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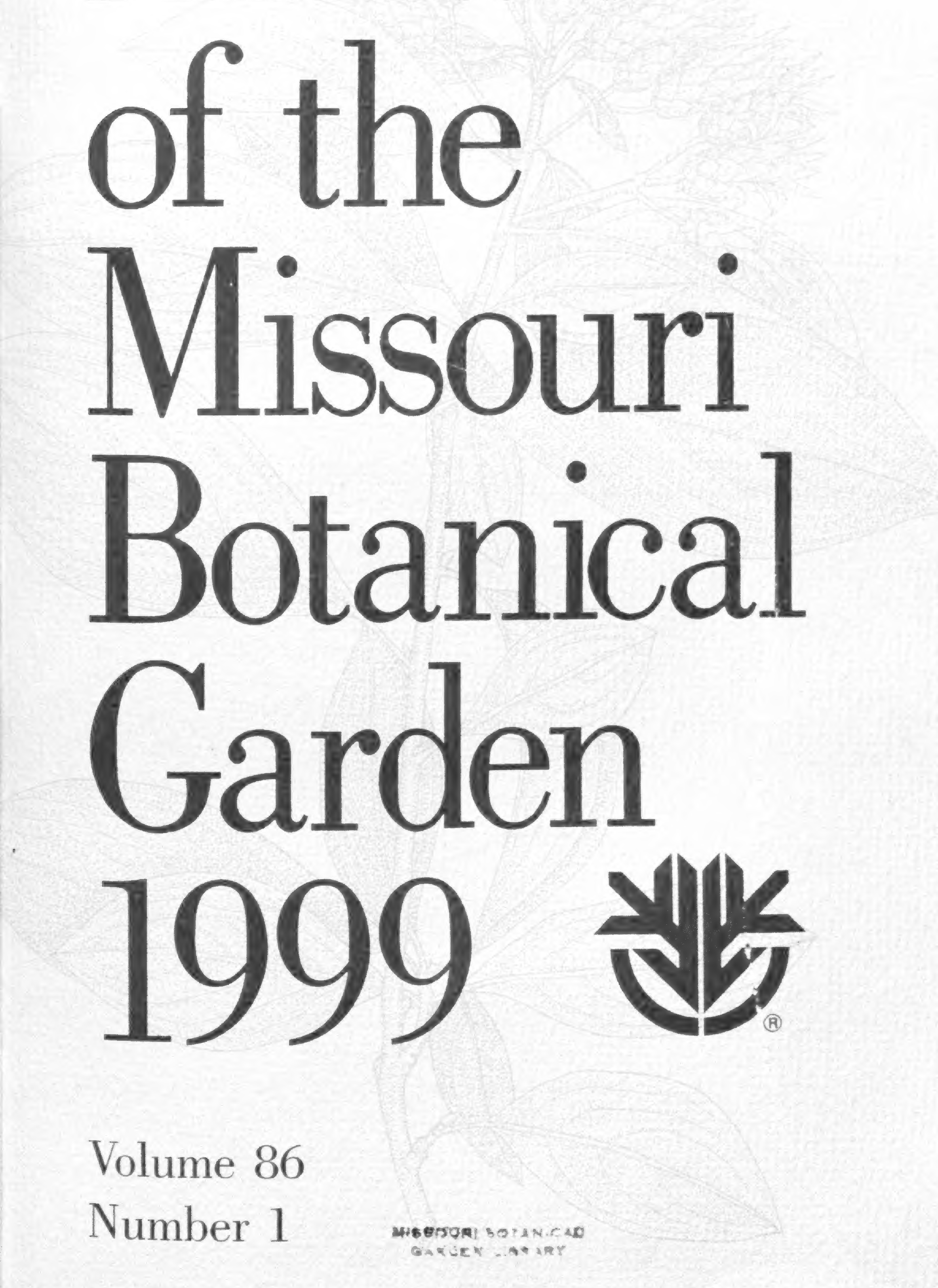

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PHYLOGENY OF BASAL EUDICOTS BASED ON THREE MOLECULAR DATA SETS: *atp*B, *rbc*L, AND 18S NUCLEAR RIBOSOMAL DNA SEQUENCES[1]

Sara B. Hoot,[2] *Susana Magallón,*[3] *and Peter R. Crane*[4]

ABSTRACT

Phylogenetic analyses were conducted for 73 genera of "lower" eudicots (Ranunculidae and "lower" Hamamelididae), magnoliid outgroups, and appropriate representatives for higher taxa within the "higher" eudicot clade (e.g., Rosidae, Dillenidae, Asteridae) based on sequences of three genes: the two chloroplast genes *atp*B and *rbc*L and nuclear ribosomal 18S DNA. Based on the partition homogeneity test, the three data sets were relatively congruent ($P \geq 0.13$). The data were analyzed using heuristic parsimony searches and bootstrap analyses in three ways: individually, the two chloroplast sequences combined, and all three sequences combined. Both ingroup and outgroup sampling were varied to test the stability of the tree topology. The trees resulting from a combination of the chloroplast data and all three data sets had the best resolution and the strongest branch support. The following higher taxonomic groups were recognized with high bootstrap values (> 90%): Eudicots (including *Nelumbo*), Ranunculidae (including *Euptelea*), Papaverales, "core" ranunculids, a clade consisting of "lower" hamamelids and "core" eudicots, "core" eudicots (including caryophyllids, asterids, and rosids), Dilleniaceae, caryophyllids (including *Simmondsia*), and asterids. All ranunculid families, including Circaeasteraceae s.l. (including *Kingdonia*) and Lardizabalaceae s.l. (including *Sargentodoxa*), formed well-supported monophyletic groups. Other well-supported eudicot clades were *Platanus*/Proteaceae, Buxaceae/*Didymeles*, Trochodendraceae/Tetracentraceae, and a group with poor internal resolution that included genera in Hamamelidaceae, various rosids, and *Paeonia*. Morphology (especially floral features) and other characteristics are described in some detail for well-supported clades determined by the molecular data.

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Recent cladistic analyses of phylogenetic relationships within angiosperms recognize two major clades, eudicots and monocotyledons, both nested within a small assemblage of "basal" dicotyledons at the magnoliid grade (Crane, 1989; Drinnan et al., 1994; APG, 1998). Eudicots are characterized by the possession of triaperturate or triaperturate-derived pollen, and monophyly of the group is further supported by phylogenetic analyses based on morphological and/or molecular data (Chase et al., 1993; Albert et al., 1994; Doyle et al., 1994; Hoot & Crane, 1995; Soltis et al., 1997). Eudicots comprise approximately 75% of extant angiosperm species (subclasses Nelumbonidae, Ranunculidae, Caryophyllidae, Hamamelididae, Dilleniidae, Rosidae, Cornidae, Asteridae, and Lamiidae sensu Takhtajan, 1997). Clarification of phylogenetic patterns at the base of this clade is therefore important to our understanding of relationships among angiosperms as a whole.

Recent discussions have highlighted two assemblages of families as potentially "basal" within the eudicots as a whole: the ranunculids and the "lower" hamamelids (Crane, 1989; Drinnan et al., 1994; Hoot & Crane, 1995). Ranunculidae have sometimes been placed within Magnoliidae (e.g., Ranunculales of Cronquist, 1981), largely on the basis of their frequently polymerous flowers (Drinnan et al., 1994), but are more appropriately included within the eudicots because of their triaperturate pollen (Takhtajan, 1997; Crane, 1989; Drinnan et al., 1994). "Lower" hamamelids, such as *Trochodendron*, *Tetracentron*, and to a lesser extent *Euptelea* and *Cercidiphyllum*, have been thought to retain a variety of unmodified plesiomorphic features from their putative ancestors at the magnoliid grade (cf. Endress, 1986; Crane, 1989).

Because of the extreme diversity in the eudicot clade (ca. 175,000 species), one problem in resolving eudicot phylogeny has been the development of a strategy that provides adequate representation of the group while at the same time allowing sample size to be maintained at a level that is manageable given currently available techniques for phylogenetic analyses. To minimize sampling size, we conducted an extensive survey of phylogenetic patterns within the eudicot clade based on existing molecular data. We then used a "placeholder" strategy to represent the major eudicot groups currently recognized. Also factored into the selection of appropriate taxa were previous phylogenetic analyses of major ranunculid and "lower" hamamelid families, by us and others, which provide acceptable representation of large groups such as the Papaverales, Ranunculaceae, and Berberidaceae (e.g., Hoot et al., 1995, 1997; Kim & Jansen, 1995).

In this paper, we present the results of phylogenetic analyses of the "lower" eudicots (Ranunculidae and "lower" Hamamelididae) using 73 taxa including appropriate magnoliid outgroups and placeholders for higher taxa within the eudicot clade (e.g., Rosidae, Dillenidae). Analyses are based on three sequence data sets, both individually and combined: the two chloroplast genes, *atp*B and *rbc*L, and nuclear ribosomal 18S DNA. Because relationships within the magnoliid grade are unresolved (see below), we explore potential changes in tree topology that may result from the use of alternative outgroups. We also explore the effects on tree topology of different sampling strategies within the "lower" eudicot ingroup. Phylogenetic trees resulting from the analyses of molecular data are used to examine evolution of specific morphological, anatomical, and chemical characters.

MATERIALS AND METHODS

TAXON SAMPLING—INGROUP

The 73 taxa included in the analyses presented here were selected to maximize systematic coverage within the Ranunculidae, "lower" Hamamelidae, and other subclasses (Tables 1, 2). Unless otherwise noted, taxonomic groupings are as in Takhtajan (1997; Table 1).

Ranunculidae. Most of the families in the ranunculid complex recognized by various workers (Dahlgren, 1980; Cronquist, 1981; Thorne, 1992; Takhtajan, 1997) were included in our sampling (Table 1). To represent relatively large ranunculid families, placeholders were selected based on previous analyses of molecular and morphological data.

Pteridophyllum, *Hypecoum*, *Dicentra*, and *Corydalis* were chosen as placeholders for Papaverales based on morphological analyses (Kadereit et al., 1995) and combined analyses of molecular and morphological data sets (Hoot et al., 1997). These studies show a sister-group relationship between *Pteridophyllum* and all remaining Papaverales (Fumariaceae and Papaveraceae). The Fumariaceae (represented here by *Hypecoum*, *Dicentra*, and *Corydalis*) are sister to Papaveraceae s. str.

Kingdonia and *Circaeaster*, frequently treated as monotypic families, were included as genera of uncertain affinities within Ranunculidae. Previous analyses have shown that together they form the sister group to a clade composed of *Sargentodoxa* and Lardizabalaceae (Hoot & Crane, 1995).

Table 1. Genera of basal eudicots sampled based on Takhtajan's classification (1997).

- **Magnoliidae**
  - Magnolianae
    - Winterales
      - Winteraceae
        - *Drimys*
        - *Pseudowintera*
        - *Tasmannia*
    - Illiciales
      - Illiciaceae
        - *Illicium*
      - Schisandraceae
        - *Schisandra*
    - Austrobaileyales
      - Austrobaileyaceae
        - *Austrobaileya*
    - Aristolochiales
      - Aristolochiaceae
        - *Aristolochia*
        - *Asarum*
  - Piperanae
    - Piperales
      - Peperomiaceae
        - *Peperomia*
      - Saururaceae
        - *Houttuynia*
        - *Saururus*
  - Lauranae
    - Chloranthales
      - Chloranthaceae
        - *Chloranthus*
        - *Sarcandra*
- **Nelumbonidae**
  - Nelumbonales
    - Nelumbonaceae
      - *Nelumbo*
- **Ranunculidae**
  - Ranunculanae
    - Papaverales
      - Pteridophyllaceae
        - *Pteridophyllum*
      - Hypecoaceae
        - *Hypecoum*
      - Fumariaceae
        - *Corydalis*
        - *Dicentra*
    - Circaeasterales
      - Circaeasteraceae
        - *Circaeaster*
      - Kingdoniaceae
        - *Kingdonia*
    - Lardizabalales
      - Sargentodoxaceae
        - *Sargentodoxa*
      - Lardizabalaceae
        - *Decaisnea*
        - *Sinofranchetia*
    - Menispermales
      - Menispermaceae
        - *Menispermum*
        - *Tinospora*
    - Glaucidiales
      - Glaucidiaceae
        - *Glaucidium*
    - Hydrastidales
      - Hydrastidaceae
        - *Hydrastis*
    - Berberidales
      - Nandinaceae
        - *Nandina*
      - Podophyllaceae
        - *Caulophyllum*
        - *Podophyllum*
    - Ranunculales
      - Ranunculaceae
        - *Coptis*
        - *Xanthorhiza*
    - Paeoniales
      - Paeoniaceae
        - *Paeonia*
- **Hamamelididae**
  - Trochodendranae
    - Trochodendrales
      - Trochodendraceae
        - *Trochodendron*
      - Tetracentraceae
        - *Tetracentron*
    - Cercidiphyllales
      - Cercidiphyllaceae
        - *Cercidiphyllum*
    - Eupteleales
      - Eupteleaceae
        - *Euptelea*
  - Myrothamnanae
    - Myrothamnales
      - Myrothamnaceae
        - *Myrothamnus*
  - Hamamelidanae
    - Hamamelidales
      - Platanaceae
        - *Platanus*
      - Hamamelidaceae
        - *Corylopsis*
        - *Disanthus*
        - *Exbucklandia*
        - *Hamamelis*
      - Altingiaceae
        - *Altingia*
        - *Liquidambar*
  - Daphniphyllanae
    - Daphniphyllales
      - Daphniphyllaceae
        - *Daphniphyllum*
  - Buxanae
    - Didymelales
      - Didymelaceae
        - *Didymeles*
    - Buxales
      - Buxaceae
        - *Buxus*
        - *Pachysandra*
        - *Styloceras*
    - Simmondsiales
      - Simmondsiaceae
        - *Simmondsia*
- **Caryophyllidae**
  - Caryophyllanae
    - Caryophyllales
      - Phytolaccaceae
        - *Phytolacca*
      - Molluginaceae
        - *Limeum*
      - Chenopodiaceae
        - *Spinacia*
  - Polygonanae
    - Polygonales
      - Polygonaceae
        - *Rheum*
- **Dilleniidae**
  - Nepenthanae
    - Nepenthales
      - Nepenthaceae
        - *Nepenthes*
  - Dillenianae
    - Dilleniales
      - Dilleniaceae
        - *Dillenia*
        - *Hibbertia*
        - *Schumacheria*
  - Ericanae
    - Bruniales
      - Bruniaceae
        - *Berzellia*
- **Rosidae**
  - Saxifraganae
    - Cunoniales
      - Eucryphiaceae
        - *Eucryphia*
    - Saxifragales
      - Saxifragaceae
        - *Heuchera*
      - Iteaceae
        - *Itea*
    - Francoales
      - Francoaceae
        - *Francoa*
    - Haloragales
      - Haloragaceae
        - *Haloragis*
    - Gunnerales
      - Gunneraceae
        - *Gunnera*
  - Rutanae
    - Sabiales
      - Sabiaceae
        - *Sabia*
    - Coriariales
      - Coriariaceae
        - *Coriaria*
  - Geranianae
    - Geraniales
      - Geraniaceae
        - *Geranium*
  - Proteanae
    - Proteales
      - Proteaceae
        - *Placospermum*
        - *Roupala*
- **Cornidae**
  - Cornanae
    - Hydrangeales
      - Hydrangeaceae
        - *Hydrangea*
  - Aralianae
    - Araliales
      - Araliaceae
        - *Hedera*

Sargentodoxa is often assigned to a family of its own, usually considered to be closely related to, or within, Lardizabalaceae (Hoot & Crane, 1995). *Sinofranchetia* and *Decaisnea* were included as placeholders for Lardizabalaceae s. str. based on previous analyses of morphological (Loconte & Estes, 1989; Loconte et al., 1995) and molecular sequence data (Hoot et al., 1995).

We selected *Tinospora* and *Menispermum* as placeholders for Menispermaceae, based on their diverse fruit and floral morphology (Thanikaimoni, 1984). Preliminary phylogenetic analyses of 17 genera within the family, based on molecular data (*atp*B and *rbc*L), confirmed the monophyly of the family and the relative divergence of *Tinospora* and *Menispermum* (Hoot, unpublished results).

Nandina, *Caulophyllum*, and *Podophyllum* were selected as placeholders for Berberidales based on

Table 2. Species sequenced, voucher information, sources of sequences and accession numbers. KBG = Kirstenbosch Botanical Garden (accession numbers for living plants); SA = Strybing Arboretum.

Family	Species	*atp*B Voucher information/ source of sequence/ GenBank	*rbc*L Voucher information/ source of sequence/ GenBank	18S Voucher information/ source of sequence/ GenBank
Altingiaceae	*Altingia excelsa* Noronha	*Hoot 9225* (UWM) Hoot AF092103		
Altingiaceae	*Altingia* sp.		*Qiu 93006* (NCU) Qiu AF061996	*Qiu 93006* (NCU) Soltis U42552
Altingiaceae	*Liquidambar styraciflua* L.	*Kron 162* (NCU) Hoot AF092104	Bousquet M58394	*Soltis & Soltis 2516* (WS) Soltis U42553
Araliaceae	*Hedera helix* L.	*Hoot 972* (UWM) Hoot AF092105	*Jansen s.n.* (MICH) Olmstead et al. 1992 L01924	*Plunkett 1368* (WS) Soltis & Soltis U42500
Aristolochiaceae	*Aristolochia macrophylla* Lam.		*Qiu 91019* (NUC) Qiu L12630	
Aristolochiaceae	*A. tomentosa* Sims	*Nickrent 2922* (SIU) Hoot AF092106		*Nickrent 2922* (SIU) Nickrent L24083
Aristolochiaceae	*Asarum canadensis* L.	*Hoot 923* (UWM) Hoot U86383	Olmstead L14290	*Nickrent 2888* (SIU) Nickrent L24043
Austrobaileyaceae	*Austrobaileya scandens* C. T. White	*Qiu 90030* (NCU) Hoot AF092107	*Qiu 90030* (NCU) Qiu L12632	*Nickrent 2953* (SIU) Nickrent U42503
Berberidaceae	*Caulophyllum thalictroides* (L.) Michx.	*Hoot 925* (UWM) Hoot AF092108	*Les s.n.* (CONN) Les L08760	*Hoot 925* (UWM) Hoot L54064
Berberidaceae	*Podophyllum peltatum* L.	*Hoot 943* (UWM) Hoot AF092109	*Hoot 943* (UWM) Hoot AF093716	*Nickrent 2891* (SIU) Nickrent L24413

Table 2. Continued.

Family	Species	*atp*B Voucher information/ source of sequence/ GenBank	*rbc*L Voucher information/ source of sequence/ GenBank	18S Voucher information/ source of sequence/ GenBank
Bruniaceae	*Berzelia lanuginosa* (L.) Brongn.	KBG 7589 Savolainen AF095731	*Price s.n.* (IND) Price & Rodman L14391	*Price s.n.* (IND) Soltis U42508
Buxaceae	*Buxus sempervirens* L.	*Hoot 921* (UWM) Hoot AF092110	*Hoot 921* (UWM) Hoot AF093717	*Hoot 921* (UWM) Hoot L54065
Buxaceae	*Pachysandra procumbens* Michx.	*Hoot 917* (UWM) Hoot AF092111	*Hoot 917* (UWM) Hoot AF093718	*Hoot 917* (UWM) Hoot AF094533
Buxaceae	*Styloceras laurifolium* (Willd.) Kunth	*Dillon et al. 6398* (F) Hoot AF093421	*Dillon et al. 6398* (F) Hoot AF093733	*Dillon et al. 6398* (F) Hoot AF094563
Cercidiphyllaceae	*Cercidiphyllum japonicum* Siebold & Zucc.	*Olmstead 90-016* (COLO) Hoot AF092112	*Olmstead 90-016* (COLO) Olmstead L11673	*Olmstead 90-016* (COLO) Hoot AF094534
Chenopodiaceae	*Spinacia oleracea* L.	Zurawski U23082	Zurawski V00168	*Nickrent 2896* (SIU) Nickrent L24420
Chloranthaceae	*Chloranthus japonicus* Siebold		*Chase 204* (NCU) Hills L12640	
Chloranthaceae	*C. oldhami* Solms	*Lammers 8575* (F) Hoot AF092113		*Lammers 8575* (F) Hoot AF094535
Chloranthaceae	*Sarcandra glabra* (Thunb.) Nakai	*Lammers 8542* (F) Hoot AF092114		*Lammers 8542* (F) Hoot AF094536
Chloranthaceae	*S. grandifolia* (Miq.) Subr. & A. N. Henry		*Qiu 92002* (NCU) Qiu L12663	

Table 2. Continued.

Family	Species	*atp*B Voucher information/ source of sequence/ GenBank	*rbc*L Voucher information/ source of sequence/ GenBank	18S Voucher information/ source of sequence/ GenBank
Circaeasteraceae	*Circaeaster agrestis* Maxim.	*Chase 506* (K) Hoot AF092116	*Chase 506* (K) Hoot AF0937120	*Chase 506* (K) Hoot AF094538
Coriariaceae	*Coriaria myrtifolia* L.	*Chase 245* (NCU) Hoot AF092117	*Chase 245* (NCU) Hoot L01897	*Chase 245* (NCU) Hoot AF094539
Daphniphyllaceae	*Daphniphyllum* sp.	*Wagner et al. 6599* (HAST) Hoot AF092118	*Qiu 91026* (NCU) Qiu L01901	*Wagner et al. 6599* (HAST) Hoot AF094540
Didymelaceae	*Didymeles* sp.	*Andrianantonnina 387* (MO) Hoot AF092119	*Andrianantonnina 387* (MO) Chase AF061994	*Andrianantonnina 387* (MO) Hoot AF094541
Dilleniaceae	*Dillenia alata* (DC.) Mart.		*Chase 234* (NCU) Kron L01903	*Nickrent 2956* (SIU) Nickrent U38314
Dilleniaceae	*D. retusa* Thunb.	*Chase 2103* (K) Savolainen & Morton AF095732		
Dilleniaceae	*Hibbertia volubilis* Andr.	*Hoot 9222* (UWM) Hoot AF092120	*Hoot 9222* (UWM) Hoot AF093721	*Hoot 9222* (UWM) Hoot AF094542
Dilleniaceae	*Schumacheria* sp.	*Chase 308* (K) Hoot AF092121	*Chase 308* (K) Hoot AF095734	*Chase 308* (K) Hoot AF094543
Eucryphiaceae	*Eucryphia cordifolia* Cav.	*Hoot 9224* (UWM) Hoot AF092122		
Eucryphiaceae	*E. lucida* Druce		SA 86-0250 Morgan & Soltis L01918	SA 86-0250 Soltis U42533

Table 2. Continued.

Family	Species	*atp*B Voucher information/ source of sequence/ GenBank	*rbc*L Voucher information/ source of sequence/ GenBank	18S Voucher information/ source of sequence/ GenBank
Eupteleaceae	*Euptelea polyandra* Siebold & Zucc.	*Qiu 90026* (NCU) Hoot U86384	*Qiu 90026* (NCU) Qiu L12645	*Qiu 90026* (NCU) Hoot L75831
Francoaceae	*Francoa appendiculata* A. Juss.	*Chase 2502* (K) Morton & Savolainen AF035905		
Francoaceae	*F. sonchifolia* Cav.		*Soltis & Soltis 2479* (WS) Soltis L11184	*Soltis & Soltis 2479* (WS) Soltis L28137
Fumariaceae	*Corydalis nobilis* Pers.	*Hoot 9225* (UWM) Hoot AF093372	*Hoot 9225* (UWM) Hoot AF093722	*Hoot 9225* (UWM) Hoot AF094544
Fumariaceae	*Dicentra eximia* Torr.	*Reznicek 9756* (MICH) Hoot L37927	*Reznicek 9756* (MICH) Hoot L37917	*Reznicek 9756* (MICH) Hoot L37908
Geraniaceae	*Geranium cinereum* Cav.	*Hoot 971* (UWM) Hoot AF093373	*Price s.n.* (IND) Price L14695	*Price s.n.* (IND) Soltis U42541
Glaucidiaceae	*Glaucidium palmatum* Siebold & Zucc.	*Hoot 924* (UWM) Hoot AF093375	*Hoot 924* (UWM) Hoot L75848	*Hoot 924* (UWM) Hoot L75829
Gunneraceae	*Gunnera hamiltonii* Kirk ex W. S. Ham.	*Chase 562* (K) Hoot AF093374	*Chase 562* (K) Hoot AF093724	*Chase 562* (K) Hoot AF094546
Haloragaceae	*Haloragis erecta* Eichler	*Chase 594* (K) Hoot AF093376		*Chase 594* (K) Hoot AF094547
Haloragaceae	*H. serra* Brongn.		*Conti 195* (WIS) Conti U26325	

Table 2. Continued.

Family	Species	*atp*B Voucher information/ source of sequence/ GenBank	*rbc*L Voucher information/ source of sequence/ GenBank	18S Voucher information/ source of sequence/ GenBank
Hamamelidaceae	*Corylopsis pauciflora* Siebold & Zucc.	*Reznicek 9239* (MICH) Hoot AF093377	*Reznicek 9239* (MICH) Hoot AF060710	*Reznicek 9239* (MICH) Hoot AF094548
Hamamelidaceae	*Disanthus cercidifolius* Maxim.	*Hoot 9221* (UWM) Hoot AF093378	*Hoot 9221* (UWM) Hoot AF060709	*Hoot 9221* (UWM) Hoot AF094549
Hamamelidaceae	*Exbucklandia populnea* R. Br. ex Griff.	*Chase 619* (K) Hoot AF093379	*Chase 619* (K) Hoot AF060708	*Chase 619* (K) Hoot AF094550
Hamamelidaceae	*Hamamelis mollis* Oliv.		*Qiu 91035* (NCU) Qiu L01922	
Hamamelidaceae	*H. virginiana* L.	*Hoot 910* (UWM) Hoot AF093380		*Hoot 910* (UWM) Hoot AF094551
Hydrangeaceae	*Hydrangea arborescens* L.	*Hoot 971* (UWM) Hoot AF093381		
Hydrangeaceae	*H. macrophylla* Torr.		*Morgan 2150* (WS) Soltis L11187	*Morgan 2150* (WS) Soltis U42781
Hydrastidaceae	*Hydrastis canadensis* L.	*Naczi 2883* (MICH) Hoot AF093382	*Naczi 2883* (MICH) Hoot L75849	*Naczi 2883* (MICH) Hoot L75828
Hypecoaceae	*Hypecoum imberbe* Sm.	*Chase 528* (K) Hoot U86398	*Chase 528* (K) Hoot U86628	*Chase 528* (K) Hoot AF094553
Illiciaceae	*Illicium parviflorum* Michx. ex Vent.	*Naczi 2784* (MICH) Hoot U86385	*Qiu 83* (NCU) Qiu L12652	*Naczi 2784* (MICH) Hoot L75832

Table 2. Continued.

Family	Species	*atp*B Voucher information/ source of sequence/ GenBank	*rbc*L Voucher information/ source of sequence/ GenBank	18S Voucher information/ source of sequence/ GenBank
Iteaceae	*Itea ilicifolia* Oliv.	*MacDougal 5060* (MO) Hoot AF093383		
Iteaceae	*I. virginica* L.		*Ware 9401* (WS) Soltis L11188	*Ware 9401* (WS) Soltis U42545
Kingdoniaceae	*Kingdonia uniflora* Balf. f. & W. W. Sm.	*Qin s.n.* (PE) Hoot AF092115	*Qin s.n.* (PE) Hoot AF093719	*Qin s.n.* (PE) Hoot AF094537
Lardizabalaceae	*Decaisnea fargesii* Franch.	*Reznicek 9236* (MICH) Hoot L37926	*Reznicek 9236* (MICH) Hoot L37907	*Reznicek 9236* (MICH) Hoot L37916
Lardizabalaceae	*Sinofranchetia chinensis* Helmsl.	*Hoot 9220* (UWM) Hoot/Culham L37931	*Hoot 9220* (UWM) Hoot L37912	*Hoot 9220* (UWM) Hoot L37921
Menispermaceae	*Menispermum canadensis* L.	*Naczi 2837* (MICH) Hoot AF093384	*Naczi 2837* (MICH) Hoot AF093726	*Naczi 2837* (MICH) Hoot L75834
Menispermaceae	*Tinospora caffra* Miers	*Jaarsveld 2131* (NBG) Hoot L37933	*Jaarsveld 2131* (NBG) Hoot L37923	*Jaarsveld 2131* (NBG) Hoot L37914
Molluginaceae	*Limeum* sp.	*Hoot 983* (UWM) Hoot AF093385	*Hoot 983* (UWM) Hoot AF093727	*Hoot 983* (UWM) Hoot AF094554
Myrothamnaceae	*Myrothamnus flabellifolius* Welw.	*Winter 72* (RAV) Hoot AF093386	*Winter 72* (RAV) Hoot AF060707	*Winter 72* (RAV) Hoot AF094555
Nandinaceae	*Nandina domestica* Thunb.	*Hoot 922* (UWM) Hoot L37930	*Hoot 922* (UWM) Hoot L37920	*Hoot 922* (UWM) Hoot L37911

Table 2. Continued.

Family	Species	*atpB* Voucher information/ source of sequence/ GenBank	*rbc*L Voucher information/ source of sequence/ GenBank	18S Voucher information/ source of sequence/ GenBank
Nelumbonaceae	*Nelumbo lutea* (Willd.) Pers.	*Hoot 974* (UWM) Hoot AF093387	*Les s.n.* (CONN) Les/Qiu M77032	*Hoot 974* (UWM) Hoot AF094556
Nepenthaceae	*Nepenthes alata* Blanco	*Chase 145* (NCU) Hoot AF093388	*Chase 145* (NCU) Chase L01935	
Nepenthaceae	*Nepenthes* sp.			*Nickrent 3056* (SIU) Soltis U42787
Paeoniaceae	*Paeonia suffruticosa* Andrews	*Reznicek 9235* (MICH) Hoot AF093389		*Chase 486* (K) Soltis U42792
Paeoniaceae	*P. tenuifolia* L.		*Kron 2115* (NCU) Kron L13187	
Peperomiaceae	*Peperomia serpens* (Sw.) Loudon	*DN 2907* (SIU) Hoot AF093390		*DN 2907* (SIU) Nickrent L24411
Peperomiaceae	*Peperomia* sp.		*Qiu 91047* (NCU) Qiu L12661	
Phytolaccaceae	*Phytolacca americana* L.	*Hoot 942* (UWM) Hoot AF093391	*Rettig 1651* (TAMU) Rettig et al. M62567	*Hoot 942* (UWM) Hoot AF094557
Platanaceae	*Platanus occidentalis* L.	*Qiu P90005* (NCU) Hoot U86386	*Qiu P90005* (NCU) Qiu L01943	*Soltis & Soltis 2514* (WS) Sweere, Zimmer & Soltis U42794
Polygonaceae	*Rheum rhaponticum* L.	*Hoot 953* (UWM) Hoot AF093392	Giannassi et al. M77702	*Hoot 953* (UWM) Hoot AF094558

Table 2. Continued.

Family	Species	*atp*B Voucher information/ source of sequence/ GenBank	*rbc*L Voucher information/ source of sequence/ GenBank	18S Voucher information/ source of sequence/ GenBank
Proteaceae	*Placospermum coriaceum* C. T. White & W. D. Francis	*Douglas 110* (MEL) Hoot AF060391	*Douglas 110* (MEL) Hoot AF093729	*Douglas 110* (MEL) Hoot L75837
Proteaceae	*Roupala macrophylla* Pohl	*Douglas 131* (MEL) Hoot AF060416	*Douglas 131* (MEL) Hoot AF093728	*Douglas 131* (MEL) Hoot AF094559
Pteridophyllaceae	*Pteridophyllum racemosum* Siebold & Zucc.	*Chase 531* (K) Hoot U86400	*Chase 531* (K) Hoot U86631	*Chase 531* (K) Hoot AF094560
Ranunculaceae	*Coptis trifolia* (L.) Salisb.	*Voss & Howard s.n.* (MICH) Hoot AF093393	*Voss & Howard s.n.* (MICH) Hoot AF093730	*Voss & Howard s.n.* (MICH) Hoot L75838
Ranunculaceae	*Xanthorhiza simplicissima* Marshall	*Qiu 91030* (NCU) Hoot AF093394	*Qiu 91030* (NCU) Qiu L12669	*Qiu 91030* (NCU) Hoot L75839
Sabiaceae	*Sabia swinhoei* Hemsl. ex F. B. Forbes & Hemsl.	*Wagner 6158* (HAST) Hoot AF093395		*Wagner 6518* (HAST) Hoot L75840
Sabiaceae	*Sabia* sp.		*Qiu 91025* (NCU) Qiu L12662	
Sargentodoxaceae	*Sargentodoxa cuneata* (Oliv.) Rehder & E. H. Wilson	*Qin s.n.* (PE) Hoot AF093396	*Qin s.n.* (PE) Hoot AF093731	*Qin s.n.* (PE) Hoot L75841
Saururaceae	*Houttuynia cordata* Thunb.	*Reznicek 9238* (MICH) Hoot AF093397	*Les s.n.* (CONN) Les L08762	*Nickrent 2940* (SIU) Nickrent L24147
Saururaceae	*Saururus cernuus* L.	*Olmstead 88-006* (COLO) Hoot AF093398	*Olmstead 88-006* (COLO) Olmstead L14294	*Suh 128* (US) Sweere, Zimmer & Soltis U42805

Table 2. Continued.

Family	Species	*atp*B Voucher information/ source of sequence/ GenBank	*rbc*L Voucher information/ source of sequence/ GenBank	18S Voucher information/ source of sequence/ GenBank
Saxifragaceae	*Heuchera micrantha* Douglas		*Soltis & Soltis 1949* (WS) Soltis & Soltis L01925	*Soltis & Soltis 1949* (WS) Soltis & Soltis X28139
Saxifragaceae	*H. sanguinea* Engelm.	*Hoot 932* (UWM) Hoot AF093399		
Schisandraceae	*Schisandra chinensis* (Turcz.) Baill.	*Reznicek 10720* (MICH) Hoot AF093400		*Reznicek 10720* (MICH) Hoot AF094561
Schisandraceae	*S. sphenanthera* Rehder & E. H. Wilson		*Qiu 73* (NCU) Qiu L12665	
Simmondsiaceae	*Simmondsia chinensis* C. K. Schneid.	*S. Boyd et al. 3355* (F) Hoot AF093401	*S. Boyd et al. 3355* (F) Hoot AF093732	*S. Boyd et al. 3355* (F) Hoot AF094562
Tetracentraceae	*Tetracentron sinensis* Oliv.	*Qiu 90009* (NCU) Hoot AF093422	*Qiu 90009* (NCU) Qiu L12668	*Qiu 90009* (NCU) Hoot AF094564
Trochodendraceae	*Trochodendron aralioides* Siebold & Zucc.	*Qiu 90026* (NC) Hoot AF093423	*Qiu 90026* (NC) Qiu L01958	*Qiu 90026* (NC) Hoot AF094565
Winteraceae	*Drimys winteri* J. R. Forst. & G. Forster	*Nickrent 3013* (SIU) Hoot AF093425	*Nickrent 3013* (SIU) Hoot AF093734	*Suh* 47 (US) Sweere, Zimmer & Soltis U42823
Winteraceae	*Pseudowintera colorata* Dandy	*Hoot 9223* (UWM) Hoot AF093426	*Hoot 9223* (UWM) Hoot AF093735	*Hoot 9223* (UWM) Hoot AF094567
Winteraceae	*Tasmannia insipida* R. Br. ex DC.		*A. N. Rodd 5540* (NSW) Qiu L01957	
Winteraceae	*T. lanceolata* (Poir.) A. C. Smith	*Raleigh 109* (MEL) Hoot AF093424		*Raleigh 109* (MEL) Hoot AF094566

the frequent separation of *Nandina* as Nandinaceae (e.g., Dahlgren, 1980; Takhtajan, 1997) and the position of *Caulophyllum* and *Podophyllum* close to the base of the Berberidales (Kim & Jansen, 1995; Nickol, 1995).

Glaucidium, Hydrastis, Coptis, and *Xanthorhiza* were selected as representatives of Ranunculaceae s.l. based on extensive morphological and molecular phylogenetic studies of the family, which place these genera close to the base of the family (Hoot, 1991, 1995; Johansson & Jansen, 1993; Johansson, 1995).

"Lower" Hamamelididae. The "lower" hamamelids have been only loosely defined by previous workers, but are generally considered to include the orders Trochodendrales (Trochodendraceae, Tetracentraceae), Cercidiphyllales (Cercidiphyllaceae), Eupteleales (Eupteleaceae), Myrothamnales (Myrothamnaceae), Hamamelidales (Platanaceae, Hamamelidaceae, Altingiaceae), Daphniphyllales (Daphniphyllaceae), Didymelales (Didymelaceae), Buxales (Buxaceae), and Simmondsiales (Simmondsiaceae), all belonging to subclass Hamamelididae sensu Takhtajan (1997; Table 1). With the exception of Hamamelidaceae, Altingiaceae, and Buxaceae, each of the families included in these orders contains a single genus, and all were included in our analyses (Table 1).

Hamamelidaceae (sensu Endress, 1989a) include 30 genera distributed among four subfamilies, of which Hamamelidoideae is the largest with 22 genera (Endress, 1989a, 1993). Because results of previous phylogenetic analyses suggest that Hamamelidaceae are not monophyletic (e.g., Morgan & Soltis, 1993; Manos et al., 1993; Chase et al., 1993; Qiu et al., 1998), three of the four subfamilies, i.e., Hamamelidoideae, Exbucklandioideae, and Altingioideae, were represented in our study. A more detailed assessment of the monophyly of Hamamelidaceae and the relationships among the genera will require more extensive sampling within the family.

Several taxa that have been identified as putatively closely related to Hamamelidaceae (sensu Endress, 1989a) based on recent phylogenetic analyses of molecular data were also included in our sampling (e.g., Chase et al., 1993; Morgan & Soltis, 1993; Drinnan et al., 1994; Soltis et al., 1997). In addition to *Cercidiphyllum* and *Daphniphyllum,* these taxa are Saxifragaceae s. str. (equivalent to the Saxifragoideae of Engler, 1930, and Schulze-Menz, 1964, and represented here by *Heuchera*; Soltis et al., 1993; Soltis & Soltis, 1997), other genera of saxifragoid affinity (represented here by *Itea*), Haloragaceae (represented here by *Haloragis*), and the isolated genus *Paeonia* (placed in Ranunculidae by Takhtajan, 1997).

Preliminary analyses of molecular data for five genera and nine species of Buxales (including *Styloceras*) indicated three genera are appropriate as placeholders for the family: *Styloceras, Buxus,* and *Pachysandra* (Hoot, unpublished data). Cronquist (1981) tentatively included Buxaceae in Euphorbiales. However, Takhtajan's (1997) superorder Buxanae, which includes Didymelales, Buxales, and Simmondsiales, is placed in subclass Hamamelididae. The genus *Simmondsia,* which was separated by Cronquist (1981) and Takhtajan (1997) from Buxaceae and placed within a monogeneric family, was also included in our sampling.

Taxa that have been identified by previous phylogenetic analyses (e.g., Chase et al., 1993; Williams et al., 1994; Drinnan et al., 1994, Soltis et al., 1997) as putatively related to "lower" hamamelids were also included in the taxonomic sampling. These include *Nelumbo* (Nelumbonaceae), *Roupala* and *Placospermum* (Proteaceae), *Sabia* (Sabiaceae), and *Gunnera* (Gunneraceae).

Core eudicots. Results of recent phylogenetic analyses (Olmstead et al., 1992; Chase et al., 1993; Drinnan et al., 1994; Williams et al., 1994; Soltis et al., 1997) converge in identifying a large clade, which we term here as "core" eudicots, that includes the majority of eudicot species diversity. Based on recent results derived mainly from analyses of molecular data, the core eudicots are largely distributed in three distinct clades: the "caryophyllids," "asterids," and "rosids" (Chase et al., 1993; Soltis et al., 1997), all of which were represented in our sampling.

The "caryophyllid clade," equivalent to the "caryophyllids" of Search II from Chase et al. (1993) or the Caryophyllidae s.l. of Soltis et al. (1997), was represented in our analyses by genera belonging to five families: Polygonaceae (*Rheum*), Chenopodiaceae (*Spinacia*), Molluginaceae (*Limeum*), Phytolaccaceae (*Phytolacca*), and Nepenthaceae (*Nepenthes*). Nepenthaceae have been recognized recently as closely related to Caryophyllidae (Albert et al., 1992; Chase et al., 1993; Williams et al., 1994; Soltis et al., 1997). Because *Dillenia* appears as either sister to a largely caryophyllid clade (Chase et al., 1993) or closely associated with several "lower" hamamelid species (Qiu et al., 1998), three representatives of the Dilleniaceae were included in our sampling: *Dillenia, Hibbertia,* and *Schumacheria.*

The "rosid clade," corresponding to the "rosids" of Search II in Chase et al. (1993) and roughly to the Rosidae of Soltis et al. (1997), was represented in our analyses by four placeholders: *Francoa* and *Geranium* (Rosid II), and *Coriaria* and *Eucryphia* (Rosid I). Genera of Hamamelidaceae, *Cercidiphyllum, Daphniphyllum,* and other taxa have been identified as forming a paraphyletic grade at the base of the rosid clade (e.g., Morgan & Soltis, 1993; Soltis et al., 1993; Williams et al., 1994) or have been included within the most basal group (i.e., "Rosid III" of Chase et al., 1993, or "Saxifragoids" of Soltis et al., 1997) of the rosid clade (e.g., Chase et al., 1993; Soltis et al., 1997; Soltis & Soltis, 1997).

The "asterid clade," equivalent to the "asterids" of Search II of Chase et al. (1993) and to Asteridae s.l. of Olmstead et al. (1993), was represented in our analyses by three placeholders. The "Cornales" of Olmstead (1993) or "asterid IV" clade of Chase et al. (1993) was represented by *Hydrangea* (Hydrangeaceae). The "asterid II" clade of Chase et al. (1993), which includes the Apiales, Dipsacales, Asterales s.l., and several genera of varied taxonomic affinity (Olmstead et al., 1992; Olmstead et al., 1993; Cosner et al., 1994; Plunkett et al., 1996), was represented by *Hedera* (Araliaceae) and *Berzelia* (Bruniaceae).

TAXON SAMPLING—OUTGROUP

The sister-group relationships of the eudicots as a whole with respect to groups at the magnoliid grade are not resolved, and many different phylogenetic arrangements have been suggested (e.g., Donoghue & Doyle, 1989a; Chase et al., 1993; Doyle et al., 1994; Soltis et al., 1997). Because of these uncertainties and the absence of critical eudicot features in potential outgroup taxa, rooting the basal eudicots is problematic (Donoghue & Doyle, 1989b; Doyle & Donoghue, 1993). Therefore, we selected a broad taxonomic sample of potential woody and herbaceous outgroup taxa within subclass Magnoliidae, representing 13 genera in eight families within six different orders (all sensu Takhtajan, 1997): Winterales (Winteraceae), Illiciales (Illiciaceae, Schisandraceae), Austrobaileyales (Austrobaileyaceae), Aristolochiales (Aristolochiaceae), Piperales (Peperomiaceae, Saururaceae), and Chloranthales (Chloranthaceae; Table 1). For the analyses presented here, *Austrobaileya* was designated as outgroup, allowing for an additional check of eudicot monophyly (Figs. 1–6). In addition, alternative outgroup configurations were chosen to check the effect of outgroup sampling on the tree topologies (described below).

MOLECULAR METHODS

Total cellular DNA was isolated from fresh, herbarium, or silica-dried material using the miniprep method of Doyle and Doyle (1987). The amplification primers and polymerase chain reaction (PCR) protocol are as described in Hoot et al. (1995). Purification of PCR product and manual double-stranded sequencing protocols are as described in Hoot (1995). Automated sequencing from purified PCR product was performed on an ABI automated sequencer (Applied Biosystems, Model 373A) and contigs were assembled using Sequencher™ 3.0 (Gene Codes Corporation).

Sequence comparisons for *atp*B, *rbc*L, and 18S included 1493, 1397, and 1635 bp, respectively. Both strands of DNA were sequenced for all regions with approximately 80% overlap. Several regions were removed from the 18S data set due to alignment and/or compression problems at the following positions in relation to the soybean 18S sequence (Eckenrode et al., 1985): 131–133, 224–231, 666–669, 1363–1366, and 1512–1517. In addition, three informative sites were removed due to compensatory changes (paired sites indicated in parentheses): 734 (708), 1050 (1076), and 1074 (1052). See Hoot (1995) for details of data collection.

DATA ANALYSIS

Phylogenetic analyses with the complete sampling were performed separately on the *rbc*L, *atp*B, and 18S data as well as on the combined data sets *atp*B/*rbc*L and *atp*B/*rbc*L/18S. Analyses were performed with PAUP* 4.0d64 (kindly provided by D. Swofford) using the heuristic search option with 20 random additions, TBR (tree bisection-reconnection branch swapping), and MULPARS (retention of all equally parsimonious trees) in effect. Bootstrap analyses (Felsenstein, 1985) with 100 replications were perfomed on each individual and combined data set using the heuristic search option with simple addition sequence. In the case of individual data sets (*atp*B, *rbc*L, and 18S), the maxtree limit of 2000 was reached on some bootstrap replications. Alternative tree topologies and resultant changes in tree length were explored using MacClade 3.0 (Maddison & Maddison, 1992).

Alternative analyses. Several additional analyses of the combined data sets were performed as described above to check the effect of taxon sampling on the tree topology. Five alternative samplings were examined as follows: (1) exclusion of paleoherbs (*Chloranthus, Sarcandra, Asarum, Aristolochia, Peperomia, Saururus,* and *Houttuynia*;

Table 3. Comparison of indices for the various trees illustrated in Figures 1–5. Tree length includes uninformative characters; consistency index (CI) excludes uninformative characters. RI = retention index, RC = rescaled consistency index.

Data set	No. variable characters	No. informative characters	No. of trees	Length of trees	CI	RI	RC
*atp*B	576	435	108	2233	0.34	0.59	0.23
*rbc*L	630	431	2	2478	0.31	0.54	0.20
*atp*B/*rbc*L	1206	866	6	4744	0.32	0.56	0.21
18S nrDNA	307	175	270	939	0.33	0.58	0.25
*atp*B/*rbc*L/18S	1513	1041	15	5714	0.32	0.56	0.21

designated outgroup *Austrobaileya*); (2) exclusion of "woody" magnoliids (*Austrobaileya, Illicium, Schisandra, Pseudowintera, Tasmannia*, and *Drimys*; designated outgroup *Chloranthus*); (3) ranunculids reduced to six placeholders (*Euptelea, Pteridophyllum, Sargentodoxa, Menispermum, Nandina, Hydrastis*); (4) ranunculids reduced to three placeholders (*Euptelea, Pteridophyllum, Hypecoum*); and (5) separate analysis of "core" eudicots (see Fig. 6) using *Tetracentron* and *Trochodendron* as outgroups.

Congruence of data sets. Before combining the data sets, data (or character) congruence was assessed using the partition homogeneity test (Farris et al., 1995; implemented with PAUP* vers. 4.0), a bootstrap approach that randomly partitions characters. It tests the null hypothesis that a given partition of a data set (for example, *rbc*L and *atp*B data sets) represents a random partition of the data. All combinations of data sets were analyzed with 100 replicates, the heuristic search option with simple addition sequence, TBR, and MULPARS in effect. To reduce computation time, the analyses were done with reduced sampling (50 taxa). The following outgroup and placeholder taxa were omitted from the analyses: *Schisandra, Chloranthus, Sarcandra, Pseudowintera, Tasmannia, Drimys, Asarum, Aristolochia, Peperomia, Saururus, Houttuynia, Berzelia, Hedera, Coriaria, Francoa, Dillenia, Schumacheria, Nepenthes, Spinacia, Limeum, Phytolacca, Haloragis*, and *Itea*. To test the effect of the reduced sampling, a heuristic parsimony search of the combined data with reduced sampling was performed. It resulted in a strict consensus tree (of six trees) that was virtually identical in topology to that found in the strict consensus tree with complete sampling (Fig. 6).

Table 4. *P*-values from partition-homogeneity test, with 100 replications for various partitions of data. To reduce computation time, analyses were done with reduced sampling (see "Materials and Methods"). *P*-values of 0.05 or more indicate that the partition of data sets is random, indicating congruence between data sets.

Data sets	*P*-value
*atp*B vs. *rbc*L	0.41
*atp*B vs. 18S	0.13
*rbc*L vs. 18S	0.26
*atp*B/*rbc*L vs. 18S	0.21

RESULTS

The number of variable and potentially phylogenetically informative characters found in each data set, the number and length of most parsimonious trees obtained, and the consistency, retention, and rescaled consistency indices of the various analyses performed are presented in Table 3. The results from the incongruence tests of the reduced data sets are found in Table 4. The *P*-values resulting from the partition homogeneity test indicate that the data partitions are random (*P*-values ranges between 0.13 and 0.41) and that the data sets are reasonably congruent.

One of the most parsimonious trees produced from each analysis is presented to illustrate the support at different nodes (Figs. 1–5). In the results and discussion presented here, clades with bootstrap values of 70% or more are regarded, provisionally, as "well supported" (Hillis & Bull, 1993). Tables 5 and 6 present the bootstrap support for various systematic groupings.

RESULTS BASED ON THE CHLOROPLAST GENES

The two chloroplast sequences, *atp*B and *rbc*L, are most congruent (*P*-value = 0.41, Table 4). Comparison of the strict consensus trees derived from each data set (Figs. 1, 2) indicates minor differences in the degree of resolution of some clades and some positional differences in branches with weak bootstrap support (< 70%). Because the data are congruent and topologically similar, only the

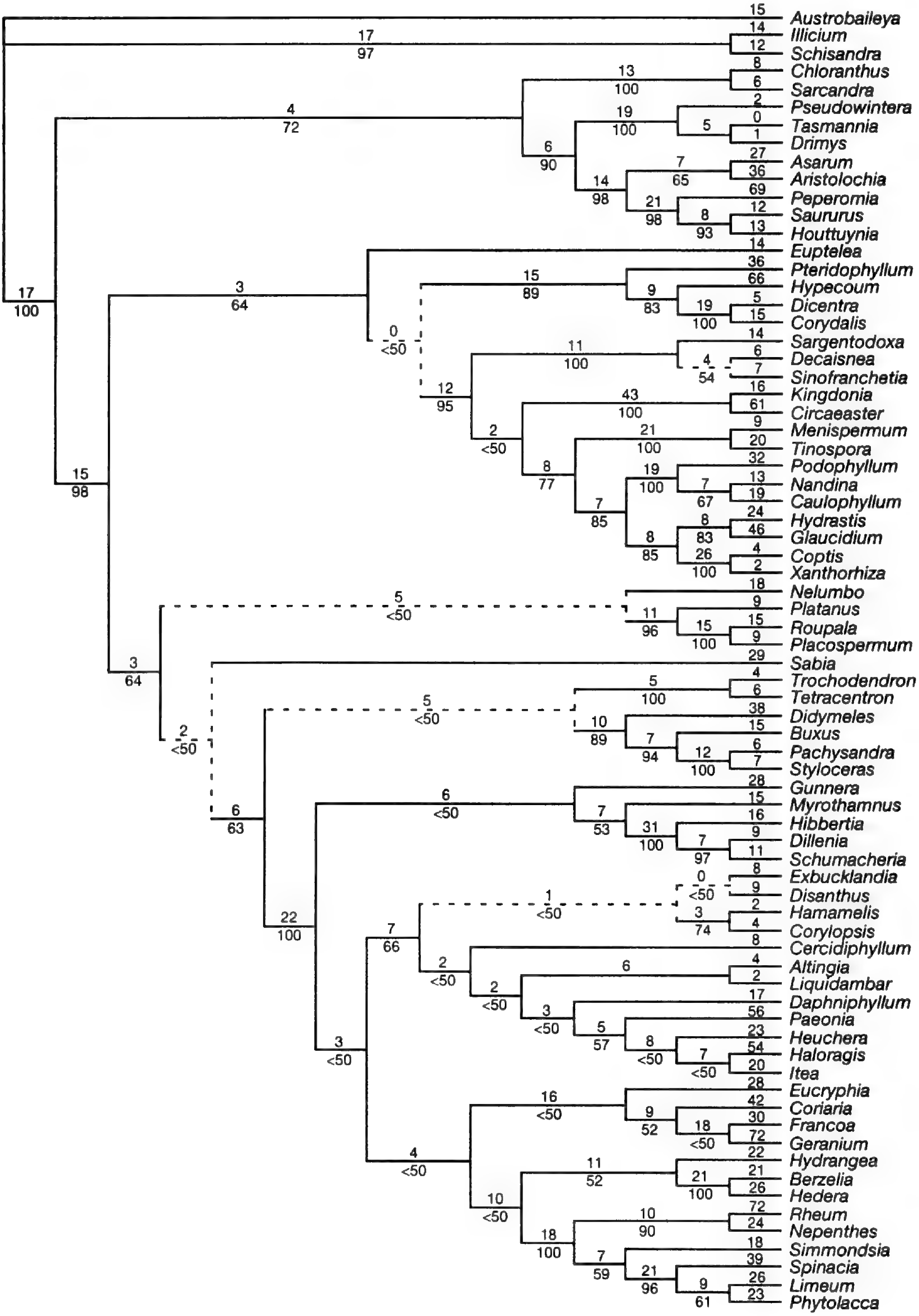


Figure 1. One of 108 shortest trees based on the *atp*B sequence data. Numbers above the line indicate the number of nucleotide changes supporting each branch. Numbers below the branches are the percentage of times that the branch was recovered in 100 bootstrap replications. Dotted lines indicate branches that collapse in the strict consensus tree derived from multiple shortest trees. See Table 3 for tree statistics.

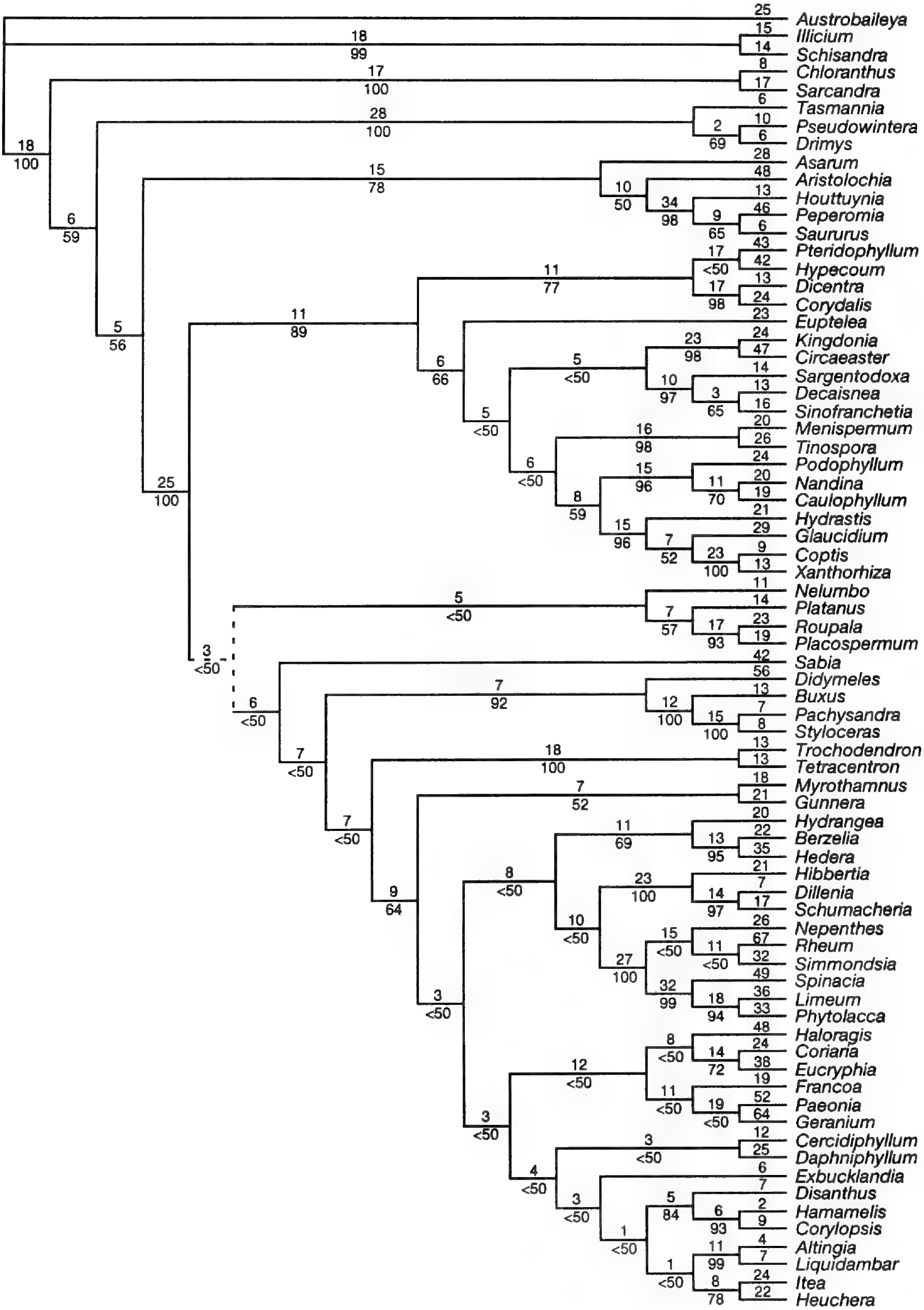


Figure 2. One of two shortest trees based on the *rbc*L sequence data. Numbers above and below the lines and dotted lines are as in Figure 1. See Table 3 for tree statistics.

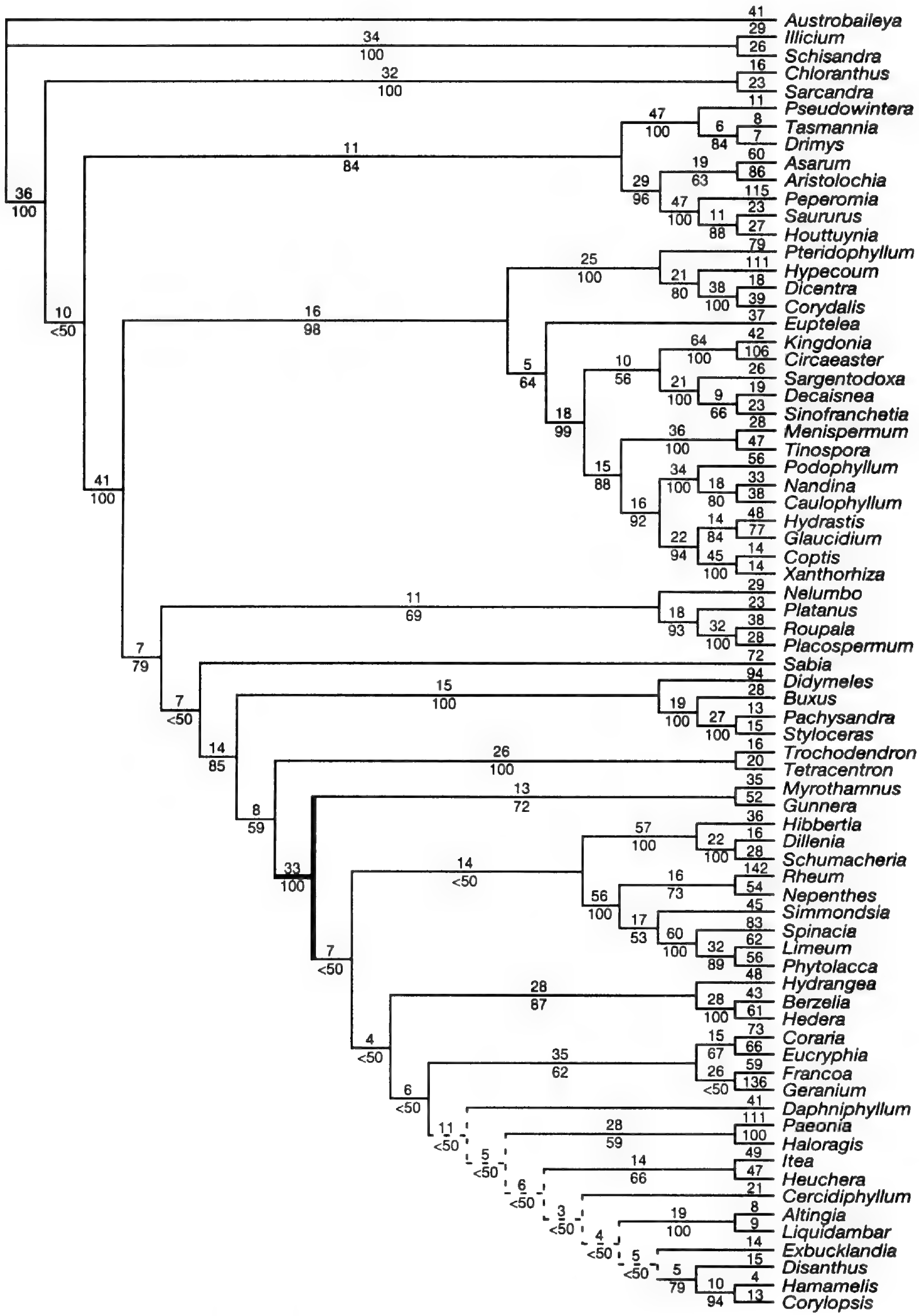


Figure 3. One of six shortest trees based on a combination of *atp*B and *rbc*L sequence data. Numbers above and below the lines and dotted lines are as in Figure 1. Node in bold indicates the well-supported core eudicot clade. See Table 3 for tree statistics.

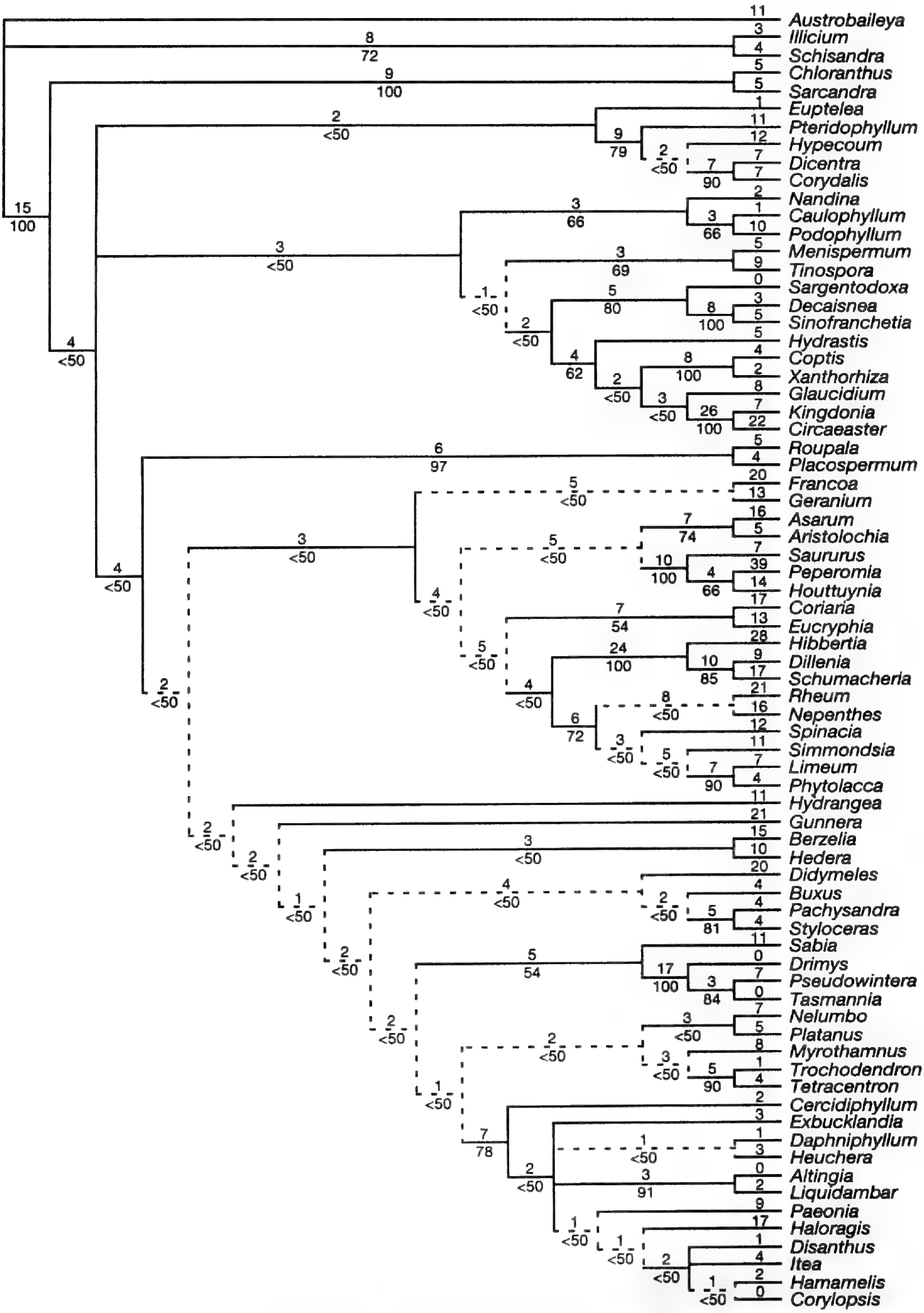


Figure 4. One of 270 shortest trees based on the nr18S sequence data. Numbers above and below the lines and dotted lines are as in Figure 1. See Table 3 for tree statistics.

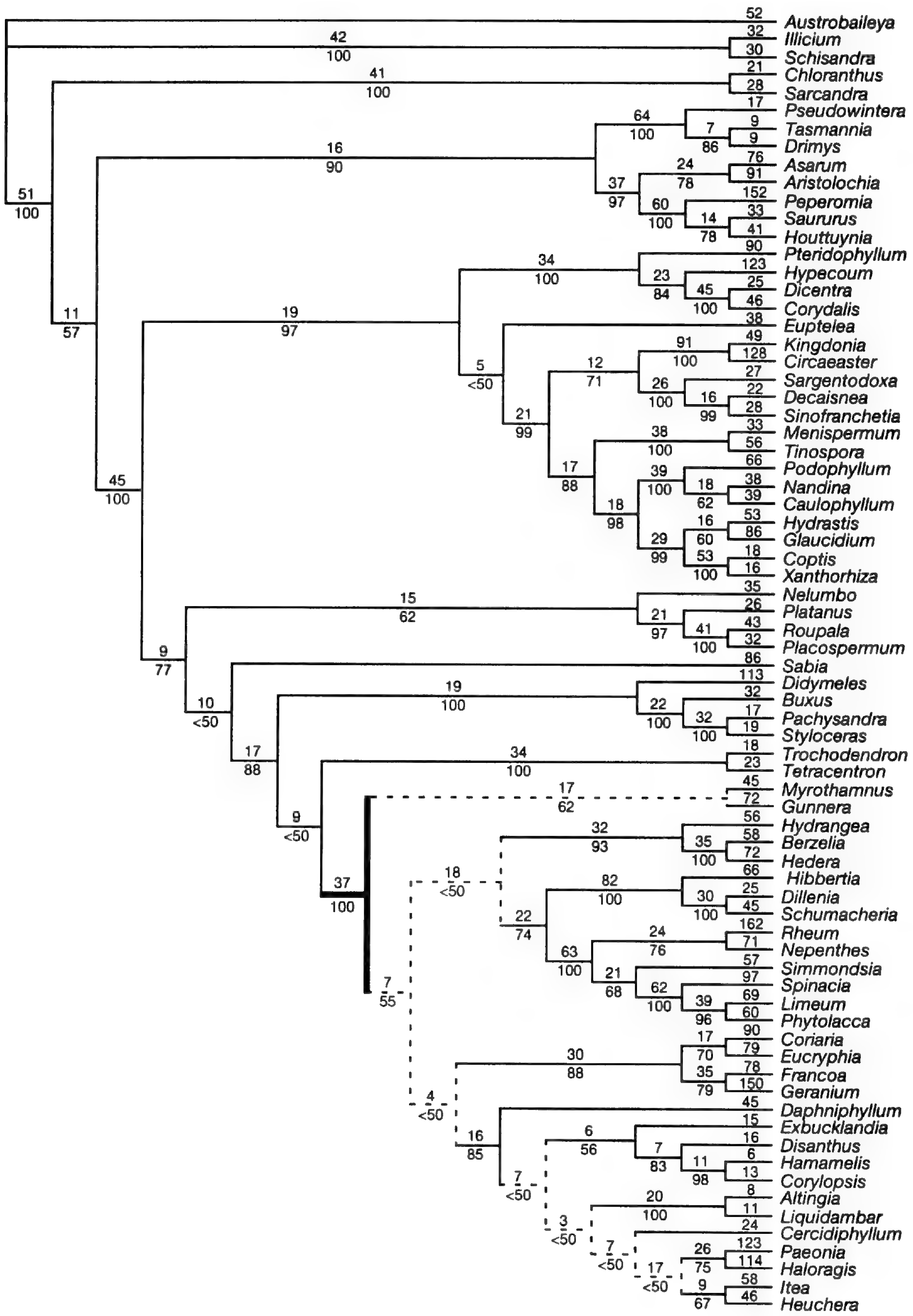


Figure 5. One of 15 shortest trees based on a combination of *atp*B, *rbc*L, and 18S sequence data. Numbers above and below the lines and dotted lines are as in Figure 1. Node in bold indicates the well-supported core eudicot clade. See Table 3 for tree statistics.

results of the combined chloroplast data analysis will be discussed here in detail (Fig. 3).

The six trees resulting from analysis of the combined chloroplast data (*atp*B and *rbc*L) strongly support the monophyly of the eudicots as a whole (bootstrap = 98%). Within the group there are two major well-supported clades, the Ranunculidae (including *Euptelea*) and the "core eudicots" (Fig. 3, node highlighted in bold).

In Ranunculidae, there is strong support for the monophyly of traditionally recognized taxa including Papaverales, Circaeasteraceae (including *Kingdonia*), Lardizabalaceae (including *Sargentodoxa*), Menispermaceae, Berberidales, and Ranunculaceae. Within Ranunculidae, Papaverales and *Euptelea* are basal, while Berberidales and Ranunculaceae are found in a derived position.

Within the non-ranunculid "lower" eudicots, there is moderate support for an expanded hamamelid clade (bootstrap = 79%) consisting of several basal eudicot lineages forming a paraphyletic series: (1) *Platanus*/Proteaceae/*Nelumbo*, (2) *Sabia*, (3) Buxaceae/*Didymeles*, (4) *Trochodendron*/*Tetracentron*, and (5) the core eudicots. The core eudicots are well supported (33 substitutions, bootstrap = 100%) and consist of a highly unresolved clade of "lower" hamamelids and placeholders for various eudicot groups (Fig. 3). The "lower" hamamelids, as previously suggested, are clearly polyphyletic (Crane, 1989; Albert et al., 1994; Chase et al., 1993; Drinnan et al., 1994; Williams et al., 1994; Soltis et al., 1997; Qiu et al., 1998).

RESULTS BASED ON 18S SEQUENCE DATA

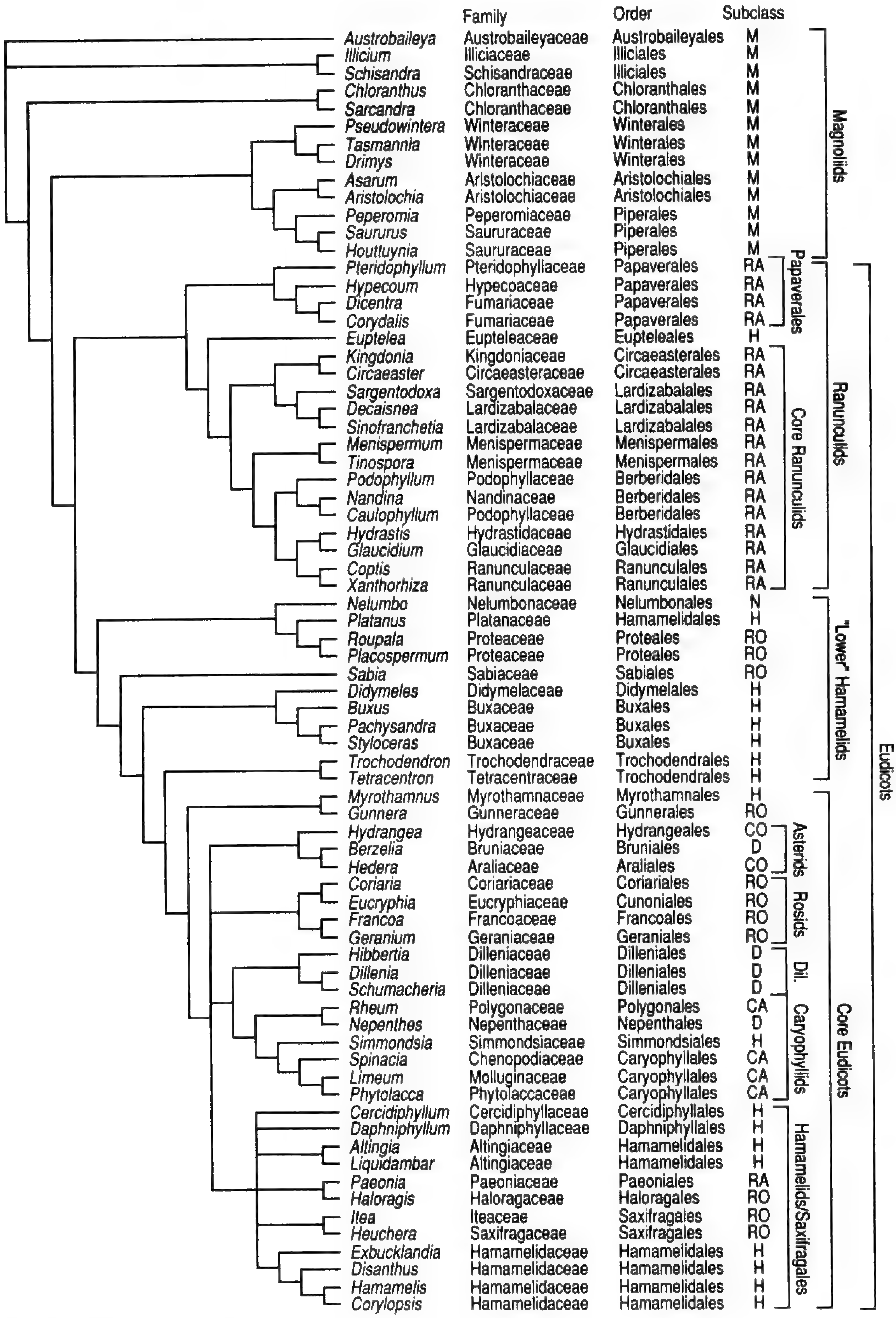
The consensus tree resulting from 18S nuclear ribosomal DNA (Fig. 4) is less resolved, and deeper branching patterns are less well supported (lower bootstrap values), than in the consensus trees resulting from the individual chloroplast data sets. This is highlighted in Table 5, which contrasts the level of support for the chloroplast and 18S data at the order/subclass level. Major factors contributing to this lack of basal support in the analyses based on 18S data are: less information (approximately half as many variable and informative sites compared to *atp*B and *rbc*L, Table 3) and a larger number of sites in highly variable regions that exhibit high levels of homoplasy (Hoot, unpublished data). At lower taxonomic levels, however, many of the more terminal clades with adequate bootstrap support are identical to those found in the cladograms based on the chloroplast sequence data (Table 6).

The anomalous placement of some magnoliid taxa within the eudicots seen in previous analyses of 18S data (Nickrent & Soltis, 1995; Soltis et al., 1997) is also found in the analysis presented here (Fig. 4). Interestingly, although the sampling differs in the two studies, two of the same families are involved: Aristolochiaceae and Winteraceae. In our 18S analysis, the paleoherb order Piperales is also placed within the eudicots, while it remained nested among other magnoliid groups in the Soltis et al. (1997) analysis. However, in both analyses, the branches involved in this anomalous placement of magnoliid taxa have bootstrap values < 50%. Indeed, if all branches with bootstrap values < 50% are collapsed, the tree (Fig. 4) reads as a highly unresolved polytomy with little or no information about higher-level taxonomic relationships.

RESULTS BASED ON COMBINED *RBCL*, *ATPB*, AND 18S SEQUENCE DATA

The trees (Figs. 5, 6) based on a combination of all the data are very similar in topology to the trees derived from analyses of the data from the two chloroplast genes, but, in general, the addition of 18S data resulted in higher bootstrap support for many of the branches (Tables 5, 6). Four clades are not supported (bootstrap values ≤ 50%) by any of the individual data sets, but are supported in the combined analyses (Tables 5, 6): Circaeasteraceae/Lardizabalaceae, Rosid I & II, *Nelumbo*/*Platanus*/Proteaceae, and Hamamelidaceae s. str. (i.e., Hamamelidoideae sensu Endress, 1989a, 1993).

The results of the first four alternative analyses with varied taxon sampling (see "Materials and Methods") were very similar in tree topology to the tree resulting from complete sampling (Fig. 5). Varying the outgroup by removing either the paleoherbs or the "woody" magnoliids resulted in trees with the same topology as presented in Figure 5, except that *Euptelea* formed a trichotomy within the ranuculids when only woody magnoliids were used as the outgroup, whereas it was resolved as sister group to all ranunculids except Papaverales when the paleoherbs were the outgroup. Reducing the sample size of the ranunculids to three or six genera (see "Materials and Methods") resulted in identical tree topologies to the tree based on complete sampling with only one exception: the tree based on three ranunculid genera resulted in a lack of resolution for *Sabia* in relation to other eudicots in the "lower" hamamelid/core eudicot clade (Fig. 6). Analysis of just the core eudicot group (as delimited in Fig. 6) using *Tetracentron* as an outgroup, resulted in one fully resolved tree. However, bootstrap support was < 50% for the identical branches



	Family	Order	Subclass
Austrobaileya	Austrobaileyaceae	Austrobaileyales	M
Illicium	Illiciaceae	Illiciales	M
Schisandra	Schisandraceae	Illiciales	M
Chloranthus	Chloranthaceae	Chloranthales	M
Sarcandra	Chloranthaceae	Chloranthales	M
Pseudowintera	Winteraceae	Winterales	M
Tasmannia	Winteraceae	Winterales	M
Drimys	Winteraceae	Winterales	M
Asarum	Aristolochiaceae	Aristolochiales	M
Aristolochia	Aristolochiaceae	Aristolochiales	M
Peperomia	Peperomiaceae	Piperales	M
Saururus	Saururaceae	Piperales	M
Houttuynia	Saururaceae	Piperales	M
Pteridophyllum	Pteridophyllaceae	Papaverales	RA
Hypecoum	Hypecoaceae	Papaverales	RA
Dicentra	Fumariaceae	Papaverales	RA
Corydalis	Fumariaceae	Papaverales	RA
Euptelea	Eupteleaceae	Eupteleales	H
Kingdonia	Kingdoniaceae	Circaeasterales	RA
Circaeaster	Circaeasteraceae	Circaeasterales	RA
Sargentodoxa	Sargentodoxaceae	Lardizabalales	RA
Decaisnea	Lardizabalaceae	Lardizabalales	RA
Sinofranchetia	Lardizabalaceae	Lardizabalales	RA
Menispermum	Menispermaceae	Menispermales	RA
Tinospora	Menispermaceae	Menispermales	RA
Podophyllum	Podophyllaceae	Berberidales	RA
Nandina	Nandinaceae	Berberidales	RA
Caulophyllum	Podophyllaceae	Berberidales	RA
Hydrastis	Hydrastidaceae	Hydrastidales	RA
Glaucidium	Glaucidiaceae	Glaucidiales	RA
Coptis	Ranunculaceae	Ranunculales	RA
Xanthorhiza	Ranunculaceae	Ranunculales	RA
Nelumbo	Nelumbonaceae	Nelumbonales	N
Platanus	Platanaceae	Hamamelidales	H
Roupala	Proteaceae	Proteales	RO
Placospermum	Proteaceae	Proteales	RO
Sabia	Sabiaceae	Sabiales	RO
Didymeles	Didymelaceae	Didymelales	H
Buxus	Buxaceae	Buxales	H
Pachysandra	Buxaceae	Buxales	H
Styloceras	Buxaceae	Buxales	H
Trochodendron	Trochodendraceae	Trochodendrales	H
Tetracentron	Tetracentraceae	Trochodendrales	H
Myrothamnus	Myrothamnaceae	Myrothamnales	H
Gunnera	Gunneraceae	Gunnerales	RO
Hydrangea	Hydrangeaceae	Hydrangeales	CO
Berzelia	Bruniaceae	Bruniales	D
Hedera	Araliaceae	Araliales	CO
Coriaria	Coriariaceae	Coriariales	RO
Eucryphia	Eucryphiaceae	Cunoniales	RO
Francoa	Francoaceae	Francoales	RO
Geranium	Geraniaceae	Geraniales	RO
Hibbertia	Dilleniaceae	Dilleniales	D
Dillenia	Dilleniaceae	Dilleniales	D
Schumacheria	Dilleniaceae	Dilleniales	D
Rheum	Polygonaceae	Polygonales	CA
Nepenthes	Nepenthaceae	Nepenthales	D
Simmondsia	Simmondsiaceae	Simmondsiales	H
Spinacia	Chenopodiaceae	Caryophyllales	CA
Limeum	Molluginaceae	Caryophyllales	CA
Phytolacca	Phytolaccaceae	Caryophyllales	CA
Cercidiphyllum	Cercidiphyllaceae	Cercidiphyllales	H
Daphniphyllum	Daphniphyllaceae	Daphniphyllales	H
Altingia	Altingiaceae	Hamamelidales	H
Liquidambar	Altingiaceae	Hamamelidales	H
Paeonia	Paeoniaceae	Paeoniales	RA
Haloragis	Haloragaceae	Haloragales	RO
Itea	Iteaceae	Saxifragales	RO
Heuchera	Saxifragaceae	Saxifragales	RO
Exbucklandia	Hamamelidaceae	Hamamelidales	H
Disanthus	Hamamelidaceae	Hamamelidales	H
Hamamelis	Hamamelidaceae	Hamamelidales	H
Corylopsis	Hamamelidaceae	Hamamelidales	H

Figure 6. Strict consensus tree of the 15 shortest trees obtained from the combined data (*atp*B, *rbc*L, and 18S). Families, orders, and subclass acronyms are listed in the first three columns (taxonomic designations according to

that collapsed in the strict consensus tree derived with complete taxon sampling (dotted lines, Fig. 5).

DISCUSSION

As in other work involving the combination of large molecular data sets (e.g., Hoot et al., 1995, 1997; Soltis et al., 1998), the analyses based on the combined data (both the combined chloroplast sequences and a combination of all three sequences) had shorter computer run times and resulted in trees with better resolution and improved bootstrap support. The increases in resolution and support for groupings at the subclass and family levels are indicated in Tables 5 and 6. Of the individual data sets, bootstrap values and resolution were the highest with *atp*B and *rbc*L sequences from the chloroplast genome and the lowest with nr18S DNA sequences. In addition, the tree topology derived from a combination of all the data was not sensitive to variations in either outgroup or ingroup sampling. Any differences occurring as a result of various sampling experiments were minor and confined to branching patterns with weak support.

In the following paragraphs, we briefly discuss the congruence of our results with previous work based on non-molecular characters, with an emphasis on floral morphology. A more detailed morphological study of the "lower" eudicots is in progress (Magallón & Crane).

RANUNCULID CLADE

A ranunculid clade, which corresponds largely to subclass Ranunculidae of Takhtajan (1997), is strongly supported (bootstrap = 97%, 19 substitutions; Fig. 5) in the combined analysis of *atp*B, *rbc*L, and 18S sequence data. The ranunculids are characterized by unusually large and homogeneous S_s sieve element plastids (Behnke, 1995), benzylisoquinoline alkaloids of the berberine and morphine type (Jensen, 1995), and epicuticular wax tubules (also found in a few non-ranunculid families, including Nelumbonaceae; Barthlott & Theisen, 1995). There are no clear synapomorphies in floral morphology for the Ranunculidae (Endress, 1995). The flowers are often large and conspicuous with brightly colored petals with whorled phyllotaxis, but there are many exceptions. A di- or trimerous floral plan seems to be basic in the group (Drinnan et al., 1994).

Euptelea. A surprising result that emerged from previous studies (Chase et al., 1993; Drinnan et al., 1994; Hoot & Crane, 1995; Soltis et al., 1997), and that is supported by this work utilizing three gene sequences and more extensive sampling, is the inclusion of *Euptelea* within the ranunculid clade in a basal position near the Papaverales. Because of the low bootstrap value (< 50%) in the total evidence tree, phylogenetic patterns involving *Euptelea* are best considered as a trichotomy that includes Papaverales and the remaining "core" ranunculids (Figs. 5, 6).

Euptelea has traditionally been placed among the "lower" hamamelids, characterized by relatively inconspicuous flowers (e.g., *Trochodendron, Cercidiphyllum*; Endress, 1986; Cronquist, 1981; Takhtajan, 1997). Flowers of *Euptelea* are small, bisexual, lack a perianth, and have a variable number of stamens and carpels, apparently in whorls. Developmental studies indicate that the floral primordium is bilaterally symmetrical (Endress, 1986), perhaps indicating a basically dimerous floral plan. The floral features of *Euptelea* are significantly different from those of other Ranunculidae. One possible similarity between the flowers of *Euptelea* and several Ranunculales and Papaverales is a dimerous floral organization, but the distribution of this character state among ranunculids and "lower" hamamelids is complex. There is apparently no uniquely derived floral feature that links this genus with Papaverales and Ranunculales.

Papaverales. A clade corresponding to the order Papaverales of Cronquist (1981) and Takhtajan (1997), represented in this study by *Pteridophyllum, Hypecoum,* and two genera of Fumariaceae, is solidly supported as a monophyletic group (bootstrap = 100%, 34 substitutions) and appears as sister to all remaining ranunculids (core ranunculids) in the strict consensus tree resulting from the combined three-gene analysis (Figs. 5, 6). The position of Papaverales as sister to *Euptelea* and the core ranunculids is consistent with the results of previous analyses based on molecular data (Chase et al., 1993; Hoot & Crane, 1995; Soltis et al., 1997), but conflicts with previous cladistic analyses

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Takhtajan, 1997). Acronyms for subclasses: CA = Caryophyllidae, CO = Cornidae, D = Dilleniidae, H = Hamamelididae, M = Magnoliidae, N = Nelumbonidae, RA = Ranunculidae, RO = Rosidae. Dil. = Dilleniaceae. Brackets to the right indicate major taxonomic groups discussed in text.

Table 5. Bootstrap support (%) for various groups of order to subclass rank sensu Takhtajan (1997) found in separate and combined data analyses (Figs. 1–6). See Figure 6 for generic makeup of various groups. * As defined in Chase et al. (1993). "—" indicates bootstrap values ≤ 50%.

Higher taxonomic groupings	*atp*B	*rbc*L	*atp*B/*rbc*L	18S	*atp*B/*rbc*L/ 18S
Winteraceae/Aristolochiaceae/Piperales	90	—	84	—	90
Piperales	98	98	100	100	100
Eudicots + *Nelumbo*	98	100	100	—	100
Ranunculidae + *Euptelea*	64	89	98	—	97
Papaverales	89	77	100	79	100
Ranunculales	95	—	99	—	99
Circaeasteraceae/Lardizabalaceae s.l.	—	—	56	—	71
Menispermaceae/Berberidaceae/Ranunculaceae s.l.	77	—	88	—	88
Berberidaceae/Ranunculaceae s.l.	85	59	92	—	98
Lower eudicots excluding ranunculids	64	—	79	—	77
Hamamelididae	—	—	—	—	—
Core eudicots (hamamelids, caryophyllids, asterids, rosids)	100	64	100	—	100
Dilleniidae	100	100	100	100	100
Rosid I & II*	—	—	62	—	88
Asterids*	52	69	87	—	93
Caryophyllids + *Simmondsia*	100	100	100	72	100
Hamamelidales + *Paeonia*, *Haloragis*, *Itea*, and *Heuchera*	66	—	—	78	85

of morphological data (Loconte & Stevenson, 1991; Loconte et al., 1995), which placed Papaverales as sister to Ranunculaceae in a relatively derived position with respect to other ranunculid families. Based on results from the combined *atp*B, *rbc*L, and 18S data, the latter conclusion is unparsimonious. Moving Papaverales into a derived position as sister to Ranunculaceae adds an additional 24 steps (total

Table 6. Bootstrap support (%) for various clades at the family level. "—" indicates bootstrap values ≤ 50%.

Family-level groupings	*atp*B	*rbc*L	*atp*B/*rbc*L	18S	*atp*B/*rbc*L/ 18S
Illicium/*Schisandra*	97	99	100	72	100
Chloranthaceae	100	100	100	100	100
Winteraceae	100	100	100	100	100
Aristolochiaceae	65	—	63	74	78
Saururaceae	93	—	88	—	78
Fumariaceae (including *Hypecoum*)	83	—	80	—	84
Circaeasteraceae	100	98	100	100	100
Lardizabalaceae s.l. (including *Sargentodoxa*)	100	97	100	80	100
Lardizabalaceae s. str.	54	65	66	100	99
Menispermaceae	100	98	100	69	100
Berberidaceae (including *Nandina*)	100	96	100	66	100
Ranunculaceae s.l. (including *Hydrastis*/*Glaucidium*)	86	96	94	62	99
Ranunculaceae s. str.	100	100	100	100	100
Nelumbo/*Platanus*/Proteaceae	—	—	69	—	62
Platanus/Proteaceae	96	57	93	—	97
Proteaceae	100	93	100	97	100
Trochodendron/*Tetracentron*	100	100	100	90	100
Buxaceae/Didymelaceae	89	92	100	—	100
Buxaceae	94	100	100	—	100
Hamamelidaceae s.l. (including *Altingia*/*Liquidambar*)	—	—	—	—	—
Hamamelidaceae s. str.	—	—	—	—	56

tree length = 5714 steps); moving Ranunculaceae into a relatively basal position as sister to Papaverales incurs an additional 25 steps.

Papaverales constitute a coherent group that has been recognized traditionally as a distinct natural entity, characterized by paracarpous gynoecia and the presence of secretory idioblasts or lacticifers (except for *Pteridophyllum*; Kadereit et al., 1995; Hoot et al., 1997). The flowers are bisexual and range from regularly symmetrical to markedly zygomorphic. They have a whorled and basically dimerous, opposite-decussate organization.

Pteridophyllum is strongly supported as sister to Hypecoaceae plus Fumariaceae based on the analysis of the combined data (Fig. 5). The flowers of *Pteridophyllum* have a perianth composed of one pair of sepals and two pairs of petals. The androecium consists of four stamens arranged in two opposite-decussate pairs, and the gynoecium has two connate carpels, forming a unilocular ovary.

The sister-group relationship between *Hypecoum* and Fumariaceae is well supported (bootstrap = 84%, 23 substitutions; Fig. 5). The flowers of *Hypecoum* have a similar organization to those of *Pteridophyllum* but differ in that the stamens of the inner pair have anthers in which the two thecae are separated. The gynoecium is unilocular, formed by two connate carpels.

Results of the combined three-gene analysis indicate that the two representatives of Fumariaceae s. str. (*Dicentra, Corydalis*) are monophyletic (bootstrap = 100%, 45 substitutions; Fig. 5). The flowers of Fumariaceae are strongly zygomorphic, which is clearly a synapomorphy with respect to the condition found in *Pteridophyllum* and *Hypecoum.* The androecium consists of two compound stamens, each with a central bithecal portion and two lateral monothecal portions. The gynoecium has two connate carpels that form a unilocular ovary. Flowers of Papaveraceae, which were not sampled in this study, are constructed upon the same basic pattern as those of *Pteridophyllum, Hypecoum,* and Fumariaceae. In some Papaveraceae, the production of numerous stamens and the development of multiple internal placentae in unilocular ovaries formed from one to a few carpels are clearly derived features (Hoot et al., 1997).

"CORE" RANUNCULIDS

A "core" ranunculid clade composed of Circaeasteraceae, Lardizabalaceae, Menispermaceae, Hydrastidaceae, Glaucidiaceae, Berberidaceae, and Ranunculaceae is strongly supported (bootstrap = 99%, 21 substitutions) in the combined analysis of *atp*B, *rbc*L, and 18S sequence data (Figs. 5, 6). This clade corresponds approximately to the order Ranunculales of Cronquist (1981). Floral morphology in the core ranunculid group is extremely varied. Flowers may be unisexual (e.g., Lardizabalaceae, Menispermaceae) or bisexual, with radial to bilateral symmetry. Merosity varies from dimerous (e.g., *Circaeaster, Glaucidium*) or trimerous (e.g., Lardizabalaceae, Menispermaceae, Berberidaceae) to 4–12-merous with helical or whorled phyllotaxy (e.g., Ranunculaceae). Hypogyny and apocarpy are characteristic of this group.

Circaeasteraceae s.l. *Circaeaster* and *Kingdonia* form a moderately well-supported sister group to Lardizabalaceae and *Sargentodoxa* (bootstrap = 71%, 12 substitutions) in the tree resulting from a combination of all the data (Fig. 5). Morphological comparisons of Circaeasteraceae with *Sargentodoxa* and Lardizabalaceae s. str. (e.g., *Decaisnea* and *Sinofranchetia*) reveal little similarity in vegetative and floral features. Significant differences between Circaeasteraceae s.l. and Lardizabalaceae s.l. are also reflected in the unusually long branches associated with Circaeasteraceae and its two genera, *Circaeaster* and *Kingdonia* (Figs. 1–5).

Circaeaster and *Kingdonia* form an extremely well-supported monophyletic group (bootstrap = 100%, 91 substitutions; Fig. 5). This is consistent with past interpretations (Foster, 1961, 1963; Oxelman & Liden, 1995), but conflicts with suggestions that *Kingdonia* should be placed within Ranunculaceae in a position close to *Anemone* (Tamura, 1962, 1995; Kosuge et al., 1989). Based on our combined data set, moving *Kingdonia* to the base of Ranunculaceae s.l. (represented here by four genera) adds 82 steps to the shortest tree length. Experiments involving a larger sampling of Ranunculaceae are similarly unparsimonious (Hoot, unpublished results).

In terms of floral organization and life history, *Circaeaster* and *Kingdonia* differ markedly. The flowers of *Circaeaster* are usually bisexual, with a whorled phyllotaxy and irregular floral merosity. Most flowers have a perianth of two or three undifferentiated tepals, two stamens, and one carpel (Hu et al., 1990). The flowers of *Kingdonia* are bisexual, also with irregular and variable floral merosity. Flowers are apparently based on a helical phyllotaxy (Kosuge et al., 1989; Drinnan et al., 1994). There are 5 to 7 undifferentiated tepals, 8 to 12 external staminodes, 3 to 6 internal stamens, and 5 to 8 helically arranged carpels. In addition, *Circaeaster* is an annual and *Kingdonia* is a perennial, rhizomatous plant. However, the dichotomous venation in the leaves of both genera is one clear and remarkable morphological character that unites *Circaeaster* and *Kingdonia.*

Lardizabalaceae. The monophyly of Lardizabalaceae s. str. and the sister-group relationship of *Sargentodoxa* to Lardizabalaceae are both strongly supported (bootstrap = 99% and 100%, respectively; Figs. 5, 6). Lardizabalaceae s. str. are monoecious or dioecious. The flowers have a whorled phyllotaxy with regular symmetry. The perianth usually consists of six petaloid sepals and six petals, each arranged in two whorls. The petals are thought to be staminodial in origin (Drinnan et al., 1994). In staminate flowers, the androecium usually consists of six stamens that are opposite the petals, and pistillodes may be present. Pistillate flowers usually have three free carpels, but in some genera there may be more. Species of *Sargentodoxa* are andromonoecious or dioecious and have flowers with 48–90 helically arranged, free carpels (Cronquist, 1981; Wu & Kubitzki, 1993).

Menispermaceae. Menispermaceae is well supported as sister to a clade consisting of Berberidaceae and Ranunculaceae s.l. (bootstrap = 88%, 17 substitutions; Figs. 5, 6) and as a monophyletic family (bootstrap = 100%, 38 substitutions). Menispermaceae share a trimerous floral construction with most Berberidaceae but differ in being dioecious. The perianth is formed by relatively differentiated sepals and petals, organized in two whorls of three sepals and two whorls of three petals. The staminate flowers have six stamens in two whorls, and the pistillate flowers have mostly three (occasionally one to six) free carpels in one or more whorls, forming an apocarpous gynoecium.

Berberidaceae. The sister-group relationship between Berberidaceae and Ranunculaceae s.l. (including *Hydrastis* and *Glaucidium*) is stable and strongly supported (bootstrap = 98%, 18 substitutions; Fig. 5). This relationship is also supported by an important phytochemical character, the presence of the isoquinoline alkaloid berberine in Berberidaceae and the basal members of Ranunculaceae s.l. (Hegnauer, 1966; Jensen, 1995). Molecular data provide no support for a sister-group relationship between Berberidaceae and Papaveraceae proposed on the basis of several shared morphological characters (i.e., gynoecium congenitally closed to the level of the stigma, placentae protruding-diffuse in some genera, fruit dehiscence transverse; Endress, 1995).

The placeholders for Berberidaceae form a strongly supported monophyletic group in the analyses presented here (bootstrap = 100%, 39 substitutions; Figs. 5, 6). The typically trimerous flowers of Berberidaceae are bisexual with regular symmetry and whorled phyllotaxy. The perianth consists of one or more whorls of three sepals, and one or more whorls of three petals, which may or may not have nectaries. Morphological differentiation between sepals and petals is not very strong. There are usually six stamens, apparently in two whorls of three, and opposite the petals. The gynoecium consists of two or three carpels, but is pseudomonomerous.

Ranunculaceae s.l. The sister-group relationship between Ranunculaceae and *Hydrastis/Glaucidium* (bootstrap = 99%, 29 substitutions; Fig. 5) derived from our data supports previous classifications and phylogenetic analyses based on morphological and molecular characters (Hoot, 1991, 1995). Given the strongly supported phylogenetic pattern among Lardizabalaceae, Menispermaceae, and Berberidaceae, it is more parsimonious to suppose a basically trimerous condition for the flowers of Ranunculaceae (including *Hydrastis* and *Glaucidium*) that has been modified within Ranunculaceae into a dimerous or pentamerous plan. The flowers of *Hydrastis* show a tendency toward trimery with a perianth of three tepals (sometimes two or four). *Glaucidium,* sister to *Hydrastis,* has bisexual, dimerous flowers with an opposite-decussate plan that consists of four tepals arranged in two pairs; numerous, spirally arranged stamens, and two partially fused carpels.

Floral morphology is diverse within Ranunculaceae, but most taxa have bisexual hypogynous flowers with regular symmetry and floral organs frequently arranged in a helical phyllotaxy on the floral receptacle. The innermost organs of the perianth are thought to be staminodial in nature (Tamura, 1965). The perianth parts may be in threes, fives, or variable numbers. The stamens and carpels are numerous, and the gynoecium is apocarpous.

"LOWER" HAMAMELID GRADE

Placed between the ranunculid clade, which constitutes a basal eudicot lineage, and the core eudicot clade, which includes the majority of the taxonomic diversity within the eudicots, is a paraphyletic grade that includes taxa of "lower" Hamamelididae and other affinities, which we term here the "lower" hamamelid grade (Fig. 6). There appear to be no universal morphological features shared among the independent lower hamamelid lineages and the core eudicots and, in spite of the limited number of lineages and species within the lower hamamelid grade, the disparity in floral form and structure encompassed by these lineages is considerable. The flowers belonging to the lower hamamelid lineages may have a conspicuous perianth (e.g., *Nelumbo*), a perianth formed by small, bract-like organs (e.g., Buxaceae), or no perianth (e.g., *Trochodendron*). The androecium may consist of few (e.g., *Tetracentra*) to numerous (e.g., *Nelumbo*) stamens, and the gynoecium may be formed of few to many free or fused carpels. The ovaries are superior, with the exception of Trochodendrales (with the basal part of the ovary embedded in the floral receptacle). Floral merosity may be dimerous, tetramerous, pentamerous, or irregular, either by presumed reduction or increase in the number of floral organs. With the exception of Sabiaceae, the perianth is not differentiated into a single whorl of sepals and a single whorl of petals, apparently a plesiomorphic feature which also occurs in several lineages of the ranunculid clade. The generalized absence of a differentiated perianth (as described above) among basal eudicot lineages suggests that the perianth has not yet developed the specialized level of organization that characterizes the core eudicots.

Nelumbo/Platanaceae/Proteaceae. One of the main lineages of the lower hamamelid grade is a weakly supported clade (bootstrap = 62%, 15 substitutions) comprising *Nelumbo*, Proteaceae, and Platanaceae (Figs. 5, 6). The somewhat unexpected relationship of *Nelumbo* with Platanaceae/Proteaceae, and with non-magnoliid dicotyledons as a whole, has been previously suggested in other phylogenetic analyses (e.g., Chase et al., 1993; Drinnan et al., 1994). The placement of *Nelumbo* within the eudicots is supported by the observation that it produces (usually) tricolpate pollen grains (diagnostic of eudicots). Floral organization in *Nelumbo* is unique. The flowers are large, conspicuous, bisexual, and hypogynous, with irregular merosity. The perianth consists of greenish sepals arranged in opposite-decussate pairs, and numerous conspicuous petals arranged helically on the floral axis (Moseley & Uhl, 1985). The numerous stamens continue the helical phyllotactic pattern of the petals. The 2 to 30 carpels are free from one another, but embedded in a modified, terminally expanded, floral receptacle.

Proteaceae and Platanaceae are well supported as sister taxa (bootstrap = 97%, 21 substitutions; Fig. 5). There are several interesting similarities among the flowers of Proteaceae and Platanaceae, especially when considering fossil platanoids. Proteaceae have bisexual flowers with whorled phyllotaxy and a superior ovary. Except for the gynoecium, floral merosity is tetramerous. The perianth consists of a single whorl of four tepals. The androecium has four stamens, each placed opposite one tepal, and the gynoecium consists of a single carpel. The flowers of *Platanus* are unisexual, individually inconspicuous, and grouped in compact, strictly unisexual, spherical inflorescences. Although sepals and petals have been described, morphological differentiation between the two types of organs is ambiguous. Staminate flowers typically have four stamens. Pistillate flowers have a variable number of reproductive organs. Several fossils attributed to Platanaceae on the basis of a distinctive combination of characters have flowers with relatively conspicuous perianth parts and fixed tetramery (Magallón-Puebla et al., 1997) or pentamery (e.g., Manchester, 1986; Friis et al., 1988; Crane et al., 1993). Developmental studies of the pistillate flowers of extant *Platanus* have also revealed an initially tetramerous organization (A. W. Douglas, pers. comm.). The occurrence of a basically tetramerous organization in the flowers of *Platanus*, together with the discovery of tetramerous fossil flowers apparently referable to Platanaceae, provides morphological links with Proteaceae, suggesting the possibility that this condition was shared by these two families and has subsequently been modified one to several times within Platanaceae.

Sabiaceae. While the inclusion of the genus *Sabia* in the basal eudicot grade has been supported by this work and previous phylogenetic analyses (e.g., Chase et al., 1993; Drinnan et al., 1994), its exact placement with respect to other basal eudicot lineages is not securely resolved. The sister-group relationship of *Sabia* and all remaining eudicots is weakly supported in the trees derived from the combined data (bootstrap < 50%, 10 substitutions; Fig. 5). The flowers of *Sabia* exhibit several seemingly derived features, and those of *Meliosma*, included in Sabiaceae (e.g., Cronquist, 1981) or segregated into its own family within Sabiales (Takhtajan, 1997), display several modifications presumably derived from the pattern in *Sabia*. Flowers of *Sabia* are bisexual (or rarely unisexual), hypogynous, pentamerous, with whorled phyllotaxy and regular symmetry. The perianth has one whorl of apparently bract-like sepals, and one whorl of relatively elongate petals. The androecium consists of one whorl of five stamens, and a 4- or 5-lobed disk between the androecium and corolla has been reported (Li, 1993). The gynoecium consists of two to three carpels (Li, 1993). The organs in the two perianth whorls and in the androecium are opposite one another. Flowers of *Meliosma* exhibit a modified pentamerous plan that resembles trimery. Sabiaceae are the only family among the basal eudicot lineages to have flowers with a perianth consisting of a single whorl of sepals and a single whorl of petals, organized under a pentamerous plan. Because of these seemingly advanced features, which appear equivalent to the condition found in the flowers of core eudicots (see below), a clear understanding of the phylogenetic placement of Sabiaceae with respect to other basal eudicot lineages (and especially the core eudicot lineages) becomes critical to understanding the pattern of floral evolution in core eudicots.

Didymelaceae/Buxaceae. The genus *Didymeles*, endemic to Madagascar, is confirmed as a well-supported sister group to Buxaceae (bootstrap = 100%; Figs. 5, 6). A close relationship between *Didymeles* and Buxaceae had been proposed previously based on morphological (e.g., Takhtajan, 1997) and molecular characters (Qiu et al., 1998). *Didymeles* is dioecious; the staminate flowers are reported as being dimerous, lacking a perianth, and with two opposite stamens. The pistillate flowers are described as unicarpellate, lacking a perianth or with bract-like tepals, and placed in opposite pairs or in groups of three (Cronquist, 1981; Takhtajan, 1997). Preliminary observations of the pistillate flowers of *D. madagascarensis* Willd. show that the pistillate flowers consist of opposite bracts or bract-like tepals at the tip of a pedicel. There is usually one large carpel subtended by one of the tepals; the opposite tepal is empty. However, in several specimens, each of the tepals subtends a carpel, one smaller than the other. The dimerous organization of the staminate flowers of *Didymeles*, and the general aspect of the carpels, suggest similarities with Buxaceae. More detailed comparisons are currently in progress (Magallón, in prep.).

Buxaceae are strongly supported as monophyletic in the results of the combined analysis of the three data sets. Within Buxaceae, the sister-group relationship between *Pachysandra* and *Styloceras*, and the placement of *Buxus* as sister to this clade are both strongly supported (bootstrap = 100%, 32 substitutions and bootstrap = 100%, 22 substitutions, respectively; Fig. 5). The inflorescences of Buxaceae usually include both staminate and pistillate flowers. The staminate flowers are organized in a dimerous, opposite-decussate plan. The perianth is weakly differentiated from the inflorescence bracts, and two or three pairs of tepals are present. The androecium is composed of two or three pairs of stamens, and the staminate flowers contain a central pistillode. The pistillate flowers are difficult to delimit because there is no clear-cut morphological distinction between the opposite-decussate pairs of inflorescence bracts and the helically arranged tepals. Typically there are three (rarely two) carpels united in a syncarpous ovary.

Trochodendrales. Buxaceae and *Didymeles* form a well-supported sister group to Trochodendrales and the core eudicots (bootstrap = 88%, 17 substitutions; Fig. 5). However, the relationship of Trochodendrales as sister group to the core eudicots is not supported (bootstrap < 50%, 9 substitutions), and it seems best to consider the phylogenetic placement of Trochodendrales as yet unresolved within the lower hamamelid grade. However, a sister-group relationship between *Trochodendron* and *Tetracentron* is solidly supported in the combined three-gene analysis (bootstrap = 100%, 34 substitutions; Fig. 5).

Although superficially different, the flowers of *Trochodendron* and *Tetracentron* share several distinctive attributes. Both genera have bisexual flowers with semi-inferior ovaries. The flowers of *Tetracentron* are clearly constructed on a dimerous plan with four tepals and four stamens arranged in opposite-decussate pairs. The gynoecium consists of four carpels, basally embedded in the floral receptacle and placed diagonally with respect to the tepal and stamen pairs. The flowers of *Trochodendron* are different from those of *Tetracentron*, but there is some indication that they are derived from an originally dimerous plan. Early in floral development, the floral meristem is bilaterally symmetrical. The perianth is absent in adult flowers, but two small, irregularly placed scales between the prophylls and the androecium have been interpreted as possible remains of a reduced perianth (Endress, 1986). The androecium is composed of numerous, irregularly arranged stamens. The gynoecium consists of several to many (4 to 17) collaterally arranged carpels which are embedded proximally in the floral receptacle. The pattern of carpellary fusion, the mode of fruit dehiscence, and especially, the presence of a nectarial surface on the abaxial surface of the carpels and the absence of vessels in the wood (Endress, 1986), are some of the features shared by these two genera.

"CORE" EUDICOTS

The strong support for the "core" eudicot clade (including *Myrothamnus* and *Gunnera*; bootstrap = 100%, 37 substitutions) is one of the most significant results from our combined analysis of *atp*B, *rbc*L, and 18S sequence data (Figs. 5, 6). A similar clade was found in other phylogenetic analyses based on one gene and/or with less thorough sampling of the basal eudicot taxa (e.g., Olmstead et al., 1992; Chase et al., 1993; Drinnan et al., 1994; Williams et al., 1994; Soltis et al., 1997). Except for the inclusion of *Myrothamnus* (not sampled in previous studies) and *Gunnera*, our "core" eudicot clade is comparable to the "higher eudicots" recognized by Chase et al. (1993).

The strict consensus tree obtained from the combined analysis of the three-gene data sets (Fig. 6) recognizes a major polytomy of the following relatively well-supported clades within the core eudicots: (1) an asterid clade consisting of placeholders *Hydrangea, Berzelia,* and *Hedera*; (2) a clade equivalent to "rosid I and II" in search II of Chase et al. (1993), consisting of the four relatively derived placeholders *Francoa, Geranium, Coriaria,* and *Eucryphia*; (3) a caryophyllid clade plus Dilleniaceae (*Rheum, Nepenthes, Simmondsia, Spinacia, Limeum, Phytolacca, Hibbertia, Dillenia,* and *Schumacheria*); and (4) a hamamelid/Saxifragales clade (*Cercidiphyllum, Daphniphyllum, Altingia, Liquidambar, Paeonia, Haloragis, Itea, Heuchera, Exbucklandia, Disanthus, Hamamelis,* and *Corylopsis*) comparable to the rosid III clade of Chase et al. (1993) and the "saxifragoids" of Soltis et al. (1997). The poorly supported and unstable phylogenetic patterns among the major clades of the core eudicots (Figs. 5, 6), together with the conflicting patterns of relationships obtained in independent analyses (e.g., Chase et al., 1993; Morgan & Soltis, 1993; Williams et al., 1994; Soltis & Soltis, 1997), suggest that relationships among these major clades are currently best expressed as a polytomy.

Floral morphology among the core eudicots is extremely diverse. However, the core eudicot floral groundplan apparently consists of a whorled phyllotaxy with a fixed number of organs in each whorl (usually five in calyx and corolla, five or ten in the androecium, and two in the gynoecium) and alternation in the radial placement of organs of adjacent floral whorls. The perianth consists of a single whorl of sepals and a single whorl of petals that are morphologically differentiated from each other.

Myrothamnus/Gunnera. The sister-group relationship of *Myrothamnus* and *Gunnera* is not well supported (bootstrap = 62%, 17 substitutions; Fig. 5) and these two genera are best thought of as forming an unresolved polytomy with clades that include the remaining core eudicots. These two genera differ greatly in vegetative and reproductive morphology. *Myrothamnus* is a shrub with small, xeromorphic, fan-like leaves. The plants are dioecious, and the flowers have a perianth generally formed by four bract-like tepals. The androecium consists of four stamens, apparently arranged in a single whorl. The pistillate flowers have three or four carpels that are basally fused and distally free, and are reported to alternate with the tepals (Endress, 1989b; Kubitzki, 1993).

Gunnera consists of herbaceous plants that produce tiny (e.g., *G. magellanica* Lam.) to gigantic leaves (e.g., *G. chilensis* Lam.). The flowers are usually unisexual, apparently dimerous, and epigynous. The perianth is formed by two or three small sepals and two petals that are larger than the sepals. The androecium consists of one or two stamens, and the gynoecium of two fused carpels. The placement of organs with respect to those of neighboring whorls is not well understood.

Caryophyllids/Dilleniaceae. The phylogenetic placement of Dilleniaceae within the core eudicots has been problematic (e.g., Chase et al., 1993; Morgan & Soltis, 1993; Rice et al., 1997). In this study, a sister-group relationship between Dilleniaceae and the caryophyllid clade is supported (bootstrap = 74%, 22 substitutions; Figs. 5, 6). The caryophyllids and Dilleniaceae are each supported as monophyletic with high bootstrap values (100%; Fig. 5). The genus *Simmondsia,* frequently classified close to Buxaceae, although generally regarded as constituting a monotypic and somewhat isolated family (e.g., Cronquist, 1981; Takhtajan, 1997), appears within the caryophyllid clade in a weakly supported sister-group relationship with Caryophyllales (bootstrap = 68%, 21 substitutions; Fig. 5). A close relationship between *Simmondsia* and the Centrospermae (i.e., Caryophyllales) was proposed by van Tieghem (1897) and is supported by palynological, chemical, and microstructural characters (Jarvis, 1989).

Hamamelids/Saxifragales. In our analysis of the combined three-gene data sets, the "hamamelid/Saxifragales" clade is recognized as a monophyletic group with moderate support (bootstrap = 85%, 16 substitutions; Fig. 5). The occurrence of the hamamelid/Saxifragales clade as an independent lineage within the core eudicots has been reported in analyses that include a broad sample of eudicots (e.g., Rice et al., 1997). Alternatively, the hamamelids/Saxifragales have been resolved as sister to a largely rosid clade (e.g., Chase et al., 1993; Soltis et al., 1997). Most clades within the hamamelid/Saxifragales clade are poorly supported (bootstrap < 70%; Fig. 5). The only clades with reliable support are: *Disanthus/Hamamelis/Corylopsis* (Hamamelidaceae), *Altingia/Liquidambar* (Altingiaceae), and *Paeonia/Haloragis.*

CONCLUSIONS

The analyses presented here were designed to explore the pattern of phylogenetic relationships at the base of the eudicot clade. Data from *rbc*L, *atp*B, and 18S genomic sequences were analyzed independently and in combination to provide an assessment of phylogenetic patterns among an extensive representation of previously identified basal eudicot taxa, as well as selected representatives of more derived clades. Because phylogenetic patterns among major angiosperm lineages and the sister-group relationships for the eudicot clade are not yet resolved, the outgroup comprised a taxonomically broad selection of magnoliid lineages, including herbaceous and woody representatives. Analyses in which different magnoliid taxa were used as outgroups documented the stability of ingroup phylogenetic patterns.

Analyses of *rbc*L, *atp*B, combined *rbc*L/*atp*B, and combined *rbc*L/*atp*B/18S sequence data support the previously detected basic structure of the eudicot clade, with the ranunculid clade (Papaverales and Ranunculales) forming the sister group to all other eudicots ("lower" hamamelids plus core eudicots). Within the "lower" hamamelid/core eudicot clade several independent lineages, mostly of "lower" Hamamelididae, constitute a grade leading to a major clade, the core eudicots. The core eudicots include taxa of Caryophyllidae, Dilleniidae, Rosidae, and Asteridae, as well as some additional genera of "lower" Hamamelididae. The use of placeholders to represent the ranunculid clade did not have any major effect on the pattern of relationships among the remaining basal eudicots.

Among previously suggested phylogenetic patterns that were confirmed by this study are: the placement of *Euptelea* within the ranunculid clade; the close relationship of Berberidaceae to Ranunculaceae rather than Papaverales; the inclusion of *Nelumbo* within the eudicot clade and its placement among the lineages of the "lower" hamamelid grade; and the detection of major caryophyllid, asterid, and rosid clades within the core eudicot clade. A result that emerged in other phylogenetic analyses, but which is not universally supported, is the presence of a hamamelid-rosid clade (hamamelids/Saxifragales, Fig. 6) separate from more derived rosids, forming an independent branch within the core eudicot clade. The sister-group relationship of *Didymeles* with Buxaceae and the close relationship of *Simmondsia* with Caryophyllales, both of which had been suggested previously based on traditional analysis of morphological evidence, are strongly supported by our molecular results.

Although this study provides considerable information about phylogenetic patterns at the base of the eudicot clade, issues that still require resolution include: the placement of Sabiaceae among the basal eudicot lineages; whether the hamamelid/Saxifragales clade is part of the main rosid clade or constitutes an independent lineage within the core eudicots; and the monophyletic status of the Hamamelidaceae (sensu Endress, 1989a).

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PHYLOGENETIC ANALYSIS OF BIGNONIACEAE BASED ON THE cpDNA GENE SEQUENCES *rbc*L AND *ndh*F[1]

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ABSTRACT

A phylogenetic analysis of the Bignoniaceae and related families was conducted using the DNA sequences of the chloroplast genes *rbc*L and *ndh*F. Trees were constructed using each gene separately and in a combined data set. The analysis suggested that the family is more derived within the order Lamiales sensu lato than once believed. *Paulownia* and *Schlegelia* previously have been placed in Bignoniaceae or Scrophulariaceae. However, the sequence data presented here do not support their placement in Bignoniaceae. Excluding *Paulownia* and *Schlegelia*, Bignoniaceae were found to be monophyletic. Tribes Bignonieae, Crescentieae, and Coleeae each forms a monophyletic group based on this analysis. Tribe Tecomeae is paraphyletic.

Bignoniaceae are called "one of the most important families of woody plants and the most important family of lianas in the Central American forest ecosystems" (Gentry, 1974: 728). Gentry spent much of his career working on this family, and his contributions to Bignoniaceae systematics were extensive. Bignoniaceae are a family of 7 or 8 tribes, 112 genera, and 800 species, composed primarily of lianas, trees, and some shrubs. The family is essentially pantropical, although a few species reach the temperate zone, with 78% (620) of the species occurring in the Neotropics and a center of diversity in Brazil (Gentry, 1980). The origin of the family is not clear; however, Goldblatt and Gentry (1979) speculated that some Old World species may be among the most primitive members of the family. Bignoniaceae are united phylogenetically by such characters as the presence of two distinct placental ridges, each bearing one to several rows of ovules, and lack of endosperm in the mature seeds (Armstrong, 1985). Additionally, a cup-shaped calyx, tubular corolla morphology, woody habit, a chromosome number of $n = 20$, bilamellate stigma with an elongate style, and seeds with a hyaline wing surrounding the embryo are also characteristic taxonomically (Gentry, 1980). However, many members of the Scrophulariaceae share some of these character states, leading to confusion in the placement of morphologically intermediate taxa.

A traditional placement for Bignoniaceae is in the order Scrophulariales (sensu Cronquist, 1981) in subclass Asteridae (Cronquist, 1981; Takhtajan, 1980), considered an evolutionarily derived subclass within the dicots. Molecular studies (Olmstead et al., 1992; Olmstead et al., 1993a) have suggested that the Lamiales (sensu Takhtajan, 1980; primarily Lamiaceae and Verbenaceae) and the Scrophulariales together form a monophyletic group (along with Cronquist's small orders Plantaginales and Callitrichales), but that neither is monophyletic. This expanded group, which we refer to as Lamiales sensu lato, is recognized by Thorne (1992), who nevertheless retained the two traditional groups at the level of suborder within the order. In at least one study based on *rbc*L (Olmstead et al., 1993a), Bignoniaceae appeared basal in the Lamiales s.l., a placement consistent with traditional expectations (e.g., Goldblatt & Gentry, 1979). However, subsequent molecular studies including more taxa in the Lamiales s.l. and/or additional sequence data (Olmstead & Reeves, 1995; Wagstaff & Olmstead, 1997) found Bignoniaceae nested within the order. Ambiguity arises because characters traditionally used to infer ancestral lineages

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in the Lamiales s.l. (e.g., woodiness and many ovules per carpel) co-occur with characters that have been considered characteristics of more recent lineages (e.g., lack of endosperm, climbing habit, winged seeds, and compound leaves).

Early treatments of Bignoniaceae relied on fruit morphology to divide the family into tribes. De Candolle (1838) recognized two tribes: Bignonieae, with dehiscent fruits, and Crescentieae, with indehiscent fruits. Bentham and Hooker (1876) followed his lead but divided de Candolle's tribe Bignonieae into three separate tribes based on locule number and orientation of the septum relative to the capsule valves: Bignonieae, with two locules and the septum parallel to the valves; Tecomeae, with two locules and septum perpendicular to the valves; and Jacarandeae, with one locule and partially or completely missing the septum. Bignonieae and Tecomeae were subtribes in de Candolle's (1838) system, while Jacarandeae was considered an unnatural group. Schumann (1894) distributed the genera of Bentham and Hooker's Jacarandeae among the three large tribes Bignonieae, Crescentieae, and Tecomeae, and recognized two monogeneric tribes, Eccremocarpeae (first described by Endlicher in 1839) and Tourrettieae (first described by Don in 1838). Bojer (1837) created the tribe Coleeae for a small group of Madagascan genera with fleshy, indehiscent fruits. In all subsequent major treatments, these genera usually were included in Crescentieae, until tribe Coleeae was resurrected by Gentry (1976). Tribe Oroxyleae was defined (Gentry, 1980) to include four Old World genera formerly put in Bignonieae that have reduced chromosome numbers ($n = 14, 15$): *Oroxylum, Millingtonia, Nyctocalos,* and *Hieris* (Gentry, 1980). Chromosome numbers of $n = 20$ are typical in the family and are found almost universally among tribes Bignonieae, Coleeae, Crescentieae, Schlegelieae, and Tourrettieae (Goldblatt & Gentry, 1979). Tribe Schlegelieae was erected to include *Schlegelia, Gibsoniothamnus, Synapsis,* and recently, *Exarata* (Gentry, 1980, 1992a). Reveal (1995) later segregated tribe Schlegelieae into its own family, Schlegeliaceae, based on the molecular evidence of Olmstead and Reeves (1995). A summary of classifications, key characteristics, and geographic distribution of tribes in Bignoniaceae is presented in Table 1. For a comprehensive discussion of the taxonomic and nomenclatural history of Bignoniaceae, see Gentry (1980).

Gentry (1980) maintained that it is very difficult to understand the phylogeny within Bignoniaceae because of "rampant parallelisms and convergence in nearly every taxonomically important characteristic." He speculated that tribes Tecomeae and Oroxyleae were "closest to the ancestral stock of Bignoniaceae," although he acknowledged that tribe Schlegelieae may have diverged from the common ancestor that gave rise to both Bignoniaceae and Scrophulariaceae. Oroxyleae were suggested to be primitive on the basis of the presence of five stamens in some members and the putatively ancestral chromosome base number of $x = 14$. Tecomeae were suggested to be primitive on the basis of having a world-wide distribution and a few Old World genera with five anthers. Tecomeae were believed to have given rise to the other tribes with more restricted distributions such as Bignonieae, Coleeae, and Crescentieae (Gentry, 1980). This scenario depicts Tecomeae as a paraphyletic group, and implies that dehiscent fruits with the septum perpendicular to the valves gave rise to indehiscent fruits (Coleeae, Crescentieae) and to dehiscent fruits with the septum parallel to the valves (Bignonieae).

Paulownia and the tribe *Schlegelieae* have both been considered intermediate between Bignoniaceae and Scrophulariaceae, and their placement is still in doubt (Armstrong, 1985; Gentry, 1980). *Schlegelia* and *Paulownia* both have a haploid complement of $n = 20$, suggesting a relationship with the Bignoniaceae (Gentry, 1980; Goldblatt & Gentry, 1979; Westfall, 1949). Presence of endosperm, gynoecial anatomy, embryo and placental morphology, and winged seeds morphologically different from those of Bignoniaceae suggests a relationship with the Scrophulariaceae (Armstrong, 1985). Molecular systematic studies in the Scrophulariaceae (Olmstead & Reeves, 1995) indicated that these taxa may not belong to either family, but to two of many small, independent lineages in the Lamiales s.l. (Wagstaff & Olmstead, 1997).

In the present study, we used sequences from the chloroplast genes *rbc*L and *ndh*F to construct a phylogenetic hypothesis for Bignoniaceae. Recent publications have used these two chloroplast genes for phylogenetic studies within the Asteridae (Olmstead & Sweere, 1994), and even within the Lamiales s.l. (Olmstead & Reeves, 1995; Scotland et al., 1995). The phylogenetic hypothesis based on these gene sequences is here used to determine whether Bignoniaceae are a monophyletic family, especially regarding the phylogenetic relatedness of *Schlegelia* and *Paulownia* to the "core" Bignoniaceae. The position of the family within the Lamiales s.l. is examined. We also discuss the relationships among primary lineages within the Bignoniaceae. The phylogenetic hypotheses complement recent monographic work (D'Arcy, 1997; Gentry, 1980,

Table 1. Tribes recognized in major classifications of Bignoniaceae and features of taxa placed into each tribe. Geographic distribution is listed for tribes recognized by the most recent classification of Gentry (1980).

de Candolle (1838)	Bentham and Hooker (1876)	Schumann (1894)	Gentry (1980)	Geographic distribution of taxa
Crescentieae	Crescentieae	Crescentieae	Crescentieae	Central America and the West Indies
Indehiscent fruit	Indehiscent fruit	Indehiscent fruit and seeds without wings	Trees with indehiscent fruits; seed wings can be vestigial, New World distribution	
Bignonieae	Bignonieae	Bignonieae	Bignonieae	New World tropics
Dehiscent fruit	Two locules in the fruit; septum parallel to the valves	Two locules in the fruit; septum parallel to the valves	Mostly lianas with two locules in the fruit; septum parallel to the valves	
	Tecomeae	Tecomeae	Tecomeae	Pantropical
	Two locules in the fruit; septum perpendicular to the valves	Two locules in the fruit; septum perpendicular to the valves	Trees with two-loculate fruit and the septum perpendicular to valves	
	Jacarandeae	Eccremocarpeae	Eccremocarpeae	Andes
	Unilocular fruit with a partial or missing septum	Unilocular fruit opening downward; spiny and apically fused capsule	Unilocular fruit opening downward; spiny and apically fused capsule	
		Tourrettieae	Tourrettieae	Andes
		Four-locular fruit	Four-locular fruit	
			Coleeae	Madagascar and tropical Africa
			Indehiscent fruits with an Old World distribution	
			Schlegelieae	Central and South America and Cuba
			Lianas with indehiscent fruits and seed wings developed, but see *Exarata* (Gentry, 1992a)	
			Oroxyleae	Southeast Asian tropics
			Chromosome numbers of $n = 14$ or 15, not $n = 20$ as in most of the rest of the family	

1992b; Hauk, 1997), as well as continuing systematic studies on the family (M. Zjhra, pers. comm.; G. Dos Santos, pers. comm.). The monographic studies deal primarily with taxa from the New World, whereas this study provides a framework phylogeny for the entire family, including both Old and New World taxa.

MATERIALS AND METHODS

This study included sequences from 19 species of Bignoniaceae plus *Paulownia* and *Schlegelia*, an additional 14 members of the Lamiales s.l., and 4 outgroup taxa from related orders (Table 2). Seven tribes of Bignoniaceae are represented (following Gentry, 1980), in addition to *Paulownia* (sometimes included in the tribe Tecomeae) and *Schlegelia* (Schlegeliaceae, or formerly in Bignoniaceae tribe Schlegelieae). Only the monotypic tribe Tourrettieae was not included in this study because DNA was not readily available at the time of this study.

Total genomic DNA was extracted from leaf material using the CTAB procedure (Doyle & Doyle, 1987), followed by cesium-chloride ultracentrifugation. The chloroplast genes *rbc*L and *ndh*F were amplified following a two-stage PCR process to generate single-stranded DNA (Kaltenboeck et al., 1992). Sequencing was done using ^{32}P-labeled dideoxy nucleotides, and sequences were visualized using autoradiography. Amplification and internal primer sequences for each gene and details of sequencing methods were as in Olmstead et al. (1992, 1993a, b), Olmstead and Sweere (1994), and Olmstead and Reeves (1995). Both DNA strands were sequenced and compared for all taxa to ensure accuracy, and sequences generated for the present study were submitted to GenBank. Both *rbc*L and *ndh*F sequences for each taxon were obtained from the same accession except for *Nicotiana*, *Barleria*, *Digitalis*, and *Verbena*. Sequences were aligned manually, and "gaps" introduced into sequences due to taxon specific insertion/deletion events were not treated as separate characters. Missing data were coded as a question mark in the data matrix.

The sequences were analyzed using a test version of PAUP* version 4.0d56 (kindly provided by D. Swofford) on a Sun Ultra 1 computer. The *rbc*L and *ndh*F data sets each were analyzed separately and in a combined data set. For each data set (*rbc*L, *ndh*F, and combined) a heuristic search of 100 replications with random order taxon entry, TBR branch swapping, and MULPARS was used to find the shortest trees. Bootstrap analyses (Felsenstein, 1985) were conducted as a quantitative evaluation of the relative strength of monophyletic groupings in each tree. The *ndh*F and combined data sets had 100 bootstrap replicates with TBR swapping and MULPARS in effect, and the *rbc*L data set underwent 1000 bootstrap replicates with MULPARS off. A decay analysis (Donoghue et al., 1992) was performed on the combined data using the computer program AutoDecay version 2.9.9 (Eriksson, 1997). The data in the combined analysis were partitioned into their respective *rbc*L and *ndh*F components, and an Incongruence Length Difference Test (partition-homogeneity test) (Farris et al., 1995) was conducted to determine if the partitions differed significantly from random partitions of the combined data. A maximum-likelihood analysis using the discrete gamma-approximation model was conducted on the combined data set for comparison with the parsimony analysis. The trees resulting from these two analyses were compared using the Kishino-Hasegawa test (Kishino & Hasegawa, 1985) under the Hasegawa-Kishino-Yano (Hasegawa et al., 1985) likelihood model using a discrete gamma approximation.

RESULTS

Sequence data from the two chloroplast genes included a total of 3545 bp of aligned sequence, with 709 phylogenetically informative sites. The *rbc*L sequences were 1411 bp in length (40% of the total sequence in the combined data set), and had 194 phylogenetically important characters (14% of the total *rbc*L sequence length and 27% of the total number of informative characters in the combined data). Aligned *ndh*F sequences were 2134 bp in length (60% of the total in the combined data set) with 515 phylogenetically informative characters (24% of the total *ndh*F sequence length and 73% of the total number of informative characters in the combined data). One 6 bp insertion was found in all taxa except *Nyctanthes* and the outgroups, and a single shared deletion occurred in *Petunia* and *Nicotiana*. Each of these indels denotes groups with 100% bootstrap support based on nucleotide substitutions. Another insertion was shared between two distantly related taxa, *Radermachera* (Bignoniaceae) and *Nematanthus* (Gesneriaceae), but there is overwhelming evidence from the remainder of the sequence data against their grouping.

The analysis of the *rbc*L sequences generated 63 equally parsimonious trees of 826 steps. These trees occurred in islands of 15 and 48 trees (called tree island-15 and tree island-48, respectively). One of the most parsimonious trees is depicted with branch lengths in Figure 1, along with the strict consensus of all 63 trees. Bignoniaceae formed one of several clades emerging from a basal polytomy in the Lamiales s.l. The family formed a monophyletic group in the *rbc*L tree, but with low bootstrap support. *Schlegelia* and *Paulownia* emerged as independent lineages from this polytomy and did not occur in a clade with the Bignoniaceae in any of the 63 trees. Tribe Tecomeae (taxa denoted with a "T" in Fig. 1) was not monophyletic within the family, while the other tribes were monophyletic (Bignonieae, Coleeae, and Crescentieae) or were represented by only one taxon in this analysis (Oroxyleae and Eccremocarpeae).

The *ndh*F analysis yielded four trees of 2420 steps (Fig. 2). Bignoniaceae were not found to be monophyletic, but a subset of Bignoniaceae, excluding *Jacaranda* and *Podranea,* formed a single clade with 82% bootstrap support. Resolution and support for internal nodes below the ordinal level was greater for the *ndh*F tree than for the *rbc*L tree. *Jacaranda* and *Podranea,* both usually included in the family (tribe Tecomeae), formed a weakly supported group with *Schlegelia* separate from the rest of the Bignoniaceae. A search constraining *Jacaranda* and *Podranea* to monophyly with the rest of Bignoniaceae resulted in trees only two steps longer (length = 2422). Constraining *Schlegelia* and these two taxa to a monophyletic Bignoniaceae required one additional step (length = 2423). *Paulownia* formed a well-supported clade with the Lamiaceae that was sister to a weakly supported clade composed of the majority of Bignoniaceae + *Sesamum* (Pedaliaceae).

The parsimony analysis of the combined *rbc*L and *ndh*F sequences produced three most-parsimonious trees of 3285 steps (Fig. 3). The partition-homogeneity test resulted in a value of $P = 0.01$, so the null hypothesis that the partitions represent two random partitions of the same homogeneous data pool was statistically rejected by this test. The combined analysis identified a monophyletic Bignoniaceae, excluding *Paulownia* and *Schlegelia.* Maximum likelihood analysis produced a tree (not shown) almost identical to the combined tree, except in the ML tree *Catalpa* and *Oroxylum* did not form a clade, *Cydista* and *Martinella* switched places within tribe Bignonieae, *Jacaranda* was the sister group to the rest of Bignoniaceae, *Stachytarpheta* was sister to the clade containing *Antirrhinum, Digitalis, Barleria,* and *Sesamum* (rather than forming a clade with *Verbena*), and a clade comprised of *Schlegelia* and *Verbena* was sister to Bignoniaceae. The tribes within the Bignoniaceae were still monophyletic in the ML tree, with the exception of a paraphyletic Tecomeae, as also seen in the other analyses. The Kishino-Hasegawa test was not significant ($P = 0.60$), indicating statistical congruence between the ML and the parsimony trees despite minor topological differences. In the parsimony tree, constraining *Schlegelia* with Bignoniaceae added two steps, constraining *Paulownia* with Bignoniaceae added six steps, and constraining *Schlegelia* and *Paulownia* with Bignoniaceae added seven steps.

DISCUSSION

The increased internal resolution for the *ndh*F alone trees relative to the *rbc*L trees is consistent with previous studies (Olmstead & Reeves, 1995; Olmstead & Sweere, 1994; Wagstaff et al., 1998). Phylogenetic signal from *rbc*L becomes more apparent when data sets are combined. The combined data provide a more reliable hypothesis of relationships than either gene tree alone, taking the signal from both genes and producing a better resolved tree with increased statistical support, as also seen by Olmstead and Sweere (1994). For example, Bignoniaceae were found to be monophyletic with *rbc*L, but with only ca. three nucleotide substitutions and 14% bootstrap support, and were not found to be monophyletic with *ndh*F. However, with the combined data, Bignoniaceae have 15 inferred substitutions and bootstrap support of 63%. In general, areas of low support in the combined data tree reflect lack of support in both of the individual gene trees. This is not the case, though, for the *Pandorea* + *Podranea* and the *Tecoma* + *Pandorea* + *Podranea* clades; in the *rbc*L tree they have 85% and 80% bootstrap support, respectively, and they do not occur in the combined tree at all.

The result that the partitions of the data (in this case, each gene sequence) are not random partitions of a homogeneous data pool may reflect dependence of unknown cause for some characters within one or both gene sequences. Congruence tests are sensitive to localized regions of heterogeneity and can produce significant results even when a small portion of a single partition is giving misleading results. Fine partitioning of data sets may help to identify problem areas that would lead to rejection of homogeneous data partitions, but reasons for the incongruence would still not be revealed. However, because the two genes sampled here were drawn from the same non-recombining genome, they are presumed to have the same underlying phylogeny, and the combined data set was assumed to give the best estimate of phylogeny for the group. Other data sets using the same two regions of the genome have yielded similar results for

Table 2. Taxon voucher information and GenBank numbers for sequences used in the analyses. References are listed for voucher information of previously published sequences. Taxa are arranged according to the classification of Thorne (1992).

Taxon	Voucher specimen, deposit location, and references	GenBank number for *rbc*L sequences	GenBank number for *ndh*F sequences
GENTIANALES			
Gentianaceae			
Gentiana procera Holm.	none cited (Olmstead et al., 1993a; Olmstead & Reeves, 1995)	L14398	L36400
BORAGINALES			
Boraginaceae			
Borago officinalis L.	none cited (Olmstead et al., 1992; Olmstead & Reeves, 1995)	L11680	L36393
SOLANALES			
Solanaceae			
Nicotiana tabacum L.	(Lin et al., 1986; Olmstead et al., 1993b)	M16896	L14953
Petunia parviflora Juss.	*A. C. Sanders 5835* (COLO) (Olmstead et al. 1998, in press)	In press	In press
LAMIALES s.l.			
Acanthaceae			
Barleria prionitis L.	*Uppsala B.G. 1977-3036* (UPS) (Chase et al., 1993; Scotland et al., 1995)	L01886	U12653
Bignoniaceae			
Amphitecna apiculata A. H. Gentry	*R. Spangler B1* (MO)	AF102640	AF102624
Arrabidaea pubescens (L.) A. H. Gentry	*A. H. Gentry 10234* (MO)	AF102641	AF102625
Campsis radicans Seem.	DNA from R. Jansen, voucher unknown	AF102642	AF102626
Catalpa sp.	*C. W. dePamphilis s.n.* (COLO) (Olmstead et al., 1992; Olmstead & Reeves, 1995)	L11679	L36397
Crescentia portoricensis Britton	*Gentry & Zardini 50458* (MO)	AF102643	AF102627
Cybistax donnell-smithii (Rose) Seibert	*Collector unknown*, Waimea Bot. Gard. 89p166	AF102644	AF102628
Cydista aequinoctialis Miers	*R. Spangler B2* (MO)	AF102645	AF102629
Eccremocarpus scaber Ruiz & Pav.	*Chase 2999* (K)	AF102646	AF102630
Jacaranda sparrei A. H. Gentry	*H. Descimmon s.n.*, Waimea Bot. Gard. 82s772	AF102647	AF102631
Kigelia africana Benth.	*R. C. A. Rica s.n.*, Waimea Bot. Gard. 74s980	AF102648	AF102632
Macfadyena unguis-cati (L.) A. H. Gentry	*R. Spangler B3* (MO)	AF102649	AF102633
Martinella obovata Bureau & K. Schum.	*A. H. Gentry 50277* (MO) (Olmstead & Reeves, 1995)	L36444	L36402
Ophiocolea floribunda (Boj. ex Lindl.) H. Perrier	*G. Schatz 3448* (MO)	AF102650	AF102634
Oroxylum indicum (L.) Kurz	*A. H. M. Jayasuriya s.n.*, Waimea Bot. Gard. 79s51	AF102651	AF102635
Pandorea jasminoides Schum.	*Collector unknown*, Matthaei Bot. Gard. Ann Arbor, Michigan	AF102652	AF102636

Table 2. Continued.

Taxon	Voucher specimen, deposit location, and references	GenBank number for *rbc*L sequences	GenBank number for *ndh*F sequences
Podranea ricasoliana Sprague	*Collector unknown*, Waimea Bot. Gard. 84p524	AF102653	AF102637
Radermachera frondosa Chun & How	*Gentry & Ortiz 78009* (MO)	AF102654	AF102638
Tabebuia heterophylla (A. deCandolle) Britton	none cited (Olmstead & Reeves, 1995)	L36451	L36416
Tecoma stans Juss.	DNA from R. Jansen, voucher unknown	AF102655	AF102639
Buddlejaceae			
Buddleja davidii Franch.	*R. G. Olmstead 88-007* (WTU) (Olmstead et al., 1993a; Olmstead & Reeves, 1995)	L14392	L36394
Gesneriaceae			
Nematanthus hirsutus (Mart) Wiehler	*Collector unknown* (SEL) (Olmstead & Reeves, 1995)	L36446	L36404
Lamiaceae			
Callicarpa dichotoma (Lour.) K. Koch	*R. G. Olmstead 88-012* (WTU) (Olmstead et al., 1993a; Olmstead & Reeves, 1995)	L14393	L36395
Lamium purpureum L.	*S. J. Wagstaff 88-031* (BHO) (Wagstaff & Olmstead, 1997; Wagstaff et al., 1988)	U75702	U78694
Myoporaceae			
Myoporum mauritianum A. de Candolle	*R. G. Olmstead 92-299* (WTU) (Olmstead & Reeves, 1995)	L36445	L36403
Oleaceae			
Nyctanthes arbor-tristis L.	*RBG, Kew 099.86.00993* (K) (Wagstaff & Olmstead, 1997)	U28877	U78708
Pedaliaceae			
Sesamum indicum L.	none cited (Olmstead et al., 1993a; Olmstead & Reeves, 1995)	L14408	L36413
Scrophulariaceae			
Antirrhinum majus L.	*C. W. dePamphilis s.n.* (Olmstead et al., 1992; Olmstead & Reeves, 1995)	L11688	L36413
Digitalis grandiflora Lam.	none cited (Olmstead & Reeves, 1995)		L36399
Digitalis purpurea L.	none cited (Olmstead et al., 1993a)	L01902	
Paulownia tomentosa (Thunb.) Steudel	*R. G. Olmstead 88-008* (WTU) (Olmstead & Reeves, 1995)	L36447	L36406
Schlegelia parviflora (Oerst.) Monachino	*Gentry & Puig-Ross 14221* (MO) (Olmstead & Reeves, 1995)	L36448	L36410
Scrophularia sp.	*C. W. dePamphilis s.n.* (Olmstead & Reeves, 1995)	L36449	L36411
Verbascum thapsus L.	none cited (Olmstead & Reeves, 1995)	L36452	L36417
Verbenaceae			
Stachytarpheta dichotoma (Ruiz et. Pav.) Vahl.	*R. G. Olmstead 951* (WTU) (Olmstead & Reeves, 1995)	U32161	L36414
Verbena bonariensis L.	none cited (Olmstead et al., 1993a)	L14412	
Verbena bracteata Lagasca & Rodriguez	*R. G. Olmstead 92-131* (WTU) (Olmstead & Reeves, 1995)		L36418

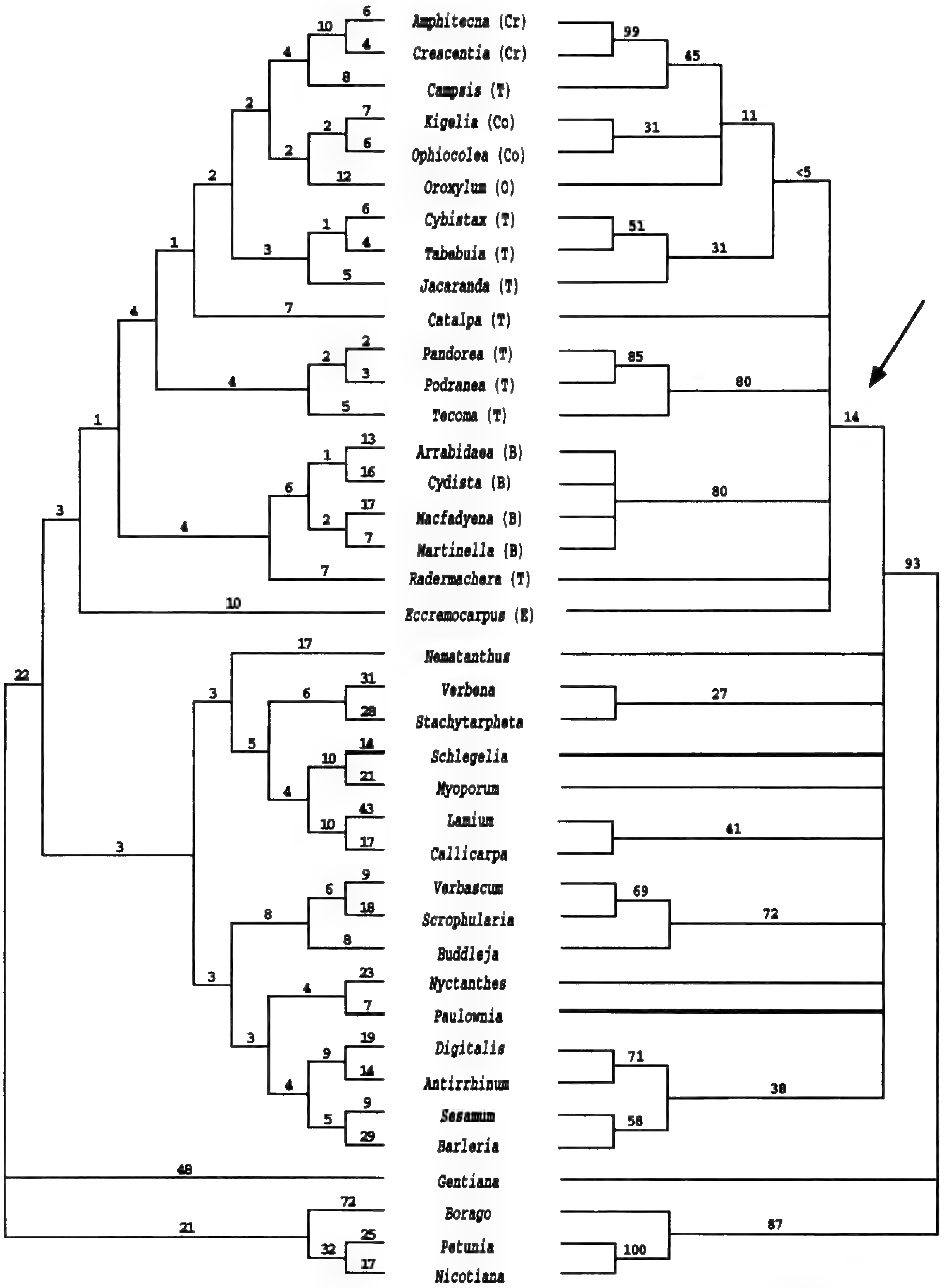

Figure 1. On the left is one of the most parsimonious trees from *rbc*L tree island-48 (length = 826, CI = 0.58, RI = 0.48). Branch lengths are indicated. On the right is the strict consensus of all 63 trees found with bootstrap values indicated. The arrow indicates the internode defining the Bignoniaceae. A letter next to a taxon name designates the tribe that taxon is a member of (B = Bignonieae, Co = Coleeae, Cr = Crescentieae, E = Eccremocarpeae, O = Oroxyleae, T = Tecomeae). Bold branches indicate *Schlegelia* and *Paulownia*.

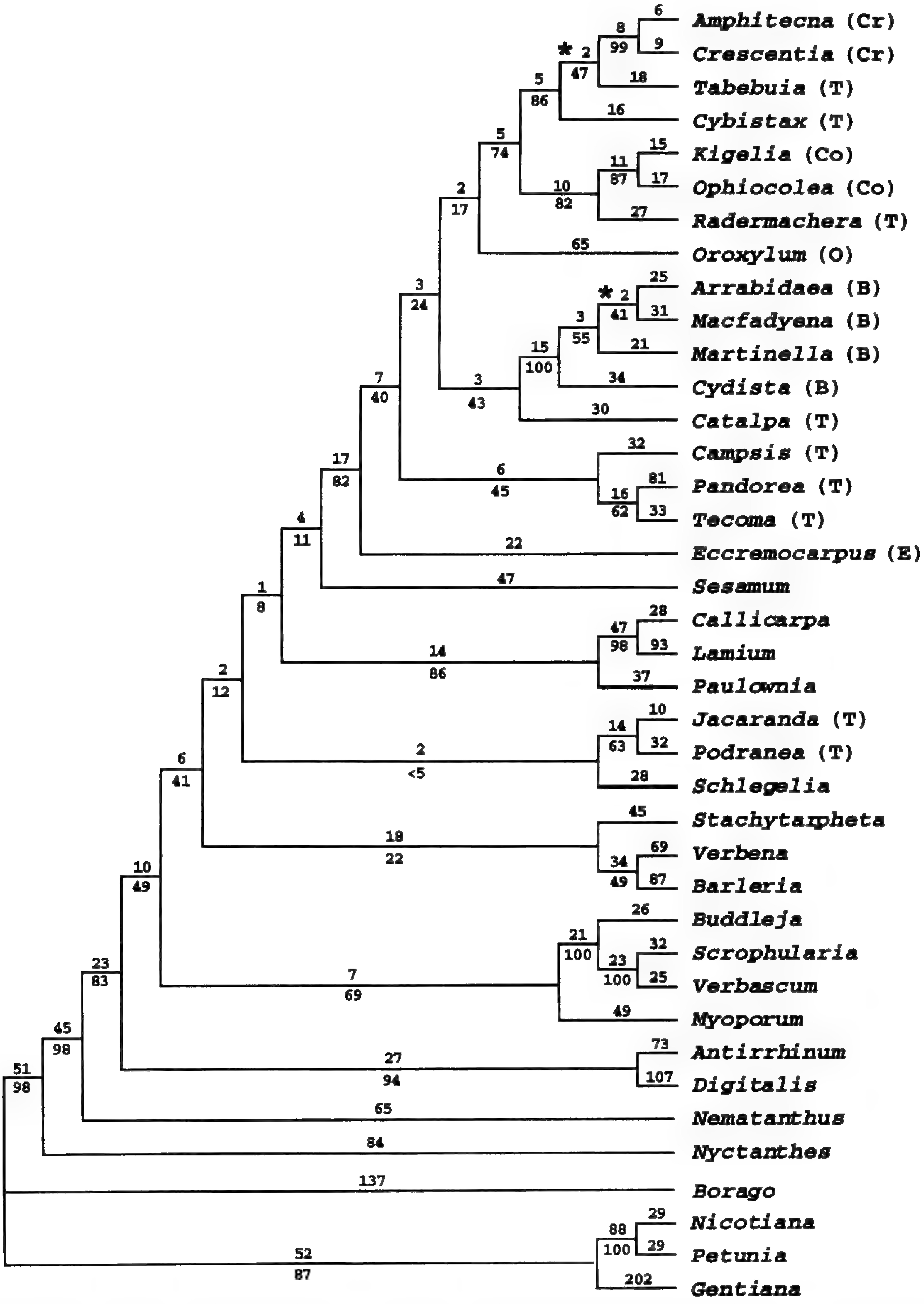

Figure 2. One of four most parsimonious trees based on the *ndh*F sequences. Branch lengths are indicated above branches, bootstrap numbers are indicated below. Asterisks indicate internodes that collapse in the strict consensus of all four trees (length = 2432, CI = 0.56, RI = 0.48). A letter next to a taxon name designates the tribe that taxon is a member of (B = Bignonieae, Co = Coleeae, Cr = Crescentieae, E = Eccremocarpeae, O = Oroxyleae, T = Tecomeae). Bold branches indicate *Schlegelia* and *Paulownia*.

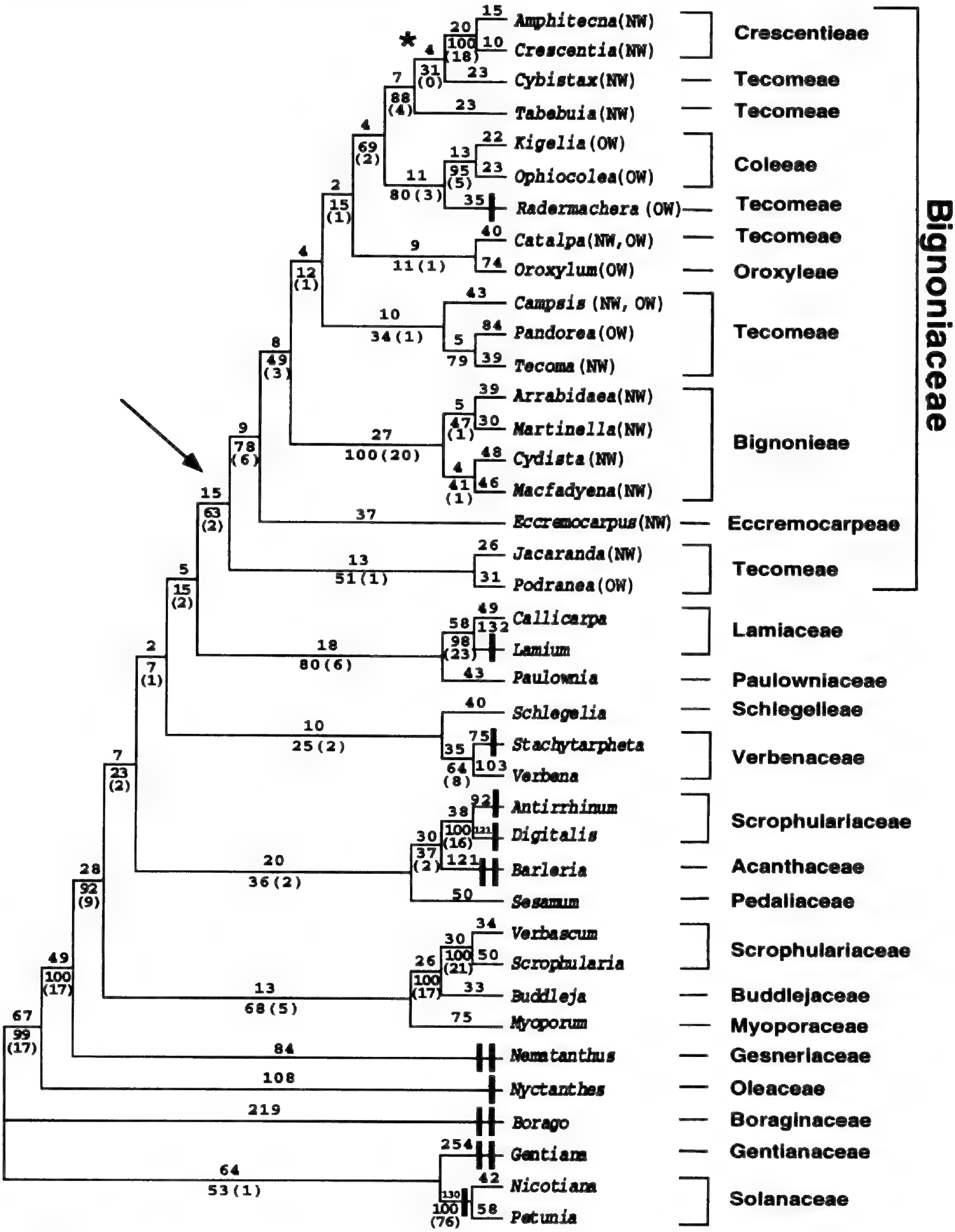

Figure 3. One of three most parsimonious trees based on the combined *rbc*L and *ndh*F data (length = 3285, CI = 0.56, RI = 0.47). Branch lengths are indicated above branches. Bootstrap numbers are below internodes with decay values in parentheses. The arrow denotes the clade comprising the Bignoniaceae. "NW" indicates a New World member of the Bignoniaceae, "OW" designates the taxon occurs in the Old World. The asterisk denotes the only internode that collapses in the strict consensus of the three trees, and vertical bars indicate inferred insertions or deletions.

this test of congruence. Data from Solanaceae (Olmstead & Sweere, 1994) gave a value of $P = 0.04$, and data from Scrophulariaceae (Olmstead & Reeves, 1995) had $P = 0.01$, significant in both cases. Lamiaceae (Wagstaff et al., 1998), on the other hand, gave $P = 0.39$ for the partition-homogeneity test, a non-significant result. Beyond the inherent problems congruence tests have, it remains unclear why these independent data sets, each representing groups of relatively closely related species, gave results indicating significant heterogeneity between data sets for these genes.

Bignoniaceae monophyly based on the combined cpDNA data agrees with the hypothesis Gentry (1980) proposed based on morphological characters, except for *Schlegelia.* Gentry considered *Schlegelia* to be part of, but distant from, the rest of Bignoniaceae (see discussion below). Morphological characters shared between Bignoniaceae and Scrophulariaceae that have caused confusion in the placement of taxa such as *Paulownia* and *Schlegelia* can now be examined in the context of the molecular data. True morphological synapomorphies for Bignoniaceae may be characters such as lack of endosperm, compound leaves, and unique type of winged seeds. A clear sister group to Bignoniaceae based on the present results is not evident. The *rbc*L analysis leaves relationships unresolved among the Lamiales s.l., the *ndh*F analysis places Pedaliaceae as sister to Bignoniaceae, and the combined data analysis places *Paulownia* sister to Lamiaceae, all with low support. Indeed, there is no evidence that Scrophulariaceae, or any part of this family (Olmstead & Reeves, 1995), are sister to Bignoniaceae. Future studies using morphology, cytology, and anatomy (as formerly done by Armstrong, 1985; Guédès, 1974; Westfall, 1949) to decipher the connection between these groups can now make use of a more complete phylogenetic hypothesis to direct the scope of their comparisons.

The sequence data do not support Bignoniaceae as a basal lineage in the Lamiales s.l., as suggested by Goldblatt and Gentry (1979); rather, they are nested high in the order. Oleaceae (*Nyctanthes*) are sister to the rest of the order in the combined analysis. This result agrees with other previously published studies (Hedren et al., 1994; Olmstead et al., 1993a; Wagstaff & Olmstead, 1997). Woody habit has been used as a character indicating a basal placement of Bignoniaceae in the Lamiales s.l., but it cannot be polarized easily due to its widespread occurrence in the order and poor resolution among clades.

Clues to the placement of the problematic genera *Paulownia* and *Schlegelia* can be found in the results presented here (Figs. 1–3). However, limited sampling among outgroup families, particularly the polyphyletic Scrophulariaceae, limits the strength of any conclusions concerning their placement. Various molecular studies (Olmstead & Reeves, 1995; Wolfe et al., 1997; Nickrent et al., 1998; Wolfe & dePamphilis, 1998; Young et al., 1997) have all focused on particular groups of Lamiales s.l., and sampling has not been comprehensive in any one study with respect to all possible placements for these two taxa. Several studies in press have included *Paulownia* and/or *Schlegelia* in surveys of the chloroplast genes *rbc*L, *ndh*F, *mat*K, and *rps*2. A large study using three genes and many taxa from the Scrophulariaceae (Olmstead et al., unpublished) suggests that *Paulownia* belongs with the Orobanchaceae (broadly defined to include all parasitic Scrophulariaceae), but weakly so (no members of Orobanchaceae were included in the present study or in Olmstead & Reeves, 1995). The results of the unpublished study of Olmstead et al. grouped *Schlegelia* with Bignoniaceae, but with weak support, and only *Kigelia* and *Catalpa* were included as Bignoniaceae representatives. The results here and in other molecular studies (Olmstead & Reeves, 1995; Wolfe et al., 1997; Nickrent et al., 1998; Wolfe & dePamphilis, 1998; Young et al., 1997; Olmstead et al., unpublished) contradict Westfall's (1949) inference, based on cytology, that *Paulownia* belongs in Bignoniaceae, whereas some studies also contradict Armstrong's (1985) placement of *Paulownia* with the Scrophulariaceae (Olmstead & Reeves, 1995; Wolfe et al., 1997). Still other studies suggest a connection to the Orobanchaceae s.l. (Nickrent et al., 1998; Wolfe & dePamphilis, 1998; Young et al., 1997; Olmstead et al., unpublished data) or Lamiaceae (this study). *Schlegelia* has not been found to belong with any group of the Scrophulariaceae in any of the molecular studies in which it has been included. However, some studies suggest *Schlegelia* may be related to Bignoniaceae (Nickrent et al., 1998, *rps*2 sequences; Young et al., 1997; Olmstead et al., unpublished data), while others contradict that relationship (Olmstead & Reeves, 1995; Nickrent et al., 1998, *rbc*L sequences; Wolfe & dePamphilis, 1998). Perhaps the only safe conclusions are that *Paulownia* does not belong with Bignoniaceae and that *Schlegelia* does not belong with Scrophulariaceae.

Restricting Bignoniaceae to the moderately supported clade that excludes tribe Schlegelieae and *Paulownia* better reflects our current uncertainty about the true placement of these problematic taxa. If, one day, one of these groups is found to be sister to the core Bignoniaceae, a classification that considers them as separate groups still will be consistent with phylogeny. We can now identify the morphological characters that have led to confusion in placement of these taxa, and the actual synapomorphies for Bignoniaceae may be characters such as the lack of endosperm, compound leaves, and unique type of winged seeds. It may be best for us now to recognize Schlegelieae and *Paulownia* as distinct families, rather than fit them into existing families. Nakai (1949) recognized the family Paulowniaceae, separating *Paulownia* from the Bignoniaceae based on the presence of endosperm in the seeds. The family name Schlegeliaceae has been proposed (Reveal, 1995) to include the four genera comprising the tribe Schlegelieae. Reveal's proposals for the recognition of many of the lineages in the Lamiales s.l. are a step forward in bringing the taxonomy of the order into agreement with phylogeny. However, his recognition of the Crescentiaceae (after Dumortier, 1829) would render the Bignoniaceae paraphyletic (see below). Caution should be used in making family-level classifications at this time, when our knowledge of relationships within the Lamiales is still incomplete. Current work on a molecular phylogeny of the entire Lamiales s.l. (R. Olmstead, unpublished data) should provide a framework for a new family-level classification upon its completion.

Within Bignoniaceae, clades corresponding to the tribes Crescentieae, Bignonieae, and Coleeae are well supported. These clades are in agreement with circumscriptions suggested by previous authors (Gentry, 1980; Goldblatt & Gentry, 1979). Tecomeae, however, do not form a monophyletic group in any of the trees presented here, and the Crescentieae, Bignonieae, Coleeae, Oroxyleae, and Eccremocarpeae are each derived from within Tecomeae.

Gentry (1980) considered the indehiscent fruits of the Crescentieae to be derived from the dehiscent fruits of the neotropical Tecomeae. The derivation of Crescentieae from within the Tecomeae is strongly supported in all analyses done for the present study. *Tabebuia* groups strongly with tribe Crescentieae (88% bootstrap in Fig. 3), and in the absence of a name to recognize this strongly supported clade, expanding Crescentieae to include *Tabebuia* may warrant consideration. Our data support recognition of Crescentieae as a distinct taxon within Bignoniaceae; however, Reveal's (1995) recognition of a family Crescentiaceae would make the rest of Bignoniaceae paraphyletic.

Bignonieae are the largest tribe in the family, with their center of diversity in Brazil. All trees from this study show Bignonieae to be monophyletic, consistent with Gentry's (1980) hypothesis. However, our limited sampling makes this conclusion preliminary. Additional sampling from this group would enhance our knowledge of lineages that compose the family. Gentry (1976, 1980) segregated tribe Oroxyleae from the rest of Bignonieae and suggested it is allied with tribe Tecomeae. Our results confirm this by placing it among the lineages that together comprise the paraphyletic tribe Tecomeae, sister to *Catalpa*. The unique chromosome numbers of Oroxyleae ($n = 14, 15$) indicate a possible synapomorphy for this tribe. Gentry and Tomb (1979) believed the base chromosome number of Bignoniaceae to be $x = 7$, and on this basis, plus the retention of five stamens, placed Oroxyleae basal within the family, or even within the Tubiflorae (essentially Lamiales s.l.) as a whole. These hypotheses have no support from the molecular data. *Jacaranda*, one of the basalmost Bignoniaceae, has four stamens and one staminode, and a chromosome number of $n = 18$. A chromosome count has not been published for *Podranea*.

Our analysis places the monogeneric Andean tribe Eccremocarpeae near the base of Bignoniaceae. Three species were recognized in a recent revision of the tribe (D'Arcy, 1997), but previous treatments recognized as many as six species (Gentry, 1980; Gentry & Tomb, 1979). The clade comprising *Eccremocarpus* and all Bignoniaceae except *Jacaranda* and *Podranea* is strongly supported (78% bootstrap), yet has not been formally named. We declined to name this clade at this point due to limited sampling. Further sampling from Tecomeae is necessary to more rigorously evaluate the monophyly of the Eccremocarpeae.

The paraphyly of tribe Tecomeae presents some major taxonomic problems. The basalmost Bignoniaceae (*Jacaranda* and *Podranea* in Fig. 3) belong to Tecomeae, but other members of this tribe (e.g., *Cybistax, Tabebuia, Radermachera*) are highly derived within the family. Gentry (1974) suggested that Tecomeae was phylogenetically basal relative to Bignonieae. However, the evidence presented here suggests Bignonieae as sister to much of the rest of the family, including most of the Tecomeae, although support for several branches near the divergence of Bignonieae is weak. Most Tecomeae, as currently circumscribed, share features such as fruits dehiscing perpendicular to the septum and an arborescent habit, but these may be plesiomorphies. Members with palmately compound leaves are usually found in the Neotropics ("NW" in Fig. 3), and the Old World members ("OW" in Fig. 3) usually have pinnately compound leaves. Gentry

(1980) used this information to suggest that Old and New World taxa may represent distinct groups derived from different ancestors within the tribe. The molecular evidence presented here does not support a simple split along geographic lines. It is the only tribe occurring in both the Old and New Worlds, but given the paraphyly of the tribe (Fig. 3), biogeographic interpretations within the tribe have little meaning. The tribe should be split into several smaller lineages (R. Olmstead, unpublished data), or placed with existing lineages where data strongly support groupings. For example, *Radermachera* and tribe Coleeae form a clade with strong support (80% bootstrap in Fig. 3), so these data suggest expanding tribal limits of Coleeae to include *Radermachera.* Taxonomic revision of tribal boundaries in Bignoniaceae should focus on redefining Tecomeae to identify monophyletic lineages.

Increased sampling among members of Bignoniaceae has provided further information for the delimitation of the family. Additional support is provided for the exclusion of *Paulownia* and *Schlegelia* as well as for tribal relationships traditionally based on morphological reproductive characters. It is hoped that the present work will continue to expand our knowledge of Bignoniaceae by providing a phylogenetic framework for current and future work on the family.

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POLLINATION OF *MORAEA* SPECIES (IRIDACEAE) WITH A STAMINAL COLUMN[1]

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ABSTRACT

The ancestral and most common flower in the African genus *Moraea* is *Iris*-like and consists of three functional units (meranthia). Each unit consists of an outer tepal opposed to a broad style branch terminating in prominent paired crests, together forming a gullet-like unit. However, many species in this genus of some 200 species have mechanically protandrous flowers in which the three stamens form a sheath surrounding the style and the style branches are narrow, with reduced stigmatic crests, and the subequal inner and outer tepal whorls form a shallow or deep bowl sometimes fully enclosing the stamens and style branches. The flowers secrete hexose-dominant nectar and, except for *M. collina*, are self-incompatible. Flowers of the nine species in two sections studied comprise two different modes of pollination based on the presentation of the staminal column and perianth, pigmentation, scent, and edible rewards. In five species, *M. collina, M. comptonii, M. elegans, M. ochroleuca*, and *M. vallisbelli*, the perianth forms a wide or narrow bowl and produces strong, sweet or musk-like odors, and the weakly diverging anthers are appressed to the narrow, inconspicuous style branches. These flowers are pollinated primarily by flower flies, scarab beetles, and honey bees that land on the perianth and brush against the anthers and/or receptive stigmas while foraging for nectar or pollen, or in the case or beetles merely assembling on the flowers. In the second group of species, *M. bifida, M. miniata, M. pseudospicata*, and *M. reflexa*, the perianth is stellate, pink, yellow, or blue, usually without discernable scent, the filaments are united into a column that is exserted from the flower, and the anthers are usually coherent. These flowers are pollinated primarily by polylectic bees in the families Apidae (*Anthophora diversipes, Apis mellifera*) and Melittidae (*Rediviva* spp.). The bees land on the staminal column and forage for pollen, sometimes later moving onto the perianth to take nectar present at the base of the tepals. The columns of these species are interpreted as both morphological and functional intermediates between pollen presenters or protostigmas (e.g., in Asterales, Campanulales, Proteales) and true gynostemia/gynostegia (in Asclepiadaceae, Orchidaceae, and Stylidiaceae). These flowers represent a profound shift in the ancestral pollination strategy in the genus from one of passive pollen deposition on bees foraging for nectar on meranthia to one of active foraging for nectar or pollen on whole flowers.

Floral morphology in the Iridaceae is usually closely correlated with the diversity of pollinators. For example, most species in the genera *Lapeirousia* and *Nivenia* have flowers with elongated floral tubes and are pollinated by nemestrinid and tabanid flies and sphinx moths that have probosces longer than their bodies and often forage for nectar while hovering (Vogel, 1954; Goldblatt & Bernhardt, 1990; Goldblatt et al., 1995; Manning & Goldblatt, 1996, 1997). Conversely, North American *Sisyrinchium* species, and some species of the southern African genera, including *Aristea, Ixia, Romulea*, and *Sparaxis*, have stellate or rotate perianths, the latter with reduced, often non-functional floral tubes. The primary pollinators of these flowers include small- and large-bodied bees, large scarab beetles (Hopliinae), and short-tongued flies that must land on the tepals to collect nectar and/or pollen (Henderson, 1976; Cholewa & Henderson, 1984; Goldblatt et al., 1998a; Goldblatt & Manning, 1997). In southern Africa scarab beetles also use the flowers as sites for assembly and mating. Genera pollinated primarily by large bees with long probosces (e.g., *Gladiolus*) have zygomorphic, bilabiate flowers in which the lower tepals form a landing platform (Vogel, 1954; Goldblatt et al., 1998b).

In *Iris* and most species of *Moraea* the individual flowers comprise three functionally separate pollination units, or meranthia (Faegri & van der Pijl, 1979). Each meranthium resembles a bilabiate gullet flower and consists of a large outer tepal, the claw of which is closely opposed to a flattened style branch that bears a transverse stigma and terminal, petal-like crests (Fig. 1). The major pollinators are large bees that land on the outer tepal limb and

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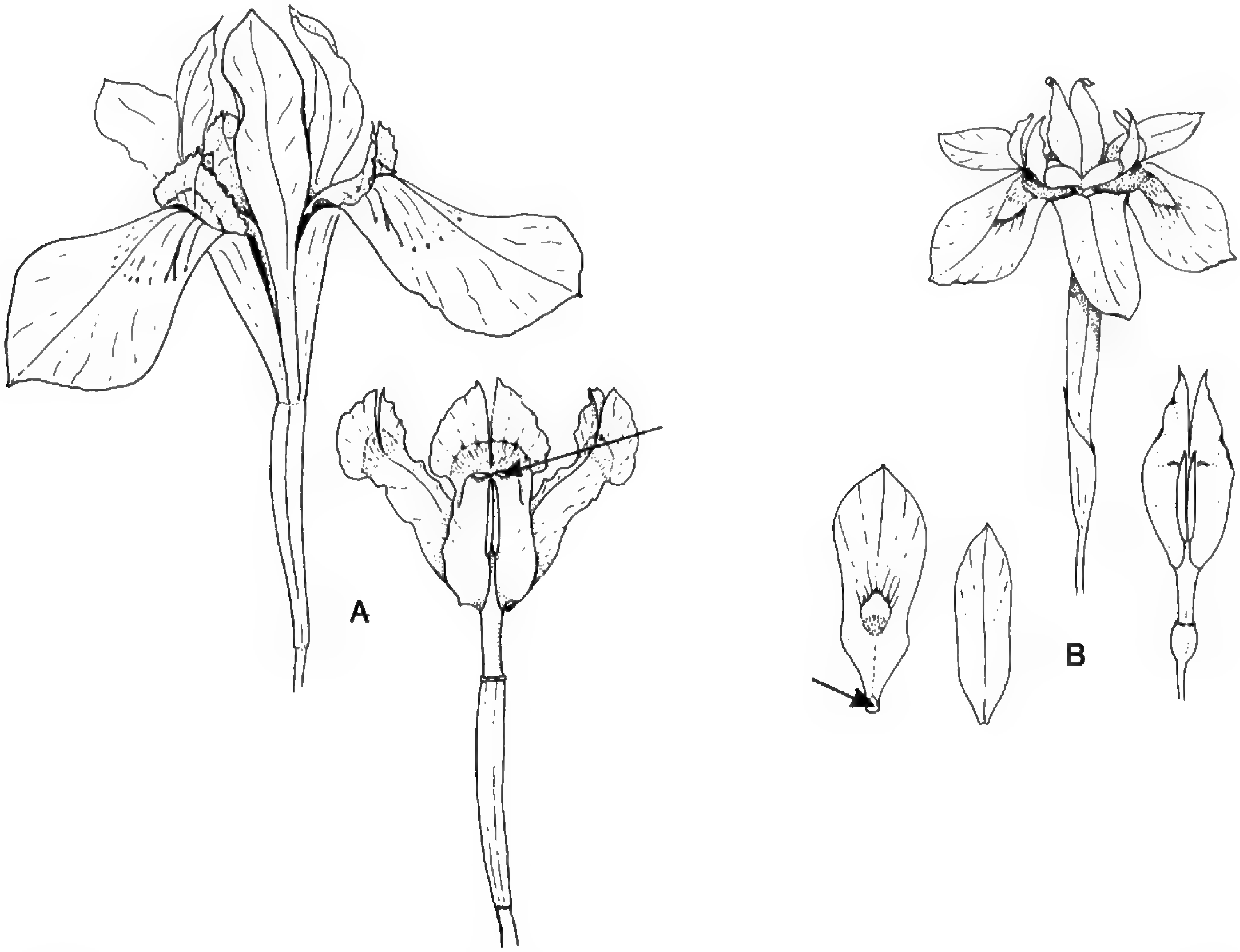

Figure 1. Classic *Iris*-type flower of *Moraea*. —A. *M. huttonii* (Baker) Oberm., with stamens and style branch enlarged and arrow indicating the stigmatic lobes of one style branch. —B. *M. inclinata* Goldblatt, with one stamen and the opposed style branch and an inner and outer tepal enlarged with arrow indicating position of perigonal nectary. Whole flowers ×1.5, dissections much enlarged. Drawn by Margo Branch.

push their bodies between the style branch and tepal claw to forage for nectar (Müller, 1883; Goldblatt et al., 1989; Proctor et al., 1996).

Among the southern African species of *Moraea*, now including *Homeria* and *Hexaglottis* (Goldblatt, 1998), there are some striking modifications to the ancestral flower (Goldblatt, 1981, 1986). Some 60 species of the genus belonging to several different lineages have flowers in which the three-part, bilabiate form has been lost. Style crests are reduced or absent, filaments form a column, anthers are often coherent, and the outer whorl of tepals does not differ from the inner whorl at all in orientation and hardly in size and shape. In these flowers the tepal claws are not associated with the style branches to form a floral throat or gullet (Figs. 2, 3). These floral forms suggest alternative pollination systems. Here we examine nine representative species with these flowers and compare them with what is known of pollination in the remaining species of *Moraea* and other Iridaceae specifically, and within the angiosperms in general.

METHODS

Field studies were conducted in the winter-rainfall zone of southern Africa over the past 25 years as opportunity arose while in the course of research on the systematics of various genera of the Iridaceae (Table 1). Observation of insect foraging involved 4–10 hours per plant species and included recording of floral attractants (pigment patterns, scent, nectar), the behavior of insects on the flower, and the taxonomic diversity of floral foragers. Casual observations made in other years have confirmed many of the observations reported for particular study sites. Flower visitors were captured if they were seen to contact the sexual organs of the flower or while they foraged for floral nectar and/or pollen. Netted insects were killed in a jar using ethyl acetate fumes. To prevent contamination with pollen carried by another insect in the killing jar, specimens were isolated from each other by wrapping them in tissue. Insect length was measured from the pronotum to the posterior tip of the abdomen.

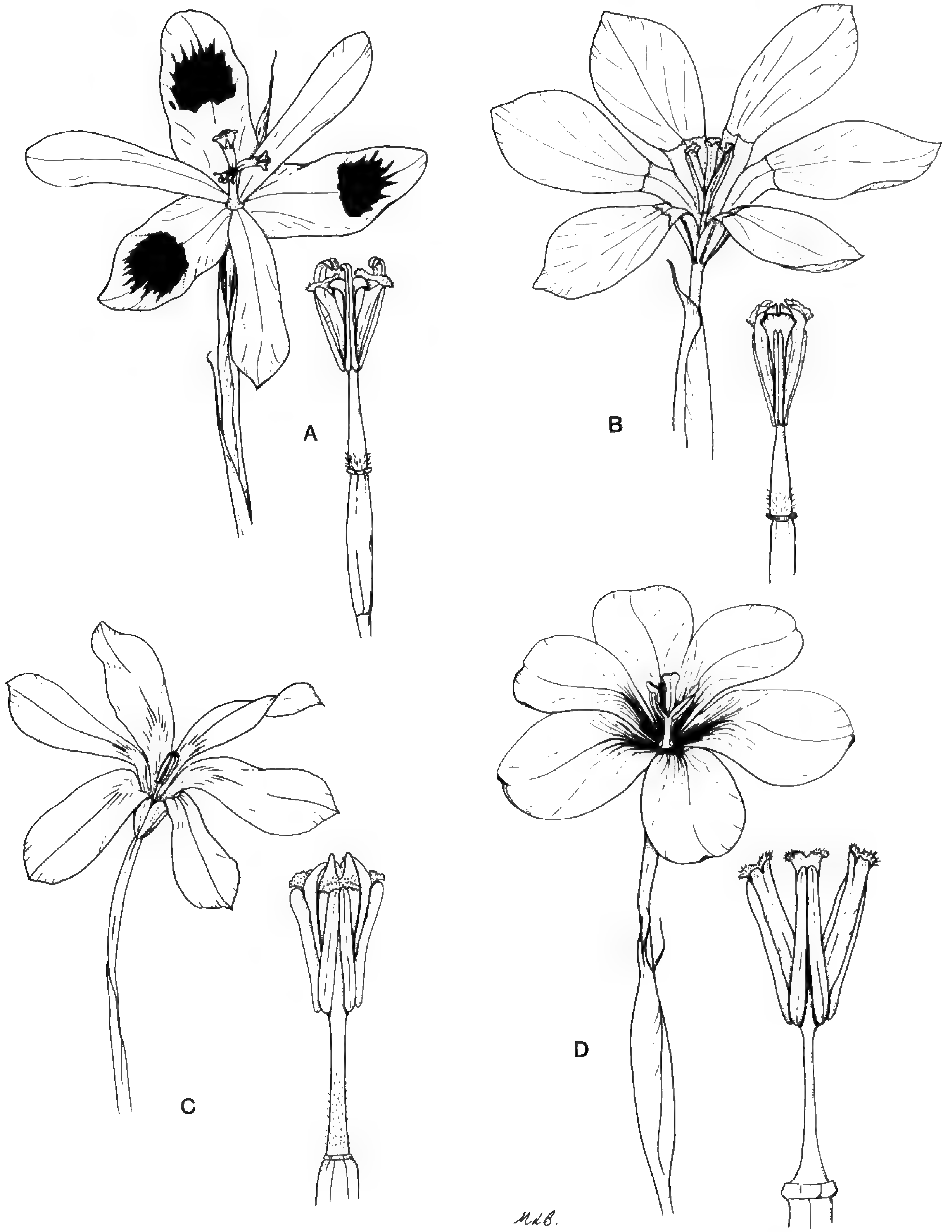

Figure 2. Bowl flowers of *Moraea* species studied with detail of the stamen–style branch unit. —A. *Moraea elegans.* —B. *M. comptonii.* —C. *M. collina.* —D. *M. ochroleuca.* Whole flowers ×1.5, stamen–style unit much enlarged. Drawn by Margo Branch.

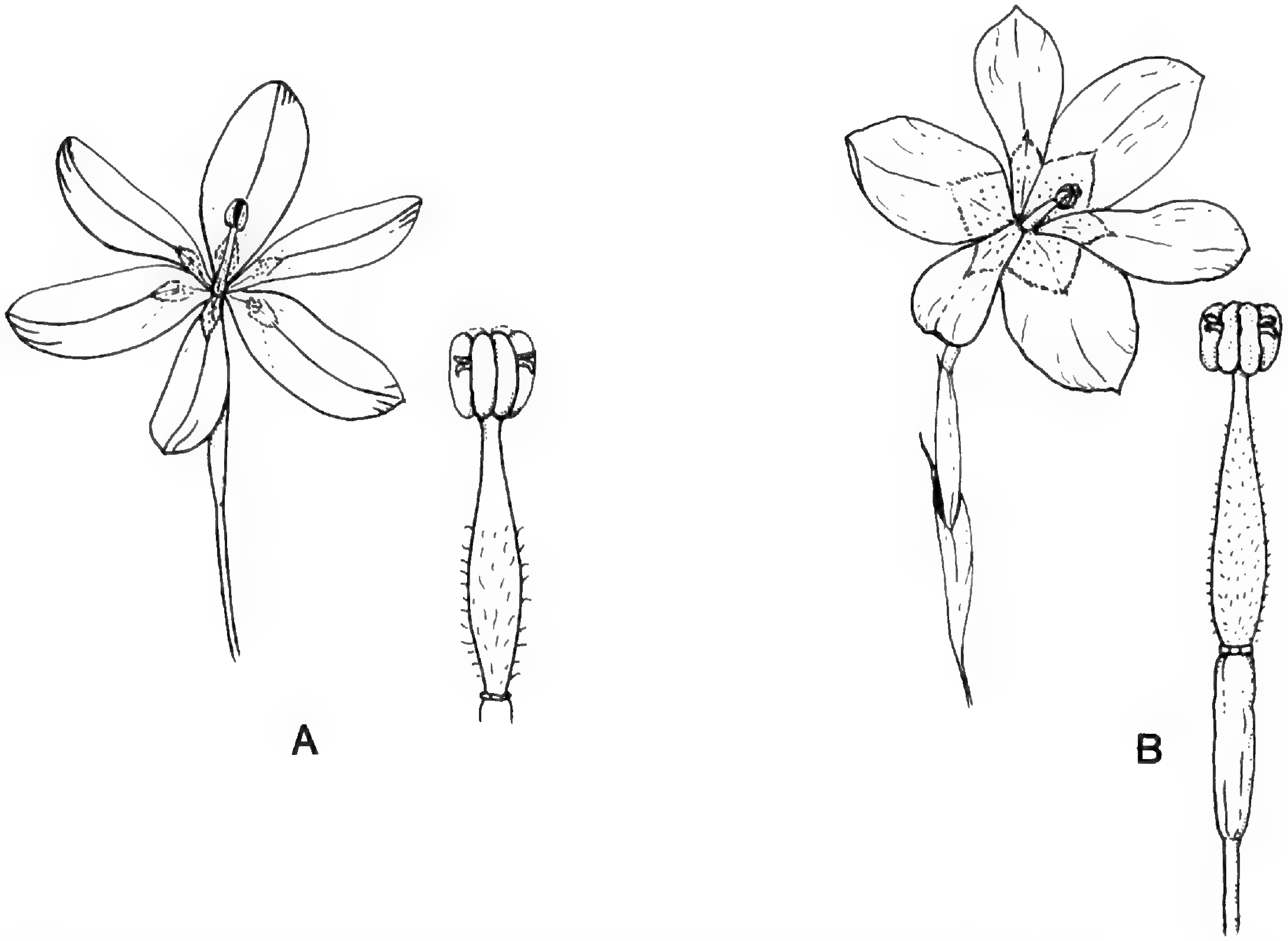

Figure 3. Stellate flowers of *Moraea* species studied with detail of the stamen–style branch unit. —A. *Moraea miniata*. —B. *M. bifida*. Whole flowers ×1.5, stamen–style unit much enlarged. Drawn by Margo Branch.

Pollen was removed from insects by placing the pinned specimen on a glass slide and either scraping pollen off the body with a dissecting needle or gently washing the specimen in drops of 95% ethanol. The residue from needle probes or washes was collected on glass slides and mounted in 1–2 drops of Calberla's fluid (Ogden et al., 1974). Pollen was scored as present on an insect if more than 10 grains (or polyads) were observed on the slide (Table 4). Pollen grains were identified by comparison with a reference set of pollen preparations made from plants flowering at study sites.

Insects were identified by H. Dombrow, Wurms, Germany (beetles), D. Barraclough, KwaZulu-Natal Museum, Pietermaritzburg (most Diptera), and V. Whitehead, South African Museum, Cape Town

Table 1. Research sites and voucher data for species studied. All localities are in Western Cape Province, South Africa. All vouchers are deposited at MO.

Species	Locality	Voucher
M. bifida (L. Bolus) Goldblatt	Nieuwoudtville, Glenlyon Estate, Aug. 1976, and Sep. 1996	*Goldblatt 3969*
M. collina Thunb.	Cape Town, Signal Hill, Aug. 1996	*Goldblatt s.n.* (no voucher)
M. comptonii (L. Bolus) Goldblatt	Near Bot River, Aug. 1997	*Goldblatt 3997*
M. elegans Jacq.	Napier, Fairfield Estate, Aug.–Sep. 1996	*Goldblatt 10255*
M. miniata Andr.	Near Clanwilliam, Sep. 1996	*Goldblatt 2563*
M. ochroleuca (Salisb.) Drapiez	Foot of Sir Lowry's Pass, Aug. 1996	*Goldblatt 10248*
	Cape Peninsula, near Kommetje, July 1976	*Goldblatt 3615*
M. reflexa Goldblatt	Calvinia, top of Hantamsberg, Oct. 1995	*Goldblatt 10555*
M. vallisbelli (Goldblatt) Goldblatt	West of Nieuwoudtville, Oct. 1996	*Goldblatt 4032*
M. pseudospicata Goldblatt	Nieuwoudtville Wild Flower Reserve, Apr. 1997	*Goldblatt 10797*

Table 2. Floral characteristics of species of *Moraea* studied, including shape, perianth color and marking, presence of nectar, and flowering time. Abbreviations: + = presence, − = absence.

	Flower					
	Shape	Color	Scent	Nectar	Flowering time	Floral longevity
Moraea sect. *Homeria*						
M. bifida	star	pink	−	+	Sep.–Oct.	ca. 12–5 PM (ca. 6 hr.)
M. collina	bowl	yellow or pink	+	+	Aug.–Sep.	ca. 12–4 PM, 2 days (ca. 36 hr.)
M. comptonii	bowl	yellow or pink	+	+	Aug.–Sep.	10 AM–4 PM, 2 days (30 hr.)
M. elegans	bowl	yellow	+	+	Sep.	10 AM–5 PM, 2 days (30 hr.)
M. miniata	star	pink (or yellow)	−	+	Sep.	1–6 PM (ca. 5 hr.)
M. ochroleuca	bowl	yellow	+	+	Aug.–Oct.	10 AM–5 PM, 2 days (ca. 30 hr.)
M. reflexa	star	yellow	+	+	Oct.	1 day (ca. 6 hr.)
M. vallisbelli	bowl	yellow or pink	−	+	Sep.–Oct.	11 AM–4 PM (ca. 6 hr.)
Moraea sect. *Polyanthes*						
M. pseudospicata	star	blue	−	+	Mar.–Apr.	ca. 3:30–6 PM (2.5 hr.)

(*Rediviva* bees). Plant voucher specimens have been deposited at the Missouri Botanical Garden (MO), and insects at the KwaZulu-Natal and South African Museums. Bee taxonomy followed is that of Roig-Alsina and Michener (1993).

The presence of nectar was determined in the field by withdrawing nectar from the base of the floral tube with 2-μl capillary tubes after separating the ovary from the perianth. When volumes were too small to sample in the field, stems were cut and placed in water and nectar was sampled in the laboratory within 18 to 24 hours. Experience showed that nectar characteristics gradually change in *Moraea* species if stems are retained in water for longer periods. Volume and solute content are based on laboratory measurements of flowers of plants maintained in water (Table 3). Nectar samples were dried on Whatman's filter paper no. 1 and sent to B.-E. van Wyk, Rand Afrikaans University, Johannesburg, for HPTCL analysis (Table 3). The percentage of sugars dissolved in fresh nectar (Table 3) was recorded on a Bellingham & Stanley hand-held refractometer (0–50%) using nectar extracted from flowers in the manner described above. When volumes were too small to measure or to determine sugar concentration, the presence of nectar was estimated by brushing nectariferous areas of flowers against the tongue.

Floral scent was noted in the field and in cultivated plants. Flowers of species with scents too weak to be discerned by the human nose were recorded after individual flowers were picked and placed in clean, lidded glass jars and stored in a warm place. The contents of each jar was smelled after a minimum of 60 minutes (Buchmann, 1983).

Compatibility was determined in the greenhouse by self- or cross-pollinating emasculated flowers. Sufficient pollen was applied to the stigma to be visible to the naked eye. Two types of pollination were made. One: cross-pollinations of at least five emasculated flowers received pollen from a second genotype of the same species. Two: self-pollinations of at least five emasculated flowers each received pollen of the same genotype.

RESULTS

Floral phenology and habit. Species studied are corm-bearing, seasonal geophytes native to the winter-rainfall region of southern Africa, that is, the southern and western coast and near interior of the subcontinent. Eight species bloom from late winter to mid spring, while *M. pseudospicata* blooms in the autumn (Table 2). All nine species typically form clumped populations with over five individuals per square meter not uncommon and with each flowering shoot bearing two to four open flowers per day.

Flowers last one or two days depending on the species. One-day flowers usually last 6–8 hours, but only 2.5 hours in *M. pseudospicata*. Flowering is strongly synchronized. On some days no flowers are produced in a population and on other days most individuals with flowering stems produce flowers. The time of flower opening is species specific (Table 2). The flowers of *Moraea collina, M. comptonii, M. elegans,* and *M. ochroleuca* close in the late afternoon and reopen on the following day, withering by late afternoon.

The flowers of all nine species show morphological protandry. That is, anthers dehisce within one hour after tepals expand but stigmatic surfaces remain folded against opposed stylar tissue for at least 2 hours in those species in which flowers last a single day. In *M. collina, M. comptonii,* and *M.*

Table 3. Nectar characteristics of species studied. Nectar analyses were provided by B.-E. van Wyk, Rand Afrikaans University, Johannesburg, South Africa (n = number of individuals sampled).

	Nectar		Sugar ratios %			
Species	Volume μL (n)	Conc. % (± SD)	Fru	Glu	Suc	Sucrose/ F + G (n)
M. bifida	trace amount present		50–51	49–50	0	0 (2)
M. collina	0.2–0.6 (4)	47.8 (2.1)	47–52	48–53	0	0 (4)
M. reflexa	2.5–5.0 (2)	9.0–12.0	50.5	49.5	0	0 (2)
M. ochroleuca	trace amount present		49–50	50–51	0	0 (2)

elegans the stigmas are not exposed until the mid afternoon of the first day of flowering, and in *M. ochroleuca* not until the second day of the floral lifespan.

Floral compatibility. *Moraea collina* was the only species that set seed following self-pollination. All remaining species were strongly self-incompatible, as no capsules were produced after at least five hand self-pollinations; full capsules were produced by cross pollinations. Flowers of *M. collina* are thus self-compatible and are in addition weakly autogamous, as shown by flowers of greenhouse-grown plants that were not hand pollinated.

Floral presentation and rewards. Flowers of *Moraea* species are produced in several-flowered monochasial cymose inflorescences (rhipidia) with the buds enclosed until the day before anthesis in a pair of large, green, leathery sheathing bracts (spathes) (Goldblatt, 1986, 1990). Flowers are actinomorphic and are produced sequentially from a rhipidium 1–3 days apart during the flowering season, when they are exserted from the spathes as the pedicels elongate.

Flowers are of two contrasting forms (Table 2). In the first (Fig. 2), the tepals have elongated, ascending claws forming a narrow to wide bowl while the tepal limbs spread horizontally. The perianths are either yellow or pale salmon pink, but other species (not included in this study) may have blue or white flowers, e.g., *M. polyanthos* L.f. Flowers are usually uniformly colored within a population, but at our study site for *M. comptonii* plants had either yellow or salmon flowers, and some populations of this species have green markings on the outer or all tepals. Individuals of *M. vallisbelli* also may have yellow or pink flowers within a population. Pale yellow nectar guides, typically outlined in dark gray, are usually present at the base of the tepal limbs, but *M. ochroleuca* has no visible nectar guides (Fig. 2D), although some individuals have the floral cup a deeper shade of yellow. Flowers of *M. elegans* have prominent, large, dark green and or orange markings on the distal halves of the outer tepals (Fig. 2A).

The bowl-shaped flowers are typically scented, with odors reminiscent of musk (*M. ochroleuca*), honey (*M. collina*), or fruity odors with a strong component of coconut (*M. comptonii, M. elegans*). The united filaments enclose the style, and the weakly divergent anthers are appressed to narrow style branches. The style branches reach to the middle or just beyond the anther tips and have terminal, bilobed stigmatic surfaces. The staminal column and the style branches are included in the floral bowl, but barely so in *M. comptonii* and *M. elegans* in which the bowl is wide and shallow.

In the second floral type (Fig. 3) the tepal claws are short and erect while the limbs spread horizontally or are reflexed. The perianth is thus more or less stellate. The perianths are usually pink, sometimes yellow or blue, but are typically uniformly colored within populations. *Moraea reflexa* always has yellow flowers, and *M. pseudospicata* blue flowers (Table 2). Yellow nectar guides, often with minute blackish dots, are present at the base of the tepal limbs. Only *M. reflexa* has flowers that produce a light sweet odor. None of the remaining species with stellate flowers produces a discernable scent even when kept in lidded glass jars. In these flowers the stamens form an elongated, and disproportionately prominent column with the fused filaments enclosing the style and the anthers either diverging (*M. reflexa*) or coherent (Fig. 3). The filament column is smooth and slender (*M. pseudospicata*) or lightly papillate and inflated and bulbous above the base. When the filament column is bulbous a small chamber is formed between the tepal claws and lower portion of the column. The staminal column is well exserted from the flower, and the anthers and pollen are prominently displayed. When the anthers are contiguous the stigmatic tips of the style branches emerge between the anthers after anther dehiscence (Fig. 3), and in the field are usually visible after pollen has been removed from the anthers by insect visitors. Pollen and stigmatic

Table 4. Pollen load anlaysis of collected beetles. Taxonomic affiliations are as follows: Coleoptera: *Anisochelus, Anisonyx, Peritrichia, Platychelus* (Scarabaeidae). Diptera: *Anthomyia* (Anthomyiidae); *Orthellia* (Muscidae); *Scathophaga* (Scathophagidae). Hymenoptera–Apoidea: *Andrena* (Andrenidae); *Anthophora* (Anthophoridae); *Apis* (Apidae); *Lasioglossum, Patellapis* (Halictidae); *Rediviva* (Melittidae).

	Number of insects carrying pollen loads of:			
Plant and insect taxon	Host flr only	Host flr + other sp.	Other sp. only	No pollen
Bowl flowers:				
M. collina				
Anisonyx ursus	3	0	0	0
Apis mellifera	0	4	0	0
Lasioglossum pearstonensis	0	0	3	4
Patellapis sp.	0	3	0	1
M. comptonii				
Apis mellifera	0	3	0	0
Anthophora diversipes	0	2	0	0
Orthellia sp.	5	0	0	0
Platychelus sp.	2	2	0	0
M. elegans				
Apis mellifera	2	0	0	0
Orthellia sp.	0	2	0	1
Peritrichia pseudoplebia	7	2	0	1
Scathophaga stercoraria	0	0	0	3
M. ochroleuca				
Anisonyx ursus	2	0	0	0
Anthomyia sp.	0	0	0	1
Apis mellifera	3	1	0	0
Calliphoridae	0	0	1	0
Orthellia sp.	10	0	0	0
Musca sp.	0	2	0	1
Scathophaga stercoraria	0	2	0	3
Syrphidae	0	1	0	0
M. vallisbelli				
Anisochelus inarmatus	6	5	0	2
	40	29	4	17
Stellate flowers:				
M. bifida				
Apis mellifera	0	3	0	0
Rediviva macgregorii	0	2	0	0
M. miniata				
Apis mellifera	0	3	0	0
Rediviva parva	0	3	0	0
Rediviva longimanus	0	1	0	0
Anthophora diversipes	0	3	0	0
M. pseudospicata				
Apis mellifera	5	2	0	0
Halictidae	1	1	0	1
M. reflexa				
Apis mellifera	2	0	0	0
	6	18	0	1

surfaces are, however, in close proximity during anthesis, and pollen inevitably comes into contact with stigmatic surfaces unless removed by insect visitors.

Nectar. A small nectar gland (perigonal nectary) is located at the base of each tepal in seven species but only at the base of the outer tepals in *Moraea comptonii* and *M. elegans*. In species with bowl-shaped flowers nectar droplets are visible after flowers open. Discrete nectar glands are not present in *M. ochroleuca*, but nectar is secreted over the lower surface of the tepals above vascular traces, visible as darker streaks on the tepals. Nectar is concealed between the tepal claws and filament column in a small nectar chamber in species with stellate flowers. In all nine species nectar is available in such small quantities in the field that it could not be measured for volume and solute concentration. The nectar sugars of all species for which there are data are hexose dominant and have trace amounts of sucrose or none at all.

Insect pollination of bowl vs. stellate flowers. Bowl flowers are visited by a wide variety of insects, with short-tongued flies and scarab beetles predominant (Table 4). All insects observed on these bowl-shaped flowers land on the tepals and then crawl into the floral bowl. As they enter the flower, dorsal parts of the bodies of beetles, flies, and *Apis mellifera* brush against the anthers and stigma lobes. Beetles may remain at rest in the floral cup for at least 15 minutes with their heads lying against the base of the filament column and their abdomens or entire bodies visible from above. Of the 69 insects found to carry pollen of their host flowers (Table 4), 58% carried pure loads of the species on which they were captured.

The four species with stellate flowers are visited exclusively by bees in the families Apidae (*Apis mellifera, Anthophora diversipes*), Halictidae, and Melittidae (*Rediviva* spp.). Bees normally land directly on the anthers where they actively remove the pollen from dehisced anthers. After foraging for pollen some bees crawl onto the tepals and forage for nectar in the chamber at the base of the filament column. Of the 24 bees netted on stellate flowers and found to carry pollen of their host flowers (Table 4), only 6 individuals (25%) carried pure loads of the species on which they were captured.

While *Apis mellifera* forages for nectar and pollen on six species included in the study, field observation and pollen load analyses show that individuals foraged for pollen on co-blooming species including *Drimia* (Hyacinthaceae) and *Oxalis* (Oxalidaceae). *Anthophora diversipes*, collected on *M. miniata*, carried pollen of *Gladiolus* sp. (Iridaceae), *Lachenalia* sp. (Hyacinthaceae), and *Lobostemon* sp. (Boraginaceae). *Rediviva* species, collected on *M. bifida* and *M. miniata*, also forage on co-blooming *Diascia* sp. (Scrophulariaceae) and *Oxalis* sp.

DISCUSSION

The columnar organization of the androecium and gynoecium in combination with the shape of the perianth of the nine species of *Moraea* studied shows a clear correlation with the major pollen vectors. Species with bowl-shaped perianths are pollinated primarily by insects that are more likely to consume nectar or pollen. Contact between the pollinator and the anthers and stigmas at the apex of the column is passive and dorsal. In contrast, the apex of the column of species with stellate flowers offers pollen as the primary reward to female bees, and contact is typically active and ventral (Bernhardt, 1996).

It is noteworthy that the flowers of *Moraea* species studied here produce hexose-dominant nectar in contrast to sucrose-rich to sucrose-dominant nectar found in the vast majority of the many species in several other genera of Iridaceae examined for nectar sugars (Goldblatt et al., 1995, 1998b; Manning & Goldblatt, 1996, 1997). Hexose-rich to -dominant nectar is found elsewhere in the Iridaceae only in species of subfamily Nivenioideae and some species of Ixioideae that have flowers adapted for pollination by sunbirds (Goldblatt, 1993). Hexose-rich nectar is commonly associated both with flowers pollinated by passerine (perching) birds and some insects with short mouth parts including certain flies (Baker & Baker, 1983, 1990). Most of the many members of Iridaceae subfamily Ixioideae so far examined for nectar chemistry, whether pollinated by short- or long-tongued insects, have sucrose-rich to sucrose-dominant nectar (e.g., Goldblatt et al., 1998a, b; van Wyk, pers. comm.), and the presence of hexose-dominant nectar appears to be the result of pollinator-driven selection. The difference in *Moraea* (subfamily Iridoideae) may simply be due to the nectar source, from perigonal nectaries in bowl-shaped or stellate flowers in contrast to nectar produced from septal nectaries in species of Ixioideae and Nivenioideae, rather than reflecting pollinator selection for a particular nectar type. Species of Ixioideae pollinated by short-tongued insects including andrenid bees, hopliine beetles, and tabanid flies consistently have sucrose-rich nectar.

Stellate or bowl-shaped flowers with prominent staminal columns in *Moraea* are specialized relative to the ancestral (plesiomorphic) condition in the genus, the *Iris*-like flower composed of meranthia (Goldblatt, 1990, 1991), and are closely correlated with a particular pollination system. The meranthium organization has been lost in some 60 of the estimated 195 species of *Moraea* (Goldblatt, 1981, 1986, 1991; Goldblatt & Manning, 1995), including those studied here, as a result of a complete structural reorganization of the floral parts that includes the reduction in size of the style branches, suppression of stigmatic crests, and loss of the close relationship of the outer tepal to its opposed style branch and stamen.

The mode of pollination in these species appears to depend primarily on shape and depth of the floral cup, and thus the degree to which the staminal column is exserted from the flower, and secondarily to the degree of coalescence between anthers in the column. These two architectural features determine whether anthers will swab the back of pollinators entering a flower in search of nectar or serve as a site of active pollen collection for polylectic bees. Both systems occur extensively within *Moraea* and also characterize the genus *Ferraria* (Iridaceae tribe Irideae) (de Vos, 1979), the ancestors of which have an *Iris*-type flower. Stellate flowers with the stamens and style arranged in a column in *Moraea* appear to reflect an unusual modification to exploit polylectic bees in a genus in which pollination by bees is ancestral but based on an entirely different floral organization. ***Moraea bifida*, *M. miniata***, and ***M. pseudospicata*** are thus representative examples of several species in the genus that display a shift toward the evolution of a pollen flower derived from bilabiate, nectariferous ancestors. Pollen flowers are relatively uncommon in *Moraea*, and are derived in the genus. In contrast, floral evolution in *Moraea* species with bowl-shaped flowers appears to exploit a wide range of potential pollen vectors. These flowers often use scent as an attractant, offer visible nectar, and are pollinated by insects that may acquire pollen loads passively.

One of the more striking modes of floral convergence in the angiosperms has been in the evolution of stamens and carpels into columnar units. This occurs at two different levels. In such families as the Marantaceae, Fabaceae, Proteaceae, Polygalaceae, Meliaceae, and the orders Asterales, Campanulales, and Rubiales, part of the style or stigma becomes a pollen presenter or cup-like indusium (Kennedy, 1978; Ladd & Donaldson, 1993; Burns-Balogh & Bernhardt, 1985). In these flowers the anthers dehisce in the bud and empty their contents onto a sticky or hairy portion of the carpel. In the other example, most well known in the Asclepiadaceae, Orchidaceae, and Stylidiaceae, flowers show true adnation between the androecium and gynoecium forming gynostemia or gynostegia (sensu Lawrence, 1951). The arrangement of stamens and style in the ***Moraea*** species with flowers like ***M. pseudospicata*** is intermediate between these two major columnar developments. Self-fertilization due to the close proximity of the anthers and pollen to the stigmatic surfaces is avoided by self-incompatibility.

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REVISIÓN DEL GÉNERO *BARNADESIA* (ASTERACEAE: BARNADESIOIDEAE, BARNADESIEAE)[1]

Estrella Urtubey[2]

RESUMEN

El género *Barnadesia* de América del Sur comprende 18 especies de árboles o arbustos espinosos, distribuidas principalmente en los Andes desde Colombia hasta Argentina, y una especie llega a Brasil. El presente trabajo incluye aspectos taxonómicos y filogenéticos. El análisis taxonómico comprende: descripción e historia del género, claves para la identificación de los géneros de la subfamilia Barnadesioideae, y de las especies de *Barnadesia*, descripciones, sinónimos, caracteres morfológicos y anatómicos (espinas, hojas, pelos, corolas, anteras, aquenios, papus y polen), ilustraciones, mapas de distribución para cada especie, listas de nombres dudosos y de taxones excluídos. Se proponen 2 subgéneros, *Bacasia* (Ruiz & Pav.) Urtubey y *Barnadesia*, y una nueva combinación *Barnadesia lehmannii* Hieron. var. *villosa* (I. C. Chung) Urtubey. Se establecen las siguientes sinonimías: *Barnadesia media* D. Don = *B. arborea* Kunth; *B. wurdackii* Ferreyra = *B. arborea* Kunth; *B. caryophylla* (Vell.) S. F. Blake var. *macrospinosa* (Loefgr.) I. C. Chung = *B. caryophylla* (Vell.) S. F. Blake; *B. hutchisoniana* Ferreyra = *B. lehmannii* Hieron. var. *lehmannii*; *B. polyacantha* Wedd. var. *velutina* I. C. Chung = *B. polyacantha* Wedd. El análisis filogenético de *Barnadesia*, fue realizado usando caracteres morfológicos. La polaridad de los caracteres se determinó por el método del grupo hermano, se usó como grupo externo al género monotípico *Fulcaldea*. Para confirmar la monofilia de *Barnadesia* se incluyó en el análisis al género *Huarpea*. Se reconocieron dos principales grupos monofiléticos: (1) *B. corymbosa* y *B. parviflora* y (2) *B. lehmannii*, *B. reticulata*, *B. caryophylla*, *B. polyacantha*, *B. glomerata*, *B. odorata*, *B. macbridei*, *B. jelskii*, *B. aculeata*, *B. horrida*, *B. macrocephala*, *B. pycnophylla*, *B. spinosa*, *B. arborea*, *B. dombeyana* y *B. blakeana*.

ABSTRACT

Barnadesia is a South American genus with 18 species of trees and shrubs, mainly distributed in the Andes. This work represents a modern revision, which comprises taxonomic and phylogenetic aspects. The taxonomic aspect includes a description and history of the genus, keys for identification of the genera of the subfamily Barnadesioideae and the species of *Barnadesia*, descriptions, an account of morphological and anatomical characters (spines, leaves, hairs, corollas, anthers, achenes, pappi, and pollen), synonyms, illustrations, and distribution maps for each species, as well as a list of doubtful and excluded taxa. Two new subgenera, subg. *Bacasia* (Ruiz & Pav.) Urtubey and *Barnadesia*, and a new combination, *Barnadesia lehmannii* Hieron. var. *villosa* (I. C. Chung) Urtubey, are proposed. The following new synonymies are established: *Barnadesia media* D. Don = *B. arborea* Kunth; *B. wurdackii* Ferreyra = *B. arborea* Kunth; *B. caryophylla* (Vell.) S. F. Blake var. *macrospinosa* (Loefgr.) I. C. Chung = *B. caryophylla* (Vell.) S. F. Blake; *B. hutchisoniana* Ferreyra = *B. lehmannii* Hieron. var. *lehmannii*; *B. polyacantha* Wedd. var. *velutina* I. C. Chung = *B. polyacantha* Wedd. The phylogenetic analysis of *Barnadesia* was proposed using morphological characters. Polarity of characters was based on outgroup comparison with the genus *Fulcaldea*. The genus *Huarpea* was included to test the monophyly of *Barnadesia*. Two monophyletic groups were resolved: (1) *B. corymbosa* and *B. parviflora*, and (2) *B. lehmannii*, *B. reticulata*, *B. caryophylla*, *B. polyacantha*, *B. glomerata*, *B. odorata*, *B. macbridei*, *B. jelskii*, *B. aculeata*, *B. horrida*, *B. macrocephala*, *B. pycnophylla*, *B. spinosa*, *B. arborea*, *B. dombeyana*, and *B. blakeana*.

El género *Barnadesia* (Asteraceae) fue descripto por Mutis en 1781 y pertenece a la subfamilia Barnadesioideae, tribu Barnadesieae (Bremer & Jansen, 1992). *Barnadesia* comprende 18 especies arbustivas o arbóreas de los Andes de América del Sur; sólo una especie crece también en Brasil. Has-

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ta el momento existen solamente estudios parciales del género: Ferreyra (1964) trató las especies peruanas de *Barnadesia,* y Chung (1965) estudió el género sin incluir las cuatro especies nuevas descriptas por Ferreyra en el año anterior. Robinson (1975) estableció una nueva especie, y finalmente Harling (1991) trató las especies ecuatorianas, y elevó una variedad de Chung a categoría de especie. La presente revisión comprende un estudio sistemático-filogenético del género, que tiene como objetivos: (1) definir la posición del género *Barnadesia* dentro de la subfamilia Barnadesioideae; (2) clarificar la taxonomía de las especies (delimitar las especies, ampliar las descripciones, resolver problemas nomenclaturales y proporcionar claves de determinación de las especies); (3) ampliar el conocimiento actual sobre los aspectos morfológicos, anatómicos y palinológicos del género; (4) establecer la distribución geográfica de las especies; (5) establecer una hipótesis acerca de las relaciones filogenéticas entre las especies de *Barnadesia.*

MATERIAL Y MÉTODOS

El estudio se realizó sobre la base de ejemplares de herbario provenientes de las siguientes instituciones: F, GH, HUT, K, LIL, LP, MCNS, MO, NY, S, SI, UC, US, USM. En la cita de los materiales examinados de cada especie, se señala con un asterisco (*) los ejemplares examinados en los estudios anatómicos.

Los datos del color de las flores, hábitat y época de floración de las plantas se tomaron de las etiquetas de herbario y de observaciones en el campo.

Las partes florales se reconstituyeron hirviéndolas unos minutos y se conservaron luego en alcohol 70°.

Para los estudios anatómicos, las hojas fueron reconstituidas colocándolas en etilenglicol durante 3–4 días. Los cortes se realizaron a mano alzada incluyendo el material en médula de hinojo; se aclararon en hipoclorito de sodio al 50% y se tiñeron con violeta de cresilo o con safranina diluida. Los preparados cuticulares se obtuvieron por maceración de los tejidos en hipoclorito de sodio diluido al 50% y se colorearon con safranina. El montaje de los preparados se realizó en glicerina diluida al 10%.

Los aspectos morfológicos de las especies se ilustraron con ayuda de una cámara clara adicionada a una lupa binocular Wild M5, y tubo de dibujo adicionado a un microscopio óptico Olympus CH-2.

El contorno de las hojas, los aquenios y los capítulos se describieron de acuerdo con la terminología de "The Systematics Association Committee for Descriptive Biological Terminology, II" (Taxon 11: 145–156, 1962). La terminología empleada en las descripciones de las epidermis es la de Stace (1965). Los diferentes tipos de pelos foliares fueron asignados de acuerdo con Ramayya (1962) y Bremer & Jansen (1992). El taxon infragenérico propuesto conserva el estatus de variedad, dado que el cambio de estatus de las variedades anteriores implica nuevas combinaciones.

Para el análisis cladístico se consideraron 25 caracteres morfológicos correspondientes a 8 caracteres vegetativos y 17 caracteres florales (Tabla 1). La Tabla 2 muestra la matriz de datos (especies × caracteres) usada en el análisis. La polaridad de los caracteres se determinó por el método de comparación con el grupo hermano (Watrous & Wheeler, 1981), se usó como grupo externo al género monotípico *Fulcaldea.* Además, de las especies de *Barnadesia,* se incluyó en el análisis a *Huarpea andina,* para confirmar la monofilia de *Barnadesia.* En el caso en que la determinación con el grupo externo no es posible (caracteres 1 y 20) se tomó como segundo grupo externo a *Arnaldoa.* Los estados plesiomórficos (presentes en el outgroup y en el grupo estudiado) fueron codificados con 0, y los estados apomórficos (sólo presentes en el grupo estudiado) con 1, 2 ó 3. En los casos en que el carácter presentaba variabilidad dentro del taxón (polimorfismos) se indicó con "?" ("missing data" para el software). Los caracteres con más de dos estados de carácter (1, 12, 13, 17, 19 y 24) fueron tratados como no aditivos.

Se usó el programa Hennig86 versión 1.5 (Farris, 1988), usando el algoritmo ie* ("implicit enumeration"). Se calcularon los índices de consistencia (Kluge & Farris, 1969) y retención (Farris, 1989), donde para no sobre estimar los valores de estos índices se excluyeron las autapomorfías y las sinapomorfías totales. El árbol de consenso estricto se obtuvo con la opción nelsen. La evolución de los caracteres fue interpretada usando el programa Clados versión 1.21 (Nixon, 1992).

HISTORIA TAXONÓMICA DEL GÉNERO *BARNADESIA*

El género *Barnadesia* fue fundado por Mutis en 1781 (Suppl. pl.: 55), sin mencionar un binomio. En el mismo trabajo (p. 348), Linneo (f.) describió *Barnadesia spinosa* sobre materiales colectados por Mutis en Colombia. David Don (1833) creó 5 especies y, junto con *Barnadesia spinosa,* sobre la base de caracteres florales, las reunió en tres grupos: (1) *Propriae* (*B. spinosa, B. media, B. reticulata, B. lanceolata*); (2) (*B. corymbosa*); (3) *Penthea*

Tabla 1. Caracteres y estados de los caracteres.

Caracteres	Estados
1. Hábito	arbusto (0); árbol (1); subarbusto (2)
2. Tallos	espinosos (0); inermes (1)
3. Disposición de las hojas	alterna (0); fasciculada (1)
4. Base de la hoja	peciolada (0); sésil o subsésil (1)
5. Forma de la lámina	tercio superior igual de ancho que el tercio inferior (0); tercio superior más ancho que el tercio inferior (1)
6. Apice de la lámina	acuminado (0); atenuado (1); obtuso (2)
7. Apice de la lámina	espinoso (0); mucronado (1)
8. Nerviación en la base de lámina	3-nervia (0); 1-nervia (1)
9. Apice de las filarias	mucronado (0); espinoso (1)
10. Base del capítulo	sésil o subsésil (0); pedunculada (1)
11. Número de flores del disco	una (0); tres (1)
12. Tipo de corola de las flores del disco	tubulosa (0); bilabiada (1); ligulada (2); subligulada (3)
13. Simetría de la corola de las flores del disco	actinomorfa (0); levemente cigomorfa (1); cigomorfa (2)
14. Longitud de los dientes de las corolas del disco	menos de un tercio de longitud de la corola (0); más de la mitad de la longitud de la corola (1)
15. Pubescencia en la región de inserción de los filamentos en las flores del disco	presencia (0); ausencia (1)
16. Sexualidad de las flores del disco	perfecta (0); imperfecta (1)
17. Filamentos de los estambres de las flores del margen	libres (0); parcialmente fusionados (1); fusionados (2)
18. Filamentos de los estambres de las flores del disco	libres (0); fusionados (1)
19. Inserción de los filamentos en las flores del disco	entre la garganta y la base (0); garganta (1); base (2); garganta y parte media (3)
20. Base de las anteras de las flores del margen	decurrente (0); cortamente sagitada (1)
21. Base de las anteras de las flores del disco	cortamente sagitada (0); decurrente (1)
22. Tipo del grano polen	no lofado (0); lofado (1)
23. Simetría del grano del polen	radiosimétrico (0); radioasimétrico (1)
24. Tipo de papus de las flores del disco	cortamente plumoso (0); barbelado (1); simple (2)
25. Longitud del papus de las flores del disco	más largo que el tubo de la corola (0); igual o menor que el tubo de la corola (1)

(*B. laxa*). Don consideró al género *Diacantha* Less. como un sinónimo de *Barnadesia.* En 1833, Lessing ubicó al género *Barnadesia* en la tribu Mutisieae. De Candolle (1836) trató 8 especies de *Barnadesia* en cuatro secciones, de acuerdo a caracteres florales: (1) ***Diacanthoides*** (***B. spinosa, B. dombeyana, B. media, B. reticulata, B. lanceolata***); (2) ***Bacazia*** (***B. corymbosa***); (3) ***Diacantha*** (***B. arborea***); (4) ***Penthea*** (***B. laxa***). En 1841, Spach elevó la sección ***Penthea*** D. Don a la categoría de género y lo ubicó en la secc. Barnadésiées Cass. Bentham and Hooker (1873) crearon cinco subtribus para la tribu Mutisieae, siendo una de ellas la subtribu Barnadesinae.

Desde 1873 hasta 1938, fueron asociados con *Barnadesia* 20 nombres (Spruce, 1873; Grisebach, 1879; Kuntze, 1893; Hieronymus, 1895, 1901; Rusby, 1896–1899, 1905–1907; Löfgren, 1897; Muschler, 1914; Blake, 1925; Benoist, 1938). Ferreyra (1964) describió cuatro especies nuevas de *Barnadesia*: *B. blakeana, B. hutchisoniana, B. macbridei* y *B. wurdackii* para Perú. Finalmente, Chung (1965) en su tratamiento del género *Barnadesia* no incluyó las especies descriptas por Ferreyra en el año anterior y consideró 21 especies. Dividió a *Barnadesia* en 2 subgéneros y 5 secciones: subgén. *Penthea* (secc. *Pauciflora* y secc. *Penthea*) y subgén. ***Barnadesia*** (secc. ***Bacasia***, secc. ***Diacantha*** y secc. ***Barnadesia***). Describió una nueva especie, ***B. chachapoyasensis*** para Perú, y 9 variedades (***B. glomerata*** var. ***mucronata, B. glomerata*** var. ***distincta, B. polyacantha*** var. ***velutina, B. polyacantha*** var.

Tabla 2. Matriz de datos. El número e carácter corresponde al usado en el texto y en el cladograma.

	Carácter																								
										1										2					
Taxon	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5
Fulcaldea laurifolia	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0
Huarpea andina	2	1	0	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	?	?	1	0	0	1
B. aculeata	0	0	1	1	?	?	1	?	0	0	0	3	1	1	0	0	2	0	1	0	0	1	1	1	0
B. arborea	?	0	1	1	1	?	?	?	?	0	1	1	2	0	0	0	2	0	1	0	0	1	1	1	0
B. blakeana	0	0	1	1	?	1	0	?	1	0	1	1	2	0	1	0	1	0	1	0	0	1	1	1	0
B. caryophylla	0	0	1	1	?	?	1	0	0	0	1	?	2	0	0	0	0	0	1	0	0	1	1	2	0
B. corymbosa	?	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	2	0	2	0	0	1	0	0	1
B. dombeyana	0	0	1	1	1	?	?	?	?	0	1	?	2	?	1	0	2	0	1	0	0	1	1	1	0
B. glomerata	0	0	1	1	?	1	?	0	?	0	0	?	2	0	1	0	0	0	1	1	1	1	0	2	1
B. horrida	0	0	1	1	1	1	0	?	1	0	0	3	1	1	0	0	0	0	1	0	0	1	1	1	0
B. jelskii	0	0	1	1	?	?	?	?	?	0	0	1	2	0	0	0	2	0	1	0	0	1	1	1	0
B. lehmannii	0	0	1	1	?	?	0	0	0	0	1	1	2	0	0	0	0	0	1	?	?	1	1	2	0
B. macbridei	0	0	1	1	?	1	0	0	1	0	0	1	2	?	0	0	0	0	3	0	0	1	1	2	0
B. macrocephala	0	0	1	1	1	?	0	?	1	0	0	3	1	1	0	0	0	0	1	0	0	1	1	1	0
B. odorata	0	0	1	1	?	1	?	0	?	0	1	2	2	0	1	0	0	0	1	1	1	1	1	2	1
B. parviflora	1	0	0	0	?	?	1	0	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0
B. polyacantha	0	0	1	1	?	?	1	0	1	0	1	2	2	0	0	0	0	0	1	1	1	1	0	2	0
B. pycnophylla	0	0	1	1	1	1	0	?	1	0	0	3	1	1	1	0	0	0	1	0	0	1	1	1	0
B. reticulata	0	0	1	1	1	?	?	0	?	0	1	1	2	0	0	0	1	0	1	0	?	1	1	2	0
B. spinosa	?	0	1	1	1	?	?	0	?	0	1	?	2	0	0	0	2	1	1	0	0	1	0	1	0

villosa, B. polyacantha var. *attenuata, B. lehmannii* var. *ciliata, B. lehmannii* var. *angustifolia, B. jelskii* var. *acuta* y *B. spinosa* var. *recurvata).*

UBICACIÓN SISTEMÁTICA

La subfamilia Barnadesioideae, tribu Barnadesieae, exclusiva de América del Sur, se caracteriza morfologicamente por presentar espinas axilares en sus tallos y pelos barnadesioideos (Cabrera, 1959, 1961, 1977; Bremer, 1987; Bremer & Jansen, 1992) en corolas, aquenios y papus, y molecularmente por la ausencia de una inversión en la molécula de ADN del cloroplasto, registrada en tres géneros *Barnadesia, Chuquiraga* y *Dasyphyllum.* Dicha inversión se halla en 250 géneros pertenecientes a las dos subfamilias restantes (Jansen & Palmer, 1987, 1988). La subfamilia Barnadesioideae comprende 9 géneros y ca. de 90 especies.

Barnadesia está caracterizada por tratarse de arbustos y árboles, siempre espinosos, siendo una novedad evolutiva para el género los filamentos de los estambres fusionados en varias de sus especies.

El género más afin a *Barnadesia* es *Huarpea,* de los Andes de San Juan (Argentina), con el cual comparte el polen psilolofado y las bases de las anteras decurrentes o cortamente sagitadas. *Huarpea* se diferencia de *Barnadesia* por su hábito subarbustivo y la ausencia de espinas en sus tallos. Ambos géneros conforman el grupo más avanzado de la subfamilia Barnadesioideae (Bremer, 1994).

CLAVE PARA LOS GÉNEROS DE LA SUBFAMILIA BARNADESIOIDEAE

1a. Hierbas.
  2a. Anteras obtusas en la base .... *Schlechtendalia*
  2b. Anteras largamente sagitadas.
    3a. Receptáculo plano; papus plumoso .... *Doniophyton*
    3b. Receptáculo ligeramente convexo; papus lanceolado con margen ciliado .... *Duseniella*
1b. Subarbustos, arbustos o árboles.
  4a. Capítulos unifloros .... *Fulcaldea*
  4b. Capítulos plurifloros.
    5a. Capítulos heteromorfos; polen psilolofado.
      6a. Arbustos o árboles, de 0.60–20 m de alto, espinosos .... *Barnadesia*
      6b. Subarbusto, hasta 5 cm de alto, inerme .... *Huarpea*
    5b. Capítulos homomorfos; polen nunca psilolofado.
      7a. Anteras cortamente sagitadas (caudículas ca. 0.5 mm); apéndice conectival bilobado o emarginado .... *Dasyphyllum*

7b. Anteras largamente sagitadas (caudículas ca. 1–4 mm); apéndice conectival lanceolado y agudo.
  8a. Corolas con labio externo 4-lobado o 4-dentado; inserción del filamento en la garganta de la corola .... *Arnaldoa*
  8b. Corola con el labio externo con incisiones más profundas; inserción del filamento en la base del tubo de la corola .... *Chuquiraga*

RESULTADOS

MORFOLOGÍA Y ANATOMÍA

Todas las especies de *Barnadesia* son plantas leñosas, en su mayoría arbustivas. *Barnadesia arborea* y *B. corymbosa* pueden ser también arbóreas, en tanto *B. parviflora* es exclusivamente arbórea, llegando hasta los 20 m de altura.

Los tallos presentan ramificación pseudomonopodial, con ramas de crecimiento indefinido (macroblastos) y ramas con crecimiento definido (braquiblastos); pueden ser glabros, subglabros o densamente pubescentes.

Transección del tallo. La zona cortical está formada por epidermis, colénquima angular y parénquima colenquimático. La zona vascular está constituida por floema primario representado por fibras dispuestas en casquetes discontinuos, floema secundario, xilema secundario formando un cilindro continuo y polos de xilema primario en la parte más interna. La médula presenta células parenquimáticas esclerificadas.

Todas las especies de *Barnadesia* son espinosas. Estas espinas axilares se ubican de a pares (geminadas) o en fascículos, comunmente por arriba o a los lados de las hojas, o por debajo de yemas de braquiblastos o de macroblastos. Se tratan de estructuras vascularizadas, macizas o huecas en la madurez, con pelos barnadesioides en la base. Si bien Cabrera (1959), describió a las espinas de *Dasyphyllum* como carentes de haces conductores y como "un apéndice del pulvínulo o hipopedio donde se insertan las hojas," tanto en *Barnadesia* como en *Chuquiraga* (Ezcurra, 1985) se tratan de espinas vascularizadas.

En cuanto al origen de estas estructuras, Troll (1967) como Goebel (1932) sugirieron un origen apartir de profilos. Asimismo, Ezcurra (1985) para *Chuquiraga*, sustentó un origen foliar sobre la base de la ausencia de nudos, y por la presencia espinas foliáceas en *C. jusseui.*

La disposición de las hojas varía desde hojas alternas hasta hojas agrupadas en fascículos. Las hojas son sésiles o subsésiles, raramente pecioladas; con láminas coriáceas; oblanceoladas, obovadas o elípticas; enteras en el margen, mucronadas o espinosas en el ápice; el indumento puede faltar o ser desde escaso hasta denso.

Transección de la hoja. Es plana o involuta, ocasionalmente con los márgenes levemente involutos. El mesófilo es dorsiventral, formado por una o dos capas de parénquima en empalizada en la cara superior y parénquima esponjoso en la cara inferior. El haz vascular medio está rodeado por una vaina parenquimática de una o dos capas. Los haces vasculares colaterales, el haz medio y los haces vasculares primarios poseen casquetes esclerenquimáticos adaxiales y abaxiales. También suele haber esclerénquima en el margen de las hojas. Esta estructura foliar es similar a la descripta por Cabrera (1959) para algunas especies de *Dasyphyllum.* (Fig. 1A, B.)

Estomas presentes en la cara inferior (hojas hipostomáticas), ligeramente elevados con respecto a las restantes células epidérmicas. Los estomas son anomocíticos, y estan rodeados por 5–7 células epidérmicas. (Fig. 2Y, Z.)

Se diferencian los siguientes tipos de pelos:

Pelo barnadesioide (Cabrera, 1959, 1961, 1977; Bremer, 1987; Bremer & Jansen, 1992): pie unicelular, semejante a las restantes células epidérmicas, cuerpo formado por dos células, una basal y corta, con paredes gruesas, y una célula apical larga, de paredes delgadas. (Fig. 2V.)

Pelo birramoso o malpighiáceo asimétrico: pie unicelular, semejante a las restantes células epidérmicas, cuerpo formado por una célula basal corta de paredes gruesas, y una célula apical alargada con extremos aguzados de inserción dorsal (presente sólo en las hojas). (Fig. 2W.)

Pelo glandular uniseriado: 2–10-celular, con la célula terminal redondeada en el ápice (presentes en hojas y filarias). (Fig. 2X.)

Los capítulos son sésiles, subsésiles o pedunculados. Homógamos (con flores perfectas) o heterógamos (con flores marginales perfectas y flores del disco imperfectas). La disposición de los capítulos en las especies de *Barnadesia* varía desde: (a) solitarios o geminados, (b) cimas racemiformes hasta (c) cimas corimbiformes. (Fig. 2E–H.)

Los involucros son acampanados, ligeramente cilíndricos o turbinados, con 6–14 series de brácteas involucrales.

Las brácteas involucrales son glabras en el dorso sólo en *B. lehmannii* var. *ciliata,* comúnmente subglabras o pubescentes en el dorso, y siempre con márgenes ciliados; las exteriores ovado-acuminadas, gradualmente más largas hacia el interior, las

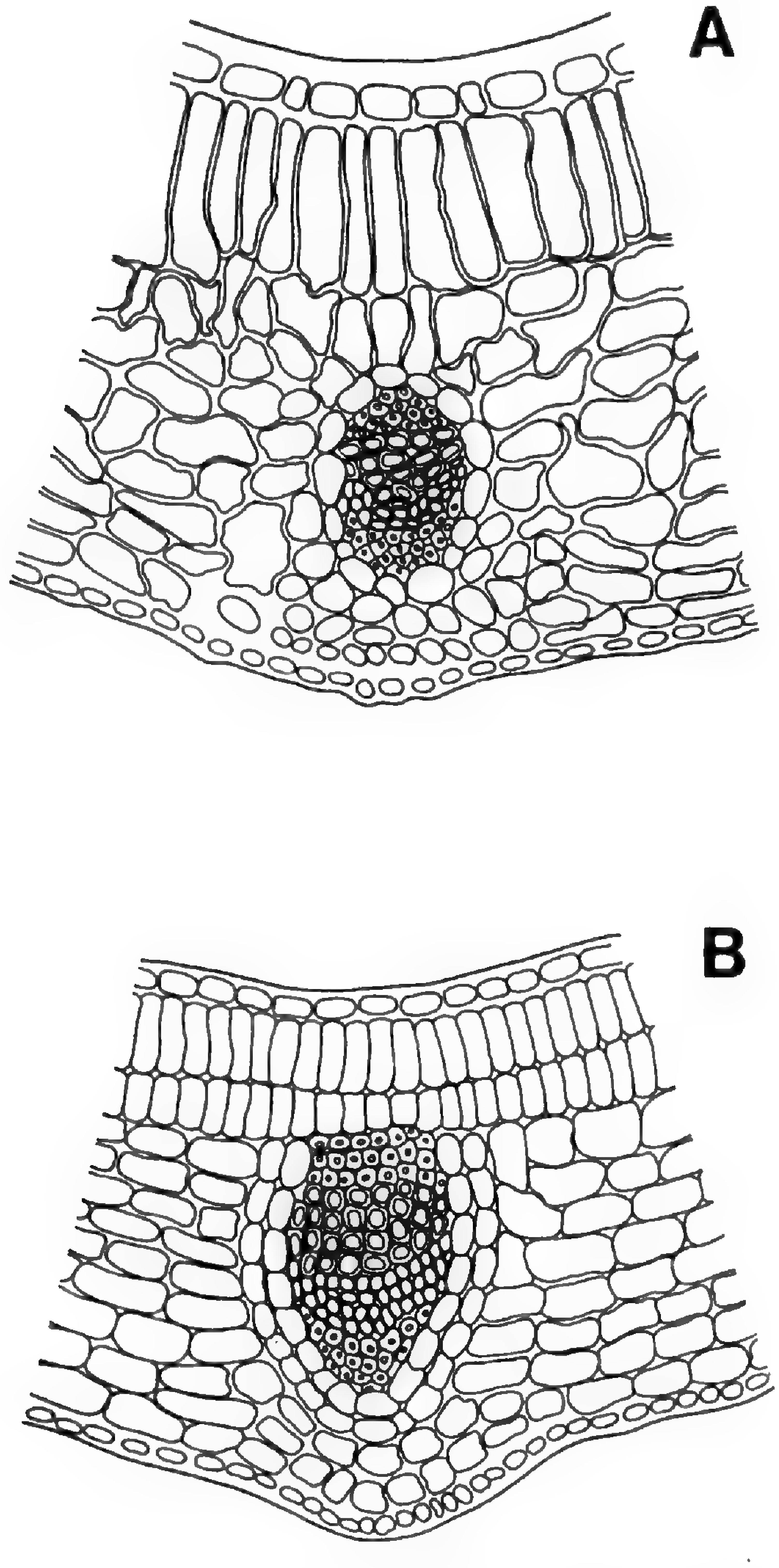


Figura 1. Transección de la hoja. Mesófilos dorsoventrales. —A. *Barnadesia dombeyana* (*López & Sagástegui 2755*, LP). —B. *B. spinosa* (*Schultes & Villarreal 7912*, GH).

intermedias linear-lanceoladas y las internas linear-obovadas; mucronadas o espinosas.

Las corolas son de color blanco, rosado, rojo, morado, azul o violáceo. Densamente cubiertas de pelos barnadesioideos en la cara externa, comunmente en la garganta de la corola de las flores del disco (raro en las flores del margen), y en *B. corymbosa* en la base interna del tubo de la corola del disco. Los capítulos presentan corolas ligeramente dimorfas, dimorfas o trimorfas.

La corola de las flores del margen es siempre bilabiada (4+1), labio interno filiforme e indiviso (Fig. 2A) y de mayor tamaño que las corolas de las flores del disco.

Los distintos tipos de corolas de las flores del disco representan el carácter más variable del género *Barnadesia*. Siguiendo el criterio de Cabrera (1959), el cual consideró a las corolas actinomorfas como las más primitivas, y de las cuales evolucionarían las corolas bilabiadas y por último las corolas liguladas, en *Barnadesia* se pueden interpretar los distintos tipos de corolas con el siguiente esquema evolutivo: a partir de una corola tubular actinomorfa presentes en *B. corymbosa* (5-lobada) y en *B. parviflora* (4-lobada o 3-lobada), se pasa a las corolas bilabiadas 4+1 ó 3+1 de *B. arborea, B. blakeana, B. jelskii, B. lehmannii, B. macbridei* y *B. reticulata* (Fig. 2C), y de estas últimas a una corola subliguda (5-secta, con una incisión más profunda y levemente cigomorfa) en *B. aculeata, B. horrida, B. macrocephala* y *B. pycnophylla* (Fig. 2B), o a una corola ligulada 5-lobada de *B. odorata* y *B. polyacantha* (Fig. 2D).

Esta hipótesis coincidente con lo propuesto por Bremer (1994), y no asi con lo propuesto por Jeffrey (1977) quien sugirió a las corolas bilabiadas como primitivas. Tanto *Barnadesia caryophylla, B. dombeyana, B. glomerata* y *B. spinosa* presentan corolas bilabiadas y liguladas en las flores el disco.

El androceo está formado por 5 estambres en las flores del margen; en las flores del disco 5, 4 ó 3 estambres. La base de las anteras puede ser decurrente o cortamente sagitada, con o sin papilas (Fig. 2J, K). El conectivo se prolonga en forma de asta, y es levemente triangular.

Los filamentos de los estambres de las flores del margen, en su porción libre de la corola pueden estar libres entre sí (Fig. 2L), parcialmente fusionados en *B. blakeana* y *B. reticulata* (Fig. 2M) o totalmente fusionados formando un tubo estaminal en *B. aculeata, B. arborea, B. corymbosa, B. dombeyana* y *B. jelskii* (Fig. 2N). *Barnadesia spinosa* es la única especie que presenta tubo estaminal en ambos tipos de flores.

La inserción de los filamentos en las flores del margen siempre es en la garganta de la corola. En las flores del disco en la mayoría de las especies la inserción de los filamentos es en la garganta de la corola (Fig. 2Ñ), en *B. macbridei* tres filamentos se insertan en la parte media de la corola y dos en la garganta de la corola (Fig. 2O), o todos los filamentos insertos en la base de la corola en *B. corymbosa* (Fig. 2P).

Las flores del margen son perfectas, mientras que las flores del disco pueden ser perfectas o imperfectas por atrofia del gineceo *(B. parviflora)* o del androceo o gineceo (*B. corymbosa*).

Los aquenios de las flores del margen son cilíndricos o raramente algo turbinados; los aquenios de las flores del disco son siempre turbinados y más

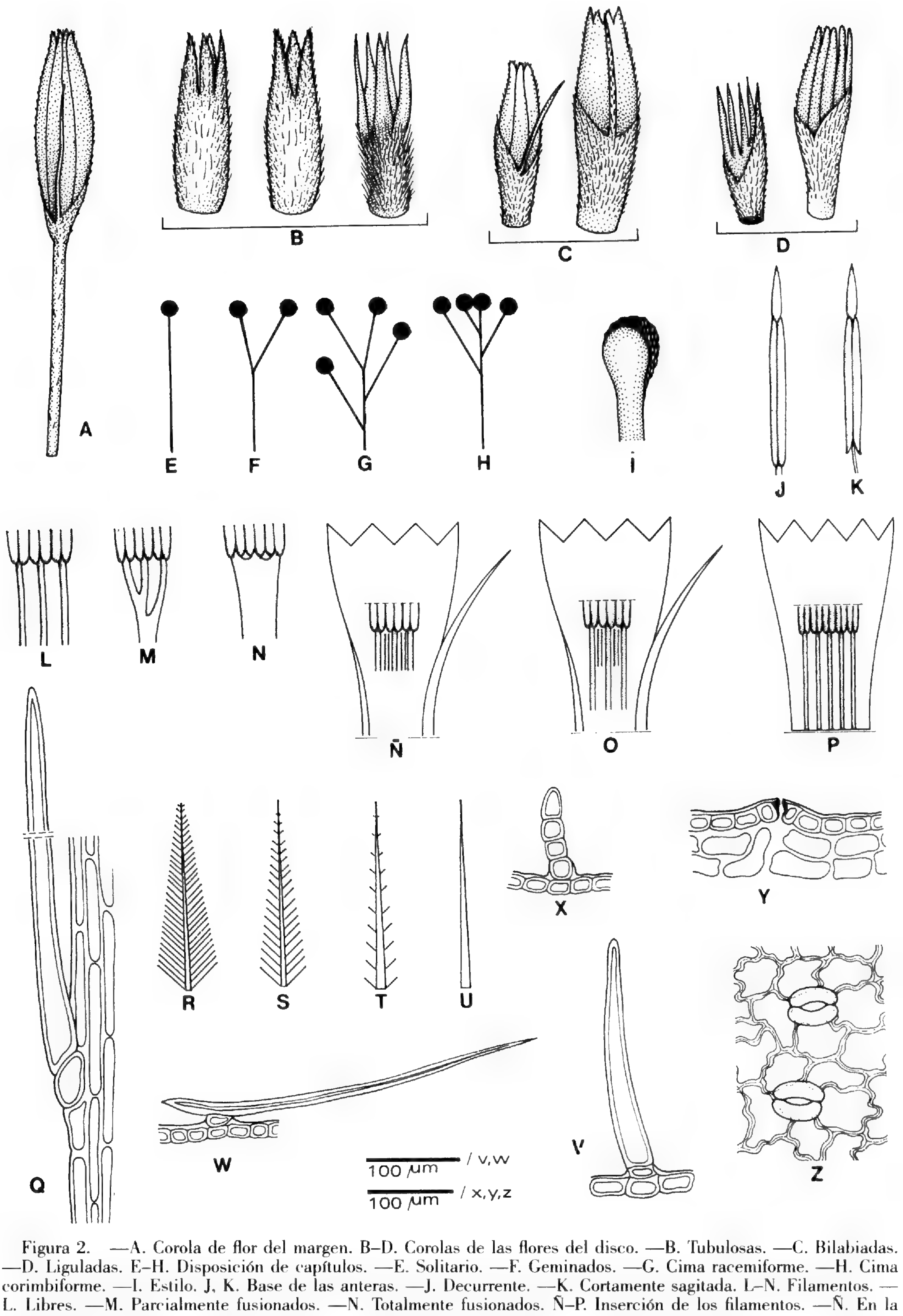


Figura 2. —A. Corola de flor del margen. B–D. Corolas de las flores del disco. —B. Tubulosas. —C. Bilabiadas. —D. Liguladas. E–H. Disposición de capítulos. —E. Solitario. —F. Geminados. —G. Cima racemiforme. —H. Cima corimbiforme. —I. Estilo. J, K. Base de las anteras. —J. Decurrente. —K. Cortamente sagitada. L–N. Filamentos. —L. Libres. —M. Parcialmente fusionados. —N. Totalmente fusionados. Ñ–P. Inserción de los filamentos. —Ñ. En la garganta de la corola. —O. Dos en la garganta y tres en la parte media. —P. En la base de la corola. —Q. Detalle de la cerda del papus. R–U. Tipos de papus. —R. Plumoso. —S. Cortamente plumoso. —T. Barbelado. —U. Simple. V–Z. Pelos. —V. Barnadesioide. —W. Malpighiáceo. —X. Glandular. —Y. Corte transversal de epidermis. —Z. Estomas.

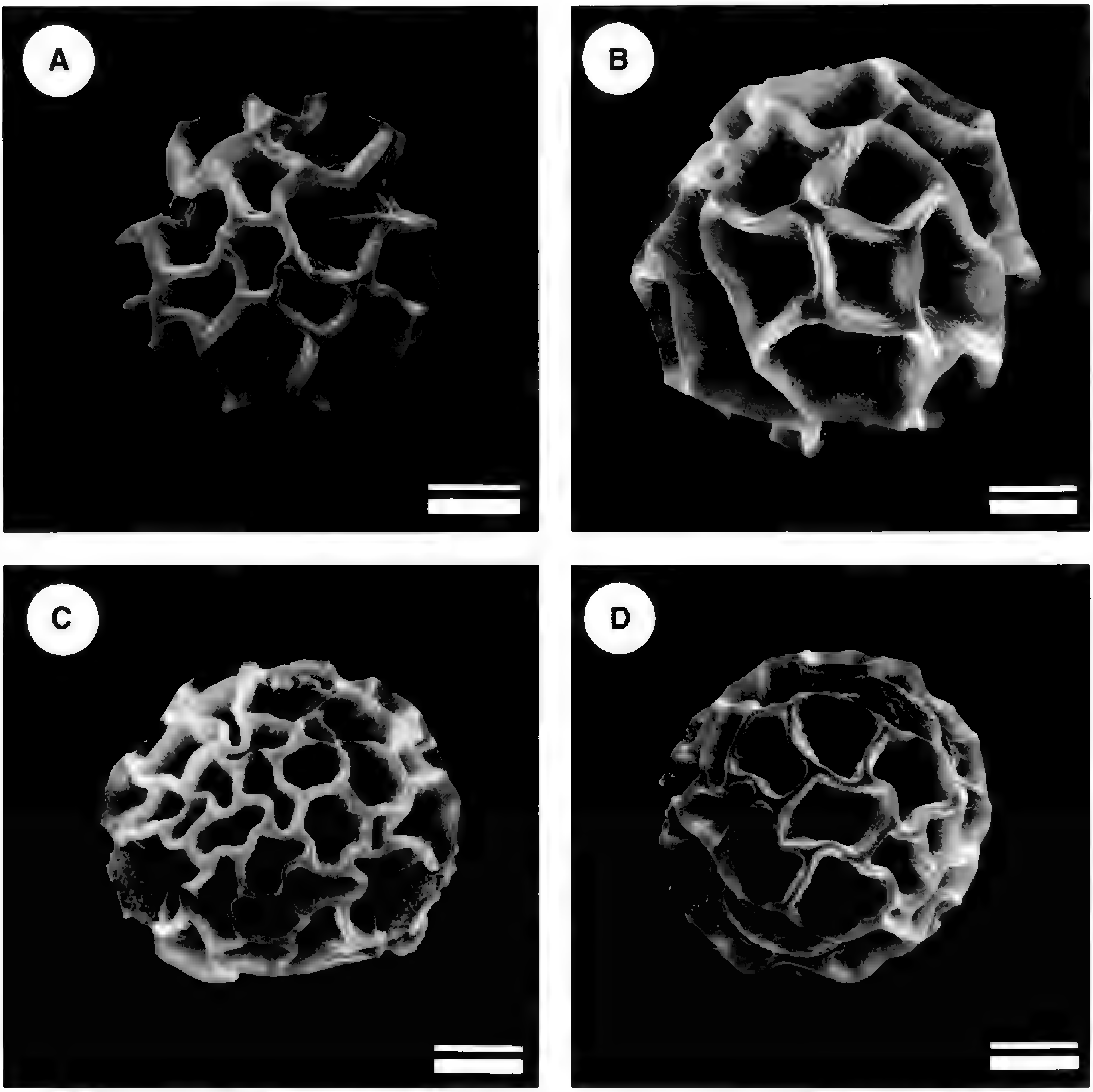


Figura 3. Polen. A, B. *Barnadesia parviflora*. Plan de lagunas radiosimétrico: —A. Vista polar. —B. Vista ecuatorial. C, D. *B. pycnophylla*. Plan de lagunas radioasimétrico: —C. Vista polar. —D. Vista ecuatorial.

grandes que los aquenios de las flores del margen. Los aquenios están densamente cubiertos por pelos barnadesioides.

Las cerdas del papus de las flores del margen son plumosas (Fig. 2R) y las cerdas de las flores del disco pueden ser cortamente plumosas, barbeladas o simples (Fig. 2S–U).

Las cerdas barbeladas y plumosas, poseen pelos barnadesioideos con una célula de articulación (Fig. 2Q).

Las cerdas barbeladas y las cerdas simples al secarse se curvan hacia afuera.

La longitud del papus puede ser menor a igual, o de mayor longitud que el tubo de la corola.

El polen de *Barnadesia* fue estudiado por Wodehouse (1929, 1935), Skvarla et al. (1977), Gamerro (1985) y Urtubey (1997).

Los granos de polen son tricolporados, subesferoidales a esferoidales, psilolofados con plan de distribución de lagunas radiosimétrico (también presente en *Huarpea*: Gamerro, 1985) o radioasimétrico presente en la mayoría de las especies (Fig. 3A–D). La endoapertura es larga, lolongada; comunmente sobre la membrana apertural se observan placas de exina (Fig. 3C). El fondo de las lagunas es escábrido y las superficies de las crestas lisas. La sexina es esponjosa, y se adelgaza hacia el fondo de las lagunas; la nexina es homogénea y se adelgaza hacia las aberturas. El tamaño de los granos de polen es: para las flores del margen diámetro polar de 42.50–81.00 µm y el diámetro ecuatorial es de 40.00–82.50 µm y, para las flores del disco el diámetro polar de 42.50–67.50 µm y el diámetro ecuatorial de 44–74 µm.

El polen psilolofado presente en *Barnadesia* y *Huarpea,* constituye un caracter avanzado para la subfamilia (Bremer, 1994).

BIOLOGÍA FLORAL

La polinización ornitófila por colibríes ha sido mencionada para *Barnadesia* y *Chuquiraga* (Müller, 1873; Leppik, 1977; Ezcurra, 1985). Sin embargo, Galeto (1995) sugirió la polinización esfingófila (mariposas nocturnas) sobre la base del color blanco y perfume de las corolas de *B. odorata;* no obstante, indica que la concentración de azúcar presente en esta especie corresponde tanto a polinizaciones esfingófilas como ornitófilas.

A través de observaciones de campo pude corroborar la visita de colibríes a *B. dombeyana* en Perú, y en etiquetas de ejemplares de herbario se menciona que *Barnadesia caryophylla* es visitada por *Agleactis cupripennis* y *Lesbia victoria; B. corymbosa* es visitada por especies del género *Eriocnimus.* Asimismo, observé la presencia de guias nectaríferas en *B. odorata* y *B. polyacantha.*

CITOLOGÍA

Los números cromosómicos básicos reportados para *Barnadesia* son: $n = 25$ (*B. spinosa;* Heiser, 1963), $n = 12, 24$ (*B. arborea*; Olsen, 1980; Strother & Panero, 1994), $n = 26$ (*B. odorata;* Cristóbal, 1986), $2n = 50–52$ (*B. lehmannii;* Strother & Panero, 1994; Stuessy et al., 1996), $n = 48$ (*B. parviflora;* Stuessy et al., 1996). Recientemente Wulff (1995) describió el cariótipo de *B. odorata,* el cual está compuesto por: 5 pares de cromosomas submetacéntricos, 11 subtelocéntricos y 10 telocéntricos.

Hasta el presente se conocen los números cromosómicos de especies en otros cuatro géneros de los nueve que constituyen la subfamilia Barnadesioideae (Wulff, 1990; Diers, 1961; Cialdella & López, 1981; Stuessy & Sagástegui, 1993): *Chuquiraga* (*C. avellanedae, C. echegarayi, C. erinacea* subsp. *hystrix, C. oppositifolia, C. spinosa* subsp. *australis, C. rosulata, C. ruscifolia*) con $n = 27$; *Doniophyton* (*D. anomalum* y *D. weddellii*; Katinas & Stuessy, 1997) con $n = 25$ y $n = 24$; *Schlechtendalia* con $n = 8$; por último *Arnaldoa weberbaueri* con $n = 24–27$.

DISTRIBUCIÓN Y HÁBITAT

El género *Barnadesia* es exclusivo de América del Sur. La mayor concentración de especies se encuentra en Perú (*B. arborea, B. blakeana, B. caryophylla, B. corymbosa, B. dombeyana, B. horrida, B. jelskii, B. lehmannii, B. macbridei, B. polyacantha, B. pycnophylla* y *B. reticulata*), en Bolivia (*B. caryophylla, B. corymbosa, B. glomerata, B. macrocephala, B. odorata, B. polyacantha* y *B. pycnophylla*) y en Ecuador (*B. aculeata, B. arborea, B. jelskii, B. lehmannii* y *B. parviflora*), disminuyendo hacia el norte hasta Colombia (*B. parviflora* y *B. spinosa*) y hacia el sur hasta el NW de la Argentina (*B. odorata*) y Brasil (*B. caryophylla*).

Desde el punto de vista biogeográfico (Cabrera & Willink, 1973) las especies ocupan los dominios Andino–Patagónico, Amazónico y Chaqueño. En el dominio Andino–Patagónico crecen 13 de las 18 especies: *B. dombeyana, B. macrocephala, B. parviflora, B. polyacantha, B. pycnophylla* y *B. spinosa* llegan a los bosques que limitan con la provincia Altoandina. *Barnadesia blakeana, B. lehmannii* y *B. reticulata* crecen en la provincia del Desierto, caracterizada por clima seco, y cálido. *Barnadesia corymbosa, B. glomerata, B. horrida, B. macrocephala, B. odorata, B. polyacantha,* y *B. pycnophylla* crecen en la provincia Puneña de clima frío y seco.

En el dominio Amazónico, crecen 11 especies: *B. caryophylla, B. dombeyana, B. macbridei* y *B. parviflora* en la provincia Amazónica; *B. caryophylla, B. odorata, B. parviflora, B. polyacantha* y *B. pycnophylla* en la provincia de las Yungas; y *B. lehmannii* en la provincia Pacífica. Estas tres provincias se caracterizan por clima cálido y húmedo. Mientras que *B. spinosa* crece en la provincia de la Sabana y *B. caryophylla* en la provincia del Cerrado, ambas con clima cálido y marcada estación seca. *Barnadesia aculeata, B. arborea* y *B. spinosa* se encuentran en la provincia del Páramo, con clima frío y húmedo. Por último, en el dominio Chaqueño, dentro de la provincia Chaqueña, se hallan *B. corymbosa, B. glomerata, B. odorata, B. polyacantha* y *B. pycnophylla* donde el clima es continental con lluvias estivales (Fig. 4).

FILOGENIA Y CLASIFICACIÓN INFRAGENÉRICA

Las 18 especies de *Barnadesia* constituyen un grupo monofilético sustentado por las siguientes sinapomorfías: hojas obovadas u oblanceoladas y filamentos de los estambres de las flores del margen insertos en la garganta de la corola.

Barnadesia y su género hermano monotípico *Huarpea* ocupan una posición avanzada en los cladogramas de la subfamilia Barnadesioideae (Bre-

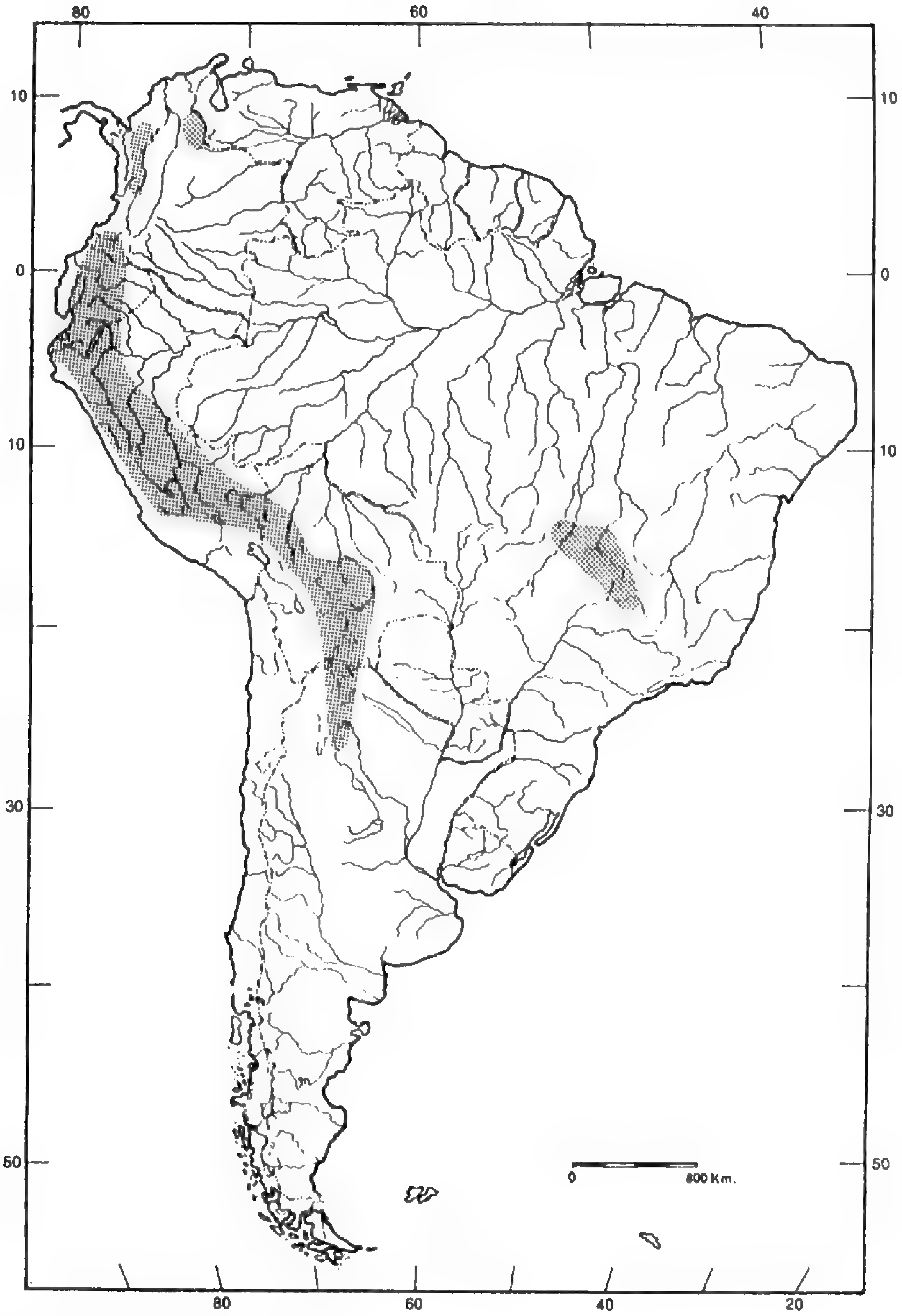


Figura 4. Distribución de *Barnadesia* Mutis.

mer, 1994; Stuessy et al., 1996), donde constituyen un grupo monofilético definido por las anteras decurrentes en la base, apéndice conectival agudo, tejido endotecial con adelgazamientos radiales y el polen psilolofado (Bremer, 1994) y por los capítulos heterógamos, corolas bilabiadas 4+1 con lobulos lineales, ramas estigmáticas lobuladas, redondeadas y alargadas, y estilo liso (Stuessy et al., 1996).

A partir de la matriz de datos (Tabla 2) se obtuvieron 12 árboles de 50 pasos de longitud, índice de consistencia de 0.60 e índice de retención de 0.74. La monofilia de *Barnadesia* está sustentada por las sinapomorfías 5.1 (hojas obovadas u oblanceoladas) y 19.1 (inserción de los filamentos de los estambres de las flores del margen en la garganta de la corola). El árbol de consenso estricto (Fig. 5) muestra 10 grupos monofiléticos que se repiten en los 12 árboles: (1) grupo corymbosa: (*B. corymbosa* y *B. parviflora*); (2) grupo macbridei: todos los taxa excepto (*B. corymbosa* y *B. parviflora*); (3) (*B. caryophylla*, *B. lehmannii*, *B. reticulata*, (*B. polyacantha*, (*B. glomerata* y *B. odorata*))); (4) (*B. polyacantha*, (*B. glomerata* y *B. odorata*)); (5) (*B. glomerata* y *B. odorata*); (6) (*B. macbridei*, (*B. jelskii*, (*B. arborea*, *B. spinosa*, (*B. blakeana*, y *B. dombeyana*)), (*B. aculeata*, *B. horrida*, *B. macrocephala* y *B. pycnophylla*)); (7) (*B. jelskii*, (*B. arborea*, *B. spinosa*, (*B. blakeana*, y *B. dombeyana*)), (*B. aculeata*, *B. horrida*, *B. macrocephala* y *B. pycnophylla*)); (8) (*B. aculeata*, *B. horrida*, *B. macrocephala* y *B. pycnophylla*); (9) (*B. arborea*, *B. spinosa*, (*B. blakeana*, y *B. dombeyana*)); y (10) (*B. blakeana*, y *B. dombeyana*).

Los 12 árboles obtenidos pueden ser simplificados en cuatro topologías, dado que el Hennig86 muestra árboles con ramas no justificadas o que

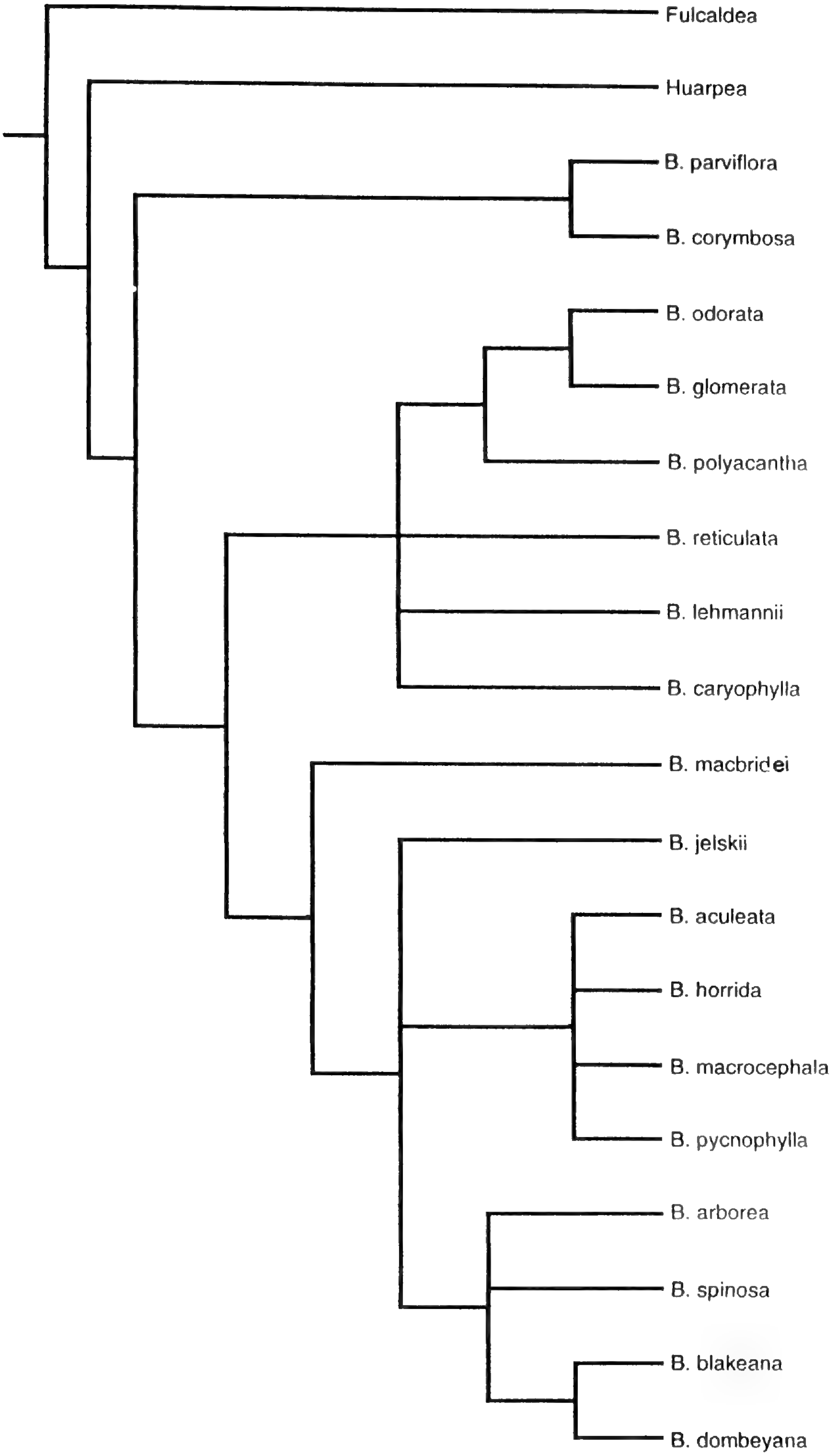


Figura 5. Arbol de consenso estricto.

difieren en la interpretación de alguno de los caracteres (Carr et al., 1990). En los 4 cladogramas aparecen simultáneamente 9 grupos monofiléticos: (1) (*B. corymbosa* y *B. parviflora*); (2) todos los taxa excepto (*B. corymbosa* y *B. parviflora*); (3) (*B. caryophylla, B. lehmannii, B. reticulata,* (*B. polyacantha,* (*B. glomerata* y *B. odorata*))); (4) (*B. polyacantha,* (*B. glomerata* y *B. odorata*)); (5) (*B. glomerata* y *B. odorata*); (6) (*B. macbridei,* (*B. jelskii,* (*B. arborea, B. spinosa,* (*B. blakeana* y *B. dombeyana*)), (*B. aculeata, B. horrida, B. macrocephala* y *B. pycnophylla*))); (7) (*B. aculeata, B. horrida, B. macrocephala* y *B. pycnophylla*); (8) (*B. arborea, B. spinosa,* (*B. blakeana,* y *B. dombeyana*)); y (9) (*B. blakeana,* y *B. dombeyana*).

La Figura 6 muestra los cuatro árboles con el mismo número de pasos donde los cambios de las configuraciones resultan del carácter 7 (ápice de las hojas) y del carácter 17 (filamentos de los estambres de las flores del margen). El carácter 7 es no comparable para *B. reticulata.* La presencia del ápice mucronado ocurre en la Figura 7A y B. Las distintas posiciones del carácter 17 (filamentos de los estambres de las flores del margen) ocurren: la presencia de los filamentos fusionados en forma paralela en *B. aculeata* y el grupo *B. jelskii, B. arborea, B. spinosa, B. blakeana* y *B. dombeyana* (Fig. 7C). En la Figura 7D ocurre en forma paralela en *B. jelskii, B. aculeata, B. arborea, B. spinosa, B. blakeana, B. dombeyana.* En tanto la condición filamentos libres revierte en el grupo *B. horrida, B. macrocephala* y *B. pycnophylla.*

De los cuatro árboles igualmente simples, fue selecionado uno para ilustrar la evolución de los caracteres (Fig. 8).

La topología del cladograma de consenso confirma la monofilia de *Barnadesia* como un género independiente, afín a *Huarpea.* Esta afinidad ya fue señalada por Cabrera (1951), sobre la base de las corolas, la base de las anteras, estilo y polen.

En el género *Barnadesia* existen dos grupos monofiléticos principales: (1) formado por dos especies *B. corymbosa* y *B. parviflora,* justificado por las hojas pecioladas, ápice de la hoja mucronado y capítulos pedunculados; y (2) formado por las especies restantes, *B. macbridei, B. lehmannii, B. caryophylla, B. reticulata, B. polyacantha, B. glomerata, B. odorata, B. jelskii, B. aculeata, B. horrida, B. macrocephala, B. pycnophylla, B. arborea, B. spinosa, B. blakeana* y *B. dombeyana,* sustentado por su hábito arbustivo, hojas reunidas en fascículos, ápice atenuado, flores del disco con corolas bilabiadas, cigomorfas y perfectas, polen radioasimétrico y papus barbelado.

CLASIFICACIÓN (FIG. 9)

La clasificación infragenérica de *Barnadesia* propuesta por Chung (1965) no se corresponde con los resultados del análisis cladístico. Los subgéneros *Penthea* I. C. Chung (secciones *Pauciflora* y *Penthea*) y *Barnadesia* (secciones *Bacasia, Diacantha* y *Barnadesia*) no forman grupos monofiléticos en el presente análisis. La sección *Pauciflora* I. C. Chung (*) es polifilética por incluir a *B. parviflora* y *B. glomerata,* sólo es monofilético el grupo formado por *B. horrida, B. macrocephala* y *B. pycnophylla.* Las especies de la sección *Penthea* D. Don (▲) constituyen un grupo parafilético por incluir a *B. lehmannii, B. caryophylla, B. polyacantha* y *B. odorata* y no incluir a *B. reticulata* y a *B. glomerata.* Las especies de la sección *Diacantha* (Less.) DC. (●) constituyen un grupo polifilético por incluir a *B. reticulata, B. arborea* y *B. dombeyana,* y es parafilética por no incluir a *B. spinosa* y *B. blakeana. Barnadesia corymbosa,* sección *Bacasia* (■), se encuentra en la base del cladograma, mientras que *B. aculeata* junto con *B. jelskii* comparten un grupo monofilético con las especies de las secciones *Diacantha* (*B. dombeyana, B. arborea*), *Pauciflora* (*B. horrida, B. macrocephala, B. pycnophylla*) y *Barnadesia* (□) (*B. spinosa*). Sobre la base de los resultados obtenidos se establece una nueva clasificación infragenérica que comprende dos subgéneros: (1) el subgénero *Bacasia,* representado por dos especies (*B. corymbosa* y *B. parviflora*); y (2) el subgénero *Barnadesia* representado por las restantes 16 especies (*B. aculeata, B. arborea, B. blakeana, B. caryophylla, B. dombeyana, B. glomerata, B. horrida, B. jelskii, B. lehmannii, B. macbridei, B. macrocephala, B. odorata, B. polyacantha, B. pycnophylla, B. reticulata* y *B. spinosa*).

EVOLUCIÓN DE LOS CARACTERES FLORALES

Estambres (Fig. 10). El tubo estaminal constituye la novedad evolutiva exclusiva del género *Barnadesia.* La presencia del tubo estaminal en las flores del margen fue utilizada por Chung (1965) para la creación del subgénero *Barnadesia.* Este carácter, presente en las flores del margen en *B. aculeata, B. arborea, B. corymbosa, B. dombeyana, B. jelskii* y en ambos tipos de flores en *B. spinosa,* ocurrió en forma independiente en los dos subgéneros.

Número de flores en el disco (Fig. 11). Este carácter fue utilizado para la creación de secciones (Chung, 1965). Sin embargo, en el cladograma este carácter no justifica grupos monofiléticos. En *Barnadesia* la evolución del número de flores parte de

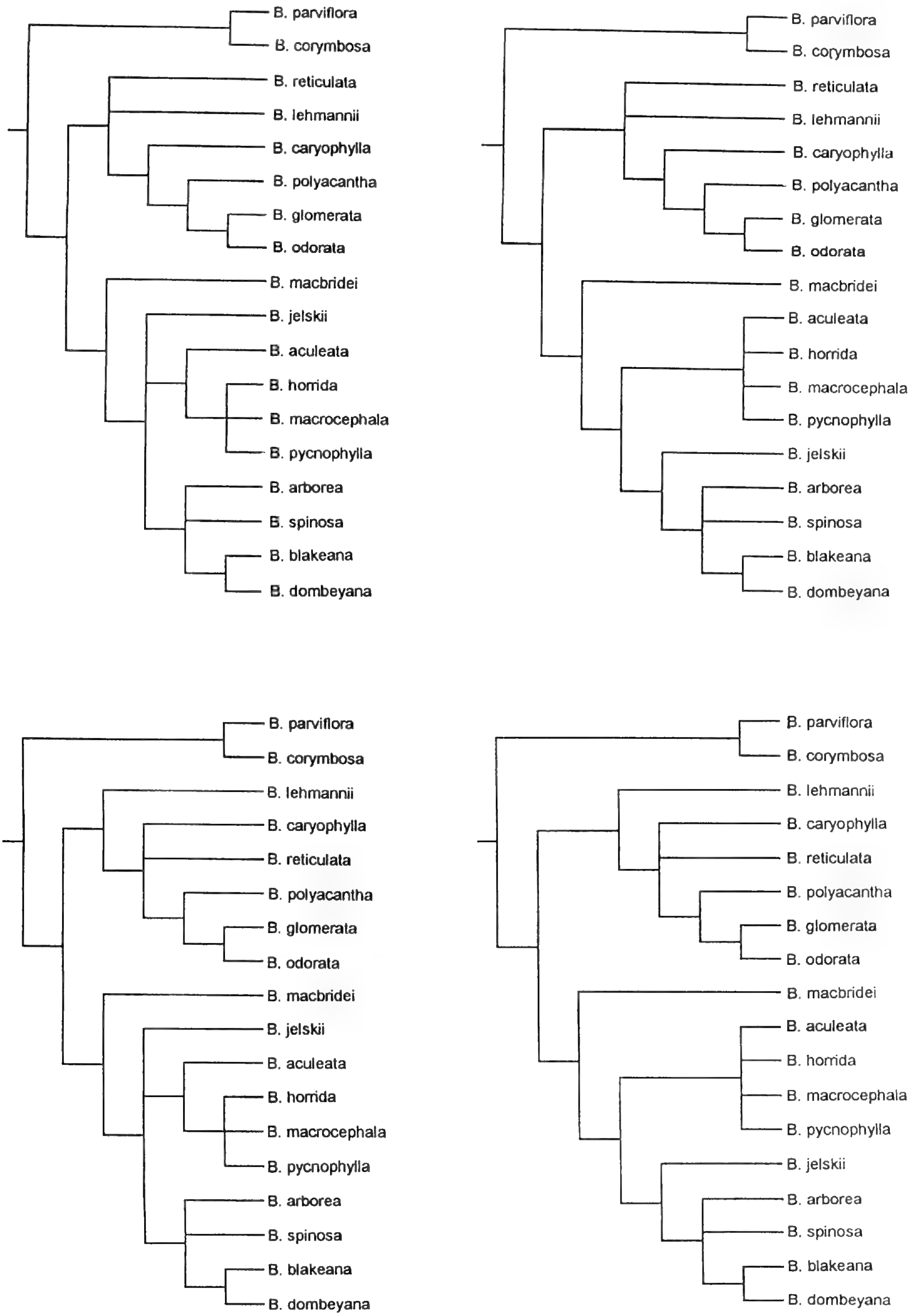


Figura 6. Cladogramas igualmente simples.

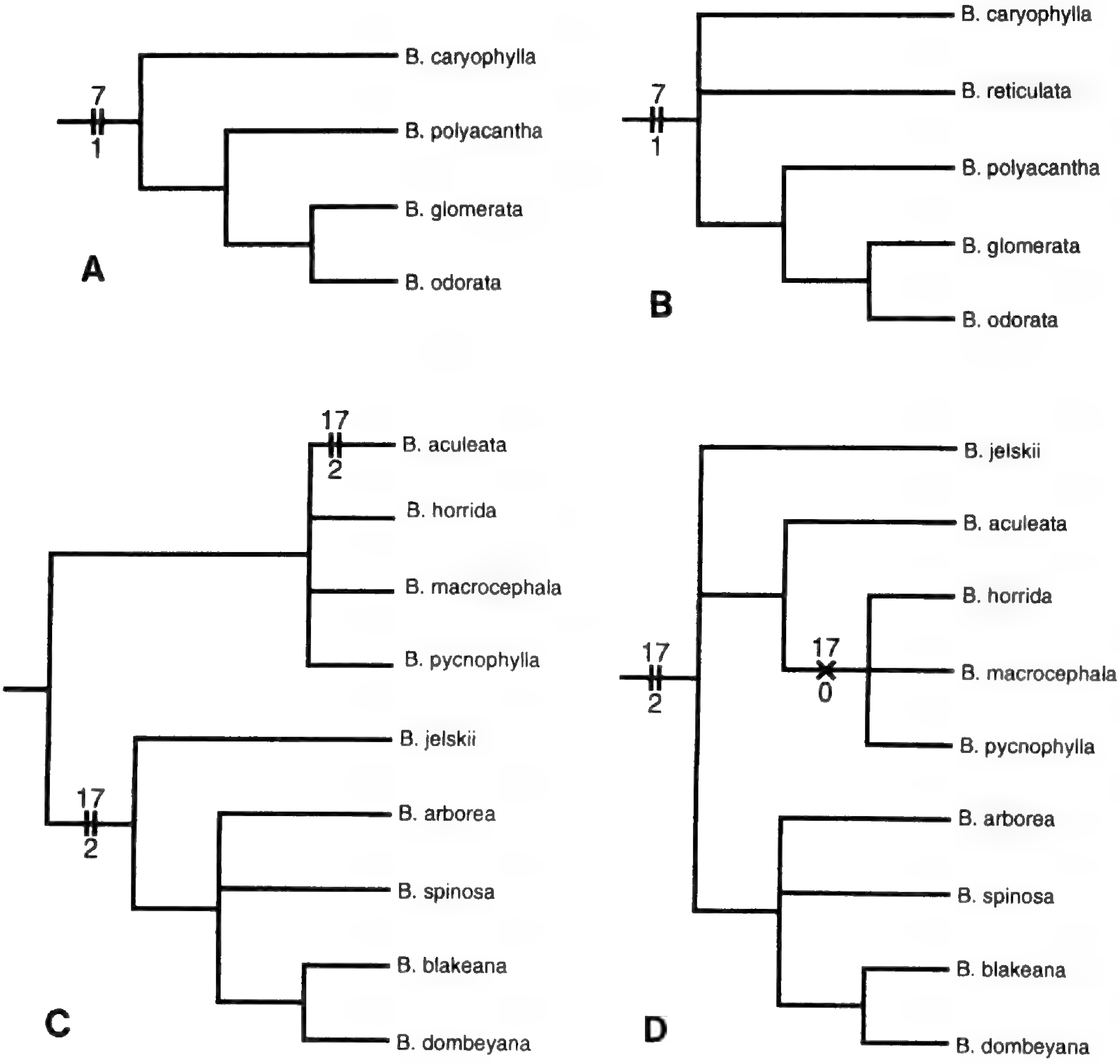


Figura 7. Variación de las topologías de los 4 árboles igualmente simples.

capítulos unifloros en el disco, pasando a trifloros (*B. lehmannii, B. reticulata, B. caryophylla, B. polyacantha, B. odorata,* y el grupo *B. arborea, B. spinosa, B. blakeana* y *B. dombeyana),* a nuevamente unifloro en *B. glomerata.*

Corolas de las flores del disco (Fig. 12). La interpretación de la evolución de las corolas en el género *Barnadesia* coincide con lo propuesto por Cabrera (1959) y Bremer (1994): a partir de las corolas tubulosas presentes en *B. corymbosa* y *B. parviflora* evolucionan las corolas bilabiadas presentes en la mayoría de las especies, y de estas evolucionan en forma independiente las liguladas en *B. polyacantha, B. glomerata* y *B. odorata,* y las subliguladas en el grupo monofilético *B. aculeata, B. horrida, B. macrocephala* y *B. pycnophylla.* Esta hipótesis se contrapone a lo propuesto por Jeffrey (1977), quien consideró las corolas bilabiadas como las más primitivas.

TAXONOMÍA

Barnadesia Mutis, in L.f., Suppl. pl. 55. 1782 ("1781"). TIPO: *Barnadesia spinosa* L.f.

Bacasia Ruiz & Pav., Fl. peruv. prodr. 105, t. 22. 1794. *Barnadesia* secc. *Bacasia* (Ruiz & Pav.) DC., Prodr. 7: 3. 1938. TIPO: *Bacasia corymbosa* Ruiz & Pav. (lectótipo, designado por Chung (1965)).

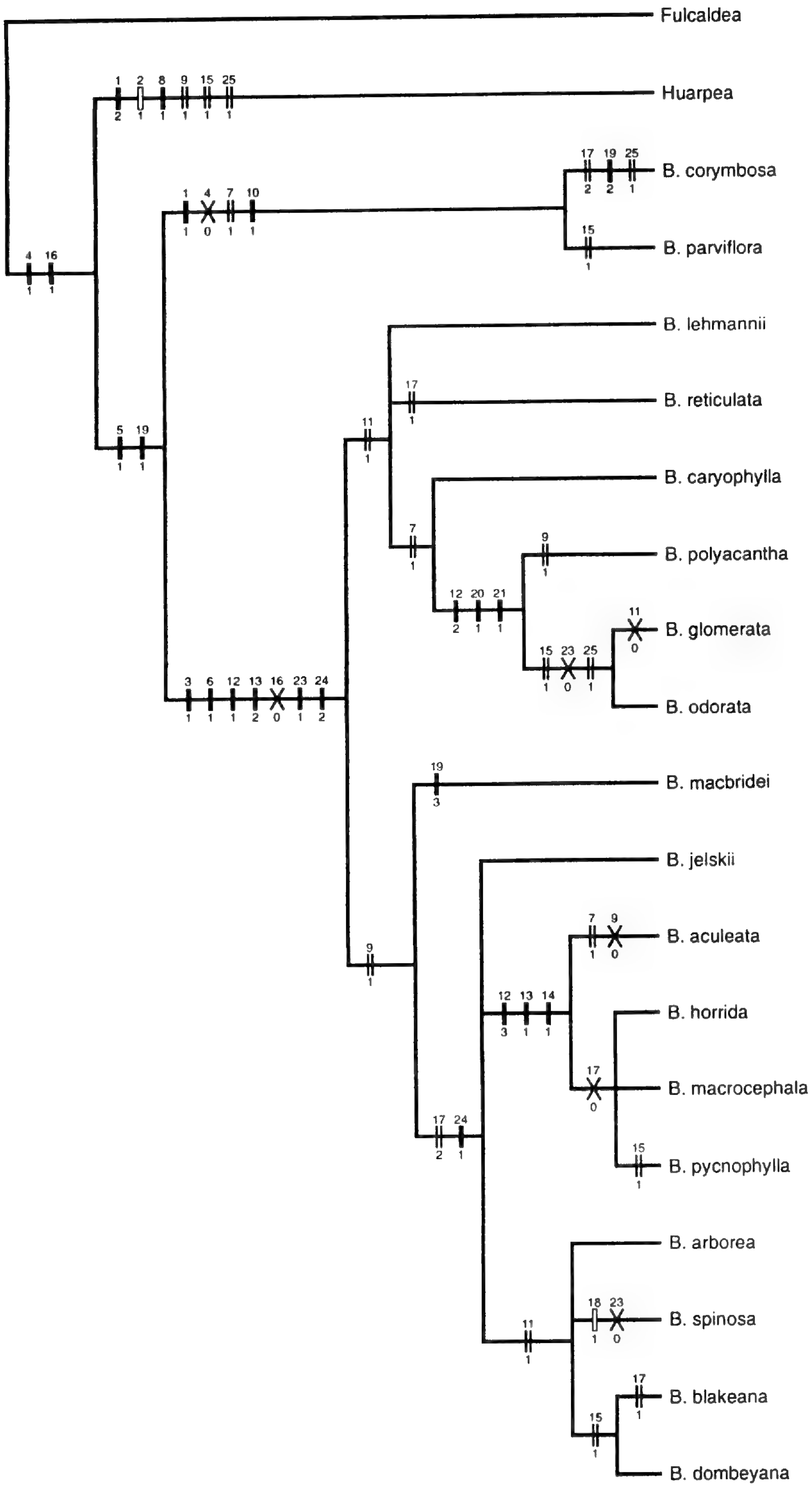
Xenophontia Vell., Fl. flumin. 346. 1829. TIPO: *Xenophontia caryophylla* Vell.

Diacantha Less., Linnaea 5: 243. 1830, non Lag. (1811). TIPO: *Diacantha arborea* (Kunth) Less. (*Barnadesia arborea* Kunth).

Penthea (D. Don) Spach, Hist. nat. vég. 10: 9. 1841, non Lindl. (1838). *Barnadesia* secc. *Penthea* D. Don, Trans. Linn. Soc. London 16: 280. 1830. *Barnadesia*

→

Figura 8. Arbol seleccionado para la interpretación de los caracteres. Cambios de los estados de los caracteres superpuestos en el cladograma. Sinapomorfía (I); paralelismo (II); reversión (x).


Fulcaldea
1 2 8 9 15 25
2 1 1 1 1 1
Huarpea
17 19 25
2 2 1
B. corymbosa
1 4 7 10
1 0 1 1
15
1
B. parviflora
4 16
1 1
B. lehmannii
17
1
B. reticulata
5 19
1 1
11
1
B. caryophylla
9
1
B. polyacantha
7
1
12 20 21
2 1 1
11
0
B. glomerata
15 23 25
1 0 1
3 6 12 13 16 23 24
1 1 1 2 0 1 2
B. odorata
19
3
B. macbridei
B. jelskii
7 9
1 0
B. aculeata
12 13 14
3 1 1
B. horrida
9
1
17
0
B. macrocephala
17 24
2 1
15
1
B. pycnophylla
B. arborea
18 23
1 0
11
1
B. spinosa
17
1
B. blakeana
15
1
B. dombeyana

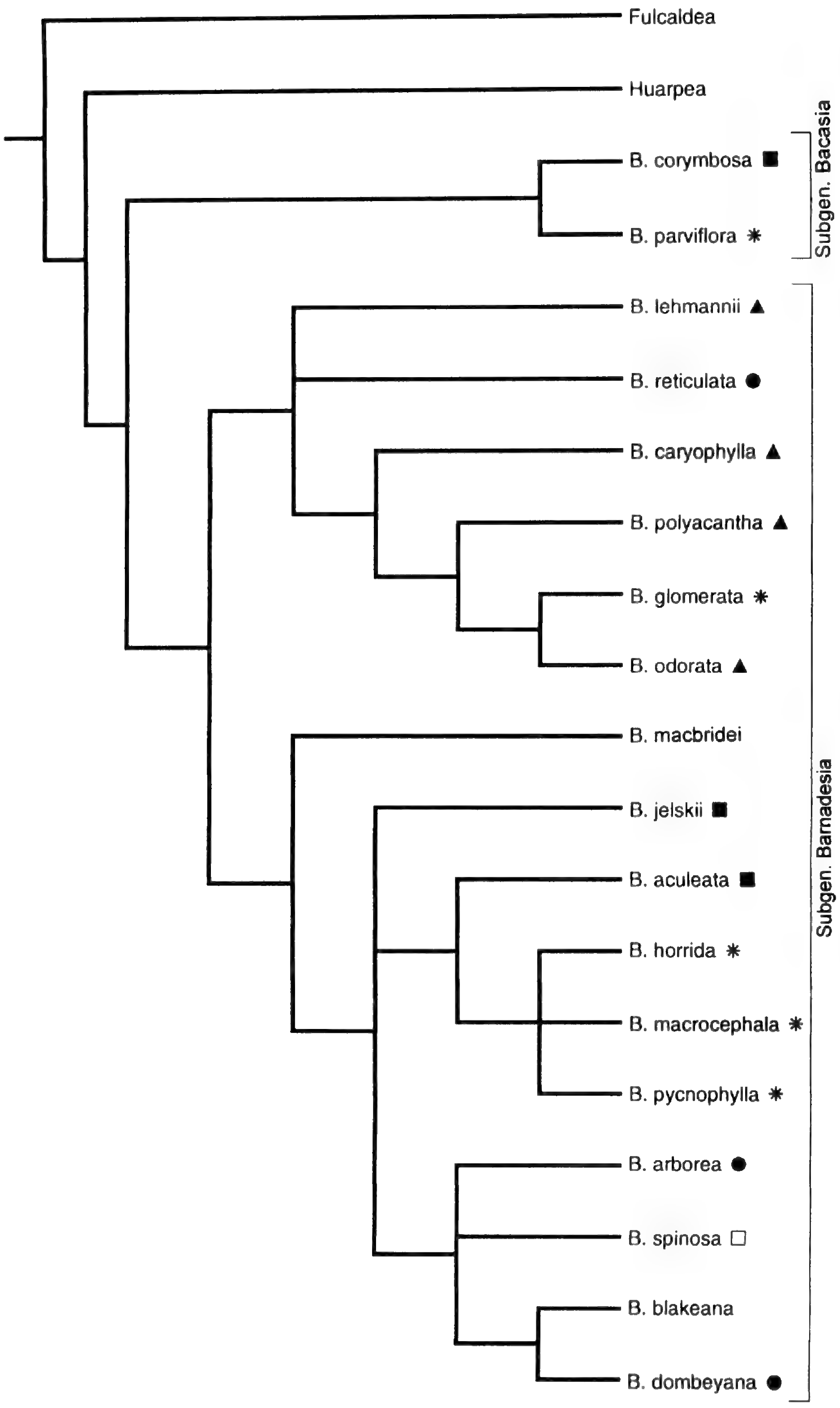


Figura 9. Interpretaciones de las clasificaciones infragenéricas de Chung (1965): sección *Pauciflora* (*), sección *Penthea* (▲), sección *Diacantha* (●), sección *Bacasia* (■), sección *Barnadesia* (□); y Urtubey: subgénero *Bacasia* y subgénero *Barnadesia*.

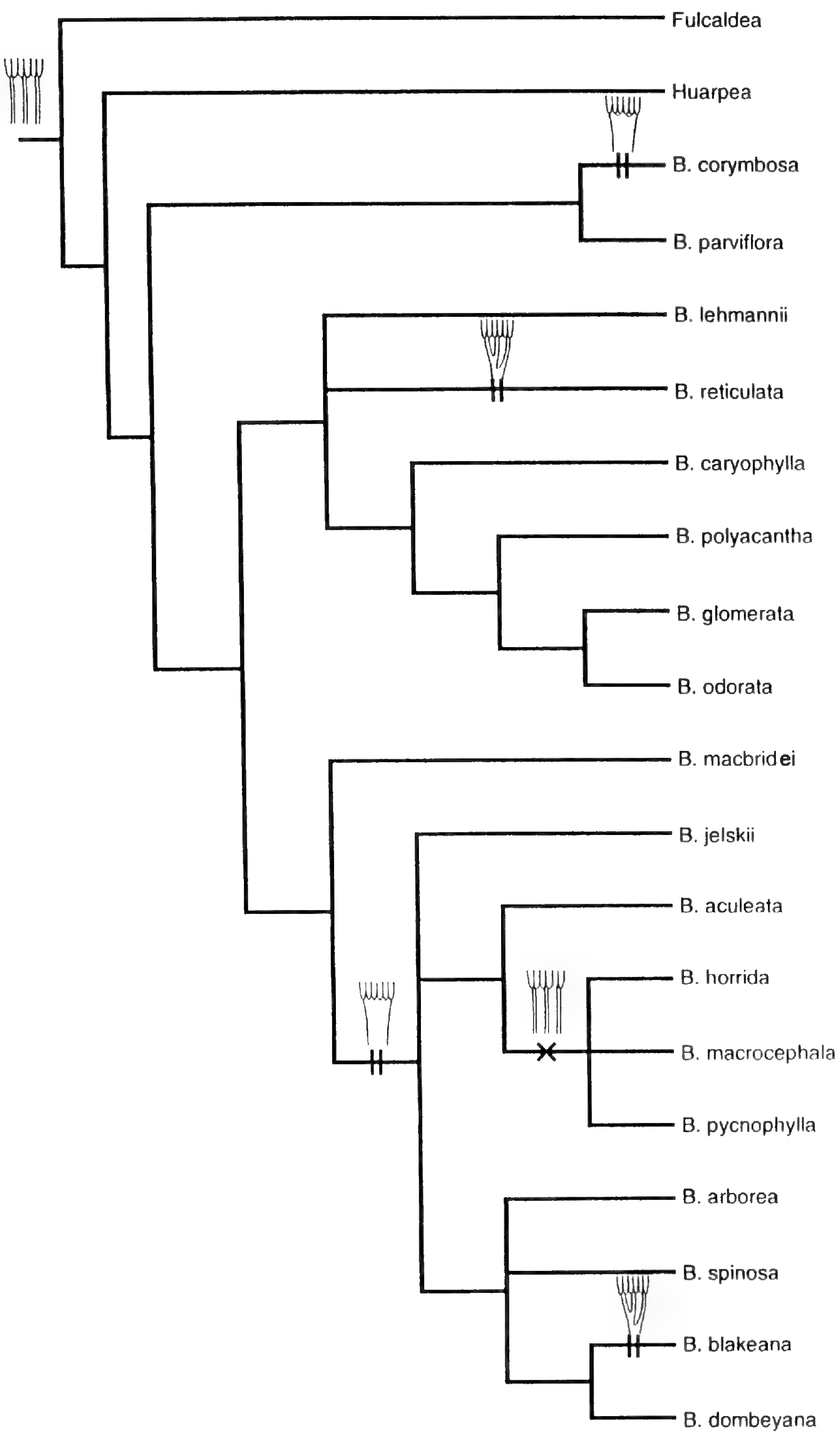


Figura 10. Evolución del tubo estaminal en *Barnadesia*.

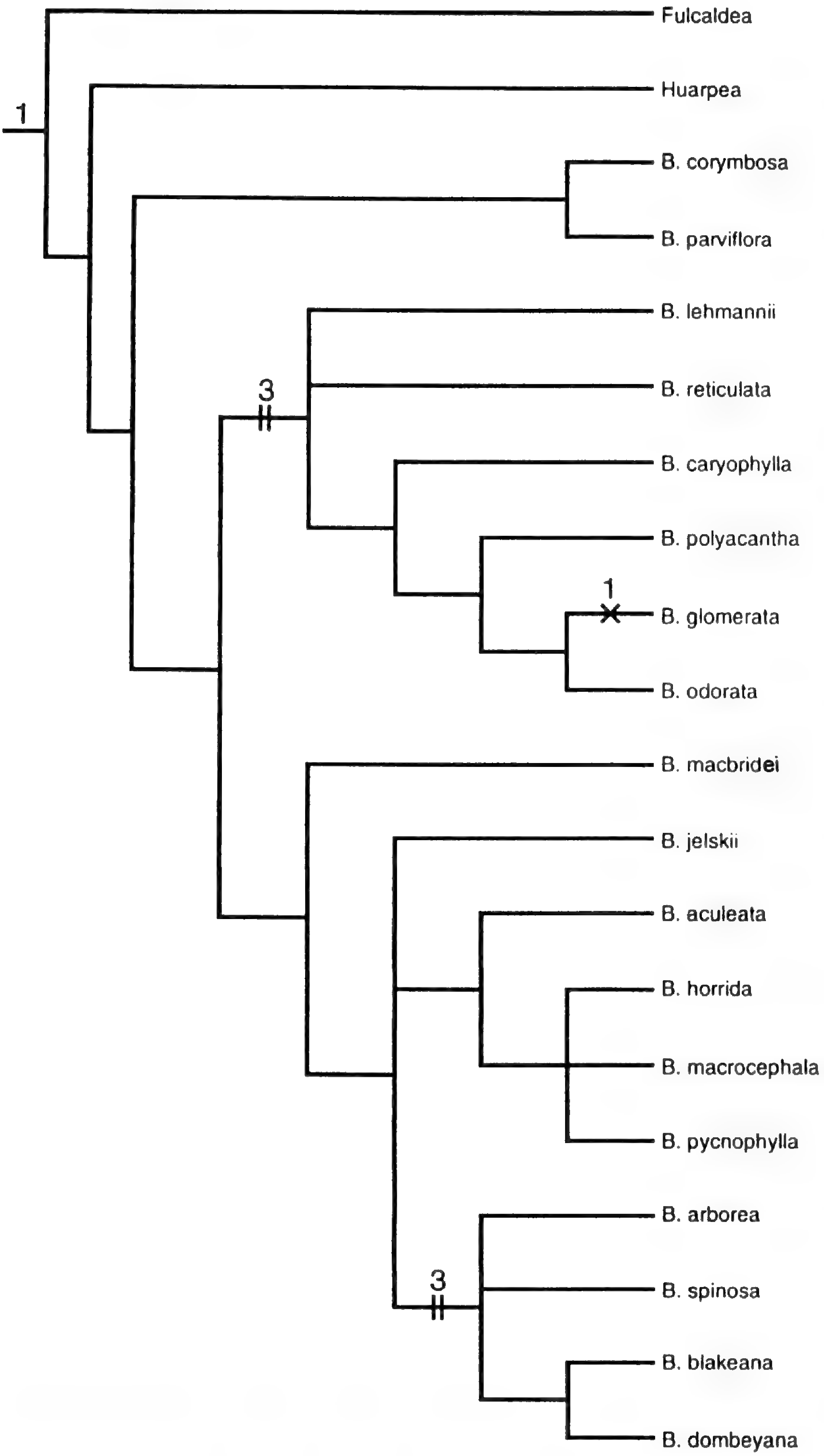


Figura 11. Evolución del número de flores del disco en *Barnadesia*.

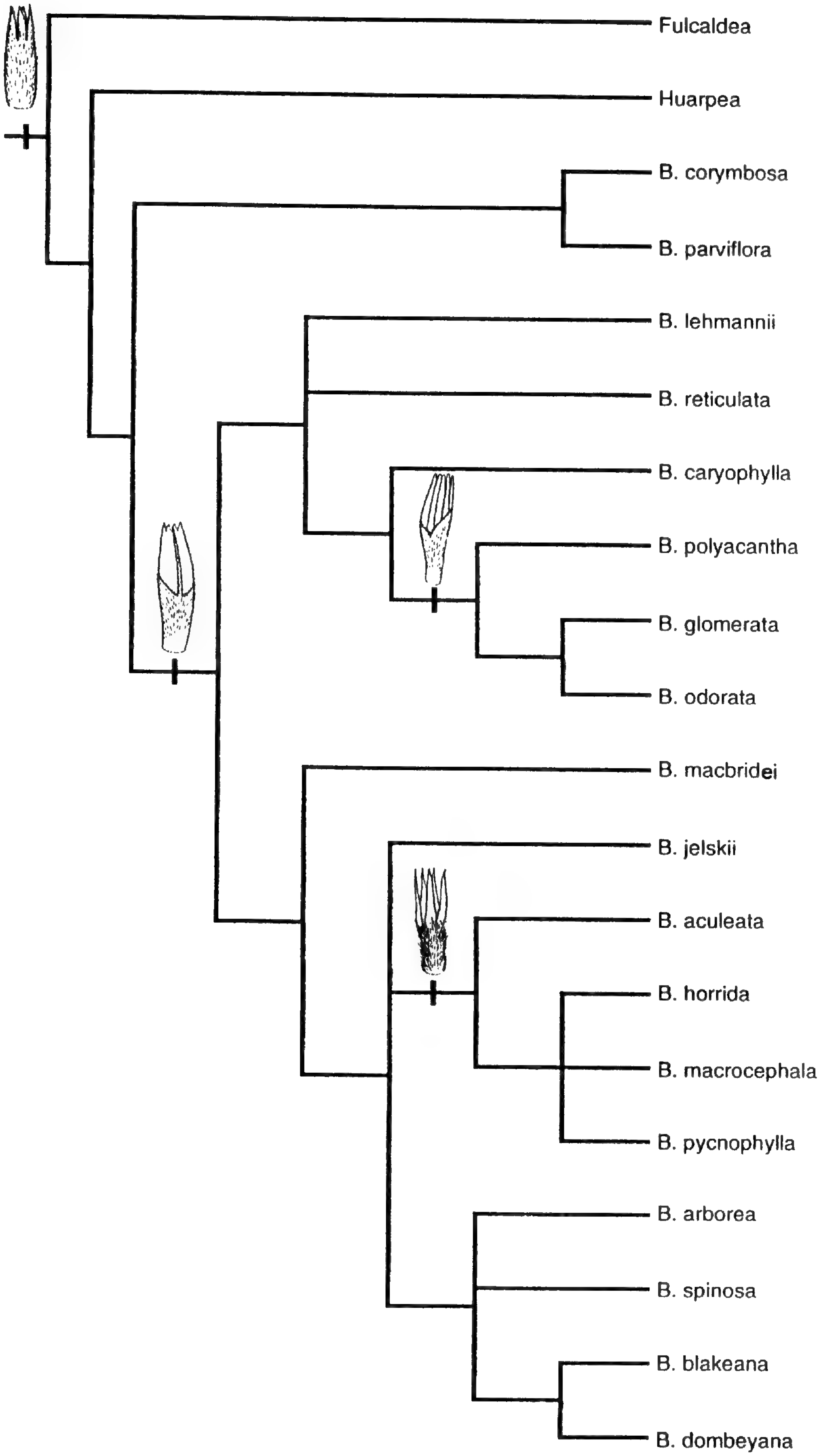


Figura 12. Evolución de las corolas de las flores del disco en *Barnadesia*.

subg. *Penthea* (D. Don) I. C. Chung, Rev. *Barnadesia*. 23. 1965. TIPO: *Barnadesia laxa* D. Don.

Rhodactinea Gardner, London J. Bot. 6: 449. 1847. TIPO: *Rhodactinea rosea* (Lindl.) Gardner (*Barnadesia rosea* Lindl.).

Arboles o arbustos de 0.60–20 m de alto. Tallos con crecimiento pseudomonopodial. Espinas geminadas o en fascículos. Hojas dispuestas en fascículos o alternas, sésiles, corta o largamente pecioladas, elípticas, oblanceoladas u obovadas, glabras hasta densamente pubescentes, de 9.5–190 mm de largo; enteras en el margen; ápice atenuado u obtuso, mucronado o espinoso. Capítulos radiados; homógamos o heterógamos; sésiles o pedunculados; solitarios, geminados, dispuestos en cimas racemiformes o cimas corimbiformes. Involucro cilíndrico, acampanado o turbinado. Receptáculo hueco, plano y piloso. Filarias mucronadas o espinosas, con pelos en el dorso y cilias en el margen, o sólo ciliadas, dispuestas en 6–14 series; las exteriores ovadas, las intermedias linear-lanceoladas, las interiores linear-oblanceoladas. Corolas de color blanco, rosado, rojo, lilacino a morado, exteriormente pubescentes, con o sin pelos en la garganta; anteras decurrentes en la base o cortamente sagitadas; conectivo prolongado en forma de asta; filamentos libres, parcialmente fusionados o totalmente unidos entre sí formando un tubo estaminal; estilo columnar, ramas estilares cortamente bilobadas, con papilas en la cara ventral. Flores del margen ocho o trece, perfectas, isomorfas; corola bilabiada (4+1); estambres 5, insertos en la garganta; aquenios cilíndricos o ligeramente turbinados, densamente pubescentes; papus plumoso. Flores del disco una o tres; perfectas o imperfectas; corolas ligeramente dimorfas, dimorfas o trimorfas; corola bilabiada, ligulada, tubulosa (3–5-lobada o 4–5-secta); estambres 3–5, insertos en la garganta, ocasionalmente en la parte media o en la base de la corola; aquenios turbinados, densamente pubescentes; papus cortamente plumoso, barbelado o simple. Pelos barnadesioides en corolas, aquenios y papus. Polen psilolofado con plan de lagunas radiosimétrico o radioasimétrico.

Comprende 18 especies, cuya distribución geográfica va desde los Andes orientales de Colombia hasta el noroeste argentino, una especie llega al sudeste del Brasil; desde los 400–5000 m.

CLAVE DE LOS SUBGÉNEROS DE *BARNADESIA*

1a. Hojas sésiles o subsésiles, fasciculadas; capítulos sésiles o cortamente pedunculados; flores del disco con corolas bilabiadas, subliguladas o liguladas, y papus simple o barbelado .... *Barnadesia* subg. *Barnadesia*
1b. Hojas pecioladas, alternas; capítulos pedunculados; flor del disco con corola tubulosa y papus plumoso .... *Barnadesia* subg. *Bacasia*

Barnadesia subgénero **Barnadesia**

Barnadesia subg. *Penthea* (D. Don) I. C. Chung, Rev. *Barnadesia*. 23. 1965. *Barnadesia* secc. *Penthea* D. Don, Trans. Linn. Soc. London, Bot. 16: 280. 1833. *Penthea* (D. Don) Spach, Hist. nat. vég. 10: 9. 1841, non Lindl. (1838). TIPO: *Barnadesia laxa* D. Don.

Barnadesia secc. *Diacantha* (Less.) DC., Linnaea 5: 243. 1830. TIPO: *Barnadesia arborea* Kunth.

Barnadesia subg. *Penthea* secc. *Pauciflora* I. C. Chung, Rev. *Barnadesia* 23. 1965. TIPO: *Barnadesia pycnophylla* Muschl.

Hojas sésiles o subsésiles, fasciculadas (ocasionalmente algunas hojas alternas). Capítulos sésiles o subsésiles. Flores del disco 1 u 8; con corolas bilabiadas, liguladas, subliguladas; papus con cerdas barbeladas o simples.

El subgénero *Barnadesia* comprende 16 especies que habitan desde Colombia hasta en NO argentino, llegando a Brasil.

1a. Flores del margen: estambres con filamentos fusionados.
  2a. Estambres con los filamentos parcialmente fusionados en las flores del margen.
    3a. Flores del disco con papus barbelado .... 3. *B. blakeana*
    3b. Flores del disco con papus simple .... 15. *B. reticulata*
  2b. Estambres con los filamentos totalmente fusionados en las flores del margen.
    4a. Flores del disco con filamentos de los estambres totalmente fusionados. .... 16. *B. spinosa*
    4b. Flores del disco con filamentos de los estambres libres.
      5a. Flores del margen ocho; flores del disco una.
        6a. Flor del disco con corola subligulada .... 1. *B. aculeata*
        6b. Flor del disco con corola bilabiada .... 8. *B. jelskii*
      5b. Flores del margen trece; flores del disco tres.
        7a. Flor del disco: corolas con garganta pubescente .... 2. *B. arborea*
        7b. Flor del disco: corolas con garganta glabra .... 5. *B. dombeyana*
1b. Flores del margen: estambres con filamentos libres.
  8a. Flores del margen trece; flores del disco tres.
    9a. Papus de la flor del disco de menor a igual longitud que el tubo de la corola .... 12. *B. odorata*
    9b. Papus de la flor del disco más largo que el tubo de la corola.
      10a. Flores del disco tetrámeras, ocasionalmente pentámeras .... 9. *B. lehmannii*

10b. Flores del disco exclusivamente pentámeras.
11a. Corolas de las flores del disco bilabiadas, ocasionalmente liguladas; involucro turbinado, 10–12-seriado .... 4. *B. caryophylla*
11b. Corolas de las flores del disco liguladas; involucro acampanado, 8–9-seriado .... 13. *B. polyacantha*
8b. Flores del margen ocho; flor del disco una.
12a. Papus de la flor del disco de menor a igual longitud que el tubo de la corola; anteras cortamente sagitadas .... 6. *B. glomerata*
12b. Papus de la flor del disco de mayor longitud que el tubo de la corola; anteras decurrentes en la base.
13a. Flor del disco con corola bilabiada (4+1) .... 10. *B. macbridei*
13b. Flor del disco con corola subligulada.
14a. Flor del disco con garganta glabra .... 14. *B. pycnophylla*
14b. Flor del disco con garganta pubescente.
15a. Capítulos de 25–35 mm de largo; involucro 7–8-seriado .... 7. *B. horrida*
15b. Capítulos de 45–50 mm de largo; involucro 10–11-seriado .... 11. *B. macrocephala*

1. Barnadesia aculeata (Benth.) I. C. Chung, Rev. *Barnadesia.* 53. 1965. *Barnadesia corymbosa* var. *aculeata* Benth., Pl. hartw. 136. 1844. TIPO: Ecuador. In montibus Loxa. *Hartweg 769* (holótipo, K; isótipos, BM, K, NY, P no vistos; fotografía, LP).

Arbusto de 1–4 m de alto. Hojas en fascículos; pecíolo de hasta 3 mm de largo; láminas elípticas u oblanceoladas, pubescentes, de 23.0–30.5 × 7.0–11.5 mm; ápice atenuado u obtuso, mucronado. Capítulos sésiles o cortamente pedunculados, cimas corimbiformes o racemiformes. Involucro cilíndrico o ligeramente acampanado, de 33–43 × 9–20 mm, filarias ca. 71, mucronadas, dispuestas en 8–10 series: las exteriores de 3–7 mm de largo; las intermedias de 10.5–30.0 mm de largo; las interiores de 19–39 mm de largo. Corolas de color rosa brillante o purpúreas, dimorfas. Flores del margen ocho; corola bilabiada (4+1), de 28–47 mm de largo, labio interno de 10–12 mm de largo, labio externo de 13.0–18.5 × 4–6 mm, tubo de 15.0–28.5 mm de largo; anteras decurrentes en la base, de 6–9 mm de largo; tubo estaminal ca. 9 mm de largo; estilo de 37.8–45.0 mm de largo, ramas estilares de 0.8 mm de largo; papus de 13–21 mm de largo; aquenios cilíndricos o ligeramente turbinados de 2.2–3.5 × 2.0–2.2 mm. Flor del disco una, perfecta; corola subligulada, densamente pubescente en el tubo y el ápice de los dientes, con pelos en la garganta, de 12.8–19.0 mm de largo; anteras 5, decurrentes en la base, de 7.4 mm largo; filamentos libres, parte libre de la corola ca. 9.6 mm de largo; estilo de 32.2 mm de largo, ramas estilares de 1 mm de largo; papus barbelado, más largo que el tubo de la corola, de 11–17 mm de largo, aquenio de 3.8–6.0 × 3–5 mm. Polen radioasimétrico. Figuras 13, 31.

Distribución y ecología. Ecuador. Crece en el subpáramo, entre 2400–3200 m. Epoca de floración: febrero–septiembre.

Material adicional examinado. ECUADOR. **Loja:** Cerro Villanaco, 7 km W of the city of Loja, 8000–9000 ft., *Camp E-230** (NY); Cuenca–Loja road, 26 km N of Saraguro, 3060 m, *Clements et al. 2238** (NY); road to Saraguro at summit of Loma del Oro, 3200 m, *Dodson & Thien 614** (MO, US). **Zamora-Chinchipe:** Road Gualaceo–Limón (Gral. Plaza) 4–6 km of the pass, *Bohlin et al. 1425* (S).

Esta especie se caracteriza por la corola subligulada y el papus barbelado de la flor del disco.

2. Barnadesia arborea Kunth, in Humb., Bonpl. & Kunth, Nov. gen. sp. Quarto ed. 4: 16. Folio ed. 4: 12. 1820. *Diacantha arborea* (Kunth) Less., Linnaea 5. 244, figs. 56, 57. 1830. TIPO: Ecuador. Crescit in frigidis montis Guamani, alt. 1600 hex. (regno Quitensis), floret Februario, *Bonpland 3505* (holótipo, P no visto, fotocopia, LP; isótipo, P no visto, fotografía, LP).

Barnadesia media D. Don, sin. nov. Trans. Linn. Soc. London., Bot. 16: 276. 1833. TIPO: In Peruvia, *Ruiz & Pav. s.n.* (holótipo, BM, fotografía, LP).
Barnadesia sodiroi Hieron., Bot. Jahrb. Syst. 29: 78. 1901. TIPO: Ecuador. Crescit in regione superiore silvarum in monte vulcanico Pululahua, *Sodiro 62/1* (holótipo, B probablemente destruido; fotografía serie Field Museum Nº 15919, GH, LP, MO). Ecuador. Pichincha: Volcán Pululahua, *Sodiro s.n.* (neótipo, designado por Chung (1965), P no visto, fotografía, LP).
Barnadesia vestita Benoist, Bull. Soc. Bot. France 84: 634. 1938. *Barnadesia arborea* var. *vestita* (Benoist) I. C. Chung, Rev. Barnadesia. 62. 1965. TIPO: Ecuador. Borma, arbuste d'une hauteur moyenne de 2.50 m., à fleurs roses, sep. 1904, *Rivet 673* (holótipo, P no visto, fotografía, LP; isótipo, P no visto, fotografía, LP).
Barnadesia wurdackii Ferreyra, sin. nov. Publ. Mus. Hist. Nat. "Javier Prado" Ser. B, Bot. 18: 16, lám. 5. 1964. TIPO: Perú. Amazonas: Prov. Chachapoyas, Puma-Urcu cerca a Chachapoyas, 2700–3000 m, *Wurdack 681* (holótipo, USM; isótipos, GH, MO, UC, US, USM).
Barnadesia chachapoyasensis I. C. Chung, Rev. Barnadesia 64. 1965. TIPO: Perú. Amazonas: Cerro Chunchula (Chachapoyas), *Ochoa 1665* (holótipo, US).

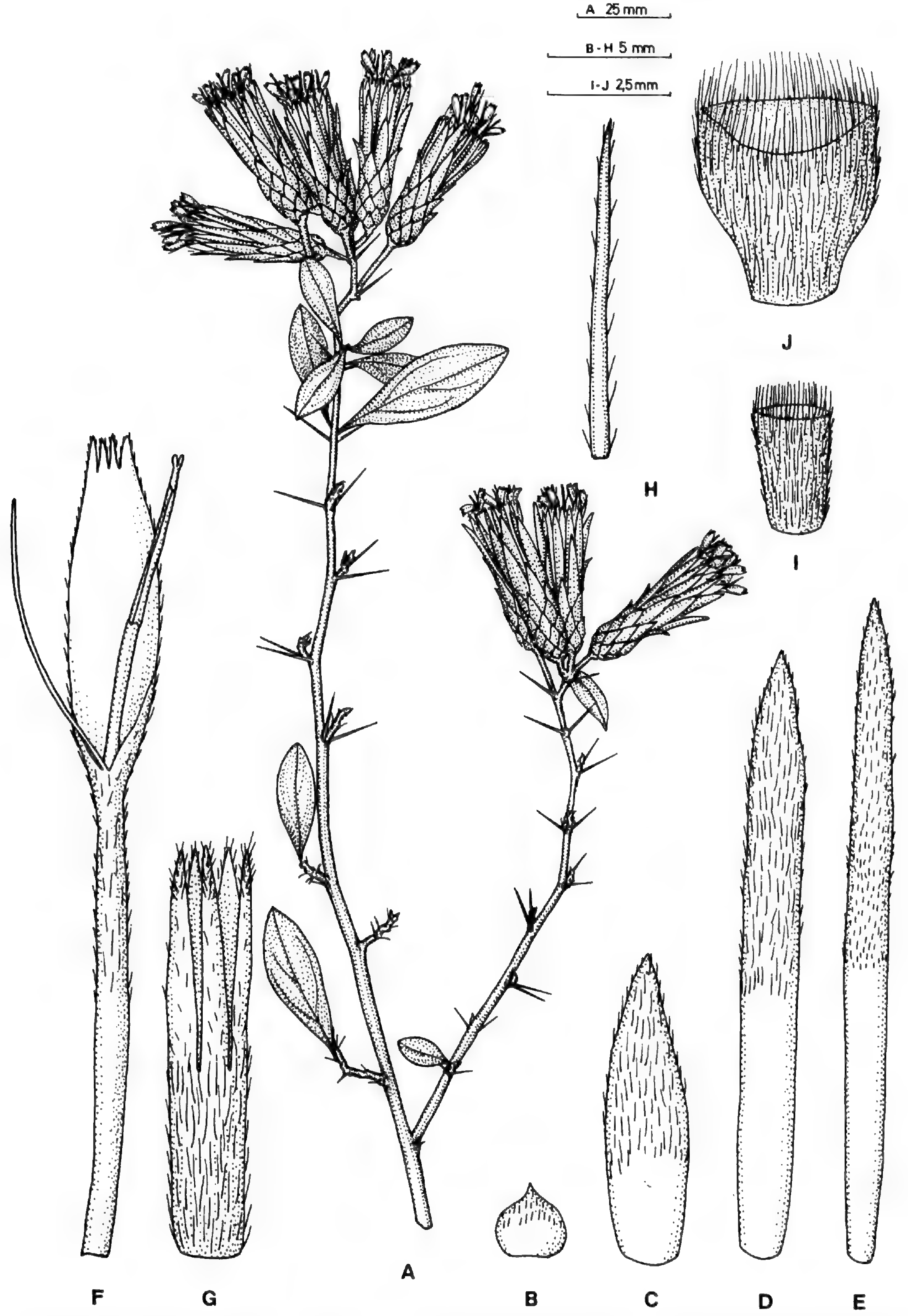


Figura 13. *Barnadesia aculeata.* —A. Rama. —B–E. Brácteas involucrales. —F. Corola: (4+1), estambres y estilo de la flor del margen (*Clements et al. 2238,* NY). —G. Corola de la flor del disco: (5+0) (*Dodson & Thien 614,* US). —H. Cerda del papus de la flor del disco. —I. Aquenio de la flor del margen. —J. Aquenio de la flor del disco (*Clements et al. 2238,* NY).

Nombres vulgares. "Chian" (*Prieto 74*), "chuquirahua" (*Cerón et al. 6980*), "espino" (Harling, 1991), "espino santo" (Harling, 1991), "espino de gato" (Harling, 1991), "espino de estrella" (*Cerón et al. 6885*), "chivocaspi" (Harling, 1991).

Arbusto o arbolito de 1–5 m de alto. Espinas geminadas o en fascículos, de 11–27 mm de largo. Hojas en fascículos; pecíolo menos de 2 mm; láminas oblanceoladas u obovadas, pubescentes a subglabras en la cara adaxial, de 18.0–32.5 × 8.5–13.8 mm; ápice atenuado u obtuso, mucronado o espinoso. Capítulos sésiles o cortamente pedunculados, en cimas racemiformes, cimas corimbiformes o en panoja. Involucro acampanado o turbinado, de 25–39 × 8–16 mm, filarias 95–99, mucronadas o espinosas, dispuestas en 8–10(–11) series: las exteriores de 3.8–7.0 mm de largo; las intermedias de 7.0–24.2 mm de largo; las interiores de 17.5–26.0 mm de largo. Corolas de color rosa brillante, rosa oscuro, rojo, morado o purpúreas, ligeramente dimorfas o dimorfas. Flores del margen trece; corola bilabiada (4+1), de 26.4–41.5 mm de largo, labio interno de 10–14 mm de largo, labio externo de 13–18 × 3.8–5.0 mm, tubo de 13.4–23.5 mm de largo; anteras decurrentes en la base, de 6.0–7.5 mm de largo, tubo estaminal de 6–11 mm de largo; estilo de 28–47 mm de largo, ramas estilares de 0.3–0.4 mm de largo; papus de 9–16 mm de largo; aquenios cilíndricos de 2.2–4.5 × 1–2 mm. Flores del disco tres, perfectas; corola bilabiada (3+1 ó 4+1), densamente pubescente en el tubo y el ápice de los dientes, de 11.0–16.5 mm de largo, labio interno de 8–10 mm de largo, labio externo 4-dentado o 3-dentado, de 8.0–14.5 × 4.0–7.8 mm, tubo de 2–5 mm de largo, con pelos en la garganta; anteras 4 ó 5, decurrentes en la base, de 5.0–6.8 mm de largo; filamentos libres, parte libre de la corola de 7.0–8.8 mm de largo; estilo de 9–19 mm de largo, ramas estilares de 0.3–0.8 mm de largo; papus barbelado, más largo que el tubo de la corola, de 7.0–11.9 mm de largo; aquenios de 2.5–4.6 × 1.5–3.0 mm. Polen radioasimétrico. Figuras 14, 32.

Distribución y ecología. Ecuador y Perú. Crece en el páramo, bosque andino lluvioso, bosque premontano y bosque montano, entre 1800–5000 m. Epoca de floración: Todo el año.

Material adicional examinado. ECUADOR. **Azuay:** Cantón Cuenca, parroquia Baños Yanasacha, 2925 m, *Boeke 619* (NY); 6.8 km SE Gualaceo on road to Mendez, *Dorr & Barnett 5921* (NY); 8–10 km S of Cumbe on the road to Loja, 9050–9400 ft., *King & Almeda 7762* (MO, US); along road to Loja, ca. 17 km S of Cumbe, 9700 ft., *King & Garvey 6893* (MO, NY, UC, US); 40 km from Cuenca on route to Loja, 9700 ft., *Maguire & Maguire 44277* (NY); about 30 mi. before Cuenca, en route from Guayaquil, 10,400 ft., *Maguire & Maguire 44276* (NY); Giron, 3700 m, *Hirsch E-24* (NY). **Bolívar:** Carretera Guaranda–Pueblo Viejo, 18 km Guaranda, 2850 m, *Larsen 95* (NY); 3200 m, *Penland & Summers 547* (GH, US). **Cañar:** 31 km S of Chunchi, on Chunchi–Cañar, 3000 m, *Dorr & Barnett 5793* (NY, US); Páramo de Inganilla, between Biblián and Cañar, 3400 m, *Harling 25665* (GH); 20 km S of Cañar on the road to Cuenca, 9700 ft., *King & Almeda 7742* (MO, US); along the road to Cuenca, ca. 20 km from Azogues, 9800 ft., *King & Garvey 6885** (MO, NY, UC, US); región of San Marcos, about 10 km NE of Azogues, 9500 ft., *Prieto P-74* (NY). **Chimborazo:** Río Puela, vertientes del Tungurahua, 2500–2800 m, *Mena 620* (NY); ostlich Riobamba, Paramo Gebiet, 3200 m, *Schimpf 884* (MO). **Cotopaxi:** Corazón, *André K-271* (NY); Volcán Cotopaxi, *Gilmartin 796* (US); Mt. Cotopaxi, 4000–4500 m, July 1977, *Norman s.n.* (US). **Imbabura:** environs of Otavalo, road from Otavalo to Apuela, Páramo of Cotacachi, *Davis 238* (US); Cantón Pimampiro, Carretera de Ibarra a Mariano Acosta, 3500 m, *Rubio & Quelal 489* (US). **Loja:** road from Loja to Latuna, km 14–34, 1600–2600 m, *Dodson & Thien 1509* (US). **Napo:** carretera Quito–Tena vía Baeza, 3300 m, *Dodson et al. 15176* (US); cerca de baños termales, 2 km N Papallacta, *González 17* (MO); Cerro Antisana, 3500 m, *Grubb et al. 717* (MO, NY). **Pichincha:** Potrerillo, Pululahua, 7700 ft., *Bell 572** (GH); Reserva Geobotánica Pululahua, camino a Lulumbamba alrededor del Pan de Azúcar, 1800–3356 m, *Cerón 1147* (MO, NY); Lloa, al sur del Volcán Pichincha, 10 km al SW Quito, 2800 m, *Cerón et al. 6980* (MO); between Quito and Nanegal, vía Cotocollao and Nono, 18–21 km NW Quito (between Cotocollao and Nono), 3100–3200 m, *Croat 38794* (MO); Ventanas del Pululahua, 2800 m, *Flora ecuatoriana 1015** (GH); declives de Pichincha, 3000 m, *Flora ecuatoriana 1016* (GH), *1017* (GH), *1018* (GH); Bosque Protector Pasochoa, 30 km SE de Quito, 2850–3900 m, *Granda 8* (NY); cráter del Volcán Pululahua, "death" volcano, 34 km N Quito, *Ledingham et al. 4575* (NY); prope Quito, *Sodiro 754* (GH). **Tungurahua:** slope of volcano Tungurahua, *Popenoe 1285* (GH). PERÚ. **Amazonas:** Bongará, hills W-NW (310°–320°) of Pomacocha, 2300–2700 m, *Wurdack 930** (LP, UC); Chachapoyas, 10 km along road ascending mountain SE of Chachapoyas, ca. 8700 ft., *King & Bishop 9259* (MO); Pomacocha entre Leimabamba y Balsas, 2575 m, *López et al. 4406* (LP). **Cajamarca:** La Encañada, jalca de Cumulca, 3300 m, *Sagástegui et al. 8095* (MO, SI); 28 km along road from Leimebamba SW towards Celendín, 9700 ft., *King & Bishop 9254* (MO).

Barnadesia arborea es una de las especies con mayor variabilidad, tanto en sus caracteres vegetativos como reproductivos, y con el mayor rango de distribución altitudinal (3200 m). Esta especie se caracteriza por el tubo estaminal en las flores del margen y la garganta pubescente en las corolas de las flores del disco.

Barnadesia media comparte con *B. arborea,* las hojas fasciculadas, subsésiles, obovadas y mucronadas; filarias reflexas; y la presencia de tres flores en el disco, por lo cual la considero un sinónimo de *B. arborea,* si bien he contado sólo con el fototipo y la diagnosis original.

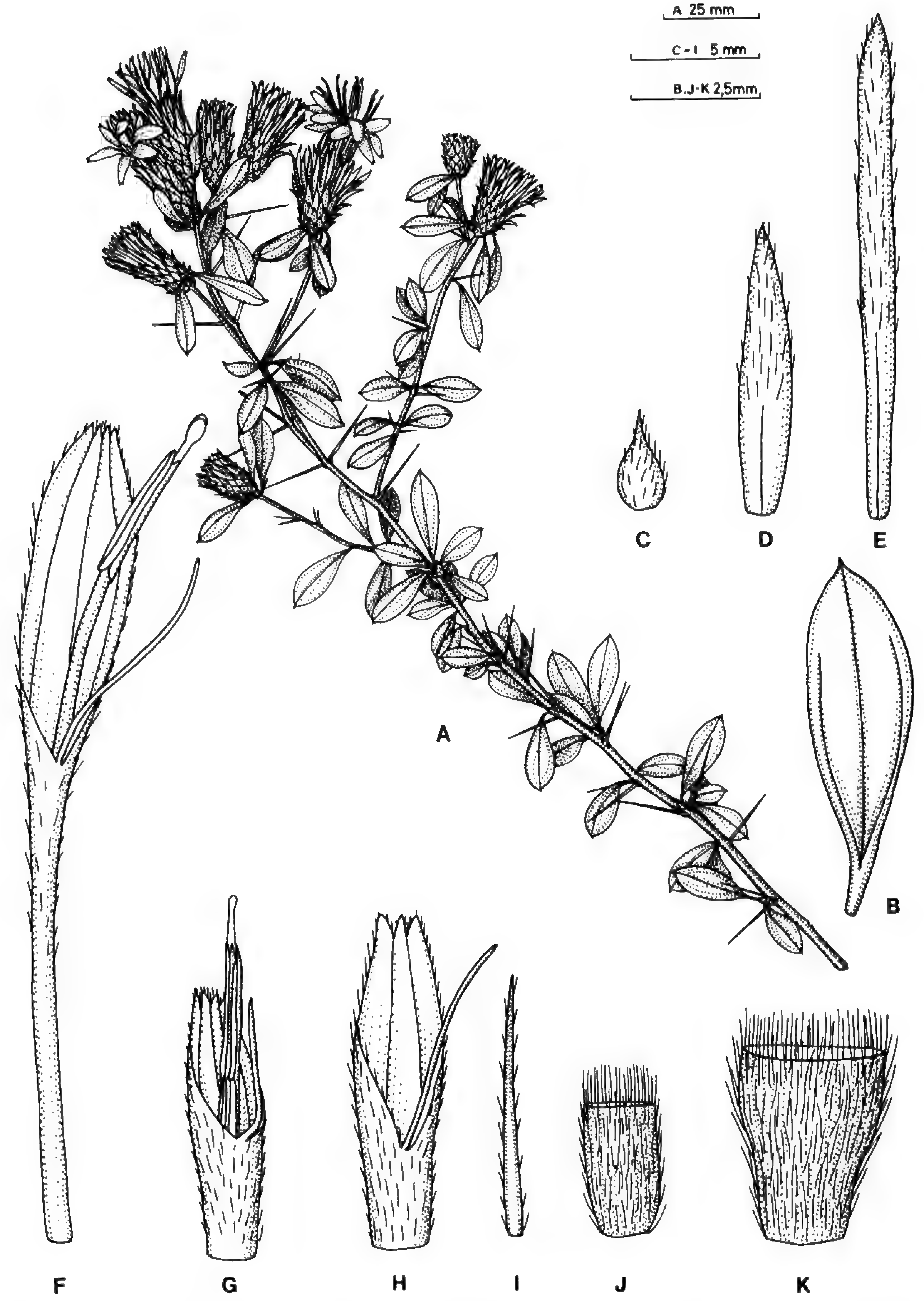


Figura 14. *Barnadesia arborea.* —A. Rama. —B. Hoja. —C–E. Brácteas involucrales. —F. Corola: (4+1), tubo estaminal y estilo de la flor del margen. —G. Corola: (4+1), estambres y estilo de la flor del disco (*UC 1333177*). —H. Corola de la flor del disco (3+1) (*King & Garvey 6885*, US). —I. Cerda del papus de la flor del disco. —J. Aquenio de la flor del margen. —K. Aquenio de la flor del disco (*UC 1333177*).

Ferreyra (1964), en la descripción original de *Barnadesia wurdackii*, la caracterizó por el hábito arbustivo; por sus hojas dispuestas en fascículos alternos, cortamente pecioladas; brácteas cuando secas involutas; capítulos terminales o axilares, y corolas bilabiadas 3+1 para las flores del disco. Sin embargo, estos caracteres son parte de la variabilidad de *B. arborea* y carecen por lo tanto de validez taxonómica. Por otra parte, el material tipo me permitió confirmar la presencia de tubo estaminal en las flores del margen y la ausencia en las flores del disco, así como también la presencia de pelos en la garganta de la corola de las flores del disco, los cuales son caracteres diagnósticos de *B. arborea*. Esto confirma nuevamente que *B. wurdackii* es un sinónimo de *B. arborea*.

Chung (1965) designó el lectótipo *Bonpland s.n.* para *Barnadesia arborea*. De acuerdo al herbario de tipos P, el holótipo correspondiente a *Barnadesia arborea* es el ejemplar *Bonpland 3505*, por lo tanto queda invalidado el lectótipo designado por Chung según el art. 9.13(a) del Código Internacional de Nomenclatura Botánica (Greuter et al., 1994).

Usos. En la etiqueta del ejemplar *Cerón et al. 6885* (MO), se menciona "la utilización de sus hojas como infusión, para ser aplicadas en el cuerpo de niños para curar espasmos."

3. **Barnadesia blakeana** Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, Bot. 18: 14. 1964. TIPO: Perú. Lima: Huarochirí, Monte de Zárate, encima de San Bartolomé, entre Lima y Matucana, 6 Nov. 1954, 2900 m, *Ferreyra 10427* (holótipo, USM; isótipos, MO, USM).

Arbusto de 1.5–2.0 m de alto. Espinas geminadas, ca. 28.5 mm de largo. Hojas en fascículos; pecíolo ca. 2 mm; láminas oblanceoladas o elípticas, subglabras (sobre la vena media en la cara adaxial), de 18–36 × 7–10 mm; ápice atenuado, espinoso. Capítulos sésiles, solitarios o geminados. Involucro acampanado de 45–50 × 19–40 mm, filarias mucronadas, densamente pubescentes, en 8–9 series: las exteriores de 41–45 mm de largo, las intermedias de 11–39 mm de largo, las interiores ca. 7 mm de largo. Corolas ligeramente dimorfas o dimorfas. Flores del margen trece; corola bilabiada (4+1), de 48–62 mm de largo; labio interno ca. 15 mm de largo, labio externo de 19–23 × 2.5–5.0 mm, tubo de 25–39 mm de largo; anteras decurrentes en la base, 10–11 mm de largo; filamentos parcialmente fusionados; estilo ca. 38 mm de largo; aquenios cilíndricos, ca. 5 × 2 mm. Flores del disco tres, perfectas; corola bilabiada (3+1), ocasionalmente (4+1), de 19.8–21.0 mm de largo, labio externo de 12.1–14.0 × 4–5 mm; anteras 4 ó 5, decurrentes en la base, de 8.5–9.8 mm de largo; filamentos libres; estilo ca. 27.5 mm de largo, ramas estilares ca. 0.6 mm de largo; papus barbelado, más largo que el tubo de la corola, de 13–14 mm de largo; aquenios turbinados. Polen radioasimétrico. Figuras 15, 33.

Distribución y ecología. *Barnadesia blakeana* es endémica de Monte Zárate, Perú. Crece en el monte bajo, entre 2600–3300 m. Epoca de floración: abril–noviembre.

Material adicional examinado. PERÚ. **Lima:** Huarochiri, Ventanilla, 3300 m, *Valencia 719* (USM); 3000–3150 m, *Valencia 1308* (USM); Puquio Blanco, 3100 m, *Valencia 1314** (USM); Qda. Monte Zárate, 2800 m, *Valencia 1596* (USM); Gatera, 2800–3000 m, *Valencia 1605** (USM); 3090–3150 m, *Valencia & Franke 3* (USM); Zárate, 2800 m, *Valencia & Franke 96* (USM); Dist. San Bartolomé, Monte Zárate, arriba de San Bartolomé, 2600–2700 m, July 1977, *Valencia & Franke s.n.** (USM).

Barnadesia blakeana es afín a *B. reticulata* de la cual se diferencia por poseer espinas de menor longitud, dispuestas más próximas, y por el papus barbelado.

4. **Barnadesia caryophylla** (Vell.) S. F. Blake, Proc. Biol. Soc. Wash., 38: 86. 1925. *Xenophontia caryophylla* Vell., Fl. flumin. 346. 1825. TIPO: Ic. 8 in Vell., Fl. Flumin. 1831 (holótipo).

Barnadesia spinosa Less., Linnaea 5: 245. 1830. TIPO: figs. 58–62 in Less., Linnaea 5: 239, 243–246. 1830 (holótipo).

Barnadesia laxa D. Don, Trans. Linn. Soc. London, Bot. 16: 280. 1833. TIPO: "In Brasilia," *Sello s.n.* (holótipo, B probablemente destruido; neótipo, aqui asignado, K no visto, fotografía, LP).

Barnadesia rosea Lindl., Bot. Reg. 29: t. 29. 1843. *Rhodactinea rosea* (Lindl.) Gardner, London J. Bot. 6: 449. 1947. TIPO: Ic. 29. in Lindl., Bot. reg. 29. 1843 (holótipo).

Barnadesia rosea var. *macrospinosa* Loefgr., Bol. Commiss. Geogr. Estado São Paulo 12: 488. 1897. *Barnadesia caryophylla* var. *macrospinosa* (Loefgr.) I. C. Chung, sin. nov. Rev. *Barnadesia* 42. 1965. TIPO: *Herbario da Commissão 346* (holótipo, SP no visto, fotocopia, LP).

Nombre vulgar. "Espinho de agulha" (*Hoehne 389*).

Arbusto de 0.60–4.00 m de alto. Espinas geminadas, rectas o curvas, de 12–28 mm de largo. Hojas dispuestas en fascículos, ocasionalmente algunas hojas alternas; pecíolo menos 4 mm; láminas oblanceoladas, obovadas o elípticas, pubescentes a subglabras en la cara adaxial, de 28–78 × 11.8–42.0 mm; ápice atenuado u obtuso, mucronado; ocasionalmente con la nerviación marcada. Capí-

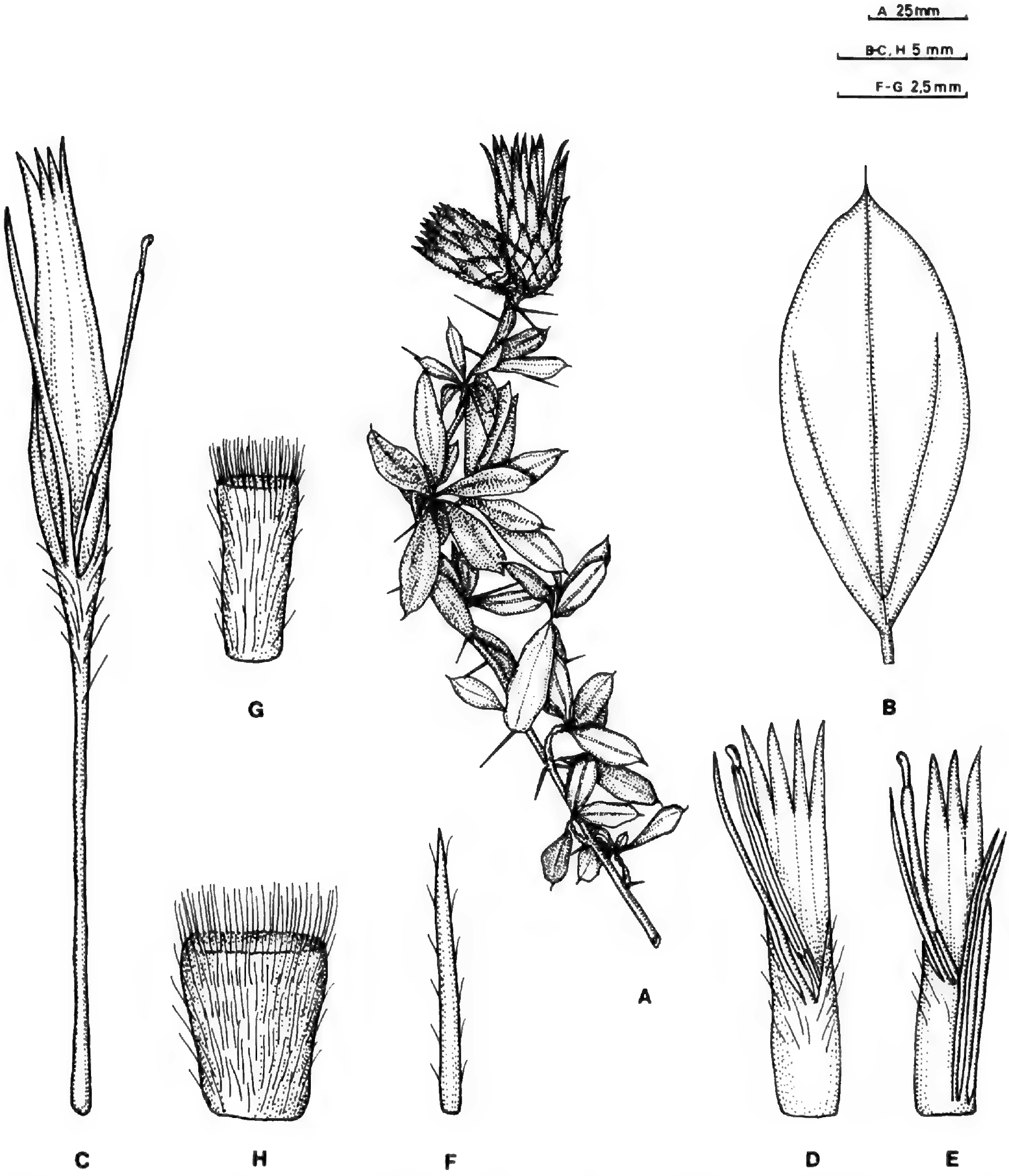


Figura 15. *Barnadesia blakeana.* (*Ferreyra 10427,* MO) —A. Rama. —B. Hoja. —C. Corola: (4+1), estambres y estilo de la flor del margen. —D, E. Corola: (4+1, 3+1), estambres y estilo de la flor del disco. —F. Cerda del papus de la flor del disco. —G. Aquenio de la flor del margen. —H. Aquenio de la flor del disco.

tulos sésiles, solitarios, geminados o en cimas racemiformes. Involucro turbinado, de 33–46 × 20–32 mm, filarias ca. 95, mucronadas o espinosas, con pelos en el dorso y cilias en el margen, dispuestas en 10–12 series: las exteriores de 2.2–4.5 mm de largo, las intermedias de 4.2–32.8 mm de largo, las interiores de 24.4–37.0 mm de largo. Corolas de color rosado, rosado fuerte, rojo, rojo fuerte o purpúreo-lilacinas, ligeramente dimorfas o dimorfas. Flores del margen trece; corola bilabiada (4+1), de 25.8–50.0 mm de largo, labio interno de 10.0–12.5 mm de largo, labio externo de 11.8–18.0 × 3–4 mm, tubo de 16.0–34.5 mm de largo; anteras decurrentes en la base, de 7.2–10.0 mm de largo, filamentos libres, parte libre de la corola de 2.2–3.0 mm de largo; estilo de 21.5–48.0 mm de largo, ramas estilares de 0.5–1.0 mm de largo; papus de 17–23 mm de largo; aquenios cilíndricos o levemente turbinados, de 3.0–5.5 × 1.0–2.5 mm. Flores del disco tres, perfectas; corola bilabiada (4+1), de 14–18 mm de largo, labio interno de 9.8–13.0 mm de largo, labio externo de 9.8–13.0 × 3.8–5.0 mm, o corola ligulada 5-lobada, de 15.0–18.8 mm de largo, tubo de 3–8 mm de largo; anteras 5, decurrentes en la base, de 6.5–8.8 mm de largo; filamentos libres, parte libre de la corola de 3.2–7.0 mm de largo; estilo de 14.0–18.8 mm de largo, ramas estilares de 0.5–0.8 mm de largo; papus simple, más largo que el tubo de la corola, de 12.4–21.5 mm de largo; aquenios de 4–7 × 2.0–3.2 mm. Polen radioasimétrico. Figuras 16, 34.

Distribución y ecología. Bolivia, Brasil y Perú. Crece en la selva, selva lluviosa, bosque talado, bosque bajo, matorral y monte; entre 600–2700 m. Epoca de floración: febrero–noviembre.

Material adicional examinado. BOLIVIA. **La Paz:** Prov. Sud Yunga, near Irupana, *Cárdenas 4370* (GH); Cañamina, 4500 m, *White 258* (US). BRASIL. **Distrito Federal:** Corrego da Papuda, *Ezechias et al. 1291* (LP, US); entre Brasilia e Nique Landia, *Pires et al. 9703* (LP); Brasilia, *Vindobon s.n.* (NY). **Goiás:** Mpio. de Pirenópolis, Fazenda Olaria, *Pereira 1084* (US), *Saint-Hilaire 736* (GH); vicinity of Estrela do Norte, Belém–Brasilia, *Prance & Silva 58432* (NY); upper Río Araquaia, 700 m, *Irwin et al. 17486* (US); Serra Dourada, ca. 17 km S Goiás Velho, ca. 6 km NE of Mossamedis, ca. 750 m, *Anderson 9937* (MO). **Matto Grosso:** Serra do Chapada, *Malme 1648** (GH, NY). **Minas Gerais:** Caldas, 1854, *Regnell s.n.* (MO), *198* (GH, NY), *Regnell 190* (NY), *Widgren 192* (US); Fazenda Monte Alegre, Monte Belo, *Soraya 30* (NY); Planalto do Brasil, Serra do Caiapo, 950 m, *Irwin et al. 17807* (NY); Pinheirinho, *Porto 360* (LP). **Rio de Janeiro:** Rio de Janeiro, environs de Río de Janeiro et d'Ouropreto, *Glaziou 14942* (GH); Jardín Botánico, *Damazio D–4805* (LP). **São Paulo:** Museo Paulista, cultivada, *Hoehne 389* (NY); Agua Funda, Jardín Botánico do Estado (cultivada), *Teixeira 255* (GH); Capital, Bairro do Ipiranga, proximo ao Museu Paulista, 1 Oct. 1942, *Pickel s.n.* (MO); Morro Pellado, *Edwall 16983** (LP, US); S. Paulo inter Mongimerins et Urisanga, *Burchell 5186* (US); São Paulo, *Kiehl 3711* (US). PERÚ. **Amazonas:** Mendoza, 1400 m, *Woytkowski 8121* (MO). **Cajamarca:** Colasay, 2700 m, *Woytkowski 6880** (GH, MO). **Junín:** Chanchamayo, near La Merced, *Soukup 2510* (US); 2 km N of San Ramón, *Whalen & Salick 868** (NY); Yucapata, *Woytkowski 6637* (MO); entre La Merced y Quimiri, valle de Chanchamayo, 800–900 m, *Ferreyra 3696* (MO); Chanchamayo, *Isern 36** (LP); 6 km S of Vitoc, along road between San Ramón and Pucara, 1100 m, *Wasshausen & Encarnación 1141* (US). **Lima:** Lima, in the Botanical Garden at the O.E.A (cultivada), *Robertson & Austin 12* (MO). **Puno:** Sandía, San Juan del Oro, 1300 m, *C. Vargas 16401* (US). **San Martín:** Moyobamba, 890 m, *Woytkowski 15482* (MO); Zepelacio, near Moyobamba, 1100–1200 m, *Klug 3318* (GH, MO, NY, US); Lamas, San Roque, 1350–1500 m, *Williams 7241* (GH, US).

Barnadesia caryophylla es la única especie del género que crece en el Brasil. Se caracteriza por sus capítulos brillantes vistosos, dispuestos en forma solitaria, geminada o en cimas racemiformes.

Si bien en la descripción original del género *Xenophontia* se menciona como especie típica a *X. caryophyla,* con una sola l, en la iconografía se lee *X. caryophylla,* esta diferencia ortográfica ya ha sido sugerida como un error tipográfico por Blake (1925), por lo cual el nombre válido es *X. caryophylla.*

Chung (1965) designa para *Barnadesia caryophylla* el neótipo *Gardner 4268.* Dado que existe una iconografía en la descripción original de *Xenophontia caryophylla* no es válido el neótipo mencionado de acuerdo con el artículo 9.13(a) del Código Internacional de Nomenclatura Botánica (Greuter et al., 1994).

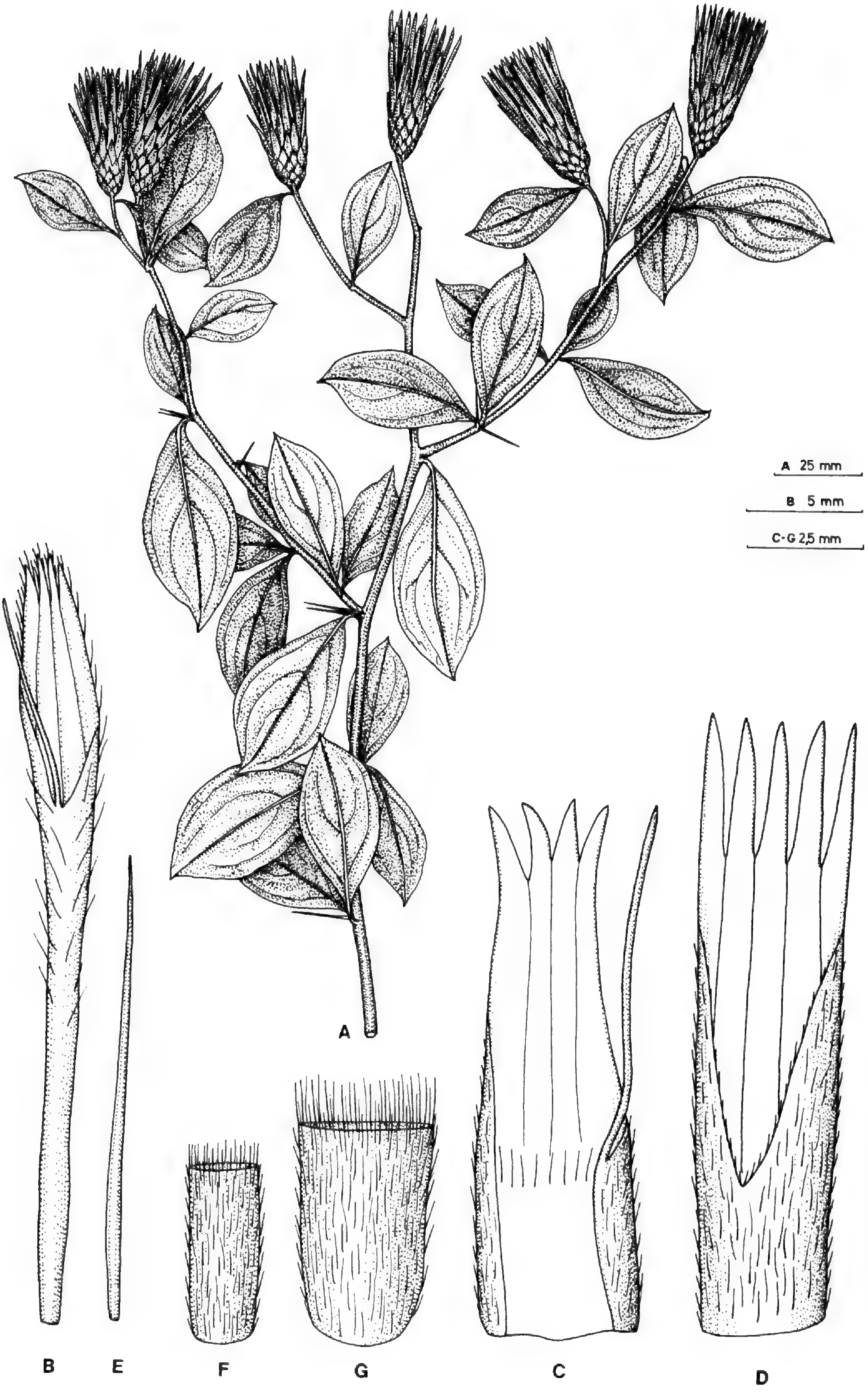
Löfgren (1897) creó la variedad *macrospinosa* para *B. caryophylla,* sobre la base de dos caracteres vegetativos: (1) hojas menores que la variedad típica y (2) espinas hasta 40 mm. Através de la fotocopia del ejemplar tipo de *B. rosea* var. *macrospinosa,* pude observar que las espinas no superan los 20 mm y la longitud de sus hojas queda comprendida en las medidas tomadas para la variedad típica. Como resultado de las observaciones considero a la variedad *macrospinosa* como un sinónimo de *B. caryophylla.*

5. **Barnadesia dombeyana** Less, Linnaea 5: 246. 1830. TIPO: Perú, *Dombey s.n.* (lectótipo, designado por Chung (1965), P no visto, fragmentos del tipo USM; fotografía, LP).

Bacasia spinosa Ruiz & Pav., Syst. veg. fl. peruv. chil. 188. 1798 (non *Barnadesia spinosa* L.f.). TIPO: Perú. Habitat in Peruviae subalpinus et praeruptis frigides ad huarocheri, Tarmae et Cantae Provincias, *Ruiz & Pavón s.n.* (holótipo, MA no visto, fragmentos del tipo USM, fotografía, LP).
Barnadesia lanceolata (Ruiz & Pav. ex DC.) D. Don, Trans. Linn. Soc. London, Bot. 16: 277. 1833.
Bacasia lanceolata Ruiz & Pav. ex DC., Prodr. 7: 3. 1838. TIPO: Perú. In Peruvia, *Dombey s.n.* (holótipo, BM no visto; isótipos, B probablemente destruido, fotografía serie Field Museum N° 8264; GH, MO).

Nombres vulgares. "Bindote" (*Sagástegui et al. 9385*), "chungal" (*Angulo & López 1381, López & Sagástegui 2755*), "coñor" (*Becker & Terrones 1013*), "punas" (*López Miranda 311, 1059*), "quincha" (*Cerrate 276, 523, 1318*).

Arbusto de 1–3 m de alto. Espinas en fascículos, de 9–50 mm de largo. Hojas en fascículos; pecíolo menos 2 mm; láminas oblanceoladas, pubescencia en ambas caras, en la cara adaxial escasa, aumentando hacia el borde y la vena media, de 14.5–29.4 × 4.8–10.2 mm; ápice atenuado u obtuso, mucro-


A 25 mm
B 5 mm
C-G 2,5 mm
A
B
E
F
G
C
D

nado o espinoso. Capítulos sésiles, geminados, en cimas racemiformes o corimbiformes. Involucro acampanado, de 22–32 × 12–19 mm, filarias ca. 82, mucronadas o espinosas, dispuestas en 7–9 series: las exteriores de 3.5–9.0 mm de largo, las intermedias de 5.5–24.5 mm de largo, las interiores de 18.5–30.0 mm de largo. Corolas de color rosado fuerte o lilacino, ligeramente dimorfas, dimorfas o trimorfas. Flores del margen trece; corola bilabiada (4+1), de 23.5–38.8 mm de largo; labio interno de 10.2–13.0 mm de largo, labio externo de 12–17 × 3–5 mm; tubo de 13–21 mm de largo; anteras decurrentes en la base, de 6.0–9.8 mm de largo, tubo estaminal de 4.0–6.8 mm de largo; estilo de 19.2–40.0 mm de largo; ramas estilares de 0.5–0.9 mm de largo; papus de 9–15 mm de largo; aquenios cilíndricos de 2.0–3.9 × 1–2 mm. Flores del disco tres, perfectas; corola bilabiada (4+1), (3+1), ocasionalmente ligulada, 5-secta, corolas bilabiadas de 12.2–17.8 mm de largo, pubescente en el tercio medio, y disminuyendo la pubescencia hacia la base y el ápice, labio interno de 9.4–14.5 mm de de largo, labio externo de 10.3–14.6 × 4.0–5.6 mm; tubo de 2–5 mm de largo, y corola ligulada, 5-secta, de 13–15 mm de largo, tubo de 4–5 mm de largo; anteras 4 ó 5, decurrentes en la base, de 5.5–8.5 mm de largo; filamentos libres entre sí, parte libre de la corola 4.0–8.5 mm de largo; estilo de 15.9–23.8 mm de largo, ramas estilares de 0.8 mm de largo; papus barbelado, más largo que el tubo de la corola, de 6–14 mm de largo; aquenios de 3–4 × 1.5–4.0 mm. Polen radioasimétrico. Figuras 17, 36.

Distribución y ecología. Perú. En quebradas, laderas de montañas, matorrales, entre 1790–4300 m. Epoca de floración: enero–noviembre.

Material adicional examinado. PERÚ. **Ancash:** Bolognesi, Cerca de Chiquián, 3500 m, *Cerrate 1318* (MO); Mararrackra, cerro NO Chiquián, 3520–3560 m, *Cerrate 17* (MO); Chiquián, 3800–3850 m, *Ferreyra 6216* (MO); Bolognesi, *Cerrate 276* (MO); Cerros al E de Chiquian, *Cerrate 523* (MO); Pasamarca, 3680 m, *Cerrate 1407* (MO); Casma, El Tambo, 3600 m, *Mostacero et al. 532* (MO, NY, US); km 13, 3800 m, *Zardini 1511* (MO); Huascarán National Park, Quebrada Carhuazcancha, 3970 m, *Smith et al. 12360** (MO); Recuay, edge of Río Santa, 3390 m, *Gentry et al. 37463* (MO); Catac, entre Conococha y Tipapampa, 3600–3700 m, *Ferreyra 14292* (MO). **Apurimac:** Abancay, 3200 m, *Stork et al. 10615* (UC). **Cajamarca:** 38 km N Huamachuco, cerca de Cajamarca, 2900–3000 m, *Ferreyra 3039* (MO); bajando cumbre "El Gavilán hacia Chile," 3000 m, *Ferreyra 3331* (MO); Huarhuashpata, Chamis Bajo, 3100 m, *Becker & Terrones 1013* (US); 3 km E Encañada, road to Celendín, 3470 m, *Hutchison & Wright 5120* (MO, UC, US); N along road from Cajamarca to Bambamarca, 10,600 ft., *King & Bishop 9115** (MO, US); Coscabamba, arriba de Contumazá, *Sagástegui et al. 9013* (MO, SI); Jalca de Chuño, 4000 m, *Sagástegui et al. 9385* (MO). **Huánuco:**Yanahuanca, about 10,000 ft., *Macbride & Featherstone 1222* (GH); Chasqui, 10,500 ft., *Macbride & Featherstone 1759* (GH, US); Huamalies, Llata, about 7000 ft., *Macbride & Featherstone 2250* (GH, US). **La Libertad:** Bolívar, Camino de Las Quisbus, 3000 m, *López & Sagástegui 3280* (LP); Otuzco, 9 km W of and below shore toward Trujillo, *Hutchinson et al. 6289* (MO, NY, UC); Chota, Yamobamba shore, 2900 m, *Sagástegui et al. 11066* (MO, NY); Agallpampa, 3200 m, *López 311* (LP), *1059* (LP); Sánchez Carrión, near Huamachuco, *Smith 2236* (SI); alrededores de Yamobamba, 1790 m, *Angulo & López 1381* (LP); entre Yanazaca y Huaquil, 3750 m, *López Sagástegui 2755* (LP); Pataz, camino al Nevado Huaylillas, 3400–3500 m, *Riccio & La Rosa 3625* (US); entre Yanazaray Huaquil, carretera al Río Marañón, 3750 m, *López & Sagástegui 2755** (LP). **Lima:** Obrajillo, near Canta, *US exploring expedition under the command of Charles Wilkes* (US-65078); along Río Chillón, above Obrajillo, 2800–3200 m, *Pennell 14397* (GH); cerca de San Juan, Valle de Chancay, 3000–3200 m, *Ferreyra 18415* (MO). **Pasco:** Daniel Carrion, 16 km NE Yanahuanca, 1 km NW of Paucar, along fencerow, 3450 m, *Bird 1258* (MO); cerca de Salcachupán, carretera cerro de Pasco–Huánuco, 3300–3400 m, *Ferreyra 8062* (MO).

Barnadesia dombeyana es afín a *Barnadesia arborea* de la cual se distingue por sus tallos más armados, cuyas espinas alcanzan los 50 mm, y por las corolas de las flores del disco glabras en la garganta.

Usos. En varias etiquetas de herbario se cita el uso de estos arbustos para cercos.

6. **Barnadesia glomerata** Kuntze, Revis. gen. pl. 3 (2): 135. 1893. TIPO: Bolivia. Cochabamba: Tunari, 4 Mayo 1892, *Kuntze s.n.* (lectótipo, designado por Chung (1965), NY no visto, fotografía, LP; isolectótipo, US).

Arbusto de 1–3 m de alto. Espinas geminadas o en fascículos, de 9–21 mm de largo. Hojas en fascículos, ocasionalmente algunas hojas alternas; subsésiles, pecíolo menos 3 mm; elípticas o ligeramente oblanceoladas, pubescencia en ambas caras, cara adaxial de pubescente a subglabra, de 40–70 × 14–18 mm; ápice atenuado, mucronado o

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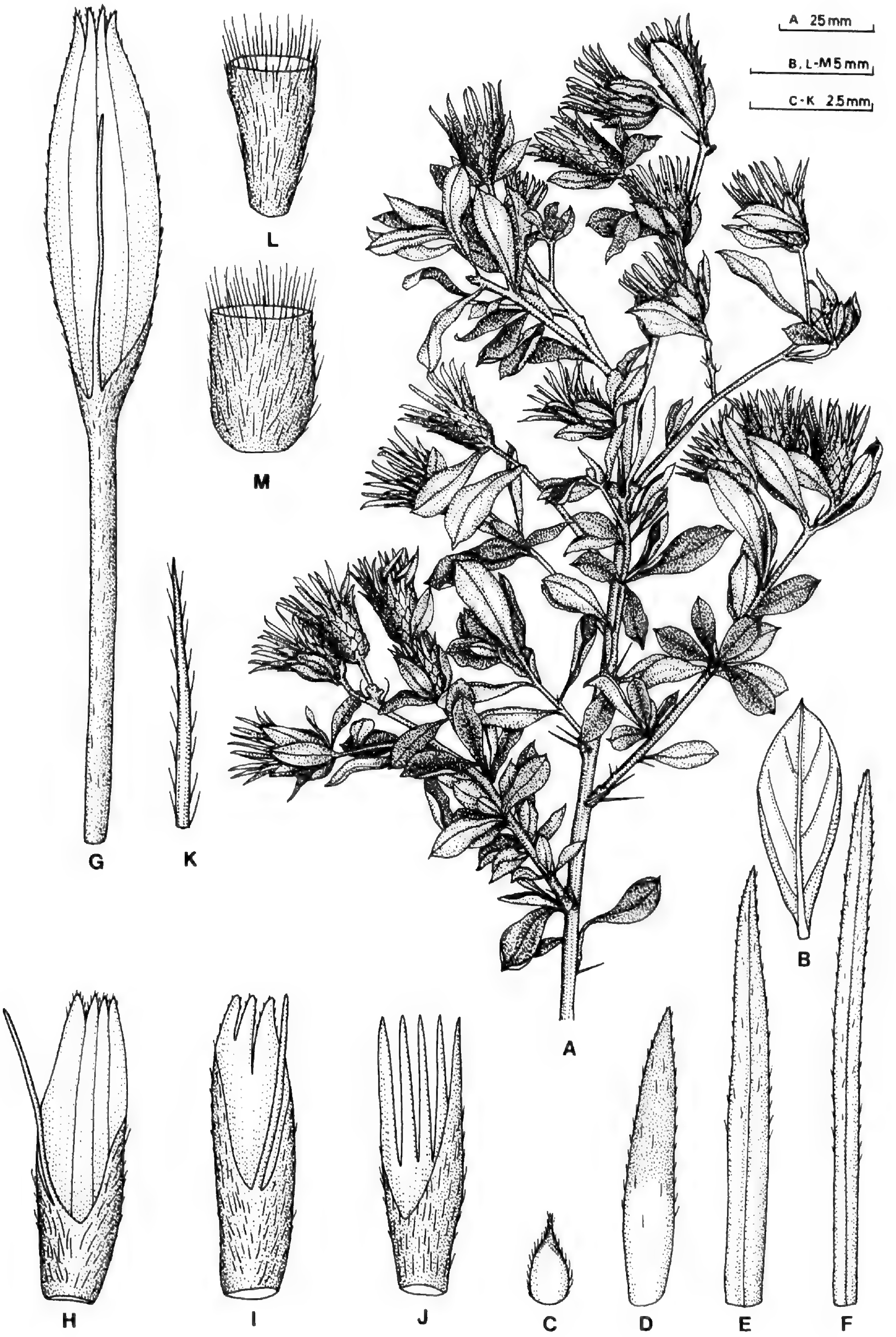
Figura 16. *Barnadesia caryophylla.* —A. Rama. —B. Corola de la flor del margen: (4+1) (*Irwin et al. 17486*, US). —C. Corola de la flor del disco: (4+1) (*Edwall 16983*, LP). —D. Corola de la flor del disco: (5+0). —E. Cerda del papus de la flor del disco. —F. Aquenio de la flor del margen. —G. Aquenio de la flor del disco (*Irwin et al. 17486*, US).


A 25mm
B, L-M 5mm
C-K 2.5mm
L
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espinoso. Capítulos sésiles, en cimas corimbiformes o en panojas. Involucro acampanado, de 16–22 × 15–18 mm, filarias dispuestas en 8–9 series: las exteriores de 2.5–6.0 mm de largo, las intermedias de 7–12.0 mm de largo, las interiores de 16.5–17 mm de largo. Corolas de color blanco, crema, rosado o purpúreas, ligeramente dimorfas o dimorfas. Flores del margen ocho; corola bilabiada (4+1), de 19–25 mm de largo, labio interno de ca. 7.2 mm de largo, labio externo de 9.0–13.2 × 4 mm, tubo de 9–12 mm de largo; anteras cortamente sagitadas en la base, de 6.1–6.8 mm de largo; filamentos libres, parte libre de la corola de 2 mm de largo; estilo de 17.5–24.2 mm de largo, ramas estilares de 0.5 mm de largo; papus de 11.5 mm de largo; aquenios levemente turbinados de 2–3 × 1.0–1.4 mm. Flor del disco una, perfecta, corola bilabiada (4+1 ó 3+2) o ligulada 5–lobada ca. de 15 mm de largo; tubo 7–7.5 mm de largo; anteras 5, sagitadas en la base, de 5.8–6.0 mm de largo; filamentos libres, parte libre de la corola de 9.0–9.4 mm de largo; estilo de 15–17 mm de largo, ramas estilares de 0.4–0.5 mm de largo; papus simple, más corto que el tubo de la corola, de 5–7 mm de largo; aquenios de 3–4 × 2.2–2.5 mm. Polen radiosimétrico. Figuras 18, 37.

Barnadesia glomerata es afín a *B. macbridei* de la cual se distingue por el papus de la flor del disco más corto que el tubo de la corola y por el polen radiosimétrico.

Barnadesia glomerata es endémica de Bolivia; comprende 2 variedades:

1a. Filarias espinosas .... 6a. *B. glomerata* var. *glomerata*
1b. Filarias mucronadas .... 6b. *B. glomerata* var. *mucronata*

6a. **Barnadesia glomerata** var. **glomerata**

Esta variedad se caracteriza por los involucros de menor longitud (16–20 mm), formado por filarias espinosas; por las corolas de las flores del margen de hasta 19 mm, y por presentar en la flor del disco corola bilabiada (4+1) o ligulada (5+0).

Distribución y ecología. *Barnadesia glomerata* var. *glomerata* es endémica del departamento de Cochabamba. Crece en las laderas de montañas, cerca de los 2800 m. Epoca de floración: abril–mayo.

Material adicional examinado. BOLIVIA. **Cochabamba:** Prov. Ayapaya. Naranjito–El Chovo–Ayopaya–Cochabamba, 2800 m, *Cárdenas 4290* (US).

6b. **Barnadesia glomerata** var. **mucronata** I. C. Chung, Rev. *Barnadesia* 33. 1965. TIPO: Bolivia. Santa Cruz: Comaropa, Jungas de San Mateo, 2500 m, 22 Oct. 1928, *Steinbach 8400* (holótipo, GH; isótipos, MO, UC, US).

Esta variedad se caracteriza por sus involucros de mayor tamaño (ca. 22 mm), formado por filarias mucronadas; por las corolas de las flores del margen de mayor longitud (ca. 25.2 mm) y por presentar en la flor del disco corola bilabiada (4+1 ó 3+2). Figura 37.

Distribución y ecología. *Barnadesia glomerata* var. *mucronata* es endémica del departamento de La Paz. Crece en bosques y bosque nublado, entre 2500 y 3000 m. Epoca de floración: junio–octubre.

Material adicional examinado. BOLIVIA. **La Paz:** Inquisivi, N-facing slope of Loma El Abra just below ridgeline, ca. NW from Inquisivi, *Lewis 88899* * (MO, NY); along the first creek E of and 1 km E of Loma El Abra, ca. 6 km NW of Inquisivi, 2800 m, *Lewis 881138* (US); along the trail between Loma El Abra and cerro Negro Khota 6 km hike, ca. 6 km N from Inquisivi, 2900–3000 m, *Lewis 881108* (MO).

7. **Barnadesia horrida** Muschl., Bot. Jahrb. Syst. 50, Beibl. 111: 100. 1914. TIPO: Perú. Colles Sacsaihuamam prope Cuzco, in formatione aperta sed interdum densa herbis fruticibusque composita, 3500–3600 ms.m., 24 mayo 1905, *Weberbauer 4859* (holótipo, B probablemente destruido; fotografía serie Field Museum N° 15911: GH, LP, MO). Perú: Cusco: Saxaihuaman hills, *Herrera 1544* (neótipo, designado por Chung (1965), US).

Nombres vulgares. "Llaulli" (*Vargas 1896, 4360*).

Arbusto de 1.2–3.0 m de alto. Espinas geminadas de 17.0–26.5 mm de largo. Hojas en fascículos; peciolos menos de 2.5 mm; láminas oblanceoladas, pubescentes en ambas caras, la pubescencia más abundante en la vena media y el borde de la superficie abaxial; de 14–29 × 3.3–6.9 mm; ápice

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Figura 17. *Barnadesia dombeyana* (*Hutchison & Wright 5120,* UC). —A. Rama. —B. Hoja. —C–F. Brácteas involucrales. —G. Corola de la flor del margen: (4+1). —H–J. Corolas de la flor del disco: (4+1, 3+1, 5+0). —K. Papus de la flor del disco. —L. Aquenio de la flor del margen. —M. Aquenio de la flor del disco.

Figura 18. *Barnadesia glomerata* var. *glomerata* (*Cárdenas 4290,* US). —A. Rama. —B–E. Brácteas involucrales. —F. Corola: (4+1), estambres y estilo de la flor de margen. —G. Flor del disco sin el ovario: (5+0). —H. Aquenio de la flor del margen. —I. Aquenio de la flor del disco.

atenuado, espinoso. Capítulos sésiles, solitarios, cimas racemiformes o en panoja. Involucro acampanado de 25–35 × 12–15 mm, filarias en número ca. 61–69, espinosas; con pelos en el dorso y cilias en el margen, dispuestas en 7–8 series: las exteriores de 4–11 mm de largo, las intermedias de 9.5–29.1 mm de largo, las interiores de 22.0–29.4 mm de largo. Corolas de color blanco, rosa-rojizo o rojo oscuro, dimorfas. Flores del margen ocho; corola bilabiada (4+1), de 20.0–35.7 mm de largo, labio interno de 10–14 mm de largo, labio externo de 2.0–3.4 × 3–4 mm; tubo cilíndrico de 14.2–19.5 mm de largo; anteras decurrentes en la base, de 8.0–10.2 mm de largo; filamentos libres, parte libre de la corola de 3.2–5.4 mm de largo; estilo de 19.2–35.0 mm de largo, ramas estilares de 0.4–0.9 mm de largo; papus de 13.0–16.5 mm de largo; aquenios cilíndricos o levemente turbinados, de 2.5–3.5 × 1.1–2.6 mm. Flor del disco una, perfecta; corola subligulada 5-secta (raro 4-secta), pubescente en el tubo disminuyendo la pubescencia hacia el ápice, de 12.5–14.0 mm de largo, con pelos en la garganta; anteras 5(–4), decurrentes en la base, de 7.7–9.6 mm de largo; filamentos libres parte libre de la corola de 2.0–5.6 mm de largo; estilo de 13.1–19.2 mm de largo; ramas estilares de 0.5–1.0 mm de largo; papus barbelado, más largo que el tubo de la corola, de 10.5–15.3 mm de largo; aquenio de 2.0–3.8 × 1.6–2.8 mm. Polen radioasimétrico. Figuras 19, 33.

Distribución y ecología. Perú. Crece en las laderas de las montañas entre 2100–3800 m. Epoca de floración: marzo–agosto.

Material adicional examinado. PERÚ. **Apurimac:** Valle of Río Colcacha at Cotarusi–Colca ca. 1 km above junction W Río Chalhuanca ca. 15 km (air) S of Chalhuanca, 9900–10100 ft., *Iltis et al. 541* (US). **Ayacucho:** Huanta, N of Abancay at km 200, above Chineros, 3700 m, *Hutchison 1718* (GH, NY, US); between Huanta and Hacienda Pargora, 3700 m, *Killip & Smith 22187* (NY); Dist. of Humanguilla, ca. 15 km before Ayacucho left of road Huanta–Ayacucho, *Saunders 725* (NY). **Cusco:** alrededores de Cusco, *Cabrera & Fabris 13531* (LP); 4.5 km from Cusco on road to Pisac, *Ugent & Ugent 3853* (US); Quenco, *Krapovickas & Cristóbal 38162** (SI); 55 km E of Cusco on road to Paucartambo, 19 km of Huancarana, 3300 m, *Gentry et al. 23407* (NY); N of Cusco, 1 km above ruins of Tambomachay, 3600 m, *Ugent 4372* (US); Tambomachay bei Cusco, 3600 m, 1 mar. 1969, *Doppelbaur & Doppelbaur s.n.* (MO); Paururo, Mpio. Huaynacancha, along road from Yaurisque to Cusco, 10,800 ft., *Grifo et al. 1065* (MO). **Huancavelica:** Tayacaja, Hacienda Tocas, entre Colcabamba y Paucarbamba, 3000–3100 m, *Tovar 1931* (MO); Paucartambo, Valle de Paucartambo, hacienda Pfuyucalla, 2400 m, *Herrera 2956* (US); quebrada de Llulluchayoco, 3100 m, *C. Vargas 4360* (LP); Paucartambo, 11,500 ft., *Balls B–6683** (UC, US); Inspicanchi, 3500 m, *Herrera 1055** (US); Urubamba, 2870 m, *Zamalloa D–66* (LP); Urubamba, alrededores de Peñas, 3600 m, *C. Vargas 16336* (US). **Puno:** Sandía, entre Sandía y Cuyocuyo, 3200–3300 m, *Ferreyra 16740* (MO).

Barnadesia horrida es afín a *B. macrocephala,* de la cual se diferencia por tener capítulos y flores más pequeños, y menor número de series de filarias.

8. Barnadesia jelskii Hieron., Bot. Jahrb. Syst. 36: 511. TIPO: Perú. Crescit inter Chota et Cutervo, Jun. 1879, *Jelski 748* (holótipo, B probablemente destruído; foto serie Field Museum Nº 15912: MO). Perú: Amazonas: Chachapoyas. *Mathews s.n.* (neótipo, designado por Chung (1965), K no visto; isoneótipo, GH).

Barnadesia jelskii var. *acuta* I. C. Chung, Rev. *Barnadesia.* 56. 1965. TIPO: Ecuador. Pichincha: Malchingui to Pomasqui, 3000–3600 m, *Hitchcock 20968* (holótipo, US; isótipo, GH).

Nombre vulgar. “Coñor” *(Sagástegui et al. 8798).*

Arbusto de 2–6 m de alto. Espinas geminadas o en fascículos, de 11.5–33.0 mm de largo. Hojas en fascículos; pecíolo menos 2.5 mm; láminas elípticas u oblanceolas, pubescencia en ambas caras (en la cara adaxial sobre la vena media y en la cara abaxial más en toda la superficie), de 19.0–27.8 × 9–13 mm; ápice atenuado u obtuso, mucronado o espinoso. Capítulos sésiles en cimas racemiformes, cimas corimbiformes o en panoja. Involucro acampanado, de 21–28 × 7–17 mm, filarias ca. 63, mucronadas o espinosas, con pelos en el dorso y cilias en el margen, dispuestas en 7–9 series: las exteriores de 2.3–6.0 mm de largo, las intermedias de 7.0–20.2 mm de largo, las interiores, de 20.0–22.5 mm de largo. Corolas de color rosado, purpúreo o lilacino, ligeramente dimorfas o dimorfas. Flores del margen ocho; corola bilabiada (4+1), de 22–33 mm de largo, labio interno de 8–13 mm de largo, labio externo de 11.5–16.0 × 3.8–4.0 mm, tubo de 9–17 mm de largo; anteras decurrentes en la base, de 5.5–7.6 mm de largo; tubo estaminal de 3.5–8.5 mm de largo; estilo de 20.8–34.0 mm de largo, ramas estilares de 0.5–1.0 mm de largo; papus de 13.5 mm de largo; aquenios levemente turbinados, de 2–5 × 1.2–2.0 mm. Flores del disco una, perfectas; corola bilabiada (4+1) ocasionalmente (3+1), de 10.0–12.2 mm de largo, labio interno de 7.0–10.5 mm de largo, labio externo de 7.0–9.2 × 4–7 mm, densamente pubescente en el tubo, con pelos en la garganta; anteras 5, decurrentes en la base, de 5.0–6.8 mm de largo; filamentos libres, parte libre de la corola de 5.0–8.8 mm de largo; estilo de 15.4–18.0 mm de largo, ra-

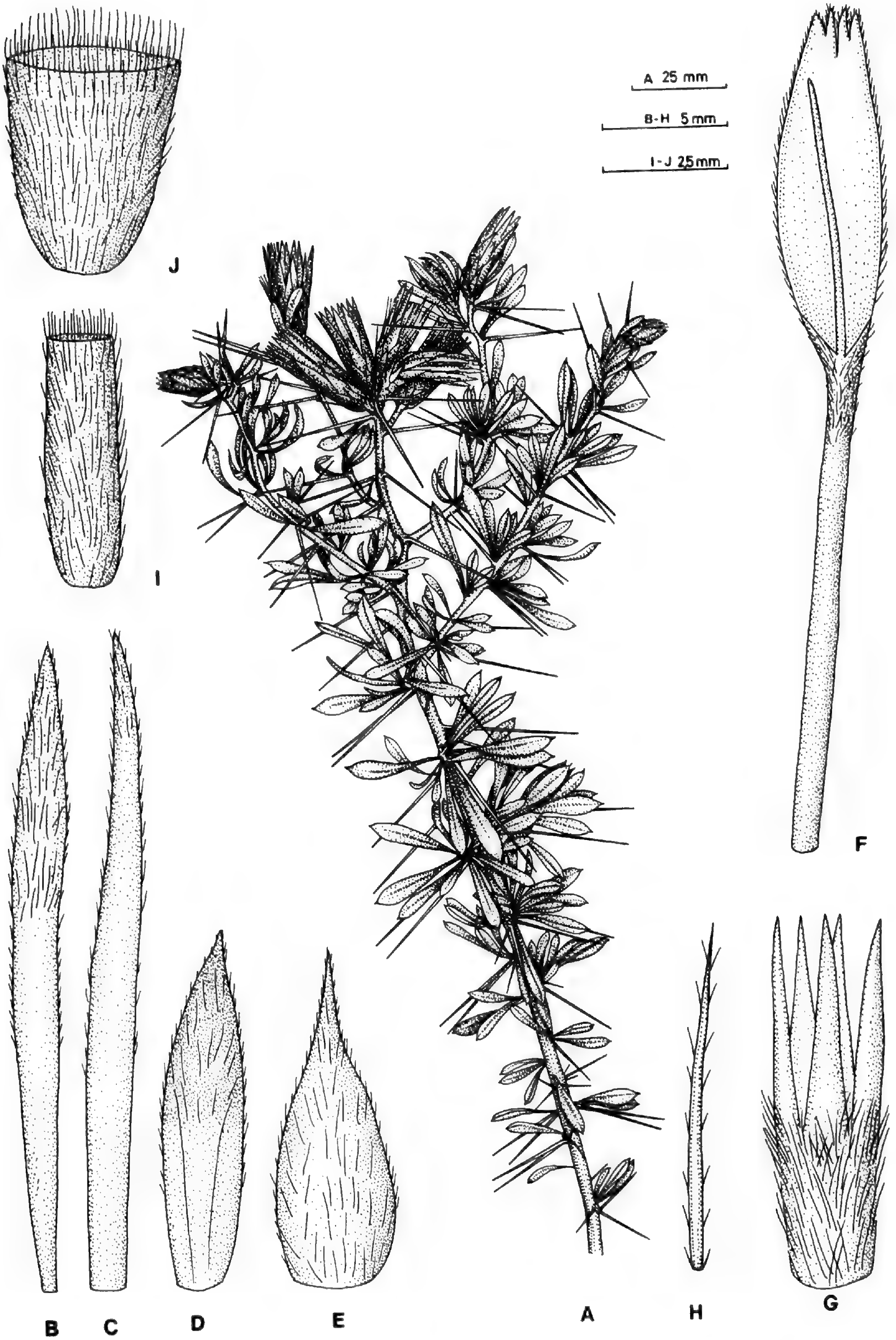


Figura 19. *Barnadesia horrida* (*Balls B-6683*, UC). —A. Rama. —B–E. Brácteas involucrales. —F. Corola de la flor del margen: (4+1). —G. Corola de la flor del disco. —H. Papus de la flor del disco. —I. Aquenio de la flor del margen. —J. Aquenio de la flor del disco.

mas estilares de 0.4–0.8 de mm de largo; papus barbelado, más largo que el tubo de la corola, de 7.0–10.5 mm de largo; aquenios de 2.2–3.5 × 2–3 mm. Polen radioasimétrico. Figuras 20, 31.

Distribución y ecología. Perú y Ecuador. En laderas de montañas y bosques bajos, entre 2500–3619 m. Epoca de floración: enero–agosto.

Material adicional examinado. PERÚ. **Cajamarca:** Celendín, Cruz Conga, entre Cumullca y Celendín, *Ferreyra 13281* (MO); Sendamal (ruta a Celendín), 3100 m, *Sagástegui et al. 12235** (NY); cerca de Celendín, 3400–3500 m, *Ferreyra 15032* (MO); Chota, arriba de Chota, Chaupelanche, 2800 m, *Ferreyra 8493** (MO); Cutervo, entre Cutervo y Cochabamba, 2500–2600 m, *Ferreyra 838* (MO); San Miguel, El Tingo (Agua–Blanca), 2750 m, *Sagástegui et al. 8798* (MO). **Piura:** Huancabamba (Mitopampa), Huancabamba–Cuello del Indio, 2650 m, *Sagástegui et al. 8239* (MO).

Barnadesia jelskii se distingue por presentar tubo estaminal en las flores del margen, corola bilabiada y papus barbelado en la flor del disco.

9. Barnadesia lehmannii Hieron., Bot. Jahrb. Syst. 29: 77. 1901. TIPO: Ecuador. Chimborazo: Pallatanga, *Lehmann 5238* (lectótipo, designado por Chung (1965), K no visto, fotografía, LP; isolectótipo, GH, USM).

Arbusto de 1–5 m de alto. Espinas geminadas, de 15–55 mm de largo. Hojas subsésiles, pecíolo menos de 4 mm; oblanceoladas, obovadas o elípticas; pubescencia en ambas caras; de 21–82 × 11–45 mm; ápice atenuado u obtuso, espinoso o mucronado. Capítulos solitarios, geminados o en cimas racemiformes. Involucro acampanado o ligeramente cilíndrico, de 25–45 × 12–30 mm, filarias en 8–14 series: las exteriores de 2.5–9.0 mm de largo, las intermedias 10–28 mm, las interiores 20–45 mm largo, glabras o pubescentes. Corolas de color rosado, rosado-violáceo, liláceo o rojo, ligeramente dimorfas o dimorfas. Flores del margen trece; corola bilabiada (4+1), de 32–46 mm de largo; labio interno de 8–17 mm de largo, labio externo de 10.5–28.0 × 3–5 mm, tubo de 20.0–31.5 mm de largo; estilo de 31.5–41.0 mm de largo; ramas estilares de 0.7–0.8 mm de largo; anteras decurrentes o cortamente sagitadas en la base, de 6–12 mm de largo; filamentos libres, parte libre de la corola de 1.5–2.5 mm de largo; papus de 17–24 mm de largo; aquenios cilíndricos o ligeramente obovados de 4–5 × 1.8–4.0 mm. Flores del disco tres, perfectas; corola bilabiada (3+1), ocasionalmente (4+1), de 13–22 mm de largo, tubo de 4–7 mm de largo, con pelos en la garganta; estilo de 15–28 mm de largo; ramas estilares ca. 0.5 mm de largo; anteras 4 ó 5, decurrentes o cortamente sagitadas en la base, de 8.5–12.5 mm de largo; filamentos libres, parte libre de la corola de 3.0–12.5 mm de largo; papus simple, más largo que el tubo de la corola, de 8–20 mm de largo; aquenios de 4 × 3–4 mm. Polen radioasimétrico.

Barnadesia lehmannii es la especie con mayor variabilidad de caracteres vegetativos e involucrales, caracterizada por las corolas de las flores del disco bilabiadas (3+1) raro (4+1), pubescentes en la garaganta. *Barnadesia lehmannii* reune 4 variedades:

1a. Involucro 13–14-seriado; filarias glabras en el dorso y ciliadas en el margen .... 9c. *B. lehmannii* var. *ciliata*
1b. Involucro 8–12(–13)-seriado; filarias pubescentes en el dorso y ciliadas en el margen.
  2a. Capítulos lustrosos .... 9d. *B. lehmannii* subsp. *villosa*
  2b. Capítulos no lustrosos.
    3a. Hojas elípticas u obovadas .... 9a. *B. lehmannii* var. *lehmannii*
    3b. Hojas angostamente oblanceoladas .... 9b. *B. lehmannii* var. *angustifolia*

9a. Barnadesia lehmannii var. lehmannii

Barnadesia hutchisoniana Ferreyra, sin. nov. Publ. Mus. Hist. Nat. "Javier Prado" Ser. B., Bot. 18: 1964. TIPO: Perú. Amazonas: Prov. Bongará, 2200–2300 m, *Ferreyra 15201* (holótipo, USM; isótipo, MO).

Nombre vulgar. "Cachambique" (dato de etiqueta).

Barnadesia lehmannii var. *lehmannii* posee hojas elípticas u obovadas. Capítulos no lustrosos. Involucro acampanado o ligeramente cilíndrico, 10–12 seriado, 32–45 × 19–30 mm. Corolas de las flores del margen de 32–46 mm long. Corolas de la flores del disco bilabiadas (3+1), ocasionalmente (4+1). Figuras 21, 38.

Distribución y ecología. Ecuador y Perú. Crece en el monte, suelos pedregosos–arcillosos, entre 300 y 2500 m. Epoca de floración: mayo–septiembre.

Material adicional examinado. ECUADOR. **Cañar:** valley of Río Cañar, near Rosario; 3500 ft., *Prieto CP–24A, CP–24B** (NY). **Chimborazo:** vicinity of Huigra, mostly on the Hacienda de Licay, *Rose & Rose 22134* (GH, US). PERU. **Cajamarca:** Chota, cerca de Llama, 2000 m, *Ferreyra 8394* (MO); entre Llama y Chongoyape, 2200–2500 m, *Ferreyra 862* (MO). **Contumazá:** 2100 m, *Sagástegui 9819* (MO); arriba de Trinidad, 2200 m, *Sagástegui et al. 8945* (MO). **Lambayeque:** Lambayeque, W side of Abra de Porculla pass, 35 Km E of Olmos, 1650 m, *Hutchison 1378* (GH, NY, UC). **Piura:** Ayabaca, on road to Ayabaca, 18 km above Puente Tandopa, 1700 m, *Hutchison & Wright 6684* (UC). **Huancabamba:** arriba de Palambla, 1300 m, *López & Sagástegui 8802* (MO);

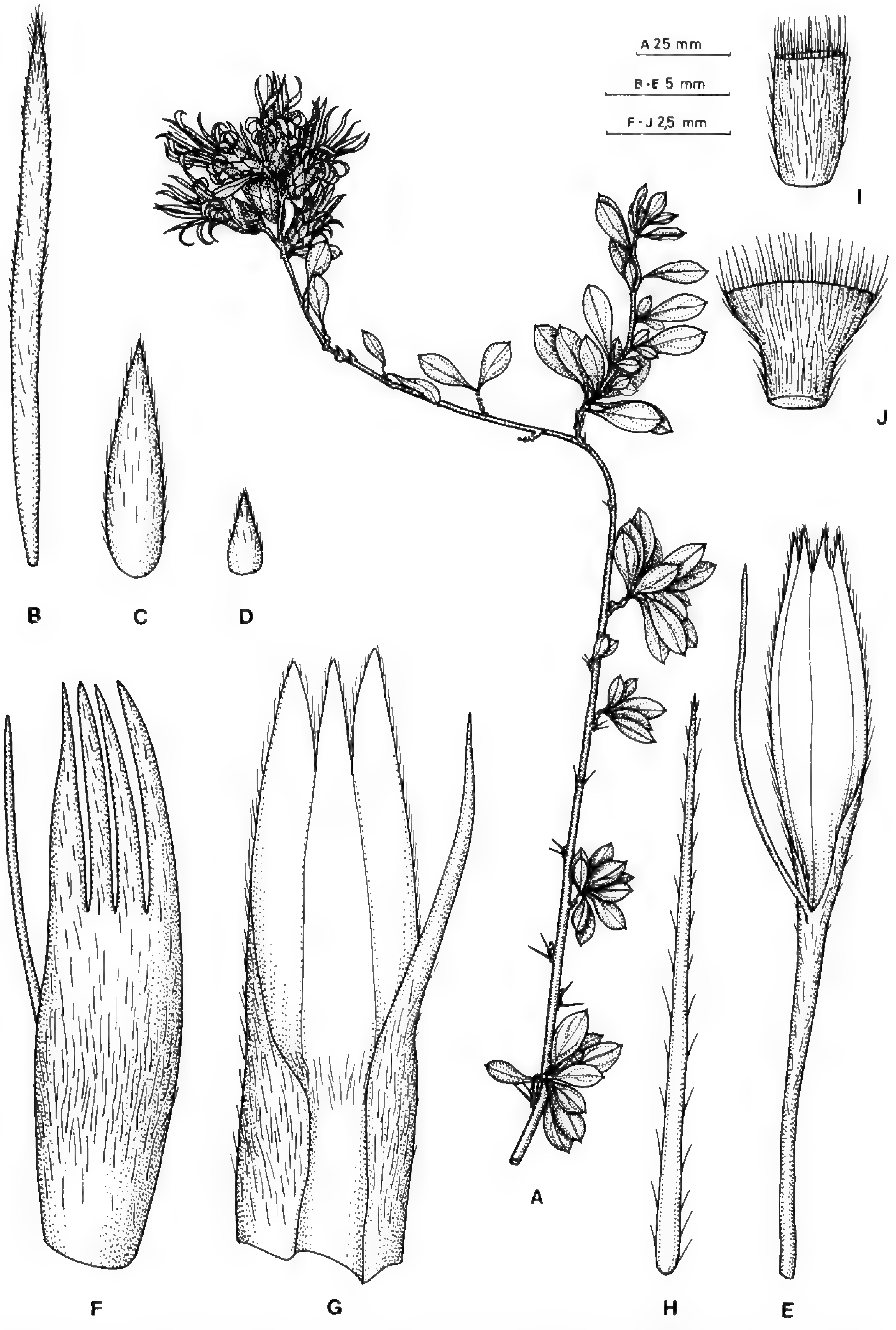


Figura 20. *Barnadesia jelskii* (*Ferreyra 15032*, MO). —A. Rama. B–D. Brácteas involucrales. —E. Corola de la flor del margen: (4+1). —F, G. Corolas de la flor del disco (4+1; 3+1). —H. Papus de la flor del disco. —I. Aquenio de la flor del margen. —J. Aquenio de la flor del disco.

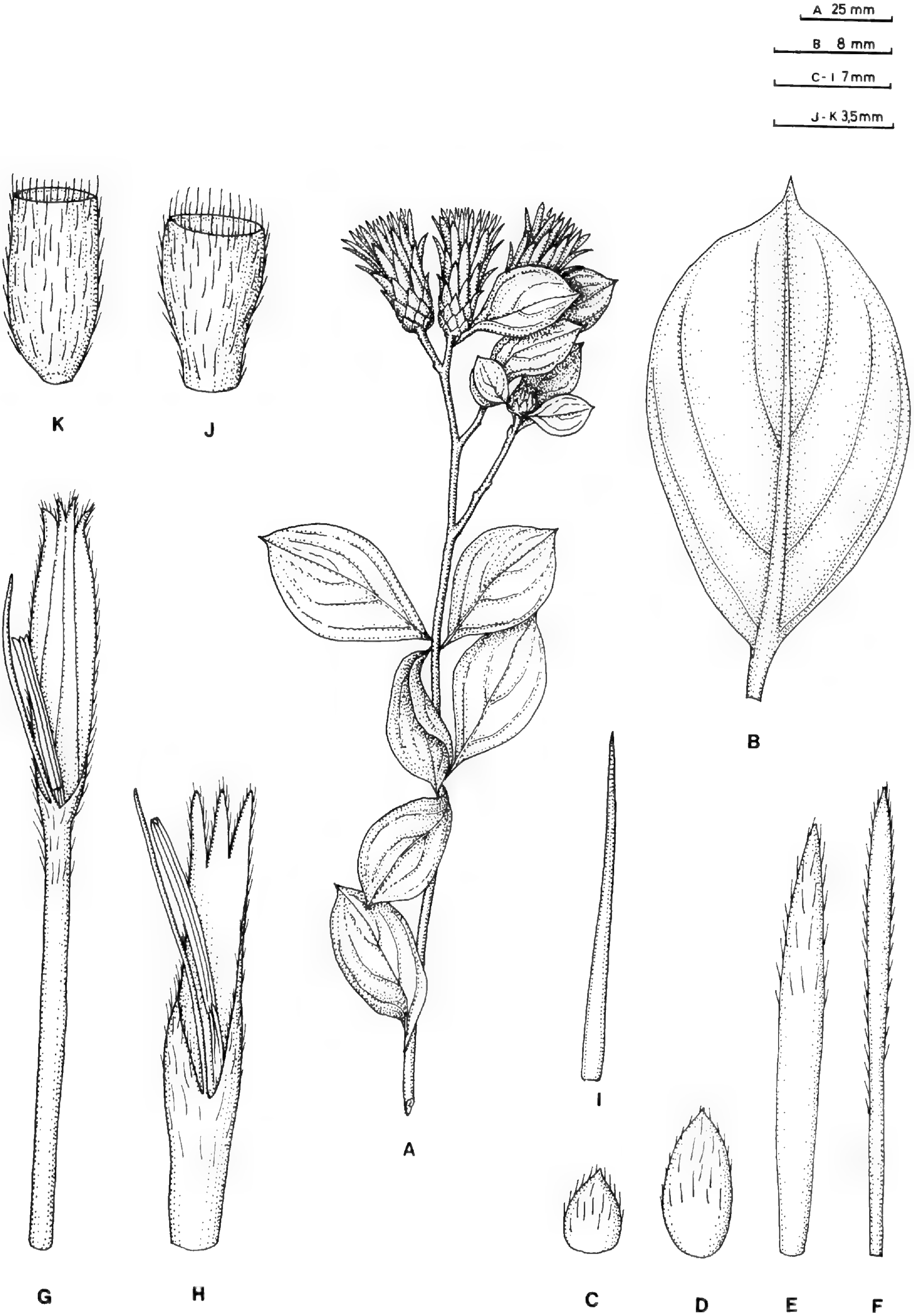


Figura 21. *Barnadesia lehmannii* var. *lehmannii* (*Hitchcock 20751*, US). —A. Rama. —B. Hoja. C–F. Brácteas involucrales. —G. Corola: (4+1), estambres y estilo de de la flor del margen. —H. Corola: (3+1), estambres y estilo de la flor del disco. —I. Cerda del papus de la flor del disco. —J. Aquenio de la flor del margen. —K. Aquenio de la flor del disco.

Palambla, 2000 m, *Soukup 4283* (US). **Tumbes:** Zarumilla, El Gaucho, 300–400 m, *Maekawa s.n.* (MO).

Barnadesia lehmannii var. *lehmannii* es la variedad con mayor distribución: crece desde la provincia de Chimborazo (Ecuador) hasta el departamento de Cajamarca (Perú).

Ferreyra (1964) funda a *Barnadesia hutchisoniana* considerándola afín a *B. lehmannii* y distinguiéndola de esta por sus hojas de menor tamaño, el involucro acampanado y las brácteas involucrales con ápice involuto y dorso glabrescente. Sin embargo, el estudio de los materiales tipo y adicionales me permitieron observar que el tamaño de las hojas y la forma del involucro están comprendidos en la variabilidad morfológica de *B. lehmannii* var. *lehmannii*. En cuanto al ápice de las brácteas involucrales, no observé que sean involutos. Por lo tanto, considero a *B. hutchisoniana* un sinónimo de *B. lehmannii* var. *lehmannii*.

9b. Barnadesia lehmannii var. **angustifolia** I. C. Chung, Rev. *Barnadesia* 50. 1965. TIPO: Perú. Lima: Canta, June 1938, *Sandeman 216* (holótipo, BM no visto; isótipo, K).

Barnadesia lehmannii var. *angustifolia* posee hojas ligeramente oblanceoladas. Capítulos no lustrosos. Involucro acampanado, 8 seriado, 32–35 × 22–25 mm. Corolas de las flores del margen de 39 mm long. Corolas de la flores del disco bilabiadas (4+1).

Distribución. Esta variedad es endémica del departamento de Lima, Perú.

Material adicional estudiado. PERÚ. **Lima:** Moyobamba, *Mathews 1389* (K); above Huamantanga and Obrajilla, *Mathews 643* (K).

Esta variedad es muy afín a *B. lehmannii* var. *lehmannii* diferenciándose por sus hojas ligeramente oblanceoladas, de hasta 35 mm de largo y espinosas en el ápice. Figura 38.

9c. Barnadesia lehmannii var. **ciliata** I. C. Chung, Rev. *Barnadesia* 50. 1965. *Barnadesia ciliata* (I. C. Chung) Harling, Fl. Ecuador. 190(10): 10. 1991. TIPO: Ecuador. Zaruma, Río Calera, *Espinosa 1853** (holótipo, F).

Barnadesia lehmannii var. *ciliata* posee hojas oblanceoladas. Capítulos lustrosos. Involucro ligeramente cilíndrico, 13–14 seriado, 40 × 25 mm. Corolas de las flores del margen de ca. 45 mm long. Corolas de las flores del disco bilabiadas (3+1). Figura 38.

Distribución y hábitat. *Barnadesia lehmannii* var. *ciliata* es endémica de la provincia de Loja, Ecuador.

Hasta el momento sólo ha sido colectado el material tipo, el cual corresponde a la localidad de Zaruma.

9d. Barnadesia lehmannii var. **villosa** (I. C. Chung) Urtubey, comb. et stat. nov. Basionimo: *Barnadesia polyacantha* var. *villosa* I. C. Chung, Rev. *Barnadesia*. 46. 1965. TIPO: Ecuador. Chimborazo: Alansi, 2500 m, 19, 27 July 1923, *Hitchcock 20692* (holótipo, GH; isótipos, NY, US).

Barnadesia polyacantha var. *attenuata* I. C. Chung, Rev. *Barnadesia* 47. 1965. TIPO: "Ecuador. Loja, near Chinchas about 60 km W of Loja, 2200–2300 m, July 11, 1947," *R. Espinosa E. 1608* (holótipo, F).

Barnadesia kingii H. Rob., Phytologia 32: 414. 1975. TIPO: Ecuador. Azuay: along the road to Girón, ca. 6 km generally SW of Girón, 6500 ft., *King 6685* (holótipo, US; isótipo, MO).

Barnadesia lehmannii var. *villosa* posee hojas oblanceoladas, elípticas o ligeramente obovadas. Capítulos lustrosos. Involucro acampanado, 8–9 seriado, 25–31 × 12–22 mm. Corolas de las flores del margen de 32.5–34.5 mm long. Corolas de la flores del disco bilabiadas (3+1 ó 4+1), de 13–17 mm long. Figura 38.

Distribución. Crece en Perú y Ecuador, entre 2200 y 3250 m. Epoca de floración abril–agosto.

Material adicional examinado. ECUADOR. Sin prov. determinada: Cotacocha, *Espinosa 596* (F). **Chimborazo:** Carretera Alsusí–Yocon grande García Moreno, 10 km de la población, 2600 m, *Jaramillo et al. 8975* (US); Cañón of the Río Chanchan about 5 km N of Huigra, 5000–6500 ft., *Camp C-3423* (NY); Cerro de Calubín, estribaciones de la Cord. Occ., Parroquia Sibambe, 2950–3250 m, *Acosta Solís 5485* (F). **Loja:** Región Central, 2250 m, *Acosta Solís 7775* (F); San Pedro, 2200 m, *Harling 6104* (S). PERU. **Piura:** Ayabaca, Pingola, 2250 m, *López Miranda 7803** (NY).

Barnadesia lehmannii var. *villosa* es afín a la variedad *ciliata* de la cual se diferencia principalmente por el tamaño del involucro formado por 8–9 series de filarias y por las corolas de la flores del disco ocasionalmente bilabiadas (4+1).

Sobre la base del análisis de los tipos y de los materiales adicionales pude comprobar la presencia de 13 flores en el margen y 3 flores en el disco, las corolas bilabiadas 3+1 o 4+1 y la pubescencia en la garganta de las corolas de las flores del disco, siendo estos caracteres diagnósticos de *B. lehmannii*. Como resultado de estas observaciones considero a *B. kingii* como otra variedad de *B. lehmannii*.

Al existir variedades de Chung (1965) que quedan comprendidos en *Barnadesia lehmannii*, *B. kingii* resulta un sinónimo de la nueva combinación *B. lehmannii* var. *villosa* (I. C. Chung) Urtubey.

10. Barnadesia macbridei Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, Bot. 18: 23. 1964. TIPO: Perú. Huánuco: Huacachi, cerca a Muña, *Macbride 3878* (holótipo, F; isótipo, USM).

Barnadesia glomerata var. *distincta* I. C. Chung, Rev. *Barnadesia* 36. 1965. TIPO: Perú. Junín: Prov. Jauja, 5 km to Comas, 3350 m, 8 July 1948, *Ochoa 553* (holótipo, US; isótipo, F).

Arbusto ca. 2 m de alto. Espinas geminadas o en fascículos, de 12.0–21.1 mm de largo. Hojas en fascículos, ocasionalmente algunas hojas alternas; pecíolo menos 3 mm; láminas elípticas u oblanceoladas, ambas caras pubescentes, de 35–39 × 14–16 mm; ápice atenuado, espinoso. Capítulos sésiles, en cimas corimbiformes o en panoja. Involucro acampanado, de 23–31 × 12–19 mm, filarias espinosas dispuestas en 7–8 series: las exteriores de 2.1–5.4 mm de largo, las intermedias de 8–14 mm de largo, las interiores de 20.5–27.0 mm de largo. Corolas de color rosado oscuro, ligeramente dimorfas. Flores del margen ocho; corola bilabiada (4+1), de 29.5–35.8 mm de largo; labio interno de 8.4–9.2 mm de largo, labio externo de 9.5–11.8 × 4–5 mm; tubo de 19–24 mm de largo; anteras decurrentes en la base, ca. 7 mm de largo; filamentos libres, parte libre de la corola ca. 1.3 mm de largo; estilo de 30.5–36.5 mm de largo; ramas estilares de 0.4–0.5 mm de largo; papus de 12 mm de largo; aquenios levemente turbinados, ca. 3 × 1 mm. Flores del disco una, perfecta; corola bilabiada (4+1), labio interno de 5 mm de largo; labio externo ca. 7.8 × 5.0–5.5 mm, tubo de 2.5–3.0 mm de largo; anteras 5, decurrentes en la base, de 6.0–6.5 mm de largo; filamentos libres, 3 insertos en la parte media interna del tubo de la corola y 2 en la garganta, parte libre de la corola ca. 5 mm de largo; estilo ca. 15 mm de largo; ramas estilares de 0.5 mm de largo; papus simple, más largo que el tubo de la corola, de 8.5–13.0 mm de largo; aquenio de 4.0 mm × 2.1 mm. Polen radioasimétrico. Figuras 22, 33.

Distribución y ecología. Perú. En laderas abiertas y quebradas estrechas húmedas, entre 2200–3350 m. Epoca de floración: febrero–julio.

Material adicional examinado. PERÚ. **Huánuco:** on open slope of ravine, 3 km E of Acomayo, 2200 m, *Woytkowski 34335** (MO, UC, US). **Lima:** Jardín Bot. de la U. N. M. San Marcos (cultivada), *Ferreyra 12946* (MO).

Barnadesia macbridei se distingue de las restantes especies por la flor del disco con papus de mayor longitud que el tubo de la corola, por las anteras decurrentes en la base y el polen radioasimétrico.

11. Barnadesia macrocephala Kuntze, Revis. gen. pl. 3 (2): 135. 1893. TIPO: Bolivia. Cochabamba: Sierra of Colomi between Cochabamba and Río Juntas, 1–4 Apr. 1892, *Kuntze s.n.* (lectótipo, designado por Chung (1965), NY).

Arbusto de 1–3 m de alto. Espinas geminadas, de 24–27 mm de largo. Hojas en fascículos; pecíolo menos 2 mm; láminas oblanceoladas, pubescencia en ambas caras, de 17–62 × 5.5–16.0 mm; ápice atenuado u obtuso, espinoso. Capítulos sésiles, dispuestos en cimas racemiformes o solitarios. Involucro acampanado o ligeramente cilíndrico, de 45–50 × 15–25 mm, filarias ca. 77, espinosas, con pelos en el dorso y cilias en el margen, dispuestas en 10–11 series: las exteriores 6.0–7.5 mm de largo, las intermedias 10.0–45.5 mm de largo, las interiores ca. 45.5 mm de largo. Corolas de color rosa o rosa oscuro, dimorfas. Flores del margen ocho; corola bilabiada (4+1), de 54–63 mm de largo; labio interno de 16–19 mm de largo, labio externo de 20–27 × 4.5–5.0 mm; tubo de 32–38 mm de largo; anteras decurrentes en la base, de 12.0–13.5 mm de largo; filamentos libres, parte libre de la corola de 3.5–4.5 mm de largo; estilo de 51–56 mm de largo; ramas estilares de 0.5 mm de largo; papus de 21–22 mm de de largo; aquenios cilíndricos o ligeramente turbinados, de 3.5 × 2.0 mm. Flores del disco una, perfecta; corola 5-secta, de 15–19 mm de largo, tubo de 3–5 mm de largo, con pelos en la garganta; anteras 5, decurrentes en la base, de 10 mm de largo; filamentos libres, parte libre de la corola de 4.0–7.5 mm de largo, estilo de 21–29 mm de largo, ramas estilares de 1 mm de largo; papus barbelado, más largo que el tubo de la corola, de 13.0–19.5 mm de largo, aquenios de 3.5–4.0 × 3.5 mm. Polen radioasimétrico. Figuras 23, 35.

Distribución y ecología. Bolivia. Crece en sitios semiáridos, entre 2800–3650 m. Epoca de floración: julio–noviembre.

Material adicional examinado. BOLIVIA. **Cochabamba:** Quebradas von Tiraque, 2900 m, *Steinbach 8723** (GH, MO); Nordosthange der Sierra de Cochabamba, Umgebung von Incachaca, 2800 m, *Wedermann 2009* (MO); Chaparre, 9.8 km S of Colomi (junction of the road to Candelaria), on the road to Cochabamba, 3500 m, *Solomon 14502** (MO, NY).

Barnadesia macrocephala es semejante a *B. ho-*

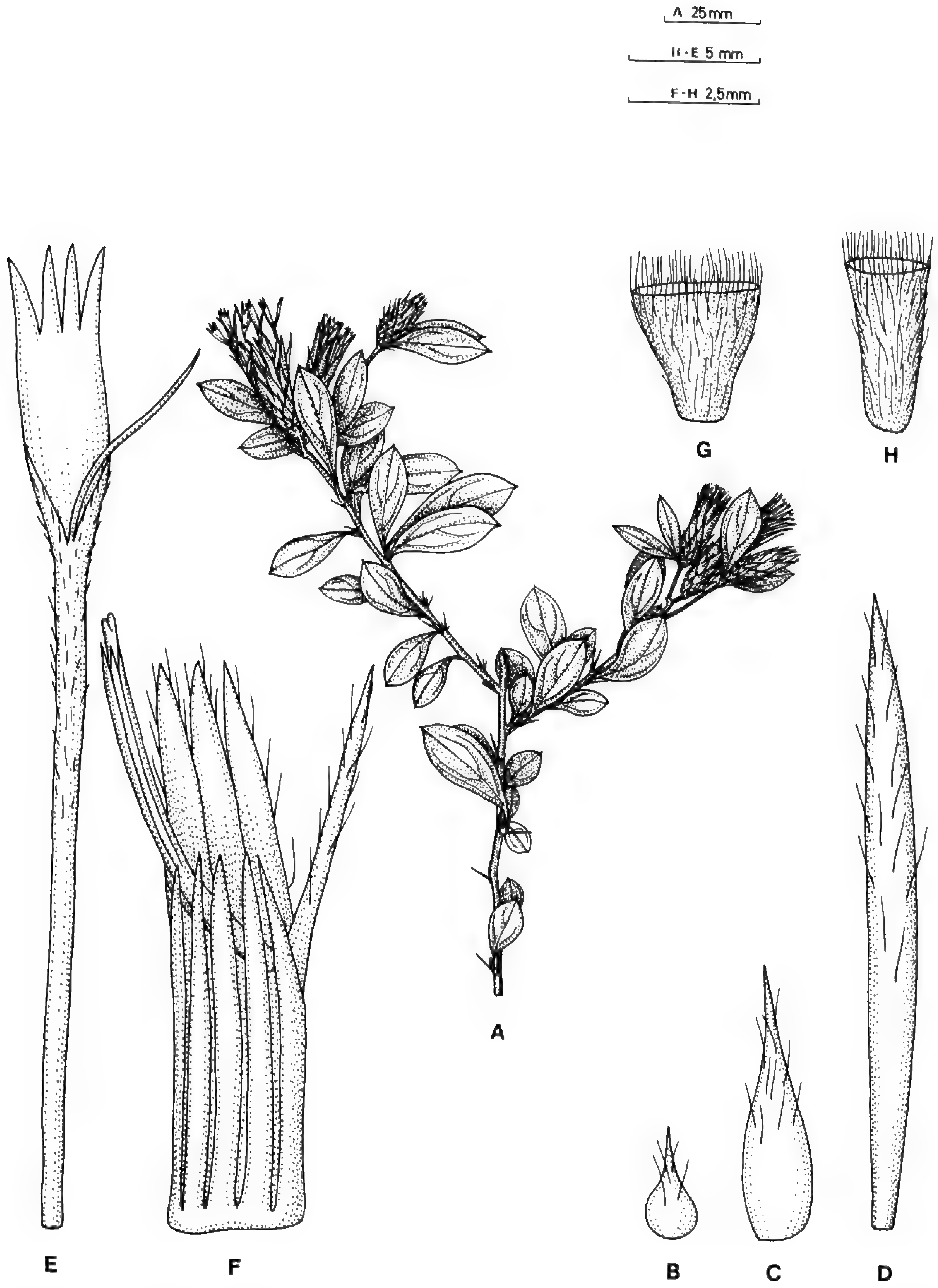


Figura 22. *Barnadesia macbridei* (*Ochoa 553*, US). —A. Rama. —B–D. Brácteas involucrales. —E. Corola de la flor del margen: (4+1). —F. Flor del disco sin el ovario: (3+1). —G. Aquenio de la flor del disco. —H. Aquenio de la flor del margen.

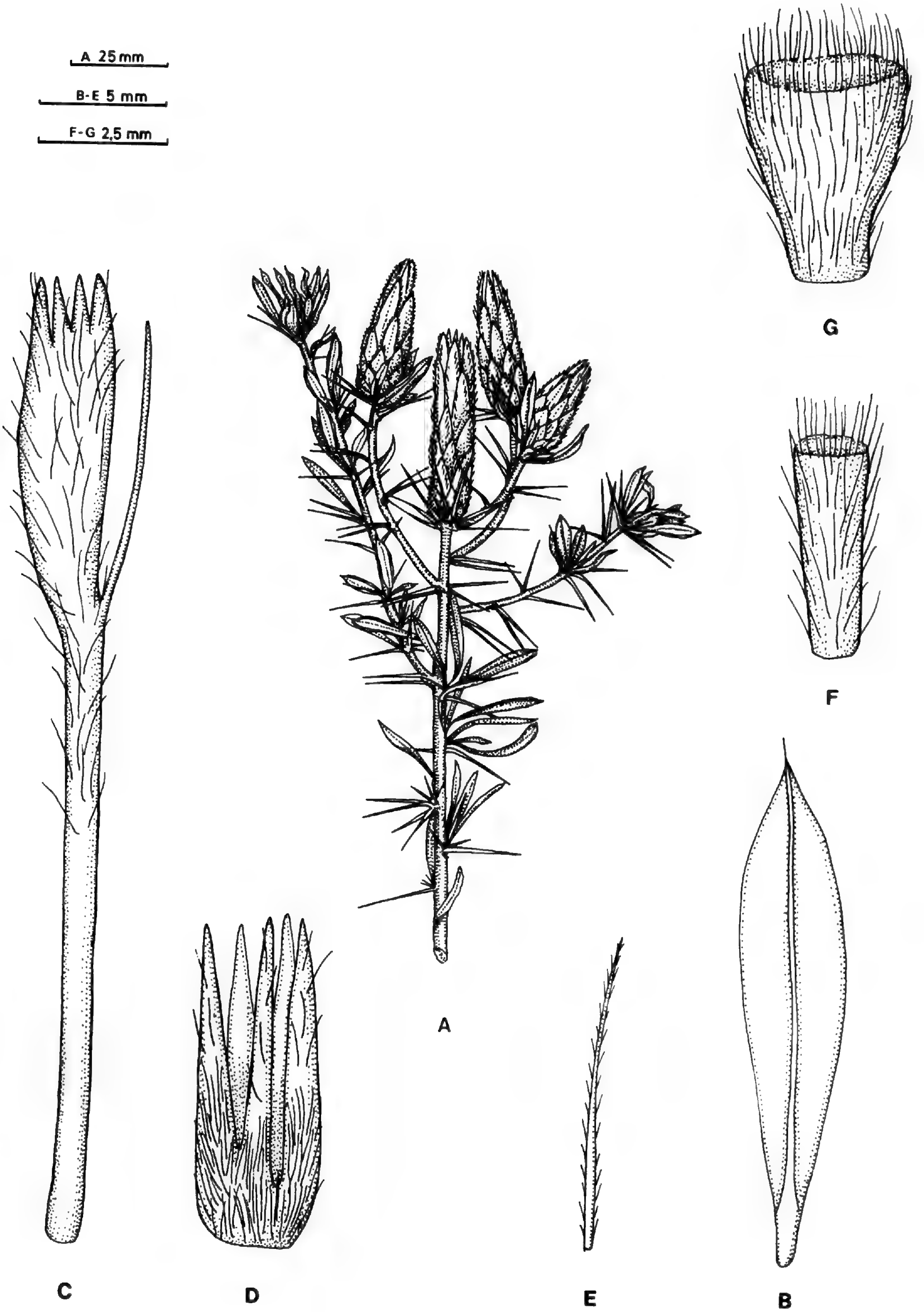


Figura 23. *Barnadesia macrocephala* (*Steimbach 8723*, MO). —A. Rama. —B. Hoja. —C. Corola de la flor del margen: (4+1). —D. Corola de la flor del disco. —E. Cerda del papus de la flor del disco. —F. Aquenio de la flor del margen. —G. Aquenio de la flor del disco.

rrida de la cual se distingue por los capítulos de mayor tamaño.

12. Barnadesia odorata Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 210. 1879. TIPO: Argentina. Tuscán and Taruca Pampa near La Cruz, 22–28 dic. 1872, *Lorentz & Hieronymus s.n.* (lectótipo, designado por Chung (1965), G no visto; fotocopia, LP).

Nombres vulgares. "Alfiler" (*Venturi 9503*), "alfilerillo" (*Krapovickas 42714, Nuñez et al. 56, 307*), "clavel" (Cabrera, 1978); "clavel de la puna" (*Hicken SI8084*), "clavelillo" *(Nuñez et al. 307, Ortin 17, Tolaba 186*; Cabrera, 1978), "zunchu kisca" (*Vargas 7*).

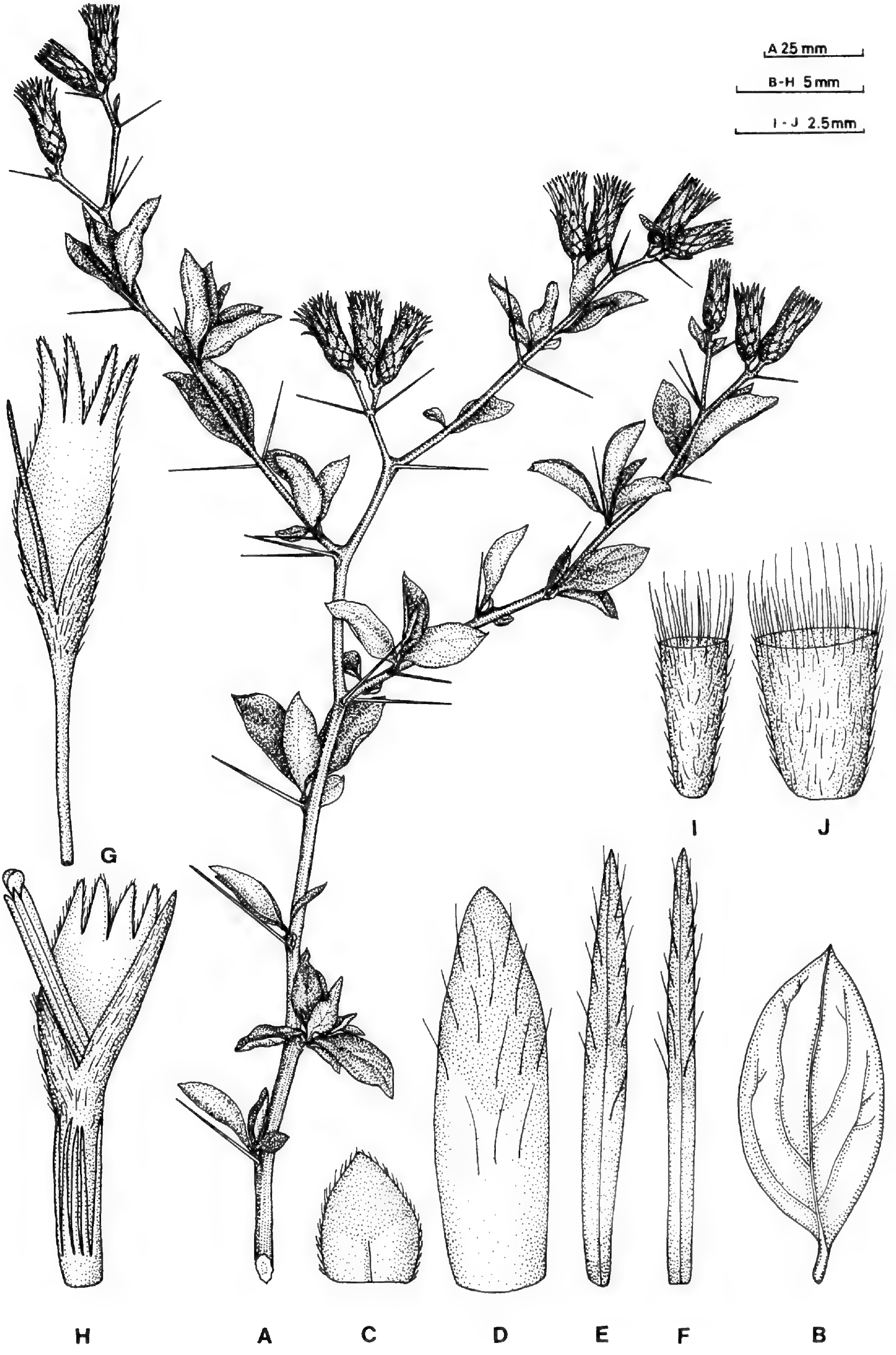
Arbusto de 1.0–3.5 m de alto. Espinas geminadas o fasciculadas, de 11–26 mm de largo. Hojas en fascículos ocasionalmente algunas hojas alternas; pecíolo menos 3 mm de largo; láminas elípticas u oblanceoladas, pubescentes en ambas caras, la pubescencia más abundante en la cara abaxial, de 29–71 × 10.5–21.2 mm; ápice atenuado, mucronado o espinoso. Capítulos sésiles, solitarios o geminados. Involucro acampanado, de 20–29 × 10–16 mm, filarias entre 84–102, mucronadas, con pelos en el dorso y cilias en el margen, dispuestas en 7–9 series: las exteriores de 2–6 mm de largo, las intermedias de 5–13 mm de largo, las interiores de 16.3–19.4 mm de de largo. Corolas de color blanco, rosado o lilacino, dimorfas. Flores del margen trece; corola bilabiada (4+1), de 18–23 mm de largo, labio interno de 8–10 mm de largo, labio externo de 10.8–12.4 × 3–4 mm, tubo cilíndrico de 6.5–12.0 mm de largo, anteras cortamente sagitadas en la base, de 5.8–7.1 mm de largo; filamentos libres, parte libre de la corola de 2–3 mm de largo; estilo de 15.0–19.8 mm de largo; ramas estilares de 0.4–1.0 mm de largo; papus de 9.5–12.0 mm de largo; aquenios cilíndricos de 2.4–4.0 × 0.7–1.2 mm. Flores del disco tres, perfectas; corola ligulada (5+0), densamente pubescente en el 1/3 medio, disminuyendo hacia la base y el ápice, de 13.8–19.8 mm de largo, tubo de 5.8–9.0 mm de largo; anteras 5, cortamente sagitadas en la base, de 5.5–6.8 mm de largo; filamentos libres, parte libre de la corola de 2–3 mm de largo; estilo de 14–20 mm de largo, ramas estilares de 0.4–1.0 mm de largo; papus simple, más corto o igual que el tubo de la corola, de 4.8–7.8 mm de largo; aquenios de 2.8–4.2 × 1.6–2.2 mm. Polen radiosimétrico. Figuras 24, 39.

Distribución y ecología. Habita en Argentina y Bolivia, en los bosques húmedos, en las laderas de montaña y en el borde de la selva de transición, entre 400–2500 m. Epoca de floración: febrero–noviembre.

Material adicional examinado. BOLIVIA. Sin Dpto. determinado: Salada bei Chiquiacá, 1500 m, *Fiebrig 2459* (GH). **Cochabamba:** Carrasco, Siberia–Cochabamba, 2800 m, *Cárdenas 5736* (LP, US); Yungas de San Mateo, Comaropa, 2500 m, *Steinbach 8418* (GH). **Santa Cruz:** Vallegrande, Huasacañada, 5 km S de la ciudad de Vallegrande, 2050 m, *I. G. Vargas 7* (NY, US). **Tarija:** O'Connor, San Diego, 1400 m, *Coro 1339* (SI); entre Riós a Cañada, *Zuloaga et al. 1334* (SI). ARGENTINA. **Jujuy:** Bárbara, El Fuerte, camino a la Laguna, *Guaglianone et al. 1940* (SI); alrededores de Jujuy, *Cabrera et al. 14389* (GH); Qda. de Lozano, *Kiesling 104* (SI); Yala, cerca del cementerio, *Krapovickas 42714* (GH); camino a Tiraxi a 9 km de Lozano, 1650 m, *Hunziker et al. 10359* (SI); camino a Laguna de Yala, *Urtubey 27* (LP); Termas de Reyes, *Cabrera 4558* (GH, US); Ledesma, Sierra de Calilegua, 700 m, *Venturi 5235* (SI, US); San Pedro, Cerro de San Pedro, 650 m, *Venturi 9608* (GH, MO, SI, US). **Salta:** camino Salta–Jujuy, por Las Cuestas, *Boelcke 2893* (SI); Lagunillas, *Hicken 20* (SI-1588); cerro San Bernardo, 14 July 1922, *Castellanos s.n.* (SI-8505); Yacones, Cuenca Mojotoro, *Yussen & Contino 10* (MCNS); camino de cornisa de Salta a Jujuy, pasando Lago Madera, *Urtubey 25* (LP); Anca, Parque Nacional del Rey, Filo Aguas Negras, *Brown et al. 1606* (SI); Ciudad de Salta, 1200 m, *Zapata 74* (MCNS); pie del cerro San Bernardo, 1250 m, *Novara 5491* (MCNS); Barrio Tres Cerritos, 1300–1400 m, *Gentry & Palací 51734* (MO, NY, SI); Qda. de San Lorenzo, 12 Oct. 1963, *Juárez s.n.** (LIL); camino a Los Yacones, entre San Lorenzo y Lesser, *Zardini 1183* (MO); Chicoana, Quebrada de Tilián, 1300 m, *Ortin 68* (MCNS); Finca Los-Los, arroyo Pantheón, 1400 m, *Rupnik 14* (MCNS); Guachipas, El Cebilar, 1400 m, *Varela & Del Castillo 214* (MCNS); La Caldera, 1400–1500 m, *Ortin 17* (MCNS); Alto La Sierra, km 1638, *Núñez & Marmol 307* (MCNS); A° Peñas Blancas, *Palací 74* (MCNS); Río La Caldera, ruta 9 (68) yendo a Jujuy 1 km más allá del puente La Caldera, *Novara 217* (MCNS); ruta Nac. N° 9 km 1620, 1 km S del paredón del Dique Campo Alegre, 1455 m, *Tolaba 266* (MCNS); La Candelaria, Sierra de La Candelaria, 1000 m, *Venturi 9503* (GH, MO); Unquillo, 1200 m, *Peirano 27145* (GH, UC); La Viña, Dique Cabra Corral, *Cabrera et al. 29765** (SI); Rosario de Lerma, La Silleta, fuera El Manantial, 10 km W del Pueblo La Silleta, 1400–1500 m, *Del Castillo 75* (MCNS); Campo Quijano, cerros al N del camping Municipal, 1520 m, *Tolaba 186* (MCNS); El Corralito, Río El Manzano, en la Usina, 10 km S de Campo Quijano, 1600–1700 m, *Novara 7371* (MCNS); Vaqueros, Arroyo Chaite, Zona I, *Núñez et al. 56* (MCNS). **Tucumán:** Burruyacú, Qda. Porcel–Sierra La Ramada,

→

Figura 24. *Barnadesia odorata* (*Charpin & Eslenche 20538*, US). —A. Rama. —B. Hoja. —C–F. Brácteas involucrales. —G. Corola de la flor del margen: (4+1). —H. Flor del disco sin el ovario: (5+0). —I. Aquenio de la flor del margen. —J. Aquenio de la flor del disco.


A 25 mm
B-H 5 mm
I-J 2.5 mm
G
I
J
H
A
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B

zona Norte, 450 m, *Peirano 58500* (GH); La Ramada, ladera del Cerro, 500 m, *Venturi 756* (GH); Cerro del Duraznillo, 700 m, *Monetti 1989* (GH); Sierra Medina, 1400 m, *Burkart 26536* (SI); Tafí, Tafí Viejo a Granja La Guillermina, 550 m, *Schreiter 4053* (UC); Tafí Viejo, faldas del Cerro, 700 m, *Venturi 756* (US); Tafi Viejo, 800 m, *Venturi 756* (GH, SI); Tafí del Valle, Cumbre de San Javier, R.P. N° 340, 1000 m, *Renvoize 3340* (MO, SI, US); Las Tipas, *Pedersen 9891* (NY).

Barnadesia odorata es la especie que llega más al sur (Prov. de Tucumán, Argentina). Se caracteriza por presentar capítulos verde-violáceos muy llamativos y por sus corolas de variado color en la misma planta.

Usos. Su madera es usada como leña.

13. Barnadesia polyacantha Wedd., Chlor. andina 1: 13. 1855. TIPO: Bolivia. Larecaja: near Sorata, *Weddell 4468* (lectótipo, designado por Chung (1965), P no visto, fotografía, LP; isolectótipos, GH, P no visto).

Barnadesia polyacantha var. *velutina* I. C. Chung, sin. nov. Rev. *Barnadesia* 46. 1965. TIPO: Bolivia. Larecaja: near Ananea, 2400 m, *Mandon 5* (holótipo, BM no visto; isótipos, G, K, NY, P no vistos, fotocopia, F).

Arbusto de 3–4 m de alto. Espinas geminadas o en fascículos, de 6.5–19.0 mm de largo. Hojas en fascículos; pecíolo menos de 3 mm; láminas elípticas, ocasionalmente obovadas o ligeramente lanceoladas, con pelos en ambas caras; de 9.5–44.0 × 4.5–16.0 mm; ápice atenuado u obtuso, mucronado. Capítulos sésiles, en cimas racemiformes, en cimas corimbiformes o en panojas. Involucro acampanado, de 24–42 × 13–28 mm, filarias ca. 88, dispuestas en 8–9 series: las exteriores de 2–9 mm de largo, las intermedias de 25.5–36.5 mm de largo, las interiores de 25.0–36.8 mm de largo. Corolas de color rosado o morado, dimorfas. Flores del margen trece; corola bilabiada (4+1), densamente pubescente en la parte media, de 23–51 mm de largo, labio interno de 9–17 mm de largo, labio externo de 12–22 × 3.5–4.4 mm, tubo cilíndrico de 14–32 mm de largo; anteras cortamente sagitadas, de 7–12 mm de largo; filamentos libres, parte libre de la corola de 2.5–4.0 mm de largo; estilo de 13.4–49.5 mm de largo, ramas estilares de 0.5–1.0 mm de largo; papus de 13–20 mm de largo; aquenios cilíndricos, de 2–4 × 1.6–2.0 mm. Corolas del disco tres, perfectas; corola ligulada, 5-lobada, pubescente por encima del tubo, de 15.4–19.0 mm de largo; tubo cilíndrico de 3.8–8.5 mm de largo, con pelos en la garganta; anteras 5, cortamente sagitadas, de 6.8–9.0 mm de largo; filamentos libres, parte libre de la corola de 1.9–10.4 mm de largo; estilo de 15.2–27.0 mm de largo; ramas estilares de 0.3–0.6 mm de largo; papus simple, más largo que el tubo de la corola, de 8.4–17.0 mm de largo; aquenios de 2.9–5.0 × 2.2–3.6 mm. Polen radioasimétrico. Figuras 25, 36.

Distribución y ecología. Bolivia y Perú. Crece en ambas laderas de los Andes, desde 2300–4470 m. Epoca de floración: enero–noviembre.

Material adicional examinado. BOLIVIA. **Cochabamba:** Incachaca, 3000 m, *Cárdenas 2183* (US); Ayapampa, Sailopato, 2700 m, *Cárdenas 3268* (US); Carrasco, 11 km ESE del pueblo de Siberia, 2600 m, *Saldías 288* (NY); carretera Cochabamba–Comarapa, a 207 km Cochabamba, 2600 m, *Smith et al. 13606* (MO, US); 17.5 km E Pojo (puente) por el camino a Cochabamba, 2700 m, *Solomon 18669* (MO); Siberia, *Cárdenas 6152* (US); Chaparre, 2500 m, *Steinbach 9547* (GH, MO); Totora, upper canyon of Río Huairamayo (r. Montepunco) 40 km N Totora, *Fosberg 28424* (GH, MO, US). **La Paz:** vic. La Paz, 10,000 ft., *Britton & Rusby 718* (GH, MO, US); Inquisivi, 2700 m, *Ochoa & Salas 15491* (US); along Río Khatu at the mouth of the Río Irupaya, ca. 3 km NE of Quime, 2800 m, *Lewis 881077* (MO, US); along trail between Loma El Abra and Cerro Negro Khota, ca. 6 km N from Inquisivi, 2900–3000 m, *Lewis 881107* (MO, US); Chichipata Trail, along the trail between Hospital San Antonio de Quime and the Río Chichipata, 3000–3100 m, *Lewis 88626* (MO). **Larecaja:** entre Acachachi y Sorata, pasando Humanata, 3670 m, *Ceballos et al. 596* (SI); Sorata, orillas del camino de Sorata a Consata, 2 km después de entrada hacia San Pedro, 2200 m, *Acevedo & Vargas 1758** (MO, NY); Sorata, 10,000 ft., *Rusby 1553** (GH); Ilabaya, 3400–3550 m, *Krach 9475* (SI); Cordillera Real, top of the pass on Tipuani–Ancona–Sorata trail docunto Sorata, 11,500 ft., *Tate 797* (NY); Murillo, 4 km después de la cumbre bajando el valle de Zungo, 4470 m, *Beck 2068* (SI); Nor Yungas, near Chuspipata, 2800 m, *Gentry et al. 44199* (MO, US); 25 km después de la cumbre Cerropal, 1 km hacia mina Salvador, 3080 m, *Beck 3733* (SI); 1.2 km E of Cotapata on road between Unduavi and Chuspipata, 3100 m, *Solomon 15341* (MO, US); Sud Yungas, Unduavi, 8000 ft., *Rusby 1552* (GH, NY, US); Unduavi, 4 km hacia Chulumani sobre camino antiguo, 3000 m, *Beck 8605* (SI); 69 km from Chulumani, along the road to La Paz, *King & Bishop 7476* (MO); Tamayo, 3050–2850 m, *Krach 9158* (SI); Kanton, Khurva, 3700–3500 m, *Krach 6585* (SI); Bautista Saavedra, 2600 m, *Feuerer 4904* (SI). **Santa Cruz:** Prov. Manuel María Caballero, 50 km al N de Maratal (en la carretera Sta. Cruz–Comaropa) pasando por San Juan del Potrero y bajando a la cuenca del alto Río Ichilo, 2000 m, *Smith et al. 13383* (MO). PERÚ. **Cusco:** Ollanta, 3000 m, *Herbario Zamalloa Díaz 2042* (LP); Urubamba, km 88–95, 2300–2500 m, *C. Vargas 3395* (LP); Machu Picchu, near the ruin Huayna Quente, 1.5 km down river along the Urubamba River from km 88 of the Urubamba railroad, 2820 m, *Peyton & Peyton 1541* (MO); Machu Picchu, along the Inca trail in Tres Piedras Blancas, 1 km from Huayabamba, 3130 m, *Peyton & Peyton 1563* (MO); Calca, Cañon Mantio, 2300 m, *C. Vargas 22951* (SI); Vilcabamba, 2700 m, *C. Vargas 3966* (LP); Amparaes, 3450 m, *Chávez 3271* (MO). **Junín:** Carpapata, above Huacapistana, 2700–3200 m, *Killip & Smith 24391* (US). **Puno:** Sandía, entre Sandía y Cuyocuyo, 3100–3200 m, *Ferreyra 16742* (MO).

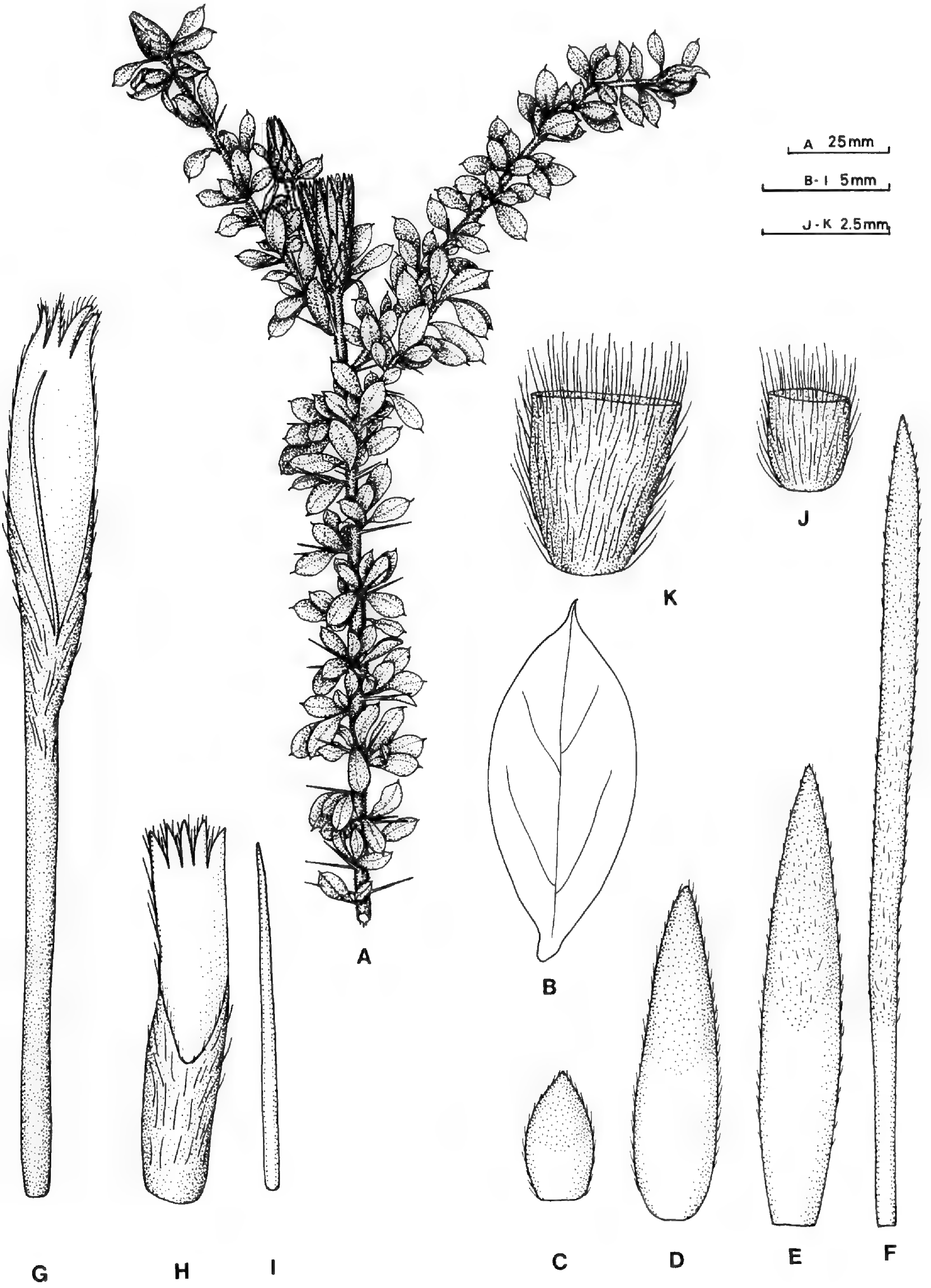


Figura 25. *Barnadesia polyacantha* (*Feuerer 4290*, SI). —A. Rama. —B. Hoja. C–F. Brácteas involucrales. —G. Corola de la flor del radio: (4+1). —H. Corola de la flor del disco: (5+0). —I. Cerda del papus de la flor del disco. —J. Aquenio de la flor del margen. —K. Aquenio de la flor del disco.

Barnadesia polyacantha se distingue por sus espinas reunidas en fascículos densos, las cuales miden hasta ca. 19 mm, y por las flores del disco con corolas liguladas y papus más largo que el tubo de la corola.

Chung (1965) diferenció la variedad *velutina* por sus ramas purpúreas oscuras, tallos jóvenes densamente villosos, y hojas aterciopeladas y elíptico-lanceoladas; espinas axilares jóvenes; y escamas involucrales villosas. Como resultado de la observación del material tipo de la variedad *polyacantha*, y sobre la base del material analizado pude observar que: (1) la variedad *velutina*, presenta variación continua en el color de las ramas, desde purpúreas a purpúreas oscuras; (2) no existe diferencia en la pilosidad de las ramas jóvenes con la variedad *polyacantha*; (3) la variedad *velutina* no presenta diferencia con la variedad *polyacantha* en la forma de la hoja y la pilosidad de las espinas jóvenes. De este análisis de caracteres considero a la variedad *velutina* como un sinónimo de *B. polyacantha*.

14. Barnadesia pycnophylla Muschl., Bot. Jahrb. Syst. 50, Beibl. 111: 101. 1914. TIPO: Peruvia. Via inter Tambo et Apurimac flumen in Departimento Ayacucho, provincia Huanta, frutices parvi in formatione herbis et graminibus composita, 3500–3600 m, 31 mayo 1910, *Weberbauer 5558* (B probablemente destruido; fotografía serie Field Museum Nº 15907: GH, MO). Perú. 6 mi. S of Mito, 10,000 ft., *Macbride & Featherstone 1830* (neótipo, designado por Chung (1965), US no visto, fotografía, LP).

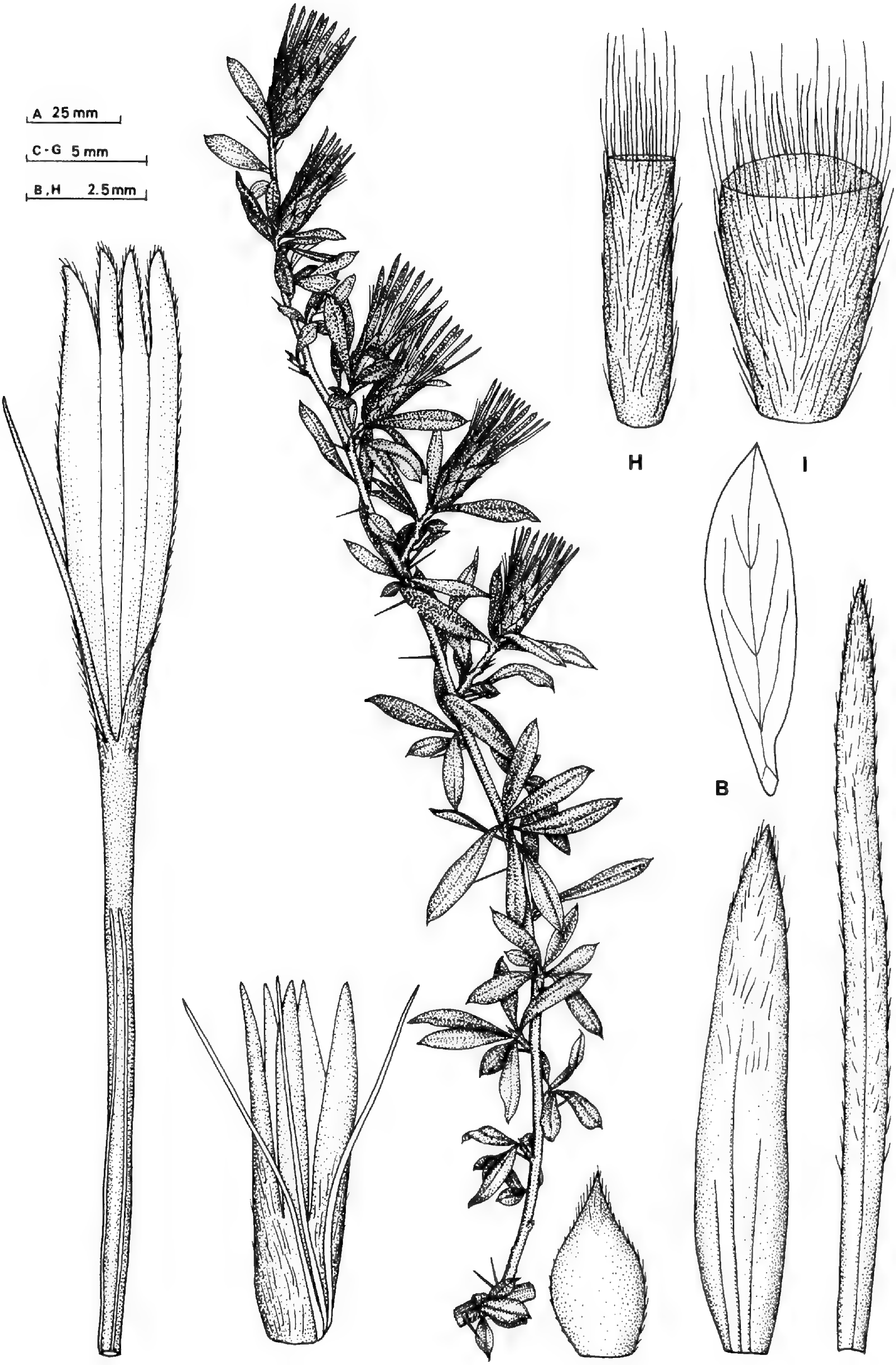
Arbusto de 1.0–3.5 m de alto. Espinas geminadas o en fascículos, de 8.5–25.0 mm de largo. Hojas en fascículos; pecíolo menos 1.5 mm; láminas oblanceoladas; pubescentes en ambas caras; de 28.0–62.5 × 6.5–14.0 mm; ápice espinoso. Capítulos sésiles, solitarios, en cimas racemiformes o panojas. Involucro ligeramente acampanado de 24–46 × 11–24 mm, filarias ca. 59, dispuestas en 7–9(–10) series, dorso pubescente y cilias en el margen, las exteriores de 6–10 mm de largo, las intermedias de 7–24 mm de largo, las interiores lineares, de 15.5–42.0 mm de largo. Corolas de color rosa, lilacino-rosado o rojo-violáceo, dimorfas. Flores del margen ocho; corola bilabiada (4+1), de 29.0–56.2 mm de largo, labio interno de 12.1–20.0 mm de largo, labio externo de 13.9–27.2 × 4.0–6.0 mm, tubo cilíndrico de 15–29 mm de largo; anteras decurrentes en la base, de 9.0–11.7 mm de largo; filamentos libres, parte libre de la corola de 2.6–5.0 mm de largo; estilo de 22.8–47.8 mm de largo, ramas estilares de 0.6–1.1 mm de largo; papus de 14.6–24.0 mm de largo; aquenios cilíndricos, de 3.0–7.0 × 1.2–2.0 mm. Flor del disco una, perfecta; corola subligulada, 5-secta, de 12.5–16.0 × 7.0–9.0 mm, tubo de 3.0–4.8 mm de largo; anteras 5, decurrentes en la base, de 8.8–9.2 mm de largo; filamentos libres, parte libre de la corola de 5.4–8.0 mm de largo; estilo de 14–22 mm de largo, ramas estilares de 0.4–0.8 mm de largo; papus barbelado, más largo que el tubo de la corola, de 14–21 mm de largo; aquenios, de 3–6 × 3–4 mm. Polen radioasimétrico. Figuras 26, 40.

Distribución y ecología. Bolivia y Perú. Crece en los bosques montanos bajos y en los matorrales, entre 2700–3890 m. Epoca de floración: febrero–diciembre.

Material adicional examinado. BOLIVIA. Sin dpto. determinado: near Pelichuco, *Williams 2469* (US); Pongo, 12,000 ft., *Tate 241* (NY); Pongo, 11,500 ft., *White 188* (NY, US); Pongo, valley near stream, 13,500 ft., *Rusby 17* (GH, NY, US). **Cochabamba:** Incachaca, 2700 m, *Cárdenas 692* (US); Río Juntas, 3500 m, Apr. 1892, *Kuntze s.n.* (NY); Carrasco, 5 km E del puente sobre el Río López Mendoza por el camino entre Cochabamba y Santa Cruz (19 km O de Epizana), 2900 m, *Solomon & Nee 16043* (US); Siberia, 3000 m, *Steinbach 193* (GH, NY, UC, US). **La Paz:** Inquisivi, along the trail, and slopes W of trail Pongo Chico and Laguna Naranjani, *Lewis 881032* (NY, US); along the trail between Chichipata y hacienda Jucumarini, ca. 2 km N Quime, 3400–3500 m, *Lewis 881010* (MO); Río Huallatan, following the Río Huallantani from where it crosses the Quime–Caxata road ca. 1 km E Pongo, 0.3 km up the cascade and waterfalls, 3550–3600 m, *Lewis 88655* (MO); Murillo, valle del Río Zongo, 21.1 km N de la cumbre, 3200 m, *Solomon 16453** (MO, NY, US); Zongo valley (below Botijlaca), ca. 40 km N La Paz, 3300 m, *Barker 366* (MO, NY); valle del Río Zongo, Santa Rosa 11 km hacia La Paz, 3890 m, *Beck 1116* (US); Nor Yungas, 3200 m, *Buchtien 474* (GH); Sud Yungas, Yungas debajo de Unduavi, subiendo al valle de Cerromarca, 3300 m, *Beck 14652* (US); 19.8 km E of pass between Mururata and Illimani, 3500 m, *Solomon 15118* (MO, US). PERÚ. **Ayacucho:** La Mar, along roadside from Ayacucho to San Francisco, shortly after crossing over the high pass ca. 34 km S of Tambo, ca. 10 km from Rinconado, 3500 m, *Dudley 9053* (US). **Cusco:** Calca, alrededores de Laves, 3100–3650 m, *C. Vargas 3607* (LP); Quispicanchis, 47 mi. from Quincime on road to Cusco,

→

Figura 26. *Barnadesia pycnophylla* (*Solomon 16453*, NY). —A. Rama. —B. Hoja. C–E. Brácteas involucrales. —F. Corola: (4+1), estambres y estilo de la flor del margen. —G. Corola de la flor del disco y papus. —H. Aquenio de la flor del margen. —I. Aquenio de la flor del disco.


A 25 mm
C-G 5 mm
B, H 2.5 mm
H
I
B
F
G
A
C
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E

3160 m, *Maguire & Maguire 61626* (NY); antes de Marcapata, 3600–3000 m, *C. Vargas 14559* (US); 23 km past the peal on road to Ocongate and Marcapata, 3640 m, *Aronson & Berry 509* (MO); Paucartambo, 9–12 km NE Paucartambo, 2980–3050 m, *Gentry et al. 23420* (MO). **Huánuco:** 15 mi. SE Huánuco, 10,500 ft., *Macbride & Featherstone 2230* (US). **Junín:** Carhnish, camino a Satipo, 3000 m, *Soukup 2883** (US). **Pasco:** entre Victoria y Paucartambo, 3600 m, *Tovar 1099* (MO). **Puno:** Carabaya, 3 km S of Ollachea, *Boeke & Boeke 2997* (US); Sandía, 2–6 km S Limbani, 3550–3650 m, *Metcalf 30446* (GH, MO, UC, US); Phara, 3400 m, *Ochoa OCH–5199* (US).

Barnadesia pycnophylla es afín a *B. horrida*, de la cual se diferencia por presentar la corola de la flor del disco glabra en la garganta, y generalmente con mayor número de series en el involucro.

15. **Barnadesia reticulata** D. Don, Trans. Linn. Soc. London, Bot. 16: 277. 1833. TIPO: Perú. Junín: Segetibus Tarmae Peruvianorum, *Ruiz & Pavón s.n.* (holótipo, MA no visto; isótipo, BM no visto, fotografía, GH).

Nombre vulgar. "Shaule" (*Ferreyra 6914*).

Arbusto de 2–3 m de alto. Espinas geminadas, de 32–48 mm de largo. Hojas en fascículos, ocasionalmente algunas hojas alternas; pecíolo menos de 1.5 mm de largo; láminas oblanceoladas, pubescencia en la superficie abaxial; de 42–54 × 15–18 mm; ápice obtuso o atenuado, mucronado o espinoso. Capítulos en cimas racemiformes o solitarios. Involucro acampanado, de 44–46 × 28–30 mm, filarias dispuestas en 8–9 series. Corolas de color rosado, purpúreo o amarillo, ligeramente dimorfas o dimorfas. Flores del margen trece, corola bilabiada (4+1), labio externo ca. 19 mm de largo, tubo ca. 24 mm de largo; anteras decurrentes en la base, ca. 13 mm de largo; filamentos parcialmente unidos; papus de 21 mm de largo; aquenios cilíndricos o levemente turbinados, de 2.0–5.5 × 1.0–2.5 mm. Flores del disco tres, perfectas; corola bilabiada (3+1) u ocasionalmente (4+1), ca. 18 mm de largo; labio externo de 13.5 × 4.5 mm, tubo ca. 4.5 mm de largo, con pelos en la garganta; anteras 4 ó 5, decurrentes en la base; filamentos libres; ramas estilares ca. 0.8 mm de largo; papus simple, más largo que el tubo de la corola, de 14.5 mm de largo; aquenios turbinados. Polen radioasimétrico. Figuras 27, 40.

Distribución y ecología. Perú. Crece en monte pluvifolio y laderas subxerófilas, entre 2700–2950 m. Epoca de floración: enero–marzo.

Material adicional examinado. PERÚ. **Ica:** Pisco, Arriba de Pisco, 2900 m, *Rauh 386* (MO, USM). **Lima:** alrededores de Canta, 2900–2950 m, *Ferreyra 6914** (MO, USM); Loc. Pachacama, a 2 km de Canta, 2700 m, *Meza 86** (USM).

Barnadesia reticulata se caracteriza por los filamentos de los estambres de las flores del margen parcialmente fusionados, por el papus simple en las flores del disco y por la nerviación marcada de sus hojas.

16. **Barnadesia spinosa** L.f., Suppl. pl.: 348. 1782 ("1781"). TIPO: Colombia (America meridionalis), 1778, *Mutis 88* (holótipo, LINN no visto, fotocopia, LP).

Barnadesia spinosa var. *recurvata* I. C. Chung Rev. *Barnadesia* 70. 1965. TIPO: Ecuador. Carchi: Tufino, *Mexía 7551* (holótipo, US).

Nombres vulgares. "Espina" (*Mexía 7551*), "espina de Tatequieta" (*John 20738*), "espinillo" (*Bristol 858*), "espino" (*Jaramillo 3511*), "guasco" (*Jaramillo 3511, Niemeyer 157*), "guncianguishe" (*Chindoy 202*), "guntsianga" (*Bristol 858*).

Arbol o arbusto de 2–10 m de alto. Espinas geminadas de 10–27 mm de largo. Hojas en fascículos; pecíolo menos 2.5 mm de largo; láminas oblanceoladas, pubescencia en ambas caras (la cara adaxial subglabra, en la superficie abaxial pubescente, más abundantes en la vena media y en los bordes), de 9.6–50.6 × 6.2–16.0 mm; ápice atenuado u obtuso, mucronado o espinoso. Capítulos en cimas corimbiformes o panoja. Involucro acampanado, de 21–37 × 8–17 mm, filarias ca. 82, dispuestas en 8–9 series: las exteriores de 3.0–7.5 mm de largo, las intermedias de 5.5–22.1 mm de largo, las interiores de 19.0–23.5 mm de largo. Corolas de color blanco, rosado, purpúreo o violáceo, ligeramente dimorfas o dimorfas. Flores del margen trece, corola bilabiada (4+1), de 17.3–35.8 mm de largo, labio interno de 10.0–12.5 mm de largo, labio externo de 10.3–19.5 × 3.1–6.0 mm, tubo cilíndrico de 7–19 mm de largo; estilo blanco, rosado o rojizo, de 16.0–37.8 mm de largo; ramas estilares de 0.4–1.0 mm de largo; anteras moradas, castaño-purpúreas o rosadas, decurrentes en la base, de 5.8–10.0 mm de largo; tubo estaminal de 3.5–11.0 mm de largo; papus de 9–21 mm de largo; aquenios cilíndricos o levemente turbinados, de 2.0–5.5 × 1.0–2.5 mm. Flores del disco tres, perfecta; corola bilabiada (4+1) o ligulada (5+0), densamente pubescente en los 2/3 superiores o los 2/3 inferiores, de 11–19 mm de largo; labio interno de 8.2–12.0 mm de largo, labio externo de 8–11 × 5–8 mm; tubo cilíndrico de 3–8 mm de largo, con pelos en la garganta; estilo de 16.5–22.2 mm de largo, ramas estilares 0.3–0.6 mm de largo; anteras 4 ó 5, decurrentes en la base, de 5–6 mm de largo; tubo estaminal de 3.0–7.8 mm de largo; papus barbelado, más largo que el tubo de la corola, de 7.4–

Figura 27. *Barnadesia reticulata* (*Meza 86*, USM). —A. Rama. —B. Hoja. —C. Corola: (4+1), estambres y estilo de la flor del margen. —D, E. Corolas (4+1, 3+1), estambres y estilo de las flores del disco. —F. Aquenio de la flor del margen. —G. Aquenio de la flor del disco.

10.4 mm de largo; aquenios de 2.5–9.0 × 2.0–4.0 mm. Polen radiosimétrico. Figuras 28, 41.

Distribución y ecología. Ecuador y Colombia. Crece en bosques húmedos premontanos, bosques montanos, bosques secundarios y páramo, entre 2200–4100 m. Epoca de floración: enero–diciembre.

Material adicional examinado. COLOMBIA. **Boyacá:** Valle de Uvita, *Cuatrecasas 1143* (US); Cordillera Oriental, Sierra Nevada del Cocuy, Quebrada de San Paulino próximo Ritacuva, 3500 m, *Barclay & Juajibioy 7305* (MO, US). **Cauca:** Coconuco, 2300–2500 m, *Killip 6837* (GH); El Cauca, Río Vinagritatibia, Amacé, 3000 m, *Dryander 1636* (US); Municipio Purace, N slope of the Volcan de Purace, 2700–2800 m, *Barclay & Schultes 137* (GH, NY); between Piaspampa and Chapa near headwaters of Río Quilcace, along camino, 2850 m, *Core 884* (US). **Cundinamarca:** near Río San Cristóbal, *Bro. Ariste–Joseph A155* (GH, US); Bogotá Plateau, San Cristóbal, *Niemeyer 157* (US); Bogotá, "páramo" in vía a Cabras, *Woronow & Juzepczuk 5118* (US); Cordillera Oriental, vertiente Occidental, Páramo Cruz–Verde, 2880 m, *Gutiérrez 256* (GH); Quebrada de Chicó, 8500–9500 ft., *Schultes 18562* (US); Mpio. de La Calera, al W del Páramo de La Siberia, Valle de Sopó, Carretera a Guasca, Hacienda El Salitre, *Humbert et al. 26923* (LP, US); Páramo de Sumapaz, cerca de lagunitas al S de San Juan, *Cleef 8423* (US); Páramo de Usme, 1922, *Bro. Ariste s.n.* (US); S of Sibaté on road to Fusagasugá, near km marker 25, 2650 m, *Barclay et al. 3382* (US); Usaquén, 2700 m, *Guevara Amórtegui A–39* (US); km 16 on road from Mosquera to La Mesa, 2700 m, *Gentry et al. 17070* (MO); Sibate, 2700–2800 m, *Pennell 2516* (NY); Salto Tequendama, 2400 m, *Haught 6539* (US). **Nariño:** 18 km above Pasto, on Tangua road, 2700 m, *Ewan 15924* (US); Cebadal, on highway to Yacuanquer, km 15–25, 2700–2800 m, *Schultes & Villarreal 7919* (US); highway between Santa Rosa and Tuquerres, 2750–2850 m, *Schultes & Villarreal* 7912* (GH); near top of divide on Tuquerres–Ricaurte road, 3000 m, *Gentry et al. 34833* (MO); carretera a Ipiales, de Túquerrés a Ipiales, 3100–2950 m, *García-Barriga & Hawkes 13068* (NY, US); Mpio. Tuquerres, 2 m N del pueblo en el camino de Olaya, 3000 m, *Bernal 1274* (MO); Finca La Planada, 1950 m, *Libenson et al. 30654* (MO). **Meta:** Puerto López, 3000 m, *Jaramillo M. 402* (US). **Putumayo:** Sibunday, 7600 ft., *Foster & Foster 1938* (GH); Sibunday, hill of valley, 2220–2270 m, *Schultes & Villarreal 7479* (GH); Valle de Sibunday, 2225 m, *Bristol 858* (GH, US). **Santander:** Vecindad de Veta, 3100–3250 m, *Killip & Smith 17316* (GH, NY, US); País, Río La Baja, 3445 m, *John 20738** (LP, NY, UC, US); road from Pamplona to Toledo, crossing the divide between Río La Teja (Maracaibo drainage) and Río Mesme (Orinoco drainage), 2800–3000 m, *Killip & Smith 20013* (GH); Páramo del Puente, above La Baja, 3500–3700 m, *Killip & Smith 18250* (GH, NY, US); Páramo El Romeral, 3800–4100 m, *Killip & Smith 18573* (GH, NY). **Valle:** Barragán, Finca La Florida, 2800 m, *Devia 157* (MO); Mpio. de Tuluá, corregimiento Sta. Lucía, Finca San Luis, 2800 m, *Devia 724* (MO); La Cruz, *Bro. A305* (US). ECUADOR. **Carchi:** wooded hills about 5 mi. S of Tulcán, *Hitchcock 21012* (GH, NY); road to Maldona, ca. 15 km W Tulcán, 2930 m, *Fallen & Escobar 741* (MO); SE slopes of Volcán de Chile, near village of Tufino, 11,000 ft., *Wiggins 10631* (UC).

Barnadesia spinosa y *B. parviflora* son las especies que llegan más al norte de América del Sur (Colombia).

Barnadesia spinosa y *B. dombeyana* presentan la mayor variabilidad de corolas (bilabiadas 3+1, 4+1; y liguladas 5+0) en las flores del disco. *Barnadesia spinosa* se distingue de las restantes especies por los filamentos de los estambres totalmente fusionados, tanto en las flores del margen como en las flores del disco.

Barnadesia subgén. **Bacasia** (Ruiz & Pav.) Urtubey, stat. nov. *Barnadesia* secc. *Bacasia* (Ruiz & Pav.) DC., Prodr. 7: 3. 1938. *Bacasia* Ruiz & Pav., Fl. peruv. prodr. 105, t. 22. 1794. TIPO: *Barnadesia corymbosa* (Ruiz & Pav.) D. Don.

Hojas pecioladas, alternas. Capítulos pedicelados. Flor del disco 1, con corola tubulosa y papus plumoso.

El subgénero *Bacasia* comprende dos especies; habitan desde Colombia, Ecuador, Perú hasta Bolivia.

1a. Involucro de 24–34 mm de long; flores del margen con filamentos de los estambres totalmente fusionados .... 17. *B. corymbosa*
1b. Involucro de 14–19 mm de long; flores del margen con filamentos de los estambres libres .... 18. *B. parviflora*

17. Barnadesia corymbosa (Ruiz & Pav.) D. Don, Trans. Linn. Soc. London, Bot. 16: 278. 1833. *Bacasia corymbosa* Ruiz & Pav., Syst. veg. fl. peruv. chil. 1: 189. 1798. TIPO: Perú. In Andium memoribus prope Muña vicun, *Ruiz & Pavón s.n.* (Ferreyra (1995) holótipo, MA no visto, fotografía, LP; isótipo, BM, fotografía, LP).

Barnadesia venosa Rusby, Mem. Torrey Bot. Club 6: 69. 1899. TIPO: Bolivia. Espíritu Santo: 1891, *Bang 1205* (holótipo, GH; isótipos, MO, US).

Arbusto o arbolito de 1–8 m de alto. Espinas geminadas, de 11.5–22.5 mm de largo, comúnmente las ramas floríferas inermes. Hojas alternas, ocasionalmente algunas hojas en fascículos; pecíolo de 13–25 mm; láminas oblanceoladas o ligeramente obovadas, subglabras en la cara adaxial y algo más pubescentes en la cara abaxial, con nerviación secundaria marcada; de 10.6–18.9 × 3.8–4.9 cm; ápice acuminado, mucronado. Capítulos pedunculados, en cimas corimbiformes compuestas. Involucro acampanado, de 24–34 × 12–16 mm, filarias

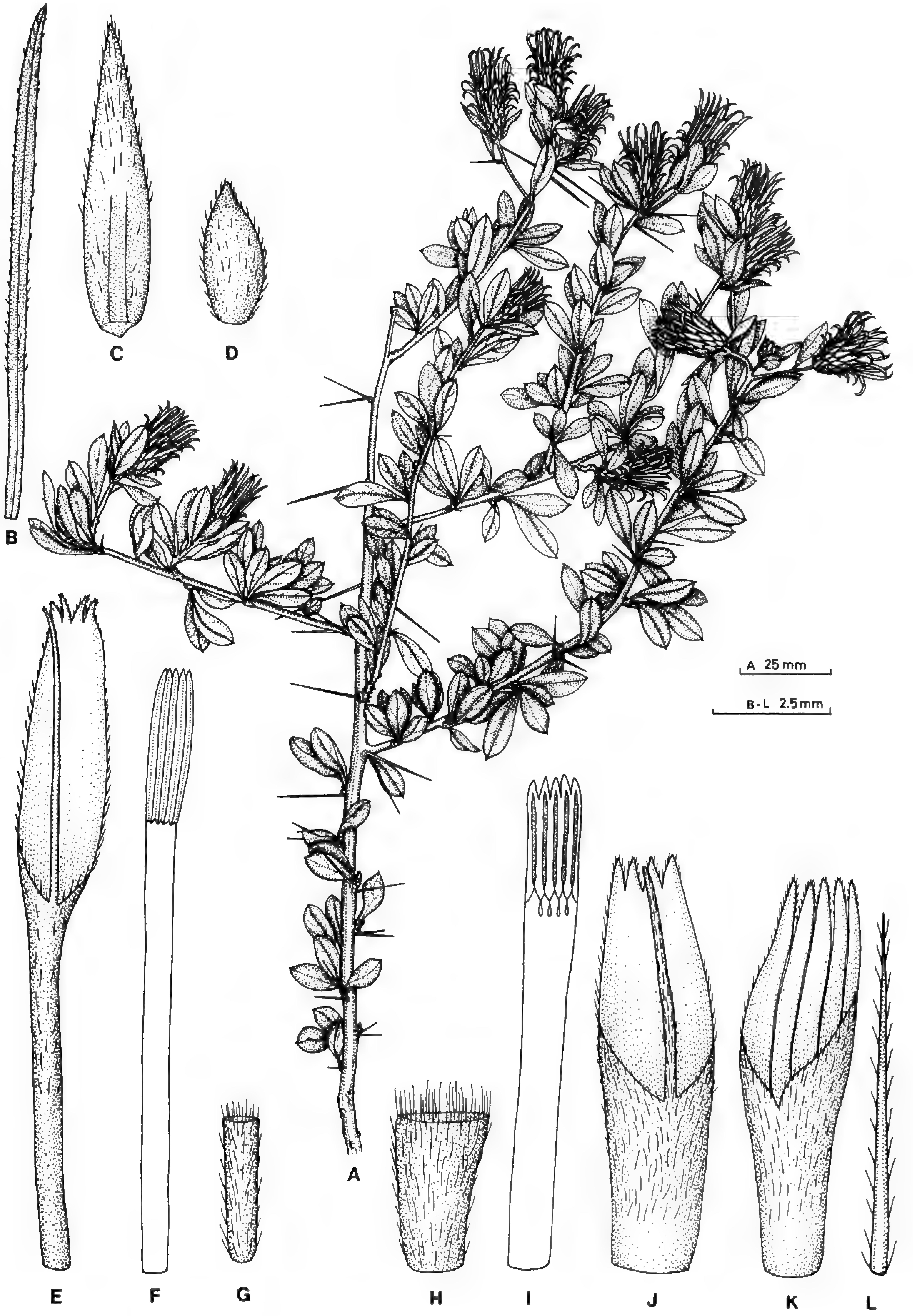

Figura 28. *Barnadesia spinosa* (*Schultes & Villarreal 7912*, GH). —A. Rama. —B–D. Brácteas involucrales. —E. Corola de la flor del margen: (4+1). —F. Tubo estaminal de la flor del margen. —G. Aquenio de la flor del margen. —H. Aquenio de la flor del disco. —I. Tubo estaminal de la flor del disco. —J, K. Corolas de la flor del disco: (4+1, 5+0). —L. Papus de la flor del disco.

ca. 62, mucronadas, dispuestas en 7–8 series: las exteriores de 25.2–30.4 mm de largo, las intermedias de 11.5–22.0 mm de largo, las interiores de 4–10 mm de largo. Corolas de color blanco, dimorfas. Flores del margen ocho; corola bilabiada (4+1), de 35.5–55.0 mm de largo, labio interno de 16–18 mm de largo, labio externo de 15.5–23.0 × 3.3–4.0 mm, tubo de 20–32 mm de largo, con pelos en la garganta; anteras decurrentes en la base, de 9–10 mm de largo; tubo estaminal de 10.0–12.5 mm de largo; estilo de 35.0–44.5 mm de largo, ramas estilares de 0.6–1.0 mm de largo; papus de 14.5–19 mm de largo; aquenios cilíndricos o ligeramente turbinados, de 4–6 × 2.0–2.5 mm. Flor del disco una, imperfecta; corola tubulosa, 5-lobada, pubescente externamente y con pelos en la base interna, de 22.2–27.2 mm de largo; flores pistiladas: estambres reducidos; estilo de 31.5 mm de largo, ramas estilares de 1.2 mm de largo; flores estaminadas: anteras 5, decurrentes en la base, de 5–6 mm de largo; filamentos libres, parte libre de la corola de 6 mm de largo, inserción en la base del tubo; estilo reducido; papus cortamente plumoso, más corto que el tubo de la corola, de 8.2–14.0 mm de largo; aquenio de 4.0–7.5 × 2.2–5.0 mm. Polen radiosimétrico. Figuras 29, 35.

Distribución y ecología. Bolivia y Perú. Crece en los bosques y a orillas de los rios entre 800–2500 m. Epoca de floración: marzo–agosto.

Material adicional examinado. BOLIVIA. **Santa Cruz:** Florida, Río La Negra, Las Yungas de las Negras, 85 km along Santa Cruz, Cochabamba road, along trail leading up to mountains, 800 m, *Balick et al. 1387** (US); Sara, orillas del Río Surutú, de su salto por arriba, 1300 m, *Steinbach 3380* (GH). PERÚ. **Cusco:** Quispicanchis, Río Marcapata, ceja de montaña, 2800 m, *Hirsh P1320** (NY); Paucartambo, Yamayo, valle de Kosñipa, borde de monte en barranca, 2000 m, *C. Vargas 14710* (USM); Paucartambo, Santa Isabel, 1000 m, borde del bosque, 1000 m, *C. Vargas 5170* (USM). **Huánuco:** Huallaga, Muña, *Weberbauer 6717** (GH, US). **Puno:** Carabaya, Ollachea, across San Gaban river from town, *Boeke & Boeke 3171* (MO).

Barnadesia corymbosa se caracteriza por sus hojas de gran tamaño, largamente pecioladas y generalmente alternas, papus cortamente plumoso en las flores del disco, características que comparte con *B. parviflora*, de la cual se diferencia por sus capítulos de mayor tamaño y por el tubo estaminal presente en las flores del margen.

En la descripción original de *Barnadesia venosa* se cita como ejemplar tipo: Espíritu Santo, 1891 (1205). En una fotografía del ejemplar tipo depositado en Kew figura: *Bang 1265*; un segundo rótulo aclara que el número *Bang 1265* corresponde a *Vitis sigmoides*. Es probable que la diferencia se deba a un error de impresión. Por lo tanto el número de colección del tipo de *Barnadesia venosa* es *Bang 1205*.

18. Barnadesia parviflora Spruce ex Benth. & Hook. f., Gen. pl. 2: 485. 1873. TIPO: Ecuador. Arbor in sylvis Baños frequens Palo santo Quitensium, *Spruce 5123* (holótipo, K no visto, fotografía, LP; isótipos, GH, K).

Barnadesia trianae Hieron., Bot. Jahrb. Syst. 19: 71. 1895. TIPO: Colombia. Antioquia: Prov. Mariquita, San José, 1900 m, *Triana 1492* (lectótipo designado por Chung (1965), P no visto, fotografía, LP; isolectótipo, P, fotografía, LP).

Nombre vulgar. "Espino santo" (Harling, 1991), "palo santo" (*Cerón 4292, Freire Fierro 1227, Lehmann 5239*).

Arbol de 5–20 m de alto. Espinas ca. 21 mm de largo. Hojas alternas, ocasionalmente algunas hojas en fascículos; pecíolo de 15–35 mm; láminas elípticas raramente oblanceoladas, pubescencia en ambas caras; nerviación marcada; de 10–16 × 3.2–6.0 cm; ápice acuminado o atenuado, mucronado. Capítulos pequeños, pedúnculados, cimas corimbiformes compuestas. Involucro acampanado, de 14–19 × 9–14 mm, filarias 82–92, con pelos en el dorso y cilias en el margen, mucronadas, dispuestas en 6–7 series: las exteriores de 2.0–4.1 mm de largo, las intermedias de 3.5–14.1 mm de largo, las interiores de 12.0–15.8 mm de largo. Corolas de color lilacino, azul-lilacino o violáceo, dimorfas. Flores del margen ocho; corola bilabiada (4+1), de 15–20 mm de largo, labio interno de 6–9 mm de largo, labio externo de 8–11 × 2.5–4.0 mm, tubo de 5.2–10.0 mm de largo; anteras decurrentes en la base, de 3.0–5.5 mm de largo; filamentos libres, parte libre de la corola de 1.2–4.5 mm de largo; estilo de 13–19 mm de largo; ramas estilares de 0.3–0.8 mm de largo; papus de 7–12 mm de largo; aquenios cilíndricos o ligeramente turbinados, de 2–4 × 0.8–2.0 mm. Flor del disco una, imperfecta; corola tubulosa, 3–4-lobada, de 9–15 mm de largo, sin estilo, raramente presente y atrofiado; anteras 3 ó 4, decurrentes en la base, de 2.8–4.0 mm de largo; filamentos libres, parte libre de la corola de 1–3 mm de largo; papus cortamente plumoso, más largo que el tubo de la corola, de 7–10 mm de largo; aquenios de 2–6 × 1.2–2.0 mm. Polen radiosimétrico. Figuras 30, 31.

Distribución y ecología. Ecuador y Colombia. Crece en bosque húmedo premontano y montano, en valles y en quebradas, entre 1400–5000 m. Epoca de floración: enero–noviembre.

Material adicional examinado. COLOMBIA. **Caldas:**

Figura 29. *Barnadesia corymbosa* (*Boeke 3171*, MO). —A. Rama. —B–E. Brácteas involucrales. —F. Corola abierta de la flor del margen: (4+1). —G. Corola de la flor del disco abierta (con pelos en la base): (5+0). —H. Cerda del papus de la flor del disco. —I. Aquenio de la flor del margen. —J. Aquenio de la flor del disco.

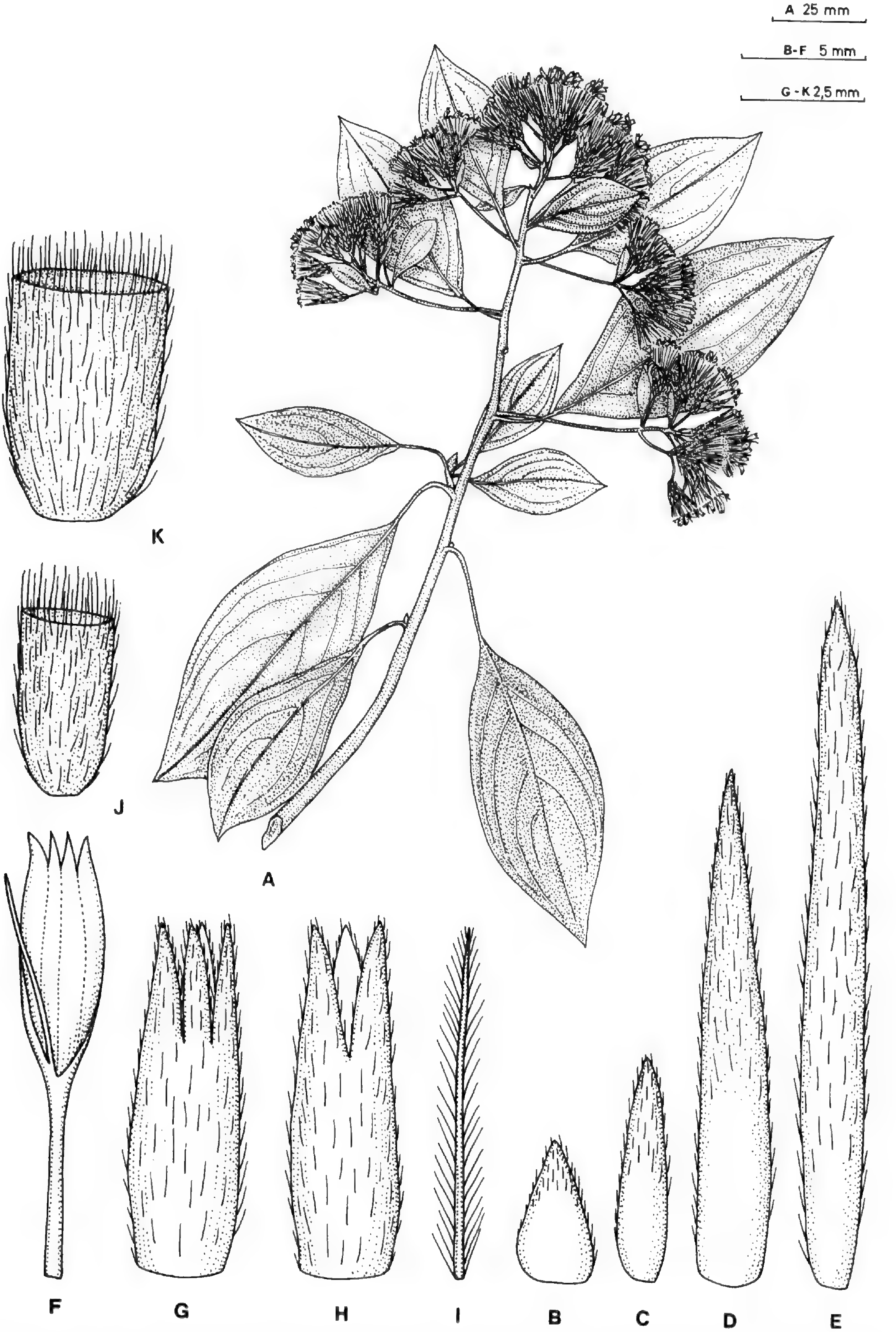

Figura 30. *Barnadesia parviflora* (*Asplund 17121*, NY). —A. Rama. —B–E. Brácteas involucrales. —F. Corola de la flor del margen: (4+1). —G, H. Corolas de la flor del disco: (3+0, 4+0). —I. Cerda del papus de la flor del disco. —J. Aquenio de la flor del margen. —K. Aquenio de la flor del disco.

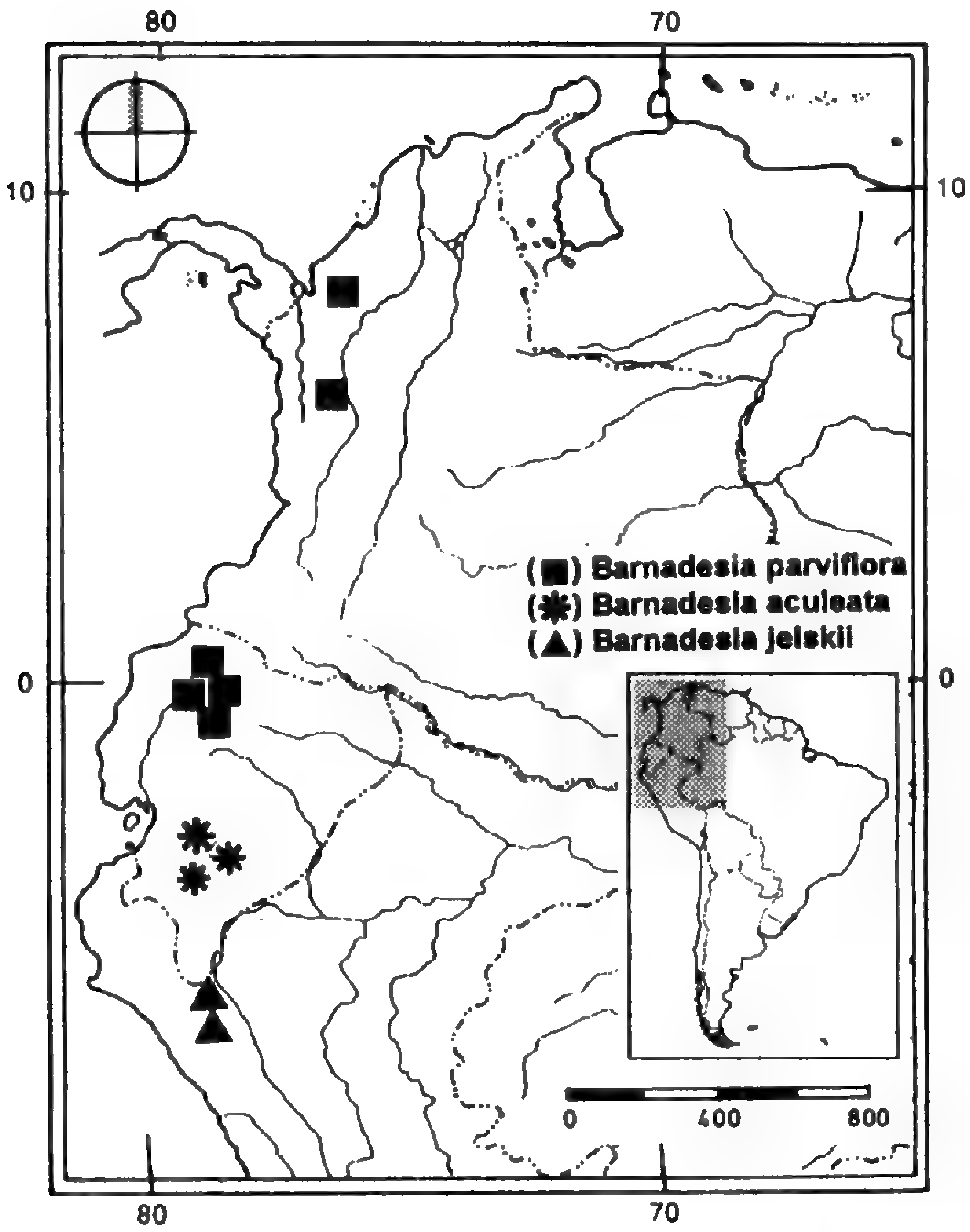

Figura 31. Distribución de *Barnadesia aculeata*, *B. parviflora* y *B. jelskii*.

7 km carretera Córdoba–Pijao, 1840 m, *Arbeláez et al. 2227* (MO); carretera a Cocora, 200 m antes de Retén Inderena, 1850 m, *Arbeláez et al. 1292* (MO); Salento, 1700–2400 m, *Pennell 8861* (GH, US); laguneta, Salento, 2300 m, *von Sneidern 3111* (GH). ECUADOR. **Imbabura:** Cantón Cotocachi, carretera de Cotachi a Nangulbi y Apuela, 3000 m, *Rubio & Quelal 606* (MO, US). **Napo:** Carretera Quito–Tena via Baeza, al lado de la carretera, *Dodson et al. 15165* (MO, US); Unión of Río Borja and Río Quitos, 1750 m, *Holm-Nielsen et al. 26134* (NY); Cantón El Chaco, Las Palmas, Finca Carmita de Luis Salazar, 1600–1750 m, *Palacios 6244* (US); Baeza, 1900 m, *Palacios 6277* (US). **Pastaza:** valley of Río Papallacta, 2600–2800 m, *Fosberg 27472** (US). **Pichincha:** Cerca de Chiriboga, *Balslev 2733** (GH, MO, US); Reserva Geobotánica de Pululahua, camino a Lulubamba, *Cerón 4292* (MO); Cerro Antisana, 1 mi. NE of Borja, 5000 m, *Grubb. et al. 1298* (NY); road Nono–Pacto, Río Yacuambi, 5–10 km above Nanegalito, 1700 m, *Holm-Nielsen et al. 24428* (MO, NY); Cantón Quito, along the Río Alambi, 7.5 km by road SE Tandayapa, 2100–2200 m, *Webster 28669*

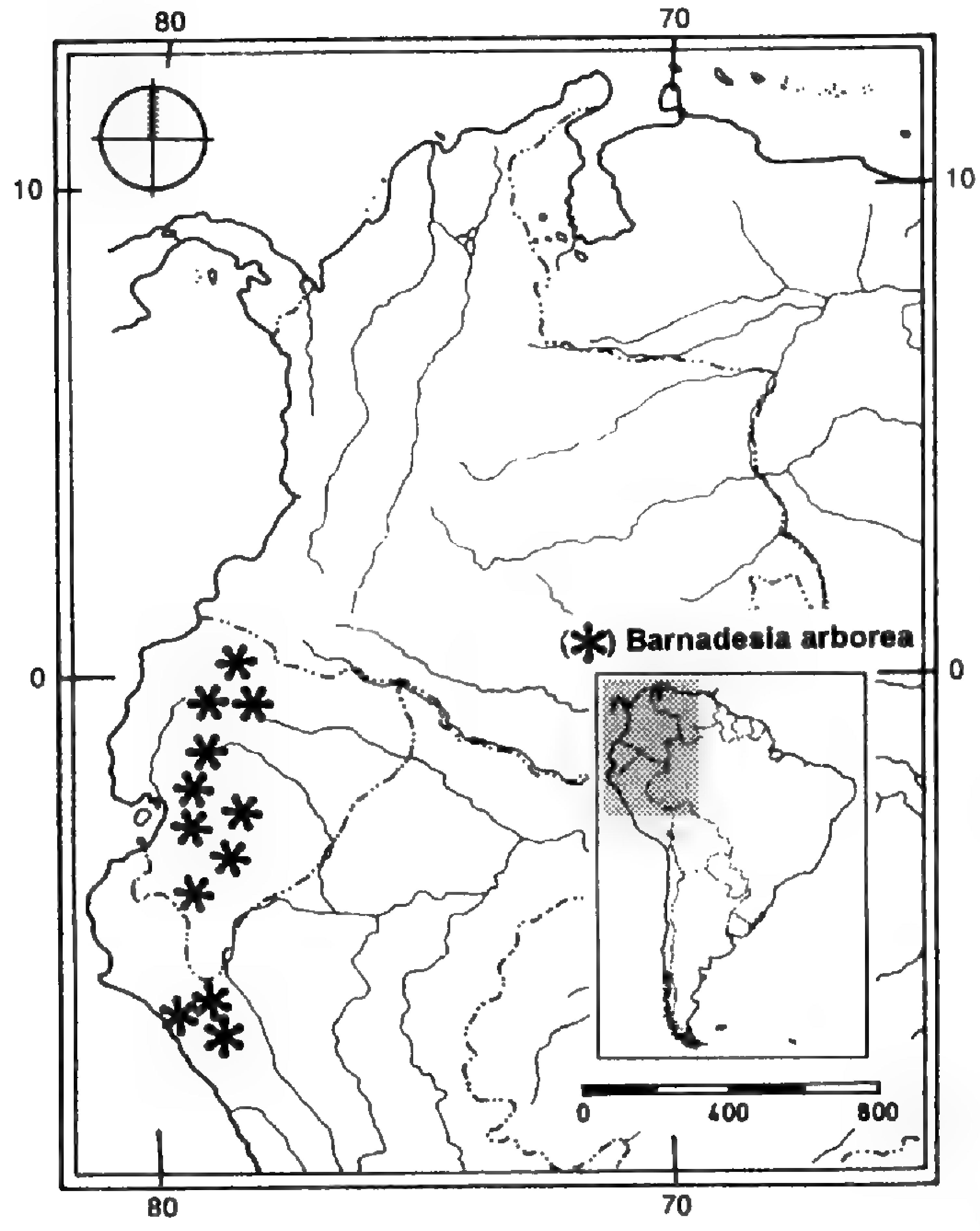

Figura 32. Distribución de *Barnadesia arborea*.

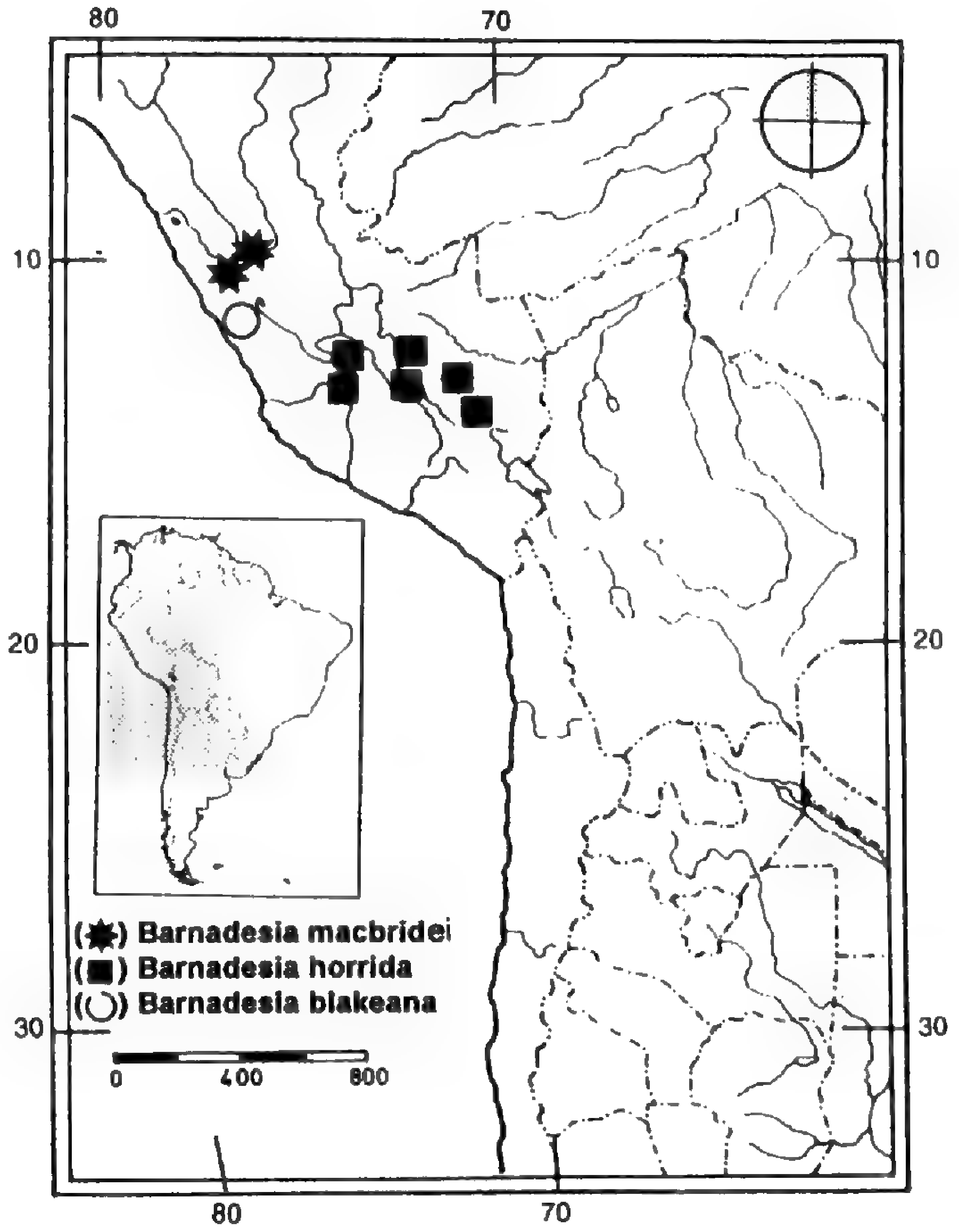

Figura 33. Distribución de *Barnadesia blakeana*, *B. horrida*, y *B. macbridei*.

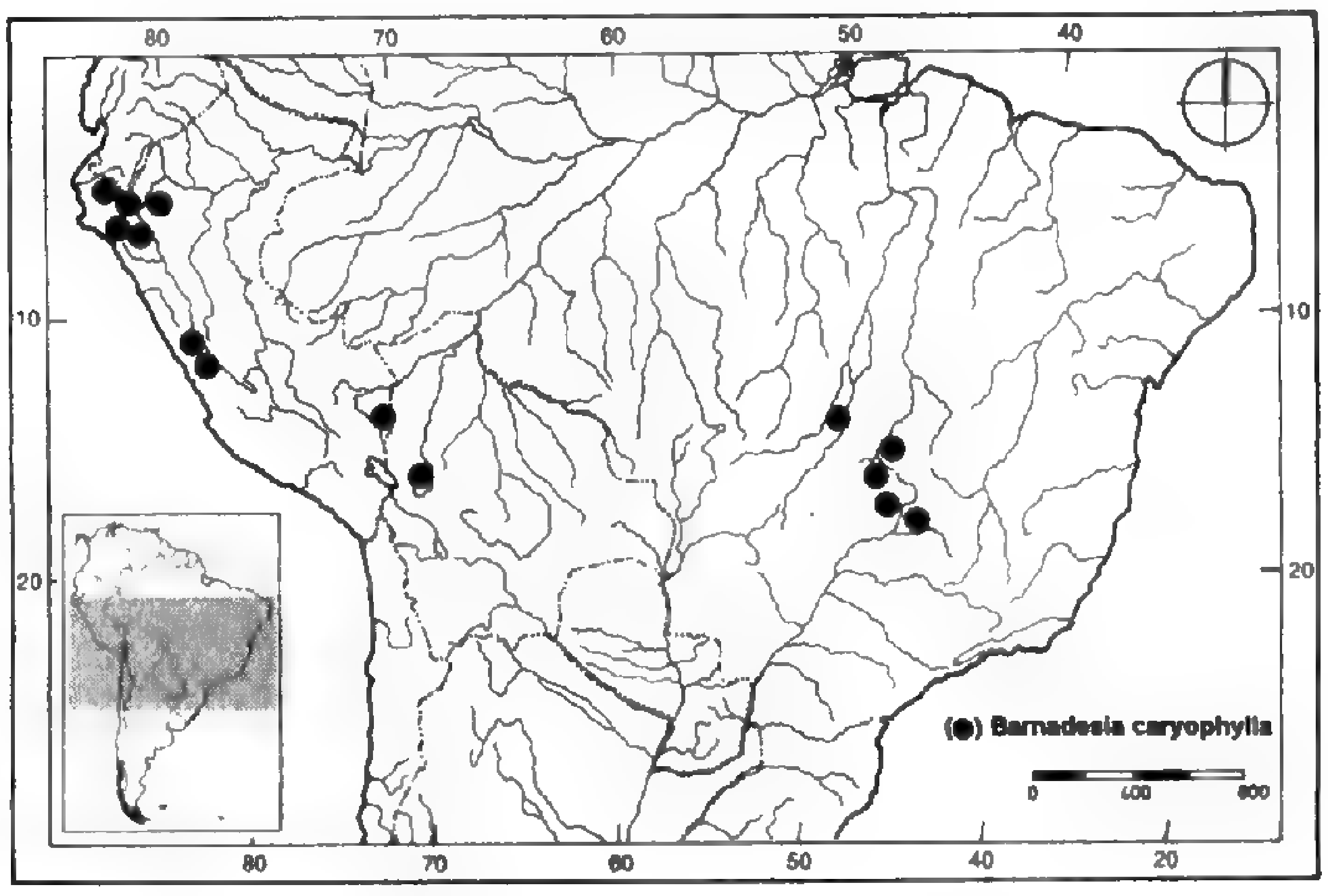

Figura 34. Distribución de *Barnadesia caryophylla*.

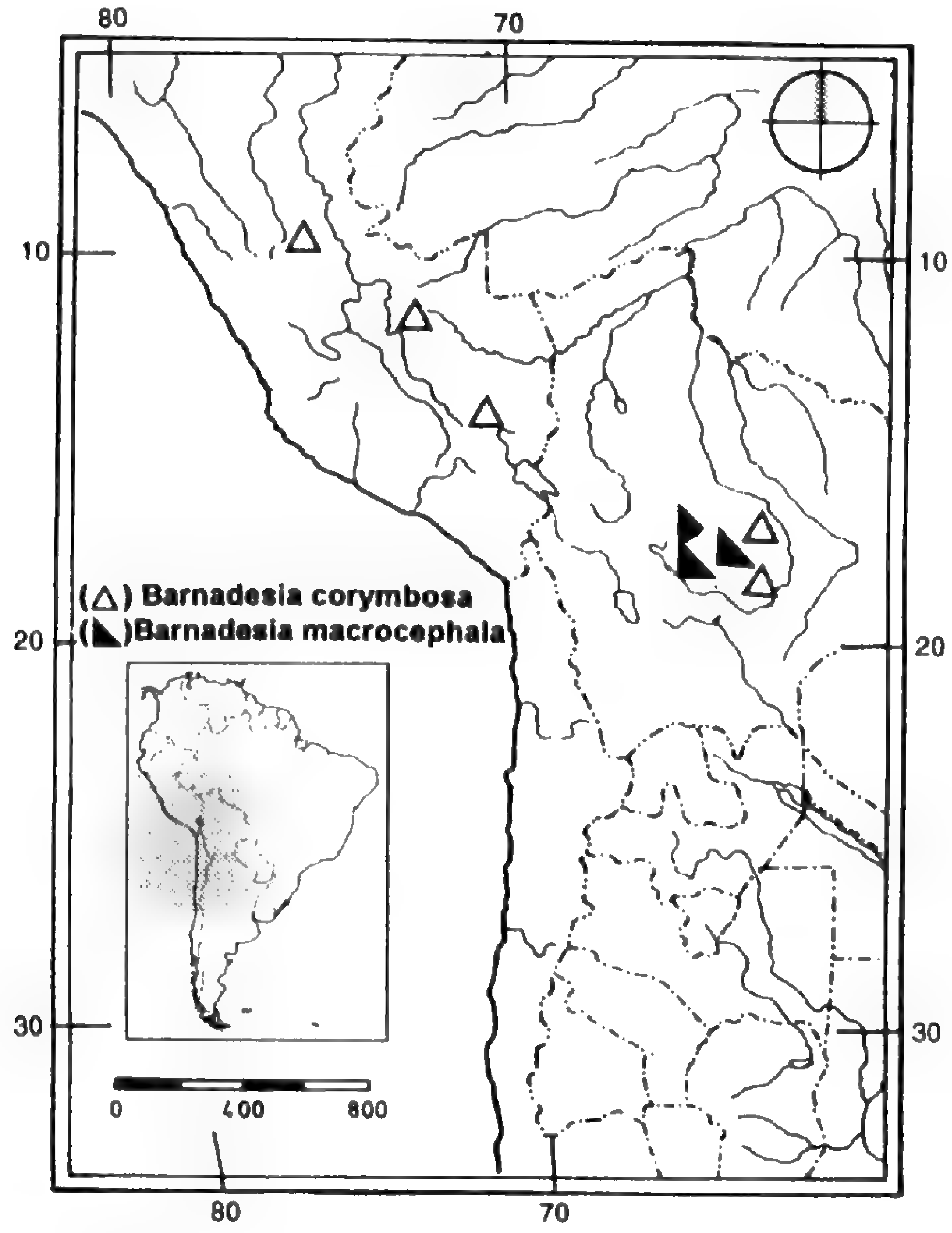

Figura 35. Distribución de *Barnadesia corymbosa* y *B. macrocephala*.

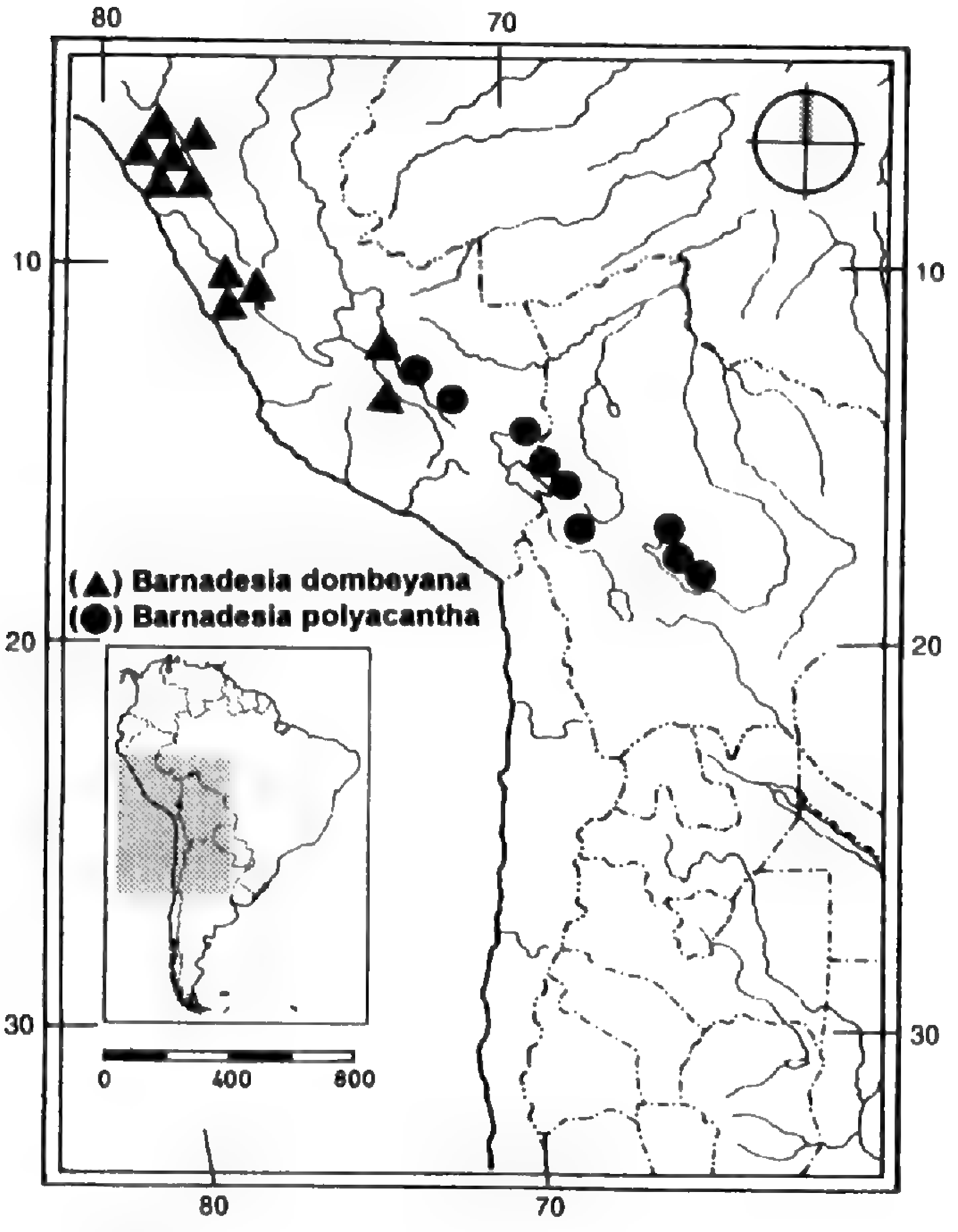

Figura 36. Distribución de *Barnadesia dombeyana* y *B. polyacantha*.

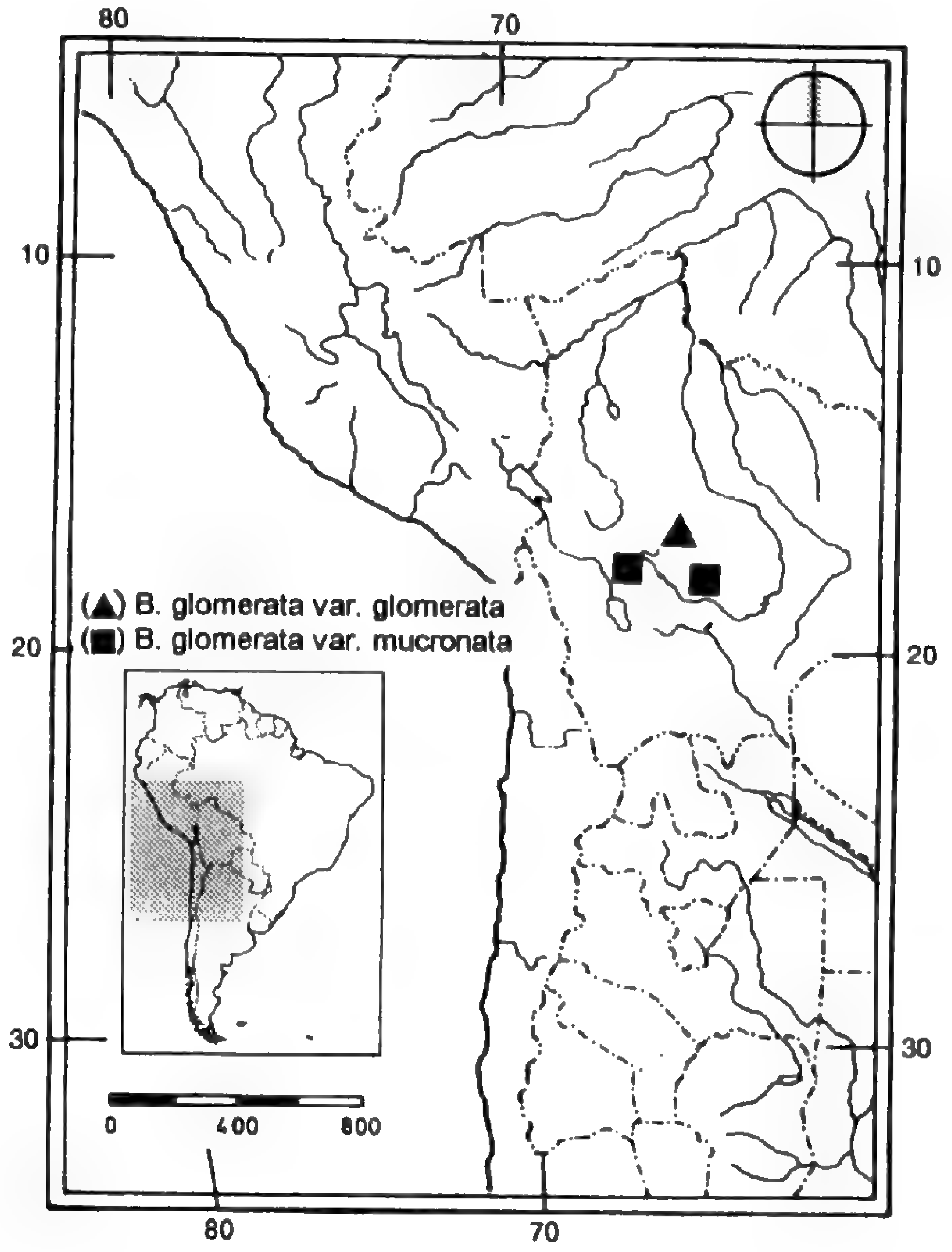

Figura 37. Distribución de *Barnadesia glomerata* var. *glomerata* y *B. glomerata* var. *mucronata*.

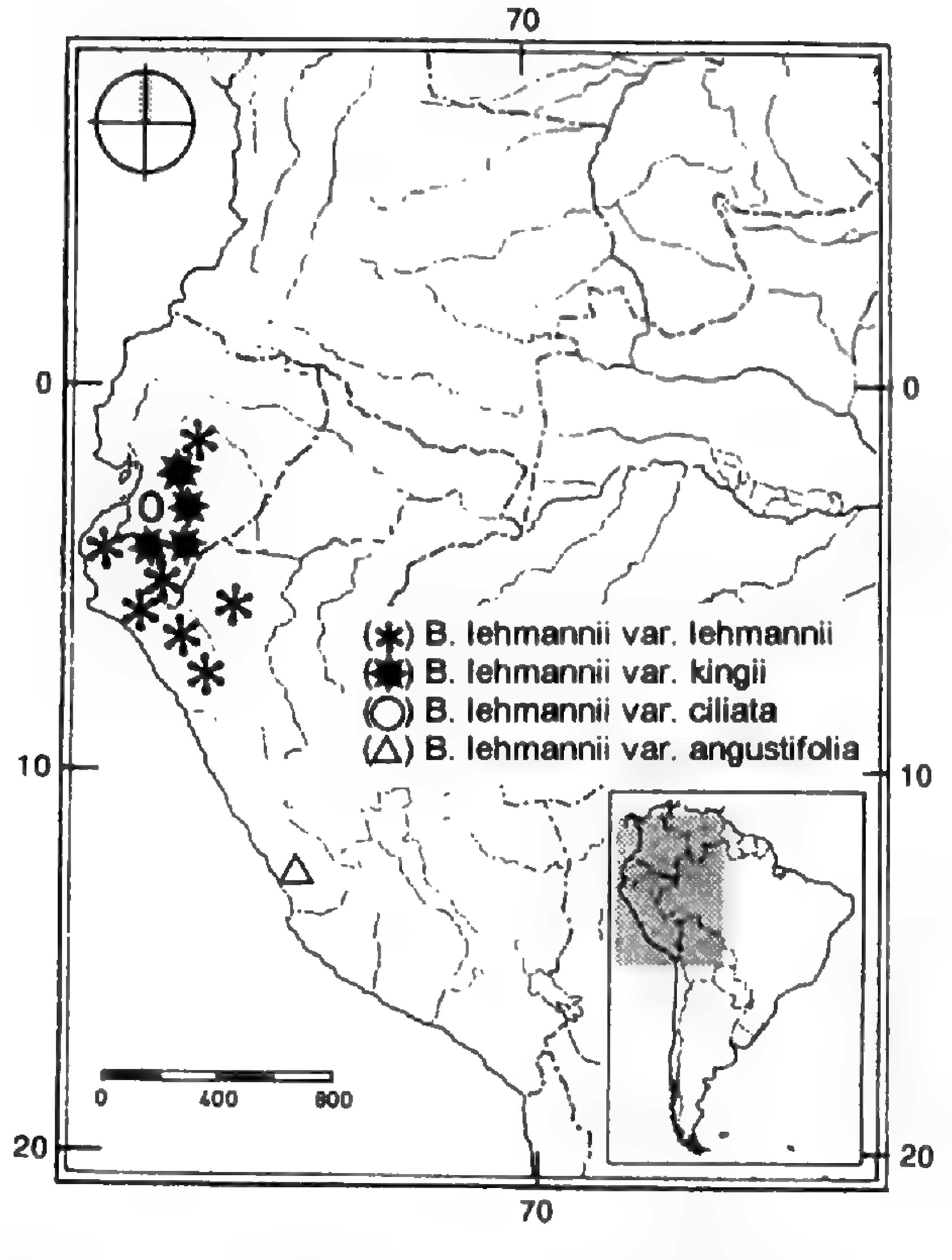

Figura 38. Distribución de *Barnadesia lehmannii* var. *lehmannii*, *B. lehmannii* var. *kingii*, *B. lehmannii* var. *ciliata* y *B. lehmannii* var. *angustifolia*.

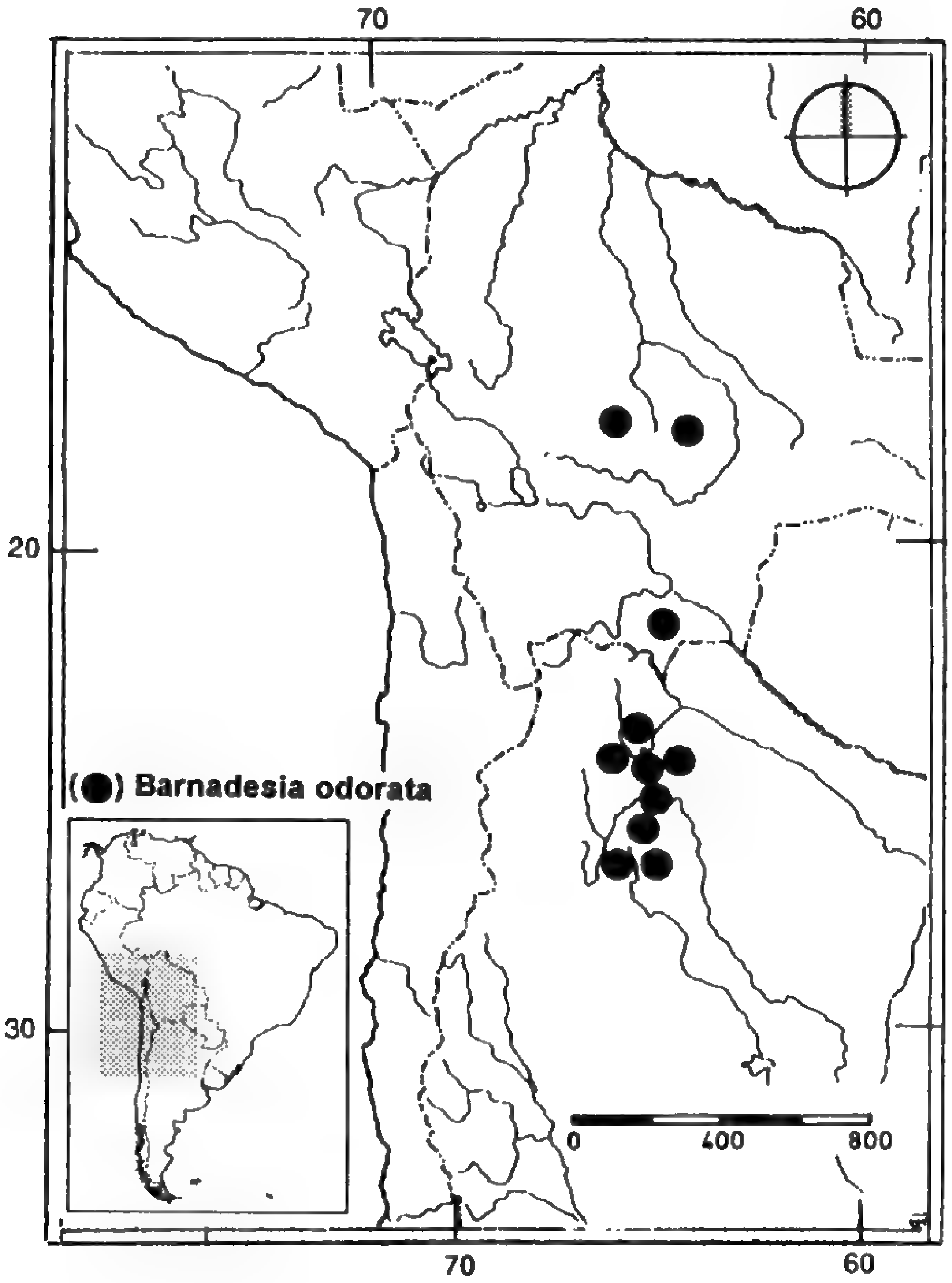

Figura 39. Distribución de *Barnadesia odorata.*

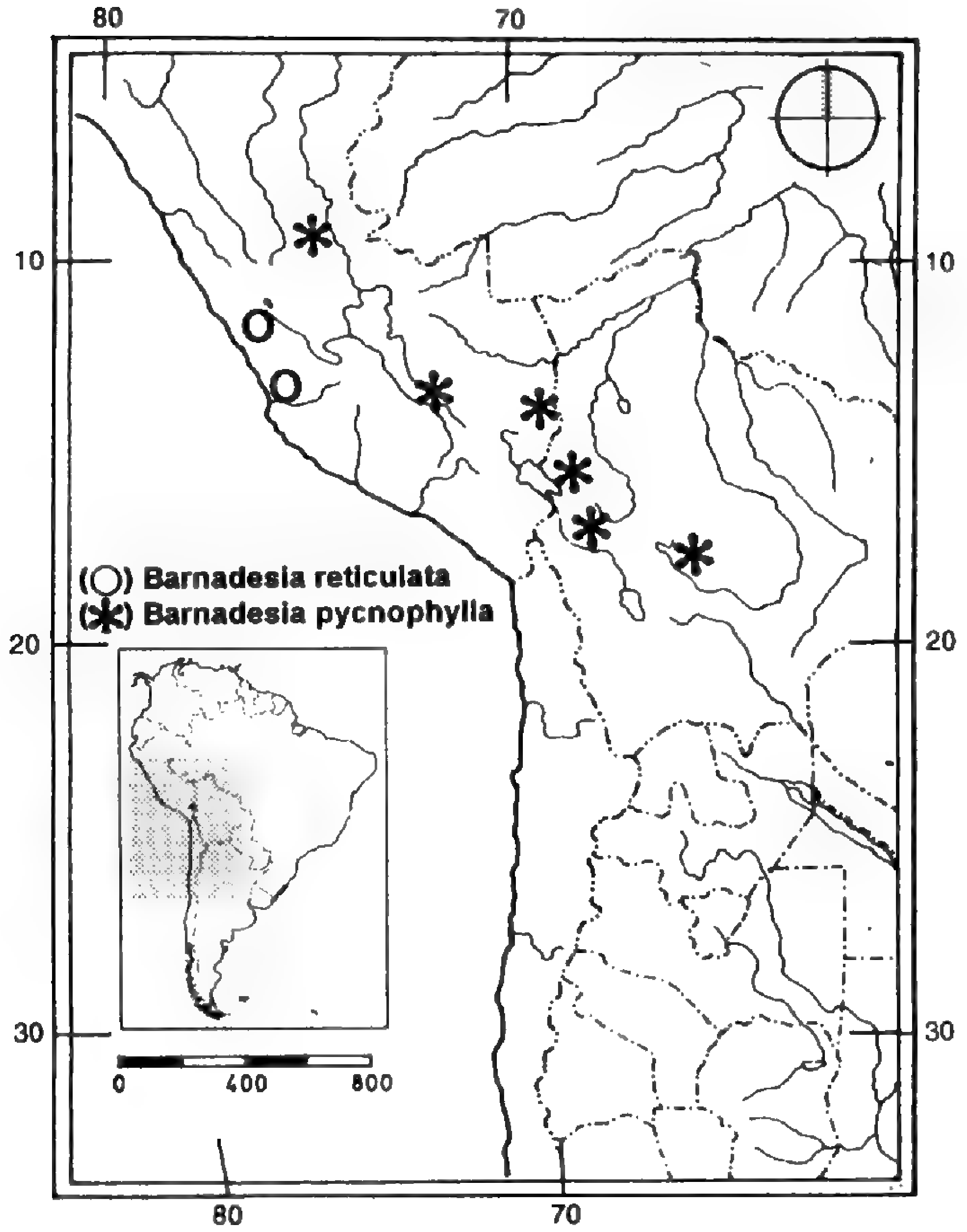

Figura 40. Distribución de *Barnadesia reticulata* y *B. pycnophylla.*

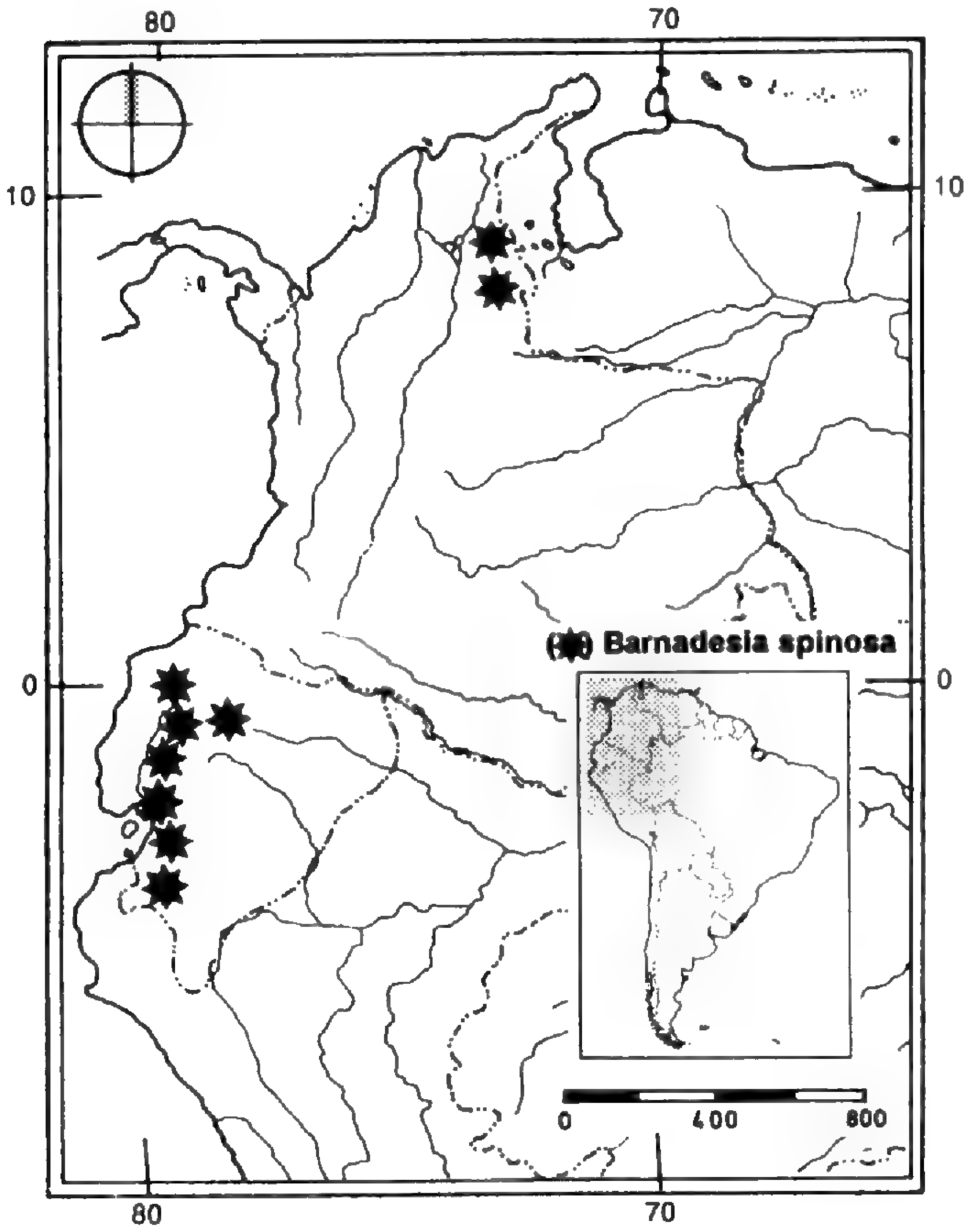

Figura 41. Distribución de *Barnadesia spinosa.*

(US). **Tungurahua:** valley of Río Pastaza, Hacienda Río Verde Grande, 1500 m, *Asplund 7837* (US); valley of Pastaza River, between Baños and Cashurco, 8 hours E of Baños, 1300–1800 m, *Hitchcock 21778* (GH, US); along the road to Negro, ca. 11 km SE Baños, 5500 ft., *King 6545* (MO); Pastaza river, 1700 m, *Rimbach 263* (US); camino El Triunfo–Los Llanganates, antes del Playón del Río Muyu, 2800 m, *Freire Fierro 1227* (NY, US); Volcán Tungurahua, 1900–2500 m, *Lehmann 5239* (GH); near Baños, 6400 ft., *Plowman & Davis 4460* (GH).

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LISTA ENUMERADA DE ESPECIES

(1) B. aculeata; (2) B. arborea; (3) B. blakeana; (4) B. caryophylla; (5) B. dombeyana; (6a) B. glomerata var. glomerata; (6b) B. glomerata var. mucronata; (7) B. horrida; (8) B. jelskii; (9a) B. lehmannii var. lehmannii; (9b) B. lehmannii var. angustifolia; (9c) B. lehmannii var. ciliata; (9d) B. lehmannii subsp. kingii; (10) B. macbridei; (11) B. macrocephala; (12) B. odorata; (13) B. polyacantha; (14) B. pycnophylla; (15) B. reticulata; (16) B. spinosa; (17) B. corymbosa; (18) B. parviflora.

ÍNDICE DE MATERIAL EXAMINADO

Los ejemplares de herbario se mencionan con el nombre del primer colector.

Acevedo 1758 (13); Acosta Solís 5485 (9d), 7775 (9d); Ahumada 4163 (12), 4283 (12); Alexander 28119 (12); Allen 2998 (16); Anderson 9937 (4); André K-271 (2), 3794 (18); Angulo 1381 (5); Arbeláez 1292 (18), 2227 (18); Ariste Joseph, Bro. A155 (16), A305 (16); Aronson 509 (14); Asp 158 (12); Asplund 6439 (2), 7837(18), 17121(18), 17267 (18).

Balik 1387 (17); Balls 5767 (16), B–6683 (7); Balslev 2014 (2), 2482 (18), 2733 (18), 10385 (18); Barclay 137(16), 3382 (16), 7305 (16), 7798 (2); Barker 366 (14); Bartlett 20295 (12); Beck 1116 (14), 1353 (13), 2068 (13), 3733 (13), 8605 (13): 14652 (14); Becker 1013 (5); Bell 438 (18), 572 (2); Bernal 1274 (16); Bernardi 16685 (5); Bird 1258 (5); Biloni 6065 (12); Blohm 81 (7); Boeke 619 (2), 2462 (2), 2997 (14), 3171 (17); Boelcke 2893 (12); Bohlin 1425 (1); Bristol 426 (16), 648 (16), 858 (16); Britton 718 (13); Brown 1606 (12); Buchtien 474 (14), 690 (13); Burchell 5186 (4); Burkart 26536 (12), 30660 (12).

Cabrera 4558 (12), 13476 (7), 13531 (7), 14389 (12), 15717 (12), 29765 (12); Camp E–230 (1), E–3046 (9a), E–3423 (9d), E–4013 (2); Campos Porto 2907 (4); Cárdenas 692 (14), 2183 (13), 3268 (13), 4182 (7), 4290 (6a), 4370 (4), 5736 (12), 5950 (13), 6152 (13); Casas FC 6535 (13); Ceballos 596 (*aff.* 13); Cerón 1147 (2), 1930 (18), 4292 (18), 5238 (2), 5239 (2), 6885 (2), 6980 (2); Cerrate 17 (5), 276 (5), 523 (5), 1318 (5), 1407 (5); Charpin AC–20538 (12); Chávez 3271 (13); Cleef 8423 (16); Clements 2238 (1); Core 884 (16); Coro 1339 (12); Croat 38794 (2); Cuatrecasas 1143 (16), 5199 (16).

Damazio D–2007(4), D–4805 (4); D'Arcy 13824 (13); Davidson 5044 (13); Davis 238 (2); Del Castillo 63 (12), 75 (12); Devia 157 (16), 724 (16); Diers 1147 (3); Dillon 1637 (8); Dodson 614 (1), 1509 (2), 14365 (18), 15165 (18), 15176 (2); Dorr 5793 (2), 5921 (2), 6385 (2), 6962 (13); Dryander 1636 (16); Dudley 9053 (14); Duque Jaramillo 3511 (16).

Edwall 16983 (4); Edwin 3651 (2); Ellenberg 8386 (5); Espinosa 596 (9d); Eyerdam 22225 (12); Ewan 15924 (16), 16461 (2); Ezechias 1291 (4).

Fallen 741 (16); Ferreyra 838 (8), 862 (9 a), 3039 (5), 3331 (5), 3696 (4), 5595 (5), 6216 (5), 6914 (15); 7325 (5), 8062 (5), 8394 (9a), 8493 (8), 9843 (7), 12136 (5), 12946 (10), 13281 (8), 14292 (5), 15032 (8), 15325 (2), 16740 (7), 16742 (13), 18415 (5); Feuerer 4290 (13), 4478 (13), 4904 (13); Fiebrig 2759 (12); Firmin 101 (2); Flora ecuatoriana 1015 (2), 1016 (2), 1017 (2), 1018 (2); Fosberg 27472 (18), 27556 (2); 20579 (16), 28424 (13); Foster 1938 (16); Freire Fierro 1227 (18).

García-Barriga 13068 (16); Gardner 4268 (4); Gentry 9481 (2), 12348 (2), 23188 (2), 16429 (4), 17070 (16), 23407 (7), 23420 (14), 34833 (16), 37463 (5), 44199 (13), 51734 (12), 54986 (18); Gilmartin 796 (2); Glaziou 14942 (4); González 17 (2); Graf 203 (13); Granda 8 (2); Grifo 1065 (7); Grimes 2492 (2); Grubb 717 (2), 1298 (18), 1342 (18); Guaglianone 1940 (12); Guevara Amórtegui A–39 (16); Gutiérrez 256 (16), 378 (16).

Harling 6104 (9d), 25665 (2); Haught 5959 (16), 6539 (16); Henrichs 620 (2); Herbario Marín 161 H (13), 398 (7); Herbario Zamalloa Díaz 2042 (13); Herrera 1055 (7), 2956 (7); Herzog 1938 (13); Hicken 20 (12), 8084 (12); Hirsch E24 (2), 1052 (7), P–1320 (17); Hitchcock 20343 (9a), 20751 (9a), 21012 (16), 21778 (18); Hoehne 389 (4); Holm-Nielsen 18087 (2), 24428 (18), 25120 (2); 26134 (18); Holmberg SI–10640 (12); Holton 392 (16); Humbert 21120 (12), 26923 (16), 30537 (7), 30548 (7); Humbles 6236 (2); Hunziker 10333 (12), 10359 (12); Hutchison 1378 (9a), 1718 (7), 5120 (5), 5312 (2), 6289 (5), 6684 (9a), 6972 (2).

Idrobo 1091 (16); Iltis 541 (7); Irwin 17486 (4), 17807 (4); Isern 36 (4).

Jaramillo M. 402 (16), 2491 (2), 4699 (2), 8589 (2), 8880 (2), 8975 (9d); Jiménez 92 (13); John 20738 (16); Juajibioy Ch. 202 (16); Julio, Bro. 69 (13), 343 (13).

Kiehl 3711 (4); Kiesling 104 (12); Killip 6837 (16), 17238 (16), 17280 (16), 17316 (16), 18250 (16), 18573 (16), 20013 (16), 22187 (7), 24391 (13), 25043 (4), 25142 (4); King 6545 (18), 6704 (2), 6731 (2), 6885 (2), 6893 (2), 7742 (2), 7762 (2), 7788 (2), 9254 (2), 9259 (2), 7476 (13), 7664 (13), 9115 (5); Klatt 2597 (16); Klug 3318 (4); Krach 6585 (13), 9158 (13), 9475 (13); Krapovickas 38162 (7), 42714 (12).

Larsen 95 (2); Ledingham 4575 (2); Lehmann 2597 (16); 5239 (18); Lewis 88626 (13), 88655 (14), 88899 (6b), 881010 (14), 881032 (14), 881077 (13), 881107 (13), 881108 (6b), 881138 (6b); Libenson 30654 (16); Linden 65 (16); Little 129 (18); López, A. 311 (5), 1059 (5), 2755 (5), 3280 (5), 4406 (2), 7803 (9d), 8802 (9a).

Macbride 849 (18), 1222 (5), 1759 (5), 2250 (5), 2230 (14), 3953 (17); MacBryde 188 (2), 1236 (2); Maguire 44276 (2), 44277 (2), 61626 (14); Malme 1648 (4); Mathews 643 (9b), 1389 (9b); Mena 620 (2); Metcalf 30446 (14); Meza 86 (15); Monetti 1989 (12), 3091 (12); Mostacero 532 (5).

Niemeyer 157 (16); Novara 217 (12), 562 (12), 3533 (12), 5491 (12), 7371 (12), 8098 (12); Núñez 56 (12), 307 (12).

Ochoa 2669 (2), OCH–5199 (14), 15491 (13); Oldeman 3372 (2); Øllgaard 8018 (2); Ortin 17 (12), 68 (12).

Palací 74 (12); Palacios 6244 (18), 6277 (18); Pasco 350 (2); Pearce 1868 (17); Pedersen 9891 (12); Peirano 9117 (12), 27145 (12), 58500 (12); Penland 547 (2); Pennell 2290 (16), 2516 (16), 8861 (18), 13556 (7), 14397 (5), 15553 (2); Pereira 1084 (4); Peyton 1541 (13), 1563 (13); Piergentili 3421 (12), 3477 (12); Pires 9703 (4); Plowman 4460 (18), 14200 (4); Popenoe 1285 (2); Porto 360 (4); Prance 58432 (4); Prescott 226 (2); Prieto CP–24A (9a), CP–24B (9a), P–74 (2); Pring 22 (16).

Rauh 386 (15), 26063 (14); Regnell 190 (4), 198 (4); Rentzell von 12544 (13); Renvoize 3340, 3439 (12); Riccio 3625 (5); Rimbach 34 (2), 263 (18); Robertson 12 (4); Rose 19036 (7), 22134 (9a), 23544 (2); Rubio 489 (2), 606 (18); Rupnik 14 (12); Rusby 17 (14), 1552 (13), 1553 (13).

Sagástegui 8095 (2), 8239 (8), 8798 (8), 8945 (9a), 9013 (5), 9385 (5), 9819 (9a), 10001 (5), 11066 (5), 12235 (8); Saint-Hilaire 736 (4); Saldías 288 (13); Saunders 725 (7); Scolnik-Luti 540 (13); Schiefer 346 (16); Schimpff 683 (18), 884 (2); Schreiter 4053 (12), 11415 (12), 58537 (12); Schultes 7479 (16), 7912 (16), 7919 (16), 18562 (16); Smith 2236 (5), 8295 (5), 9708 (5), 11072 (5), 11152 (5), 11248 (5), 12360 (5), 13383 (13), 13606 (13); Sneidern, K. von 2805 (16), 3085 (16), 3111 (18); Sodiro 754 (2); Soejarto 286 (16); Solomon 2942 (7), 5989 (13), 6039 (13), 11984 (13), 15341 (13), 18669 (13), 8341 (14), 15118 (14), 16043 (14), 16453 (14), 16646 (14), 14502 (11); Soraya 30 (4); Soukup 2510 (4), 3391 (4), 4415 (4), 2883 (14), 4283 (9a); Soukuz 4981 (8); Spruce 4393 (4), 5197 (2), 5532 (9a); Steinbach, J. 193 (14), 3380 (17), 8418 (12), 8578 bis (13), 9547 (13), 8723 (11); Stork 10615 (5); Stuessy 4893 (2).

Tate 241 (14), 797 (13), 879 (13); Teixeira 255 (4); Teppner 218 (4); Tolaba 186 (12), 266 (12); Tovar 1099 (14), 1931 (7); Townsend 945 (9a); Triana 65 (16), 1492 (18).

Ugent, D. 3853 (7), 4372 (7), 5595 (2); Urtubey 23 (12), 25 (12), 27 (12).

Valencia 3 (3), 96 (3), 719 (3), 1308 (3), 1314 (3), 1596 (3), 1605 (3); Vanni 463 (12); Varela 214 (12); Vargas, C. 1896 (7), 3395 (13), 3607 (14), 3627 (7), 3966 (13), 4360 (7), 5170 (17), 14559 (14), 14710 (17), 16336 (7), 16401 (4), 22951 (13); Vargas, I. G. 7 (12); Velarde Núñez 4778 (4); Venturi 756 (12), 5235 (12), 9503 (12), 9608 (12); Vuilleumier 110 (2), 247 (14).

Wasshausen 1141 (4); Weberbauer 6717 (17); Webster 28669 (18); Wedermann 2009 (11); Whalen 868 (4); White 188 (14), 258 (4); Widgren 192 (4); Wiggins 10631 (16); Williams 2469 (14), 7241 (4); Woronow 5118 (16); Woytkowski 6637 (4), 6880 (4), 7398 (4), 8121 (4), 15482 (4), 35300 (4), 34335 (10); Wurdack 930 (2).

Yussen 10 (12).

Zak 2347 (18); Zamalloa D–66 (7); Zapata 74 (12); Zardini 1183 (12), 1274 (12), 1511 (5); Zuloaga 1334 (12).

Índice de Nombres Científicos y Vulgares

Los sinónimos se presentan en letra cursiva.

A REVISION OF *GRIMMIA* (MUSCI, GRIMMIACEAE) IN THE AMERICAS. 1: LATIN AMERICA[1]

Jesús Muñoz[2]

ABSTRACT

Grimmia comprises 29 (plus 2 probable) species in Latin America. The centers of highest species diversity are the Mexican Volcanic Belt and the Andean Range between central Peru and southern Patagonia. All taxa are keyed and described, and they are typified if it has not been done previously. Each species is illustrated and its distribution mapped. *Grimmia molesta* is described as new from Peru. Previous records of *G. tergestina* from Mexico correspond to *G. involucrata. Grimmia kidderi, G. ochyriana,* and *G. tergestina* are reported for the first time from the Americas.

Grimmia comprises about 100 species worldwide (Muñoz, in prep.), and its taxonomy is reputedly difficult. Most of this difficulty arises because hundreds of names were published without proper evaluation of existing taxa, and because currently there are only a few updated regional treatments available. For example, at this time there is no complete survey for Latin America, a region rich in described taxa according to *Index Muscorum* (van der Wijk et al. 1962, 1969). Papers on Patagonian and Peruvian taxa by Deguchi (1984, 1987) do not cover all the species known from those areas, in spite of which they are of great value and the only source of reliable information for South American *Grimmia.* The only other treatment available is by Crum (1994), which covers the Mexican species. My results, however, differ in several ways from his, mostly in terms of accepted species.

Species of *Grimmia* are typical members of plant communities above the tree line, growing on rocks and fed by thawed snow, withstanding extremely harsh enviromental conditions. In the geographic area covered for this study, only a few widespread species are present outside the main mountain ranges, mainly associated with man-made habitats.

Some 1500 herbarium specimens were studied to determine the geographical distribution and morphological variation of the species. Types of many taxa described from areas not covered in this revision were also studied in order to determine the correct names for the taxa; these names are listed in the appropiate nomenclatural sections. World distributions follow the Hollis and Brummitt (1992) scheme. All distributions are based on specimens actually studied by the author.

GEOGRAPHICAL DISTRIBUTION OF *GRIMMIA* IN LATIN AMERICA

Figure 1 plots the number of species per country, clearly showing that *Grimmia* is more species-rich in temperate regions. Conversely, in the Neotropics the genus is found only in montane to alpine habitats, mainly above tree line.

Mexico has the highest number of species, reflecting its larger variety of habitats suitable for the establishment of *Grimmia.* Species with a temperate distribution (*G. americana, G. laevigata, G. lisae, G. montana, G. ochyriana, G. ovalis, G. pilifera, G. poecilostoma, G. pulvinata,* and *G. ungeri*) reach their southernmost limit in the Mexican Volcanic Belt (or north of it). Two species, *G. ochyriana* (Fig. 29) and *G. ovalis* (Fig. 31), have outlying populations in the highest peaks of northern Guatemala.

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Figure 1. Number of *Grimmia* species per country in Latin America.

Noteworthy is the bipolar temperate distribution of *G. laevigata* (Fig. 12) and *G. pulvinata* (Fig. 40), species not occurring in the intervening Neotropics. Two endemic species, *G. involucrata* (Fig. 6) and *G. pulla* (Fig. 34), increase the number of taxa known from Mexico. The number of *Grimmia* species decreases south of the Mexican Volcanic Belt. The predominance of tropical lowland to montane vegetation in Central America and the Caribbean seems to be responsible for the paucity of *Grimmia* taxa in the area (Fig. 1).

Grimmia anodon, G. atrata, G. donniana, G. elongata, G. fuscolutea, G. longirostris, G. plagiopodia, G. reflexidens, G. tergestina, and *G. trichophylla* are widespread species following the main South American Andean chain. Two of these, *G. elongata* and *G. longirostris,* have disjunct populations in the mountains of southeastern Brazil (Itatiaia and Santa Catarina). Figure 1 shows that the diversity is low in the northern countries of South America, but increases southward, especially around the Bolivia–Peru border. Indeed, there are several species almost restricted to this area: *G. bicolor* (Fig. 10), *G. molesta* (Fig. 10), *G. pseudoanodon* (Fig. 34), and *G. trinervis* (Fig. 29). This may be an artifact since much of this area is better collected than other sites in Argentina and Chile similarly suitable for *Grimmia* establishment.

Two more species can be considered endemic to areas covered by this study. *Grimmia navicularis* (Fig. 26) grows in the Andean range, and *G. tortuosa* (Fig. 40) is known only from the type collection in the Falkland Islands.

TAXONOMIC CHARACTERS

The taxonomic characters of *Grimmia* have been surveyed in depth by Deguchi (1978). Variability in taxonomic characters was considered by Muñoz (1998d) in his revision of *Grimmia* subg. *Orthogrimmia,* with four Latin American species. Some taxonomic characters, however, deserve further comment here.

Hair-points. Features associated with hair-points should be used with extreme caution due to their variability. In this study, only *G. atrata* and *G. ochyriana* constantly lack hair-points. *Grimmia pulla* has short hair-points that are strongly dentate and usually brownish, at least proximally, features only observed in this taxon. *Grimmia elongata* usually has short hair-points, which are absent in many leaves, but some Bolivian specimens of this species have long hair-points. Hair-point length and structure in remaining species show high infraspecific variability, from lacking to more than 1 mm, and from entire to dentate. I discard any taxonomic entity based solely on this structure.

Costae. The structure of the costae and its relative differentation from the lamina are considered of major taxonomic importance in this study, and can be easily ascertained in transverse sections. Kawai (1965, 1968) wrote the best survey of costae structure and ontogeny in Grimmiaceae.

Three types of costae (as seen in cross section) can be distinguished in *Grimmia*: (1) undifferentiated or weakly differentiated from the lamina, not or only scarcely prominent on the dorsal side of the leaf (Figs. 2C, 18C, D, 20E, F, 30B, C, 35B, 42B, C); (2) reniform, consisting of 2 to 6 cells in the ventral epidermis, differentiated from the lamina and prominent (occasionally weakly) on the dorsal side of the leaf (Figs. 5B–D, 21B, C, 22B, C, 28B–D); and (3) terete, consisting of 2 cells in the ventral epidermis, differentiated from the lamina and prominent on the dorsal side of the leaf (e.g., Figs. 4B, C, 7B–D, 9G–I, 13B–D, 43B, C).

Propagula. The main source of information about vegetative propagation in mosses is still Correns (1899), who recognized three main modes of gemma formation in *Grimmia*: (1) complete modification of the leaf apex into massive gemmae, causing the destruction of the leaf (*G. anomala* Schimp. and *G. hartmanii* Schimp., both alien); (2) gemmae generated at the tips of stalks, branched or not, developed on the dorsal axillary side of leaves, causing minor leaf damage, if any (*G. austrofunalis*, *G. lisae*, and the alien *G. muehlenbeckii* Schimp. and *G. torquata* Drumm.); and (3) modification of the laminal cells into propagula, destroying the leaf (*G. trichophylla*).

Features associated with the development of gemmae are critical to distinguish the closely related *G. austrofunalis* and *G. trichophylla* and are treated in detail under these species.

Perichaetial leaves. Perichaetial leaves are convolute and larger than other leaves except for *G. atrata*, in which they are convolute but otherwise undifferentiated. Five species in the area (*G. americana*, *G. involucrata*, *G. poecilostoma*, *G. tergestina*, and *G. trinervis*) have perichaetial leaves strongly modified, hyaline and filmy except for a patch of green cells at the apex. Except for *G. trinervis*, with strongly plicate leaves, these taxa are identical in gametophyte morphology and anatomy, differing either in sexuality or sporophyte characteristics.

Annulus. Deguchi (1978, fig. 7) described three types of annulus: (1) *Schistidium* type: simple and persistent, composed of undifferentiated cells (*G. montana*, *G. plagiopodia*, and *G. ungeri*); (2) *elongata* type: compound and revoluble, composed of 1 to 2 rows of inflated, isodiametric cells (e.g., *G. atrata*, *G. elongata*, *G. ochyriana*, and *G. pseudoanodon*); and (3) *affinis* type: compound and revoluble, composed of (2)3 to 4 rows of inflated, rectangular cells becoming larger from the lower to the upper rows (e.g., *G. involucrata*, *G. longirostris*, *G. poecilostoma*, and *G. trichophylla*).

The annulus of all the species studied can be assigned to one of Deguchi's three types except for *G. anodon* and *G. trinervis*. Discrepancies are apparent in the interpretation of the annulus morphology in *G. anodon*. It has been defined as "narrow, persistent. . ." (Deguchi, 1987: 22), "wanting" (Cao & Vitt, 1986: 205), "simple" (Jones, 1933: 22), "persistent, of 1 layer of cells" (Crum, 1994: 395), or as "1(2)reihig, bleibend, gewölbt, stumpf genabelt, gleichfarbig [in 1(2) layers, persistent, arched, bluntly umbilicate, concolorous]" (Limpricht, 1890: 727). In *G. trinervis*, the annulus was characterized as "imperfectly developed, of quadrate, thick-walled, translucent cells" (Deguchi, 1987: 32). In fact, *Grimmia anodon* and *G. trinervis* share a similar annulus: 1 to 2 layers of inflated cells, differentiated from both the exothecial and operculum cells, and persisting for a long time on the capsule mouth. These annular cells are identical to those of the *elongata* type, but the annulus in these two gymnostomous species persists longer on the capsule mouth, and can be termed "tardily deciduous."

In this treatment, laminal length excludes hair-point, laminal width has been measured at the broadest part of the leaf, and fractions (e.g., "margin recurved in the proximal ½") always refer to laminal length. Cellular measurements include the wall, except when otherwise stated. Proximal juxtacostal and marginal cells refer to the two or three rows of cells closest to the costa and margin, respectively. The size of the perichaetial leaves refers to the area of the rectangle defined by their length and width. Finally, setae length includes the vaginula.

TAXONOMIC TREATMENT

Grimmia Hedw., Sp. Musc. Frond. 75. 1801. TYPE: *Grimmia plagiopodia* Hedw. (lectotype, designated by Mårtensson (1956: 106–107)).

Cladautoicous, *gonioautoicous*, or *dioicous*. *Plants* in dense cushions or compact to loose tufts, glaucous, green, greenish yellow, or olive-green. *Stems* erect or ascending, with or without a central strand. *Leaves* erect, appressed or flexuous, occasionally with homomallous tips when dry, erect to spreading when moist, linear, ovate, lanceolate, ligulate, oblong to triangular, obtuse to acuminate, concave, canaliculate or keeled, plane or plicate; *margins* entire, plane, recurved or incurved; *costa* single, percurrent, terete, semi-terete, semi-elliptic or almost indistinct in cross section; *lamina* 1–4-stratose in the distal half; *distal cells* isodiametric to rectangular or oblate, bulging or plane, with straight or sinuous walls; *proximal cells* quadrate to rectangular or oblate, the walls straight or sinuous, uniformly thickened or the transverse walls thicker than the longitudinal walls; with or without *hyaline hair-points*. *Perichaetial leaves* convolute and larger or similar in shape but slightly larger than vegetative leaves. *Androecia* axillary or terminal. *Setae* straight or curved, longer or shorter than capsules. *Capsules* immersed, emergent or exserted, subglobose, ovoid, ellipsoid or fusiform, symmetric or asymmetric and ventricose at the base, smooth or ribbed, stramineous or castaneous, with stomata at the urn base or lacking stomata; *exothecial cells* isodiametric or rectangular, thin- or thick-walled; *annulus* simple and persistent, compound and revoluble, or compound and tardily deciduous; *peristome teeth* 16, triangular, entire, perforate in the distal half or cribrose throughout and irregularly cleft at apex, orange to brown; *opercula* conic to long-rostrate; *calyptrae* cucullate or mitrate, smooth, covering to the capsule mouth; *columella* persistent; *spores* smooth to coarsely granulose.

KEY TO SPECIES OF *GRIMMIA* IN AMERICA SOUTH OF THE U.S.A.

Notes for using the key:

Leaf length is *without* hair-points.

Cross sections: They are essential to correctly identify a specimen. Superficial examination, as indicated by Sayre (1952: 255–256), can result in errors. Cross sections are made between ½ and ⅔ of laminal length above base.

Capsules: Some species have immersed capsules hidden by the perichaetial leaves that are often overlooked. Immersed capsules can be found when looking carefully under the dissecting microscope for inflated distal stem parts, where leaves have longer hair-points. It is surprising how many specimens with immersed capsules are considered sterile even though some sporophytes can be easily found in the packet.

Propagula: If the specimen has propagula, go directly to couplet 36, but check also *G. lisae* (European specimens of this taxon sometimes have propagula). Although it is commonly stated that fertile specimens of *G. trichophylla* have no propagula, this is not correct. Propagula are most likely detected around perichaetial buds, even on the perichaetial leaves themselves. Propagula may be first sought on the youngest innovations and perichaetial buds. If not located, propagules may be found in older stem bifurcations, among decayed perichaetia. It is important to note where the propagula are generated on the leaves, whether on the back of the costa or directly over the lamina (see couplet 36 in the key). *Grimmia austrofunalis* and *G. trichophylla* can be difficult, if not impossible, to separate without propagula.

1a. Leaves strongly plicate on both sides of costa.
2a. Setae curved; capsules asymmetric and ventricose at base, gymnostomous; calyptrae mitrate, not exceeding further down than capsule mouth, not plicate .... 30. *G. trinervis*
2b. Setae straight; capsules symmetric with seta centrally placed at base, species in the area with peristomes; calyptrae campanulate, extending below capsule mouth, plicate .... *[Coscinodon]*
1b. Leaves not plicate or only weakly so.
3a. Capsules asymmetric and ventricose at base; seta eccentrically attached to the capsule, curved, shorter than the capsule.
4a. Peristome lacking; leaves keeled .... 2. *G. anodon*
4b. Peristome present; leaves concave .... 21. *G. plagiopodia*
3b. Sterile specimens, or capsules symmetric; seta centrally attached to the capsule and, if curved, longer than the capsule.
5a. Proximal marginal cells of leaves oblate .... 12. *G. laevigata*
5b. Proximal marginal cells of leaves quadrate to rectangular.
6a. Proximal marginal cells of leaves with all walls similar, thin.
7a. Margins plane throughout or incurved above, no trace of recurvation.
8a. Leaves crisped when dry; exothecial cells strongly incrassate, lumen almost obliterated .... 28. *G. tortuosa*
8b. Leaves erect and appressed to weakly flexuous when dry, but never crisped; exothecial cells thin-walled .... 6. *G. donniana*
7b. At least one margin recurved for part of its length.
9a. Longest hair-points longer than 0.3 mm, most of the leaves piliferous; autoicous, male buds small and lateral, hidden just below perichaetia; setae curved (the species is always found with sporophytes) .... 8. *G. fuscolutea*
9b. Longest hair-points to 0.3 mm long, most of the leaves muticous; dioicous, male buds terminal; setae straight .... 7. *G. elongata*
6b. Proximal marginal cells of leaves with transverse walls thicker than longitudinal walls.
10a. All leaves constantly muticous.
11a. Dry plants with leaves flexuous and crisped; 1 to 2 basal marginal cell rows inflated, usually reddish, forming 2-stratose alar areas; perichaetial leaves virtually identical to vegetative leaves (2.3–3.2 mm vs. 1.5–3.2 mm long); seta 3–10 mm; capsule completely exserted .... 3. *G. atrata*
11b. Dry plants with leaves erect, only flexuous at apical part; basal marginal cell rows not inflated, not colored, similar to adjacent inner rows, 1-stratose; perichaetial leaves longer than vegetative leaves (4.0–5.5 mm vs. 2–3 mm long); seta 1.5–2.1 mm; capsule immersed .... 18. *G. ochyriana*
10b. At least perichaetial leaves with a trace of a hyaline hair-point.
12a. Margins plane or incurved.
13a. Distal half of lamina unistratose, only 1 or 2 marginal rows 2-stratose.
14a. Hyaline hair-points terete; seta more than 1 mm, curved; capsules exserted, with peristome .... 9. *G. humilis*
14b. Hyaline hair-points flat at base; seta less than 1 mm, straight; capsules immersed, gymnostomous .... 23. *G. pseudoanodon*
13b. Distal half of lamina 2 to 3(4)-stratose.
15a. Costae semicircular (cross section), prominent on dorsal surface.
16a. Lamina concave to U-shaped (cross section) in the proximal part

of leaf; perichaetial leaves 5–15 times larger in area than the other leaves; capsules immersed .... 11. *G. kidderi*

16b. Lamina V-shaped (cross section) in the proximal part of leaf; perichaetial leaves 2–3 times larger in area than the other leaves; capsules exserted.

17a. Laminar cells bulging (cross section) .... 26. *G. reflexidens*

17b. Laminar cells not bulging (cross section). (NOTE: Sterile or poor specimens of the following three taxa can be impossible to name.)

18a. Blades of lamina in cross section (distal half) forming a < 30° angle, parallel at the junction with the costa, furrow very narrow; stomata present at the urn base .... 26. *G. reflexidens*

18b. Blades of lamina in cross section (distal half) forming a > 45° angle, divergent at base, furrow more open; stomata lacking.

19a. Operculae long-rostrate; setae 2–4 mm long; peristome teeth 50–90 µm wide at mouth, irregularly splitting above and ± cribrose; proximal juxtacostal leaf cells mostly long-rectangular, to 4.5:1; dioicous .... 16. *G. montana*

19b. Operculae obtuse to rostellate; setae to 2 mm long; peristome teeth 40–50 µm wide at mouth, entire or slightly cribrose at apex; proximal juxtacostal leaf cells isodiametric to rectangular, to 3:1; autoicous .... 31. *G. ungeri*

15b. Costae elliptical (cross section), scarcely prominent on dorsal surface, occasionally of the same thickness as lamina, scarcely differentiated.

20a. Proximal juxtacostal cells long-rectangular (4–8:1), walls nodulose; perichaetial leaves of mature sporophytes green and firm, neither hyaline nor filmy; setae 3–7 mm long; capsules exserted .... 19. *G. ovalis*

20b. Proximal juxtacostal cells shorter (1–4:1), walls straight; perichaetial leaves of mature sporophytes almost entirely hyaline and filmy (look carefully around capsules: inner perichaetial leaves are almost invisible except under high contrast in the compound microscope); setae to 1 mm; capsules immersed. (NOTE: Sterile specimens of the following four taxa are gametophytically identical and impossible to name with confidence.)

21a. Setae curved; capsules ventricose and asymmetric at base.

22a. Autoicous, male buds small and hidden just below perichaetia .... 1. *G. americana*

22b. Dioicous, male buds terminal .... 22. *G. poecilostoma*

21b. Setae straight; capsules symmetric at base.

23a. Autoicous, male buds small and hidden just below perichaetia .... 10. *G. involucrata*

23b. Dioicous, male buds terminal .... 27. *G. tergestina*

12b. Margin recurved, at least on one side for part of its length.

24a. Ventral layer of costae 2 to 6 cells wide, cross section of costae reniform.

25a. Proximal juxtacostal cells of leaves with nodulose walls; setae straight; capsules cylindrical .... 14. *G. longirostris*

25b. Proximal juxtacostal cells of leaves with uniformly thickened walls; setae curved; capsules ovoid .... 13. *G. lisae*

24b. Ventral layer of costae 2 cells wide, cross section of costae semicircular, never reniform.

26a. Leaves lingulate to elliptic, widest near middle or sides parallel, of equal width ± from base to little above middle.

27a. Hyaline hair-points sharply dentate, to 0.6 mm long; dioicous .... 24. *G. pulla*

27b. Hyaline hair-points smooth or weakly denticulate, to 2 mm long; autoicous, perigonia below perichaetia .... 25. *G. pulvinata*

26b. Leaves ovate to lanceolate, widest near base and conspicuously tapering upward from there.

28a. Laminar cells bulging (cross section) .... 26. *G. reflexidens*

28b. Laminar cells not bulging (cross section).

29a. Lamina 2 to 3(4)-stratose for most of its upper ⅔.

30a. Leaves ovate, broad proximally, ± suddenly nar-

rowed into an upper subulate part, forming shoulders; leaves 2–3 mm long .... 20. *G. pilifera*
30b. Leaf base not forming shoulders; leaves shorter than 1.9 mm.
    31a. Blades of lamina in cross section forming a < 30° angle, parallel at the junction with the costa, furrow very narrow.
        32a. Leaves lanceolate to narrowly lanceolate; plants commonly reddish; setae curved .... 17. *G. navicularis*
        32b. Leaves ovate-lanceolate to lanceolate; plants never reddish; setae straight .... 26. *G. reflexidens*
    31b. Blades of lamina in cross section forming a > 50° angle, divergent at base, furrow open.
        33a. Leaves appressed, straight; setae straight; capsules immersed; autoicous .... 15. *G. molesta*
        33b. Leaves flexuous; setae curved; capsules exserted; dioicous .... 5. *G. bicolor*
29b. Lamina mostly unistratose in its upper ⅔, with bistratose margins and/or occasional and small 2-stratose patches.
    34a. Leaves ovate .... 9. *G. humilis*
    34b. Leaves narrowly lanceolate to lanceolate.
        35a. Blades of lamina in cross section forming a < 30° angle, parallel at the junction with the costa, furrow very narrow .... 17. *G. navicularis*
        35b. Blades of lamina in cross section forming a > 45° angle, divergent at base, furrow more open.
            36a. Propagula sessile on lamina, seldom on the costa, no stalk remaining after propagula liberation, which causes leaf destruction; lamina bistratose at margins and in streaks; plants less than 3 cm; spores minutely granulose, apparently smooth under light microscope .... 29. *G. trichophylla*
            36b. Propagula on stalks at dorsal base of costa, the stalk 1(2) cells long remaining attached to the costa after propagula liberation, which does not affect the leaf; lamina unistratose except the sometimes 2-stratose 1 or 2 marginal rows; plants to 8 cm; spores coarsely and distinctly granulose under compound microscope .... 4. *G. austrofunalis*

1. Grimmia americana E. B. Bartram, Bryologist 32: 8, pl. 1. 1929. TYPE: U.S.A. Texas: Jeff Davis Co., Fort Davis, *Orcutt 7082* (lectotype, here designated, FH; isolectotype, NY).

Gonioautoicous. Plants olive-green. *Stems* erect, to 2 cm, with central strand. *Leaves* erect and appressed when dry, erect to patent when moist, 1.1–1.6 × 0.4–0.7 mm, triangular to ovate, obtuse to acute, concave, not plicate; *margins* plane; *costa* semi-elliptical, undifferentiated, ventral epidermis 3–7 cells wide in cross section; *lamina* 2-stratose in the distal ⅔; *distal cells* 7–12 µm long, isodiametric, rectangular and oblate, not bulging, walls sinuous; *proximal juxtacostal cells* 20–60 × 10–14 µm, rectangular (2–5 : 1), walls medium-thick and straight; *proximal marginal cells* 7–20 × 10–18 µm, oblate to rectangular (0.5–1.5 : 1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete distally and flat proximally, somewhat decurrent, straight, to 2 mm, denticulate. *Perichaetial leaves* 1.8–2.5 × 0.8–1.3 mm, convolute, hyaline and filmy, scarcely discernible, larger than vegetative leaves (3–3.5 : 1). *Androecia* below perichaetia. *Setae* curved, 0.4–0.6 mm long. *Capsules* immersed, ovoid, ventricose, smooth, castaneous, with stomata at the base; *exothecial cells* 35–70 × 20–35 µm, rectangular (1.5–2.5 : 1), thin-walled; *annulus* compound and revoluble, *affinis* type; *peristome teeth* 80–120 µm wide at the mouth, cribrose throughout and irregularly cleft at apex, external surface nearly smooth proximally and papillose distally, internal surface papillose

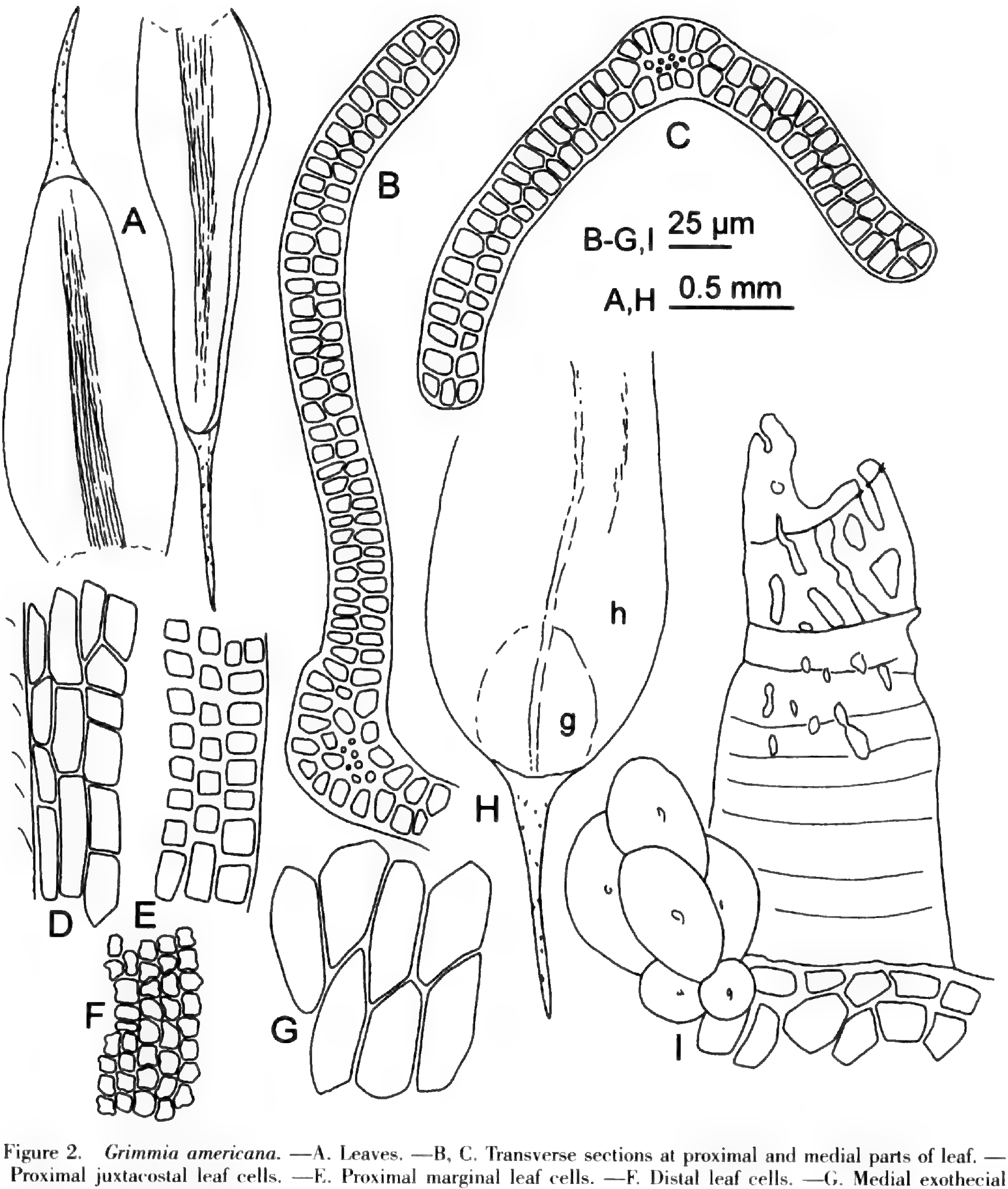

Figure 2. *Grimmia americana.* —A. Leaves. —B, C. Transverse sections at proximal and medial parts of leaf. —D. Proximal juxtacostal leaf cells. —E. Proximal marginal leaf cells. —F. Distal leaf cells. —G. Medial exothecial cells. —H. Perichaetial leaf (h = hyaline area; g = green area). —I. Peristome tooth and annulus (only contour shown, not papillosity). (*Orcutt 7082*, FH.)

throughout, orange-brown, concolorous with the urn; *opercula* rostrate; *calyptrae* mitrate; *spores* 14–18 µm, smooth.

Illustrations. Figure 2; Bartram (1929: pl. 1); Crum and Anderson (1981: fig. 195 A–G); Jones (1933: pl. 6).

Distribution (Fig. 3). Northern America. *Grimmia americana* is known only from the southwestern and south-central U.S.A. It grows in Arizona and Texas close to the Mexican border, and it should be expected in suitable places in northern Mexico.

Grimmia americana has concave leaves with an undifferentiated costa in the distal part; it is gonioautoicous and has immersed capsules on curved setae. It is a member of the complex of taxa with strongly modified perichaetial leaves, which are hyaline and filmy except for a small patch of green cells in the distalmost part of the leaf. Species in

Figure 3. Distribution of: ● *Grimmia americana*; ▲ *Grimmia anodon*.

this group cannot be distinguished from sterile specimens, as discussed under *G. poecilostoma.*

Additional specimens examined. U.S.A. **Arizona**: Pima Co., near Agua Caliente, *Bartram 189* (FH). **Texas**: Jeff Davis Co., Fort Davis, *Orcutt 7082* (FH, NY).

2. **Grimmia anodon** Bruch & Schimp., Bryol. Europ. (fasc. 25–28) 3: 110, tab. 236. 1845. *Schistidium anodon* (Bruch & Schimp.) Loeske, Laubm. Eur. Part I: 49. 1913. TYPE: Germany. Heidelberg, *Braun s.n.* (lectotype, designated by Cao & Vitt (1986), BM not seen).

Grimmia alpina Kindb., Christiania Vidensk.-Selsk. Forh. 1888(6): 30. 1888 [1889]. TYPE: Norway. Dovre, Drivstuen, *Kindberg s.n.* (lectotype, here designated, S; isolectotype, S).

Grimmia anodon var. *anomala* E. B. Bartram, Bryologist 27: 59. 1924. *Grimmia anodon* f. *anomala* (E. B. Bartram) G. N. Jones, in Grout, Moss Fl. N. Amer. 2(1): 22. 1933. TYPE: U.S.A. Arizona: Pima Co., steep shaded banks of dry washes in Tuscon Mountains, *Bartram s.n.* (lectotype, here designated, FH; isolectotype, H-BR).

Gonioautoicous. Plants yellowish green to olive-green. *Stems* erect, to 2 cm, with central strand. *Leaves* erect and appressed when dry, erect to patent when moist, 0.9–1.6 × 0.35–0.70 mm, oblong or ovate to lanceolate, obtuse to acute, keeled (seldom rather flat distally), not plicate; *margins* recurved proximally or in middle part of one side; *costa* semi-terete, differentiated, ventral epidermis 2 cells wide in cross section; *lamina* 1-stratose, 2-stratose at margins and in streaks in the distal ⅔; *distal cells* 7–16 μm long, mostly rectangular, not bulging, walls straight to sinuous; *proximal juxtacostal cells* 20–40 × 9–12 μm, rectangular (2–4 : 1), walls medium-thick and straight; *proximal marginal cells* 14–25 × 10–12 μm, rectangular (1.5–2 : 1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* sometimes lacking, terete, straight, to 1.5 mm, denticulate. *Perichaetial leaves* 1.6–2.0 × 0.8–1.2 mm, convolute and larger than vegetative leaves (2–3×). *Androecia* below perichaetia. *Setae* curved, 0.3–0.5 mm long. *Capsules* immersed, subglobose, ventricose, smooth, stramineous, with stomata at the base; *exothecial cells* 40–80 × 14–25 μm, rectangular (2–3 : 1), thin-walled; *annulus* compound and tardily deciduous, *elongata* type; *peristome* lacking; *opercula* plano-convex, bluntly mammillate; *calyptrae* mitrate; *spores* 8–11 μm, minutely granulose.

Illustrations. Figure 4; Braithwaite (1888: tab. 46 fig. E); Chałubiński (1882: tab. 4 fig. 3); Deguchi (1984: fig. 1; 1987: pl. 1); Ignatov and Cao (1994: fig. 18); Lawton (1971: pl. 57 fig. 15–24); Maier and Geissler (1995: abb. 2); Petrov (1975: tab. 62 fig. 6); Smith (1978: fig. 147 16–18); Vaněk (1940: figs. 12–20).

Distribution (Fig. 3). Europe, northern Africa, temperate and tropical Asia, northern and southern America; Mexico, Peru, and Bolivia. On crevices and surfaces of calcareous rocks in open areas between 100 and 4000 m elevation.

Grimmia anodon has ovate leaves and immersed, subglobose, and ventricose eperistomate capsules on a curved seta. Although its gametophytes resemble several other species such as *G. humilis*, *G. molesta*, or *G. pseudoanodon*, the sporophyte is unmistakable. In areas in which they cohabit (e.g., Europe, North America), *G. anodon* can be also misidentified as *Schistidium flaccidum* (De Not.) Ochyra, but the seta in *Schistidium* is straight, and the study of this feature precludes any confusion.

Hair-point presence and length, as well as the number of cell layers in leaf cross section, are variable in *G. anodon*. Several taxa have been described based on muticous specimens (e.g., *G. alpina* Kindb. and *G. limprichtii* Kern, both described from European materials) or supposed differences in leaf lamina stratification (e.g., *G. anodon* var. *anomala* E. B. Bartram from Arizona). Random variation in laminal characters occurs across the entire distributional range of *G. anodon*. No correlation can be seen to other characters, and *G. alpina* and *G. anodon* var. *anomala* are herein reduced to synonymy.

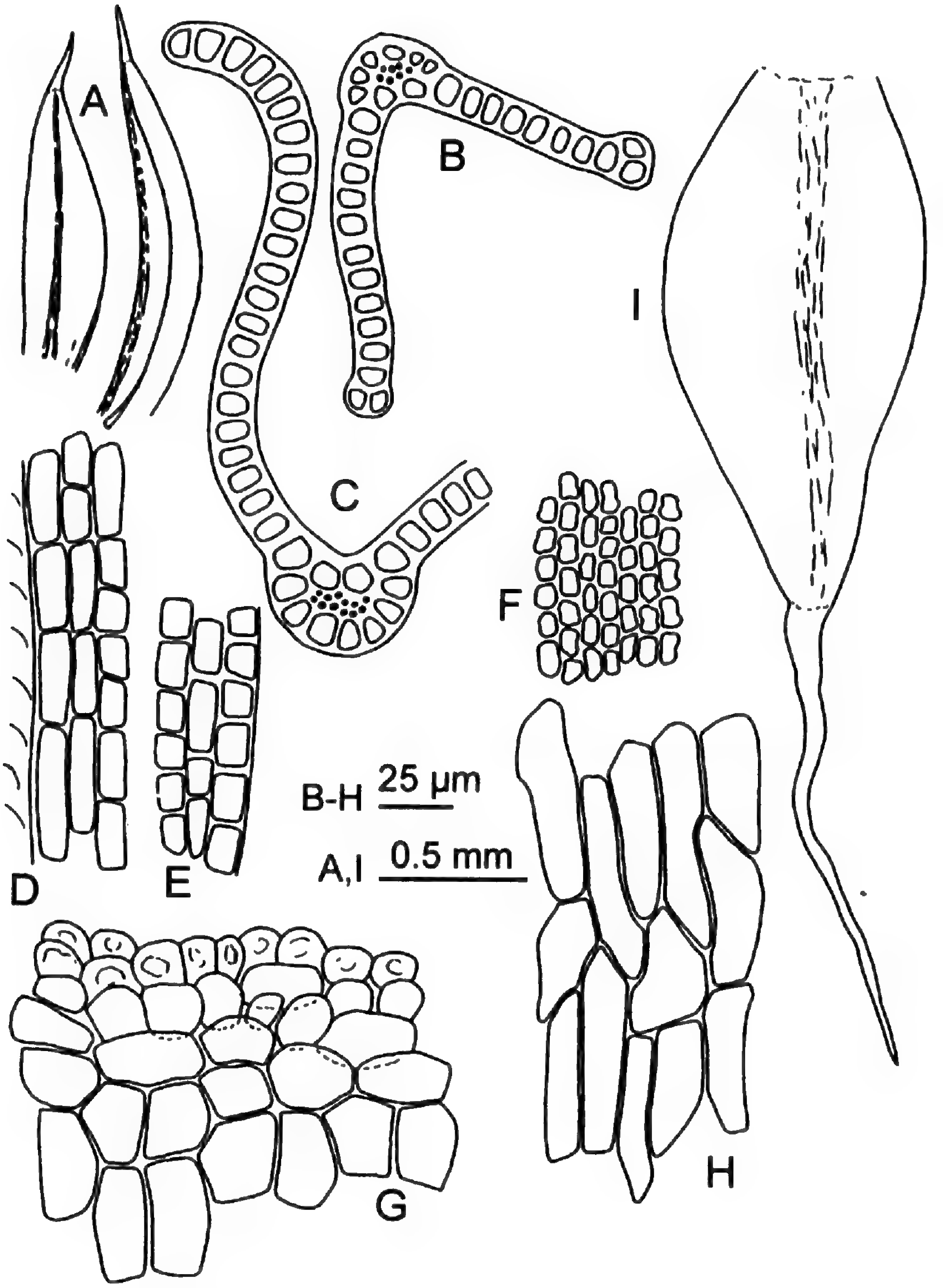

Figure 4. *Grimmia anodon.* —A. Leaves. —B, C. Transverse sections at medial and proximal parts of leaf. —D. Basal juxtacostal leaf cells. —E. Basal marginal leaf cells. —F. Distal leaf cells. —G. Mouth of capsule showing the annulus. —H. Medial exothecial cells. —I. Perichaetial leaf. (*Delgadillo 2414*, TENN.)

Specimens examined. MEXICO. **Nuevo León**: summit of Cerro Potosí, *Delgadillo 2361* (TENN), *2414* (TENN), *2429* (TENN); Cerro Potosí near Galeano, *Sharp 3912* (TENN).

BOLIVIA. **Oruro**: Atahuallpa, Cerro Pumiri, near Sabaya, NW of Laguna Coipasa, *Lewis 79-1947* (F); Pallallkkollu, SE of Pagador, W of Laguna Coipasa, near Chilean border, *Lewis 79-2008B* (F). CHILE. **Magallanes**: Parque Nacional Torres del Paine, *Deguchi 26028* (HIRO), *26070* (HIRO), *26074* (HIRO), *26102* (HIRO). PERU. **Arequipa**: Arequipa, laguna Las Salinas, *Hegewald & Hegewald 5483b* (HIRO). **Puno**: prov. Azángaro, around laguna Ascanocha, about 5 km SW of Asillo, *Deguchi 29980* (HIRO), *29983* (HIRO), *29996* (HIRO).

3. **Grimmia atrata** Miel. ex Hornsch., Flora 2: 85. 1819. *Grimmia alpestris* var. *brevipila* Bruch ex Mont., Arch. Bot. 1: 219. 1833, nom. inval. in synon. *Dryptodon atratus* (Miel ex Hornsch.) Hartm., Handb. Skand. Fl. ed. 3: 271. 1838. TYPE: Austria. Grosarl, *Hornschuch s.n.* (lectotype, designated by Deguchi (1978), B).

Grimmia strictifolia Mitt., J. Linn. Soc., Bot. Suppl. 1: 44. 1859. *Racomitrium strictifolium* (Mitt.) A. Jaeger, Ber. Tätigk. St. Gallischen Naturwiss. Ges. 1872–73:

89 (Gen. Sp. Musc. 1: 371). 1874. TYPE: India. Sikkim: Jongri, *Hooker 295* (lectotype, here designated, NY).

Grimmia tristicha Herzog, Biblioth. Bot. 87: 58. 1916, nom. illeg., non Schwaegr., 1811. *Grimmia tristichoides* Margad., Lindbergia 1: 128. 1972. TYPE: Bolivia. Hochtal von Viloco, *Herzog 3152* (lectotype, here designated, JE; isolectotype, PC).

Grimmia tristicha var. *comosa* Herzog, Biblioth. Bot. 87: 59. 1916. *Grimmia tristichoides* f. *comosa* (Herzog) Margad., Lindbergia 1: 128. 1972. TYPE: Bolivia. Hochtal von Viloco, *Herzog 3188* (lectotype, here designated, JE; isolectotype, PC).

Dioicous. Plants dark green, reddish, or blackish. *Stems* erect, to 5.5 cm, central strand lacking or weakly developed. *Leaves* flexuous and crisped when dry, erect to patent when moist, 1.5–3.2 × 0.30–0.75 mm, lingulate-lanceolate, obtuse, canaliculate, not plicate; *margins* recurved proximally, to ⅓ the leaf length on one side; *costa* reniform, differentiated, ventral epidermis 4–6 cells wide in cross section; *lamina* 2-stratose at margins and in streaks in the distal ⅔; *distal cells* 7–20 μm long, isodiametric to rectangular, not bulging, walls sinuous; *proximal juxtacostal cells* 30–50 × 7–12 μm, rectangular (3–5 : 1), walls thick and nodulose; *proximal marginal cells* 14–34 × 8–10 μm, rectangular (1.5–4.0 : 1), inflated and forming bistratose alar parts, the transverse walls thicker than the longitudinal walls; *hyaline hair-points* lacking. *Perichaetial leaves* 2.3–3.2 × 0.6–0.8 mm, similar to vegetative leaves but convolute proximally. *Androecia* terminal. *Setae* straight, 3–10 mm long. *Capsules* exserted, ovoid to ellipsoid, with attenuate base, symmetric, smooth, castaneous, with stomata at the base; *exothecial cells* 25–55 × 20–35 μm, isodiametric to rectangular (1–2 : 1), thick-walled; *annulus* compound and revoluble, *elongata* type; *peristome teeth* 60–90 μm wide at the mouth, entire to cribrose and irregularly cleft at apex, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, castaneous, concolorous with the urn; *opercula* mammillate to rostrate; *calyptrae* cucullate or mitrate; *spores* 13.5–17.5 μm, coarsely granulose.

Illustrations. Figure 5; Cao and Churchill (1995a: pl. 2 figs. 1–7); Herzog (1916: fig. 20, as *G. tristicha*); Maier and Geissler (1995: abb. 5); Noguchi (1988: fig. 145A); Smith (1978: fig. 154 8–11).

Distribution (Fig. 6). Europe, temperate and tropical Asia, southern America. In Latin America *Grimmia atrata* is known only from a few Bolivian collections. It grows on moist acidic rocks in open areas above tree line, between 4350 and 4800 m elevation.

Grimmia atrata has muticous, flexuous, more or less curled leaves that are bistratose marginally and at the alar areas. The lamina is usually unistratose, with the margins and occasional streaks bistratose. However, the type of *Grimmia tristicha* has leaves almost entirely bistratose. *Grimmia atrata* is similar to *G. ochyriana,* another taxon with muticous leaves. However, alar cells in *G. ochyriana* are similar to other basal cells, the perichaetial leaves are strongly differentiated from vegetative leaves, and the capsules are immersed.

Grimmia atrata shows little morphological variability, except for sporophyte dimensions. Throughout its world range specimens occur with longer sporophytes. Seta length can reach to 10 mm, and longer setae are usually correlated with longer capsules.

Additional specimens examined. BOLIVIA. **La Paz**: Chojñacota, *Herzog 2979* (JE, PC); prov. Inquisivi, Mina Poldi, *Lewis 87–884* (MO), *87–901* (MO), *87–914* (MO), *87–926* (MO); Loayza, im Hochtal von Viloco, *Herzog 3170* (JE, NY).

4. Grimmia austrofunalis Müll. Hal., Hedwigia 37: 165. 1898. TYPE: [Australia. Victoria:] Mt. William, Mar. 1883, *Sullivan s.n.* (holotype, MEL).

Grimmia pansa R. S. Williams, Bull. New York Bot. Gard. 3: 125. 1903 [19 Oct.]. TYPE: Bolivia. Pelechuco, *Williams 2823* (lectotype, here designated, NY; isolectotypes, FH, JE).

Racomitrium austrosudeticum Broth., in Herzog, Biblioth. Bot. 87: 60. 1916. TYPE: [Bolivia. Cochabamba:] Tablas, *Herzog 2859* (lectotype, here designated, H; syntypes, *Herzog 3179,* H; *Herzog 4366,* H; *Herzog 4807,* H).

Grimmia crassiretis Cardot & Broth., Kongl. Svenska Vetenskapsakad. Handl. 63(10): 27, tab. 2 fig. 7. 1923. TYPE: [Argentina. Santa Cruz:] Patagonie: lac San Martín, *Skottsberg 380* (lectotype, here designated, PC; isolectotypes, H-BR, UPS; syntype, [Valle Frías. . .] PC).

Grimmia benoistii Thér., Rev. Bryol. Lichénol. 9: 10. 1936. TYPE: [Ecuador.] Pichincha: Massif du Pichincha, en face de Condorguachana, *Benoist 3116* (lectotype, here designated, PC; isolectotypes, F, PC; syntypes, [*Benoist 3117*] F, PC).

Dioicous. Plants olive-green to reddish or blackish, strongly glossy. *Stems* ascending, to 8 cm, central strand lacking on sterile stems. *Leaves* erect and appressed or somewhat flexuous apically when dry, patent when moist, 2.0–2.8 × 0.5–0.8 mm, lanceolate, acuminate, keeled, not plicate; *margins* recurved proximally, to ½–⅔ the leaf length on one side and flat or more narrowly recurved proximally, to ⅓–½ the leaf length on the other side, occasionally both margins plane; *costa* semi-terete, differ-

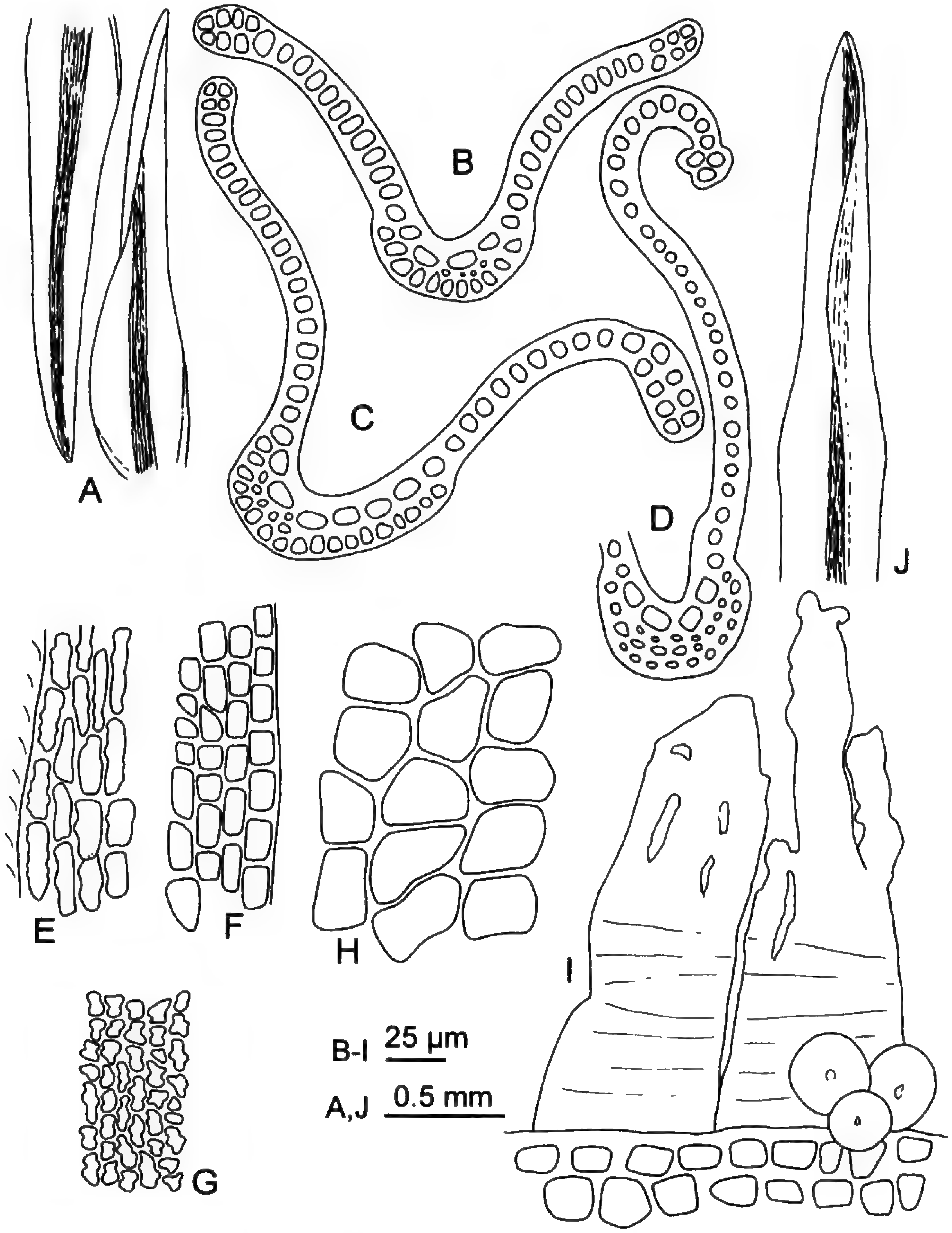

Figure 5. *Grimmia atrata.* —A. Leaves. —B–D. Transverse sections at distal, medial and proximal parts of leaf, the latter showing bistratose alar areas. —E. Proximal juxtacostal leaf cells. —F. Proximal marginal leaf cells. —G. Distal leaf cells. —H. Medial exothecial cells. —I. Peristome teeth and annulus (only contour shown, not papillosity). —J. Perichaetial leaf. (*Lewis 87-914,* MO.)

Figure 6. Distribution of: ● *Grimmia atrata*; ▲ *Grimmia humilis*; ■ *Grimmia involucrata*; ★ *Grimmia lisae*.

entiated, ventral epidermis 2 cells wide in cross section; *lamina* 1-stratose, seldom 2-stratose at one or two marginal rows in the distal ⅔; *distal cells* 6–18 μm long, isodiametric and rectangular, some oblate intermingled, not bulging, walls sinuous; *proximal juxtacostal cells* 45–85 × 8–18 μm, rectangular (2–10:1), walls thin and straight to medium-thick and nodulose; *proximal marginal cells* 13–30 × 9–12 μm, rectangular (1.5–3.0:1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete, straight, to 0.4 mm, smooth to denticulate. ***Propagula*** 100–200 × 50–130 μm, ellipsoid, composed of several multicellular clusters, on branched stalks at dorsal basal part of costa, brownish with brown to reddish walls. ***Perichaetial leaves*** 3–4 × 0.7–0.9 mm, convolute proximally and prolonged in a very narrow acuminate distal half, larger than vegetative leaves (1.5 ×). ***Androecia*** terminal. ***Setae*** curved, 4.0–5.5 mm long. ***Capsules*** exserted, ellipsoid, symmetric, ribbed, stramineous, with stomata at the base; *exothecial cells* 22–65 × 14–24 μm, isodiametric to rectangular (1–2:1), thin-walled; *annulus* compound and revoluble, *affinis* type; *peristome teeth* 45–65 μm wide at the mouth, entire, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, orange, contrasting with the urn; *opercula* rostrate; *calyptrae* mitrate; *spores* 10–16 μm, minute to coarsely granulose.

Illustrations. Figures 7, 8; Deguchi (1984: figs. 12, 13; 1987: pl. 12–14, all as *G. trichophylla*).

Distribution (Fig. 31). Australasia, southern America; Andean Range from Venezuela to Patagonia. *Grimmia austrofunalis* grows on dry to seepy rocks, seldom on bark of *Polylepis* sp., in every kind of habitat, from open sunny grassland to shaded forests in deep ravines, between 160 (Patagonia) and 5180 (Bolivia) m elevation.

Grimmia austrofunalis is the largest South American species within the genus, with the stems sometimes reaching 8 cm. Most specimens are strongly glossy, with brownish to reddish tints. Leaves are tightly appressed to the stem and not or weakly flexuous, and unistratose (seldom 1 or 2 marginal rows are bistratose). In *G. austrofunalis*, gemmae arise on stalks from the proximal dorsal costae. In one strongly propaguliferous collection stalks on the laminar cells occur at both sides of the costa. After the release of the gemmae, both costa and leaf remain undamaged. This represents the best character differentiating *G. austrofunalis* from *G. trichophylla*. Gemmae in *G. trichophylla* are sessile on the lamina, leading to the destruction of underlying cells. Gemmae formation in *G. trichophylla* is described specifically under that taxon (Fig. 44). The developmental formation of propagula in *G. austrofunalis* is illustrated in Figure 8.

Gemma formation starts with the development of hyaline filaments at the basal dorsal side of the costa. These filaments are uniseriate, 4- to 8-celled, and hyaline. They subsequently ramify at the distal extremes. Cells in each filament branch undergo several consecutive perpendicular divisions to form a more or less spherical to ellipsoid body. These multicellular bodies remain attached to the main filament, which functions like a hilum. Finally, just prior to the release of propagula, the cell walls of the propagula become thickened and pigmented. When a gemma detaches, the basal cell of the stalk, strongly reddish or brownish in color, remains on the costa. Propagula so formed compose a large cluster of gemmae resembling those found in *G. trichophylla*, but are obviously much larger in *G. austrofunalis*.

Names included here under *Grimmia austrofunalis* have usually been considered synonyms of *G. trichophylla* (Deguchi, 1987: 30, *G. pansa*; Deguchi, 1984: 25, *G. crassiretis*; and Churchill, 1994: 2, *G. benoistii*).

Selected specimens examined. ARGENTINA. **Chubut:** vallée Frías, *Skottsberg 381* (PC). **Santa Cruz:** Lac San Martín, *Skottsberg 380* (PC). BOLIVIA. **Cochabamba:** prov. Arani, 14 km S of Tiraque, *Lewis 85-115* (F, IBA);

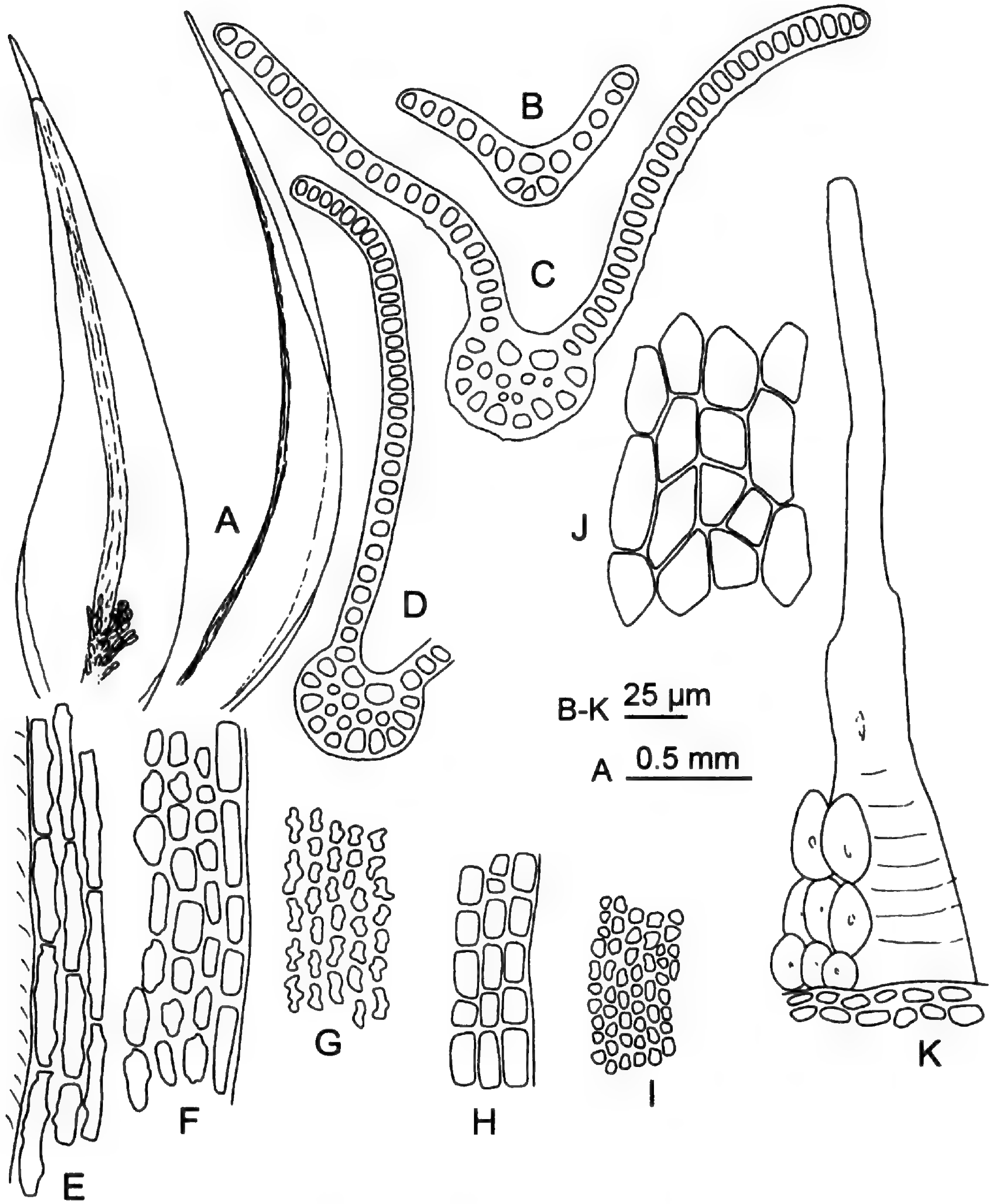

Figure 7. *Grimmia austrofunalis.* —A. Leaves. —B–D. Transverse sections at distal, medial, and proximal parts of leaf. —E. Proximal juxtacostal leaf cells. —F & H. Proximal marginal leaf cells. —G & I. Distal leaf cells. —J. Medial exothecial cells. —K. Peristome tooth and annulus (only contour shown, not papillosity). (A–D, H, I: *Lewis 87–1882,* MO; E–G, I, K: *Williams s.n.,* UBC.)

prov. Carrasco, río Monte Puncu, *Lewis 83-1826* (F, IBA); prov Chapare, río Espíritu Santo, *Lewis 85-1649* (F, IBA); prov. Quillacollo, *Lewis 79-2568* (MO). **La Paz**: prov. Camacho, 1 km below Escoma–Charasani road, *Lewis 79-793* (F, IBA); prov. Inquisivi, Cumbre Sayaquira, *Lewis 87321* (PC); prov. Larecaja, Pelechuco, 5 May 1902, *Williams s.n.* (UBC); prov. Loayza, río Acoroma Chuma, *Lewis 87-1789B* (MO); prov. Los Andes, Cerro Jankho Karka, *Lewis 84-145A* (F, IBA); prov. Murillo, head of río Zongo at SW slope of Cerro Chekhara, N of La Paz, *Lewis 79-1809* (F); prov. Sur Yungas, Bolsa Negra, *Lewis 83-2229* (F, MO). CHILE. **La Araucanía**: Cautín, Dep. Villarrica, Pucón, Halbinsel, *Hosseus 394* (FH). **Libertador General Bernardo O'Higgins**: Las Palmas, 60 km W of Rancagua, *Bartlett 19123* (NY). **Los Lagos**: Llanquihue, Lago Todos los Santos, *Seki 1/70-72* (H). COLOMBIA.

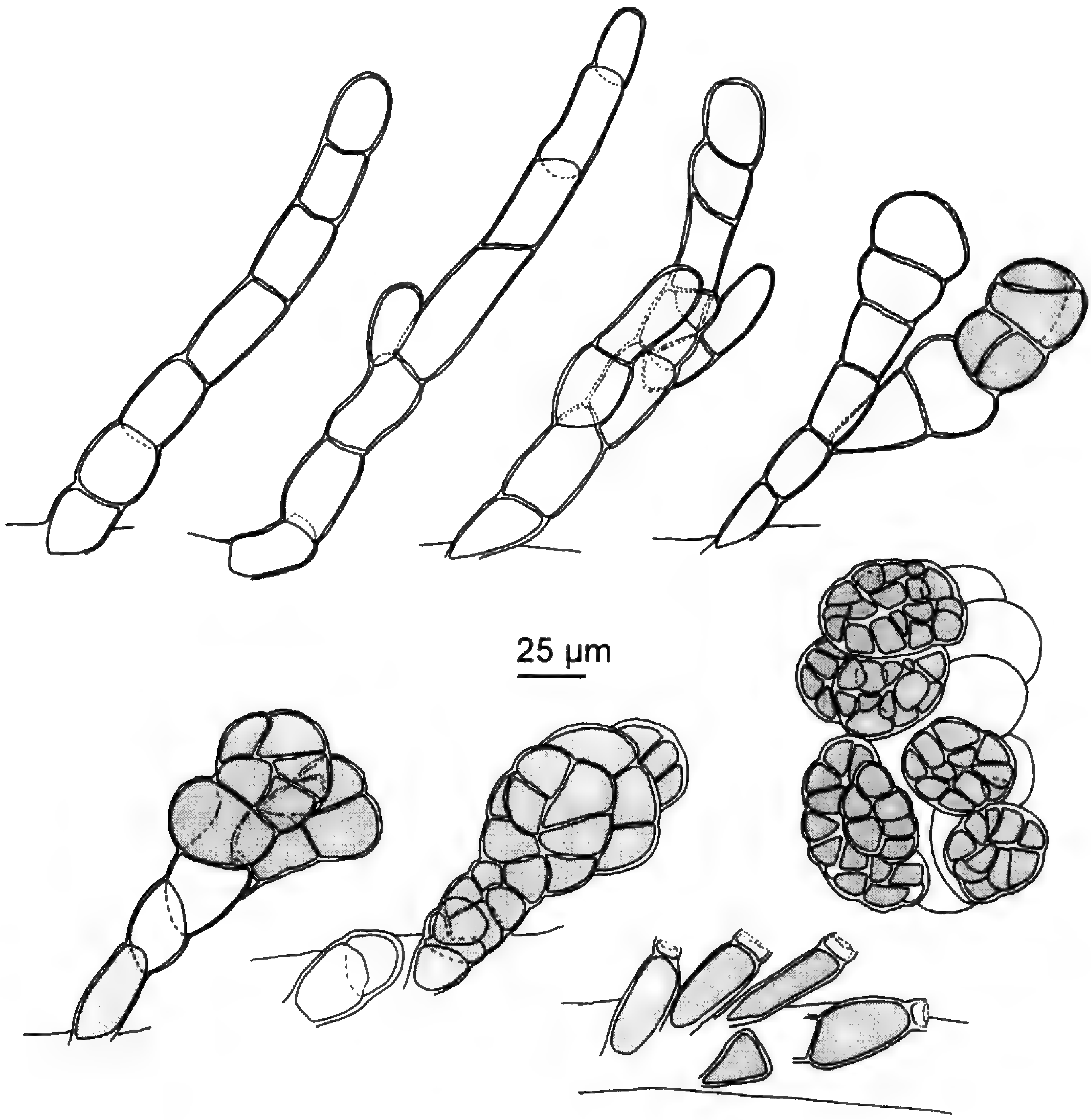

Figure 8. *Grimmia austrofunalis.* Sequence of gemmae formation.

Arauca: Sierra Nevada del Cocuy, quebrada El Playón, *Cleef 8855* (COL). **Boyacá**: páramo de la Rusia, *Cleef 7006c* (COL). **Caldas**: Villamaría, carretera Manizales–Bogotá, sobre la carretera que conduce al Nevado del Ruiz (km 213), *Churchill et al. 16307A* (IBA). ECUADOR. **Pichincha**: Pichincha, *Bell 375* (FH). PERU. **Ancash**: Huari, an der Ostseite des Tunnel Cahuish, *Hegewald & Hegewald 7698* (IBA, MO). **Ayacucho**: an der Strasse Huanta–San Francisco, Pass zwischen Tambo und Quinoa, *Frahm 824021* (IBA). VENEZUELA. **Mérida**: en el cañón justamente al S de Gavidia, *Griffin III et al. PV-1170* (CAS).

5. Grimmia bicolor Herzog, Beih. Bot. Centralbl. 26: 66. 1909. TYPE: Bolivia. Cochabamba: Llavethal, Jan. 1908, *Herzog s.n.* (lectotype, here designated, JE; isolectotype, PC).

Grimmia subquatricruris Broth., in Herzog, Biblioth. Bot. 87: 57. 1916. TYPE: Bolivia. Huaillattanisee, *Herzog 2973* (lectotype, here designated, H-BR; isolectotype, JE).

Dioicous. Plants glaucous-green to blackish, occasionally rusty-brownish. *Stems* erect, to 2 cm, with central strand. *Leaves* strongly flexuous, creased along the costa, twisted and incurved at apex, sigmoid in lateral view when dry, erect to patent when moist, 1–2 × 0.5–0.9 mm, ovate to lanceolate, acute, keeled, not plicate; *margins* recurved proximally, to ½ the leaf length on one side; *costa* semi-terete, differentiated, ventral epidermis 2 cells wide in cross section; *lamina* 2(3)-stratose in the distal ⅔; *distal cells* 5–12 μm long, isodiametric, rectangular and oblate, not bulging, walls sinuous; *proximal juxtacostal cells* 20–50 × 8–12 µm, mostly rectangular ([1]2–6 : 1), walls medium-thick and straight; *proximal marginal cells* 10–20 × 7–12 µm, isodiametric to rectangular (1–2 : 1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete, flexuous, to 0.9 mm, entire or with few denticulations. *Perichaetial leaves* 2–3 × 0.8–1.0 mm, convolute and larger than vegetative leaves (2 ×). *Androecia* terminal. *Setae* curved, 2.0–2.6 mm long. *Capsules* exserted, ovoid to ellipsoid, symmetric, smooth, stramineous to light brown, with stomata at the base; *exothecial cells* 30–50 × 14–25 µm, mostly rectangular (2 : 1), thin-walled; *annulus* compound and revoluble, *affinis* type; *peristome teeth* 70–130 µm wide at the mouth, entire or moderately cribrose, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, orange, contrasting with the urn; *opercula* conic to mammillate; *calyptrae* not seen; *spores* 9–12 µm, minutely granulose.

Illustrations. Figure 9; Herzog (1916: fig. 19).

Distribution (Fig. 10). Southern America. *Grimmia bicolor* is rare, known only from scattered collections in Bolivia. It was collected on rocks between 3600 and 5180 m.

Grimmia bicolor has bistratose, keeled, ovate to lanceolate flexuous leaves and curved setae. Noteworthy in dry plants are the leaves with wide bases clasping most of the stem circumference. They are folded distally along the costa, and are also flexuous (Fig. 9A).

Only two fertile collections are known (*Herzog 4772*, JE; *Lewis 87-1879*, MO). Sporophytes are very old in the Herzog specimen, and thus exostome characters are difficult to see. This could account for his observation (Herzog, 1916: 58) of “stomatibus deficientibus.” However, stomata do appear at the urn bases.

I have identified *Lewis 87-1879* as *G. bicolor*, although it is quite different from the other collections known. Most of the stems in this specimen are sprouts with strongly differentiated, small and muticous leaves that are well developed only at the very apex of the shoots. Furthermore, the apical leaves of these sprouts are lanceolate and less flexuous than in the other specimens of *G. bicolor* I know. Nonetheless, there are several more or less typical stems scattered in the cushion, some of them fertile. Similar stem and deviant leaf morphology in plants subject to extreme conditions is known in other genera (e.g., *Bryum*, *Philonotis*). This is especially true from high-altitude locations where the plants receive water from melting snow or, as in this case, plants are subject to freezing conditions at night and extremely high insolation during the day.

Additional specimens examined. BOLIVIA. **Cochabamba**: bei der Saittulaguna, *Herzog 2680* (JE); oberen Chocayatal, *Herzog 3587* (PC); Llavetal, *Herzog 308* (JE, PC); prov. Quillacollo, near summit of Cerro Tunari, *Lewis 79-2581* (F), *79-2585* (F, IBA), *Herzog 4772* (JE). **La Paz**: prov. Loayza, (Glacier Camp) alongside the glaciers of Cerro Jankho Loma, 11 km SE of Viloco, *Lewis 87-1879* (MO); prov. Los Andes, Cerro Jankho Karka, *Lewis 84-209a* (F, IBA); prov. Murillo, 5 km NE of Milluni, *Lewis 79-1727* (F, IBA).

6. Grimmia donniana Sm., Engl. Bot. 18: 1259. 1804. TYPE: United Kingdom. North Wales, pales at Beddgelart, July 1802, *Turner s.n.* (lectotype, designated by Muñoz (1998d), BM).

For a list of synonyms, see Muñoz (1998d).

Cladautoicous or goniautoicous. Plants greenish yellow above, dark green to blackish below. *Stems* erect, to 1.5 cm, with central strand. *Leaves* erect and appressed, occasionally flexuous when dry, patent when moist, 1.3–2.2 × 0.25–0.60 mm, lanceolate, acute, keeled, not plicate; *margins* plane; *costa* semi-terete, differentiated, ventral epidermis 2 cells wide in cross section; *lamina* 2-stratose at margins and in streaks in the distal ⅔; *distal cells* 7–11 µm long, isodiametric to rectangular (1–1.5 : 1), not bulging, walls straight to slightly sinuous; *proximal juxtacostal cells* 38–80 × 5.5–15.0 µm, narrowly rectangular (4–9 : 1), walls thin and straight to thick and slightly sinuous; *proximal marginal cells* 35–95 × 8–25 µm, narrowly rectangular (4–9 : 1), the walls thin and straight, all alike, scarcely discernible; *hyaline hair-points* terete or flat when long, slightly flexuous, to 2.2 mm, entire to weakly denticulate. *Perichaetial leaves* 2.0–2.5 × ca. 0.8 mm, convolute and larger than vegetative leaves (2.0–2.5 ×). *Androecia* axillary or terminal. *Setae* erect and straight, 3.5 mm long. *Capsules* exserted, ovoid, symmetric, smooth, stramineous, with stomata at the base; *exothecial cells* 35–55 × 24–46 µm, isodiametric to rectangular (1–2 : 1), thin-walled; *annulus* compound and revoluble, *elongata* type; *peristome teeth* 50–70 µm wide at the mouth, entire or irregularly cleft at apex, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, orange, contrasting with the urn; *opercula* conic or mammillate; *calyptrae* mitrate (only one specimen known with some cucullate calyptrae; see Muñoz, 1998d); *spores* 7–11 µm, minutely granulose.

Illustrations. Figure 11; Bruch and Schimper

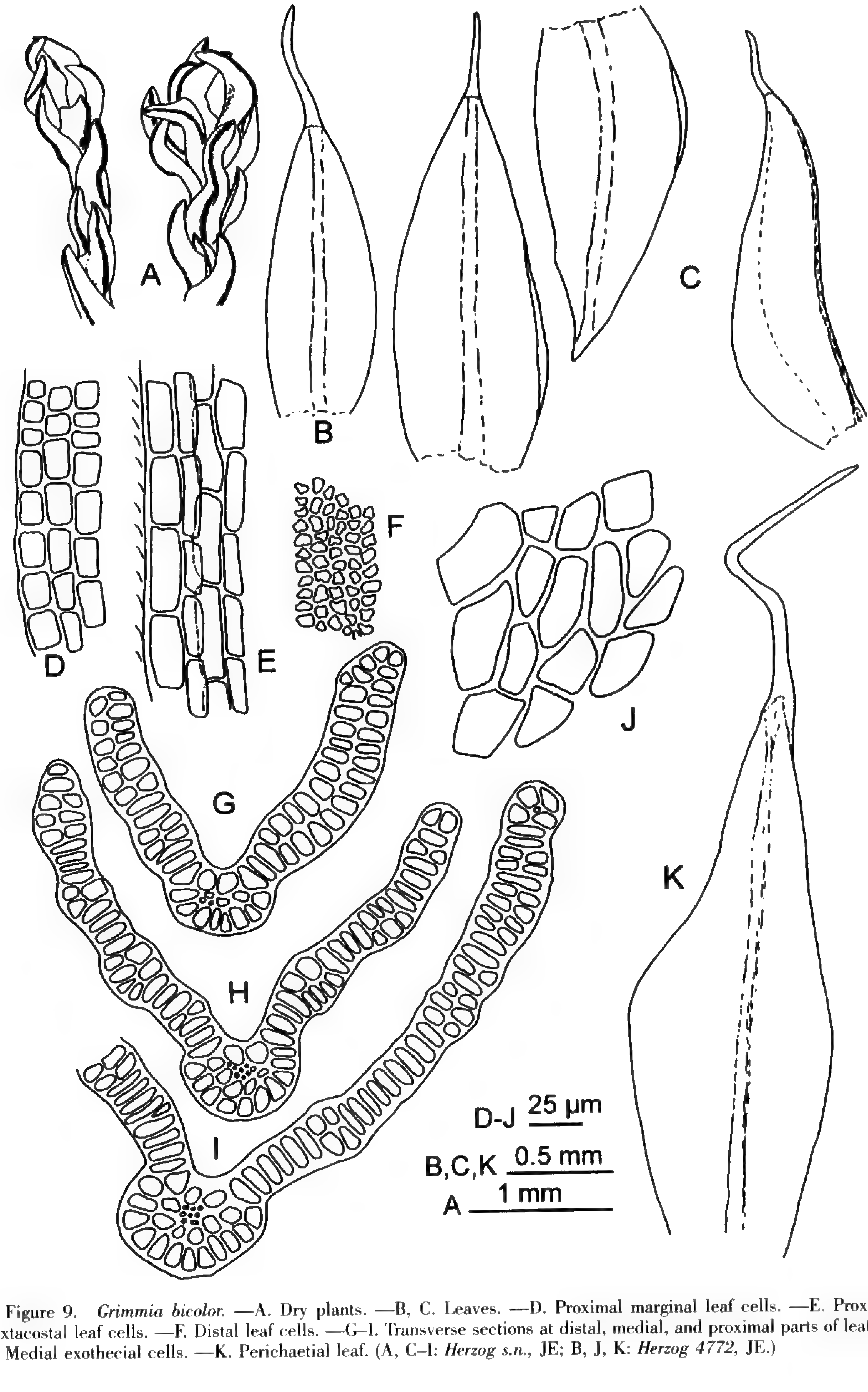

Figure 9. *Grimmia bicolor.* —A. Dry plants. —B, C. Leaves. —D. Proximal marginal leaf cells. —E. Proximal juxtacostal leaf cells. —F. Distal leaf cells. —G–I. Transverse sections at distal, medial, and proximal parts of leaf. —J. Medial exothecial cells. —K. Perichaetial leaf. (A, C–I: *Herzog s.n.,* JE; B, J, K: *Herzog 4772,* JE.)

Figure 10. Distribution of: ● *Grimmia bicolor*; ▲ *Grimmia kidderi*; ■ *Grimmia molesta*; ★ *Grimmia pilifera*.

(1845: tab. 249, as *G. obtusa*); Cao and Vitt (1986: figs. 15, 16a–c); Chałubiński (1882: tab. 7 fig. 11); Deguchi (1978: fig. 27); Ignatov and Cao (1994: fig. 10, but not figs. 8, 9); Jóhannsson (1993: fig. 32); Limpricht (1890: fig. 198); Muñoz (1998d: fig. 4); Noguchi (1988: fig. 140B); Nyholm (1956: fig. 69F).

Distribution (Fig. 12). Europe, temperate Asia, northern and southern America. *Grimmia donniana* is fairly common in temperate regions of the Northern Hemisphere. However, in Latin America it is rare, known only from scattered localities in Mexico, Ecuador, and Bolivia. It grows on igneous rocks in open areas between 3560 and 4670 m elevation.

The leaves of *G. donniana* are characterized by more or less homogeneous, hyaline, and thin-walled cells extending from the costa to margins in the proximal quarter of the leaves. The setae are straight, the capsules are exserted, pale yellowish or stramineous with thin-walled exothecial cells, and the peristome teeth are entire and rather narrow below. The specimen from Popocatépetl (*Sharp 4761 p.p.*, TENN) has very short setae for the species (1 mm), and the capsules are mostly immersed. It could be confused with the Eurosiberian *G. triformis* Carestia & De Not. because that species is identical in gametophyte features and has immersed sporophytes. However, *G. triformis* has thick-walled exothecial cells, and broader (70–100 µm rather than 50–70 µm), cribrose peristome teeth (Muñoz, 1998d).

In the area of the Nevado Sajama (Oruro, Bolivia), *G. donniana* grows closely intermingled in the same cushions with *G. pseudoanodon* and *G. longirostris*. The three species are autoicous and have abundant sporophytes, and identification is therefore easy. *Grimmia pseudoanodon* has immersed, stramineous, gymnostomous capsules, and the leaf margins are plane. *Grimmia longirostris* has exserted, brownish capsules with peristome of the same color, and leaves with recurved margins. In these two species the proximal marginal cells of the leaves have transverse walls thicker than longitudinal walls. *Grimmia donniana* has exserted, pale-yellowish to stramineous capsules topped by orange-reddish peristomes contrasting in color with the capsule. The leaf margins are plane, with the proximal cells being hyaline and more or less inflated and homogeneous from margins to costa.

Additional specimens examined. MEXICO. **México:** Popocatépetl, *Sharp 4761A* (TENN). **Veracruz:** monte Orizaba, *Galeotti s.n.* (PC).

BOLIVIA. **La Paz:** prov. Inquisivi, Cerro Naranuani, *Lewis 83-3243* (F). **Oruro:** Nevado Sajama, *Lewis 84-293* (F, IBA), *308A* (F). ECUADOR. **Napo:** Cerro Antisana in moraine S of W glacier, *Grubb 2501B* (FH).

7. **Grimmia elongata** Kaulf., in Sturm, Deutschl. Fl. Abtheilung II, Cryptogamie 4(13): 24. 1812. *Dryptodon elongatus* (Kaulf.) Hartm., Handb. Skand. Fl. ed. 3: 271. 1838. TYPE: [Austria. Steyermark:] Styria, *Kaulfuss s.n.* (lectotype, designated by Geissler & Maier (1995), B not seen).

Grimmia fuliginosa Schimp. ex Müll. Hal., Syn. Musc. Frond. 1: 778. 1849. *Schistidium fuliginosum* (Müll. Hal.) Ochyra, Fragm. Florist. Geobot. 43: 105. 1998. TYPE: Mexico. [Veracruz:] Pic d'Orizaba, *Liebmann s.n.* (lectotype, here designated, BM).

Grimmia andreaeacea Müll. Hal., Linnaea 43: 453. 1882. TYPE: Argentina. Cuesta de Caldeira, 27 May 1873, *Lorentz s.n.* (lectotype, here designated, BM; isolectotype, PC).

Grimmia montana var. *epilosa* Grav. ex Delogne, Ann. Soc. Belge Microscop. 9: 21. 1885. *Grimmia montana* f. *epilosa* (Delogne) Podp., Consp. Musc. Eur: 281. 1954. TYPE: Belgique. Namur: Willerzie, 14 Sep. 1882, *Gravet s.n.* (lectotype, here designated, PC; isolectotype, PC).

Grimmia tolucensis Cardot, Rev. Bryol. 38: 1. 1911. TYPE: Mexico. México: volcano of Toluca, *Pringle s.n.* Plantae mexicanae, n° 27a (lectotype, here designated, PC; isolectotypes, FH, JE, PC 2 replicates, TENN).

Dioicous. Plants olive-green to reddish, blackish at high-elevation or exposed habitats. *Stems* erect, to 4 cm, with a central strand. *Leaves* erect and appressed, occasionally flexuous when dry, erect when moist, 1.6–2.4 × 0.3–0.4 mm, lanceolate, acuminate, keeled, not plicate; *margins* re-

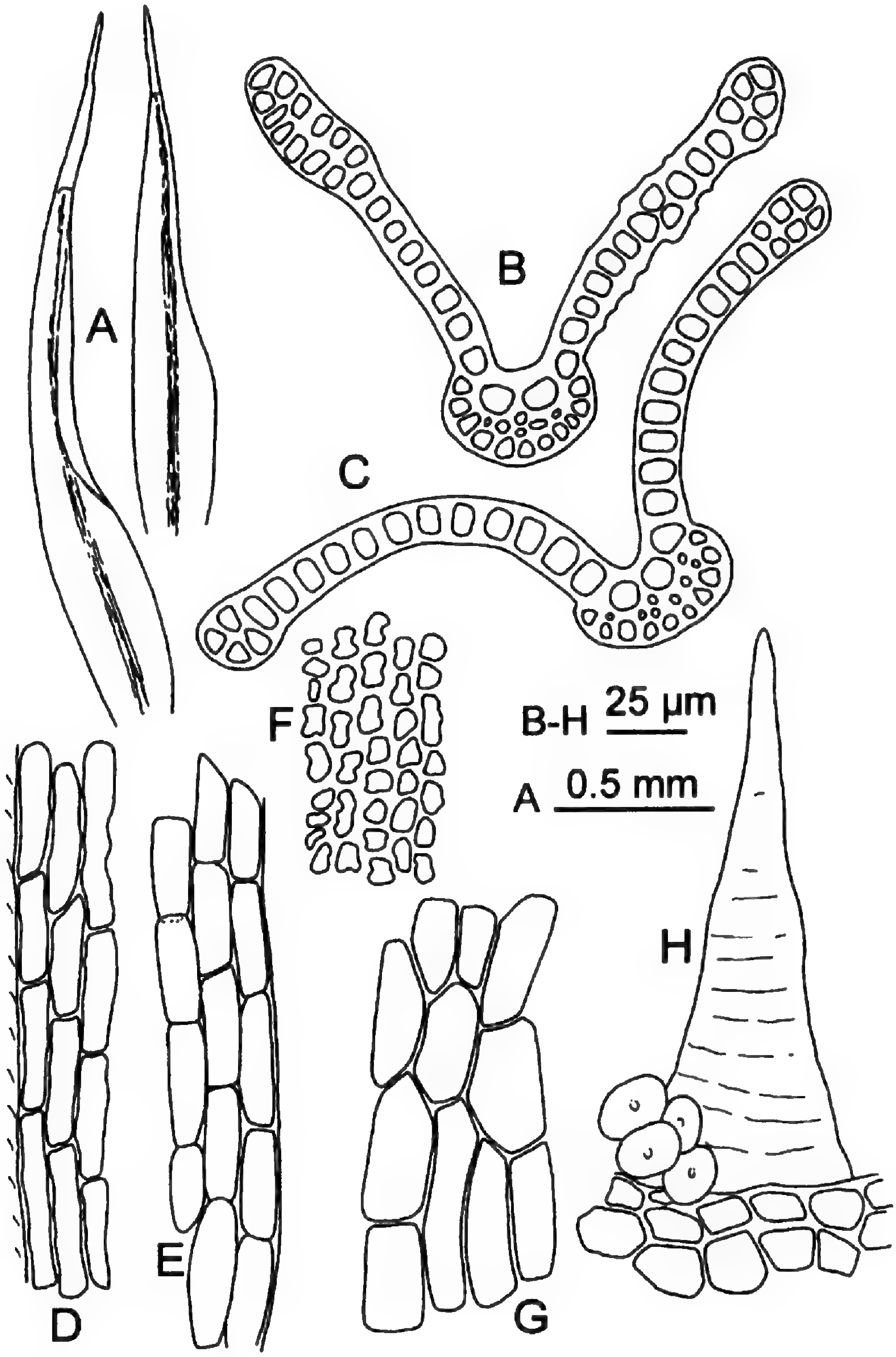

Figure 11. *Grimmia donniana.* —A. Leaves. —B, C. Transverse sections at medial and proximal parts of leaf. —D. Proximal juxtacostal leaf cells. —E. Proximal marginal leaf cells. —F. Distal leaf cells. —G. Medial exothecial cells. —H. Peristome tooth and annulus (only contour shown, not papillosity). (A–F: *Galeotti s.n.*, PC; G, H: *Sharp 4761 p.p.*, TENN.)

curved proximally, to ½ the leaf length on one side and flat or more narrowly recurved proximally, to ⅓ the leaf length on the other side; *costa* semiterete to nearly terete, differentiated, ventral epidermis 2 cells wide in cross section; *lamina* 1–2-stratose, 2-stratose at margins in the distal ⅔; *distal cells* 6–9 µm long, isodiametric to rectangular, not bulging, walls sinuous; *proximal juxtacostal cells* 30–50 × 6–10 µm, rectangular (3–5 : 1), walls thin and straight; *proximal marginal cells* 40–65 × 6–10 µm, rectangular (4–10 : 1), the walls thin and straight, all alike; *hyaline hair-points* sometimes lacking, terete, straight, to 0.3 mm, entire. *Perichaetial leaves* 3.25 × 0.7 mm, convolute and larger than vegetative leaves (2–3 ×). *Androecia* terminal. *Setae* erect and straight, 1.0–2.5 mm long. *Capsules* emergent to exserted, ovoid, symmetric, smooth, stramineous, with stomata at the base; *exothecial cells* 20–50 × 12–30 µm, mostly isodiametric (1[2] : 1), thin-walled; *annulus* compound

Figure 12. Distribution of: ● *Grimmia donniana*; ▲ *Grimmia laevigata*.

and revoluble, *elongata* type; *peristome teeth* 50–60 μm wide at the mouth, entire, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, orange, contrasting with the urn; *opercula* conic to rostrate; *calyptrae* mitrate, seldom cucullate; *spores* 9–14 μm, minutely granulose.

Illustrations. Figure 13; Chałubiński (1882: tab. 10 fig. 18); Jóhannsson (1993: fig. 23); Lawton (1971: pl. 59 figs. 11–18); Maier and Geissler (1995: abb. 12); Noguchi (1988: fig. 139 B); Petrov (1975: tab. 64 fig 3); Smith (1978: fig. 149 6–8).

Distribution (Fig. 14). Europe, Reunion, temperate and tropical Asia, southern America; Mexico, Guatemala, Bolivia, Argentina, southeastern Brazil. On sandstone and igneous, either granite or basalt, rocks in open areas, mainly in places with water available from melt, between 2100 and 4600 m elevation.

Plants of *G. elongata* are usually red-tinged. The leaves have recurved margins, short hair-points, and basal marginal cells with thin, uniformly thickened walls. The setae are straight, and the capsules exserted. It is likely to be confused only with *Grimmia navicularis*, a species with curved setae, but rarely fertile. *Grimmia navicularis* has also a red tint and narrow leaves strongly keeled. However, its leaves have basal marginal cells with transverse walls thicker than the longitudinal walls.

Usually quite stenotypic, the only feature that really varies is the length and sinuousity of the distal cells. These are commonly rectangular and strongly sinuous, but short isodiametric cells are also seen. The calyptrae are seldom cucullate instead of mitrate, e.g., PC isolectotypes of *G. tolucensis*.

Additional specimens examined. GUATEMALA. **San Marcos**: between San Sebastián and summit of Volcán Tajamulco, *Steyermark 35547A* (FH), *35548* (FH), *35549A* (FH); near summit of Tajamulco, *Sharp 5429* (TENN). MEXICO. **México**: Mt. Popocatépetl, *Kiener 18554* (FH, TENN), *18591A* (FH), *18591B* (FH), *18592B* (FH), *Vitt 17469* (ALTA), *17486* (ALTA); Nevado del Toluca, *Balls 4100* (FH), *Dunn et al. 21901* (TENN), *Hahn s.n.* (TENN), *Horton 7859* (TENN), *Iltis & Iltis 3221* (TENN), *3228* (TENN), *3229* (TENN), *Patrick 292* (FH), *Pringle s.n.* (FH, JE, PC, UC), *Saint-Pierre 1781A* (PC), *1795* (PC), *1797A* (PC), *1797B* (PC), *1899* (PC), *Sharp et al. 1506B* (TENN), *1514* (TENN), *Vitt 17887* (ALTA), *17902* (ALTA, TENN). **Puebla**: ladera NW del Pico de Orizaba, *Delgadillo 4081* (ALTA), *Purpus 4277A* (UC). **Veracruz**: road from Perote to Cofre, *Sharp et al. 7175B* (TENN).

ARGENTINA. **Salta**: Cuesta de Caldeira, 27 May 1873, *Lorentz s.n.* (BM, PC). BOLIVIA. **Chuquisaca**: prov. Sur Cinti, 6 km E of Salitre, *Lewis 84-1827* (F, IBA), *84-1868* (F, IBA). **Cochabamba**: prov. Cercado, laguna Taquiña, *Lewis 83-2051* (F, IBA); prov. Tapacari, 3 km NE of Challa, *Lewis 83-3938a* (F, IBA), *83-3945* (F, IBA), *83-3961* (F, IBA), *83-3971* (F, IBA). **La Paz**: prov. Inquisivi, Cerro Colque Mata, *Lewis 83-3291* (F, IBA), *83-3301* (F, IBA), *83-3306A* (F, MO), *83-3314* (F, IBA), *83-3317* (F, MO); prov. Sur Yungas, Taquesi Pass, *Lewis 83-2129A* (F, IBA); prov. Sur Yungas, between Tres Ríos and Empresa Minera Bolsa Negra, *Lewis 83-2232* (F, IBA), *83-2235* (F, IBA), *83-2138* (F, IBA). BRAZIL: **Minas Gerais**: Serra do Itatiaia, May 1902, *Dusén s.n.* (PC), *611* (H-BR).

8. **Grimmia fuscolutea** Hook., Musci Exot. 1: 63. 1818. TYPE: [Mexico.] In frigidis Tobeccae et Islahuacae, *Humboldt & Bonpland s.n.* (syntype, BM not seen).

Grimmia affinis Hornsch., Flora 2: 85. 1819 [non *G. affinis* Hornsch. Flora 2: 442 = *G. longirostris* Hook.]. *Grimmia apiculata* Hornsch., Flora 1: 329. 1818, nom. nud. *Grimmia apiculata* Hornsch., Flora 2: 442. 1819, nom. illeg. incl. sp. prior. *Grimmia pulvinata* var. *apiculata* (Hornsch.) Huebener, Muscol. Germ: 710. 1833, nom. nud. err. cit. *Dryptodon apiculatus* (Hornsch.) Hartm., Handb. Skand. Fl. ed. 3: 270. 1838. TYPE: [Austria.] Windischmattreyer Tauern, *Hornschuch s.n.* (lectotype, designated by Deguchi (1978), B; isolectotype, H-SOL).

Grimmia flexicaulis Müll. Hal., Linnaea 43: 454. 1882. TYPE: Argentina. Cuesta de Pinos, 27 Mar. 1873, *Lorentz s.n.* (lectotype, designated by Deguchi (1987), JE; isolectotype, BM).

Grimmia quatricruris Müll. Hal., Linnaea 43: 462. 1882. TYPE: Argentina. Cuesta de Pinos in descensu ab alta Puna in convallem Tarija Boliviae, 27 Mar. 1873, *Lorentz s.n.* (lectotype, here designated, BM; isolectotype, PC).

Grimmia unicruris Müll. Hal., Linnaea 43: 463. 1882. TYPE: Argentina. Cuesta de Pinos, 27 Mar. 1873,

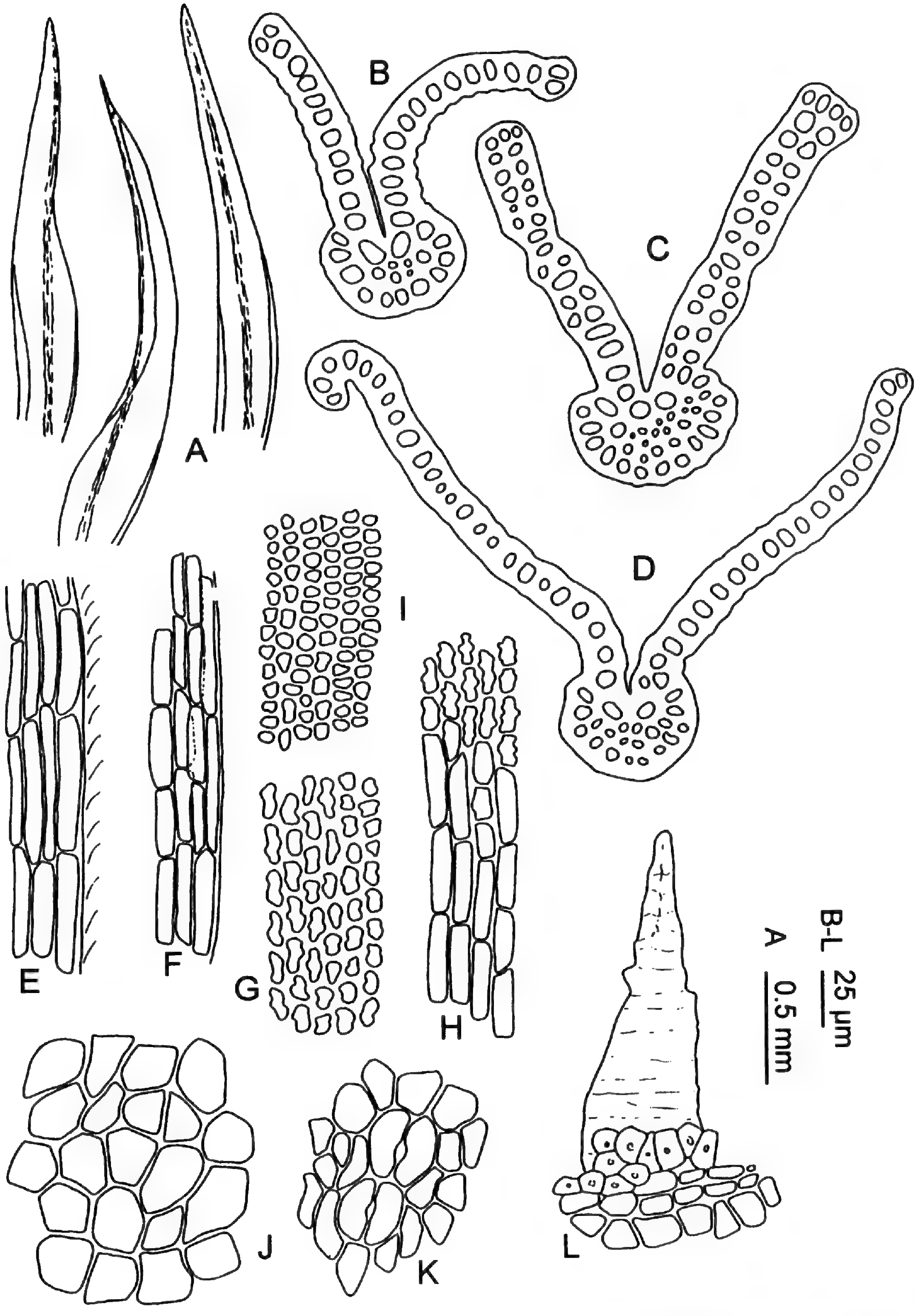

Figure 13. *Grimmia elongata.* —A. Leaves. —B–D. Transverse sections at distal, medial, and proximal parts of leaf. —E. Proximal juxtacostal leaf cells. —F. Proximal marginal leaf cells. —G & I. Distal leaf cells. —H. Transition proximal-medial leaf cells. —J. Medial exothecial cells. —K. Proximal exothecial cells and stomata. —L. Peristome tooth and annulus (only contour shown, not papillosity). (A, B, D–H: *Steyermark 35547a,* FH; C: *Saint-Pierre s.n.,* 1889, PC; J-L: *Saint-Pierre s.n.,* 1887, PC.)

Figure 14. Distribution of *Grimmia elongata.*

Lorentz s.n. (lectotype, here designated, BM [N.B. 3 isotypes in JE are all *G. longirostris* Hook.]).

Grimmia trichophylloidea Schimp. ex Müll. Hal., Nuovo Giorn. Bot. Ital., n.s. 4: 127. 1897. TYPE: Bolivia. Larecaja: vicinitis Sorata, prope Vancuiri, *Mandon 1633* (lectotype, here designated, NY; isolectotypes, F, PC).

Grimmia fastigiata Cardot, Bull. Herb. Boissier, sér. 2, 5: 1003. 1905. TYPE: Argentina. Tierra del Fuego: Ushuaia, mt. Martial, *Skottsberg 70* (lectotype, here designated, PC; isolectotype, H-BR).

Grimmia sanii Greven, Bryologist 99: 429, fig. 2. 1996. TYPE: South Africa. Natal: Drakensberg, Crow's Nest, Mount aux Sources, *Schelpe 2115* (holotype, PRE not seen; isotypes, MO 2 replicates).

Gonioautoicous. Plants green, yellowish green to golden brown. *Stems* erect, to 6 cm, with central strand. *Leaves* erect and flexuous when dry, erect when moist, 1.5–3.0 × 0.3–0.6 mm, lanceolate, acuminate, keeled, not plicate; *margins* recurved proximally, to ⅔ the leaf length on one side and more narrowly recurved proximally, to ⅓–½ the leaf length on the other side, sometimes only shortly and narrowly recurved proximally, in the middle on one side; *costa* semi-terete, differentiated, ventral epidermis 2 cells wide in cross section; *lamina* 1-stratose, 2-stratose at margins and in streaks, seldom 2-stratose throughout the distal half in the distal ⅔; *distal cells* 10–30 × 7–11 μm long, isodiametric to rectangular, not bulging, walls sinuous; *proximal juxtacostal cells* 40–110 × 8–12 μm, rectangular (3.5–13 : 1), walls medium-thick and straight or nodulose; *proximal marginal cells* 35–80 × 8–12 μm, rectangular (3–10 : 1), the walls thin and straight, all alike, scarcely discernible; *hyaline hair-points* terete, flexuous, to 2 mm, entire. *Perichaetial leaves* 3–4 × 0.6 mm, convolute and larger than vegetative leaves (2–3 ×). *Androecia* below perichaetia. *Setae* curved, 1.5–3.0 mm long. *Capsules* emergent to exserted, ovoid, symmetric, smooth or ribbed, stramineous, with stomata at the base; *exothecial cells* 30–60 × 10–20 μm, rectangular (2.5–5.0 : 1), thin-walled, but incrassate at the corners; *annulus* compound and revoluble, *affinis* type; *peristome teeth* 70–90 μm wide at the mouth, entire or moderately cribrose, both surfaces papillose throughout, orange, contrasting with the urn; *opercula* mammillate to rostellate; *calyptrae* mitrate; *spores* 10–16 μm, minutely granulose.

Illustrations. Figure 15; Chałubiński (1882: tab. 4 fig. 5, as *G. apiculata*); Deguchi (1978: figs. 17–19, as *G. apiculata*; 1987: pl. 2, 3, as *G. flexicaulis*); Maier and Geissler (1995: abb. 4, as *G. apiculata*); Noguchi (1988: fig. 139B, as *G. apiculata*).

Distribution (Fig. 16). Europe, Africa, temperate and tropical Asia, Antarctic, northern and southern America; Mexico, Andean Range from Venezuela to northern Argentina and Tierra del Fuego. On granite, slate, quartzite, and basalt in forested and open areas, also on strongly compacted earth in grass tussocks and shrub bases in open areas above the tree line, mainly in places with water available from melt, between 3900 and 4700 m elevation.

Grimmia fuscolutea varies in both gametophytic and sporophytic features (Deguchi, 1978: 169, figs. 18, 19). Plants from drier habitats have longer and more incrassate laminal cells, a modification common in many other species in the genus. Capsule shape and surface vary independently of the habitat conditions. Despite this variability, *G. fuscolutea* can be recognized under the dissecting microscope by the combination of the yellowish-shiny bases of the leaves, the recurved margin, and the perigonia located just below the perichaetia. The plant is autoicous and fruits abundantly, making it easy to find male buds. The yellowish shine of the leaf bases is due to the long cells with mostly thin walls, especially toward the margins.

Two specimens (Ecuador. Pichincha: *Bell 153,* FH; Argentina. Tucumán: Cumbre de Calehuaqui, *Kühn s.n.,* JE) have proximal marginal cells with transverse walls slightly thicker than the longitudinal walls. Both are sterile and morphologically deviant from normal *G. fuscolutea* and could prove to be a different taxon. I include them in *G. fuscolutea,* but fertile specimens would be necessary to definitively place them.

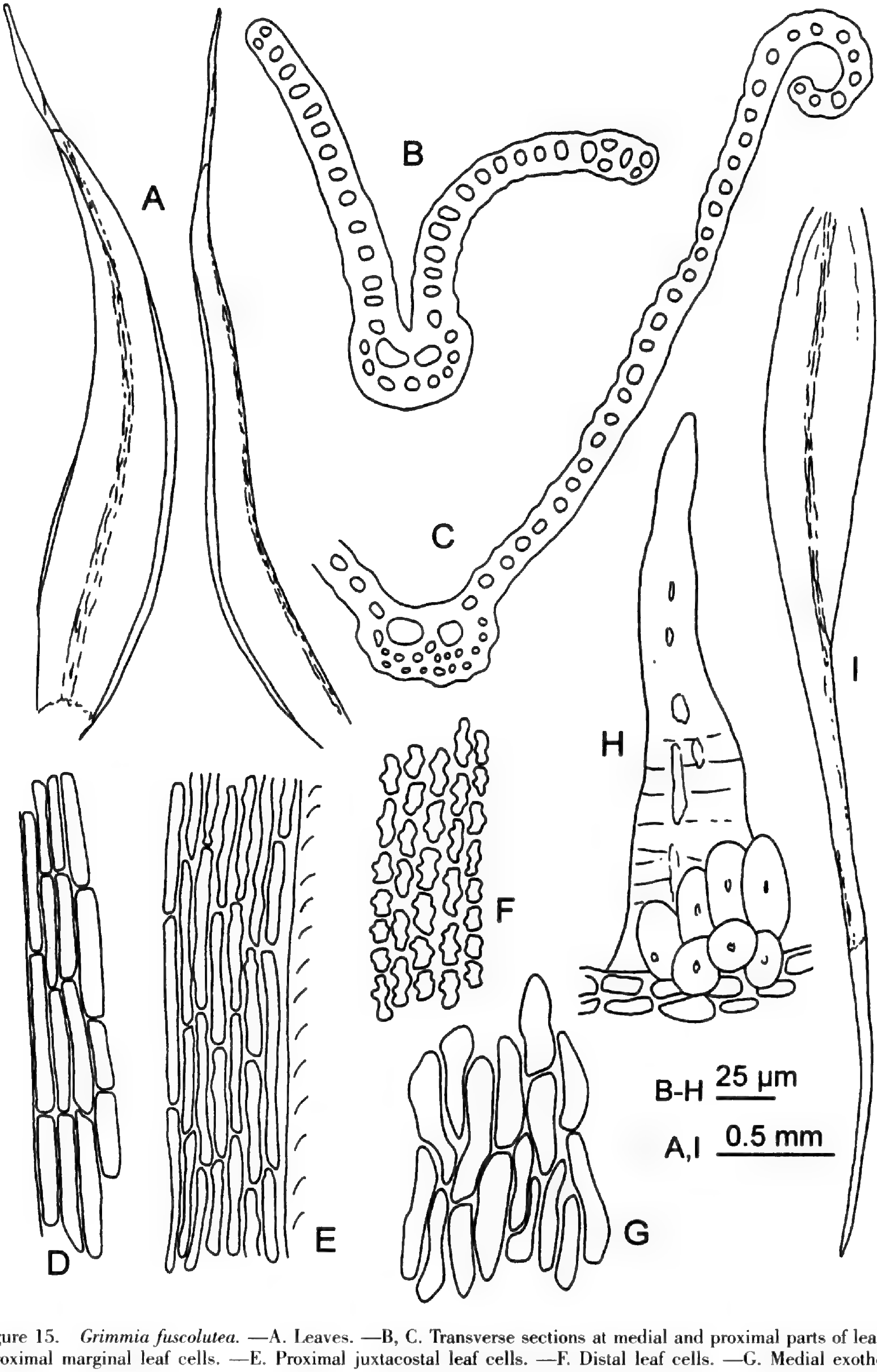

Figure 15. *Grimmia fuscolutea*. —A. Leaves. —B, C. Transverse sections at medial and proximal parts of leaf. —D. Proximal marginal leaf cells. —E. Proximal juxtacostal leaf cells. —F. Distal leaf cells. —G. Medial exothecial cells. —H. Peristome tooth and annulus (only contour shown, not papillosity). —I. Perichaetial leaf. (*Vitt 17921*, TENN.)

Figure 16. Distribution of *Grimmia fuscolutea.*

Selected specimens examined. MEXICO. **México**: Nevado de Toluca, *Cárdenas 3512* (ALTA). **Puebla**: ladera NW del Pico de Orizaba, *Cárdenas 647* (ALTA). **Veracruz**: cima del Cofre de Perote, *Delgadillo 3057* (ALTA); Orizaba, *Schiede 1070B* (PC).

ARGENTINA. **Catamarca**: Yakatula, Grandillas [sic] et Vayas, Feb. 1872, *Lorentz s.n.* (JE). **Salta**: Cuesta de Pinos, in descensu ab alta Puna inconvallem Tarija Boliviae, 27 Mar. 1873, *Lorentz s.n.* (BM, JE, PC). **Tucumán**: depto. Tafi, Infiernillo, *Glummer 1976* (FH). **Tierra del Fuego**: Ushuaia, Mt. Martial, *Skottsberg 70* (PC). BOLIVIA. **Cochabamba**: prov. Ayopaya, laguna Cayuntani, *Lewis 83-4354B* (F, MO); prov. Quillacollo, head of río Suturi, S of Serranías Tarucani, *Lewis 79-2427* (F, FH); prov. Tapacari, Vicuña, *Lewis 83-3932* (F, IBA). **La Paz**: La Cumbre, *Raeymaekers 550* (FLAS); Mururata, *Jaffuel 247* (PC, FH); prov. Camacho, 1 km below Escoma–Charasani road, about 3 km S of Amarate turnoff, NNW of Chuma, *Lewis 79-824* (F, MO, UBC); prov. Inquisivi, cumbre Sayaquira, ca. 2.5 km S of Estancia Huaña Hkota, *Lewis 87414* (FLAS); prov. Larecaja, vicinitis Sorata, prope Vancuiri, *Mandon 1633* (F, NY, PC); prov. Los Andes, Cerro Jankho Karka, *Lewis 84-205A* (F, IBA); prov. Murillo, upper río Chuquiaguillo, *Lewis 88-417* (FLAS); prov. Sur Yungas, between Abra and Estancia Taquesi, *Lewis 83-2183* (F, IBA). **Oruro**: prov. Dalence, 3 km S of Ñaquela, *Lewis 84-1540* (F, IBA). **Potosí**: prov. Tomás Frías, cerro Kari Kari, *Lewis 79-206* (F). ECUADOR. **Pichincha**: Rucu Pichincha, *Benoist 3457* (PC), *3458* (F, PC). PERU. **Lima**: Oroya–Bahn, Hacienda Arana bei Yauli, *Weberbauer 373* (H-BR, PC). VENEZUELA. **Mérida**: Rangel, páramo de Piedras Blancas, *Griffin, III et al. 1498* (ALTA, F, MO).

9. Grimmia humilis Mitt., J. Linn. Soc., Bot. 12: 100. 1869. TYPE: [Chile. Magallanes:] Sandy Point [Punta Arenas], *Lechler s.n.* (lectotype, here designated, NY; isolectotypes, BM, PC).

Gonioautoicous. Plants green, yellowish green to rusty. *Stems* erect, to 1 cm, with central strand. *Leaves* erect and appressed when dry, erect to patent when moist, 0.7–1.2 × 0.3–0.5 mm, ovate, acute, keeled, not plicate; *margins* plane, occasionally weakly recurved distally; *costa* semi-terete, differentiated, ventral epidermis 2 cells wide in cross section; *lamina* 1-stratose except for the 2-stratose two marginal rows in the distal ⅔; *distal cells* 10–18 μm long, isodiametric, rectangular and oblate, not bulging, walls sinuous; *proximal juxtacostal cells* 24–37 × 10–13 μm, rectangular (2–3 : 1), walls thin and straight; *proximal marginal cells* 12–25 × 10–13 μm, isodiametric to rectangular (1–2 : 1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete, straight, to 1.1 mm, denticulate. *Perichaetial leaves* 1.0–1.4 × 0.5–0.7 mm, convolute and larger than vegetative leaves (2–3 ×). *Androecia* below perichaetia. *Setae* curved, 1.6 mm long. *Capsules* exserted, ovoid, symmetric, smooth to weakly ribbed, stramineous, with stomata at the base; *exothecial cells* 25–55 × 12–27 μm, rectangular (2–3 : 1), thin-walled; *annulus* compound and revoluble, *affinis* type; *peristome teeth* 50–75 μm wide at the mouth, entire, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, orange, contrasting with the urn; *opercula* conic; *calyptrae* cucullate; *spores* 10–15 μm, minutely granulose.

Illustrations. Figure 17; Deguchi (1984: figs. 3, 4).

Distribution (Fig. 6). Southern America. *Grimmia humilis* is known from Argentina and Chile. It has been collected on dry rocks between 100 and 800 m elevation.

Grimmia humilis has small, ovate and unistratose leaves with flat margins, and curved setae. The only species with similar leaf shape and sporophyte morphology is *G. bicolor,* but this taxon has bistratose, larger leaves.

Additional specimens examined. ARGENTINA. **Río Negro**: Parque Nacional Argentino Nahuel Huapi, Valle Limay, *Donat 110* (JE, PC). **Santa Cruz**: lac Buenos Aires, *Skottsberg 377* (PC); Lago San Martín, Nana, *Donat 28* (JE); Cañadón de las Cuevas, Jan. 1905, *Dusén s.n.* (PC); estancia Güer Aike, río Gallegos, *Santesson M542* (FH). CHILE. Feria, *Gay s.n.* (BM). **Aisén**: en route from Coihaique to Coihaique Alto, *Deguchi 26528* (HIRO). **Magallanes**: Sierra Carmen Silva, *Roivainen 326* (FH); Natales, *Siple 391.3* (FH); Patagonia, 1912, *Cormack s.n.* (BM); río San Martín, *Dusén 141* (FH, NY, PC); Morro Chico, *Deguchi 26407* (HIRO); Parque Nacional Torres del Paine, *Deguchi 26027* (HIRO).

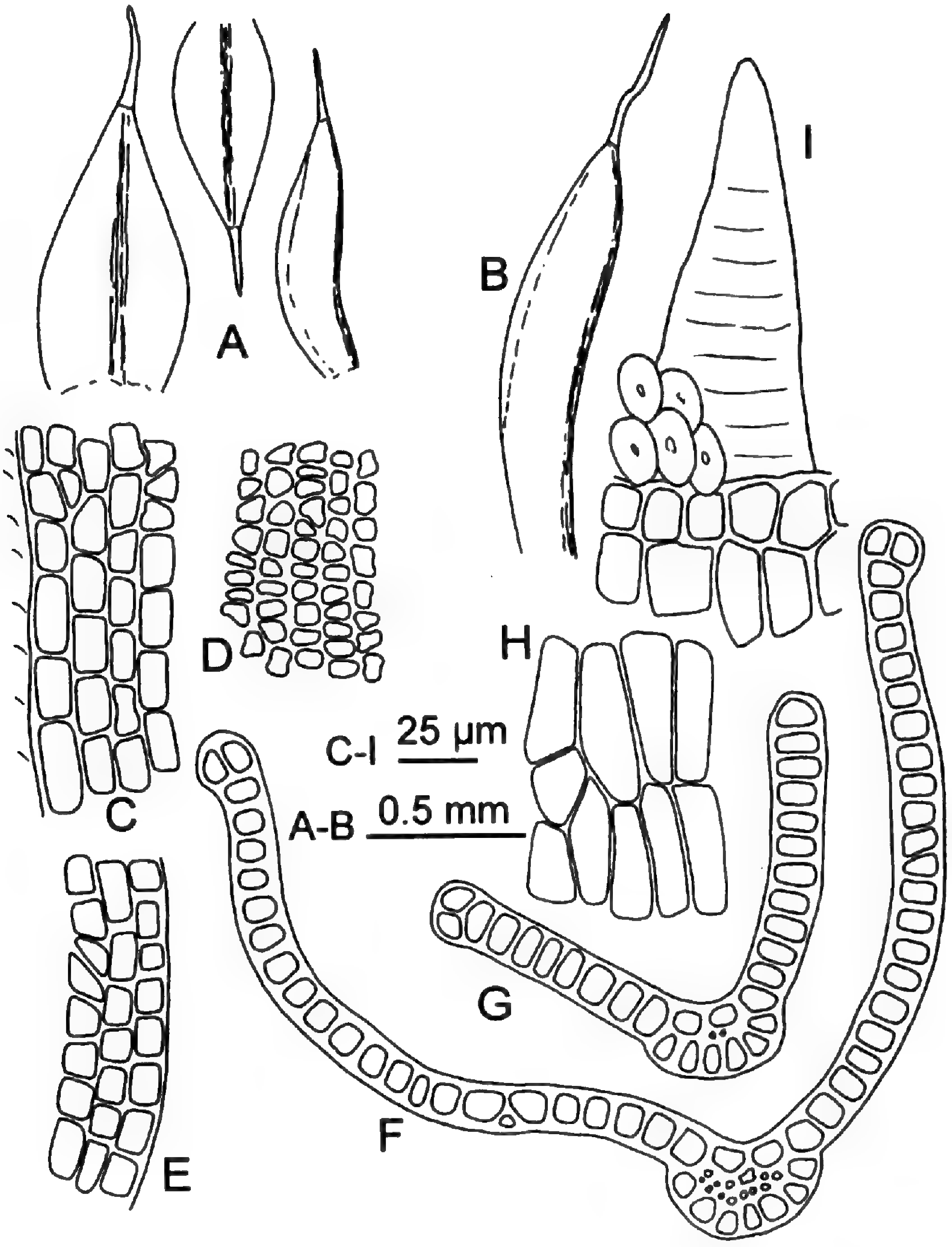

Figure 17. *Grimmia humilis.* —A. Leaves. —B. Perichaetial leaf. —C. Proximal juxtacostal leaf cells. —D. Distal leaf cells. —E. Proximal marginal leaf cells. —F, G. Transverse sections at proximal and medial parts of leaf. —H. Medial exothecial cells. —I. Peristome tooth and annulus (only contour shown, not papillosity). (*Donat 110*, PC.)

10. Grimmia involucrata Cardot, Rev. Bryol. 36: 105. 1909. TYPE: Mexico. Cuyamaloya, 17 Sep. 1908, *Pringle s.n.*, Plantae mexicanae n° 10598 p.p. (lectotype, here designated, PC; isolectotype, PC).

Gonioautoicous. Plants olive-green to blackish. *Stems* erect, to 2 cm, with central strand. *Leaves* erect and appressed when dry, erect to patent when moist, 0.9–1.5 × 0.35–0.60 mm, triangular to ovate, obtuse to acute, concave, not plicate; *margins* plane; *costa* semi-elliptical, undifferentiated, ventral epidermis 2–6 cells wide in cross section; *lamina* 2-stratose in the distal ⅔; *distal cells* 5–14 µm long, mostly isodiametric, not bulging, walls straight to slightly sinuous; *proximal juxtacostal cells* 20–50 × 10–15 µm, rectangular (1.5–4.0 : 1), walls medium-thick and straight; *proximal marginal cells* 10–22 × 10–18 µm, isodiametric, rectangular or oblate (0.7–2.0 : 1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete distally and flat proximally, somewhat decurrent, straight, to 2 mm, denticulate. *Perichaetial leaves* 1.7–2.2 × 0.9–1.2 mm, convolute, hyaline and filmy, scarcely discernible, larger than vegetative leaves (3.0–3.5 : 1). *Androecia* below perichaetia. *Setae* erect and straight, 1 mm long. *Capsules* immersed, ovoid, ventricose, smooth, stramineous, with stomata at the base; *exothecial cells* 30–70 × 15–35 µm, rectangular (2–4 : 1), thin-walled; *annulus* compound and revoluble, *affinis* type; *peri-*

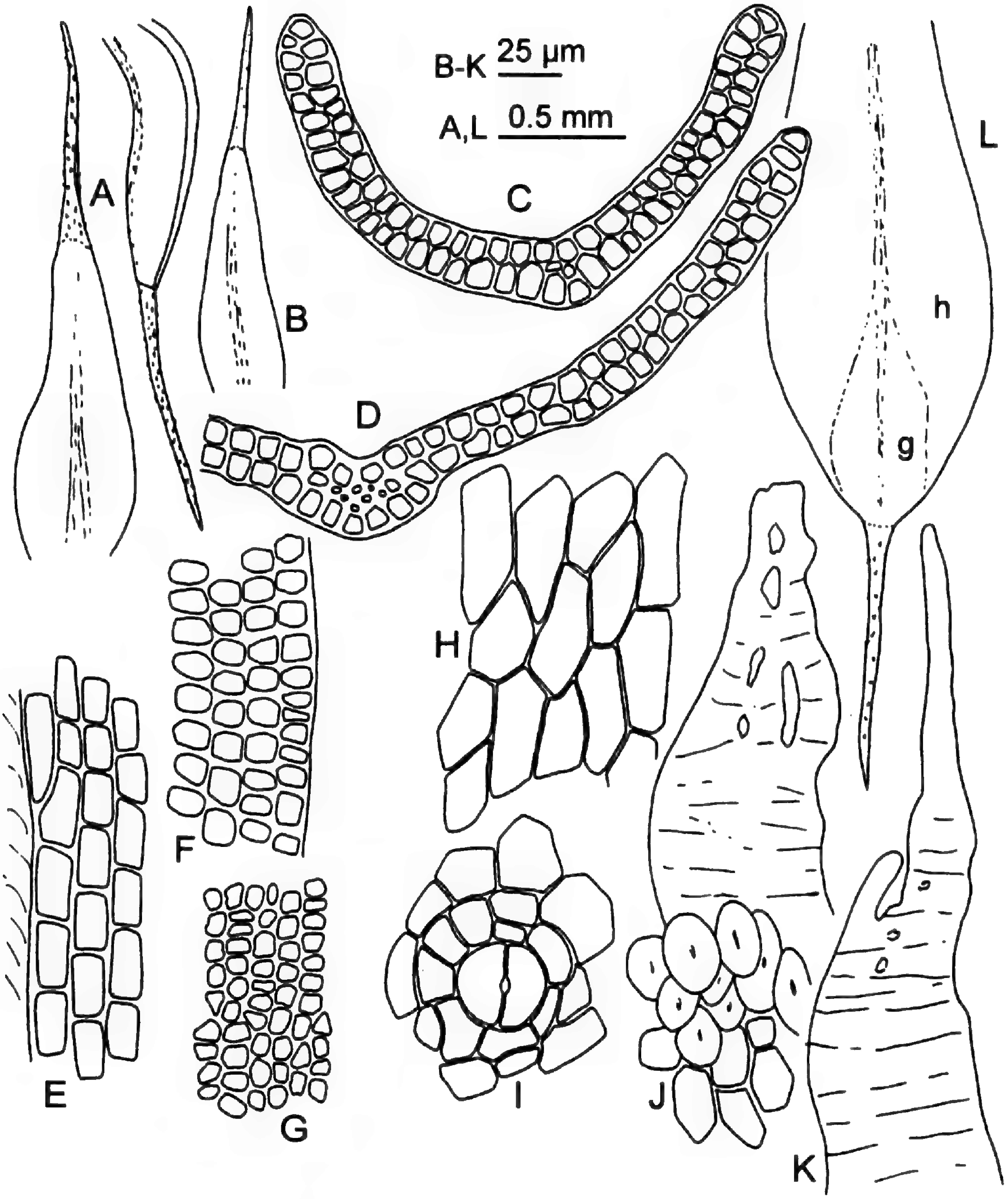

Figure 18. *Grimmia involucrata.* —A, B. Leaves. —C, D. Transverse sections at medial and proximal parts of leaf. —E. Proximal juxtacostal leaf cells. —F. Proximal marginal leaf cells. —G. Distal leaf cells. —H. Medial exothecial cells. —I. Proximal exothecial cells and stoma. —J. Peristome tooth and annulus (only contour shown, not papillosity). —K. Peristome tooth (only contour shown, not papillosity). —L. Perichaetial leaf (h = hyaline area; g = green area). (A, H, I, K: *Pringle 10598*, TENN; B–G, J, L: *Amable 1448*, TENN.)

stome teeth 55–80 µm wide at the mouth, cribrose throughout and irregularly cleft at apex, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, orange-brown, contrasting with the urn; *opercula* rostrate; *calyptrae* mitrate; *spores* 12–16 µm, minutely granulose.

Illustrations. Figure 18; Delgadillo (1999: fig. 1).

Distribution (Fig. 6). Northern America. *Grimmia involucrata* is known only from a few localities in Mexico, where it grows on rocks of unspecified nature around 2500 m elevation.

Grimmia involucrata is characterized by the bistratose concave leaves, undifferentiated costa, the gonioautoicous sexual condition, the strongly modified perichaetial leaves, and the straight setae. For differences between this taxon and the closely related *Grimmia americana, G. poecilostoma,* and *G. tergestina,* see the discussion under *G. poecilostoma.*

Crum (1994) considered *Grimmia involucrata* synonymous with *G. affinis* and included the specimens of *G. involucrata* under *G. tergestina. Grimmia longirostris* (= *G. affinis*) is a totally different taxon, but some type collections of *G. involucrata* have stems of *G. longirostris* intermingled. This, combined with the similarity of *G. involucrata* and *G. tergestina,* may explain Crum's mistake.

A description and illustration of *Grimmia involucrata* appears in Delgadillo (1999).

Additional specimens examined. MEXICO. **Hidalgo**: Cuyamaloya, Sierra de Pachuca, *Pringle 10599* (ALTA, TENN). **México**: Tlalpan, *Amable 1448* (PC).

11. **Grimmia kidderi** James, Bull. Torrey Bot. Club 6: 54. 1875. TYPE: Kerguelen Island, 1874, *Kidder s.n.* (lectotype, here designated, FH; isolectotype, FH).

Grimmia frondosa James, Bull. Torrey Bot. Club 6: 54. 1875. TYPE: Kerguelen Island, *Kidder s.n.* (lectotype, here designated, FH; isolectotypes, FH 2 replicates, NY, PC).

For additional synonyms, see Ochyra and Hertel (1990) and Bell (1984).

Dioicous. Plants olive-green, yellowish brown or blackish. *Stems* erect, to 3 cm, with central strand. *Leaves* erect and appressed when dry, erect to patent when moist, (0.75)1.0–1.5 × 0.2–0.4 mm, lanceolate, acuminate, concave to keeled distally, not plicate; *margins* plane; *costa* semi-terete, differentiated, ventral epidermis 2 cells wide in cross section; *lamina* 1–2-stratose in the distal ⅔; *distal cells* 7–16 μm long, isodiametric and rectangular, some oblate intermingled, bulging on the dorsal surface, walls straight to sinuous; *proximal juxtacostal cells* 30–60 × 8–12 μm, rectangular (3–8: 1), walls thin and straight to thick and nodulose; *proximal marginal cells* 20–35 × 6–8 μm, rectangular (3–6 : 1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete distally or when short, flat proximally or when long, straight to flexuous, to 1.5 mm, smooth to denticulate. *Perichaetial leaves* 3.0–4.5 × 0.7–0.9 mm, convolute and larger than vegetative leaves (5–15 ×). *Androecia* terminal. *Setae* straight, 0.6–1.4 mm long. *Capsules* immersed, ovoid, symmetric, smooth, stramineous, with stomata at the base; *exothecial cells* 35–60 × 15–25 μm, rectangular (1.5–3.0 : 1), thin-walled, but incrassate at the corners; *annulus* compound and tardily deciduous, *elongata* type; *peristome teeth* 100–130 μm wide at the mouth, entire to cribrose and irregularly cleft at apex, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, orange, contrasting with the urn; *opercula* conic to rostrate; *calyptrae* not seen; *spores* 10–12 μm, minutely granulose.

Illustrations. Figure 19; Bell (1984: fig. 3 as *G. immerso-leucophaea*); Cardot (1908: 52 as *G. nordensjoldii*); van Zanten (1971: fig. 11–1 as *G. kerguelensis*).

Distribution (Fig. 10). Antarctic, middle Atlantic (Ascension), Subantarctic islands (Kerguelen, Marion-Prince Edward, South Georgia, Tristan de Cunha), southern America. In Latin America *G. kidderi* is known only from two Patagonian collections. Nevertheless, it is one of the commonest *Grimmia* species in the Southern Hemisphere archipelagos. The South American specimens lack habitat information, but collections from other areas grow on rocks in open and exposed areas, between sea level in South Georgian islands to 1800 m in Tristan de Cunha.

Grimmia kidderi is rarely fertile, yet despite this it is not difficult to recognize. The leaves are narrowly lanceolate and concave for most of their length; a few distal cross sections can appear V-shaped. The proximal cells are long-rectangular, and often somewhat nodulose in the juxtacostal rows. If fertile, the species can be immediately recognized by the immersed capsules surrounded by disproportionately large perichaetial leaves, 5–15 times larger in area than the normal vegetative leaves (Fig. 19K). It is interesting to note that the vast majority of species of *Grimmia* have large perichaetial leaves, commonly 2–5 times larger than other leaves. Nevertheless, the genera *Grimmia* and *Schistidium* have been distinguished historically by the larger, strongly differentiated perichaetial leaves of *Schistidium* as opposed to the largely undifferentiated perichaetial leaves of *Grimmia* (cf. the keys in Crum, 1994; Crum & Anderson, 1981).

In a previous work (Muñoz, 1998d), I cited the specimen *Gunckel 1768* as *Grimmia reflexidens,* but, on reexamination, it clearly has the characteristics of *G. kidderi.*

Additional specimens examined. ARGENTINA. **Santa Cruz**: à l'ouest du lac Azara, *Skottsberg 371* (H-BR). CHILE. **La Araucanía**: Lonquimay, *Gunckel 1768* (PC).

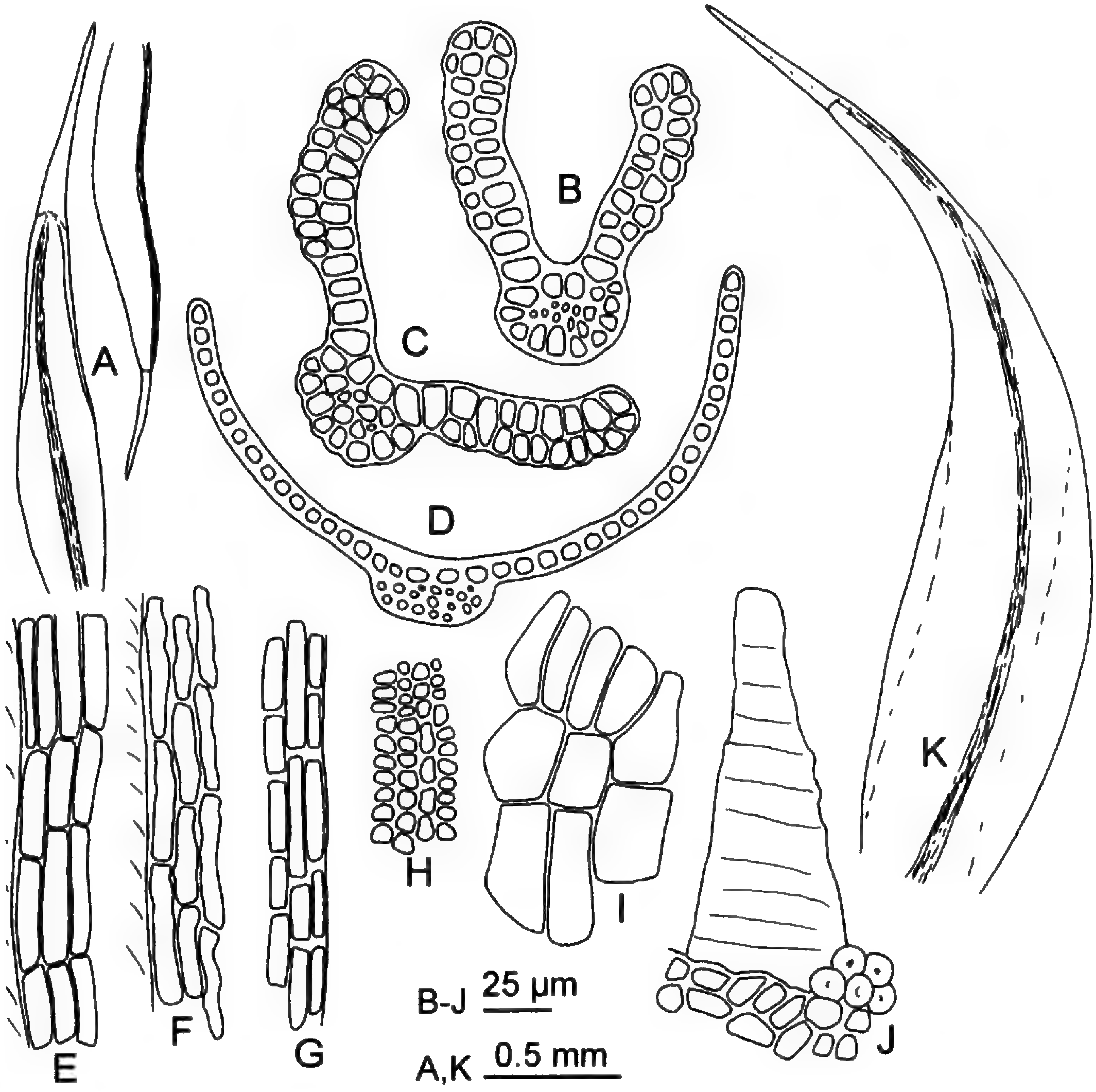

Figure 19. *Grimmia kidderi.* —A. Leaves. —B–D. Transverse sections at distal, medial, and proximal parts of leaf. —E, F. Proximal juxtacostal leaf cells. —G. Proximal marginal leaf cells. —H. Distal leaf cells. —I. Medial exothecial cells. —J. Peristome tooth and annulus (only contour shown, not papillosity). —K. Perichaetial leaf. (A–H: *Gunckel 1768*, PC; I–K: *Skottsberg*, H-BR.)

12. Grimmia laevigata (Brid.) Brid., Bryol. Univ. 1: 183. 1826. *Campylopus laevigatus* Brid., Muscol. Recent. Suppl. 4: 76. 1819. TYPE: Italy. *Anonymous s.n.* (lectotype, designated by Cao & Vitt (1986), B).

Grimmia leucophaea Grev., Mem. Wern. Nat. Hist. Soc. 4: 87, pl. 6. 1822. *Dryptodon leucophaeus* (Grev.) Brid., Bryol. Univ. 1: 773. 1827. TYPE: United Kingdom. Edinburgh, King's Park, *Greville s.n.* (lectotype, here designated, BM; isolectotypes, FH, NY 3 replicates).

Dryptodon brevifolius Brid., Bryol. Univ. 1: 775. 1827. TYPE: no data, labeled: "Dryptodon brevifolius N. Schleich. Herb. De Cand." (lectotype, here designated, B).

Grimmia leiocarpa Taylor, London J. Bot. 5: 44. 1846. TYPE: Australia. Swan River, 1843, *Drummond s.n.* (lectotype, here designated, FH; isolectotypes, H-SOL, NY 2 replicates).

Grimmia calotricha Müll. Hal., Linnaea 43: 454. 1882. TYPE: Argentina. Sierra de Córdoba, Las Peñas, 1871, *Lorentz s.n.* (lectotype, here designated, BM; isolectotype, PC).

Grimmia leucophaea var. *latifolia* Limpr., Laubm. Deutschl. 1: 742. 1889. *Grimmia leucophaea* var. *latifolia* Limpr., Bryoth. Siles. n° 163. 1867, nom. nud. *Grimmia campestris* var. *latifolia* (Limpr.) Paris, Index Bryol. ed. 2: 269. 1904. *Grimmia campestris* f. *latifolia* (Limpr.) Mönk., Laubm. Eur. 356. 1927. *Grimmia laevigata* f. *latifolia* (Limpr.) Podp., Consp. Musc. Eur. 276. 1954. TYPE: [Poland. Silesia:] Spitzberg bei Hirschberg, 1867, *Limpricht s.n.* (lectotype, here designated, FH).

Grimmia sarcocalyx Kindb., in Macoun, Cat. Canad. pl., Musci: 66. 1892. *Grimmia sarcocalyx* Kindb., in Macoun, Bull. Torrey Bot. Club 17: 271. 1890, nom. nud. *Grimmia campestris* subsp. *sarcocalyx* (Kindb.) Kindb., Eur. N. Amer. Bryin. 2: 219. 1898. TYPE: Canada. British Columbia: Spence's Bridge, 28 May 1889, *Macoun s.n.* (lectotype, here designated, S; isolectotype, CANM-198098).

Grimmia murina Müll. Hal., Hedwigia 36: 105. 1897. TYPE: [Argentina. Buenos Aires:] Sierra de la Ventana, 1881, *Lorentz s.n.* (lectotype, here designated, JE; isolectotypes, JE, PC).

Dioicous. *Plants* olive-green to blackish. *Stems* erect, to 2 cm, with central strand. *Leaves* erect and appressed when dry, spreading when moist, 0.8–1.4 × 0.3–0.8 mm, triangular or cordate to ovate, obtuse to acuminate, concave, not plicate; *margins* plane; *costa* semi-elliptical, undifferentiated, ventral epidermis 2–6 cells wide in cross section; *lamina* 2-stratose in the distal ⅔; *distal cells* 5–10 µm long, isodiametric, rectangular and oblate, not bulging, walls straight to slightly sinuous; *proximal juxtacostal cells* 20–30 × 12–16 µm, rectangular (1.5–2.5 : 1), walls thick and straight; *proximal marginal cells* 6–10 × 10–16 µm, oblate (0.4–0.7 : 1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete, straight, to 2 mm, dentate, seldom nearly smooth. *Perichaetial leaves* ca. 2 × 0.8–1.3 mm, convolute and larger than vegetative leaves (2–4 ×). *Androecia* terminal. *Setae* erect and straight, 1–3 mm long. *Capsules* exserted, ovoid, symmetric, smooth, castaneous, with stomata at the base; *exothecial cells* 30–65 × 15–30 µm, rectangular (1.5–2.5 : 1), thin-walled; *annulus* compound and revoluble, *affinis* type; *peristome teeth* 50–60 µm wide at the mouth, entire or weakly cribrose, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, castaneous, concolorous with the urn; *opercula* rostrate; *calyptrae* mitrate; *spores* 12–16 µm, minutely granulose.

Illustrations. Figure 20; Deguchi (1984: fig. 5); Dirkse (1982: figs. 1–12); Lawton (1971: pl. 61 figs. 1–9); Maier and Geissler (1995: abb. 16); Orbán and Vajda (1983: fig. 328a–c); Petrov (1975: tab. 62 fig. 7); Smith (1978: fig. 148 1–4).

Distribution (Fig. 12). Europe, Africa, temperate and tropical Asia, Australasia, northern and southern America; central and eastern Argentina, south Brazil, central Chile. On acidic and slightly basic rocks on cliffs, outcrops, and other exposed, open places usually dry and sunny between 180 and 2000 m elevation.

Grimmia laevigata is readily recognized by the basal marginal cells oblate and the undifferentiated costae in the distal part of leaves. It is macroscopically similar to *Grimmia americana*, *G. involucrata*, *G. poecilostoma*, *G. tergestina*, and populations of *G. ovalis* with short acumina. For example, all reports of *G. laevigata* from Chihuahua, Durango, and Tlaxcala (Mexico; Crum, 1994: 391) are *G. ovalis* with short leaves. All previous species have basal marginal cells that are isodiametric to rectangular, and are not oblate as in *G. laevigata*. Some authors have stressed that *G. laevigata* has more strongly dentate hair-points. This is usually correct, but some populations of *G. laevigata* have almost smooth hair-points, and *G. tergestina* can have strongly dentate hair-points, leading to misidentifications. Basal leaf areolation is the best diagnostic character in *G. laevigata* because sporophytes are rarely produced.

Additional specimens examined. MEXICO. **Baja California**: 75 km S of Tijuana on Ensenada Rd., 6 Sep. 1962, *Sharp s.n.* (TENN); below Melting Ranch, E of Colenett, Sierra de San Pedro Mártir, *Sharp et al. 6086* (TENN), *6090* (TENN), *6097a* (TENN); Sonorabampo Canyon near La Misión, *Mulroy 8* (TENN); ca. 12 km W de Tecate, *Meyer 33* (TENN); 3.5 km S of Tecate, *Meyer 34A* (TENN); 1 km W of Tijuana, Presa de Rodríguez, *Meyer 32A* (TENN).

ARGENTINA. **Buenos Aires**: Sierra Ventana, *Kühnemann 4137* (TENN). **Córdoba**: Depto. Punilla, Weg von Tanti nach Cerro Los Gigantes, unterhalb La Hoyada, *Hosseus & Weihmüller 2216* (FH), *2217* (FH), *2218* (FH), *2227* (FH), *2309* (FH), *2372* (FH); Weg von Tanti nach Cosquín bei der Cueva de los Pajaritos, *Hosseus & Weihmüller 886* (FH), *887* (FH), *888* (FH), *889* (FH); Sierra Chica, Weg von Río Ceballos nach La Falda, *Hosseus & Weihmüller 1487* (FH); Río Juspe, Weg nach La Candelaria, *Hosseus 910* (FH); bei der Estafeta Casa Nueva (Pedernera), *Hosseus 1856* (FH); Depto. Colón, Los Quebrachitos, 10 km oberhalb Unquillo, *Hosseus 761* (FH). BRAZIL. **Rio Grande do Sul**: Lavras do Sul, *Vital 9196* (FLAS). CHILE. **Bio-Bio**: Los Ángeles, *Dusén 366* (FH, JE, NY, PC). **Maule**: Caurico, *Barros 6877* (FH). **Región Metropolitana**: prope Santiago urbem, *Dusén 136* (FH, NY, PC); San Cristóbal, *Bertho 100* (FH, PC). URUGUAY. **Montevideo**: Montevideo, *Gibert 1243* (PC).

13. Grimmia lisae De Not., Muscol. Ital. Spic: 15. 1837. *Grimmia muehlenbeckii* var. *lisae* (De Not.) Bott., in Venturi & Bott., Atti Soc. Crittog. Ital. 3: 217. 1884. *Grimmia trichophylla* subsp. *lisae* (De Not.) Boulay, Musc. France 1: 378. 1884. *Dryptodon lisae* (De Not.) Loeske, Stud. Morph. Syst. Laubm. 111. 1910. *Grimmia trichophylla* var. *lisae* (De Not.) Bott., in Luisier, Brotéria, Sér. Bot. 14: 32. 1916. TYPE: Italia. In collibus taurinensibus, 1836, *Lisa s.n.* (lectotype, here designated, RO; isolectotypes, H-SOL, NY, RO).

Grimmia sardoa Müll. Hal., Syn. Musc. Frond. 1: 786. 1849. *Grimmia trichophylla* var. *sardoa* (Müll. Hal.)

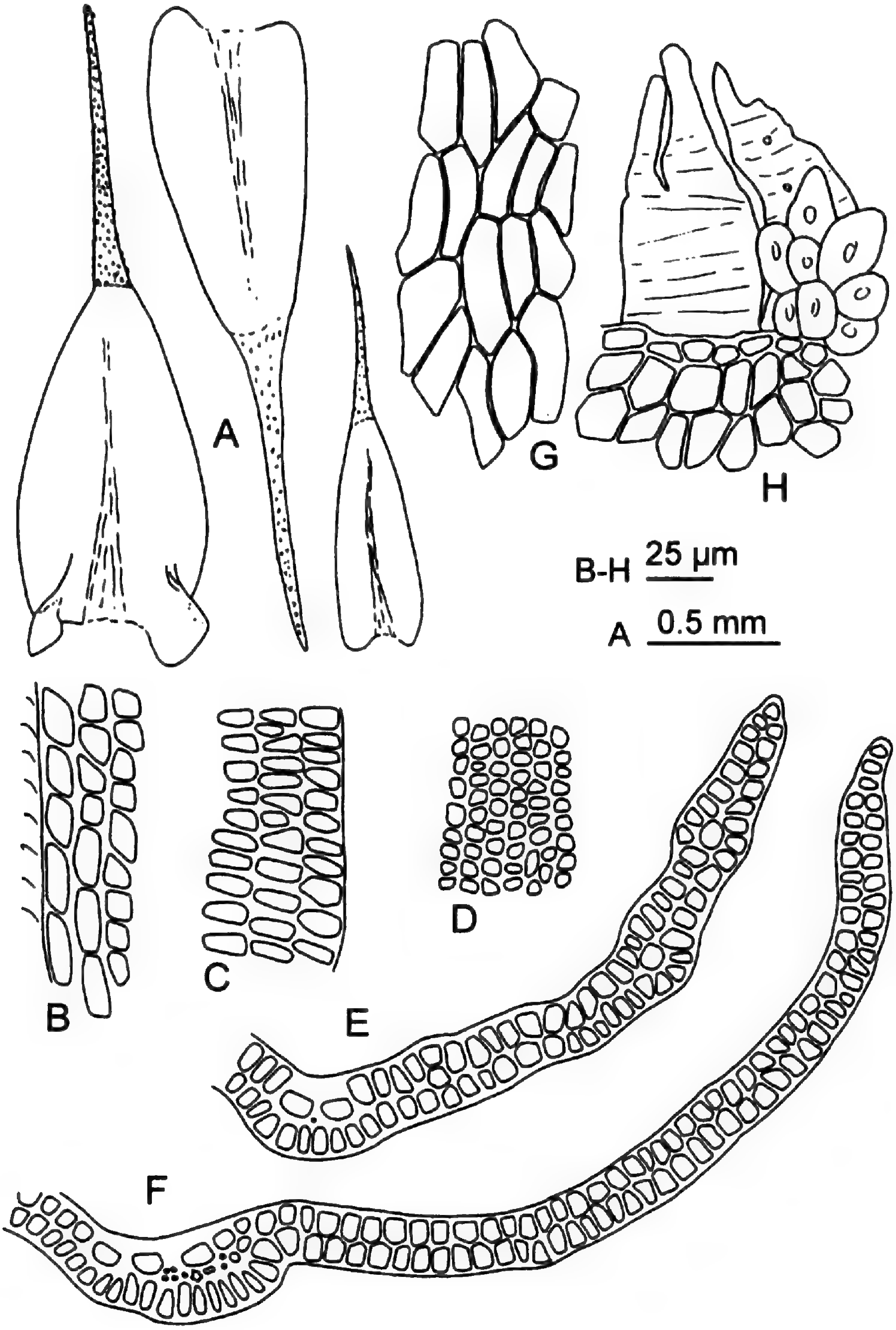

Figure 20. *Grimmia laevigata.* —A. Leaves. —B. Proximal juxtacostal leaf cells. —C. Proximal marginal leaf cells. —D. Distal leaf cells. —E, F. Transverse sections at medial and proximal parts of leaf. —G. Medial exothecial cells. —H. Peristome teeth and annulus (only contour shown, not papillosity). (*Mulroy 8,* TENN.)

Boulay, Musc. France 1: 379. 1884. *Grimmia muehlenbeckii* var. *sardoa* (Müll. Hal.) M. Fleisch., Malpighia 7: 329. 1893, nom. inval. pro synon. *Grimmia lisae* subsp. *sardoa* (Müll. Hal.) Kindb., Eur. N. Amer. Bryin. 2: 223. 1898. *Dryptodon sardoa* (Müll. Hal.) Loeske, Stud. Morph. Syst. Laubm. 111. 1910. *Grimmia trichophylla* subsp. *sardoa* (Müll. Hal.) Bott., in Loeske, Laubm. Eur. Part I: 133. 1913. TYPE: Italia. Sardinia, *De Notaris s.n.* (lectotype, here designated, RO).

Grimmia californica Sull., Expl. Railroad Mississippi Pacific, Descr. Moss. Liverw: 187, pl. 4. 1857 "1856." TYPE: U.S.A. California: near Oakland, *Bigelow 2.b* (lectotype, here designated, FH).

Grimmia canadensis Kindb., Eur. N. Amer. Bryin. 2: 226. 1898. TYPE: Canada. British Columbia: Vancouver Isl., 26 May 1893, *Macoun s.n.* (lectotype, here designated, S; isolectotypes, CANM-198079, CANM-198080).

Grimmia azorica Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 41: 58. 1905. *Grimmia trichophylla* subsp. *azorica* (Renauld & Cardot) Luisier, Brotéria, Sér. Bot. 17: 42. 1919. TYPE: Portugal. Azores: Sta. Maria, *Trelease 1393c* (lectotype, here designated, PC; isolectotype, MO; syntype, [Graciosa, *Brown s.n.*] PC).

Grimmia trichophylla f. *propagulifera* H. Winter, Hedwigia 55: 101. 1914, nom. illeg., non Limpr., 1889. TYPE: Spain. Santa Cruz de Tenerife: Guímar, auf Felsen dem Sanatorium, Mar. 1912, *Winter s.n.* (lectotype, here designated, JE).

Dioicous. Plants olive-green. *Stems* erect or ascending, to 3 cm, with central strand. *Leaves* erect and appressed when dry, spreading to squarrose when moist, 1.7–3.0 × 0.5–0.7 mm, lanceolate, acute, keeled, not plicate; *margins* recurved proximally, to ½–⅔ the leaf length on one side and flat or more narrowly recurved proximally, to ⅓–½ the leaf length on the other side; *costa* reniform, differentiated, ventral epidermis (2)4–6 cells wide in cross section; *lamina* 1–2-stratose, 2-stratose at margins and in streaks in the distal ⅔; *distal cells* 5–12 μm long, isodiametric, rectangular and oblate, not bulging, walls straight to slightly sinuous; *proximal juxtacostal cells* 17–50 × 7–14 μm, rectangular (1.5–6.0 : 1), walls thick and straight; *proximal marginal cells* 10–35 × 8–12 μm, isodiametric to rectangular (1–3 : 1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete, straight, to 1.2 mm, denticulate. *Propagula* (not seen in American specimens; description from Mediterranean specimens) 40–60 μm diam., spherical to broad-ellipsoid, multicellular, on branched stalks on the dorsal side of leaf base, olive-green or brownish with yellowish green to brownish walls. *Perichaetial leaves* 2.6–3.6 × 0.6–0.9 mm, convolute and larger than vegetative leaves (2–4 ×). *Androecia* terminal. *Setae* curved, 3–5 mm long. *Capsules* exserted, ellipsoid, symmetric, weakly ribbed, stramineous, with stomata at the base; *exothecial cells* 20–35 × 14–25 μm, mostly rectangular ([1]2 : 1), thin-walled; *annulus* compound and revoluble, *affinis* type; *peristome teeth* 40–70 μm wide at the mouth, entire or irregularly cleft at apex, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, orange, contrasting with the urn; *opercula* rostrate; *calyptrae* mitrate; *spores* 12–18 μm, minutely granulose.

Illustrations. Figure 21.

Distribution (Fig. 6). Europe, northern Africa, northern America. *Grimmia lisae* occurs commonly along the Pacific coast from Vancouver Island to Baja California. The Mexican localities of this species lie in the southernmost area of Californian vegetation. It is found on rocks and soil over rocks in coastal sage shrub vegetation at low elevations near sea level.

Grimmia lisae has straight non-flexuous leaves not folded along the costae, short hair-points, and costae reniform in cross section. Under the dissecting microscope the leaves are quite flat in the distal part, and closely appressed to the stem. It has usually been considered a synonym of *G. trichophylla*, but they are readily distinguished by costa structure. *Grimmia trichophylla* has more flexuous leaves usually folded along the costae. When sporophytes are present, the ovoid, weakly ribbed capsules of *G. lisae* markedly contrast with the ellipsoid to cylindrical, strongly ribbed capsules of *G. trichophylla*. Propagula, when found, are distinctive, although I have never seen them in American specimens of *G. lisae*. In *G. lisae*, they originate from dorsal bases of leaves. In *G. trichophylla* propagula are sessile on the laminae. European collections of *G. lisae* sometimes have propagula, in contradiction to Greven (1995: 90). Greven (1995: 90) also mistakenly attributed this taxon to specimens collected in "Toros Daglari in Turkey," confusing the Latin *taurinensibus* (= "from Taurinum," Turin, Italy) and *tauricus* (= "from Taurus," Toros Dağlari, Turkey, or "from Tauria," Crimea, Ukraine) (Stearn, 1983).

Additional specimens examined. MEXICO. **Baja California**: 75 km S of Tijuana on Ensenada Road, 6 Sep. 1962, *Sharp s.n.* (TENN); Punta Banda, near Los Arbolitos, *Mulroy 3* (TENN); Sonorabampo Canyon near La Misión, *Mulroy 5* (TENN), *6* (TENN).

14. Grimmia longirostris Hook., Musci Exot. 1: 62. 1818. TYPE: [Ecuador. Chimborazo: mt. Chimborazo], *Humboldt 76* (lectotype, designated by Deguchi (1984), BM; isolectotypes, BM, PC).

Grimmia affinis Hornsch., Flora 2: 443. 1819 [July], nom. illeg. [non Hornsch. 1819, Flora 2: 85 [February] (= *Grimmia fuscolutea* Hook.)]. *Dryptodon ovatus* var. *affine* (Hornsch.) Hartm., Handb. Skand. Fl. ed. 3: 271. 1838. *Grimmia ovata* var. *affinis* (Hornsch.) Bruch & Schimp., in Bruch, Schimp. & W. Gümbel, Bryol. Europ. 3: 123, tab. 255ß. 1845. *Grimmia ovalis* var. *affinis* (Hornsch.) Broth., Acta Soc. Sci. Fenn. 19: 86. 1892. *Grimmia ovalis* f. *affinis* (Hornsch.) Mönk., Laubm. Eur. 360. 1927. TYPE: [Austria:] Windissmattrey Tauern, *Hornschuch s.n.* (lectotype, designated by Deguchi (1978), B).

Grimmia columbica De Not., Mem. Reale Accad. Sci. To-

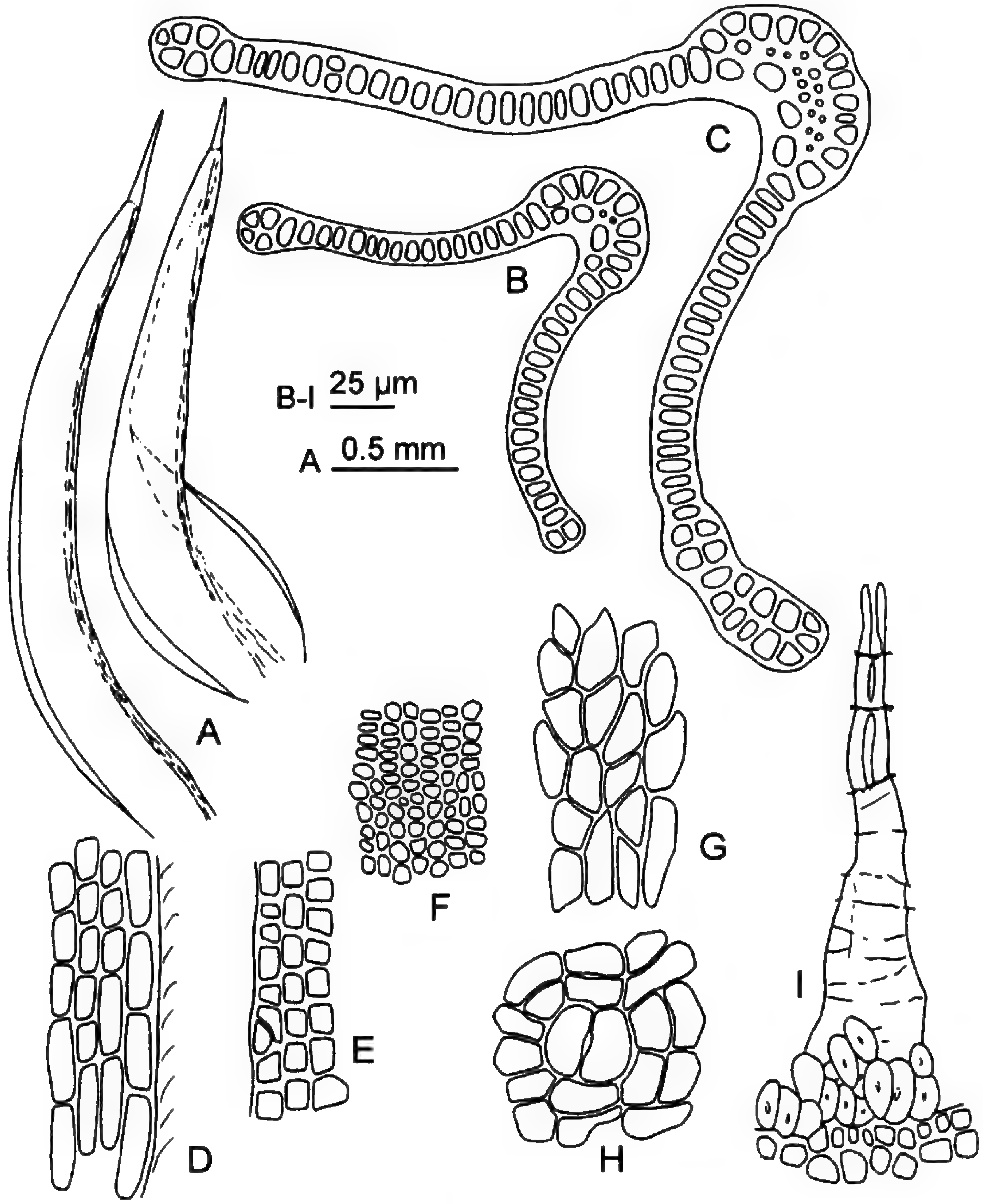

Figure 21. *Grimmia lisae.* —A. Leaves. —B, C. Transverse sections at medial and proximal parts of leaf. —D. Proximal juxtacostal leaf cells. —E. Proximal marginal leaf cells. —F. Distal leaf cells. —G. Medial exothecial cells.—H. Proximal exothecial cells and stoma. —I. Peristome tooth and annulus (only contour shown, not papillosity). (*Mulroy 5*, TENN.)

rino, ser. 2, 18: 447, fig. 7. 1859. TYPE: [Ecuador. Napo:] ad rivum Napo, *Osculati s.n.* (holotype, RO?; isotype, H-SOL).

Grimmia peruviana Sull., U. S. Expl. Exped., Musc. 8, Tab. 5A. 1860. TYPE: Peru. Andes, [*Rick & Brackenridge s.n.*] (lectotype, designated by Muñoz (1998c), BM; isolectotypes, BM, FH, NY).

Grimmia bogotensis (Hampe) A. Jaeger, Ber. Tätigk. St. Gallischen Naturwiss. Ges. 1872–1873: 70. 1874. *Guembelia bogotensis* Hampe, Linnaea 32: 142. 1863. TYPE: Colombia. Cundinamarca: Bogotá, Los Laches, *Lindig 2011* (lectotype, designated by Muñoz (1998c), PC; isolectotype, NY).

Grimmia integridens Müll. Hal., Linnaea 43: 460. 1882. TYPE: Argentina. Tucumán: in der Cienaga, 1893, *Lorentz s.n.* (lectotype, designated by Muñoz (1998c), PC).

Grimmia leucophaeola Müll. Hal., Linnaea 43: 456. 1882.

TYPE: Argentina. Tucumán: Tafi, 1872, *Lorentz s.n.* (lectotype, designated by Muñoz (1998c), JE; isolectotypes, BM, JE, NY).

Grimmia raphidostega Müll. Hal., Linnaea 43: 459. 1882. TYPE: Argentina. Salta: Nevado de Castillo, 1873, *Lorentz s.n.* (lectotype, designated by Muñoz (1998c), JE).

Grimmia vernicosula Müll. Hal., Linnaea 43: 458. 1882. TYPE: Argentina. Salta: Orán, *Lorentz s.n.* (lectotype, designated by Muñoz (1998c), JE; isolectotype, BM).

Grimmia rufa Müll. Hal., Bot. Jahrb. Syst. 5: 81. 1884. TYPE: [South Africa.] Kerguelen Isl., Nov. 1874, *Naumann s.n.* (lectotype, here designated, PC; isolectotype, H-BR).

Grimmia nanoglobosa Müll. Hal. ex E. Britton, Bull. Torrey Bot. Club 23: 477. 1896. TYPE: Bolivia. La Paz: Mapiri, May 1886, *Rusby s.n.* (holotype, NY).

Grimmia breviexserta Müll. Hal., Bull. Herb. Boissier 5: 200. 1897. TYPE: Guatemala. Quezaltenango: Quezaltenango, *Bernoulli & Cario 115* (lectotype, designated by Muñoz (1998c), PC).

Grimmia micro-ovata Müll. Hal., Nuovo Giorn. Bot. Ital., n.s. 4: 128. 1897. TYPE: Bolivia. Cochabamba: prope Choquecamata, *Germain 1142* (lectotype, designated by Muñoz (1998c), JE; isolectotype, NY).

Grimmia subovata Schimp. ex Müll. Hal., Nuovo Giorn. Bot. Ital., n.s. 4: 128. 1897. TYPE: Bolivia. Larecaja: vicinitis Sorata, Ancouma, hacienda Peñas, *Mandon 1634* (lectotype, designated by Muñoz (1998c), BM; isolectotype, BM 2 replicates, FH, G).

Grimmia itatiaiae Müll. Hal., Bull. Herb. Boissier 6: 109. 1898. TYPE: Brazil. Minas Gerais: Serra do Itatiaia, Agulhas-Negras, *Ule 1830* (lectotype, designated by Muñoz (1998c), H-BR).

Grimmia itatiaiensis Broth. ex Müll. Hal., Bull. Herb. Boissier 6: 108. 1898. TYPE: Brazil. Minas Gerais: Serra do Itatiaia, 2100 m, Mar. 1894, *Ule 1913* [Ule & Brotherus, Bryotheca brasiliensis, n° 124] (lectotype, designated by Muñoz (1998c), H-BR; isolectotypes, GOET, JE, NY, PC, UPS).

Grimmia praetermissa Cardot, Rev. Bryol. 36: 105. 1909. TYPE: Mexico. México: in the crater of the Volcano of Toluca, 25 Sep. 1892, *Pringle s.n.* [Pringle, Plantae mexicanae n° 26a] (lectotype, designated by Muñoz (1998c), NY; isolectotypes, JE, PC 2 replicates).

Grimmia herzogii Broth., in Herzog, Biblioth. Bot. 87: 55. 1916. TYPE: [Bolivia. Cochabamba:] An Felsen eines Gipfel der Yanakakabastion, 4500 m, *Herzog 3826* (lectotype, designated by Deguchi (1987), JE; isolectotype, H-BR).

Grimmia nigella Herzog, Biblioth. Bot. 87: 55, fig. 17. 1916. TYPE: Bolivia. Bei der Saittulaguna, *Herzog 2679* (lectotype, designated by Muñoz (1998c), JE).

Grimmia speirophylla Herzog, Biblioth. Bot. 87: 55. 1916. TYPE: Bolivia. Cochabamba: Yanakakabastion, *Herzog 3827* (lectotype, designated by Muñoz (1998c), JE; isolectotype, JE; syntypes, *Herzog 4871*, *Herzog 3148*, JE; *Herzog 3811*, NY; *Herzog 4811*, PC).

Grimmia speirophylla f. *humilis* Herzog, Biblioth. Bot. 87: 55. 1916. TYPE: Bolivia. Cochabamba: Torreni-Yanakaka, July 1911, *Herzog s.n.* (holotype, JE).

Grimmia allionii Broth., Rev. Bryol. 47: 9. 1920. TYPE: [Ecuador.] Azuay: in rupibus montis prope Cañar, 16 Nov. 1909, *Allioni s.n.* (lectotype, designated by Muñoz (1998c), H-BR; isolectotypes, H-BR, PC).

Grimmia trollii Herzog, Hedwigia 74: 102. 1934. TYPE: Bolivia. [Oruro:] Curahuara, *Troll 58* (lectotype, designated by Deguchi (1987), JE).

Grimmia cinerea Thér., Rev. Bryol. Lichénol. 9: 9, fig. 3. 1936. TYPE: [Ecuador. Pichincha:] rochers du Condorguachana, *Benoist 3153* (holotype, PC).

Grimmia stenopyxis Thér., Rev. Bryol. Lichénol. 9: 8. 1936. TYPE: [Ecuador. Pichincha:] Pichincha, 24 Oct. 1930, *Benoist s.n.* (lectotype, designated by Muñoz (1998c), PC).

Grimmia antillarum Thér., Rev. Bryol. Lichénol. 13: 13. 1944. TYPE: Dominican Republic. Azua: Cordillera Central, Los Vallecitos de Yaque, *Ekman 13630* (lectotype, designated by Muñoz (1998c), PC; isolectotype, NY).

For additional synonyms, see Muñoz (1998c).

Cladautoicous. Plants yellowish green, olive-green, rusty, golden, or black above, brownish to black in the internal parts. *Stems* erect, to 6 cm but commonly 1–3 cm, with central strand. *Leaves* erect and appressed, occasionally flexuous when dry, erect to patent when moist, 1.7–2.6 × 0.3–0.6 mm, lanceolate to ovate-lanceolate, acute, canaliculate, not plicate; *margins* recurved proximally, to ½–⅔ the leaf length on one side, plane elsewhere, seldom recurved in both sides; *costa* reniform, slightly to clearly differentiated, ventral epidermis 2–6 cells wide in cross section; *lamina* 2(3)-stratose, occasionally with 3(4)-stratose margins and streaks in the distal ⅔; *distal cells* 4–11 μm long, isodiametric, rectangular and oblate intermingled, not bulging, walls sinuose; *proximal juxtacostal cells* 25–60 × 7–13 μm, rectangular (3–7 : 1), walls thick and nodulose; *proximal marginal cells* 9–25 × 6–11 μm, usually rectangular ((1)–3 : 1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* seldom lacking, flat or terete, straight to moderately flexuous, to 3 mm, entire to denticulate. *Perichaetial leaves* 2.6–3.5 × 0.6–0.7 mm, convolute and larger than vegetative leaves (2–3 ×). *Androecia* terminal. *Setae* erect and straight, 1–4 mm long. *Capsules* immersed to exserted, ovoid to cylindric, symmetric, smooth, stramineous, with stomata at the base; *exothecial cells* 18–50 × 18–20 μm, rectangular (2 : 1), although many isodiametric intermingled, thin-walled; *annulus* compound and revoluble, *affinis* type; *peristome teeth* 50–80 μm wide at the mouth, entire or irregularly cleft at apex, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, orange to reddish, contrasting with the urn; *opercula* mammillate to long-rostrate; *calyptrae* mitrate (very rarely cucullate); *spores* 8–12 μm, minutely granulose.

Illustrations. Figure 22; Afonina (1986: ris. 1 figs. 1–8, as *G. affinis*; ris. 2 figs. 9–16, as *G. ovalis*); Cao and Churchill (1995a: pl. 1, as *G. af-*

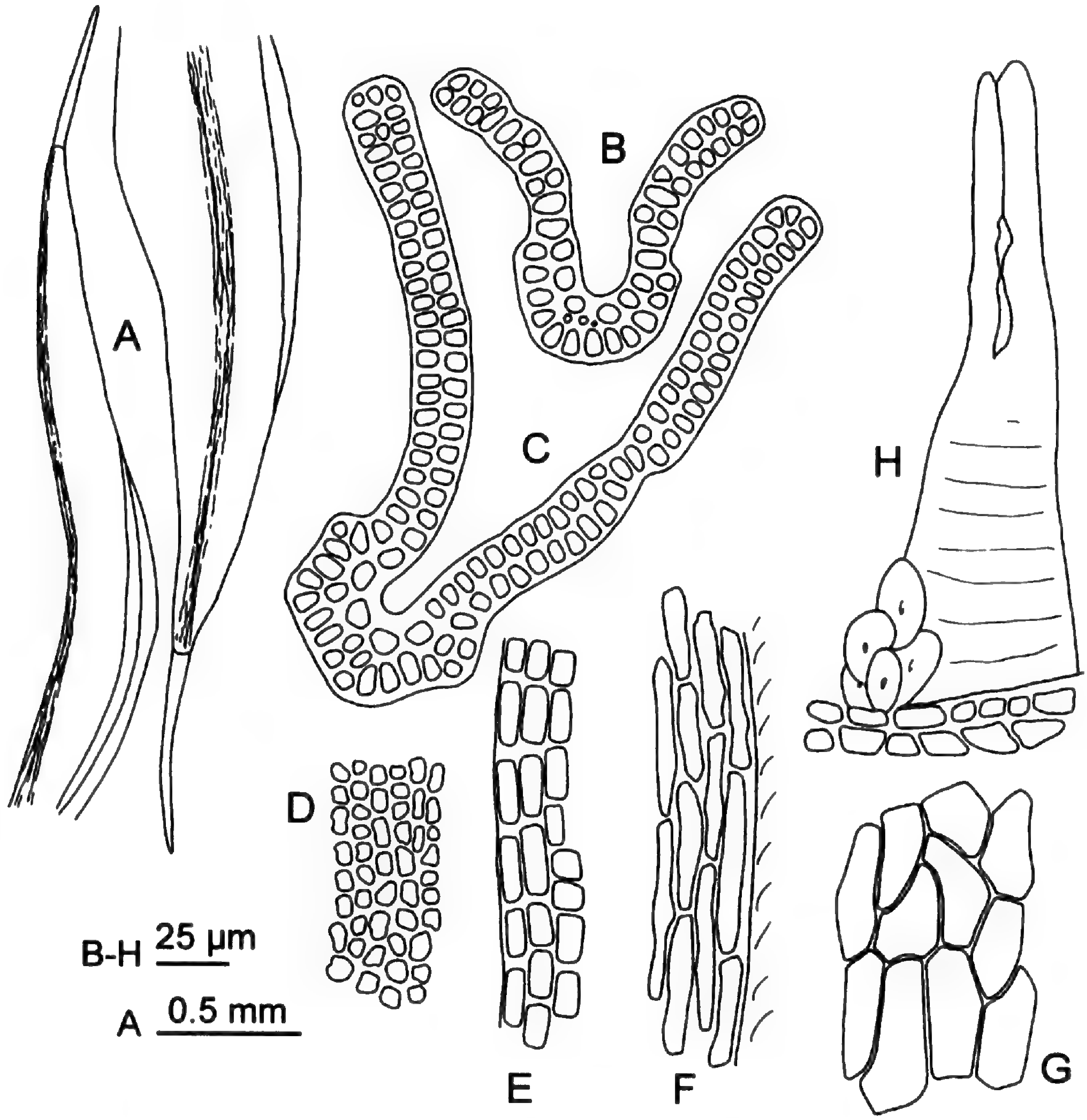

Figure 22. *Grimmia longirostris.* —A. Leaves. —B, C. Transverse sections at distal and medial parts of leaf. —D. Distal leaf cells. —E. Proximal marginal leaf cells. —F. Proximal juxtacostal leaf cells. —G. Medial exothecial cells. —H. Peristome tooth and annulus (only contour shown, not papillosity). (*Sharp 1833,* TENN.)

finis); Deguchi (1978: figs. 12, 13; 1984: fig. 6; 1987: pl. 4, 5, as *G. herzogii,* pl. 6, 7); Eddy (1990: fig. 313, as *G. affinis*); Herzog (1916: fig. 17, as *G. nigella*); Ignatov and Cao (1994: fig. 7, as *G. affinis*); Ireland (1982: pl. 134, as *G. affinis*); Jóhannsson (1993: fig. 36, as *G. affinis*); Maier and Geissler (1995: fig. 1, as *G. affinis*); Muñoz (1998c: fig. 1); Noguchi (1988: fig. 140 A, as *G. affinis*).

Distribution (Fig. 23). Europe, Africa, temperate and tropical Asia, Australasia, northern and southern America; Mexico, Mesoamerica, Caribbean, Andean Range from Venezuela to northern Argentina, central Argentina, southeast Brazil, Tierra del Fuego. On any kind of rock, from acidic to ultrabasic, seldom on bark. Forests and open areas, between 1800 and 5300 m elevation.

Grimmia longirostris has canaliculate leaves that are distally flattened when dry. At least one of the leaf margins is recurved proximally. The costae are reniform in cross section, and the ventral epidermis consists of 2 to 6 cells. Along with long-rectangular, nodulose, proximal juxtacostal cells, and an *affinis*-type annulus, those characters are stenotypic, separating *G. longirostris* from every other taxon in the genus. The species is widespread, and is also morphologically variable. The setae are erect and straight, although one Philippine specimen (Luzón, *Tan 82-195,* FH) was observed with arcuate setae. Setae vary

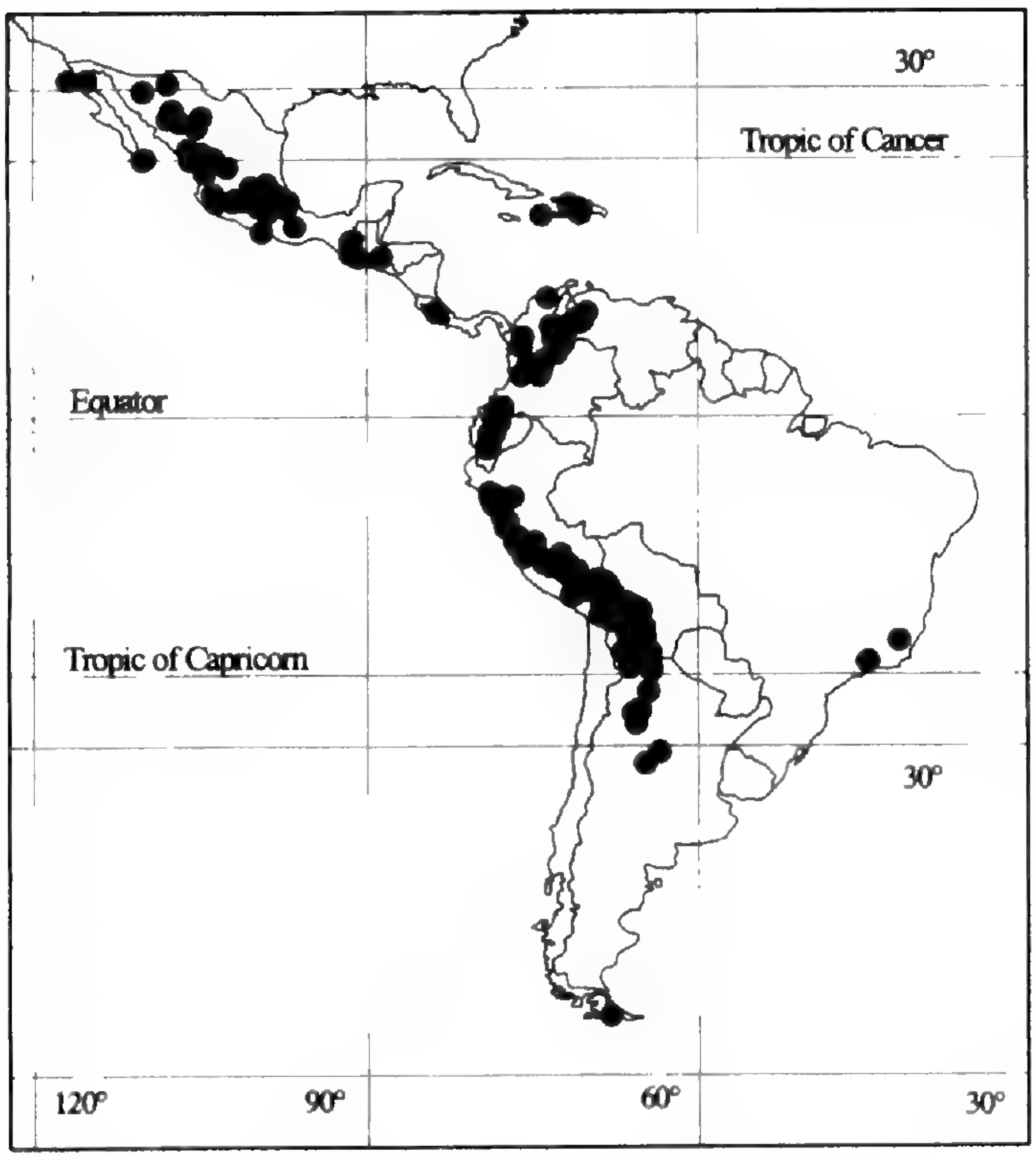

Figure 23. Distribution of *Grimmia longirostris.*

broadly in length, from 1 to 4 mm, and consequently the capsules range from immersed to long-exserted. Operculum shape is quite variable, as has been illustrated by Cao and Vitt (1986: fig. 2). The taxonomy and distribution of *Grimmia longirostris* have been studied by Muñoz (1998c), placing 55 validly published names into synonymy for this taxon.

Selected specimens examined. COSTA RICA. **Cartago**: near summit of Inter American Highway at La Ascensión, *Crosby & Crosby 6137* (MO). **San José**: summit of Pan-American Hwy. at Cerro de la Muerte, *Crosby 3917* (TENN). DOMINICAN REPUBLIC. **Azua**: Cordillera Central, Los Vallecitos del Yaque, *Ekman 13630* (PC). **La Vega**: 6.3 km S of Valle Nuevo, *Steere 23052* (G). **San Juan**: summit of Pico Duarte, *Buck 8396* (NY). GUATEMALA. **Huehuetenango**: near Paquix above Huehuetenango, *Sharp 4777* (TENN). **Quezaltenango**: Cerro La Pedrera, S of Quezaltenango, *Standley 65530* (FH). **Sacatepéquez**: slopes of Volcán de Agua, above Santa María de Jesús, *Standley 65262* (FH). **Totonicapán**: entre Las Trojadas y Empuxet, *Smith 780* (F). HONDURAS. **Lempira**: Montaña Celaque, summit of Cerro Mojón, *Allen 12260* (MO). MEXICO. **Distrito Federal**: Ajusco, *Orcutt 5353* (FH). **Baja California**: Lomas de San Pedro Mártir, ca. 41 km SW of Observatory, *Meyer 21A* (TENN). **Baja California Sur**: Sierra de La Laguna, 15 mi. E of Todos los Santos, *Bowers et al. 5205A* (TENN). **Chihuahua**: 21 mi. N of San Juanito, *Bowers et al. 5403* (TENN); Ejido de Bocoyna, SW part of Creel Valley, *Bye 7295* (TENN). **Distrito Federal**: 12 km W de San Miguel Ajusco, 15 Aug. 1985, *Cárdenas s.n.* (ALTA). **Durango**: below El Salto, *Sharp 1833* (FH). **Guanajuato**: 4 km S de San José Iturbide, *Cárdenas S. 5344* (MO). **Hidalgo**: 14 km E de Pachuquilla, carretera Pachuca–Tulancingo, 14 Feb. 1984, *Cárdenas 3378* (ALTA). **Jalisco**: ladera N del Nevado de Colima, 27 July 1983, *Delgadillo s.n.* (ALTA). **México**: volcán de Toluca, *Pringle 26A* (JE). **Michoacán**: Paracho, about 6 km N on way to Cheran, *Frey & Frey 3072* (FH, UC). **Nayarit**: Acaponeta, 4 mi. E of La Ciénaga on ridge about 5 mi. NW of Mesa de Nayar, *Norris & Taranto 14330* (UC). **Oaxaca**: 13 km E of La Cumbre pass between Oaxaca and Ixtlán de Juárez, *Sharp et al. 2607* (TENN). **Puebla**: ladera NW del Pico de Orizaba, 22 Apr. 1980, *Delgadillo s.n.* (ALTA). **Sinaloa**: along Hwy. 40, about 2 mi. E of Las Palmitas, *Norris et al. 20567* (H, UC); 11 mi. NE of Baviácora, *Richards et al. 675* (TENN). **Veracruz**: cima del Cofre de Perote, 7 Dec. 1979, *Delgadillo s.n.* (ALTA).

ARGENTINA. **Córdoba**: Depto. Punilla, Sierra Grande de Córdoba, Pampa de Achala, südl. La Posta, *Hosseus 207* (FH, PC). **Jujuy**: Cochinoca, 1.5 km W of the top of Abra Rechaite, *Taylor 11268* (IBA). **Salta**: Nevado de Castillo prope Salta, 1881, *Lorentz s.n.* (BM, JE). **Santa Cruz**: Lac Cami, baie de la Chaloupe, *Skottsberg 370* (PC). **Tucumán**: in alpinis prope Ciénaga, 1871, *Lorentz s.n.* (JE, PC). BOLIVIA. **Chuquisaca**: prov. Yamparaez, Tarabuco, *Lewis 83-1661* (F, MO). **Cochabamba**: NW slope of Mt. Tunari, near Liriuni Aguas Termales Hotel, *Hermann 25149* (ALTA, MO). **La Paz**: Loayza, río Atoroma Chuma (Glacier Camp), *Lewis 87-1908* (MO); Murillo, Lago Choquecota, *Asplund 13* (JE); Omasuyos, vicinitis Achacache, *Mandon 1635* (BM); Pacajes, Estación General Campero, *Asplund 53* (JE); Saavedra, trail between Charasani and Niño Karine, NNW of Chuma, *Lewis 79-946* (F). **Oruro**: Carangas, Cerro Lajama, *Asplund 75* (JE). **Potosí**: Tomás Frías, Cerro Kari Kari, SE de Potosí, *Lewis 79-214* (FH, MO, UBC). **Tarija**: Méndez, 5 mi. NE of Iscyachi, *Lewis 79-691* (F). BRAZIL. **Espírito Santo**: National park Serra de Caparaó, *Schäfer-Verwimp & Verwimp 11500* (FLAS). **Minas Gerais**: Serra do Itatiaia, Mar. 1894, *Ule s.n.* (GOET, H-BR, PC, UPS). **Rio de Janeiro**: Serra do Itatiaia, Pico das Agulhas Negras, *Vitt 21541* (FLAS). CHILE. **Magallanes**: Porvenir, *Dusén 113* (PC). COLOMBIA. **Antioquia**: Urrao, Páramo de Frontino, ca. 17 km N of Urrao, *Churchill 13335* (ALTA, UC). **Boyacá**: Valle de las Playas, Sierra Nevada de Cocuy, *Grubb & Guymer B.216-A* (BM). **Cundinamarca**: from Bogotá (vía La Calera) to Mundo Nuevo, Cordillera Oriental, *Steere 7713* (IBA). **Magdalena**: Sierra Nevada de Santa Marta, *Mägdefrau 1187* (COL). **Nariño**: Carchi, just N of Bolívar, Interandean Valley, *Steere 9498* (IBA). **Risaralda**: Pereira, Nevado de Santa Isabel, *Reenen 582* (FLAS). **Santander**: Páramo Frailejonale, near Vetas, *Killip & Smith 17987* (BM, FH). ECUADOR. **Azuay**: Area Nacional de Recreación "Cajas," WNW of Sayausí, *Lewis 78-2336* (F-1064894). **Bolívar**: Guaranda, río Salinas, *Acosta Solís 5858* (MO). **Chimborazo**: NW Seite, Paramo-region, *Meyer 5518* (JE). **Cotopaxi**: Parque Nacional Cotopaxi, *Raeymaekers 1013* (FLAS). **Imbabura**: E side of Cerro Cotacachi, NW of Cotacachi, *Lewis 78-2675* (F). **Napo**: Cerro Antisana, near the main western glacier at Antisana, 1960, *Grubb 2500* (FH). **Pichincha**: Pichincha, *Spruce s.n.* (FH-SULL). **Tungurahua**: El Altar, Paramoregion, *Meyer 5435* (JE). PERU. **Ancash**: Huaraz, Monterrey bei Huaraz, *Hegewald & Hegewald 7482* (MO). **Apurimac**: Andahuaylas, Pampa Runtojoch bei Chincheros, *Hegewald & Hegewald 5761* (MO). **Arequipa**: Sumbay, 16 Aug. 1939, *Schmidt s.n.* (F). **Ayacucho**: Huamanga, Pass Huamina zw. Andahuaylas und Ayacucho, *Hegewald & Hegewald 8993* (MO). **Cajamarca**: Contumazá, 2 km südlich Contumazá, *Hegewald & Hegewald 7280* (MO). **Cuzco**: Calca, Pisaja, *Vargas 7099* (FH). **Huancavelica**: Tayacaja, Quebrada Pucayacu zw. Ayacucho u. Huancayo, *Hegewald & Hegewald 9125* (IBA, MO). **Junín**: Tarma, Río Yanamayo hinter Palca zw. Tarma u. San Ramón, *Hegewald & Hegewald 8377* (IBA, MO). **La Libertad**: Otuzco, Huancamarca, Quebrada Hornillo, *Hegewald & Hegewald 5156* (MO). **Lima**: Canta Province, 2 km vor Canta an der Straße nach Lima, *Hegewald & Hegewald 7425* (MO). **Pasco**: from Cerro de Pasco to Lima, *Vitt 21717* (FLAS). **Puno**: San Román, Panamericana zw. Laguna Maquera u. Laguna La Calzada, *Hegewald & Hegewald 8586* (IBA, MO). **San Martín**: prov. Marical Cáceres, Pampa del Cuy, *B. León & K. Young 2118* (FLAS). VENEZUELA. **Barinas**: páramo de Santo Cristo, *Griffin III & Díaz M. PV-119* (FLAS). **Mérida**: Cañada Cerrada above Cachopo, *Pittier 13183* (NY); Distr. Libertador, Sierra Nevada de Mérida, near Laguna de Los Anteojos just below the loma R, *Griffin III et al. 398* (ALTA, MO, NY); Distr. Rangel, páramo de Piedras Blancas, *Griffin III et al. 1451* (FLAS); Distr. Rivas Dávila, páramo La Negra, above the town of Bailadores, *Griffin III et al. 2047* (ALTA, MO, NY). **Trujillo**: Distr. Carache, páramo El Jabón, *Griffin III & López PV-1360* (FLAS).

15. Grimmia molesta J. Muñoz, sp. nov. TYPE: Peru. Arequipa: Arequipa, am Weg nach Puno, *Hegewald & Hegewald 5480* (holotype, MO; isotypes, H, IBA, NY).

A *G. pseudoanodon* foliis bistratosis margineque recurvatis atque peristomio exsistenti dignoscitur.

Cladautoicous. Plants olive-green to brownish. *Stems* erect, to 2 cm, with central strand. *Leaves* erect and appressed when dry, erect to patent when moist, 1.6–1.9 × 0.4–0.5 mm, lanceolate, acuminate, keeled, not plicate; *margins* recurved proximally, to ⅓ the leaf length on one side, occasionally recurved only in the middle part of the leaf; *costa* semi-terete, differentiated, ventral epidermis 2 cells wide in cross section; *lamina* 2-stratose in the distal ⅔; *distal cells* 8–15 μm long, isodiametric, rectangular and oblate, not bulging, walls straight to slightly sinuous; *proximal juxtacostal cells* 30–60 × 15–20 μm, rectangular (1.5–3.0 : 1), walls medium-thick to thick, nodulose; *proximal marginal cells* 15–55 × 10–12 μm, rectangular (1.5–5.0 : 1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete, straight to flexuous, to 1 mm, denticulate. *Perichaetial leaves* 3.0–3.5 × ca. 1 mm, convolute and larger than vegetative leaves (4 ×). *Androecia* terminal. *Setae* straight, 0.6–0.8 mm long. *Capsules* immersed, cylindrical, symmetric, smooth, stramineous, with stomata at the base; *exothecial cells* 35–80 × 13–30 μm, rectangular (2–4 : 1), thin-walled; *annulus* compound and revoluble, *elongata* type; *peristome teeth* 70–90 μm wide at the mouth, cribrose throughout and irregularly cleft at apex, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, orange, contrasting with the urn; *opercula* mammillate to rostellate; *calyptrae* mitrate; *spores* 10–12 μm, minutely granulose.

Illustration. Figure 24.

Distribution (Fig. 10). Southern America. Known only from the type collection in Arequipa (Peru), where it grows on rocks at 4000 m elevation.

Grimmia molesta has lanceolate, bistratose leaves with recurved margins, short straight setae, and immersed peristomate capsules with a compound and revoluble annulus. The male buds arise at the ends of branches separated from perichaetia.

Deguchi (1987: 29) considered *Hegewald & Hegewald 5480* to be *G. pseudoanodon.* However, the specimen in MO (Hegewald's original herbarium) contains no material of this species. *Grimmia pseudoanodon* differs from *G. molesta* in having unistratose leaves with plane margins and gymnostomous capsules.

Etymology. Molesta: burdensome, annoying, irksome.

Specimens examined. PERU. **Arequipa**: Arequipa, am Weg nach Puno, *Hegewald & Hegewald 5480* (H, IBA, MO, NY).

16. Grimmia montana Bruch & Schimp., Bryol. Europ. (fasc. 25–28) 3: 128, tab. 250. 1845. TYPE: [Germany. Rhineland-Palatinate:] Donnersberg, Apr. 1843, *Gümbel s.n.* (lectotype, designated by Cao & Vitt (1986), BM).

Grimmia laxa Müll. Hal., Bot. Zeitung (Berlin) 5: 801. 1847. *Guembelia laxa* (Müll. Hal.) Müll. Hal., Syn. Musc. Frond. 1: 771. 1849. TYPE: Mexico. In monte Orizabae, *Deppe & Schiede s.n.* (lectotype, designated by Muñoz (1998d), PC).

Grimmia schiedeana Müll. Hal., Bot. Zeitung (Berlin) 13: 765. 1855. TYPE: Mexico: [no locality given] *Deppe & Schiede s.n.* (lectotype, here designated, BM; isolectotype, PC).

Grimmia arctophila Kindb., Rev. Bryol. 23: 18. 1896. TYPE: Greenland. Claushavn, 1870, *Berggren s.n.* (lectotype, here designated, S).

For additional synonyms, see Muñoz (1998d).

Dioicous. Plants olive-green above, dark green or blackish below. *Stems* erect, to 1 cm, with central strand. *Leaves* erect, loosely appressed and flexuous when dry, with patent proximal part and incurved apex, sigmoid in lateral view when moist, 1–2 × 0.3–0.6 mm, lanceolate, acuminate, keeled, not plicate; *margins* plane proximally and incurved distally; *costa* semi-terete, slightly to clearly differentiated, ventral epidermis 2 cells wide in cross section; *lamina* 2(3–4)-stratose in the distal ⅔; *distal cells* 4–8 μm long, isodiametric, not bulging or bulging weakly on the dorsal surface, walls straight

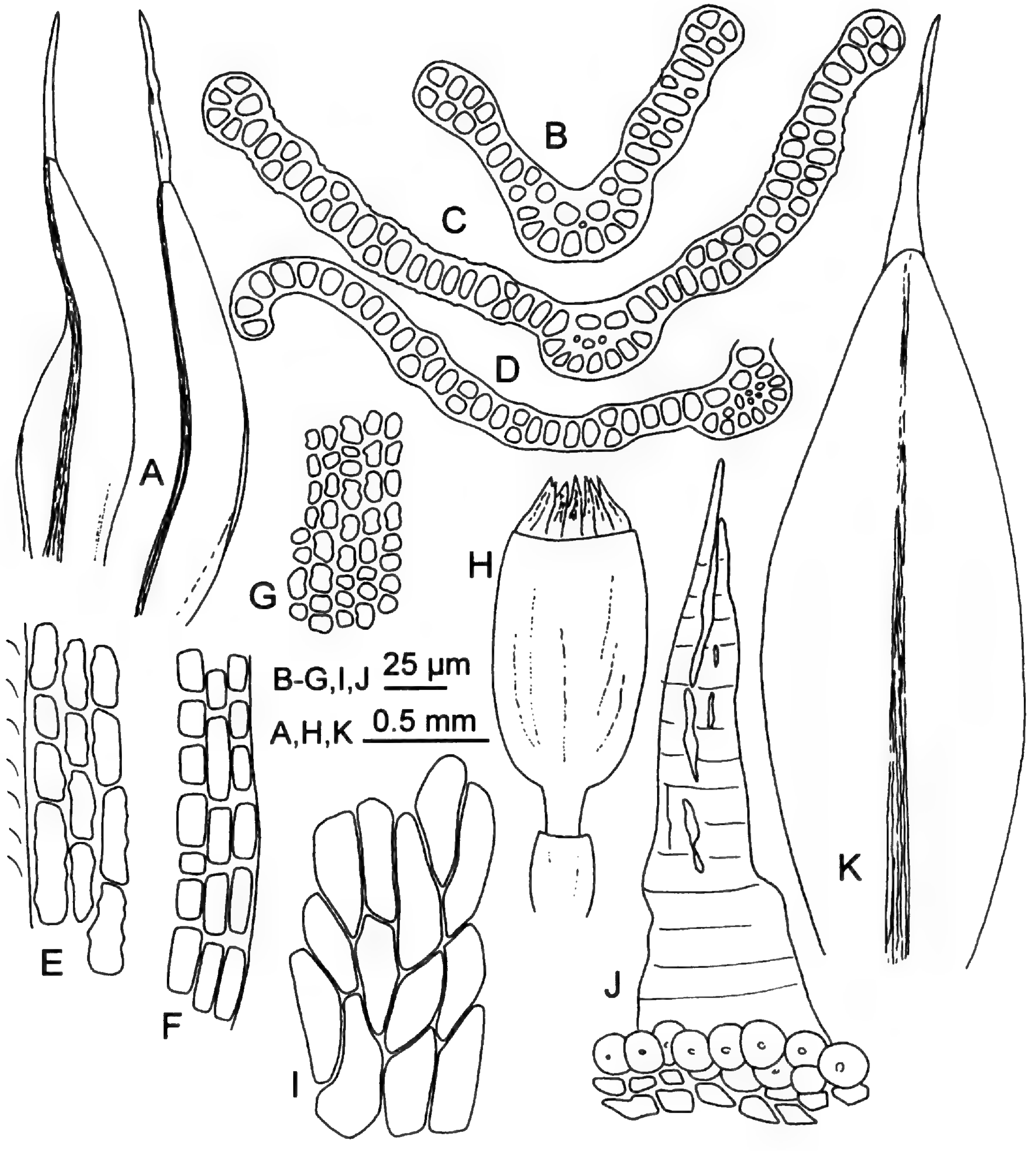

Figure 24. *Grimmia molesta.* —A. Leaves. —B–D. Transverse sections at distal, medial, and proximal parts of leaf. —E. Basal juxtacostal leaf cells. —F. Basal marginal leaf cells. —G. Distal leaf cells. —H. Capsule. —I. Medial exothecial cells. —J. Peristome tooth and annulus (only contour shown, not papillosity). —K. Perichaetial leaf. (*Hegewald & Hegewald 5480,* MO.)

to slightly sinuous; *proximal juxtacostal cells* 20–50 × 8–15 µm, rectangular (2.0–4.5 : 1), walls medium-thick and straight; *proximal marginal cells* 20–50 × 8–15 µm, rectangular (2.0–4.5 : 1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete, straight, to 1.5 mm, obtusely denticulate, seldom serrate. *Perichaetial leaves* 1.7–2.4(4) × 0.6–0.9 mm, convolute and larger than vegetative leaves (2–4 ×). *Androecia* terminal. *Setae* erect and straight, 2–4 mm long. *Capsules* exserted, ovoid or ellipsoid, symmetric, smooth, castaneous, lacking stomata; *exothecial cells* 30–70 × 10–25 µm, rectangular (2–4 : 1), thin-walled; *annulus* simple and persistent, *Schistidium* type; *peristome teeth* 50–90 µm wide at the mouth, cribrose throughout and irregularly cleft at apex, external surface nearly smooth proximally and papillose distally, internal surface papillose

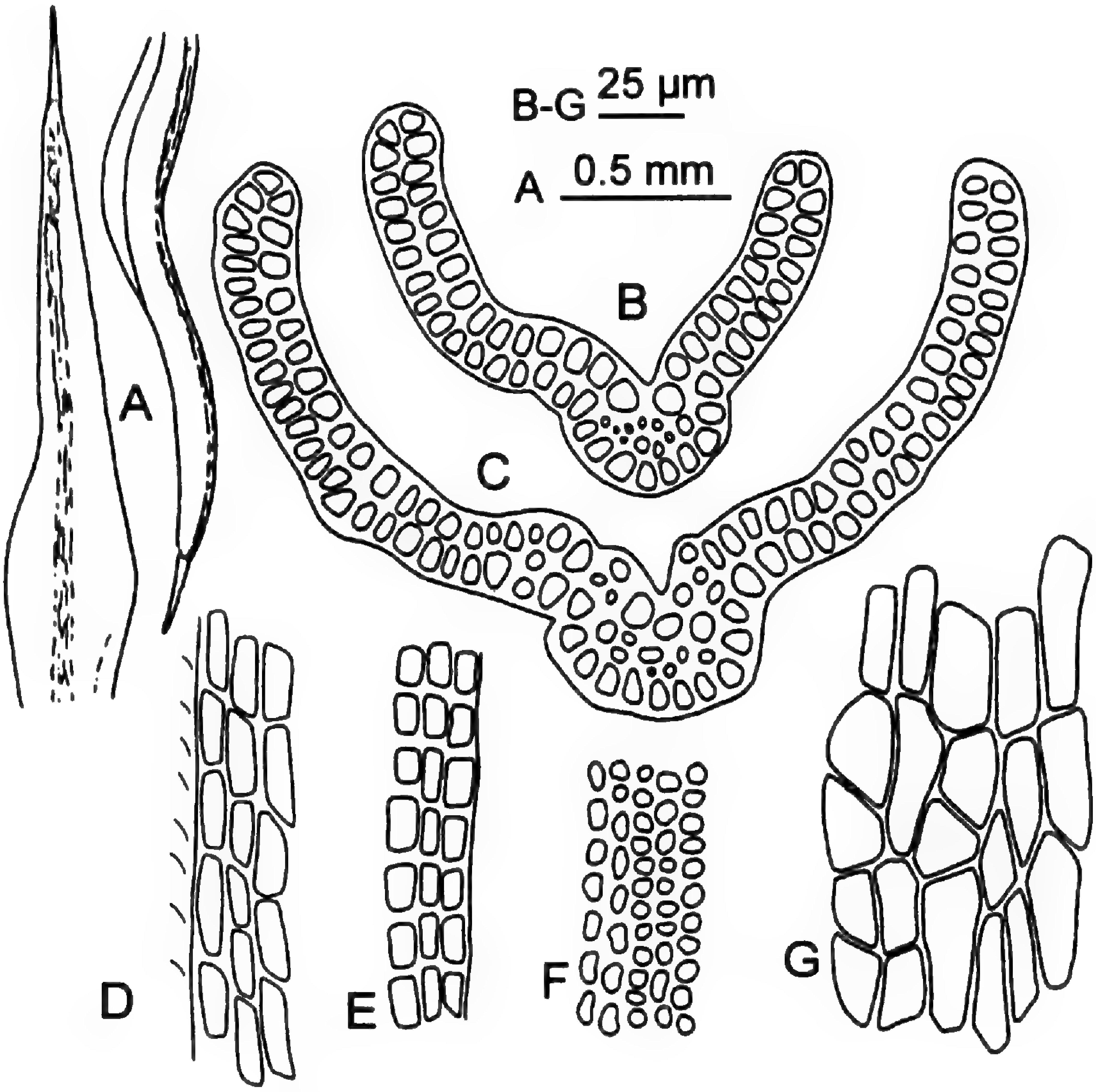

Figure 25. *Grimmia montana.* —A. Leaves. —B, C. Transverse sections at medial and proximal parts of leaf. —D. Proximal juxtacostal leaf cells. —E. Proximal marginal leaf cells. —F. Distal leaf cells. —G. Medial exothecial cells. (*Vitt 17520,* TENN.)

throughout, castaneous, concolorous with the urn; *opercula* rostrate, the beak oblique; *calyptrae* cucullate; *spores* 10–14 µm, minutely granulose.

Illustrations. Figure 25; Bruch and Schimper (1845: tab. 250); Chałubiński (1882: tab. 8 fig. 14); Jóhannsson (1993: fig. 26); Maier and Geissler (1995: fig. 17); Muñoz (1998d: fig. 12); Nyholm (1956: fig. 69 B).

Distribution (Fig. 26). Europe, northern America. *Grimmia montana* is common in western Europe and western North America. In the area here covered it is known only from Mexico, where it has been collected on igneous rocks in open pine forests and in subalpine areas above the tree line, between 2250 and 4800 m elevation.

Grimmia montana has keeled, bistratose or thicker leaves and rostrate opercula. The species is dioicous, and the capsules lack stomata. In leaf morphology and anatomy it is almost inseparable from *G. ungeri.* However, *G. ungeri* is an autoicous species with mammillate to rostellate opercula. Another useful character is the length of the setae. Setae are longer in *G. montana* (2–4 mm) than they are in *G. ungeri* (less than 2 mm). Unfortunately, the autoicous condition of the latter is usually difficult to demonstrate, and poor specimens are generally impossible to name with confidence.

The variability of *G. montana* and its relationships with other species of *Grimmia* subg. *Orthogrimmia* have been studied by Muñoz (1998d). The Mexican specimens have, like other American or northern European ones, a relatively short leaf acumen. Otherwise they fall in the expected range of variation for the species.

For the differences between *G. montana* and *G. reflexidens,* see the latter species.

Additional specimens examined. MEXICO. **Baja California**: Guadalupe Island, summit, *Moran 5664* (FH); National Park, San Pedro Mártir Mts., *Hammond 10837* (NY); Sierra de San Pedro Mártir, Cerro de la Encantada, pass below observatory, *Sharp et al. 5594* (TENN), *5663A*

Figure 26. Distribution of: ● *Grimmia montana*; ▲ *Grimmia navicularis*.

(TENN), *5668* (TENN), *5671* (TENN), *6055* (TENN). **México**: Popocatépetl, *Sharp 4749* (TENN). **Puebla**: Mt. Ixtaccíhuatl, *Hermann 20845* (TENN), *Kiener 18518* (FH), *18518B* (FH), *Vitt 17520* (ALTA, TENN); above Huejotzingo, *Sharp 4289* (TENN); ladera SW del pico Orizaba, *Delgadillo 4117* (ALTA). **Veracruz**: monte Orizaba, *Little 1* (TENN), *Smith s.n.* (FH), *Purpus 4277* (F, PC); road from Perote to the Cofre, *Sharp et al. 71646* (TENN).

17. Grimmia navicularis Herzog, Beih. Bot. Centralbl. 26: 65. 1909. TYPE: Bolivia. Cochabamba: Abra de San Benito, Jan. 1908, *Herzog s.n.* (lectotype, designated by Deguchi (1987), JE; syntypes, [Cochabamba: über dem Tunarisee, Jan. 1908, *Herzog s.n.*], JE, PC).

Grimmia chilensis Thér., in Herzog, Darwiniana 11: 217. 1957. TYPE: [Argentina. Río Negro:] Parque Nacional Argentino Nahuelhuapi, Cerro López, *Donat 114* (lectotype, here designated, JE; isolectotype, JE).

Dioicous. Plants olive-green to reddish green. *Stems* erect, to 1 cm, with central strand. *Leaves* erect and appressed when dry, erect when moist, 1.0–1.8 × 0.3–0.4 mm, lanceolate, acute, keeled, not plicate; *margins* recurved proximally, to ½–⅔ the leaf length on one side and flat or more narrowly recurved proximally, to ⅓–½ the leaf length on the other side, occasionally both margins plane; *costa* semi-terete, differentiated, ventral epidermis 2 cells wide in cross section; *lamina* 1–2-stratose, 2-stratose at margins and in streaks in the distal ⅔; *distal cells* 7–13 μm long, isodiametric to rectangular, not bulging, walls sinuous; *proximal juxtacostal cells* 30–60 × 10–14 μm, rectangular (2–4:1), walls thin and straight to medium-thick and nodulose; *proximal marginal cells* 15–50 × 7–12 μm, rectangular (2–5:1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete, flexuous, but straight if short, to 1 mm, denticulate. *Perichaetial leaves* 2.5–3.5 × 0.7–0.8 mm, convolute and larger than vegetative leaves (2–4 ×). *Androecia* terminal. *Setae* curved, 2.3–3.2 mm long. *Capsules* exserted, ellipsoid, symmetric to slightly asymmetric at base, smooth, stramineous, with stomata at the base; *exothecial cells* 25–65 × 12–30 μm, oblong (2–5:1), somewhat collenchymatous, thin-walled; *annulus* compound and revoluble, *elongata* type; *peristome teeth* 60–75 μm wide at the mouth, entire, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, orange, contrasting with the urn; *opercula* conic to short-rostrate; *calyptrae* cucullate; *spores* 9–13 μm, minutely granulose.

Illustrations. Figure 27; Deguchi (1984: fig. 2, as *G. chilensis*; 1987: pl. 8, 9).

Distribution (Fig. 26). Southern America; Andean Range between Venezuela and Patagonia. *Grimmia navicularis* grows on rocks in open grassy areas above the tree line between 1500 and 5300 m elevation.

Grimmia navicularis has lanceolate leaves with recurved margins and proximal marginal cells with transverse walls thicker than the longitudinal ones. The sporophytes, which are not common, are characterized by the curved setae and the smooth capsules occasionally weakly asymmetric at the base. At high elevations, filiform shoots arising from basal stems are commonly found. These shoots have small, tightly appressed, ovate leaves that are muticous and mucronate, appearing very different from normal vegetative leaves.

Grimmia navicularis is gametophytically similar to *G. elongata* in that both are usually reddish, with strongly keeled leaves. Hair-points are longer in *G. navicularis*, to 1 mm, and the proximal marginal cells have the transverse walls thicker than the longitudinal walls. Hair-points are seldom longer than 0.3 mm in *G. elongata*, and the walls of the proximal marginal cells are thin with wall diameters similar. If fertile, both taxa can be readily separated: *G. navicularis* has curved setae whereas those of *G. elongata* are straight.

Additional specimens examined. ARGENTINA. **Río Negro**: Parque Nacional Argentino Nahuel-Huapi, Tronador, *Donat 175* (JE, PC); Puerto Moreno, 12 July 1897,

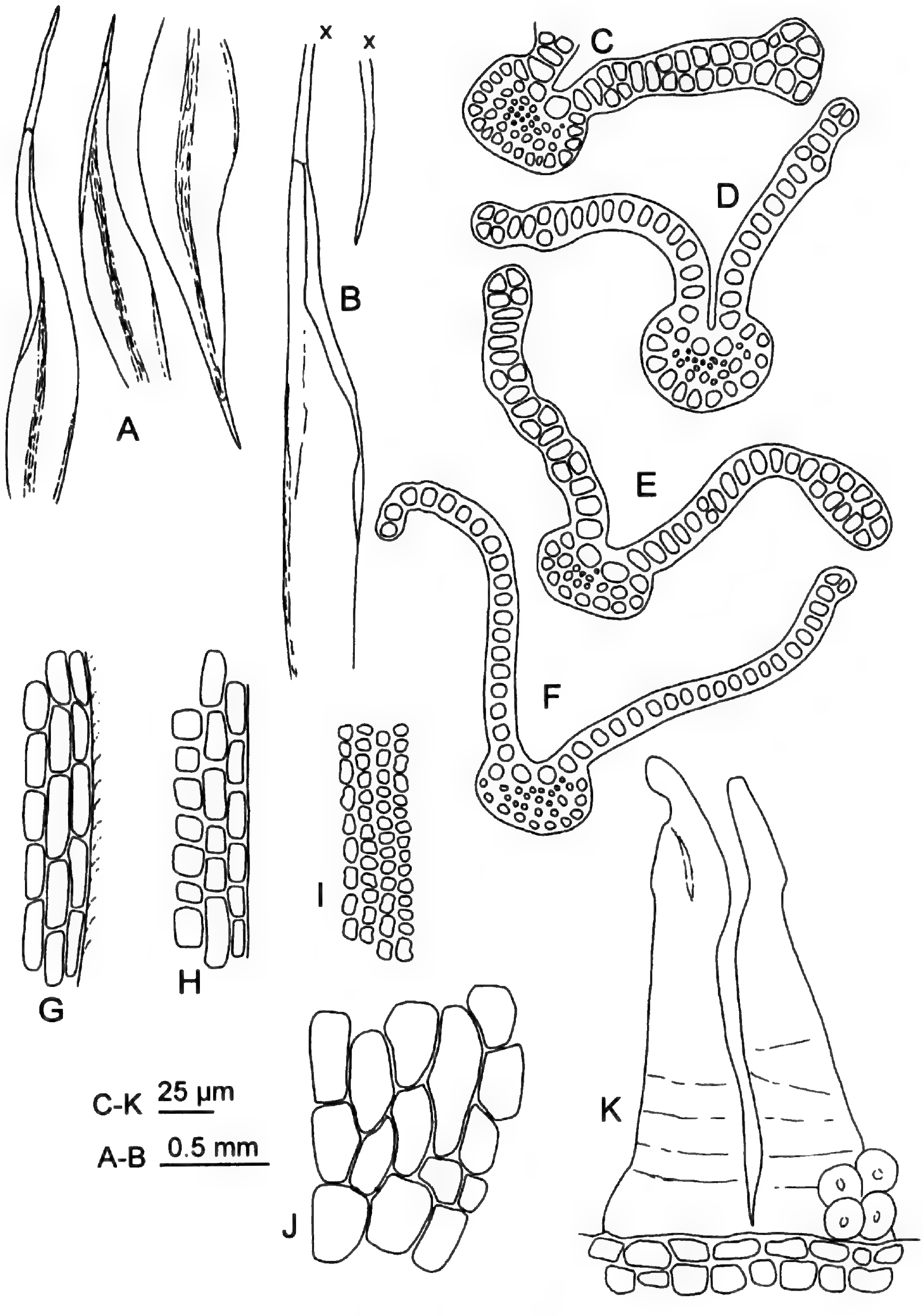

Figure 27. *Grimmia navicularis.* —A. Leaves. —B. Perichaetial leaf. —C, D. Transverse sections at distal part of leaf. —E, F. Transverse sections at medial and proximal parts of leaf. —G. Proximal juxtacostal leaf cells. —H. Proximal marginal leaf cells. —I. Distal leaf cells. —J. Medial exothecial cells. —K. Peristome teeth and annulus (only contour shown, not papillosity). (A, B, D, G–K: *Donat 175*, PC; C, E, F: *Herzog s.n.*, JE.)

Dusén s.n. (PC). BOLIVIA. **Cochabamba**: Abra de San Benito, Jan. 1908, *Herzog s.n.* (JE); über dem Tunarisee, *Herzog s.n.* (JE), *306* (JE), *4913* (JE). **La Paz**: Huallata pass, *Williams 1781* (F); prov. Inquisivi, Mina Poldi, *Lewis 87-875* (MO); Cumbre Sayaquira, *Lewis 87335* (CAS); prov. Loayza, 11 km SE from Viloco, *Lewis 87-1819* (MO), *Herzog 3146A* (JE); Yanakakaberge, July 1911, *Herzog s.n.* (BM); bei der Saittulaguna, *Herzog 2675* (JE); prov. Los Andes, Cerro Jankho Karka, *Lewis 84-199* (F, IBA), *83-209* (F, IBA); prov. Murillo, 5 km NE of Milluni, *Lewis 79-1728B* (F, IBA), *79-1731* (F). **Potosí**: above Solapampa, *Williams 1782* (F); prov. Quijarro, cerro Purgatorio Mundo, SW of Estación Yura, *Lewis 79-368* (F). COLOMBIA. **Boyacá**: Municipio Güicón, Sierra Nevada del Cocuy, sitio Las Cabañas, carretera Güicón–Cubara, *Escobar & Santa 403* (MO), *404* (IBA, MO, NY); páramo de La Rusia, *Cleef 6965* (FLAS); farm Ritacuva, *Grubb & Guymer B.68* (FH). ECUADOR: **Chimborazo**: Paramo-region, NNW Seite, July 1903, *Meyer 5478* (H), *5500* (H), *5510* (H), *5511* (H), *5512* (H), *5513* (H), *5514* (H), *5515* (H), *5516* (H), *5517* (H), *5519* (H), *5522* (H), *5531* (H). PERU. **Ancash**: Huari, zwischen Tunnel Cahuish und Chavín, quebrada Pucavado, *Hegewald & Hegewald 7718* (IBA, MO), *7798A* (MO); Ostseite des Tunnel Cahuish, *Hegewald & Hegewald 7697* (IBA, MO); Cordillera Blanca, Parque Nacional Huascarán, Laguna Llanganuco, *Frahm 824071* (IBA). **Junín**: Jauja, La Oroya, bei der laguna Añascocha bei Canchayllo, *Hegewald & Hegewald 5427* (MO). **La Libertad**: Santiago de Chuco, Pampas de Julia bei Quiruvilca, *Hegewald 6001* (MO). **Puno**: Melgar, 7 km W of La Raya Pass, *Hegewald & Hegewald 5512A* (MO), *5526A* (MO). VENEZUELA. **Mérida**: distr. Miranda, above pico El Águila, *Griffin III et al. 1318* (FLAS); distr. Rangel, páramo de Piedras Blancas, *Griffin III et al. 1444* (FLAS), *1485* (FLAS), *1494* (FLAS), *1495* (FLAS).

18. **Grimmia ochyriana** J. Muñoz, Nova Hedwigia 66: 235. 1998. TYPE: Nepal. Près du Camp de Base, direction de Lobuje, *Zimmermann 558* (holotype, G; isotype, IBA).

Dioicous. Plants yellowish to brownish green, glossy. *Stems* erect, to 3 cm, with central strand. *Leaves* erect and appressed, flexuous apically when dry, patent to spreading when moist, 2–3 × 0.5–0.7 mm, lingulate-lanceolate, acuminate, canaliculate, not plicate; *margins* recurved proximally, to ½ the leaf length on one side and flat on the other side, occasionally only shortly and narrowly recurved proximally, in the middle of one side; *costa* reniform, differentiated, ventral epidermis 6–8 cells wide in cross section; *lamina* 2-stratose in the distal ⅔; *distal cells* 5–16 µm long, isodiametric to rectangular, not bulging, walls sinuous; *proximal juxtacostal cells* 25–80 × 6–12 µm, rectangular (2–10 : 1), walls thin and straight to medium-thick and nodulose; *proximal marginal cells* 10–30 × 10–16 µm, isodiametric to rectangular (1–3 : 1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* lacking. *Perichaetial leaves* 4.0–5.5 × 0.6–1.2 mm, convolute and larger than vegetative leaves (3–5 ×). *Androecia* terminal. *Setae* erect and straight, 1.5–2.1 mm long. *Capsules* immersed, ovoid, symmetric, smooth, stramineous, with stomata at the base; *exothecial cells* 24–50 × 15–35 µm, isodiametric to oblong (1.0–3.5 : 1), somewhat collenchymatous, thin-walled; *annulus* compound and revoluble, *elongata* type; *peristome teeth* 60–80 µm wide at the mouth, entire, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, yellowish orange, contrasting with the urn; *opercula* rostellate to rostrate; *calyptrae* mitrate; *spores* 10–16 µm, minutely granulose.

Illustrations. Figure 28; Muñoz (1998a: figs. 1–11).

Distribution (Fig. 29). Tropical Asia, northern America; Mexico, Guatemala. Previously known only from the type locality in Nepal, the species seems not to be rare in Mexico. It grows on igneous rocks, either granite and basalt, between grasses in open areas above the tree line, mainly in places with melting water, between 3700 and 4200 m elevation.

Grimmia ochyriana has muticous, glossy leaves 2(3 to 4)-stratose in thickness. The costa is 7 to 8 cells wide in the ventral epidermis, and reniform in cross section. The most striking characteristics are the length of the muticous perichaetial leaves and its immersed capsules. Although not always found with capsules, the easily recognizable perichaetial leaves are conspicuously longer than other leaves, even at very early stages of perichaetial development.

The only other species with muticous leaves and wide costae in the study area is *G. atrata.* Known only from Bolivia to date, it could be also found at high elevations in Mexico. *Grimmia atrata* differs from *G. ochyriana* in the bistratose proximal alar regions of the leaves, the perichaetial leaves that are undifferentiated, as well as the exserted capsules on long setae.

Additional specimens examined. GUATEMALA. **San Marcos**: near summit of Tajamulco, *Sharp 5428* (TENN); upper slopes of Volcán Tacaná, *Steyermark 36091A* (FH). MEXICO. **México**: Mt. Popocatépetl, *Kiener 18554A* (TENN, FH), *18591BA* (FH), *Sharp 4753* (TENN), *4747* (TENN), *Horton 7463* (TENN), *Vitt 17488* (ALTA, TENN); Nevado de Toluca, *Iltis & Iltis 2128* (TENN), *3128A* (TENN), *Horton 7837, 7890A* (TENN). **Puebla**: Mt. Ixtaccíhuatl, *Kiener 18518C* (FH); Las Cuevas on Ixtaccíhuatl above Huejotzingo, *Sharp 4270, 4276* (TENN). **Veracruz**: cerca del Cofre de Perote, *Ortega 630* (TENN).

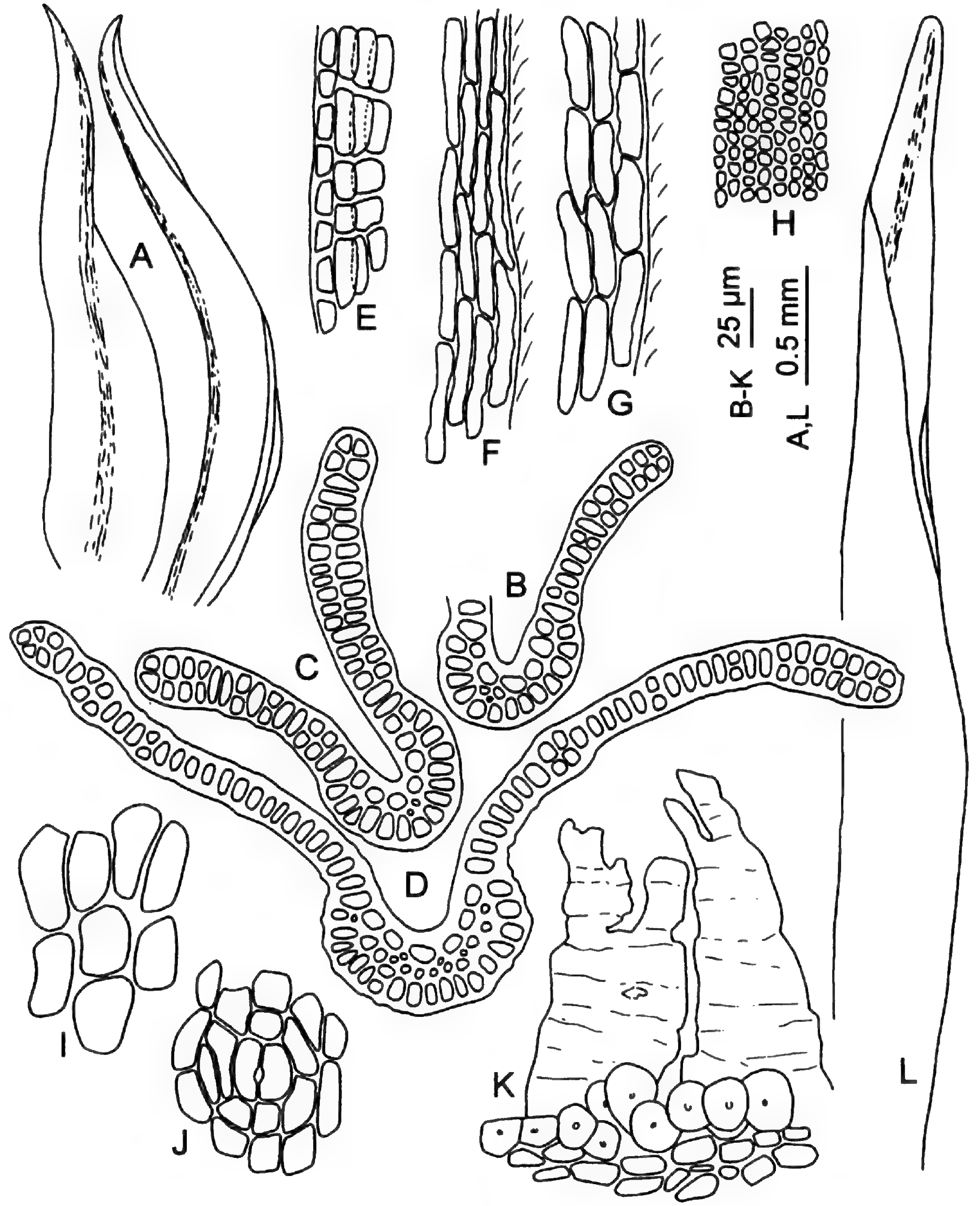

Figure 28. *Grimmia ochyriana.* —A. Leaves. —B–D. Transverse sections at distal, medial, and proximal parts of leaf. —E. Proximal marginal leaf cells. —F, G. Proximal juxtacostal leaf cells. —H. Distal leaf cells. —I. Medial exothecial cells. —J. Proximal exothecial cells and stoma. —K. Peristome teeth and annulus (only contour shown, not papillosity). —L. Perichaetial leaf. (*Vitt 17488*, ALTA.)

19. Grimmia ovalis (Hedw.) Lindb., Acta Soc. Sci. Fenn. 10: 75. 1871. *Dicranum ovale* Hedw., Sp. Musc. Frond: 140. 1801. *Dicranum ovale* Hedw., Descr. Micr.-Anal. Musc. Frond. 3: 81, tab. 34 figs. 1–6. 1792, nom. inval. *Dicranum ovatum* Sw., Kongl. Vetensk. Acad. Nya Handl. 16: 243. 1795, nom. inval. *Bryum ovale* Hoffm., Deutschl. Fl. 2: 35. 1795

Figure 29. Distribution of: ● *Grimmia ochyriana*; ▲ *Grimmia trinervis.*

"1796," nom. inval. *Trichostomum ovatum* P. Beauv., Prodr. Aethéogam: 91. 1805, nom. illeg. incl. sp. prior. *Dicranum ovatum* Brid., Muscol. Recent. Suppl. 1: 214. 1806, nom. illeg. incl. sp. prior. *Grimmia elliptica* Funck, Deutschl. Moose: 16, tab. 11 fig. 1. 1820, nom. illeg. incl. sp. prior. *Trichostomum ovale* (Hedw.) Roehl. ex Steud., Nomencl. Bot. 2: 99 [also 421]. 1824, nom. inval. in synon. *Campylopus ovalis* (Hedw.) Wahlenb., Fl. Suec. 2: 748. 1826. *Dryptodon ovatus* (Hedw.) Brid., Bryol. Univ. 1: 202. 1826. *Grimmia commutata* Huebener, Muscol. Germ.: 185. 1833, nom. illeg. incl. sp. prior. *Dryptodon ellipticus* (Funck) Hartm., Handb. Skand. Fl. ed. 3: 271. 1838, nom. illeg., non Brid. 1826. *Guembelia elliptica* (Funck) Hampe, Bot. Zeitung (Berlin) 4: 125. 1846. *Guembelia ovalis* (Hedw.) Müll. Hal., Syn. Musc. Frond. 1: 774. 1849. *Guembelia commutata* (Huebener) Rabenh., Krypt. Fl. Sachsen 1: 444. 1863, nom. illeg. incl. sp. prior. *Dryptodon ovalis* (Hedw.) Hartm. ex H. Möller, Ark. Bot. 26A(2): 14. 1934 "1933," nom. inval. in synon. err. pro *Dryptodon ovatus* Brid. TYPE: Germany. "Grimmia commutata B & S Specimina ab Hedw. ad iconem Dicrani ovali adhibita [manu Schwägrichen]" (lectotype, designated by Geissler & Maier (1995), G not seen).

Grimmia ovata F. Weber & D. Mohr, Naturh. Reise Schweden: 132, tab. 2 fig. 4a–c. 1804. *Campylopus ovalis* var. *ovatus* (F. Weber & D. Mohr) Wahlenb., Fl. Suec. ed. 2, 2: 776. 1833. *Dryptodon ovatus* (F. Weber & D. Mohr) Hartm., Handb. Skand. Fl. ed. 3: 271. 1838, nom. illeg., non Brid., 1826. *Grimmia ovata* var. *euovata* Loeske, Laubm. Eur. Part I: 113. 1913, nom. inval. TYPE: [Sweden.] Holmiae. (lectotype, here designated, BM).

Grimmia commutata f. *epilifera* J. E. Zetterst., Revis. Grimm. Scand: 90. 1861. *Grimmia commutata* var. *imberbis* Lindb. ex H. Möller, Ark. Bot. 26A(2): 17. 1934 "1933," nom. inval., pro synon. *Grimmia commutata* var. *mutica* J. E. Zetterst. ex H. Möller, Ark. Bot. 26A(2): 17. 1934 "1933," nom. inval., pro synon. TYPE: [Sweden.] Juxta Gottsunda prope Upsaliam, 5 May 1858, *Zetterstedt s.n.* (lectotype, here designated, H).

Grimmia cossonii Besch., Cat. Mouss. Alg. 18. 1882. TYPE: Algeria. Djebel Ksel pr. Geryville, 30 May 1856, *Cosson s.n.* (lectotype, here designated, PC).

Grimmia bernoullii Müll. Hal., Bull. Herb. Boissier 5: 200. 1897. TYPE: [Guatemala.] Quezaltenango: *Bernoulli & Cario s.n.* (lectotype, here designated, PC).

Dioicous. Plants dark green above, blackish or rusty below, sometimes the entire plant blackish. *Stems* erect or ascending, to 5 cm, with central strand. *Leaves* erect and appressed or flexuous when dry, erect, sigmoid in lateral view when moist, 1.7–2.5 × 0.4–0.7 mm, lanceolate or from an ovate ± sheathing base extended into an acuminate apical part, acuminate, concave, not plicate; *margins* plane; *costa* semi-elliptical to flat, undifferentiated, ventral epidermis 4–7 cells wide in cross section; *lamina* 2–4(5)-stratose in the distal ⅔; *distal cells* 4–8 μm long, isodiametric to rectangular, not bulging, walls sinuous; *proximal juxtacostal cells* 50–105 × 8–14 μm, rectangular (4–8:1), walls thick and nodulose; *proximal marginal cells* 20–40 × 8–14 μm, rectangular (2–3:1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete, straight, to 2 mm, denticulate. *Perichaetial leaves* 3.5–4.0 × 0.8–1.0 mm, convolute and larger than vegetative leaves (2–3 ×). *Androecia* terminal. *Setae* erect and straight, 3.5–7.0 mm long. *Capsules* exserted, ovoid, symmetric, smooth, stramineous, with stomata at the base; *exothecial cells* 20–60 × 14–35 μm, rectangular ([1]2–3:1), thin-walled; *annulus* compound and revoluble, *affinis* type; *peristome teeth* 50–70 μm wide at the mouth, cribrose throughout and irregularly cleft at apex, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, orange, contrasting with the urn; *opercula* rostrate; *calyptrae* cucullate; *spores* 10–14 μm, minutely granulose.

Illustrations. Figure 30; Abramov et al. (1961: ris. 137 figs. 8–14); Jóhannsson (1993: fig. 38); Lawton (1971: pl. 63 figs. 1–8); Maier and Geissler (1995: abb. 20); Petrov (1975: tab. 62 fig. 5); Smith (1978: fig. 150 5–9).

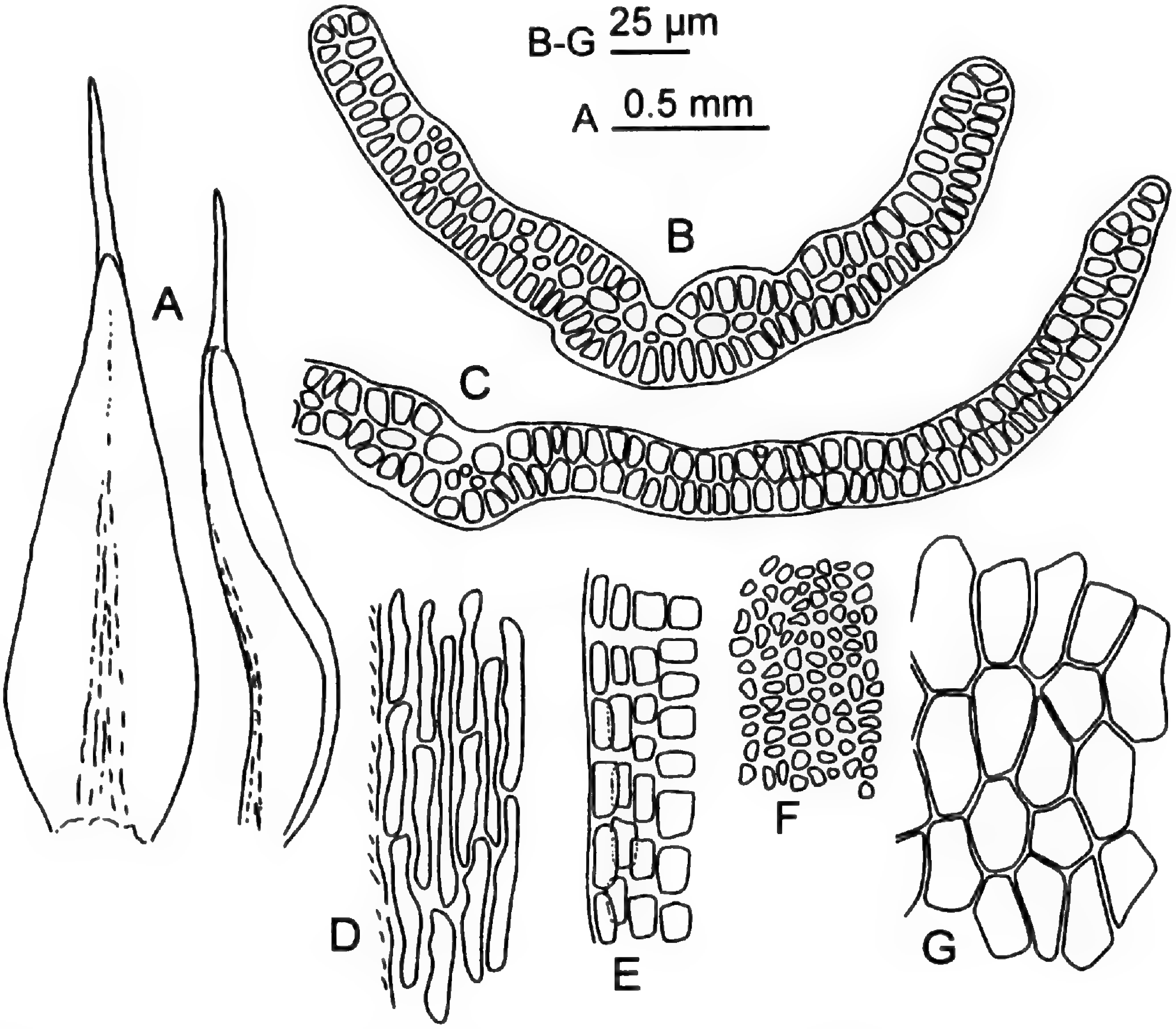

Figure 30. *Grimmia ovalis.* —A. Leaves. —B, C. Transverse sections at medial and proximal parts of leaf. —D. Proximal juxtacostal leaf cells. —E. Proximal marginal leaf cells. —F. Distal leaf cells. —G. Medial exothecial cells. (*Bernoulli & Cario 115,* PC.)

Distribution (Fig. 31). Europe, northern Africa, temperate and tropical Asia, northern America; Mexico, Guatemala. *Grimmia ovalis* grows mainly on granite and slate, but also on ultrabasic rocks like basalt, on sunny and dry places. It occasionally also covers rocks along streams and rivers. In Mexico it has been collected on igneous rocks and boulders in pine-oak forests and open areas between 2000 and 2730 m elevation.

Grimmia ovalis is readily recognized in the field by its large size, dark green color, ascending stems, and distally indistinct costae. The taxon is rather stenotypic, with most variation related to hair-point length. However, for genus *Grimmia,* hair-point length variation is often greater within than among populations or taxa, and is therefore mostly useless. Despite this, some specimens show puzzling features noteworthy of comment:

The type of *G. bernoullii* (*Bernoulli & Cario s.n.,* PC) and some, but not all, Mexican specimens (e.g., *Bowers 5270A,* TENN) have mitrate calyptrae. This could constitute a basis for recognition as a separate taxon. Nevertheless, except for this character, these plants are identical to other collections of *G. ovalis* from Eurasia and North America.

Setae in *G. ovalis* are straight, but I have studied one specimen from Punjab, India (*Koeltz 7304,* MO), with slightly curved setae.

Additional specimens examined. GUATEMALA. **Quetzaltenango**: Quetzaltenango, *Bernoulli & Cario s.n.* (PC). MEXICO. **Baja California**: Sierra de Juárez, ca. 8.5 km W of Cóndor–La Rumorosa Jct., *Meyer 44C* (TENN). **Chihuahua**: Ejido de Bocoyna, SW part of Creel Valley, *Bye 7297* (TENN); valley of Basihuare, 21 km S of Cusarare, *Weber & Bye B-60309* (TENN); 21 mi. N of San Juanito, *Bowers et al. 5402* (TENN), *5414B* (TENN). **Durango**: a few km before Palos Colorados, W of Durango, *Sharp 1749* (TENN); along Hwy. 40 about 4 mi. W of La Ciudad, *Bowers et al. 5270A* (TENN), *Norris et al. 20878* (UC); below Salto, *Sharp 1833A* (TENN); near Estación Coyotes E of El Salto, *Norris et al. 20991* (UC). **Michoacán**: vicinity of Morelia, Campanario, *Arsène 7449* (PC). **Puebla**: near San Agustín bridge E of Serdan, *Sharp 784* (TENN). **Tlaxcala**: top of falls on Río Zuahuapán near Amaxas, *Sharp 417* (TENN); mt. Tlacuapango, *Sharp 443* (TENN). **Zacatecas**: Cerro de la Bufa, *Cárdenas 354*

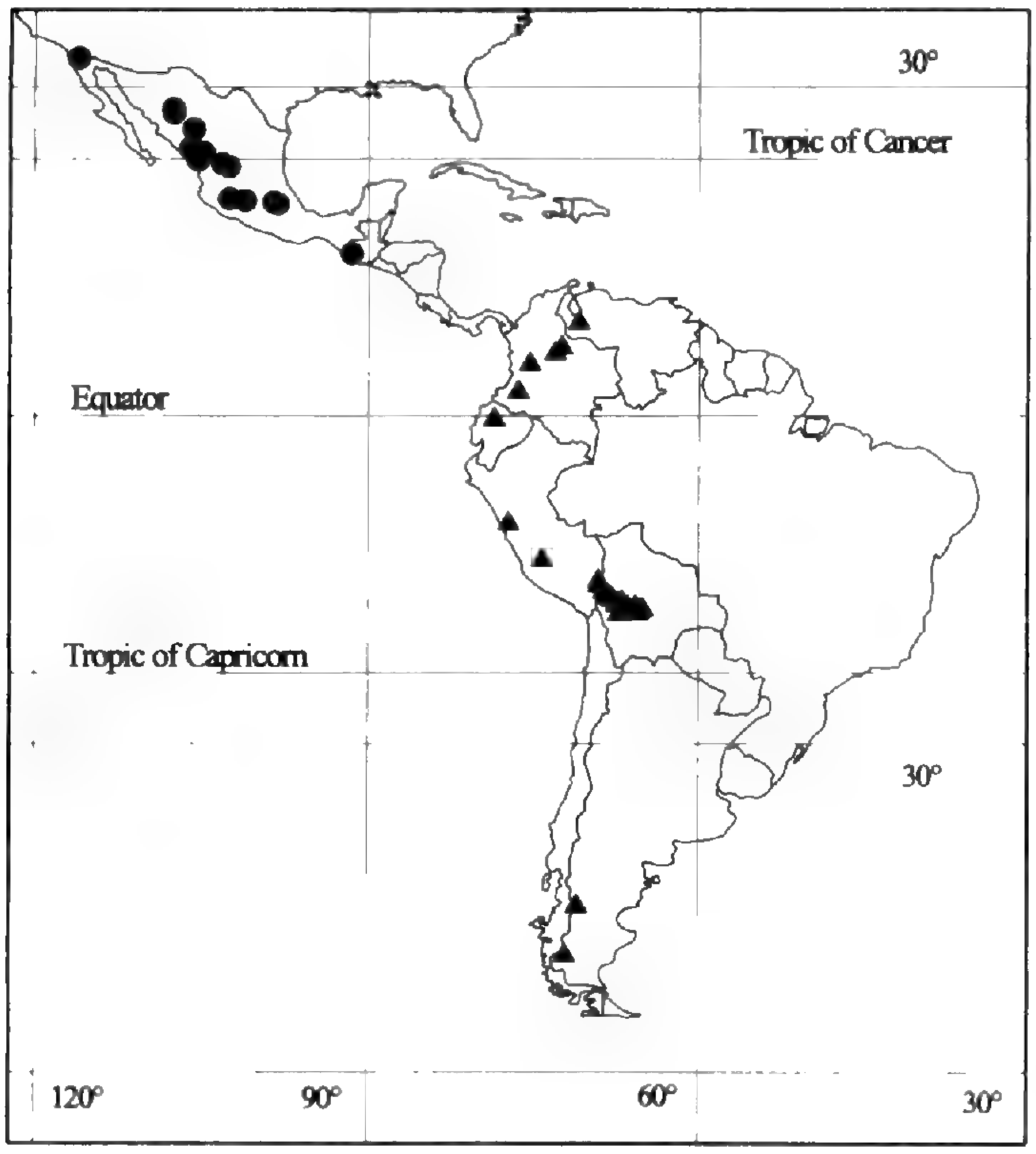

Figure 31. Distribution of: ● *Grimmia ovalis*; ▲ *Grimmia austrofunalis*.

(ALTA); Fresnillo, 2 km de San Juan de los Hornillos, cerca de la Presa Hornos, *Cárdenas 781* (ALTA).

20. Grimmia pilifera P. Beauv., Prodr. Aethéogam: 58. 1805. TYPE: "Etats-Unis d'Amerique" (holotype, G? not seen).

Grimmia arizonae Renauld & Cardot, Rev. Bryol. 19: 85. 1892. TYPE: U.S.A. Arizona: Fort Grand, *La Forêt s.n.* (lectotype, here designated, PC; isolectotypes, FH, NY).

Grimmia arsenei Cardot, Rev. Bryol. 40: 37. 1913. TYPE: Mexico. Michoacán: vicinity of Morelia, *Arsène 7894* (lectotype, here designated, PC; isolectotypes, F, PC 2 replicates).

Grimmia santaritae E. B. Bartram, Bryologist 27: 60, pl. 9. 1924. TYPE: U.S.A. Arizona: Santa Cruz Co., White House Canyon, Santa Rita Mountains, *Bartram 694* (lectotype, here designated, FH; isolectotypes, FH, NY).

Grimmia santaritae f. *propagulifera* E. B. Bartram, Bryologist 27: 60. 1924. *Grimmia arizonae* f. *propagulifera* (E. B. Bartram) G. N. Jones, in Grout, Moss Fl. N. Amer. 2: 33. 1933. TYPE: U.S.A. Arizona: Santa Cruz Co., Patagonia Mountains, *Bartram 618* (lectotype, here designated, FH).

Dioicous. Plants olive-green. *Stems* erect to ascending, to 6 cm, central strand lacking on sterile stems. *Leaves* erect and appressed when dry, patent to spreading when moist, 2–3 × 0.5–0.8 mm, lanceolate or from an ovate ± sheathing base extended into an acuminate apical part, acuminate, concave, not plicate; *margins* recurved; *costa* semi-terete to semi-elliptical, differentiated, sometimes weakly, ventral epidermis 2 cells wide in cross section; *lamina* 2–3(4)-stratose in the distal ⅔; *distal cells* 6–9 µm long, isodiametric, rectangular and oblate, not bulging, walls sinuous; *proximal juxtacostal cells* 28–80 × 7–11 µm, rectangular (3–11 : 1), walls thick and nodulose; *proximal marginal cells* 10–35 × 7–14 µm, isodiametric to rectangular (1.0–3.5 : 1), the transverse walls thicker than the longitudinal walls; *hyaline hairpoints* terete, straight to flexuous, to 3 mm, dentate. *Perichaetial leaves* 3–4 × 0.9–1.2 mm, convolute and larger than vegetative leaves (2–3 ×). *Androecia* terminal. *Setae* erect and straight, 1.0–1.3 mm long. *Capsules* immersed, ovoid to ellipsoid, symmetric, smooth, stramineous, with stomata at the base; *exothecial cells* 17–55 × 14–25 µm, mostly rectangular (1–3 : 1), thin-walled; *annulus* compound and revoluble, *affinis* type; *peristome teeth* 50–90 µm wide at the mouth, entire or irregularly cleft at apex, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, orange, contrasting with the urn; *opercula* rostrate; *calyptrae* mitrate; *spores* 13–17 µm, minutely granulose.

Illustrations. Figure 32; Deguchi (1978: figs. 38, 39); Ignatov and Cao (1994: fig. 6); Noguchi (1988: fig. 142 B).

Distribution (Fig. 10). Temperate Asia, northern America. In Mexico, *G. pilifera* grows on rocks in open areas as well as pine and oak forests, from full sun and dry to shady and more or less moistened places at the bottom of deep ravines, between 1500 and 2730 m elevation.

Typical specimens of *Grimmia pilifera* have distinctive leaves, with a broad base abruptly narrowing to an acuminate apical part, forming "shoulders" at the base-acumen transition, and with the margins proximally recurved. This distinctive leaf morphology along with the immersed capsules on short setae, make it easy to recognize. Unfortunately, *G. pilifera* is commonly sterile, and gametophytically variable. Specimens from eastern North America or growing in shade have long-acuminate apices quite distinct from the ovate bases, and with costae clearly differentiated from the lamina. However, specimens from southwestern North America, or from sunny habitats, have lanceolate leaves with bases scarcely differentiated from apices, and costae less clearly differentiated from laminae. This morphological gradation of lanceolate leaves in eastern North America to ovate ones in the southwest occurs continuously from east to west. No sharp distinction can be drawn separating typical eastern *G. pilifera* from taxa described from southwestern specimens (i.e., *G. arizonae*, *G. arsenei*, *G. santaritae*, and *G. santaritae* f. *propagulifera*). This

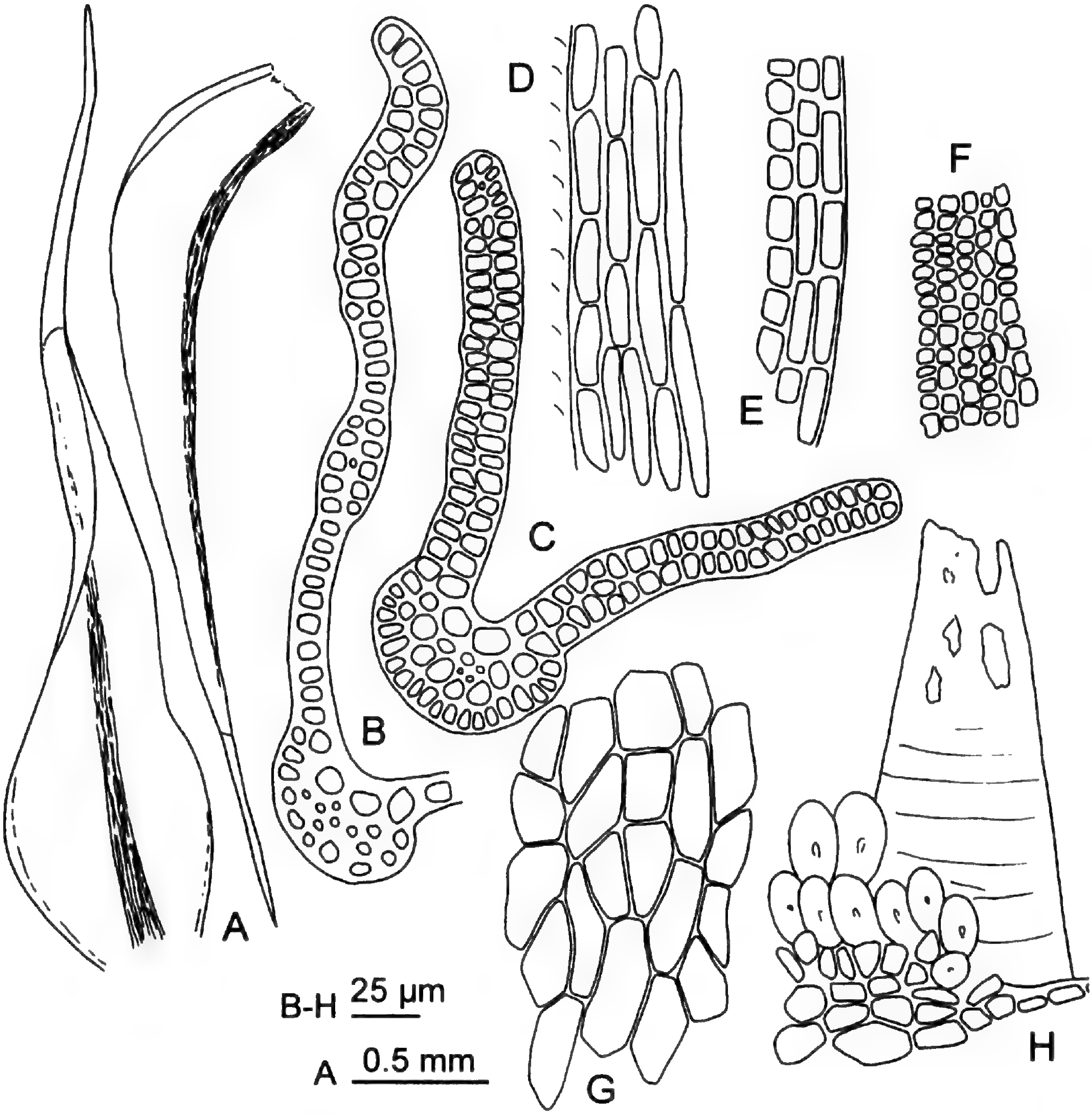

Figure 32. *Grimmia pilifera.* —A. Leaves. —B, C. Transverse sections at proximal and medial parts of leaf. —D. Proximal juxtacostal leaf cells. —E. Proximal marginal leaf cells. —F. Distal leaf cells. —G. Medial exothecial cells. —H. Peristome tooth and annulus (only contour shown, not papillosity). (*White 4210,* TENN.)

variability in acumen shape was previously noted by Deguchi (1978: 205–206).

This gametophytic variability makes it difficult to separate *G. pilifera* from sterile *G. longirostris,* or from populations of the latter with short setae (described from Arizona as *G. catalinensis,* but found across the entire world range of *G. longirostris*). Their principal difference lies in the morphology of costae cross sections. Costae in *G. longirostris* are reniform (2- to 6-celled on the ventral epidermis), but can be weakly distally differentiated. In *G. pilifera* costae are semi-terete, distinct, and only 2-celled on the ventral epidermis.

The presence or absence of a central strand in the stem is too variable to be a reliable character. Fertile stems usually have a distinct central strand; sterile stems or those with unfertilized perichaetia usually lack it.

Additional specimens examined. MEXICO. Cerro San Miguel, pr. Morelia, Dec. 1910, *Arsène 5070a* (FH, PC). **Chihuahua**: Puerto del Río Urique 38 mi. S of Creel, *Bowers et al. 5315A* (TENN), *5371C* (TENN); Cusarare, 20 km S of Creel, *Weber & Bye B-60292* (TENN). **Durango**: below El Salto, *Sharp 1892A* (TENN); near Palos Colorados, W of Durango, *Sharp 1786* (TENN). **Hidalgo**: Dublan, 2 July 1901, *Pringle s.n.* (PC). **Jalisco**: 9 mi. above San Martín Hidalgo, *Sharp et al. 2737* (TENN), *3233* (TENN), *3245B* (TENN). **Michoacán**: vicinity of Morelia, *Arsène 5070* (PC, FH) *7894* (PC), *7906* (PC); Cerro de la Campana, 4 km E of Tuxpán, *Delgadillo 4960* (ALTA); Uripitío, 11 km NE de Maravatio, *Delgadillo 4909* (ALTA); Negro Country, *LeSeur C8A* (F), *C9A* (F), *D5A* (F), *D7A* (F, FH). **Nuevo León**: Monterrey, *Arsène s.n.* (PC). **Oaxaca**: 38 km N of Oaxaca, between Oaxaca and Ixtlán de Juárez, *Sharp et al. 2608B* (TENN). **San Luis Potosí**: 44 mi. W of Antiguo Morelos on road to Huizache, *Pursell 5435* (TENN). **Sonora**: rancho El Roble, NE of El Tigre, *White 4210* (TENN). **Tlaxcala**: mt. Tlacuapango, *Sharp 443A* (TENN). **Zacatecas**: 7 km S de la Laguna Grande, al N de Monte Escobedo, 27 Aug. 1983, *Cárdenas s.n.* (H); Fresnillo, 2 km S de San Juan de los Hornillos, cerca de la presa Hornos, *Cárdenas 767* (ALTA); Valparaíso, 14 km N de Valparaíso, *Cárdenas 805* (ALTA); Tlaltenango, Cerro del Moro, 29 km W de Jalpa, *Cárdenas 832* (ALTA).

21. Grimmia plagiopodia Hedw., Sp. Musc. Frond.: 78, tab. 15 figs. 6–13. 1801. *Grimmia plagiopus* Spreng., Bot. Zeitung (Regensburg) 1: 74. 1802, nom. inval., orthogr. err. *Schistidium plagiopodium* (Hedw.) Loeske, Laubm. Eur. Part I: 52. 1913. TYPE: Germany. Saxoniae, *Flügge s.n.* (holotype, G not seen).

Grimmia brandegei Austin, Bull. Torrey Bot. Club 6: 45. 1875. TYPE: U.S.A. Colorado: 1874, *Brandegee s.n.* (lectotype, here designated, NY).

Grimmia nivea Dusén, Bot. Not. 1905: 303. 1905. TYPE: Argentina. Santa Cruz: Patagonia australis, in valle rivuli Aryo. Pelque, 16 Jan. 1905, *Dusén s.n.* (holotype, S not seen (Deguchi, 1984: 22); isotypes, H-BR, PC).

Cladautoicous or goniautoicous. Plants green, yellowish green to rusty. *Stems* erect, to 1 cm, with central strand. *Leaves* erect and appressed when dry, erect to patent or homomallous when moist, 0.5–1.5 × 0.25–0.40 mm, oval, obtuse, concave, not plicate; *margins* plane, occasionally weakly recurved distally; *costa* semi-terete, differentiated, ventral epidermis 2 cells wide in cross section; *lamina* 1-stratose, occasionally the marginal row 2-stratose in the distal ⅔; *distal cells* 9–20 µm long, isodiametric and rectangular, not bulging, walls sinuous; *proximal juxtacostal cells* 12–40 × 12–15 µm, isodiametric to rectangular (1.0–2.5 : 1), walls thin to medium-thick and straight; *proximal marginal cells* 20–27 × 10–14 µm, isodiametric to rectangular (1.0–2.5 : 1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* sometimes lacking (but always present in perichaetial leaves), plane, straight or flexuous, to 1 mm, denticulate. *Perichaetial leaves* 1.3–1.6 × 0.7–0.8 mm, convolute and larger than vegetative leaves (3–5 ×). *Androecia* terminal or below perichaetia. *Setae* curved, 0.5–1.2 mm long. *Capsules* immersed, ovoid to subglobose, ventricose, smooth, stramineous, with stomata at the base; *exothecial cells* 30–50 × 12–25 µm, rectangular (1.5–3.0 : 1), thick-walled, occasionally thin-walled proximally and thick-walled in the distal ⅓; *annulus* simple and persistent, *Schistidium* type; *peristome teeth* 80–115 µm wide at the mouth, cribrose throughout and irregularly cleft at apex, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, occasionally both surfaces almost smooth, orange, contrasting with the urn; *opercula* mammillate to rostellate; *calyptrae* mitrate; *spores* 9–14 µm, smooth.

Illustrations. Figure 33; Deguchi (1984: fig. 7); Ignatov and Cao (1994: fig. 17); Jóhannsson (1993: fig. 23); Limpricht (1890: 190); Maier and Geissler (1995: abb. 21); Ochyra (1993: fig. 1).

Distribution (Fig. 34). Europe, temperate Asia, Australasia, Antarctic, northern and southern America. *Grimmia plagiopodia* is known from three localities in South America; only two were available for this study, both lacking habitat information. Besides the specimens here studied, Ochyra (1993) reported another collection from Mendoza (Argentina, *Anonymous 10749,* FH, on loan, not seen). *Grimmia plagiopodia* grows on rocks of any composition, granites, limestone, or sandstone, usually in open and exposed situations below 1600 m elevation.

Grimmia plagiopodia has unistratose leaves usually tipped with flat hair-points, with curved setae asymmetrically attaching to immersed, ventricose, and peristomate capsules. Confusion of this plant with any other is very unlikely, although it has been described as novel several times from the Southern Hemisphere.

Although a characteristic seen in specimens beyond Latin America, it is interesting to note that *G. plagiopodia* sometimes has muticous leaves. Otherwise these plants fit within the expected normal range of variation of *G. plagiopodia.* As reiterated under *G. anodon* and *G. ovalis,* hair-point length is too variable in Grimmiaceae to be taxonomically valuable.

Grimmia brandegei was synonymized under *G. plagiopodia* by Ochyra and Bednarek-Ochyra (1994: 669). Its type packet contains a mixture of *Grimmia plagiopodia* and *G. poecilostoma* plants. A further microscope slide from the type is identified as *G. poecilostoma.* The protologue for *G. brandegei* describes features from both *G. plagiopodia* and *G. poecilostoma.* It seems best to select as lectotype *G. plagiopodia* plants to preserve the usage of Ochyra and Bednarek-Ochyra (1994).

Additional specimens examined. ARGENTINA. **Santa Cruz**: in valle rivulis Pelque, *Dusén 5713* (H-BR, PC). CHILE. **Magallanes**: Natales, *Siple 391-6* (FH).

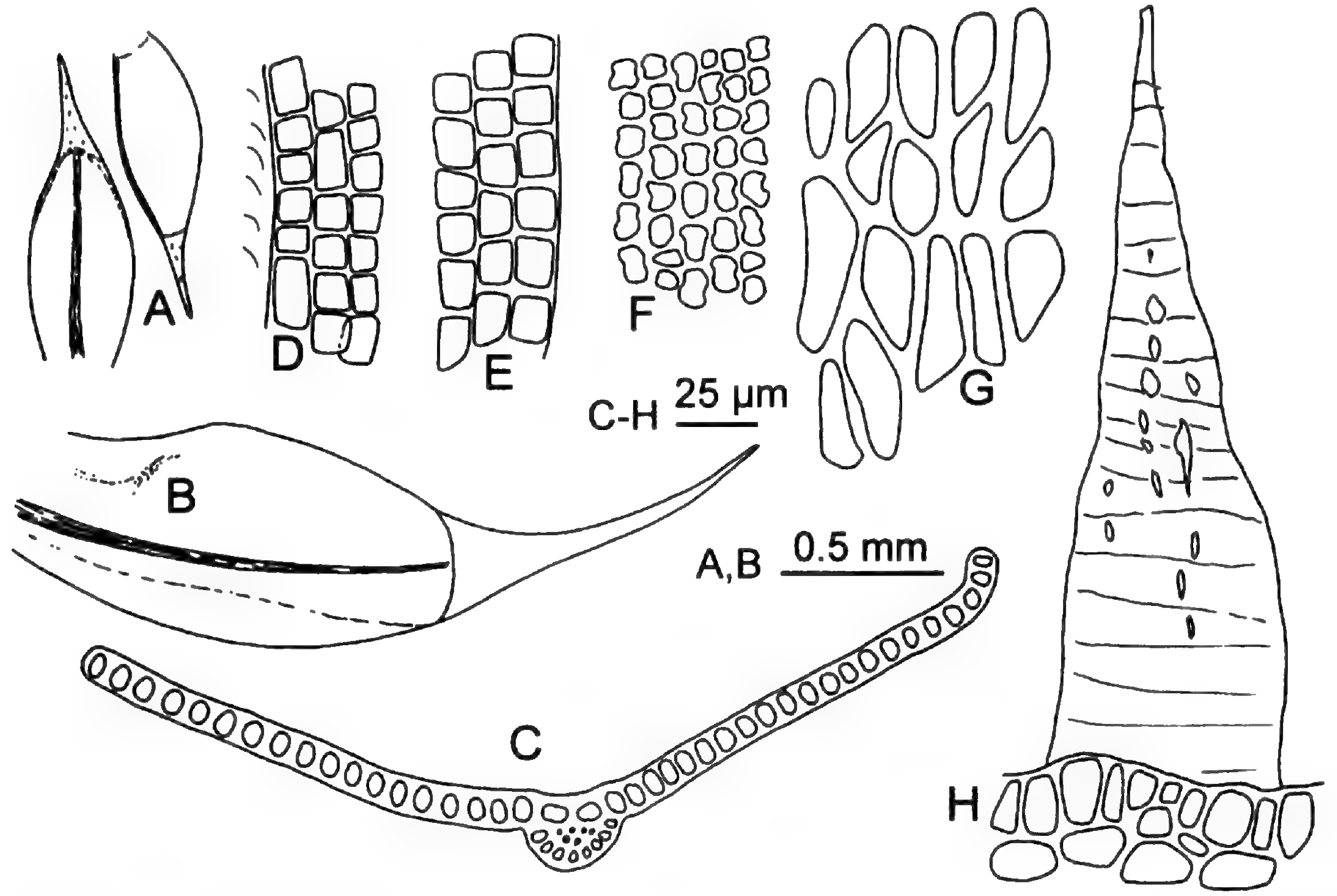

Figure 33. *Grimmia plagiopodia.* —A. Leaves. —B. Perichaetial leaf. —C. Transverse section at medial part of leaf. —D. Basal juxtacostal leaf cells. —E. Basal marginal leaf cells. —F. Distal leaf cells. —G. Medial exothecial cells. —H. Peristome tooth and capsule mouth showing the annulus simple and persistent. (*Dusén s.n.*, PC.)

Figure 34. Distribution of: ● *Grimmia plagiopodia*; ○ *Grimmia plagiopodia* (Argentina. Mendoza: Depto. Las Heras, quebrada del Portero Puerta, *Anonymous 10749*, FH not seen, *fide* Ochyra, 1993); ▲ *Grimmia pseudoanodon*; ■ *Grimmia pulla.*

22. Grimmia poecilostoma Cardot & Sebille, in Sebille, Rev. Bryol. 28: 118, tab. 5. 1901. *Grimmia tergestina* var. *poecilostoma* (Cardot & Sebille) Loeske, Laubm. Eur. Part I: 84. 1913. *Grimmia crinitoleucophaea* Cardot, Rev. Bryol. 17: 18–19. 1890, nom. inval., published as a formula (Greuter et al., 1994, ICBN H.10.3). *Grimmia cardotii* Hérib., Mém. Acad. Sci. Clermont-Ferrand, sér. 2, 14: 358. 1899, nom. inval., not accepted by the author (ICBN art. 34.1a). TYPE: France. Isère: Clapier de Saint-Christophe-en-Oisans, *Sèbille s.n.* (lectotype, here designated, PC; syntype, [Pont-de-Longe près Clermont, Auvergne, 3 Avril 1888, *Gasilien*], PC).

Grimmia crassifolia Lindb. ex Broth., Acta Soc. Sci. Fenn. 19(12): 84. 1892. TYPE: [Russia. North Ossetia:] in valle fl. Ardon inter Alagir et Misurtsy, July 1877, *Brotherus s.n.* (lectotype, here designated, H-BR; isolectotypes, H, JE, PC, UPS).

Grimmia gymnostoma Culm., Rev. Bryol. 23: 108. 1896. *Grimmia tergestina* var. *gymnostoma* (Culm.) G. Roth, Eur. Laubm. 1: 410. 1903 "1904." *Grimmia tergestina* f. *gymnostoma* (Culm.) Loeske, Laubm. Eur. Part I: 82. 1913, comb. inval., pro synon. TYPE: Switzerland. Appenzell: Ostabhang der Ebenalp, 24 Aug. 1896, *Culmann s.n.* (lectotype, here designated, PC).

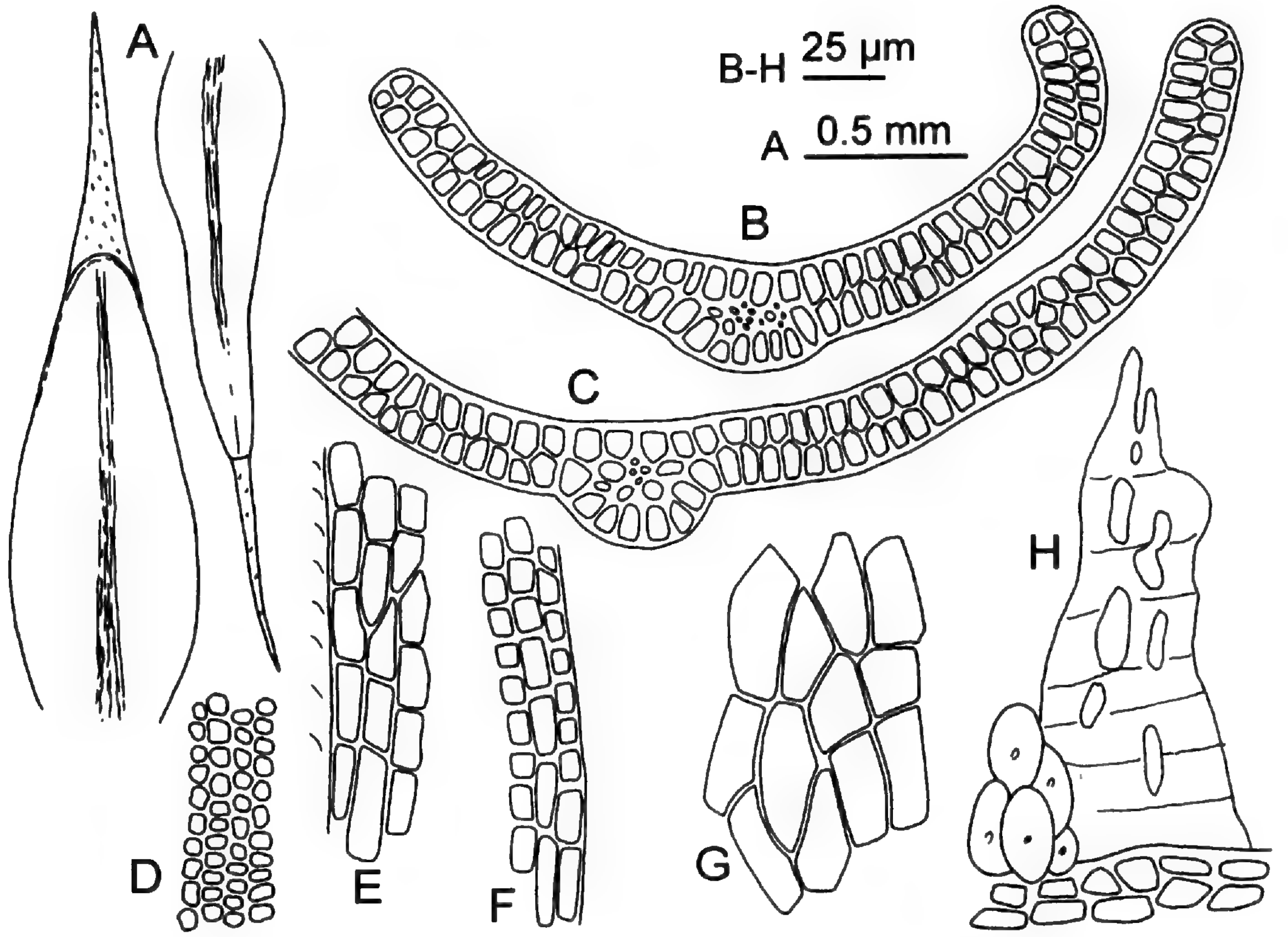

Figure 35. *Grimmia poecilostoma.* —A. Leaves. —B, C. Transverse sections at distal and medial parts of leaf. —D. Distal leaf cells. —E. Proximal juxtacostal leaf cells. —F. Proximal marginal leaf cells. —G. Medial exothecial cells. —H. Peristome tooth and annulus (only contour shown, not papillosity). (*Stark & Castetter 1182,* MO.)

Dioicous. Plants olive-green to blackish. *Stems* erect, to 2 cm, with central strand. *Leaves* erect and appressed when dry, erect to patent when moist, 1.1–2.0 × 0.4–0.6 mm, ovate to lanceolate, obtuse to acuminate, concave, not plicate; *margins* plane; *costa* semi-elliptical, undifferentiated, ventral epidermis 3–7 cells wide in cross section; *lamina* 2-stratose in the distal ⅔; *distal cells* 8–12 µm long, mostly isodiametric, but also rectangular and oblate, not bulging, walls straight to slightly sinuous; *proximal juxtacostal cells* 20–40 × 10–14 µm, rectangular (1.5–3.5 : 1), walls thin to moderately thick and straight; *proximal marginal cells* 7–25 × 10–18 µm, oblate to rectangular (0.7–2 : 1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete distally and flat proximally, somewhat decurrent, straight, to 2 mm, entire to dentate. *Perichaetial leaves* 1.8–2.5 × 0.8–1.2 mm, convolute, hyaline and filmy, scarcely discernible, larger than vegetative leaves (3–3.5 : 1). *Androecia* terminal. *Setae* curved, 0.4–0.6 mm long. *Capsules* immersed, ovoid, ventricose, smooth, stramineous, with stomata at the base; *exothecial cells* 35–70 × 20–35 µm, rectangular (1.5–2.5 : 1), thin-walled, seldom internal side thickened; *annulus* compound and revoluble, *affinis* type; *peristome teeth* 60–115 µm wide at the mouth, cribrose throughout and irregularly cleft at apex, both surfaces papillose throughout, orange, contrasting with the urn; *opercula* rostrate; *calyptrae* mitrate; *spores* 9–12 µm, smooth.

Illustrations. Figure 35; Jones (1933: pl. 6); Nowak and Poelt (1979: figs. 13–14, as *G. tergestina* var. *poecilostoma*); Sebille (1901: pl. 5).

Distribution (Fig. 36). Europe, temperate Asia, northern America. *Grimmia poecilostoma* is unknown from Latin America, but it grows in New Mexico close to the Mexican border, and its presence in Mexico is likely. In New Mexico it grows on dry and sunny granite at about 2000 m elevation.

Grimmia poecilostoma is extremely variable in leaf shape. Leaves range from small, triangular and obtuse to larger, acuminate, resembling those of *G. ovalis.* Sporophytes appear less variable, with the only deviation seen in a specimen from France (*Sèbille s.n.,* PC, the lectotype). This specimen has proximal exothecial cells that are thin-walled, but

Figure 36. Distribution of: ● *Grimmia poecilostoma*; ▲ *Grimmia reflexidens*; ■ *Grimmia ungeri*.

distal exothecial cells are incrassate on the inner capsule wall.

The gametophyte morphology and anatomy of *G. poecilostoma* are identical to those of *G. americana*, *G. involucrata*, and *G. tergestina*. All four species have strongly modified perichaetial leaves, which are almost completely hyaline and filmy, and much larger than other leaves. Perichaetial leaves are usually overlooked because they are difficult to discriminate even under the compound microscope. These four species form an interesting group of two pairs differing in sexuality and sporophyte morphology as well as geographical distribution. *Grimmia poecilostoma* and *G. americana* have ventricose capsules on curved setae. However, *G. poecilostoma* is dioicous and holarctic; *G. americana* is gonioautoicous and North American. In contrast, *Grimmia tergestina* and *G. involucrata* bear symmetric capsules on straight setae. Again, the former is dioicous and holarctic, whereas the latter is gonioautoicous and North American.

Greven (1995: 30, 115) stated that *G. poecilostoma* can be separated from *G. tergestina* by its ecology. According to him, *G. poecilostoma* occurs only on acidic rocks, whereas *G. tergestina* grows only on basic substrata. Despite this, indisputable fertile collections reveal most of the Asiatic and some European specimens of *G. poecilostoma* have been collected from calcareous rocks, and that *G. tergestina* also grows on quarzite (e.g., *Handel-Mazzetti 2948*, from Turkey). Already Cardot (1890: 18–19) had stressed in the protologue the subcalcareous nature of the substrate where the type of *G. poecilostoma* was collected.

Study of the types of *Grimmia crassifolia* reveals this taxon to be identical with *G. poecilostoma*, having curved setae and ventricose capsules. Greven (1995: 57) applied this name, *G. crassifolia*, to a different taxon, with straight setae and symmetric capsules. From its illustration it appears to resemble, indeed it is identical, to *G. tergestina*. If it proved to be a distinct taxon, it would need a new name.

Additional specimen examined. U.S.A. **New Mexico:** Dona Ana Co., slopes and ravines of the Organ Mountains, E side, Sugarloaf Peak, *Stark & Castetter 1182* (MO).

23. Grimmia pseudoanodon Deguchi, in Inoue, Studies on Cryptogams in Southern Peru: 29, pl. 11. 1987. TYPE: Peru. Puno: prov. Puno, Chucuito, near Acora, *Deguchi 30008* (holotype, TNS not seen; isotype, NY).

Cladautoicous. *Plants* olive-green to reddish or blackish. *Stems* erect, to 1 cm, with central strand. *Leaves* erect and appressed when dry, erect to patent when moist, 0.8–1.2 × 0.30–0.45 mm, ovate to lanceolate, acute, keeled, not plicate; *margins* plane; *costa* semi-terete, differentiated, ventral epidermis 2 cells wide in cross section; *lamina* 1-stratose except for the 2-stratose marginal row in the distal ⅔; *distal cells* 7–20 μm long, isodiametric to rectangular, not bulging, walls straight to slightly sinuous; *proximal juxtacostal cells* 18–36 × 8–15 μm, rectangular (1.5–5.0 : 1), walls medium-thick, straight to somewhat sinuous; *proximal marginal cells* 14–30 × 10–15 μm, isodiametric to rectangular (1–3 : 1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* flat, straight, to 1 mm, smooth to denticulate. *Perichaetial leaves* 1.6–1.8 × ca. 0.8 mm, convolute and larger than vegetative leaves (2–4 ×). *Androecia* terminal. *Setae* straight, 0.5–0.7 mm long. *Capsules* immersed, ovoid to cylindric, symmetric, smooth, stramineous, with stomata at the base; *exothecial cells* 40–70 × 12–24 μm, rectangular (3–6 : 1), thin-walled; *annulus* compound and revoluble, *elongata* type; *peristome teeth* lacking; *opercula* conic to mammillate; *calyptrae* mitrate; *spores* 11–20 μm, coarsely granulose.

Illustrations. Figure 37; Deguchi (1987: pl. 11).

Distribution (Fig. 34). Southern America. *Grimmia pseudoanodon* was originally described from southern Peru. Subsequently, Hastings (1997) re-

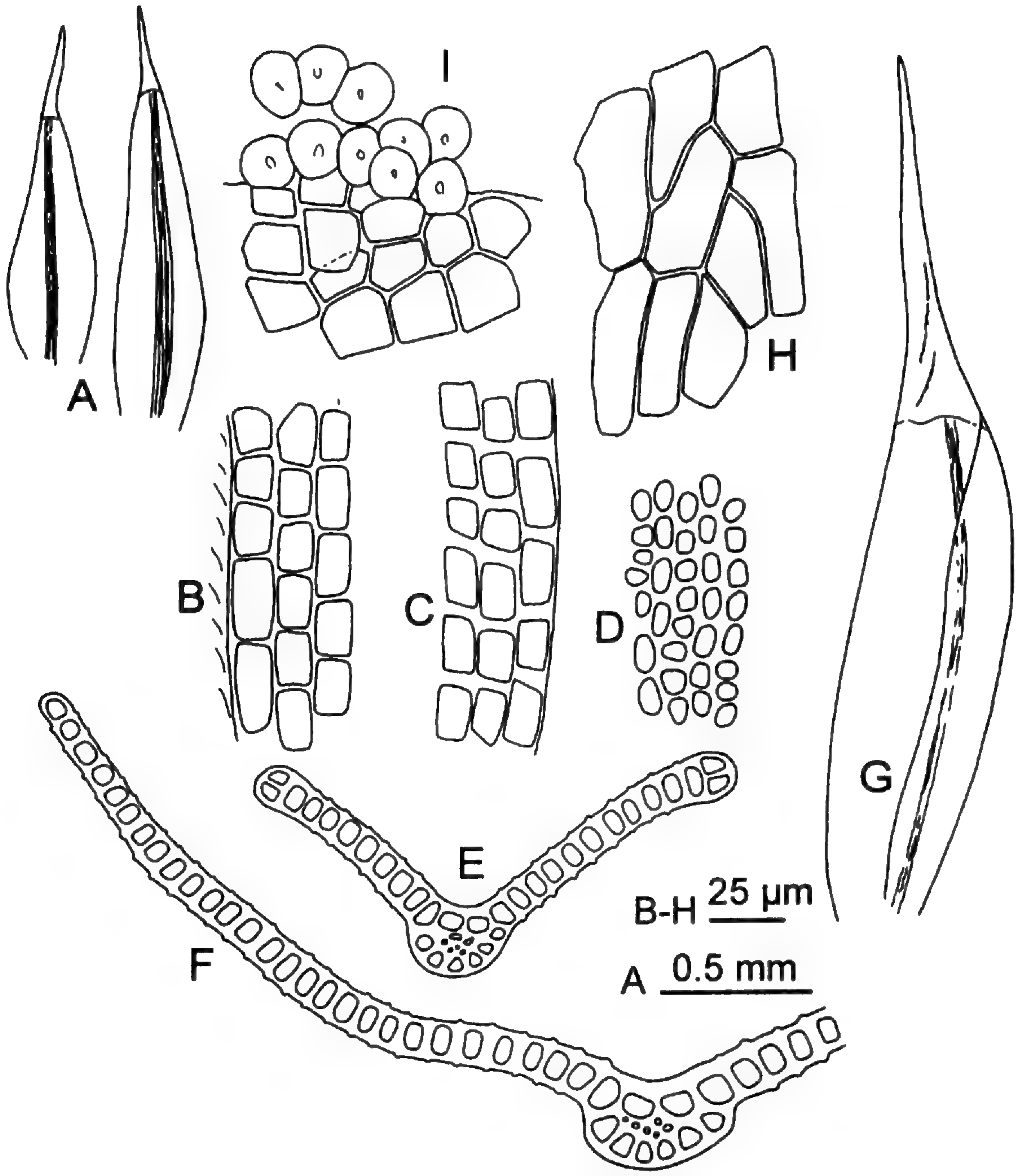

Figure 37. *Grimmia pseudoanodon.* —A. Leaves. —B. Proximal juxtacostal leaf cells. —C. Proximal marginal leaf cells. —D. Distal leaf cells. —E, F. Transverse sections at medial and proximal parts of leaf. —G. Perichaetial leaf. —H. Medial exothecial cells. —I. Capsule mouth and annulus. (*Hegewald 5438a,* IBA.)

ported its presence from Bolivia, and its range is here extended to northern Argentina. It grows on rocks in open areas above the tree line between 4000 and 4900 m elevation.

Grimmia pseudoanodon is characterized by ovate to lanceolate leaves with flat margins, and symmetric, gymnostomous capsules on straight setae. It is similar to *G. anodon* as already indicated by Deguchi (1987: 30). However, considering the overall variability of *G. anodon,* it is difficult to discriminate their gametophytes except by male bud position. Male buds are terminal on separate branches in *G. pseudoanodon,* but remain hidden below the perichaetia in *G. anodon.* Both taxa are unequivocally identified by their sporophytic characters.

Additional specimens examined. ARGENTINA. **Salta:** Nevado de Castillo, *Lorentz s.n.* (JE). BOLIVIA. **Oruro:** prov. Atahuallpa, SE slope of Cerro Separaya, *Lewis 79-2004* (F); prov. Atahuallpa, Cerro Tata Sabaya, *Lewis 79-2015* (F, IBA); prov. Sajama, Cerro Achuta, *Lewis 84-260* (F, IBA), *84-271* (F, IBA), *84-286* (F, IBA), *84-315* (F, IBA); prov. Sajama, Nevado Sajama, *Lewis 84-266* (F, MO). PERU. **Arequipa:** Arequipa, laguna Las Salinas, *Hegewald & Hegewald 5483A* (IBA, MO). **Puno:** Puno, Chucuito, near Acora, *Deguchi 30008* (NY).

24. Grimmia pulla Cardot, Rev. Bryol. 36: 106. 1909. TYPE: Mexico. Hidalgo: Honey Station, *Pringle s.n.* [Pringle, Plantae mexicanae, n° 10423] (lectotype, here designated, PC; isolectotypes, CANM-197543, FH, JE, NY, PC 2 replicates, TENN, UC-133015).

Grimmia pulla var. *squarrosa* Thér., Rev. Bryol. Lichénol. 5: 99. 1933. TYPE: Mexico. México: San Rafael, *Amable 1857* (lectotype, here designated, PC; syntypes, [Mexico. México: Contreras, *St. Pierre 1472*], H-BR, PC).

Dioicous. Plants yellowish green above, brownish below. *Stems* erect or ascending, to 2 cm, with central strand. *Leaves* erect and appressed or somewhat flexuous apically when dry, spreading to squarrose when moist, 1.5–2.0 × 0.3–0.4 mm, lingulate, acute, keeled, not plicate; *margins* recurved from ⅓ to ½–⅔ the leaf length on one or both sides; *costa* semi-terete, differentiated, ventral epidermis 2 cells wide in cross section; *lamina* 1-stratose except for the 2-stratose two marginal rows in the distal ⅔; *distal cells* 6–8 μm long, isodiametric, rectangular and oblate, not bulging, walls sinuous; *proximal juxtacostal cells* 20–50 × 8–12 μm, rectangular (2–5 : 1), walls medium-thick and straight; *proximal marginal cells* 12–35 × 8–14 μm, isodiametric to rectangular (1–2 : 1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* usually brownish at base, terete, straight, to 0.6 mm, dentate. *Perichaetial leaves* 2 × 0.5–0.6 mm, convolute and larger than vegetative leaves (1.5 ×). *Androecia* terminal. *Setae* curved, 3–4 mm long. *Capsules* exserted, ellipsoid, symmetric, ribbed, stramineous, with stomata at the base; *exothecial cells* 30–60 × 14–25 μm, rectangular (1.5–2 : 1), thin-walled; *annulus* compound and revoluble, *affinis* type; *peristome teeth* 50–70 μm wide at the mouth, entire, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, orange, contrasting with the urn; *opercula* rostrate; *calyptrae* mitrate; *spores* 10–16 μm, minutely granulose.

Illustrations. Figure 38; Crum (1994: fig. 306).

Distribution (Fig. 34). Northern America. *Grimmia pulla* is known only from Mexico. It grows on acid rocks and bases of tree trunks in open areas and forests between 2300 and 2600 m elevation.

Grimmia pulla is a very stenotypic species typified by its narrowly lingulate leaves and short, sharply dentate, brownish hair-points. The only species to be confused with it is *G. pulvinata*. However, *G. pulvinata* has wider leaves, and longer, smoother hair-points. *Grimmia pulvinata* is autoicous, with perigonial buds found just below the perichaetia, and is typically fertile.

Additional specimens examined. MEXICO. **Distrito Federal**: La Venta, *Saint-Pierre 1803* (PC); near Cerro Zacayuca in Pedrigal near Contreras, *Sharp & Miranda 1176B* (TENN). **Durango**: Hwy. 40 about 9 mi. W of La Ciudad, *Bowers et al. 5068B* (TENN). **Hidalgo**: river ledges, near Honey Station, 12 Dec. 1909, *Pringle s.n.* (NY). **Jalisco**: between Cd. Venustiano Carranza and Tapalpa, *Valentine 8–14* (TENN). **Michoacán**: near Las Cabras, between Chilchota and Zacapú, *Sharp 3715* (TENN); along Hwy. 15 near Zacapú, *Norris & Taranto 15408* (TENN); about 1 mi. E of Las Penas on Hwy. 15, *Norris & Taranto 15642A* (UC). **México**: 2 mi. S of Hwy. 15 on road to Valle Bravo, *Sharp & Cárdenas 8713A* (TENN), *8716* (TENN); Contreras, *Amable 1475* (FH); La Escondida, 8 mi. E of Lerma, *Hermann & Crum 20884* (TENN); San Rafael, *Amable 1860* (PC); near Llano Grande, near Río Frío, *Sharp 178* (TENN). **Morelos**: at mirador, near km 67 on Cuernavaca–México City toll road, Hwy. 95D, *Magill 2527* (TENN); old Rt. 95, 42.5 km from México to Cuernavaca, *Snider 262* (TENN). **Oaxaca**: Mts. Oaxaca, *Spotts 1757* (FH). **Veracruz**: Ixhuacán de los Reyes, al SW de Teocelo, *Viveros-Juárez 465* (TENN).

25. Grimmia pulvinata (Hedw.) Sm., Engl. Bot. 24: 1728. 1807. *Fissidens pulvinatus* Hedw., Sp. Musc. 158, tab. 40 fig. 1–3. 1801. TYPE: Germany (lectotype, designated by Cao & Vitt (1986), G not seen).

Fissidens pulvinatus var. *africanus* Hedw., Sp. Musc. Frond. 159, tab. 40 figs. 4–6. 1801. *Dicranum africanum* (Hedw.) F. Weber & D. Mohr, Index Mus. Pl. Crypt.: 2. 1803. *Dicranum pulvinatum* (Hedw.) Lag., D. García & Clemente var. *africanum* (Hedw.) Schleich., Cat. Pl. Helv. ed. 4: 40. 1821. *Dryptodon obtusus* Brid., Bryol. Univ. 1(1): 198. 1826. *Grimmia africana* (Hedw.) Arn., Arnott, G.A.W. Mém. Soc. Linn. Paris 5: 243. 1827. *Grimmia pulvinata* var. *obtusa* Huebener, Muscol. Germ. 194. 1833. *Dryptodon obtusus* Hartm., Handb. Skand. Fl. ed. 3: 270. 1838. *Grimmia pulvinata* var. *africana* (Hedw.) Wilson, in Hooker, Bot. Antarct. Voy., Fl. Nov.-Zel. 2: 75. 1854. *Grimmia obtusa* (Brid.) Loeske, Laubm. Eur. Part I: 165. 1913. *Grimmia pulvinata* f. *obtusa* Vilh., Věstn. Král. Ceské Společn. Nauk, Tř. Mat.-Přir. 1924: 27. 1924. TYPE: [South Africa.] Ad Cap. bonae Spei lecta specimina misit O. Swartz. (lectotype, here designated, G).

Dicranum cribrosum Brid., Muscol. Recent. Suppl. 1: 212. 1806. *Dryptodon cribrosus* (Brid.) Brid., Bryol. Univ. 1: 198. 1826. TYPE: South Africa. Promontorium Bonae Spei, *Thunberg s.n.* (lectotype, here designated, H-SOL).

Grimmia cygnicolla Taylor, London J. Bot. 5: 45. 1846. TYPE: Australia. Swan River, *Drummond s.n.* (lectotype, here designated, FH; isolectotypes, FH, H-SOL, NY).

Grimmia callosa Müll. Hal. & Hampe, Linnaea 26: 498. 1855. TYPE: Australia. Victoria: Barossa range, *Müller s.n.* (lectotype, here designated, JE).

Grimmia gibertii Mitt., J. Linn. Soc., Bot. 12: 100. 1869. TYPE: Uruguay. Montevideo, *Gibert 729* (lectotype, here designated, NY; isolectotypes, FH, H-BR, NY, PC).

Grimmia auresia Besch., Cat. Mouss. Alg. 17. 1882. TYPE: Algeria. Aurès, *Balansa s.n.* (lectotype, here designated, PC; isolectotype, F).

Grimmia campbelliae Müll. Hal., Hedwigia 37: 162. 1898. TYPE: Australia. Hume River, *Campbell s.n.* (lectotype, here designated, JE; isolectotypes, H-BR, JE).

Grimmia woollsiana Müll. Hal., Hedwigia 37: 162. 1898. TYPE: [Australia.] New South Wales: *Woolls s.n.* (lectotype, here designated, H-BR; isolectotype, JE).

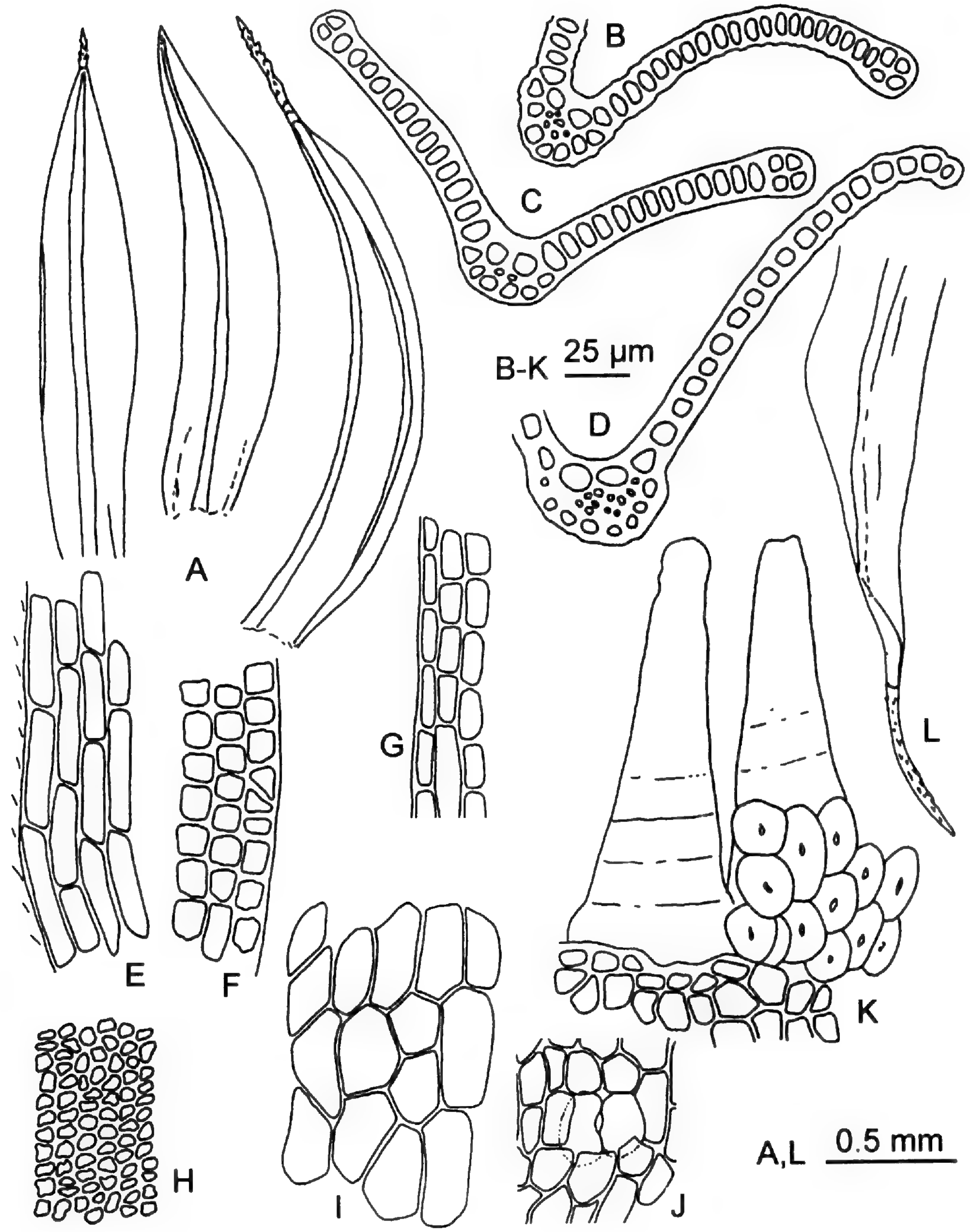

Figure 38. *Grimmia pulla.* —A. Leaves. —B, C. Transverse sections at medial part of leaf, B showing pseudopapillosity. —D. Transverse section at proximal part of leaf. —E. Proximal juxtacostal leaf cells. —F, G. Proximal marginal leaf cells. —H. Distal leaf cells. —I. Medial exothecial cells. —J. Proximal exothecial cells and stoma. —K. Annulus and peristome teeth (only contour shown, not papillosity). —L. Perichaetial leaf. (*Pringle 10423*, PC.)

Grimmia subcurvula Kindb., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 57: 1007. 1900 "1899." TYPE: [Sweden.] Dalsland, Rostock, 14 Aug. 1898 *Kindberg s.n.* (lectotype, here designated, S; isolectotype, PC).

Grimmia orbicularis var. *patagonica* Cardot, Wiss. Erg. Schwed. Südpolar-Exp. 4(8): 284. 1908. *Grimmia arachnoidea* Dusén, Rep. Princeton Univ. Exped. Patagonia 8: 122. 1903, nom. nud. TYPE: Chile. Aisén: Patag. occ. in valle fluminis Aysen, 18 Feb. 1897, *Dusén s.n.* (lectotype, here designated, H-BR).

Grimmia phyllorhizans Broth., Nat. Hist. Juan Fernandez 2(3): 419, tab. 26 fig. 21–24. 1924. TYPE: [Chile. Valparaíso:] Juan Fernández, Masatierra, Villagra, *Skottsberg 129* (lectotype, here designated, H-BR; isolectotypes, FH, NY, UPS).

Grimmia decurrentipilis Thér., in Felipp., Rev. Bryol. Lichénol. 2: 216, fig. 8. 1929. TYPE: Uruguay. [Canchones:] La Paz, *Felippone 837* (lectotype, here designated, PC).

Grimmia montevidensis Thér., in Felipp., Rev. Bryol. Lichénol. 2: 216, fig. 7. 1929. TYPE: Uruguay. Montevideo: Montevideo, *Felippone 839* (lectotype, here designated, BM; isolectotype, PC).

Gonioautoicous. Plants yellowish green above, brownish below. *Stems* erect, to 2 cm, with central strand. *Leaves* erect and appressed or somewhat flexuous apically when dry, patent to spreading when moist, 1.0–1.8 × 0.3–0.6 mm, lingulate to elliptic, obtuse to acute, keeled, not plicate; *margins* recurved from ⅓ to ½–⅔ the leaf length on one or both sides; *costa* semi-terete, differentiated, ventral epidermis 2 cells wide in cross section; *lamina* 1-stratose except for the 2-stratose two marginal rows and occasional streaks in the distal ⅔; *distal cells* 6–14 μm long, isodiametric, rectangular and oblate, not bulging, walls sinuous; *proximal juxtacostal cells* 10–70 × 10–15 μm, rectangular (1–4[8]: 1), walls thin and straight, occasionally thickened and nodulose; *proximal marginal cells* 15–35 × 10–15 μm, isodiametric to rectangular (1–2: 1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete, straight, to 2 mm, smooth to weakly denticulate. *Perichaetial leaves* 2 × 0.5–0.8 mm, convolute and larger than vegetative leaves (2 ×). *Androecia* below perichaetia. *Setae* curved, 3–4 mm long. *Capsules* exserted, ellipsoid or ovoid, symmetric, ribbed, stramineous, with stomata at the base; *exothecial cells* 30–50 × 13–20 μm, mostly rectangular ([1]2–3: 1), thin-walled; *annulus* compound and revoluble, *affinis* type; *peristome teeth* 50–60 μm wide at the mouth, entire, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, orange, contrasting with the urn; *opercula* rostellate to rostrate; *calyptrae* mitrate; *spores* 10–12 μm, minutely granulose.

Illustrations. Figure 39; Chałubiński (1882: tab. 4 fig. 4); Deguchi (1984: figs. 8, 9, as *G. pulvinata* var. *africana*); Lawton (1971: pl. 64 figs. 1–8); Maier and Geissler (1995: abb. 22); Smith (1978: fig. 151 1–5).

Distribution (Fig. 40). Europe, Africa, temperate and tropical Asia, Australasia, northern and southern America; Mexico, central Chile and Juan Fernández Islands, central Argentina, Tierra del Fuego, southern Brazil, Uruguay. This species is usually found in man-made habitats, such as concrete and limestone walls, roofs, and other kinds of constructions. In Latin America it grows on basic as well as acidic rocks like slate, seldom on tree bark, either dry or moist, in man-made habitats, rocky grasslands, and *Nothofagus* forests between sea level in southernmost Patagonia and 2250 m elevation.

Grimmia pulvinata has lingulate to elliptic leaves. Its perigonia lie cryptic just below the perichaetia and calyptrae are mitrate. Proximal juxtacostal cells are usually short-rectangular with thin, uniformly thickened walls. However, some populations have long-rectangular basal juxtacostal cells (up to 8: 1 length: width ratio) with wavy walls. Sporophytes are more variable, for capsule and opercula lengths. However, this variability is not taxonomically significant. A related taxon not present in Latin America is *G. orbicularis* Wilson, which is a cladautoicous taxon with elongate, nodulose, basal juxtacostal cells, and cucullate calyptra. Scattered across the world range of *G. pulvinata* there are collections gametophytically similar to *G. orbicularis* in their long, wavy basal juxtacostal cells. All of these are gonioautoicous, have mitrate calyptrae, and, for the most part, long rostrate operculae (e.g., U.S.A. California *Crosby 17705*, MO).

Differences between *G. pulvinata* and *G. pulla* are discussed under the latter species.

Described from the Juan Fernández Islands off the coast of Chile, *G. phyllorhizans* is a small plant to 0.3 cm high. It displays remarkably long hair-points, to 2 mm, relative to the overall size of the plants. Capsules are short, ovoid. Bulbiform terminal male buds are occasionally seen, but axillary perigonia predominate.

In his treatment on Patagonian mosses, Dusén (1903: 122) listed *G. arachnoidea* as a nomen nudum. In a later publication, he changed his identification to *G. orbicularis* (Dusén, 1906: 14). Cardot (1908: 109) considered this specimen to be *G. orbicularis*, but in the "Additions" appendix (Cardot, 1908: 284) he described the specimen *Dusén 587* as *G. orbicularis* var. *patagonica*. From this it is clear that there is only one specimen on hand, although renamed several times. Neither PC nor S has specimens collected by Dusén in the protologue locality and determined to *Grimmia orbicularis* or its variety *patagonica* by Cardot. Under these circumstances, the specimen identified as *G. arachnoidea* Dusén serves as lectotype of *G. orbicularis* var. *patagonica*, although the actual collection number does not appear on the label.

Additional specimens examined. MEXICO. **Baja California:** Sierra de San Pedro Mártir, Cerro de la Encantada, pass below observatory, *Sharp et al. 5596* (TENN), *5661-B* (TENN), *5663* (TENN), *6074* (TENN); Sierra de

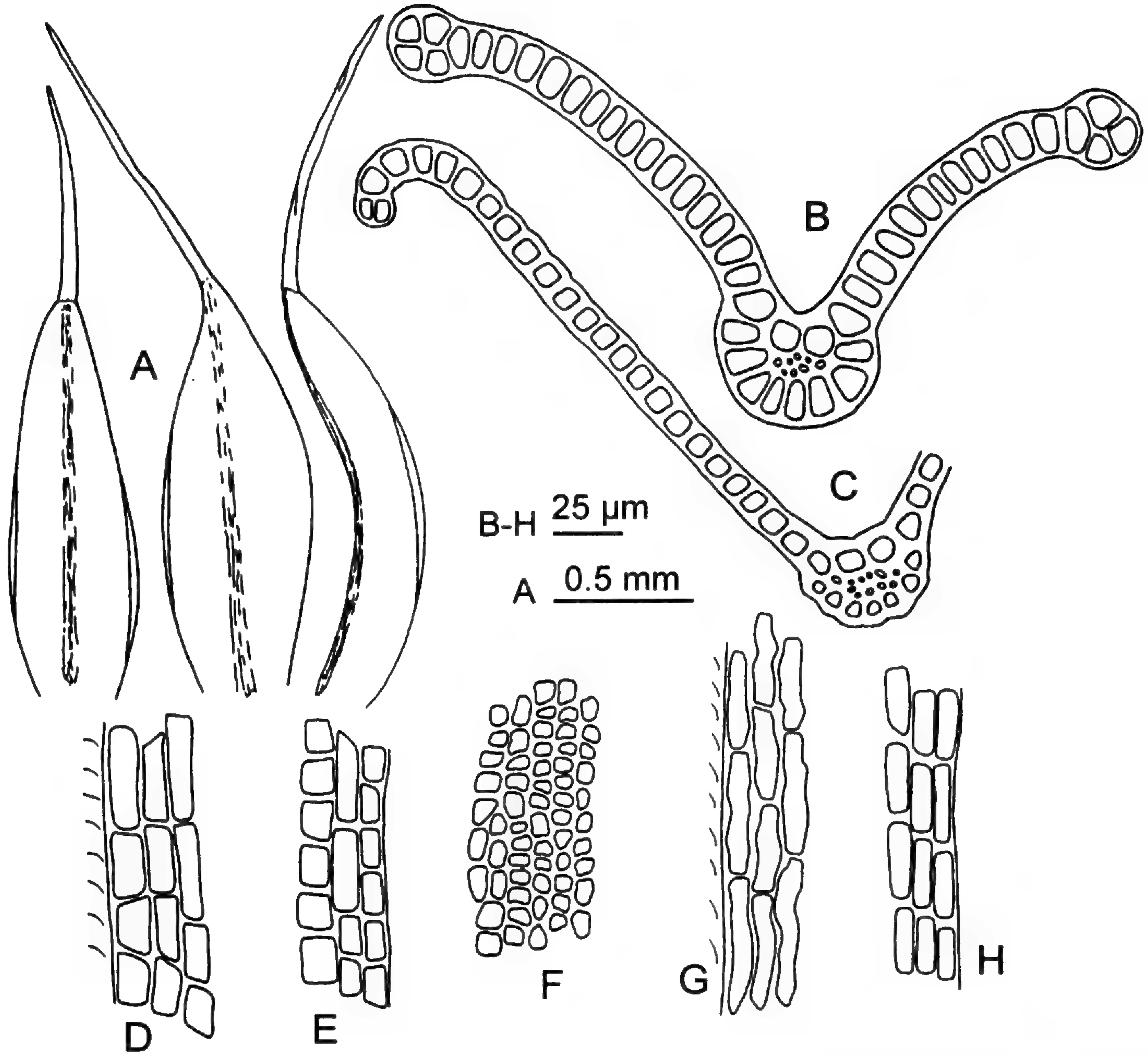

Figure 39. *Grimmia pulvinata.* —A. Leaves. —B, C. Transverse sections at medial and proximal parts of leaf. —D & G. Proximal juxtacostal leaf cells. —E & H. Proximal marginal leaf cells. —F. Distal leaf cells. (A–F: *Sharp et al. 6074*, TENN; G, H: *Dusén s.n.*, H-BR.)

San Pedro Mártir, below Meling Ranch, E of Colenett, *Sharp et al. 6099-A* (TENN); ca. 18 km SW de El Cóndor en Sierra de Juárez, *Meyer 43B* (TENN); Guadalupe Island, *Palmer 113* (MO).

ARGENTINA. **Catamarca**: Dept. Capital, lomas vecinas a la capital, *Castillón 1002* (MO, FH). **Córdoba**: Depto. Punilla, Río Yuspe, Weg nach La Candelaria, *Hosseus & Weihmüller 911* (FH), *911A* (FH), *913* (FH); bei des Estafeta Casa Nueva (Pedernera), *Hosseus 1830B* (FH); Weg von Tanti nach Los Gigantes, *Hosseus 2220* (FH), *2221* (FH), *2228* (FH); Weg von Ascochinga nach La Cumbre, *Hosseus & Weihmüller 2598* (FH); Depto. Colón, pedanía Río Ceballos, cerca de Colonchanga, *Hosseus 2433* (FH); Anfang der Quebrada de Los Cóndores, *Hosseus 2447* (FH), *2447A* (FH), *2447B* (FH), *2448* (FH), *2449* (FH). **Río Negro**: Parque Nacional Argentino Nahuel Huapi, 11 Sep. 1936, *Donat s.n.* (JE). BRAZIL. **Rio Grande do Sul**: Pinheiro Machado, *Vital 9155* (FLAS). CHILE. **Los Lagos**: Llanquihué, Saltos de Petrohué, *Deguchi 25159* (HIRO). **Magallanes**: Parque Nacional Torres del Paine, *Deguchi 26063* (HIRO), *26074* (HIRO), *26090* (HIRO), *26091* (HIRO), *26102A* (HIRO); Península de Brunswick, around Puerto del Hambre, *Deguchi 26374* (HIRO). **Valparaíso**: Islas Juan Fernández, Masatierra, Quebrada Mono, *Hatcher & Engel 470* (NY). URUGUAY. **Canelones**: La Paz, *Felippone 720* (H-BR), *837* (PC); Colonia, Estanzuela, July 1928, *Herter s.n.* (JE). **Montevideo**: Montevideo, *Arechavaleta s.n.* (H-BR, JE), *201* (NY), *215* (NY), *Felippone 990* (PC), *2439* (PC), *Gibert 1262* (NY), *Herter 1267* (FH); Pocitos, pr. Montevideo, *Felippone 960 p.p.* (PC).

26. Grimmia reflexidens Müll. Hal., Syn. Musc. Frond. 1: 795. 1849. TYPE: Chile. *Pöppig s.n.* (lectotype, designated by Muñoz (1998d), BM; isolectotypes, JE, NY, PC).

For a list of synonyms, see Muñoz (1998d).

Cladautoicous or goniautoicous. Plants yellowish green at the tips. *Stems* erect, to 1 cm, with

Figure 40. Distribution of: ● *Grimmia pulvinata*; ▲ *Grimmia tergestina*; ■ *Grimmia tortuosa.*

central strand. *Leaves* erect and appressed when dry, patent to spreading when moist, 1.0–1.8 × 0.25–0.45 mm, ovate to lanceolate, acute, keeled, plane or very weakly plicate; *margins* plane or recurved proximally, to ½ the leaf length on one side, occasionally both sides briefly recurved proximally; *costa* semi-terete, differentiated, ventral epidermis 2 cells wide in cross section; *lamina* 2-stratose in the distal ⅔; *distal cells* 8–12 µm long, isodiametric, bulging or not, walls straight to slightly sinuous; *proximal juxtacostal cells* 15–55 × 8–15 µm, usually rectangular ([1]1.5–6.0 : 1), walls medium-thick and straight; *proximal marginal cells* 10–50 × 8–15 µm, isodiametric to rectangular (1–5 : 1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete, straight, to 1.5 mm, entire or very weakly denticulate. *Perichaetial leaves* 1.8–2.7 × 0.5–0.85 mm, convolute and larger than vegetative leaves (2×). *Androecia* axillary or terminal. *Setae* erect and straight, 1.5–3.0 mm long. *Capsules* exserted, ovoid, symmetric, smooth, stramineous, with stomata at the base; *exothecial cells* 35–70 × 10–35 µm, rectangular (1.5–3 : 1), thin-walled; *annulus* simple and persistent, *Schistidium* type; *peristome teeth* 45–70 µm wide at the mouth, entire or irregularly cleft at apex, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, orange, contrasting with the urn; *opercula* conic or mammillate; *calyptrae* cucullate; *spores* 8–14 µm, minutely granulose.

Illustrations. Figure 41; Bell (1984: fig. 1); Cao and Vitt (1986: fig. 20 a, c, e–l, n, p, q, s, u); Cardot (1908: fig. 51); Deguchi (1978: fig. 41, as *G. subsulcata*); Maier and Geissler (1995: fig. 23, as *G. sessitana*); Muñoz (1998d: fig. 16).

Distribution (Fig. 36). Europe, Africa, temperate and tropical Asia, Australasia, Antarctic, northern and southern America; Andean Range from Bolivia to Tierra del Fuego. *Grimmia reflexidens* grows on rocks of unknown nature in open areas above the tree line, in snow beds and other harsh environments fed by thawing snow, between 1400 and 2600 m elevation in southern South America, but it reaches 5060 m in Bolivia.

Grimmia reflexidens is an autoicous taxon with narrowly keeled, bistratose leaves, straight setae, and stramineous capsules with stomata. It is widely distributed and gametophytically variable: identification of sterile specimens may be impossible.

To date, the geographical distributions of *G. montana*, *G. reflexidens*, and *G. ungeri* are not known to overlap. Consequently, incomplete specimens from South America can be assumed to be *G. reflexidens*. However, *G. reflexidens* is likely to be also present in high elevations in Mexico, within the geographic range of *G. montana* and *G. ungeri*. The use of sporophyte characters for correct identification is therefore indispensable within this species grouping.

Additional specimens examined. ARGENTINA. **Río Negro**: west. Bariloche am S. Ufer des L. Nahuel Huapi, 21 Feb. 1922, *Schiller s.n.* (JE); lac Nahuelhuapí, *Dusén 718* (H-BR). **Santa Cruz**: près des sources du río Ñirchuao, au sud de Pampa Chica, *Skottsberg 976* (PC); río Tarde, *Halle 369* (BM, H-BR, PC). BOLIVIA. **Oruro**: prov. Sajama, Cerro Chucarero, *Lewis 79-2092* (F, IBA), *79-2095A* (F, IBA); prov. Sajama, Cerro Achuta, *Lewis 84-305a* (F, IBA). CHILE. **Aisén**: Coyhaique, Cerros Divisaderos (Cordón de Bella Vista), *Santesson M340* (FH). **Libertador General Bernardo O'Higgins**: Colchagua, Vegas del Flaco, *Mahú & Tapia 50220, 50221* (MO). **La Araucanía**: Cautín, volcán Llaima, *Sparre 4832* (FH). **Los Lagos**: Osorno, Ottoshöhe, S Ufer des Lago Nahuel Huapi, *Schiller 25* (PC). **Región Metropolitana**: Santiago, laguna Lo Encanado, *Mahu 5539* (NY); El Volcán, *Santesson M123* (FH).

27. Grimmia tergestina Tomm. ex Bruch & Schimp., Bryol. Europ. 3: 126, tab. 258. 1845. *Grimmia tergestina* var. *eutergestina* Loeske, Laubm. Eur. Part I: 80. 1913, nom. inval. TYPE: Italy. Bosco de Melara bei Triest [. . .] zwischen Longera und Bozzal, Mar. 1845, *Tommasini s.n.* (lectotype, designated by Cao & Vitt (1986), BM; isolectotypes, BM 3 replicates, H-SOL).

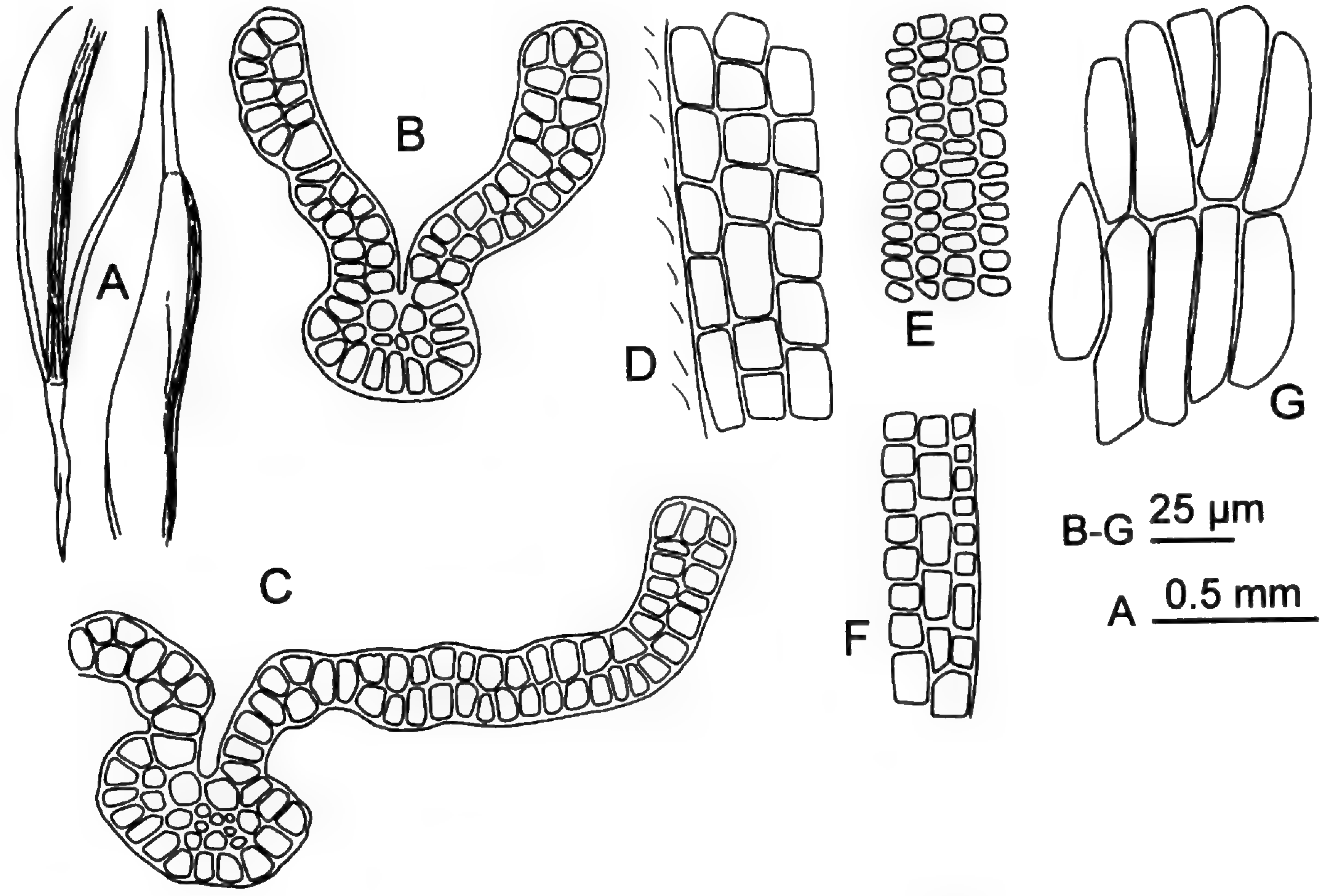

Figure 41. *Grimmia reflexidens.* —A. Leaves. —B, C. Transverse sections at distal and medial parts of leaf. —D. Proximal juxtacostal leaf cells. —E. Distal leaf cells. —F. Proximal marginal leaf cells. —G. Medial exothecial cells. (*Mahú 5539,* MO.)

Dioicous. Plants olive-green to blackish. *Stems* erect, to 2 cm, with central strand. *Leaves* erect and appressed when dry, erect to patent when moist, 0.9–1.5 × 0.3–0.5 mm, ovate to lanceolate, obtuse to acuminate, concave, not plicate; *margins* plane; *costa* semi-elliptical, undifferentiated, ventral epidermis 2–6 cells wide in cross section; *lamina* 2-stratose in the distal ⅔; *distal cells* 6–13 µm long, isodiametric, rectangular and oblate, not bulging, walls straight to slightly sinuous; *proximal juxtacostal cells* 17–50 × 9–15 µm, rectangular (2–3: 1), walls thin to moderately thick and straight; *proximal marginal cells* 10–30 × 10–20 µm, isodiametric to rectangular (1–2: 1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete distally and flat proximally, occasionally somewhat decurrent, straight, to 2 mm, smooth to dentate. *Perichaetial leaves* 2.0–2.5 × 1.0–1.2 mm, convolute, hyaline and filmy, scarcely discernible, larger than vegetative leaves (3.0–3.5: 1). *Androecia* terminal. *Setae* erect and straight, 0.7–1.0 mm long. *Capsules* immersed, ovoid, symmetric, smooth, stramineous, with stomata at the base; *exothecial cells* 20–70 × 15–35 µm, rectangular (1.5–3.0: 1), thin-walled; *annulus* compound and revoluble, *affinis* type; *peristome teeth* 65–85 µm wide at the mouth, cribrose throughout and irregularly cleft at apex, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, orange, contrasting with the urn; *opercula* rostrate; *calyptrae* mitrate; *spores* 10–16 µm, minutely granulose.

Illustrations. Figure 42; Bruch and Schimper (1845: tab. 21); Cao and Vitt (1986: fig. 29, but basal marginal cells inaccurate, drawn from outer perichaetial leaves); Chałubiński (1882: tab. 8 fig. 13); Maier and Geissler (1995: abb. 26); Nowak and Poelt (1979: figs. 8–11); Orbán and Vajda (1983: fig. 330 a–c); Vaněk (1940: figs. 1–11).

Distribution (Fig. 40). Europe, temperate Asia, northern and southern America; Caribbean, Peru, Bolivia. *Grimmia tergestina* grows in rocks and outcrops of undefined nature in open areas above the tree line in Bolivia and Peru, and in outcrops in pine forests in the Dominican Republic, between 2840 and 4520 m elevation.

Plants of *Grimmia tergestina* have bistratose leaves, indistinct costae, strongly modified perichaetial leaves, and symmetric capsules on a straight and erect seta. For its discrimination from

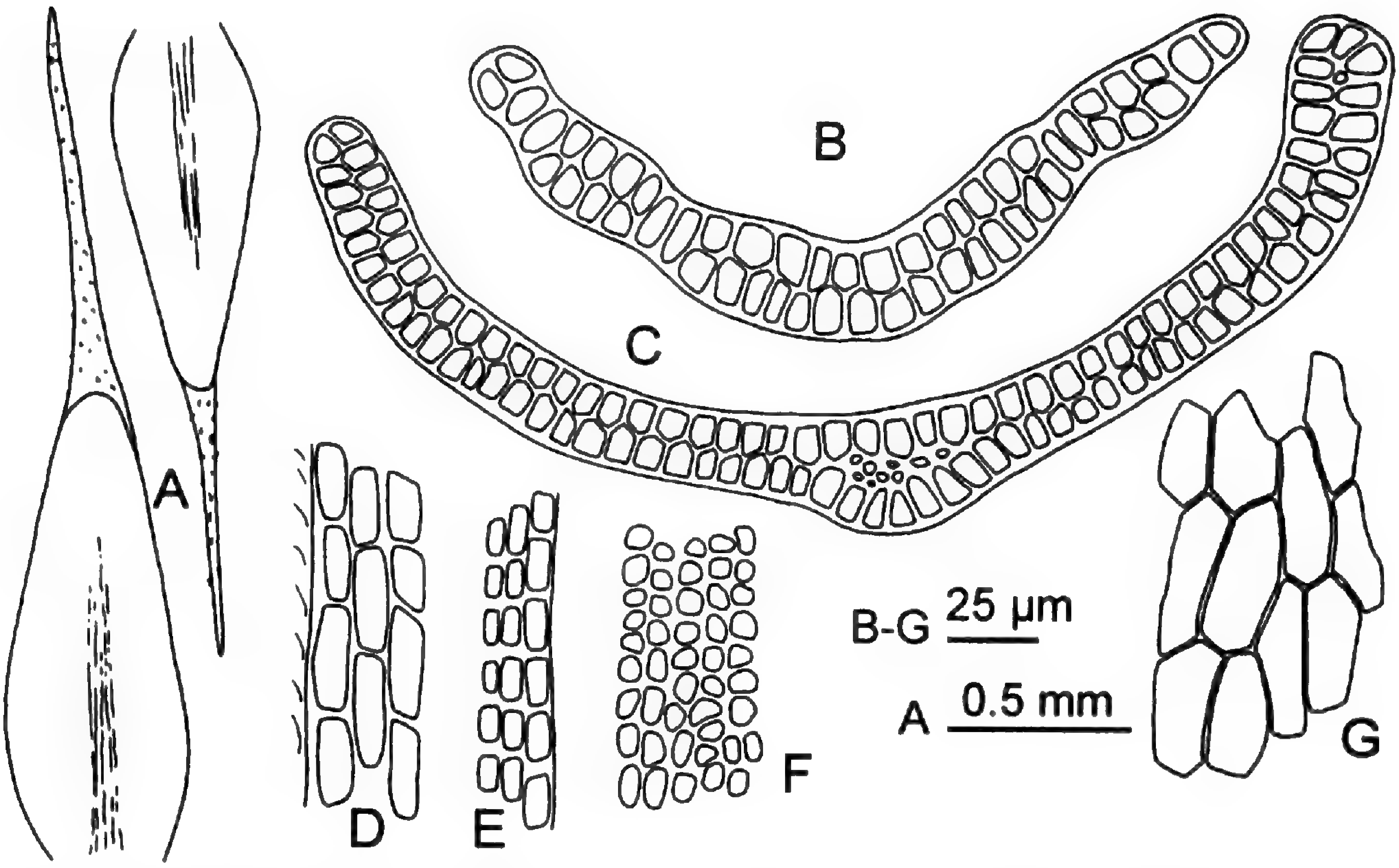

Figure 42. *Grimmia tergestina.* —A. Leaves. —B, C. Transverse sections at distal and medial parts of leaf. —D. Proximal juxtacostal leaf cells. —E. Proximal marginal leaf cells. —F. Distal leaf cells. —G. Medial exothecial cells. (*Buck 8575,* NY.)

G. americana, G. involucrata, and *G. poecilostoma,* see the discussion under *G. poecilostoma.*

Bolivian and Dominican specimens have mature sporophytes, allowing unequivocable identifications. Unfortunately, Peruvian specimens are totally barren. As stated under *G. poecilostoma, Grimmia tergestina* belongs to a complex of taxa that can only be confidently determined from sporophytic material. Peruvian specimens are tentatively placed in *G. tergestina* based on these species distribution ranges.

Additional specimens examined. DOMINICAN REPUBLIC. **La Vega**: Alto de la Bandera, near summit, *Buck 8575* (NY).

BOLIVIA. **Potosí**: prov. Chayanta, 1 km NE of Macha, *Lewis 84-1641* (F, IBA); prov. Tomás Frías, cerro Kari Kari, *Lewis 79-243* (F). PERU. **Junín**: Jauja, südlich Canchayllo, *Hegewald & Hegewald 5848A* (MO); Tarma, Cerro Quinchomachay bei Tarma, vor Pueblo Coches Bajo, *Hegewald & Hegewald 6262* (IBA, MO).

28. Grimmia tortuosa Hook.f. & Wilson, London J. Bot. 3: 540. 1844. TYPE: Falkland Islands, 1839–1843, *Hooker s.n.* (lectotype, here designated, BM; isolectotypes, BM 7 replicates, FH 4 replicates, H-SOL, NY).

Gonioautoicous. Plants dark green to blackish. *Stems* erect, to 1.5 cm, central strand lacking or weakly developed. *Leaves* flexuous and crisped when dry, erect to patent when moist, 2.5–3.2 × 0.5–0.7 mm, lanceolate, acuminate, keeled, not plicate; *margins* plane; *costa* semi-terete to terete, differentiated, ventral epidermis 2 cells wide in cross section; *lamina* 1-stratose, 2-stratose at margins and seldom in streaks in the distal ⅔; *distal cells* 6–9 µm long, isodiametric, seldom oblate, not bulging, walls straight to slightly sinuous; *proximal juxtacostal cells* 30–100 × 12–20 µm, rectangular (1.5–7.0 : 1), walls thin and straight to slightly nodulose; *proximal marginal cells* 40–120 × 10–16 µm, rectangular (3–10 : 1), the walls thin and straight, all alike, scarcely discernible; *hyaline hair-points* terete, straight, to 1.2 mm, smooth to denticulate. *Perichaetial leaves* 3–4 × ca. 0.8 mm, somewhat larger than vegetative leaves (1.5 ×), otherwise undifferentiated. *Androecia* below perichaetia. *Setae* straight, 0.5–0.6 mm long. *Capsules* immersed, cyathiform, symmetric, smooth, blackish, with stomata at the base; *exothecial cells* 14–30 × 4–10 (lumen) µm, elliptical (2–7 : 1), strongly thick-walled; *annulus* compound and tardily deciduous, *elongata* type; *peristome teeth* 90–110 µm wide at the mouth, entire to cribrose and irregularly cleft at apex, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, orange, contrasting with the urn; *opercula* conic to mammillate; *calyptrae* mitrate; *spores* 8–10 µm, minutely granulose.

Illustrations. Figure 43; Cao and Churchill

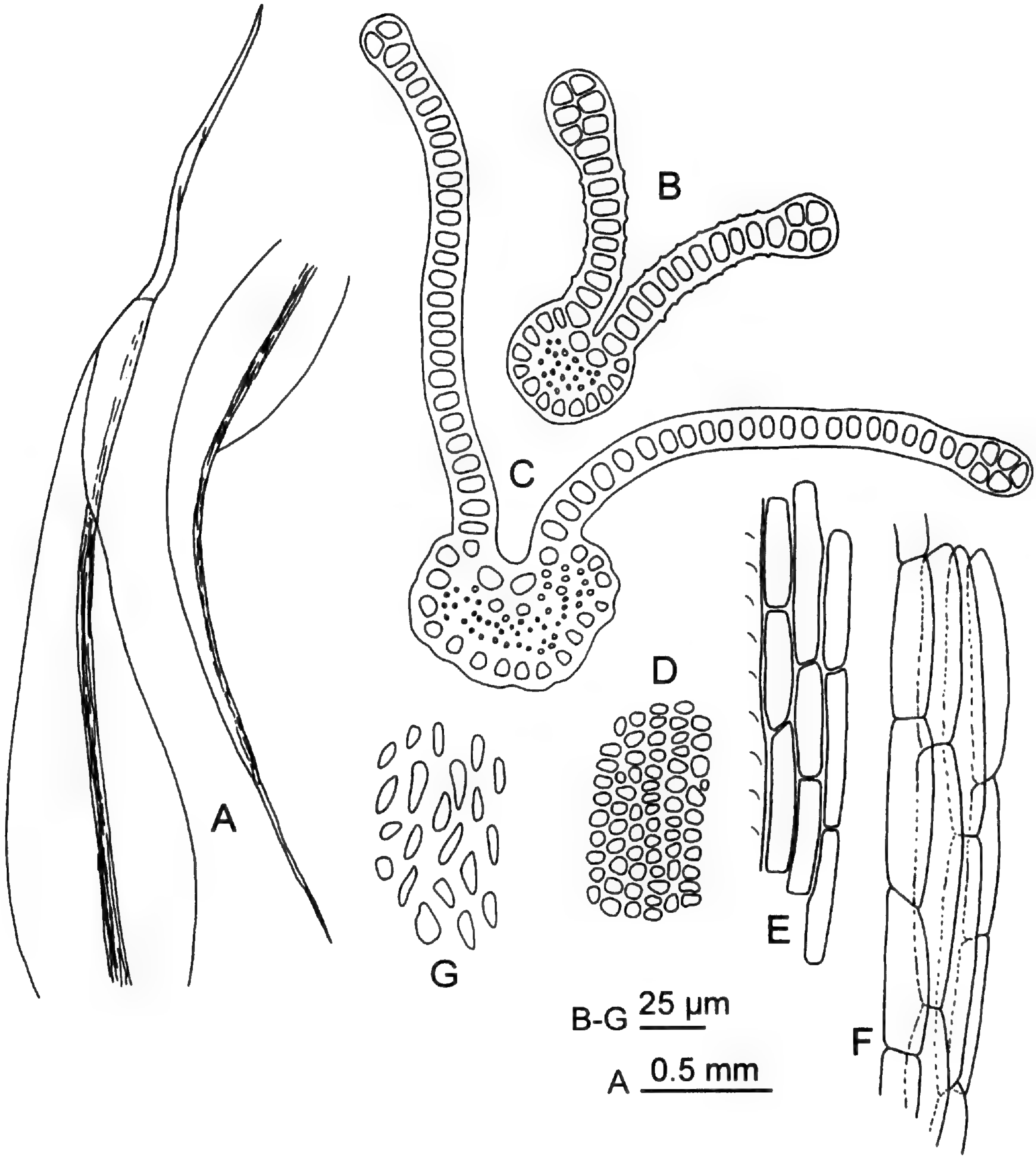

Figure 43. *Grimmia tortuosa.* —A. Leaves. —B, C. Transverse sections at distal and medial parts of leaf. —D. Distal leaf cells. —E. Proximal juxtacostal leaf cells. —F. Proximal marginal leaf cells. —G. Medial exothecial cells. (*Hooker s.n.*, BM.)

(1995b: pl. 1); Wilson and Hooker (1847: pl. 151 fig. 7).

Distribution (Fig. 40). Antarctic. Known only from the original collection made by J. D. Hooker on Mount Vernet, Falkland Islands, but its presence in southern South America is likely. According to Wilson and Hooker (1847: 400), the plants were growing on dry quartz rocks at 300 m elevation.

Material of *Grimmia tortuosa* is characterized by straight setae, immersed capsules with strongly incrassate exothecial cell walls, perigonia situated just below the perichaetia, and proximal cells of the leaves being thin-walled, lax, and inflated.

Ochyra (1993: 227) reported *G. tortuosa* from South Georgia (***Walton et al. BAS Misc. 166,*** BM), but this specimen is better referred to *G. incrassicapsulis* Bell. The latter can be differentiated from *G. tortuosa* by its asymmetric, ventricose capsules on curved setae.

Cao and Churchill (1995: 515) erroneously reported that Cardot (1902) had cited *G. tortuosa* from "the antarctic." However, Cardot (1902: 7) only cited *G. tortuosa* in a list of the species of the "Terres Magellaniques" considered endemic to that area. New collections were not listed by Cardot. His report obviously refers to the Falkland Islands specimen collected by Hooker, with Cardot (1902: 5) stating, "Sous le dénomination de Terres magellaniques, je comprends . . . et les îles Falkland ou Malouines. . . ."

Specimens examined. FALKLAND ISLANDS. Mount Vernet, 1839–1843, *Hooker s.n.* (BM, FH, FH-SULL, H-SOL, NY, TCD).

29. Grimmia trichophylla Grev., Fl. Edin: 235. 1824. *Grimmia affinis* Hornsch. ex Brid., Bryol. Univ. 1: 771. 1827, nom. nud. pro synon. *Dryptodon trichophyllus* (Grev.) Brid., Bryol. Univ. 1: 771. 1827. *Grimmia trichophylla* subsp. *eutrichophylla* Loeske, Laubm. Eur. I: 128, fig. 37, 38. 1913, nom. inval. TYPE: [United Kingdom.] Scotland: Edinburgh, *Greville s.n.* (lectotype, designated by Geissler & Maier (1995), E not seen; isolectotypes, FH, H-SOL).

Grimmia consobrina Kunze ex Müll. Hal., Syn. Musc. Frond. 1: 785. 1849. TYPE: Chile. *Pöppig s.n.* (lectotype, here designated, NY; isotypes BM 2 replicates).

Grimmia imberbis Kunze ex Müll. Hal., Syn. Musc. Frond. 1: 788. 1849. TYPE: Chile. *Kuntze s.n.* (lectotype, here designated, JE).

Grimmia trichophylla var. *meridionalis* Müll. Hal., Syn. Musc. Frond. 1: 785. 1849. *Grimmia trichophylla* subsp. *meridionalis* (Müll. Hal.) Loeske, Biblioth. Bot. 101: 171. 1930. TYPE: Spain. Granada: In coll. siccis prope Granatam, *Schimper s.n.* (lectotype, here designated, H-SOL; isolectotype, NY; syntype, NY [Spain. Madrid: El Escorial, *Schimper s.n.*]).

Grimmia crispatula Müll. Hal. & Hampe, Linnaea 26: 499. 1855. *Grimmia crispata* Müll. Hal. & Hampe ex Mitt., Trans. Roy. Soc. Victoria 19: 55. 1882, nom. inval. orthogr. err. TYPE: [Australia. South Australia:] Flinders range. (lectotype, here designated, H-SOL; isolectotype, MEL; syntypes, [. . . juxta rivulum Fift creek] H-SOL, MEL).

Grimmia densa Kindb., Bull. Torrey Bot. Club 17: 271. 1890. *Grimmia depilata* Kindb., in Macoun & Kindberg, Cat. Canad. Pl., Musci 69, 1892, nom. illeg. incl. sp. prior. TYPE: [Canada. British Columbia:] Vancouver Island, Mt. Benson, 8 June 1887, *Macoun s.n.* (lectotype, here designated, S; isolectotype, CANM-198083).

Grimmia sardoa var. *gracilis* Warnst. & M. Fleisch., Bot. Centralbl. 65: 299. 1896. *Grimmia trichophylla* var. *gracilis* (Warnst. & M. Fleisch.) Paris, Index Bryol. Suppl. 176. 1900. *Grimmia trichophylla* f. *gracilis* (Warnst. & M. Fleisch.) Podp., Consp. Musc. Eur. 288. 1954. TYPE: Italy. Romano: Monti Albani, Mt. Cavo, 7 June 1895, *Fleischer s.n.* [Fleischer & Warnstorf, Bryotheca europaea meridionalis. Cent. 1, n° 55. 1896] (lectotype, here designated, FH).

Grimmia trichophylla var. *teneriffae* Renauld & Cardot, Bull. Herb. Boissier, sér. 2, 2: 436. 1902. TYPE: [Spain.] Santa Cruz de Tenerife: Las Cañadas, 1896, *Tullgren s.n.* (lectotype, here designated, PC).

Grimmia macropulvinata Dusén, Rep. Princeton Univ. Exped. Patagonia 8: 78, fig. 8, pl. 8 fig. 7. 1903. TYPE: "Patagonia austr." [verosimiliter Chile. Magallanes: in territorio fontinali fluminis Río Chico in saxis], 1896–1897, *Hatcher s.n.* (lectotype, here designated, S; isolectotypes, FH, NY).

Grimmia flexicaulis var. *dicksonii* Dusén, Bot. Not. 1905: 303. 1905. *Grimmia dicksonii* (Dusén) Dusén, Ark. Bot. 6(10): 14. 1907, nom. nov., nom. illeg., non Turner, 1804. TYPE: Chile. Aisén: Patagonia, in vallis fluminis Aysén, 11 Feb. 1897, *Dusén s.n.* (lectotype, designated by Deguchi (1984), S-PA not seen; isolectotypes, FH 2 replicates).

Grimmia pachyphylla Dusén, Bot. Not. 1905: 302. 1905, nom. illeg., non Müll. Hal., 1885. TYPE: [Chile. Aisén:] Patagonia occ. in valle flumini Aysen, 11 Feb. 1897, *Dusén s.n.* (lectotype, here designated, H-BR).

Grimmia trichophylla var. *subincurva* H. Winter, Hedwigia 55: 101. 1914. TYPE: Portugal. Madeira: Levada de Gordon, May 1912, *Winter s.n.* (lectotype, here designated, JE).

Grimmia gusindei J. Froehl., Ann. Naturhist. Mus. Wien 59: 117. 1953. TYPE: [Chile. Magallanes:] Canal Beagle, *Gusinde 359* (lectotype, here designated, S).

Dioicous. Plants green to yellowish green. *Stems* erect, to 3 cm, with central strand. *Leaves* flexuous when dry, erect to spreading when moist, 1.5–3.0 × 0.4–0.7 mm, lanceolate, acuminate, keeled, not plicate; *margins* recurved proximally, to ½–⅔ the leaf length on one side and flat or more narrowly recurved proximally, to ⅓–½ the leaf length on the other side, occasionally both margins plane; *costa* semi-terete, differentiated, ventral epidermis 2 cells wide in cross section; *lamina* 1–2-stratose, 2-stratose at margins and in streaks in the distal ⅔; *distal cells* 7–12 μm long, isodiametric to rectangular, not bulging, walls sinuous; *proximal juxtacostal cells* 20–90 × 7–14 μm, rectangular (2–11 : 1), walls thin and straight to medium-thick and nodulose; *proximal marginal cells* 15–35 × 10–14 μm, rectangular (2–4 : 1), the transverse walls thicker than the longitudinal walls; *hyaline hairpoints* terete, straight to flexuous, to 1.2 mm, smooth to denticulate. *Propagula* 35–60 μm diam., spherical to broad-ellipsoid, multicellular, sessile on the dorsal side of upper lamina, seldom on the costa, olive-green to brownish with brownish walls. *Perichaetial leaves* 2.0–2.7 × 0.6 mm, convolute proximally and prolonged in a very narrow acuminate distal half, larger than vegetative leaves (1.5 ×). *Androecia* terminal. *Setae* curved, 3–5 mm long. *Capsules* exserted, ellipsoid, symmetric, ribbed, stramineous, with stomata at the base; *exothecial cells* 20–50 × 15–30 μm, rectangular (2.0–3.5 : 1), thin-walled; *annulus* compound and revoluble, *af-*

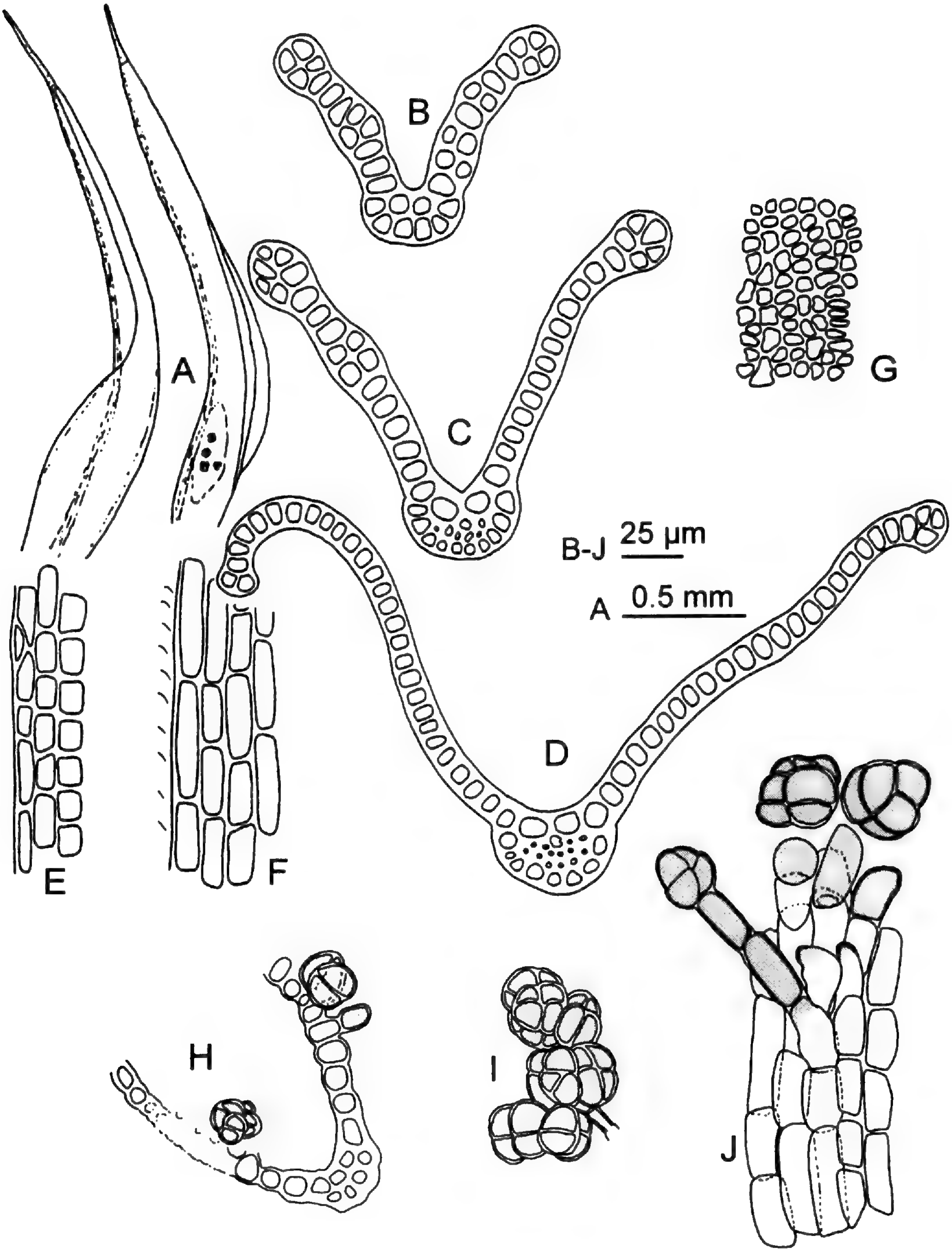

Figure 44. *Grimmia trichophylla.* —A. Leaves. —B–D. Transverse sections at distal, medial, and proximal parts of leaf. —E. Proximal marginal leaf cells. —F. Proximal juxtacostal leaf cells. —G. Distal leaf cells. —H. Transverse section at propaguliferous area. —I. Cluster of propagula. —J. Propaguliferous area showing hyaline, inflated cells and liberated propagula. (A–G, J: *Sharp 6058*, TENN; H, I: *Hatchmann s.n.*, NY.)

finis type; *peristome teeth* 55–70 µm wide at the mouth, irregularly cleft at apex, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, orange, contrasting with the urn; *opercula* rostrate; *calyptrae* mitrate; *spores* 11–14 µm, minutely granulose.

Illustrations. Figure 44; Maier and Geissler

Figure 45. Distribution of *Grimmia trichophylla.*

(1995: abb. 28 a, c, g, but b and d–f, are most probably *G. lisae*); Petrov (1975: tab. 61 fig. 3); Smith (1978: fig. 152 1–6, 10–12, as var. *tenuis*; 13–15, as var. *subsquarrosa*; 16–19, as var. *stirtonii*).

Distribution (Fig. 45). Europe, Africa, temperate and tropical Asia, Australasia, northern and southern America; Mexico, Mesoamerica, Andean Range from Venezuela to Tierra del Fuego. On acid, seldom basic, dry rocks and trunk bases in open areas, paramos and forests between sea level in southernmost Patagonia and 5200 m elevation in Ecuador.

Plants of *G. trichophylla* have semi-terete costae with 2 cells in the ventral epidermis cross sections. Propagula are sessile on the lamina; the leaves are bistratose along the margins and in streaks, and are usually flexuous, yellowish and dull. Stems are erect, to 3 cm, and are generally shorter and more branched than those of related *G. austrofunalis.* For problematic specimens, features related to the propagula best identify the species. Propagula attributes appear stable, and only one specimen of *G. trichophylla* (Mexico, *Sharp et al. 1660b*, TENN) has been seen with two long, slightly branched filaments, but producing small propagula. The sequence of formation of the propagula in *G. trichophylla* is illustrated in Figure 44.

In *Grimmia trichophylla,* a patch of otherwise normal mature green cells of the lamina, with thick and nodulose walls, typically dedifferentiate, becoming hyaline, thin-walled, and inflated. Subsequently these laminar cells distally protrude (either ventrally or dorsally) outward from the lamina, forming a 1- or 2-celled brownish filament. Each cell of the filament divides several times to generate the propagula, a process initiating with the distalmost cell. Proximal cells of each filament, appearing in the first stages of development like a short stalk, also undergo consecutive perpendicular divisions and become part of the gemma, whereas the mother cell shrinks. The eventual collapse of all laminar cells originally involved in the gemmae development produces the degeneration and subsequent destruction of the leaf. Several propagula occasionally coalesce to form a bigger cluster, of the type seen in *G. austrofunalis,* but this is not common in *G. trichophylla.* In fact, typical small propagula are always abundant in these populations of *G. trichophylla* with only some larger, clustered propagula evident. This was first observed by Correns (1899: 108, fig. 63L), who recognized the differences in propagula morphology and development between *G. trichophylla* and *G. muehlenbeckii.*

I have studied several specimens from southern Chile that deviate markedly in leaf shape (e.g., *Barros 6856, 6957, 8629, 8652, Dusén 123, 366 p.p., 555,* and *Skottsberg 378*). These Chilean collections have widely ovate leaves, wider even than typical in *G. austrofunalis,* and developing distinct auricles. Nevertheless, these specimens bear small, sessile propagula on the lamina, and all other characters are consistent with typical *G. trichophylla.* These collections are maintained in *G. trichophylla* because specimens with similar characters are seen from other localities outside the range of *G. austrofunalis.*

Grimmia trichophylla has been confused with *G. austrofunalis* and *G. lisae.* Costae reniform in cross section, with 4 to 6 cells in the ventral layer, rapidly discriminate *G. lisae.* Specimens of *G. austrofunalis* and *G. trichophylla* are more difficult to distinguish. *Grimmia austrofunalis* is a larger plant, to 8 cm tall, with ascendent and scarcely branched stems; leaves are straight (or slightly flexuous at apices), strongly glossy, and with a reddish tinge. Leaves of *G. austrofunalis* usually have wider bases than those of typical *G. trichophylla* (but see prior discussion about Chilean anomalous specimens). Finally, leaves in *G. austrofunalis* are essentially unistratose. The best characters to separate both species remain the point of origin and morphology of the gemmae (Figs. 7, 8, 44).

Grimmia trichophylla is a problematic species for most bryologists. It often tends to be the specific assignment given to otherwise unnameable specimens. The identification to species of most *Grimmia* can be confidently determined from sporophytic material. However, sporophytes are of little value in the *G. austrofunalis–G. trichophylla* pair, being identical in both taxa except for spore ornamentation. Additionally, the synonymy of several disparate taxa under *G. trichophylla* has contributed to its problematic status. Nevertheless, the removal of extraneous taxa such as *G. austrofunalis* and *G. lisae* minimizes variability within *G. trichophylla.* Granted the taxon is variable; however, if considered in the restricted sense of this paper, it probably does not vary more than other species in the genus, e.g., *G. longirostris* or *G. pilifera.*

Additional specimens examined. COSTA RICA. **Cartago**: El Guarco Cantón, Cordillera de Talamanca, páramo Buenavista, carretera interamericana km 85, *Dauphin 1690* (MO). GUATEMALA. **Quetzaltenango**: Getena area, N of Sija, *Sharp 2211* (TENN, FH). **San Marcos**: near summit of Tajamulco, *Sharp 5415* (TENN), *5421* (TENN), *5434* (TENN), *5439* (TENN), *5441* (TENN); upper slopes of Volcán Tacaná, *Steyermark 36091* (FH); mountains along the road between San Marcos and Serchil, *Standley 85410* (FH). **Totonicapán**: Región de Chiu Jolom, mountains above Totonicapán, on road to Desconsuelo, *Standley 84451* (FH, UC), *84462* (FH), *84474* (FH, UC). MEXICO. **Baja California**: Sierra de San Pedro Mártir, Cerro de la Encantada, *Sharp et al. 5660-B* (TENN), *5662* (TENN), *5664* (TENN), *6058* (TENN), *6073* (TENN); Guadalupe Island, Oct. 1896, *Anthony s.n.* (NY), *Palmer 113A* (MO). **Chiapas**: cima del Cerro Mozotal, 30 km NW de Motozintla, *Delgadillo 4779* (CAS). **Distrito Federal**: monte Alegre, 19 Feb. 1927, *Antipovitch s.n.* (PC). **Durango**: 9 mi. W of La Ciudad, *Bowers et al. 5061* (TENN), *Norris et al. 20896A* (UC). **Hidalgo**: National Park near Mineral del Chico, *Sharp et al. 81* (TENN), *95D* (TENN), *1686* (TENN). **Michoacán**: Cerro del Águila, 15 km N de Capácuaro, *Cárdenas S. 5502* (MO), *5981* (MO); about 1 mi. E of Las Penas on Hwy. 15, *Norris & Taranto 15642* (UC). **México**: 14 km E of San Pedro Nexapa, *Delgadillo 1148* (TENN), *1151* (TENN); Desierto de Los Leones near México City, *Sharp 72A* (TENN); Ixtapaluca, lado S del Cerro del Telapón, *Flores 308* (ALTA); Mt. Ixtaccíhuatl, *Kiener 18518A* (FH); Popocatépetl, *Hermann 20796* (TENN), *Hermann 20822* (TENN), *Horton 7457* (TENN), *Sharp 4761* (TENN); NW slopes of Nevado de Toluca, *Pócs 9550/J* (MO), *Sharp et al. 1334* (TENN), *Sharp et al. 1335* (TENN), *Sharp et al. 1341A* (TENN); Zinacantepec, Raíces, *Rzedowski 27260* (TENN, UC); above Río Frío, *Sharp et al. 1660C* (TENN), *Mexía 2702* (UC). **Oaxaca**: along route 175, Sierra Juárez, 20 mi. N of Ixtlán, *Hermann 26223* (TENN). **Puebla**: along route 119, 15 mi. S of Chignahuapan, *Hermann 26444* (TENN); below las cuevas de Ixtaccíhuatl above Huejotzingo, *Sharp 4296* (TENN), *Sharp 4296A* (TENN), *Sharp 4306* (TENN); near Tlamacas, *Delgadillo 1165* (TENN). **Veracruz**: in summo Pic d'Orizaba, *Liebmann s.n.* (PC); Xalapa, *Bonpland s.n.* (PC); La Muñeca, above Perote, *Sharp 3656* (TENN); Cofre de Perote, 2 Oct. 1984, *García s.n.* (ALTA), *Iltis et al. 891* (TENN), *892* (TENN), *893* (TENN), *897* (TENN), *Sharp et al. S6AB* (TENN). **Zacatecas**: Cerro de la Bufa, 9 June 1979, *Cárdenas 343* (ALTA). PANAMA. **Chiriquí**: at summit of volcán Barú, *Allen 9093* (MO).

ARGENTINA. **Chubut**: Vallée 16 Oct., *Skottsberg 378* (BM, PC). **Río Negro**: Parque Nacional Argentino Nahuel Huapi, Puerto Guerrero, Isla Victoria, *Donat 77* (JE, PC), *78* (JE); San Carlos de Bariloche, *Donat 166* (JE); Nauelhuapí, *Dusén 717* (FH). **Santa Cruz**: Lago San Martín, *Skottsberg 380* (UPS). **Tucumán**: Cumbre de Cauhagui, Cuesta de las Cañas, Ostseite, June 1920, *Kühn s.n.* (BM). BOLIVIA. **La Paz**: prov. Larecaja, Nevado Jankho Uma, *Lewis 79-1546* (F, IBA); prov. Loayza, río Atoroma Chuma (Meta Camp), 11 km SE of Viloco, *Lewis 87-1812* (MO). CHILE. **Aisén**: río Aisén, *Dusén 502* (NY, PC), *555* (FH). **Bío-Bío**: Antuco, *Barros 6870* (FH); Chillán, Bureo, *Barros 6858* (FH), *8629* (FH), *8652* (FH); Calbuco, O. Küste, *Schwabe 114* (FH, PC); Coquimbo, 1838, *Gay s.n.* (PC); Los Ángeles, *Dusén 347* (JE, NY, PC), *366A* (FH, JE, NY, PC). **La Araucanía**: Malleco, Angol, El Vergel, *Hosseus 766* (JE); La Ermita, Los Condes, 60 km de Santiago, *Jaffuel 152* (PC); Cautín, Dept. Villarrica, Pucón, *Hosseus 407A* (JE); Villarrica, *Barros 6856* (FH). **Libertador General Bernardo O'Higgins**: Colchagua, Baños de Cauquenes, *Dusén 143* (PC), *145* (FH, JE, NY), *149* (FH, JE, NY), *151* (NY). **Los Lagos**: lago Pillaifa, río Llancahue, *Schawbe 10* (JE); Calbuco, *Schawbe 114* (JE); Chiloé, Dep. Llanquihué, Puerto Varas, in der Nähe des río Maullín, *Hosseus 294A* (JE); Valdivia, Dep. Corral, Amargos, *Hosseus 567* (JE), *589* (JE), *590A* (JE); Los Perales, Sep. 1919, *Bertho s.n.* (FH); Los Perales, Sep. 1923, *Bertho s.n.* (FH); Marga-Marga, 1916, *Costes s.n.* (BM); San José de la Mariquina, *Barros 6957* (FH). **Magallanes**: Jan. 1897, *Dusén s.n.* (BM). **Maule**: Linares, E of Linares along river Atchibuena, *Taylor & Gereau 11044* (FH). **Ñuble**: San Fabián ca. 60 km E of San Carlos, *Landrum 1504B* (NY); Panguipulli, *Hollermayer 72* (NY, PC); Recinto, 20 Apr. 1929, *Roivainen s.n.* (H). **Región Metropolitana**: Linares, Bullileo ca. 50 km E of Parral, *Landrum 1525A* (NY), *1526* (NY), *1528* (NY), *1538* (NY); Santa Lucia, *Schwabe 17B* (PC, JE). **Valparaíso**: Estero Marga Marga, *Schwabe 102/B* (JE); El Salto prope Valparaíso urbem, *Dusén 123* (NY); Alto del Puerto, *Santesson M150* (FH). COLOMBIA. **Antioquia**: Urrao, Páramo de Frontino, ca. 17 km directamente N de Urrao, *Churchill 13329* (MO). **Caldas**: Villamaría, carretera Manizales–Bogotá, sobre la carretera que conduce al Nevado del Ruiz (km 213), *Churchill et al. 16307* (IBA). ECUADOR. Avenida volcanica del Cotopaxi, *Espinosa 19* (JE). **Imbabura**: E side of Cerro Cotacachi, NW of Cotacachi, *Lewis 78-2705* (F), *78-2769* (F, UBC); E side of Cerro Imbabura above La Esperanza, ENE of Otavalo, *Lewis 78-2917* (F), *78-2918* (F), *78-2981* (F). **Pichincha**: second camp on Chimborazo, *Bell 153* (FH), *Whymper 1347* (BM). PERU. **Ancash**: Huari, zwischen Tunnel Cahuish und Chavin, Quebrada Pucavado, *Hegewald & Hegewald 7729* (MO). **Arequipa**: Arequipa, am Weg nach Puno, *Hegewald & Hegewald 5467* (MO), *5479* (MO). VENEZUELA. **Barinas**: distr. Urdaneta, páramo de La Estrella, *Griffin III et al. 1400* (FLAS). **Mérida**: páramo de Piñango, *Griffin III & Díaz M. PV-21* (FLAS); páramo de Los Conejos, *Griffin III & López F. PV-543* (FLAS); distr. Libertador, páramo de Don Pedro, *Ruiz-Terán & López-Palacios 8695* (FLAS); distr. Rangel, páramo de Mucubají, *Vareschi 8872* (FLAS), *8874* (FLAS). **Trujillo**: Ribas, páramo de la Teta de Niquitao, *Ruiz-Terán & López-Palacios 7525* (FLAS).

30. Grimmia trinervis R. S. Williams, Bull. New York Bot. Gard. 3: 124. 1903. *Coscinodon trinervis* (R. S. Williams) Broth., in Herzog, Biblioth. Bot. 87: 52. 1916. TYPE: Peru. Juliaca, *Williams 2814* (holotype, NY; isotype, F).

Dioicous. Plants glaucous or dark green to blackish. *Stems* erect, to 1 cm, with central strand. *Leaves* erect and appressed when dry, erect to patent when moist, 0.8–1.4 × 0.3–0.5 mm, obovate base suddenly narrowed into an acuminate apical part, acute, keeled, plicate; *margins* plane in the proximal half, incurved in the distal half and cucullate at tip; *costa* semi-terete, differentiated, ventral epidermis 2 cells wide in cross section; *lamina* 2-stratose in the distal ⅔; *distal cells* 6–14 μm long, isodiametric to rectangular, not bulging, walls straight to slightly sinuous; *proximal juxtacostal cells* 15–50 × 10–15 μm, rectangular, seldom isodiametric ([1]2–5:1), walls thin and straight to medium-thick and somewhat sinuous; *proximal marginal cells* 15–40 × 9–15 μm, isodiametric to rectangular (1–3:1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete, straight, to 1.3 mm, smooth. *Perichaetial leaves* 1.8–2.2 × 0.8–1.2 mm, convolute, hyaline and filmy, scarcely discernible, larger than vegetative leaves (3–5:1). *Androecia* terminal. *Setae* curved to coiled, 0.9–1.5 mm long. *Capsules* immersed, ovoid to subglobose, ventricose, smooth, stramineous, with stomata at the base; *exothecial cells* 25–60 × 24–30 μm, rectangular (1.5–2.5:1), thin-walled; *annulus* compound and tardily deciduous, *elongata* type; *peristome teeth* lacking; *opercula* conic; *calyptrae* mitrate; *spores* 10–12 μm, minutely granulose.

Illustrations. Figure 46; Deguchi (1987: pl. 15); Hastings (1996: figs. 1–10).

Distribution (Fig. 29). Southern America. *Grimmia trinervis* is known to date from northwestern Bolivia and southeastern Peru. It grows on dry sandstone and basalt cliffs in open puna areas and in forests of *Polylepis racemosa* between 3850 and 5100 m elevation.

Grimmia trinervis has strongly plicate leaves and gymnostomous capsules immersed and ventricose on a curved seta. Sterile specimens cannot be separated with confidence from species of *Coscinodon*, despite Hastings's (1996) work on South American *Coscinodon*.

Grimmia trinervis was transferred to *Coscinodon* by Brotherus (in Herzog, 1916: 52), a placement followed later by Churchill (1981) and recently by Hastings (1996). Hastings discussed at length the generic placement of *Grimmia trinervis*, concluding that *G. trinervis* should be within *Coscinodon* based on: (1) gametophytic similarities between *Coscinodon cribrosus* (Brid.) Jur. and *G. trinervis*, as no member of *Grimmia* subg. *Grimmia* has plicate leaves; (2) capsule/seta length ratios being smaller in *G. trinervis* than in natural members of *Grimmia* subg. *Grimmia*; (3) the length of the seta cells, isodiametric in *Grimmia anodon* and *G. plagiopodia* (members of *Grimmia* subg. *Grimmia*), but rectangular in *G. trinervis, Coscinodon pseudocribosus* Hastings, and *C. calyptratus* (Drumm.) Kindb.; (4) setae in *G. trinervis* sometimes longer than expected for a member of *Grimmia* subg. *Grimmia.* Furthermore, Hastings found these setae to be "considerably different than that found in the *Gasterogrimmia*" (1996: 421–422). (5) Finally, the dioicous nature of *G. trinervis* was significant for this author, because all other members of *Grimmia* subg. *Grimmia* are autoicous.

However, none of the aforementioned characters are generically reliable for *Coscinodon*: all of them show parallel unreliable variation in both *Grimmia* and *Coscinodon.*

(1) *Plication of leaves. Grimmia caespiticia* (Brid.) Jur. shares similar leaf morphology and areolation with *Coscinodon cribrosus.* When sterile these two species may be impossible to separate (Muñoz, 1998d). In contrast, the leaves of *Coscinodon calyptratus* are nonplicate. Plication occurs in both genera and is not a diagnostic character at the generic level.

(2) *Capsule/seta length ratio. Coscinodon calyptratus* has long setae, resulting in emergent to exserted capsules. At the other extreme is *C. cribrosus*, with short setae and immersed capsules. The same situation can be found in *Grimmia. Grimmia* species may typically have exserted capsules, such as *G. ovalis.* Conversely, species such as *G. pseudoanodon* display immersed capsules. An extreme example that seta lengths are variable and generically uninformative is *G. longirostris* Hook., with capsules ranging from immersed to longly exserted (Muñoz, 1998c).

(3) *Length of seta cells.* This character strongly correlates with capsule/seta length. In general, the longer the seta cells, the longer the setae will be. The same can also be observed in relation to leaf length. Leaves with longer acumina usually have longer laminal cells.

(4) *Seta length.* Hastings (1996) referred *Grimmia anodon* and *G. plagiopodia* to his "*Gasterogrimmia,*" both species with short setae. Within *Grimmia* subg. *Grimmia*, seta length in *G. crinita* Brid. and *G. pitardii* Corb. ranges from 0.6 to 1.1 mm and capsule length ranges from 0.7 to 1.1 mm, with these values exceeding Hastings's observations. Capsule/seta length ratio for subgenus *Grimmia* varies much more than Hastings observed. *Grimmia trinervis* capsule/seta ratio (1:1) falls within the range of variation for subgenus *Grimmia.*

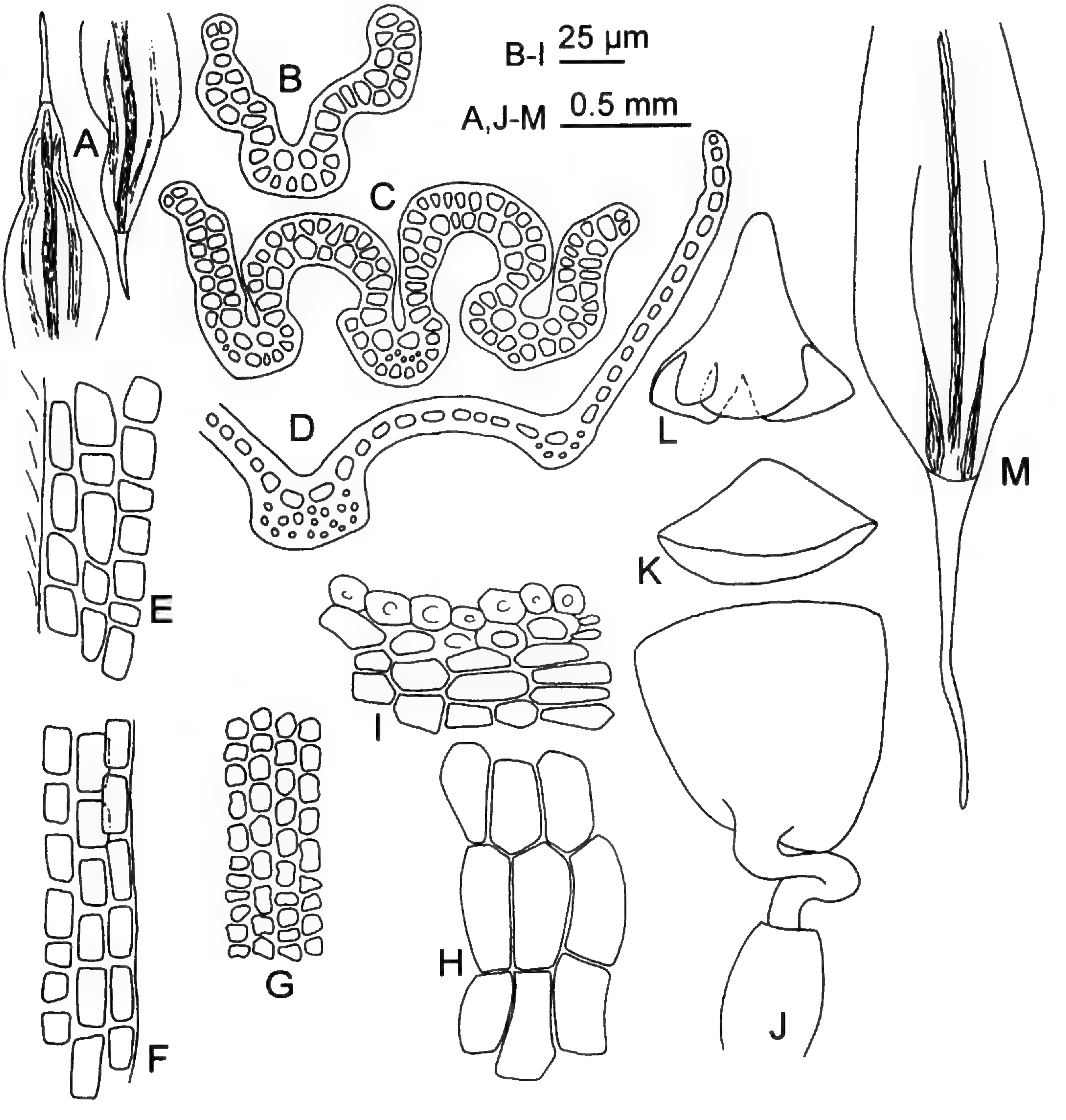

Figure 46. *Grimmia trinervis.* —A. Leaves. —B–D. Transverse sections at distal, medial, and proximal parts of leaf. —E. Proximal juxtacostal leaf cells. —F. Proximal marginal leaf cells. —G. Distal leaf cells. —H. Medial exothecial cells. —I. Capsule mouth and annulus. —J. Deoperculate sporophyte. —K. Operculum. —L. Calyptra. —M. Perichaetial leaf. (A, E–M: *Williams 2814*, NY; B–D: *Lewis 79–2073A*, MO.)

Both *G. crinita* and *G. pitardii* have seta cells rectangular (20–45 × 10–15 µm, ratio 2–3 : 1), with these being three times longer than reported by Hastings (1996: 421), even exceeding his report for *G. trinervis.*

(5) *Sexual condition.* Sexuality in *Coscinodon* and *Grimmia* cannot be used to decide generic placements. *Coscinodon calyptratus* is autoicous (Muñoz, 1998b) whereas the rest of the genus, with 5 to 7 species, is dioicous. In *Grimmia*, about 40% of the species are autoicous, with no apparent pattern to the distribution of sexual condition among subgenera.

In summary, the five characters considered by Hastings supporting the inclusion of *G. trinervis* in *Coscinodon* are widely variable within both genera *Grimmia* and *Coscinodon* and are systematically useless for defining these genera.

In marked contrast, *G. trinervis* does share with other members of *Grimmia* subg. *Grimmia* four character states strongly supporting its inclusion within this subgenus: (1) the setae are short and curved or even coiled; (2) these setae attach asymmetrically to the capsules; (3) the capsules are ventricose; and (4) the calyptrae are smooth, not plicate, and extend only to the capsule mouth. Deguchi (1987: 32–33) also suggested the lack of peristome teeth as a character to retain this species in *Grimmia* subg. *Grimmia*. However, this character is shared with *Coscinodon arctolimnius* and other species among other taxa of Grimmiaceae, such as *Schistidium flaccidum* (De Not.) Ochyra.

Additional specimens examined. BOLIVIA. Huaillattenisee, *Herzog 2971* (H-BR). **Cochabamba**: prov. Tapacari, 3 km N of Challa, *Lewis 83-3938* (F, IBA). **La Paz**: prov. Aroma, 1 km S of Villa Santa Cruz, *Lewis 86-2115* (F, IBA); prov. Camacho, W of Escoma, N side of Lago Titicaca, *Lewis 79-778* (IBA, MO); Chacaltaya, Mar. 1908, *Buchtien s.n.* (PC). **Oruro**: Sajama, Cerro Kohuiri Tarak, W of Nevado Sajama, *Lewis 79-2073A* (MO). **Potosí**: prov. Bustillos, 3 km SE of Uncia, *Lewis 84-1587* (F, IBA); prov. Quijarro, cerro Purgatorio Mundo, *Lewis 79-371* (F). PERU. **Ancash**: Huaraz, Monterrey, *Hegewald & Hegewald 7483* (MO). **Arequipa**: Arequipa, laguna Las Salinas, *Hegewald & Hegewald 5483* (MO); Juliaca, *Rose 19091A* (NY). **La Libertad**: Otuzco, Huancamarca, Quebrada Hornillo, *Hegewald & Hegewald 5158* (MO). **Puno**: prov. Azángaro, Jarjani, about 7 km SW of Asillo, *Deguchi 29943* (HIRO), *29952* (HIRO), *29962* (HIRO); prov. Lampa, Cara Cara, near Pucará, *Deguchi 29871* (HIRO), *29872* (HIRO), *26879* (HIRO); prov. Melgar, 7 km W of La Raya Pass, *Hegewald & Hegewald 5512* (MO), *5526* (MO); prov. Puno, around laguna Umayo, *Deguchi 29848* (HIRO), *29851* (HIRO).

31. Grimmia ungeri Jur., in Unger & Kotschy, Ins. Cypern: 169. 1865. TYPE: Cyprus. In Olimpo Cypri, vere 1862, *Unger s.n.* (lectotype, designated by Muñoz (1998d), BM; isolectotype, BM 2 replicates, GOET 2 replicates, H-SOL, S).

For a list of synonyms, see Muñoz (1998d).

Cladautoicous. Plants olive-green to blackish. *Stems* erect, to 1.5 cm, central strand weakly developed. *Leaves* erect and appressed when dry, patent when moist, 1.0–1.7 × 0.3–0.5 mm, ovate, acute, weakly keened, not plicate; *margins* plane proximally and incurved distally; *costa* semi-terete, slightly to clearly differentiated, ventral epidermis 2 cells wide in cross section; *lamina* 2–3(4)-stratose in the distal ⅔; *distal cells* 5–7 μm long, isodiametric, not bulging or bulging weakly on dorsal surface, walls straight to slightly sinuous; *proximal juxtacostal cells* 20–35 × ca. 16 μm, isodiametric to rectangular (1–3 : 1), walls medium-thick and straight; *proximal marginal cells* 10–25 × 6–10 μm, isodiametric to rectangular (1–2 : 1), the transverse walls thicker than the longitudinal walls; *hyaline hair-points* terete, straight, to 1.5 mm, entire. *Perichaetial leaves* 1.5–2.5 × 0.5–0.9 mm, convolute and larger than vegetative leaves (2–3 ×). *Androecia* terminal. *Setae* erect and straight, to 2 mm long. *Capsules* exserted, ovoid or ellipsoid, symmetric, smooth, castaneous, lacking stomata; *exothecial cells* 17–65 × 13–45 μm, rectangular (1.5–3 : 1), thin-walled; *annulus* simple and persistent, *Schistidium* type; *peristome teeth* 40–50 μm wide at the mouth, entire or moderately cribrose at apex, external surface nearly smooth proximally and papillose distally, internal surface papillose throughout, castaneous, concolorous with the urn; *opercula* conical to rostellate; *calyptrae* cucullate; *spores* 9–13 μm, minutely granulose.

Illustrations. Figure 47; Muñoz (1998d: fig. 18).

Distribution (Fig. 36). Europe, Macaronesia, northern America; Mexico. *Grimmia ungeri* is common along the west coast of North America, becoming rarer to the south (Muñoz, 1998d). In Mexico it is known from scattered localities, but further exploration may fill in the gaps in its known distribution. It grows on igneous rocks between 1500 and 4000 m elevation.

Grimmia ungeri is the only species in the genus combining autoicous sexuality with the absence of stomata in the capsules. In spite of this clear definition, its differentiation from *G. montana* can be impossible in poor or sterile material. Both taxa have keeled, 2 to 3(4)-stratose leaves, erect setae, and capsules lacking stomata. *Grimmia ungeri* has conical to rostellate opercula, and is autoicous. *Grimmia montana* has rostrate opercula and is dioicous. The latter usually has longer proximal juxtacostal cells, but the length of the juxtacostal cells appears intermediate in some collections, so the likelihood of misidentifications using this character alone is great.

Additional specimens examined. MEXICO. **Baja California**: Las Cuevitas, Sierra Juárez, ca. 10 mi. S of Laguna Hanson, *Wiggins 9177* (FH). **México**: Mt. Popocatépetl, *Kiener 18590* (F, FH), *18591* (FH).

Taxa Excluded from *Grimmia*

The following taxa have been described or included in Grimmia, but they pertain to other genera.

Grimmia abscondita Cardot, Wiss. Erg. Schwed. Südpolar-Exp. 4(8): 107, fig. 19. 1908. *Schistidium absconditum* (Cardot) Ochyra, Fragm. Florist. Geobot. 43: 104. 1998. TYPE: [Chile. Magallanes:] lac San Martin, Río Fósiles, *Du-*

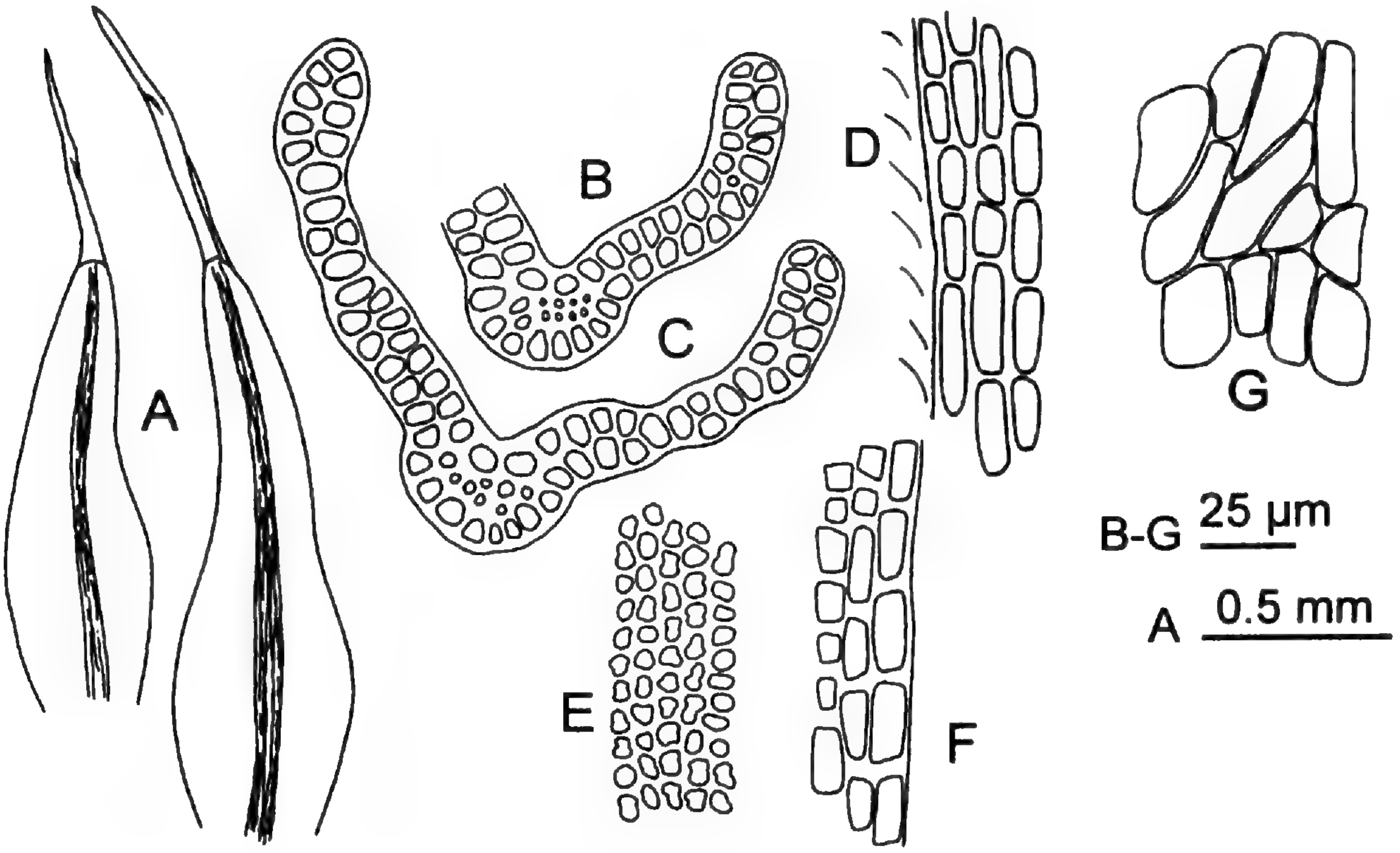

Figure 47. *Grimmia ungeri*.—A. Leaves. —B, C. Transverse sections at medial and proximal parts of leaf. —D. Proximal juxtacostal leaf cells. —E. Distal leaf cells. —F. Proximal marginal leaf cells. —G. Medial exothecial cells. (*Kiener 18590*, FH.)

sén 5944 (type, PC not seen). This taxon belongs in *Schistidium.*

Grimmia amblyophylla Müll. Hal., Syn. Musc. Frond. 1: 779. 1849. *Schistidium amblyophyllum* (Müll. Hal.) Ochyra & Hertel, Polish Bot. Stud. 1: 26. 1990. TYPE: [Chile. Magallanes:] Hermite Island, Cap Horn, *Hooker 122* (lectotype, designated by Ochyra & Hertel (1990), BM; isolectotypes, NY 2 replicates). This taxon belongs in *Schistidium.*

Grimmia austroleucophaea Besch., Bull. Soc. Bot. France 32: LIV–LXIX. 1885. *Guembelia austroleucophaea* (Besch.) Müll. Hal., in Paris, Index Bryol. 2: 540. 1895. *Willia austroleucophaea* (Besch.) Broth., Nat. Pflanzenfam. 3(1): 453. 1902. TYPE: "Terre de Feu, île Horn" *Hariot 157* (type, BM? not seen). This taxon belongs in *Willia* Broth. (Pottiaceae).

Grimmia calycina Herzog, Beih. Bot. Centralbl. 27: 354. 1910. *Schistidium calycinum* (Herzog) Ochyra, Fragm. Florist. Geobot. 43: 105. 1998. TYPE: Bolivia. Chacaltaya, 1908, *Buchtien s.n.* (isotype, S not seen). This taxon belongs in *Schistidium.*

Grimmia chubutensis Cardot & Broth., Kongl. Svenska Vetenskapsakad. Handl. 63(10): 26, tab. 2 fig. 6. 1923. *Schistidium chubutense* (Cardot & Broth.) Ochyra, Fragm. Florist. Geobot. 43: 105. 1998. TYPE: Argentina. Chubut, Valle Diez-y-seis de Octubre, *Skottsberg 439* (isotypes, H-BR, UPS). This taxon belongs in *Schistidium.*

Grimmia donatii Herzog & Thér., Repert. Spec. Nov. Regni Veg. 41: 290, tab. 236 e–n. 1937. *Schistidium donatii* (Herzog & Thér.) Ochyra & Matteri, Fragm. Florist. Geobot: 1008. 1996. TYPE: [Chile.] Aisén, Ventisquero, *Donat 48* (holotype, JE; isotype, JE). This taxon belongs in *Schistidium.*

Grimmia fallax Dusén, Rep. Princeton Univ. Exped. Patagonia 8: 77, fig. 7, pl. 8, figs. 5, 6. 1903. *Schistidium fallax* (Dusén) Ochyra & Matteri, Fragm. Florist. Geobot: 1008. 1996. TYPE: "Princeton Scientific Expedition to Patagonia 1896–1897." [Chile. Magallanes:] South Patagonia, *Hatcher s.n.* (holotype, S not seen; isotype, NY). This taxon belongs in *Schistidium.*

Grimmia fasciculata Dusén, Bot. Not. 1905: 302. 1905, nom. illeg., non Brid., 1819. TYPE: (lectotype, designated by Ochyra & Bell (1984), S not seen; isolectotype, UPS not seen). This taxon belongs in *Schistidium falcatum* (Hook.f. & Wilson) B. Bremer.

Grimmia julacea R. S. Williams, Bull. New York Bot. Gard. 6: 260. 1910, nom. illeg., non F. Weber & D. Mohr, 1803. *Grimmia williamsii* Deguchi, Studies on Cryptogams in Southern Peru: 33. 1987. TYPE: [Peru.] Arequipa, *Williams 2805* (holotype, NY; isotypes, F, JE 2 replicates). This name is a synonym of *Jaffueliobryum wrightii* (Sull.) Thér.

Guembelia lorentziana Müll. Hal., Linnaea 43: 450. 1882. *Grimmia lorentzi* (Müll. Hal.) Kindb., Enum. Bryin. Exot., Suppl. 1: 91. 1889. *Grimmia lorentziana* (Müll. Hal.) Paris, Index Bryol. 2: 529. 1895. *Schistidium lorentzianum* (Müll. Hal.) Ochyra & Matteri, Fragm. Florist. Geobot: 1008. 1996. TYPE: Argentina. Tafi, *Lorentz s.n.* (lectotype, designated by Ochyra & Matteri (1996), JE; isolectotype, BM). This taxon belongs in *Schistidium.*

Grimmia macrotyla Cardot & Broth., Kongl. Svenska Vetenskapsakad. Handl. 63(10): 26, tab. 2, fig. 5. 1923. *Schistidium macrotylum* (Cardot & Broth.) Ochyra, Fragm. Florist. Geobot. 43: 106. 1998. TYPE: [Argentina.] Chubut: meseta Chalia, *Skottsberg 382* (isotypes, H-BR, UPS). This taxon belongs in *Schistidium.*

Grimmia olivacea Herzog, Biblioth. Bot. 87: 56, fig. 18g–m. 1916. TYPE: Bolivia. Im oberen Chocayatal, *Herzog 3587* (isotypes, JE, PC). This taxon belongs in *Schistidium.*

Grimmia perplexa Thér., Revista Chilena Hist. Nat. 27: 11, Lám. 2. 1923. *Schistidium perplexum* (Thér.) Ochyra, Fragm. Florist. Geobot. 43: 106. 1998. TYPE: Chile. La Ermita (Las Condes), Oct. 1919, *Bertho s.n.* (isotypes, FH 2 replicates). This taxon belongs in *Schistidium.*

Guembelia praemorsa Müll. Hal., Linnaea 43: 452. 1882. *Grimmia praemorsa* (Müll. Hal.) Kindb., Enum. Bryin. Exot., Suppl. 1: 91. 1889. TYPE: Argentina. Catamarca: Yakutula, in Vayas altas [sic], convallis altas Grandillas [sic], Feb. 1872, *Lorentz s.n.* (isotypes, BM, JE). This taxon belongs in *Schistidium.*

Grimmia rivulariopsis R. S. Williams, Bull. Torrey Bot. Club 43: 327, pl. 19. 1916. *Schistidium rivulariopsis* (R. S. Williams) Ochyra, Fragm. Florist. Geobot. 43: 106. 1998. TYPE: Peru. Ollantaytambo, *Cook & Gilbert 753* (lectotype, designated by Deguchi (1987), NY; isolectotype, F). This name is a synonym of *Schistidium rivulare* (Brid.) Podp.

Grimmia saxatilis Mitt., J. Linn. Soc., Bot. 12: 97. 1869. *Schistidium saxatile* (Mitt.) Ochyra, Fragm. Florist. Geobot. 43: 106. 1998. TYPE: [Ecuador.] Chimborazo, *Spruce 132* (lectotype, designated by Bremer (1980), NY; isolectotype, FH). This taxon belongs in *Schistidium.*

Grimmia scabripes E. B. Bartram, Farlowia 2: 310. 1946. *Schistidium scabripes* (E. B. Bartram) Deguchi, in Inoue, Studies on Cryptogams in Southern Chile: 27. 1984. TYPE: Chile. Ñuble: Recinto, Las Trancas, *Roivainen 1003* (holotype, FH). This name is now *Schistidium scabripes* (E. B. Bartram) Deguchi.

Grimmia squamatula Herzog, Biblioth. Bot. 87: 56, fig. 18a–f. 1916. TYPE: Bolivia. Yanakakabastion, July 1911, *Herzog s.n.* (lectotype, here designated, JE). This taxon belongs in *Schistidium.*

Grimmia yaulensis Broth., Bot. Jahrb. Syst. 56(2), Beibl. 123: 11. 1920. TYPE: Peru. An der Lima-Oroya-Bahn, Hacienda Arana bei Yauli, *Weberbauer 373 ex p.* (lectotype, here designated, H-BR; isolectotype, PC 2 replicates). This taxon belongs in *Schistidium.*

TAXA FOR WHICH TYPE SPECIMENS HAVE NOT BEEN LOCATED

Grimmia depressa Müll. Hal., Flora 68: 421. 1885. TYPE: "Fuegia, Staten Island, Port Cook, ad truncos putridos in sylvis, Martio 1882. Fuegia australis, Burnst Island, ad ramos Chilostrii amelloidis in sylvis, Majo 1882: Spegazzini."

Grimmia depressa var. *terrestris* Müll. Hal., Flora 68: 421. 1885. TYPE: "Beagle Channel, in sinu Fandagaia, ad glaream orae maritimae, Majo 1882: Spegazzini."

Although none of the consulted herbaria house type specimens of these two names, they might belong in *Racomitrium,* according to the protologue ("*. . . dentibus densis angustis in crura duo adglutinata asperula lutescentia usque fere ad basin fissis*").

NOMINA NUDA

Grimmia anodon var. *mutica* Broth. ex Paris, Index Bryol. ed. 2, 2: 263. 1904 (= *G. poecilostoma*).

Grimmia biplicata Broth., in H. J. A. Mey., In den Hoch-Anden von Ecuador: 518. 1907 (= *G. navicularis*).

Grimmia flexiseta Dusén, Rep. Princeton Univ. Exped. Patagonia 8: 122. 1903 (= *G. trichophylla*).

Grimmia flexiseta Schimp. ex Jard., Bull. Soc. Linn. Normandie, sér. 2, 9: 263, 264. 1875 (= *G. lisae*).

Grimmia meridensis Vareschi, Flora de los Páramos de Venezuela: 87. 1970 (= *G. longirostris*).

Grimmia nivalis Liebm. ex Besch., Mexic. pl. 1: 19. 1872 (= *G. donniana*).

Grimmia ovata f. *dioica* Cardot, in Pringle, Plantae mexicanae n° 10539 (= *G. longirostris*).

Grimmia pycnophylla Dusén, Rep. Princeton Univ. Exped. Patagonia 8: 122. 1903 (= *G. trichophylla*).

Grimmia paramophila Broth., in H. J. A. Mey., In den Hoch-Anden von Ecuador: 518. 1907 (= *G. navicularis*).

Grimmia sardoa var. *robusta* M. Fleisch. & Warnst., Bryotheca meridionalis n° 342. *Grimmia trichophylla* f. *robusta* (M. Fleisch. & Warnst.) Podp., Consp. Musc. Eur. 288. 1954, nom. inval. (= *G. lisae*).

Grimmia serripila Dusén ex Paris, Index Bryol. ed. 2: 287. 1904 (= *G. laevigata*).

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List of Species

1. *Grimmia americana* E. B. Bartram
2. *Grimmia anodon* Bruch & Schimp.
3. *Grimmia atrata* Hornsch.
4. *Grimmia austrofunalis* Müll. Hal.
5. *Grimmia bicolor* Herzog
6. *Grimmia donniana* Sm.
7. *Grimmia elongata* Kaulf.
8. *Grimmia fuscolutea* Hook.
9. *Grimmia humilis* Mitt.
10. *Grimmia involucrata* Cardot
11. *Grimmia kidderi* James
12. *Grimmia laevigata* (Brid.) Brid.
13. *Grimmia lisae* De Not.
14. *Grimmia longirostris* Hook.
15. *Grimmia molesta* J. Muñoz
16. *Grimmia montana* Bruch & Schimp.
17. *Grimmia navicularis* Herzog
18. *Grimmia ochyriana* J. Muñoz
19. *Grimmia ovalis* (Hedw.) Lindb.
20. *Grimmia pilifera* P. Beauv.
21. *Grimmia plagiopodia* Hedw.
22. *Grimmia poecilostoma* Cardot
23. *Grimmia pseudoanodon* Deguchi
24. *Grimmia pulla* Cardot
25. *Grimmia pulvinata* (Hedw.) Sm.
26. *Grimmia reflexidens* Müll. Hal.
27. *Grimmia tergestina* Bruch & Schimp.
28. *Grimmia tortuosa* Hook.f. & Wilson
29. *Grimmia trichophylla* Grev.
30. *Grimmia trinervis* R. S. Williams
31. *Grimmia ungeri* Jur.

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Index to Scientific Names (Accepted Names in Italics)

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HOW RICH IS THE FLORA OF BRAZILIAN CERRADOS?[1]

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ABSTRACT

An attempt is made to summarize what is known about the richness of the total terrestrial angiosperm flora of the "cerrados" (as a complex of formations) in Brazil, based on published surveys and species lists. A "refined" list of arboreal and shrubby species was compiled from a total of 145 individual lists from 78 localities, taking into account synonymy and recent taxonomic changes. The refined list had 1709 references to taxonomic entities at the species level (973 identified with confidence and 31 with *aff.* or *cf.*), 572 references to generic entities (363 genera identified with confidence), and 210 references to the family level (88 families identified with confidence). There are many unidentified arboreal and shrubby taxa at the specific, generic, and family levels, indicating that a considerable amount of taxonomic research remains to be done on the cerrado flora, and that this flora may be much richer than is generally assumed. Depending on the assumptions made, these data suggest a total of around 1000 to 2000 arboreal and shrubby species and 2000 to 5000 herbaceous ones, yielding estimates for the total cerrado flora (terrestrial angiosperms) ranging from 3000 to 7000 species. These limits, especially the upper one, are dubious, but give an idea of the magnitude of the angiosperm flora in the Brazilian cerrados. Surveys of cerrados are very unevenly distributed, and studies of relatively unknown sites may reveal much more diversity than that presently known.

On reading accounts of floristic studies on cerrados in Brazil, one rapidly comes to realize that the majority of authors, either implicitly or explicitly, consider the cerrado flora to be well known and to have low richness. For example, Rizzini (1963, 1971) estimated around 600 species and a little over 200 genera for the whole cerrado arboreal and shrubby flora, but Heringer et al. (1977) cited 193 arboreal and shrubby species and confirmed less than 150 genera. Even recent studies (e.g., Leitão Filho, 1992; Ratter et al., 1997) have estimated the number of arboreal-shrubby species for the cerrados as being around 800. Eiten (1990) has been one of the few authors to suggest that the thick-stemmed arboreal-shrubby flora contains more than 1000 species and that the denser physiognomies may reach more than 150 arboreal and shrubby species per hectare. Castro (1994; see Ratter et al., 1997) made an extensive survey of the literature in order to gather support for the idea that the arboreal and shrubby flora of the Brazilian cerrados is much richer than previously assumed.

It could be argued that as the cerrados consist of physiognomies that are predominantly grasslands, the greatest floristic richness should be encountered in the non-woody (herbaceous-subshrubby) component of the vegetation. Surveys of this component have been rare in Brazil (Mantovani & Martins, 1993). Comparing the non-woody component in different localities in Brazil, Mantovani (1983) found a local richness that varied between 165 species in the Serra Dourada (state of Goiás) and 640 in the municipality of Lagoa Santa (state of Minas Gerais). In an area of 343.42 ha of a cerrado in the Reserva Biológica de Moji Guaçu (state of São Paulo), Mantovani and Martins (1993) found 403 species of non-woody angiosperms. The herbaceous-subshrubby angiosperm flora of the cerrados therefore appears to be richer than the arboreal-shrubby flora, but its richness varies with physiognomy (Mantovani, 1987).

It can also be argued that the maximum physiognomic and floristic expression, together with maximum spatial continuity, should occur in the "nuclear" (Labouriau, 1966), "central" (Rizzini, 1963), or "core" (Eiten, 1972; Ferri, 1977a) areas. An implication of this reasoning is that marginal and disjunct areas (Ratter et al., 1988a) should have a relatively impoverished flora in comparison to the nuclear area, although they may be supplemented by floristic elements from the surrounding vegetation formations (Eiten, 1972; Fernandes & Bezerra, 1990; Rizzini, 1963). These elements, which occur preferentially in other formations and

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sporadically in cerrados, were called "accessory" species or elements by Rizzini (1963). Species that occur exclusively in cerrado formations, or show a marked preference for cerrados, were termed "characteristic" species ("espécies peculiares ou próprias") by Rizzini (1963). He considered that only the woody species occurring in the "cerradão" (forest physiognomy) could be designated characteristic species, that is, essentially the arboreal-shrubby species. However, because of a large number of accessory species (sensu Rizzini, 1963), marginal and disjunct cerrado areas generally show considerable floristic richness.

Although this might suggest that cerrados in marginal or disjunct areas should gradually grade into other formations, they are usually fairly easily distinguished from other formations in the neighborhood by their physiognomy and floristic composition, often with a number of common well-known species. The fact that a species occurs, grows, and reproduces successfully in an area shows that it is adapted to the local conditions. It is possible to construct a *continuum* of species ranging from those restricted to very local areas within a single vegetation type to those that are very widespread and occur in several different formations. The distinction between "characteristic" and "accessory" species therefore seems rather artificial and debatable, lacking in ecological significance. The spatial and temporal abundance of the different species also cannot be ignored. While it might be argued that a species typical of other formations and occurring only sporadically in cerrados should be considered an accessory species (e.g., *Ficus* spp.), it is possible to find examples of species that occur with very low abundance but only in cerrado areas (such as *Eugenia aurata*), along with numerous intermediate situations (such as *Copaifera langsdorffii* or *Vochysia tucanorum*) in which species that are common in other formations also occur in some abundance in many cerrados. Once again, it is virtually impossible to find a clear distinction between "accessory" and "characteristic" species. Most floristic studies, moreover, do not include information on abundance, making it difficult to use this criterion.

Although cerrados are among the best studied vegetation types in Brazil, a number of fundamental questions remain unanswered. Just how rich, floristically, is the cerrado? How many and which taxa are already known? What is the proportion of still unknown/unidentified/undescribed taxa? What are the taxa that cause most problems for identification? In addition, knowledge of the flora of a given type of vegetation depends fundamentally on collections in the field. Which areas have been well collected? To what extent have collections been widely spread or have they concentrated in certain areas? In which regions are collections sparse or nonexistent? These represent priority areas for future work and should be clearly identified.

Answers to these questions are essential for any attempt to establish plans for conservation and further investigation of the cerrado vegetation, tasks which are, sadly, increasingly urgent given the rapid destruction and exploitation of this vegetation type in Brazil today.

In the present study we tried to summarize what is known from floristic studies in the cerrados of Brazil, at least for the arboreal-shrubby component of the vegetation, and to provide some indications of where further work might most usefully be invested to improve our knowledge for conservation and rational sustainable exploitation.

MATERIAL AND METHODS

This study was based on material published and theses defended up to 1992, supplemented by 12 unpublished field surveys from the states of Piauí and São Paulo (Castro et al., in press). A literature survey uncovered 135 publications and theses that included floristic surveys of cerrados. Of these, 92 were selected for the present study. It is likely that other studies exist, but they were not localized or could not be obtained.

An initial survey was based on Garcia et al. (1981), Huber (1974), Lemos (1976), Pinto (1979), and Silva (1982), together with publications by Eiten (1972), Ferri (1963, 1971, 1973, 1977b, 1979), Goodland (1979), Labouriau (1966), Marchetti (1988), and Marchetti and Machado (1982). A second survey was based on the citations in these publications and on theses defended, as well as on the literature cited in them. In many cases, the authors contacted supplied complementary information in the form of extended species lists and revised identifications. Surveys were selected based on the following criteria:

(1) Where the authors designated the vegetation surveyed as some type of "cerrado."
(2) Where the authors distinguished the growth form of the species surveyed. We consider only trees and shrubs; other growth forms were excluded.
(3) When the publication omitted growth form, the authors were contacted and they sent us their field observations. In some cases, indications in the literature were used (Ferri, 1969, 1977b; Heringer et al., 1977; Martius et al., 1840,

1906; Rizzini, 1963, 1971). In a few cases, growth forms were designated based on the field experience of the authors themselves.

(4) Only surveys that made periodic collections or quantitative sampling in a limited area at a given locality were included. We excluded lists based on single or sporadic visits, or that were not relatively localized.

According to Coutinho (1990), different vegetation types are included under the word "cerrados," whose physiognomies vary from pure grassland ("campo limpo de cerrado"), through savanna ("campo sujo," "campo cerrado," "cerrado sensu stricto," in order of growing woody biomass), to pure forest ("cerradão"). A similar concept of the cerrados can be found in Castro (1996), Eiten (1972), Ratter and Dargie (1992), and Ratter et al. (1996, 1997). They are classified in the world biome of savannas, which occur between the tropics, on dystrophic, allic or acid, deep, heavily intemperized soils under a seasonal climate where recurrent fires are normal events (Sarmiento, 1983). We accept the broad concept of cerrados as a complex of different vegetation formations, and in the present study we accepted the classification of the vegetation surveyed as some type of cerrado by the author of the survey, as stated in criterion 1 above.

The cerrados show two distinct floras, termed "silvestre" (from the Latin *sylva* = forest) and "campestre" (from the Latin *campus* = field) by Rizzini (1963, 1971), mutually exclusive because both are heliophilous (Coutinho, 1990). In the physiognomies of the cerrados they constitute roughly the woody layer and the ground layer, respectively, in Eiten's (1972) terminology. The dominant life forms in the woody layer are arboreal phanerophytes (here called trees) and shrubby chamaephytes (here called shrubs). In the ground layer the dominant life forms are subshrubby chamaephytes (here called subshrubs), hemicryptophytes (the dominant life form), and geophytes (here called herbs) and all qualified as non-woody. A key for plant life-forms can be found in Mueller-Dombois and Ellenberg (1974). We use the term "woody" to include trees and shrubs and apply the qualifier "woody" according to the appearance of the aerial system of a dicotyledonous plant: all that can be seen of a plant in a normal survey. A woody plant has at least one orthotropic stem axis arising from the soil that, along some extension from its base, is hard, relatively thick, and has a bark (not a thin, green epidermis). Most quantitative surveys in Brazilian cerrados have sampled woody plants with a minimum stem diameter of 3 cm at ground level. To categorize species belonging to the "silvestre" or "campestre" floras we use here the expressions arboreal-shrubby and subshrubby-herbaceous components. We prefer to use the word "component" because it is abstract and not so concrete as "layer," which has a well-defined meaning in physiognomy: a layer can be seen in the vegetation, but not in a flora.

In several cases, more than one species list was presented for a given site, since a number of adjacent areas had been studied, thus resulting in 145 floristic lists for 78 sites. A preliminary list of identified species and those with dubious identification was prepared. Dubious identifications included those such as *aff.* or *cf.* Unidentified taxa were those unknown at species, genus, or family levels. From this preliminary list, a refined list was prepared where synonyms were combined under a single epithet, based on the taxonomic literature (floras, revisions, theses, etc.). No attempt was made to ensure that the epithet chosen was taxonomically up to date, but only to make sure that different binomials belonging to the same species were included under a single name, although wherever possible, the nomenclature used in the most recent revision was followed.

Calculations of proportions of dubious and unknown taxa were based on the refined list. Each unidentified taxon was considered to be different among samples; that is, unknown taxa identified to a given genus or family were considered to be different if they occurred in different surveys, so that if *Myrcia* sp. appeared in two lists, the final list contained *Myrcia* sp1 and *Myrcia* sp2. In the same way, any plant unknown in one survey was considered to be a different taxon from the unknowns occurring in other surveys. Dubious binomials were considered to be different among themselves and were also considered to be different from confident identifications. Infraspecific taxa were treated as separate taxa. All these were taken as references to taxonomic entities at the species (or genus or family) level, and not as "true" different species (or genera or families) in themselves, in order to estimate lower and upper limits for the richness of the flora. We used this method of calculating the number of taxonomic entities for operational facility and greater objectivity. Nevertheless, since it was impossible to know whether the unidentified, unknown, or dubious entities represented the same or different taxa in different lists, by adopting this procedure we introduced an overestimation of the upper limit of the cerrado floristic richness.

The surveys included in the present study are listed in Table 1 (pp. 204–212), which shows the

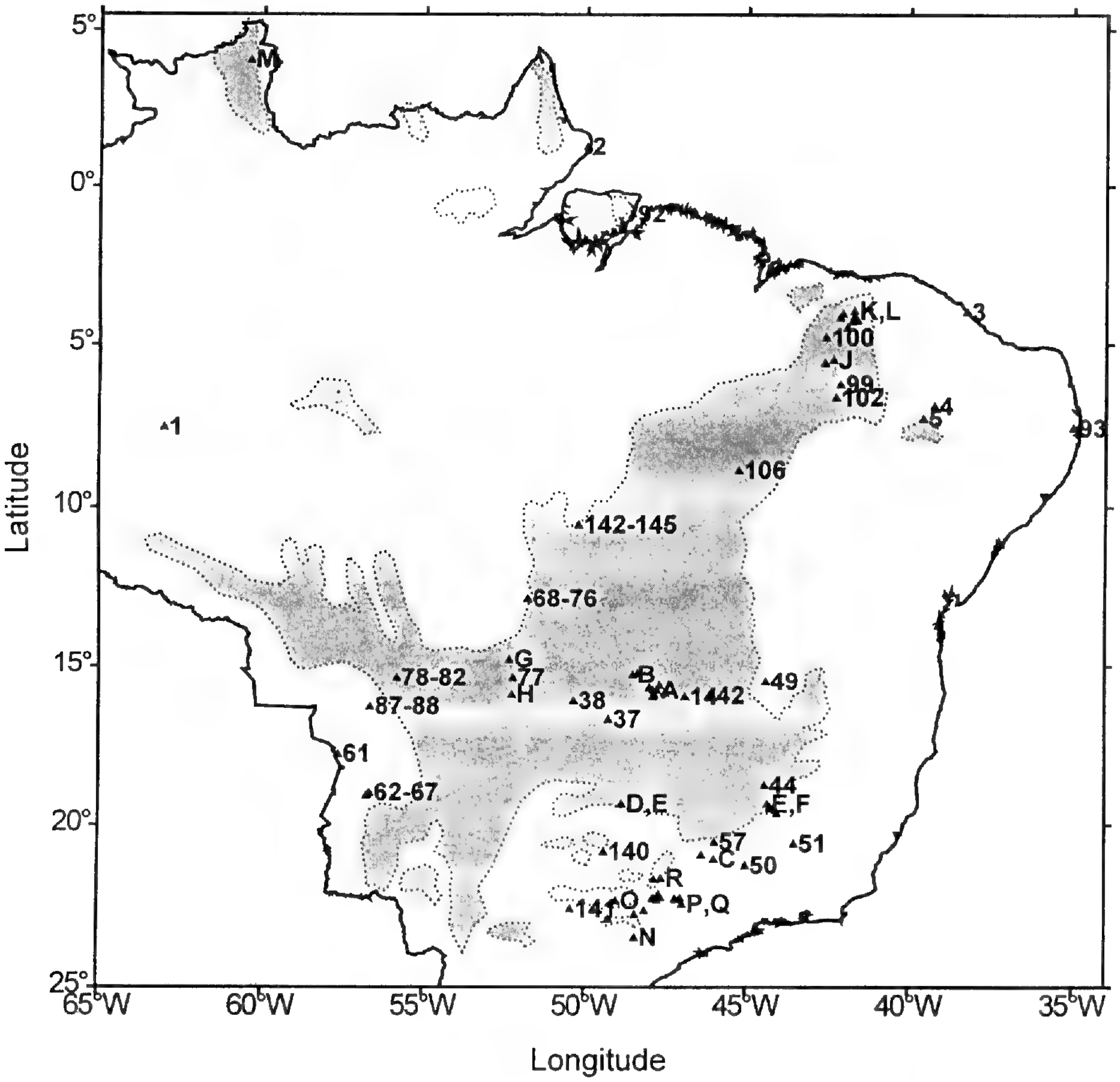

Figure 1. Cerrado vegetation sites included in the present survey. The dotted area represents the approximate distribution of cerrado vegetation in Brazil. Numbers and letters on the map correspond to municipalities where the surveys were done. See Table 1 for number code. The letters represent the following lists: A 6–36; B 39, 40; C 41–43; D 45–48; E 52–56, F 58–60; G 83–86; H 89–91; J 97, 101; K 94–96, 98; L 103–105; M 107–109; N 110–118; O 119, 120; P 121–132, 138; Q 134–137; R 133, 139.

sites surveyed, the municipality where they are located, their geographical location, and the author of the survey.

The distribution map (Fig. 1) showing the nuclear and disjunct cerrados was adapted from Fernandes and Bezerra (1990), Ferri (1977b, 1979), Malavolta and Klieman (1985), Ogata (1986), and Wagner (1986). It also shows the localization of the municipalities in which the surveys included in the present study were done.

RESULTS

The refined list (Table 2, pp. 213–223) indicates a total of 210 references to taxonomic entities at the family level, 572 references to the genus level, and 1709 references to the species and subspecies levels, including dubious identifications and non-identified material. Of the 210 references to taxa at the family level, 122 could not be identified by the authors of the original studies. They are here called "unknowns," representing 58.1% of the total. This would indicate that the number of families lies between 88 (the number of families definitely identified) and 210 (if none of the unknowns could be attributed to a family already identified). Of the 572 references to taxonomic entities at the generic level, 363 were identified, but 209 were not. These "unknowns" at the generic level represent 36.5% of the total. From the 1709 references to taxonomic entities at the species level, there are only 973 identified with confidence, 31 with dubious identifications, 36 with dubious identifications where the same species had already been identified in other sites, and a further 5 infraspecific taxa that belonged to species already included without indications of infraspecific categories. Also from the total 1709 references, 455 were identified to the generic level only, and 209 remained "unknown"

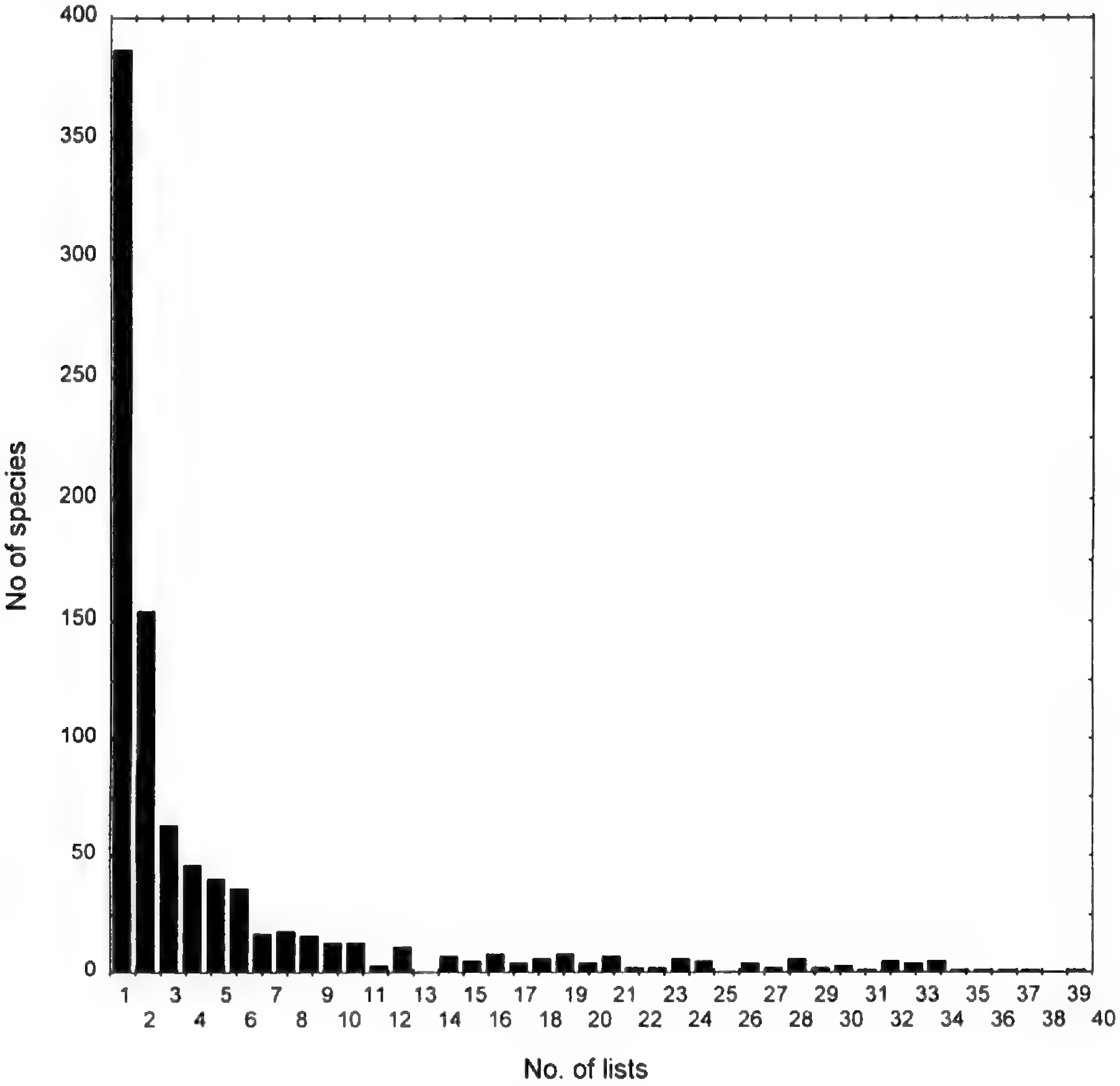

Figure 2. Frequency distribution of confidently identified species of arboreal and shrubby plants of Brazilian cerrados according to the number of lists in which they were recorded.

at the generic level (of these, 122 are references only to the family level). These results are summarized in Table 3 (p. 224).

Of the well-identified species, 387 (39%) occurred in a single list, while species with two occurrences made up a further 16%. This means that more than half of the species were present in less than 3 out of 145 lists. Figure 2 shows the frequency distribution of species according to the number of sites at which they were recorded.

Discussion

It is difficult to obtain a reliable estimate of the number of arboreal-shrubby taxa occurring in the cerrado, since a large number of factors may inflate or diminish the total obtained. In spite of this, we can arrive at two distinct estimates, with variable degrees of reliability: (1) an *upper limit* represented by the list taken as it stands, assuming that all of the references to taxonomic entities are new to the list and represent species, genera, or families not previously identified; (2) a *lower limit*, which assumes that all of the unknowns are in fact taxa that have already been recorded and that there remain no more taxa to be added beyond the ones already identified. The assumptions for both of these estimates are highly implausible, especially for the upper limit, but they provide a means of establishing probable upper and lower limits. The numbers implied by both of these limits are shown in Table 4 (p. 224).

The lower limit would seem to offer a reasonably secure minimum estimate for the arboreal-shrubby cerrado flora of around 1000 species, 370 genera, and 90 families. Three main objections might be raised: (1) The list includes a number of species that certainly would not be regarded as typical cerrado species (e.g., *Talauma ovata*). (2) A number of species that are not typically woody in most sites are also included (e.g., *Oxalis*). (3) Some unrecorded rarer species are likely to be "hidden" in this list, having been misidentified as common cerrado species.

The question of "non-cerrado" species is very difficult to resolve. As mentioned in the introduction, we have taken the position that if a species has been recorded in some form of cerrado vegetation, it should be included here, since we feel that it is almost impossible to supply a consistent criterion to distinguish Rizzini's "accessory species."

The second objection is the question of how to define "woody" forms. This is also practically impossible, since again there is no hard and fast criterion that can be applied universally, and authors differ considerably in the concepts that they utilize. A number of species also vary considerably in habit and may range from small, virtually herbaceous forms up to quite large trees in different cerrado sites (e.g., *Andira, Caryocar, Cochlospermum*), so that a species that is clearly woody and included in a survey of woody species in one site may be excluded in another. In all of the species listed, at least one author considered the species to be a shrub or tree in the site where he made his survey, and in many cases this information was confirmed by personal contacts with the author of the publication.

The final objection is almost impossible to quantify. The proportion of rarer species that have been confused with common cerrado species is likely to vary widely with the experience and thoroughness of the researchers who carry out a survey and the degree to which the flora of the region being studied is more or less well known. The availability of recent revisions and more easily accessible literature will also have a strong influence, and this will tend to be unequal among different taxonomic groups.

The upper limit for the cerrado woody flora is much more debatable. It is obviously unrealistic to assume that all of the unknowns represent "new" taxa (taxa not included in the lists; these are not new species from the taxonomic viewpoint), so that the number given here would tend to overestimate the number of taxa in the cerrado woody flora quite considerably. This is most evident in the number of families: it is highly unlikely that many of the unknowns at the family level do, in fact, represent "new" families. Once again, the proportion of "new" species is likely to vary widely, depending on the region where the survey was made. In relatively well-known cerrado areas such as the Distrito Federal, the state of São Paulo, and the southern part of the state of Minas Gerais, the cerrado woody flora is quite well known, and it is improbable that a large number of "new" species will be added, at least for the woody component. In less well-known regions such as northern Mato Grosso state and northern Minas Gerais, however, this proportion could be much higher. We have no reliable estimate of what proportion of the unknowns represents "new" species. It might be possible to estimate this by sampling and re-examining the unknowns from a number of surveys for taxonomic groups where recent revisions or expert taxonomic assistance are available. This is very difficult, however, since most publications do not cite voucher specimens, which would allow the unidentified material to be refound. We recommend that, in future studies, voucher specimens be deposited and cited for *all* species, even where only vegetative material is available.

Although the upper limit given here is likely to represent a gross overestimate of the number of cerrado woody species, it is necessary to be somewhat cautious before discarding this estimate completely. Any sampling scheme is certain to miss a number of species in a given area. For example, Gibbs et al. (1980) estimated that in a relatively restricted area of riparian forest, sampling by quadrats or point-centered quarters missed approximately 20% of the species present. This percentage is likely to be rather lower in cerrado—Ratter et al. (1988a) found that only about 5% of the woody species were not included in a quadrat survey in São Paulo state—but it is very unpredictable and likely to vary widely with sample size and local richness. A preliminary study of data from quantitative surveys (Castro, 1994) suggested that at least 1000 individuals should be included to give a reasonable representation of the woody flora of a given locality. Surveys that do not sample quantitatively frequently miss less conspicuous species, unless the survey is very thorough and visits are repeated in different seasons. In a number of cases, our field experience has shown that a quantitative sampling scheme (with statistical planning) will bring to light a much larger number of species than a series of sporadic visits. It might be argued that even if one survey misses a number of species, the repeated sampling by different studies should be enough to ensure an almost complete species list. This argument, however, supposes that the vegetation is relatively uniform. Comparison of different areas has shown that composition may vary widely, even between cerrado areas that are geographically close (Castro, 1994; Ratter et al., 1988a, b, 1996, 1997, Ratter & Dargie, 1992, and citations of A. A. J. F. Castro therein), and that many species have very sporadic or patchy distributions. It has also become clear that more intensive studies of even relatively well known areas and well known groups are still uncovering a surprising number of new species (Pereira et al., 1993). Besides these arguments, the map in Figure 1 clearly shows that sampling has been uneven, with an enormous concentration of surveys in relatively few well-studied areas, while large and potentially interesting and heterogeneous regions have remained unsampled. Even in comparatively well-worked states such as São Paulo and Minas Gerais, the distribution of cerrado surveys has been uneven. Surveys in these areas would almost certainly contribute a considerable number of "new" species to the list. In consequence, it seems premature to declare that the upper limit given in Table 2 is totally wrong, and it is possible that the cerrado flora could have a much greater number of woody species than that established as the lower limit.

We are left, therefore, with a range of around 1000 to 2000 for the number of woody species in the cerrado flora. Comparing the lower limit with estimates in the literature, it can be seen that this is somewhat higher than those proposed by most authors, but is quite close to Eiten's (1990) value. Our upper limit is considerably higher than any of the published estimates, and is more than double the number of woody cerrado species that most authors have assumed. Although we consider this upper limit rather unlikely, it suggests that the cerrado woody flora may be much richer than has usually been indicated and that much work is still necessary, particularly in under-sampled regions, to reach a more satisfactory conclusion.

The almost complete absence of studies of the herbaceous-subshrubby component of the cerrado flora means that it is not possible, at present, to make comprehensive lists of species. Mantovani and Martins (1993) have found proportions of 1 : 2 to 1 : 3 for the number of arboreal-shrubby species: herbaceous-subshrubby species. Extrapolation from these ratios gives the results found in Table 5 (p. 224), which shows the estimated number of herbaceous-subshrubby species under various assumptions. The number of herbaceous-subshrubby species would therefore lie between 2000 and 5250, with the total cerrado flora of 3000 to 7000 angiosperm species. These numbers are clearly not very reliable, since we have insufficient knowledge of the ratio of woody : non-woody species, but they do at least suggest an order of magnitude. In general, it seems likely that the proportion of confidently identified species is lower in studies of the non-woody flora of the cerrado (Mantovani, 1983), so that the percentage of "new" species among the unknowns may be much higher in this group.

Because the spatial distribution of the surveys in the cerrados in Brazil has been very uneven (Fig. 1), a number of areas merit high priority for future investigations. Among these we particularly emphasize the following:

(1) The state of Mato Grosso do Sul has extensive areas of cerrado outside the pantanal region, which is the only part to have been studied. This region is particularly vulnerable, since large areas have already been cleared for agriculture. The neighboring cerrados in the southeast of Goiás are also unstudied and extremely vulnerable.
(2) Northwestern Mato Grosso state has also been very little studied and is being rapidly opened up to colonization.
(3) The state of Tocantins (formerly north of Goiás) and adjoining areas in Ceará are practically untouched and almost nothing has been published about these areas. They are likely to be particularly interesting, since they are in contact with the forests of the Amazon basin and are likely to show high diversity in common with sites in Mato Grosso, which have provided the highest species richness encountered in the cerrado flora (Castro, 1994).
(4) The west of Bahia and south of Piauí also have considerable areas of cerrado that have scarcely been studied. These offer the opposite extreme from the previous region, since they come into contact with the caatinga vegetation and are likely to contain a number of unique elements adapted to drier climates (Castro et al., in press).

CONCLUSIONS

The greatest source of error and uncertainty in compilation of lists of the cerrado flora is the relatively large number of "unknowns," together with the uneven geographic distribution of the studies that have been made. The unknowns and dubious identifications in the present list amount to more than 40% at the species level. Although this percentage must contain many "unknowns" that are in fact known species that were not identified as such when the survey was made, and must also contain many species that are common to several sites, there is still a sizeable residue that represents genuinely new species or species that have not been correctly identified as occurring in cerrado vegetation. There is clearly still a need for much taxonomic work on the cerrado flora.

Good taxonomy depends on good collecting, and it is clear that much work remains to be done in the cerrados. On the one hand, typical floristic studies tend to collect flowering material, which can usually be identified to species level with confidence, but will often tend to miss species that were not in flower at the times visits were made, that tend to flower sporadically or rarely, that are very ephemeral, or are relatively inconspicuous. On the other hand, quantitative studies on community structure often collect more completely, since all the individuals within certain size classes will be included, but much of the material may be sterile or atypical (attacked by herbivores, etc.). Thorough collecting and complete identification of material therefore require repeated visits to a site, making the whole exercise time-consuming and costly, particularly in more remote areas where access is difficult and considerable time may be spent in traveling to the site. This problem is more acute with herbaceous-subshrubby species, where the problems mentioned above are even more serious. In many areas the accelerated rates of destruction of cerrado areas mean that it is very difficult, if not impossible, to make a number of return visits to a site, since it may have been destroyed or heavily altered in the meantime.

A further source of difficulties in the compilation of species lists is the problem of updating identifications. In most cases, once a survey has been published, no attempt is made to update the species lists or publish corrections where erroneous identifications have been made. Since many surveys do not cite individual voucher specimens, it can often be impossible to relocate the material collected in order to check identifications or try to resolve unidentified material. In the case of a list like the present one, even if the voucher lists were published, verifying them would involve consulting dozens of herbaria. The collections in a herbarium may have been recently reworked by a specialist, but the new identifications that have been made are generally not easily accessible. This is one area where the use of data banks and on-line access to collections would be genuinely useful, rather than just a fashionable thing to do in order to say that the herbarium is "up-to-date." If it were possible to consult herbaria on line and discover whether specific specimens cited in published reports have been reidentified, many of the difficulties and errors in the compilation of the present list would be avoidable. We therefore urge that more attention be given to publishing corrections and additions to already published species lists or quantitative surveys, and that efforts be made to extend and facilitate the use of computer data banks and on-line access to collections.

In the Brazilian Constitution, the vegetation formations of the Amazon, the Atlantic Forest, coastal areas, and the pantanal of Mato Grosso are considered to be a national heritage. Riparian forest is also the subject of special legislation. This implies that different categories of ecosystems have been recognized and that the formations cited above are considered to be of greater importance, while the remaining vegetation formations are not. Among the latter, the cerrado is being destroyed most rapidly. In addition, historically the cerrados have never been considered deserving of specific conservation measures, and there are few official cerrado reserves. Contrary to the assumptions made by many authors, however, the cerrados do have a relatively rich and diverse flora, which is still relatively under-investigated.

The cerrado has species that evolved under conditions of strong selective pressures from herbivores (Fowler & Duarte, 1991; Oliveira & Leitão Filho, 1987). Moreover, they are adapted to dystrophic, acid, often aluminum-rich soils, and are resistant to (often prolonged) periodic drought. As such, they represent an important genetic resource and are much more than a simple source of vegetable charcoal or areas to be exploited for cultivation of crops, often stimulated more by economic interests than any real necessity. Their protection, and the preservation of the genetic diversity that they contain, is a matter of considerable importance and urgency.

Any attempt to create a rational scheme for preservation of cerrados and to identify particularly critical areas for conservation is hampered by our incomplete knowledge of the flora as a whole and by the uneven coverage of studies in the vast region originally covered by this vegetation. We are still unable to determine what would be a sufficient size of reserve to maintain a reasonable level of cerrado biodiversity, or even to state with any confidence what is a reasonable level of biodiversity for this formation.

A potentially valuable resource that is still relatively unknown is now being subjected to increasing levels of genetic erosion and is not being exploited in a rational or wise manner. We therefore urge that increased efforts be made to improve our knowledge of the cerrado flora as a whole, both in terms of basic taxonomy and in improving the geographic coverage of cerrado studies.

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Table 1. Selected surveys of cerrado sensu lato in Brazil and their authors. In the column "Authors," when not indicated, the authors are the same as above. Map Code: locality of the municipality on the map of Figure 1. State: AM Amazonas, AP Amapá, CE Ceará, DF Distrito Federal, GO Goiás, MG Minas Gerais, MS Mato Grosso do Sul, MT Mato Grosso, PA Pará, PE Pernambuco, PI Piauí, RR Roraima, SP São Paulo, TO Tocantins. Altitude in meters. (a) no information.

Map Code	State	Municipality	Sites	Latitude S	Longitude W	Altitude	Authors
1	AM	Humaitá	Puciari-Humaitá	7°31'	63°00'	51	Gottsberger and Morawetz (1986)
2	AP	(a)	Macapá e Calçoene	1°17' N	50°00'	13	Rabelo and Berg (1982)
3	CE	Aquiraz	(a)	3°58'	38°16'	35	Granjeiro (1983)
4	CE	Aurora, Caririaçu, Farias Brito, Granjeiro, Lavras da Mangabeira e Várzea Alegre	(a)	6°52'	39°15'	440	Figueiredo (1989a, b), Figueiredo and Fernandes (1987)
5	CE	Crato, Nova Olinda e Santana do Cariri	Chapada do Araripe	7°15'	39°35'	871	Albuquerque (1987)
6(A)	DF	Brasília	Fazenda Água Limpa	15°57'	46°53'	1100	Moura (1983)
7(A)	DF	Brasília	Fazenda Água Limpa	15°57'	46°53'	1100	Ratter (1980, 1985[a],1986)
8(A)	DF	Brasília	Fazenda Água Limpa	15°57'	46°53'	1100	
9(A)	DF	Brasília	Fazenda Água Limpa	15°57'	46°53'	1100	
10(A)	DF	Brasília	Fazenda Água Limpa	15°57'	46°53'	1100	
11(A)	DF	Brasília	Fazenda Água Limpa	15°57'	46°53'	1100	
12(A)	DF	Brasília	Fazenda Água Limpa	15°57'	46°53'	1100	Felfili and Silva Jr. (1992)
13(A)	DF	Brasília	Fazenda Água Limpa	15°57'	46°53'	1100	
14(A)	DF	Brasília	Fazenda Água Limpa	15°57'	46°53'	1100	Santos (1988)
15(A)	DF	Brasília	Parque Nacional de Brasília	15°40'	47°59'	1135	Oliveira et al. (1982)
16(A)	DF	Brasília	Parque Nacional de Brasília	15°40'	47°59'	1135	
17(A)	DF	Brasília	Campus da Universidade de Brasília	15°45'	47°52'	1172	Heringer (1971), Heringer and Barroso (1968)
18(A)	DF	Brasília	Estação Ecológica do Roncador	15°57'	47°53'	1170	Santos (1988)
19(A)	DF	Brasília	Reserva da TERRACAP	15°54'	47°50'	1155	Araújo (1984)
20(A)	DF	Brasília e Gama	(a)	15°45'	47°45'	1125	

Table 1. Continued.

21(A)	DF	Brasília e Planaltina	Área de Proteção Ambiental da Bacia do Rio São Bartolomeu	15°50'	47°30'	963	Pereira et al. (1990)
22(A)	DF	Brasília e Planaltina	Área de Proteção Ambiental da Bacia do Rio São Bartolomeu	15°50'	47°30'	963	
23(A)	DF	Brasília e Planaltina	Área de Proteção Ambiental da Bacia do Rio São Bartolomeu	15°50'	47°30'	963	
24(A)	DF	Brasília, Gama e Planaltina	(a)	15°45'	47°45'	1125	Aoki and Santos (1980, 1982), Santos and Aoki (1992)
25(A)	DF	Brasília, Gama, Planaltina e Taguatinga	(a)	15°45'	47°45'	1125	
26(A)	DF	Planaltina	Centro de Pesquisa Agropecuária dos Cerrados	15°36'	47°40'	975	Ribeiro et al. (1982)
27(A)	DF	Planaltina	Centro de Pesquisa Agropecuária dos Cerrados	15°36'	47°40'	975	
28(A)	DF	Planaltina	Centro de Pesquisa Agropecuária dos Cerrados	15°36'	47°40'	975	
29(A)	DF	Planaltina	Centro de Pesquisa Agropecuária dos Cerrados	15°36'	47°40'	975	
30(A)	DF	Planaltina	Centro de Pesquisa Agropecuária dos Cerrados	15°36'	47°40'	975	Ribeiro et al. (1985)
31(A)	DF	Planaltina	Centro de Pesquisa Agropecuária dos Cerrados	15°36'	47°40'	975	

Table 1. Continued.

32(A)	DF	Planaltina	Centro de Pesquisa Agropecuária dos Cerrados	15°36'	47°40'	975	
33(A)	DF	Planaltina	Centro de Pesquisa Agropecuária dos Cerrados	15°36'	47°40'	975	Santos (1988)
34(A)	DF	Planaltina	Centro de Pesquisa Agropecuária dos Cerrados	15°36'	47°40'	975	Ribeiro and Haridasan (1990)
35(A)	DF	Planaltina	Centro de Pesquisa Agropecuária dos Cerrados	15°36'	47°40'	975	
36(A)	DF	Planaltina	Reserva Biológica de Águas Emendadas	15°35'	47°40'	1175	Brandão (1976), Distrito Federal (1977)
37	GO	Goiania	(a)	16°40'	49°15'	730	Rizzo et al. (1973)
38	GO	Goiás e Mossâmedes	Serra Dourada	16°05'	50°20'	700	Rizzo (1970)
39(B)	GO	Padre Bernardo	(a)	15°15'	48°30'	629	Ratter and Dargie (1992), Ratter et al. (1977)
40(B)	GO	Padre Bernardo	Fazenda Lagoa Santa	15°12'	48°21'	640	
41(C)	MG	Alpinópolis	Fazenda Monte Alto	20°54'	46°21'	876	Carvalho (1987)
42(C)	MG	Arinos	Sagarana	15°55'	46°03'	480	Ratter and Dargie (1992)
43(C)	MG	Campo do Meio	Fazenda Campo das Flores	21°02'	45°58'	785	Carvalho (1987)
44	MG	Curvelo	(a)	18°45'	44°25'	633	Rizzini (1975)
45(D)	MG	Frutal, Ituiutaba, Tupaciguara e Uberlândia	Triângulo Mineiro	19°20'	48°50'	752	Goodland (1970, 1979)
46(D)	MG	Frutal, Ituiutaba, Tupaciguara e Uberlândia	Triângulo Mineiro	19°20'	48°50'	692	

Table 1. Continued.

47(D)	MG	Frutal, Ituiutaba, Tupaciguara e Uberlândia	Triângulo Mineiro	19°20'	48°50'	742	
48(D)	MG	Frutal, Ituiutaba, Tupaciguara e Uberlândia	Triângulo Mineiro	19°20'	48°50'	713	
49	MG	Januária	Pandeiros	15°28'	44°23'	434	
50	MG	Lavras	Reserva Biológica Municipal de Poço Bonito	21°14'	45°00'	801	Gavilanes et al. (1990)
51	MG	Ouro Preto	(a)	20°33'	43°30'	1061	Zurlo (1978)
52(E)	MG	Paraopeba	Estação Florestal de Experimentação de Paraopeba	19°20'	44°20'	742	Silva Jr. (1984), Silva Jr. And Silva (1988)
53(E)	MG	Paraopeba	Estação Florestal de Experimentação de Paraopeba	19°20'	44°20'	742	Thibau et al. (1975)
54(E)	MG	Pedro Leopoldo	Fazenda da Jaguara	19°37'	44°02'	698	(Rizzini, 1975)
55(E)	MG	Pedro Leopoldo	Fazenda da Jaguara	19°37'	44°02'	698	
56(E)	MG	Pedro Leopoldo	Fazenda da Jaguara	19°37'	44°02'	698	Castro (1975)
57	MG	Pimenta	Fazenda Serra dos Lopes	20°30'	45°57'	776	
58(F)	MG	Prudente de Morais	Fazenda Experimental de Santa Rita	19°29'	44°09'	732	Brandão et al. (1981)
59(F)	MG	Sete Lagoas	Instituto de Pesquisa Agropecuária do Centro-Oeste	19°28'	44°15'	775	Silva et al. (1974/76)
60(F)	MG	Sete Lagoas	(a)	19°25'	44°15'	771	Brandão et al. (1984)
61	MS	Corumbá	Fazenda Acurizal	17°45'	57°37'	90	Prance and Schaller (1982)
62	MS	Corumbá	Fazenda Ipanema	18°59'	56°39'	89	Ratter et al. (1988b)
63	MS	Corumbá	Fazenda Nhumirim (Bahia Suja)	19°00'	56°40'	89	
64	MS	Corumbá	Fazenda Nhumirim (Salina Grande)	19°05'	56°45'	89	

Table 1. Continued.

65	MS	Corumbá	Fazenda Nhumirim (Salina Grande)	19°05'	56°45'	89	
66	MS	Corumbá	Fazenda Nhumirim (Cerrado)	19°03'	56°43'	89	
67	MS	Corumbá	Fazenda Nhumirim (Cerrado)	19°03'	56°43'	89	
68	MT	(a)	Serra do Roncador (Base de Campo da Expedição Xavantina-Cachimbo)	12°49'	51°46'	400	Eiten (1975), Ratter et al. (1973)
69	MT	(a)	Serra do Roncador (Base de Campo da Expedição Xavantina-Cachimbo)	12°49'	51°46'	400	
70	MT	(a)	Serra do Roncador (Base de Campo da Expedição Xavantina - Cachimbo)	12°49'	51°46'	400	
71	MT	(a)	Serra do Roncador (Base de Campo da Expedição Xavantina - Cachimbo)	12°49'	51°46'	400	
72	MT	(a)	Serra do Roncador (Base de Campo da Expedição Xavantina-Cachimbo)	12°49'	51°46'	400	
73	MT	(a)	Serra do Roncador (Base de Campo da Expedição Xavantina - Cachimbo)	12°49'	51°46'	400	
74	MT	(a)	Serra do Roncador (Base de Campo da Expedição Xavantina - Cachimbo)	12°49'	51°46'	400	
75	MT	(a)	Serra do Roncador (Base de Campo da Expedição Xavantina - Cachimbo)	12°49'	51°46'	400	
76	MT	(a)	Serra do Roncador (Base de Campo da Expedição Xavantina - Cachimbo)	12°49'	51°46'	400	Ratter and Dargie (1992), Ratter et al. (1977)

Table 1. Continued.

77	MT	Barra do Garças	Vale dos Sonhos	15°21'	52°13'	318	Ratter and Dargie (1992), Ratter et al. (1977)
78	MT	Cuiaba	Salgadeira	15°21'	55°49'	375	Oliveira Filho (1984), Oliveira Filho et al. (1989)
79	MT	Cuiabá	Salgadeira	15°21'	55°49'	515	Oliveira Filho and Martins (1986)
80	MT	Cuiabá	Salgadeira	15°21'	55°49'	515	
81	MT	Cuiabá	Salgadeira	15°21'	55°49'	515	
82	MT	Cuiabá	Salgadeira	15°21'	55°49'	515	
83(G)	MT	Nova Xavantina	Serra do Roncador	14°45'	52°20'	400	Eiten (1975), Ratter et al. (1973)
84(G)	MT	Nova Xavantina	Serra do Roncador	14°45'	52°20'	400	
85(G)	MT	Nova Xavantina	Serra do Roncador	14°45'	52°20'	400	
86(G)	MT	Nova Xavantina	Serra do Roncador	14°45'	52°20'	400	Ratter and Dargie (1992), Ratter et al. (1973)
87	MT	Poconé	Fazenda São Vicente do Rio Claro	16°16'	56°38'	93	
88	MT	Poconé	Fazenda São Vicente do Rio Claro	16°16'	56°38'	93	Ratter et al. (1977), Ratter and Dargie (1992)
89(H)	MT	Torixoréu	Morro da Fumaça (Fazenda Alvorada)	15°53'	52°15'	40	Furley et al. (1988)
90(H)	MT	Torixoréu	Morro da Fumaça (Fazenda Alvorada)	15°53'	52°15'	40	
91(H)	MT	Torixoréu	Morro da Fumaça (Fazenda Alvorada)	15°53'	52°15'	40	
92	PA	Salvaterra	Ilha de Marajó (Vila de Joanes)	0°53'	48°35'	8	Bastos (1984)
93	PE	Goiania	(a)	7°33'	35°00'	13	Haynes (1970), Tavares (1964a, b)
94(K)	PI	Barras	Fazenda Lagoa Seca	4°14'	41°37'	75	
95(K)	PI	Batalha	Fazenda Caiçara	4°01'	42°04'	80	
96(K)	PI	Batalha	Fazenda Bom Principio	4°08'	42°09'	80	
97(J)	PI	Beneditinos	Fazenda Descanso	5°27'	42°21'	80	Castro et al. (in press)
98(K)	PI	Capitão de Campos	Fazenda Santana	4°27'	41°56'	140	
99	PI	Elesbão Veloso	Fazenda Vista Alegre	6°12'	42°08'	230	

Table 1. Continued.

100	PI	José de Freitas	Fazenda Tucum	4°45'	42°35'	137	
101(J)	PI	Monsenhor Gil	Fazenda Toti Negra	5°33'	42°37'	115	
102	PI	Oeiras	Fazenda Piloto Chapada Grande	6°36'	42°16'	430	Castro et al. (in press)
103(L)	PI	Piracuruca	Fazenda Alto Bonito	3°56'	41°43'	70	
104(L)	PI	Piracuruca e Piripiri	Parque Nacional de Sete Cidades	4°06'	41°43'	275	Barroso and Guimarães (1980)
105(L)	PI	Piripiri	Fazenda Carnaubal	4°16'	41°47'	160	
106	PI	Ribeiro Gonçalves	Estação Ecológica de Uruçuí-Una	8°51'	45°15'	400	Castro (1984), Castro et al. (in press)
107(M)	RR	(a)	Campos de Roraima (Milagre, Normandia, Paricarana, Pedra do Passarão e Surumu)	4°03' N	60°25'	133	Dantas and Rodrigues (1982)
108(M)	RR	(a)	Campos de Roraima	4°03' N	60°25'	133	Rodrigues (1971)
109(M)	RR	(a)	Campos de Roraima (Milagre, Normandia, Paricarana, Pedra do Passarão e Surumu)	4°03' N	60°25'	133	Dantas and Rodrigues (1982)
110(N)	SP	Águas de Santa Bárbara	Estação Ecológica de Santa Bárbara	22°53'	49°14'	510	Meira Neto (1991)
111(N)	SP	Águas de Santa Bárbara	Estação Ecológica de Santa Bárbara	22°53'	49°14'	510	
112(N)	SP	Águas de Santa Bárbara	Estação Ecológica de Santa Bárbara	22°53'	49°14'	510	
113(N)	SP	Águas de Santa Bárbara	Estação Ecológica de Santa Bárbara	22°53'	49°14'	510	
114(N)	SP	Águas de Santa Bárbara	Estação Ecológica de Santa Bárbara	22°53'	49°14'	510	
115(N)	SP	Analândia	Área de Proteção Ambiental de Corumbataí	22°08'	47°40'	685	
116(N)	SP	Angatuba	Instituto Florestal de São Paulo	23°27'	48°25'	598	Ratter et al. (1988a)

Table 1. Continued.

117(N)	SP	Angatuba	Instituto Florestal de São Paulo	23°27'	48°25'	598	
118(N)	SP	Angatuba	Instituto Florestal de São Paulo	23°27'	48°25'	598	
119(O)	SP	Bauru	(a)	22°20'	49°00'	499	Ferracini et al. (1983)
120(O)	SP	Bauru	Parque Ecológico Municipal de Bauru	22°20'	49°00'	580	Cavassan (1990)
121(P)	SP	Botucatu	Fazenda Treze de Maio	22°45'	48°25'	550	Silberbauer-Gottsberger and Eiten (1983, 1987), Silberbauer-Gottsberger et al. (1977)
122(P)	SP	Botucatu	Fazenda Treze de Maio	22°45'	48°25'	550	Gottsberger and Silberbauer-Gottsberger (1983)
123(P)	SP	Botucatu	Fazenda Treze de Maio	22°45'	48°25'	550	
124(P)	SP	Brotas e Itirapina	Represa do Lobo	22°16'	47°52'	715	Souza (1977)
125(P)	SP	Corumbataí	Campus da Universidade Estadual Paulista (Rio Claro)	22°15'	47°00'	815	Cesar et al. (1988)
126(P)	SP	Corumbataí	Área de Proteção Ambiental de Corumbataí	22°13'	47°37'	570	Pagano et al. (1989a, b)
127(P)	SP	Itirapina	Estação Experimental de Itirapina	22°15'	47°49'	760	Giannotti (1986), Giannotti and Leitão Filho (1992)
128(P)	SP	Itirapina	Estação Experimental de Itirapina	22°15'	47°49'	760	
129(P)	SP	Itirapina	Área de Proteção Ambiental de Corumbataí	22°18'	47°44'	700	
130(P)	SP	Itirapina	(a)	22°16'	47°10'	760	Mantovani (1990)
131(P)	SP	Itirapina	(a)	22°16'	47°10'	760	
132(P)	SP	Itirapina	(a)	22°16'	47°10'	760	
133(R)	SP	Luis Antonio	Estação Experimental de Luis Antonio	21°40'	47°49'	670	Toledo Filho (1984)
134(Q)	SP	Moji Guaçu	Reserva Biológica de Moji Guaçu	22°18'	47°09'	680	Batista (1982, 1988), Batista and Couto (1992)

Table 1. Continued.

135(Q)	SP	Moji Guaçu	Reserva Biológica de Moji Guaçu	22°18'	47°09'	600	Mantovani (1983), Mantovani et al. (1985)
136(Q)	SP	Moji Guaçu	Fazenda Campininha	22°18'	47°09'	600	Gibbs et al. (1983)
137(Q)	SP	Moji Mirim	Estação Experimental de Moji Mirim	22°26'	46°57'	631	Toledo Filho et al. (1984)
138(P)	SP	Santa Maria da Serra	Área de Proteção Ambiental de Corumbataí	22°38'	48°07'	500	
139(R)	SP	Santa Rita do Passa Quatro	Parque Estadual de Vaçununga (Gleba Pé de Gigante)	21°38'	47°36'	700	Castro (1987)
140	SP	São José do Rio Preto	(a)	20°48'	49°23'	475	Camargo and Marinis (1966)
141	SP	Assis	Estação Experimental de Assis	22°35'	50°25'	562	Durigan et al. (1987)
142	TO	Cristalândia, Formoso do Araguaia e Pium	Ilha do Bananal (Parque Nacional do Araguaia)	10°31'	50°12'	205	Ratter (1985b, 1987)
143	TO	Cristalândia, Formoso do Araguaia e Pium	Ilha do Bananal (Parque Nacional do Araguaia)	10°31'	50°12'	205	
144	TO	Cristalândia, Formoso do Araguaia e Pium	Ilha do Bananal (Parque Nacional do Araguaia)	10°31'	50°12'	205	
145	TO	Cristalândia, Formoso do Araguaia e Pium	Ilha do Bananal (Parque Nacional do Araguaia)	10°31'	50°12'	205	

Table 2. "Refined" list of families (according to Cronquist, 1981, 1988) and species of shrubs and trees reported to occur in cerrado vegetation. *spp. x* indicates x taxonomic entities not identified at species level. *unknown x* indicates x taxonomic entities not identified at the genus level. The asterisk (*) means that the binomial was taken as it stands in the original publication: no synonym or author was found for it in the taxonomic literature.

Acanthaceae
Ruellia geminiflora Kunth

Amaranthaceae
Gomphrena macrocephala A. St.-Hil.

Anacardiaceae
Anacardium humile A. St.-Hil.
Anacardium occidentale L.
Astronium fraxinifolium Schott
Astronium cf. fraxinifolium Schott
Astronium cf. lecointe Ducke
Astronium ulei Mattick
Lithraea molleoides (Vell.) Engl.
Lithraea sp.
Miracrodruon urundeuva Alemão
Schinus terebinthifolius Raddi
Spondias purpurea L.
Tapirira guianensis Aubl.
Tapirira marchandii Engl.
Tapirira sp.

Annonaceae
Annona campestris R. E. Fr.
Annona coriacea Mart.
Annona cornifolia A. St.-Hil.
Annona crassiflora Mart.
Annona crotonifolia Mart.
Annona dioica A. St.-Hil.
Annona muricata L.
Annona pygmaea (Warm.) Warm.
Annona reticulata L.
Annona tomentosa R. E. Fr.
Annona cf. tomentosa R. E. Fr.
Annona spp. 6
Bocageopsis mattogrossensis (R. E. Fr.) R. E. Fr.
Cardiopetalum calophyllum Schltdl.
Duguetia echinophora R. E. Fr.
Duguetia furfuracea (A. St.-Hil.) Benth. & Hook. f.
Duguetia lanceolata A. St.-Hil.
Ephedranthus parviflorus S. Moore
Guatteria aff. minarum R. E. Fr.
Guatteria nigrescens Mart.
Guatteria silvatica R. E. Fr.
Guatteria subsessilis Mart.
Guatteria spp. 3
Rollinia emarginata Schltdl.
Rollinia sylvatica (A. St. Hil.) Mart.
Rollinia sp.
Unonopsis lindmani R. E. Fr.
Xylopia aromatica (Lam.) Mart.
Xylopia brasiliensis Spreng.
Xylopia emarginata Mart.
Xylopia sericea A. St.-Hil.
Xylopia spp. 2

Apocynaceae
Aspidosperma cuspa (Kunth) S. T. Blake

Table 2. Continued

Aspidosperma cylindrocarpon Müll. Arg.
Aspidosperma macrocarpon Mart.
Aspidosperma multiflorum A. DC.
Aspidosperma nobile Müll. Arg.
Aspidosperma polyneuron Müll. Arg.
Aspidosperma pyricolium Müll. Arg.
Aspidosperma pyrifolium Mart.
Aspidosperma subincanum Mart. ex A. DC.
Aspidosperma tomentosum Mart.
Aspidosperma verbascifolium Müll. Arg.
Aspidosperma spp. 9
Hancornia speciosa M. Gómez
Himatanthus articulatus (Vahl) Woodson
Himatanthus bracteatus (A. DC.) Woodson
Himatanthus cuneatus Sm.
Himatanthus obovatus (Müll. Arg.) Woodson
Himatanthus phagedaenicus (Mart.) Woodson
Himatanthus sp.
Mandevilla erecta (Vell.) Woodson
Mandevilla gentianoides (Mill.) Woodson
Odontadenia lutea (Vell.) Markgr.
Peschiera affinis (Müll. Arg.) Miers
Peschiera hystrix (Steud.) A. DC.
Rauvolfia ternifolia Kunth

Aquifoliaceae
Ilex affinis Gardner
Ilex asperula Mart.
Ilex cerasifolia Reissek
Ilex conocarpa Reissek
Ilex cf. conocarpa Reissek
Ilex sp.

Araliaceae
Dendropanax cuneatum (DC.) Decne. & Planch.
Dendropanax sp.
Didymopanax distractiflorum Harms
Didymopanax macrocarpum (Cham. & Schltdl.) Seemann
Didymopanax morototoni (Aubl.) Decne. & Planch.
Didymopanax vinosum Cham. & Schltdl.
Didymopanax spp. 3

Arecaceae
Acanthococos emensis Toledo
Acrocomia aculeata (Jacq.) Lodd.
Acrocomia totai Mart.
Acrocomia sp.
Allagoptera campestris (Mart.) Kuntze
Astrocaryum campestre Mart.
Astrocaryum vulgare Mart.
Astrocaryum spp. 2
Attalea exigua Drude
Attalea geraensis Barb. Rodr.
Attalea humilis Mart.
Attalea phalerata Mart. & Spreng.
Attalea sp.
Bactris spp. 2
Butia leiospatha (Mart.) Becc.

Table 2. Continued.

Butia paraguayensis (Barb. Rodr.) L. H. Bailey
Copernicia prunifera (Mill.) H. E. Moore
Mauritia martiana Spruce
Maximiliana regia Mart.
Oenocarpus distichus Mart.
Orbignya phalerata Mart.
Orbignya sp.
Syagrus comosa (Mart.) Mart.
Syagrus flexuosa (Mart.) Becc.
Syagrus loefgrenii Glassman
Syagrus petraea (Mart.) Becc.
Syagrus romanzoffiana (Cham.) Glassman
Syagrus spp. 9
Unknown 5

Asclepidaceae

Hemipogon setaceus Decne.
Hemipogon sp.
Pseudibatia sp.

Asteraceae

*Baccharis aff. campestris
Baccharis concinna G. M. Barroso
Baccharis dracunculifolia DC.
Baccharis lymannii G. M. Barroso
Baccharis cf. microdonta DC.
Baccharis pseudotenuifolia I. L. Teodoro
Baccharis ramosissima Gardner
Baccharis reticularia DC.
Baccharis semiserrata DC.
Baccharis tridentata Vahl
Baccharis trimera DC.
Baccharis spp. 4
Brickellia pinifolia A. Gray
Clibadium rotundifolium DC.
Dasyphyllum orthacantum (DC.) Cabrera
Elephantopus biflora Sch. Bip.
Eremanthus glomeratus Less.
Eremanthus goyazensis (Gardner) Sch. Bip.
Eremanthus mattogrossensis Kuntze
Eremanthus sphaerocephalus (DC.) Baker
Eremanthus spp. 3
Eupatorium barbacense Hieron.
Eupatorium cuneatum DC.
Eupatorium laevigatum Lam.
Eupatorium maximiliani Schrad. ex DC.
Eupatorium squalidum DC.
Eupatorium trixoides Mart. ex Baker
Eupatorium vauthierianum DC.
Eupatorium spp. 8
Gochnatia barrosii Cabrera
Gochnatia floribunda Cabrera
Gochnatia plymorpha (Less.) Cabrera
Gochnatia pulchra Cabrera
Gochnatia velutina (Bong.) Cabrera
Gorceixia sp.
Hoehnephytum trixioides (Gardner) Cabrera
Ichthyothere cunabi Mart.
Lychnophora ericoides Mart.
Mikania sessilifolia DC.
Piptocarpha rotundifolia (Less.) Baker
Piptocarpha sp.
Senecio brasiliensis Less.
Senecio aff. oxyphyllus DC.

Table 2. Continued.

Symphyopappus polystachyus (DC.) Baker
Trichogonia alternata*
Trichogonia campestris Gardner
Trixis verbasciformis Less.
Vanillosmopsis erythropappa Sch. Bip.
Vanillosmopsis sp.
Vernonia bardanoides Less.
Vernonia brasiliensis (Spreng.) Less.
Vernonia chamissonis Less.
Vernonia diffusa (Spreng.) Less.
Vernonia ferruginea Less.
Vernonia fruticulosa Mart. ex DC.
Vernonia glabrata Less.
Vernonia grandiflora Less.
Vernonia missionis Gardner
Vernonia mucronulata Less.
Vernonia oligolepis Sch. Bip. ex Baker
Vernonia phosphorea (Vell.) H. Monteiro*
Vernonia polyanthes (Spreng.) Less.
Vernonia rubriramea Mart. ex DC.
Vernonia ruficoma Schltdl. ex Mart.
Vernonia cf. ruficoma Schltdl. ex Mart.
Vernonia aff. varroniaefolia DC.
Vernonia spp. 5
Wunderlichia mirabilis Riedel ex Baker
Unknown 4

Bignoniaceae

Anemopaegma arvense (Vell.) Stellfeld
Anemopaegma glaucum Mart.
Anemopaegma sp.
Arrabidaea brachypoda (DC.) Bureau & K. Schum.
Arrabidaea corallina (Jacq.) Sandwith
Arrabidaea inaequalis Baill.
Arrabidaea sceptrum (Cham.) Sandwith
Arrabidaea sp.
Crescentia cujete L.
Cybistax antisyphilitica (Mart.) Mart.
Distictella mansoana (DC.) Urb.
Fridericia speciosa Mart.
Jacaranda acutifolia Humb. & Bonpl.
Jacaranda brasiliana (Lam.) Pres.
Jacaranda caroba (Vell.) DC.
Jacaranda copaia (Aubl.) D. Don
Jacaranda cusipidifolia Mart.
Jacaranda decurrens Cham.
Jacaranda jasminoides (Thunb.) Sandwith
Jacaranda paucifoliolata Mart. ex DC.
Jacaranda puberula Cham.
Jacaranda rufa J. Silva Manso
Jacaranda ulei Bureau & K. Schum.
Jacaranda spp. 7
Memora axilaris Bureau & K. Schum.
Memora cuspidata Hassl.
Memora nodosa (J. Silva Manso) Miers
Memora peregrina (Miers) Sandwith
Memora sp.
Tabebuia alba (Cham.) Sandwith
Tabebuia aurea (J. Silva Manso) Benth. & Hook.
Tabebuia chrysantha (Jacq.) G. Nicholson
Tabebuia impetiginosa (Mart. ex DC.) Standley
Tabebuia insignis (Miq.) Sandwith
Tabebuia ochracea (Cham.) Standley
Tabebuia roseo-alba (Ridl.) Sandwith

Table 2. Continued.

Tabebuia serratifolia (Vahl) G. Nicholson
Tabebuia spp. 13
Tecoma leucoxylon Mart. ex DC.
Zeyheria montana Mart.
Unknown 2

Bixaceae

Cochlospermum regium (Schrank) Pilg.
Cochlospermum vitifolium (Willd.) Spreng.

Bombacaceae

Bombax cyathophorum (Casar.) K. Schum.
Bombax sp.
Eriotheca gracilipes (K. Schum.) A. Robyns
Eriotheca pubescens (Mart. & Zucc.) Schott & Endl.
Pseudobombax longiflorum (Mart. & Zucc.) A. Robyns
Pseudobombax marginatum (A. St.-Hil., A. Juss. & Chambess.) A. Robyns
Pseudobombax tomentosum (Mart. & Zucc.) A. Robyns
Pseudobombax spp. 2

Boraginaceae

Cordia alliodora (Ruiz & Pav.) Oken
Cordia bicolor A. DC.
Cordia discolor Cham.
Cordia ecalyculata Vell.
Cordia glabrata (Mart.) A. DC.
Cordia insignis Cham.
Cordia nodosa Lam.
Cordia sellowiana Cham.
Cordia superba Cham.
Cordia spp. 2
Tournefortia sp.

Burseraceae

Bursera leptophloeos Engl.
Bursera simaruba (L.) Sarg.
Bursera sp.
Protium almecega Marchand
Protium aracouchini (Aubl.) Marchand
Protium brasiliense (Spreng.) Engl.
Protium elegans Engl.
Protium heptaphyllum (Aubl.) Marchand
Protium ovatum Engl.
Protium pilosissimum Engl.
Protium spp. 3
Tetragastris unifoliolata (Engl.) Cuatrec.

Cactaceae

Cereus jamacaru DC.

Caesalpiniaceae

Apuleia leiocarpa (Vog.) J. F. Macbr.
Bauhinia amplifolia Ducke
Bauhinia brevipes Vogel
Bauhinia aff. cheilantha (Bong.) Steud.
Bauhinia cupulata Benth.
Bauhinia cuyabensis (Bong.) Steud.
Bauhinia dubia Don
Bauhinia goyazensis Harms
Bauhinia macrostachya Benth.
Bauhinia mollis D. Dietr.
Bauhinia pulchella Benth.
Bauhinia rufa (Bong.) Steud.
Bauhinia tenella Benth.
Bauhinia ungulata L.

Table 2. Continued.

Bauhinia spp. 5
Caesalpinia bracteosa Tul.
Caesalpinia ferrea Mart. ex Tul.
Cassia moschata Kunth
Cassia pendula Humb. & Bonpl. ex Willd.
Cassia spp. 8
Cenostigma gardnerianum Tul.
Cenostigma macrophyllum Tul.
Chamaecrista cathartica (Mart.) H. S. Irwin & Barneby
Chamaecrista claussenii (Benth.) H. S. Irwin & Barneby
Chamaecrista conferta (Benth.) H. S. Irwin & Barneby
Chamaecrista cotonifolia (Don) H. S. Irwin & Barneby
Chamaecrista dalbergiifolia (Benth.) H. S. Irwin & Barneby
Chamaecrista desvauxii (Collad.) Killip
Chamaecrista ensiformis (Vell.) H. S. Irwin & Barneby
Chamaecrista isidorea (Benth.) H. S. Irwin & Barneby
Chamaecrista juruenensis (Hoehne) H. S. Irwin & Barneby
Chamaecrista orbiculata (Benth.) H. S. Irwin & Barneby
Chamaecrista rotundata (Vogel) H. S. Irwin & Barneby
Chamaecrista zygophyloides (Taub.) H. S. Irwin & Barneby
Chamaecrista sp.
Copaifera coriacea Mart.
Copaifera langsdorffii Desf.
Copaifera luetzelburgii Harms
Copaifera martii Hayne
Dimorphandra gardneriana Tul.
Dimorphandra mollis Benth.
Dimorphandra cf. wilsonii Rizzini
Diptychandra aurantiaca Tul.
Diptychandra glabra Benth.
Hymenaea courbaril L.
Hymenaea maranhensis Y. T. Lee & Langenh.
Hymenaea martiana Hayne
Hymenaea stigonocarpa Mart. ex Hayne
Hymenaea velutina Ducke
Hymenaea spp. 3
Macrolobium bifolium (Aubl.) Pers.
Macrolobium sp.
Martiodendron mediterraneum (Mart. ex Benth.) Koeppen
Peltogyne confertiflora (Hayne) Benth.
Peltogyne paniculata Benth.
Peltogyne sp.
Peltophorum vogelianum Benth.
Pterogyne nitens Tul.
Schizolobium parayba (Vell.) Blake
Sclerolobium aureum (Tul.) Benth.
Sclerolobium hypoleucum Benth.
Sclerolobium paniculatum Vogel
Sclerolobium cf. paniculatum Vogel
Sclerolobium spp. 2
Senna alata (L.) Roxb.
Senna bicapsularis (L.) Roxb.
Senna latifolia (G. Mey) H. S. Irwin & Barneby
Senna macranthera (Collad.) H. S. Irwin & Barneby
Senna obtusifolia (L.) H. S. Irwin & Barneby
Senna rugosa (Don) H. S. Irwin & Barneby
Senna silvestris (Vell.) H. S. Irwin & Barneby
Senna spectabilis (DC.) H. S. Irwin & Barneby
Senna trachypus (Benth.) H. S. Irwin & Barneby
Senna velutina (Vogel) H. S. Irwin & Barneby

Table 2. Continued.

Senna sp.
Swartzia flaemingii Raddi
Swartzia latifolia Benth.
Swartzia racemosa Benth.
Swartzia sp.

Caricaceae

Jacaratia sp.

Caryocaraceae

Caryocar brasiliense Cambess.
Caryocar coriaceum Wittm.

Cecropiaceae

Cecropia adenopus Mart.
Cecropia cinerea Miq.
Cecropia cf. cinerea Miq.
Cecropia concolor Willd.
Cecropia obtus Trécul
Cecropia pachystachya Trécul
Cecropia cf. pachystachya Trécul
Cecropia spp. 4

Celastraceae

Austroplenckia populnea (Reissek) Lundell
Austroplenckia sp.
Maytenus alaternoides Reissek
Maytenus aff. alaternoides Riessek
Maytenus cf. alaternoides Reissek
Maytenus communis Reissek
Maytenus evonymoides Reissek
Maytenus obtusifolia Mart.
Maytenus rigida Mart.
Maytenus spp. 3

Chrysobalanaceae

Couepia grandiflora (Mart. & Zucc.) Benth. ex Hook. f.
Exellodendron gardneri (Hook. f.) Prance
Hirtella ciliata Mart. & Zucc.
Hirtella glandulosa Spreng.
Hirtella gracilipes (Hook. f.) Prance
Hirtella hoehnei Pilg.
Hirtella racemosa Lam.
Hirtella spp. 2
Licania apetala (E. Mey.) Fritsch
Licania blackii Prance
Licania gardneri (Hook. f.) Fritsch
Licania hoehnei Pilg.
Licania humilis Cham. & Schltdl.
Licania kunthiana Hook. f.
Licania minuscula Cuatrec.
Licania octandra (Hoffmanns. ex Roem. & Schult.) Kuntze
Licania rigida Benth.
Licania spp. 5
Parinari campestre Aubl.
Parinari obtusifolia Hook. f.

Clethraceae

Clethra brasiliensis Cham. & Schltdl.

Clusiaceae

Calophyllum brasiliense Cambess.
Clusia cf. insignis Mart.
Clusia microphylla Klotzsch ex Engl.
Clusia sellowiana Schltdl.

Table 2. Continued.

Clusia sp.
Kielmeyera abdita Saddi
Kielmeyera coriacea (Spreng.) Mart.
Kielmeyera corymbosa (Spreng.) Mart.
Kielmeyera grandiflora (Wawra) Saddi
Kielmeyera rubriflora Cambess.
Kielmeyera speciosa A. St.-Hil.
Kielmeyera suberosa
Kielmeyera variabilis (Spreng.) Mart.
Kielmeyera cf. variabilis (Spreng.) Mart.
Kielmeyera spp. 6
Mahurea exstipulata Benth.
Platonia insignis Mart.
Symphonia globulifera L. f.
Vismia amazonica Ewan
Vismia brasiliensis Choisy
Vismia cayennensis (Jacq.) Pers.
Vismia guianensis (Aubl.) Choisy
Vismia magnoliaefolia Cham. & Schltdl.
Vismia spp. 3

Combretaceae

Buchenavia grandis Ducke
Buchenavia tomentosa (Mart.) Eichler
Combretum ellipticum Kuhlmann
Combretum fruticosum (Loefl.) Stuntz
Combretum leprosum Mart.
Combretum mellifluum Eichler
Combretum sp.
Terminalia argentea Mart. & Zucc.
Terminalia brasiliensis (Camb.) Eichler
Terminalia fagifolia Mart. ex Zucc.
Terminalia januariensis DC.
Terminalia phaeocarpa Eichler
Terminalia spp 2
Thiloa glaucocarpa (Mart.) Eichler
Unknown 1

Connaraceae

Connarus perrottetii (DC.) Planch.
Connarus suberosus Planch.
Connarus spp. 4
Rourea induta Planch.

Convolvulaceae

Ipomoea albiflora Moric.
Ipomoea sp.
Merremia aturensis (Kunth) Hallier

Cunoniaceae

Lamanonia ternata Vell.

Dilleniaceae

Curatella americana L.
Davilla cearensis Huber
Davilla elliptica A. St.-Hil.
Davilla grandiflora A. St.-Hil. & Tul.
Davilla aff. multiflora A. St.-Hil.
Davilla rugosa Poir.
Davilla sp.

Ebenaceae

Diospyros brasiliensis Mart.

Table 2. Continued.

Diospyros burchellii Hiern
Diospyros coccolobaefolia Mart.
Diospyros hispida A. DC.
Diospyros sericea A. DC.
Diospyros spp. 2
Maba inconstans (Jacq.) Griseb.

Ericaceae

Gaylussacia brasiliensis Meisn.
Gaylussacia pseudo-gaultheria Cham. & Schltdl.
Leucothoe pohlii (Don) Sleumer
Leucothoe serrulata DC.

Erythroxylaceae

Erythroxylum ambiguum Peyr.
Erythroxylum campestre A. St.-Hil.
Erythroxylum citrifolium A. St.-Hil.
Erythroxylum cuneifolium (Mart.) O. E. Schulz
Erythroxylum daphinites Mart.
Erythroxylum deciduum A. St.-Hil.
Erythroxylum engleri O. E. Schulz
Erythroxylum flexuosum O. E. Schulz
Erythroxylum gonocladum (Mart.) O. E. Schulz
Erythroxylum aff. micranthum Bong. ex Peyr.
Erythroxylum orinocense Kunth
Erythroxylum cf. orinocense Kunth
Erythroxylum aff. rufum Cav.
Erythroxylum strobilaceum Peyr.
Erythroxylum suberosum A. St.-Hil.
Erythroxylum tortuosum Mart.
Erythroxylum spp. 9

Euphorbiaceae

Actinostemon communis (Müll. Arg.) Pax
Alchornea discolor Endl. & Poepp.
Alchornea schomburgkii Klotzsch
Alchornea triplinervia (Spreng.) Müll. Arg.
Alchornea spp. 2
Chaetocarpus echinocarpus (Baill.) Ducke
Cnidosculus vitifolius Pohl
Croton floribundus Spreng.
Croton pohlianus Müll. Arg.
Croton salutaris Casar.
Croton spp. 3
Mabea fistulifera Mart.
Mabea sp.
Manihot coerulescens Pohl
Manihot pruinosa Pohl
Manihot tripartita (Spreng.) Müll. Arg.
Manihot violacea Pohl
Manihot spp. 4
Maprounea brasiliensis A. St.-Hil.
Maprounea guianensis Aubl.
Maprounea sp.
Pera bicolor (Klotzsch) Müll. Arg.
Pera ferruginea (Schott) Müll. Arg.
Pera glabrata (Schott) Baill.
Pera obovata (Klotzsch) Baill.
Pera sp.
Sapium biglandulosum Müll. Arg.
Sapium marginatum (Müll. Arg.) Müll. Arg.
Sapium sp.
Savia dictyocarpa Müll. Arg.
Sebastiania bidentata (Mart.) Pax
Unknown 1

Table 2. Continued.

Fabaceae

Acosmium dasycarpum (Vogel) Yakovlev
Acosmium lentiscifolium Schott
Acosmium subelegans (Mohlenbr.) Yakovlev
Acosmium sp.
Aeschynomene paniculata Willd. ex Vogel
Amburana cearensis (Alemão) A. C. Sm.
Andira anthelmia (Vell.) J. F. Macbr.
Andira cuyabensis Benth.
Andira fraxinifolia Benth.
Andira inermis (Sw.) Kunth
Andira laurifolia Benth.
Andira legalis (Vell.) Toledo
Andira nanum
Andira paniculata Benth.
Andira cf. riverina Arroyo
Andira spectabilis Saldanha
Andira surinamensis (Bondt) Splitg. ex Pulle
Andira vermifuga Mart. ex Benth.
Andira spp. 7
Ateleia glazioveana Baill.
Bocoa mollis (Benth.) R. Cowan
Bowdichia nitida Spruce ex Benth.
Bowdichia virgilioides Kunth
Camptosema coriaceum (Nees & Mart.) Benth.
Camptosema pedicellatum Benth.
Centrolobium tomentosum Guill. ex Benth.
Clitoria sp.
Coursetia arborea Griseb.
Dalbergia miscolobium Benth.
Dioclea bicolor Benth.
Dioclea glabra Mart. ex Benth.
Dioclea huberii Ducke
Dioclea reflexa Hook. f.
Dipteryx alata Vogel
Dipteryx odorata (Aubl.) Willd.
Eriosema aff. congestum Benth.
Eriosema spp. 3
Galactia glaucescens Kunth
Harpalyce brasiliana Benth.
Indigofera suffruticosa Mill.
Lonchocarpus araripensis Benth.
Lonchocarpus cf. sericeus (Poir.) Kunth
Luetzelburgia auriculata (Alemão) Ducke
Machaerium acutifolium Vogel
Machaerium aff. acutifolium Vogel
Machaerium arobreum (Jacq.) Vogel
Machaerium hirtum (Vell.) Stellfeld
Machaerium lanatum Tul.
Machaerium opacum Vogel
Machaerium stipitatum (DC.) Vogel
Machaerium villosum Vogel
Machaerium spp. 2
Ormosia arborea (Vell.) Harms
Platymiscium trinitatis Benth.
Platypodium elegans Vogel
Platypodium grandiflorum Benth.
Pterocarpus rohrii Vahl
Pterocarpus violaceus Vogel
Pterodon emarginatus Vogel
Tephrosia purpurea (L) Pers.
Vatairea macrocapra (Benth.) Ducke

Table 2. Continued.

- Vigna firmula (Benth.) Maréchal, Mascherpa & Stainier
- Zollernia paraensis Huber

Flacourtiaceae

- Banara sp.
- Casearia arborea (Rich.) Urb.
- Casearia commersoniana Cambess.
- Casearia decandra Jacq.
- Casearia gossypiosperma Briq.
- Casearia grandiflora Cambess.
- Casearia guianensis (Aubl.) Urb.
- Casearia lasiophylla Eichler
- Casearia sylvestris Sw.
- Casearia spp. 5
- Laetia procera (Peoppig) Eichler
- Lindackeria latifolia Benth.
- Ryania mansoana Eichler

Hippocrateaceae

- Cheiloclinium cognatum (Miers) A. C. Sm.
- Cheiloclinium sp.
- Peritassa campestris (Camb.) A. C. Sm.
- Salacia campestris Walp.
- Salacia crassifolia (Mart.) Peyr.
- Salacia micrantha (Mart.) Peyr.
- Salacia spp. 5
- Tontelea micrantha (Mart. ex Schult.) A. C. Sm.
- Unknown

Humiriaceae

- Humiria balsamifera Aubl.
- Sacoglottis guianensis Benth.

Icacinaceae

- Emmotum nitens (Benth.) Miers
- Emmotum sp.

Krameriaceae

- Krameria argentea Mart. ex. Sperng.
- Krameria tomentosa A. St.-Hil.
- Krameria sp.

Lacistemataceae

- Lacistema aggregatum (Bergius) Rusby
- Lacistema hasslerianum Chodat
- Lacistema sp.

Lamiaceae

- Hyptis cana Pohl ex Benth.
- Hyptis eriophylla Pohl ex Benth.
- Hyptis macrantha A. St.-Hil. ex Benth.
- Hyptis pauliana Epling

Lauraceae

- Mezilaurus crassiramea (Meisn.) Taub. ex Mez
- Mezilaurus lindaviana Schwacke & Mez
- Mezilaurus aff. lindaviana Schwacke & Mez
- Nectandra lanceolata Nees & Mart. ex Nees
- Nectandra membranaceae (Sw.) Griseb.
- Nectandra nitidula Nees & Mart. ex Nees
- Nectandra sp.
- Ocotea acutifolia (Nees) Mez
- Ocotea corymbosa (Meisn.) Mez
- Ocotea diospyrifolia (Meisn.) Mez
- Ocotea cf. macropoda (Humb., Bonpl. & Kunth) Mez
- Ocotea odorifera (Vell.) Rohwer
- Ocotea pulchella (Nees) Mez
- Ocotea spixiana (Nees) Mez
- Ocotea velutina (Nees) Rohwer
- Ocotea spp. 10
- Persea caerulea (Ruiz & Pav.) Mez
- Persea major Kopp
- Persea pyrifolia Nees & Mart. ex Nees
- Persea sp.
- Phoebe erythropus (Mart. & Spix) Mez
- Unknown 12

Lecythidaceae

- Eschweilera brancoensis (R. Knuth) Mori
- Eschweilera nana (Berg) Miers
- Eschweilera sp.
- Lecythis sp.

Loganiaceae

- Antonia ovata Pohl
- Mitreola sp.
- Strychnos martii Progel
- Strychnos pseudoquina A. St.-Hil.
- Strychnos sp.

Lythraceae

- Cuphea thymoides Cham. & Schltdl.
- Cuphea sp.
- Diplusodon ramosissimus Pohl
- Diplusodon virgatus Pohl
- Diplusodon sp.
- Lafoensia densiflora Pohl
- Lafoensia pacari A. St.-Hil.
- Lafoensia puniciifolia DC.
- Lafoensia replicata Pohl
- Lafoensia sp.
- Physocalymma scaberrimum Pohl

Magnoliaceae

- Talauma ovata A. St.-Hil.

Malpighiaceae

- Banisteria paraisia*
- Banisteriopsis argirophylla (A. Juss.) B. Gates
- Banisteriopsis campestris (A. Juss.) Little
- Banisteriopsis clausseniana (A. Juss.) W. R. Anderson & B. Gate
- Banisteriopsis irwiing B. Gates
- Banisteriopsis laevifolia (A. Juss.) B. Gates
- Banisteriopsis latifolia (A. Juss.) B. Gates
- Banisteriopsis malifolia (Nees & Mart.) B. Gates
- Banisteriopsis megaphylla (A. Juss.) B. Gates
- Banisteriopsis oxyclada (A. Juss.) B. Gates
- Banisteriopsis pubipetala (A. Juss.) Cuatrec.
- Banisteriopsis schizoptera (A. Juss.) B. Gates
- Banisteriopsis variabilis B. Gates
- Banisteriopsis spp. 4
- Byrsonima basiloba A. Juss.
- Byrsonima blanchetiana Miq.
- Byrsonima coccolobifolia Kunth
- Byrsonima aff. coccolobifolia Kunth
- Byrsonima coccolobifolia f. parvifolia Nied.
- Byrsonima coriacea (Sw.) Kunth
- Byrsonima crassa Nied.
- Byrsonima crassifolia Kunth
- Byrsonima cydoniifolia A. Juss.
- Byrsonima fagifolia Nied.

Table 2. Continued.

Byrsonima gautherioides Griseb.
Byrsonima guilleminiana A. Juss.
Byrsonima cf. guilleminiana A. Juss.
Byrsonima indorum S. Moore
Byrsonima intermedia A. Juss.
Byrsonima intermedia f. latifolia Nied.
Byrsonima lancifolia A. Juss.
Byrsonima laxiflora Griseb.
Byrsonima linguifera Cuatrec.
Byrsonima orbignyana A. Juss.
Byrsonima pachyphylla A. Juss.
Byrsonima schomburgkiana Benth.
Byrsonima sericea DC.
Byrsonima stipulacea A. Juss.
Byrsonima cf. umbellata Mart.
Byrsonima vacciniifolia A. Juss.
Byrsonima aff. vacciniifolia A. Juss.
Byrsonima variabilis A. Juss.
Byrsonima verbascifolia (L.) Rich. ex A. Juss.
Byrsonima verbascifolia ssp. discolor f. leiocarpa Griseb.
Byrsonima spp. 9
Galphimia brasiliensis (L.) A. Juss.
Heteropterys acutifolia A. Juss.
Heteropterys byrsonimiifolia A. Juss.
Heteropterys cf. escalloniifolia A. Juss.
Heteropterys pteropetala A. Juss.
Heteropterys tomentosa A. Juss.
Heteropterys umbellata A. Juss.
Heteropterys xanthophylla A. Juss.
Heteropterys spp. 3
Peixotoa hirta A. Juss.
Peixotoa parviflora A. Juss.
Peixotoa sp.
Pterandra pyroidea A. Juss.
Tetrapterys ramiflora A. Juss.
Tetrapterys sp.
Unknown 3

Malvaceae

Hibiscus furcellatus Lam.
Mollia sp.
Pavonia malacophylla Garcke

Marcgraviaceae

Norantea guianensis Aubl.
Norantea sp.

Melastomataceae

Cambessedesia espora (A. St.-Hil.) DC.
Clidemia hirta (L.) D. Don
Clidemia rubra (Aubl.) Mart.
Clidemia sp.
Leandra involucrata DC.
Leandra lacunosa Cogn.
Leandra lancifolia Cogn.
Leandra polystachia (Naudin) Cogn.
Leandra purpurascens (DC.) Cogn.
Leandra cf. solenifera (Schrank ex DC.) Cogn.
Leandra cf. xanthopogon (Naudin) Cogn.
Leandra sp.
Macairea aff. calvescens Naudin
Miconia adenostemon Cogn.
Miconia albicans (Sw.) Triana
Miconia albo-rufescens Naudin

Table 2. Continued.

Miconia argentea DC.
Miconia burchellii Triana
Miconia chamissois Nuadin
Miconia chartacea Triana
Miconia cinerea Cogn.
Miconia cinnamomifolia (Mart. ex DC) Naudin
Miconia cuspidata Naudin
Miconia fallax DC.
Miconia ferruginata (Schrank & Mart. ex DC.) DC.
Miconia guianensis (Aubl.) Cogn.
Miconia holosericea (L.) Triana
Miconia ibaquensis (Bonpl.) Triana
Miconia langsdorffii Cogn.
Miconia ligustroides (DC.) Naudin
Miconia minutiflora (Bonpl.) DC.
Miconia paulensis Naudin
Miconia pepericarpa DC.
Miconia pohliana Cogn.
Miconia rubiginosa DC.
Miconia rufescens (Aubl.) DC.
Miconia sellowiana (Cham.) Naudin
Miconia stenostachya (Schrank & Mart. ex DC.) DC.
Miconia theaezans (Bonpl.) Cogn.
Miconia tiliaefolia Naudin
Miconia spp. 17
Mouriri acutiflora Naudin
Mouriri elliptica Mart.
Mouriri guianensis Aubl.
Mouriri pusa Gardner
Mouriri spp. 2
Ossaea congestiflora (Naudin) Cogn.
Tibouchina adenostemon (Schrank ex DC.) Cogn.
Tibouchina aspera Aubl.
Tibouchina barbigera (Naudin) Baill.
Tibouchina candolleana (Mart. ex DC.) Cogn.
Tibouchina cf. candolleana (Mart. ex DC.) Cogn.
Tibouchina clidemoides (Berg ex Triana) Cogn.
Tibouchina gracilis (Bonpl.) DC.
Tibouchina papyrifera (Pohl ex Naudin) Cogn.
Tibouchina pogonanthera (Naudin) Cogn.
Tibouchina sellowiana (Cham.) Cogn.
Tibouchina stenocarpa (Schrank & Mart. ex DC.) Cogn.
Tibouchina spp. 2
Tococa formicaria Mart. ex DC.
Trembleya parviflora (D. Don) Cogn.
Trembleya phlogiformis (Mart. & Schrank ex DC.) DC.
Unknown 5

Meliaceae

Cabralea canjerana (Vell.) Mart.
Cabralea sp.
Cedrela fissilis Vell.
Guarea macrophylla Vahl
Trichilia elegans A. Juss.
Trichilia pallida Sw.
Trichilia sp.

Menispermaceae

Abuta grandifolia (Mart.) Sandwith
Abuta selloana (Benth.) Eichler
Cissampelos sp.

Mimosaceae

Acacia plumosa Lowe

Table 2. Continued.

Acacia sp.
Anadenanthera colubrina (Vell.) Brenan
Anadenanthera falcata (Benth.) Speg.
Anadenanthera macrocarpa (Benth.) Brenan
Anadenanthera peregrina (L.) Speg.
Calliandra abbreviata Benth.
Calliandra dysantha Benth.
Calliandra foliolosa Benth.
Calliandra microphylla Benth.
Calliandra parviflora Benth.
Chloroleucon dumosum (Benth.) G. P. Lewis
Chloroleucon foliolosum (Benth.) G. P. Lewis
Chloroleucon mangense (Jacq.) Britton & Rose
Enterolobium contortisiliquum (Vell.) Morong
Enterolobium gummiferum (Mart.) J. F. Macbr.
Enterolobium schomburgkii (Benth.) Benth.
Enterolobium spp. 2
Inga affinis DC.
Inga fagifolia (L.) Willd. ex Benth.
Inga heterophylla Willd.
Inga scabriuscula Benth.
Inga sessilis (Vell.) Mart.
Inga spp. 3
Mimosa acutistipula (Mart.) Benth.
Mimosa albolanata Taub.
Mimosa caesalpiniifolia Benth.
Mimosa claussenii Benth.
Mimosa dolens Vell. ssp. rigida (Benth.) Barneby var. rigida
Mimosa foliolosa Benth.
Mimosa lanuginosa Glaz. ex Burkart
Mimosa laticifera Rizzini & A. Mattos
Mimosa millefoliata Scheele
Mimosa pithecolobioides Benth.
Mimosa platyphylla Benth.
Mimosa pteridifolia Benth.
Mimosa aff. somnians Humb. & Bonpl. ex Willd.
Mimosa sonderstromii Barneby*
Mimosa xanthocentra Mart. spp. subsericea (Benth.) Barneby var. subsericea
Mimosa verrucosa Benth.
Mimosa spp. 3
Parkia platycephala Benth.
Piptadenia gonoacantha (Mart.) J. F. Macbr.
Piptadenia obliqua (Pers.) J. F. Macbr.
Piptadenia sp.
Pithecellobium incuriale (Vell.) Benth.
Pithecellobium marginatum Spruce ex Benth.
Plathymenia foliolosa Benth.
Plathymenia reticulata Benth.
Stryphnodendron adstringens (Mart.) Coville
Stryphnodendron coriaceum Benth.
Stryphnodendron cf. coriaceum Benth.
Stryphnodendron obovatum Benth.
Stryphnodendron polyphyllum Mart.
Stryphnodendron spp. 2

Monimiaceae

Siparuna cujabana (Mart.) DC.
Siparuna guianensis Aubl.
Siparuna spp. 2
Unknown 1

Moraceae

Brosimum gaudichaudii Trécul

Table 2. Continued.

Brosimum guianensis (Aubl.) Huber
Brosimum spp. 2
Ficus citrifolia Mill.
Ficus gomelleira Kunth & Bouche ex Kunth
Ficus guyanensis Desv. ex Ham.
Ficus obtusifolia Humb., Bonpl. & Kunth
Ficus spp. 9
Pseudolmedia laevigata Trécul
Pseudolmedia sp.
Sorocea ilicifolia Miq.
Sorocea sprucei (Baill.) J. F. Macbr.
Sorocea sp.
Unknown 1

Myristicaceae

Virola malmei A. C. Sm.
Virola sebifera Aubl.
Virola sessilis (A. DC.) Warb.
Virola surinamensis (Rol.) Warb.
Virola spp. 3

Myrsinaceae

Cybianthus boissieri DC.
Cybianthus detergens Mart.
Cybianthus goyazensis Mez
Cybianthus sp.
Rapanea ferruginea (Ruiz & Pav.) Mez
Rapanea guyanensis Aubl.
Rapanea lancifolia (Mart.) Mez
Rapanea leuconeura (Mart.) Mez
Rapanea parvifolia (DC.) Mez
Rapanea umbellata (Mart.) Mez
Rapanea cf. umbellata (Mart.) Mez
Rapanea spp. 2
Stylogyne warmingii Mez
Unknown 2

Myrtaceae

Blepharocalyx salicifolius (Humb., Bonpl. & Kunth) Berg
Blepharocalyx sp.
Calycorectes acutatus (Miq.) Toledo
Campomanesia adamantium (Camb.) Berg
Campomanesia dichotoma (Berg) Mattos
Campomanesia eugenioides (Camb.) D. Legrand
Campomanesia lineatifolia Ruiz & Pavon
Campomanesia pubescens (DC.) Berg
Campomanesia rufa (Berg) Nied.
Campomanesia xanthocarpa Berg
Campomanesia spp. 4
Eugenia albo-tomentosa Camb.
Eugenia aurata Berg
Eugenia bimarginata DC.
Eugenia chrysantha Berg
Eugenia dysenterica Mart. ex DC.
Eugenia gamaeana Glaz.
Eugenia hiemalis Camb.
Eugenia livida Berg
Eugenia mansonii Berg
Eugenia cf. mansonii Berg
Eugenia aff. oblongata Berg
Eugenia obversa Berg
Eugenia pitanga (Berg) Kiaersk.
Eugenia pluriflora Mart.
Eugenia punicifolia (Humb., Bonpl. & Kunth) DC.

Table 2. Continued.

Eugenia spathulata Berg
Eugenia uniflora L.
Eugenia aff. uniflora L.
Eugenia spp. 24
Gomidesia affinis (Camb.) D. Legrand
Gomidesia lindeniana Berg
Myrceugenia aff. alpigena (DC.) Landrum
Myrcia albo-tomentosa DC.
Myrcia bella Camb.
Myrcia canescens Berg
Myrcia castrensis (Berg) D. Legrand
Myrcia cuprea (Berg) Kiaersk.
Myrcia daphnoides DC.
Myrcia floribunda Miq.
Myrcia formosiana DC.
Myrcia guajavaefolia Berg
Myrcia hayneana Berg
Myrcia intermedia (Berg) Kiaersk.
Myrcia aff. intermedia (Berg) Kiaersk.
Myrcia laevigata Berg
Myrcia laruotteana Camb.
Myrcia lasiantha DC.
Myrcia lingua Berg
Myrcia longipes (Berg) Kiaersk.
Myrcia cf. longipes (Berg) Kiaersk.
Myrcia multiflora (Lam.) DC.
Myrcia nigro-punctata DC.
Myrcia obtusata (Schauer) D. Legrand
Myrcia pallens DC.
Myrcia polyantha DC.
Myrcia pubipetala Miq.
Myrcia rorida (Berg) Kiaersk.
Myrcia rostrata DC.
Myrcia rufipes DC.
Myrcia schottiana Berg
Myrcia stricta (Berg) Kiaersk.
Myrcia superba Berg
Myrcia aff. ternifolia Berg
Myrcia tomentosa DC.
Myrcia aff. tomentosa DC.
Myrcia cf. tomentosa DC.
Myrcia cf. torta DC.
Myrcia uberavensis Berg
Myrcia variabilis DC.
Myrcia venulosa DC.
Myrcia spp. 20
Myrcianthes pungens (Berg) D. Legrand
Myrciaria floribunda (West ex Willd.) Berg
Myrciaria aff. floribunda (West ex Willd.) Berg
Psidium acutangulum DC.
Psidium aerugineum Berg
Psidium australe Camb.
Psidium aff. australe Camb.
Psidium bergianum (Nied.) Burret
Psidium cambessedianum*
Psidium cinereum DC.
Psidium firmum Berg
Psidium guajava L.
Psidium guineense Sw.
Psidium myrsinoides Berg
Psidium rufum DC.
Psidium submetrale McVaugh
Psidium spp. 19
Siphoneugena densiflora Berg

Table 2. Continued.

Siphoneugena spp. 2
Unknown 36

Nyctaginaceae

Guapira graciliflora (Mart. ex J. A. Schmidt) Lundell
Guapira noxia (Netto) Lundell
Guapira opposita (Vell.) Reitz
Guapira subferruginea (Mart.)
Guapira tomentosa (Casar.) Lundell
Guapira spp. 9
Neea macrophylla Britton
Neea aff. macrophylla Britton
Neea spruceana Heimerl
Neea theifera Oerst.
Neea spp. 2
Unknown 2

Ochnaceae

Ouratea acuminata (DC.) Engl.
Ouratea castanaefolia (DC.) Engl.
Ouratea confertiflora (Pohl) Engl.
Ouratea cuspidata (A. St.-Hil.) Engl.
Ouratea fieldingiana (Gardner) Engl.
Ouratea floribunda (A. St.-Hil.) Engl.
Ouratea hexasperma (A. St.-Hil.) Baill.
Ouratea nana (A. St.-Hil.) Engl.
Ouratea schomburgkii (Planch.) Engl.
Ouratea spectabilis (Mart.) Engl.
Ouratea spp. 4

Olacaceae

Dulacia sp.
Heisteria densifrons Engl.
Ximenia americana L.

Oleaceae

Linociera hassleriana Hassl.

Opiliaceae

Agonandra brasiliensis Miers
Agonandra sp.

Oxalidaceae

Oxalis hirsutissima Mart. & Zucc.

Piperaceae

Piper spp. 2

Poaceae

Actinocladum verticillatum (Nees) MacClure & Sonderstron
Arundinaria cannavieira Silveira
Guadua sp.
Unknown 1

Polygalaceae

Bredemeyera altissima A. W. Benn.
Bredemeyera laurifolia Klotzch

Polygonaceae

Coccoloba grandifolia Jacq.
Coccoloba mollis Casar.
Coccoloba cf. mollis Casar.
Coccoloba spp. 4

Proteaceae

Euplassa inaequalis (Pohl) Engl.
Roupala brasiliensis Klotzsch

Table 2. Continued.

Roupala montana Aubl.
Roupala spp 3

Rhamnaceae

Rhamnidium elaeocarpum Reissek
Rhamnus sphaerosperma Sw.

Rosaceae

Prunus brasiliensis (Cham. & Schltdl.) D. Dietr.
Prunus myrtifolia (L.) Urb.
Prunus sellowii Koehne
Rubus brasiliensis Mart.

Rubiaceae

Alibertia concolor (Cham.) K. Schum.
Alibertia edulis (L. C. Rich.) A. Rich.
Alibertia elliptica (Cham.) K. Schum.
Alibertia macrophylla (Mart.) K. Schum.
Alibertia cf. macrophylla (Mart.) K. Schum.
Alibertia obtusa K. Schum.
Alibertia sessilis (Vell.) K. Schum.
Alibertia cf. sessilis (Vell.) K. Schum.
Alibertia verrucosa S. Moore
Alibertia spp. 4
Amaioua guianensis Aubl.
Borojoa lanceolata (Cham.) Cuatrec.
Calycophyllum multiflorum Griseb.
Chimarrhis sp.
Chiococca nitida Benth.
Chomelia anisomeris Müll. Arg.
Chomelia obtusa Cham. & Schltdl.
Chomelia pohliana Müll. Arg.
Chomelia ribesioides Benth. ex A. Gray
Coccocypselum lanceolatum (Ruiz & Pav.) Pers.
Coussarea hydrangeaefolia (Benth.) Benth. & Hook. ex Müll. Arg.
Declieuxia lysimachioides Zucc. ex Schult. & Schult. f.
Faramea crassifolia Benth.
Faramea sp.
Ferdinandusa elliptica Pohl
Genipa americana L.
Genipa sp.
Guettarda angelica Mart. ex Müll. Arg.
Guettarda platypoda DC.
Guettarda viburnoides Cham. & Schltdl.
Guettarda sp.
Ixora gardneriana Benth.
Ladenbergia chapadensis S. Moore
Palicourea crocea (Sw.) Roem. & Schult.
Palicourea rigida Kunth
Palicourea rigida var. genuina Müll. Arg.
Palicourea xanthophylla Müll. Arg.*
Palicourea sp.
Psychotria carthagenensis Jacq.
Psychotria officinalis (Aubl.) Raeusch. ex Sandw.
Psychotria sessilis (Vell.) Müll. Arg.
Psychotria spp. 2
Randia nitida (Humb., Bonpl. & Kunth) DC.
Randia sp.
Remijia amazonica K. Schum.
Remijia ferruginea (A. St.-Hil.) DC.
Rudgea amazonica Müll. Arg.
Rudgea viburnoides (Cham.) Benth.
Rudgea villosa Benth. ex Glaz.
Rudgea sp.

Table 2. Continued.

Sabicea cana Hook. f.
Sipanea sp.
Tocoyena bullata (Vell.) Mart.
Tocoyena aff. foetida Poepp. & Endl.
Tocoyena formosa (Cham. & Schltdl.) K. Schum.
Tocoyena neglecta N. E. Brown
Tocoyena spp. 2
Unknown 6

Rutaceae

Dictyoloma incanescens DC.
Erythrochiton brasiliensis Nees & Mart.
Esenbeckia febrifuga (A. St.-Hil.) A. Juss. ex Mart.
Esenbeckia pumila Pohl
Fagara sp.
Hortia brasiliensis Vand. ex DC.
Spiranthera odoratissima A. St.-Hil.
Zanthoxylum cinereum Engl.
Zanthoxylum cf. cinereum Engl.
Zanthoxylum aff. hasslerianum (Chodat) Pirani
Zanthoxylum cf. hasslerianum (Chodat) Pirani
Zanthoxylum rhoifolium Lam.
Zanthoxylum cf. rhoifolium Lam.
Zanthoxylum rieldelianum Engl.
Zanthoxylum rugosum A.-St. Hil. & Tul.

Sapindaceae

Allophylus quercifolius (Mart.) Radlk.
Allophylus sericeus (Camb.) Radlk.
Allophylus sp.
Cupania racemosa (Vell.) Radlk.
Cupania revoluta Radlk.
Cupania cf. scrobiculata Rich.
Cupania vernalis Camb.
Cupania spp. 2
Diatenopteryx sorbifolia Radlk.
Dilodendron bipinnatum Radlk.
Magonia pubescens A. St.-Hil.
Matayba arborescens (Aubl.) Radlk.
Matayba elaeagnoides Radlk.
Matayba guianensis Aubl.
Matayba sp.
Serjania erecta Radlk.
Unknown

Sapotaceae

Chrysophyllum brevipes (Pierre) T. D. Penn.
Chrysophyllum marginatum (Hook. & Arn.) Radlk.
Chrysophyllum sp.
Manilkara bidentata (A. DC) Chev.
Manilkara triflora (Alemão) Monach.
Manilkara spp. 2
Micropholis venulosa (Mart. & Eichler) Pierre
Pouteria ramiflora (Mart.) Radlk.
Pouteria torta (Mart.) Radlk.
Pouteria sp.
Sideroxylon aff. venulosum Mart. & Eichler
Unknown 1

Simaroubaceae

Simaba trichilioides Engl.
Simaba warmingiana Engl.
Simaba sp.
Simarouba amara Aubl.
Simarouba versicolor A. St.-Hil.

Table 2. Continued.

Solanaceae

- Cestrum corymbosum Schltdl.
- Cestrum obovatum Sendtn.
- Cestrum sendtnerianum Mart. ex Sendtn.
- Solanum baturitense Huber
- Solanum cordifolium Dunal
- Solanum grandiflorum Ruiz & Pavon
- Solanum horridum Dunal
- Solanum jamaicense Mill.
- Solanum lycocarpum A. St.-Hil.
- Solanum macranthum Dunal
- Solanum subinerme Jacq.
- Solanum spp. 2

Sterculiaceae

- Guazuma ulmifolia Lam.
- Helicteres brevispira A. St.-Hil.
- Helicteres corylifolia Nees
- Helicteres guazumifolia Kunth
- Helicteres macropetala A. St.-Hil.
- Helicteres ovata Lam.
- Helicteres sacarolha A. St.-Hil.
- Helicteres sp.
- Melochia hirsuta Cav.
- Sterculia striata A. St.-Hil. & Naudin
- Sterculia sp.
- Waltheria indica L.
- Waltheria polyanthos K. Schum.

Styracaceae

- Styrax camporum Pohl
- Styrax ferrugineum Nees & Mart.
- Styrax sp.

Symplocaceae

- Symplocos fallax Brand
- Symplocos lanceolata (Mart.) DC.
- Symplocos cf. lanceolata (Mart.) DC.
- Symplocos nitens (Pohl) Benth.
- Symplocos platyphylla (Pohl) Benth.
- Symplocos pubescens Klotzsch ex Benth.
- Symplocos rhamnifolia DC.
- Symplocos tenuifolia Brand
- Symplocos tetrandra Mart. ex Miq.
- Symplocos uniflora (Pohl) Benth.
- Symplocos spp. 4

Theaceae

- Ternstroemia brasiliensis Cambess.
- Ternstroemia oleaefolia Wawra

Thymelaeaceae

- Daphinopsis fasciculata (Meisn.) Nevling

Tiliaceae

- Apeiba tibourbou Aubl.
- Luehea divaricata Mart.
- Luehea paniculata Mart.
- Luehea speciosa Willd.
- Luehea spp. 2
- Triumfetta semitriloba Jacq.

Turneraceae

- Piriqueta aurea (Cambess.) Urb.

Ulmaceae

- Celtis iguanea (Jacq.) Sarg.
- Celtis pubescens Kunth
- Celtis sp.

Table 2. Continued.

- Trema micrantha (L.) Blume

Velloziaceae

- Vellozia flavicans Mart. ex Schult. f.
- Vellozia spp. 2

Verbenaceae

- Aegiphila amazonica Moldenke
- Aegiphila intermedia Moldenke
- Aegiphila lhotszkiana Cham.
- Aegiphila parviflora Moldenke
- Aegiphila pernambucensis Moldenke
- Aegiphila sellowiana Cham.
- Aegiphila splendens Schauer
- Aegiphila verticillata Vell.
- Aegiphila sp.
- Lantana camara L.
- Lantana fucuta Lindl.
- Lantana trifolia L.
- Lippia corymbosa Cham.
- Lippia eupatorium Schauer
- Lippia glandulosa Schauer
- Lippia gracilis Schauer
- Lippia lacunosa Mart. & Schauer
- Lippia lasiocalycina Cham.
- Lippia lupulina Cham.
- Lippia martiana Schauer
- Lippia salviaefolia Cham.
- Petrea racemosa Nees
- Vitex cymosa Bertero
- Vitex flavens Kunth
- Vitex megapotamica (Spreng.) Moldenke
- Vitex polygama Cham.
- Vitex cf. polygama Cham.
- Vitex schomburgkiana Schauer
- Vitex spp. 2
- Unknown 2

Vochysiaceae

- Callisthene fasciculata Mart.
- Callisthene hassleri Briq.
- Callisthene major Mart.
- Callisthene major var. pilosa Warm.
- Callisthene microphylla Warm.
- Qualea cordata Spreng.
- Qualea densiflora Spreng.
- Qualea dichotoma (Mart.) Warm.
- Qualea grandiflora Mart.
- Qualea multiflora Mart.
- Qualea parviflora Mart.
- Qualea sp.
- Salvertia convallariodora A. St.-Hil.
- Vochysia cinnamomea Pohl
- Vochysia elliptica Mart.
- Vochysia aff. ferruginea Mart.
- Vochysia gardneri Warm.
- Vochysia haenkeana Mart.
- Vochysia herbacea Pohl
- Vochysia petraea Warm.
- Vochysia pruinosa Pohl
- Vochysia rufa Mart.
- Vochysia thyrsoidea Pohl
- Vochysia tucanorum Mart.
- Vochysia spp. 2
- Family unknown—122

Table 3. Numbers (N) of references to taxonomic entities at different levels found in surveys of trees and shrubs in Brazilian cerrados.

		N	%
Families			
Identified		88	41.9
"Unknown"		122	58.1
	Total	210	
Genera			
Identified		363	63.3
"Unknown"		209	36.5
	Total	572	
Species			
Identified		973	57.1
Dubious		31	1.8
Dubious, but species already identified at another site		36	2.1
Subspecies or variety of species already included		5	0.3
Genus only		455	26.6
"Unknown"		209	12.2
	Total	1709	

Table 4. Estimates of the number of taxa of arboreal and shrubby plants at different levels in Brazilian cerrados. See text for details on calculation.

Level	Lower limit	Upper limit
Families	88	210
Genera	363	572
Species	973	1709

Table 5. Estimates of the number of terrestrial herbaceous-subshrubby species and total terrestrial angiosperm flora of Brazilian cerrados, assuming different proportions (1 : 2 and 1 : 3) of woody : herbaceous-subshrubby components and considering a lower (minimum) and an upper (maximum) limit (see Table 4) for the woody flora.

	Minimum		Maximum	
	1:2	1:3	1:2	1:3
Herbaceous-subshrubby species	1946	2919	3418	5127
Total flora	2919	3892	5127	6836

Statistical Summary of Some of the Activities in the Missouri Botanical Garden Herbarium, 1998

	Vascular	Bryophyte	Total
Acquisition of Specimens			
Staff Collections	17,314	3,093	20,407
Purchase	55,433	0	55,433
Exchange	27,576	2,847	30,423
Gifts	25,028	2,210	27,238
Total acquisitions	125,351	8,150	133,501
Mountings			
Newly mounted	52,168	14,815	66,983
Mounted when received	64,839*	0	64,839
Total specimens filed	117,007	14,815	131,822
Repairs			
Specimens repaired	21,015	n/a	21,015
Specimens stamped	187	n/a	187
Total repairs	21,202	0	21,202
Specimens sent			
On exchange	31,960	4,934	36,894
As gifts	17,693	992	18,685
Total	49,653	5,926	55,579
Loans sent			
Total transactions	444	17	461
Total specimens	21,784	1,008	22,792
To U.S. institutions			
Transactions	228	14	242
Specimens	11,386	915	12,301
To foreign institutions			
Transactions	216	3	219
Specimens	10,398	93	10,491
To student investigators			
Transactions	58	1	59
Specimens	5,857	742	6,599
To professional investigators			
Transactions	374	16	390
Specimens	15,804	266	16,070
Loans received			
Transactions	251	83	334
Specimens	18,890	4,821	23,711

* 55,139 of the "Mounted when received" vascular plants are specimens of Chinese plants purchased directly from China.

	From U.S.A.	From abroad	Total
Visitors	295	93	388

After correcting the number of bryophytes packeted in 1996 by 521 specimens, on 31 December 1998 the total number of mounted, accessioned specimens in the herbarium was 4,909,747 (4,600,053 vascular plants and 309,694 bryophytes).

The Garden's herbarium is closely associated with its database management system, TROPICOS. For example, many of the numbers in the above chart are taken from TROPICOS, since it is used as a herbarium management tool. Herbarium labels for newly collected specimens are generated through TROPICOS, and the information is retained there for further use. The charts below summarize some of the statistics from TROPICOS both for the calendar year 1998 and as year-end totals. Note that the specimen records in TROPICOS are primarily based on MO specimens, meaning that about twenty percent of the bryophytes (an increase of about three percent over 1997) and twenty-seven percent of the vascular plants (an increase of about one percent) in the herbarium are now computerized, with an overall total of about twenty-seven percent (an increase of about one percent). Distributional records are taken both from herbarium specimens and from literature records, and these are distinguished in TROPICOS. Similarly, information concerning types is taken both from the literature (protologues) and from specimens.

TROPICOS records—1998 additions

	Bryophytes	Vascular Plants	Total
Specimens	10,513	64,874	75,387
Names	2,773	24,857	27,630
Synonyms	1,335	15,333	16,668
Distributions	111	19,056	19,167
Types	92	17,516	17,608
Bibliography	979	2,514	3,493

TROPICOS records—Year-End 1998 Totals

	Bryophytes	Vascular Plants	Total
Specimens	60,851	1,244,091	1,304,942
Names	95,894	722,598	818,492
Synonyms	58,949	351,290	410,239
Distributions	36,441	711,569	748,010
Types	6,763	226,497	233,260
Bibliography	19,263	55,692	74,955
Specimens in herbarium	309,694	4,600,053	4,909,747
Percent computerized	20	27	27

—Marshall R. Crosby

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Cover illustration. *Barnadesia corymbosa* (Ruiz & Pavón) D. Don, by Iona Nieva.

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Garden

THE ORIGIN OF MODERN TERRESTRIAL ECOSYSTEMS: INTRODUCTION[1]

Peter R. Crane[2] *and*
Patrick S. Herendeen[3]

Fifteen years ago the *Annals of the Missouri Botanical Garden* (volume 71[2], 1984) published an important collection of papers on the fossil history of flowering plants edited by David Dilcher and William Crepet. Like the *Origin and Early Evolution of Angiosperms* edited by C. B. Beck in 1976 (New York: Columbia Univ. Press), these papers comprised a watershed in the development of studies of the angiosperm fossil record. The 1984 *Annals* volume included classic papers by Muller, and by Walker and Walker on fossil angiosperm pollen, as well as important work on the fossil history of insect pollination (Crepet), angiosperm dispersal syndromes (Tiffney), enigmatic Early Cretaceous and other Mesozoic fossil plants (Krassilov, Hughes), pollen ultrastructure (Zavada), and Early Cretaceous angiosperm cuticles (Upchurch). Also included in the 1984 volume were several important contributions on fossil flowers, including a landmark early paper by Friis on small charcoalified angiosperm flowers from the Cretaceous of southern Sweden, a consideration of Eocene flowers from the Messel locality by Schaarschmidt, and the description of *Archaeanthus* and other early magnoliid flowers by Dilcher and Crane and Crane and Dilcher. Since the mid 1980s studies of the angiosperm fossil record, particularly of flowers from the Cretaceous, have expanded dramatically and have substantially enhanced our understanding of the history of angiosperm diversity. In addition, increasingly rigorous research on angiosperm fossils of all kinds has produced a wealth of useful and reliable data pertaining to angiosperm diversification as well as

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[1] This volume comprises the proceedings of the 44th Annual Systematics Symposium of the Missouri Botanical Garden on "The Origin of Modern Terrestrial Ecosystems: Fossils, Phylogeny, and Biogeography," held 17–18 October 1997 at the Missouri Botanical Garden, St. Louis, Missouri, U.S.A.

We are grateful to Peter H. Raven and P. Mick Richardson for the opportunity to organize this symposium and publish the proceedings, to Kathy Hurlbert for her organizational skills and handling of symposium details, to our reviewers for providing technical critiques of the papers, to Donna Herendeen for preparing the index, and to Victoria Hollowell, Amy McPherson, and Diana Gunter for their editorial and production assistance. We are also indebted to the contributors for their efforts to develop both an interesting symposium and an informative volume based on the proceedings. Only one of the papers presented at the symposium does not appear here. We are especially grateful to Elizabeth McIver and James F. Basinger, as well as Bonnie F. Jacobs, John D. Kingston, and Louis L. Jacobs for contributing excellent papers to this volume even though time limitations precluded their inclusion in the symposium. The paper by Herendeen et al. also was not presented orally. The symposium was supported in part by National Science Foundation grant DEB-9420140.

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many aspects of biotic and environmental change over the last 140 million years.

The collection of nine papers in this volume reflects the current status and future promise of a range of different approaches to the study of the angiosperm fossil record, and their importance for elucidating angiosperm diversification and the origin of modern terrestrial ecosystems. Six of these papers were presented at the 44th Annual Systematics Symposium of the Missouri Botanical Garden in October 1997 on "The Origin of Modern Terrestrial Ecosystems." Three additional papers have also been added to highlight specific topics that we felt would be of particular interest to those concerned with the interplay between the origin of angiosperm diversity and the history of modern vegetation. The collection of papers is by no means comprehensive with respect to the full range of research currently being pursued in this field, but it nevertheless provides a sense of the current excitement, relevance, and breadth of modern approaches to the angiosperm fossil record.

A common theme running through the papers collected here is the extent to which angiosperm paleobotany connects to other disciplines in illuminating the origin of modern terrestrial ecosystems. It is self evident that research on angiosperm fossils is strongly and naturally linked to comparative structural and biological studies of living plants that provide the basis for our interpretations of fossils. Papers presented here further show that modern research in angiosperm paleobotany connects even more broadly to topics ranging from molecular systematics and vertebrate and invertebrate paleontology, to paleoclimatology, tectonics, and isotope paleobiology. When properly integrated into these and other disciplines, the study of angiosperm fossils helps us understand how the modern terrestrial ecosystems on which we all depend have been assembled and shaped over millions of years. It is from these connections that much of the current and future vitality of angiosperm paleobotany is inevitably derived.

The volume begins with a paper by Novacek that sets the stage for studies of angiosperm evolution through a sweeping review of the vertebrate fossil record and environmental change through the critical Cretaceous-Early Tertiary interval. Novacek emphasizes the antiquity of many vertebrate lineages and the selectivity of extinctions among vertebrate groups at the Cretaceous-Tertiary boundary. He also highlights the undeniably explosive diversification of mammals in the Early Tertiary—a pattern of presumed adaptive radiation comparable in terms of its magnitude, and perhaps its speed, to that which occurred 70 million years earlier during the extraordinary and equally dramatic diversification of angiosperms.

The paper by Friis, Pedersen, and Crane represents the culmination of intensive studies of some of the best preserved suites of early angiosperm fossil reproductive structures from the Early Cretaceous. Based on materials from Portugal, it reveals that even as early as the Barremian-Aptian, approximately 130–110 million years ago, angiosperms were highly diverse and possibly ecologically dominant in some environments. However, it is also significant that this diversity was almost exclusively at the level of magnoliids and perhaps early monocotyledons. It did not include representation of the extraordinarily diverse groups of living angiosperms that comprise the bulk of extant eudicots, thus providing no comfort for those who would extrapolate the history of derived eudicot lineages back to the Late Jurassic or earlier.

The following paper by Magallón, Crane, and Herendeen addresses the question of eudicot diversity through a substantial synthesis that integrates patterns of eudicot evolution derived from molecular phylogenetics with evidence on the first appearance of eudicot clades in the fossil record. The results establish a framework for examining the tempo of angiosperm evolution and, because the paper includes preliminary quantification of the species-level diversity of angiosperm clades, the study raises new questions about the processes underlying speciation, extinction, and diversification rates in different angiosperm lineages. The results provide a further indication of what had long been suspected, that some of the most diverse clades of extant angiosperms appear only relatively late in the fossil record—further underscoring the extraordinary diversification rates achieved not just by angiosperms as a whole, but especially by some of the most speciose modern clades.

The origin of angiosperm diversity, at least in terms of enhanced speciation rates, has often been attributed in large part to coevolution with insects, based on the concept that faithful specialized modes of insect pollination create new opportunities for reproductive isolation, and hence speciation. The paper by Grimaldi provides a critical review of the Cretaceous fossil history of insects and begins to provide an empirical basis for models of angiosperm diversification that invoke extensive angiosperm-insect coevolution through the Cretaceous. Grimaldi concludes that there is good evidence for the diversification of a variety of insect pollinators approximately synchronous with the major Cretaceous radiation of angiosperms.

The last five papers in the volume focus on different aspects of the origin of modern vegetation and how that relates to patterns of angiosperm diversification. The paper by Herendeen et al. provides the first complete description of one of the many Cretaceous mesofossil floras that have been discovered in the last 20 years, and in so doing helps to place the angiosperm diversification in a context including other components of the Cretaceous vegetation. It documents unequivocally that by the end of the Santonian (ca. 84 million years before present) vegetation in at least some parts of the world was dominated, both in terms of abundance and in terms of species numbers, by angiosperms. In the Allon flora conifers were also important, but ferns are relatively underrepresented, except in the palynofloras. The complete, albeit preliminary, description of the flora also provides a starting point for comparisons among mesofloras that will ultimately lead to an improved understanding of how angiosperm diversification relates to biogeographic patterns during the Cretaceous.

The question of how modern biogeographic patterns have developed is pursued in the paper by Manchester, which provides a major synthesis of the temporal and paleogeographic patterns exhibited by selected Early Tertiary angiosperms. A wealth of new data are presented based on extensive fieldwork and original research on some of the most distinctive angiosperm fossils, mainly fruits and seeds, in the Early Tertiary floras of North America, Europe, and Asia. Based on this paleobotanical synthesis, which is unrivaled in its systematic rigor and biogeographic coverage, Manchester concludes that biogeographic patterns have involved multiple migrations at different times between the major Northern Hemisphere continents via high-latitude land connections across the North Atlantic and Beringia.

The following paper by McIver and Basinger provides striking paleobotanical evidence of the relative warmth of Early Tertiary climates and the viability of the kinds of high-latitude migration routes envisaged by Manchester. They provide an overview of the Paleocene and Eocene vegetation of the Canadian High Arctic, which included a surprising diversity of broad-leaved angiosperms. The paper highlights just one facet of the extraordinary data acquired over the last decade unequivocally documenting the relative warmth of the Early Tertiary, and especially the Early Eocene, compared to climates of the present day. At the same time, the contrast between the vegetation of these areas today and in the Early Tertiary emphasizes the relentless climatic deterioration that has occurred at high latitudes over the last 35 million years.

The last two papers address how the climatic changes of the Tertiary contributed to the origin of two of the most distinctive and productive of present-day biomes. Burnham and Graham provide an important synthesis of the scattered data relating to the origin of neotropical vegetation. They show that Andean and lowland Amazonian floras have been highly diverse since at least the Miocene and that tropical diversity cannot simply be ascribed to speciation in association with climatic changes during the Pleistocene. They also explain that there is no evidence for displacement of lowland tropical plant species in South America by northern immigrants after emergence of a continuous Panamanian land connection—a pattern that stands in stark contrast to that exemplified by the history of South American mammals.

In the final paper of this volume, Jacobs, Kingston, and Jacobs take on a similar topic as they synthesize the paleobotanical, faunal, and isotopic data relevant to understanding the origin of grass-dominated vegetation, which now comprises approximately one-third of the Earth's vegetational cover but that appears to have been widespread for perhaps only the last 20 million years. They note in particular that the dramatic expansion of C_4 grasses occurred quite recently, between about 9 and 4 million years ago, probably correlating with the origin of modern climatic patterns of seasonality and rainfall.

The collection of papers in this volume documents the speed with which the study of angiosperm fossils has progressed in the 15 years since the publication of the last issue of the *Annals* devoted to this topic. Much of this progress has been fueled by new paleobotanical data, hard-won in both the field and the laboratory. It is also significant that the development of the field has not followed a single narrow trajectory. Rather, it has expanded in scope to build a robust network of new intellectual connections through which it contributes to an integrated view of changes in terrestrial ecosystems over the last 140 million years. The central message from these papers is that any consideration of the history of modern terrestrial ecosystems, on a scale of millions of years, that fails to take into account the changing nature and composition of terrestrial vegetation, is fundamentally flawed. The evolutionary development of angiosperms and the origin of our modern terrestrial ecosystems are intimately interconnected, and therein lies the power and relevance of angiosperm paleobotany in the coming decades.

100 MILLION YEARS OF LAND VERTEBRATE EVOLUTION: THE CRETACEOUS-EARLY TERTIARY TRANSITION[1]

Michael J. Novacek[2]

ABSTRACT

A critical time interval for vertebrate evolution—between 100 and 112 million years in duration—spans the beginning of the Cretaceous period to the late Eocene epoch of the Cenozoic. This interval encompasses the appearance in the Cretaceous of many of the modern vertebrate groups that persist today, the extinction event at the Cretaceous-Tertiary (K/T) boundary, and the restructuring of the vertebrate megafauna dominated by mammals in the Paleocene and Eocene. Cretaceous turnover in the dinosaur fauna has been tied to the radiation and diversification of angiosperms, but these correlations do not apply to all continental regions represented by a fossil record. The Cretaceous also marks the emergence and radiation of certain groups of mammals, birds, lizards, and freshwater fishes. Reconstructions, however, that push back the diversification of modern lineages of birds and mammals (groups that include extant representatives) to the Early or middle Cretaceous are not supported by the fossil record. Despite the severity of the Cretaceous-Tertiary (K/T) extinction event of 65 million years ago, effects on vertebrates are strikingly selective, with a number of groups, including actinopterygians (ray-finned fishes), multituberculate mammals, eutherian mammals, turtles, lizards, champsosaurs, and crocodiles surviving across the K/T boundary. Subsequent to the K/T event, the basic organization and dynamics of the larger vertebrate fauna were radically transformed. Of general evolutionary interest is the protracted "rebound" of the larger vertebrate fauna and the nature of its controlling factors. The loss of the non-avian dinosaurs meant a loss of larger herbivorous browsers not replenished for some millions of years into the Paleocene. Diversification in the smaller mammal fauna shows a new emphasis on frugivory and granivory. Some of the modern groups of mammals first appear in the late Paleocene-early Eocene. Subsequent climate and habitat changes coincide with the radiation of large herbivorous mammals such as perissodactyls and artiodactyls. The coevolutionary relationships of the terrestrial mammalian megafauna and the changing flora likely promoted the spread of more open habitats that characterized the later Cenozoic.

The fossil record, like a daily clock, can be divided into any number of critical phases whose relative importance might reflect mere arbitration as much as objective evidence. Yet terrestrial ecosystems, including the vertebrates comprising them, experienced a particularly profound transformation between the beginning of the Cretaceous some 146 million years ago and the end of the Eocene epoch of the Tertiary between 40 and 34 million years ago. Why is this interval so remarkable? First, it begins with what has been called one of the most significant evolutionary events of life on land (Wing & Sues, 1992)—namely, the appearance and radiation in the middle Cretaceous of angiosperms and more modern insect groups, including key groups of pollinating insects. These dramatic radiations further set in motion important coevolutionary interactions between herbivorous vertebrates and diversifying angiosperm-dominated habitats (Weishampel & Norman, 1989) and established the framework for modern ecosystems. Second, this interval encompasses the K/T extinction event, which had an unmistakable and profound ecological impact. The event is tied to the disappearance of several groups of terrestrial vertebrates (primarily non-avian dinosaurs) and the subsequent persistence and emergence of terrestrial mammals of radically smaller body size than dinosaurs and concomitantly different trophic connections with the flora. Third, this interval sets the stage for the rise of the modern mammal-dominated communities synchronous with the emergence of ecosystems involving fauna and flora that persist today.

The drama of these transitions notwithstanding, the Cretaceous-early Tertiary is marked by endurance as well as vicissitude. Indeed, one of the remarkable aspects of this phase is the resilience of many higher taxa—flowering plants, pollinating insects, even various vertebrate groups such as croc-

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[1] The author thanks Gao Keqin, Mark Norell, Guillermo Rougier, Maureen O'Leary, Louis Chiappe, and Lowell Dingus for comments and information on aspects covered in this paper. Drawings are by Ed Heck. This work was supported by NSF grants DEB 9300770 and DEB 952811.

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odiles, lizards, turtles, frogs and salamanders, and certain mammals—that thwarted whatever shocks to the global system that came with the K/T extinction event. In its broadest outlines, "modern" terrestrial ecosystems essentially took form in the Cretaceous. Some organismic groups came and went, but the basic architecture of the present system is the legacy of the Late Mesozoic. This is not meant to minimize the waves of turnover that characterized many of the intervals thereafter. It is merely meant to emphasize that the new world established in the Cretaceous has, despite the K/T extinction event, more in common biologically with the living world than the Jurassic world. This paper is meant as an elaboration of this thesis drawing on a summary of the vertebrate record against what is known of relevant physical, environmental, faunal, and floral changes. The paper also addresses an important issue relating to the study of any geologic interval. This concerns the juxtaposition of theories of ecosystem change against what is actually known about the fossil evidence. Although such evidence includes anatomical and morphometric data for inferring ecological roles in fossil taxa, the major and most critical aspect of the evidence concerns distributions of taxa in space and time. Such distributions are based on raw occurrence data and ranges inferred (but not necessarily observed) from reconstructed phylogenies (Norell, 1992; Norell & Novacek, 1992).

THE CRETACEOUS-EARLY TERTIARY RECORD

GEOGRAPHIC PATTERNS

Advances in paleogeographic reconstruction have been fed by data from sea floor spreading patterns, polar wander curves, and many other sources. The intensity of that coverage has not spared the Cretaceous-early Tertiary. Here are just a few salient aspects of the broad-scale geographic history of this interval, covered to much greater depth in the references cited.

By the Cretaceous, the fragmentation and drifting of continental blocks well under way in the Jurassic (Fig. 1) had transformed the terrestrial geography of the globe (see Smith et al., 1994; Scotese, 1997). This fragmentation on a gigantic scale, the so-called break up of Pangea, represents a reversal in the pattern of continental coalescence recorded in the earlier Mesozoic. Its potential influence in isolating and reshaping the biota is obvious. A vast belt of amphitropical seaway, the Tethys, split Pangea asunder, isolating the Gondwana landmasses from the northern Laurasian blocks. Both these Pangean subdivisions were subjected to further fragmentation (Fig. 2). While Africa and South America still remained sutured across the Amazon-Gabon basin region in the Early Cretaceous, this connection was being severed by the opening of the Atlantic both in the north and south. Other southern blocks, such as Antarctica and India, became separated from the Gondwana core. Western and southern Europe were a fragmented mosaic of landmasses: an archipelago in the nascent northern Atlantic and a huge embayment in the region of present-day eastern Europe and Russia. North America, isolated from both South America and northern Africa by formidable oceanic barriers, was also flooded by epicontinental seas, especially along its western margin. The massive supercontinent of Asia was also eroded along its southern and western margins by extensive seaways. The long arm of its Siberian extension made only intermittent and tenuous connections with the Alaska region of North America.

This trend toward continental fission and marine ingression reached its acme in the Latest Cretaceous (Smith et al., 1994; Scotese, 1997). South America and Africa were well separated by the southern Atlantic (Fig. 3). Europe was still very much an archipelago. North America was essentially two landmasses nearly bisected by a north-south epicontinental seaway in what is now the Western Plains-Rocky Mountain area. A similar seaway separated fragments of western from eastern Asia. There is both geologic and paleontologic evidence for a corridor between Siberia and Alaska, but this connection was, as in earlier times, ephemeral, depending on the cycles of marine ingression that characterized this phase. Indeed, so profound is the fragmentation of large landmasses in the middle and Late Cretaceous that it has been associated with the isolation and diversification of modern and extant lineages of birds and mammals, at a time before that diversification is indicated by the first occurrences of representative fossils (see Hedges et al., 1996; Kumar & Hedges, 1998; and discussion below).

The Paleocene terrestrial world is the expected product of the continental fission in the Late Mesozoic. Southern landmasses like Antarctica, India, and Madagascar were further isolated from their original moorings. Yet in the early to middle Paleocene there is evidence of reversal in the pattern of marine invasion that so characterized the later Cretaceous. The mid-epicontinental seaway in North America had retreated to an embrasure along the continent's southern margin, a mere extension of what is the present-day Gulf of Mexico. Europe and western Asia, though still separated from eastern

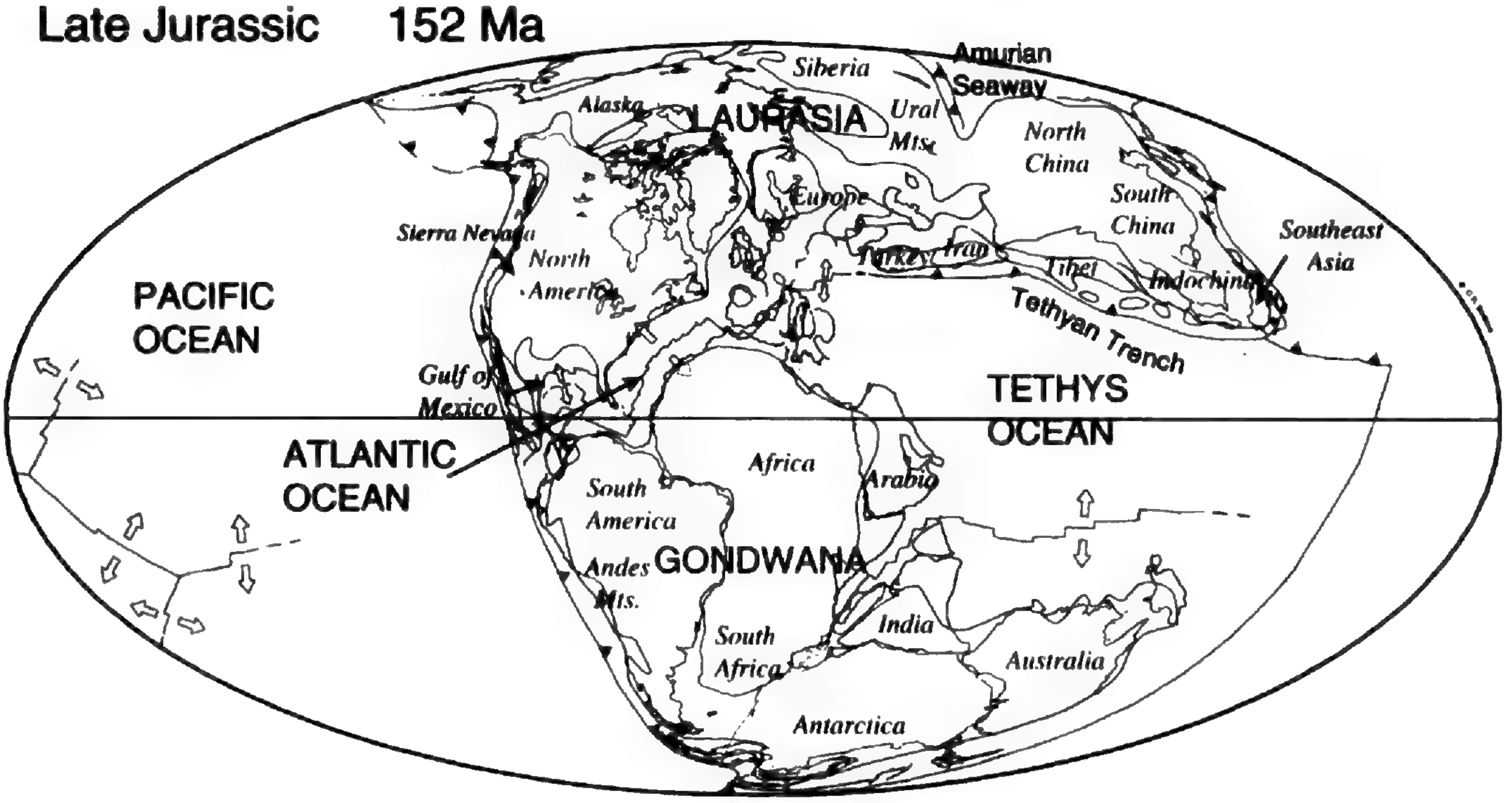

Figure 1. Reconstruction of continental positions for the Late Jurassic. Map from Scotese (1997).

Asia by the north-south trending Turgai straits (Szalay & McKenna, 1971), showed more coalescence than during the previous interval. Importantly, stronger and more enduring connections were forged between Europe and eastern North America as well as between Asia and North America in the Bering region. Opportunities for biotic exchange across emergent landmasses are also evident from the common occurrence of various mammal taxa across the northern continents (Szalay & McKenna, 1971; Savage & Russell, 1983; Janis, 1993; Beard, 1998).

These northern land connections were maintained in the early Eocene (ca. 55 million mybp), but a notable break between eastern North America and Europe did occur with the merging of the far northern Atlantic with the Arctic oceans by middle Eocene times (Fig. 4). This isolation event was mirrored by the subsequent divergence of European and North American mammal faunas (McKenna,

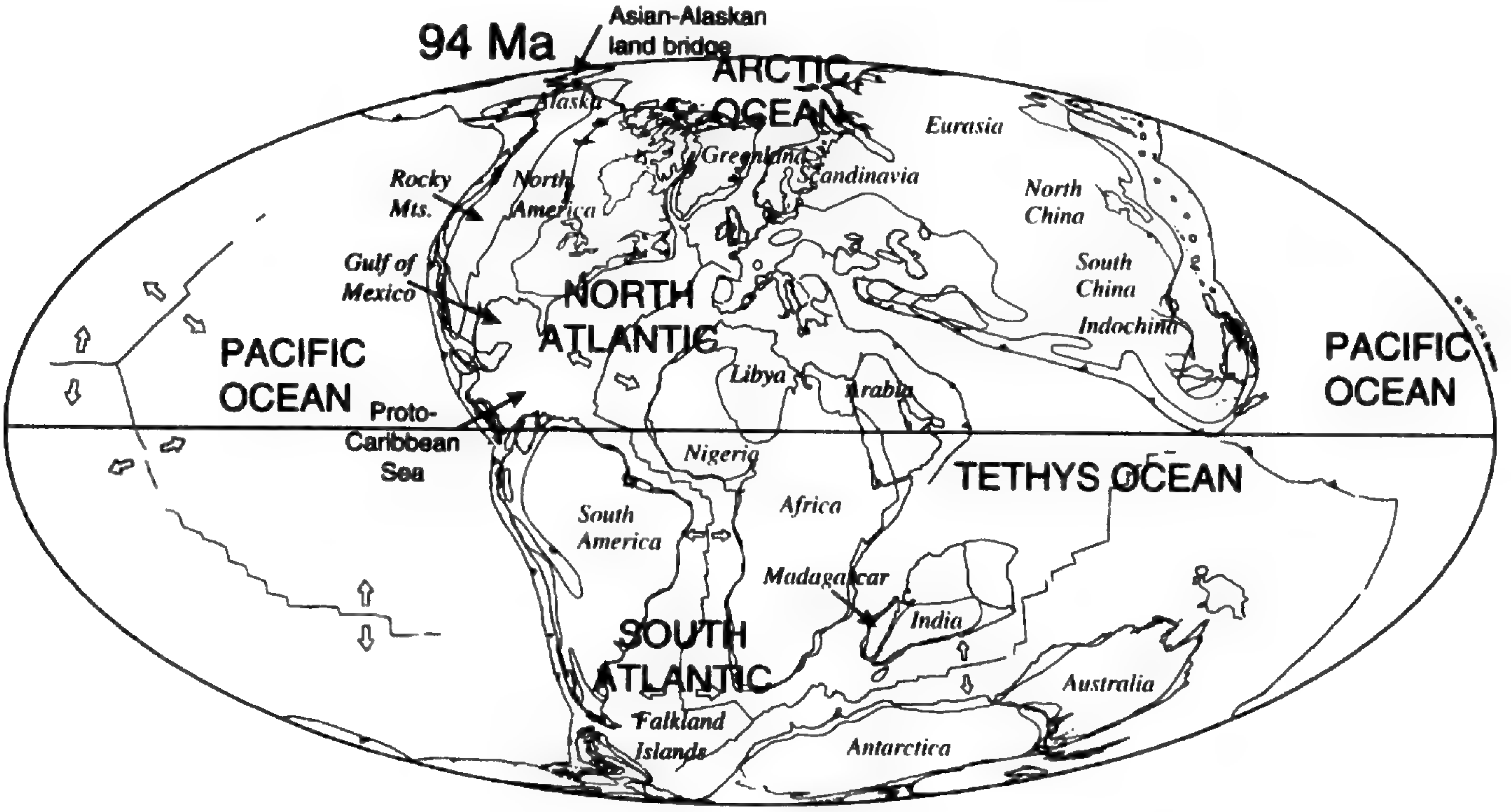

Figure 2. Reconstruction of continental positions for the Mid Cretaceous. Map from Scotese (1997).

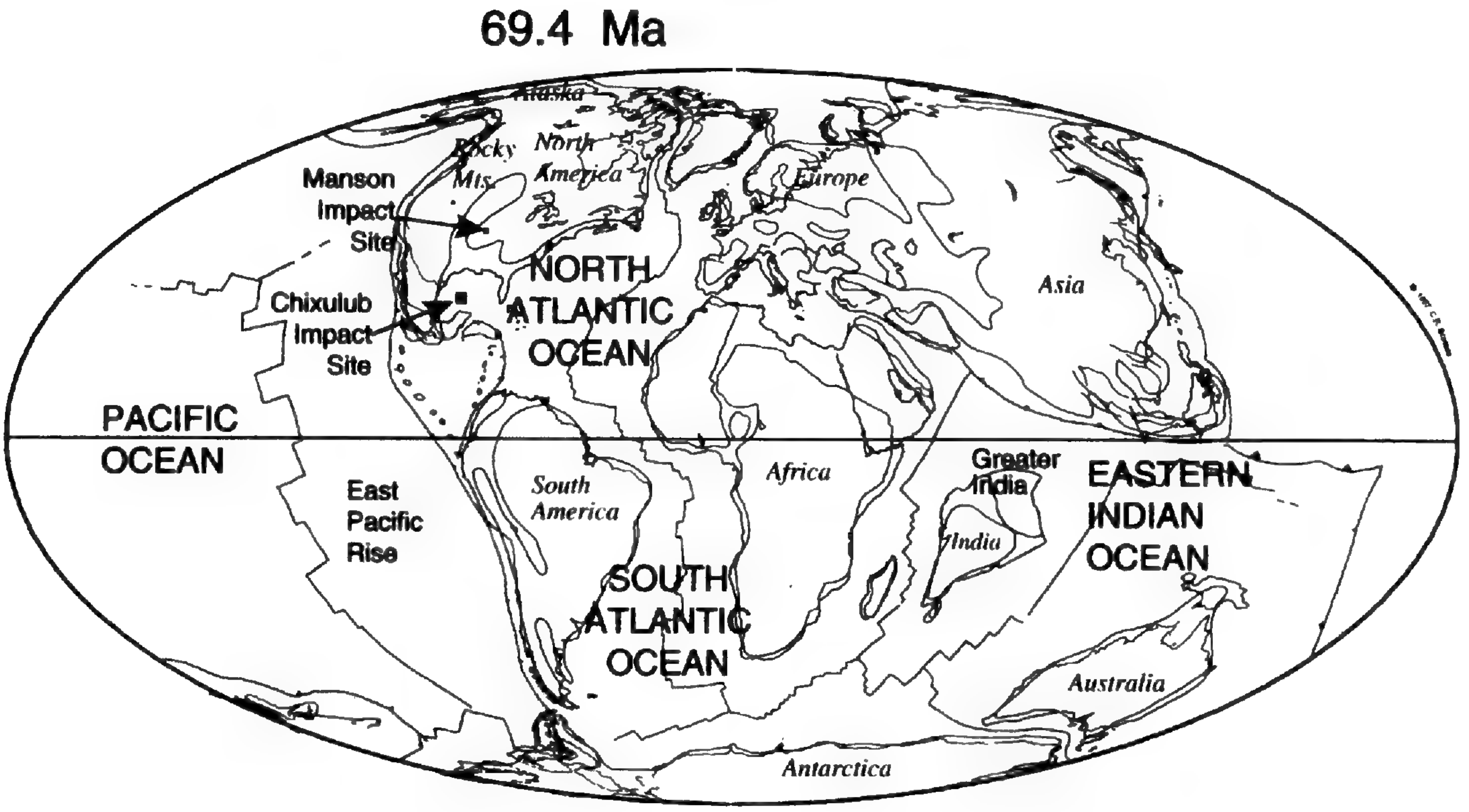

Figure 3. Reconstruction of continental positions for the Late Cretaceous. Map from Scotese (1997).

1983; Flynn, 1986). During the Eocene, the far southern landmasses showed increasing isolation, with India drifting farther northward toward the underbelly of Asia and the Antarctica-Australia megamass drifting from southern South America and Africa. Although some dispersal to South America from either Africa or North America is suggested by the Eocene mammalian record, any such migrations were over substantial tracts of ocean. Indeed, South America remained essentially a giant island through most of the Cenozoic, preceding the closure of the Panamanian land bridge and a marked exchange in fauna between the Americas in the Pliocene between 2.7 and 2.5 million mybp (Marshall & Cifelli, 1990; Woodburne & Swisher, 1995). Not all trends in the middle and later Eocene, however, involved a reprise of continental isolation and separation. Further regression of the mid-latitudinal Tethys seaway in the region of the present-day Mediterranean Sea (Scotese, 1997) enhanced pos-

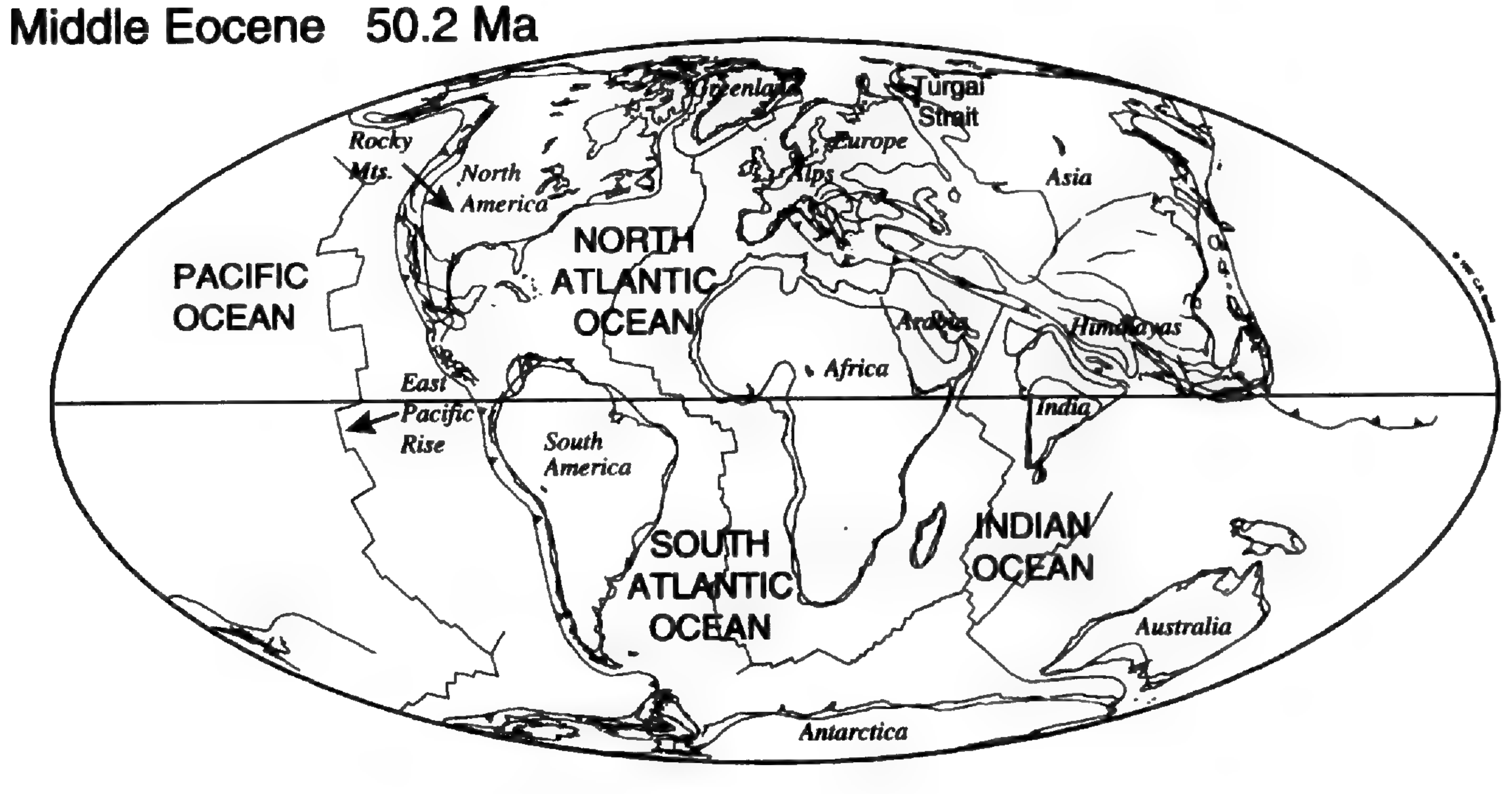

Figure 4. Reconstruction of continental positions for the Middle Eocene. Map from Scotese (1997).

sibilities for biotic exchange between Africa and Europe and western Asia.

To summarize, the oscillation of continental fragmentation and coalescence during the Cretaceous-Early Tertiary is particularly dynamic and is better chronicled than geographic change during earlier intervals. Highlights of this phase include the marked isolation of many landmasses during the Cretaceous, a pattern related to geographic differences noted among terrestrial floras and faunas (Wing & Sues, 1992). By the Late Cretaceous, the amount of marine ingression, in combination with continental fragmentation, produced a marked extent of shallow epicontinental seas, continental shelves, and coastline. Many of the best-known vertebrate assemblages, such as the Late Cretaceous localities in the western interior of North America, represent communities at the margin of these seas. As noted above, it is appealing to relate the diversification of some major clades of more modern vertebrates, e.g., birds and mammals, to the pulse of continental rifting and fragmentation that occurred in the Middle to Late Cretaceous (Hedges et al., 1996). Yet the fossil record does not so far show evidence of extensive radiation of such groups at such an early time (see discussion below). Nonetheless, a degree of endemism for certain vertebrate groups can be documented. For example, a diverse group of Mesozoic and early Tertiary herbivorous mammals, the multituberculates, are well represented in Late Cretaceous assemblages from both North America and central Asia. Virtually all the multituberculate taxa represented in either continent are, however, highly distinctive. Most of the central Asian taxa from rich Mongolian sites have even been identified as an endemic, monophyletic group (Rougier et al., 1997). This obtains despite the fact that central Asia and western North America were at least intermittently connected through Siberia-Alaska in the Late Cretaceous.

In the early Tertiary, patterns of continental isolation, and their biotic effects, differ between the northern and Southern Hemispheres. In the north, landmasses were relatively stabilized and interchange, or isolation, of the vertebrate fauna tracked the severance or suture of land connections between western and eastern Asia, eastern Asia and North America, and Europe and North America. Expectedly, a marked similarity among Holarctic vertebrate faunas has long been recognized. Moreover, Asia has been increasingly recognized as a staging area for the invasion of many higher-level mammalian taxa (e.g., primates, rodents, lagomorphs, perissodactyls, artiodactyls, cetaceans, and others) into North America (Beard, 1998). Homogenization of mammalian faunas between North America and Europe is especially apparent during certain intervals like the early Eocene where northern connections were broadly developed (Savage & Russell, 1983). In the south, by contrast, the breakup of Gondwana initiated in the middle Mesozoic progressed, with further rifting and drift of India, Antarctica, Australia, and other landmasses. Doubtless, this geologic fragmentation contributed substantially to the marked patterns of endemism in present-day fauna and flora documented for the southern continents. Unfortunately, the early Tertiary vertebrate record is less complete and less geographically comprehensive in the Southern Hemisphere. Although important fossil localities document a rich and highly endemic mammalian fauna in South America, early Tertiary faunas in continents such as Australia are limited. A small sample of Eocene mammals from Antarctica (polydolopoid marsupials, edentates, and ungulates) indicates faunal relationships between that continent and South America (Woodburne & Zinsmeister, 1982; Hooker, 1992). The early Tertiary vertebrate record for Africa is extremely poor, a hiatus that critically constrains reconstructions of the diversification and deployment of vertebrates from the southern continents.

CLIMATIC PATTERNS

Continental drift, sea level rise and fall, and oceanic circulation during the Cretaceous-early Tertiary "age of fragmentation" obviously relate to global climatic patterns whose documentation is rapidly improving. Much of the evidence here comes from fossil pollen and plant localities (see below) as well as isotopic analysis for paleotemperatures. Naturally, the late Mesozoic-early Cenozoic global climate, as today, was a mosaic of climatic regimes, some of which are much more precisely documented than are others. Yet some generalizations about overall trends are possible, as temperature curves, especially in the case of the northern latitudes, have distinctive profiles (see Fig. 5 and Burchardt, 1978; Wolfe, 1978; Janis, 1993; Askin & Spicer, 1995).

The earliest phase of the Cretaceous generally experienced a warming trend that peaked about 100 million years ago. Thereafter a slow and steady decline in mean temperature ended in a rather abrupt drop in the last few million years of the Cretaceous. Fossil wood and oxygen isotope data derived from marine mollusk shells of the Antarctic Peninsula also record declining temperatures during the Santonian-Campanian interval to the Maastrichtian during the Late Cretaceous (Pirrie & Mar-

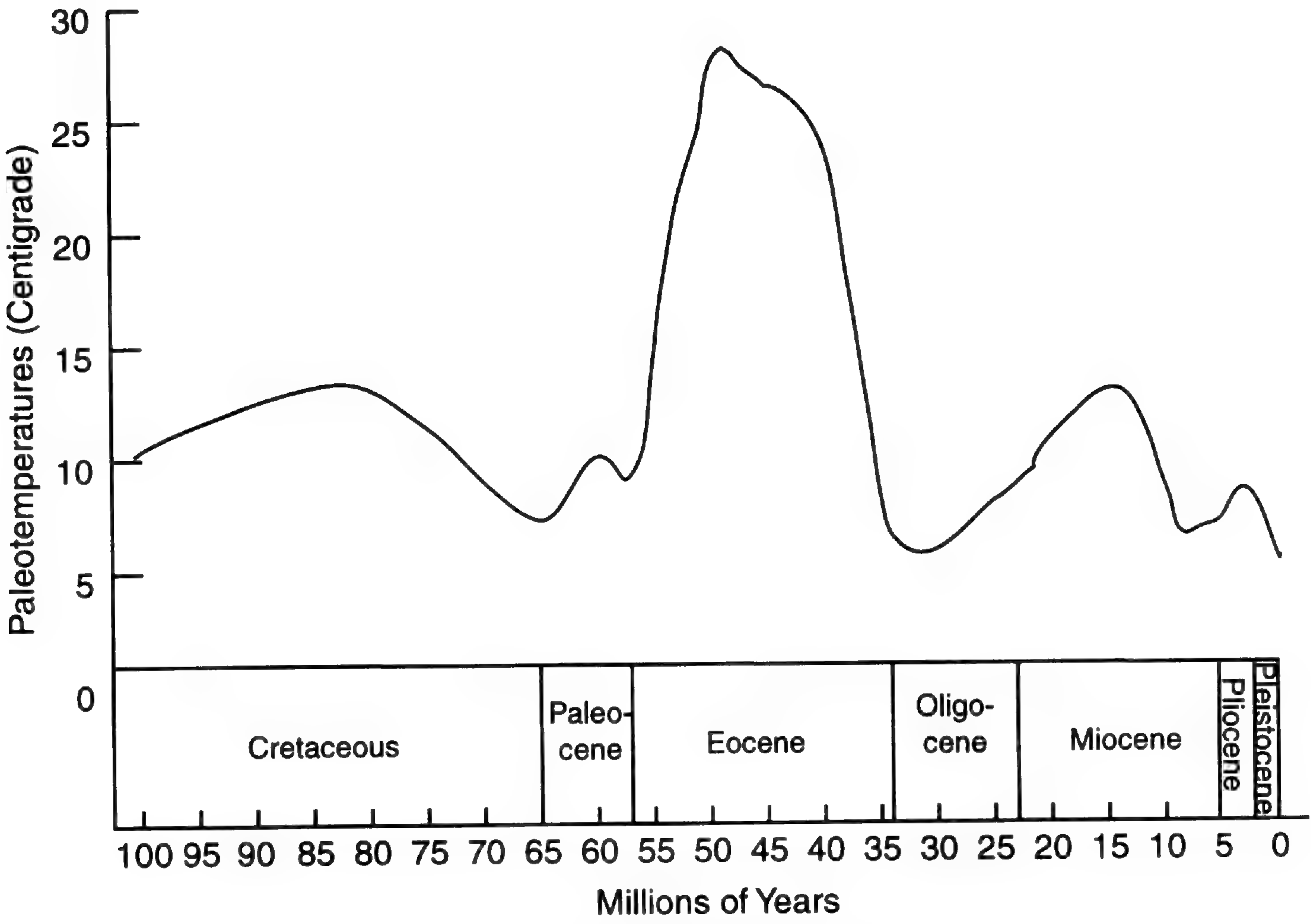

Figure 5. Curve for mean annual temperature in northern latitudes derived from oxygen isotope and paleobotanical data. After information in Burchardt (1978), Wolfe (1978), Janis (1993), and Askin & Spicer (1995).

shall, 1990). Similar patterns are indicated in both northern and southern latitudes: Late Cretaceous cooling was global.

The early Cenozoic in general shows a reversal in this global cooling pattern. A warm early Paleocene was succeeded by an even more tropical middle Paleocene (see Janis, 1993, and references cited therein). Temperatures retreated in the late Paleocene, but the lapse was temporary. The early Eocene was a time of dramatic rise in global temperature and marked equability. Indeed, tropical habitats are evident at very high latitudes, and the cosmopolitan nature of fauna and flora, especially in the holarctic continents, is striking. By the end of the early Eocene (about 51 Ma), this warming trend reached a thermal global high for the entire Tertiary (Fig. 5). A cooling and drying phase beginning in the middle Eocene accelerated markedly between 43 and 40 Ma and continued through the end of the Eocene. The more marked seasonality and climatic latitudinal zonation that came with this cooling trend likely influenced the coincident turnover in mammal lineages, and the radiation of larger more modern mammal groups that persisted through the rest of the Cenozoic (Prothero, 1985; Janis, 1993). Such turnover was also likely promoted by mammalian dispersal and immigration, especially in Holarctica where continents were broadly, if intermittently, connected. Although the affect of climate on such dispersal seems to have been indirect for much of the Cenozoic, the relationship between climate, sea level change, and mammalian faunal exchange is strongly etched for the late Eocene-early Oligocene transition (Woodburne & Swisher, 1995). Indeed, the interplay of climatic and biotic change relates to the controversy over the boundary line for the end of the Eocene (Prothero & Berggren, 1992). A major climatic shift occurred about 40 million years ago, but a major biotic reshuffling, well documented in the case of mammals, occurred over an extended transition span of about 16 million years between the middle Eocene and through most of the Oligocene.

Again, it is important to note that these general global scale trends in temperature should not obscure the heterogeneity in climatic regimes that also characterized different, shorter-term phases of the late Mesozoic and early Cenozoic. In the Early to middle Cretaceous, climates at midlatitudes (southern Laurasia and northern Gondwana) were seasonally dry, but the dominance of fern and conifer palynomorphs in northern Laurasian and southern Gondwanan regions indicated cooler and wetter climates (Brenner, 1976; Ziegler et al., 1987). Late Cretaceous climatic regimes were doubtless diverse, as indicated by the pastiche of different floras in higher and lower latitudes (see review in Wing & Sues, 1992). Higher-latitude floras show greater loss of diversity with the climatic deterioration in the last (Maastrichtian) age of the Cretaceous. But the heterogeneity in climate is not simply indicated by variance in the composition of paleofloras. During the Late Cretaceous, major areas, such as Central Asia, preserve extensive sand dunes, abundant dinosaurs, mammals, and other vertebrates, but few plant remains. These were environments subject to intense drying and seasonality, mixed with intermittent torrential rains and flash floods. Such conditions are typical of deserts or semi-arid regions today (Jerzykiewicz et al., 1993; Loope et al., 1998).

A mosaic of climatic regimes is also apparent in the early Tertiary. There is evidence of a sharp but long-lasting transition to wetter climates over most of North America in the early Paleocene (Fastovsky & McSweeney, 1987; Retallack et al., 1987; Wolfe & Upchurch, 1987; Lehman, 1990), a shift that has been related by some authors (Wolfe & Upchurch, 1987) to the effects of the K/T bolide impact. Nonetheless, higher latitudes of both North America and Asia probably maintained extensive subtropical woodland or gallery forests typical of drier, more seasonal climates. The marked warming trend in the early Eocene clearly expanded the tropical rainforests through higher latitudes, but a narrow belt of more seasonal climates probably remained in the far north of Asia and North Africa, as well as in parts of Antarctica and Australia (Janis, 1993). Expectedly, the contraction of tropical rainforest habitat, and the expansion of habitats that indicate drier and more seasonal climates—namely, paratropical forests, more open woodlands, and temperate forests (mixed coniferous and deciduous)—accompanied the marked global cooling trend in the later Eocene (Miller, 1992). Likewise, the Eocene/Oligocene boundary in the marine realm shows a sharp increase in temperature seasonality similar to that indicated by contemporaneous terrestrial floras (Swisher & Prothero, 1990).

EXTRATERRESTRIAL IMPACTS AND VOLCANISM

In addition to changing geography, sea level, and climate, other physical environmental events doubtless have wide-ranging and enduring effects on the biota. Notable among those events cited for the late Mesozoic and early Cenozoic are extraterrestrial impacts and pulses of volcanism. Archibald (1996a) provided a very useful overview of these occurrences in the geologic record and their likely affects. The timing and reality of a major bolide impact at the end of the Cretaceous (ca. 65 million years ago) is now widely recognized (Alvarez et al., 1982). The evidence for impact is the preservation of the massive (110 miles in diameter) Chicxulub Crater near the Yucatan Peninsula of Mexico. Attendant disasters have been widely imagined and reconstructed; they include but are not restricted to global cooling due to prolonged cloud cover (Alvarez & Asaro, 1990), acid rain (D'Hondt et al., 1994), and global wildfire (Wolbach et al., 1990). Although such catastrophic phenomena are certainly expected, matching these events with a highly selective pattern of extinction, especially in the terrestrial record, is problematic (see further discussion below). There is geologic evidence for other much smaller bolide impacts in the Early Cretaceous, the Late Cretaceous just preceding the Chicxulub impact, and in the early Tertiary (Grieve & Robertson, 1987; Newsom et al., 1990; Raup, 1991; Izett et al., 1993; Hildebrand et al., 1995). The timing and relation of these smaller impacts to major pulses of extinction and turnover are not clearly documented.

A second physical trauma related to extinction patterns is widespread volcanism. Even isolated volcanic eruptions, like the recent Mount Pinatubo eruption in the Philippines, can dramatically influence present-day weather patterns. One can imagine the magnitude of such effects with volcanism on a much wider scale. Marked phases of volcanism are recorded throughout the Cretaceous-early Tertiary interval, but the greatest intensity of broad-scale volcanism seems coincident with the K/T boundary (Courtillot, 1990: Campbell et al., 1992). Flood basalt data taken from the Deccan Traps of India suggest an enormous volume of lava: as much as 350,000 cubic miles. It has been argued that the Deccan event would have produced significant atmospheric changes, such as increased ash and other particulate matter, carbon dioxide, and cloud cover, that may have induced either global warming (through the greenhouse effect) or global cooling (an option more in line with the recorded drop in global temperature at the end of the Cretaceous). Another scenario ties volcanic eruption and the release into the atmosphere of elements like selenium that could be harmful to the developing embryos of dinosaurs and other vertebrates. Selenium or other possibly toxic trace elements have been identified in the eggshells of dinosaurs from localities at or near the K/T boundary (Hansen, 1991; Stets et al., 1995), although there is little comparative data on eggs from older Cretaceous levels. As in the case of the bolide impact, the most straightforward effect of marked volcanism would be cloud cover, atmospheric accumulation of carbon dioxide, prolonged darkness, climatic cooling, and possible temporary disruption of photosynthesis (Archibald, 1996a).

The hypothesized link between marked volcanism and the K/T extinction event, however, does entail problems. The Deccan event may have been much broader in time than the extinction event—between 69 and 65 million years ago (Prasad et al., 1994). This broad span, as well as the nature of the Deccan basalts, suggests continual and long-term activity much like the shield volcanoes of Hawaii rather than sudden and catastrophic explosions like the eruption of Mount Saint Helens. Moreover, intense volcanic activity, like the bolide impact, does not effectively explain the highly selective extinction at the K/T boundary (see below).

THE TERRESTRIAL FLORAL RECORD

Major contributions to this issue of the *Annals* deal with the dramatic floral changes of the late Mesozoic-early Cenozoic. The summary here derives from those papers and a few earlier reviews, notably Wing and Sues (1992) and Askin and Spicer (1995).

Earliest Cretaceous floras were generally thought to lack angiosperms and to look like preceding Late Jurassic floras, but pollen data from strata of Hauterivian age and scattered records from the Valanginian, now show that angiosperms were well established by the earliest Cretaceous (Friis et al., 1999). The record is nonetheless spotty, with diverse floras found mainly in terrestrial strata with poor age control, or more readily datable marine strata with depauperate floras. By Barremian-Aptian times rapid diversification of angiosperms is evident, though this radiation seems less explosive at middle to high latitudes where extensive ferns suggest persistence of open foliage (Wing & Sues, 1992).

Early Late Cretaceous angiosperm diversity increased dramatically, especially in middle and high latitudes. By the end of the Late Cretaceous, 50–80% of the fossil flora were flowering plants (Crabtree, 1987; Lidgard & Crane, 1990). This radiation was coincident with a significant drop in diversity and abundance of cycadophytes and ferns, but not a decline in the proportion of conifer species in these assemblages (Lidgard & Crane, 1990). Indeed, specimen counts at the Late Cretaceous Black Hawk locality show that 4 of the 9 taxa represented by more than 100 specimens (out of a total of 7400 specimens) are conifers or cycadophytes (Parker, 1976). The data suggest a Late Cretaceous co-dominance of gymnosperms with flowering plants, at least in certain localities were such a census is feasible.

This diversification notwithstanding, angiosperms, prior to the Campanian and Maastrichtian, did not compare with the present-day angiosperm floras in their range of ecological roles. Angiosperm wood is rarer than contemporaneous flowers, as well as coniferous wood (Wing & Tiffney, 1987). In addition, latitudinal variation in angiosperm diversity persisted throughout the Cretaceous. For example, Cretaceous floras from Alaska show a lower proportion of angiosperms than do lower-latitude floras (Spicer & Parrish, 1986; Parrish & Spicer, 1988). By Maastrichtian times, these high-latitude floras were drastically reduced in diversity and show signs of lower productivity (Spicer & Parrish, 1986), plausibly a result of Late Cretaceous climatic deterioration. A more stable pattern of diversity and productivity, however, is indicated in Antarctica during the Late Cretaceous (Askin & Spicer, 1995).

Following the K/T event, the replenishment and diversification of angiosperms shows marked heterogeneity on a global scale. This has strong implications for any scenario concerning the range and magnitude of the extinction event, its cause, and its effects on the biota. In the North American earliest Paleocene a drastic decrease in angiosperms is indicated by the presence of a "fern spike" only a few centimeters above the K/T boundary (Orth et al., 1981; Nichols et al., 1986). This fern flora was succeeded by an angiosperm-dominated flora of quite different composition than the conifer-abundant floras of the latest Cretaceous of North America (Orth et al., 1981; Tschudy et al., 1984; Tschudy & Tschudy, 1986). Wolfe (1987) attributed preferential extinction of evergreen species at the K/T boundary to relatively low tolerance to the cold snap caused by the impact cloud. But the floral record for North America displays notable variation. Megafloras in New Mexico and Colorado show low diversity for the first few million years of the Paleocene (Wolfe & Upchurch, 1986, 1987), but floras in western North Dakota show a more rapid increase in diversity (Johnson et al., 1989; Johnson & Hickey, 1991).

One of the most provocative aspects of the paleobotanical evidence is that the dramatic fall-off in angiosperm, indeed floral, diversity at the K/T boundary does not hold for certain other regions of the world. Paleofloras from Japan (Saito et al., 1986), New Zealand (Raine, 1988), and Seymour Island off Antarctica (Askin, 1988) show little or no turnover at the boundary. This is in strong contrast to the terrestrial faunal picture, where non-avian dinosaurs were supposedly decimated worldwide (but see discussion below on the paucity of non-North American vertebrate sites bracketing the K/T boundary) and the large tetrapod herbivore component was erased. The discrepancy in the global pattern between faunal and floral change still eludes explanation.

Early-middle Paleocene floras of the Northern Hemisphere show low diversity and strong homogeneity, as exemplified by very similar floras from the late Paleocene of Mongolia, China, and western North America (Crane et al., 1990; Manchester, 1999). During the early Eocene the rise in global paleotemperatures corresponds with a high point in tropicality and the flourishing of angiosperm-dominated closed forests; subtropical vegetation may have ranged as far north as 60° latitude and multistratal tropical rainforests occurred at 30°N (Wolfe, 1985). In the Eocene, Australia (then between 30 and 60°S) harbored diverse angiosperm-dominated tropical to subtropical rainforests (Hill, 1982). Argentine floras were tropical but were subject to seasonal wet and dry periods (Romero, 1986). The African floral record shows evidence of wet tropical forests beginning in the middle Tertiary, though such habitats likely did not spread on a continental scale until the Miocene (Axelrod & Raven, 1978). Late Eocene floras from Egypt were wet and tropical with indications of seasonality (Wing & Sues, 1992).

The cooling and drying phase during the middle to late Eocene doubtless inaugurated the extinction or marginalization of the thermophilic plants (Manchester, 1999). Likewise, increased aridity during the late Eocene in the Rocky Mountain region promoted loss of conifers, even in wetter habitats at lower elevations (Wing, 1987). A global decline in temperatures and greater seasonality at about 33 Ma resulted in a shift to more broad-leafed types of vegetation in coastal North America (Wolfe, 1978), a pattern essentially duplicated in Europe (Collinson & Hooker, 1987). It is noteworthy that by mid-Oligocene, most woody genera that typify modern North American forests were already present (Manchester, 1999). Thus floral changes, as well as vertebrate faunal turnover, during the late Eocene-early Oligocene interval established the persisting terrestrial ecosystems of most continents.

The plant record, therefore, shows both oscillation and resilience during the late Mesozoic-early Tertiary. Angiosperm floras, though still spottily sampled, were definitely established by the earliest Cretaceous (Crane & Lidgard, 1990). Angiosperm diversification, though subject to a number of pulses, seems to have been progressive rather than instantaneous during the Cretaceous. Differences in these patterns of diversification from the Late Cretaceous through the early Cenozoic in high-latitude northern and southern regions can be attributed to different continental configurations. The extensive continuity of land in the north favored floral dispersal in contrast to Antarctica and adjacent landmasses, which offered increasingly restricted dispersal corridors (Askin & Spicer, 1995). Considerable floral heterogeneity, including the persistence of more open vegetation during the Cretaceous at certain latitudes and on certain continents, also has been related to the trophic impact of large terrestrial herbivores, namely dinosaurs (see below). Heterogeneity likewise obtains for the global pattern of floral extinction and replacement at the K/T boundary. In North America, turnover of the flora is marked, but in Asia and the Southern Hemisphere little turnover coincident with the K/T event is evident. In the Paleocene and early Eocene, floral diversification was fed by global warming and the concomitant latitudinal spread of tropical and subtropical forests. Homogeneity among Northern Hemisphere early Eocene floras matches that seen in the vertebrate fauna. Starting in the middle Eocene, marked global cooling and increasing aridity catalyzed the loss or restriction of these warm temperature floras and their replacement, by the early-middle Oligocene, by woody-dominated floras that essentially persist today.

THE TERRESTRIAL FAUNAL RECORD: NON-VERTEBRATES

The terrestrial non-vertebrate fauna obviously encompasses a vast range of organisms, including freshwater invertebrates, soil infauna, protozoans, and microbes. Yet the biostratigraphic record for these elements is generally so poor that it provides little insight on biotic transitions of non-vertebrates during the late Mesozoic-early Cenozoic. Brief discussion here is restricted to insects where the record, though inconsistent, is impressive and rapidly improving. Comprehensive treatment of the early fossil record of pollinating insects can be found in D. Grimaldi's contribution to this volume (Grimaldi, 1999). The first occurrences of aphids (Homoptera), short-horned grasshoppers (Orthoptera), and gall wasps (Hymenoptera) are in the Cretaceous. The equivocal Late Cretaceous record of ants (Hennig, 1981; Wilson, 1987; Agosti et al., 1998) is now confidently established based on well-preserved specimens in Turonian-age (Late Cretaceous) amber from New Jersey in the northeastern United States (Agosti et al., 1998).

Perhaps the most interesting aspect of the insect record in the Cretaceous is the radiation of pollinating insects. The major groups in question are the Lepidoptera (butterflies and moths), Hymenoptera (bees, wasps), and Diptera (flies) within the Brachycera. Lepidoptera have a clear record since the Early Cretaceous (Whalley, 1986), but there is evidence of their first appearance in the Upper Jurassic with extensive diversification in the middle to Late Cretaceous (Grimaldi, 1999). Likewise, the Brachycera have a record dating back to the Upper Jurassic. The pollination motive in Late Cretaceous angiosperms seems somewhat different than that in mid-Tertiary floras. Most flowers were radially symmetrical (actinomorphic) and probably either pollinated by wind or by a broad range of insects rather than just the Hymenoptera (Friis & Crepet, 1987; Crepet & Friis, 1987). But advanced eusocial bees are known from the Campanian (Michener & Grimaldi, 1988), and the presence of lauraceous flowers in the Cenomanian is consistent with bee pollination (Drinnan et al., 1990). A suggested lag between the rise of angiosperms and a putative later appearance of pollinating insects has been disputed (Grimaldi, 1999). Assessment of fossil occurrence data against patterns of phylogeny suggests a coincidence between the radiation of angiosperms and their insect pollinators, a coincidence expected by the strong ecological interdependence of these groups.

The fossil record suggests a continual increase in the number of insect families throughout the Paleocene, with the appearance of modern groups of moths and butterflies by the Eocene. Formicoid ants also show significant diversification from the Late Cretaceous through the Paleocene (Wilson, 1987).

The insect record for this crucial interval is of course still patchy. Yet what we know of this record seems to indicate two essential patterns of insect evolution. First, the radiation of pollinating insects is now extended back to a time coincident with the radiation of flowering plants. Second, there is no evidence of perturbation of insect diversification that is clearly related to the K/T extinction event.

THE TERRESTRIAL FAUNAL RECORD: VERTEBRATES

Although vertebrates have a much more enriched record of faunal change from the Cretaceous through the early Cenozoic than do other animal groups, the emphasis of that history largely concerns the non-avian dinosaurs and mammals. For the sake of completeness, the basic aspects of the known record of the major terrestrial and freshwater vertebrate groups (Fig. 6) are provided here, with the weight of the discussion centering on the groups with particularly well-documented records. These summaries focus on distribution evidence for groups during the Late Cretaceous-early Tertiary, with emphasis on differential survival across the K/T boundary.

Elasmobranchs. Sharks, rays, and relatives have a long and comparatively rich fossil record, to a large extent due to the abundance of taxonomically informative teeth. The tooth record is complemented in some cases by spectacular fossils of calcified cartilaginous skeletons. The elasmobranch fossil record, which is overwhelmingly marine, is notable for the waves of succession of major groups (Cappetta et al., 1993). Many archaic clades traditionally known as families of the mid and late Paleozoic dwindled or went extinct by the Triassic. The Mesozoic radiation comprised clades extending back to the Carboniferous (e.g., Polyacrodontidae), clades originating in the Triassic or Jurassic but disappearing by the earliest Tertiary (e.g., Orthacodontidae), and clades first appearing in the Jurassic or Cretaceous and persisting through the Cenozoic to the present day (e.g., several squalimorph, squatinomorph, and galeomorph familial lines). The lineages emerging during the later Mesozoic far outnumber the modern higher clades that have first occurrences in the Tertiary (e.g., Heptranchidae, Dalatiinae, and Rhincodontidae).

The persistence of higher clades of elasmobranchs across the K/T boundary contrasts with some evidence for at least local extinction at the species level. Archibald and Bryant (1990) and Archibald (1996a) documented the disappearance in lowermost Paleocene beds of five species of elasmobranchs known from the uppermost Cretaceous Hell Creek beds of Montana. These species were freshwater forms, as the fossil localities in the Hell Creek Formation represent habitats that were 100 to 150 miles west of the receding epicontinental marine sea. Thus these freshwater sharks and rays seemed to have been among the victims of the K/T extinction event, at least where sufficient evidence exists in the North American record.

Bony fishes. The present-day diversity of bony fishes (Osteichthyes) is overwhelmingly embraced by the actinopterygian or ray-finned fishes, which number above 20,000 species, nearly half the

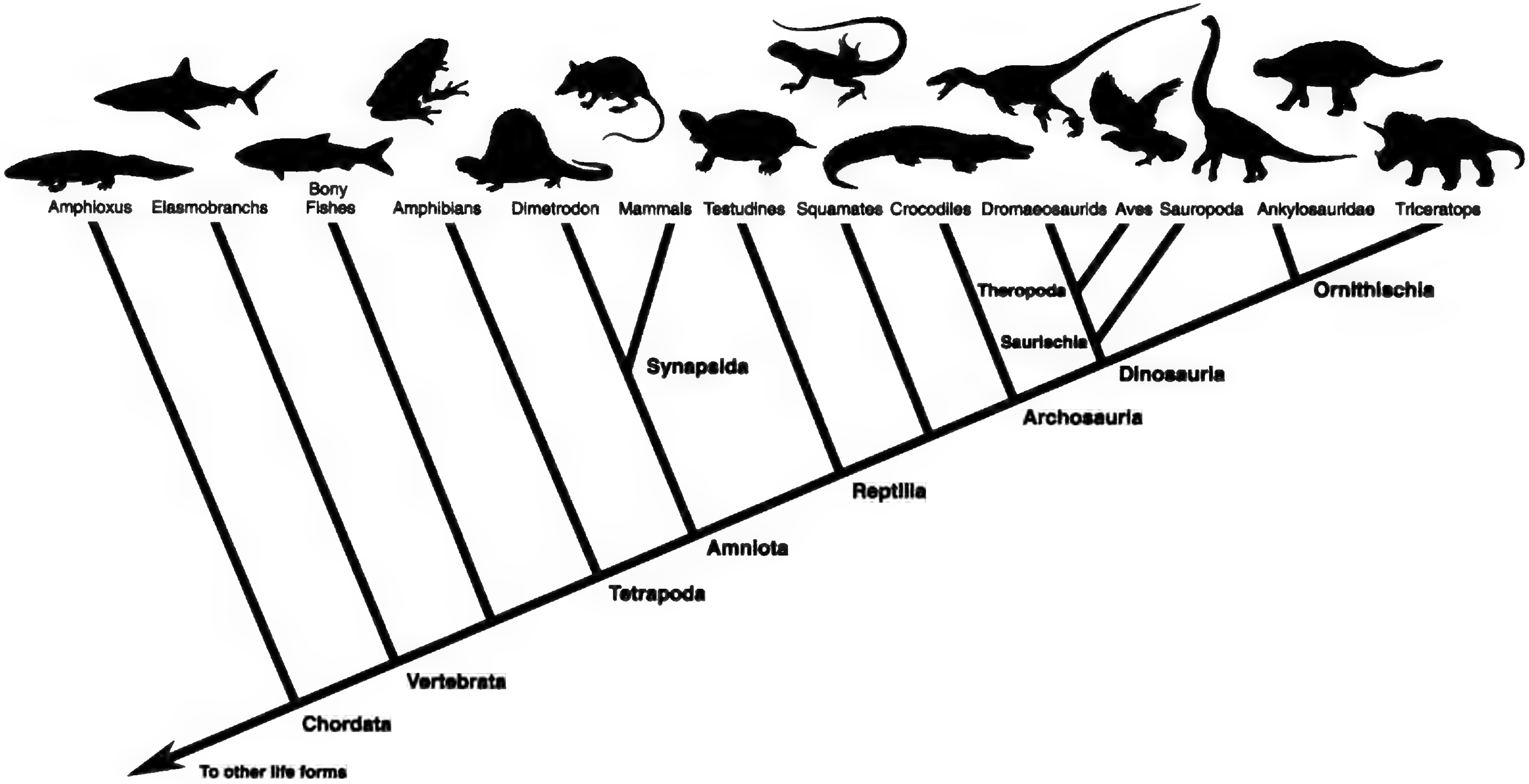

Figure 6. Cladogram depicting interrelationships of the major vertebrate clades.

named species of all living vertebrates (Moyle & Cech, 1988). This great radiation began at least by the Silurian, with the appearance and short duration of *Andreolepis,* followed by the Devonian and Carboniferous radiation of many archaic clades (Gardiner, 1993). Waves of successive clades of basal actinopterygians also characterize the Triassic and, to a lesser extent, the Jurassic and Cretaceous (Gardiner, 1993). The spectacular diversification of clades of more modern bony fishes, the teleosts, began at least in the Early Mesozoic, with an impressive number of lineages recorded by the Cretaceous (Patterson, 1993). A distinctive quality of the teleost record is the very large number of living clades whose first appearances are recorded in the earliest Tertiary (see figs. 36.1–36.6 in Patterson, 1993).

Within actinopterygians, the vast majority of terrestrial (freshwater) fishes are members of the Ostariophysi, a major clade that includes carps, characins, suckers, loaches, and catfish. Ostariophysans have largely a Tertiary record, with a few clades either appearing and terminating in the Cretaceous (e.g., Otophysi and some *incertae sedis* Siluroidea and Characiformes) or originating in the Cretaceous and persisting to the present (e.g., Diplomystidae, Ariidae). Nonetheless, a few basal freshwater actinopterygian groups straddle the K/T boundary, a pattern evident even at the species level. These include the chondrosteans—the acinpenserids (sturgeons) and the polyodontids (paddlefish). These more primitive forms, along with the lepisosteids (gars) and amiids (bowfins), account for 7 of the 15 species of actinopterygians known from the Upper Cretaceous Hell Creek Formation of Montana (Archibald, 1996a). Remarkably, all these groups of fishes, originally the denizens of Cretaceous river systems, not only persisted through the Tertiary but are still found today in the Mississippi river drainage. The remaining eight groups of bony fishes preserved in the Hell Creek Formation are teleost clades, although the more basal actinopterygians dominate the sample of fish remains from this sequence. Wilson et al. (1992) reassigned some Hell Creek teleosts previously described as the extinct *Platacodon* as extant Esocoidei. These authors also argued that the dearth of Cretaceous teleost lineages is a problem of sampling and monographic bias, and that many of the Tertiary clades probably have Mesozoic occurrences awaiting description. Revised studies of teleosts, as well as the records of basal actinopterygians noted above, underscore the geochronological endurance of many freshwater fish clades. In contrast to the marked extinction of elasmobranchs, 9 of 15 species of bony fishes (60%) in the Hell Creek Formation persist into the Tertiary (Archibald, 1996a). Moreover, the prospects for marked improvements in documenting the Cretaceous record of teleosts argue against linking the impressive diversification of this group strictly with environmental changes that post-date the Mesozoic.

The other division of Osteichthyes, the sarcopterygians, are primarily a Paleozoic radiation with a few clades (Gnathorizidae, Ceratodontidae, Laugiidae) persisting through the Mesozoic and in some cases early Cenozoic (Shultze, 1993). Some sarcopterygian clades show remarkable longevity; these include Neoceratodontidae (Triassic to present), Latimeriidae (Jurassic to present), and Lepidosirenidae (Cretaceous to present). Many of these lineages are monotypic or contain very few taxa. The more marked sarcopterygian diversification in the Paleozoic thus gave way to a few very persistent clades whose diversity was greatly overshadowed by that of the actinopterygians.

Lissamphibians. The modern amphibian groups—frogs, salamanders, and caecelians—belong to the Lissamphibia, some of whose surviving lineages have a long fossil history (Milner, 1993). The earliest lissamphibian records, represented by the extinct Triadobatracidae, date back to the earliest Triassic. Both frogs (Anura) and salamanders (Caudata) appear by the mid Jurassic, and some of these lineages (e.g., the anuran Discoglossidae) persist today (Estes, 1969). Many lineages of lissamphibians, some of them extant groups, have records extending back at least to the Cretaceous (Nessov, 1988). As in the case of some other vertebrate groups, the apparent restriction of a large number of lineages of frogs and salamanders to the Cenozoic may reflect sampling and monographic bias. Amphibian remains are usually fragmentary and often elude identification. Estes (1969, 1982) pioneered much of the taxonomic work on Cretaceous and Tertiary amphibians as well as squamates (see below).

As in the case of several other vertebrate groups, the primary reference sections for latest Cretaceous and earliest Tertiary lissamphibians are in western North America. Lissamphibians are less common in the Upper Cretaceous Hell Creek Formation of Montana (Archibald, 1996a) than they are in the Upper Cretaceous Lance Formation in eastern Wyoming (Estes, 1964). The faunal contrast has been attributed to more fluvial conditions in the Lance sequence (Archibald, 1996a). Of the five families of lissamphibians in the Hell Creek, only one, the Sirenidae, includes extant species. The remaining four families, though extinct, extend into the Tertiary. In fact, all eight of the lissamphibian species identified from Hell Creek are survivors of the K/T event (Archibald, 1996a).

Testudines (turtles). Turtles are an ancient group of vertebrates whose remains of shell fragments are among the most common fossils found at many terrestrial sites. The record of the group extends back to the Triassic, but the Cretaceous is notable for marking the first appearances of many turtle lineages, several of which (Chelydridae, Pelomedusiidae, Trionychidae, Cheloniidae, Carettochelydae) survive today (Hutchison & Archibald, 1986). Virtually all other extant turtle clades date back to the Paleocene (Benton, 1993). With respect to the Cretaceous-Tertiary transition, turtles, like lissamphibians and actinopterygian fishes, show a high survival rate. Eleven higher taxa of Cretaceous turtles have records that cross the K/T boundary, while only five clades disappear before the end of the Cretaceous (fig. 39.1 in Benton, 1993). This pattern pertains to more refined, albeit more local, analyses. Fifteen of seventeen (89%) turtle species from the Cretaceous Hell Creek fauna are also known from Tertiary faunas (Archibald & Bryant, 1990; Gaffney & Meylan, 1988; Brinkman & Nicholls, 1993; Archibald, 1996a).

Squamates (lizards and snakes). The early squamate record, though spotty, is lately much improved. Inspired by important analyses by Estes (1964, 1983), recent work has expanded greatly the taxonomic treatment of Cretaceous lizards (e.g., Nessov, 1985, 1988; Richter, 1994; Gao, 1994; Gao & Fox, 1996; Gao & Hou, 1995; Cifelli & Nydam, 1995). Extremely large and diverse samples of Late Cretaceous lizards (see Novacek et al., 1994; Novacek, 1996) are now under study by Gao Keqin. Accordingly, even some of the most recent reference work on squamate geological distributions (Benton, 1993) warrant revision. At present it is apparent that the record of fossil lizards extends back at least to the Late Jurassic, but no Jurassic lizard can be referred to any of the modern clades (Seiffert, 1973; Estes, 1983).

Diversification of many of the modern lizard groups is first recorded in the Cretaceous and early Tertiary (Estes, 1983; Sullivan, 1987; Benton, 1993; Cifelli & Nydam, 1995; Gao & Fox, 1996). Recent work has pushed back the minimum age of first occurrence in several cases. For example, the Iguanidae* (* asterisks indicate a metataxon not diagnosed by apomorphies; see Gauthier et al., 1988; Estes et al., 1988), Scincidae, Xenosauridae, and Necrosauridae* have been listed as first appearing in the latest Cretaceous, Maastrichtian stage (ca. 75–65 Ma) in recent compendia (e.g., Benton, 1993). It is clear now that these clades date back at least to the preceding Campanian stage (ca. 83–80 Ma) in North America (Gao & Fox, 1996). Possibly contemporaneous occurrences of Iguanidae* and Necrosauridae* are known from Central Asia (Borsuk-Bialynicka, 1991). The extant family Anguidae is first recorded from the early Campanian of North America (Gao & Fox, 1996). Other groups of at least Campanian age include the more advanced varanoids, Varanidae and Helodermatidae, and the diverse Teiidae, although Winkler et al. (1990) identified possible teiids from the Early Cretaceous (Aptian or Albian) of Texas. Early Cretaceous occurrences are also cited for the Gekkonidae (Alifanov, 1989), a possible relative of Necrosauridae* (Cifelli & Nydam, 1995), and a scincomorphan relative (?Anguidae in Winkler et al., 1990, reassigned by Gao & Fox, 1996). Notably, the extant Cordylidae, Amphisbaenidae, and Xantusiidae, listed by Benton (1993) as first appearing in the Paleocene, are now known from possibly referable taxa in the Late Cretaceous (Borsuk-Bialynicka, 1991; Gao & Fox, 1996).

Given the above-noted ranges, it is clear that many lizard higher clades survived the K/T extinction event. Of some 19 Tertiary or extant clades usually designated as families, 13 (e.g., Iguanidae*, Agamidae, Amphisbaenidae, Gekkonidae, Xantusiidae, Teiidae, Scincidae, Cordylidae, Anguidae, Xenosauridae, Necrosauridae*, Helodermatidae, and Varanidae) have first occurrences in the Cretaceous. Nonetheless, selective extinction is apparent at lower taxonomic levels. For example, teiids, the most diverse group of Late Cretaceous lizards in both North American and Asian faunas (Estes, 1983; Borsuk-Bialynicka, 1991; Gao & Fox, 1996) show marked extinction at the K/T boundary. All four species of teiids from the Hell Creek Formation are not known above the boundary (Archibald, 1996a). [Before the end of the Cretaceous, teiids likely entered South America and later diversified there during the Tertiary (Gao & Fox, 1996).] In fact, only three of the ten lizard species assigned to seven different families persist into the Tertiary (Archibald, 1996a). This pattern should be tested against records in the Gobi Desert of Mongolia and northern China, where Late Cretaceous lizard faunas are even more diverse and much better preserved than in North America. Unfortunately, an Upper Cretaceous-Lower Paleocene sequence preserving the K/T boundary has yet to be found in the Gobi (Novacek et al., 1994).

This improving document of lizard distributions does not, unfortunately, extend to its squamate sister taxon, the snakes (Serpentes). Snakes have a record extending back to the Early Cretaceous, and several of the extant or Tertiary higher clades (Aniliidae, Boidae, Madstoiidae) have occurrences in the Late Cretaceous (Benton, 1993). The emergence and impressive diversification of some of the more modern groups, like Colubridae, Viperidae, and Elapidae, are currently restricted to the Tertiary. Doubtless, occurrences of snakes in the Cretaceous record will increase when the fragmentary squamate remains from many collections receive more expert study.

Champsosaurs. The crocodile-like appearance of the champsosaurs is misleading, as this group, also denoted choristoderans, lies outside crocodilians and their archosaur relatives, the dinosaurs (including birds) and pterosaurs. The group ranges at least from the Early Cretaceous to the middle Eocene (see summary in Benton, 1993). Champsosaurs are very common, if fragmentary, fossils in Late Cretaceous and early Tertiary faunas. Archibald and Bryant (1990) and Archibald (1996a) claimed that *Champsosaurus* straddled the K/T boundary, but the lack of a comprehensive classification precludes any analysis of distributions for species of this taxon.

Crocodiles. The impressive and enduring fossil record of crocodilians extends from the Middle Triassic to the present. Appreciable radiations of lineages are recorded in the Late Jurassic, the middle to Late Cretaceous, and the early Tertiary. Five out of nine higher clades that have Tertiary or Recent records are known from the Cretaceous (Benton, 1993). This includes the earliest occurrences of the extant "families" Alligatoridae and Crocodylidae. On the other hand, several crocodilian higher clades (Baurusichidae, Peirosauridae, Hsisosuchidae, Paralligatoridae, and Dolichochampsidae) disappear at or slightly earlier than the K/T boundary. Species-level analysis in the Hell Creek-Tullock Formation section shows that four of the five crocodilian species from the Hell Creek Formation extend into the Paleocene (Archibald, 1996a).

Non-avian dinosaurs. Dinosaurs, long the subject of intense and unabated scientific and popular interest, have in more recent years been the focus of massive systematic revision (e.g., Weishampel et al., 1990; Sereno, 1997). Such studies apply cladistic methods adopted earlier in the case of many other vertebrate groups. In addition, there has been a great surge during the last decade of discoveries of dinosaur fossils worldwide. Both field discoveries and modern systematic treatment allow revisions and refinement of the dinosaur record and a scrutiny of numerous theories on dinosaur evolution (Currie & Padian, 1997).

One evolutionary scenario of particular relevance here is the correlation between the Late Mesozoic radiation of herbivorous hadrosaurs, ankylosaurs, and ceratopsians and the emergence of the angiosperm flora (Weishampel & Norman, 1989). This scenario was derived partly from the observation that Cretaceous tetrapod faunas showed pronounced differences between Northern and Southern Hemispheres. In the north (but primarily the North American record–see comments below) there is an apparent decrease during the Cretaceous of high-browsing sauropods (Weishampel & Norman, 1989) and stegosaurs, but a concomitant increase and diversification of ankylosaurs (Maryánská, 1977; Coombs, 1978), ornithopods (Weishampel & Norman, 1989; Sereno, 1997), and especially ceratopsians. Radiation of the latter began with Psittacosauridae in the Early Cretaceous (Sereno, 1997), and later with protoceratopsids in East Asia and North America (Russell, 1970; Maryánská & Osmólska, 1975) and huge ceratopsians in the latest Cretaceous of North America (Sereno, 1997). In the Southern Hemisphere, sauropods continued to dominate and hadrosaurid ornithopods remained rare throughout the Cretaceous (Bonaparte, 1987). Pachycephalosaurids also appeared in the Early Cretaceous (Maryánská & Osmólska, 1974; Sues & Galton, 1987) and diversified throughout the period, especially in central Asia and western North America (Sereno, 1997).

This increase in relative abundance and diversity of two groups of large herbivores—the hadrosauriid ornithopods and ceratopsid ceratopsians—has been claimed to track the increase in relative abundance and diversity of angiosperms in disturbed areas (Bakker, 1978; Wing & Tiffney, 1987; Weishampel & Norman, 1989). These groups probably foraged in herds, with the effect of considerable harvest on foliage dominated by "weedy" angiosperms. Accordingly, this interaction represents a putative case of coevolution where low-browsing herbivorous dinosaurs set up conditions for favorable selection of weedy foliage, typical of angiosperms (Bakker, 1978). Under this scheme, South American Late Cretaceous plant floras, where high-browsing sauropods continued to flourish, should differ significantly from contemporaneous North American vegetation. Namely, disturbed angiosperm-dominated vegetation should show low abundance and diversity (see discussion in Wing & Sues, 1992). There is some evidence to suggest that the diversification of angiosperms in higher southern latitudes was slower, at least up until Cenomanian times (Drinnan & Crane, 1990). Nonetheless, the correlation between the diversification of low-browsing herbivorous dinosaurs and angiosperms is biased toward the North American record. Indeed, it is difficult to draw the contrast between simply the Northern and Southern Hemispheres. High-browsing sauropods, for example, continued to flourish alongside hadrosaurs and ankylosaurs in the Late Cretaceous in Mongolia and China, where there is also evidence for angiosperm assemblages (Gradzínski et al., 1977; Novacek, 1996). Sauropods, and for that matter hadrosaurs, are very rare, however, in Upper Cretaceous red bed sequences of central Asia that represent semi-arid or desert conditions. Here protoceratopsians and ankylosaurs are found in abundance (Gradzínski et al., 1977; Jerzykiewicz et al., 1993; Novacek et al., 1994). Unfortunately, the rich concentrations of vertebrate fossils in these red-bed facies are not accompanied by adequate concentrations of plants and pollen. One might be forced to the conclusion that a rough correlation between the relative dominance of certain dinosaur taxa and more open-habitat, angiosperm-dominated vegetation typified local conditions and intervals but not necessarily global-scale patterns.

One aspect of the non-avian dinosaur record is of course incontrovertible: there is no unambiguous evidence of dinosaur occurrence in Tertiary sequences anywhere in the world, and dinosaur extinction at the end of the Mesozoic is one of the famous hallmarks of the fossil record. Two issues concerning this record, however, must be considered. First, there is an uneasy reliance on the North American record for calibrating the dinosaur extinction event. Although Late Cretaceous dinosaur faunas are well documented in numerous localities on most continents, latest Cretaceous dinosaurs—namely, occurrences just below the K/T boundary—are virtually confined to localities in western North America (Archibald, 1996a). The only possible exceptions to this isolated record are controversial latest Cretaceous occurrences in China and South America (see Archibald, 1996a). This dearth of global-scale data still leaves open the possibility that dinosaurs may have persisted into the Paleocene, or alternatively may have disappeared before the end of the Cretaceous, in some regions of the world.

A second and related issue concerns the tempo and timing of dinosaur extinction. It is clear that the K/T boundary in North America shows the abrupt termination of notable dinosaurs, such as *Tyrannosaurus* and *Triceratops*, but there is an argument that dinosaur diversity was on the wane for several million years preceding the end of the Cretaceous (see Archibald, 1996a). This is based on documentation of North American assemblages distributed between Judithian and Lancian Land Mammal Ages (75 Ma to 65 Ma), showing a reduction in dinosaur (primarily ceratopsian and hadrosaurid) diversity from 33 genera (Weishampel, 1990) to 19 genera (Archibald & Clemens, 1982). Russell's (1984) counterclaim that Lancian dinosaur diversity was maintained above the level of 30 genera has been disputed by Archibald (1996a) because many of the critical taxa from the Lancian have not received published descriptions, and Russell's rarefaction analysis introduced incorrect assumptions concerning sample sizes. Archibald (1996a: 37) concluded: "This means for the best, and really only well-sampled, latest Cretaceous dinosaur faunas in the world, the fossils themselves reveal a 40% decline in genera of dinosaurs in the waning ten million years of the Cretaceous. The dinosaurs were indeed on a slippery slope of decline long before the K/T boundary."

Despite such a generalization about dinosaur decline, many ambiguities concerning the relevant record persist. Archibald (1977) and others noted a 10-foot gap between the uppermost occurrence of dinosaur bones in the Hell Creek Formation and the K/T pollen shift and iridium layer. In the more southern localities of New Mexico, dinosaur fossils were found three to six feet—and trackways 15 inches—below the layer with iridium concentrations (Pillmore et al., 1994). These observations might be taken to dispute the firm coincidence between dinosaur extinction and the asteroid event. However, Archibald (1996a) noted that the uppermost section of the Hell Creek Formation is generally depauperate in fossil vertebrates, and the apparent gap between the last dinosaur occurrences and the iridium layer could be a function of samples denuded by leaching of bone, low rates of sediment accumulation, and soil development unfavorable to preservation. Other attempts to document dinosaur diversity and distribution through this critical section include work by Sheehan et al. (1991), who claim to record steady numbers of individuals and taxa of dinosaurs through the Hell Creek. This analysis, however, focused on family-level taxa, where the disappearance of genera or species would not be recorded. At the present time, it seems reasonable to claim that there is some indication of decline in dinosaur generic diversity over the last ten million years of the Cretaceous, at least in selected areas of western North America, but finer-scale patterns bearing on dinosaur diversity approaching the K/T boundary are unclear.

Avian dinosaurs (birds). Birds as well as other dinosaurs have enjoyed a recent wave of paleontological discovery and monographic study, resulting in a much improved picture of their early history and phylogeny (Gauthier, 1986; Chiappe, 1992, 1995; Padian & Chiappe, 1998a, b). Although bird specimens from the Mesozoic are still comparatively rare, they include some of the most exquisitely preserved and important fossils from the Mesozoic record. That assemblage includes *Archaeopteryx lithographica* from the Upper Jurassic Solenhofen limestones, still the earliest and most basal member of birds (Padian & Chiappe, 1998a). These spectacular fossils are augmented by skeletons, many of which have been found only in recent years, of a variety of Cretaceous birds. Argentina, Spain, and China have produced the short-winged enantiornithines, which vary from the sparrow-sized *Sinornis* to the turkey vulture-sized *Enantiornis.* Cretaceous sequences of Patagonian Argentina have yielded the flightless *Patagopteryx,* and the Upper Cretaceous of North America preserves skeletons of the flightless loon-like *Hesperornis,* and the tern-sized *Ichthyornis* (Chiappe, 1995). A particularly spectacular addition to this sample is represented by new finely preserved skeletons with feather impressions of both non-avian theropods (*Sinosauropteryx, Protarchaeopteryx*) and birds from the Liaoning Province of China, an assemblage dated as Late Jurassic or Early Cretaceous (Padian & Chiappe, 1998a). Other recent discoveries include the flightless bird *Mononykus* from the Late Cretaceous of Mongolia (Chiappe et al., 1998), a form that shows a suite of features common to both more modern birds and non-avian maniraptoran theropods. Fossil evidence extends to embryos and eggs of the Late Cretaceous form *Gobipteryx* (Elzanowski, 1995) as well as a nestling enantiornithine bird from the Lower Cretaceous of Spain (Sanz et al., 1997).

The dramatic influx of new information on Mesozoic birds does not radically alter a primary aspect of the avian fossil record. The diverse lineages of modern and extant bird lineages are overwhelmingly restricted to the Tertiary (see compilation in Unwin, 1993). The Mesozoic bird groups noted above do much to elucidate the close affinities and transitions between birds and other theropod dinosaurs (though this theory has a few detractors; see Martin, 1991; Tarsitano, 1991; and Feduccia & Wild, 1993), but they cannot be placed within the crown-group (neornithines) that contains all extant birds and their common ancestor. Instead, these Mesozoic stem lineages, primarily the Enantiornithes, *Patagopteryx,* and Ornithurae, fail to survive into the Tertiary (Padian & Chiappe, 1998b). Conversely, few extant higher taxa (orders) of birds, and no extant families, are known from the Cretaceous. The putative Mesozoic candidates include Charadriiformes and Procellariformes from the latest Cretaceous of Wyoming and New Jersey (Olson, 1985), possible neornithines from the Late Cretaceous of Canada (Tokaryk & James, 1989), Gaviiformes from the Late Cretaceous of Antarctica and Chile (Chatterjee, 1989; Olson, 1992), and Anseriformes from the Late Cretaceous of Antarctica (Noriega & Tambussi, 1995). In addition, some fragmentary Cretaceous remains of possible neornithines have been recovered from Europe and Asia (Nessov & Jarkov, 1989, 1992; Hou & Liu, 1984; Kurochkin, 1988). In contrast, the early Tertiary shows abundant, though often fragmentary, evidence of the radiation of modern birds. Virtually all of the 35 or so extant avian orders, with the possible exception of the speciose passeriformes, were present by the Eocene (Unwin, 1993; Feduccia, 1995).

This gap between the ranges of stem Mesozoic birds and modern bird lineages has prompted the view that the latter underwent an explosive radiation over a 5-to-10-million-year period during the early Tertiary (Feduccia, 1995). This pattern suggests a latest Cretaceous demise of more archaic lineages, a subsequent bottleneck in bird diversity, and a dramatic reorganization and diversification of bird lineages a few million years after the Cretaceous extinction event. The origins of extant orders, families, and then genera are claimed to track the temporal cascade often applied to Cenozoic mammals (Feduccia, 1995). Others (e.g., Padian & Chiappe, 1998b) have argued that this is an overinterpretation of a spotty fossil record which may, over time, reveal abundant and unambiguous evidence of Cretaceous neornithines. Moreover, comparisons of gene differences among neornithine bird orders that assume clock-like rates of molecular evolution have been interpreted to indicate a time span of 90–100 million years (Hedges et al., 1996) or even earlier (Cooper & Penny, 1997) for the divergence of these lineages. Thus, both a skepticism concerning the quality of the Cretaceous bird record and a reliance on extrapolations based on gene comparisons might lead one to argue that the radiation of modern birds began in the late Mesozoic and persisted through the K/T extinction event with minimal disruption. An attractive feature of this scenario is the obvious synchrony between divergence of major bird clades and the marked continental fragmentation and isolation that characterized the Cretaceous (Hedges et al., 1996).

Which of these alternative hypotheses for the origin and timing of the modern bird lineages seems more persuasive? One might argue that both the implications of the molecular evidence and the expectations for the fossil record (it always gets better, with revelations of older fossils) provide a strong rationale for a Late Mesozoic radiation of these groups. It is, however, difficult to leap to this conclusion; divergence dates based on assumptions of clock-like rates in genes have been the subject of much skepticism that reflects observations of varying rates among many lineages. With respect to the paleontological data, it is noteworthy that the markedly improved record for Mesozoic birds includes extremely well-preserved fossils of avian stem taxa, but no comparable evidence for modern groups. Many of these stem taxa are small delicate forms, no less vulnerable to damage or loss in preservation than are various neornithines. Furthermore, phylogenetic analysis that might predict an earlier occurrence of some Cenozoic bird lineages based on the known fossil range of their nearest sister taxa (Norell, 1992; Norell & Novacek, 1992) cannot be readily applied here. This is because all the well-represented Mesozoic forms are basal to the more modern lineages, and the relationships among the extant clades are very poorly resolved. The only Cretaceous neornithine forms, as noted above, are fragmentary, and their affinities with particular members of the modern bird orders are not readily identifiable. Thus, although it may be tempting to extend the divergence of more modern lineages well into the Cretaceous, this is not clearly indicated by the fossil record. What is known of that record and the higher-level phylogenetic relationships of birds fails to refute the notion that the explosive radiation of modern bird lineages largely occurred after the K/T extinction event.

Given the above-noted uncertainties in the early fossil record of birds, one might expect that finer-scale patterns across the K/T boundary are even more elusive. Studies of vertebrates in the Cretaceous Hell Creek-Paleocene Tullock sequence included only 30 specimens representing only four bird species (Bryant, 1989). The scanty sample precluded any kind of range analysis comparable to those described for most other terrestrial vertebrate groups in the local section (Archibald & Bryant, 1990). Little with respect to bird distribution during the Late Cretaceous-early Paleocene interval can be ventured except for the observation that the best represented group of Cretaceous birds, the enantiornithines, do not survive the end of the Cretaceous. Extinction of this basal bird group by the end of the Cretaceous is in fact agreed upon by authors who argue for either a Cretaceous (Chiappe, 1995) or a Cenozoic (Feduccia, 1995) radiation of the modern bird lineages.

Mammals. Of all the groups of terrestrial fossil vertebrates, the mammals perhaps offer the most sensitive picture of faunal transitions during the Cretaceous-early Tertiary. While the fossil record for mammals during this interval is inconsistent, it is much enriched and much studied compared to data on other vertebrate groups. Mammals are known from diverse lineages on either side of the K/T boundary (Fig. 7). Apparent patterns of mammalian distribution are not so easily ascribed to biases due to an impoverished record, as they might be for birds, amphibians, or other groups. Moreover, mammals themselves show a dramatic evolutionary reorganization that has been critical to describing and subdividing the whole of the Cenozoic. Finally, it is clear that mammals represent the primary successors to the non-avian dinosaurs as the dominant terrestrial megafauna in the evolving Cenozoic ecosystems.

Stem mammal groups first appear in the fossil record 210 million years ago, during the Late Triassic (see review in Rougier & Novacek, 1998). Diversification during the Jurassic involved several major lineages primarily represented by fragmentary teeth and jaws in isolated localities in Europe, western North America, South Africa, and Asia. By the Early Cretaceous, several basal clades are represented (Stucky & McKenna, 1993; McKenna & Bell, 1997): triconodonts, symmetrodonts, cladotheres (amphitheriids, dryolestids, and other groups), and herbivorous multituberculates, as well as a number of *incertae sedis* taxa (e.g., docodontids). The extant monotremes (duck-billed platypus and echidna) are doubtless very primitive mammals that shared an early history with the many Mesozoic groups. The Cretaceous occurrence of monotremes, however, was not revealed by fossils from Australia until recent years (Archer et al., 1985). Early Cretaceous faunas also include the first allies of the more modern Theria, the group comprising living marsupials and placentals (Kielan-Jaworowska & Dashzeveg, 1989; Cifelli, 1993b). The most intriguing, and controversial, record for an Early Cretaceous therian is claimed for Australia, where a jaw with cheek teeth described as *Ausktribosphenos* is identified as a basal placental mammal (Rich et al., 1997). However, this allocation is widely questioned, as *Ausktribosphenos* seems more likely an archaic mammal with some similarities to the cheek

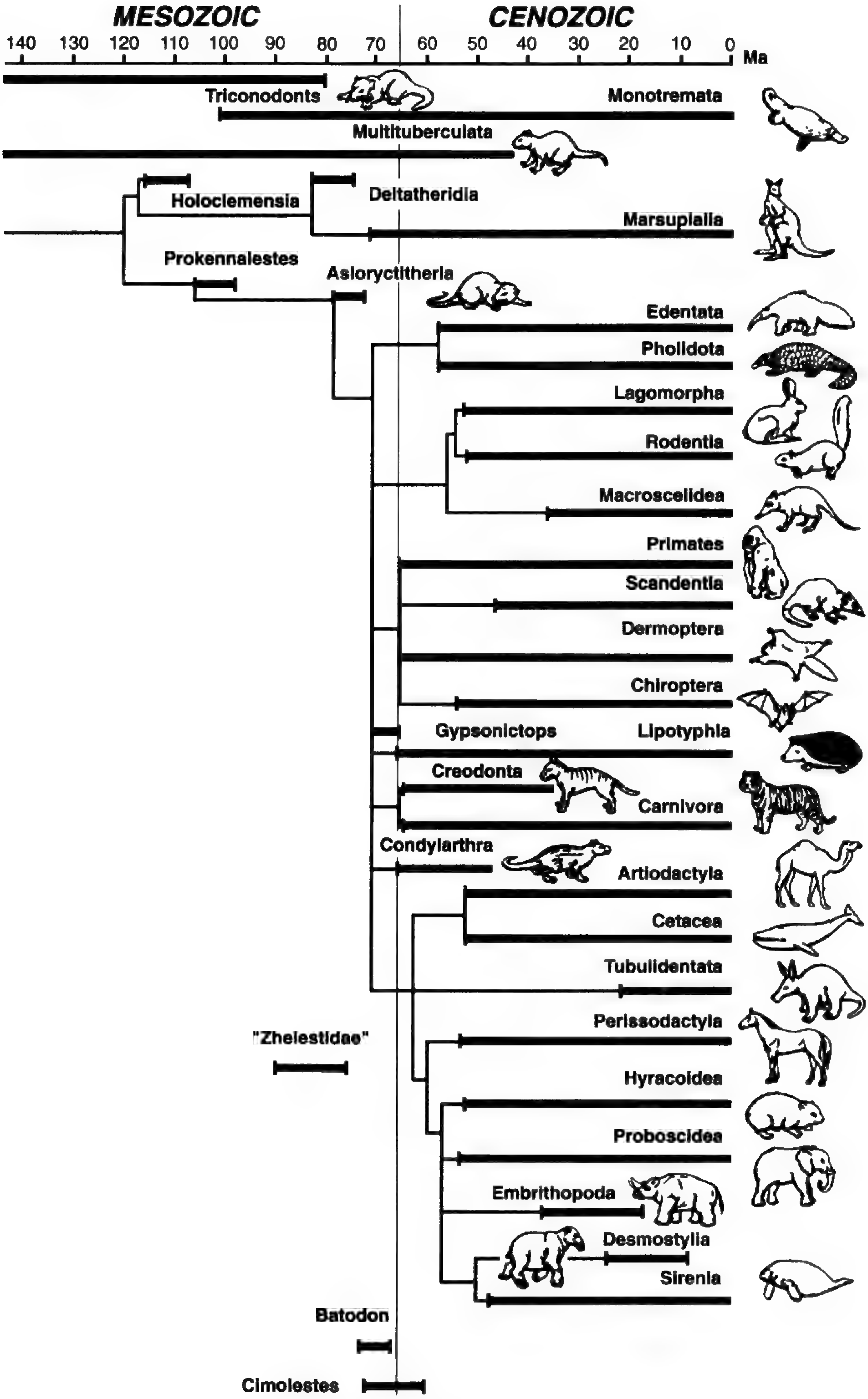

Figure 7. Relationships (thin lines) and geochronological ranges (horizontal bars) for major clades of therians and selected other mammals. Thin lines also depict ghost lineages necessary to calibrate the age of origin of a given taxon based on the known age of its nearest sister taxon. Internodal distances are slightly exaggerated to represent the resolution among clades.

tooth anatomy of more modern placentals (Wuetrich, 1997; Rougier & Novacek, 1998).

Later Cretaceous mammalian faunas mark the appearance of more advanced therians and the diversification of more basal forms such as the multituberculates. Although most of the literature of Late Cretaceous mammals is concentrated on the less complete jaws and teeth representing many taxa from North American sequences (Clemens, 1966, 1973; Clemens & Kielan-Jaworowska, 1979; Lillegraven, 1969; Lillegraven & McKenna, 1986; Fox, 1984; Cifelli, 1990, 1993a; Archibald, 1996a), that record has been greatly enhanced by a dramatic array of complete skeletons and skulls representing Late Cretaceous therians and multituberculates from Mongolia (Gregory & Simpson, 1926; Kielan-Jaworowska, 1974, 1992; Novacek et al., 1994, 1997; Dashzeveg et al., 1995; Rougier et al., 1996, 1997; Rougier & Novacek, 1998). Later Cretaceous faunas from Uzbekistan now are known to include a diversity of zhelestids, mammals known only from rather broad molars that suggest herbivorous habits and possible phylogenetic affinities with the extant ungulate placentals (Archibald, 1996b). Late Cretaceous mammal assemblages from South America are highly endemic, as indicated by *Gondwanatherium* (Bonaparte, 1987, 1990) and other nontherian taxa. Gondwanatheres have recently been discovered in the Cretaceous of Madagascar (Krause et al., 1997).

Mammalian diversity during the Mesozoic reflects a variety of ecological roles. These include insectivorous and carnivorous forms (e.g., symmetrodonts, deltatheridians, and asioryctitheres) as well as the herbivorous multituberculates. The latter show an interesting parallel to the placental order Rodentia in having dentitions suited for fruit and seed eating. Multituberculates lack any affinity with rodents; they also appear some 100 million years before the first occurrence of rodents (Novacek, 1997). Nonetheless, because of their specialized dentitions and skulls, multituberculates are commonly labeled as the ecological equivalent to the rodents. Multituberculates also compare with extant rodents in their relative diversity and abundance in fossil assemblages. A very rich Late Cretaceous assemblage from Mongolia (Dashzeveg et al., 1995) has yielded more than 800 skulls of fossil mammals, of which at least 80% represent several species of multituberculates. This dominance of small herbivorous forms resembles the high proportion of rodent species in many extant habitats that support small mammals (Dashzeveg et al., 1995). The basic trophic organization of Cretaceous small mammal communities thus foreshadowed rodent-dominated communities during the Cenozoic, even though Cretacous communities comprised much fewer species and the transition involved dramatic taxonomic turnover. Various groups of Mesozoic mammals show locomotory specializations relating to burrowing (multituberculates) or even hopping (zalambdalestid therians). Despite this heterogeneity in form and inferred habit, Mesozoic mammals are rather stereotypic for at least one quality: none of them were very large. In fact, the average estimated body mass for 29 species of Late Cretaceous mammals is 150 g, in contrast to the average mass of 1.01 kg for 33 mammal species (27 of them new) occurring only one million years after the K/T event (Alroy, 1998). This extraordinary size increase for mammalian lineages in the Cenozoic has of course been associated with the opportunities that emerged in terrestrial ecosystems in the absence of competition from other large species, such as dinosaurs.

Subsequent to the K/T event, mammals increased not only in terms of body mass but also in diversity. In western North America, mammalian diversity rose from 20 to 45 genera within 250,000 years of the K/T event, and reached 70 genera 2 million years into the Paleocene (Archibald, 1983). The fossil record provides an incontrovertible picture of the early Tertiary radiation of mammals. Nonetheless, a central question concerning this transition remains. Is this radiation largely a phenomenon that post-dates the Mesozoic, or does it extend back to the Late Cretaceous or even earlier times? In the local Cretaceous Hell Creek-Paleocene Tullock sequence, the picture of mammalian survival across the K/T boundary is heterogeneous (Archibald & Bryant, 1990; Archibald, 1996a). Only 9% of the marsupial species survive the K/T event, whereas 50% of the multituberculates and 100% of eutherians (the group that includes the living placental orders) manage to make it through the boundary. This suggests a nascent development of the radiation of at least eutherians back as far as the Late Cretaceous. Other estimates point to even more dramatic Cretaceous diversification of the modern groups. Similar gene studies as applied to birds suggest a window of divergence of 90–100 million years for the major clades (orders) of marsupials and placentals (Hedges et al., 1996; Kumar & Hedges, 1998). Analyses sensitive to phylogenetic relationships and the age of sister taxa also suggest a Cretaceous radiation of the major clades of more modern mammals (Norell, 1992). Complementary evidence comes from the fossils themselves, as forms representing sister taxa to extant marsupials on the one hand and extant placentals on the other are known from Early Cretaceous assemblages (Kielan-Jaworowska & Dashzeveg, 1989; Cifelli, 1993b). Finally, if ungulate affinities of the later Cretaceous zhelestids are accepted, there is even evidence for a subclade of placentals that predates the Cenozoic.

This combination of evidence and assertion fails, however, to firmly establish the greater antiquity of the radiation of the extant therian clades. As in the case of birds, the Mesozoic therians are virtually all stem taxa: they are related to but outside of the crown-groups representing extant marsupials and placentals (Fig. 7). In fact, Cretaceous Mongolian forms like *Kennalestes, Asioryctes,* and *Zalambdalestes,* taxa long thought to be intimately associated with placental insectivorans, are now known to preserve features that suggest their basal position relative to all placentals and their last common ancestor (Novacek et al., 1997). Likewise, well-represented metatherians from the Cretaceous of Mongolia are excluded from the group that includes extant marsupials and their common ancestor (Rougier et al., 1998). As for the Late Cretaceous North American therians, the limited evidence provided by dentitions and isolated teeth frustrates any unambiguous assignment to a modern placental or marsupial clade. There is nothing known about the dental anatomy of these forms that would allow one to claim they were members of either of the two therian crown-groups, even though certain species of these Cretaceous lineages survived the K/T event. The major contradiction here is the Cretaceous Zhelestidae (Archibald, 1996b), but again the limited evidence of dentitions prevents their confident assignment or even close alliance with some placental ungulate clade. Given the dramatically enriched sampling of Cretaceous mammalian faunas (there is no Paleocene mammal assemblage better represented by diverse and abundant skulls and skeletons than the Upper Cretaceous assemblage from Ukhaa Tolgod in Mongolia; see Dashzeveg et al., 1995; Novacek, 1996), it is surprising that bona fide lineages of placentals and marsupials have not yet been discovered. Indeed, here it is more difficult to argue, as in the case of birds, that the Cretaceous record is simply too impoverished to turn up these forms. The available evidence suggests that diversification of the therian clade is rooted in the Cretaceous, but does not refute the more traditional view that the intense pulse of radiation of the more modern placental and marsupial subclades took place in the early Tertiary.

During the early Paleocene, many of the smaller mammal lineages had enlarged, elaborated incisors, canine, and premolars, suggesting diversification and refinement of diets for fruits, seeds, and small prey. More robust forms were squat, heavy-legged creatures such as pantodonts with generalized dentitions suitable for mashing vegetation, but virtually none of these Paleocene mammals were specialized browsers (Stucky, 1990). The Paleocene/Eocene transition shows significant turnover involving the replacement of archaic groups by more modern forms (Rose, 1981, 1984; Stucky, 1990). The more modern herbivores (those with extant members) first occur at the Paleocene/Eocene boundary, including rodents at the end of the Paleocene. Major biotic interchange in the Northern Hemisphere during the early Eocene resulted in marked homogenization of the mammalian faunas (McKenna, 1983; Flynn, 1986). The dominant modern ungulates, the even-toed artiodactyls (camels, hippos, antelope, bovines, and others) and the odd-toed perissodactyls (horses, rhinos, tapirs, and some extinct lineages), appeared in the Northern Hemisphere at the beginning of the Eocene. Diversification of these forms in the early Eocene also involved a trend to larger body size (Rose, 1984; Stucky, 1990).

The highest alpha-level diversity in mammals was reached in the late Paleocene and early-middle Eocene. Thereafter, a decrease in diversity and more dominance of certain keystone species abides. This clumped distribution of species seems characteristic of more open habitats, which expanded during the cooling phase in the later Eocene-early Oligocene interval (Stucky, 1990). The late Eocene shift toward more open savanna-like habitats with plants of lower stature (Wing, 1987) was accompanied by evolution in plant-eating mammal lineages of larger body size, increased lophodonty, emphasis of cursorial features, and a decline in arboreal forms (Webb, 1977; Stucky, 1990; Wing & Sues, 1992). This coincidence in fauna and floral trends suggests coevolution and perhaps a reprise of the dinosaur-angiosperm interdependence in the Cretaceous. More open vegetation caused by increased seasonality certainly favored diversification of large, wide-ranging grazers and browsers. These animals likely reciprocated in maintaining vegetation at levels that favored the diversification and increased abundance of weedy plants, particularly herbaceous angiosperms (Wing & Tiffney, 1987).

Discussion and Conclusions

The foregoing summaries of the vertebrate record, as well as the brief synopsis of related geographic, climatic, floral, and non-vertebrate faunal trends, provide a matrix for a few generalizations concerning the crucial Cretaceous-early Tertiary interval. Clearly this interval is among the best sampled within the Phanerozoic for terrestrial ecosystems, with a picture that is rapidly improving. Nonetheless, several persistent issues, such as those relating to the source and specific impact of Cretaceous extinction, the disparity between fossil occurrences and extrapolations for the time of origin of some key modern groups, and the relationship between local events and global-scale patterns have not been completely resolved by the recent accumulation of fossil data. Below are a few of the principal issues that relate to the evidence reviewed herein.

EARLY CRETACEOUS ORIGINS OF THE MODERN TERRESTRIAL ECOSYSTEM

There seems little doubt that the Early Cretaceous was the crucial time of origin for a terrestrial ecosystem that forecast the environments persisting today. The primary representatives of this dramatic shift are the angiosperms and the insects (especially the pollinating forms). Despite some argument for a lag between these components, their broad coincidence in appearance and diversification seems well established (Grimaldi, 1999), a logical reflection of the ecological interdependence of these components. The question remains as to whether any of the vertebrate groups show changes that reinforce the sweeping transformations indicated by plants and non-vertebrate groups. As summarized above, most vertebrate groups for which an adequate fossil record is available show moderate or marked turnover between the Late Jurassic and Early Cretaceous. Nonetheless, it is difficult to argue that these changes were very different in scope and magnitude from the frequent cycles of turnover throughout the Mesozoic and were directly related to the emergence of an angiosperm-dominated flora. The most notable proposal for a coevolutionary relationship concerns the coincidence of angiosperm diversification and the replacement of high-browsing herbivores (e.g., sauropods) by lower-browsing forms (notably ceratopsians and hadrosaurs) in the Cretaceous (Weishampel & Norman, 1989). The argument depends on the logical inference that low-browsing forms had an impact on vegetation that opened opportunities for weedy and woody foliage typified by angiosperms. The problem with this correlation is its uncertain scope. Although the shift in dinosaur faunal composition is clearly seen in North America, this is not so clearly demonstrated elsewhere. In fact, certain regions, such as central Asia, show a persistence of sauropods combined with less dramatic diversification of ceratopsians throughout the later Cretaceous (Gradzínski et al., 1977; Novacek, 1996). It is then uncertain whether the angiosperm radiation worldwide can be intimately associated with dinosaur transitions recognized in some regions. Part of the problem of course is the lack of an adequate record and sampling of both fossil plants and vertebrates at many of the key Cretaceous localities. Increased emphasis on pollen sampling and study at well-known vertebrate sites would be a contribution here.

Another event that may have coincided with the Early Cretaceous angiosperm radiation was the diversification of several groups of vertebrates, namely, lizards (and snakes), therian mammals, and birds. In this way, the modern ecosystem that emerged and endured the K/T extinction event would have comprised several vertebrate groups as well as flora and non-vertebrate fauna. The appeal of this scenario also stems from the alleged coincidence between the diversification of modern groups (with extant representatives) and the patterns of biogeographic isolation and continental fragmentation that so characterized the Cretaceous (Hedges et al., 1996). The fossil record, however, fails to offer compelling evidence that indicates an Early to middle Cretaceous radiation for these modern groups. Although some advanced lizard groups are known from the Early Cretaceous, the majority of the families are not recorded until the Late Cretaceous. The Mesozoic record for modern groups of birds and mammals is even sketchier. Virtually all the better represented taxa (those preserved as skulls and skeletons) of either group are stem lineages that lie outside their respective crown-groups. The putative Cretaceous candidates for membership within modern lineage of birds are limited and represented by fragmentary evidence (see Padian & Chiappe, 1998b, and comments above). It cannot be distinguished whether many of these forms are actually members within the lineages or are sister taxa to the groups containing the common ancestor of the extant forms. Moreover, the lack of higher-level resolution among the modern bird clades compromises more precise resolution of the affinities of these Cretaceous forms.

These problems echo the situation with mammals, except the evidence for modern placentals and marsupials is perhaps even less certain, being represented largely by fragmentary dentitions from the Late Cretaceous of North America and west-central Asia. Extending groups farther back based on the geometry of their phylogenetic relationships (Norell, 1992; Norell & Novacek, 1992) does not effectively alter the pattern, because, as noted above, Cretaceous taxa formerly thought to belong to the crown-group placentals are now recognized as stem-group taxa (Novacek et al., 1997). Thus, a discrepancy persists between the fossil evidence at hand and an attractive theory for an Early or middle Cretaceous radiation of several modern vertebrate groups. At present, it is realistic to recognize that vertebrates do not show patterns of distribution, relative abundance, and diversity that can be readily matched with the rise of the modern flora in the Cretaceous. The only exception here seems to be the proposed correlation between the angiosperm radiation and the turnover of certain dinosaur taxa, which can only be invoked in some regional situations.

CRETACEOUS-TERTIARY (K/T) EXTINCTION EVENT—TIMING AND BIOTIC IMPACTS

It is now confirmed that a major asteroid impact—as indicated by a marked spike in iridium as well as evidence of major crustal disruption in the Caribbean region—occurred 65 million years ago, at the time of the end of the Cretaceous extinction event. Moreover, it is widely believed that the impact of the bolide, drastic devastation of some of the fauna and flora, and subsequent appearance of successional vegetation were causally related, at least in the case of the record from western North America (Wing & Sues, 1992). We must nonetheless recognize the geographic limitations of the evidence for terrestrial vertebrate faunal change at the K/T boundary. As noted above, the only definitive latest Cretaceous-earliest Tertiary interval for terrestrial vertebrates is confined to western North America (Archibald, 1996a). Patterns outside this region for turnover at lower taxonomic levels are highly uncertain. Indeed, one cannot even confidently assert that non-avian dinosaurs failed to survive the K/T extinction event, at least for a very brief interval, outside western North America. In this regard, it is noteworthy that the taxonomic composition of certain floras outside North America are not drastically transformed from the Late Cretaceous to the Paleocene (Saito et al., 1986; Raine, 1988; Askin, 1988; and discussion above). Over a broader interval, of course, the absence of dinosaurs in Paleocene faunas worldwide is readily demonstrable.

Despite the magnitude of the Cretaceous-Tertiary (K/T) extinction event and its obvious impacts on non-avian dinosaurs, the extinction of vertebrates across the K/T boundary is strikingly selective. Indeed it is the marine and not the terrestrial record that shows a comprehensive level of biotic transformation (e.g., see Smith & Jeffrey, 1998). Recent compilations (Archibald & Bryant, 1990; Archibald, 1996a) show that just five groups—sharks and their relatives, marsupials, lizards, and non-avian dinosaurs—suffered complete or more than 75% species extinction in the local section represented by the uppermost Cretaceous Hell Creek Formation and the lowermost Paleocene Tullock Formation in Montana. In contrast, species survival of actinopterygians (ray-finned fishes), multituberculate mammals, eutherian mammals, turtles, champsosaurs, and crocodiles across the K/T boundary ranges between 50 and 100%. Despite the strong evidence for extraterrestrial impact coincident with the K/T extinction event, these heterogeneous extinction patterns still elude satisfactory explanation (see Archibald, 1996a).

When we move beyond the fine-scale documentation unique to sections in North America, we can still recognize a striking mosaic of extinction and survival for higher-vertebrate taxa. The above summary and update of relevant records, clearly show that as many as 13 modern lizard families appearing in the Cretaceous survived across the K/T boundary. Other such enduring taxa include acinpenserids (sturgeons), polyodontids (paddlefish), lepisosteids (gars), amiids (bowfins), neoceratodontids, latimeriids, lepidosirenids, discoglossid frogs, many turtle lineages (Chelydridae, Pelomedusiidae, Trionychidae, Cheloniidae, and Carettochelydae first occur in the Cretaceous but several surviving groups date back earlier), champsosaurs, alligatorids and crocodylids, multituberculate mammals, and selected therian mammal groups.

This impressive list of survivors of course has one exception. Dinosaurs, including a number of Cretaceous bird lineages (Padian & Chiappe, 1998b), remain the higher-level terrestrial vertebrate taxon most affected by K/T extinction. Theories for this distinction are many and varied (see Archibald, 1996a). The large size of many dinosaur taxa does not explain their particular vulnerability, as the K/T boundary marks the termination of many of the smaller and more gracile dinosaurs as well as their robust relatives. Conversely, turtles, crocodilians, and other survivors include some very large taxa. Perhaps the traumatic climatic/environmental shifts that marked the end of the Cretaceous, and had a direct and detrimental affect on vegetation, also had severe impacts on large herbivorous tetrapods. In turn, the devastation of the herbivorous megafauna could have had reverberations that affected all dinosaurs, including smaller predaceous forms. On the other hand, periods of climatic deterioration may not necessarily lead to such a cascade of events; vegetation changes might even favor large herbivores, depending on the nature of the succeeding flora (Wing & Sues, 1992). The environmental changes caused by a single event, such as a bolide impact, would have to be sudden and intense in order to have such sweeping effects over a range of taxa and trophic levels. Still, the logical argument that such events were catastrophic and sudden sits oddly with a fossil record that shows the persistence of so many terrestrial groups across the K/T boundary.

EMERGENCE OF THE TERTIARY TERRESTRIAL MEGAFAUNA

The mosaic of extinction and survival that marked the Cretaceous-Tertiary transition has a quality that does suggest reorganization of the ecosystem. Dinosaurs represented most of the large terrestrial vertebrates during the Mesozoic, and their disappearance left a vacuum of size and trophic types that was not filled for a remarkably long time. Despite the rapid diversification of mammal taxa (Archibald, 1983) and the extraordinary increase in the size of many lineages (Alroy, 1998) during the Paleocene, mammals did not match the ecological range or the average body size of a herbivorous megafauna represented by the dinosaurs. For example, it has been noted that from the beginning of the Paleocene until the mid Cenozoic there were no high-browsing herbivores. Such forms, above 2 m in height, did not appear before the Oligocene, leaving a trophic gap of some 30 million years (see also comments in Wing & Sues, 1992). The influence of large browsing herbivores is evident in terms of their less discriminating feeding habits and greater potential alteration of the habitat (Peters, 1983; Crawley, 1983). Such a trophic impact could easily favor thorns, compensatory growth, and chemicals for defense of the assaulted vegetation. The coevolutionary relationships between the flora and the herbivorous megafauna may have set in motion conditions that stimulated the spread of grasslands and savannas in ways that augmented the effects of climate change in the Oligocene and later. This pattern of interdependence and ecosystem modification echoes that proposed for the radiations of browsing herbivorous dinosaurs and angiosperm-dominated flora in the Cretaceous. Authors (e.g., Webb & Opdyke, 1995) have also strongly emphasized the close relationship between climatic change, ecosystem disruption, and rapid pulses of turnover in the Cenozoic mammal fauna.

There remains the whole question of opportunity for diversification of both taxa and their adaptations in the wake of the K/T extinction event. It is most popular here to suggest that the empty adaptive zones at the beginning of the Paleocene afforded such opportunities (Van Valen, 1978; Erwin et al., 1987). The emergence of many mammalian lineages with dentitions specialized for granivory and frugivory presumably opened up a great range of food sources and in turn provided a relatively new means of vertebrate-mediated dispersal of seeds and fruits so critical today in tropical rainforests (Tiffney, 1986). Still it is important to emphasize that during much of the Paleocene these explosive radiations were represented by mammals of comparatively small size. Indeed the diversity of dental, cranial, and skeletal specializations in Cretaceous mammals has been underemphasized, as have the potential adaptive opportunities for these creatures in Mesozoic terrestrial ecosystems. The easiest adaptive opportunity to characterize, namely, that for large, browsing herbivores, remained vacant for an appreciable period of some millions of years after the end of the Cretaceous, and persistently vacant for the largest body sizes. If these adaptive opportunities, these empty adaptive zones, were so readily available, why were their occupants so long in coming? The reasons for this lag in exploitation, as well as explanations for many other fascinating patterns that characterize the Cretaceous-Tertiary transition, remain elusive.

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EARLY ANGIOSPERM DIVERSIFICATION: THE DIVERSITY OF POLLEN ASSOCIATED WITH ANGIOSPERM REPRODUCTIVE STRUCTURES IN EARLY CRETACEOUS FLORAS FROM PORTUGAL[1]

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ABSTRACT

Studies of five mesofossil floras from the Early Cretaceous (Barremian or Aptian?) of Portugal document a previously unrecognized diversity of angiosperms exceeding that currently known from other localities of this age. At the Famalicão, Vale de Agua, and Buarcos localities angiosperms are represented by about 100 different kinds of flowers, fruits, seeds, and stamens. At the other two localities (Torres Vedras and Catefica) angiosperm diversity is lower but still significant. At each of the five localities between 7 and 26 types of angiosperm pollen have been recognized based on pollen grains in situ within anthers, or on stigmatic or fruit surfaces. Monocolpate, dicolpate, periporate, and tricolpate angiosperm pollen have been recognized, but in all cases monocolpate grains, of probable magnoliid or monocotyledonous affinity, are the most diverse element. The diversity of angiosperm pollen in situ, or associated with other angiosperm reproductive structures, is greater than that of the dispersed palynoflora from the same localities. The diversity and abundance of angiosperms in the Portuguese mesofloras contrast strongly with the apparent paucity of angiosperm pollen in dispersed palynofloras, as well as the scarcity of angiosperm wood and leaves in Barremian-Aptian fossil plant assemblages. This discrepancy may reflect the widespread occurrence of both insect pollination and herbaceous habit among the angiosperms in the initial phases of their Early Cretaceous diversification.

Numerous fossil floras of Cretaceous age that comprise three-dimensionally preserved angiosperm flowers, fruits, seeds, and dispersed stamens have been discovered within the past 15 to 20 years. These floras are particularly abundant in Upper Cretaceous sediments and have been reported from widely separate geographic regions in the Northern Hemisphere. The first comprehensive studies were based on European material, and rich Late Cretaceous floras are known from Cenomanian to Maastrichtian strata of the Czech Republic, Germany, Austria, the Netherlands, Portugal, and Sweden (Friis & Skarby, 1981, 1982; Friis, 1983, 1984; Knobloch & Mai, 1984; Friis, 1985a, b; Knobloch & Mai, 1986; Friis et al., 1988; Friis & Crane, 1989; Friis, 1990; Knobloch & Mai, 1991; Friis et al., 1992; Eklund et al., 1997; Eklund & Kvaček, 1998). In North America, similarly rich Late Cretaceous floras are known from Cenomanian to Campanian strata of Massachusetts, Maryland, New Jersey, North Carolina, and Georgia (Friis, 1988; Friis et al., 1988; Drinnan et al., 1990, 1991; Herendeen, 1991; Herendeen et al., 1993; Nixon & Crepet, 1993; Crepet & Nixon, 1994; Herendeen et al., 1994; Crane & Herendeen, 1996; Frumin & Friis, 1996; Magallón-Puebla et al., 1996, 1997). In Asia, fossil flowers and fruits have been reported from Coniacian to Campanian strata of Japan (e.g., Nishida & Nishida, 1988; Nishida, 1994; Nishida et al., 1996) and have recently been discovered from Cenomanian-Turonian strata of Kazakhstan (Frumin & Friis, 1996, 1999). The angiosperms recovered in

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these Late Cretaceous floras exhibit great taxonomic diversity and document the presence of many major angiosperm lineages at the ordinal and family level (Magallón-Puebla et al., 1999, this issue).

From the Early Cretaceous, well-preserved floras with flowers, fruits, seeds, and stamens are known from North America (the Potomac Group sequence) and from Portugal. From the Potomac Group, the best preserved and most diverse floras are from the late Aptian-Albian (Friis et al., 1986, 1988; Drinnan et al., 1991; Crane et al., 1994; Friis et al., 1994a; Pedersen et al., 1994b; Friis et al., 1995; Crane & Herendeen, 1996; Friis et al., 1997a). From Portugal, rich floras with angiosperm reproductive organs have been discovered in the Western Portuguese Basin, and the most important localities are in the area around Torres Vedras and the Runa Basin, the vicinity of Cós-Juncal-Leiria, and the area around Buarcos-Tavarede (Friis et al., 1994b; Pedersen et al., 1994a; Friis et al., 1997a, b). The Portuguese floras are thought to be of Barremian or possibly Aptian age and contain the most diverse assemblages of early angiosperms currently known.

The earliest angiosperm remains that can be recognized reliably in the fossil record are dispersed pollen grains in palynofloras of Early Cretaceous age (Valanginian-Hauterivian). In these earliest Cretaceous palynofloras angiosperm pollen is rare but occurs over a large area that includes Israel, Italy, and southern England. From the Valanginian of Italy monoaperturate angiosperm pollen with reticulate-columellate wall structure was reported but not illustrated from a sequence dated partly by marine dinoflagellate cysts (Trevisan, 1988). Trevisan (1988) noted considerable morphological diversity among these Valanginian grains. Angiosperm pollen is also present, but extremely rare, in late Valanginian to early Hauterivian strata of Israel where it comprises less than 2‰ of the total palynomorph assemblage (Brenner, 1984; Brenner & Bickoff, 1992; Brenner, 1996). In palynofloras from the Hauterivian of southern England, angiosperm pollen grains are also rare but show a considerable diversity in the form of the reticulum and the ornamentation of the tectum. Hughes (1994) illustrated more than 10 different dispersed monoaperturate pollen taxa from this time interval, each typically represented by a few specimens only. In Barremian and younger palynofloras there is a marked increase in diversity and abundance of dispersed angiosperm pollen, and tricolpate pollen is first reported from this time interval.

In this paper we discuss the angiosperm component of five Early Cretaceous (Barremian or Aptian?) fossil floras from Portugal that contain flowers, fruits, seeds, and stamens. We focus particularly on documenting the diversity of angiosperm pollen grains found in situ in stamens, within flowers adhering to the stigmatic or fruit surfaces of carpels, or on dispersed fruits. We show that the diversity of fossil pollen assessed in this way is higher than the diversity of angiosperm pollen taxa currently recognized in mid-Cretaceous dispersed palynofloras.

MATERIAL AND METHODS

The five floras discussed in this work include the Torres Vedras flora (northeast of Forte da Forca), the Catefica flora, the Vale de Agua flora, the Famalicão flora, and the Buarcos flora. The effort expended so far in studying each of these floras is about equivalent and therefore the quantitative estimates of their composition provided below are broadly comparable.

The Torres Vedras flora was collected in 1989 (KRP, EMF, PRC) and in 1990, 1992, 1994, and 1995 (KRP, EMF) from a large clay pit northeast of Torres Vedras, about 1 km northeast of Forte da Forca on the road toward Sarge (39°06′13″N, 9°14′47″W, Carta Geológica de Portugal Torres Vedras 30C, Zbyszewski et al., 1955). The sediments exposed in the clay pit include light yellowish and purple silts and clays, as well as grayish clays, silts, and sands with horizons of coalified material. The angiosperm component is less diverse in the Torres Vedras flora than in the other Portuguese floras, but some samples are distinctive in containing many angiosperm stamens.

The Catefica flora was collected in 1989 (KRP, EMF, PRC) and in 1992, 1994, and 1995 (KRP, EMF) in a road cut close to the village of Catefica, about 4 km south of Torres Vedras (39°3′30″N, 9°14′30″W, Carta Geológica de Portugal 30-D Alenquer, Zbyszewski & Torre de Assunção, 1965). The Cretaceous strata at Catefica are deposited close to the western margin of the Runa Basin (cf. Rey, 1972) and consist of crossbedded sands with intercalated clay beds and darker organic-rich horizons. The fossil flora extracted from these fluviatile sediments comprises several angiosperm flowers, fruits, and seeds as well as stamens with pollen in situ, cheirolepidiaceous twigs (*Pseudofrenelopsis* Nathorst), a variety of ferns, selaginellaceous shoots, and numerous fragments of thalloid liverworts.

The Vale de Agua flora was collected in 1989 (KRP, EMF, PRC), in 1992 and 1994 (KRP, EMF), and in 1997 (KRP) in a large complex of clay pits close to the small village of Vale de Agua, and about 5 km southwest of Batalha (39°37′15″N, 8°51′30″W, Carta Geológica de Portugal 27-A Vila Nova de Ourém, Zbyszewski et al., 1974). The sediments are predominantly gray, reddish, or greenish clays belonging to the "Complexos gresosos de Nazaré e de Cós-Juncal." The flora includes numerous angiosperm flowers, fruits, seeds, and dispersed stamens, as well as many twigs and cones of cheirolepidiaceous plants. In situ angiosperm pollen grains have been observed in many of the flowers and dispersed stamens.

The Famalicão flora was collected in 1989 (KRP, EMF, PRC) in the outskirts of the small village of Famalicão, about 5 km SSE of Leiria (39°42′16″N, 8°46′12″W, Carta Geológica de Portugal 23-C Leiria, Teixeira et al., 1968). The plant-bearing horizon was a thin gray and organic-rich clay discovered in the basal part of the pit. The deeper part of the clay pit is now infilled, and the plant-bearing horizon no longer accessible for collecting. The flora includes diverse and numerous angiosperm flowers, fruits, and seeds, as well as some dispersed stamens. Compared to the other Portuguese floras, remains of cheirolepidiaceous plants are rare.

The Buarcos flora was collected in 1992, 1994, and 1995 (KRP, EMF) in the town of Buarcos north of Figueira da Foz (40°09′54″N, 8°52′11″W, Carta Geológica de Portugal 19C Figueira da Foz, Rocha et al., 1981). The plant-bearing sediments are coarse, crossbedded sands with intercalated layers of silt and clay and belong to the "Arenitos de Carrascal" complex. The flora includes a rich assemblage of angiosperm flowers, fruits, seeds, and anthers, as well as many twigs of cheirolepidiaceous plants. Palynological analysis of a clay sample from the same exposure tentatively indicated a Barremian-Aptian age (Pais & Reyre, 1981). The rich Early Cretaceous leaf flora of Buarcos described by Saporta (1894) and Teixeira (1948) was collected at another site and is perhaps not contemporaneous with the mesoflora described here. The leaf flora contains a diversity of angiosperm leaves in addition to ferns and conifers and is one of the richest angiosperm macrofloras from the Early Cretaceous.

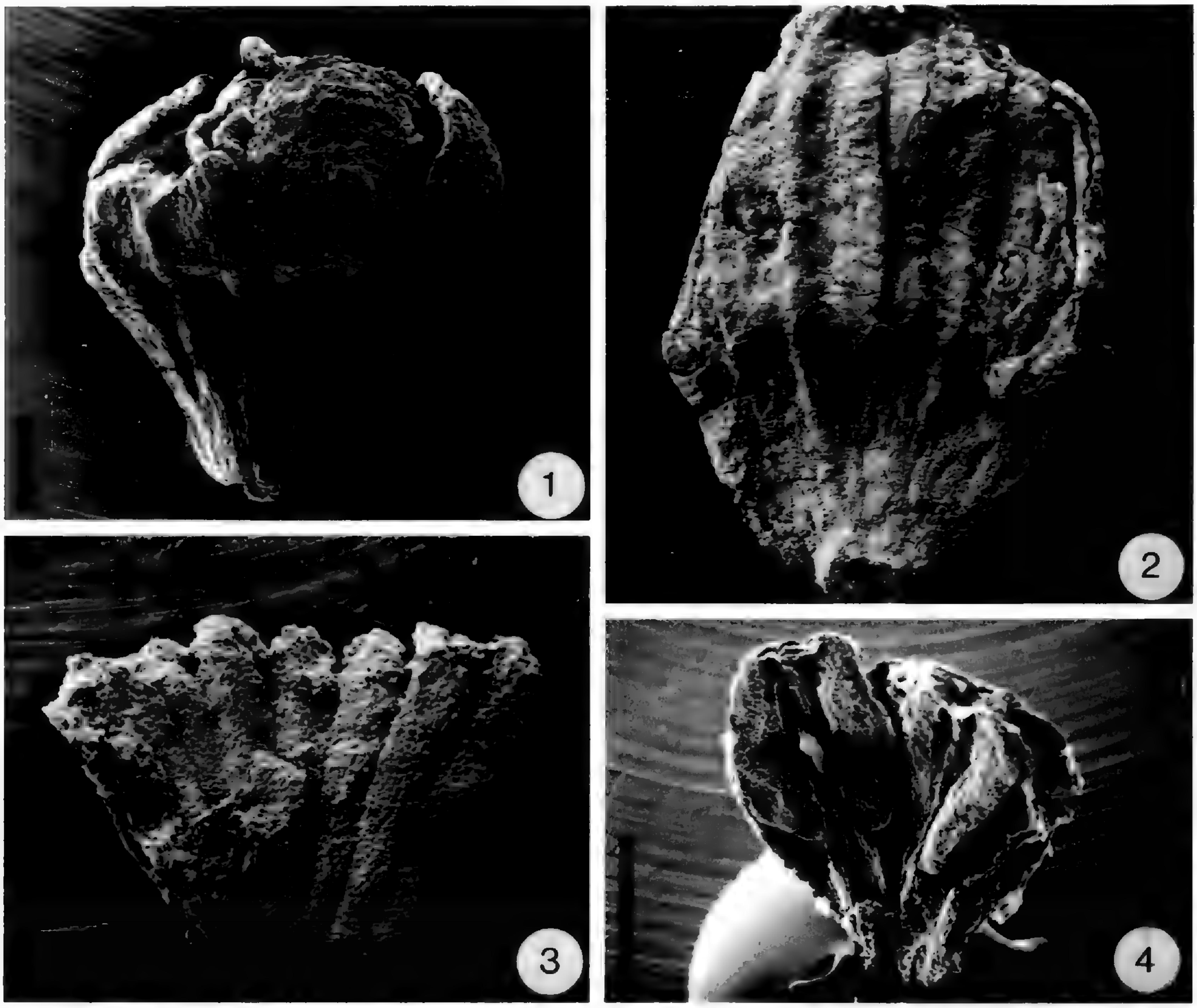
The five mesofloras have many taxa in common indicating that they are probably more or less contemporaneous, and in all cases the fossils occur in terrestrial sediments of lacustrine or fluviatile origin. Marine control is generally absent and the dating of these terrestrial plant assemblages is problematic, but the age of the five mesofossil floras considered here is thought to be Barremian or possibly Aptian (Friis et al., 1997a). Detailed geological mapping is available for the Estremadura region including the Torres Vedras-Runa area (Rey, 1972, 1979, 1982). According to Rey (1972), the strata northeast of Forte da Forca that yield the Torres Vedras flora are Valanginian to early Barremian in age (Valanginian-Hauterivian at the collection site for the Torres Vedras flora). No Aptian strata were indicated for this area. The strata south of Catefica, where the Catefica flora was collected, are Hauterivian-early Barremian (Rey, 1972). The presence of several different types of tricolpate pollen in the Torres Vedras flora and in some of the other floras may indicate a slightly younger age than is suggested by the geological data, but tricolpate pollen grains are known from Barremian strata in England (Hughes & McDougall, 1990; Penny, 1991), and it is possible that the tricolpate grains in the Portuguese floras are also pre-Aptian. Palynological analyses of samples from the Buarcos site tentatively indicate a Barremian-Aptian age (Pais & Reyre, 1981). Most of the in situ pollen discovered in the Portuguese floras are monoaperturate, and many are comparable to forms reported from the Hauterivian, Barremian, or Aptian, and sometimes also from the Albian and Cenomanian in other areas, but there are also many angiosperm pollen types that apparently have not been described from dispersed palynofloras.

The fossil fruits, seeds, and stamens in all five floras are typically preserved as three-dimensional charcoal fossils or as slightly compressed lignite fossils. They were extracted from the sediment samples and prepared for scanning and transmission electron microscopy (SEM and TEM) using standard methods as described by Friis et al. (1988). The specimens were studied using a Philips SEM 515 scanning electron microscope and a Jeol-100S transmission electron microscope. Specimens described in this work are stored in the Palaeobotanical Department of the Swedish Museum of Natural History, Stockholm (S).

Results

DIVERSITY IN REPRODUCTIVE ORGANS

Among the five Early Cretaceous assemblages discussed here the angiosperm component of the Famalicão flora is by far the most diverse and includes many thousands of specimens representing at least 105 different types of angiosperm flowers, fruits, and seeds. Pollen grains occur in situ in flowers and dispersed stamens, and also adhering to the carpels. So far, 13 different angiosperm pollen types have been recognized. Associated with the angiosperm reproductive organs are about 15 different types of gymnospermous seed, which are probably of cheirolepidiaceous and gnetalean affin-



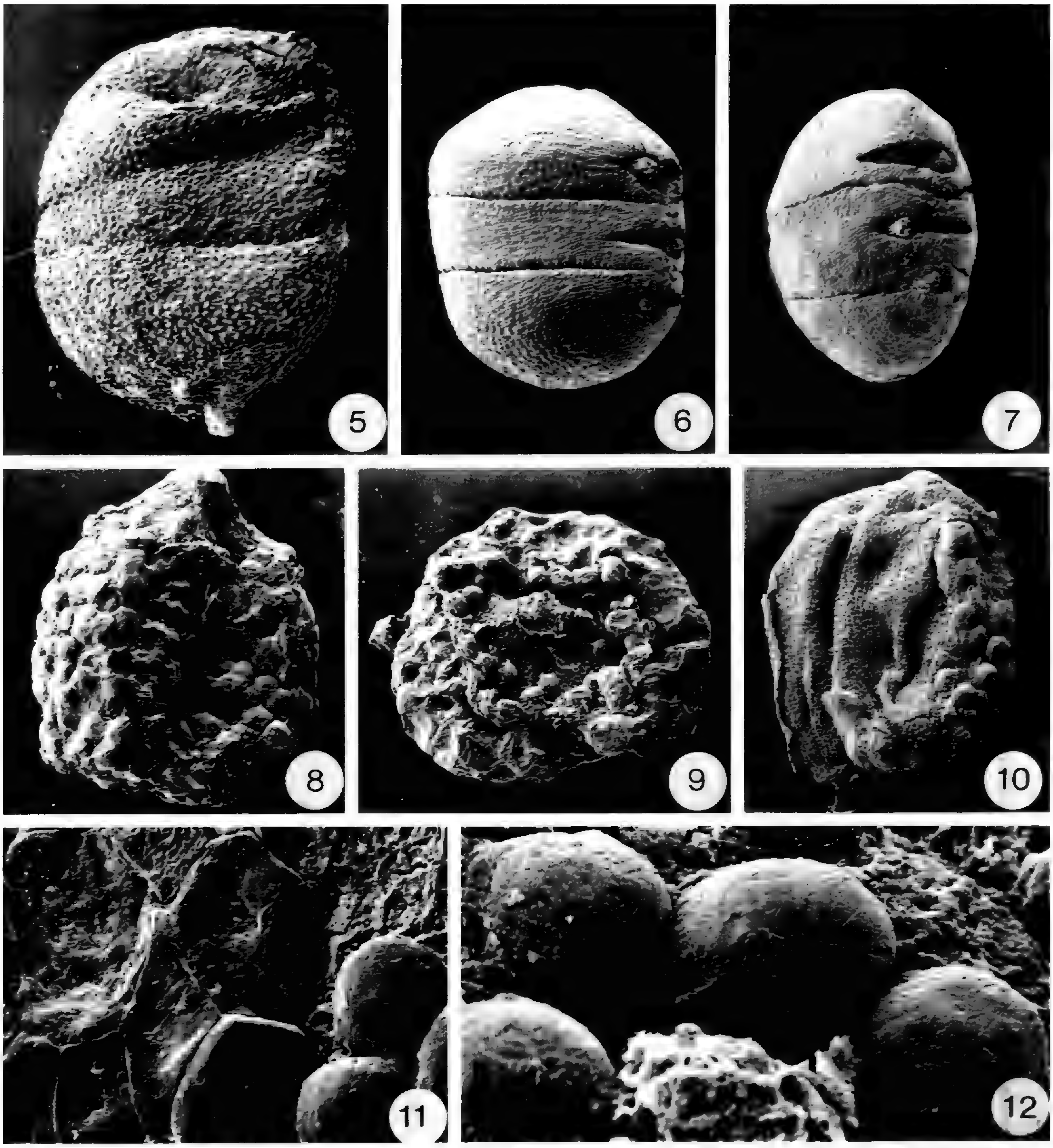
Figures 1–4. Scanning electron micrographs of angiosperm flowers and stamens from the Early Cretaceous (Barremian or Aptian?) of western Portugal. —1. Epigynous flower from the Catefica flora (sample 49), S100757, ×40; scale equal to 250 μm. —2. Epigynous flower from the Famalicão flora (sample 25), S105906, ×40; scale shown in Figure 1. —3. Several stamens from a possible chloranthaceous staminate inflorescence from the Torres Vedras flora (sample 44), S105015, ×60; scale equal to 250 μm. —4. Fragment of a small flower with two complete stamens from the Buarcos flora (sample 209), S101739, ×70; scale equal to 250 μm.

ity. The sample also contains many twigs of cheirolepidiaceous plants. All stamens and anthers discovered so far in the Famalicão flora, and many of the flowers, fruits, and seeds, have been studied preliminarily using SEM. However, there are still many taxa that have not been studied in detail, and it is likely that the diversity of angiosperm reproductive organs and pollen in situ will increase as our studies progress.

The fossil floras from Vale de Agua, Catefica, and Torres Vedras are less diverse than that from Famalicão, and most of the angiosperm flowers, fruits, and seeds recorded are also present in the Famalicão flora. The Buarcos flora also shares many taxa with that from Famalicão, but it is distinct from the other four fossil assemblages in having a higher percentage of unique taxa.

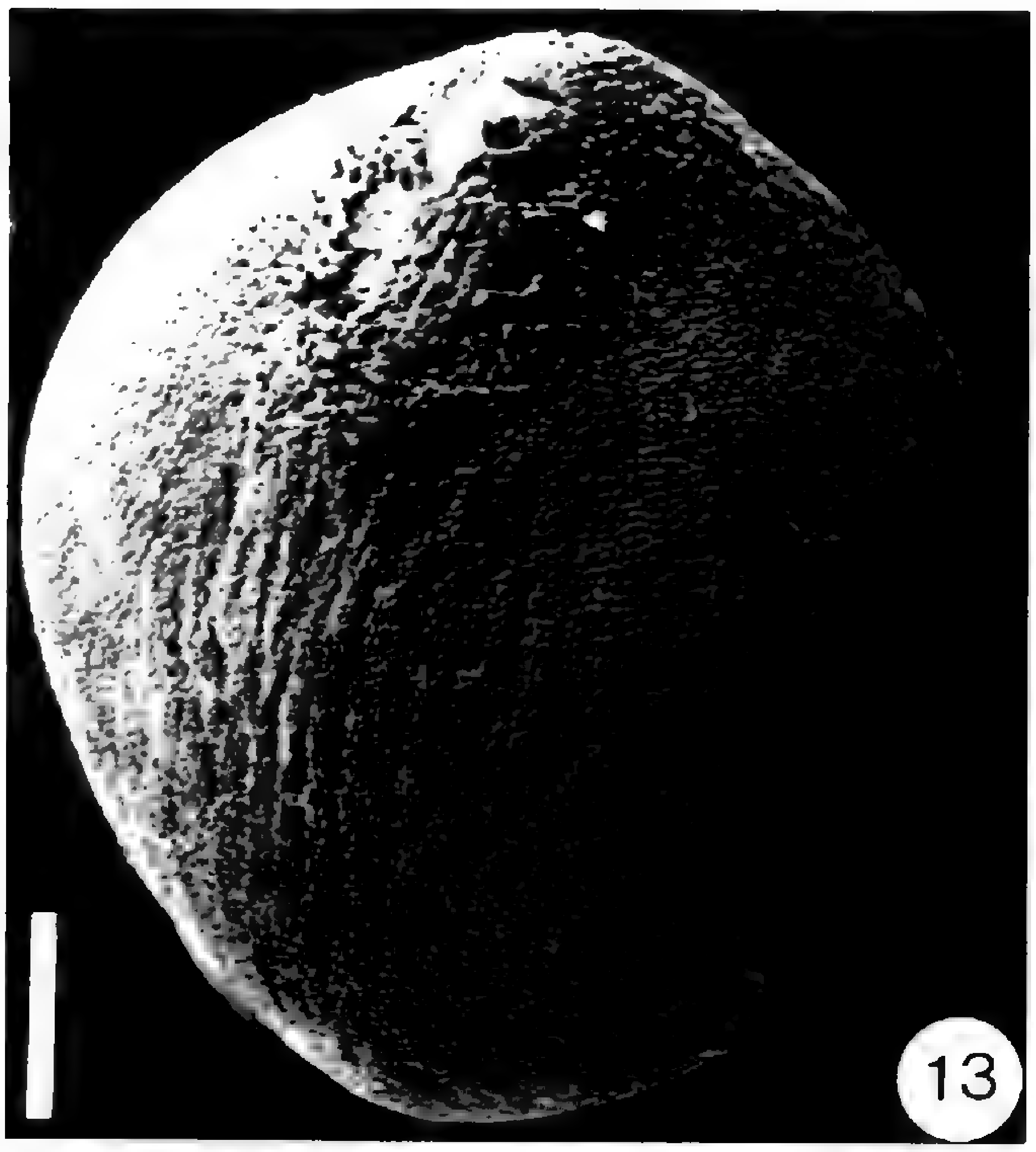
All of the angiosperm taxa represented by reproductive organs, and probably most of the non-angiospermous seed-plant taxa recorded in the Portuguese floras, appear to be new to science, and formal descriptions and comparison with extant angiosperms are still in progress. The angiosperm component in the floras consists mostly of fruits and seeds, but there are also several flowers and dispersed stamens. Some of this material has been figured in previous studies (Friis et al., 1994b, 1997a, b). Our main focus here is on the diversity of pollen in situ, but we also illustrate a small selection of flowers, fruits, and seeds that have not been published previously to indicate the quality of preservation and diversity of the angiosperm reproductive structures in these assemblages (Figs. 1–29).

Flowers. Many of the taxa in the Portuguese floras show character combinations that indicate a



Figures 5–12. Scanning electron micrographs of angiosperm fruits and seeds from the Early Cretaceous (Barremian or Aptian?) Famalicão flora (sample 25), western Portugal. 5–7. Fruit with tightly co-adhering exotestal seeds. —5. Fruit showing thin fruit wall and several seeds, S105130, ×35; scale equal to 500 μm. —6. Oblique lateral view of three co-adhering seeds from a single fruit, S105154, ×35; scale shown in Figure 5. —7. Apical view of three co-adhering seeds from a single fruit showing slit in outer integument and projecting inner integument that forms the micropyle, S105155, ×35; scale shown in Figure 5. 8–12. Fruit with abundant resin bodies in the fruit wall. —8. Lateral view of fruit showing thin fruit wall and prominent resin bodies, S105187, ×50; scale equal to 250 μm. —9. Apical view of fruit showing stigmatic area, S105184, ×50; scale shown in Figure 8. —10. Fruit with most of fruit wall and resin bodies abraded showing two seeds, S105191, ×50; scale shown in Figure 8. —11, 12. Details of fruit wall showing polygonal epidermal cells and spherical resin bodies in fruit wall. 11: S105188, ×250; scale equal to 40 μm.; 12: S105186, ×400; scale equal to 25 μm.

magnoliid or perhaps monocotyledonous affinity. There are several distinct flower types in the Portuguese floras (Friis et al., 1994b). Some are represented by a single specimen, others are more abundant and occur in more than one flora. One of the more abundant types includes small epigynous, bisexual flowers with one whorl of triangular leathery tepals and perhaps two whorls of stout stamens (Figs. 1, 2; flowers with pollen types A.1 and A.2, Figs. 30–38). The stamens have anthers with val-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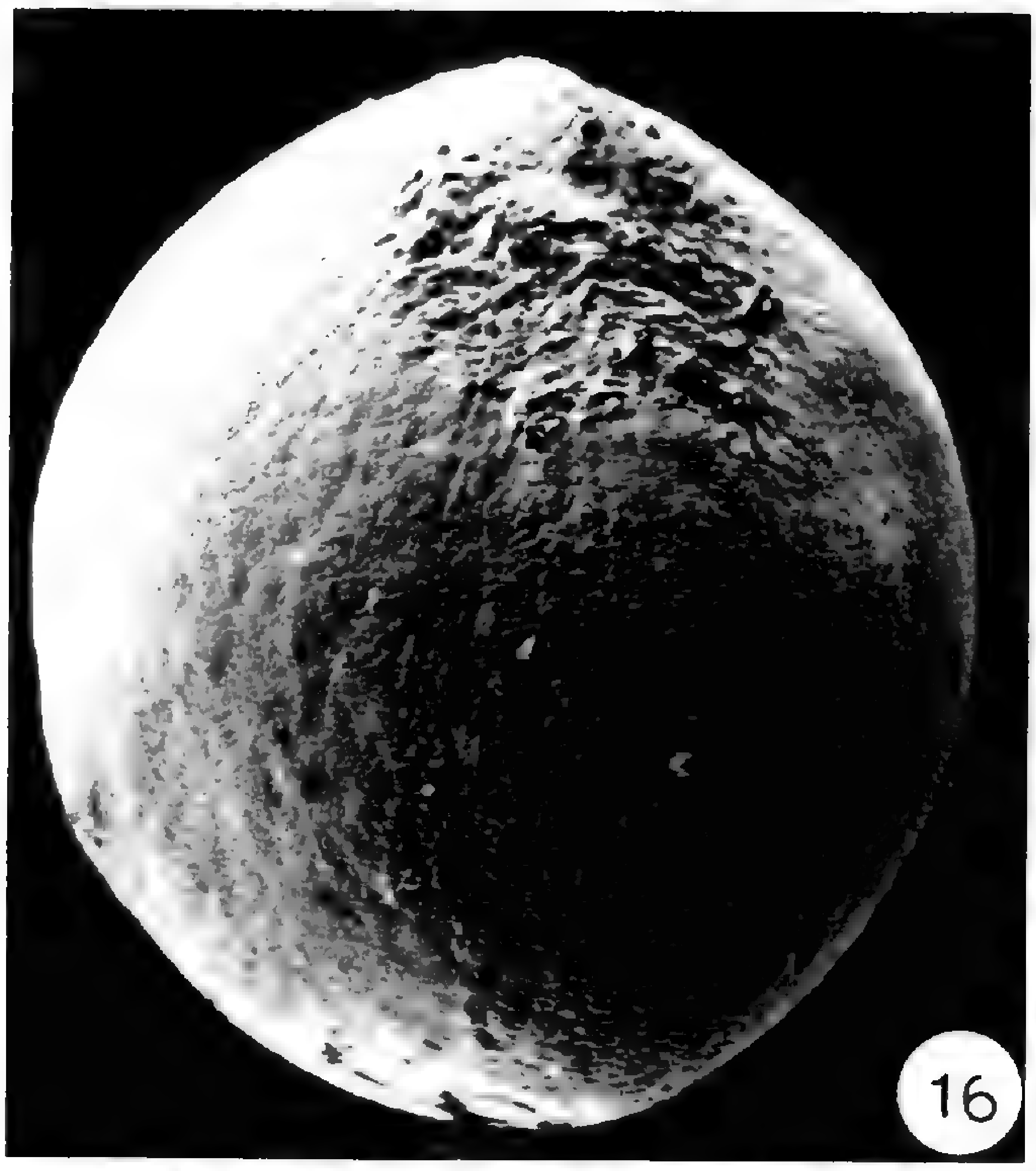
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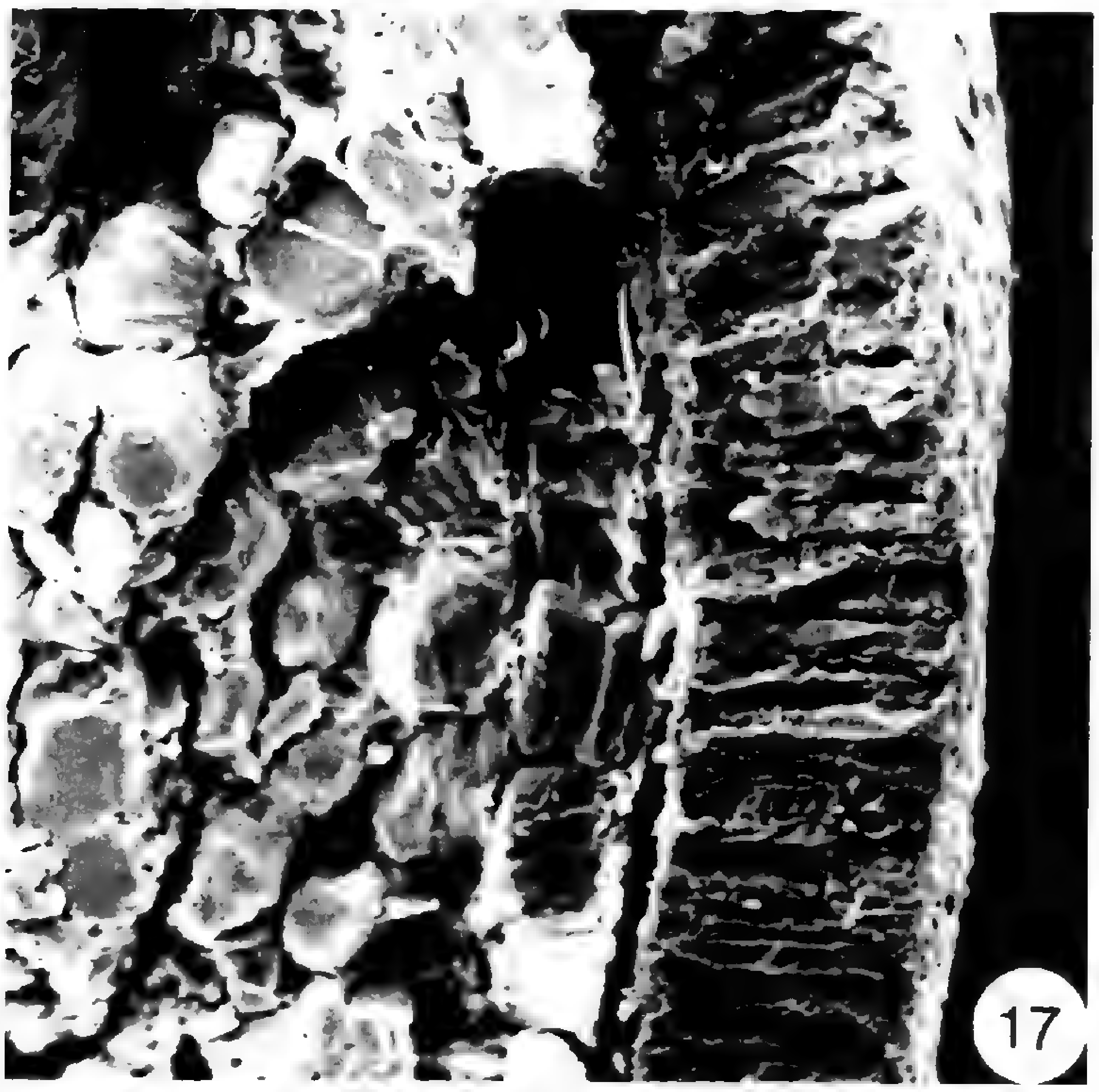
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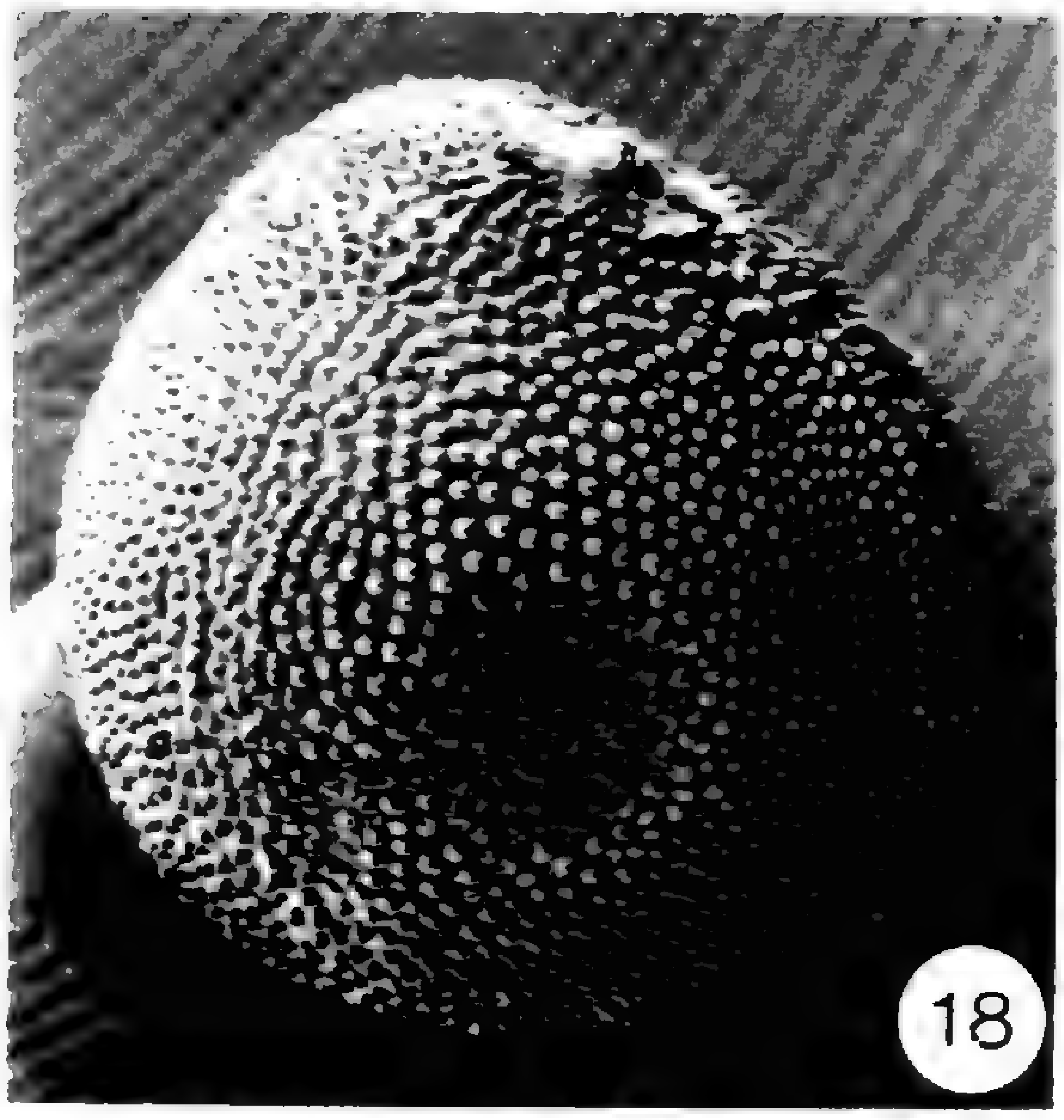
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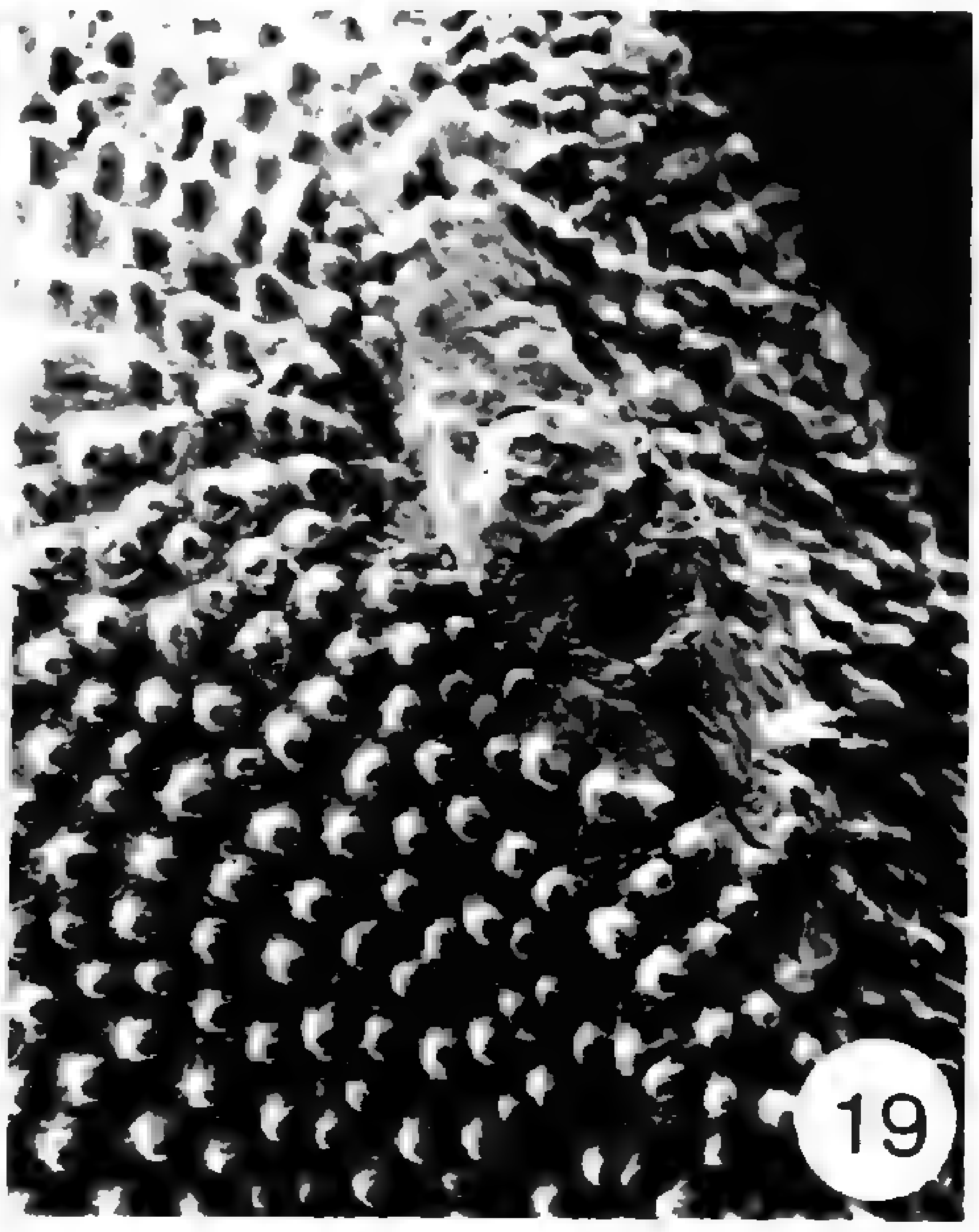
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vate dehiscence and a distinct apical protrusion of the connective. The number of parts is apparently variable with five to seven parts in each whorl. The gynoecium is bicarpellate, but usually only a single seed is developed. At least two different species are present and are distinguished mainly based on differences in size and shape of tepals, stamens, and ovary. Pollen grains have been found in situ in both species and have a characteristic finely striate tectum ornamentation that forms a fingerprint-like pattern (pollen types A.1 and A.2, Figs. 30–38). The pollen from the two different species differs in aperture configuration and fine details of the ornamentation, with monocolpate and trichotomocolpate grains in one species and dicolpate grains in the other. Extant *Cabomba* Aubl. has similar striate pollen, but the fossil flowers are distinct from those of *Cabomba* or other members of the Cabombaceae, which all have trimerous, hypogynous flowers. Trichotomocolpate and dicolpate aperture configuration has not been reported for pollen of extant *Cabomba,* but it does occur in several monocotyledons, and in the magnoliid family Hydnoraceae.

Another common flower in the Portuguese fossil floras is a minute epigynous, pistillate form closely related to the extant Chloranthaceae genus *Hedyosmum* Sw. Such flowers are known from all five of the Portuguese floras (flower with pollen type J.7, Figs. 114–116). They are extremely simple, consisting of three tepal-like structures at the apex of a unilocular and uniovulate ovary. The flower has a characteristic opening in the hypanthium wall, the so-called "window" (Friis et al., 1997b). Pollen grains attached to the surface of the female flowers are of the *Asteropollis*-type, a dispersed pollen genus that is closely similar to pollen of extant *Hedyosmum* (e.g., Walker & Walker, 1984). Pollen is monoaperturate with a star-shaped aperture and a reticulate tectum with muri that have a characteristic beaded ornamentation. *Asteropollis*-type pollen similar to that observed on the fruits has also been found in situ in stamens from the Portuguese floras, and a variety of other pollen types (pollen types J.1–12, Figs. 97–121) resembling pollen of extant *Hedyosmum* and *Ascarina* J. R. & G. Forst. have been found in dispersed stamens or fragments of staminate inflorescences (e.g., Fig. 3 with pollen type J.2, Figs. 100–102). Several have distinct trichotomocolpate apertures.

Among the hypogynous floral structures from the Portuguese localities is a small flower with a trimerous androecium and gynoecium (flower with pollen type D.5, Figs. 61–63). Pollen in situ within the stamens is small, monocolpate, and reticulate. The flower was previously described as "epigynous (?) flower with reticulate pollen" by Friis et al. (1994b), but removal of the perianth has now demonstrated that the flower is hypogynous. The androecium is incomplete, but the position of the stamens that are preserved shows that the flower originally had nine stamens. The base of the flower is broken, and it is not possible to establish whether the stamens are in one or several whorls. Each stamen consists of a broad filament bearing a tetrasporangiate anther, about 0.6 mm long. The gynoecium consists of three carpels. The number of perianth parts and their organization are unclear. The systematic affinity of the flower remains to be established, but the trimerous arrangement of the androecium and gynoecium combined with the monocolpate pollen may indicate a monocotyledonous affinity. A reticulum supported by densely spaced columellae is also common among many extant monocotyledons, e.g., some Agavaceae and palms (Alvarez & Köhler, 1987; Harley, 1997).

Another small hypogynous flower is represented by a single, fragmentary specimen (Fig. 4; flower with pollen type B.4, Figs. 47–49). It consists of an outer whorl of membranous tepals and an inner whorl of stamens. Stamens and tepals are of about the same length, and stamens consist of a distinct filament bearing a tetrasporangiate anther with valvate dehiscence. Two tepals and two complete stamens as well as a fragment of a third stamen are present, but the specimen is incompletely preserved, and the original number of parts is un-

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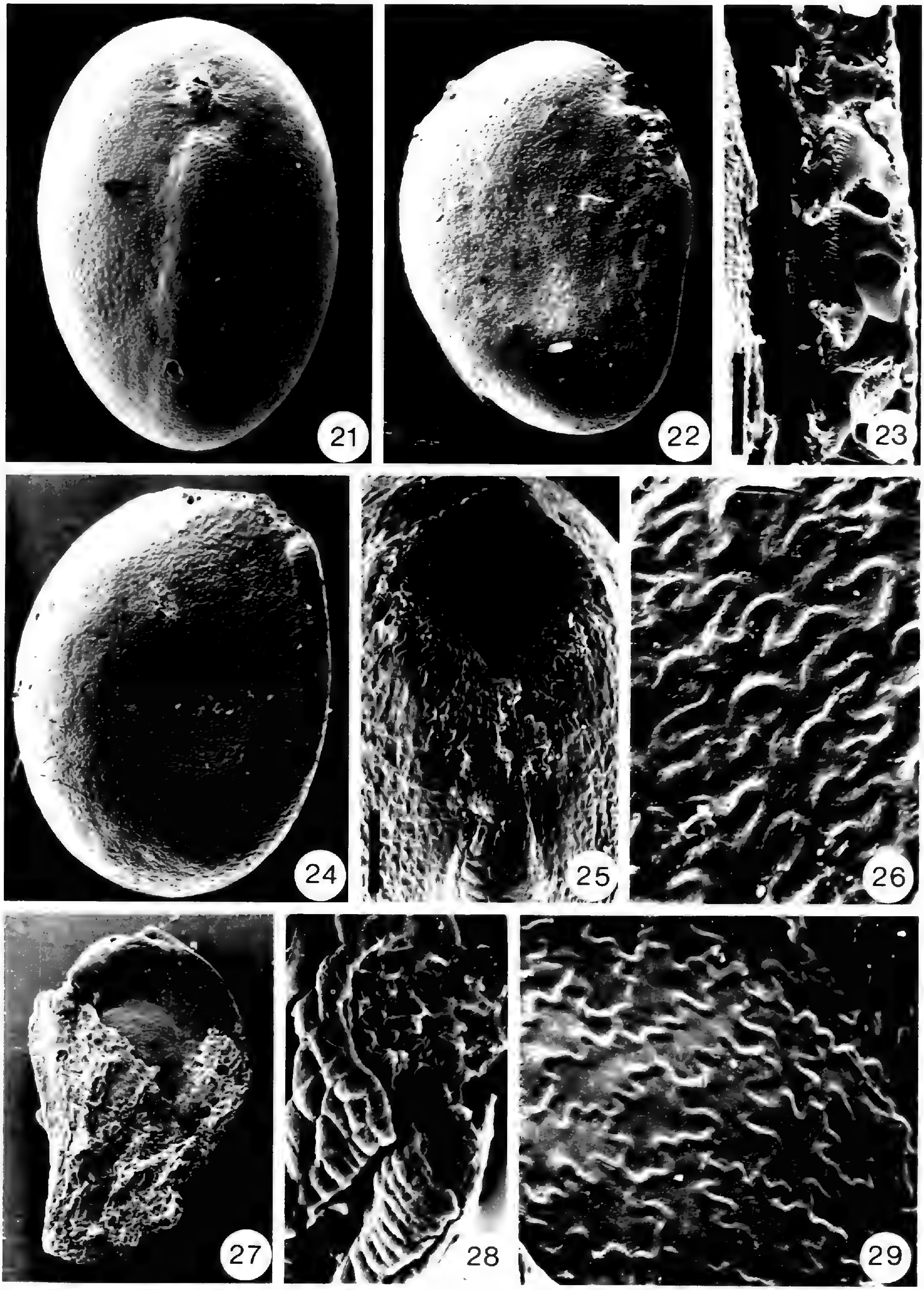
Figures 13–20. Scanning electron micrographs of exotestal angiosperm seeds from the Early Cretaceous (Barremian or Aptian?) Famalicão flora (sample 25), western Portugal. 13–15. Exotestal seed with slightly verrucate surface. —13. Oblique dorsiventral view showing seed and micropylar area, S105221, ×50; scale equal to 250 μm. —14. Detail of micropylar area enlarged, S105221, ×120; scale equal to 100 μm. —15. Detail of seed surface showing verrucate ornamentation, S105221, ×300; scale equal to 50 μm. 16, 17. Exotestal seed with almost smooth surface and narrow, high palisade cells. —16. Dorsiventral view of seed and micropylar area, S105224, ×50; scale shown in Figure 13. —17. Detail of seed wall showing palisade cells of exotesta, S105223, ×300; scale shown in Figure 15. 18–20. Exotestal seed with fine spines and short palisade cells. —18. Lateral view of seed, S105225, ×50; scale shown in Figure 13. —19. Detail of seed showing micropylar area, S105225, ×120; scale shown in Figure 14. —20. Detail of seed wall showing outer short palisade cells of testa and spiny surface of seed, S105228, ×300; scale shown in Figure 15.



Figures 21–29. Scanning electron micrographs of angiosperm seed with exotestal seeds and digitate anticlinal cells from the Early Cretaceous (Barremian or Aptian?) Famalicão flora (sample 25), western Portugal. 21–23. Seed type with digitate palisade cells over raphe. —21. Dorsiventral view of seed and raphe, S105218, ×50; scale equal to 250 µm. —22. Lateral view of seed, S105220, ×50; scale shown in Figure 21. —23. Detail of palisade cells, S105219, ×600; scale equal to 25 µm. 24–26. Seed type with non-digitate cells over raphe, S105027. —24. Lateral view, ×50;

known. The pollen grains are monoaperturate, with both monocolpate and trichotomocolpate pollen produced by the same anther. The graded (*Similipollis*-type) tectum of the pollen wall from psilate to reticulate indicates a possible relationship with the monocotyledons, but the systematic affinity of the fossil flower cannot be established based on our current knowledge of the floral structure.

Fruiting units. There are many unilocular fruiting units, some of which may be from unicarpellate gynoecia, while others may be dispersed fruitlets from apocarpous, multicarpellate structures. Usually there are only one, or a few, seeds per carpel, and the stigmatic area is sessile (Figs. 5–10). One type of fruiting unit that occurs abundantly in the Portuguese floras belongs to the extinct genus *Anacostia* Friis, Crane & Pedersen, which is based on unicarpellate, apparently baccate, fruiting units with a single anatropous, bitegmic, and exotestal seed (Friis et al., 1997a). The stigmatic area is indistinct and sessile. Monoaperturate (monocolpate and trichotomocolpate) pollen grains with a characteristic graded reticulum have been observed on many specimens (see description of pollen type F). The fruit wall contains scattered resin bodies, thought to represent the remains of ethereal oil cells. Fruit characters indicate a possible magnoliid affinity, while pollen features indicate a possible affinity to monocotyledons. In the Portuguese floras two species have been distinguished: *Anacostia portugallica* Friis, Crane & Pedersen described from Vale de Agua, Famalicão, and Buarcos, and *A. teixeirae* Friis, Crane & Pedersen described from Famalicão and Buarcos (Friis et al., 1997a). Two other species of *Anacostia* were described from the Early Cretaceous of North America (Friis et al., 1997a). Other unilocular and one-seeded fruiting units in the Portuguese floras are related to the extinct genera *Couperites* Pedersen, Crane, Drinnan & Friis and *Appomattoxia* Friis, Pedersen & Crane, described earlier from mid-Cretaceous strata of North America (Pedersen et al., 1991; Friis et al., 1995).

Like *Anacostia* several of the angiosperm fossils in the Portuguese Early Cretaceous floras have resin bodies that probably represent the remains of ethereal oil cells. This feature is characteristic for many extant magnoliids, and among the monocotyledons is only reported from the genus *Acorus* L. One resinous fruit type that has been reported from all floras studied is particularly abundant in the Famalicão flora (Figs. 8–12). The material is thought to include two different species of the same genus. Resin bodies are densely spaced under the cuticle of the fruit wall. Each fruit includes two anatropous and apparently endotestal seeds with a small, subbasal heteropyle. The seed wall has an endotestal tissue with distinct crystal cells. The seeds are very similar to those of *Liriodendron* L. and other Magnoliaceae in organization and wall structure. Pollen grains are found in large quantities on the surface of the fruit, particularly in the stigmatic area. They are monoaperturate with a loose, coarse reticulum and long columellae (see described pollen type D.9, Figs. 72–74). They are unlike pollen of extant Magnoliaceae, and the fossil may belong to an extinct group of magnoliids.

Seeds. Both endotestal and exotestal angiosperm seeds occur in the Portuguese fossil floras, but exotestal seeds are especially abundant and diverse (Figs. 13–29). These seeds have the mechanical layer in the outer seed wall, and the outer epidermis is often developed as a palisade layer. Frequently, they can be recognized in fossil assemblages as black, shiny objects. They are all anatropous and vary in size, shape, and testa ornamentation, as well as in anatomical details. Some of them show similarities to seeds of extant Nymphaeales in having distinctly digitate anticlinal cell walls of the outer palisade layer (Figs. 21–29), but only one (not figured here) has the characteristic micropylar lid of the Nymphaeales and their relationships may be to other magnoliids, or some may be on the Nymphaeales stem lineage. Exotestal seeds with palisade cells and digitate cell wall occur also in the Illiciales, and it is possible that some of the Early Cretaceous angiosperm seeds from Portugal are related to this group. Seeds with unequivocal features of Illiciaceae have been documented from younger (Cenomanian-Turonian) strata of Kazakhstan (Frumin & Friis, 1999).

A distinctive exotestal seed type encountered in all five fossil floras is particularly abundant at Famalicão. Several thousand specimens have been isolated (Figs. 6, 7). Several different species per-

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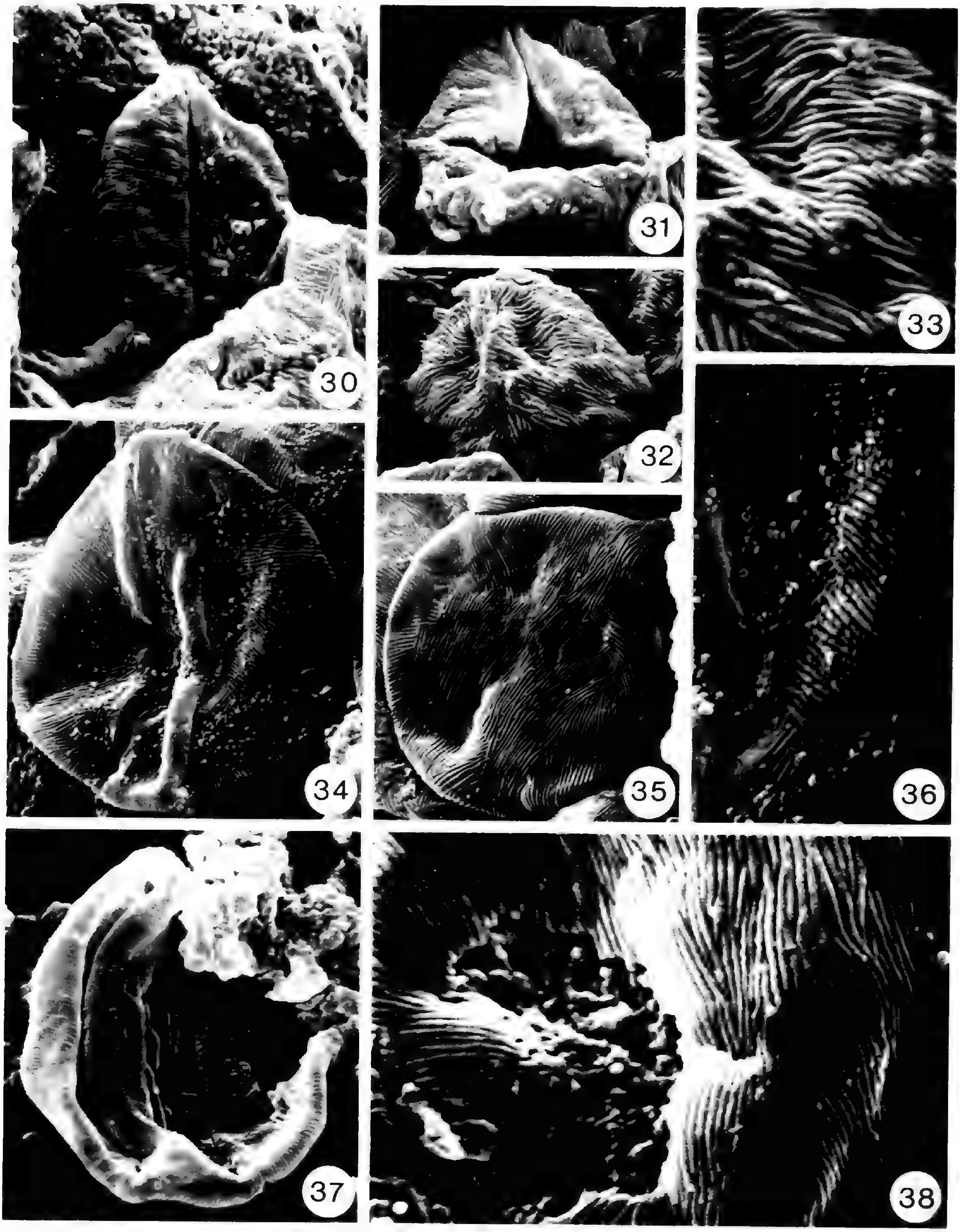
scale shown in Figure 21. —25. Detail of micropylar area, ×120; scale equal to 100 μm. —26. Detail of external surface showing digitate outlines of the palisade cells, ×500; scale equal to 25 μm. 27–29. Thin-walled seed in unilocular fruit, S105096. —27. Lateral view of seed surrounded by fragmentary fruit wall, ×50; scale shown in Figure 21. —28. Detail of micropylar area, ×400; scale equal to 25 μm. —29. Detail of external surface showing digitate outlines of the palisade cells, ×400; scale shown in Figure 28.



Figures 30–38. Scanning electron micrographs of pollen type A from the Early Cretaceous (Barremian or Aptian?) Vale de Agua flora, western Portugal. 30–33. Pollen type A.1, monocolpate-trichotomocolpate, finely striate pollen, S105030 (Vale de Agua sample 19). —30. Distal view showing monocolpate aperture, ×4000; scale equal to 5 μm. —31. Distal view showing trichotomocolpate aperture, ×4000; scale shown in Figure 30. —32. Proximal view showing fingerprint-like striations, ×4000; scale shown in Figure 30. —33. Detail of finely striate exine, ×10,000; scale equal to 1 μm. 34–38. Pollen type A.2, dicolpate, tectate, finely striate pollen, S101288 (Vale de Agua sample 141). —34. Distal view showing two colpi, ×4000; scale shown in Figure 30. —35. Proximal view showing finely striate exine, ×4000; scale shown in Figure 30. —36. Detail of finely striate exine, ×10,000; scale shown in Figure 33. —37. Distal view showing two colpi, ×4000; scale shown in Figure 30. —38. Detail of finely striate exine showing apparently granular infratectal structure where the surface is broken, ×10,000; scale shown in Figure 33.

haps belonging to different genera have been recognized. One species has one to six seeds per carpel, the most common number being three seeds (Figs. 6, 7). The seeds are anatropous and bitegmic and laterally co-adhering to each other. The micropyle is formed by the thin inner integument, while the outer integument forms an elongated slit around it. The seeds occur in unilocular fruits (Fig. 5) with a thin fruit wall without mechanical tissue. The fruit wall was perhaps originally fleshy and is mostly abraded. The stigma is indistinct and sessile. No pollen grains have been observed on the stigmatic area, although numerous specimens have been examined. The second, presumably closely related species, differs in having larger and more elongated seeds. A third species typically has four laterally fused seeds per carpel, and the fruits are of more regular, almost spherical shape.

DIVERSITY OF IN SITU POLLEN

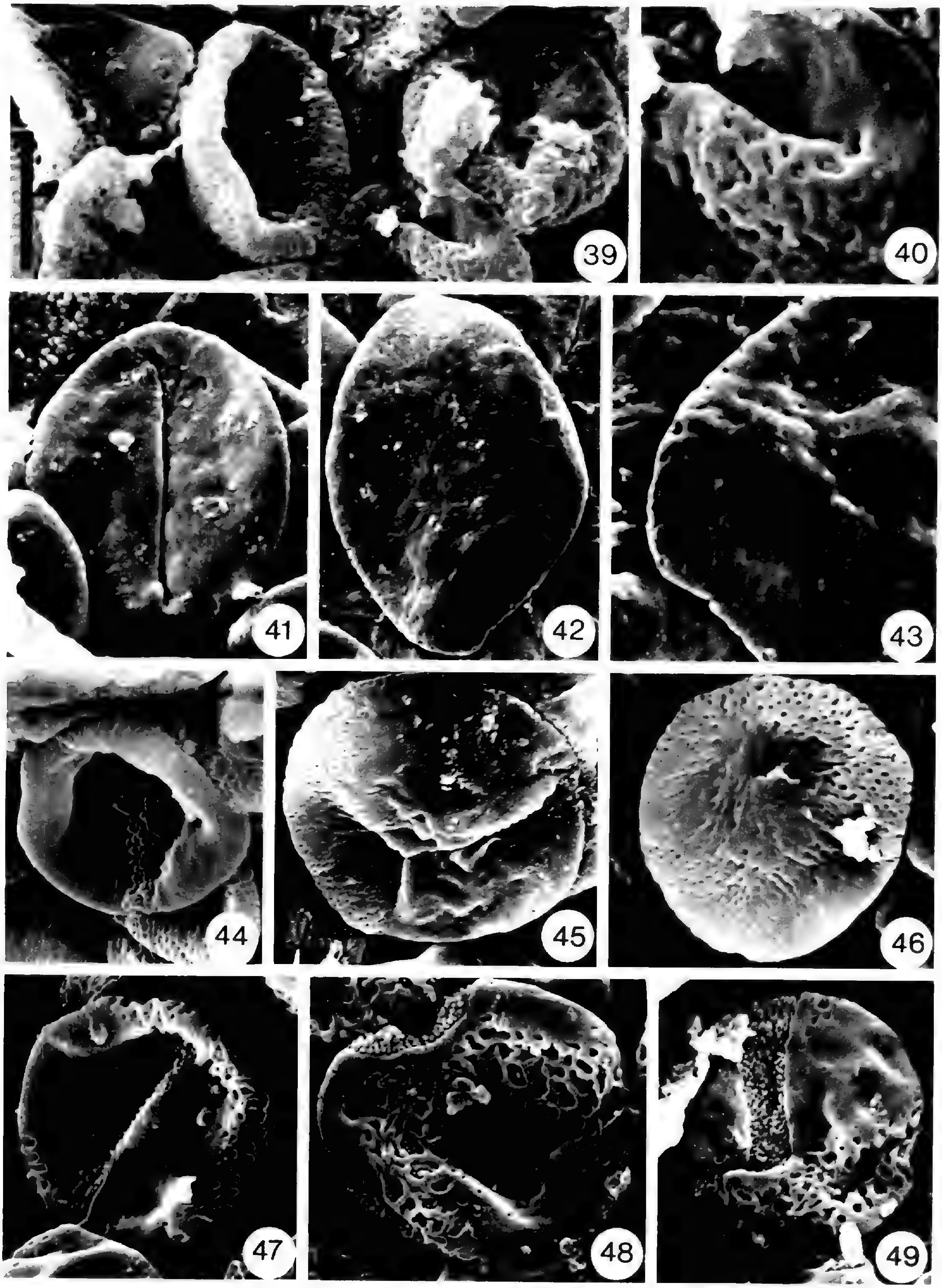
In all five of the Portuguese floras discussed here pollen grains have been found in situ in flowers or dispersed stamens or on the surface of dispersed fruits. Several of these pollen grains are closely similar to pollen described from dispersed palynofloras, but detailed comparisons are often problematic because the dispersed pollen species are usually characterized based only on light microscopy (LM). Light microscopy does not provide sufficient information on ornamentation and other fine details that are readily observed by the SEM and that are of clear taxonomic importance. For example, studies of an assemblage of minute, monocolpate, and finely reticulate angiosperm pollen grains from the Barremian of southern England based on LM studies resulted in the recognition of only a single species, *Clavatipollenites hughesii* Couper, while details retrieved by SEM demonstrated that this assemblage included ten or more distinct species (e.g., Hughes et al., 1979; Hughes, 1994). A similar example was discussed by Penny (1988) based on SEM studies of an extensive collection of semitectate-acolumellate pollen grains from the Early Cretaceous of Egypt. Other SEM-based palynological studies show similar results with higher diversity of pollen taxa than retrieved by LM studies from comparable samples.

About 60 different pollen types have been found in situ from the five Portuguese Early Cretaceous floras. Monoaperturate, dicolpate, and periporate pollen grains of probable magnoliid and monocotyledonous affinity are by far the most diverse with 48 different taxa identified so far of which 44 are described here. About 10 different tricolpate pollen types of presumed eudicotyledons have been observed. All of the early angiosperm pollen grains described here are small, ranging from about 9 to 25 μm in their maximum diameter. Only one pollen type is larger than 30 μm, and most are in the size range of 12–16 μm. Semitectate and reticulate forms predominate and comprise about 75% of the pollen types recognized so far. The remainder are tectate-foveolate or tectate-striate. Trichotomo-, tetrachotomo-, and pentachotomocolpate apertures are common. In two different species monocolpate and trichotomocolpate grains were observed in situ in the same anther. Pollen grains associated with the fruits of *Anacostia* also include both monocolpate and trichotomocolpate forms (Friis et al., 1997a).

In this study we concentrate on the diversity of probable magnoliid and monocotyledonous pollen, providing brief descriptions, comments on their occurrence in the five Portuguese floras, and a brief consideration of the type of organ with which they are associated. The pollen grains are grouped according to their morphological features. They are not referred to genera or species based on dispersed grains, although possible links to dispersed taxa are discussed when relevant.

A. Monocolpate-trichotomocolpate and dicolpate, tectate and finely striate pollen (Figs. 30–38). Two very similar tectate and finely striate pollen species have been identified. Both are found in situ in small epigynous flowers with a distinct perianth of leathery tepals (Figs. 1, 2). These flowers occur in the Catefica, Vale de Agua, Buarcos, and Famalicão floras, and their systematic position remains to be investigated in detail.

The pollen grains are similar to pollen of extant *Cabomba* (Cabombaceae, Nymphaeales) in wall ornamentation, but dicolpate or trichotomocolpate apertures have not been observed in pollen of Cabombaceae, and the epigynous organization of the flowers, as well as number of floral parts, precludes an affinity with members of this family. Dicolpate pollen with two closely spaced (distal) colpi and monocolpate/trichotomocolpate pollen is common among monocotyledons and is also known for the magnoliid family Hydnoraceae. We have not seen similar tectate-striate pollen grains reported from dispersed Early Cretaceous palynofloras. The two species of pollen are distinguished from each other in size, aperture configuration, and details of ornamentation. Despite these differences they are thought to be closely related. They occur in very similar flowers and both have the characteristic striate ornamentation.



Figures 39–49. Scanning electron micrographs of pollen type B from the Early Cretaceous (Barremian or Aptian?) Vale de Agua, Buarcos, and Torres Vedras floras, western Portugal. 39, 40. Pollen type B.1, monocolpate, psilate-foveolate pollen, S105257 (Vale de Agua sample 141). —39. Several pollen grains: grain at right in distal view showing monocolpate aperture, ×4000; scale equal to 5 μm. —40. Detail of exine at the equatorial region, ×10,000; scale equal to 1 μm. 41–43. Pollen type B.2, monocolpate, psilate-finely foveolate pollen, S105024 (Buarcos sample 243). —41. Distal view showing monocolpate aperture, ×4000; scale shown in Figure 39. —42. Proximal view, ×4000; scale shown in Figure 39. —43. Detail of exine in equatorial region, ×10,000; scale shown in Figure 40. 44–46. Pollen

A.1. Monocolpate-trichotomocolpate pollen (Figs. 30–33). Pollen grains small, elliptical to circular or almost triangular in equatorial outline, about 8–10.5 μm in diameter, and with monocolpate (Fig. 30) or trichotomocolpate apertures (Fig. 31). The two aperture types co-occur in the same stamen and were clearly produced by the same plant. The tectum has a finely striate supratectal ornamentation that forms a fingerprint-like pattern (Figs. 31–33).

The pollen grains have been observed in situ in several flowers from the Vale de Agua and Famalicão floras. The same flower type also occurs in the floras from Buarcos and Catefica, but no pollen was observed in these specimens.

A.2. Dicolpate pollen (Figs. 34–38). Pollen grains very similar to the monocolpate-trichotomocolpate grains described above, but distinct in having a dicolpate aperture configuration (Figs. 34, 37), and in being larger with an equatorial diameter of about 13.5–15 μm. Pollen grains of this species also differ in having slightly finer striations on the tectum (Figs. 35, 36, 38). The two colpi are parallel and closely spaced and extend almost to the equator of the grains. The margins of the colpi are distinctly marked by a smooth tectum. The striate ornamentation becomes less prominent toward the aperture margins, and in the narrow intercolpal area the pollen wall is psilate (Figs. 34, 37). A fracture in the pollen wall shows that the pollen grains have apparently a granular infratectal structure (Fig. 38).

The pollen grains were observed in situ in several flowers from the Vale de Agua flora. Similar flowers are also known from the Buarcos flora, but no pollen grains were observed in the Buarcos specimens.

B. Monoaperturate, tectate, psilate pollen with foveolate or reticulate equatorial zone (Figs. 39–49). Four different pollen types have been grouped together under this heading because they share the unusual feature of having psilate grains with a distinctive foveolate to reticulate equatorial zone. Such features are not common in angiosperm pollen. One of the pollen types is from the Vale de Agua flora, two are from the Buarcos, and one is from Torres Vedras. The Vale de Agua pollen type (Figs. 39, 40) apparently has a broader equatorial zone than the other three. In the two different types from the Buarcos flora (Figs. 41–46) the equatorial zone is foveolate, while in the polar regions the tectum is more or less psilate. The size and density of the foveolae differ in the two pollen types. In the pollen type from Torres Vedras (Figs. 47–49) the equatorial belt grades from foveolate to coarsely reticulate. All pollen types have similar granular membranes in the colpi. These types of pollen grains show some resemblance to pollen grains of the *Anacostia-Similipollis* type (pollen type F.1 and F.2, Figs. 83–85), which have a graded reticulate to foveolate reticulum that has smaller lumina and foveolae in the polar areas, and larger lumina in the equatorial region. This kind of graded tectum structure, here referred to as *Similipollis*-type grading (see pollen F), has been reported from extant palms (e.g., Harley, 1997) but is apparently not present in the pollen of extant magnoliid angiosperms. Another type of graded reticulum, here referred to as *Liliacidites*-type grading (see pollen type E), has smaller lumina in equatorial position at the ends of the apertures and is known for many monocotyledons (e.g., Erdtman, 1952; Alvarez & Köhler, 1987; Le Thomas et al., 1996).

B.1. Monocolpate, psilate-foveolate pollen (Figs. 39, 40). Pollen grains small, elliptical to circular in equatorial outline, and about 8.5–9 μm in diameter. Aperture monocolpate with rather short colpi and a granular colpus membrane (Fig. 39). Pollen wall psilate except for a broad foveolate zone around the equator (Fig. 40).

The pollen grains were observed in a small fragmentary stamen, about 0.4 mm long, from the Vale de Agua flora. We have not seen any reports of dispersed pollen taxa that match this pollen type.

B.2. Monocolpate, psilate-finely foveolate pollen (Figs. 41–43). Pollen grains elliptical in outline, and about 12–13.5 μm long. Aperture monocolpate with the colpus reaching almost to the equator of the grain (Fig. 41). Colpus membrane granular, and the colpus margin distinct. Pollen wall psilate with

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type B.3, monocolpate, finely foveolate pollen, S101739 (Buarcos sample 209). —44. Distal view showing monocolpate aperture and granular aperture membrane, ×4000; scale shown in Figure 39. —45. Oblique distal view showing trichotomocolpate aperture, ×4000; scale shown in Figure 39. —46. Proximal view showing foveolate equatorial zone, ×4000; scale shown in Figure 39. 47–49. Pollen type B.4, monocolpate, psilate-reticulate pollen, S105002 (Torres Vedras sample 144). —47. Distal view showing monocolpate aperture and granular aperture membrane, ×4000; scale shown in Figure 39. —48. Proximal view showing foveolate to reticulate equatorial zone, ×4000; scale shown in Figure 39. —49. Oblique lateral view showing colpus and equatorial zone, ×4000; scale shown in Figure 39.

scattered foveolae and with a narrow, finely foveolate zone around the equator (Figs. 42, 43).

The pollen grains were observed in situ in a stamen with tetrasporangiate anther from the Buarcos flora. We are not aware of any dispersed pollen taxon similar to this in situ form.

B.3. Monocolpate-trichotomocolpate, finely foveolate pollen (Figs. 44–46). Pollen grains almost circular in equatorial outline and about 9–11 μm in diameter. Aperture monocolpate or trichotomocolpate. Both aperture forms have been observed in situ in the same anther. Colpus reaches almost to the equator. Colpus margin is distinct and the colpus membrane granular. Pollen wall psilate grading into a narrow, foveolate equatorial zone.

The pollen grains were found in a small, fragmentary flower from the Buarcos flora consisting of two stamens and perianth parts. The stamens have distinct filaments and the anthers are tetrasporangiate. We are not aware that similar pollen grains have been illustrated from dispersed palynofloras.

B.4. Monocolpate, psilate-reticulate pollen (Figs. 47–49). Pollen grains almost circular in equatorial outline and about 9–12 μm in diameter. Aperture monocolpate with a long broad colpus reaching almost to the equator of the grain (Fig. 47). Colpus margin is distinct and the colpus membrane is granular. Tectum distinctly heterogeneous, psilate over most of the proximal and distal surfaces, with a narrow foveolate to reticulate zone around the equator and a narrow foveolate zone flanking the aperture margins (Figs. 48, 49).

This pollen type has been recovered in a tetrasporangiate anther from the Torres Vedras locality. The grains show some resemblance to dispersed pollen from the late Barremian-early Aptian of Gabon assigned to *Similipollis* Góczán & Juhász (Doyle & Hotton, 1991) that also has a narrow foveolate-reticulate equatorial zone, but the African pollen is distinct in having a long extended colpus.

C. Monoaperturate, tectate pollen with finely spiny ornamentation. Pollen grains monocolpate, elliptical (?) in equatorial outline, about 15 μm in diameter. Colpus margin and colpus membrane not well exposed. Grains are tectate. Tectum faintly rugulate-verrucate and covered by minute echinae.

The pollen is poorly preserved and not illustrated here. It occurs on a small spiny fruit very similar to those of *Appomattoxia ancistrophora* Friis, Pedersen & Crane described from the early to middle Albian Puddledock flora, Virginia, U.S.A. (Friis et al., 1995). The pollen is also closely similar to that of *Appomattoxia,* and comparable to dispersed grains from Lower Cretaceous strata assigned to *Tucanopollis* (Regali) Regali and *Transitoripollis* Góczán & Juhász (see discussion in Friis et al., 1995). In extant plants pollen of this type is known in the Piperales, and the fruits of *Appomattoxia* also show a possible relationship with extant members of the Piperales, although the fossils cannot with certainty be placed in this group.

D. Monoaperturate, semitectate, reticulate pollen with smooth muri (Figs. 50–74). Monoaperturate columellate pollen with a non-graded reticulum that lacks supratectal ornamentation on the muri is common among the in situ pollen types from the Portuguese floras. Pollen grains of this type have been found associated with diverse gynoecia and also in anthers. They vary in size, details of the reticulum, and length and spacing of the columellae. They probably represent several distinct genera, and probably also belong to different families, orders, or other higher-level taxa. Dispersed pollen grains similar to these Portuguese reticulate pollen have been described from several Early Cretaceous palynofloras and are often assigned to various species of the genus *Retimonocolpites* Pierce (e.g., Doyle & Robbins, 1977; Schrank, 1983; Ward, 1986). Several taxa of this general type were also

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Figures 50–60. Scanning electron micrographs of pollen types D.1–D.4 from the Early Cretaceous (Barremian or Aptian?) Vale de Agua flora, western Portugal. 50–52. Pollen type D.1, monocolpate, heterogeneous reticulate pollen with widely spaced columellae, S105277 (Vale de Agua sample 19). —50. Distal view showing monocolpate aperture, ×4000; scale equal to 5 μm. —51. Two grains showing distal and proximal views, ×4000; scale shown in Figure 50. —52. Detail of reticulum showing widely spaced columellae, ×10,000; scale equal to 1 μm. 53–55. Pollen type D.2, monocolpate, homogeneous reticulate pollen with widely spaced columellae, S105256 (Vale de Agua sample 141). —53. Distal view showing monocolpate aperture, ×4000; scale shown in Figure 50. —54. Proximal view, ×4000; scale shown in Figure 50. —55. Detail of reticulum showing widely spaced columellae, ×10,000; scale shown in Figure 52. 56, 57. Pollen type D.3, monocolpate, heterogeneous reticulate pollen with widely spaced columellae, S105029 (Vale de Agua sample 19). —56. Three grains showing distal and proximal views, ×4000; scale shown in Figure 50. —57. Detail of reticulum showing widely spaced columellae, ×10,000; scale shown in Figure 52. 58–60. Pollen type D.4, monocolpate, homogeneous reticulate pollen with densely spaced columellae, S105661 (Vale de Agua sample 139). —58. Distal view showing monocolpate aperture, ×3000; scale equal to 5 μm. —59. Proximal view, ×3000; scale shown in Figure 58. —60. Detail of reticulum showing densely spaced columellae, ×10,000; scale shown in Figure 52.


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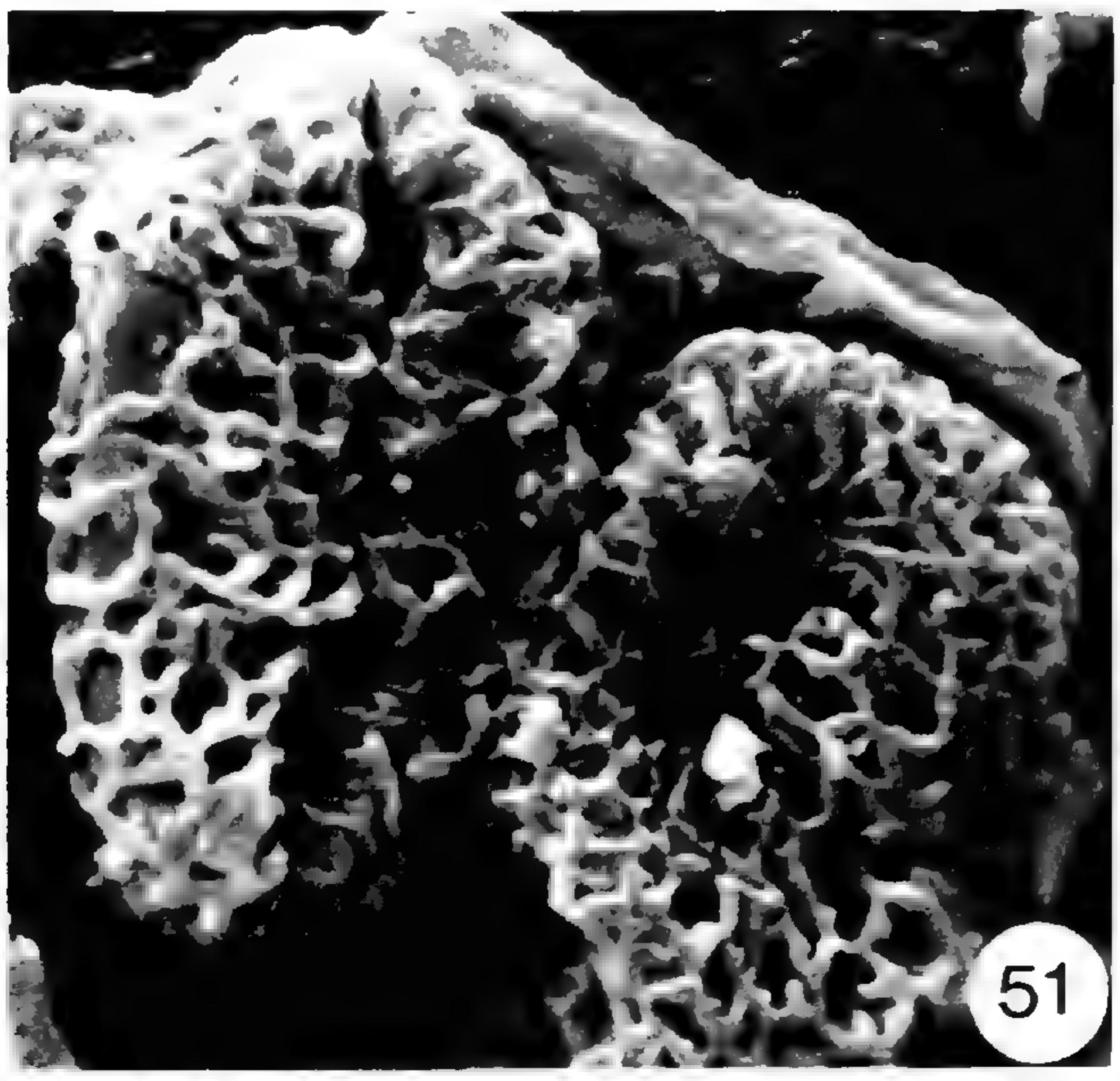
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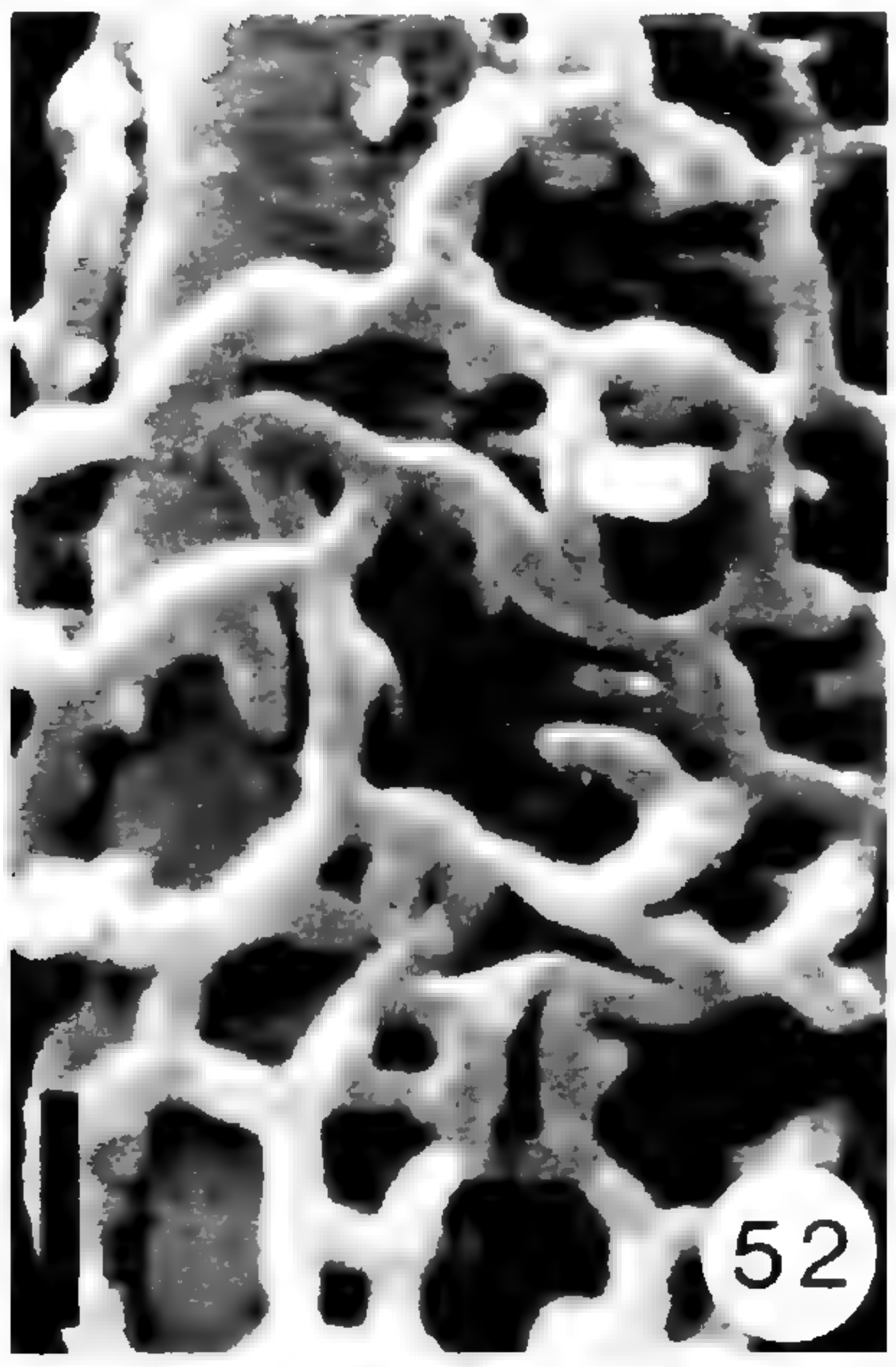
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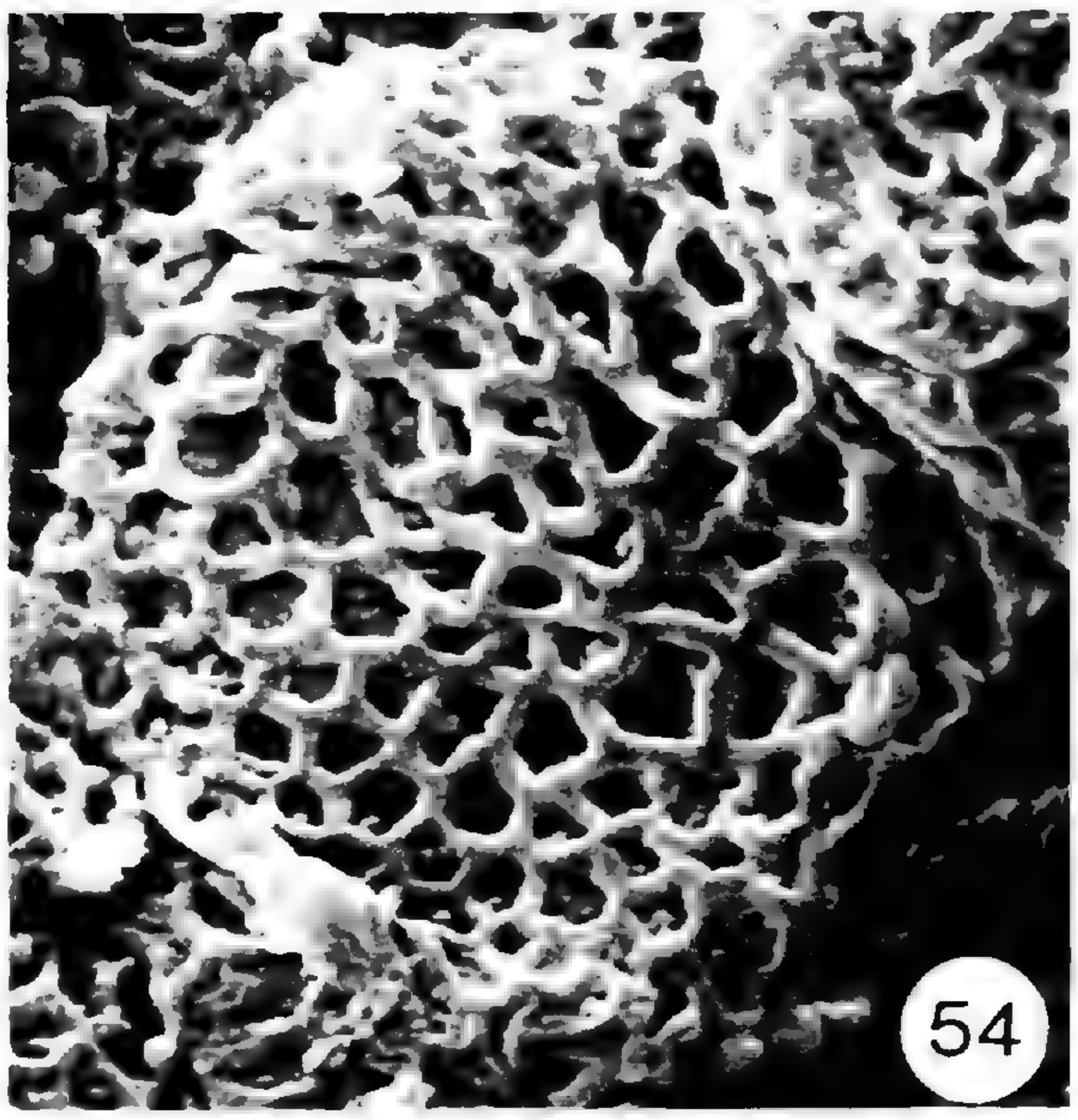
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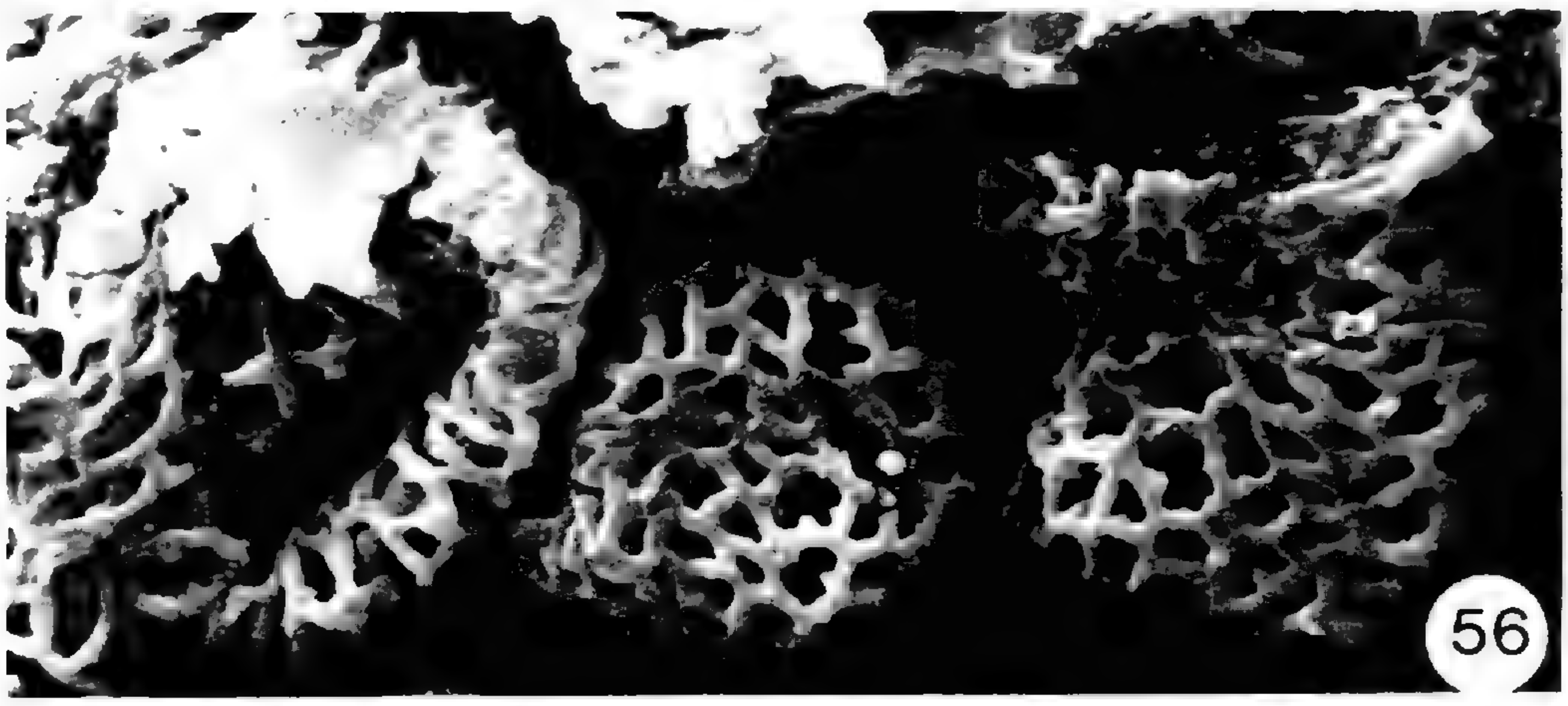
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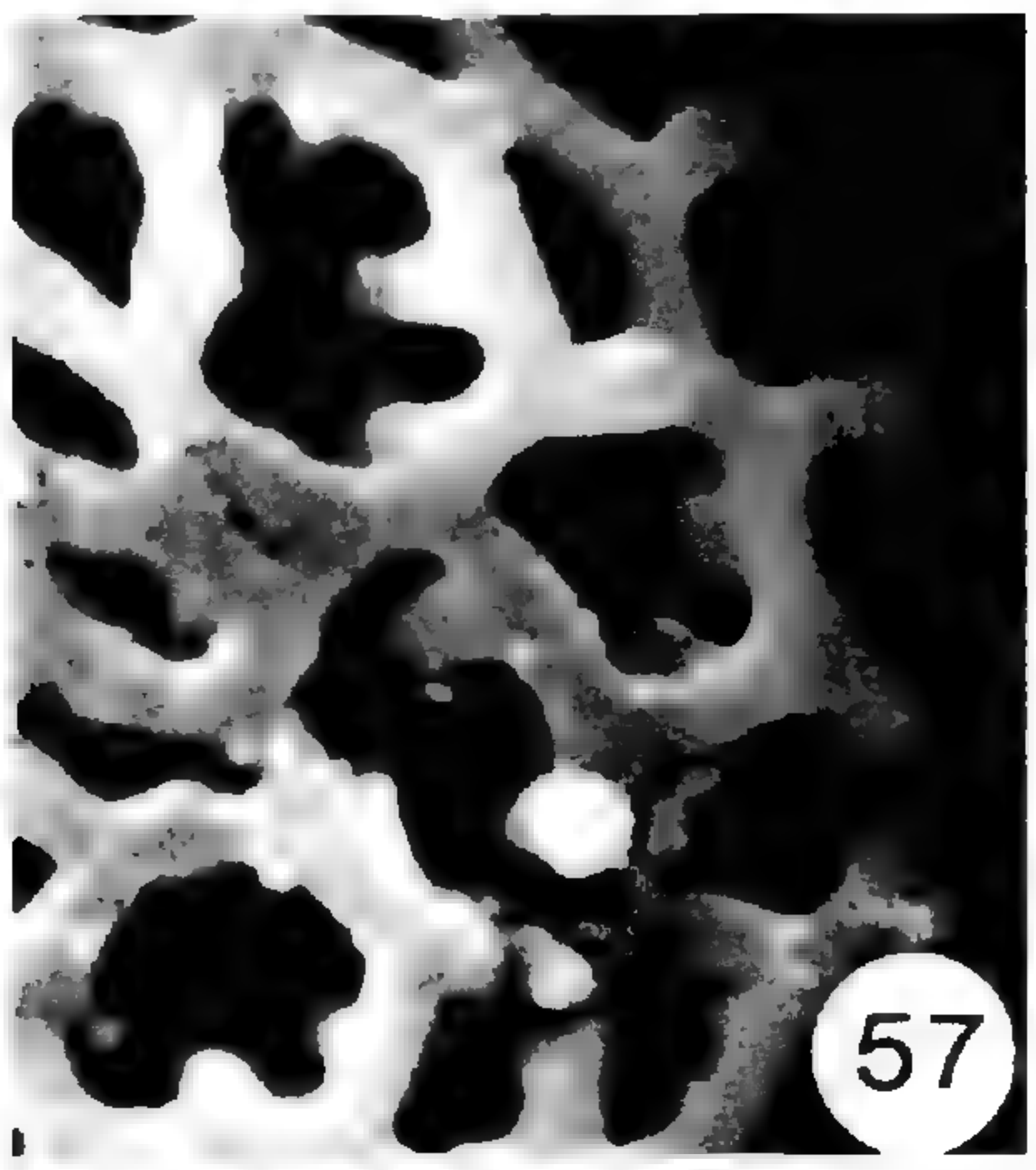
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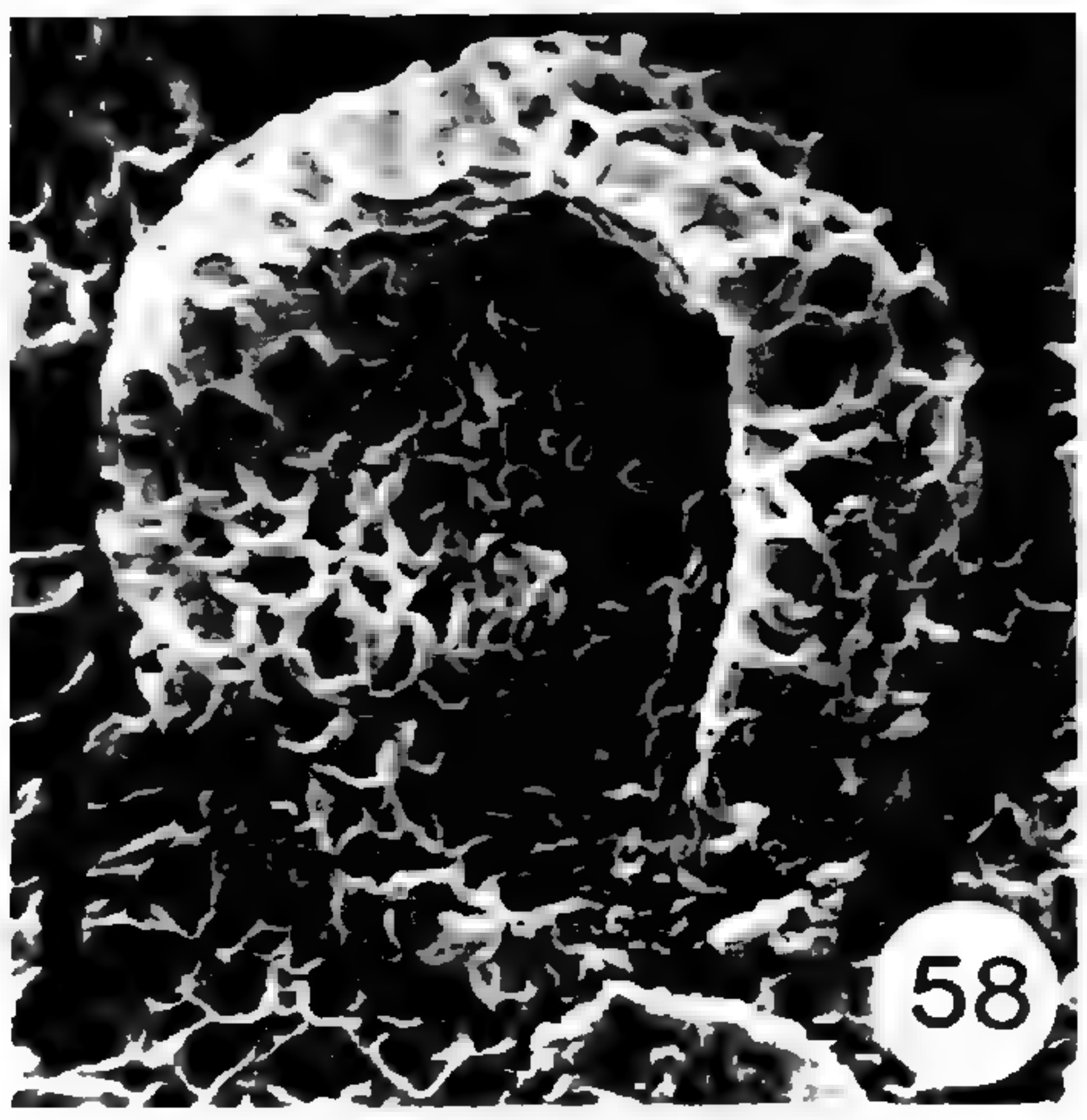
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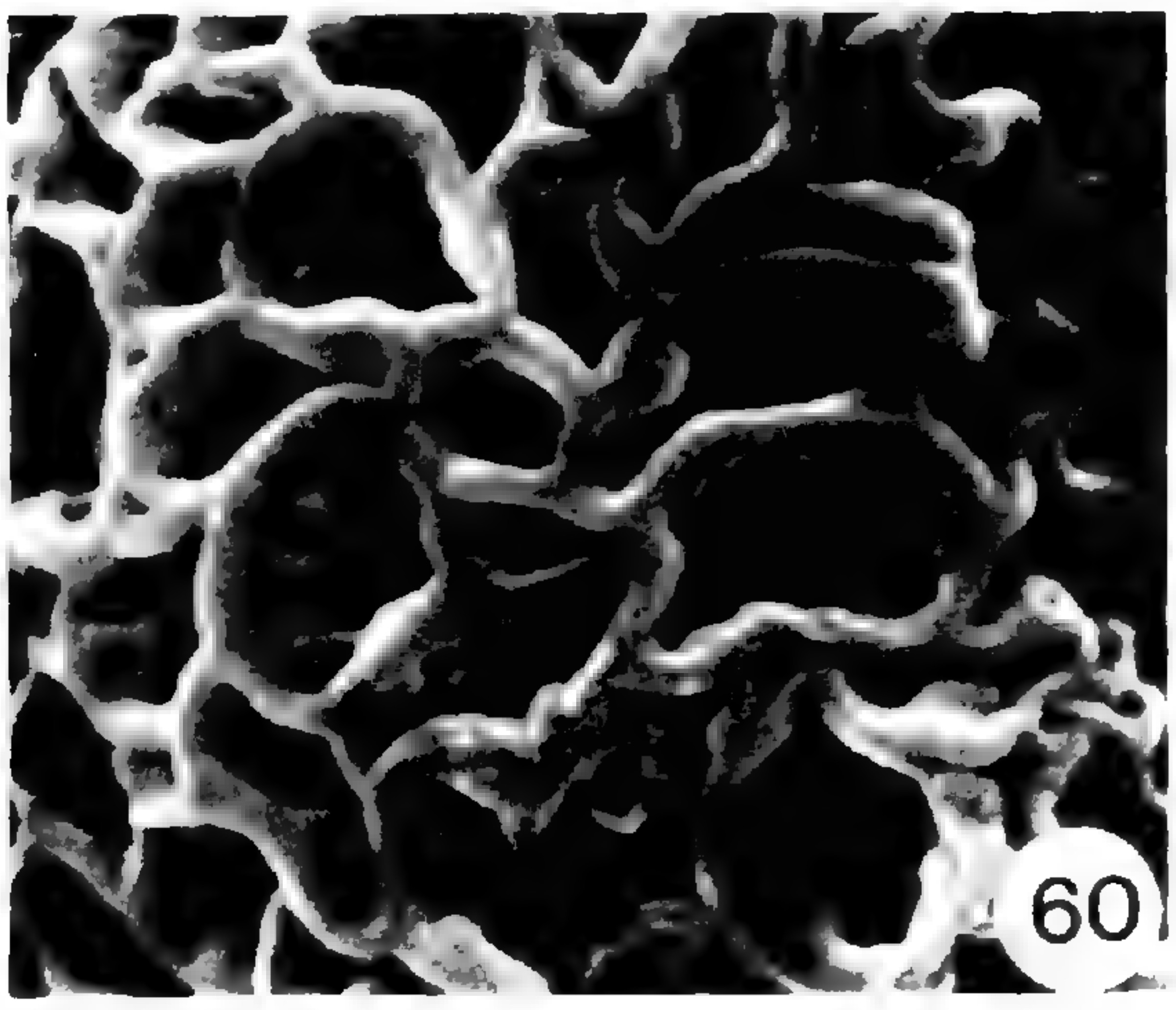
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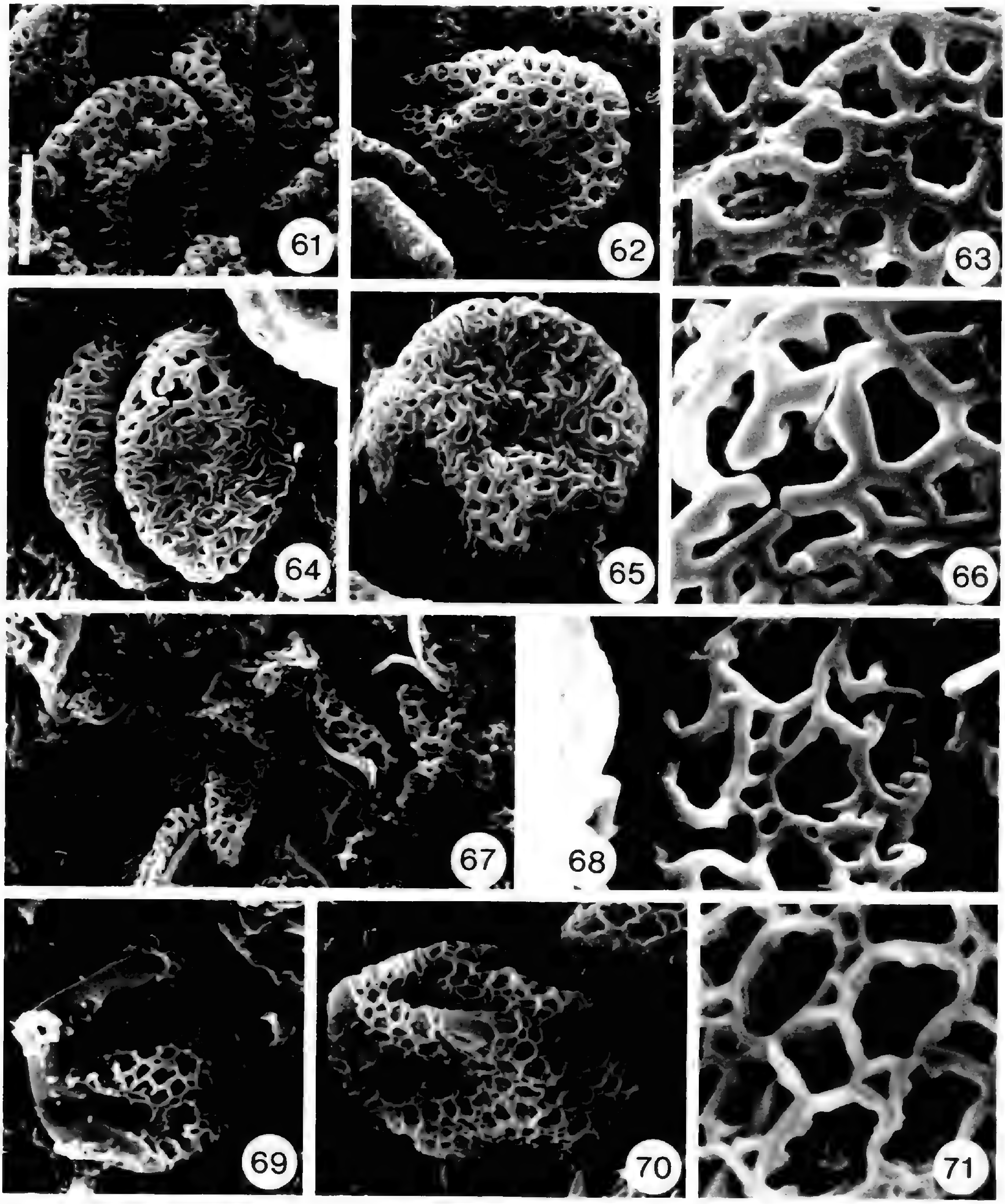
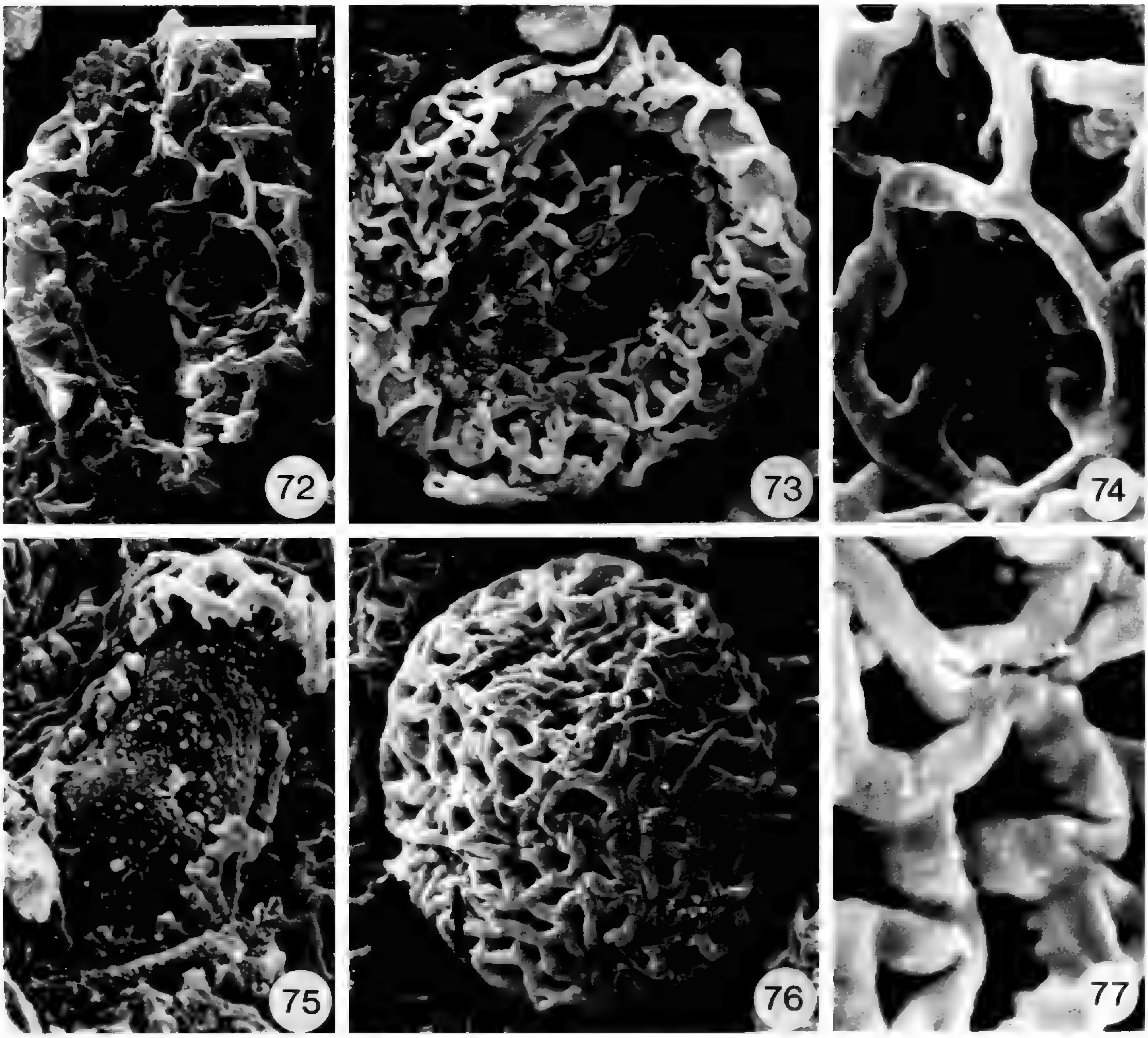


Figures 61–71. Scanning electron micrographs of pollen types D.5–D.8 from the Early Cretaceous (Barremian or Aptian?) Torres Vedras and Catefica floras, western Portugal. 61–63. Pollen type D.5, monocolpate, heterogeneous, reticulate pollen with densely spaced columellae, S101306 (Torres Vedras sample 39). —61. Two pollen grains in distal view showing monocolpate aperture, ×3000; scale equal to 5 μm. —62. Proximal view, ×3000; scale shown in Figure 61. —63. Detail of reticulum showing densely spaced columellae, ×10,000; scale equal to 1 μm. 64–66. Pollen type D.6, monocolpate, heterogeneous, reticulate pollen with widely spaced columellae, S105018 (Torres Vedras sample 44). —64. Oblique distal view showing monocolpate aperture, ×3000; scale shown in Figure 61. —65. Proximal view, ×3000; scale shown in Figure 61. —66. Detail of reticulum showing widely spaced columellae, ×10,000; scale shown in Figure 63. 67, 68. Pollen type D.7, monocolpate, heterogeneous reticulate pollen with densely spaced columellae, S105021 (Torres Vedras sample 44). —67. Numerous pollen grains showing distal and proximal views, ×3000; scale shown in Figure 61. —68. Detail of reticulum showing widely spaced columellae, ×10,000; scale shown in Figure 63. 69–71. Pollen type D.8, monocolpate, heterogeneous reticulate pollen with densely spaced columellae, S105281 (Catefica sample 151). —69. Proximal view of pollen grain with reticulum partially abraded, ×3000; scale shown in Figure 61. —70. Proximal view, ×3000; scale shown in Figure 61. —71. Detail of reticulum showing densely spaced columellae, ×10,000; scale shown in Figure 63.



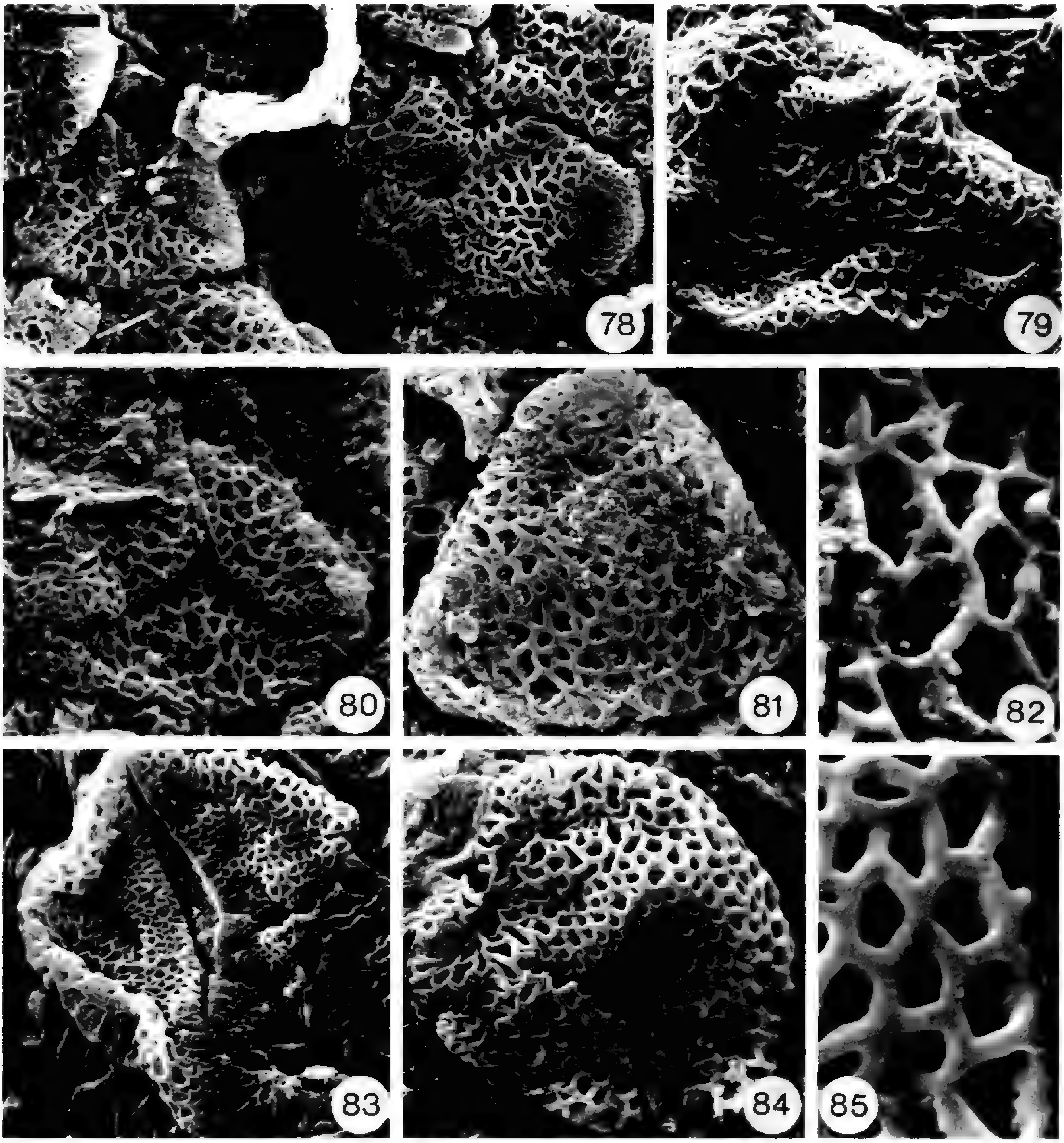
Figures 72–77. Scanning electron micrographs of pollen types D.9 and H from the Early Cretaceous (Barremian or Aptian?) Famalicão flora (sample 25), western Portugal. 72–74. Pollen type D.9, monocolpate, homogeneous reticulate pollen with widely spaced columellae, S105285. —72. Distal view showing monocolpate aperture, ×3000; scale equal to 5 μm. —73. Proximal view, ×3000; scale shown in Figure 72. —74. Detail of reticulum showing widely spaced columellae, ×10,000; scale equal to 1 μm. 75–77. Pollen type H, periporate and reticulate pollen, S105073. —75. Pollen grain with reticulum partially abraded, ×3000; scale shown in Figure 72. —76. Pollen grain showing reticulum and location of several pores (arrows), ×3000; scale shown in Figure 72. —77. Detail of reticulum showing muri and columellae/granules, ×10,000; scale shown in Figure 74.

reported from Egypt by Penny (1991), who described forms with a heterogeneous reticulum (lumen size distribution bimodal) as various Biorecords of the Genusbox "Crocheret." Forms with a homogeneous reticulum (lumen size distribution unimodal) were described as Biorecords of the Genusbox "Reticoll." Most dispersed species of this general type are illustrated by LM images only and typically do not show the fine details of the reticulum and columellae that distinguish the pollen types from Portugal.

D.1. Monocolpate, heterogeneous reticulate pollen with widely spaced columellae (Figs. 50–52). Pollen grains monocolpate, elliptical to circular in equatorial outline, about 10.5–13 μm in diameter, and with a long colpus reaching to the equator (Figs. 50, 51). Reticulum is heterogeneous with lumina of various sizes. The smaller lumina are about 0.2–0.5 μm in diameter, and the larger are up to about 2 μm in diameter. Muri are narrow, smooth, and low, with rounded profile, about 0.3 μm wide. Columellae are long and widely spaced (Fig. 52).

These pollen grains were observed on the surface of small spiny fruits from the Vale de Agua flora.

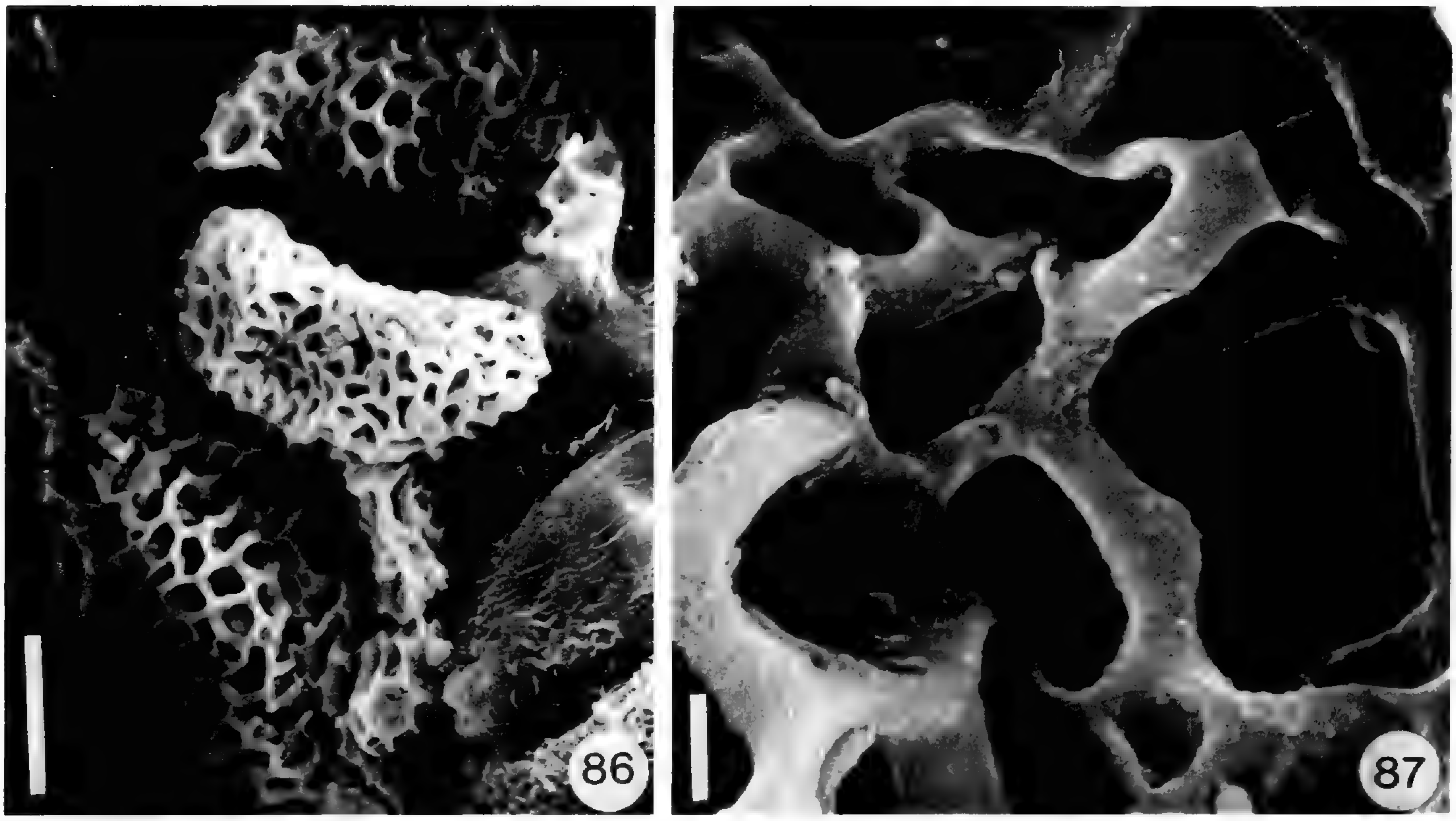
D.2. Monocolpate, homogeneous reticulate pollen with widely spaced columellae (Figs. 53–55). Pollen



Figures 78–85. Scanning electron micrographs of pollen type E and F from the Early Cretaceous (Barremian or Aptian?) Vale de Agua flora (sample 141), western Portugal. 78–82. Pollen type E, trichotomocolpate, semitectate, and reticulate pollen with graded reticulum and smooth muri, S101425. —78. Pollen grains showing distal and proximal views, ×2000; scale equal to 5 μm. —79. Distal view showing trichotomocolpate aperture, ×3000; scale equal to 5 μm. —80. Distal view showing trichotomocolpate aperture, ×3000; scale shown in Figure 79. —81. Proximal view, ×3000; scale shown in Figure 79. —82. Detail of reticulum showing short densely spaced columellae, ×10,000; scale equal to 1 μm. 83–85. Pollen type F.1, monocolpate-trichotomocolpate, and reticulate pollen with graded reticulum and smooth muri (*Anacostia portugallica*), S105039. —83. Distal view showing monocolpate aperture, ×3000; scale shown in Figure 79. —84. Proximal view showing graded reticulum, ×3000; scale shown in Figure 79. —85. Detail of reticulum showing densely spaced columellae, ×10,000; scale shown in Figure 82.

grains monocolpate, circular in equatorial outline, about 14.5 μm in diameter, and with a long colpus reaching almost to the equator (Figs. 53, 54). Reticulum is homogeneous with lumina of about the same size all over the grain, up to about 1.5 μm in diameter (Fig. 55). Muri are low, with a rounded profile, and about 0.5 μm wide. Columellae are long and widely spaced.

These pollen grains were observed in stamen fragments with elongated pollen sacs, about 0.6 mm long, from the Vale de Agua flora. They are similar in shape and reticulum pattern to dispersed grains



Figures 86, 87. Scanning electron micrographs of pollen type G from the Early Cretaceous (Barremian or Aptian?) Vale de Agua flora (sample 141), western Portugal. Monocolpate reticulate pollen with extended colpus, S101303. —86. Distal view showing extended colpus, ×1500; scale equal to 10 μm. —87. Detail of reticulum showing long, widely spaced columellae, ×10,000; scale equal to 1 μm.

illustrated and described from the Potomac Group sequence (Zone IIB, middle to late Albian) as *"Liliacidites" minutus* (= *Clavatipollenites minutus* Brenner) (Walker & Walker, 1984), but the columellae are longer and more widely spaced. As pointed out by Walker and Walker (1984) this kind of pollen differs from typical *Liliacidites* Couper grains, which have a graded reticulum. According to Walker and Walker (1984) the *"Liliacidites" minutus* grains that they described are probably identical to grains occurring throughout the Potomac Group sequence and originally assigned by Brenner (1963) to *Clavatipollenites minutus* Brenner.

D.3. Monocolpate, heterogeneous reticulate pollen with widely spaced columellae (Figs. 56, 57). Pollen grains monocolpate, more or less spherical in outline, and about 10–11 μm in diameter (Fig. 56). Colpus is weakly marked. Reticulum is heterogeneous with most lumina of more or less the same size, up to about 1.5 μm in diameter, but with some small lumina scattered over the surface. Muri are smooth and low, with a rounded profile, and about 0.4 μm wide. Columellae are medium-sized to short and widely spaced (Fig. 57).

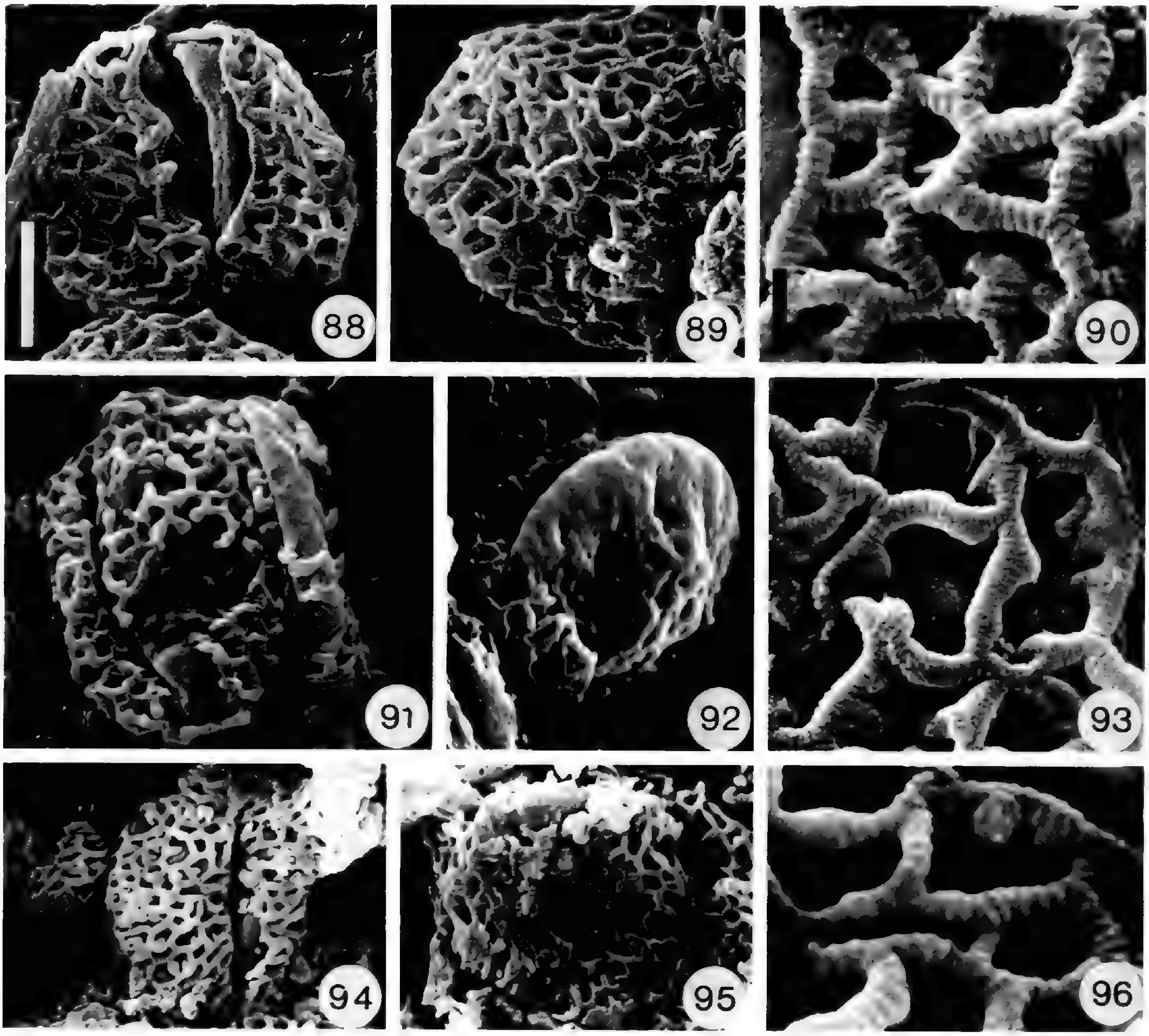
The pollen grains were found in situ in a dispersed tetrasporangiate anther, about 0.5 mm long, with few morphological details preserved, from the Vale de Agua flora.

D.4. Monocolpate, homogeneous reticulate pollen with densely spaced columellae (Figs. 58–60). Pollen grains monocolpate, elliptical to circular in equatorial outline, about 13–14 μm in diameter (Figs. 58, 59). Colpus is broad and long, reaching almost to the equator. The colpus margin is indistinct, and the colpus membrane is verrucate. Reticulum is homogeneous with lumina of more or less equal size, up to about 1.2 μm in diameter. Muri are high and narrow, about 0.2 μm wide, with rounded to triangular profile. Columellae are short and densely spaced (Fig. 60).

The pollen was observed in a fragmentary stamen from the Vale de Agua flora.

D.5. Monocolpate, heterogeneous reticulate pollen with densely spaced columellae (Figs. 61–63). Pollen grains monocolpate and elliptical to circular in outline, and about 12–13 μm in diameter (Figs. 61, 62). Colpus is long, reaching to the equator, and has a distinct margin. Reticulum heterogeneous and fine with larger lumina up to about 1.2 μm in diameter, and smaller lumina about 0.2 μm in diameter. Muri are low, with a rounded profile, and about 0.3 μm wide. Reticulum grades into a narrow foveolate to psilate zone along the colpus margin. Columellae are short and densely spaced (Fig. 63).

These pollen grains were found in situ in a small incompletely preserved and strongly abraded hypogynous and trimerous flower from the Torres Vedras flora.

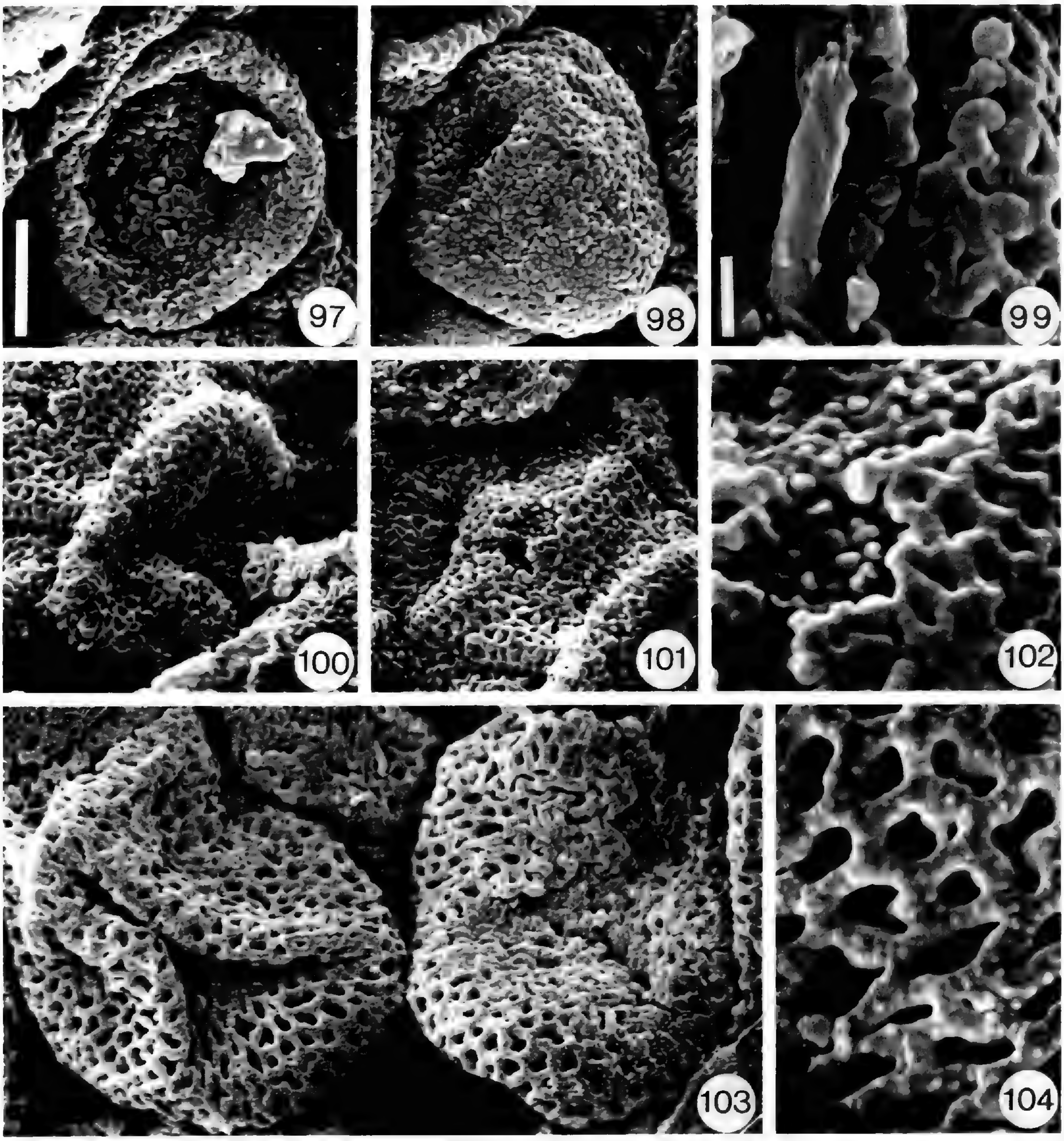


Figures 88–96. Scanning electron micrographs of pollen type I from the Early Cretaceous (Barremian or Aptian?) Vale de Agua flora, western Portugal. 88–90. Pollen type I.1, monocolpate, reticulate pollen with coarsely striate muri, S101316 (Vale de Agua sample 141). —88. Distal view showing monocolpate aperture, ×3000; scale equal to 5 μm. —89. Proximal view, ×3000; scale shown in Figure 88. —90. Detail of reticulum showing muri with coarse, transverse, striations and long columellae, ×10,000; scale equal to 1 μm. 91–93. Pollen type I.2, monocolpate, reticulate pollen with finely striate muri, S101320 (Vale de Agua sample 141). —91. Oblique distal view showing monocolpate aperture, note reticulum partially abraded and exposing the foot-layer, ×3000; scale shown in Figure 88. —92. Oblique lateral view showing partially abraded reticulum, ×3000; scale shown in Figure 88. —93. Detail of reticulum showing muri with fine, transverse, striations and long columellae, ×10,000; scale shown in Figure 90. 94–96. Pollen type I.3, monocolpate, reticulate pollen with weakly striate muri, S105602 (Vale de Agua sample 139). —94. Distal view showing monocolpate aperture, ×3000; scale shown in Figure 88. —95. Proximal view, ×3000; scale shown in Figure 88. — 96. Detail of reticulum showing muri with weak, transverse, striations, ×10,000; scale shown in Figure 90.

D.6. Monocolpate, heterogeneous reticulate pollen with widely spaced columellae (Figs. 64–66). Pollen grains monocolpate, circular in equatorial outline, and about 11.5–13.5 μm in diameter. Colpus is long with a distinct margin, and appears to extend slightly beyond the equator (Figs. 64, 65). Reticulum is heterogeneous and loosely attached, with larger lumina up to about 1.2 μm in diameter. Muri are smooth and low, with a rounded profile, about 0.5 μm wide. Columellae are medium in size to short and widely spaced (Fig. 66).

The pollen grains were found in a fragmentary stamen from the Torres Vedras flora.

D.7. Monocolpate, heterogeneous reticulate pollen with densely spaced columellae (Figs. 67, 68). Pollen grains circular in equatorial outline and about 10 μm in diameter. Reticulum is heterogeneous and loosely attached. The smaller lumina are about 0.2–0.3 μm



Figures 97–104. Scanning electron micrographs of pollen types J.1–J.3 from the Early Cretaceous (Barremian or Aptian?) Torres Vedras flora (sample 44), western Portugal. 97–99. Pollen type J.1, monocolpate pollen with a round aperture, dense reticulum and broad muri, S105019. —97. Distal view showing round aperture, ×3000; scale equal to 5 μm. —98. Proximal view, ×3000; scale shown in Figure 97. —99. Detail of reticulum and exine structure, ×10,000; scale equal to 1 μm. 100–102. Pollen type J.2, trichotomocolpate pollen with dense reticulum and broad muri, S105015. —100. Oblique distal view showing trichotomocolpate aperture, ×3000; scale shown in Figure 97. —101. Proximal view, ×3000; scale shown in Figure 97. —102. Detail of reticulum; note foot layer and columellae exposed where reticulum is partially abraded, ×10,000; scale shown in Figure 99. 103–104. Pollen type J.3, trichotomocolpate pollen with dense reticulum and broad muri, S105012. —103. Distal view of two pollen grains showing trichotomocolpate aperture, ×3000; scale shown in Figure 97. —104. Detail of reticulum with blunt protrusions, ×10,000; scale shown in Figure 99.

in diameter, and are often arranged in rows around the larger lumina, which are up to about 1.7 μm in diameter. Muri are narrow and low, with a rounded profile, and about 0.2 μm wide. Columellae are medium in size and densely spaced (Fig. 68).

The pollen grains were found in a fragmentary stamen from the Torres Vedras flora. Dispersed pollen grains from Egypt assigned by Penny (1991) to "Crochetret-Tallmur" have a comparable heterogeneous reticulum with smaller lumina in rows. However, the Egyptian grains are much larger than those from Portugal.

D.8. Monocolpate, heterogeneous reticulate pollen with densely spaced columellae (Figs. 69–71). Pollen grains monocolpate, circular in equatorial outline, about 15.5 μm in diameter. Reticulum is heterogeneous and loosely attached. Larger lumina are up to about 1.6 μm in diameter. Smaller lumina are 0.2–0.3 μm in diameter, sometimes arranged in rows. Muri narrow with an almost triangular profile, about 0.2 μm wide. Columellae very short and densely spaced (Fig. 71).

The pollen grains were found in a fragmentary laminar, dithecate and tetrasporangiate stamen from the Catefica flora. The pollen sacs are arranged in two pairs on the same side of the stamen. There is abundant sterile tissue between the two pairs of pollen sacs and also lateral to them. The stamen is broken both distally and proximally. The pollen grains resemble those described above from the Torres Vedras flora (pollen type D.7), but the columellae are shorter and more densely spaced.

D.9. Monocolpate, homogeneous reticulate pollen with widely spaced columellae (Figs. 72–74). Pollen grains monocolpate, elliptical to circular in equatorial outline, about 16.5–20.5 μm in diameter (Figs. 72, 73). All grains observed appear to be infolded over the aperture, and neither aperture margin nor aperture membrane has been observed. Reticulum is coarse and loosely attached. Lumina are of more or less equal size over the whole grain, up to about 4.5 μm in diameter. Muri are narrow and high with a rounded to triangular profile, sometimes with a narrow crest, and about 0.4 μm wide. Columellae are long and widely spaced (Fig. 74).

This pollen type occurs abundantly on the surface of small fruits with resin bodies from the Famalicão flora (Figs. 1–6). The fruits contain two endotestal and anatropous seeds with a layer of distinct crystal cells. Anatomically and morphologically the seeds are similar to those of some extant Magnoliaceae, but fruit and pollen features are unlike those of this family. The same kind of fruit has been seen in the fossil floras from Vale de Agua, Catefica, and Buarcos, but pollen grains have not been observed on the fruits from any of these other floras.

D.10. Monocolpate, heterogeneous reticulate pollen with widely spaced columellae. Pollen grains elliptical in equatorial outline, and about 10–11 μm in diameter. Aperture monocolpate with short colpus, and distinct aperture margin. Reticulum is heterogeneous with smaller lumina along the aperture margin. Muri are broad and smooth, with a rounded profile, about 0.2 μm wide. Columellae are of medium size and widely spaced.

The pollen is poorly preserved and not illustrated here. It occurs in a small fragmentary anther from the Famalicão flora.

D. 11. Monocolpate, homogeneous reticulate pollen. Pollen grain elliptical to circular in equatorial outline and about 13 μm in diameter. All grains are strongly folded, and aperture configuration is difficult to study. Reticulum dense with broad, low muri. Columellae not visible in any of the grains.

The pollen is poorly preserved and not figured here. It occurs on the stigmatic surface of a small rugulate fruit with sessile stigma from the Catefica flora.

D.12. Monocolpate, homogeneous reticulate pollen with widely spaced columellae. Pollen grains elliptical in equatorial outline, about 12 μm in diameter. Aperture monocolpate with long colpus extending to the equator. Reticulum homogeneous, loosely attached. Lumina are about 0.7 μm in diameter. Muri are smooth and low, with a rounded profile, about 0.35 μm wide. Columellae are long and widely spaced.

The pollen occurs in a small tetrasporangiate anther from the Catefica flora. They are not figured here.

D. 13. Monocolpate, heterogeneous reticulate pollen with widely spaced columellae. Pollen more or less spherical in outline, about 10–11 μm in diameter. Aperture monocolpate with long colpus reaching to the equator. Aperture margin is distinct. Reticulum is homogeneous, loosely attached. Larger lumina are up to about 1.4 μm in diameter. Muri are smooth and low, with a rounded profile, about 0.35 μm wide. Columellae are long and widely spaced.

The pollen grains were found in a small group of stamens from the Torres Vedras locality. They are not figured here.

E. Trichotomocolpate and semitectate, reticulate pollen with Liliacidites-type grading of reticulum (Figs. 78–82). One pollen type with a reticulum that grades into smaller lumina or almost psilate areas toward the ends of the aperture arms (in the equatorial region) has been observed in the Early Cretaceous floras of Portugal. This kind of graded reticulum is characteristic for many extant members of Liliales, Asperagales, and other monocotyledons (e.g., Erdtman, 1952; Alvarez & Köhler, 1987; Le Thomas et al., 1996). Dispersed fossil pollen grains with this type of reticulum were first described as *Liliacidites* (Couper, 1953) from the Late Cretaceous of New Zealand and have been reported from numerous Cretaceous palynofloras (Doyle et al., 1977; Doyle & Robbins, 1977; Walker & Walker, 1984; Ward et al., 1989). *Liliacidites*-type pollen from the Aptian of Egypt was assigned to the Biorecord "Crochetret-Endsmall" (Penny, 1991). We refer to this kind of grading of the reticulum as *Liliacidites*-type grading in contrast to the *Similipollis*-type of grading, in which the larger lumina occur around the equator and decrease in size toward the aperture margins and the proximal pole (see pollen type F).

The Portuguese pollen grains are triangular in equatorial outline and about 13.5–16 μm in diameter (Figs. 78–80). Aperture is trichotomocolpate. Arms of aperture long, extending over the equatorial rim to the proximal side of the grain (Figs. 78, 79). Only trichotomocolpate forms were observed in the anther, and apparently this plant produced only pollen grains with one type of aperture (in contrast to the *Anacostia*-plant described below, pollen type F.1 and F.2). Aperture margin is distinct. Tectum is coarsely reticulate over most of the grain with lumina up to about 1.5 μm in diameter. Toward the aperture margin and around the three corners of the grains at the ends of the aperture arms the reticulum grades into a narrow foveolate to psilate zone (Fig. 78). Muri are low, with rounded profile and a smooth surface, about 0.3 μm wide. They are supported by short, densely spaced columellae (Fig. 82). Ultrathin sections of the grains show that the pollen wall has a thick foot layer and well-developed endexine under the aperture.

The pollen grains were observed in a dispersed stamen from the Vale de Agua flora. The stamen is about 1 mm long and consists of a short, broad filament bearing a tetrasporangiate anther with a triangular apical extension of the connective (Friis et al., 1994b, fig. 8d).

These pollen grains are similar to dispersed grains assigned to *Liliacidites* in having the foveolate-psilate part of the tectum concentrated around the aperture margin and at the ends of the aperture arms, but *Liliacidites* typically has a monocolpate aperture. Monocolpate *Liliacidites* grains illustrated from the Potomac Group sequence (Zone IIB, middle-late Albian) have similar low, rounded and psilate muri supported by short, densely spaced columellae, but the foot layer is extremely thin in these grains. A graded reticulum, similar to that of *Liliacidites*, is known for pollen of several monocotyledonous plants (e.g., Liliaceae) and to our knowledge has not been reported from the Magnoliidae. Previous authors (e.g., Doyle, 1973; Walker & Walker, 1984) also noted several monocotyledonous features for the North American *Liliacidites* grains.

F. Monocolpate, semitectate, and reticulate pollen with Similipollis-type grading of reticulum (Figs. 83–85). Two-pollen type with a graded reticulum in which the lumina decrease in size from the equatorial area toward the aperture margins and proximal pole. Dispersed pollen grains with a comparable graded reticulum have been reported from various Early Cretaceous palynofloras in Europe, North America, and Africa (Doyle, 1973; Doyle et al., 1977; Walker & Walker, 1986). The genus *Similipollis* was established to accommodate this kind of dispersed fossil pollen (Góczán & Juhász, 1984), but in earlier studies such grains were typically assigned to the genera *Liliacidites* and *Retimonocolpites* (see discussion in Friis et al., 1997a). Pollen grains of this type closely resemble those of some extant palms (Walker & Walker, 1986; Harley, 1997). We refer to this kind of grading as the *Similipollis*-type to distinguish it from the type of grading in which the smaller lumina occur at the ends of the aperture in the equatorial regions (*Liliacidites*-type grading, see pollen type E).

F.1. Monocolpate-trichotomocolpate pollen (Anacostia portugallica) (Figs. 83–85). Pollen grains more or less circular in equatorial outline and 14.5–18.3 μm in diameter. Aperture is symmetrical or asymmetrical monocolpate or trichotomocolpate (Fig. 83). Arms of the aperture sharply delimited with rounded ends. Tectum is foveolate to reticulate with lumina decreasing in size toward the aperture and toward the proximal pole (Figs. 83, 84). Larger lumina are up to about 1.2 μm. Muri are smooth and low, with rounded profile, and about 0.35–0.4 μm wide. Columellae are short and densely spaced (Fig. 85).

This pollen type was found associated with the fruits of *Anacostia portugallica* in the Vale de Agua flora (Friis et al., 1997a). Fruits of *Anacostia portugallica* with pollen grains attached to the surface have also been recorded from the Buarcos flora. Fruits of this species also occur in the Famalicão flora, but none of these have pollen preserved. Fruits assigned to another species of *Anacostia*, *A. teixeirae*, occur abundantly in the Famalicão flora and are also reported from Buarcos, and pollen grains observed on a specimen from Famalicão are very similar to those of *A. portugallica*. In the Potomac Group sequence numerous fruits of *Anacostia* have been recovered from the Kenilworth and Puddledock localities. These are assigned to two distinct species: *A. marylandensis* Friis, Crane & Pedersen and *A. virginiensis* Friis, Crane & Pedersen, both with similar monocolpate-trichotomocolpate grains adhering to the stigma and fruit wall (Friis et al., 1997a). The pollen grains in the two North American species and the Portuguese material are distinguished from each other by subtle details of the reticulum.

Although the pollen adhering to *Anacostia* show resemblance to that of some palms, the *Anacostia* fruiting units are unlike palm fruits and show some similarities in fruit and seed characters to magnoliid taxa (Friis et al., 1997a).

F.2. Monocolpate-trichotomocolpate pollen (Anacostia teixeirae). Pollen grains observed on the fruits of *Anacostia teixeirae* from the Famalicão flora are poorly preserved. They are closely similar to those of *A. portugallica* in form and reticulum grading but are slightly smaller, about 11–13 μm in diameter. Fruits of this species also occur in the Buarcos flora, but no pollen was observed on this material.

G. Monocolpate, semitectate, reticulate pollen with extended colpus (Figs. 86, 87). One monocolpate pollen type with a distinctly extended colpus has been observed in the Early Cretaceous floras from Portugal. Pollen grains are circular in equatorial outline and about 23–25 μm in diameter. Colpus is long, extending beyond the equator (Fig. 86), but its total extent is not clear in any of the specimens observed. Tectum is coarsely reticulate. Lumina typically of the same size, up to about 4.5 μm in diameter, with a few smaller lumina scattered over the grain. Muri are high with an acute triangular profile and about 0.6 μm wide. Columellae are long and widely spaced (Fig. 87).

The pollen grains were found in a dispersed stamen from the Vale de Agua flora figured by Friis et al. (1994b, fig. 8a, b). The stamen is dorsiventrally flattened and has a strongly thickened filament that is not well differentiated from the anther. The fertile portion of the stamen is small compared to the rest of the structure. The anther is dithecate and tetrasporangiate with two pairs of pollen sacs in a lateral position separated by a massive connective. The connective is extended apically into an almost quadrangular protrusion above the pollen sacs. The filament and connective have irregular hemispherical swellings on the surface that are thought to indicate the position of ethereal oil cells. We have not identified similar dispersed pollen in any Early Cretaceous palynoflora.

H. Periporate, semitectate, reticulate pollen (Figs. 75–77). One periporate pollen type has been observed in the Early Cretaceous floras of Portugal. Pollen grains almost spherical in outline, about 19 μm in diameter (Fig. 76). Pores are poorly defined and are seen as small, slightly sunken granular areas that are scattered over the entire grain (Figs. 75, 76). Pollen wall is coarsely reticulate with a homogeneous reticulum. The reticulum often appears contracted with muri closely appressed. Lumina are up to about 2 μm in diameter. Muri are smooth and high, with a rounded to triangular profile, about 0.5 μm wide. Columellae are short, densely spaced, and sometimes have the appearance of granulae rather than columellae (Fig. 77).

The pollen grains were found in a tetrasporangiate anther from the Famalicão locality. Dispersed pollen matching these in situ grains has not been observed in Cretaceous palynofloras as far as we are aware. The pollen grains are closely similar to those of the extant genus *Sarcandra* Gard. of the Chloranthaceae, but the stamen differs from those of modern *Sarcandra* and *Chloranthus* Sw. (the other insect-pollinated genus of the Chloranthaceae) in having larger pollen sacs and in lacking an extensive connective between them. Periporate pollen also occur in several monocotyledonous families (Dahlgren & Clifford, 1981). Eudicototyledonous taxa with periporate pollen occur in widely separate orders.

I. Monoaperturate, semitectate, reticulate pollen with transversely striate muri (Figs. 88–96). Three closely similar pollen types have been found in the Portuguese fossil floras. All three occur in the Vale de Agua flora, and one type also occurs in the Famalicão flora. They are distinguished from each other mainly by their size and details of the supratectal ornamentation, which varies from very fine in one species (Figs. 91–93) to relatively coarse in the two other species (Figs. 88–90, 94–96). Dispersed pollen comparable to these three types has been tentatively assigned to *Retimonocolpites* (Walker & Walker, 1984). From Egypt Penny (1991) assigned similar pollen with striate muri from the late Barremian-early Aptian to the biorecord "Reticoll-Springmur." Similar grains have also been reported from the Barremian of southern England as various forms of the biorecords "Barremian-teebac" (Hughes, 1994) and "Retisulc-muriverm" (Hughes & McDougall, 1987).

I.1. Monocolpate pollen with coarsely striate muri (Figs. 88–90). Pollen grains elliptical to spherical in outline, about 13–14 μm in diameter. Aperture monocolpate with a long colpus extending to the equator (Fig. 88). Colpus margin is distinct. Tectum is reticulate with a homogeneous reticulum and lumina of more or less equal size, up to about 2 μm in diameter. Muri are low, with a rounded profile, about 0.4 μm wide. They are ornamented with distinct transverse ridges that give the muri a coarse transversely striate appearance. Columellae are long and widely spaced (Fig. 90).

The pollen grains occur in a small stamen with resin bodies from the Vale de Agua flora and have also been found in the same flora on the surface of small unilocular fruits and single-seeded hairy fruits. Very similar pollen also occurs abundantly on a fruit type from the Famalicão flora, but this fruit type differs from that of the Vale de Agua flora in several respects.

I.2. Monocolpate pollen with finely striate muri (Figs. 91–93). Pollen grains elliptical to spherical in outline, about 12–14 μm in diameter. Aperture monocolpate with a long colpus extending to the equator (Figs. 91–92). Colpus margin is distinct. Tectum is reticulate with a homogeneous, loosely attached reticulum and lumina of more or less equal size, up to about 2.5 μm in diameter. Muri are low, with a rounded profile, about 0.3 μm wide. They are ornamented with fine, densely spaced transverse ridges that give the muri a fine transversely striate appearance. Columellae are long and more closely spaced than in pollen type I.1 (Fig. 93).

The pollen grains were found on the surface of a hairy fruiting structure from the Vale de Agua flora, and were also observed in a fragmentary stamen from the Torres Vedras flora.

I.3. Monocolpate pollen with coarsely striate muri (Figs. 94–96). Pollen grains elliptical to spherical in outline, about 10–11 μm in diameter. Aperture monocolpate with a long colpus extending to the equator (Figs. 94, 95). Colpus margin is distinct. Tectum is reticulate with a homogeneous and loosely attached reticulum and lumina of more or less equal size, up to about 2 μm in diameter. Muri are low, with a rounded profile, about 0.3 μm wide. They are ornamented with transverse ridges that give the muri a coarse transversely striate appearance. Columellae are short and widely spaced (Fig. 96).

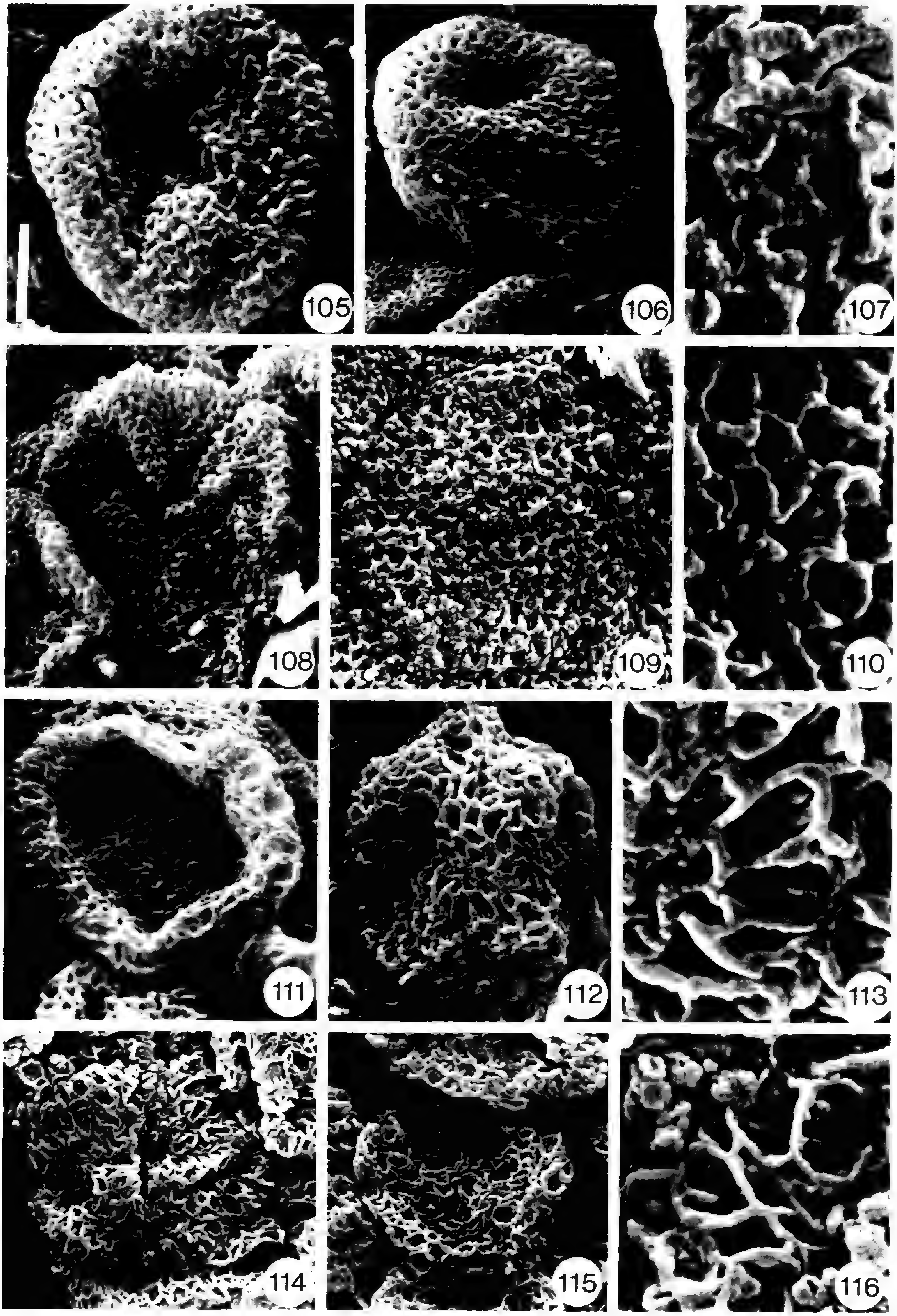
This pollen type is slightly smaller than the two other pollen types with striate muri (I.1, I.2). Ornamentation of the muri is rather coarse and similar to that described for pollen type I.1, but lumina are larger. The pollen grains were found in a well-preserved tetrasporangiate anther from the Vale de Agua flora.

J. Monocolpate, trichotomocolpate, and pentachotomocolpate, semitectate, reticulate pollen with beaded muri (Clavatipollenites-Asteropollis-type) (Figs. 97–121). Several closely similar pollen types with mono-, trichotomo-, and tetrachotomocolpate apertures and beaded ornamentation of the muri have been found in all five of the Portuguese floras. Pollen of this general type is also common in dispersed palynofloras from the Early Cretaceous, where they are typically assigned to species of *Clavatipollenites* and *Asteropollis* Hedlund & Norris. From the Early Cretaceous of southern England similar grains were assigned to the biorecord taxa "Retichot-baccat," "Retisulc-monbac," "Aptianlongcol," and "Retisulc-dident" (Hughes, 1994), and one type with beaded muri was reported from the late Barremian of Egypt as "Reticoll-speckle" (Penny, 1991). Species of *Clavatipollenites* have been compared to pollen of extant *Ascarina* (Couper, 1958; Walker & Walker, 1984), while species of *Asteropollis* have been compared to pollen of extant *Hedyosmum* (Walker & Walker, 1984); both are Chloranthaceae. The Chloranthaceae affinity of at least some *Asteropollis* pollen has now been established by the discovery of pollen grains associated with *Hedyosmum*-like pistillate flowers and stamens in the Early Cretaceous floras of Portugal (see above). However, monoaperturate pollen with beaded ornamentation of the muri also occur outside the Chloranthaceae (e.g., Lactoridaceae, Saururaceae; Walker, 1976), and some of the pollen types may belong to other families.

J.1. Monoaperturate pollen with a round aperture, dense reticulum, and broad muri (Figs. 97–99). Pollen grains almost circular in equatorial outline (Figs. 97, 98), about 14–16 μm in diameter, with a broad and round aperture that is indistinctly delimited and has a verrucate colpus membrane (Fig. 97). Tectum is densely reticulate. Lumina are typically condensed, about 0.6 μm in diameter. Muri are low, with a rounded profile, about 0.5 μm wide. They are ornamented with very small blunt protrusions that are often arranged in two rows along the edge of the muri. Columellae are of medium size and spacing (Fig. 99).

The pollen grains were found in stamens from the Torres Vedras locality.

J.2. Trichotomocolpate pollen with dense reticulum and broad muri (Figs. 100–102). Pollen grains circular in equatorial outline and about 12.5–13.5 μm in diameter (Figs. 100, 101). In most specimens the aperture is not visible, but in all grains where the aperture is visible it appears be trichotomocolpate with rather short arms. Tectum is semitectate and densely reticulate with lumina up to about 0.6 μm in diameter. Muri are low, with rounded profile, about 0.3 μm wide. They are ornamented with very small blunt protrusions that are



Figures 105–116. Scanning electron micrographs of pollen types J.4 —J.7 from the Early Cretaceous (Barremian or Aptian?) Vale de Agua flora, western Portugal. 105–107. Pollen type J.4, trichotomo- to tetrachotomocolpate pollen

often arranged in two rows. Columellae are of medium size and spacing.

The pollen grains were observed in a group of several stamens from the Torres Vedras flora (Fig. 3). The arrangement of the stamens shows that they were originally arranged in densely spaced whorls. The anthers are tetrasporangiate and elongated, about 0.7 mm long. The arrangement and shape of the stamens is similar to that seen in male inflorescences of extant *Hedyosmum* of the Chloranthaceae. This pollen type is very similar to that described above (pollen type J.1) in shape and reticulum pattern but differs in its clearly different aperture configuration.

J.3. Trichotomocolpate pollen with dense reticulum and broad muri (Figs. 103, 104). Pollen grains almost circular in equatorial outline and about 18–22 µm in diameter (Fig. 103). Aperture weakly defined, trichotomocolpate with aperture arms that reach almost to the equator, and a verrucate colpus membrane. Tectum is semitectate with a relatively dense homogeneous reticulum with lumina up to about 1.2 µm in diameter. Muri are low, with rounded profile, about 0.4 µm wide. They are ornamented by very small blunt protrusions that are typically arranged in two rows. Columellae are of medium size and widely spaced (Fig. 104). This pollen type shows resemblance to pollen type J.1 and J.2 in shape and tectum structure, but it is larger and has somewhat larger lumina.

The pollen grains were observed in an elongate tetrasporangiate anther, about 0.7 mm long, from the Torres Vedras flora.

J.4. Trichotomo- to pentachotomocolpate pollen with dense reticulum and broad muri (Figs. 105–107). Pollen grains more or less circular in outline, about 15–20 µm in diameter (Figs. 105, 106). Aperture trichotomo-, tetrachotomo-, or pentachotomocolpate with short aperture arms, weakly defined aperture margin, and verrucate aperture membrane. Tectum is densely reticulate with lumina of approximately equal size, up to about 1.5 µm in diameter. Muri are low, with rounded profile, about 0.5 µm wide. They are ornamented by very small blunt protrusions that are often arranged in two rows. Columellae are of medium size and spacing (Fig. 107).

Pollen grains of this type have been found in stamens and on the surface of *Hedyosmum*-like pistillate flowers from the Catefica, Torres Vedras, Vale de Agua, and Buarcos localities. *Hedyosmum*-like pistillate flowers also occur in the Famalicão flora, but no pollen was observed in this material.

J.5. Monoaperturate (monocolpate to tetrachotomocolpate?) pollen with open reticulum and narrow muri (Figs. 108–110). Pollen grains more or less circular in equatorial outline and about 16–17 µm in diameter (Figs. 108, 109). The aperture is very indistinct, apparently with up to four or five arms and verrucate colpus membrane. Tectum with an open reticulum and lumina of more or less equal size up to about 1.5 µm in diameter. Muri are narrow and low, with a rounded profile, and about 0.2 µm wide. They are ornamented by low blunt protrusions arranged in a single row. Columellae are long, broad, and medium spaced (Fig. 110).

This type of pollen was recovered in an elongated stamen, about 0.7 mm long, from the Vale de Agua flora.

J.6. Monoaperturate pollen with an irregular aperture, open reticulum and narrow muri (Figs. 111–113). Pollen grains more or less circular in equatorial outline and about 15 µm in diameter (Figs. 111, 112). The aperture is broad and weakly delimited, irregularly rounded to slightly triangular in outline. The tectum is open reticulate with lumina of more or less the same size, up to about 2.5 µm in diameter. Muri are narrow and low, with a rounded profile, about 0.3 µm wide. They are ornamented by small blunt protrusions arranged in a single row. Columellae are high and occasionally densely spaced (Fig. 113).

The pollen occurs in a fragmentary stamen, about 0.6 mm long, from the Vale de Agua flora,

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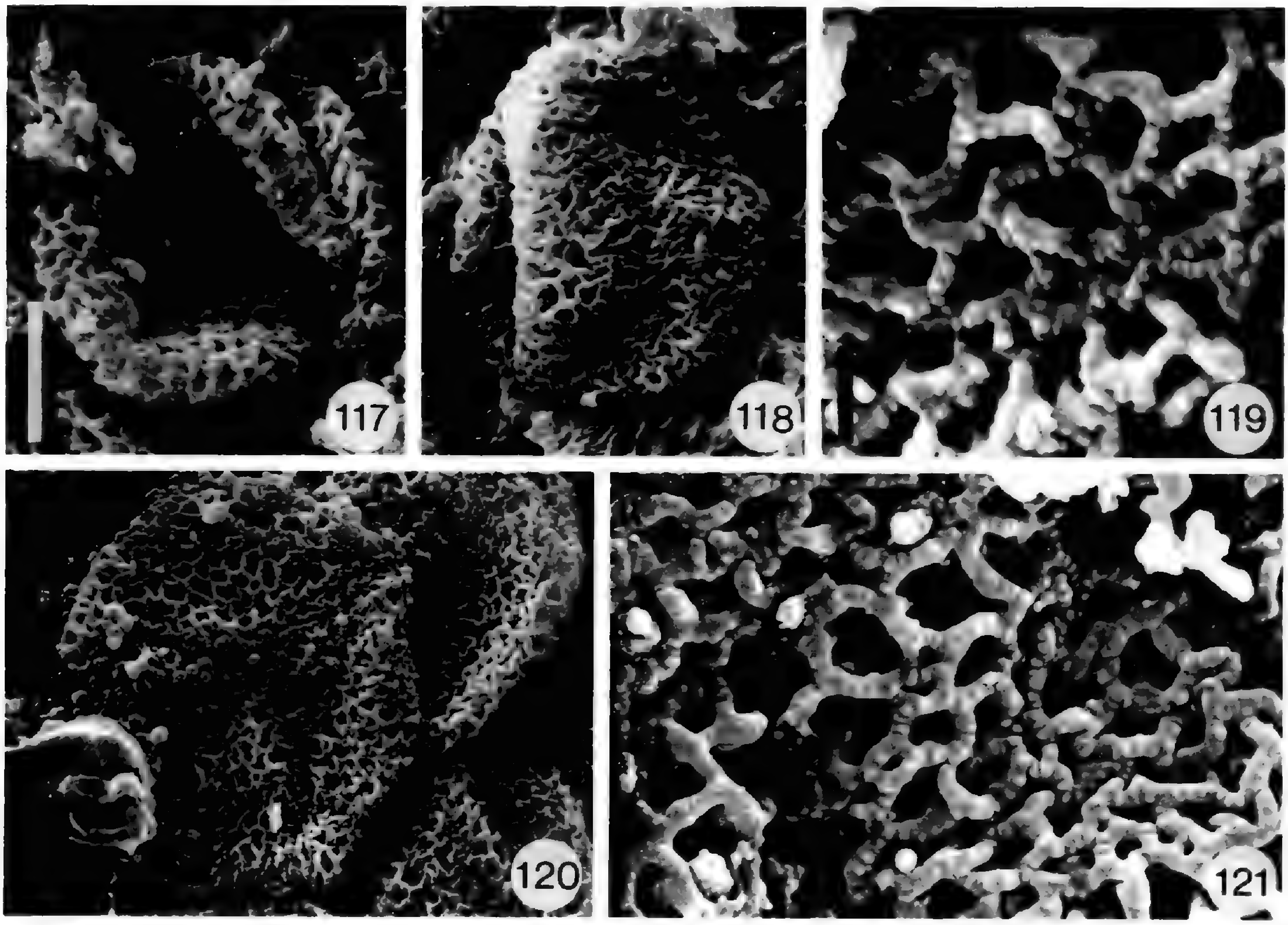
with dense reticulum and broad muri, S105259 (Vale de Agua sample 141). —105. Distal view showing tetrachotomocolpate aperture, ×3000; scale equal to 5 µm. —106. Proximal view, ×3000; scale shown in Figure 105. —107. Detail of reticulum, ×10,000; scale equal to 1 µm. 108–110. Pollen type J.5, monoaperturate (monocolpate to tetrachotomocolpate?) pollen with open reticulum and narrow muri, S105324 (Vale de Agua sample 139). —108. Distal view, ×3000; scale shown in Figure 105. —109. Proximal view, ×3000; scale shown in Figure 105. —110. Detail of reticulum, ×10,000; scale shown in Figure 107. 111–113. Pollen type J.6, Monoaperturate pollen with irregular aperture, open reticulum, and narrow muri, S105659 (Vale de Agua sample 139). —111. Distal view, ×3,000; scale shown in Figure 105. —112. Proximal view, ×3000; scale shown in Figure 105. —113. Detail of reticulum, ×10,000; scale shown in Figure 107. 114–116. Pollen type J.7, monocolpate pollen with open reticulum and narrow muri, S105322 (Vale de Agua sample 139). —114. Distal view showing monocolpate aperture, ×3000; scale shown in Figure 105. —115. Proximal view, ×3000; scale shown in Figure 105. —116. Detail of reticulum, ×10,000; scale shown in Figure 107.



Figures 117–121. Scanning electron micrographs of pollen types J.8 and J.9 from the Early Cretaceous (Barremian or Aptian?) Famalicão flora (sample 25) western Portugal. 117–119. Pollen type J.8, trichotomocolpate pollen with open reticulum and narrow muri, S105176. —117. Distal view showing trichotomocolpate aperture, ×3000; scale equal to 5 μm. —118. Proximal view, ×3000; scale shown in Figure 117. —119. Detail of reticulum, ×10,000; scale equal to 1 μm. 120–121. Pollen type J.9, trichotomocolpate pollen with open reticulum and narrow muri, S101222. —120. Distal view showing distinct trichotomocolpate aperture, ×3000; scale shown in Figure 117. —121. Detail of reticulum, ×10,000; scale shown in Figure 119.

and similar grains have also been observed on the surface of a fruit in the same flora.

J.7. Monocolpate pollen with open reticulum and narrow muri (Figs. 114–116). Pollen grains circular in equatorial outline and about 12–13 μm in diameter (Figs. 114, 115). Aperture is monocolpate with a long colpus that reaches to the equator. Aperture margin is distinct, but the membrane has not been observed in any of the specimens. The tectum is open reticulate with lumina of two sizes. Larger lumina are up to 1.4 μm in diameter, and smaller lumina are about 0.25 μm in diameter. Muri are narrow and low, with a rounded profile, about 0.2 μm wide. They are ornamented by faintly developed protrusions. Columellae are long and widely spaced (Fig. 116).

The pollen grains were found in a fragmentary stamen from the Vale de Agua flora.

J.8. Trichotomocolpate pollen with open reticulum and narrow muri (Figs. 117–119). Pollen grains almost circular in outline, about 13 μm in diameter, with a trichotomocolpate aperture (Figs. 117, 118). Arms of the aperture short and broad. Reticulum is open and heterogeneous with lumina ranging in size from about 0.2 μm to 1.2 μm in diameter. Muri are narrow, about 0.3 μm wide, with a rounded profile. They are ornamented by one row of small blunt to spiny protrusions. Columellae are high and relatively densely spaced (Fig. 119).

This pollen type was found in dispersed tetrasporangiate anthers from the Famalicão flora. The anther is about 0.8 mm long and 0.35 mm broad with little sterile tissue between the pollen sacs.

J.9. Trichotomocolpate pollen with open reticulum and narrow muri (Figs. 120, 121). Pollen grains almost circular in outline, about 15 μm in diameter (Fig. 120). Aperture is distinct and trichotomocolpate in most specimens showing the aperture, but monocolpate specimens are apparently also present. Reticulum is heterogeneous with smaller lumina about 0.1 μm and larger lumina up to about 0.6 μm. Muri are narrow, about 0. 3 μm broad, rounded in cross section. They are ornamented by one row of small rounded to spiny processes. Columellae are high and widely spaced (Fig. 121). Ultrastructural study of the pollen wall shows that the endexine is thick and granular under the aperture, but lacking or extremely thin in non-apertural regions (Pedersen et al., 1994a).

This pollen type was found in dispersed anthers from the Famalicão flora. The pollen grains are very similar to those described above (pollen type J.8), but they are slightly larger and have more widely spaced columellae.

The pollen grains from Famalicão are comparable to dispersed grains reported from the Barremian to early Albian of Egypt as "Trichoto-Beatle" (Penny, 1991). They also show some resemblance to slightly larger grains described from the Barremian of southern England as "CfA Retichot-*baccat*" (Hughes, 1994).

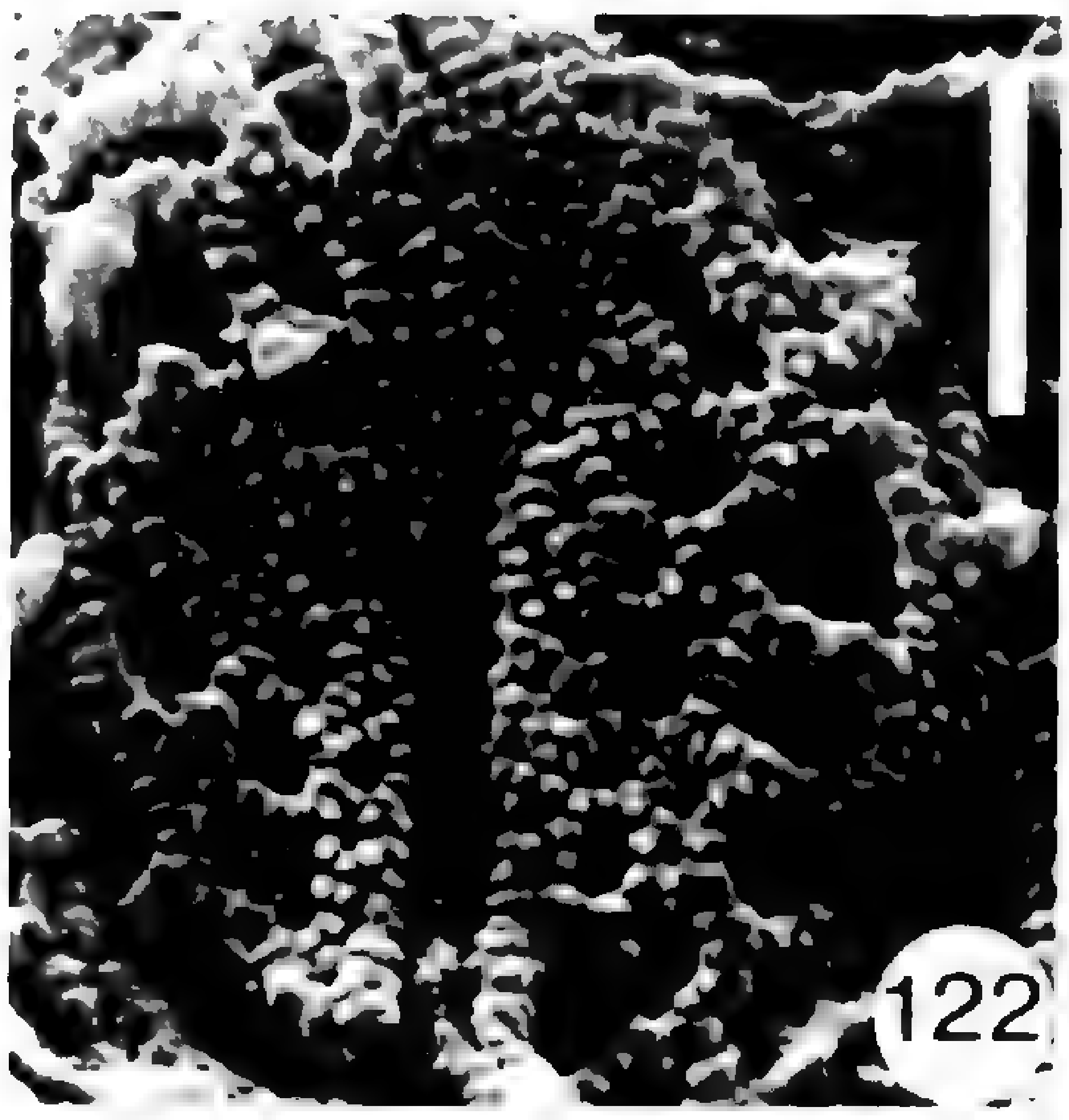
J.10. Monoaperturate pollen with a round aperture, dense reticulum, and broad muri. Pollen grains elliptical in equatorial outline and about 16 μm in diameter. Aperture margin and aperture membrane not exposed. Tectum reticulate with lumina of various sizes. Muri are low, with rounded profile, about 0.3 μm wide. They are ornamented with low blunt processes that are often arranged in two rows. Columellae are of medium size and widely spaced.

The pollen is poorly preserved and not illustrated here. It occurs in a small anther with resin bodies from the Torres Vedras flora. It is very similar to pollen grains associated with fruits of *Couperites mauldinensis* Pedersen, Crane, Drinnan & Friis described from the early Cenomanian of Maryland, U.S.A. (Pedersen et al., 1991) and to dispersed pollen grains assigned to the genus *Clavatipollenites*. Similar pollen was reported from the Barremian of southern England as "Reticulc-monbac" (e.g., Hughes, 1994).

K. Monoaperturate, semitectate, acolumellate, and reticulate pollen with spinulate muri (Figs. 122–132). Pollen grains of this very distinctive type lack columellae and have a very coarse and loosely attached reticulum. They occur abundantly in one sample from the Vale de Agua locality where they are found within stamens and adhering to many specimens of one particular type of fruit. They also occur in many coprolites where they are apparently the only constituents (Figs. 131, 132). Material from this Vale de Agua sample is generally of poor preservation, but some of the anthers are sufficiently well preserved to show the tetrasporangiate organization and the presence of an apical extension of the connective. The stamens differ in size and shape and include pollen grains that differ from each other in details of muri ornamentation and lumen size. Three different species have been distinguished so far. A cluster of dispersed stamens with similar pollen has also been recovered from the early Cenomanian Elk Neck Beds near Mauldin Mountain in northern Maryland, U.S.A. (Crane & Herendeen, 1996). These stamens are also tetrasporangiate with a short apical connective and a very short filament.

Closely similar dispersed pollen grains have been reported from many localities in Europe, Africa, and North America and are sometimes very abundant (Penny, 1988). They range from the Barremian through to the Cenomanian and perhaps to the Turonian (Penny, 1988). The Barremian record from southern England includes pollen with scattered columellae, while the younger records are all acolumellate. They are particularly prominent in Early Cretaceous palynofloras from Egypt and are also common in the Early Cretaceous of North America. From Egypt, 13 different taxa were distinguished from the Mersa Matruh borehole, ranging in age from the earliest Aptian to the Early Albian (Penny, 1988). In these Egyptian samples pollen grains of this type attained their maximum abundance and diversity in the Aptian. The acolumellate taxa from the Mersa Matruh borehole are assigned to the Genusbox "RETIMONO," and different biorecords are distinguished based on pollen size, lumen size and distribution, muri configuration, and supratectal ornamentation. Pollen of this distinctive complex was first described from dispersed grains observed in the Potomac Group sequence and assigned to the genus *Peromonolites* Couper, a dispersed genus established for pteridophyte spores. Two species were recognized, *P. peroreticulatus* Brenner and *P. reticulatus* Brenner (Brenner, 1963). Subsequently both were transferred to the genus *Retimonocolpites* by Doyle et al. (1975) and later to the genus *Brenneripollis* Juhász & Góczán (Juhász & Góczán, 1985). The type species of both *Retimonocolpites* and *Brenneripollis* are different from the acolumellate pollen described here, and Penny (1988) pointed out that neither of these genera are appropriate for this pollen type. Although Doyle (1992) later argued that the holotype of *Brenneripollis*, which was studied using LM only, was perhaps also acolumellate, we follow Penny and exclude the *peroreticulatus* and *reticulatus* species from *Brenneripollis*.

TEM studies of ultrathin sections of the pollen wall of the Portuguese specimens show that although the grains are acolumellate, there is a thin finely granular infratectal layer at the base of the muri. The ektexine is otherwise thick with a thick foot layer and high muri of the tectum. The inner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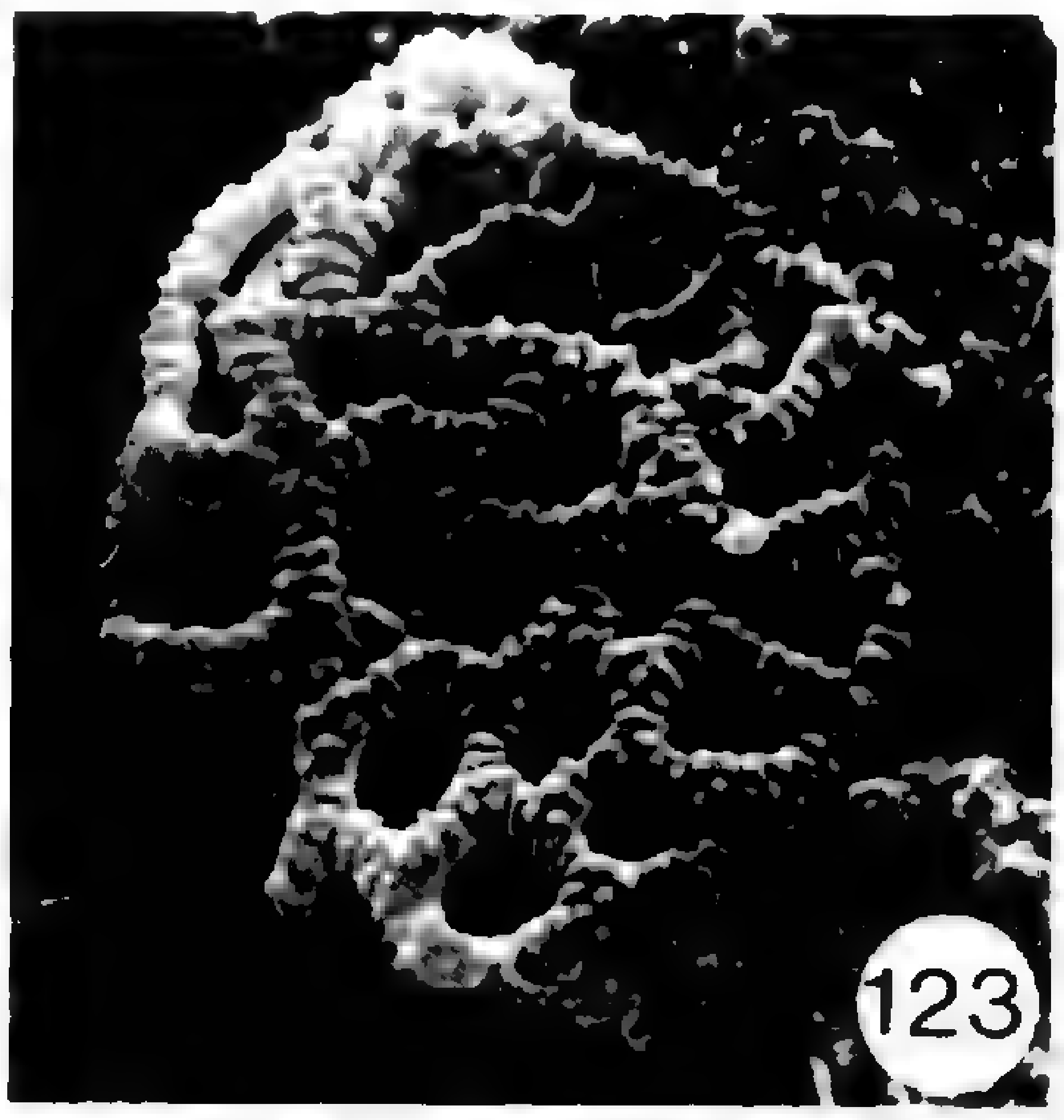
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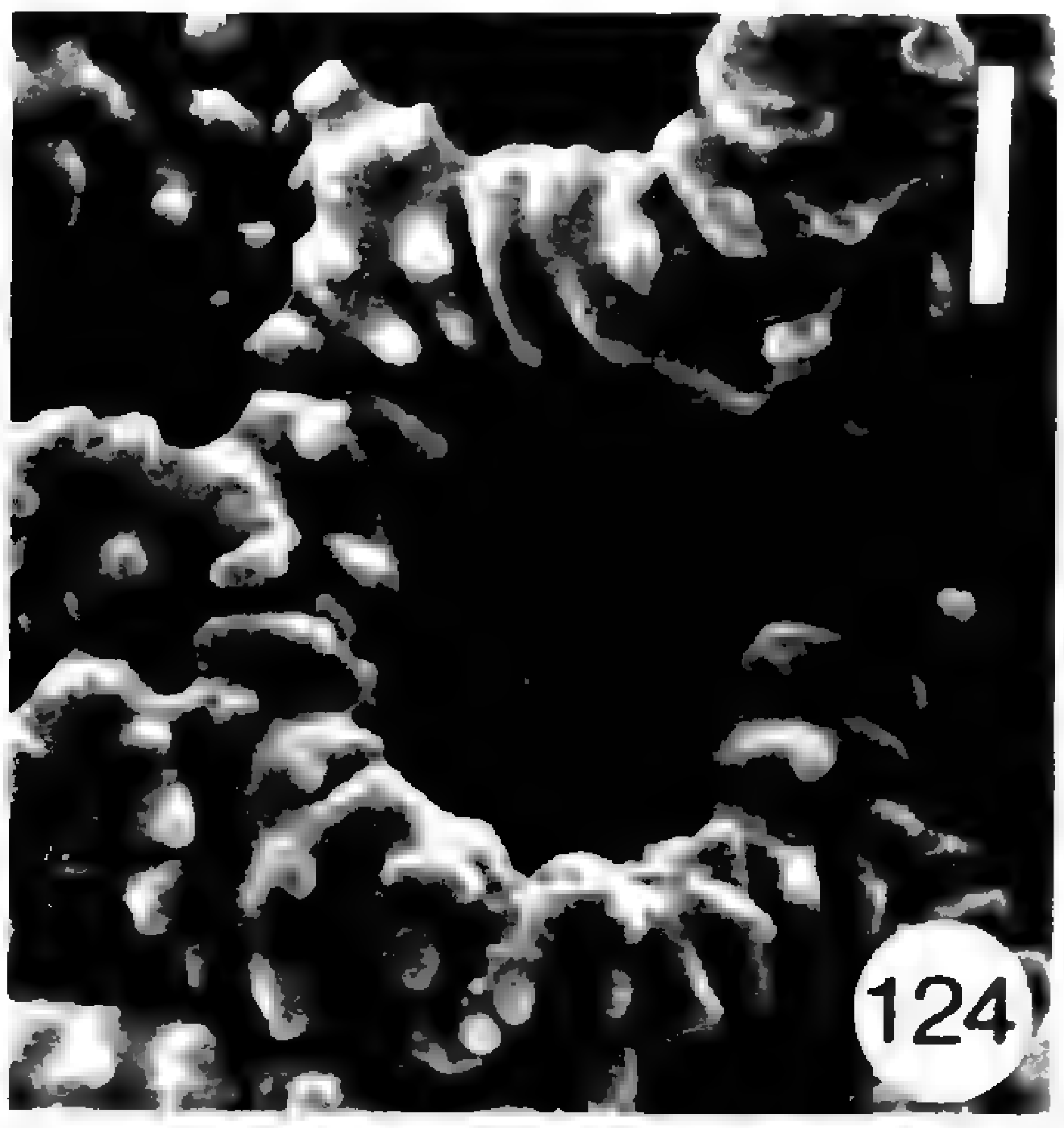
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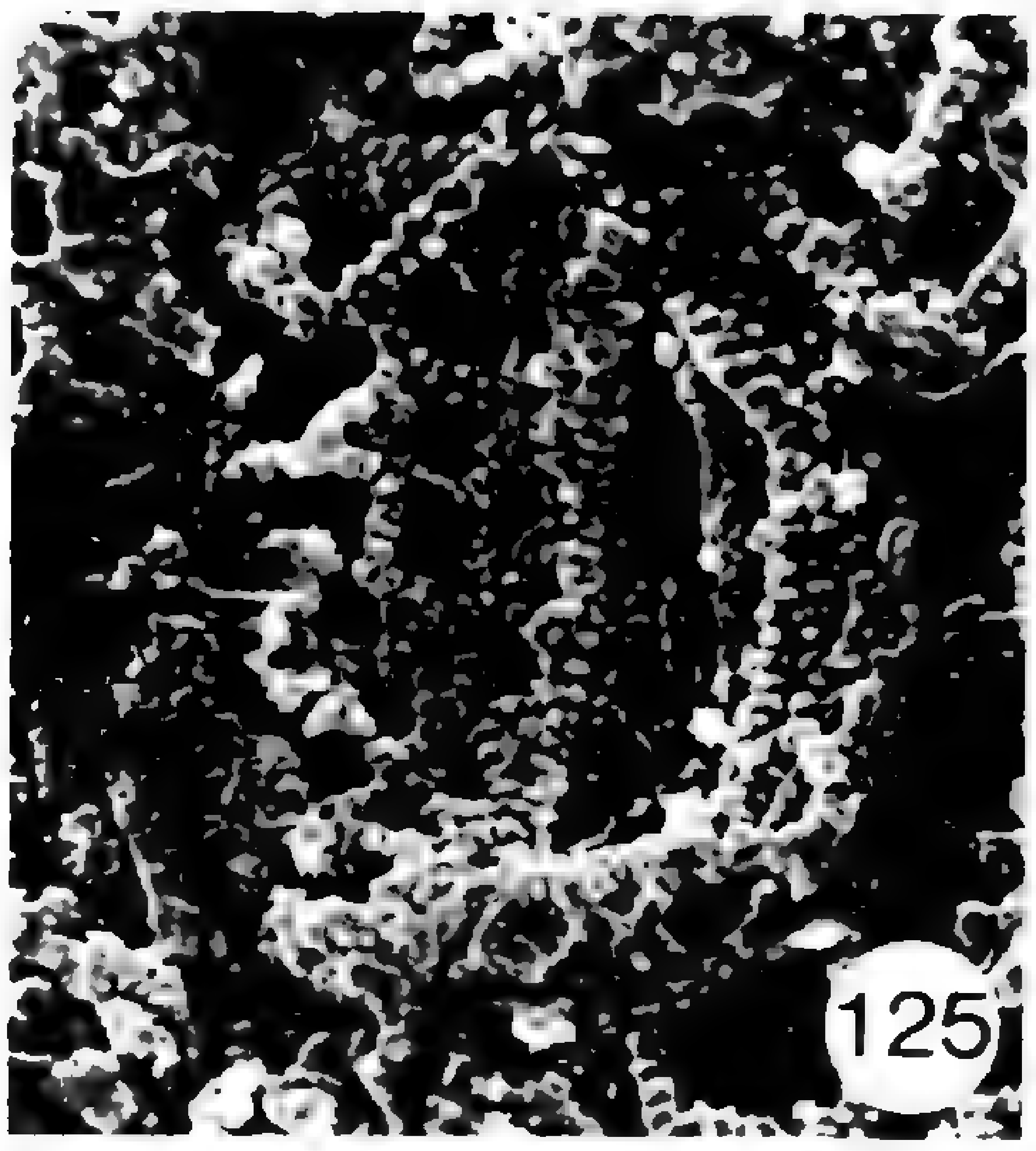
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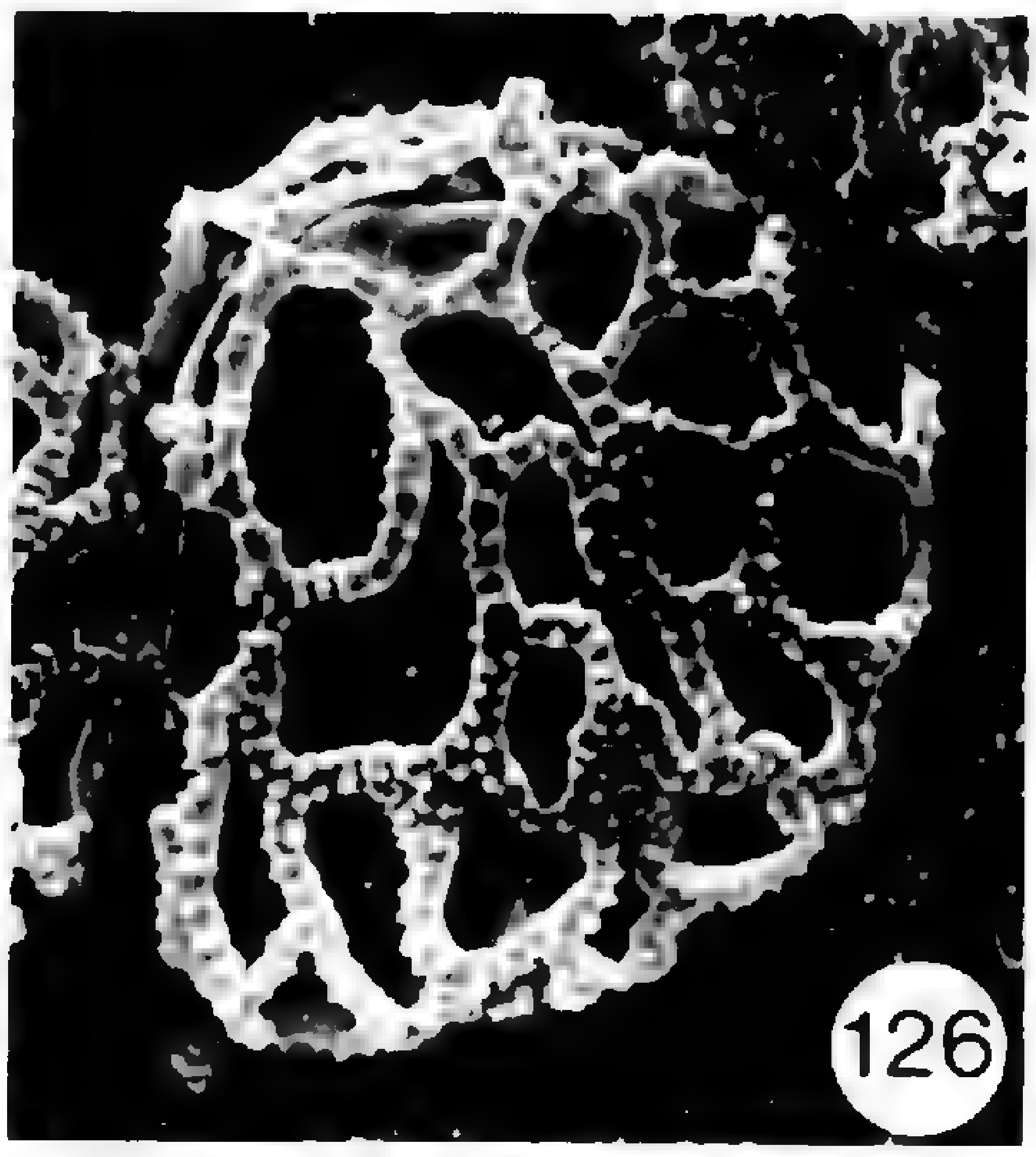
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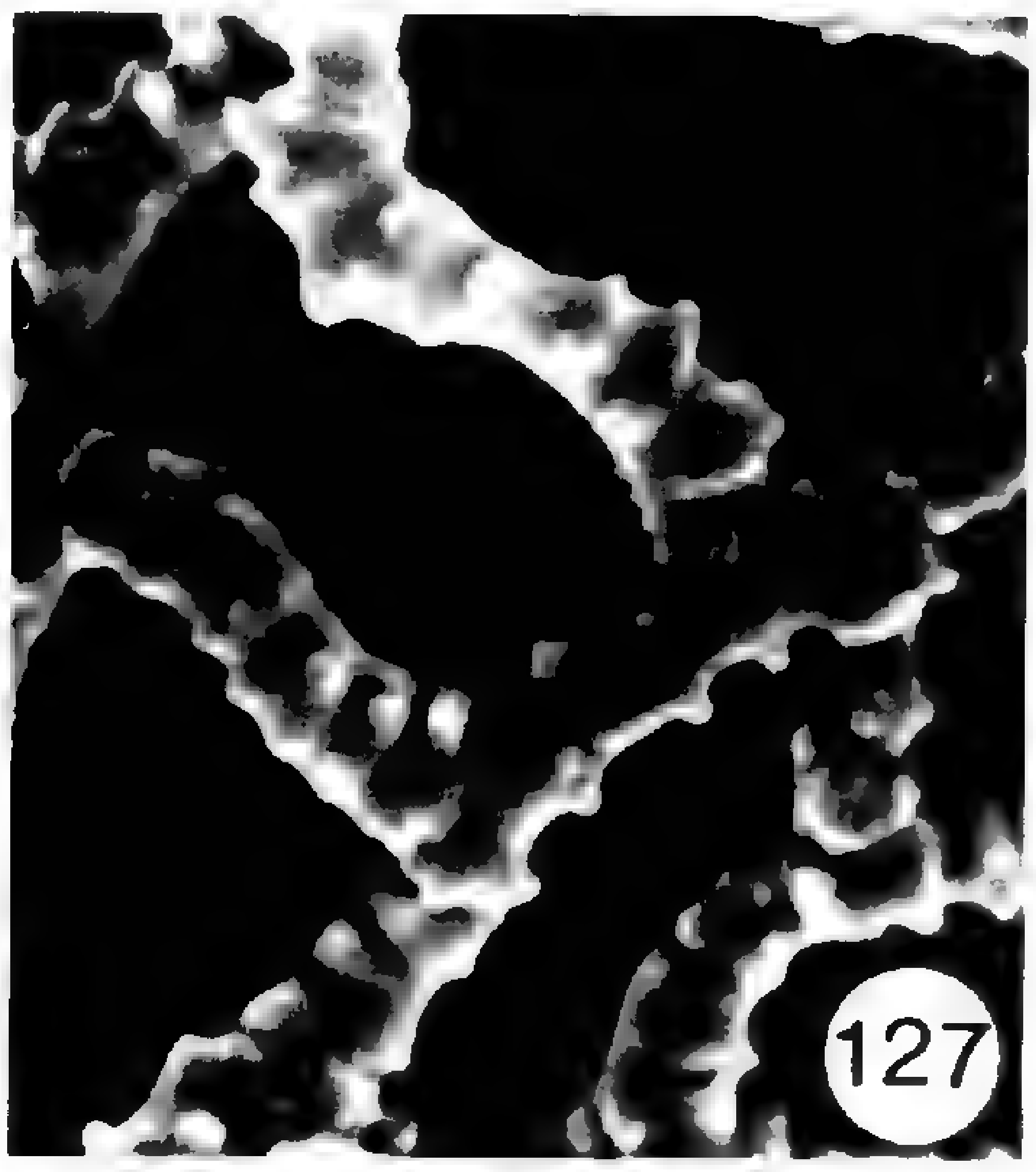
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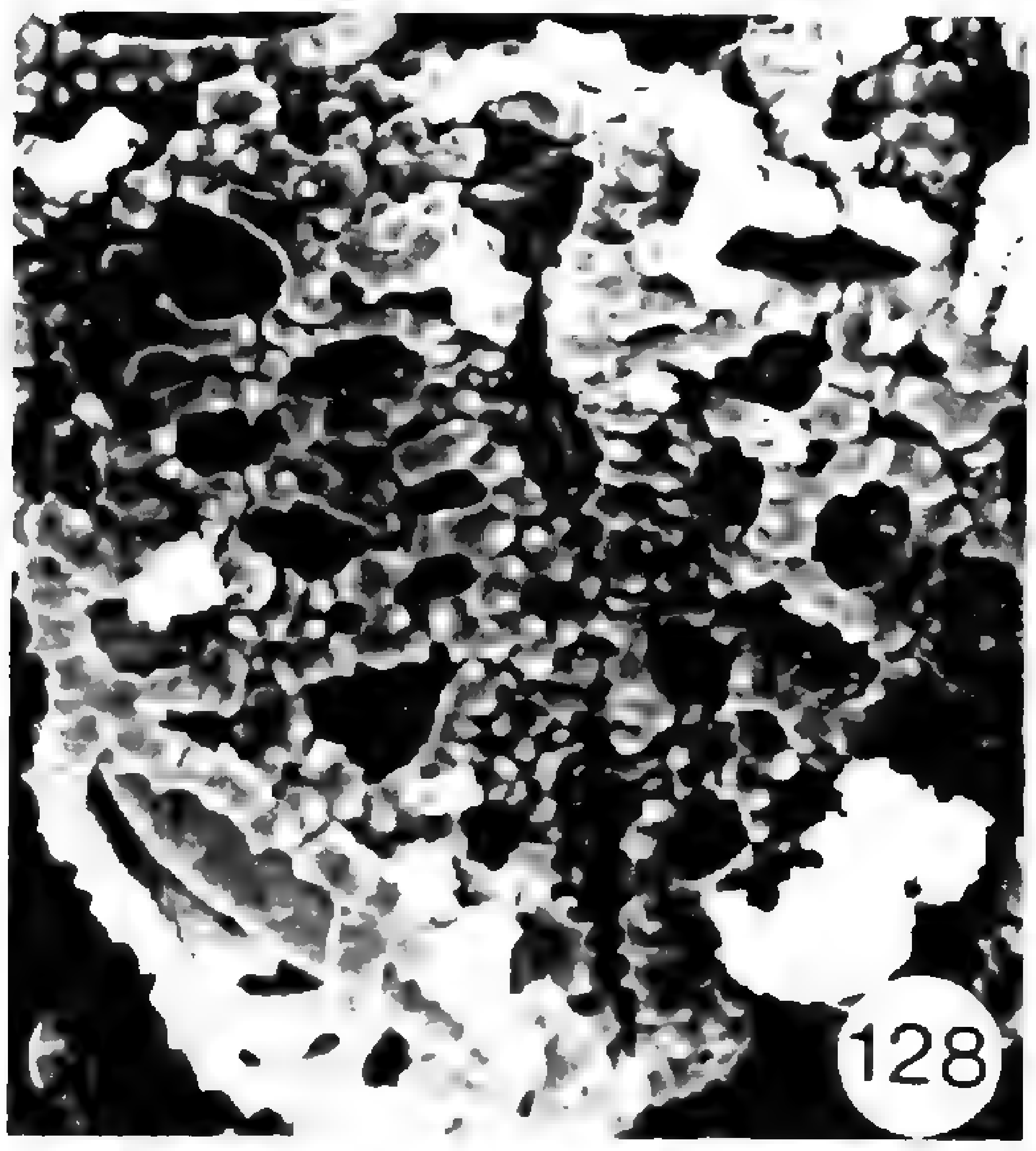
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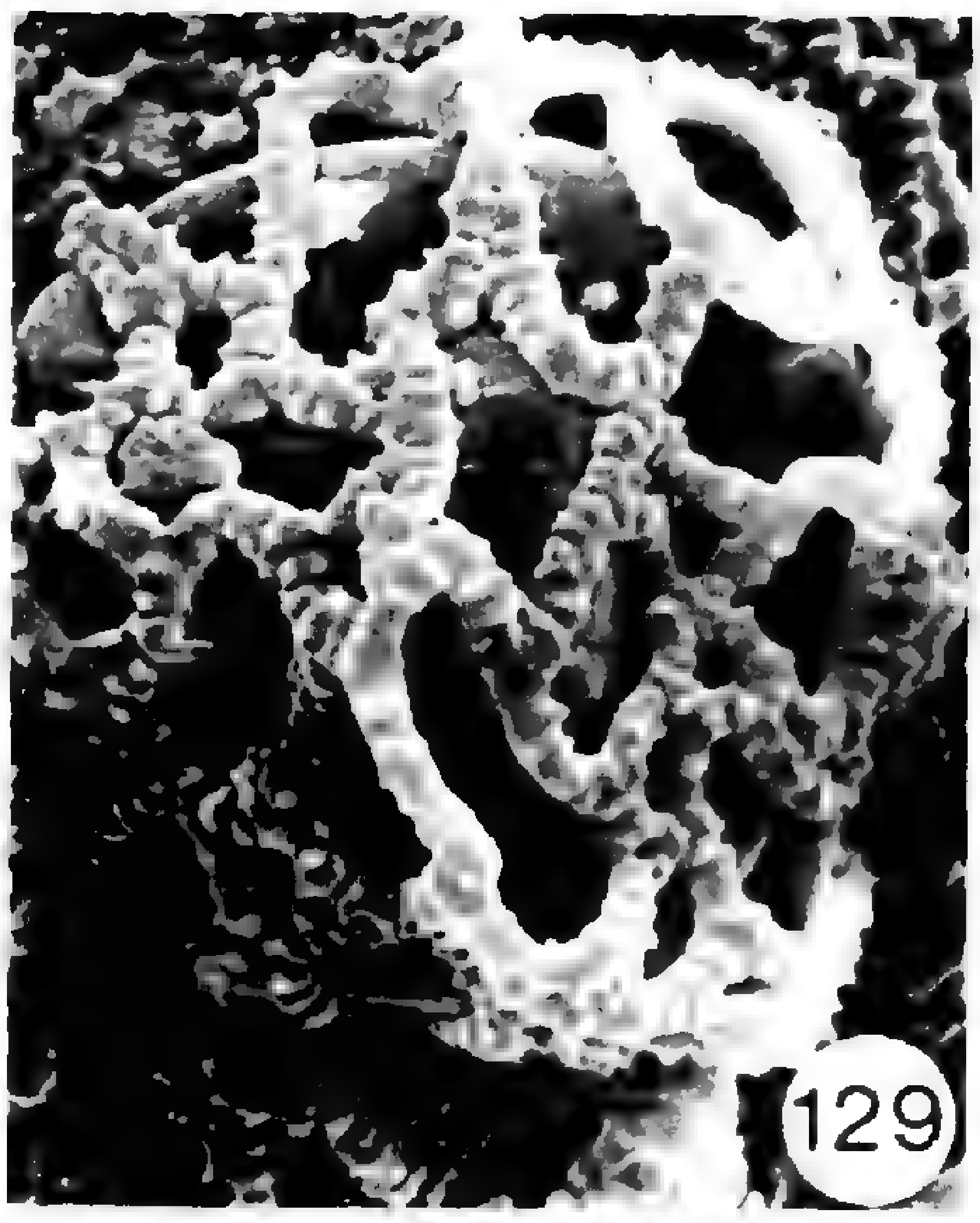
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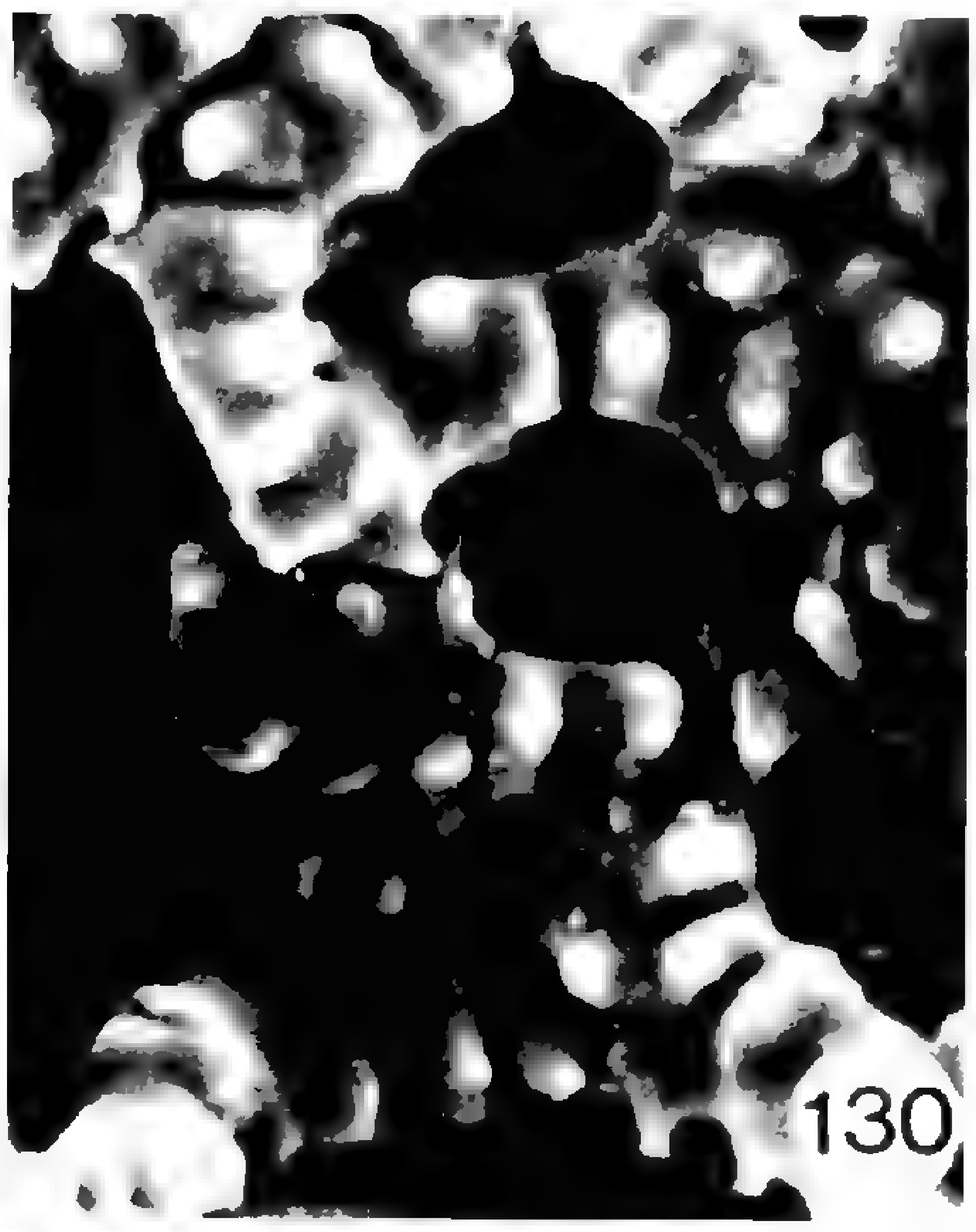
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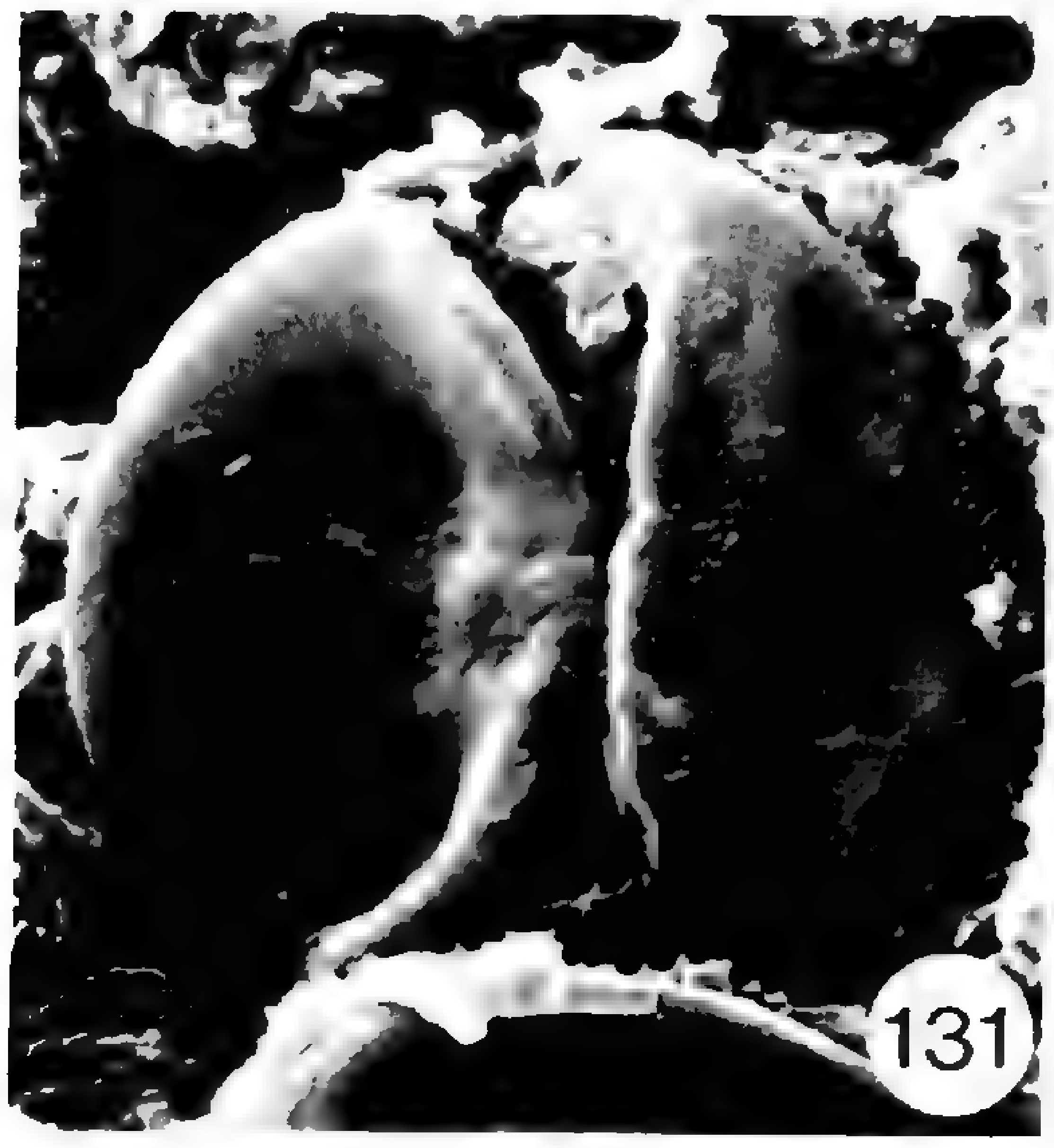
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darker staining layer is very thin in non-apertural regions, but thick under the aperture (work in progress).

K.1. Monocolpate, acolumellate, and reticulate pollen with broad muri ornamented by two to three rows of spinules (Figs. 122–124). Pollen grains monocolpate and elliptical to circular in equatorial outline, about 14–17 μm in diameter (Figs. 122, 123). Colpus is long, reaching to the equator, and has a distinct solid margin with spinules. The tectum is reticulate with a coarse and loosely attached reticulum. Lumina are irregularly rounded, up to about 3 μm in diameter, and of more or less equal size. Small lumina are absent except along the colpus margin where they become very small. Muri are relatively broad, about 1.2 μm wide, and have a flattened and rounded profile. Muri are ornamented by indistinct transverse ridges with distinct spinules that are irregularly aligned in two to three rows (Fig. 124). The spinules tend to extend down the sides of the muri. There are no columellae, except perhaps for single isolated columellae (Fig. 124).

The pollen grains were found in situ in a fragmentary stamen, about 0.4 mm long and 0.32 mm wide, with a tetrasporangiate anther. This species differs from the two other species from the Vale de Agua flora mainly in having broader muri and more than two rows of spinules.

K.2. Monocolpate, acolumellate, and reticulate pollen with narrow muri ornamented by two rows of spinules (Figs. 125–127). Pollen grains monocolpate and elliptical to circular in equatorial outline, about 12.5–15 μm in diameter (Figs. 125, 126). Colpus is long, reaching to the equator, and has a solid narrow margin with spinules. Tectum consists of a coarse and loosely attached reticulum. Lumina are irregular, angular to rounded, varying in size. Small lumina are absent except along the colpus margin. The largest lumina are up to about 5 μm in diameter. Toward the colpus margin the lumina become gradually smaller. Muri are narrow, about 0.6 μm wide, and have a flattened and rounded profile. They are ornamented by transverse ridges with distinct spinules that are typically arranged in pairs and aligned in two rows along the margins of the muri (Fig. 127). There are apparently no columellae.

The pollen grains were found in situ in a fragmentary anther, about 0.5 mm long and 0.15 mm broad, consisting of two elongated pollen sacs. This species differs from the two other species in the Vale de Agua flora mainly in the narrower muri and the two regular rows of spinules.

K.3. Monocolpate, acolumellate, and reticulate pollen with broad muri ornamented by one or two rows of spinules (Figs. 128–130). Pollen grains monocolpate and elliptical to circular in equatorial outline, about 15–19 μm in diameter (Figs. 128, 129). Colpus is long, reaching to the equator, and has a distinct solid margin. The tectum is reticulate with a coarse and loosely attached reticulum. Lumina are irregular, angular to rounded in shape, and of various sizes with small lumina scattered on the proximal surface of the grain. Larger lumina are up to about 5 μm in diameter. Toward the colpus margin the lumina become very small. Muri have a flattened and rounded profile and are about 0.9 μm wide. They are ornamented by irregular transverse ridges and distinct, rather stout spinules that are typically arranged in two longitudinal rows along the margins of the muri. More rarely the spinules are arranged in a single row (Fig. 130). There are apparently no columellae.

The pollen grains were found in situ in small stamens about 0.45 mm long and 0.25 mm broad consisting of a tetrasporangiate anther bearing a short apical extension of the connective. This pollen type is mainly distinguished from pollen type K.1 and K.2 from the Vale de Agua flora in having

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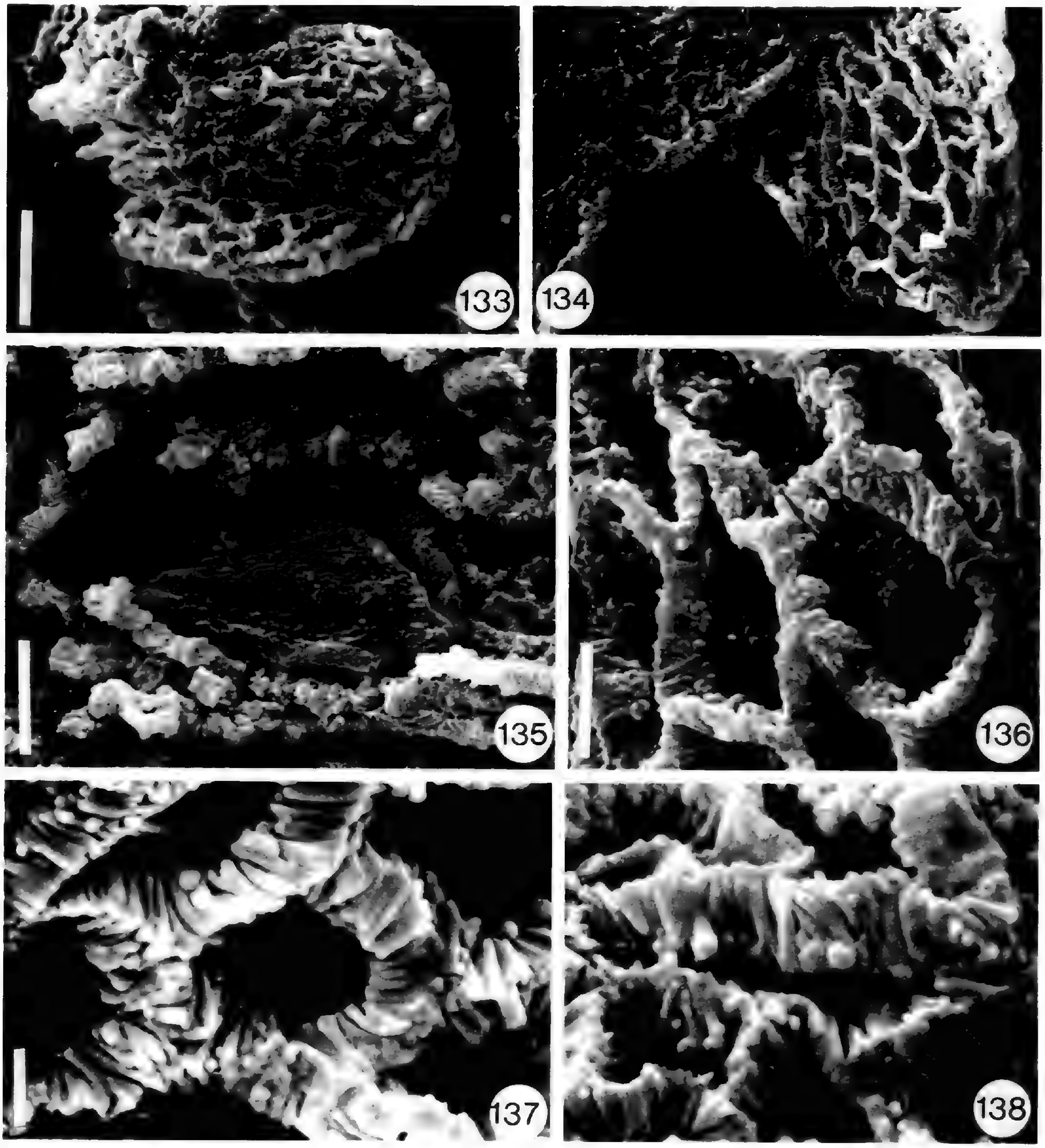
Figures 122–132. Scanning electron micrographs of pollen type K from the Early Cretaceous (Barremian or Aptian?) Vale de Agua flora (sample 139), western Portugal. 122–124. Pollen type K.1, monocolpate, acolumellate, and reticulate pollen with broad muri ornamented by two to three rows of spinules, S105319. —122. Distal view showing monocolpate aperture, ×3000; scale equal to 5 μm. —123. Proximal view, ×3000; scale shown in Figure 122. —124. Detail of reticulum (with a single columella?), ×10,000; scale equal to 1 μm. 125–127. Pollen type K.2, monocolpate, acolumellate, and reticulate pollen with narrow muri ornamented by two rows of spinules, S105323. —125. Distal view showing monocolpate aperture, ×3000; scale shown in Figure 122. —126. Proximal view, ×3,000; scale shown in Figure 122. —127. Detail of reticulum, ×10,000; scale shown in Figure 124. 128–130. Pollen type K.3, monocolpate, acolumellate, and reticulate pollen with broad muri ornamented by one to two rows of spinules, S105320. —128. Distal view showing monocolpate aperture, ×3000; scale shown in Figure 122. —129. Proximal view, ×3000; scale shown in Figure 122. —130. Detail of reticulum, ×10,000; scale shown in Figure 124. 131–132. Acolumellate pollen of type K.2 from coprolite specimens. —131. Distal view of pollen grain from which the reticulum has been lost, S105327, ×3000; scale shown in Figure 122. —132. Several pollen grains, some from which the reticulum has been lost, S105328, ×2000; scale equal to 5 μm.



Figures 133–138. Scanning electron micrographs of pollen type L from the Early Cretaceous (Barremian or Aptian?) Vale de Agua flora (sample 141), western Portugal. Inaperturate (?), acolumellate, and reticulate pollen with segmented muri (*Afropollis*). —133. Single pollen grain showing reticulum, S105253, ×1500; scale equal to 10 μm. —134. Pollen grain showing reticulum and central body, S105250, ×1500; scale shown in Figure 133. —135. Detail of body of pollen grain with reticulum missing, S105250, ×3000; scale equal to 5 μm. —136. Detail of reticulum showing segmented muri and granules, S105250, ×6000; scale equal to 2.5 μm. —137. Detail of reticulum showing segmented muri and granules, S105253, ×10,000; scale equal to 1 μm. —138. Detail of reticulum showing segmented muri and granules, S105253, ×10,000; scale shown in Figure 137.

small lumina scattered on the proximal surface of the grain. In the two other types small lumina only occur on the distal surface close to the colpus margin.

Coprolites with acolumellate and reticulate pollen (Figs. 131, 132). Several small coprolites, about 0.5–1.5 mm long, consisting exclusively of acolumellate pollen of the same type as described above, have been recovered in the same Vale de Agua sample. In some pollen grains the reticulum is lost exposing the psilate foot layer (Figs. 131, 132). In these naked specimens the colpus is distinct and extends to the equator. At least some of the coprolites appear to include only a single pollen type.

The coprolite illustrated in Figures 131 and 132 contains pollen similar to pollen type K.2.

L. Inaperturate (?), acolumellate, and reticulate pollen with segmented muri (Afropollis-type) (Figs. 133–138). Pollen grains of this unique and distinct type lack columellae; they have an open, loosely attached reticulum that is typically free from the much smaller central body and characteristically segmented muri. They are observed in the Vale de Agua flora and are similar to dispersed pollen assigned to the genus *Afropollis* Doyle, Jardiné & Doerenkamp. This genus was established by Doyle et al. (1982) based on pollen grains from the Albian of Peru first assigned by Brenner (1968) to the spore genus *Reticulatasporites* Leschik. *Afropollis* is widespread in Early to mid-Cretaceous strata and is particularly common at low palaeolatitudes in Africa and South America (e.g., Doyle et al., 1982; Penny, 1989, 1991). It is also reported from North America and Europe, with the earliest record in the late Barremian (e.g., Doyle et al., 1982; Penny, 1989). Aperture configuration varies from inaperturate to possibly monocolpate (cryptoaperturate) and zonacolpate, with a ring-furrow that is either displaced toward one pole or is in a symmetrical position dividing the grains in two equal halves (Doyle et al., 1982; Penny, 1989). A winteraceous affinity for the *Afropollis* grains was suggested by Doyle et al. (1990a, 1990b), but in Portugal they occur in separate pollen sacs that are unlike those of extant Winteraceae or any other angiosperms. The structure of the pollen wall is also unlike that in Winteraceae, and currently the systematic affinity of this unique pollen type is unresolved. The presence of a thick endexine may even indicate a non-angiospermous affinity for these grains, but similar segmented muri do occur in some monocotyledonous pollen (e.g., Takahashi, 1982; Le Thomas et al., 1996), and pollen with segmented muri supported by a granular intratectal layer was described for the Liliaceae genus *Erythronium* L. (Takahashi, 1987).

The in situ pollen grains from Portugal are elliptical in outline, about 33 μm in maximum diameter (Fig. 133). No aperture has been observed in the reticulum. The tectum is reticulate with a coarse and open reticulum that is detached from the central body of the grain. The central body known from TEM studies to consist of the foot layer and endexine is much smaller than the reticulum and is about 15–20 μm in diameter (Figs. 134, 135). Lumina are angular and of more or less the same size, up to about 5 μm in diameter. Muri are high, with a triangular profile, about 1 μm wide, and are distinctly segmented transversely. At the base of the muri the segmented part grades into small spherules or granules (Figs. 136–138). TEM sections of the pollen wall show that the wall of the central body consists mainly of a thick endexine, lined by an extremely thin foot layer. A similar wall structure was also shown by Doyle et al. (1990a).

The pollen grains have been found in two separate pollen sacs from the Vale de Agua flora. The pollen sacs are strongly compressed with few details preserved, but unlike other fragments of angiosperm anthers/stamens the pollen sacs are unusual in occurring singly, and may not be angiospermous.

The Portuguese pollen particularly resembles the Egyptian biorecords "Afropol-lumps" from the late Barremian-late Aptian (Penny, 1989, 1991) and "Afropol-jard" from the early Aptian-early Albian (Penny, 1991).

DISCUSSION

The preliminary study of the Torres Vedras, Catefica, Vale de Agua, Famalicão, and Buarcos fossil mesofloras presented here documents an unexpected diversity of angiosperms for this early stage in the evolution of the group. It also documents that in these well-preserved fossil assemblages the number of angiosperm taxa represented by reproductive organs preserved as mesofossils greatly exceeds that previously recognized at other localities of comparable age. In terms of simple species numbers some of the Early Cretaceous floras (e.g., Famalicão, Vale de Agua, and Buarcos) show a level of angiosperm diversity that is comparable to that of rich Tertiary localities. The results presented here also show that there is marked local variation in diversity and abundance of angiosperms among the five floras examined. Even for assemblages collected only a short distance from each other at the same locality, and in the same sedimentary horizon, there is great variation in the abundance and diversity of angiosperms.

RECOGNITION AND REPRESENTATION OF ANGIOSPERMS IN EARLY CRETACEOUS MESOFLORAS AND PALYNOFLORAS FROM PORTUGAL

In the fossil assemblage from the Famalicão locality there is a very distinct discrepancy between the diversity of angiosperm floral organs recovered and the diversity of angiosperms assessed from dispersed pollen, or from pollen associated with angiosperm reproductive structures. Currently, 105 different taxa based on angiosperm flowers, fruits, and seeds have been identified from the Famalicão flora. Dispersed stamens have not been included in the counts. Our estimate of 105 different taxa is a minimal estimate, and when possible we have tried to avoid counting different organs of the same species twice. Compared to other localities (e.g., Vale de Agua) there are remarkably few dispersed anthers and very few pollen grains in situ in flowers, or adhering to fruits or stigmatic surfaces. In total 13 different pollen types have been identified in situ from the Famalicão flora. Two are tricolpate, while nine are monoaperturate (monocolpate or trichotomocolpate). One is dicolpate, and one is periporate. Standard palynological preparation of the plant-bearing clay at the Famalicão locality for light microscopy yielded no dispersed angiosperm pollen or other palynomorphs. The paucity of angiosperm pollen in situ in the Famalicão flora may perhaps be explained by the fact that most fossils are charcoalified rather than lignitized, resulting in a lower fossilization potential for pollen. The lack of dispersed pollen in the Famalicão samples may also be explained by differential preservation of organs perhaps in combination with low dispersal of angiosperm pollen to the depositional environment.

The Vale de Agua flora, obtained from several samples collected from the same sedimentary sequence in a large complex of clay pits, has many lignitic fossils and also has the most diverse in situ pollen assemblage of all the Portuguese floras studied so far. Light microscopy of standard palynological preparations revealed only three species of dispersed angiospermous pollen in a palynoflora of about 100 different palynomorph taxa (C. Konradsen, pers. comm., 1997), but currently 26 different angiosperm pollen types have been observed in situ in flowers and dispersed stamens, or on the surface of fruits. Of these, 22 are monoaperturate, one is dicolpate, and three are tricolpate. Many species of flowers, fruits, and seeds occur commonly and consistently in all the various samples, but superimposed on this basic uniformity there is also considerable variation in abundance, diversity, and preservation of the angiosperm reproductive organs. From some samples we have recovered less than one hundred specimens, while from others we have recovered several thousand. Some taxa have been encountered in one sample only. For example, Vale de Agua sample 19 is rich in reproductive organs, but rather poor in in situ angiosperm pollen (5 different types: 4 monocolpate, 1 tricolpate), while Vale de Agua sample 141 includes the most diverse assemblage of in situ pollen that we have encountered (15 different types: 13 monoaperturate, 2 tricolpate). Vale de Agua sample 139 exhibits further variation and has only rare and mostly poorly preserved reproductive organs. However, in this sample stamens are generally better preserved, and 10 different pollen types are known in situ (9 monoaperturate, 1 tricolpate).

Among the pollen types at the Vale de Agua locality (sample 139) are a variety of characteristic semitectate, reticulate, and acolumellate pollen grains (pollen type K). These grains occur in stamens and abundantly on one kind of fruit. They are also the only component in many small coprolites. The plants producing these pollen grains were probably common in the local vegetation, but so far this pollen type has not been encountered in situ in other samples from the Vale de Agua locality. Pollen grains of this type are also absent from the dispersed palynofloras at the Vale de Agua locality. Similar local variation in floristic composition is shown by samples from the Torres Vedras locality. Samples collected in a lignitic horizon in the lower part of the sequence include several monoaperturate pollen types in situ. However, a sample (Torres Vedras sample 144) collected 25 m to the east in the same lignitic horizon yielded several in situ tricolpate forms, not observed in other samples from the same locality.

Like the Famalicão flora, the Buarcos flora is also rich and includes almost 100 different types of angiosperm flowers, fruits, and seeds. There is also a very distinct discrepancy between the diversity of angiosperm reproductive structures and the diversity of pollen associated with the floral organs and the dispersed pollen. Seven angiosperm pollen types have been recorded in the mesoflora (all monoaperturate), and the dispersed palynoflora from the same site studied using light microscopy by Pais and Reyre (1981) is dominated by a variety of fern spores and conifer pollen. Angiosperm pollen is rare and only two taxa were recorded, *Clavatipollenites* cf. *hughesii* and *Apiculatisporis vulgaris* Groot & Groot (later transferred to *Asteropollis* by Singh, 1983). One of these (*Asteropollis*-type pollen) has been detected among the in situ pollen types in the Buarcos flora, where it occurs both in dispersed stamens and on the surface of pistillate *Hedyosmum*-like flowers (pollen type J.4). The remaining six in situ pollen types have not yet been recognized in the dispersed pollen flora. The famous leaf flora from Buarcos (Buarcos-para-Tavarede, Saporta, 1894; Teixeira, 1948) is also collected along the old road from Buarcos to Taverede. The age of this flora is also uncertain, and it is perhaps not contemporaneous with the mesoflora. Saporta (1894) described about 18 different species of angiosperms, but according to studies by Teixeira

(1948) the number of angiosperm taxa is lower, perhaps less than 10.

IMPLICATIONS FOR THE BIOLOGY AND ECOLOGY OF EARLY ANGIOSPERMS

The results presented above document conclusively that angiosperms were more diverse in the Early Cretaceous vegetation around the Torres Vedras, Catefica, Vale de Agua, Famalicão, and Buarcos localities than is indicated by standard LM studies of dispersed palynofloras from those sites. Standard palynological approaches thus provide only a minimum estimate of angiosperm diversity, which may need to be modified based on studies of mesofossils or SEM investigations of dispersed palynofloras (e.g., Penny, 1988; Hughes & McDougall, 1990; Hughes et al., 1991; Penny, 1991; Hughes, 1994). In particular, results from the Portuguese localities suggest that standard palynological studies of the earliest phases of the angiosperm radiation are likely to seriously underestimate both the abundance and diversity of the group. Growth habit and pollination biology of the early angiosperms may have been important factors in the low content of angiosperm pollen in the Early Cretaceous palynofloras. It is interesting that of the 54 pollen types recognized here only *Asteropollis*-type pollen is found in all five Portuguese floras. *Asteropollis*-type pollen also occurs in stamens that have little connective tissue, produced large quantities of pollen, and have elongate pollen sacs that dehisced by simple longitudinal slits. These are all features associated with wind pollination among extant taxa. In addition, *Asteropollis*-type pollen and the floral organs associated with the pollen are closely comparable to extant *Hedyosmum*, which is wind pollinated (Endress, 1987).

The plants that produced the *Asteropollis*-type pollen appear to have been the exception, rather than the rule, in the five floras surveyed here. For example, acolumellate pollen (pollen type K) and most other in situ pollen types are more sporadic in their occurrence in the Portuguese samples. These acolumellate pollen are found in anthers that have an apical expansion of the connective, produced small quantities of pollen, and have small pollen sacs. These are all features that indicate that the plants may have been insect pollinated (Endress, 1996). In addition, there is direct evidence of interaction with insects because these pollen grains occur abundantly in presumed insect coprolites, where they are typically the only component preserved. Many other stamens in the Portuguese floras have similar features indicating insect pollination and low pollen production. Under these circumstances the pollen of this type may not have reached the sedimentary basins in any substantial quantities and will thus require intensive search to detect by standard palynological techniques.

The contrast between the high diversity of angiosperms recognized from mesofossils and low diversity of angiosperms recognized based on dispersed pollen is consistent with the widely accepted hypothesis that most early angiosperms were insect pollinated. In addition, the abundance of angiosperm mesofossils in the Portuguese floras suggests that these plants were a significant component of Early Cretaceous vegetation near the site of deposition. The preservation of delicate structures (e.g., flowers) also suggests minimal transport and implies that the source vegetation was nearby, but as in many other mid-Cretaceous mesofloras angiosperm wood has not been detected, and fragments of angiosperm leaves are rare. Together with the uniformly small size of all the flowers and fruits recovered, these observations suggest that angiosperms represented in the Portuguese floras were of low stature, perhaps small shrubs and herbs. One possible contemporaneous leaf flora from Portugal with angiosperm leaf remains is the flora "Buarcos-para-Tavarede" (Saporta, 1894; Teixeira, 1948), which includes about 10 different angiosperm taxa (Teixeira, 1948), and several of these fossil leaves also have a herbaceous appearance (e.g., *Braseniopsis venulosa* Saporta, *Adoxia praeatavia* Saporta). The Cercal flora, which is probably slightly older, includes 3 angiosperm taxa, all with an herbaceous appearance (*Dicotylophyllum ceriforme* Saporta, *Hydrocotylephyllum lusitanicum* Teixeira, *Nymphaeites choffatii* (Saporta) Teixeira (Teixeira, 1948)). Our results are consistent with the hypothesis advanced by Stebbins (1965) that the earliest angiosperms were perhaps woody shrubs or subshrubs rather than large trees. They are also consistent with evidence from recent phylogenetic analyses of extant angiosperms suggesting that the herbaceous habit was perhaps basal in angiosperms (Taylor & Hickey, 1992; Chase et al., 1993; Qiu et al., 1993). The systematic position of most of the fossil flowers, fruits, and seeds from the Portuguese floras remains to be investigated in detail, but 44 of the 54 pollen taxa identified are of magnoliid or possible monocotyledonous affinity. Among the magnoliids the few taxa for which systematic affinities can be accurately determined have been related to modern families or orders including herbaceous forms (Piperales, Chloranthaceae).

CONCLUSIONS

The discovery and description of mesofossil floras containing well-preserved angiosperm flowers, stamens, fruits, seeds, and other reproductive structures from the Late Cretaceous has stimulated a major advance in our current understanding of large-scale patterns in angiosperm evolution (Crane et al., 1995). As these techniques are now applied to a greater range of Early Cretaceous floras, an unexpected diversity of fossil angiosperms is beginning to emerge. In particular, the five mesofossil floras from the Early Cretaceous of Portugal treated in this paper include more than 100 taxa of angiosperm reproductive organs and document the presence of 48 different pollen types with systematic affinities either to extant plants at the magnoliid grade or monocotyledons. A further 10 species referable to the eudicots will be described in a subsequent paper. The diversity of angiosperms recovered from the Portuguese floras contrasts with indications from standard LM studies of dispersed palynofloras, as well as the scarcity of angiosperm wood and leaves in Barremian-Aptian fossil plant assemblages. These discrepancies may reflect important features of the biology and ecology of early angiosperms, including the widespread occurrence of insect pollination and a herbaceous or shrubby habit during the initial phases of their Early Cretaceous radiation.

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PHYLOGENETIC PATTERN, DIVERSITY, AND DIVERSIFICATION OF EUDICOTS[1]

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ABSTRACT

The implementation of explicit phylogenetic techniques to the study of relationships among angiosperms has led to the recognition of a major monophyletic group, the eudicot clade, characterized by the production of tricolpate or tricolpate-derived pollen grains. Eudicots comprise nearly 75% of extant angiosperm species (subclasses Hamamelididae, Caryophyllidae, Dilleniidae, Rosidae, and Asteridae, as well as the order Ranunculales in the Magnoliidae sensu Cronquist). Recent phylogenetic analyses, based on both morphological data and molecular sequences, have begun to clarify higher-level phylogenetic relationships within the eudicot clade. The basalmost branch within the eudicots separates a small ranunculid clade, which includes the Ranunculales and Papaverales. The main group within the eudicots, here referred to as the main eudicot clade, is formed by a basal grade of species-poor lineages, mostly of "lower" Hamamelididae, and a large monophyletic group, here referred to as core eudicots, which includes ca. 97% of eudicot species diversity. Within the core eudicots, three distinct groups can be recognized. (1) The caryophyllid clade (ca. 6% of eudicot species diversity) includes the Caryophyllidae as traditionally defined and a few additional taxa previously thought to be of dilleniid and rosid affinity. (2) The rosid clade (ca. 39% of total eudicot species diversity) is composed mostly of taxa previously included in Dilleniidae and Rosidae, and includes a well-supported clade that we term here the core rosids (ca. 24% of total eudicot species diversity). Among the taxa in the core rosid clade are the Fabaceae, Rosaceae, Linales, and Cunoniaceae, as well as some families of Violales, and the "higher" Hamamelididae. (3) The asterid clade (ca. 50% of eudicot species diversity) consists of two large clades composed mostly of taxa previously assigned to Asteridae, and additional members of Rosidae and Dilleniidae. One of these large asterid clades is dominated by the Asterales s.l. (ca. 17% of total eudicot species diversity), while the other corresponds to a broadly defined Lamiidae (ca. 26% of total eudicot species diversity). Paleobotanical data first document the presence of early eudicots ca. 125 million years before the present (Barremian-Aptian boundary, Lower Cretaceous), prior to the major diversification and ecological radiation of angiosperms. Well-preserved floral remains and other fossils provide a minimum age for the origin of eudicot lineages. Sediments of Albian age contain floral remains of Platanaceae and probable Buxaceae, both of which fall within the species-poor lineages at the base of the main eudicot clade. In slightly younger sediments, the taxonomic diversity of eudicots increases considerably. Basal taxa in the core eudicots are represented by Hamamelidaceae and by several flowers of broad saxifragalean affinity in Turonian-Campanian strata. Among taxa within the rosid clade, the Capparales and Myrtales are documented from the Turonian and Santonian-Campanian, respectively. The core rosids are represented by several flowers with affinities to Juglandales, Myricales, and Fagales in the Santonian-Campanian. Flowers with possible affinities to Hydrangeaceae, from the Coniacian-Santonian, represent the basalmost group within the asterid clade, and flowers of broad ericalean affinity (including Actinidiaceae), from the Turonian-Campanian, document the presence of several groups within the ericalean clade. The Asteridae s.l. are not securely represented in the Upper Cretaceous, and, to our knowledge, there is no reliable Cretaceous record for any member of the Lamiidae s.l. Although nearly all of the main eudicot clades are represented by at least one of their included lineages in the Upper Cretaceous, the earliest well-documented records of the Fabaceae, Asteraceae, Lamiales s.l., and Gentianales, which together comprise ca. 45% of total eudicot species diversity, are found in uppermost Cretaceous (Maastrichtian) or Tertiary sediments. The three subfamilies of Fabaceae are well documented by flowers and fruits in the Eocene, although the presence of pollen grains assigned to Caesalpinioideae from Maastrichtian strata suggests that the family extends back into the uppermost Cretaceous. The Asteraceae, Lamiales s.l., and Gentianales are known from the Paleogene based mostly on vegetative remains. The uneven distribution of species diversity among the major clades of eudicots, and the fact that the most species-rich groups are known only from relatively young fossils, suggests that a significant portion of eudicot diversity is the result of relatively recent radiations that occurred during the second half of angiosperm evolutionary history. The evolutionary basis for the explosive diversification of specific eudicot clades—in terms of exceptionally high speciation rates, low extinction rates, or both—remains uncertain.

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Throughout the history of life, major evolutionary radiations have resulted in radical changes in the taxonomic composition and biotic organization of the Earth's ecosystems (e.g., Erwin, 1992). One such radiation occurred during the Cretaceous as angiosperms (flowering plants) diversified rapidly and initiated a radical modification of the composition of vegetation in nearly all terrestrial biomes—in which they ultimately became the dominant plants. The number and complexity of unique biological and structural features that all angiosperms share, especially in their reproductive cycles, provide strong evidence that angiosperms are a monophyletic group (e.g., Crane, 1985; Doyle & Donoghue, 1986; Loconte & Stevenson, 1990; Nixon et al., 1994; Rothwell & Serbet, 1994; Doyle et al., 1994).

The application of cladistic techniques has identified two major monophyletic groups within the angiosperms: the monocotyledons and the eudicotyledons (i.e., non-magnoliid dicotyledons: Crane, 1989; eudicots: Doyle & Hotton, 1991). These two distinct and well-supported clades are embedded among a basal grade of magnoliid angiosperms composed of several independent woody and herbaceous lineages (Donoghue & Doyle, 1989; Loconte & Stevenson, 1991; Chase et al., 1993; Doyle et al., 1994; Drinnan et al., 1994). Monocots can be defined by their unique single cotyledon, among several other features (Herendeen & Crane, 1995), whereas eudicots are characterized by the production of triaperturate or triaperturate-derived pollen. Most of the vegetative and reproductive morphological disparity of angiosperms is encompassed within the eudicot clade, which includes more than 175,000 species, corresponding to nearly 75% of all extant angiosperm species. Eudicots are first documented in the fossil record from tricolpate pollen grains in late Barremian-early Aptian strata from Gabon (ca. 125 MYBP, Doyle & Hotton, 1991; Doyle, 1992), indicating that eudicots had evolved prior to the initial diversification of angiosperms that took place during the Aptian-Albian (ca. 112 MYBP, Lidgard & Crane, 1988, 1990; Crane, 1989; Crane & Lidgard, 1989, 1990).

In the last 10 to 15 years, numerous explicit phylogenetic studies have been directed toward resolving relationships among angiosperms at all taxonomic levels. These studies have applied parsimony and/or maximum likelihood techniques to traditional morphological, anatomical, and sometimes chemical characters, but especially to sequence data from nuclear and chloroplast genomes. Sophisticated computer-based analytical approaches have also significantly increased the number of taxa that can be analyzed in cladistic analyses, and various ad hoc strategies of analysis (e.g., Chase et al., 1993; Soltis & Soltis, 1996; Rice et al., 1997; Nixon et al., 1998) have been successfully employed in studies with an extensive representation of angiosperm diversity. Current approaches recognize that all types of evidence are potentially useful for phylogenetic analysis (e.g., Hillis, 1987; Sytsma, 1990; Donoghue & Sanderson, 1992), and that, in principle, the simultaneous analysis of different types of evidence in combined phylogenetic analyses is desirable (e.g., Kluge, 1989; Barrett et al., 1991; Bull et al., 1993; Chippindale & Wiens, 1994). Together with the development of explicit methods to evaluate compatibility among different data sets (e.g., Bull et al., 1993; de Queiroz, 1993; Rodrigo et al., 1993; Huelsenbeck et al., 1996; Cunningham, 1997), and the empirical evaluation of the properties and usefulness of these methods (e.g., Lutzoni & Vilgalys, 1995; Lutzoni, 1997; Davis et al., 1998), these approaches have provided an improved theoretical background in which phylogenetic relationships in angiosperms can be evaluated with increased reliability.

In this study, we provide an initial working hypothesis of the higher-level pattern of phylogenetic relationships within and among major eudicot clades. We attempt to synthesize results that are currently scattered in a large number of individual analyses in a published literature that is expanding rapidly. Our approach is to present a phylogenetic pattern that provides a heuristically useful summary of recurrent higher-level associations among eudicot taxa. Theoretical considerations and practical limitations on the size of phylogenetic analyses that are currently feasible preclude explicit analysis of all the data presently available. Nevertheless, we believe it is important to attempt an integrative synthesis that summarizes agreement among the studies completed to date and that highlights problematic areas for future research. In addition, for those major clades that can be identified, we summarize the number of extant species that are included to provide an initial assessment of the distribution of species diversity among major eudicot clades. We also summarize the earliest reliable appearance in the fossil record for each of the major eudicot clades, to constrain the time of origin of stem lineages and provide a minimum age for diversification of crown groups. Combining information about the number of species encompassed in major eudicot clades with information on their minimum age, allows a preliminary assessment of the relationship between the presumed age of clades and present-day species diversity.

MATERIALS AND METHODS

PHYLOGENETIC PATTERN

The synthesis presented in this paper attempts to identify major clades within the eudicots, and the pattern of phylogenetic relationships among them, based on a comparison of results from numerous published phylogenetic studies that include a broad taxonomic sample, and thus provide information about higher-level patterns of relationship. The summary of phylogenetic patterns presented here was approached conservatively with special attention given to the density of taxonomic sampling within the various monophyletic groups. The most significant criterion for favoring a particular pattern was its recurrent appearance in different analyses, particularly when that pattern was supported by independent analyses of different types of evidence. Patterns were also considered more reliable if they were supported by formal combined analyses of two or more data sets from different types of evidence (e.g., molecular sequences and morphology, or combined data from two or more kinds of genes). An assessment was also made of the variation in alternative phylogenetic patterns for similar taxa. In most cases, the incongruent patterns were different from one another, and varied in an apparently random way with respect to the most recurrent pattern. In these cases, we utilized the most recurrent pattern and attempted to summarize other suggested patterns. In a few cases, however, there were clearly two alternative recurrent phylogenetic patterns. In these cases, we describe both hypotheses of relationship and highlight the type of data upon which the alternatives are based.

While there are many important and useful studies of large-scale patterns of phylogenetic relationships in angiosperms using implicit (e.g., Cronquist, 1981; Dahlgren, 1983; Takhtajan, 1997) or explicit (e.g., Hufford, 1992) syntheses of traditional (largely morphological) characters, recent phylogenetic results from the widespread use of molecular data have been especially informative. Molecular characters have provided a more straightforward basis for initial comparative studies across a broad taxonomic sample, and in several cases also show significant congruence with results from rigorously analyzed morphological data sets. Phylogenetic analyses of Hydrangeaceae, for example, based on *rbc*L sequence data (Soltis et al., 1995a) and on morphological characters (Hufford, 1997), document similar relationships within the family, with differences restricted to only a few specific branches.

Many of the molecular phylogenetic studies of higher-level relationships in angiosperms are based on evidence from the *rbc*L gene, which encodes for the large subunit of ribulose-1, 5-bis-phosphate carboxylase/oxygenase (RuBisCO). The rate of change in *rbc*L sequences is appropriate for assessing relationships at relatively high taxonomic levels, and the numerous studies based on this gene currently provide the most extensive comparative analyses for eudicots, and for angiosperms as a whole (e.g., Albert et al., 1992; Chase et al., 1993; Williams et al., 1994; Rice et al., 1997). Especially important is the initial large-scale phylogenetic analysis for angiosperms of Chase et al. (1993), which provides a pioneering general assessment of phylogenetic patterns in eudicots, and of the composition of major clades. In this review we focus on results from the analysis of the second data set (Chase et al., 1993; search II; figs. 1B–15B), because it included a larger taxonomic sample, it involved a strategy for searching for islands of equally parsimonious trees, and it did not use relative character weighting. Also especially influential in our synthesis was the recent study of Soltis et al. (1997a), which provides an assessment of phylogenetic relationships of angiosperms based on 18S nuclear ribosomal DNA sequence data. In this case, we focused on the results from analysis of the fourth data set (Soltis et al., 1997a; fig. 4A–4C) because it excluded dubious sequences, but included presence/absence information for two indels in highly conserved regions of the gene. Our synthesis also leaned heavily on the recently completed combined analysis of *rbc*L and 18S sequence data (Soltis et al., 1997b), and a yet-unpublished combined analysis of *rbc*L, *atp*B, and 18S sequences for all angiosperms (Soltis et al., 1998).

For each major clade that we recognize in the eudicots, we include its taxonomic composition (Table 1), an outline of the pattern of relationships within the group, and its relationship with respect to other major eudicot clades. In cases where taxa are known to be para- or polyphyletic, available information about the phylogenetic placement of their component parts is provided (Table 2). Definition and content of taxa, and the use of taxonomic names, follow Cronquist (1981), unless otherwise indicated. Brief consideration is also given to suggested relationships among taxa based on previous macrotaxonomic treatments (Cronquist, 1981; Dahlgren, 1983; Takhtajan, 1997). These comparisons with traditional classifications were made a posteriori, and served only to corroborate phylogenetic associations detected based on more explicit published analyses.

Table 1. Taxonomic content and species diversity for eudicot clades. Names of major clades are given in the left column. For each major clade, included subclades and taxa are listed. Names of orders and families are sensu Cronquist (1981). Included and excluded families/genera from orders/families are indicated in parentheses after the taxon name. The number of species in each taxon was obtained from Mabberley (1993). Percentage of total eudicot species diversity (TESD) for major clades is indicated.

Clade	Included taxa	Extant species	% extant eudicots
RANUNCULID CLADE			
Ranunculales	Ranunculaceae (incl. *Glaucidium* and *Hydrastis*)	1750	
	Berberidaceae	570	
	Menispermaceae	520	
	Lardizabalaceae	21	
	Sargentodoxaceae	1	
	Circaeasteraceae (incl. *Kingdonia)*	2	
	TOTAL RANUNCULALES	2864	1.64%
Eupteleaceae	Eupteleaceae	2	
	TOTAL EUPTELEACEAE	2	<0.01%
Papaverales	Papaveraceae	210	
	Fumariaceae (incl. *Pteridophyllum* and *Hypecoum*)	450	
	TOTAL PAPAVERALES	660	0.38%
	TOTAL RANUNCULID CLADE	**3526**	**2.01%**
MAIN EUDICOT CLADE			
BASAL EUDICOT GRADE	Nelumbonaceae	2	
	Platanaceae	7	
	Proteaceae	1350	
	Sabiaceae	48	
	Buxaceae	60	
	Didymelaceae	2	
	Trochodendrales	2	
	TOTAL BASAL EUDICOT GRADE	**1471**	**0.84%**
CORE EUDICOT CLADE			
CARYOPHYLLID CLADE			
Caryophyllales	Caryophyllales	9177	
	Simmondsiaceae	1	
Plumbaginales/Polygonales	Polygonaceae	1150	
	Plumbaginaceae	440	
	Nepenthaceae	70	
	Droseraceae	85	
	Tamaricaceae	78	
	Frankeniaceae	30	
	Ancistrocladaceae	12	
	Dioncophyllaceae	3	
	Rhabdodendraceae	3	
	TOTAL CARYOPHYLLID CLADE	**11,049**	**6.31%**
SAXIFRAGOIDS	Cercidiphyllaceae	1	
	Daphniphyllaceae	10	
	Hamamelidaceae	115	
	Saxifragoideae (Saxifragaceae)	449	
	Penthoroideae (Saxifragaceae)	2	
	Iteoideae (Grossulariaceae)	10	
	Pterostemonoideae (Grossulariaceae)	2	
	Ribesoideae (Grossulariaceae)	150	
	Tetracarpaeoideae (Grossulariaceae)	1	
	Haloragaceae	66	
	Paeoniaceae	33	
	Crassulaceae	1500	

Table 1. Continued.

Clade	Included taxa	Extant species	% extant eudicots
	Hydrobryum (Podostemaceae)	10	
	Cladopus (Podostemaceae)	5	
	TOTAL SAXIFRAGOIDS	**2354**	**1.34%**
ROSID CLADE			
GERANIACEAE	Geraniaceae (excl. *Wendtia* and *Viviania*)	721	
	Hypseocharis (Oxalidaceae)	8	
	TOTAL GERANIACEAE	729	0.42%
FRANCOA CLADE	*Francoa* (Francooideae; Saxifragaceae)	1	
	Greyiaceae	3	
	Viviania (Geraniaceae)	6	
	Wendtia (Geraniaceae)	3	
	Bersama (Melianthaceae)	2	
	TOTAL *FRANCOA* CLADE	15	0.01%
CAPPARALES/SAPINDALES/MALVALES			
expanded Capparales	Capparales	3766	
	Limnanthaceae	8	
	Bataceae	2	
	Salvadoraceae	11	
	Gyrostemonaceae	14	
	Caricaceae	31	
	Bretschneideraceae	1	
	Akaniaceae	1	
	Tropaeolaceae	88	
	TOTAL EXPANDED CAPPARALES	3922	2.24%
expanded Malvales	Malvales (excl. Elaeocarpaceae)	4025	
	Thymelaeaceae	720	
	Sarcolaenaceae	39	
	Dipterocarpaceae	530	
	Bixaceae	16	
	Cistaceae	175	
	Sphaerosepalaceae	17	
	Neuradaceae	9	
	Muntingia (Flacourtiaceae)	1	
	TOTAL EXPANDED MALVALES	5532	3.16%
Sapindales	Simaroubaceae (excl. *Irvingia*, *Picrammia* and *Alvaradoa*)	122	
	Rutaceae	1700	
	Burseraceae	540	
	Kirkiaceae	5	
	Ptaeroxylaceae	3	
	Aceraceae	113	
	Sapindaceae	1325	
	Anacardiaceae	850	
	Cneoraceae	3	
	Meliaceae	575	
	Hippocastanaceae	15	
	Leitneriaceae	1	
	Peganum (Zygophyllaceae)	5	
	Malacocarpus (Zygophyllaceae)	1	
	Nitraria (Zygophyllaceae)	6	
	TOTAL SAPINDALES	5264	3.01%
	TOTAL CAPPARALES/SAPINDALES/MALVALES	14,718	8.41%
MYRTALES	Myrtales (excl. Thymelaeaceae)	10,384	
	Qualea (Vochysiaceae)	59	
	TOTAL MYRTALES	10,443	5.97%

Table 1. Continued.

Clade	Included taxa	Extant species	% extant eudicots
CORE ROSID CLADE			
Cucurbitales	Begoniaceae	900	
	Cucurbitaceae	760	
	Datiscaceae	4	
	Coriariaceae	5	
	Corynocarpaceae	4	
	TOTAL CUCURBITALES	1673	0.96%
Urticales	Urticales	2594	
	Elaeagnaceae	45	
	Rhamnus (Rhamnaceae)	125	
	Ceanothus (Rhamnaceae)	55	
	TOTAL URTICALES	2819	1.61%
Rosaceae	Rosaceae (excl. *Quillaja*)	3296	
	TOTAL ROSACEAE	3296	1.88%
"Higher" Hamamelididae	Betulaceae	150	
	Casuarinaceae	70	
	Juglandaceae	59	
	Myricaceae	50	
	Fagaceae (incl. *Nothofagus*)	1050	
	TOTAL "HIGHER" HAMAMELIDIDAE	1379	0.79%
Fabaceae/Surianaceae/ Polygalaceae	Fabaceae	16,400	
	Polygalaceae	950	
	Surianaceae	5	
	Quillaja (Rosaceae)	4	
	TOTAL FABACEAE/SURIANACEAE/POLYGALACEAE	17,359	9.92%
Expanded Cunoniaceae	Cunoniaceae (incl. *Bauera*)	340	
	Tremandraceae	43	
	Cephalotaceae	1	
	Elaeocarpaceae	520	
	Oxalidaceae (excl. *Hypseocharis*)	567	
	Davidsoniaceae	1	
	TOTAL EXPANDED CUNONIACEAE	1472	0.84%
Euonymus clade	*Euonymus* (Celastraceae)	117	
	Hippocratea (Celastraceae)	120	
	Siphonodon (Celastraceae)	7	
	Plagiopteron (Flacourtiaceae)	2	
	Brexia (Brexioideae; Grossulariaceae)	1	
	Lepuropetaloideae (Saxifragaceae)	1	
	Parnassioideae (Saxifragaceae)	15	
	Stackhousiaceae	28	
	Huaceae	3	
	TOTAL *EUONYMUS* CLADE	294	0.17%
Linales/Euphorbiaceae/ Malpighiaceae	Linales	631	
	Euphorbiaceae	7950	
	Chrysobalanaceae	460	
	Malpighiaceae	1100	
	Lacistemataceae	2	
	Trigoniaceae	26	
	Passifloraceae	530	
	Dichapetalaceae	125	
	Balanopaceae	9	
	Caryocaraceae	24	
	Quiinaceae	44	
	Clusiaceae	1350	

Table 1. Continued.

Clade	Included taxa	Extant species	% extant eudicots
	Turneraceae	110	
	Malesherbiaceae	27	
	Medusagynaceae	1	
	Achariaceae	4	
	Salicaceae	435	
	Ochnaceae	86	
	Carallia (Rhizophoraceae)	10	
	Goupia (Celastraceae)	3	
	Kiggelaria (Flacourtiaceae)	1	
	Pangium (Flacourtiaceae)	1	
	Hydnocarpus (Flacourtiaceae)	40	
	Abatia (Flacourtiaceae)	9	
	Flacourtia (Flacourtiaceae)	15	
	Idesia (Flacourtiaceae)	1	
	Casearia (Flacourtiaceae)	180	
	Marathrum (Podostemaceae)	25	
	Viola (Violaceae)	400	
	TOTAL LINALES/EUPHORBIACEAE/MALPIGHIACEAE	13,599	7.77%
Other core rosids	Krameriaceae	15	
	Guaiacum (Zygophyllaceae)	6	
	Connarus (Connaraceae)	100	
	Irvingia (Simaroubaceae)	3	
	TOTAL CORE ROSID CLADE	42,015	24.00%
Other rosids	Crossosomataceae	2	
	Stachyuraceae	5	
	Aphloia (Flacourtiaceae)	1	
	Ixerba (Brexioideae; Grossulariaceae)	1	
	Picrammia (Simaroubaceae)	40	
	Alvaradoa (Simaroubaceae)	5	
	Staphylea (Staphyleaceae)	11	
	Tapiscia (Staphyleaceae)	1	
	TOTAL ROSID CLADE	**67,986**	**38.84%**
ASTERID CLADE			
CORNALEAN CLADE	Nyssaceae (incl. *Mastixia*)	8	
	Cornus (Cornaceae)	45	
	Diplopanax (Cornaceae)	1	
	Curtisia (Cornaceae)	1	
	Alangiaceae	17	
	Loasaceae	260	
	Hydrangeaceae	170	
	Hydrostachydaceae	22	
	TOTAL CORNALEAN CLADE	524	0.30%
ERICALEAN CLADE	Fouquieriaceae	11	
	Impatiens (Balsaminaceae)	850	
	Polemoniaceae	275	
	Marcgraviaceae	108	
	Tetrameristaceae	2	
	Pelliceraceae	1	
	Diapensiaceae	13	
	Primulales	2140	
	Scytopetalaceae	22	
	Lecythidaceae	280	
	Theaceae	520	
	Sapotaceae	1000	

Table 1. Continued.

Clade	Included taxa	Extant species	% extant eudicots
	Ebenaceae	485	
	Styracaceae	165	
	Symplocaceae	250	
	Cyrillaceae	14	
	Clethraceae	64	
	Grubbiaceae	3	
	Actinidiaceae	355	
	Sarraceniaceae	15	
	Roridula (Byblidaceae)	2	
	Ericaceae	3350	
	Epacridaceae	400	
	Empetraceae	5	
	Pyrolaceae	42	
	Monotropaceae	15	
	TOTAL ERICALEAN CLADE	10,387	5.93%
CORE ASTERID CLADE			
ILEX CLADE	*Ilex* (Aquifoliaceae)	400	
	Helwingia (Cornaceae)	3	
	Phyllonomoideae (Grossulariaceae)	4	
	TOTAL ILEX CLADE	407	0.23%
ASTERIDAE S.L.			
Apiales	Apiaceae	3100	
	Araliaceae	800	
	Pittosporaceae	240	
	Aralidium (Cornaceae)	1	
	Melanophylla (Cornaceae)	8	
	Toricellia (Cornaceae)	3	
	Griselinia (Cornaceae)	6	
	TOTAL APIALES	4158	2.38%
Dipsacales	Dipsacales	1018	
	Desfontainia (Loganiaceae)	1	
	TOTAL DIPSACALES	1019	0.58%
Asterales s.l.	Asteraceae	21,000	
	Calyceraceae	55	
	Goodeniaceae (incl. *Brunonia*)	430	
	Menyanthaceae	40	
	Campanulaceae (incl. Lobeliaceae, Cyphiaceae, Cyphocarpaceae and Nemacladaceae; excl. Sphenocleaceae)	1948	
	Pentaphragmataceae	25	
	Brunoniaceae	1	
	Donatiaceae	2	
	Stydiliaceae	170	
	Alseuosmiaceae	8	
	Argophyllaceae	11	
	Corokia (Cornaceae)	4	
	TOTAL ASTERALES S.L.	23,774	13.58%
Other Asteridae s.l.	Escallonioideae (Grossulariaceae)	54	
	Eremosynoideae (Saxifragaceae)	1	
	Berzelia (Bruniaceae)	12	
	Phelline (Aquifoliaceae)	4	
	TOTAL ASTERIDAE S.L.	29,022	16.58%
GARRYA CLADE	*Garrya* (Garryaceae)	13	
	Aucuba (Cornaceae)	4	
	Eucommiaceae	1	
	TOTAL *GARRYA* CLADE	18	0.01%

Table 1. Continued.

Clade	Included taxa	Extant species	% extant eudicots
LAMIIDAE S.L.			
Boraginales	Boraginaceae	2500	
	Hydrophyllaceae	275	
	TOTAL BORAGINALES	2775	1.59%
Solanales	Solanaceae	2600	
	Convolvulaceae	1650	
	Duckeodendraceae	1	
	TOTAL SOLANALES	4251	2.43%
Gentianales	Gentianaceae	1200	
	Rubiaceae	10,400	
	Apocynaceae	2100	
	Asclepiadaceae	2850	
	Loganiaceae (excl. *Desfontainia*, *Plocosperma*, *Polypremnum*)	596	
	TOTAL GENTIANALES	17,146	9.80%
Lamiales s.l.	Verbenaceae	1900	
	Scrophulariaceae	4450	
	Lamiaceae	5600	
	Gesneriaceae	2400	
	Callitrichaceae	17	
	Plantaginaceae	255	
	Acanthaceae	4300	
	Pedaliaceae	95	
	Globulariaceae	250	
	Buddlejaceae	100	
	Bignoniaceae	725	
	Myoporaceae	220	
	Lentibulariaceae	245	
	Retziaceae	1	
	Oleaceae	900	
	Plocosperma (Loganiaceae)	1	
	Polypremnum (Loganiaceae)	1	
	Byblis (Byblidaceae)	2	
	Vahlioideae (Saxifragaceae)	5	
	TOTAL LAMIALES S.L.	21,467	12.26%
Other Lamiidae s.l.	Sphenocleaceae	2	
	Montinioideae (Grossulariaceae)	1	
	TOTAL LAMIIDAE S.L.	45,642	26.08%
Other core asterids	*Icacina* (Icacinaceae)	6	
	Gonocaryum (Icacinaceae)	10	
	Oncothecaceae	2	
	TOTAL CORE ASTERID CLADE	**75,107**	**42.91%**
	TOTAL ASTERID CLADE	**86,018**	**49.14%**
TAXA OF UNCERTAIN PLACEMENT WITHIN CORE EUDICOTS			
Santalales	Santalales (incl. 10 families)	2186	
Dilleniaceae	Dilleniaceae	300	
Vitis-Leeaceae	*Vitis* (Vitaceae)	65	
	Leeaceae	34	
Gunnera-Myrothamnus	Gunneraceae	40	
	Myrothamnaceae	2	
Aextoxicon-Berberidopsis	Aextoxicaceae	1	
	Berberidopsis (Flacourtiaceae)	2	
	TOTAL CORE EUDICOT CLADE	**170,037**	**97.15%**
	TOTAL MAIN EUDICOT CLADE	**171,508**	**97.99%**
	TOTAL EUDICOT CLADE	**175,034**	**100%**

Table 2. Placement of orders and families according to eudicot phylogenetic pattern presented here. Orders are in bold, and their circumscription follows Cronquist (1981). The phylogenetic placement in which each taxon is most frequently resolved is indicated, with supporting references. References supporting possible monophyly for each taxon are indicated, although monophyly of taxa was explicitly addressed in only very few studies. Monophyly status of orders and families for which only a few representatives have been included in phylogenetic analyses (insufficient to presume monophyly) is denoted by a question mark. Monogeneric families are indicated. Documented para- or polyphyletic orders/families are indicated as such, and placement of their members is provided.

Taxon	Phylogenetic placement	Reference for placement	Monophyly status
ORDERS			
Caryophyllales (including 12 families)	Caryophyllid cl., Caryophyllales	Albert et al., 1992; Giannasi et al., 1992; Olmstead et al., 1992; Chase et al., 1993; Williams et al., 1994; Soltis et al., 1997a	Rodman et al., 1984; Albert et al., 1992; Downie & Palmer, 1992; Olmstead et al., 1992; Rettig et al., 1992; Chase et al., 1993; Williams et al., 1994; Soltis et al., 1997a
Capparales (including 5 families)	Rosid cl., Capparales/Sapindales/Malvales, expanded Capparales	Rodman, 1991; Rodman et al., 1993, 1994, 1996; Gadek et al., 1992; Chase et al., 1993	paraphyletic, all components in similar phylogenetic placement
Dipsacales (including 4 families)	Asterid cl., Asteridae s.l., Dipsacales	Olmstead, 1992, 1993; Chase et al., 1993; Cosner et al., 1994; Gustafsson et al., 1996	Olmstead, 1992, 1993; Chase et al., 1993; Cosner et al., 1994; Gustafsson et al., 1996
Linales (including 5 families)	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Albert et al., 1992; Chase et al., 1993; Morgan & Soltis, 1993; Swensen et al., 1994; Williams et al., 1994; Soltis et al., 1995b	paraphyletic, all components in similar phylogenetic placement
Malvales (excluding Elaeocarpaceae; including 4 families)	Rosid cl., Capparales/Sapindales/Malvales, expanded Malvales	Gadek et al., 1992; Chase et al., 1993; Fernando et al., 1993, 1995; Rodman et al., 1996	Gadek et al., 1992; Chase et al., 1993; Fernando et al., 1993; Price & Palmer, 1993
Myrtales (excluding Thymelaeaceae; including 11 families)	Rosid cl., Myrtales	Gadek et al., 1992; Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Price & Palmer, 1993; Rodman et al., 1993; Williams et al., 1994; Conti et al., 1996	Albert et al., 1992; Swensen et al., 1994; Williams et al., 1994
Primulales (including 3 families)	Asterid cl., ericalean cl.	Chase et al., 1993; Kron & Chase, 1993; Olmstead et al., 1993; Cosner et al., 1994; Morton et al., 1996, 1997	Chase et al., 1993; Kron & Chase, 1993; Olmstead et al., 1993; Morton et al., 1996, 1997
Santalales (including 10 families)	uncertain placement within core eudicots		Nickrent & Soltis, 1995; Nickrent & Franchina, 1990; Chase et al., 1993; Swensen et al., 1994; Williams et al., 1994; Soltis et al., 1997a
Trochodendrales (including 2 families)	basal eudicot grade	Chase et al., 1993; Drinnan et al., 1994; Hoot et al., 1999	Drinnan et al., 1994; Soltis et al., 1997a; Hoot et al., 1999
Urticales (including 6 families)	Rosid cl., core rosids	Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Swensen et al., 1994; Soltis et al., 1995b	Chase et al., 1993; Morgan et al., 1994; Swensen et al., 1994; Soltis et al., 1995b

Table 2. Continued.

Taxon	Phylogenetic placement	Reference for placement	Monophyly status
FAMILIES			
Acanthaceae (including *Thunbergia* and *Nelsonia*)	Asterid cl., Lamiidae s.l., Lamiales s.l.	Albert et al., 1992; Downie & Palmer, 1992; Chase et al., 1993; Morgan & Soltis, 1993; Olmstead et al., 1993; Cosner et al., 1994; Hedrén et al., 1995	Chase et al., 1993; Olmstead et al., 1993; Hedrén et al., 1995
Aceraceae	Rosid cl., Capparales/Sapindales/Malvales, Sapindales	Gadek et al., 1992, 1996; Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Price & Palmer, 1993; Rodman et al., 1993; Fernando et al., 1995	?
Achariaceae (only *Acharia*)	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	?
Actinidiaceae	Asterid cl., ericalean cl.	Albert et al., 1992; Anderberg, 1992; Chase et al., 1993; Kron & Chase, 1993; Olmstead et al., 1993; Cosner et al., 1994; Williams et al., 1994; Morton et al., 1996; Morton et al., 1997	Morton et al., 1996
Aextoxicaceae	uncertain placement within core eudicots; associated with *Berberidopsis* (Flacourtiaceae)	Soltis et al., 1998	single genus
Akaniaceae	Rosid cl., Capparales/Sapindales/Malvales, expanded Capparales	Rodman, 1991; Rodman et al., 1994, 1996; Gadek et al., 1992; Chase et al., 1993; Fernando et al., 1993	single genus
Alangiaceae	Asterid cl., cornalean cl.	Chase et al., 1993; Olmstead et al. 1993; Xiang et al., 1993; Hempel et al., 1995; Soltis et al., 1995a	single genus
Alseuosmiaceae	Asterid cl., Asteridae s.l., Asterales s.l.	Gustafsson et al., 1996	Gustafsson et al., 1996
Anacardiaceae	Rosid cl., Capparales/Sapindales/Malvales, Sapindales	Gadek et al., 1992, 1996; Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Fernando et al., 1995	?
Ancistrocladaceae	Caryophyllid cl., Polygonales/Plumbaginales	Lledó et al., 1998; Soltis et al., 1998	single genus
Apiaceae	Asterid cl., Asteridae s.l., Apiales	Olmstead et al., 1992, 1993; Chase et al., 1993; Cosner et al., 1994; Plunkett et al., 1996; Soltis et al., 1997a	Plunkett et al., 1996, 1997
Apocynaceae	Asterid cl., Lamiidae s.l., Gentianales	Bremer & Struwe, 1992; Downie & Palmer, 1992; Olmstead et al., 1992, 1993; Chase et al., 1993; Cosner et al., 1994; Struwe et al., 1994; Sennblad & Bremer, 1996; Soltis & Soltis, 1997	paraphyletic, all components in similar phylogenetic placement

Table 2. Continued.

Taxon	Phylogenetic placement	Reference for placement	Monophyly status
Aquifoliaceae			paraphyletic
Ilex	Asterid cl., *Ilex* cl.	Chase et al., 1993; Olmstead et al., 1993; Cosner et al., 1994; Gustafsson et al., 1996; Plunkett et al., 1996	—
Phelline	Asterid cl., Asteridae s.l.	Soltis et al., 1998	—
Araliaceae	Asterid cl., Asteridae s.l., Apiales	Olmstead et al., 1992, 1993; Chase et al., 1993; Cosner et al., 1994; Gustafsson et al., 1996; Plunkett et al., 1996; Soltis et al., 1997a	?
Argophyllaceae	Asterid cl., Asteridae s.l., Asterales s.l.	Gustafsson et al., 1996	single genus
Asclepiadaceae	Asterid cl., Lamiidae s.l., Gentianales	Downie & Palmer, 1992; Chase et al., 1993; Olmstead et al., 1993; Cosner et al., 1994; Sennblad & Bremer, 1996	Struwe et al., 1994; Sennblad & Bremer, 1996
Asteraceae	Asterid cl., Asteridae s.l., Asterales s.l.	Olmstead, 1992, 1993; Chase et al., 1993; Michaels et al., 1993; Cosner et al., 1994; Gustafsson & Bremer, 1995; Gustafsson et al., 1996; Soltis et al., 1997a	Chase et al., 1993; Olmstead et al., 1993; Cosner et al., 1994
Balanopaceae	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	single genus
Balsaminaceae (only *Impatiens*)	Asterid cl., ericalean cl.	Chase et al., 1993; Kron & Chase, 1993; Olmstead et al., 1993; Cosner et al., 1994; Morton et al., 1996, 1997	—
Bataceae	Rosid cl., Capparales/Sapindales/Malvales, expanded Capparales	Rodman, 1991; Rodman et al., 1993, 1994, 1996; Chase et al., 1993; Morgan & Soltis, 1993	single genus
Begoniaceae	Rosid cl., core rosids, Cucurbitales	Albert et al., 1992; Chase et al., 1993; Swensen et al., 1994; Soltis et al., 1995b	?
Berberidaceae	Ranunculid cl., Ranunculales	Chase et al., 1993; Drinnan et al., 1994; Hoot & Crane, 1995; Hoot et al., 1995b, 1999; Soltis et al., 1997a	Drinnan et al, 1994; Hoot & Crane, 1995; Hoot et al., 1999
Betulaceae	Rosid cl., core rosids, "higher" Hamamelididae	Albert et al., 1992; Chase et al., 1993; Manos et al., 1993; Gunter et al., 1994; Swensen et al., 1994; Soltis et al., 1995b; Manos & Steele, 1997	?
Bignoniaceae	Asterid cl., Lamiidae s.l., Lamiales s.l.	Downie & Palmer, 1992; Olmstead et al., 1992; Chase et al., 1993; Cosner et al., 1994; Hedrén et al., 1995; Olmstead & Reeves, 1995; Soltis & Soltis, 1997	Olmstead & Reeves, 1995
Bixaceae	Rosid cl., Capparales/Sapindales/Malvales, expanded Malvales	Soltis et al., 1998; Alverson et al., 1998	Alverson et al., 1998
Boraginaceae	Asterid cl., Lamiidae s.l., Boraginales	Downie & Palmer, 1992; Olmstead et al., 1992, 1993; Chase et al., 1993; Morgan & Soltis, 1993; Cosner et al., 1994; Gustafsson et al., 1996; Soltis & Soltis, 1997	?

Table 2. Continued.

Taxon	Phylogenetic placement	Reference for placement	Monophyly status
Bretschneideraceae	Rosid cl., Capparales/Sapindales/ Malvales, expanded Capparales	Gadek et al., 1992; Rodman, 1991; Rodman et al., 1993, 1994, 1996; Chase et al., 1993	single genus
Bruniaceae (only *Berzelia*)	Asterid cl., Asteridae s.l.	Chase et al., 1993; Olmstead et al., 1993; Gustafsson et al., 1996	?
Brunoniaceae	Asterid cl., Asteridae s.l., Asterales s.l.	Cosner et al., 1994; Gustafsson & Bremer, 1995; Gustafsson et al., 1996	single genus
Buddlejaceae	Asterid cl., Lamiidae s.l., Lamiales s.l.	Downie & Palmer, 1992; Chase et al., 1993; Olmstead et al., 1993; Cosner et al., 1994	single genus
Burseraceae	Rosid cl., Capparales/Sapindales/ Malvales, Sapindales	Gadek et al., 1992, 1996; Chase et al., 1993; Fernando et al., 1993, 1995; Morgan & Soltis, 1993; Rodman et al., 1993	?
Buxaceae	basal eudicot grade	Chase et al., 1993; Drinnan et al., 1994; Hoot et al., 1999	Drinnan et al., 1994; Hoot et al., 1999
Byblidaceae			polyphyletic
Byblis	Asterid cl., Lamiidae s.l., Lamiales s.l.	Albert et al., 1992; Chase et al., 1993; Olmstead et al., 1993; Williams et al., 1994; Hedrén et al., 1995	—
Roridula	Asterid cl., ericalean cl.	Albert et al., 1992; Anderberg, 1992; Chase et al., 1993; Kron & Chase, 1993; Olmstead et al., 1993; Cosner et al., 1994; Williams et al., 1994; Morton et al., 1996, 1997	—
Callitrichaceae	Asterid cl., Lamiidae s.l., Lamiales s.l.	Downie & Palmer, 1992; Chase et al., 1993; Olmstead et al., 1992, 1993; Cosner et al., 1994; Hedrén et al., 1995	?
Calyceraceae	Asterid cl., Asteridae s.l., Asterales s.l.	Olmstead, 1992, 1993; Chase et al., 1993; Michaels et al., 1993; Cosner et al., 1994; Gustafsson & Bremer, 1995; Gustafsson et al., 1996	?
Campanulaceae	Asterid cl., Asteridae s.l., Asterales s.l.	Olmstead, 1992, 1993; Chase et al., 1993; Michaels et al., 1993; Cosner et al., 1994; Gustafsson & Bremer, 1995; Gustafsson et al., 1996	?
Caricaceae	Rosid cl., Capparales/Sapindales/ Malvales, expanded Capparales	Gadek et al., 1992; Chase et al., 1993; Morgan & Soltis, 1993; Rodman et al., 1993, 1994, 1996, 1998; Swensen et al., 1994; Alverson et al., 1998	Rodman, 1991
Caryocaraceae (only *Caryocar*)	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	?

Table 2. Continued.

Taxon	Phylogenetic placement	Reference for placement	Monophyly status
Casuarinaceae	Rosid cl., core rosids, "higher" Hamamelididae	Albert et al., 1992; Chase et al., 1993; Manos et al., 1993; Morgan & Soltis, 1993; Gunter et al., 1994; Morgan et al., 1994; Swensen et al., 1994; Soltis et al., 1995b; Manos & Steele, 1997	Soltis et al., 1995b
Celastraceae			paraphyletic
Euonymus	Rosid cl., core rosids, *Euonymus* cl.	Chase et al., 1993; Morgan & Soltis, 1993; Swensen et al., 1994; Williams et al., 1994; Soltis et al., 1995b; Conti et al., 1996; Soltis et al., 1997a	—
Goupia	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	—
Hippocratea	Rosid cl., core rosids, *Euonymus* cl.	Soltis et al., 1998	—
Siphonodon	Rosid cl., core rosids, *Euonymus* cl.	Soltis et al., 1998	—
Cephalotaceae	Rosid cl., core rosids, expanded Cunoniaceae	Albert et al., 1992; Chase et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Williams et al., 1994; Soltis et al., 1995b; Conti et al., 1996; Soltis & Soltis, 1997	single genus
Cercidiphyllaceae	Saxifragoids	Chase et al., 1993; Manos et al., 1993; Morgan & Soltis, 1993; Soltis et al., 1993, 1997a; Williams et al., 1994; Soltis & Soltis, 1997; Hoot et al., 1999	single genus
Chrysobalanaceae	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Swensen et al., 1994; Soltis et al., 1995b	Chase et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Soltis et al., 1995b
Circaeasteraceae	Ranunculid cl., Ranunculales	Drinnan et al, 1994; Hoot & Crane, 1995; Hoot et al., 1995a, 1999	single genus
Cistaceae (only *Helianthemum* and *Cistus*)	Rosid cl., Capparales/Sapindales/Malvales, expanded Malvales	Soltis et al., 1998; Alverson et al., 1998	?
Clethraceae	Asterid cl., ericalean cl.	Anderberg, 1992, 1993; Chase et al., 1993; Kron & Chase 1993; Olmstead et al., 1993; Cosner et al., 1994; Morton et al., 1996, 1997	single genus
Clusiaceae (only *Mesua* and *Hypericum*)	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	?
Cneoraceae	Rosid cl., Capparales/Sapindales/Malvales, Sapindales	Fernando et al., 1995; Gadek, 1996	single genus

Table 2. Continued.

Taxon	Phylogenetic placement	Reference for placement	Monophyly status
Connaraceae (only *Connarus*)	Rosid cl., uncertain position within core rosids	Fernando et al., 1993; Morgan et al., 1994	?
Convolvulaceae	Asterid cl., Lamiidae s.l., Solanales	Downie & Palmer, 1992; Chase et al., 1993; Morgan & Soltis, 1993; Olmstead et al., 1992, 1993; Cosner et al., 1994; Soltis & Soltis, 1997	Chase et al., 1993; Olmstead et al., 1993
Coriariaceae	Rosid cl., core rosids, Cucurbitales	Albert et al., 1992; Chase et al., 1993; Swensen et al., 1994; Soltis et al., 1995b	single genus
Corynocarpaceae	Rosid cl., core rosids, Cucurbitales	Soltis et al., 1998	single genus
Cornaceae			polyphyletic
Aralidium	Asterid cl., Asteridae s.l., Apiales	Plunkett et al., 1996	—
Aucuba	Asterid cl., *Garrya* cl.	Olmstead et al., 1993; Cosner et al., 1994; Gustafsson et al., 1996	—
Cornus	Asterid cl., cornalean cl.	Chase et al., 1993; Morgan & Soltis, 1993; Olmstead et al. 1993; Xiang et al., 1993; Hempel et al., 1995; Soltis et al., 1995a	—
Corokia	Asterid cl., Asteridae s.l., Asterales s.l.	Chase et al., 1993; Michaels et al., 1993; Olmstead et al., 1993; Cosner et al., 1994	—
Curtisia	Asterid cl., cornalean cl.	Xiang et al., 1993; Hempel et al., 1995; Soltis et al., 1995a	—
Diplopanax	Asterid cl., cornalean cl.	Chase et al., 1993; Xiang et al., 1993; Soltis et al., 1995a	—
Helwingia	Asterid cl., *Ilex* cl.	Chase et al., 1993; Olmstead et al., 1993; Gustafsson et al., 1996; Plunkett et al., 1996	—
Griselinia	Asterid cl., Asteridae s.l., Apiales	Chase et al., 1993; Olmstead et al., 1993; Cosner et al., 1994; Gustafsson et al., 1996; Plunkett et al., 1996	—
Melanophylla	Asterid cl., Asteridae s.l., Apiales	Plunkett et al., 1996	—
Toricellia	Asterid cl., Asteridae s.l., Apiales	Plunkett et al., 1996	—
Crassulaceae	Saxifragoids	Chase et al., 1993; Morgan & Soltis, 1993; Soltis et al., 1993, 1997a; Williams et al., 1994; Soltis & Soltis, 1997	Chase et al., 1993; Morgan & Soltis, 1993; Soltis et al., 1993, 1997; Swensen et al., 1994; Williams et al., 1994; Soltis & Soltis, 1997
Crossossomataceae	uncertain placement within rosid clade	Chase et al., 1993; Fernando et al., 1993; Price & Palmer, 1993; Soltis & Soltis, 1997; Soltis et al., 1993	single genus
Cucurbitaceae	Rosid cl., core rosids, Cucurbitales	Chase et al., 1993; Swensen et al., 1994; Soltis et al., 1995b	Chase et al., 1993; Soltis et al., 1995b

Table 2. Continued.

Taxon	Phylogenetic placement	Reference for placement	Monophyly status
Cunoniaceae (including *Bauera*)	Rosid cl., core rosids, expanded Cunoniaceae	Albert et al., 1992; Hufford, 1992; Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Swensen et al., 1994; Williams et al., 1994; Soltis et al., 1995b; Conti et al., 1996; Soltis & Soltis, 1997	Hufford, 1992; Chase et al., 1993; Morgan & Soltis, 1993; Soltis et al., 1995b; Soltis & Soltis, 1997
Cyphocarpaceae	Asterid cl., Asteridae s.l., Asterales s.l.	Gustafsson & Bremer, 1995; Gustafsson et al., 1996	single genus
Cyphiaceae	Asterid cl., Asteridae s.l., Asterales s.l.	Gustafsson & Bremer, 1995; Gustafsson et al., 1996	single genus
Cyrillaceae	Asterid cl., ericalean cl.	Albert et al., 1992; Anderberg, 1992, 1993; Kron & Chase, 1993; Olmstead et al., 1993; Cosner et al., 1994; Morton et al., 1996, 1997	Morton et al., 1996
Daphniphyllaceae	Saxifragoids	Chase et al., 1993; Morgan & Soltis, 1993; Soltis et al., 1993, 1997a; Soltis & Soltis, 1997; Hoot et al., 1999	single genus
Datiscaceae	Rosid cl., core rosids, Cucurbitales	Chase et al., 1993; Morgan & Soltis, 1993; Swensen et al., 1994; Soltis et al., 1995b	paraphyletic, all components in similar phylogenetic placement
Davidsoniaceae	Rosid cl., core rosids, expanded Cunoniaceae	Soltis et al., 1998	single genus
Diapensiaceae	Asterid cl., ericalean cl.	Anderberg, 1992, 1993; Chase et al., 1993; Kron & Chase, 1993; Olmstead et al., 1993; Cosner et al., 1994; Morton et al., 1996, 1997	?
Dichapetalaceae (only *Dichapetalum*)	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	?
Didymelaceae	basal eudicot grade	Hoot et al., 1999	single genus
Dilleniaceae	uncertain within core eudicots	Albert et al., 1992; Chase et al., 1993; Williams et al., 1994; Hoot et al., 1999; Soltis et al., 1998	Hoot et al., 1999
Dioncophyllaceae (only *Triphyllophyllum*)	Caryophyllid cl., Plumbaginales/Polygonales	Lledó et al., 1998; Soltis et al., 1998	?
Dipterocarpaceae (only *Shorea*, *Monotes*, and *Anisoptera*)	Rosid cl., Capparales/Sapindales/Malvales, expanded Malvales	Chase et al., 1993; Fernando et al., 1995; Soltis et al., 1998; Alverson et al., 1998	Chase et al., 1993; Fernando et al., 1995; Alverson et al., 1998

Table 2. Continued.

Taxon	Phylogenetic placement	Reference for placement	Monophyly status
Donatiaceae	Asterid cl., Asteridae s.l., Asterales	Gustafsson & Bremer, 1995; Gustafsson et al., 1996	?
Droseraceae	Caryophyllid cl., Polygonales/Plumbaginales	Albert et al., 1992; Chase et al., 1993; Williams et al., 1994; Soltis et al., 1997a	Albert et al., 1992; Chase et al., 1993; Williams et al., 1994
Duckeodendraceae	Asterid cl., Lamiidae s.l., Solanales	Soltis et al., 1998	single genus
Ebenaceae	Asterid cl., ericalean cl.	Chase et al., 1993; Kron & Chase, 1993; Olmstead et al., 1993; Cosner et al., 1994; Morton et al., 1996, 1997	?
Elaeagnaceae	Rosid cl., core rosids, Urticales	Soltis et al., 1995b	Soltis et al., 1995b
Elaeocarpaceae	Rosid cl., core rosids, expanded Cunoniaceae	Soltis et al., 1998	Soltis et al., 1998
Empetraceae	Asterid cl., ericalean cl.	Anderberg, 1992, 1993; Chase et al., 1993; Judd & Kron, 1993; Kron & Chase, 1993; Olmstead et al., 1993; Cosner et al., 1994	Anderberg, 1994
Ericaceae	Asterid cl., ericalean cl.	Albert et al., 1992; Anderberg, 1992, 1993; Chase et al., 1993; Judd & Kron, 1993; Kron & Chase, 1993; Olmstead et al., 1993; Cosner et al., 1994; Kron, 1996; Morton et al., 1996, 1997	paraphyletic, all components in similar phylogenetic placement
Epacridaceae	Asterid cl., ericalean cl.	Albert et al., 1992; Anderberg, 1992, 1993; Chase et al., 1993; Judd & Kron, 1993; Kron & Chase, 1993; Olmstead et al., 1993; Cosner et al., 1994; Kron, 1996; Morton et al., 1996	Kron & Chase, 1993; Kron, 1996; Morton et al., 1996
Eucommiaceae	Asterid cl., *Garrya* cl.	Albert et al., 1992; Chase et al., 1993; Olmstead et al., 1993; Cosner et al., 1994; Gustafsson et al., 1996	single genus
Euphorbiaceae	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Chase et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Swensen et al., 1994; Williams et al., 1994; Soltis et al., 1997a	paraphyletic, with components in similar phylogenetic placement
Eupteleaceae	Ranunculid cl.	Chase et al., 1993; Drinnan et al., 1994; Hoot & Crane, 1995; Hoot et al., 1995b, 1999	single genus
Fabaceae s.l.	Rosid cl., core rosids, Fabaceae/Surianaceae/Polygalaceae	Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Swensen et al., 1994; Soltis et al., 1995b	Chase et al., 1993; Fernando et al., 1993; Soltis et al., 1995b; Doyle et al., 1997
Fagaceae (including *Nothofagus*)	Rosid cl., core rosids, "higher" Hamamelididae	Chase et al., 1993; Manos et al., 1993; Morgan & Soltis, 1993; Gunter et al., 1994; Morgan et al., 1994; Swensen et al., 1994; Soltis et al., 1995b, Manos & Steele, 1997	paraphyletic, with components in similar phylogenetic placement

Table 2. Continued.

Taxon	Phylogenetic placement	Reference for placement	Monophyly status
Flacourtiaceae			polyphyletic
Abatia	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	—
Aphloia	uncertain within rosid clade	Soltis et al., 1998	—
Berberidopsis	uncertain within core eudicots	Soltis et al., 1998	—
Casearia	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	—
Flacourtia	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	—
Hydnocarpus	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	—
Idesia	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	—
Kiggelaria	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	—
Muntingia	Rosid cl., Capparales/Sapindales/Malvales, expanded Malvales	Alverson et al., 1998; Soltis et al., 1998	—
Pangium	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	—
Plagiopteron	Rosid cl., core rosids, *Euonymus* cl.	Soltis et al., 1998	—
Fouquieriaceae	Asterid cl., ericalean cl.	Chase et al., 1993; Kron & Chase, 1993; Olmstead et al., 1993; Cosner et al., 1994; Morton et al., 1996, 1997	Morton et al., 1997
Frankeniaceae (only *Frankenia*)	Caryophyllid cl., Polygonales/Plumbaginales	Lledó et al., 1998; Soltis et al., 1998	?
Fumariaceae	Ranunculid cl., Papaverales	Chase et al., 1993; Drinnan, et al., 1994; Hoot & Crane, 1995; Hoot et al., 1999	Drinnan et al., 1994; Hoot et al., 1999
Garryaceae	Asterid cl., *Garrya* cl.	Albert et al., 1992; Chase et al., 1993; Olmstead et al., 1993; Cosner et al., 1994; Gustafsson et al., 1996	single genus
Gentianaceae	Asterid cl., Lamiidae s.l., Gentianales	Downie & Palmer, 1992; Olmstead et al., 1992, 1993; Chase et al., 1993; Struwe et al., 1994; Gustafsson et al., 1996; Soltis et al., 1997a	Bremer & Struwe, 1992; Chase et al., 1993; Olmstead et al., 1993
Geraniaceae (excl. *Wendtia* and *Viviania*)	Rosid cl., Geraniaceae	Chase et al., 1993; Morgan & Soltis, 1993; Williams et al., 1994	Albert et al., 1992; Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Price & Palmer, 1993; Williams et al., 1994

Table 2. Continued.

Taxon	Phylogenetic placement	Reference for placement	Monophyly status
Viviania	Rosid cl., *Francoa* cl.	Chase et al., 1993; Morgan & Soltis, 1993; Price & Palmer, 1993; Williams et al., 1994	—
Wendtia	Rosid cl., *Francoa* cl.	Chase et al., 1993; Price & Palmer, 1993	—
Gesneriaceae	Asterid cl., Lamiidae s.l., Lamiales s.l.	Downie & Palmer, 1992; Chase et al., 1993; Hedrén et al., 1995; Gustafsson et al., 1996; Smith et al., 1997; Soltis & Soltis, 1997	Smith et al., 1997
Goodeniaceae (including *Brunonia*)	Asterid cl., Asteridae s.l., Asterales s.l.	Chase et al., 1993; Michaels et al., 1993; Olmstead et al., 1993; Cosner et al., 1994; Gustafsson & Bremer, 1995; Gustafsson et al., 1996	?
Globulariaceae	Asterid cl., Lamiidae s.l., Lamiales s.l.	Downie & Palmer, 1992	?
Greyiaceae	Rosid cl., *Francoa* cl.	Chase et al., 1993; Morgan & Soltis, 1993; Price & Palmer, 1993	single genus
Grossulariaceae			polyphyletic
Brexioideae			polyphyletic
Brexia	Rosid cl., core rosids, *Euonymus* cl.	Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Soltis et al., 1997a	—
Ixerba	uncertain within rosid clade	Soltis et al., 1998	—
Escallonioideae	Asterid cl., Asteridae s.l.	Olmstead et al., 1993; Cosner et al., 1994; Gustafsson et al., 1996	?
Iteoideae	Saxifragoids	Chase et al., 1993; Morgan & Soltis, 1993; Soltis et al., 1993, 1997a; Soltis & Soltis, 1997	single genus
Montinioideae	Asterid cl., Lamiidae s.l.	Chase et al., 1993; Morgan & Soltis, 1993; Cosner et al., 1994; Gustafsson et al., 1996; Soltis & Soltis, 1997; Soltis et al., 1997a	single genus
Phyllonomoideae	Asterid cl., *Ilex* cl.	Chase et al., 1993; Olmstead et al., 1993; Cosner et al., 1994; Gustafsson et al., 1996; Plunkett et al., 1996	single genus
Pterostemonoideae	Saxifragoids	Chase et al., 1993; Morgan & Soltis, 1993; Soltis et al., 1993; Soltis et al., 1997a; Soltis & Soltis, 1997	single genus
Ribesoideae	Saxifragoids	Chase et al., 1993; Morgan & Soltis, 1993; Williams et al., 1994; Soltis & Soltis, 1997; Soltis et al., 1997a	single genus
Tetracarpoideae	Saxifragoids	Chase et al., 1993; Morgan & Soltis, 1993; Soltis et al., 1997a; Soltis & Soltis, 1997	single genus
Grubbiaceae	Asterid cl., ericalean cl.	Anderberg, 1992	single genus

Table 2. Continued.

Taxon	Phylogenetic placement	Reference for placement	Monophyly status
Gunneraceae	uncertain within core eudicots, associated with *Myrothamnus*	Chase et al., 1993; Drinnan et al., 1994; Hoot et al., 1999; Soltis et al., 1998	single genus
Gyrostemonaceae	Rosid cl., Capparales/Sapindales/ Malvales, expanded Capparales	Rodman et al., 1994	Rodman et al., 1994
Haloragaceae	Saxifragoids	Chase et al., 1993; Morgan & Soltis, 1993; Soltis & Soltis, 1997; Soltis et al., 1997a; Hoot et al., 1999	Soltis & Soltis, 1997
Hamamelidaceae	Saxifragoids	Chase et al., 1993; Manos et al., 1993; Morgan & Soltis, 1993; Soltis et al., 1993, 1997a; Williams et al., 1994; Hoot et al., 1999	paraphyletic, all components in similar phylogenetic placement
Hippocastanaceae	Rosid cl., Capparales/Sapindales/ Malvales, Sapindales	Fernando et al., 1995; Gadek et al., 1996	?
Huaceae (only *Afrostyrax*)	Rosid cl., core rosids, *Euonymus* cl.	Soltis et al., 1998	?
Hydrangeaceae	Asterid cl., cornalean cl.	Hufford, 1992; Chase et al., 1993; Morgan & Soltis, 1993; Olmstead et al. 1993; Xiang et al., 1993; Hempel et al., 1995; Soltis et al., 1995a	Hufford, 1992; Chase et al., 1993; Morgan & Soltis, 1993; Olmstead et al., 1993; Soltis et al., 1995a
Hydrophyllaceae	Asterid cl., Lamiidae s.l., Boraginales	Albert et al., 1992; Downie & Palmer, 1992; Olmstead et al., 1992; Chase et al., 1993; Morgan & Soltis, 1993; Olmstead et al., 1993; Cosner et al., 1994	Chase et al., 1993; Olmstead et al., 1993; Cosner et al., 1994
Hydrostachydaceae	Asterid cl., cornalean cl.	Hempel et al., 1995; Soltis et al., 1998	single genus
Icacinaceae (only *Icacina* and *Gonocaryum*)	Asterid cl., uncertain within core asterids	Soltis et al., 1998	paraphyletic
Juglandaceae	Rosid cl., core rosids, "higher" Hamamelididae	Chase et al., 1993; Manos et al., 1993; Gunter et al., 1994; Swensen et al., 1994; Soltis et al., 1995b; Manos & Steele, 1997	?
Kirkiaceae	Rosid cl., Capparales/Sapindales/ Malvales, Sapindales	Fernando et al., 1995; Gadek et al., 1996	single genus
Krameriaceae	uncertain within core rosids	Chase et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994	single genus
Lacistemataceae (only *Lacistema*)	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	?

Table 2. Continued.

Taxon	Phylogenetic placement	Reference for placement	Monophyly status
Lamiaceae	Asterid cl., Lamiidae s.l., Lamiales s.l.	Albert et al., 1992; Downie & Palmer, 1992; Olmstead et al., 1992; Chase et al., 1993; Morgan & Soltis, 1993; Cosner et al., 1994; Hedrén et al., 1995; Olmstead & Reeves, 1995; Soltis & Soltis, 1997; Wagstaff & Olmstead, 1997	Olmstead & Reeves, 1995
Lardizabalaceae	Ranunculid cl., Ranunculales	Chase et al., 1993; Drinnan et al., 1994; Hoot & Crane, 1995; Hoot et al., 1999	Drinnan et al., 1994; Hoot et al, 1995a, 1995b, 1998
Lecythidaceae	Asterid cl., ericalean cl.	Morton et al., 1996, 1997	paraphyletic, all components in similar phylogenetic placement
Leeaceae	uncertain within core eudicots, associated with *Vitis*	Soltis et al., 1998	single genus
Leitneriaceae	Rosid cl., Capparales/Sapindales/Malvales, Sapindales	Gadek et al., 1992, 1996; Chase et al., 1993; Morgan & Soltis, 1993; Fernando et al., 1995	single genus
Lentibulariaceae	Asterid cl., Lamiidae s.l., Lamiales s.l.	Albert et al., 1992; Chase et al., 1993; Olmstead et al., 1993; Cosner et al., 1994; Williams et al., 1994; Hedrén et al., 1995	Chase et al., 1993; Olmstead et al., 1993
Limnanthaceae	Rosid cl., Capparales/Sapindales/Malvales, expanded Capparales	Gadek et al., 1992; Chase et al., 1993; Morgan & Soltis, 1993; Price & Palmer, 1993; Rodman et al., 1993, 1994, 1996; Williams et al., 1994	Chase et al., 1993; Rodman et al., 1993, 1994, 1996
Loasaceae	Asterid cl., cornalean cl.	Hufford, 1992; Hempel et al., 1995; Soltis et al., 1995a	Hempel et al., 1995
Lobeliaceae	Asterid cl., Asteridae s.l., Asterales s.l.	Chase et al., 1993; Cosner et al., 1994; Gustafsson & Bremer, 1995; Gustafsson et al., 1996	?
Loganiaceae (excluding *Desfontainia*, *Plocosperma*, and *Polypremnum*)	Asterid cl., Lamiidae s.l., Gentianales	Downie & Palmer, 1992; Chase et al., 1993; Olmstead et al., 1993; Cosner et al., 1994	?
Desfontainia	Asterid cl., Asteridae s.l., Dipsacales	Struwe et al., 1994; Gustafsson et al., 1996	—
Plocosperma	Asterid cl., Lamiidae s.l., Lamiales s.l.	Struwe et al., 1994	—
Polypremnum	Asterid cl., Lamiidae s.l., Lamiales s.l.	Struwe et al., 1994	—
Malesherbiaceae	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	single genus

Table 2. Continued.

Taxon	Phylogenetic placement	Reference for placement	Monophyly status
Malpighiaceae	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Albert et al., 1992; Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Swensen et al., 1994; Williams et al., 1994; Soltis et al., 1995b	Chase et al., 1993
Marcgraviaceae	Asterid cl., ericalean cl.	Morton et al., 1996, 1997	?
Medusagynaceae	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	single genus
Meliaceae	Rosid cl., Capparales/Sapindales/Malvales, Sapindales	Fernando et al., 1995; Gadek et al., 1996	?
Melianthaceae (only *Bersama*)	Rosid cl., associated with *Francoa* cl.	Soltis et al., 1998	?
Menyanthaceae	Asterid cl., Asteridae s.l., Asterales s.l.	Olmstead et al., 1992, 1993; Chase et al., 1993; Michaels et al., 1993; Cosner et al., 1994; Gustafsson & Bremer, 1995; Gustafsson et al., 1996	?
Menispermaceae	Ranunculid cl., Ranunculales	Chase et al., 1993; Drinnan et al., 1994; Hoot & Crane, 1995; Soltis et al., 1997a; Hoot et al., 1999	Hoot & Crane, 1995; Drinnan et al., 1994; Hoot et al., 1999
Monotropaceae	Asterid cl., ericalean cl.	Anderberg, 1992, 1993; Judd & Kron, 1993	?
Myoporaceae	Asterid cl., Lamiidae s.l., Lamiales s.l.	Downie & Palmer, 1992	?
Myricaceae	Rosid cl., core rosids, "higher" Hamamelididae	Chase et al., 1993; Manos et al., 1993; Morgan & Soltis, 1993; Gunter et al., 1994; Morgan et al., 1994; Swensen et al., 1994; Soltis et al., 1995b; Manos & Steele, 1997	?
Myrothamnaceae	uncertain within core eudicots, associated with *Gunnera*	Drinnan et al., 1994; Hoot et al., 1999; Soltis et al., 1998	single genus
Nelumbonaceae	basal eudicot grade	Chase et al., 1993; Drinnan et al., 1994; Hoot et al., 1999	single genus
Nemacladaceae	Asterid cl., Asteridae s.l., Asterales s.l.	Gustafsson & Bremer, 1995; Gustafsson et al., 1996	single genus
Nepenthaceae	Caryophyllid cl., Polygonales/Plumbaginales	Chase et al., 1993; Soltis et al., 1997a; Lledó et al., 1998; Hoot et al., 1999	single genus
Neuradaceae (only *Neurada*)	Rosid cl., Capparales/Sapindales/Malvales, expanded Malvales	Soltis et al., 1998; Alverson et al., 1998	?
Nyssaceae (including *Mastixia*)	Asterid cl., cornalean cl.	Hufford, 1992; Chase et al., 1993; Morgan & Soltis, 1993; Olmstead et al. 1993; Hempel et al., 1995; Soltis et al., 1995a	?

Table 2. Continued.

Taxon	Phylogenetic placement	Reference for placement	Monophyly status
Ochnaceae	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Chase et al., 1993; Soltis et al., 1995b	single genus
Oleaceae	Asterid cl., Lamiidae s.l., Lamiales s.l.	Albert et al., 1992; Downie & Palmer, 1992; Olmstead et al., 1992, 1993; Hedrén et al., 1995; Gustafsson et al., 1996; Soltis & Soltis, 1997; Soltis et al., 1997a	Chase et al., 1993; Olmstead et al., 1993
Oncothecaceae	Asterid cl., associated to *Garrya* clade and Lamiidae s.l.	Soltis et al., 1998	single genus
Oxalidacae (excluding *Hypseocharis*)	Rosid cl., core rosids, expanded Cunoniaceae	Albert et al., 1992; Chase et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Swensen et al., 1994; Williams et al., 1994; Soltis et al., 1995b; Conti et al., 1996	?
Hypseocharis	Rosid cl., Geraniaceae	Chase et al., 1993	—
Paeoniaceae	Saxifragoids	Chase et al., 1993; Soltis & Soltis, 1997; Soltis et al., 1997a; Hoot et al., 1999	single genus
Papaveraceae	Ranunculid cl., Papaverales	Chase et al., 1993; Drinnan et al., 1994	Drinnan et al., 1994
Passifloraceae	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Albert et al., 1992; Chase et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Swensen et al., 1994; Soltis et al., 1995b, 1998	?
Pedaliaceae	Asterid cl., Lamiidae s.l., Lamiales s.l.	Albert et al., 1992; Downie & Palmer, 1992; Chase et al., 1993; Morgan & Soltis, 1993; Olmstead et al., 1993; Cosner et al., 1994	Olmstead et al., 1993; Hedrén et al., 1995
Pelliceraceae	Asterid cl., ericalean cl.	Soltis et al., 1998	single genus
Pentaphragmataceae	Asterid cl., Asteridae s.l., Asterales s.l.	Cosner et al., 1994; Gustafsson & Bremer, 1995; Gustafsson et al., 1996	?
Pittosporaceae	Asterid cl., Asteridae s.l., Apiales	Chase et al., 1993; Olmstead et al., 1993; Cosner et al., 1994; Gustafsson et al., 1996; Plunkett et al., 1996; Soltis et al., 1997a	Plunkett et al., 1996
Plantaginaceae (only *Plantago*)	Asterid cl., Lamiidae s.l., Lamilaes s.l.	Olmstead & Reeves, 1995; Reeves & Olmstead, 1998	?
Platanaceae	basal eudicot grade	Chase et al., 1993; Drinnan et al., 1994; Hoot et al., 1999	single genus
Plumbaginaceae	Caryophyllid cl., Polygonales/Plumbaginales	Rodman et al., 1984; Albert et al., 1992; Olmstead et al., 1992; Chase et al., 1993; Williams et al., 1994; Soltis et al., 1997a; Lledó et al., 1998	Lledó et al., 1998

Table 2. Continued.

Taxon	Phylogenetic placement	Reference for placement	Monophyly status
Podostemaceae			polyphyletic
Marathrum	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	—
Hydrobryum	Saxifragoids	Ueda et al., 1997a	—
Cladopus	Saxifragoids	Ueda et al., 1997a	—
Polemoniaceae	Asterid cl., ericalean cl.	Chase et al., 1993; Kron & Chase, 1993; Olmstead et al., 1993; Cosner et al., 1994; Williams et al., 1994; Morton et al., 1996	Johnson et al., 1996; Morton et al., 1996
Polygalaceae	Rosid cl., core rosids, Fabaceae/Surianaceae/Polygalaceae	Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Swensen et al., 1994; Soltis et al., 1995b	Chase et al., 1993; Fernando et al., 1993; Soltis et al., 1995b
Polygonaceae	Caryophyllid cl., Polygonales/Plumbaginales	Rodman et al., 1984; Albert et al., 1992; Olmstead et al., 1992; Chase et al., 1993; Williams et al., 1994; Soltis et al., 1997a; Lledó et al., 1998	Downie & Palmer, 1994, Lledó et al., 1998
Proteaceae	basal eudicot grade	Chase et al., 1993; Drinnan et al., 1994; Hoot et al., 1999	Drinnan et al., 1994; Hoot et al., 1999
Ptaeroxylaceae	Rosid cl., Capparales/Sapindales/Malvales, Sapindales	Gadek et al., 1996	?
Pyrolaceae	Asterid cl., ericalean cl.	Anderberg, 1992, 1993; Chase et al., 1993; Judd & Kron, 1993; Kron & Chase, 1993; Olmstead et al., 1993; Morton et al., 1996	?
Quiinaceae (only *Quiina*)	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	?
Ranunculaceae	Ranunculid cl., Ranunculales	Chase et al., 1993; Drinnan et al., 1994; Hoot, 1995; Soltis et al., 1997a; Hoot et al., 1999	Chase et al., 1993; Drinnan et al., 1994; Hoot, 1995; Soltis et al., 1997a; Hoot et al., 1999
Retziaceae	Asterid cl., Lamiidae s.l., Lamiales s.l.	Hedrén et al., 1995; Struwe et al., 1994	single genus
Rhabdodendraceae	Caryophyllid cl., Polygonales/Plumbaginales	Lledó et al., 1998; Soltis et al., 1998	single genus
Rhamnaceae (only *Rhamnus* and *Ceanothus*)	Rosid cl., core rosids, Urticales	Morgan & Soltis, 1993; Morgan et al., 1994; Swensen et al., 1994; Soltis et al., 1995b	?
Rhizophoraceae (only *Carallia*)	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	?

Table 2. Continued.

Taxon	Phylogenetic placement	Reference for placement	Monophyly status
Rosaceae (excluding *Quillaja*)	Rosid cl., core rosids	Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Swensen et al., 1994; Soltis et al., 1995b	Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Swensen et al., 1994; Williams et al., 1994; Soltis et al., 1995b; Soltis et al., 1997a
Quillaja	Rosid cl., core rosids, Fabaceae/Surianaceae/Polygalaceae	Morgan et al., 1994; Soltis et al., 1995b; Doyle et al., 1997	—
Rubiaceae	Asterid cl., Lamiidae s.l., Gentianales	Bremer & Struwe, 1992; Downie & Palmer, 1992; Chase et al., 1993; Olmstead et al., 1993; Cosner et al., 1994; Struwe et al., 1994; Gustafsson et al., 1996; Soltis & Soltis, 1997; Soltis et al., 1997a	Bremer & Struwe, 1992; Olmstead et al., 1993; Struwe et al., 1994
Rutaceae	Rosid cl., Capparales/Sapindales/Malvales, Sapindales	Gadek et al., 1992, 1996; Chase et al., 1993; Fernando et al., 1993, 1995; Morgan & Soltis, 1993	?
Sabiaceae	basal eudicot grade	Chase et al., 1993; Drinnan et al., 1994; Hoot et al., 1999; Soltis et al., 1998	Soltis et al., 1998
Salicaceae	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	Soltis et al., 1998
Salvadoraceae	Rosid cl., Capparales/Sapindales/Malvales, expanded Capparales	Rodman et al., 1998	?
Sapindaceae	Rosid cl., Capparales/Sapindales/Malvales, Sapindales	Gadek et al., 1992, 1996; Chase et al., 1993; Morgan & Soltis, 1993; Fernando et al., 1993, 1995	?
Sapotaceae	Asterid cl., ericalean cl.	Albert et al., 1992; Chase et al., 1993; Kron & Chase, 1993; Olmstead et al., 1993; Cosner et al., 1994; Morton et al., 1996, 1997	Chase et al., 1993; Kron & Chase, 1993; Olmstead et al., 1993; Morton et al., 1997
Sarcolaenaceae	Rosid cl., Capparales/Sapindales/Malvales, expanded Malvales	Conti et al., 1996; Soltis et al., 1998; Alverson et al., 1998	Conti et al., 1996
Sargentodoxaceae	Ranunculid cl., Ranunculales	Hoot & Crane, 1995; Hoot et al., 1999	single genus
Sarraceniaceae	Asterid cl., ericalean cl.	Albert et al., 1992; Chase et al., 1993; Kron & Chase, 1993; Olmstead et al., 1993; Cosner et al., 1994; Williams et al., 1994; Morton et al., 1996, 1997	Albert et al., 1992; Chase et al., 1993; Bayer et al., 1996; Morton et al., 1997
Saxifragaceae			polyphyletic
Eremosynoideae	Asterid cl., Asteridae s.l.	Hibisch-Jetter et al., 1997; Soltis et al., 1997a	single genus
Francooideae	Rosid cl., *Francoa* cl.	Chase et al., 1993; Morgan & Soltis, 1993; Price & Palmer, 1993; Williams et al., 1994	?
Lepuropetaloideae	Rosid cl., core rosids, *Euonymus* clade	Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Soltis et al., 1995b; Soltis et al., 1997a	single genus

Table 2. Continued.

Taxon	Phylogenetic placement	Reference for placement	Monophyly status
Parnassioideae	Rosid cl., core rosids, *Euonymus*-clade	Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Swensen et al., 1994; Williams et al., 1994; Soltis et al., 1997a	single genus
Penthoroideae	Saxifragoids	Chase et al., 1993; Morgan & Soltis, 1993; Soltis & Soltis, 1997; Soltis et al., 1997a	single genus
Saxifragoideae	Saxifragoids	Chase et al., 1993; Morgan & Soltis, 1993; Soltis et al., 1993, 1997a; Williams et al., 1994; Soltis & Soltis, 1997	Chase et al., 1993; Morgan & Soltis, 1993; Soltis et al., 1993, 1997a; Williams et al., 1994; Soltis et al., 1997a
Vahlioideae	Asterid cl., Lamiidae s.l., Lamiales s.l.	Chase et al., 1993; Morgan & Soltis, 1993; Gustafsson et al., 1996; Soltis & Soltis, 1997; Soltis et al., 1997a	single genus
Scrophulariaceae	Asterid cl., Lamiidae s.l., Lamiales s.l.	Albert et al., 1992; Downie & Palmer, 1992; Olmstead et al., 1992, 1993; Chase et al., 1993; Morgan & Soltis, 1993; Cosner et al., 1994; Williams et al., 1994; Hedrén et al., 1995; Olmstead & Reeves, 1995; Gustafsson et al., 1996	paraphyletic, all components in similar phylogenetic placement
Scytopetalaceae	Asterid cl., ericalean cl.	Morton et al., 1996, 1997	Morton et al., 1997
Simaroubaceae (excluding *Irvingia*, *Picramnia*, and *Alvaradoa*)	Rosid cl., Capparales/Sapindales/Malvales, Sapindales	Gadek et al., 1992, 1996; Chase et al., 1993; Fernando et al., 1993, 1995; Morgan & Soltis, 1993; Price & Palmer, 1993; Rodman et al., 1993	paraphyletic
Irvingia	Rosid cl., uncertain within core rosids	Fernando et al., 1995	—
Picramnia	uncertain within rosid clade	Fernando et al., 1995	—
Alvaradoa	uncertain within rosid clade	Fernando et al., 1995	—
Simmondsiaceae	Caryophyllid cl., Caryophyllales	Lledó et al., 1998; Soltis et al., 1998; Hoot et al., 1999	single genus
Solanaceae	Asterid cl., Lamiidae s.l., Solanales	Albert et al., 1992; Downie & Palmer, 1992; Olmstead et al., 1992, 1993; Chase et al., 1993; Morgan & Soltis, 1993; Cosner et al., 1994; Williams et al., 1994; Gustafsson et al., 1996; Soltis & Soltis, 1997; Soltis et al., 1997a	Chase et al., 1993; Olmstead et al., 1993
Sphaerosepalaceae (only *Rhopalocarpus*)	Rosid cl., Capparales/Sapindales/Malvales, expanded Malvales	Alverson et al., 1998	?
Sphenocleaceae	Asterid cl., Lamiidae s.l.	Cosner et al., 1994; Gustafsson et al., 1996	single genus

Table 2. Continued.

Taxon	Phylogenetic placement	Reference for placement	Monophyly status
Stachyuraceae	uncertain within rosid clade, associated with *Crossosoma*, *Aphloia*, and *Ixerba*	Soltis et al., 1998	single genus
Stackhousiaceae (only *Stackhousia*)	Rosid cl., core rosids, *Euonymus* cl.	Soltis et al., 1998	?
Staphyleaceae			paraphyletic
Staphylea	uncertain within rosid cl., associated with *Stachyurus*, *Crossosoma*, *Aphloia*, and *Ixerba*	Soltis et al., 1998	—
Tapiscia	uncertain within rosid cl., associated with Capparales/Sapindales/Malvales	Soltis et al., 1998	—
Stylidiaceae	Asterid cl., Asteridae s.l., Asterales s.l.	Cosner et al., 1994; Gustafsson & Bremer, 1995; Gustafsson et al., 1996	?
Styracaceae	Asterid cl., ericalean cl.	Chase et al., 1993; Kron & Chase, 1993; Olmstead et al., 1993; Cosner et al., 1994; Morton et al., 1996, 1997	paraphyletic, all components in similar phylogenetic placement
Surianaceae	Rosid cl., core rosids, Fabaceae/Surianaceae/Polygalaceae	Fernando et al., 1993; Morgan et al., 1994; Soltis et al., 1995b	Fernando et al., 1993
Symplocaceae	Asterid cl., ericalean cl.	Chase et al., 1993; Kron & Chase, 1993; Olmstead et al., 1993; Cosner et al., 1994; Morton et al., 1996, 1997	?
Tamaricaceae (only *Tamarix*)	Caryophyllid cl., Polygonales/Plumbaginales	Lledó et al., 1998; Soltis et al., 1998	?
Tetrameristaceae	Asterid cl., ericalean cl.	Morton et al., 1996, 1997	?
Theaceae	Asterid cl., ericalean cl.	Chase et al., 1993; Kron & Chase, 1993; Olmstead et al., 1993; Cosner et al., 1994; Morton et al., 1996, 1997	paraphyletic, all components in similar phylogenetic placement
Thymelaeaceae	Rosid cl., Capparales/Sapindales/Malvales, expanded Malvales	Conti et al., 1996; Alverson et al., 1998	Conti et al., 1996; Alverson et al., 1998
Ticodendraceae	Rosid cl., core rosids, "higher" Hamamelidae	Manos & Steele, 1997	single genus
Tremandraceae	Rosid cl., core rosids, expanded Cunoniaceae	Albert et al., 1992; Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Swensen et al., 1994; Soltis et al., 1995b	?
Trigoniaceae (only *Trigonia*)	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Soltis et al., 1995b	?

Table 2. Continued.

Taxon	Phylogenetic placement	Reference for placement	Monophyly status
Tropaeolaceae	Rosid cl., Capparales/Sapindales/Malvales, expanded Capparales	Rodman, 1991; Gadek et al., 1992; Chase et al., 1993; Morgan & Soltis, 1993; Price & Palmer, 1993; Rodman et al., 1993, 1994, 1996; Swensen et al., 1994; Williams et al., 1994	single genus
Turneraceae (only *Turnera*)	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Soltis et al., 1998	?
Verbenaceae	Asterid cl., Lamiidae s.l., Lamiales s.l.	Downie & Palmer, 1992; Olmstead et al., 1992; Chase et al., 1993; Morgan & Soltis, 1993; Cosner et al., 1994; Hedrén et al., 1995; Olmstead & Reeves, 1995; Gustafsson et al., 1996; Wagstaff & Olmstead, 1997	Olmstead & Reeves, 1995
Violaceae (only *Viola*)	Rosid cl., core rosids, Linales/Euphorbiaceae/Malpighiaceae	Chase et al., 1993; Morgan & Soltis, 1993; Swensen et al., 1994; Williams et al., 1994; Soltis et al., 1995b	?
Vitaceae (only *Vitis*)	uncertain within core eudicots	Albert et al., 1992; Chase et al., 1993; Williams et al., 1994; Soltis et al., 1998	?
Vochysiaceae (only *Qualea*)	Rosid cl., Myrtales	Gadek et al., 1992; Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Price & Palmer, 1993; Rodman et al., 1993; Conti et al., 1996	?
Zygophyllaceae			polyphyletic
Nitraria	Rosid cl., Capparales/Sapindales/Malvales, Sapindales	Gadek et al., 1996	—
Malacocarpus	Rosid cl., Capparales/Sapindales/Malvales, Sapindales	Gadek et al., 1996	—
Peganum	Rosid cl., Capparales/Sapindales/Malvales, Sapindales	Fernando et al., 1995; Gadek et al., 1996	—
Guaiacum	Rosid cl., core rosids	Chase et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994	—

A preliminary evaluation of the monophyletic status of families or taxa of higher order included in each major clade is also provided (Table 2). In general, we found that phylogenetic analyses that cover a broad taxonomic sample rarely include significant representation of individual putatively monophyletic taxa (e.g., within a family). On the other hand, studies that assess phylogenetic relationships within presumed monophyletic taxa, while often including a good taxonomic representation of the group under study, usually do not include a significant representation of potentially related outgroup taxa, and as a result, do not provide a rigorous test of monophyly. Only a few of the phylogenetic studies that we investigated include an explicit two-stage approach (e.g., Fernando et al., 1993, 1995; Price & Palmer, 1993; Cosner et al., 1994; Gadek et al., 1996; Gustafsson et al., 1996). The first stage consists of a taxonomically broad analysis, with carefully selected placeholders, that provides information about the general phylogenetic placement for the taxon in question and identifies phylogenetically closely related taxa. The second stage consists of a taxonomically more restricted analysis that includes significant representation of the taxon under study, together with closely related taxa. In our view, these types of studies currently offer the most reliable basis for evaluating the monophyletic status of higher-level taxa.

DISTRIBUTION OF SPECIES DIVERSITY

The taxonomic composition of each major clade is described at the most inclusive taxonomic level for which there is reasonable indication of monophyly. In most cases this is the family level, but occasionally there is clear evidence for monophyly of orders (e.g., Santalales, Caryophyllales). In some cases, orders as traditionally circumscribed (Cronquist, 1981) are monophyletic except for the exclusion of a few entities of lower rank (e.g., Myrtales with Thymelaeaceae excluded), or the inclusion of a few taxa that were not previously thought to be close to that group (e.g., Malvales s. str. plus Thymelaeaceae, Sarcolaenaceae, and Dipterocarpaceae). In the former case, the excluded families or genera are indicated, and in the latter case, the definition of the order is considered to be expanded. The use of a family name indicates that currently there is no contradiction to its presumed monophyly. We have attempted to avoid the use of families that are clearly paraphyletic or polyphyletic. In the case of monogeneric families, the family name is used, and its monogeneric status is indicated. Generic names are used when the family to which they have been assigned has been documented as non-monophyletic.

The number of living species included within each major eudicot clade was estimated by adding the number of species for all of the included taxonomic entities. Information about the number of species in particular families and genera was obtained from Mabberley (1993). When a family is assumed to be monophyletic (see above), the number of species contained in the family is used. When a family has been shown to be unequivocally non-monophyletic, the distribution of the genera for which phylogenetic placement is known usually allowed for a general partitioning of species diversity among the different segments of the family in question (e.g., Cornaceae). The estimated total number of eudicot species used here is the total of species for which phylogenetic placement has been addressed, or can be reasonably assumed (i.e., 175,034; Table 1). The percentage of species included in each major eudicot clade was calculated based on this number (here referred to as total eudicot species diversity [TESD]), to provide an indication of the distribution of species among the major eudicot groups.

FOSSIL RECORD

Inferences about the minimum age of major eudicot clades are based on the earliest well-documented appearance in the fossil record of one or more of their component taxa. Data were obtained mostly from the compendium of Collinson et al. (1993), supplemented with information on more recent paleobotanical discoveries. We adopted a critical approach to ensure that, as far as possible, the earliest appearance of taxa is based on the most reliable evidence available. In selecting these key paleobotanical records we have emphasized those based on mesofossil or macrofossil reproductive remains. However, data from pollen grains or vegetative remains are also used when there are distinctive features that allow the unambiguous paleobotanical identification of particular eudicot taxa.

The quality of the fossil record for eudicots, and for angiosperms in general, has been enormously enhanced over the last 15 years by a more critical approach to the identification of Early Tertiary fossils, as well as the discovery and ongoing description of exquisitely preserved, small (typically 0.5–5 mm), three-dimensionally preserved, charcoalified or mummified flowers and other reproductive remains. These fossils preserve excellent morphological and anatomical details that provide a secure basis for detailed comparison with extant taxa. These types of fossils are currently known from Cretaceous strata that range possibly from the early Barremian (several localities in Portugal; Friis et al., 1994, 1999) to the Campanian-Maastrichtian (Esgueira locality, Portugal; Friis et al., 1992). Important localities that have yielded these types of fossils are known along the Atlantic Coastal Plain of North America, from Georgia to New Jersey and Massachusetts, U.S.A. (e.g., Tiffney, 1977; Crepet & Nixon, 1994; Crane & Herendeen, 1996), in Europe from central Portugal (e.g., Friis et al., 1994), southern Sweden (e.g., Friis, 1984), and many localities from central Europe (e.g., Knobloch & Mai, 1986), and in Asia from Kazakhstan (e.g., Frumin & Friis, 1996, in press) and Japan (Takahashi & Crane, in prep.).

THE PHYLOGENETIC POSITION OF EUDICOTS

The eudicots, as previously defined, form a monophyletic group in nearly all phylogenetic analyses in which a significant sample of eudicot taxa is included (Loconte & Stevenson, 1991; Chase et al., 1993; Doyle et al., 1994; Rice et al., 1997; Hoot et al., 1999). Results of analyses based on 18S sequence data (Soltis et al., 1997a) identify a major assemblage that is broadly equivalent to the eudicot clade, but differs by excluding *Nelumbo* Adans. (Nelumbonaceae) and by including two distinct small magnoliid clades near its base. There are relatively few studies that sample a broad range of magnoliid taxa, as well as of monocots and eudicots, and that also include quantitative indications of support for the clades detected (e.g., Doyle et al., 1994; Soltis et al., 1997a, fig. 1A). The strongest support for the recognition of the eudicot clade comes from combined analysis of three molecular data sets (*atp*B, *rbc*L, and 18S), which includes a broad representation of lineages of woody and herbaceous magnoliid taxa and an extensive representation of basalmost eudicots (Hoot et al., 1999). This analysis shows 100% bootstrap support for the eudicot clade, and 45 substitutions along the branch leading to eudicots (Hoot et al., 1999). These results, combined with the recurrence of a clade that includes all triaperturate pollen-producing plants in numerous analyses based on different taxonomic samples and on several types of evidence, strongly suggest that the eudicots are a monophyletic group.

The question of how eudicots are related to taxa at the magnoliid grade is unresolved, reflecting the currently poorly understood relationships among the earliest diverging angiosperm lineages. Analyses based on different types of evidence and with different taxonomic sampling have suggested different sister groups for eudicots. The density of taxonomic sampling of magnoliid lineages in the studies published to date also clearly affects resolution of the sister group for eudicots (cf., e.g., Donoghue & Doyle, 1989, fig. 3.2; Loconte & Stevenson, 1991; Chase et al., 1993; Rice et al., 1997; Soltis et al., 1997a). In the combined morphological and rRNA analysis of Doyle et al. (1994), the sister group to eudicots includes Magnoliales, Laurales, Winteraceae, and Chloranthaceae. In the combined *rbc*L, *atp*B, and 18S analysis of Hoot et al. (1999), the sister group to eudicots includes Saururaceae, Piperaceae, Aristolochiaceae, and Winteraceae. *Ceratophyllum* L. appears as the sister to eudicots, and a clade that includes Magnoliales, Piperales, Laurales, Aristolochiales, and the monocotyledons is the sister to *Ceratophyllum* plus eudicots in the combined analysis of *atp*B, *rbc*L, and 18S data by Soltis et al. (1998).

The various possible placements of eudicots within angiosperms have different implications for the origin of the group in the early angiosperm radiation. A relatively derived position with respect to the magnoliid grade is supported by analyses based on morphological data (Loconte & Stevenson, 1991), 18S sequence data (Soltis et al., 1997a), and combined morphological and rRNA evidence (Doyle et al., 1994), which suggests that the origin of eudicots was preceded by the differentiation of numerous lineages at the magnoliid grade. In contrast, a near basal placement of eudicots within the angiosperms is supported by *rbc*L evidence (Chase et al., 1993; Rice et al., 1997). This presumed early origin of the eudicot branch is in agreement with the very early appearance of tricolpate pollen grains in the fossil record, which first occur in sediments only slightly younger than those containing the oldest unequivocal angiosperm pollen (Doyle, 1992; Brenner, 1996).

EUDICOT PHYLOGENETIC PATTERN

The main elements of the phylogenetic structure in the eudicot clade are as follows (Fig. 1). There is a basalmost branch that separates a small clade composed mainly of the Ranunculales and Papaverales, which we term here the ranunculid clade. The ranunculid clade is sister taxon to the bulk of eudicots, which we term here the main eudicot clade. Within the main eudicot clade, there is a basal eudicot grade, composed of a few genera of "lower" Hamamelididae and taxa that have been

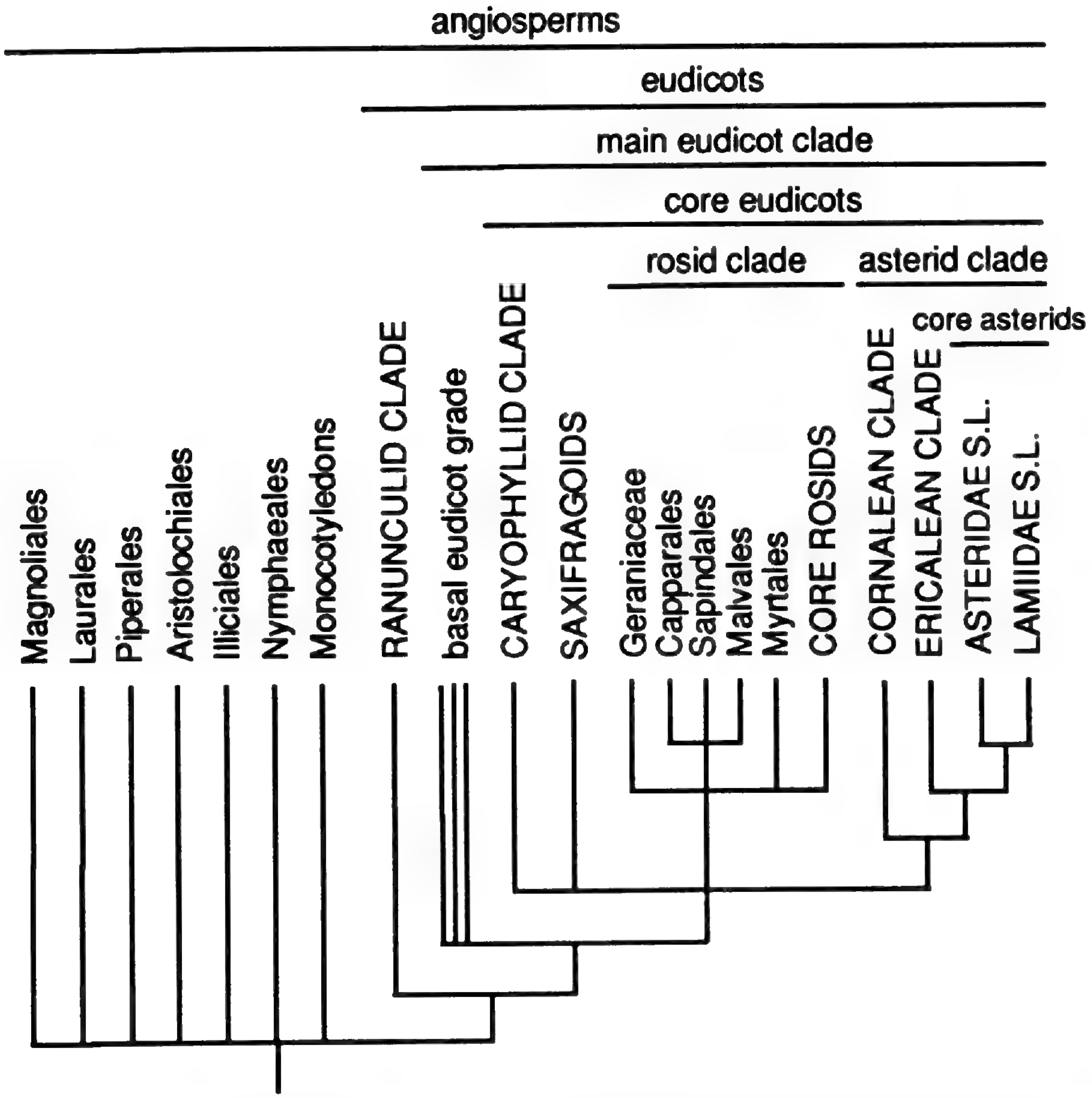

Figure 1. General eudicot phylogenetic pattern. Pending more detailed study, the eudicot clade is shown in an unresolved relationship with other major angiosperm lineages. Within the eudicots, the ranunculid clade is sister to all other eudicots. The main eudicot clade includes a basal eudicot grade, and the core eudicot clade. The core eudicot clade encompasses the majority of extant species diversity in the eudicots and includes three major groups, namely, the caryophyllid clade, the rosid clade, and the asterid clade, as well as several smaller lineages. The relationships among these lineages are unresolved. The rosid clade includes several smaller lineages and a major core rosid clade. The asterid clade includes a cornalean and an ericalean clade near its base, and a core asterid clade. The core asterid clade has two main components: the Asteridae s.l. and the Lamiidae s.l. Taxa included in each of these clades are listed in Table 1.

regarded previously as having widely differing affinities (e.g., Sabiaceae, Proteaceae). Then there follows a very large and inclusive clade, which we term the core eudicots. The core eudicots include the "higher" Hamamelididae, Caryophyllidae, Dilleniidae, Rosidae, and Asteridae (sensu Cronquist, 1981), distributed in three distinct major subclades, which we term here the caryophyllid clade, the rosid clade, and the asterid clade, and a few other small, apparently independent lineages. The core eudicots encompass the great majority of eudicot species diversity (ca. 97%, Table 1). Relationships among the three major clades within the core eudicots are unresolved.

The ranunculid clade, the basal eudicot grade, the core eudicots and the three major clades of which it is composed, and the general phylogenetic scheme described above, are recognized in most analyses based on *rbc*L sequence data (e.g., Chase et al., 1993; Morgan & Soltis, 1993; Williams et al., 1994) as well as in recent combined analyses of *rbc*L, *atp*B, and 18S data (Hoot et al., 1999; Soltis et al., 1998).

RANUNCULID CLADE (= ranunculids sensu Chase et al., 1993; Soltis et al., 1997b; APG, 1998)

The placement of the ranunculid clade as the basalmost branch within the eudicots is now securely supported by the results of combined analysis of *rbc*L, *atp*B, and 18S sequence data for a

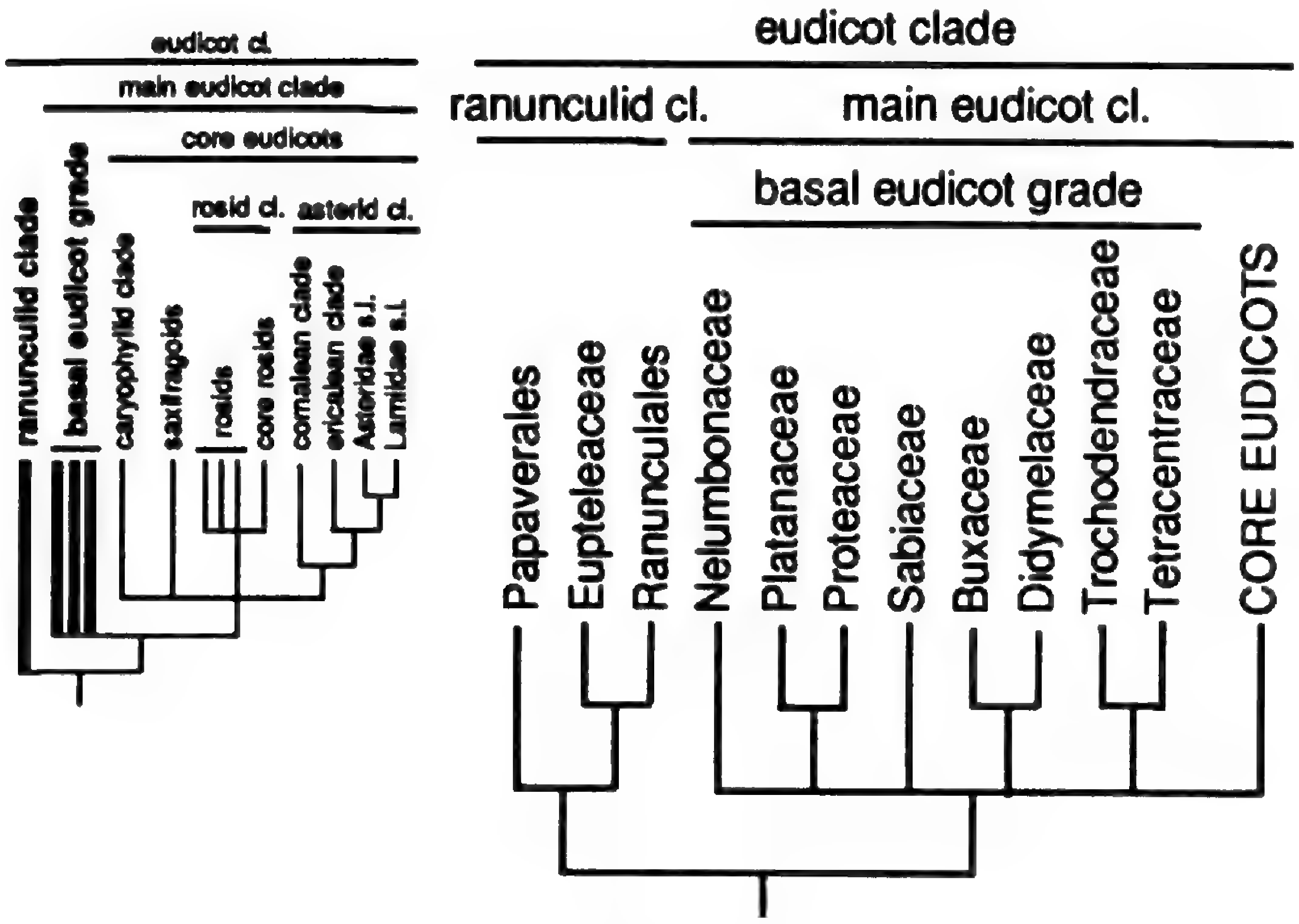

Figure 2. Ranunculid clade and basal eudicot grade. The cladogram on the left summarizes the general eudicot phylogenetic pattern, and the ranunculid clade and basal eudicot grade are indicated in bold. The ranunculid clade is sister to all other eudicots, and is composed of two major clades, the Papaverales and the Ranunculales, and additionally, the genus *Euptelea*. The main eudicot clade includes a basal grade composed mostly of taxa of "lower" Hamamelididae, but the exact pattern of relationships among them is not fully resolved.

broad sample of woody and herbaceous magnoliids (outgroups), ranunculids, lineages of the basal eudicot grade, and placeholders for the core eudicot clade (Hoot et al., 1999). The ranunculid clade includes the genus *Euptelea* Siebold & Zucc. and two distinct subclades that correspond closely to the orders Ranunculales and Papaverales. The Ranunculales include all the families of the order as defined by Cronquist (1981), except for Coriariaceae and Sabiaceae (Table 1), and receive clear support as a monophyletic group (Table 2; e.g., Drinnan et al., 1994; Hoot & Crane, 1995; Soltis et al., 1997a; Hoot et al., 1999). The monophyletic Papaverales include the families Papaveraceae and Fumariaceae (both themselves monophyletic), and the genera *Hypecoum* L. and *Pteridophyllum* Siebold & Zucc. (Table 1; e.g., Chase et al., 1993; Drinnan et al., 1994; Williams et al., 1994). With approximately 3500 living species, the diversity of the ranunculid clade is relatively small, representing only ca. 2% of the total eudicot species diversity (= TESD; Table 1). A close relationship between Ranunculales and Papaverales has been acknowledged in almost all recent taxonomic treatments. The ranunculid clade, as defined above (except for the inclusion of *Euptelea*), corresponds exactly to the superorder Ranunculiflorae of Dahlgren (1983), which is subdivided into the orders Ranunculales and Papaverales. The ranunculid clade is also nearly equivalent to Takhtajan's (1997) superorder Ranunculanae, except for the inclusion of *Paeonia* L. in Takhtajan's treatment. Cronquist (1981) recognized the Ranunculales and Papaverales as two distinct orders within Magnoliidae, but did not combine them into a category of higher rank.

The apparent close relationship of Ranunculales and Papaverales with *Euptelea* (e.g., Hoot et al., 1999) is a new result based on molecular data that had not been previously suggested. Relationships among Ranunculales, Papaverales, and *Euptelea* are not securely resolved, although the analyses based on *rbc*L sequence data (Chase et al., 1993), and combined *rbc*L, *atp*B, and 18S data (Hoot & Crane, 1995; Hoot et al., 1999), all suggest a sister group relationship between *Euptelea* and the Ranunculales, with the Papaverales basal in the ranunculid clade (Fig. 2).

Flowers in the ranunculid clade are often based on a dimerous or trimerous plan. However, they lack a single or a combination of diagnostic features. The flowers of Papaverales are bisexual, regular to strongly zygomorphic, have a whorled phyllotaxy, and a basically dimerous, opposite-decussate plan. The perianth is differentiated into one whorl of sepals and two whorls of petals. Among taxa of Ranunculales, the flowers may be bisexual and fundamentally dimerous (e.g., *Circaeaster* Maxim., *Glaucidium* Siebold & Zucc.), or unisexual, trimerous, and hypogynous with regular symmetry (e.g., Lardizabalaceae, Menispermaceae), or bisexual with helical phyllotaxy and sometimes with five petals (e.g., some Ranunculaceae). The flowers of *Euptelea* are small, bisexual, naked, and have a variable number of stamens and carpels. Developmentally, the flowers of *Euptelea* are derived from a bilaterally symmetric primordium (Endress, 1986).

The fossil record of ranunculids is relatively sparse, and mostly from Tertiary strata. The earliest reports for the clade in the fossil record are fruits similar to *Thalictrum* L. from the Early Cretaceous of Portugal (Friis et al., 1994). Fossil fruits from the lower Albian of Virginia, U.S.A. (*Appomattoxia ancistrophora* Friis, Pedersen & Crane) show some similarities to Circaeasteraceae (Friis et al., 1995), but the monosulcate pollen grains on the stigmatic surfaces suggest a possible piperalean affinity. Menispermaceae are represented in the fossil record by distinctive endocarps, which are first recorded in the Maastrichtian and then become abundant and diverse in the Eocene (Collinson et al., 1993, and references therein). Seeds of Sargentodoxaceae are known from the Middle Eocene (Manchester, 1999). Reproductive structures of *Euptelea* are not known in the fossil record, although leaves assigned to *Euptelea orientalis* (Sanborn) Wolfe are reported from the Upper Eocene of North America (Wolfe, 1977; Collinson et al., 1993). The fossil record of Papaverales is limited to seeds of *Corydalis* DC. from Miocene strata (Dorofeev, 1964; Collinson et al., 1993). In spite of the limited representation of ranunculids in the fossil record, the presence of unequivocal menispermaceous endocarps in the Maastrichtian documents securely that at least some lineages had differentiated by the latest Cretaceous.

MAIN EUDICOT CLADE (= hamamelid I, hamamelid II, and higher eudicots sensu Chase et al., 1993)

A clade formed by several independent lineages of "lower" Hamamelididae together with the core eudicots appears in several phylogenetic analyses (Chase et al., 1993; Williams et al., 1994; Hoot et al., 1999). This clade, which includes all the eudicots except for the ranunculid clade, is termed here the main eudicot clade. However, this group is not supported in all broadly spanning analyses. The analyses of Albert et al. (1992), based on *rbc*L data, and of Soltis et al. (1998), based on combined *rbc*L, *atp*B, and 18S data, do not provide resolution at the base of the eudicot clade and instead show a polychotomy among the ranunculids, lineages of "lower" Hamamelididae, and the core eudicots.

Nevertheless, a recent integrative study, which was designed to resolve the relationships at the base of the eudicot clade, provides strong support for a clade that includes all the non-ranunculid eudicots (Hoot et al., 1999). This analysis is based on combined *rbc*L, *atp*B, and 18S sequence data for all representatives of basal eudicot lineages, placeholders for the core eudicots, and a broad selection of woody and herbaceous magnoliids as outgroups. The study includes experiments in which different combinations of taxa are placed in the ingroup and outgroup, and in all cases the ranunculid clade is the basalmost branch within the eudicots. The "lower" Hamamelididae lineages are more closely associated with the placeholders for core eudicots, forming the equivalent of the main eudicot clade (Hoot et al., 1999). The main eudicot clade includes approximately 171,500 species (ca. 98% TESD; Table 1).

BASAL EUDICOT GRADE (= hamamelid I and hamamelid II sensu Chase et al., 1993)

Lineages at the base of the main eudicot clade comprise several groups that have traditionally been considered of varied and often problematic systematic affinity. They include Nelumbonaceae, Platanaceae, Didymelaceae (all monogeneric families), the order Trochodendrales (including the monogeneric Trochodendraceae and Tetracentraceae), Sabiaceae, Proteaceae, and Buxaceae (Table 1). Species diversity in the basal eudicot grade is low. Most families are monogeneric, except for Buxaceae (4 or 5 genera) and Sabiaceae (3 genera), and usually include a small number of extant species (fewer than 100). Proteaceae are the only exception, with 75 genera and ca. 1350 species (Table 1). The total number of species in the basal eudicot grade is approximately 1470, which represents less than 1% TESD (Table 1).

The genus *Nelumbo* has usually been considered to be closely related to herbaceous, aquatic taxa in the Magnoliidae (Cronquist, 1981; Dahlgren, 1983), or to be of isolated taxonomic position (Takhtajan, 1997). Close association with "lower" hamamelid taxa had not been previously suggested, but its placement within the eudicots is supported by the production of tricolpate pollen. A position close to the base of the eudicots is also consistent with the occasional production of monosulcate pollen grains. *Nelumbo* is the only eudicot known to produce both monosulcate and tricolpate pollen.

Several taxa in the basal eudicot grade have traditionally been considered to hold a transitional position between Magnoliidae and other subclasses of dicotyledons. The Platanaceae, Trochodendrales, and Didymelaceae were considered to be primitive members of the Hamamelididae by Cronquist (1981) and Takhtajan (1997), but were assigned to different orders within the Rosiflorae by Dahlgren (1983). The close relationship between Buxaceae and Didymelaceae was recognized by Takhtajan (1997), who grouped the two families as two orders that comprise the Buxanae, and by Dahlgren (1983), who treated both families as comprising the Buxales.

The phylogenetic placement of Proteaceae and Sabiaceae has been controversial. Proteaceae, although consistently recognized as a natural group, have been placed with Elaeagnaceae in Proteales within Rosidae (Cronquist, 1981), or included in an order of their own, and considered to be taxonomically isolated (Dahlgren, 1983; Takhtajan, 1997). Sabiaceae (including *Sabia* Colebr., *Meliosma* Blume, and *Ophyocaryon* Endl.) have been assigned to Ranunculales (Cronquist, 1981), or placed within Sapindales in Rutiflorae (Dahlgren, 1983). Sabiaceae, together with Meliosmaceae, also have been assigned to an order of their own within Rutanae (Takhtajan, 1997).

Phylogenetic relationships among taxa at the level of the eudicot grade are not fully resolved (Fig. 2). However, several analyses agree in finding a close association among *Nelumbo*, Platanaceae, and Proteaceae, which are usually placed near the base of the eudicots (e.g., Chase et al., 1993; Williams et al., 1994; Hoot et al., 1999). The relationship between Proteaceae and Platanaceae is especially strongly supported (Hoot et al., 1999). Proteaceae are usually represented in phylogenetic analyses by only a few placeholders, but recent studies based on molecular data from an extensive sample of taxa support the family's monophyletic status (Hoot & Douglas, 1998), as has long been recognized based on morphological data. In agreement with evidence from morphology and anatomy (Endress, 1986; Crane, 1989), the two vesselless genera *Trochodendron* Siebold & Zucc. and *Tetracentron* Oliver are consistently linked to form a monophyletic Trochodendrales in analyses based on molecular data (Table 2; e.g., Chase et al., 1993; Drinnan et al., 1994; Soltis et al., 1997a), and their position with respect to magnoliids and other basal eudicots implies that vessels have been lost in this group. Based on current molecular results, the Trochodendrales are usually placed in a relatively derived position within the basal eudicot grade. Buxaceae, with the inclusion of *Styloceras* Knuth ex A. Juss., are supported as a monophyletic entity (Drinnan et al., 1994; Hoot et al., 1999) and are also closely linked to the Madagascan endemic *Didymeles* Thouars (Hoot et al., 1999). These taxa occur in an unresolved, but generally more or less intermediate, position among other taxa in the basal eudicot grade. *Sabia* also has a particularly uncertain position at intermediate levels within the basal eudicot grade.

The flowers of taxa at the basal eudicot grade do not have the pentamerous floral groundplan commonly found in the core eudicots. In many cases, the flowers are based on a dimerous, opposite decussate plan (e.g., Buxaceae, *Tetracentron*) or have an irregular merosity (e.g., *Trochodendron*, *Platanus* L.). If a multiradiate arrangement is present, the organs of adjacent floral whorls are arranged opposite to one another (e.g., Sabiaceae, Proteaceae). With the possible exception of Sabiaceae, flowers of taxa at the basal eudicot grade lack a perianth formed by a single whorl of sepals, and a single whorl of petals.

Several lineages in the basal eudicot grade have a well-documented, early, and extended presence in the fossil record, and are among the oldest records of pollen grains and macroscopic vegetative and reproductive structures for eudicots as a whole. Reproductive structures probably closely related to *Nelumbo* are known from upper Albian strata of Virginia (Upchurch et al., 1994); endocarps assigned to *Sabia* and *Meliosma* have been reported from Maastrichtian strata of Europe (Knobloch & Mai, 1986). Probable Proteaceae are known from the mid-Cretaceous based on fossil pollen (Ward & Doyle, 1994), and from the early Tertiary based on macrofossils (Christophel, 1984; Collinson et al., 1993).

The oldest reproductive structures of Platanaceae are from early to middle Albian strata of the Potomac Group, Virginia, U.S.A. (Crane et al., 1993). Isolated stamens of probable platanoid affinity are known from the early Albian Puddledock locality, Virginia, U.S.A. (Crane & Herendeen, 1996). Reproductive and vegetative remains of Platanaceae are known from many other younger Upper Cretaceous and Tertiary fossiliferous localities (e.g., Manchester, 1986; Crane et al., 1988, 1993; Friis et al., 1988; Boulter & Kvaček, 1989; Pigg & Stockey, 1991; Pedersen et al., 1994; Magallón et al., 1997). Fossil reproductive structures of Platanaceae consist of spherical pistillate or staminate inflorescences that bear closely packed flowers. The only known exception is possibly *Tanioplatanus cranei* Manchester, which is interpreted as a cylindrical platanoid infructescence (Manchester, 1994). Flowers of Cretaceous Platanaceae (Friis et al., 1988; Crane et al., 1993; Pedersen et al., 1994) differ significantly from those of Tertiary and extant representatives (Manchester, 1986, 1994; Pigg &

Stockey, 1991) in having a well-developed perianth, and a fixed number of usually five stamens and carpels. Recently, a modification of this pattern has been documented through the discovery of tetramerous flowers of Platanaceae from Coniacian-Santonian strata of Georgia, U.S.A. (Upatoi Creek locality). Staminate flowers have a single whorl of perianth with four tepals, and four stamens, each opposite a tepal. Pistillate flowers have two undifferentiated whorls of perianth, each with fused tepals, and eight carpels (Magallón et al., 1997). Similar staminate inflorescences are known from the Turonian of New Jersey (Crepet et al., 1992).

Reproductive structures similar to those of Buxaceae, assigned to the extinct genus *Spanomera* Drinnan, Crane, Friis & Pedersen, are known from middle Albian and Cenomanian strata of the Potomac Group in Maryland, U.S.A. (Drinnan et al., 1991). The fossils consist of inflorescences with a terminal pistillate flower and lateral staminate flowers that are all based on an opposite decussate plan. The staminate flowers are formed by two pairs of scale-like tepals, two pairs of stamens, and a central pistillode (Drinnan et al., 1991).

Some of the earliest tricolpate pollen in the fossil record has striate ornamentation similar to that of extant Trochodendrales (Penny, 1988), and fossil leaves assigned to *Populus potomacensis* Ward from the Aptian Potomac Group of eastern North America are broadly similar to those of extant *Tetracentron* (Doyle & Hickey, 1976). Reproductive structures assigned to *Nordenskioldia borealis* Heer emend. Crane, Manchester & Dilcher are known from the Maastrichtian Hell Creek Formation (K. Johnson, pers. comm.), and are common through the Paleocene in high-latitude areas of the Northern Hemisphere. *Nordenskioldia* is closely related to the Trochodendrales (Crane et al., 1986, 1991; Manchester et al., 1991) and includes axes that bear laterally attached, sessile, subglobose fruits. The fruits are similar in structure and form to those of extant *Trochodendron* (Crane et al., 1991) but differ in having a distally bilateral outline, dispersion of carpels as mericarps, and in apparently lacking nectariferous tissue on the adaxial surface of the carpels.

CORE EUDICOTS (= higher eudicots plus *Gunnera* L. sensu Chase et al., 1993; core eudicots sensu APG, 1998)

The core eudicots include the traditional subclasses Caryophyllidae, Dilleniidae, Rosidae, and Asteridae, as well as the more derived orders typically placed within the Hamamelididae (Table 1). The core eudicots include more than 170,000 species and approximately 97% TESD (Table 1). This clade is recognized in almost all phylogenetic analyses that include a significant taxonomic sample of dicotyledons. These analyses are based on different types of evidence, i.e., *rbc*L sequence data (Olmstead et al., 1992; Chase et al., 1993; Morgan & Soltis, 1993; Williams et al., 1994), 18S sequence data (Soltis et al., 1997a), combined *atp*B and *rbc*L (Drinnan et al., 1994), and combined *atp*B, *rbc*L, and 18S sequence data (Soltis et al., 1998; Hoot et al., 1999). The core eudicots are equivalent to the "higher eudicots" plus *Gunnera* of Chase et al. (1993, fig. 7B), which includes the "caryophyllids," "rosids," and "asterids" (Chase et al., 1993, figs. 8B–15B). The analysis of 18S sequence data by Soltis et al. (1997a) recognizes a major core eudicot assemblage equivalent to "Rosidae" plus "Asteridae s.l." (e.g., fig. 4B).

Within the core eudicots, three major groups (the caryophyllid clade, the rosid clade, and the asterid clade) and several smaller isolated lineages (Saxifragoids, Santalales, Dilleniaceae, *Vitis* L., *Gunnera*, and *Myrothamnus* Welw.) can usually be recognized in large-scale phylogenetic analyses (Table 1; e.g., Chase et al., 1993; Williams et al., 1994; Hoot et al., 1999), but the pattern of relationships among them is not resolved (Fig. 1). All three possible arrangements for the three major clades emerge from the results of different analyses. In some cases, the caryophyllid clade appears as sister taxon to the rosid clade plus the asterid clade (Chase et al., 1993). In other cases, it is resolved as sister to the asterid clade, with the rosid clade sister to both (Morgan & Soltis, 1993), while in still other analyses, it is closer to the rosid clade (Williams et al., 1994; Soltis & Soltis, 1997).

Most of the morphological disparity and complexity of eudicot floral form is displayed among the taxa that comprise the core eudicot clade. This disparity and complexity are superimposed on a basic groundplan (not seen in the basal eudicot grade) that consists of flowers with whorled phyllotaxy, a fixed number of organs per whorl (five organs in the perianth and androecium, two in the gynoecium), multiple planes of radial symmetry, alternation in the radial placement of organs of adjacent whorls, and a perianth formed by a single whorl of sepals (i.e., calyx) and a single whorl of petals (i.e., corolla). Although some of these characters are found in other angiosperms, they may all occur simultaneously only in flowers of core eudicots.

CARYOPHYLLID CLADE (= caryophyllids sensu Chase et al., 1993; Caryophyllales sensu APG, 1998)

The caryophyllid clade includes the orders Caryophyllales, Polygonales, and Plumbaginales, several families of Nepenthales, Violales, Rosales, and Simmondsiaceae (Euphorbiales, monogeneric; Table 1). The total number of species included in the caryophyllid clade is about 11,000 (ca. 6.3% TESD; Table 1). A close link among the Caryophyllales, Polygonales, and Plumbaginales has long been recognized. Cronquist (1981) and Takhtajan (1997) placed them together as different orders or superorders, respectively, within Caryophyllidae. The association of the other families with these core caryophyllids is an important and new result of recent molecular studies (e.g., Lledó et al., 1998). *Nepenthes* L. and Droseraceae have previously been recognized as close to one another and have been placed together either in the Nepenthales (Cronquist, 1981) or in separate single-family orders in Nepenthanae (Takhtajan, 1997). Both Cronquist (1981) and Takhtajan (1997) considered Droseraceae and Nepenthaceae to be distantly related to the Caryophyllidae, and placed them within Dilleniidae. *Simmondsia* Nutt. has usually been considered close to Buxaceae (e.g., Cronquist, 1981; Takhtajan, 1997), and distantly related to the above taxa (e.g., Dahlgren, 1983). Interestingly, the genus was included within the Centrospermae as a monotypic family by van Tieghem (1897, in Jarvis, 1989).

The caryophyllid clade is consistently supported in phylogenetic analyses using *rbc*L sequence data (e.g., Albert et al., 1992; Chase et al., 1993; Williams et al., 1994), 18S sequence data (e.g., Soltis et al., 1997a), and combined *rbc*L, *atp*B, and 18S sequence data (Soltis et al., 1998; Hoot et al., 1999). The caryophyllid clade is equivalent to the "caryophyllids" of Chase et al. (1993, fig. 9B), and to "Caryophyllidae s.l." of Soltis et al. (1997a, fig. 4D). Within the caryophyllid clade, the Caryophyllales constitute a well-supported monophyletic group and are characterized morphologically by having curved embryos and chemically by the production of betalanin (Table 2; e.g., Rodman et al., 1984; Giannasi et al., 1992; Olmstead et al., 1992; Rettig et al., 1992; Downie & Palmer, 1994; Williams et al., 1994; Soltis et al., 1997a). The remaining taxa apparently form a separate group within the caryophyllid clade (see below).

Polygonaceae and Plumbaginaceae have been represented each by one genus in most phylogenetic analyses based on molecular data. Lledó et al. (1998) documented monophyly for both families based on a more extensive taxonomic sample. The Droseraceae are supported as a monophyletic group based on the relationships among the genera *Drosera* L., *Dionaea* Ellis, and *Drosophyllum* Link. in analyses based on molecular sequence data (e.g., Williams et al., 1994), and this is also supported by the presence of structural and other specializations associated with the insectivorous habit.

There is agreement among different studies regarding the close relationship between Polygonaceae and Plumbaginaceae, and between Droseraceae and *Nepenthes*, but relationships of these two groups to the Caryophyllales are not fully resolved (Fig. 3). Analyses using *rbc*L sequence data support Polygonaceae and Plumbaginaceae as sister taxa (Lledó et al., 1998). Closely associated with this clade are Tamaricaceae plus Frankeniaceae, and a clade that includes Ancistrocladaceae, Dioncophyllaceae, Droseraceae, and Nepenthaceae (Lledó et al., 1998). These taxa together constitute the sister to Caryophyllales (Albert et al., 1992; Chase et al., 1993; Williams et al., 1994). Results based on analyses of 18S sequence data (Soltis et al., 1997a) place Polygonaceae plus Plumbaginaceae as the sister to Caryophyllales, with Droseraceae plus *Nepenthes* as the sister taxon to this clade. A combined analysis of *rbc*L, *atp*B, and 18S sequence data (Hoot et al., 1999) indicates a sister relationship between Caryophyllales and *Simmondsia*, and these two taxa comprise the sister to *Nepenthes* plus *Rheum* L. (Polygonaceae).

Unequivocal caryophyllid fossils are scarce and known mostly from Tertiary strata. Seeds with possible affinities to Caryophyllaceae and Droseraceae have been reported from Eocene strata (Chandler, 1964; Mai, 1985a; Collinson et al., 1993). Seeds of Chenopodiaceae and fruits of Polygonaceae are known from Miocene strata (Gregor, 1982; Friis, 1985a; van der Burgh, 1987; Dorofeev, 1988; Collinson et al., 1993). The possible presence of caryophyllid lineages in the Late Cretaceous is documented by seeds tentatively assigned to Amaranthaceae from the Santonian-Campanian of southern Sweden (Collinson et al., 1993), and by permineralized infructescences, fruits, and seeds that resemble those of Phytolaccaceae from the Campanian of Mexico (Pérez-Hernández et al., 1997).

SAXIFRAGOIDS (= rosid III sensu Chase et al., 1993; saxifragoids sensu Soltis et al., 1997a, 1997b; Saxifragales sensu APG, 1998)

One of the smaller groups within the core eudicot clade, which is here referred to as the saxifragoid clade, includes the Hamamelidaceae, Cercidiphyllaceae, Daphniphyllaceae, Saxifragaceae s. str. (equivalent to Saxifragoideae of Engler, 1930, and Schulze-Menz, 1964), Crassulaceae, Haloragaceae,

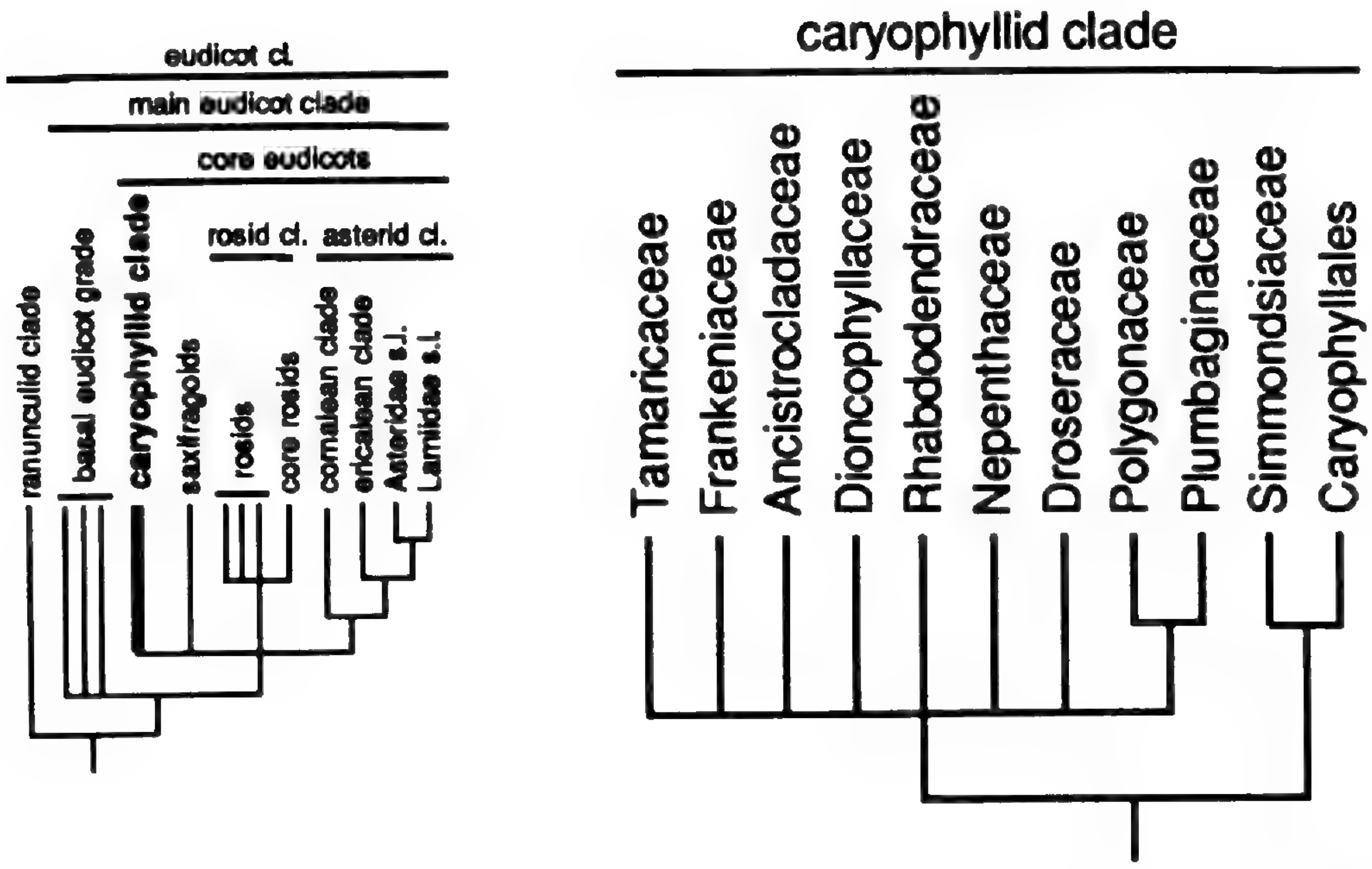

Figure 3. Caryophyllid clade. The cladogram on the left summarizes the general eudicot phylogenetic pattern. The caryophyllid clade is indicated in bold. The caryophyllid clade is one of the three major clades within the core eudicots. Within the caryophyllid clade, there are two major clades, one that includes the Caryophyllales plus Simmondsiaceae, and another that includes Polygonaceae plus Plumbaginaceae. Additionally, Droseraceae and Nepenthaceae, as well as several other families and taxa, are included (Table 1), but the exact pattern of relationships among them is not securely resolved.

and the genera *Itea* L., *Ribes* L., *Penthorum* L., *Pterostemon* Schauer., *Tetracarpaea* Hook., each of which is assigned to a different subfamily within the Saxifragaceae in the system of Engler (1930), and *Paeonia* (Paeoniaceae; Table 1). The number of species belonging to this saxifragoid assemblage is approximately 2350 (ca. 1.3% TESD; Table 1). The Hamamelidaceae, Cercidiphyllaceae, and Daphniphyllaceae have been considered to be relatively primitive members of the Hamamelididae, while the remaining taxa, except for *Paeonia,* are usually placed within Rosidae (Cronquist, 1981; Takhtajan, 1997). A relationship between Saxifragaceae s. str., other saxifragoid genera, and Crassulaceae, as well as more distantly with Haloragaceae, was recognized by Takhtajan (1997), who included all the above taxa within superorder Saxifraganae. The genus *Paeonia* has been placed within Dilleniales (Cronquist, 1981), within Theiflorae (Dahlgren, 1983), or in an order of its own within Ranunculales (Takhtajan, 1997).

The taxa included in the saxifragoids have been resolved in three different placements within the core eudicots: (1) as forming a paraphyletic series basal to the rosid clade (Soltis et al., 1993; Williams et al., 1994; Morgan & Soltis, 1993; Fig. 4B); (2) as forming a clade that is sister to the rosid clade (Chase et al., 1993; Soltis et al., 1997a; Fig. 4A); or (3) as forming an independent lineage within the core eudicots (Soltis & Soltis, 1997; Rice et al., 1997; Hoot et al., 1999). Here we tentatively treat the saxifragoids as an independent lineage within the core eudicots.

Saxifragaceae s. str. are documented as a monophyletic entity (e.g., Chase et al., 1993; Morgan & Soltis, 1993; Soltis et al., 1993; Soltis & Soltis, 1997), and genera of Crassulaceae consistently appear more closely related to one another than they are to any other taxon (e.g., Morgan & Soltis, 1993; Soltis et al., 1993, 1997b; Swensen et al., 1994). All phylogenetic analyses where at least two different subfamilies of Hamamelidaceae and other basal rosid taxa are sampled suggest that the Hamamelidaceae are paraphyletic, with some of its genera (i.e., *Liquidambar* L. and *Altingia* Noronha. [Altingioideae]), being more closely related to *Cercidiphyllum* Siebold & Zucc. and/or *Daphniphyllum* Blume than to other genera of Hamamelidaceae (e.g., Chase et al., 1993; Manos et al., 1993; Morgan & Soltis, 1993; Hoot et al., 1999). However, in all published analyses the taxonomic sample for Hamamelidaceae has been sparse, with a maximum of six genera included (Hoot et al., 1999). With respect to Haloragaceae, most phylogenetic analyses based on molecular data include either *Haloragis* Forster & Forster or *Myriophyllum* L., but generally not both. However, both genera were included simultaneously in the analysis of Soltis and Soltis (1997), where they were resolved as sister taxa, thus suggesting monophyly for Haloragaceae. *Cercidiphyllum, Daphniphyllum,* and the fragments of Hamamelidaceae are usually linked

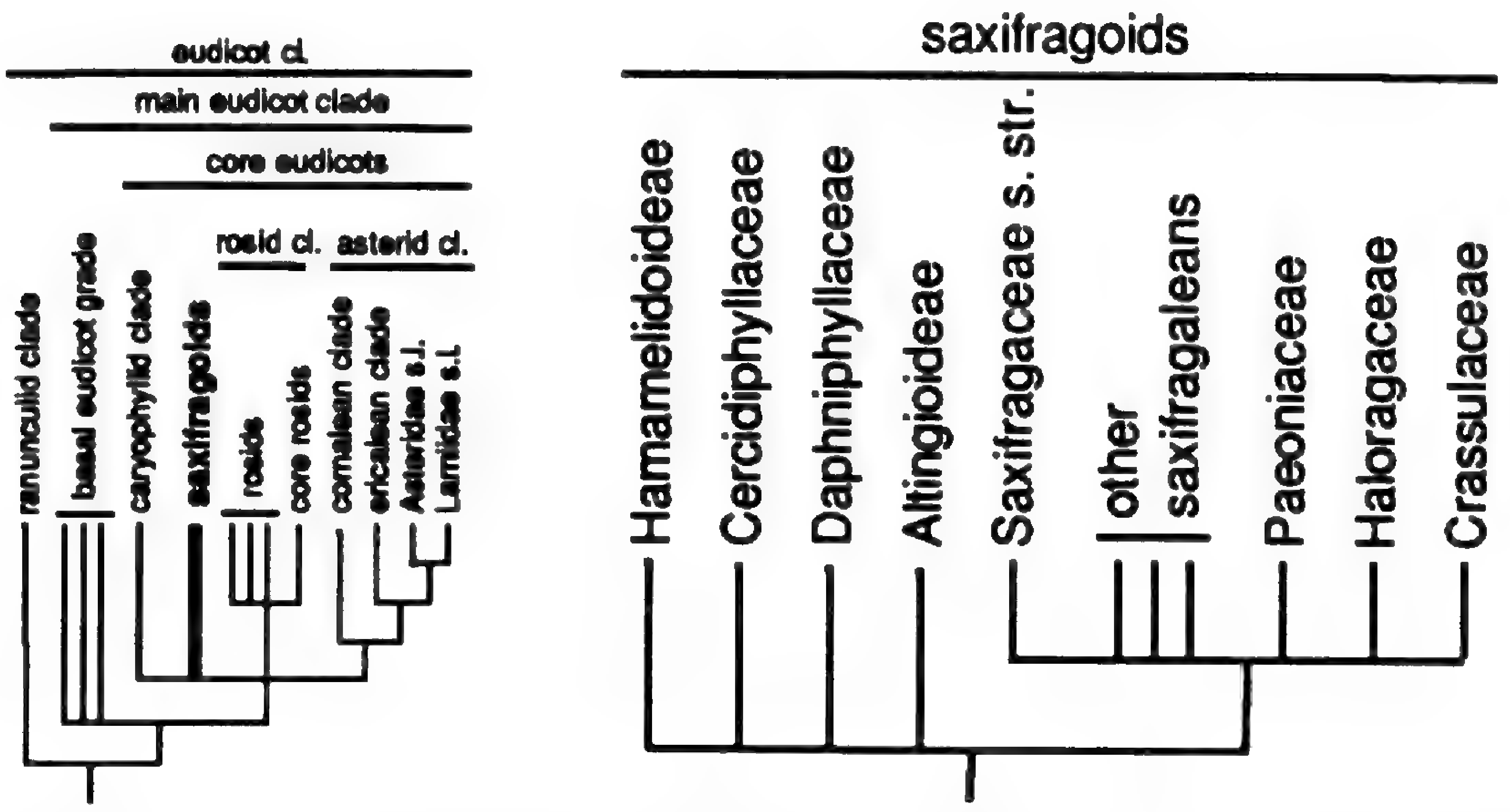

Figure 4. Saxifragoids. The cladogram on the left summarizes the general eudicot phylogenetic pattern. The saxifragoid clade is indicated in bold. The saxifragoid clade is tentatively considered here as an independent branch within the core eudicots. Hamamelidoideae, Cercidiphyllaceae, Daphniphyllaceae, and Altingioideae appear to be closer to the base of the clade. Saxifragaceae s. str., other saxifragalean genera, Paeoniaceae, Haloragaceae, and Crassulaceae appear to be more closely related to each other.

closely to one another (Chase et al., 1993; Morgan & Soltis, 1993; Soltis et al., 1993, 1997a; Fig. 4B; Williams et al., 1994). The Saxifragaceae s. str., other saxifragoid genera, Haloragaceae, *Paeonia*, and Crassulaceae appear at a more derived level within the clade (e.g., Morgan & Soltis, 1993; Soltis et al., 1993, Williams et al., 1994). Recently, representatives of Podostemaceae (*Hydrobryum* Endl. and *Cladopus* H. Möller) have been resolved as closely related to Crassulaceae (Ueda et al., 1997a).

Several taxa of the saxifragoid clade are well documented in the fossil record as early as the Upper Cretaceous. Reproductive structures of probable affinity with Cercidiphyllaceae are known from Upper Cretaceous (Maastrichtian) and Paleocene strata of the Northern Hemisphere (Crane, 1984; Crane & Stockey, 1985, 1986). *Nyssidium articum* (Heer) Iljinskaya and *Joffrea speirsii* Crane & Stockey are whole plant reconstructions based on vegetative and reproductive material for extinct taxa that are closely related to extant *Cercidiphyllum*. Unlike extant *Cercidiphyllum*, the gynoecium often consists of paired carpels.

The subfamily Hamamelidoideae (Hamamelidaceae) is well documented in the Upper Cretaceous. Flowers assigned to *Archamamelis bivalvis* Endress & Friis, from Santonian-Campanian strata of Sweden, have anthers in which each theca has a single pollen sac, suggesting an affinity with extant *Embolanthera* Merr., or more likely, with *Hamamelis* L. However, features of floral organization and the variability in the number of organs per floral whorl preclude the placement of this fossil within a modern taxon (Endress & Friis, 1991). *Allonia decandra* Magallón, Herendeen & Endress, from the late Santonian of Georgia, U.S.A. (Allon locality), shows distinct similarities with taxa of subtribe Loropetalinae (Hamamelideae; Hamamelidoideae). Cladistic analysis of several genera of Hamamelideae places *Allonia* as sister to the extant genus *Maingaya* Oliver (Magallón et al., 1996). The subfamily Altingioideae (Hamamelidaceae) is represented by a recently discovered fragmentary portion of an infructescence from Coniacian-Santonian sediments of Georgia, U.S.A. (Upatoi Creek locality). The carpel configuration, mode of dehiscence, and aggregation of fruits in a spherical infructescence all suggest an affinity with *Liquidambar* (Magallón, unpublished).

The Saxifragaceae s. str. are possibly represented by two types of flowers from Upper Cretaceous strata. Flowers assigned to the genus *Scandianthus* Friis & Skarby, from Santonian-Campanian strata of Sweden, may be a possible fossil representative of Saxifragaceae s. str. However, these fossil flowers also show important similarities with Hydrangeaceae, Vahliaceae, and Escalloniaceae (Friis & Skarby, 1982). A fossil flower from the Turonian of New Jersey, U.S.A., shows features that suggest affinity with Saxifragaceae s. str., although similarities with Hydrangeaceae are also apparent (Gandolfo et al., 1995, 1998a).

ROSID CLADE (= "rosid II" plus "rosid I" sensu Chase et al., 1993; rosids sensu APG, 1998)

The group here referred to as rosid clade includes taxa placed traditionally in the Rosidae, Dilleniidae, and derived orders of Hamamelididae.

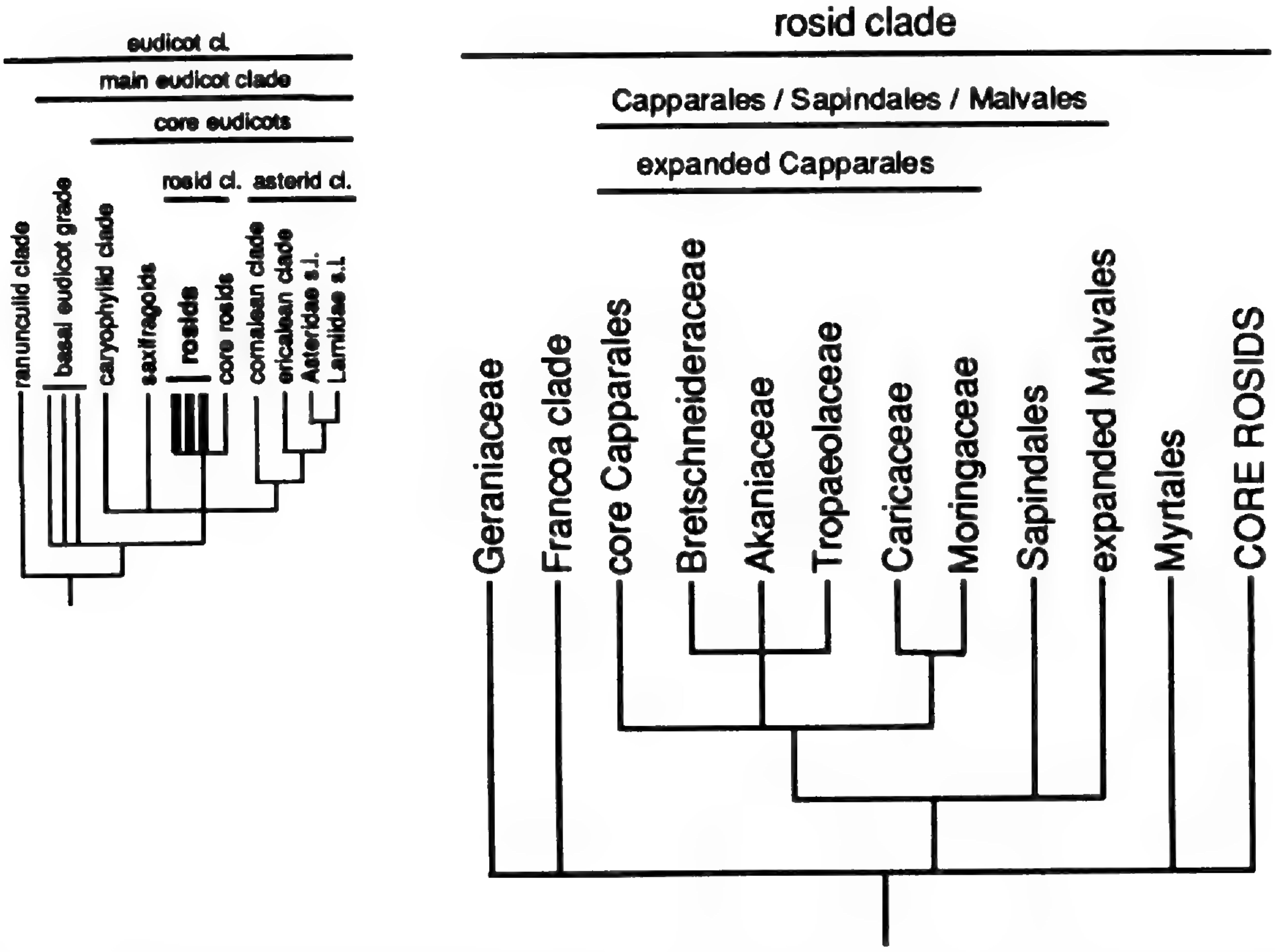

Figure 5. Rosid clade. The cladogram on the left summarizes the general eudicot phylogenetic pattern. The rosid clade is indicated in bold. Phylogenetic relationships among the major lineages in the rosid clade are not fully resolved. However, the expanded Capparales, Sapindales, and expanded Malvales form a clade, and the Myrtales are apparently closely related to the Capparales/Sapindales/Malvales and/or to the core rosid clade.

The rosid clade includes about 68,000 species (ca. 38.8% TESD; Table 1). The component taxa fall into several distinct lineages, the relationships among which are not fully resolved, broadly corresponding to "rosid II" of Chase et al. (1993), but also including the Myrtales and a small clade that includes *Francoa* Cav., and in the core rosids, corresponding to "rosid I" of Chase et al. (1993), but excluding Myrtales and the *Francoa* clade (Fig. 1). The rosid clade has been recognized in several large-scale phylogenetic analyses using *rbc*L (Chase et al., 1993; Morgan & Soltis, 1993; Williams et al., 1994), 18S (Soltis et al., 1997a), and combined *rbc*L, *atp*B, and 18S sequence data (Soltis et al., 1998; Hoot et al., 1999). There are five distinct groups within the rosid clade: (1) Geraniaceae, (2) the *Francoa* clade, (3) a large clade containing the Capparales, Malvales, and Sapindales and a few other genera of varied taxonomic affinity, (4) a clade corresponding roughly to the order Myrtales, and (5) a large and complex core rosid clade (Fig. 5). Relationships among these groups are not fully resolved.

Geraniaceae (included in Geraniales sensu APG, 1998). The family Geraniaceae (excluding *Wendtia* Meyen and *Vivania* Cav.) plus the genus *Hypseocharis* Remy (Oxalidaceae) form a clade according to the results of several phylogenetic analyses (e.g., Chase et al., 1993; Price & Palmer, 1993). *Hypseocharis* has been assigned traditionally to Oxalidaceae within Geraniales (Cronquist, 1981), or treated as a monogeneric family within Geranianae, relatively distant from Oxalidaceae, and in the same order as Geraniaceae (Takhtajan, 1997). The genus *Crossosoma* Nutt. (Crossosomataceae) appears phylogenetically close to Geraniaceae and *Hypseocharis* (Price & Palmer, 1993; Chase et al., 1993; Fernando et al., 1993), but the phylogenetic placement of *Crossosoma* is different according to 18S evidence (e.g., Soltis & Soltis, 1997; Soltis et al., 1997a) and is only weakly supported by *rbc*L analyses. The total number of species in Geraniaceae is 729 (< 0.5% TESD; Table 1).

Analyses based on *rbc*L sequence data place Geraniaceae as sister to the Capparales/Sapindales/Malvales (Chase et al., 1993), or to the latter clade plus Myrtales (Fernando et al., 1993). Alternatively, Geraniaceae are resolved as sister taxon to the *Francoa* clade, and together form the sister taxon to the Capparales/Sapindales/Malvales (Morgan & Soltis, 1993), or are basal to all other rosids (Williams et al., 1994; Price & Palmer, 1993). A different phylogenetic placement for Geraniaceae suggests that the clade is sister to rosids plus saxifragoids (Conti et al., 1996), but only *Geranium* L. was included in this analysis. According to analyses of 18S sequence data, *Geranium* is sister to the *Francoa* clade, and together they form the sister taxon to the caryophyllid clade, which is embedded within the rosid clade (Soltis & Soltis, 1997). An alternative result based on 18S data placed *Geranium* within a clade roughly equivalent to the Linales/Euphorbiaceae/Malpighiaceae in the core rosids (Soltis et al., 1997a). In most phylogenetic analyses, the sample for Geraniaceae has been small, although Price and Palmer (1993) included all five genera of Geraniaceae in addition to *Wendtia* and *Viviania*. There appears to be no reliable macrofossil record for the Geraniaceae (Collinson et al., 1993).

Francoa clade (included in Geraniales sensu APG, 1998). A small monophyletic group consisting of *Francoa* (Francooideae, Saxifragaceae), *Greyia* Hook. & Harvey (Greyiaceae; Rosales), *Viviania* (Geraniaceae), and *Wendtia* (Geraniaceae) is here referred to as the *Francoa* clade (Table 1; Fig. 5). The *Francoa* clade, as described above, includes only 13 species (Table 1), but apparently other genera are also related to this assemblage (e.g., *Bersama* Fres. [Melianthaceae]; Soltis et al., 1998). Monophyly of this assemblage is supported by analyses of *rbc*L and 18S sequence data (e.g., Chase et al., 1993; Morgan & Soltis, 1993; Price & Palmer, 1993; Soltis & Soltis, 1997; Soltis et al., 1997a). A close relationship among these four genera had not been previously suggested. *Viviania* and *Wendtia* were assigned to Geraniaceae by Cronquist (1981), but *Viviania* was separated into a monogeneric family by Dahlgren (1983) and Takhtajan (1997). *Greyia* and *Francoa* have been assigned to different orders within Saxifraganae (Takhtajan, 1997), or to the Saxifragales (Dahlgren, 1983). None of the genera included in the *Francoa* clade is known in the fossil record (Collinson et al., 1993).

Capparales/Sapindales/Malvales (included in "Eurosids II," sensu APG, 1998). A major group comprising an expanded Capparales, an expanded Malvales, and a large part of Sapindales has been detected in numerous phylogenetic studies based on *rbc*L sequence data in which a significant sample of the rosid clade is included (e.g., Gadek et al., 1992, 1996; Chase et al., 1993; Fernando et al., 1993, 1995; Price & Palmer, 1993; Rodman et al., 1993, 1994, 1996; Swensen et al., 1994; Williams et al., 1994; Table 1; Fig. 5). The Capparales/Sapindales/Malvales clade comprises approximately 14,700 species (ca. 8.4% TESD; Table 1), and is equivalent to "rosid II" of Chase et al. (1993), except for the inclusion in the latter of the Geraniaceae (Chase et al., 1993, fig. 10B). Studies based on 18S data, although recognizing a monophyletic Malvales and the expanded Capparales clade, do not support their close association either with each other or with the Sapindales (Soltis & Soltis, 1997; Soltis et al., 1997a). However, a combined analysis of 18S and *rbc*L sequence data supports the association of the expanded Capparales, expanded Malvales, and Sapindales in a clade (Rodman et al., 1998). A close association among these three major taxa has not been recognized in traditional classification systems. The Capparales and Malvales have been treated as different orders of Dilleniidae, and the Sapindales have been included in Rosidae (Cronquist, 1981; Takhtajan, 1997). Dahlgren (1983) placed each taxon in a different superorder (Violiflorae, Malviflorae, and Rutiflorae).

The expanded Capparales (= glucosinolates sensu Soltis et al., 1997a, 1997b; Brassicales sensu APG, 1998) include the families in the order Capparales plus the Limnanthaceae (Geraniales), Gyrostemonaceae (Batales), Bataceae (Batales, monogeneric), Bretschneideraceae (Sapindales, monogeneric), Akaniaceae (Sapindales, monogeneric), Tropaeolaceae (Geraniales), Caricaceae (Violales), and Salvadoraceae (Celastrales; Table 1). All genera of the expanded Capparales, except for *Koeberlinia* Zucc., produce mustard oil glucosides. Among the plants that produce these chemical compounds only *Drypetes* Vahl. (Euphorbiaceae) is placed elsewhere (in the core rosid clade, e.g., Rodman et al., 1996). The number of species included in the expanded Capparales is approximately 3900 (ca. 2.2% TESD; Table 1). Takhtajan (1997) recognized a close relationship between Capparales and Moringales with Bataceae and *Carica* L., by including all within Violanae. Dahlgren (1983) included Gyrostemonaceae and Bat(id)aceae within the order Capparales. *Carica* was included within Violales, but placed in the same superorder as the Capparales. The Tropaeolales, which include Limnathaceae and Tropaeolaceae, were placed within Rutiflorae, but an alternative placement near the Capparales was suggested (Dahlgren, 1983). The close relationship of Bretschneideraceae and Akaniaceae with the Capparales had not been suspected based on traditional sources of data. Both families are generally considered to be of broad sapindalean affinity (Cronquist, 1981; Dahlgren, 1983; Takhtajan, 1997).

The expanded Capparales clade has been documented in phylogenetic analyses based on morphology (Rodman, 1991), *rbc*L sequence data (e.g., Gadek et al., 1992; Fernando et al., 1993; Price & Palmer, 1993; Rodman et al., 1993, 1994, 1996, 1998; Swensen et al., 1994), and 18S sequence data (Soltis & Soltis, 1997; Soltis et al., 1997a). All the component families of the Capparales are closely related and form part of the expanded Capparales clade (e.g., Rodman et al., 1993, 1996), but the order itself, as traditionally defined, is not monophyletic.

Relationships within the expanded Capparales are relatively well resolved. The Limnanthaceae, which include only two genera, are monophyletic (Chase et al., 1993; Rodman et al., 1993, 1994, 1996), and genera of Gyrostemonaceae appear more closely related to one another than they are to any other taxon (Rodman et al., 1994). A core Capparales clade includes Bataceae, Brassicaceae, Capparaceae, Koeberliniaceae, Tovariaceae, Pentadiplandraceae, Gyrostemonaceae, Resedaceae, and Salvadoraceae (e.g., Rodman et al., 1996, 1998). *Carica* and *Moringa* Adans., and *Bretschneidera* Hemsley, *Akania* Hook. f., and *Tropaeolum* L. occur near the base of the clade (e.g., Gadek et al., 1992; Chase et al., 1993; Morgan & Soltis, 1993; Rodman et al., 1996). Limnanthaceae and *Setchellanthus* Brandegee apparently have an intermediate position within the expanded Capparales (e.g., Gadek et al., 1992; Chase et al., 1993; Morgan & Soltis, 1993; Rodman et al., 1994, 1996).

The Malvales have been found to be closely related to the Thymelaeaceae (Myrtales), Sarcolaenaceae, Dipterocarpaceae and Sphaerocarpaceae (Theales), Bixaceae and Cistaceae (Violales), Neuradaceae (Rosales), and *Muntingia* L. (Flacourtiaceae), constituting an expanded Malvales clade (Conti et al., 1996; = malvoids sensu Soltis et al., 1997b; Malvales sensu APG, 1998) that includes approximately 5500 species (ca. 3.2% TESD; Table 1). A close relationship between Malvales and Sarcolaenaceae and Dipterocarpaceae was suggested by Takhtajan (1997). Dahlgren (1983) grouped the families of Malvales s. str., Sarcolaenaceae, and Dipterocarpaceae within his Malvales, and also included the Thymelaeales within Malviflorae. The expanded Malvales correspond closely to the Malvales plus Thymelaeales of Dahlgren (1983), except for the inclusion of Gonystylidaceae, for which there is currently no information regarding its phylogenetic placement. Except for Elaeocarpaceae, Malvales sensu Cronquist (1981) are apparently monophyletic, although the internal phylogenetic pattern is not fully resolved (Chase et al., 1993; Fernando et al., 1993; Price & Palmer, 1993). A core Malvales clade includes Malvaceae, Bombacaceae, Sterculiaceae, and Tiliaceae (Alverson et al., 1998). Thymelaeaceae and Sarcolaenaceae are sister taxa, and together form the sister group to Malvales (Conti et al., 1996). Dipterocarpaceae appear basal to the Malvales (Chase et al., 1993; Fernando et al., 1995), but relationships among representatives of Dipterocarpaceae, Thymelaeaceae, and Sarcolaenaceae have not been analyzed and are unknown. In the analysis of Alverson et al. (1998), based on *rbc*L sequences, the core Malvales, Thymelaeaceae, as well as Bixaceae plus Sphaerosepalaceae form a trichotomy. A clade that includes Dipterocarpaceae, Sarcolaenaceae, Cistaceae, *Muntingia*, and *Neurada* L. is placed in a trichotomy with the previous malvalean clade and with the expanded Capparales (Alverson et al., 1998).

The Sapindales (= Sapindales sensu APG, 1998) include the Rutaceae, Burseraceae, Aceraceae, Sapindaceae, Anacardiaceae, Cneoraceae, Meliaceae, Hippocastanaceae, Ptaeroxylaceae, Simaroubaceae (excluding *Picramnia* Sw. and *Alvaradoa* Liebm.), and at least the genera *Peganum* L., *Malacocarpus* Fischer & C. Meyer, and *Nitratia* L. of Zygophyllaceae (Table 1; Gadek et al., 1992, 1996; Chase et al., 1993; Fernando et al., 1993, 1995; Morgan & Soltis, 1993; Price & Palmer, 1993; Rodman et al., 1993). The monogeneric Kirkiaceae (Gadek et al., 1996) and Leitneriaceae (Leitneriales; Gadek et al., 1992, 1996; Chase et al., 1993; Morgan & Soltis, 1993; Fernando et al., 1995) are also included in this group. The sapindalean clade, as described above, includes approximately 5260 species (ca. 3% TESD; Table 1). The taxa listed above, except for Leitneriaceae, were included within Sapindales by Cronquist (1981). However, Dahlgren (1983) and Takhtajan (1997) included them and the Leitneriaceae in different orders of Rutanae and Rutiflorae, respectively. *Peganum* is considered to have a somewhat isolated position: within Geraniales (Rutiflorae; Dahlgren, 1983), or as a monogeneric family of Zygophyllales within Geranianae (Takhtajan, 1997). Within the sapindalean clade, the families Cneoraceae, Rutaceae, Meliaceae, Ptaeroxylaceae, and part of Simaroubaceae, together with *Leitneria* Chapman, are closely related. The Anacardiaceae, Aceraceae, Hippocastanaceae, Sapindaceae, and other genera of Simaroubaceae form a second association, while the Burseraceae may appear in either of these two groups (Chase et al., 1993; Morgan & Soltis, 1993; Gadek et al., 1992, 1996; Fernando et al., 1995). Kirkiaceae and Zygophyllaceae p.p. are resolved as the basalmost branches in the sapindalean clade

(Gadek et al., 1992, 1996; Chase et al., 1993; Morgan & Soltis, 1993; Fernando et al., 1995).

Phylogenetic relationships among the expanded Capparales, expanded Malvales, and Sapindales are not fully resolved (Fig. 5). The expanded Malvales and the Sapindales usually appear as sister taxa, and together are the sister taxon to the expanded Capparales (Gadek et al., 1992; Chase et al., 1993; Morgan & Soltis, 1993; Rodman et al., 1993, 1994; Swensen et al., 1994; Soltis et al., 1995b). However, other results, generally obtained with a smaller sample for Malvales and Sapindales, suggest that the expanded Malvales and expanded Capparales are sister taxa (Albert et al., 1992; Fernando et al., 1993; Price & Palmer, 1993; Williams et al., 1994; Rodman et al., 1996). Phylogenetic analyses based on 18S sequence data contrast strongly in suggesting that the Malvales, Sapindales, and Capparales are distantly related (Soltis & Soltis, 1997; Soltis et al., 1997a). However, combined analyses of molecular sequence data support the association among these groups (Rodman et al., 1998; Soltis et al., 1998).

When the Capparales/Sapindales/Malvales are closest to one another, their position with respect to other rosid clades is not fully resolved (Fig. 5). In several analyses, they are the sister taxon to the Myrtales (Fernando et al., 1993; Price & Palmer, 1993; Soltis et al., 1995b) and together form the sister group to the core rosids (Gadek et al., 1992; Williams et al., 1994; Conti et al., 1996). However, according to the results of Morgan and Soltis (1993), the Capparales/Sapindales/Malvales are the sister group to the core rosids plus Myrtales, and, according to Chase et al. (1993), the Capparales/Sapindales/Malvales are the sister group to Geraniaceae (i.e., "rosid II"), and together form the sister taxon to a clade including *Francoa*, the Myrtales, and the core rosids (i.e., "rosid I").

Lineages belonging to the expanded Capparales, Malvales, and Sapindales are known from at least the early Tertiary. A leaf impression of putative Akaniaceae from the Paleocene (Romero & Hickey, 1976; Collinson et al., 1993) and fruits and seeds assigned to Capparaceae from the Lower Eocene of England (Chandler, 1964; Collinson et al., 1993) are some of the earliest reports in the fossil record. A recently discovered, three-dimensionally preserved flower from Turonian strata of New Jersey, U.S.A., shows a combination of characters found in families of Capparales (Crepet & Nixon, 1996; Gandolfo et al., 1996, 1998b). Vegetative and reproductive remains assigned to Malvaceae (Chandler, 1964; Collinson et al., 1993), Sterculiaceae (Wilde, 1989; Collinson et al., 1993), Tiliaceae (Chandler, 1964; Collinson et al., 1993), Thymelaeaceae (Taylor, 1990; Collinson et al., 1993), and Dipterocarpaceae (Wolfe, 1977; Collinson et al., 1993), all from Eocene strata, document the existence of distinct lineages of the expanded Malvales by the early Tertiary. The genus *Florissantia* Manchester includes well-preserved flowers, fruits, and pollen of affinity within Malvales from the Eocene and Oligocene (Manchester, 1992). Seeds of putative Rutaceae from Maastrichtian-Paleocene strata of Europe (Knobloch & Mai, 1986), and fruits and leaves of *Acer* L. from the Upper Paleocene (Wolfe & Tanai, 1987; Collinson et al., 1993; Crane et al., 1990), comprise the earliest evidence of sapindalean lineages in the fossil record.

Myrtales (= Myrtales, included in "Eurosids II" sensu APG, 1998). The families of Myrtales, with the exception of Thymelaeaceae, form a monophyletic group in a relatively derived position within the rosid clade (Table 2; Fig. 5; Gadek et al., 1992; Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Price & Palmer, 1993; Rodman et al., 1993; Williams et al., 1994; Conti et al., 1996). The genus *Qualea* Aublet (Vochysiaceae) consistently appears close to the Myrtales, either embedded within the Myrtales (Chase et al., 1993; Conti et al., 1996) or as sister to a monophyletic Myrtales (Fernando et al., 1993; Morgan & Soltis, 1993; Soltis et al., 1995b), although in the last three studies the sample size for Myrtales is small. There is currently no information regarding the phylogenetic position or monophyletic status of Myrtales, nor about their close relationship with *Qualea*, from molecular evidence other than *rbc*L. The Myrtales plus *Qualea* form a clade that includes about 10,440 species (ca. 5.9% TESD; Table 1). The Myrtales are recognized as a natural group in traditional classification systems (Cronquist, 1981; Dahlgren, 1983; Takhtajan, 1997). Takhtajan (1997) recognized the Thymelaeaceae as independent and distant from Myrtales. A relationship between the Myrtales and Vochysiaceae (specifically *Qualea*) has never been proposed in traditional classification systems, although the two groups are similar in the presence of vestured pits and other wood anatomical features.

The phylogenetic position of Myrtales relative to other major monophyletic groups within the rosid clade is not fully resolved (Fig. 5). In several analyses, Myrtales appear as sister taxon to the Capparales/Sapindales/Malvales (Gadek et al., 1992; Fernando et al., 1993; Price & Palmer, 1993; Rodman et al., 1993; Williams et al., 1994; Soltis et al., 1995b; Conti et al., 1996), but in some of these

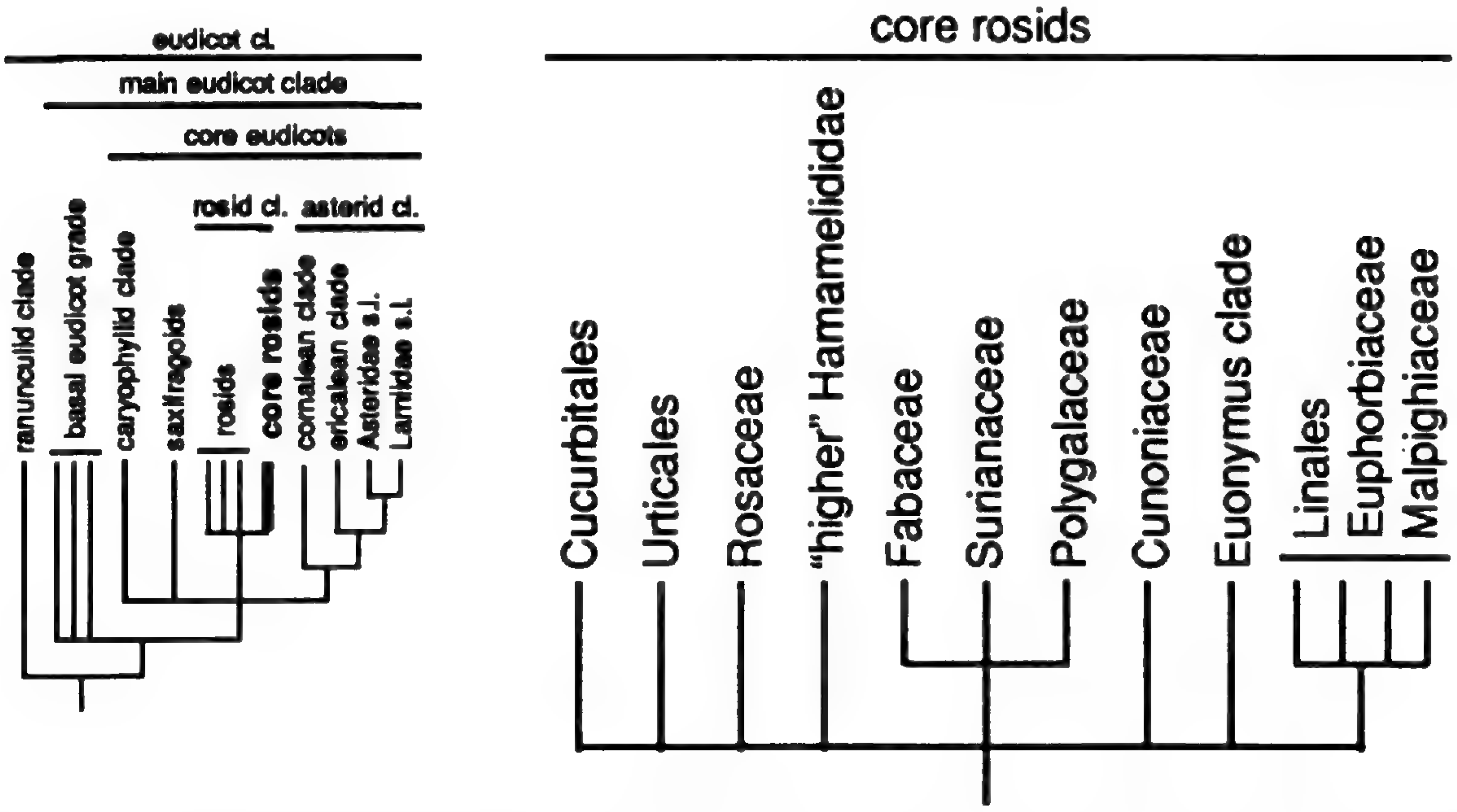

Figure 6. Rosid clade: core rosids. The cladogram on the left summarizes the general eudicot phylogenetic pattern. The core rosid clade is indicated in bold. The core rosid clade includes eight main lineages, the relationships among which are not resolved.

studies the taxonomic sample for groups other than these two major clades is limited. Myrtales also have been resolved as sister taxon to the core rosids (Chase et al., 1993; Morgan & Soltis, 1993), and the observed phylogenetic placement of Myrtales is apparently sensitive to the density of taxonomic sampling within and outside the group. As stated by Conti et al. (1996: 230), ". . . the issue of identifying the sister group of Myrtales cannot be considered definitely settled."

Macrofossil reproductive remains assigned to Lythraceae (Collinson, 1986; Collinson et al., 1993) and Myrtaceae (Crane et al., 1990) have been reported from the Paleocene, and reproductive remains assigned to Onagraceae and Rhizophoraceae are known form the Eocene (Collinson et al., 1993). Three-dimensionally preserved flowers and fruits belonging to the extinct genus *Esgueiria* Friis, Pedersen & Crane (of probable affinity with Combretaceae) are known from the Campanian-Maastrichtian of Portugal (Friis et al., 1992) and the early Santonian of Japan (Takahashi & Crane, in prep.). Features of the flowers, including the distinctive peltate trichomes on the inferior ovary, are very similar to features of extant Combretaceae, but the presence of three free stylar branches in *Esgueiria* is a significant difference. Extant Combretaceae have a single style (Friis et al., 1992). Fossils of myrtalean affinity are also reported for the Cenomanian-Turonian of Kazakhstan (Frumin & Friis, in press).

Core rosids (nearly equivalent to rosid I sensu Chase et al., 1993; = "nitrogen-fixing clade" sensu Soltis et al., 1995b, 1997b; "Eurosids I" sensu APG, 1998)

Many taxa considered to be derived within the subclass Rosidae, together with certain Dilleniidae, and the derived orders of Hamamelididae form a large clade, which we term here the core rosids (Table 1). The core rosids have been recognized in phylogenetic analyses using *rbc*L sequence data (Albert et al., 1992; Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Swensen et al., 1994; Williams et al., 1994; Conti et al., 1996). Results of analyses based on 18S sequence data also recognize a core rosid clade, although with a somewhat different taxonomic composition (Soltis & Soltis, 1997; Soltis et al., 1997a). There are eight major subclades in the core rosids (Fig. 6): (1) Cucurbitales; (2) Urticales; (3) Rosaceae; (4) "higher" Hamamelididae; (5) Fabaceae/Surianaceae/Polygalaceae; (6) the expanded Cunoniaceae; (7) *Euonymus* L. clade; and (8) Linales/Euphorbiaceae/Malpighiaceae. Additionally, the genera *Krameria* L. (Krameriaceae) and *Guaiacum* L. (Zygophyllaceae) also form part of the core rosids in the results of some analyses (Chase et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994), but are more closely related to the Myrtales in the results of Soltis et al. (1995b). The total species number included in the core rosid clade is approximately 42,000 (ca. 24% TESD; Table 1). The core rosid clade is closely equivalent to "rosid I" of Chase et al. (1993, figs. 11B, 11C), except for the inclusion in the latter of Geraniaceae, the *Francoa* clade, and Myrtales. Because all of the known dicot genera that form symbiotic associations with nitrogen-fixing bacteria in root nodules are included in different lineages of the core rosids (along with other non N-fixing taxa), this clade has been termed the "nitrogen-fixing clade" (e.g., Soltis et al., 1995b, 1997a, b).

Phylogenetic patterns among the major taxa in the core rosids are uncertain (Fig. 6). In some analyses the Linales/Euphorbiaceae/Malpighiaceae and the *Euonymus* clade are relatively well supported as sister taxa (Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Williams et al., 1994; Soltis et al., 1995b). However, in other studies, the Linales/Euphorbiaceae/Malpighiaceae are sister to the expanded Cunoniaceae (Morgan et al., 1994), or include *Geranium* (Geraniaceae), *Muntingia* (Flacourtiaceae), and the Malvales, and are sister to the Rosaceae (Soltis et al., 1997a). The *Euonymus* clade, in addition to the relationship described above, may be resolved as the sister group to Linales/Euphorbiaceae/Malpighiaceae plus the expanded Cunoniaceae (Morgan et al., 1994), or as sister to the expanded Cunoniaceae (Swensen et al., 1994).

The expanded Cunoniaceae are also resolved as sister group to Linales/Malpighiaceae/Euphorbiaceae plus the *Euonymus* clade (Fernando et al., 1993; Williams et al., 1994), or as sister taxon to the Cucurbitales (represented only by Datiscaceae; Morgan & Soltis, 1993). Alternatively, the expanded Cunoniaceae are sister to all other core rosids (Chase et al., 1993) or constitute an independent branch within an unresolved core rosid clade (Soltis et al., 1997a).

The Fabaceae/Surianaceae/Polygalaceae are resolved as sister to Urticales plus Rosaceae (Chase et al., 1993; Fernando et al., 1993), or alternatively, they are closely related to *Krameria* (Krameriaceae) and *Guaiacum* (Zygophyllaceae), and together form the sister group to Linales/Euphorbiaceae/Malpighiaceae plus the *Euonymus* clade (Morgan & Soltis, 1993). Other analyses result in a similar pattern, in which Fabaceae/Surianaceae/Polygalaceae are sister to a clade that includes the Linales/Euphorbiaceae/Malpighiaceae, the expanded Cunoniaceae, and the *Euonymus* clade (Morgan & Soltis, 1993). A further alternative placement for the Fabaceae/Surianaceae/Polygalaceae is as the basalmost lineage within the core rosids (Williams et al., 1994).

The "higher" Hamamelididae are apparently closely related to the Urticales. These two clades are resolved as sister taxa (Fernando et al., 1993; Williams et al., 1994), or the "higher" Hamamelididae are sister to the Urticales plus Rosaceae (Morgan & Soltis, 1993; Morgan et al., 1994). An alternative result recognizes a sister relationship between the "higher" Hamamelididae and the Cucurbitales (Chase et al., 1993).

The Rosaceae are resolved as sister to the Urticales (Chase et al., 1993; Morgan & Soltis, 1993; Soltis et al., 1995b), or to the Urticales plus the "higher" Hamamelididae (Fernando et al., 1993; Morgan et al., 1994; Williams et al., 1994). Alternatively, the Rosaceae are the sister to a modified Linales/Euphorbiaceae/Malpighiaceae (Soltis et al., 1997a; see above). The possible phylogenetic relationships of the Urticales and the Cucurbitales are described above, but their relationships are currently not securely resolved (Swensen et al., 1994; Soltis et al., 1995b, 1997a).

Cucurbitales (= Cucurbitales sensu APG, 1998). Recognition of a Cucurbitales clade containing the families Begoniaceae, Cucurbitaceae, and Datiscaceae (Dilleniidae), and its placement within the core rosids is supported by phylogenetic analyses based on *rbc*L (Albert et al., 1992; Chase et al., 1993; Morgan & Soltis, 1993; Swensen et al., 1994; Soltis et al., 1995b), and 18S sequence data (Soltis et al., 1997a; Soltis & Soltis, 1997). This group corresponds exactly to the order Cucurbitales (Violiflorae) of Dahlgren (1983). In addition to Begoniaceae, Cucurbitaceae, and Datiscaceae, the Corynocarpaceae (Celastrales) and Coriariaceae (Ranunculales) have been recognized as belonging to this clade (Table 1; Albert et al., 1992; Chase et al., 1993; Swensen et al., 1994; Soltis et al., 1998). A close relationship between these families and the genus *Coriaria* L. has never been suggested in traditional classification systems. The Begoniaceae, Cucurbitaceae, and Datiscaceae have been placed previously within a large and heterogeneous Violales (Cronquist, 1981; Takhtajan, 1997). The number of species encompassed in the Cucurbitales, including Coriariaceae and Corynocarpaceae, is approximately 1670 (ca. 1% TESD; Table 1)

Begonia L. and *Symbegonia* Warb. appear as sister taxa in the analysis by Soltis et al. (1997a), suggesting a monophyletic Begoniaceae. A limited number of genera have been used as placeholders for Cucurbitaceae, and therefore the monophyletic status of this relatively large family has not yet been assessed adequately. Datiscaceae have been shown to be paraphyletic, with all component genera placed within the Cucurbitales (Table 2; Swensen et al., 1994). The fossil record for the families of Cucurbitales is limited to seeds assigned to Cucurbitaceae from Paleocene strata (Collinson et al., 1993), and seeds assigned to Coriariaceae from

Miocene strata (Gregor, 1980; Collinson et al., 1993).

Urticales (included in Rosales sensu APG, 1998). The placement of the Urticales clade within the core rosids is documented by phylogenetic analyses both of *rbc*L (Albert et al., 1992; Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Swensen et al., 1994; Willams et al., 1994; Soltis et al., 1995b), and 18S sequence data (Soltis & Soltis, 1997; Soltis et al., 1997a). The Urticales are resolved as monophyletic in *rbc*L-based analyses where two or more taxa of the order are included (e.g., Soltis et al., 1995b), but are paraphyletic in analyses based on 18S data. Within Urticales, Ulmaceae consist of a monophyletic Ulmoideae and a paraphyletic Celtidoideae (Zavada & Kim, 1996; Ueda et al., 1997b). *Rhamnus* L. (Chase et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Swensen et al., 1994; Soltis et al., 1995b) and *Ceanothus* L. (Morgan et al., 1994; Soltis et al., 1995b), both of Rhamnaceae, as well as Elaeagnaceae (Soltis et al., 1995b), appear to be closely related to Urticales. The number of species encompassed by the urticalean clade, including *Rhamnus* and *Ceanothus*, is about 2820 (ca. 1.6% TESD; Table 1).

Although usually recognized as a distinct group in traditional classifications, the Urticales have never been linked closely with rosid taxa. Instead, they have been placed in the Hamamelididae (Cronquist, 1981), in their own superorder within a large Malviflorae (Dahlgren, 1983), or treated as a separate superorder within Dilleniidae (Takhtajan, 1997). A close link between Urticales and Rhamnales was not previously suspected, although Dahlgren (1983) placed Rhamnaceae in an order of its own, also within Malviflorae. Urticales are represented in the Upper Cretaceous fossil record by fruits of Moraceae (Collinson et al., 1993), and by flowers, fruits, and leaves of Celtidoideae (Manchester, 1989). The Ulmoideae are well represented in the Tertiary fossil record by abundant vegetative and reproductive remains (Manchester, 1989).

Rosaceae (included in Rosales sensu APG, 1998). The Rosaceae are consistently nested within the core rosid clade in phylogenetic analyses based both on *rbc*L and 18S sequence data (Table 1; e.g., Chase et al., 1993; Fernando et al., 1993; Swensen et al., 1994; Soltis & Soltis, 1997; Soltis et al., 1997a). Rosaceae have been identified as a distinct family, either as part of a large Rosales (Cronquist, 1981; Dahlgren, 1983), or close to *Crossosoma* and Chrysobalanaceae in a relatively restricted Rosales (Takhtajan, 1997). The family Rosaceae, excluding *Quillaja* Molina, was found to be monophyletic in a study where taxa representing all but one of the recognized 17 subtribes and 4 subfamilies within the family were included in phylogenetic analysis of *rbc*L data (Morgan et al., 1994). Monophyly of Rosaceae is also supported by other studies based on *rbc*L (e.g., Chase et al., 1993; Fernando et al., 1993; Swensen et al., 1994; Williams et al., 1994; Soltis et al., 1995b) and 18S sequence data (Soltis & Soltis, 1997; Soltis et al., 1997a). Within Rosaceae, the subfamilies Rosoideae s. str., Amygdaloideae s.l., and Maloideae s.l. were suggested as monophyletic (Morgan et al., 1994). The Rosaceae, excluding *Quillaja*, include about 3300 species (ca. 1.9% TESD; Table 1). Rosaceae are represented in the fossil record by fossil wood of Prunoideae (Cevallos-Ferriz & Stockey, 1990), flowers of uncertain affinities within the family (Taylor, 1990), flowers assigned to *Paleorosa similkameenensis* Basinger (Basinger, 1976; Cevallos-Ferriz et al., 1993), and fruits of *Prunus* L. (Mai, 1984; Collinson et al., 1993; Manchester, 1994), all from Eocene strata.

"Higher" Hamamelididae (= Fagales sensu APG, 1998). The "higher" Hamamelididae include the classic "amentiferous" families with reduced, typically wind-pollinated flowers that produce tricolporate-triporate pollen grains often with reduced apertures and granular infratectal exine (Crane & Blackmore, 1989). Included families are Betulaceae, Casuarinaceae, Myricaceae, Juglandaceae, Rhoipteleaceae, Ticodendraceae, Fagaceae, and Nothofagaceae. The number of species of "higher" Hamamelididae is about 1380 (ca. 0.8% TESD; Table 1). All the families listed above have been considered to be derived within the Hamamelididae, but have been assigned to different orders (Cronquist, 1981) or superorders (Takhtajan, 1997) within the subclass. The classification system of Dahlgren (1983) places these families in different orders of a broad Rosiflorae, which also includes "lower" hamamelids (sensu Crane & Blackmore, 1989) among others.

A close relationship between the "higher" Hamamelididae and rosid taxa has been previously suggested (e.g., Dickison, 1989; Nixon, 1989), and placement of the group in a major rosid clade is supported by phylogenetic analyses based on morphological (Hufford, 1992), 18S (Soltis et al., 1997a), *rbc*L (e.g., Chase et al., 1993; Morgan & Soltis, 1993; Gunter et al., 1994; Morgan et al., 1994; Soltis et al., 1995b; Manos & Steele, 1997), and *mat*K data (Manos & Steele, 1997), as well as chloroplast DNA restriction site variation (Manos et al., 1993) and analyses of combined data (Gunter et al., 1994; Manos & Steele, 1997). The families of "higher" Hamamelididae are resolved as more closely related to one another than to any other taxon in studies where a significant taxonomic sample has been included (Manos et al., 1993; Gunter et al., 1994; Soltis et al., 1995b; Manos & Steele, 1997), but in most cases the taxonomic sample has been small, and in these cases, relationships have been resolved in various ways (Albert et al., 1992; Chase et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Williams et al., 1994; Soltis et al., 1997a).

Within the "higher" Hamamelididae, the Betulaceae, Casuarinaceae, Myricaceae and Juglandaceae, *Rhoiptelea* Diels & Hand.-Mazz., and *Ticodendron* Gómez-Laurito & Gómez P. are grouped together into what we term the Normapolles clade (core "higher" hamamelids), in reference to the diverse late Cretaceous Normapolles pollen, much of which was produced by early representatives of these families (e.g., Friis, 1983; Friis & Crane, 1989; Sims et al., 1995 and in press). Relationships within the Normapolles group are not fully resolved. Sister to the Normapolles group are a monophyletic Fagaceae s. str., and sister to Normapolles plus Fagaceae is *Nothofagus* Blume. This arrangement has been supported by the separate and combined analyses of *rbc*L and *mat*K sequence data of Manos and Steele (1997) and by the combined morphology and *rbc*L analysis of Gunter et al. (1994). In the *rbc*L analysis of Chase et al. (1993), genera of Fagaceae form a grade between *Nothofagus* and the Normapolles group. A different pattern of relationships is supported by the separate *rbc*L and morphology analyses of Gunter et al. (1994). The analysis based on *rbc*L data resolves Fagaceae and Myricaceae as sister taxa to the remaining Normapolles families. The morphological analysis places Betulaceae as sister taxon to Fagaceae plus Myricaceae, and these three families as sister group to Juglandaceae plus Casuarinaceae.

The "higher" Hamamelididae have an abundant and well-documented fossil record in Upper Cretaceous and Tertiary strata (e.g., Manchester, 1987; Crane & Blackmore, 1989). Flowers and pollen assigned to Betulaceae have been reported from the Maastrichtian (Crane & Stockey, 1987; Collinson et al., 1993), and flowers possibly referable to Betulaceae are known from the late Santonian of Georgia, U.S.A. (Sims et al., in press). Cupules and leaves of extant subgenera of *Nothofagus* are known from the Oligocene (Hill, 1991a; Collinson et al., 1993), while characteristic *Nothofagus* pollen is known as early as the Campanian (e.g., Dettman et al., 1990). Most of the distinctive and diverse pollen grains that constitute the Normapolles complex were probably produced by lineages of "higher" hamamelids. Normapolles pollen was diverse and abundant in mid-latitudes of eastern North America and Europe (Normapolles Province) during the late Cretaceous (Campanian-Maastrichtian; Lupia et al., in press). Three-dimensionally preserved fossil flowers containing Normapolles pollen grains provide unequivocal information about the features of the flowers that produced these grains, and their probable phylogenetic relationships. Three different Normapolles flowers, assigned to the genera *Manningia* Friis, *Antiquocarya* Friis, and *Caryanthus* Friis, from Santonian-Campanian strata of Sweden, have been related to the Myricaceae or Juglandaceae (Friis, 1983). Three additional types of flowers with anthers containing Normapolles grains, probably related to Juglandales/Myricales and possibly Betulaceae, have been recently discovered in late Santonian strata of Georgia, U.S.A. (Sims et al., 1995 and in press).

Exquisitely preserved fossils representing two extinct genera of Fagaceae s.l. have been described from the late Santonian of central Georgia (Herendeen et al., 1995; Sims et al., 1998). *Protofagacea allonensis* Herendeen, Crane & Drinnan is known from associated staminate inflorescences and flowers, cupules, and fruits (Herendeen et al., 1995). *Antiquacupula sulcata* Sims, Herendeen & Crane is known from staminate and bisexual flowers with well-developed nectary-like structures that are unknown among extant Fagaceae. The presence of nectaries in an extinct flower of the characteristically wind-pollinated "higher" Hamamelididae may be a plesiomorphic feature retained from insect-pollinated precursors (Sims et al., 1998).

Fabaceae/Surianaceae/Polygalaceae (= Fabales sensu APG, 1998). The Fabaceae/Surianaceae/Polygalaceae have been identified within the core rosid group by phylogenetic analyses based on *rbc*L sequence data (Table 1; Chase et al., 1993; Fernando et al., 1993; Swensen et al., 1994; Soltis et al., 1995b). The Polygalaceae (Albert et al., 1992; Chase et al., 1993; Morgan & Soltis, 1993; Swensen et al., 1994; Williams et al., 1994; Soltis et al., 1995b), Surianaceae (Fernando et al., 1993; Morgan et al., 1994; Soltis et al., 1995b), and possibly the genus *Quillaja* (Rosaceae; Morgan et al., 1994; Soltis et al., 1995b) appear to be closely related to the Fabaceae. The number of species included in the Fabaceae/Surianaceae/Polygalaceae is approximately 17,360 (ca. 10% TESD), of which 16,400 species comprise the Fabaceae (Table 1). Traditional classification systems recognize Fabaceae (or Fabales, including Caesalpiniaceae, Mimosaceae, and Fabaceae s. str.) as a distinct natural group, placed in its own order (Fabales; Cronquist, 1981), or superorder (Fabiflorae, Dahlgren, 1983; Fabanae, Takhtajan, 1997). A close link between Polygalaceae or Surianaceae with Fabaceae has never been suggested in traditional classification systems.

The Fabaceae, Polygalaceae, and Surianaceae are each monophyletic (Table 2), although in the large-scale phylogenetic analyses completed to-date, the taxonomic sample for Fabaceae and Polygalaceae has been very limited. The Fabaceae include two distinct monophyletic subgroups, Mimosoideae and Papilionoideae, embedded within a paraphyletic Caesalpinioideae (e.g., Doyle et al., 1997). Sampling of Caesalpinioideae for molecular analyses has been especially sparse. The pattern of relationships among Fabaceae, Polygalaceae, and Surianaceae is not resolved. Fernando et al. (1993), in a study that included a significant generic representation of Surianaceae, documented the sister relation of Surianaceae to Fabaceae plus Polygalaceae. However, Morgan et al. (1994), in a study centered in the Rosaceae, found that Polygalaceae plus Surianaceae formed the sister taxon to Fabaceae, and *Quillaja* was sister to the previous group. In marked contrast, a limited sample of 18S data has yielded the anomalous result that Fabaceae appear as paraphyletic (Soltis & Soltis, 1997) or polyphyletic (Soltis et al., 1997a).

Polygalaceae are represented in the fossil record by putative samaras of *Securidaca* L. from Paleocene strata (Crane et al., 1990), and by leaves assigned to the same genus, from Miocene strata (Collinson et al., 1993). The Fabaceae are securely documented by reproductive structures in Paleocene strata (Herendeen & Crane, 1992), and the three subfamilies were distinct and diverse by the Eocene (Herendeen, 1992; Herendeen et al., 1992). Some of the earliest representatives for Caesalpinioideae are fruits of *Caesalpinia* subg. *Mezoneuron* (Desf.) Vidal ex Herendeen & Zarucchi, from Tertiary localities in eastern and western North America and southern England (Herendeen & Dilcher, 1991; Herendeen & Crane, 1992). One of the earliest reliable records for Mimosoideae is provided by spicate inflorescences and flowers, assigned to *Eomimosoidea plumosa* Crepet & Dilcher, from Middle Eocene strata of the Claiborne Formation, in western Tennessee, U.S.A. (Crepet & Dilcher, 1977). Fossil flowers and fruits assigned to *Barnebyanthus buchananensis* Crepet & Herendeen, corresponding to the subfamily Papilionoideae, are known from early Eocene strata from the Claiborne Formation, in western Kentucky, Tennessee, and northern Mississippi (Crepet & Herendeen, 1992). The absence of connation between the keel petals and among the stamen filaments in the fossil, as well as the occurrence of numerous ovules in the carpel and the absence of seed chambers, suggest that *Barnebyanthus buchananensis* occupies a near-basal position within the Papilionoideae (Crepet & Herendeen, 1992).

Expanded Cunoniaceae (= cunonioids sensu Soltis et al., 1997a, 1997b; included in Oxalidales sensu APG, 1998). The Cunoniaceae, including *Bauera* Banks ex Andrews, have been supported as monophyletic based on analyses of morphological evidence (Hufford & Dickison, 1992), as well as *rbc*L (e.g., Chase et al., 1993; Morgan & Soltis, 1993; Soltis et al., 1995b) and 18S sequence data (Soltis & Soltis, 1997). Tremandraceae (e.g., Albert et al., 1992; Fernando et al., 1993; Swensen et al., 1994; Soltis et al., 1995b), Cephalotaceae (e.g., Chase et al., 1993; Morgan et al., 1994; Soltis et al., 1995b; Conti et al., 1996; Soltis & Soltis, 1997), Oxalidaceae, excluding *Hypseocharis* (e.g., Chase et al., 1993; Morgan et al., 1994; Swensen et al., 1994; Soltis et al., 1995b), Elaeocarpaceae, and Davidsoniaceae (Soltis et al., 1998) have been resolved as closely related to Cunoniaceae, and together these families constitute the expanded Cunoniaceae. A single representative for Connaraceae (*Connarus* L.; Fernando et al., 1993; Morgan et al., 1994) has also been resolved as closely related to the expanded Cunoniaceae, but this relationship requires more detailed study.

The total number of species included in the expanded Cunoniaceae is about 1470 (ca. 0.8% TESD; Table 1). Cunoniaceae have been included within Rosales (Cronquist, 1981), as part of Cunoniales, within Saxifraganae (Rosidae; Takhtajan, 1997), or within a relatively restricted Cunoniales, within Rosiflorae (Dahlgren, 1983). Other taxa in the expanded Cunoniaceae have not been previously linked with this family, although all were included within Rosidae, either in different orders (Cronquist, 1981) or superorders (Takhtajan, 1997). Dahlgren recognized some link between Cunoniaceae and Cephalotaceae by including both within Rosiflorae, although he assigned them to different orders.

The position of the expanded Cunoniaceae within the core rosids has been recognized by analyses based on *rbc*L (Chase et al., 1993; Williams et al., 1994; Conti et al., 1996) and 18S sequence data (Soltis et al., 1997a; Soltis & Soltis, 1997), but its exact phylogenetic placement is unresolved (Fig.

6). The earliest representatives of members of the expanded Cunoniaceae in the fossil record are leaf remains assigned to *Eucryphia* Cav., from Paleocene strata of Australia (Hill, 1991b; Collinson et al., 1993). Fruits similar to those of *Sloanea* L. (Elaeocarpaceae) are known from the Paleocene of North America and Greenland (Manchester, 1999).

Euonymus clade (= celastroids sensu Soltis et al., 1997a, b; included in Oxalidales sensu APG, 1998).

The genus *Euonymus* (Celastraceae) is consistently placed with *Brexia* Noronha ex Thouars, *Lepuropetalon* Elliott, and *Parnassia* L. *Hippocratea* L. and *Siphonodon* Griffith (Celastraceae), *Stackhousia* Sm. (Stackhousiaceae), *Afrostyrax* Perkins & Gilg. (Huaceae), and *Plagiopteron* Griffith (Flacourtiaceae) are apparently linked to the previous genera (Soltis et al., 1998) and together form the *Euonymus* clade. This clade includes nearly 300 species (< 0.2% TESD; Table 1). *Brexia, Lepuropetalon,* and *Parnassia* have been considered to be of broad saxifragalean affinity (e.g., Engler, 1930; Cronquist, 1981). *Parnassia* and *Lepuropetalon* were placed within Saxifragaceae (Cronquist, 1981) or as different families within Droserales (Dahlgren, 1983). *Brexia,* and especially *Euonymus,* have often been placed more distantly, although Takhtajan (1997) recognized a link among the four genera of the *Euonymus* clade by placing all within different orders of Celastranae. *Lepuropetalon* and *Parnassia* were assigned to different monogeneric families within Parnassiales. *Euonymus, Brexia, Lepuropetalon,* and *Parnassia* are included in the core rosids in phylogenetic analyses based on *rbc*L (e.g., Chase et al., 1993; Morgan & Soltis, 1993) and 18S sequence data (Soltis & Soltis, 1997; Soltis et al., 1997a). The representation of the *Euonymus* clade in the fossil record is limited to pollen grains assigned to *Brexia* from Oligocene strata of New Zealand (Muller, 1981).

Linales/Euphorbiaceae/Malpighiaceae (= Malpighiales sensu APG, 1998). A large clade of heterogeneous composition that includes members of Linales, Euphorbiales, Polygalales, Celastrales (Rosidae), Violales, Salicales, Theales (Dilleniidae), and several families and genera of varied affinity (Table 1) is termed here Linales/Euphorbiaceae/Malpighiaceae. The number of species included in this clade is approximately 13,600 (ca. 7.7% TESD; Table 1). The Linales/Euphorbiaceae/Malpighiaceae clade, and its presence within the core rosids, has been documented mostly by analyses based on *rbc*L data (Albert et al., 1992; Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Swensen et al., 1994; Williams et al., 1994; Soltis et al., 1995b) and on combined *rbc*L, *atp*B, and 18S data (Soltis et al., 1998). Analyses based on 18S sequence data recognize an assemblage that approximately corresponds to the above-described clade (Soltis & Soltis, 1997; Soltis et al., 1997a). Taxa that form the Linales/Euphorbiaceae/Malpighiaceae are not considered to be closely related to one another in traditional classification systems, but rather are scattered in the Linales, Euphorbiales, Rosales, Polygalales, and Sapindales (Rosidae), and in Violales and Theales (Dilleniidae; Cronquist, 1981); or in the superorders Malviflorae, Myrtiflorae, Rutiflorae, Violiflorae, and Theiflorae (Dahlgren, 1983), or in the superorders Geranianae, Euphorbianae, and Rosanae (Rosidae), and Violanae and Theanae (Dilleniidae; Takhtajan, 1997).

The Chrysobalanaceae (Chase et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Soltis et al., 1995b, 1998) and Malpighiaceae (Chase et al., 1993; Soltis et al., 1995b, 1998) appear to be monophyletic (Table 2), although in all published analyses only very small taxonomic samples for each family have been included. The Euphorbiaceae (Chase et al., 1993; Soltis et al., 1995b, 1997a) and the order Linales (Chase et al., 1993; Morgan & Soltis, 1993; Swensen et al., 1994; Williams et al., 1994; Soltis et al., 1995b) are paraphyletic, but apparently all their components are included in the Linales/Euphorbiaceae/Malpighiaceae clade. The pattern within the clade is unstable and varies depending on sampling density and on the selection of placeholders for component taxa.

Pollen grains assigned to Euphorbiaceae from Upper Paleocene strata (Muller, 1981), fruits and seeds from the Eocene London Clay Flora (Collinson, 1983), and a fruit similar to that of extant *Hippomane* L. from the Middle Eocene Claiborne Formation (Dilcher & Manchester, 1988) probably constitute the earliest reliable reports for the Linales/Euphorbiaceae/Malpighiaceae in the fossil record. Fossil flowers assigned to *Eoglandulosa warmanensis* Taylor & Crepet, with likely affinities within Malpighiaceae, have been recorded from Middle Eocene strata of the Claiborne Formation, in northwestern Tennessee, U.S.A. (Taylor & Crepet, 1987). Glands on the surface of sepals of this fossil flower have been interpreted as the characteristic elaiophores present in most neotropical members of Malpighiaceae, and together with the presence of clawed petals and the occurrence of two-branched trichomes, support the assignment of these fossil flowers with Malpighiaceae (Taylor & Crepet, 1987).

ASTERID CLADE (= asterids sensu Chase et al., 1993; Asterids sensu APG, 1998)

The asterid clade includes taxa previously assigned to Rosidae, Dilleniidae, and Asteridae (e.g., Cronquist, 1981), distributed in four major and two smaller clades that appear repeatedly in different analyses (Table 1). Two major clades, termed here the cornalean clade and the ericalean clade, are placed at the base of the asterid clade and are dominated respectively by taxa of Rosidae and of Dilleniidae (sensu Cronquist, 1981). These clades correspond to "asterid IV" and "asterid III" of Chase et al. (1993) and have been recognized in phylogenetic analyses of both morphological (Hufford, 1992) and *rbc*L sequence data (e.g., Olmstead et al., 1993, strict consensus of island 2784; Williams et al., 1994; Hibisch-Jetter et al., 1997). In addition, there are two large derived clades, both composed mainly of taxa of Asteridae (sensu Cronquist, 1981), which we term Asteridae s.l., and Lamiidae s.l. (Chase et al., 1993; Olmstead et al., 1993, strict consensus of island 2784; Williams et al., 1994; Hibisch-Jetter et al., 1997; Soltis & Soltis, 1997; Soltis et al., 1997a). A small clade, which includes the genus *Ilex* L. (*Ilex* clade), frequently appears as sister taxon to Asteridae s.l., and together these groups correspond to "asterid III" of Chase et al. (1993). Another small clade, which includes the genus *Garrya* Douglas ex Lindley (*Garrya* clade), is often close to Lamiidae s.l., and together these groups comprise the "asterid IV" of Chase et al. (1993). Asteridae s.l. plus the *Ilex* clade and Lamiidae s.l. plus the *Garrya* clade comprise a large clade that we term the core asterids (Fig. 1).

The general phylogenetic pattern described above within the asterid clade, although apparent in several phylogenetic analyses based mainly on *rbc*L sequence data, is not universally supported. In a few analyses, the cornalean and ericalean clades and Asteridae s.l. have appeared as nonmonophyletic (e.g., Olmstead et al., 1993, strict consensus of island 2784, Soltis & Soltis, 1997; Soltis et al., 1997a) or in "unusual" positions within the asterid clade. For example, in some analyses, the cornalean clade is sister to Lamiidae s.l. plus the *Garrya* clade (Downie & Palmer, 1992), or Lamiidae s.l. are the basalmost branch within the asterid clade (Olmstead et al., 1993, strict consensus of island 102). The asterid clade includes approximately 86,000 species (ca. 49% TESD; Table 1), which represent a substantial proportion of living angiosperm species.

Cornalean clade (= asterid IV sensu Chase et al., 1993; Cornales sensu APG, 1998)

The cornalean clade includes Hydrangeaceae, Loasaceae, Hydrostachydaceae, Nyssaceae (including *Mastixia* Blume), Alangiaceae, and *Cornus* L., *Diplopanax* Hand.-Mazz., and *Curtisia* Aiton (Cornaceae), which together amount only to 524 species (0.3% TESD; Table 1). Nyssaceae, Alangiaceae, and the genera *Cornus*, *Diplopanax*, and *Curtisia* have been assigned to the Cornales in traditional classification systems (Cronquist, 1981; Dahlgren, 1983; Takhtajan, 1997). The Hydrangeaceae are also a member of Cornales in the systems of Dahlgren (1983) and Takhtajan (1997). However, the affinity of Hydrostachydaceae and Loasaceae with the former taxa had not been previously recognized.

The cornalean clade has been recognized as part of the asterid clade in phylogenetic analyses based on morphological (Hufford, 1992), *rbc*L (e.g., Olmstead et al., 1993; Xiang et al., 1993; Cosner et al., 1994), and chloroplast DNA inverted repeat data (Downie & Palmer, 1992). However, a cornalean clade is not recognized in analyses based on 18S sequence data (Soltis & Soltis, 1997; Soltis et al., 1997a). Loasaceae and Hydrangeaceae each appear to be monophyletic (Table 2; Xiang et al., 1993; Soltis et al., 1995a; Hufford, 1997), but genera of Hydrangeaceae are paraphyletic and closely related to *Hydrostachys* Thouars (Hydrostachydaceae) in the analysis based on *rbc*L sequence data by Hempel et al. (1995) and on the combined three-gene analysis of Soltis et al. (1998).

Phylogenetic relationships within the cornalean clade are not fully resolved, although some associations are relatively well supported (Fig. 7). The Loasaceae and Hydrangeaceae (plus Hydrostachydaceae) are apparently most closely related (Hempel et al., 1995; Soltis et al., 1995a). *Diplopanax* appears closely related to Nyssaceae (Chase et al., 1993; Xiang et al., 1993; Hempel et al., 1995; Soltis et al., 1995a), and species of *Cornus*, *Alangium* Lam., and *Curtisia* usually group with one another (Chase et al., 1993; Hempel et al., 1995; Soltis et al., 1995a; but see Olmstead et al., 1993, strict consensus of island 102, for a different pattern). The position of the cornalean group at the base of the asterid clade is supported by analyses based on morphological (Hufford, 1992), *rbc*L (Chase et al., 1993; Morgan & Soltis, 1993; Williams et al., 1994; Hibisch-Jetter et al., 1997), and 18S sequence data (Soltis & Soltis, 1997, as a paraphyletic series). However, the cornalean clade is resolved as sister to Lamiidae s.l. plus the *Garrya* clade, based on evidence from restriction site mapping of the chloroplast DNA inverted repeat (Downie & Palmer, 1992), as sister to Asteridae s.l. according to an analysis of *rbc*L sequence data (Olmstead et al.,

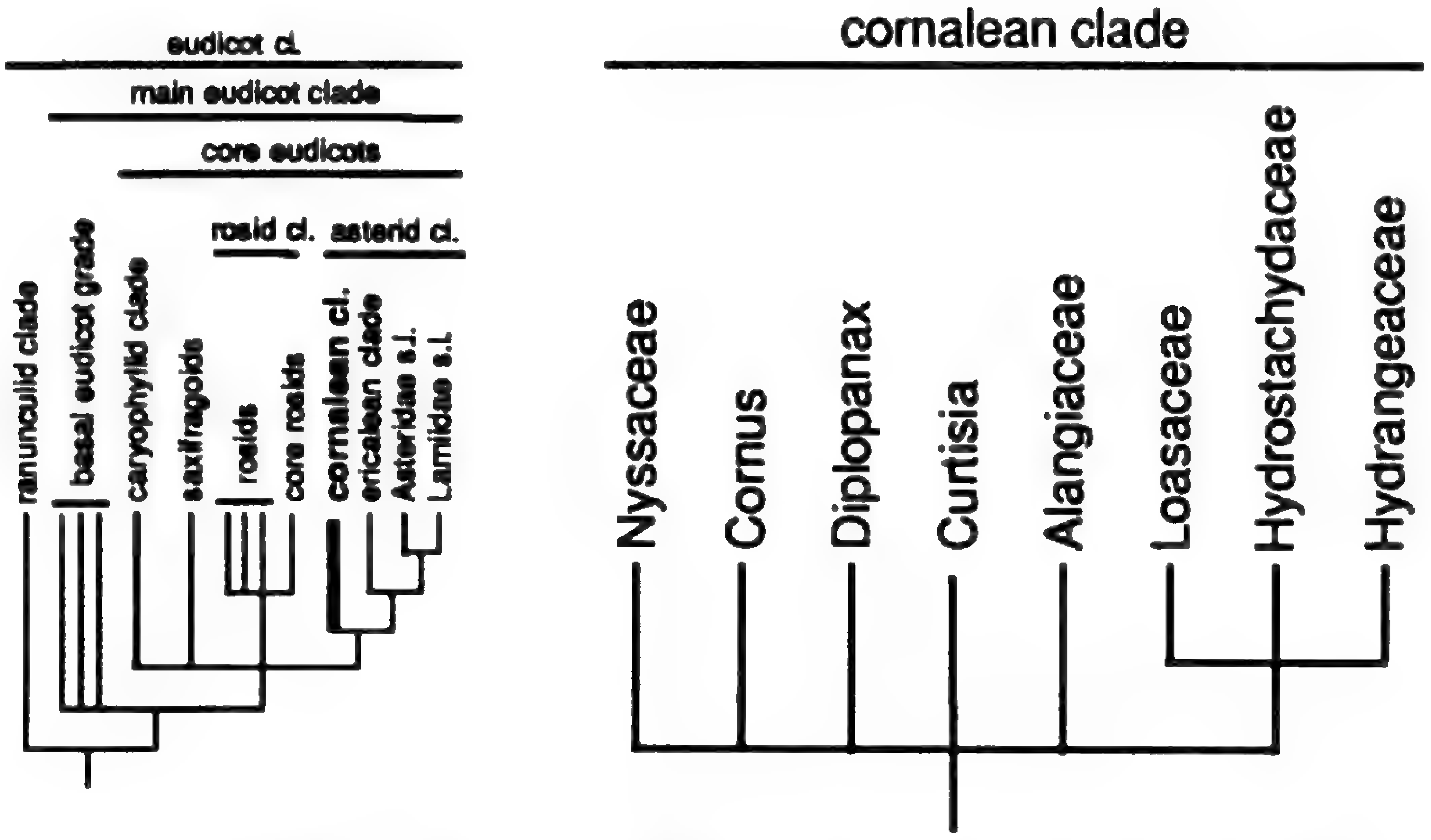

Figure 7. Asterid clade: cornalean clade. The cladogram on the left summarizes the general eudicot phylogenetic pattern. The cornalean clade is indicated in bold. The cornalean clade is apparently the sister to all other taxa in the asterid clade. It includes the Loasacae, Hydrangeaceae, and Hydrostachydaceae, which apparently form a clade, and several genera and families of broad cornalean affinity. The exact phylogenetic pattern among them is not fully resolved.

1993, strict consensus of island 102), and forming a trichotomy with the ericalean clade and the core asterids in the combined three-gene analysis of Soltis et al. (1998).

Fruits of four extinct mastixioid genera from Maastrichtian strata (Knobloch & Mai, 1986) and flowers similar to those of *Hydrangea* L. from Eocene strata (Mai, 1985b; Manchester & Meyer, 1987; Collinson et al., 1993) are some of the earliest appearances in the fossil record for lineages of the cornalean clade. In addition, there are reports of possible endocarps of *Cornus* from Campanian strata (Eyde, 1988). A possible addition to the fossil record of the cornalean clade are recently discovered, three-dimensionally preserved flowers from Coniacian-Santonian strata of western Georgia, U.S.A. (Upatoi Creek locality), which show similarities with Hydrangeaceae (Magallón, 1997). The fossil flowers have a general similarity with those of *Fendlerella* A. A. Heller and *Whipplea* Torrey. However, the presence of dorsifixed stamens and psilate pollen grains is unknown among extant Hydrangeaceae and therefore, the assignment of these flowers to the family is not secure (Magallón et al., in prep.).

Ericalean clade (= asterid III sensu Chase et al., 1993; Ericales sensu APG, 1998)

The ericalean clade is a heterogeneous assemblage of taxa, most of which have been assigned previously to orders or superorders within Dilleniidae (Cronquist, 1981; Takhtajan, 1997). It includes all families of Ericales, Ebenales and Primulales, the Actinidiaceae, Theaceae, Marcgraviaceae, Scytopetalaceae, *Tetramerista* Miq. (Theales), Sarraceniaceae (Nepenthales), Lecythidaceae (Lecythidales), Diapensiaceae (Diapensiales), Polemoniaceae (Solanales), Fouquieriaceae (Violales), and the genera *Impatiens* L. (Balsaminaceae) and *Roridula* Burm. f. ex L. (Byblidaceae). In the classification of Cronquist (1981), taxa included in the ericalean clade belong to five families of Theales, one family of Violales, one family of Nepenthales, and the orders Primulales, Diapensiales, Lecythidales (including only Lecythidaceae), Ebenales, and Ericales. Additionally, one family assigned to Asteridae (i.e., Polemoniaceae), and two genera assigned to orders of Rosidae (i.e., *Impatiens* and *Roridula*) are also included. In the system of Takhtajan (1997), taxa included in the ericalean clade are also scattered within Dilleniidae. In the classification of Dahlgren (1983) the taxa in the clade belong to six different superorders. The number of species in the ericalean clade is approximately 10,390 (ca. 5.9% TESD; Table 1).

The ericalean clade has been recognized in analyses of *rbc*L sequence data (e.g., Olmstead et al., 1992, 1993; Chase et al., 1993; Cosner et al., 1994; Morton et al., 1996), and also in analyses based on chloroplast DNA inverted repeat (Downie & Palmer, 1992) and 18S sequence data (Soltis & Soltis, 1997). However, another analysis of 18S sequence data (Soltis et al., 1997a) resulted in an ericalean grade that appears closely linked to the caryophyllid clade, within an asterid assemblage. The families Epacridaceae (Kron, 1996; Kron & Chase, 1993; Morton et al., 1996), Empetraceae (Anderberg, 1994), Sarraceniaceae (Albert et al., 1992; Chase et al., 1993; Bayer et al., 1996; Morton et

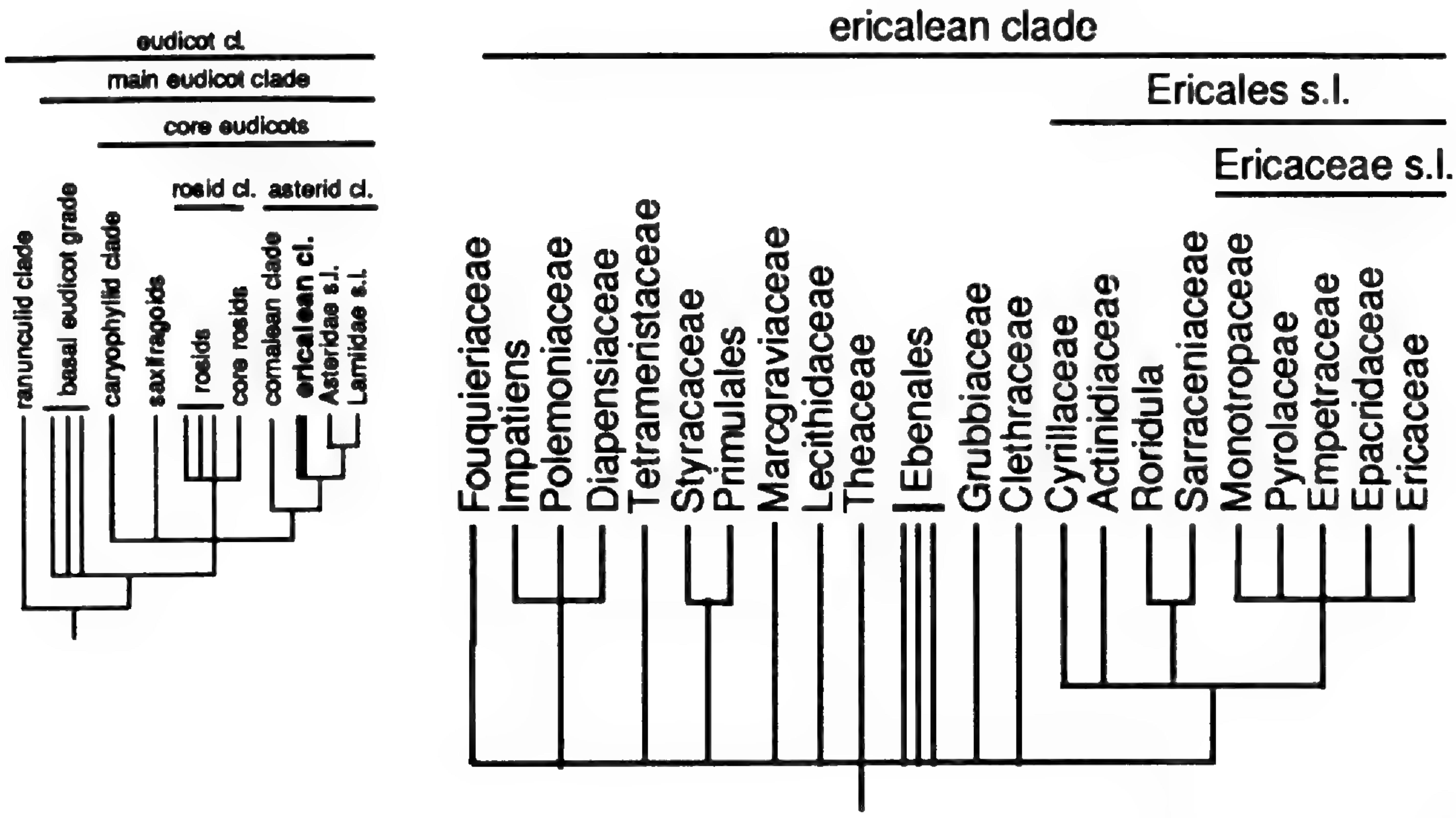

Figure 8. Asterid clade: ericalean clade. The cladogram on the left summarizes the general eudicot phylogenetic pattern. The ericalean clade is indicated in bold. The ericalean clade mostly includes taxa of dilleniid affinity, the phylogenetic relationships among which are unresolved. The Polemoniaceae, Diapensiaceae, and *Impatiens*, and the Primulales and Styraceaeae are apparently more closely related to each other. The Ericales s.l., which include Cyrillaceae, Actinidiaceae, *Roridula* plus Sarraceniaceae, and the Ericaceae s.l., are recurrent in phylogenetic analyses. The Ericaceae s.l. are a presumably monophyletic assemblage that includes Monotropaceae, Pyrolaceae, Empetraceae, Epacridaceae, and Ericaceae. Several taxa in the ericalean clade have been documented as non-monophyletic (e.g., Ebenales, Ericaceae s. str., Lecythidaceae, Styraceaeae; see Table 2).

al., 1996), Cyrillaceae (Morton et al., 1996), Sapotaceae (Chase et al., 1993; Kron & Chase, 1993; Olmstead et al., 1993; Morton et al., 1997), Actinidiaceae (Morton et al., 1996), Fouquieriaceae (Morton et al., 1997), and Polemoniaceae (Johnson et al., 1996; Morton et al., 1996) are presumably monophyletic (Table 2). Other "ericalean" taxa have been found to be non-monophyletic (e.g., Ericales s. str., Ericaceae, Ebenales, Styracaceae, Theaceae, Lecythidaceae), but their component parts appear to be included within the ericalean clade.

Phylogenetic relationships within the ericalean clade are largely unresolved, apparently with few generally supported patterns (Fig. 8). An assemblage that we term the Ericales s.l. includes the Cyrillaceae, Actinidiaceae, Sarraceniaceae, and *Roridula*, and sometimes *Clethra* L., together with a core ericalean clade (Ericaceae s.l.). This core ericalean group includes Ericaceae, Empetraceae, Epacridaceae, Monotropaceae, and Pyrolaceae and is recognized in analyses based mainly on morphological characters (Anderberg, 1992, 1993; Judd & Kron, 1993), as well as those based on *rbc*L sequence data (e.g., Albert et al., 1992; Kron & Chase, 1993; Olmstead et al., 1993; Bayer et al., 1996; Morton et al., 1996, 1997). Sarraceniaceae and *Roridula* are sister taxa in most analyses (e.g., Albert et al., 1992), but in some analyses they are not placed with the core Ericales (Kron, 1996; Morton et al., 1996). *Impatiens* (Balsaminaceae), Polemoniaceae, and Diapensiaceae are usually closely linked (e.g., Chase et al., 1993; Kron & Chase, 1993; Olmstead et al., 1993; Bayer et al., 1996). Primulales, Styracaceae, and sometimes *Clethra*, also frequently appear closely related (e.g., Chase et al., 1993; Bayer et al., 1996; Morton et al., 1996, 1997).

The ericalean clade is sister taxon to the core asterids (i.e., Asteridae s.l. and the *Ilex* clade plus Lamiidae s.l. and the *Garrya* clade) according to results of several broad phylogenetic analyses based on morphology (Hufford, 1992) and on *rbc*L sequence data (Chase et al., 1993; Williams et al., 1994; Hibisch-Jetter et al., 1997), although this placement is not universally supported. A relatively similar pattern has also been detected, in which the ericalean clade is sister to Hydrangeaceae, and together they form the sister taxon to the core asterids (Soltis & Soltis, 1997). Alternatively, the ericalean clade is sister group to a modified core asterid clade that excludes Lamiidae s.l. (Olmstead et al., 1993, strict consensus of island 102). In the results of other analyses, the ericalean clade appears basalmost within the asterid clade (Downie & Palmer, 1992), or as an independent branch within a basally unresolved asterid clade (Olmstead et al., 1993, strict consensus of island 2784), or forming a trichotomy with the cornalean clade and the core asterids (Soltis et al., 1998). A still different pattern resolves the ericalean clade as sister to Asteridae s.l. plus the *Ilex* clade, forming a clade that is sister to Lamiidae s.l. plus the *Garrya* clade (Morgan & Soltis, 1993).

Some of the earliest putative representatives of the ericalean clade are fruits and seeds of extinct genera assigned to Cyrillaceae (Mai & Walther, 1978, 1985; Knobloch & Mai, 1986; Collinson et al., 1993), and fruits and seeds assigned to Ericaceae (Knobloch & Mai, 1986), from Maastrichtian strata. Seeds like those of *Rhododendron* L. are also known from the Paleocene (Collinson & Crane, 1978). Several ericalean families (e.g., Theaceae, Sapotaceae, Ebenaceae) are known from the Eocene (Collinson et al., 1993). Studies of three-dimensionally preserved flowers from Upper Cretaceous strata also document that taxa within or closely related to the Ericaceae s.l. are a common component of fossil floras in the Normapolles province.

Fossil flowers from Santonian-Campanian strata of Sweden, assigned to *Actinocalyx bohrii* Friis, have been considered to belong to the order Ericales and are similar to flowers of extant Diapensiaceae, although there are differences in thecal configuration, pollen characters, and the presence of three free styles in the fossil flowers (Friis, 1985b). Flowers from the Turonian of New Jersey, assigned to *Palaeoenkiananthus sayrevillensis* Nixon & Crepet, are thought to be related to the Ericaceae s.l. (Nixon & Crepet, 1993). The structure of the fossil flower, and the presence of inverted anthers with pseudoterminal dehiscence, strongly suggests affinity within the Ericales, and especially with families of Ericaceae s.l. However, because the combination of features in the fossil flower, as well as characters of its style, are unknown among extant Ericales, it may represent a member of the order with plesiomorphic features (Nixon & Crepet, 1993). Two additional flower types of probable affinity within the Ericaceae s.l. are known from the Turonian of New Jersey (Crepet & Nixon, 1996), and from two Upper Cretaceous sites in Georgia, U.S.A (Coniacian-Santonian and late Santonian; Herendeen et al., 1999). A further fossil flower, *Parasurauia allonensis* Keller, Herendeen & Crane, also known from both Georgia localities, shows strong similarities with the Actinidiaceae (Keller et al., 1996). This fossil is very similar to flowers of extant *Saurauia* Willd., except for the presence of only ten stamens. A cladistic analysis placed this fossil as sister to *Saurauia* plus *Actinidia* Lindley (Keller et al., 1996).

Ilex clade (= Aquifoliales, included in "Euasterids II" sensu APG, 1998)

The recurring association in phylogenetic analyses of *Ilex* (Aquifoliaceae), *Helwingia* Willd. (Cornaceae), and *Phyllonoma* Willd. ex Schultes (Grossulariaceae) is here referred to as the *Ilex* clade. The *Ilex* clade includes 407 species (< 1% TESD; Table 1) and has been recognized in studies based on *rbc*L (e.g., Chase et al., 1993; Olmstead et al., 1993; Cosner et al., 1994) and 18S sequence data (Soltis & Soltis, 1997; Soltis et al., 1997a), although the genera in the clade have not previously been considered to be closely related. The *Ilex* clade frequently appears as the sister taxon to Asteridae s.l. in studies based on *rbc*L sequence data (Fig. 11; Chase et al., 1993; Morgan & Soltis, 1993; Olmstead et al., 1993, strict consensus of island 102; Cosner et al., 1994; Hibisch-Jetter et al., 1997). A similar placement results in the combined three-gene analysis of Soltis et al. (1998), although *Gonocaryum* Miq. (Icacinaceae) plus *Irvingia* Hook. f. (Simaroubaceae) form the immediate sister to the *Ilex* clade. Alternatively, the *Ilex* clade is sister to a group that includes a paraphyletic Asteridae s.l. and Lamiidae s.l. (Olmstead et al., 1993, strict consensus of island 2784). A further alternative position for the Ilex clade, based on 18S data, is as sister to *Aucuba* Thunb., which together form the sister group to Lamiidae s.l. (Soltis & Soltis, 1997; Soltis et al., 1997a). Fruits similar to those of *Ilex* have been reported from Maastrichtian strata (Knobloch & Mai, 1986; Collinson et al., 1993).

Asteridae s.l. (included in "Euasterids II," sensu APG, 1998)

A close phylogenetic link among the Dipsacales, Asterales s.l. (Asteridae), and Apiales (Rosidae) has been documented by phylogenetic analyses based on *rbc*L (Table 1; e.g., Olmstead et al., 1992, 1993; Chase et al., 1993; Cosner et al., 1994; Gustafsson et al., 1996) and 18S sequence data (Soltis & Soltis, 1997; Soltis et al., 1997a). We term this group the Asteridae s.l., which includes more than 29,000 species (ca. 16.6% TESD). Approximately 21,000 of these species belong to the family Asteraceae (Table 1). The Asterales, Dipsacales, and Apiales have sometimes been associated, although somewhat remotely, in traditional classification systems. In the system of Cronquist (1981), Dipsacales and Asterales were included in Asteridae, but Apiales were included in Rosidae. Takhtajan (1997) included Araliales (i.e., Apiales) and Dipsacales in different superorders within Cornidae, while Asterales correspond closely to subclass Asteridae.

The Asterales s.l. (= Asterales sensu APG, 1998) include Asteraceae, Calyceraceae (Calycerales), and the Campanulales (including Campanulaceae, Pentaphragmataceae, Stylidiaceae, Donatiaceae, Brunoniaceae, and Goodeniaceae, but excluding the monogeneric Sphenocleaceae), plus Menyanthaceae (Solanales), Alseuosmiaceae (Rosales), *Argophyllum* Forster & Forster (Grossulariaceae), and *Corokia* Cunn. (Cornaceae; Table 1). A close association between Alseuosmiaceae, *Argophyllum,* and *Corokia* with asterid taxa had not been previously proposed. The close relationship between Asterales and Campanulales has been widely acknowledged in traditional classification systems (Cronquist, 1981; Dahlgren, 1983; Takhtajan, 1997), but the association with other taxa in the Asterales s.l. is not usually recognized. However, in the system of Takhtajan (1997), Asterales and Calycerales were grouped in Asteranae, and the Campanulales, Goodeniaceae, Stylidiaceae, and Menyanthaceae were grouped within Campanulanae. These two superorders constitute subclass Asteridae in Takhtajan's (1997) system. The Asteridae sensu Takhtajan (1997) correspond closely to the Asterales s.l. clade, except for the inclusion of Sphenocleaceae, which Takhtajan (1997) placed within Lamiidae s.l. (Table 2).

The phylogenetic relationship of Asterales s.l. with Dipsacales and Apiales is supported by analyses based on *rbc*L sequence data (e.g., Michaels et al., 1993; Cosner et al., 1994; Gustafsson et al., 1996), and morphological and chemical data (Gustafsson & Bremer, 1995). The genus *Desfontainia* Ruíz & Pavón (Loganiaceae) is apparently closely related to the Dipsacales (Table 1; Struwe et al., 1994; Gustafsson et al., 1996), even though it has been considered to be taxonomically isolated in traditional classification systems (e.g., assigned to a monogeneric family within Gentianales; Dahlgren, 1983). A close relationship with Dipsacales has not been suggested previously.

The Apiales (= Apiales sensu APG, 1998) include the families Apiaceae and Araliaceae, as well as Pittosporaceae (Rosales; Table 1, e.g., Chase et al., 1993; Olmstead et al., 1993; Soltis et al., 1997a), and *Aralidium* Miq., *Melanophylla* Baker, *Toricellia* DC., and *Griselinia* Forster f. of Cornaceae (Table 1, e.g., Plunkett et al., 1996). A close relationship between Apiales and Pittosporaceae was suggested by Dahlgren (1983), who placed both taxa within Araliiflorae. Also included were Tremandraceae and Byblidaceae, which have been found to have a more distant phylogenetic placement (Table 2). Takhtajan (1997) placed Araliales (i.e., Apiales) and Pittosporaceae within superorder Aralianae, but also included *Helwingia* and Byblidaceae. The close relationship of the Apiales with taxa traditionally included in the Asteridae is supported by studies based on *rbc*L (e.g., Olmstead et al., 1992, 1993; Cosner et al., 1994; Plunkett et al., 1996) and 18S sequence data (Soltis & Soltis, 1997; Soltis et al., 1997a). Genera that are also phylogenetically close to the Asterales s.l., Dipsacales, and Apiales are *Berzelia* Brong. (Bruniaceae; Chase et al., 1993; Olmstead et al., 1993; Gustafsson et al., 1996), *Escallonia* Mutis ex L.f. and *Quintinia* A. DC. (Escallonioideae, Grossulariaceae; Olmstead et al., 1993; Cosner et al., 1994; Gustafsson et al., 1996), and *Eremosyne* Endl. (Eremosynoideae, Saxifragaceae; Hibisch-Jetter et al., 1997), but in current analyses relationships among them are not clearly resolved.

The Asteraceae, Campanulaceae, Apiaceae, and Pittosporaceae are all supported as monophyletic taxa (Table 2, e.g., Chase et al., 1993; Cosner et al., 1994; Gustafsson et al., 1996), but the monophyly of Dipsacales (including Caprifoliaceae, Adoxaceae, Valerianaceae, and Dipsacaceae; Donoghue et al., 1992; Plunkett et al., 1996) and Araliaceae (Olmstead et al., 1993; Plunkett et al., 1997) is not firmly established. Within the Asterales s.l., the Asteraceae, Goodeniaceae, Calyceraceae, Menyanthaceae, and *Corokia* appear to be more closely related to each other (Michaels et al., 1993; Olmstead et al., 1993; Cosner et al., 1994; Gustafsson & Bremer, 1995), forming a clade that corresponds to the "asterads" of Lammers (1992). The Campanulaceae and Lobeliaceae (including closely associated taxa, i.e., Cyphiaceae, Cyphiocarpaceae, and Nemacladaceae), as well as Brunoniaceae, Donatiaceae, Stylidiaceae, and Pentaphragmataceae, form a clade that corresponds to the "campanulads" of Lammers (1992; Michaels et al., 1993; Olmstead et al., 1993; Cosner et al., 1994; Gustafsson & Bremer, 1995). Within the Dipsacales, Caprifoliaceae appear to be paraphyletic (Chase et al., 1993; Donoghue et al., 1992; Olmstead et al., 1993; Cosner et al., 1994). In the Apiales clade, the Apiaceae have been documented as a monophyletic group embedded within a paraphyletic Araliaceae (Olmstead et al., 1993; Plunkett et al., 1996), which is consistent with the hypothesis of Judd et al. (1994). Alternatively, Apiaceae plus Araliaceae appear as the sister taxon to *Pittosporum* Banks ex Gaertner (Chase et al., 1993; Cosner et al., 1994), or to a presumably monophyletic Pittosporaceae (Plunkett et al., 1996).

A pattern of relationship in which the Apiales

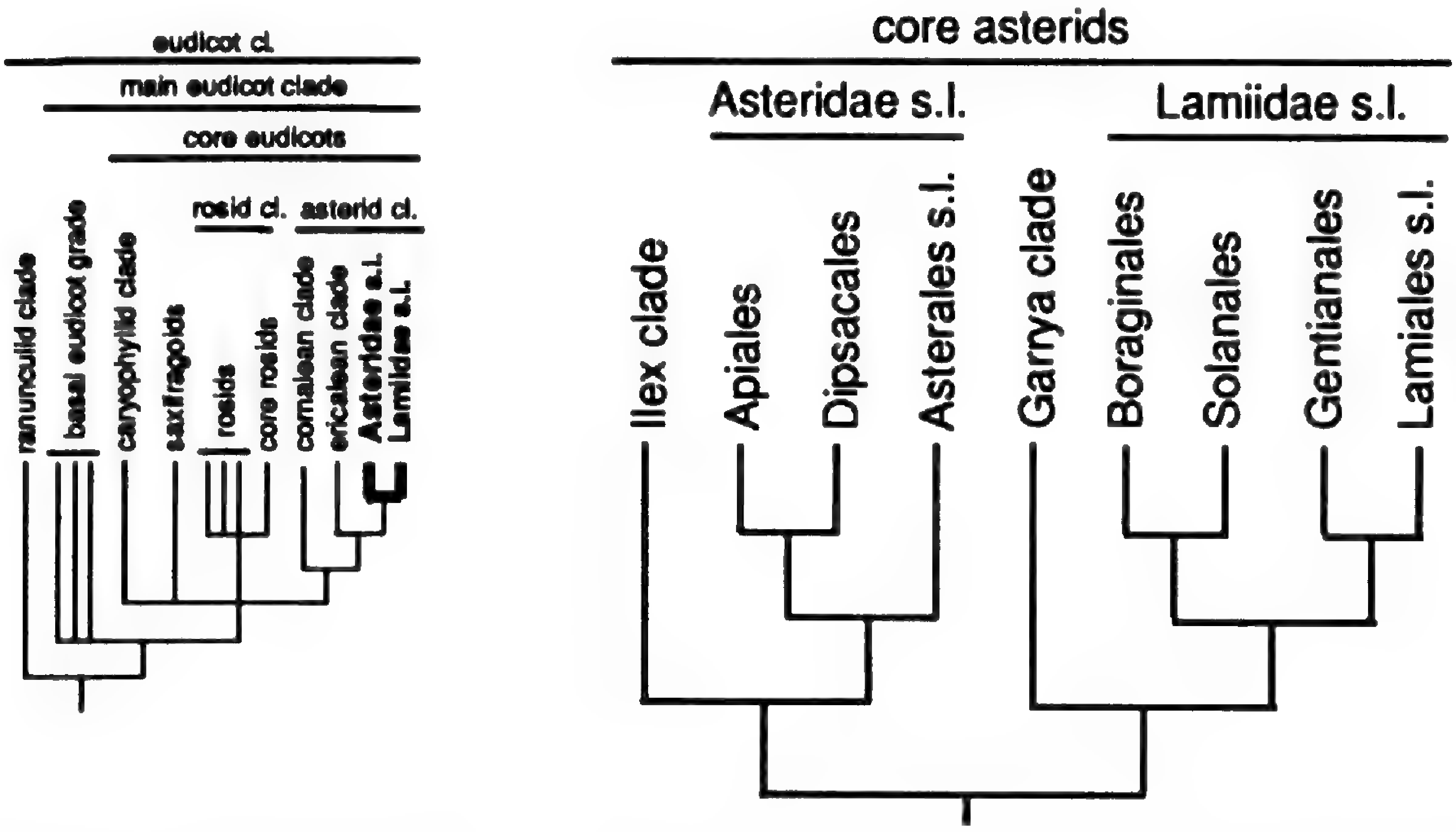

Figure 9. Asterid clade: core asterids. The cladogram on the left summarizes the general eudicot phylogenetic pattern. The core asterid clade is indicated in bold. The core asterid clade has two major components: the Asteridae s.l. and the Lamiidae s.l. Asteridae s.l. include the Apiales and Dipsacales, which apparently form the sister taxon to Asterales s.l. A small *Ilex* clade is the sister taxon to the Asteridae s.l. Lamiidae s.l. include the Boraginales plus Solanales, which together form the sister taxon to the Gentianales and Lamiales s.l. The small *Garrya* clade is the sister taxon to the Lamiidae s.l.

and Dipsacales are sister taxa, and together form the sister group to the Asterales s.l., is relatively constant in results from different phylogenetic analyses (Fig. 9; Olmstead et al., 1992, 1993; Chase et al., 1993; Cosner et al., 1994; Soltis & Soltis, 1997). An alternative pattern, obtained from analysis of morphological and chemical characters, suggests a sister group relationship between Dipsacales and Asterales s.l., with Araliaceae appearing as an independent branch of a basal paraphyletic series (Gustafsson & Bremer, 1995). The Asteridae s.l. and the *Ilex* clade are frequently linked as sister taxa (Fig. 9; e.g., Chase et al., 1993; Olmstead et al., 1993, strict consensus of island 102), and together appear as the sister group to Lamiidae s.l. plus the *Garrya* clade (Chase et al., 1993; Williams et al., 1994; Hibisch-Jetter et al., 1997). This pattern of relationship is supported by *rbc*L sequence data, but other analyses based on *rbc*L, as well as other types of data, suggest alternative relationships. A roughly similar pattern, obtained from analyses of 18S sequence data, places the Asteridae s.l. as sister taxon to Lamiidae s.l. plus an assemblage including members of the *Ilex* and *Garrya* clades (Soltis & Soltis, 1997; Soltis et al., 1997a). The ericalean clade (Morgan & Soltis, 1993) or the cornalean clade (Olmstead et al., 1993, strict consensus of island 102) has been resolved as sister taxon to Asteridae s.l. plus the *Ilex* clade. Asteridae s.l. are paraphyletic according to the results of Downie and Palmer (1992), based on chloroplast DNA inverted repeat, and Olmstead et al. (1993, strict consensus of island 2784), based on *rbc*L sequence data.

Flowers of Dipsacales and Asterales s.l. have fused petals, forming tubular or campanulate corollas. The fused corollas in nearly all studied taxa of Asterales s.l. and Dipsacales begin development as a ring primordium, which initially forms a tube-like structure, and in later stages forms free petal primordia that become the corolla lobes. This developmental origin for fused corollas has been termed "early sympetaly" (Erbar & Leins, 1996) and occurs in nearly all families of Dipsacales studied by Erbar and Leins (1996), except for *Adoxa* L. (i.e., Caprifoliaceae s. str., Dipsacaceae, Morinaceae, Valerianaceae, *Sambucus* L., and *Viburnum* L.), and in all studied families of Asterales s.l. (i.e., Asteraceae, Calyceraceae, Goodeniaceae, Brunoniaceae, Menyanthaceae, Campanulaceae, Lobeliaceae, and Stylidiaceae). Representatives of Apiaceae, Araliaceae, and Pittosporaceae, which have very weakly sympetalous or choripetalous mature corollas, were found to have a brief early sympetalous stage. A ring primordium is initiated, but its development stops at an early stage, and most of the mature corolla results from growth of separate petal primorida (Erbar & Leins, 1996).

Flowers of possible affinity with Araliaceae/Apiaceae are known from the late Santonian of Georgia, U.S.A. (Allon locality; Herendeen et al., 1999). Another possible early representative of the Asteridae s.l. are flowers assigned to *Silvianthemum suecicum,* from Santonian-Campanian strata of Sweden. These flowers have been considered to be of broad saxifragalean affinity and found to be most similar to those of Escalloniaceae, in particular to those of *Quintinia* (Friis, 1990). *Escallonia* and *Quintinia* are now thought to be closely related to the Asterales s.l. (see above). Conclusive documentation of Asterales s.l. from the Upper Cretaceous is not known.

Reproductive organs assigned to genera of Caprifoliaceae have been reported from the Eocene (Chandler, 1964; Lancucka-Srodoniowa, 1979; Dorofeev, 1988; Collinson et al., 1993). Other reliable fossils of Dipsacales, and Asterales s.l., are known only from much younger strata (Collinson et al., 1993). Recently, *Diplodipelta* Manchester & Donoghue was described as a fossil fruit of Caprifoliaceae (Manchester & Donoghue, 1995). Among the Asterales s.l., pollen grains assigned to Goodeniaceae and seeds like those of *Menyanthes* L. are known from the Oligocene (Muller, 1981; Mai, 1985a; Collinson et al., 1993), and seeds of Campanulaceae are known from the Miocene (Lancucka-Srodoniowa, 1979; Collinson et al., 1993). The earliest reports for Asteraceae are pollen grains from the Oligocene, and a reliable fruit record is present in Miocene and younger strata (Collinson et al., 1993).

Garrya clade (= Garryales, included in "Euasterids I" sensu APG, 1998)

A very small assemblage including *Garrya* (Garryaceae), *Aucuba* (Cornaceae), and *Eucommia* Oliver (Eucommiaceae), here referred to as the *Garrya* clade, is nested within the asterid clade according to phylogenetic analyses based on *rbc*L sequence data (Table 1; e.g., Chase et al., 1993; Morgan & Soltis, 1993; Olmstead et al., 1993; Cosner et al., 1994). Additionally, the genus *Icacina* A. Juss. (Icacinaceae) appears as sister to the three previous genera in the combined three-gene analysis of Soltis et al. (1998). However, analyses based on 18S data do not indicate the close relationship among *Garrya, Aucuba,* and *Eucommia,* although the three fall within the asterid clade (Soltis & Soltis, 1997; Soltis et al., 1997a). *Garrya* and *Aucuba* were placed in different families within Cornales by Cronquist (1981) and Dahlgren (1983). Takhtajan (1997) assigned the three genera to different orders within Cornanae. The *Garrya* clade includes only 18 species (<1% TESD; Table 1).

The *Garrya* clade is sister to Lamiidae s.l. in the analysis of Chase et al. (1993). The *Garrya* clade is sister to a clade that includes the *Ilex* clade, the Asteridae s.l., and Lamiidae s.l. (Olmstead et al., 1993, strict consensus of island 2784). Based on 18S evidence, *Aucuba* is sister to the *Ilex* clade, and *Garrya* is closely related to *Pittosporum,* within the Asteridae s.l. (Soltis & Soltis, 1997; Soltis et al., 1997a). Fruits and leaves of *Eucommia* are well known from Eocene and younger strata (Collinson et al., 1993; Call & Dilcher, 1997). Seeds, inflorescences, and leaves similar to those of *Garrya* have been reported from the Miocene (Collinson et al., 1993).

Lamiidae s.l. (included in "Euasterids I" sensu APG, 1998)

The Lamiidae s.l. appear as a distinct monophyletic entity in phylogenetic analyses based on *rbc*L (e.g., Olmstead et al., 1992, 1993; Cosner et al., 1994; Gustafsson et al., 1996), 18S (Soltis & Soltis, 1997; Soltis et al., 1996), and morphological data (Hufford, 1992), and include four major clades, corresponding broadly to Lamiales s.l., Gentianales, Solanales, and Boraginales, all of which are placed in Asteridae in the classification system of Cronquist (1981). Dahlgren (1983) and Takhtajan (1997) recognized the close relationship among these taxa, but assigned them to three different superorders in each of their classification systems. Lamiidae s.l. include a significant percentage of eudicot species: There are about 2775 species in the Boraginales, about 4251 in the Solanales, about 17,146 in the Gentianales, and about 21,467 in Lamiales s.l., which together with 3 species of Sphenocleaceae and Montinioideae, constitute an estimated total of 45,642 species in the Lamiidae s.l. (ca. 26% TESD; Table 1).

The Lamiales s.l. (= Lamiales sensu APG, 1998) include the Scrophulariales (including at least Buddlejaceae, Oleaceae, Scrophulariaceae, Globulariaceae, Myoporaceae, Gesneriaceae, Acanthaceae, Pedaliaceae, Bignoniaceae, and Lentibulariaceae), the families Verbenaceae and Lamiaceae (Lamiales), Callitrichaceae (Callitrichales), and the genera *Retzia* Thunb., *Plocosperma* Benth., and *Polypremnum* L. of Loganiaceae (Gentianales), as well as *Byblis* Salisb. (Byblidaceae) and *Vahlia* Thunb. (Saxifragaceae; Table 1). A close relationship among the Scrophulariales, Lamiaceae, Verbenaceae, and Callitrichaceae is usually recognized in traditional systems of classification, by their association within Lamianae (Takhtajan, 1997) or Lamiiflorae (Dahlgren, 1983). The family Oleaceae, while included in Scrophulariales by Cronquist (1981), was placed within Gentianiflorae by Dahlgren (1983), and more distantly in an order of its own, within Loasanae (Lamiidae), by Takhtajan

(1997). *Retzia* was placed within Scrophulariales by Dahlgren (1983) and Takhtajan (1997). A close relationship between Scrophulariales, Lamiaceae, Verbenaceae, and Callitrichaceae with *Byblis* and *Vahlia* had not been previously suggested.

Phylogenetic relationships within Lamiales s.l. are unresolved. Combined analysis of *rbc*L and *ndh*F data (Olmstead & Reeves, 1995; Reeves & Olmstead, 1998) separates the families of Scrophulariales into two distinct clades, which also include taxa of other orders. One of these clades includes some members of Scrophulariaceae and *Plantago* L. (Plantaginaceae; Plantaginales), *Hippuris* L. (Hippuridaceae; Callitrichales), and *Callitriche* L. (Callitrichaceae; Callitrichales). The other clade includes additional members of Scrophulariaceae, and also two genera of Buddlejaceae, and *Selago* L. (Globulariaceae). Representatives of Lamiaceae and Verbenaceae appear as more closely related to one another than to any other taxa according to results of *rbc*L analyses, supporting the monophyly of Lamiales s. str. (Olmstead et al., 1992; Chase et al., 1993; Cosner et al., 1994). However, Lamiaceae (monophyletic) and Verbenaceae (single representative) are separate from each other according to the *rbc*L analysis of Olmstead et al. (1993). According to the results of combined analysis of *rbc*L and *ndh*F sequence data (Olmstead & Reeves, 1995), the monophyly of both families is supported, but they are separated from one another, with genera of Scrophulariaceae, Pedaliaceae, and Bignoniaceae interspersed among them. The Gesneriaceae are supported as monophyletic (e.g., Smith et al., 1997), as well as the Oleaceae, which consistently appear as the basalmost branch of the Lamiales s.l. (Olmstead et al., 1992, 1993; Cosner et al., 1994; Olmstead & Reeves, 1995; Wagstaff & Olmstead, 1997).

The Gentianales (= Gentianales sensu APG, 1998), including Gentianaceae, Apocynaceae, Asclepiadaceae, Loganiaceae p.p. (Gentianales), and Rubiaceae (Rubiales), are resolved as closely related in phylogenetic analyses based on *rbc*L data (Olmstead et al., 1992, 1993; Chase et al., 1993; Cosner et al., 1994), as well as on morphological evidence (Struwe et al., 1994). The phylogenetic association among these taxa corresponds closely to the superorder Gentiananae of Takhtajan (1997), and to a lesser extent, to the order Gentianales of Dahlgren (1983), which includes some taxa that are placed elsewhere in molecular studies (e.g., *Desfontainia*). The Apocynaceae and Asclepiadaceae are both monophyletic and are sister taxa in large-scale analyses based on *rbc*L data (Chase et al., 1993; Olmstead et al., 1993; Cosner et al., 1994). However, broader sampling of Apocynaceae results in a paraphyletic assemblage that includes a monophyletic Asclepiadaceae (Struwe et al., 1994; Sennblad & Bremer, 1996), in conformity with the ideas of Judd et al. (1994). Rubiaceae are supported as monophyletic (Bremer & Struwe, 1992; Olmstead et al., 1993; Struwe et al., 1994), while the Loganiaceae are recognized as paraphyletic, with most of their component genera included in this clade. However, *Plocosperma* and *Polypremnum* are included in Lamiales s.l. (Olmstead et al., 1993; Cosner et al., 1994; Struwe et al., 1994), and *Desfontainia* is closely related to the Dipsacales, within the Asteridae s.l. (Struwe et al., 1994; Gustafsson et al., 1996).

The Solanaceae s.l. and Convolvulaceae are resolved as monophyletic sister taxa according to analyses of *rbc*L data (Chase et al., 1993; Olmstead et al., 1993; Cosner et al., 1994), and together with Duckeodendraceae (Soltis et al., 1998) form a clade that corresponds closely to the Solanales of Dahlgren (1983; Table 1; included in Solanales sensu APG, 1998). The phylogenetic placement of other families included in this taxon has not been fully assessed. The genera *Montinia* Thunb. (Montinioideae, Grossulariaceae; Chase et al., 1993; Olmstead et al., 1993; Cosner et al., 1994) and *Sphenoclea* Gaertner (Sphenocleaceae, Campanulales; Cosner et al., 1994) are resolved as closely related to the Solanales, either with *Montinia* as the sister taxon to Solanales, or forming a clade that includes *Montinia, Hydrolea* L. (Hydrophyllaceae), and *Sphenoclea,* which is the sister group to Solanales.

The Boraginales (included in Solanales sensu APG, 1998) comprise the Boraginaceae and Hydrophyllaceae, which are consistently linked in phylogenetic analyses based on *rbc*L sequence data (e.g., Olmstead et al., 1992, 1993; Chase et al., 1993; Cosner et al., 1994). This circumscription corresponds closely to the Boraginales of Dahlgren (1983) and Takhtajan (1997). However, in both cases the phylogenetic placement of other families traditionally included in the order has not been sufficiently addressed. The Hydrophyllaceae are apparently monophyletic and are nested among genera of a paraphyletic Boraginaceae (Table 1; Chase et al., 1993; Olmstead et al., 1993; Cosner et al., 1994).

A relatively well supported pattern of relationships among the four major subclades within the Lamiidae s.l. is obtained in analyses based on *rbc*L sequence data. Results indicate a sister group relationship between Lamiales s.l. and Gentianales, and between Solanales and Boraginales. In turn, these two clades are also resolved as sister taxa

(Fig. 9; Chase et al., 1993; Olmstead et al., 1993; Cosner et al., 1994). The Solanales-Boraginales clade corresponds closely to superorder Solaniflorae (Dahlgren, 1983), and approximately to superorder Solananae (Takhtajan, 1997). Analyses based on *rbc*L sequence data of Morgan and Soltis (1993) and Hibisch-Jetter et al., (1997) also suggest a phylogenetic pattern in which Solanales and Boraginales are sister taxa and together form the sister taxon to Lamiales s.l., while Gentianales are resolved as the sister group to all other Lamiidae s.l. A different pattern, also based on the results of analysis of *rbc*L sequence data, but with more limited taxonomic sampling, suggests a sister group relationship that results in a Lamiales s.l.-Gentianales clade. These two taxa form the sister taxon to Boraginales, while Solanales are the sister group to all other taxa within Lamiidae s.l. (Gustafsson et al., 1996). Results of analyses based on 18S sequence data suggest that Boraginales and Gentianales are closely related to one another, but whether they are monophyletic or paraphyletic is uncertain. The Solanales are then placed as the sister taxon to the Boraginales plus Gentianales, and various taxa of Lamiales s.l. form a paraphyletic series at the base of Lamiidae s.l. (Soltis & Soltis, 1997; Soltis et al., 1997a).

The Lamiidae s.l. usually occupy a terminal position within the asterid clade, and, according to most phylogenetic analyses, are closely related to the *Garrya* clade (Fig. 9). In studies based on *rbc*L sequence data, Lamiidae s.l. and the *Garrya* clade form the sister group to the Asteridae s.l. plus the *Ilex* clade (Chase et al., 1993; Morgan & Soltis, 1993; Hibisch-Jetter et al., 1997). Results also based on *rbc*L data, but with a different taxonomic sample, suggest that the Lamiidae s.l. are sister to the Asterales (Olmstead et al., 1993, strict consensus of island 2784), or, together with the *Garrya* clade (represented only by *Aucuba*), form an independent lineage within the asterid clade (Olmstead et al., 1993, strict consensus of island 102). Analyses of chloroplast DNA inverted repeat data suggest that Lamiidae s.l. plus the *Garrya* clade are sister to the cornalean clade, in a terminal position within the asterid clade (Downie & Palmer, 1992). Results based on 18S sequence data also support the derived position of Lamiidae s.l., which are resolved as the sister taxon to a small group containing the *Ilex* clade and members of a paraphyletic *Garrya* clade (Soltis & Soltis, 1997; Soltis et al., 1997a).

The flowers of Lamiidae s.l. are characterized by having sympetalous corollas that are sometimes modified and associated with other floral cycles, often forming extremely elaborated organ complexes (e.g., Asclepiadaceae; Endress, 1990, 1994). Ontogenetic initiation of the sympetalous corollas begins with the development of independent petal primordia, which later become connected by the extension of their basal areas, or by the growth of interprimoridal bridges (Erbar & Leins, 1996). This "late sympetaly" has been found to occur exclusively in members of the Lamiidae s.l. (e.g., Boraginaceae, Solanaceae, Gentianaceae, Apocynaceae, Scrophulariaceae, and Bignoniaceae). However, some members of Lamiidae s.l. (i.e., Oleaceae and Rubiaceae) develop fused corollas through "early sympetaly," and the Asclepiadaceae and some Gentianaceae exhibit transitions between early and late sympetaly (Erbar & Leins, 1996).

Fossil reproductive remains assigned to the families Boraginaceae (Chandler, 1964; Collinson et al., 1993), Solanaceae (Collinson et al., 1993), Rubiaceae (Vaudois-Mieja, 1976; Friis, 1985a; Mai & Walther, 1985; Collinson et al., 1993), Apocynaceae-Asclepiadaceae (Chandler, 1964; Collinson et al., 1993), Scrophulariaceae (Mai & Walther, 1985; Collinson et al., 1993), and Oleaceae (Chandler, 1964; Collinson et al., 1993; Call & Dilcher, 1992) have been reported from Eocene strata and comprise the earliest appearances in the fossil record of Lamiidae s.l. The Lamiaceae (Lancucka-Srodoniowa, 1979; Mai, 1985a; Collinson et al., 1993), Callitrichaceae (Mai, 1985a; Collinson et al., 1993), and Bignoniaceae (Wolfe & Schorn, 1989; Collinson et al., 1993) have been reported from the Oligocene, while Loganiaceae (Mai, 1968; Collinson et al., 1993) and Pedaliaceae (Mai, 1985a; Collinson et al., 1993) are known from the Miocene.

TAXA OF UNCERTAIN PLACEMENT WITHIN THE CORE EUDICOTS

Dilleniaceae and Vitis-Leeaceae

A close association between Dilleniaceae and *Vitis* is found in several analyses (e.g., Chase et al., 1993; Morgan & Soltis, 1993; Williams et al., 1994), and together they form the sister group to Santalales (Williams et al., 1994), to the asterid clade (Chase et al., 1993), or to the caryophyllid clade (Morgan & Soltis, 1993). In the results of Rice et al. (1997), *Dillenia* L. plus *Vitis* form one of the lineages within an unresolved core eudicot clade. Dilleniaceae have been also resolved as sister to the caryophyllid clade (e.g., Albert et al., 1992; Hoot et al., 1999; Soltis et al., 1998). Although its phylogenetic placement is not secure, the family Dilleniaceae appears to be monophyletic (Soltis et al., 1998; Hoot et al., 1999). Dilleniaceae have been viewed as relatively isolated (e.g., Cronquist, 1981; Dahlgren, 1983; Takhtajan, 1997). The earliest records of Dilleniaceae are seeds similar to those of *Tetracera* L. and *Hibbertia* Andrews, from the Lower Eocene (Chandler, 1964; Collinson et al., 1993).

Leea Royen ex L., the single genus in Leeaceae (Rhamnales), is the sister to *Vitis* in the combined three-gene analysis of Soltis et al. (1998), and together they are the sister to the rosid clade. The taxonomic placement of Vitaceae has been controversial. Cronquist (1981) placed the family in the Rhamnales, and Takhtajan (1997) placed it within the superorder Vitanae, both within Rosidae. Dahlgren (1983) placed Vitaceae in the Celastrales, within Santaliiflorae. The family Vitaceae is known in the fossil record from characteristic seeds from the Upper Paleocene and younger strata (e.g., Mai & Walther, 1978, 1985; Collinson et al., 1993).

Santalales

The Santalales (= santaloids sensu Soltis et al., 1997a; Santalales sensu APG, 1998) are consistently documented as monophyletic (Table 2; Nickrent & Franchina, 1990; Chase et al., 1993; Swensen et al., 1994; Williams et al., 1994; Nickrent & Soltis, 1995; Soltis et al., 1997a, 1998), but their phylogenetic position is uncertain. According to results of two analyses based on *rbc*L sequence data, the Santalales appear closely related to the caryophyllid clade (Chase et al., 1993; Williams et al., 1994). However, phylogenetic analyses of *rbc*L data by Nickrent and Soltis (1995, fig. 5) indicate that Santalales are close to some of the major monophyletic groups usually included in the asterid clade. Phylogenetic analysis based on 18S sequence data in the same study indicates a relationship of Santalales with fragments of a paraphyletic rosid clade, in a deeply unresolved strict consensus tree (Nickrent & Soltis, 1995, fig. 7). According to analysis of 18S sequence data (Soltis et al., 1997a), the Santalales are related to Polygalaceae, *Pisum* L. (Papilionoideae, Fabaceae), and *Gunnera,* which together form an assemblage that is the sister taxon to a modified rosid clade. The Santalales constitute an isolated branch within a basally unresolved core eudicot clade in the combined three-gene analysis of Soltis et al. (1998).

The Santalales are a distinctive group that includes approximately 2190 species (ca. 1.25% TESD; Table 1) most of which are hemiparasitic to fully parasitic. Traditionally, the group has been interpreted as isolated within Rosidae (Cronquist, 1981; Takhtajan, 1997), or as an independent superorder within the dicotyledons (Dahlgren, 1983). Presumed fruits of Olacaceae from the Lower Eocene (Chandler, 1964; Collinson et al., 1993) and seeds similar to *Santalum* L. from the Middle Eocene (Mai, 1976; Collinson et al., 1993) represent the earliest appearances in the macrofossil record for Santalales. However, it has been suggested that pollen grains of the *Aquillapollenites*-complex were produced by members of Santalales, based on their resemblance to some extant pollen grains of Loranthaceae and Santalaceae (Muller, 1984; Jarzen, 1977). The *Aquillapollenites*-complex, which includes pollen grains with distinctive equatorial projections, was abundant in high northern latitudes (the *Aquillapollenites* province) during the late Cretaceous. Flowers that produced the *Aquillapollenites*-type of pollen grains are not known, and thus the systematic affinity of these pollen grains is not firmly established.

Gunnera and Myrothamnus

When *Gunnera* (Gunneraceae) and *Myrothamnus* (Myrothamnaceae) are included simultaneously in phylogenetic analyses, they appear as sister taxa, and usually one or both appear as sister taxon to all other core eudicots (Chase et al., 1993; Drinnan et al., 1994; Hoot et al., 1999). Different results were obtained by Williams et al. (1994), in which *Gunnera* is sister taxon to *Trochodendron* plus the core eudicots, and by Soltis et al. (1997a), in which *Gunnera* has a slightly more derived position and is included in the basalmost group within the "Rosidae" (Soltis et al., 1997a, fig. 4C). The placement of *Gunnera* and *Myrothamnus* within the core eudicot clade is supported by a 100% bootstrap value in a combined analysis of *rbc*L, *atp*B, and 18S data for basal eudicots and basal core eudicots (Hoot et al., 1999). Both genera constitute one of several independent lineages within a basally unresolved core eudicot clade in the combined three-gene analysis of Soltis et al. (1998).

A relationship between the monogeneric Gunneraceae and Myrothamnaceae has not been proposed previously. Gunneraceae have been usually considered to be of broad rosid affinity, and included in Haloragales (Cronquist, 1981), or placed in an order of their own within Rosiflorae (Dahlgren, 1983) or Saxifraganae (Takhtajan, 1997). Myrothamnaceae were related to Hamamelidales or Hamamelididae by Cronquist (1981), Takhtajan (1997), and Dahlgren (1983). These genera occupy widely dissimilar habitats and are very different in vegetative and floral form.

Aextoxicon Ruíz & Pavón and Berberidopsis Hook. f.

The genera *Aextoxicon* (Aextoxicaceae) and *Berberidopsis* (Flacourtiaceae) constitute one of the independent lineages within an unresolved core eudicot clade in the combined three-gene analysis of Soltis et al. (1998). A relationship between these genera has never been suggested in classification systems, and both have been considered of uncertain affinities. The monogeneric Aextoxicaceae were assigned to Celastrales by Cronquist (1981), or to Euphorbiales by Dahlgren (1983) and Takhtajan (1997). *Berberidopsis* was included in Flacourtiaceae by Cronquist (1981) or assigned to a monogeneric family by Takhtajan (1997), both in Violales. Neither genera has a known fossil record.

Discussion

The patterns of eudicot phylogenetic relationships presented here provide an overview of recent hypotheses based on analyses at different taxonomic levels, utilizing a variety of taxonomic samples. In many cases, the results are not definitive, but they provide a useful working hypothesis of higher-level patterns of relationships and a framework for further research. A comparison of the results in our synthesis with the subclasses and orders recognized by Cronquist (1981) is presented in Table 3. Most members of Magnoliidae do not belong to the eudicot clade, but two orders of this subclass form the main part of the ranunculid clade, and one genus (i.e., *Nelumbo*) belongs to the basal eudicot grade. Hamamelididae are polyphyletic, but its members are distributed mostly in the basal eudicot grade, in the saxifragoid clade, and in the core rosid clade. Caryophyllidae remain as a coherent unit, with its orders included in the caryophyllid clade. Dilleniidae are confined to the core eudicot clade, but are widely scattered within this group. Significant portions of the subclass are included in the expanded Malvales, the expanded Capparales, the core rosids, and the ericalean clade. As circumscribed by Cronquist (1981), the Rosidae are also polyphyletic and are scattered from the basal eudicot grade to all levels within the core eudicots. However, a significant component of the subclass is part of the core rosid clade. Asteridae are almost completely restricted to the asterid clade and comprise the major part of Asteridae s.l. and Lamiidae s.l. (Table 3).

PROBLEMATIC AREAS FOR FUTURE RESEARCH

Placement of eudicots among other angiosperm lineages. The position of the eudicot clade within angiosperms and the identity of its sister taxon are two major issues for which there are currently no unambiguous answers. In studies based on different types of evidence and with different taxonomic sampling, nearly all magnoliid lineages have been resolved as the possible sister taxon to the eudicots. Furthermore, because eudicots appear to have diverged very early in angiosperm evolutionary history, determining the phylogenetic position of the group with respect to taxa at the magnoliid grade is intimately related to the difficult question of "rooting" the angiosperm tree as a whole (Crane et al., 1995).

Future strategies for clarifying the phylogenetic position of the eudicots might usefully attempt to separate the question of the identity of the eudicot sister group from the issue of the rooting of the angiosperms, by exploring the different phylogenetic patterns that result from using different subsets of magnoliid and monocot lineages as outgroups in analyses that include dense sampling of other magnoliids plus an adequate selection of eudicots. The ideal analysis would combine data from slow-evolving and fast-evolving genes, as well as from a careful assessment of morphological and other traditional sources of information. Efforts should also be directed toward finding structural changes in either the nuclear or chloroplast genomes that help to delimit major groups.

Basal eudicot grade. The exact pattern of relationships among basal eudicot lineages, including the placement of a presumably monophyletic Sabiaceae, is not well resolved, and this precludes a clear understanding of the origin and evolution of the derived vegetative and reproductive syndromes that characterize core eudicots (Magallón, in prep.). Given the relatively small number of extant species in the lineages of the basal eudicot grade, it will be important to obtain a complete, or nearly complete, representation of these lineages in phylogenetic analyses that combine different morphological and molecular data sets. In addition, several lineages of the basal eudicot grade are well represented in the fossil record and can be compared in detail with extant taxa. Inclusion of such fossils in morphology-based phylogenetic analyses can provide evidence of within-lineage changes that may otherwise obscure relationships based on morphological data.

Core eudicots. Most phylogenetic analyses that include a broad taxonomic representation of core eudicot taxa recognize three major clades of dominantly caryophyllid, rosid, and asterid composition, but the pattern of relationships among them is not

Table 3. Placement of orders of dicotyledons (Magnoliopsida) of Cronquist (1981) within the eudicot clade.

Subclass/Order	Phylogenetic placement
MAGNOLIIDAE	
1. Magnoliales	not eudicot
2. Laurales	not eudicot
3. Piperales	not eudicot
4. Aristolochiales	not eudicot
5. Illiciales	not eudicot
6. Nymphaeales	not eudicot, basal eudicot grade
7. Ranunculales	ranunculids
8. Papaverales	ranunculids
HAMAMELIDIDAE	
1. Trochodendrales	basal eudicot grade
2. Hamamelidales	ranunculids, basal eudicot grade, saxifragoids, uncertain in core eudicots
3. Daphniphyllales	saxifragoids
4. Didymelales	basal eudicot grade
5. Eucommiales	core asterids
6. Urticales	core rosids
7. Leitneriales	Sapindales
8. Juglandales	core rosids
9. Myricales	core rosids
10. Fagales	core rosids
11. Casuarinales	core rosids
CARYOPHYLLIDAE	
1. Caryophyllales	caryophyllids
2. Polygonales	caryophyllids
3. Plumbaginales	caryophyllids
DILLENIIDAE	
1. Dilleniales	saxifragoids, uncertain in core eudicots
2. Theales	expanded Malvales, core rosids, ericaleans
3. Malvales	expanded Malvales, core rosids
4. Lecythidales	ericaleans
5. Nepenthales	caryophyllids, ericaleans
6. Violales	caryophyllids, expanded Malvales, core rosids, cornaleans, ericaleans, uncertain in core eudicots
7. Salicales	core rosids
8. Capparales	expanded Capparales
9. Batales	expanded Capparales
10. Ericales	ericaleans
11. Diapensiales	ericaleans
12. Ebenales	ericaleans
13. Primulales	ericaleans
ROSIDAE	
1. Rosales	caryophyllids, saxifragoids, *Francoa* clade, expanded Malvales, core rosids, cornaleans, ericaleans, Asteridae s.l., Lamiidae s.l., uncertain in core eudicots
2. Fabales	core rosids
3. Proteales	basal eudicot grade, core rosids
4. Podostemales	saxifragoids, core rosids
5. Haloragales	saxifragoids, uncertain in core eudicots
6. Myrtales	Myrtales, expanded Malvales
7. Rhizophorales	(?) core rosids
8. Cornales	cornaleans, core asterids, Asteridae s.l.
9. Santalales	uncertain in core eudicots
10. Rafflesiales	(?)
11. Celastrales	expanded Capparales, core rosids, core asterids, uncertain in core eudicots

Table 3. Continued.

Subclass/Order	Phylogenetic placement
12. Euphorbiaceae	basal eudicot grade, caryophyllids, core rosids
13. Rhamnales	core rosids, uncertain in core eudicots
14. Linales	Myrtales, core rosids
15. Polygalales	core rosids
16. Sapindales	*Francoa* clade, expanded Capparales, Sapindales, core rosids
17. Geraniales	Geraniaceae, expanded Capparales, core rosids, ericaleans
18. Apiales	Asteridae s.l.
ASTERIDAE	
1. Gentianales	Asteridae s.l., Lamiidae s.l.
2. Solanales	Lamiidae s.l.
3. Lamiales	Lamiidae s.l.
4. Callitrichales	cornaleans, Lamiidae s.l.
5. Plantaginales	Lamiidae s.l.
6. Scrophulariales	Lamiidae s.l.
7. Campanulales	Asteridae s.l., Lamiidae s.l.
8. Rubiales	Lamiidae s.l.
9. Dipsacales	Asteridae s.l.
10. Calycerales	Asteridae s.l.
11. Asterales	Asteridae s.l.

clearly resolved. Phylogenetic analyses based on different samples of *rbc*L sequence data have resulted in all possible combinations of relationships among these three clades (Chase et al., 1993; Morgan & Soltis, 1993; Williams et al., 1994), or are unresolved (Albert et al., 1992; Olmstead et al., 1992; Rice et al., 1997). An additional issue is the placement of the saxifragoids, especially because they are apparently close to the rosid clade (e.g., Chase et al., 1993; Soltis et al., 1997a). Also problematic are the relationships of the Santalales, Dilleniaceae, *Vitis*-Leeaceae, and other apparently isolated genera. Resolution of the unstable phylogenetic patterns among major core eudicot clades, which in part reflect sensitivity to different taxonomic sampling strategies, different sources of evidence, and different analytical approaches, will be critical to understanding the initial patterns of phylogenetic and morphological divergence in the core eudicot clade.

Rosid clade. The interrelationships of the major groups within the rosid clade are uncertain—even in studies based on the same type of evidence (cf. results based on *rbc*L, e.g., Chase et al., 1993; Fernando et al., 1993; Rodman et al., 1993; Conti et al., 1996). One significant issue is whether the rosid clade is formed by two major groups, one including the core rosids and another including all other major rosid clades, or if the non-core rosid lineages form a paraphyletic series basal to the core rosids. Phylogenetic relationships of Capparales/Sapindales/Malvales, and of Myrtales with respect to other rosid clades have not yet been sufficiently addressed with molecular evidence other than *rbc*L. However, strong support for the association of the expanded Capparales, expanded Malvales, and Sapindales in a clade is provided by studies based on *rbc*L (Gadek et al., 1992; Chase et al., 1993; Fernando et al., 1993; Price & Palmer, 1993; Rodman et al., 1993, 1994; Swensen et al., 1994; Williams et al., 1994; Conti et al., 1996), and more recently by combined molecular evidence (Rodman et al., 1998; Soltis et al., 1998).

Core rosids. Several analyses have addressed phylogenetic relationships within particular core rosid lineages, (e.g., Morgan et al., 1994, for Rosaceae; Manos & Steele, 1997, for "higher" hamamelids; Doyle, 1995, and Doyle et al., 1997, for Fabaceae), but relatively few have focused on the pattern of relationships among these groups. Because of the enormous species numbers involved, and their exceptional structural and ecological diversity, detailed resolution of phylogenetic patterns within the core rosid clade is difficult, but extremely important. For example, all angiosperm taxa that have symbiotic associations with nitrogen-fixing bacteria in root nodules are included within the core rosid clade, but they occur mixed with several non-nitrogen-fixing taxa (e.g., Soltis et al., 1995b). More detailed understanding of the origin (and potential loss) of nitrogen-fixing ability will require more secure and more detailed resolution of phylogenetic relationships among these diverse lineages.

Also in need of more detailed attention is the relationship of the Fabaceae to other core rosids (Herendeen & Bruneau, in progress). Analyses based on *rbc*L sequence data suggest a close relationship among Fabaceae s.l., Polygalaceae, Surianaceae, and the genus *Quillaja* (Albert et al., 1992; Chase et al., 1993; Fernando et al., 1993; Morgan & Soltis, 1993; Morgan et al., 1994; Swensen et al., 1994; Williams et al., 1994; Soltis et al., 1995b). However, the exact pattern of relationships is poorly resolved. Current data suggest that the sister group to Fabaceae is the Polygalaceae, but other potentially relevant groups have not yet been investigated adequately. The Fabaceae themselves have so far been represented in large-scale analyses only by an insufficient sample of their overall diversity.

The assemblage that we term Linales/Euphorbiaceae/Malpighiaceae has been recognized as a clade that includes taxa considered to be derived within the subclass Rosidae, together with assorted genera of Violales, Theales, and other groups. Relationships within this clade are extremely problematic, and clear patterns are not evident. Most higher-level phylogenetic analyses have included only a small number of relevant taxa, and there have been few specific attempts to resolve relationships among the lineages in the group. The fact that analyses based on *rbc*L and on 18S data detect equivalent clades within the core rosids suggests that improved sampling, perhaps together with other genes and morphological data, will provide improved resolution of phylogenetic patterns among them.

Ericalean clade. The ericalean clade is a distinctive assemblage that mostly includes dilleniid taxa and is recognized in analyses based on *rbc*L (e.g., Olmstead et al., 1992, 1993; Chase et al., 1993; Cosner et al., 1994; Gustafsson et al., 1996; Morton et al., 1996) and 18S (Soltis & Soltis, 1997) data. While there is a recurrent close association among the taxa included, phylogenetic relationships among them are unresolved. The recognition of Ericaceae s.l. (Ericaceae, Empetraceae, Epacridaceae, Monotropaceae, Pyrolaceae), and its placement within the Ericales s.l. (Ericaceae s.l. plus Cyrillaceae, Actinidiaceae, Sarraceniaceae, *Roridula*, and possibly *Clethra*), is a relatively constant result of different phylogenetic analyses. However, relationships among the Ericales s.l. and other lineages in the ericalean clade are not well understood. Several analyses have either addressed higher-level phylogenetic patterns for the ericalean clade as a whole (e.g., Olmstead et al., 1992, 1993; Chase et al., 1993; Soltis & Soltis, 1997), or have focused on the relationships within particular ericalean lineages (e.g., the Ericales s.l. and Ericaceae s.l. by Anderberg 1992, 1993, 1994; Kron & Chase, 1993; Kron, 1996; Keller et al., 1996; Polemoniaceae by Steele & Vilgalys, 1994; Johnson et al., 1996). Relatively few studies have so far approached phylogenetic relationships within the broader ericalean clade by including a representative sample of all potentially relevant taxa.

Lamiidae s.l. In the results of several *rbc*L-based phylogenetic analyses, phylogenetic relationships among the four major clades within Lamiidae s.l. are relatively congruent: Lamiales s.l. plus Gentianales are the sister taxon to Solanales plus Boraginales (e.g., Chase et al., 1993; Olmstead et al., 1993; Cosner et al., 1994). However, this pattern is not supported by all *rbc*L-based analyses (Morgan & Soltis, 1993; Gustafsson et al., 1996; Hibsch-Jetter et al., 1997), nor by 18S studies (Soltis & Soltis, 1997; Soltis et al., 1997a), and given the large proportion of eudicot species diversity in this group, further analyses of the relationships among the major clades of the Lamiidae s.l. are needed.

Within Lamiales s.l., some generally recognized patterns are the placement of Oleaceae in a basal position within the clade (e.g., Olmstead et al., 1992, 1993; Chase et al., 1993), support for the monophyletic status of Acanthaceae, Bignoniaceae, Gesneriaceae, Verbenaceae, and possibly Lamiaceae (e.g., Hedrén et al., 1995; Olmstead & Reeves, 1995; Smith et al., 1997), and the detection of two main assemblages including members of Scrophulariaceae. "Scrophs I" includes genera such as *Verbascum* L., *Scrophularia* L., and *Selago*, and Buddlejaceae, while "scrophs II" includes, for example, *Antirrhinum* L. and *Digitalis* L., as well as derived genera that are usually thought to be related to Scrophulariaceae, but are frequently segregated into different families (i.e., *Plantago*, *Hippuris*, and *Callitriche*; Olmstead & Reeves, 1995; Reeves & Olmstead, 1998). At a broader level, however, phylogenetic relationships among lineages within Lamiales s.l. are incompletely resolved.

TOWARD EXPLICIT INTEGRATION OF PHYLOGENETIC STUDIES

We used the presence of recurring phylogenetic patterns, especially those resulting from studies based on different types of evidence, as a main criterion for summarizing higher-level eudicot phylogenetic relationships. Integration of data sets from different types of evidence in combined phylogenetic analyses, emerging techniques to evaluate congruence in different phylogenetic signals, and other powerful methodological approaches are needed to assess the generalizations about the phylogenetic patterns made here. Integration of the numerous currently available studies of intrafamilial phylogenetic relationships within the framework of a higher-level phylogenetic pattern may have the potential to provide information about monophyletic status of families, placement of members of nonmonophyletic taxa, and possibly, contribute to the resolution of internal nodes in detected clades. In particular, the development of methods for integrating information from partially overlapping taxonomic samples into an integrative solution provides a major advance of great significance for attempting to resolve patterns of phylogenetic relationships on a broad scale (e.g., Sanderson et al., 1998).

DISTRIBUTION OF EUDICOT SPECIES DIVERSITY

The availability of a phylogenetic framework permits an estimate of the number of species encompassed by each major eudicot clade, which documents great heterogeneity in diversity with respect to phylogenetic pattern. It is especially striking that a few well-supported clades and monophyletic taxa comprise a significant proportion of eudicot species (Fig. 10). The great majority of eudicot species (ca. 97% TESD) are included in the core eudicots. Within the core eudicots, ca. 39% of TESD are encompassed by the rosid clade, and nearly 50% of living eudicots belong to the asterid clade. Within each of these two major clades, distribution of species diversity is also heterogeneous. More than

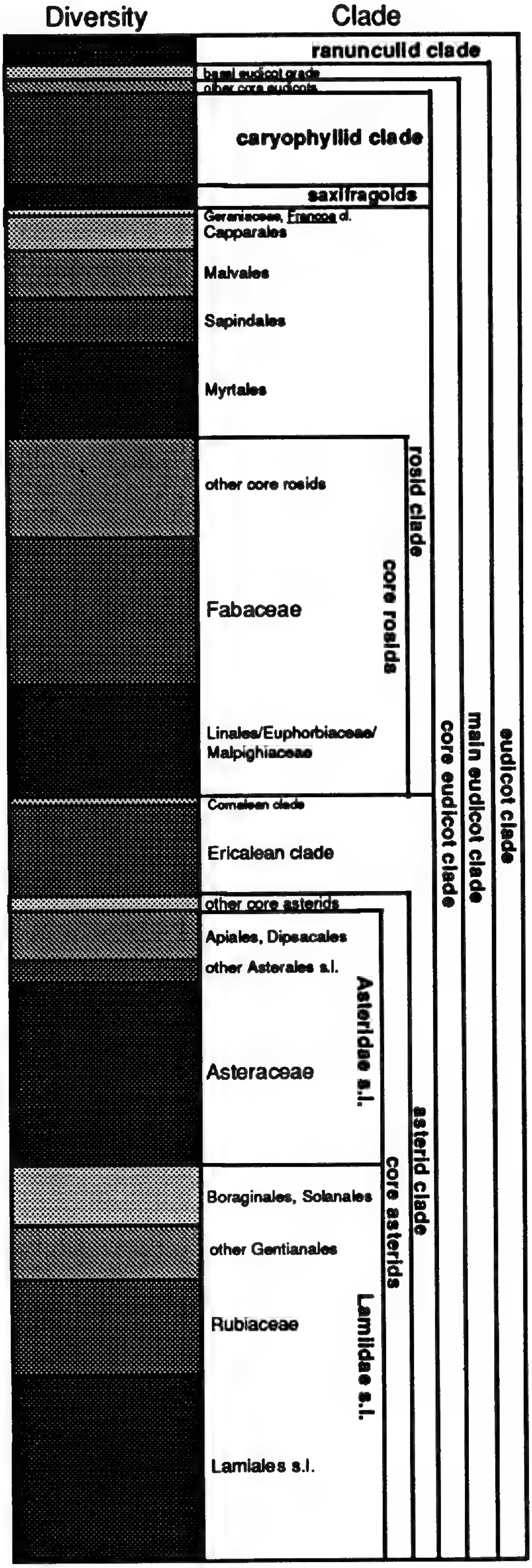

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Figure 10. Distribution of species diversity among major eudicot clades. The approximate percentage of TESD for major eudicot clades is as follows: ranunculid clade: 2.01%; main eudicot clade: 97.99%; basal eudicot grade: 0.84%; core eudicots: 97.15%; caryophyllid clade: 6.31%; Saxifragoids: 1.34%; rosid clade: 38.84%; Geraniaceae plus the *Francoa* clade: 0.43%; expanded Capparales: 2.24%; expanded Malvales: 3.16%; Sapindales: 3.01%; Myrtales: 5.97%; core rosids: 24%; Fabaceae: 9.37%; Linales/Euphorbiaceae/Malpighiaceae: 7.77%; all other core rosids: 6.86%; asterid clade: 49.14%; cornalean clade: 0.3%; ericalean clade: 5.93%; core asterids: 42.91%; Asteridae s.l.: 16.58%; Apiales plus Dipsacales: 2.96%; Asteraceae: 12%; other Asterales s.l.: 1.58%; Lamiidae s.l.: 26.08%; Boraginales plus Solanales: 4.02%; Rubiaceae: 5.94%; all other Gentianales, except for Rubiaceae: 3.86%; Lamiales s.l.: 12.26%; other core asterids: 0.01%.

half of the species in the rosid clade belong to the core rosids (ca. 24% TESD), while nearly half of the species within the core rosid clade are grouped within the Fabaceae/Surianaceae/Polygalaceae (ca. 10 % TESD). Within the asterid clade, the majority of species (87%) are accounted for by the core asterids (ca. 43% TESD). Asteridae s.l. include 16.6% of TESD, of which 13.6% belong to the Asterales s.l. Within the eudicots, Lamiidae s.l. are the group that encompasses the single largest percentage of species (ca. 26% TESD). There are nearly as many species in Lamiidae s.l. (ca. 45,600) as in the monocotyledons as a whole (ca. 50,000). Five taxa include significant percentages of eudicot species diversity. Myrtales (ca. 6% TESD), Fabaceae (9.4% TESD), Asteraceae (12% TESD), Rubiaceae (ca. 6% TESD), and Lamiales s.l. (12.3% TESD) together account for almost half of eudicot species (ca. 45.7% TESD).

Explicit recognition of considerable heterogeneity in the distribution of species diversity within eudicots provides greater precision to the general impression that angiosperms as a whole are very diverse. It shows very clearly that, in the present day, a few angiosperm taxa are extremely diverse, while many other taxa include relatively few members. This uneven partitioning of diversity is also apparent in other plant groups, for example, the Orchidaceae within the monocots (Herendeen & Crane, 1995) and the Polypodiaceae s.l. within the Filicales (Pryer et al., 1995). The basis for the observed heterogeneous partitioning of species diversity, its relationship to phylogenetic patterns, and possible selective causes are important aspects of angiosperm evolution that have so far received relatively little attention (e.g., Crane & Lidgard, 1990; Sanderson & Donoghue, 1994; Magallón, 1996). In particular, the extreme diversity of a limited number of taxa needs to be evaluated from a standpoint that addresses the relationship between the evolution of clade-restricted key innovations and an increase in diversification rates (e.g., Hodges, 1997).

MINIMUM AGES AND IDENTIFICATION OF ANGIOSPERM TAXA IN THE FOSSIL RECORD

The earliest appearance in the fossil record of a taxon indicates the minimum age that can be assigned to its lineage. However, the assumption that the earliest appearance in the fossil record accurately represents a lineage's time of origination, or crown-group radiation, is problematic (e.g., Doyle & Donoghue, 1993), especially given the characteristics of plant macrofossil record, and the taphonomic biases inherent in the plant fossil record (different dispersed organs that need to be associated into whole-plant reconstructions). The angiosperm macrofossil record is very uneven in its representation of angiosperm lineages, and even at its best comprises mainly intermittent occurrences of members of particular lineages, separated by gaps (e.g., Platanaceae). Continuous, unequivocal, and detectable representation of lineages through prolonged stratigraphic intervals is very rare. Estimation of probability intervals to the time of origination of angiosperm taxa based on their first and subsequent occurrences in the fossil record (e.g., Strauss & Sadler, 1989; Marshall, 1990, 1994, 1997) is problematic.

These difficulties are further exacerbated by the significant challenges inherent in determining the phylogenetic affinity of isolated and fragmentary angiosperm fossil remains. First, a strict delimitation of many higher taxa of extant angiosperms is not currently feasible because discrete sets of constant characters or combinations of characters that define most living angiosperm families and higher taxa have not yet been recognized (Stebbins, 1951). Second, isolated and fragmentary angiosperm macrofossils may not display all the characters that in combination allow recognition of membership within a particular taxon. Third, an extinct angiosperm that does not fall within the morphological range displayed by extant members of the lineage to which it belongs may be difficult to recognize as a member of that lineage.

Reliable identification of the early members of extant angiosperm lineages is often difficult. Most fossil angiosperms that have been correctly assigned to living taxa are most likely members of crown groups. These fossils therefore provide a minimum age for the radiation of crown groups, but they do not provide information regarding the extent to which stem lineages extend back in time, nor about the probable diversification rate associated with that lineage. Integration of phylogenetic patterns with earliest appearances in the fossil record for sister taxa may provide an indirect but independent source of evidence about time of origin of lineages. Estimated times of differentiation for eudicot lineages, obtained from data of minimum ages placed within a phylogenetic pattern, are shown in Figure 11.

AGE OF LINEAGES AND PRESENT-DAY SPECIES DIVERSITY

An assessment of the minimum time of origin of the five major monophyletic groups of extant seed plants indicates that, with the exception of angiosperms, the presumed origins of cycads, *Ginkgo* L.,

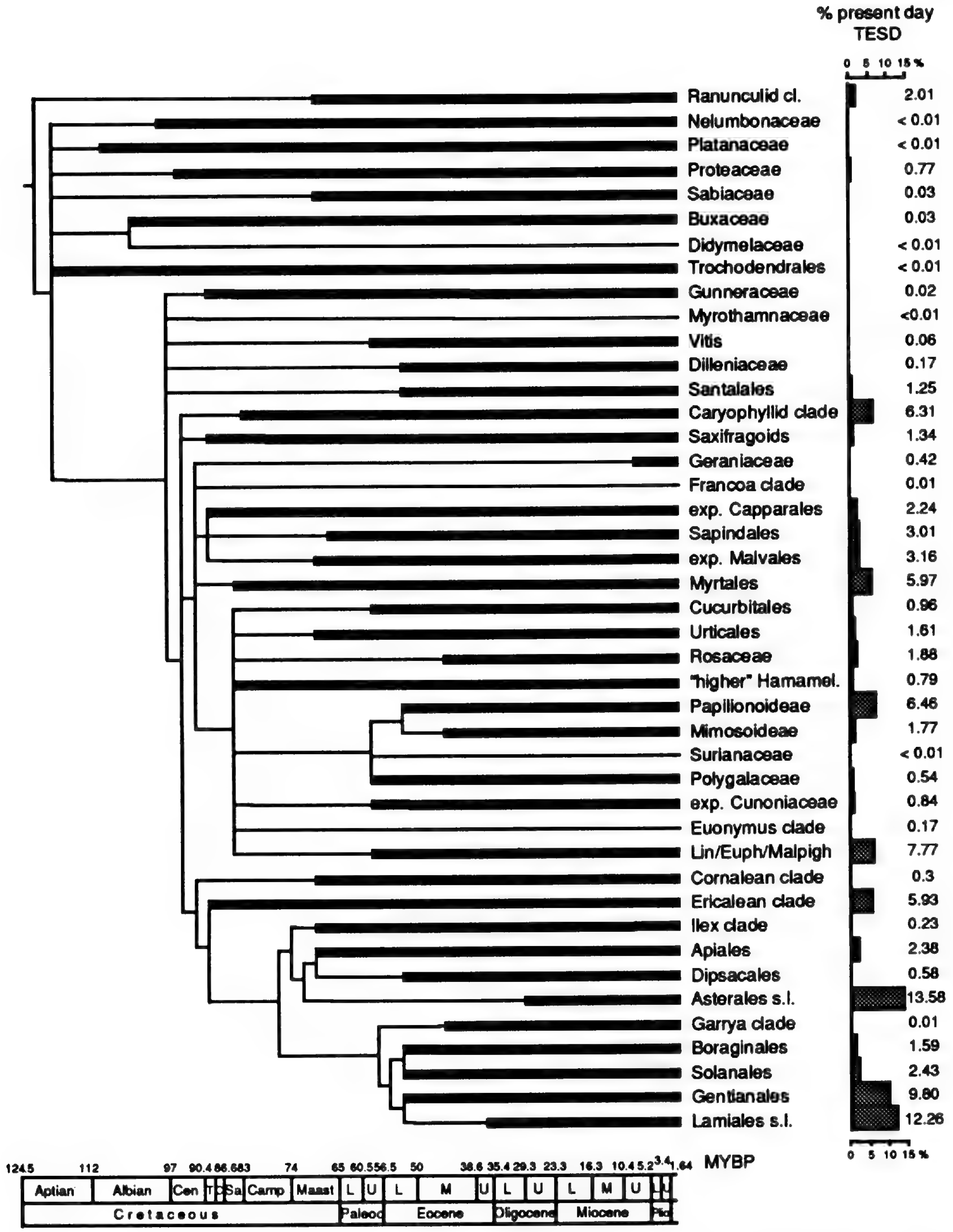

Figure 11. Earliest documented appearance in the fossil record for major eudicot clades, integrated to general phylogenetic pattern. Thick horizontal lines represent geologic time by which the clade is securely known in the fossil record. Thin horizontal lines represent that the clade is inferred to have differentiated, given the documented existence of its sister taxon. Time scale after Harland et al. (1989). The column on the right shows the percentage of present-day TESD for each major eudicot clade.

Table 4. First appearance in the fossil record of the five major extant groups of seed plants. Time scale is based on Harland et al. (1989). Number of living species for gymnosperms is based on Gifford and Foster (1988). Estimate of extant angiosperm species diversity is based on Cronquist (1981) and Mabberley (1993).

Taxon	Age	MYBP	Present-day species diversity	% present-day species diversity
Cycads	Lower Pennsylvanian (Namurian B or C)	310	160	0.07
Ginkgoaceae	Triassic	235	1	<0.01
Conifers	Carboniferous (Westphalian B)	307	550	0.24
Gnetales	Triassic	235	100	0.04
Angiosperms	Lower Cretaceous (Valanginian-Hauterivian)	135	230,000	99.65
TOTAL:			230,811	

conifers, and gnetaleans range from the Pennsylvanian (ca. 310 million years before the present [MYBP]) to the Triassic (ca. 235 MYBP). However, in the present day, these ancient plant taxa comprise only a small percentage of total plant species diversity (Table 4). Angiosperms, which include the overwhelming majority of present-day seed plant species diversity (> 99%, Table 4, Fig. 12), occur unambiguously in the fossil record in Valanginian-Hauterivian strata (ca. 135 MYBP; Brenner, 1996). Comparison of the estimated time of origination of major, non-inclusive plant clades with the number of species in present-day floras for each of these groups (Fig. 12) shows that although the number of angiosperm species is larger by orders of magnitude than the number of species of all other seed plants, the group is also the most recent in terms of its appearance in the fossil record.

Within the angiosperms, an assessment of the presumed time of origination of major eudicot clades, derived from their earliest reliable appearance in the fossil record, compared to present-day eudicot species diversity, indicates that the most species-rich clades (i.e., Papilionoideae, Asterales, Gentianales, Lamiales s.l.) have distinctly late times of origination (Table 5, Fig. 13). Small or medium-sized clades may be old or young, but the most ancient eudicot clades (i.e., Nelumbonaceae, Platanaceae, Buxaceae, Trochodendraceae s.l.) include only a small number of species in the present day (Table 5, Fig. 13). While the earliest angiosperm remains are found in Valanginian-Hauterivian strata (Brenner, 1996), the earliest eudicots appear soon afterward in the Barremian-Lower Aptian (Doyle, 1992). Based on the occurrence of reliable, mostly macrofossil reproductive remains, the origins of clades that comprise less than 1% of present-day TESD can be traced to the Aptian (Trochodendraceae s.l.), the Albian (Nelumbonaceae, Platanaceae, and Buxaceae), and the Cenomanian (Proteaceae). Clades that together include ca. 46% of present-day TESD originated during different stages of the Upper Cretaceous (Turonian to Maastrichtian) and the Paleocene. Minimum ages of eudicot clades that together include ca. 22% of present-day TESD (i.e., Papilionoideae, Dipsacales, Boraginales, Solanales, Gentianales, Santalales, and Dilleniaceae) show that they existed by the Lower Eocene. Clades that today comprise ca. 68% of present-day TESD had originated by the early Eocene, but a significant proportion of TESD appears to be the result of diversification in relatively recent times. The earliest occurrence in the fossil record of Lamiales s.l. is in the Upper Eocene, providing a minimum time for the initiation of diversification that resulted in 12.3% of present-day TESD. The Asterales s.l. are documented from Oligocene strata, indicating that the clade that includes ca. 13.6% of present-day TESD had begun to diversify by at least 30 MYBP. The sister taxon to the Asterales s.l. (i.e., Apiales-Dipsacales) can be traced back to (at least) the Maastrichtian (Fig. 11), which indicates that the stem lineage of the Asterales s.l. had differentiated at least by the latest Upper Cretaceous. However, the absence of the distinctive pollen grains of Asteraceae from the pre-Oligocene fossil record suggests that the lineage's crown-group radiation may be close to its time of appearance in the fossil record. By the Upper Miocene, the clades that today comprise more than 98.7% TESD are known in the fossil record. The remaining 1.3% corresponds to small clades and isolated lineages that are not known in the fossil record (e.g., the *Euonymus* clade, the *Francoa* clade, Surianaceae).

While estimates of the time of origin of eudicot lineages may be obtained by combining information on phylogenetic pattern and stratigraphic ranges (Fig. 11), and approximations to the time of crown-group radiations of eudicot lineages may be ob-

Table 5. Minimum age for major eudicot clades, as documented by their earliest occurrence in the fossil record. Earliest records for clades are taken from the earliest appearance of the oldest family included in each clade, from Collinson et al. (1993), and other sources (see main text). Time scale is based on Harland et al. (1989). Extant species diversity for each clade is estimated from data in Mabberly (1993). Eudicot clades without a known fossil record are not included. Names in parentheses after the age indicate the specific taxon on which minimum age is based. Numbers in the first column correspond to numbers in Figure 13.

Taxon	Minimum age	MYBP	Present-day species diversity	% Present-day species diversity
1 Ranunculid clade	Maastrichtian (Menispermaceae)	69.5	3526	2.01
2 Nelumbonaceae	Upper Albian	100	2	<0.01
3 Platanaceae	Lower Albian	108	7	<0.01
4 Proteaceae	mid-Cretaceous	97	1350	0.77
5 Sabiaceae	Maastrichtian	69.5	48	0.03
6 Buxaceae	mid-Albian	104.5	60	0.03
7 Trochodendrales	Aptian (Tetracentraceae)	118	2	<0.01
8 Caryophyllid clade	Santonian-Campanian (Amaranthaceae)	83	11,049	6.31
9 Saxifragoids	Turonian (saxifragaleans)	89.5	2354	1.34
10 Geraniaceae	Upper Miocene (pollen)	7.8	729	0.42
11 expanded Capparales	Turonian (Capparales)	89.5	3922	2.24
12 Sapindales	Upper Maastrichtian (Rutaceae, Aceraceae)	67.2	5264	3.01
13 expanded Malvales	Maastrichtian (Bombacaceae, pollen)	69.5	5532	3.16
14 Myrtales	late Santonian (Myrtales)	84	10,443	5.97
15 Cucurbitales	Upper Paleocene	58.5	1673	0.96
16 Urticales	Maastrichtian (Celtidoideae)	69.5	2819	1.61
17 Rosaceae	Middle Eocene	44.3	3296	1.88
18 "higher" Hamamelididae	late Santonian (Normapolles flowers)	84	1379	0.79
19 Polygalaceae	Upper Paleocene	58.5	950	0.54
20 Mimosoideae	Middle Eocene	44.3	3100	1.77
21 Papilionoideae	Lower Eocene	53.2	11,300	6.46
22 expanded Cunoniaceae	Upper Paleocene	58.5	1472	0.84
23 Linales/ Euphorbiaceae/Malpighiaceae	Upper Paleocene (Euphorbiaceae, pollen)	58.5	13,599	7.77
24 Cornalean clade	Maastrichtian (Mastixiaceae)	69.5	524	0.30
25 Ericalean clade	Turonian (Ericaceae s.l.)	89.5	10,387	5.93
26 *Ilex* clade	Maastrichtian (*Ilex*)	69.5	407	0.23
27 Apiales	Maastrichtian (Araliaceae)	69.5	4158	2.38
28 Dipsacales	Lower Eocene (Caprifoliaceae)	53.2	1019	0.58
29 Asterales s.l.	Oligocene (Asteraceae, Goodeniaceae [pollen], Menyanthaceae)	29.3	23,774	13.58
30 *Garrya* clade	Middle Eocene (*Eucommia*)	45.9	18	0.01
31 Boraginales	Lower Eocene (Boraginaceae)	53.2	2775	1.59
32 Solanales	Lower Eocene (Convolvulaceae)	53.2	4251	2.43
33 Gentianales	Lower Eocene (Apocynaceae, Rubiaceae)	53.2	17,146	9.80
34 Lamiales s.l.	Upper Eocene (Scrophulariaceae, Oleaceae)	37	21,467	12.26
35 Santalales	Lower Eocene (Olacaceae)	53.2	2186	1.25
36 Dilleniaceae	Lower Eocene	53.2	300	0.17
37 *Vitis*-Leeaceae	Upper Paleocene	58.5	99	0.06
38 Gunneraceae	Turonian (pollen)	89.5	40	0.02

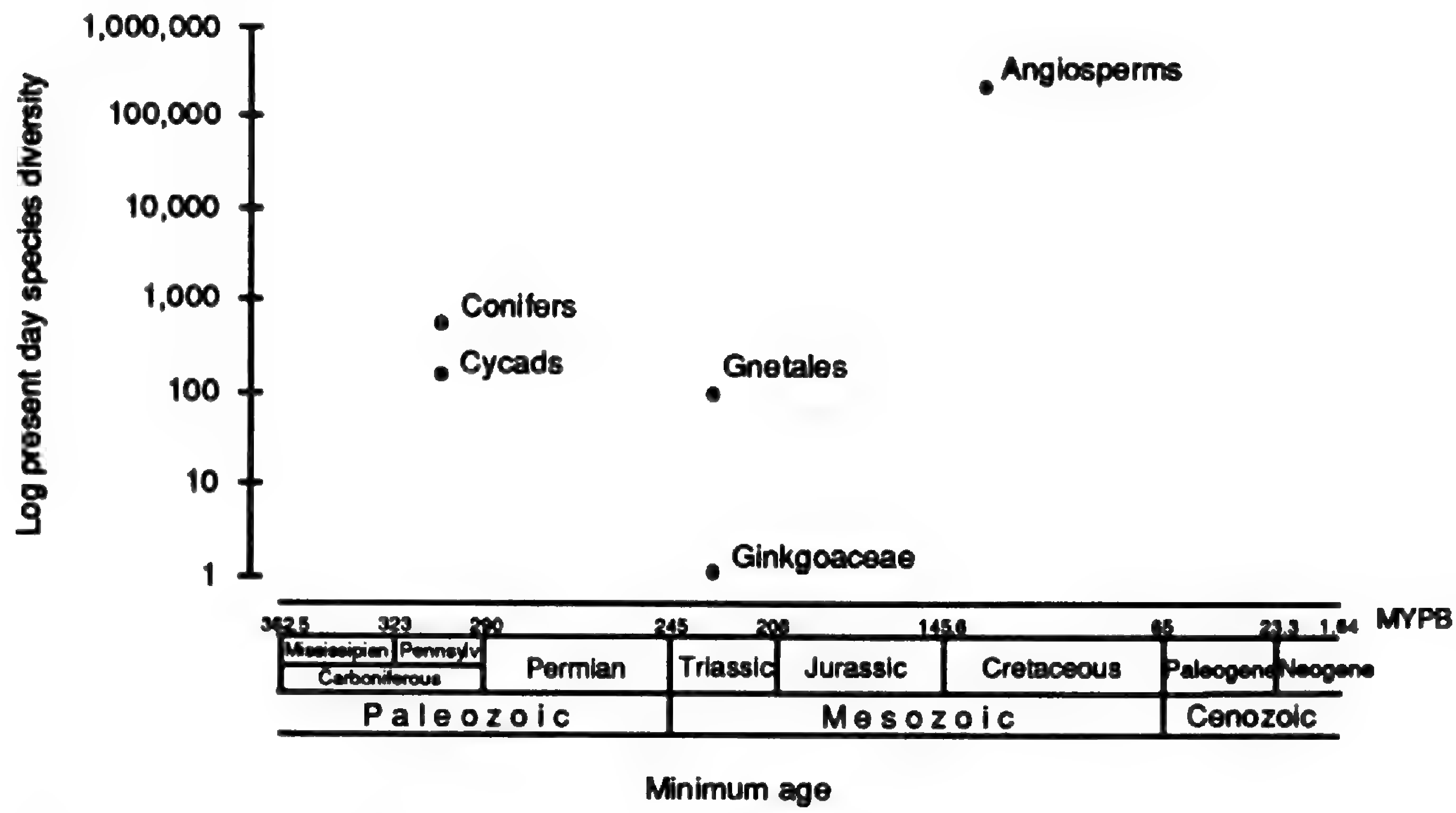

Figure 12. Minimum age for major plant taxa vs. log present-day species diversity. Data for minimum age and for present-day species diversity are from Table 4. Most plant taxa are known from the Paleozoic or the Triassic (gnetaleans). Nevertheless, these ancient taxa comprise a small percentage of present-day plant species diversity. The angiosperms include nearly 88% of present-day plant species diversity. However, the angiosperms are unambiguously recorded in the fossil record only as far back as the Early Cretaceous (Hauterivian-Valanginian).

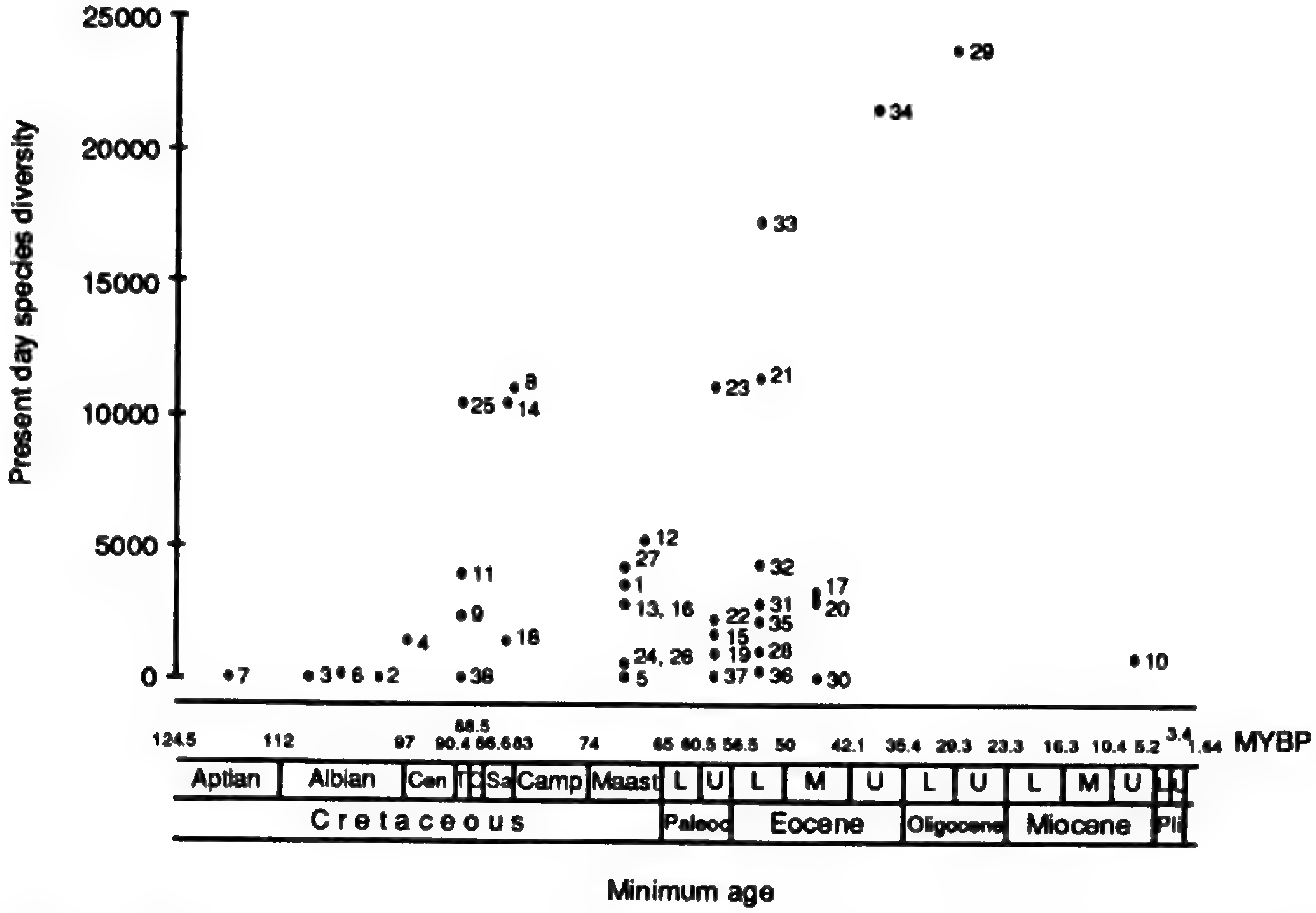

Figure 13. Minimum age for major eudicot taxa vs. present-day TESD. Data for minimum ages and diversity of major eudicot clades are from Table 5. Numbers next to data points correspond to numbers for clades in Table 5. Eudicot clades with small species numbers range from very old to young. However, the most ancient taxa (7 = Trochodendraceae; 3 = Platanaceae; 6 = Buxaceae; and 2 = Nelumbonaceae) have very few species in the present day. The most species-rich eudicot taxa in the present day (33 = Gentianales; 34 = Lamiales s.l.; and 29 = Asterales s.l.) appear relatively late in the fossil record.

tained from earliest appearances in the fossil record, there is little reliable information about the overall diversity history of clades of eudicots (i.e., the distribution species diversity within a lineage through time; Raup et al., 1973; Gould et al., 1977). In a few cases, however, the fossil record suggests that some of the most ancient eudicot taxa (i.e., Trochodendrales, Platanaceae, Buxaceae, and Hamamelidoideae; Fig. 13) probably never included a large number of species. Detailed analyses of features of flowers and inflorescences of extinct members of these taxa indicate that, while extinct representatives display some structural and morphological differences with respect to living members, the distinctive features of floral structure and form for each clade are constant among extinct and living representatives (e.g., Crane et al., 1986; Friis et al., 1988; Drinnan et al., 1991; Endress & Friis, 1991; Magallón et al., 1996, 1997). For taxa such as these, our working hypothesis is that the small number of species in the present day is not the result of massive clade-specific extinction, but rather, that these lineages have always had relatively few species. Simulation experiments (Gould et al., 1977) suggest that clades with these characteristics (i.e., a prolonged representation through geologic time with a constantly small diversity) result from a combination of low speciation rates and low extinction rates.

In contrast, the Papilionoideae, Asterales s.l., Gentianales, and Lamiales s.l. seem to have appeared relatively late in the evolution of eudicots, but nevertheless, comprise a large proportion of present-day TESD. If the earliest representation of each of these taxa in the fossil record accurately represents the time of diversification of their respective crown groups, then these lineages must have undergone very rapid radiations, involving high speciation rates, and perhaps also reduced extinction rates. The late appearance in the fossil record of the Asterales s.l., together with its sister group relationship with a clade that can be traced back to (at least) the Maastrichtian (Fig. 11), suggests that the lineage of the Asterales s.l. diversified (probably corresponding to the crown-group radiation) after a long period of relatively low diversity (presumably corresponding to the stem lineage). The pattern of appearance of eudicot clades through geologic time suggests that, through the evolutionary history of eudicots different clades may have comprised significant proportions of species diversity at different time periods. On the whole, the evidence suggests the relatively recent evolution of species-rich taxa. High species diversity is apparently not associated with early evolution of eudicot lineages. On the contrary, a significant proportion of extant eudicot species diversity appears to be the result of radiations during the Tertiary. Further effort needs to be directed toward testing this preliminary hypothesis and exploring the factors underlying what appear to be extraordinary diversification rates in some angiosperm clades.

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THE CO-RADIATIONS OF POLLINATING INSECTS AND ANGIOSPERMS IN THE CRETACEOUS[1]

David Grimaldi[2]

ABSTRACT

The origins of many groups of flower-visiting insects are generally believed to have been in the Cretaceous. However, a recent hypothesis has concluded that many modern families of insects originated in the Jurassic, and that the Cretaceous radiation of angiosperms had little positive effect on the diversity of insect families. It is shown here, based on critical and phylogenetic interpretation of Mesozoic fossils, that radiations of major anthophilic groups of insects took place in the late part of the Lower Cretaceous to Upper Cretaceous: the bees (Apoidea/Apidae sensu lato), pollen wasps (Vespidae: Masarinae), various families of brachyceran flies (Acroceridae, Apioceridae, Bombyliidae, Empididae, Nemestrinidae, Stratiomyidae, and Syrphidae), and the Lepidoptera. The pattern of diversification of these insects, centered in the mid-Cretaceous, is consistent with the chronology of appearance of entomophilous syndromes in Cretaceous flowers, and not with a model of late Jurassic or earliest Cretaceous diversification of pollinating insects. Despite a more refined understanding of the timing of Cretaceous insect-angiosperm co-radiations, cause and effect relationships remain obscure.

Working on a group of organisms with perhaps 5 million species, entomologists are not easily impressed by groups other than insects. Nonetheless, even they admit to the central role that the angiosperms have in terrestrial communities. Based simply on the dazzling array of colors, patterns, and morphologies of flowers specialized for attracting insects, it is reasonable to estimate that at least two-thirds of the 250,000–300,000 living angiosperm species are insect pollinated. On this basis alone insects would be the most ecologically important group of terrestrial animals, without even taking into consideration their other ecological roles. The intimate and obligate associations that have evolved between thousands of species of angiosperms and insects are among the most significant mutualistic relationships to occur among all organisms. Understanding the origins of this relationship is, thus, hardly a trivial consideration.

Insects feeding on, or from, the reproductive structures of plants is an ancient habit, probably beginning in the Carboniferous with the Paleodictyopteroidea (Taylor & Scott, 1983; Labandeira, 1998). This assemblage of extinct insect orders had sucking mouthparts, presumably used for obtaining plant fluids or reaching into small spaces, such as the sporangia of Carboniferous medullosan pteridosperms. Indeed, the very large pollen (to 600 μm diam.) of some of these plants is thought to have precluded wind pollination, and they may have been pollinated by paleodictyopterans. It was the Coleoptera, though, that clearly set the stage for pollination of the early seed plants, probably beginning as early as the debut of beetles in the Permian (reviewed in Carpenter, 1992). Evidence that Mesozoic beetles were significant pollinators is largely circumstantial, and is based on the fact that various kinds of beetles today are facultative, and some even obligate, visitors to flowers of generalized morphology and exposed floral rewards (Armstrong & Irvine, 1990; Dafni et al., 1990; Gazit et al., 1982; Proctor et al., 1996). For example, En-

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dress (1987a, b) reported bisexual members of the primitive family Chloranthaceae to be pollinated by beetles and short-tongued flies, whereas unisexual species were wind pollinated. Also, certain weevils have been found to be essential to the pollination of some cycads (Norstog, 1987; Ornduff, 1997). Because beetles have chewing (mandibulate) mouthparts, they are not restricted to feeding on exposed pollen or nectar, but can also consume the ovules. It has been hypothesized that the fundamental angiosperm structure of closed carpels evolved as a mechanism to protect the ovules from visitors like beetles. The common occurrence of inferior ovaries may also have afforded a protective function. Despite their presumed early dominance of the anthophilous niche, Coleoptera were eclipsed as pollinators by Lepidoptera, aculeate wasps (including bees), and various brachyceran flies. The hardened forewings, or elytra, enable beetles to exploit tight spaces in which the wings of other insects would be damaged; as a result, however, beetles fly poorly compared to most other insects, which makes them less efficient at visiting many flowers.

EVIDENCE FOR INTERPRETING ANCIENT INSECT POLLINATION

DIRECT EVIDENCE

Direct evidence of insect-pollen interactions is provided by fossil insects with pollen preserved on or in them. Impressive examples are provided by the insects *Idelopsocus diradiatus* Rasnitsyn (Hypoperlida), *Tshekardaenigma pollinivorum* Rasnitsyn (Grylloblattida?), and *Sojanidelia florea* Rasnitsyn (Grylloblattida), from the Lower Permian (Kungurian) of the Urals (Rasnitsyn & Krassilov, 1996a, b), all found with masses of pollen in their guts. The pollen varied in preservation and was referred to the genera *Lunatisporites*, *Protohaploxypinus*, and *Vittatina* (Gymnospermae, Peltaspermales). The amount of pollen in the gut, and the fact that each gut was filled with only one pollen type, indicates that the insects were selectively feeding on pollen, and thus perhaps transporting it from plant to plant.

Several similar examples are known from the Cretaceous. Three species of sawflies in the primitive, living family Xyelidae (Hymenoptera), from the Lower Cretaceous (?Neocomian) of Baissa, Transbaykalia, are known to have fed as adults on the pollen of *Alisporites* (a pollen form-genus probably produced by the macrofossil conifer *Wilsiostrobus*), *Pinuspollenites* (?Pinaceae), and *Vitimipollis* (taxon unknown) (Krassilov & Rasnitsyn, 1982). Another xyelid with *Afropollis* pollen (possibly angiospermous) is briefly reported from the Santana Formation limestone of Brazil (Aptian: Lower Cretaceous) (Caldas et al., 1989).

In the Tertiary, apine bees in the Eocene shales of Germany (Lutz, 1990, 1993) have corbicula filled with angiosperm pollen. Stingless bees, ***Proplebeia dominicana*** (Wille), which are quite common in the Miocene amber from the Dominican Republic, can be found with masses of pollen in their abdomen preserved with perfect fidelity (Grimaldi et al., 1994; Grimaldi, 1996), although the pollen has not been identified.

The preservation of pollen in the guts of fossil insects appears to be more widespread than previously believed, and investigations on specimens from diverse Mesozoic deposits with exceptional preservation are likely to reveal fascinating data. Of particular interest would be the examination of the gut contents of beetles from the Lower Cretaceous and Upper Jurassic, and sphecid wasps from the Lower and mid-Cretaceous, since these groups are implicated as faithful visitors to early angiosperms. Nonetheless, pollen in the gut of fossil insects will probably always be a sporadic occurrence and not very illuminating for elucidating major patterns of insect-angiosperm diversification.

INDIRECT EVIDENCE

1. Pollinators of Extant, Primitive Angiosperms and Close Relatives.

Documenting the pollinators of primitive angiosperms and close relatives has been an active field of inquiry: for *Magnolia* (Thien, 1974), Chloranthaceae (Endress, 1987a, b), Winteraceae (Thien et al., 1985), *Illicium* (Thien et al., 1983), *Ephedra*, and *Gnetum* (Kato & Inoue, 1994). Gottsberger (1988) and Endress (1990) provided useful reviews and new information on several additional systems. In general, pollination of these gnetaleans and basal angiosperms is done by insects with a relatively generalized morphology, like beetles, short-tongued flies, and primitive Lepidoptera. Primitive insects can be engaged in some very specialized pollination relationships (e.g., *Tegiticula* moths and *Yucca*), but this is rare. Basal angiosperms visited by generalized insects is a rather consistent pattern, but it is difficult to tease out the extent to which this is due to a persistent symbiotic relationship or to the generalized, non-exclusionary morphology of these flowers. Also, it is not intuitively obvious as to why an ecological relationship that originated perhaps 100 Ma should persist to modern descendants virtually unmodified, in the face of dramatically changing ecological conditions as well as opportunities to develop new ecological interactions. Bees are the most dedicated and significant group of anthophilous insects; but even some species of the recently derived meliponines (stingless honeybees) have reverted to gathering spores of cycads (Ornduff, 1997) and even to feeding on carrion (Roubik, 1989).

2. Fossil Record of Angiosperms and Pollination Syndromes.

It has been well established that angiosperms are closely related to the relict and largely extinct Gnetales, as well as extinct Bennettitales, all three taxa comprising the Anthophyta (Doyle & Donoghue, 1986; Crane et al., 1995). The non-angiospermous anthophytes originated in the Triassic and reached a peak of diversification in the mid Cretaceous (Crane & Lidgard, 1990). Angiosperms, on the other hand, have their earliest palynological and macrofossil geological records in the Lower Cretaceous (Crane et al., 1995). Crane and Lidgard (1990) and Lidgard and Crane (1988) surveyed the generic and species diversity of angiosperms in the fossil record and found that generic diversity dramatically rises in the Albian to the Turonian (115–90 Ma), with a slightly less dramatic trend when species are surveyed. Thus, the explosive diversification of the angiosperms is well documented to be in a rather narrow window of time in the mid-Cretaceous.

Crepet (1985, 1996) and Crepet and Friis (1987) focused on the chronology of first appearance in the fossil record of morphological features associated specifically with insect pollination. Flowers often have suites of such features ("syndromes") that not only reflect whether the flowers are pollinated by insects, but may also indicate the order(s) of insects that visit the flowers. Data summarized by Crepet (1996) have considerably narrowed the time frame for radiations of pollinating insects, and the timing is consistent with the pattern of overall diversification (e.g., Lidgard & Crane, 1988). Crepet (1996) surveyed the earliest appearances of 36 reproductive features of angiosperms, many of them associated with insect pollination; the earliest of these appear in the Aptian (2), in the Albian (10), in the Cenomanian (20), and by the Turonian all 36 features had appeared. Based on these data, insect anthophily was well established by the Cenomanian (100 Ma), and virtually fully intact by the Turonian (90 Ma). Some highlights of this chronology are: sepals, petals, and long, filamentous stamens in the Cenomanian; and bilateral symmetry, corolla tubes, clawed petals, polyads and viscin threads on pollen, resin rewards, floral nectaries, and various modified anthers in the Turonian.

These data provide an essential basis of comparison with the insect fossil record. If the diversifications of angiosperms and anthophilous insects were coupled, we would expect major radiations of these insects between the Albian and Turonian/Campanian.

3. Insect Fossil Record.

Labandeira and Sepkoski (1993) statistically analyzed insect families in the fossil record and reported that the number of insect families decreased since the mid Cretaceous radiation of the angiosperms. They concluded (Labandeira & Sepkoski, 1993: 313): "The more startling interpretation that can be drawn from the data . . . is that the appearance and expansion of angiosperms had no influence on insect *familial* diversification" (italics mine). According to their data, it does indeed appear true that many insect families appeared before the angiosperm radiation; but as will be shown and discussed later, it would be very misleading to extrapolate from this data that the angiosperm radiations had no effect on diversification of insects in general, such as species, genera, and other subfamilial taxa (see also Crepet, 1996). Also, insect families and orders are dramatically uneven in their species diversity, their relationship to plants, and in their significance as pollinators.

The oldest fossils of various insect families or orders are usually cited as evidence for the earliest records of pollinators or potential pollinators, but this can be very misleading. For example, some empidid flies today are facultative visitors to flowers, but this does not mean that early empidids in the Mesozoic were as well (in fact, they were probably predaceous). Ideally, there should be some morphological indicator in the fossil that reflects a feeding specialization for pollination. Compared to entomophilous angiosperms, insects have very few overt morphological specializations for anthophily. In part this may reflect the variety of behavioral rather than structural adaptations that pollinating insects employ, such as bee "buzzing," nectar robbing and theft, grooming pollen from the body, and learning differential rewards. Bees (Sphecoidea: Apidae s.l.) have the greatest number of anthophilic specializations: scopae and corbiculae, or brushes and baskets of hairs in which pollen is carried; plumose body hairs, to which pollen adheres particularly well; various combs and scrapers, for grooming pollen from the body hair; and, in many bees there is a long, maneuverable, retractile glossa (tongue) (Thorp, 1979). Unless preserved in amber, only some of these minute features are likely to be observed in a fossil.

Other major groups of anthophilous insects have few morphological specializations, but the most obvious and repeatedly derived feature is a proboscis. In most Lepidoptera, some Diptera, and Hymenoptera (and even an instance in the Coleoptera [*Nemognatha*]), the mouthparts are elongate, which allows the extraction of nectar and pollen from deep and narrow flowers. An elongate proboscis has evolved numerous times in association with other lifestyles, such as in eight families of Diptera where females suck blood of vertebrates or prey on other insects. (One cannot always determine from structure alone if proboscides function primarily for anthophily or hematophagy. The females of many ceratopogonids and mosquitoes supplement their diet with nectar, or at least the male feeds on nectar. In some cases hematophagous midges are primary pollinators, such as ceratopogonids visiting *Theobromia cacao* [Young et al., 1984] and mosquitoes visiting the small North American orchid *Habenaria obtusata* [Dexter, 1913; Thien, 1969a, b]).

The ground plan for insects is to have mouthparts with three paired structures (maxillae, labial appendages, and mandibles) and three main central structures (the labium, labrum, and hypopharynx). In the many convergent cases where a proboscis has evolved, the constituent parts of the mouthparts are modified in different ways. Unfortunately, while an elongate proboscis may be preserved even as a compression fossil, the component parts are usually not distinguishable, and this can lead to ambiguity about the function of long proboscides in some fossil insects. *Pseudopolycentropus latipennis* Martynov (Paratrichoptera: Mecoptera), from the Upper Jurassic of Karatau, Kazakhstan, has a long, slender proboscis nearly twice the length of the head, which is much longer and more slender than any living mecopteran (Novokshonov, 1996). Since some mecopterans, the Bittacidae, have predatory adults, it is possible that this species had similar habits. If the detailed morphology of the proboscis components were preserved well enough, one could probably resolve whether *Pseudopolycentropus* used the proboscis for impaling prey or probing flowers.

Tracking the appearance of an elongate proboscis in the fossil record as an index to insect anthophily is a conservative approach. Without documentation of ingested fossil pollen, insects with a generalized morphology that visited flowers are easily overlooked. Most insects visiting flowers, in fact, have a generalized morphology. A four-year study of the insects visiting flowers of wild carrot (*Daucus carota*) in Logan, Utah, revealed 334 species in 37 families (Hawthorne et al., 1956). In a similar study of the insects on ragwort flowers (*Senecio jacobaea*), 178 species were found (Harper & Wood, 1957). In one area of Nova Scotia, 93 species of insects in 15 families were found visiting blueberries, *Vaccinium angustifolium* Aiton and *V. myrtilloides* Michaux (Finnamore & Neary, 1978). A total of 192 species of insects are known to visit blueberry flowers in eastern North America. Many of these species are itinerant, casual visitors without specialized structures for feeding from flowers. However, also included are some obligate anthophiles, like *Apis* (honeybees), halictids (sweat bees), and syrphids (flower flies), which are morphologically specialized and also the most persistent insect visitors. On the whole, obligate anthophiles are the most efficient pollinators, the most morphologically specialized, and ecologically most important for pollination; their history should better reflect angiosperm history than other groups of insects.

4. Phylogeny and Fossils of Obligate Anthophiles.

The approach taken here was to examine the phylogeny, fossil record, and biogeography (where applicable) of those insect lineages that predominantly comprise obligate visitors of flowers: Lepidoptera, Apidae sensu lato (bees), masarine wasps, and various families of lower Brachycera flies. The fossil record of each of these groups is spotty—typical for most insects—such that a generic or species-level diversity analysis will add little further resolution. Rather, a chronology is more accurately inferred by understanding the phylogenetic position of those few, critical fossils. I have attempted to superimpose cladistic relationships on a geological chronology by assessing the phylogenetic positions of fossils. This approach relies on phylogenetic studies for the various groups and scrutinizing the fossil for evidence of salient, diagnostic features (for the latter I often had to rely on accuracy of the published descriptions). Ages of clades, then, are strictly based on minimum estimates. However, I have also tried to estimate absolute ages based on correlations between phylogenetic position and fossil age.

HYMENOPTERA

BEES: SPHECOIDEA: APIDAE SENSU LATO

Bees are, by far, the most important group of insect pollinators. Many bees are foraging specialists, thus making them efficient pollen vectors. According to a study by Moldenke (1976), about 2000 species of bees occur in the Great Basin, Sonoran Desert, and xeric regions of the western U.S., 60% of which are specialists on a genus or family of flowering plants. The social bees, in particular, are spectacularly efficient at foraging, because the division of labor allows specialization of tasks and rapid recruitment to new resources. This is why colonies of *Apis* can harvest honey in such surplus that it is productive for agriculture, and why they can outcompete wild bee species wherever they colonize.

Traditionally, the bees are put into the superfamily Apoidea, with varying numbers of families, although it has been known for a long time that the bees were closely related to and perhaps derived from within the Sphecidae. Alexander's (1992) exploratory cladistic study of the tribes of Sphecoidea is the most comprehensive analysis of the group thus far. Instability in the sphecoid cladogram varies with the use of characters having problematic polarity, inclusion of enigmatic taxa, and methods of analysis. Some regions of the most parsimonious cladograms, however, are quite stable. In particular, the Apidae appear closest to a clade that consistently groups together the sphecid tribes Philanthini + Aphilanthopini + Cercini + Pseudoscolini + Psenini + Xenosphecini. Relationships among these tribes were highly unstable in Alexander's analysis, but as expected, the bees are a monophyletic group. All bees should best be phylogenetically categorized as a family in the Sphecoidea. In the cladogram of bee families and significant genera, though (Fig. 1), I have retained the traditional bee taxonomy simply for ease of recognition.

The fossil record of bees needs to be considered in the context of the fossil record of all aculeates (the stinging wasps, including ants and bees), but particularly the Sphecidae. The earliest fossil aculeates are the extinct family Bethylonymidae, from the Upper Jurassic of Kazakhastan, which is also the only family of aculeates known from the Jurassic. Modern families of aculeates appear first in the Cretaceous, most of them in the mid- to Upper Cretaceous (e.g., Grimaldi et al., 1997, for ants; review of aculeate families up to 1984 in Carpenter, 1992). The Sphecidae are no exception, with 11 records from the Cretaceous, 6 of them in various ambers: *Archisphex* Evans (Santonian, Siberia; Hauterivian, Weald Clay, England), *Angarosphex* Rasnitsyn (Lower Cretaceous, Baissa; Weald Clay), *Cretosphex* Rasnitsyn (Aptian, Brazil; and others), *Eopinoecus* Budrys (Santonian, Siberia), *Gallosphex* Schlüter (Cenomanian, France), *Lisponema* Evans (Santonian, Siberia), *Pittoecus* Evans (Campanian, Canada), an undescribed genus from the Turonian of New Jersey, and several very primitive, undescribed forms from the Lebanese Neocomian amber. The genera from Brazilian limestone (Darling & Sharkey, 1990), and from Canadian, Siberian, and New Jersey amber are pemphredonines, and Jarzembowski (1991) considered *Archisphex* and *Angarosphex* to possibly be pemphredonines. According to Alexander's (1992) analysis, the Pemphredoninae are of intermediate phylogenetic position in the Sphecidae. It is virtually certain that sphecoids originated in the Lower Cretaceous, perhaps in the uppermost Jurassic, which helps explain the chronology of bees.

Bee phylogeny was most recently and comprehensively treated by Alexander and Michener (1995) and Roig-Alsina and Michener (1993). The cladograms in both studies were highly unstable, so the topology on which fossils are superimposed in Figure 1 is one of several of the most parsimonious schemes. This should not affect basic conclusions on bee origins. With the exception of stingless honeybees (Meliponini) in some Cenozoic ambers, bees are not common fossils. In fact, until the last decade, the fossil record of bees was almost entirely reflected by fossils from particularly rich Lagerstätten, especially the vast deposits of Eocene-Oligocene Baltic amber, and the Oligocene shales of Florissant, Colorado. Evaluating the systematic position of most fossil bees, particularly those preserved as compressions, is complicated by the lack of crucial, minute details, such as of the mouthparts.

A report of bees from the Triassic is easily dismissed, particularly since it antedates by 50 Ma the earliest appearance of the most primitive aculeate wasps, the Bethylonymidae. In the Chinle Formation (Upper Triassic, Arizona) are nest cells preserved in araucarioid wood (Wilford, 1995), but critical features of wood-nesting bee cells are not preserved, such as pollen clumps and special linings. It is most likely that these "cells" are gallery chambers of wood-boring beetles, such as cupedoids.

The oldest definitive fossil bee is *Trigona prisca* (Michener & Grimaldi, 1988a, b), in Cretaceous amber from New Jersey (Fig. 2). (A fossil wasp, *Paleapis beiboziensis* Hong, 1983, from the lower Cretaceous of China, can be dismissed as clearly not a bee; C. D. Michener, pers. comm. 1997). *Trigona prisca* is a controversial fossil for various reasons, several of which are discussed in Rasnitsyn and Michener (1991). Firstly, it belongs to one of the most highly derived groups of bees, the Meliponini, which to some experts is implausibly of

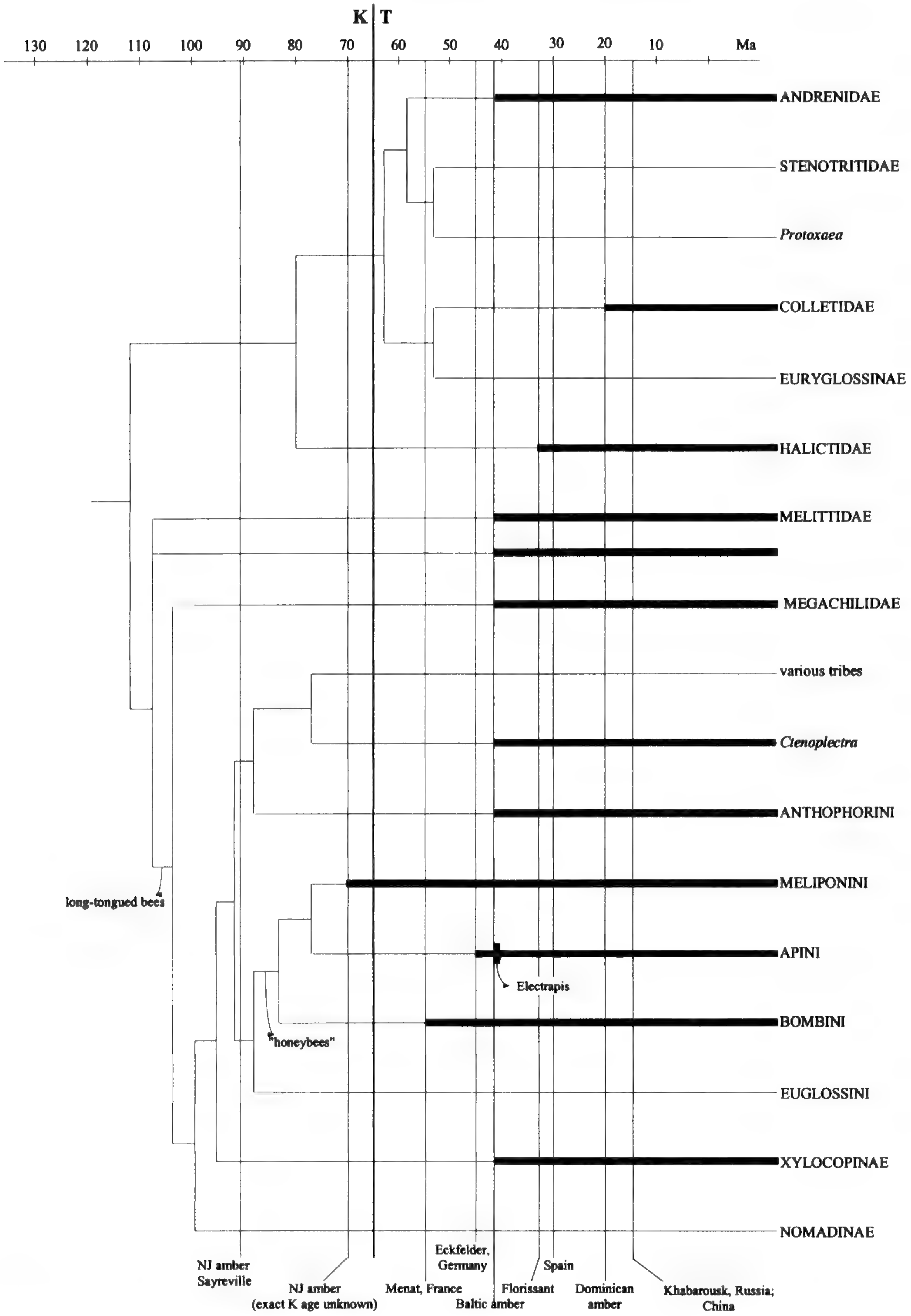


Figure 1. One of several most parsimonious cladograms of families, subfamilies, and some genera of bees, taken from Alexander and Michener (1995) and Roig-Alsina and Michener (1993), with dates of representative fossils included. The basal diversification of bees in the Cretaceous is constrained by the fossil record of the Sphecidae, from which bees are derived. The earliest sphecid is from the Barremian.

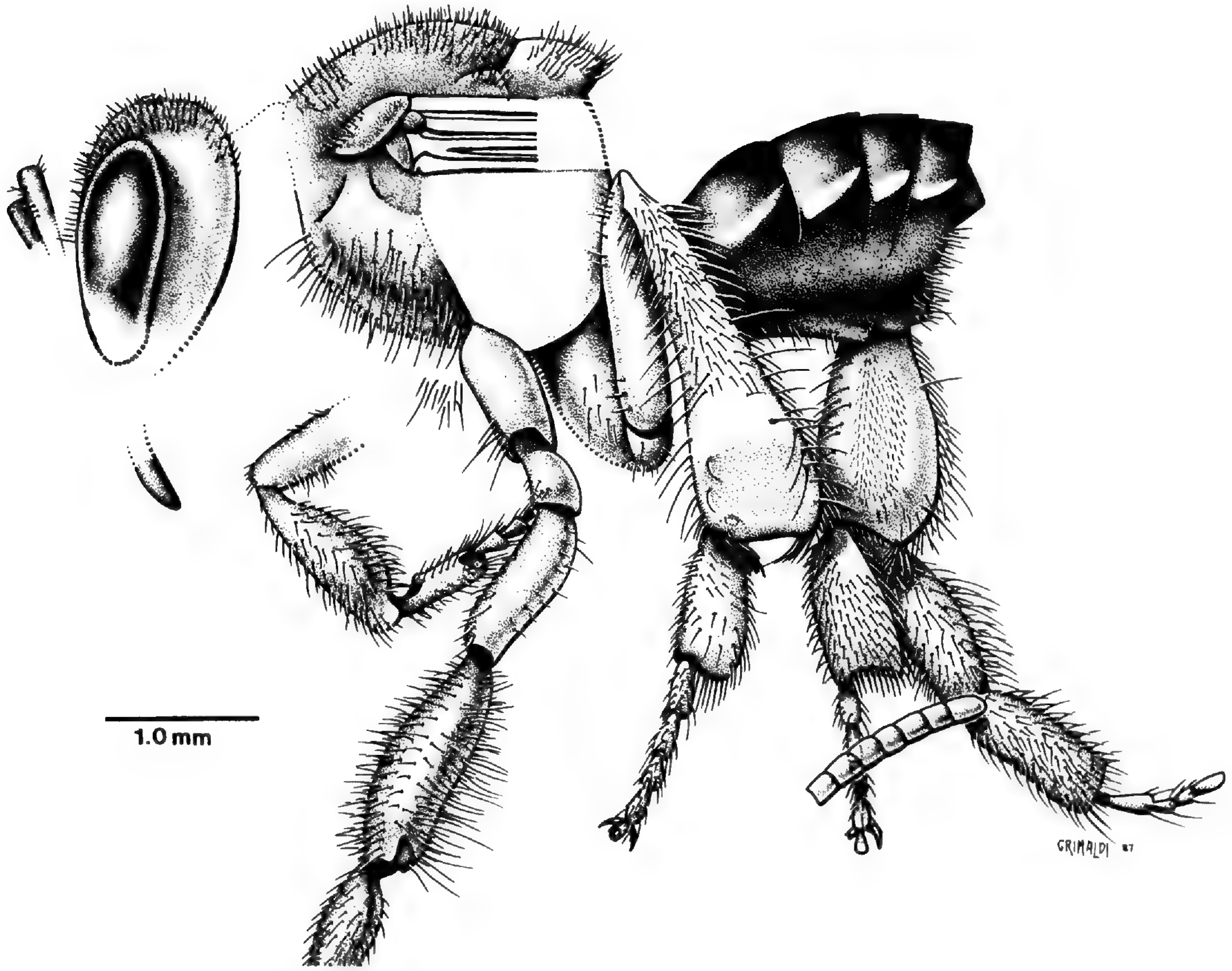


Figure 2. The oldest known bee, *Trigona prisca* (Apidae: Meliponini), in amber from the (presumably uppermost) Cretaceous of New Jersey.

Cretaceous age (Alexandr Rasnitsyn, pers. comm. 1990). Secondly, it was discovered in an old collection of amber fossils, labeled with the collector and town of origin (Kinkora, New Jersey), but stratigraphy is unknown, leading some to believe it is not even Cretaceous. Lastly, there are various other insects preserved in the same piece of amber as *Trigona prisca*, such as a wing of a termitid or rhinotermitid termite, a milichiid fly, and an emesine reduviid. All are fossils of rather derived insect groups that are regarded by some as improbably of Cretaceous age.

Evidence consistent with the Cretaceous origin of the *Trigona prisca* amber piece is the following: (1) Infrared spectroscopy and pyrolysis gas chromatography of barren fragments taken from the piece compares closely with amber samples collected in New Jersey by myself, which have well-documented stratigraphy (Grimaldi et al., 1989). (Since these samples have been taken, the fragile piece has been embedded in synthetic casting resin to protect it from accidental damage and oxidative degradation). (2) Based on some mayflies, staphylinids, neuropterans, dipterans, and other groups in amber from New Jersey that is accurately dated to Turonian, it is not at all unusual for there to be from this time period extinct species belonging to extant genera, or genera very closely related to modern ones. Also, since rampant morphological convergence in meliponines obscures tribal relationships, it is not even entirely clear that *T. prisca* is a *Trigona* (Michener, 1990). (3) The mid-Cenozoic diversity of bees is probably biased by the vast deposits of Baltic amber; excellent preservation of a sphecoid in such amber allows unequivocal determination of whether it is a bee or not. If, for example, a fossil bee that did not possess an obvious derived feature, like corbiculae, were preserved as a compression, it is doubtful it would be recognized as a bee at all. In contrast, some Cretaceous compression fossil sphecids are plausibly bees, but the exact relationships of the fossils are obscured because critical characters like branched hairs are not preserved. For example, some species of the Cretaceous genus *Cretosphex* are plausibly bees (see Darling & Sharkey, 1990). It is only in the Cenozoic that we find compression fossilized bees with unequivocal identity, because many other, derived characters like enlarged corbiculae are preserved (e.g., *Eckfeldapis*, which actually appears to be synonymous with *Electrapis* in Baltic amber; M. Engel, pers. comm. 1997). Also, Cretaceous nests of aculeates may be halictid bees but lack definitive, diagnostic features. Nests of cells from the Upper Cretaceous of Uruguay were considered to be halictids (Zeuner & Manning, 1976), while nests of similar morphology, age, and location, tentatively identified as *Sceliphron* (Sphecidae) or Eumeninae (Vespidae) (Schlüter, 1984) have cells with one convex and one concave wall, as in the nests of bees and particularly similar to ground-nesting halictids (J. Wenzel, pers. comm. 1997). (4) The existence of undisputed, mid- (Turonian) and Lower (Aptian) Cretaceous pemphredonine sphecids is consistent with the presence of bees during the Cretaceous. (5) The existence of some bees in the Apinae from the lower Cenozoic is also consistent with Upper Cretaceous meliponines. These include extinct species from the Oligocene of Germany belonging to the living genus of honeybees, *Apis* (Engel, 1998a); a bombine (bumblebee) from the Paleocene of France; and eusocial bees in the extinct sister genus to *Apis*, *Electrapis*, from Eocene Baltic amber (e.g., Engel, 1998b). (6) True, resinous amber from New Jersey is known only from the Upper Cretaceous, but varies in age from Cenomanian to latest Maastrichtian (the latter being at the K/T boundary) (Grimaldi et al., 1989). Thus, it is quite possible, even likely, that *T. prisca* comes from the uppermost Cretaceous, ca. 65 Ma. *Trigona prisca* minimally indicates that the history of bees reaches into the Cretaceous. In Figure 1 I have concentrated the basal divergences of bees near the Cenomanian and Aptian based on indications from the much better fossil record of the sphecids. This scenario hypothesizes a very explosive radiation of bees in the mid-Cretaceous, with the origins of many bee subfamilies, tribes, and other such taxa somewhat later.

VESPIDAE: MASARINAE (POLLEN WASPS)

The Masarinae are a relatively small group (ca. 300 species worldwide) of solitary vespid wasps, one of six extant subfamilies of Vespidae. The eumenines, by contrast, have approximately 3000 species. The masarines are the only wasps besides bees that provision nests with nectar and pollen. Most species are found in South Africa (155 species), the Mediterranean region (90 spp.), Australia (32), and then southern South America (16) and western North America (14). Carpenter (1993) provided a general area cladogram of world genera, with relationships being: Australia (South America (south Africa (Palearctic + Nearctic)))—a classic Gondwanan distribution. Gess (1996) reviewed the natural history, distributions, behavior, and ecology of the masarines, and Carpenter (1989, 1997) examined phylogenetic relationships of masarine genera. The wasps are small, 4–20 mm in length, with proboscides 0.14–1.3 times the length of the body, depending on the species (Fig. 3). The records of flower associations indicate a high degree of oligolecty in these wasps and their importance as pollinators (Gess, 1996).

There are no fossil masarines, but fossil vespids in other subfamilies (Carpenter & Rasnitsyn, 1990; Wenzel, 1990), some patterns of biogeographic distributions (Carpenter, 1993), and the phylogeny of vespid subfamilies (Carpenter, 1981, 1990) allow a fairly good estimate of masarine age. The oldest vespids are *Priorvespa*, in the extinct subfamily Priorvespinae; and *Curiosivespa* in the most primitive, living subfamily (Euparagiinae). Both of the fossil genera are known from the Lower Cretaceous (Barremian/Aptian) of Baissa, with *Curiosivespa* also known from the mid-Cretaceous (Turonian) of Kzyl-zhar. An undescribed, primitive eumenine is known from Turonian amber from New Jersey (Carpenter, in litt.); and the oldest fossil of social vespids (Polistinae + Vespinae) is *Celliforma* Brown, a fossil nest comb from Upper Cretaceous deposits of undetermined age from Utah (Wenzel, 1990). Another ichnogenus, *Desertina* Nessov, from the Upper Cretaceous of the Kyzylkum desert in Kazakhstan, appears very similar to *Celliforma* (J. Wenzel, pers. comm. 1997). Because *Celliforma* and *Desertina* are form genera, it is impossible to determine their phylogenetic position among the social vespids.

Excellent correspondence is found among the phylogenetic position of the Mesozoic fossil vespids and their ages (Fig. 4): the most primitive ones are Lower Cretaceous and mid-Cretaceous (Turonian); another Turonian fossil is of intermediate phylogenetic position; and a social vespid nest, the most derived of all vespids, is found in the Upper Cretaceous. The Vespidae probably originated in the lowermost Cretaceous, and most of the living subfamilies appear to have originated in the mid Cretaceous, which is consistent with the disjunct Gondwanan distribution of the masarines. Since genera and generic groups of masarines are highly endemic to continental areas (e.g., within southern Africa), most of the diversification of masarines has taken place since the mid-Cretaceous.

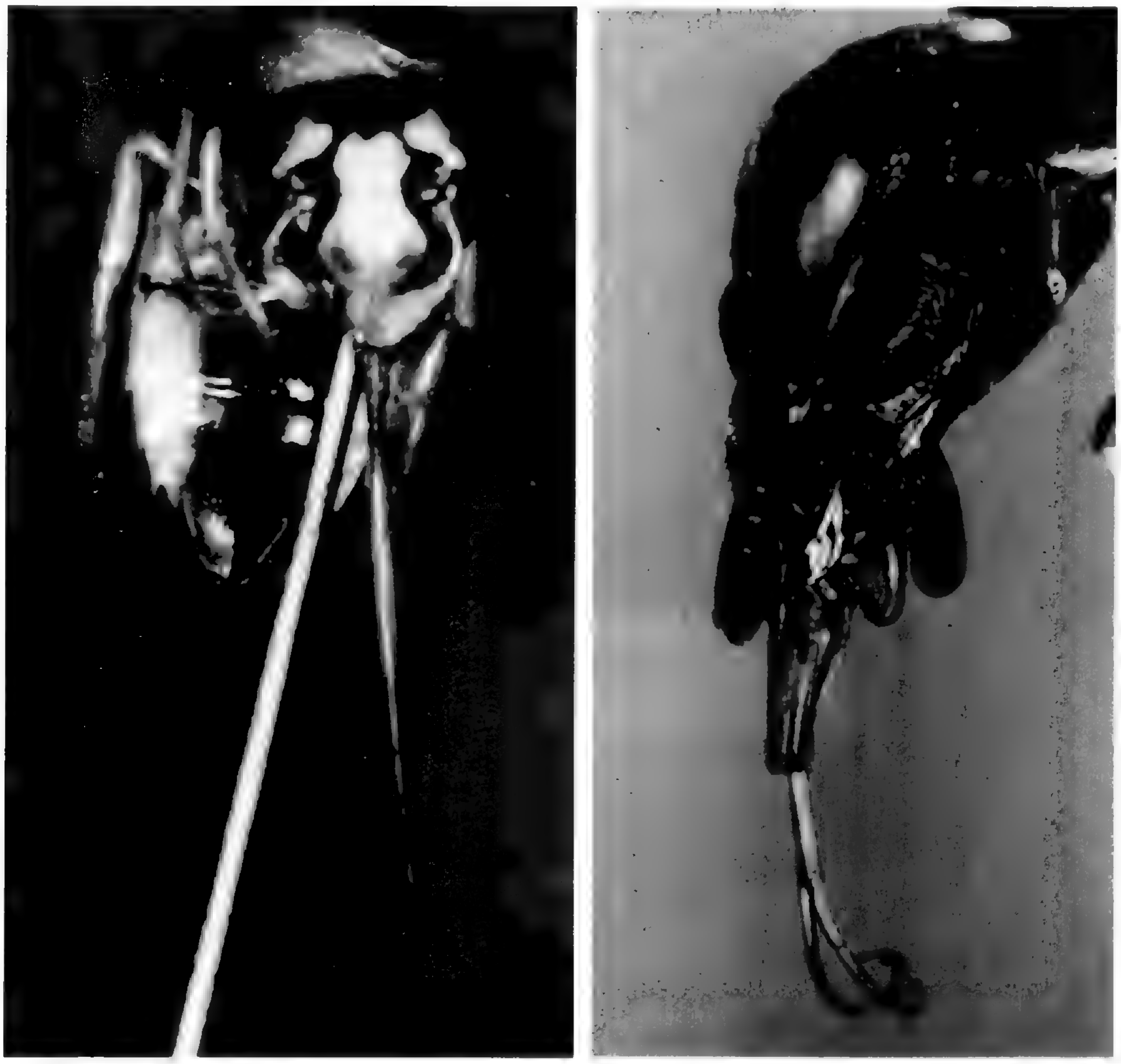


Figure 3. Extant species of masarine wasps, *Celonites varipennis* (left) and *Trimeria americana* (right). The glossa of *Celonites* is fully distended. Photos by J. M. Carpenter.

DIPTERA

The ecological significance of the Diptera, or true flies, is often overlooked, especially with regard to pollination. Judging from morphology, obligate anthophiles are probably more widespread in the Diptera than are presently recognized. Long proboscides that are clearly not used for sucking blood, but are probably used for feeding from flowers, are scattered throughout the nematocerous Diptera, despite the characterization by Proctor et al. (1996) that nematocerous Diptera have generalized, short proboscides. In North America alone, genera of nematocerous Diptera with elongate probsocides are ***Elephantomyia*, *Ornithodes*, *Toxorhina*,** and ***Limonia*** (Geronomyia) (Tipulidae: craneflies); ***Lygistorrhina*** and ***Gnoriste*** (Mycetophilidae: fungus gnats); and ***Eugnoriste*** (Sciaridae). In addition, elongate proboscides occur in various phorids (scuttleflies); and in empidids, or dance flies (***Iteaphila*, *Toreus*, *Anthepiscopus*,** and some ***Empis***), which employ them for predation and/or flower feeding. In regions where bees are scarce, Diptera are often the dominant pollinating group. For example, McAlpine (1965) found at least 18 species of flies feeding on flowers on Ellesmere Island in the Canadian Arctic, making this order the primary pollinator group in that region.

The recent reports by Ren (1998a, b) have emphasized the importance of Diptera as earliest pollinators. He reported three families of flies in Upper Jurassic rocks from Lianoning, China, which belong to the lower Brachycera. Representatives of two of these families, the Tabanidae and Nemestrinidae, had long proboscides equal to or longer than the head length. The third family, the extinct Protapioceridae, is dismissed as anthophilous by lack of evidence (see below under Apioceridae). The conclusion that the fossil Nemestrinidae were anthophilous is compelling (see below), but the evidence that the Jurassic tabanids were anthophilous is unconvincing.

Ren (1998a, b) described three Upper Jurassic tabanids from the Yixian Formation, which he placed in the family on the basis of pulvilliform empodia (on the feet) and the apices of wing veins R_4 and R_5 encompassing the wing tip; he placed

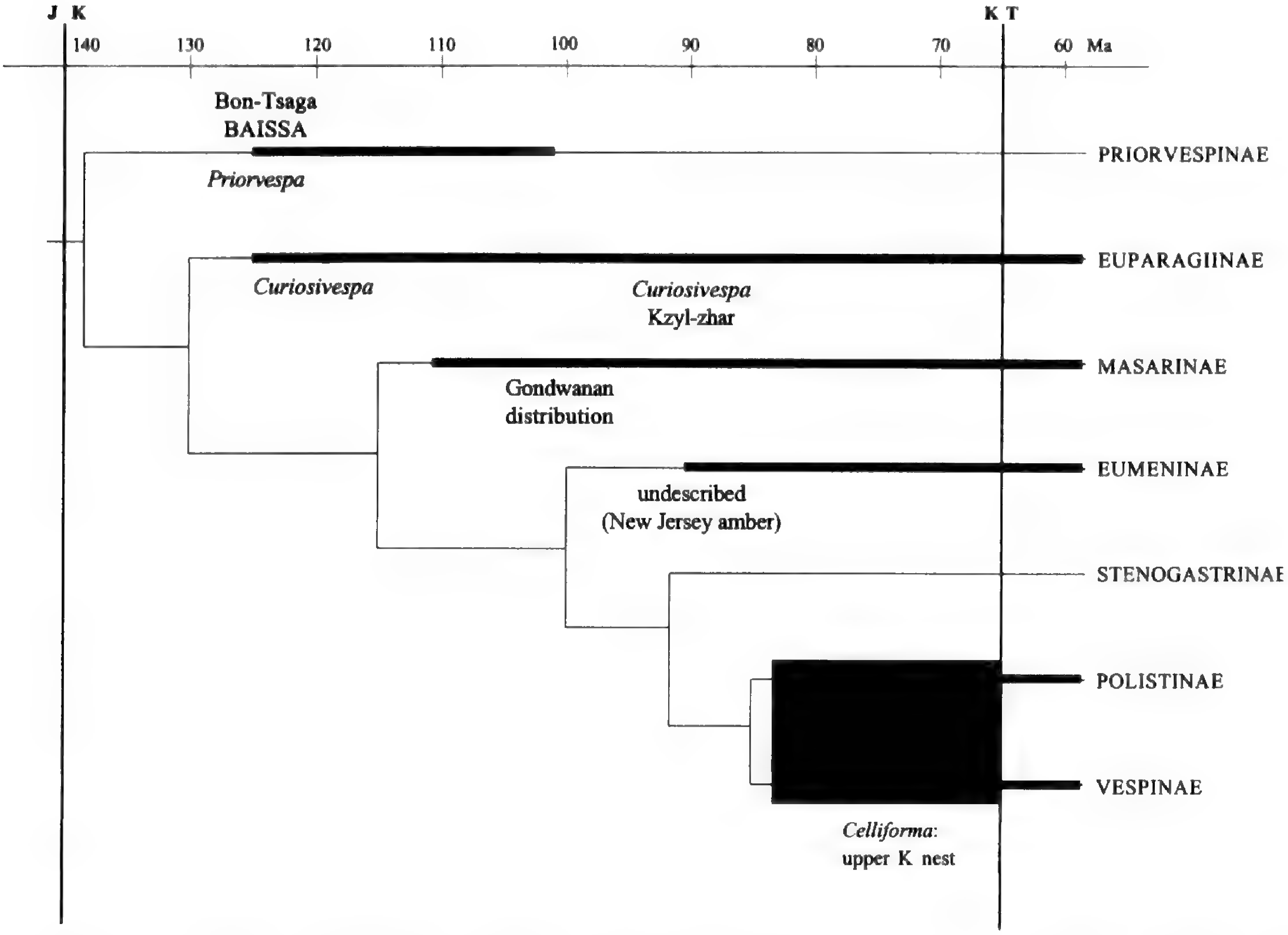


Figure 4. Cladogram of subfamilies of Vespidae, from Carpenter (1981, 1990; Carpenter & Rasnitsyn, 1990), with positions of all known Mesozoic fossils included. Age of the Masarinae, or pollen wasps, is inferred on the basis of a Gondwanan distribution.

the flies specifically in the subfamily Pangoniinae on the basis of a long proboscis. Further, he cited Colless and McAlpine (1991), that "most extant pangoniines are exclusively flower feeders" (Ren, 1998b: 85). Colless and McAlpine (1991: 755) actually said: "Most of the Australian [pangoniine] species suck blood, but some species of *Scaptia* appear to be exclusively flower-feeders . . . ."

Identification of the Chinese Jurassic fossils as tabanids is uncertain, since a pulvilliform empodium is plesiomorphic for this family (and found throughout the lower Brachycera). In addition, the structure of radial wing vein apices seen in the fossils is also found in other families, like Pelecorhynchidae and *Pseudoerrina*, and even in the fossils they are less divergent than in living tabanids; veins R_{4-5} in the fossils diverge near the posterior m crossvein, unlike modern tabanids and more like Rhagionidae; and the large lower calypter typical of tabanids is not preserved or is absent in the fossils. Ren's "tabanids" are therefore most likely to be rhagionid ("snipe") flies, a primitive family (suspected to be paraphyletic) that is well represented in Mesozoic deposits. Modern rhagionids are predatory and some even hematophagous. Some Mesozoic rhagionids had projecting, but not particularly long, proboscides (Grimaldi & Cumming, 1999).

The main groups of pollinators in the Diptera are large-bodied species in various families of lower Brachycera: Acroceridae, Conopidae, Mydidae, Scenopinidae, Stratiomyidae, Nemestrinidae, Apioceridae, Bombyliidae, and Syrphidae, with the last four being the most ecologically significant pollinators. Most of these flies are fast fliers and excellent hoverers, making them very efficient for foraging from flowers. A convergent feature among the hovering, anthophilous Diptera is a concentration of the apical wing veins, which are also upturned (Fig. 5). These modified wing veins strengthen the apex of the wing blade from the intense forces generated at very high wing-beat frequencies. The only other kinds of flies with this apical wing vein scaffold are a few blood-sucking, parasitic, and insectivorous flies, like some tabanids (horseflies/deerflies) and asilids (robberflies), the tsetse flies (Glossinidae), and botflies (Oestridae); rarely, though, are the veins in these flies as distorted as in the hovering anthophiles. Nagatomi and Soroida

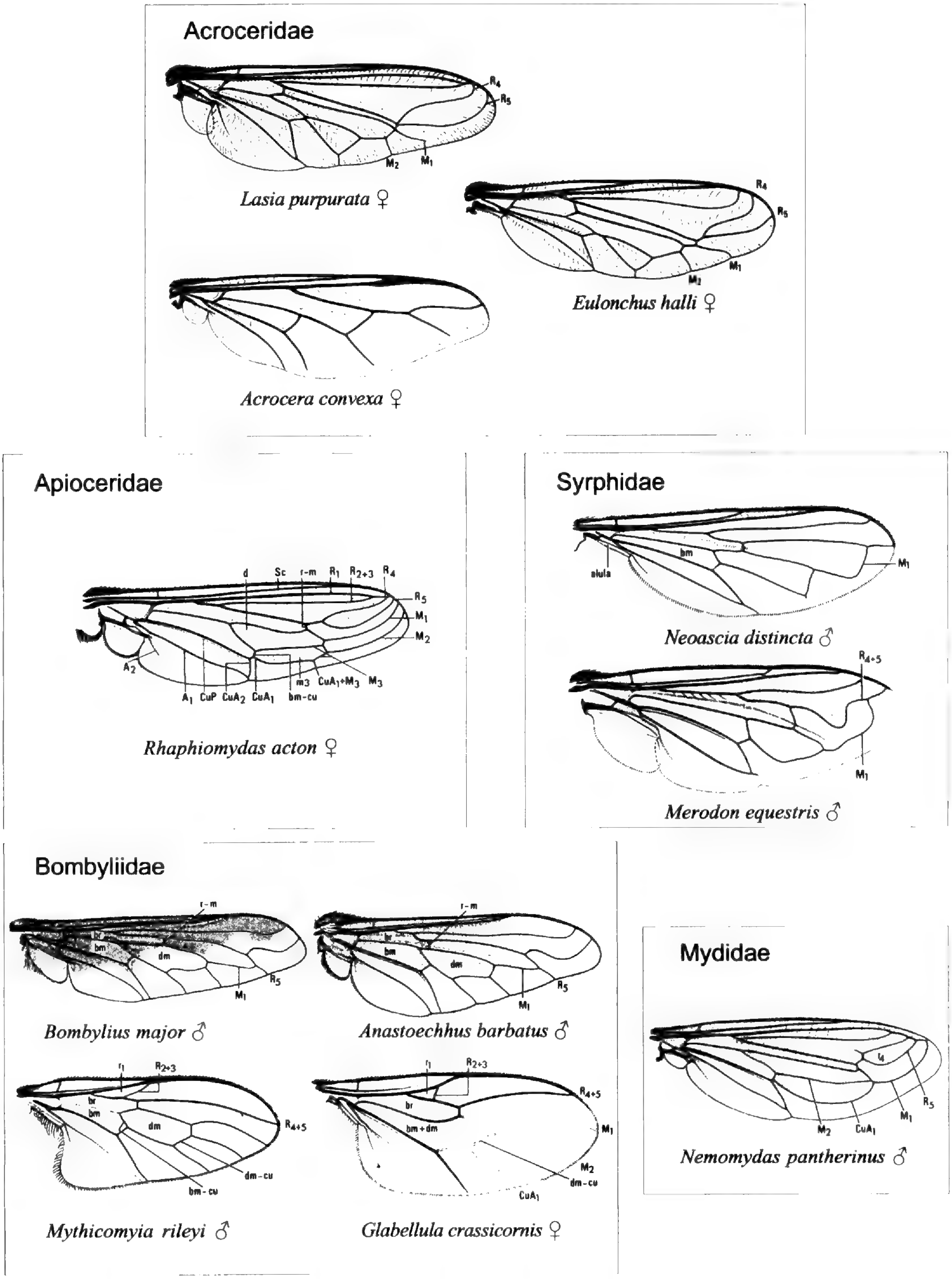


Figure 5. Wings of representative, extant anthophilic Diptera. Note the coalescence and curvature of the apices of the veins in some species. Development of this feature is strongly correlated with development of an elongate proboscis (see Fig. 6). Modified from McAlpine (1981).

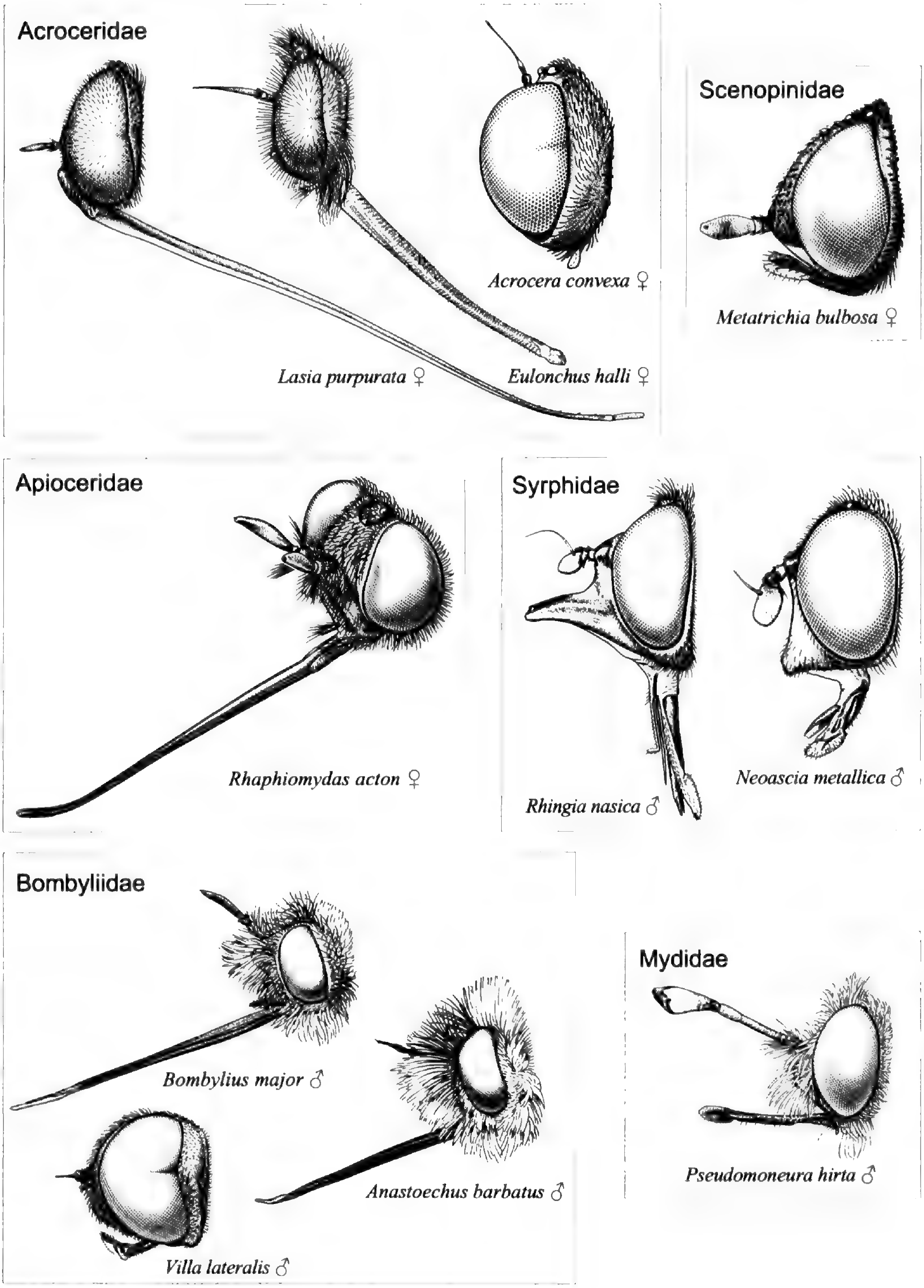


Figure 6. Heads and proboscides of representative species of Diptera belonging to anthophilic families.

(1985) presented a comparative morphological study of the mouthparts of "orthorrhaphous" flies, illustrating various ways in which mouthparts are elongated into a proboscis.

Mesozoic fossils of "lower" Diptera are relatively abundant compared to the other orders, and the phylogenetic relationships within the order have been intensively investigated (Fig. 7). Nematocerous Diptera first appear in the Triassic (Shcherbakov et al., 1995; Fraser et al., 1996), and the Brachycera appear in the Lower Jurassic. Understanding of the biogeography of Diptera has also progressed, with development of phylogenetic systematics in the group and studies like those of Hennig (1960) and Brundin (1966) on austral Diptera. The south temperate Diptera, in fact, roughly reflect what is known about relationships and fossils. The Cyclorrhapha (= Muscomorpha), a monophyletic group and the most derived infraorder, shows barely any austral distributions. The suggestion is that this assemblage of about 70 families and some 60,000 described species is a post-Gondwanan radiation; that is, one that post-dated the separation of Australia, South America, and Africa some 100 Ma. The Conopidae are one family for which there are just several Cenozoic records and the phylogenetic relationships of genera have not been at all explored, so little can be said about the origin of this family.

ACROCERIDAE

Acroceridae, or "small-headed flies," have very uniform life histories as internal, larval parasitoids of spiders, but their adult morphology is extremely varied. Some genera, like *Acrocera*, *Ocnaea*, and *Ogcodes*, have vestigial mouthparts and probably do not feed as adults. Other genera, like *Eulonchus*, *Lasia*, and *Philopota*, have among the longest proboscides in the Diptera, equal in length to the body. It is interesting to note that the long-proboscis genera also have wing venation that is complete and with apical veins that are crowded and upturned, typical of excellent hoverers (other genera have a venation that is so reduced that they probably cannot hover). Indeed, these genera are excellent hoverers, and even though acrocerids in general are rarely seen, the long-proboscis genera are usually encountered visiting flowers. For example, Schlinger (1960) and Grant and Grant (1965) reported *Eulonchus* to be faithful visitors to species of *Gilia* and *Linanthus* (Polemoniaceae), the flowers of which have long, slender corolla tubes.

Fossils of acrocerids are exceptionally rare; also, despite the fact that the family is small (50 genera with 500 described species), the phylogenetic relationships of acrocerid genera have not been examined. The oldest fossils of the family are *Archocyrtus gibbosus* Ussatchov and *Juracyrtus kovalevi* (Nartshuk, 1996), from the Upper Jurassic (Kimmeridgian) of Karatau, Kazakhstan. *Archocyrtus* does not possess a long proboscis; the wing venation is simplified as in many acrocerid genera, and lacks the apical vein buttress. This fly certainly did not hover and probably did not feed on pollen. *Juracyrtus*, however, has similar, simplified venation but is reported as having a proboscis considerably longer than the length of the body. The rendering of the fossil (Fig. 8a) indicates that the interpretation of the long, thin structure as a proboscis is ambiguous: connection to the base of the head is not definite, nor is there any fine structure confirming it as a proboscis (or possibly a stray object). Most importantly, the wing venation is definitely not of the hovering type, which all living acrocerids have that also have proboscides of this length. Unfortunately, there are no Cretaceous acrocerid fossils, and the only other fossils are in Cenozoic amber. In Baltic amber (Eocene/Oligocene) there are *Glaesoncodes* Hennig (1968), *Prophilopota* and *Villalites* Hennig (1966a), all of which are closely related to extant genera. In Miocene Dominican amber, *Ogcodes exotica* is closely related to several African and Asian species (Grimaldi, 1995). The age and plesiomorphic nature of *Archocyrtus* and *Juracyrtus*, combined with two Tertiary amber records, are consistent with a late Mesozoic origin and Cretaceous diversification of the family.

MYDIDAE AND APIOCERIDAE

These families, although not particularly closely related, are discussed together because several genera in both families have had a confused taxonomy. Fortunately, the phylogenetic work of Yeates and Irwin (1996) has rectified the taxonomic problems and even reported an illuminating biogeographic pattern. The fossil record of the two families is scant. An Oligocene fossil mydid is placed in the living genus *Mydas*, as *M. miocenicus* Cockerell. Two Mesozoic species exist, of the extinct genus *Protapiocera*, from the Upper Jurassic of China (Ren, 1998a, b). Ren placed *Protapiocera* in a separate family from the living Apioceridae, and the coalescence and near-coalescence of the apical parts of the radial wing veins definitely indicate a close relationship of the two taxa.

Mydids and apiocerids are mostly large flies of xeric habitats. They are excellent fliers, and particularly the Apioceridae are renowned for their hov-

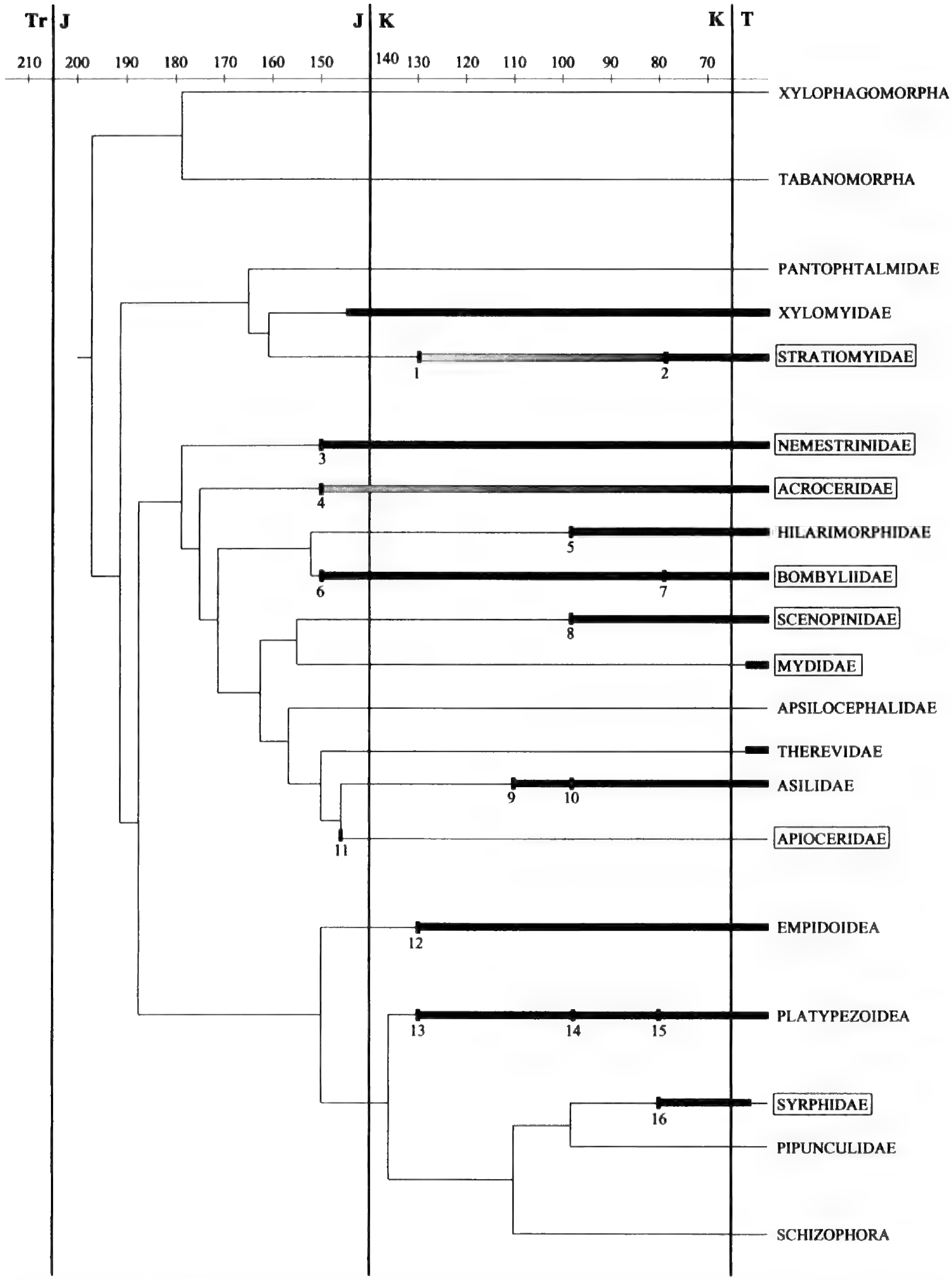


Figure 7. Relationships of families of lower Brachycera flies, derived from Woodley (1986), Yeates (1994), and Cumming et al. (1995). Total lengths of lines indicating clades provide a broad estimate of ages of various clades. Records of undescribed specimens from New Jersey and Lebanon are based on Grimaldi and Cumming (1999). Families in boxes are major anthophilic groups.

Numbers on cladogram: 1, undescribed stratiomyid, lower Cretaceous of Montsec, Spain; 2, *Cretaceogaster*, Canadian amber; 3, various described nemestrinids, Karatau, Kazakhstan; 4, *Archocyrtus* (placement is questionable); 5, undescribed hilarimorphid, Turonian amber, New Jersey; 6, *Paleoplatypygus*, Karatau; 7, *Procyrtosia*, *Proplatypygus*, in Sanering ability. Some genera have short or vestigial mouthparts, while others have long proboscides (subgenus *Apiocera*, and in the Mydidae: *Rhaphiomidas* and *Neorhaphiomidas*). Species with medium to long proboscides are typically found feeding from flowers. According to the cladistic results of Yeates and Irwin (1996), the genus *Rhaphiomidas*, traditionally placed in the Apioceridae, is actually the sister group to the Mydidae, including the plesiomorphic subfamily Megascelinae of the Mydidae; the Megascelinae have an austral distribution. There is, in fact, perfect correspondence in the cladistic biogeography between the subgenera of *Apiocera* (the sole genus of the Apioceridae) and the plesiomorphic mydids. The biogeographic relationships are (western) North America (Africa (Australia + South America)). One must conclude that the ancestral clades of Apioceridae and Mydidae existed in the late Mesozoic, prior to the major Albian rifting ca. 110 Ma (Barron, 1987). An Upper Jurassic origin of these families suggested by Yeates and Irwin (1996) is supported by the recent discovery of the Chinese Jurassic *Protapiocera.*

Since *Rhaphiomidas* has a long proboscis and is the most primitive clade of the mydids, this might be suggestive of an Upper Jurassic-Lower Cretaceous origin of a long proboscis. Actually, this inference could only be made if all/most other primitive clades in *Apiocera* and Megascelinae also had a long proboscis, but in fact a long proboscis evolved three times in both groups. Thus, the long proboscis could have evolved at any time between the earliest Cretaceous and throughout the Cenozoic, and it is also significant that *Protapiocera* fossils, from the Upper Jurassic of China, do not have the mouthparts preserved. Ren (1998b), however, still concluded that these fossil flies were anthophilous, because of the hirsute body—a feature possessed by many anthophilous insects. This is entirely speculative, since species with hirsute bodies are scattered throughout non-anthophilous Diptera: many Asilidae, Therevidae, and some Empididae (predatory); some Tabanidae (hematophagous); and the Heleomyzidae, Psychodidae, and Scathophagidae (saprophagous and coprophagous). Conversely, many anthophilous Diptera are not particularly hirsute, such as the proratine scenopinids, Stratiomyidae, and many Syrphidae. A reasonable estimate is that a long proboscis and pollen feeding in apiocerids and mydids appeared in the Upper Cretaceous.

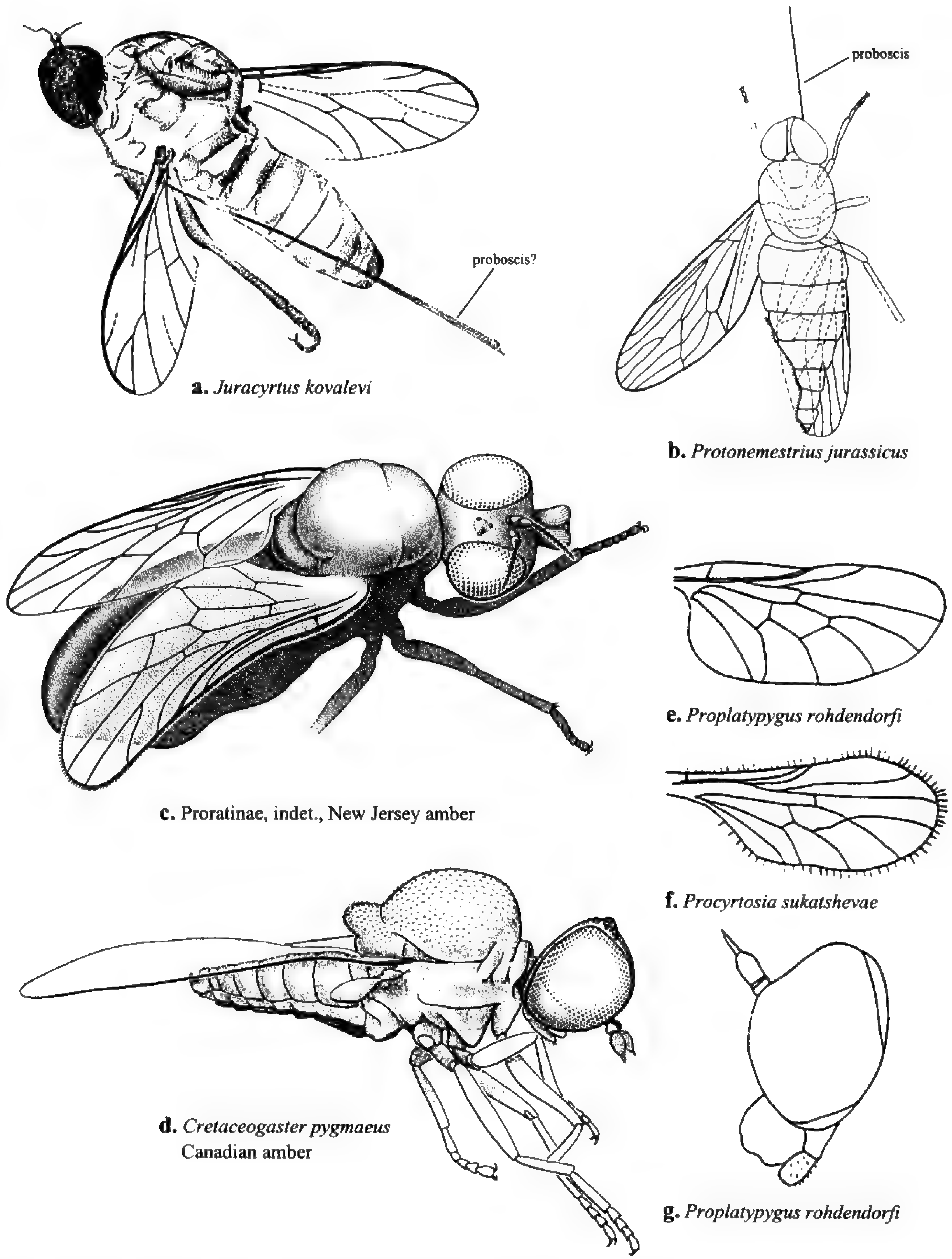
NEMESTRINIDAE

These are relatively large and hirsute flies that are superb fliers and that have the apical venation of the wing buttressed by extreme coalescence (hence their common name, "tangle-veined flies"). Among the 300 species and 20 living genera, all but a few genera (e.g., *Trichopsidea*) have a slender proboscis that is as long as the head or longer (the trichopsideines have a very reduced, vestigial, or even non-existent proboscis). The South African *Moegistorhynchus longirostris* has the longest proboscis of all insects relative to the body size, nearly four times the body length. Nemestrinids with the longest proboscides have extreme buttressing of the apical wing veins, to the point of the veins becoming reticulate. The apical veins in the wing of *Moegistorrhynchus*, for example, form a lacey network. Understanding the evolution of this group is greatly facilitated by the fact that it is probably the best represented family of Brachycera in the fossil record.

The oldest Nemestrinidae are from the very rich Upper Jurassic (Kimmeridgian) beds of Karatau, Kazakhstan (*Archinemestrius* Rohdendorf, *Protonemestrius* Rohdendorf, and *Eohirmoneura* Rohdendorf), and from the Yixian Formation, Upper Jurassic, of Liaoning, China (*Protonemestrius jurassicus* Ren, *P. beipaiaoensis*, and *Florinemestrius pulcherrimus* Ren [Ren, 1998a, b]). Fortunately, the venation of nemestrinids is so distinctive that there is little ambiguity about placing fossils of these flies: they possess a "diagonal vein" composed of several other veins and running obliquely through the middle of the wing. Bernardi (1973b) placed *Archinemestrius* and *Protonemestrius* in the most primitive subfamily, the Archinemestriinae Rohd.; and *Eohirmoneura* was placed close to the living genus *Hirmoneura*, also a basal lineage. Bernardi (1973b: 285) qualified this placement by indicating (285) that *Hirmoneura* is possibly a polyphyletic group.

←

tonian amber from Taymyr, Siberia; 8, undescribed scenopinid, Turonian amber, New Jersey; 9, *Araripogon*, Aptian, Brazil; 10, undescribed asilid, Turonian amber, New Jersey; 11, biogeographic dating (see text, based on Yeates & Irwin, 1996); 12, various taxa, oldest definitive Empididae in Neocomian amber, Lebanon; 13, undescribed, Neocomian amber, Lebanon; 14, undescribed Platypezidae, Phoridae in New Jersey amber; 15, *Prioriphora*, *Sciadophora* (Phoridae), and *Ironomyia* (Ironomyiidae) in Canadian amber; 16, undescribed, Santonian amber, Taymyr, Siberia.



a. *Juracyrtus kovalevi*

b. *Protonemestrius jurassicus*

c. Proratinae, indet., New Jersey amber

e. *Proplatypygus rohdendorfi*

f. *Procyrtosia sukatshevae*

d. *Cretaceogaster pygmaeus*
Canadian amber

g. *Proplatypygus rohdendorfi*

Figure 8. Fossil Diptera belonging to anthophilic families. —a. *Juracyrtus kovalevi* (Acroceridae) (from Nartshuk, 1996). Note that the apical wing veins are not coalesced or upturned in *Juracyrtus*, *Proplatypygus*, or *Procyrtosia*. —b. *Protonemestrius jurassicus* (Nemestrinidae), from Jurassic of China (from Ren, 1998a). —c. Undescribed scenopinid in New Jersey amber (original). —d. *Cretaceogaster pygmaeus* (Stratiomyidae) in Canadian amber (original). e–g: Bombyliidae. —e. *Proplatypygus rohdendorfi* (Siberian amber). —f. *Procyrtosia sukatshevae* (wing) (Siberian amber: upper Cretaceous). —g. *Proplatypygus rohdendorfi* (head) (Siberian amber). f and g from Zaitsev (1987).

Not including the enigmatic genus *Rhagionemestrius* Ussatchev from Karatau, which is of questionable family placement (Bernardi, 1973a), two other Jurassic genera are described, from the Tithonian (uppermost Jurassic): *Sinonemestrius* Hong & Wang, from China, and *Prohirmoneura* Handlirsch, from the Solnhofen beds of Bavaria. Wing venation of *Prohirmoneura* is distinctly nemestrinid, but not well enough preserved to make a more accurate placement (unfortunately, the type and only known specimen cannot be located, so the accuracy of the original description cannot be checked). The taxa from Karatau have consolidated apical veins on the wing, but are not strongly curved upward nor are as consolidated as in many modern species. Thus, they probably did not hover at all, or at least not as well as the Cenozoic forms. Most fascinating is that some species of *Protonemestrius* are reported to have a proboscis (Rohdendorf, 1964; M. Mostovsky, pers. comm. 1997). Bernardi (1973b: 285) mentioned the proboscis in Archinemestriinae being ". . . short . . . rarely equal to the length of the head . . . ." If this is the case, *Protonemestrius* appears to be the earliest appearance of a proboscis in the fossil record that was almost certainly used for feeding on pollen or some other anthophyte reproductive reward, but interpretation of the proboscis may be as ambiguous as that of *Juracyrtus* (Acroceridae), discussed above. New hirmoneurine nemestrinids from Montsec, Spain (Aptian), lack a proboscis, but a new nemestrinine genus from Baissa, Siberia (Albian), possesses a *short* proboscis. In *Eohirmoneura,* the oral region is not well preserved, making preservation of a proboscis uncertain.

Most recently, several new taxa of fossil nemestrinids from the Upper Jurassic of China have reinforced the view that the nemestrinids were probably among the earliest obligate pollinators (Ren, 1998b). Of the three taxa described by Ren, two have anthophilic-type proboscides: *Protonemestrius jurassicus* and *Florinemestrius pulcherrimus* (proboscis of the latter is of moderate length, 1.2 times depth of head). Even though Ren (1998a) mentioned that many Late Jurassic examples were collected, only the holotype specimen of *P. jurassicus* was figured and discussed (Ren, 1998a, b). The one specimen makes it difficult to evaluate the structure of the proboscis, which is peculiar in being much finer than in any living species.

It is important to note that the Nemestrinidae are the most plesiomorphic family in the Asiloidea (Fig. 7), an assemblage of 10 families, half of which are important pollinators. This antiquity can account for the impressive late Jurassic diversification of this brachyceran family. Moreover, the distributions of the subfamilies Nemestrininae and Cyclopsideinae are austral (Bernardi, 1973b), which is again suggestive of a Gondwanan pattern.

The main Cenozoic record of nemestrinid flies is in the Oligocene shales of Florissant, Colorado, with five species belonging to three extant genera (Bequaert & Carpenter, 1936), although Bernardi (1973b) indicated that the fossil genus *Palembolus* Scudder should be maintained for one of these species. *Neorhynchocephalus occultator* Cockerell, in fact, was indistiguishable from the living species *N. volaticus* largely on the basis of wing venation. At least one species, *Prosoeca florigera* (Scudder) (the genus is presently South African), had an elongate proboscis. Given the remarkable diversification of the nemestrinids by the Upper Jurassic (some 6 genera from Eurasia), one can conclude that somewhere between the Upper Jurassic and the Lower Cenozoic the radiations of modern nemestrinid genera took place. This family is at present the best candidate for the earliest obligate pollinator of angiosperms, and certainly the earliest record of a morphological structure specialized for feeding from flowers.

SCENOPINIDAE

Scenopinidae, or "window flies" (ca. 700 species described), are rarely encountered, with the exception of a few common species. Most genera have a short, jutting proboscis (Fig. 6), but some have a slender probsocis that is equal to the length of the head or slightly longer. The higher-level relationships of the family were studied (Yeates, 1992), but there are only two fossils: *Metatrichia pria,* in Miocene amber from the Dominican Republic (Yeates & Grimaldi, 1993), which belongs to a rare extant genus; and an undescribed species from mid Cretaceous (Turonian) amber from New Jersey (Grimaldi & Cumming, 1999) (Fig. 8c). Certain apomorphies diagnostic of the Scenopinidae are not visible in the Cretaceous fossil, such as the pair of sensory patches on abdominal tergite 2, but the wing venation is very similar to certain proratine scenopinids, notably the genera *Acaenotus, Jackhallia,* and *Prorates.* These genera and two others belong to the proratines, which used to be placed in the Bombyliidae (e.g., Hall, in McAlpine, 1981; Hull, 1973). The proratines were reviewed by Nagatomi et al. (1994), classifying them according to Yeates's (1992) work. Proratines with a proboscis have a similar habit to bombyliids in their feeding from flowers, but some species have vestigial mouthparts (Liu & Nagatomi, 1995). Figure 9 is a cladogram of the higher relationships of the prora-

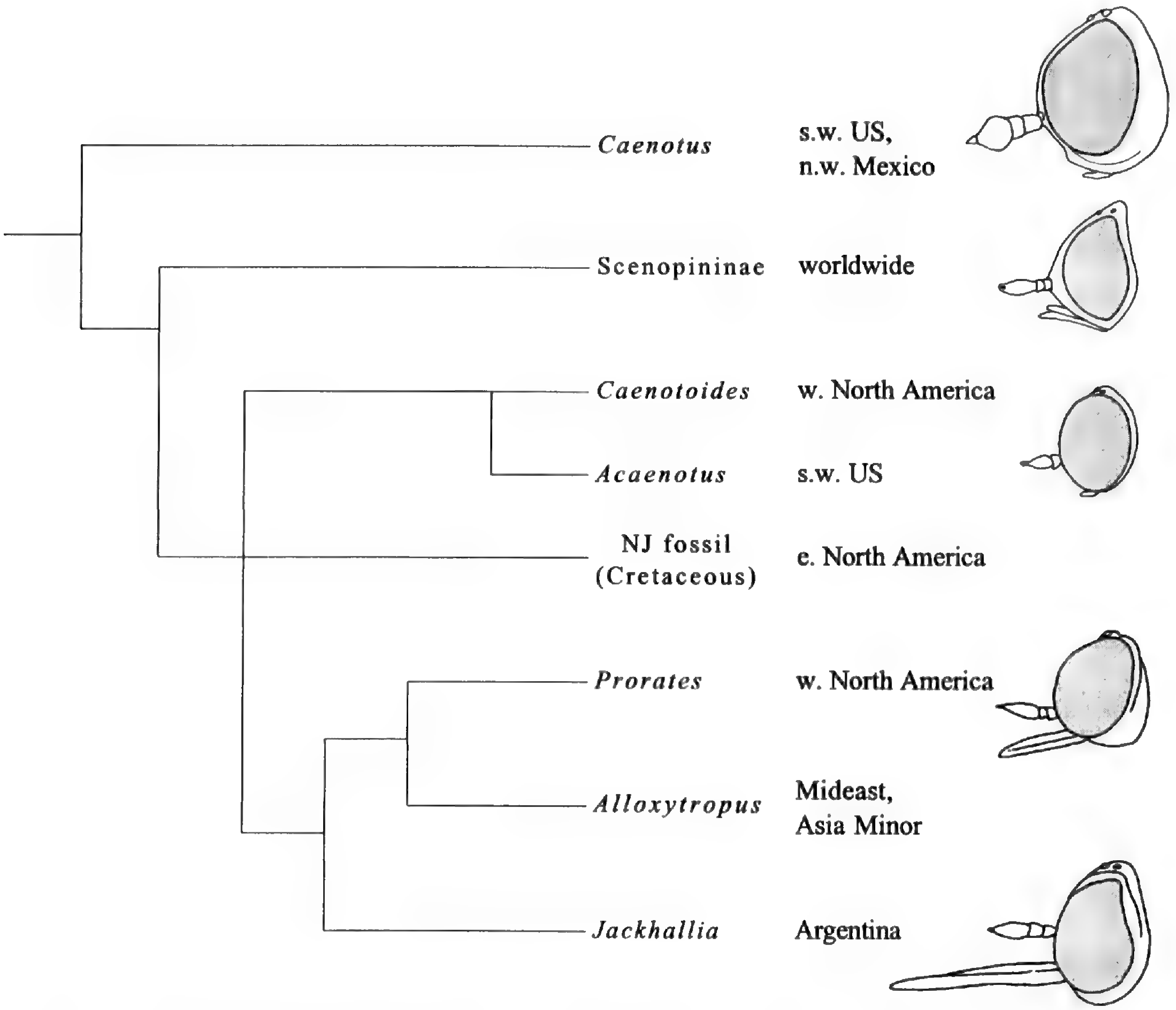


Figure 9. Cladogram of proratine scenopinids, showing diagram of heads and proboscides. Cladogram derived principally from Yeates (1992), with additional taxa from Nagatomi et al. (1994).

tines. The three most derived genera have the longest proboscides; the New Jersey amber fossil has a short proboscis that extends slightly beyond the oral margin. This is consistent with a Cretaceous origin of an anthophilic proboscis and of proratine scenopinid genera.

The distribution of proratines is centered in the arid regions of western North America, where most of the diversification appears to have occurred. There are some dramatic disjunctions, involving this area (four genera), the Mid East and central Asia (*Alloxytropus*), and Argentina (*Jackhallia*). Such disjunctions are suggestive of formerly widespread genera, which the Cretaceous fossil corroborates, but they must be interpreted very cautiously for such notoriously poorly collected and rare flies.

STRATIOMYIDAE

Stratiomyidae, or "soldier flies," superficially resemble syrphids in their bold yellow and black color patterns. There are approximately 2000 described, extant species. Among the groups of flies discussed here, they are the least specialized for anthophily. Wing venation is not particularly modified for hovering, and their flight is not as maneuverable as in the other groups; with a few exceptions, the proboscis has a generalized structure. Of the described fossils, there are 16 Cenozoic genera (catalogued in Evenhuis, 1994, with several additional genera in Dominican amber), all of them extant or very close to extant genera. Only three Cretaceous fossils are known: *Cretaceogaster pygmaeus* Teskey, in Santonian amber from Canada (Fig. 8d); an undetermined beridine-like specimen in Turonian amber from New Jersey (Grimaldi & Cumming, 1999); and undetermined larvae from Lower Cretaceous limestone of Montsec, Spain (Gomez Pallerola, 1986).

The relationships of *Cretaceogaster* were discussed by Woodley (1986). The genus is most closely related to *Parhadrestia* from south temperate South America. Together, they are the sister group to the Chiromyzinae + all other stratiomyids. Interestingly, the Chiromyzinae have an austral distribution that also includes Andean South America and southern Central America. Without knowledge of *Cretaceogaster* from the Northern Hemisphere, one might conclude that the basal clades of the Stratiomyidae had a Gondwanan distribution, whereas it had a much wider distribution in the Upper Cretaceous. The basal position of *Cretaceogaster* is consistent with a Lower Cretaceous origin of the stratiomyids. The position of the Lower Cretaceous specimens from Spain will probably not be particularly revealing since they are larvae. Unlike *Cretaceogaster,* the specimen in New Jersey amber is too fragmentary for accurate systematic placement, but its features are consistent with the Beridinae, a primitive clade of stratiomyids. The little data on Cretaceous stratiomyids indicate they were plesiomorphic at this time period.

EMPIDIDAE

These flies are often implicated as significant pollinators because some species have long, rigid proboscides, which are used for preying on other insects and probing narrow corollas for nectar and pollen. *Empis tessellata,* for example, is recorded visiting 20 species of flowers in Britain (Hobby & Smith, 1961). In actuality, there are only a handful of empidid genera that are obligate or even largely pollen feeders, namely *Anthalia* (Ocydromiinae), *Iteaphila* and *Anthopiscopus* (Oreogetoninae), some *Empis* species, and possibly *Philetas* and *Hesperempis* (Empidinae).

The relationships among empidid subfamilies are well investigated (Cumming et al., 1995), as are the relationships of genera of some subfamilies (Sinclair, 1995). The family is also one of the best known from the Cretaceous, with extensive representation in ambers from the Neocomian of Lebanon, Cenomanian of France, and various Upper Cretaceous ages of Manitoba and Alberta, (Canada) New Jersey (U.S.A.), and Taymyr (Siberia) (Hennig, 1970, 1971; Kovalev, 1974, 1978; Negrobov, 1978; Grimaldi & Cumming, 1999). The oldest empidoid is *Protempis,* from the Upper Jurassic of Karatau, which has very primitive wing venation and is considered to be the sister group to the empidids on this basis. None of the Mesozoic empidoids have a proboscis that is even as long as the head, and in most other respects they are quite plesiomorphic. The oldest records of the living subfamilies Empidinae, Atelestinae/*Nemedina*-genus group, and Trichopezinae occur in Turonian amber from New Jersey, and of Tachydromiinae and Ocydromiinae in Campanian amber from Canada (Grimaldi & Cumming, 1999). Strangely, one of the most derived clades, the Microphorinae and Dolichopodidae, occurs in the oldest fossiliferous amber, from the Neocomian of Lebanon, as well as in younger ambers. The origin of empidid subfamilies is therefore definitely a Cretaceous event, and modern genera did not appear until the latest Cretaceous and early Cenozoic.

SYRPHIDAE

Syrphidae, or “flower flies,” are almost certainly the most ecologically important group of anthophilous Diptera (Proctor et al., 1996), not because of any particular specializations, but rather because of their ubiquity, with some 6000 species and 180 genera worldwide. Species in the Syrphinae and Eristalinae visit flowers; those in the smaller subfamily Microdontinae do not, with most having small and vestigial mouthparts. None of the syrphines and eristalines have particularly long mouthparts, and there seem to be various degrees of specialization of pollen and/or nectar feeding.

There is, unfortunately, only one Cretaceous fossil syrphid, preserved in Santonian amber (ca. 84 Ma) from Taymyr, Siberia. It is very incomplete and appears to belong to the modern subfamily Cheilosiinae (M. Mostovsky, pers. comm. 1997). Also, the phylogenetic relationships of tribes and genera have been explored only piecemeal. The fossil record of the Syrphidae is summarized best by Vockeroth and Thompson (1986: 52): “There are 32 species known from Baltic amber [Eocene] . . .; the others are from [Oligocene and Eocene] sedimentary deposits from western North America and Europe. Forty-five species are assigned to recent genera; the others belong to extinct genera, *which do not differ markedly from living Syrphidae* [italics mine]. Because of many changes in classification and the use of many additional taxonomic characters since Hull’s [1945, 1949] study, the available material should be critically studied.”

Thus, by the Eocene-Oligocene, a basically modern diversity of hoverflies was intact. The basal diversification of this family was almost certainly Cretaceous, probably Upper Cretaceous, based on constraints of only primitive platypezoids found thus far in the Cretaceous (Grimaldi & Cumming, 1999). Vockeroth (1969), in discussing the biogeography of syrphids, concluded that syrphids are like other groups of the Schizophora in showing no apparent austral distributions. The indication is that the origin of major syrphid lineages postdates the rifting of Gondwanaland between the Aptian and Turonian.

BOMBYLIIDAE (BEE FLIES)

Besides the Syrphidae, this is the fly family of greatest significance for pollination. These flies are generally very hirsute and are most diverse in xeric environments around the world where they are found hovering close to the ground and on flowers. Some species have small or vestigial mouthparts, many have a proboscis that projects beyond the head, but the ones with the longest proboscides (3–4 times the length of the head) are in the Bombyliinae (Fig. 6). Most of the species for which behavior is known occur in temperate regions, generally in the spring. These studies have revealed a remarkable degree of flower-constant foraging among various long-proboscis species. With their superb hovering ability, and "trap-lining" behavior, they are no doubt efficient pollinators of various herbaceous plants, especially those with flowers having narrow corolla tubes (Scott-Elliot, 1896; Graenicher, 1910; Knoll, 1921; Straw, 1963; Grant & Grant, 1965; van Someren, 1978; Evenhuis, 1983; Daniels, 1983; Grimaldi, 1988; Proctor et al., 1996).

Mesozoic fossils of the family are sparse, but the phylogenetic relationships of bombyliid subfamilies have been studied in detail by Yeates (1994) (Fig. 10). The oldest fossil is *Paleoplatypygus zaitsevi* Kovalev, from the mid-Jurassic of Siberia. According to Evenhuis (1994), who has been monographing the mythicomyiines, the wing venation of *Paleoplatypygus* is similar to extant members of the *Psiloderoides* group of genera. The adults of these genera have small to vestigial mouthparts. [Evenhuis (e.g., 1994) placed the Mythicomyiinae, the most primitive clade of a monophyletic Bombyliidae, into a separate family. The cladistic results of Yeates (1994) indicate that such splitting into families is unwarranted.] The only other Mesozoic bombyliids are in Upper Cretaceous (Santonian) amber from Taymyr, Siberia: *Procyrtosia sukatshevae* Zaitsev, and *Proplatypygus rohdendorfi* Zaitsev (Figs. 8e, g). All are mythicomyiines and have small to rudimentary mouthparts, while the Eocene *Proplatypygus succineus* Hennig and some recent *Platypygus* have proboscides that protrude even to several times the length of the head. *Zarzia* Zaitsev, also in Siberian amber, was transferred from the Bombyliidae to the Rhagionidae by Evenhuis (1994). Lastly, Evenhuis (1994) commented that *Crosaphis*, from the Upper Triassic (Carnian) of Australia and Virginia, may be a mythicomyiine; it is actually an anisopodoid nematoceran (Fraser et al., 1996).

The fossil record of the non-mythicomyiine, higher bombyliids is entirely in the Cenozoic and includes some 32 genera and 50 species, reviewed by Evenhuis (1994). Lack of non-mythicomyiine Cretaceous bee fly fossils is a concern, but probably accurately reflects their absence given that various Brachycera are abundant in vast compression deposits from Botswana, Brazil, China, England, Mongolia, Siberia, and Spain. Although modern study of Cenozoic bee fly fossils is necessary, they all appear either close to or equivalent to modern genera. The Mesozoic fossils are few but consistent with the cladistics of the family: primitive, mythicomyiine bombyliids appear in the Upper Jurassic and Lower Cretaceous, and more derived taxa in the Cenozoic. Major radiations of bombyliids probably occurred in the Upper Cretaceous and Lower Cenozoic, contrary to Zaitzev's (1987) hypothesis that basal radiations of non-mythicomyiines occurred in the Upper Jurassic. Unfortunately, no biogeographic synthesis of even part of the bombyliids has been done, and is made difficult by the current tradition of faunistic-style systematics of the genera.

LEPIDOPTERA

In terms of the number of species (ca. 110,000 worldwide), and their biomass in vegetated habitats, this is certainly among the most successful of the insect orders. Many lepidopterans are tiny, with wing spans down to 3 mm. Others have wingspans of nearly 30 cm, more expansive than any other living insect.

Lepidopterans are intimately associated with flowers, feeding on the pollen and nectar with their proboscis, a structure that is found in all but the most primitive lepidopterans. There are some extremely specialized relationships with flowers among Lepidoptera (Proctor et al., 1996), but it must also be noted that many Lepidoptera do not feed exclusively on flowers. The diet of many species is supplemented with, and sometimes made up exclusively of, fluids from puddles, dung, rotting fruit, and even the eye secretions of large animals. Some species of noctuids from southeast Asia have evolved a proboscis capable of piercing the rind of fruits in order to feed (Bänziger, 1982). The groundplan function of the lepidopteran proboscis is actually uncertain, and not necessarily used for probing flowers (Kristensen, 1997). Feeding habits of the primitive, mandibulate moths, the Agathiphag-

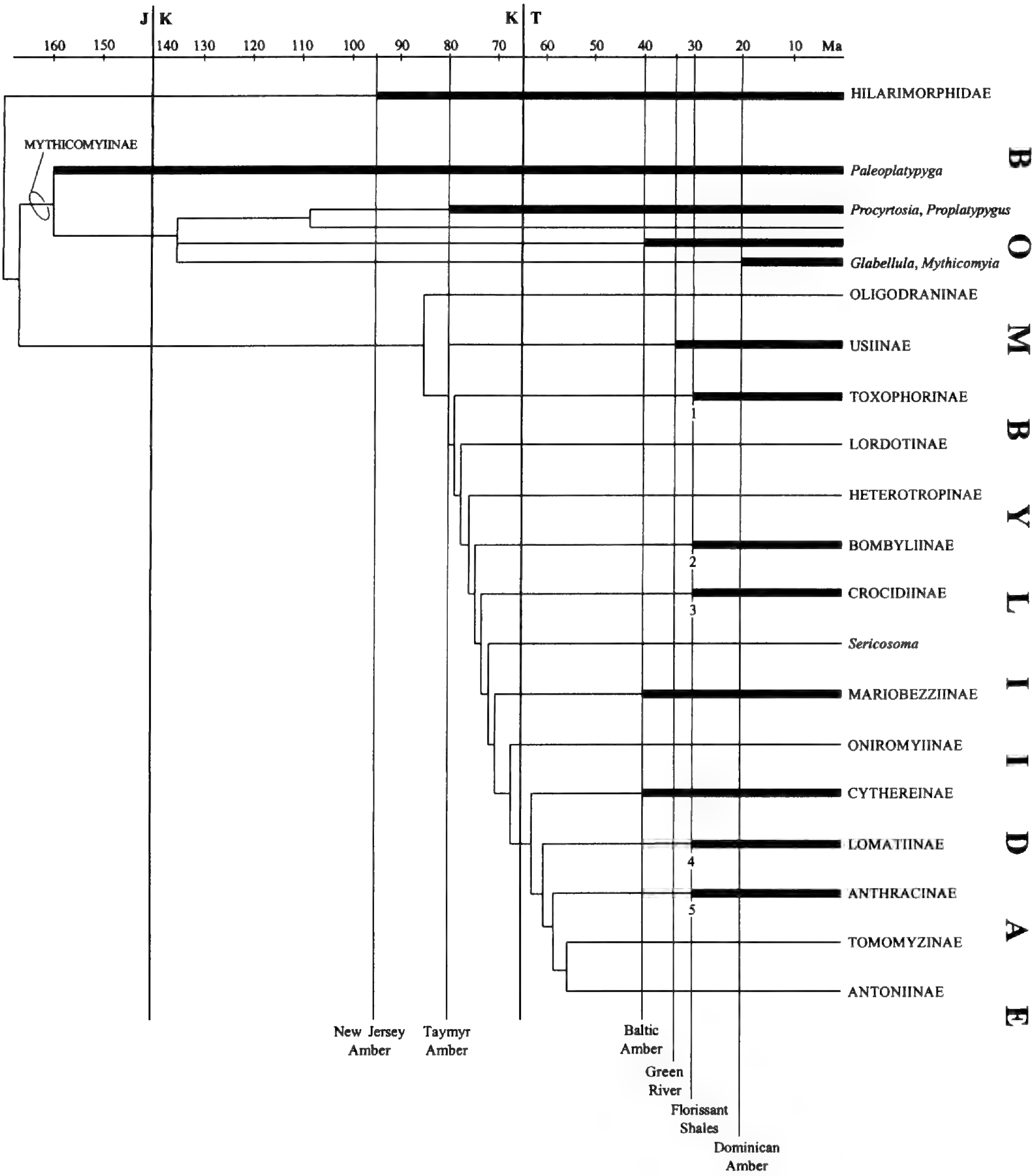


Figure 10. Cladogram of bee fly (family Bombyliidae) subfamilies, from Yeates (1994), with geological ages and fossils overlaid. Lengths of branches grossly estimate ages of clades but will need refinement as fossils are more carefully re-studied and placed. Major radiation of "advanced," non-mythicomyiine bombyliids is hypothesized to be sudden and occurring in the late Cretaceous, in contrast to the hypothesis of Zaitzev (1991). Numbers on cladogram: 1, *Dolichomyia, Systropus*; 2, *Alepidophora, Bombylius*; 3, *Desmatomyia*; 4, *Alomatia*; 5, *Exoprosopa.*

idae, are unknown, but the other two mandibulate moth families (the Micropterigidae and Heterobathmiidae) feed on pollen and fern spores (Kristensen, 1997). With exception of the most primitive lepidopterans, the heteroneuran moths represent the largest clade of insects so wedded to vascular plants, and angiosperms in particular, as larval phytophages and adult anthophiles.

The Lepidoptera are highly modified, with 27 apomorphies proposed for the order (Kristensen, 1984). The most primitive lineages of lepidopterans, though, are only subtly different phenetically from the sister group, the order Trichoptera (caddisflies). The external apomorphies most easily observed are much more likely to be seen in amber fossils rather than compression fossils, and this has complicated the interpretation of some Mesozoic fossils as discussed below. Critical lepidopteran apomorphies are: (1) vein M_4 lost (except in *Agathiphaga*); (2) presence of an epiphysis (a setulose spur) in the middle of the foretibia of most species; (3) scales on the fore *and* hind wing (where Trichoptera have scales, they are on the forewing only).

Excellent morphological work by Kristensen, Nielsen, and Davis has established a phylogenetic classification of basal Lepidoptera better than virtually any other major group of insects (Kristensen, 1984; Kristensen & Nielsen, 1979; Nielsen, 1987; Nielsen & Kristensen, 1996; Davis, 1986). DNA sequence data have been unable to revise or modify the morphologically based cladograms (Friedlander et al., 1996). The work of these morphologists has revealed and revised numerous apomorphies within the Lepidoptera, the most significant for present purposes being the proboscis, or tongue. This structure is an elongation of the paired galeae, which have also become fused. All but three of the most primitive families (Micropterygidae, Agathiphagidae, and Heterobathmiidae) possess a proboscis, and all but three of the most primitive glossatan families possess intrinsic musculature in the proboscis. Intrinsic musculature allows great elongation of the proboscis, by controlling the coiling and uncoiling of the structure and its probing movements. It must be stressed that the non-ditrysians represent only about 2% of all Lepidoptera, and that the relationships of ditrysian families as currently known are almost entirely polytomous (fig. 41.13 in Nielsen & Common, 1991). Understanding the basal, non-ditrysian relationships of the Lepidoptera, though, is essential to interpreting the Mesozoic lepidopteran fossils.

Table 1 summarizes the Mesozoic records of Lepidoptera. Figure 11 is an attempt to place these fossils into the currently recognized phylogeny of extant, basal Lepidoptera. Labandeira et al. (1994) also superimposed a phylogeny of lepidopterans on a geological time scale, but they placed all of the fossils into taxa where they were originally described. As Kristensen and Skalski (1997: 16) mentioned: "The bulk of the Mesozoic Lepidoptera so far described are believed to belong to the non-glossatan grade, but it is admittedly only in exceptional cases (*Parasabatinca*) that head structures are so well conserved that there is direct evidence for this assumption." Here, a critical view is also taken of the morphological evidence in the Mesozoic lepidopteran fossils (see Appendix); placement of the fossils seriously affects the hypothesized timing of lepidopteran radiations. The records of Mesozoic Lepidoptera were broken down into several categories, based on re-evaluation of the published evidence: Possible Lepidoptera; Lepidoptera incertae sedis; Lepidoptera Non-Glossata; Lepidoptera-Glossata; and Lepidoptera plausibly assigned to particular families/superfamilies. Justification for the placement of the fossils is discussed in detail in Appendix 1. This evaluation is hardly definitive since it is virtually essential to reexamine specimens of fossil insects, particularly compressions where venation and other critical but subtle details can be difficult to observe or appear ambiguous over the background texture of the matrix. Whalley (1986) and Skalski (1990) provided earlier, general reviews of Mesozoic Lepidoptera. I will not discuss Triassic records of putative lepidopterans, which were thoroughly discussed and mostly dismissed by Whalley (1986). However, my hypothesis differs from that of Whalley (1986) and Labandeira et al. (1994) in not postulating the existence of Lepidoptera in the Triassic, among other aspects.

Placement of the Mesozoic compression fossils is more conservative here than that in Labandeira et al. (1994), with our hypotheses on ages of various lineages differing dramatically. Labandeira et al. (1994) hypothesized the basal radiation of the order in the Lower Jurassic, the basal radiation of the Myoglossata in the mid Jurassic, and the basal radiation of the Ditrysia in the late Jurassic. This hypothesis critically depends on the placement of certain Jurassic and Lower Cretaceous fossils. One such fossil is a putative incurvarioid, which is a fragment of a wing in the Acra collection of Lebanese amber (Neocomian) and which is discussed in Appendix 1 as being Glossata incertae sedis.

The other old Mesozoic records concern mines, which have pivotal chronological effects on the dates hypothesized by Labandeira et al. (1994), so some discussion on the diagnostic characters of mines is germane. Mines are caused by a larva feeding in spaces it creates between the epidermal layers of a leaf. Leaf mines occur among the Hymenoptera (Pergidae, Argidae), Coleoptera (Chrysomelidae: Hispinae), Diptera (Agromyzidae, and a few others), and most commonly in primitive Lepidoptera. Among the 10 major families of "microlepidopteran" leaf miners, there is considerable variation in the morphology of the mine. Indeed, there are numerous features on which leaf mines can be recognized: geometry of mine (straight, serpentine, blotch, etc.), growth pattern of mine, pupation chambers, pattern of frass deposition, and taxon of host plant (although this is most useful for Cenozoic records and becomes problematic for mid- to Lower Cretaceous leaves, which are often

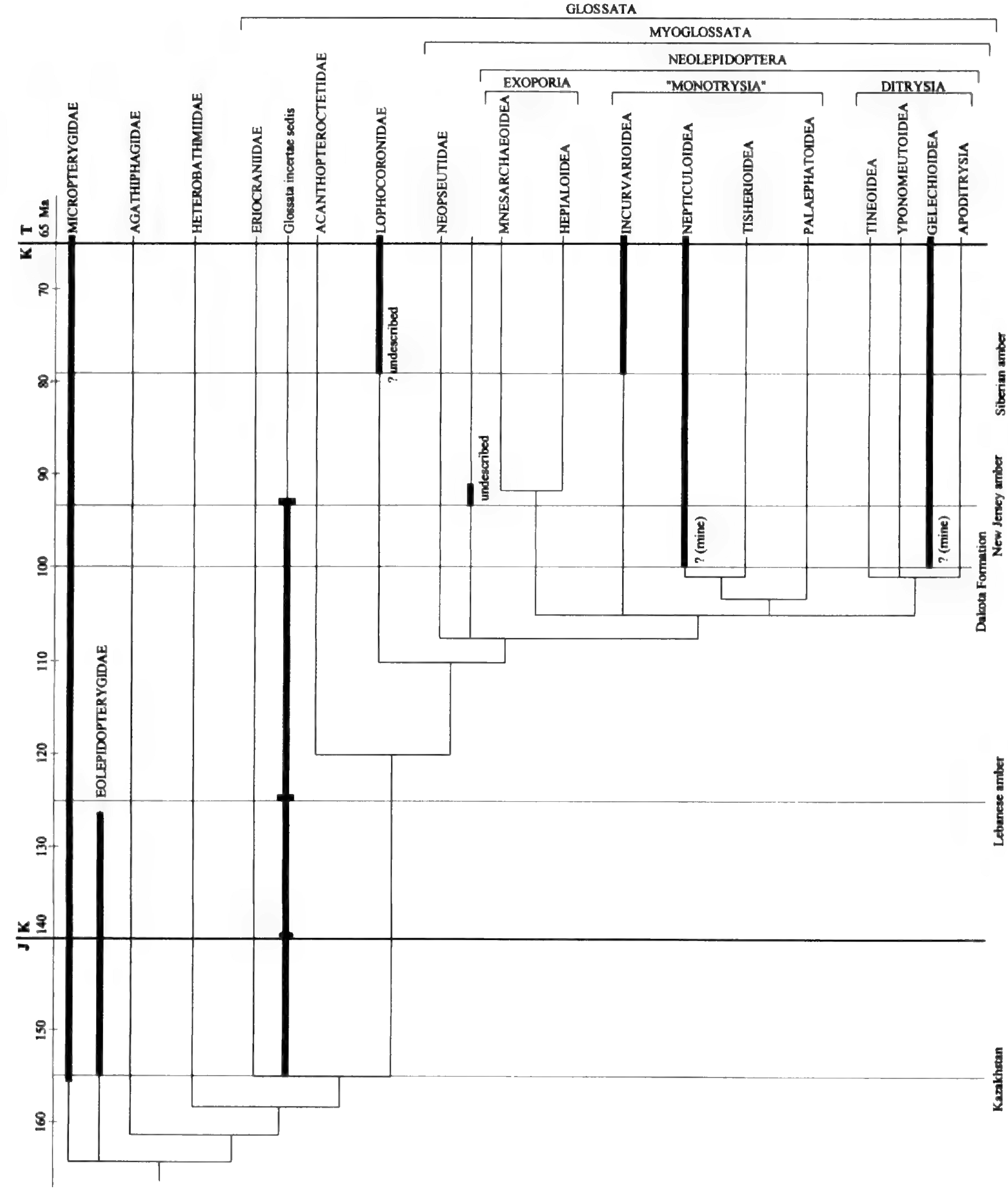
Table 1. Records of Mesozoic Lepidoptera. Placements are discussed in Appendix 1.

Taxon/family	Age/locality	Reference
	POSSIBLE LEPIDOPTERA	
Archaeolepis mane	L. Lias/Dorset	Whalley, 1985
Auliepterix mirabilis	U. Jurassic/Kazakhstan	Kozlov, 1989
Auliepterix minima	UJ/LK/Mongolia	Kozlov, 1989
Daiopterix olgae	LK/Chitinsk Oblast	Kozlov, 1989
Karataunia lapidaria	U. Jurassic/Kazakhstan	Kozlov, 1989
Parasabatinca caldasae	Aptian/Brazil	Martins-Neto & Vulcano, 1989
Undopterix carirensis	Aptian/Brazil	Martins-Neto & Vulcano, 1989
Gracilepterix pulchra	Aptian/Brazil	Martins-Neto & Vulcano, 1989
	LEPIDOPTERA, INCERTAE SEDIS	
Daiopterix rasnitsyni	Aptian/Transbaykalia	Skalski, 1984
Eolepidopterix jurassica	U. Jurassic	Rasnitsyn, 1983
Paleolepidopterix aurea	U. Jurassic/Kazakhstan	Kozlov, 1989
Undopterix sukatshevae	Aptian/Transbaykalia	Skalski, 1979a
Micropteryx pervetus	Cretaceous?/Myanmar	Cockerell, 1919
	MICROPTERYGIDAE	
Parasabatinca aftimacrai	Neocomian/Lebanon	Whalley, 1977, 1978
indet. (scales)	Cenomanian/France	Kühne et al., 1973
	GLOSSATA	
Protolepis cuprealata	U. Jurassic/Kazakhstan	Kozlov, 1989
undescribed (larva)	Neocomian/Lebanon	Grimaldi, 1996
Incurvarioidea (scales)	Neocomian/Lebanon	Whalley, 1986
Glossata indet. (adults)	Turonian/New Jersey	Grimaldi, unpubl.
indet. (larval head capsule)	Santonian/Canada	MacKay, 1970
Dyseriocrania perveta	Cretaceous?/Myanmar	Cockerell, 1919
?Nepticulidae (mines)	U. Jurassic/Karatau	Skalski, 1979a
?Nepticulidae (mines)	U. Jurassic/Karatau	Kozlov, 1989
?Nepticulidae (mine)	UJ/LK/Queensland	Rozefelds, 1988
Nepticulidae (mines)	Cenomanian/Dakota Form.	Labandeira et al., 1994
Gracillariidae (mines)	Cenomanian/Dakota Form.	Labandeira et al., 1994
	FAMILIES: GLOSSATA	
Lophocoronidae?	Santonian/Siberia	Skalski, 1979b
Incurvariidae	Santonian/Siberia	Skalski, 1979b

of uncertain relationships). As a result, some studies have attributed Miocene through Lower Eocene leaf mines as belonging to living genera of microlepidopterans (Opler, 1973, 1982), although one study of Paleocene leaves was more cautionary (Crane & Jarzembowski, 1980).

Mines of putative Nepticulidae, in the Monotrysia, are among the oldest records of all Lepidoptera (Kozlov, 1989; Labandeira et al., 1994; Rozefelds, 1988; Skalski, 1979a, b). If truly nepticulid, these mines would push the basal diversification of the Lepidoptera deep into the Jurassic. The leaves in which these mines occur are a non-angiosperm seed plant (Rozefelds, 1988: Upper Jurassic/Lower Cretaceous); Trochodendraceae (Kozlov, 1989: Turonian); and Platanaceae and Rosidae (Labandeira et al., 1994: Cenomanian) (Skalski, 1979b, did not indicate the kind of plant from which the Upper Jurassic mines from Karatau, Kazakhastan, are recorded). Today, 70% of the known nepticulid mines are on Fagaceae and, to a lesser extent, Rosidae.

Based on hosts, the Cenomanian records would appear least problematic, but some of the characters used to make this identification are widespread among leafminers in general. These include gradual widening of the mine, culminating in a large blotch that obliterates some of the early mine, and a serpentine mine that has a central frass trail that is intermittently broken and culminates in "modestly expanded frass-free chamber"—a very generalized morphology of all sorts of mines, not just lepidopteran (Hering, 1951; Needham et al., 1928). That these Cenomanian mines were identified as the living genera *Stigmella* and *Ectoedemia*, in lieu of adult characters, is open to alternative interpretation. There are only about 600 species of extant


GLOSSATA
MYOGLOSSATA
NEOLEPIDOPTERA
EXOPORIA
"MONOTRYSIA"
DITRYSIA
K | T
65 Ma
MICROPTERYGIDAE
AGATHIPHAGIDAE
HETEROBATHMIIDAE
ERIOCRANIIDAE
Glossata incertae sedis
ACANTHOPTEROCTETIDAE
LOPHOCORONIDAE
NEOPSEUTIDAE
MNESARCHAEOIDEA
HEPIALOIDEA
INCURVARIOIDEA
NEPTICULOIDEA
TISHERIOIDEA
PALAEPHATOIDEA
TINEOIDEA
YPONOMEUTOIDEA
GELECHIOIDEA
APODITRYSIA
EOLEPIDOPTERYGIDAE
? undescribed
undescribed
? (mine)
? (mine)
70
80
90
100
110
120
130
J | K
140
150
160
Siberian amber
New Jersey amber
Dakota Formation
Lebanese amber
Kazakhstan

nepticulids described worldwide, and this is probably only a fraction of the entire fauna. Nepticulidae are generally poorly collected and studied, some genera in the family being the smallest lepidopterans. Judging from the proportions of described (16) and undescribed (estimated to be about 300) species of this family from Australia (Nielsen & Common, 1991), the actual world fauna is likely to be immense, particularly since the tropics have hardly been surveyed.

This point raises a serious concern about the identification of Mesozoic leaf mines in general. Powell (1980) estimated that 20–25% of the world's *described* species of microlepidopterans have hosts that are known (not just leafminers). These records are heavily biased toward the north temperate regions, and biased against tropical leafminers. Also, this does not include estimates of undescribed species. A reasonable approximation would be that *5% of the mines of the total world species of lepidopteran leafminers is known.* For several presumed leafmining families, the Acanthopteroctectidae, Lophocoronidae, and Mnesarchaeoidae, the hosts and habits are entirely unknown. With that kind of sampling, what kind of confidence do we really have in the identification of leaf mines to family and especially to genus, particularly from the Mesozoic? In other words, how widespread or convergent are leaf-mine characters that are used to diagnose a certain genus, subfamily, or family? Modern leaf mines are never used to formally diagnose a genus or other taxon of microlepidopteran; adult morphology is considered the most reliable source of characters. In Figure 11 and Appendix 1 more conservative placements are made by assigning the Jurassic "nepticulid" mines as Lepidoptera-Glossata fossils incertae sedis; the Cenomanian mines from the Dakota Formation are included under the Nepticuloidea.

Also critical are mines from the Dakota Formation that have been assigned to living genera of the Gracillariidae, in the most derived subfamily Phyllocnistinae (Labandeira et al., 1994). The Gracillariidae are a large extant family with 1700 described species and 70 genera. The mines were found on leaves of Chloranthaceae and Lauraceae. If these are indeed gracillariid mines, they would be the oldest Ditrysia. Living species of gracillariids are most common on Fagaceae, then Fabaceae, with Aceraceae, Betulaceae, Salicaceae, and Rosaceae also used. Magnoliidae are virtually unknown as hosts, although a genus from Chile mines leaves of *Drimys* (Winteraceae). The critical feature used to identify these mines as gracillariids is a central, zigzagging trail of frass. Although Kristensen and Skalski (1997) agreed with Labandeira et al. on the placement of the Dakota Formation leaf mines, the confidence in this identification depends on whether a zigzagging frass trail is eventually found to be entirely restricted to the gracillariids or not. The Gracillariidae are the largest family of leafminers and have the greatest host diversity, so the true diversity of mines in this group is very incompletely known.

Figure 11 hypothesizes the basal radiations of the Lepidoptera in the mid- to Upper Jurassic, the basal radiation of the Myoglossata in the mid-Cretaceous, and the basal radiation of the Ditrysia in the early Upper Cretaceous. Eventually, with the accrual of sufficient Mesozoic body fossils (especially from amber), we will be able to assess the evidence that the leaf mines from the Cenomanian Dakota Formation are indeed ditrysians.

It should be noted that Labandeira et al. (1994) postulated all basal radiations of Lepidoptera, even of basal Ditrysia, on Jurassic gymnosperms. This is contrary to evidence from the extant fauna (Powell, 1980). There are no radiations—significantly speciose, extant lineages—on pteridophytes or conifers, and angiosperms account for the vast majority of all phytophagous host records. In fact, no major living lineage subsists on a primitive subclass of angiosperms (e.g., Magnoliidae, Ranunculidae, and lower orders of Hamamelidae, with the exception of some Liliales in the monocots). Labandeira et al.'s (1994) hypothesis would assume the simultaneous shift of all basal lepidopteran lineages onto the more derived subclasses of angiosperms. Kristensen (1997) mentioned the "real possibility" that the ancestral heterobathmiid-glossatan moths were leafminers in the Fagaceae [sensu lato]. Primitive Fagaceae are documented from the Campanian of Georgia, U.S.A. (Herendeen et al., 1995), and Turonian of New Jersey (Nixon et al., in litt.). These are the oldest records thus far and are consistent with the diversification of "higher" Hamamelidae in the Turonian-Campanian (Herendeen et al., 1995). Since there is no evidence for gymnosperm-

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Figure 11. Cladogram of basal families of the Lepidoptera, from Davis (1986), Kristensen (1984), Kristensen and Nielsen (1979), Nielsen (1987), and Nielsen and Kristensen (1996). Approximate positions of Mesozoic fossils are located on the cladogram, based on discussion provided in text and detailed discussion in Appendix.

based diversification in the Lepidoptera, a largely Cretaceous basal radiation of Lepidoptera is the most likely scenario. This timing is most consistent with a critical interpretation of the Mesozoic fossils.

CONCLUSIONS

The earliest apparent adaptation to flower feeding is exhibited by several nemestrinid flies, from the Upper Jurassic of Karatau and China, which had proboscides several times the lengths of the heads. Other Jurassic flies reported to be long-tongued, like *Juracyrtus* (Acroceridae), have an elongate structure that is only questionably a proboscis; the report by Ren (1998b) that Jurassic tabanid-like and apiocerid-like flies were anthophilous is discussed above as not convincingly substantiated. It would be important that the fossil nemestrinids be critically re-studied to confirm the fine structure of the apparent long proboscis. Given that living nemestrinids today with long proboscides feed from flowers, it is difficult to say from what else the Jurassic forms could have been feeding. Ren (1998b) has forced the conclusion that these insects fed on flowers and used this as evidence to predict the existence of highly modified, entomophilous angiosperms in the Jurassic. However, it is possible that these ancient nemestrinids gleaned pollen from flower-like structures of Jurassic Bennettitales and gnetaleans. These non-angiospermous anthophytes originated in the Triassic and diversified until the late Cretaceous (Crane, 1996). The Bennettitales had flower-like reproductive structures composed of ovules/seeds and pollen-producing organs surrounded by perianth-like bracts (e.g., Pedersen et al., 1989). It is unclear how exposed the pollen would be for flies to harvest it. Judging from the living gnetaleans, reproductive structures of these plants certainly could have supported anthophilous insects. At least *Welwitschia* has exposed pollen and a decaying odor (Crane & Hult, 1988), which, in angiosperms, is known to be attractive to flies. Evenhuis (1994) even found mythicomyiine bombyliids feeding from flowers of *Welwitschia*. Thus, one need not infer the presence of angiosperms to account for the anthophilic specializations in Jurassic insects, like *Protonemestrius* (e.g., Ren, 1998b).

It is actually not until the late Early Cretaceous that there appear many of the first, definitive representatives of insects belonging to present-day anthophilic groups, and all these fossil forms are clearly generalized in morphology. Not until the Cenozoic do insects consistently appear with structures specialized for flower-feeding, most notably, the repeated appearance of elongate proboscides.

Despite the virtual absence of bee fossils in the Cretaceous, save for a single controversial specimen, the phylogenetic and stratigraphic constraints imposed by the much better record of the sphecid wasps indicate that bees could not have radiated prior to the mid Cretaceous. The historical record for vespid wasps is much better understood, based on thoroughly studied phylogenetic relationships and fossils for most of the subfamilies, save the one most germane to pollination, the Masarinae. But, again, constraints from phylogenetics and ages of other fossil vespids, as well as a compelling biogeographic pattern, indicate that the masarines did not arise and radiate until the post-Gondwanan Cretaceous, between the Aptian and Turonian.

Several families of Diptera were definitely in existence by the Upper Jurassic, notably the Acroceridae, Bombyliidae, and Nemestrinidae. But for the acrocerids and bombyliids, only primitive forms existed, and it is not until the Cenozoic that species with anthophilic adaptations are found. The families Apioceridae, Scenopinidae, and Stratiomyidae, paleontologically and biogeographically, appear not to have originated prior to the earliest Cretaceous, and to have their basal diversification in the Cretaceous. The flower flies, or Syrphidae, one of the most significant modern groups of anthophilic Diptera (with Bombyliidae) are clearly the youngest group. Although there is only one Cretaceous fossil syrphid, the occurrence of only primitive Cretaceous members of the closely related Platypezoidea indicates that syrphids probably did not diversify significantly until the Upper Cretaceous and especially Lower Cenozoic.

Phylogenetic relationships of the primitive Lepidoptera are exceptionally well known, which allows critical interpretation of fossilized adults (in rocks, amber, based just on scales, etc.), larvae, and even larval traces (e.g., leaf mines). Scrutiny of the evidence places the origins of the tongued Lepidoptera, the Glossata, possibly in the Upper Jurassic, with radiations of basal glossatan families in the Cretaceous. The Ditrysia, which comprise 98% of the current species diversity, probably did not radiate until the latest Cretaceous and certainly by the early Cenozoic.

All the available evidence is entirely consistent with the model proposed by Crepet (1996) based on a Cenomanian to Turonian diversification of entomophilous flowers. While many families of anthophilic insects existed prior to the Cenomanian, as Labandeira and Sepkoski (1993) concluded, there is little evidence for radiations of anthophilic groups (e.g., clades of species) prior to the Cenomanian.

The only plausible scenario is that the original pollinators of the earliest angiosperms were generalized insects like beetles; primitive, short-tongued, and mandibulate moths; possibly sphecid wasps ancestral to bees; and various flies. The diversity of anthophilic Diptera indicates that this order was probably pivotal in early angiosperm pollination, including long- and short-tongued nemestrinids, short-tongued mythicomyiine bombyliids, proratine scenopinids, acrocerids, stratiomyids, empidids, as well as perhaps ceratopogonids and other nematocerans. The Masarinae, Syrphidae, Apidae, and Ditrysia almost certainly did not radiate until the major diversification of angiosperm families was intact. There is a consistent and rather perplexing pattern of very small flowers in the Cretaceous, perhaps due to preservational bias by charcoalification—the greatest source of angiosperm fossil flowers (e.g., Friis et al., 1994; Crane et al., 1994; Crepet & Nixon, 1994; and many other papers). If this pattern of diminutive Cretaceous flowers is real, it is also consistent with the early roles of flies and small, generalized aculeate wasps and lepidopterans as the earliest dedicated pollinators.

Such a scenario is based on various kinds of data, but as a whole the result is little different from the traditional view of Cretaceous co-radiations of insects and plants. It must be stressed that concomitant with the development of pollination symbioses is the development of various insect herbivore relationships, which spawned a dazzling array of angiosperm chemical defenses. The effects of pollination on breeding systems and genetic isolation in species of angiosperms is obvious, but the cladogenetic impact on plants of insect herbivory remains to be deciphered.

It may be significant to note that most of the pollinator groups that are discussed here have distributions concentrated in xeric regions, or areas of Mediterranean-type flora. As a result, many of these pollinators feed on flowers from shrubby and decumbent plants. This is particularly true of all the Diptera that were discussed, the vespids, and many of the bees (although there are significantly speciose groups of tropical bees, like the meliponines and euglossines). This pattern is consistent with Taylor and Hickey's (1992) hypothesis that the first angiosperms were decumbent herbaceous plants, and also with theories that the Cretaceous climate was globally drier than it is now (e.g., Wolfe & Upchurch, 1987; Spicer et al., 1993). Present-day distributions of greatest pollinator diversity may reflect Cretaceous "refugia."

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APPENDIX 1. Discussion of Mesozoic Lepidopteran Fossils.

Most records listed in Table 1 are discussed below for diagnostic features. Qualifying remarks about the leaf mine fossils are presented in the main text of the paper; no remarks are made about the two taxa in amber from Myanmar, given the equivocal age of this amber (Grimaldi, 1996; Grimaldi et al., 1997).

POSSIBLE LEPIDOPTERA

Archaeolepis mane Whalley. A small (5 mm long) wing covered with scales from the Lower Lias of Britain (Whalley, 1985). Even though preservation of the wing is incomplete, such that no diagnostic venation shows, Whalley ruled out the possibility that the wing was not derived from other orders where scaled wings sporadically occur. He even concluded that the wing was a hind wing, which is very significant because those Trichoptera with scales have them on the forewings only. Unfortunately, Whalley's evidence that it is a hindwing is meager, based largely on the fact that the shape of the wing, according to Whalley, is most similar to the hind wings of Micropterygidae. All but the most distal tips of veins R and M are lost, and it is unclear how Whalley could have homologized these short segments in lieu of connections; yet he concluded that M_4 is lost—a lepidopteran apomorphy. He admitted to this uncertainty (Whalley, 1985: 180): "The exact number of median veins in *Archaeolepis* is difficult to determine but there are *probably* three branches. . ." (italics mine). Labandeira et al. (1994) assigned this fossil to the Zeugloptera (Micropterygidae) in their figure 2 cladogram. Kristensen and Skalski (1997) stated that this is the oldest fossil that can be referred to the Lepidoptera "with great certainty . . ." (p. 16) and "with reasonable certainty" (p. 17). The lack of critical features are only suggestive of its lepidopterous nature.

Auliepterix mirabilis Kozlov. Wing venation of this very small (3.4 mm wing length), Upper Jurassic fossil (Kimmeridgian/Oxfordian of Chayan, Kazakhastan) (Kozlov, 1989) is not completely preserved, but unusual for primitive Lepidoptera. The venation apomorphically possesses only M_1 and M_2, no M_3, and also a radial-cubital cell and reduced stem of the M vein. Kozlov attributed these features to miniaturization. A marginal fringe on the wing is mentioned, but wing scales are otherwise unknown. Neither mouthparts nor foreleg (e.g., ephysis) are preserved. Kozlov assigned the genus to the Micropterygidae on the basis of wing shape, shape of the pronotum, and lack of an ovipositor (a primitive feature)—all features of "gestalt."

Auliepterix minima Kozlov. From Ara-Khangayskiy, near Khotont Somon, Mongolia (Upper Jurassic/Lower Cretaceous) (Kozlov, 1989). This is an exceedingly small specimen (1.9 mm wing length), with a scaly wing covering. Only two wings are figured, and Kozlov did not mention if both were forewings (the right one certainly is, the left one appears too incomplete to be certain). Thus, it probably cannot be confirmed if the forewings and hindwings are scaled, nor if mouthparts and forelegs (e.g., ephysis) are preserved. Wing venation is incomplete, but Kozlov indicated that only three medial veins are present, which would be the best evidence for the fossil being lepidopteran. Labandeira et al. (1994) apparently assigned both *Auliepterix* species to the Micropterygidae on their cladogram (their fig. 2).

Daiopterix olgae Kozlov. This is another compression fossil, from Shelopugino, Glushkovskaya series, Transbaykal (Lower Cretaceous: exact age not provided) (Kozlov, 1989). Scales on the wing surface are either not present or not preserved, except for a fringe of "piliform" scales on the margin of the forewing, which was the evidence used to assign the fossil to the Lepidoptera by Kozlov. The mouthparts are apparently mandibulate; forelegs are not preserved; the wing venation is complete, including veins M_1–M_3, although Kozlov did not mention the absence of M_4 as evidence for its placement in the Lepidoptera. Beyond the absence of M_4 it would be useful to have other apomorphic features of the Lepidoptera preserved to confirm placement in the order.

Karataunia lapidaria Kozlov. A small specimen (forewing length 2.8 mm) from Chayan, Kazakhastan, Aulye locality, Upper Jurassic (Kozlov, 1989). Scales on the wings were not preserved or are absent. A foreleg or mouthparts are not preserved. At least the presence of a proboscis would need to be demonstrated before assigning this fossil (as Kozlov did) to possibly different families of Ditrysia, particularly on such tentative basis as incomplete wing venation.

Parasabatinca caldasae, Undopterix carirensis, Gracilepterix pulchra. From the Aptian limestone of Ceará, Brazil (Martins-Neto & Vulcano, 1989). None of the specimens have scales or mouthparts preserved. For most, the fragmentary remains of the legs are also insufficient to detect the presence of an epiphysis. In *Gracilipterix* and *U. carirensis* the wings apparently have vein M_4 lost, which would appear to be the only preserved evidence for placing them in the Lepidoptera. Labandeira et al. (1994) apparently put *Parasabatinca caldasae* on the Micropterygidae clade in their cladogram figure 2.

DEFINITIVE LEPIDOPTERA

LEPIDOPTERA INCERTAE SEDIS

Daiopterix rasnitsyni Skalski (1984). Based on an almost complete specimen from the Aptian/Albian of Russia. The specimen has traces of scales on the fore and hind wings, veins Sc and R_1 are forked, and vein M_4 is lacking—indicating that this beautiful specimen is a lepidopteran. Forelegs and mouthparts are not preserved, but long apodemes connecting with the ovipositor are preserved.

Nepticulidae? Leaf mines, from the Battle Camp Formation (Early Cretaceous/Late Jurassic) of northern Queensland (Rozefelds, 1988). According to Rozefelds, the mines are poorly preserved, and although a noted lepidopterist (I. F. B. Common) examined the material and agrees the structure of the mines is similar to nepticulids, diagnostic features of the frass and the exit hole were not preserved. Kristensen and Skalski (1997) indicated that an assignment of this trace fossil to the Heteroneura "cannot be easily accepted on the basis of present knowledge" (p. 16), with which I concur. Skalski (1979b) reported leaf mines from the Upper Jurassic of Karatau, which he also assigned to the Nepticulidae on the basis of shape. Structure of the mines are highly suggestive of Lepidoptera.

LEPIDOPTERA NON-GLOSSATA

Eolepidopterix jurassica Rasnitsyn (Fig. 12b). Found in the Upper Jurassic of Karatau (Kimmeridgian), Kazakhastan (Rasnitsyn, 1983). The specimen is small, ca. 7 mm. long, with a wing span approximately 12 mm (wings are incomplete), but with a virtually complete body. Since the foretibia has an epiphysis, examined by Skalski (cited in Whalley, 1986, and Kristensen, pers. comm. to DG), the fore *and* hind wings are scaled, and a pair of small brush-like structures flank the oral region (similar to lepidopteran pilifers), this is almost certainly a lepidopteran. The specimen has no proboscis, indicating that it is very primitive; but the presence of an apparent ovipositor with long internal apodemes is compatible with but not necessarily indicative of the Agathiphagidae, as was concluded by Skalski (1990). Long internal apodemes are even found in the Trichoptera and may be an amphiesmenopteran ground-plan feature.

Paleolepidopterix aurea Kozlov (Fig. 12c). A compression fossil with wings 5.2 mm long, from Chayan District, Kazakhastan, Upper Jurassic (Kimmeridgian/Oxfordian) (Kozlov, 1989). Kozlov mentioned scaled fore wings, but not the hind wings. Legs are not preserved, so the presence of a foretibial epiphysis cannot be determined. The wing venation is barely preserved, but the apparent presence of a well-developed jugum with a cluster of setae indicate it is a lepidopteran. Apophyses, again, indicate just a basal amphiesmenopteran. Kozlov placed the fossil in the Eolepidopterigidae with *Eolepidopteryx* Rasnitsyn. If this is the case, it would belong in the Agathiphagidae, but most of the mouthparts are not preserved.

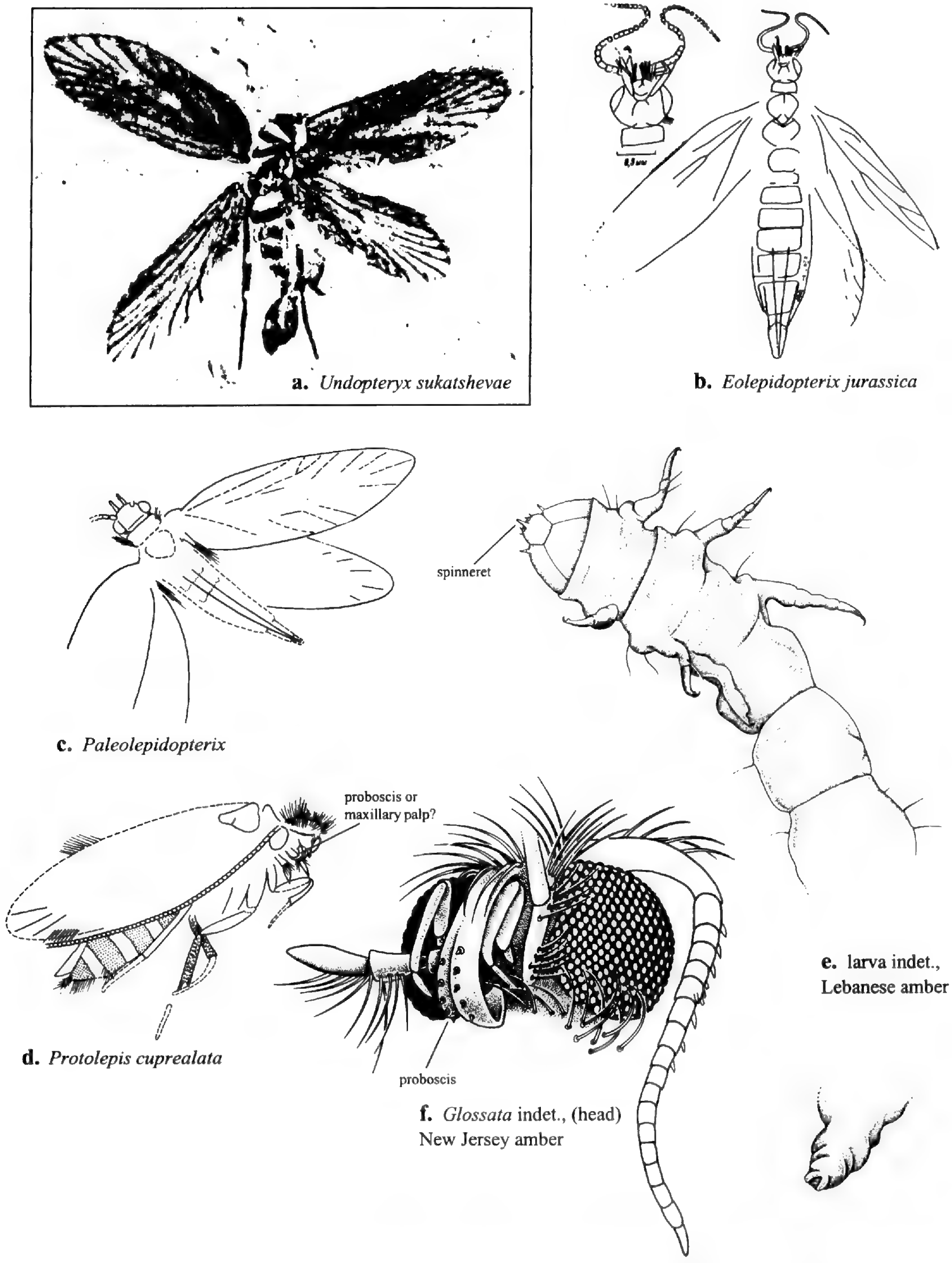
Parasabatinca aftimacrai Whalley. A nearly complete, and well-preserved specimen in Lebanese amber, with venation, details of mouthparts, and fine structure of the scales preserved. Mouthparts and scales indicate the specimen is unequivocally a micropterigid.

?Micropterigidae (scales) (Kühne et al., 1973). These are loose scales in Cenomanian amber from Bezonnais, France. The fine structure of the scales indicates the plesiomorphic nature of the ribs and lacunae, similar to micropterigids.

LEPIDOPTERA GLOSSATA

Protolepis cuprealata Kozlov (1989) (Fig. 12d). From the Upper Jurassic (Oxfordian/Kimmeridgian) of Kazakhastan. This may be the oldest glossatan. The presence of a short, curled proboscis would place this fossil in the Lepidoptera. Unfortunately, the wing venation is totally obscured by overlapping wings, and the presence of thickly scaled wing surface on both pairs of wings cannot be confirmed. Also, an epiphysis on the foretibia appears to be lacking. Presence of these features would be valuable independent confirmation that the short curled structure is indeed the proboscis. At a forewing length of 4.6 mm, the resolution of such minute structures like a proboscis is difficult against the background texture of the matrix. Also, the uncurled proboscis in lower Glossata is usually concealed between the larger labial and maxillary palps (the latter often extended in front of the head). Incredibly, Kozlov placed this species in the Ditrysia, probably near the Tineoidea (on the basis of overall similarity), because of ". . . short secondary ovipositor with distinctly pronounced anal papillae" (p. 38 of English translation). The concern about resolution of the proboscis pertains to the putative anal papillae. It would seem imperative that this specimen be re-examined using an SEM, so that presence and structure of the proboscis (is it the maxillary palp?), anal papillae, and wing scales (e.g., advanced/primitive) could be assessed.

The anal papillae are a pair of usually soft, fleshy lobes flanking the ovipore at the apex of the abdomen. There



a. *Undopteryx sukatshevae*

b. *Eolepidopterix jurassica*

c. *Paleolepidopterix*

d. *Protolepis cuprealata*

e. larva indet., Lebanese amber

f. *Glossata* indet., (head) New Jersey amber

Figure 12. Cretaceous Lepidoptera. —a. *Undopterix sukatshevae* (from Skalski, 1979a). —b. *Eolepidoteryx jurassica* (from Rasnitsyn, 1983). —c. *Paleolepidopterix aurea* (from Kozlov, 1989). —d. *Protolepis cuprealata* (from Kozlov, 1989). —e. Larva, in Lebanese amber (from Grimaldi, 1996). —f. Glossata indet. (head), in New Jersey amber (original).

are two pairs of internal apodemes present in female ditrysians, one pair connecting to the anal papillae and one pair connecting to segment VIII. Given that there is preservation of apodemes in other Jurassic putative moths, and soft structures like the putative anal papillae in *Protolepis* are preserved, it is interesting that the apodemes cannot be observed and do not appear to be preserved. As drawn by Kozlov (1989) (fig. 1e), the apical segmentation of the abdomen cannot confirm if this fossil is ditrysian. The antennae, which are as long as or longer than the length of the wing, are unusually long for a ditrysian. In lieu of re-examination of the fossil it is prudent to place the fossil as Glossata incertae sedis.

Larva. Lebanese amber (Neocomian, Lower Cretaceous). First figured in Grimaldi (1996) (fig. 12e), this is a well-preserved larva with the underside of the head beautifully preserved, displaying the critical glossatan synapomorphy of the spinneret. This is the oldest definitive glossatan, although it is possible that a spinneret predated the adult proboscis, even though both features occur on the same node in the cladogram of modern lepidopterans. There are three pairs of thoracic legs, but no prolegs, and the head is prognathous, features consistent with it being a leaf-mining taxon. Crochet-bearing prolegs are an apomorphy of the Neolepidoptera; very different prolegs of the primitive living genus *Micropteryx* are convergent.

?Incurvariidae. In Lebanese amber, identified by Whalley (1977, 1978) on the basis of two very fragmentary specimens with scaled wings. Apparently, the scales on the margin of the wing are strongly toothed and most closely match incurvariid marginal scales (particularly the genus *Prodoxus* Riley). I do not consider the emargination of marginal scales of the wings diagnostic for any one family.

?Incurvariidae. A specimen in Santonian amber from Taymyr, northern Siberia, mentioned by Skalski (1979b: 64) as being "very near recent incurvariids," and which possesses a frenulum with a single bristle.

?Lophocoronidae. Another Siberian amber specimen mentioned by Skalski (1979b) as being in or very near the Lophocoronidae. Nielsen and Kristensen (1996) questioned this placement. According to Nielsen and Kristensen, a postapical Rs_4 is found in the fossil, the Lophocoronidae, and the Exoporia (where Rs_4 is displaced even more posteriorly), as well as some *Sabatinca*. Convergence of the Rs_4 is apparently reflected in its configuration. The valve shape in the fossil as originally reported by Skalski (1979) as *Lophocorona*-like is apparently unlike the valves in this family.

Undescribed forms, Turonian amber, New Jersey. Various undescribed Glossata have recently been discovered in Turonian amber from central New Jersey (Grimaldi, unpublished). With nearly 20 complete specimens, this site is probably the most significant for Mesozoic Lepidoptera. Scale morphology, details of mouthparts and legs, male genitalia—even wing color patterns—are observable on many specimens. A comprehensive study of the specimens is presently under way, although preliminarily all specimens appear to be primitive Glossata and Myoglossata: none apparently are Ditrysia.

A PRELIMINARY CONSPECTUS OF THE ALLON FLORA FROM THE LATE CRETACEOUS (LATE SANTONIAN) OF CENTRAL GEORGIA, U.S.A.[1]

Patrick S. Herendeen[2], *Susana Magallón-Puebla*[3], *Richard Lupia*[3], *Peter R. Crane*[3], *and Jolanta Kobylinska*[3]

ABSTRACT

A preliminary conspectus of the fossil flora from the Allon locality, in Crawford County central Georgia, documents the presence of at least 63 distinct plant organs, based on macrofossils and mesofossils, but excluding dispersed pollen and spores. The fossils are preserved in a clay lens within the Buffalo Creek Member of the Gaillard Formation, and are of late Santonian (Late Cretaceous) age. In general, macrofossils are sparse at this site, but abundant mesofossils have been isolated from bulk samples by sieving. The flora includes sporophytes and gametophytes of fossil mosses (e.g., *Eopolytrichum antiquum*, *Campylopodium allonense*), ferns (e.g., cf. *Boodlepteris*), and conifers, but is dominated by the diverse and abundant remains of angiosperms. Angiosperms in the flora include cf. *Detrusandra* (Magnoliales), *Mauldinia* sp. (Lauraceae), *Allonia decandra* (Hamamelidaceae), and *Parasaurauia allonensis* (Actinidiaceae). Especially abundant are flowers and cupules of two species of Fagaceae sensu lato (*Protofagacea allonensis*, *Antiquacupula sulcata*). The flora also includes fossil flowers of *Caryanthus* sp. (Juglandales/Myricales) and *Bedellia pusilla* (cf. Betulaceae), which comprise the first record of Normapolles-producing flowers from North America. The structural and systematic diversity of angiosperms in the Allon flora is comparable to that at other Turonian-Campanian sites in eastern North America and Europe. Together, these fossil floras indicate that angiosperms, and especially eudicots, were already diverse at this relatively early stage in angiosperm evolution. The source vegetation represented by the Allon fossil assemblage was dominated by angiosperms, probably with taxodiaceous conifers also common. Preservation of most of the mesofossils as charcoal indicates that fire may have been an important factor contributing to frequent disturbance of the source plant community.

Over the last two decades, investigations of Cretaceous floras have been revitalized by the emergence of a wealth of new paleobotanical data and the application of a more rigorous approach to the comparison of Cretaceous fossil plants with their living relatives. Especially striking have been rapid advances in the study of mesofossil assemblages isolated from plant debris beds, which have included remarkable discoveries of fossil flowers, and other small, delicate, plant fossils (e.g., moss gametophytes and sporophytes) that have not been recognized previously. Mesofossil assemblages are generally obtained by wet sieving and panning of unconsolidated sediments that can be disaggregated in water. Typically, they are comprised of three-dimensionally preserved fossils 0.5–5 mm in maximum dimension: too small to be seen easily in the field and too large to survive standard palynological preparation techniques.

Mesofossil assemblages from the Cretaceous have yielded extremely well-preserved angiosperm flowers, fruits, seeds, stamens, and wood, as well as cones, pollen organs, and wood of other seed plants (especially conifers), fern pinnules and rhizomes, remains of other pteridophytes, and bryophyte sporophytes and gametophytes. Specimens may be lignified or charcoalified, and both modes of preservation can be studied easily with scanning electron microscopy to reveal morphological and anatomical information. Charcoalified specimens,

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in particular, are often exquisitely preserved and yield a level of fine structural detail comparable to that obtained from extant plants.

Studies of mesofossils have greatly expanded our knowledge of previously described plant fossils (e.g., *Eucommiidites*-producing plants, Pedersen et al., 1989) and have provided new insights into the diversity and systematic relationships of Cretaceous angiosperms (e.g., Crane et al., 1989, 1994, 1995; Crepet & Nixon, 1994, 1996, 1998; Friis, 1984, 1985, 1990; Friis & Skarby, 1982; Friis et al., 1986, 1988, 1995, 1997a; Gandolfo et al., 1998a, b; Herendeen, 1991a, b; Herendeen et al., 1994, 1995; Keller et al., 1996; Magallón-Puebla et al., 1996, 1997; Pedersen et al., 1991, 1994; Sims et al., 1998). In addition, because pollen is frequently preserved in situ within mesofossil reproductive structures, these studies have led to the identification of the parent plants of many Cretaceous angiosperm pollen grains that were previously only known from dispersed palynofloras (Friis, 1983; Crane et al., 1989; Pedersen et al., 1989, 1991; Sims et al., 1999).

The impact of research on mesofossils has been especially pronounced in changing our understanding of the Cretaceous fossil history of flowering plants. New discoveries, especially from the Late Cretaceous of Europe and eastern North America, have substantially extended the known fossil record of many angiosperm groups (e.g., Herendeen et al., 1995; Sims et al., 1998) and have documented the presence of many lineages that previously were not known to have a reliable fossil record (Friis et al., 1997b; Magallón-Puebla et al., 1999). Information on fossil flowers has provided new insights into floral architecture, pollination, and dispersal in extinct angiosperms, and how these structural and biological features may have changed through time. Morphological and systematic studies of mesofossils have yielded new information on the fossil history of bryophytes (Konopka et al., 1997, 1998), ferns (Gandolfo et al., 1997b; Herendeen & Skog, 1998), conifers (Srinivasan, 1992, 1995; Srinivasan & Friis, 1989), and other gymnosperms (Pedersen et al., 1989, 1993). Paleoecological studies based on mesofloras are also contributing valuable new information for interpreting Cretaceous vegetation (Lupia, 1994, 1997).

Mesofossil assemblages have been described from sediments in North America and Europe that range in age from Barremian-Aptian to Maastrichtian. In Europe, the most intensively studied site is the Åsen locality in Scania, southern Sweden (e.g., Friis & Skarby, 1982; Friis, 1983, 1984, 1985, 1988, 1990), which includes a large number of different assemblages that are of late Santonian to early Campanian age. Other mesofossil assemblages have been recovered from the Early Cretaceous of southern England (e.g., Herendeen & Skog, 1998), and many localities in the Late Cretaceous of central Europe (Knobloch & Mai, 1984, 1986, 1991). Also intensively studied are a sequence of rich mesofossil assemblages from the Cretaceous of western Portugal that have yielded important data on early angiosperm evolution and that range from Barremian-Aptian to Maastrichtian in age (e.g., Friis et al., 1992, 1994, 1999). In Asia, important mesofossil assemblages are known from the Coniacian-Santonian of Japan (Takahashi, Crane & Ando, in prep.) and the Cenomanian-Turonian of Kazakhstan (Frumin & Friis, 1996, 1999).

In North America the most intensively studied mesofossil localities are from the Cretaceous of the Atlantic Coastal Plain, where a series of floras are known from Martha's Vineyard (Tiffney, 1977) and New Jersey (e.g., Crepet & Nixon, 1994; Gandolfo et al., 1997b) in the north, to central Georgia in the south (Crane & Herendeen, 1996; Crane et al., 1994; Friis et al., 1986, 1988, 1997a). These fossil assemblages range in age from Aptian to Campanian and are continuing to yield a great diversity of well-preserved mesofossil material (e.g., Crane & Herendeen, 1996). Other mesofossil floras from the Great Plains and Rocky Mountain regions of North America have been less intensively studied than those in eastern North America and in general they appear less well preserved (Herendeen, unpublished).

Most studies of mesofossils published to date have presented detailed treatments of the morphology and systematic relationships of particular fossil taxa. This approach has drawn attention to some of the most common components of mesofossil assemblages and has clarified fossil history of many groups of angiosperms and other plant lineages. However, a by-product of this focused approach has been that only a small fraction of the total plant diversity preserved as mesofossils has been described. Complete paleofloristic descriptions that illustrate and describe the diverse structures in a single mesofossil assemblage using modern techniques, and that also include both the angiosperm and non-angiosperm components of these floras, have not been presented.

In this paper we present a preliminary conspectus of the Allon flora: a diverse and well-preserved late Santonian (Late Cretaceous) mesofossil assemblage from central Georgia. Several other diverse mesofossil assemblages from Georgia are currently under investigation, but the Allon flora has been

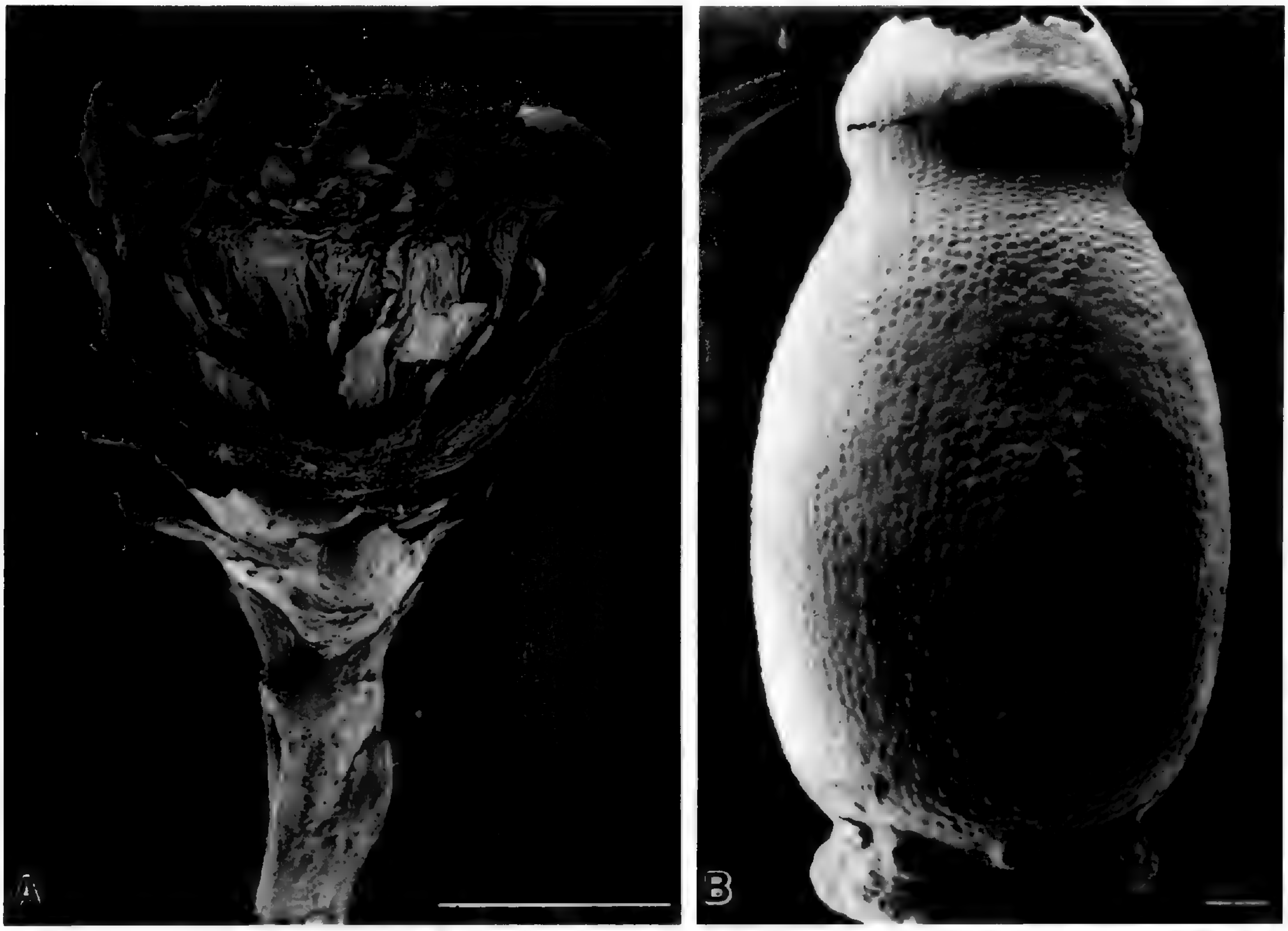

Figure 1. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 1, *Eopolytrichum antiquum* Konopka, Herendeen, Smith Merrill & Crane (Polytrichaceae). —A. Oblique view of fertile gametophyte shoot apex showing elongated antheridia and numerous leaves with photosynthetic lamellae on their adaxial surface; PP44724. —B. Lateral view of sporophyte capsule showing the line of separation of the operculum, swollen apophysis at the base and prominent stomata; PP44717. Scale bars; A = 1 mm. B = 100 μm.

studied for several years, and several detailed treatments of specific taxa are already published (Crane & Herendeen, 1996; Herendeen et al., 1995; Keller et al., 1996; Konopka et al., 1997, 1998; Magallón-Puebla et al., 1996; Sims et al., 1998, 1999). Most taxa from the Allon flora, however, have not yet been described. Some components of the mesofossil assemblages have not been treated because they belong to plant groups that are not yet the focus of a major research effort (e.g., conifers), while in other cases there has been insufficient material to prepare a detailed description that could serve as the basis for systematic analysis. For many angiosperm mesofossils, uncertainty over systematic relationships has also served as a disincentive for publication.

To our knowledge, the treatment of the Allon flora in this paper is the first time that a Cretaceous mesofossil assemblage has been documented in its entirety based on scanning electron microscopy. Preliminary descriptions and photographs (excluding details of anatomy and pollen/spores for reasons of space) are presented of all bryophyte, fern, conifer, and angiosperm mesofossil remains that we have been able to discriminate and characterize. Only the dispersed pollen and spores, as well as a small number of poorly preserved dispersed seeds, stamens, and coprolites, are not treated. We also provide documentation of the leaf impression/compression fossils that are known from the Allon locality, and present an initial estimate of the relative abundance of the different elements in the mesofossil assemblage. A preliminary estimate of the relative diversity of different major plant groups in the flora is also provided.

Future research on the Allon flora will undoubtedly result in the recognition of new taxa. In the meantime, however, the preliminary conspectus presented here will provide useful data for comparison with other mid and late Cretaceous mesofossil localities (Lupia, work in progress) and will help place the diversity of late Santonian angiosperms in a broader context that includes other elements of Late Cretaceous vegetation.

MATERIALS AND METHODS

The fossil material described here was collected from a clay lens in the south pit ("Allon" quarry) of the Atlanta Sand and Supply Company (Knoxville Quadrangle, lat. 32°37′47″N, long. 83°59′10″W) in Gaillard, Georgia, ca. 9.5 km southeast of Roberta in Crawford County. The clay lens has been assigned to the Buffalo Creek Member of the Gaillard Formation (Huddlestun & Hetrick, 1991). The Buffalo Creek Member is considered to be of late Santonian age. This is based on the presence of terrestrial palynomorphs that are considered to be biostratigraphically equivalent to those in marine units assigned to the late Santonian based on calcareous nannofossils (i.e., equivalent to the lower part of calcareous nannofossil zone CC17, which Burkett [1996] considered to be late Santonian) (Christopher, unpublished data).

The clay lens yielding the mesofossils varies from 0.2 to 0.8 m thick, is truncated at both ends, and has a lateral extent of at least 16 m in the outcrop. The clay is microlaminated, dark gray, and carbonaceous. It is inferred to represent a lower floodplain pond, and the presence of rare dinoflagellates in the palynoflora perhaps indicates some tidal influence (Lupia & Sims, unpublished). In terms of the mesofossils, the productivity of the Allon locality varies across the outcrop from about 250 specimens per 20-kg sample where the lens is thick, to about 2500 specimens per 20-kg sample at the extreme edge where the lens is thinnest. There is also considerable variation in the composition of the mesofossil assemblage among different samples (Lupia, 1997; in prep.). The Allon flora contains a diverse assemblage of angiosperms, gymnosperms, ferns, and bryophytes preserved as fusainized and lignitic mesofossils (Herendeen et al., 1995; Crane & Herendeen, 1996; Keller et al., 1996; Magallón-Puebla et al., 1996; Konopka et al., 1997, 1998; Sims et al., 1998, 1999). The clay also contains a macrofossil assemblage, which is preserved as impressions or thin compressions, and a diverse palynoflora.

The material was prepared by dissolving bulk samples of clay in water and then washing the slurry through a series of sieves (finest mesh 125 μm). Isolated plant material was cleaned with HCl, followed by HF, and then thoroughly washed in water. The fossil material was air-dried and examined using a binocular stereomicroscope. Specimens picked from the organic debris were mounted on stubs, coated with gold, and examined with an Amray 1810 scanning electron microscope. After initial scanning, selected specimens were partially dissected to reveal internal morphology, and then recoated and scanned. Except where noted all illustrations are scanning electron micrographs. All fossil specimens are deposited in the paleobotanical collections of the Department of Geology, The Field Museum, Chicago (PP).

DESCRIPTIONS AND DISCUSSION OF FOSSIL PLANTS

MOSSES

Polytrichaceae

1. *Eopolytrichum antiquum* Konopka, Herendeen, Smith Merrill & Crane
Figure 1.

Sporophyte capsules are terete to somewhat dorsiventrally flattened in cross section, 0.9–1.1 mm long, 0.6–0.8 mm wide, and have a swollen, asymmetrical apophysis and mammillose exothecium. Stomatal complexes, each surrounded by a ring of subsidiary cells, are confined to the apophysis (Fig. 1B). The operculum is tall and dome-shaped, but the calyptra and beak of the operculum are not preserved. Remains of a peristomial membrane are present around the rim of the capsule after the operculum has dehisced, but peristome teeth are absent and the epiphragm is retained in the operculum. Spores are alete, spherical, and echinulate (Konopka et al., 1997). Associated sterile and fertile male (Fig. 1A) gametophytes have leaves with adaxial, presumed photosynthetic, lamellae on the blade surface as well as other anatomical structures comparable to those of leaves in extant Polytrichaceae.

The structure and relationships of *Eopolytrichum antiquum* were described by Konopka et al. (1997).

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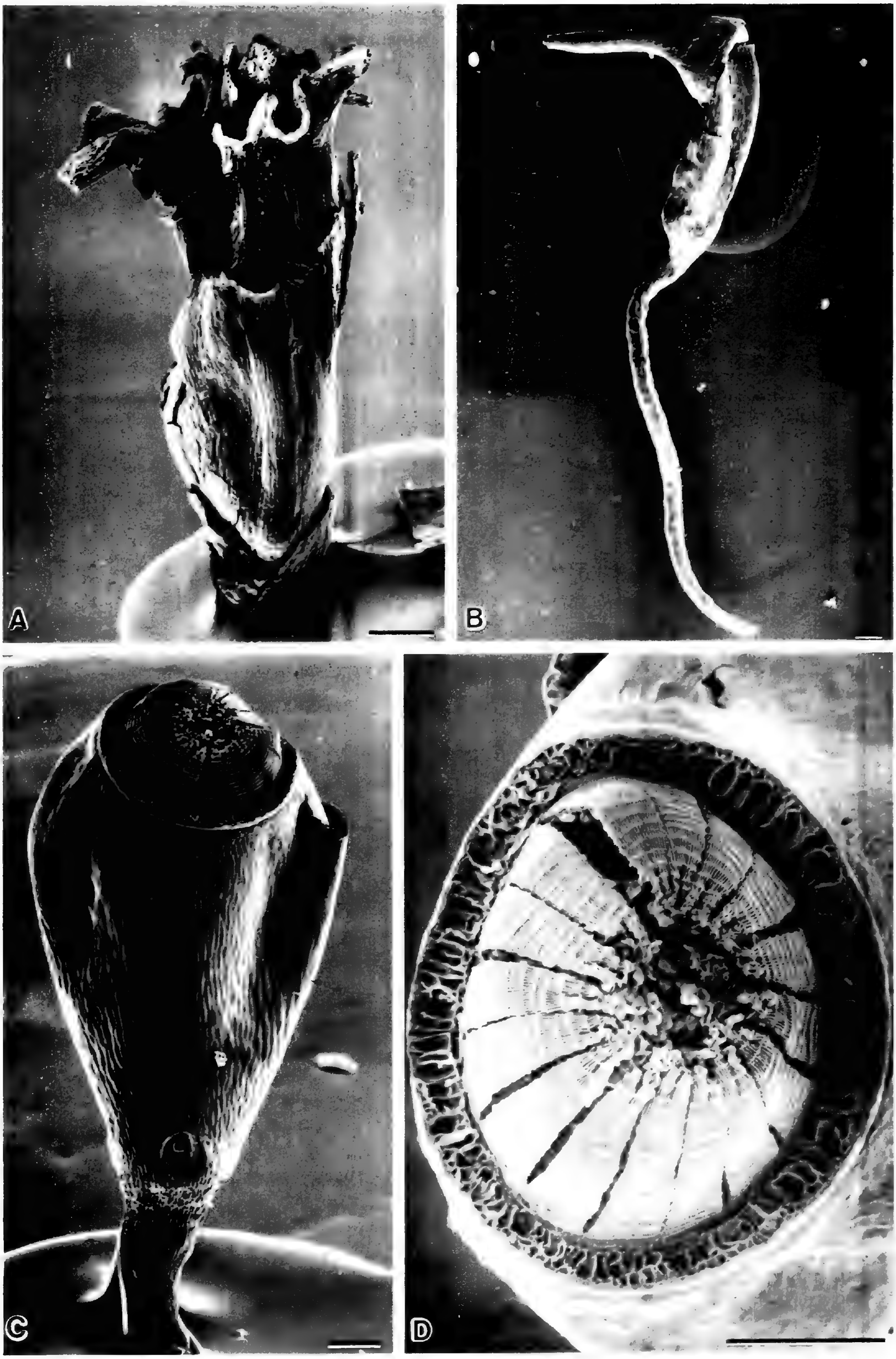
Figure 2. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 2, *Campylopodium allonense* Konopka, Herendeen & Crane (Dicranaceae). —A. Lateral view of gametophyte axis fragment showing leaves with broadly sheathing bases and abruptly narrowed blades; PP44740. —B. Lateral view of sporophyte capsule showing attached seta, slightly swollen apophysis, prominent stomata and cuculate operculum; PP45163. —C. Lateral view of sporophyte capsule showing narrowed base, prominent stoma and attachment to the seta; operculum missing and exposing the peristome teeth; PP44725. —D. Apical view of peristome showing compound annulus, teeth with divided tips and numerous spores in the center; PP44725. Scale bars = 100 μm.


A
B
C
D

Morphological and anatomical details clearly indicate that the fossil sporophytes belong to the family Polytrichaceae, but the combination of features in the fossils does not occur in any extant genus (Konopka et al., 1997; Table 1). Associated fossil gametophytes exhibit the distinctive lamellae and leaf anatomy of the Polytrichaceae, and the male gametophytes contain characteristic clavate paraphyses and antheridia. Toothed leaf margins and pyriform marginal cells of lamellae occur in several extant genera of Polytrichaceae, but the rounded abaxial protuberances of the leaf sheath are unique to the fossil. More detailed information is needed about the epiphragm, columella, peristomial membrane, and tooth structure in extant taxa in order to determine structural homologies within and among Polytrichales, Bryales, Tetraphidales, and other major lineages of mosses. A more precise understanding of the relationships of *Eopolytrichum* within the Polytrichaceae will require cladistic analysis that includes the fossil and relevant extant taxa.

Eopolytrichum antiquum is known from two sporophyte capsules and four gametophyte specimens.

Dicranaceae

2. *Campylopodium allonense* Konopka, Herendeen & Crane
   Figure 2.

Fossil sporophyte capsules are curved, cylindrical, and strumose (Fig. 2B), 1.7–2.4 mm long, with an obliquely rostrate operculum (Fig. 2C), cucullate calyptra, and compound annulus (Fig. 2D). The peristome is haplolepidous with 16 dicranoid, apically bifid teeth that are vertically striate on the outer surface (Fig. 2D) and asymmetrically trabeculate on the inner surface. Spores are alete, spherical, and finely rugose, and thus differ from the finely papillose spores of extant *Campylopodium* (Konopka et al., 1998). Spores identical to those found within the sporangium have been found on the leaf surfaces of one of the gametophyte specimens, providing circumstantial evidence that both sporophyte and gametophyte belong to the same species. Fossil gametophytes are consistent with the morphology of extant *Campylopodium* and have leaves with a broad sheathing base and a narrow blade (Fig. 2A).

Sporophytes and gametophytes of *Campylopodium allonense* were described by Konopka et al. (1998). *Campylopodium allonense* represents the first appearance of Dicranaceae in the fossil record. This material, along with *Eopolytrichum antiquum* also from the Allon locality, represents two different subclasses of mosses, and provides the first definitive evidence of modern families of mosses in the Cretaceous. In a phylogenetic context, these fossils imply that mosses were already diverse at the family and genus level by the Late Cretaceous.

Campylopodium allonense is represented in the Allon flora by ca. 20 sporophyte capsules and at least 10 gametophyte specimens.

FERNS

Gleicheniaceae

3. cf. *Boodlepteris* Gandolfo, Nixon, Crepet & Ratcliffe
   Figure 3.

Ultimate pinnules are alternate, sessile, and broadly rounded to obtuse, 0.5 mm long, 0.7 mm wide (Fig. 3A, B). The midvein does not reach the apex of the pinnules, and lateral veins are not evident (Fig. 3B). The ultimate rachis is slightly sinuous (Fig. 3A). Fertile specimens have not been found.

Only two specimens of these fern pinnule fragments are known and both are similar to those of *Boodlepteris turoniana* Gandolfo, Nixon, Crepet & Ratcliffe (1997b) from a Turonian age locality (lower Magothy Formation) in Sayreville, New Jersey (Old Crossman Clay Pit). Fertile specimens have not been found at the Allon site, but the Turonian material bears exindusiate sori composed of 10–20 sporangia (Gandolfo et al., 1997b). Based on cladistic analysis, *Boodlepteris turoniana* is thought to be most closely related to the extant genus *Stromatopteris* (Gleicheniaceae) (Gandolfo et al., 1997b). Another fossil representative of Gleicheniaceae was described by Herendeen and Skog (1998) based on charcoalified pinnule fragments from a mesofossil assemblage in the Early Cretaceous of Bedfordshire, England. These fossils were described as an extinct species of the extant genus *Gleichenia*. The extensive fossil record of the family Gleicheniaceae is reviewed by Herendeen and Skog (1998).

Fern, family *incertae sedis*

4. Fern leaf type 1
   Figure 4.

Leaf fragments are pinnate with ultimate pinnules alternate, sessile, narrowly triangular, and with an acute apex, 3 mm long, 1.5 mm wide at base (Fig. 4A–C). Presumed mature pinnules are more broadly triangular (Fig. 4D) and have revolute margins, and the midvein is raised on the abaxial side (Fig. 4E). Stomata have not been observed.

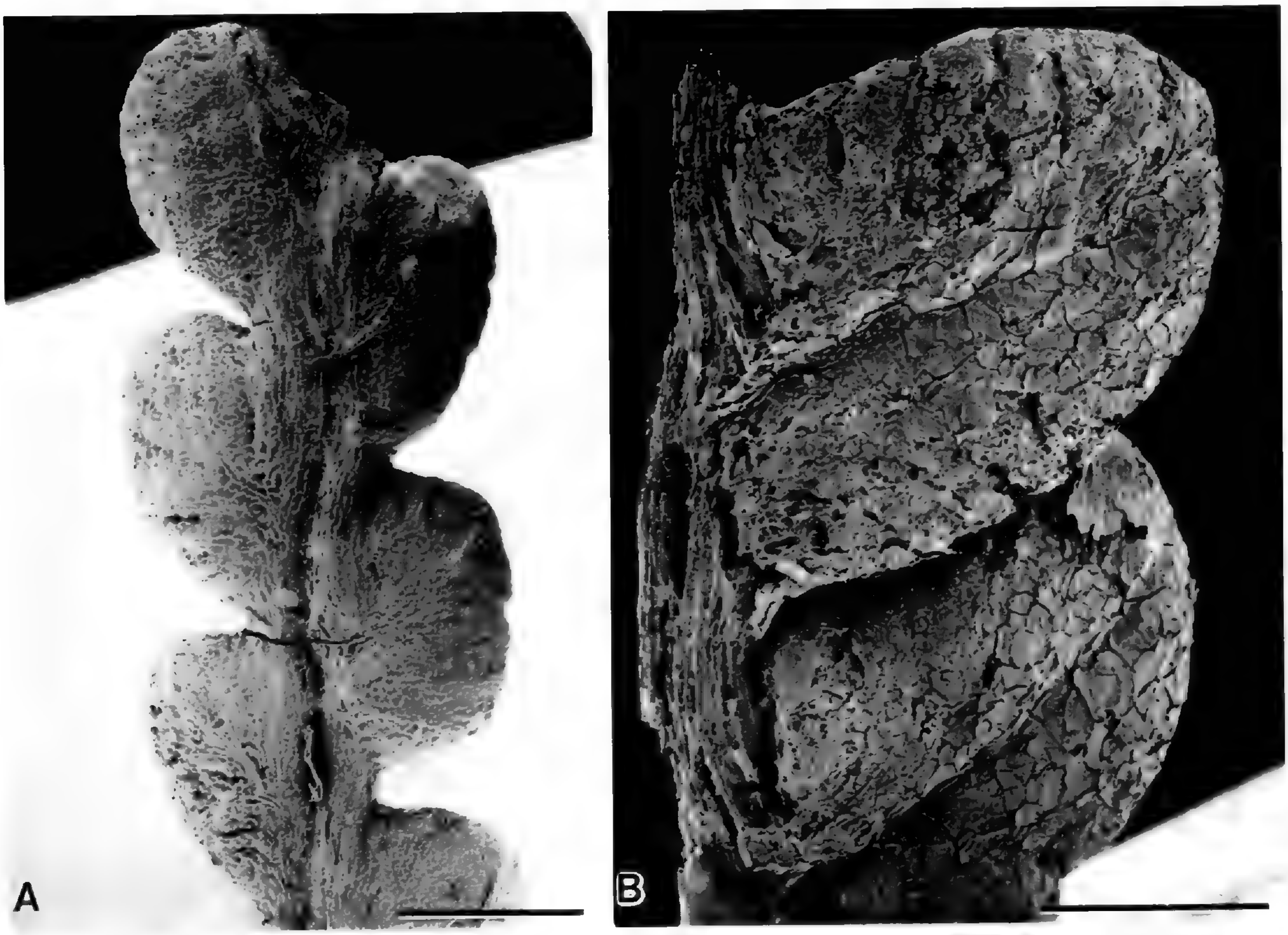


Figure 3. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 3, cf. *Boodlepteris* Gandolfo, Nixon, Crepet & Ratcliffe (Gleicheniaceae). —A. Fern pinna with alternate, rounded pinnules; PP45158. —B. Fern pinna with alternate, rounded pinnules; PP45159. Scale bars = 0.5 mm.

Only sterile specimens are known. Simple trichomes are abundant on the abaxial leaf surface. Rachis and rhizome anatomy are unknown.

The available details are insufficient to evaluate the affinities of these few fragmentary specimens. Specimens of fern leaf type 1 are rare in the Allon fossil assemblage.

5. Fern leaf type 2 (macrofossil)
   Figure 5A.

Leaf fragment pinnatifid, 20 mm long. Proximal pinnules broadly triangular with 1–2 teeth. Distal pinnules narrowly triangular and lacking teeth. Details of pinnule venation not preserved.

This single fragment, of unknown systematic relationships, is the only evidence of ferns in the Allon macroflora. The specimen is similar to pinnules of *Dryopterites stephensonii* Berry (1914, pl. 17, fig. 1) from the Eutaw Formation (Santonian-Campanian) of Georgia, but the absence of pinnule venation in the Allon material precludes more detailed comparison.

CONIFERS

Conifers, family *incertae sedis*

6. Conifer foliage type 1 (cf. *Brachyphyllum* Brongniart) (macrofossil)
   Figure 5B.

Branched, planated conifer leafy shoot bearing numerous, tightly appressed, helically arranged scale leaves with acute apices. Shoots up to 3–4 mm wide.

Only a single fragment of this conifer leaf shoot has been found. In overall form it resembles leafy shoots often assigned to *Brachyphyllum* and assumed to be of araucariaceous or cheirolepidiaceous affinity. In this context it may be significant that *Classopollis* pollen (Cheirolepidiaceae) has not been detected in the Allon palynoflora. The specimen resembles shoots from the Allon mesoflora assigned to conifer foliage type 4 (taxon 9).

7. Conifer foliage type 2 (macrofossil)
   Figure 5C.

Conifer leafy shoot bearing helically arranged, acicular, leaves up to 5 mm long, with pointed api-

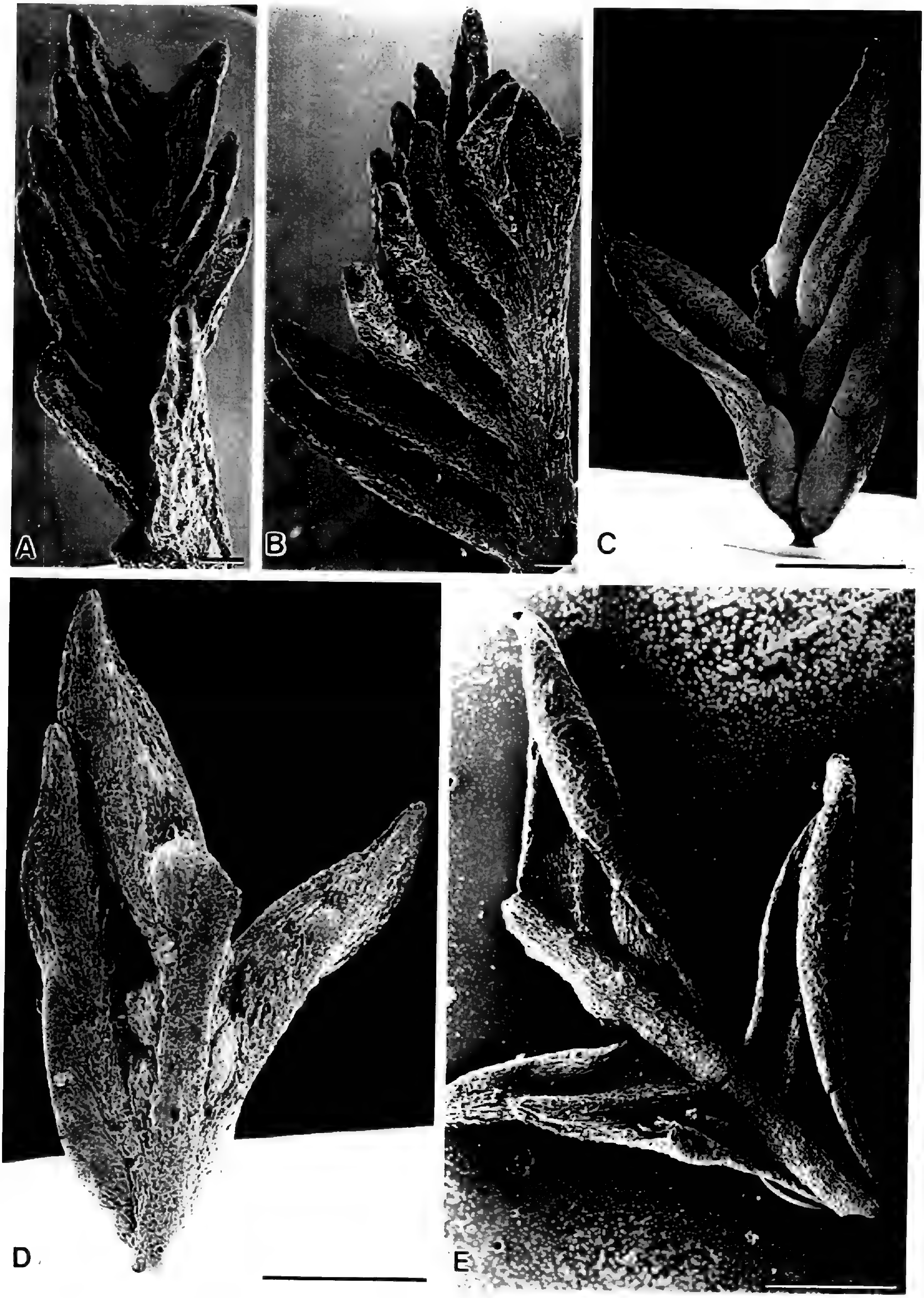


Figure 4. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 4, Fern leaf type I. —A. Frond fragment with alternate, narrowly triangular acute pinnules; PP45160. —B. Abaxial surface of specimen shown in A. —C. Frond fragment with alternate, acute pinnules, showing the abaxial surface; PP45161. —D. Adaxial surface of specimen shown in C. —E. Fern with alternate, acute pinnules, showing the adaxial surface with a prominent rachis and pinnule midvein; PP45162. Scale bars; A, B = 100 μm. C, D, E = 1 mm.

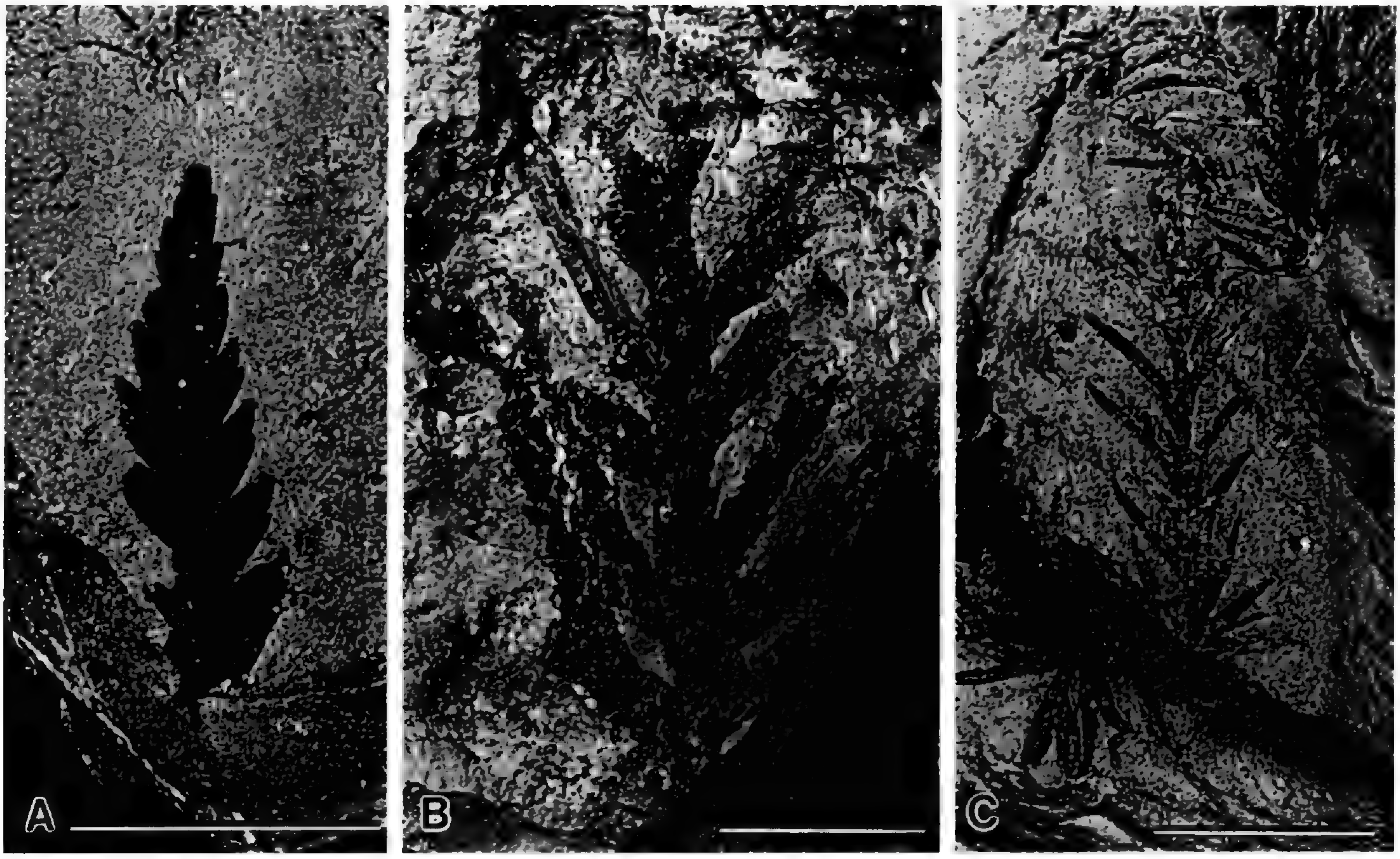


Figure 5. Macrofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxa 5, 6, and 7, Ferns and conifers; light micrographs. —A. Taxon 5, Fern leaf type 2, frond fragment showing pinnules, macrofossil; PP45376. —B. Taxon 6, Conifer foliage type 1 (cf. *Brachyphyllum*), shoot bearing numerous scale-like leaves, macrofossil; PP4537. —C. Taxon 7, Conifer foliage type 2, shoot bearing elongated leaves, macrofossil; PP45378. Scale bars = 10 mm.

ces. Many fragments of this conifer leafy shoot have been found. Among the conifers described by Berry (1914) from the Santonian-Campanian of Georgia, the Allon material is most similar to the specimens described as *Sequoia reichenbachi* (Geinitz) Heer, but the absence of anatomical information for both the Allon material and the specimens illustrated by Berry (1914, pl. 4) precludes more detailed comparison. Isolated conifer leaves (Fig. 6F) similar to those of conifer foliage type 2 are described below under conifer foliage type 3 (taxon 8).

cf. Taxodiaceae

8. Conifer foliage type 3
   Figure 6.

The material consists of a variety of leafy shoots (Fig. 6A–E) and isolated leaves (Fig. 6F). The leaves have an acute apex and decurrent base, and when observed attached are helically arranged. Some leaves have parallel margins and a short triangular apex (Fig. 6A, B), while others have a more extensively tapering apex (Fig. 6D, E). Additionally, there are larger, narrow tapering leaves with stomata that are oriented parallel to the leaf axis (Fig. 6F). One leafy shoot has structures in the leaf axes that may be the broken stalks of pollen cones (Fig. 6A, B).

Conifer foliage type 3 is abundant at the Allon locality, and more than one taxon may be represented. In gross morphology some specimens of this leaf type are similar to *Taxodium wallisii* Aulenback & LePage (1998) from the Maastrichtian of Alberta. However, Aulenback and LePage (1998) noted that foliage of *Taxodium* Rich., *Cryptomeria* D. Don., and *Glyptostrobus* Endl. can be difficult to distinguish without associated reproductive material, and that material previously assigned to these genera from the Cretaceous and Tertiary is in need of re-evaluation. One difference between the isolated leaves from Allon (Fig. 6F) and *Taxodium wallisii* is that the stomata on the former are oriented parallel to the leaf axis, whereas they are randomly oriented in *Taxodium wallisii* (Aulenback & LePage, 1998). Some of the Allon conifer shoots (e.g., Fig. 6A, B, D) are broadly similar to specimens from the Late Cretaceous (late Santonian-early Campanian) of southern Sweden assigned to the fossil genus *Quasisequoia* Srinivasan & Friis (1989). Other specimens (e.g., Figs. 6E, F) more closely resemble specimens from southern Sweden assigned to *Elatidopsis* Srinivasan & Friis (1989).

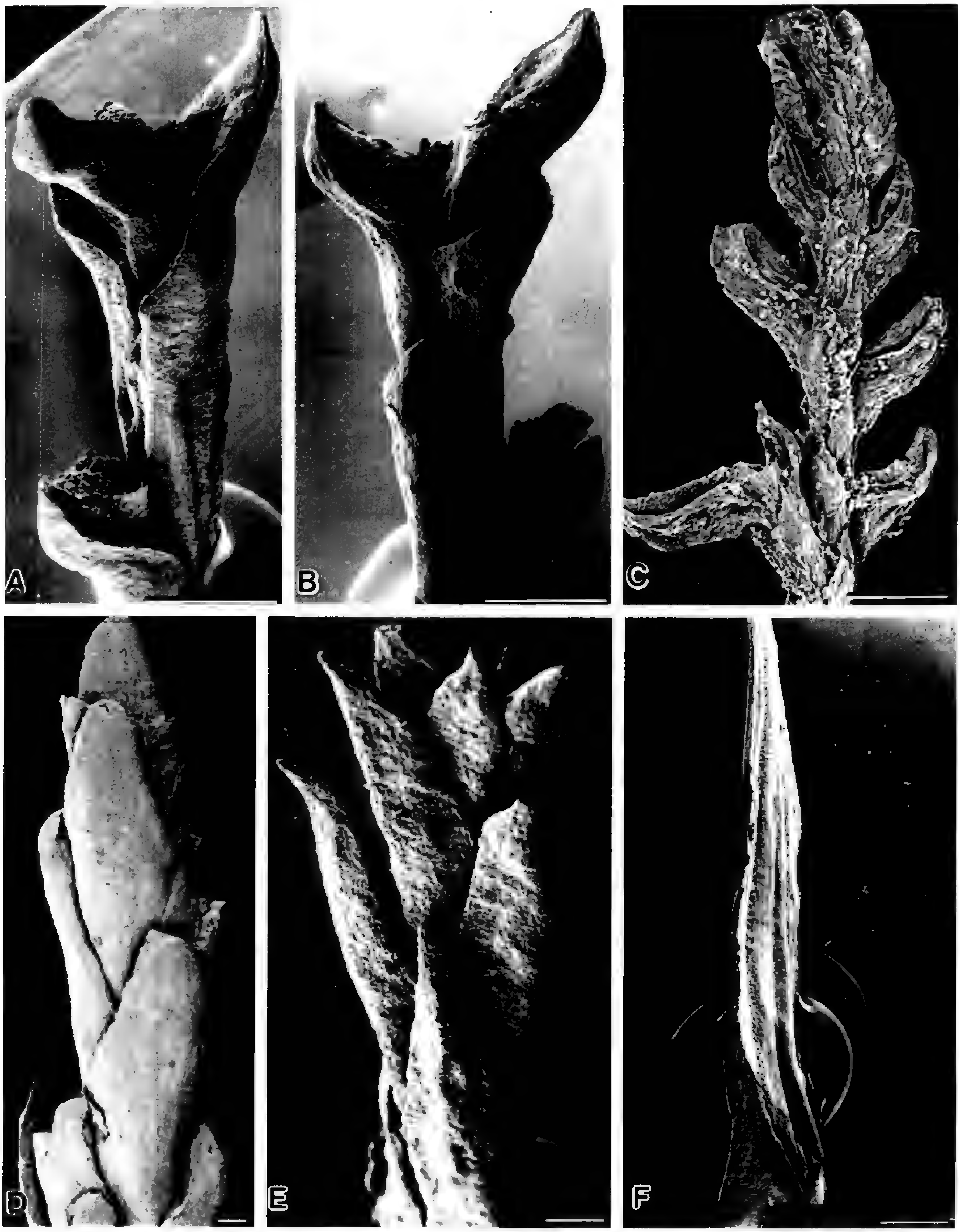


Figure 6. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 8, Conifer foliage type 3. —A. Conifer shoot with short, scale-like leaves with parallel margins, acute apex, and decurrent base showing possible cone stalk in leaf axil; PP45164. —B. Other surface of specimen shown in A. —C. Conifer shoot with short, thick, scale-like leaves with an acute apex and decurrent base; PP45165. —D. Conifer shoot with short, scale-like leaves with a tapering rounded apex and decurrent base; PP45166. —E. Conifer shoot with short, scale-like leaves with a tapering acute apex and decurrent base; PP45167. —F. Isolated conifer leaf with acute apex and two parallel lines of stomata on the adaxial surface; PP45168. Scale bars: A–C, F = 0.5 mm; D, E = 100 μm.

Both *Quasisequoia* and *Elatidopsis* are of probable taxodiaceous affinity.

Conifer family *incertae sedis*

9. Conifer foliage type 4 (cf. *Brachyphyllum*)
Figure 7.

Conifer shoot fragments with short, broadly triangular, tightly appressed helically arranged scale leaves (Fig. 7A–C). Leaves are 3–4 mm long, 2–3 mm wide. The abaxial epidermis bears numerous, longitudinally oriented, parallel rows of stomata (Fig. 7D). The leaves have thin fimbriate margins.

These specimens are common in the Allon mesofossil assemblage and may represent the mesofossil equivalent of taxon 6 (conifer foliage type 1 [cf. *Brachyphyllum*]), which is known as a macrofossil, but more detailed study is required based on additional material.

10. Conifer pollen cone and dispersed cone scales
Figure 8.

Conifer pollen cones bear helically arranged, imbricate cone scales (Fig. 8A, B). The cones are ca. 8 mm long, 5–6 mm wide. Cone scales have a narrow stalk proximally and a broad peltate limb with a fimbriate margin distally (Fig. 8C–E). Pollen grains are not preserved.

Epidermal details have not yet been studied to determine whether these cones were produced by the same plant species as one of the conifer foliage types, but the strongest morphological similarities are with the leaves of conifer foliage type 4 (cf. *Brachyphyllum*). The Allon pollen cone is similar to probable taxodiaceous pollen cones and sporophylls that were described from the Åsen locality in southern Sweden (Srinivasan & Friis, 1989, plate 8). Fragments of conifer cones are relatively common in the Allon flora, and more than one taxon may be represented.

ANGIOSPERMS

Magnoliales

11. cf. *Detrusandra* Crepet & Nixon
Figure 9.

Flowers ca. 5 mm tall, 3 mm wide, with numerous helically arranged perianth parts that are connate basally to form a deep floral cup (Fig. 9A, B). Stamens numerous, laminar, inserted on inner surface of cup; filament and anther are not differentiated. Carpels numerous, apparently spirally arranged, inserted in the base of the floral cup. Pollen unknown.

Crepet and Nixon (1994, 1998) described several types of fossil flowers with deep floral cups from the Turonian of New Jersey. They concluded that some of the flowers are most similar to the Eupomatiaceae (Magnoliales), and that others are more similar to the Calycanthaceae (Laurales). Cladistic analyses of relationships of two fossil taxa of magnoliid flowers showed that these taxa cannot be referred to any extant family (Crepet & Nixon, 1998). The flowers described here are most similar to the fossil *Detrusandra mystagoga* Crepet & Nixon (1998). Although similar to Calycanthaceae in many respects, these fossils differ from members of the extant family in the absence of elongated stigmas on the carpels and other features (Crepet & Nixon, 1998).

This taxon is represented in the Allon flora by three specimens.

Lauraceae

12. *Mauldinia* sp. Drinnan, Crane, Friis & Pedersen
Figure 10.

Flowers borne on flattened, bilobed inflorescence units, 6–7 mm wide, 5–6 mm long (Fig. 10A, B). Flowers trimerous with perianth in two cycles of three; the tepals of the outer cycle are shorter than those of the inner cycle. Details of androecium and pollen unknown. The gynoecium consists of a single carpel with a superior ovary.

Mauldinia was originally described by Drinnan et al. (1990) from an early Cenomanian locality in northern Maryland, and has since been found at other mid and Late Cretaceous localities in North America, Europe, and Asia (Drinnan et al., 1990; Eklund & Kvaček, 1998; Herendeen & Crane, unpublished data). The inflorescence structure of *Mauldinia* is unique and unlike that found in extant Lauraceae, but in those cases where flower structure is understood in detail it is consistent with extant members of the family (Drinnan et al., 1990; Eklund & Kvaček, 1998). The inflorescence of *Mauldinia* is spicate with helically arranged lateral cladode-like inflorescence units that are flattened, deeply bilobed, and typically bear five flowers and associated subtending bracts (Drinnan et al., 1990). The material described here is preserved as lignitized and compressed specimens, not as charcoal.

Wood of *Mauldinia mirabilis* Herendeen (*Paraphyllanthoxylon marylandense*) was described by Herendeen (1991a). *Paraphyllanthoxylon* is one of the most common types of angiosperm wood in the Late Cretaceous, and it is likely that much of it is referable to the Lauraceae (Herendeen, 1991a).

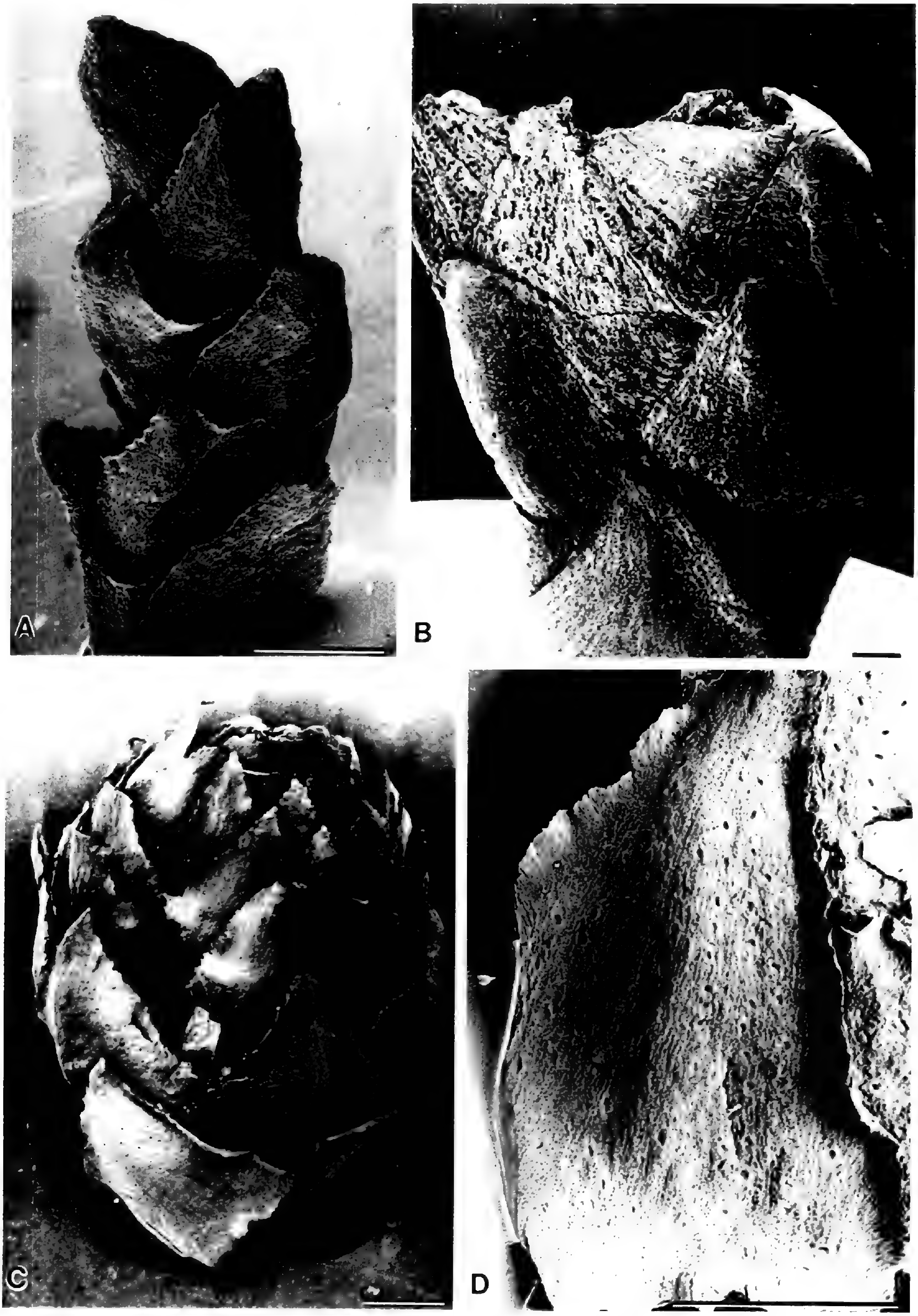


Figure 7. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 9, Conifer foliage type 4 (cf. *Brachyphyllum*). —A. Conifer shoot with short, broad scale-like leaves; note upturned acute apices (cf. Fig. 5B); PP45169. —B. Conifer shoot with short, broad scale-like leaves; PP45170. —C. Conifer shoot with short, broad

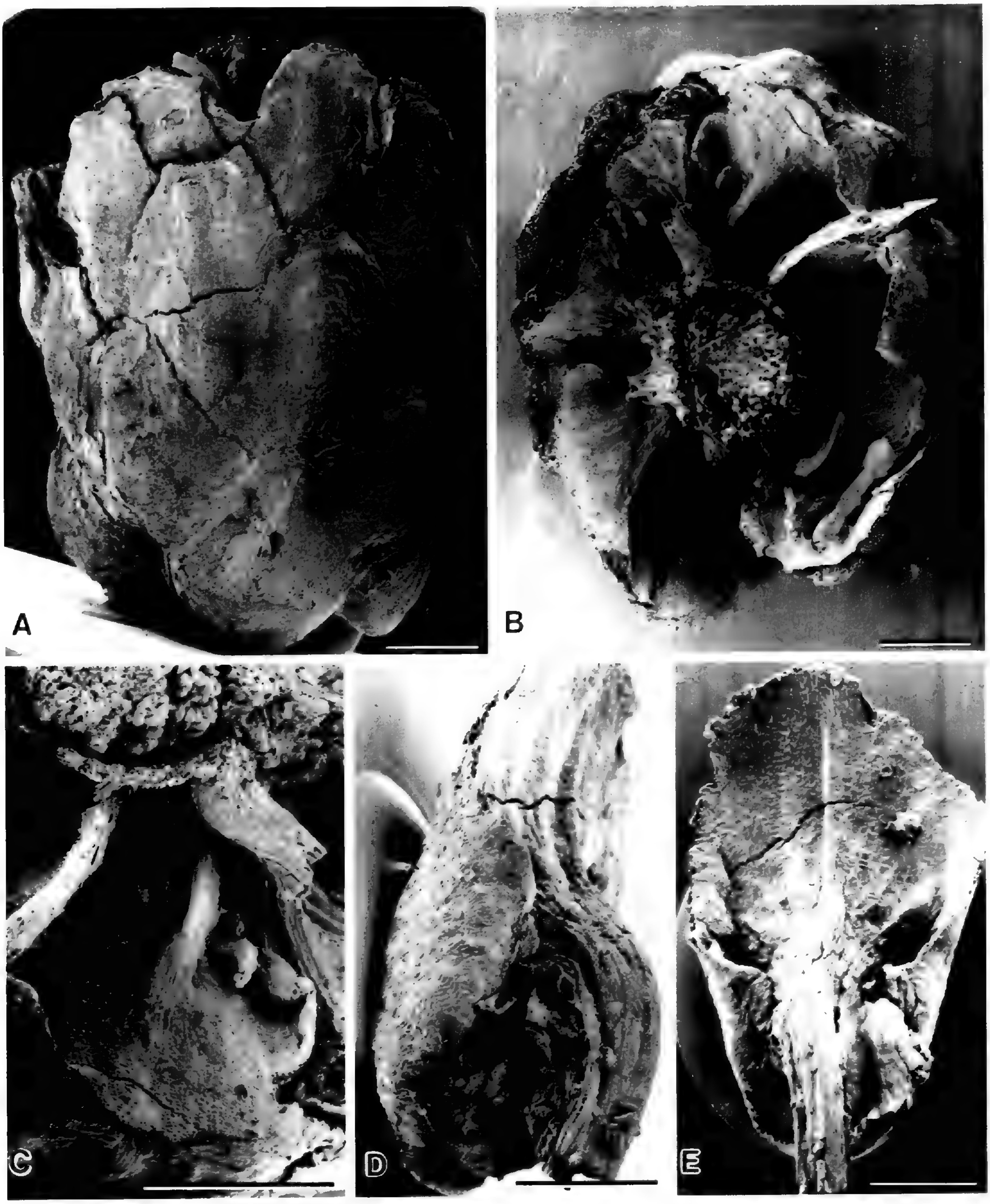


Figure 8. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 10, Conifer pollen cone and dispersed cone scales. —A. Lateral view of conifer pollen cone with imbricate cone scales; PP45172. —B. Apical view of conifer pollen cone in A. —C. Detail of pollen cone in A showing attachment of scale to axis. —D. Lateral view of isolated pollen cone scale; PP45173. —E. Cone scale in D viewed from inner (adaxial) surface. Scale bars: A–C = 1 mm; D, E = 0.5 mm.

←

scale-like leaves; note stomata on adaxial surface; PP45171. —D. Detail of leaf from specimen in C showing detail of fimbriate leaf margin and abaxial surface with stomata. Scale bars = 0.5 mm.

Figure 9. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 11, cf. *Detrusandra* Crepet & Nixon (Magnoliales). —A. Lateral view of longitudinally fractured flower showing numerous tepals incurved at the apex and numerous carpels; PP45174. —B. Same specimen as A from opposite side; lateral view showing hypanthial cup bearing numerous free tepals incurved toward the apex and along the margin. Scale bars = 1 mm.

cf. Triuridaceae

13. Trimerous staminate flower
    Figure 11.

Staminate flowers are actinomorphic with six perianth parts and three stamens. The perianth parts are basally united forming a zone ca. 0.1 mm wide. Distally the perianth parts are free, 0.8–1.0 mm long, 0.6–0.7 mm wide, and taper to a rounded apex. The androecium consists of three stamens in a single cycle. The stamens are united at the base. In some specimens the anthers are sessile in the center of the flower (Fig. 11A, D), while in others they are elevated on a thick, central column, which apparently results from fusion of the filaments (Fig. 11B, C). The anther connective is thick and extends beyond the anther sacs. Anthers dehisce longitudinally and are extrorse. Pollen is monosulcate. Pistillate flowers are unknown.

Flowers similar to the specimens from Allon were described by Gandolfo et al. (1997a, 1998b) from the Turonian of New Jersey as the oldest representatives of the achlorophyllous monocot family Triuridaceae. Gandolfo et al. (1997a) observed variation in tepal and connective morphology among their specimens and concluded that the fossils represent at least four species of related plants. The specimens from Allon also exhibit morphological variation, and one of the variants (with the anthers attached to the apex of a swollen column Fig. 11B, D) is apparently not represented among the suite of specimens from New Jersey (Gandolfo et al., 1997a, 1998b). This taxon is represented in the Allon assemblage by about five specimens.

Monocot, family *incertae sedis*

14. Tricarpellate flower
    Figure 12.

Flowers trimerous, actinomorphic, apparently bisexual, ca. 0.7 mm diameter, 0.5–0.8 mm long; perianth abraded, apparently consisting of one cycle of three tepals (Fig. 12A, D); androecium incompletely preserved, only filament bases present, apparently consisting of two cycles of three stamens (Fig. 12C, D); pollen grains preserved on the fruit surfaces, monosulcate, exine reticulate, coarse near the middle of the grain and becoming finer toward the ends; polar axis 22 μm, equatorial axis 12 μm. The gynoecium consists of three free carpels; the

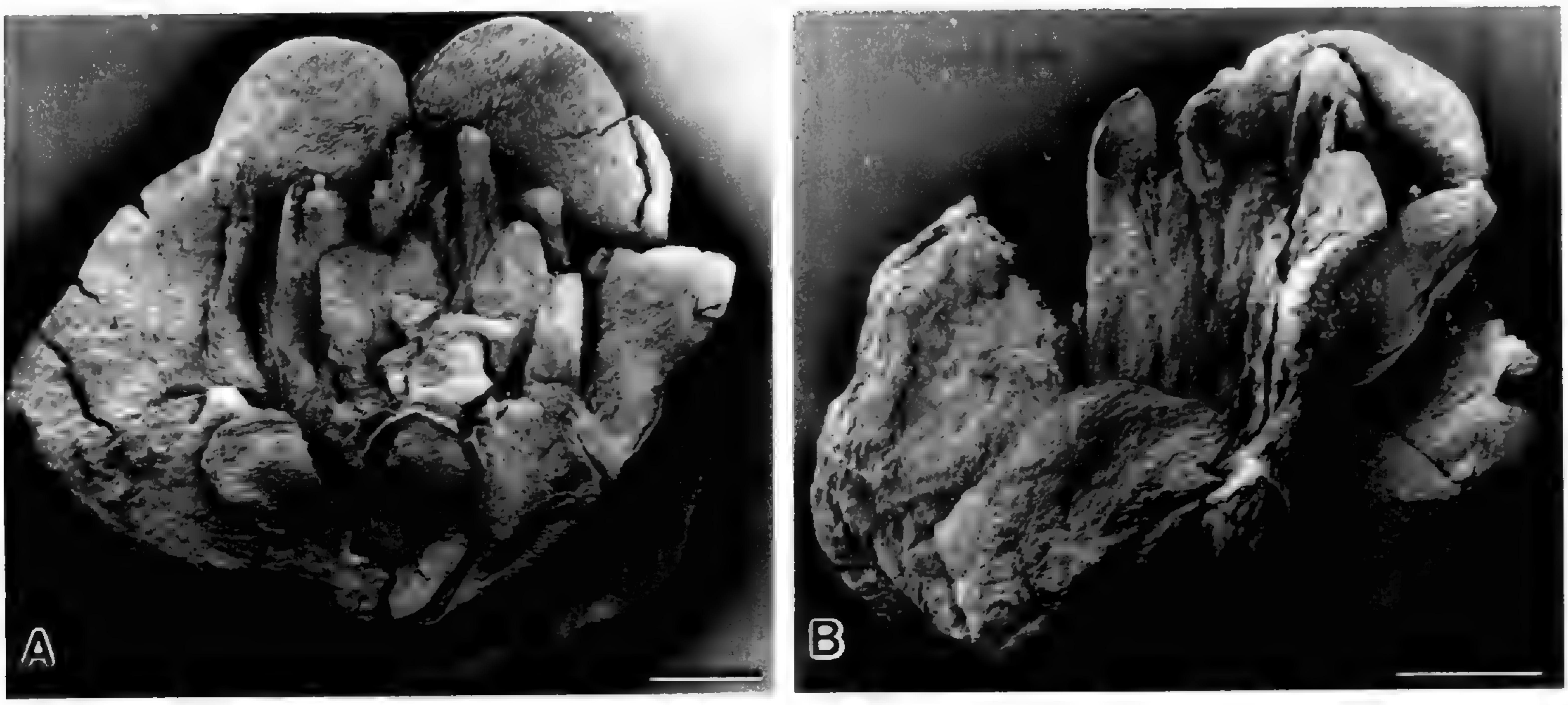


Figure 10. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 12, *Mauldinia* sp. Drinnan, Crane, Friis & Pedersen (Lauraceae). —A. Adaxial surface of flattened, bilobed inflorescence unit with several attached flowers; PP45175. —B. Adaxial surface of inflorescence unit showing tepals and other floral parts of several flowers; PP45153. Scale bars = 1 mm.

ovary is superior; styles are well differentiated and distinct, although confluent for most of their length (Fig. 12B).

Only two specimens of this fossil type are known. Both specimens, which are well-developed fruits, contain only abraded perianth remnants. The perianth and androecium are poorly understood. Additional material is required for detailed characterization. The monosulcate pollen associated with this taxon is similar to fossil pollen grains assigned to *Liliacidites* (Walker & Walker, 1984, 1986). Pollen grains of this type are similar to those of some monocotyledons (Doyle, 1973; Friis et al., 1999).

15. Monocot leaf type 1
Figure 13A.

Leaf fragments with very fine parallel venation (Fig. 13A). Maximum length ca. 200 mm (incomplete), maximum width ca. 70 mm (incomplete).

This leaf type is represented by two specimens. It differs from similar leaves grouped as monocot leaf type 2 (taxon 16) in its more fragile (less coriaceous) texture, its greater width and the absence of a thicker midrib region. Monocot leaf type 1 is similar in overall form to *Doryanthites cretacea* described by Berry (1914, pl. 17, fig. 3) from the Eutaw Formation (Santonian-Campanian) of Georgia, but additional details are needed to pursue this comparison further.

16. Monocot leaf type 2
Figure 13B.

Leaf fragments with fine parallel venation; apparently with parallel margins. Maximum length ca. 60 mm (incomplete). Maximum width ca. 16 mm. Center of the leaf occupied by a darker region perhaps indicating greater leaf thickness (Fig. 13B). It is unclear whether there is a single thick central vein or just a cluster of parallel veins embedded in thicker leaf tissue.

This leaf type is represented by a single specimen in our collections. While almost certainly a monocot, the systematic affinity of this leaf type within the group is uncertain. This specimen may ultimately be resolved as a variant of monocot leaf type 1.

Hamamelidaceae subfamily Hamamelidoideae

17. *Allonia decandra* Magallón-Puebla, Herendeen & Endress
Figure 14A–C.

Flowers actinomorphic, pentamerous, ca. 2.75 mm from base to tip of anthers. Perianth consists of a poorly preserved calyx represented by irregular, abraded lobes on the floral cup, and narrow, linear petals (apparently five in number). The androecium is composed of ten stamens in two alternating cycles of five (Fig. 14A). The stamens have a very short filament and a long anther with a well-developed extension of the connective (Fig. 14B). Pollen grains are spherical to slightly oblate, 21–26 μm in diameter, tricolpate with a prominent reticulum. Internal to the stamens are structures that may represent a nectariferous disk. The gynoecium is unknown. Isolated seeds similar to those of extant subfamily Hamamelidoideae also occur in the Allon flora (Fig. 14D, E). The seeds

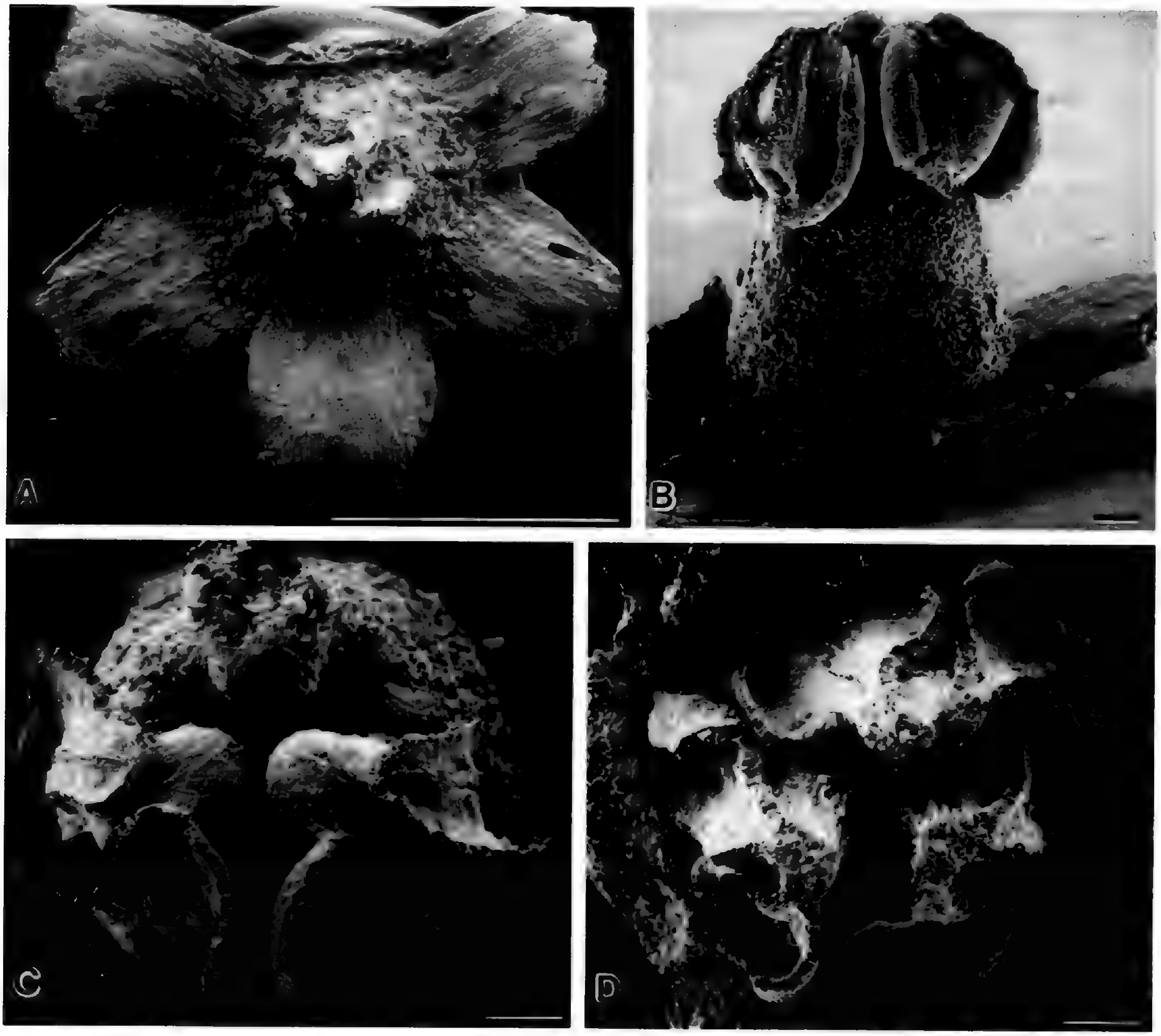


Figure 11. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 13, Trimerous staminate flowers (cf. Triuridaceae). —A. Staminate flower with six perianth parts (one broken at base) and three stamens with remains of open sessile anthers; PP45176. —B. Lateral view of staminate flower with three anthers borne on a central fleshy column; PP45177. —C. Apical view of stamens from B showing open thecae and fleshy apical extension of the connective; PP45177. —D. Detail of broken staminate flower with sessile extrorse anthers showing details of the anther wall in cross section; PP45178. Scale bars: A = 1 mm; B–D = 100 μm.

are 1.0–1.2 mm long, 0.25–0.36 mm wide, approximately oval in outline with an oblique, elongate hilum.

This fossil flower was described in detail by Magallón-Puebla et al. (1996). The morphological and palynological features observed in *Allonia* indicate an affinity to the subtribe Loropetalinae (tribe Hamamelideae). Cladistic analysis of the relationships within Hamamelideae placed *Allonia* as sister taxon to the extant southeast Asian genus *Maingaya* Oliver, which includes a single species. *Allonia* is represented in the Allon flora by one incomplete flower specimen and numerous dispersed anthers. Dispersed seeds number ca. 15.

cf. Hamamelidaceae

18. Flower with apically connate stamen connectives
    Figure 15.

Flower small, ca. 1.5 mm in diameter, actinomorphic, hypogynous and 5-parted. The perianth is represented by five petals or their bases. The androecium is formed by ten stamens in two whorls of five. The stamens have a very massive filament (Fig. 15D, F), short anthers, and a long apical expansion of the connective. The filaments are laterally connate near their base, forming a proximal continuous androecial ring (Fig. 15A). The stamens

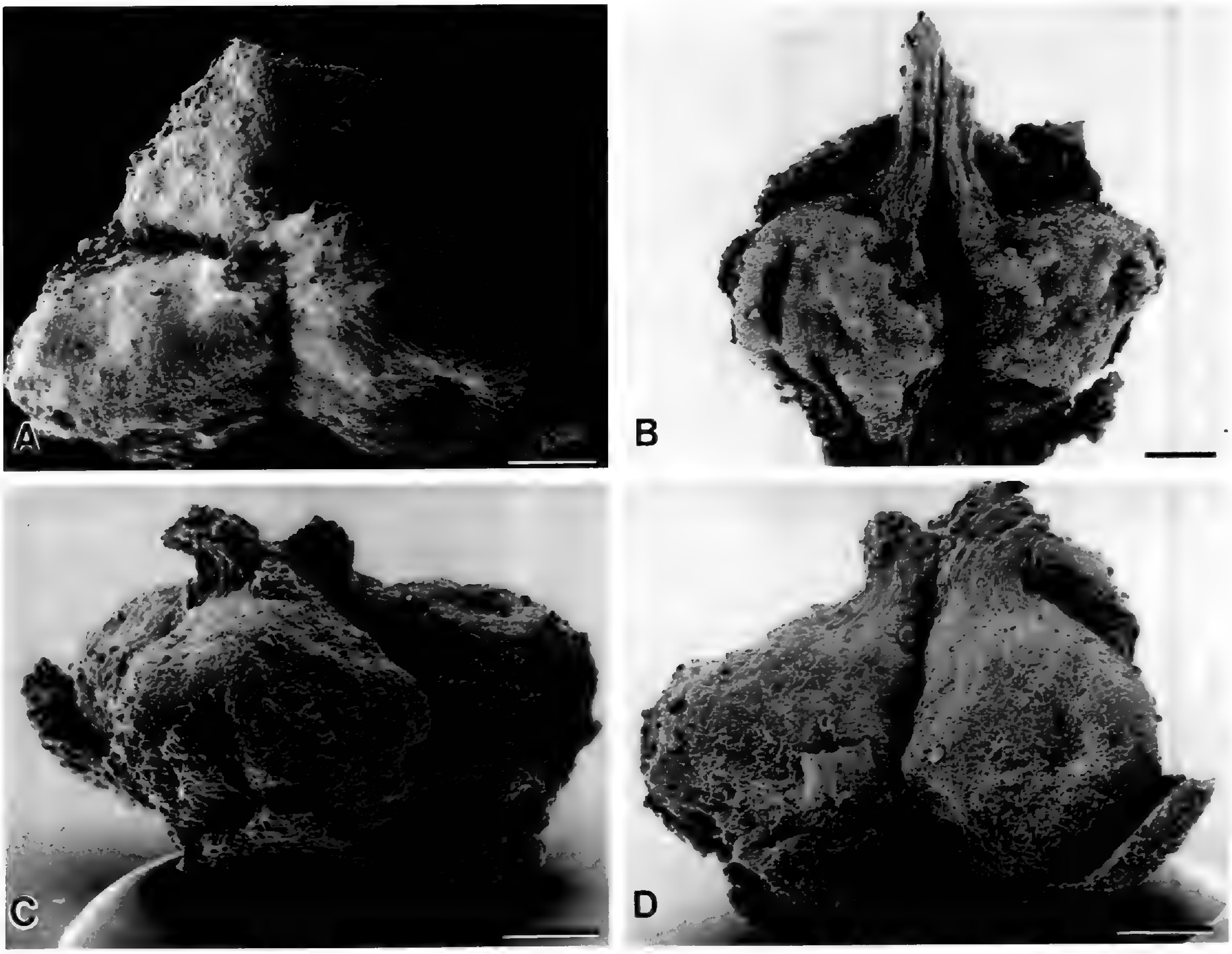


Figure 12. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 14, Tricarpellate flower (cf. monocots). —A. Apical view of trimerous flower showing tricarpellate gynoecium; PP45179. —B. Lateral view of young fruit showing elongated, separate but confluent, styles; PP45180. —C. Oblique view of specimen in A showing remains of perianth and filament bases. —D. Lateral view of specimen in A and C showing perianth part. Scale bars = 100 μm.

of the inner whorl have four pollen sacs, but the stamens of the outer whorl are bisporangiate. Abundant pollen grains are found on the adaxial surface of stamens and on the center of the flower. Pollen grains are tricolpate, with a coarse, slightly heterogeneous reticulate exine ornamentation. The details of structures in the center of the flower are currently uncertain.

This complex flower is known from only two specimens. The crowding of parts in the center of the flower, and the presumed modified condition of several floral organs have precluded a secure identification of the nature of the available structures, and the interpretation of floral organs. Therefore, the floral structure described here is currently tentative. Detailed examination and dissection of additional specimens will be necessary to fully understand the organization of this flower type. Based on the preliminary data currently available, the elongate apical extensions of the connective, the basically pentamerous architecture, and the exine sculpture of the pollen grains suggest a possible relationship to the subfamily Hamamelidoideae (Hamamelidaceae). However, further comparisons, including comparisons with other families of basal eudicots, are necessary once additional specimens are discovered.

cf. subfamily Altingioideae, Hamamelidaceae

19. Capitate inflorescence
Figure 16.

Inflorescence capitate, spherical, diameter 1.6 mm, flowers sessile (Fig. 16A, B). Material consists of a single, abraded specimen in fruit. The inflorescence bore at least 20 flowers. Perianth and androecium are unknown. The gynoecium consists of two united and at least partially inferior carpels. The styles are free. Each ovary has two locules and numerous ovules (Fig. 16C, D). Pollen unknown.

Only a single specimen of this taxon is available. The available character information is currently in-

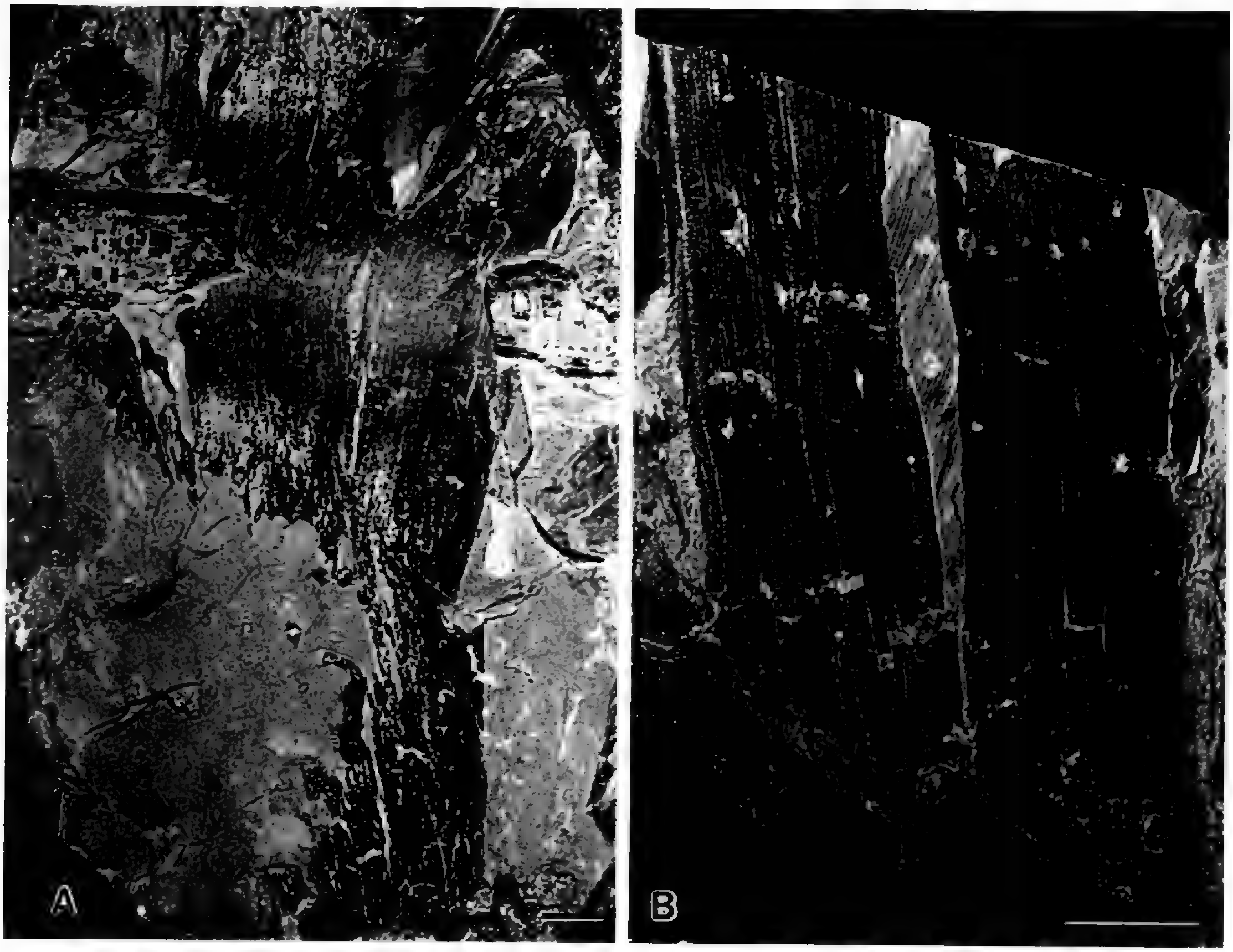


Figure 13. Macrofossils for the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxa 15 and 16, Monocot leaves: light micrographs. —A. Taxon 15, Monocot leaf type 1, macrofossil; PP45379. —B. Taxon 16, Monocot leaf type 2, macrofossil; PP45380. Scale bars = 10 mm.

sufficient to assess systematic relationships, but the morphology of the inflorescence and fruits is suggestive of altingioid Hamamelidaceae. Additional specimens are needed to pursue this comparison further.

Fagaceae sensu lato

20. *Protofagacea allonensis* Herendeen, Crane & Drinnan
Figure 17.

Material consists of staminate inflorescence units, dispersed staminate flowers, fruits, and cupules. Staminate flowers are typically borne in seven-flowered dichasia subtended by three series of bracts (Fig. 17A). Flowers have six small imbricate tepals in two cycles of three, 12 stamens in two cycles of six, and a vestigial gynoecium with three styles surrounded by a mass of simple trichomes (Fig. 17B). Pollen is very small, prolate, tricolporate, and reticulate to microfoveolate. Associated fruits are triangular or lenticular in cross section and develop from epigynous flowers with two (Fig. 17D) or three (Fig. 17C) carpels. The triangular fruits bear six short tepals at the apex (Fig. 17C). Associated cupules are pedunculate, four-lobed, and bear three or more fruits (Fig. 17E). The cupule lobes bear three series of bracts similar to those subtending the staminate dichasia.

This fossil taxon was treated in detail by Herendeen et al. (1995). Comparisons of *Protofagacea allonensis* with extant taxa clearly indicate a relationship to extant Fagaceae sensu lato, based particularly on the presence of the cupule, the form of the fruits, and the morphology of staminate inflorescences and flowers. However, pollen morphology (probably plesiomorphic) differs from that of extant taxa. Detailed resolution of the affinities of *Protofagacea* will require a clearer understanding of characters and relationships among extant Fagaceae sensu stricto and Nothofagaceae. *Protofagacea allonensis* is one of the five most abundant angiosperm mesofossils in the Allon flora (> 1000 whole or partial specimens).

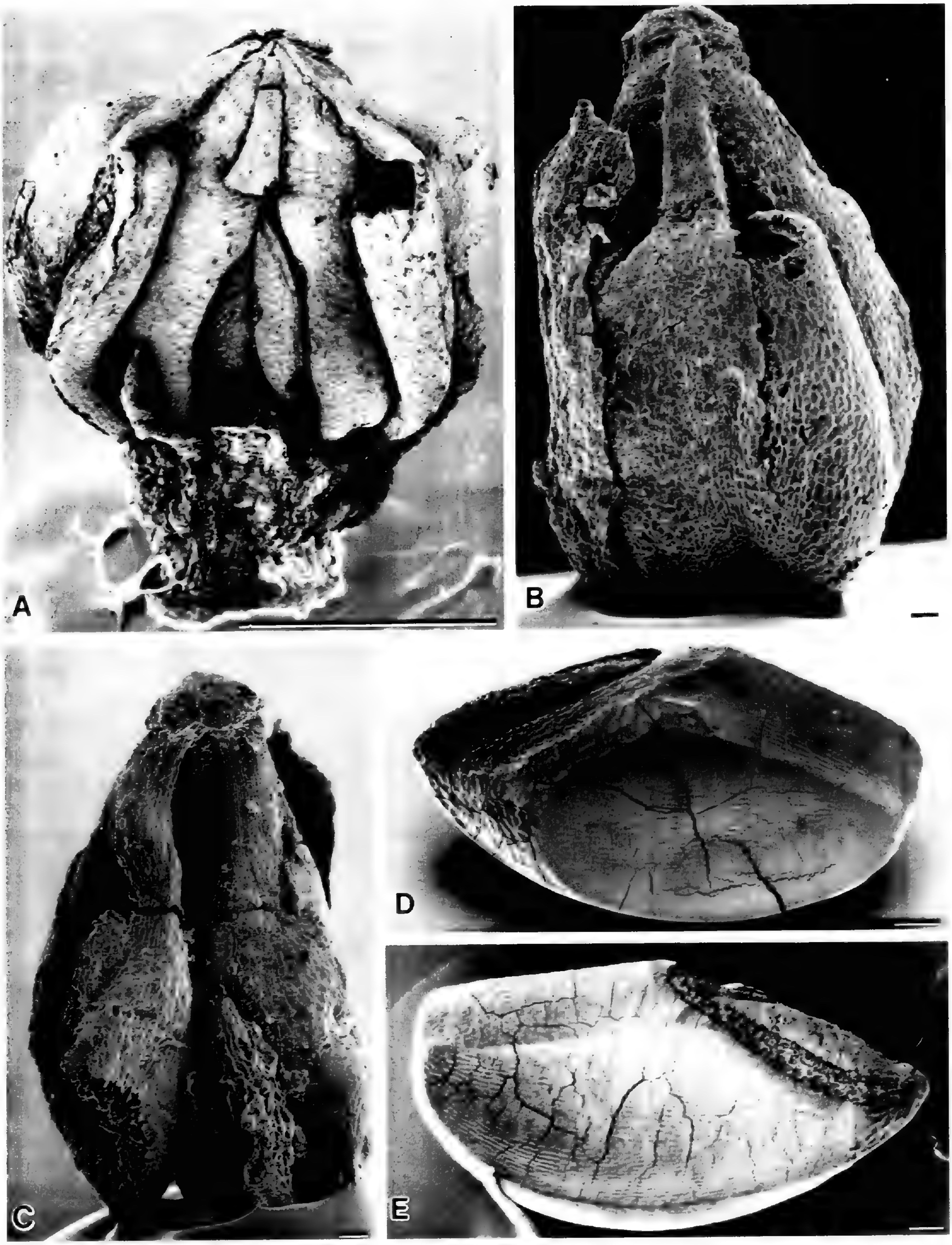
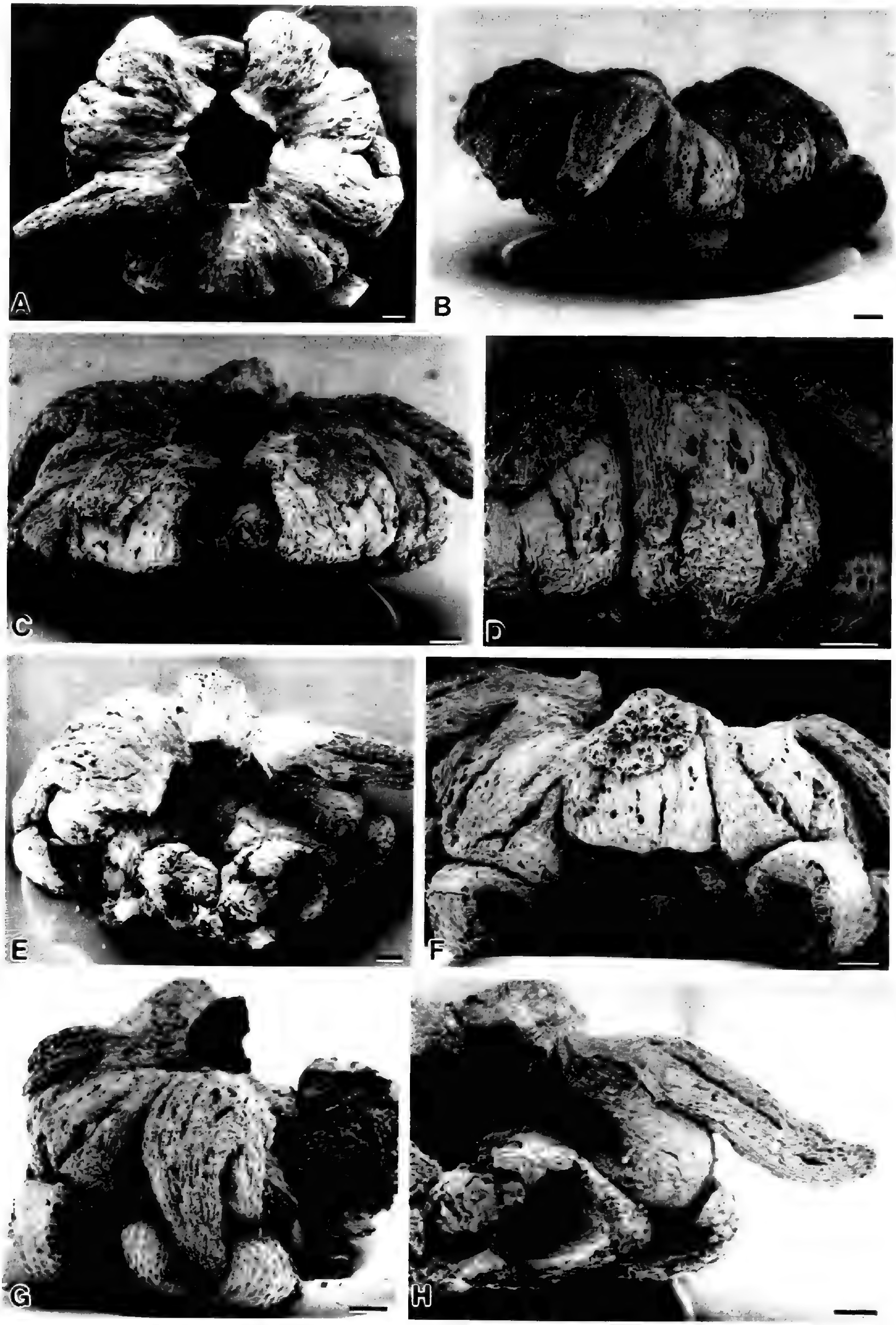


Figure 14. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 17, *Allonia decandra* Magallón-Puebla, Herendeen & Endress (A–C) and associated seeds (D, E) (Hamamelidaceae). —A. Oblique view of flower with ten stamens and sepal remnants; PP44595. —B. Abaxial view of stamen with long anther and a linear petal on the left; PP44676. —C. Adaxial view of specimen in B showing portions of two anthers and possible lobe of nectariferous disk. —D. Seed characteristic of Hamamelidoideae showing oblique elongate hilum scar; PP44685. —E. Seed characteristic of Hamamelidoideae showing oblique elongate hilum scar; PP44680. Scale bars: A = 1 mm; B–E = 100 μm.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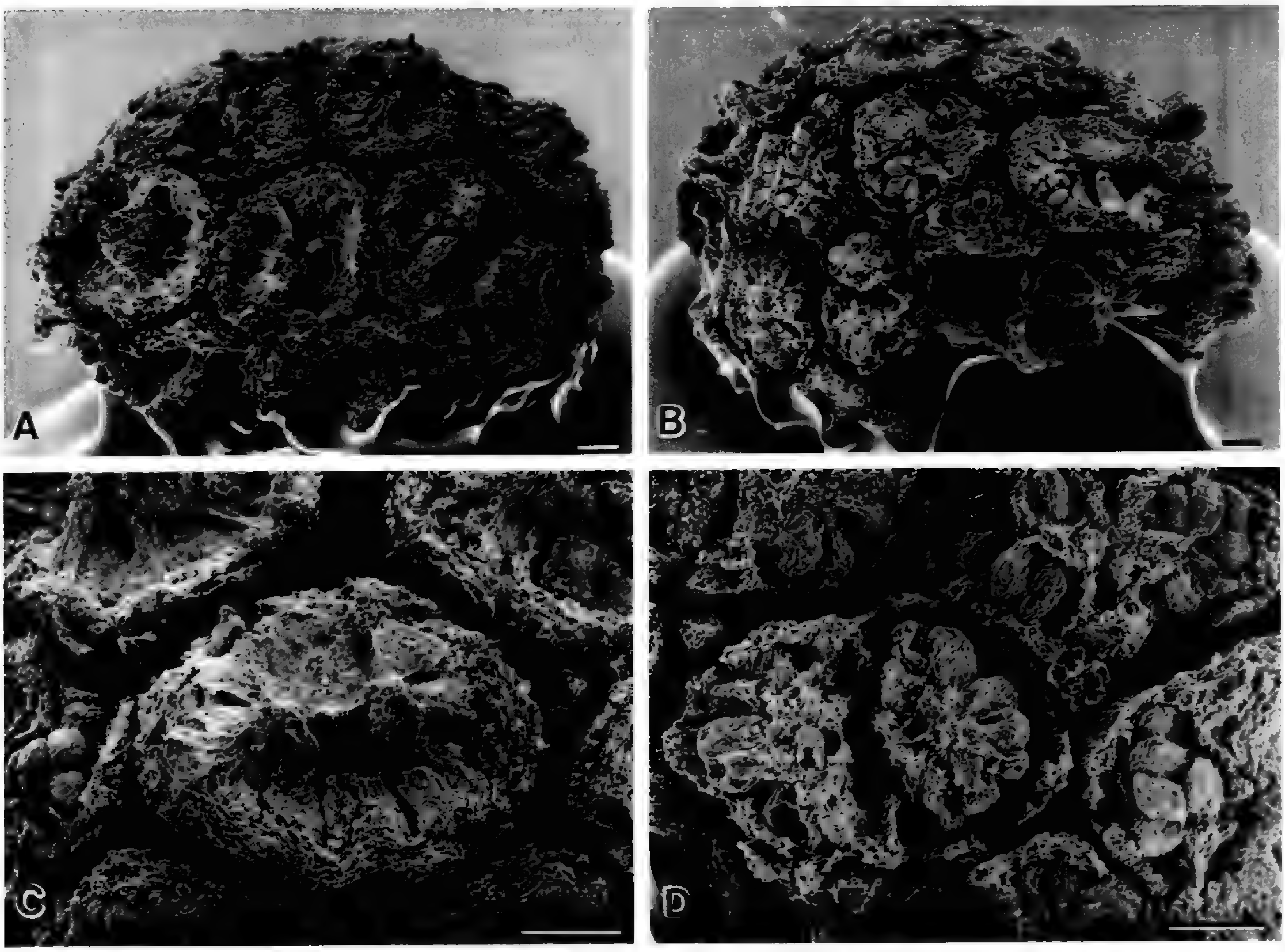

Figure 16. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 19, Capitate infructescence (cf. Hamamelidaeae subfamily Altingioideae). —A. Oblique view of infructescence showing arrangement of young fruits; PP45181. —B. Lateral view of specimen in A. Note the walls of some fruits are abraded, revealing numerous rounded ovules or seeds. —C. Apex of single fruit from infructescence in A, showing remains of two style bases. —D. Transverse section of fruit from infructescence in A, showing two locules and numerous rounded ovules or seeds. Scale bars = 100 μm.

21. *Antiquacupula sulcata* Sims, Herendeen & Crane
Figure 18.

Material consists of staminate flowers, bisexual flowers, fruits, and cupules. Staminate flowers are pedicellate (Fig. 18G), with six tepals in two cycles of three, 12 stamens, and a vestigial gynoecium with three styles (Fig. 18G–I). Bisexual flowers are epigynous and actinomorphic (Fig. 18D, E), with six free tepals in two whorls, 12 free stamens, and a syncarpous gynoecium with three styles that are partially connate below, with trichomes around and between the style bases. The ovary is trilocular with two anatropous, apically pendulous ovules per locule. Fruits are triangular in cross section, with nearly equal sides (Fig. 18C). Cupules contain at least six fruits (Fig. 18A, B). The staminate and bisexual flowers both have slender, thin-walled nec-

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Figure 15. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 18, Flower with apically connate stamen connectives (cf. Hamamelidaceae). —A. Apical view of flower, showing nine apically connate stamen connectives, with one empty space that probably corresponds to a stamen that has broken off; PP45232. —B. Lateral view of flower in A, showing pollen sacs and massive apical extensions of the stamen connectives. —C. Lateral view of flower, opposite side as in B, with empty space corresponding to a missing stamen. —D. Detail of extended stamen connective showing pollen sac below (right). —E. Oblique view of partially dissected flower showing broken pollen sacs and apical extension of the connectives. The center of the flower is comprised of a ring of bulbous structures (?nectaries). —F. Detail of stamens showing broken pollen sacs and prominent extensions of the connectives. —G. Detail of a stamen showing small pollen sacs and massive apical extension of the connective. —H. Lateral view of a stamen showing broken pollen sacs and apical extension of the connective. Scale bars = 100 μm.

Figure 17. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 20, *Protofagacea allonesis* Herendeen, Crane & Drinnan (Fagaceae sensu lato). —A. Dichasium of trimerous staminate flowers; PP44457. —B. Single staminate flower showing anthers removed from dichasium; PP43838. —C. Tricarpellate fruit with epigynous perianth and three style bases; PP445777. —D. Small bicarpellate fruit showing remains of tepals; PP45183. —E. Cupule specimen showing fruit scars; PP44567. Scale bars = 100 μm.

tary lobes between the filament bases (Fig. 18I), and distinctive, multicellular glandular structures on the surface of the gynoecium. Pollen grains found in situ, and also on the surface of the flowers and fruits, are small and tricolporate, with a finely perforate tectum.

This fossil taxon was described in detail by Sims et al. (1998). *Antiquacupula* (and *Protofagacea*) shares several characters with extant rosids and hamamelids, and may prove to be a key taxon in future work examining relationships among these groups, as well as within the Fagaceae. The presence of a cupule, which is widely considered a synapomorphy of the family, plus trimerous flowers, and an inferior, trilocular ovary with two apically attached, pendulous, anatropous ovules per locule, are all characters of extant Fagaceae sensu lato, and support the relationship of *Antiquacupula* to this group. Current data are insufficient for confident assignment to a particular taxon within Fagaceae sensu lato.

Antiquacupula and *Protofagacea* share characters with both Nothofagaceae and Fagaceae sensu stricto, as well as with some families of Rosidae. Evaluating the relationships of *Antiquacupula* and *Protofagacea* is complicated by uncertainties regarding the relationships among extant Fagaceae. Recent cladistic analyses of morphological and/or molecular data have shown the Fagaceae sensu lato to be paraphyletic, and have therefore placed *Nothofagus* in a separate family from Fagaceae sensu stricto (Nixon, 1989; Chase et al., 1993; Manos et al., 1993; Manos & Steele, 1997). Under this interpretation, the presence of a cupule is no longer an unambiguous synapomorphy for the group. In this context, the presence of a cupule in the fossil taxon may support a relationship to the fagaceous grade, but it does not help to resolve relationships with respect to Fagaceae sensu stricto and Nothofagaceae. *Antiquacupula sulcata* is one of the five most abundant angiosperm mesofossils in the Allon assemblage (> 1000 whole or partial specimens).

cf. Juglandales/Myricales (family *incertae sedis*)

22. *Caryanthus* sp. Friis
Figure 19.

Flowers small, 1.1 mm long, 0.75 mm wide, apparently bisexual; epigynous (Fig. 19A, B), tepals free, imbricate; stamens six, free. Associated dispersed anthers are basifixed with longitudinal dehiscence slits. Pollen grains in situ within dispersed anthers, and on the surface of the flowers, are triaperturate with three very short colpi. Gynoecium composed of an inferior ovary (Fig. 19A–C) and a single style, locule number unknown; simple trichomes are present on the outer surface of the fruit wall. Pollen associated with these specimens is referable to the Normapolles pollen taxon *Pseudoplicapollis endocuspis* Tschudy (1975: 22, pl. 13, figs. 1–7, text-fig. 20).

A detailed treatment of this taxon is presented by Sims et al. (1999). Normapolles-type pollen grains are diverse and abundant in Late Cretaceous floras from eastern North America and Europe, but so far flowers with in situ Normapolles pollen have only been recovered from Europe (Friis, 1983; Friis & Crane, 1989) and the Allon locality (Sims et al., 1999). *Caryanthus knoblochii* Friis (1983), with which the Allon material shares many significant features, is probably closely related to extant Juglandales/Myricales. The species is represented in the Allon flora by five specimens.

23. Normapolles flower type A.
Figure 20.

The single known specimen is bisexual (designated as "Unnamed Normapolles flower A" by Sims et al., 1999), approximately 1.7 mm long, strongly flattened, and 1.1 mm in maximum width. The perianth and the androecium are poorly preserved (Fig. 20A, B). Apparently three stamen filaments are present, each opposite a tepal (Fig. 20C). Although none of the stamens are preserved with attached anthers, the filaments are covered with more than 30 grains of a single type of palynomorph. Pollen grains are triporate and small (ca. 10–11 μm in equatorial diameter), with a verrucate tectum. The ovary is inferior, style number is unclear. Although it is not possible to refer the pollen to a Normapolles pollen taxon without more data on internal structure, the grains appear to show polar thinning of the exine and circular external apertures, features exhibited by the post-Normapolles genus *Momipites*. The structural similarities of this flower to the Normapolles flowers described by Friis (1983) and the presence of probable *Momipites* pollen (Nichols & Ott, 1978; Frederiksen & Christopher, 1978) are both suggestive of a relationship to the Juglandales/Myricales.

cf. Betulaceae

24. *Bedellia pusilla* Sims, Herendeen, Lupia, Christopher & Crane
Figure 21.

Staminate flowers are actinomorphic, ca. 0.25–0.4 mm in diameter. Tepals free, imbricate, in two cycles of five, ca. 0.5–1.0 mm long, 0.1–0.2 mm maximum width (Fig. 21A–C). Stamens ten, free, filaments long, extending beyond tepals (Fig. 21C). Anthers ca. 0.6–0.9 mm long, basifixed, dehiscing by longitudinal slits (Fig. 21D). Ovary absent. Pollen grains oblate to peroblate, equatorial outline triangular with concave to occasionally straight sides and rounded corners. Pollen triaperturate with three very short colpi, weakly developed arci on


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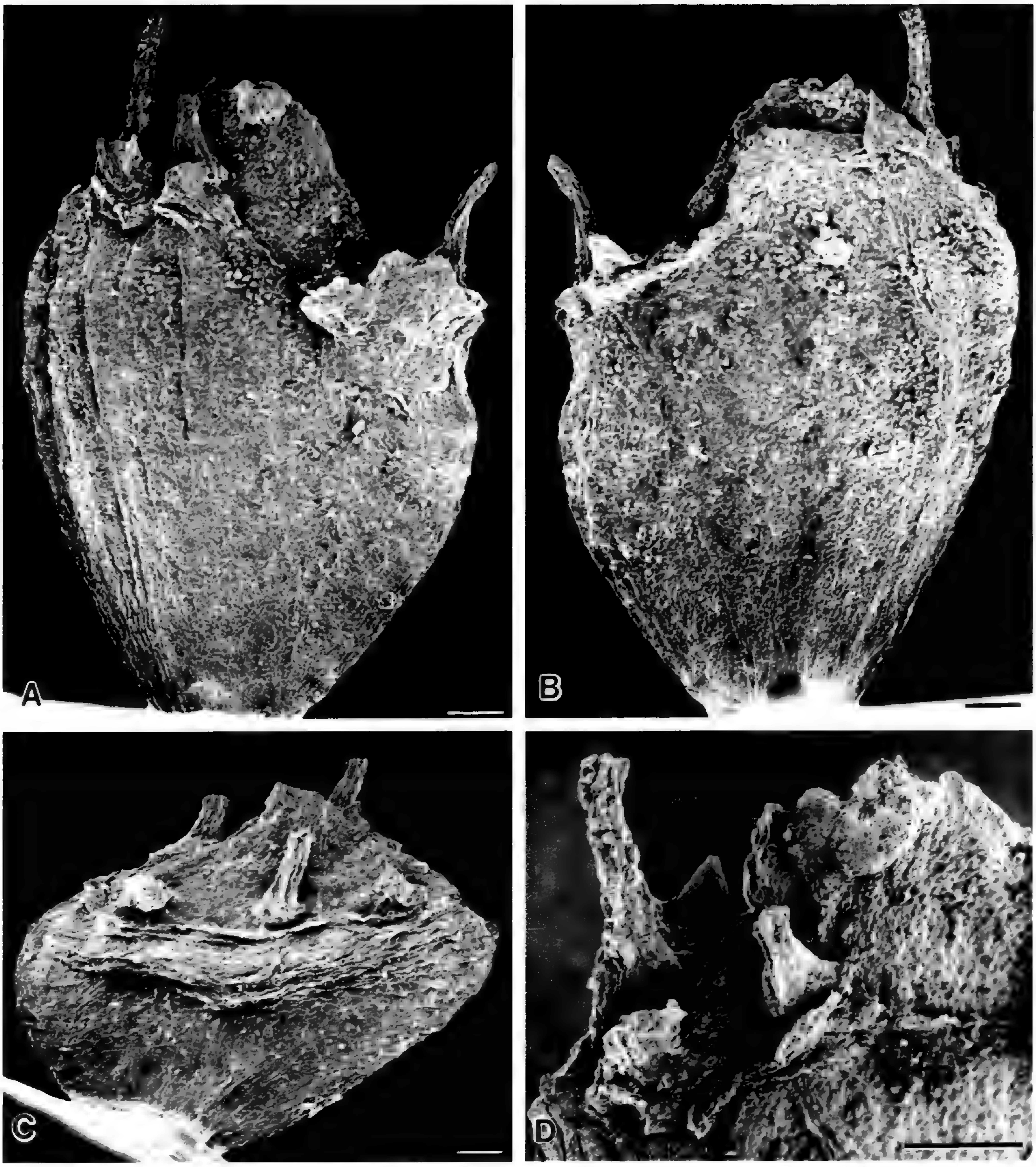

Figure 19. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 22, *Caryanthus* sp. Friis (cf. Juglandales/Myricales). —A. Lateral view of flower with remains of perianth and stamen filaments; PP45095. —B. Opposite side of flower shown in A. —C. Flower with remains of stamen filaments and single style; PP45096. —D. Oblique view of apex of flower in A showing numerous pollen grains around filament bases. Scale bars = 100 μm.

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Figure 18. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 21, *Antiquacupula sulcata* Sims, Herendeen & Crane (Fagaceae sensu lato). —A. Lateral view of cupule with young fruits; PP44751. —B. Apical view of cupule with fruits shown in A. —C. Incomplete cupule with one fruit; PP44752. —D. Lateral view of young fruit with attached perianth parts and stamen filaments; PP44764. —E. Apical view of fruit shown in D. —F. Lateral view of mature fruit showing longitudinal ribbing; note abraded perianth at apex; PP44814. —G. Lateral view of pedicellate staminate flower; PP44771. —H. Apical view of young staminate flower showing stamens and pistillode; PP44768. —I. Apical view of mature staminate flower; note filament bases alternating with presumed nectary lobes; PP44769. Scale bars: A–F, I = 1 mm; G, H = 100 μm.

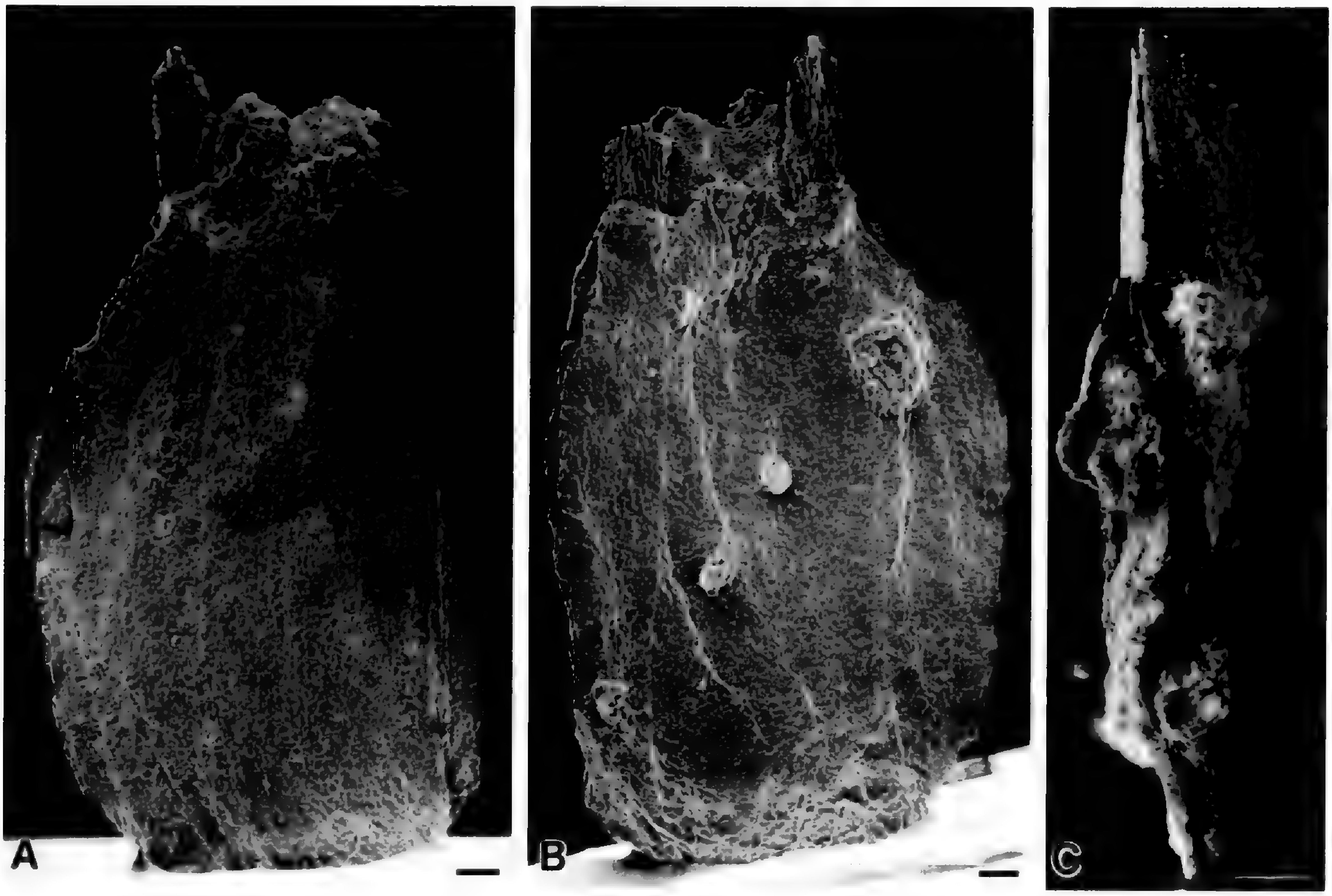


Figure 20. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 23, Normapolles flower type A (cf. Juglandales/Myricales). —A. Poorly preserved fruit with remains of perianth and stamen filaments; PP45097. —B. Opposite side of fruit shown in A. —C. Apical view of fruit shown in A and B. Scale bars = 100 μm.

each hemisphere and between apertural regions. Pistillate flowers and fruits are unknown.

The pollen associated with these specimens is referable to the Normapolles pollen taxa "New Genus D sp. D and New Genus D sp. A" of Christopher (1979), which were initially separated as two putatively distinct forms. The presence of arci (although weakly developed) and pollen ornamentation both suggest a relationship to Betulaceae. Some species of *Alnus* also have basically pentamerous flowers, although no extant Betulaceae have staminate flowers bearing ten perianth parts. *Bedellia* is represented in the Allon flora by four specimens.

Actinidiaceae

25. *Parasaurauia allonensis* Keller, Herendeen & Crane

Figure 22.

Flowers are actinomorphic, 0.7–1.2 mm long, 0.6–0.8 mm wide. Calyx composed of five imbricate sepals with multicellular trichomes on the abaxial surface (Fig. 22A). Corolla composed of five imbricate petals (Fig. 22B). Androecium of ten stamens, five of which are large, with the other five smaller, arranged in an alternating pattern (Fig. 22C, D). Anthers basifixed and deeply sagittate (Fig. 22C, D); pollen unknown. Gynoecium tricarpellate, with a syncarpous, superior ovary and three free styles emerging from an apical depression (Fig. 22E). The ovary is trilocular with intruded axile placentae bearing numerous ovules (Fig. 22F); mature fruit structure unknown.

The structure, phylogenetic relationships, and evolutionary significance of *Parasaurauia allonensis* were treated in detail by Keller et al. (1996). The fossil flowers and fruits are most similar to those of the family Actinidiaceae, which includes three extant genera, *Clematoclethra* (Franchet) Maxim., *Actinidia* Lindley, and *Saurauia* Willd. (Keller et al., 1996). Of these, *Parasaurauia allonensis* is most similar to *Saurauia*, differing only in the number of stamens (10 in the fossil vs. 15 to numerous in *Saurauia*). Like *Parasaurauia allonensis*, *Saurauia* has free styles with an adaxial longitudinal groove, simple stigmas, and three to five carpels. *Actinidia* has numerous stamens, frequently up to 30 carpels, and free styles with capitulate stigmas. Flowers of *Parasaurauia* are similar to Clethraceae and Diapensiaceae in being consistently tricarpellate, and are like most members of

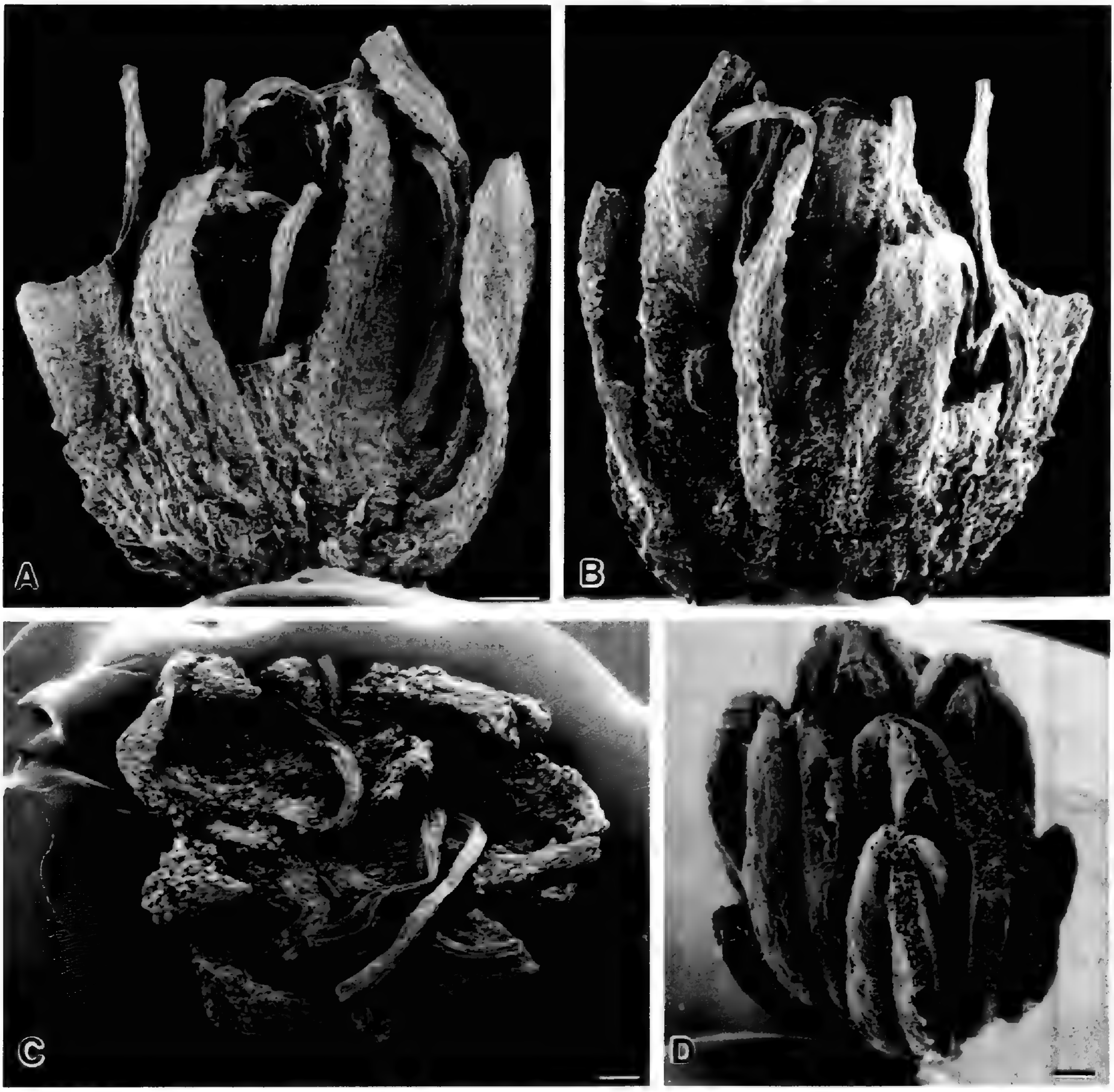


Figure 21. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 24, *Bedellia pusilla* Sims, Herendeen, Lupia, Christopher & Crane (cf. Betulaceae). —A. Staminate flower with well-developed perianth and stamen filaments; PP45099. —B. Opposite side of flower in A showing two whorls of perianth parts. —C. Apical view of compressed staminate flower showing perianth and stamen filaments with abundant adhering pollen; PP45100. —D. Lateral view of young staminate flower showing anthers and in situ pollen grains; PP45101. Scale bars = 100 μm.

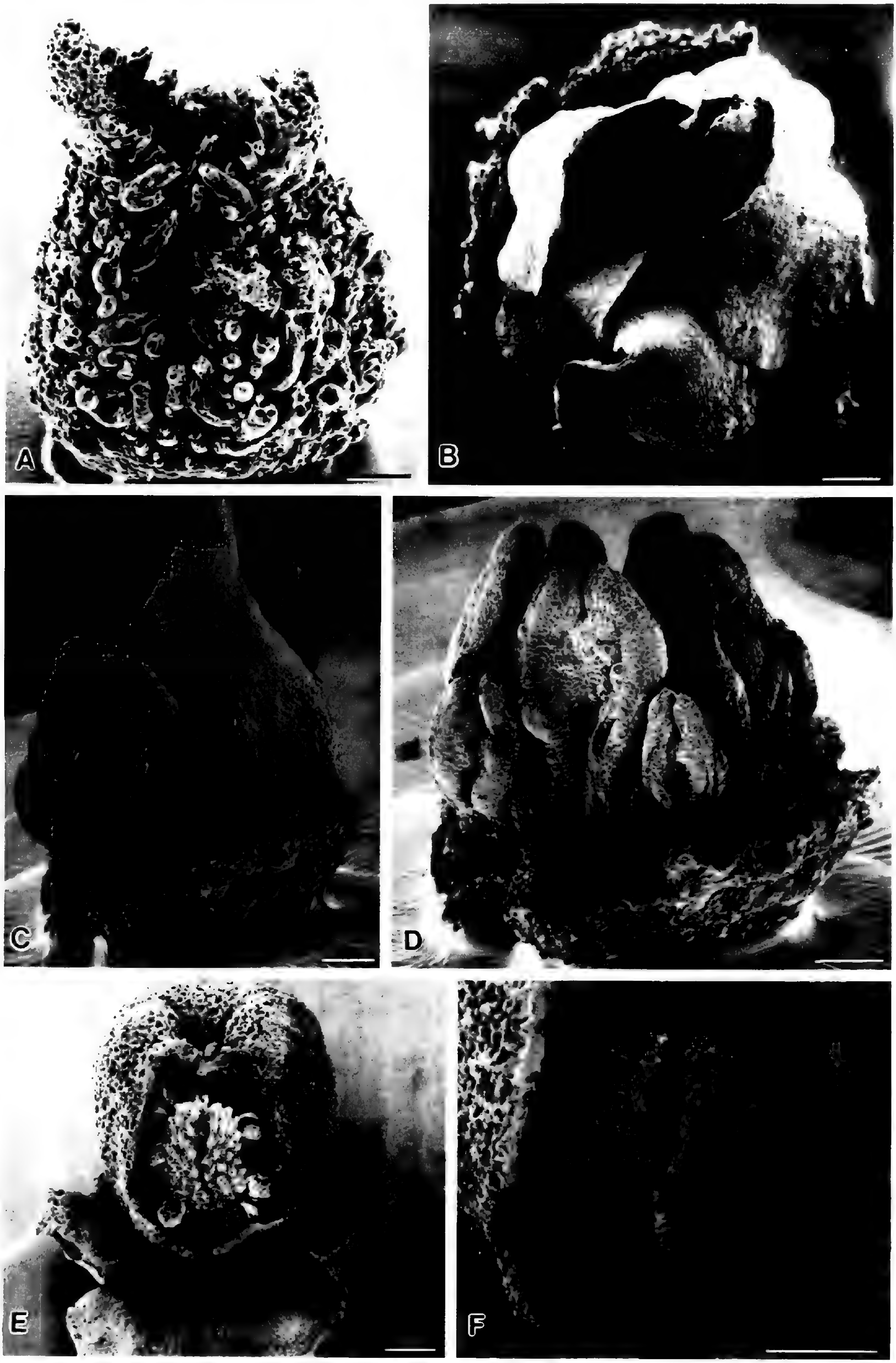
the Ericales in bearing 10 stamens. However, *Parasaurauia* differs most conspicuously from Clethraceae, Diapensiaceae, and other Ericales in having free styles.

Phylogenetic relationships of *Parasaurauia* were evaluated through a cladistic analysis (Keller et al., 1996). *Parasaurauia* is placed within the Actinidiaceae as sister to *Actinidia* plus *Saurauia*. *Clematoclethra* is resolved as the basal genus in the family. In this configuration, the free styles of *Parasaurauia*, *Actinidia*, and *Saurauia* are best interpreted as a synapomorphy that unites these genera, rather than a retained plesiomorphy in this group. Similarly, within the Actinidiaceae the presence of numerous stamens is a synapomorphy uniting *Actinidia* and *Saurauia* rather than a retained plesiomorphy.

cf. Ericales

26. Flower with stellate trichomes, type 1. Figure 23.

Flowers are bisexual, hypogynous, actinomorphic, and pentamerous, ca. 3 mm long, 2 mm wide (Fig. 23A, B). The five sepals are free to the base, taper gradually to an acute apex, and apparently have only sparse stellate trichomes on their abaxial surface. The corolla is represented only by the ba-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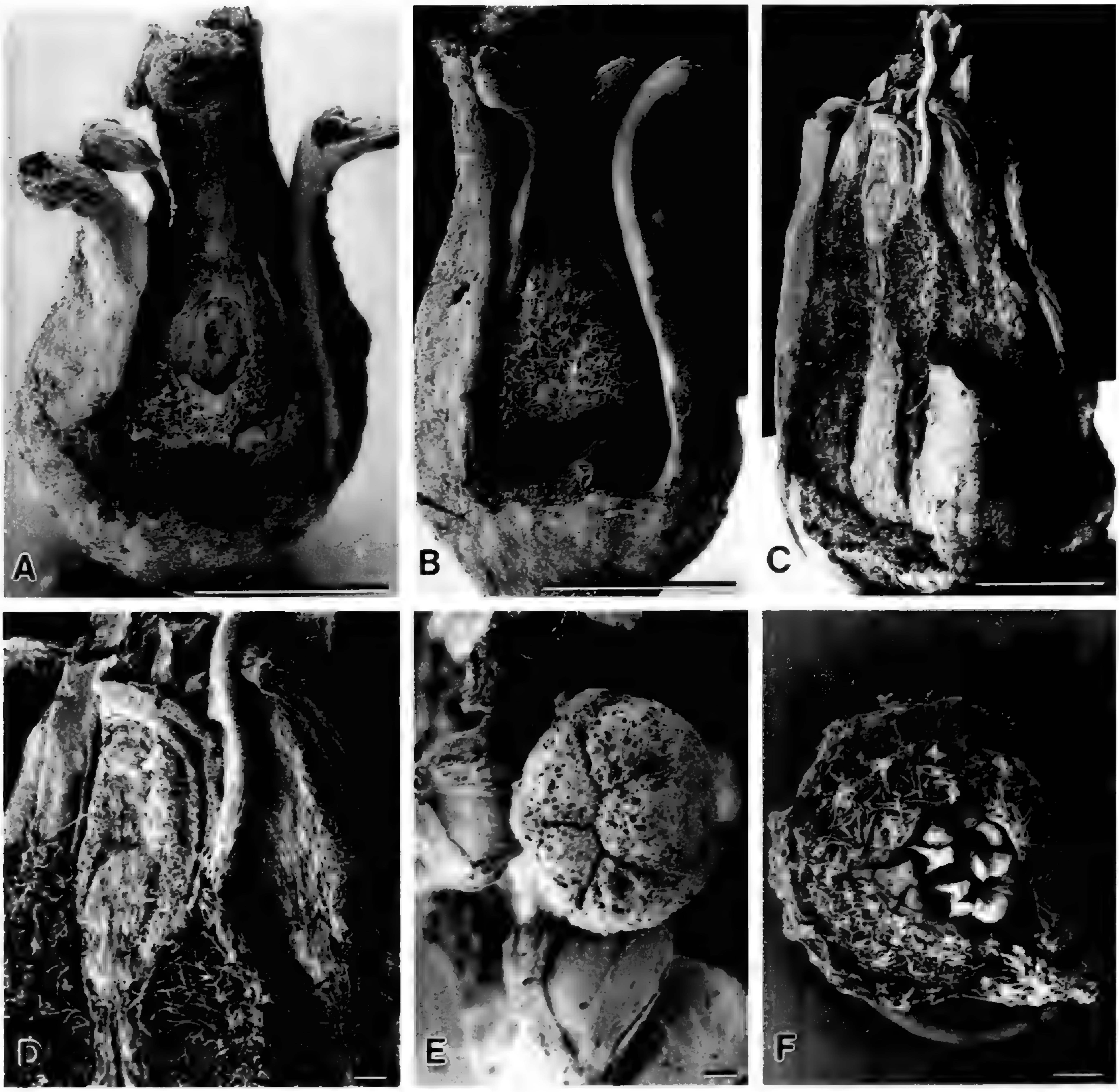

Figure 23. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 26, Flower with stellate trichomes, type 1 (cf. Ericales). —A. Oblique view of flower with valvate sepals, showing stellate trichomes and capitate stigma; PP45184. —B. Lateral view of specimen in A showing stamens with basifixed anthers and numerous stellate trichomes on ovary. —C. Specimen with sepals removed showing base of clawed petal, stamens, and numerous stellate trichomes; PP45185. —D. Detail of basifixed anther from specimen shown in C. —E. Capitate stigma with five lobes; PP45184. —F. Fruit with numerous stellate trichomes on fruit wall. Apex of fruit is broken showing tips of the internal septae; PP45186. Scale bars. A–C = 1 mm; D–F = 100 μm.

ses of clawed petals (Fig. 23C). The androecium consists of five free stamens with tangentially flattened filaments and basifixed anthers (Fig. 23D, E). Alternating with the stamen bases are five short, broad nectary lobes. The gynoecium consists of five connate carpels with a single style and a five-lobed, capitate stigma (Fig. 23E). Ovary locule number is unknown. The surface of the gynoecium and the

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Figure 22. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 25, *Parasaurauia allonensis* Keller, Herendeen & Crane (Actinidiaceae). —A. Flower bud showing sepals with conspicuous multicellular trichomes; PP44609. —B. Flower with sepals removed showing five imbricate petals; PP44612. —C. Lateral view of flower in B with three petals removed showing stamens with sagittate anthers. —D. Lateral view of flower shown in B, C with all petals removed. Note sagittate anthers and free styles in the center. —E. Fruit with locule broken open showing placentae and numerous seeds; PP44476. —F. Detail of specimen in E showing seeds. Scale bars = 100 μm.

filaments are covered by numerous stellate trichomes (Fig. 23F).

Fossil flowers very similar to these specimens from Allon were first described from the Campanian of Martha's Vineyard, Massachusetts (Tiffney, 1977). They are also known from the Turonian of New Jersey (Crepet, 1996, plate IV, 1–9; Crepet & Nixon, 1996, fig. 11A–G). The same flower is also known from fossil localities of similar age on Upatoi Creek in western Georgia (Herendeen et al., unpublished data). Flowers of this type are rare at the Allon locality.

27. Flower with stellate trichomes, type 2. Figure 24.

Flowers are bisexual, hypogynous, actinomorphic, 3 mm long, 2.5 mm wide, with pentamerous calyx, corolla, and androecium; number of carpels unknown. The five sepals are imbricate and free (Fig. 24B), with obtuse to acute apices. Numerous stellate trichomes cover the abaxial surface of the sepals (Fig. 24A). The corolla is represented only by the bases of clawed petals. The androecium apparently consists of five free stamens; filaments are not markedly flattened; anthers are unknown. Alternating with the stamen bases are five short, broad structures that we infer to be nectary lobes (Fig. 24D). The gynoecium consists of a syncarpous ovary with a single style (Fig. 24C); stigmas are not preserved. Ovary locule number is unknown. The ovary is roughly triangular in outline with rounded corners. The surface of the gynoecium, the filaments, and abaxial surface of the calyx also are covered by numerous stellate trichomes.

This fossil flower is similar in general organization to the previous taxon (taxon 26), except that the sepals are broader and are densely covered by stellate trichomes, the filaments are less strongly flattened, and the ovary is broader, shallower, and has a triangular outline. This taxon and the previous one may be variants of a single species or two species in the same genus. Similar variation was observed among the comparable fossils that were recorded from the Turonian of New Jersey (Crepet, 1996; Crepet & Nixon, 1996). Flowers of this type are very rare at the Allon locality.

28. Fruits bearing large peltate trichomes Figure 25.

Flowers bisexual, hypogynous, somewhat bilaterally symmetrical, ca. 3 mm long, 2 mm wide. Calyx composed of five thick, triangular, valvate sepals, three of which are broader than the other two (Fig. 25A, B). Corolla not preserved. Androecium composed of eight stamens, which alternate with eight square-shaped structures that we interpret as nectary lobes. The gynoecium consists of a superior ovary that is roughly triangular in outline, with a single style that appears to have a hollow, fluted central canal, and a stigma that is three-lobed. Internally, the ovary has three locules and massive axile placentae bearing numerous ovules (Fig. 25C). The fruit is a loculicidally dehiscent capsule (Fig. 25D). The abaxial surface of the sepals and the gynoecium are covered by numerous, overlapping, peltate trichomes.

Flowers identical to these have been reported from the Turonian of New Jersey (Weeks et al., 1996) and are also known from the Coniacian-Santonian of Georgia (Upatoi Creek; Herendeen & Crane, unpublished data). Weeks et al. (1996) used a cladistic analysis to assess the systematic relationships of the fossils from New Jersey, and they tentatively concluded that this taxon may be a basal member of the order Ericales. Fossils of this taxon are rare at the Allon locality.

Miscellaneous Fossil Angiosperm Flowers, Fruits, and Other Structures: Order and Family *Incertae Sedis*

29. Pentamerous flower with inferior ovary Figure 26.

The flowers are epigynous, presumably bisexual, ca. 2 mm long, 1.75 mm wide, with a pentamerous calyx (Fig. 26A). The sepal lobes are triangular with an obtuse, rounded apex. The corolla and androecium are not preserved. The hypanthium has slightly prominent longitudinal ridges. The gynoecium consists of an inferior ovary and three free styles (Fig. 26B). Pollen grains on the style surfaces are tricolporate.

These flowers are comparable in general morphology to flowers of Hydrangeaceae, Saxifragaceae, and Grossulariaceae, but currently available details are insufficient to evaluate their possible systematic relationships. Flowers of this type are very rare at the Allon locality.

30. Pentamerous flower with semi-inferior ovary Figure 27.

Flowers bisexual, 1 mm long, 0.9 mm wide, with a semi-inferior ovary (Fig. 27A, B). Calyx composed of five free sepals that are abruptly narrowed above the base (Fig. 27D); distal portions of sepals are short and blunt (Fig. 27A, D). Corolla not preserved. The androecium is composed of five stamens that alternate with five apparent staminodes (Fig. 27A, D). The five fertile stamens are opposite the sepals and have short filaments and small, dor-

Figure 24. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 27, Flower with stellate trichomes, type 2 (cf. Ericales). —A. Lateral view of flower with numerous stellate trichomes on outer surface of sepals; PP45187. —B. Apical view of flower in A showing imbricate sepals. —C. Oblique view of flower showing remains of perianth and single style; PP45188. —D. Apical view of specimen in C showing sepals, large nectary lobes alternating with sepals, and the bases of two filaments. Scale bars = 1 mm.

sifixed anthers. The presumed staminodes (or possibly stamens that have lost their anthers) alternate with the sepals and are approximately one-third longer than the fertile stamens. The gynoecium consists of a half inferior ovary and two short styles. Locule number and mature fruit structure are unknown.

This flower is similar in some respects to *Tylerianthus crossmanensis* Gandolfo, Nixon & Crepet (1998) from the Turonian of New Jersey. However, the specimens described here differ in shape of the sepals, the dorsifixed rather than basifixed anthers, and details of in situ pollen. The abruptly narrowed sepals, stamens opposite the sepals, staminodes alternate to the sepals, and the bicarpellate half inferior ovary are all features consistent with a rela-

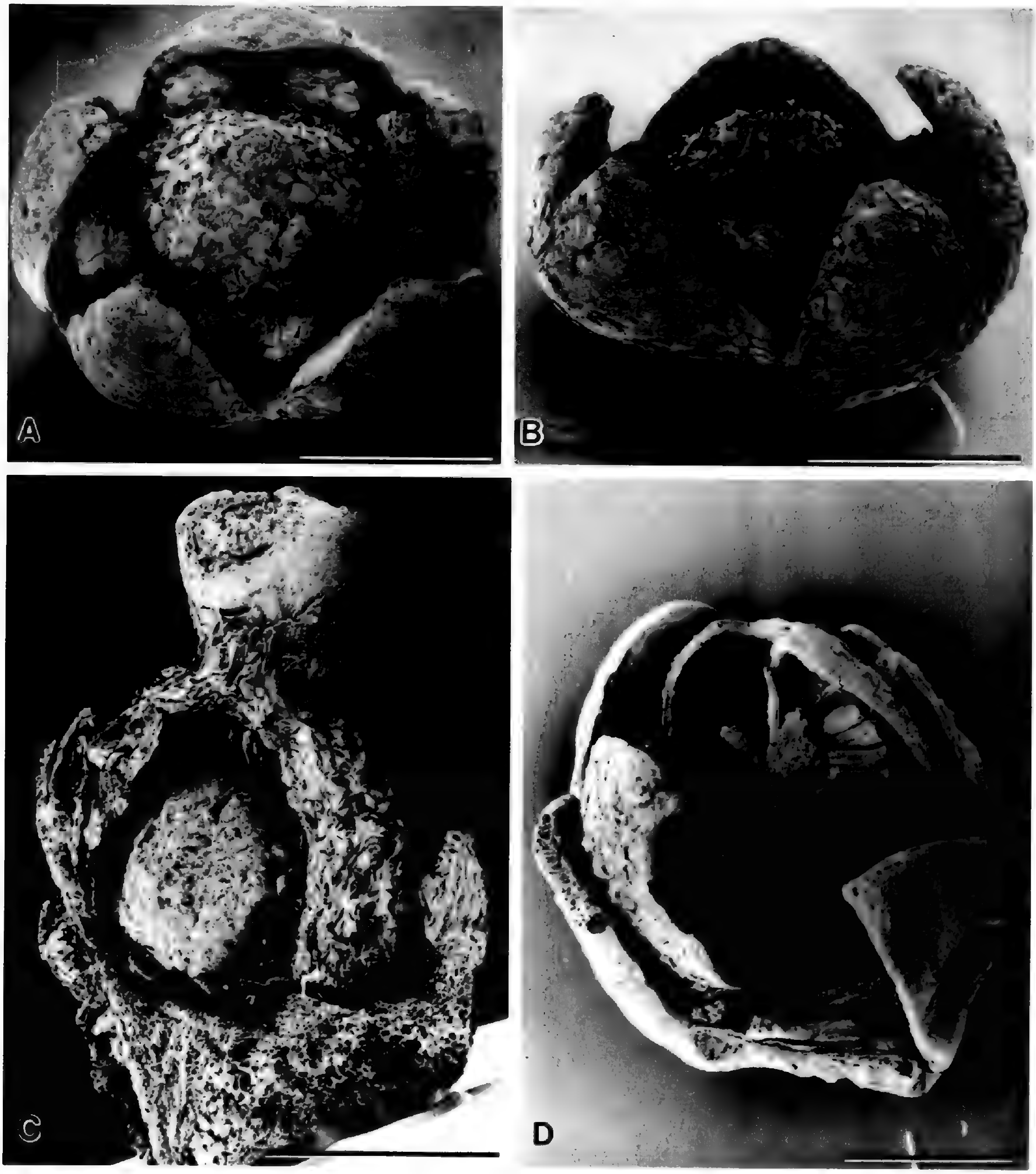

Figure 25. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 28, Fruits bearing large peltate trichomes (cf. Ericales). —A. Young fruit with five fleshy sepals and eight well-developed nectary lobes; note triangular outline of young fruit and numerous peltate trichomes on the sepals and young fruit; PP45189. —B. Lateral view of specimen in A showing peltate trichomes on sepals and ovary. —C. Abraded fruit specimen showing massive placenta and numerous ovules; note basal (united) portion of style; PP45190. —D. Mature trilocular capsule with numerous seeds and persistent sepals; note loculicidal dehiscence; PP45191. Scale bars = 1 mm.

tionship to Hydrangeaceae and Grossulariaceae. Few specimens of this taxon are known.

31. Flower with spindle-shaped inferior ovary Figure 28.

Flowers bisexual, epigynous, forming a long, spindle-shaped fruit that is 4–8 mm long. Calyx abraded, connate at least at the base, number of sepals unknown. Corolla abraded, connate at least at the base, number of petals unknown. Stamens, possibly five, enclosed within corolla (Fig. 28A, E), exserted at maturity (Fig. 28H). Filaments free, attached at base of corolla tube (Fig. 28H). Anthers apparently dorsifixed. Gynoecium composed of

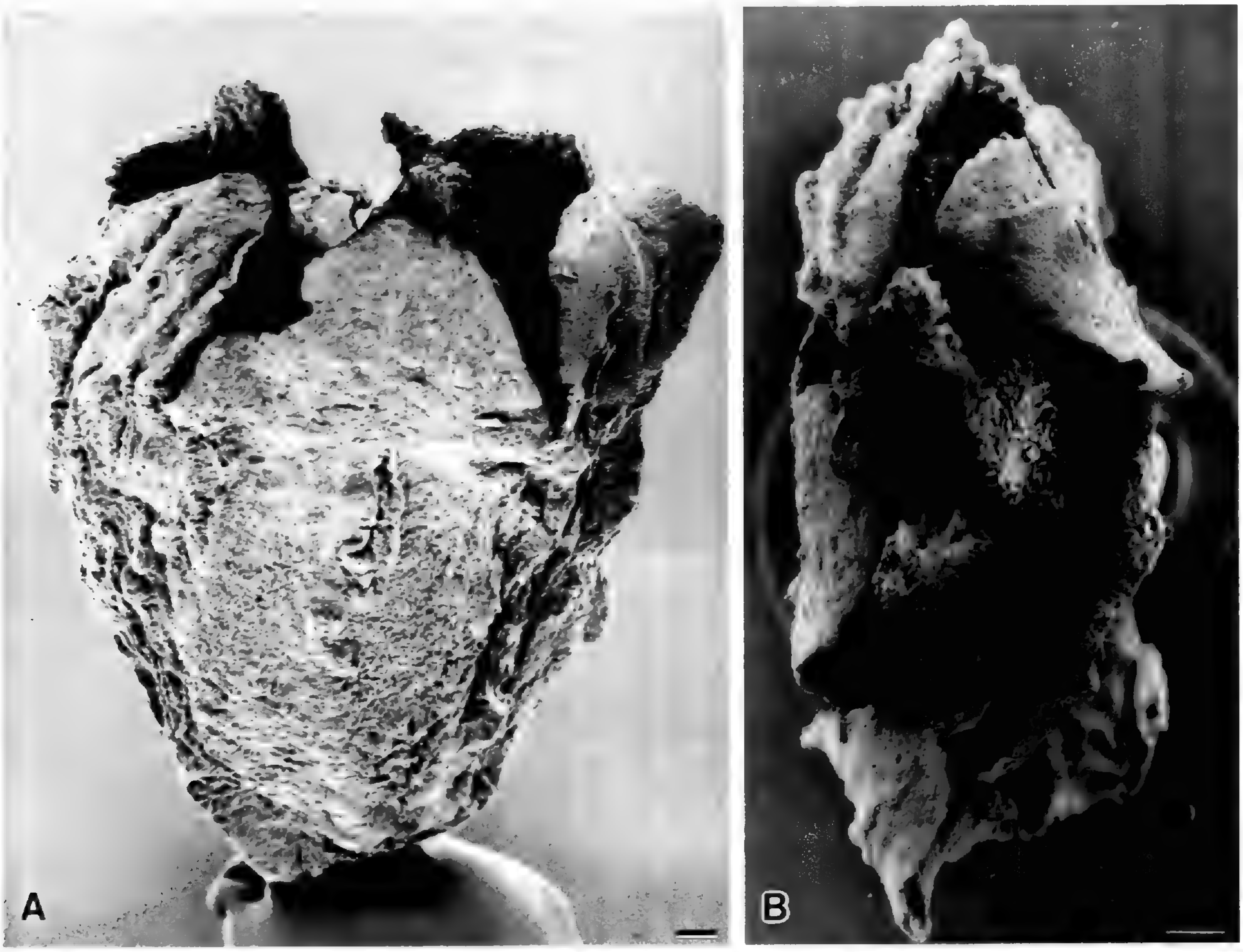

Figure 26. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 29, Pentamerous flower with inferior ovary. —A. Lateral view of flower showing inferior ovary, three styles, and five sepals; PP44603. —B. Apical view of flower in A showing three styles. Scale bars = 100 μm.

long, slender inferior ovary. Styles three, basally united, but free for most of their length and recurved at maturity (Fig. 28C, G). The stigma is decurrent on the distal third of the style. Locule and ovule number unknown. Large open pores (?modified stomata) at base of style may represent nectariferous tissue. Mature fruits are spindle-shaped with longitudinal ridges (Fig. 28B, C). Pollen grains are prolate, tricolporate, with an open reticulum that becomes closed toward the colpi.

Complete specimens of this flower have not been recovered, and details of perianth structure are poorly known. The fruits are especially abundant in the Allon samples and are almost always preserved as compressed lignitized specimens. The pollen grains are distinctive and have been found on all of the dispersed parts (Lupia et al., 1995). The flowers may have been protandrous. Some specimens are preserved with the three style lobes tightly appressed (Fig. 28D, H), while others have the style lobes recurved with the presumed stigmatic surfaces exposed (Fig. 28C, G). One specimen with appressed style lobes has an elongated filament still attached (Fig. 28H). This specimen may indicate that the stamens were exserted, and reached maturity, before the stigmatic surfaces were exposed.

These fossils are broadly similar to *Esgueiria* Friis, Pedersen & Crane (1992), which was described from the Late Cretaceous of Portugal and recently discovered also from the Late Cretaceous of Japan (Takahashi, Crane & Ando, unpublished data). Friis et al. (1992) suggested that *Esgueiria* has a close relationship with the Combretaceae (Myrtales), although free style lobes do not occur in any extant member of the family. Free style and stigma lobes are present in some other members of Myrtales. Additional details of perianth structure, and locule number, are needed for a more complete assessment of possible relationships. This morphotype is one of the five most abundant angiosperms at Allon (> 1000 whole or partial specimens) and is the only mesofossil that has also been recognized in the compression flora (Fig. 28C).

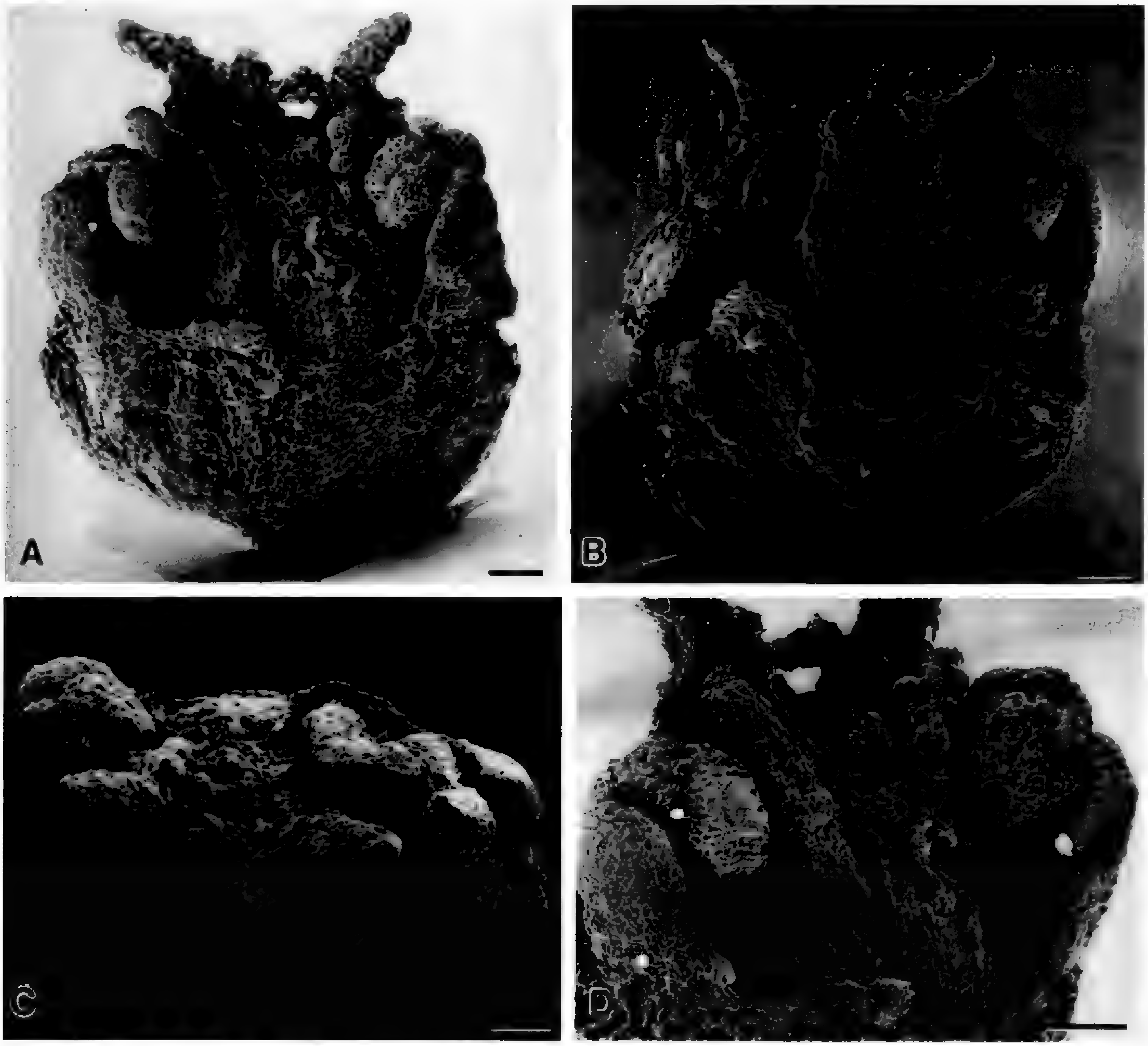

Figure 27. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 30, Pentamerous flower with semi-inferior ovary. —A. Lateral view of flower showing semi-inferior ovary, two styles, stamens with dorsifixed anthers, and long stamen filaments or staminodes; PP45192. —B. Opposite side of flower shown in A. —C. Apical view of flower shown in A. —D. Detail of flower in A showing narrow sepals and anther. Scale bars = 100 μm.

32. Flower with lobed petals
Figure 29.

Flowers bisexual, epigynous, 2 mm long, 1 mm wide. Perianth composed of a calyx, which is abraded in the available specimens, and lobed petals. Petals have either three (Fig. 29A) or two lobes (Fig. 29B). Stamen number unknown but possibly five; details of filaments and anthers unknown. Gynoecium bicarpellate with a semi-inferior ovary with two placentae and several ovules (Fig. 29E). Two short, free styles are inserted between two large, prominent, spongy structures at the apex of the ovary (Fig. 29C, D). Pollen grains are small (polar axis 6 μm), prolate, tricolporate, tectate, and microechinate. Fruits are small, triangular in outline, with a thin epidermis or epicarp that is frequently not preserved, and a thicker endocarp that dehisces to yield two valves. Mature fruits have a single locule (Fig. 29E), and apparently only a single seed develops to maturity.

One of the most distinctive features of these flowers is the large, spongy, bilobed structure that is located above the insertion of perianth and stamens (Fig. 29C, D). Two short styles are located between these structures. Most specimens are lignitized and compressed, and these structures appear as wings or a continuation of the ovary (Fig. 29A, D). However, several charcoalified specimens (e.g., Fig. 29C) clearly show that these structures are not part of the ovary. They are similar in appearance to a massive bilobed nectary disk.

The fossil flowers and fruits are similar in many respects to those of the Araliaceae and Apiaceae. A minute calyx, lobed petals, large nectary disk, bicarpellate gynoecium with an inferior ovary, and free styles are all features found in these families. However, parietal placentation and more than one ovule per locule are features not found in extant Araliaceae or Apiaceae. Additional study of the fossil specimens, and extant Araliaceae and Apiaceae, is needed before the relationships of these fossils can be understood in more detail.

This taxon is one of the five most abundant taxa in the Allon flora (> 1000 whole or partial specimens).

33. Trimerous flower with numerous coarse trichomes
Figure 30.

Flowers are slender, pedicellate, 2–3 mm long, 1–1.5 mm wide, with numerous long, coarse trichomes on all flower parts. Most specimens are abraded with perianth and androecium broken. Perianth usually composed of six tepals (Fig. 30D, E), but flowers with five tepals also occur. Tepals are narrow and taper to an acute apex (Fig. 30A, B). Stamen filaments are broken, and anthers are unknown. At least six filaments are present, but the exact number is unknown (Fig. 30C). Filaments bear numerous coarse trichomes. Some specimens contain three relatively long, slender styles; others have no evidence of styles. Other details of the gynoecium are unknown. Pollen is tricolporate, ca. 15–17 μm long, with a perforate tectum.

This flower type is very common, but it is poorly known because most specimens are broken. The long, coarse trichomes covering all surfaces are distinctive. Abraded specimens in which the trichomes have been broken have a distinctive pock-marked surface. The flowers are similar to the staminate flowers of *Antiquacupula sulcata* (taxon 21) but differ in several respects, especially the more numerous trichomes, larger pollen grains, and absence of the obvious united style base. It is possible that these flowers represent another taxon of Fagaceae sensu lato but more structural details are needed to pursue this comparison further.

34. Capitate inflorescence of pentamerous flowers
Figure 31.

Inflorescence capitate, borne terminally on a slender stalk, small, diameter ca. 1.2 mm, containing ca. 20 sessile flowers (Fig. 31A, B). Flowers small, diameter ca. 0.4 mm. Calyx composed of five free sepals with broadly rounded apices and scattered simple trichomes on the abaxial and adaxial surfaces. Internal to, and alternating with, the sepals are five long, slender structures that may be stamen filaments (Fig. 31C, D). Anthers not preserved. Pollen has not been found on the specimen. The center of the flower contains a cycle of 10 awl-shaped structures (Fig. 31B, D) that are presumed to represent the gynoecium, but details are unknown.

This inflorescence is known from a single specimen. Many aspects of the flower structure are uncertain, and additional specimens are needed for more detailed characterization.

35. Flower with pentamerous perianth and trimerous gynoecium
Figure 32.

Flowers are hypogynous, pedicellate (Fig. 32A), actinomorphic, ca. 1.2 mm in diameter. The calyx is pentamerous (Fig. 32B, D), the sepals are basally united for ca. 0.2 mm, free lobes ca. 0.7–0.8 mm long; sepal apex obtuse to acute. Corolla and androecium unknown. Gynoecium syncarpous, tricarpellate, ovary superior, locule number unknown (Fig. 32D). Single style long, slender, hollow, fluted, apex acute. Surface of ovary papillose. Pollen grains tricolporate, exine slightly rugose.

The short, broad ovary of these flowers, with a papillose surface, is one of their most distinctive features (Fig. 32C). These flowers are similar in some respects to those of some taxa in the Ericales, especially in the hollow, fluted style, but currently there is insufficient information to investigate relationships further.

36. Flower with pentamerous calyx composed of thick valvate sepals
Figure 33.

Flowers are hypogynous (Fig. 33A), actinomorphic, and possibly unisexual, 1–2 mm long, 1 mm wide. Calyx composed of five valvate, thick sepals that taper to an acute apex (Fig. 33B, C). Stamens apparently five, alternate with the sepals (Fig. 33D). Gynoecium not observed. Pollen grains are tricolporate, polar axis 12 μm, with a finely reticulate exine sculpture.

There are relatively few specimens available for this flower type, and few structural details have been documented. As a consequence, little is known regarding the possible systematic relationships of this fossil within the eudicots.

37. Slender epigynous flower
Figure 34.

Flowers slender, epigynous (Fig. 34A–C), actinomorphic, apparently bisexual, 2.4 mm long, 1 mm wide. Perianth composed of six narrow, free

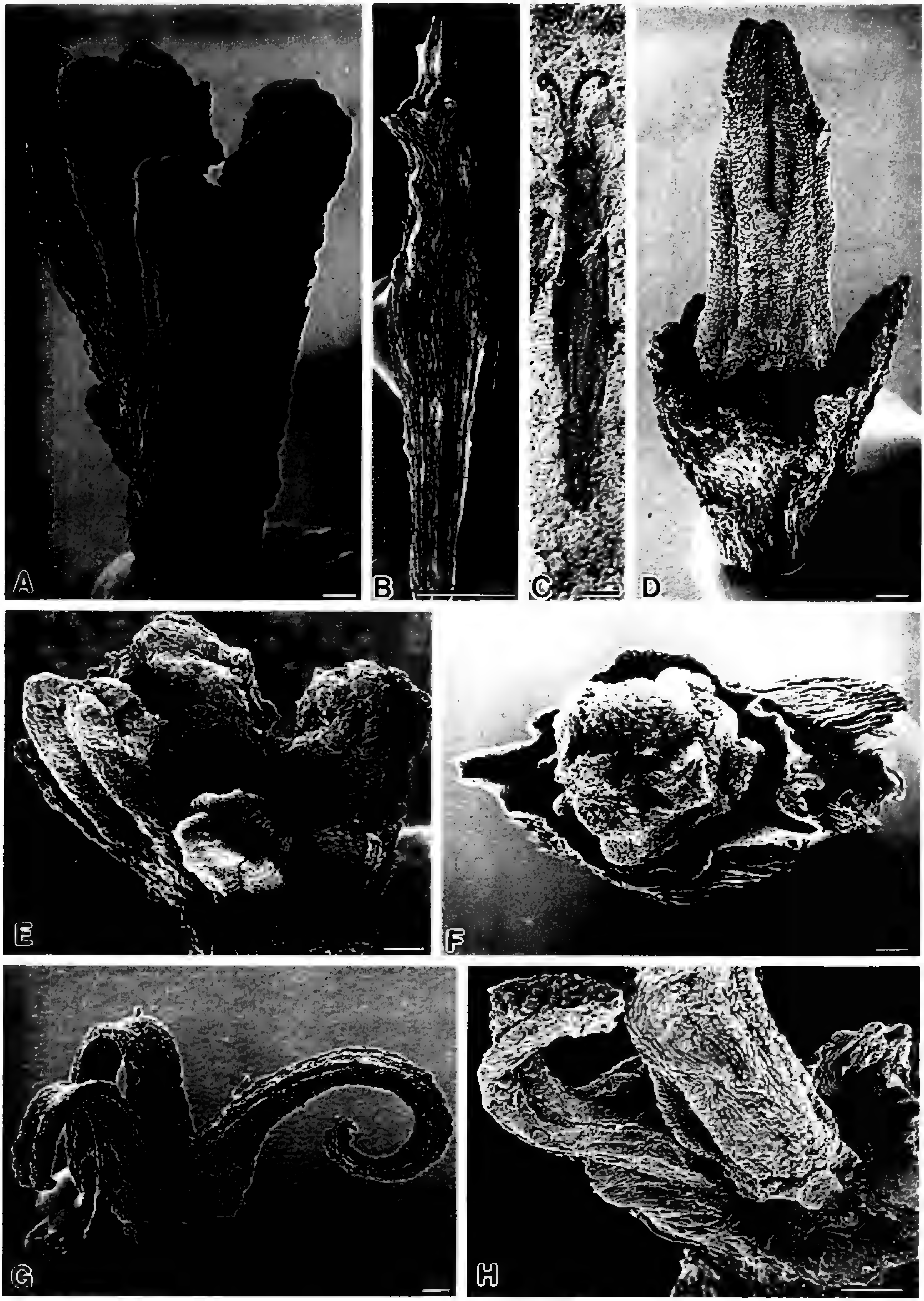

Figure 28. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 31, Flower with spindle-shaped inferior ovary. —A. Lateral view of abraded flower showing stamens; PP45193. —B. Young spindle-shaped fruit showing apex of the gynoecium protruding above the remains of the perianth; PP45194. —C. Compression fossil of spindle-shaped fruit; note recurved style lobes (light micrograph); PP45151. —D. Apical portion of gynoecium

Figure 29. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 32, Flower with lobed petals. —A. Flower with one trilobed petal; PP44597. —B. Flower with one bilobed petal; PP45198. —C. Young fruit with large, bilobed nectary present; note that two short, free styles are present between nectary lobes; PP45199. —D. Flower with several stamen filaments attached; note two styles in center; PP45200. —E. Transverse fracture of fruit showing placenta along suture on left; placenta on other suture removed during preparation; PP45201. Scale bars = 100 μm.

tepals with an acute apex. Stamens 12, represented by filaments only, anthers not preserved, pollen grains unknown. Six filaments alternate with the tepals, six are opposite the tepals. Filaments are tangentially flattened and at least as long as the tepals (Fig. 34D, E). The filaments alternate with thin, slender structures (Fig. 34E). Ovary inferior, triangular in cross section with somewhat thickened corners. Styles lobes three.

These flowers are very similar to the pistillate flowers of *Antiquacupula* (taxon 21) (Sims et al., 1998) but differ in several features. The filaments

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showing remains of perianth and two of three style lobes; PP44599. —E. Oblique apical view of specimen in A showing anthers. —F. Apical view of flower showing remains of calyx tube and corolla tube; PP45195. —G. Apical portion of style showing three recurved style lobes; compare with styles in C; PP45196. —H. Oblique view of flower showing style with lobes tightly appressed and remains of stamen covered with numerous pollen grains; PP45197. Scale bars: A, D–H = 100 μm; B = 10 mm; C = 1 mm.

Figure 30. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 33, Trimerous flower with numerous coarse trichomes. —A. Lateral view of flower showing perianth with numerous, coarse, densely spaced trichomes; PP45202. —B. Opposite side of flower shown in A; note two perianth parts are missing, revealing several narrow filaments covered with numerous trichomes. —C. Lateral view of flower with several perianth parts removed showing several filaments and abundant trichomes; PP45203. —D. Flower bud with intact calyx comprised of six tepals; PP45204. —E. Apical view of flower showing arrangement of tepals; PP45205. Scale bars: A–C = 0.5 mm; D, E = 100 μm.

are flattened, whereas they are terete in *Antiquacupula*, and there is no evidence of swollen filament bases in these specimens, while this is a consistent feature of *Antiquacupula sulcata.* There is also no evidence of longitudinal ridges and grooves on the ovary of these specimens, whereas again, this feature is consistently observed on fruits of *Antiquacupula sulcata.* These flowers may represent a second species of *Antiquacupula*, but additional specimens and details are needed to pursue this

Figure 31. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 34, Capitate inflorescence of pentamerous flowers. —A. View of base of inflorescence showing central axis and several flowers with broken perianth; PP45206. —B. Lateral view of specimen in A, showing perianth of several flowers; flower at center has three of five sepals present. —C. Detail of specimen in A showing a single flower with five fragmentary perianth parts (?sepals), filaments, and possible gynoecium. —D. Oblique view of specimen in A showing a single flower. Scale bars = 100 μm.

possibility further. This taxon is represented in the Allon flora by only two specimens.

38. Epigynous flower with spherical ovary Figure 35.

Flowers epigynous, bisexual, apparently actinomorphic, 4.2 mm long, 2.7 mm wide (Fig. 35A, B). Perianth abraded, poorly preserved. Calyx composed of possibly five sepals. Corolla not preserved. Fusiform structures (?stamens) numerous, grouped in possibly five bundles opposite the sepals (Fig. 35B, C). Filaments of putative stamens short, anthers with an acute apical extension of the connective (Fig. 35C, D). Pollen not preserved. Gynoecium composed of a large, spherical inferior ovary and single thick style possibly with five distal free lobes (Fig. 35A, B).

This taxon is known from only one poorly preserved specimen. An inferior ovary together with numerous stamens in bundles occurs in several orders of Dilleniidae, but more structural details are needed before possible systematic relationships can be assessed.

39. Flower with very broad perianth parts and coarse fimbriate trichomes Figure 36.

Flowers hypogynous with a perianth composed of a single cycle of 4–6 tepals (commonly 5), ca. 4 mm long, 3 mm wide (Fig. 36A). Tepals very broad with prominent venation, apparently persistent in fruit. Tepals thin and foliose, glabrous, broadly rounded at the apex, with a relatively narrow base, but not clawed. Androecium and pollen grains not

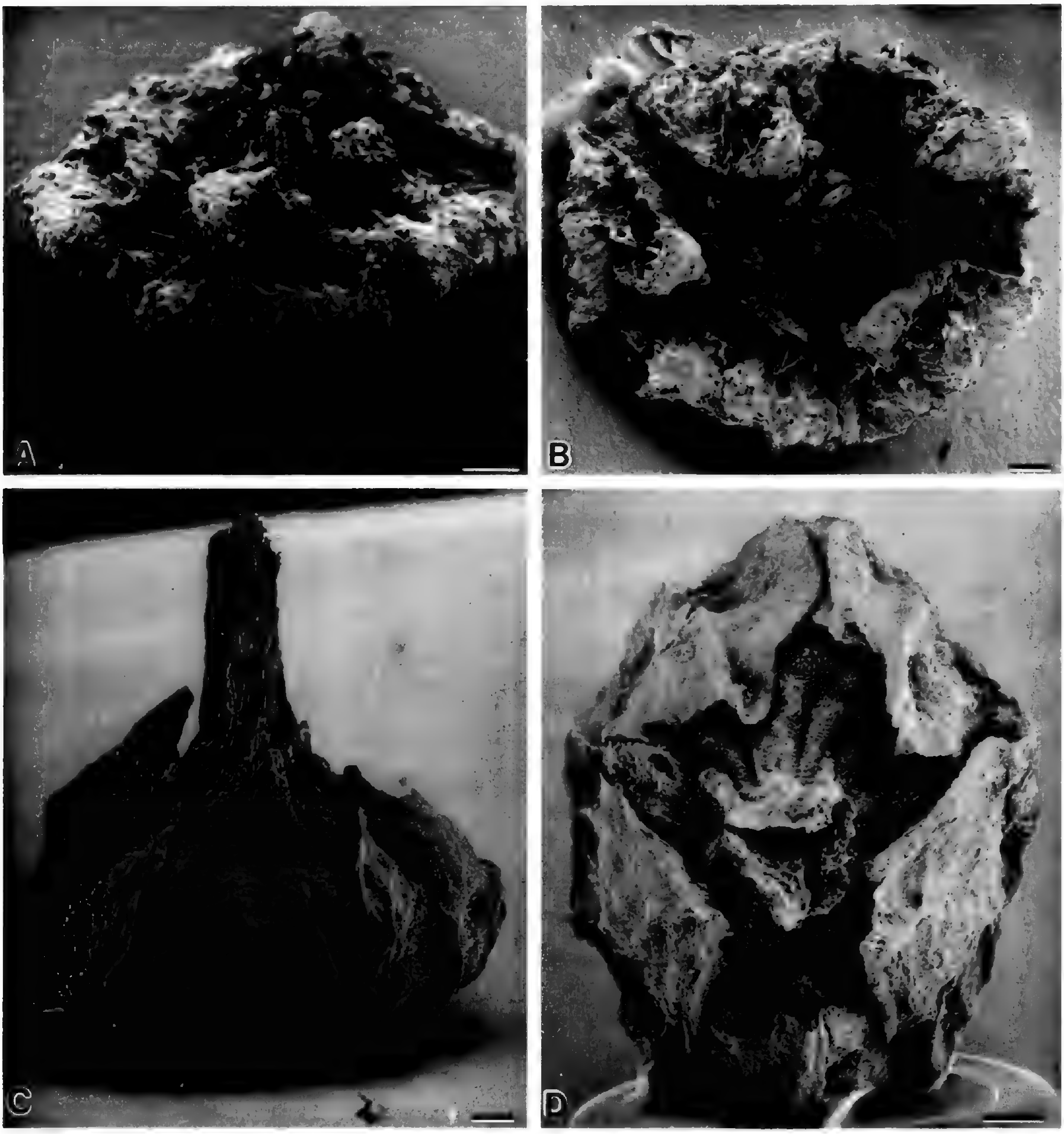


Figure 32. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 35, Flower with pentamerous perianth and trimerous gynoecium. —A. Lateral view of vertically compressed flower showing pedicel and thin sepals; PP45207. —B. Apical view of specimen in A showing pentamerous calyx. —C. Lateral view of flower showing imbricate sepals and long style; PP45208. —D. Apical view of flower showing hollow style and papillose surface of the ovary; PP45209. Scale bars = 100 μm.

preserved. Gynoecium composed of a superior ovary with three locules and three free, but confluent, styles (Fig. 36B). The surface of the ovary is covered by numerous large, coarse, fimbriate trichomes (Fig. 36C). The fruits are loculicidal capsules, with at least two seeds per locule (Fig. 36D).

This taxon is represented by several hundred specimens, nearly all of which are preserved as compressed lignitized material rather than as charcoal. None of the specimens provide any evidence of an androecium, and no staminate flowers are known from the Allon flora that have a comparable perianth. Although specimens of this taxon are abundant, they currently provide insufficient structural details to evaluate systematic relationships.

40. Ovate fruit
Figure 37.

Fruits derived from a superior ovary, ovate, 3–4 mm long, 3.0–3.5 mm wide, with an acute apex bearing a single style scar (Fig. 37A, B). Fruits apparently unilocular with partial septae. Ovule

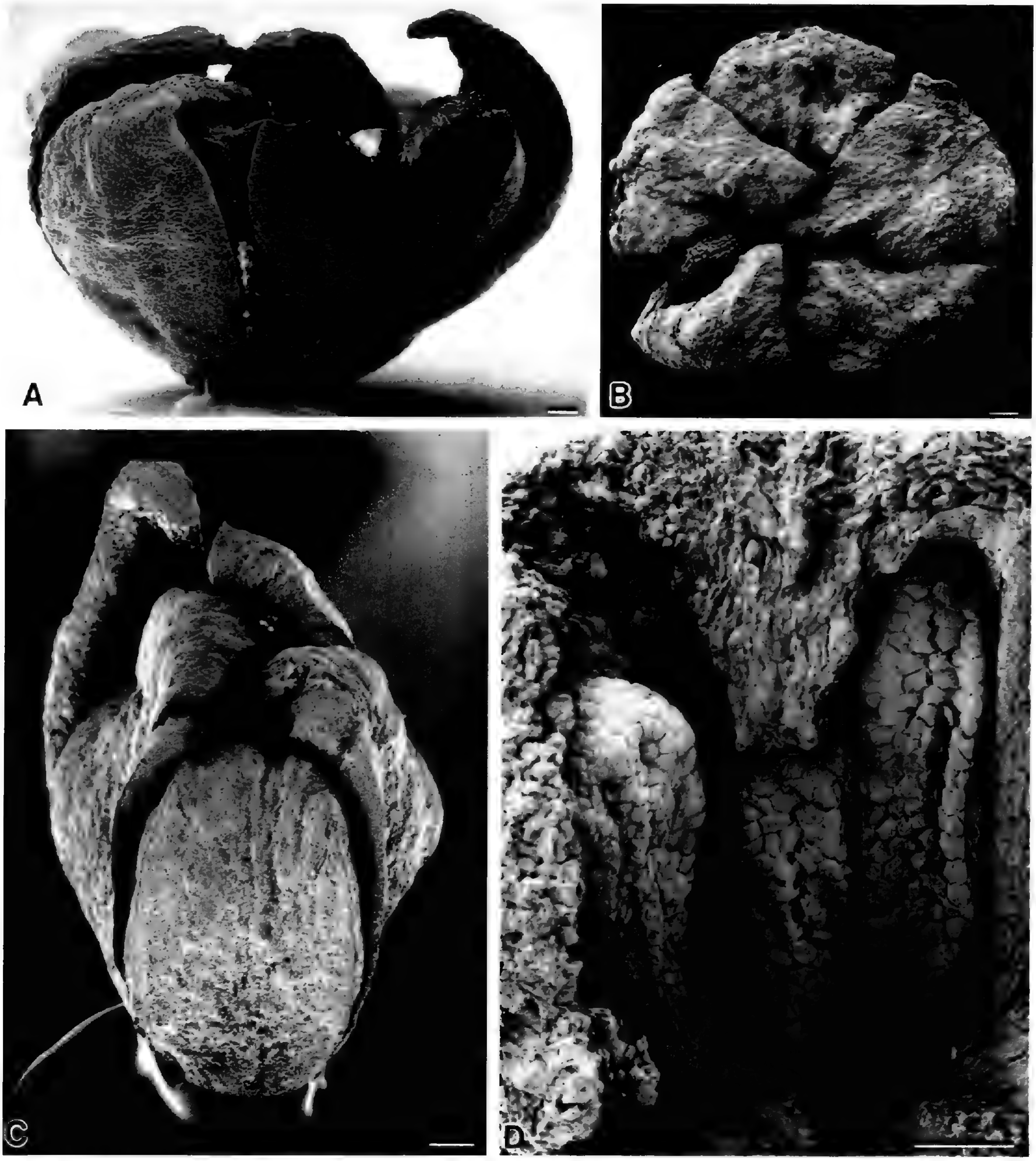
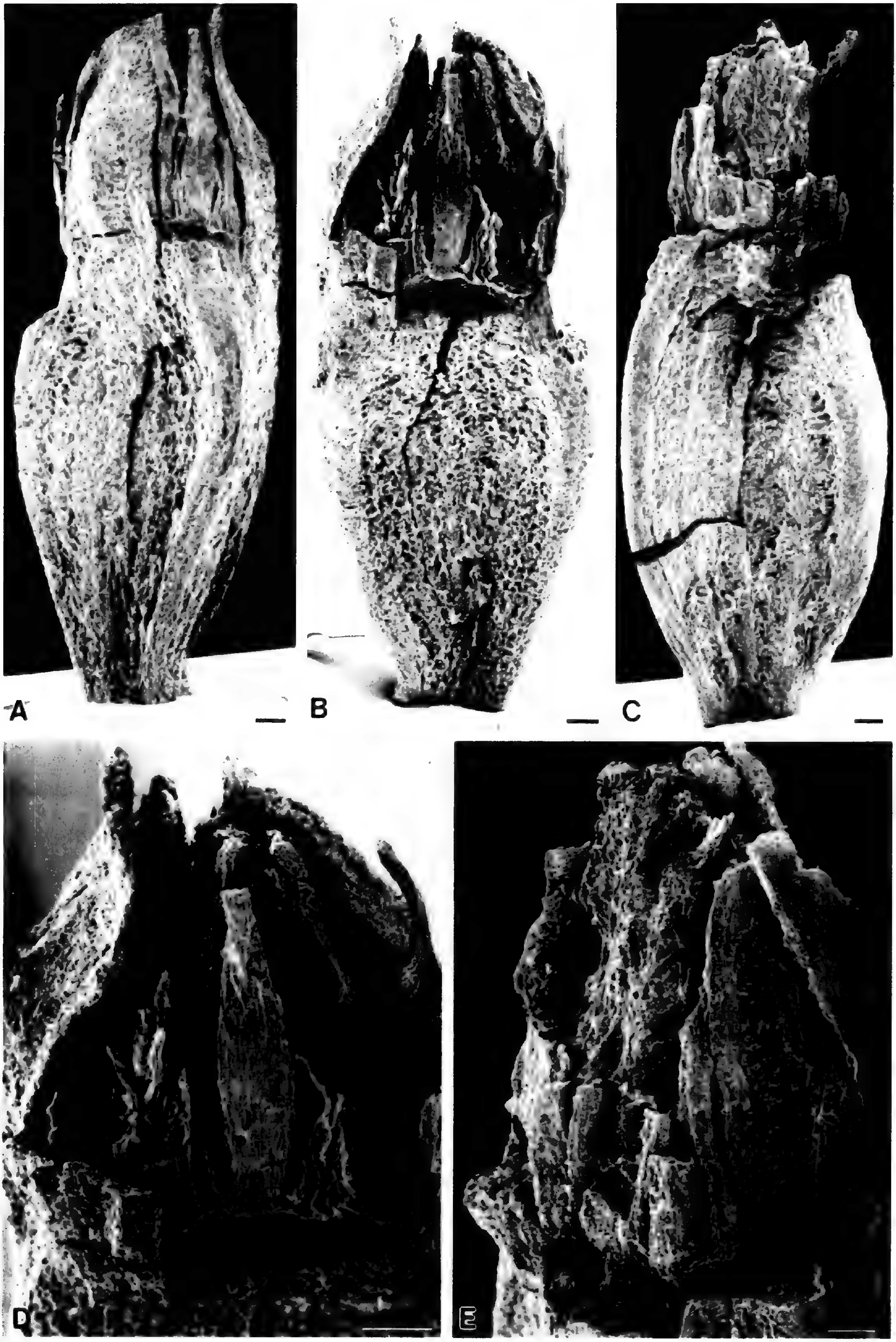


Figure 33. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 36. Flower with pentamerous calyx composed of thick, valvate sepals. —A. Lateral view of flower showing valvate sepals with acute apices; PP45210. —B. Apical view of flower showing sepals with acute apices; PP45211. —C. Oblique view of flower showing thick, valvate sepals; PP45212. —D. Flower with broken perianth revealing anthers; PP45213. Scale bars 100 μm.

and seed number are unknown. The fruit wall apparently consisted of a fleshy outer layer and a more resistant endocarp. The endocarp is characterized by the presence of lacunae that are clearly visible externally but apparently do not connect with the locule (Fig. 37D). The fruit wall is marked by three prominent longitudinal ribs that extend from base to apex. Nine less well developed ribs are also present, three between each major rib, and these generally do not extend all the way to the fruit apex. A poorly preserved perianth is present in some specimens (Fig. 37A). The perianth is apparently trimerous, but the quality of preservation is insufficient to confirm this feature.

This morphotype is one of the five most abundant angiosperms at Allon (> 1000 whole or partial


A
B
C
D
E

specimens). However, there are insufficient distinctive characters to determine systematic relationships for this fossil fruit. The fruits are usually preserved as laterally compressed specimens (Fig. 37A, B), but a few charcoalified, three-dimensional specimens are also present in the Allon assemblage (Fig. 37D).

41. Bicarpellate superior fruit
Figure 38.

Fruits ca. 2.25 mm long, 1.75 mm wide, 1 mm thick, apparently derived from a superior ovary, lenticular, bicarpellate with two persistent style bases. Locule, ovule, seed, and pollen details are unknown. Possible perianth remnants are preserved on the base of one specimen (Fig. 38A).

This fruit type is known from two poorly preserved specimens, one of which is very abraded (Fig. 38B). The fruit is apparently derived from a superior ovary because remains of a perianth are present on one specimen (Fig. 38A). This feature confirms that this fruit is not the same as the lenticular fruit of *Protofagacea.* This fruit type is similar in many features to specimens from Upatoi Creek in western Georgia (Herendeen et al., unpublished data). Absence of pollen precludes comparisons with fossils bearing Normapolles pollen and relevant extant taxa. Additional material is needed before this taxon can be understood in more detail.

42. Epigynous flower with rounded sepals
Figure 39.

Flowers are epigynous, apparently actinomorphic, 3.5–3.7 mm long, 2.5 mm wide, with a pentamerous calyx composed of short, broadly rounded sepal lobes, and a gynoecium with a single style. The ovary and calyx are covered by numerous short, blunt trichomes. Corolla and androecium are not preserved. Details of ovary structure are unknown.

This flower type is represented by only a few poorly preserved specimens. The short, blunt, and often downwardly directed, trichomes are distinctive and have not been observed in other fossils from the Allon locality. Additional better preserved specimens are needed before systematic relationships can be evaluated.

43. Pentamerous flower with bracteoles
Figure 40.

Flowers are pedicellate, subtended by a pair of fleshy bracteoles (Fig. 40A, B), hypogynous, apparently actinomorphic, ca. 1.5 mm long, and 1.5 mm wide. The calyx is pentamerous, basally united for ca. 1/3 of its length, thick and fleshy except at the margins of the free lobes (Fig. 40C). Ovary composed of five carpels, superior, locule number unknown. There is a single style scar present at the apex of the ovary in a slight depression (Fig. 40C, D). Corolla and androecium are not preserved.

Only a single specimen of this taxon is known. The style appears to have been inserted in a slight depression in the apex of the ovary. This feature is commonly present in flowers of Ericales. The calyx structure, gynoecium of five carpels, and the presence of paired bracteoles are also consistent with a relationship to Ericales. Additional details, especially of corolla and androecium, are needed for a more precise assessment of the systematic relationships of this fossil.

44. Immature bicarpellate fruit
Figure 41.

Flower epigynous with a thick hypanthium cup, which has small conical protuberances on its inner wall and slight longitudinal ribbing externally toward the base. Gynoecium bicarpellate, composed of a single inferior ovary and two free but confluent styles. The styles are shorter than the hypanthium cup. Details of perianth and androecium are unknown.

This fossil is known from a single incomplete specimen of an immature fruit. The thick, well-developed hypanthium cup is distinctive. No other details are known for this fossil.

45. Inflorescence with trimerous flowers
Figure 42.

Inflorescence pedunculate, cymose, bearing flower buds with a trimerous perianth. Flower buds are 0.8 mm long and 0.4 mm wide. The peduncle is short and thick (Fig. 42B, C). At the apex of the

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Figure 34. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 37, Slender epigynous flower. —A. Lateral view of flower showing inferior ovary and perianth; PP45214. —B. Opposite side of specimen in A with perianth removed showing filaments flanked by narrow, thin-walled structures. —C. Specimen with abraded perianth; PP45215. —D. Detail of specimen in A and B showing perianth, flattened filaments, and thin-walled structures alternating with the filaments. —E. Detail of specimen in C showing perianth, flattened filaments, and thin structures alternating with the filaments. Scale bars = 100 μm.

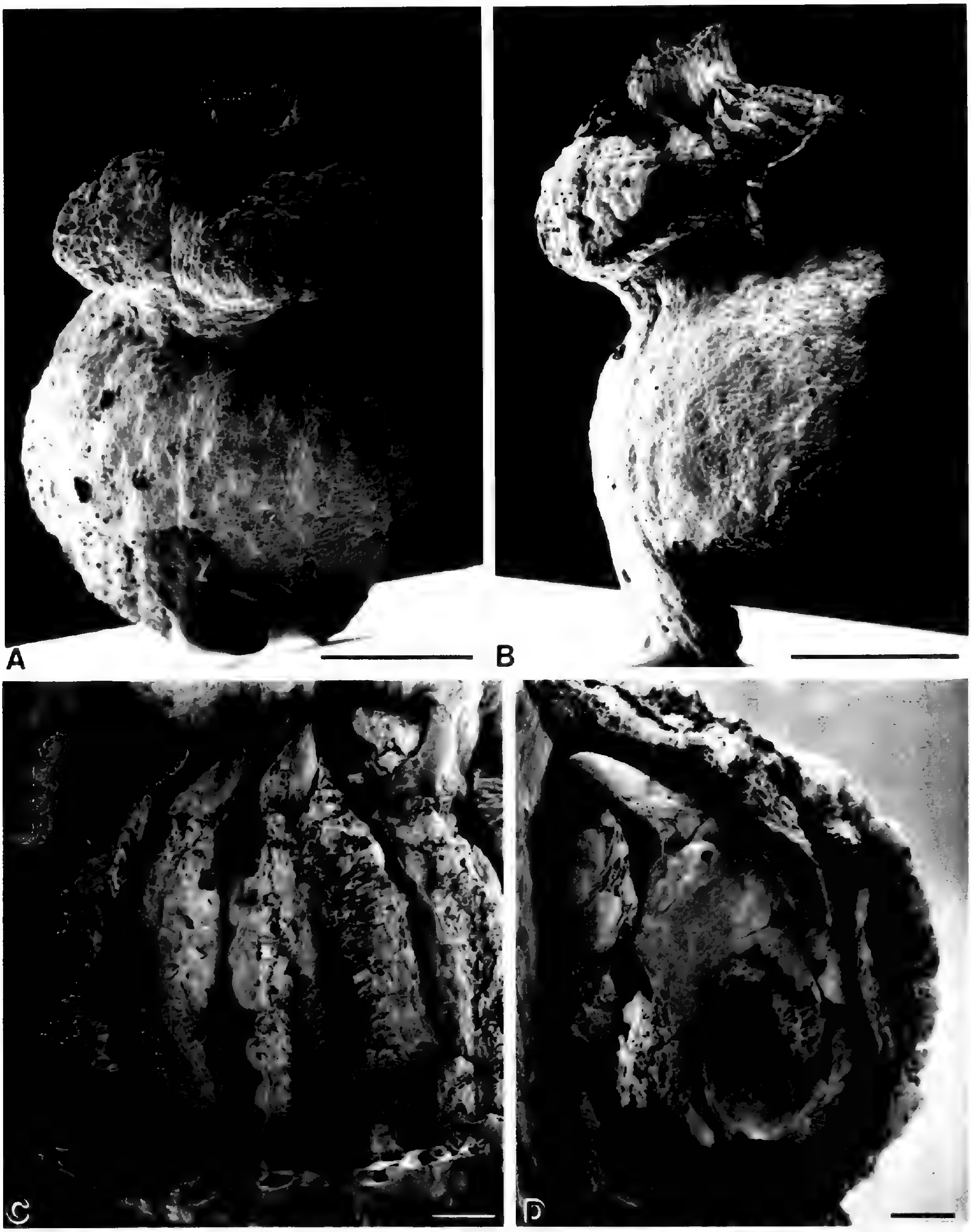


Figure 35. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 38. Epigynous flower with spherical ovary. —A. Lateral view of flower showing ovary and sepals; PP45216. —B. Specimen in A showing broken ovary, clusters of stamens opposite two sepals, and base of thick style. —C. Detail of abraded stamens showing connective extension. —D. Lateral view of stamen showing connective extension. Scale bars: A, B = 1 mm; C, D = 100 μm.

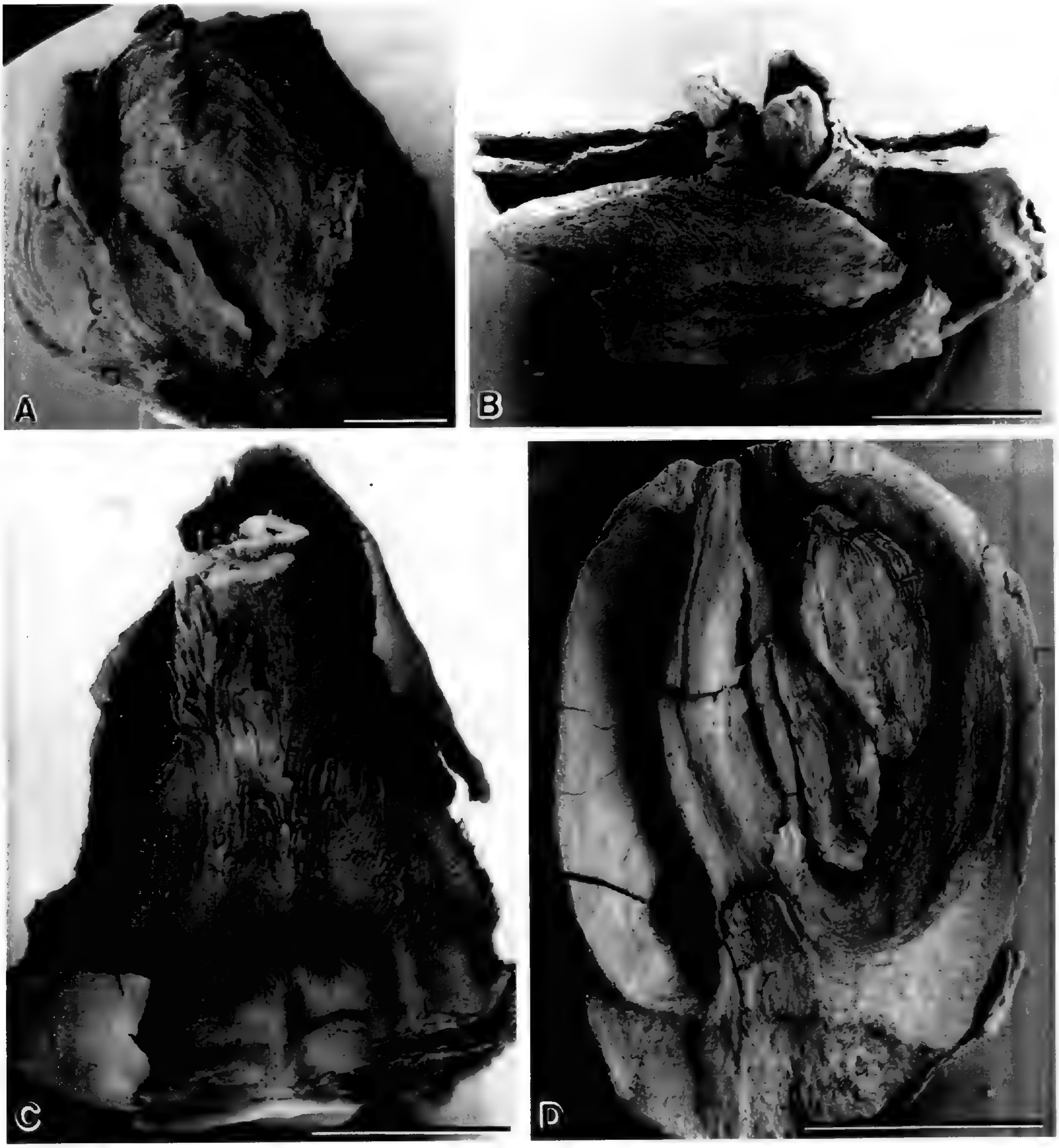


Figure 36. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 39, Flower with very broad perianth parts and coarse trichomes. —A. Lateral view of flower showing perianth; PP45217. —B. Oblique view showing broad perianth members and three free styles; PP45218. —C. Flower with perianth parts removed to show superior ovary covered with coarse trichomes; PP45219. —D. Longitudinally fractured fruit showing ovules in situ; PP45220. Scale bars = 1 mm.

peduncle there is a single flower pedicel, flanked by two clusters of flowers that are subtended by digitately divided bracts (Fig. 42D). Most flowers are broken off, and their position is indicated by pedicel bases only. The organization of the lateral groups of flowers is difficult to discern because the flowers are tightly clustered. In some specimens the lateral clusters appear to have a cymose organization. Flower buds, pedicels, and bracts are all covered by numerous simple trichomes.

The flower buds that are present on some specimens are too small to dissect for internal structural details, and no specimens with larger flowers attached are available. The flower buds are somewhat similar in gross morphology and trichome structure to young staminate flowers of *Antiquacupula sulcata* (taxon 21; Sims et al., 1998, fig. 4), but it has not yet been possible to compare details of flower structure. Because there are other pedicellate flowers with trimerous perianth and long simple trichomes

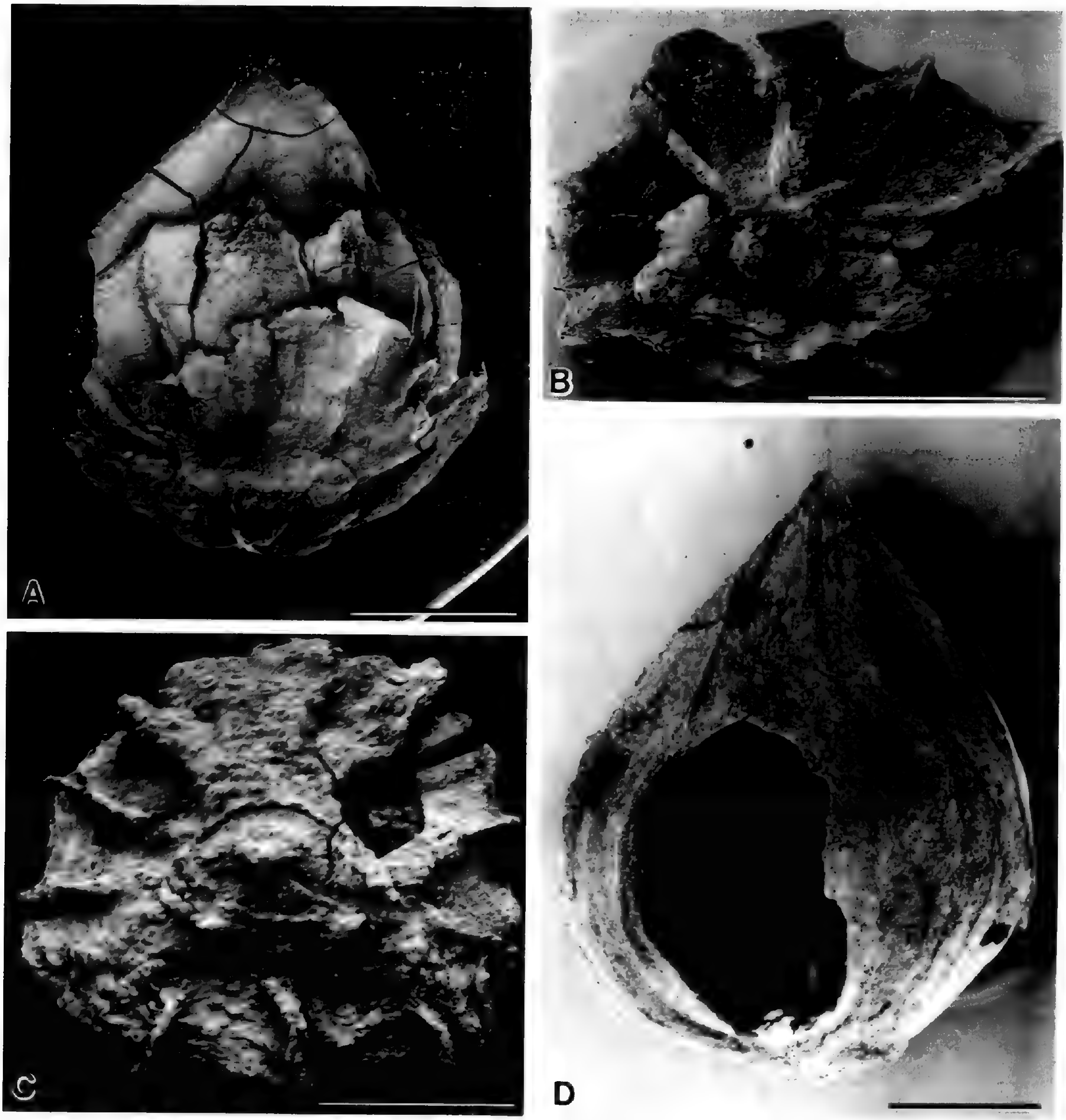


Figure 37. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 40, Ovate fruit. —A. Lateral view of endocarp with remains of other fruit layers and perianth; PP45221. —B. Base of fruit showing attachment scar, remains of perianth, and fleshy tissue adhering to endocarp; PP45222. —C. Basal view of fruit showing attachment scar and remains of perianth; note numerous small spherical structures (?galls) on surface; PP45223. —D. Lateral view of endocarp with broken fruit wall showing locule; note lacunae in endocarp; PP45224. Scale bars = 1 mm.

in the Allon flora, it is premature to associate this fossil with *Antiquacupula sulcata*. The cymose organization with bracts subtending the lateral flowers is consistent with inflorescence structure in Fagaceae sensu lato. This taxon is common in the Allon assemblage.

46. Strobiloid spicate axis
Figure 43A, B.

Axis fragment 2 mm long, 1.7 mm wide, fleshy in appearance, with helically arranged scars (Fig. 43A). The axis bears approximately 40 round attachment scars, each of which is flanked by two flange-like structures (Fig. 43B). No other structural details are available.

This taxon is known from only a single specimen. It is not certain that this taxon is an angiosperm.

47. Spherical capitate inflorescence
Figure 43C, D.

Capitate inflorescence on pedunculate axis. The specimen is 9 mm long. The presumed inflores-

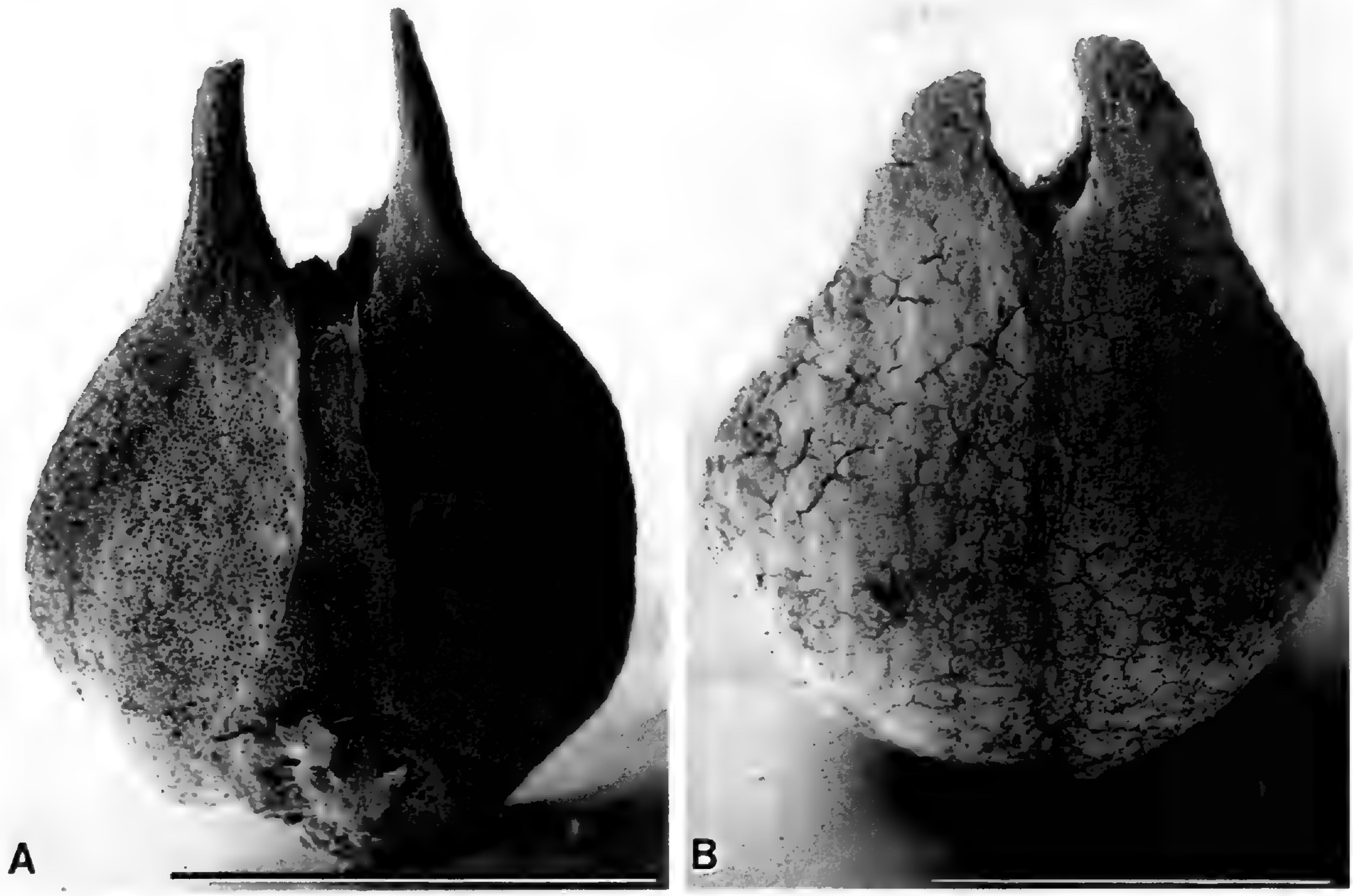


Figure 38. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 41, Bicarpellate superior fruit. —A. Lateral view of specimen showing two style bases and remains of perianth; PP45225. —B. Lateral view of abraded fruit; PP45226. Scale bars = 1 mm.

cence is represented by a spherical cluster of numerous presumed pedicel bases interspersed with trichomes (Fig. 43D).

The single specimen is severely abraded, and other structural details are unknown.

48. Miscellaneous axes with attached leaves/ bracts, type 1
Figure 44A–C.

There are two types of axes bearing closely spaced, helically arranged leaves/bracts. The first (taxon 48, Fig. 44A–C) has numerous, gradually tapering leaves (or bracts), each of which subtends a three-parted axillary structure (Fig. 44C). The leaves/bracts are entire-margined with scattered simple trichomes on the abaxial surface and margins. The shoot axis is longitudinally furrowed with raised peg-like leaf bases (Fig. 44B, C). The axillary structures included under type 1 may include more than one taxon but are too immature or poorly preserved to determine key structural details.

49. Miscellaneous axes with attached leaves/ bracts, type 2
Figure 44D, E.

The second axis type (taxon 49, Fig. 44D, E) has numerous, abruptly apically narrowed leaves (or bracts), each of which subtends one to several rounded structures, the details of which are unclear from the available material. The leaves are entire-margined with scattered simple trichomes on the abaxial surface and margins.

Axis type 2 shares some similarities with axis type 1 (taxon 48), but they differ most noticeably in the form of the leaves/bracts. It is uncertain whether this structure was produced by an angiosperm.

50. Axis with pinnate bracts
Figure 45.

The axis is 1.7 mm long, 0.7 mm wide, and bears bracts (or leaves) of two forms. The basalmost structure on the axis is a pinnately divided bract with numerous narrow, finger-like "pinnae" (Fig. 45A). The other leaves on the axis are simple and entire-margined (Fig. 45B). The central (distal) portion of the axis bears numerous smaller, narrower entire-margined structures. The margins and abaxial surfaces of all bracts/leaves support numerous simple trichomes. Internal anatomy of the axis is unknown.

This axis is known from only a single specimen. The pinnately divided structure is similar in some respects to the preserved young leaves of fern leaf type 1 (taxon 4, Fig. 4).

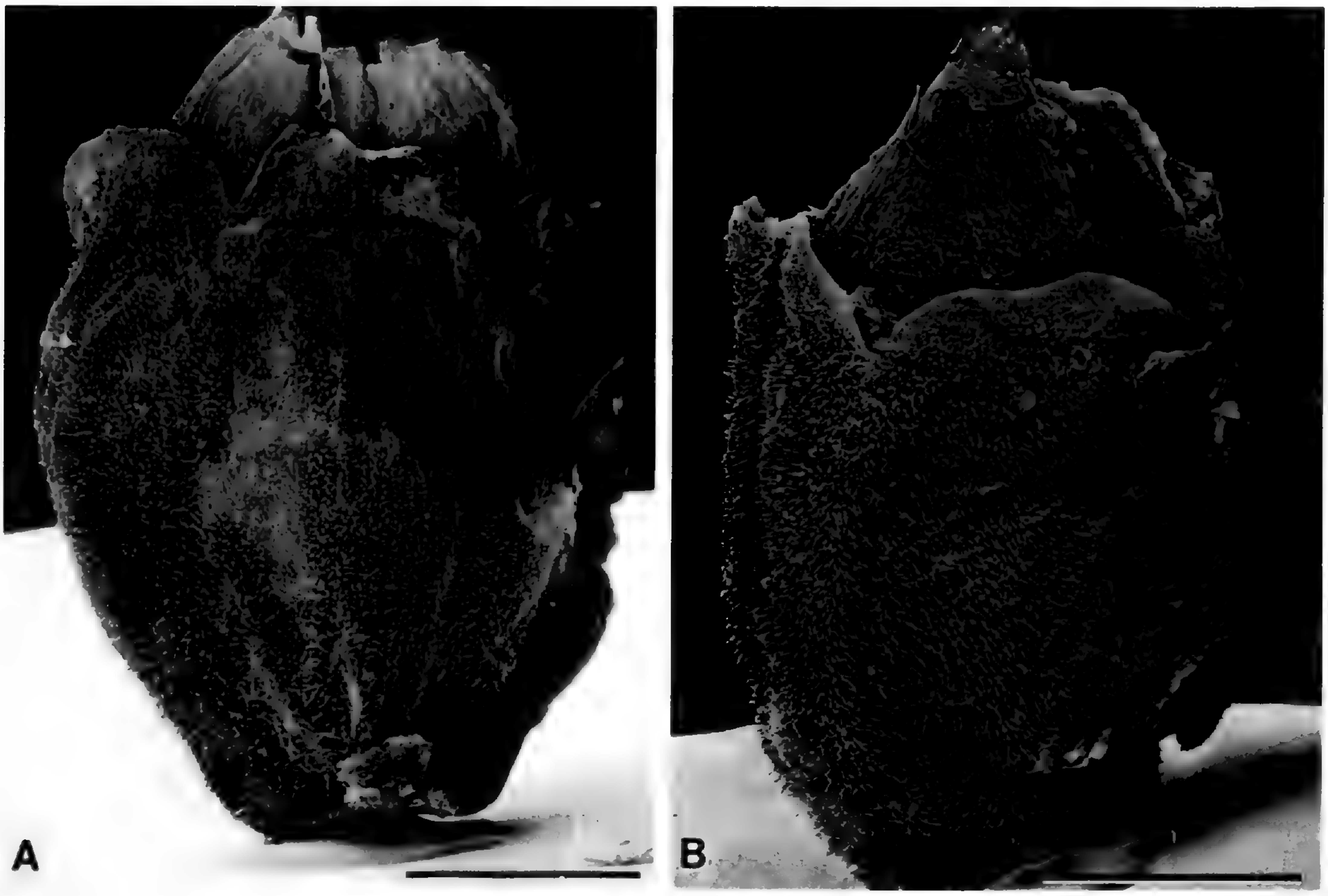


Figure 39. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 42, Epigynous flower with rounded sepals. —A. Lateral view of flower showing inferior ovary and rounded sepal lobes; note numerous short trichomes covering surface of ovary; PP45227. —B. Lateral view of flower; PP45228. Scale bars = 1 mm.

Several types of dispersed seeds are known from the Allon flora. We describe and illustrate three types that are among the most common in the Allon assemblage.

51. Miscellaneous seed type 1
Figure 46A.

Small seed with characteristic exfoliating outer cell layer of seed coat (taxon 51, Fig. 46A). Seeds are ovate, ca. 1 mm long, and 0.5–0.6 mm wide. The seed coat must have been fleshy or corky because most specimens are preserved with an outer layer that is exfoliating to reveal the cellular pattern underneath. This seed has not been found in any of the fruits that have been recovered with seeds in situ.

52. Miscellaneous seed type 2
Figure 46B.

Large seed with oblique fissure lines (taxon 52, Fig. 46B). The seeds are oblong, relatively large, ca. 2.5 mm long, 1.3 mm wide, with characteristic oblique fissure lines (Fig. 46B, arrows) that demarcate two presumed abortive seeds. One end of the seed is symmetrical, rounded, and obtuse, the other end is nearly acute and asymmetrical with a flattened face on one side (Fig. 46B). The two oblique fissures demarcate one large central section and two small flanking sections (Fig. 46B). The three sections often separate near the obtuse end of the seed. The overall structure has the appearance of a single seed with a gross morphology comparable to seeds of Hamamelidaceae subfamily Hamamelidoideae. This seed is common in the Allon assemblage but has not yet been found in a fruit.

53. Miscellaneous seed type 3
Figure 46C.

Large seed with finely pitted surface (taxon 53, Fig. 46C). This seed is oval with one end more broadly rounded than the other, relatively large, 2.5 mm long, 1.5 mm wide. The seed coat has a distinctive pitted surface. No specimens have been recovered in situ.

A great variety of non-reproductive plant parts are commonly encountered in mesofossil assemblages such as Allon, including pieces of wood and bark, leaves, bracts, and sometimes roots. We illustrate here a selection of bracts and fossil roots from the Allon assemblage.

54. Bracts
Figure 47A–D.

Bracts are represented in a diversity of morphologies. The more distinctive ones have margins that are deeply incised or toothed (taxon 54, Fig. 47A–D). One distinctive form is a relatively large, bilaterally symmetrical structure that is deeply incised with ca. 11 slender digitate processes that are 1.0–1.5 mm long with a swollen tip (Fig. 47A). The swollen structures appear to be glandular. These specimens are similar to bracts found in some species of Hamamelidoideae (Endress, pers. comm., 1998). Another specimen (Fig. 47B) is similar but has fewer digitate lobes and appears to be pinnate rather than palmate. The tips of the lobes are broken so it is unknown whether there were glandular structures present. Other bracts are asymmetrical with a margin that bears slender acute teeth (Fig. 47C). There is also a rounded form with numerous triangular teeth (Fig. 47D). Unless bracts have a very distinctive morphology, or are found attached to an axis that bears reproductive structures, it will be difficult to identify these structures.

55. Root with nodules?
Figure 47E, F.

Among the other dispersed plant parts recovered at Allon, several specimens that appear to be nodulated roots are especially interesting (taxon 55, Fig. 47E, F). The root is slender, ca. 0.15 mm in diameter, and bears clusters of oblong nodules. In one specimen (Fig. 47E) there is a cluster of four nodules that are 1 mm long, 0.3 mm wide, with a blunt, rounded apex. Another specimen bears at least six nodules that have a constriction near the apex (Fig. 47F). Unfortunately, details are insufficient to determine the systematic relationships of these roots.

56. Dicot leaf type 1
Figure 48A.

Leaf narrowly elliptical, up to 230 mm long, 45 mm wide. Base acute. Petiole unknown. Apex attenuate. Margin entire. Midrib curved, gradually thinning and becoming very fine toward the leaf apex. Secondary veins pinnately arranged, not prominent, apparently eucamptodromous. Tertiary and quaternary venation not visible.

This species resembles several leaf forms from the Middendorf and Eutaw Formations that were assigned by Berry (1914) to the extant genera *Ficus* or *Laurus*, but the accuracy of these determinations remains uncertain. This leaf is one of two leaf types (see also taxon 57) that is abundant in the Allon macrofossil assemblage.

57. Dicot leaf type 2
Figure 48B.

Leaf narrowly elliptical, maximum length (estimated) ca. 150–200 mm (distal portion unknown), maximum width ca. 25–31 mm. Base decurrent into a broad petiole (length unknown). Margin entire. Venation pinnate. Midrib very broad at the base, tapering distally. Secondary veins diverging at angles of ca. 40°, widely spaced at intervals of up to 10 mm sometimes with intersecondaries not prominent. Tertiary venation fine, not strongly developed. Quaternary venation not visible.

This leaf type is one of the two most abundant leaf forms in the Allon macrofossil assemblage. Details of venation and its systematic relationships are unknown.

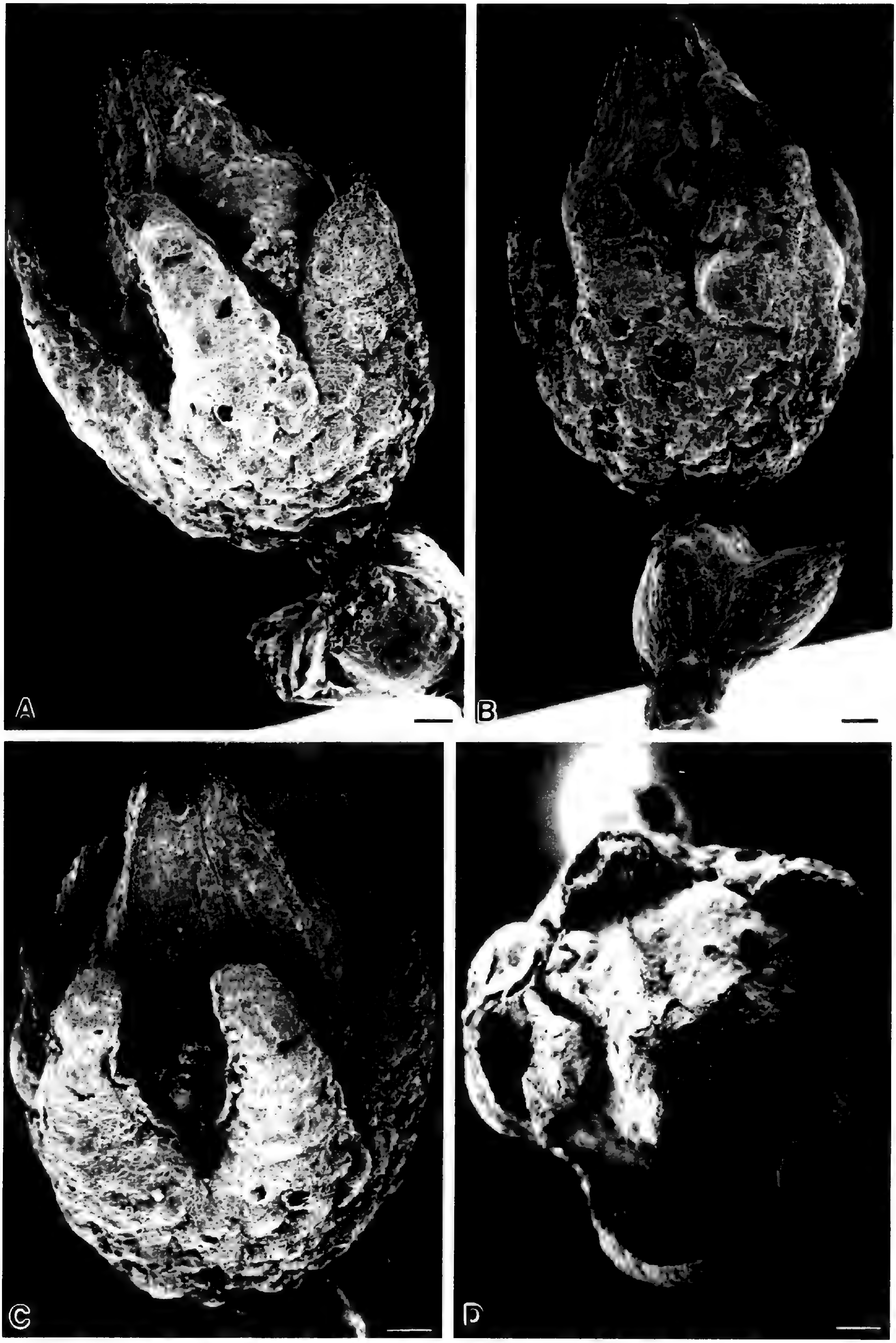
58. Dicot leaf type 3
Figure 48C.

Leaf narrowly elliptical, up to 50 mm long, 13 mm wide. Base acute. Apex acute. Margin entire. Venation acrodromous with three primary veins diverging at the leaf base and becoming thinner distally. Two additional weak secondary veins also diverge at the leaf base and run just inside the leaf margin in the distal third of the leaf. Lateral primary veins persist for more than two-thirds of the distance to the leaf apex. Secondary veins not prominent, best developed in the distal third of the leaf, especially between the outer primary veins and the leaf margin where they diverge at angles of ca. 60°. Tertiary and quaternary venation not visible.

This leaf type is similar to *Cinnamomum middendorfensis* Berry (1914, pl. 9, fig. 1) from the Middendorf and Eutaw Formations of Georgia. The yellowish coloration of these specimens may indicate that they possessed a thicker cuticle than most of the other leaves in life. This is often a feature of lauraceous leaves in other fossil leaf floras, and despite the occurrence of lauraceous reproductive structures at Allon (taxon 12), Berry's systematic determination should nevertheless be treated with caution. This leaf type is common in the Allon macrofossil assemblage.

59. Dicot leaf type 4
Figure 48D.

Leaf broadly elliptical, maximum length ca. 60 mm (incomplete), maximum width ca. 40 mm (details of base and apex unknown). Margin entire. Leaf texture thin. Venation pinnate, eucamptodromous with widely spaced secondary veins diverging at an angle of about 60° from the midrib. Prominent tertiary veins (intersecondaries) diverge from the midrib between the secondary veins and form a poorly organized, more or less orthogonal, reticulum of tertiary and quaternary veins. Ultimate venation not visible.


A
B
C
D

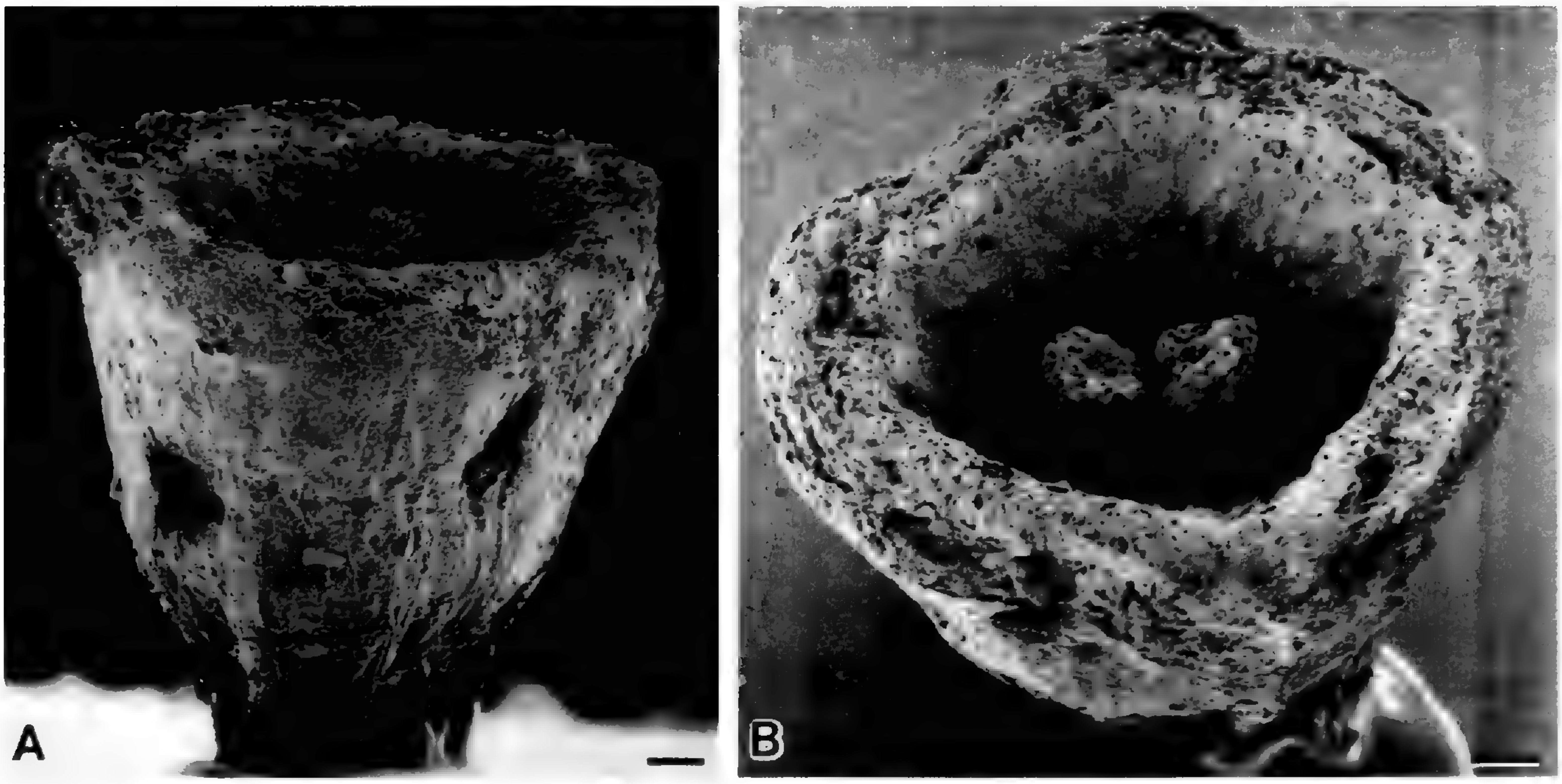


Figure 41. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 44, Immature bicarpellate fruit. —A. Lateral view of young fruit showing slight longitudinal ribbing in the basal region of the hypanthium; PP45231. —B. Oblique view of specimen in A showing two short styles inside the very thick hypanthium cup. Scale bars = 100 μm.

This leaf type is represented in the Allon macrofossil assemblage by a single specimen. The pattern of venation, in so far as it can be compared, is similar to that in leaf type 7 (taxon 62, fig. 49B). The systematic affinities of leaf type 4 are uncertain.

60. Dicot leaf type 5
Figure 48E.

Leaf of medium size, at least 100 mm in maximum length (incomplete), ca. 60 mm in maximum width (details of base, apex, and margin not preserved). Midrib prominent with a pair of strong secondaries on either side that diverge close to the leaf base. Lowermost secondary veins not prominent and diverging at angles of ca. 60° well above the leaf base. Tertiary and quaternary venation not observed.

This leaf type is rare in the Allon macrofossil assemblage. Its systematic affinities are uncertain.

61. Dicot leaf type 6
Figure 49A.

Leaf broadly elliptical or ovate. Estimated leaf length ca. 50 mm (incomplete). Maximum width ca. 25 mm. Base rounded. Petiole short (ca. 4 mm long) (leaf apex not preserved). Margin finely serrate with small, bluntly rounded teeth separated by bluntly rounded sinuses. Venation pinnate. Secondary veins thin, straight, slightly curved toward the leaf apex; diverging from the midrib at ca. 40°; regularly spaced at intervals of about 5 mm. Tertiary venation forming a poorly organized, more or less orthogonal network weakly percurrent between the secondaries. Details of tertiary and quaternary venation not observed.

The teeth on the specimen are difficult to interpret. On one side they appear distinct with a dark glandular tip, whereas on the other side the margin is irregular and perhaps damaged by insect feeding. The systematic affinities of this leaf type are uncertain. It is represented by a single specimen in the collection.

62. Dicot leaf type 7
Figure 49B.

Leaf elliptical to ovate, up to ca. 60 mm long (incomplete), up to ca. 23 mm wide. Base unknown. Apex acute to attenuate. Leaf margin entire. Ve-

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Figure 40. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 43, Pentamerous flower with bracteoles. —A. Lateral view of flower showing sepals, superior ovary, and paired bracteoles subtending flower; PP45230. —B. Opposite side of flower in A. —C. Oblique view of flower in A showing partially united calyx with acute sepal lobes. —D. Apical view of flower in A showing superior ovary with longitudinal ridges demarcating five carpels. Scale bars = 100 μm.

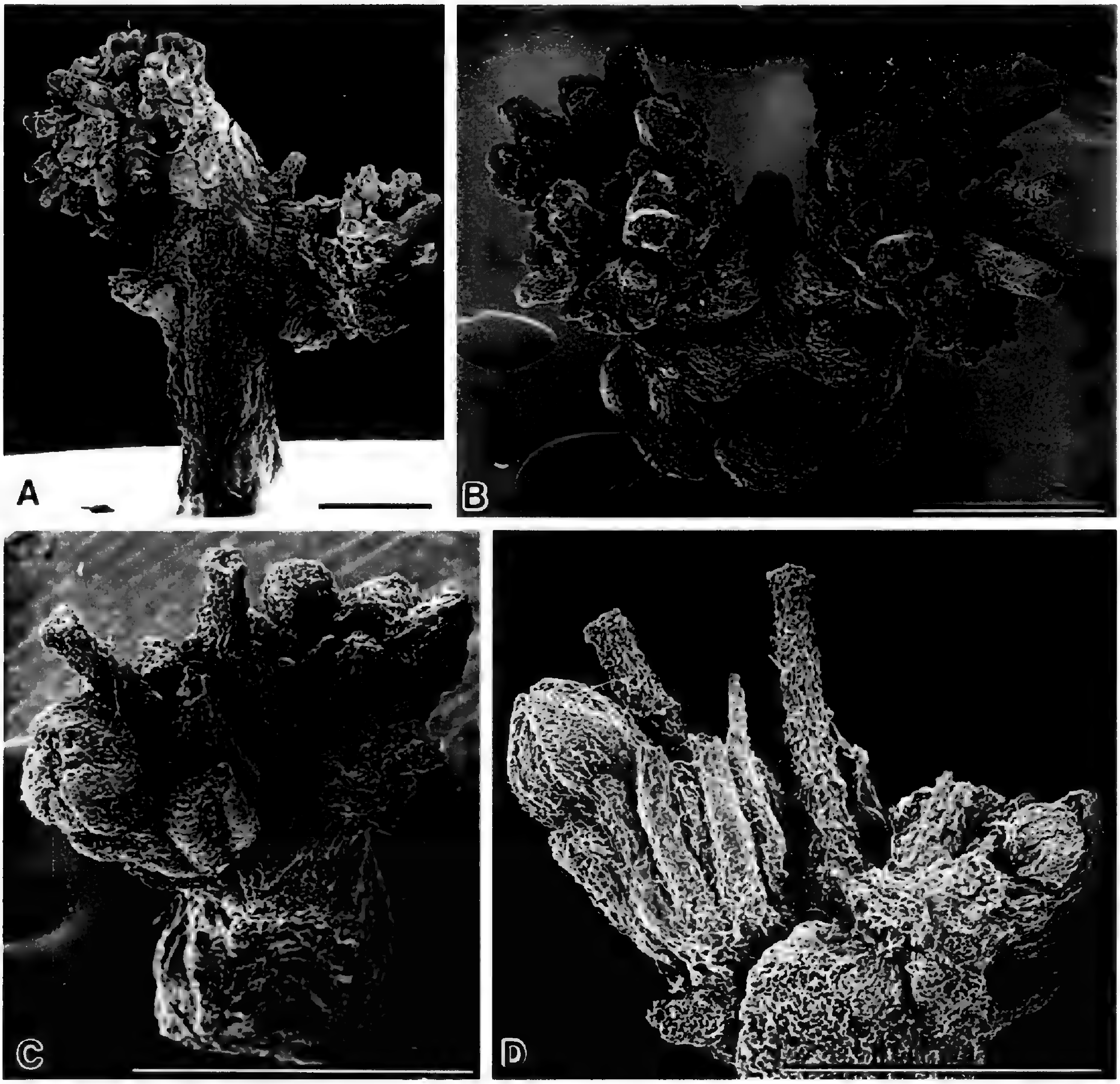

Figure 42. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 45, Inflorescence with trimerous flowers. —A. Lateral view of inflorescence with two clusters of pedicel bases; PP45233. —B. Oblique view of specimen showing cymose organization consisting of a central pedicel base and two lateral inflorescence units; note flowers are broken and only pedicel bases remain; PP45234. —C. Oblique view of inflorescence with lateral flower bud present; PP45235. —D. Lateral view of specimen in C showing flower bud subtended by a digitately divided bract. Scale bars = 1 mm.

nation pinnate, eucamptodromous. Secondary veins gently curved toward the leaf apexes, widely spaced, and diverging from the midrib at intervals of ca. 10 mm. Tertiary veins (intersecondaries) also diverge from the midrib between the major secondaries. Tertiary venation forming an irregular, more or less orthogonal network. Details of quaternary venation not observed.

This leaf type is very rare in the Allon macroflora. In general form this leaf is similar to *Diospyros* aff. *primaeva* described by Berry (1914, pl. 14, figs. 12–13) from the Santonian Middendorf and Eutaw Formations of Georgia, although this systematic determination should be treated with caution. This leaf type is similar to, and potentially conspecific with, taxon 59, leaf type 4 (Fig. 48D).

63. Dicot leaf type 8
Figure 49C.

Leaf elliptical to narrowly elliptical, estimated up to ca. 90 mm long (incomplete), width ca. 24 mm (apex and base unknown). Margin entire. Venation pinnate, eucamptodromous to weakly brochidodromous. Midrib prominent. Secondary veins fine, diverging from the midrib at angles of ca. 30–40°, straight to irregular in their course, branching

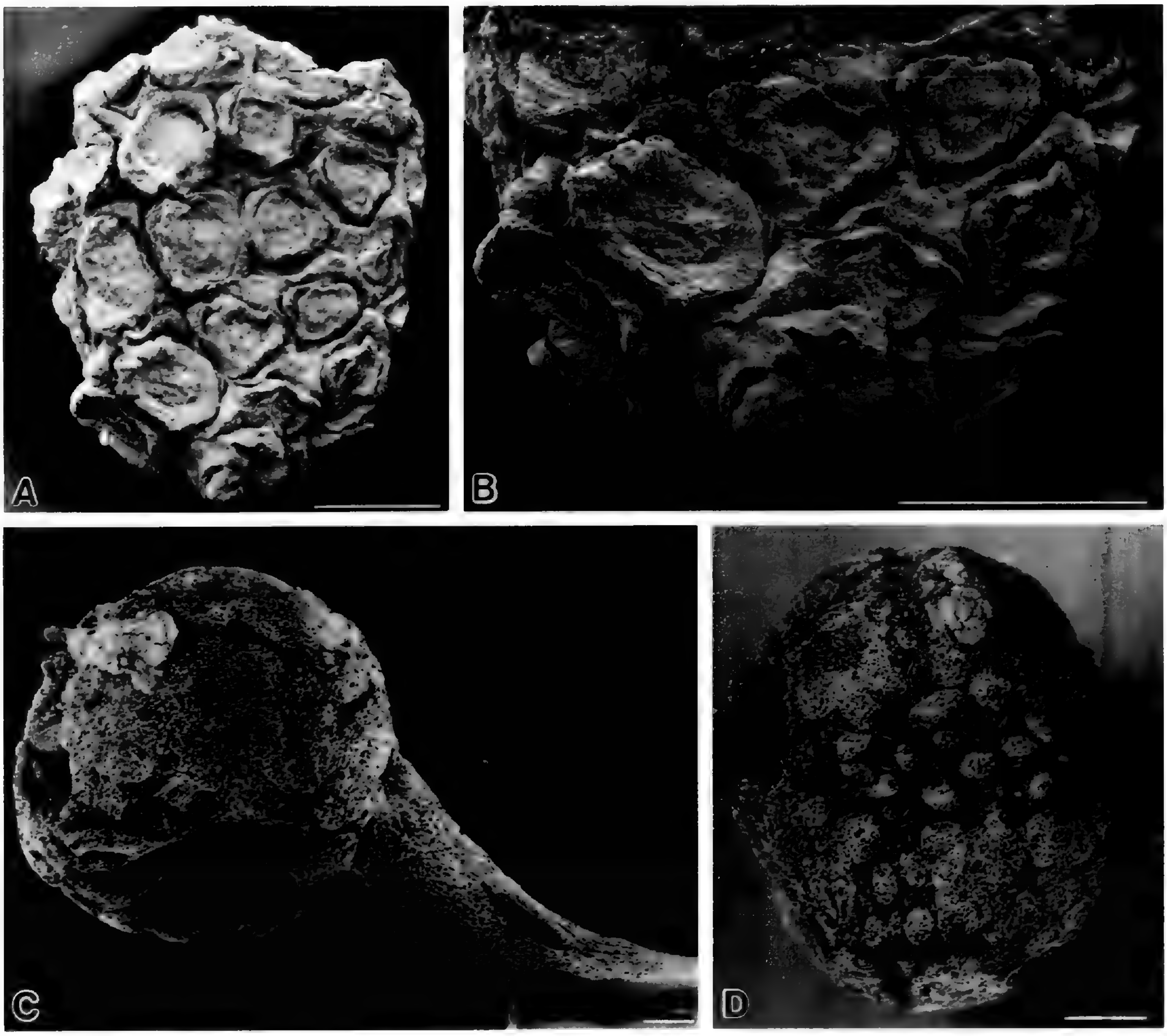

Figure 43. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxa 46 and 47, Miscellaneous reproductive axes. —A. Taxon 46, Strobiloid spicate axis; PP45236. —B. Taxon 46, Detail of specimen in A; note each scar has two flanking flange-like structures. —C. Taxon 47, Spherical capitate reproductive axis; PP45237. —D. Taxon 47, Apical view of head from specimen in C showing numerous presumed pedicel bases. Scale bars = 0.5 mm.

toward the margin to form a more or less irregular, orthogonal, network of tertiary veins, which is also developed between the secondaries. Quaternary and ultimate venation not observed.

This leaf type is very rare in the Allon macroflora, and its systematic affinities are uncertain.

Discussion

The late Santonian Allon flora from central Georgia, U.S.A., is one of many mesofossil assemblages known from the Barremian-Aptian to the Maastrichtian of North America, Europe, central Asia, and Japan (Crane & Herendeen, 1996; Friis & Skarby, 1982; Friis, 1983; Friis et al., 1999; Crepet, 1996; Takahashi, Crane & Ando, unpublished data), but it is the first to be described almost in its entirety. Systematically, the excellent preservation of flowers, fruits, seeds, and other organs provides detailed information for comparison with extant plants. Ecologically, a survey of the entire mesofossil assemblage (Table 1) provides insights into the composition of the living vegetation from which the Allon flora was derived, and a basis for estimating the abundance of the constituent taxa. Some of the taxa are known in detail, and systematic relationships are well resolved (e.g., *Parasaurauia*, Keller et al., 1996; *Allonia*, Magallón-Puebla et al., 1996; *Campylopodium*, Konopka et al., 1998), while others remain poorly characterized and their systematic relationships are unknown. Many of these fossils may never be understood in sufficient detail to justify a separate detailed treat-

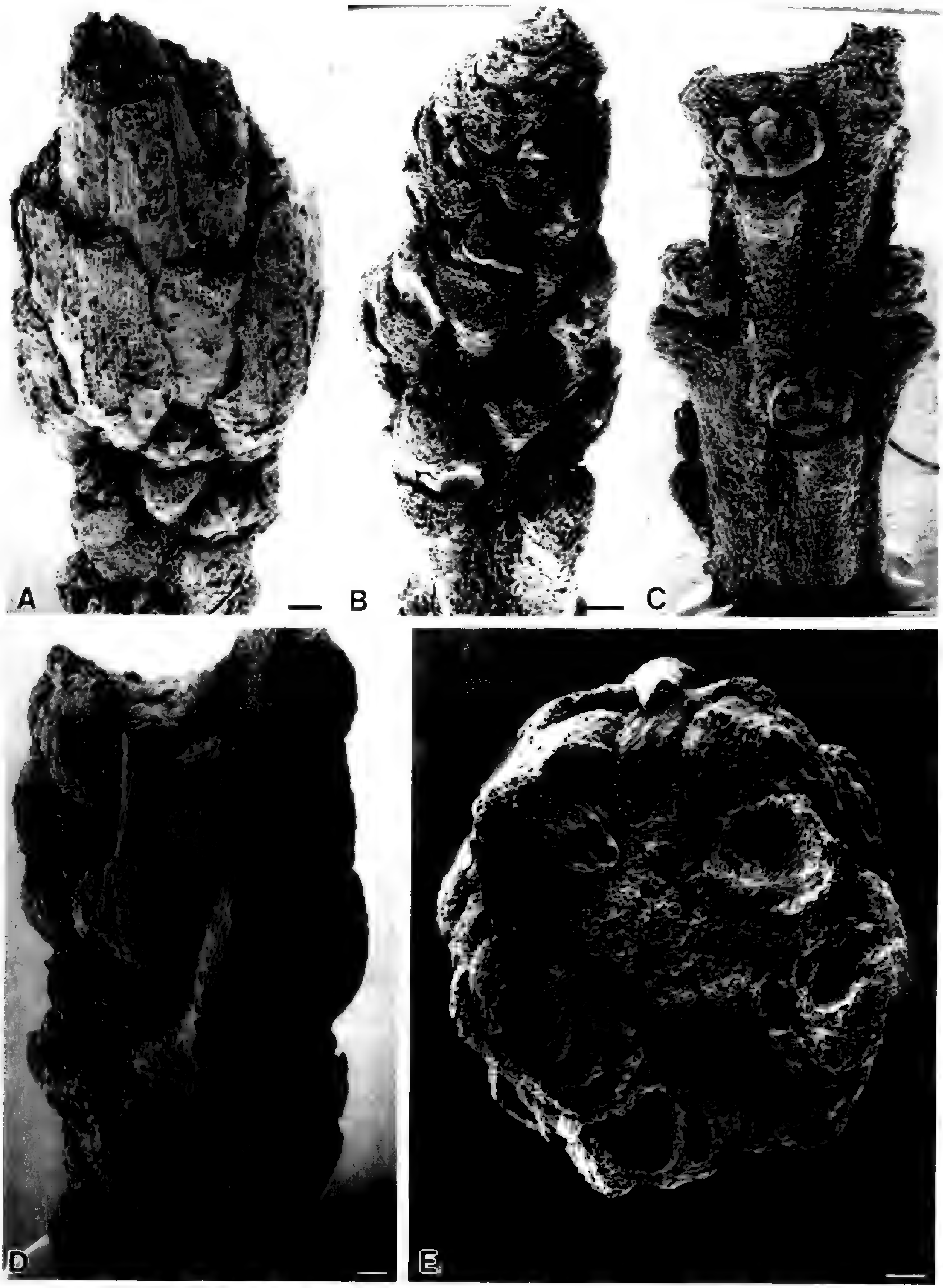

Figure 44. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxa 48 and 49, Miscellaneous axes with attached leaves/bracts. —A. Taxon 48, Axis Type 1, Oblique view of axis with bracts/leaves at apex and scars below; PP45238. —B. Taxon 48, Axis Type 1, Lateral view of axis showing broken bases of bracts/leaves; PP45239. —C. Taxon 48, Axis Type 1, Axis showing leaves/bracts with bulbous structures in their axils; PP45240. —D. Taxon 49, Axis Type 2, Axis bearing bracts/leaves that have an abruptly narrowed apex; PP45241. —E. Taxon 49, Axis Type 2, Apical view of specimen in D. Scale bars = 100 μm.

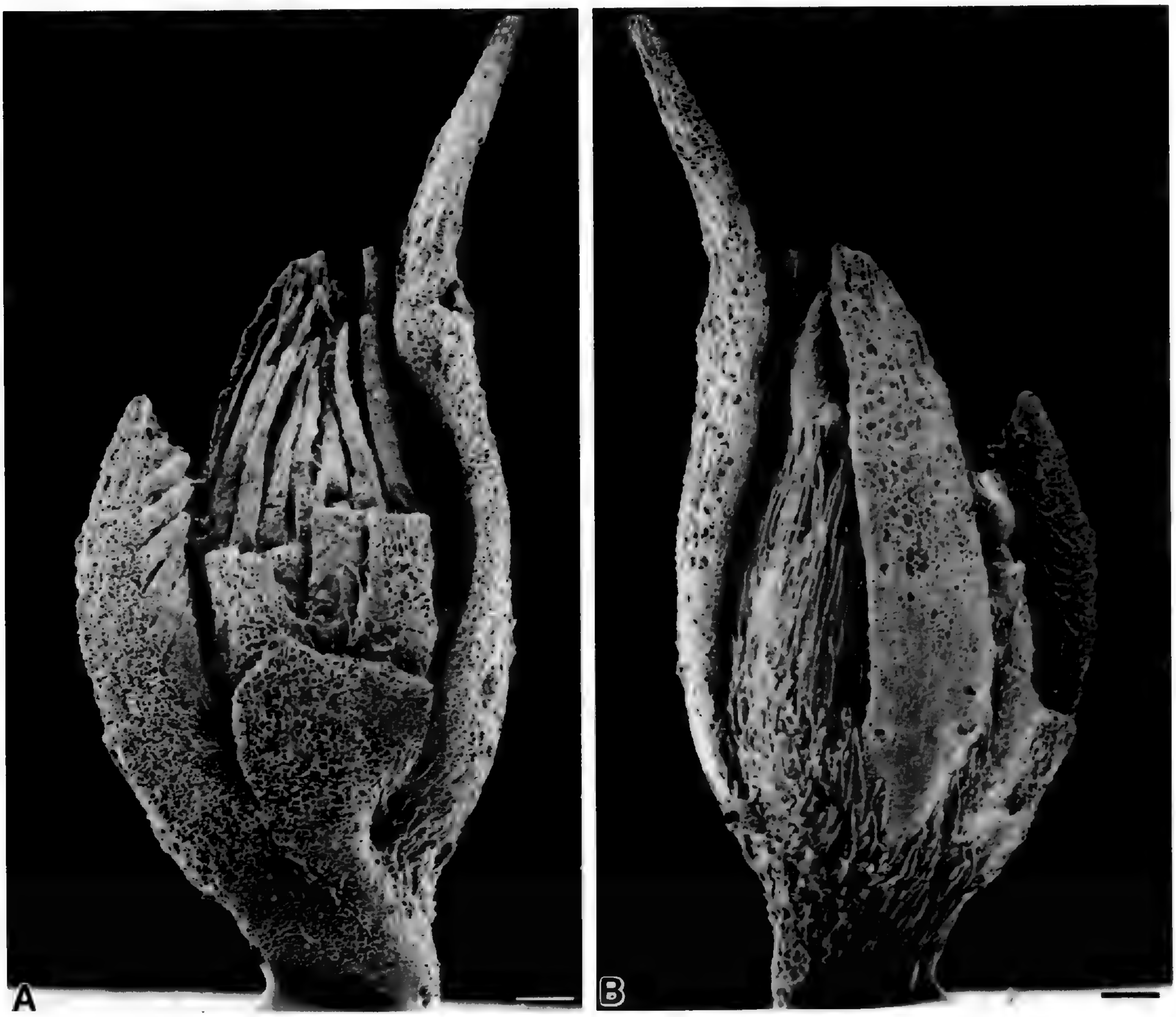

Figure 45. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 50, Axis with pinnate bracts. —A. Lateral view of axis with pinnate bract (left) and entire bract (right); note numerous awl-shaped structures at center; PP45242. —B. Opposite side of axis shown in A. Scale bars = 100 μm.

ment, but they may nevertheless be important for systematic, paleoecological, and biogeographic comparisons with other mesofossil assemblages.

Studies of mesofossil assemblages have greatly expanded our knowledge of Late Cretaceous plants from southeastern North America and until recently, studies of Late Cretaceous fossil plants from this area have focused almost entirely on leaves (Berry, 1914, 1919, 1925) or palynomorphs (e.g., Christopher, 1978; Frederiksen & Christopher, 1978). Mesofossils were first described from the Black Creek Formation, exposed in the "Neuse River Cut-Off" near Goldsboro, North Carolina (Friis, 1988; Friis et al., 1988; Frumin & Friis, 1996), from plant-bearing sediments considered to be of early Campanian age (Owens & Sohl, 1989). Although perhaps slightly older (late Santonian), the Allon assemblage from central Georgia is similar in many respects to that from Neuse River. The Allon assemblage is also approximately contemporaneous with the fossil leaf floras described by Berry (1914) from the Middendorf Arkose Member of the Black Creek Formation in South Carolina (now Middendorf Formation; Gohn, 1992), and the two floras may share several leaf species (Berry, 1914). Some of the Allon macrofossils are also similar to species from the Eutaw Formation (Berry, 1914, 1919), which is of early Santonian age (Huddlestun & Hetrick, 1991), probably slightly older than the Allon assemblage. Well-preserved mesofossil floras from early Coniacian sediments along Upatoi Creek in western Georgia are currently under study (Magallón-Puebla et al., 1997; Herendeen & Crane, unpublished). The Allon assemblage also shares several taxa with the older Turonian-age Crossman flora from New Jersey.

In relation to other fossil assemblages from southeastern North America, the Allon flora is older

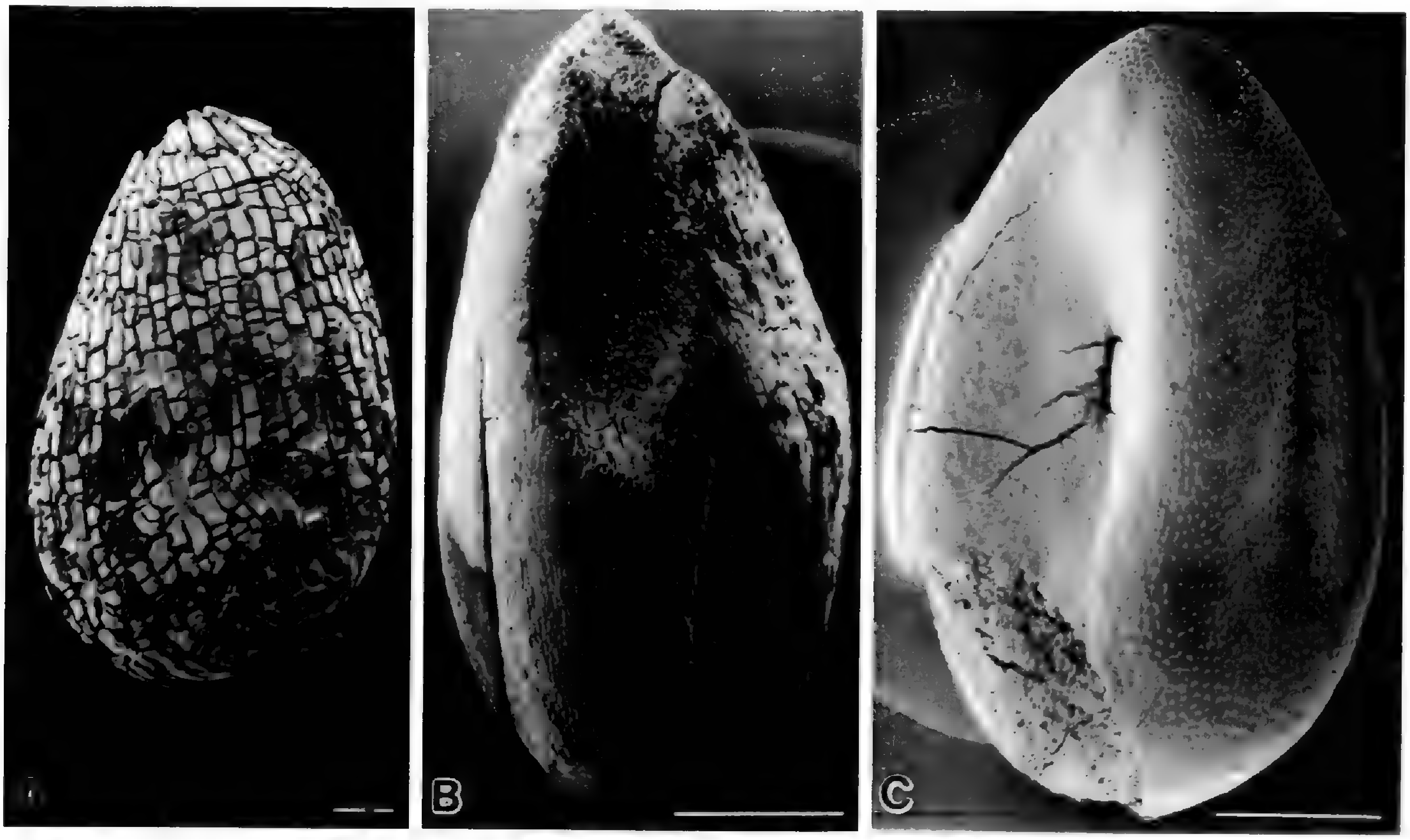

Figure 46. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxa 51, 52, and 53, Miscellaneous seeds. —A. Taxon 51, Miscellaneous seed type 1, small seed with characteristic exfoliating outer cell layer of seed coat; PP44678. —B. Taxon 52, Miscellaneous seed type 2, large seed with oblique fissure lines demarcating two presumed abortive seeds; PP45245. —C. Taxon 53, Miscellaneous seed type 3, large seed with finely pitted surface; PP45246. Scale bars: A = 100 μm; B, C = 0.5 mm.

than the fossil leaf assemblages described from the Ripley Formation (Berry, 1919, 1925), which are of early Maastrichtian age, and younger than the fossil leaf floras described from the Tuscaloosa Formation (Berry, 1919), which are of late Cenomanian age. Interpretations based on these and other leaf floras from southeastern North America, which range in age from late Cenomanian to early Maastrichtian, have suggested that the climate was wet and warm (ca. 25–30°C mean annual temperature) resulting in paratropical closed canopy forest (Upchurch & Wolfe, 1993; Wolfe & Upchurch, 1987; Wolfe, 1997). The mean annual temperature for the Middendorf leaf flora in particular was estimated at 23–25°C. Using the calculation of Wilf (1997) results in a mean annual temperature estimate of 26 ± 4°C.

The Allon flora is typical of Late Cretaceous mesofossil assemblages from the Atlantic Coastal Plain of North America in being dominated, both in terms of diversity of species, and in terms of abundance of specimens, by angiosperm remains. Flowers, fruits, and seeds of angiosperms far outnumber specimens of all other groups of plants combined. Conifers, primarily represented by fragments of leafy shoots, are next in abundance and are sufficiently common that they were almost certainly an important component of the original source vegetation. Sporophytes and gametophytes of mosses are not as frequent as the conifer remains, but they are not uncommon at this site. Ferns are the least abundant of the major plant groups in the Allon mesofossil assemblage. Nonconiferous gymnosperms (*Ginkgo*, cycads, Gnetales), sphenopsids, or lycopods have not yet been recognized. Also, no megaspores have been recovered from Allon.

This pattern in the representation of different major groups of plants contrasts strikingly with that at certain other Late Cretaceous localities from North America. For example, Late Cretaceous floras from distal floodplains on the North Slope of Alaska are dominated by ferns, cycadophytes, ginkgos, and conifers (Spicer, 1987). Similarly, the relatively poor representation of ferns in the Allon flora (both in diversity and abundance) is very different from the vegetation dominated by ferns and monocots in the Maastrichtian Meteetsee Formation of Wyoming (Wing et al., 1993). A primary factor in accounting for these differences may be marked latitudinal differences in climatic conditions.

Among the angiosperms at the Allon site, four taxa comprise more than 75% of specimens recovered. In decreasing abundance they are: ovate fruit (taxon 40), flower with a spindle-shaped inferior

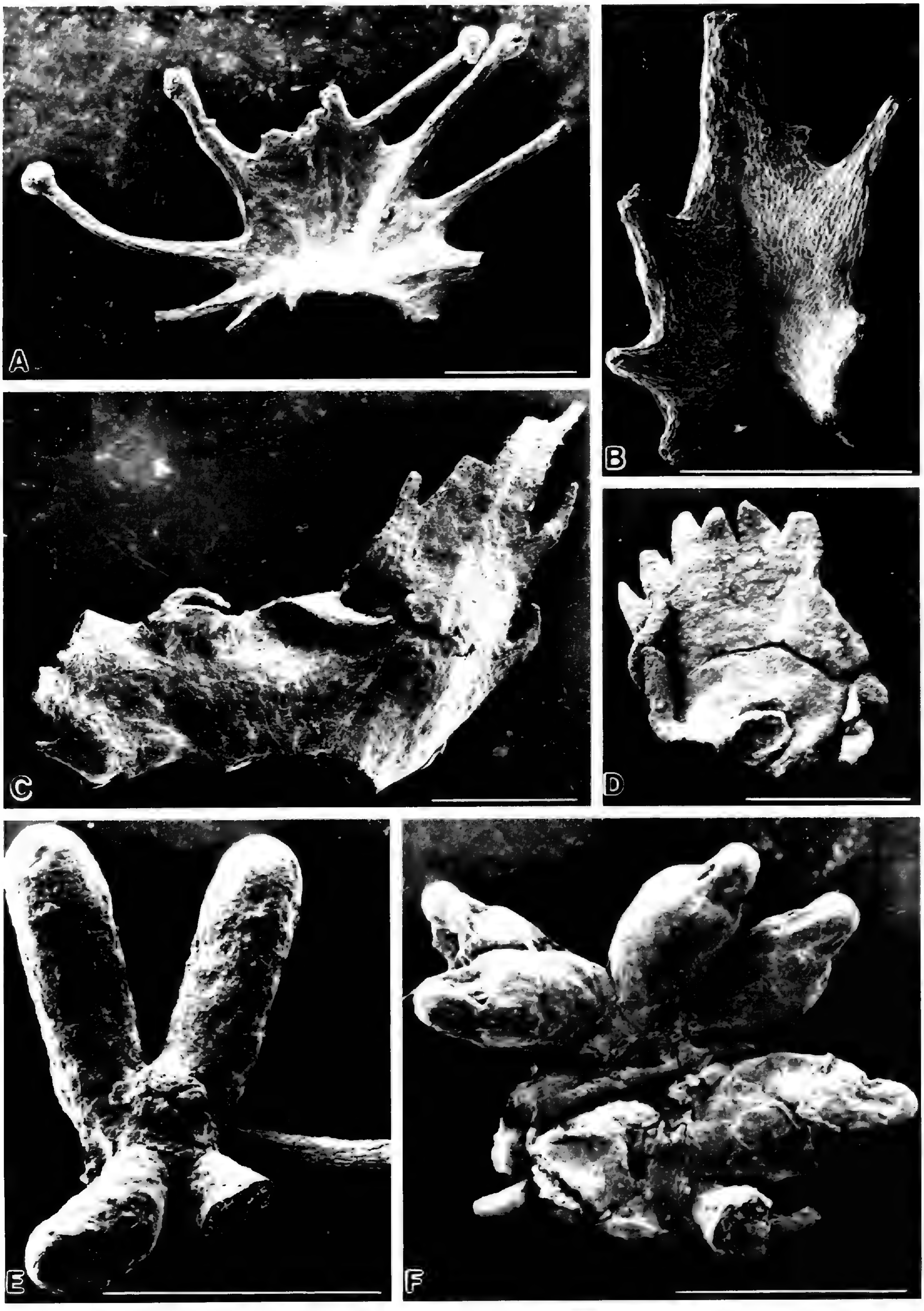

Figure 47. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxa 54 and 55, Miscellaneous bracts and roots. —A. Taxon 54, Bract with stalked glandular structures; PP45247. —B. Taxon 54, Presumed bract with acute pinnate lobes; PP45248. —C. Taxon 54, Asymmetrical bract; PP45249. —D. Taxon 54, Rounded bract with dentate margin; PP45250. —E. Taxon 55, Root with presumed nodules; PP45251. —F. Taxon 55, Root with presumed nodules; PP45252. Scale bars = 1 mm.

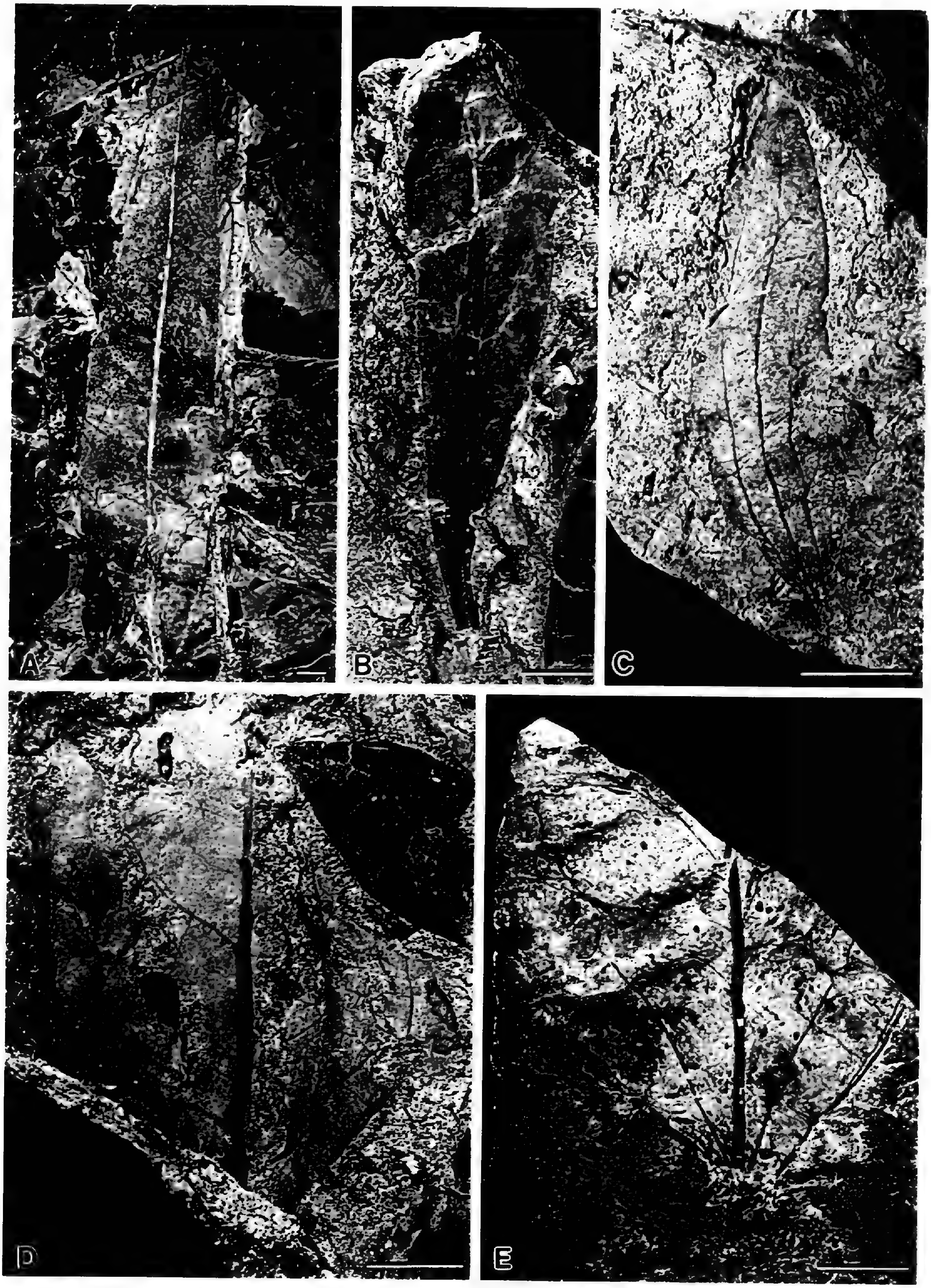

Figure 48. Macrofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxa 56–60. Miscellaneous dicot leaves, light micrographs. —A. Taxon 56. Dicot leaf type 1, macrofossil; PP45381. —B. Taxon 57. Dicot leaf type 2, macrofossil; PP45382. —C. Taxon 58. Dicot leaf type 3, macrofossil; PP45383. —D. Taxon 59. Dicot leaf type 4, macrofossil; PP45384. —E. Taxon 60. Dicot leaf type 5, macrofossil; PP45385. Scale bars = 10 mm.

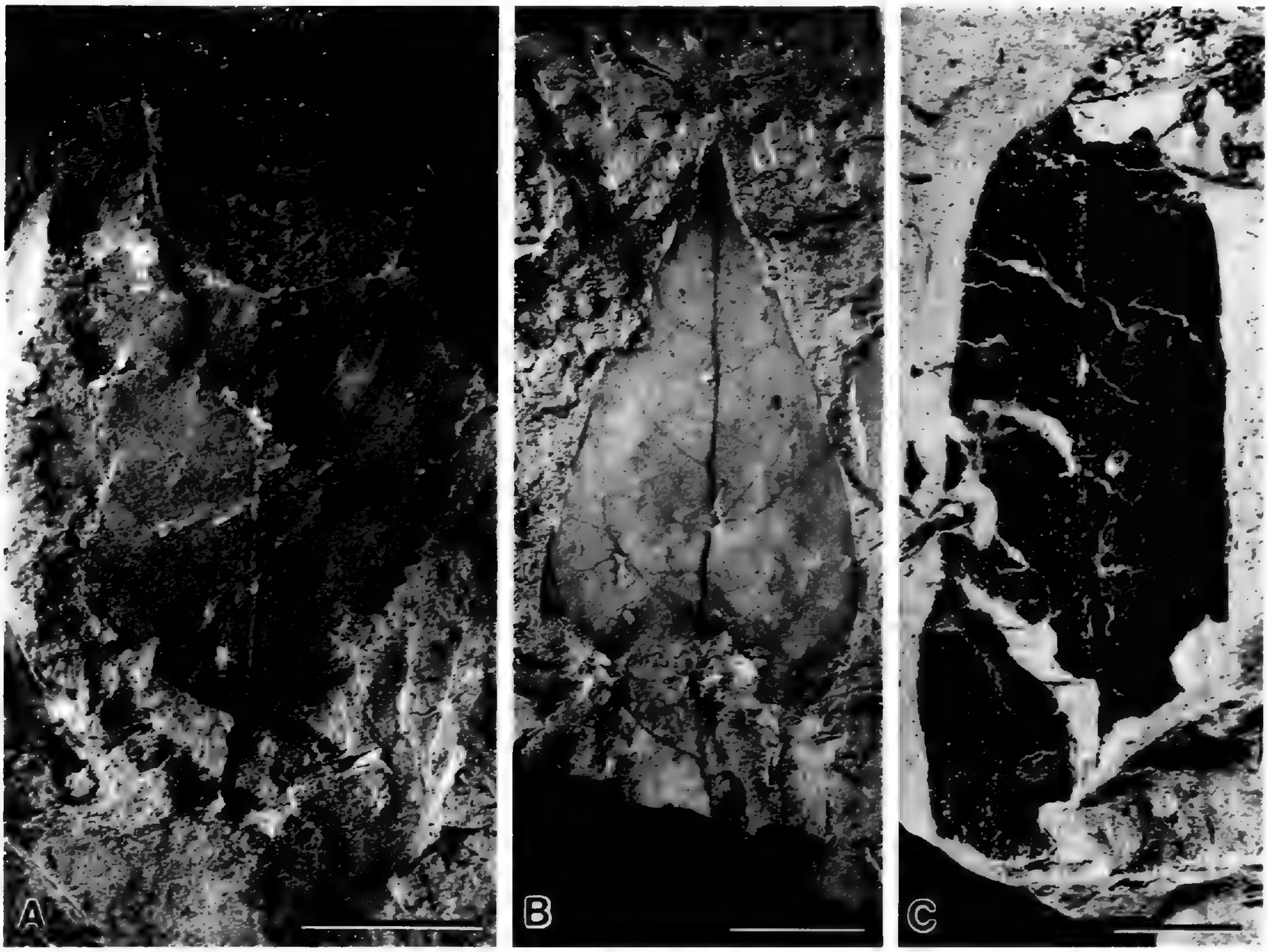

Figure 49. Macrofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxa 61–63, Miscellaneous dicot leaves, light micrographs. —A. Taxon 61, Dicot leaf type 6, macrofossil; PP45386. —B. Taxon 62, Dicot leaf type 7, macrofossil; PP45387. —C. Taxon 63, Dicot leaf type 8, macrofossil; PP45388. Scale bars = 10 mm.

ovary (taxon 31), flower with lobed petals (taxon 32), and *Antiquacupula sulcata* (taxon 21). The abundance of *Antiquacupula* and *Protofagacea* (the sixth most abundant taxon) implies that Fagaceae sensu lato were an important element in the source vegetation. Probable taxodiaceous conifers are the fifth most abundant element in the Allon flora and were probably also common. The relative paucity of ferns, and good representation of mosses, may also indicate a relatively poorly developed understory vegetation. More detailed analyses of the diversity and abundance of different taxa in the Allon flora and other mesofossil assemblages are currently under way (Lupia, work in progress). These studies will compare the composition of the Allon mesofossil assemblage with the palynoflora and macroflora at the same site.

Preliminary results from the Allon locality (Lupia, work in progress) indicate that plants represented in the mesofossil assemblage are often not recognized in the dispersed pollen spore flora. The diversity of plants represented as mesofossils is also much greater than the diversity of plants represented as macrofossils (Table 1). Only 11 types of leaf macrofossils have been recognized at the Allon site, whereas the mesofossil assemblage records between 40 and 50 distinct botanical entities, including some (e.g., the mosses) that would be unlikely to be represented in the macroflora even under the most favorable circumstances. It is also interesting that while only two types of leaf macrofossil are abundant at the site, seven taxa are as abundant in the mesofossil assemblage (Table 1).

Mesofossil assemblages at Allon, as is typical of localities on the Atlantic Coastal Plain of North America, contain a mixture of lignified and charcoalified specimens. Pollen is frequently better preserved in lignified material, whereas charcoalification generally preserves finer anatomical and morphological details. The quality of preservation of the charcoalified material from the Allon flora suggests that it was not transported extensively prior to deposition and is consistent with preservation under quiet, near allochthonous, conditions. Actualistic studies do, however, show that fossil plant structures preserved as charcoal are significantly

Table 1. Composition of the Allon flora from the Late Cretaceous (late Santonian) of central Georgia, based on macrofossils and mesofossils. Unless otherwise indicated, fossils are angiosperms *incertae sedis*. Relative abundance is based on over 11,000 mesofossil specimens counted from 12 samples (Lupia, in prep.). Rank follows Spicer and Hill (1979) but combining the "rare" and "rare or localized" categories; asterisk (*) preceding rank indicates taxa with > 1000 specimens. Mesofossil taxa not appearing in the 12 samples were considered "very rare." Relative abundance for macrofossils is indicated in italics, based on an estimate of the approximately 100 blocks in our collection.

Taxon or structure	Organ	Relative abundance
1. *Eopolytrichum antiquum* Konopka, Herendeen, Smith Merrill & Crane (Polytrichaceae)	sporophyte capsules and gametophytes	rare
2. *Campylopodium allonense* Konopka, Herendeen & Crane (Dicranaceae)	sporophyte capsules and gametophytes	rare
3. cf. *Boodlepteris* Gandolfo, Nixon, Crepet & Ratcliffe (Gleicheniaceae)	pinnules	common
4. Fern leaf type 1	pinnules	common
5. Fern leaf type 2, macrofossil	frond fragment	*very rare*
6. Conifer foliage type 1 (cf. *Brachyphyllum*) macrofossil	shoot with leaves	*very rare*
7. Conifer foliage type 2, macrofossil	shoot with leaves	*very common*
8. Conifer foliage type 3 (cf. Taxodiaceae)	shoots with leaves	abundant
9. Conifer foliage type 4 (cf. *Brachyphyllum*)	shoots with leaves	common
10. Conifer pollen cone and dispersed cone scales	cone and dispersed cone scales	common
11. cf. *Detrusandra* Crepet & Nixon (Magnoliales)	flowers	very rare
12. *Mauldinia* sp. Drinnan, Crane, Friis & Pedersen (Lauraceae)	inflorescence units and flowers	rare
13. Trimerous staminate flower (cf. Triuridaceae)	staminate flowers	very rare
14. Tricarpellate flower (cf. monocots)	flowers	very rare
15. Monocot leaf type 1, macrofossil	leaf	*very rare*
16. Monocot leaf type 2, macrofossil	leaf	*very rare*
17. *Allonia decandra* Magallón-Puebla, Herendeen & Endress (Hamamelidaceae)	flowers and associated seeds	rare
18. Flower with apically connate stamen connectives (cf. Hamamelidaceae)	flower	very rare?
19. Capitate inflorescence (cf. subfamily Altingioideae, Hamamelidaceae)	inflorescences and pistillate flowers	very rare
20. *Protofagacea allonensis* Herendeen, Crane & Drinnan (Fagaceae sensu lato)	staminate inflorescence units and flowers, fruits, and cupules	abundant
21. *Antiquacupula sulcata* Sims, Herendeen & Crane (Fagaceae sensu lato)	staminate and bisexual flowers, fruits, and cupules	*abundant
22. *Caryanthus* sp. Friis (cf. Juglandales/Myricales)	flowers	very rare
23. Normapolles flower type A (cf. Juglandales/Myricales)	flower	very rare
24. *Bedellia pusilla* Sims, Herendeen, Lupia, Christopher & Crane (cf. Betulaceae)	staminate flowers	very rare
25. *Parasaurauia allonensis* Keller, Herendeen & Crane (Actinidiaceae)	flowers	rare
26. Flower with stellate trichomes, type 1 (cf. Ericales)	flowers	rare
27. Flower with stellate trichomes, type 2 (cf. Ericales)	flowers	very rare
28. Fruits with large peltate trichomes (cf. Ericales)	flowers	rare
29. Pentamerous flower with inferior ovary	flowers	very rare
30. Pentamerous flower with semi-inferior ovary	flowers	very rare

Table 1. Continued.

Taxon or structure	Organ	Relative abundance
31. Flower with spindle-shaped inferior ovary	flowers and fruits	*abundant
32. Flower with lobed petals	flowers	*abundant
33. Trimerous flowers with numerous coarse trichomes	flowers	very common
34. Capitate inflorescence of pentamerous flowers	inflorescence and flowers	very rare
35. Flower with pentamerous perianth and trimerous gynoecium	flowers	abundant
36. Flower with pentamerous calyx composed of thick valvate sepals	flowers	rare
37. Slender epigynous flower	flowers	very rare
38. Epigynous flower with spherical ovary	flowers	very rare
39. Flower with very broad perianth parts and coarse fimbriate trichomes	flowers	very common
40. Ovate fruit	fruits	*abundant
41. Bicarpellate superior fruit	fruits	very rare
42. Epigynous flower with rounded sepals	flowers	very rare
43. Pentamerous flowers with bracteoles	flowers	very rare
44. Immature bicarpellate fruit	fruit	very rare
45. Inflorescence with trimerous flowers	inflorescence with flower buds	common
46. Strobiloid spicate axis	axis	very rare
47. Spherical capitate inflorescence	inflorescence	very rare
48. Miscellaneous axes with attached leaves/bracts, type 1	axis	very rare
49. Miscellaneous axes with attached leaves/bracts, type 2	axis	very rare
50. Axis with pinnate bracts	axis	very rare
51. Miscellaneous seed type 1	seed	very rare
52. Miscellaneous seed type 2	seed	rare
53. Miscellaneous seed type 3	seed	very rare
54. Bract	bract	very rare
55. Root with nodules?	roots	very rare
56. Dicot leaf type 1, macrofossil	leaf	*abundant*
57. Dicot leaf type 2, macrofossil	leaf	*abundant*
58. Dicot leaf type 3, macrofossil	leaf	*common*
59. Dicot leaf type 4, macrofossil	leaf	*very rare*
60. Dicot leaf type 5, macrofossil	leaf	*rare*
61. Dicot leaf type 6, macrofossil	leaf	*very rare*
62. Dicot leaf type 7, macrofossil	leaf	*very rare*
63. Dicot leaf type 8, macrofossil	leaf	*very rare*

smaller than they were in life (McGinnes et al., 1976; Scott, 1989; Herendeen, 1991b), and care must be used in comparing the absolute dimensions of fossils preserved in this way (Lupia, 1995). In a study of charcoalification of angiosperm reproductive structures Lupia (1995) documented shrinkage of 14% to 47%, with substantial variation among plant organs studied.

The proportion of mesofossils preserved as charcoal or lignite varies among, and sometimes within, sites. Some localities are dominated by lignified specimens while others consist almost entirely of charcoal, formed as a by-product of natural fires. Interestingly, at Allon, as at other localities on the Atlantic Coastal Plain, the mode of preservation sometimes varies by taxon. Some taxa are represented exclusively, or almost exclusively, by charcoalified specimens, others are represented by both charcoalified and lignified specimens, while others are represented by only lignified material. These differences could represent a variety of factors, such as differences in phenology relative to (?seasonal) fire patterns, or the effects of habitat variation resulting in differences in fire susceptibility, and deserve further investigation including actualistic studies in contemporary plant communities subject to forest fires. At the Allon locality the preservation of some specimens of almost all taxa as charcoal indicates that fire may have been an important factor contributing to frequent disturbance of the source plant community. The extent to which such fires may have been a function of a particular climatic regime, thereby introducing potential large-scale biases into studies of the mesofossil record, remains to be determined.

Previous publications on plants from the Allon locality have presented detailed descriptions and analyses of relationships of specific fossil taxa. In many cases the excellent structural details preserved in these fossils have made it possible to carefully integrate paleontological and neontological data and document the presence of synapomorphies of extant groups of families, subfamilies, or even genera (e.g., Keller et al., 1996; Magallón-Puebla et al., 1996). Such studies have substantially modified previous estimates of the time of differentiation of several groups of extant angiosperms (e.g., Hamamelidaceae: Magallón-Puebla et al., 1996; Fagaceae sensu lato: Herendeen et al., 1995; Sims et al., 1998).

The combined effect of this work, together with information from other mesofossil localities, has been to modify our current understanding of the "modernization" of the angiosperm flora through the Late Cretaceous. Syntheses of data from dispersed fossil pollen (Muller, 1981, 1984) suggest that most extant angiosperm families differentiated during the latest Cretaceous or Early Tertiary, but the rapidly accumulating evidence from mesofossils, with the increased systematic precision provided by information on flowers and fruits, indicates that many extant angiosperm lineages were already differentiated at the level of family, or even genus, by the Turonian-Campanian. Continued study of rich mesofossil assemblages such as Allon, other localities in southeastern North America (Herendeen & Crane, work in progress), the Potomac Group localities in Virginia and Maryland (Crane, Friis & Pedersen, work in progress), the Crossman site in New Jersey (Crepet & Nixon, work in progress), the Åsen flora in southern Sweden (Friis, Pedersen & Schönenberger, work in progress), the numerous localities in Portugal (Friis, Pedersen & Crane, work in progress), and recently discovered mesofossil floras in Asia (Frumin & Friis, work in progress; Takahashi, Crane & Ando, work in progress) is certain to further expand the spectrum of angiosperm lineages that can be recognized.

Mesofossil assemblages such as Allon also offer to provide new and valuable information about ferns (Gandolfo et al., 1997b; Herendeen & Skog, 1998), cheirolepidiaceous conifers (Srinivasan, 1995), and other pteridophyte and gymnosperm taxa (Pedersen et al., 1989, 1993). Especially interesting is the new information on Late Cretaceous fossil mosses (Konopka et al., 1997, 1998), which suggests that careful examination of other mesofossil floras may substantially expand current knowledge of the bryophyte fossil record (e.g., Crandall-Stotler et al., 1996).

CONCLUSIONS

A rapid increase in our knowledge of Cretaceous mesofossil assemblages is contributing to a substantially improved understanding of the composition of Cretaceous vegetation, and providing new and more precise insights into the phylogenetic relationships and evolutionary significance of Cretaceous plants. However, the full wealth of systematic and paleoecological information that can be obtained from these assemblages is only just beginning to be exploited. A very large number of new taxa remain to be described in the mesofossil assemblages that are already known, and many more mesofossil assemblages will be discovered as additional areas are explored and the techniques of bulk sieving are applied more widely.

The mesofossil approach, which so far has been mainly applied to studies of Cretaceous and Tertiary sediments, also holds great promise for studies of other time periods and a broader range of taxonomic groups. For example, exquisitely preserved mesofossils from early Devonian sediments are already providing important new information on early land plants (Edwards, 1997), while the recognition of such floras from late Paleozoic and early Mesozoic could be extremely helpful in studies of a variety of pteridophyte and gymnosperm groups.

The study of mesofossils has already resulted in a much improved knowledge of Cretaceous angiosperms. However, much work remains to be done in terms of describing the full range of taxa present, characterizing the individual plants, and understanding their relationship to their living relatives. The documentation of complete assemblages, such as we have attempted here for the Allon flora, combined with detailed studies of individual fossil plants, has much to contribute to a more refined understanding of early angiosperm evolution and global environmental change in terrestrial environments during the Cretaceous.

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BIOGEOGRAPHICAL RELATIONSHIPS OF NORTH AMERICAN TERTIARY FLORAS[1]

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ABSTRACT

Comparisons of Tertiary floras of North America with those of Europe and Asia document a long history of floristic interchange. The stratigraphic and geographic ranges of selected conifer and angiosperm genera that are easily recognized in the fossil record provide a basis for discerning patterns in the routes and timings of intercontinental dispersals through the Tertiary.

The origin of the extant flora and vegetation of North America has been the subject of much interest and debate ever since the floristic similarities between North America and Asia were first documented. Many of the woody genera comprising North America's present-day forests have excellent fossil records that can be traced through the Tertiary in North America and other continents of the Northern Hemisphere (Wolfe, 1975; Graham, 1993; Tiffney, 1985a, b; Mai, 1995). In addition, many genera that are no longer native to North America have well-documented Tertiary records. Patterns of geographic disjunction among extinct and extant genera provide important clues to the history of North American flora and the former continuity of Tertiary forests in the Northern Hemisphere. By comparing the stratigraphic records of genera shared among two or more continents it is possible to consider the pathways and timing of plant interchange through the Tertiary.

Many ideas have been published on the paleobotanical origins and development of extant flora and vegetation of the Northern Hemisphere (e.g., Engler, 1879; Chaney, 1940, 1947; Wolfe, 1975; Raven & Axelrod, 1974; Latham & Ricklefs, 1993; Mai, 1995; Akhmetiev, 1996). In the attempt to be as comprehensive as possible, investigators have sometimes relied uncritically upon genera reported in the literature. Closer scrutiny reveals many erroneous generic determinations (Dilcher, 1974). The purpose of this review is to highlight Tertiary records of selected conifer and angiosperm genera that may be considered soundly identified and which are significant in understanding the biogeographic affinities of North American Tertiary floras. I present a review of about 90 genera with reliable Tertiary records in North America and other continents. Examination of the stratigraphic ranges of different taxa in North America, Europe, and Asia provides the basis for assessing phytogeographic patterns and pathways of biotic dispersal through the Tertiary. South American and African records are mentioned when known, but the emphasis is on affinities within the Northern Hemisphere. For a review of relationships between North and South America, see Burnham and Graham (1999, this issue).

Because of our familiar vantage point of the present day, neobotanists and paleobotanists alike tend to regard the modern flora as an endpoint showing the "true" floristic patterns of extant genera and species. Thus a genus such as *Ginkgo*, with a wide paleogeographic distribution (Tralau, 1968), may be classified as an "East Asian element." Clearly, such "elements" have more to do with extinctions elsewhere than they do to the natural geographic affinity or origin of the genus (Wolfe, 1975). Fossils can document former geographic distribution patterns of both extinct and extant genera and thus provide a means of tracking the changing floristic relation-

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ships among different landmasses through time. Recent studies have emphasized morphological and molecular phylogenetics as a framework to construct phytogeographic history of disjunct taxa (reviewed by Wen, in press). Biogeographic hypotheses developed from phylogenetic and molecular studies can be tested by observations from the fossil record.

It might be argued that the fossil record is too fragmentary to provide a thorough understanding of phytogeographic history; however, the alternative of using only modern distributions or phylogenetic hypotheses to determine phytogeographic history leads to an even more incomplete picture. If forced to rely only on extant generic distributions, we would be unlikely to predict that *Carya* had its greatest diversification in the Tertiary of Europe (Mai, 1981; Manchester, 1987a) despite its absence from the extant European flora, or that *Ensete* and *Pyrenacantha* (both native to Africa and Asia today) would be present in the early Tertiary of North America (Manchester, 1994b).

In this article, I review the North American Tertiary fossil record of selected conifer and angiosperm genera in comparison with their stratigraphic ranges in other parts of the Northern Hemisphere. These case history studies illustrate a variety of biogeographic patterns that may be analyzed to gain insight into the timing of past intercontinental migrations.

METHODS

It is a well-known problem that paleobotanical literature includes a large number of generic assignments of dubious validity. In North America the problem applies to much of the literature prior to the 1970s and actually persists to the present day. This is because different investigators apply different standards of what is necessary to identify a genus. It may also reflect the need for stratigraphic geologists to obtain quick, tentative names for fossils that may not be well preserved or that may not provide sufficient characters for a more secure determination. In many instances assignment to a particular extant genus is justified by discussing a few similarities between the fossil species and the modern genus, but the criteria that distinguish it from all other possible candidates are not considered. For this reason, it is inadvisable to accept reports from the literature as valid without critical evaluation. Databases and surveys that simply take generic names from the literature must be used with considerable caution.

One of the most thorough and critical reviews of Tertiary genera is that of Kirchheimer (1957), which emphasizes the European fossil record but also reports selected reliable occurrences of genera in North America and Asia. Many of the age assignments in Kirchheimer's catalog have since been revised, but Kirchheimer was careful to give locality information, so that it is possible to determine current age assignments by attention to more recent literature. Helpful, but less comprehensively documented, reviews of taxa reported in the paleobotanical literature are provided by Taylor (1990), Collinson et al. (1993), and Mai (1995). Useful guides to Asian literature on Cenozoic Paleobotany include Tanai (1992a, 1994) and Liu et al. (1996). Published critical reviews of the fossil record of particular phylogenetic groups, for example, that of the magnoliid angiosperms (Friis et al., 1997), and individual families (e.g., Betulaceae, Crane, 1989) or genera (e.g., *Nyssa*, Eyde, 1997) are also very useful.

The decision whether to accept generic records for this summary was based on whether the organ(s) and morphological/anatomical features preserved and described can be considered truly diagnostic of the genus indicated. As in the taxonomy of modern plants, it is often difficult to make reliable generic determinations of fossil material based upon sterile specimens. Rare paleobotanical specimens showing fruits and/or flowers attached to twigs with foliage have revealed "mosaic" plants, in which the leaves closely resemble those of a modern genus, while the fruits or flowers reveal novel characters that indicate they belong to an extinct genus (Manchester, 1989a; Manchester et al., 1998). In the usual case, when interconnected vegetative and reproductive parts are unavailable, studies of fertile material, particularly flowers and fruits, provide the best systematic resolution.

Reports based on fossil foliage are also important, particularly since leaves are more commonly preserved than fruits in many depositional environments, but they require careful scrutiny to determine the likelihood of correct generic determinations. Leaves in some families are so distinctive as to be reliable in diagnosing a genus, as in Platanaceae and Berberidaceae. More commonly there are instances of convergence and parallelism in foliage that cause me to be less confident of generic assignments. In the Betulaceae, Juglandaceae, and Menispermaceae, for example, identification of the family using leaf morphology is relatively easy, but secure generic determinations require fruits. In these families the leaves may provide a good "best estimate" of genera that are present, but identifications should be viewed with caution if corroborating fruit records are lacking.

I emphasize megafossil reports of fruits, flowers, and leaves, because I am more confident with the evaluation of these organs. Wood and pollen also provide biogeographically important records, but often with coarser systematic resolution. In the case of pollen the decreased systematic resolution is balanced by the relatively high stratigraphic resolution (wind-dispersed pollen may be found throughout a sedimentary sequence, whereas megafossils are confined to specific facies). For critical systematic review of the voluminous literature on fossil pollen, refer to Muller (1981).

In addition, before accepting records for inclusion in this summary, it was necessary that they be fully documented in the literature with convincing photographs or that I had the opportunity to observe the specimens in museum collections. For access to study critical specimens, I am indebted to curators of the following collections: University of California, Berkeley (specimen numbers cited have the prefix UCMP); University of Idaho, Moscow; Denver Museum of Natural History; Peabody Museum of Natural History, Yale University (YPM); United States National Museum, Washington, D.C. (USNM); Burke Museum of Natural History and Culture, Seattle (UWBM); Department of Biological Sciences, University of Alberta; Natural History Museum, London (BM-V); National Museum, Prague; Senckenberg Museum of Natural History, Frankfurt (SM); Botanical Department, Hungarian Natural History Museum, Budapest; Geological Institute and Geological Museum, Moscow; Komarov Botanical Institute, St. Petersburg; National Science Museum, Tokyo; Nanjing Institute of Geology and Paleontology, Academia Sinica, Nanjing; Institute of Botany, Academia Sinica, Beijing. Specimens cited with the prefix UF are from the Florida Museum of Natural History, Gainesville. Extant comparative material was studied at herbaria including A, FLAS, MO, and PE.

The authorities for extant genera mentioned in the paper may be found in Mabberley (1997). The authors of fossil genera not presented by Mabberley are specified at their first mention in the text.

Stratigraphic charts presented in this paper are simplistic in that they condense diverse records from different parts of each northern continent into a single column. However, this enables a quick visual summary that provides some constraints on the timing of intercontinental exchange events for each taxon. More details for each genus are provided in the family narratives of the following section, leading to the more informative literature for the genera considered. Another weakness of this overview is that the southern continents are not included in the stratigraphic charts. The Tertiary record for South America and Africa is still poorly known relative to that for the northern continents, and evidence for direct exchange of plant species between North and South America during the early to late Tertiary remains weak. For more detailed accounts of relationships inferred between the fossil record of North America and the living genera of Africa and South America, see Raven and Axelrod (1974), Taylor (1990), and Burnham and Graham (1999).

The million-year chronology of Tertiary epochs follows Berggren et al. (1995). The Brandon Lignite flora of Vermont is significant as one of the few informative Tertiary megafossil floras in the northeastern United States. Unfortunately, there are no associated datable rocks or animal fossils to provide an independent means of determining the age. Although for many years considered likely to be Oligocene, the current consensus is that it may be early Miocene (Tiffney, 1994a; Traverse, 1994). I adopt this age for the discussions involving Brandon fossils. There are also problems with the precise age of many floras in eastern Asia. I have usually accepted the assignments given by the most recent authors, but in some cases there continue to be disagreements among different investigators and it may be expected that the ages of many sites will continue to be revised in the future.

I have attempted to be conservative in the positioning of stratigraphic ranges. Thus the ranges presented here are often shorter (begin later) than those indicated by other authors, e.g., Mai (1995). For example, it is possible to find reports of *Engelhardia* based on pollen from the Paleocene. However, the fruits diagnostic of this tribe do not occur until the Eocene, and *Engelhardia*-like pollen (usually called *Momipites* Wodehouse) is known to have been produced by other genera of Juglandaceae in the Tertiary (Manchester, 1989b). Likewise, there are reports of *Alnus* from the Cretaceous, but without convincing infructescences. Because the scope of this treatment is limited to genera known from the Tertiary and/or Recent flora of North America, I have omitted some interesting examples of taxa shared only between Europe and Asia, many of which are reviewed by Mai (1995).

CASE HISTORIES

The following section highlights records that I consider useful in evaluating the biogeographic affinities of North American Tertiary floras. These paragraphs cite the references upon which the stratigraphic ranges plotted in the summary chart (Fig. 19) and in Figures 21–25 are based. This section is arranged alphabetically by families under the headings Gymnosperms and Angiosperms, with angiosperms of uncertain affinities treated last, under the heading Incertae Sedis. Common patterns are reviewed in the subsequent section.

GYMNOSPERMS

Cupressaceae. Distinctive leaves of the extinct *Fokieniopsis* McIver & Basinger and associated cones occur in the Paleocene of Wyoming, Saskatchewan, Alberta (McIver & Basinger, 1990; McIver, 1992) and in the Paleocene of Altai, Xinjing, China (Guo et al., 1984, as *Ditaxocladus* Guo), indicating a transberingial distribution.

Tetraclinis, with one species living in the western Mediterranean today, has a good Tertiary record in Europe (Kvaček, 1989; Mai, 1995). In addition, one species is known from the early Oligocene to Miocene of western North America based upon cones, seeds, and foliage (Meyer & Manchester, 1997). As it has not been observed in the east Asian Tertiary, it appears likely that this genus traversed the North Atlantic in the late Eocene.

Ginkgoaceae. The record of *Ginkgo* in the Northern Hemisphere extends back to the Jurassic, but its record in the Tertiary is of biogeographic interest, documenting the relatively late confinement to Asia. The Tertiary records in North America extend from the Paleocene of the Rocky Mountains (Brown, 1962) to the Miocene of Oregon (Chaney, 1920). A worldwide review of the distribution of this genus through space and time was presented by Tralau (1968).

Pinaceae. Various genera of the Pinaceae are well represented in the Cretaceous and Tertiary of the Northern Hemisphere, including, for example, *Abies* (Schorn & Wehr, 1986), *Keteleeria* (Meyer & Manchester, 1997), *Larix* (LePage & Basinger, 1991; Schorn, 1994), *Picea* (Crabtree, 1983), *Pinus* (Miller & Malinky, 1986), and *Pseudolarix* (LePage & Basinger, 1995). Most of these genera are widespread in the Northern Hemisphere today, but *Keteleeria* and *Pseudolarix* are limited to eastern Asia in their modern distribution. LePage and Basinger (1991) provided a comprehensive analysis of the phytogeographic history of *Pseudolarix* in the Northern Hemisphere based on its distinctive seeds, cones, and foliage, with earliest records in the Cretaceous of Asia and North America followed by Oligocene establishment in Europe. They concluded that the genus became extinct in North America by the middle to late early Miocene, and in Europe after the Pliocene. *Keteleeria*, found today only in the broad-leaved evergreen forests of China and Taiwan, is known based on distinctive seeds from the Eocene of the Quilchena flora of British Columbia (R. Mathewes, unpublished data), and Oligocene of Oregon (Meyer & Manchester, 1997).

Taxaceae. *Amentotaxus*, with four extant species in China and southeast Asia, has an excellent fossil record in North America and Europe. It is readily recognized by its broad needle-like leaves with a pair of prominent stomatal bands and distinctive epidermal anatomy (Ferguson et al., 1978). *Amentotaxus* extends from the Upper Cretaceous (Santonian) to Miocene of North America and from the Paleocene to Upper Miocene of Europe (Ferguson et al., 1978; Jähnichen, 1990). Other genera of the Taxaceae, including *Taxus* and *Torreya*, and at least one extinct genus, are well represented in the Tertiary of western North America (Manchester, 1994b; Meyer & Manchester, 1997) and central Europe (Kvaček, 1982), but their history is best explored through attention to Mesozoic floras.

Taxodiaceae. This family includes several genera with relictual extant distribution. *Metasequoia* has become famous as an example of a genus once widespread in the Northern Hemisphere that is now native only to China. I do not see the need to review this again here as there are already many accounts (most recently in Meyer & Manchester, 1997).

Cunninghamia grows today in mixed mesophytic and broad-leaved evergreen forests of China and Taiwan. Its fossil record includes cones, seeds, and foliage from the Eocene to Miocene of western North America (reviewed in Meyer & Manchester, 1997), the Tertiary of Europe (Mai, 1995), and the Eocene to Miocene of Japan (Matsuo, 1967; Horiuchi, 1996).

Glyptostrobus is native today only in southeastern China, but, like *Metasequoia* and *Cunninghamia*, was widespread in the Tertiary. It extends from the Paleocene (Boulter & Kvaček, 1989) to the Pliocene in Europe (Mai, 1995; Martinetto, 1998). *Glyptostrobus europaeus* twigs with attached cones occur in the Eocene to Pliocene of Japan (Tanai, 1961; Matsumoto et al., 1997b). In North America, *Glyptostrobus* is well represented in the Paleocene to Eocene of the Rocky Mountain region (Brown, 1962; Hoffman, 1996), and in the Miocene of Idaho, Oregon, and Washington (Brown, 1936; Chaney & Axelrod, 1959; Fields, 1996).

Sequoia and *Taxodium*, although restricted in their modern distribution to Pacific Coastal North America and eastern North America, respectively, were widespread in the Northern Hemisphere in the

Tertiary. Cones of *Sequoia* occur as late as the Pliocene in Italy (Martinetto, 1994).

ANGIOSPERMS

Actinidiaceae. *Actinidia* is distributed in Indomalesia and eastern Asia today, but was present in North America and Europe during the Tertiary. In North America, it is known based on seeds from the Eocene Clarno Formation of Oregon (Manchester, 1994b). In Europe, fossil seeds occur from the Eocene to the Pliocene (Tralau, 1963; Friis, 1985; Martinetto, 1998).

Anacardiaceae. *Pentoperculum* Manchester is an extinct genus of fruits belonging to the Spondieae shared between the middle Eocene of Oregon (Manchester, 1994b) and the lower Eocene of England (Reid & Chandler, 1933, as *Dracontomelon*). The calyces called *Astronium truncatum* by MacGinitie (1953) from the Eocene and Oligocene of the western United States are very different in venation and fruit morphology from the extant genus and are no longer believed to represent Anacardiaceae (Manchester & Wang, 1998). The leaves that MacGinitie placed in the same species may in fact represent Anacardiaceae, but they are at least as similar to *Rhus* as they are to *Astronium*. *Rhus* is known from anatomically preserved fruits from the Eocene of Oregon (Manchester, 1994b).

Apocynaceae. Elongate seeds with a terminal streamer-like tuft of hairs two to four times the length of the seed body are found in many extant genera of Apocynaceae, e.g., *Anodendron, Cleghornia, Echites, Forsteronia, Holarrhena, Kibatalia, Odontadenia, Pottsia, Prestonia, Strophanthus*, and *Wrightia*. Apocynaceous seeds can be recognized with ease, but the distinction of genera based only on seed characters is a difficult challenge. Thus, the fossil generic name *Echitonium* Unger 1850 (= *Cypselites* Heer = *Apocynospermum* Reid & Chandler, 1926) is applied to fossil remains. In the North American Tertiary, such seeds occur in the middle Eocene Green River Formation (*Apocynospermum coloradensis* Brown in MacGinitie, 1969: pl. 18, fig. 4), the Clarno shales of Oregon (Manchester, unpublished), and the late Eocene of Florissant, Colorado (Manchester, unpublished). They are not known in North America after the Eocene, but in Europe they extend from the Middle Eocene (Messel, Germany: Senckenberg Collection-ME 7624), the Late Eocene of England (Reid & Chandler, 1926), Early Oligocene of Budapest-Obuda, Hungary (Botanical Department, Hungarian Natural History Museum Collection, BP 63.1039), and the České středohoří Mountains (Kvaček & Walther, 1995: pl. 9, fig. 2) to the Middle Miocene of Switzerland.

Araliaceae. *Toricellia* of western and eastern Asia, sometimes placed in its own family, was considered by some taxonomists to be allied to the Cornaceae, but recent molecular work indicates a position within the Araliaceae (Plunkett et al., 1996). *Toricellia* has distinctive fruits (Fig. 1A, B) with three locules: a single-seeded central locule with a terminal germination valve and two enlarged, bladder-like lateral chambers that are infertile. The endocarp tissue is composed of isodiametric sclereids. These same characters occur in Eocene fruits (Fig. 1D, G) that I had previously described as the fossil genus *Tripartisemen* Manchester (1994b). Therefore, I now offer the new combination, *Toricellia bonesii* (Manchester) Manchester comb. nov. (see Appendix 1). *Toricellia bonesii* occurs in the middle Eocene of the Clarno Formation, Oregon (Fig. 1C–F), Roslyn Formation, Washington (Fig. 1G), and Messel, Germany (Collinson, 1988: pl. 1, fig. 11). Fruits are also present in the lower Miocene Oberdorf locality of Austria (Meller, 1996, and pers. comm. 1998). These occurrences indicate that *Toricellia* was shared between Europe and North America during the Eocene, although it is still unknown from the Asian Tertiary. The timing of its arrival in Asia, where it occurs today, remains a mystery.

Bignoniaceae. *Catalpa* lives today in eastern Asia, eastern North America, and the Caribbean region. Small biwinged seeds of *Catalpa* have been recognized from the Early Oligocene of Oregon (Meyer & Manchester, 1997). Similarly small *Catalpa* seeds (*Catalpa microsperma* Saporta) occur in the late Oligocene of France and Germany (Saporta, 1889; Weyland, 1937), suggesting a possible North Atlantic linkage during or prior to the Oligocene.

Berberidaceae. *Mahonia* is distributed in Asia, Malesia, and North and Central America today. Although sometimes subsumed within *Berberis* (Whittemore, 1997), *Mahonia* is easily distinguished by its compound foliage. This genus is readily recognized by the distinctive architecture of its imparipinnately compound leaves and spiny leaflets, without the need for associated flowers or fruits, and thus is a good candidate for recognition in the fossil record. *Mahonia* is well represented in western North American Tertiary floras, extending from the Eocene to Pleistocene (Schorn, 1966). Although not native in Europe today, it occurs in the Oligocene of France (Saporta, 1865) and North Bohemia (Bůžek et al., 1990), in the Neogene of Hungary (Andreánszky, 1959), and in the late Miocene of Abkhasia (see Takhtajan, 1974). *Mahonia bil-*

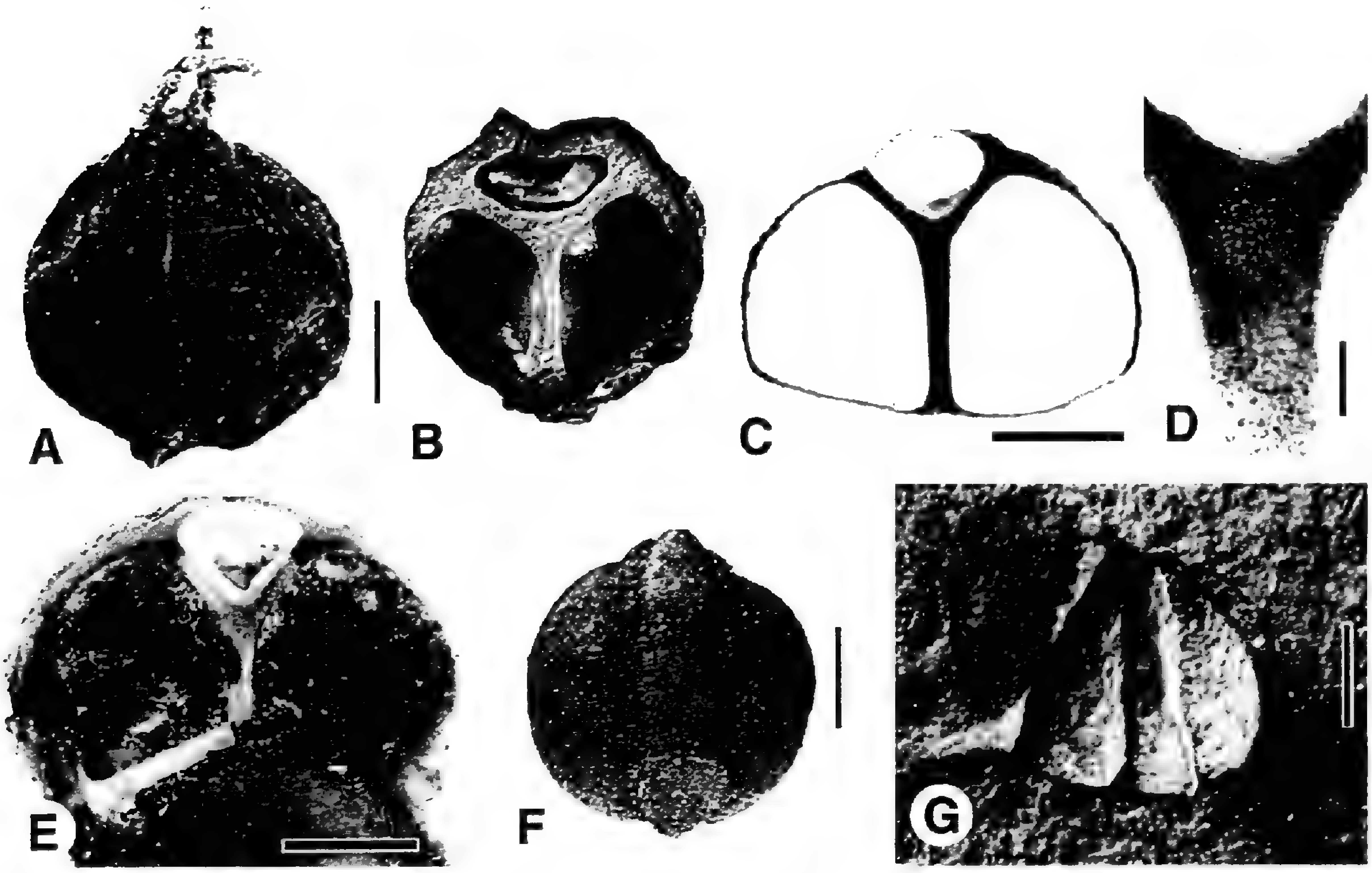


Figure 1. Extant and fossil *Toricellia* (Araliaceae) fruits from Asia and North America. —A. Fruit of *Toricellia tiliaefolia*, Yunnan, China, MO 52556: *A Henri 11907*. —B. Transverse section of the same fruit, showing three chambers: two large and empty, one smaller and containing a seed. C–F. *Toricellia bonesii* (Manchester) comb. nov. from the Eocene Clarno Nut Beds, Oregon. —C. Transverse section showing small central chamber and large laterals, UF 9578. —D. Detail of the septum of specimen in C, enlarged to show isodiametric sclereids. —E. Transversely sectioned specimen showing a small chamber containing a seed, and two larger lateral chambers filled with sediment, UF 9577. —F. Dorsal surface of a silicified fruit with the pericarp partially stripped away showing two symmetrically placed lateral chambers, and the median chamber with a small facet corresponding to the germination valve, holotype, UF 9288. —G. Sedimentary cast of *Toricellia bonesii* from the Eocene of Ronald, Washington, showing the small fertile chamber and larger lateral chambers, UWBM 95238-B4738. Scale bars = 1 mm in A–C, E–G, 0.1 mm in D.

inica (Unger) Kvaček & Bůžek from early Miocene of Bilina, western Czech Republic, is similar to *M. simplex* Arnold from the Oligocene of western North America (Kvaček & Bůžek, 1994).

Although most diverse in Asia today, *Mahonia* is poorly represented in the Asian fossil record. Tanai and Suzuki (1963) described *Mahonia lanceofolia* from the Miocene of southwestern Hokkaido, but the single known leaflet lacks spinose teeth and its affinity to *Mahonia* may be questioned. Based on the available fossil record, it appears that *Mahonia* spread from North America to Europe in the early Tertiary and to Asia in the late Tertiary. Its arrival in Asia may have been either from Europe or North America.

Betulaceae. The birch family has an excellent fossil record in the Northern Hemisphere (Crane, 1989). *Alnus*, which is distributed today around the Northern Hemisphere and south into the Andes, is confirmed on the basis of infructescences and associated leaves in the early Eocene in Wyoming and in the middle Eocene of Oregon (Crane, 1989). It continues to be a common element of subsequent Tertiary flora in North America. In Asia, *Alnus* is confirmed from infructescences by the Middle Eocene (Ube coal field in southwestern Honshu; Huzioka & Takahashi, 1970), and from strata in Kamchatka that Budantsev (1997) considers to be late Paleocene. In Europe, it is first recorded from the Eocene Bournemouth Beds of England (Chandler, 1963).

Betula, which is widespread in the Northern Hemisphere today, has commonly been reported in the fossil record on the basis of leaves, but because of overlap in venation patterns between *Betula* and other genera of the Betulaceae, such reports remain speculative unless accompanied by the diagnostic trilobed infructescence bracts. In North America the earliest *Betula* documented by such bracts is *B. leopoldae* Wolfe & Wehr from the middle Eocene of One Mile Creek, British Columbia (Crane & Stockey, 1987). Subsequently, another species with broader bracts, *B. angustifolia* Newberry, is documented in the Bridge Creek flora of Oregon (Meyer

& Manchester, 1997). In Asia *Betula* is already confirmed by bracts in the Paleocene of the Takhobe flora in Sikhote-Alin (Akhmetiev, pers. comm. 1997). In Europe, the earliest example confirmed by bracts is in the early Oligocene of Markvartice, Czech Republic (Bůžek et al., 1978).

Carpinus occurs in North Temperate areas today, and is easily identified by the enlarged asymmetrical leaflike bract attached to the ribbed nutlet. The genus is common in the Tertiary of Asia beginning in the late Eocene (Tanai, 1972; Uemura & Tanai, 1993). In Europe the genus is confirmed by two kinds of bracts from the Middle Eocene Eckfeld flora (Wilde & Frankenhäuser, 1998) and continues as a common element in Oligocene and later floras (Berger, 1953; Roiron & Vernet, 1978; Mai, 1995). It is much more rare in the North American Tertiary. Possibly the oldest record is an undescribed species from the middle Eocene of Republic, Washington (Wehr, 1995: pl. 3, fig. 3). It conforms to *Carpinus* in the size and morphology of the nutlet, and the venation, asymmetry, and serration of the bract, but the bract differs from modern species in the obovate, rather than ovate, outline. Curiously, *Carpinus* appears to be lacking from the subsequent Tertiary record of North America. Its presence in the forests of eastern North America today indicates either that the genus persisted on this continent after the Eocene without leaving a record, or that the Eocene populations perished, followed by a later Tertiary or Quaternary recolonization from Europe or Asia. Leaves formerly referred to *Carpinus* from the late Eocene and Oligocene of western North America are now placed in *Paracarpinus*, and are considered the probable candidate for the foliage of the extinct fruit *Asterocarpinus* (Manchester & Crane, 1987; Crane, 1989; Meyer & Manchester, 1997).

Corylus, which occurs in North America, Europe, and Asia today, is first confirmed on the basis of nuts with multilobed, both foliar and spiny bracts in the Middle Eocene of Republic, Washington (Wehr, 1995). *Corylus*-like leaves are known from many Paleocene and Eocene sites around the Northern Hemisphere, but it is virtually impossible to determine whether they are the leaves of *Corylus*, or *Palaeocarpinus*. Hence, they are best placed in the fossil leaf genus *Corylites* Gardner (Boulter & Kvaček, 1989; Kvaček et al., 1994; Manchester & Chen, 1996). Silicified nuts of *Coryloides* Manchester from the Eocene of Oregon resemble *Corylus* in morphology and anatomy, but differ from modern species by being perfectly spherical (Manchester, 1994b).

Cranea Manchester & Chen (1998) is an extinct betulaceous genus common in the Paleocene of Wyoming with elongate, cone-like infructescences bearing small wingless nuts. As this genus has not been recovered from regions outside North America, it may have been endemic to North America.

Ostrya, which occurs in North Temperate areas today, is readily recognized by the persistent bladderlike involucre which surrounds the nutlet. It is first observed in the early Oligocene of central Europe (Engelhardt, 1885: 320; Kvaček & Walther, 1998, pl. 12, figs. 6, 7) and western North America (Meyer & Manchester, 1997) and in the Miocene of China (WGCPC, 1978) and Japan (Tanai, 1972). Although absent from northwestern North America today, the genus occurred as late as the middle Miocene in Oregon and Idaho (Chaney & Axelrod, 1959; Fields, 1996). In Asia, *Ostrya* fruits occur in the fossil record by the middle Miocene (Huzioka, 1963; WGCPC, 1978; Tanai, 1961).

Palaeocarpinus Crane is an extinct genus of fruit with bract characters similar to *Corylus* and nutlet characters similar to *Carpinus*. It was circumboreal during the Paleocene, with occurrences in England (Crane, 1981), France (Crane, 1989), China (Manchester & Guo, 1996), and North America (Crane et al., 1990; Sun & Stockey, 1992; Manchester & Chen, 1996). *Palaeocarpinus* persisted into the Eocene in western North America (Republic flora; Wehr, 1995: pl. 3, fig. 4) and eastern Asia (Buoy flora, Sikhote Alin; Akhmetiev & Manchester, in progress).

Caprifoliaceae. *Diplodipelta* from the Eocene to Miocene of the western United States is an extinct genus of fruits related to extant *Dipelta* of Asia (Manchester & Donoghue, 1995). Both genera have elongate fruits with persistent epigynous sepals, but the dispersal units differ. Dispersal units of *Dipelta* consist of a single fruit subtended by three wings developed from the inflorescence bracts. *Diplodipelta* dispersal units also have three bract-derived wings, but the involucre subtends a pair of fruits rather than just one. The occurrence of *Dipelta* based upon fruits in the late Eocene of England (Reid & Chandler, 1926) indicates that the genus was not always confined to Asia and apparently crossed directly between Europe and Asia. In addition, the morphologic similarity between *Diplodipelta* and *Dipelta* suggests early Tertiary geographic continuity.

Cercidiphyllaceae. Cercidiphyllaceae are represented by one living genus with two species native to eastern Asia. The family has an excellent fossil record, with leaves and fruits extending back to the late Cretaceous. Cretaceous and early Tertiary leaves are usually placed in the fossil genus *Troch-*

odendroides Berry (Crane, 1984). Fruits of *Nyssidium* Heer (syn. *Trochodendrocarpus* Kryshtofovich), commonly found in the same localities as *Trochodendroides* leaves, are pod-like follicles similar to those of *Cercidiphyllum,* but they are obliquely striated, and are borne in elongate racemes rather than clusters (Crane, 1984). *Nyssidium* is common in the late Cretaceous, Paleocene, and Eocene of North America, the late Cretaceous to Paleocene of Asia, and the Paleocene to Eocene of Europe, Greenland, and Spitsbergen. The southernmost occurrence in North America is from Hope, Arkansas (UF loc. UF 18607).

At one locality in the Paleocene of Alberta, Canada, *Nyssidium* fruits, *Trochodendroides* leaves, and associated seeds and seedlings were placed together as a single species in a separate genus, *Joffrea* Crane & Stockey (1985a). Elsewhere, the more conservative practice of providing separate names to the fruits and leaves continues.

Detailed multiple organ investigations on *Nyssidium*-related plants from Paleocene localities in Canada, England, and Far Eastern Russia reveal that these plants were diverse in phyllotaxy, shoot growth, and inflorescence position (Crane & Stockey, 1985b). *Joffrea speirsii* from Alberta had opposite phyllotaxy (possibly also alternate) on long and short shoots with inflorescences in the leaf axils of monopodial short shoots. *Nyssidium arcticum* from the Paleocene of England had long shoots with whorled, or pseudowhorled, leaves and terminal inflorescences. The plant referred to as *Trochodendrocarpus arcticus* (Krassilov, 1976; Crane & Stockey, 1985b) has alternate phyllotaxy and bears inflorescences in the leaf axils of long shoots. Although it is clear that infructescences and fruits corresponding to *Nyssidium* were widespread in the Northern Hemisphere, more work is needed to determine the geographic ranges of the different species. For example, it remains uncertain whether plants with the *Joffrea speirsii* type of growth architecture occurred outside North America.

Cercidiphyllum, native today in China and Japan, is first recognized on the basis of clustered fruits and associated leaves like those of the extant species in the lower Oligocene both in Oregon and central Europe (Meyer & Manchester, 1997). In North America it continues through the Middle Miocene of Idaho (Smiley & Rember, 1985). In Europe, *Cercidiphyllum* fruits and leaves are known from the Early Oligocene to Pliocene (Jähnichen et al., 1980; Kovar-Eder et al., 1998). Staminate flowers found with the fruits and leaves in the Miocene of Bohemia differ from extant species by the development of a perianth (Kvaček & Konzalová, 1996). In the Asian Tertiary, the genus is confirmed by clustered fruits and associated foliage in the Miocene of Zaliv Korfa, eastern Kamchatka (Chelebaeva, 1978).

Cornaceae. The Cornaceae sensu lato (including Nyssaceae, Mastixioideae; Alangiaceae) have an excellent fossil record in the Northern Hemisphere that includes both extant and extinct genera.

Alangium is distributed today from China to eastern Australia and in tropical Africa. *Alangium* leaves are strikingly convergent in shape and the primary, secondary, and tertiary venation to the leaves of some genera in the Malvales, and there are many cases of mistaken identity in the literature. However, the endocarps are very diagnostic. *Alangium* has unequivocal fossil fruit remains in the Tertiary of North America, Europe, and Asia (Eyde et al., 1969). In North America species are known from the Eocene of Oregon (Manchester, 1994b) and Miocene of Vermont (Eyde et al., 1969). In Europe, it ranges from the Eocene of England (Chandler, 1961) and Germany (Mai, 1970) to the Pliocene in Alsace, France (Geissert & Gregor, 1981). In Asia, fruits are known from the Pliocene and Pleistocene of Japan (Miki, 1956; Miki & Kokawa, 1962; Eyde et al., 1969). The fossil fruits all correspond to section *Marlea,* which occurs in eastern Asia and Indonesia today (Eyde et al., 1969).

Infructescences and fruits of the extinct genus *Amersinia* Manchester, Crane & Golovneva (1999), related to the extant Chinese endemics *Davidia* and *Camptotheca,* occur in association with leaves formerly called "*Viburnum*" *cupanioides* both in North America and Asia. The infructescences are heads of tricarpellate fruits with four or five prominent bract scars on the peduncle below the head. Permineralized fruits have been sectioned to show trilocular endocarps composed of fibers, lacking an axial bundle, and having single-seeded locules with apical-dorsal germination valves. These fruits, and the associated foliage, *Beringiaphyllum* Manchester, Crane & Golovneva (1999), occur together at eight localities in the Rocky Mountains of the U.S. and Canada, in northeastern China, and in southern Primorye, Koryak Highland, and western Kamchatka, Russia. The apparent absence of *Amersinia* from the Tertiary of Europe, Greenland, and Spitzbergen suggests that the genus dispersed across Beringia but did not populate the North Atlantic or Turgai region.

Cornus occurs in North Temperate regions, and extends into South America and Africa today. The genus is known in the Paleocene of North America both from leaves (e.g., *Cornus hyperborea* Heer, in Hickey, 1977: 144, pl. 47, fig. 1) and fruits (Crane et al., 1990: fig. 31G–I) in the Paleocene of North Dakota. Leaves are readily identified to the genus (sensu lato) because of the smoothly curving acrodromous secondaries, thin, widely spaced, percurrent tertiary veins, and entire margin, but discrimination of subgenera or sections requires reproductive material. Paleocene *Cornus* fruits from North Dakota, and those described from the Early Eocene of England (Reid & Chandler, 1933, as *Dunstanea*) are anatomically preserved, showing resin cavities in the wall that indicate affinities with the Cornelian Cherry group of dogwoods. Thus, the Cornelian Cherry group seems to have traversed the North Atlantic during the early Tertiary. Evidence of the big-bracted dogwoods is provided by the fruit of *Cornus clarnensis* from the Eocene of Oregon, which resembles extant *C. florida* (Manchester, 1994b).

Nyssa, with a disjunct distribution in eastern Asia, eastern North America, and Central America, has an excellent fossil record in the Northern Hemisphere (Eyde, 1997). *Nyssa* fruits have woody stones composed of fibers and have one to three locules with apical-dorsal germination valves. Transverse sections of permineralized specimens reveal that the endocarps are composed of tortuous fibers, lack an axial bundle, and possess apical dorsal germination valves—a syndrome diagnostic of *Nyssa*. The genus is well represented in the Eocene and later Tertiary of North America (Manchester, 1994b) and Europe (Mai, 1995). In Asia, it extends from the Oligocene to Recent (Eyde, 1997).

Mastixia, which occurs in Asia today, is well known for its excellent representation by fruits in the European Tertiary, extending from the Eocene (Reid & Chandler, 1933) to the Miocene (Kirchheimer, 1957; Mai, 1993). *Mastixia* endocarps are anatomically similar to *Nyssa*, but the endocarps have more pronounced dorsal infolds, resulting in locules that are u-shaped in cross section, and the germination valves extend the entire length of the endocarp, rather than being confined to the apical end. *Mastixia* also occurs in the Eocene of Oregon and California (Manchester, 1994b; Tiffney & Haggard, 1996). In addition to *Mastixia* itself, there is a complex of closely related extinct genera of mastixioids in the Tertiary of Europe (Kirchheimer, 1936, 1957; Mai, 1993) distinguished by differences in size, surface sculpture and presence or absence of gum/resin cavities, with some members extending back to the late Cretaceous (Maastrichtian; Knobloch & Mai, 1986). The living mastixioid genus *Diplopanax* is a native of Asia today, but has fossil occurrences in North America (Stockey et al., 1998) and Europe (Eyde & Xiang, 1990). The taxonomic levels to be accorded different taxa within the mastixioids are still not agreed upon. Murrell (1993) recommended that *Diplopanax* be treated as a section within *Mastixia*. If this proposal were to be accepted, then most of the taxa now treated as extinct mastixioid genera (Mai, 1993) would need to be subsumed within the extant genus *Mastixia*. Whichever approach might be taken in the future, it is clear that the fruit morphological diversity of this complex was much greater in the Tertiary than it is today.

Langtonia is one of the most distinctive of the extinct mastixioids. These bilocular ellipsoid fruits conform to the Mastixioideae by having an endocarp composed of tortuous fibers, single-seeded locules, and elongate germination valves. The fruit differs from other modern and fossil mastixioids by the occurrence of paired dorsal infolds in each locule, giving a W-shaped cross section of the locule and seed in contrast to the usual U- or V-shape. This genus was first described based on specimens from the Early Eocene of England (Reid & Chandler, 1933) and was subsequently recognized in the middle Eocene of Oregon (Manchester, 1994b) and Paleocene of Wyoming (Tiffney & Haggard, 1996).

Elaeocarpaceae. *Sloanea* occurs today in tropical and subtropical America, Asia, and Australia. Fruits of four to five spiny valves corresponding to those of extant *Sloanea* occur in the Paleocene of North America, where they have gone under the name *Carpolithes spinosus* (Fig. 2A–C; Newberry, 1898: 138, pl. 68, figs. 2, 3), and in the Paleocene of Greenland (Fig. 2D, E; "*Castanea ungeri*" in Heer, 1869: 470, pl. 45, fig. 2). These remains occur at numerous sites in the Paleocene and into the Eocene of the Rocky Mountain region. *Sloaneaecarpum* is a genus based on a similar spiny valve from the lower Oligocene of Hungary (Rásky, 1962).

Eucommiaceae. *Eucommia*, native only to central China today, has distinctive samaroid fruits (Fig. 3A). Such fruits have an excellent record in the Eocene of the western and southeastern United States (Fig. 3B; Call & Dilcher, 1997), and extending into the Oligocene or Miocene of southern Mexico (Fig. 3C; Magallón-Puebla & Cevallos-Ferriz, 1994a). The generic determination of these fruits is unquestionable because of the unique morphology and venation, and the presence of latex strands observable in the fossils that correspond in position to the laticifers of extant fruits (Szafer, 1954; Tralau, 1963; Call & Dilcher, 1997). In Asia, *Eucommia* is well documented by fruits in the Eocene of Yubari, Hokkaido, Japan (Huzioka, 1961), the lower Oligocene of Kiin Kerish, Kazakhstan (Akhme-

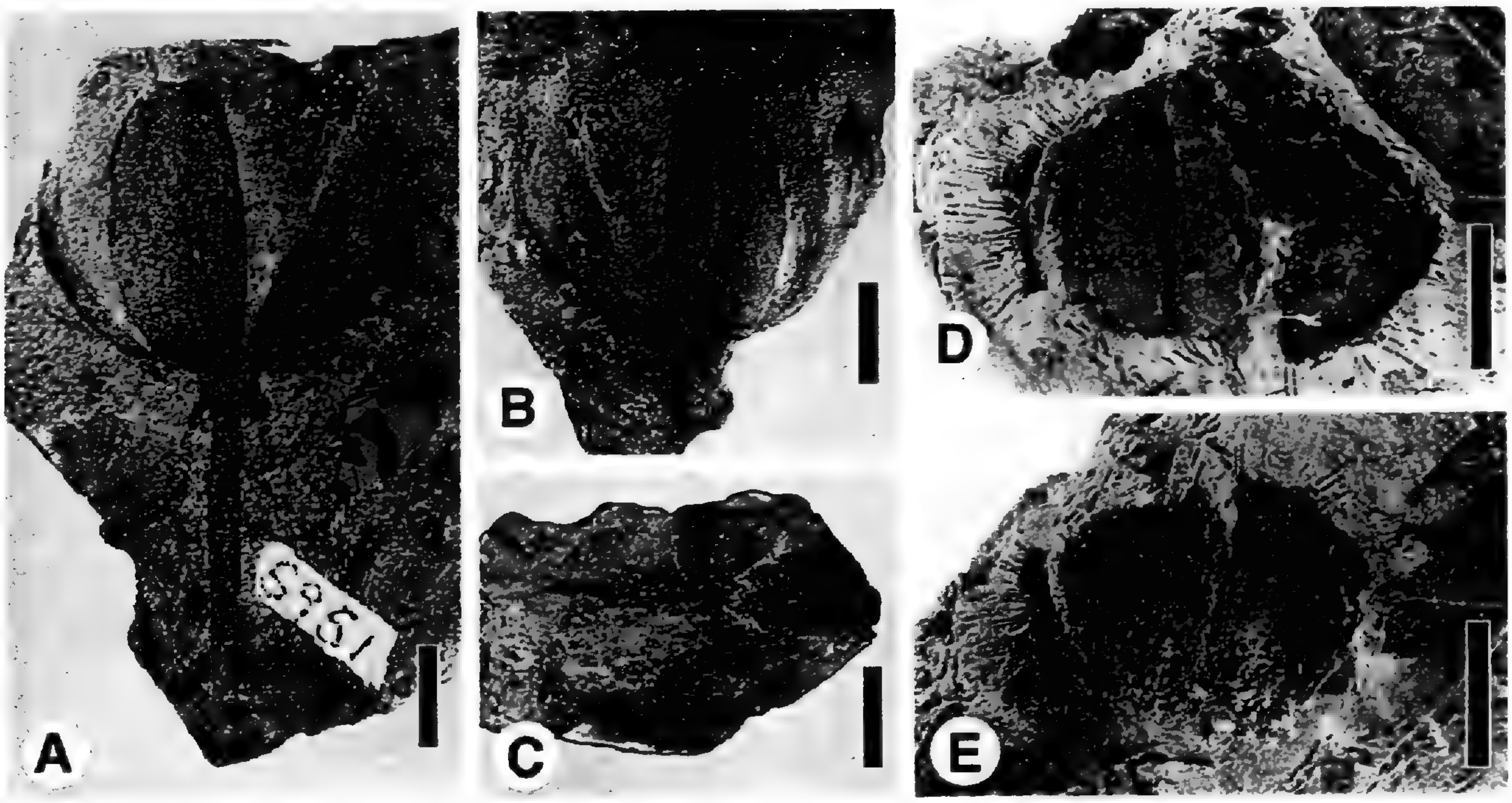


Figure 2. Fruits of *Sloanea* (Elaeocarpaceae) from the Paleocene of North America and Greenland. A–C. *Carpolithus spinosus* Newberry, 1898, USNM 6960, 6961, North Fork of Purgatoire River. —A. Lateral view showing the opened fruit valves, hypogynous perianth scar, and stout peduncle. Note the needle-like spines preserved on the external surface of the valve on the right. —B. Counterpart internal cast, showing the impressions left by internal keels on the fruit valves. —C. Apical view of the same, showing three locules; two more can be inferred from the symmetry and are observed in other specimens. —D, E. Specimen illustrated as *Castanea ungeri* Heer from Paleocene of Atanekerdluk, Greenland, by Heer (1869; Philos. Trans., p. 470, pl. 45, fig. 2), Natural History Museum, London, V/11326. Scale bars = 1 cm.

tiev, 1991), and the Miocene Kraskino flora of Khasan Basin, south Primorye, Russia (Ablaev et al., 1993). The numerous fruit records in Europe extend from the Oligocene to the Pleistocene (Tralau, 1963; Mai, 1995). The North American fruits are about half as large as fruits of the extant species and are slightly more asymmetrical in the placement of stigma at the fruit apex (Call & Dilcher,

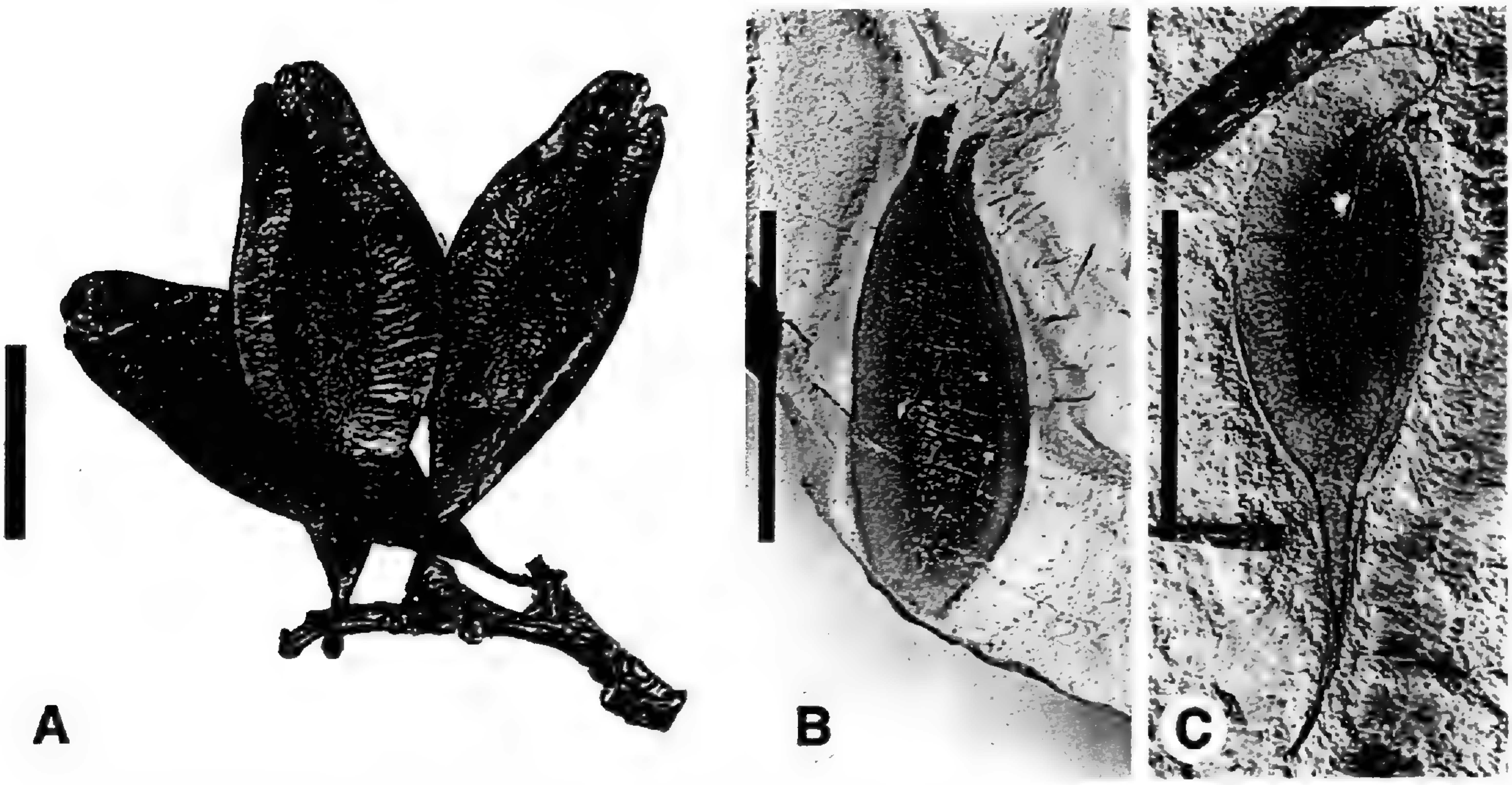


Figure 3. *Eucommia* (Eucommiaceae) fruits from Asia and North America. —A. Extant *Eucommia ulmoides*, Hupeh, China, A: *P. C. Silvestri 7378.* —B. *Eucommia eocenica* (Berry) Brown from the Bovay Clay Pit, Mississippi, UF 15737–8218. —C. *Eucommia constans* Magallón-Puebla & Cevallos-Ferriz from the Oligocene or Miocene Pie de Vaca Formation, Puebla, Mexico. IGM-PB 2573–632. Scale bars = 1 cm.

1997). The Japanese Eocene species is intermediate in size between the North American fossils and the living species, but it resembles the American fossils in the asymmetry of stigma position.

Fagaceae. Fagaceous flowers are now known to date back to the Santonian stage of the Late Cretaceous in North America (Herendeen et al., 1995; Sims et al., 1998), but the focus here is on Tertiary occurrences.

Castanea, which occurs in North Temperate areas today, has often been reported in literature on Tertiary leaves, but many of these reports are questionable. *Castanea* leaves lack a fimbrial vein, which is present on the leaves of otherwise similar-leaved species of *Quercus.* According to this criterion, many, if not all, of the *Castanea* leaves reported from western North America may represent *Quercus.* No *Castanea* cupules are known from western North America prior to the Miocene (Chaney, 1920). *Castanea* is present, however, in the Eocene of Tennessee based on spiny cupules and associated leaves and staminate inflorescences (Crepet & Daghlian, 1980). This assemblage of organs was given different fossil generic names due to the differences in systematic resolution afforded by isolated organs.

Castanopsis, which occurs today in tropical and warm temperate eastern Asia, occurs in the Eocene Clarno Nut Beds of Oregon based upon fruits with identical anatomy of cupule and nut to that of extant *Castanopsis piriformis* of Vietnam (Manchester, 1994b). Younger records have not been discovered. In Europe, the genus has also been recognized by fruits (Kirchheimer, 1957), but they are most similar to those of different extant species, and are morphologically distinct from the Clarno fossil. No fruit records are known to me from Asia, although the genus grows there today.

Fagopsiphyllum groenlandicum (Heer) Manchester comb. nov. (see Appendix 1 for generic diagnosis) is a taxon based on leaves of possible fagaceous affinities from the Paleocene of North America, Greenland, Scotland, and with similar species in the Eocene of Far East Russia and Japan. The leaves have simple, triangular to rounded teeth, pinnate, craspedodromous secondaries, and percurrent tertiaries. These leaves have commonly been placed in *Fagopsis* Hollick, a genus with very similar foliage (Wolfe, 1977; Boulter & Kvaček, 1989; Tanai, 1995). However, *Fagopsis* was diagnosed on the basis of twigs with attached leaves and infructescences (Hollick, 1909; Manchester & Crane, 1983) from the late Eocene of Colorado with fruits that are unlike any found in association with the Paleocene leaves. Despite a careful search for the distinctive fruits of *Fagopsis* where the leaves of *Fagopsiphyllum groenlandicum* occur, both in the field and at museum collections, I have never seen them. This also applies to the localities producing the leaves identified as *Fagopsis nipponica* Tanai from the Eocene of Hokkaido (Tanai, 1995). Therefore, despite the foliar similarity, these fossils lack diagnostic characters of *Fagopsis* (namely, those of the infructescence) and should not be placed in that genus. *Fagopsiphyllum* has an interesting pattern of distribution that indicates communication across the North Atlantic during the Paleocene exemplified by its occurrences in the Rocky Mountains (Brown, 1962), Greenland (Koch, 1963), and Scotland (Boulter & Kvaček, 1989), followed by arrival in Asia during the Eocene exemplified by the occurrences in eastern Russia and Japan. True *Fagopsis* is known on the basis of leaves and infructescences from the Eocene of Washington (Wehr, 1995), Montana (Becker, 1961), and Colorado (MacGinitie, 1953; Manchester & Crane, 1983). So far, it is not known outside North America.

Fagus is distributed at temperate latitudes of the Northern Hemisphere but is not native to western North America today. Nevertheless, the genus is documented by beech nuts and associated foliage in the lower Oligocene of Oregon (Meyer & Manchester, 1997). The fossil record and evolution of *Fagus* foliage has been reviewed by Tanai (1974, 1995), Zetter (1984), and Kvaček and Walther (1991, 1992). The genus extends through the Miocene in western North America and from the upper Oligocene through the Pliocene in Europe and Asia.

Pseudofagus, a North American endemic extinct genus, makes its appearance in the Miocene of Idaho (Smiley & Huggins, 1981; type material at UCMP). Although the leaves are virtually indistinguishable from those of *Fagus,* the attached fruits have a single trikeeled nut (unlike the paired trikeeled nuts of *Fagus*), and a highly dissected cupule that covers only the basal part of the nut (Smiley & Huggins, 1981).

Quercus is widespread in the Northern Hemisphere and extends into Malesia and Colombia. It is first recognized on the basis of silicified nuts with cupules from the Middle Eocene Clarno Nut Beds, Oregon (Manchester, 1994b). Lobed oak leaves are described along with acorns and staminate catkins from the Oligocene of Huntsville, Texas (Daghlian & Crepet, 1983). Reports of unlobed leaf impressions attributed to *Quercus* should be viewed with caution if not accompanied by acorns because of the difficulty in distinguishing from other genera

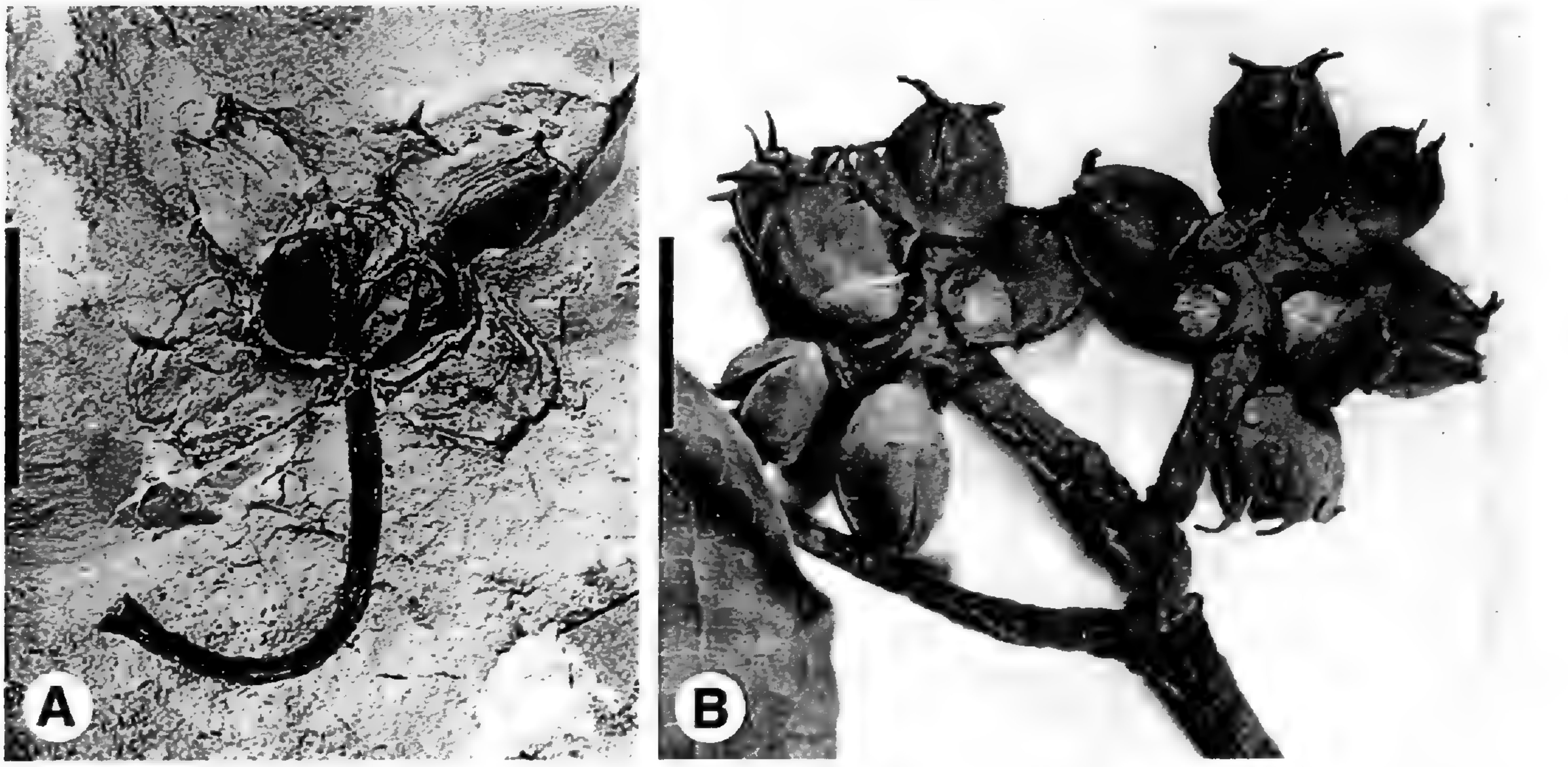


Figure 4. *Exbucklandia* (Hamamelidaceae). —A. *Exbucklandia oregonensis* Brown, 1946, Miocene Spokane flora, Washington, USNM 42366. —B. Extant *Exbucklandia populnea* (R. Br.) R. W. Brown from Yunnan, China, A: *T. T. Yu 17269*. Scale bars = 1 cm.

such as *Lithocarpus* and *Castanopsis*. *Quercus* species with lobed leaves became widespread in the Northern Hemisphere in the early Oligocene (Tanai & Uemura, 1994). The North American fossil record of *Quercus* was reviewed by Borgardt and Pigg (1999) with special attention to anatomically preserved acorns.

The Trigonobalanoids include three extant species that were formerly placed together in the single genus *Trigonobalanus*, but now segregated by Nixon and Crepet (1989) into separate monotypic genera: *Trigonobalanus verticillata* (Borneo and the Malay Peninsula), *Formanodendron doichangensis* (Thailand and southern China), and *Colombobalanus excelsa* (Colombia). Fossils of the extinct genus *Trigonobalanoidea* from the Eocene of Buchanan, Tennessee, resemble *Formanodendron* and *Colombobalanus* on the basis of alternate cupule arrangement and winged fruits (Crepet & Nixon, 1989).

Hamamelidaceae. *Corylopsis* ranges from the Himalayas to Japan today, but was formerly distributed in Europe and North America. The fossil record of the genus, with many European Tertiary seed occurrences, was reviewed by Tralau (1963). Grote (1989) recognized *Corylopsis* on the basis of seeds from the Eocene of Tennessee. He noted that the large, narrow, very asymmetrical, hilar scar facilitates the distinction of *Corylopsis* seeds from other extant genera of the Hamamelidaceae. Infructescences of *Fortunearites* from the Eocene of Oregon bear seeds with a combination of characters found today only in the Chinese genera *Fortunearea* and *Sinowilsonia* (Manchester, 1994b).

Exbucklandia, a genus endemic to China today, was identified on the basis of leaves and associated globose infructescences from the Miocene of Idaho (Brown, 1946a; Lakhanpal, 1958). *Exbucklandia* has a globose infructescence of bilocular woody capsules (Fig. 4B) that are closely similar to the specimens identified to this genus from the North American Tertiary (Fig. 4A). The fossil infructescences are clearly hamamelidaceous, but the enlarged persistent stipules diagnostic of extant *Exbucklandia* have not been observed at these fossil localities, and further work on these fossil occurrences would be desirable to confirm the identification.

Liquidambar, which is well known for its disjunct distribution between eastern North America, Mexico, the eastern Mediterannean, and eastern Asia, is first recognizable by leaves from the middle Eocene of California (MacGinitie, 1941), but the infructescences attributed to the same species by MacGinitie were later determined to be platanaceous (Manchester, 1986). The genus persists through the Oligocene (Meyer & Manchester, 1997) and is common in the Miocene of western North America (Chaney & Axelrod, 1959; Rember, 1991). *Liquidambar* leaves occur in the late Eocene of Kamchatka (Budantsev, 1997) and are common in the Miocene of Japan (Huzioka & Uemura, 1979) and early Oligocene to Pliocene in Europe (Mai & Walther, 1978). Some reports of the genus based on leaves, including that from the Eocene Green River Formation (MacGinitie, 1969), are equivocal because the teeth are absent from the basal part of

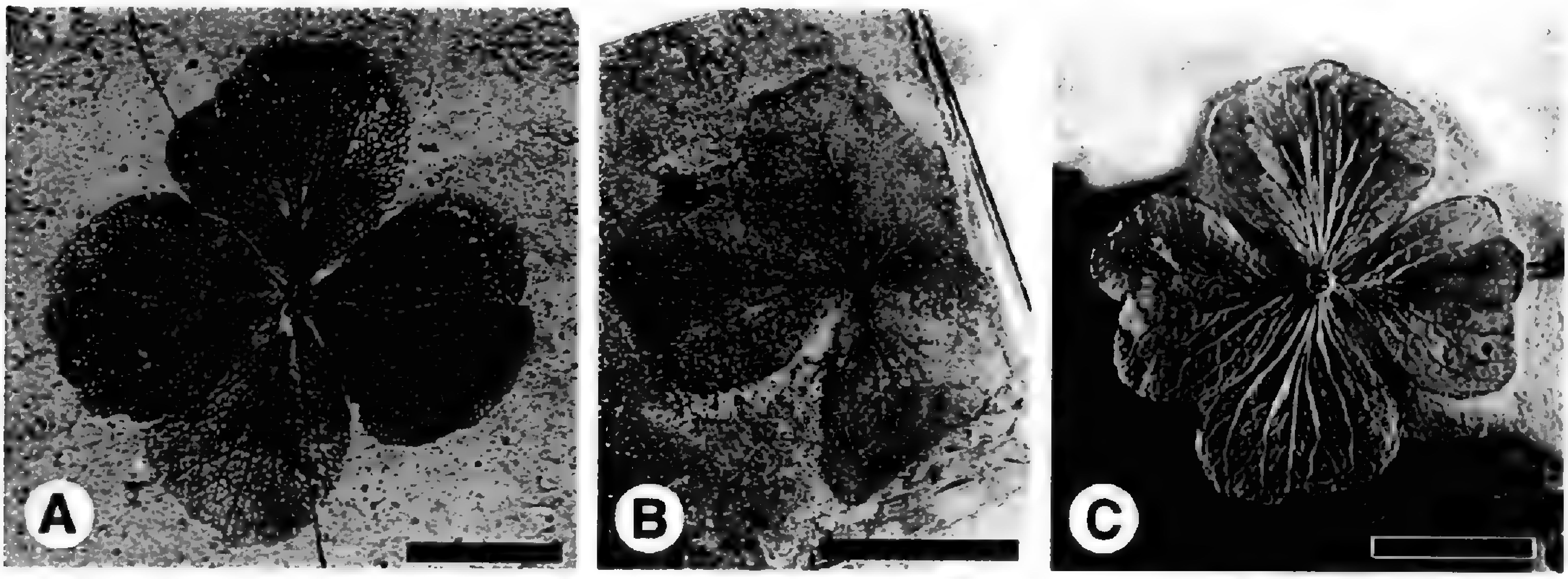


Figure 5. *Hydrangea* (Hydrangeaceae). Sterile calyces of the infructescence. —A. *Hydrangea* sp. from the Gosner Road locality of the Eocene Clarno Formation, Oregon, UF 238–9962. —B. "*Getonia oeningensis* Unger," originally figured by Weber (1852: 24, fig. 2), Oligocene of Rott, Germany. —C. Extant *Hydrangea oerstedii*, *Utley 3844* (MO 2592036), epiphytic habit, Costa Rica. Scale bars = 1 cm.

the lamina next to the petiole in contrast to the teeth in extant species, which are uniformly distributed over the entire lamina.

Hydrangeaceae. This family is now considered to be a close relative of Cornaceae (Soltis et al., 1995; Xiang et al., 1993). *Hydrangea*, which occurs in Asia, Atlantic North America, and to Chile today, is readily recognized by the large persistent calyces of its sterile flowers (Fig. 5C), also occasionally by infructescences of capsular fruits (Mai, 1985a; Manchester, 1994b; Meyer & Manchester, 1997). In North America the calyces range from middle Eocene (Fig. 5A; Manchester, 1994b) to middle Miocene (Knowlton, 1902; Fields, 1996). Permineralized fruits of *H. knowltonii* from the Eocene of Oregon were found to contain winged seeds diagnostic of *Hydrangea* sect. *Hydrangea*, subsection *Calyptranthe*, which has a single extant species *H. anomala*, extending from the eastern Himalayas to Japan (Manchester, 1994b). In Europe calyces of *Hydrangea* range from the late Eocene of Kučlin, Czech Republic (Sieber, 1881), and late Oligocene of Rott, Germany (Fig. 5B; *Getonia oeningensis* Unger of Weber, 1852), to the Pliocene (Mai, 1995). Asian examples of these calyces include *Hydrangea* sp. from Miocene Kraskino flora of Khasan Basin, south Primorye, Russia (Ablaev et al., 1993: pl. 20, fig. 7) and *H. sendaiensis* from the Late Miocene flora near Sendai, Japan (Okutsu, 1940).

Icacinaceae. The tribes Phytocreneae and Iodeae of the Icacinaceae are presently paleotropical in distribution, but both are well represented by unilocular endocarps in the early Tertiary of North America and Europe. In the Iodeae, the fruits of modern *Iodes* (Asia, Africa), *Natsiatum* (Asia), and *Hosiea* (Asia) are similar in the possession of reticulately ridged endocarp surfaces, and papillate locule lining. These genera are distinguished by phyllotaxy, which is opposite in *Iodes*, and alternate in the others, but the distinction of these genera based on their fruits requires details of internal morphology and endocarp sculpture (Manchester, 1994b; Kvaček & Bůžek, 1995). *Iodes* has a funicular canal within the endocarp, whereas *Hosiea* and *Natsiatum* lack this canal, and have the funicle to the outside of the endocarp. Endocarps and locule casts consistent in morphology and anatomy with *Iodes* occur in the Eocene London Clay (Reid & Chandler, 1933) and Clarno (Manchester, 1994b) floras. A new genus, *Palaeohosiea* Kvaček & Bůžek (1995), was recognized on the basis of endocarp fossils from the Eocene and Oligocene of central and western Europe. It is not clear whether the fossils assigned to this fossil genus are truly an extinct genus, or whether they simply lack sufficient characters to specify the correct extant genus to which they belong. The species assigned to *Palaeohosiea* would be difficult to distinguish from those ascribed to *Iodes* in England and western North America. In the distribution chart (Fig. 19), I have lumped the occurrences of *Palaeohosiea* with those of *Iodes*. It is clear that the Iodeae were widely distributed both in western North America and Europe during the early Tertiary. The extinct genus *Iodicarpa* Manchester includes fruits that are morphologically similar to *Iodes*, but three or more times larger than those of extant *Iodes* species (Manchester, 1994b). I am not aware of any Neogene fruits of Iodeae nor of any paleobotanical record of the fruits in Asia.

Fruits of the Phytocreneae are ellipsoidal, with lignified endocarps characterized by conspicuous cylindrical, conical, or laterally elongate invaginations that may appear as pits on the endocarp sur-

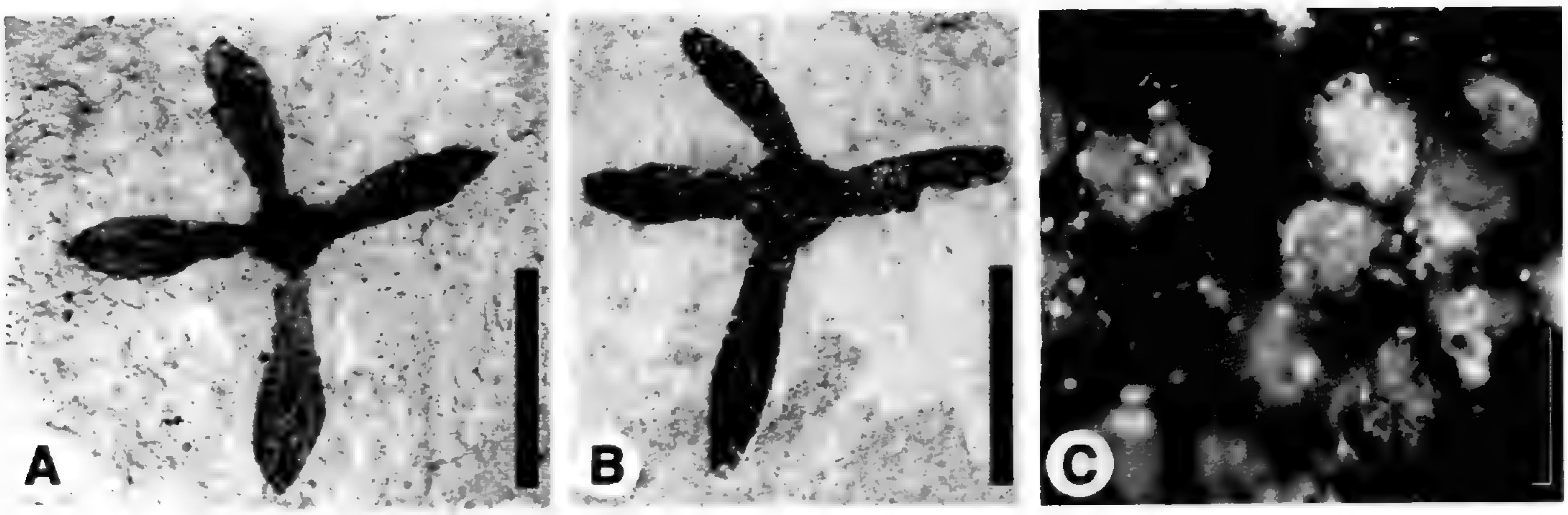


Figure 6. *Cruciptera* (Juglandaceae) from the Eocene of North America and Europe. —A. Samara of *Cruciptera simsonii* with four wings attached to a central globose nut that shows the impression of primary and secondary septa. Middle Eocene, Clarno Gosner Road, Oregon, UF238–9486. —B. Holotype of *C. schaarschmidtii* from the Middle Eocene of Messel, Germany, SM.B. Me 7152. —C. Peltate scales typical of Juglandaceae on surface of the nutlet in B, viewed by epifluorescence microscopy. Scale bars = 1 cm in A, B, 100 μm in C.

face, and/or protrusions into the locule. Fossil endocarps and locule casts conforming in these features to the Phytocreneae, but not attributable to an extant genus, are assigned to *Palaeophytocrene* Reid & Chandler. Such fruits are common in the Eocene of England (Reid & Chandler, 1933) and western North America (Manchester, 1994b; Manchester & Tiffney, 1993).

The extant genus *Pyrenacantha,* which currently is disjunct between Asia and Africa, is recognized in the fossil record on the basis of endocarps with parallel-sided (not broadly conical), spine-like projections extending into the locule. This genus is known from the Eocene of Oregon (Manchester, 1994b), California, and Egypt (Manchester & Tiffney, 1993). These occurrences indicate that *Pyrenacantha* may be a remnant of the Eocene boreotropical forest with early biogeographic ties to Africa.

Illiciaceae. *Illicium* occurs today from India to eastern Asia and western Malesia, and in eastern North America, Mexico, and the Caribbean. It is known on the basis of fruits from the Miocene of Vermont (Tiffney & Barghoorn, 1979) and Germany (Mai, 1970).

Juglandaceae. Several genera of the Juglandaceae give clues to the biogeographic pathways. The identification of juglandaceous precursors such as the flowers and fruits of *Caryanthus* Friis in the late Cretaceous of the southeastern United States (Crane & Herendeen, 1996) and Europe (Friis, 1983) indicates an early connection across the North Atlantic. Modern genera of the family were not recognizable on the basis of fruits until the lower Paleocene (Manchester, 1989b). Since my earlier review of the biogeographic history of this family (Manchester, 1987a), an additional genus has been recognized in the Eocene of western North America and Europe (*Cruciptera*: Manchester, 1991; Manchester et al., 1994), and a comprehensive review of the Russian fossil record of the family has been published (Budantsev, 1994b).

Carya, which occurs in eastern Asia and eastern North America today, is first confirmed by fruits in the late Eocene of Florissant, Colorado. The greatest diversity occurs in Europe, with many species recognized from the Oligocene to the Pliocene (Kirchheimer, 1957; Mai, 1981). Although *Carya*-like pollen occurs in the Paleocene, these grains are much smaller than those of most modern species and appear to be associated with fruits of *Juglandicarya simplicarpa* Manchester (1989b).

Cruciptera Manchester is an extinct genus with four wings radiating from the equator of a globose nutlet. It is known from the Middle Eocene to Oligocene of western North America (Fig. 6A; Manchester, 1991, 1994b; Wehr, 1995; Meyer & Manchester, 1997), and from the middle Eocene of England and Germany (Fig. 6B; Manchester et al., 1994). Peltate scales visible on the nutlet surface (Fig. 6C), together with the nutlet internal morphology, confirm affinities within the Juglandaceae. *Cruciptera* is absent from any of the known Tertiary deposits of Asia.

Cyclocarya, although native to southern and central China today, is recognizable based on distinctive fruits in the Paleocene of North America (Manchester & Dilcher, 1982; Manchester, 1987a). A Paleocene specimen from northeastern China was described as *Cyclocarya macroptera* Tao and interpreted to be a fruit by Tao and Xiong (1986). However, I have reexamined the specimen and exclude it from *Cyclocarya* because there is no nutlet impression at the axis of the radiating veins. It might be the remains of a peltate leaf similar to *Nelumbo*. Similarly, *C. minuta* Krassilov (1976) may be dismissed from *Cyclocarya* because the "fruit" lacks a nut and the wing does not possess veins. A winged fruit illustrated as *Cyclocarya* from the Eocene of Hokkaido (Tanai, 1992b) appears likely to be that of the rhamnaceous genus *Paliurus*. The criteria that I find useful to distinguish these highly convergent fruits are presented later under the discussion of *Paliurus*. *Cyclocarya* ranges from the Oligocene to Upper Pliocene in Europe and Asia (Manchester, 1987a; Mai, 1995).

Engelhardieae. Most genera of this tribe are readily recognized by having wings formed by persistent trilobed bracts. They are unknown from the Paleocene but are widespread by the middle Eocene both in Europe and North America and in the Oligocene of Asia. Fruits with deeply trilobed bracts similar to those of extant *Engelhardia* (Asia) and *Oreomunnea* (Central America) are placed in the organ genus *Palaeocarya* Saporta. *Palaeocarya* is well represented in the Tertiary of Europe, North America, and Asia. In addition, two extinct genera are known from the Eocene of southeastern North America. *Paleoengelhardtia* Berry has a small nutlet and a shallowly trilobate bract. *Paleooreomunnea* Dilcher, Potter & Crepet has a large nut and a shallowly trilobate bract (Dilcher et al., 1976; Manchester, 1987a). This greater diversity in southeastern North America at the time when this tribe makes its first appearance in the fossil record suggests that the group may have actually diversified in North America prior to dispersing to Europe and Asia.

Platycarya, native to China and Japan today, provides good evidence for a late Paleocene/early Eocene North Atlantic crossing, followed by a much later Tertiary arrival in Asia. The genus is confirmed on the basis of infructescences and fruits from the early Eocene of England (Reid & Chandler, 1933; Manchester, 1987a), North Dakota (Wing & Hickey, 1984), and Wyoming (Dennison Cap; UF localities 18120, 18216). Although Mai (1987) described a specimen from the Paleocene of Gonna, Germany, as *Platycarya cordiformis*, the locule cast, lacking nutlet and wings, is more properly placed in *Juglandicarya*. The lack of dorsiventral compression, and presence of four, rather than two, basal lobes excludes it from *Platycarya* and indicates similarity with the locule casts of *Cruciptera* and *Cyclocarya*. The extinct genera *Paleoplatycarya* Manchester and *Hooleya* Reid & Chandler are also believed to have affinities with *Platycarya* (Wing & Hickey, 1984; Manchester, 1987a).

Pterocarya is no longer native to North America but has one species in the Caucausus region and several in eastern Asia. It is known from fruits first from the lower Oligocene of the Lyons and Bridge Creek floras of Oregon (Meyer & Manchester, 1997), and additional fruit records indicate that the genus survived into the Miocene in the Pacific Northwestern states (Manchester, 1987a). Fruits reported as *Pterocarya* by MacGinitie (1969) from the Eocene Green River Flora are now thought to more accurately be assigned to the extinct genus *Hooleya* Reid & Chandler. *Pterocarya* has excellent fruit records from the Oligocene to Pliocene of Europe and Asia (Budantsev, 1994b).

Polyptera Manchester & Dilcher is a Paleocene fruit genus known from one locality in Montana and several in Wyoming (Manchester & Dilcher, 1982, 1997). The morphology and symmetry of the fruit are somewhat similar to *Cyclocarya*, but the wing is divided into 8 to 12 prominent lobes. The fruits are associated with pinnately compound leaves of *Juglandiphyllites glabra* (Brown) Manchester & Dilcher, and catkins containing an extinct type of juglandaceous pollen (*Maceopolipollenites anellus* (Nichols & Ott) Manchester & Dilcher). *Polyptera* fruits are unknown outside North America, but the occurrence of pollen resembling *Maceopolipollenites anellus* in the Paleocene of China (Zhuang, 1990) indicates that *Polyptera* may have been present in Asia, or that *Maceopolipollenites* pollen corresponded to more than one kind of fruit (Manchester & Dilcher, 1997).

Leitneriaceae. *Leitneria*, with a single living species confined to the southeastern United States, has drupes with reticulately ribbed, slightly asymmetrical, ellipsoid, and somewhat flattened endocarps. Although still unknown from the North American fossil record, these distinctive endocarps have been identified from the Oligocene of western Siberia and the Miocene to Pliocene of Germany (Dorofeev, 1963, 1994; Mai, 1980). Transverse sections of the endocarp reveal virtually identical anatomy in extant *Leitneria floridana* and in the fossil species (Dorofeev, 1994).

Lemnaceae. *Limnobiophyllum* Krassilov emend Kvaček (1995) was a floating aquatic plant with reniform to nearly orbicular laminae attached in small rosettes interconnected by stolons with simple adventitious roots. Recent work on specimens from the Paleocene of Alberta (Stockey et al., 1997) revealed attached stamens containing globose, monoulcerate, echinate pollen. The combined characters of this plant indicate affinities both with the Araceae and the Lemnaceae (Kvaček, 1995; Stockey et al., 1997). In North America, *Limnobiophyllum* occurs in the Paleocene of Alberta (Stockey et al., 1997) and Saskatchewan (McIver & Basinger, 1993, as *Spirodela scutatum* Dawson) and in the Middle to Late Eocene of Colorado (Kvaček, 1995). In Asia, the same genus is known from the early Paleocene of Primorye (Krassilov, 1976: pl. 11, fig. 5 only). Other specimens illustrated under this name by Krassilov (1976) and Golovneva (1994) are actually an unrelated genus called *Porosia* Hickey (see below). In Europe, *Limnobiophyllum* is represented by a similar species in the Early Miocene of Bilina and Zelenky, western Czech Republic, the Middle Miocene of Oeningen and Kreuzau, Germany, and the Late Miocene of Sosnica, Poland (Kvaček, 1995).

Lythraceae. *Decodon* is endemic to swampy areas of southeastern North America today and has a good fossil record in Europe and Asia, as well as North America. Silicified fruits are known from the Eocene of Princeton, British Columbia (Cevallos-Ferriz & Stockey, 1988), and Oregon (Manchester, 1994b). The distinctive seeds are known from the Eocene to Pliocene in Europe (Mai & Walther, 1978; Friis, 1985) and from the Oligocene and Miocene of Asia (Dorofeev, 1977; Matsumoto et al., 1997a). The extinct *Microdiptera* Chandler occurs from the Middle Eocene to Miocene of Europe and also in the Miocene Brandon Lignite of Vermont (Tiffney, 1981a).

Magnoliaceae. The fossil record of Magnoliaceae includes some extinct genera that extend well into the Cretaceous (Friis et al., 1997), but extant genera are not confirmed by reproductive structures prior to the Tertiary. Magnolia seeds have a distinctive morphology that allows them to be easily identified in the fossil record (Reid & Chandler, 1933; Tiffney, 1977b). *Magnolia* seeds occur in the upper Paleocene of Wyoming (UF loc. 18132) and are well documented in the middle Eocene of Tennessee (Grote, 1989) and Oregon (three species; Manchester, 1994b). Miocene records include seeds from the Brandon Lignite of Vermont (Tiffney, 1977b) and a multifolicular fruit from the Clarkia beds of Idaho (Rember, 1991). The identification of leaves to this genus is more difficult because of the convergence with similar leaf architecture among many different dicotyledonous families. In Europe and Asia, the record of *Magnolia* extends from the Paleocene to Pliocene (Mai, 1995).

Liriodendron, which is disjunct between eastern North America and China today, is readily recognized by its distinctive, apically notched, bisymmetrical, lobed leaves, and by its elongate-winged fruitlets. Leaves of *Liriophyllum* Lesquereux from the mid-Cretaceous and *Liriodendrites* K. Johnson (1996) from the late Cretaceous are similar to *Liriodendron* and are considered to represent Magnoliaceae, but can be distinguished by the depth of the apical sinus and the nature of the midvein as it nears the apical sinus. Although magnoliaceous infructescences and seeds sometimes occur together with these leaves, no samaroid fruitlets of the *Liriodendron* type have been found prior to the Tertiary (Friis et al., 1997). *Liriodendrites* Knobloch & Mai seeds from the Late Cretaceous are anatomically similar to the seeds of *Liriodendron* except that the fossil seeds are winged, rather than the fruitlets (Friis et al., 1997). Leaves and fruits that can be attributed unequivocally to the extant genus occur relatively late in North America, in the Miocene of Idaho (Baghai, 1988). The genus has an earlier record in the Oligocene of Markvartice (Bůžek et al., 1976), where it is noted to have a lower leaf cuticle that is smooth like that of the extant North American species *L. tulipifera*, in contrast to the finely papillate lower cuticle of the extant Chinese *L. chinense*. The last European records are upper Pliocene (Wilde et al., 1992). *Liriodendron* occurs in the middle and late Miocene of Japan (Uemura, 1988) based on leaves of *L. honshuensis* Endo and winged fruitlets of *L. fukushimaensis* Suzuki. The genus is absent from the Pliocene of Japan and is no longer native to the islands.

Malvales. Judd and Manchester (1997) proposed, based upon cladistic analyses, that the Tiliaceae, Sterculiaceae, Bombacaceae, and Malvaceae should be combined into one family, the Malvaceae s.l. To alleviate confusion prior to a general consensus on this matter, I refer to the group here simply as the order Malvales. The extant genus *Craigia*, traditionally placed in the Tiliaceae, has two species in southern China. It was widely distributed through the Tertiary, and its fruits were formerly thought to be an extinct genus, *Pteleacarpum* Weyland (Bůžek et al., 1989). With the recognition that the fossil fruits represent *Craigia* (Kvaček et al., 1991), it has been possible to document an extensive history of this genus in the Northern Hemisphere (Kvaček, 1994). The distinctive fruits are known from the Eocene of Spitzbergen and of John Day Gulch, Oregon, and Bonanza, Utah. In North America, the latest record of *Craigia* is early Oligocene (Meyer & Manchester, 1997), but in Europe the fruits extend from the Oligocene to the Pliocene, and in Asia they are known in the fossil record from the Eocene to the Miocene (Bůžek et al., 1989).

Tilia is a tree of North Temperate distribution that also extends south to Indochina and Mexico today. Bracts of *Tilia* suggest an interesting phytogeographic scenario (Manchester, 1994a). The ear-

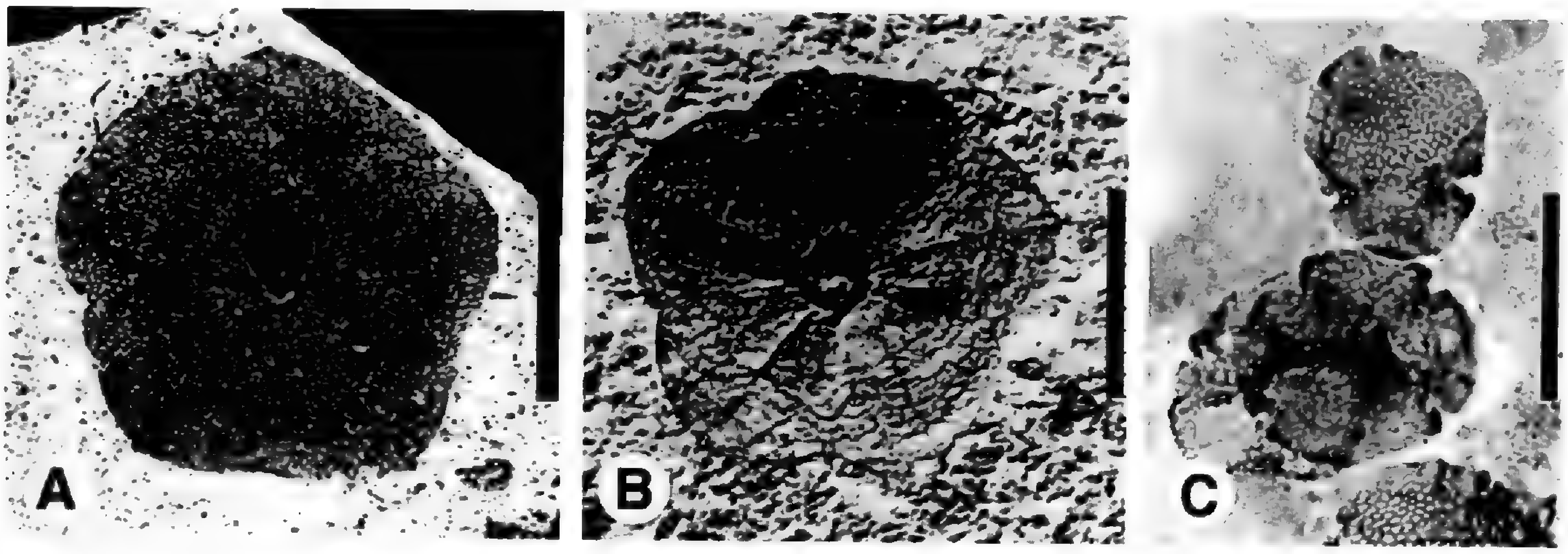


Figure 7. *Florissantia* (Malvales) calyces from the Eocene of western North America and Miocene of Asia. —A. *Florissantia quilchenensis* (Mathewes & Brooke) Manchester, from the Middle Eocene Republic flora of Washington, western North America, UWBM 57556. —B. *Florissantia sikhote-alinensis* (Kryshtofovich) Manchester comb. nov. from the Miocene Amgu flora of Sikhote Alin. Specimen missing, figure reproduced from Kryshtofovich (1921). —C. Malvalean pollen removed from the anther of a *Florissantia speirii* flower (Manchester, 1992). Scale bars = 1 cm in A, B, 30 μm in C.

liest known *Tilia* bracts are from the late Eocene of North America. They are elongate and have the peduncle adnate only to the base of the bract ("type B" morphology), as seen in only a few Chinese species today. Also in the late Eocene of Idaho and early Oligocene of Oregon, an extinct type of bract with a circular, rather than elongate, outline became common ("type A" morphology). This kind of bract is not known from floras outside western North America. In Europe, *Tilia* bracts are unknown prior to the Oligocene, and they conform to type B, suggesting dispersal across the North Atlantic. By the Pliocene in Europe, a third type appeared that is elongate and has the peduncle adnate along the lower 1/4 to 1/3 of the bract. This "type C" morphology also extends from the Oligocene to the Pliocene in Asia and characterizes most extant species in North America, Europe, and Asia. Thus, the kind of bract that is widespread in the Northern Hemisphere today occurs only in Asia in the middle Tertiary and evidently arrived relatively late in the Tertiary of Europe and North America (Manchester, 1994a).

Florissantia Knowlton (Fig. 7) is an extinct genus with fruit, flower, and pollen morphology indicating malvalean affinity, common in the Eocene to Oligocene of western North America. At the time the record was summarized (Manchester, 1992), I overlooked its occurrence in the Miocene of eastern Asia. Kryshtofovich (1921) had earlier described a calyx that he considered similar to *Florissantia speirii* (then known under the name *Porana speirii* Lesq.) from the Miocene of Amgu, Sikhote-Alin. Although the specimen has not been relocated, the published description and photograph (Fig. 7B) leave little doubt that it represents the same genus. The species that Kryshtofovich described now provides the basis for a new combination: *Florissantia sikhote-alinensis* (Krysh.) Manchester comb. nov. (see Appendix 1).

The stratigraphic ranges of *Florissantia* in Asia and North America do not overlap, so the fossil record is clearly insufficient to resolve the precise timing of the migration between continents. However, the complete absence of these fruits from European Tertiary indicates that the likely route was across Beringia in the early to mid Tertiary.

Menispermaceae. This family is diverse in the tropics today but has a few outliers in temperate areas, e.g., *Menispermum, Calycocarpum.* The family can be recognized by its leaves, although different genera can be difficult to discriminate because of very similar venation patterns. The tribes and genera are recognizable from the endocarps. Although apparently absent from the Tertiary of southeastern North America, the family has a rich record in western North America. The family is relatively rare in the Paleocene (Crane et al., 1990), but it becomes common in the Eocene, with more than 12 genera of Menispermaceae based upon endocarps in the Eocene Clarno Nut Beds (Manchester, 1994b). Of these, *Tinospora, Tinomiscoidea, Atriaecarpum, Davisicarpum, Diploclisia, Eohypserpa,* and *Palaeosinomenium* are shared with the Eocene London Clay flora. *Anamirta,* known both from leaves in the Kulthieth Formation of Alaska (Wolfe, 1977) and endocarps from the Clarno Formation (Manchester, 1994b), grows today from India to Indochina and throughout Malesia. In North America Menispermaceae diminished in diversity by the end of the Eocene, and the family is known only from cf. *Menispermum* in the Oligocene Bridge Creek flora (Meyer & Manchester, 1997). The numerous reports of *Cocculus* and *Menispermites* leaves were formerly thought to represent Menispermaceae (LaMotte, 1952; Hickey, 1977), but based on co-occurrence at numerous localities through the Northern Hemisphere, many of these are now considered to belong to the extinct trochodendraceous plant *Nordenskioldia* (Crane et al., 1991; Manchester et al., 1991).

Musaceae. The banana family is represented by *Ensete* on the basis of seeds (Manchester & Kress, 1993) and fruits (Manchester, 1994b) from the Eocene of Oregon, and by fruits from the Eocene of Republic, Washington (Wehr & Manchester, 1996). Today this genus is distributed in Asia and Africa.

Myricaceae. *Comptonia*, which today is restricted to eastern North America, has distinctive, pinnately lobed leaves (Fig. 8A) that are easily recognized in the fossil record. It was widespread in the Tertiary of the Northern Hemisphere. Eocene occurrences include the Clarno Formation of Oregon; Republic, Washington (Wolfe & Wehr, 1987); Alum Bay, England (Fig. 8D); and Messel and Eckfeld, Germany (Wilde, 1989; Wilde & Frankenhäuser, 1998). In western North America, the leaves are known as late as the Miocene (Fig. 8C; Boyd, 1985). In Europe, *Comptonia* extends into the upper Pliocene of Willershausen (Wilde et al., 1992). Leaves also occur in the Lower Oligocene of central Kazakhstan (Zhilin, 1989; Akhmetiev, 1991). In eastern Asia the genus is known, for example, from the Eocene of Fushun (WGCPC, 1978) and Yilan (Fig. 8B), China, the Miocene of Sikhote-Alin (Fig. 8E) and is diverse in the Middle Miocene of Japan (Tanai, 1961; Huzioka & Uemura, 1979). In Europe and western Asia, the record also includes endocarps (Dorofeev, 1994).

Although *Myrica* is well represented in the extant flora of eastern North America, its fossil record in North America is poor or nonexistent (Chourey, 1974). *Myrica* is known based on leaves from the Late Eocene of western Kamchatka (Budantsev, 1983, 1997) and by well-preserved fruits from the mid to late Tertiary of Europe and Asia (Dorofeev in Budantsev, 1994b).

Myrtaceae. This family is represented by permineralized fruits from the Paleocene of North Dakota and the Eocene of British Columbia with distinctive seeds similar to those of the guava, referred to *Paleomyrtinaea* Pigg, Stockey & Maxwell (1992). An extinct myrtaceous genus, *Syzygioides* Manchester, Dilcher & Wing, was recently established based on leaves and fruits from the Eocene Green River Formation of Colorado and Utah (Manchester et al., 1998). Leaves of *Syzygioides americana* (Lesquereux) Manchester, Dilcher & Wing were formerly attributed to extant *Eugenia* (MacGinitie, 1969), but they have been found attached to twigs with an extinct kind of fruit (Manchester et al., 1998). Budantsev (1994a: pl. 5, figs. 4–6) illustrated strikingly similar leaves from the Eocene of Cape Rebro, northwest Kamchatka, which he also referred to *E. americana*. The close similarity of these leaves to those from North America suggests the possibility of a Beringial connection; however, there is considerable overlap in patterns of venation among different genera in the family even today, and it is possible that the similarities are due to parallelism or convergence. A comparison of associated fruits is needed to assess whether the Kamchatka and Rocky Mountain species are indeed conspecific.

Oleaceae. *Fraxinus*, which occurs around the Northern Hemisphere today and is easily identified based upon its distinctive fruits, is known from the Eocene of both western and eastern North America (Call & Dilcher, 1992) and has records continuing through the Oligocene (Meyer & Manchester, 1997) and Miocene of the Pacific Northwest (Chaney & Axelrod, 1959). In Europe, fruits of *Fraxinus* are known from the lower Oligocene to Pliocene (Kirchheimer, 1957; Kvaček & Walther, in press). Asian fruit records include *Fraxinus honshuensis* Tanai & Onoe from the Late Miocene to Pliocene of Hokkaido and Honshu, Japan (Tanai, 1961), *F. stenoptera* from the lower Miocene of Orzhilansay, Turgayan Plateau (Zhilin, 1991), and *F. dayana* and *F. microcarpa* from the Miocene Shanwang flora of China (WGCPC, 1978).

Palmae. *Sabal* is distributed today in southeastern North America, Central America, and the Caribbean region. It has an ancient record in North America extending back to the Campanian stage of the Upper Cretaceous based upon seeds from Big Bend, Texas (T. Lehman, E. Wheeler & S. Manchester, unpublished obs.), as well as leaves. The genus is known from seeds and foliage from the Eocene of Oregon and from foliage with epidermal preservation in the Eocene of Tennessee, etc. (Daghlian, 1978). By the Eocene this genus had become widespread in the Northern Hemisphere. It is known from seeds in the early Eocene London Clay, the late Eocene/early Oligocene Bembridge beds (Reid & Chandler, 1926), and the middle Eocene Geiseltal of Germany, as well as by leaves from the Eocene of Europe (Paris Basin and Czech Republic; Knobloch et al., 1996) and Kamchatka (Budantsev, 1979, 1994a). Its range diminished after the terminal Eocene cooling, and the genus was

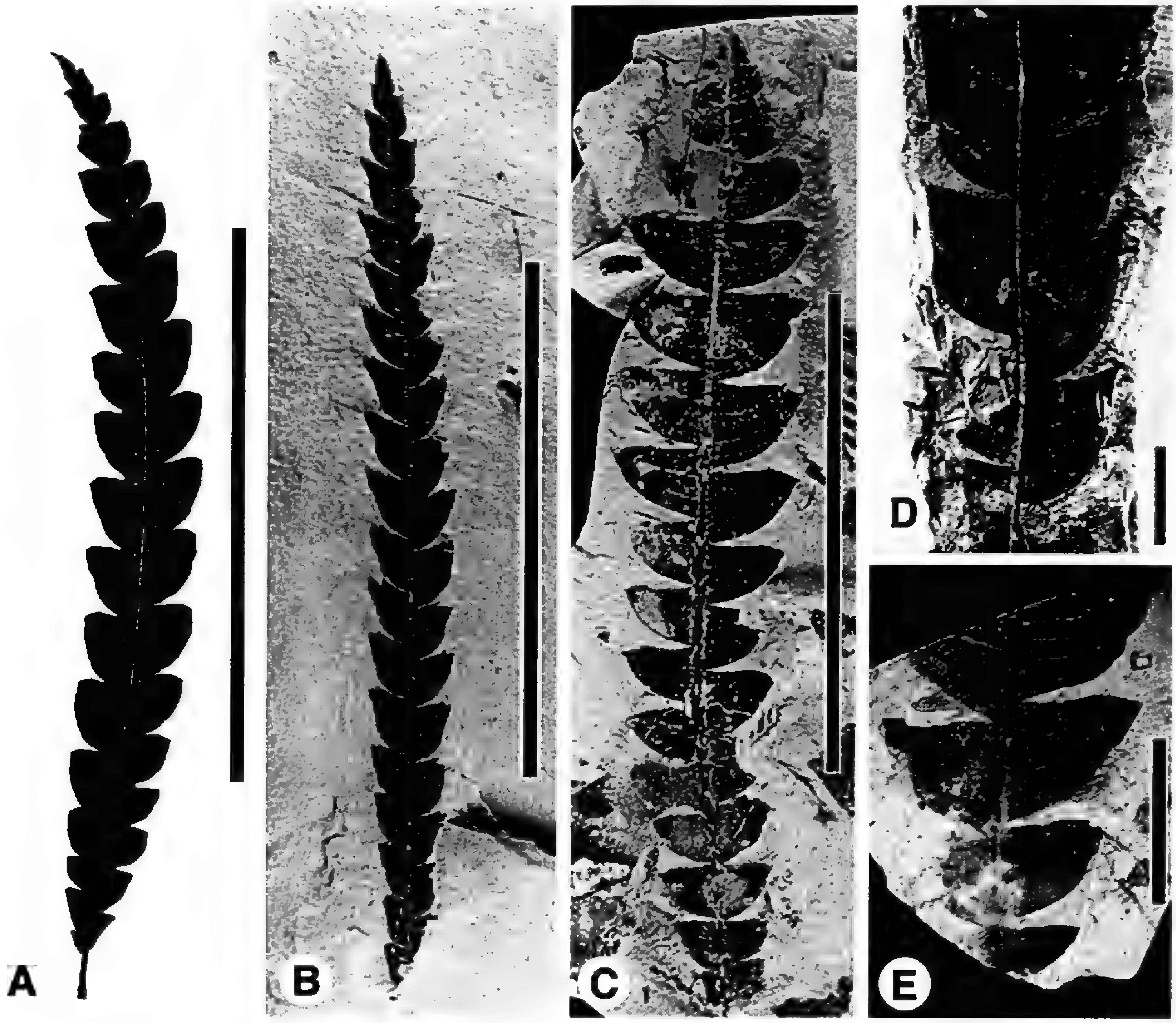


Figure 8. *Comptonia* (Myricaceae) from North America, Europe, and Asia. —A. Extant *Comptonia peregrina* (L.) Coulter from Baltimore, Maryland, FLAS 186865: *E Baltars 1212.* —B. *Comptonia* sp. from the Eocene of Yilan, China. Beijing Paleobotanical Coll. 9456. —C. *C. hesperia* Berry, Miocene of Oviatt Creek, Idaho, UF 18343–25433. —D. *Comptonia* sp. from the Eocene of Alum Bay, Gardner Coll., Natural History Museum, London, V46154. —E. *Comptonia* sp. from the Miocene of Velikaja Kema, Eastern Sikhote-Alin, Akhmetiev coll., Geol. Inst. Russ. Acad. Sci. no. 3820/801. Scale bars = 5 cm in A–C, 1 cm in D, E.

eradicated from Eurasia after the Miocene. It is known from the Miocene in Florida (Berry, 1916).

Platanaceae. The Platanaceae were already widespread in the Northern Hemisphere in the mid Cretaceous, represented mainly by palmately lobed simple leaves with palinactinodromous venation of a type that continued to be abundant during the Tertiary. Similar leaves occur today in extant *Platanus* sect. *Platanus.* Although the fruits were borne in globose infructescences, as today, the fruits of Cretaceous and some early Tertiary Platanaceae lacked dispersal hairs (Manchester, 1986; Friis et al., 1988). The occurrence of *Platanus*-like leaves in the Cenomanian of Bohemia and Kansas indicates that the Platanaceae had spread across the Northern Hemisphere long prior to the Tertiary. Leaves and infructescences attributable to modern *Platanus* occur in the Paleocene (Maslova, 1996).

Platanites is characterized by ternate leaves with a terminal leaflet that is indistinguishable from the simple leaf of extant *Platanus,* accompanied by a pair of smaller asymmetrical lateral leaflets. It occurs in the Paleocene of North America and Scotland (Crane et al., 1988; McIver & Basinger, 1993). This distribution, and its apparent absence in Asia, suggests a North Atlantic crossing during or perhaps prior to the Paleocene. Ternate-leaved Platanaceae were more common in the late Cretaceous as indicated by the occurrence of *Platanites marginatus* (Lesq.) Johnson in the Maastrichtian of Colorado, Montana, South Dakota, and North Dakota, and the segregate genus *Erlingdorfia* Johnson in the upper Maastrichtian of North Dakota, South Dakota, and Montana (Johnson, 1996). The latest known records for *Platanites* are in the Eocene of Wyoming (MacGinitie,

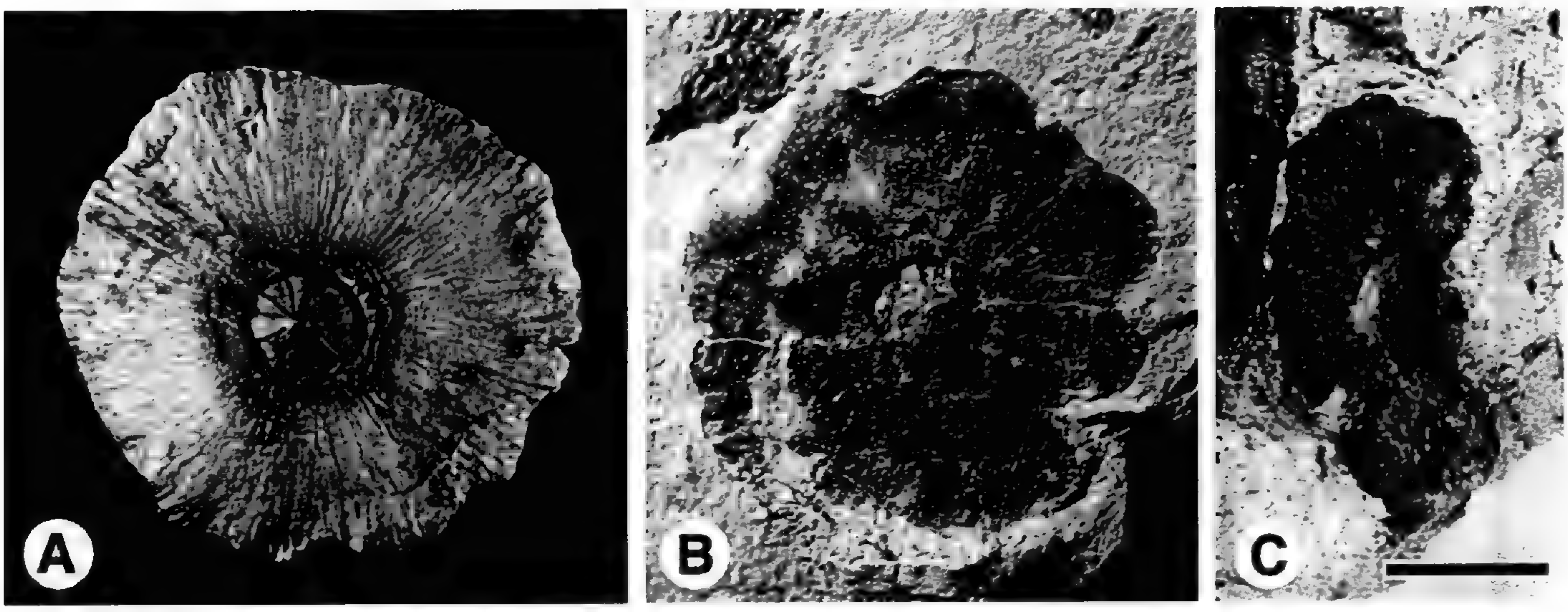


Figure 9. Fruits of extant and fossil *Paliurus* (Rhamnaceae). —A. Extant *Paliurus spina-christi* Gilan, Iran, MO 1983529: *M. L. Grant 16425.* —B. *Paliurus* sp. from the Early Eocene Wind River Formation, Wyoming, UCMP 168324. —C. *Paliurus* fruit impression, Middle or Upper Miocene Alum Bluff, Florida, UF 18048–26117. Bar = 1 cm, applies to A–C.

1974: pl. 14, fig. 1) and Oregon (John Day Gulch, UF 265–27869, 27870).

Macginitiea Wolfe & Wehr was a digitately lobed platanaceous leaf common at some localities in the upper Paleocene and Eocene of western North America (Manchester, 1986). Recently, *Macginitiea* has also been discovered in the Paleocene to Eocene of Kamchatka (Budantsev, 1996). Thus, it appears that *Macginitiea* dispersed across Beringia in the late Cretaceous and/or early Tertiary, perhaps at about the same time that *Platanites* spread across the North Atlantic bridge.

Rhamnaceae. *Paliurus,* which occurs today in southern Europe and eastern Asia, is readily recognized by its disk-winged nuts (Fig. 9A). There is remarkable convergence in general form and wing venation with fruits of the juglandaceous genus *Cyclocarya,* and this has led to some confusion in the assignment of paleobotanical specimens. However, the two genera can be readily distinguished if the fossils are well preserved. *Paliurus* fruits have a persistent perianth disk scar on the basal side of the ovary, which can be observed in fossils as a circular raised rim on the fruit body below the wing, surrounding the pedicel scar. Such a disk is lacking in *Cyclocarya,* which merely has four separate sepals near the apex. If the internal morphology is preserved, *Paliurus* can be distinguished by having two or three distinct locules. *Cyclocarya* fruits have a single locule with incomplete primary and secondary septa that frequently preserve in fossil specimens (Manchester & Dilcher, 1982; Manchester, 1987a).

Although *Paliurus* is no longer native in North America, the genus is documented by fruits as early as the early Eocene from the Wind River Formation of Wyoming (Fig. 9B). In North America it persisted through the Miocene both in the West (Washington: Berry, 1928) and Southeast (Fig. 9C; Alum Bluff, Florida, from the locality of Berry, 1916). In Asia, the earliest fruit records are middle Eocene (e.g., Ube flora, Japan, Huzioka & Takahashi, 1970). Later records include those from the middle Miocene Shanwang flora of China (WGCPC, 1978), the late Miocene of northeast Honshu, Japan (Tsukagoshi & Suzuki, 1990), and the late Miocene of Kazakhstan (Zhilin, 1989: fig. 3b). In Europe, *Paliurus* is known from the Upper Oligocene and Miocene (Kirchheimer, 1957; Bůžek, 1971).

Rosaceae. Although Rosaceae are rare or absent in Paleocene floras, fossil foliage indicates that the family was becoming diverse in northwestern North America by the middle Eocene. Because of overlap in leaf architectural patterns among different extant genera, it is sometimes difficult to specify precise generic affinities without flowers and/or fruits. Extant *Prunus* is verified based on endocarps from the Middle Eocene of Princeton, British Columbia (Cevallos-Ferriz & Stockey, 1991), and the Clarno Formation of Oregon (Manchester, 1994b), and a diversity of rosaceous foliage is known from the Middle Eocene Republic flora of Washington (Wehr & Hopkins, 1994). *Rosa* itself is confirmed by rose hip fruits and compound leaves in the Early Oligocene of Oregon (Meyer & Manchester, 1997). The Rosaceae are well suited for a critical investigation of their phytogeographic history in the Northern Hemisphere, but such a study was not undertaken for this review.

Rubiaceae. *Emmenopterys,* endemic to China today, is represented by well-preserved infructescences, fruits, and seeds from the Eocene of Oregon

(Manchester, 1994b). *Pinckneya,* endemic to the southeastern United States today, is known from the Oligocene of Oregon based on seeds (Meyer & Manchester, 1997). An extinct genus, *Paleorubiaceophyllum* Roth & Dilcher, from the Eocene of Tennessee and Kentucky was a Rubiaceae, and showed similarities of cuticle and a distinctive adnate stipule indicating similarity with the Cinchonoideae. However, a more recently collected specimen from the Eocene of Mississippi (Bolden Clay Pit, UF 15738–27774) shows the leaves attached to a twig with alternate phyllotaxy. Extant Rubiaceae, including the genera cited as most similar to the fossil by Roth and Dilcher (1979) have opposite phyllotaxy. The significance of this discovery to the systematic position of *Paleorubiaceophyllum* requires further study.

Rutaceae. Seeds with morphology diagnostic of *Euodia,* a genus now found in tropical Africa, Asia, Australia, and the Pacific, have been recognized from the Upper Eocene of England and Miocene Brandon Lignite of Vermont (Tiffney, 1981b). Two additional genera recorded from the Brandon lignite are *Zanthoxylon* and *Phellodendron* (Tiffney, 1981a). Seeds assigned to the fossil genus *Rutaspermum* Chandler from the Eocene of Messel, Germany, share characters with extant *Zanthoxylon, Toddalia,* and *Euodia* (Collinson & Gregor, 1988).

Ptelea, which is endemic to North America today, appears to have been confined to this continent also during the Tertiary. Although it has been mistakenly reported in many instances of leaves and fruits in North America and Europe, the only unequivocal fruit records are a few specimens of *Ptelea enervosa* H. V. Smith from the Miocene of Idaho and Oregon (Call & Dilcher, 1995).

Sabiaceae. *Meliosma* occurs in tropical to warm temperate areas of Asia, North America, and South America today. Its distinctive endocarps are known from the late Cretaceous (Maastrichtian) of Walbeck, Germany (Knobloch & Mai, 1986), from the upper Paleocene of Gonna, Germany (Mai, 1987), from the Eocene of England (Reid & Chandler, 1933), and the Miocene to Pliocene of Germany, Poland, Italy (Martinetto, 1994, 1998), and Bulgaria (Mai & Palamarev, 1977). In North America the record of *Meliosma* endocarps extends from the latest Cretaceous and Paleocene to the Eocene (Manchester, 1994b). *Sabia* is recognized based on endocarps from the Maastrichtian of Germany (Knobloch & Mai, 1986) and from as late as the *Pliocene* in Alsace, France (Geissert & Gregor, 1981), and northwestern Italy (Martinetto, 1994, 1998) and from the Eocene of Oregon and Montana (Manchester, 1994b).

Sapindaceae (including Aceraceae). Schizocarpic samaras closely resembling those of extant *Acer* first occur in the late Paleocene (Crane et al., 1990), and the genus has an excellent record based on both fruits and leaves in the Eocene and later Tertiary of North America with at least 91 species (Wolfe & Tanai, 1987). The genus is also diverse in the Tertiary of eastern Asia (Tanai, 1972, 1983) and Europe (Walther, 1972; Procházka & Bůžek, 1975). Interpretations of the subgeneric ranking of fossil species are often provided in the paleobotanical literature, but usually without specifying the characters unique to the group to which the fossil species are assigned. Because *Acer* is an exceptionally diverse genus, often with more than one species occurring at a single location, it is difficult or impossible to link the isolated fruits with the isolated leaves as the same species, yet determination to extant section often requires both fruit and leaf characters. Because the fossil record of this genus is so abundant, there is potential to unravel details of the history of intercontinental exchanges through the Tertiary (Wolfe & Tanai, 1987; Kvaček, 1996); however, it is likely that only the most distinctive sections or species groups can realistically be traced. Also, the natural relationships of extant *Acer* species should be reevaluated with help from molecular studies. The early occurrences of *Acer* in North America, together with the related extinct Eocene fruit, *Deviacer* (Manchester, 1994b; Wehr, 1995), and the North American records of *Dipteronia* mentioned below, all point to North America as a possible center of origin for the "Aceraceae" clade of the Sapindaceae.

Dipteronia has one living species that is restricted to China that is readily recognized by its distinctive elliptical schizocarpic samaras (Fig. 10A). The genus has an excellent record of these fruits in North America, beginning in the late Paleocene (Hells Half Acre, Wyoming; UF 15740D–23086), and continuing through the Eocene (Fig. 10B) and early Oligocene (Meyer & Manchester, 1997). Several complete specimens from the middle Eocene of Republic, Washington, show that the fruits were borne in threes (a typical feature of Sapindaceae) rather than in pairs as in the modern species (e.g., pl. 3, fig. 8 in Wehr, 1995). Whether fruits from the other North American Tertiary occurrences were borne in threes or in pairs is unknown, but the morphology of the schizocarps leaves no question that they are closely related and belong to the same genus. The Republic specimens were sometimes placed in the sapindaceous leaf genus *Bohlenia* Wolfe & Wehr, but without attachment or repeated close association to prove the connection. A single

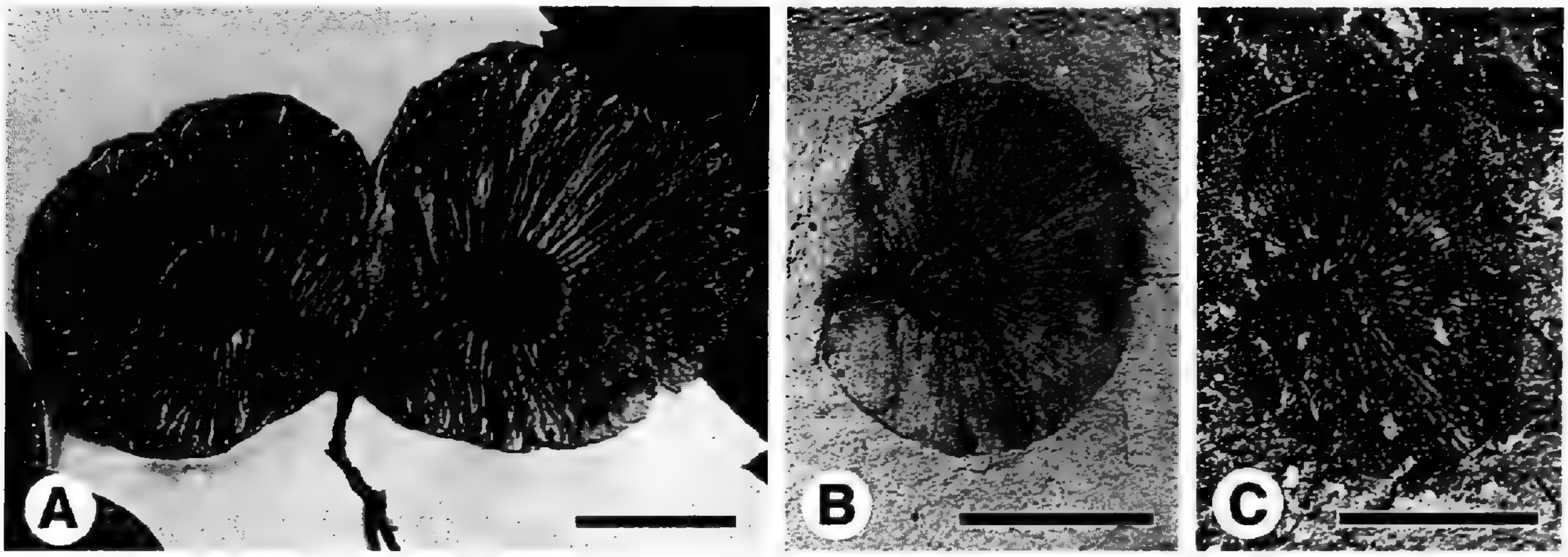


Figure 10. Fruits of *Dipteronia* (Sapindaceae/Aceraceae) from Asia and North America. —A. *Dipteronia sinensis* Oliv. from western Szechuan, China, A: *E. H. Wilson 883*. —B. *Dipteronia insignis* (Lesq.) Brown from the Oligocene Ruby flora, Montana, H. F. Becker Coll., YPM 35346 (orig. Becker, 1960: 393, fig. 11). —C. *Dipteronia* sp. from late Eocene Fushun flora, northeastern China, UCMP 168225. Scale bars = 1 cm.

Dipteronia fruit specimen was recovered from the late Eocene Fushun flora of northeastern China (Fig. 10C), but the genus has not been found in Europe.

Although Asian today, *Koelreuteria* is recognizable by its distinctive inflated winged capsules (Fig. 11B), which are first known in the Eocene of the Green River (Fig. 11A) and Florissant Formations of North America (Edwards, 1927; MacGinitie, 1953, 1969) and from the Oligocene (Weyland, 1937) to Miocene of Germany (Rüffle, 1963), Czech Republic, and Hungary (Bůžek, 1971). In Asia the fruit valves are also known from the Miocene Shanwang flora of China (Hu & Chaney, 1940). In some instances fruit valves of *Craigia* (= *Pteleaecarpum*, Tiliaceae) have been mistaken for *Koelreuteria*, but they can be distinguished by the serial attachment of seeds and the complete septum. *Koelreuteria* has an incomplete septum with seeds borne at a single level within the pod.

Sargentodoxaceae. *Sargentodoxa*, which is native to China today, was recognized by Tiffney

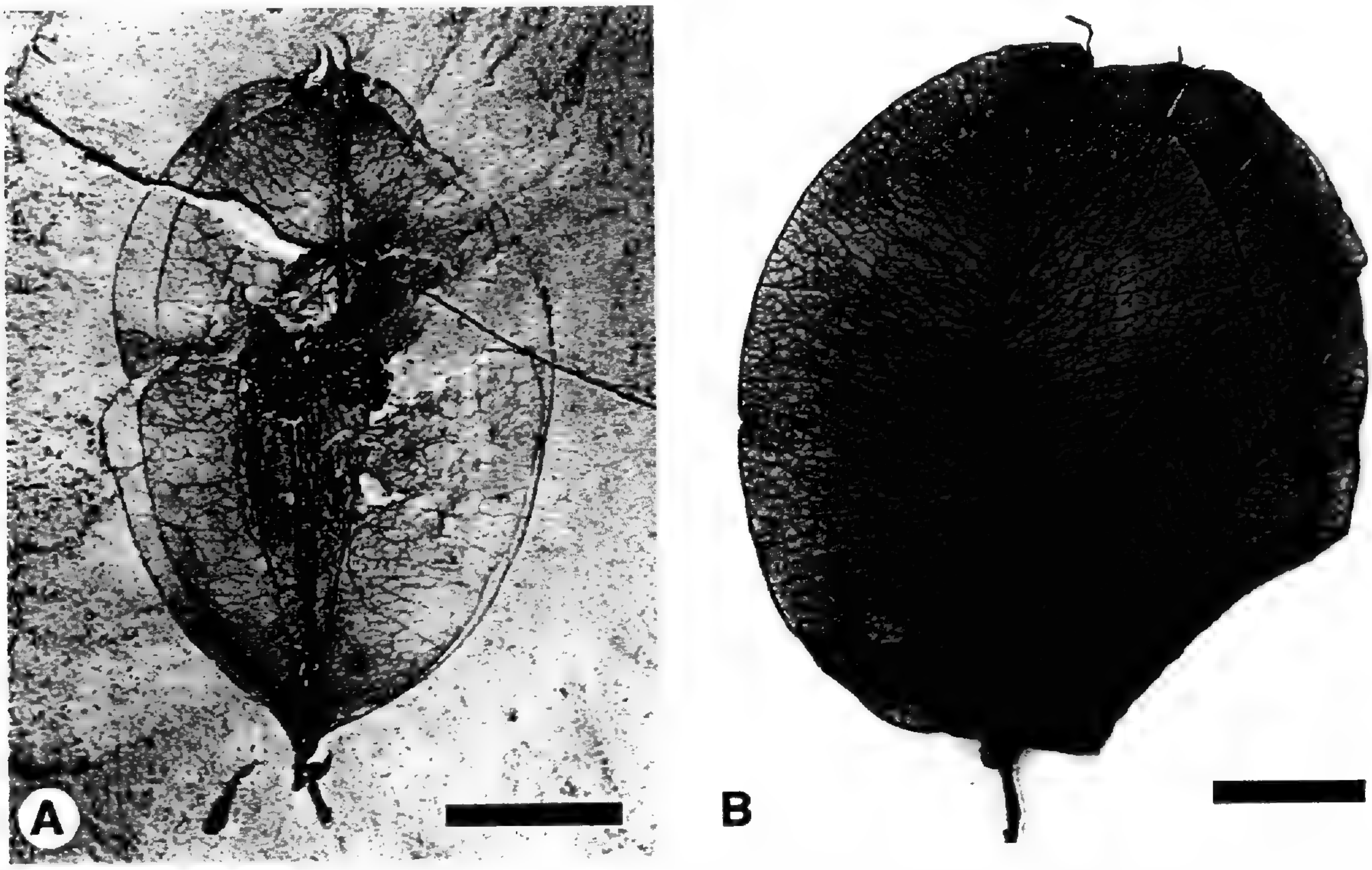


Figure 11. *Koelreuteria* (Sapindaceae) fruits. —A. *Koelreuteria nigricans* (Lesq.) Brown [*Staphylea viridifluminsis* Hollick (1929, Bull. Torrey Bot. Club 56: pl 2, fig. 3)], Green River Formation, DeBeque, Colorado, YPM 20681. —B. Extant *Koelreuteria bipinnata* Franch. Cult., US National Arboretum, FLAS 186865: *F. G. Meyer NA34048*. Scale bars = 1 cm.

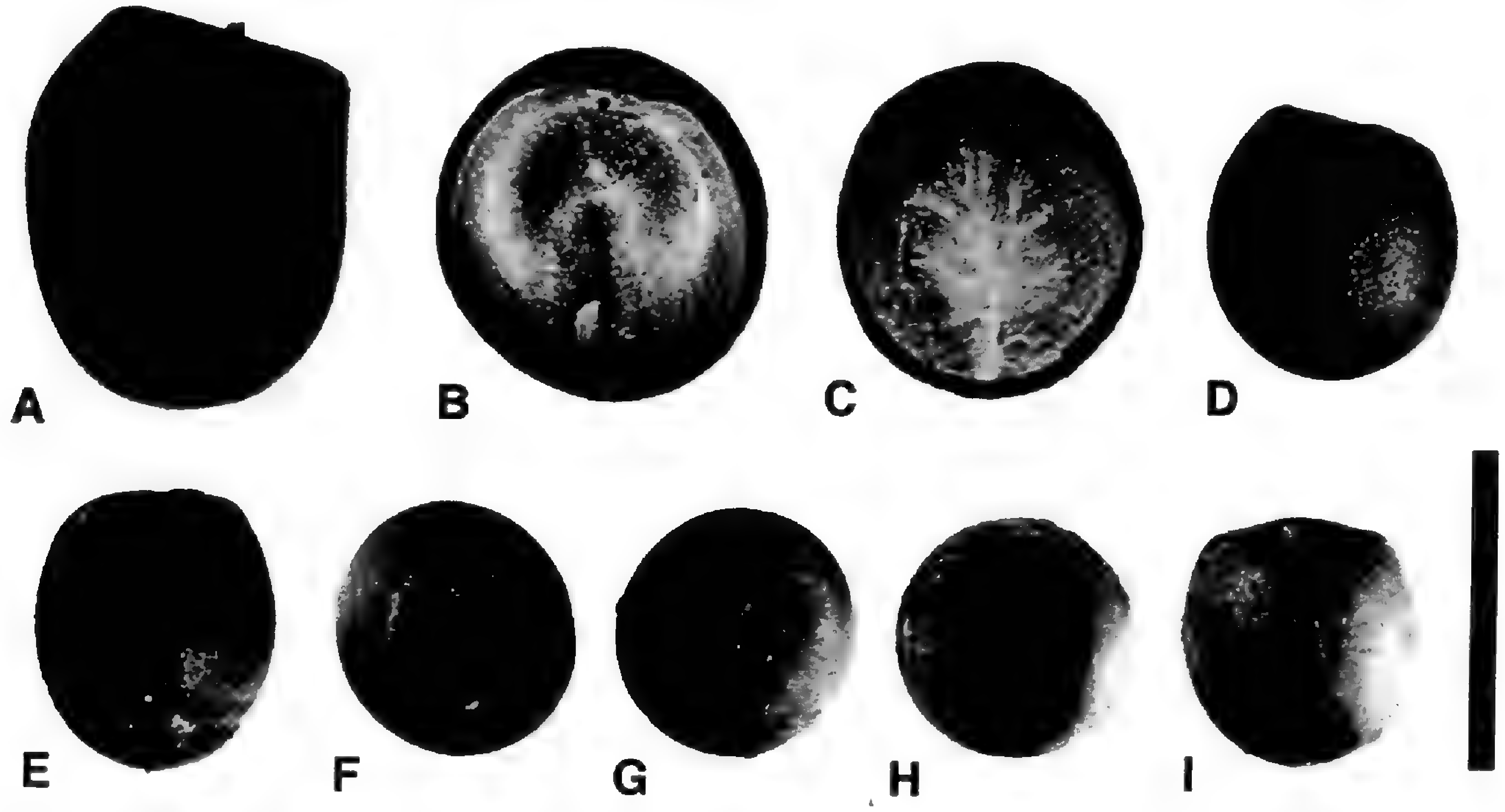


Figure 12. *Sargentodoxa* (Sargentodoxaceae) seeds from Asia and North America. A–C. Extant *Sargentodoxa cuneata* (Oliver) Rehder & Wilson from Anwhei Prov., China, PE 1137193. —A. Lateral view of seed showing smooth shiny testa, hemispherical base, obliquely truncate apical surface. —B. Transversely fractured seed showing thin black seed coat at periphery. Endosperm removed, looking inside toward the apex to reveal the circular facet with micropyle at top, and raphe at bottom. —C. Looking into the basal half of the fractured seed coat, showing the radiating strands of chalaza. D–H. *Sargentodoxa globosa* (Manchester) Manchester comb. nov. from the Middle Eocene Clarno Nut Beds, Oregon. —D. Lateral view showing obliquely truncate apical surface, USNM 424663. —E. Holotype, face view, showing raphe leading between chalaza at base and hilar facet apically, USNM 424644. —F. Same as D, apical view. —G. Specimen in apical view, showing aperture through which raphe passed, USNM 424662; compare with B. —H. Basal view of a specimen showing radiating fibers of chalaza; compare with C. UF 8669. —I. Same specimen in face view, showing chalaza at base and apical facet. Scale bar = 5 mm.

(1993) from the Miocene Brandon Lignite. In addition, the seeds that I described as *Bumelia? globosa* from the middle Eocene of Oregon (Manchester, 1994b) are in reality internal seed molds of the seed coat of *Sargentodoxa*. Both *Bumelia* and *Sargentodoxa* have ovoid seeds with an oblique hilar facet and a thick seed coat; however, the distal end of *Bumelia* is pointed, whereas that of *Sargentodoxa* is more smoothly rounded. In addition, the fossil seeds match *Sargentodoxa* perfectly in the placement of the raphe, micropyle, and chalaza (Fig. 12). Accordingly, I now provide the following new combination, *Sargentodoxa globosa* (Manchester) Manchester comb. nov. (see Appendix 1).

Sargentodoxa also occurs in the uppermost Miocene-lower Pliocene Saugbagger flora of Alsace (Geissert et al., 1990), indicating that it was in Europe at least by the late Tertiary. Bruce Tiffney (pers. comm. 1997) brought to my attention that a seed identified as *Pulmonaria gossmannii* Geissert, Gregor & Mai (pl. 16, figs. 24, 25) is actually *Sargentodoxa*. However, the holotype of *Pulmonaria gossmannii* is not *Sargentodoxa*.

Schisandraceae. *Schisandra*, with 1 extant species in eastern North America and about 24 in Asia, is known from fossil seeds in the Eocene of Oregon (Manchester, 1994b), Miocene of western Czech Republic (Bůžek et al., 1996), and Pliocene of Alsace, France (Gregor, 1981).

Simaroubaceae. *Ailanthus* has distinctive winged fruits that are both easily recognized (Fig. 13A) and readily preserved in lacustrine deposits where leaves are preserved. Although distributed from western China to Korea and in Australia today, the genus was widespread in the Tertiary of the Northern Hemisphere (Tralau, 1963). *Ailanthus* fruits are present in the Middle Eocene of Messel, Germany (Collinson, 1988), as well as the Oligocene of France, Hungary (Rásky, 1956), the Oligocene to early Miocene in the western Czech Republic (Knobloch & Kvaček, 1993; Kvaček, 1996), and the middle Miocene of the Randecker Crater (Rüffle, 1963). In Asia, the fruits occur in the early Oligocene of Kiin Kerish, Kazakhstan (Akhmetiev, 1991), from the Eocene/Oligocene of Fushun (WGCPC, 1978), and the Miocene of Shangwang, China (Hu & Chaney, 1940; WGCPC, 1978), Velika Kema, Sikhote Alin (Fig. 13C), and Shanabuchi, Northeastern Hokkaido, Japan (Tanai & Suzuki, 1965). In North America, *Ailanthus* samaras are known from the Eocene of Colorado, Wyoming (MacGinitie, 1969), Montana (Becker, 1961),

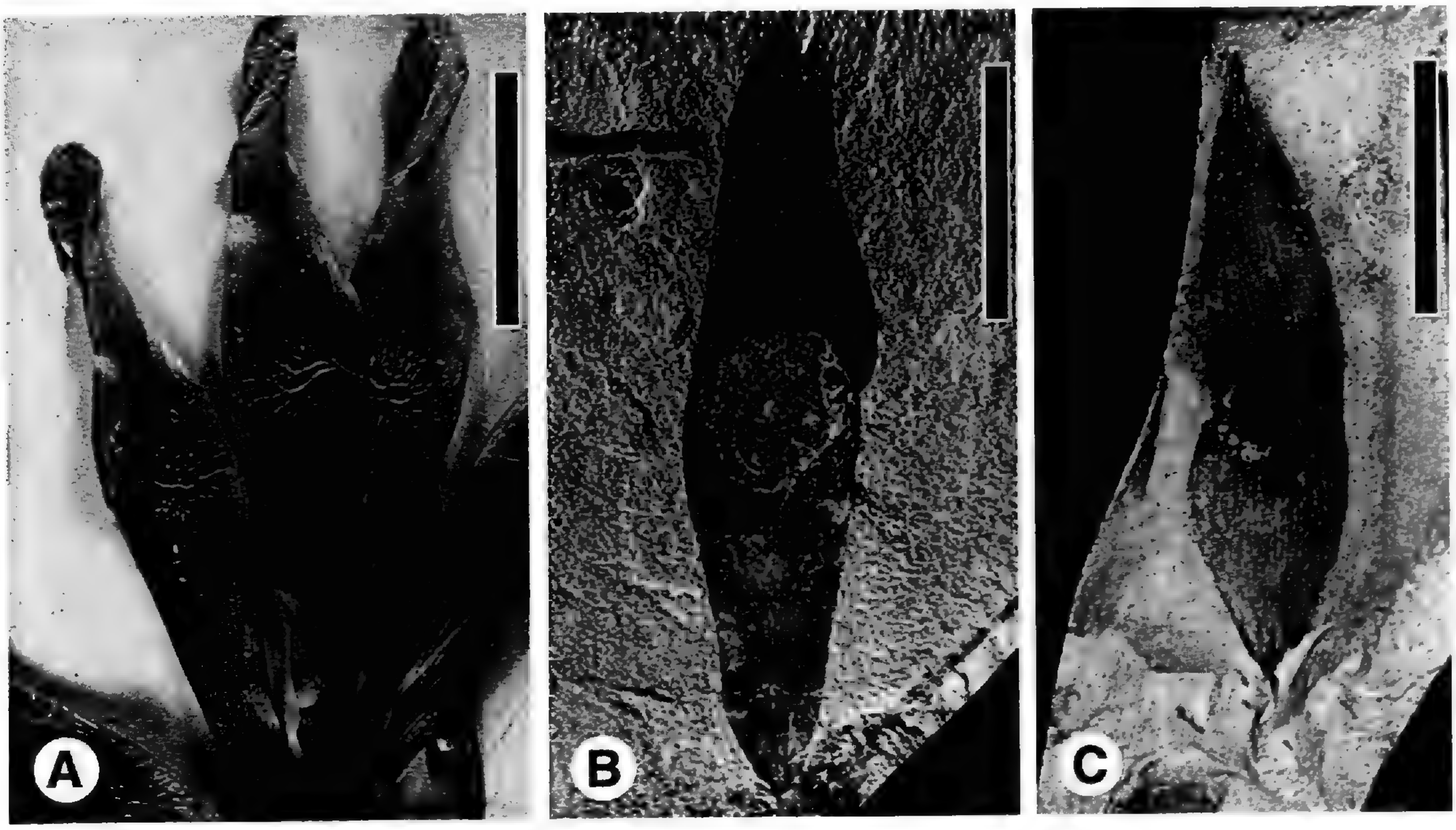


Figure 13. *Ailanthus* (Simaroubaceae) samaras from Asia and North America. —A. Extant *Ailanthus* sp. Chekiang, China, MO 1897584. —B. *Ailanthus* sp. from the late Eocene of Teater Road, Oregon. UF 256–20713. —C. *Ailanthus* sp. from the Miocene of Velikaja Kema, Eastern Sikhote-Alin, Akhmetiev Coll., Geol. Inst. Russ. Acad. Sci. no. 3820/594. Scale bars = 1 cm.

Oregon (Fig. 13B), and California (MacGinitie, 1941), and from the Miocene of Oregon and Idaho (Chaney & Axelrod, 1959; Fields, 1996).

Staphyleaceae. *Turpinia*, distributed today from Indomalesia to Japan and in tropical America, is known on the basis of seeds from the Miocene of Vermont (Tiffney, 1979) and central Europe (Mai, 1964). *Tapiscia*, which occurs today in the mixed mesophytic forests of China, has distinctive fruits and seeds (Fig. 14A, B) that are known as fossils from the Eocene of England (Fig. 14E, F), Germany (Mai, 1980), and Oregon (Fig. 14C, D; Manchester, 1988, 1994b). The extant Carribean genus *Huertea* has seeds similar to, but larger than those of *Tapiscia* (Manchester, 1988), and may be an indication of former exchange between the Caribbean and North America during the Tertiary.

Styracaceae. *Halesia* has extant five species in eastern China and eastern North America. The trees bear fruits with longitudinal wings (usually two or four) that radiate from a spindle-shaped fruit body. Fruits of this genus have been reported from the North American Tertiary (e.g., Brown, 1946a; Lakhanpal, 1958); however, those occurrences do not represent *Halesia* and are probably not even Styracaceae because they lack the diagnostic thick intramarginal vein seen on each of the fruit wings in this genus. Although no longer native to Europe, the genus is well represented by anatomically preserved endocarps in the European Tertiary (Kirchheimer, 1957). Tralau (1965) illustrated particularly well-preserved specimens from the upper Pliocene of Weilerswist, western Germany, with intact wings showing the characteristic intramarginal veins.

Symplocaceae. *Symplocos* is disjunct today between the Old World (excluding Africa) and tropical America. Characteristic fruits occur in the Eocene of Oregon (Manchester, 1994b), California (Tiffney & Haggard, 1996: 41), and Virginia (Tiffney, in press) and the Miocene of Vermont (Tiffney, 1977a). They are especially well represented in the Tertiary of Europe, ranging from the early Eocene (Reid & Chandler, 1933) through the Pliocene with several morphologically distinct species (Kirchheimer, 1950, 1957; Mai, 1995). Also in the European Tertiary are two extinct genera that fit in the Symplocaceae based on fruit morphology: *Palliopora* Kirchheimer and *Sphenotheca* Kirchheimer (Kirchheimer, 1957). In Japan, fruits are known from the upper Pliocene (fig. 9J in Miki, 1937). On the basis of paleopalynology, Krutzsch (1989) provided a summary of the fossil record of Symplocaceae, interpreted to show an upper Cretaceous origin in North America, followed by Paleocene spread across the North Atlantic into Europe, late Eocene arrival in Asia, survival of a European population into the Pliocene, and the southward extension of the genus into the Caribbean and South America, and to the South Pacific during the Pliocene.

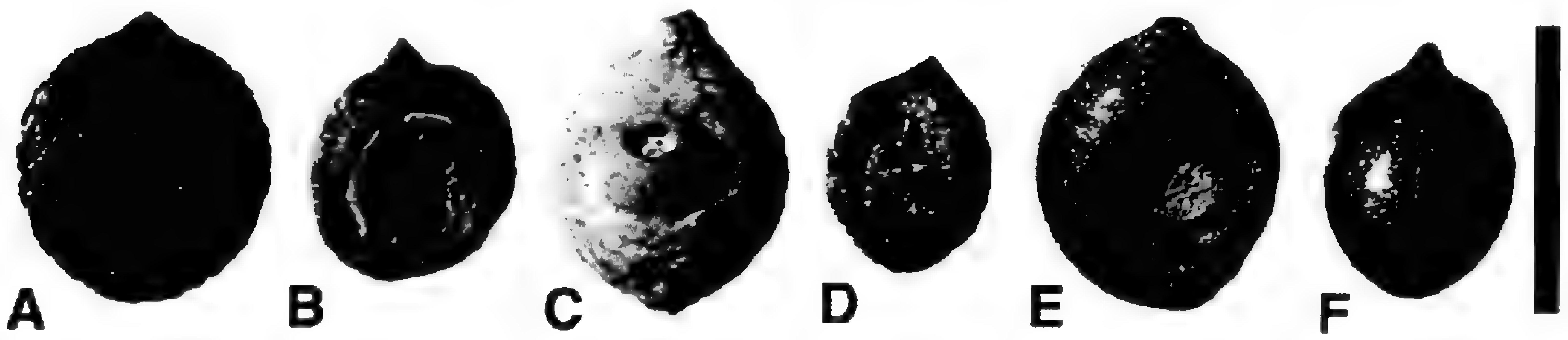


Figure 14. *Tapiscia* (Staphyleaceae) fruits and seeds. —A, B. Fruit and seed from extant *Tapiscia sinensis* Oliv. western Hupeh, China, A: *E. H. Wilson 108.* —C, D. *T. occidentalis* Manchester silica casts of fruit and seed, Middle Eocene Clarno Nut Beds, Oregon. UF 5201, 5205. —E, F. *T. pusilla* (Reid & Chandler) Mai pyrite seed casts, Early Eocene London Clay, England. Scale bar = 5 mm.

Theaceae. *Gordonia,* with about 30 species in tropical and subtropical Asia and one disjunct species in southeastern North America, has distinctive pentalocular, loculicidally dehiscent capsules and winged seeds. It is well represented in the Eocene of southeastern North America by fruits and seeds and in the Miocene of Idaho by seeds (Grote & Dilcher, 1992). *Gordonia* is also well represented in the Eocene to late Miocene of Europe, sometimes attributed to the segregate genus *Polyspora* (Gregor, 1978; Grote & Dilcher, 1992; Mai, 1995). Related extinct fruit genera, including *Andrewsiocarpon* Grote & Dilcher (1989) and *Gordoniopsis* Grote & Dilcher (1992) show that this family was diverse in the Eocene of Tennessee and Kentucky. Extant *Cleyera,* disjunct between Asia and tropical America, has fossil seed records in the Eocene of western North America (Manchester, 1994b) and in the Eocene to Miocene of Europe (Friis, 1985).

Trapaceae. *Trapa* is an aquatic plant with distinctive spiny fruits that grows today in central and southeastern Europe, temperate and tropical Asia, and Africa. Although absent from North America today, the genus is confirmed on the basis of fruits from the Late Oligocene/Early Miocene Weaverville flora of California (Tiffney, pers. comm. 1998), the Miocene of Idaho (Brown, 1937), and the Pliocene Red Bluff flora (Citronelle Formation) of Alabama (Berry, 1914). In Europe, fruits of *Trapa* first occur in the Middle Miocene and continue through the Neogene to the present day (Mai, 1985b, 1995; Wójcicki & Bajzáth, 1997).

Fruits remarkably similar in size and morphology to those of extant *Trapa* occur as early as the Late Cretaceous (Maastrichtian) in Far Eastern Russia (Golovneva, 1991). They differ from the modern species in being borne in a raceme rather than isolated and were therefore placed by Golovneva in the extinct genus *Palaeotrapa* Golovneva. If this may be taken as a direct predecessor of *Trapa,* then the lineage would appear to have its roots in Asia. Later records include fruits from the Pliocene of Japan (Miki, 1952). Despite the apparent antiquity of *Trapa* in Asia, the genus apparently did not spread to Europe or North America until the Neogene (Mai, 1985b). Certainly in Europe it would be expected to be found earlier if it were present, because of the numerous lignitic deposits favorable for preservation of hard aquatic fruits. Although the genus has sometimes been reported on the basis of rosettes of aquatic leaves (e.g., Brown, 1962), these are only superficially similar to those of *Trapa* and are now placed in a fossil genus (*Quereuxia*; see incertae sedis discussion) of unknown familial affinity.

Trochodendraceae. This family includes the extant Asian vesselless genera *Trochodendron* and *Tetracentron. Trochodendron* is known based on fossil fruiting racemes from the Eocene of Washington (Wehr, 1995), the Miocene of Idaho and Oregon (Manchester et al., 1991; Fields, 1996: 304–307), and the Miocene of Kamchatka (Chelebaeva & Chigayeva, 1988) and Japan (Manchester et al., 1991). Wolfe (1989) illustrated and discussed leaves of an extinct trochodendraceous morphology from the middle Eocene of Republic, Washington. The leaves resemble those of extant *Trochodendron* in thick texture (probably evergreen) and small appressed teeth typically confined to the apical half of the lamina, but they differ from leaves of the single extant species of the genus by having palmate venation, a possible primitive feature shared with extant *Tetracentron* (Wolfe, 1989). The subsequent discovery of *Trochodendron* fruits and infructescences from the same locality (Wehr, 1995) leads to the hypothesis that these organs were produced by the same genus, namely *Trochodendron,* but by an extinct species that retained some primitive foliar characters.

Nordenskioldia Heer is an extinct genus based on fruits and infructescences that were widespread in the Paleocene of the Northern Hemisphere. It is also known from the Upper Cretaceous in Asia and North America and from the Miocene of Idaho, in

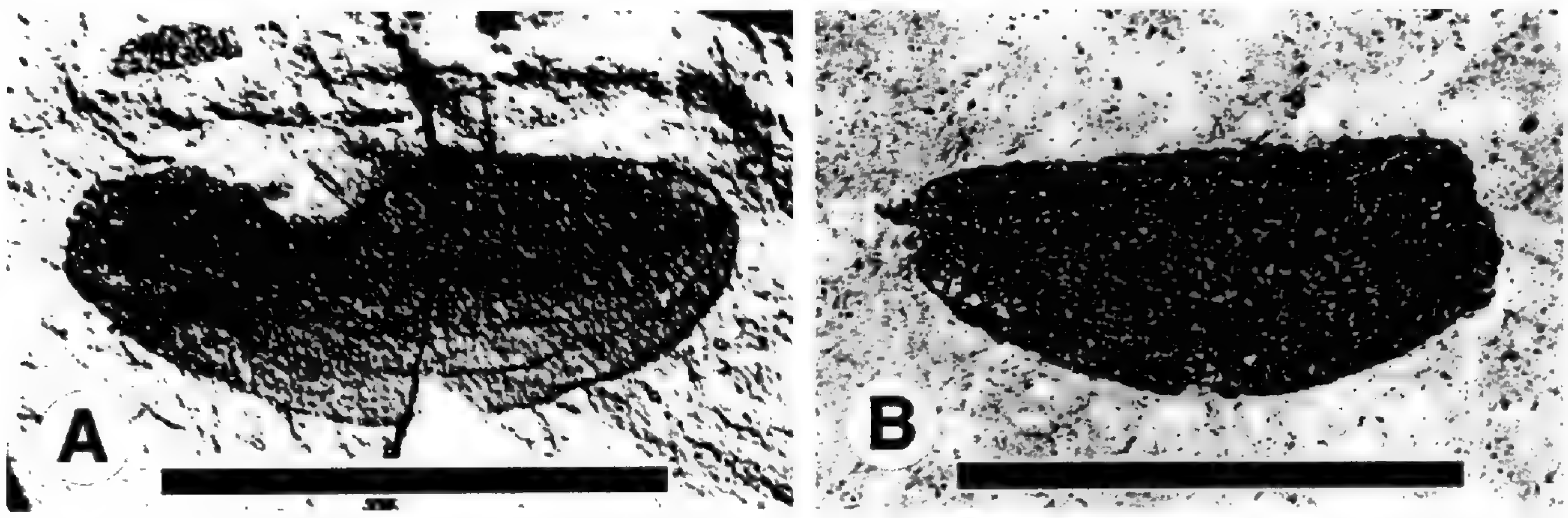


Figure 15. *Cedrelospermum* (Ulmaceae) fruits from North America and Europe. —A. *C. nervosum*, White Cliffs, Clarno Formation, Oregon, UF262–17733. —B. *C. leptospermum*, Messel, Germany, SM.B. Me 7274. Scale Bars = 5 mm.

each case associated with leaves of the "*Cocculus* type" assignable to *Ziziphoides* Seward & Conway (Crane et al., 1991). The trochodendraceous affinities of *Nordenskioldia*, first suggested by Kryshtofovich (1958), were corroborated by Crane et al. (1991), on the basis of anatomically preserved fruits and vesselless xylem of the fruiting axis and associated twigs. *Nordenskioldia* was already established in the Late Cretaceous of North America (Serbet, 1997) and Asia (Senonian of Velui River, Vakrameev, 1958) and had become widespread in northern latitudes of North America, Europe, and Asia by the Paleocene. It was evidently extinct in most areas by the Eocene, but it occurs in the middle Eocene of Washington (Wehr, 1995), and is abundant in the Miocene of Washington and Idaho (Manchester et al., 1991).

Ulmaceae. The Ulmaceae are well represented in the fossil record (Manchester, 1987b). This family is represented in the North American fossil record by both subfamilies: Ulmoideae (*Ulmus*, *Cedrelospermum*, maybe *Zelkova*) and Celtidoideae (*Aphananthe*, *Celtis*). The extant endemic of eastern North America, *Planera*, has been reported from time to time in the literature on fossil leaves of Europe and North America, but none of these are particularly convincing.

Ulmus occurs today in North Temperate areas. Leaves that compare favorably with this genus are common in the Paleocene of the Northern Hemisphere at sites in North America, Greenland, Spitzbergen, and Asia. However, the distinctive winged fruits of *Ulmus* have never been found in association. Although the Paleocene leaves certainly are correctly placed in Ulmaceae (short petioles, asymmetrical lamina, blunt teeth with submedial entry of principal vein), the lack of associated *Ulmus* fruits suggests that they belong to another, possibly extinct, genus of the family. I concur with Kvaček et al. (1994: 116) who noted in reference to specimens from the Paleogene of Spitzbergen that "until associated fruits are recovered to help identify the generic affinity, we suggest that a fossil genus is used . . . ." The name *Ulmites* Dawson is applied in this context (Kvaček et al., 1994). *Ulmites* was spread widely in the Northern Hemisphere by the Paleocene.

Ulmus itself makes its first appearance based on fruits during the Eocene with occurrences in the west-coastal part of North America including California, Oregon, Washington, and British Columbia (Manchester, 1989b). These oldest fruits have narrow wings similar to those of extant section *Chaetoptelea* (e.g., *Ulmus mexicana* and *U. alata*). A rare specimen from One Mile Creek, British Columbia, shows the fruits attached to a foliage-bearing twig (Manchester, 1989b).

Cedrelospermum is an extinct genus of Ulmaceae. Although first described based upon isolated fruits like those in Figure 15, the genus is now known from twigs with attached leaves, fruits, and flowers (Manchester, 1989a). The oldest known fruits and leaves are from the Middle Eocene both in western North America (Green River Formation, Clarno Formation) and Europe (Messel, Germany). In North America the genus persists until the Oligocene in Texas (Manchester, 1989a) and to the Oligocene or Miocene of southern Mexico (Magallón-Puebla & Cevallos-Ferriz, 1994c). But in Europe the genus survived to the middle Miocene. The absence of the distinctive fruits and leaves in any of the known Asian Tertiary floras indicates that it did not cross Beringia and did not penetrate eastward beyond the Urals.

It is interesting to note similarities and differences in apparent evolutionary trends between the European and North American populations of *Cedrelospermum*. Both in North America and in Europe, the smallest fruits (5–7 mm) occur in the oldest localities, and the largest ones occur in the

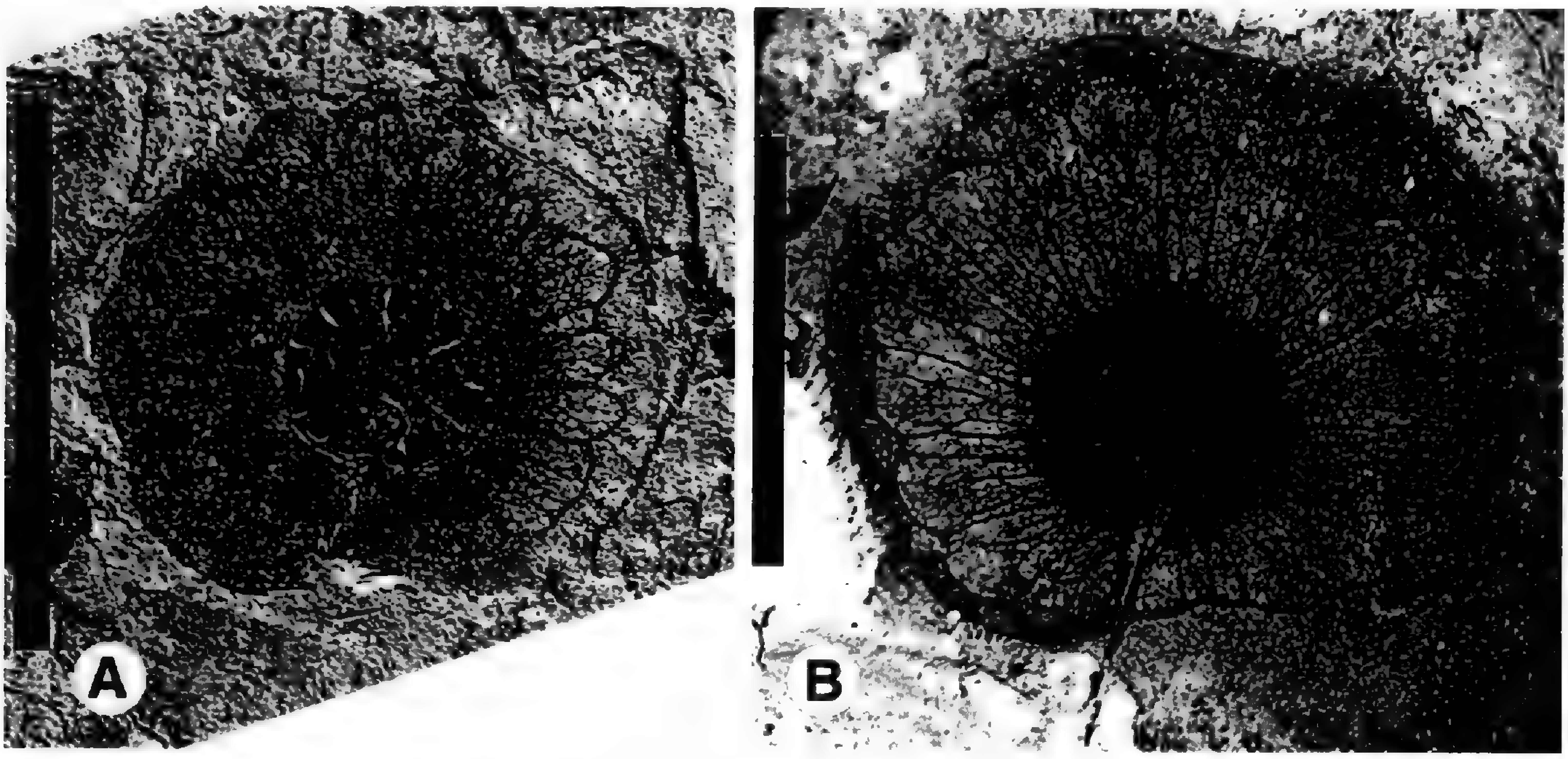


Figure 16. *Buzekia tertiaria* (Weyland) comb. nov. from the Tertiary of central Europe and western North America. —A. Specimen from the late Oligocene of Rott, Germany. Köln coll. Weyland no. 1773. —B. Specimen with identical morphology and venation from the middle Miocene of Oviatt Creek flora, Idaho, UF 18343. Scale bars = 1 cm.

youngest localities. In Europe, all observed specimens are consistent in having a single wing with a distal stigmatic notch. In the Oligocene to Miocene of North America the normal condition is to have two wings, one of them large and comparable in venation to the single wing of the European species, and a second, small vestigial wing (Manchester, 1987b). However, in the middle Eocene of North America there is variation from forms with a single wing resembling the European species, to those with two wings, of the type found later in North America. This greater variability in the North American Eocene forms may indicate that the original populations were more plastic, and that after separation of the two geographic areas, the European and American populations became canalized in different morphological patterns.

INCERTAE SEDIS

Buzekia gen. nov. (see Appendix 1 for generic diagnosis) is a distinctive winged fruit of uncertain affinities that was formerly placed provisionally in the extant legume genus *Pterocarpus* (Weyland, 1937; Bůžek, 1992). *Buzekia tertiaria* (Weyland) Manchester comb. nov. (see Appendix 1) is well known from the late Oligocene and early Miocene of central Europe (Fig. 16A) and has recently been recovered from the middle Miocene of Idaho (Fig. 16B).

A propeller-like fruit with an elongate body and six epigynous wings was named *Calycites ardtunensis* by Crane (1988). Occurrences in the Paleocene of Scotland (Crane, 1988; Boulter & Kvaček, 1989) and Wyoming (Crane, 1988) indicate a likely North Atlantic crossing. In North America, the fruits persist into the middle Eocene of the Clarno Formation, Oregon, and Republic, Washington (Crane, 1988; Wehr, 1995: pl. 5, fig. 5).

Distinctive reniform, lenticular, sometimes paired, verrucate-walled objects known as *Porosia* Hickey (1977) are present in the late Cretaceous and Paleocene of the Rocky Mountains (Fig. 17B, C; Brown, 1962, as *Hydromystria*; Hickey, 1977; McIver & Basinger, 1993; Crane et al., 1990), and in the Paleocene of the Amur region, southeastern Russia (Fig. 17A; Krassilov, 1973: pl. 23, figs. 49–61; 1976: pl. 12, figs. 1–6, as *Limnobiophyllum*), the Koryak highland of northeastern Russia (Golovneva, 1994: pl. 27, figs. 4–6, as *Limnobiophyllum*), and eastern Kazakhstan (Akhmetiev & Chelebaeva, 1989: figs. 5, 6, as *Limnobiophyllum*). They are also known from the Paleocene or early Eocene Pilot Rock flora, Oregon (Fig. 17D; Gordon, 1985: fig. 3d). *Porosia* is unknown from Europe and thus seems to be a good example of a taxon that dispersed across Beringia during the Late Cretaceous or Paleocene.

When Krassilov (1976) erected the genus *Limnobiophyllum*, he illustrated it with specimens of *Porosia* (sensu Hickey, 1977), but he based the genus on *Lemna* (*Spiradela*) *scutata* Dawson, a species with thin, orbicular leaves now known to be an extinct genus of lemnaceous affinity (Kvaček, 1995; Stockey et al., 1997). The former hypothesis that *Porosia verrucosa* represented float leaves produced by the same plant as *Limnobiophyllum* (Krassilov,

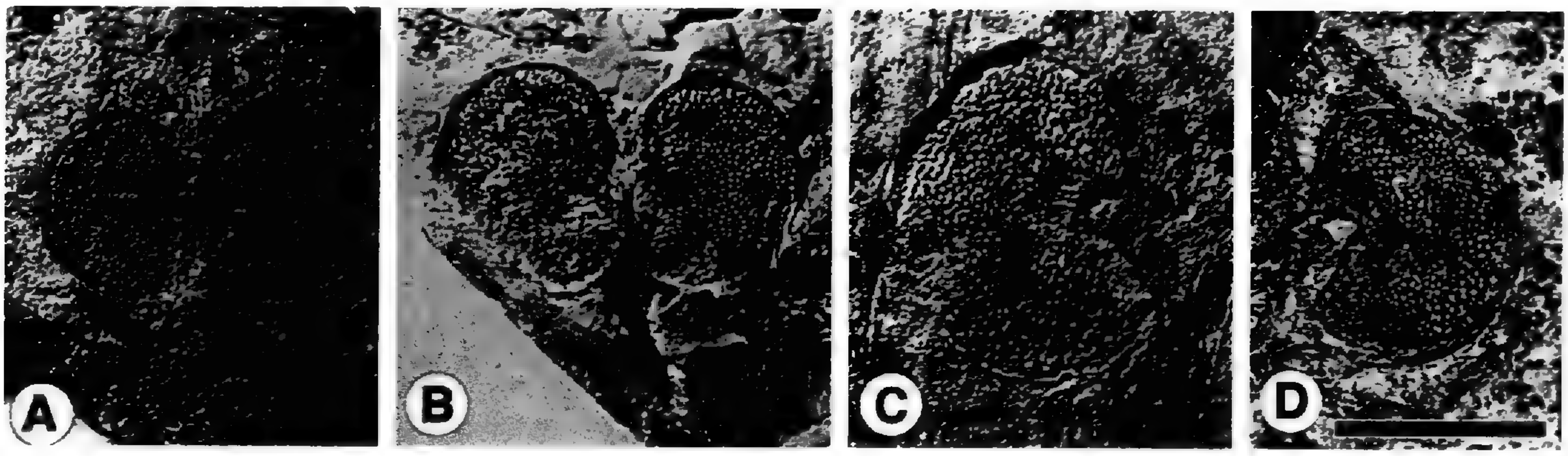


Figure 17. *Porosia verrucosa* (Lesquereux) Hickey from the Paleocene of eastern Asia and North America. —A. Pair of fruits from Belagory, Amur District, Russia, UF 18650–27771. —B. Pair of fruits on peduncle, East Fork, Razor Creek, Montana, UF 18163–25934. —C. Individual fruit showing verrucate texture, Linch, Wyoming, UF 18260–15023. —D. Similar specimen from Late Paleocene or Early Eocene Herron Formation, Pilot Rock (Denning Spring), Oregon, UF 271–27772. Scale bar = 1 cm, applies to A–D.

1976) resulted in use of the same name for two plants now considered to be unrelated. However, that hypothesis remains unsubstantiated, and the lack of *Porosia* in co-occurrence with the *Limnobiophyllum* at European localities casts doubt on their affiliation. Analysis of silicified *Porosia* specimens from the Maastrichtian of Alberta (Aulenback & Braman, 1991) has led some workers to the conclusion that these are fruits, rather than leaves (McIver & Basinger, 1993; Serbet, 1997), as Lesquereux (1878) originally supposed. Cuticularly preserved specimens from the lower Paleocene middle part of the Tsugayan Formation near the confluence of the Dermakon and Bureya Rivers of Amur District, southeastern Russia, provide useful epidermal information for *Porana* (Krassilov, 1973, 1976, as *Limnobiophyllum*). Krassilov (1973) described them as epistomatic leaf blades with rare stomata, the guard cells and lateral subsidiary cells thinly cutinized, sunken in a pit formed by polar subsidiary cells and encircling cells, and scattered simple short conical trichomes. Krassilov noted that this cuticular structure is distinct from that of Hydrocharitaceae, Nymphaeaceae, and Lemnaceae, and more comparable to the stomatal complexes present in several extant araceous genera.

Quereuxia Kryshtofovich ex Nevolina (syn. *Trapago* McIver & Basinger) is an extinct genus of floating aquatic plant with rosettes of simple and compound leaves with up to nine or eleven obovate serrated leaflets (Fig. 18). It occurs in the late Cretaceous and Paleocene of both North America and eastern Russia (Kryshtofovich, 1953). Some confusion has surrounded the name of this plant because *Quereuxia* was first published invalidly (Kryshtofovich, 1958, provided no diagnosis, hence creating a nomen nudum). Therefore, McIver and Basinger (1993) proposed a new name, *Trapago,* for the genus. However, in the intervening years, Nevolina (1977) had validated *Quereuxia* by providing a diagnosis and designating *Q. angulata* as the type species. I thank Leo Hickey for his help in unravelling the complex nomenclatural history of this taxon. The Russian occurrences were recently reviewed (Samilina, 1988; Golovneva, 1991), and a suite of relatively complete vegetative plants was described in detail from the Cretaceous of Alberta, Canada (Stockey & Rothwell, 1997). The North American representatives were sometimes misplaced in *Trapa* (Brown, 1962), but the affinities with that genus are only superficial (McIver & Basinger, 1993; Stockey & Rothwell, 1997). Although *Quereuxia* is shared between North America and Asia during the late Cretaceous and Paleocene, it is unknown from the European Tertiary and appears to have become extinct by the end of the Paleocene.

PATTERNS

The modern flora of North America is the result of evolution, immigration, and extinction of numerous taxa during a period when angiosperms had become dominant in all but the highest elevations and latitudes. Although some of the extant genera indigenous to North America have fossil records that can be traced to the Cretaceous, most have their first known records in the Tertiary.

During any given time interval, the genera found in North America can be classified into one of four main patterns of geographic distribution (Fig. 20): (1) Circumboreal, with species in Asia, North America, and Europe (usually also Greenland and Spitsbergen; Fig. 20A); (2) Euro-North American, with species found in North America and Europe (Fig. 20B); (3) Amer-Asian, with species shared between North America and Asia (Fig. 20C); and (4) North American endemics (Fig. 20D), those not known to be present in the other regions. All of

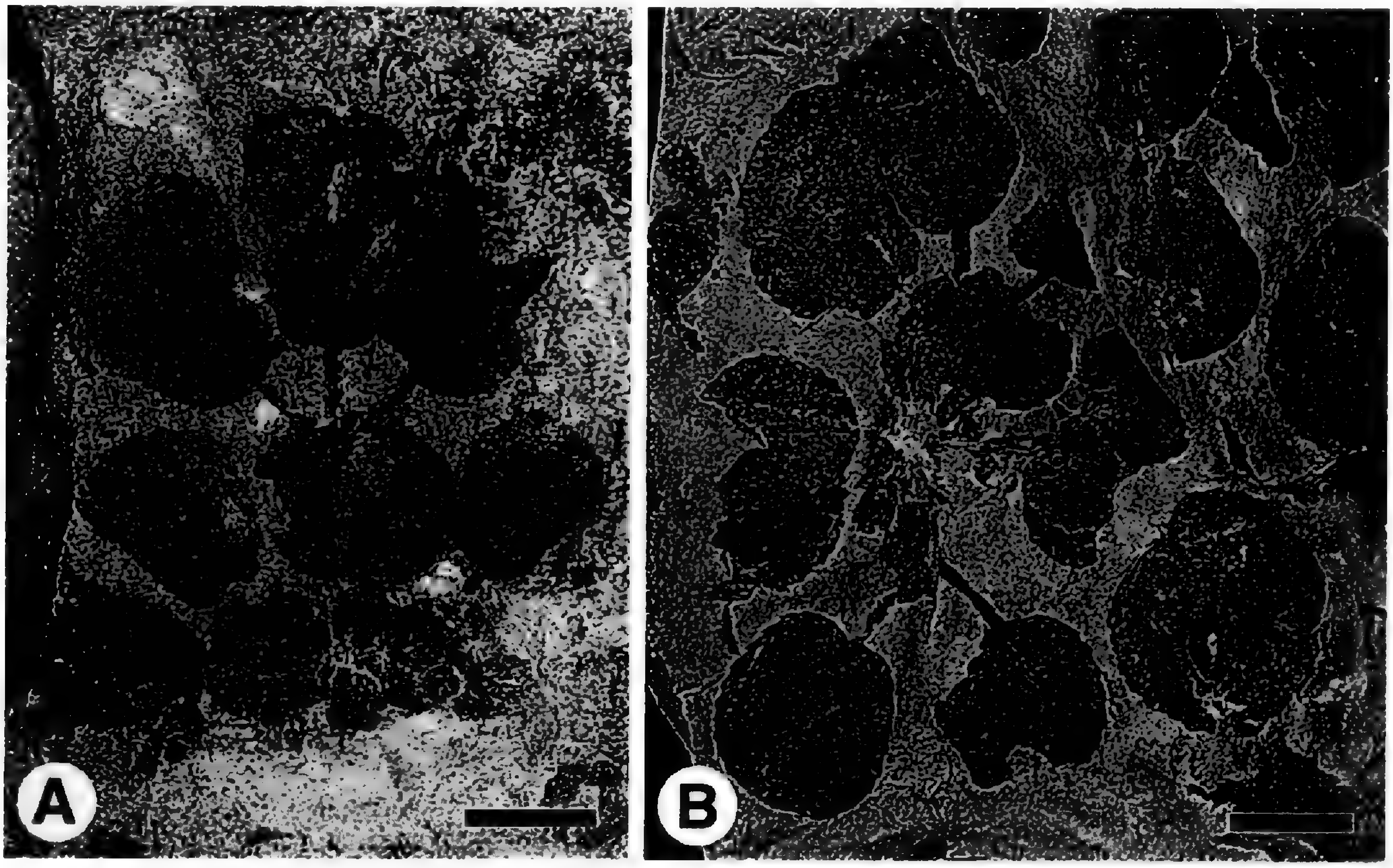


Figure 18. *Quereuxia angulata* (Newberry) Kryshtofovich from the Paleocene of Asia and North America. —A. Rosette of several leaves from Raritkin Series, Koryak Upland, northeastern Russia, Golovneva 90–642. —B. Similar specimen from the Fort Union Formation, Black Buttes, Wyoming, UF 15886–14176. Scale bars = 1 cm.

these patterns occur in each of the Tertiary epochs, but the proportion of taxa in each category differs from one epoch to the next. During the Eocene, for example, pattern 2 predominates, whereas in the Miocene, pattern 1 is the strongest. Other patterns exist that do not include North America (e.g., taxa shared between Europe and Asia, but not North America, and those endemic to Europe or Asia) but are outside the charge and scope of this article. For this overview, comparisons have been made at the generic level. Analysis at the species level is reasonable only in the case of those genera whose fossilized organs preserve characters sufficient to permit the morphological distinction of species using criteria comparable to those used to distinguish modern species in related extant genera.

The stratigraphic and modern distributions of selected genera are summarized graphically in the summary chart (Fig. 19) and and in Figures 21–25. By comparing the stratigraphic ranges of genera within different landmasses, it is possible to infer likely routes and timing of intercontinental dispersals of different taxa. Caution must be exercised in evaluating the data, because the apparent absence of a taxon from a particular time interval and/or region may be due to absence of comparable fossiliferous strata or less thorough sampling. For example, Pliocene paleobotanical localities are rare in North America but common in Europe and Japan; thus the ranges of many North American taxa appear to end in the Miocene. However, in cases of genera with Miocene records in North America that are still living in North America today, I plot the range to include the intervening Plio-Pleistocene.

PALEOCENE

Paleocene floras of Wyoming, Montana, North Dakota, Alberta, and Saskatchewan are dominated by deciduous taxa of Taxodiaceae, Ginkgoaceae, Platanaceae, Cercidiphyllaceae, Trochodendraceae, Betulaceae, and Juglandaceae. Other common elements include Cupressaceae, Lauraceae, Zingiberaceae, and aquatic plants of the Araceae/Lemnaceae (Brown, 1962; Crane et al., 1990; McIver & Basinger, 1993; Stockey et al., 1997). Many of the genera are shared with other Paleocene floras of the Northern Hemisphere. Figure 21 shows three genera that were circumboreal during the Paleocene, with records in North America, Europe, Greenland, and Asia: *Nordenskioldia*, *Nyssidium*, and *Palaeocarpinus*. The first two were already present in North America and Asia by the Maastrichtian, so their distribution in the Paleocene may be simply a function of earlier history. A similar situation is apparent for *Metasequoia*, *Glyptostrobus*, and *Platanus*. The distribution of *Palaeocarpinus*, however, suggests that overland passage was possible across Europe, North America, and Asia during the Paleocene. "Paleocene endemics" of North America (i.e., taxa not known from other continents at that time) include *Cranea, Cyclocarya,* and *Polyptera* Manchester & Dilcher (Fig. 22). *Cranea* and *Polyptera* apparently became extinct without spreading to other continents, whereas *Cyclocarya* subsequently appeared in Europe and Asia and remains today in China.

There is some evidence of provinciality during the Paleocene. Several genera of the North American Paleocene are shared with the Asian Paleocene, but apparently are lacking in the Paleocene of Greenland, Spitsbergen, and Europe (examples in Fig. 23): *Amersinia, Fokieniopsis, Limnobiophyllum, Macginitiea, Porosia,* and *Quereuxia.* This suggests probable continuity via Beringia. There are also some genera shared between North America and Europe during the Paleocene that are unknown in the Asian Paleocene (Figs. 24, 25): *Calycites ardtunensis, Fagopsiphyllum, Meliosma,* and *Platanites.*

Geophysical data have been interpreted to indicate that both the Beringial and North Atlantic corridors were present during the Paleocene (Tiffney, 1985b). However, Woodburne and Swisher (1995: 338) indicated that intracontinental overland interchange of mammals involving North America was minor during the Paleocene except in the latest part of the epoch. They inferred that the first important land mammal migration episode of the Tertiary occurred during the Clarkforkian, with the introduction of mammalian taxa of both European and Asian origin.

Paleobotanical evidence for late Paleocene/early Eocene exchange across the North Atlantic derives from the occurrence of fruit and seed taxa in the early Eocene London Clay flora (Reid & Chandler, 1933; Chandler, 1961; Collinson, 1983) that are also known from the late Paleocene (Clarkforkian) of the Rocky Mountain and Great Plains regions. Examples include *Cornus* (cornelian cherry group), *Juglandicarya cantia* Reid & Chandler (similar to *J. simplicarpa* of North America), *Langtonia* Reid & Chandler (Tiffney & Haggard, 1996), and *Meliosma* sect. *Kingsboroughia* (Van Beusekom, 1971; Crane et al., 1990). *Platycarya* may also conform to this pattern, being known from pollen in the Paleocene Reading Beds of England and some sites in the Rocky Mountain region (Wing, 1984) and confirmed on the basis of infructescences and fruits in the early Eocene of both regions.

EOCENE

The Eocene was the longest epoch of the Tertiary (ca. 21 million years), about twice as long as the Paleocene. This was an especially important interval in the history of the North American flora, during which climate reached the warmest conditions of the Tertiary. With the addition of genera suited to warmer climate, floras of the Eocene became more diverse than those of the Paleocene. All of the dicotyledonous families common in the North American Paleocene persisted into the Eocene, and many underwent further radiation producing both extinct and extant genera.

Woodburne and Swisher (1995) recognized three mammalian faunal interchange "events" during the Eocene. The first, in the Early Eocene (Wasatchian), is a major overland dispersal between North America and western Europe, with greater generic similarity between the faunas of North America and western Europe than any time in the Cenozoic before or since (McKenna, 1975; Woodburne & Swisher, 1995). The second, during the Middle Eocene (Late Uintan), records an influx of probable Asian immigrants (Woodburne & Swisher, 1995). The third interchange interval, during the Late Eocene (Chadronian), involves fewer taxa, but also appears to indicate exchange across Beringia. Through the early and middle Eocene, similarities between the flora of western North America and western to central Europe became very pronounced with numerous shared genera, including both thermophilic and mesophytic elements. Some taxa were also shared between the Eocene of North America and Asia, but most of these seem to be holdovers from the Paleocene, rather than new appearances (examples: *Fagopsiphyllum* gen. nov., *Ginkgo, Nordenskioldia* Heer, *Nyssidium* Heer, *Palaeocarpinus* Crane, and *Platanus*). A few newly appearing genera that were shared between the Eocene of Asia and North America include *Craigia, Eucommia,* and *Paliurus.* In general, the Asian Eocene flora appears to lack the diversity of thermophilic elements such as Icacinaceae and Menispermaceae observed in North America and Europe. It remains possible that the apparent dissimilarity of the floras results from fewer sampled sites in Asia and the lack of rich fruit and seed assemblages there for comparison with those in Europe and North America.

It is noteworthy that the Aceraceae, Betulaceae, Cercidiphyllaceae, Icacinaceae, Menispermaceae, Pinaceae, Taxodiaceae, and Vitaceae, which are common in western North American Eocene localities, are lacking from the Eocene of southeastern

Genus	Stratigraphic and Geographic Distribution							Comments
	K	PA	EO	OL	MI	PL	RE	
Acer		NA	NA AS	NA EU AS	NA EU AS	> EU AS	NA EU AS	Paleogene Beringial crossing; subsequent arrival in Europe.
Actinidia			NA	EU	EU	EU	AS	Asian endemic today with Euramerican Tertiary record.
Ailanthus			NA EU AS	EU AS	NA EU AS	EU AS	AS	Now native from Asia to Australia; formerly widespread in Northern Hemisphere.
Alangium			NA EU	EU	NA EU	EU AS	AS	Now native in Asia and Africa, once common in Europe and N Amer. Ignore leaf reports.
Alnus			NA EU AS	NA EU AS	NA EU AS	NA EU AS	NA EU AS	These ranges are plotted based on the diagnostic woody infructescences.
Amentotaxus	NA	NA EU	NA EU	> >	NA EU		AS	Paleogene North Atlantic crossing; subsequent arrival in Asia.
Amersinia		NA AS						Eocene Beringial crossing; absent from Europe.
Anamirta			NA				AS	Tertiary Beringial crossing.
Betula		AS	NA	NA EU AS	NA EU AS	NA EU AS	NA EU AS	Occurrences confirmed from diagnostic trilobate inflorescence bracts.
Buzekia				EU	NA EU			Possible middle or late Tertiary Beringial crossing.
Calycites ardtunensis		NA EU	NA					North Atlantic crosser.
Carya			NA	NA EU	NA EU AS	NA EU AS	NA AS	Highly diverse in Miocene of Europe.
Catalpa				NA EU			NA AS	Plotted on the basis of winged seeds.

Figure 19. Chart showing the stratigraphic and geographic distribution of selected conifer and angiosperm genera in the Northern Hemisphere. K = Cretaceous; PA = Paleocene; EO = Eocene; OL = Oligocene; MI = Miocene; PL = Pliocene + Pleistocene; RE = Recent; NA = North America; EU = Europe; AS = Asia. The symbol > indicates fossils unknown from that interval but inferred because of related species in both older and younger intervals.

Genus	Stratigraphic and Geographic Distribution							Comments
	K	PA	EO	OL	MI	PL	RE	
Cedrelospermum			NA EU	NA EU	EU			Eocene North Atlantic crossing; absent from Asia.
Cercidiphyllum				NA EU	NA EU	EU AS	AS	Fruits in clusters. Racemose fruit occurrences are treated here as *Nyssidium.*
Comptonia		AS	NA EU AS	NA EU AS	NA EU AS	> EU AS	NA	Eastern North American endemic today with circumboreal Tertiary distribution.
Cornus		NA	NA EU	NA EU AS	NA EU	> EU	NA EU AS	Also native today in South America and Africa.
Corylopsis			NA EU	EU	EU	EU	AS	Eocene North Atlantic crossing; subsequent arrival in Asia.
Craigia			NA SP AS	NA EU AS	EU AS	EU AS	AS	North America, Asia and Spitsbergen (SP) in Eocene; Oligocene appearance in central Europe.
Cruciptera			NA EU	NA				Eocene North Atlantic crossing; absent from Asia.
Cyclocarya		NA	NA	EU AS	EU AS	EU AS	AS	First appearance in N. America; survival in Europe through Pliocene and in Asia through Recent.
Decodon			NA EU	EU AS	EU AS	EU	NA	Eocene North Atlantic crossing, subsequent arrival in Asia.
Dipteronia		NA	NA AS	NA			AS	Tertiary Beringial crossing.
Emmenopterys			NA				AS	Possible Beringial crossing.
Ensete			NA				AS	Also extant in Africa.
Eucommia			NA AS	NA AS	EU AS	EU AS	AS	Paleogene Beringial crossing; subsequent arrival in Europe.

Figure. 19. Continued.

Genus	Stratigraphic and Geographic Distribution							Comments
	K	PA	EO	OL	MI	PL	RE	
Fagopsiphyllum		NA EU	AS					Paleocene North Atlantic crossing, Eocene arrival in Asia.
Fagus				NA EU AS	NA EU AS	> EU AS	NA EU AS	Dispersed rapidly across Northern Hemisphere in early Oligocene.
Florissantia			NA	NA	AS			Tertiary Beringial crossing; absent from Europe.
Fraxinus			NA	NA EU	NA EU AS	> > AS	NA EU AS	Ignore leaf reports in favor of samaras.
Gordonia			NA EU	> EU	NA EU	>	NA AS	Eocene North Atlantic crossing, subsequent arrival in Asia.
Glyptostrobus		NA EU AS	NA EU AS	EU AS	NA EU AS	EU AS	AS	Asian endemic today with former circumboreal distribution.
Halesia					EU	EU	NA AS	Winged fruits with prominent intramarginal veins.
Hydrangea			NA EU	NA EU	NA EU AS	> EU >	NA AS	Occurrences confirmed from calyces.
Illicium			EU		NA	>	NA AS	North American fossil occurrence based on fruit; European based on seeds.
Iodes			NA EU	EU			AS	Plotted distribution includes *Palaeohosiea*. Also occurs in Africa today.
Juglans			NA	NA EU AS	NA EU AS	NA EU AS	NA EU AS	Sec. *Rhysocaryon* confined to N America. Sec. *Cardiocaryon* circumboreal in Oligocene.
Koelreuteria			NA	EU	EU AS		AS	Eo-Oligocene North Atlantic crossing, subsequent appearance in Asia.
Langtonia		NA	NA EU					Late Paleocene or Eocene North Atlantic crossing.

Figure. 19. Continued.

Genus	Stratigraphic and Geographic Distribution							Comments
	K	PA	EO	OL	MI	PL	RE	
Leitneria				AS	EU AS	EU	NA	North American endemic with Eurasian fossil record.
Limnobiophyllum		NA AS	NA		EU			Paleocene Beringial crossing; subsequent arrival in Europe.
Liquidambar			NA AS	NA EU AS	NA EU AS	EU AS	NA AS	Distinctive leaves and infructescences.
Liriodendron				EU	NA EU AS	EU >	NA AS	Good Tertiary record in Europe despite absence there today.
Macginitiea		NA AS	NA AS					Paleocene Beringial crossing.
Mahonia			NA	NA EU	NA EU	>	NA AS	Initial North Atlantic crossing; subsequent arrival in Asia.
Mastixia			NA EU	EU	EU	EU	AS	Initial North Atlantic crossing; subsequent arrival in Asia.
Meliosma	NA EU	NA EU	NA EU	EU	EU	EU	NA AS	Initial North Atlantic crossing; subsequent arrival in Asia.
Metasequoia	NA AS	NA EU AS	NA AS	NA AS	NA AS	AS	AS	Classic example of Chinese living fossil.
Nordenskioldia	NA NA	NA EU AS	NA AS		NA			Circumboreal in Paleocene, North American endemic in Miocene.
Nyssa		NA	NA EU	NA EU AS	NA EU AS	NA EU AS	NA AS	Classic Amer-Asian disjunct modern distribution with former European distribution.
Nyssidium	NA AS	NA EU AS	NA EU AS					Circumboreal Paleocene to Eocene; precursor of *Cercidiphyllum*.
Palaeocarpinus		NA EU AS	NA AS					Paleocene circumboreal.

Figure. 19. Continued.

Genus	Stratigraphic and Geographic Distribution							Comments
	K	PA	EO	OL	MI	PL	RE	
Palaeophytocrene		NA	NA EU	NA				Eocene North Atlantic crossing.
Paliurus			NA AS	NA EU AS	NA EU AS	> AS	EU AS	Eocene Beringial crossing; Late Oligocene appearance in Europe.
Pentoperculum			NA EU					Eocene North Atlantic crossing.
Platanites	NA	NA EU	NA					Maastrichtian or Paleocene North Atlantic crossing.
Platycarya			NA EU				AS	Early Eocene North Atlantic crossing; Late Tertiary arrival in Asia.
Porosia	NA ?	NA AS	NA ?					Paleocene Beringial crossing.
Pterocarya				NA EU	NA EU AS	EU AS	EU AS	Distribution plotted on the basis of diagnostic biwinged fruits.
Pyrenacantha			NA EU				AS	Also in Oligocene Fayum flora, Egypt. Disjunct between Asia and Africa today.
Quereuxia	NA AS	NA AS						Maastrichtian Beringial crossing.
Sabal	NA	NA EU	NA EU AS	NA EU AS	NA EU AS	> EU	NA	Distribution plotted on the basis of distinctive seeds and costapalmate leaves.
Sargentodoxa			NA		NA	EU	AS	Chinese endemic with Eur-American history.
Schisandra			NA			EU	NA AS	Classic Amer-Asian disjunct distribution with former European distribution.
Symplocos			NA EU	EU	NA EU	EU	NA AS	Eocene North Atlantic crossing.
Tapiscia			NA EU				AS	Eocene North Atlantic crossing; subsequently in Asia. Sister genus *Huertea* extant in Cuba.

Figure. 19. Continued.

Genus	Stratigraphic and Geographic Distribution							Comments
	K	PA	EO	OL	MI	PL	RE	
Tetraclinis			EU	NA EU	EU	EU	EU	Eo-Oligocene North Atlantic crossing.
Tilia			NA	NA EU AS	NA EU AS	> EU AS	NA EU AS	Bract characters indicate initial North Atlantic crossing with subsequent arrival in Asia.
Toricellia			NA EU		EU		AS	Eocene North Atlantic crossing with subsequent arrival in Asia.
Trapa	AS				NA EU AS	EU	EU AS	Earliest known occurrence is *Palaeotrapa* from Maastrichtian of Koryak Upland.
Trochodendron			NA		NA AS		AS	Miocene or prior connection across Beringia.

Figure. 19. Continued.

North American localities in Tennessee, Kentucky, and Mississippi. The Eocene Mississippi Embayment floras have a diversity of legumes and Theaceae not observed in the western North American Tertiary. These floristic differences may indicate barriers to dispersal as well as environmental dissimilarity due to the differences in latitude and physiographic relief.

Some components of the Middle Eocene Claiborne flora in Tennessee and Kentucky, although assigned to extinct genera, seem to show closest affinities to taxa living in South America today (Roth & Dilcher, 1979; Taylor & Crepet, 1987). Investigating the diversity of legumes in the Eocene of southeastern North America, Herendeen (1992) recognized three genera of tropical South American affinity, two of tropical Asia and Africa, two of pantropical distribution, and two of temperate North America and Asia. Noting that many legumes are tolerant of saline conditions and can be dispersed across ocean barriers, Herendeen (1992) proposed that there may have been exchange between the Mississippi Embayment and South America by way of ocean currents. This scenario would also explain the occurrence of *Crepetocarpon* Dilcher & Manchester, a close relative of *Hippomane* (Euphorbi-

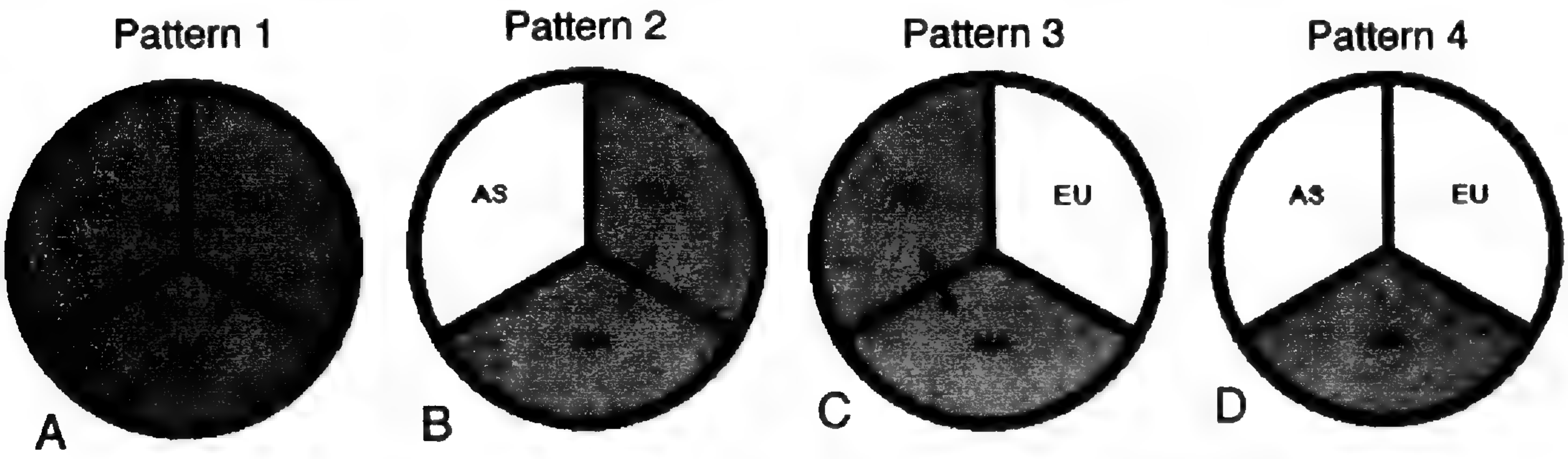


Figure 20. Four main patterns of geographic distribution of taxa in the Northern Hemisphere, emphasizing the possible ties between North America and adjoining northern landmasses. —A. Circumboreal. —B. Euro-American, indicating interchange between Europe and North America, usually inferred to have occurred via land bridge(s) in the North Atlantic. —C. Amer-Asian, indicating interchange between North America and Asia, probably via Beringia. —D. Endemic, taxa that are not known outside North America during a particular time interval. NA = North America; AS = Asia; EU = Europe.

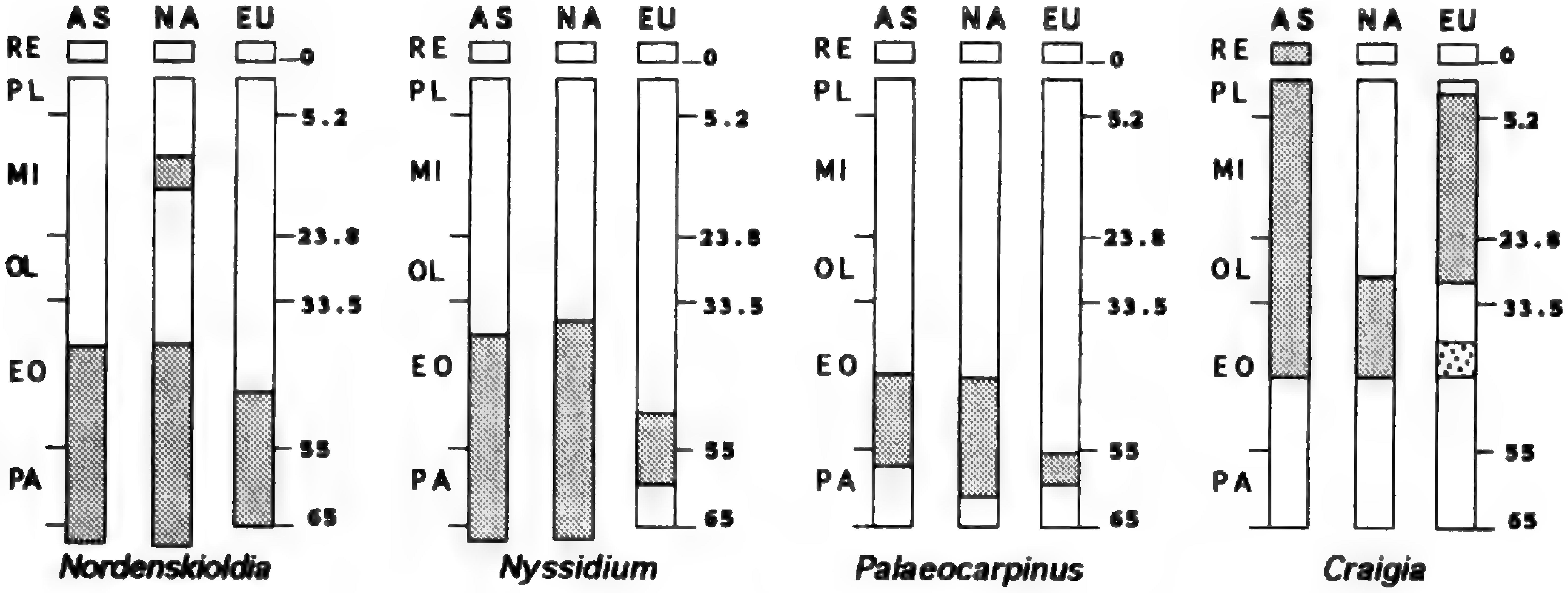


Figure 21. Examples of genera with circumboreal distribution patterns during the Paleocene (*Nordenskioldia*, *Nyssidium*, *Palaeocarpinus*) and Eocene (*Craigia*). Spitsbergen occurrence stippled in the column for Europe.

aceae), in the Eocene of the Mississippi embayment area (Dilcher & Manchester, 1988).

OLIGOCENE

Climatic cooling near the end of the Eocene resulted in the reduction in range of numerous thermophilic taxa in North America and Europe. Few North American Oligocene floras have been studied in detail, but an overview of assemblages that are available for study reveals that the diversity of broad-leaved evergreen taxa such as Icacinaceae, Lauraceae, Menispermaceae, and others had declined considerably since the middle Eocene. Temperate genera, many of which were already established by the late Eocene, become dominant elements. Still, approximately 13% of genera from the early Oligocene Bridge Creek flora, Oregon, are extinct (Meyer & Manchester, 1997).

Comparison of early Oligocene floras in North America and central Europe reveals high levels of generic similarity, indicating either that these plants were still able to migrate across the North Atlantic or that they had already spread across both continents prior to the Oligocene and maintained their similarity through evolutionary stasis on either side of the Atlantic Ocean. Studies at the species level are needed to determine the extent of taxonomic similarity between these floras.

MIOCENE

The maximum expansion of mixed mesophytic forest across the Northern Hemisphere was reached by the Middle Miocene. Useful overviews of Miocene floras are presented in Chaney and Axelrod (1959), Rember (1991), Graham (1993), Fields (1996), and Tiffney (1977a–1994a). A large proportion of the arborescent genera known from the Miocene of North America are also seen in the Mio-

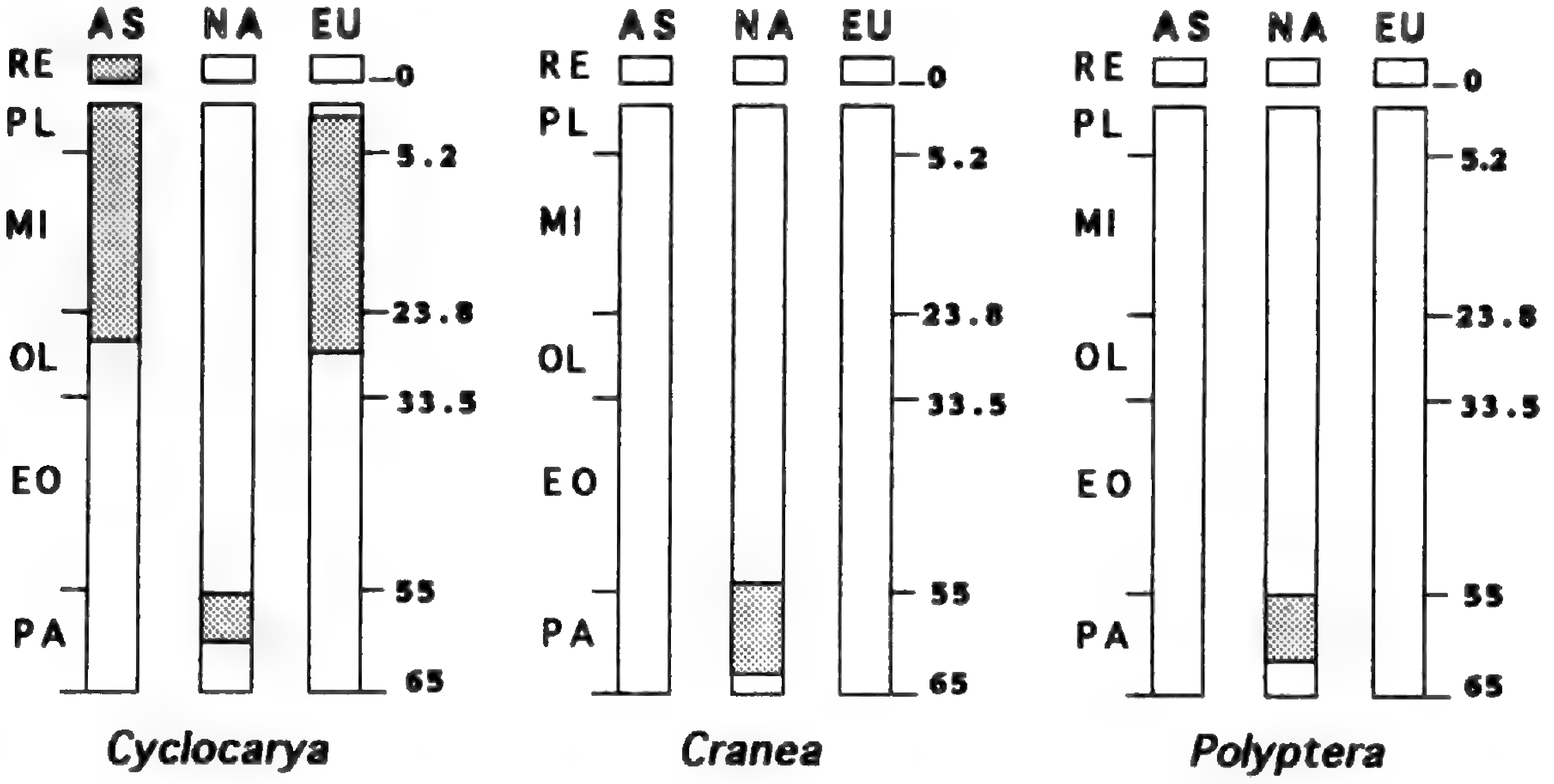
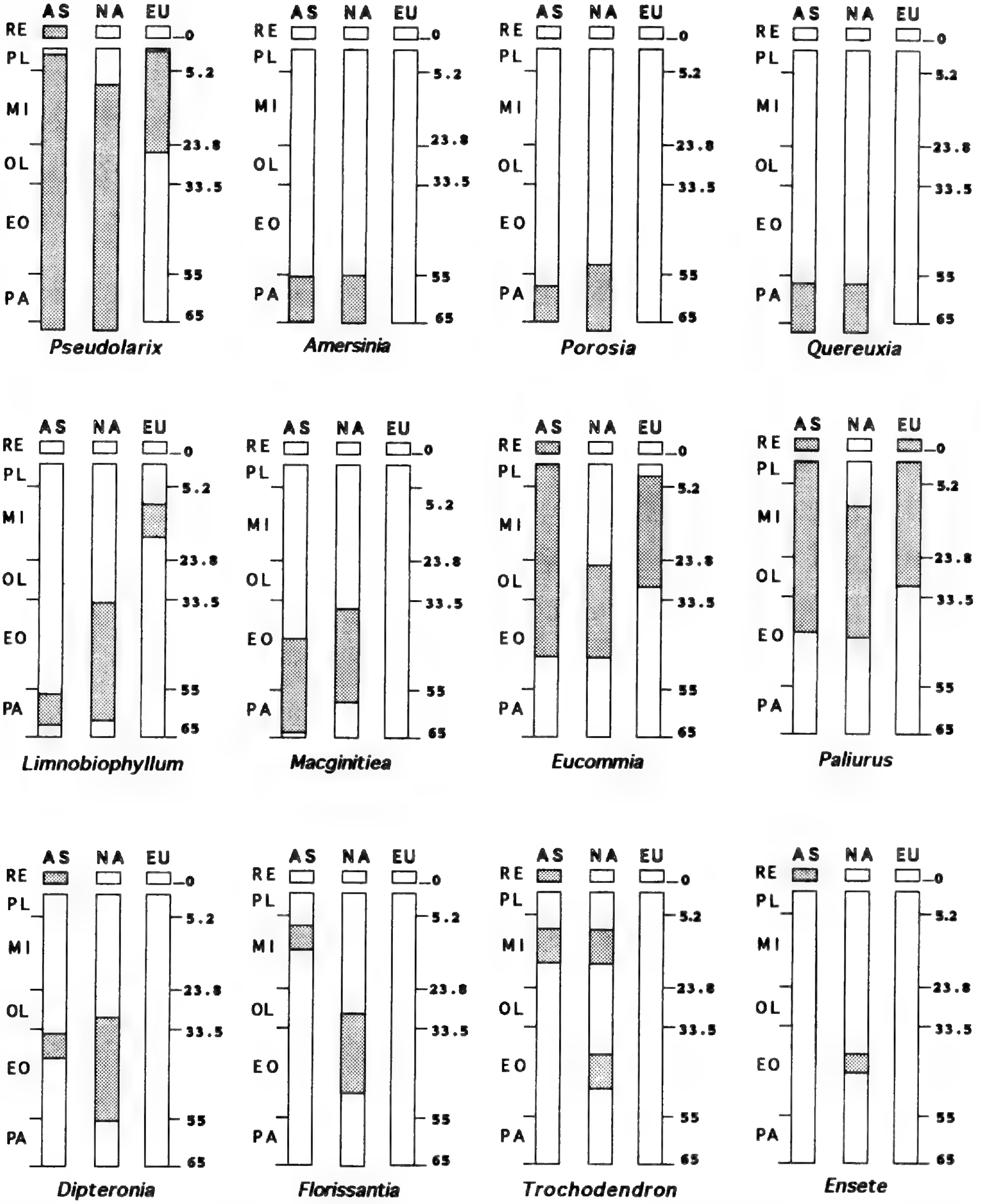


Figure 22. Examples of North American Paleocene endemic genera.



Pseudolarix *Amersinia* *Porosia* *Quereuxia*

Limnobiophyllum *Macginitiea* *Eucommia* *Paliurus*

Dipteronia *Florissantia* *Trochodendron* *Ensete*

Figure 23. "Beringia crossers." The first six examples suggest direct interchange between Asia and North America during the Paleocene. The other examples appear to indicate a later, perhaps Eocene, interval of interchange between the two continents. In three instances (*Eucommia*, *Paliurus*, *Pseudolarix*), the genera subsequently colonized Europe.

cene of Europe and Asia, indicating that by this time the Euro-American flora had spread into Asia. At the same time we may expect that Asian elements were invading Europe and North America, such as *Trapa*. The first North American record of *Liriodendron* occurs at this time; either it was "hiding out" prior to the Miocene, or it arrived relatively late from another continent. The arrival of Euro-American elements in Asia may have been by both routes, Beringia and Turgai. Presumably, however,

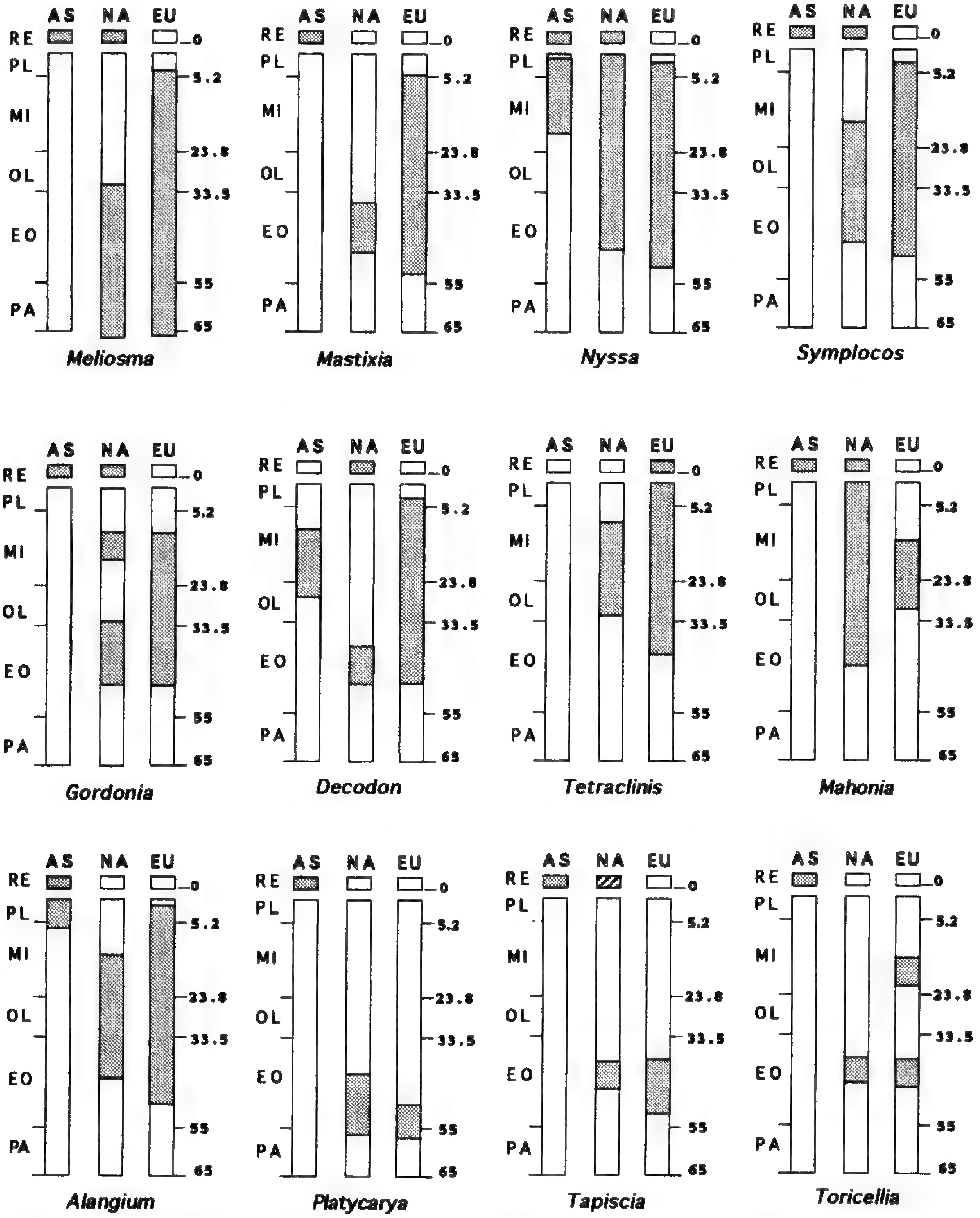
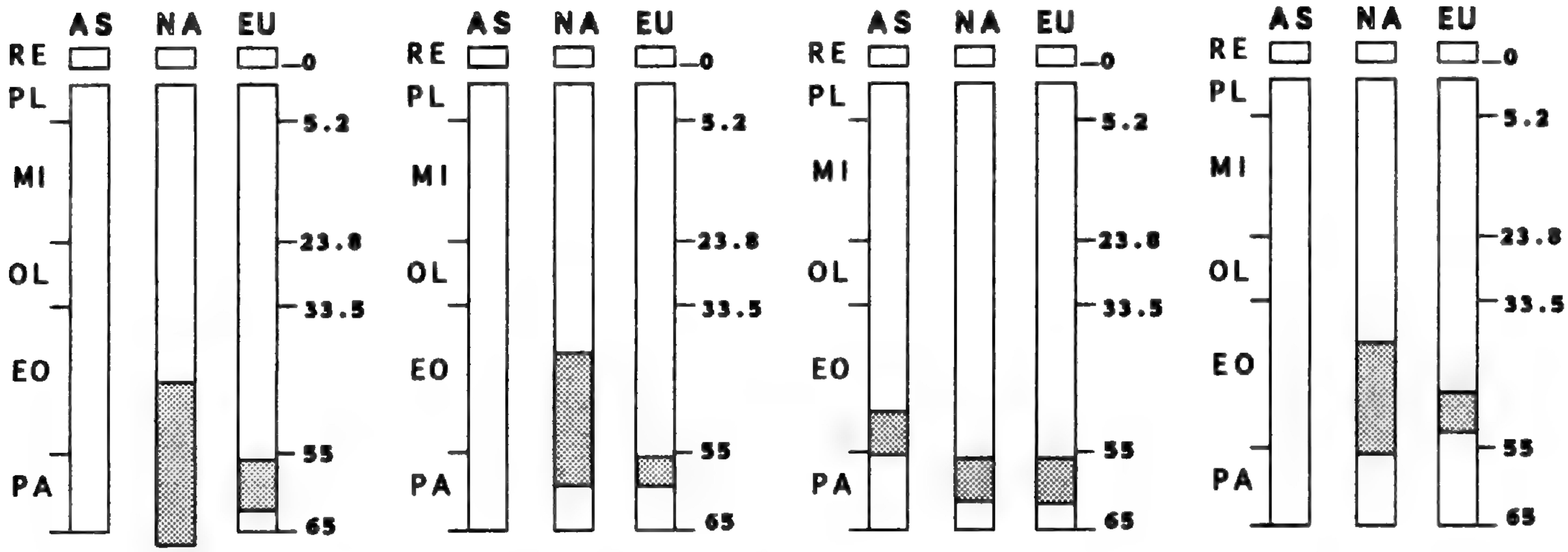


Figure 24. Extant genera of initial Euramerican distribution, in some cases with subsequent arrival in Asia. Diagonally stippled box represents *Huertea*, the extant Cuban sister genus to *Tapiscia*.

the more thermophilic elements would have come by way of Europe and the Turgai crossing, because the relatively high latitude of the Beringial connection would have been inhospitable for tropical species (Tiffney, 1994b).

The majority of North American Miocene genera are still living in the Northern Hemisphere today. Even in the Middle Miocene, however, there are some conspicuous extinct genera remaining, including *Diplodipelta* Manchester & Donoghue, *Nordenskioldia* (Fig. 21), and *Pseudofagus* Smiley & Huggins.

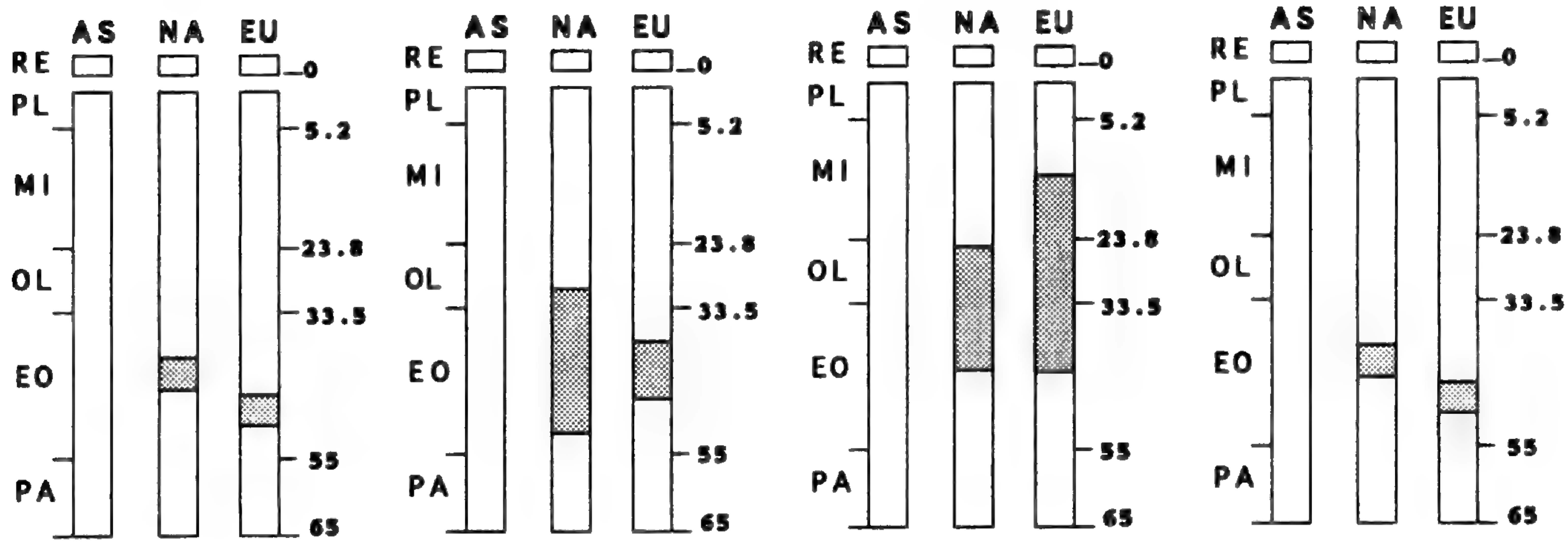


Platanites

Calycites ardtunensis

Fagopsiphyllum

Langtonia



Pentoperculum

Cruciptera

Cedrelospermum

Saxifragispermum

Figure 25. Extinct genera that apparently crossed the North Atlantic. The first four examples appear to indicate interchange between Europe and North America during or prior to the Paleocene, whereas the other examples appear to indicate Eocene interchange.

GENERAL OBSERVATIONS

Extinct genera have commonly been overlooked or ignored in phytogeographic studies, possibly because of the lack of modern analogs for direct environmental interpretations. Nevertheless, extinct genera are useful to illustrate important paleogeographic patterns. Figure 25 shows the ranges of extinct genera that appear to have crossed the North Atlantic: *Cedrelospermum* Saporta, *Cruciptera* Manchester, *Fagopsiphyllum* gen. nov., *Langtonia* Reid & Chandler, *Pentoperculum* Manchester, *Platanites* Forbes, and *Saxifragispermum* Reid & Chandler. *Platanites* was established in North America already in the Maastrichtian, and it is possible that the passage between Europe and North America occurred prior to the Paleocene. From the other examples we may infer passage across the North Atlantic during the late Paleocene (*Fagopsiphyllum, Langtonia*) or later. Most of these genera became extinct by the end of the Eocene, but *Cruciptera* persisted into the early Oligocene in North America, and *Cedrelospermum* made it into the late Miocene of Europe. Of these genera, only *Fagopsiphyllum* arrived later in Asia. The others are unknown from the Asian record. The absence of most of these genera from the Asian fossil record cannot be attributed solely to lack of adequate sampling in Asia. The winged fruits *Cedrelospermum* and *Cruciptera* are distinctive, easily recognized taxa that commonly preserve in lacustrine localities. Thus, if they were present near areas of deposition, we would expect to find them among the numerous Asian shale deposits from which leaves have been collected over the past century.

Figure 24 shows the distribution of selected modern genera with records indicating early Tertiary exchange between North America and Europe. A common pattern observed in these data is that of taxa shared between the Eocene of Europe and North America that are indigenous to Asia today. In many instances the genera have become extinct both in North America and Europe but survive only in Asia today. Examples include *Actinidia, Ailanthus, Amentotaxus, Cercidiphyllum, Corylopsis, Diplopanax, Mastixia, Toricellia,* and *Platycarya.* These genera, including both thermophilic and mesophytic taxa, evidently were able to cross between North America and Europe, but were blocked from entering Asia until later in the Tertiary. The paucity or lack of *Mahonia* in the Asian fossil record is striking because this leaf type would easily be recognized if present. It is also worth noting that *Platycarya* has very distinctive pollen that could easily be recognized if present in the Tertiary of Asia. Some other taxa shared between the Eocene of Europe and North America are found both in Asia and tropical America today (*Meliosma, Symplocos*). *Tapiscia* is native to Asia today, and its sister genus *Huertea* of the Caribbean region suggests a fragmentation of a more continuous ancestral range (Manchester, 1988). Some genera found in the Eocene of North America that now occur both in Africa and Asia include *Ensete, Iodes,* and *Pyrenacantha.*

Figure 23 shows some taxa that appear to have dispersed directly between North America and Asia, i.e., across Beringia. These include *Amersinia* Manchester, Crane & Golovneva, *Dipteronia, Eucommia, Florissantia* Knowlton, *Quereuxia* Kryshtofovich ex Nevolina, *Limnobiophyllum* Krassilov emend. Kvaček, *Macginitiea* Wolfe & Wehr, *Paliurus, Porosia,* and *Trochodendron.* These taxa suggest crossings of Beringia during the Paleocene (*Macginitiea, Amersinia, Porosia*), Eocene (*Eucommia*), and later. *Florissantia,* distributed from the Eocene to Oligocene in western North America, is known only in the Miocene of eastern Asia, suggesting a post-middle Eocene, pre-middle Miocene crossing. Thus, it appears that crossings were possible at various times during the Tertiary. Indeed, it has been suggested that a land connection existed, and that the only barrier was climate. Three of the genera shown in Figure 23 succeeded in colonizing Europe later in the Tertiary, after the initial dispersal between Asia and North America.

Some of the genera endemic today to North America, such as *Sequoia, Sabal, Comptonia,* and *Decodon,* have fossil records showing former widespread distribution in the Northern Hemisphere (examples in Fig. 19). *Decodon,* which survives today only in eastern North America, has a good fossil record in both North America and Europe. *Pinckneya* is limited to the southeastern United States today, but is known from the Oligocene of western North America. Although endemic to the southeastern United States, *Leitneria* has no confirmed North American fossil record, but it is well documented in central Europe to western Siberia.

Extant genera that have attracted special attention because of their modern disjunct distribution between North America and Asia and/or the Caucasus region include *Carya, Catalpa, Gordonia, Halesia, Liquidambar, Liriodendron, Magnolia, Nyssa, Platanus, Pterocarya,* and *Schisandra.* Each of these has reliable fossil records throughout the northern continents (examples in Fig. 19). Others are found today in all three northern continents, but have their earliest known megafossil records in North America, e.g., *Fagus, Ostrya,* and *Tilia.* Still others occur in both Europe and Asia today but are absent from the extant flora of North America despite their presence in the Tertiary, e.g., *Trapa, Paliurus.* Additional examples are provided by Tiffney (1994b).

Many of the genera found as fossils in the western part of North America are no longer native to that region today, but survive in eastern North America or in Asia. The extirpation of these taxa in western North America may have been brought on by increasing summer drought in the late Tertiary (Axelrod & Schorn, 1994).

Those taxa that are found first in Europe and North America and subsequently in Asia (Fig. 24, except *Tetraclinis*) are likely to have crossed the North Atlantic prior to arriving in Asia. However, it is difficult to determine the more parsimonious route to explain their arrival in Asia. They could have arrived from Europe as the Turgai seaway receded, or they could have arrived from North America via Beringia. Indeed, it is likely that both directions were involved and that different taxa followed independent courses.

In instances where the primary crossing was between North America and Asia, the subsequent arrival in Europe could be attributed either to a North Atlantic crossing or to a Turgai crossing. Comparative phylogenetic analyses at the species level may be required to unravel the probable sequences and directions of migration. It is likely, for example, that *Acer* first crossed between North America and Asia, and then from Asia into Europe. This conclusion derives from the observation that several Tertiary species belong to sections that are shared between the Eocene and Oligocene of North America and Asia (and not Europe), and that *Acer* arrived later in Europe with some species corresponding to the Asian, rather than American, sections. The occurrences of *Dipteronia* and the extinct genus, *Deviacer* Manchester (1994b; Wehr, 1995), in the North American early Tertiary suggest an initial radiation of "Aceraceae" in North America followed by successive emigration to Asia and to Europe.

How late was migration between North America and Europe possible? It is considered likely that separation of landmasses in the North Atlantic severed biogeographic ties between Europe and North America by the late Eocene (Tiffney, 1985a, b; Woodburne & Swisher, 1995). In this context, it is interesting that *Buzekia* samaras are found both in the late Oligocene and early Miocene of central Europe (Fig. 16A), and in the middle Miocene of Idaho (Fig. 16B). This might be an indication that plants could still disperse between the two continents in the Oligocene or Neogene. Alternatively, it may be that the known fossil occurrences reflect an earlier, perhaps Eocene, dispersal of a species that remained morphologically unchanged for millions of years following isolation of the two populations.

Although the main sources of North American vegetation appear to be Laurasian, Dilcher (1973), Taylor (1990), and Herendeen (1992) have called attention to apparent ties with South America and/or Africa. Particularly in the Eocene of southeastern North America, there appear to be some affinities with the flora of South America. In most of these instances it is not known whether the taxa were already in South America during the early Tertiary, but their presence there in the modern-day flora indicates that floristic exchange did occur at some times in the past. *Juglans* appears to have had a North American origin, with first occurrences in the Eocene (Manchester, 1987a). Black walnuts from the late Miocene or early Pliocene Punta Gorda Formation of Ecuador (Brown, 1946b) indicate that *Juglans* sect. *Rhysocaryon* entered South America by the Pliocene. Today the black walnuts are also distributed in the Caribbean, suggesting that a route through the Caribbean area may have facilitated its colonization of South America.

Although there seems to be some support for limited floristic exchange between the floras of southeastern North America and South America, there is very little evidence for the introduction of southern elements into western North America during the Tertiary. Although MacGinitie (1953) reported some extant South American elements in the Florissant flora (e.g., *Astronium*, *Lomatia*, *Petrea*), none of these have withstood more detailed comparative analyses (Manchester, in press). Clearly, there was some interchange with Mexico, as indicated by the correspondence of *Populus wilmattae* of the Green River formation with extant *P. mexicana* Wesmael (Eckenwalder, 1980; Manchester et al., 1986), the occurrence of several "arctotertiary elements" in the mountains of Mexico, and by the occurrence of *Cedrelospermum* and *Eucommia* as far south as Puebla Province during the late Tertiary (Magallón & Cevallos, 1994a–c).

The Arctotertiary concept, that many of the Northern Hemisphere temperate taxa evolved at high latitudes and moved southward across North America, Europe, and Asia as the climate cooled, is neither confirmed nor disproved by this review. Clearly, land connections at high latitude were important to the intercontinental dispersal of plants during the Tertiary, and it is plausible that the high latitudes may have served as a "cradle" for some species. However, few if any of the taxa reviewed in this study show identical patterns of geographic dispersal, and it is unlikely that any single mechanism can account for the separate histories of so many different taxa. Although some temperate elements may have descended from the North, many others may have evolved at high elevations in the early Tertiary and spread across lower elevations subsequently as climate cooled near the end of the Eocene.

As paleobotanical work continues, and carefully determined stratigraphic and geographic occurrences of particular taxa are added to computer databases, it is becoming possible to study the distribution patterns of particular species, and the vegetation that they comprise, through the Tertiary in some regions (Kovar-Eder et al., 1996). Eventually such studies can be expanded to allow direct comparison of the patterns in different continents with higher taxonomic, geographic, and temporal resolution than I have been able to provide here. In addition, molecular and morphological phylogenetic investigations of extant genera disjunct between two or more of the refugial regions can be compared with the paleobotanical data to provide improved resolution of the times and places of divergence between extant species (Wen, 1998, in press).

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APPENDIX 1

In the process of preparing this review, several nomenclatural revisions became necessary, including new generic names and new combinations. Information required to validate these names is provided below in alphabetical sequence.

Buzekia Manchester, gen. nov.

DIAGNOSIS (from species diagnosis of Bůžek, 1992: 20): "Fruits small, winged, indehiscent, with one central locule and a single seed. The wing surrounds the seed locule (fruit body) and has a small incision at the base. Stipe short, narrow, tapering. The fruit body is circular or subcircular and 0.3–0.4 cm in diameter. The wing is up to 0.6 cm wide. The width of the entire fruit is 0.7–1.3 cm (in vertical direction up to 1.5 cm). The fruit body and wing are covered with a prominent, single venation system. The venation pattern of the fruit body consists of an irregular network of polygonal meshes and is connected with the wing venation which consists of radially oriented veins that form loops near the wing margin and give rise to an intramarginal vein."

ETYMOLOGY. This genus is named in memory of Čestmír Bůžek, honoring his many contributions to paleobotany of central Europe, including his detailed investigation of the European representatives of this species (Bůžek, 1992).

TYPE SPECIES: *Buzekia tertiaria* (Weyland) Manchester, comb. nov. (Figs. 16A, B).

BASIONYM. *Pterocarpus tertiarius* Weyland, 1937, Palaeontgraphica, Abt. B, Paläophytol. 83: 95, text fig. 38, pl. 13, figs. 2, 3. TYPE: Weyland (1937) illustrated two specimens but did not designate a holotype. His Plate 13, fig. 1, is hereby designated the lectotype. Although the specimen is now lost, the original published high-resolution photograph shows all of the salient features. A topotypic specimen is illustrated here (Fig. 16A). The type locality is the Rott flora of Germany, of late Oligocene age.

OCCURRENCE. *Buzekia tertiaria* occurs in the late Oligocene of Germany (Fig. 16A; Weyland, 1937), the Miocene of Bohemia (Bůžek, 1992), and is now known from a single specimen from the Miocene of Idaho (Fig. 16B). Although Weyland placed it in the extant legume genus *Pterocarpus*, Bůžek expressed reservations by placing the generic name in quotes. Although both Weyland and Bůžek favored affinities with the legumes, the similarities with *Pterocarpus* are likely the result of convergence. Modern species of *Pterocarpus* have much larger fruits, do not possess the prominent intramarginal vein, and lack the fine reticulum seen in both the European and North American fossils. The familial affinities remain uncertain. The fine reticulum observed in these fruits is similar to that of *Dipteronia*, but *Dipteronia* fruits lack an intramarginal vein and usually show a scar where the schizocarp splits apart.

Fagopsiphyllum Manchester, gen. nov.

DIAGNOSIS. Leaves simple, elliptical to ovate, l/w ratio 1.5–3.5. Base rounded to cuneate and slightly decurrent along petiole, margin serrate except at base, teeth simple, broadly triangular, sharp to rounded, evenly spaced, with nonglandular, nonspinose apices. Venation craspedodromous, very regularly pinnate, with strikingly parallel, nearly straight, evenly spaced secondaries, each terminating in a marginal tooth. Tertiary veins percurrent, perpendicular to the secondary veins.

TYPE SPECIES: *Fagopsiphyllum groenlandicum* (Heer) Manchester, comb. nov.

BASIONYM. *Quercus groenlandica* Heer, 1868, Flora fossilis Artica 1. Die fossile Flora der Polarländer enthaltend die in Nordgrönland, auf der Melville-Insel, im Banksland, am Mackenzie, in Island und in Spitzbergen entdeckten fossilen Pflanzen. F. Schulthess, Zurich p. 108.

TYPE: Heer, 1868, pl. 8, fig. 8 was selected as the lectotype by Iljinskaja (p. 100, in Takhtajan, 1982).

SYNONYMY. *Quercophyllum groenlandicum* (Heer) E. Koch, 1963, Medd. Groenland, 172, 5: 34, pl. 6, figs. 1–3. *Fagopsis groenlandicus* (Heer) Wolfe, 1977, Profess. Pap. U.S. Geol. Surv. 997: 88.

OCCURRENCE. This species is common in the Paleocene of western Greenland (Heer, 1868; Koch, 1963), the Rocky Mountains and Great Plains of the United States (Brown, 1962), and is known from the Paleocene of Mull, Scotland (Boulter & Kvaček, 1989).

DISCUSSION. As mentioned in the text of this article, the name *Fagopsis* Hollick applies to a middle to late Eocene plant known from twigs with attached leaves, inflorescences, and infructescences (Hollick, 1909; Manchester & Crane, 1983). Although this generic name has been applied loosely to similar leaves from older localities that lack appropriate reproductive structures, it is unlikely that those isolated leaves really represent *Fagopsis*. A separate generic name is needed for such isolated leaves that lack features of the reproductive structures necessary to diagnose *Fagopsis* sensu Hollick. Koch (1963) proposed the combination *Quercophyllum groenlandicus* (Heer) Koch, but the type of *Quercophyllum* Fontaine is an unrelated taxon from the Lower Cretaceous of the Potomac Group.

Fagopsiphyllum nipponica (Tanai) Manchester, comb. nov.

BASIONYM. *Fagopsis nipponica* Tanai, Bull. Natl. Sci. Mus. Tokyo, Ser. C., 21 (3, 4): 76–78, Pl. 5, figs. 1, 2; Pl. 6, figs. 1, 2, 5, 6; Fig. 1–Ea, b. TYPE: Late Middle Eocene Kabato Formation, Tsukigata-Cho, Hokkaido, Japan (holotype, NSM-PP 10579).

Fagopsiphyllum rarytkinensis (Akhmetiev & Samsonenko) Manchester, comb. nov.

BASIONYM. *Fagopsis rarytkinensis* Akhmetiev & Samsonenko, Paleontol. Zhurn. 31: 94–102, Pl. 12, figs. 2, 4, 6. TYPE: Late Eocene Pravotaljainskaya Formation (holotype, Geol. Inst. Russ. Acad. Sci. no. 4812/244).

Florissantia sikhote-alinensis (Kryshtofovich) Manchester, comb. nov. (Fig. 7B).

BASIONYM. *Porana sikhote-alinensis* Kryshtofovich, 1921, Materials on geology and mineral resources of the Far East. No. 15, p. 331, pl. 2, fig. 7. TYPE: Miocene Amgu flora, Sikhote Alin. Figured specimen of Kryshtofovich 1921, pl. 2, fig. 7 (reprinted here, Fig. 7B). In 1998 the specimen could not be relocated.

Sargentodoxa globosa (Manchester) Manchester, comb. nov. (Fig. 12D–H).

BASIONYM. *Bumelia? globosa* Manchester, Palaeontogr. Amer. 58: 86, pl. 39, figs. 7–16. TYPE: Eocene Clarno Nut Beds, Oregon (holotype, USNM 424644).

Toricellia bonesii (Manchester) Manchester, comb. nov. (Fig. 1C–F).

BASIONYM. *Tripartisemen bonesii* Manchester, 1994, Paleontogr. Amer., 58: 113, pl. 62, figs. 8–15. TYPE: Eocene Clarno Nut Beds, Oregon (holotype, UF 9288).

EARLY TERTIARY FLORAL EVOLUTION IN THE CANADIAN HIGH ARCTIC[1]

E. E. McIver and J. F. Basinger[2]

ABSTRACT

Discovery of fossil remains of Tertiary high-latitude forest vegetation during 19th century polar exploration was recognized as critical to an understanding of long-term global climatic evolution and origins of modern mid-latitude northern temperate vegetation. An extensive record of early Tertiary plants is preserved within rocks of the Eureka Sound Group exposed in the Canadian Arctic Archipelago, and intensive collecting from this Group over the past 15 years has provided a basis for paleofloristic and paleoenvironmental interpretations. Fossil locality data and preliminary floral lists are included for all principal collection sites on Ellesmere and Axel Heiberg islands from the four constituent units of the Group, the Expedition, Strand Bay, Iceberg Bay, and Buchanan Lake formations, ranging in age from early Paleocene through middle Eocene and representing paleolatitudes of 75–80°N. Flora and vegetation are consistent with a mesothermal, humid climatic regime with little or nonexistent frost at low elevations throughout the polar regions. Although the four formations are floristically distinct, Paleocene through early Eocene assemblages are vegetationally similar. Assemblages from the youngest formation, the middle to late Eocene Buchanan Lake, are more complex and are correlated with both structural reorganization of the ancient Sverdrup Basin during the Eurekan Orogeny and the onset of Tertiary global climatic deterioration. The origins of some of the lineages that characterize northern deciduous vegetation may have been influenced by tectonically induced regional environmental complexity and global cooling.

Knowledge of Canadian Arctic Tertiary floras began with late 19th and early 20th century polar exploration (Heer, 1868, 1878; Brainard, 1886; Schei, 1903, 1904; Nathorst, 1915). These discoveries, and others elsewhere in high latitudes, revealed the existence of a ubiquitous type of deciduous Tertiary circumpolar vegetation (e.g., Schloemer-Jäger, 1958; Manum, 1962, 1994; Koch, 1963; Schweitzer, 1974, 1980; Budantsev, 1983, 1992; Hickey et al., 1983; Axelrod, 1984; Guo et al., 1984; Wolfe, 1985; Boulter & Kvaček, 1989; Spicer & Parrish, 1990; Boyd, 1990; Basinger, 1991; Francis, 1991; Kvaček & Manum, 1993; Kvaček et al., 1994). Originally referred to as the "Arctic Miocene" Flora, most of these fossil assemblages were later recognized as of Paleocene to Eocene age. The resemblance of this vegetation, in character and to some degree composition, to Neogene mid-latitude floras as well as the modern mixed-deciduous floras of southeastern North America and southeastern Asia, led eventually to the concept of a widespread Arcto-Tertiary Geoflora that retained a similar composition through long periods of geologic time (Engler, 1879/1882; Chaney, 1947, 1959) (see: Wolfe, 1977; Mai, 1991; and references therein). With disagreement over the validity of the Geoflora concept, vegetation of this Northern Polar Region was referred to as the Polar Broadleaved Deciduous Flora by Wolfe (1985).

Although early Tertiary plant remains were reported periodically in the 20th century from the Arctic Archipelago (Tozer, 1963; McMillan, 1963; Riediger & Bustin, 1987), until recently no systematic attempt had been made to explore the Eureka Sound Group, the principal plant-bearing unit of the region, for plant fossils. Recent work by Hickey et al. (1983), McIver and Basinger (1989), Basinger (1991), Lepage and Basinger (1991, 1995), and Basinger et al. (1994) represents ongoing investigation of the floras of this Group. Exposures of the coal-bearing Eureka Sound Group are found throughout much of the northern and western Arctic Archipelago (Ricketts, 1986, 1994), but those on Ellesmere and Axel Heiberg islands are the most

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ANN. MISSOURI BOT. GARD. 86: 523–545. 1999.

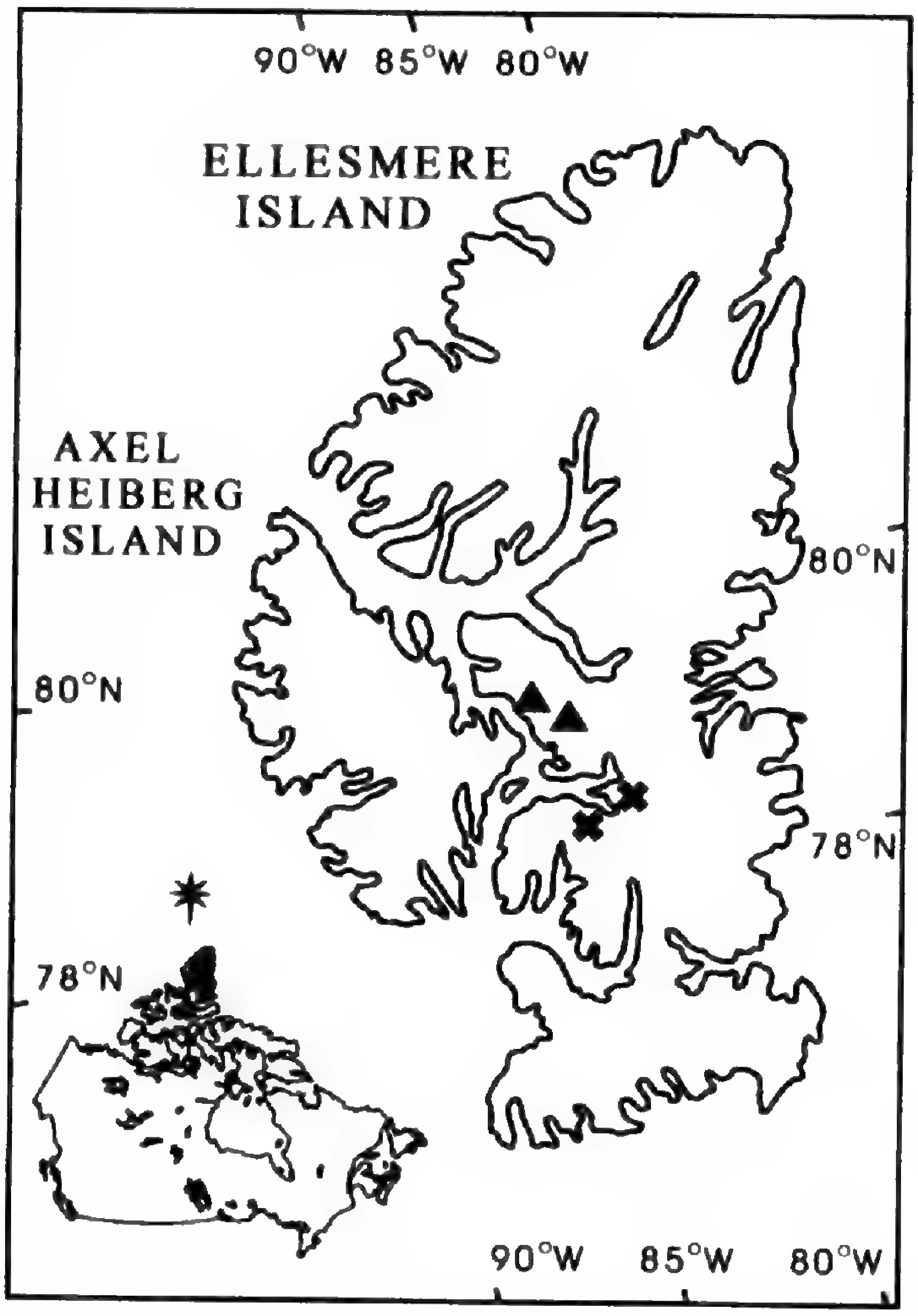

Figure 1. Location of plant fossil sites from the Expedition Formation. Fosheim Peninsula (triangles); Strathcona Fiord (X).

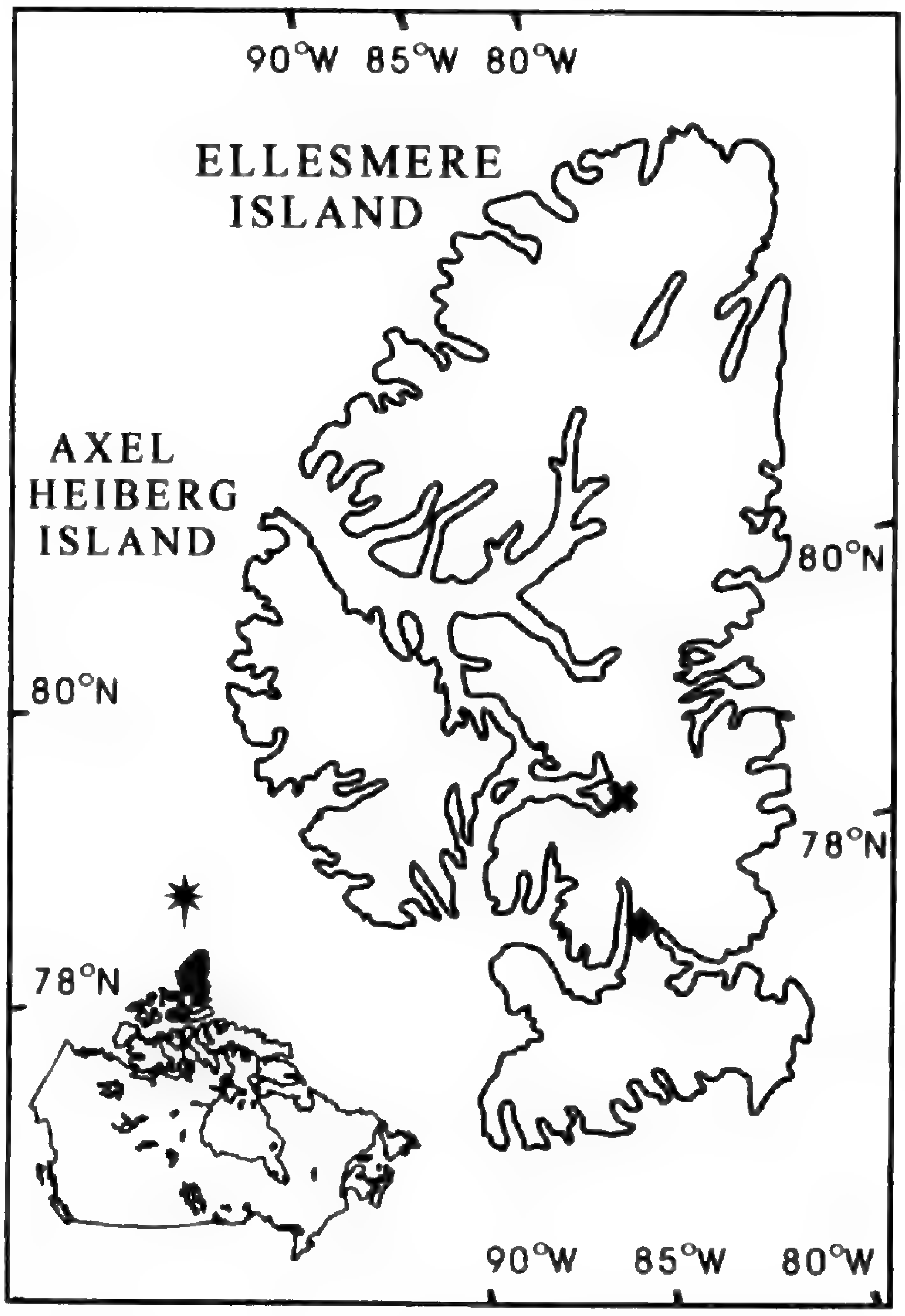

Figure 2. Location of plant fossil sites from the Strand Bay Formation (= Mount Lawson Formation). Strathcona Fiord (X); Vendom Fiord (diamond).

extensive and have been the subject of most of the current work.

The contrast between early Tertiary and modern polar floras dramatically illustrates the extent of Tertiary climatic deterioration resulting from global climatic change during the late Cenozoic. That climate and vegetation have an intimate relationship is well established, and although climate may be primary, other factors can be crucial to determining vegetational structure and composition. Walter (1973: 32) stated, "The natural limit of distribution of a particular species is reached when, as a result of changing physical environmental factors, its ability to compete, or its competitive power is so much reduced that it can be ousted by other species." For example, acquired data indicate that geomorphology has played an important role in floral evolution of the Canadian High Arctic during the early Tertiary. Recent advances in understanding the geological history of the Canadian Arctic Archipelago have substantially clarified the important role of the physical environment in contributing to patterns of vegetational stability and change. Regional geological analysis of the Eureka Sound Group by Miall (1986), Ricketts (1986, 1987, 1988, 1994), and Ricketts and Stephenson (1994) provides a basis for interpretation of paleoenvironments, and makes possible correlation of the many plant localities.

In this report we present a preliminary account of the fossil plants of the Eureka Sound Group. A monographic systematic analysis of taxa is not presented, but all significant fossil localities discovered as part of this research are enumerated, and lists of taxa occurring at each locality are appended. Most systematic assignments are at the generic level, because without inclusion of more detailed descriptions, specific assignments are generally of limited value. The fossils reported here contribute the foundation for a comprehensive systematic treatment of the early Tertiary flora of the Canadian High Arctic in the future.

MATERIALS

The fossil plants included in this report were collected from Ellesmere and Axel Heiberg islands in the Canadian Arctic from 1982 to 1993 (Figs. 1–4) and are housed in the University of Saskatche-

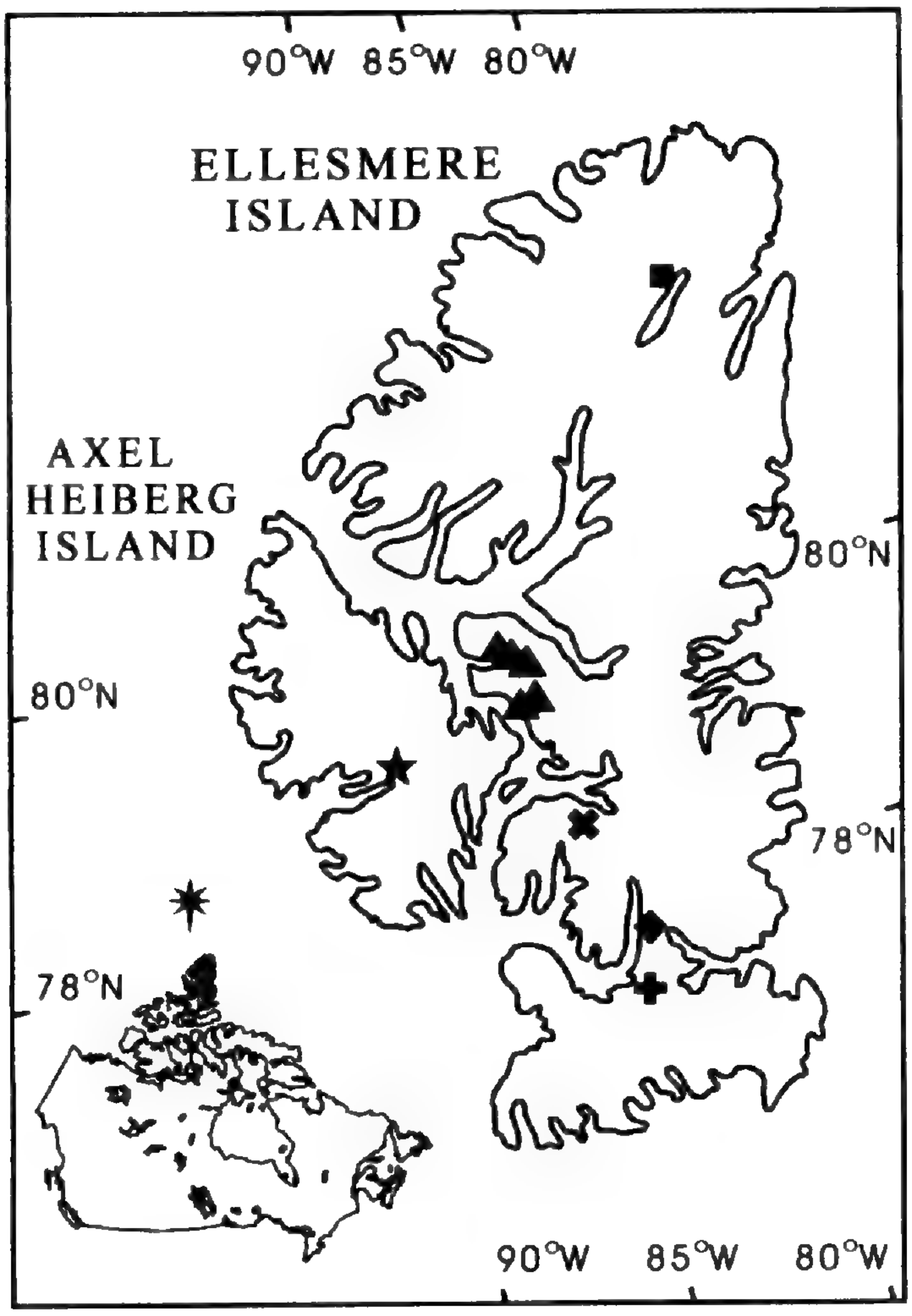

Figure 3. Location of plant fossil sites from the Iceberg Bay Formation (= Margaret Formation). Lake Hazen (square); Fosheim Peninsula (triangles); Strathcona Fiord (X); Vendom Fiord (diamond); Stenkul Fiord (cross); Strand Bay (star).

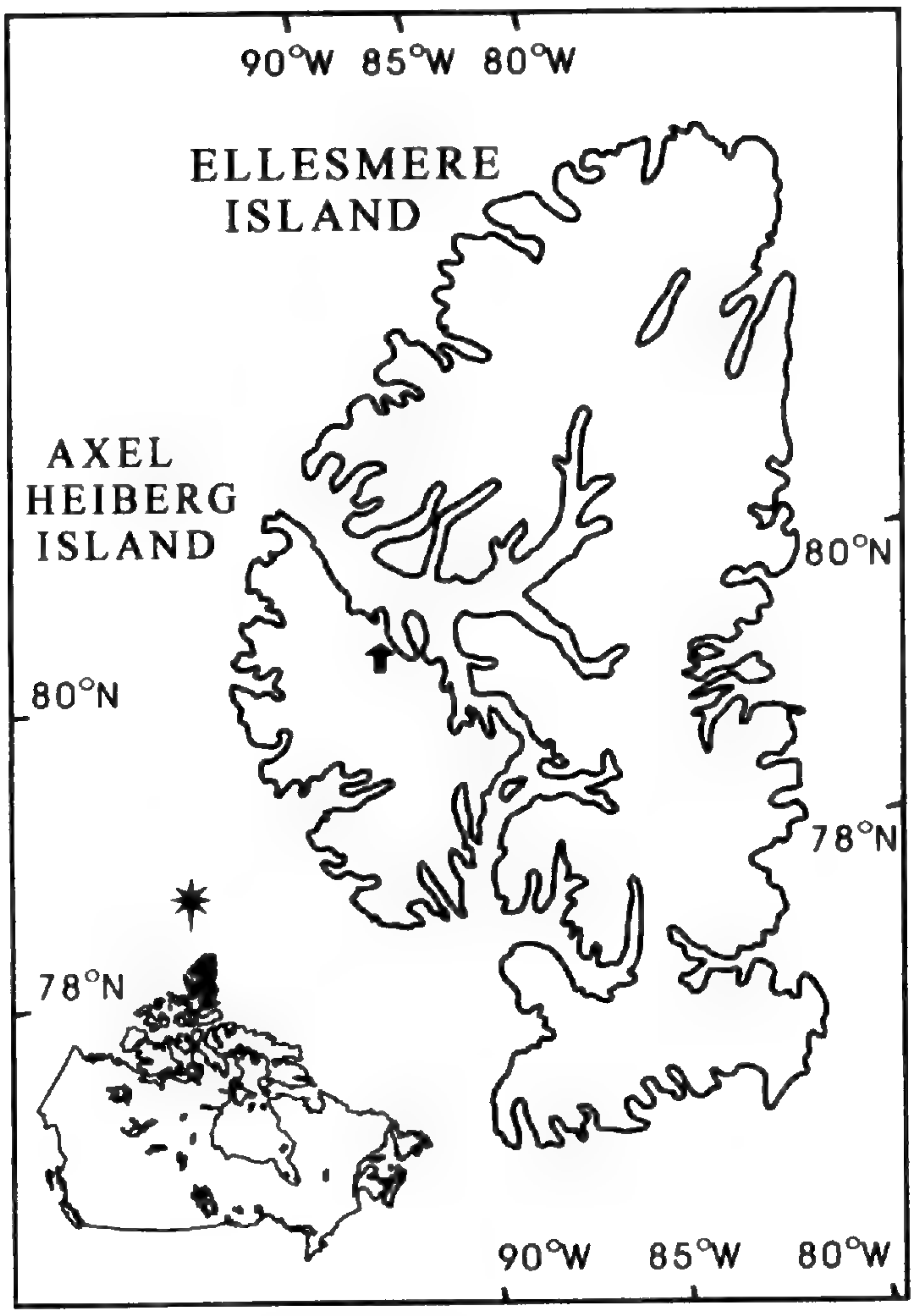

Figure 4. Location of plant fossil sites (arrow) from the Buchanan Lake Formation.

wan Paleobotanical Collection. All specimens are designated by the locality number (e.g., US188) and specimen number (e.g., 5731). Lists of fossil plants and pollen follow the classification of Hutchinson (1973) at the suprageneric level. Authorities are included in the floral lists found in appendices; plant identifications are preliminary (Appendices 1–8). All plants were recovered from sediments of the Eureka Sound Group and are interpreted as early Paleocene to middle or late Eocene in age (Fig. 5). Early Tertiary paleolatitudes of this region were approximately 75–80°N (McKenna, 1980, 1983; Irving & Wynne, 1991; Dawson et al., 1993).

Late Cretaceous to early Tertiary coal-bearing sediments deposited within the Sverdrup Basin of the Arctic Archipelago, and deformed during the early Tertiary Eurekan Orogeny, were recognized by Troelsen (1950), Tozer (1963), and Souther (1963) as the Eureka Sound Formation. Ricketts (1986) and Miall (1986) independently elevated the formation to group status, both authors recognizing that the sediments reflected the complex paleogeographic evolution of the Arctic Islands immediately prior to and during the Eurekan Orogeny. Ricketts subdivided the group into four lithologically distinct formations of regional extent; Miall recognized nine constituent formations.

The lithostratigraphical scheme of Ricketts (1986, 1991, 1994) used here includes, from oldest to youngest, the Expedition Formation (Fm.), Strand Bay Fm., Iceberg Bay Fm., and Buchanan Lake Fm. Ricketts's units are based on lithologic homogeneity, have mappable boundaries, and are biostratigraphically and paleomagnetically constrained. They are extremely useful for discussions on floral evolution and distribution. Furthermore, recent modeling of the Late Cretaceous to Paleogene stratigraphic sequences of the Eureka Sound Group by Ricketts (1994) and Ricketts and Stephenson (1994) greatly enhances an understanding of the depositional environments represented through the sequence, therefore allowing more detailed interpretations of plant paleoenvironments.

We have used data from both Ricketts (1986, 1987, 1988, 1991, 1994) and Miall (1986, 1988) in correlating the different fossil assemblages; nevertheless, the resulting interpretation is ours and may not in all cases correspond to that of either Ricketts or Miall. Although Ricketts's stratigraphic

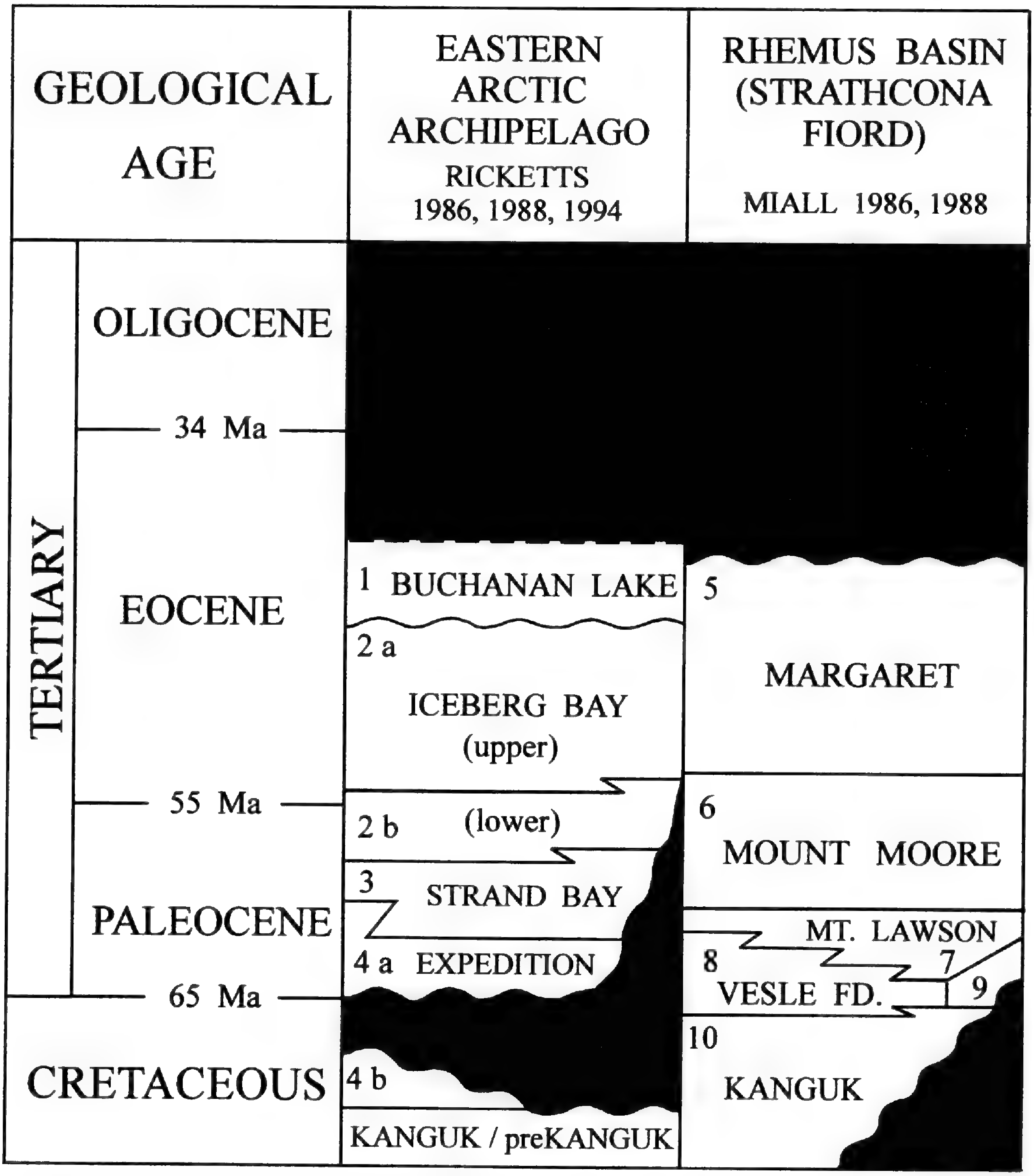

Figure 5. The Eureka Sound Group: generalized correlation of lithostratigraphical schemes of Ricketts (1986, 1987, 1994) and Miall (1986, 1988) applicable to this study (scheme comparison adapted from Ricketts (1988)). 1 = Buchanan Lake Formation; 2a = Iceberg Bay Formation (Coal Member); 2b = Iceberg Bay Formation (Lower Member); 3 = Strand Bay Formation; 4a = Expedition Formation (Upper Member); 4b = Expedition Formation (Lower Member); 5 = Margaret Formation; 6 = Mount Moore Formation; 7 = Mount Lawson Formation; 8 = Vesle Fiord Formation; 9 = Mount Bell Formation; 10 = Kanguk Formation (and may include preKanguk). Numerical ages after Berggren et al. (1995).

scheme is preferred when correlating plant localities and discussing arctic vegetative change during the Paleocene and Eocene, Miall's classification, based mainly on facies types (Miall, 1986), is especially helpful in consideration of the fossil-bearing beds from southern Ellesmere Island. In this region, Miall's formations are more easily recognized even though the units may be markedly diachronous. However, correlation of plant beds within the Eureka Sound Group may be difficult under either lithological scheme in the absence of additional biostratigraphic data, which are avail-

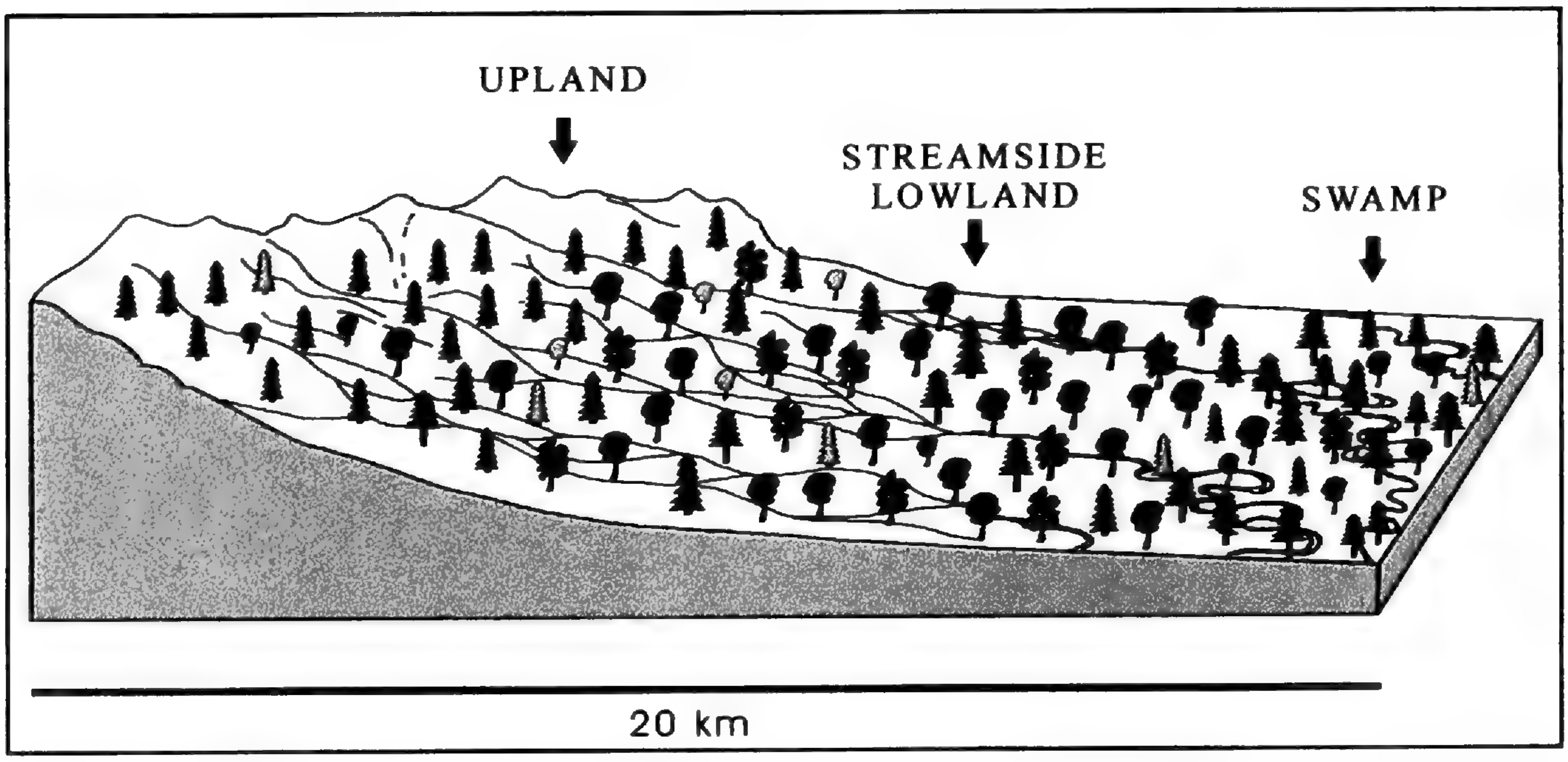

Figure 6. Model of depositional environment of Buchanan Lake Formation, Axel Heiberg Island. Adapted from Ricketts (1991).

able currently for only a few sites; for example, Miall's type sections from near Strathcona Fiord, our data from the Taggart River section, and the Buchanan Lake fossil site on Axel Heiberg Island. In the Strathcona and Stenkul fiord regions, we could assign the fossil assemblages to Miall's scheme and correlate them with those of Ricketts (a comparison of the schemes is shown in Fig. 5).

Sediments of the Eureka Sound Group conformably or unconformably overlie Mesozoic and Paleozoic rocks of the Sverdrup Basin and Franklinian Mobile Belt in the Canadian Arctic. In the eastern Arctic, which includes all sites reported here, the sediments accumulated as deposits of wave- and fluvial-dominated deltas, barrier islands, estuaries, lagoons, coastal plains, and shelves (Ricketts, 1991, 1994). Sediments of the Paleocene upper member of the Expedition Formation preserve the oldest plants reported from the current study; sites yielding plant fossils are not common, and only one assemblage revealed more than six taxa (Fig. 1; Appendix 1). Deposition of the Strand Bay Formation occurred during regional transgression and the subsequent sea-level highstand, and plant-bearing beds are rare. All Strand Bay sites were on Ellesmere Island and interpreted as middle Paleocene in age (Fig. 2; Appendix 2). Plant remains are most abundant in the coal-bearing sediments of the late Paleocene to early Eocene Iceberg Bay Formation, from which substantial collections have been made at numerous localities on Ellesmere and Axel Heiberg islands (Fig. 3; Appendix 3).

During the early to middle Eocene, possibly extending into the late Eocene, the entire region of the Sverdrup Basin underwent structural reorganization during the Eurekan Orogeny (Ricketts, 1986, 1991, 1994). As a result, sediments of the Expedition, Strand Bay, and Iceberg Bay formations experienced moderate to severe deformation. Folding and thrusting throughout the region, and involving Eureka Sound Group rocks, resulted in development of syn- to late-orogenic foredeep basins in the eastern Arctic Islands, including several on Ellesmere Island and one on Axel Heiberg Island (Ricketts, 1991). On northeastern Axel Heiberg Island, fragmentation of the older basin and uplift of the ancestral Princess Margaret Arch caused clastic detritus to accumulate in a narrow, synorogenic intermontane basin superimposed on older stratigraphic foundations (Ricketts, 1991). Because this basin developed as a direct response to uplift and faulting, the sediments of the Buchanan Lake Formation that accumulated within it experienced only minor deformation. These sediments preserve the spectacular remains of Eocene forests (Christie & McMillan, 1991, and papers therein). Plant remains of the Buchanan Lake Formation are known primarily from a single area on Axel Heiberg Island, but here they are abundant and beautifully preserved (Fig. 4; Appendix 4).

METHODS

Most plants in our collection can be assigned to one of three major environmental settings: streamside-lowland forest environments; swamp environments; and probable upland environments (Fig. 6). Plants collected from sites interpreted as streamside or lowland forests make up the bulk of the plant specimens and the majority of taxa. Evaluation of sampling techniques (unpublished data) indicates that sampling of these environments was good if sites were visited for more than one season. Our most reliable data are from sites visited over several field seasons; nevertheless, these data are typically from sites that preserve vegetation growing outside swamps that by themselves are unlikely to well represent regional floral diversity.

Studies of modern swamp vegetation indicate that samples from peat or coal seams represent more accurately the local swamp vegetation than the streamside sediments do the remaining regional flora. Except during highstand flooding, swamps tend to filter out plant debris produced by vegetation from outside the swamps. Typically, swamps also preserve more non-canopy members than drier sites. Taphonomic biases are therefore less pronounced for forest assemblages deposited in swamps as opposed to streamside sites. Together with the intensive work done on the Buchanan Lake swamp floras, this leads us to believe that paleobotanical samples from swamp habitats closely mirror the actual swamp vegetation. Preservation of plant remains from swamp environments, particularly for Eocene deposits, is also notably better than in other environments, thus facilitating taxonomic identification and detailed comparison with living plants.

Allochthonous remains of possible stream-side or upland vegetation occur within sandy fluvial facies of the Buchanan Lake Formation in some sections. For example, wood, conifer seed cones, and nuts occur in the channel lag deposits of stream systems. Because of the likely substantial taphonomic bias, the extent to which these remains accurately represent the dominant taxa of the upland floras is unknown.

A comparison of macrofloras and palynofloras provides a general indication of how well the macrofossil species identified characterize the regional flora. For example, Table 1 presents macrofossil data and McIntyre's palynological data from the Buchanan Lake Formation; only taxa assigned or tentatively assigned to extant families and interpreted as woody species are included in these lists. A total of 20 families are recognized in the macrofossil collections from the Buchanan Lake Formation; 21 families are recognized from the pollen record. Considered together, 25 extant families are represented, with approximately 45 genera, and thus probably providing a reasonable representation of the diversity of woody plants in the regional flora.

At this site the vegetation appears to be reasonably well characterized by either macrofossil or palynofloral data alone, although the level of diversity is lower when only one data set is considered. Rare (or yet unrecognized) in the macrofloras are probable understory plants, although some are represented in the palynofloras (e.g., *Pachysandra*, *Lonicera*). Also among the palynomorphs are more than 13 taxa of unknown modern affinity. While the recognition of these taxa contributes to our understanding of the total regional plant diversity, it does not further clarify the composition or structure of the vegetation. In the Buchanan Lake flora there is an apparent absence or near-absence, as is typical prior to the Oligocene, of many herbaceous groups that contribute significantly to the diversity of modern angiosperm-dominated vegetation, including grasses, sedges, composites, etc. (Muller, 1981).

Over a broad region throughout the Paleocene and early Eocene of the Sverdrup Basin the species composition is very similar, suggesting that a similar vegetation and depositional environment covered much of the land surface over a long interval of time. This is also consistent with Ricketts's (1994) geological synthesis and Manum's (1994) interpretation of the Paleogene floras of Spitsbergen. For this report, we assume that leaves common at a locality, and commonly recovered from most localities in a restricted area, represent local dominants; leaves commonly recovered from most localities throughout a region are assumed to be those of regionally dominant species. For floras with great diversity in the canopy, such assumptions might be suspect (see Greenwood, 1992); however, for floras of moderate to low diversity, as appears to be the case for the Paleocene and early Eocene lowland floras, monotony in the canopy should allow counts to provide a useful guide to the dominant tree taxa. Organ counts from specific sites are included in the text in the discussion of the floras.

RESULTS

ENVIRONMENTS AND FLORAS OF THE EARLY TO MIDDLE PALEOCENE

Marine transgression, initiated in the early Paleocene, filled valleys and covered lowlands of the Sverdrup Basin that had been exposed to erosion during Maastrichtian/earliest Paleocene regression. Along the western margin of the Fosheim sub-basin (eastern Axel Heiberg Island), wave-dominated deltas and strandplains dominated. To the east and south (western Ellesmere Island), delta plains, coastal plains, and estuaries provided habitats for

Table 1. Preliminary comparison of palynofloral and macrofloral data from the Buchanan Lake Formation, Axel Heiberg Island at the generic and family level. Data from this study (see Appendix 4) and adapted from McIntyre (see Appendix 8). Only taxa assigned or tentatively assigned to extant families and interpreted as woody species are included.

Family	Macrofloral genera	Palynofloral genera
Ginkgoaceae	1	0
Pinaceae	6	5
Taxodiaceae	5	2
Cupressaceae	2	represented
Menispermaceae	1	0
Cercidiphyllaceae	1	1
Platanaceae	1	0
Hamamelidaceae	1	1
Ulmaceae	1	2
Juglandaceae	1	4
Myricaceae	1	1
Fagaceae	2	3
Betulaceae	3	3
Tiliaceae	1	1
Salicaceae	0	1
Ericaceae	1	1
Rosaceae	represented	1
Nyssaceae	1	1
Aquifoliaceae	0	1
Buxaceae	0	1
Vitaceae	1	0
Aceraceae	0	1
Anacardiaceae	1	1
Oleaceae	1	1
Caprifoliaceae	0	3

early Paleocene vegetation (see Ricketts, 1994; Ricketts & Stephenson, 1994).

Fossil plants are found in the upper member of the Expedition Formation which, based on litho- and biostratigraphy, is primarily lower Paleocene (Ricketts, 1994). All plant fossil sites of this age reported here are on Ellesmere Island (Fig. 1). Fossil plants from the Expedition Formation occur in siltstones and mudstones commonly interbedded with sandstones and are interpreted as fluvial deposits. Thick coal seams, in some cases with permineralized tree trunks up to 3 m in diameter (unpublished data), are rare, but indicate the periodic existence of long-lasting swamps of regional extent.

The fossil plants recovered indicate that the vegetation was composed primarily of a mixture of deciduous conifers and deciduous angiosperms. The deciduous *Metasequoia* (Fig. 8) and *Glyptostrobus* were dominant among the conifers, although rare evergreen conifers have also been recovered (Appendix 1). The most common broadleaf angiosperm taxa were *Ushia* and a *Trochodendroides* species with its putative fruits *Nyssidium arcticum*. Recovered from one site were leaves of *Corylites* (Figs. 7, 9), *Archeampelos* (Vitaceae), cf. *Trema*, and *Pseudoprotophyllum* (Fig. 11).

The presence of *Pseudoprotophyllum* in the Paleocene is of interest. This is a widespread fossil leaf form of the Late Cretaceous of Alaska (Hollick, 1930), Western Canada (Bell, 1963), and Siberia (Vakhrameev, 1991), but we are not aware of any other occurrence in Tertiary sediments. A Paleocene age is indicated by both the macroflora and palynoflora (McIntyre, pers. comm. 1998; McIntyre, in Ricketts, 1994: see Appendix 5). It therefore seems that *Pseudoprotophyllum* persisted in high latitudes after its extinction further south.

Equisetum and the aquatic angiosperm *Trapago*[3] (Fig. 10) are present in most plant assemblages of the upper Expedition Formation, indicating that quiet, shallow-water habitats were common and widespread.

The few available plant fossils and the poor pollen record provide little data by which to charac-

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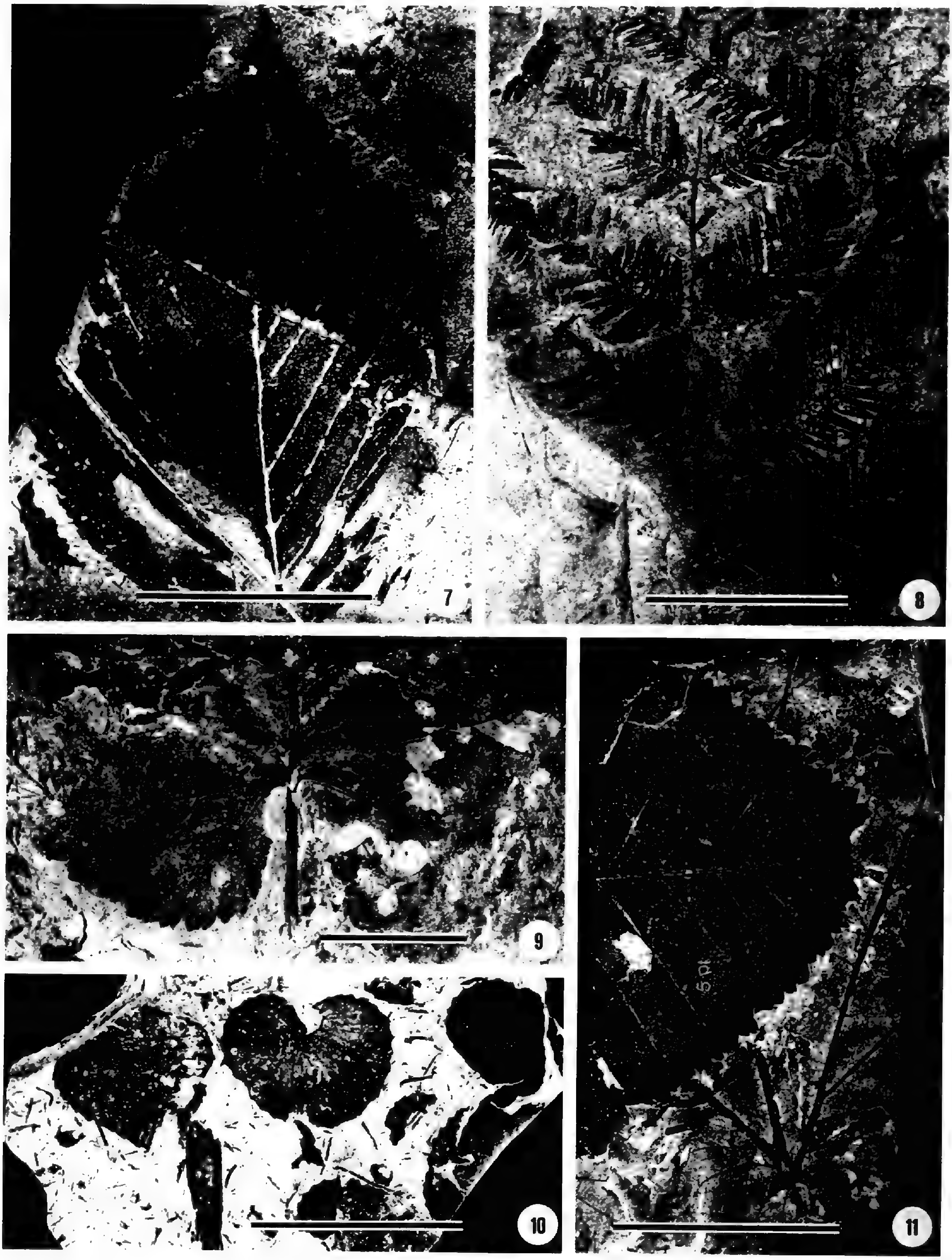
[3] We use *Trapago angulata* (Newberry) McIver & Basinger (1993) rather than *Quereuxia angulata* (Newb.) Krysht. for this species. Kryshtofovich (1953) transferred *Neuropteris angulata* Newb. (= *Trapa angulata* (Newb.) Brown) to *Quereuxia*, a genus that he created invalidly in 1938 for *Trapa*-like fruits from Russia. In 1953, when he transferred *N. angulata* to *Q. angulata*, he made reference to his 1938 use of the genus in the combination *Quereuxia aculeata* Krysht. within an article that does not appear to have been made available. *Quereuxia aculeata* was later validly published by Kryshtofovich in 1958.

Because *Quereuxia* was used as the generic name for his 1953 transfer, it has been assumed by some that the type of the basionym (*Neuropteris angulata*) is the generitype, although Kryshtofovich did not indicate this (see Golovneva, 1991). We believe Kryshtofovich (1953, 1958) clearly indicated that it is the similarity between his unattached fruits of *Quereuxia aculeata* and the unattached fruits that Brown (1962) inappropriately included with *Trapa angulata* that led him to create a new generic name, and that therefore his concept of the genus is based not on foliar material, but on fruits. It would be inappropriate to accept the type of the basionym *N. angulata* (a leaf) as the generitype for *Quereuxia*. Although Krystofovich did not follow the rules of the ICBN in 1953, his intent is clear and should be followed. Kryshtofovich's 1958 description of *Q. aculeata* should be viewed as the basis for the establishment of the genus, with this species being recognized as the type and basionym for the genus. To be consistent with Kryshtofovich's stated intent, his transfer of leaf material from *Neuropteris* and *Trapa* to *Quereuxia* must be viewed as an error. *Trapago* represents the subsequent and valid name to which foliage of this type has been transferred. The only basis for transfer of foliage of *Trapago angulata* to the genus *Quereuxia* would be the demonstration that fruits of the *Q. aculeata* type were found in attachment.



Figures 7–11. —7. cf. *Corylites* Seward & Holttum. US368–3906.1. Scale bar = 3.0 cm. —8. *Metasequoia* Miki. US200–6259. Scale bar = 4.0 cm. —9. cf. *Corylites* Seward & Hottum. US367–3897. Scale bar = 4.0 cm. —10. *Trapago* McIver & Basinger. US443–2834.2. Scale bar = 3.0 cm. —11. *Pseudoprotophyllum* Hollick (base of leaf) overlain by cf. *Corylites* Seward & Holttum (leaf apex). US367–3898. Scale bar = 4.0 cm.

terize regional vegetation (Appendices 1, 5). The fossil floras from the Expedition Formation appear very low in diversity. Although this low diversity may be attributable to poor preservation and limited sampling of plant remains, it is probable that the vegetation of this region during Expedition time was depauperate relative to the vegetation that succeeded it.

ENVIRONMENTS AND VEGETATION OF THE MIDDLE PALEOCENE

Throughout the Sverdrup Basin, the Strand Bay Formation is characterized by prodelta and muddy shelf facies, all of which represent regressive-progradational conditions that followed the mid-Paleocene regional transgression (Ricketts, 1994). The sediments are interpreted as shallow marine, but palynological data from some sites, together with fossil plants, indicate that terrestrial and freshwater environments were also present, although rare (Fig. 2).

The age of the Strand Bay Formation is considered middle Paleocene; however, as palynomorph recovery from this primarily marine unit of the Eureka Sound Group is poor, it may range from middle to late Paleocene (Ricketts, 1994).

Plant macrofossils are rare in the Strand Bay Formation and comprise mainly aquatic or emergent aquatic plants, including *Trapago*, the fern *Azolla*, and *Equisetum*. Probable swamp or wetland trees, including *Metasequoia*, are also represented. The paucity of plant remains (Appendix 2), including pollen (Appendix 6), supports the primarily prodeltaic to muddy shelf paleoenvironmental interpretation of Ricketts (1994). It appears that little emergent land surface was available throughout much of the High Arctic Islands for plant growth. Forests no doubt existed outside the wetlands, and certainly in the mountainous areas of the eastern margin of the Sverdrup Basin. Pollen data reveal bisaccate conifer pollen of the *Picea* and *Pinus* type, *Alnus*, *Betula*, and at least two members of the Juglandaceae (McIntyre in Ricketts, 1991).

ENVIRONMENTS AND FLORA OF THE LATE PALEOCENE AND EARLY EOCENE

Continuing regression characterized the eastern and southern Sverdrup Basin during the latter half of the Paleocene (Ricketts & Stephenson, 1994). On Ellesmere Island, from the Fosheim Peninsula to south of Strathcona Fiord, regressive river-dominated delta facies were predominant. This aggradational phase left a succession of coarsening-upward mudstone to sandstone cycles, with minor coals, forming the Lower Member of the Iceberg Bay Formation of Ricketts (1986, 1994). Carbonaceous mudstones and coal beds up to a meter thick, with abundant plant remains, commonly cap the uppermost sandstone beds of these cycles. Ricketts (1994) distinguished the Upper Coal Member from the Lower Member in part on the presence of fining-upward sequences and on the prevalence of thick, extensive coal seams.

By the end of the Paleocene, the sea had fully withdrawn, and most of Axel Heiberg and Ellesmere islands were covered with delta and alluvial plains (Ricketts, 1994). River systems dominated the landscape, producing either high-sinuosity fluvial environments, or broad floodplains with swamps and woodlands. Flood plain deposits can be recognized by the presence of thick coal seams, many with spectacular permineralized tree trunks and associated plant-fossil deposits (Francis, 1988; unpublished data). A greater land surface was exposed than at any other time during the deposition of the Eureka Sound Group, and the lush vegetation provided extensive habitats for diverse vertebrate faunas (West et al., 1977; Estes & Hutchinson, 1980; McKenna, 1980; Dawson et al., 1993; Ricketts, 1994).

Fossil plants of the Lower Member of the Iceberg Bay Formation are primarily of late Paleocene age, and Ricketts (1994) placed the Paleocene-Eocene boundary within this Lower Member. Neither the plant macrofossils nor palynofloras give clear evidence of the Paleocene-Eocene transition (McIntyre in Ricketts, 1994; McIntyre, pers. comm. 1997). Macrofloras are also not useful in distinguishing between beds of the Lower Member and the Coal Member of the Iceberg Bay Formation (Appendix 3). Assignment of the beds to either member was based on lithostratigraphy if possible, or beds were left unassigned.

Consistency of species composition throughout the Arctic Islands from the late Paleocene to early Eocene (Appendix 3) allows the Iceberg Bay floras to be considered as a single unit despite the time span of about 10 million years.

The vegetation of the late Paleocene and early Eocene, like the earlier floras, was essentially deciduous and composed of mixed conifer and broadleaf taxa. *Metasequoia* (523 specimens) is more commonly recovered than *Glyptostrobus* (41). *Ginkgo* (7), although present in many assemblages, is locally rare. The most abundant broadleaf angiosperm leaves were those of *Trochodendroides* (480 specimens; Fig. 14), with *Ushia* (328; Fig. 12) and *Ulmus* (264; Fig. 15) slightly less common. From fruits, we believe there were at least three cercidiphylloid species; in addition to the common *Nyssidium arcticum* and *Nordenskioldia borealis* types, there are fruits of a yet undescribed form (Fig. 17). *Carya* (72 specimens; Figs. 13, 32) was obviously one of the dominant taxa, as was *Archeampelos* (99; Fig. 16), the latter interpreted to be a vine. Less common members of the flora are the Betulaceae (46 specimens), *Osmunda, Thuja,* cf. *Amelanchites,* and taxa with leaves at least superficially resembling *Smilax, Trema, Prunus, Tilia,* and *Rhus* (i.e., Fig. 44).

The major swamp or wetland taxa of the early Paleocene persist as dominants in the floras of the late Paleocene and early Eocene, as do many of the deciduous broadleaf elements. Missing, however, is the relict *Pseudoprotophyllum.* The previously common aquatic angiosperm *Trapago* is extremely rare.

Not found earlier, but common in macrofloral assemblages of this age, are members of the Ulmaceae and Juglandaceae, although both families are represented in older palynofloras (Appendix 6). Also present in the palynofloras are the remains of evergreen conifers, including *Picea* and *Pinus* (Appendix 6). The near absence of these evergreen conifers in macrofloral assemblages of the Iceberg Bay suggests that they did not inhabit the same environments as did the plants commonly preserved. It is possible that they thrived in uplands; but up to 25% of the palynomorphs of some coal seams are pinaceous (D. J. McIntyre, pers. comm. 1997), suggesting that the conifers producing them lived nearby or within the swamps.

The late Paleocene to early Eocene Iceberg Bay floras appear moderate to low in diversity; about 28–30 species are recognized at present from macrofossils, and about 30 from the palynomorphs (Kalkreuth et al., 1993; Ricketts, 1994; Appendix 7). Based on preliminary identifications, we estimate that about 20 to 22 tree and shrub taxa are represented in the floral assemblages. All but Cupressaceae, Pinaceae, and perhaps Ericaceae (known from palynofloras only) are interpreted as deciduous.

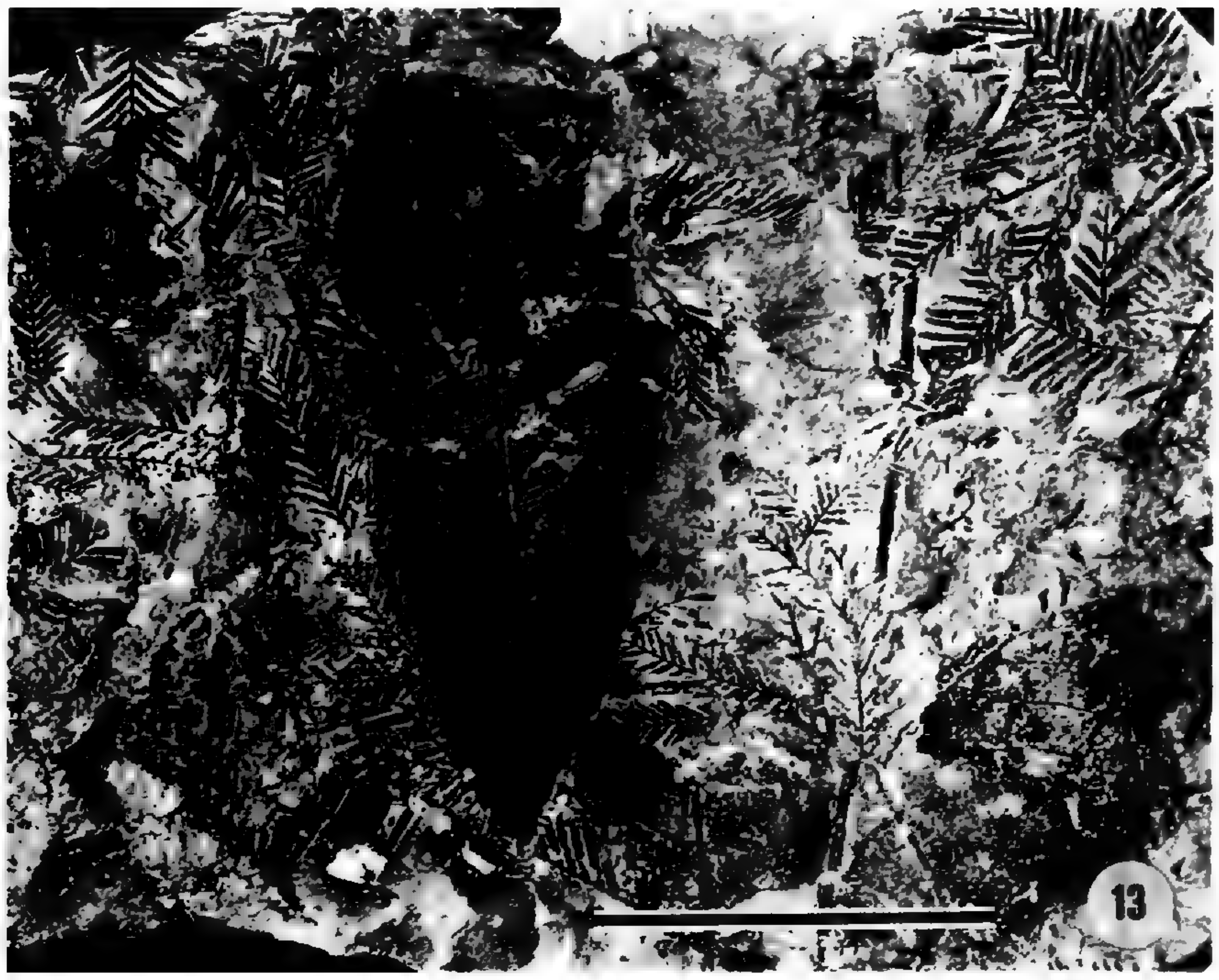
ENVIRONMENTS AND FLORA OF THE MIDDLE TO LATE EOCENE

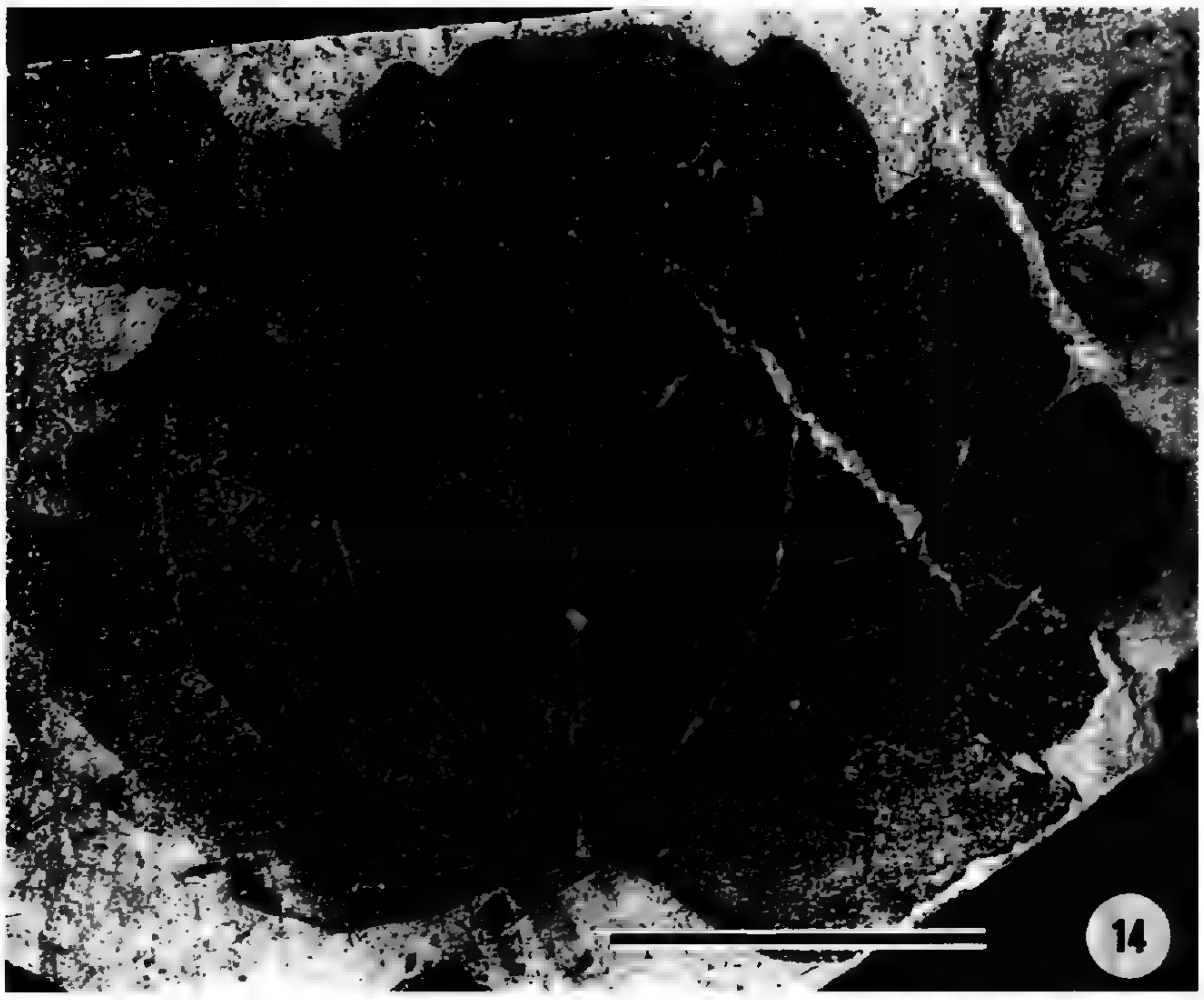
Late middle or late Eocene fossil floras are preserved in sediments of the Buchanan Lake Formation, which unconformably overlies the Iceberg Bay Formation. The Buchanan Lake Formation is diachronous; the sediments were deposited into synorogenic intermontane basins that formed at different stages of Eurekan tectonism, which may have commenced as early as the early Eocene or possibly latest Paleocene (Ricketts, 1991).

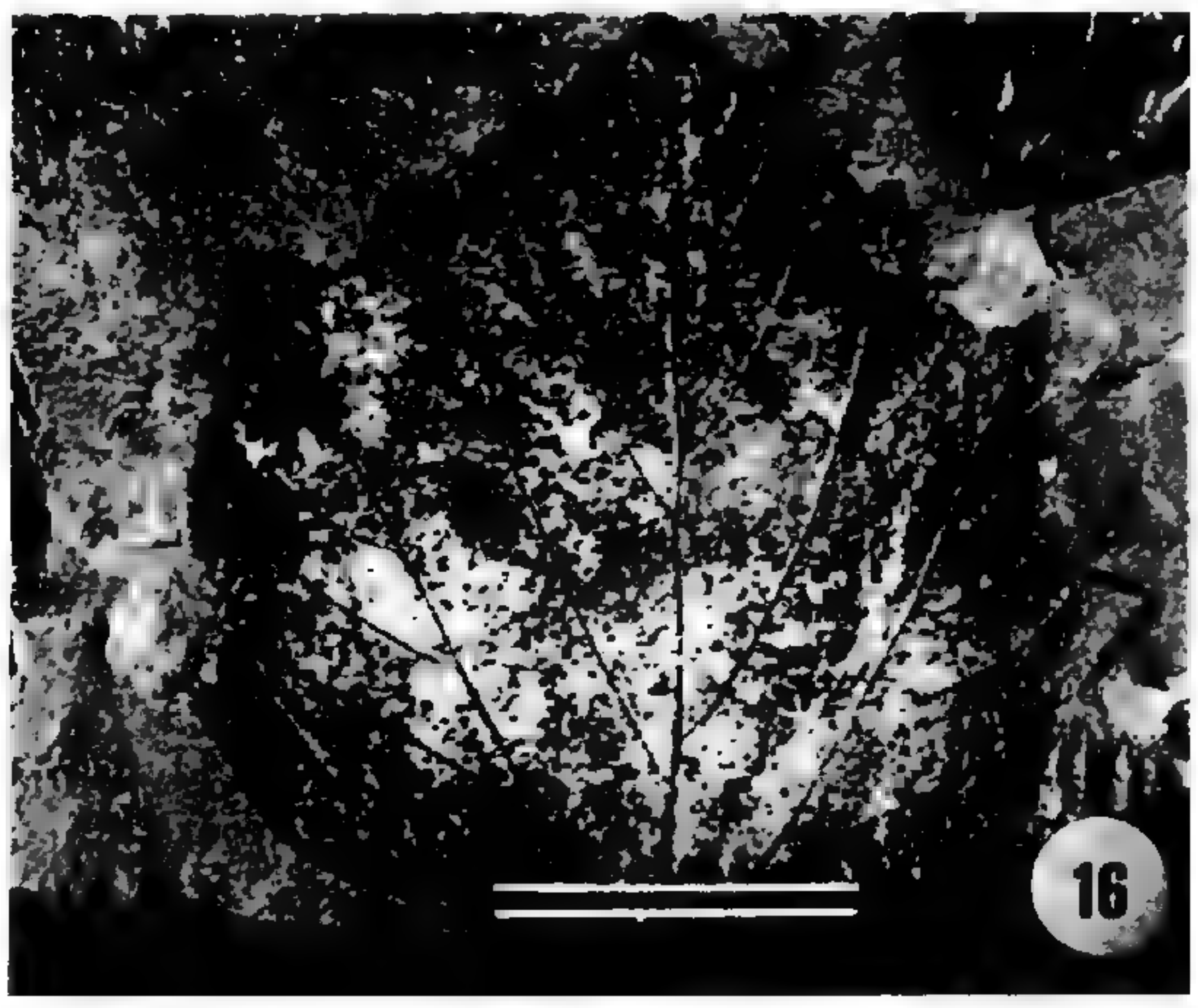
The demise of the Sverdrup Basin and the formation of at least six of these syntectonic, intermontane basins by the middle Eocene profoundly altered the geography of the Canadian High Arctic Islands, and is also reflected in distinct changes in the taxonomic composition of macrofossil assemblages. In one particular basin on eastern Axel Heiberg Island, plant remains are exquisitely preserved (Fig. 4). Sediments shed from the ancestral Princess Margaret Arch on the western margin of this basin were deposited in proximal fans, braidplains, and forest-bearing meanderplains (Ricketts, 1991), preserving the remains of vegetation from numerous habitats. Extensive study of this formation near the Geodetic Hills on Axel Heiberg Island provides data for modeling the depositional environment and interpretation of the vegetational mosaic (Fig. 6). The fossil plants from this site are used as the basis for interpreting the Buchanan Lake floras, as fossil plants are unreported from other contemporaneous basins. At the center of the basin, repetitive fining-upward cycles, commonly terminating in laterally extensive lignites that may be traced over several kilometers, indicate that periodically the floor of the basin was covered by shallow wetlands or swamp forests. Interbedded fluvial deposits, paleosols, and siltstones containing broad-leaved angiosperms indicate that at other times the lowlands were characterized by better drained floodplains, and that deciduous broadleaf angiosperm vegetation extended across the basin.

From stratigraphic and structural evidence, Ricketts (1994) interpreted the Buchanan Lake Formation as middle Eocene in age. A rich and diverse pollen assemblage is similar to middle Eocene assemblages from elsewhere in the Canadian Arctic, and although a late Eocene age cannot be ruled out on the basis of palynology, there is no evidence that the sediments are as young as Oligocene (McIntyre, 1991). Tooth fragments of a large herbivore have recently been recovered from the plant-bearing beds of the Buchanan Lake Formation. Based on their morphology and size, they are tentatively identified as belonging to a diplacodont (Brontotheriidae) and are indicative of a Uintan or Duchesnian age (middle Eocene) (J. J. Eberle & J. E. Storer, pers. comm. 1998), falling within the age range of 47 to 37 Ma (Prothero, 1995).

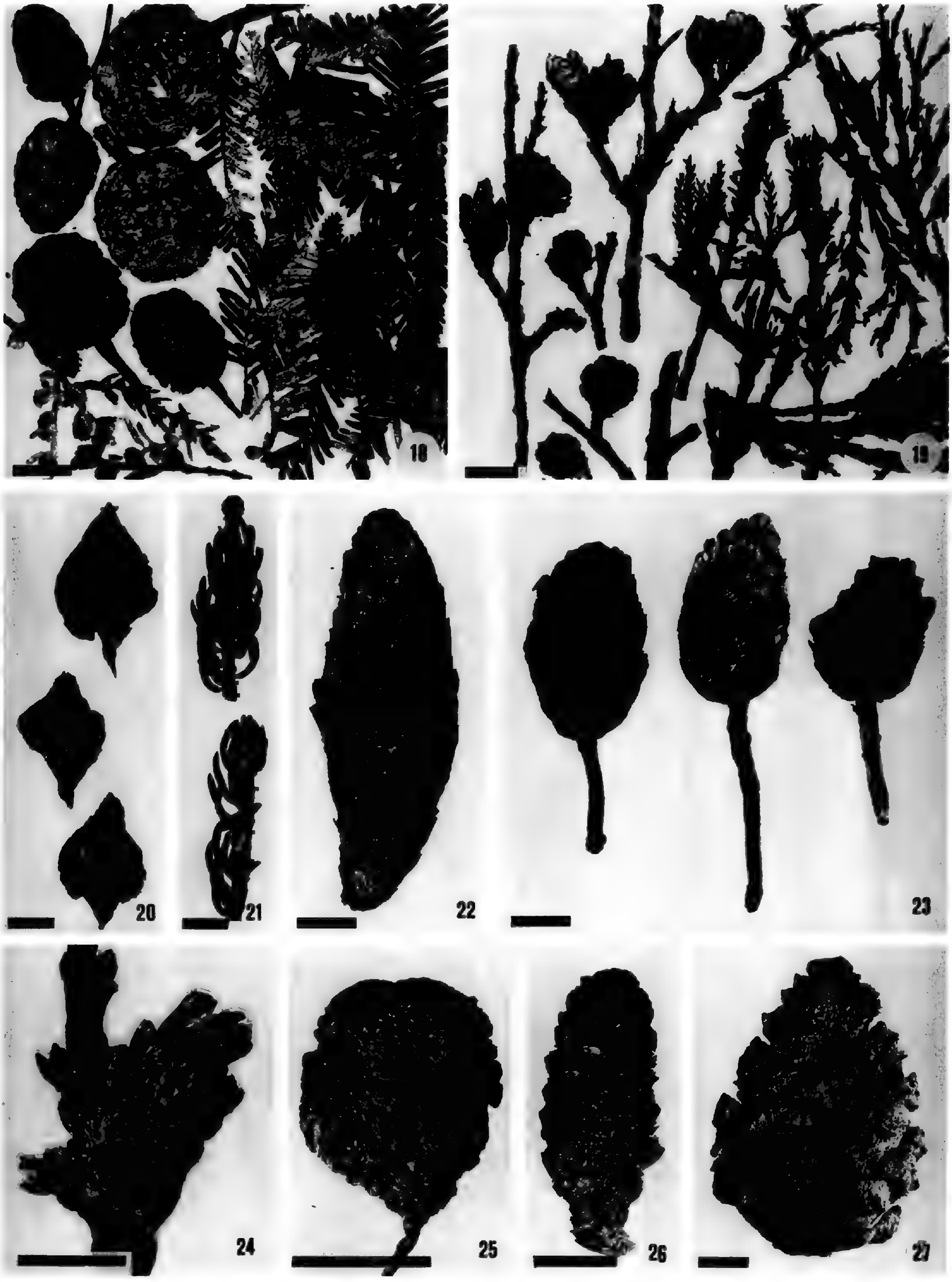
The regional flora of the Buchanan Lake Formation was briefly discussed by Basinger (1991) and Basinger et al. (1994). These works concentrated on the swamp vegetation, with only brief mention of fossil plants from fluvial deposits. Data







Figures 12–17. —12. *Ushia* Kolakovskij. US111–6293. Scale bar = 5.0 cm. —13. *Carya* Nutt. with *Metasequoia* Miki. US200–6259. Scale bar = 8.0 cm. —14. *Trochodendroides* Berry. US436–2696.1. Scale bar = 3.0 cm. —15. *Ulmus* L. US111–6314. Scale bar = 3.0 cm. —16. *Archeampelos* McIver & Basinger. US436–2134.1. Scale bar = 4.0 cm. —17. Unidentified Cercidiphyllaceae fruit. US6–498. Scale bar = 1.0 cm.



Figures 18–27. —18. *Metasequoia* Miki. Seed cones, pollen cones, foliage. US220. Scale bar = 10.0 mm. —19. *Glyptostrobus* Endl. Seed cones, foliage. US220. Scale bar = 10.0 mm. —20. *Pseudolarix* Gord. Ovuliferous scales. US220. Scale bar = 5.0 mm. —21. *Picea* A. Dietr. Twigs. US185. Scale bar = 5.0 mm. —22. *Picea* A. Dietr. Seed cone. US185. Scale bar = 10.0 mm. —23. *Tsuga* (L.) Carr. Seed cones. US220. Scale bar = 10.0 mm. —24. *Chamaecyparis* Spach. Twig. US220–6363. Scale bar = 5.0 mm. —25. *Chamaecyparis* Spach. Seed cone. US220–6358. Scale bar = 5.0 mm. —26. *Taiwania* Hayata. Seed cone. US220. Scale bar = 5.0 mm. —27. *Pinus* L. Seed cone. US115. Scale bar = 5.0 mm.

on the swamp floras come primarily from the site of the fossil forests of Axel Heiberg that are known for the beautifully preserved in situ mummified tree stumps and leaf litter (Francis, 1991; Basinger, 1991; Basinger et al., 1994; Greenwood & Basinger, 1993). At this site, numerous peat and coal beds, some up to a meter thick, are interbedded with fine-grained to coarse sediments in a section that is more than 400 m thick.

Swamp floras were dominated by the deciduous conifers *Metasequoia* (Fig. 18) and *Glyptostrobus* (Fig. 19), but diverse floral assemblages are apparent among the numerous peat layers that characterize the site. Palynological data show no biostratigraphical change in the floras within the unit (McIntyre, 1991), indicating that observed floral variation can be attributed to successional changes in a continually evolving floodplain environment. This is also supported by macrofossil data. Within-formation vegetational changes are therefore considered to be related to changes in sedimentary facies and depositional environment rather than time, and local floras are considered parts of a vegetation mosaic (Basinger et al., 1994).

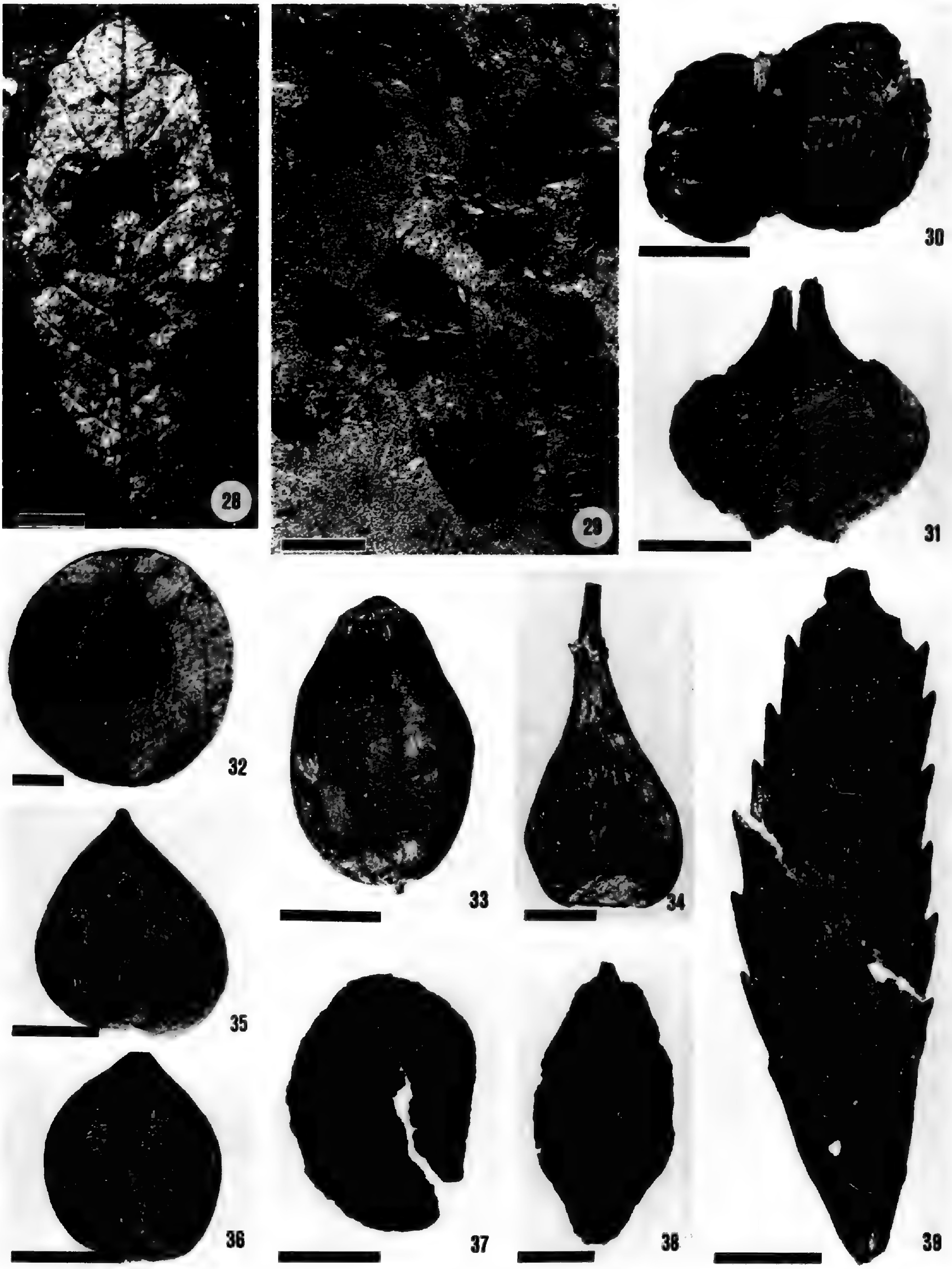
Other than the deciduous Taxodiaceae, conifers such as *Larix,* cf. *Keteleeria, Pseudolarix* (Fig. 20), *Picea* (Figs. 21, 22), *Tsuga* (Fig. 23), *Chamaecyparis* (Figs. 24, 25), *Taiwania* (Fig. 26), and *Pinus* (Fig. 27) are rare to locally common. Angiosperms were a significant component of swamp vegetation even though this may not be immediately apparent from the floral lists (Appendix 4), due to over-representation of conifers as a result of both taphonomy and collecting bias. Conifer remains are more resistant to decay and much more easily reclaimed from the peat than those of deciduous angiosperms and ferns. When present in abundance, broad leaves are typically decomposed and compressed into a thick mat, making them less easily identified in the field. They are commonly unreported. While studies of the swamp flora so far have concentrated on the conifers (Lepage & Basinger, 1991, 1995; Lepage, 1993), most peat layers producing conifer reproductive organs also produce angiosperm seeds and fruits; most of which remain unidentified. Many peat layers bear thick mats of broadleaf taxa that may include Betulaceae, *Osmunda,* and others.

Although included here as "swamp flora," the most productive and diverse peat layers do not likely represent typical swamp conditions, but rather lowland forests within a broad swamp environment. For example, the thick peat layer designated as locality US184 reveals the following assemblage: *Osmunda,* cf. *Keteleeria, Larix, Pseudolarix, Picea, Pinus, Tsuga, Chamaecyparis, Glyptostrobus, Metasequoia, Betula,* Juglandaceae, unidentified Taxodiaceae, unidentified angiosperm leaves (i.e., Figs. 28, 39), and numerous seeds and fruits (i.e., Figs. 30, 31, 33–38), including a likely Fagaceae, cf. *Trigonobalanus* (Manchester, pers. comm. 1998). Locality US220, at the same level but separated laterally by more than a kilometer, bears an almost identical flora. Based on their living relatives, many of the taxa collected at these two localities would not have been tolerant of standing water. This suggests the presence of microhabitats, on a scale of meters to 10s of meters, that were capable of supporting a diverse forest of large trees. Such diversity in the Buchanan Lake peat-forming environments, however, is exceptional, and most peat layers apparently represent low diversity or monotypic stands.

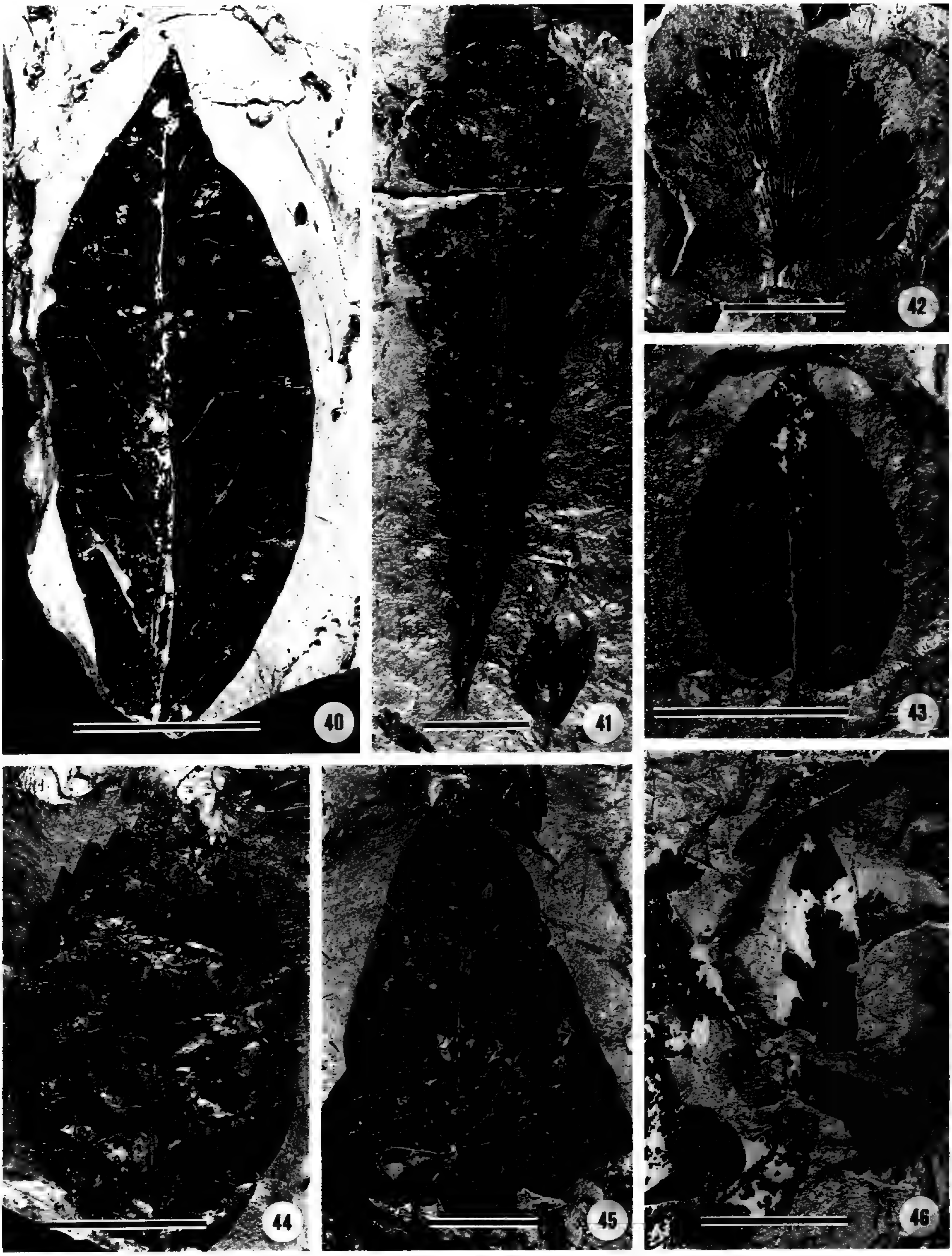
Many peat layers are composed entirely of *Metasequoia* or *Glyptostrobus,* or a combination of both. In some cases, only the seed cones of *Metasequoia* are well preserved, with the foliage hardly recognizable, suggesting typical cypress swamp environments with advanced peatification (diagenesis). Coalification (metamorphism) commonly renders components of Paleogene or older peats unrecognizable, making accurate characterization of Buchanan Lake swamp forests especially significant.

While peat-forming environments have left an extraordinary fossil record, they commonly cover only a small part of the land surface in depositional environments such as that interpreted for the Buchanan Lake Formation, as is illustrated in the model (Fig. 6). The regional vegetation is best typified by the plants that flourished on the well- or at least better-drained sites, as this would be most representative of cover of low to moderate elevations.

The "stream site" on Axel Heiberg Island near the fossil forest site includes fossiliferous mudstones and siltstones that are interpreted as overbank and floodplain sediments. Fossils from these deposits are interpreted as remains of plants that grew on the floodplains. Organ counts from collections made at this site indicated that the most commonly preserved leaves were Betulaceae (493 leaves; Fig. 43), which included both *Betula* and *Alnus,* as fruits of both were present, and perhaps *Corylus. Equisetum* (common) and *Metasequoia* (186 specimens) were found at most sites, as was *Trochodendroides* (102 leaves), the latter representing two species based on fruits (*Nyssidium arcticum* and *Nordenskioldia borealis*) and probably underrepresented in the collection. *Ginkgo* (79 leaves; Fig. 42), *Osmunda* (53 specimens; Fig. 46), and *Sparganium* (63 fruiting heads; confirmed non-pla-



Figures 28–39. —28. Unidentified coriaceous leaf. US220. Scale bar = 5.0 mm. —29. Unidentified bract-like structures. US436–2778. Scale bar = 5.0 mm. —30. *Nordenskioldia borealis* Heer. US220. Scale bar = 5.0 mm. —31. cf. *Trigonobalanus* (Fagaceae), bicarpellate fruit, styles incomplete. US220. Scale bar = 5.0 mm. —32. cf. *Carya* Nutt. Fruit husk. US522. Scale bar = 5.0 mm. —33. Unidentified fruit. US220. Scale bar = 3.0 mm. —34. Single carpel from same fruit type as Figure 31, style incomplete. US220. Scale bar = 2.0 mm. —35. cf. *Juglans* L. US220. Scale bar = 5.0 mm. —36. cf. *Juglans* L. Nut, inner view of valve. US220. Scale bar = 5.0 mm. —37. Unidentified fruit. US220. Scale bar = 5.0 mm. —38. cf. *Nyssa* L. Fruit. US220. Scale bar = 5.0 mm. —39. Unidentified leaf. US220. Scale bar = 5.0 mm.



Figures 40–46. —40. cf. *Nyssa* L. US188–5897. Scale bar = 3.0 cm. —41. *Quercus* L. US188–5894. Scale bar = 2.0 cm. —42. *Ginkgo* L. US188–5896. Scale bar = 2.0 cm. —43. Betulaceae. US188–6069. Scale bar = 2.0 cm. —44. cf. *Rhus* L. US188–6068. Scale bar = 3.0 cm. —45. Menispermaceae. US652–5716. Scale bar = 3.0 cm. —46. *Osmunda* L. US188–5822. Scale bar = 2.0 cm.

tanoid) were present, as were cf. *Nyssa* (107 leaves; Fig. 40), *Quercus* (59 leaves; Fig. 41), and a Menispermaceae (interpreted as a vine; 39 leaves; Fig. 45). Less common at the site were leaves of *Glyptostrobus, Ushia, Platanus,* Juglandaceae, *Archeampelos,* cf. *Rhus* (Fig. 44), two additional ferns, and other taxa yet unidentified (Appendix 4).

The local vegetation at this site is interpreted as primarily broadleaf deciduous, with deciduous conifers present and likely dominating the wettest sites, given their dominance of swamp facies. The canopy was apparently dominated by hardwoods, including many of the taxa that flourished in the High Arctic during the Paleocene and early Eocene. Many are related to taxa that are typically found today in mesothermal climates at midlatitudes; some taxa have modern relatives that are more typically megathermal, such as Menispermaceae (known from macrofloras), and Sterculiaceae, Olacaceae, and Aquifoliaceae (known from palynofloras). At least 20 extant families and 33 extant genera are represented by leaves that are interpreted as either trees or shrubs (see Table 1). Ferns appear to have been the most abundant plants of the forest understory, while *Sparganium* and *Equisetum* flourished in wetlands.

Vegetation of the uplands is difficult to characterize because of the scarcity of fossil remains known to have come from these environments. Common in fluvial sands are seed cones of *Picea, Pinus,* and *Metasequoia,* although fruits of Juglandaceae have also been recovered (Basinger, 1991; Lepage, 1993). These remains are associated with stems and wood fragments preserved as lag deposits. Unlike wood from peats and lignites, woods of these lag deposits are commonly resinous and attributable to the Pinaceae, most probably *Pinus* or *Picea.* The abundance of *Picea* cones relative to all other taxa strongly suggests that plants in these deposits were brought in from outside of the depositional environment, as the genus is largely unknown from the other facies and occurs only rarely in a few lignite beds (Lepage, 1993). *Picea* may have been common in the uplands and may have dominated at higher altitudes. The common occurrence of bisaccate grains in the palynological record (McIntyre, in Ricketts, 1991, 1994), in the absence of a corresponding macrofossil record, supports this interpretation. Near-absence of angiosperms in these fluvial sands, with the exception of robust fruits of Juglandaceae, is most probably a consequence of taphonomic processes.

The regional vegetation at the time of Buchanan Lake deposition can be described as: lowlands dominated by mixed deciduous angiospermous and coniferous forests; swamps and wetlands dominated by deciduous conifers; and uplands probably covered by mixed deciduous angiospermous and evergreen coniferous forests.

DISCUSSION

Paleoclimates can be interpreted from plant macrofossil data using either nearest-living-relative or physiognomic approaches. A correlation between leaf form and climate is well established (Bailey & Sinnott, 1916; Wolfe, 1971, 1979), and foliar physiognomic techniques appear relatively robust when fossil plant assemblages have extant vegetational equivalents (Wolfe, 1993; Wilf, 1997). However, it has become clear that physiognomic techniques are not useful for interpreting climate of high paleolatitudes during most of the Earth's past, because analogous vegetation does not exist today. Basinger et al. (1994) found that temperature predictions based on data drawn from extant deciduous vegetation were too low, given arguments from sea-surface temperature data, nearest living relatives, and threshold taxa such as crocodilians. In the modern world deciduousness as a response to cold winter temperatures is apparently correlated with the same physiognomic signatures as deciduousness induced by high-latitude winter darkness in the past.

Tiffney (1994) has shown that the climatic tolerances of living species of genera with distributions in both Old and New Worlds can be used to assess arctic paleoclimates. These taxa must have inhabited the arctic regions during the past in order to achieve their present distributions. Most of the nearest living relatives of the fossil species inhabit frost-free environments, and Tiffney (1994) suggested that during the early Eocene, the cold-month mean temperature in the High Arctic was about 10°C with the possibility of mild frost. Interpretations based on fossil remains from the Buchanan Lake Formation, including wood and leaf fossils, indicate that winters were not cold and that frost was rare or absent (Basinger, 1991). Minimum cold-month mean temperatures of 0 to 4°C, warm-month mean of more than 25°C, and mean annual temperatures of 12 to15°C were estimated for the Buchanan Lake floras by Basinger et al. (1994).

Preliminary examination of fossil plants for this study suggests that a cold-month mean of 0–4°C may be slightly low for sites at sea level. As noted by Basinger et al. (1994), cold-month temperatures in the modern mid-latitudes exhibit strong diurnal fluctuation and may vary widely throughout a month. Minimum daily and extreme monthly values, which are critically important to vegetation, are masked by the mean. Under polar winter-dark regimes, diurnal temperature fluctuation essentially ceases, fostering long-term stability of weather patterns and temperature. In this case, the mean more closely represents actual minima experienced, irrespective of moderation of coastal habitats by a warm polar ocean. Therefore, cold-month mean temperatures associated with analogous modern vegetation (i.e., 10°C of Tiffney, 1994) would be expected to be several degrees higher than mean polar cold-month paleotemperatures. Based on the data currently available, we conclude that climates of this time were mesothermal, moist, and mainly without severe winter frosts at low elevations, despite the dark winters.

It is well established that global warming occurred during the early Tertiary (Frakes et al., 1992). Benthic foraminiferal oxygen isotope records indicate that the thermal maximum occurred shortly after the Paleocene-Eocene transition (Miller et al., 1987). By the middle Eocene, temperatures had returned to Paleocene levels, and continued to deteriorate to present lows. Early Tertiary warming and cooling are reflected in the arctic fossil plant assemblages, and appear to have been responsible for some of the floral changes identified. Nevertheless, other factors apparently played an important role in the evolution of the composition of the younger plant assemblages.

Throughout the Paleocene and early Eocene, most land surfaces of the Canadian Arctic Archipelago appear to have been of low relief and covered with a similar deciduous vegetation. Most forests flourished at or near sea level in situations representing swamps, wetlands, and moist lowlands. By the early Eocene, evergreen conifers were rare elements in fossil assemblages. On the alluvial plains, deciduous broadleaf taxa, such as the elms and hickories, became common members of regional floras. Although rarely represented in the lowland macrofloral assemblages, members of the Buxaceae, Tiliaceae, Nyssaceae, Aceraceae, and Caprifoliaceae are known from their pollen (Appendix 7).

By the middle Eocene, floras had become considerably more diverse and complex. Evergreen conifers were then forming integral parts of local assemblages. Sharing dominance in the forests were elms, hickories, oaks, lindens, and plane trees, as well as more ancient forms such as the trochodendroides, dawn redwood, ginkgos, and grapes. New to the flora were plants interpreted as most closely related to extant taxa of tropical regions today (i.e., Menispermaceae, Sterculiaceae, Olacaceae, and Aquifoliaceae).

The presence of megathermal elements in the middle Eocene Buchanan Lake floras could be interpreted as reflecting poleward dispersal of these taxa during the Eocene thermal optimum as they became adapted to polar seasonality. Their presence, and the persistence of the same frost-intolerant taxa that characterize the early Eocene swamp and lowland floras, indicate that at or close to sea level, climates remained within the limits of tolerance of these taxa and continued to be mesothermal and without significant winter frost. The appearance of diverse evergreen Pinaceae, the dominance of Betulaceae, and the inclusion of many other taxa commonly associated with winter frosts today, such as *Platanus, Juglans, Fagus, Tilia, Salix, Acer,* and *Fraxinus,* in the middle Eocene Buchanan Lake assemblages would then be unexpected, as hard winter freezing is not indicated. Most of these genera, however, do have extant species that inhabit regions that are not associated with hard winter frosts; for example, *Salix* and *Fraxinus* are common in bald cypress swamps of southern Florida (Duever et al., 1984a).

Basinger et al. (1994) suggested that the appearance of diverse evergreen Pinaceae in the Buchanan Lake assemblage may reflect achievement of some temperature threshold that permitted evergreen plants to become dormant and to survive the dark winter at low elevation, noting that the pollen record of evergreen Pinaceae is extensive in the Paleocene and Eocene polar Tertiary, in contrast to the general absence of such taxa in the lowland macrofossil record. Profound climatic deterioration, however, did not occur until after deposition of the Buchanan Lake Formation. Nevertheless, we believe that the development of greater diversity and complexity of floral assemblages is more likely attributable to increased environmental heterogeneity associated with regional tectonism.

Correlation between mountain building and quantum evolution of angiosperms was noted by Axelrod (1967). During the Eocene, the Eurekan Orogeny fundamentally altered the tectonostratigraphic organization of the ancient Sverdrup Basin. Uplift and subsidence changed the broad, relatively flat coastal plains into isolated valleys and mountain ranges, creating increased environmental diversity. Two consequences would be to bring lowland (frost intolerant) and montane (frost tolerant) vegetation into close proximity, and thereby increase preservational potential of the latter in the fossil record, and to contribute to fragmentation of populations, and thereby increase potential for speciation.

There is no evidence that any of the fossil localities were deposited at significant elevation, but elevation is an important factor of local microclimate in high mountain-deep valley terrain. Regional climates may be generally frost-free at sea level, but adiabatic lapse would have caused the highlands to have been cooler. Mountains can also cause temperature depression and greater temperature fluctuations in adjacent lowlands, allowing frost-tolerant vegetation to invade otherwise frost-free sites. On the other hand, in mature hardwood forests with a closed canopy, a well established understory can provide protection from occasional frosts, allowing more sensitive megathermal species to invade (Duever et al., 1984b).

The apparently rapid appearance and diversification during the Eocene in the High Latitudes of groups now typical of frost-tolerant northern mid-latitude assemblages is correlated with the structural reorganization of the ancient Sverdrup Basin during Eurekan tectonism, and with the onset of Tertiary global climatic deterioration. Both factors may have influenced the origin and evolution of some lineages now characterizing northern mid-latitude vegetation. It could be that frost tolerance within these lineages evolved after adaptation to polar seasonal light regimes and in response to mid-Tertiary climatic cooling. Alternatively, frost tolerance within lineages could have developed at high altitude. Nevertheless, there is not at present sufficient data to consider the high latitudes, as opposed to high altitudes, as primary centers of origin and diversification of frost-tolerant taxa. Further study of these fossil collections from the Canadian High Arctic and better integration of macrofossil and palynological data will contribute to the resolution of the role of the high latitudes in the evolution of northern ecosystems.

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APPENDIX 1

Plant Remains from the Upper Expedition Formation: Early to Middle Paleocene.

FOSHEIM ANTICLINE WEST, ELLESMERE ISLAND

US191, 193 79°34′N 84°02′W

Metasequoia Miki, *Glyptostrobus* Endl., *Trochodendroides* Berry, cf. *Ushia* Kolakovskij, *Trapago* McIver & Basinger.

FOSHEIM ANTICLINE EAST, ELLESMERE ISLAND

US250–253 79°42.5′N 84°15′W

Equisetum L., Unidentified conifer (Cupressaceae-Taxodiaceae), *Trochodendroides* Berry, cf. *Ushia* Kolakovskij, *Trapago* McIver & Basinger, Unidentified angiosperm leaves.

STRATHCONA FIORD, ELLESMERE ISLAND

US358, 359, 362–364,
367, 368, 371 78°38–40′N 81°55–57′W

Equisetum L., cf. *Pseudolarix* Gord., *Metasequoia* Miki, *Trochodendroides* Berry, *Nyssidium arcticum* (Heer) Iljinskaja, *Ushia* Kolakovskij, Betulaceae, cf. *Corylites* Seward & Holttum, cf. *Trema* Lour., *Trapago* McIver & Basinger, *Archeampelos* McIver & Basinger, *Pseudoprotophyllum* Hollick.

US421 78°36′N 82°48′W

Equisetum L., cf. *Filicites* Forbes, Unidentified conifer (Cupressaceae-Taxodiaceae).

Appendix 2

Plant Remains from the Strand Bay Formation: Middle Paleocene.

Strathcona Fiord, Ellesmere Island

US360, 361, 365, 369, 370 78°38–40′N 81°57–59′W

Equisetum L., *Azolla* Lam., *Metasequoia* Miki, *Trapago* McIver & Basinger, cf. *Ushia* Kolakovskij, Unidentified angiosperm leaves.

Split Lake, Ellesmere Island

US441, 443 77°51′N 83°38–40′W

Equisetum L., *Trapago* McIver & Basinger.

Appendix 3

Plant Remains from the Iceberg Bay Formation.

Lower Member: Late Paleocene

FOSHEIM ANTICLINE WEST, ELLESMERE ISLAND

US111 79°43′N 84°45′W

Equisetum L., Unidentified fern, *Ginkgo* L., *Metasequoia* Miki, cf. *Glyptostrobus* Endl., cf. *Smilax* L., *Trochodendroides* Berry, *Nordenskioldia borealis* Heer, *Ushia* Kolakovskij, *Ulmus* L., *Carya* Nutt., Betulaceae, *Archeampelos* McIver & Basinger, Unidentified dicotyledon leaf.

Coal Member: Early Eocene

LAKE HAZEN, ELLESMERE ISLAND

US261–263, 267, 268, 274 Near 81°54′N 69°40″W

Equisetum L., *Ginkgo* L., *Metasequoia* Miki, cf. *Glyptostrobus* Endl., *Trochodendroides* Berry, *Nyssidium arcticum* (Heer) Iljinskaja, *Ushia* Kolakovskij, cf. *Ulmus* L., cf. *Carya* Nutt., cf. *Amelanchites* McIver & Basinger, cf. *Archeampelos* McIver & Basinger, Unidentified dicotyledon leaf.

STRAND FIORD, AXEL HEIBERG ISLAND

US163 79°16′N 91°26′W

Ginkgo L., *Metasequoia* Miki, *Trochodendroides* Berry, cf. *Carya* Nutt., Unidentified dicotyledon leaves.

US164 79°14′N 91°26′W

Metasequoia Miki, cf. *Glyptostrobus* Endl., cf. *Ulmus* L., *Comptonia* Banks.

US165–167, 172 79°15′N 91°16′W

Metasequoia Miki, *Trochodendroides* Berry, *Nyssidium arcticum* (Heer) Iljinskaja, *Ushia* Kolakovskij, Betulaceae, *Comptonia* Banks, *Archeampelos* McIver & Basinger, Unidentified dicotyledon leaves.

US168–170 79°15′N 91°10′W

Metasequoia Miki, *Trochodendroides* Berry, *Nyssidium arcticum* (Heer) Iljinskaja, cf. *Ulmus* L., cf. *Carya* Nutt., *Archeampelos* McIver & Basinger, cf. *Viburnum* L., Unidentified dicotyledon leaves.

US173 79°16′N 91°17′W

Trochodendroides Berry, *Nordenskioldia borealis* Heer, *Ushia* Kolakovskij.

US174 79°15′N 91°10′W

Metasequoia Miki, *Trochodendroides* Berry, *Ushia* Kolakovskij, cf. *Carya* Nutt., *Archeampelos* McIver & Basinger.

US175–177 79°15′N 91°16′W

cf. *Filicites* Forbes, *Metasequoia* Miki, Unidentified monocotyledon, *Trochodendroides* Berry, Betulaceae, cf. *Carya* Nutt., Unidentified dicotyledon leaves.

US176 79°15′N 91°16′W

cf. *Carya* Nutt., Unidentified dicotyledon leaves.

US178–180 79°14′N 91°16′W

Metasequoia Miki, *Trochodendroides* Berry, *Archeampelos* McIver & Basinger, Unidentified dicotyledon leaves.

Iceberg Bay Formation, Undivided: Late Paleocene to Early Eocene

OXHEAD CREEK, ELLESMERE ISLAND

US6 79°43′N 85°05′W

Metasequoia Miki, *Trochodendroides* Berry, Unidentified Cercidiphyllaceae fruit, *Ushia* Kolakovskij, *Carya* Nutt., Unidentified dicotyledon leaf.

US22–26 79°43′N 85°05′W

Equisetum L., *Osmunda* L., cf. *Filicites* Forbes, *Metasequoia* Miki, cf. *Glyptostrobus* Endl., Unidentified monocot, *Trochodendroides* Berry, Betulaceae, Unidentified dicotyledon leaf.

MOSQUITO CREEK, ELLESMERE ISLAND

US100, 101, 195–201 79°57′N 84°43′W

Equisetum L., *Metasequoia* Miki, *Thuja polaris* McIver & Basinger, *Trochodendroides* Berry, *Nordenskioldia borealis* Heer, *Ushia* Kolakovskij, *Ulmus* L., cf. *Trema* Lour., cf. *Carya* Nutt., Betulaceae, cf. *Prunus* L., *Archeampelos* McIver & Basinger, Unidentified dicotyledon leaf, Unidentified fruits and seeds.

HOT WEATHER CREEK, ELLESMERE ISLAND

US100–104, 107, 108 79°56′N 84°45′W

Equisetum L., *Osmunda* L., Unidentified fern, *Metasequoia* Miki, cf. *Smilax* L., Unidentified monocot, *Trochodendroides* Berry, *Nordenskioldia borealis* Heer, *Ushia* Kolakovskij, *Carya* Nutt.

FOSHEIM PENINSULA

US254–259 79°45′N 85°01′W

Equisetum L., *Osmunda* L., cf. Pinaceae, *Metasequoia* Miki, *Glyptostrobus* Endl. (seed cones), *Trochodendroides* Berry, *Ushia* Kolakovskij, cf. *Amelanchites* McIver & Basinger, Unidentified dicotyledon leaf.

STRATHCONA FIORD, ELLESMERE ISLAND (MARGARET FORMATION)

US422 78°38′N 82°52.5′W

Metasequoia Miki, *Trochodendroides* Berry, cf. *Trema* Lour., *Carya* Nutt., cf. *Vitis* (Tourn.) L., Unidentified dicotyledon leaf

STENKUL FIORD, ELLESMERE ISLAND (MARGARET FORMATION)

US430–439 77°52′N 81°38′W

Equisetum L., *Osmunda* L., *Metasequoia* Miki, cf. *Nelumbo* Adanson, *Trochodendroides* Berry, *Nyssidium arcticum* (Heer) Iljinskaja, Unidentified Cercidiphyllaceae fruit, *Ushia* Kolakovskij, cf. *Trema* Lour., *Ulmus* L., *Carya* Nutt., Betulaceae, cf. *Tilia* L., *Archeampelos*

McIver & Basinger, cf. *Rhus* L., cf. *Grewia* L., Unidentified dicotyledon leaf, Unidentified fruits and seeds.

SPLIT LAKE, ELLESMERE ISLAND (MARGARET FORMATION)

US442 77°52′N 83°37′W

Equisetum L., cf. *Trema* Lour., *Trapago* McIver & Basinger, *Archeampelos* McIver & Basinger.

US444 77°53.2′N 83°36′W

Metasequoia Miki, *Trochodendroides* Berry, Unidentified Cercidiphyllaceae fruit, cf. *Archeampelos* McIver & Basinger, *Carya* Nutt., cf. *Trema* Lour., Unidentified dicotyledon leaf.

APPENDIX 4

Plant Remains from the Buchanan Lake Formation: Middle to Late Eocene.

AXEL HEIBERG ISLAND: Swamp sediments (peats and coals)

US184, 220 70°55″N 88°58′W

Osmunda L., cf. *Keteleeria* Carr., *Larix altoborealis* Lepage & Basinger, *Picea* A. Dietr., *Pinus* L., *Pseudolarix* Gord., *Tsuga* Carr., *Glyptostrobus* Endl., *Metasequoia* Miki, cf. *Sequoia* Endl., *Taiwania* Hayata, *Chamaecyparis* Spach, *Carya* Nutt., cf. Myricaceae, cf. *Trigonobalanus*, *Betula* L., cf. Ericaceae, Unidentified Taxodiaceae, Unidentified angiosperms.

US116

Picea A. Dietr., *Metasequoia* Miki, Unidentified angiosperms.

US182

Picea A. Dietr., *Carya* Nutt.

US186

Picea A. Dietr., *Metasequoia* Miki.

US236

Picea A. Dietr., *Pinus* L., *Larix altoborealis* Lepage & Basinger, *Pseudolarix* Gord., *Tsuga* Carr., *Metasequoia* Miki, Unidentified conifers and angiosperms.

US415

Pinus L., *Larix altoborealis* Lepage & Basinger, *Pseudolarix* Gord., *Glyptostrobus* Endl., *Metasequoia* Miki, *Chamaecyparis* Spach, Unidentified Taxodiaceae, Unidentified angiosperms.

US516

Larix altoborealis Lepage & Basinger, *Pinus* L., *Tsuga* Carr., *Metasequoia* Miki.

US554

Pinus L., *Pseudolarix* Gord.

US564

Osmunda L., *Pinus* L., *Pseudolarix* Gord., cf. *Betula* L., Unidentified Cupressaceae.

US585

Picea A. Dietr.

US588

Picea A. Dietr., *Pinus* L., *Pseudolarix* Gord., *Metasequoia* Miki.

AXEL HEIBERG ISLAND: Fluvial sediments (mudstones)

US187, 592 79°55′N 88°58′W

Equisetum L., *Ginkgo* L., *Trochodendroides* Berry, *Ushia* Kolakovskij, *Alnus* L., Unidentified dicotyledon leaves.

US188, 216, 652 79°56.5′N 89°08′W

Equisetum L., *Osmunda* L., *Onoclea* L., Unidentified fern, *Ginkgo* L., *Glyptostrobus* Endl., *Metasequoia* Miki, cf. *Sparganium* (Tourn.) L., Menispermaceae, *Trochodendroides* Berry, *Nyssidium arcticum* (Heer) Iljinskaja, *Platanus* L., *Ushia* Kolakovskij, cf. Ulmaceae, *Juglans* L., *Quercus* L., *Betula* L., *Alnus* L., *Tilia* L., cf. Rosaceae, cf. *Nyssa* L., *Archeampelos acerifolia* (Newberry) McIver & Basinger, cf. *Rhus* L., cf. *Fraxinus* L., Unidentified dicotyledon leaves, Unidentified fruits and seeds.

US210–212, 502, 503, 506, 507 79°5′N 89°08′W

Equisetum L., *Osmunda* L., Unidentified fern, *Ginkgo* L., *Pinus* L., *Metasequoia* Miki, cf. *Sparganium* (Tourn.) L., Menispermaceae, *Trochodendroides* Berry, *Nyssidium arcticum* (Heer) Iljinskaja, *Nordenskioldia borealis* Heer, *Platanus* L., *Juglans* L., *Quercus* L., Betulaceae, cf. *Nyssa* L., *Archeampelos acerifolia* (Knowlton) McIver & Basinger, Unidentified angiosperm leaves.

US213–215, 500, 501, 504, 505,
510, 550, 589 79°56 89°08′W

Osmunda L., Unidentified fern, *Metasequoia* Miki, *Glyptostrobus* Endl., cf. *Sparganium* (Tourn) L., Unidentified monocotyledon leaves, Menispermaceae, *Trochodendroides* Berry, *Ushia* Kolakovskij, *Quercus* L., *Betula* L., *Alnus* L., cf. *Nyssa* L., *Archeampelos acerifolia* (Knowlton) McIver & Basinger, Unidentified fruits and seeds.

US323, 324, 409, 508 79°55 89°04′W

Osmunda L., *Metasequoia* Miki, cf. *Sparganium* (Tourn) L., Menispermaceae, *Trochodendroides* Berry, *Betula* L., cf. *Nyssa* L., *Archeampelos acerifolia* (Knowlton) McIver & Basinger, cf. *Rhus* L.

US588 79°56.5′N 89°08′W

Unidentified Taxodiaceae.

AXEL HEIBERG ISLAND: Plants from fluvial sediments (ironstones)

US187 70°55″N 88°58′W

Ginkgo L., *Pseudolarix* Gord., *Metasequoia* Miki, *Alnus* L., *Betula* L.

AXEL HEIBERG ISLAND: Fluvial sediments (sandstones)

US114, 119, 587 70°55″N 88°58′W

Picea A. Dietr., *Metasequoia* Miki.

US115, 234, 235, 567, 568

Picea A. Dietr., *Pinus* L., *Metasequoia* Miki.

US237

Larix altoborealis Lepage & Basinger, *Picea* A. Dietr., *Pinus* L., *Metasequoia* Miki, *Carya* Nutt., Unidentified angiosperm leaves.

US520

Larix altoborealis Lepage & Basinger, *Picea* A. Dietr., *Metasequoia* Miki.

US563

Larix altoborealis Lepage & Basinger, *Picea* A. Dietr., *Pinus* L.

US586

Picea A. Dietr.

US533

cf. *Keteleeria* Carr.

APPENDIX 5

List of Palynomorphs Assigned to Extant Genera or Families from the Expedition Formation from Ellesmere Island. Adapted from McIntyre (in Ricketts, 1994), and see reference for additional palynomorphs. Sediments are considered probable early Paleocene age.

Ulmus L. (*Ulmipollenites undulosus* Wolff), Ericaceae (*Ericipites* Wodehouse, *Simplicepollis rallus* (Stanley) Nichols & Brown, *Alnus* L., *Betula* L.

Report on Palynomorphs from the Taggart River Section (US372: Samples 1–14), Near Strathcona Fiord, 78°38′08″N, 81°56′37″W, Ellesmere Island. (Report by D. J. McIntyre.)

The palynological preparations in the section from Taggart River contain abundant plant tissue. This is mainly cuticular or leafy type, and vascular or woody tissue is also present. Pollen and spore floras are similar throughout, and any differences are primarily because of dominance and abundance of pollen and spore types. In most samples pollen of conifers are dominant, particularly types referable to *Picea* and *Pinus.* Other conifer pollen present includes rare *Larix* and *Abies* and some probable *Podocarpidites.* Pollen of Taxodiaceae is common in many samples but rare in others. Most of the small-sized grains are considered to be of *Taxodium* and *Metasequoia.* Some large grains are probably of *Sequoia* type. In samples 9, 11, and 12 Taxodiaceae pollen is dominant. Fern spores of *Osmunda, Laevigatosporites,* and *Deltoidospora* are domiant in samples 10, 13, and 14.

Pollen of angiosperm species is present in all samples. However, there is limited representation of species, and most samples have only a few of the species recorded in the section. The pollen types present in the section are *Alnus, Betula, Ulmus, Paraalnipollenites alterniporus, Momipites wyomingensis, Caryapollenites imparalis, Triporopollenites mullensis, Triporopollenites bituitus, Simplicepollis rallus, Ericipites* (Ericaceae), *Arecipites* (Liliaceae), *Trudopollis barentsii,* and *Insulapollenites rugulatus.* The fungal type *Pesavis parva* occurs in many samples, and other fungal forms are also present in some samples.

The pollen and spore floras indicate a Paleocene age, probable middle, for the section. All taxa noted above occur in the Paleocene. *Alnus* first appears in the Arctic in the early Paleocene. *Pesavis parva* is a Paleocene and late Maastrichtian species. *Simplicepollis rallus* last occurs in the middle Paleocene, and *Insulapollenites rugulatus* is known only from the middle and late Paleocene. *Trudopollis barentsii* was described from the Paleocene of Spitzbergen and has also been recorded from the Paleocene of the Arctic Islands. *Momipites wyomingensis* and *Caryapollenites imparalis* occur in the middle and late Paleocene, but other species of the two genera that are present in the late Paleocene were not recorded. The fern spore *Hazaria sheopiariae,* which is rare, is a Campanian to middle Paleocene species. The pollen and spore assemblages indicate that the section is probably middle Paleocene in age and do not provide evidence of an age as young as late Paleocene. Cretaceous dinoflagellates are present in some samples, but the pollen evidence clearly indicates that these are reworked.

APPENDIX 6

List of Palynomorphs Assigned to Extant Genera or Families from the Strand Bay Formation from Ellesmere Island. Adapted from McIntyre (in Ricketts, 1994), and see reference for additional palynomorphs. Sediments are considered middle to late Paleocene in age.

Juglandaceae (*Momipites wyomingensis* Nichols & Ott).

List of Palynomorphs Assigned to Extant Genera or Families from the Strand Bay Formation from Axel Heiberg Island. Adapted from McIntyre (1991), and see reference for additional palynomorphs. Sediments are considered Paleocene in age.

Picea L., *Pinus* L., Taxodiaceae/Cupressaceae (*Metasequoia* Miki), *Alnus* L., *Betula* L., Juglandaceae (*Caryapollenites imparalis* Nichols & Ott, *Caryapollenites inelegans* Nichols & Ott, *Momipites wyomingensis* Nichols & Ott), Ericaceae.

APPENDIX 7

List of Palynomorphs Assigned to Extant Genera or Families from the Iceberg Bay Formation (Coal Member) from Ellesmere Island. Adapted from McIntyre (1991), and see reference for additional palynomorphs. Sediments are considered not older than middle Paleocene and not younger than middle Eocene. See also Manum (1962) for additional data and comments.

Sphagnum L., *Osmunda* L., *Picea* A. Dietr., *Pinus* L., Taxodiaceae, *Sparganium* (Tourn.) L., *Liquidambar* L., *Ulmus* L., *Carya* Nutt., *Alnus* L., *Betula* L., *Corylus* (Tourn.) L., *Tilia* L., Ericaceae, *Diervilla* Miller.

List of Palynomorphs Assigned or Tentatively Assigned to Extant Genera from the Iceberg Bay Formation (= Margaret Formation), Strathcona Fiord Area. Adapted from Kalkreuth, McIntyre, and Richardson (1993) and considered late Paleocene to early Eocene in age.

Picea L., *Pinus* L., *Metasequoia* Miki, cf. *Glyptostrobus* Endl., cf. *Taxodium* Rich, cf. *Sequoia* Endl., *Cercidiphyllum* Sieb. & Zucc., *Liquidambar* L., *Ulmus* L., *Carya* Nutt., *Pterocarya* Kunth, *Quercus* L., *Alnus* L., *Betula* L., *Corylus* L., *Tilia* L., *Nyssa* L., *Pachysandra* Michx., *Acer* L., *Fraxinus* L., *Diervilla* Miller, *Viburnum* L.

APPENDIX 8

List of Palynomorphs Assigned or Tentatively Assigned to Extant Genera and Families from the Buchanan Lake Formation. Adapted from McIntyre (1991) and considered middle to possibly late Eocene.

Lycopodium L., *Gleichenia* Sm., *Osmunda* L., cf. *Polypodium* L., cf. *Cryptogramma* R. Br., cf. *Abies* (Tourn.) Hill, cf. *Larix* (Tourn) Adans., *Picea* A. Dietr., *Pinus* L., *Tsuga* (L.) Carr., *Metasequoia* Miki, cf. *Glyptostrobus* Endl., cf. *Taxodium* Rich., *Sparganium* (Tourn.) L., *Cercidiphyllum* Sieb. & Zucc., *Liquidambar* L., *Ulmus* L., cf. *Planera* J. F. Gmelin, *Carya* Nutt., *Engelhardia* Leschen, *Juglans* L., *Pterocarya* Nutt., *Myrica* L., *Castanea* Adams, *Fagus* L., *Quercus* L., *Alnus* L., *Betula* L., *Corylus* L., *Tilia* L., *Salix* L., Ericaceae, Rosaceae, *Nyssa* L., *Ilex* L., *Pachysandra* Michx., *Acer* (Tourn.) L., cf. *Rhus* (Tourn.) L., *Fraxinus* L., *Diervilla* Miller, *Lonicera* L., cf. *Viburnum* L.

THE HISTORY OF NEOTROPICAL VEGETATION: NEW DEVELOPMENTS AND STATUS[1]

Robyn J. Burnham[2] *and Alan Graham*[3]

ABSTRACT

The isolation of South America from Central America and Africa during the Tertiary Period left a strong imprint on the flora of the Neotropics. South American Eocene through Miocene fossil assemblages, both pollen and macrofossils, document a rich tropical flora on the continental margins, and represent some of the only data on pre-landbridge lowland taxa in South America. Lowland Miocene floras from Amazonia are remarkably similar in their high diversity to Amazonian floras today based on lists of dominant families. Recent geophysical data on the uplift of the northern Andes show a strong correlation between uplift and the development and diversification of montane forests in Colombia and Venezuela. The emergence of a continuous landbridge at 3 Ma between Central and South America is well documented and is demonstrated by the arrival of temperate elements in South American highlands and concurrent appearance of South American taxa in Central America. There is no evidence for displacement of lowland tropical plants in South America by northern immigrants, which appears to stand in contrast to the published record for mammals. The mix of taxa in extant Mexican tropical floras derived from tropical South America, tropical Central America, and from remnants of northern tropical Eocene floras is strong evidence for the impact that the landbridge through the Panamanian isthmus had on the neotropical flora. The early appearance of low-elevation savannas is inferred from an increase in grass pollen in the middle Pliocene of Panama; however, widespread savannas are not indicated by pollen data from the Central American region. Rather, beginning in the latest Miocene Epoch and continuing up to the Quaternary, a mix of tropical rainforest and mixed tropical woodlands is suggested for the lowlands, based on pollen evidence. Accumulating data on temperature changes during the late Tertiary and Quaternary Periods points to low-latitude temperature fluctuations of up to 6°C. Proposals of accompanying widespread rainfall fluctuations are more equivocal. Rainfall probably varied regionally, resulting in a mosaic of habitats controlled by river migration, sea level fluctuations, local dryness, and local uplift. Zones postulated as refugia provide testable hypotheses using neoecological and paleoecological data. The paleoecological data to test these hypotheses are still limited taxonomically and spatially. It is important to stress that the effect of the isolation of South American neotropical floras has not been erased in the 3 million years since their connection with Central America. New data from middle and late Miocene floras in South America will be critical in determining the degree to which the composition of South American floras has been influenced by immigration of plants from the better-known Central American area to the north.

The neotropics extend geographically from the Tropic of Cancer to the Tropic of Capricorn, including environments as diverse as dry desert or humid rainforest. Mean annual temperatures range from over 30°C to as low as 10°C. Elevations from sea level up to well over 6000 m are included. This wide range of climate and topography has a profound effect on the composition and structure of neotropical vegetation. The area also has a distinctive geographic outline. It is roughly hour-glass shaped, with the narrow isthmus of Panama composing the fragile, primarily lowland connection between large northern and southern land masses. In addition, both the northern and southern neotropics lie contiguous to subtropical and temperate areas to the north and south: no barriers to immigration from these extra-tropical sources are present. There are as many reasons for neotropic patterns of diversity and distribution today as there are different landforms and climatic regimes. If these differences are played out over the course of the late Mesozoic and Cenozoic, when data from fossil deposits can inform us about the sequence of changes that has taken place, the history of neotropical vegetation takes on a dizzying complexity.

We approach this review of the vegetational history of the Neotropics by outlining four important events (Fig. 1). We initially treat the two major land areas separately, because for much of their history they were indeed isolated from one another. Then, we summarize the interactions that postdate the connection and treat selected aspects of the Neo-

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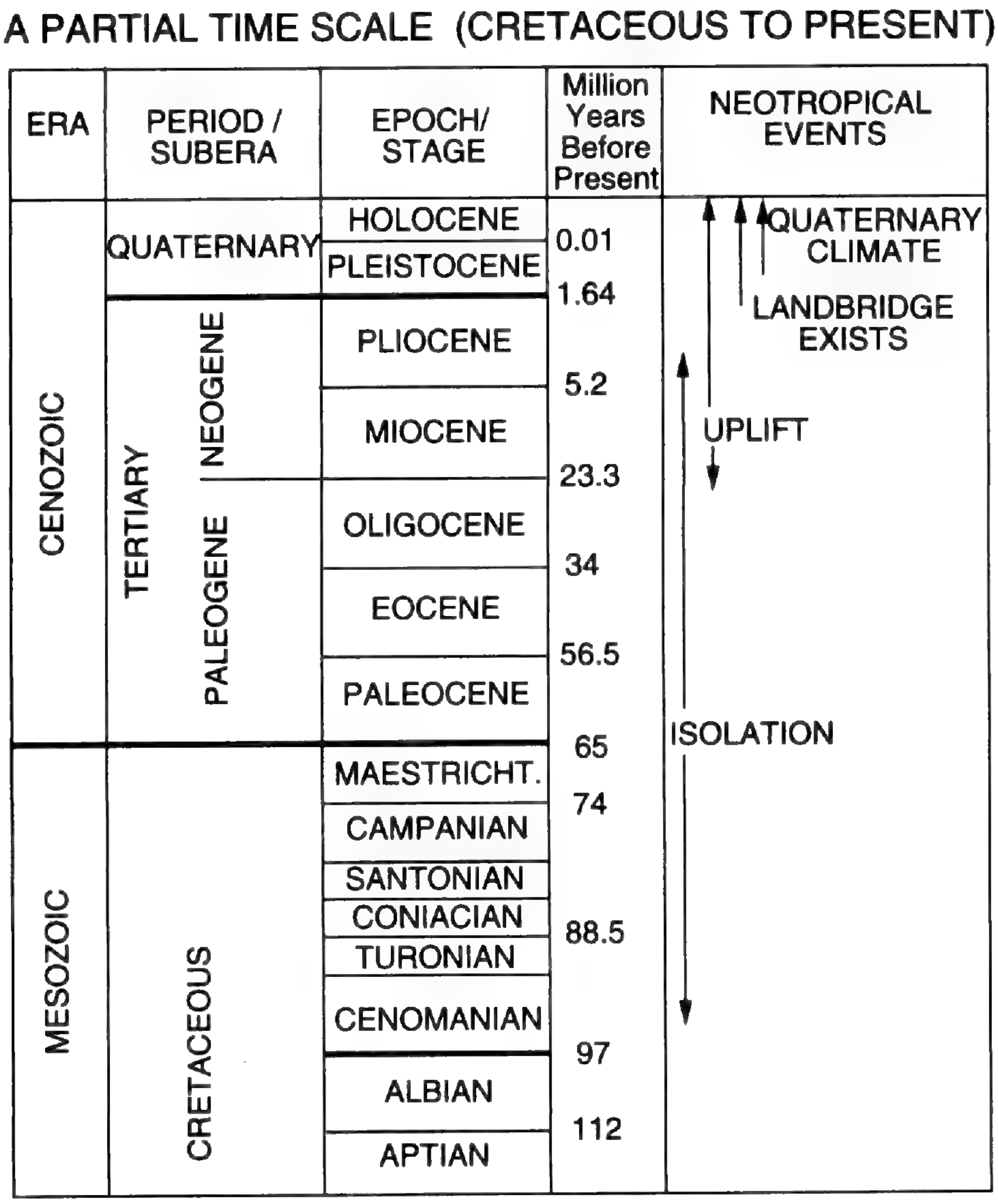

Figure 1. Time scale for the mid-Cretaceous to Present showing the four events discussed in the text. Note that the events are not temporally distinct from one another.

tropics as a whole up to the present. The unique history of the vegetation of the Neotropics is, in large part, due to the geographic isolation of its southern half during most of the past 90 million years, subsequent uplift of the Andes, and interactions between the northern and southern elements.

We review data on the pollen and macrofossil records from the late Cretaceous Period up to about 5000 years ago, when climates and physiography took on essentially modern aspects. We address the Neotropics as geographically defined: from 23° South to 23° North latitude. At the southern extreme we have included fossil floras from Bolivia, but have excluded floras from Argentina, Paraguay, and southern Brazil. At the northern extreme, we have included fossil floras from Mexico up to 23° North latitude. Our review of the history of the vegetation in this broad geographic area incorporates all the published data known, insofar as it can be integrated into databases on plant macrofossils and microfossils. Figure 2 shows the location of published fossil floras from Costa Rica to Bolivia, which are referenced in Appendix 1.

A BRIEF HISTORY OF THE ACCUMULATION OF MACROFOSSIL AND MICROFOSSIL DATA IN THE NEOTROPICS

Among the oldest reports of plant fossil assemblages from the Neotropics are the works of T. Wolf, a geologist who mapped areas of southern Ecuador in the late 1800s in company with G. vom Rath (Wolf & vom Rath, 1876). His work on paleontology and geology in southern Ecuador coincided temporally with the explorations on extant plant biology of Richard Spruce in the Amazon and Andes. Wolf's reports of fossils from the inter-Andean basins of southern Ecuador were followed by H. Engelhardt, who published several taxonomic treatments of plant fossils from 1887 through 1895. From about 1915 through 1945, E. W. Berry published extensively on neotropical paleobotany with works on macrofossil floras from Mexico through Patagonia (Berry, 1921a, 1929a, 1945a). Berry

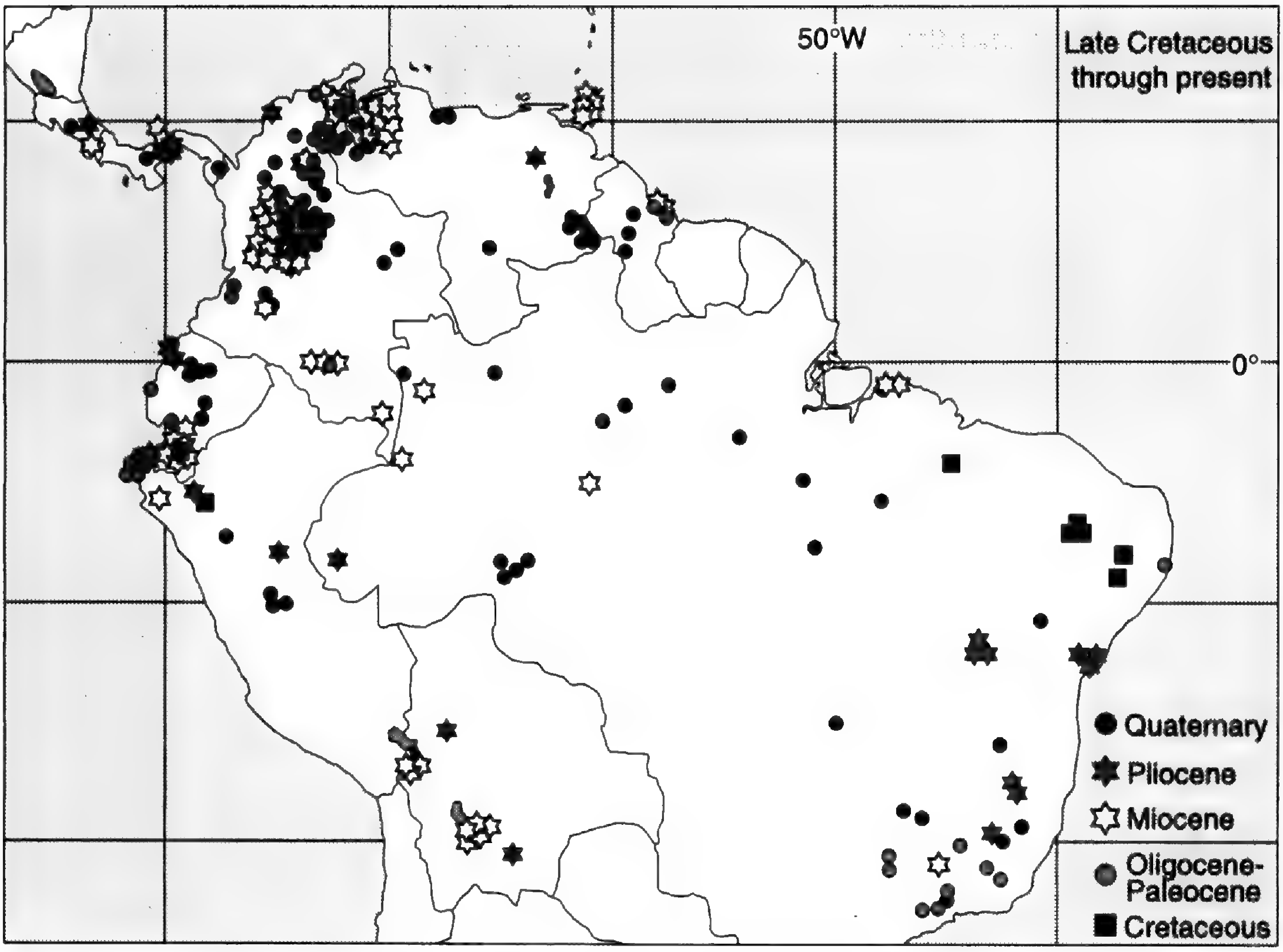

Figure 2. Distribution of published fossil plant localities in northern South America and southern Central America of Late Cretaceous to Quaternary age, referenced in Appendix 1.

published more than 55 papers on South American paleobotany alone, detailing the systematic affinities of the floras and reconstructing vegetation, altitude, and paleoclimate. Although Berry's treatments of the floras were classic for the time, his identifications were based on a comparatively small number of known modern taxa. His firsthand experience in South America appears to have been quite limited. Berry's identifications of Eocene fossil plants from the United States may be at least 60% in error (Dilcher, 1974), and it is also a concern that pollen samples processed from the same Costa Rican localities (Graham, 1987) turned up none of the genera identified by Berry (1921a). Nonetheless, the paleobotanical literature was dominated by Berry's publications on the Neotropics up to the time of his death (Appendix 1).

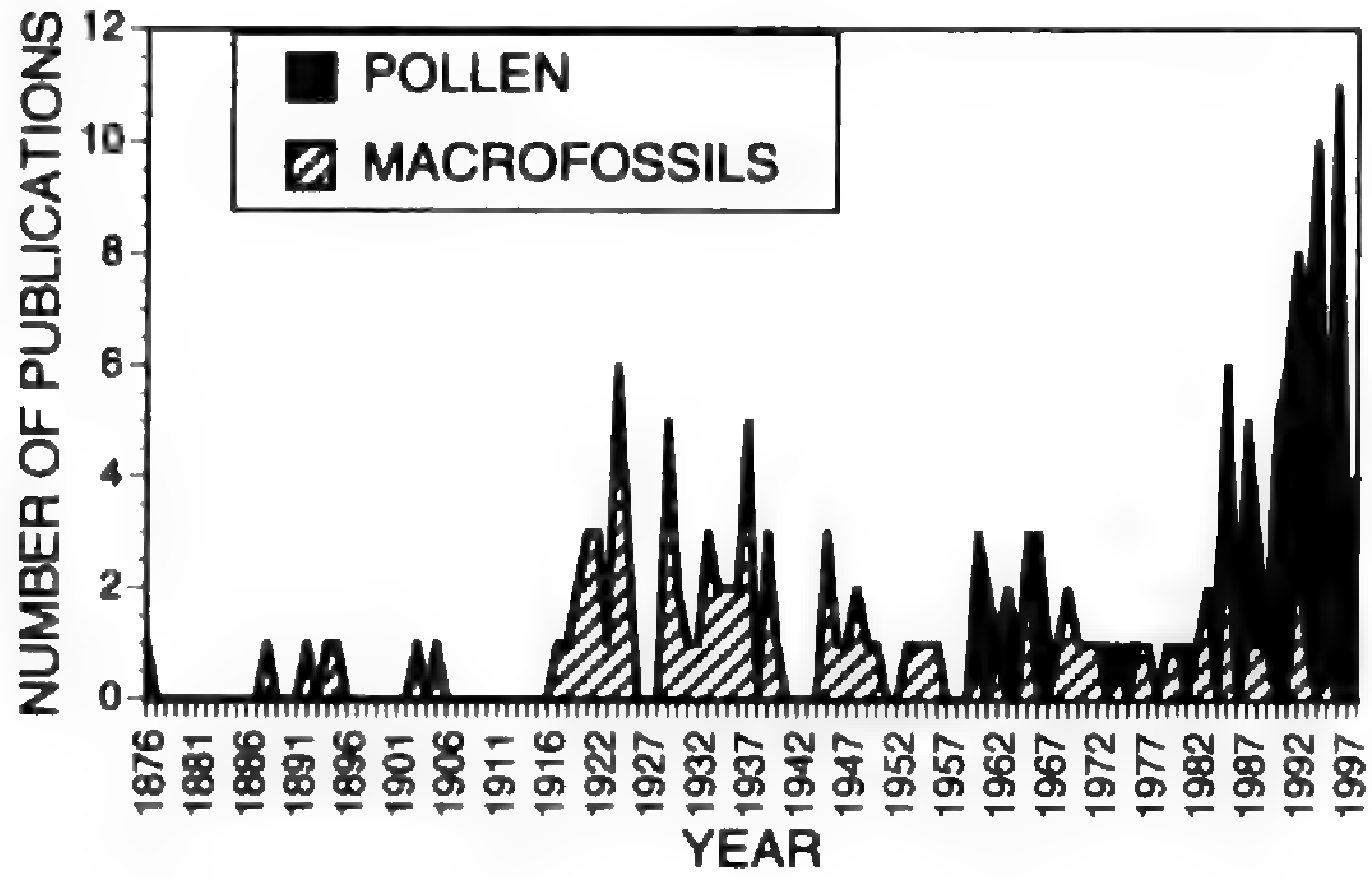

Figure 3. Publication activity in neoptropical paleobotany since 1876. Publications are coded with respect to the dominant organ reported: all macrofossils (leaves, fruits, seeds, wood) are grouped. Publications listed are primary reports of localities and fossil plant remains; no summaries or reviews are included.

After Berry there was a relative lull in publication activity (Fig. 3) until palynology became an established research tool in tropical America. In 1954 the first of the monumental works of T. van der Hammen on vegetation reconstruction, using palynology of the Colombian Andes, was published (van der Hammen, 1954). Some of this work used artificial, form-generic taxonomy, making comparisons with macrofossils difficult. However, other research was focused on creating a pollen zonation for the High Plain of Bogotá. From the dominant taxa, reconstructions of vegetation zones were achieved and directly related to the uplift of the northern Andes.

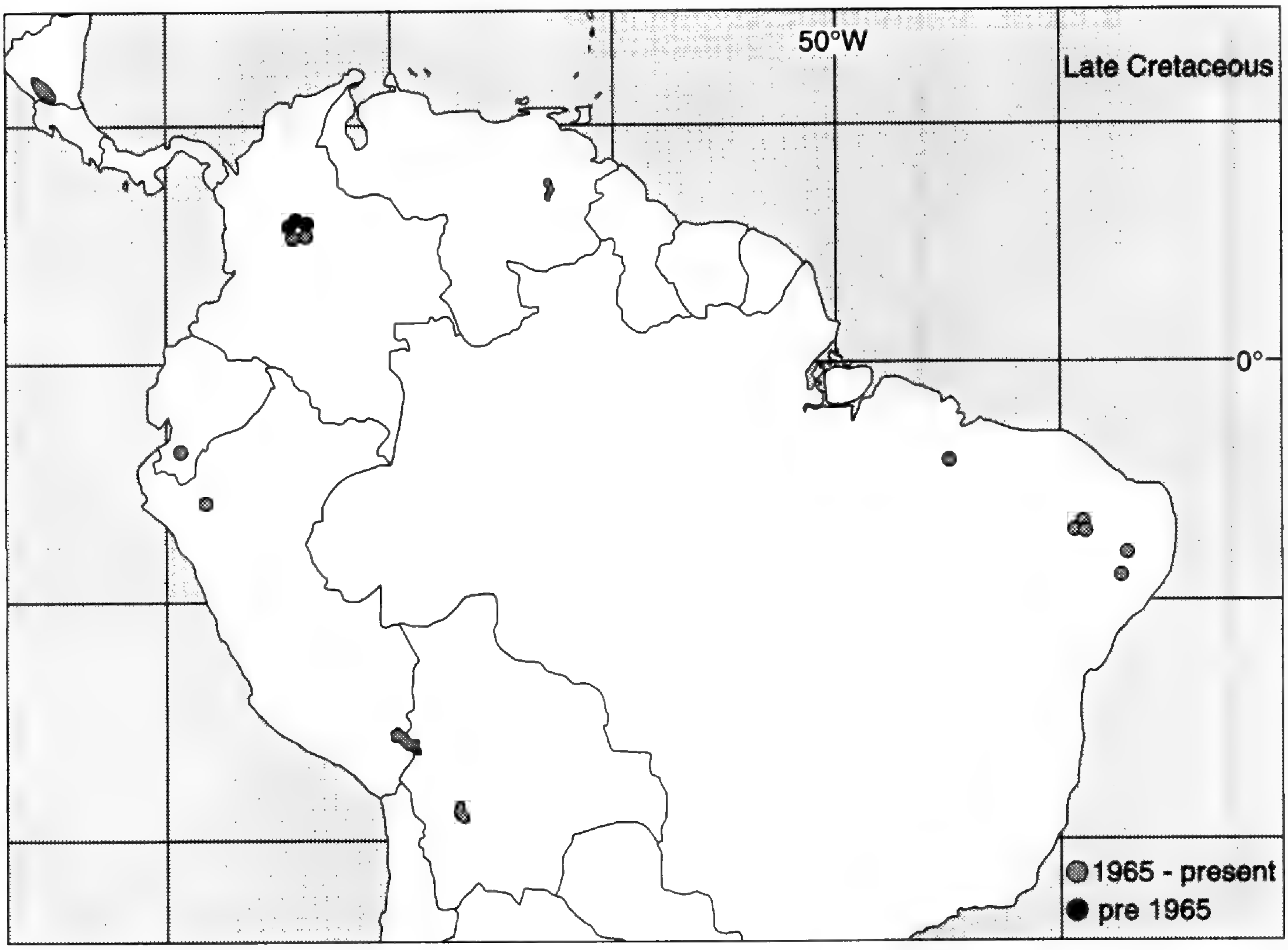

Figure 4. Distribution of published fossil plant localities in northern South America and southern Central America of Late Cretaceous age.

The potential for assessing the nature of past vegetation depends upon the methodologies of macrofossil paleobotany and paleopalynology. Each has its strengths and weaknesses. Pollen provides an inventory of many canopy trees, shrubs, and understory herbaceous plants, identifiable mostly to genus, and is useful for reconstructing larger-scale vegetational patterns (tens of square kilometers of vegetation may contribute to a single sample). Macrofossils provide an inventory mostly of canopy trees and shrubs, identifiable to species, and allow detailed reconstruction of vegetation in the immediate vicinity of the depositional basin; less than a square kilometer of vegetation usually contributes to a single fossil assemblage (Burnham, 1994). Clearly, the integrated use of both methodologies creates the highest resolution picture of vegetation and vegetational change. Although pairing of samples from localities is a logical goal, it is only rarely that such studies have been carried out in paleobotany (Hollick, 1928; Graham & Jarzen, 1969; Leopold & MacGinitie, 1972; Farley & Dilcher, 1986; Farley & Wing, 1989; Taggart & Cross, 1990; Skog & Dilcher, 1994; Willard et al., 1995; Wijninga, 1996a).

DISTRIBUTION OF THE DATA IN TIME AND SPACE

In Figure 2 we show the geographical distribution of data used in this review. Localities from which fossil floras have been described, either with a goal of vegetation reconstruction or floristic census, were plotted and coded for the geological time period represented. Sites shown on these maps are listed by country and stratigraphic position in Appendix 1. The distribution of sites mentioned in the text in Mexico, Central America, and the Antilles are presented in publications by Graham (1988c). In South America there is a clear preponderance of localities on continental margins. Amazonia is particularly poor in pre-Quaternary sites, and it is important to continue exploration for additional palynological or macrofossil assemblages in the rich Cenozoic deposits (Tschopp, 1953; Duarte, 1972, 1983, 1985).

We have also displayed the data for northern South America in two categories: pre-1965 and post-1965 (Figs. 4–8). This distinction is entirely arbitrary, chosen only on the basis of a visible break in publication activity at 1965. In addition, radiometric dating was being widely applied by this time, and some tropical Cenozoic floras could be dated independently of the estimates based on the fossil assemblages. Thus the two categories also reflect greater possibility for independent age confirmation in the more recently published works.

FOUR MAJOR EVENTS STRUCTURING NEOTROPICAL VEGETATION

EVENT I: ISOLATION

The physical setting

Geophysical and biological evidence now indicate that rifting between Africa and South America was under way by about 95 mya (Pitman et al., 1993; 106–84 mya, Goldblatt, 1993). By 85 million years ago, it is estimated that a seaway covering as much as 10° longitude (up to 800 km) existed between the two southern continents. Plant communities in South America of this age are too fragmentary to provide much evidence on the degree of isolation of the floras of the two continents. However, from other regions we know that angiosperms were diversified by this time (Muller, 1981, 1984; Wing et al., 1993), and several modern families are recognizable (Wolfe & Upchurch, 1987; Friis & Crepet, 1987). The ecological dominance of angiosperms in most habitats becomes apparent after the Cenomanian (Wing & Tiffney, 1987a, b; Wing et al., 1993).

At the same time that Africa and South America were separated, South America was also isolated from North America by a marine portal through Central America. This condition had existed since the inception of the Tethys seaway (Early Jurassic) and continued until the emergence of the Panamanian Landbridge in the Late Pliocene. Thus, notwithstanding the possibility of small-scale chance dispersal events, South America from about 100 to about 3 million years ago was an island continent (McKenna, 1980; Simpson, 1980; Marshall et al., 1982; Simpson & Neff, 1985; Webb, 1985; Marshall, 1988). The isolation of South America attracted the attention of vertebrate paleontologists because fossil mammals in South America, older than the connection with North America, were easily distinguished from their northern counterparts. Paleobotanists were slower to recognize the discontinuities, perhaps because the extant angiosperm flora of northern South America and Central America was bewilderingly diverse to Northern Hemisphere plant biologists, but also because many plant collections from South America were limited and this provided few opportunities for comparison. In addition, Berry was not an adherent of the theory of continental drift (Sullivan, 1974; Graham, 1988c), a situation that did not encourage critical comparison of the fossil floras of the two continents. In fact, theories on the origin and development of the biogeographic affinities of the South American flora were derived more through study of the modern flora (Raven & Axelrod, 1974; Gentry, 1982a, b, 1990; Simpson & Neff, 1985) rather than through the efforts of paleobotanists of the time (but see reviews by Taylor, 1991, 1995). Thus, the meager history of comparison of floristic patterns between Central and South America may be due to the high diversity of the floras and an early lack of acceptance of the concepts of continental drift.

Floristic similarity between northern and southern Neotropics

Fossil angiosperm floras in northern South America older than 65 mya are few (Fig. 4). More are available for assessing the degree of isolation from fossil floras of early Tertiary age (Fig. 5). The majority of the reported floras are from Colombia, Venezuela, and Ecuador, with over half published before 1965. To the north, well-preserved early Tertiary pollen floras are reported from Panama (Graham, 1985, 1999a) and Mexico (Martinez-Hernandez et al., 1980). The percent similarity between palynomorphs in Early to Middle Eocene pollen floras from Panama and northern South America was calculated by Graham (1992) and is reported here in Table 1. The low degree of floristic similarity (2.6%) is in accord with the physical reconstructions of the Panamanian landbridge (Coates et al., 1992; Coates & Obando, 1996), as well as with the data on the distinctiveness of mammalian faunas at that time. The taxonomic determinations made on the leaf floras are either limited in number or too unreliable to reconstruct vegetation types in the Paleocene. Recently, however, Eocene mangrove vegetation flanked by inland palm

Table 1. Similarity of palynomorphs between Central and South America from the Early Eocene Epoch through Quaternary Period.

Time period	Similarity of palynomorphs between Central America and South America
Early to Middle Eocene	2.6%
Early Miocene	10.7%
Middle Pliocene	8.9%
—Landbridge established—	
Quaternary	29.7%

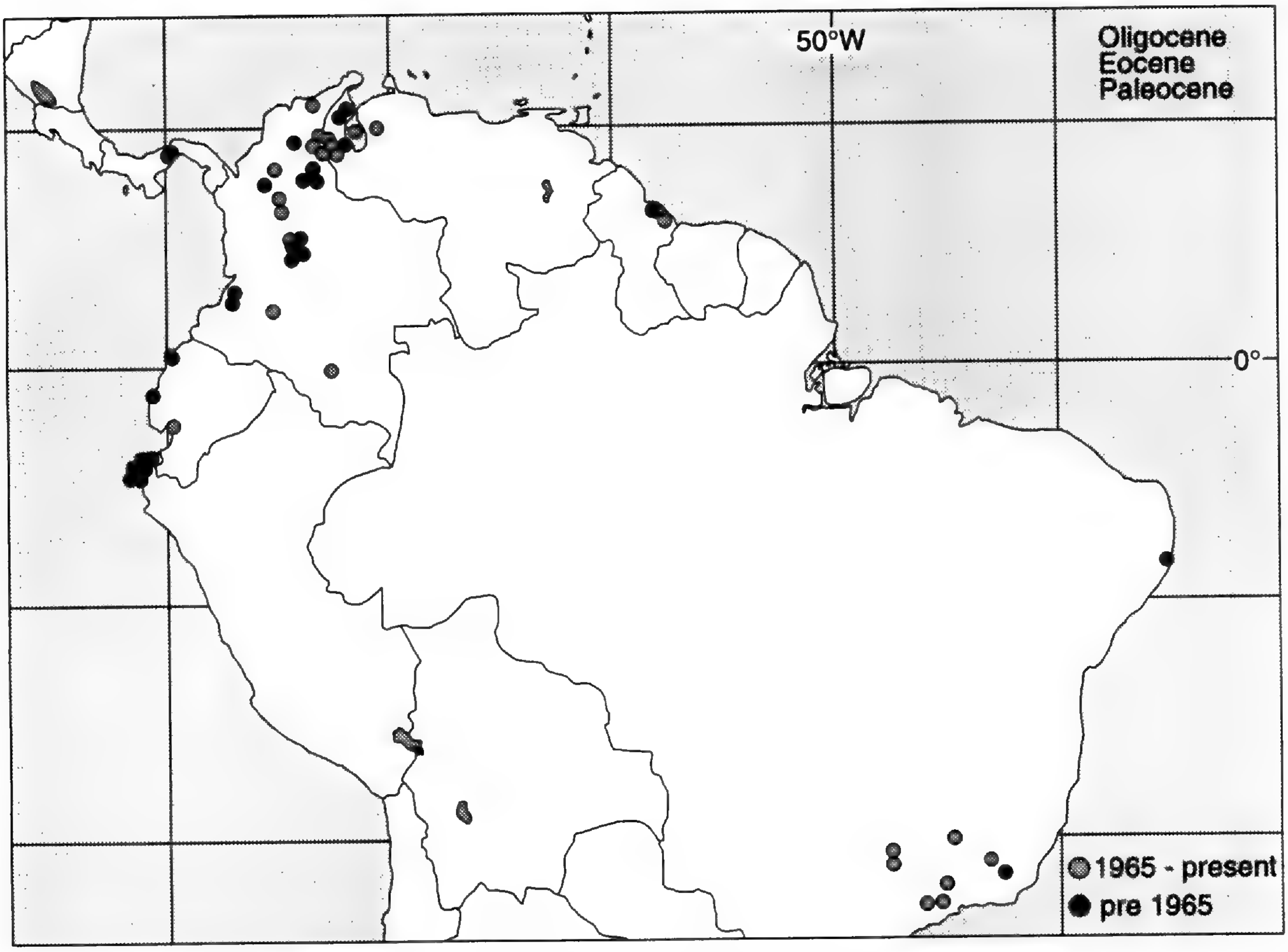

Figure 5. Distribution of published fossil plant localities in northern South America and southern Central America of Paleocene through Oligocene age.

and dicotyledon-dominated forests has been reconstructed by Rull (1998a) from the northern coast of South America.

Disjunctions recognized in modern distributions

The isolation of South America during the Tertiary Period can also be inferred from the distribution of extant taxa as presented by Gentry (1992), Wendt (1993), and Hammel and Zamora (1990, 1993). The predicted diversity for a group of plants isolated in South America until establishment of the landbridge would be a high number of species in South America, with only a few, perhaps widespread, taxa extending into Central America. This pattern was documented for many genera by Gentry (1982b) and more recently for *Serjania* sect. *Platycoccus* by Acevedo-Rodriguez (1993). Such a pattern, however, might also derive from narrow ecological amplitudes in the restricted taxa and wider ecological amplitudes in the geographically wide-ranging taxa. Nonetheless, in many of the cases cited by Gentry (1982a), the ranges of South American taxa extend north into Colombia, but not across the Isthmus of Panama. This suggests that a recent geographic barrier is responsible for many of the observed patterns.

Fossil and modern family diversity

During the period of isolation, northern South America harbored a rich assemblage of angiosperm families. The high diversity of Amazonian forests today is due in part to recent speciation and immigration of taxa from Central America starting 3 million years ago, but the high diversity within prominent neotropical families most likely is due to the long evolutionary history of many taxonomic groups in South America. Although Tertiary fossil floras from Amazonia are few, none of them completely documented, and most from moderate paleoaltitudes (probably close to 1000 m), fossil assemblages of Miocene deposits from southern Ecuador (Berry, 1929a, 1945a) do reveal family-level diversity. Fossil taxa were assessed only at the family level because the identifications by Berry have been repeatedly questioned over the past 40 years. Floras from these basins are currently under study by one of us (RJB), and our research on Berry's family-level taxonomic determinations shows

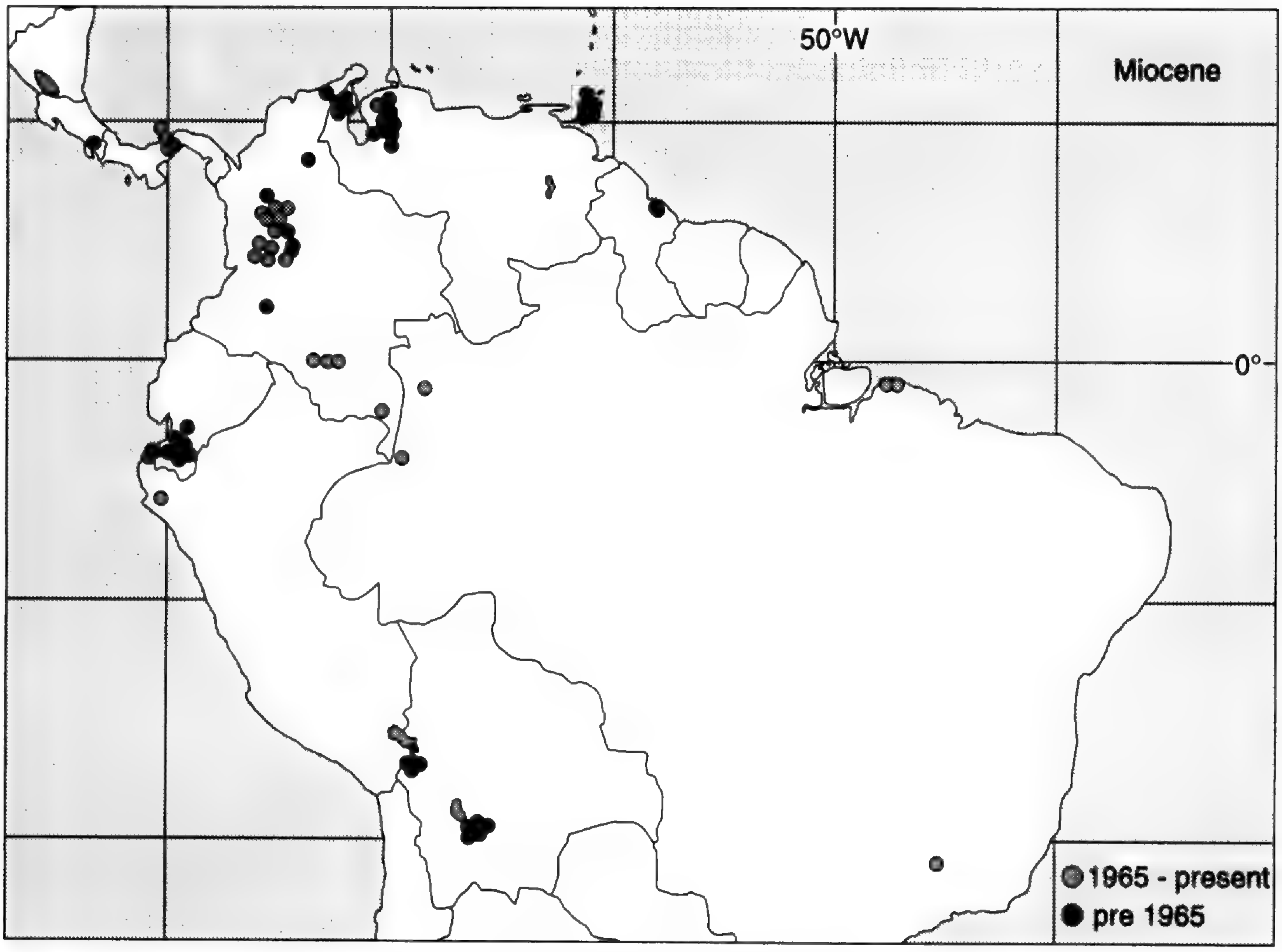

Figure 6. Distribution of published fossil plant localities in northern South America and southern Central America of Miocene age.

that they are reasonable in about 70% of the cases. Four modern lowland tropical floras were reported (Gentry, 1990) in which the percentage of species in 20 angiosperm families are listed, and these can be compared to the proportion of species in the same families of fossil plants from Ecuador (Fig. 9). At this crude level of comparison, the most common angiosperm families in the four modern Amazonian forests are also represented in the fossil assemblage. Similarly, Rull (1998a) indicated that the Eocene mangrove communities of northern Venezuela were similar in diversity and composition to other equivalent-age mangrove floras worldwide. Hoorn (1994a) reported Miocene palynological diversity in Amazonian Colombia that is at least as high, if not higher, than modern diversity in the area today (see also discussion by Hooghiemstra & van der Hammen, 1998). Lundberg and Chernoff (1992) and Lundberg (1997) reported that freshwater fish diversity in Middle Miocene deposits of Colombia was probably as rich as in the fish faunas from Amazonian basins today. Mammalian diversity was also high before the interchange (Marshall, 1985; Marshall & Cifelli, 1990).

Endemism as an effect of isolation

A pattern expected from the isolation of a landmass for a considerable amount of time is a high level of endemism. This is well documented on islands. For example, the island continent of Madagascar includes close to 10,000 endemic plant species due in part to its isolation from Africa since the mid-Cretaceous (Takhtajan, 1986). The 3 million years of contact between Central America and northern South America has certainly decreased the extent of endemism in both areas, but high endemism in some groups still can be documented. Table 2 lists genera with at least three species that probably evolved in South America and are endemic there today. Genera known from the Tertiary fossil record in South America are indicated. Likewise, Wendt (1993) listed genera that may have diversified in Central America or Mexico and are endemic there today.

EVENT II: UPLIFT AND PHYSIOGRAPHIC CHANGE

The second important time in northern South America is the period from about 15 million years

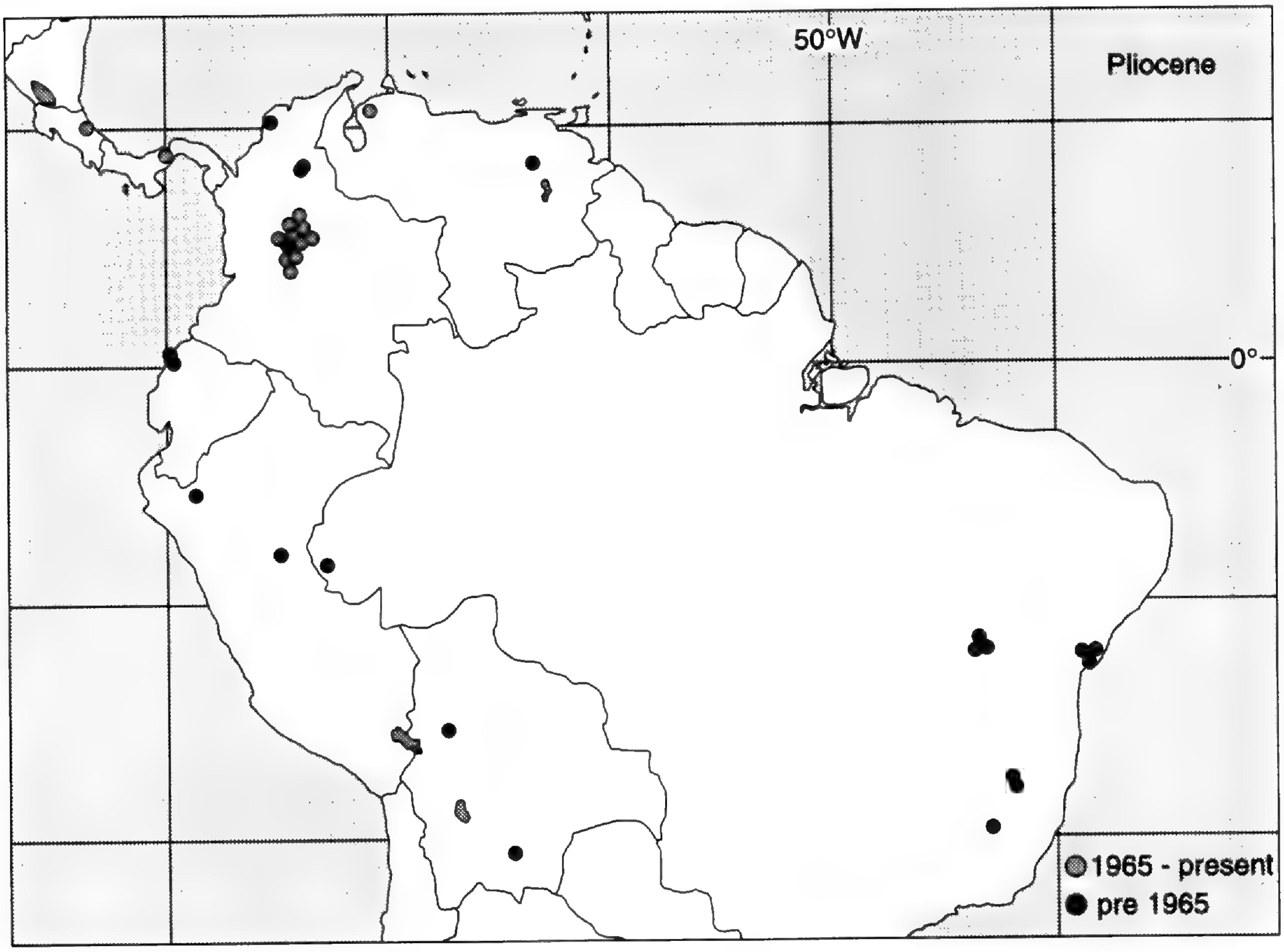

Figure 7. Distribution of published fossil plant localities in northern South America and southern Central America of Pliocene age.

ago to the present. Note that this phase, including uplift of the Andes and changing drainage patterns, overlaps with the younger period of landbridge connection and also with the older period of isolation. Part of the difficulty in interpreting the present vegetation in South America derives from events that overlap. This underscores the care that must be taken in attributing patterns noted in modern distribution to recent fluctuations in climate.

Altitudinal changes

The major period of uplift in northern South America occurred in the Miocene Epoch, although there is strong evidence for uplift in the central and southern part of South America earlier than the Miocene Epoch (Jordan & Alonso, 1987; Sempere et al., 1990). Exact altitudes are difficult to determine because this requires latitudinally paired lowland and upland equivalent-age floras that can provide lapse rates or enthalpy estimates (and thus altitudes: Wolfe, 1992; Forest et al., 1995; Gregory-Wodzicki, 1997; Gregory & McIntosh, 1996). Despite the large number of floras studied by Berry, few are tied to radiometric dates, and many appear to be from areas of moderate paleoelevation. Lowland coastal or lowland Amazonian floras exist in Colombia, Ecuador, Peru, and Brazil, but these have not been studied or are not tied to well-established biostratigraphic sections.

The paleophysiography in western Colombia has been reconstructed as an elongated peninsula with a mountainous backbone. Elevations during the middle Miocene Epoch in the northern Andes have been estimated by palynological records from the High Plain of Bogotá as being less than 700 m, while by the late Miocene Epoch the area is estimated to have been close to 1000 m (Wijninga, 1996b). Middle Miocene sediments in central Colombia preserve the exquisite La Venta mammal fauna, interpreted to indicate lowland tropical conditions (Kay & Madden, 1997) probably below 500 m. Situated on the eastern cordillera of the Colombian Andes, the mammal fossils and their sedimentary environments indicate that uplift began as early as 12.9 mya (Guerrero, 1997). The La Venta sites would be ideal for calibrating up-

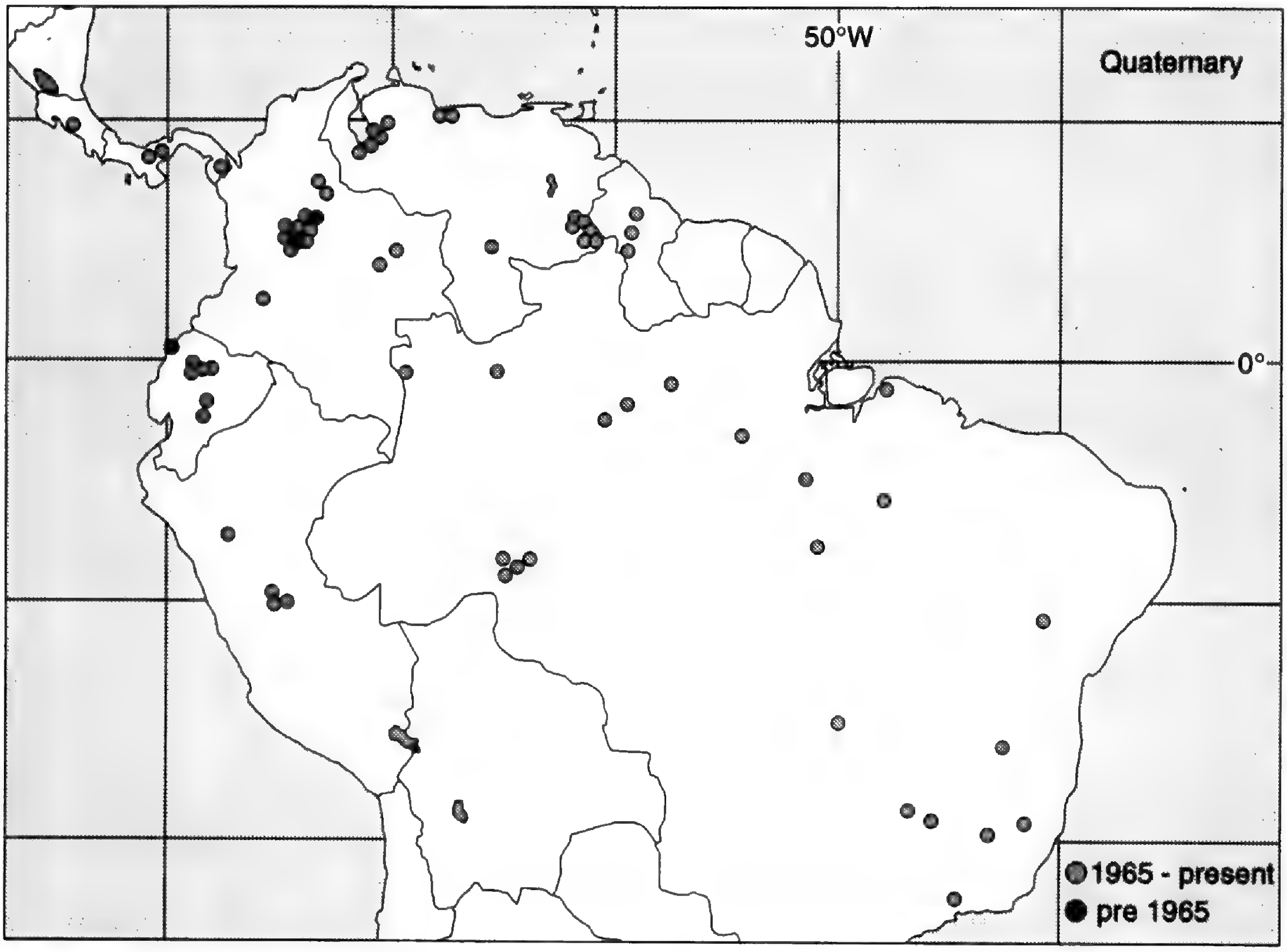

Figure 8. Distribution of published fossil plant localities in northern South America and southern Central America of Quaternary age.

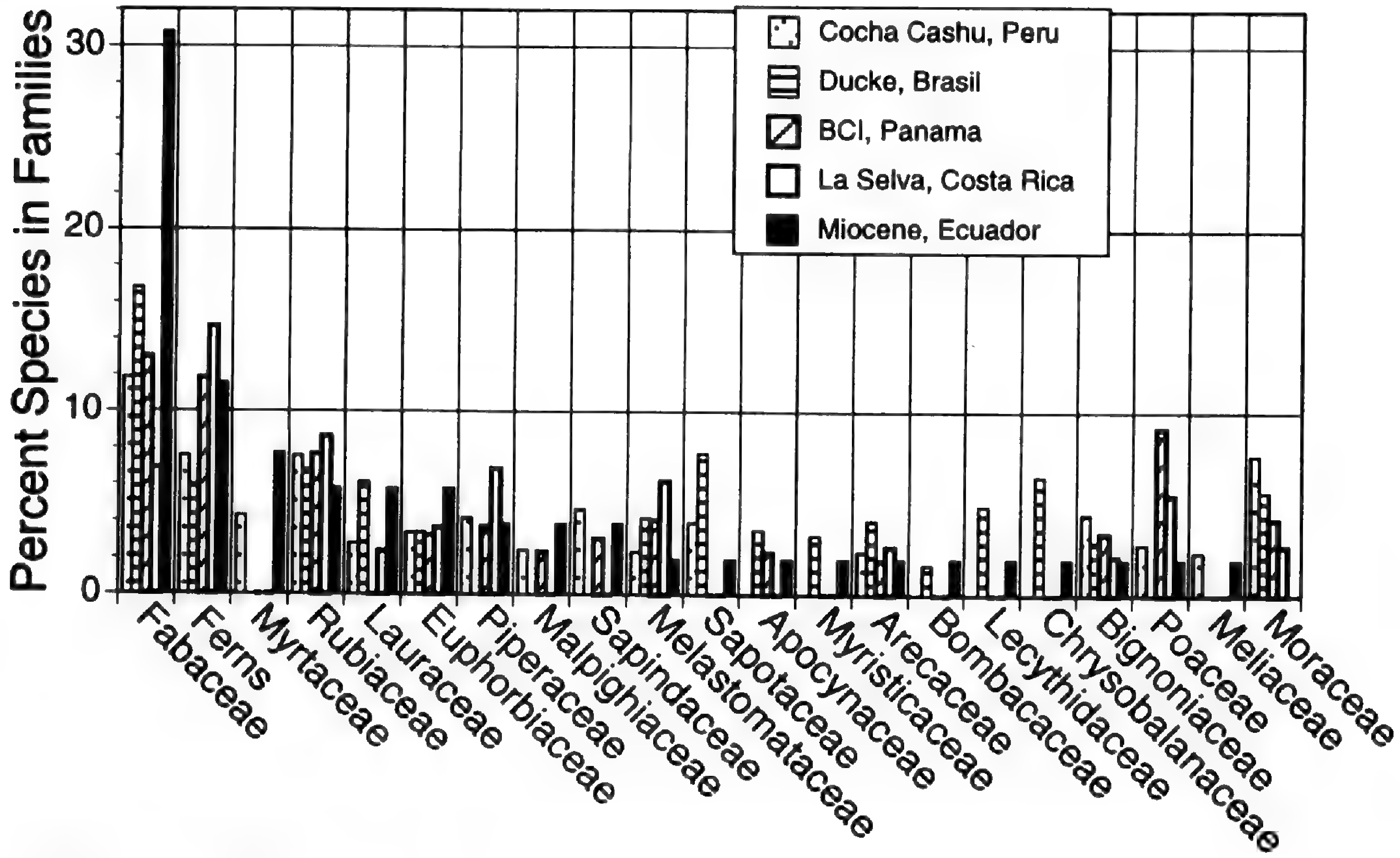

Figure 9. Comparison of modern and Miocene neotropical floras using proportional species diversity within families at all sites. Modern floral data from Gentry (1990).

land floras if fossil leaf floras could be recovered from this volcanically influenced terrane. Fossil wood from the area was reported by Schönfeld (1947). Fish faunas dating from the middle Miocene Epoch and preserved in the present Magdalena Valley of Colombia document a strong affinity to current Amazonian freshwater fish faunas. This indicates that the Eastern Cordillera of Colombia had not created sufficient barriers to migration of fish until at least 11 mya (Lundberg & Chernoff, 1992).

Drainage and physiographic change

Reconstructions of the physiography of northern South America presented by Hoorn (1994a, b, 1995) and by Vonhof et al. (1998) and synthesized by Kay and Madden (1997) show that in the early Miocene Epoch, the Western Cordillera of Colombia was high enough to deflect sediment in an eastward direction and potentially isolate the current Choco region. The major sediment source to the Amazon Basin was from the moderately uplifted Guyana Shield (Fig. 10). A controversial portal (Marañon Portal) in the area of Guayaquil has been proposed (Nuttall, 1990; Hoorn, 1994a), but by the middle Miocene Epoch, the Andes in southern Ecuador probably no longer allowed westward transport of sediments from the Amazon Basin to the Guayaquil area (Vonhof et al., 1998). Instead, primary sediment flux was northeastward, with sediments directed toward the major depositional basin off the coast of present eastern Venezuela. Currently, the Andes provide the bulk of sediments to the Amazon and Orinoco systems, with the largest sediment flux now directed east to the Amazon mouth, rather than north toward the Orinoco.

The simplified physiography presented here suggests that the middle Miocene is the time during which the distinctive nature of the flora in the Choco region began its development. Habitat diversity in the Choco region was probably higher in the mid-Miocene than suggested by Gentry (1982a), which would give a much greater age to the endemism documented there today. The Choco, including coastal Ecuador, was isolated from the Amazon by the rising Andes and from Panama by the deep trench off the northwestern coast of Colombia.

Evidence from palynology

Certainly the most useful paleobotanical research in northern South America in the past 50 years is that of T. van der Hammen, H. Hooghiemstra, and their associates at the University of Amsterdam (summarized in Hooghiemstra & van der Hammen, 1998). The palynological work of Hoorn (1994a, b) and Wijninga (1996a, b) addressed the eastern and central regions of Colombia, respectively. Hoorn documented a variety of habitats including palm swamps, riparian vegetation, and diverse tropical forests in eastern Colombia. Flooding was common, and the majority of sediment came from the east. She also presented strong evidence for vegetation change due to uplift in the Andes during the middle to late Miocene (Hoorn, 1994b). Wijninga, whose work involved sediments of middle Miocene through late Pliocene age, indicated that in the present High Plain of Bogotá lowland conditions existed through the end of the Miocene Epoch. Lowland forests developed on well-drained floodplains. Higher elevations supported only lower montane forests. By the early Pliocene sub-Andean taxa appeared on the present High Plain of Bogotá, along with the pollen of a few high-Andean taxa, which were interpreted as coming from nearby highlands. Wijninga (1996a) documented the progressive uplift of the Andes through the Pliocene using a combined pollen and macrofossil approach. Analysis of the upper stratigraphic sequence was presented by Hooghiemstra (1994), who documented the arrival of northern temperate taxa (see below).

The effects of the changing drainage patterns in northern South America are also preserved in strata at the mouths of the major rivers. One such study (Diaz de Gamero, 1995) indicated that in the early through middle Miocene the proto-Orinoco River built a delta in northern Venezuela, east of the Maracaibo Basin. Through uplift of the Eastern Cordillera of Colombia, the river was deflected progressively eastward during the late middle and late Miocene. This uplift to the west of the depositional center isolated the floras of western Colombia, as well as fragmented and diversified habitats that previously existed as contiguous tropical lowland swamps.

Evidence from plant macrofossils

The record of Miocene plant macrofossils in northern South America is seemingly rich, with 50 published reports. However, much of this work was completed prior to 1960, and lacks a modern systematic and plate tectonic perspective. One of us (RJB) has recently initiated macrofossil plant studies in Ecuador and Bolivia (Burnham, 1995a, b). Three Miocene basins in southern Ecuador and two in Bolivia are under investigation. The three Ecuadorian basins each include 55–75 species of fossil plants, of which most are dicotyledonous angio-

Table 2. Selected Gondwanan-derived genera, still primarily endemic to South America today. Estimated number of species per genus is indicated in parentheses. Only genera with at least three species are listed. * indicates Tertiary fossil record in South America.

Trees	Lianas and vines
Amaioua (25)	*Clytostoma* (9)
**Apeiba* (10)	*Mansoa* (15)
Campomanesia (80)	*Maripa* (19)
Catoblastus (17)	*Selysia* (3)
**Coussapoa* (30)	*Siolmatra* (3)
Crematosperma (17)	*Apondandra* (4)
Cyclolobium (5)	*Dicella* (6)
Ecclinusa (21)	**Trigonia* (24)
Geoffroea (3)	
Herrania (20)	
Hexachlamys (3)	
**Humiria* (4)	
Jessenia (6)	
Leonia (6)	
**Loxopterygium* (5)	
Parapiptadenia (3)	
Peritassa (14)	
Ptilochaeta (5)	
Seguieria (6)	
Schinopsis (7)	
Siparuna (150)	
Socratea (5)	
**Thinouia* (12)	
**Ticorea* (3)	

sperms. Species richness is high in some localities (up to 33 species). Over 80% of the species in each basin bear entire-margined leaves, and the leaf size is about 35% notophyll, 40% microphyll, and the remainder evenly divided between very small and very large leaves. Provisionally identified angiosperms from the Cuenca Basin are: *Loxopterygium* (Anacardiaceae), *Tipuana* (Fabaceae: Burnham, 1995a), *Coussapoa* (Cecropiaceae), Lauraceae, Malpighiaceae, and Arecaceae, while the Nabon Basin includes *Tipuana* (Fabaceae), *Roupala* (Proteaceae), Sapindaceae, Clusiaceae, and Melastomataceae. The Loja Basin was studied by Berry (1929a, 1945a); taxa from that basin verified by recent work include *Coussapoa* (Cecropiaceae), *Trema* (Sterculiaceae), *Tipuana* (Fabaceae), *Ruprechtia* (Polygonaceae), Meliaceae, Lauraceae, and Malpighiaceae.

The Miocene basins of southern Ecuador are well suited to provide information on the rate of uplift and degree of influence of a rain shadow in the northern Andes during the middle Miocene. All three floras have been tied to radiometric dates ranging from 13 to 10 mya (R. H. Madden, unpublished data). Mean annual paleotemperature indi-

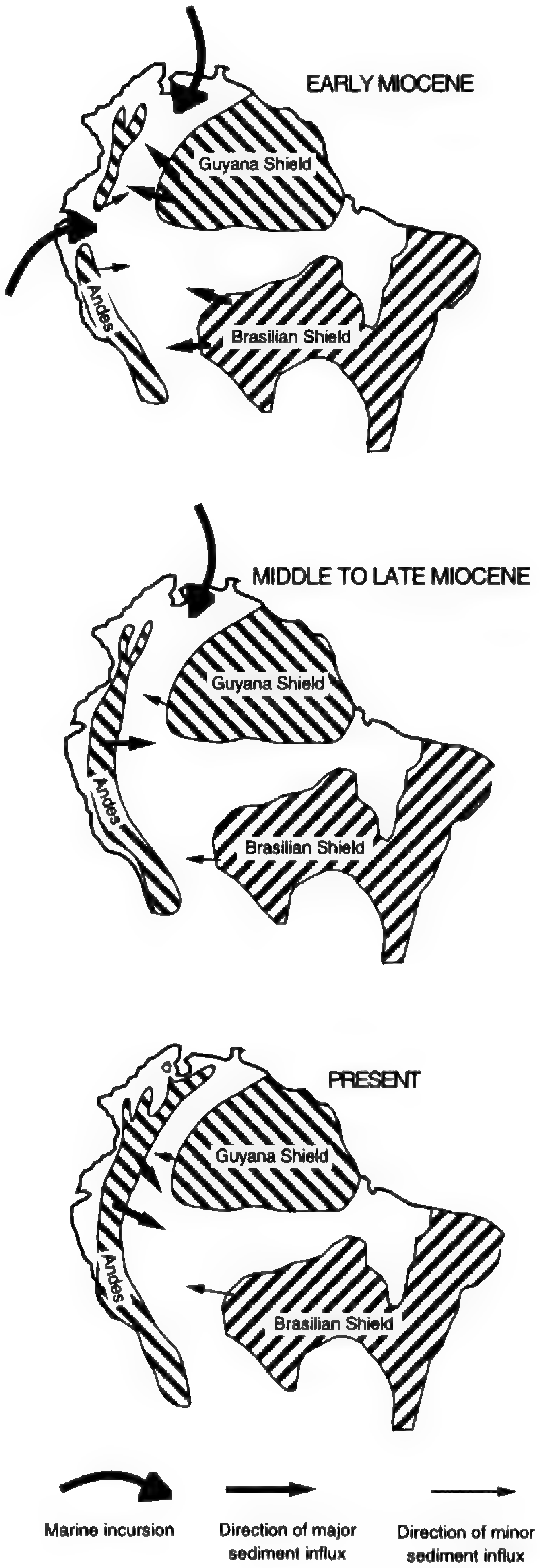

Figure 10. Major sedimentary sources, highland areas, and seaways in Early Miocene, Middle to Late Miocene, and Present South America. From Hoorn (1994b).

cated by leaf margin analysis varies among the basins from 22 to 28°C. All plant-bearing deposits include a large proportion of small leaflets of Fabaceae (up to 30% of the species), which may indicate a seasonally dry climate. Of the three sites, Loja has the largest-leaved species indicating relatively wetter conditions based on correlations of leaf size and precipitation in modern floras (Wilf et al., 1998). Like today, Loja may have been to the east of the Andes, whereas the other two basins may have been between rising parallel chains of the Andes. This eastern position would have diminished the effect of a rain shadow on the flora of the Loja basin.

Changes in physiography and its effect on vegetation are well documented in sections from Colombia, but new evidence from the Pebas formation in eastern Peru (Räsänen et al., 1987, 1995) indicates that changes dating to the middle Miocene are present throughout northern South America. Indeed, as noted by Guerrero (1997), the time of uplift of the Eastern Cordillera of Colombia was a period of global importance, which included the closure of the east end of the Mediterranean seaway; the collision of the Australian plate with Indonesia, thus closing the faunal gap recognized as Wallace's line; the deep sea sedimentation hiatus at 12.0–11.8 Ma reported by Keller and Barron (1987); and a major cooling event that expanded the Antarctic Ice Cap (Woodruff et al., 1981). Increases in the seasonality of precipitation have been cited from many areas, which would have substantially increased habitat diversity at this time.

EVENT III: CLOSURE OF THE ISTHMUS OF PANAMA

Physical changes

The formation of land connections between North and South America had profound climatic (Burton et al., 1997) and biogeographic consequences for the flora and fauna of both continents. Prior to the middle Miocene at ~15 Ma tropical marine waters interchanged between the Atlantic and Pacific Oceans, and there was only weak marine-water transport northward via the Gulf Stream. At ~15 Ma a sill began forming in the Isthmian region that intensified flow of the Gulf Stream. This provided warm water to the North Atlantic region that together with Milankovitch orbital cycles, and decreasing atmospheric CO_2 concentration from waning plate tectonic activity, eventually produced conditions favorable to the development of glacial climates.

Interchange of flora and fauna

Of particular biogeographic importance for the floral and faunal interchange is the timing of the formation of the Panama landbridge. This has been estimated recently from three independent sources: provincialization of eastern Pacific/Caribbean marine biotas (Coates & Obando, 1996; Coates et al., 1992; Jackson et al., 1996), interchange of terrestrial mammals between North and South America (Stehli & Webb, 1985; Webb & Rancy, 1996), and the similarity between palynomorphs on either side of the Isthmus at different times during the Cenozoic (Graham, 1992).

Through the middle Miocene (16–15 Ma) there were marine passages across present-day Central America, and deep-water sediments and biotas are especially evident between the southern (eastern) terminus of proto-Central America and the cordillera of northwestern South America (Fig. 11). By the late Miocene (7–6 Ma) marine portals were more restricted (Fig. 12), and by the late Pliocene (~3 Ma) they existed only across the eastern and western extremes of the Isthmus (Fig. 13). Sedimentological and marine invertebrate provincialism date the establishment of an essentially complete structural connection between North and South America at between 3.5 and 3.1 Ma (Coates et al., 1992; Coates & Obando, 1996). Sometime after 3.5–3.1 Ma the interchange of terrestrial organisms lacking means for long-distance dispersal was facilitated by the development of land corridors that were elevated above the low-lying coasts and marshlands. Although waif dispersal events prior to 3.5 mya have been noted (Reig, 1980; Gingerich, 1985; Gentry, 1992; Marshall & Sempere, 1993; Webb & Rancy, 1996), there is no conclusive evidence that a continuous terrestrial corridor existed between Central America to South America prior to the late Pliocene, about 3 to 3.5 mya.

Recent summaries of the mammalian fossil record provide important information on the climates, kinds of habitats, and the time of appearance and expansion of the terrestrial corridors. First, the affinities of the Early and Middle Tertiary faunas of Central America are almost exclusively with North America, while the relationship of the modern fauna is with South America. This was recognized early on by Wallace (1876): "The portion of North America that lies within the tropics (Mexican Subregion) closely resembles the [Brazilian Subregion] in general zoological features," and he noted "unmistakable evidence of an extensive immigration from South into North America, not long before the Glacial epoch" (quoted from Webb & Rancy, 1996:

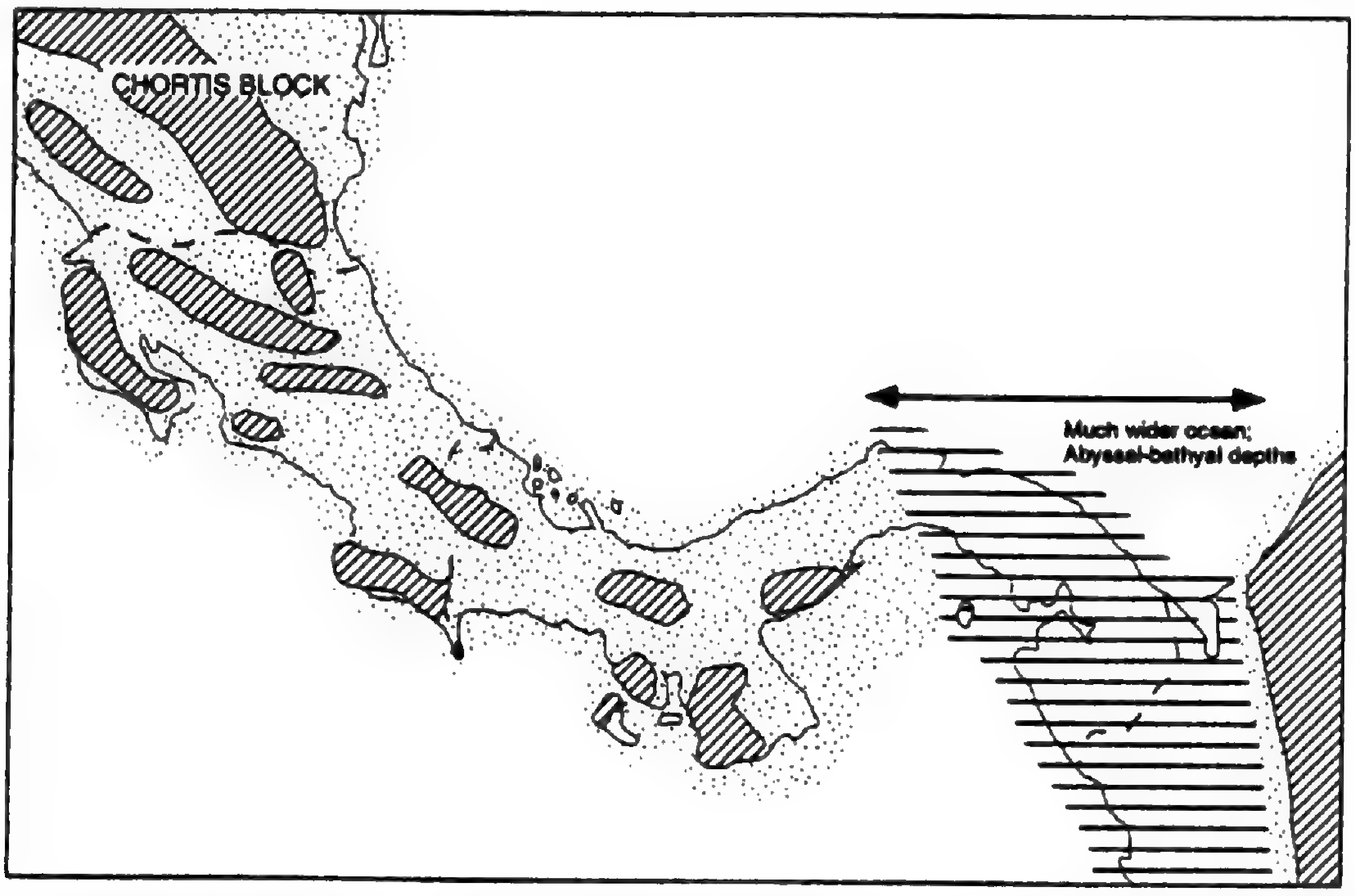

Figure 11. Central American Isthmus during the middle Miocene (16–15 Ma). Oblique parallel lines = emergent land; dots = shelf sediments; parallel lines = abyssal oceanic sediments. From Coates and Obando (1996). Used with permission of the University of Chicago Press.

335–336). Second, large numbers of immigrants from North and Central America are first found in South America after the establishment of the landbridge. Relatively fewer, but still a large number, of South American mammal genera are first noted in North and Central America after the landbridge was completed. These Pliocene migrants were mostly characteristic of temperate climates and savanna habitats. Evidence from fossil mammalian faunas is further interpreted to suggest that by the middle Pleistocene the savanna corridor was giving way to tropical rainforest, especially during interglacial times (Webb & Rancy, 1996: 348).

The flow of mammalian immigrants from north to south appears to have been larger than from south to north (Marshall et al., 1982; Webb, 1985). In addition, there appears to have been a higher speciation rate among taxa that moved to the south, compared to the northward-moving immigrants (Fig. 14). Thus, in addition to different numbers of species successfully migrating in each direction, there were also different rates of subsequent diversification among mammalian taxa involved in the interchange. This resulted in the asymmetrical pattern of distribution among extant North and South American mammals. According to Webb (1991),

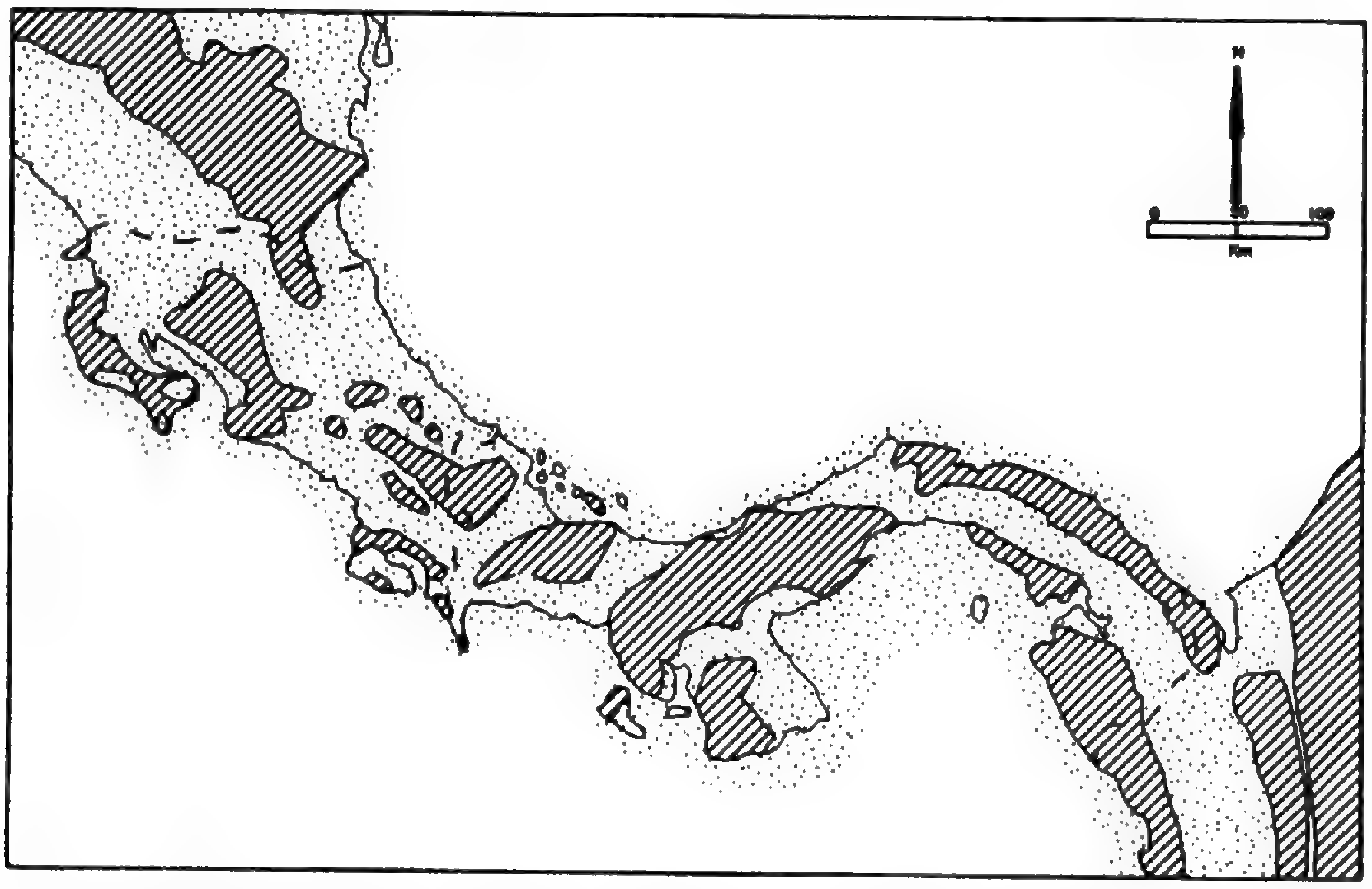

Figure 12. Central American Isthmus during the late Miocene (7–6 Ma). Symbols and source as in Figure 11.

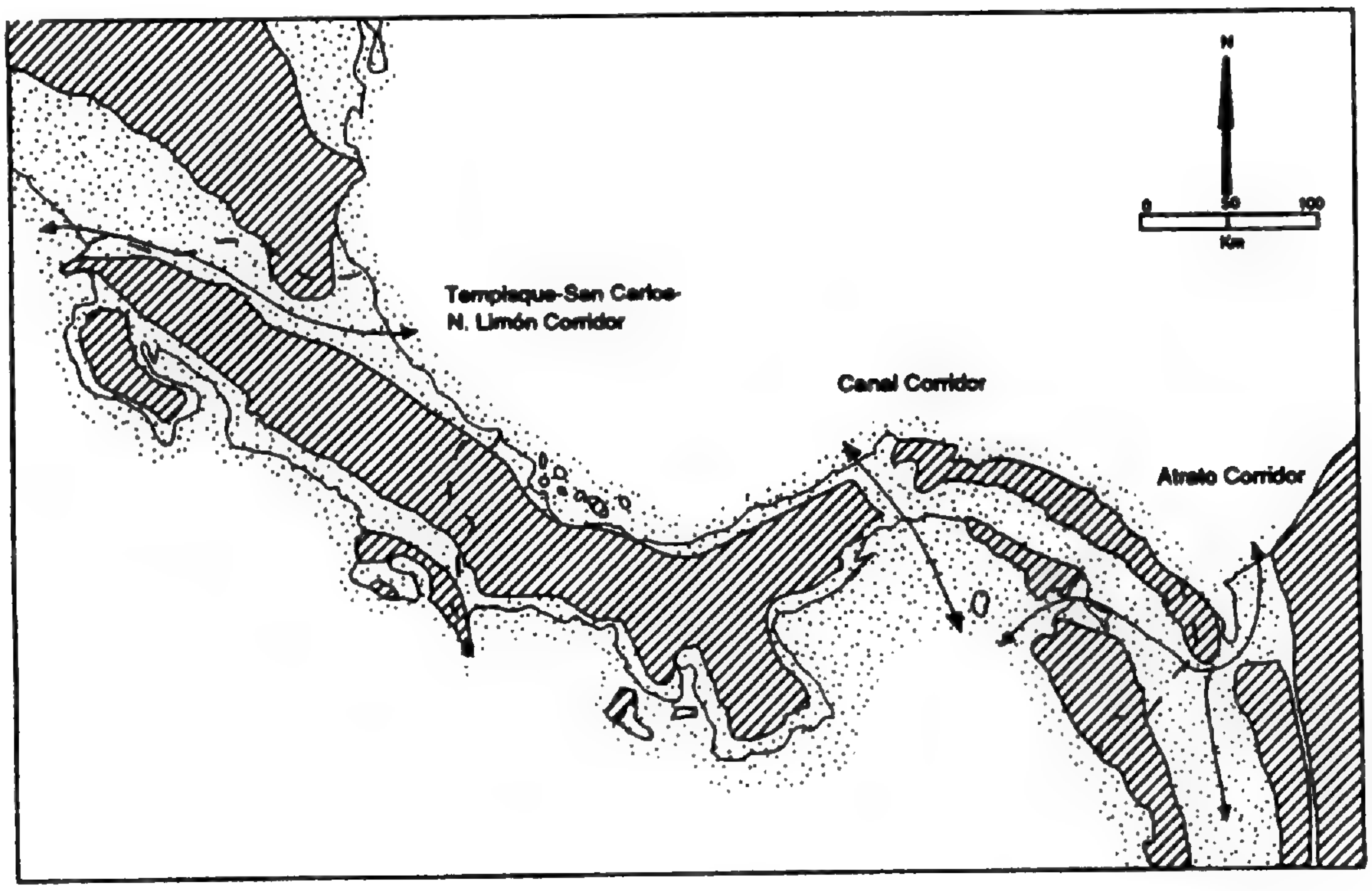

Figure 13. Central American Isthmus during the late Pliocene (~3 Ma). Symbols and source as in Figure 11.

roughly 53% of the extant South American mammal fauna is derived from descendants of immigrants from North America, while only 10% of the extant mammalian fauna of North America is ascribed to descendants of the interchange.

An early introduction from the north into South America, near the end of the Miocene Epoch, was a raccoon known from the late Miocene of Argentina (Webb, 1985), while two genera of South American ground sloths appear in the late Miocene of North America. By the late Pliocene and Pleistocene, the number of land mammals of northern or-

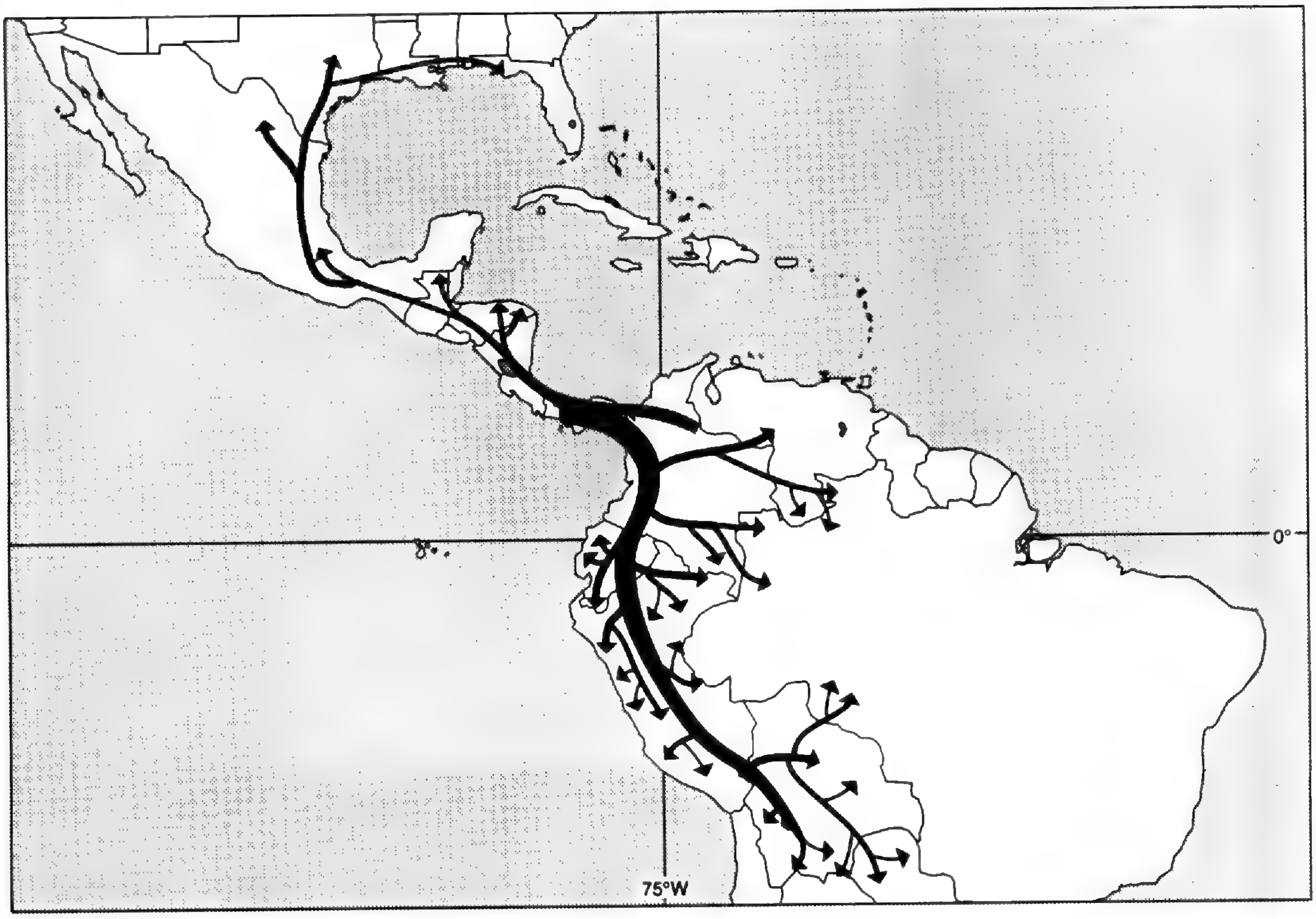

Figure 14. Mammalian migration and diversification following establishment of the Central American landbridge.

igin in South America increases to 15 families and 29 genera (Webb, 1985: table I). These include modern, extinct, or ancestral genera of the Chiroptera (bats), Soricidae (shrews), Leporidae (hares), Heteromyidae (pocket mice), Geomyidae (pocket gophers), Sciuridae (squirrels), Sigmodontine rodents (field mice), the first introduction of Carnivora–Felidae [cats; *Smilodon* (New World Pleistocene saber-toothed tiger), *Puma, Panthera, Felis*], Mustelidae (weasels, skunks, otters), Canidae (fox and wolf), Procyonidae (raccoons), Ursidae (bears), Gomphotheriidae (elephantids), Tapiridae (tapirs), Equidae (horses), Tayassuidae (peccaries, pig-like forms), early Camelidae (camel line), and Cervidae (deer).

Groups moving from South America into Central and North America include the Dasypodidae (armadillos), Mylodontidae (sloths), Glyptodontidae (an extinct group related to the armadillos), Erethizontidae (porcupines), Hydrochoeridae (capybara), Trichechidae (manatees), Phorusrhachidae (large predaceous ground birds), Megatheriidae (giant ground sloths), Megalonychidae (large extinct edentate mammals), Camelidae (represented by llama-like camelids), Didelphidae (opossums), and Toxodontidae (rhino-like ungulates).

The mammalian record indicates that connections suitable for the migration of dry-land species across the Isthmus were essentially complete by ~2.5 Ma. According to Webb and Rancy (1996), savanna habitats were at least locally available at that time. The origin of the modern tropical mammalian fauna of Central America is placed at approximately the middle Pleistocene or ~780 ka.

The Cenozoic fossil plant record also reflects distinct South American and Central American vegetation through the early and middle Tertiary. As noted previously here (Table 1), in the early to middle Eocene only ~2.6% of palynomorphs are common to assemblages on both sides of the Isthmus. In the early Miocene the figure is 10.7% and decreases to 8.9% in the middle Pliocene. The decrease correlates with rising sea levels during a middle Pliocene interval of increasing warmth (Cronin & Dowsett, 1991). The various factors that affect the calculations are discussed by Graham (1992), and it is especially important to note that they represent similarities in palynomorphs and not in vegetation directly. In the original tabulations, the percent similarity for the late Quaternary (15.7%) was especially approximate because most of the few studies available from Central America were from the lowlands (e.g., Bartlett & Barghoorn, 1973, Panama; Bush & Colinvaux, 1990, Panama; Horn, 1985, off-shore Costa Rica; see also Phillips et al., 1997), while many of those from northern South America are from the highlands of Colombia (Hooghiemstra, 1984; Hooghiemstra & van der Hammen, 1993; van der Hammen & Hooghiemstra, 1995; 2000–4000 m). However, studies from upland deposits in Central America (Hooghiemstra et al., 1992, Iselbe et al., 1996, Costa Rica, 2310 m; Martin, 1961, Costa Rica, 2400 m) and from the lowlands of Amazonia (Colinvaux et al., 1996a, b; Liu & Colinvaux, 1988; van der Hammen & Absy, 1994) allow new calculations from comparable localities. Appendix 2 lists 235 palynomorphs reported from Quaternary deposits on both sides of the Isthmus of Panama. Seventy of the palynomorphs occur both in southern Central America and in northern South America for a similarity value of 29.7%. Thus, the paleobotanical trend is consistent with that of the marine invertebrate record, tectonics, and mammalian fossil faunas. The floras are distinct until late in the Tertiary (through about the Mio-Pliocene interval) with greater similarities developing in the Plio-Pleistocene and especially in the Pleistocene.

Habitats of the interchange

The fossil plant data are also generally consistent with estimates of habitats (savannas) and climate (temperate) based on mammalian fossil faunas, but with some differences. The paleobotanical evidence indicates predominantly tropical forest throughout the Cenozoic, with restricted grassy savannas developing in about the late Miocene. The early Miocene microfossil floras from Panama (Culebra, Cucaracha, La Boca; ~9°N latitude; Fig. 15) and Costa Rica (Uscari; ~10°N latitude) contain virtually no pollen of the Gramineae, while in the Mio-Pliocene Gatun flora of Panama, grass pollen reaches a maximum of 7.5%. This marks the beginning of at least local savannas that presumably continued to develop through the Pliocene, and expanded during glacial intervals, as reflected by the increase in grazing and browsing members of mammalian faunas. However, in the Cenozoic pollen floras from southern Central America, the dominant components of the paleovegetation are tropical forest elements. This apparent inconsistency between mammalian faunas indicating open savanna vegetation, and paleobotanical evidence for mostly closed tropical forest, is paralleled in the Tertiary record of northwestern North America. There the explanation appears to be frequent disturbance of the vegetation by ash falls associated with extensive volcanism (Cross & Taggart, 1982; Taggart & Cross, 1990; Taggart et al., 1982). This was interpreted as a

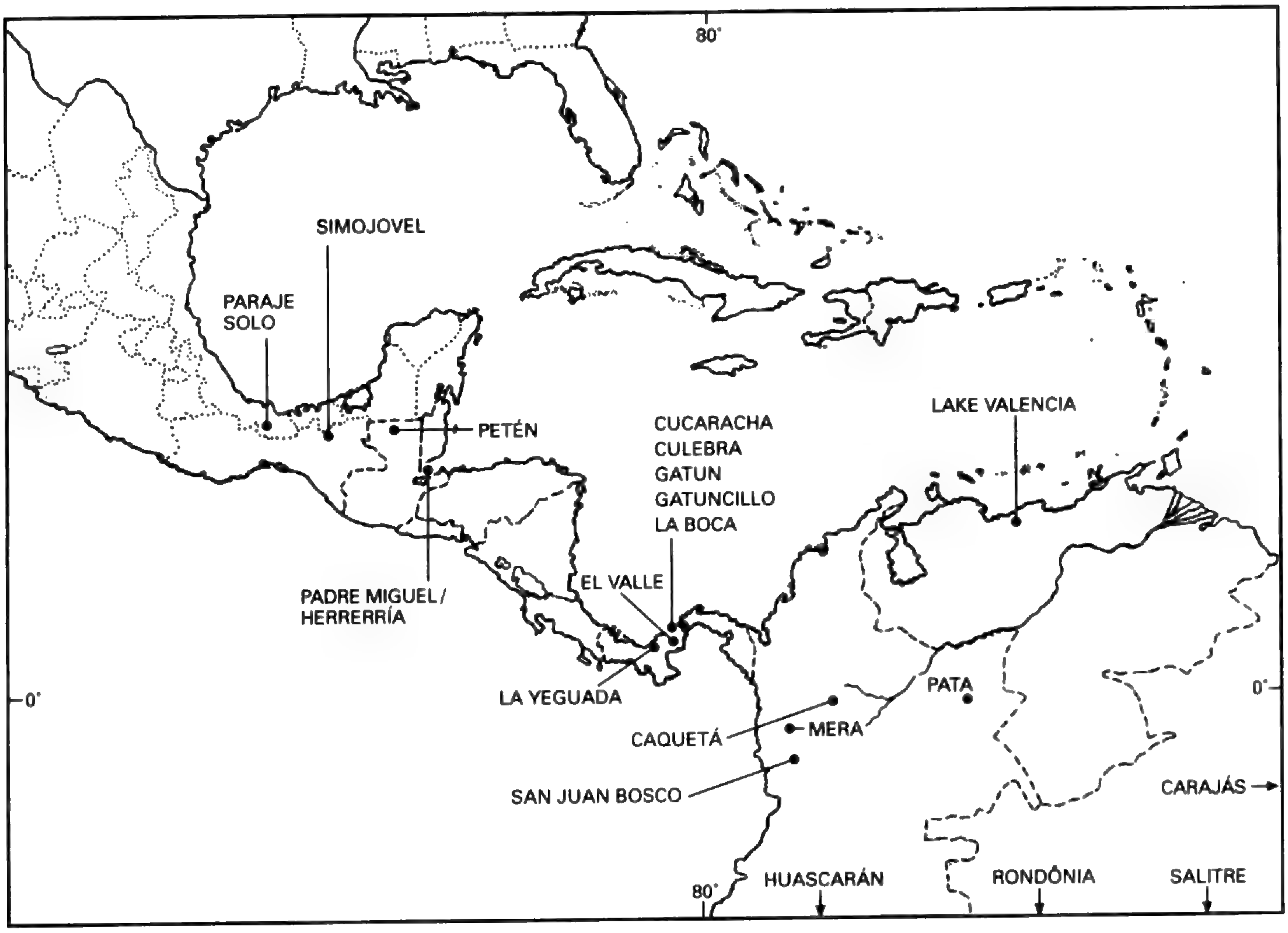

Figure 15. General location of fossil palynofloras mentioned in the text.

shifting mosaic of open, short-lived habitats sufficient to support mobile herds of browsing and grazing ungulates within a mostly temperate forested vegetation. The frequent ash layers in the Cucaracha Formation of Panama suggests a similar mechanism (Graham, 1988b). Evidence of extensive savanna development is only present in Quaternary floras, but is never abundant in Central America. Comparable data have not yet been presented in South America. Savanna, as recognized today in Central America, may be a Pleistocene development augmented by recent anthropogenic factors.

There is also evidence to suggest that drier habitats supporting more open vegetation began developing locally in the late Miocene and early Pliocene. The early Tertiary floras from southern Central America contain a few elements of dry habitats. By the Mio-Pliocene these elements increase and include 11 taxa that collectively suggest an early form of tropical dry forest—Poaceae, *Acacia, Allophylus, Busera, Cedrela, Ceiba, Combretum,* cf. *Jatropha, Posoqueria, Pseudobombax,* and *Serjania* (Graham, 1991).

It is likely that these local drier conditions resulted, at least in part, from a developing rain shadow due to increasing elevations during the Tertiary Period. Through the early Miocene all elements in the fossil floras from southern Central America can be accommodated at elevations between sea level and ~1400 m. By the Mio-Pliocene (Gatun flora) paleoelevations, based on modern analog distributions, had increased to ~1700 m (lower montane moist forest, lower montane wet forest, premontane dry forest, montane moist forest, montane wet forest). Present maximum elevations are 3820 m (Cerro Chirripó) and 3432 m (Volcán Irazú) in Costa Rica, and 3475 m (Volcán Barú) in Panama. The appearance of these highlands in the Mio-Pliocene began to deflect moisture-laden winds from the north and initiated the differentiation between a wetter Atlantic and drier Pacific side, as at present.

The development of temperate habitats in proto-Central America during the Middle and Late Cenozoic is complex. The initial appearance of northern temperate elements is in the Mio-Pliocene Gatun flora of Panama, where a few pollen grains of *Quercus* are first recovered. This corresponds in time to the appearance of the paleoelevations that began differentiating the region into wetter and drier sides. By the late Quaternary pollen of *Alnus, Juglans, Liquidambar, Myrica, Quercus, Salix,* and *Ulmus* is present in terrestrial Central American sediments, although *Juglans* and *Liquidambar* in off-shore deposits from Costa Rica (Horn, 1985) may have been transported from farther north. Localized temperate habitats first appear in the Mio-Pliocene and it is likely they resulted, at least in part, from increasing elevations rather than exclusively from marked changes in climate. We assume that the low-lying, peninsular area in question received ameliorating sea breezes and precipitation that may have dampened the global signal of changes caused by trends in CO_2 concentration and solar fluctuations.

Another factor influencing climates, especially along coastal areas, is upwelling. As the Panama landbridge became established, the flow of the Gulf Stream intensified and brought cold bottom water to the surface in some regions. This is a likely explanation for the cooler climates indicated by the middle Pliocene Paraje Solo flora of southeastern Veracruz, Mexico (17°N), during an interval of overall warming (Graham, 1976, 1998b). Ocean circulation, orogeny, lower CO_2 concentrations (van der Berg et al., 1993; Kürschner et al., 1996), concentrations from globally waning post-Mesozoic plate tectonic activity, and solar-induced fluctuations in climate via Milankovitch mechanisms all influenced the Cenozoic history of environments. In proto-Central America a combination of factors periodically produced local conditions suitable for the interchange of temperate biotas of open habitats in the late Tertiary Period. These conditions prevailed especially in the highlands and became more prevalent toward the end of the Tertiary Period.

Comparison of the mammalian and angiosperm records

Comparison of the pattern of migration and speciation between plant and animal groups involved in the exchange across the Panamanian landbridge has received surprisingly little attention. Simpson and Neff (1985) noted the lack of similarity between plant and mammal records but did not expand on the specific patterns in each lineage. The plant data required for such a comparison is based on two sources of information. First, direct fossil evidence from comparison of taxonomic lists of fossil pollen in Colombia and the Guianas with fossil pollen in Panama and Costa Rica (Graham, 1992) as well as comparison of sites of first fossil occurrences of taxa believed to have been involved in the interchange (Taylor, 1988), and second, evidence from modern distributions of plant taxa (Gentry, 1982a, 1992; Hammel & Zamora, 1990, 1993; Wendt, 1993). Raven and Axelrod (1974) and Simpson (1975) documented taxa that, based on extant distribution, must have been immigrants to South America from the north. The list is short, and few genera show radiation following their arrival in South America. Woody plant taxa that are well known for their appearance in South America following establishment of the landbridge include *Alnus, Myrica, Quercus, Cornus,* and *Salix* (Table 3). These genera include only one or a few species in South America (Brako & Zarucchi, 1993), although they can be ecologically important in many Andean areas. Pollen records cannot be used to resolve the issue of speciation in these cases because the pollen cannot be recognized to species. A more evolutionarily successful group of shrubs and herbs includes *Berberis, Lupinus, Rubus, Scutellaria,* and *Viburnum* (Table 3). The South American species of these genera very likely came into existence after their immigrant ancestors reached South America, similar to the radiation proposed within mammalian genera. However, the timing of the immigrant arrival, relative to the establishment of the landbridge, is difficult to establish without direct information from the fossil record. Their arrival could predate the landbridge, and in this case examination of dispersal mechanisms might prove useful. These plant taxa are absent or are recovered rarely from the palynological record, most likely because they are insect-pollinated. The arrival of the successful sigmodontine rodents was proposed to have predated the landbridge (Hershkovitz, 1966; Reig, 1980, 1986; Marshall & Sempere, 1993), but a consensus has not been reached on this point among vertebrate paleontologists (Patterson & Pascual, 1972; Flynn et al., 1985; Marshall & Sempere, 1993). The fact that South American sigmodontines

Table 3. Laurasian genera now in tropical South America. South American species numbers are approximated from guides and floras (e.g., Gentry, 1993; Brako & Zarucchi, 1993; Killeen et al., 1993).

Trees	Shrubs and herbs
Alnus (1)	*Ambrosia* (?)
Boehmeria (8)	*Berberis* (32)
Cornus (1)	*Erigeron* (?)
Morus (2)	*Lupinus* (171)
Myrica (3)	*Ribes* (16)
Prunus (19)	*Rubus* (18)
Quercus (1)	*Salvia* (76)
Rhamnus (2)	*Satureja* (26)
Salix (2–3)	*Scutellaria* (15)
Sambucus (1)	*Valeriana* (100)
	Vaccinium (9)
	Viburnum (12)

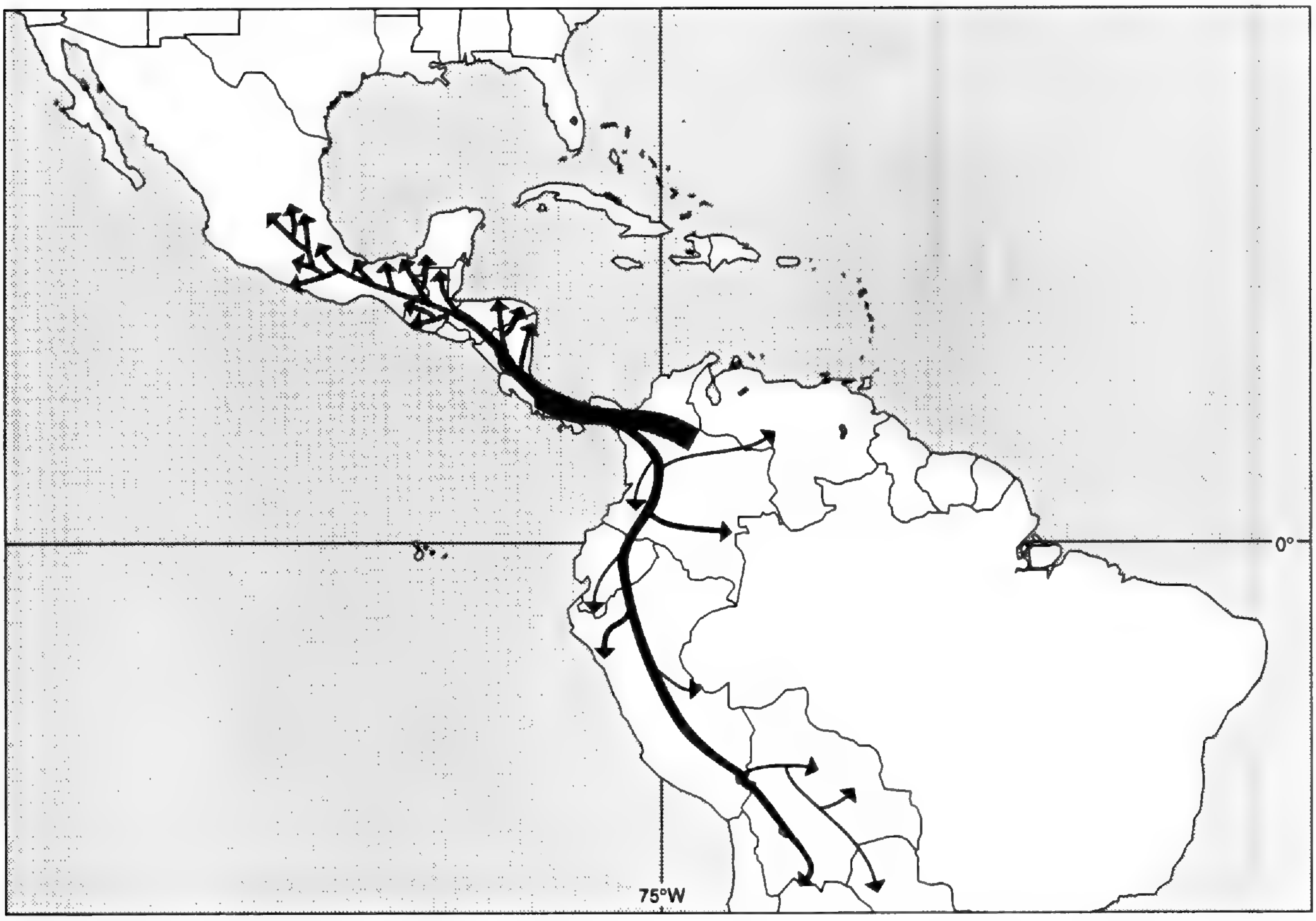

Figure 16. Woody plant migration and diversification following establishment of the Central American landbridge.

appear to be more primitive than North American forms, at least in penile morphology and in host-parasite relationships, casts doubts on their arrival in South America via the landbridge (Jacobs & Lindsay, 1984; B. D. Patterson, pers. comm. 1998). The plant immigration pattern viewed from South America is that establishment of the landbridge resulted in significant changes in the composition of South American upland forests. However, the number of species, and certainly the number of genera descended from northern immigrants, is low. The landbridge appears to have been far less significant for speciation in lowland angiosperms in South America than it was for mammals. To our knowledge, there are no estimates of the number of species in the South American flora that were derived from northern immigrants, but we would place it at about 10%.

From a northern perspective, Wendt (1993) documented taxa based on modern distributions that had most likely immigrated from South America and speciated in Mexico and Central America. These were not compared to the mammalian patterns. Radiations into central Mexico and the Antilles have been suggested by specialists on Bignoniaceae, Malpighiaceae, and Sapindaceae (Gentry, 1992; Acevedo-Rodríguez, 1993, 1996; W. R. Anderson, pers. comm. 1997). These include radiations into the moist forests of Mexico (Wendt, 1993), but appear to be more typical of the dry tropical forests of Central America, which were widespread until recent deforestation (Janzen, 1988).

In summary, the plant and animal migration and radiation patterns are interestingly different (Figs. 14 and 16). Mammalian radiations in South America are noted in many different groups of larger mammals (deer, canids, camelids, tapirs), but are particularly important among the sigmodontine rodents. These rodents are abundant in many habitats throughout South America, and are perhaps most species-rich in uplands and open habitats (Hershkovitz, 1972). However, when their current distribution is mapped on their phylogenetic diversification it appears that lowland sigmodontines gave rise to highland sigmodontines, rather than being derived from them (Patterson, in press). This contrasts with the situation in plants where uplands do correspond to the site of ecological dominance of the immigrant angiosperms from North America, but in the case of immigrant woody plants, ecological dominance is not accompanied by evolutionary diversification. Once arriving in Central and North America, southern mammals were relatively unsuccessful in an evolutionary sense, where only one or a few species of each group (sloths, capybara, agoutis, and opossums) are found (Emmons, 1990). Conversely, while some northward-moving plants extend just into the wet forests of Panama or southern Costa Rica, the more successful plant groups that extend farther north show strong diversification into the drier, seasonal habitats of Central America. The pollen records that are rapidly accumulating, together with refinements of species lists from both sides of the landbridge, should make it possible to establish the ecological conditions under which taxa migrated. With this added ecological perspective it may be easier to postulate reasons for a particular migration event and the environments in which speciation may have occurred.

Origin of the northern temperate element in neotropical vegetation

Two scenarios have been proposed for the origin of north-temperate plants in Mexico, Central America, and northern South America. One is that many of these elements were part of an ancient widespread vegetation existing in northern Latin America since the Paleogene (Axelrod, 1975). The other is that many migrated southward with cooling climates, the appearance of upland habitats, and the establishment of land connections through the Isthmian region (Graham, 1973). There is also the possibility of random and occasional introductions throughout the Cenozoic by long-distance transport. Three tests are available for assessing the likelihood of each model. First, if there was a general progressive introduction from the north into Mexico, Central America, and northern South America, the oldest temperate plant fossils should be in the north with the younger ones toward the south. Second, the introductions into northern South America should coincide generally with closure of the Isthmus; that is, they should mostly appear in South America after about the Mio-Pliocene. Third, the introductions into northern Latin America should correspond with some global climatic event that favored the southward migration of north-temperate organisms.

In the southeastern United States, pollen similar to *Alnus, Betula,* and *Carya* is present in deposits of Paleocene age (Frederiksen, 1991). In the Eocene (Claibornian) there are added *Pinus, Castanea, Celtis, Fagus, Quercus, Nyssa, Juglans, Ostrya-Carpinus, Platanus, Tilia,* and *Ulmus,* and in the younger Jacksonian *Picea, Tsuga, Acer*(?), *Diospyros*(?), *Fraxinus*(?), and *Nyssa* appear (Frederiksen, 1981, 1988, 1991; Gray, 1960). Although there are no fossil floras of Paleocene age known from northern Latin America, north-temperate elements are absent from the Eocene Burgas Basin assemblage in northern Mexico (Graham, 1999a; Martinez-Hernandez et al., 1980), the Gatuncillo assemblage in Panama (Graham, 1985), and from early Miocene assemblages in Costa Rica (Graham, 1987) and Panama (Graham, 1988a, b, 1989). These elements are known from a few grains of *Quercus* in the Mio-Pliocene Gatun Formation of Panama, and from a richer assemblage in the middle Pliocene Paraje Solo Formation of southeastern Veracruz, Mexico (*Abies, Picea, Pinus, Alnus, Celtis, Juglans, Liquidambar, Myrica, Populus, Quercus,* and *Ulmus*). Based on this evidence, it appears that the origin of the northern temperate component of the Latin American vegetation was primarily through relatively recent introductions. If north-temperate elements were present prior to the late Miocene, these phantom forests left no substantive record in the fossil assemblages published to date.

Until recently the number of fossil floras by which the models could be evaluated was relatively low. New data from microfossil floras in Chiapas (Mexico), Guatemala, and Costa Rica provide further information on the principal time of origin for north-temperate elements in northern Latin America. The evidence previously discussed would suggest that fossil floras older than about the middle to late Miocene should contain few or no representatives of these elements; rather, they should be present in floras of younger age, and their diversity in the fossil floras should decrease toward the south. The Simojovel flora in Chiapas, Mexico, is Early Miocene in age (Frost & Langenheim, 1974), and it is within the present-day distribution of deciduous trees and shrubs disjunct from eastern North America (Breedlove, 1973; Gómez-Pompa, 1973; Miranda & Sharp, 1950). With the exception of *Pinus,* the fossil flora contains no representatives of eastern deciduous temperate elements (Graham, 1998a, 1999b; Graham & Palacios Chávez, 1996; Langenheim et al., 1967). Temperate habitats were available, but they were occupied by plants such as *Podocarpus* and *Engelhardia.*

In Guatemala, a late Miocene to Mio-Pliocene assemblage of pollen and spores has been recovered from the Padre Miguel-Herrería complex of formations (Graham, 1998a). *Picea, Pinus, Juglans, Quercus,* and *Ulmus* have been identified, revealing a north-temperate component in the late Miocene and Mio-Pliocene that was absent in the older early Miocene Simojovel flora from adjacent Chiapas. Farther south in Costa Rica these elements are absent in the Pliocene Rio Banano Formation (Gra-

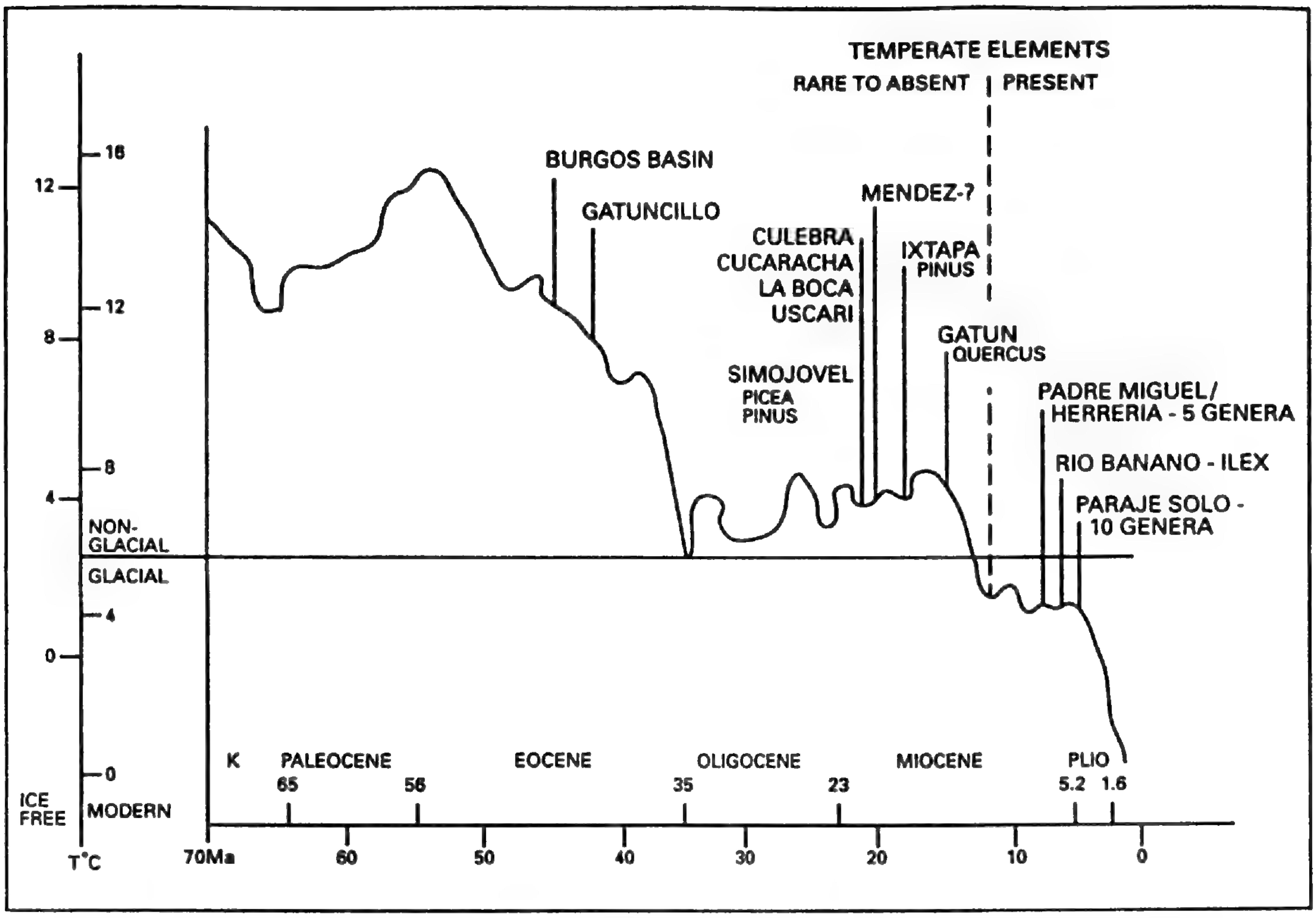

Figure 17. Benthic paleotemperature curve, Tertiary palynofloras from northern Latin America mentioned in the text, and occurrences of northern temperate elements. Paleotemperature curve based on Miller et al. (1987).

ham & Dilcher, 1998). Thus, northern temperate elements are absent from the Eocene Burgas Basin Flora of Mexico, the Eocene Gatuncillo flora of Panama, the early Miocene Simojovel flora of Chiapas, Mexico, the early Miocene Uscari Formation and the Pliocene Rio Banano Formation of Costa Rica, and the early Miocene Culebra, Cucaracha, and La Boca floras of Panama. They are present in Mio-Pliocene floras of Guatemala; in the middle Pliocene Paraje Solo flora of Veracruz, Mexico; and just appear (*Quercus* only) in the Mio-Pliocene Gatun flora of Panama.

The second test is whether these temperate elements appear in northern South America primarily after closure of the Isthmus of Panama (after about the Mio-Pliocene interval). In South America *Salix* appears in the early Pliocene, *Myrica* in the middle Pliocene, *Alnus* at ~1 Ma, and *Quercus* at 330 ka (Hooghiemstra, 1989, 1994; Hooghiemstra & Ran, 1994; Hooghiemstra & Sarmiento, 1991; Wijinga, 1996). One exception may be seeds of *Juglans* reported from presumed Miocene deposits in Ecuador (Brown, 1946), but Manchester (pers. comm. 1997) suggested that radiometric dates are needed to confirm the age of the specimens. *Juglans* may be represented in South America today by as many as five species (Brako & Zarucchi, 1993; Killeen et al., 1993).

The third test is whether some climatic event occurred at the appropriate time that facilitated the introduction of north-temperate elements into Latin America, and that is evident from an independent line of inquiry. In Figure 17 the floras are plotted on the global benthic paleotemperature curve. A major drop in temperature is evident in the middle Miocene that initiated Antarctic glaciations, expanded continental glaciers on Antarctica, and contributed to the spread of seasonally dry habitats in North America (see discussion in Graham, 1999c, chapters 3 and 7). This drop in temperature is consistent with the timing of the introductions based on the available paleobotanical evidence, and provides a plausible mechanism for the early appearance of the northern temperate component in the neotropical vegetation. Evidence for the slightly later appearance of uplands (Mio-Pliocene) supplementing effects of Late Cenozoic cooling, has been discussed previously (this paper). The pre-existing uplands and rising mountain areas in Central and South America would have been expected to experience more pronounced climate changes than the lowland, coastal areas. It is these upland areas that likely provided habitats for the early temperate elements.

Origin of the tropical element in the northern Latin American vegetation

New analyses also are providing insights into the origin of the tropical component in northern Latin American vegetation. It has generally been assumed that trees and shrubs in the tropical forests of Mexico and Central America were derived from South America: "Indigenous tropical plants in modern North America are descendants of Tertiary and Quaternary immigrants from South America" (Cronquist, 1988: 153). In general this is true, but it is proving too simplistic.

Wendt (1993) studied the affinities of rainforest canopy trees in Mexico. As expected, the majority of the taxa (75%) are related to ones in South America, and probably arrived via an Isthmian route after formation of the Panama landbridge, and/or by long-distance transport throughout the Cenozoic Era. However, the modern distribution and affinities, and the fossil record of a significant number (~25%), suggest a different history. According to Wendt (1993), modern distributions and relationships indicate that some are of Laurasian origin and probably migrated from the north via the North Atlantic landbridge—*Antirhea, Aphananthe, Berrya, Bourreria, Bursera, Ehretia, Erblichia, Federovia,* Flacourtiaceae (subtribe Hydnocarpinae), *Lonchocarpus, Sideroxylon, Styphnolobium,* and *Trichospermum.* The fossil record provides evidence for others of Laurasian origin that followed a northern route into Mexico. These are taxa known from the Eocene of the southeastern United States, but which presently have no or only later fossil records in South America—*Celtis, Clethra, Cordia, Ilex, Populus, Saurauia, Salix, Talauma, Trema,* and *Turpinia.*

A group of African-Gondwanan origin probably arriving from the north includes *Acacia, Beilschmiedia, Bursera, Caesalpinia, Cassia, Cedrela, Chrysophyllum, Dalbergia, Diospyros, Ficus, Lonchocarpus, Nectandra, Ocotea, Oreopanax, Persea, Sabal, Sapindus, Sapium, Sterculia,* and *Terminalia,* while others of Gondwanan origin arriving prior to the landbridge but still via South America may include *Alchornea, Allophyllus, Apeiba, Astronium, Bauhinia, Bernoullia, Casearia, Dendropanax, Erythrina, Eugenia, Homalium, Luehea, Mabea, Ochroma, Pouteria, Tapiria, Thouinia,* and *Trichilia.*

The presence of plants of Old World origin in the tropical forests of northern Latin America also has been assessed by a cladistic analysis of two legume groups (*Dichrostachys* group, tribe Robinieae and allies; Lavin & Luckow, 1993). If a taxon has a modern center of distribution and an early Tertiary fossil record in tropical North America, then there is a high probability that its sister-group will be in the paleotropics and derived relatives will be in South America if it has been introduced from the north from Gondwanan ancestors. The results of the analysis for these legumes supported the hypothesis; namely, the taxa in South America were derived from, and not a source for, the northern tropical ones. In contrast, a similar analysis of the Costa Rican *Ruptiliocarpon* in Lepidobotryaceae (Hammel & Zamora, 1993) showed that it is likely an example of the majority of taxa that arrived from South America. The emerging picture is that the tropical forests of northern Latin America, although primarily South American in origin, are more complex than earlier thought and are composed of elements arriving from several sources via different routes and at different times (Graham, 1995; Wendt, 1993).

EVENT IV: QUATERNARY CLIMATE FLUCTUATIONS

The first broad assessment of global Quaternary climates was from the Climate Long-Range Investigation and Mapping Program (CLIMAP) project (CLIMAP Project Members, 1976, 1981, 1984). The resulting model, based on changes in the composition and distribution of planktonic microfossils (e.g., foraminifera), indicated that while high latitudes chilled at glacial maximum at ~ 18 ka, temperatures in the low latitudes remained about the same or to a maximum of about 2° cooler. This is at variance with new oxygen isotope evidence (Guilderson et al., 1994; Schrag, et al., 1996), noble gasses dissolved in ^{14}C-dated ground water (Stute et al., 1995), snow-line depression (Rind & Peteet, 1985), continental climate records from pollen analysis, and with global circulation model (GCM) simulations that predict a MAT (mean annual temperature) cooling in the equatorial regions of 5°–6°C at glacial maximum (Colinvaux et al., 1996a, b, and see review in Kerr, 1997). New calcium-strontium ratios from submerged coral reefs (*Acropora palmata*) drilled off the south coast of Barbados (13°N) also favor cooler climates. The element strontium is chemically similar to calcium and can replace calcium in the walls of the corals. The rate of replacement is temperature-sensitive, and measurements indicate temperatures lower by ~ 5°C at ~ 18 ka (Guilderson et al., 1994). Modeling by Webb et al. (1997) demonstrated the mechanism potentially responsible for equatorial cooling.

Other recent data also suggest that the middle and low latitudes responded to fluctuations in Quaternary temperatures (Charles, 1997; Beck et al., 1997; Curry & Oppo, 1997; Webb et al., 1997). A cool interval called the Little Ice Age occurred at ~ 400 years ago and at that time MAT in the Sargasso Sea (~ 32°N) was ~ 1°C cooler than at present. During a warm interval at ~ 1 ka it was ~ 1°C warmer (Keigwin, 1996).

Among the unsettled aspects of Quaternary vegetational history in South America are the history of tropical lowland biotas and the related Haffer model of diversification. Early pollen profiles from the High Plain of Bogotá revealed that treeline fluctuated by ~ 1700 m during the late Pliocene and Quaternary (van der Hammen & Gonzalez, 1960, 1964). This corresponds to a difference in MAT of ~ 8°C at ~ 2500 m; the present MAT is 17–19°C. By extrapolation, a potential lowering of up to ~ 6°C was indicated for the lowlands during the coldest intervals. Glacial climates were also frequently drier because cooler temperatures reduce the rate of evaporation of water from the ocean surface into the atmosphere. In the northern Andes, rainfall was periodically reduced by up to 50% (van Geel & van der Hammen, 1973). The question is whether these changes suggested by geochemical and oxygen isotope data, and evident in the Andean highlands, affected biotas in the lowland Amazon Basin.

Haffer (1969, 1970, 1974, 1982) observed that species diversity among toucans and jaçanas was not uniform across the basin, but was focused at certain locales. These areas of high species diversity corresponded to sites that by their physiography appeared likely to perpetuate moist conditions during periods of aridity (river margins, base of mountain slopes). The model envisioned rainforest biota concentrated in refugia during cooler/drier glacial cycles, while drier forest and savanna-like vegetation occupied the intervening area. During warmer/moister interglacial cycles, the rainforest expanded from these sites and coalesced, while the drier communities either persisted on edaphically dry tablelands with sandstone substrata in the lowlands, or occupied the surrounding slopes, as at present. The periodic fragmentation and reuniting of ranges facilitated speciation by allopatry and hybridization, and was proposed as one mechanism accounting for the high diversity of the lowland tropical biota. Several other lines of evidence were interpreted as supporting the model, including the presence of stone lines which form under arid conditions, and the concentration of plant and insect species at sites identified as refugia on the basis of bird distribution (see papers in Prance, 1982).

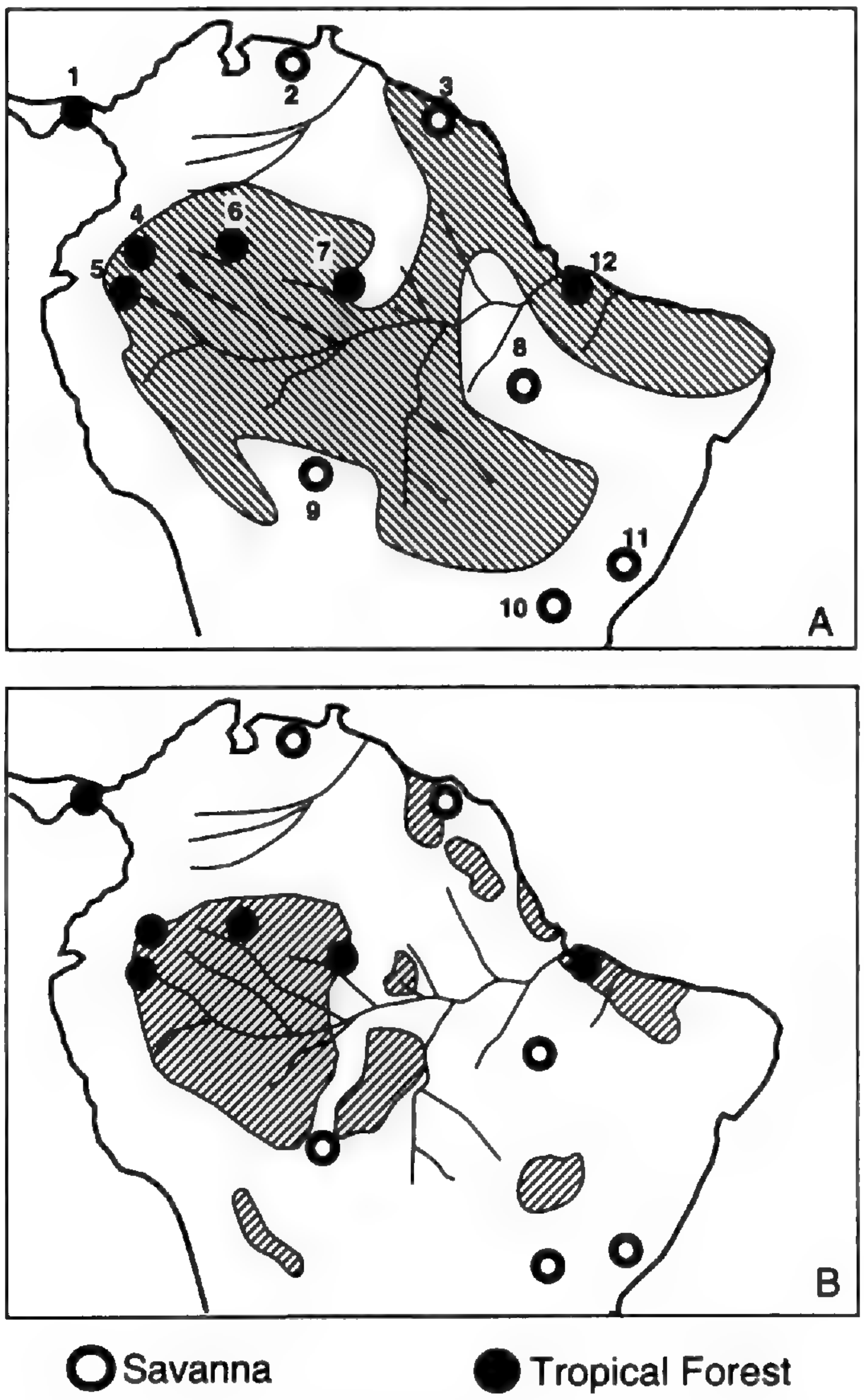

Figure 18. Projected rainforest distribution in Amazonia during the Pleistocene, with (A) 25% and (B) 40% reductions in rainfall from present-day values. Shaded area shows rainfall over 1500 mm annually. Palynological samples from Amazonia shown by symbols, with interpreted vegetation indicated by symbol coding. After Absy and van der Hammen, 1994; Colinvaux, 1996; Behling, 1998. Sites are (informal names): 1, La Yeguada; 2, Lake Valencia; 3, Guianas; 4, Mera; 5, San Juan Bosco; 6, Caqueta River; 7, Lake Pata; 8, Carajas; 9, Katira (Rondonia); 10, Lagoa Campestre; 11, Catas Altas; 12, Lagoa Curuça.

Lacking was paleobotanical information directly from the lowland Amazon Basin, and ancillary information on neotropical Quaternary environments derived from independent lines of inquiry. New data were recently published for lower-elevation sites around the Amazon Basin and for other locations in the lowlands (Fig. 18). Considering the immense complexity of the tropical ecosystem, and the difficulties and limitations inherent in trying to reconstruct its past, it is not surprising that a consensus has not yet been achieved. Only a few plant-bearing sites that extend into the last glacial interval (older than ~ 12 ka) have been published. Haberle (1997) reported data from Amazon fan cores spanning 160,000 years that show percentages of grass and shrub pollen less than or equal to 25%, a value interpreted as indicating limited savanna development in the Amazon basin. As noted by Haberle (Haberle, 1997; see also Kerr, 1996), a few hundred sites in the Amazon Basin may be necessary to get a clear picture of environmental change and biotic response. In assessing the present information it is also necessary to distinguish between evidence for cool temperatures and for aridity. There is a broad association between warm-moist climates and tropical vegetation in the lowlands during the interglacials (as at present), and cool-dry climates and drier forest/more open savanna-like vegetation during glacial times. It has been suggested, however, that significant cooling occurred in the lowlands of Amazonia without the accompanying dryness that would have converted areas occupied by rainforest to savanna (Colinvaux, 1996). There are insufficient data for dogmatic conclusions about Quaternary environments in the Amazon, and an even-handed review must include much that is a matter of opinion.

Along the eastern slopes of the Andes at Mera (~ 1°S; 1100 m elevation) and San Juan Bosco (~ 3°S; 900 m elevation) in Ecuador, pollen profiles show that the upper range of temperature-sensitive plant populations was lower by ~ 700 m between 33,500 and 26,500 yr B.P. (late middle Glacial) and that elements from the uplands intermingled with lowland forest communities. This implies a MAT lower by ~ 4°C (earlier estimates) to 7–9°C (more recent estimates; Bush et al., 1990; Colinvaux, 1996; Colinvaux & Liu, 1987; Liu & Colinvaux, 1985) and a moist rainfall regime. However, the sites are near the base of the eastern Andes where the present annual rainfall is ~ 5 m. This physical setting qualifies as a potential refugium that would have remained moist during dry intervals.

At Lake Pata in northwestern Brazil (0°N; 300 m elevation) the pollen record extends back to ~ 42 ka. Throughout the profile, tree pollen constitutes 70–90% of the assemblage, while herb pollen remains below 10%. Pollen from trees that now grow mostly 800–1000 m above the Pata site were present (*Podocarpus*, 10%; associated Ericaceae, *Hedyosmum, Humiria, Ilex,* Melastomataceae, *Rapanea, Weinmannia*) at glacial maximum, and this was interpreted to mean a MAT 5–6°C lower than at present (Colinvaux et al., 1996a, b). The inference is that at glacial maximum the area was forested, and was not occupied by savanna. Also, if the area was sufficiently moist throughout the past ~ 42 ka to support forest, even though 5–6°C cooler, this supports the contention that lower temperatures prevailed throughout the lowlands without appreciable dryness. One complication is that on the basis of meterological evidence, the area of Lake Pata also has been considered a refugium, and by the Haffer model it would be expected to support forest during dry intervals (van der Hammen & Absy, 1994). In addition, large reproductive stands of *Podocarpus* are found at sea level in Central America, on both the Atlantic and Pacific Coasts, which throw into question the use of this genus as an exclusively cooler-climate indicator.

Data from other sites suggest that a patchwork of vegetation may have existed in the lowlands at the coldest intervals which included moist forests and drier communities. At Carajás (southeastern Amazonia, Brazil; 6°S), pollen profiles reflect changes in vegetation for the last 60 ka (Absy et al., 1991). The site is on a table mountain at 700–800 m elevation, today covered with forest and edaphic savanna, and surrounded by Amazonian forest. The pollen diagrams were interpreted as showing that wet intervals (forest on the hills and in the lowlands; lake levels high) alternated with drier intervals (expansion of savanna on the hills and in the lowlands; lake levels low). At Rondónia, Brazil (9°S) in lowland Amazonia, the sequence is from primarily rainforest (interglacial), to savanna (glacial; 42,500 ± 2,500 to 18,500 yr B.P.), to modern rainforest after ~ 11 ka (Absy, 1979; Absy & van der Hammen, 1976; van der Hammen, 1972). Geomorphic and pollen data from the middle Caquetá River area in Colombia and eastern Peru also are interpreted to show that local vegetation alternated between Amazonian forest and more open caatinga (van der Hammen et al., 1992a, b).

In the "Lagoa Campestre" (Lake) of Salitre in southern Brazil (19°S; 970 m elevation), pollen diagrams show an arid phase between ~ 50 and 40 ka (Ledru et al., 1996). This interval is characterized by low frequencies of arboreal pollen (0.5–3%). Asteraceae (18.5–28%) and Poaceae (69–70%) are dominant among the non-arboreal taxa. This pollen assemblage is poor in taxa and indicates open, treeless vegetation surrounding a shallow pond with no fringe of aquatic vegetation. The low frequency of arboreal taxa indicates that trees were growing only at a distance. This suggests the presence of landscapes found today in central and northern Argentina, where the climate is cool and dry (Ledru et al., 1996). Other areas where reduced rainfall (~ 10–20%) and dry vegetation replaces forest in the Quaternary include the Guianas (Wijmstra & van der Hammen, 1966; Salgado-Labouriau, 1980) and the Galápagos Islands (Colinvaux, 1972), as well as East Africa (Livingstone, 1975). In an extensive review of the geology and geomorphology of South America, Clapperton (1993a: 162) concluded, "The important message is that climatic conditions appear to have fluctuated between humid and dry, and as the present interglacial climate is humid, it seems reasonable to assume that dry intervals corresponded to periods of global glaciation."

A study of ice cores from Huascarán in the north-central Andes of Peru (~ 9°S, 6000 m elevation) has revealed Quaternary climatic fluctuations back 20 ka that parallel those from the North Atlantic (Thompson et al., 1995). Oxygen isotope ratios show that between 20 ka and 14.5 ka temperatures at this elevation were 8–12°C cooler than at present. This would be consistent with the ~ 6°C lowering of temperatures estimated for the lowlands. In addition, there was a 200-fold increase in dust and lower nitrate levels in the cores. Thompson and co-authors (1995: 47) concluded, "The extreme dustiness of the LGS [late glacial stage] ice on Huascarán is consistent with reconstructions [Clapperton, 1993b; van der Hammen & Absy, 1994] for South America that indicate a reduction in atmospheric humidity, precipitation, and forest and grass cover during the LGS along with an enhancement of eolian deposits such as dune fields and deflation basins [Clapperton, 1993a], because winds were stronger and surface conditions were drier." With reference to the low nitrate levels, Thompson et al. (1995: 47) further noted they "may imply that forest cover was significantly reduced in response to dry conditions and the expansion of grassland, as suggested by palynological studies in Brazil [Clapperton, 1993b]."

To the north, the history of Quaternary vegetation in lowland Panama is preserved in sediments from El Valle (500 m elevation; > 30,700 ± 800 to 8,350 ± 150 yr B.P.) and Lake La Yeguada (650 m; 14 ka to the present). These records have been interpreted to indicate lowland representation of taxa currently found at elevations ~ 800 m higher (Bush & Colinvaux, 1990; Bush et al., 1992). The MAT is estimated at 4–6°C cooler, but still moist, and the vegetation as remaining forested throughout the sections. In the Petén of Guatemala, the temperature depression is estimated at ~ 8°C cooler in the late Quaternary (Leyden, 1984; Leyden et al., 1993), but Leyden also emphasized increased aridity at interglacial-glacial transitions.

In addition to temperature and precipitation, another factor affecting lowland tropical biotas is sea-level change associated with glacial history. A recent estimate is for a lowering of ~ 121 ± 5 m at glacial maximum (Geophysics Study Committee, 1990). Considering that much of the Amazon Basin is near sea level, a change of this magnitude must have had some drying effect on vegetation through fluctuations in water table.

There are a number of indications that late Glacial and early Holocene climates in the neotropical lowlands included cooler and drier intervals, and variously supported a mosaic of moist forests and drier forests to savanna-like vegetation. These are: (1) fossil mammalian faunas in Central and South America (Webb & Rancy, 1996), (2) a trend toward drier conditions and a more complex array of communities developing near the end of the Tertiary Period in Costa Rica and Panama (Graham, 1992); (3) aridity at interglacial-glacial transitions in Guatemala (Leyden, 1984; Leyden et al., 1993); (4) geomorphic features suggesting aridity during the Quaternary in the Amazon lowlands (Ab'Sáber, 1982; Clapperton, 1993a); (5) marked changes in sea level (Geophysics Study Committee, 1990); and (6) Quaternary aridity demonstrated from other adjacent and distant parts of the world (the Guianas, Wijmstra & van der Hammen, 1966; Galápagos Islands, Colinvaux, 1972; Lake Valencia, Venezuela, Leyden, 1985; East Africa, Livingstone, 1975). This evidence is open to other interpretations: either that the lower rainfall was insufficient to cause forest to be replaced by dry-forest or savanna, or that such replacements were localized (Colinvaux, 1996).

The consensus developing is that late Tertiary and Quaternary sea level and climatic fluctuations affected the lowland biotas of the Neotropics, and that the magnitude of the temperature change was ~ 6°C. There is less agreement about aridity and the closed forest versus more open forest or savanna-like nature of the vegetation. Colinvaux (1996) has emphasized cooler climates, sustained moisture, and forested vegetation throughout much of the late Quaternary. This would negate any significant role for refugia-like mechanisms in accounting for the high level of diversity in neotropical biotas. In contrast, other authors see evidence for periods of aridity and open vegetation in the pollen profiles and from other kinds of data. Revisions may become necessary in the proposed locations, extent, and patterns of some forest refugia and savannas in the Amazonian lowlands as envisioned in the original Haffer model. It is further true that climate-induced refugial events in the Quaternary Period were not the only mechanisms influencing rainforest diversity. Recently, it has been discovered that the modern distributions of some lineages of rodents and marsupials in the Amazon Basin conform not to the present barriers formed by river drainage systems, but to ancient ridges that divide the basin into sub-basins (Patton & da Silva, 1998; summary by Morell, 1996). These ridges formed when the Andes were uplifted ~ 2–5 Ma and divided the range of some species into reproductively isolated subsets that are still detectable by mtDNA analysis. Subsequent erosion and basin filling have nearly obliterated these Pliocene barriers. They suggest changes in the physical landscape are another mechanism generating neotropical species diversity. Nonetheless, the combination of temperatures ~ 6°C cooler, sea level ~ 120 m lower, and pollen sequences indicating at least locally dry habitats and open vegetation are compelling. They create a view of lowland neotropical vegetation alternating between closed forest and more dry open forest or savanna-like vegetation during the environmental fluctuations of the late Tertiary and Quaternary Period.

Our concept of the pace of these fluctuations has also undergone substantial renovation. The older view of four major glacial advances each lasting ~ 175 ka, separated by three interglacials of about equal duration, has been replaced by a model depicting 18–20 cycles within the past 1.6 Ma and 9 within the past 800 ka [Davis, 1983; Johnson, 1982; Greenland Ice-core Project (GRIP) Members, 1993], and shorter ones on the order of several hundred (Dansgaard-Oeschger or D-O events) to several thousand years duration (Heinrich events). Whatever the disruptions of neotropical vegetation from temperature, precipitation, physical, and sea-level changes, they were taking place at a much more rapid pace than previously envisioned. Thus, the older concept of stable and unchanging tropical vegetation has given way to one of a dynamic, ephemeral, and delicately balanced assemblage.

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Appendix 1. Published plant fossil localities ranging geographically from Costa Rica to Bolivia, and temporally from Late Cretaceous to Quaternary Periods. Localities are sorted by country, and within country by geologic age and then ordered alphabetically by author of the work. When several countries are treated by a single publication, the publication is listed under the first country in alphabetical order.

Country	Geological age	Author(s)	Date of publication	Local place name	Organs studied
Bolivia	Pliocene	Berry	1939a	Potosi	leaves
Bolivia	Pliocene	Berry	1917	Potosi & Corocoro	leaves & fruits
Bolivia	Mio-Pliocene	Berry	1940	Agua Salada	fruit
Bolivia	Mio-Miocene	Berry	1922a	Pisllypampa	fruits
Bolivia	Miocene	Berry	1922b	Jancocata	leaves
Bolivia	Miocene	Britton	1892	Potosi	leaves
Bolivia	Miocene	Engelhardt	1888	Cerro de Potosi	leaves
Bolivia	Miocene	Engelhardt	1894	Potosi	leaves
Bolivia	Miocene	Gregory et al.	1998	Jakokkota (=Jancocata)	leaves
Bolivia	Miocene	Singewald & Berry	1922	Corocoro	leaves
Br. Guiana/Suriname	Paleocene to Miocene	Van der Hammen & Wymstra	1964		pollen
Brazil	Quaternary	Absy	1985		pollen
Brazil	Quaternary	Absy & van der Hammen	1976	Rondonia, Katira, Capoeira & Río Preto	pollen
Brazil	Quaternary	Absy et al.	1991	Serra dos Carajas	pollen
Brazil	Quaternary	Behling	1995	Lagoa do Pires	pollen
Brazil	Quaternary	Behling	1996	Lagoa de Curuca	pollen
Brazil	Quaternary	Behling	1998	Morro de Itapeva, SP	pollen
Brazil	Quaternary	Behling	1998	Cata Altas	pollen
Brazil	Quaternary	Behling & Hooghiemstra	1998	Laguna Angel & Laguna Sardinas	pollen
Brazil	Quaternary	Colinvaux et al.	1996a	Lake Pata—Hill of Six Lakes	pollen
Brazil	Quaternary	DeOliveira	1992		pollen
Brazil	Quaternary	Duarte & Nogueira	1985	Morro do Chapeu, Bahia	leaves
Brazil	Quaternary	Duarte & Vasconcelos	1980	Umbuzerio	leaves
Brazil	Holocene	Ledru	1992	Lake Carajas & Lake Salitre	pollen
Brazil	Quaternary	Salgado-Labouriau et al.	1997	Goias, Crominia	pollen
Brazil	Pliocene	Berry	1935a	Bahia & Minas Gerais	leaves
Brazil	Pliocene	Berry	1937d	Acre	leaves
Brazil	Pliocene	Bonnet	1905	Bahia	leaves
Brazil	Pliocene	Dolianiti	1949	Minas Gerais, Fonseca	leaves
Brazil	Pliocene	Dolianiti	1950	Minas Gerais, Fonseca	leaves
Brazil	Pliocene	Hollick & Berry	1924	Bahia	leaves
Brazil	Pliocene	Krasser	1903	Ouricanga, Alagoihas, Bahia	leaves
Brazil	Pliocene?	Selling	1945	Bahia	fruit
Brazil	Miocene	De Lima & Angulo	1990	Alexandra Formation near Curitiba, Parana	pollen
Brazil	Miocene?	Duarte	1972	Pirabas, Para	leaves
Brazil	Miocene	Hoorn	1993	Solimoes Formation	pollen
Brazil	Miocene	Mandarim-de-Lacerda	1992	Taubate Basin	leaves
Brazil	Oligocene	De Lima et al.	1985	São Paulo	pollen
Brazil	Eocene-Oligocene	Martins-Neto	1989	Taubate Basin	leaves
Brazil	Eocene-Oligocene	Beurlen & Sommer	1954	Rio de Janeiro	leaves & fruit
Brazil	Oligo-Eocene	De Lima & Salard-Cheboldaeff	1981	Gandarela & Fonseca, Minas Gerais	pollen

Appendix 1. Continued.

Country	Geological age	Author(s)	Date of publication	Local place name	Organs studied
Brazil	Eocene	De Lima, Junior & Stefani	1996	Macacu-Rifte de Guanabara	pollen
Brazil	Tertiary	Dolianiti	1955	Recife	fruits
Brazil	Eocene-Oligocene	Duarte & Rezende-Martins	1983	Vargem Grande do Sul	leaves & fruits
Brazil	Eocene-Oligocene	Duarte & Rezende-Martins	1985	Vargem Grande do Sul	leaves
Brazil	Eocene	Fittipaldi et al.	1987	Bacia de São Paulo	leaves
Brazil	Cretaceous	Crane & Maisey	1991	Santana	pollen
Brazil	Cretaceous	Duarte	1985	Santana	leaves
Brazil	Aptian	Duarte & Silva-Santos	1993	Maranhão	leaves
Brazil	Cretaceous	Herngreen	1975	Alagoas	pollen
Brazil	Cretaceous	Osborn et al.	1993	Santana (NE Brazil)	pollen
Brazil	Cretaceous	Pons et al.	1992	Pernambuco	fruits & leaves
Brazil & Guyana	Quaternary	Van der Hammen & Absy	1994	Rondonia & Carajas	pollen
Brazil, Ecuador, Colombia	Tertiary	Langenheim & Beck	1968	Capanema & Para	ambers
Colombia	Pleistocene	Bakker et al.	1989	Pitalito Basin	pollen
Colombia	Quaternary	Behling et al.	1999	Pantano de Monica	pollen
Colombia	Quaternary	Gonzalez et al.	1965	Sierra Nevada del Cocuy	pollen
Colombia	Quaternary	Helmens & Kuhry	1986	Paramo de Agua Blanca	pollen
Colombia	Quaternary	Hooghiemstra & Ran	1994		pollen
Colombia	Quaternary	Hooghiemstra & Van der Hammen	1993	Cundinamarca	pollen
Colombia	Holocene	Van der Hammen & Gonzalez	1960	Eastern Cordillera: Laguna de La América	pollen
Colombia	Quaternary	Van der Hammen & Gonzalez	1960	Sabana de Bogotá: Palacio A	pollen
Colombia	Quaternary	Van der Hammen & Gonzalez	1965	Boyaca	pollen
Colombia	Pliocene-Present	Andriessen et al.	1993	Eastern Cordillera	pollen & sediments
Colombia	Pliocene	Boureau & Salard	1962	Bolívar	wood
Colombia	Pliocene-Present	Hooghiemstra	1994	Eastern Cordillera	pollen
Colombia	Pliocene-Present	Hooghiemstra & Sarmiento	1991	Bogotá	pollen
Colombia	Pliocene	Howe	1974	Magdalena Valley	leaves
Colombia	Pliocene	Solé de Porta	1960	Cerro de la Popa, Cartagena	pollen
Colombia	Pliocene-Present	Van der Hammen & Hooghiemstra	1997	High Plain of Bogotá	pollen
Colombia	Pliocene-Present	Van der Hammen et al.	1973	Sabana de Bogotá	pollen
Colombia	Pliocene	Wijninga	1996a	Cordillera Oriental	pollen, leaves, wood, seeds
Colombia	Pliocene	Wijninga	1996b	High Plain	pollen, seeds, fruits, wood, leaves
Colombia	Pliocene	Wijninga & Kuhry	1990	Subachoque Valley	pollen & leaves
Colombia	Pliocene	Wijninga & Kuhry	1993	Guasca Valley	pollen & leaves
Colombia	Miocene	Berry	1936b	Santander	leaves

Appendix 1. Continued.

Country	Geological age	Author(s)	Date of publication	Local place name	Organs studied
Colombia	Mio-Pliocene	Berry	1945b	East of Cordillera de Bogotá	leaves
Colombia	Miocene	Hoorn	1994a	Caqueta River	pollen
Colombia	Oligocene through Pliocene probably	Mirioni	1965	Amaga, Prov. Bolívar, Magdalena Valley	wood
Colombia	Miocene or Pliocene	Pons	1965	Tolima Province	leaves
Colombia	Miocene	Pons	1969	Magdalena Valley	wood
Colombia	Miocene	Pons	1976	Tolima	leaves
Colombia	"Late Tertiary"	Pons	1979	Hato Grande, Tolima	leaves
Colombia	Miocene	Pons	1985	Magdalena Valley	leaves
Colombia	Miocene	Solé de Porta	1963	Cira del Valle Formation, Magdalena Valley	pollen
Colombia	Miocene	Wijninga	1996b	Tequendama	pollen, leaves, wood, fruits
Colombia	Oligocene-Miocene	Duenas	1977	Planeta Rica	pollen
Colombia	late Eocene or Oligocene	Berry	1924a	Cundinamarca	fruits
Colombia	Oligocene	Berry	1925b	East of Bogotá	seeds
Colombia	Oligocene	De Porta & Solé de Porta	1962	Magdalena Valley	pollen
Colombia	Oligocene & Miocene	Hoorn	1988	Araracura	pollen
Colombia	Oligocene	Marty	1933	near Yurumangui & Naya	leaves
Colombia	Oligo-Miocene	Pons	1983	Planeta Rica	seed
Colombia	Oligo-Miocene	Solé de Porta	1961a, b	Magdalena Valley, Santander	pollen
Colombia	Oligocene and Eocene	Berry	1924a	Cundinamarca & Bolívar	fruits & seeds
Colombia	Oligocene	Reid	1933	near Yurumangui & Naya	fruits
Colombia	Eocene, Miocene	Berry	1929c	Bolívar; Cundinamarca; Boyaca	leaves
Colombia	Paleocene-Eocene	Doubinger & Pons	1970	Magdalena Valley	leaves & fungi
Colombia	Eocene	Gonzalez-Guzman	1967	Tibu	pollen
Colombia	Eocene	Huertas	1977	near Medellin	leaves
Colombia	Eocene-Oligocene	Schuler & Doubinger	1970	D'Amaga	pollen
Colombia	Tertiary	Solé de Porta	1961b	near Monteria & Planeta Rica	pollen
Colombia	Eocene-Oligocene	Van der Hammen & Garcia de Mutis	1966		pollen
Colombia	Paleocene	Van der Kaars	1983	Guajira Province	pollen
Colombia	Paleogene	Doubinger & Pons	1970	Guajira	cuticle
Colombia	Cretaceous	Huertas	1960	Sabana de Bogotá, Zipaquira	leaves
Colombia	Cretaceous	Huertas	1969	Cundinamarca	fruit
Colombia	Cretaceous	Huertas & Van der Hammen	1953	Villeta	fruit
Colombia	Cretaceous	Stough	1968	Sabana de Bogotá	pollen
Colombia	Cretaceous through lower Tertiary	Van der Hammen	1954	High Plain of Bogotá	pollen
Colombia & Guyana	Quaternary	Wijmstra & Van der Hammen	1966	Laguna Agua Sucia-Rupununi	pollen
Colombia, Brazil, Peru	Miocene	Hoorn	1994b	Pebas, Solimoes	pollen

Appendix 1. Continued.

Country	Geological age	Author(s)	Date of publication	Local place name	Organs studied
Colombia	Miocene	Hoorn & Lorente	1992	Caqueta River	pollen
Costa Rica	Quaternary	Hooghiemstra et al.	1992	Talamanca	pollen
Costa Rica	Pliocene	Graham & Dilcher	1998	Río Banano near Zent	pollen
Costa Rica	Miocene	Berry	1921a	Talamanca Valley	leaves
Costa Rica	Miocene	Graham	1987	Uscari	pollen
Ecuador	Quaternary	Bush & Colinvaux	1988	Lake Ayauch	pollen
Ecuador	Pleistocene	Bush et al.	1990	Mera, San Juan Bosco	pollen, phytoliths
Ecuador	Pleistocene	Heine	1994	Mera	pollen, radiocarbon
Ecuador	Pleistocene	Liu & Colinvaux	1985	Mera	pollen, wood
Ecuador	Miocene	Berry	1929a	Loja	leaves
Ecuador	Miocene	Berry	1933	Loja Basin	fern
Ecuador	Miocene	Berry	1934a	Cuenca Basin	leaves
Ecuador	Miocene	Berry	1935b	Malacatos	leaves
Ecuador	Miocene	Berry	1945a	Loja Basin	leaves
Ecuador	Mio-Pliocene	Brown	1946	Esmeraldas	seeds
Ecuador	Mio-Pliocene	Brown	1956	Punta Gorda	seeds
Ecuador	Miocene	Burnham	1955a, b	Loja	fruit
Ecuador	Miocene	Wolf & vom Rath	1876	Loja	leaves
Ecuador	Eocene	Berry	1929d	Santa Elena	fruits
Ecuador	Eocene	Berry	1932	Santa Elena	fruits
Ecuador	Cretaceous	Shoemaker	1982	El Oro	leaves & wood
Ecuador & Colombia	Miocene	Engelhardt	1895	Loja & Santa Ana	leaves
Guyana	Paleocene-Eocene	Leidelmeyer	1966	near Georgetown, Mombaka	pollen
Panama	Quaternary	Bush & Colinvaux	1990	El Valle	pollen
Panama	Quaternary	Bush & Colinvaux	1994	Darien—Lake Wodehouse	pollen
Panama	Pleistocene	Bush et al.	1992	Veraguas Province	pollen, phytoliths
Panama	Oligocene	Berry	1918	Canal Zone	leaves & wood
Panama	Miocene	Berry	1921b	Canal Zone	nut
Panama	Eocene	Graham	1985	Alcalde Díaz	pollen
Peru	Quaternary	Hansen et al.	1994	Andean	pollen
Peru	Miocene	Berry	1920a	Tumbes	leaves
Peru	Pliocene	Berry	1923	Cajamarca	leaves
Peru	Pliocene?	Berry	1925a	Loreto	leaves
Peru	Miocene	Cruzado-Casteneda & Celi-Navarrete	1985	Tumbes Province	pollen
Peru	Miocene	Wood et al.	1992	Tumbes	pollen
Peru	Oligocene	Berry	1924b	Parinas Point, Piura	fruits
Peru	Eocene	Berry	1929b	Belen	fruits & seeds
Peru	Oligocene	Berry	1934b	Chira Valley	seeds
Peru	Eocene	Berry	1937e	Piura	leaves
Peru	Cretaceous	Mourier et al.	1988	Morerilla	wood
Peru/Ecuador	Pleistocene/Holocene	Hansen & Rodbell	1995	Laguna Baja	pollen
Puerto Rico	Oligocene	Graham	1996	San Sebastian	pollen, leaves
Trinidad	Miocene	Berry	1925c	Siparia & Moruga	leaves
Trinidad	Miocene	Berry	1937a	Forest Reserve, Fyzabad	leaves
Trinidad	Mio-Pliocene	Berry	1937b	Mud Plant Forest Reserve	leaves

Appendix 1. Continued.

Country	Geological age	Author(s)	Date of publication	Local place name	Organs studied
Venezuela	Quaternary	Leyden	1985	Lake Valencia	pollen
Venezuela	Holocene	Rinaldi et al.	1990	Gran Sabana	pollen
Venezuela	Holocene	Rull	1987	Venezuelan Andes	pollen
Venezuela	Holocene	Rull	1991	Guaiquinima, Chimanta & Auyan	pollen
Venezuela	Holocene	Rull	1992	Gran Sabana	pollen
Venezuela	Holocene	Rull	1996a	Pantepui Province	pollen
Venezuela	Pleistocene-Recent	Rull	1996b	Lake Valencia	pollen
Venezuela	Pleistocene	Rull	1998b	Mesa de Caballo	pollen
Venezuela	Holocene	Rull & Vegas-Vilarrubia	1993	Carinapay	pollen
Venezuela	Holocene	Rull et al.	1987	Piedras Blancas	pollen
Venezuela	Pleistocene	Salgado-Labouriau	1987	Piedras Blancas	pollen
Venezuela	Quaternary	Salgado-Labouriau	1991	Merida Andes	pollen
Venezuela	Pleistocene	Schubert & Rull	1988	Auyan tepui	pollen
Venezuela	Miocene	Berry	1920b	near Lake Maracaibo	seed
Venezuela	Miocene	Berry	1921c	Trujillo	leaves
Venezuela	Miocene	Berry	1937c	Falcon	leaves & fruit
Venezuela	Pliocene?	Berry	1939b	Anzoategui	leaves
Venezuela	Miocene	Hambalek et al.	1994	Urumaco trough	pollen
Venezuela	Miocene	Hoffman	1931	Betijoque	leaves
Venezuela	Eocene and Miocene	Berry	1936a	Trujillo; Zulia; Falcon;	leaves
Venezuela	Eocene	Berry	1939b	Maracaibo Basin	leaves
Venezuela	Eocene	Colmenares & Teran	1993	Maracaibo Basin	pollen
Venezuela	Eocene	De Di Giacomo & Van Erve	1987	Falcon	pollen
Venezuela	Eocene	Norem	1955	Maracaibo Basin	pollen
Venezuela	Eocene	Rull	1998a	Misoa Formation	pollen
West Indies	Miocene	Hollick	1924	all islands of the West Indies mentioned separately	leaves

Appendix 2. Comparison of principal palynomorphs from Quaternary deposits in southern Central America and northern South America. Numbers refer to the following references: 1 = Bartlett & Barghoorn, 1973; 2 = Bush & Colinvaux, 1988; 3 = Bush & Colinvaux, 1990; 4 = Bush et al., 1990; 5 = Colinvaux, 1996; 6 = Hooghiemstra, 1984 (table 2); 7 = Hooghiemstra et al., 1992; 8 = Hooghiemstra & van der Hammen, 1993; 9 = Horn, 1985; 10 = Liu & Colinvaux, 1988; 11 = Martin, 1961; 12 = van der Hammen & Absy, 1994. Cheno-Am = Chenopodiaceae-Amaranthaceae undifferentiated; ERA = Euphorbiaceae-Rutaceae-Anacardiaceae undifferentiated. Taxa are presented in the following order: ferns and fern allies, gymnosperms, monocots, and dicots.

Taxon	Lowland Central America	Upland Central America	Lowland South America	Upland South America
Acrostichum 1	x			
Cnemidaria 1, 7, 9	x	x		
Ctenitis 1	x			
Cyatheaceae: *Cyathea* 1, 3, 6, 7, 8, 9, 11	x	x	x	x
Danaea-type 1	x			
Elaphoglossum 7		x		
Hymenophyllaceae: *Hymenophyllum* 7, 9	x	x		
Isöetes 7, 8, 11, 12		x	x	x
Jamesonia 7		x		
Lophosoria 7		x		
Lycopodium 1, 7, 8, 11	x	x		x
Monolete fern spore 1, 3, 4, 7, 8, 9, 10, 12	x	x	x	x
Ophioglossaceae 7, 9	x	x		
Pteris 9	x			
Trilete fern spore 1, 4, 5, 8, 9, 10, 12	x		x	x
Selaginella 1	x			
Araucaria 5			x	
Pinus 9	x			
Podocarpus 1, 4, 5, 6, 7, 8, 9, 10, 11, 12	x	x	x	x
Cyperaceae 1, 2, 3, 4, 5, 7, 8, 9, 10, 11, 12	x	x	x	x
Eichhornia 12			x	
Eriocaulaceae 7		x		
Gramineae 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12	x	x	x	x
Iriartea 1	x		x	
Iriartea-type 9	x			
Liliaceae 9	x		x	
Mauritia 5, 10, 12			x	
Palmae 2, 4, 5, 7, 9, 10, 12	x	x	x	
Phytelephas 1	x			
Potomogeton 8				x
Sagittaria 12			x	
Typha 1, 3, 7, 9	x	x		
Abutilon-type 9	x			
Acalypha 1, 2, 6, 7, 8, 9, 10, 12	x	x	x	x
Alchornea 1, 2, 4, 5, 6, 7, 8, 9, 10, 12	x	x	x	x
Alnus 1, 4, 5, 6, 7, 8, 9, 11	x	x	x	x
Alfaroa/*Oreomunnea* 7, 9, 11	x	x		
Alternanthera 3, 5, 9	x		x	
Ambrosia-type 10			x	
Anacardiaceae 1, 8, 9	x			x
Anacardium-type 9	x			
Annonaceae 1	x			
Antidaphne 7		x		
Apeiba 1, 9	x			
Aphelandra 1, 9	x			
Apocynaceae 1, 12	x		x	

Appendix 2. Continued.

Taxon	Lowland Central America	Upland Central America	Lowland South America	Upland South America
Avicennia 1, 9	x			
Bauhinia emarginata 1	x			
Billia colombiana 6, 8				x
Bocconia 6, 8				x
Bombacaceae: *Bombacopsis* 1, 12	x		x	
Borreria 1, 8	x			x
Bravaisia 9	x			
Brunellia 6, 8				x
Byttneria 1	x			
Bursera 1, 5, 9	x		x	
Byrsonima 1, 3, 5, 9, 10	x		x	
Calliandra 1	x			
Canavalia 1	x			
Cardiospermum 9	x			
Caryophyllaceae 5, 7, 8, 9	x	x	x	x
Cassipourea 1	x			
Catopsis 1	x			
Cavanillesia 1	x			
Cecropia 3, 5, 6, 7, 8, 9, 10, 12	x	x	x	x
Celtis 2, 9, 10, 12	x		x	
Cestrum 6				x
Cheno-Am 1, 3, 8, 9, 10	x		x	x
Cissus 1	x			
Clethra 6				x
Clusia C.-type 7, 8		x		x
Coccoloba-type 1	x			
Combretaceae-Melastomataceae 3, 9	x			
Combretum 1	x			
Compositae 1, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12	x	x	x	x
Compsoneura 1	x			
Conocarpus 1	x			
Copaifera 1, 5	x		x	
Cordia 6, 9, *C. alliodora* 1	x			x
Coriaria 8				x
Couroupita 1	x			
Croton: Crotonoideae 1, 7, 8, 9	x	x		x
Cruciferae 7, 8		x		x
Cupania 1	x			
Cuphea 12			x	
Curatella 12			x	
Daphnopsis 6, 7		x		x
Dialyanthera 1	x			
Didymopanax 2, 7, 10, 12		x	x	
Dodonaea 6, 7, 8		x		x
Dorstenia 9	x			
Drepanocarpus lunatus-type 1	x			
Drimys 6, 7, 8, 9, 11	x	x		x
ERA 9, 10, 12	x		x	
Ericaceae 1, 4, 5, 6, 7, 8, 9, 11	x	x	x	x
Erythrina 1	x			
Escallonia 7		x		
Eugenia 9	x			

Appendix 2. Continued.

Taxon	Lowland Central America	Upland Central America	Lowland South America	Upland South America
Euphorbia 8				x
Ficus 2, 9, 10, 12	x		x	
Faramea 1	x			
Fuchsia 7, 8		x		x
Gaiadendron 6, 7, 8		x		x
Galium 8				x
Gentianaceae 7		x		
Geranium 7, 8		x		x
cf. *Glycydendrum* 1	x			
G. amazonicum 1	x			
Gomphrena 9	x			
Guazuma 9	x			
Gunnera 7		x		
Gryanthera darienensis-type 1	x			
Hedyosmum 1, 3, 4, 5, 6, 7, 8, 9, 12	x	x	x	x
Heliocarpus 6, 7, 8		x		x
Hesperomeles 6, 7		x		x
Hibiscus 9	x			
Hieronyma 1, 6, 7, 8, 10	x	x	x	x
Hippocratea volubilis 1	x			
Humiria 5			x	
Hura 3, 5	x		x	
Hydrangea 1	x			
Hydrocotyle 8				x
Hydrophila 9	x			
Hypericum 6, 7, 8		x		x
Ilex 1, 4, 5, 6, 7, 8, 9, 12	x	x	x	x
Ipomoea 1	x			
Juglans 6, 8, 9	x			x
Jussiaea 1	x			
Justicia 1	x			
Labiateae 8, 12			x	x
Lafoensia 1	x			
Laguncularia 9	x			
Lecythidaceae-*Eschweilera* 5			x	
Leguminosae 2, 4, 5, 8, 10			x	x
Caesalpinioideae 5			x	
Mimosoideae 1, 9, 10	x		x	
Leucaena multicapitula 1	x			
Licania arborea 1	x			
Limnocharis 3	x			
Liquidambar 9	x			
Liriosma 1	x			
Loranthaceae 7, 12		x	x	
Luehea 1, 9	x			
Lysipomia 7		x		
Lythraceae 8				x
Mabea 1	x			
Machaerium-Dalbergia 5			x	
Malouetia 1	x			
Malpighiaceae 1, 8, 9, 10, 12	x		x	x

Appendix 2. Continued.

Taxon	Lowland Central America	Upland Central America	Lowland South America	Upland South America
Malvaceae 1, 8, 9	x			x
Manihot 1	x			
Maripa 1	x			
Melastomataceae-Combretaceae 1, 2, 4, 5, 6, 7, 8, 10	x	x	x	x
Meliaceae-Sapotaceae 1, 3, 5, 9, 12	x		x	
Mendoncia 1	x			
Menispermaceae 1	x			
Merremia 1	x			
Miconia 6, 8, 12			x	x
Montia 7		x		
Moraceae, Urticaceae, Urticales 1, 2, 3, 4, 5, 6, 7, 8, 9, 10	x	x	x	x
Mortoniodendron 9	x			
Mucuna 1	x			
Mollugo 1	x			
Myrica 1, 3, 5, 6, 7, 8	x	x	x	x
Myriophyllum 8				x
Myrrhiodendron-Niphogenton 7		x		
Myrtaceae 1, 3, 4, 5, 6, 7, 12	x	x	x	x
Ochroma 1	x			
Oreopanax 7		x		
Oryctanthus 1	x			
Ouratea O. guatemalensis 1, 12	x		x	
Onagraceae 9	x			
Pachira 1	x			
Pacouria 1	x			
Paullinia 1	x			
Panopsis 8				x
Pelliceria 9	x			
Phyllanthus 1	x			
Pilea P. trema 2, 5, 6, 8			x	x
Piper 9, 10	x		x	
Piperaceae 1, 2, 4, 5, 7	x	x	x	
Plantago 7, 8, 9	x	x		x
Polygalaceae 1, 6, 8, 12	x		x	x
Polygonum 1, 7, 8, 9	x	x		x
Polylepis-Acaena 6, 8				x
Pontederiaceae 1	x			
Portulacaceae 1, 8	x			x
Proteaceae 4, 5, 6			x	x
Pseudobombax 1	x			
Psidium 9	x			
Pterocarpus-type 1	x			
Puya 7		x		
Quararibea 1	x			
Quassia 1	x			
Quercus 3, 5, 6, 7, 8, 9, 11	x	x	x	x
Randia 1	x			
Ranunculaceae 7, 8, 12		x	x	x
Rapanea R.-type 5, 6, 7, 8, 9	x	x	x	x
Rauwolfia 1	x			
Relbunium 8				x
Rhizophora 1, 9	x			

Appendix 2. Continued.

Taxon	Lowland Central America	Upland Central America	Lowland South America	Upland South America
Rosaceae 9, 10	x		x	
Rubiaceae 1, 7, 12	x	x	x	
Rumex costaricensis 7		x		
Salix-S.-type 7, 9	x	x		
Sapium 1, 2, 7, 8, 12	x	x	x	x
S.-type 1, 9	x			
Sapotaceae 5			x	
Scrophulariaceae 8				x
Sechium edule-type 1	x			
Solanaceae 7, 8, 10, 12		x	x	x
Spondias-type 9	x			
Styloceras 6, 8				x
Swartzia panamensis-type 1	x			
Symphonia 1, 4, 5, 9, 12	x		x	
Symplocos Symplocaceae 1, 5, 6, 8	x		x	x
Tabernaemontana 1	x			
Tetracera 1	x			
Thalictrum T.-type 8, 9	x			x
Tiliaceae 4, 5			x	
Tournefortia 9	x			
Trema 2, 5, 9, 10	x		x	
Trichanthera 1	x			
Tristicha 1	x			
Ulmus 7, 9	x	x		
Umbelliferae 9, 10, 11	x	x	x	
Utricularia 1	x			
Valeriana 7		x		
Vallea 6				x
Viburnum 6, 7, 8		x	x	x
Virola 1, 9	x			
Vochysia 1	x			
Weinmannia W.-type 4, 5, 6, 7, 8, 9, 10, 12	x	x	x	x
Zanthoxylum 1, 9	x			
Zea 1, 2, 10	x		x	

THE ORIGIN OF GRASS-DOMINATED ECOSYSTEMS[1]

Bonnie F. Jacobs[2], *John D. Kingston*[3], *and Louis L. Jacobs*[2]

ABSTRACT

Approximately one-third of the Earth's vegetative cover comprises savannas, grasslands, and other grass-dominated ecosystems. Paleobotanical, paleofaunal, and stable carbon isotope records suggest five major phases in the origin of grass-dominated ecosystems: (1) the late Maastrichtian (or Paleocene) origin of Poaceae; (2) the opening of Paleocene and Eocene forested environments in the early to middle Tertiary; (3) an increase in the abundance of C_3 grasses during the middle Tertiary; (4) the origin of C_4 grasses in the middle Miocene; and (5) the spread of C_4 grass-dominated ecosystems at the expense of C_3 vegetation in the late Miocene. Grasses are known from all continents except Antarctica between the early Paleocene and middle Eocene. Herbivore morphology indicative of grazing, and therefore suggestive of grass-dominated ecosystems, appears in South America by the Eocene-Oligocene boundary, prior to the occurrence of grazing morphology elsewhere, and persists throughout the Cenozoic. Clear vertebrate and paleobotanical evidence of widespread grass-dominated ecosystems in northern continents does not occur until the early to middle Miocene. C_4 grasses are present from approximately 15 Ma and undergo a dramatic expansion in the lower latitudes of North America, South America, East Africa, and Pakistan between 9 and 4 Ma. The expansion may have taken place in a shorter interval in some regions. C_4 grasses are characteristic of seasonal, arid, and warm environments and are more tolerant of lower atmospheric CO_2 (< 400 ppmv) than C_3 plants. C_4 grass distribution, therefore, is climatically controlled. The late Miocene spread of C_4 grasses possibly involved a decrease in atmospheric CO_2 and heralded the establishment of modern seasonality and rainfall patterns.

Grass-dominated ecosystems, savannas and natural grasslands, comprise about one-third of the Earth's vegetative cover (Fig. 1, Shantz, 1954). In addition, grasslands and savannas are highly productive, supporting vast numbers of mammalian herbivores and an associated fauna. Humans depend upon domesticated grasses, especially corn, wheat, and rice, to support a burgeoning world population through direct consumption of grain and through animal husbandry built upon grasses. As a consequence, extensive areas of once natural grasslands and savannas have been converted to agricultural uses. It follows that ecological study of natural grasslands and savannas is essential not only for their management and conservation, but also because of their relevance to agriculture. Paleoecology provides a framework for understanding the original development of grass-dominated ecosystems, the basis of their plant-animal interactions, and their role in human evolution. Moreover, because the modern distribution of grassland and savanna biomes is correlated with specific climatic parameters, their origins are linked to global climate evolution.

Our purpose is to address the origin of grass-dominated ecosystems by reviewing evidence from the paleobotanical, vertebrate paleontological, and stable carbon isotope records. It is meant to provide an adequate and reasonably thorough, but not exhaustive, coverage of the literature pertaining to each continental region with a focus on those geographic areas that are most informative with respect to the fossil or isotope records. We aim to answer the following questions: When do grass-dominated ecosystems first appear on each of the continents studied? Is the first appearance of grass-dominated ecosystems synchronous worldwide? Do the paleobotanical, paleofaunal, and stable carbon isotope data yield concordant evidence with respect to the origin of grass-dominated ecosystems for specific time intervals and regions?

There are a variety of grass-dominated ecosystems. Savannas are tropical and subtropical grass-dominated landscapes with varying densities of

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trees and shrubs. Density of the woody component and species composition are sensitive to a complex of factors including climate, soil, and disturbances such as fires, human land use practices, and grazing pressure (Pratt et al., 1966; Bourlière & Hadley, 1983; Cole, 1986; Morell, 1997). Savannas exhibit a range of physiognomic forms such as grass savanna (in which trees and shrubs are absent), bushland and thicket, shrubland, tree savanna, and wooded savanna (Boughey, 1957; White, 1983). Menaut (1983), based on work in Africa, recognized a more inclusive savanna biome, restricted to the tropics and subtropics, but within which are found all variants between desert and forest. For the purposes of this paper, the most important part of any definition of savanna is the key phrase, "grass-dominated." Savannas are found today where precipitation is seasonal, if not monsoonal. Rainfall varies widely from as little as 500 mm/year over one to two months, to as much as 1500 mm/year with a short dry season (Bourlière & Hadley, 1983).

Temperate grasslands, as opposed to savannas, are found in middle latitudes or at upper elevations where precipitation is too scant to support tree growth, but greater than that resulting in deserts (Ripley, 1992). As with savannas, grassland climates are seasonal and have a wide range in mean annual precipitation, between about 500 and 1500 mm/year (Ripley, 1992). Typically, temperate grasslands are nearly continuous expanses of grasses and sedges without trees, but including small shrubs and varying amounts of herbaceous dicots (Coupland, 1992a). However, similar to savannas, grasslands vary in species composition and physiognomy depending on variations in climate, soil, topography, and land use. For example, in cold, dry, continental interiors, grass and shrubs form the grassland variant known as steppe.

Traditionally, the primary means of recognizing and evaluating grass-dominated ecosystems in the paleontological past was through the interpretation of the mode of life of fossil vertebrates. The evolution of horses has played a central and deserved role in interpreting the origin of grass-dominated ecosystems because of the high-crowned teeth characteristic of Miocene and later members of the horse family Equidae, the grazing habits of the living species, their dispersal history, and the high quality of their fossil record (e.g., Kowalevsky, 1873; Osborn, 1910; and many good reviews of the subject including Simpson, 1951, 1953; Webb, 1977; MacFadden, 1992). Improvements in the paleobotanical record (both macrofossil and pollen) provide a more direct route to plant communities of the past (Elias, 1942; Thomasson, 1979; Morley & Richards, 1993). A third approach is the assessment of stable carbon isotopes in fossil material such as herbivore enamel and in paleosol components that yield information on the photosynthetic pathways of vegetation in ancient ecosystems (Cerling, 1984; Quade et al., 1989a; Kingston et al., 1994; Morgan et al., 1994). Together these disciplines provide a robust means of evaluating the origin of grass-dominated ecosystems.

The continents of North America, Eurasia, South America, Africa, and Australia are reviewed for relevant paleontological and stable carbon isotope data. The record starts in each region with the earliest documented occurrence of grass, which provides a maximum potential age for the origin of grass-dominated ecosystems for that particular region. We use published age estimates. If improvements in an age assignment have been made, we use the revised estimate as indicated in our text.

Consideration must be given separately to the strengths and weaknesses in the quality of the paleobotanical, paleofaunal, and isotopic records, and to the individual development of these lines of evidence on each continent. First we will address aspects of the paleobotanical, paleofaunal, and isotopic records that relate to grasses in terrestrial biomes; then we will review the records for each continent beginning with a summary of all three lines of evidence for each region.

THE PALEOBOTANICAL RECORD

Grass pollen is much more common in the Tertiary paleobotanical record than grass macrofossils. Grasses are primarily wind pollinated, and therefore they produce copious amounts of pollen that can be carried long distances by wind and water, as evidenced by grass pollen in marine cores. Pollen provides a regional view of vegetation. Unfortunately, grass pollen is fairly uniform throughout the family precluding identification at lower taxonomic levels.

Maastrichtian and early Tertiary grass pollen is identified as the form taxon, *Monoporites annulatus* van der Hammen (= *Graminidites* I. C. Cookson ex R. Potonié). The botanical name describes the single pore surrounded by a thickening, or annulus, that characterizes the pollen in all species of the grass family. However, the five or six other small families in the order Poales (Linder, 1986) also have a single pore, some with an annulus (Linder & Ferguson, 1985). Although the presence of fine channels in the pollen wall and absence of scrobiculae (minute pits in the wall) distinguish grass pollen, the fine channels can only be seen with

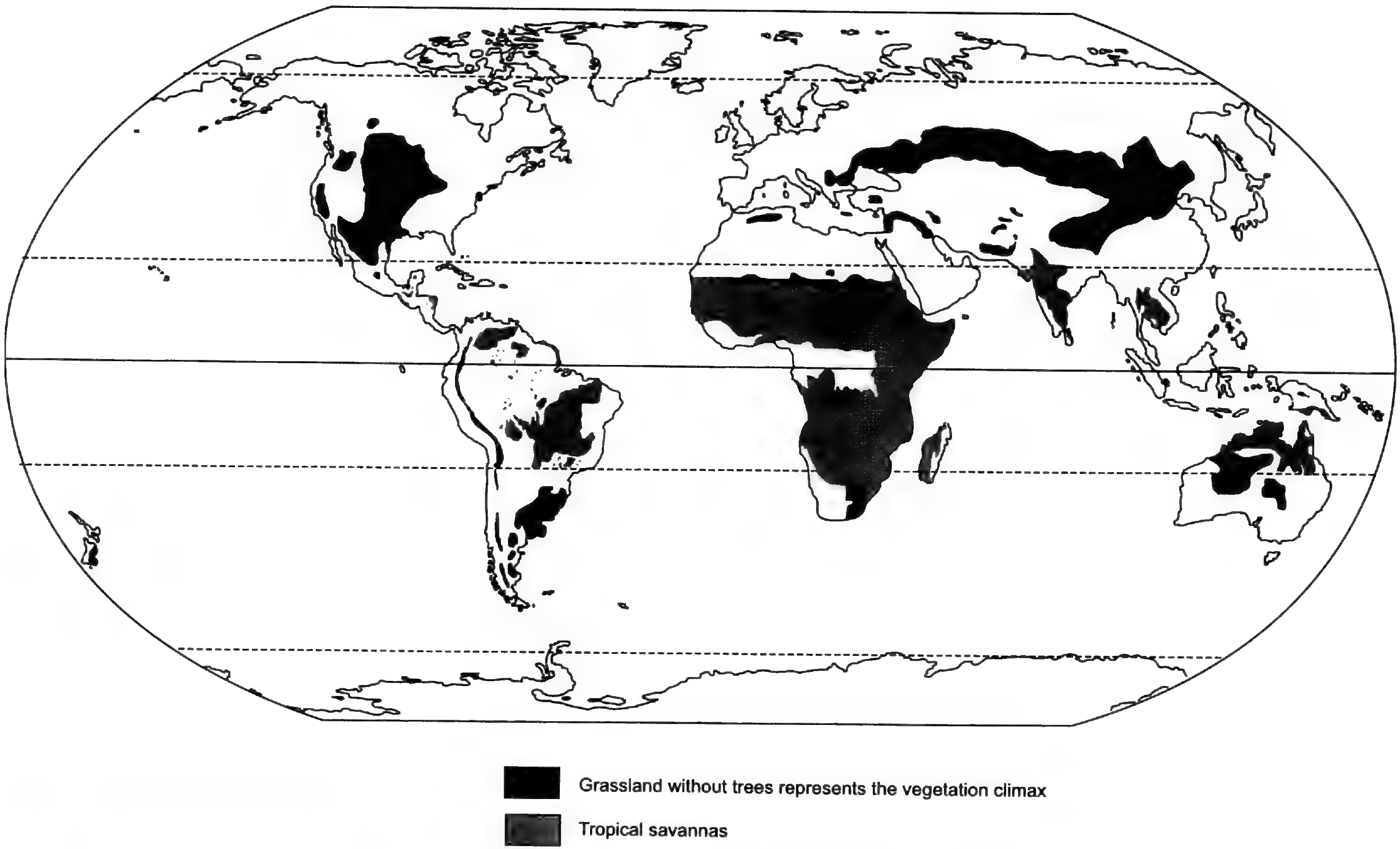

Figure 1. Modern distribution of grass-dominated ecosystems. Redrawn from Bourlière & Hadley (1983) and Coupland (1992d).

transmission electron microscopy, a technique not used routinely in pollen identification. Thus, the reevaluation and recognition of scrobiculae in some Maastrichtian and Paleocene pollen grains that originally were identified as *Monoporites annulatus* led to their reassignment to families other than Poaceae. This calls into question other early grass pollen identifications that have not been similarly re-evaluated (Muller, 1981; Linder, 1986). Nevertheless, Linder (1986) accepted at least some of the Maastrichtian identifications of *Monoporites annulatus* from Egypt as valid (Kedves, 1971), and more recent studies in northern South America document frequent occurrence (no quantitative data supplied) of *Monoporites annulatus* in the early Paleocene (Muller et al., 1987). Undoubted grass macrofossils occur in the early Eocene Claiborne Formation of Tennessee (Crepet & Feldman, 1991; Crepet & Herendeen, 1992), although no further age refinement was supplied, confirming the presence of Poaceae by at least the early Tertiary. The grass pollen record is well established with the consistent occurrence of *Monoporites annulatus* after the middle to late Eocene, especially in tropical regions (see discussions for South America and Africa below).

Palynological publications reviewed here report abundance data either categorically (rare, frequent, or common), as relative percentages, or simply as present or absent. If no paleoenvironmental interpretation is provided by the author(s), where possible the record is interpreted here. Leopold et al. (1992) compiled data from studies of grass pollen in modern soils to serve as a coarse guide to the paleoenvironmental significance of fossil grass pollen percentages. Grass pollen percentages from modern soils of steppe, grassland, and savanna environments vary widely: from 1% to 25% in Wyoming steppe, to 20% to 55% in Ethiopian savanna. To make the most reasonable interpretation of fossil pollen assemblages, the abundance and composition of associated non-grass pollen taxa are also considered.

Grass phytoliths are the opaline silica remains of silica cells (silica bodies) deposited mainly in the leaf epidermis. Silica bodies vary in shape, even on the same leaf, but generally grass subfamilies are recognized as having characteristic silica bodies. Consequently, phytoliths found in ancient soils may document past changes in grass composition at the subfamily level (Fredlund & Tieszen, 1997).

Grass macrofossils provide greater taxonomic resolution than pollen because of taxonomically diagnostic characters that facilitate broad comparisons and phylogenetic studies. Grass leaves are not shed but remain on the plant, even after death. Therefore, grass leaves in non-aquatic settings are not likely to become part of the sedimentary record. Grass reproductive structures are often adapted for dispersal by wind or animals, separating readily from the parent plant, and more commonly enter the fossil record. North America has a unique and spectacular record of fossil grass reproductive parts replaced by silica and calcium carbonate (Thomasson, 1990), as opposed to the poor record of leaves.

THE PALEOFAUNAL RECORD

Mammals are a diverse group of species with a wide range of morphological and behavioral adaptations (Eisenberg, 1981). Herbivorous mammals play a fundamental role in the recycling of nutrients in the ecosystem by processing food through their digestive systems, by becoming prey, by trampling vegetation into the soil, or by other behaviors (McNaughton et al., 1988). They are major influences on plant and ecosystem physiognomy, as is readily observed by the destruction of trees by elephants in Africa (McNaughton et al., 1988; Dublin, 1995), for example, or less apparently by the actions of small mammal herbivores, such as the pruning of picturesque junipers by packrats in the American Southwest (Vaughan, 1980). Coevolutionary relationships between herbivores and plants are reflected by adaptations for processing and digesting vegetation exhibited by herbivores and the attributes of plants that limit their digestibility or palatability (McNaughton et al., 1985; Vicari & Bazely, 1993; Seldal et al., 1994; Karban & Baldwin, 1997). In short, herbivores help to create the environment in which they live.

The most directly relevant mammalian herbivores for recognizing grass-dominated ecosystems based on morphological adaptations are derived ungulates, a large suite of hoofed mammals that includes equids. Derived ungulates have limbs modified such that the body weight is borne by the last joints of the digits, the ungual phalanges. The most useful ungulate groups are the perissodactyls (most notably horses, rhinoceroses, and their relatives) and the ruminant artiodactyls (Janis & Scott, 1987), which in the modern fauna include mouse deer or chevrotains (Tragulidae), giraffe and okapi (Giraffidae), musk deer (Moschidae), deer and muntjacs (Cervidae), pronghorn (Antilocapridae), and cattle, antelope, bison, duikers, and goats (Bovidae). The role of ungulates in South America throughout the Tertiary was filled by endemic groups, e.g., notoungulates. The mammalian herbivore fauna of Australia was effectively comprised of marsupials, such as kangaroos, during the Tertiary.

The interpretation of past grass-dominated ecosystems relies most heavily on ungulates because they rely directly on plants for food, they exhibit recognizable adaptations associated with diet, they have an abundant fossil record, and their utility has been more thoroughly tested than in other groups. Their long legs are suited for running, an adaptation for life in open environments. Living ungulates provide models for interpreting the ecology of more obscure, extinct ungulate groups, such as the unfamiliar herbivores characteristic of the South American Tertiary (MacFadden, 1997).

Mammalian carnivores may provide additional indications of habitat, such as cursorial adaptations associated with the pursuit of fleet prey species inhabiting open country (Hunt & Solounias, 1991; Van Valkenburgh, 1985; Van Valkenburgh & Janis, 1993; Werdelin & Solounias, 1996). Among nonmammalian groups, snakes, for example, which are cold-blooded predators, have a fossil record that seems to parallel the achievement of grass-dominated ecosystems in North America (Parmley & Holman, 1995). This link presumably reflects the complex ecological connections among evolving climate, changing habitat, and the adaptations of their prey, which consists in large part of small mammal herbivores (rodents). None of these groups, however, has the demonstrably close link to grass and grass-dominated ecosystems exhibited by ungulates.

Recently, the study of ungulate paleoecology has been revitalized, providing a theoretical and quantitative basis for evaluating the feeding strategies of extinct herbivores (see review by Janis, 1995). Grazers are defined as herbivores whose year-round diets comprise 90% grass; browsers consume less than 10% grass; and mixed-feeders fall somewhere in between. These appear to be realistic categories defined by observation of extant ungulates and correlated with stomach anatomy (Hofmann & Stewart, 1972; Hofmann, 1973). Recognition of these dietary categories in the fossil record is based primarily on anatomical features of the teeth, premaxilla, and maxilla, and on microwear patterns in tooth enamel caused by abrasion during the chewing of food (Walker et al., 1978; Janis & Ehrhardt, 1988; Solounias et al., 1995b).

Grazers usually have teeth with high crowns, providing long-wearing ridges of enamel for the mastication of fibrous and tough food. Such high-crowned or rootless and ever-growing (hypsodont or hypselodont) teeth are relatively common among mammalian taxa, occurring in about half of the 34 orders, in species of a variety of body sizes, and with a wide range of diets (White, 1959; Janis & Fortelius, 1988). Janis (1988) determined that the amount of grit or other abrasive material ingested with food is the most important factor in predicting hypsodonty in ungulates, and thus explained why hypsodonty is not limited to grazers, as for example in the pronghorn or the Miocene stenomyline camels. It is conceivable but not proven that grass and grazing may play coevolutionary roles in the development of hypsodonty with grass responding to cropping by increasing the amount of silica (McNaughton & Tarrants, 1983; McNaughton et al., 1985; Vicari & Bazely, 1993; Karban & Baldwin, 1997), which, in turn, may select for high-crowned teeth in grazers (Van Valen, 1960; Janis & Fortelius, 1988).

Uncertainty of the significance for grazing of high-crowned teeth in individual cases is minimized when other morphological features of the species are taken into account. Grazers have square, straight premaxillae and broad muzzles; browsers have narrow muzzles; mixed-feeders fall in between (Janis & Ehrhardt, 1988; Solounias & Moelleken, 1993a, b; Dompierre & Churcher, 1996). In addition, grazers have relatively larger masseteric chewing musculature than mixed-feeders and browsers, which can be ascertained from the morphology of the jaw (Solounias et al., 1995b). Furthermore, diets can be evaluated by scanning electron microscopy of wear surfaces on teeth, grazing leaving a quantifiably different pattern of microwear on teeth compared to browsing, and mixed-feeders having elements of both patterns (e.g., Solounias et al., 1988). However, "the Last Supper Syndrome," in which rapid wear betrays previous microwear patterns, leaving only a reflection of the most recent meals, may well introduce a bias if the final meals of an animal do not accurately reflect the food preferences or normal diet of the species (Solounias et al., 1994).

As with ungulates, the skeletal and dental adaptations of small mammals are of use in interpreting open and grassland environments. The high-crowned dentition of voles and their African ecological counterparts, the groove-toothed rats, allows for mastication of fibrous, relatively low-nutrition food (Rensberger, 1973, 1975, 1978; Butler, 1980). In contrast, modern beavers have high-crowned teeth, but they also have a diet of bark with no relevance for the origin of grass-dominated ecosystems. The situation is less clear when Miocene beavers, some of which burrowed, are taken into account (Korth, 1994). Rodents and other small mammals may exhibit other adaptive features, such as ricochetal locomotion, that are reflected in the skeleton and are indicative of open environments (Lyon, 1901; Hatt, 1932; Howell, 1932). The bipedal adaptations in jerboas, the most extremely adapted ricochetal rodents, have developed to the extent that the fused foot bones (metatarsus) are convergent with the tarsometatarsus of birds (Rich, 1973). Size is correlated with many facets of the natural history of a species, including home range (McNab, 1963; Western, 1979), which is much smaller for a rodent than for a long-legged ungulate, and the area required for foraging is less. Therefore, information regarding the distribution of open habitats provided by large versus small mammals may not be comparable in scale.

Given that the adaptations of individual species reflect habitat, then the suite of mammalian species found in a region and the resulting community structure should provide a more robust reflection of the environment than the adaptations of any particular species alone. Thus, by comparison with modern assemblages from known habitats, a fossil assemblage can be used to evaluate ecosystems and the roles of the component species of the past (Andrews & Van Couvering, 1975; Andrews et al., 1997). The pattern of changing species composition within assemblages over time should reflect changing environmental parameters or other factors that affect species distribution (Barry et al., 1985; Janis, 1984, 1988, 1993; Legendre, 1987), demonstrating open versus closed habitats, or a preponderance of grazers versus browsers and mixed-feeders. Grass-dominated ecosystems containing trees and shrubs support a more diverse fauna than pure grasslands because browsers and mixed-feeders are included in the community (Bourlière, 1963).

The paleofaunal record can be compared to the plant fossil record to discern patterns of coevolution assessed by coincident changes in both records that appear ecologically correlated. Examples include the evolutionary relationship between large nuts and rodents, or primates and fleshy fruits, both appearing in the early Tertiary (Collinson & Hooker, 1987, 1991; see also Wing & Tiffney, 1987), or between grass fossils and mammals as is reviewed here. More direct evidence of herbivore diet, and therefore indications of the relative importance of grass to a species, is obtained by analysis of the animal, as discussed above, or by the ratio of stable isotopes in fossils (e.g., Koch et al., 1994, 1995; Morgan et al., 1994; MacFadden, 1998; MacFadden & Cerling, 1996; MacFadden & Shockey, 1997), as discussed below.

THE ISOTOPIC RECORD

Recognition and characterization of biogeochemical cycles that mediate distribution of light stable isotopes (C, O, H, and N) in terrestrial ecosystems have contributed substantially to reconstructions of past environments. The relative abundance of two naturally occurring stable isotopes of carbon (^{12}C and ^{13}C) in fossils and paleosols has proved particularly useful in reconstructing aspects of the vegetation. The premise underlying this approach is that the tissue of plants utilizing alternative photosynthetic pathways can be differentiated on the basis of the ratio of ^{13}C /^{12}C. This isotopic signature can be retrieved from the fossil record, either by direct analysis of ancient organic residues or from inorganic material that formed in isotopic equilibrium with the paleovegetation.

Terrestrial plants assimilate carbon from the atmospheric CO_2 reservoir by one of three photosynthetic pathways. These pathways, referred to as C_3 (Calvin-Benson), C_4 (Hatch-Slack or Kranz), and CAM (Crassulacean Acid Metabolism), represent adaptations to variable atmospheric and climatic conditions. In all three pathways, during the first stage of photosynthesis (carboxylation), carbon incorporated into the organic plant matrix is significantly depleted in the heavy isotope (^{13}C) relative to atmospheric CO_2 (Craig, 1953; Park & Epstein, 1960; Smith & Epstein, 1971; O'Leary, 1981; Farquhar et al., 1982). This discrimination against ^{13}C (fractionation) is due to small differences in physical and chemical properties imparted by the difference in mass between ^{12}C and ^{13}C. The extent to which fractionation occurs varies significantly depending on the pathway utilized. C_3 plants are most depleted, whereas plants endowed with the C_4 metabolic pathway are least depleted. There is a distinct non-overlapping bimodal distribution of the isotopic composition (denoted as $\delta^{13}C$) of C_3 versus C_4 plants. Plants that fix CO_2 by CAM display intermediate isotope values overlapping the range of both C_3 and C_4 flora (O'Leary, 1988).

C_3 plants dominate terrestrial environments and account for approximately 85% of all plant species, including almost all trees and shrubs as well as high-latitude or high-altitude grasses preferring wet, cool growing seasons. Environmental influences affecting the isotopic composition of C_3 plants include water stress, nutrient availability, light intensity, CO_2 partial pressure, atmospheric $\delta^{13}C$, temperature, and extent of forest canopy (Farquhar et al., 1982; van der Merwe & Medina, 1989; Tieszen, 1991). These environmental factors, coupled with genetic differences, result in substantial stable carbon isotopic variation in C_3 vegetation that should be considered in attempting to document the relative amount of C_3 vegetation in a past ecosystem.

Although C_4 physiology is present in a number of monocots and diverse dicots, the bulk of C_4 global biomass is represented by graminoids, especially grasses growing in hot, arid habitats (Ehleringer et al., 1997). Modern C_4-dominated ecosystems include tropical savannas, temperate grasslands lower than about 37° latitude, and desert scrubland. The C_4 photosynthetic pathway represents a modification of the C_3 mechanism and is considered to have evolved independently at least 26 times among the plant families that have it (Peisker, 1986), at least 5 times within the grass family itself (Renvoize & Clayton, 1992; Sinha & Kellogg, 1996). In C_4 plants, CO_2 is fixed initially in mesophyll cells as a 4-carbon compound that is transported to bundle sheath cells and then enters the C_3 pathway. The internal concentration of CO_2 in the bundle sheath cells is much greater ($>$ 2000 ppmv) than atmospheric CO_2 thereby reducing the loss of C to photorespiration and increasing the overall efficiency of photosynthesis. C_4 plants generally tolerate higher temperatures and solar irradiance, drier conditions, greater seasonality, and lower atmospheric p CO_2 levels than C_3 species. C_4 photosynthesis, however, is energetically more costly (Salisbury & Ross, 1985), and C_4 species are outcompeted by C_3 plants at mean maximum temperatures below 25°C and at higher p CO_2 levels (400 ppmv). In tropical to subtropical regions there is an altitudinal transition from C_4 to C_3 grasses between 2000 and 3000 m (Tieszen et al., 1979). Grasses in closed canopy forests in these regions are C_3 except where the canopy is broken.

Crassulacean acid metabolism (CAM) evolved independently in many succulent plants including the cacti (Cactaceae) and stonecrops (Crassulaceae). CAM plants may fix atmospheric CO_2 via the C_3 pathway or in a time-separated sequence similar to C_4 pathway in which CO_2 is fixed at night (when the temperature and humidity are lower) and is photosynthesized during the day (when light levels are higher). The extent to which each pathway is utilized depends on environmental conditions, resulting in a range of $\delta^{13}C$ values spanning that of C_3 and C_4 plants (O'Leary, 1981; Deines, 1980). Under high light intensity or high temperatures, CAM vegetation has $\delta^{13}C$ values similar to C_4, whereas under environmental conditions of low light intensity and cold temperatures, they exhibit values similar to C_3. The strategy of CAM plant physiology to endure extremely xeric conditions severely limits their ability to take in and fix CO_2, and in general, the net photosynthetic rate is much lower than C_3 or C_4 plants. In modern ecosystems, ungulates specializing on CAM succulents are rare, and we assume this to be the case in the past as well.

As the C_3 and C_4 photosynthetic pathways are associated with different environmental conditions and often plant physiognomy, documenting relative proportions of C_3 and C_4 vegetation by isotopic analyses is a useful tool in paleoenvironmental reconstructions. Specifically, the link between C_4 metabolism and grasses provides a means of identifying grass-dominated plant communities such as open woodlands, savannas, and grasslands. However, the large variety of C_3-dominated habitats, ranging from lowland rainforest to arid bushland to cold-climate grassland, limits the resolving power of a C_3 isotopic signal in reconstructing vegetation. In addition, in adopting a uniform approach, modern ecosystems typically provide the template for interpreting isotopic records of the past. Past habitats may in fact have no modern analogues. An isotopic signal indicating a mixture of C_3 and C_4 species could represent tropical savanna with a significant woody component, a cool temperate prairie with a mixture of C_3 and C_4 grasses, or a tropical grassland with no modern analogue having a mixture of C_3 and C_4 grasses. The possibility of C_3 grass-dominated ecosystems at latitudes dominated by C_4 grasses today may complicate interpretations of past landscapes.

Assuming that CAM plants comprised an insignificant portion of the biomass, the key to using metabolic pathways to interpret paleoenvironment is in retrieving an intact isotopic record reflecting the relative proportion of vegetation using C_3 versus C_4 photosynthetic pathways in the past. There are a number of approaches, including isotopic analyses of: (1) preserved organic plant matter in paleosols (Ambrose & Sikes, 1991; Kingston et al., 1994); (2) organic material within opal phytoliths (Kelly et al., 1991, 1993; Fredlund & Tieszen, 1994, 1997); (3) paleosol carbonates, which formed in equilibrium with local paleovegetation and provide an average isotopic signature of plant biomass during the interval in which the paleosol formed (Cerling & Hay, 1986; Amundson & Lund, 1987; Quade et al., 1989b; Kingston et al., 1994; Sikes, 1994, 1996); (4) carbonate occluded in fossil bone, enamel, or eggshells, which reflects available dietary plants (Lee-Thorp & van der Merwe, 1987; Quade et al., 1992; Morgan et al., 1994; Stern et al., 1994; Cerling et al., 1997b; Johnson et al., 1997); and (5) terrestrial organic carbon in marine sediments (France-Lanord & Derry, 1994; Bird et al., 1995; Gonl et al., 1997). Of these techniques, analyses of fossil herbivore enamel and paleosol components have been most widely applied and are most relevant to the discussion of the origin of grass-dominated ecosystems.

Theoretical models and studies of modern soils have established a correlation between the stable carbon isotopic composition of soil components and prevailing climatic and ecological conditions (Cerling, 1984; Amundson et al., 1989; Quade et al., 1989b). In general, where plant respiration is high, the carbon isotopic composition of soil CO_2, and soil carbonate equilibrating with soil CO_2, are controlled by the proportion of surface vegetation utilizing the C_3 versus C_4 photosynthetic pathway. As soils usually form over hundreds or even thousands of years, they preserve a paleoenvironmental record averaged over an interval spanning many generations of plants.

Soil carbonates typically form in semiarid to subhumid climates (rainfall normally less than 75–85 cm/yr.) at some depth below surface. Pedogenic carbonate generally precipitates in relatively dry soils where net evaporation exceeds precipitation, conditions that are typically associated with grass or mixed grass and shrub-dominated ecosystems. Buried paleosols with associated soil carbonates and organic matter can retain the biogenic isotopic signal of the original soil system. Although soil carbonate nodules can be reworked, where preserved, they are generally not subjected to the taphonomic and sampling filters that can seriously bias representation of the faunal and floral records. Ecosystems commonly associated with surfaces subjected to erosion, such as alluvial fans, may be underrepresented in paleosol studies. Non-calcareous paleosols may be indicative of environmental conditions that inhibit formation or preservation of pedogenic carbonate nodules (e.g., forested habitats with acidic soils, heavy precipitation that leaches carbonates from soil profiles, or lack of Ca in the parent material).

Analysis of the isotopic signature in fossil enamel corroborates analyses of paleosol components documenting relative proportions of C_3 and C_4 vegetation in the past. The carbon isotopic composition of modern herbivore tissue, including tooth enamel, is directly related to the ingested $\delta^{13}C$ value of the primary photosynthesizing plants in the food chain (DeNiro & Epstein, 1978; Tieszen et al., 1983; Ambrose & DeNiro, 1986). The relationship between the carbon isotopic composition of body tissue and diet was initially exploited primarily to address archaeological issues such as the introduction of maize, a C_4 domesticate, into previously C_3-dominated New World agricultural economies (Vogel & van der Merwe, 1977; van der Merwe & Vogel, 1978). Within the last decade, this approach has been extended to fossil assemblages in which the focus of isotopic analysis has shifted from bone collagen and minerals to enamel apatite. Application of isotopic analyses to fossil enamel strictly for paleodietary studies has been limited (e.g., Ericson et al., 1981; Lee-Thorp et al., 1989), and instead its use has been primarily for paleoecological reconstruction (Thackeray et al., 1990; Kingston, 1992; Quade et al., 1992; Wang et al., 1993; Morgan et al., 1994; Quade et al., 1994; Cerling et al., 1997b).

Reconstructions of past habitats based on isotopic analysis of fossil enamel must be carefully interpreted as the paleoenvironment has not been sampled directly but rather through a dietary filter. Specific aspects of feeding behavior are dictated not only by available food items but also by selectivity, competitive exclusion, and migration. Modern giraffes, for example, typically inhabit open biomes dominated by C_4 grasses yet their enamel yields a C_3 isotopic signature. Modern ruminant herbivore species have traditionally been placed in three broad dietary categories: browsers, grazers, and mixed-feeders conveniently associated with C_3, C_4, and mixed C_3/C_4 isotopic signals, respectively. This set of categories is based on the assumption that all available grass is C_4, an unrealistic presumption in the past, or in the present in areas where C_4 plants do not grow (Morgan et al., 1994; MacFadden, 1997).

NORTH AMERICA

SUMMARY

The largest continuous grasslands of North America, the Great Plains, are bounded to the west by the Rocky Mountains, to the east by deciduous or coniferous forest, to the north by coniferous forest, and to the south by the Gulf of Mexico (Fig. 1). More restricted grassland areas include the California prairies, the Palouse prairie of the northwestern U.S. and southern British Columbia, and the desert grasslands of the Sonoran and Chihuahuan deserts in the southwestern U.S. and Mexico (Coupland, 1992b).

The oldest record of grasses in North America is a macrofloral assemblage from the early Eocene of Tennessee (Crepet & Feldman, 1991; Crepet & Herendeen, 1992), but grass pollen and macrofossils are rare throughout the Eocene and Oligocene (Fig. 2). In the early Miocene of the Great Plains

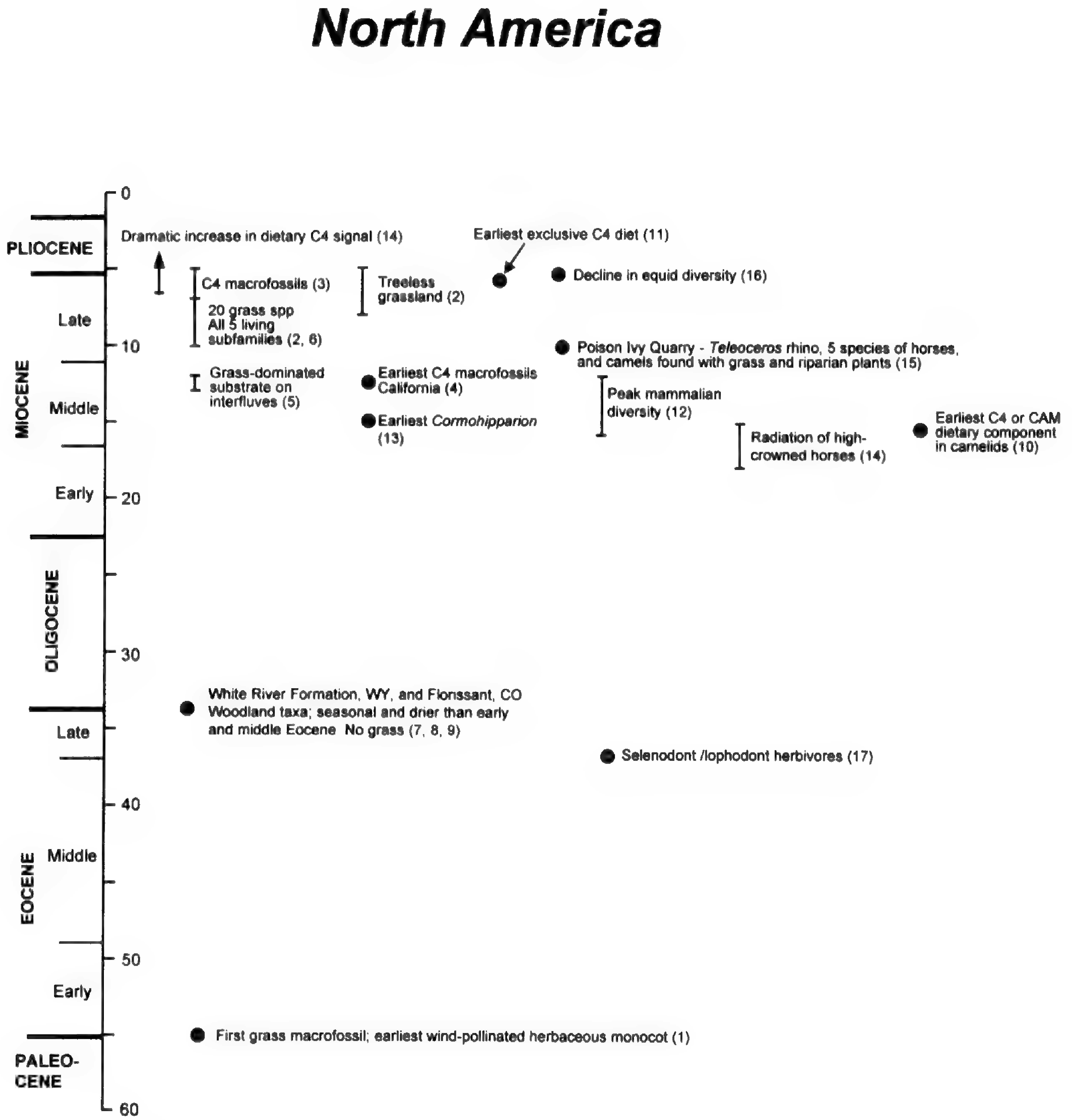
North America

Figure 2. Summary of paleobotanical, paleofaunal, and isotopic evidence for the origin of grass-dominated ecosystems in North America. Solid lines denote the presence of fossil data throughout the time interval shown. Dots indicate data from specific, well-constrained times. Sources: (1) Crepet & Feldman (1991), (2) Thomasson (1990), (3) Thomasson et al. (1986), (4) Nambudiri et al. (1978), (5) MacGinitie (1962), (6) Thomasson et al. (1990), (7) MacGinitie (1953), (8) Leopold & MacGinitie (1972), (9) Leopold et al. (1992), (10) La torre et al. (1997), (11) Cerling et al. (1997b), (12) Webb & Opdyke (1995), (13) Bernor et al. (1996a), (14) MacFadden & Hulbert (1988), (15) Voorhies & Thomasson (1979), (16) MacFadden & Cerling (1994), (17) Jernvall et al. (1996).

region, only one grass species is recognized based on macrofossils (Elias, 1942). Macrofloras document the emergence of grass-dominated environments between 13 and 10 Ma (MacGinitie, 1962; Thomasson, 1990). Relatively treeless grasslands may have been present by 8 Ma (Thomasson, 1990; see also Axelrod, 1985). By 7 Ma grass diversity includes all five living subfamilies (Thomasson, 1990). Leaf anatomical evidence for C_4 photosynthesis is documented by 12.5 Ma (Nambudiri et al., 1978; Whistler & Burbank, 1992).

The adaptive radiation of grazing horses occurs in the Miocene (18 to 15 Ma; MacFadden & Hulbert, 1988). The ungulate community as a whole is diverse in the Miocene; however, from 12 Ma until the end of the Miocene, diversity declines, especially among larger, more specialized browsing forms. After 5 Ma, grazing horse diversity drops precipitously.

The earliest potential evidence for a C_4 dietary component is from 15.6 Ma (Latorre et al., 1997). Mixed C_3/C_4 diets are clearly evident by 7 Ma

(MacFadden & Cerling, 1996), and by 6.8 Ma there appears to be a dramatic increase in the dietary C_4 component of horses in the southern portion of North America (Cerling et al., 1997b). Earliest reports of enamel isotopic values consistent with a pure C_4 diet are at 5.7 Ma from sites in Mexico (Cerling et al., 1997b). The transition from C_3 to predominately C_4 dietary signatures suggests that up until that time the contribution of grass in the ecosystem to diet was mainly from C_3 species. More northerly sites document the presence of C_4 grasses around 4 Ma. However, isotopes do not at any time suggest exclusive reliance on C_4 grasses by equids above 37°N. The extent to which C_4 grasses expand into North American biomes appears to be a function of latitude.

PALEOBOTANY

The earliest known record of Poaceae in North America consists of entire plants, spikelets, and inflorescence fragments from the early Eocene Claiborne Formation of Tennessee (Crepet & Feldman, 1991; Crepet & Herendeen, 1992). However, grass macrofossils and pollen are rare or absent in the other Paleogene deposits where forest or woodland vegetation was prevalent (Dilcher, 1973; Hickey, 1977; Wolfe, 1977; Graham, 1993; Manchester, 1994; Wing et al., 1995; Wing, 1998, and references therein).

Seasonal climates appear by the middle Eocene in western North America and along the Gulf Coast based on pollen and plant macrofossils (Dilcher, 1973; Frederiksen, 1991; Wolfe, 1994; Wing, 1998). However, only 8 of 56 Gulf Coast middle Eocene to early Oligocene pollen assemblages contain (infrequent) grass pollen, indicating the lack of grass dominance even in possible marsh settings (Frederiksen, 1981). In the Rocky Mountain region, the Florissant flora of Colorado ($\approx$ 34 Ma), containing woody xerophytes and riparian taxa, represents open evergreen oak and pine woodlands on slopes leading to riparian settings (MacGinitie, 1953; Leopold et al., 1992). A fossil grass from Florissant, *Stipa florissanti* Knowlton, is not interpreted as indicating a grassland environment (MacGinitie, 1953). Pollen assemblages from Florissant and other middle to late Eocene localities indicate that grasses were absent in woodland understories (Leopold & MacGinitie, 1972; Leopold et al., 1992). A single silicified grass caryopsis (grain with enclosing palea and lemma) is reported from the Cedar Creek Member of the White River Formation, Colorado ($\approx$ 33 Ma, Emry & Russell, 1987; Woodburne & Swisher, 1995), but additional specimens have not been found despite a decade of continued searching (Galbreath, 1974). Pollen samples from the Poison Spring locality in the White River Formation, Wyoming, yielded a pollen assemblage similar to that at Florissant, with which it is approximately equivalent in age. No grass pollen was found in the assemblage (Leopold & MacGinitie, 1972; Leopold et al., 1992). The paleofloral data contradict interpretations based on paleosols indicating wooded grasslands by 34 Ma and open treeless grassland on interfluves by the middle Oligocene (Retallack, 1992; for a discussion of paleoenvironmental interpretations based on soil classification, see Dahms et al., 1998; Retallack, 1998; Dahms & Holliday, 1998).

The Kilgore flora (Cherry County, Nebraska, MacGinitie, 1962) occurs in the Crookston Bridge Member of the Valentine Formation (Skinner & Johnson, 1984), which has yielded mammals indicative of the Barstovian Land Mammal Age (12–13 Ma, Tedford et al., 1987). Most woody taxa assigned to extant genera are riparian (e.g., *Juglans* L., *Fraxinus* L., *Carya* Nutt., *Nyssa* L., *Acer* L., and *Alnus* Mill.). Others such as *Quercus* L. and *Pinus* L. prefer drier substrates. These taxa are interpreted as forming a mixed open chaparral on interfluves, with grasses dominating the open areas (MacGinitie, 1962: 84). The pollen flora supplements macrofossil assemblages by providing a record of herbaceous families, such as Poaceae, Chenopodiaceae, Compositae, and Cyperaceae; however, relative pollen percentages are not published (MacGinitie, 1962).

The earliest C_4 grass macrofossil, *Thomlinsonia thomassonii* Tidwell & Nambudiri (1989), is from the Dove Spring Formation in the Ricardo Group of California (Nambudiri et al., 1978) now dated to approximately 12.5 Ma (Whistler & Burbank, 1992). Roots, culms, and leaves, including Kranz anatomy in leaf cross section, are preserved and are characteristic of C_4 grasses. Stable carbon isotope values from the fossils confirm the plants were C_4 photosynthesizers (Nambudiri et al., 1978). However, carbon isotope values for equid tooth enamel from the same locality indicate that the majority of equid diet consisted of C_3 vegetation (Cerling et al., 1998). Fossil wood from this locality is comprised most commonly of *Robinia* L. and a palm, with *Quercus*, *Cupressus* L., and *Pinus* species less common (Webber, 1933). The paleoenvironment reconstructed by Webber (1933) is similar to the grassy woodlands in the lower uplands of the modern Sonoran Desert region, but the amount of grass cover relative to wooded area is indeterminable from the data.

The Miocene record of macrofossils from the Great Plains of North America is unique for the Tertiary in providing information about phylogenetic relationships, species richness, and paleoecology of grasses (Elias, 1942; Thomasson, 1978, 1979, 1987, 1990). Grass taxa are documented by silicified or calcified reproductive parts (e.g., Elias, 1932, 1942; Thomasson, 1979, 1985; Gabel et al., 1998) and leaves preserving micromorphology and internal anatomy (Thomasson, 1984). Only one species is known from the early Miocene, but there appears to be continuous diversification from the early to middle Miocene (Elias, 1942). Between 10 and 7 Ma, Thomasson (1990) reported at least 20 species representing the five extant grass subfamilies. Grass fossils from the Great Plains are found in the same lithologic units that produce dated vertebrate assemblages, permitting age assignments for paleofloras based on vertebrate biochronology (Thomasson, 1990; Woodburne & Swisher, 1995).

The Poison Ivy flora from the Ash Hollow Formation (≈ 10 Ma, Antelope County, Nebraska, Thomasson, 1990) overlies the Valentine Formation, and occurs in an ashfall containing a late Clarendonian mammal fauna (see below). The flora includes hackberry, walnut or hickory, forbs, sedges, horsetails, and three grass taxa dominated by fossil species *Berriochloa communis* Thomasson (= *Stipidium commune* Elias). The early Hemphillian Russ's flora (between 8.5 and 7 Ma, Garden County, Nebraska, Thomasson, 1990) contains 10 grass species among four of the five living subfamilies. Extant species of the genus *Panicum* L. (subfamily Panicoideae) that occur at Russ's flora exhibit both C_3 and C_4 photosynthesis. A leaf fragment from Russ's flora is in the subfamily Arundinoideae, which includes both C_3 and C_4 extant genera. The Minium Quarry (approximately 7 Ma, Graham County, Kansas, Thomasson et al., 1990) has a diverse grass assemblage including 12 species among all 5 living subfamilies, and a C_4 fossil identified by Kranz anatomy in leaf cross section (Thomasson et al., 1986). Although scattered trees were present at the Russ's and Poison Ivy sites, Thomasson (1990) reported that grassland was most likely the dominant community at all localities.

Other significant Miocene paleofloras include the Beaver County floras of western Oklahoma (late Clarendonian, ≈ 10 Ma), and the Logan County, Kansas, flora (Berry, 1918; Chaney & Elias, 1936). These are lacustrine deposits preserving aquatic and riparian taxa, approximately equivalent in age to the grass and forb assemblages of Elias (1942, and discussed in Chaney & Elias, 1936). Both are interpreted as representing a prairie environment with primarily riparian trees preserved. The Logan County flora represents a drier environment than the Beaver County assemblages based on species composition and smaller size of leaves.

Thomasson (1990) interpreted the rich middle to late Miocene fossil grass record of the central and northern Great Plains as a grass-dominated landscape with scattered trees, at least by 10 to 11 Ma, and a treeless grassland by 5 to 8 Ma. Chaney and Elias (1936) assumed that grassy interfluves of 10 to 11 Ma were much like the treeless prairie of today. Axelrod (1985), in contrast, reconstructed woodlands and forests for the interfluves with parklike grassy openings until 7 to 5 Ma, by which time grasses had become dominant on the landscape. More recent analyses of Ogallala Group macrofossils from South Dakota and northern Nebraska support the contention that by the middle Miocene grass-dominated environments were present throughout the northern and southern Great Plains (Gabel et al., 1998).

Paleogene and early Miocene floras from the Pacific Northwest record widespread forests as far east as the modern Columbia Plateau (Chaney, 1959; Manchester, 1987, 1994). A precipitous cooling is evident in leaf assemblages from western North America near the Eocene-Oligocene boundary (Wolfe, 1994). Increasing aridity or continentality is indicated by the middle Miocene (Barnosky, 1984; Wolfe, 1994). Pollen from the late Barstovian (≈ 13 Ma) Succor Creek Formation indicates local grass-dominated parklands in early successional communities on volcanic ash (Taggart & Cross, 1990). By 10 Ma, forests gave way to a more open landscape in response to a rainshadow created by uplift of the Cascade Range (Clements & Chaney, 1937), but grass-dominated vegetation was probably uncommon until the middle to late Pliocene (Leopold & Denton, 1987).

PALEOFAUNA

The most recent review of the North American mammalian fauna is provided by Webb and Opdyke (1995; see also Webb, 1977, 1983a, b, 1984, 1989; Krause & Maas, 1990; Stucky, 1990; Janis, 1993; Janis et al., 1998; Woodburne & Swisher, 1995). The Cenozoic Era, as recorded in terrestrial rocks in North America, is divided on the basis of fossil mammals into 19 Land Mammal Ages (LMAs) to refine chronological resolution. In addition, Tertiary vertebrate assemblages can be grouped into six ecologically significant chronofaunas that remain relatively stable in composition and diversity throughout their duration, yet within which minor change can be demonstrated. These chronofaunas are bounded primarily by periods of immigration accompanied by extinction, which dramatically change the character of succeeding chronofaunas, but their boundaries do not necessarily coincide with those of LMAs. Each chronofauna exhibits distinct ecological attributes, providing clear indications, based on mammals, of the environmental history of North America.

As summarized by Webb and Opdyke (1995), the Tertiary began with a Paleocene Chronofauna comprised at the ordinal level primarily of Late Cretaceous holdovers. Arboreal adaptations were common. Most species were small to medium-sized, although there is a general increase in size and diversity of herbivores through the Paleocene, including the precociously hypsodont taeniodonts, the horned, browsing dinoceratans, and pantodonts, all three immigrants from Asia. During the Clarkforkian and Wasatchian (56.5–50 Ma) land mammal ages, waves of immigrants changed the character of the North American fauna, giving rise to the Eocene Chronofauna. Rodents, coryphodonts, and tillodonts entered from Asia. Strong similarities exist between the North American and European faunas of the early Eocene, reflecting a North Atlantic immigration route (Thulean Bridge). Perissodactyls and artiodactyls appear for the first time in North America. Low-crowned perissodactyls and rodents diversify greatly. Arboreal mammals, including primates, are most abundant during the middle Eocene. Forest-dwelling primates are found within the Arctic Circle on Ellesmere Island (West & Dawson, 1978).

Selenodont, or crescent-shaped, tooth cusps are characteristic of the early Eocene (Wastachian) genus *Meniscotherium* Cope. Special environmental significance was previously accorded *Meniscotherium* based on its selenodont teeth and perceived distribution across North America. A more recent analysis based on dental microwear indicates food with a high grit content without significance for a diet or environment predominated by grass (Williamson & Lucas, 1992).

By the middle Eocene seasonal aridity is suggested by evaporite and oxidized redbed deposits associated with Green River lakes (Bradley, 1947). The Uintan rodent *Protoptychus* Scott (44–45 Ma) from Wyoming has inflated bullae; its elongate hindlimbs, short forelimbs, and other skeletal features are indicative of ricochetal locomotion (Wahlert, 1973; Brown & Yalden, 1973; Turnbull, 1991). *Protoptychus* strongly resembles kangaroo rats and jerboas in its adaptations, both of which are characteristic of arid, open regions, thus suggesting to Turnbull (1991) that in the area of the Uinta and Washakie basins, riverine subtropical forests were separated by arid divides between the alluvial drainages.

The Eocene Chronofauna drew to a close at approximately 40 Ma (late Eocene), culminating in the Duchesnean LMA. New waves of immigration introduced the White River Chronofauna. The number of herbivorous species, including browsers, especially selenodont species, increased. New to this chronofauna were camels, peccaries, oreodonts, and rhinoceroses. Among the smaller mammals, shrews, squirrels, beavers, pocket mice and some other rodent families, and rabbits were new. For the first time in North America, hypsodont mammals, both larger and smaller, were diverse. Some of the ungulates [e.g., *Leptomeryx* (Leidy)] are interpreted to have behaved similarly to gazelles, as herbivores that ate green grass in the growing season but subsisted on browse during the dry season (Janis, 1982). None of the White River herbivores appears to have been a strict grazer. Burrowing species indicative of well-drained soils increased, and arboreal species decreased. Aquatic reptile diversity declined (Hutchison, 1992). The early Miocene Runningwater Chronofauna, followed by the Sheep Creek Chronofauna, are characterized by immigrations and relatively diverse faunas indicative of mixed, but progressively more open habitats.

The Clarendonian Chronofauna, beginning about 18 Ma in the Hemingfordian LMA, spans the Barstovian, Clarendonian, and Hemphillian land mammal ages, which end about 5 Ma. Between 18 and 15 million years ago, during the inception of the Clarendonian Chronofauna, horses appear to include greater amounts of graze in their diets. Beginning with *Merychippus* Leidy, high-crowned horses rapidly radiated and diversified (MacFadden & Hulbert, 1988; MacFadden et al., 1991; Hulbert & MacFadden, 1991; Hulbert, 1993), presumably signifying the increasing prevalence of grass in their diets and in the environment (Webb, 1983a; Hayek et al., 1992). This rich chronofauna exhibits its highest levels of mammalian diversity in the Barstovian, between about 16 and 12 Ma (141 species in 60 genera in 16 families).

Voorhies (1990) listed 28 ungulate species from the Barstovian Norden Bridge Quarry, Nebraska. Grazing horse diversity reached 16 contemporaneous species. The large rhinoceroses *Teleoceras* Hatcher and *Aphelops* Cope, the proboscideans *Miomastodon* Osborn and *Gomphotherium* Burmeister, and other taxa dispersed from Asia into North America early in this interval. Beginning about 12

Ma, ungulates began a decline in diversity from their Barstovian peak.

The three-toed hipparionine horse genus *Cormohipparion* Skinner & MacFadden first appears at approximately 15 Ma (Barstovian) and is widely distributed in North America until about 8 Ma. *Cormohipparion* is important because closely related equids dispersed throughout Eurasia subsequent to the first record of *Cormohipparion* in North America. This hipparionine dispersal (see discussion of the Eurasian paleofauna below) has been interpreted as representing the spread of grass-dominated ecosystems in the Old World during the Miocene, although the pattern may actually be more complex ecologically. The New World origin of the Old World hipparionine radiation can be narrowed to a subset of species that has been suggested to be within the *Cormohipparion occidentale* Leidy group (Bernor et al., 1996c; Woodburne, 1996), whose earliest record is 12.7 Ma (late Barstovian), and which lasted until slightly younger than 10 Ma (late Clarendonian or early Hemphillian; Woodburne & Swisher, 1995).

Cormohipparion occidentale occurs in the Clarendonian Dove Spring Formation, California, along with a diverse suite of mammals, including five other species of horses (Whistler & Burbank, 1992). As seen above in the discussion of North American paleobotany, the Dove Spring flora includes grass blades with Kranz anatomy, documenting the presence of C_4 grass at 12.5 Ma, yet isotopic values for tooth enamel of *Cormohipparion occidentale* and *Pliohippus tantalus* Merriam indicate that C_4 plants were insignificant components in the diets of those horses (Cerling et al., 1998).

The Poison Ivy Quarry ($\approx$ 10 Ma, Clarendonian) in Antelope County, Nebraska, is particularly significant with respect to the origin of grass-dominated ecosystems because the vertebrate assemblage is associated with paleobotanical remains in a volcanic ash (see above). Remains of the barrel-shaped rhinoceros *Teleoceros major* Hatcher were found with grass remnants in the oral cavity and rib cage, demonstrating that this hypsodont rhino ate grass (Voorhies & Thomasson, 1979; see also MacFadden, 1998). Other taxa at the site include five species of horses and several camels. The vegetation was mixed, including riparian woody species and a significant grass component, consistent with the mammalian assemblage.

The diversity of mammals in the early part of the Clarendonian Chronofauna presumably reflects a rich mosaic of environments accommodating the spectrum of feeding adaptations that had been evolving throughout the Cenozoic. As one correlate of this diversity, elements of the Barstovian fauna were able to take advantage of grassy parkland successional habitats created by volcanic activity as demonstrated in the Succor Creek Formation, Oregon (Taggart & Cross, 1990). By the end of the Hemphillian (5 Ma), generic diversity was reduced to half that of the Barstovian near the beginning of the chronofauna (Webb & Opdyke, 1995). Browsers were initially affected more than grazers. Webb and Opdyke (1995) suggested that this pattern indicates the development of an extensive grassland. The inferred increase in grass cover coincided with a reduction in ungulate diversity. Between about 7 and 5 million years ago, equid diversity in North America precipitously declined, only hipparionines and *Equus* L. remaining into the Pliocene (MacFadden & Hulbert, 1988). Accompanying these changes in the Hemphillian was an increase in faunal provincialism, an introduction of immigrants, and an increase in rodents with high-crowned teeth (Hulbert, 1987; Jacobs, 1977; MacFadden et al., 1979; Shotwell, 1958, 1961; Tedford & Gustafson, 1974; Webb, 1989). Stable carbon isotopes (see below) indicate a dramatic dietary shift from C_3 to C_4 plants in the late Miocene, during the interval when ungulate diversity was decreasing (Cerling et al., 1998).

The ungulate component of the Clarendonian Chronofauna was convergently similar to the modern African savanna fauna (Hulbert, 1982; Webb, 1983a; Janis, 1984). However, toward the end of the Miocene in North America, unlike modern Africa, the fauna was deficient in hypsodont bovids, having instead a variety of horses, and lacked the diversity of small, lower-crowned browsing ungulates (Janis, 1984, 1995).

STABLE ISOTOPES

Initial investigations of equid enamel collected from western North American fossil localities indicated that C_4 grasses became an important dietary component starting between 7 and 6 Ma (Cerling et al., 1993). This dietary shift, in conjunction with isotopic data from Pakistan (Quade et al., 1989a, 1992), was interpreted to reflect a rapid global expansion of C_4-dominated biomes attributed to global changes in both the carbon budget and the meteoric water cycle, rather than reflecting only regional climatic change. Specifically, this expansion was linked to decreasing atmospheric pCO_2 levels that would favor C_4 grasses over C_3 vegetation. Cerling et al. (1993) observed that the late Miocene $\delta^{13}C$ shift in equid enamel from North America did not correspond to the early to middle

Miocene development of hypsodonty and suggested a revision in the interpretation of the relationship of high-crowned teeth to the spread of grass-dominated environments.

Subsequent studies of fossil herbivore enamel (MacFadden & Cerling, 1994, 1996; Wang et al., 1994; Cerling et al., 1997b, 1998; Latorre et al., 1997) provide additional support for C_4 biomass expansion in the late Miocene. Based on isotopic analyses of 50 fossil horse enamel samples from various localities throughout North America up to 52 Ma, Wang et al. (1994) noted that the first strongly enriched $\delta^{13}C$ values in tooth enamel, indicating a significant to exclusive C_4 dietary component, occurred between 7 and 5 Ma. They pointed out that the early to middle Miocene equid diversity climax and development of hypsodonty cannot be linked to the expansion of strictly modern savanna ecosystems, which contain significant proportions of C_4 biomass. However, they suggested that C_3 grasslands and savannas could have existed under atmospheric pCO_2 levels higher than today (Wang et al., 1994).

The carbon isotopic signature of fossil enamel from equids, gomphothere proboscideans, and camelids from the late Miocene to Pliocene of New Mexico and Arizona indicates that C_3 plants dominated diets there until 6.3 Ma (Latorre et al., 1997). However, the isotopic values for camelid enamel as old as 15.6 Ma are interpreted as indicating a minor C_4 or CAM dietary component. After 6.3 Ma there is a dramatic increase in C_4 vegetation in the diet of the fossil horses. During this transition, the isotopic signal of camelid and gomphothere enamel indicates only moderate shifts toward an increase in the dietary C_4 component.

Dividing isotopic data on equid enamel from North America into a high-latitude group (> 37°N) and a low-latitude group (< 37°N), Cerling et al. (1997b) noted a significant dietary shift in low-latitude equids during the late Hemphillian. Sites older than 7 Ma have $\delta^{13}C$ values consistent with a C_3-dominated diet, but by 6.8 Ma a significant C_4 component is evident and by 5.7 Ma exclusive C_4 diets are indicated. Equid enamel analyzed from the high-latitude group do not indicate a C_4 dietary component until about 4 Ma, and northern horses consumed a smaller fraction of C_4 biomass than their southern counterparts. The variability in C_4 dietary component noted in North America and at intermediate latitudes (25–40°N and S) elsewhere in the world potentially reflects the variability of growing seasons in different regions, variability in the amount of C_4 biomass during different parts of the growing season, or greater sensitivity at higher latitudes to climatic fluctuations (Cerling et al., 1997b).

Analyses of the enamel of fossil mammalian herbivores comprising the orders Proboscidea, Perissodactyla, and Artiodactyla from 17 fossil localities in Florida ranging in age from 9.5 to 0.1 Ma indicate an isotopic shift toward a C_4 diet starting at 7.0 Ma (MacFadden & Cerling, 1996). Prior to 7 Ma, the carbon isotopic values of all tooth samples are consistent with a diet comprised only of C_3 plants. At about 7 Ma, the $\delta^{13}C$ values of fossil enamel indicate both C_3 and mixed C_3/C_4 diets, presumably reflecting the spread of C_4-based plant communities in this region of North America. By the latest Hemphillian (about 5 Ma) there is evidence for pure C_4 grass diets, although there is a gap in the fossil record between 5 and 7 Ma and exclusive C_4 diets may have occurred earlier. MacFadden and Cerling (1996) noted that the mixed dietary signals from teeth of *Cormohipparion* in the latest Hemphillian could reflect either a mixed diet of C_4 grass and C_3 browse or a diet of a mixture of C_3 and C_4 grasses.

One of the more interesting features of the isotopic record of North America is the significant time difference between the middle Miocene radiation of equids, usually interpreted as reflecting adaptations to grazing, and the spread of C_4 vegetation in the late Miocene. These data suggest that either C_3 grasses comprised a significant proportion of the vegetation during the middle Miocene and probably dominated communities in some regions, or that early high-crowned horses were not obligate grazers. The roughly contemporaneous spread of C_4-dominated biomes and a precipitous decline in equid diversity as well as other faunal groups is also interesting. An increase in dietary C_4 grasses reflects an expansion of C_4 grasslands that would traditionally be expected to favor a grazing fauna. MacFadden and Cerling (1994) suggested the late Miocene isotopic shift may have involved the replacement of savanna and forest biomes with lower-productivity C_4 grasslands.

EURASIA

SUMMARY

Eurasia exhibits a great deal of regional provincialism as might be expected from the longitudinal and latitudinal extent of the landmass and the significant tectonic processes that have affected it throughout the Tertiary, including such events as the retreat of the Turgai Straits, the collision of India with Asia, the closure of the Tethys, the Alpine Orogeny, and the desiccation of the Mediterranean

Basin. This large region includes the temperate grasslands of easternmost Europe, the Ukraine, Russia, and interior northern China, as well as the tropical and subtropical savanna regions of Asia and the Indian subcontinent. The natural vegetation of most of Europe is forest today and has been throughout the Tertiary (Fig. 1).

Graminidites pollen and probable grass macrofossils occur in the early Eocene London Clay flora, England (Chandler, 1964; Thomasson, 1987; Boulter, 1988). Nevertheless, the Tertiary paleobotanical record of western Europe documents the widespread presence of forest communities (Fig. 3). A period of drying and cooling begins in the late Eocene. Species richness declines into the Oligocene, and evergreen tropical and subtropical species are replaced by deciduous taxa and conifers. This trend continues throughout the Tertiary, progressing from north to south. Pollen evidence indicates the initial spread of grassland and steppe communities in the region around the Black Sea beginning in the late Miocene. However, grass pollen is not abundant in Europe until the middle Pliocene (Traverse, 1982; Benda, 1971).

Pollen records from the northern interior of China indicate open environments in the Oligocene, but significant grass cover is absent until the early Miocene (Leopold et al., 1992). Rare *Graminidites* pollen is present in the early Tertiary Subathu Formation of northwestern India (Mathur, 1984; Singh & Sarkar, 1990), along with palynological evidence of coastal, semi-evergreen tropical conditions. Early Miocene plant macrofossils from the Siwalik section of northwestern India indicate forest environments, although pollen samples from the same region contain 8% grass pollen. An increase in abundance of grass pollen occurs in the late Miocene, documenting the development of a grass-dominated ecosystem (Mathur, 1984). In Nepal, late Miocene macrofossils indicate deciduous forest, but after the late Miocene grasses are represented by pollen and a few macrofossils (Awasthi & Prasad, 1990; Sarkar, 1990; Prasad & Awasthi, 1996).

The vertebrate record of central Asia is consistent with open habitat beginning in the Oligocene. Throughout the Neogene, the fauna of western Europe indicates closed habitats, as compared to more open habitats to the east. Hipparionine horses originated in North America, but dispersed across Eurasia between 10.9 and 10.7 Ma, with an Old World radiation of browsing, mixed-feeding, and grazing species. The late Miocene fauna of Greece (8.3–7 Ma) is characterized by a diverse suite of some 30 species of mainly mixed-feeding and browsing ungulates with few grazers. Between 9 and 7 Ma, significant faunal changes occur in the Siwalik sequence of Pakistan, including the presence of hypsodont bovids, porcupines, and rabbits, and the disappearance of large hominoids, which indicate the opening of habitats.

Isotopic studies of paleosol components and fossil herbivore enamel from Europe do not indicate significant C_4 biomass at any time during the Neogene. The isotopic record of Europe throughout the Miocene indicates a predominance of C_3 vegetation. In Asia, on the other hand, C_4 plants are isotopically recorded as a minor dietary component at 9.4 Ma in the Siwalik sequence of Pakistan, increasing gradually as a foraging resource until exclusively C_4 diets are documented about 5 Ma (Morgan et al., 1994; Cerling et. al., 1997b). Analyses of paleosol carbonates from Pakistan and Nepal (Quade et al., 1989a, 1995a) and organic matter from the Bengal Fan (France-Lanord & Derry, 1994) indicate a more abrupt shift from C_3- to C_4-dominated vegetation between 8.1 and 6.5 Ma.

PALEOBOTANY

Europe. The European Tertiary paleobotanical record primarily documents a history of changing forest composition. Grass leaf and inflorescence fragments are reported from the early Eocene London Clay flora (Chandler, 1964; Thomasson, 1987). A palynological survey of aquatic monocotyledons from the Tertiary of southern England and northern France includes the occurrence of *Graminidites* pollen beginning in the early Eocene with the London Clay (Boulter, 1988), but these have not been evaluated to determine the absence of scrobiculae or presence of microchannels. Moreover, Wilkinson and Boulter (1980: 46) reported that Oligocene samples from England have up to 3% *Graminidites* having a poorly defined pore without a distinct annulus, thus implying these pollen are probably not Poaceae.

Late Eocene to Oligocene paleobotanical records from western and central Europe indicate a general increase in seasonality, cooling, and drying (Collinson, 1992). Plant communities show an increasing dominance of deciduous and coniferous taxa accompanied by an overall decrease in species richness and the occurrence of arid-adapted taxa such as *Ephedra* L., and *Acacia* Mill. (Collinson, 1992, and many references therein; Cavagnetto & Anadon, 1996). An extensive herbaceous component is lacking in most Paleogene non-aquatic communities; however, pollen of herbaceous plants, including grass, occurs in the early Oligocene of northeastern Spain (Cavagnetto & Anadon, 1996).

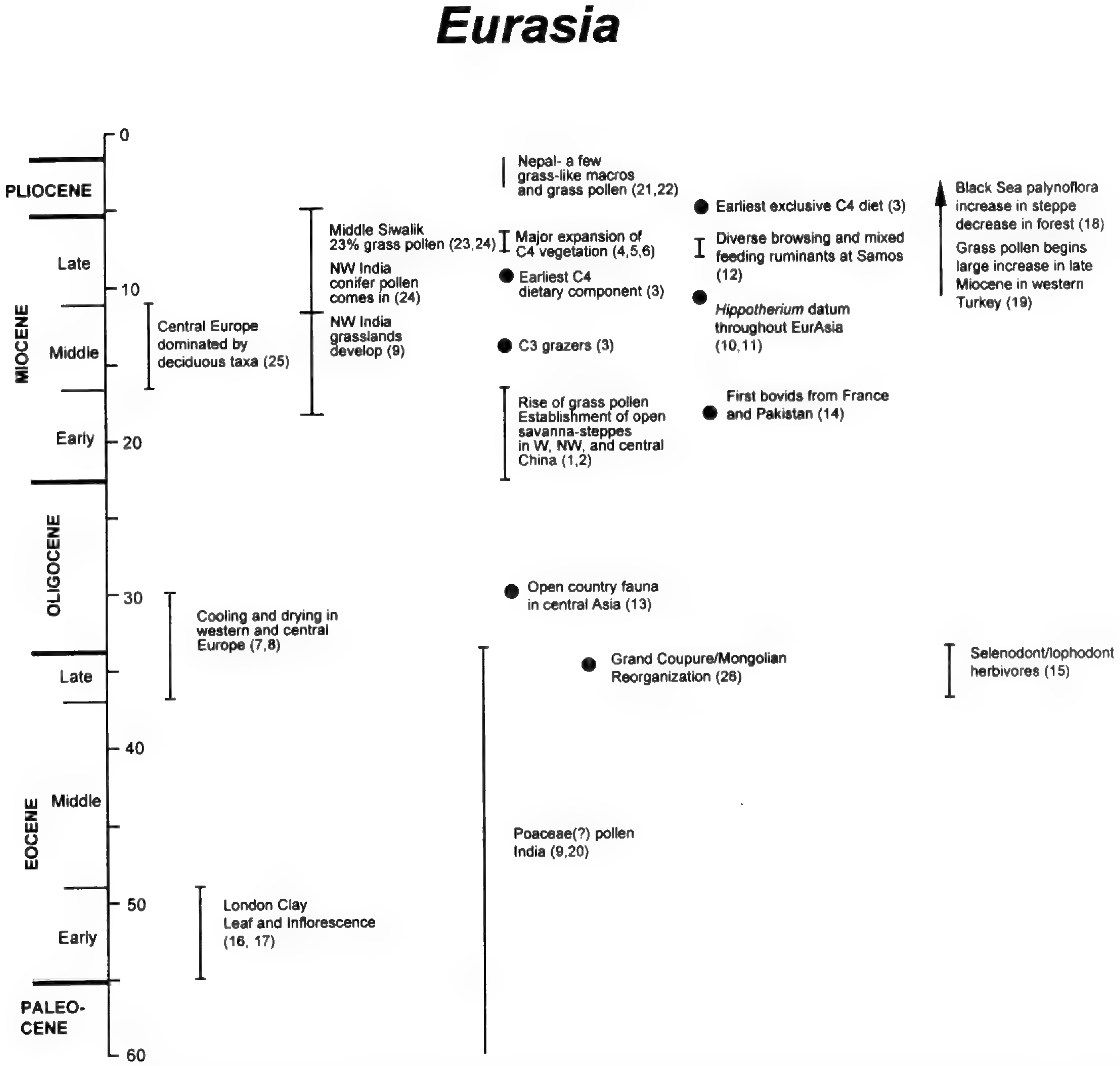

Figure 3. Summary of paleobotanical, paleofaunal, and isotopic evidence for the origin of grass-dominated ecosystems in Eurasia. Symbols as in Figure 2. Sources: (1) Leopold et al. (1992), (2) Song et al. (1981), (3) Morgan et al. (1994), (4) Quade et al. (1989a), (5) Quade et al. (1995a), (6) France-Lanord & Derry (1994), (7) Collinson (1992), (8) Cavagnetto & Anadon (1996), (9) Mathur (1984), (10) Bernor et al. (1996a), (11) Woodburne (1996), (12) Bernor et al. (1996b), (13) Wang (1997), (14) Solounias et al. (1995a), (15) Jernvall et al. (1996), (16) Chandler (1964), (17) Thomasson (1987), (18) Traverse (1982), (19) Benda (1971), (20) Singh & Sarkar (1990), (21) Prasad & Awasthi (1996), (22) Sarkar (1990), (23) Nandi (1975), (24) Sarkar et al. (1994), (25) Kovar-Eder et al. (1996), (26) Meng & McKenna (1998).

The cooling and drying trend continues into the Neogene. Paleotropical species (e.g., *Tetraclinis salicornoides* Unger, *Daphnogene* sp. Kovar, *Engelhardia orsbergensis* cf. Kovar) are replaced by deciduous, cool-adapted taxa (*Quercus pseudocastanea* Kovar-Eder and ruberoid oaks, *Alnus ducalis* Kovar-Eder, *Acer vindobonensis* Kovar-Eder) from north to south across central, eastern, and southeastern Europe. Thus, there is a time-transgressive and latitudinal trend from evergreen thermophilous taxa in the Paleogene to temperate deciduous forest in the Neogene (Kovar-Eder et al., 1996). Central Europe was dominated by deciduous taxa by the middle Miocene, while in the southern regions and the western Balkan Peninsula evergreen taxa were abundant until the beginning of the late Miocene (Kovar-Eder et al., 1996; Pantic & Mihajlovic, 1977).

Five middle Miocene pollen samples from lacustrine sediments at Samos Island in the eastern Aegean, dated to 11.2 Ma, are interpreted as representing closed to open woodlands with conifers on nearby uplands (Ioakim & Solounias, 1985). Two samples have 5% and 10% grass pollen, respectively, and the remaining three have none. Ground cover is interpreted to have consisted of a variety of herbaceous plants, including grasses, which were not a significant component of the vegetation.

A continuous core from the Black Sea spanning the last 10 million years provides a large-scale palynological record of vegetation for the more arid interior of eastern Europe, the Ukraine, and north-central Turkey (Traverse, 1982). The late Miocene was dominated by warm-temperate adapted trees such as *Engelhardia* Leschenault ex Blume, *Nyssa*, *Liquidambar* L., oak relatives, and palms (Traverse, 1982). However, a steppe-forest index, consisting of *Artemisia* L. (sage), Chenopodiaceae, and Amaranthaceae pollen, relative to the total pollen flora, indicates the steady spread of steppe beginning 10 Ma and reaching a maximum at the Plio-Pleistocene boundary. Dry, cold climate favors steppe species and grasses, which are inferred to have increased together (Traverse, 1982: 205). A palynological record from western Turkey documents an increase in conifers and herbaceous taxa, including Poaceae, in the late Miocene, with grass becoming very abundant in the middle Pliocene (Benda, 1971).

Asia. The northern and western interior regions of China have grass-dominated, cool, and arid environments today. Paleocene and early Eocene assemblages from north, west, and central China contain significant percentages (as much as 80%) of arid-adapted shrubs, such as *Nitraria* L. and *Ephedra*, sometimes associated with forest taxa, such as *Alnus*, *Betula* L., *Engelhardia*, *Carya*, *Juglans*, and *Liquidambar* (Li et al., 1984; Leopold et al., 1992). Although *Nitraria* and *Ephedra* are abundant, grass pollen in Paleogene samples is rare (Leopold et al., 1992). *Nitraria* remained widespread in the Oligocene, but *Ephedra* retreated to the northwest beginning in the late Eocene (Li et al., 1984). Miocene pollen samples from western and northern China are dominated by herbaceous pollen (as much as 40%) including grass (Leopold et al., 1992) and are interpreted as indicating a broadly open steppe with local forest meadows and pines at higher elevations (Song et al., 1981). Consequently, the Neogene has been classified by Tao (1992) as a "stage of flourishing herbs."

In the Indian subcontinent, Paleocene to Oligocene palynofloral assemblages are reported from northwestern India. Sediments associated with the Paleocene Dras volcanics have a palynoflora interpreted to represent dry, sandy, coastal vegetation based on the occurrence of palms including *Nypa* Steck, together with *Casuarina* L. and *Ephedra*, with *Carpinus* L., *Corylus* L., and *Carya* derived from uplands (Singh & Sarkar, 1990). Fern spores are also present.

The Subathu Formation of Himachal Pradesh is reported as early to late Eocene by Mathur (1984) and Paleocene-Eocene by Singh and Sarkar (1990). *Graminidites* sp. is reported by Mathur (1984) as rare in the upper Subathu, and Poaceae are reported as present by Singh and Sarkar (1990). The report of Poaceae is probably based on the assumption that *Graminidites* is a grass, although we know of no detailed studies of pollen wall structure and sculpture on these pollen. The vegetation is interpreted as coastal, semi-evergreen, and tropical. Co-occurring taxa include dinoflagellates, palms, *Cycas* L., Betulaceae, Juglandaceae, and the tropical *Anacolosa* (Blume) Blume (Singh & Sarkar, 1990). Samples from the Oligocene Dharmsala Formation are dominated by fern spores with a few angiosperms and no grass pollen reported (Mathur, 1984).

Neogene plant macrofossils and pollen are found in Siwalik and related sediments throughout the foothills of the Himalayas in India and Nepal. Siwalik deposits are the direct result of mountain building associated with the collision of the Indian and Asian plates, and range in age from early Miocene ($\approx$ 22 Ma) to the present (Barry, 1995). The Siwalik sequence of the Potwar Plateau, Pakistan, has precise time control based on the paleomagnetic time scale but contains no paleofloras (Barry, 1995, and references therein). Paleobotanical sites in India are generally designated as lower, middle, or upper Siwalik, and are thus only loosely lithologically correlated to dated sections of the Potwar, or to other vertebrate-bearing sections. The lower Siwaliks of the Potwar Plateau are of early to late Miocene age, ranging from greater than 18 Ma to less than 11 Ma. The superposed middle Siwaliks of the Potwar continue the record into the early Pliocene.

Lower Siwalik wood from the Kalagarh, northeast of Delhi, includes taxa with affinities to Dipterocarpaceae, and the genera *Sterculia* L., *Bursera* Jacq. ex L., *Dialium* L., *Millettia* Wight & Arn., *Diospyros* L., *Artocarpus* J. R. Forst. & G. Forst., and *Ficus* L. (Prasad, 1993). These plants inhabit tropical evergreen or moist deciduous forests today (Prasad, 1993). Lower Siwalik pollen assemblages from northwestern India are dominated by pteridophyte spores and angiosperm pollen, including palm, rare gymnosperms, and approximately 8% *Monoporites* sp. (Banerjee, 1968; Nandi, 1975).

Middle Siwalik pollen assemblages are more species rich than those of lower or upper Siwalik samples. Most show an increase in gymnosperm pollen (primarily Pinaceae). Macrobotanical sites lack conifers; therefore, conifer pollen is assumed to be allocthonous (e.g., Awasthi, 1982; Prasad & Awasthi, 1996), from upper elevations associated with uplift of the Himalaya (Nandi, 1972, 1975; Ghosh, 1977; Sarkar et al., 1994). Both pollen and macrofossil assemblages indicate increasing seasonality, or decreasing moisture, or both, toward the end of the lower Siwaliks and through the middle Siwaliks, particularly in the northwestern part of the subcontinent (Prakash, 1973). Grass pollen increases to 23% in middle to upper Siwalik sediments (Nandi, 1975; Sarkar et al., 1994). Mathur (1984) interpreted the increase in grass pollen as indicative of established savanna vegetation by the late Miocene (upper part of the middle Siwaliks).

Paleobotanical studies of the Surai Khola Siwaliks, Nepal, are of particular interest because there is a stable carbon isotope record from the same formation (see following isotope section). Plant macrofossils comprise 53 species among 15 families with affinities to extant evergreen and moist deciduous taxa. The proportion of dry deciduous taxa increases toward the top of the middle Siwalik section (Awasthi & Prasad, 1990; Sakar, 1990; Prasad & Awasthi, 1996). Upper Siwalik sediments from Surai Khola are poorly fossiliferous and preserve a few graminoid specimens (Prasad & Awasthi, 1996). Pollen assemblages from the upper Siwalik portion of the sequence include Pinaceae and other wind-pollinated groups, and more than 30% Poaceae in the uppermost sample (*Monoporopollenites kasauliensis*, Singh & Sarkar referred to as "grass pollen," Sarkar, 1990: 322; Prasad & Awashti, 1996).

PALEOFAUNA

Europe. The European record is, in some ways, similar to that of North America because of direct dispersals via the northern Atlantic region in the early Tertiary and because of dispersals from Asia to Europe and North America throughout the Tertiary (Schmidt-Kittler, 1987; Lindsay et al., 1989; Bernor et al., 1996a). Nevertheless, despite similarities due to episodic faunal exchanges, the records are distinct. The greatest faunal similarity is shown at ≈ 56 Ma (early Eocene; Wasatchian of North America and Sparnacian of Europe), during which time there is no evidence of extensive grass-dominated ecosystems in Europe.

Of major significance in the European faunal record is the Grande Coupure (≈ 34 Ma, early Oligocene), during which the European biota underwent major reorganization, presumably associated with global cooling. An older vertebrate fauna characteristic of forested environments changed to a younger fauna characteristic of more open, but still relatively closed and wooded, country. Asia was probably a major source for new immigrants in Europe after the Grand Coupure, following removal of the Turgai Straits as a biogeographic barrier.

Detailed data on the chronology and distribution of mammals demonstrate a high degree of regionalism between western Europe, eastern Europe, and southwestern Asia (Bernor et al., 1996a; van Dam, 1997). Fortelius et al. (1996a, b) provided detailed comparisons from about 17 Ma onward between the west (including localities in Portugal, Spain, France, Italy, Germany, Switzerland, Austria, Poland, Czech Republic, and Slovakia) and the east (including localities in Hungary, Slovenia, Serbia, Bosnia, Macedonia, Albania, Greece, Bulgaria, Romania, Moldova, Ukraine, Georgia, Turkey, Iran, Afghanistan, and Kazakhstan). Because such large geographic areas vary locally, the aggregate faunal blocks represent the sum of sampled environments. Nevertheless, there are clearly differences between the two faunal blocks that broadly reflect ecology including the dominant vegetation. Taxon-independent ecomorphological faunal analyses indicate diversity and body size trends from initially closed and forested landscapes toward assemblages characteristic of progressively more open and seasonal environments (Bernor et al., 1996b; Fortelius et al., 1996a, b). Species richness begins to increase in the eastern region at about 10.5 Ma, while it decreases in the west. By the Messinian crisis (approximately 7 Ma and younger), diversity in the eastern region had fallen. For most time intervals from 9.5 Ma onward, the distinctions intensify between the regions with the eastern block fauna reflecting more open conditions than those in the west. This pattern suggests diachronous opening of the landscape, earlier in the east, with central Europe remaining relatively closed (Bernor et al., 1996b; Fortelius et al., 1996a, b).

During the early Miocene (Orleanian, approximately 17 Ma), *Anchitherium* von Meyer (a browsing horse), two genera of proboscideans, and five browsing ruminant artiodactyls are present in Europe. The earliest records of bovids are species of *Eotragus* Pilgrim from Artenay, France, and the Kamlial Formation, Pakistan, the latter occurrence of similar age to Artenay and dated by magnetic polarity stratigraphy at 18.3 Ma (Solounias et al., 1995a). The genus has a broad distribution throughout Eurasia, Africa, and the Middle East, its youngest record being approximately 14 Ma, possibly younger. Solounias and Moelleken (1992) examined microwear in *E. sansaniensis* (Lartét) from Sansan, France (15 Ma, Steininger et al., 1996). Microwear on the teeth indicates that this species was a browser. The fauna of Sansan is diverse, including tragulids, suids, cervids, and glirids, among other taxa, suggesting a forest environment. In general, the European faunas of this age indicate a dry subtropical to deciduous forest in the east, with a more closed habitat in the west (Bernor et al., 1996b; Fortelius et al., 1996a, b).

The first appearance of hipparionine horses has traditionally been interpreted as heralding the spread of grasslands across the Old World. In addition, as an abundant and readily identifiable taxon, hipparionine horses hold a fundamental position in Eurasian Neogene mammalian chronology, its first appearance being recognized as the *Hippotherium* Kaup Datum (fide Woodburne, 1996; Woodburne et al., 1996; = *Hipparion* Datum of other authors). Recent studies suggest an origin of *Hippotherium* close to North American *Cormohipparion occidentale* with subsequent dispersal and radiation across Eurasia between about 10.9 and 10.7 Ma (Bernor et al., 1996c; Kappelman et al., 1996; Pilbeam et al., 1996; Woodburne et al., 1996; Sen, 1997). However, the dispersal of hipparionine horses across the Old World may be more complicated than simply the spread of grass-dominated ecosystems as originally interpreted.

Microwear analysis of teeth (Hayek et al., 1992) indicates that North American *Cormohipparion* obtained a significant portion of the diet by grazing. Of the Old World species examined by Hayek et al. (1992), some species were grazers while others appear to have had mixed diets. In hipparionines, reduction of facial fossae (pits on the sides of the muzzle in front of the eyes) is associated with grazing, and retention or elaboration of the facial fossae is associated with those species that appear to be mixed-feeders or to utilize browse. Well-developed facial fossae are retained in early Eurasian *Hippotherium* (Bernor et al., 1996c). Based on the morphology of the limbs, the oldest European hipparionine species were forest dwellers, but later species were adapted for drier and more open country (Eisenmann, 1995). Thus, it appears that the dispersal of hipparionines from North America through Eurasia was associated with factors other than, or possibly in addition to, the spread of grass-dominated ecosystems across the Old World.

The Turolian faunas from the Greek island of Samos, and from Pikermi, near Athens (about 8.3 to 7 Ma; Bernor et al., 1996d), are particularly interesting because they present a diverse fauna that has historically been interpreted as representing open grassland and savanna, because isotopic studies have been conducted on samples from there (see below; Quade et al., 1994), and because the morphology and tooth wear of several ungulates in the fauna have been analyzed to infer dietary habits. The ruminant fauna consists of approximately 30 species, interpreted to be predominately browsers and mixed-feeders based on the structure of the masticatory apparatus (Solounias & Dawson-Saunders, 1988). More specifically, masseteric morphology of bovids, including two species of *Tragoportax* Pilgrim, two species of *Pachytragus* Schlosser, and one species of *Gazella* de Blainville, indicates mixed-feeding or browsing; however, microwear analysis on the teeth indicates that *Tragoportax* and *Pachytragus laticeps* Andree grazed or at least took grass in the diet seasonally (Solounias & Hayek, 1993; Solounias et al., 1995b). Moreover, premaxillary shape and microwear on the low-crowned teeth of the giraffid *Samotherium boissieri* Forsyth-Major indicates grazing or possibly mixed-feeding (Solounias et al., 1988; Solounias & Moelleken, 1993a, b). In addition, of six species of hipparionine horses for which diet was interpreted from tooth wear (Hayek et al., 1992), three were inferred to be grazers and three mixed-feeders. The mixed-feeders have facial characteristics that may indicate the presence of a proboscis used in gathering browse.

Although the traditional interpretation of the environment of Samos and Pikermi is open grassland, the fauna clearly utilized both browse and grass, and the fauna as a whole does not reflect a pure grassland. Solounias et al. (1995b) suggested that the environment was one of forest and bush country, perhaps analogous to that of the Khana National Park, India, or the Tana River, Kenya (Schaller, 1967; Andrews et al., 1975).

Asia. The trend toward increasing seasonality and open country probably began earlier in China and Mongolia than in the eastern portion of Europe and southwestern Asia. Meng and McKenna (1998) documented an abrupt reorganization from perissodactyl-dominated Eocene faunas to rodent/lagomorph-dominated faunas of the Oligocene, a change they named the Mongolian Remodeling and correlated with the European Grande Coupure (≈ 34 Ma). The cause of the Mongolian Remodeling was suggested to be global cooling, resulting in open environments. The ctenodactylid *Tataromys plicidens* Matthew & Granger from Mongolia, northern China, and Kazakhstan, and other rodents, support an open environment, but not necessarily grass-dominated, in central Asia at 30 Ma (late early Oligocene; Wang, 1997). The fauna of the beginning of the Miocene is little different from that of the late Oligocene, although rhinoceroses and other browsing ungulates diversify in the Miocene. Qiu (1989) and Qiu and Qiu (1995) recorded Neogene changes in the Chinese mammal fauna, including the appearance of proboscideans and the browsing horse *Anchitherium* at about 19 Ma (Woodburne & Swisher, 1995), and hipparionines at around 10.8 Ma. Regional variation is indicated especially in the distribution of rodents and primates (Jacobs et al., 1985; Qiu & Qiu, 1995), reflecting a suite of habitats from more forested in the southeast to more open in the interior.

Indo-Pakistan has a complicated geologic and paleogeographic history of northward drift and incorporation into the Asian landmass during the early Tertiary. The Eocene fauna of Indo-Pakistan has some Holarctic elements but includes cetaceans and primitive proboscideans and is deficient in carnivores (Gingerich et al., 1997). The Neogene fauna of Pakistan is representative of a southern Asian zoogeographic province that extended eastward to Thailand (Ducrocq et al., 1994), at least during its middle Miocene portion, changing through time by the dispersal of taxa into the region from Africa and Eurasia and by evolutionary changes occurring within the region. The early Miocene is best represented by the Dera Bugti fauna and characterized by large anthracotheres, deinothere and gomphothere proboscideans, and baluchimyine rodents (Raza & Meyer, 1984; Raza et al., 1984; Flynn et al., 1986; Friedman et al., 1992; Downing et al., 1993; Flynn & Cheema, 1994). By 18 Ma, significant microfaunal turnover had occurred (Jacobs et al., 1981; Flynn et al., 1997).

The record from 18.3 Ma through the remainder of the Miocene and into the Pliocene and Pleistocene is preserved in rocks of the Siwalik Group. The Siwalik fauna comprises 13 orders of mammals, although most species are rodents, ruminants, or perissodactyls. The great strength of the Siwalik record is its chronological control, made possible through magnetic polarity stratigraphy, allowing patterns of faunal change to be discerned in detail (Barry et al., 1982, 1985, 1990, 1991, 1995; Flynn & Jacobs, 1982; Jacobs et al., 1989, 1990; Barry & Flynn, 1989; Flynn et al., 1990; Flynn et al., 1995a; Jacobs & Downs, 1994; most recently reviewed by Barry, 1995). With few exceptions (e.g., Flynn et al., 1991; Flynn et al., 1995b; Sotnikova et al., 1997), other Asian faunas lack such precise age control.

Siwalik rodents and artiodactyls increase in diversity between about 15 and 13 Ma, after which time their diversity decreased. Bovids increase relative to tragulids. By 12.7 Ma, large hominoids appear. Hipparionine horses first occur at 10.7 Ma (Pilbeam et al., 1996), consistent with the first appearances of hipparionines elsewhere in the Old World.

Murine rodents, as represented by *Progonomys* Schaub, occur at about the same time or slightly later than hipparionines in most of Eurasia, but in the Siwaliks *Progonomys* occurs earlier (12.3 Ma). This is an interesting pattern implying that murines evolved in southern Asia. They are now major components of the African savanna fauna, reflecting an endemic radiation, but the initial dispersal of the group from southern Asia may have occurred simultaneously with the dispersal of hipparionines.

In the Siwaliks, murines became numerically abundant but not taxonomically diverse at any given stratigraphic horizon. As a group, striking size increase is apparent by 9.0 to 8.5 Ma and continues less dramatically until at least 8 Ma. Burrowing rhizomyids occur in the Siwalik section prior to 9 Ma, a gerbil (*Abudhabia* de Bruijn & Whybrow also known from the Arabian Peninsula, Flynn & Jacobs, in press) appears briefly at 8.7 Ma, and porcupines (*Hystrix* L.) and rabbits are recorded about 7 Ma. Among rodents, the late Miocene is clearly eventful. Burrowing in rhizomyids and the occurrence of a gerbil and a porcupine are consistent with more open habitat. Four lineages of hypsodont artiodactyls occur from the late Miocene. Faunal change also affects pigs, hippopotamuses, and giraffes in this time interval (Barry, 1995). Hominoids are not recorded in Pakistan after about 8.0 Ma (timescale of Cande & Kent, 1995), and the Siwalik fauna of that age resembles more closely those from northern and western Eurasia (Jacobs et al., 1985; see Qiu, 1989; Qiu & Qiu, 1995).

STABLE ISOTOPES

Analyses of fossil herbivore enamel and paleosol carbonates from middle Miocene to Pliocene sites in the eastern Mediterranean (Quade et al., 1994, 1995b), including Samos and Pikermi (see discussion above), indicate that the vegetation has been dominated consistently by C_3 plants with no evidence of significant C_4 vegetation. Data from Spain and France, as well as North Africa (Cerling et al., 1997b), also indicate that C_4 plants have not been a significant component of the Neogene biomass in western European or Mediterranean biomes.

The spread of C_4 vegetation in Asia appears to have occurred in the late Miocene. This shift was first documented by analyses of paleosol carbonates collected from the Siwalik sequence in Pakistan, where Quade et al. (1989a) noted an apparent dramatic ecological shift from C_3- to C_4-dominated biomass beginning at 7.4 Ma based on the time scale then in use (now calculated at ≈ 8.1 Ma, J. Barry, pers. comm.). They concluded that earlier C_3 biomass was mainly composed of trees and shrubs, whereas C_4 grasslands dominated the Plio-Pleistocene. Paleosol carbonates were collected primarily from floodplain environments, and Quade and Cerling (1995) noted that woodland habitats were probably present throughout this period marginal to the active floodplains. The isotopic transition reflects the replacement of C_3 vegetation (possibly including C_3 grasses) by C_4 grasses. Preliminary analyses of fossil herbivore enamel from the Siwaliks (Quade et al., 1992) indicate C_3 diet at 7.5 Ma and C_4 diet at 3.5 Ma for those taxa surveyed, although data are lacking for the intervening time period. They inferred that, in general, most herbivores examined prior to the isotopic shift were browsers and that the shift reflects displacement of tree and shrub communities on the floodplains of major rivers by nearly continuous C_4 grassland. Isotopic values on tooth enamel younger than 3.5 Ma record only C_4 diet; however, these samples do not include taxa interpreted to have been browsers.

Based on a data set with more complete taxonomic and temporal coverage, Morgan et al. (1994) also recorded the dietary shift from C_3 to C_4 vegetation in fossil herbivores from the Siwaliks, but they concluded that rather than an abrupt transition at 7.4 Ma, the change occurred over a period of 2–3 Ma. In addition, independent evidence for paleodiet based on dental microwear analyses of Siwalik artiodactyl and perissodactyl species, utilized in concert with isotopic data, indicated that C_3 grasses were an integral part of the Siwalik vegetation not only before evidence for C_4 grasses at 9.4 Ma but also subsequent to the transition (Morgan et al., 1994).

Stable carbon isotopic analyses of carbonate in fossil ostrich eggshell from the Siwaliks indicates a dietary shift from C_3-dominated to mixed C_3/C_4 and pure C_4 diets sometime between 7.5 to 4 Ma (Stern et al., 1994). A scarcity of eggshell data precludes precise conclusions about the timing of this dietary shift. Stern et al. (1994) noted that the dietary shift may have taken place as late as 3.5 Ma and suggested that differences between the timing of mammalian and ratite isotopic shifts may reflect greater dietary discrimination in the mammals.

Isotopic analyses of paleosol carbonates and organic matter from the Siwalik Group in southern Nepal record an ecological change starting ≈7.0 Ma (Quade et al., 1995a), 1.1 Ma later than the shift in Pakistan [both dates calibrated to timescale of Cande & Kent, 1995]. This shift is interpreted to mark the displacement of largely C_3 vegetation, probably semideciduous forest, by C_4 grassland in floodplain environments. C_4 biomass prior to the 7.0 Ma transition is interpreted to have been $< 20\%$ of the total. Coincident with this isotopic shift is the decline and final disappearance of leaf fossils and coalified logs from the sequence.

In a more regional examination of this isotopic shift, France-Lanord and Derry (1994) analyzed organic carbon from the Bengal Fan, which also showed a 10‰ increase in $\delta^{13}C$ beginning approximately 7 Ma. This isotopic change indicates that the expansion of C_4 habitats documented in the Siwaliks was widespread over the Himalayan foreland. The relationship between the $\delta^{13}C$ and sediments in the Bengal fan suggest that C_3 plants remained abundant in the Himalayan hinterland throughout the late Miocene and Plio-Pleistocene.

SOUTH AMERICA

SUMMARY

South America spans from about 55°S to 12°N latitude, with great topographic variation, and supports grass-dominated ecosystems over large areas (Fig. 1). Tropical and subtropical savanna, the llanos, is found associated with the alluvial plains of the Orinoco River system and the Guyana region between the Orinoco and the Amazon (Coupland, 1992c). A portion of the tablelands of Brazil, referred to as the campos cerrados, consists of open grassy savanna (campos limpos). A narrow belt of tropical to subtropical grassland occurs at middle elevations along the eastern side of the Andes from Venezuela to northwest Argentina. The largest extent of temperate grassland in South America exists in the Rio de la Plata region of central eastern Argentina (the pampas), Uruguay, and southern Brazil (the campos; Soriano et al., 1992). To the west of this region is woodland to wooded savanna, the chaco of Argentina and Paraguay (Soriano et al., 1992). In the area where Brazil, Bolivia, and Paraguay meet, there is an intermingling of the northernmost extent of chaco woodlands with a southern extension of subtropical savanna (Sarmiento, 1983). High-elevation Andean grasslands of Venezuela and Colombia are referred to as paramo. Argentina and Peru have the intermontane altiplano.

Pollen assemblages from northern South America document *Monoporites annulatus* from the early and late Paleocene (Muller et al., 1987; Rull, 1997; Fig. 4). A pantropical biostratigraphic zone, the *Mono-*

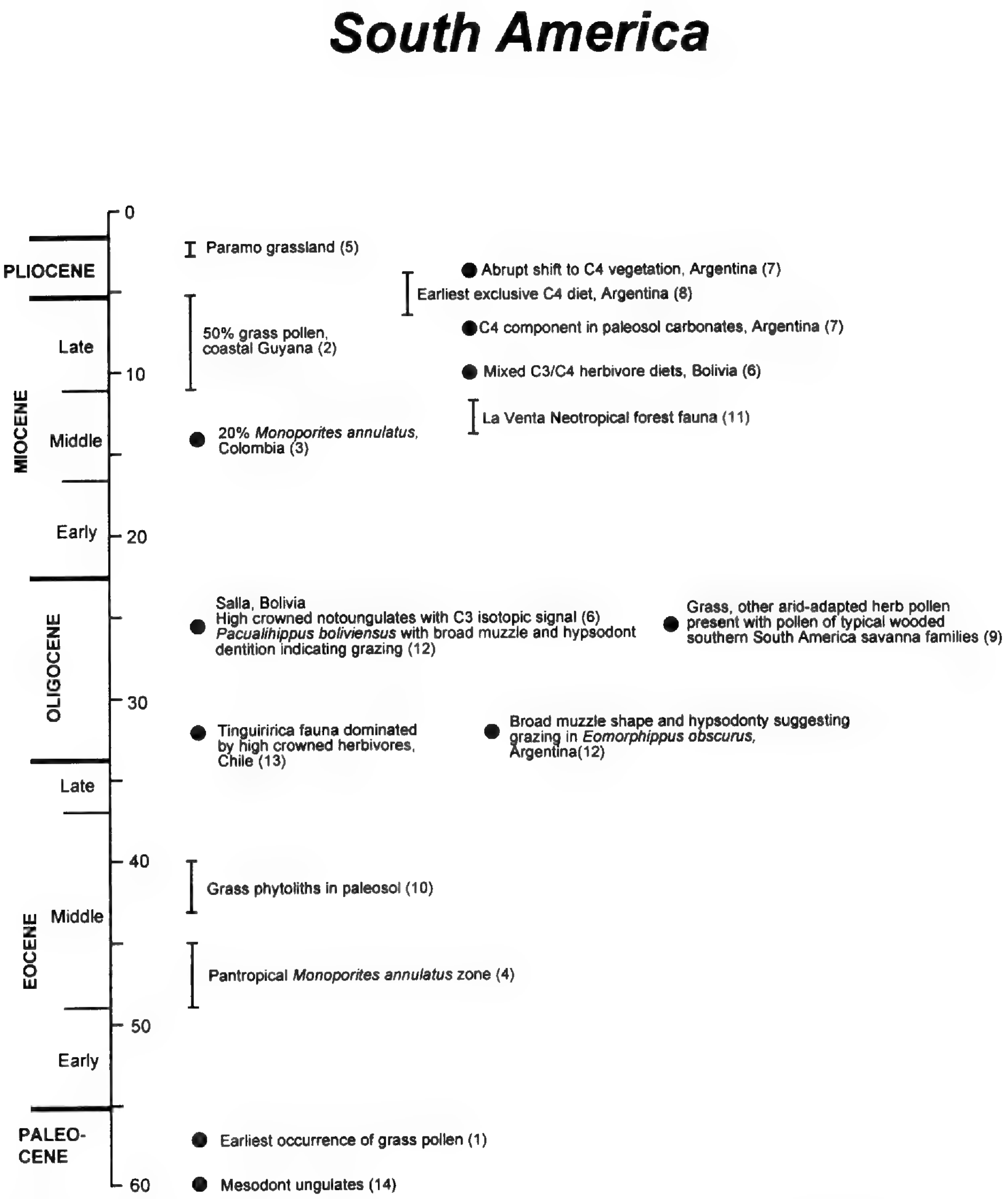

Figure 4. Summary of paleobotanical, paleofaunal, and isotopic evidence for the origin of grass-dominated ecosystems in South America. Symbols as in Figure 2. Sources: (1) Muller et al. (1987), (2) Van der Hammen & Wymstra (1964), (3) Hoorn (1993), (4) Germeraad et al. (1968), (5) Wijninga (1996), (6) MacFadden et al. (1994), (7) Latorre et al. (1997), (8) MacFadden et al. (1996), (9) Romero (1993), (10) Andreis (1972), (11) Kay et al. (1997a), (12) Shockey (1997), (13) Wyss et al. (1993), (14) Pascual & Ortiz Jaureguizar (1990).

porites annulatus Zone, of late early Eocene (49–45 Ma), recognized by the consistent presence of grass pollen, is widespread in northern South America and western Africa (Germeraad et al., 1968). Several taxa found today in the chacoan wooded savanna, including Poaceae, occur in Oligocene pollen assemblages (Romero, 1993). By the early Miocene, local grass-dominated areas are documented for coastal Guyana (Van der Hammen & Wymstra, 1964; Van der Hammen, 1983), but lowland forest is present in Colombia (Hoorn, 1993; Wijninga, 1996). By the middle Miocene, coastal savannas are documented in Colombia (Hoorn, 1993). High-elevation paramo grassland is present by the late Pliocene (Wijninga, 1996).

Endemic ungulates (notoungulates) first begin exhibiting increased crown height in the late Paleocene (Pascual & Ortiz Jaureguizar, 1990). The oldest fauna characterized by herbivores with high-crowned teeth is at least 31.5 Ma, and a similar-aged notoungulate has a muzzle shape indicative of grazing (Shockey, 1997). The locality of Salla (27 Ma) contains two notoungulates adapted for grazing based on muzzle shape and hypsodonty. Enamel samples of high-crowned notoungulates from the Salla section exhibit isotopic signatures consistent with a C_3 diet. The morphology of notoungulates and the known presence of grass in South America both earlier and later than Salla suggest that C_3 grasses may have been a major component in some South American late Oligocene ecosystems.

Evidence for C_4 grasses as a dietary component is first apparent in the enamel of 10 Ma herbivores from Bolivia, which yield isotopic values consistent with mixed C_3/C_4 diets (MacFadden et al., 1994). Exclusively C_4 grass diets are first recorded in the enamel of notoungulates from localities in Argentina (5.5 Ma ± 1 Ma). Paleosol carbonates from Argentina indicate a significant C_4 component in local biomes at 7.3 Ma (LaTorre et al., 1997). The C_4 component increases gradually until 3.7 Ma when there is an abrupt shift to environments comprised of approximately 70% C_4 biomass. There is no unequivocal evidence for C_4 grass-dominated ecosystems earlier in South America than North America. Overall, the vertebrate and isotope data suggest that the initial spread of grass-dominated ecosystems and the coevolution of grazing herbivores involved C_3 grasses as was the case in North America.

PALEOBOTANY

Grass pollen is documented in northern South America during the early and late Paleocene (middle Thanetian, ≈ 57 Ma; Muller et al., 1987; Rull, 1997), although Paleocene records from Argentina lack grass pollen or macrofossils (Menendez, 1971; Archangelsky, 1976). Argentine Paleocene to Eocene palynofloras represent tropical to subtropical forested environments (Menendez, 1971). At the base of the middle Eocene (≈ 48 Ma), Germeraad et al. (1968) defined a palynofloral zone for northern South America (and Africa) marked by the first regular occurrence of *Monoporites annulatus.* This coincides with grass leaf cells preserved in middle Eocene paleosols from the Musters Formation, Argentina (44°S), and interpreted along with pedological features to indicate an environment similar to modern pampas (Andreis, 1972). In addition, the Eocene to Oligocene Sarmiento Formation (≈ 45°S) contains loess units thought to have been formed on an extensive plain (Spalletti & Mazzoni, 1979). Romero (1993) reported the Oligocene occurrence of pollen of Poaceae and arid-adapted herbs (Chenopodiaceae), shrubs (Ephedraceae), and families characteristic of the chacoan woodlands today, suggesting the origin of South American wooded savanna communities at that time. Unfortunately, the amount of grass cover is not discernible from any of these studies.

Pollen assemblages from the southern tip of Chile (≈ 50°S), estimated to be Eocene to early middle Oligocene in age, are dominated by *Nothofagus* Blume species associated with gymnosperms and ferns (Fasola, 1969). Menendez (1971) noted a northward retreat of tropical floristic elements from Argentina and concomitant expansion of cool-temperate taxa in the late Eocene and early Oligocene. He suggested that significant aridification of the Patagonian region of Argentina did not take place until the late Miocene or early Pliocene as a result of Andean uplift, which would have cut off the source of moist Pacific air masses (Menendez, 1971).

Coastal pollen cores from Guyana document palynological zonation for much of the Tertiary with hiatuses during parts of the Oligocene, Miocene, and Pliocene (Van der Hammen & Wymstra, 1964). *Monoporites annulatus* occurs infrequently in samples from the Oligocene through the Pliocene, and rarely exceeds 10%. However, two samples from the early Miocene section of the Shelter Belt core obtain abundances of more than 10% grass pollen; one contains about 43% grass pollen (Van der Hammen & Wymstra, 1964). Van der Hammen (1983) interpreted these records to indicate savanna similar to that of today in northern South America by the Miocene.

Pollen records from the Colombian Andes of northern South America document substantial uplift of the mountains between the middle Miocene and late Pliocene (Hoorn, 1993; Hoorn et al., 1995; Hoogheimstra et al., 1994; Wijninga, 1996). Early and middle Miocene records from this area contain lowland forest assemblages. However, a noticeable increase from < 10% to 20% in grass pollen occurs in the early middle Miocene (Hoorn, 1993). This is interpreted as representing open grassy areas on alluvial plains (Hoorn et al., 1995). Wijninga (1996) documented the development of high-elevation paramo grassland in the high plain of Bogotá, Colombia, by the latest Pliocene. Palynological records from Central America represent lowland forest on isolated islands until at least the middle Pliocene (Graham, 1987, 1990a, b; see Burnham & Graham, 1999, this issue).

PALEOFAUNA

South America has a reasonably good vertebrate fossil record throughout the Tertiary (Scott, 1913; Webb, 1978; Simpson, 1980; Janis, 1993), with many localities located in what are now grass-dominated ecosystems surrounding the Amazon Basin.

However, fossil localities reflect latitudinal and orographic effects, just as the modern biota does.

The earliest record of hypsodonty among mammals, not just within South America, but globally, is found in Late Cretaceous and early Tertiary sudamericid gondwanatheres. This group has been considered related to multituberculates. Gondwanatheres are known from South America, Madagascar, and India, probably reflecting Late Cretaceous continental connections through Australia and Antarctica (Woodburne & Case, 1996; Krause et al., 1997). Other diverse multituberculates, all herbivores, have a geographically broad distribution in the Northern Hemisphere throughout the Cretaceous and early Tertiary, but no others, except gondwanatheres (if they are in fact multituberculates), developed high-crowned teeth, so far as is currently known. Hypsodonty, in the case of gondwanatheres, may indicate abrasive diet as in many other mammals with high-crowned teeth, but in any case, these small mammals first occur prior to the earliest fossil record of grasses.

The Tertiary record of mammals in South America is characterized by a number of endemic, increasingly high-crowned notoungulates and other taxa at least from the late Paleocene (Webb, 1978; and references therein; Cifelli, 1985; Pascual & Ortiz Jaureguizar, 1990). Pascual and Ortiz Jaureguizar (1990) reviewed faunal change as related to climate based on a multivariate analysis of South American land-mammal ages (SALMA), and using cheek tooth characters, particularly of ungulates, to indicate dietary preferences. Notoungulates with teeth becoming hypsodont first appear in the Paleocene (Riochican, approximately 60 Ma). High-crowned *Sudamerica* Scillato-Yané & Pascual, a gondwanathere, is also recorded in the Riochican.

From the Paleocene through most of the Tertiary the percentage of ungulates with higher-crowned teeth increased. The latest Eocene-early Oligocene Tinguiririca fauna of Chile (at least 31.5 Ma, possibly extending to 37 Ma; Flynn & Swisher, 1995) is dominated by high-crowned herbivores (Wyss et al., 1993). Shockey (1997) reported that the notoungulate *Eomorphippus obscurus* Ameghino from the Cañandón Blanco locality, Argentina, which he considers roughly the same age as the Tinguiririca fauna, has hypsodont teeth and a broad muzzle characteristic of grazers.

By 27 Ma (Deseadan, late Oligocene; Kay et al., 1997; MacFadden et al., 1985; Naeser et al., 1987), *Pascualihippus boliviensis* Shockey, another notoungulate with hypsodont teeth and a broad muzzle characteristic of grazers, was present at Salla, Bolivia (Shockey, 1997). The environment of Salla has been interpreted as being semiarid because of the large percentage of species with high-crowned teeth. The Salla primate *Branisella* Hoffstetter has features similar to ground-dwelling monkeys. The oldest known argyrolagid (*Proargyrolagus bolivianus* Wolff) is from Salla (Sánchez-Villagra & Kay, 1997). It is similar to elephant shrews, but has higher-crowned teeth, suggesting that it included seeds or other plant material gathered on the ground in its diet. The nasal region of *Proargyrolagus* is similar to that seen in desert heteromyid rodents.

The diverse Miocene fauna from La Venta, Colombia (13.5–11.8 Ma; Madden et al., 1997), is reviewed in Kay et al. (1997a). The site is located in what was at the time a Miocene peninsula in the equatorial tropics. Kay and Madden (1997) summarized the evidence for a forest environment, including the presence of a fish that exploits periodically flooded forest, forest reptiles and birds, diverse arboreal marsupials, sloths with climbing adaptations, mostly low-crowned ungulates, forest-dwelling bats, and arboreal monkeys. Five genera of primates are known from the Monkey Unit at La Venta, the number of sympatric genera today characteristic of neotropical forest receiving 1500–2000 mm annual rainfall (Kay et al., 1997b; Fleagle et al., 1997). Of the approximately 80 species of mammals recorded, only one has been suggested to be a grazer, and that is the large and rather aberrant toxodontid notoungulate *Pericotoxodon platignathus* Madden (Madden, 1997).

Ecological variation across the continent is indicated because ungulates at higher latitudes are in general more hypsodont than those at lower latitudes. Taken as a whole, middle to late Miocene diversity declined in most of South America, although hypsodont mammals seem to prevail. Caviomorph rodents, which are the only rodents occurring in South America until the Pliocene (3.5 Ma; Jacobs & Lindsay, 1984; Baskin, 1986), have fundamentally lophodont and relatively high-crowned teeth, even among the early members of the group. Their first occurrence is in the Tinguiririca fauna. During the Miocene their diversity increased, reaching a maximum in the late Miocene. The general trend in rodents was toward increased height of tooth crown and increased body size, some reaching exceptionally large size, and filling grazing niches (Simpson, 1980; Vucetich, 1984, 1986; Cifelli, 1985). After about 3 Ma, grazing horses and proboscideans entered South America via the Panamanian land bridge.

The early and widespread development of hypsodonty in South American ungulates (compared to

North American ungulates) as a response to a diet of grass has long been debated (Patterson & Pascual, 1972; Simpson, 1980; Stebbins, 1981). The mammalian fossil record is consistent with the presence of a significant grass component throughout most of the Tertiary in South America. Grass sufficient to support true grazers was present in the west-central portion of the continent, and by extension, at higher latitudes, by 27 Ma. By 31.5 Ma (minimum estimate), the Tinguiririca fauna may represent woodland or savanna grasslands as suggested by Flynn and Swisher (1995; see also Wyss et al., 1993).

STABLE ISOTOPES

Isotopic evidence for the spread of C_4 biomes in South America suggests a more complex transition to C_4 vegetation than seen in North America. Analyses of the enamel of high- and low-crowned endemic notoungulates and pyrotheres (another endemic ungulate group), as well as immigrant taxa, from Oligocene to Pleistocene fossil localities in Bolivia indicate mixed C_3/C_4 diets by about 10 Ma (MacFadden et al., 1994). Exclusively C_4 diets are not documented until the Pleistocene. Estimated paleoelevations for the middle to late Miocene Bolivian sites are 1800 m or less. MacFadden et al. (1994) concluded that if C_4 grasses were widespread they would be detected isotopically. The high-crowned dentition of notoungulates from the site of Salla (27 Ma) are interpreted as grazing adaptations (see discussion of *Pascualihippus boliviensis* above), suggesting that the C_3 dietary signal reflects the presence of C_3 grasses.

Paleosol carbonate and fossil enamel from sediments exposed in northwest Argentina indicate that although C_4 grasses were present as a dietary component by 7.6 Ma, C_4-dominated habitats were not apparent in the local landscape until about 3.7 Ma (Latorre et al., 1997). Paleosol carbonates show a gradual increase in the C_4 component starting 7.3 Ma with a sharp increase in C_4 biomass at about 3.7 Ma, interpreted as indicating 70% C_4 cover.

Carbon isotopic analyses of 65 fossil mammal tooth specimens from a number of low- to middle-elevation sites in Argentina ranging from late Oligocene to late Pleistocene also provide evidence for a late Miocene carbon shift (MacFadden et al., 1996). Their data show that herbivore enamel samples older than the Huayquerian SALMA (9–6.5 Ma) exhibit exclusively C_3 dietary signatures. During the Huayquerian, more positive $\delta^{13}C$ values of mammalian enamel indicate mixed C_3/C_4 in addition to pure C_3 diets. Exclusively C_4 diets are first apparent in herbivores of Montehermosan age (6.5 to 3.9 Ma). Preliminary analyses of the $\delta^{13}C$ composition of high-crowned mammals younger than 8 Ma collected from lowland sites spanning about 15° of latitude in Argentina and Bolivia indicate an isotopic gradient proportional to latitude. Paleoenvironmental reconstructions range from open C_4 grasslands at low-latitude sites (21° to 27°S) to mixed C_4 grassland/C_3 browse habitats at higher-latitude sites ($\approx$ 35°S).

AFRICA

SUMMARY

The modern savannas and grasslands of Africa are among the best known in the world because of the spectacular mammalian communities associated with them. A large portion of the African continent consists of grass-dominated ecosystems (Fig. 1). Semi-desert grassland occurs to the north and south of the Sahara. In central Africa, grassland savanna to woodland occurs north, south, and east of the equatorial forests. Grass-dominated environments continue into southern Africa and are widespread except in the Namib and Kalahari deserts, the southeastern coastal forest zone, and the unique sclerophyllous shrub communities (fynbos) of the South African Cape (White, 1983). Highveld grassland occurs on the high (1220–2150 m) plateau of the interior of South Africa.

The earliest record of grass in Africa is the occurrence of *Monoporites annulatus* in Paleocene pollen samples from Nigeria (Fig. 5). A core from coastal Cameroon and a Miocene to Pleistocene core from the Niger Delta document forest communities beginning in the Oligocene and expansion of grass-dominated communities beginning in the middle Miocene (Salard-Cheboldaeff, 1979, 1981; Morley & Richards, 1993).

The macrofloral record in eastern Africa documents a range of early to late Miocene environments including woodland or wooded savanna and wet and dry forests (Chaney, 1933; Chesters, 1957; Hamilton, 1968; Yemane et al., 1985; Jacobs & Kabuye, 1987; Jacobs & Deino, 1996), consistent with paleosol isotopic signals indicative of mixed C_3/C_4 environments (Kingston et al., 1994). Grass pollen and macrofossils occur at Fort Ternan, Kenya, dated at 13.9 to 14.0 Ma (Shipman et al., 1981), a site with a rich mammalian fauna consistent with a heterogeneous landscape. Abundant grass pollen in East African Pliocene samples indicates the presence of widespread grass-dominated environments by that time (Bonnefille, 1995).

The vertebrate record of the East African early

Africa

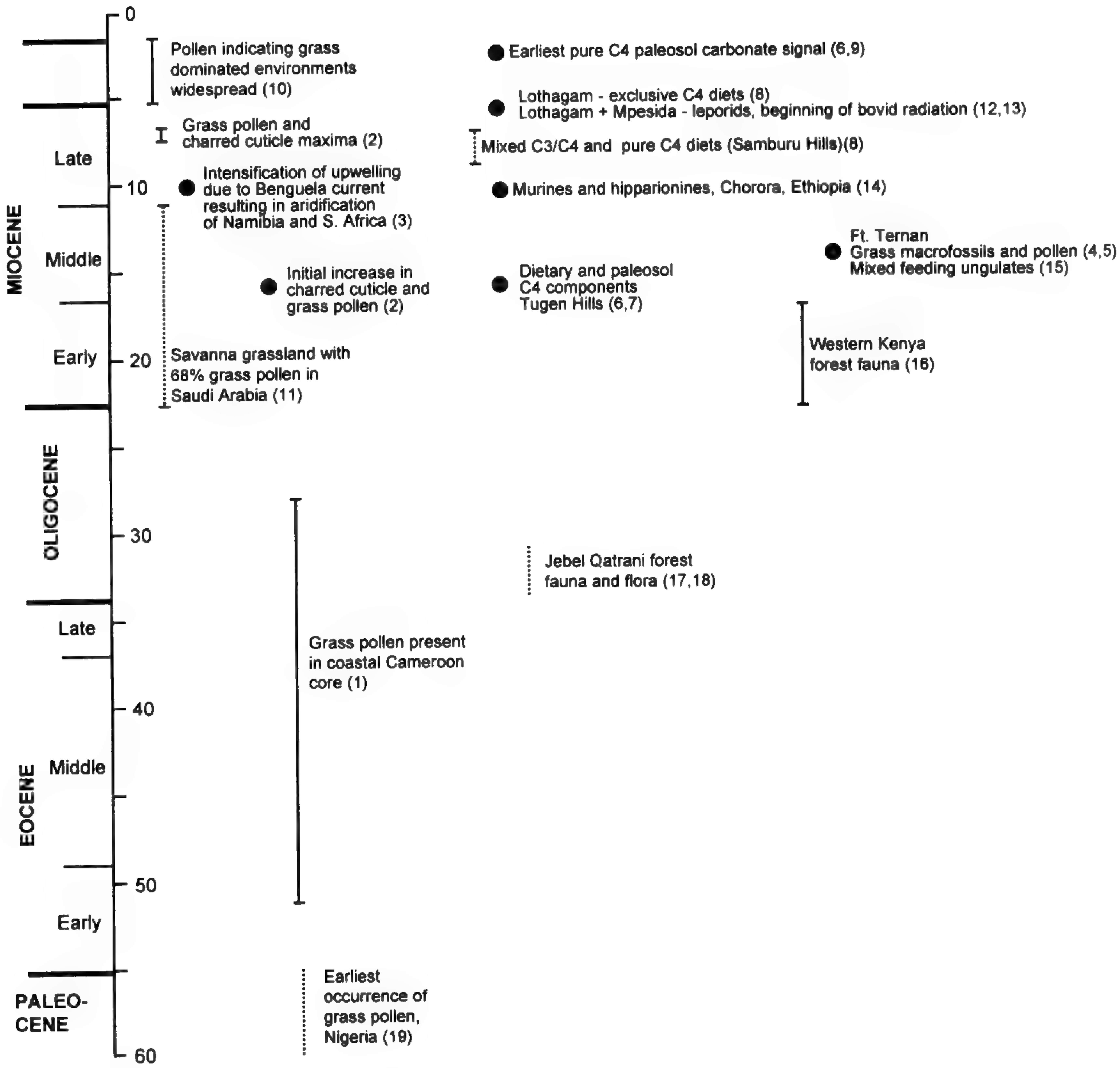

Figure 5. Summary of paleobotanical, paleofaunal, and isotopic evidence for the origin of grass-dominated ecosystems in Africa. Symbols as in Figure 2. Dashed lines indicate temporal uncertainty for the locality. Sources: (1) Salard-Cheboldaeff (1979, 1981), (2) Morley & Richards (1993), (3) Siesser (1978), (4) Dugas & Retallack (1993), (5) Bonnefille (1984), (6) Kingston et al. (1994), (7) Morgan et al. (1994), (8) Leakey et al. (1996), (9) Cerling (1992), (10) Bonnefille (1995), (11) Whybrow & McClure (1981), (12) Leakey et al. (1996), (13) Vrba (1995), (14) Hill et al. (1985), (15) Cerling et al. (1997a), (16) Andrews et al. (1997), (17) Rasmussen et al. (1992), (18) Bown et al. (1982), (19) Adegoke et al (1978).

Miocene indicates a variety of mixed habitats, giving way to more open, but still mixed, environments by at least 15 Ma. A major change in the East African fauna occurs between 8.5 and 6.5 Ma (Hill, 1995; Leakey et al., 1996), including the first introductions of high-crowned rabbits and porcupines, and significant turnover in hippos, giraffes, bovids, rhinos, and elephants. Rodents with high-crowned teeth in Namibia indicate more open conditions in southwestern Africa than in the eastern portion of the continent during the early part of the Miocene. Regional differentiation is also evident at approximately 5 Ma.

Based on isotopic analyses of fossil herbivore enamel collected from the northern Kenya rift valley, a C_4 dietary component is evident by middle Miocene times (Morgan et al., 1994), but it is not until the late Miocene that there is evidence for significant intake of C_4 biomass. Paleosol data from the Tugen Hills also indicate that C_4 plants comprised a minor part of the local ecosystems by middle Miocene times (Kingston et al., 1994). Interestingly, there is no unequivocal paleosol data from East Africa indicating C_4-dominated ecosystems similar to the modern Serengeti grasslands until well into the Pliocene (Cerling, 1992; Kingston et al., 1994).

PALEOBOTANY

Africa has an interesting paleobotanical record derived from macrobotanical remains of leaves, fruits, seeds, and wood that provide a detailed view of local vegetation, marine cores that provide a large-scale view of vegetation change on land from pollen and cuticle transported out to sea, terrestrial pollen assemblages that sample at an intermediate scale between marine cores and macrobotanical sites, and indirect evidence of past vegetation change based on modern plant systematics and biogeography. The marine cores provide data relevant to the origin of grass-dominated ecosystems in equatorial Africa because they are continuous over long time intervals and sample a broad region; macrobotanical and terrestrial pollen sites reflect more local vegetation and are discontinuous through time and space.

Monoporites annulatus pollen is first found in Africa in sediments of the Kerri-Kerri Formation of Nigeria. The taxonomic composition of this assemblage was used to determine that the formation is Paleocene in age (Adegoke et al., 1978).

Pollen contained in core sediments from coastal Cameroon document the presence of *Monoporites annulatus* pollen in early Eocene assemblages described as ". . . une quantité relativement importante de Monocotyledones (Gramineés et Palmiers) . . ." (Salard-Cheboldaeff, 1981: 412; 1979). The same pollen zone is identified in South America. Interestingly, grass pollen drops out of the African core record from the middle Oligocene to the early Miocene, the limit of the core (Salard-Cheboldaeff, 1979). Concurrent with the disappearance of grass pollen is an increase in forest taxa diversity documenting the spread of lowland tropical vegetation in West Africa during the middle Tertiary (Salard-Cheboldaeff, 1981).

A core from the Niger Delta beginning in the early Miocene and continuing to the Holocene documents changes in extent of West African savanna, and by inference, changes in aridity, based on grass pollen and charred grass cuticle assumed to be from a savanna environment (Morley & Richards, 1993). Earliest Miocene sediments in the core contain about 2% grass pollen and no charred cuticle. The pollen percentage increases to about 10% and charred cuticle to about 2% by 16 Ma. With some variation, these relative percentages remain 15% or less until a hiatus between 11 and 8.5 Ma. After 8.2 Ma both grass pollen and charred cuticle increase substantially. During the late Miocene grass pollen fluctuates between a few percent to just over 50%. There are two late Miocene maxima of charred grass cuticle (25 to 30%) at about 7.5 and 6.8 Ma. Grass pollen decreases markedly at the base of the early Pliocene but increases again around 4.5 Ma. Pleistocene relative percentages of grass pollen are over 40% with maxima approaching 60%. Charred cuticle does not exceed 20%. This record is interpreted as indicating an equable, wet climate during the early Miocene when little or no grass-dominated vegetation would have been present in West Africa. An expansion of grass cover is inferred for the middle Miocene ($\approx$ 16 Ma), but its extent is difficult to determine. The high percentages of grass pollen and charred cuticle during the late Miocene indicate periods of marked aridity with strong seasonality of rainfall. Savanna extended over most of the Niger Delta (Morley & Richards, 1993).

Deep Sea Drilling Program cores 363 and 362 off the coast of Namibia document the development of upwelling associated with the Benguela Current, which today is responsible for dry air masses and Namibia's arid climate (Siesser, 1978). On the basis of diatom productivity and sedimentation rates, cold upwelling was weak and sporadic from the late Oligocene to the middle Miocene, intensifying markedly around 10 Ma. Aridification of the Namib Desert may have begun at this time (Siesser, 1978), a hypothesis consistent with the Namibian vertebrate record.

Plant macrofossils of Oligocene age from the Jebel Qatrani Formation, Fayum Depression, Egypt, have affinities with extant Indomalaysian and African taxa. The assemblage represents a forest on the southern shore of the Tethys (Bown et al., 1982). The flora includes *Cynometra* L., a genus with several extant mangrove species.

Pollen core samples from coastal Saudi Arabia are attributed to the early Miocene Dam or middle Miocene Hofuf formations, which are indistinguishable in the subsurface (Whybrow & McClure, 1981). One of five samples contains primarily terrestrial pollen, including 68% grass and 26% nonforest taxa. The other four samples are dominated by pollen of aquatic vegetation and grasses. Together with fossil root casts identified as from mangrove plants in the Dam Formation, the assemblages are interpreted as representing an inland savanna grassland and a coastal region with freshwater marshes and mangrove vegetation. The rainfall regime is considered to have been seasonal, perhaps monsoonal (Whybrow & McClure, 1981). More recent examination of the same root casts (Whybrow et al., 1990) has revealed morphology with affinities to the family Fabaceae, which includes plants adapted to a wide variety of environments including coastal settings.

Early Miocene plant macrofossil sites from East Africa preserve both wet and dry forest, and in some cases, woodland assemblages. Leaf and wood floras from the eastern and western Ethiopian Plateau include dry forest taxa having affinities with modern Central and West Africa (Lemoigne et al., 1974; Lemoigne, 1978). Wood from Welkite, Ethiopia, shows semi-diffuse porous wood, crystals in parenchyma cells, and evidence of fire trauma, indicating a seasonally dry environment (Lemoigne, 1978). The Ethiopian sites are not dated radiometrically, but are considered early Miocene based on stratigraphic position and by comparison with other African Tertiary floras.

Flowers, fruit, and leaves from Bukwa, Uganda, underlie a 22 Ma volcanic flow (Walker, 1968, 1969; Brock & Macdonald, 1969). The assemblage has taxa with affinities to extant Ugandan forest trees such as *Bersama abyssinica* Fresen. (Melianthaceae) and *Cola cordifolia* (Cav.) R. Br. (Sterculiaceae, Hamilton, 1968). Another horizon at Bukwa contains an autochthonous leaf bed consisting primarily of grasses not identified below the family level. However, rhizomes identified as *Juncellus laevigatus* (L.) C. B. Clarke demonstrate the presence of an alkaline lake and indicate that the associated grasses are near-shore or aquatic (Hamilton, 1968).

The Bugishu flora of Uganda occurs in association with early Miocene volcanics of Mt. Elgon and contains leaves, fruit, and wood (Chaney, 1933). A total of 12 taxa comprise genera found today in dry forest or woodland. The ecology of modern relatives and the relatively small size of the leaves (when compared to Eocene leaves studied by Chaney) led to the conclusion that the flora represents savanna or savanna woodland with a dry season, although no grass fossils are reported from Bugishu (Chaney, 1933).

A small leaf flora from the Republic of Congo is considered middle Tertiary in age and is dominated by the monotypic palm genus *Sclerosperma* Mann & H. Wendland today found only in swampy areas of Central and West Africa (Lakhanpal, 1966). A wood assemblage from the Republic of Congo, associated with early Miocene mammalian fossils, contains four Fabaceae and two Meliaceae species (Lakhanpal & Prakash, 1970). Nearest living relatives occur in wet or dry forests. Two of the fossils are related to genera having species that occur in woodlands today.

The largest and most diverse assemblage of plant macrofossils from the early Miocene of equatorial Africa comes from Rusinga and Mfwangano islands, Lake Victoria, Kenya (Chesters, 1957). The age of the localities is 17.8 Ma (Drake et al., 1988). The flora contains several tree taxa found today primarily in wet forests of Central and West Africa. The abundance of lianas (half of the reported species) was taken by Chesters (1957) to indicate gallery forest, although the flora has been reinterpreted as indicating lowland wet forest (Andrews & Van Couvering, 1975).

The middle Miocene paleobotanical record of Kenya is represented by Ft. Ternan in western Kenya, and Kabarsero, in central Kenya. The fauna of Ft. Ternan, dated at 13.9–14.0 Ma (Shipman et al., 1981), has been studied extensively. A pollen assemblage is dominated by grass pollen (54%), with the remainder of the spectrum being aquatic and montane species (Bonnefille, 1984). The pollen of montane species are interpreted to have come from nearby volcanic highlands, while the local vegetation was an open woodland. An autochthonous assemblage of grass blades preserved in volcaniclastic sediment has been interpreted as representing Africa's earliest wooded grassland flora and compared with the modern Serengeti (Retallack et al., 1990; Dugas & Retallack, 1993), which is populated currently by C_4 grass species. Ft. Ternan grass specimens were assigned to five extinct species in three extant genera, two of which are C_4, and one of which is C_3 today (Dugas & Retallack, 1993). Carbon isotope studies of paleosols at Ft. Ternan document a strong C_3 signal, which indicates a minor role at best for C_4 grasses (Cerling et al., 1991, 1997a). This discrepancy between a paleoenvironment consisting of widespread C_4 grasses (as interpreted based on the grass fossils), and the C_3 carbon isotope signal may indicate that the fossil grasses were not C_4 photosynthesizers (but some possessed epidermal morphology similar to living C_4 species), or that C_4 species were uncommon in the plant community and had little or no effect on the isotope signal. Given that the fossil-bearing exposures at Ft. Ternan are limited to < 200–$300\ m^2$, the aerial extent of this past community is not known; thus, the scale implied by use of the Serengeti as a modern analogue may be inappropriate.

The Tugen Hills, a mountain range within the eastern rift in central Kenya, contains fossiliferous sediments that range in age from 16 Ma to the present. Fossil plant localities occur at 12.6, about 9.0, and 6.8 Ma. The oldest, Kabarsero, is an autochthonous assemblage of leaves, twigs, and fruit from a moist forest with taxonomic affinities to Central and West Africa (Jacobs & Kabuye, 1987, 1989; Jacobs & Winkler, 1992; Jacobs & Deino, 1996). Waril (≈ 9 Ma) contains a lacustrine assemblage of seasonally dry vegetation similar to that found associated with wooded savanna today; however, no grass fossils are known from this assemblage.

The late Miocene Kapturo site (6.8 Ma) consists of an assemblage of leaves of deciduous woodland or dry forest taxa (Jacobs & Deino, 1996), but no grass has yet been found. An approximately contemporaneous site from about 10 km to the southeast of Kapturo, the Mpesida forest, preserves abundant fossil wood in volcanic matrix. Preliminary identifications indicate affinities with Central and West African forest taxa, some species of which occur in montane settings today.

A sequence of lacustrine pollen samples from the Chilga region of the Ethiopian Plateau overlies a volcanic unit dated at 8 Ma (Yemane et al., 1985). The assemblages contain abundant wet lowland forest taxa with affinities to extant Central and West African flora. Grass pollen grains, present in some of the 46 spectra, occur in low percentages when compared with modern East African savanna soils and never exceed 27%.

Pollen samples from a variety of East African Pliocene localities consistently contain high percentages (> 50%) of grass pollen (Bonnefille, 1995), indicating a background of widespread grass-dominated environments. Changes in the amount and composition of relatively less abundant arboreal pollen indicate variations in the extent of woodland and forest vegetation (Bonnefille, 1995, and references therein).

Biogeographic analyses of extant equatorial African plants and animals document disjunctions between the coastal forests of East Africa and those of Central and West Africa. Because disjunctions occur at more than one taxonomic level in plant families (Faden, 1974), butterflies (Carcasson, 1964), and birds (Moreau, 1966), more than one period of isolation between the forests of East and Central Africa is likely. Faden (1974) postulated that the initial biogeographic isolation of the two regions took place during the middle Miocene when a nearly continuous equatorial forest belt is thought to have been replaced in East Africa by more xeric plant communities such as those found between forest remnants today (see also Carcasson, 1964; Andrews & Van Couvering, 1975; Axelrod & Raven, 1978). However, the variety of environments now known from the Miocene of the rift valley do not support a simple unidirectional breakup of continuous forest in the middle Miocene. Rather, a more heterogeneous landscape is likely throughout the Miocene in both time and space.

Paleogene and early Neogene plant fossils are uncommon in South Africa. Chronological control is especially difficult. Nevertheless, probable early Miocene pollen and macrofossil localities are interpreted as indicating subtropical woodland with swamps for the southwestern Cape, and subhumid subtropical woodland for northwest South Africa (Scott, 1995). Aridification of these regions is associated with the intensification of the Benguela Current in the early late Miocene (Coetzee, 1978; Scott, 1995).

PALEOFAUNA

The Tertiary vertebrate record of Africa (including the Arabian Peninsula) is sporadic and discontinuous (Winkler & Jacobs, 1993). Paleogene localities are concentrated in the far north with only one locality of early Oligocene age found south of the Equator (in Angola, Rasmussen et al., 1992), and its composition is consistent with localities farther to the north. At least 23 mammalian species, including the primate *Altiatlasius* Sigé, Jaeger, Sudre & Vianey-Liaud, are known from the Late Paleocene of the Ouarzazate Basin, Morocco (Sigé et al., 1990; Gheerbrant, 1992, 1994, 1995). The fauna includes endemic taxa but shows affinities with Europe and North America. All of the specimens are small, suggesting to Gheerbrant (1995) that the fauna was hydrologically sorted and biased against large specimens. Marsupials, elephant shrews, primates, and hyracoids, as well as endemic rodents and other taxa occur in Eocene faunas (Rasmussen et al., 1992; Court, 1993a).

The best known and most diverse African Paleogene fauna is that of the Jebel Qatrani Formation of the Fayum Depression, Egypt, constrained by a radiometric age of 31 Ma on an overlying basalt (Fleagle et al., 1986; Bown & Kraus, 1988). The Jebel Qatrani Formation spans the Eocene-Oligocene boundary and produces fossils of both late Eocene and early Oligocene age (Van Couvering & Harris, 1991; Rasmussen et al., 1992). At least 43 mammalian genera are known, including marsupials, pangolins, ptolemaiids, elephant shrews, primates, rodents, carnivorans, hyracoids, anthracotheres, proboscideans, and arsinotheres (Van Couvering & Harris, 1991; for species, see Bown et al., 1982, who listed 70 mammalian species plus over 20 species of other vertebrates). Within this suite, primates, hyracoids, and rodents are particularly diverse. The environment of the Jebel Qatrani Formation has been studied from a number of perspectives and appears to represent mangrove swamps near the coast, giving way to forest. This is consistent with the diversity of arboreal primates and other taxa.

The recent analysis of the postcranial skeleton of *Arsinotherium* Beadnell by Court (1993b) is interesting because of the large size and heavy dental wear of this taxon, which was previously interpreted as indicating arid savanna. However, Court (1993b) showed that the hindlimbs and pelvic girdle were weak in comparison to other large terrestrial mammals, that the forelimbs were capable of movement consistent with propelling the body forward in subaqueous locomotion, and that the limbs were graviportal with spreading feet. *Arsinotherium* was not built for prolonged terrestrial locomotion, but rather lived much of its life in water, moving by antebrachial extension and brachial retraction, its hind legs trailing behind. Its locomotion on land was not ambulant, but a slow rolling progression over soft wet substrates. Furthermore, the dentition may indicate a specialized method of browsing not represented among modern herbivores (Court, 1992; Janis, 1995).

The early Miocene in western Kenya is well known from such sites as Meswa Bridge, Mteitei Valley, Koru, Legetet, Chamtwara, Songhor, Mfwangano, and those on Rusinga Island, ranging in age from ≈ 23 Ma to ≈ 17 Ma. The faunas from these sites are not uniform, but all appear to represent forested environments based on mammalian community structure and indicator species (Andrews & Van Couvering, 1975; Van Couvering & Van Couvering, 1976; Andrews et al., 1979; Evans et al., 1981; Drake et al., 1988; Savage, 1989). The faunas are characterized by the presence of diverse primates, scaly-tailed flying squirrels, and various other rodents, tenrecids (Jacobs et al., 1987), elephant shrews (including the earliest record of the extant genus *Rhynchocyon* Peters (Novacek, 1984), tragulids, and other taxa.

Forest faunas characterize the beginning of the middle Miocene as well, although early middle Miocene faunas are not homogeneous and vary from site to site (Hill et al., 1991; Winkler, 1992). By 14.7 Ma (Feibel & Brown, 1991), the fauna from Maboko, with its relative abundance of the browsing artiodactyl *Climacoceras* MacInnes, reduction in the number of forest species, relatively abundant monkeys, and derived rodents, suggests woodland (Andrews et al., 1981; Evans et al., 1981; Winkler, 1997, 1998).

The middle Miocene site of Fort Ternan (13.9–14.0 Ma, Shipman et al., 1981) is important because it has a diverse fauna of approximately 48 species, including primates. Its environmental interpretation has become central to the issue of east African forests opening up into grass-dominated ecosystems (see Andrews & Evans, 1979; Evans et al., 1981; Kappelman, 1991; Shipman, 1986). Most recently, tooth microwear in the giraffid *Palaeotragus primaevus* Churcher and the bovids *Kipsigicerus labidotus* Thomas and *Oioceros tanyceras* Gentry from Fort Ternan was examined (Cerling et al., 1997a). *Kipsigicerus labidotus* and *O. tanyceras* are the two most common species in the fauna. Muzzle shape in *Palaeotragus* Gaudry and *Kipsigicerus* Thomas was also evaluated. Results indicate that *Palaeotragus* and *Oioceros* Gaillard were browsers, although *Oioceros* may have had habits similar to that of the common waterbuck, an extant species atypical in being adapted to grazing near waterlogged habitats. *Kipsigicerus* was a mixed-feeder, meaning that it would both browse and graze. Thus, grass may have made up part of the diet in *Oioceros* and *Kipsigicerus* at Fort Ternan (Cerling et al., 1997a), a conclusion consistent with the interpretations of Shipman (1986) and Shipman et al. (1981).

The sequence of middle Miocene localities in the Baringo Basin, Kenya, provides a well-calibrated, if sporadic, record between ≈ 13 Ma and 6 Ma, which documents a number of significant faunal changes. Hipparionine horses first occur in the Baringo sequence at Ngeringerowa (Hill et al., 1985), considered to range in age from 9.5 to 8.5 Ma (Hill, 1995), consistent with the age suggested by Flynn and Sabatier (1984) based on the relationships of rhizomyid rodents. The Ngeringerowa record of hipparionines is younger than the accepted date of 10.5 Ma for the Chorora Formation of Ethiopia, which contains both hipparionines and murine rodents (Jacobs, 1985; Winkler, 1994). In North Africa, the first record of hipparionines and the murine *Progonomys* is at Bou Hanifia, Algeria, which Woodburne et al. (1996) suggested may be as young as 9.5 Ma, although its lower age limit is set by an underlying radiometric date of approximately 12 Ma. The significance of murine rodents is that, from their introduction into Africa in the middle Miocene to the present day, they have generated a current diversity of over 100 species, and they are the most abundant group of rodents inhabiting African grass-dominated ecosystems. Their evolutionary history in Africa is closely tied to the development of those ecosystems, even to the extent that in the modern Serengeti grasses as food resources are partitioned between ungulates and the African grass rat (*Arvicanthus niloticus* Lesson), a murine (Senzota, 1983). Nevertheless, in the fossil record, the faunas of the Baringo Basin do not indicate the clear and consistent presence of a grass-dominated ecosystem throughout the middle Miocene.

In the late Miocene an important faunal change is recorded in the Mpesida Beds of Baringo ($\approx$ 6 Ma) and farther north at Lothagam ($<$ 7.9 Ma) with the introduction of porcupines, rabbits, and with turnover in hippos, giraffes, bovids, rhinos, and elephants (Leakey et al., 1996). The fauna has significant woodland elements (Cifelli et al., 1986; Leakey et al., 1996), but it also heralds the advent of a major bovid radiation in Africa (Vrba, 1995). Throughout the Miocene, the general impression of environments derived from fossil vertebrates ranges from forest to woodland, with a trend from more forested to more open environments. There is no strong evidence of Serengeti-style grasslands in eastern Africa during the Miocene.

The Miocene record from southern Africa is sparse, but several localities in southern Namibia are generally similar to those of eastern Africa (Hendey, 1978). However, more open environments than those of the early Miocene in eastern Africa may be indicated especially by the rodents, which include more hypsodont species than their east African counterparts (Flynn et al., 1983; Winkler, 1994), and in the dearth of arboreal primates in southern Africa. The younger locality of Arrisdrift is correlated with Maboko (Hendey, 1978), suggesting a middle Miocene age of approximately 15 Ma. The fauna includes suids, selenodont artiodactyls, an ochotonid, and other elements consistent with a riparian woodland. Given the early and middle Miocene faunal record of southern Namibia, the inception of the Namib desert postdates the middle Miocene. The fauna of Langebaanweg in the Cape Province of South Africa (not in the Namib Desert) is probably between 5 and 4 Ma and includes the earliest record of groove-toothed rats of the grass-eating muroid subfamily Otomyinae (Pocock, 1976; Jacobs. 1985), which, along with other taxa and evidence of fires, suggests an open environment in southern Africa at that time (Hendy, 1982).

STABLE ISOTOPES

Isotopic data relevant to the development of grass-dominated ecosystems in Africa are derived primarily from middle Miocene to Pliocene sites in the rift valleys of northern and western Kenya as well as Tanzania. As discussed earlier, the site of Ft. Ternan (13.9 to 14.0 Ma) in western Kenya has been the focus of a number of paleoecological studies. Interest in Fort Ternan was originally largely generated by the interpretation that specimens of *Kenyapithecus* Leakey recovered from the locality were central to understanding the evolution of hominids (Leakey, 1967; Simons, 1963). As *Kenyapithecus* was considered to be a hominid, there followed the implication of bipedality, which characterizes the family, and therefore of grasslands, in which bipedality was hypothesized to have evolved.

Despite the interpretation of some plant macrofossils at the site as C_4 grasses (Dugas & Retallack, 1993), carbon isotopic analysis of paleosol carbonate and associated organic matter did not yield isotopic values consistent with C_4 vegetation (Cerling et al., 1991). Isotopic values were so depleted that Cerling et al. (1991) speculated that closed canopy conditions may have prevailed during formation of the paleosols. Subsequent analyses of fossil herbivore enamel from Fort Ternan indicated diets comprised of essentially pure C_3 plants (Cerling et al., 1997a).

Based on existing isotopic data at the time, Cerling (1992) concluded from analyses of paleosol carbonates collected from a number of hominid localities in Kenya and Tanzania that the proportion of C_4 biomass in East African ecosystems increased gradually over the last 10 Ma, culminating in pure C_4 savanna grasslands during the middle Pleistocene. He noted that the earliest evidence for C_4 plants was from paleosol carbonates collected from Ngeringerowa (9.4 Ma), in the Tugen Hills, which yielded isotopic values indicating $\approx$ 20% C_4 biomass.

An isotopic study focusing on paleosol carbonates and associated organic matter from the Tugen Hills succession in the Kenya rift valley indicates that heterogeneous mixed C_3/C_4 habitats characterized this portion of the rift valley over the last 15.5 myr (Kingston et al., 1994). These isotopic data record habitats with predominantly C_3 vegetation (on average $>$ 65%) and suggest that C_4 grasses at no time dominated this portion of the rift valley during the Neogene. Associated paleosol organic matter from the Tugen Hills indicate a minor C_4 component until sometime between 8.5 and 6.5 Ma when there is an increase in paleosols yielding C_4 organic components. The carbon isotopic composition of fossil herbivore enamel from the Tugen Hills suggests that C_4 grasses were a minor dietary component at 15.3 Ma, but that there was a significant shift to a reliance on C_4 plants in addition to C_3

vegetation as a primary dietary resource sometime between 8.5 and 6.5 Ma (Kingston, 1992; Morgan et al., 1994).

Preliminary studies of the carbon isotopic composition in mammalian tooth enamel from Lothagam (≈ 7.9 to 3.7 Ma) and the somewhat older Namurungule Formation in the Samburu Hills of Kenya indicate mixed C_3/C_4 and exclusive C_4 diets throughout these horizons (Leakey et al., 1996). Published data relating to the chronology of the Namurungule Formation is limited, but radiometric dates on bracketing lavas (Matsuda et al., 1984) indicate that the sediments are between 13 and 7 Ma. A fossiliferous horizon within the Namurungule Formation, which has yielded a hominoid maxilla, has been dated to 9.5 Ma (Sawada et al., 1997, 1998), but the stratigraphic position of analyzed enamel relative to the dated horizon is unknown. Cerling et al. (1997b) interpreted tooth enamel carbon isotope data from sites in western Kenya, the Turkana basin, the Baringo Basin, and the Suguta depression as indicating a shift from C_3-dominated to C_4-dominated diet in equids and elephantids between ≈ 8 and 7 Ma.

Stable carbon isotopic values of paleosol carbonate collected from the upper Baynunah Formation in Abu Dhabi (8–6 Ma) record the presence of both C_3 and C_4 vegetation at the time during which the soils formed (Kingston, in press). Lateral variability in the $\delta^{13}C$ of pedogenic carbonate implies a heterogeneous environment, roughly analogous to what would be expected in a modern grassy woodland habitat. None of the paleosol carbonates analyzed yielded $\delta^{13}C$ values indicative of open grassland. While an analysis of 34 Baynunah enamel specimens representing five herbivore families indicates that both C_3 and C_4 plants were available for consumption, there appears to be a heavy reliance on C_4 grasses with a significant number of taxa falling within the isotopic niche occupied by committed grazers. The interpretation is that the paleosol carbonates formed in more wooded environments flanking a river system, while many of the herbivores grazed in more open grassland or wooded grassland distal to the channel.

Analyses of terrestrial fauna, flora, and lithofacies from a limited number of Tertiary sites in the Arabian Peninsula (summarized in Kingston & Hill, in press) suggest that this region may have supported forested habitats in the Eocene and Oligocene. Paleoenvironmental data from early to middle Miocene sequences in eastern Saudi Arabia and part of western Abu Dhabi indicate more open habitats with limited closed habitat areas, possibly along river or lake margins.

AUSTRALIA

SUMMARY

The continent of Australia covers a wide latitudinal range from about 38°S to 11°S, with climates supporting tropical, subtropical, arid, and temperate vegetation. The interior is vast, and grass-dominated environments are widespread, covering a large area of the continent (Fig. 1). Savanna woodland and low tree and shrub savannas range across the central portion of the continent, except in the most interior region, which is desert (Cole, 1986). Savanna variants also occur in the northern and northeastern part of the country.

The earliest record of grass from Australia is in a middle Eocene pollen flora from the western part of the continent (Frakes & Vickers-Rich, 1991; Fig. 6). In southern Australia, around the Eocene-Oligocene transition, there is a decline in species richness among forest pollen taxa, possibly indicating cooling climate (Kemp, 1978; MacPhail et al., 1994). A major change in vegetation takes place beginning around 14 Ma when samples show an increase in charcoal and Asteraceae pollen with minor increases in grass, indicating a change to drier, more open, sclerophyll forest (Martin, 1990a). In eastern Australia, at approximately 4.5 Ma there is a brief resurgence of closed, wet forest followed by an abundance of grass, other herbaceous pollen, and charcoal, indicating open grass-dominated environments (Martin, 1981, 1990a; MacPhail, 1996).

The paleofauna of Australia is unique, dominated by marsupials, and lacks placental ungulates. Faunas prior to the middle Miocene are interpreted as representing forested environments. During the middle Miocene, familial and generic diversity decreases, and by the late Miocene hypsodont wombats are present. Arboreally adapted species decline throughout the Miocene, and grazing kangaroos are present by the early Pliocene.

There are no relevant stable carbon isotope data from Australia.

PALEOBOTANY

Australian pollen floras, particularly from the eastern and southern parts of the continent, provide a regional sample of vegetation change throughout the Tertiary. Macrofossil assemblages are uncommon except in the Eocene (Christophel, 1981; Greenwood, 1994). As a result of the uneven geographic distribution of paleobotanical sites, vegetation history for the arid interior region of the continent is relatively poorly known.

Eocene macro- and microfloras are uniformly in-

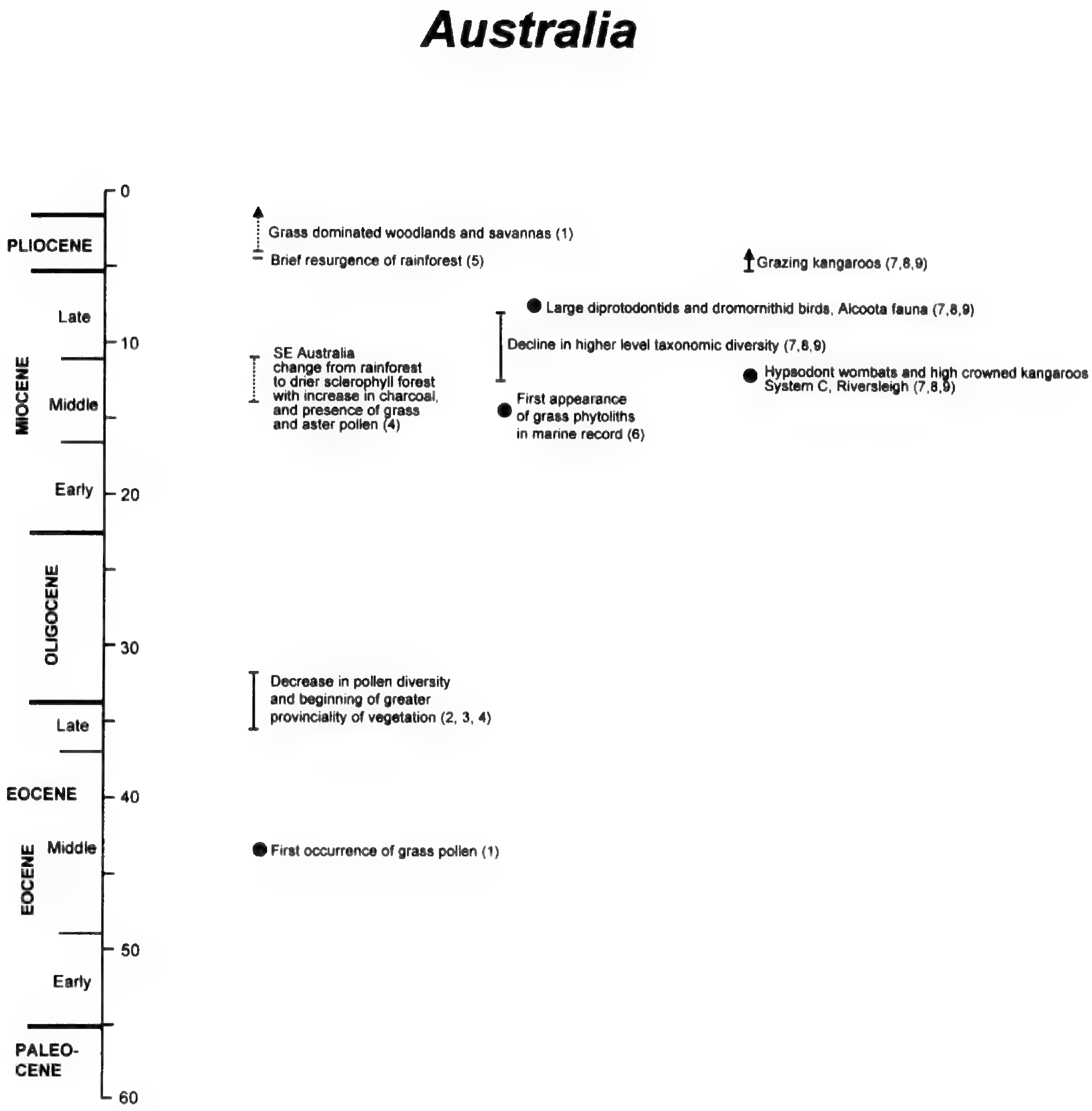

Figure 6. Summary of paleobotanical, paleofaunal, and isotopic evidence for the origin of grass-dominated ecosystems in Australia. Symbols as in Figures 2 and 5. Sources: (1) Martin (1994), (2) MacPhail (1994), (3) Archer et al. (1995), (4) Kemp (1978), (5) Martin (1990a), (6) Locker & Martini (1986), (7) Archer et al. (1994a), (8) Archer et al. (1994b), (9) Archer et al. (1995).

dicative of tropical or closed forest (Kemp, 1978). The hallmark of Australian palynofloras from the late Eocene through the middle Miocene is the presence of *Nothofagus* pollen, most significantly, *Nothofagus* subg. *Brassospora* Philipson & Philipson [formerly, *N. brassii*-type, a fossil taxon with extant species in New Guinea, New Caledonia, and the New Hebrides (Martin, 1981; Kershaw et al., 1994)]. *Nothofagus* subg. *Brassospora* pollen becomes abundant in the late Eocene and indicates cool, rainforest vegetation (Kemp, 1978; Martin, 1990a; Archer et al., 1995). Diversity decline in southern Australia between the middle and late Eocene may indicate cooling (Kemp, 1978), and the spread of *Nothofagus* subg. *Brassospora* is taken to indicate a change from megathermal rainforest in the early Eocene to mesothermal rainforest in the middle to late Eocene (MacPhail et al., 1994). Early to late middle Eocene southern Australian plant macrofossils also indicate forest conditions, but document local floristic variations in space and time not clearly evident from pollen assemblages (Christophel, 1981, 1994, 1995; Greenwood, 1994).

Oligocene to early Miocene macrofossils from Tasmania document the presence of rainforest containing Podocarpaceae, *Nothofagus* spp., Proteaceae spp., and other diverse angiosperms. Affinities lie with the lower montane rainforests of New Guinea and northernmost montane forests of New South Wales (Carpenter et al., 1994). Oligocene palynofloras are restricted to the southeastern margin of the continent and Tasmania. They indicate lower diversity than Eocene floras and further cooling in southern Australia at the Eocene-Oligocene transition (MacPhail et al., 1994). Coal and some forest taxa indicate wet conditions, although probably not as wet as the Eocene (Kemp, 1978; Greenwood, 1994; Archer et al., 1995). Physiognomically, Oligocene plant macrofloras show evidence of environments drier than the Eocene by the presence of smaller, sclerophyllous leaves (Christophel, 1995). In addition, the mesic indicators of the Eocene are replaced in Oligocene to Miocene macrofloras by such taxa as *Eucalyptus* L'Hér., *Banksia* L. f. (Proteaceae), *Allocasuarina* L. Johnson, and *Casuarina*, which have extant relatives in drier environments (Christophel, 1995). Grass pollen is present in western Australia by the late middle Eocene (≈ 40 Ma, Frakes & Vickers-Rich, 1991, and references therein) but is extremely rare until at least the early Miocene, when it is present in small amounts, constituting not more than approximately 10% of assemblages at inland sites in eastern Australia (Kershaw et al., 1994).

A palynoflora from the late Oligocene to early Miocene Namba Formation in central Australia was originally reported to contain abundant grass pollen and interpreted as an open, grass-dominated environment (Callen & Tedford, 1976; discussed in Archer et al., 1995). In a reanalysis, Martin (1990b) discovered that much of the grass-like pollen is in the family Restionaceae rather than Poaceae. Also present in the assemblages were algae (*Botryococcus* Kützing and *Pediastrum* Meyen), Cyperaceae, and Sparganiaceae, all indicators of a wetland environment and leading to the conclusion that the site was a marsh. Napperby and Hale River from the arid interior of Australia are tentatively dated to middle Eocene on the basis of palynological indicator fossils (Truswell & Harris, 1982). Both pollen floras contain taxa not usually found until the Neogene, including Cyperaceae, *Callitris* Vent., and *Micrantheum* Desf. at Napperby, and as much as 2% grass pollen at Hale River. The remainder of the pollen assemblages have more typical arboreal taxa, such as *Nothofagus*. subg. *Brassospora*, *Podocarpus* L'Hér. ex Pers., and *Casuarina* (Truswell & Harris, 1982). The vegetation reconstruction is forest with grass growing in small clearings (Truswell & Harris, 1982). Paleogene pollen assemblages of New Zealand compare favorably with vegetation reconstructions for southern Australia including the dominance of *Nothofagus* subg. *Brassospora* from the latest Eocene to early Miocene (Pocknall, 1989, 1990).

A major change in pollen floras occurs in the middle to late Miocene, beginning about 13 Ma, and documented primarily in southeastern Australia. *Nothofagus* subg. *Brassospora* disappears, Myrtaceae increase (including both dry and wet-adapted *Eucalyptus* and other rainforest taxa in this family), and grass and Asteraceae pollen occur in low percentages (Martin, 1990a; Kershaw et al., 1994). At the same time, the occurrence of charcoal in pollen samples begins to increase. Marine records document the first appearance of grass phytoliths at 14.4 Ma (Locker & Martini, 1986; Martin, 1990a). The changes in pollen and charcoal indicate tall, open, wet sclerophyll forest where eucalypts form the canopy and rainforest taxa grow in the understory (Martin, 1990a; Kershaw et al., 1994). The change to drier sclerophyll forest during the middle to late Miocene in southeastern Australia indicates increased provincialism among plant communities. Although there is some evidence for differences among regional floras during the early Tertiary, by the middle to late Miocene increasing aridity resulted in greater distinctions between northern wet, interior dry, and southern cool wet regions (Martin, 1990a; Christophel, 1995).

At about 4.5 Ma, a short-lived resurgence of rainforest taxa (including *Nothofagus* spp. other than *Nothofagus*. subg. *Brassospora*) is indicated in pollen records of the southeast (MacPhail, 1996). After this, a substantial increase in the relative percentages of Asteraceae and Poaceae pollen concomitant with high charcoal counts and a dramatic increase in grass phytoliths in marine cores indicate a change to open woodlands, savannas, and grasslands (Locker & Martini, 1986; Martin, 1981, 1990a).

PALEOFAUNA

The sporadic fossil mammal record of Australia, much of which is only loosely constrained temporally, is summarized in Archer et al. (1994a, b, 1995), Vickers-Rich et al. (1991), and Woodburne et al. (1994). Due to its long zoogeographic isolation, the composition of its Cretaceous and early Tertiary mammal fauna, and the dynamics among the early Tertiary fauna as the continent assumed its rigid isolation, Australia has a distinct marsupial-dominated fauna, lacking placental ungulates except those introduced by humans for agricultural purposes. Browsing and grazing roles throughout the Tertiary, played most conspicuously by ungulates on other continents, are filled mostly by larger kangaroos and wombats in Australia. The dental and skeletal modifications of these marsupials are different from those of placental ungulates; thus, the criteria used in interpreting environmental structure from morphology are somewhat different. Studies of morphology and diet with respect to Australian herbivores and functional similarities between kangaroos and ungulates include Janis (1990a, b), Sanson (1989, 1991), and Wright et al. (1991). The development of high-crowned teeth remains a reliable indicator of abrasive diet, often associated with a diet of grass. However, Janis (1990a) determined that most functional differences in teeth and skulls between kangaroos and ungulates are related to food handling and tooth occlusion. Moreover, Janis (1988) suggested that large kangaroos without markedly hypsodont teeth, but with other dental adaptations (Janis, 1990c), might facilitate feeding by selecting and manipulating food with their forelimbs, discarding grit and dust before ingestion.

Prior to the late Oligocene, the mammalian fauna is poorly known. The Eocene Tingamarra fauna (Godthelp et al., 1992; see Woodburne & Case, 1996, for a discussion of problems with the dating) contains about a dozen taxa of mammals recovered with frogs, turtles, crocodiles, and birds. All of the mammals are small and none appears to exhibit folivorous or other herbivorous adaptations. The locality is interpreted as representing a swamp or shallow lake. The record becomes better in the late Oligocene and early Miocene, with faunas best known from South Australia where chronology of the earlier faunas is constrained by paleomagnetic stratigraphy (Woodburne et al., 1994), and from the Riversleigh area (the Low Lyon fauna and others in stratigraphically designated systems A and B) in Queensland, farther to the north. As summarized by Archer et al. (1995), the South Australia sites (Ditjimanka, Ngapakaldi, and Ngama of the Etadunna Formation) produce a mammalian fauna less diverse than correlated faunas from Riversleigh. The interpretation is that of a relatively open, wet forest community. The overlying Kutjamarpu fauna has some taxonomic similarity to system B and C faunas from Riversleigh. None of the South Australia sites is interpreted as having significant grassland habitat. At Riversleigh, faunas are more diverse and are interpreted to represent rainforest communities. No high-crowned grazers are known from the early Miocene, although there are terrestrial browsers (macropodids and diprotodontids), as well as arboreal folivores, frugivores, and omnivores.

Middle Miocene faunas from Australia include the Bullock Creek fauna in the Northern Territory and those from System C (Dwornamor, Ringtail, Henk's Hollow) in the Riversleigh area, where there is a reduction in mammalian families and genera and turnover in species between System B and System C. Herbivorous mammals are abundant, suggesting the presence of rainforest, but not open forests. The presence of frog species whose modern relatives produce bubble nests suggests that the temperature remained below 20°C, when such nests would be utilized. Within the lower portion of System C, generic diversity in arboreal pseudocheirid possums declines. In the upper levels of System C, rainforest frogs are rare. Wombats of System B are low crowned. In contrast, only hypsodont wombats are present in most of System C assemblages. At the Encore Site, from the uppermost System C (late Miocene or possibly late middle Miocene), only rootless (hypselodont) wombats are present.

The Bullock Creek fauna of the Northern Territory has relatively fewer arboreal species, and it is dominated by a large species of the diprotodontid *Neohelos* Stirton, which also occurs in upper System C at Riversleigh. The genus *Neohelos* shows an increase in size through the Miocene. A rare, relatively high-crowned kangaroo is the only evidence of grazing, although abundant terrestrial browsers and reduced arboreal species are consistent with a more open habitat than that at Riversleigh.

The Alcoota fauna of the late Miocene (perhaps 7–8 Ma) in the Northern Territory is dominated by large diprotodontids and dromornithid birds, such as *Dromornis stirtoni* Rich, one of the largest known birds in the world. Arboreal mammals are extremely scarce. Macropodids and diprotodontids have dentitions suggestive of browsing. The Northern Territory site of Ongeva is younger, possibly 5–6 Ma, but is similar to the Alcoota. The mammalian fossil record of the Pliocene suggests further decrease in forested area and aridification of the central portion of the continent.

Australia's unique dry country fauna, derived from equally curious endemic rainforest antecedents (without the addition of ungulates from other continents), is known as the "Green Cradle Concept" (Archer et al., 1994b). The decline in species with arboreal adaptation and the increase in species adapted to more open habitats occurred through the Miocene, with the early Pliocene and younger times being characterized by grazing kangaroos.

Discussion and Conclusions

At the outset of this review we posed three fundamental questions: When do grass-dominated ecosystems first appear? Do grass-dominated ecosystems become established synchronously around the world? Is the evidence from paleobotanical, vertebrate, and isotopic data concordant? It has become clear that the origin and spread of grass-dominated ecosystems is synonymous with the evolutionary history of the Poaceae itself, and that the paleobotanical, paleofaunal, and isotopic records, individually and in concert, elucidate the major phases in that history, even if only in the most general way.

The major phases in the origin of grass-dominated ecosystems appear to have been: (1) latest Cretaceous or early Tertiary origin of Poaceae; (2) the opening of Paleocene and Eocene forested environments in the early to middle Tertiary; (3) an increase in the abundance of C_3 grasses during the middle Tertiary; (4) the origin of C_4 grasses in the middle Miocene; and (5) the spread of C_4 grass-dominated ecosystems at the expense of C_3 grasses in the late Miocene (Fig. 7).

Phylogenetic analyses of living grasses based on molecular, morphological, and anatomical characters are concordant in placing Joinvilleaceae as the sister group to Poaceae (Kellogg & Linder, 1995; Duvall & Morton, 1996; Kellogg, 1998; Soreng & Davis, 1998). Bambusoideae, Pooideae, and Oryzoideae are primitive subfamilies (which may form a clade) and must have originated early in the history of Poaceae, but their relative positions are unresolved (Renvoize & Clayton, 1992; Duvall & Morton, 1996; Kellogg, 1998). The remaining subfamilies, all of which include C_4 photosynthesizers, resulted from later radiations within the family, consistent with their younger fossil record. Resolution of the early evolution of grasses must eventually be understood through macrofossils. However, with the exception of the rare North American Eocene and Oligocene specimens, unequivocal early Tertiary grass macrofossils are currently lacking (Thomasson, 1987).

Grasses are predominately wind pollinated and able to survive seasonal climates, leading to reasonable speculation that grasses first evolved in an open environment (Stebbins, 1987), near a forest margin (Renvoize & Clayton, 1992), or in warm-temperate, subtropical, tropical dry, or seasonally dry, environments (Crepet & Feldman, 1991; Soreng & Davis, 1998). The consistent presence of *Monoporites annulatus* pollen during the early Tertiary in northern South America (Germeraad, 1968) and western Africa (Adegoke et al., 1978; Salard-Cheboldaeff, 1979, 1981) indicates that diversification may have taken place in the tropics at that time. Romero (1993) hypothesized that South American chacoan woodlands, which today have a significant grass ground cover, may have originated in the Oligocene, based on palynological assemblages. Paleogene paleobotanical records from the Northern Hemisphere indicate that grass was not a significant ground cover (Leopold & MacGinitie, 1972; Frederiksen, 1991; Leopold et al., 1992).

Clear evidence of widespread grass-dominated ecosystems does not occur until the early to middle Miocene, albeit with the intriguing possibility that grasses played a significant role in Paleogene communities of South America and West Africa. In the Northern Hemisphere, grass does not appear dominant by any criterion until the Miocene, during which time all five subfamilies of the Poaceae, and both C_3 and C_4 photosynthetic pathways, are present in North America, as documented by plant macrofossils. However, only in the late Miocene does a distribution of C_4 grasslands similar to that of the present day become established, as brought to light by isotopic analyses.

Turning to the relevance of the paleofaunal record, mammalian herbivores can be characterized by the structure of their teeth, which in turn can be correlated with ecological and environmental criteria related to the diet of the animal. Such relationships allow the ecological history of communities, as well as taxonomic composition, to be evaluated through time. Although some multituberculates occurred in the Mesozoic, the origins of most mammalian herbivore diversifications were Paleocene and Eocene in age. During that interval, forests were widespread. Mammalian herbivores were predominately low-crowned folivores and frugivores. Browsers having teeth with distinct ridges (lophodont and selenodont) became increasingly more common toward the end of the Eocene and Oligocene. Grazing mammals elaborated on those patterns, especially in the Miocene, by increasing crown height.

Jernvall et al. (1996) evaluated mammalian herbivore molar patterns in the Eocene of North America and Eurasia relative to molar patterns in the Miocene. Their approach was focused on the morphology of the crown of second molars as distinct ecological types independent of phylogeny and without regard to taxonomy. Twenty-eight crown types were identified in early Tertiary perissodactyls, artiodactyls, and primitive ungulates, or condylarths. Of those basic crown types, only eight are currently found in extant perissodactyls and artiodactyls. In the Eocene, the basic crown types were

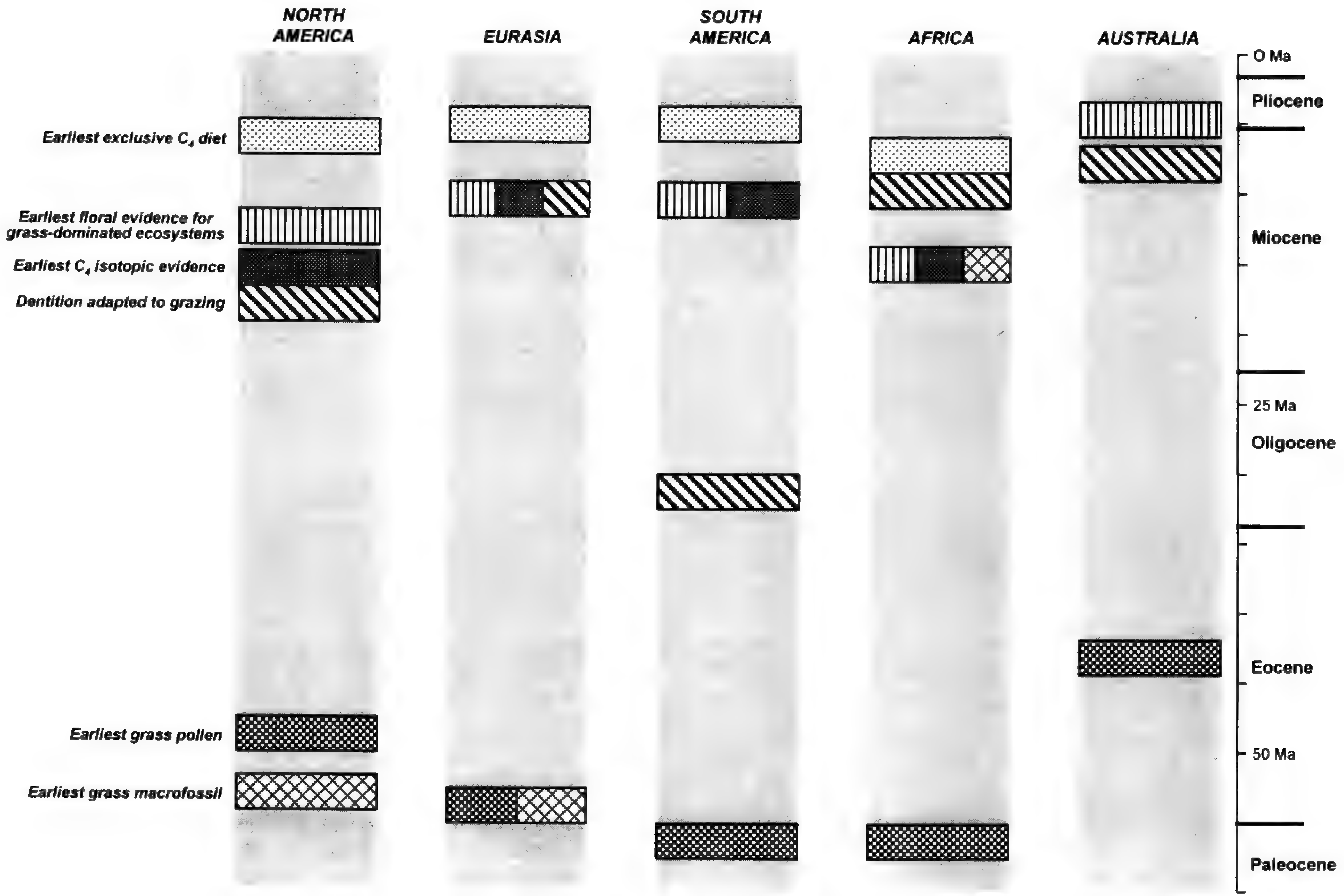

Figure 7. Generalized summary of the establishment of grass-dominated ecosystems during the Tertiary in North America, Eurasia, South America, Africa, and Australia based on paleobotanical, paleofaunal, and isotopic evidence. Patterns defined on the left apply to all columns; their order of appearance may vary.

possessed by only a few genera each, suggesting that in the early Tertiary radiation of herbivorous mammals, morphological diversification matched taxonomic diversification. Morphological diversity in crown types increased from the early to the late Eocene, followed by a decline in morphological diversity of basic crown types during the Oligocene (see also Janis, 1997).

On the other hand, Jernvall et al. (1996) found that herbivorous ungulates of the Miocene presented a very different pattern from the herbivores of the early Tertiary. Taxonomic diversification of ungulates in the Miocene was at the familial level or lower and did not lead to a similar diversity of crown types as was the case in the early Tertiary. After the Eocene, ungulate dental morphology comprised fewer basic crown types, but in the remaining types the development of lophs and ridges increased. Morphological differentiation among remaining lophodont crown types became greater, even though the total number of crown types was less than in the early Tertiary. The recurrent trend was to increase lophs in teeth, often accompanied by increased crown height, both traits related to the processing of tough, fibrous vegetation of relatively low nutritive value (Jernvall et al., 1996). Assuming a similar availability of resources, the resultant morphological disparity within a few basic crown types probably reflects greater partitioning of resources among Miocene ungulates and perhaps other taxa, as compared to the adaptive radiation of early Tertiary herbivores. The trend toward lophodonty is seen in North America, Europe, and Asia, although the basic morphological types on which the lophodont patterns are built vary among these regions, reflecting the taxon-independent ecological significance of the morphological trends.

Pascual and Ortiz Jaureguizar (1990) also noted that early Tertiary taxa are diverse but show fewer extremes of morphological differentiation than later in the Tertiary when morphologies became more divergent. In Australia, the Miocene record might show a comparable pattern with communities later in the Tertiary having fewer higher-level taxa than earlier (Archer et al., 1995). On every continent, more or less independently from other continents, the herbivore fauna was uniquely adapting along with global and regional climatic conditions that affected vegetation, and hence the food resource, which included substantial grass at some time during the middle Tertiary.

Thus, the trend toward lophodonty became prevalent in the late Eocene, affecting different taxa in different regions. In North America, Europe, and Asia, primarily perissodactyls and artiodactyls among larger mammals became lophodont. In South America, it was mainly notoungulates and other endemic ungulate groups. In Australia, marsupials eventually become lophodont. In Africa, although the record is poor and not representative for most of the continent, hyracoids exhibited the trend. In fact, we would predict that if the record for the Oligocene were to become better known, especially from northwestern Africa, diverse lophodont high-crowned hyraxes, perhaps elephant shrews, would be discovered. The patterns on different continents, so far as they can be compared, emphasize the global ecological significance of these trends. However, the differences in the starting points for each continent also help to explain some other profound biogeographic differences: such as why equids exhibit their tremendous evolutionary radiation of high-crowned forms primarily in North America, which feeds minor radiations in Eurasia through dispersal events; or why bovids are prevalent today in Africa but never had a comparable diversity in North America, an issue of relevance when evaluating the adaptive patterns and ecological deployment of bovids versus equids (see also Janis, 1976).

The importance of increased lophodonty and hypsodonty in interpreting the origin of grass-dominated ecosystems is that the earliest common occurrence of hypsodonty is taken to reflect the origin of widespread grass-dominated ecosystems because grazers generally have high-crowned teeth. The obverse of the adaptation of high-crowned grazers to a diet of grass is the protective mechanisms of grass that are induced by grazing. Initial experiments showed that silica content in Serengeti grass species increased in response to grazing intensity both in the field and in laboratory leaf-clipping experiments and that silica content was highest for grasses from the most intensely grazed areas (McNaughton & Tarrants, 1983; McNaughton et al., 1985). These data supported the hypothesis that silica production is an inducible defense against herbivory (McNaughton & Tarrants, 1983) and provided supporting data for the coevolution of grasses and grazers. However, more recent studies, reviewed by Vicari and Bazely (1993), indicate a more complicated relationship. Silica as a defense mechanism in grasses appears most effective against invertebrate herbivores; its protective role against vertebrate herbivores is inconclusive, and whether silica production can be induced in individual plants is questionable. Nevertheless, the enhanced silica content in grasses generally suggests that its effects were relevant to grazers on an evolutionary time scale.

The complexity of the relationship among vertebrate and invertebrate herbivores and grasses notwithstanding, the North American record with its radiation of high-crowned equines and corresponding record of grass macrofossils and isotope studies stands out as unique. Plant macrofossils present in North America, but not documented on other continents, provide evidence of grass species diversity and evolution during the middle to late Miocene, concomitant with the well-documented contemporary evolutionary radiation of hypsodont mammals, particularly horses.

Although it seems reasonable that grasses may have been a dietary component of some early Tertiary mammals, faunal evidence indicates that large expanses of grass-dominated environments only occurred significantly later than the early Tertiary in most areas. However, morphology indicative of grazing, and therefore suggestive of a grass-dominated ecosystem, appears in South America by the Eocene-Oligocene boundary, prior to the occurrence of grazing morphology elsewhere. Moreover, grazing adaptations persist into the late Oligocene along with indications of aridity at the locality of Salla, Bolivia. Thereafter, a case can be made for grazing ungulates throughout the remainder of the Cenozoic in South America. This pattern is accepted by us as indicating that the coevolution of grazers and grasses, and the establishment of grass-dominated ecosystems, occurred prior to the early Miocene in South America.

In the Northern Hemisphere during the Oligocene, browsing mammals diversify, but there is no clear evidence of grazing animals at that time, consistent with the paleobotanical record, which indicates a lack of grassy ground cover. Grazing and mixed-feeding mammals characterize the Miocene in North America. This pattern, in contrast to that of South America, is taken to mean that co-evolution of grasses and grazers did not occur prior to the early Miocene in North America, and by extension, that grass-dominated ecosystems developed earlier in South America, although the paleobotanical record there is relatively poor.

The relevance of geochemical investigations to the origin of grass-dominated ecosystems is in identifying the isotopic signal of C_4 grasses, as opposed to that of C_3 plants. Because C_4 grasses are restricted to open terrestrial habitats and do not include forest or aquatic species, a C_4 isotopic signal clearly indicates broad grass cover and by extension, grass-dominated ecosystems. The application of isotopic techniques to the study of grassland evolution, with the consequent definition of the late Miocene spread of C_4 grasses, is a significant advance in paleoecological studies. It does not, however, signify the initial development of grass-dominated ecosystems.

Because most plants use the C_3 photosynthetic pathway and the C_4 pathway is a supplement to basic C_3 biochemistry, C_3 photosynthesis is considered the primitive state for grasses. Although grass is known from the early Tertiary, the earliest carbon isotopic records tentatively interpreted as having a C_4 component are approximately 15 Ma (Kingston et al., 1994; Latorre et al., 1997). Furthermore, the earliest plant macrofossil with Kranz (C_4) anatomy is dated to about 12.5 Ma (Nambudiri et al., 1978; Whistler & Burbank, 1992). This record suggests that C_4 grasses were present during the middle Miocene spread of grass-dominated ecosystems, even though they did not constitute a significant portion of grass biomass until later (Cerling et al., 1998). It further suggests that the co-evolution of ungulates and grass-dominated ecosystems, accepting that it is a real phenomenon, originally involved C_3 grass. This is not an unreasonable conclusion considering that C_3 grasslands occur today at higher altitudes and latitudes, such as the northern Great Plains, and that C_3 grasses are more nutritious than C_4 grasses (Akin & Burdick, 1975; Wilson & Hacker, 1987).

The timing of the shift from C_3 to C_4 grass domination in lower latitudes is striking. Between 9 and 4 Ma, an expansion of C_4 biomass has been documented in North America, South America, East Africa, and Pakistan, although the transition may have taken place in a shorter interval in some regions (Quade et al., 1989a; Cerling et al., 1997b, 1998). This major ecological shift signifies a transformation in species composition that was undetected before the application of carbon isotope studies.

C_4 grasses are characteristic of seasonal, arid, and warm environments, and they do better than C_3 plants under lower atmospheric CO_2 conditions ($<$ 400 ppmv, Ehleringer, 1991). These attributes suggest either climatic factors, or atmospheric composition, or both, controlled the spread and distribution of C_4 grass in the late Miocene. Within the scale of this review, it suggests the establishment of essentially modern seasonality and rainfall patterns in the late Miocene. In addition, higher ratios of atmospheric CO_2/O_2 during the early to middle Miocene may have allowed C_3 grasses to occupy the niche of C_4 grasses today forming extensive grass-dominated ecosystems in tropical regions.

As C_4 grasses became more widely distributed and abundant, displacing C_3 vegetation, they became the primary diet of some ungulates. In North America, the dietary shift began in the southern

Great Plains around 7 Ma and in the central Plains by about 4 Ma (Wang et al., 1994; Cerling et al., 1998). Concomitant with this dietary change is a substantial decline in equid diversity from nine to three genera (MacFadden, 1992; Cerling et al., 1998). One explanation for this species decline is a decrease in the woody vegetation and an increase in treeless grassland, thus limiting food resources needed to support a high diversity of ungulates. That explanation retains merit because diversity of browsing and mixed-feeding species declines in the North American Miocene. However, the isotope data emphasize the intriguing possibility that the change in grass species composition, from predominantly C_3 to predominantly C_4 species, could have been a causal factor in the equid diversity decline (Cerling et al., 1998). C_3 grasses have more digestible matter than C_4 grasses due largely to anatomical attributes of C_4 grasses (especially of the cell walls in bundle sheath parenchyma and vascular tissue; Akin & Burdick, 1975; Akin et al., 1983; Wilson & Hacker, 1987; Wilson & Hattersley, 1989). The decline in ungulate diversity at the end of the Miocene paralleled the spread of less nutritious grass over much of their range.

On the other hand, decrease in nutritive value of C_4 plants relative to C_3 plants may be compensated by complex interactions between herbivores and their environments. The Serengeti, a C_4 grass-dominated ecosystem, supports the most diverse and dense ungulate fauna on earth today. Although Serengeti grazers have been shown to be sensitive to food quality, differential feeding and migration by various ungulate species enables them to coexist in this grass-dominated environment (McNaughton et al., 1985). Grazing bovids appear to have increased with the origin of C_4 grass-dominated ecosystems in Africa.

The role of grass-dominated ecosystems in human evolution has long been debated. The paleobotanical record of Africa derives special significance because the development of grass-dominated ecosystems has long been considered to play a central role in the evolution of bipedality, the defining character of the human family. A traditional perception in paleoanthropology, informally referred to as the savanna hypothesis, is that as rainforests became restricted in distribution during the late Miocene, more seasonal and drier woodland and grassland habitats became more widespread. Many of the morphological and behavioral innovations documented in the fossil hominid record have been interpreted as adaptations to these more open habitats. Deciphering the timing and biogeographic distribution of the earliest grasslands in Africa is therefore critical in assessing whether the development of grass-dominated biomes, or more specifically C_4 grass-dominated biomes (Cerling et al., 1997b), was a driving force in human evolution.

East African early and middle Miocene localities represent a variety of habitats, most of which appear to be forested, but one of which (Fort Ternan, 14 Ma) contains significant grass pollen and macrofossils. However, throughout most of the East African Miocene there is no clear record of a consistent grass-dominated ecosystem, but rather a spatial and temporal pattern of environmental heterogeneity. The pollen and charred grass cuticle record from the Niger delta clearly signifies the possibility of a grass-dominated ecosystem in western Africa by about 16 Ma, peaking in the late Miocene (about 7 Ma). However, vertebrate fossils of the relevant age, including hominoids, are unknown in western Africa. If hominids evolved in the late Miocene of East Africa, there is as yet no firm evidence to link their origins with the earlier development of grass-dominated ecosystems.

Overall, the plant, vertebrate, and isotopic records, where they occur together, are concordant with respect to the origin of grass-dominated ecosystems. However, the records are of varying detail, and severely limited by the quality and distribution of localities for plants, animals, and isotopes. Moreover, they are less definitive and less constraining than is desirable. Nevertheless, the series of five major phases in the origin of grass-dominated ecosystems listed at the beginning of this section is derived from these records, which reflect not only origins but change through time. Perhaps a sixth major stage should be added in closing: The development of agricultural grasslands. All that we know of the geological history of grass-dominated ecosystems instructs us that the processes of ecosystem evolution are profoundly influenced by large-scale changes beyond human control. However, the sixth stage in the origin of grass-dominated ecosystems, in which we find ourselves now, is unique because there are aspects, such as the maintenance of floral and faunal diversity, that can certainly be influenced by considered management.

Domesticated grass species include both C_3, e.g., wheat, and C_4, e.g., corn, physiologies naturally adapted for life in distinct environmental settings. How domesticated and genetically engineered C_3 and C_4 grasses, or naturally occurring grasses for that matter, will be affected by the combined changes in temperature, rainfall, and pCO_2 that would likely be a part of a pCO_2-caused climate change cannot be realistically predicted at this time (see discussion in Hattersley & Watson, 1992). But we do know that grass physiology is sensitive to these factors, and changes in them can result in a rapid change in species distribution, as has been demonstrated for climate and grass communities at the terminal Pleistocene in North America (Kurtén & Anderson, 1980; Fredlund & Tieszen, 1997), and has been suggested to explain the patterns in the fossil and isotope records for the Tertiary. Thus, an increased understanding and deeper consideration of both modern and ancient grass-dominated ecosystems should help us anticipate species stress in response to global climate change, such as that predicted from human-induced increases in atmospheric pCO_2.

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REVISION OF *BEILSCHMIEDIA* (LAURACEAE) IN THE NEOTROPICS[1]

Sachiko Nishida[2]

ABSTRACT

The neotropical species of *Beilschmiedia* are revised here, including general descriptions for morphology, anatomy, biogeographic distribution, and seed dispersal. The systematic position of *Beilschmiedia* within the family, as well as the systematic treatment of its neotropical species, is provided. As a result, 28 species were recognized with 4 newly described and 2 newly combined; they divide into five species groupings based on their leaf anatomical characters.

Lauraceae contain many taxa that are important ecological and economical components of tropical forests. However, the taxonomy of the family has not been sufficiently clarified at either the genus or species level. *Beilschmiedia* is an example of such a poorly understood genus.

Beilschmiedia is one of the largest pantropical genera in the Lauraceae, comprising about 250 species. It is usually distinguished from other laurel genera by the following characters: bisexual and trimerous flowers, six equal to subequal tepals, six to nine fertile stamens with 2-celled anthers, staminal glands only in the third whorl, shallow receptacles, and fruit lacking cupules.

This genus is still poorly understood taxonomically. Since Meisner (1864) revised *Beilschmiedia* with the rest of the family, no revision for the entire genus has been written. For neotropical species, Kostermans's (1938) work was the most recent comprehensive revision, and Allen (1945) treated the Mexican and Central American species. These two revisional works were not based on abundant material; 7 of 15 species in Kostermans's revision and 4 of 8 species in Allen's revision were known only

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[1] This study, undertaken as part of the author's doctoral dissertation research at Kyoto University, Japan, was mainly done during a stay at the Missouri Botanical Garden. I thank Hiroshi Tobe for his encouragement, Henk van der Werff for his guidance, and all the Garden staff for their support during my stay. I also thank the curators of the following herbaria: A, B, BM, BR, C, CR, F, IEB, INB, K, LL, MEXU, NY, P, R, RB, S, U, US, and VEN. I am especially grateful to the curators of MO, NY, and RB for allowing me to remove leaves from their specimens for leaf anatomy studies. Barry Hammel, William Haber, and the INB staff, especially Renaldo Aguilar, assisted me during my fieldwork in Costa Rica. J. L. Clark and K. Thomsen kindly sent me slides or materials of *Beilschmiedia*. Roy E. Gereau, as well as Hidetoshi Nagamasu, improved the Latin diagnoses. John Myers drew the fine illustrations. This research was supported by the Grant-in-Aid for JSPS fellowships from the Japanese Ministry of Education, Science, Sports and Culture.

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from the type collections. Additionally, 15 new species have been described under *Beilschmiedia* in the Neotropics since Kostermans's revision.

Collections of neotropical *Beilschmiedia* have increased to more than eight times as many as examined by Kostermans (1938). This present revision recognizes 28 species within *Beilschmiedia*, including 4 that are new to science.

MATERIALS AND METHODS

Approximately 850 collections from A, B, BM, BR, C, F, FCME, IEB, INB, K, LL, MEXU, MO, NY, P, R, RB, S, U, US, and VEN were examined. Fieldwork was carried out in Costa Rica in March 1996 to observe the habits and habitats for several species and to collect material for anatomical study.

TAXONOMIC HISTORY

The genus *Beilschmiedia* was first described by Nees (1831) with two Asian species, *B. roxburghiana* and *B. fagifolia*. For the Neotropics, many species now classified in *Beilschmiedia* were first described under *Hufelandia*. Nees (1833) described *Hufelandia* with *H. pendula* and *H. thomaea*, and since then 12 neotropical species were described for *Hufelandia*. Hemsley (1882) transferred the generitype of *Hufelandia* to *Beilschmiedia*, but Mez (1889) subsequently restored *Hufelandia* to generic rank. Kostermans (1938) later submerged *Hufelandia* within *Beilschmiedia* again.

Synonymous with *Beilschmiedia* in the Neotropics is *Bellota* Gay. Gay (1849–1852) described *Bellota* with a Chilean species, *B. miersii*, but Kostermans (1938) submerged this species in *Beilschmiedia*. Kostermans (1938) listed three other synonyms in his revision: *Boldu* Nees (non Feuillée), *Boldus* Kuntze (non Adanson), and *Wimmeria* Nees ex Meisner. However, *Boldu* Nees is a superfluous name. *Boldus* is a name that Kuntze (1891) reestablished from *Boldus* Molina, which actually belongs to the Monimiaceae. *Wimmeria* refers to a specimen label name for *Beilschmiedia pendula* and is not validly published. Kostermans (1952) combined the neotropical genus *Anaueria* with *Beilschmiedia*. However, Richter (1981) found that *Anaueria* differs from *Beilschmiedia* in wood anatomy. This, combined with differences in flower and fruit morphology, resulted in the current recognition of *Anaueria* as a distinct genus.

MORPHOLOGY AND TAXONOMIC CHARACTERS

Habit. All neotropical *Beilschmiedia* species are trees, with many of them growing about 30 m tall, occasionally up to 40 m tall.

Leaves. Species display two patterns of phyllotaxis, one with alternate leaves and the other with opposite leaves (for the species corresponding to each phyllotaxis, see Table 1). Species with alternate leaves rarely show a subopposite leaf arrangement near the tip of the twigs. Some species such as *Beilschmiedia anay* and *B. manantlanensis* tend to have leaves crowded at branch apices.

Leaf shape ranges from ovate to obovate. Size and shape of the leaves vary within many species. Leaves of *Beilschmiedia costaricensis* and *B. tovarensis* are especially variable.

Glaucousness on lower leaf surfaces is usually consistent within a species, but sometimes exceptions occur. A few collections of *B. mexicana* and *B. riparia* have glaucous leaves, although typical collections of these two species do not. In many southeastern Brazilian species, the presence or absence of a glaucous bloom is unknown because all the collections examined were supposedly placed in alcohol.

There has been no *Beilschmiedia* species reported to have domatia, but a few collections of *B. riparia* (*Lorea 5498, Maya 1296, L. C. Rodríguez 374,* and *Wendt & Rico 4338*) that have tufts of hairs in the axils of secondary veins appear to have domatia.

Venation patterns. Terms used here are sensu Hickey (1973, 1979), Christophel and Rowett (1996), or Nishida and Christophel (1999). Venation patterns of neotropical *Beilschmiedia* species were described in detail by Nishida and Christophel (1999). All neotropical *Beilschmiedia* species have penninerved leaves. Tertiaries of *B. alloiophylla, B. anay, B. latifolia, B. ovalioides, B. riparia,* and *B. tilaranensis* are usually strongly percurrent (directly connected to adjacent secondaries); those of *B. costaricensis, B. hexanthera, B. immersinervis, B. ovalis, B. steyermarkii,* and *B. tovarensis* are often weakly percurrent. The minor venation pattern (pattern of higher-order veins) can be used to delimit neotropical *Beilschmiedia* species. According to Nishida and Christophel (1999), the species roughly divide into two groups according to their minor venation pattern being fine or coarse. In species with a fine venation pattern, the highest vein order is seventh or more, and areoles (the smallest areas of the leaf tissue surrounded by veins) are usually less than 0.5(–0.7) mm diam. (Fig. 1A, B). In a coarse venation pattern, the highest vein order is less than fifth with larger areoles over 1.5 mm diam. (Fig. 1C). For species corresponding to each pattern, see Table 1. The veinlet pattern within areoles ranges from none (without a free-ending veinlet inside as in Fig. 1A) to branched

Table 1. Species groupings within neotropical *Beilschmiedia* based upon morphological and anatomical characters. Species with asterisks (*) were not examined for leaf anatomy.

	Phyllotaxis	Minor venation pattern	Cuticular characters	Vascular bundle arrangement in midrib	Species name	Rough geographical distribution
B. costaricensis group	alternate	fine	*B. costaricensis* type	ring	*B. alloiophylla*	Central America, Andes
					*B. anay**	Central America
					B. costaricensis	Central America, Andes
					B. hexanthera	French Guiana
					B. immersinervis	Central America
					B. latifolia	Andes
					B. mexicana	Central America
					B. ovalioides	Central America
					B. ovalis	Central America
					B. pendula	Central America, West Indies, northern South America, Andes
					B. riparia	Central America
					B. steyermarkii	Central America
					B. tilaranensis	Central America
					B. tovarensis	Central America, Andes
B. curviramea group	opposite	coarse	*B. curviramea* type	ring	*B. angustifolia*	Southeastern Brazil
					B. curviramea	Guianas
					*B. emarginata**	Southeastern Brazil
					*B. fluminensis**	Southeastern Brazil
					B. linharensis	Southeastern Brazil
					B. rigida	Southeastern Brazil
					*B. stricta**	Southeastern Brazil
					*B. taubertiana**	Southeastern Brazil
B. hondurensis group	opposite	coarse	*B. hondurensis* type	flattened arc	*B. angustielliptica*	Central America
					B. brenesii	Central America
					B. hondurensis	Central America
					*B. manantlanensis**	Central America
B. miersii group	opposite	coarse	*B. miersii* type	flattened arc	*B. miersii*	Chile
B. berteroana group	opposite	coarse	*B. berteroana* type	flattened arc	*B. berteroana*	Chile

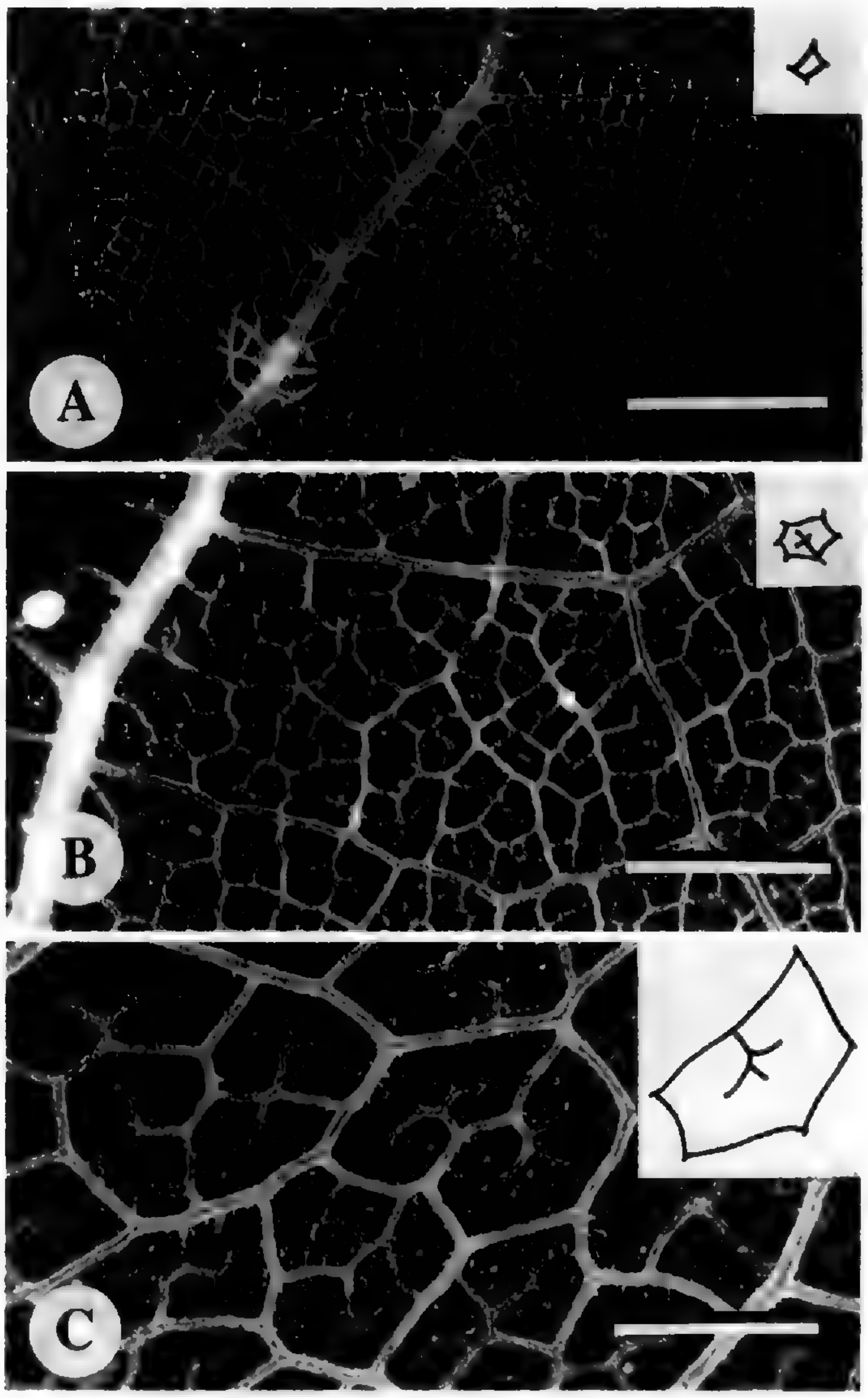


Figure 1. X-ray patterning for minor venation in neotropical *Beilschmiedia* species. —A. Fine, *B. mexicana* (*Rubio 2209*, MO). —B. Fine, *B. costaricensis* (*Bello 4882*, MO). —C. Coarse, *B. hondurensis* (*Gentle 7292*, MO). Line drawing in each corner = an areole. Scale bars = 2 mm.

(with branched, free-ending veinlets inside as in Fig. 1B) for species with a fine venation pattern. Veinlet pattern within areoles is usually branched (Fig. 1C) for species with a coarse venation pattern.

Indumentum. Indumentum can be used to delimit species, but it sometimes varies even within a species. Hairs of neotropical *Beilschmiedia* species (Fig. 2) divide into three types by their orientation (appressed, ascending, erect) and straightness (straight, wavy, curly). Appressed hairs are always straight, appearing to be somewhat silky and shiny (Fig. 2A). Ascending hairs are also straight, but their orientation is looser than the appressed ones (Fig. 2B). Erect hairs can be straight, wavy, or curly (Fig. 2C, D, E, respectively). Minutely tomentulose pubescence with short curly hairs is sometimes referred to as "appressed" in treatises, but here it is classified as erect because the orientation is not basally appressed but erect. Straightness of the hairs sometimes varies on different parts of the plant. For example, hairs on inflorescences are usually erect even in the species with appressed hairs on the terminal buds and twigs. The orientation of hairs on terminal buds and twigs is usually stable enough to delimit the species, but hair straightness is relatively variable within species, especially in *B. alloiophylla* and *B. anay.*

Inflorescences. Inflorescences of neotropical *Beilschmiedia* species are mostly axillary and paniculate. They consist of a central axis with a number of alternately positioned lateral axes. The lateral axes are usually once- or twice-branched somewhat cymosely, but actually the ultimate divisions are not strictly cymose. This character distinguishes *Beilschmiedia* from most other large genera of Lauraceae in the Neotropics (except *Cryptocarya*), which have their ultimate inflorescence divisions strictly cymose.

In most species, inflorescence bracts are small, early-deciduous, and often absent at anthesis. Bract position is variable even within an inflorescence, with the length of pedicels above the bracts often varying within a species. Central elements of the ultimate inflorescence divisions usually have much longer floral pedicels than lateral elements. It is usually not practicable to use pedicel lengths to

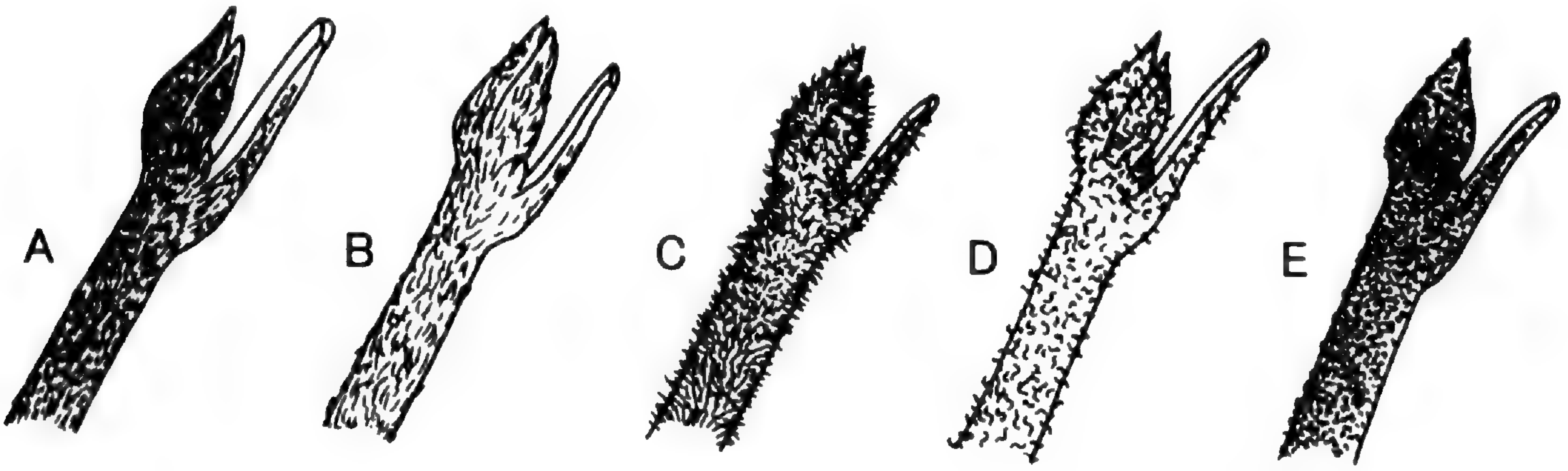


Figure 2. Five types of hairs in neotropical *Beilschmiedia* species. —A. Appressed. —B. Ascending. —C. Erect and straight. —D. Erect and wavy. —E. Erect and curly.

delimit species. However, some species, e.g., *B. brenesii*, have extremely long pedicels, and this character helps to distinguish that species from the others.

Flowers. Flowers are bisexual, small (ca. 3 mm long), and almost subspherical, except for those of *B. linharensis*, which are depressed-globose. Tepals are six, erect, almost equal, and usually ovate to elliptic. Stamens number nine in all neotropical *Beilschmiedia* species except for *B. hexanthera*, which has six. Anthers in the first and second whorls are ovate, and anthers in the third whorl are narrowly ovate to almost rectangular. Anther apices are obtuse to truncate in most species, but may be more or less acute in *B. angustielliptica*, *B. brenesii*, and *B. hondurensis*. Pubescence on anther apices distinguishes some species (*B. anay*, *B. angustifolia*, *B. curviramea*, *B. emarginata*, *B. fluminensis*, *B. linharensis*, *B. immersinervis*, *B. rigida*, *B. riparia*, *B. stricta*, and *B. taubertiana*) but, rarely, there are exceptional collections lacking this pubescence. Anther apices are glabrous in other species even if the anther sides are pubescent. Staminodia in the fourth staminal whorl are three in number and are conspicuous and sagittate or deltoid in shape. Staminodia in the third whorl in *Beilschmiedia hexanthera* are subulate in shape. Pistils are sometimes pubescent, but pubescence often varies within a species and may be easily overlooked. Receptacles are invariably shallow: this is a useful character to distinguish neotropical *Beilschmiedia* from *Cryptocarya*, in which the receptacle is deeply cupulate.

Fruits. Fruits are often ellipsoid in shape. *Beilschmiedia ovalis* and *B. ovalioides* have spherical fruits, and *B. anay* is reported to have pyriform fruits (Blake, 1919). Fruit color is usually black or purple-black at maturity.

Fruits of *Beilschmiedia* always lack cupules. Fruit pedicels are sometimes strongly constricted at their apices (Fig. 3A) or only weakly so (Fig. 3B): this is sometimes a useful character for species delimitation. In some species, e.g., *B. hondurensis* and *B. tovarensis*, the pedicels are variable, ranging from constricted to not constricted (Fig. 3C).

Cuticular characters. Cuticular characters of neotropical *Beilschmiedia* species were studied by Nishida and Christophel (1999). According to them, neotropical *Beilschmiedia* species are hypostomatic, and the cuticular characters of the species can be divided into five types (Table 2; see also Fig. 4). For the species corresponding to each type, see Table 1.

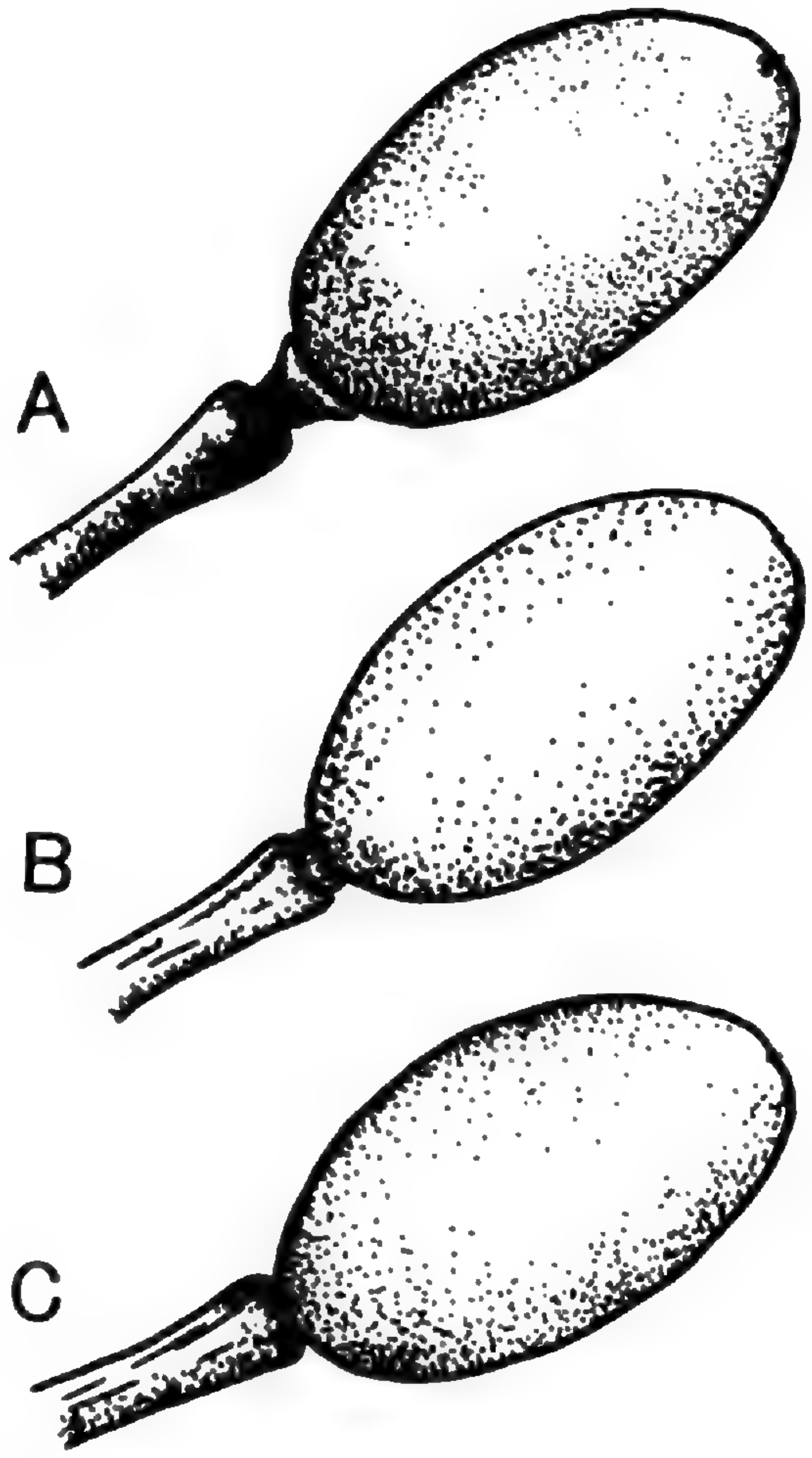


Figure 3. Fruits of neotropical *Beilschmiedia* species. —A. Fruit pedicel strongly constricted at the apex. —B. Fruit pedicel weakly constricted at the apex. —C. Fruit pedicel not constricted at the apex.

Leaf cross sections. Nishida and Christophel (1999) examined leaf sections of neotropical *Beilschmiedia* species, concluding that the most discriminating character was the arrangement of the vascular bundles in midribs. Two types are seen in neotropical *Beilschmiedia* species, one in a ring (Fig. 5A) and another in a flattened arc (Fig. 5B). For the species corresponding to each type, see Table 1.

DISTRIBUTION

In the Neotropics, *Beilschmiedia* ranges from central Mexico to southeastern Brazil and central Chile but is absent in the Amazon basin and northern Chile. Costa Rica has the highest number of species, with eight.

Many species range from tropical premontane wet forests to cloud forests. However, Chilean species are reported to occur in subtropical, semiarid vegetation (Heusser, 1971). Many species are distributed at lower and/or middle elevations. *Beilschmiedia latifolia*, *B. ovalioides*, and *B. ovalis* are also known from higher (1800–3000 m) elevations. *Beilschmiedia costaricensis* and *B. tovarensis* occur over a wide range of elevation, 600–3000 m. No

Table 2. Five cuticular types of neotropical *Beilschmiedia*. Terminology used here is sensu Christophel et al. (1996) or Nishida and Christophel (1999).

	Epidermal cell walls				
	Periclinal walls	Anticlinal walls	Dorsiventral differences in cell size	Stomatal ledge	Corresponding figures
B. costaricensis type	smooth	smooth to beaded	absent to slightly present (adaxial ≤ abaxial)	narrow	4A, B
B. curviramea type	dotted (adaxial surface), granular (abaxial surface)	branched	absent	wide	4C, D
B. hondurensis type	dotted	buttressed and strongly sinuous	absent	butterfly-shaped	4E, F
B. miersii type	smooth	smooth to beaded	conspicuously present (adaxial > abaxial)	narrow	4G
B. berteroana type	smooth	smooth to beaded	absent	strongly swollen	4H

reports are available on the altitudinal distribution of southeastern Brazilian species, but all of them are known from the Mata Atlantica region.

SEED DISPERSAL

Seeds of a few Costa Rican *Beilschmiedia* species are reported to be dispersed by birds such as quetzals (Wheelwright et al., 1984). Seeds remain in the bird's crop for more than an hour, while seeds of most of the other Lauraceae species remain there for a relatively short time (Wheelwright, 1995). Wheelwright (1986) also reported that fruit production varies greatly from year to year.

ECONOMIC USE

Some species, such as *Beilschmiedia latifolia, B. miersii,* and *B. pendula,* are useful as timber. Fruits of *B. anay* are reported to be edible by humans (Blake, 1919).

SYSTEMATIC POSITION IN LAURACEAE

Beilschmiedia had long been placed in the tribe Perseae Nees based on thyrsoid inflorescences without involucres. Kostermans (1957) regarded cupule development or its lack as an important character for lauracean systematics and placed *Beilschmiedia* close to genera such as *Endiandra, Mezilaurus, Potameia, Persea,* and *Phoebe.* Hutchinson (1964) regarded the number of anther cells as more important, placing *Beilschmiedia* in tribe Apollonieae Hutchinson with such genera as *Endiandra, Aniba, Mezilaurus, Licaria,* and *Endlicheria.*

Richter (1981) published wood and bark anatomy of Lauraceae, in which he recognized three large groups of genera. He placed *Beilschmiedia* in a group with *Endiandra, Potameia, Triadodaphne, Cryptocarya,* and *Ravensara.* Among these genera, *Cryptocarya* has fruits completely enclosed by cupules and has been regarded as a distantly related genus to *Beilschmiedia* by Kostermans (1957).

Van der Werff and Richter (1996) reviewed the classifications above and concluded that androecial characters such as the number of anther cells were not useful in a generic classification of Lauraceae. Instead, they proposed a classification based on inflorescence structure as well as wood and bark anatomy. In their study, *Beilschmiedia* was placed in the tribe Cryptocaryeae Nees and was distinguished by several characters such as paniculate inflorescences having the ultimate divisions not strictly cymose, parenchyma marginal, fibers nonseptate with conspicuously bordered pits, and ves-

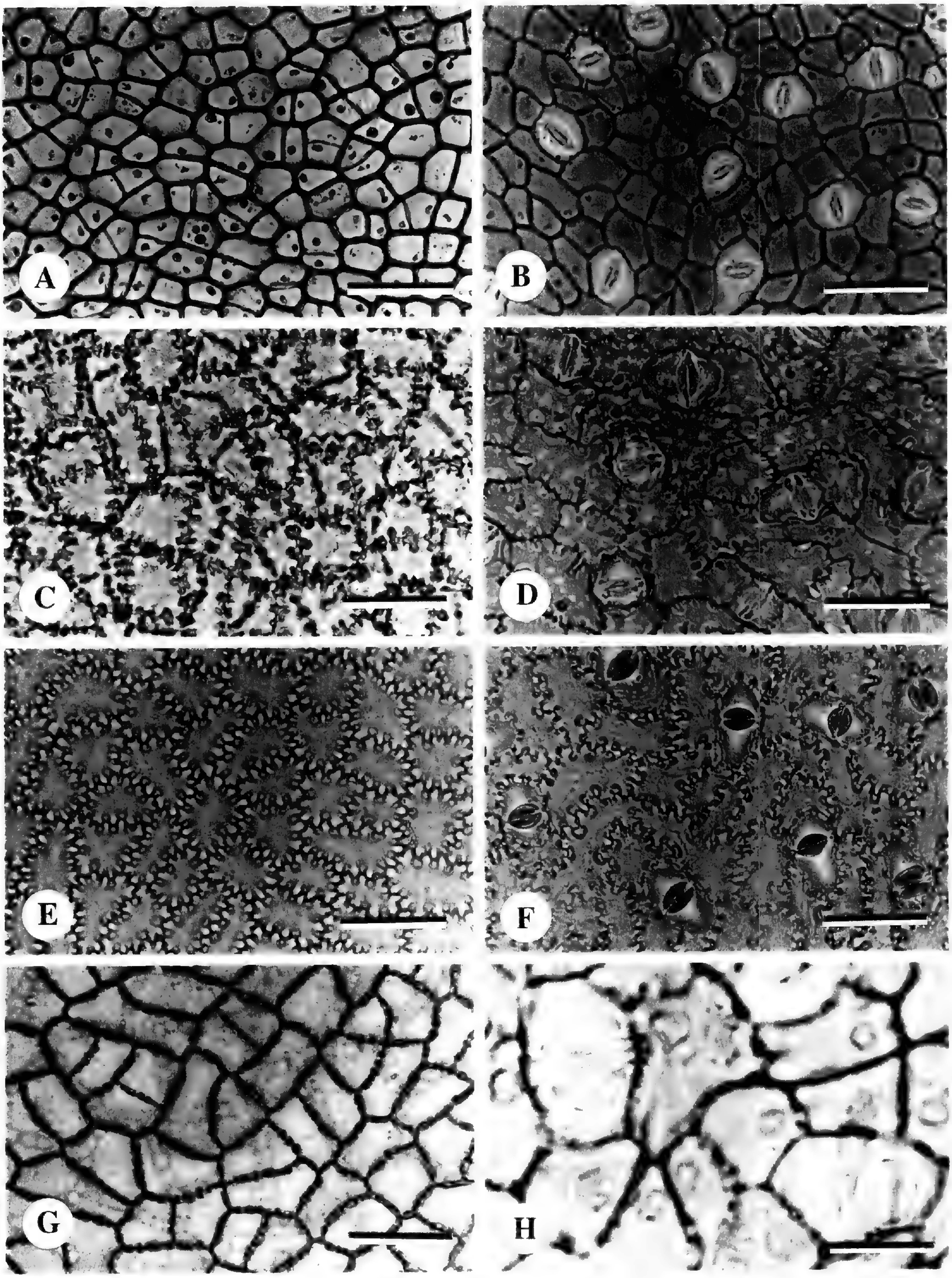


Figure 4. Cuticles of neotropical *Beilschmiedia* species on the adaxial (A, C, E, G) and abaxial leaf surfaces (B, D, F, H). —A, B. *B. costaricensis* (*van der Werff 13368, 12168*, respectively, MO). —C, D. *B. curviramea* (*Persaud 70*, NY). —E, F. *B. hondurensis* (*Lundell 19280*, MO). —G. *B. miersii* (*Taylor 10883*, MO). —H. *B. berteroana* (*s.n.*, MO). Scale bars = 50 μm in A–G, 20 μm in H.

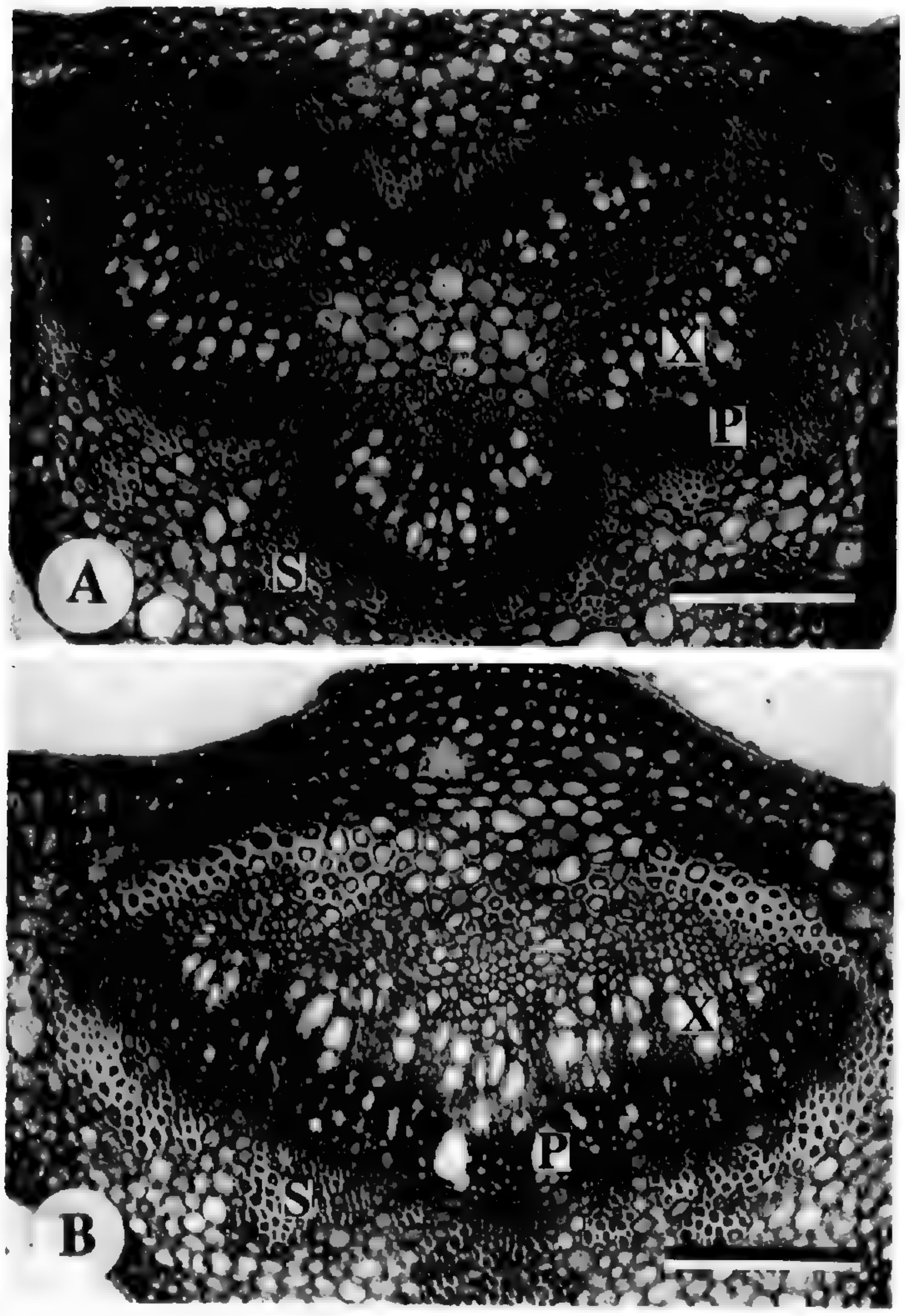


Figure 5. Leaf cross sections of neotropical *Beilschmiedia* through blade midribs. —A. Ring pattern, *B. mexicana* (*Croat 64900*, MO). —B. Flattened arc bundle pattern, *B. brenesii* (*Yasuda 1314*, MO). P = phloem, X = xylem, S = sclerenchymatous cells. Scale bars = 200 μm.

sel perforations in secondary xylem exclusively simple.

Preliminary observations of different Lauraceae genera suggests that the genus closest to *Beilschmiedia* appears to be *Cryptocarya* in the Neotropics. Neotropical species of *Beilschmiedia* and *Cryptocarya* share morphological similarity except for the pistils being short or long, receptacles being shallow or deep, and fruits without cupules or enclosed by cupules, respectively. Further studies including molecular analysis may clarify relationships between these two genera, as well as the intergeneric relationships within Lauraceae.

Relationships among Neotropical *Beilschmiedia* Species

Neotropical *Beilschmiedia* species usually share quite similar flowers and fruits, and this makes it difficult to discuss their relationships based on reproductive characters. Nishida and Christophel (1999) therefore employed leaf anatomy to investigate phylogenetic relationships. They concluded that the groupings of cuticular characters are systematically useful since they are also supported by phyllotaxis, leaf venation patterns, vascular bundle arrangements in blade midribs, and by rough geographical distributions. These species groupings are listed in Table 1 but should be considered informal until the entire genus has been revised.

These five species groups can be recognized even without examining the cuticular characters. First, all neotropical *Beilschmieidia* species with alternate leaves and a fine leaf venation pattern belong to the *Beilschmiedia costaricensis* group. Among other species, those with anthers apically pubescent and distributed in southeastern Brazil or the Guianas belong to the *Beilschmiedia curviramea* group. Mexican or Central American species whose leaves are opposite and anther apices are relatively acute belong to the *Beilschmiedia hondurensis* group. Finally, of the two Chilean species, the one with curly hairs on the twigs belongs to the *Beilschmiedia miersii* group, while the second has straight hairs on the twigs and belongs to the *Beilschmiedia berteroana* group.

Taxonomic Treatment

Beilschmiedia Nees, in Wallich, Pl. Asiat. Rar. 2: 61, 69. 1831. TYPE: *Beilschmiedia roxburghiana* Nees.

Hufelandia Nees, Plantarum Laurinarum Secundum Affinitates Naturales Expositio: 11. 1833. TYPE: *Hufelandia pendula* Nees.

Bellota Gay, Fl. Chil. 5: 297. 1851 or 1852. TYPE: *Bellota miersii* Gay.

Trees or rarely shrubs. Leaves alternate or opposite, rarely clustered, pinnately veined. Inflorescences in leaf axils, paniculate or racemose, with terminal branches of the panicles not strictly cymose. Flowers bisexual; tepals 6, equal or subequal, usually deciduous; stamens 9 or 6, filaments usually shorter than the anthers; anthers usually 2-celled, first and second whorls introrse, third whorl extrose to almost introrse, staminodia 3 in fourth whorl or absent, or rarely 6 in third and fourth whorls, staminodia representing third whorl subulate, staminodia representing fourth whorl sagittate or deltoid; ovary superior; receptacle flat to shallowly cupulate. Fruit ellipsoid, pyriform or spherical, usually purple-black, lacking cupule.

KEY TO NEOTROPICAL *BEILSCHMIEDIA* SPECIES

1a. Leaves opposite (the top leaves opposite even when leaves clustered); minor venation pattern on lower leaf surface coarse, areoles (smallest areas of the leaf tissue surrounded by veins) larger than 1.5 mm diam. (Fig. 1C).

2a. Anther apices glabrous; from Central America or Chile.

3a. Leaves roundish ovate; from Chile.

4a. Tepals glabrous outside; hairs on the terminal buds and twigs appressed or ascending, straight ..... *B. berteroana*

4b. Tepals pubescent outside; hairs on the terminal buds and twigs erect, curly to wavy ..... *B. miersii*

3b. Leaves elliptic or narrowly obovate; from Central America.

5a. Terminal buds pubescent with erect hairs; young twigs densely pubescent; secondary veins more than 14 pairs.

6a. Leaves clustered; leaf apices roundish to obtuse; filament of innermost stamens relatively densely pubescent ..... *B. manantlanensis*

6b. Leaves evenly arranged; leaf apices acute; filament of innermost stamens only sparsely pubescent ..... *B. angustielliptica*

5b. Terminal buds pubescent with appressed or ascending hairs; young twigs glabrous; secondary veins less than 13 pairs.

7a. Floral pedicels shorter than 2 mm; from Mexico to Honduras ..... *B. hondurensis*

7b. Floral pedicels longer than 3 mm; from Costa Rica and Panama ..... *B. brenesii*

2b. Anther apices pubescent; from northern South America or southeastern Brazil.

8a. Lower leaf surface pubescent; leaf base obtuse ..... *B. taubertiana*

8b. Lower leaf surface glabrous; leaf base cuneate.

9a. Hairs on the terminal buds and twigs ferrugineous, erect, very short and curly ..... *B. emarginata*

9b. Hairs on the terminal buds and twigs non-ferrugineous, appressed, relatively long and straight.

10a. Leaves obovate; leaf apex round or roundish obtuse.

11a. Flowers longer than 3 mm, wider than 3 mm; flowers globose ..... *B. rigida*

11b. Flowers shorter than 2 mm, narrower than 2.5 mm; flowers depressed-globose ..... *B. linharensis*

10b. Leaves elliptic; leaf apex acute (rarely obtuse).

12a. Leaf width less than ⅓ of the leaf length ..... *B. angustifolia*

12b. Leaf width more than ½ of the leaf length.

13a. Inflorescences racemose, ± densely pubescent ..... *B. stricta*

13b. Inflorescences paniculate, sparsely pubescent or almost glabrous.

14a. Leaf base slightly inrolled; from southeastern Brazil ..... *B. fluminensis*

14b. Leaf base flat; from northern South America ..... *B. curviramea*

1b. Leaves alternate, spirally clustered, rarely subopposite; minor venation pattern usually fine, areoles smaller than 0.5(–0.7) mm diam. (Fig. 1A, B); when venation pattern relatively coarse, leaves still alternate and from Ecuador or Colombia (*B. costaricensis*).

15a. Fertile stamens 6; staminodia 6; from French Guiana ..... *B. hexanthera*

15b. Fertile stamens 9; staminodia 3; from Central America, West Indies, or western South America.

16a. Hairs on terminal buds and twigs appressed (Fig. 2A) or ascending (Fig. 2B); when hairs ascending, minor venation pattern slightly less fine, areoles around 0.7 mm diam. (*B. costaricensis*).

17a. Leaves glaucous below.

18a. Areoles angular with branched free-ending veinlets inside (Fig. 1B); fruit pedicels strongly constricted (Fig. 3A) ..... *B. pendula*

18b. Areoles rounded, seldom with free-ending veinlets inside (Fig. 1A); fruit pedicels weakly constricted (Fig. 3B), rarely not constricted (Fig. 3C).

19a. Leaves chartaceous; from Mexico to Belize ..... *B. mexicana*

19b. Leaves usually coriaceous; from northwestern South America to Costa Rica ..... *B. tovarensis*

17b. Leaves not glaucous below.

20a. Areoles angular with branched free-ending veinlets inside; fruit pedicels not constricted (Fig. 3C); from northwestern South America to Costa Rica ..... *B. costaricensis*

20b. Areoles rounded seldom with free-ending veinlets inside (Fig. 1A); fruit pedicels weakly constricted (Fig. 3B); from Mexico to Belize ..... *B. mexicana*

16b. Hairs on terminal buds and twigs erect (Fig. 2C–E).

21a. Anther apices pubescent.

22a. Petioles longer than 2.5 cm; leaves longer than 18 cm, wider than 11 cm ..... *B. anay*

22b. Petioles shorter than 2 cm; leaves shorter than 16.5 cm, narrower than 7.5 cm.

23a. Secondary veins conspicuously raised below; lower leaf surface not glaucous; from Mexico, south to Nicaragua ..... *B. riparia*

23b. Secondary veins immersed below (visible); lower leaf surface glaucous; from Costa Rica ... *B. immersinervis*

21b. Anther apices glabrous.

24a. Leaves narrowly elliptic, the width less than 4 cm and less than ½ of the length ... *B. steyermarkii*

24b. Leaves broadly elliptic, ovate or obovate, the width more than 4 cm and more than ½ of the length.

25a. Lower leaf surface glabrous when old.

26a. Leaves longer than 22 cm ... *B. alloiophylla*

26b. Leaves shorter than 13 cm.

27a. Leaves ovate; tertiary veins weakly percurrent or reticulate; inflorescences relatively densely pubescent; fruits spherical ... *B. ovalis*

27b. Leaves obovate; tertiary veins strongly percurrent; inflorescences glabrous or sparsely pubescent; fruits ellipsoid ... *B. tilaranensis*

25b. Lower leaf surface pubescent when old.

28a. From Mexico; fruits spherical ... *B. ovalioides*

28b. From southern Central America (Costa Rica, Panama) or western South America; fruits ellipsoid.

29a. Leaves ovate to broadly elliptic; leaves shorter than 11 cm; secondary veins less than 9 pairs ... *B. latifolia*

29b. Leaves obovate (rarely broadly elliptic); leaves longer than 22 cm; secondary veins more than 9 pairs ... *B. alloiophylla*

1. **Beilschmiedia alloiophylla** (Rusby) Kosterm., Rec. Trav. Bot. Néerl. 35: 849. 1938. *Ocotea alloiophylla* Rusby, Descr. S. Amer. Pl.: 21. 1920. TYPE: Colombia. Santa Marta: mountain forest 5 mi. SE of Don Amo, ca. 750 m, 7 Mar. 1898–1901 (young fl), *H. H. Smith 2104* (lectotype, designated by Kostermans (1938), NY not seen; isolectotypes, A not seen, BM!, G-DEL not seen, K!, MO!, P!, US not seen).

Tree, to 35 m tall. Terminal buds densely pubescent with erect, short to long, straight to curly hairs. Twigs terete, sometimes sulcate or angular, sometimes corky, densely pubescent with erect, short to long, straight to curly hairs. Leaves clustered, rarely almost alternate; petioles 0.7–3.5(–4.5) cm long, canaliculate to flat above, pubescent with erect, short to long, straight to wavy hairs, concolorous with twigs; blades firmly chartaceous, elliptic to obovate, (14–)22–30 × 6–13(–17) cm; base cuneate or obtuse, not inrolled or rarely inrolled, apex acute to acuminate; upper leaf surface glabrous (sometimes pubescence left mainly on midrib when young), lower leaf surface pubescent with erect to almost appressed, short to long, straight to curly hairs, or glabrous, rarely pubescent only on major veins; lower leaf surface glaucous; midrib and secondary veins slightly impressed or immersed above, raised below, secondary veins 9 to 16 (19) pairs, tertiary veins percurrent, minor venation pattern fine, areoles rounded and seldom with free-ending veinlets inside, tertiaries and minor veins almost immersed (the pattern poorly visible) or slightly raised above, raised below. Inflorescences in axils of leaves, paniculate, (4–)8–25 cm long, pubescent with erect, wavy hairs, with (30) 60 to 250 or more flowers per inflorescence; floral pedicels of the lateral divisions 0.5–0.7 mm long, pedicels of the central flowers up to 2 mm long. Flowers green to creamy, ca. (2–)2.2–3 mm long, ca. 2 mm diam.; tepals 6, equal, ovate to elliptic, 1.5–2.1 × 1–1.5 mm, pubescent with erect and wavy hairs on both surfaces; stamens 9, filaments 0.4–0.5 mm long, pubescent, anthers 0.6–0.7 mm long, 2-celled, anther apices roundish to truncate and glabrous, glands of the innermost three stamens globose; staminodia 3, sagittate, ca. 0.7 mm long; pistil 1–1.7 mm long, glabrous, ovary longer than and gradually narrowed into the style; receptacle pubescent with appressed hairs. Fruits ellipsoid, purple-black, 3.5–4.5 × 1.5–2.5 cm, surface smooth; infructescence axis 2.5–3 mm diam., slightly thickened to 4 mm diam. near the fruit pedicel, fruit pedicels apically constricted, or rarely not constricted.

Flowering time. January to July.

Distribution and habitat. Costa Rica, Panama, western Venezuela, western Colombia, and Ecuador (Fig. 6); (35–)100–1400(–1900) m; evergreen lowland forest, premontane wet forest and montane wet forest.

Common names. Jigua de aguacate (*Dodson & Gentry 6489*), María aguacatillo (*Josse et al. 843*) (Ecuador).

Selected specimens examined. COSTA RICA. **Cartago:** Cartago Province, on slopes above Muñeco, 1550 m, 19 Mar. 1986 (fr), *Almeda et al. 5639* (MO). **Guanacaste:** Parque Nacional Guanacaste, La Cruz, Estación Pitilla, 10°59′26″N, 85°25′40″W, 700–1000 m, 1 Apr. 1991 (fl), *Morega 337* (INB, MO). **Heredia:** Finca La Selva, the OTS Field Station on the Río Puerto Viejo just E of its

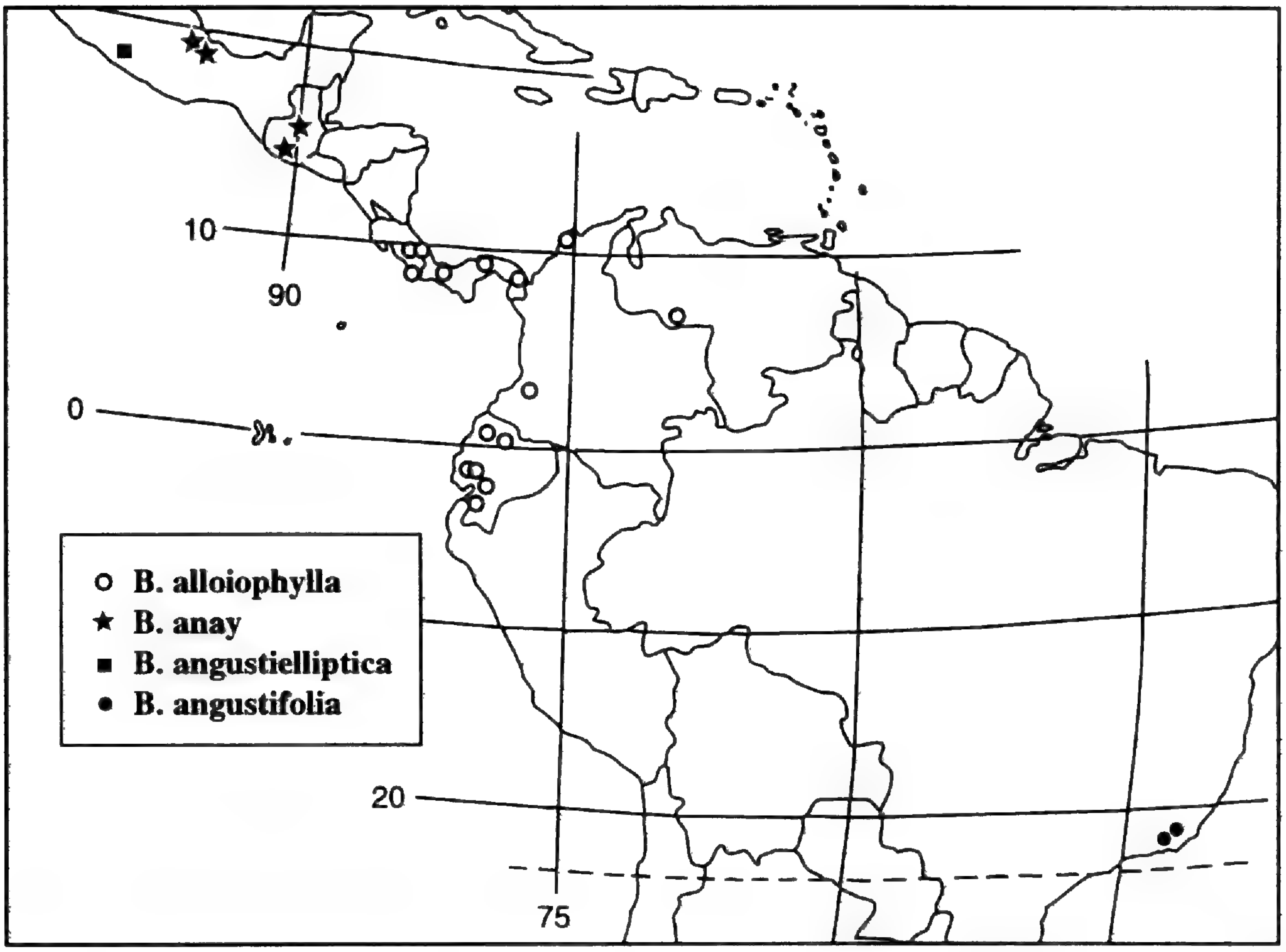


Figure 6. Representative distribution of *Beilschmiedia alloiophylla*, *B. anay*, *B. angustielliptica*, and *B. angustifolia*.

junction with the Río Sarapiquí, 100 m, 25 July 1981 (fl), *Hammel 11049* (MO, NY). **Limón:** SE region of Lago Dabagrí, cross the road to Telire, 5 Nov. 1984 (fr), *L. D. Gómez et al. 23216* (CR). **Puntarenas:** Cantón de Golfito, Corcovado National Park, Sendero Los Patos, 8°34'00"N, 83°31'00"W, 200 m, 6 June 1994 (young fl), *Aguilar 3346* (INB, MO). **San José:** along Quebrada Tablazo and on slope S of creek, NE slope of Altos Tablazo, 9°50'N, 84°03'W, 1675–1900 m, 24 Apr. 1987 (immature fr), *Grayum et al. 8263* (CR, R, MO). PANAMA. **Bocas del Toro & Chiriquí:** Cerro Colorado, from Chami station to ca. 9 mi. along road, 8°35'N, 81°54'W, 1100–1750 m, 27–31 Mar. 1986 (fr), *Hammel & Trainer 14992* (MO). **Darién:** Río Pirre, 16 Nov. 1967 (fr), *Bristan 1472 (4)* (MO). **Panamá:** Cerro Jefe, along summit road and along trail into Chagres Valley, 9°15'N, 79°30'W, 900 m, 19 Feb. 1988 (fl), *McPherson 12122* (MO). VENEZUELA. **Mérida:** Sierra de Perijá, Misión Sabana, 1300 m, 22 Mar. 1959 (young fl), *Bernardi 7452* (K, NY). COLOMBIA. **Valle:** Cordillera Occidental, La Laguna, Río Sanquininí basin, 1250–1400 m, 10–20 Dec. 1943 (fr), *Cuatrecasas 15619* (F). ECUADOR. **Azuay:** Cantón Cuenca, Parroquia Molleturo, Manta Real, 02°34'S, 79°23'W, 300–1200 m, 28 July 1992 (immature fr), *Berg 46* (MO). **El Oro:** road between Santa Rosa & Portovelo, 25 Mar. 1921 (immature fr), *Popenoe 1304* (US). **Esmeraldas:** Quininde, Bilsa Biological Station, Mache Mountains, 35 km W of Quininde, 5 km W of Santa Isabel, 0°21'N, 79°44'W, 400–600 m, 14 Nov. 1994 (young fl), *Clark & Pitman 248* (MO). **Guayas:** Cordillera Chongon-Colonche, Loha Alta Protected Forest, 1°48'S, 80°47'W, 600 m, July 1995 (immature fr), *Bonifaz & Cornejo 3091* (MO). **Los Ríos:** 56 km of Quevedo-Santo Domingo, Río Palenque Biological Station, 150–220 m, 25 Mar. 1980 (sterile), *Dodson & Gentry 9906* (MO). **Manabí:** Parque Nacional Machalilla, Piñas to the hill Avión Caído, 01°35'S, 80°41'W, 300 m, 13 Sep. 1991 (fr), *Josse 714* (MO). **Pichincha:** along road Nanegal–Palmitopamba, 1200 m, 9 July 1991 (immature fr), *van der Werff 12256* (MO).

Beilschmiedia alloiophylla belongs to the *B. costaricensis* group. This species is distinguished by the following: hairs erect on terminal buds and twigs, leaves alternate, large and obovate, anthers glabrous, and fruits ellipsoid.

Beilschmiedia alloiophylla is a complex species with variable indumentum. Collections recognized here as this species roughly separate into five groups based mainly on the hair structure and the amount of pubescence.

Group 1 species have short to long, straight to curly hairs on terminal buds and twigs, with long straight hairs on the tissue of lower leaf surfaces. Collections identified to this group include many Ecuadorian ones, all Colombian ones (including the type), all Venezuelan ones, as well as one Panamanian one. Altitudinal distribution of this group is usually around 1200 m elevation. A few collections occur lower than 300 m.

Group 2 species display short, curly hairs on terminal buds and twigs, with sparse, sericeous hairs or almost no hair on lower leaf surfaces. Petioles in this group are often shorter than those of other groups. This group has been collected mainly from relatively low elevations (150–600 m) on the Pacific coast of Ecuador. Distributions overlap between this species group and Group 1.

Group 3 features long straight hairs on terminal buds, twigs, and major veins of abaxial blade surfaces. Lower leaf surfaces in this group have dense hairs only along the blade midribs and secondary veins. Only one collection, *McPherson 12122* from Panama at 900 m, belongs to this group.

Group 4 species are characterized by short curly hairs on terminal buds and twigs but almost no hair on lower blade surfaces. There are occasional curly hairs on major veins when the leaves are young. This group has been collected from 700 to 1900 m in Costa Rica and Panama (with one collection, *Hammel 11049,* found at ca. 100 m in Costa Rica). Burger and van der Werff (1990) regarded them as a larger-leaved variation of *B. ovalis,* but they can be reliably separated from *B. ovalis* by their strongly percurrent tertiary veins and ellipsoid fruits.

Group 5 species have short curly hairs on terminal buds, twigs, and lower leaf surfaces. Lower leaf surfaces may be sparsely pubescent to almost glabrous. This group has been collected only from lower elevations (below 350 m) on the Osa Peninsula, Costa Rica.

2. **Beilschmiedia anay** (S. F. Blake) Kosterm., Rec. Trav. Bot. Néerl. 35: 847. 1938. *Hufelandia anay* S. F. Blake, J. Wash. Acad. Sci. 9: 459. 1919. TYPE: Guatemala. Suchitepézquez: Mazatenango, Finca Compromiso, ca. 420 m, 17 Jan. 1917 (immature fr), *Popenoe 754* (holotype, US!; isotype, US!).

Tree, to 40 m tall. Twigs terete to sulcate, densely pubescent with erect, curly to wavy or rarely almost straight hairs, rarely not so densely pubescent, rarely glabrescent with age. Leaves alternate, rather clustered around the terminal buds; petioles 2.5–4 cm long, canaliculate to flat above, pubescent with erect, wavy or almost straight hairs, concolorous with twigs; blades chartaceous, broadly elliptic to ovate, (14–)18–28 × 11–15 cm; base obtuse to rounded, rarely cuneate, not inrolled, apex acute, rarely cuspidate; upper leaf surface glabrous, or sometimes pubescent with wavy hairs along the midrib, lower leaf surface pubescent with erect, short curly hairs or long wavy hairs, especially densely pubescent along the midrib and secondary veins; lower leaf surface often glaucous; midrib and secondary veins immersed or slightly impressed above, raised below, secondary veins 12 to 17 pairs, tertiary veins percurrent, minor venation pattern fine, areoles rounded and seldom with free-ending veinlets inside, tertiaries and minor veins immersed above (pattern partially visible), slightly raised or almost immersed below (the pattern visible), the venation pattern visible on upper leaf surface much coarser than on lower leaf surface. Inflorescences axillary, sometimes crowded near the terminal buds, paniculate, 5–10 cm long, pubescent with erect, curly to wavy hairs, with 30 to 70 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1 mm long, pedicels of the central flowers up to 4 mm long. Flowers yellowish, 2.5–3.2 mm long, 2.8–3.5 mm diam.; tepals 6, equal, elliptic, ca. 2 mm long, 1–1.6 mm wide, ± densely pubescent with erect, wavy hairs on both sides; stamens 9, outer six filaments ca. 0.4 mm long, innermost three filaments 0.4–0.7 mm long, filaments pubescent, anthers 0.8–1 mm long, 2-celled, anther apices roundish to truncate and pubescent, glands of the innermost three stamens globose; staminodia 3, sagittate, ca. 0.6–0.8 mm long; pistil 1.3–1.6 mm long, glabrous, ovary as long as or longer than and gradually narrowed into the style; receptacle pubescent with ± appressed hairs. Fruits ellipsoid to pyriform, deep purple to black, to ca. 15 cm long (fide Blake, 1919); fruit pedicels unknown.

Flowering time. April and May.

Distribution and habitat. Eastern Mexico and Guatemala (Fig. 6); 100–920 m; montane mesophyll forest and deciduous forest, on loamy, clayish soil or limestone.

Common names. Anay (Guatemala); Anaya negra/Jani'ya (*G. Villalobos C. & Guerrero 138*) (Mexico).

Selected specimens examined. MEXICO. **Puebla:** Municipio Xochitlán de Vicente Suárez, 19°58′N, 97°44′W, 850 m, 22 Nov. 1987 (fr), *G. Villalobos C. & Guerrero 244* (MEXU). **Veracruz:** entre Maratinez de la Torre & Misantla, 100 m, 21 Oct. 1967 (sterile), *Pennington & Sarukhán 9265* (NY). GUATEMALA. **Alta Verapaz:** Chamá, ca. 270 m, 6 May 1920 (fl), *Johnson 170* (F, MO, U, US). **Escuintla:** Río Guacalate, 600 m, 16 Dec. 1938 (young fl), *Standley 60223* (F).

Kostermans (1938) reported *Beilschmiedia anay* from Guatemala, Costa Rica, and Colombia. However, he stated that he was not sure if Costa Rican specimens seen belonged to *B. anay,* and that the Colombian specimen seen had almost glabrous leaves, atypical for *B. anay.* I have not seen the specimens he cited, nor any specimen of *B. anay* from Costa Rica or Colombia. All the specimens I recognize as *B. anay* are from Guatemala or Mexico.

Beilschmiedia anay appears to be vegetatively similar to *B. alloiophylla*. However, *B. anay* differs from *B. alloiophylla* by its pubescent anthers.

Beilschmiedia anay is reported to have pyriform fruits (Blake, 1919), differing from the elliptic or spherical fruits observed for most neotropical *Beilschmiedia* species. However, I have not seen good fruiting collections of *B. anay*, only ones with very young or detached fruits. Fruit characters for this species should be confirmed through the collection of relevant material.

3. **Beilschmiedia angustielliptica** Lorea-Hern., Novon 5: 47. 1995. TYPE: Mexico. Guerrero: Municipio Atoyac de Alvarez, ca. 2 km S to El Molote, on the trail to El Edén, 1580 m, 19 May 1993 (fl & fr), *Lorea & Lozada 5540* (holotype, FCME not seen; isotype, MO!).

Tree, 7–8 m tall. Terminal buds pubescent with yellowish brown to reddish brown, erect wavy hairs. Twigs terete, compressed when young, densely pubescent with erect, long wavy hairs, becoming less dense to glabrescent with age. Leaves opposite, rarely subopposite; petioles 0.7–1.7 mm, flat or slightly canaliculate above, pubescent with erect wavy hairs but soon glabrous, concolorous with twigs or slightly discolored from twigs; blades firmly chartaceous, narrowly elliptic, margin sometimes slightly undulate, (7–)12–20(–24) × 2–6 cm, base cuneate, not inrolled, apex acute; leaf surface glabrous on both sides; lower leaf surface not glaucous; midrib immersed above, raised below, secondary veins 13 to 22 pairs, slightly raised above, raised below, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets, tertiaries and minor veinlets slightly raised above, raised below. Inflorescences in axils of leaves, paniculate, 2.5–6(–10) cm, pubescent with erect hairs, with 30 to 60 flowers per inflorescence; floral pedicels of the lateral divisions 1.2–2 mm long, pedicels of the central flowers up to 3 mm long. Flowers 2–2.7 mm long, ca. 2.5 mm diam.; tepals 6, equal, ovate, 1.3–1.7 mm long, 0.9–1.3 mm wide, outside pubescent with erect hairs, inside sparsely pubescent with appressed to erect hairs; stamens 9, outer six with filaments ca. 0.4 mm, innermost three with filaments ca. 0.5 mm long, all filaments sparsely pubescent, outer six with anthers 0.6–0.8 mm long, innermost three with anthers ca. 0.5 mm long, 2-celled, apex of the outer six anthers roundish to acute, apex of the innermost three anthers truncate, apex of all the anthers glabrous, glands of the innermost three stamens globose; staminodia 3, sagittate, 0.4–0.6 mm long; pistil ca. 1.2 mm long, glabrous or slightly pubescent, ovary slightly longer than and gradually narrowed into the style or sometimes the border between ovary and style conspicuous; receptacle pubescent with ± erect hairs, less densely pubescent toward the bottom. Fruits ellipsoid, black, 2.5–3.5 × 1.5–1.7 cm, surface smooth; infructescence axis 1.5–2 mm diam., slightly thickened to 3 mm diam. near fruit pedicels, with fruit pedicels constricted at apices.

Flowering time. May.

Distribution and habitat. Guerrero, Mexico (Fig. 6), at 1360–1630 m in mesophyllous montane forest.

Selected specimen examined. MEXICO. **Guerrero:** Municipio Atoyac de Alvarez, El Molote, 1630 m, 15 Apr. 1984 (fr), *Núñez 1159* (MO).

Among Mexican species, *Beilschmiedia angustielliptica* is distinguished by its opposite, evenly arranged, long leaves. Lorea-Hernández (1995) considered ovary pubescence as a distinctive character for this species. However, I have observed that some ovaries in this species are glabrous or only sparsely pubescent so that one can easily miss the pubescence.

4. **Beilschmiedia angustifolia** Kosterm., Rec. Trav. Bot. Néerl. 35: 857. 1938. TYPE: Brazil. Rio de Janeiro: Ad cataractam Vargem, Theresopolis, Serra dos Orgãos, 2 Feb. 1838 (fr), *Miers s.n.* (holotype, BM!).

Tree, to 10 m tall. Terminal buds pubescent with appressed straight hairs. Twigs terete, compressed when young, sparsely pubescent with appressed straight hairs or almost glabrous. Leaves opposite; petioles 0.7–1.3(–1.8) cm long, flat above, glabrous, concolorous with twigs; blades firmly chartaceous, narrowly elliptic, 7–14 × 1.5–4 cm, base acute, slightly inrolled toward the lower surface, apex acute; leaf surface glabrous on both sides; unknown whether lower leaf surface is glaucous or not; midrib immersed above, raised or almost immersed below, secondary veins 9 to 14 pairs, slightly raised or almost immersed on both sides, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins slightly raised or almost immersed on both sides. Inflorescences in axils of leaves, paniculate with few branches, 2–3.5 cm long, sparsely pubescent with appressed to erect hairs, with 10 to 15 flowers per inflorescence; floral pedicels of the lateral divisions ca. 1 mm long, pedicels of the central flowers up to 3 mm long. Flowers ca. 2.5 mm long, ca. 2.7 mm diam.; tepals 6, equal, ovate, 1.3–1.7 mm long, ca. 1.3 mm wide, pubescent with appressed to erect hairs outside, sparsely pubescent with appressed hairs inside; stamens 9, outer six filaments ca. 0.2 mm long, innermost three filaments ca. 0.4 mm long, all filaments pubescent, anthers 0.6–0.8 mm long, 2-celled, anther apices roundish to truncate and pubescent, glands on the innermost three stamens globose, ca. 0.4 mm long; staminodia 3, sagittate, ca. 0.5 mm long; pistil ca. 1.8 mm long, pubescent, ovary as long as the style, the border between ovary and style ± clear; receptacle pubescent with appressed hairs, less densely pubescent toward the bottom. Fruits roundish ellipsoid, ca. 3 × ca. 2.7 cm, surface smooth; infructescence axis ca. 3 mm diam., fruit pedicels slightly thickened to 4–7 mm diam. below the fruit, not constricted.

Flowering time. October and November.

Distribution. Rio de Janeiro, Brazil (Fig. 6).

Common name. Tapinhao (Kostermans, 1938).

Selected specimen examined. BRAZIL. **Rio de Janeiro:** Vista Chinesa, 13 Oct. 1925 (fl), *Constantino 19914* (RB).

Among southeastern Brazilian species, *Beilschmiedia angustifolia* is distinguished by its narrowly elliptic leaves. The widths of the leaves in *B. angustifolia* are usually ¼, at most ⅓, of blade lengths, while blade widths in most other southeastern Brazilian species correspond to ½ the length or more. *Beilschmiedia taubertiana* also tends to have narrow leaves; these are not narrower than ⅓ of blade lengths, and the erect pubescence of its terminal buds, twigs, and lower leaf surfaces distinguish this species from *B. angustifolia.*

In addition to its narrow leaves, *B. angustifolia* has pubescent pistils, which are characteristic only for this species and *B. rigida* among southeastern Brazilian species.

5. **Beilschmiedia berteroana** (Gay) Kosterm., Rec. Trav. Bot. Néerl. 35: 858. 1938. *Cryptocarya berteroana* Gay, Fl. Chil. 5: 301. 1851 or 1852. TYPE: Chile. Mts. La Leona, Nov. 1829 (fl & immature? fr), *Bertero s.n.* (lectotype, designated by Kostermans (1938), P!; isolectotypes, G-DEL not seen, P!, GH not seen, W not seen).

Bellota nitida Phil., Linnaea 29: 39. 1857–1858. *Boldu nitidum* (R. A. Philippi) Meisn., in DC., Prodr. 15(1): 506. 1964. TYPE: Chile. Dept. Linares: in the Andes, (fr), *Germain s.n.* (holotype, herbarium not known, not seen).

Cryptocarya nitida Phil., Linnaea 33: 228. 1864–1865. TYPE: Chile. Santiago: at the foot of the Andes, Nov. 1862 (fl), *Philippi s.n.* (W, fide Kostermans, not seen).

Bellota pauciflora Phil., Anales Univ. Chile 26: 649. 1865. TYPE: Chile. Cordillera de Linares, Jan. (fl), *Germain s.n.* (SGO not seen).

Tree, height unknown. Terminal buds pubescent with appressed to ascending, straight hairs. Twigs terete, slightly compressed when young, densely or rarely sparsely pubescent with appressed to slightly ascending, short straight hairs, less densely when older. Leaves opposite; petioles 0.2–0.5(–0.8) cm long, flat to slightly canaliculate above, pubescent with appressed hairs, concolorous with twigs; blades coriaceous, dried to light green, roundish ovate, 3–6 × 2–4 cm; base round, not inrolled, apex obtuse to retuse; leaf surface glabrous on both sides; lower leaf surface glaucous; midrib immersed above, slightly raised below, secondary veins 3 to 7 (9) pairs, almost immersed or slightly raised above, slightly raised below, tertiary veins not percurrent, minor venation pattern very coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins almost immersed or slightly raised on both sides. Inflorescences in axils of leaves, sometimes on short branchlets (with or without leaves), racemose, rarely paniculate, 0.5–2 cm long, pubescent with erect hairs, rarely only sparsely pubescent, with 3 to 10 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1 mm long, pedicels of the central flowers up to 2 (rarely 3) mm long. Flowers 2.5–3 mm long, 3–3.7 mm diam.; tepals 6, equal, almost round, 1.5–2 mm long, 1.3–1.8 mm wide, glabrous outside, sparsely to densely pubescent with almost appressed hairs at the base inside; stamens 9, outer six filaments ca. 0.2 mm long, innermost three filaments ca. 0.5 mm long, filaments pubescent, anthers 0.7–1 mm long, 2-celled, anther apices obtuse to truncate and glabrous, glands of innermost three stamens globose, 0.3–0.5 mm long; staminodia 3, sagittate, ca. 0.6 mm long; pistil ca. 1.9 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with appressed hairs. Mature fruits unknown.

Flowering time. November and May.

Distribution and habitat. Central Chile (Fig. 7); reported to grow in subtropical, semiarid vegetation (Heusser, 1971).

Common name. Ulmo (*Bertero s.n.*).

Selected specimens examined. CHILE. **Bío-bío:** Concepción, 1855 (fl), *Germain s.n.* (BM, F, K). **Maule:** Cor-

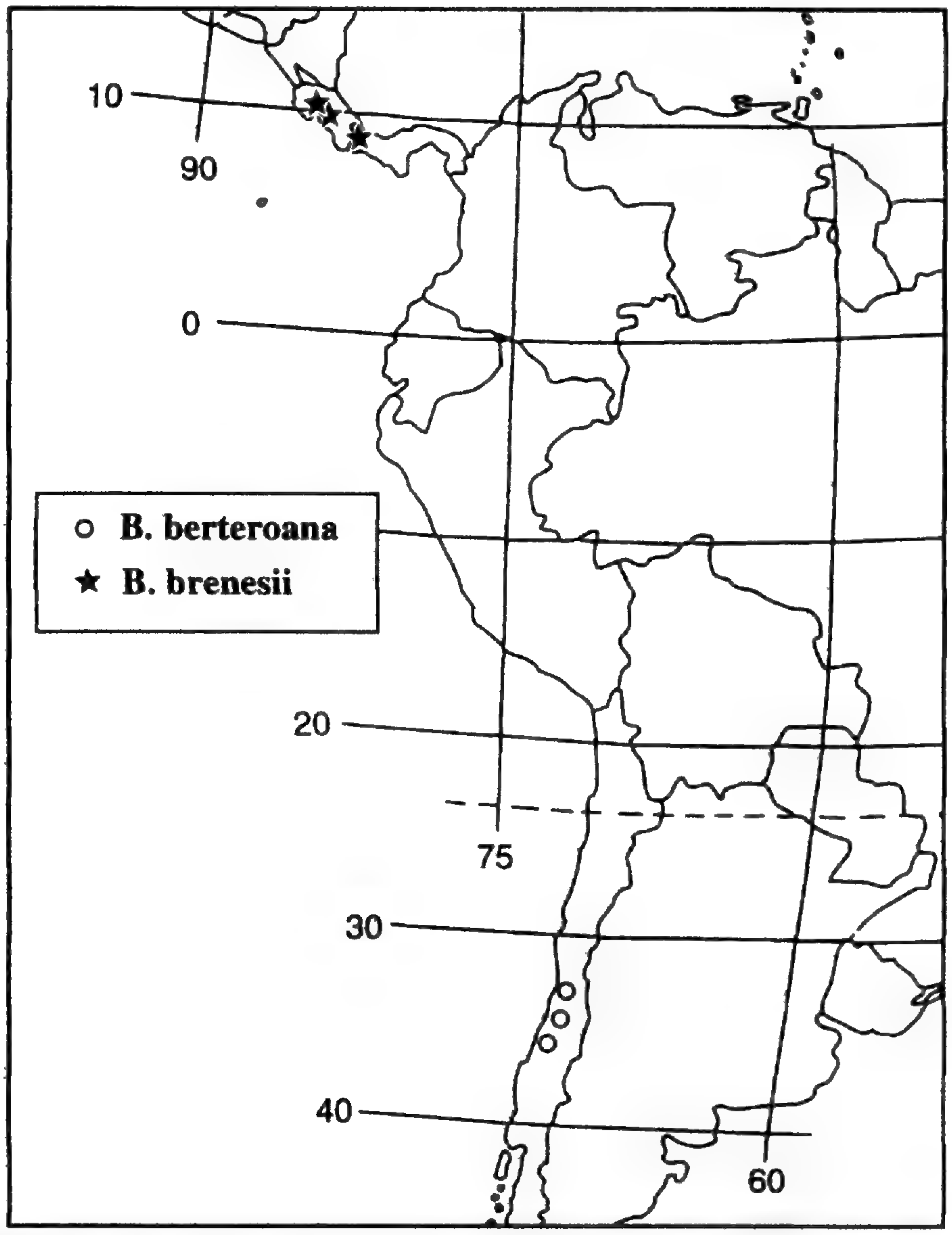


Figure 7. Representative distribution of *Beilschmiedia berteroana* and *B. brenesii.*

dillera de Linares, (fl), *Philippi 906* (K). **Valparaiso?:** Mt. la Leona, 1836 (fl), *Bertero 4* (BM).

Kostermans (1938: 859) recognized one of Bertero's collections in P as the lectotype of this species and stated, "Though Gay (Flora Chilena V, page 301) indicated no type specimen of his *Cryptocarya berteroana* it is evident that he described the specimens collected by Bertero (n. 4), as he cites the vernacular name: Ulmo and the name: *Adenostemum nitidum* Bertero, both names figuring on the labels of these specimens." I agree with Kostermans's designation, but the collection is not *Bertero 4* as he mentioned, but rather *Bertero s.n.* The specimen with a label saying "*Bertero 4*" is not in P but in BM. The label of this BM specimen does not include the vernacular name or the name *Adenostemum nitidum.* On the other hand, the Bertero specimen at P includes both of these names but without the numeral "4." Instead, the P label has the planetary symbol meaning "perennial." I suspect that Kostermans misread this planetary symbol as a "4." Since the BM and P collections appear to be taken from different trees, I would like to clarify that the lectotype of this species is not "*Bertero 4*" as present in BM, but "*Bertero s.n.*" as in P.

I have not seen the types of *Bellota nitida, Cryptocarya nitida,* or *Bellota pauciflora,* but based on the descriptions of these species, it is clear to me that these taxa are conspecific with *Beilschmiedia berteroana.*

Beilschmiedia berteroana is one of the two species from Chile, with *B. miersii* being the other. These two Chilean species are unique among neotropical *Beilschmiedia* species in their opposite, roundish ovate leaves drying to light green and with a very coarse venation pattern. These Chilean species appear similar to one another at first glance, especially in leaf shape and venation pattern. However, *B. berteroana* has appressed or ascending, straight hairs on the terminal buds and twigs and has tepals glabrous outside. *Beilschmiedia miersii* has erect, curly hairs on the terminal buds and twigs and has tepals densely pubescent outside.

Cuticular characters also distinguish these two Chilean taxa (see Table 2).

It is interesting that *Cryptocarya alba* (Molina) Looser, also endemic to central Chile, shares vegetative macromorphological characters for leaves with these two Chilean species, but a quite different venation pattern and cuticular characters distinguish *Cryptocarya alba.* The similarity of all three Chilean species might be due to their xeric adaptations.

6. Beilschmiedia brenesii C. K. Allen, J. Arnold Arbor. 26: 415. 1945. TYPE: Costa Rica. Alajuela: La Palma and El Socorro de San Ramón, 24 July 1928 (fr), *Brenes 6214* (holotype, F!; isotype, NY!).

Tree, to 20(–35) m tall. Terminal buds pubescent with ascending or appressed, straight hairs, or almost glabrous. Twigs terete, compressed when young, glabrous, rarely pubescent with ascending straight hairs. Leaves opposite, relatively clustered near the terminal buds; petioles 0.5–0.8 cm long, flat or canaliculate, slightly thickened at the base, glabrous, concolorous with twigs; blades coriaceous, elliptic, (4–)6–9(–12) × 1.7–4.2(–6) cm; base cuneate, not inrolled, apex acute, rarely obtuse; leaf surface glabrous on both sides; lower leaf surface not glaucous; midrib immersed above, raised below, secondary veins 7 to 13 pairs, slightly or conspicuously raised above, raised below, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins slightly raised or almost immersed above, slightly or conspicuously raised below. Inflorescences usually clustered around terminal buds or on short leafless shoots, rarely in axils of leaves, paniculate, 3–9 cm long, sparsely pubescent with erect hairs to glabrous, with 20 to 50 flowers per inflorescence; floral pedicels of the lateral divisions (1.5–)3–5 mm long, pedicels of the central flowers up to 7 mm long. Flowers greenish yellow to creamy, 2.5–4 mm long, 2.6–3.2 mm diam.; tepals 6, equal, ovate, 1.3–2.2 mm long, 1–1.8 mm wide, almost glabrous or sparsely pubescent with ± appressed hairs outside, sparsely pubescent with appressed to erect (wavy) hairs inside; stamens 9, outer six filaments 0.4–0.6 mm long, innermost three stamens 0.5–0.8 mm long, filaments pubescent, anthers 0.7–1.1 mm long, 2-celled, anther apices obtuse to acute and glabrous, glands of innermost three stamens globose; staminodia 3, sagittate, ca. 0.8 mm long; pistil ca. 1.8 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with appressed or rarely erect hairs, less densely toward the bottom. Fruits ellipsoid, black-purple, ca. 3.3 × ca. 1.8 cm, surface smooth; infructescence axis 2.5–3 mm diam., fruit pedicels thickened to 5 mm diam. below the fruit, but not constricted.

Flowering time. December to February.

Distribution and habitat. Costa Rica and western Panama (Fig. 7); (520–)900–1400(–1800) m; lower montane wet forest.

Common names. Chancho blanco (*Guindon & Brenes 35*), Chancho colorado (*Haber & Bello 4322*), Chancho rosado (*Haber & Bello 8434*) (Costa Rica).

Selected specimens examined. COSTA RICA. **Alajuela:** Cantón Alfaro Ruiz, 1700 m, 10 May 1941 (fr), *A. Smith 2717* (F). **Guanacaste:** Cantón de Liberia, Parque Nacional Guanacaste, Estación Cacao, 10°55′45″N, 85°28′15″W, 1100 m, 3 Oct. 1990 (fr), *Chávez 216* (CR, INB, MO). **Puntarenas:** Reserva Biológica Monteverde, Río Veracruz, 10°16′N, 84°22′W, 1300 m, 4 May 1991 (fr), *Bello et al. 2779* (INB, MO). PANAMA. **Chiriquí:** ca. 13 km from Río Sereno, Finca Hartmann, 8°50′N, 82°45′W, 1400–1800 m, 12 May 1991 (fr), *McPherson 15312* (MO).

Beilschmiedia brenesii belongs to the *B. hondurensis* group, with its closest species being *B. hondurensis* (see the discussion under *B. hondurensis*).

7. Beilschmiedia costaricensis (Mez & Pittier) C. K. Allen, J. Arnold Arbor. 26: 415. 1945. *Hufelandia costaricensis* Mez & Pittier, Bull. Herb. Boiss. II, 3: 228. 1903 (excl. *Pittier 1863* fide Kostermans). TYPE: Costa Rica. San José: forests of El Copey, 1800 m, Feb. 1898 (fl), *Tonduz 11713* (lectotype, designated by Kostermans (1938), B not seen; isolectotypes, BM!, CR!, G-BOIS not seen, K!, P!, US!).

Beilschmiedia rohliana Lasser, Bol. Acad. Cienc. Fis. Mat. y Nat. Caracas 10: 193. 1946. TYPE: Venezuela. Aragua: Henri Pittier National Park, a village of Rancho Grande, 14 Feb. 1946 (old fl & immature fr), *Lasser 2052* (holotype, VEN!).

Cryptocarya kostermansiana C. K. Allen, J. Arnold Arbor. 26: 423. 1945. TYPE: Costa Rica. Alajuela: Canton Naranjo, Naranjo, Cerro del Espiritu Santo, 1150 m, 24 Feb. 1940 (fl), *A. Smith P2418* (holotype, A photo!; isotypes, F!, US!).

Tree, to 30 m tall. Terminal buds pubescent with appressed to ascending, straight hairs. Twigs terete, compressed to angular when young, densely to sparsely pubescent with appressed to ascending, straight hairs, less densely pubescent when old. Leaves alternate; petioles 0.5–2 cm long, flat to canaliculate above, almost glabrous or pubescent

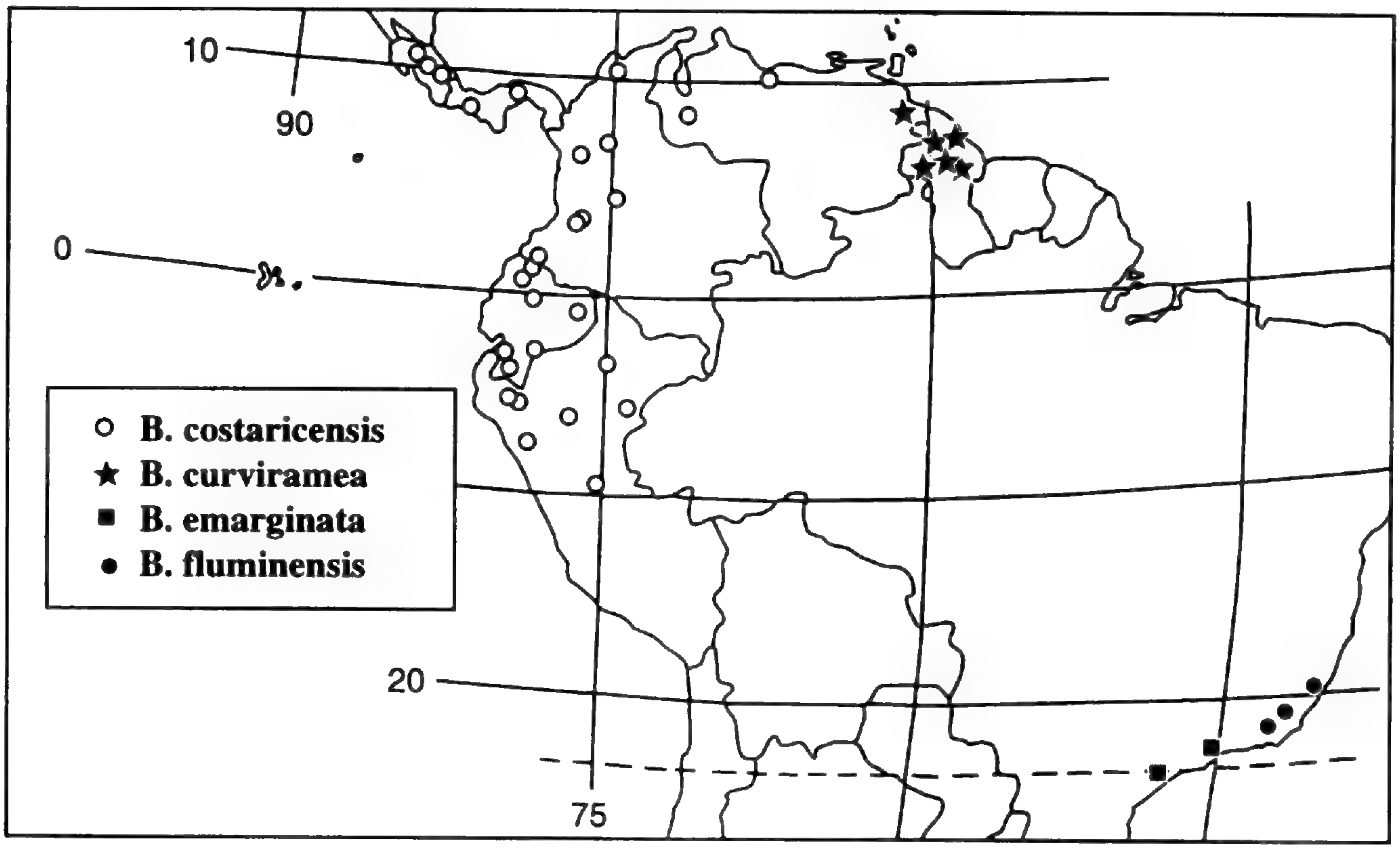


Figure 8. Representative distribution of *Beilschmiedia costaricensis, B. curviramea, B. emarginata,* and *B. fluminensis.*

with appressed to ascending hairs, concolorous with twigs; blades chartaceous to coriaceous, elliptic, 5–20(–26) × 2.5–9(–14) cm; base cuneate, not inrolled (rarely not only the base but the entire margin slightly inrolled), apex acute to acuminate, rarely obtuse; leaf surface glabrous on both sides or rarely lower leaf surface sparsely pubescent with appressed to ascending hairs, lower leaf surface not glaucous; midrib almost immersed above, raised below, secondary veins 5 to 11 (13) pairs, immersed above, raised below, tertiary veins ± percurrent, minor venation pattern fine to intermediate in size, areoles with branched free-ending veinlets inside, tertiaries and minor veins conspicuously to slightly raised on both sides. Inflorescences in axils of leaves, paniculate, 1–14(–16) cm long, sparsely pubescent with erect hairs, with (10) 25 to 50 (80) flowers per inflorescence; floral pedicels of the lateral divisions (0.3–)0.7–1.5 mm long, pedicels of the central flowers up to 4 mm long. Flowers creamy to whitish, 2–3 mm long, 2.3–2.8 mm diam.; tepals 6, equal, ovate, 1.3–1.8 mm long, 1–1.4 mm wide, pubescent with ± erect hairs on both sides; stamens 9, filaments 0.3–0.6 mm long, pubescent, anthers 0.6–0.9 mm long, 2-celled, anther apices obtuse to truncate and glabrous, glands of the innermost three stamens globose; staminodia 3, sagittate, ca. 0.7 mm long; pistil 1.1–1.8 mm long, glabrous to sparsely pubescent, ovary as long as and gradually narrowed into the style; receptacle pubescent with appressed hairs, less densely pubescent toward the bottom. Fruits ellipsoid, purple-black, 3–4(–5) × 1.5–2(–3) cm, surface smooth; infructescence axis 1.5–3.5 mm diam., fruit pedicels slightly thickened to 5 mm diam. below the fruit, but not apically constricted.

Flowering time. Usually January through May.

Distribution and habitat. Costa Rica, Panama, western Venezuela, western Colombia, Ecuador, and northern Peru (Fig. 8); (100)750–2300(3000) m; premontane wet forest to cloud forest.

Common names. Chancho (*Haber & Zuchowski 8746*) (Costa Rica); Aguacatillo (*Benalcazar & Silva 19*) (Colombia); Aguacatillo (*Poortmann s.n.*), Pacche (*Quelal & Tipaz 124*), Huevo cuguán/Malde (*Thomsen 58818*) (Ecuador); Palo oso (*Díaz & Baldeón 2464*), Puma (*Díaz 2088*), Pumapara (*Sagastegui et al. 12408*) (Peru).

Selected specimens examined. COSTA RICA. **Alajuela:** Reserva Biológica Monteverde, Río Peñas Blancas, 10°18′N, 84°45′W, 900 m, 1 Jan. 1987 (fl), *Haber & Bello 6531* (MO). **Cartago:** El Muñeco, on the Río Navarro, 1400–1500 m, 6–7 Mar. 1926 (immature fr), *Standley & Torres 51271* (US). **Guanacaste:** Chiripa, Tilarán, 4 km N of La Florida, 10°26′N, 84°54′W, 1100 m, 14 Jan. 1987 (fl), *Haber & Bello 6559* (MO). **Heredia:** Cantón Central, 11 km E of Cariblanco, 10°16′N, 84°05′W, 1060 m, 18 Apr. 1988 (young fl), *Loiselle 384* (CR). **Limón:** Cordillera de Talamanca, Fila Carbón, ca. 6 km W de Home Creek, 9°40′10″N, 82°50′35″W, 100 m, 14 Feb. 1991 (fl), *Hammel et al. 18116* (CR, F, MO). **Puntarenas:** Cantón de Coto Brus, Santa Maria de Pittier, 9°01′38″N, 82°51′56″W, 1700 m, 10 June 1995 (fr), *J. González 790* (INB). **San**

José: Sta. Ma de Dota-El Cedral, 12 June 1975 (sterile), *Póveda 1068* (CR, F). PANAMA. **Chiriquí:** Cerro Horqueta, 2100 m, 24 July 1966 (fl), *Blum & Dwyer 2624* (MO). **Panamá:** Cerro Azul, ca. 180 m, 17 July 1962 (immature fr), *Dwyer 2054* (MO). VENEZUELA. **Aragua:** Henri Pittier Parque Nacional, along road towards Rancho Grande, 1000–1200 m, 25 July 1994 (fl), *Lorea & Carnevali 5563* (MO). **Mérida:** La Chorrera, Carretera Mérida–Azulita, 3 Feb. 1987 (fl & fr), *van der Werff et al. 8786* (MO). COLOMBIA. **Antioquia:** Municipio Campamento, Vereda El Alto, 4 km W of mine "Las Brisas," 1 km from gorge "El Niño," 7°03′N, 75°19′W, 1810 m, 9 Sep. 1989 (fl), *Callejas et al. 8368* (MO). **Cundinamarca:** Laguna Pedro Palo above Finca San Jose, ca. 32 km Mosquera-La Mesa, 2000–2250 m, 1 Aug. 1976 (immature fr), *Gentry & Fallen 17136* (MO, NY). **Valle:** Peñas Blancas, cuenca río Pichindé, 1800 m, 11 June 1977 (young fl), *Benalcazar & Silva 19* (MO). **Magdalena:** Sierra de Perijá, E of Manaure, Hacienda Nuevo Horizonte, El Podrido, 1550–1600 m, 16 Nov. 1959 (immature fr), *Cuatrecasas & Romero-Castaneda 25413* (US). **Nariño:** 7 km from Chucunés, Planada Natural Reserve, 1°10′N, 77°58′W, 1800 m, 16 Nov. 1987 (fl), *de Benavides 8964* (MO). ECUADOR. **Carchi:** Gualpí Alto area, 01°02′N, 78°23′W, 900–1000 m, 18–25 May 1985 (immature fr), *Thomsen 58818* (MO). **El Oro:** Los Puntes de Guarumal, 1875 (immature fr), *Poortmann s.n.* (P). **Imbabura:** Road Otavalo–Apuela, 2000–3000 m, 14 Feb. 1989 (fl & immature fr), *van der Werff & Palacios 10574* (MO). **Loja:** El Colorado to 5 km NE of Alamor, 3°59′S, 79°58′W, 1200 m, 10 Aug. 1975 (immature fr), *Samaniego & Vivar 79* (US). **Morona-Santiago:** Bomboiza, Misión Salesiana-Shuar and around there, 03°25′S, 78°35′W, 800 m, 8–10 June 1986 (fl & fr), *Zaruma & Arguello 485* (MO). **Napo:** Aguarico, Reserva Etnica Huaorani, 245 m, 9 Mar. 1995 (immature fr), *Aulestia 3494* (MO). **Pichincha:** along new road Nanegal–Mindo, 1600–2500 m, 1 Mar. 1994 (fl & fr), *van der Werff et al. 13368* (MO). PERU. **Cajamarca:** Cutervo National Park, 12 km NE of San Andres de Cutervo, 06°10′S, 78°40′W, 2230 m, 11 Sep. 1991 (sterile), *Gentry et al. 74662* (MO). **Loreto:** C. I. Jenaro Herrera, Trocha Arboretum Braga, Tahuampa forest, 04°55′S, 73°45′W, 120–125 m, 29 Sep. 1991 (fr), *Grandez & Kovoor 2883* (MO). **Huánuco:** Prov. Puerto Inca, Dtto. Yuyapichis, 09°40′S, 75°02′W, 270 m, 1–15 Nov. 1990 (fr), *Tello 590* (MO). **Piura:** Huancabamba, Districto Canchaque, Chorro Blanco, 1500–1900 m, 18 Apr. 1987 (immature fr), *Díaz & Baldeón 2464* (MO). **San Martín:** Rioja Province, Carretera Rioja–Pedro Ruiz, Caves of Aguas Verdes, 950 m, 24 Mar. 1998 (fl), *van der Werff et al. 15585* (MO).

This species is distinguished by the following characters: appressed to ascending hairs on the terminal buds and young twigs, alternate leaves, areoles with branched free-ending veinlets, non-glaucous lower leaf surfaces, glabrous anthers, and fruit pedicels not constricted at the apices. This is sometimes misidentified as *B. pendula* due to its similar pubescence type, leaf shape, flower structure, and fruit shape (see the discussion under *B. pendula*).

Many Colombian and Ecuadorian collections for *Beilschmiedia costaricensis* appear different from collections from other countries (and some collections from Colombia) by their coriaceous leaves, coarser and less raised venation pattern, and sparsely pubescent pistils. Additionally, these collections tend to have shorter petioles and larger leaves. However, differences of the leaf texture and venation pattern between them are subtle, and it is difficult to make a clear separation: petiole lengths and leaf sizes show no clear distinction. Pubescence on pistils in the former collections cannot be used to distinguish these collections because this pistil indumentum is very sparse and easily missed. Separating these collections as a new species would only create confusion, so they are best placed within *B. costaricensis.*

8. **Beilschmiedia curviramea** (Meisn.) Kosterm., Rec. Trav. Bot. Néerl. 35: 853. 1938. *Aydendron curvirameum* Meisn., in DC., Prodr. 15(1): 90. 1864. *Hufelandia curviramea* (Meisn.) Mez, Jahrb. Königl. Bot. Gart. Berl. 5: 19. 1889. SYNTYPES: Guyana. Roraima, 1842–1843 (fl), *Schomburgk 1009* (B photo!, BM!, BR not seen, G-BOIS not seen, G-DEL not seen, LZ not seen, NY not seen, P!, W not seen); Demerara, Apr. 1844 (fl), *Schomburgk 1730* (K!).

Tree, to 25 m tall. Terminal buds pubescent with appressed hairs. Twigs terete, compressed when young, almost glabrous or sparsely pubescent with appressed hairs. Leaves opposite, rarely subopposite; petioles 0.6–1.5(–2.2) cm long, flat or canaliculate above, glabrous, slightly discolored or rarely concolorous with twigs; blades coriaceous, elliptic, (6–)9–20 × (2.5–)4–6.5(–8.5) cm; base cuneate to obtuse, not inrolled, apex acute or rarely cuspidate; leaf surface glabrous on both sides; lower leaf surface not glaucous; midrib immersed above, raised below, secondary veins 8 to 13 (16) pairs, slightly raised on both sides, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins almost immersed above, slightly raised or almost immersed below. Inflorescences in axils of leaves, very rarely clustered on a leafless short shoot, paniculate with few branches, 3–7(–12.5) cm long, sparsely pubescent with erect hairs, with 20 to 30 (50) flowers per inflorescence; floral pedicels of the lateral divisions 1–3 mm long, pedicels of the central flowers up to 5 mm long. Flowers yellow to white, ca. 2 mm long, ca. 2.5 mm diam.; tepals 6, equal, ovate to elliptic, 1.5–2 mm long, 1.2–1.7 mm wide, sparsely pubescent with ± appressed hairs outside, almost glabrous inside; stamens 9, outer six filaments 0.3–0.4 mm long, innermost three filaments 0.4–0.6 mm long, filaments pubescent, anthers 0.8–1 mm long, 2-celled, anther apices obtuse to truncate and pubescent, glands of innermost three stamens globose; staminodia 3, sagittate, ca. 0.6 mm long; pistil ca. 1 mm long, glabrous, ovary longer than and gradually narrowed into the style; receptacle pubescent with appressed hairs or glabrous. Fruits ellipsoid, black, 3–5 × 2–4 cm, surface smooth or rarely slightly warty; infructescence axis ca. 2.5 mm diam., fruit pedicels thickened to 4–5 mm diam. below the fruit and not constricted.

Flowering time. February, April to July, September to November.

Distribution. Eastern Venezuela and northern Guyana (Fig. 8); 0–650 m.

Common names. Aguacatillo moises (*Marcano-Berti 387*) (Venezuela); Lana-balli (*Persaud 70*) (Guyana).

Selected specimens examined. VENEZUELA. **Bolívar:** E of Cerro El Picacho, N of Las Nieves and Las Chicharras, 45 km N of Tumeremo, vincity of Deborah, Nuria Plateau, 600–650 m, 5–8 Feb. 1961 (fl & fr), *Steyermark 89161* (F, NY). **Amacuro:** E of Rio Grande, NE of El Palmar, near the border of Estado Bolívar, 19 Aug.–7 Sep. 1964 (immature fr), *Marcano-Berti 387* (F, MO, NY). GUYANA. **Cuyuni-Mazaruni:** W bank of Essequibo River 0–2 km S of Wolga settlement, 06°27′N, 58°38′W, 0–15 m, 24 Dec. 1992 (fl), *Henkel 650* (MO). **Upper Demerara-Berbice:** between the Demerara and Berbice Rivers, ca. 5°50′N, 15–19 July 1922 (fl), *de la Cruz 1655* (F, MO, NY).

Kostermans (1938) apparently regarded *Schomburgk 1009* and *1730* as identical. However, *Schomburgk 1009* was collected in 1842–1843, and *Schomburgk 1730* in April 1844.

Beilschmiedia curviramea is the only member of the *B. curviramea* group found outside southeastern Brazil. This species shares similar leaf and flower structures with *B. stricta*, but tends to have larger leaves, less conspicuously raised blade venation, and less pubescent flowers than seen in *B. stricta*. It is uncertain whether these characters consistently distinguish these two species since only one collection was examined for *B. stricta*.

Beyond the *Beilschmiedia curviramea* group, *B. curviramea* appears to be vegetatively similar to the Costa Rican species, *B. brenesii*, but leaves of *B. brenesii* cluster nearer the tips of branches and have a blade venation pattern conspicuously raised below. Leaves of *B. curviramea* are evenly distributed along the twigs and have a venation pattern almost immersed on both sides.

9. **Beilschmiedia emarginata** (Meisn.) Kosterm., Rec. Trav. Bot. Néerl. 35: 855. 1938. *Cryptocarya emarginata* Meisn., in DC., Prodr. 15(1): 76. 1864. *Hufelandia emarginata* (Meisn.) Mez, Jahrb. Königl. Bot. Gart. Berl. 5: 18. 1889. TYPE: Brazil. São Paulo: near Lorena, Oct. 1833 (fl), *Riedel 1585* (holotype, LE!; isotypes, G-BOIS not seen, K!, NY not seen).

Tree, to 15 m tall. Terminal buds pubescent with ferrugineous erect, short curly hairs. Twigs terete, compressed when young, sparsely pubescent with short erect curly hairs or almost glabrous. Leaves opposite; petioles ca. 0.5 cm long, flat above, sparsely pubescent or glabrous, concolorous with or slightly darker than twigs; blades chartaceous, elliptic, often asymmetrical and sinuate, 6.5–12 × 3–6.5 cm; base cuneate, not inrolled, apex emarginate to rounded; leaf surface glabrous on both sides; uncertain whether lower leaf surface glaucous or not; midrib immersed above, raised below, secondary veins 7 or 8 pairs, slightly raised or almost immersed above, raised below, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, slightly raised or almost immersed above, slightly raised below. Inflorescences in axils of leaves, paniculate, 3–5 cm long, almost glabrous or sparsely pubescent with short erect curly hairs, with 15 to 30 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1.2 mm long, pedicels of the central flowers up to 3 mm long. Flowers 2–2.8 mm long, 2.2–2.8 mm diam.; tepals 6, equal, ovate, 1.2–1.5 mm long, 0.8–1.2 mm wide, almost glabrous outside, sparsely pubescent with appressed hairs inside; stamens 9, outer six filaments ca. 0.2 mm long, innermost three filaments ca. 0.5 mm long, filaments pubescent, outer six anthers ca. 0.9 mm long, innermost three anthers ca. 0.7 mm long, all the anthers 2-celled, anther apices obtuse to truncate and pubescent, glands of innermost three stamens globose; staminodia 3, sagittate, ca. 0.7 mm long; pistil 1–1.5 mm long, glabrous, ovary as long as pistil and gradually narrowed into the style; receptacle pubescent with appressed hairs. Fruits unknown.

Flowering time. October and December.

Distribution. São Paulo, Brazil (Fig. 8).

Additional specimen examined. BRAZIL. **São Paulo:** Botanical Garden (native), 9 Dec. 1955 (sterile), *Kuhlmann 3885* (NY).

Among southeastern Brazilian *Beilschmiedia* species, *B. emarginata* is distinguished by its ferrugineous, short, and erect pubescence on terminal buds and twigs. Additionally, this species usually has undulate leaves and emarginate leaf apices, features not seen in the other southeastern Brazilian species.

10. Beilschmiedia fluminensis Kosterm., Rec. Trav. Bot. Néerl. 35: 865. 1938. TYPE: Brazil. Rio de Janeiro: Estado Rio G. Portella, Monte Sinai, 1935 (fl), *Nunes 323* (holotype, U not seen; isotype, RB!).

Tree, to 15 m tall. Terminal buds pubescent with appressed straight hairs. Twigs terete, slightly compressed when young, almost glabrous or sparsely pubescent with appressed hairs. Leaves opposite; petioles 1–2 cm long, canaliculate above, glabrous, slightly darker than twigs; blades firmly chartaceous, elliptic, (10–)13–16(–18) × 4–7 cm; base cuneate, slightly inrolled, apex acute, rarely obtuse; leaf surface glabrous on both sides, rarely lower leaf surface sparsely pubescent with short appressed hairs; lower leaf surface not glaucous; midrib immersed above, raised below, secondary veins 12 to 14 pairs, raised on both sides, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins slightly raised above, raised below. Inflorescences in axils of leaves, paniculate, 4–7 cm long, glabrous to sparsely pubescent with erect hairs, with 20 to 35 flowers per inflorescence; floral pedicels of the lateral divisions ca. 1 mm long, pedicels of the central flowers up to 2.5 mm long. Flowers greenish, 1.7–2 mm long, 2–2.5 mm diam.; tepals 6, equal, elliptic to ovate, 1–1.5 mm long, 1.1–1.5 mm wide, glabrous outside, sparsely pubescent with appressed hairs inside; stamens 9, outer six filaments ca. 0.2 mm long, innermost three filaments ca. 0.4 mm long, filaments pubescent, anthers 0.7–0.9 mm long, 2-celled, anther apices obtuse to truncate and pubescent, glands of the innermost three stamens globose; staminodia 3, sagittate, ca. 0.7 mm long; pistil ca. 1.2 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with appressed hairs around the base of stamens and staminodia. Fruits ellipsoid, 4.5–5 × ca. 3 cm, the surface warty or smooth; fruit pedicels ca. 2.5 mm diam., thickened to ca. 4 mm diam., not apically constricted.

Flowering time. September and October.

Distribution. Rio de Janeiro and Espírito Santo, Brazil (Fig. 8).

Selected specimens examined. BRAZIL. **Rio de Janeiro:** Malo Breuro, 25 Oct. 1927 (fl), *Auleuis s.n.* (RB). **Espírito Santo:** margin of Rio Paucos, road of Colomia, Colatina, 2 May 1934 (fr), *Kuhlmann 292* (RB).

Collections of *Beilschmiedia fluminensis* have sometimes been misidentified as *B. taubertiana* or *B. emarginata. Beilschmiedia fluminensis* can be distinguished from the two species by its appressed pubescence on terminal buds and twigs. *Beilschmiedia taubertiana* has erect, long pubescence while *B. emarginata* has erect, short curly pubescence. Further, petioles of *B. fluminensis* are relatively longer than the other two species. The species most similar to *B. fluminensis* is *B. stricta,* which shares a similar indument type, leaf shape, and flower structure. Differences between *B. fluminensis* and *B. stricta* are leaf bases (slightly inrolled vs. flat) and inflorescences (paniculate and almost glabrous vs. racemose and relatively densely pubescent).

11. Beilschmiedia hexanthera van der Werff, Brittonia 47: 374. 1995. TYPE: French Guiana. Vicinity of Eau Claire: near Saül, 200 m, 9–10 Aug. 1993 (fl), *van der Werff et al. 12951* (holotype, MO!; isotypes, CAY not seen, NY not seen).

Tree, to 20 m tall. Terminal buds pubescent with appressed hairs. Twigs terete, compressed when young, ± densely pubescent with short appressed hairs, less densely pubescent to glabrescent when old. Leaves alternate; petioles 0.6–1.3 cm long, flat to canaliculate, sparsely pubescent with short appressed hairs, concolorous with twigs; blades firmly chartaceous, elliptic, (5.5–)8–12(–16) × (2.5–)4–6 cm; base cuneate, not inrolled, apex acute; upper leaf surface glabrous, lower leaf surface pubescent with short appressed hairs; lower leaf surface not glaucous; midrib immersed or slightly raised above, raised below, secondary veins (5) 7 to 9 pairs, almost immersed above, raised below, tertiary veins not percurrent, minor venation pattern fine, areoles without free-ending veinlets inside, tertiaries and minor veins almost immersed on both sides (the pattern visible on both sides, coarser on the upper surface than on the lower). Inflorescences in axils of leaves, paniculate, (3–)6–11 cm long, sparsely pubescent with short erect hairs, with 25 to 50 (75) flowers per inflorescence; floral pedicels of the lateral divisions 0.3–0.5 mm long, pedicels of the central flowers up to 2 (rarely 3) mm long. Flowers greenish yellow, ca. 1.5 mm long, 1.7–2.1 mm diam.; tepals 6, equal, broadly ovate, 0.5–0.8 mm long, 0.6–1 mm wide, sparsely pubescent with short erect hairs outside, sparsely pubescent with appressed hairs inside, or with erect curly hairs at the

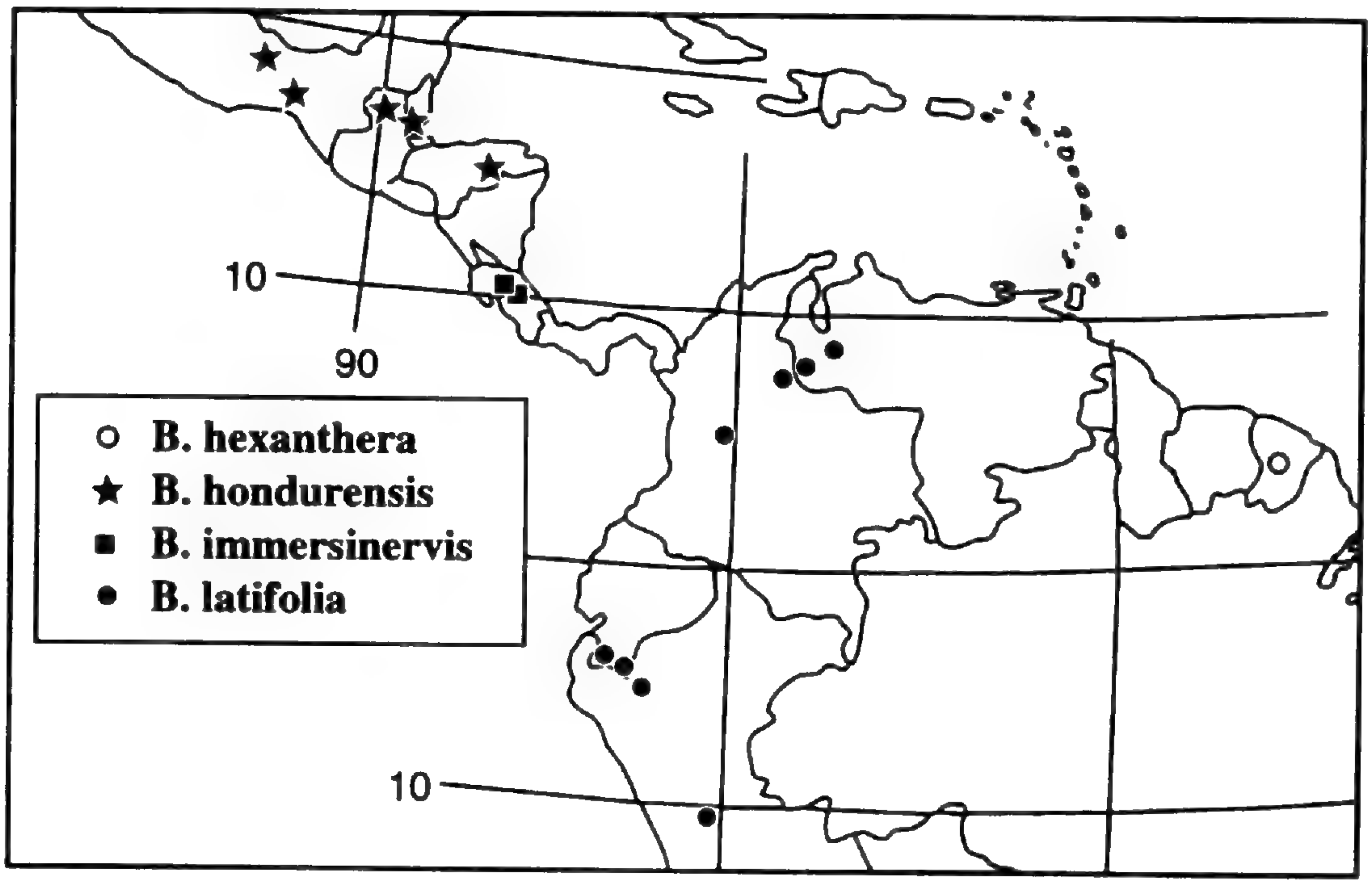


Figure 9. Representative distribution of *Beilschmiedia hexanthera*, *B. hondurensis*, *B. immersinervis*, and *B. latifolia*.

base inside; stamens 6, representing the outer two whorls, filaments ca. 0.2 mm long, pubescent, anthers ca. 0.4 mm long, 2-celled, anther apices obtuse to truncate and glabrous; staminodia 6, the three staminodia representing the third whorl subulate, 0.5–0.7 mm long, the lower half pubescent, glands on the three staminodia globose to reniform; the three staminodia representing the fourth whorl deltoid, ca. 0.5 mm long; pistil 1–1.2 mm long, glabrous, ovary ± as long as and gradually narrowed into the style; receptacle pubescent with erect curly hairs (upper part of the receptacle) and long appressed hairs (lower part of the receptacle). Fruits unknown.

Flowering time. August.

Distribution and habitat. French Guiana (Fig. 9); 200–400 m; unflooded forest.

Additional specimen examined. FRENCH GUIANA. **Saint-Laurent-du-Maroni:** Saül and vicinity, Route of Bélizon, S of Eaux Claires, 3°37′N, 53°12′W, ca. 200–400 m, 21 Aug. 1993 (fl), *Mori et al. 23377* (MO).

Beilschmiedia hexanthera is the only neotropical *Beilschmiedia* species with only six fertile stamens. According to Hyland (1989) there are several *Beilschmiedia* species with six fertile stamens in Australia, but as van der Werff (1995) suggested, it is unlikely that *B. hexanthera* and the Australian species are closely related. This reduction in stamen number probably occurred independently in French Guiana and Australia. *Beilschmiedia hexanthera* shares with *B. pendula* similar vegetative and floral characters (except for the stamens in the third whorl). However, *B. hexanthera* does not have the glaucous leaves of *B. pendula*.

12. Beilschmiedia hondurensis Kosterm., Rec. Trav. Bot. Néerl. 35: 854. 1938. TYPE: Belize: Camp 31, British Honduras-Guatemala Survey, 630 m, 7 Apr. 1934 (fr), *Schipp 1262* (holotype, K not seen; isotypes, AFS not seen, BM!, G-DEL not seen, F!, K!, NY!).

Tree, to 30 m tall. Terminal buds pubescent with appressed or slightly ascending, straight hairs. Twigs terete, compressed when young, glabrous. Leaves opposite; petioles 0.5–1(–1.2) cm, flat or canaliculate above, glabrous, darker than or concolorous with twigs; blades firmly chartaceous, elliptic, (5–)8.3–13.2(–18) × (1.5–)2.9–4.6(–6.5) cm; base cuneate, not inrolled, apex acuminate, rarely acute; leaf surface glabrous on both sides; lower leaf surface not glaucous; midrib immersed above, raised below, secondary veins (7) 9 to 12 (14) pairs, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets, tertiaries and minor veins slightly raised above, raised below. Inflorescences in axils of leaves or around terminal buds, paniculate with few branches, 3–6 cm long, sparsely pubescent with appressed to erect hairs, sometimes almost glabrous, with 10 to 30 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1.0 mm long, pedicels of the central flowers up to 2 mm long. Flowers ca. 3 mm long, ca. 2.5 mm diam.; tepals 6, equal, ovate, 1.5–2.1 mm long, 1.3–1.5 mm wide, sparsely pubescent with ± appressed hairs outside, sparsely pubescent with relatively long appressed to erect hairs inside, sometimes almost glabrous inside; stamens 9, filaments ca. 0.5 mm long, sparsely pubescent, anthers 0.6–0.8 mm long, 2-celled, anther apices acute or rarely obtuse, anther apices glabrous, glands of innermost three stamens globose; staminodia 3, sagittate, ca. 0.5 mm long; pistil ca. 1.3 mm long, glabrous, ovary as long as or longer than and gradually narrower into the style; receptacle sparsely pubescent with erect hairs, less densely toward the bottom. Fruits ellipsoid, black, 2.3–3 × ca. 1.3 cm (immature?), surface smooth; infructescence axis ca. 2 mm diam., fruit pedicels slightly thickened to 3 mm diam. below the fruit, apically constricted or rarely not constricted.

Flowering time. February.

Distribution and habitat. Eastern Mexico, Belize, northern Guatemala, Honduras (Fig. 9); (200–)750–1600(–1850) m; from wet tropical forest to montane forest.

Selected specimens examined. MEXICO. **Chiapas:** Municipio of Cintalapa, SE of Cerro Baul on the border with the state of Oaxaca, 1600 m, 8 Jan. 1973 (immature fr), *Breedlove & A. R. Smith 31417* (MEXU, MO, NY). **Oaxaca:** Municipio San Miquel Chimalapa, Cerro Salomón, near the border with Municipio Sta. Maria Chimalapa, 16°45′N, 94°11′30″W, 1850 m, 23 Dec. 1985 (immature fr), *Wendt et al. 5151* (MEXU, MO). **Veracruz:** Municipio Sn. Andres Tuxtla, Laguna Escondida, 3 km N of station of Biologia Tropical Los Tuxtlas, 200 m, 21 Feb. 1985 (fl), *Ibarra et al. 2292* (MEXU, MO). GUATEMALA. **Petén:** La Cumbre, 142/143 km E of the Cadenas Road, 11 May 1975 (young fl), *Lundell 19280* (MO). BELIZE. **Toledo:** SW of Mt. Maya, Columbia River Forest Reserve, Gloreia Camp, 16°22′N, 89°10′W, 750 m, 13–14 Apr. 1992 (immature fr), *Holst 4435* (BM, MO). HONDURAS. **Olancho:** trail between La Chorrera campsite and 1900 m camp on ridge, 14°59′N, 88°56′W, 1500 m, 31 May 1992 (fl), *Thomas 412* (MO).

The type collection of *Beilschmiedia hondurensis* is reported as a shrub, but some collections have been described as tall as 30 m.

Most closely related to *Beilschmiedia hondurensis* is *B. brenesii*. Some, if not all, Mexican collections placed in *B. hondurensis* approach *B. brenesii*, making the distinction between the two species difficult. *Beilschmiedia hondurensis* is usually distinguished from *B. brenesii* by its petioles darker than twigs, shorter floral pedicels, and fruit pedicels apically constricted. However, Mexican collections have the petioles concolorous with twigs and fruit pedicels not constricted at the apices. Typical *B. hondurensis* specimens have acuminate leaf apices, but these Mexican collections sometimes have acute leaf apices and are similar to most *B. brenesii*.

For reproductive characters, *Beilschmiedia hondurensis* differs from *B. brenesii* by its shorter floral pedicels. However, only one collection in *B. hondurensis* reveals flowers in good condition, and it is from an unusually low elevation for *B. hondurensis* (even for *B. brenesii*). More fertile material of *B. hondurensis* is clearly needed to distinguish *B. hondurensis* from *B. brenesii*.

13. Beilschmiedia immersinervis Sa. Nishida, sp. nov. TYPE: Costa Rica. Guanacaste: Cantón de Abangares, Cordillera de Tilarán, de Santa Elena hacia San Rafael, Zona Monteverde, 10°20′00″N, 84°53′00″W, 1200 m, 7 Jan. 1992 (fl & fr), *Guindon & Brenes 36* (holotype, MO!; isotype, INB!). Figure 10.

Haec species habitu *Beilschmiediae pendulae* similis, sed ab ea trichomatibus erectis atque antheris pubescentibus, ab aliis speciebus neotropicis nervis in hypophyllo immersis differt.

Tree, to 30 m tall. Terminal buds pubescent with erect, short curly hairs. Twigs terete, compressed or sulcate when young, densely to sparsely pubescent with erect curly hairs, less densely pubescent to almost glabrous when older. Leaves alternate to subopposite, rather clustered near the terminal buds; petioles 0.7–1.5 cm long, flat above, pubescent with erect curly hairs, concolorous with twigs; blades firmly chartaceous, oblanceolate to elliptic, 6–10(–13) × 2–4(–6) cm; base attenuate to cuneate, not inrolled, apex acute, rarely obtuse; leaf surface glabrous on both sides; lower leaf surface glaucous; midrib immersed above, slightly raised below, secondary veins 7 to 10 pairs, immersed on both sides (visible on lower leaf surface), tertiary veins weakly percurrent, minor venation pattern fine, areoles without free-ending veinlets inside, tertiaries and minor veins immersed and hardly visible above, almost immersed or very slightly raised below. Inflorescences in axil of the leaves near the terminal buds, paniculate with few branches, 2–6 cm long, pubescent with short erect hairs, with 10–30(–50) flowers per inflorescence; floral pedicels of the lateral divisions ca. 1 mm long, pedicels of the central flowers up to 3 mm long. Flowers greenish yellow, ca. 2.8 mm long, ca. 2.6 mm diam.; tepals 6, equal, elliptic to ovate, ca. 2.2 mm long, 1.3–1.7 mm wide, pubescent with erect or appressed hairs on both sides; stamens 9, outer six filaments ca. 0.6 mm long, innermost three filaments ca. 0.8 mm long, filaments pubescent, anthers ca. 0.8–1 mm long, 2-celled, anther apices obtuse to truncate and pubescent, glands of the innermost three stamens globose; staminodia 3, sagittate, ca. 0.7 mm long; pistil 1.3–1.8 mm long, glabrous, ovary almost as long as and gradually narrowed into the style; receptacle pubescent with appressed to erect hairs. Fruits ellipsoid, shiny black, ca. 2.5 × ca. 1.5 cm,

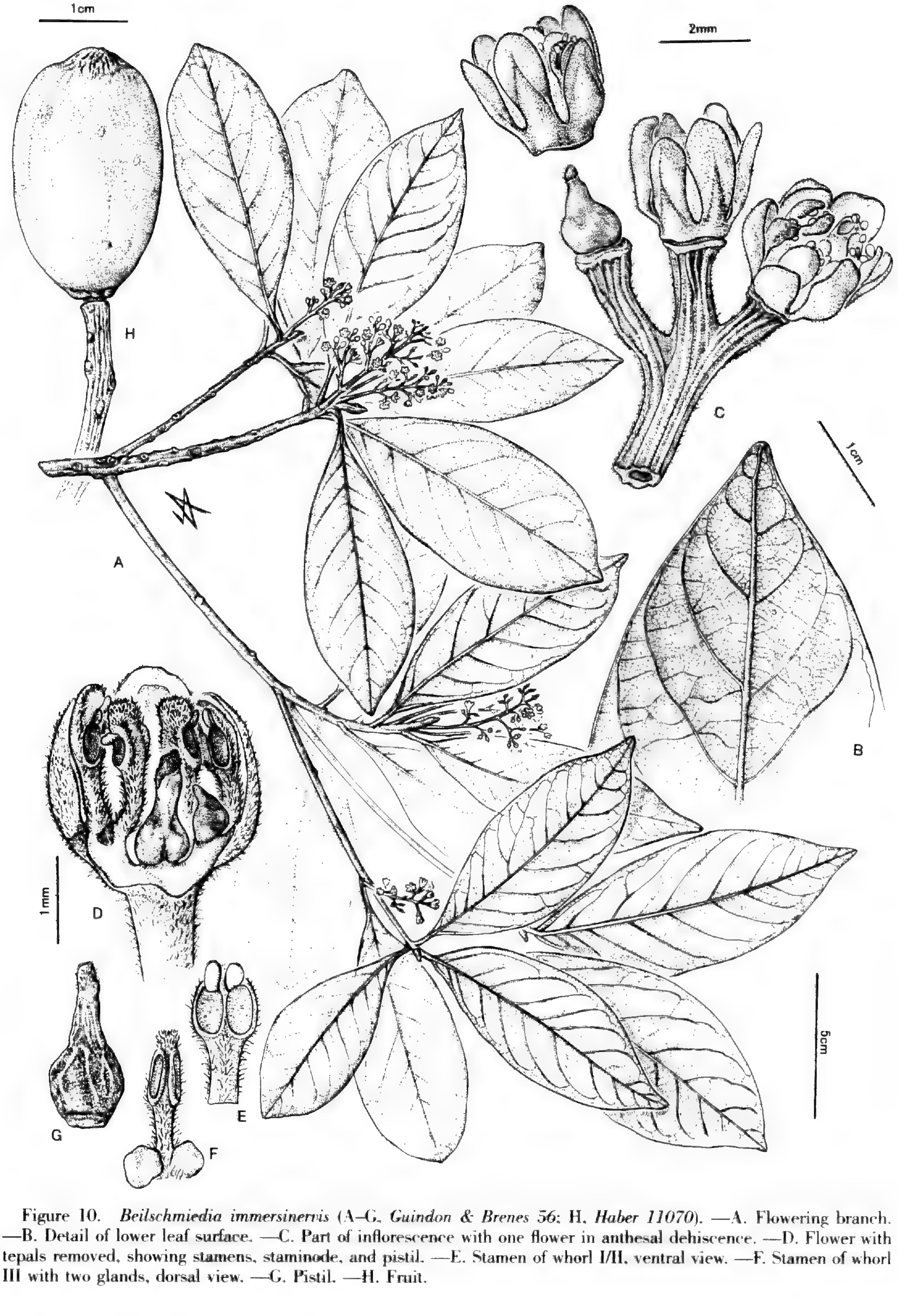


Figure 10. *Beilschmiedia immersinervis* (A–G, *Guindon & Brenes 56*; H, *Haber 11070*). —A. Flowering branch. —B. Detail of lower leaf surface. —C. Part of inflorescence with one flower in anthesal dehiscence. —D. Flower with tepals removed, showing stamens, staminode, and pistil. —E. Stamen of whorl I/II, ventral view. —F. Stamen of whorl III with two glands, dorsal view. —G. Pistil. —H. Fruit.

surface smooth; infructescence axis ca. 2 mm diam., fruit pedicels rarely slightly thickened to 3 mm diam., slightly constricted at the apices or almost not constricted.

Flowering time. December and January.

Distribution and habitat. Western Costa Rica (Fig. 9); 300–1400 m; premontane wet forest.

Paratypes. COSTA RICA. **Alajuela:** along a road between Canas and Upala, lower slopes Volcán Tenorio, 450 m, 23 Jan. 1984 (fl), *Pennington & Póveda 11416* (CR). **Guanacaste:** Parque Nacional Guanacaste, Estación Pitilla, La Pasmompa, 11°02′N, 85°25.3′W, 300 m, 17 June 1989 (fr), *Hammel et al. 17502* (INB, MO); Cantón de Tilarán, San Rafael to El Dos de Tilarán, 10°22′N, 84°53′W, 800–1100 m, 11 Mar. 1992 (fr), *Haber et al. 11070* (INB, MO); same cantón, San Rafael de Abangares, 10°20′35″N, 84°53′25″W, 1060 m, 10 Mar. 1996 (fr), *Yasuda et al. 1312* (INB, MO); Los Tornos, 10°21′N, 84°51′W, 1300 m, 14 Apr. 1987 (fr), *Haber & Bello 6967* (F, INB, MO). **Puntarenas:** Cantón de Puntarenas, Cordillera de Tilarán, Santa Elena, near Cañitas, Zona Monteverde, 10°19′30″N, 84°49′30″W, 1400 m, 1 Dec. 1992 (fl), *Guindon & Brenes 56* (CR, INB, MO, USJ).

Beilschmiedia immersinervis is distinguished by the following four characters: short curly pubescence on the terminal buds and twigs, leaves alternate, secondary veins immersed on both sides of the leaves, and anther apices pubescent. Some collections of *B. immersinervis* have been identified as *B. pendula*, probably because its leaf shape is similar to that of *B. pendula*. However, *B. immersinervis* can be separated from *B. pendula* by its erect and curly hairs on the terminal buds and pubescent anther apices.

Beilschmiedia immersinervis shares pubescence type and venation pattern with *B. steyermarkii*. However, *B. immersinervis* has pubescent anther apices and firmly chartaceous, symmetrical leaves, while *B. steyermarkii* has glabrous anther apices and more typically coriaceous, asymmetrical leaves.

This species also shares a similar venation pattern and pubescent anthers with *B. riparia*, but *B. immersinervis* is distinguished from this species by its immersed secondary veins. *Beilschmiedia immersinervis* also differs in its smaller, oblanceolate, glaucous leaves and slightly longer floral pedicels.

14. **Beilschmiedia latifolia** (Nees) Sa. Nishida, comb. nov. Basionym: *Hufelandia latifolia* Nees, Syst. Laur.: 674. 1836. TYPE: Peru. Locality not indicated, 1835 (fl), *Matthew 1433* (holotype, E!; isotypes, BM!, E!, K!, LE not seen, OXF not seen).

Tree, to 25 m tall. Terminal buds densely pubescent with brown to ferrugineous, erect, long, wavy to straight hairs. Twigs terete, angular when young, densely pubescent with long erect hairs, less densely pubescent when older. Leaves alternate; petioles 0.5–1.5 cm long, flat above, pubescent with long erect hairs to glabrous, concolorous with twigs; blades coriaceous, ovate to broadly elliptic, (5–)7–11(–18) × 4–8(–11.5) cm; base obtuse to rounded, not inrolled, apex obtuse; upper leaf surface glabrous, lower leaf surface densely pubescent with long hairs when young, less densely pubescent to rarely almost glabrous when old; lower leaf surface glaucous; midrib immersed above, raised below, secondary veins 6 to 9 pairs, immersed or impressed, rarely slightly raised above, raised below, tertiary veins usually percurrent, rarely only weakly percurrent, minor venation pattern fine, areoles lacking free-ending veinlets inside, tertiaries and minor veins immersed above, immersed (the pattern visible) or slightly raised below. Inflorescences in axils of leaves, paniculate, 6–11 cm long, densely pubescent with long erect hairs, with 20 to 40 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1 mm long, pedicels of the central flowers up to 2 mm long. Flowers 2.5–3 mm long, ca. 2.8 mm diam.; tepals 6, equal, ovate, 1.7–2.2 mm long, 1–1.5 mm wide; pubescent with erect hairs on both sides; stamens 9, outer six filaments ca. 0.3 mm long, innermost three filaments 0.3–0.5 mm long, filaments pubescent, anthers ca. 1 mm long, 2-celled, anther apices acute to truncate and glabrous, glands of the innermost three stamens globose; staminodia 3, sagittate, 0.5–0.8 mm long; pistil ca. 1.4 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with appressed long hairs. Fruits ellipsoid, black, 3–5 × ca. 2 cm, surface smooth; infructescence axis 2–3 mm diam., fruit pedicels not thickened below fruit, not constricted at the apices.

Flowering time. April, May, and September.

Distribution and habitat. Western Venezuela, western Colombia, southern Ecuador, and Peru (Fig. 9); 2100–3000 m; high montane cloud forest.

Common names. Cacoa (*Steyermark et al. 100700*), Curo (*C. K. Allen & Terrán 25*) (Venezuela); Roble palta/Sacha palta (*D. N. Smith & Pretel 8004*) (Peru).

Selected specimens examined. VENEZUELA. **Mérida:** Carbonera, 22 Jan. 1959 (sterile), *Bernardi 10955* (US). **Tachira:** from La Grita to Pregonero, 2300 m, 9 Oct. 1965 (fl & fr), *Bernardi 10954* (B, C, F, MO, NY). COLOMBIA. **Caldas:** path La Corrala, estate La Zarza, 2440 m, 22 June 1987 (fl), *Velásquez & Marulanda 7754* (MO). **Norte de Santander:** Cordillera Oriental, above Majuey, on road between Chinácota and Toledo, 7°30′N, 72°35′W, 2400–2600 m, 8 Mar. 1986 (fl), *Stein 3635* (MO, NY).

ECUADOR. **Loja:** between Tambo Cachiyacu, La Entrada and Nudo de Sabanillas, 2500–3500 m, 7 Oct. 1943 (immature fr), *Steyermark 54404* (F). **Zamora-Chinchipe:** limit with Podocarpus National Park, 04°23′N, 79°05′W, 2500–2600 m, Jan. 1995 (fl), *Palacios 13147* (MO). PERU. **Amazonas:** Luya Province, Camporredondo-Tullanya, short cut to Cerro Huicsocunga, 2350 m, 3 Sep. 1989 (sterile), *Diaz & Campos 3714* (MO). **Pasco:** Oxapampa Province, Río San Alberto valley, E of Oxapampa, 10°34′S, 75°22′W, 2500 m, 24 July 1984 (immature fr), *D. N. Smith & Pretel 8004* (MO, NY).

Kostermans (1938) placed *Hufelandia latifolia* under *Beilschmiedia sulcata.* However, the type of *H. latifolia* clearly differs from that of *B. sulcata* and is distinguished from the latter by its having erect pubescence, coriaceous leaves, and areoles without free-ending veinlets. *Beilschmiedia sulcata* itself is a problematic species, placed only imperfectly here in this study (see below).

Beilschmiedia latifolia is much more similar to *B. ovalis* or *B. tovarensis* than to *B. sulcata. Beilschmiedia latifolia* and *B. ovalis* share a very similar leaf shape, venation pattern, inflorescence, and flower structure. However, *B. latifolia* has ellipsoid fruits, whereas *B. ovalis* has spherical fruits. In vegetative characters, *B. latifolia* is distinguished from *B. ovalis* by its long hairs on the lower leaf surfaces. Usually, *B. ovalis* has its lower leaf surfaces almost glabrous even when the leaves are young. There are some exceptional specimens in *B. ovalis,* e.g., *Steyermark et al. 98480,* that have densely pubescent leaves with erect hairs when young, but rarely do the leaves retain this pubescence when they are old. Mature leaves of *B. latifolia* sometimes lose the pubescence on the lamina, but leaves of many collections, especially those from Venezuela, remain densely pubescent on the midribs and secondary veins even in old age. See Table 3 for a comparison.

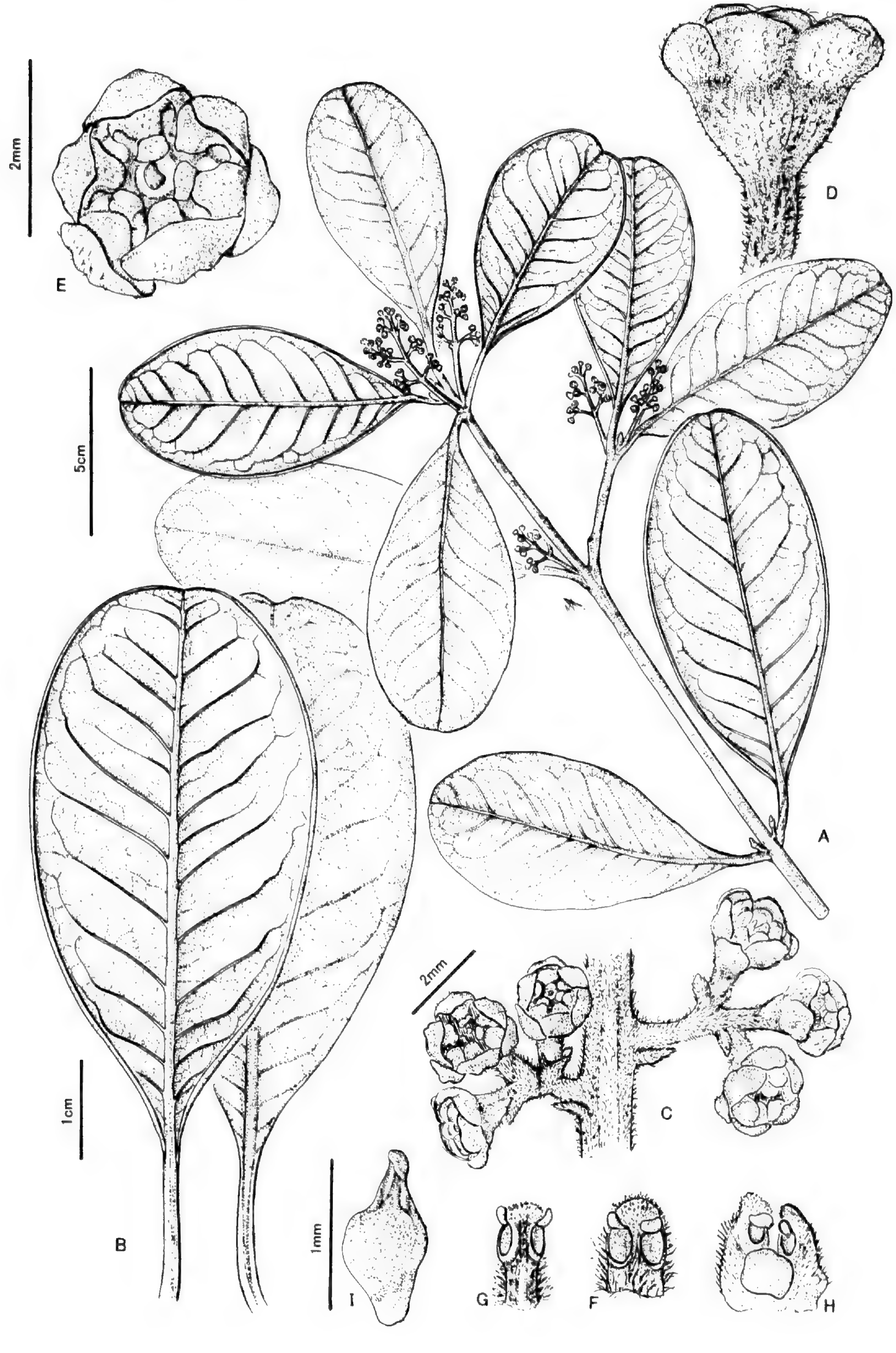
Beilschmiedia latifolia and *B. tovarensis* are also similar; *B. tovarensis* is a complex species with wide vegetative variation (see below), and some collections appear very similar to *B. latifolia.* Nonetheless, *Beilschmiedia latifolia* can be consistently distinguished from *B. tovarensis* by its erect hairs. These erect (often wavy) hairs appear on the terminal buds and the lower leaf surfaces, while appressed, sericeous hairs are seen on those parts in *B. tovarensis* (see Table 3 for the comparison).

Table 3. Differences between *Beilschmiedia ovalis* and some species morphologically close to *B. ovalis.* Country abbreviations: Ho = Honduras, CR = Costa Rica, Gu = Guatemala, Me = Mexico, Pa = Panama, Ve = Venezuela, Co = Colombia, Ec = Ecuador, Pe = Peru, Bo = Bolivia.

	B. ovalis	*B. latifolia*	*B. ovalioides*	*B. steyermarkii*	*B. tilaranensis*	*B. tovarensis*
Geographic distribution	Ho, CR, Pa	Ve, Co, Ec, Pe	Me	Gu	CR, Pa	CR, Pa, Ve, Co, Ec, Pe, Bo
Altitudinal distribution	1800–2800 m	2100–3000 m	1850–2750 m	300–400 m	1100–1580 m	500–2200 m
Pubescence on twigs and leaves	erect, short, and curly	erect, long, and straight to curly	erect, short, and curly	erect, short, and curly	erect, short, and curly	appressed, short, and straight
Leaf shape	ovate to broadly elliptic	ovate to broadly elliptic	obovate to broadly elliptic	narrowly elliptic	obovate	ovate to elliptic to obovate
Typical leaf length (cm)	4–10	7–11	11–16	5–10	6–13	8–20
Typical secondary vein number (pairs)	5 to 9	6 to 9	11 to 14	7 to 8	7 to 11	5 to 11
Pubescence on lower leaf surfaces	glabrous	pubescent	pubescent	glabrous	glabrous	pubescent
Fruit shape	spherical	ellipsoid	spherical	unknown	ellipsoid	ellipsoid

15. **Beilschmiedia linharensis** Sa. Nishida & van der Werff, sp. nov. TYPE: Brazil. Bahia: Reserva Florestal da Porto Seguro—CVRD/BA, Aceiro, 2100 km, left side, 26 Oct. 1988 (fl), *Farias 243* (holotype, MO!). Figure 11.

Haec species quoad characteres vegetativos *Beilschmie-*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E
D
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I
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H

diae rigidae similis, sed ab ea foliis angustioribus atque floribus minoribus, ab aliis speciebus neotropicis floribus depresse globosis differt.

Tree, to ca. 30 m tall. Terminal buds pubescent with appressed straight hairs. Twigs terete, compressed when young, sparsely to densely pubescent with appressed straight hairs. Leaves opposite; petioles 1.5–2 cm long, flat above, slightly darker than twigs, glabrous; blades coriaceous, obovate to elliptic, (5.5–)8–14 × 3–5 cm; base cuneate, inrolled toward lower surface (entire margin slightly inrolled toward lower surface), apex rounded to obtuse; leaf surface glabrous on both sides, lower leaf surface not glaucous; midrib immersed or slightly impressed above, raised below, secondary veins 8 to 12 (14) pairs, slightly raised on both sides, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins almost immersed on both sides. Inflorescences in axils of leaves, paniculate with few branches, 2.5–3.5 cm long, relatively densely pubescent with erect straight hairs, with ca. 15 flowers per inflorescence; floral pedicels of the lateral division ca. 0.5 mm long, pedicels of the central flowers up to 1 mm long. Flowers depressed-globose, ca. 1.6(–2) mm long, ca. 2.2 mm diam.; tepals 6, equal, curved toward inside, broadly ovate, ca. 0.5 mm long, ca. 1 mm wide, sparsely pubescent with erect hairs outside, sparsely pubescent with erect hairs to almost glabrous inside, stamens 9, outer six filaments ca. 0.2 mm long, innermost three filaments ca. 0.3 mm long, filaments pubescent, anthers ca. 0.5 mm long, 2-celled, anther apices obtuse to truncate and pubescent, glands on innermost three stamens globose; staminodia 3, sagittate, ca. 0.3 mm long; pistil ca. 1.2 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with appressed to erect hairs. Fruits unknown.

Flowering time. October.
Distribution. Espírito Santo, Brazil (Fig. 12).

Paratypes. BRAZIL. **Espírito Santo:** Reserva Florestal de CVRD. Linhares, Est. Cinco-Folhas, 1320 km right side, 16 Nov. 1982 (young fl), *Folli 409* (MO), 6 Oct. 1993 (young fl), *Folli 2033* (MO).

This species was first found in Linhares, Espírito Santo. Although I have only one collection in mature flower and two collections in flower bud, the small depressed-globose flowers of this species appear unique among neotropical *Beilschmiedia* and are diagnostic for *B. linharensis*. It shares a similar phyllotaxis, blade venation pattern, pubescence type, and leaf shape with *B. rigida*.

16. Beilschmiedia manantlanensis Cuevas & Cochrane, Novon 9: 18. 1999. TYPE: Mexico. Jalisco: municipio de Autlán de Navarro, S of Corralitos, Cañada de Alentrisco, 104°18′20″W, 19°36′19″N, 1800–1900 m, 26 Mar. 1998 (fl), *Guzmán & Santana 1616* (holotype, ZEA not seen; isotypes, BM not seen, CAS not seen, CHAPA not seen, ENCB not seen, F not seen, IBUG not seen, IEB not seen, MEXU not seen, MICH not seen, MO!, NY not seen, TEX not seen, UCR not seen, WIS not seen, XAL not seen).

Tree, to 20–30 m tall. Terminal buds densely pubescent with light brown, erect, long, straight hairs. Twigs terete, densely pubescent with long erect hairs, less densely when older. Leaves clustered (opposite on the tip of the twigs); petioles ca. 1 cm long, flat above, pubescent with long erect hairs to glabrous, concolorous with twigs; blades chartaceous, elliptic to narrowly obovate, 10–14 × 3.5–6 cm; base obtuse, not inrolled, apex obtuse to rounded; upper leaf surface glabrous, lower leaf surface pubescent with long hairs especially along the major veins when young, less densely to glabrous when old, lower surface not glaucous; midrib slightly raised above, raised below, secondary veins about 14 pairs, slightly raised above, raised below, tertiary veins usually not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins slightly raised on both surfaces. Inflorescences in axils of leaves, paniculate, 2–3 cm long, pubescent with long erect hairs or glabrous, glaucous, with less than 10 flowers per inflorescence; floral pedicels of the lateral divisions ca. 3 mm long, pedicels of the central flowers 4–7 mm long. Flowers ca. 3 mm long, ca. 3 mm diam., yellowish green; tepals 6, equal, ovate, ca. 1.8 mm long, ca. 1.2 mm wide; slightly pubescent with erect hairs to glabrous on both sides; stamens 9, outer six filaments ca. 0.5

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Figure 11. *Beilschmiedia linharensis* (*Farias 243*). —A. Flowering branch. —B. Lower leaf surface (left) and upper leaf surface (right). —C. Part of inflorescence. —D. Lateral view of flower. —E. Flower from above. —F. Stamen of whorl I/II, ventral view. —G. Stamen of whorl III, dorsal view. —H. Stamens of whorl II (right) and whorl III (left) with gland. —I. Pistil.

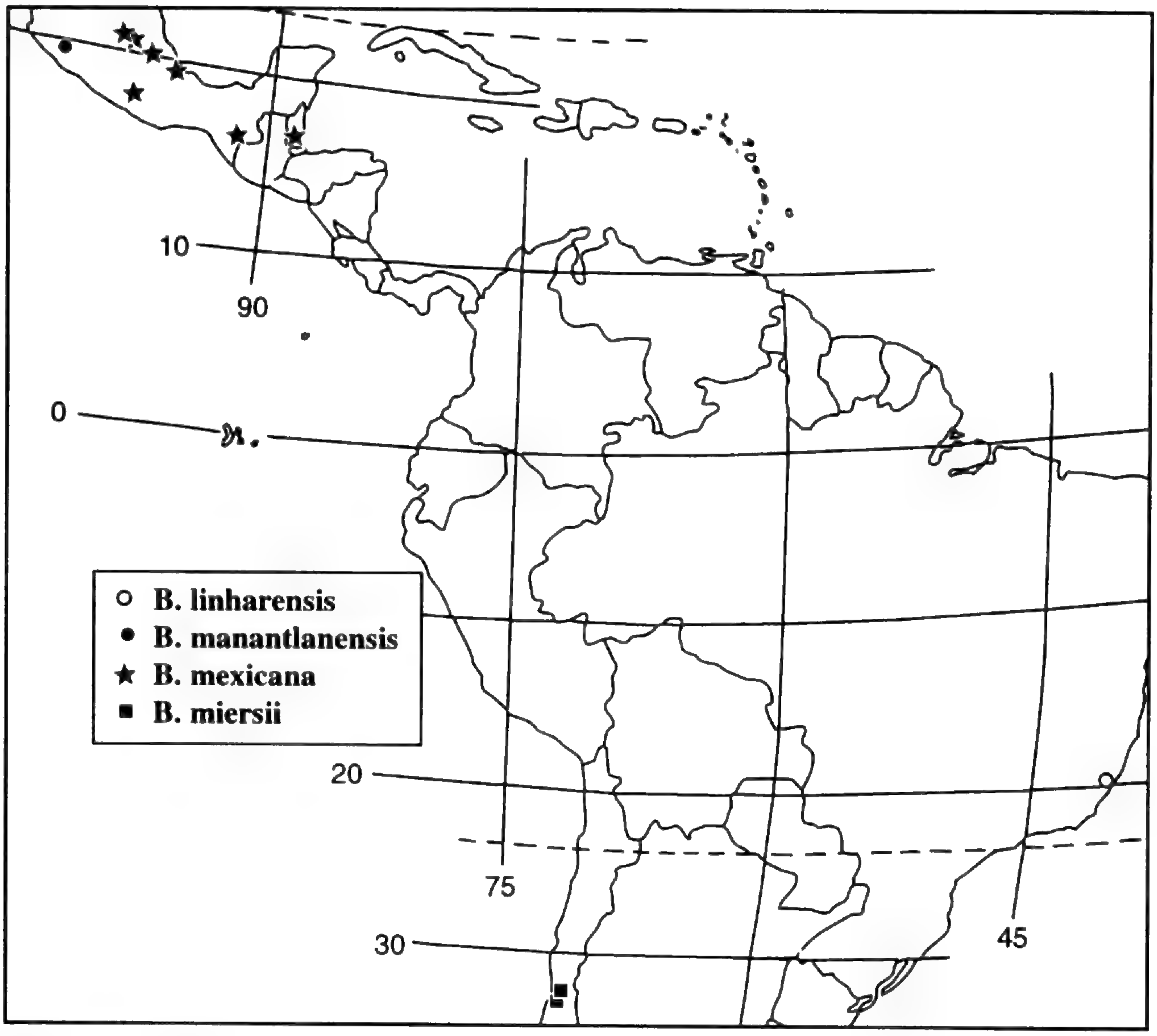

Figure 12. Representative distribution of *Beilschmiedia linharensis*, *B. manantlanensis*, *B. mexicana*, and *B. miersii*.

mm long, innermost three filaments ca. 0.7 mm long, filaments pubescent, anthers ca. 0.8 mm long, 2-celled, anther apices obtuse and glabrous, glands of the innermost three stamens globose; staminodia 3, sagittate, ca. 0.8 mm long; pistil ca. 1.5 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with erect hairs, glabrous at the bottom. Fruits unknown.

Flowering time. March.

Distribution and habitat. Jalisco, Mexico (Fig. 12), at 1800–1900 m in montane mesophyll forest.

Specimen examined. MEXICO. **Jalisco:** municipio de Autlán de Navarro, S of Corralitos, Cañada de Alentrisco, 104°18′20″W 19°36′19″N, 1900 m, 9 Mar. 1991 (fl), *Cuevas et al. 4076* (MO).

This species probably belongs to the *Beilschmiedia hondurensis* group. It has erect pubescence on the terminal buds and long leaves with coarse blade venation, approaching *B. angustielliptica*. It differs from *B. angustielliptica* in its leaf arrangement (clustered), leaf shape (with roundish to obtuse apex), and floral pedicels (being about twice as long as those of *B. angustielliptica*). *Beilschmiedia manantlanensis* also tends to have staminal filaments more pubescent than *B. angustielliptica* or others within the *B. hondurensis* group.

17. Beilschmiedia mexicana (Mez) Kosterm., Rec. Trav. Bot. Néerl. 35: 846. 1938. *Hufelandia mexicana* Mez, Jahrb. Königl. Bot. Gart. Berl. 5: 20. 1889. TYPE: Mexico. Orizaba, 1853 (fr), *F. Müller 1460* (lectotype, designated by Kostermans (1938), K!; isolectotypes, B not seen, K!, LE not seen, W not seen).

Linociera areolata Lundell, Amer. Midl. Naturalist 23: 176. 1940. TYPE: Mexico. Hidalgo: above Chapulhuacan, 1300 m, 12 July 1937 (fr), *Lundell & Lundell 7165* (holotype, AFS not seen; isotype, F!).

Tree, to 25 m tall. Terminal buds pubescent with appressed hairs, rarely almost glabrous. Twigs terete, compressed when young, pubescent with appressed hairs or glabrescent, less densely pubescent to glabrous when older. Leaves alternate, petioles 0.5–2 cm long, flat to canaliculate above, glabrous, rarely pubescent with appressed hairs, concolorous with twigs; blades chartaceous, elliptic, sometimes asymmetric, 5–13(–19) × 3–8(–10) cm; base cuneate, not inrolled, apex acute to obtuse, rarely acuminate; leaf surface glabrous on both sides; lower leaf surface not glaucous, or very rarely glaucous; midrib and secondary veins almost immersed or slightly raised above, raised below, secondary veins in 6 to 11 pairs, tertiary veins not percurrent, minor venation pattern fine, areoles rounded and lacking free-ending veinlets inside, tertiaries and minor veins raised on both sides, very rarely immersed above. Inflorescences in axils of leaves, paniculate, 1–10(–16) cm long, sparsely pubescent with short straight hairs or almost glabrous, with 10 to 20 (45) flowers per inflorescence; floral pedicels of the lateral divisions (0.3–)1–1.5 mm long, pedicels of the central flowers up to 4(–5.5) mm long. Flowers 2.5–2.7 mm long, 2.5–3 mm diam.; tepals 6, equal, ovate to elliptic, 1.3–1.7 mm long, 1.2–1.5 mm wide, sparsely pubescent with erect to appressed hairs on both surfaces. Stamens 9, outer six filaments 0.3–0.5 mm long, innermost three filaments ca. 0.5 mm long, filaments pubescent, anthers ca. 0.8 mm long, 2-celled, anther apices obtuse to truncate and glabrous, glands of the innermost three stamens globose; staminodia 3, sagittate, ca. 0.6 mm long; pistil ca. 1.5 mm long, glabrous, ovary almost as long as and gradually narrowed into the style; receptacle pubescent with appressed hairs. Fruits ellipsoid, purplish black, 2.5–3(–4) × ca. 1.5 cm, surface smooth; infructescence axis 1–2.5 mm diam., fruit pedicels scarcely thickened below the fruits, slightly constricted at the apices.

Flowering time. March to June, September.

Distribution and habitat. Southern Mexico and Belize (Fig. 12); 800–1780 m; montane mesophyll forest or semideciduous forest, rarely on limestone.

Common names. Calanique (*A. Gómez P. 795*), Tzitztez (*A. Méndez G. & Shilom 7686*) (Mexico).

Selected specimens examined. MEXICO. **Chiapas:** Municipio Oxchuc, waterfall of Río Mesbiljaz, 15 June 1984 (fr), *A. Méndez G. & Shilom 7686* (MO). **Guerrero:** Municipio Atoyac de Alvarez, in Nueva Dlhi, 17 km NE of El Paraíso, 1390 m, 29 Mar. 1983 (fl & immature fr), *Soto & Martínez 5122* (MO). **Hidalgo:** Municipio Tlanchinol, road to Tierra Colorada, 1580 m, 9 Apr. 1992 (immature fr), *Luna & Ocegueda 323* (MEXU). **Puebla:** Municipio Ahuacatlán, Agua Dulce, 4 km SE of Ahuacatlán, 20°01′N, 97°50′W, 1180 m, 12 June 1985 (immature fr), *Tenorio et al. 9000* (MO). **Queretaro:** Municipio Landa, 0.5 km SE of El Aguacate, 1520 m alt., 19 Dec. 1988 (fl), *Rubio 362* (IEB, MEXU). **San Luis Potosí:** Municipio Xilitla, 2 km SE of Ahuacatléan, 1300 m, 27 June 1959 (fl), *Rzedowski 10975* (MEXU). **Veracruz:** Cosalapa, Mar. 1922 (fl), *Purpus 8745* (MO, NY, US). BELIZE. **Toledo:** Maya Mountains, Bladen Nature Reserve, upper Bladen Branch basin, 16°30′41″N, 88°56′52″W, 900 m, 12 May 1996 (immature fr), *Holst et al. 5236* (MO).

Beilschmiedia mexicana appears close to *B. pendula*, sharing similar floral characters. However, *B. mexicana* usually has minor leaf venation conspicuously raised on both sides, acute leaf apices, and non-glaucous lower leaf surfaces, whereas *B. pendula* displays minor venation immersed above (although the pattern is visible), acuminate leaf apices, and glaucous lower leaf surfaces. These two species also have different minor venation patterns: *B. mexicana* has areoles rounded and lacking free-ending veinlets inside, while *B. pendula* has areoles angular and subtending branched veinlets. A distribution gap exists between them, with *B. pendula* found from Nicaragua to Ecuador and the West Indies and *B. mexicana* from Mexico and Belize.

18. Beilschmiedia miersii (Gay) Kosterm., Rec. Trav. Bot. Néerl. 35: 860. 1938. *Bellota miersii* Gay, Fl. Chil. 5: 298. 1851 or 1852. TYPE: Chile. Valparaiso: Aconcagua, (fl), *Gay 236* (lectotype, designated by Kostermans (1938), P!).

Tree, to 25 m tall. Terminal buds densely pubescent with erect curly hairs, or rarely with erect, slightly wavy hairs. Twigs terete, compressed when young, pubescent with erect, curly to wavy hairs, usually densely so when young, less densely pubescent when old. Leaves opposite; petioles 0.3–1 cm long, sulcate to canaliculate or rarely flat to terete above, pubescent with erect, curly to wavy hairs, concolorous with twigs; blades coriaceous, dried to light green, roundish ovate, (2.5–)5–12 × 1.5–6.5 cm; base rounded to obtuse, flat or rarely slightly inrolled toward lower surface, apex obtuse to rounded, sometimes retuse; leaf surface glabrous on both sides, rarely sparsely pubescent along the midrib; lower leaf surface glaucous; midrib immersed above, raised below, secondary veins (5) 7 to 8 (10) pairs, slightly raised or almost immersed above, slightly to conspicuously raised below, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins slightly raised or almost immersed above, slightly raised below. Inflorescences in axils of leaves (sometimes two inflorescences from one axil of the leaf), paniculate with few branches, 2–6(–9) cm long, ± densely pubescent with erect curly hairs, with 10 to 35 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1 mm long, pedicels of the central flowers up to 3.5 mm long. Flowers 2.5–3 mm long, 3.2–3.5(–4.2) mm diam.; tepals 6, equal, ovate, 1.2–1.5(–2.2) mm long, 1.2–1.7(–2.5) mm wide, ± densely pubescent with erect curly hairs outside, densely pubescent with long erect hairs inside; stamens 9, outer six filaments ca. 0.2 mm long, innermost three stamens ca. 0.3 mm long, filaments pubescent, outer six anthers 0.7–1 mm long, inner three anthers 0.6–0.8 mm long, 2-celled, anther apices obtuse to truncate and glabrous, glands of the innermost three stamens globose; staminodia 3, sagittate, ca. 0.5 mm long; pistil 1.4–1.6 mm long, glabrous or rarely sparsely pubescent, ovary longer than and gradually narrowed into the style; receptacle pubescent with long appressed hairs. Fruits ellipsoid, up to 4 × 3 cm (fide Kostermans, 1938), surface smooth; fruit pedicels in mature fruit unknown.

Flowering time. January to June and October to November.

Distribution. Central Chile (Fig. 12) at 120–900 m; reported to grow in subtropical, semiarid vegetation (Heusser, 1971).

Common name. Bellota (*Miers s.n.*).

Selected specimens examined. CHILE. **Valparaiso:** Zapallar, stream of Tigre, 27 Feb. 1952 (fl), *Boelcke 6466* (F, MO). **Santiago:** Acules, Apr. 1902 (fl), *Remy 108* (BM, MO).

Beilschmiedia miersii is one of only two *Beilschmiedia* species from Chile; both Chilean species are discussed under *B. berteroana.*

Nees (1836) used the name *Boldu chilanum* supposedly when citing a collection of this species, but it is to be treated as a superfluous name of *Boldus chilensis,* whose type belongs in the Monimiaceae.

Two collections of this species in flower, *Zöllner 11607* and *Anonymous (Nr.?) 547,* have a foliose bract on the rachis, also rare for neotropical *Beilschmiedia* species. However, this character is not consistently seen in this species.

19. Beilschmiedia ovalioides Sa. Nishida, sp. nov. TYPE: Mexico. Oaxaca: Ixtlán District, Sierra de Juárez, en route from Xiacui to Talea de Castro, ca. 25 km SSW of Talea from the route, 2750 m, 19 Apr. 1982 (fl & fr), *Lorence & Cedillo 4078* (holotype, MEXU!; isotypes, F!, MO!). Figure 13.

Haec species *Beilschmiediae ovali* affinis, sed ab ea foliis majoribus infra puberulis, nervis pluribus, venis tertiariis percurrentibus atque petiolis longioribus differt.

Tree, to 35 m tall. Terminal buds densely pubescent with ferrugineous, short erect curly hairs. Twigs terete, slightly angular when young, densely pubescent with ferrugineous, short erect curly hairs. Leaves alternate; petioles 2–3 cm long, flat above, rarely slightly canaliculate above, pubescent with ferrugineous short curly hairs, less densely pubescent when old, concolorous with twigs; blades coriaceous, broadly elliptic to obovate, sometimes slightly asymmetric, (8–)11–16 × 5–10 cm; base obtuse to cuneate, not inrolled, apex acute to acuminate; upper leaf surface glabrous, lower leaf surface puberulent with short erect hairs; lower surface usually glaucous; midrib and secondary veins immersed above, raised below, secondary veins 11 to 14 pairs, tertiary veins percurrent, minor venation pattern fine, areoles without free-ending veinlets inside, tertiaries and minor veins immersed above, slightly raised or immersed below (venation pattern visible below). Inflorescences in axils of leaves near terminal buds, paniculate, 4.5–12 cm long, pubescent with ferrugineous, short erect curly hairs, with 40 to 80 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–0.7 mm long, pedicels of the central flowers up to 1 mm long. Flowers greenish yellow, ca. 2.8 mm long, ca. 3 mm diam.; tepals 6, equal, ovate, 1.8–2.2 mm long, 1.2–2 mm wide, densely pubescent with erect hairs outside, sparsely pubescent with erect curly hairs to almost glabrous inside; stamens 9, filaments 0.3–0.8 mm long, pubescent, anthers ca. 0.9 mm long, 2-celled, anther apices obtuse to truncate and glabrous, glands of innermost three stamens globose; staminodia 3, sagittate, ca. 0.7 mm; pistil ca. 2 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with long, appressed to erect hairs. Fruits spherical, black, 3–4 × 3–4 cm, surface smooth; infructescence axis ca. 5 mm diam., fruit pedicels thickened to 10 mm in diam. below the fruit, not constricted at the apices.

Flowering time. April, May, and August.

Distribution and habitat. Southern Mexico (Fig. 14); 1850–2750 m; montane mesophyll forest.

Paratypes. MEXICO. **Chiapas:** Municipio Unión Juárez, in El Volcán Tacaná by a road from Talquián to the top of the volcano, along the border with Guatemala,

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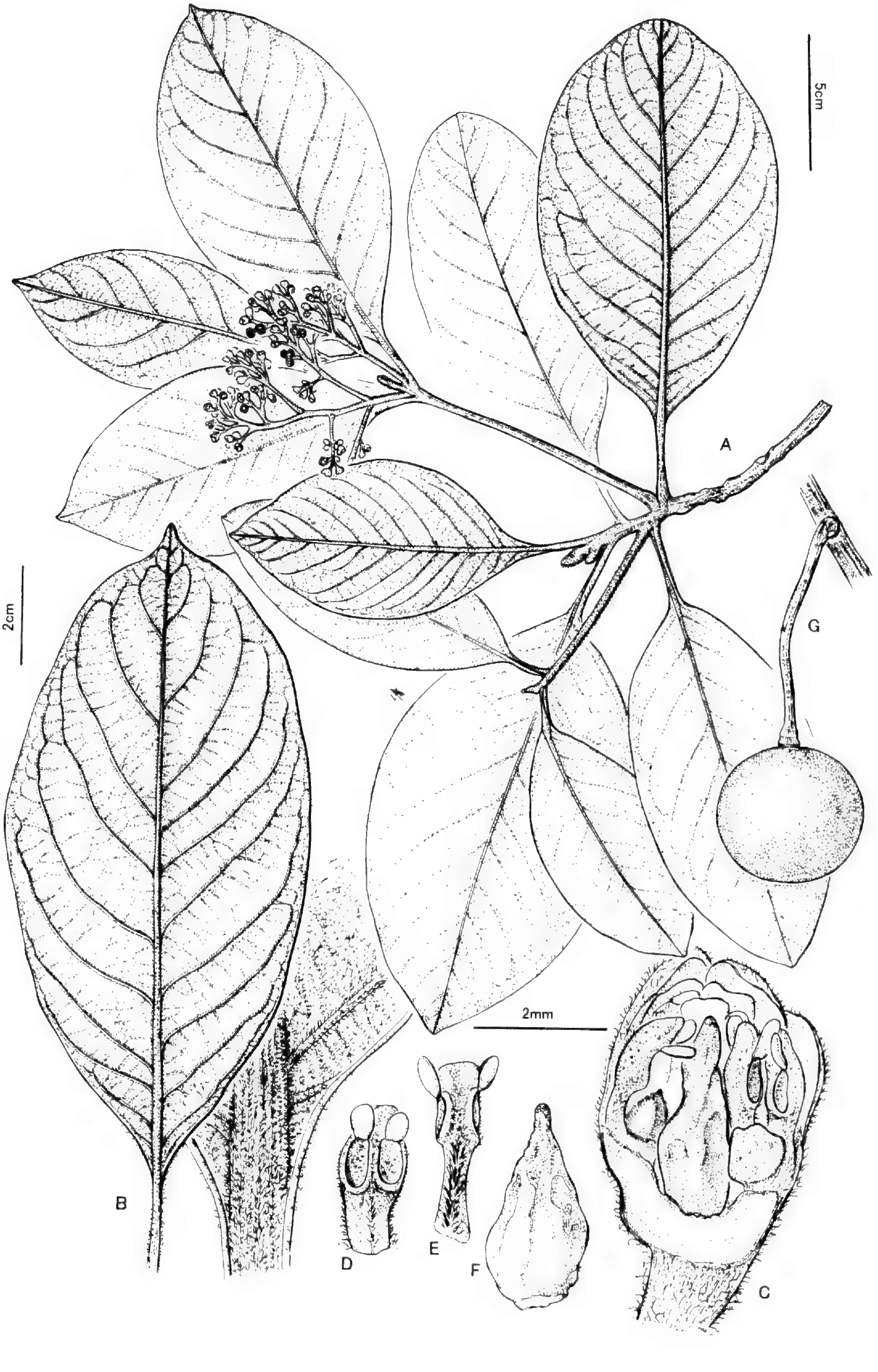
Figure 13. *Beilschmiedia ovalioides* (*Lorence & Cedillo 4078*). —A. Flowering branch. —B. Lower leaf surface with detail of pubescence. —C. Flower with tepals removed, showing stamens, gland (right), staminode (left), and pistil. —D. Stamen of whorl I/II, ventral view. —E. Stamen of whorl III, dorsal view. —F. Pistil. —G. Fruit.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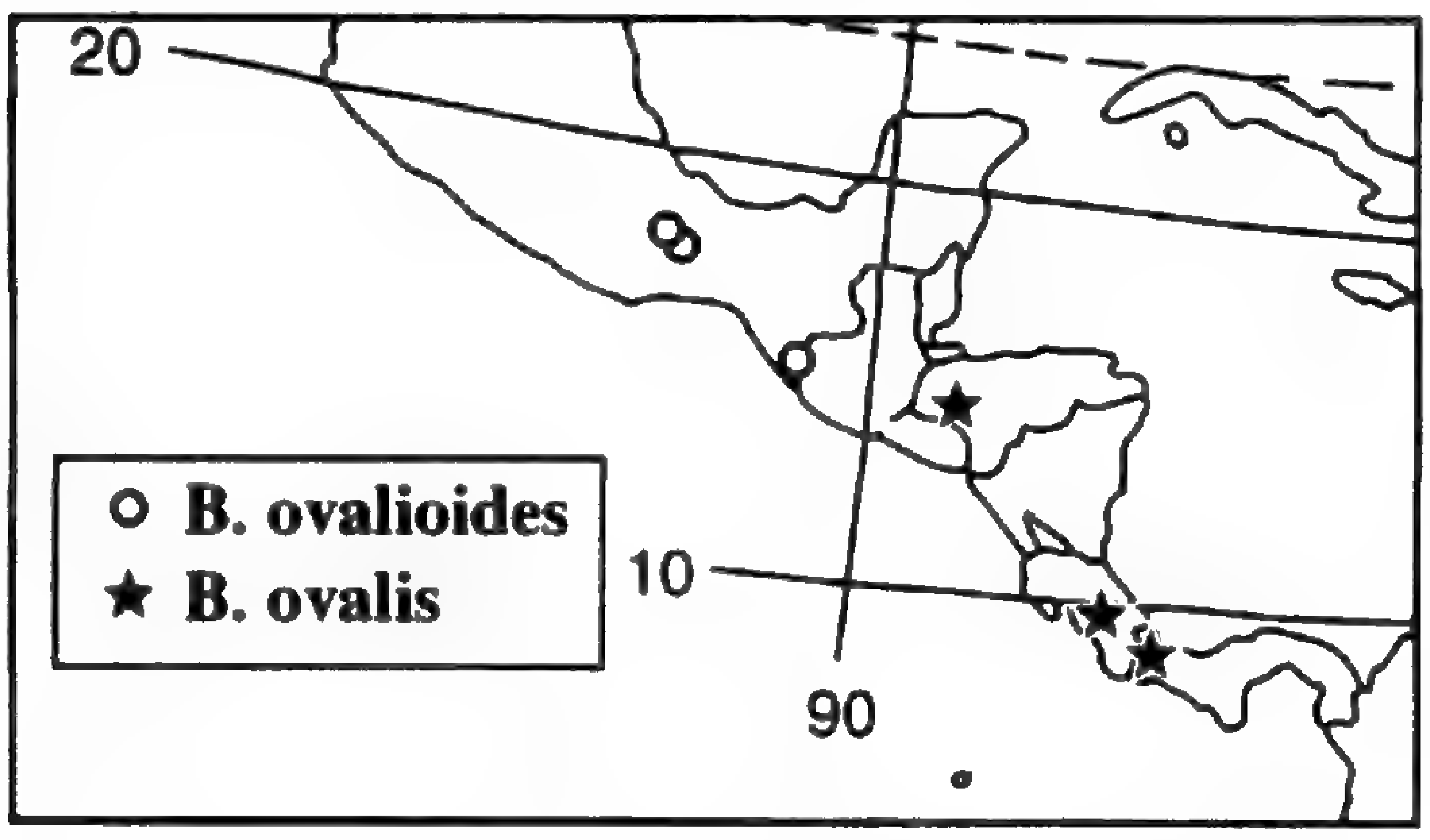

Figure 14. Representative distribution of *Beilschmiedia ovalioides* and *B. ovalis.*

2200–2700 m, 4 Feb. 1987 (fr), *Martínez et al. 19456* (MO). **Oaxaca:** Sierra de Juárez, ca. 25 km SSW of Talea de Castro, or 3 km N of the junction to Yalina, 2750 m, 31 May 1983 (fl), *Cedillo & Lorence 2372* (F, MEXU, MO); W of Municipio San Felipe Usila, 8 km straight S from Santa Cruz Tepetotutla, 17°40′06″N, 96°33′24″W, 2395 m, 31 Mar. 1994 (young fl), *Gallardo et al. 1007* (MEXU); Choapam District, road from Totontepec to Comaltepec, 5 km NE of Totontepec, 1850 m, 11 Nov. 1983 (fr), *Lorence et al. 4376* (F, MEXU, MO); 20 km SE of Totontepec, 250 m (mistake for 2500 m?), 9 Aug. 1977 (fl), *Sousa et al. 7871* (UC); Villa Alta District, 8.1 km N of Maravillas, road between Talea de Castro and Yalina, 2370 m, 15 May 1983 (fl & fr), *Torres et al. 2947* (F, MEXU, MO); Municipio San Felipe Usila, 7.3 km S (179°) of Santa Cruz Tepetotutla, 17°40′23″N, 96°33′28″W, 2220 m, 15 May 1994 (fr), *Rincón 419* (MEXU); same municipio, 7.6 km S (179°) of Santa Cruz Tepetotutla, 17°40′13″N, 96°33′28″W, 2240 m, 16 May 1994 (fl), *Rincón 433* (MEXU).

Beilschmiedia ovalioides appears close to *B. ovalis.* Both share very similar pubescence type, venation pattern, flower structure, and fruit shape. *Beilschmiedia ovalioides* has longer petioles (more than 2 cm long), lower leaf surfaces puberulent even when old, secondary veins more than 11 pairs, and conspicuously percurrent tertiary veins. *Beilschmiedia ovalis* has shorter petioles (less than 1.5 cm long), lower leaf surfaces glabrous when old, secondary veins less than 9 pairs, and tertiary veins not conspicuously percurrent. Those characters are not diagnostic individually, but in combination they discriminate these two species clearly. *Beilschmiedia ovalioides* tends to have larger (more than 11 cm long), broadly elliptic to obovate leaves, whereas *B. ovalis* usually has smaller (less than 10 cm), ovate leaves. Both species occur above 1800 m, but with some disjunction of distribution. *Beilschmiedia ovalioides* has been collected only in Mexico, whereas *B. ovalis* has been collected in Honduras, Costa Rica, and Panama.

20. Beilschmiedia ovalis (S. F. Blake) C. K. Allen, J. Arnold Arbor. 26: 418. 1945. *Hufelandia ovalis* S. F. Blake, J. Wash. Acad. Sci. 9: 461. 1919. TYPE: Costa Rica. Alajuela: Volcán de Poás, 2300 m, 31 Mar. 1907 (fl), *Pittier 2040* (holotype, US!; isotype, F!).

Beilschmiedia austin-smithii (Standl.) C. K. Allen, J. Arnold Arbor. 25: 418. 1945. *Persea austin-smithii* Standl., Field. Mus. Publ. Bot. 18: 1552. 1938. TYPE: Costa Rica. Alajuela: Cantón de Alfaro Ruiz, Palmira, 30 Apr. 1937 (fl), *A. Smith 4168* (holotype, F!).

Tree, to 30 m tall. Terminal buds pubescent with erect short curly hairs. Twigs terete to angular, densely to sparsely pubescent with short curly hairs, less dense to glabrous when old. Leaves alternate; petioles 1–1.5 cm long, flat above, glabrous or rarely pubescent with short curly hairs, concolorous with twigs; blades coriaceous, ovate to broadly elliptic, 4–10(–14) × 3–8(–10.5) cm; base obtuse to rounded, not inrolled, apex obtuse; leaf surface glabrous on both sides, rarely partly pubescent with erect curly hairs when young; lower surface glaucous; midrib immersed above, raised below, secondary veins 5 to 9 pairs, immersed above, raised below, tertiary veins not percurrent or weakly percurrent, minor venation pattern fine, areoles without free-ending veinlets inside, tertiaries and minor veins immersed or slightly raised above, slightly to conspicuously raised below. Inflorescences in axils of leaves or sometimes clustered around the terminal buds, paniculate, 3–15 cm long, pubescent with erect hairs, with 20 to 50 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1.2 mm long, pedicels of the central flowers up to 2 mm long. Flowers yellowish, 2.5–3.2 mm long, 2.9–3.7 mm diam.; tepals 6, equal, ovate to elliptic, 1.4–2.3 mm long, 1–1.7 mm wide; pubescent with erect hairs on both sides; stamens 9, outer six filaments 0.3–0.5 mm long, innermost three filaments 0.5–0.7 mm long, filaments pubescent, anthers ca. 1 mm long, 2-celled, anther apices obtuse and glabrous, glands of the innermost three stamens globose; staminodia sagittate, 0.5–1 mm long; pistil 1.3–1.7 mm long, glabrous, ovary almost as long as or longer than and gradually narrowed into the style; receptacle relatively densely pubescent with long, erect to almost appressed hairs. Fruits spherical, green when immature, ca. 3.5 × ca. 3.5 cm (or bigger), surface smooth; fruit pedicels ca. 5 mm diam., thickened to ca. 10 mm diam. below the fruit, not apically constricted.

Flowering time. February to May, September, and November.

Distribution and habitat. Western Honduras, central Costa Rica, western Panama (Fig. 14); 1800–2800 m; cloud forest.

Common names. Aguacate negro (*E. A. Lao 395*) (Costa Rica), Aguacatillo (*Thomas 584*) (Honduras).

Selected specimens examined. HONDURAS. **Comayagua:** 10.5 km E of lago Yojoa, Cerro Azul Meámbar, on the ridge leading to the Cerro Azul peak, 14°48′N, 87°53′W, 1870 m, 12 Mar. 1993 (immature fr), *Thomas 584* (MO). COSTA RICA. **Alajuela:** Palmire, 1900 m, 27 May 1938 (fl), *A. Smith NY675* (F, NY). **Heredia:** Volcán Barba, 1800–2000 m, 14 Nov. 1971 (sterile), *Holdridge 6595* (CR, NY). **San José:** Cantón Aserrí, valley of Río Grande de Tárcoles, El Cedral, Alto Hierbabuena, 9°50′30″N, 84°06′35″W, 2150 m, 6 Nov. 1993 (sterile), *J. F. Morales 1952* (INB, MO). PANAMA. **Chiriquí:** Cerro Punta, 2000 m, 24 May 1946 (fl?, missing), *P. H. Allen 3490* (MO).

Kostermans (1938) regarded *Hufelandia ovalis* as a synonym of *Beilschmiedia sulcata,* but Allen (1945) reestablished it as *B. ovalis.* However, Allen did this without seeing the type of *H. ovalis,* and in the same paper she described a new species, *B. austin-smithii,* based on a collection actually conspecific with *B. ovalis.* The type collection of *B. austin-smithii* has denser pubescence on the petioles and lower leaf surfaces than typical for *B. ovalis,* probably because this type has relatively young leaves: no other significant differences are observed.

Beilschmiedia ovalis belongs to the *B. costaricensis* group and is distinguished by its short curly pubescence on the terminal buds and twigs, alternate, coriaceous, ovate to broadly elliptic and glabrate (when old) leaves, and spherical fruits. This species shares similar leaf shape with *B. latifolia* and *B. tovarensis,* similar pubescence type with *B. steyermarkii* and *B. tilaranensis,* and similar reproductive characters with *B. ovalioides.* For differences between *B. ovalis* and each of these five species, see Table 3 and the discussion under the five species, respectively.

21. Beilschmiedia pendula (Sw.) Hemsl., Biol. Cent.-Amer., Bot. 3: 70. 1882. *Laurus pendula* Sw., Prodr.: 65. 1788. *Hufelandia pendula* (Sw.) Nees, Plantarum Laurinarum Secundum Affinitates Naturales Expositio: 22. 1833. TYPE: Jamaica: locality unknown, (fl), *Swartz s.n.* (lectotype, designated by Kostermans (1938), S not seen; isolectotypes, BM!, C!).

Hufelandia thomaea Nees, Plantarum Laurinarum Secundum Affinitates Naturales Expositio: 23. 1833. TYPE: St. Thomas. Locality and collector unknown (B not seen, P not seen).

Tree, to 35 m tall. Terminal buds pubescent with appressed straight hairs. Twigs terete, compressed when young, pubescent with appressed straight hairs, less densely pubescent to glabrous when old. Leaves alternate; petioles 0.7–2 cm long, flat or rarely canaliculate above, glabrous or sparsely pubescent with appressed hairs, concolorous with the twigs; blades firmly chartaceous, elliptic to oblanceolate, 4–13(–22) × 2–5(–10.5) cm; base cuneate, not inrolled, apex acuminate or very rarely acute to obtuse; upper leaf surface glabrous, lower leaf surface glabrous or rarely sparsely pubescent with appressed hairs; lower leaf surface glaucous; midrib immersed above, slightly raised below, secondary veins (5–)7–10(–12) pairs, immersed above, slightly to conspicuously raised or rarely almost immersed below, tertiary veins not percurrent or rarely ± percurrent, minor venation pattern fine, areoles angular with branched free-ending veinlets inside, tertiaries and minor veins immersed above (but the pattern partially visible), almost immersed or slightly raised below, the pattern visible on the upper surface much coarser than on the lower surface. Inflorescences in axils of leaves, paniculate with few branches, 3–14(–17) cm long, almost glabrous or sparsely pubescent with short appressed hairs, with 5–25(–40) flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1.5 mm long, pedicels of the central flowers up to 4 mm long. Flowers greenish yellow to whitish, 2–3 mm long, 2.3–2.8 mm diam.; tepals 6, equal, ovate, 1.2–1.7 mm long, 0.8–1.4 mm wide, sparsely pubescent with appressed to erect hairs on both sides; stamens 9, outer six filaments 0.3–0.4 mm long, innermost three filaments 0.4–0.6 mm long, filaments pubescent, anthers ca. 0.8 mm, 2-celled, anther apices obtuse-acute to truncate and glabrous, glands of the innermost stamens globose; staminodia 3, sagittate, ca. 0.8 mm long; pistil ca. 1.5 mm long, glabrous or rarely sparsely pubescent, ovary almost as long as and gradually narrower into the style; receptacle pubescent with appressed hairs. Fruits ellipsoid, black, shiny, ca. 2–3.5(–4.5) × ca. 1.5 cm, surface smooth; infructescence axis ca. 2 mm diam., fruit pedicels strongly constricted at the apices, slightly thickened below the fruit.

Flowering time. February to November.

Distribution and habitat. Honduras, Nicaragua, southern Costa Rica, Panama, the West Indies, Venezuela, Colombia, and Ecuador (Fig. 15); 0–1680 m; montane broad-leafed forest, tropical wet forest, sometimes on limestone.

Common names. Mulato (*Ekman 14826*), Carne de doucella (*A. Luna 650*) (Cuba); Vacarita (*Stern*

& Chambers 173) (Panama); Cobalongo macho (*Veillon II/12*) (Venezuela).

Selected specimens examined. CUBA. **Camagüey:** Loma del Gato and vicinity Cobre Range of Sierra Maestra, 11 July–14 Aug. 1921 (immature fr), *León et al. 10451* (NY). **Cienfuegos:** SE of Cumanayagua, Sierra de San Juan, 3–400 m, July 1941, (fl), *Howard 5695* (F, MO, NY, U). **Guantánamo:** E Cuba, Monte Verde, 1856–7 (fl & immature fr), *Wright 485* (BM, BR, MO, NY). **Holguín:** Pierra de Nipe, at Río Piedras, 500 m, 24 Aug. 1915 (immature fr), *Ekman 6402* (F, NY, US). **Sancti Spíritus:** Santa Clara, Mts. Trinidad, 650–750 m, 9 Mar. 1910 (fl), *Britton & Wilson 5320* (NY). **Santiago de Cuba:** S side of the crest of the Sierra Maestra, La Bayamesa, W of Aserradero San Antonio de los Cumbres, 1400–1500 m, 23–24 Jan. 1956 (young fl), *Morton 9563* (US). **Villa Clara:** St. Domingo, 600 m, 24 May 1887 (fl), *Eggers 2087* (NY). JAMAICA. Clarendon, along road between Ritchies & Balcarres, 900 m, 10 Nov. 1973 (immature fr), *Proctor 33607* (MO). HAITI. Ouest, Gros Cheval, Mornes des Commissaires, 1400 m, 17 Mar. 1942 (immature fr), *Holdridge 1053* (BM, F, MO, NY, US). DOMINICA. Barahona, El Gajo, ca. 7 km from the carretera de Cabral a Polo, through the way to Entrada de Cortico (Monteada Nueva), 18°07.5′N, 71°13.5′W, 1400 m, 18 Jan. 1986 (immature fr), *Zanoni & Pimentel 36009* (MO, NY). PUERTO RICO. Adjuntas, in a forest near a stream of Yunro, 22 May 1886 (fl), *Sintenis 4398* (B, BM, BR, NY, P, US). ST. KITT. Lawnent? estate, 8 Sep.–5 Oct. 1901 (immature fr), *Britton & Cowell 634* (NY). MONTSERRAT. Centre Hills, 400 m, 7 Nov. 1944 (fl), *J. S. Beard 409* (NY, U). GUADELOUPE (and dependances). St. Louis, valley of St. Louis, 700 m, 18 Sep. 1899 (fl), *Duss 4014 (4006)* (NY). MARTINIQUE. Pinte-Novie, 300–700 m, 1897 (young fl & fr), *Duss 3863* (NY). ST. LUCIA. Fouds St. La eques, 26 Mar. 1889 (sterile), *Anonymous s.n.* (BM). HONDURAS. **Yoro:** road Real de San José Texíquat to Campo Nuevo at a place called Las Letras, W of Cerro Cabeza de Negro, 15°28′00″N, 87°26′05″W, 1010 m, 24 Apr. 1995 (fr), *Aguilar & Evans 4073* (MO). NICARAGUA. **Matagalpa:** Macizos de Peñas Blancas, SE side, drainage of Quebrada El Quebradon, slopes N of Hda. San Martín, ca. 13°14–15′N, 85°39′W, 950–1100 m, 24 Nov. 1981 (fr), *Stevens et al. 20891* (MO). COSTA RICA. **Puntarenas:** Buenos Aires, Cordillera de Talamanca, Ujarrás, left margin of Quebrada Dorora, enroute to Río Lori, 09°17′50″N, 83°15′30″W, 1520 m, 11 Mar. 1993 (fl), *Herrera 5861* (MO). **San José:** along Pan American Highway, ca. 1 km N of San Isidro del General, ca. 600 m, 9 Sep. 1943 (sterile), *Barbour 1019* (F). PANAMA. **Darién:** Bahia de Piñas, slopes of bordering hills, 24 June 1957 (sterile), *Stern & Chambers 173* (NY). **Panamá:** Sendero de Interpretación, 1 km E of camp in the reserve forest of Inrenare, 8°40′N, 79°55′W, 800–900 m, 24 Mar. 1994 (fl), *Correa & Montenegro 10408* (MO). VENEZUELA. **Mérida:** Highway Panamericana, between Río Gavilan & Río Perdido, 150–500 m, 2 June 1960 (fr), *Veillon II/12* (MO). **Miranda:** Districto Paéz, road between San Juan–Montevideo, 10°04′–06′N, 65°45′–47′W, 400 m, 7 Sep. 1977 (young fl), *A. González & Ortega 1363* (MO). COLOMBIA. **Antioquia:** Municipio San Luis, stream La Cristalina, 6°N, 74°45′W, 730–770 m, 22 May 1987 (immature fr), *Guillermo & Cárdenas 933* (MO). **Nariño:** Espriella, Fumaeo, 22 June 1951 (fr), *Castañeda 2820* (F). ECUADOR. **Esmeraldas:** San Lorenzo, near rail road, right of way 3 km SE, 20 Apr. 1943 (young fl & immature fr), *Little, Jr. 6294* (MO, NY, US). **Napo:** 5 km N of Coca, El Chuncho Floristic Reserve, 0°25′S, 77°01′W, 250 m, 23 May 1993 (young fl), *Palacios 10794* (MO).

Kostermans (1938) recognized Bentham as the author of the combination *Beilschmiedia pendula*, but Bentham did not validly publish it since he did not definitely associate the epithet *pendula* with the generic name *Beilschmiedia.* Hemsley was the author who validly published the combination in 1882.

Nees (1833) established *Hufelandia thomaea* on account of its upright inflorescence and non-pendulous fruits. However, Meisner (1864) did not recognize the differences and submerged it in *Beilschmiedia pendula.* The type of *H. thomaea* was not available for this study, but Meisner's treatment should be supported because the characters Nees referred to are too subtle to discriminate these taxa.

Beilschmiedia pendula is one of the most widely distributed neotropical species in the genus. It is often confused with *B. costaricensis, B. mexicana,* and *B. tovarensis*: these four species share similar pubescence type, leaf shape (except for a group of *B. tovarensis* with ovate to broadly elliptic leaves), flower structure, and fruit shape. However, *B. pendula* can be distinguished from *B. costaricensis* by blade venation almost immersed on upper leaf surfaces, glaucous lower leaf surfaces, and its fruit pedicels apically constricted. Differences between *B. pendula* and *B. mexicana* or *B. tovarensis* are discussed under these two species respectively.

Leaves of *B. pendula* are usually small and narrowly elliptic-oblanceolate. However, some exceptional collections show large and wide leaves, especially from Puerto Rico and Martinique. Leaf apices in these collections also differ from typical, distinctively acuminate leaf apices in being obtuse.

22. Beilschmiedia rigida (Mez) Kosterm., Rec. Trav. Bot. Néerl. 35: 856. 1938. *Hufelandia rigida* Mez, in Taubert, Bot. Jahrb. Syst. 17: 519. 1893. TYPE: Brazil. Rio de Janeiro: Alto Macaé de Nova Friburgo, Oct.–Nov. (fl), *Glaziou 19790* (lectotype, designated by Kostermans (1938), B not seen; isolectotypes, BM!, C!, F!, LE not seen, P!).

Tree, height unknown. Terminal buds pubescent with appressed short straight hairs. Twigs terete, sparsely pubescent with appressed short straight hairs or almost glabrous. Leaves opposite; petioles 1.5–3.5 cm long, flat above, slightly discolored from twigs, glabrous; blades coriaceous, obovate, 14–22 × 7–11 cm; base decurrent, flat to slightly inrolled toward lower surface, apex rounded to obtuse; leaf

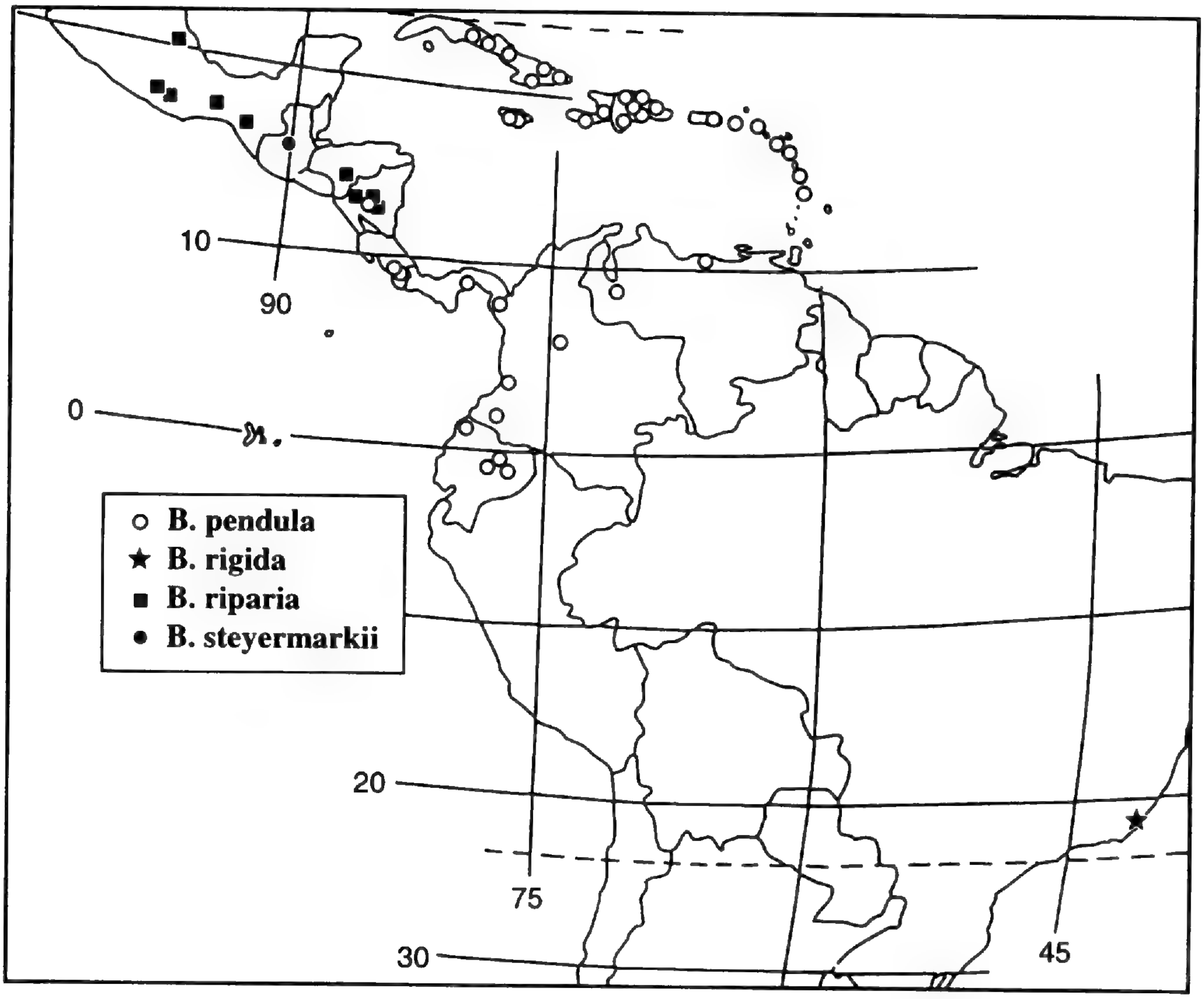

Figure 15. Representative distribution of *Beilschmiedia pendula, B. rigida, B. riparia,* and *B. steyermarkii.*

surface glabrous on both sides; lower leaf surface not known whether glaucous or not; midrib immersed above, raised below, secondary veins 9 to 12 pairs, slightly raised above, raised below, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins slightly raised on both sides. Inflorescences in axils of leaves or clustered around the terminal buds, paniculate, 4–12 (–18) cm long, sparsely pubescent with appressed to erect hairs or almost glabrous, with 10 to 30 (55) flowers per inflorescence; floral pedicels of the lateral divisions 1.5–2 mm long, pedicels of the central flowers up to 5 mm long. Flowers 3–3.5 mm long, ca. 3.5 mm diam.; tepals 6, equal, ovate, 1.5–2.3 mm long, 1.1–1.5 mm wide, pubescent with erect hairs on both surfaces; stamens 9, outer six filaments 0.3–0.5 mm long, innermost three filaments ca. 0.5 mm long, filaments pubescent, anthers 0.9–1.2 mm long, 2-celled, anther apices obtuse to truncate and pubescent, glands on innermost three stamens globose; staminodia 3, sagittate, ca. 0.7 mm long; pistil 1.6–1.9 mm long, pubescent, ovary slightly longer than and gradually narrowed into the style; receptacle pubescent with appressed hairs. Fruits known only in immature stage, ellipsoid, surface smooth; infructescence axis ca. 3 mm diam., fruit pedicels thickened to ca. 5 mm diam. below the fruit; fruit pedicels scarcely constricted at the apices.

Flowering time. September to November.

Distribution. Rio de Janeiro and Espírito Santo, Brazil (Fig. 15).

Common names. Canella tapinha (Kostermans, 1938), Canela-batata (*de Lima et al. 3707*).

Selected specimens examined. BRAZIL. **Rio de Janeiro:** Alto Macaé de Nova et Serra de Estrella, Oct.–Nov. (fl), *Glaziou 20444* (C, K, NY).

Beilschmiedia rigida belongs to the *B. curviramea* group, but has some distinct cuticular characters, showing relatively thick, straight anticlinal walls (Nishida & Christophel, 1999). This species is distinguished by its opposite, obovate leaves, rounded leaf apices, long petioles, larger flowers, and thicker inflorescence rachises.

23. Beilschmiedia riparia Miranda, Anales Inst. Biol. Univ. Nac. México 24: 75. 1953. TYPE: Mexico. Chiapas: ca. 7 km SE of Tuxtla Gutiérrez, border of the stream of Cerro Hueco, ca. 700 m, 4 Feb. 1951 (fl), *Miranda 6872* (holotype, MEXU!; isotype, F!).

Persea primatogena L. O. Williams & A. R. Molina, Econ. Bot. 31: 319. 1977. TYPE: Nicaragua. Matagalpa: Cordillera Central de Nicaragua, finca Sta. María de Ostuma, 1300–1400 m, 30 Nov. 1973 (fr), *Williams & Molina 42575* (F!, EAP not seen).

Tree, to 40 m tall. Terminal buds pubescent with erect, straight to wavy or rarely curly hairs. Twigs terete, rarely compressed when young, relatively densely pubescent with erect, straight to wavy curly hairs, less densely pubescent or rarely glabrous when old. Leaves alternate, rarely subopposite; petioles 1–2 cm long, flat above, glabrous or pubescent with erect, straight to wavy hairs, densely pubescent when young, concolorous with twigs; blades chartaceous, elliptic, rarely ovate, sometimes asymmetric, 7–16.5 × 4–7.5 cm; base cuneate, rarely obtuse, not inrolled, apex acute to obtuse; upper leaf surface glabrous, lower leaf surface pubescent with erect, straight to wavy hairs when young, glabrous when old, or sometimes hairs remaining on the midrib and secondary veins even when old; lower leaf surface not or very rarely glaucous; midrib and secondary veins immersed above, raised below, secondary veins 8 to 13 pairs, tertiary veins not percurrent or rarely ± percurrent, minor venation pattern fine, areoles without free-ending veinlets inside, tertiaries and minor veins immersed (the pattern visible) above, slightly raised below. Inflorescences in axils of leaves, rarely clustered on the buds, 2–14 cm long, pubescent with erect, wavy to curly hairs, with 15–100 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–0.7 mm long, pedicels of the central flowers up to 1.5 (rarely 2) mm long. Flowers white to creamy 2–3 mm long, 2.3–3 mm diam.; tepals 6, equal, ovate to elliptic, ca. 2 mm long, 1.5 mm wide, pubescent with erect, slightly wavy hairs on both sides; stamens 9, outer six filaments 0.3–0.5 mm long, innermost three filaments ca. 0.7 mm long, filaments pubescent; anthers 0.7–1 mm long, 2-celled, anther apices obtuse to truncate and pubescent (very rarely glabrous), glands of the innermost three stamens globose; staminodia 3, sagittate, ca. 0.8 mm long; pistil ca. 1.8 mm long, glabrous to sparsely pubescent, ovary longer than and gradually narrowed into the style; receptacle pubescent with appressed hairs. Fruits ellipsoid, black, 4 × 1.5 cm, surface smooth; fruit pedicels ca. 2 mm diam., scarcely thickened below the fruit, pedicels constricted at the apices.

Flowering time. January to May.

Distribution and habitat. Southern Mexico, southern Honduras, and Nicaragua (Fig. 15); (480–)700–1500 m; along streams in semi-deciduous forests or mixed cloud forests.

Common names. Guaquemico, Aguacate de mico, Aguacatillo (*Bachem et al. 1000*), (Mexico); Aguacatillo colorado (*von Hagen & von Hagen 1257*) (Honduras); Aguacate de monte (*Standley 10857*) (Nicaragua).

Selected specimens examined. MEXICO. **Chiapas:** Municipio Villaflores, Depresion Central and Sierra Madre, Finca Ocotlan, 740 m, 21 Apr. 1989 (immature fr), *Bachem et al. 1000* (MO). **Guerrero:** Municipio Chilpancingo, Cañada Las Hamacas, path to Soyatepec, 750 m, 2 May 1988 (fl), *L. C. Rodríguez 374* (FCME, MO). **Oaxaca:** Municipio San Miguel Chimalapa, 2 km N to Col. Rodulfo Figueroa road to Díaz Ordaz and B. Juárez, 16°34'N, 94°12'W, ca. 1400 m, 28 Mar. 1984 (fl), *Wendt & Rico 4338* (MO). **Veracruz:** Misantla, June 1866 (fr), *M. Hahn s.n.* (P). HONDURAS. **Tegucigalpa:** locality unknown, ca. 840 m, 16 Dec. 1937 (sterile), *C. & W. von Hagen 1257* (NY). NICARAGUA. **Estelí:** entre Plan Helado y la laguna de Miraflor, El Zacatón, 13°14'N, 86°15'W, 1400 m, 30 June 1983 (immature fr), *Moreno 21657* (MEXU, MO). **Jinotega:** vicinity of Finca San Roque, sierra E of Jinotega, 1300–1500 m, 5 July 1947 (sterile), *Standley 10857* (F).

Beilschmiedia riparia belongs to the *B. costaricensis* group. This species is distinguished by the following characters: erect pubescence on the terminal buds and twigs, secondary veins raised below, a fine blade venation pattern, pubescent anthers, and elliptic fruits. To separate *B. riparia* from the similar *B. immersinervis*, see the discussion under the latter.

24. Beilschmiedia steyermarkii C. K. Allen, J. Arnold Arbor. 26: 417. 1945. TYPE: Guatemala. Alta Verapaz: S of Cubilagüitz, 300–400 m, 3 Mar. 1942 (fl), *Steyermark 44494* (holotype, F!).

Tree, to 27 m tall. Terminal buds pubescent with erect, short curly hairs. Twigs terete, slightly angular when young, pubescent with erect, short wavy hairs to glabrous, less densely pubescent when older. Leaves alternate; petioles 1–1.7 cm long, flat to canaliculate above, glabrous to pubescent with erect, short curly hairs, concolorous with the twigs; blades coriaceous, elliptic to narrowly ovate, often asymmetric, 5–10 × 1.5–4 cm; base and apex acute, rarely apex obtuse, glabrous on both sides; lower leaf surface uncertain whether glaucous or not; midrib immersed above, raised below, secondary veins in 7 or 8 pairs, immersed above, slightly raised below, tertiary veins not percurrent, minor venation pattern fine, areoles without free-ending veinlets inside, tertiaries and minor veins immersed above (sometimes the pattern visible above), slightly raised below. Inflorescences in axils of leaves, tending to cluster near the top of the branchlets, paniculate, 4–8 cm long, pubescent with erect short wavy hairs, with 25 to 65 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1 mm long, pedicels of the central flowers up to 3 mm long. Flowers ca. 2.4 mm long, ca. 2.5 mm diam.; tepals 6, equal, ovate to elliptical, ca. 1.5 × 1 mm, pubescent with erect wavy hairs outside, erect and wavy, or appressed hairs inside; stamens 9, filaments 0.3–0.6 mm long, pubescent, anthers 0.6–0.8 mm long, 2-celled, anther apices obtuse to truncate and glabrous, glands of the innermost stamens globose, staminodia 3, sagittate, ca. 0.8 mm long; pistil ca. 1.4 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with erect wavy hairs, less densely pubescent to glabrous toward the bottom. Fruits unknown.

Flowering time. March.

Distribution. Guatemala (Fig. 15); 300–400 m.

Additional specimen examined. GUATEMALA. Los Arcos, 149 km of Cadenas Road, 22 Dec. 1969 (young fl), *Contreras 9448* (C, F, MO).

Beilschmiedia steyermarkii is similar to *B. ovalis* in pubescence type, venation pattern, and floral structure but differs in its narrow leaves. Additionally, the two collections annotated herein are from 300–400 m altitude, which is a too low an elevation for *B. ovalis* (which typically occurs above 1800 m elevation).

Beilschmiedia steyermarkii also vegetatively resembles *B. immersinervis* (see the discussion under the latter).

As Allen (1945) reported, the type specimen of *B. steyermarkii* has few-flowered inflorescences. However, precise floral number is uncertain because the inflorescences are broken. The second specimen, collected after Allen's description, has inflorescences with relatively many (40 to 65) flowers.

25. Beilschmiedia stricta Kosterm., Rec. Trav. Bot. Néerl. 35: 863. 1938. TYPE: Brazil. Rio de Janeiro: G. Portella, Monte Sinai, 1935 (fl), *Nunes 313* (holotype, U not seen; isotype, RB!).

Tree, height unknown. Terminal buds pubescent with appressed straight hairs. Twigs terete, younger ones compressed, sparsely pubescent with appressed hairs, less densely pubescent to glabrous when older. Leaves opposite; petioles ca. 1 cm long, canaliculate to flat above, glabrous, slightly darker than branches; blades firmly chartaceous, elliptic, (5–)8–9 × 2.5–4 cm; base cuneate, not inrolled, apex acute; leaf surface glabrous on both sides; lower leaf surface not glaucous; midrib immersed or impressed above, raised below, secondary veins 9 to 13 pairs, raised on both sides, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins raised on both sides. Inflorescences in axils of leaves, racemose, 1.5–2.5 cm long, pubescent with ± appressed hairs, with 5 to 10 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1.2 mm long, pedicels of the central flowers up to 3 mm long. Flowers ca. 2.5 mm long, ca. 2.7 mm diam.; tepals 6, almost equal, ovate, ca. 1.8 mm long, 1.2–1.5 mm wide, pubescent with appressed hairs outside, sparsely pubescent with appressed hairs or almost glabrous inside; stamens 9, outer six filaments ca. 0.4 mm long, innermost three filaments ca. 0.5 mm long, pubescent, anthers ca. 1.1 mm long, 2-celled, anther apices obtuse to truncate and pubescent, glands of innermost three stamens globose; staminodia 3, sagittate, ca. 0.8 mm long; pistil 1.4–1.6 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle sparsely pubescent with appressed hairs. Mature fruits unknown, young fruit ellipsoid, surface warty; young fruit pedicels not constricted at the apices.

Distribution. Rio de Janeiro, Brazil (Fig. 16).

Beilschmiedia stricta is known only from the type collection. It appears to be similar to *B. curviramea* and *B. fluminensis* in leaf shape and flower structure (see the discussion under these two species respectively).

26. Beilschmiedia taubertiana (Schwacke & Mez) Kosterm., Rec. Trav. Bot. Néerl. 35: 863. 1938. *Hufelandia taubertiana* Schwacke & Mez, Arb. Bot. Gart. Breslau 1: 108. 1892. TYPE: Brazil. Minas Gerais: Rio Novo, 1890 (fl & fr), *Araujo 7047* (lectotype, designated by Kostermans (1938), B photo!; isolectotypes, P!, RB!).

Tree, height unknown. Terminal buds pubescent with erect, long straight hairs. Twigs terete, younger ones compressed, pubescent with erect, long straight or slightly wavy hairs, less densely pubescent when old. Leaves opposite; petioles 0.8–1 cm long, canaliculate above, pubescent with erect long

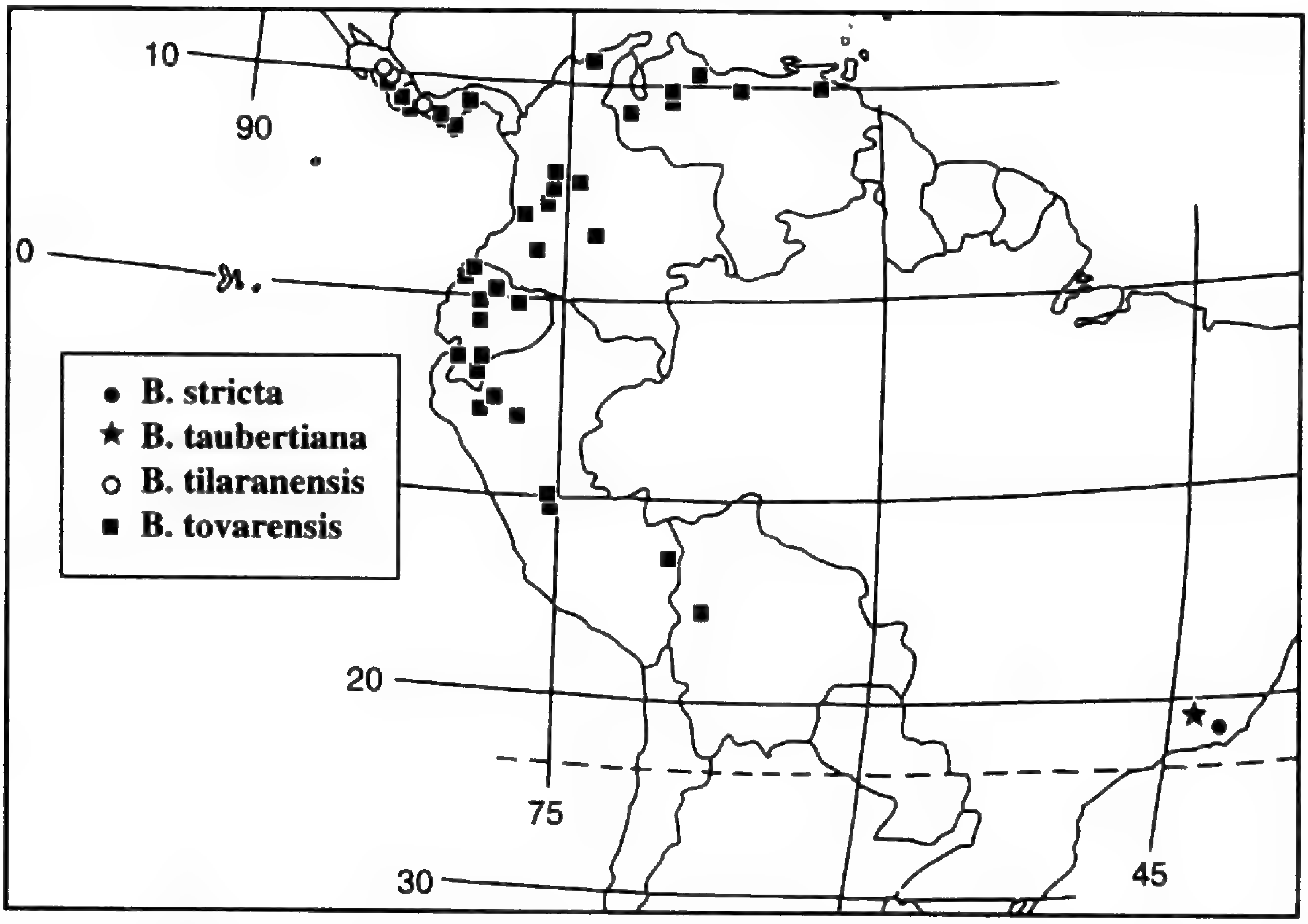

Figure 16. Representative distribution of *Beilschmiedia stricta*, *B. taubertiana*, *B. tilaranensis*, and *B. tovarensis*.

hairs, slightly discolored from twigs; blades firmly chartaceous, elliptic, 10–14 × 4–5 cm; base obtuse to rounded, not inrolled, apex acute; upper leaf surface glabrous, lower leaf surface sparsely pubescent with erect, long straight to slightly wavy hairs; lower leaf surface not known whether glaucous or not; midrib immersed above, raised below, secondary veins 9 to 14 pairs, slightly raised or almost immersed above, raised below, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins slightly raised on both sides. Inflorescences in axils of leaves, racemose, ca. 1.5 cm long, pubescent with erect long hairs, with ca. 5 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1 mm long, pedicels of the central flowers up to 4 mm long. Flowers ca. 3 mm long, ca. 3 mm diam.; tepals 6, equal, ovate, 1.9–2 mm long, 1.3–1.5 mm wide, pubescent with erect long wavy hairs outside, sparsely pubescent with appressed to erect hairs inside; stamens 9, outer 6 filaments ca. 0.3 mm long, innermost 3 filaments ca. 0.4 mm long, filaments pubescent, outer six anthers 1.2–1.3 mm long, innermost anthers 0.9–1.1 mm long, 2-celled, anther apices obtuse to truncate and pubescent, glands of the innermost 3 stamens globose; staminodia 3, sagittate, ca. 0.6 mm long; pistil ca. 1.2 mm long, glabrous, ovary shorter than and gradually narrowed into the style; receptacle densely pubescent with erect hairs. Fruits ellipsoid, ca. 5 × 3 cm, surface warty; infructescence axis ca. 3 mm diam., fruit pedicels thickened to ca. 5 mm diam. below the fruit, not constricted at the apices.

Distribution. Southern Minas Gerais, Brazil (Fig. 16).

Additional specimen examined. BRAZIL. **Minas Gerais:** Rio Novo, 1889 (sterile), *Araujo 5* (RB).

Among southeastern Brazilian species, *Beilschmiedia taubertiana* is easily distinguished by its erect, long straight pubescence on terminal buds and twigs, and by the lower leaf surfaces sparsely and similarly pubescent.

27. Beilschmiedia tilaranensis Sa. Nishida, sp. nov. TYPE: Costa Rica. Guanacaste: Cantón de Tilarán, Cordillera de Tilarán, Las Nubes de Río Chiquito, Mt. Olivo, 10°21′00″N, 84°51′00″W, 1450 m, 29 Jan. 1992 (fr), *Guindon & Brenes 40* (holotype, MO!; isotypes, CR!, INB!, USJ!). Figure 17.

Haec species *Beilschmiediae ovali* affinis, sed ab ea foliis obovatis, venis tertiariis valde percurrentibus atque fructu ellipsoideo differt, necnon quam ea in altitudinibus inferioribus habitat.

Tree, to 20 m tall. Terminal buds pubescent with erect short curly hairs. Twigs terete, angular when young, densely pubescent with erect short curly hairs, less dense when old. Leaves alternate; peti-

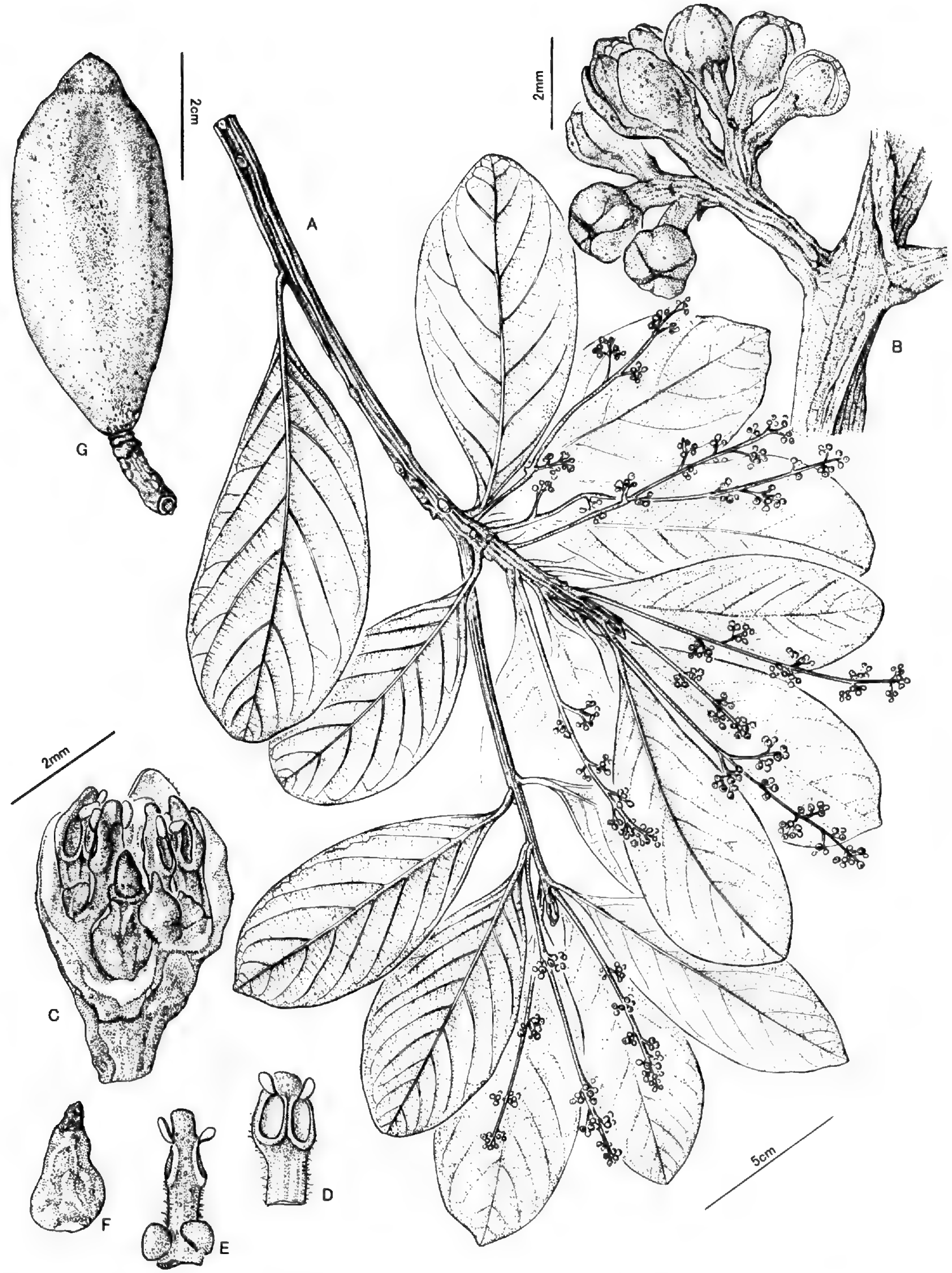

Figure 17. *Beilschmiedia tilaranensis* (A–F, *Haber 11092*, G, *Guindon 40*). —A. Flowering branch. —B. Part of inflorescence. —C. Lateral section through flower, showing stamens, two glands, staminode, and pistil. —D. Stamen of whorl I/II, ventral view. —E. Stamen of whorl III with two glands, dorsal view. —F. Pistil. —G. Fruit.

oles 1–2 cm long, almost flat above, sparsely pubescent with erect short curly hairs, concolorous with twigs; blades coriaceous, obovate, rarely elliptic, 6–13 × 4–7 cm; base cuneate, not inrolled, apex obtuse; leaf surface glabrous on both sides; lower leaf surface glaucous; midrib immersed above, raised below, secondary veins 7 to 11 pairs, almost immersed, rarely impressed above, raised below, tertiary veins percurrent, minor venation pattern fine, areoles without free-ending veinlets inside, tertiaries and minor veins immersed above, raised below. Inflorescences in axils of leaves, paniculate, 5–12 cm long, sparsely pubescent with erect short curly hairs or almost glabrous, with 20 to 30 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1 mm long, pedicels of the central flowers up to 2 mm long. Flowers creamy, ca. 2.3 mm long, ca. 2.6 mm diam.; tepals 6, equal, ovate, ca. 1.5 mm long, ca. 1.2 mm wide, sparsely pubescent with erect hairs on both sides; stamens 9, filaments 0.4–0.8 mm long, pubescent; anthers ca. 1 mm long, 2-celled, anther apices obtuse to truncate and glabrous, glands of the innermost three stamens globose; staminodia 3, deltoid, ca. 0.7 mm long; pistil ca. 1.5 mm long, glabrous, ovary as long as the style or longer than and gradually narrowed into the style; receptacle sparsely pubescent with appressed hairs. Fruits ellipsoid or obovoid, black, 5.5–6.5 × 2–2.5 cm, surface smooth; infructescence axis 3–4 mm diam., fruit pedicels thickened to 4–6 mm diam. below the fruit, not apically constricted.

Flowering time. April.

Distribution and habitat. Costa Rica and western Panama (Fig. 16); 1100–1580 m; premontane forest.

Paratypes. COSTA RICA. **Alajuela:** Cerros de la Palma de San Ramón, 1300–1500 m, 24 Jan. 1984 (fr), *J. Gómez L. 9800* (CR, F). **Guanacaste:** Parque Nacional Guanacaste, Estación Cacao, Liberia, 10°55′45″N, 85°28′15″W, 1100 m, 11 Dec. 1990 (immature fr), *Chávez 443* (MO); 1 km N of La Cruz, 10°21′N, 84°50′W, ca. 1480 m, 10 Mar. 1996 (immature fr), *Yasuda et al. 1313* (INB, MO). **Puntarenas:** Cantón de Tilarán 4–5 km NW Monteverde, 2–4 km W of Santa Elena between road to Cañitas and upper road to Las Nubes, 10°20′N, 84°49′W, 1400–1500 m, 11 Apr. 1992 (fl), *Haber et al. 11092* (INB, MO); Las Alturas de Coto Brus, 8°54′N, 82°50′W, 1150–1250 m, 20 Mar. 1987 (fr), *Burger et al. 12184* (F, MO, NY); Estación Biológica Las Alturas, 8°57′15″N, 83°50′10″W, 1580 m, 7 Mar. 1996 (sterile), *Yasuda et al. 1307* (INB). PANAMA. **Coclé:** sawmill above El Copé Pacific slope, ca. 1100 m, 9 Mar. 1979 (fr), *Hammel 6286* (MO).

Burger and van der Werff (1990) reported that a few collections in *Beilschmiedia ovalis* had atypically obovate leaves and commented that these might belong to an undescribed species. Since then, additional specimens with pubescence and leaf texture similar to *B. ovalis* but with these obovate leaves have been collected from elevations lower than where *B. ovalis* occurs. These collections consistently have ellipsoid fruits, also different from the spherical fruits of *B. ovalis.* Obovate leaves, ellipsoid fruits, and a lower-elevational habitat clearly distinguish these collections as a new species. In addition, *B. tilaranensis* has leaf tertiary veins conspicuously percurrent, a condition rarely seen in *B. ovalis.*

28. Beilschmiedia tovarensis (Meisn.) Sa. Nishida, comb. nov. Basionym: *Hufelandia tovarensis* Meisn., in DC., Prodr.15 (1): 65. 1864. SYNTYPES: Colombia. Locality unknown, *Karsten 88* (B photo!). Venezuela. Mérida: Tovar, ca. 1920 m, 28 Aug. 1854 (fl), *Fendler 1094* (NY!).

Aniba pseudo-coto (Rusby) Kosterm., Rec. Trav. Bot. Néerl. 35: 872. 1938. *Ocotea pseudo-coto* Rusby, Bull. Torrey Bot. Club 49: 261. 1922. TYPE: Bolivia. La Paz: mountains S of Huachi, near the Cochabamba River, 750–900 m, 9 Sep. 1921 (young fl), *White 1051* (lectotype, designated by Kostermans (1938), NY photo!; isolectotypes, AFS not seen, C!, G-DEL not seen, GH not seen, K!, US photo!).

Tree, to 40 m tall. Terminal buds pubescent with appressed straight hairs. Twigs terete, slightly angular when young, pubescent with appressed straight hairs, less densely pubescent when older. Leaves alternate; petioles 0.5–4.2 cm long, flat to canaliculate above, glabrous or pubescent with appressed straight hairs, concolorous with twigs; blades coriaceous to firmly chartaceous, ovate to broadly elliptic, rarely broadly oblanceolate, (5–)8–20(–28) × 4–14 cm; base cordate to obtuse, rarely cuneate, not inrolled, apex acuminate, rarely acute; upper leaf surface glabrous, lower leaf surface pubescent with appressed short straight hairs; lower leaf surface glaucous; midrib immersed above, raised below, secondary veins 5 to 11 pairs, immersed or slightly raised above, raised below, tertiary veins percurrent, minor venation pattern fine, areoles lacking free-ending veinlets inside, tertiaries and minor veins immersed above (the fine pattern sometimes slightly visible), almost immersed below (the pattern visible). Inflorescences in axils of leaves near the terminal buds, sometimes in axils of cataphylls below leaves near tips of the twigs, paniculate, 4–16(–23) cm long, pubescent with short, appressed to erect hairs, with 30 to 100 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1.5 mm long, pedicels of the central flowers up to 3 mm long. Flowers yellowish white, 2–3 mm long, 2–3 mm diam.; tepals 6, equal, ovate to elliptic, 1.3–2 mm long, 1–1.5 mm wide, pubescent with appressed to erect hairs on both sides; stamens 9, outer six filaments 0.3–0.4 mm long, innermost three filaments 0.4–0.7 mm long, filaments pubescent, anthers 0.7–1 mm long, 2-celled, anther apices obtuse to truncate and glabrous, glands of the innermost three stamens globose, staminodia 3, sagittate, ca. 0.7 mm long; pistil ca. 1.3 mm long, sparsely pubescent to glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with appressed hairs, less densely pubescent toward the bottom. Fruit ellipsoid, purple-black, 2.5–3.5 × 1.5–2 cm, surface smooth; infructescence axis 2–3 mm diam., fruit pedicels scarcely thickened below fruits, constricted or not constricted at the apices.

Flowering time. July to March.

Distribution and habitat. Southern Costa Rica, Panama, northern Venezuela, Colombia, Ecuador, Peru, and western Bolivia (Fig. 16); (1–)500–2200(–3000) m; premontane wet forest to cloud forest.

Common names. Aguacatillo (*Figueiras 8401*) (Colombia); Aguacatillo (*Alvarez et al. 625*), Aguacatillo de montaña (*Little, Jr. 6657*) (Ecuador); Roble palta (*van der Werff et al. 8329*), Palta moena, Moena (*Albán 4085*) (Peru).

Selected specimens examined. COSTA RICA. **Heredia:** Volcán Barba, 4 Mar. 1983 (fr), *Peralta s.n.* (CR). **Puntarenas:** Cantón of Golfito Jiménez, Dos Brazos de Río Tigre, enroute between the ravines, Cerro Mueller and Cerro Rincón, 8°30′35″N, 83°28′15″W, 782 m, 25 Nov. 1990 (fl), *Herrera 4643* (MO). **San José:** Cantón Pérez Zeledón San Isidro de El General, El Pilar de Cajón, plots of Las Brisas de Cajón, 9°22′50″N, 83°36′45″W, 600 m, 16 Apr. 1992 (immature fr), *Zamora et al. 1819* (MO). PANAMA. **Barro Colorado Isl.:** Lutz Trail cut-off behind Animal house, 23 May 1968 (fr), *Croat 5813* (F, MO, NY). **Canal Zone:** Pipeline Road, 6 km N of Gamboa, 3 Dec. 1971 (sterile), *Gentry 2829* (MO). **Chiriquí:** road from Volcán to Río Serano, road that turns E 7.2 km from Río Serano, 1.2 km along the side road, 29 June 1977 (fr), *Folson 4040* (MO). **Los Santos:** Coabal, Progrese, W slope above Río Cobachén, 200 m, 19 Apr. 1968 (immature fr), *Holdridge 6209* (MO). **Panamá:** Cerro Campana, 900 m, 13 Apr. 1967 (fl), *Duke 10749* (MO). **Veraguas:** District of Montijo, Cerro Hoya Nacional Park, ca. 900 m, 7 Mar. 1993 (immature fr), *N. Rivera 324* (MO). VENEZUELA. **Aragua:** Henri Pittier National Park, 31 Aug. 1990 (fl), *Cardozo et al. 1549* (MO). **Mérida:** La Trampa, highway San Juan–Azulita, 2500 m, 2 Feb. 1987 (sterile), *van der Werff et al. 8766* (MO). **Monagas:** Distrito Caripe, forest adjacent to the cave of El Guácharo, 1000–1100 m, 16 July 1985 (sterile), *Lau 16* (MO). **Portuguesa:** Distrito Sucre, Concepción division, 9°18′N, 70°06′W, 1700 m, 24 Oct. 1985 (immature fr), *van der Werff et al. 7575* (MO). **Trujillo:** Carache District, road between La Playa (9°37′N, 70°8′W), SW of Carache, & Potreritos de Cendé (9°32′N, 70°8′W), ca. 10–14 km from La Playa, 2200 m, 11 May 1988 (immature fr), *Dorr et al. 5114* (MO). **Yaracuy:** 7–10 km N of Salom, El Amparo near Candelaria, 1100–1300 m, 27–30 Dec. 1972 (young fl), *Steyermark & Espinoza 106806* (NY). COLOMBIA. **Antioquia:** Municipio of San Luís, canyon of Río Claro, S sector, right edge, 5°53′N, 74°39′W, 325–450 m, 29 Jan. 1984 (immature fr), *Cogolla 1285* (MO). **Boyaca:** 100 m NW of Bogotá, extreme W part of Department Boyaca, region of Mt. Chapon, ca. 1080 m, 23 July 1932 (immature fr), *Lawrance 353* (BM, F, K, NY, U). **Caldas:** Municipio Risaralda, Quebrada Chovarquía, 1140 m, 14 Nov. 1992 (immature fr), *Vargas 754* (MO). **Cauca:** Tierra Odentro, around Huila, Indian village in Río Paez Valley, 1600–1900 m, Jan. 1906 (immature fr), *Pittier 1286* (NY). **Magdalena:** region near Santa Marta, 2250 m, 2 Mar. 1932 (sterile), *Espina & Giacometto A170* (NY). **Meta:** Sierra de la Macarena, Caño Entrada, 550 m, 13 Jan. 1950 (immature fr), *Philipson et al. 2094* (NY). **Valle:** Cordillera Occidental, valley of Río Cali, suburb of Peffas Blancas, 23 Jan. 1963 (fl), *Figueiras 8401* (US). ECUADOR. **Bolívar:** Road Echandia–Guaranda, 2000 m, 17 July 1991 (fl), *van der Werff et al. 12406* (MO). **Esmeraldas:** Cantón San Lorenzo, Parroquia Alto Tambo, Sector El Cristal, 01°30′N, 78°30′W, 600 m, 13 Apr. 1992 (fr), *Tipaz et al. 792* (MO). **Imbabura:** Cotacachi, Hda. La Florida, 0°23′S, 78°28′W, 1900–2500 m, 28 Aug. 1992 (sterile), *Alvarez et al. 625* (MO). **Morona-Santiago:** 11.7 km SW of Taisha, 2°32′S, 77°44′W, 11–15 Sep. 1976 (sterile), *Ortega 138* (US). **Napo:** Canton Quijos, Chaco, road to Cayambe-Coca Reserve, Río San Juan Chico, following to Río Oyacachi, 00°17′S, 77°03′W, 1750 m, 12 Jan. 1992 (young fl & fr), *Palacios et al. 9554* (MO). **El Oro:** 15 km S of Piedras, Ingenio farm, 700–1000 m, 20 June 1943 (immature fr), *Little, Jr. 6657* (NY, US). **Pichincha:** along new road Nanegal–Mindo, 1500–1800 m, 2 Mar. 1994 (young fl), *van der Werff et al. 13377* (MO). PERU. **Amazonas:** Luya Province, Jaipe, Fundo El Paraíso, 1690 m, 31 May 1989 (immature fr), *Díaz & Campos 3587* (MO). **Cajamarca:** Provincia Jaen, Colasay, hills NW of town, 5°58′S, 79°03′W, 2100 m, 21 Feb. 1985 (fr), *Stein & Todzia 2231* (MO, NY). **Huánuco:** Provincia Pachitea, Honoria, Caserío Leoncio, Aug. 9, 1963 (fl), *R. Lao M. 66* (F, NY, US). **Madre de Dios:** Tambopata Tourist Camp, junction of Ríos la Torre and Tambopata, 12°50′S, 69°17′W, 260 m, 6 June 1986 (immature fr), *Gentry & Nuñez 54196* (MO). **Pasco:** Provincia Oxapampa, 1800 m, 3 Mar. 1986 (immature fr), *van der Werff et al. 8329* (MO). **San Martín:** Provincia Moyobamba, Soritor, 680 m, 23 July 1986 (sterile), *Albán 4085* (F). BOLIVIA. **La Paz:** Provincia Larecaja, Copacabana (ca. 10 km S of Mapiri), 850–950 m, 8 Oct.–15 Nov. 1939 (fl), *Krukoff 11235* (F, MO, U).

Beilschmiedia tovarensis belongs to the *B. costaricensis* group. It is distinguished by the following characters: appressed pubescence on the terminal buds and twigs, alternate leaves, lower leaf surfaces pubescent with appressed hairs, rounded areoles, glabrous anthers, and ellipsoid fruits. This species is broadly based on two specimen groups. One group has ovaries that are pubescent, whereas the second group has ovaries that are glabrous. Those with pubescent ovaries tend to have shorter petioles and coriaceous, ovate to broadly elliptic leaves with fruit pedicels not apically constricted. Those with glabrous ovaries tend to have longer petioles, rigid chartaceous, elliptic leaves, and fruit pedicels apically constricted. Careful survey of leaf morphology revealed many intermediate collections, and a clear separation between the two groups cannot be made for petiole length and leaf size. Additionally, there are some exceptions in the groups indicated by the pubescence of ovaries. Within the same collections, duplicates may have short petioles, ovate leaves, and glabrous ovaries, or long petioles, elliptic leaves, and pubescent ovaries. Both groups occur from Venezuela to Bolivia, although glabrous ovaries are more often observed in specimens from Costa Rica and Panama. This species has an unusually wide range of morphology and geographic distribution, but the two groups are retained together in this species because of the existence of many intermediate specimens.

Specimens with glabrous ovaries have sometimes been identified as *B. pendula*, but can usually be distinguished from it by the very fine areoles lacking free-ending veinlets, longer (1.5–3.5 cm long) petioles, and larger (8–20 × 4–14 cm) leaves.

IMPERFECTLY KNOWN SPECIES

Beilschmiedia sulcata (Ruiz & Pav.) Kosterm., Recueil. Trav. Bot. Néerl. 35: 850. 1938. *Laurus sulcata* Ruiz & Pav., Fl. Peruv. 4: 356. 1804. *Hufelandia sulcata* (Ruiz & Pav.) Nees, Linnaea 21: 494. 1848. *Persea sulcata* (Ruiz & Pav.) Meisn., in DC., Prodr. 15(1): 54. 1864. TYPE: Peru. Muña, (immature? fr), *Ruiz s.n.* (lectotype, designated by Kostermans (1938), MA photo!; isolectotypes, B not seen, BM!, F!, G-BOIS not seen).

In Ruiz and Pavon's (1804) illustration of *Laurus sulcata* in *Flora Peruviana*, the anthers are drawn as having 4 cells. However, there are no flowers in the holotype seen by Velayos (pers. comm.) or any isotypes I have seen. It is unknown whether the illustration is correct and this is a species of *Beilschmiedia* with 4-celled anthers, or if the illustration is erroneous. Thus far no fertile specimen has been located that corresponds to the type or illustration.

Beilschmiedia zapoteoides (Lundell) Kosterm., Reinwardtia 6: 156. 1962. *Endlicheria zapoteoides* Lundell, Wrightia 1: 145. 1946. TYPE: Mexico. Chiapas: Cascada near Siltepec, in advanced forest, 1600 m, 1 Mar. 1945 (fl & fr), *Matuda 5153* (holotype, TEX!; isotypes, MO!, US!).

The type collection of *Beilschmiedia zapoteoides* approaches *B. hondurensis*, but it is distinguished from the latter by its having relatively longer floral pedicels (ca. 2 mm long in the lateral divisions) and more or less spherical fruits. However, the type collection of *B. zapoteoides* appears to be abnormal: its leaves are diseased, and the number of cells in the stamens of the third whorls is variable, from two to zero.

EXCLUDED SPECIES

Beilschmiedia brasiliensis (Kosterm.) Kosterm. = *Anaueria brasiliensis* Kosterm.

Beilschmiedia cuneata (Meisn.) Kosterm. = *Persea cuneata* Meisn.

Beilschmiedia durifolia (Mez) Kosterm. = *Persea durifolia* Mez

Beilschmiedia inaequalis (A. C. Sm.) Kosterm. = *Caryodaphnopsis inaequalis* (A. C. Sm.) van der Werff & H. G. Richter

Beilschmiedia lundelliana Lasser = *Persea cuneata* Meisn.

Beilschmiedia sphaerocarpa H. Winkl. Affinity uncertain.

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LIST OF SPECIES

1. *Beilschmiedia alloiophylla* (Rusby) Kosterm.
2. *Beilschmiedia anay* (S. F. Blake) Kosterm.
3. *Beilschmiedia angustielliptica* Lorea-Hern.
4. *Beilschmiedia angustifolia* Kosterm.
5. *Beilschmiedia berteroana* (Gay) Kosterm.
6. *Beilschmiedia brenesii* C. K. Allen
7. *Beilschmiedia costaricensis* (Mez & Pittier) C. K. Allen
8. *Beilschmiedia curviramea* (Meisn.) Kosterm.
9. *Beilschmiedia emarginata* (Meisn.) Kosterm.
10. *Beilschmiedia fluminensis* Kosterm.
11. *Beilschmiedia hexanthera* van der Werff
12. *Beilschmiedia hondurensis* Kosterm.
13. *Beilschmiedia immersinervis* Sa. Nishida
14. *Beilschmiedia latifolia* (Nees) Sa. Nishida
15. *Beilschmiedia linharensis* Sa. Nishida & van der Werff
16. *Beilschmiedia manantlanensis* Cuevas & Cochrane
17. *Beilschmiedia mexicana* (Mez) Kosterm.
18. *Beilschmiedia miersii* (Gay) Kosterm.
19. *Beilschmiedia ovalioides* Sa. Nishida
20. *Beilschmiedia ovalis* (S. F. Blake) C. K. Allen
21. *Beilschmiedia pendula* (Sw.) Hemsl.
22. *Beilschmiedia rigida* (Mez) Kosterm.
23. *Beilschmiedia riparia* Miranda
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25. *Beilschmiedia stricta* Kosterm.
26. *Beilschmiedia taubertiana* (Schwacke & Mez) Kosterm.
27. *Beilschmiedia tilaranensis* Sa. Nishida
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TAXONOMIC REVISION OF THE GENUS *SARCOLAENA* (SARCOLAENACEAE)[1]

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ABSTRACT

A systematic study, based primarily on morphology, suggests that patterns of variation in *Sarcolaena* Thouars, a member of the Malagasy endemic family Sarcolaenaceae, are best resolved by recognizing eight species. Keys for identification of the genera of Sarcolaenaceae and species of *Sarcolaena* are provided, as well as a discussion of the overall morphology of *Sarcolaena* and complete descriptions of its species. Two species, *S. grandiflora* and *S. multiflora*, are lectotypified in the present study.

Madagascar is the world's fourth largest island with a land area of approximately 590,000 km^2. Lying in the Indian Ocean about 400 km southeast of the African mainland, it extends 1650 km from 12° to 25° latitude south (Griffiths & Ranaivoson, 1972). Madagascar the island separated from the African coastline more than 100 million years ago (Rabinowitz et al., 1983). However, debate about its paleoposition before the breakup of Gondwanaland still continues. According to Rabinowitz et al. (1983), Madagascar was attached to Africa along the Somalian, Kenyan, and Tanzanian coastlines. A more recent study of the paleomicroflora of Tanzania and Madagascar by Hankel (1993) suggested that Madagascar was contiguous with Africa further south, along the southeast Kenya, Tanzania, and northern Mozambique coasts.

Since its separation from the African mainland, Madagascar has been the center of tremendous evolutionary diversification. Madagascar's wide range of habitats and its long geographic isolation have resulted in unusually high levels of endemism of plants and animals. Its unique flora has resulted from the persistence of relic taxonomic groups associated with the process of numerous localized speciation events, a phenomenon often observed in continental islands (Whittaker, 1999). Although Madagascar has a varied and rich flora, unfortunately it is poorly characterized and, most frustrating of all, some species of plants will disappear before they are even known scientifically. Estimates of the size of the flora and levels of endemism vary widely. Phillipson (1994) suggested that the known Malagasy flora has 9345 species, of which 7581 (81%) are endemic. Lowry (1992) estimated that 75% of the 10,000 to 12,000 native species found in Madagascar are endemic. Perrier de la Bâthie (1936) estimated 20% of the 1289 plant genera were endemic. Despite modern taxonomic revision for some families and many descriptions of new species, inadequate taxonomic treatments for most of the flora continue to prevent more precise estimates of its size and levels of endemism.

The largest of the endemic families in Madagascar is Sarcolaenaceae, which consists of eight to ten genera and about 34 species. Within Sarcolaenaceae, one of the larger genera is *Sarcolaena* with eight species recognized here, one of which is recently described (Randrianasolo & Miller, 1994). The genus is well defined within the family by morphological characters such as prefoliation traces on leaf surfaces and ovary locules each containing only two ovules. However, limits among its species have been poorly defined in previous taxonomic studies. The present study incorporates new characters from morphology to address specific limits in *Sarcolaena*. The number of specimens available for study has increased greatly since the last monograph (Cavaco, 1952a), permitting much better assessment of character variability within and between species.

The goal of the present study is to resolve spe-

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Table 1. List of morphological characters and character states used to delimit *Sarcolaena* species.

Characters	Character states
1. Tree height	
2. Leaf	
a—size	
b—blade shape	lanceolate/narrowly ovate or elliptic/ovate/oblanceolate/obovate
c—indumentum	glabrous/pubescent
d—apex shape	acute/acuminate/attenuate/mucronate/retuse/obtuse
e—base shape	acute/cuneate/obtuse/rounded/subcordate
3. Inflorescence	
a—position	terminal/axillary
b—flower number	
4. Involucre	
a—shape	widely obovoid/very widely obovoid
b—size at floral and fruit stage	
c—indumentum	sericeous/setaceous/hirsute/spreading
5. Flower	
a—sepal number	3/5
b—sepal shape	ovate/widely ovate/very widely ovate/widely depressed ovate
c—petal size	
d—petal color	white/yellow
e—stamens number	
f—ovary size	
g—style length	
h—style indumentum	glabrous/pubescent
6. Fruit	
a—size	
b—enclosure in the involucre	partial/complete

cies delimitation within *Sarcolaena*, to clarify nomenclatural problems, including lectotypification of taxa, where necessary and appropriate, and to generate a complete monographic treatment for the genus. Parallel descriptions of species, as well as a key for their identification, are provided.

MATERIALS AND METHODS

Over 200 herbarium specimens were examined, with additional collections made during field studies from 1992 to 1993 in Madagascar. To understand the variation within individuals and also within and among populations, 5–10 individuals from 2–5 populations were sampled for each plant species when feasible. For each of these, 3 different collection numbers were made, distributed from the top, center, and bottom of tree crowns. Fresh buds in varying developmental stages as well as flowers were collected and preserved in formalin/acetic acid/ethanol (FAA) (Radford et al., 1974) to supplement material available from herbarium specimens. Ecological and edaphic data were compiled from both literature and herbarium labels and were supplemented with field observations.

A series of morphological characters were measured and recorded for each specimen (Table 1). Continuously ranging characters such as leaf length or width were measured and recorded. Qualitative characters, such as shape, form, position, or texture, conform to Radford et al. (1974) and Hickey (1973).

SYSTEMATICS OF SARCOLAENACEAE

The Sarcolaenaceae are the largest of ten angiosperm families endemic to Madagascar (Takhtajan, 1997; Table 2). The family is concentrated in the eastern and central regions of Madagascar. A few genera reach the Sambirano region in the northwest, which is similar climatically to the east, but very few members occur in the western region.

The family consists of trees or shrubs with alternate, simple, entire, persistent and stipulate leaves. Most species have terminal or axillary cymose inflorescences, which are less commonly corymbiform

Table 2. Endemic vascular plant families in Madagascar.

Family	Number of genera	Number of species
Sarcolaenaceae	10	35
Sphaerosepalaceae	2	17
Didieraceae	4	11
Melanophyllaceae	1	8
Kaliphoraceae	1	1
Didymelaceae	1	2
Physenaceae	1	2
Bembiciaceae	1	1
Diegodendraceae	1	1
Asteropeiaceae	1	1

Table 3. Genera of Sarcolaenaceae with number of species recognized by Cavaco (1952a) and Capuron (1970).

Genera	Number of species	
	Cavaco	Capuron
Sarcolaena Thouars (1806)	7	7
Leptolaena Thouars (1806)	7	2
Rhodolaena Thouars (1806)	4	4
Schizolaena Thouars (1806)	8	9
Xyloolaena Baillon (1879)	3	3
Xerochlamys Baker (1882)	0	4
Eremolaena Baillon (1884)	2	2
Pentachlaena P. de la Bâthie (1920)	1	2
Perrierodendron Cavaco (1952c)	1	1
Mediusella (Cavaco) Hutch. (1973)	0	1

or paniculiform, or occasionally solitary flowers. Flowers are perfect and regular, with 3 to 5 sepals and 5 to 6 petals. The number of stamens varies from 5 to 100, and the ovary is superior and has 2 to 5 locules. An involucre is present, and a nectariferous disk is sometimes present in a flower between stamens and petals.

NOMENCLATURAL HISTORY

The first description of species of Sarcolaenaceae, originally known as Chlaenaceae, was made by Aubert Du Petit-Thouars (1806). The original family description included four genera with two common characters: the presence of 3 sepals and an involucre covering the flower. The original familial name Chlaenaceae refers to this involucre, using the Greek *chlaina* or *laena*, meaning superior or exterior tunic. Other names proposed after Chlaenaceae include Sarcolaenaceae Caruel (1881) and Rhodolaenaceae Bullock (1957), of which Sarcolaenaceae was conserved (Greuter et al., 1994). Since Thouars's publication in 1806, six additional genera were subsequently described in the family. Baker (1882) described *Xerochlamys* with its dry involucre, numerous stamens, and ovary containing 2 to 4 ovules per locule. Two genera, *Xyloolaena* and *Eremolaena*, were added by Baillon in 1879 and 1884, respectively. *Pentachlaena*, with its involucre reduced to 4 or 5 bracts subtending two sessile flowers each with a large disk and unequally sized and free stamens, was described by Perrier de la Bâthie (1920). Recently, *Perrierodendron* was described by Cavaco (1952c) based essentially on its ovary and fruit characters. Finally, *Mediusella* was segregated from *Leptolaena* by Hutchinson in 1973 (Table 3). *Sarcolaena* Thouars was chosen as the type genus of the family (Greuter et al., 1994).

FOSSIL RECORD

According to Emberger (1944), Sarcolaenaceae originated from the Theales during the Cretaceous period (from 141 to 65 MYA), and species were probably widespread throughout Gondwanaland. His hypothesis was later supported by the finding of *Xyloolaena*-type pollen of estimated lower Miocene age from the Cape region of South Africa (Coetzee & Muller, 1984). The occurrence of Sarcolaenaceae outside of Madagascar would indicate that the current endemic distribution on Madagascar results from extinction on mainland Africa rather than its independent origin and adaptive radiation on the isolated island landmass after its mainland separation.

SYSTEMATIC POSITION OF SARCOLAENACEAE

The relationships and systematic positioning of Sarcolaenaceae have been unclear. The wide diversity of opinions on the relationships of Sarcolaenaceae has included placement in Theales (Hutchinson, 1926; Cronquist, 1981), Ochnales (Hutchinson, 1973), or Malvales (Heywood, 1978; Takhtajan, 1980; Dahlgren, 1983) (Table 4). The presence of imbricate sepals suggests placement in the Theales. However, the presence of mucilage cells, stratified secondary phloem in the cortex (Outer & Vooren, 1980), as well as malvalic and sterculic cyclopropene fatty acids (Gaydou & Ramanoelina, 1983) are all characters allying with Malvales. Molecular study based on *rbc*L and *atp*B sequences strongly suggests that Sarcolaenaceae belong to an expanded malvalean clade (Alverson et al., 1998; Bayer et al., 1999).

Table 4. Affinities of the Sarcolaenaceae.

Characters	References	Indicated affinity
Secondary phloem	Outer & Vooren (1980)	Malvales
Secondary xylem	Outer & Schutz (1981)	Malvales
Pollen morphology	Takhtajan (1983)	Malvales
Petiolar anatomy	Takhtajan (1983)	Malvales
Fatty acids	Gaydou & Ramanoelina (1983)	Malvales
Vessel length & diameter	Hutchinson (1973)	Ochnales
Sepals aestivation	Cronquist (1981)	Theales
*rbc*L sequence data	Alverson et al. (1998)	Malvales
*atp*B sequence data	Bayer et al. (in press)	Malvales

GENERIC RELATIONSHIPS

Cavaco (1952a) recognized 8 genera and 33 species in Sarcolaenaceae. Capuron (1970) proposed 10 genera with 35 species for the family, elevating subgenera *Xerochlamys* and *Mediusella* Cavaco of *Leptolaena* to independent generic rank (Table 3). However, this elevation of the subgenus *Mediusella* to generic rank was not validly published until Hutchinson's correct combination in 1973. Goldblatt and Dorr (1986) further published the same combination with a more direct reference to the place of valid publication of the basionym. Hutchinson's error by giving a secondary bibliographic citation does not invalidate his publication based on Article 33.3 of the *Code* (Greuter et al., 1994), rendering Goldblatt and Dorr's combination superfluous.

Previous hypotheses of relationships among genera in the Sarcolaenaceae are varied and often conflicting. Capuron (1970), by his own observations and the previous work of Straka (1963), recognized four taxonomic groupings in Sarcolaenaceae (Tables 5 and 6). The first group proposed by Capuron (1970) comprises *Xyloolaena* Baill., *Sarcolaena*, and *Leptolaena* sensu lato (including *Xerochlamys* and *Mediusella*), all genera with a well-developed involucre with one to two flowers at anthesis. The second and third groups each contain a single genus, *Schizolaena* Thouars and *Rhodolaena* Thouars, respectively. *Schizolaena* shares many characters with the first group but differs in its small, simple, ericaceous-type pollen tetrads, which Straka (1963) referred to as pollen type I. *Rhodolaena* has the same pollen type as group 1 but has a reduced involucre at anthesis. Group 4 contains *Eremolaena* Baill., *Perrierodendron* Cavaco, and *Pentachlaena* H. Perrier, which all have type III pollen (Straka, 1963). Type III pollen is characterized by discontinuous ridges beside the aperture forming triangles, with each connecting the polar regions of three grains of the tetrad. Genera of Sarcolaenaceae can be distinguished by the following key, modified from Capuron (1970).

Table 5. Generic relationships within Sarcolaenaceae as proposed by Straka (1963).

Group 1	*Schizolaena* *Rhodolaena* *Eremolaena*
Group 2	*Sarcolaena*
Group 3	*Leptolaena* *Pentachlaena*
Group 4	*Xyloolaena* *Perrierodendron*

KEY TO THE GENERA OF SARCOLAENACEAE

1a. Seed with abundant endosperm; seminal integument formed by 2 distinct layers.
  2a. Involucre partially or completely enclosing flower buds and well developed at anthesis.
    3a. Flower buds partially enclosed in the involucre; ovules more than 4 per locule .... *Xyloolaena*
    3b. Flower buds completely enclosed in the involucre; ovules (1–)2(–4) per locule.
      4a. Stipules fused into a single sheath; inflorescence bracts fused.
        5a. Leaves with induplicate prefoliation traces; ovules 2 per locule .... *Sarcolaena*
        5b. Leaves without induplicate prefoliation traces; ovules 2(–4) per locule .... *Xerochlamys*
      4b. Stipules free from one another; inflorescence bracts free.
        6a. Stamens numerous; ovary 3–5-locular with (1–)2–3 ovules per locule; pericarp of fruit ± lignified .... *Mediusella*
        6b. Stamens 10; ovary 3-locular

Table 6. Generic relationships within Sarcolaenaceae as proposed by Capuron (1970).

Group 1	*Xyloolaena* *Sarcolaena* *Xerochlamys* *Mediusella* *Leptolaena*
Group 2	*Schizolaena*
Group 3	*Rhodolaena*
Group 4	*Pentachlaena* *Eremolaena* *Perrierodendron*

with ovules 2 per locule; pericarp of fruit thin ..... *Leptolaena*
  2b. Involucre not enclosing flower buds and reduced at anthesis.
    7a. Calyx with only 3 sepals .... *Schizolaena*
    7b. Calyx with 5 sepals (2 external and reduced) .... *Rhodolaena*
1b. Seed without or with very reduced endosperm; seminal integument without distinct layers.
  8a. Ovary 5-locular with 4–6 ovules per locule .... *Pentachlaena*
  8b. Ovary 2–3-locular, with 2 ovules per locule.
    9a. Sepals persistent; ovary 3-locular; fruit dehiscent .... *Eremolaena*
    9b. Sepals caducous; ovary 2-locular; fruit indehiscent .... *Perrierodendron*

SYSTEMATICS OF *SARCOLAENA*

In his book *Histoires des végétaux recueillis dans les iles australes d'Afrique*, Du Petit-Thouars (1806) described *Sarcolaena*. This genus had previously been called *Tantalus* in an unpublished manuscript by Ferdinand de Norohna, a Spanish botanist who worked in the eastern rainforest of Madagascar (Du Petit-Thouars, 1806). Later, the French botanist A. L. de Jussieu used the name *Eriocarpus*, referring to the hairy character of the involucre, but did not publish it because Thouars convinced him that there were more distinctive characters (Du Petit-Thouars, 1806). Thouars's publication was the first valid description of *Sarcolaena*, which means fleshy, exterior tunic or covering, referring to the involucre. Thouars initial description of *Sarcolaena* included three species: *S. multiflora*, *S. eriophora*, and *S. grandiflora*.

All studies of the genus beyond basic morphology, such as pollen (Carlquist, 1964), wood anatomy (Outer & Schutz, 1981), bark anatomy (Outer & Vooren, 1980), floral morphology (Koechlin, 1972), cytology (Goldblatt & Dorr, 1986), and chemistry (Gaydou & Ramanoelina, 1983) have been parts of broader familial surveys. These have been generally based on generic representatives with few species from *Sarcolaena*. As an example, Goldblatt and Dorr (1986) reported chromosome numbers in *Sarcolaena* ($2n = 22$) but for only the species *S. oblongifolia* and *S. multiflora*. The most recent systematic treatment of *Sarcolaena* is that of Cavaco (1952a). However, according to our observations, the characters that he used to delimit species vary continuously, especially for species with overlapping geographic ranges. Despite Capuron's (1970) proposal that *Sarcolaena* might be only a single variable species, currently available morphological evidence, such as leaf size, number of stamens, and involucral indumentum, supports Cavaco's conclusion that the genus, although varying more or less continuously over a climatic and geographical continuum, does consist of discontinuous populations that can be recognized as distinct species. This morphological variation in *Sarcolaena* is best represented by recognizing eight species, one of which was recently described.

Cavaco (1952a) cited only 28 collections, as opposed to the 210 cited in the present study. This enhanced number of collections for study makes possible a more precise circumscription of morphological variation of species, with the realization that some characters previously assumed to be constant do vary over the geographic range of a species. For example, *S. multiflora* Thouars, previously characterized by only a single pair of prefoliation traces may, in fact, have from one to three. This variable pattern of leaf traces has also been demonstrated in *S. grandiflora* Thouars and *S. oblongifolia* F. Gérard.

DISTRIBUTION AND ECOLOGY

Madagascar is generally considered to be divisible into two major phytogeographic regions (Perrier de la Bâthie, 1921; Humbert, 1927; Koechlin et al., 1974). These Eastern and Western Regions are further subdivided into several domains. Four Eastern domains consist of: eastern, central, high mountains (>2000 m), and the Sambirano. Two Western domains occur: the western and southern. *Sarcolaena*'s distribution is restricted to three Eastern domains, namely eastern, Sambirano, and central (Fig. 1).

The eastern domain ranges from the coast to about 800 m and from Vohémar in the north to Tolagnaro in the south, and covers almost the entire eastern coast (Fig. 1). Five species, *S. multiflora*, *S. grandiflora*, *S. eriophora*, *S. delphinensis* Cavaco, and *S. humbertiana* Cavaco, occur here, and all except *S. eriophora* are endemic.

The Sambirano domain in northwestern Madagascar is included in the Eastern Region because of climatic affinities (Perrier de la Bâthie, 1921; Humbert, 1927; Koechlin et al., 1974). The range of *S. codonochlamys* Baker is essentially confined to this Sambirano domain with possible extensions slightly north or east (e.g., *Eaux et Forêts Tamatave 66* [P]).

The central domain is an uneven plateau ranging from 800 to 2000 m. Its northern limit is the foothills of Tsaratanana, and it extends south to the Isalo plateau. Three species occur in this domain: *S. eriophora* in the central part (Ankazobe) and close to the eastern edge (Anjozorobe); *S. oblongifolia* on western and southwestern slopes between

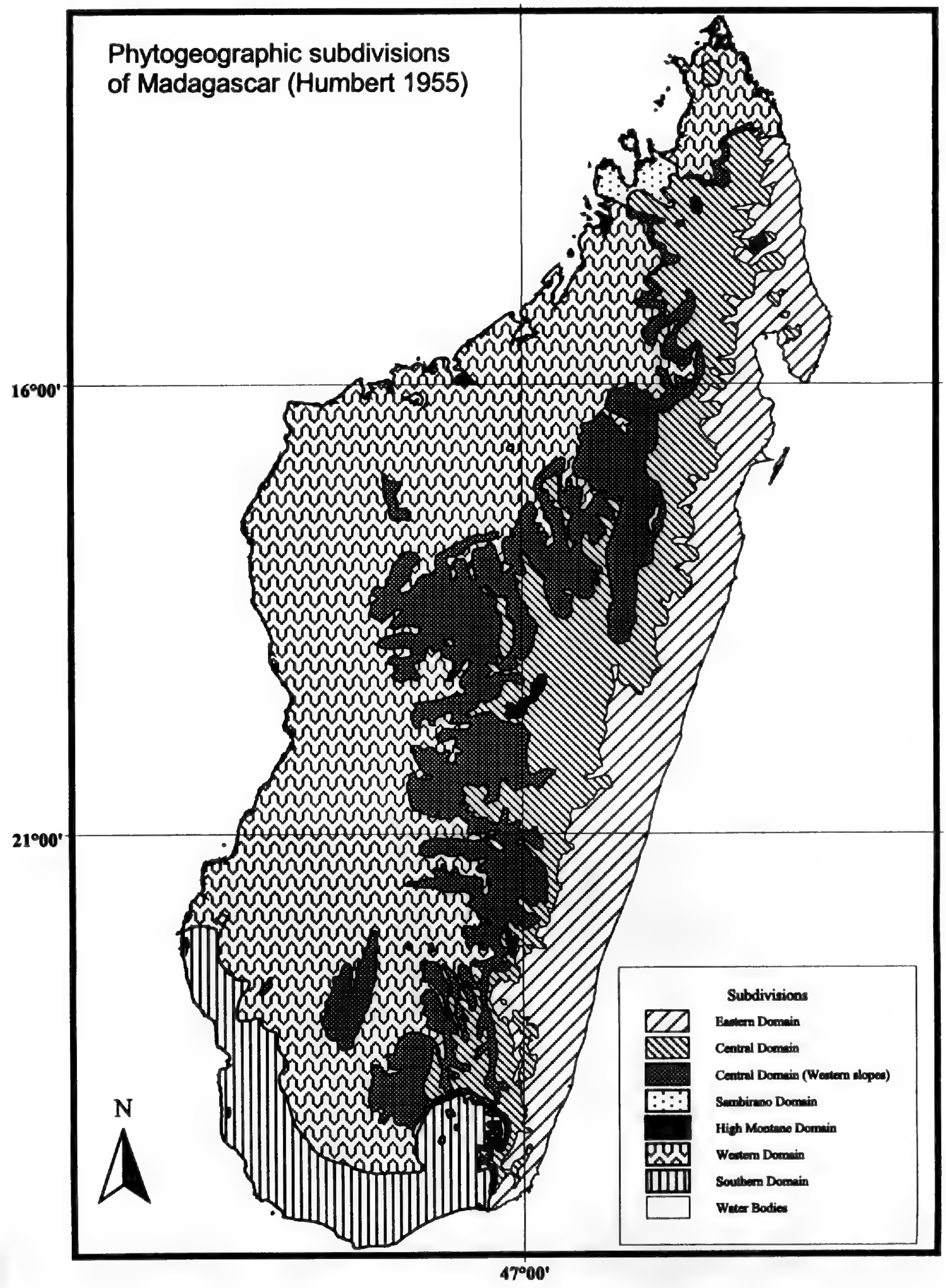


Figure 1. Phytogeographic subdivisions of Madagascar.

1500 and 2000 m; and *S. isaloensis* A. Randrianasolo & J. S. Mill. confined to the Isalo region.

Species of *Sarcolaena* occur in a great diversity of habitats. These vary from very humid, wet areas without a dry month (rainfall 2000–3500 mm per year) to areas where the dry season lasts for 5–6 months (rainfall 1000–1500 mm per year) (Griffiths & Ranaivoson, 1972; Koechlin et al., 1974). Populations range from the lowland to high elevational sites (1500–2000 m). *Sarcolaena* occurs in evergreen forests on lateritic soil, littoral forests on sand, or sclerophyllous forests on rocky substrates where water and nutrients are quite limited. The wide variation in habitats may account for the vast differences in phenotypic expression present in a taxon. Among and within species, many morphological characters vary continuously, perhaps reflecting edaphic and climatic variation. Populations of *Sarcolaena* in wet, lowland areas tend to have large leaves with few hairs on the abaxial surface, while those in dry areas have smaller, more pubescent leaves. Tree size also decreases with increasing elevation and decreasing rainfall. The most extreme case is the geographically isolated population of *S. isaloensis* at Isalo, where individual plants display very reduced leaves less than 6 cm long and very pubescent involucres.

Species of *Sarcolaena* also occupy an important place in Malagasy vegetation. *Sarcolaena multiflora* and *S. grandiflora* are the most common canopy constituents in eastern coastal littoral or sublittoral forests. On the western slopes of the central domain, at an altitude between 800 and 1600 m, *S. oblongifolia* is the second dominant species after *Uapaca bojeri* Baill. (Euphorbiaceae/Uapacaeae) in Tapia forests. *Sarcolaena oblongifolia* has a tremendous resistance to fire, a yearly occurrence in this part of the island. More interestingly, our field observations indicate that it even outcompetes *U. bojeri* because it is the only woody species that persists in some areas of the Itremo mountain chain that have been severely and repeatedly burned (Fig. 2A).

Griffiths and Ranaivoson (1972) recognized two seasons in Madagascar: the summer (rainy and hot) starting in November and ending in April, and the winter (cool and dry) from May to October. The least rainfall and the lowest temperatures in the eastern domain occur from August through October. Cavaco (1952b) speculated a relationship between rainfall, temperature, and flowering time for *Sarcolaena* species. He stated that species growing in the eastern and Sambirano domains, such as *S. multiflora*, *S. eriophora*, *S. delphinensis*, *S. grandiflora*, *S. codonochlamys*, and *S. humbertiana*, flowered during the driest months with lowest temperature. Species such as *S. oblongifolia* and *S. isaloensis* from the central domain flowered during the last three months of the rainy season. While our field observations and study of herbarium specimens indicate that Cavaco's predictions appear generally accurate, there are clearly exceptions, e.g., *Randrianasolo 233* is *S. oblongifolia* flowering in early July, and not October or November. This anthesal variation may happen as annual climatic fluctuations occur with species flowering opportunistically.

No information has been previously recorded about pollination or dispersal of *Sarcolaena* species. Now, our field observations suggest these species are pollinated by small to medium-sized bees. Some flower structures suggest bee pollination as evidenced by bright coloration of the corolla, numerous stamens, and especially a floral disk with copious nectar. Further pollination study is needed for a better understanding of this group.

MORPHOLOGY

HABIT

Species of *Sarcolaena* are all densely branched trees, with more or less conic crowns. Tree height ranges from 3 to 20 m, varying according to local climatic and edaphic conditions and thus having little utility as a taxonomic character. For example, *S. oblongifolia* stands only 3–6 m tall at col de Tapia sites between Antsirabe and Ambositra. However, in Ingaro forest, a much wetter region, these trees reach 15 m in height (*Morat 3172 & 3323*).

LEAVES

Sarcolaena has alternate, simple, entire leaves. Blades are smallest in *S. isaloensis* (2.5–5.3 cm long, 0.5–1.1 cm wide) and largest in *S. multiflora* (8.5–15.5 cm long, 3–6.5 cm wide). Leaf length and width are quite variable within species and can only be used to separate species when blade sizes do not overlap. Leaf shape in *Sarcolaena* also varies. In most species, leaves vary from lanceolate or narrowly elliptic to elliptic, narrowly ovate, or ovate, even oblanceolate in *S. delphinensis* or obovate in *S. eriophora*. Leaves are borne on canaliculate, sericeous petioles that range from 4 to 20 mm. Leaf texture is coriaceous. Pairs of traces lie on each side of the midribs due to induplicate prefoliation (Figs. 2B, 3A). These traces are unique to *Sarcolaena* in the family, although *S. isaloensis* appears not to have them. The number of pairs of

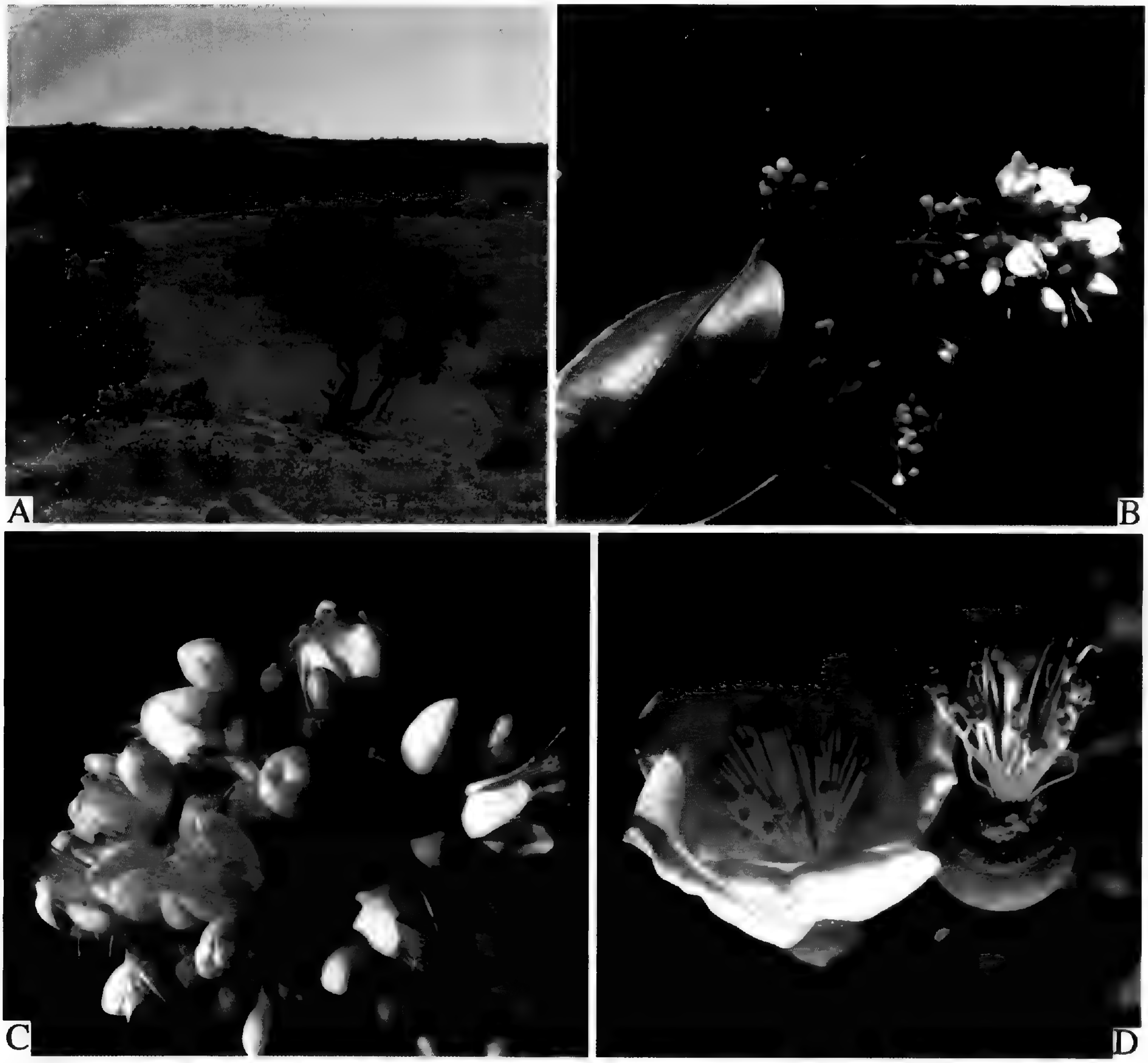


Figure 2. Photos documenting vegetative and floral morphology of *Sarcolaena*. —A. *S. oblongifolia* as a dominant woody species in the Itremo region. —B. Inflorescence and leaves of *S. multiflora*. —C. Inflorescence with opened and unopened flowers of *S. multiflora*. —D. Flower and involucres of *S. oblongifolia*.

these traces ranges from 0 to 4 and is sometimes useful for species recognition. In all species, leaf surfaces are sericeous with T-shaped hairs. There are usually fewer hairs on adaxial surfaces. Abaxial surfaces are also always covered by stellate scales. However, the density and presence or absence of hairs on leaves are variable characters and therefore of limited diagnostic value.

INFLORESCENCES

Inflorescences in *Sarcolaena* are terminal or subterminal, dichotomously branched cymes with up to 30 flowers (Fig. 2B, C). This fertile axis may be reduced to a solitary, axillary flower in *S. humbertiana*. Capuron (1970) observed that small-flowered species had more flowers per inflorescence and that large-flowered species generally had fewer. We did not conduct a quantitative study to confirm or refute Capuron's conclusion; however, we did observe that flower number is generally too variable to be of much use in delimiting species.

INVOLUCRES

Involucre as considered here was defined by Capuron (1970) as a structure distinct from the perianth of the flower (Fig. 2D). It is not a receptacle as implied by Cavaco (1952a, 1952b). However, careful anatomical study is necessary to determine the homologous nature of the involucre in *Sarcolaena*. The involucre surrounds a single flower and is well developed at anthesis. This is in contrast to some genera of Sarcolaenaceae such as *Xyloolaena*, *Rhodolaena*, *Pentachlaena*, *Eremolaena*, and *Perrierodendron*, in which the involucre may subtend more than one flower or remain reduced at anthesis. Involucral size varies in *Sarcolaena*, ranging from 5–7 mm long and 5–6 mm wide in *S. multiflora* to 7.5–12 mm long and 8–11.5 mm wide in *S. grandiflora*. Involucral shape also varies from widely to very widely obovoid. The involucre consists of two distinct parts with the body or lower portion and the top or upper part divided into separate teeth at anthesis (Fig. 3B, C_1). The involucre is covered by brown to light brown hairs of variable length. In species descriptions, short hairs are defined as less than 1 mm long, and long hairs are longer than 1 mm. Hairs on involucres of *Sarcolaena* vary in shape, length, and orientation and result in four types of indumentum (Stearn, 1992): (1) *sericeous*—with > 1 mm long, appressed, straight, silky hairs; (2) *setaceous*—with > 1 mm long, appressed, straight, thick, bristle-like, dense hairs; (3) *hirsute*—with > 1 mm long, erect, straight, dense hairs; (4) *spreading hairs*—with > 1 mm long, spreading, curved hairs.

CALYX

Terminology describing aestivation follows that of P. F. Quer (1953). The calyx of *Sarcolaena* is dialysepalous with three equal sepals, which are abaxially brown and have long appressed hairs forming apical tufts (Fig. $3C_2$). Sepals are membranaceous, contorted, and occasionally imbricate. An exception is *S. humbertiana*, which was reported to have five unequally sized sepals (2 small and 3 large) (Cavaco, 1952a, 1952b). Sepals are always included within the involucre. Sepal shape varies from ovate to very widely or widely depressed ovate, and size ranges from 2 to 8 mm long and 1.5 to 5 mm wide. The length and width of sepals vary continuously within and among species, but these measures can be used to separate species when variation ranges do not overlap.

COROLLA

All species of *Sarcolaena* have a 5-merous, white or yellow corolla (Fig. 2D). The petals are free, obovate, narrowed at the base, glabrous, membranaceous, contorted, and range in size from 12 to 23 mm long and 6 to 15 mm wide. As with the sepals, variation in size is useful in delimiting some taxa.

NECTARY

All species of *Sarcolaena* have an annular and toothed nectary located between the stamens and the corolla (Fig. $3C_2$). It secretes a limpid sticky liquid, which probably is an attractant to pollinators.

STAMENS

Stamen number varies considerably throughout the Sarcolaenaceae. It ranges from 5 to10 in *Leptolaena* (sensu stricto) to 80 to 100 in *Perrierodendron* Cavaco (1952a). In *Sarcolaena*, stamens are numerous and may be diagnostic of certain species: *S. delphinensis* has 23 to 28 stamens; *S. multiflora* has 30 to 40. All other species have more than 40. Anthers in *Sarcolaena* are dorsifixed, introrse, and bithecate dehiscing by longitudinal slits. They are approximately the same height as the corolla but generally shorter than the style. Filaments are glabrous, slender, and twisted at their bases (Fig. 2D).

POLLEN

The pollen of Sarcolaenaceae is shed in tetrahedral tetrads. Three major types of pollen have been recognized in the family by Straka (1963, 1964, 1971, 1975) and Carlquist (1964). However, a more recent study by Nilsson and Randrianasolo (1999) suggested four types of pollen. According to Nilsson and Randrianasolo (1999), Type I is the *Schizolaena*-type and includes the genus *Schizolaena* with small (25–40 μm) and simple tetrads, tricolporate or porate pollen grains with the tectum varying from scabrate to verrucate, rugulate, or foveolate. Tetrads of *Schizolaena*-type also lack raised ridges. Type II is the larger *Sarcolaena*-type (75–120 μm), which includes *Sarcolaena*, *Leptolaena*, *Rhodolaena*, and *Xyloolaena*. Here, pollen grains have a smooth tectum with very distinct, thick and continuous ridges. Type III corresponds to the *Eremolaena*-type. This includes only *E. rotundifolia* (F. Gérard) Danguy and presents relatively simple tetrads ca. 70 μm in diameter. Type IV, or the *Perrierodendron*-type, is defined as large tetrads (45–90 μm) with a smooth tectum and is known from *Pentachlaena*, *Perrierodendron*, and one of the two species of *Eremolaena* (*E. humblotiana* Baill.). The tectum of this last type also is characterized by raised, discontinuous ridges. While pollen morphology has proven useful for elucidating generic relationships, *Sarcolaena* species all share Type II pollen with only slight structural differences. Hence, pollen is of little use for delimiting species or elucidating relationships within *Sarcolaena*.

GYNOECIUM

The ovary in *Sarcolaena* is superior, trilocular, usually with two pendulous ovules in each locule, and is covered with long, reddish brown hairs (Fig. $3C_3$). The single style is as long as or slightly longer than the petals, ranges from 7 to 24 mm long, and is terminated by a trilobed, discoid stigma (Fig. 2D). Style lengths can be used to separate some species.

FRUIT

Sarcolaena fruits are indehiscent capsules with a very fragile pericarp. They are completely enclosed in the involucre in all species except *S. delphinensis*, in which they are only partially included. Fruit size ranges from 5 to 10 mm long and 5.5 to 9 mm wide, and due to extensive variation and overlap has little utility in distinguishing species. Each fruit contains 3 to 6 black, rugose seeds to 3–5 mm in length.

SYSTEMATIC TREATMENT

Sarcolaena Thouars, Hist. Veg. Isles. Austral. Afriq. 37. 1806. TYPE: *Sarcolaena multiflora* Thouars (lectotype, designated by Bullock (1960)).

Sarcochlaena orth. var. in Spreng., Linn. Syst. Veg. Vol. II, 594. 1825.

Trees, (3–)8–15 m tall, usually branched. Leaves alternate, simple, the blade petiolate, entire, coriaceous, persistent, with well-marked longitudinal traces from induplicate prefoliation (except in *S. isaloensis*) and brochidodromous venation. Stipules deciduous, leaving circular scars on the young twigs. Inflorescence terminal or subterminal, cymose, ± dichotomously branched in most species, but in *S. humbertiana* reduced to solitary flowers in terminal or axile position. Flowers pedunculate, each with a cup-shaped, hairy, generally brown involucre; calyx dialysepalous, the 3 sepals (5 in two whorls in *S. humbertiana*) widely ovate, contorted, membranaceous, brown, sparsely sericeous with an apical tuft of long, simple hairs on the abaxial surface, always enclosed in the involucre; corolla 5-merous, widely obovate, contorted, dialypetalous, membranaceous, white, white-yellow, or white-blue; nectary annular, toothed, borne between the corolla and the stamens; stamens 23 to 61, slightly exserted, the filaments unequal in length, slender, glabrous, the anthers dorsifixed, introrse, bithecate, parallel, dehiscing by longitudinal slits; ovary oblong, pubescent, trilocular with 2 pendulous ovules per locule, the placentation axillary, the style ± exserted. Fruits capsular with a very fragile pericarp in maturity, enclosed completely in the transformed involucre, except in *S. delphinensis* where they are partially enclosed.

Distribution. *Sarcolaena* is endemic to Madagascar and occurs primarily in the Eastern and Central phytogeographic regions with disjunct occurrence in the Sambirano domain, considered part of the Eastern Region because of similar climatic conditions and corresponding forest composition and profile (Koechlin, 1972).

No holotype was designated by Thouars in the original generic description, and Bullock (1960) designated *Sarcolaena multiflora* as the lectotype of the genus from the three species described by Thouars: *S. multiflora*, *S. grandiflora*, and *S. eriophora*.

Vernacular names. The Malagasy language varies from one part of the island to another, and different vernacular names are used for *Sarcolaena*. Those recorded with collections are reported here with an indication of their region: helana or mera (East coast), vondrozona (Central), and hazo atambo (Northwest). There is no indication of vernacular recognition of different species.

Uses. There are no detailed ethnobotanical studies of *Sarcolaena*. The species are reputed to have hard wood that is good for building houses, and they are also commonly used as fuelwood along the east coast. *Sarcolaena oblongifolia*, with its attractive flowers, has been cultivated in the Parc Botanique et Zoologique de Tsimbazaza for about ten years; the aesthetic beauty of *Sarcolaena* species makes them candidates as ornamental plants in tropical areas.

KEY TO THE SPECIES OF *SARCOLAENA*

1a. Leaves less than 1.1 cm wide .... 6. *Sarcolaena isaloensis*

1b. Leaves more than 1.1 cm wide.

2a. Stamens 23–28; fruit partially enclosed in the involucre; leaves oblanceolate .... 2. *Sarcolaena delphinensis*

2b. Stamens 30 or more; fruit completely enclosed in the involucre; leaves generally narrowly ovate, narrowly elliptic, or lanceolate.

3a. Hairs of the involucre dense and more than 1 mm long.

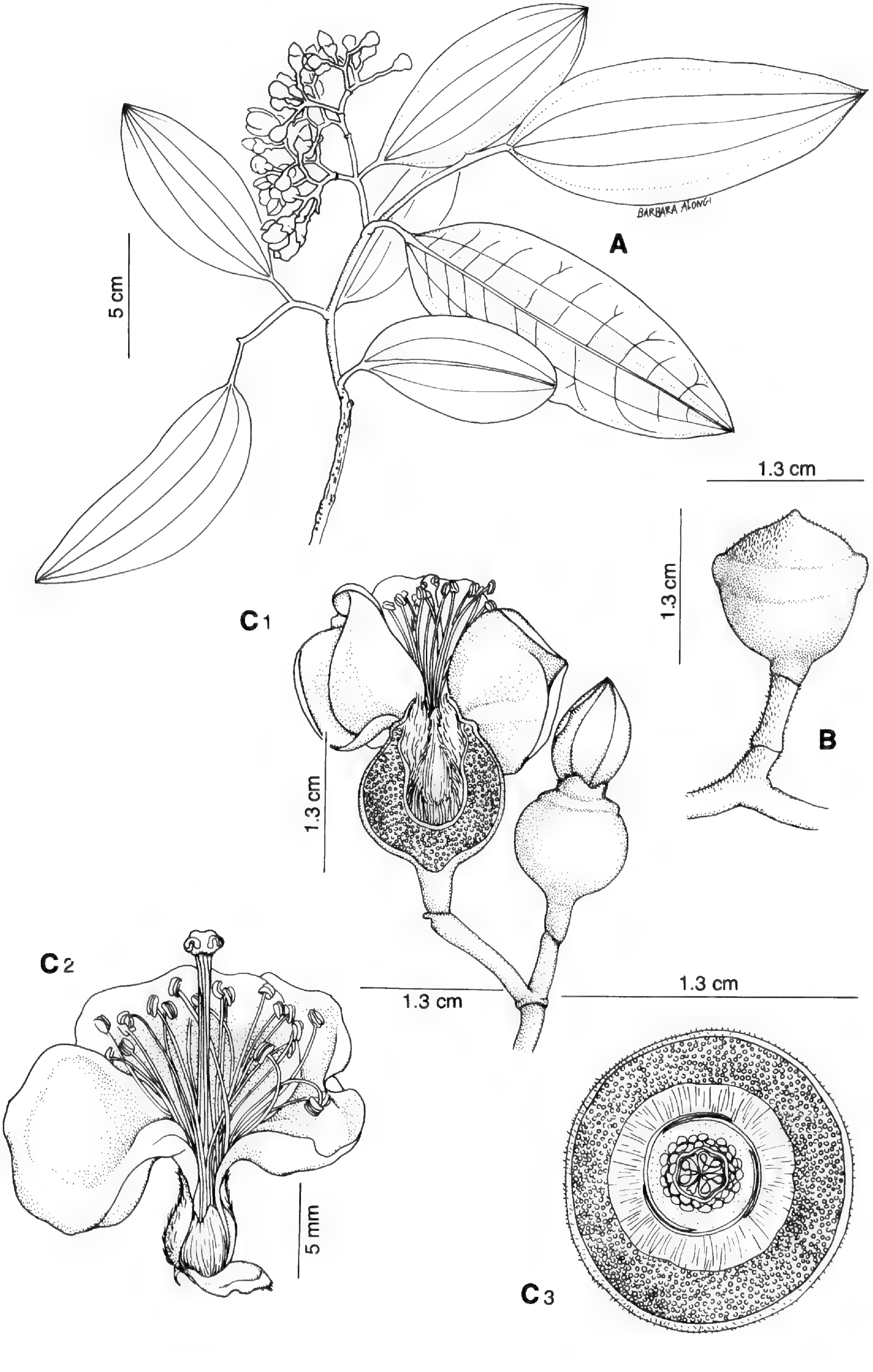
4a. Erect and spreading hairs found on the involucre; leaf apex obtuse or sometimes mucronate .... 3. *Sarcolaena eriophora*

4b. Only spreading hairs on the involucre; leaf apex acute to attenuate or slightly acuminate .... 5. *Sarcolaena humbertiana*

3b. Hairs of involucre not dense, less than 1 mm long.

5a. Style greater than 16 mm long; petals more than 12 mm wide.

6a. Style 18–24 mm long; sepals 6–8 mm long; petals 20–23 mm long; leaves 3.2–9.2 cm long; involucre widely obovate,


BARBARA ALONGI
A
5 cm
1.3 cm
1.3 cm
B
C1
1.3 cm
C2
1.3 cm
1.3 cm
5 mm
C3

± top-bottom compressed .... 8. *Sarcolaena oblongifolia*
    6b. Style 16–17 mm long; sepals 4–5 mm long; petals 16–21 mm long; leaves 8–13.5 cm long; involucre very widely obovate, cup-shaped .... 4. *Sarcolaena grandiflora*
5b. Style less than 16 mm long; petals less than 12 mm wide.
    7a. Abaxial leaf surface ferrugineous; stamens 43–61; sepals 4.5–5.5 mm long .... 1. *Sarcolaena codonochlamys*
    7b. Abaxial leaf surface not ferrugineous; stamens 32–39; sepals 2.5–3 mm long .... 7. *Sarcolaena multiflora*

1. **Sarcolaena codonochlamys** Baker, Bull. Misc. Inform., CCXCII, 11. 1893. TYPE: Madagascar. North Madagascar: Without exact locality, *Baron 6366* (holotype, K not seen; isotype, P!).

Trees, 8–15 m tall, the young twigs sericeous, glabrate. Leaf blades lanceolate, sometimes narrowly oblong, (6–)8–11(–16.5) cm long, (2–)2.2–3.5(–5.3) cm wide, apex acute, narrowing to an acuminate, mucronate or sometimes retuse apex, base obtuse, rarely acute; adaxial blade surfaces glabrous, sometimes with long appressed hairs along the midrib (more so on young leaves), abaxial blade surfaces ferrugineous, sparsely sericeous, with 1 or 2 induplicate prefoliation traces on either side of midrib; petiole sericeous, canaliculate, (6–)7–10(–12) mm long. Inflorescence terminal, 4- to 16- or more flowered. Involucre widely to very widely obovate, (5–)7–8(–10) mm long, (6–)7–8(–9) mm wide, exterior surface with short brown hairs, inside sericeous; sepals widely to very widely ovate, 4.5–5.5 mm long, 4–5 mm wide, the abaxial sepals with a few long hairs with apical tuft; petals obovate, 16–20 mm long and 9–10 mm wide, glabrous, white or blue; stamens 43 to 61, 15–18 mm long, with anthers small, 1 mm long; ovary hairy, oblong, 1.5–2 mm long, style 12–15 mm long, glabrous. Fruit 9–10 mm long and 7 mm wide, enclosed in an involucre 13–15 mm long and 11–12 mm wide.

Sarcolaena codonochlamys is distinct in having lanceolate leaves abaxially ferrugineous.

Distribution and ecology. *Sarcolaena codonochlamys* has been collected in the Sambirano, in northwestern Madagascar, particularly around Ambanja and Ambilobe. It also occurs near Rantabe in the eastern rainforest (Fig. 4).

Additional specimens examined. MADAGASCAR. **Antsiranana:** Marovato Ambanja, close to Mabibo village, *72 D 309* (P); S of Ambilobe, *Decary 14837, 14799* (P); Plateaux of Ankarana, near Ambondrofe, *Humbert 18945* (P); Sambirano basin and Zangoa, less than 500 m high, *Perrier de la Bâthie 3026* (P); vicinity of Ambilobe, *Perrier de la Bâthie 3033* (P); Bas Sambirano, *Perrier de la Bâthie 15676* (P); Tandavan'i Galoka (Chaine du Galoka), SW of Ambilobe, NE end of ridge, 5 km along road from Beramanja, *Phillipson 2014* (MO, TAN); S of Ambanja, N slope of the Ambatomenavava peak, 500 m, *RN [Ramarokoto and Ratoto] 1448* (P); Antanimandry, county of Beramanja, Ambilobe district, *SF 3515* (P); Ampondrabe, Ambanja, *SF 5838* (P); Bekaka, Benavony, Ambanja, *SF 7504, 9296* (P); Andampy, Ambilobe, *SF 10432* (P); Ankotika Ambanja, *SF 10641* (P). **Mahajanga:** Bejofo, Maromandia district, *Decary 939, 2221* (P); hills in Andranosamonta vicinity, Analalava district, *Perrier de la Bâthie 3022* (P). **Toamasina:** Ambodisira, Rantabe, *Randriamanga 139* (P). **Province unknown:** N Madagascar without exact locality, *Baron 5816, 6380* (K, P); *Decary 14795* (TAN).

2. **Sarcolaena delphinensis** Cavaco, Bull. Mus. His. Nat. (Paris) Ser. 2, 22: 615. 1950. TYPE: Madagascar. Toliara: vicinity of Fort-Dauphin, 1–25 m, 20 Sep.–6 Oct. 1928 (fl), *Humbert 5996 bis* (holotype, P!).

Trees, 8–10 m tall, densely branched; young twigs sericeous, later glabrous. Leaf blades oblanceolate, 5–9 cm long, 1.2–3 cm wide, apex acute and often abruptly acuminate, less commonly mucronate or retuse, base acute to cuneate; adaxial blade surfaces with sparsely appressed hairs, usually glabrate with age, abaxial blade surfaces sericeous, with 1 or 2 induplicate prefoliation traces on either side of midrib; petiole (6–)7–9(–10) mm long, adaxially canaliculate, brown sericeous. Inflorescences terminal, 4- to 16- or more flowered. Involucre widely obovate, 6–7 mm long, 4–5 mm wide, the interior surface setaceous, the exterior surface brown, showy with medium-sized appressed hairs; sepals 3 mm long, 2 mm wide, free, these generally contorted in opened flowers but sometimes imbricate in the buds, sparsely sericeous on abaxial surfaces with apical tufts; petals obovate, 1.2–1.5 cm long, 0.5 cm wide, glabrous, white to yellow; stamens 23–28, 1.2–1.5 cm long, attached

←

Figure 3. —A. Inflorescence branch of *S. multiflora*. —B. Unopened floral involucre of *S. grandiflora*. —C. *S. oblongifolia*: —C_1. Unopened and opened flowers. —C_2. Flower outside the involucre. —C_3. Cross section of involucre with young fruit.

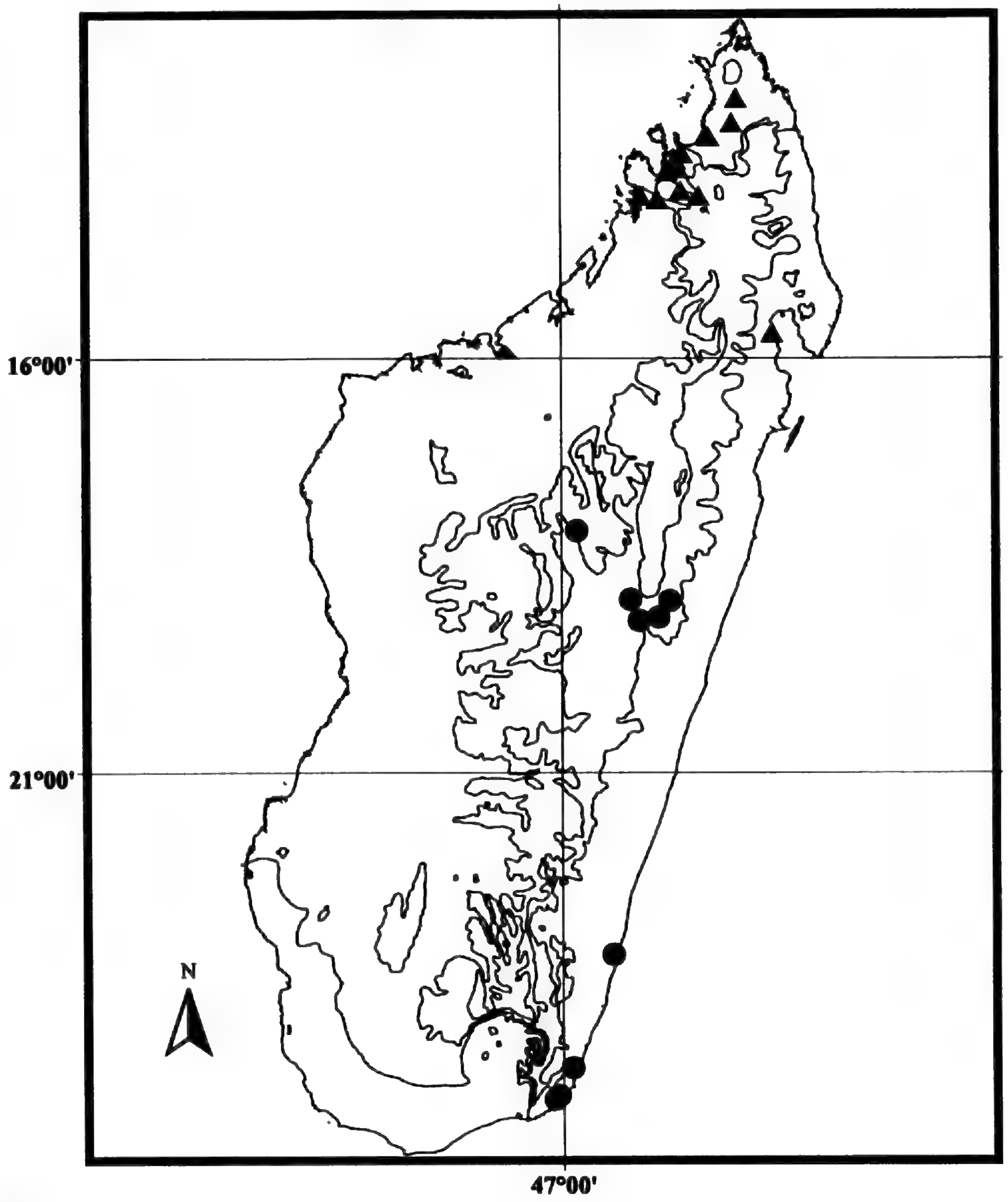


Figure 4. Geographic distribution of *Sarcolaena codonochlamys* (triangles) and *S. eriophora* (circles).

between ovary and nectary, anthers 0.8–1 mm long; ovary ± oblong, 1.8–2 mm long, very hairy, style 8–10 mm long, glabrous. Fruit ovoid, 11–12 mm long, 8–9 mm broad, incompletely included in the brownish green, very widely obovoid involucre, 8–9 mm long, 11–11.5 mm broad.

Sarcolaena delphinensis is distinctive because its fruits are only partially enclosed in the involucre, and its leaves are oblanceolate in shape. It has also 23 to 28 stamens, the fewest of any species.

Distribution and ecology. This species occurs in moist sublittoral forest from sea level to 200 m and is only known from southeastern Madagascar, in the vicinity of Tolagnaro (Fort-Dauphin) (Fig. 5).

Additional specimens examined. MADAGASCAR. **Toliara:** environs de Fort-Dauphin, *d'Alleizette 1182* (P); environs de Fort-Dauphin, 1–25 m, *Humbert 5996 bis* (P); Fort-Dauphin region, N of the town along trail following pipes to town's water source, forest called Lakandava, 100–200 m, *McPherson et al. 14894* (A, MO, P, TAN); Fort-Dauphin Lakandava, bassin du JIRAMA, just close the pipes back to town, 50–70 m, *Randrianasolo 256* (K, MO, P, TAN); vicinity of Fort-Dauphin, 2 km W of Manantantely, *Randrianasolo 278* (K, MO, P, TAN).

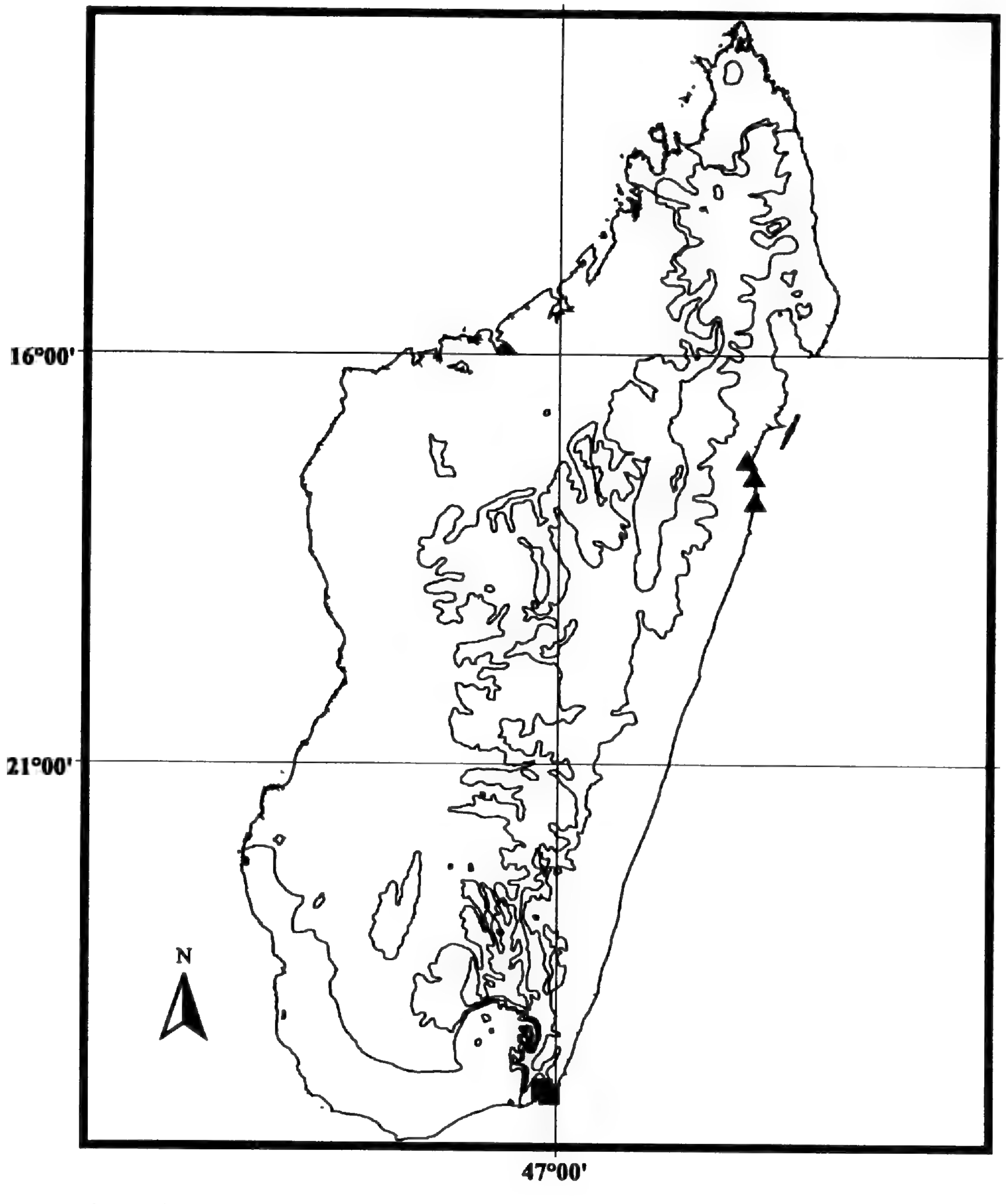


Figure 5. Geographic distribution of *Sarcolaena delphinensis* (squares) and *S. grandiflora* (triangles).

3. **Sarcolaena eriophora** Thouars, Hist. Veg. Isles Austral. Afriq. 40. 1806. TYPE: Madagascar. Without exact locality, *Commerson s.n.* (holotype, P!).

Trees, 3–10 m tall; twigs sericeous, more so in young branches. Leaf blades variable in shape, narrowly ovate, sometimes narrowly obovate or narrowly elliptic to ovate or obovate, (3.9–)4.7–6.8(–8.4) cm long, 1.7–4.3 cm wide, apex usually obtuse, sometimes mucronate, base obtuse; adaxial blade surfaces sparsely sericeous along the midrib, more so in younger leaves, but sometimes glabrous, abaxial blade surfaces sericeous, with none or one induplicate prefoliation trace on either side of midrib; petiole (6–)7–9(–12) mm, adaxially canaliculate, brown and sericeous. Inflorescence terminal, with 1 to 7 flowers per inflorescence. Involucre very widely obovate, 8–9 mm long, ca. 8 mm wide, hirsute on the lower part and sericeous on the upper part, the interior surface sericeous; sepals very widely ovate, 4–5 mm long and 4 mm wide, with a few long appressed hairs on abaxial surface, and an apical tuft of hairs at the apex; petals 14–15 mm long and 5–6 mm wide, glabrous; disk 1 mm high, yellow; stamens 44 to 47, unequally sized, 6–7 mm long, the anthers very small, 0.5–1 mm long; ovary very hairy, ± 2 mm long, style 7–12 mm long, pubescent from the base to ca. ⅔ of its length. Fruit widely ovoid to widely depressed ovoid, 5–7 mm long and 5.5–6 mm broad, included within involucre 10–11 mm long and 9–11 mm broad.

The most distinctive feature of *Sarcolaena eriophora* is differentiation between hairs on the lower and upper portions of the involucre. On the lower part the hairs are dense and erect, but on the upper part they are less dense and spreading. This species also has the narrowest petals in the genus.

Distribution and ecology. *Sarcolaena eriophora* occurs in wet littoral forests on sand along the southeast coast of Madagascar, from Fort-Dauphin to Farafangana (Fig. 4). It also occurs from the premontane forests along the escarpment between the eastern domain and the central domain to the plateau.

Additional specimens examined. MADAGASCAR. **Antananarivo:** Ankazobe, Canton Maridaza, Réserve Spéciale Ambohitantely, *RN [Jean de Dieu] 190* (P), *SF 9594, 14684, 18008, 18358, 19875* (all P); Station Forestière Mandraka, 1210 m, *SF (Rakotovazaha) 1903* (P); Station Forestière Mandraka, vallée de la Mandraka, vers PK 69, *SF 18502* (P). **Fianarantsoa:** Cote-Est, près de l'embouchure du Faraony, *Perrier de la Bâthie 3013* (P); Farafangana, coastal forest of Nosiala, *SF 16210* (P). **Toamasina:** Ampitanonoka, entre Ampitanonoka et Sahalampona, 1200 m, *Cours 2629* (P); Mangoro, entre Beparasy et Moramanga, 800 m, *Perrier de la Bâthie 17201* (P); Moramanga, Analamazaotra-Périnet Réserve Spéciale, *SF 10347, 14961, 15019, 19081* (all P); Moramanga, Niagarakely, Sarindreniny, Toby P.K 27 route d'Anosibe, *SF 25802* (P). **Toliara:** Fort-Dauphin, Petriky, Forêt littorale sur sable de Petriky, derrière les lacs, *Allorge 798* (MO); Fort-Dauphin region, NE of city, in region called Mandena, beyond the botanical garden and QIT camp, in forest remnants near coastal lake, 25 m, *McPherson & Dumetz 14319* (MO, TAN); Fort-Dauphin, forestry station of Mandena, 12 km of Fort-Dauphin, *Randrianasolo 252, 254* (K, MO, P, TAN); Mandena 12 km N of Fort-Dauphin, forest on sand, *SF 6088, 7010* (P); Bemangidy forest, N of Mahatalaky, 100 m, *SF 11782* (P); sandy dunes in Mandromondromotra, N of Fort-Dauphin, *SF 22644* (P); about 10 km NNE of Fort-Dauphin, Mandena region, coastal low forest on sand, 10 m, *Zarucchi et al. 7602* (MO, P, TAN).

4. **Sarcolaena grandiflora** Thouars, Hist. Veg. Isles Austral. Afriq. 40. 1806. TYPE: Madagascar. Without exact locality, *Thouars 806* (lectotype, selected here, P!; isolectotype, P!).

Trees, 8–15 m tall; young twigs light brown sericeous, glabrate with age. Leaf blades lanceolate to narrowly ovate or ovate, 8–13.5 cm long, (2.5–)3–4.6(–5.5) cm wide, apex acute to slightly acuminate, base obtuse; adaxial blade surfaces generally glabrous but occasionally with very few appressed long hairs, abaxial blade surfaces brown, more so in young leaves, sparsely sericeous, with 1 to 4 induplicate prefoliation traces on either side of midrib; petiole 8–15 mm long, adaxially canaliculate, brown sericeous, more so on young leaves. Inflorescences terminal, (4–)10–11(–16)-flowered. Involucre very widely obovate, 7.5–12 mm long, 8–11.5 mm wide, the interior surface setaceous, exterior surface with very short brown hairs; sepals ovate to widely ovate, 4–5 mm long and 3.5–6 mm wide, glabrous but with a tuft of hairs at the apex; petals obovate, 16–21 mm long and 14–15 mm wide, glabrous, white; stamens 46–50, filaments unequal in size, 15–19 mm long, anthers 1–1.2 mm long; ovary oblong, 2.5 mm long, with dark red-brown hair, style 16–17 mm long, pubescent from the base to ⅔ of its length. Fruit completely enclosed in a depressed obovoid involucre, 9–11 mm long, 17–19 mm broad.

Sarcolaena grandiflora is easily distinguished from other members of the genus by its very widely obovate cup-shaped involucre (Fig. 3B) and the presence of pubescence on the lower ⅔ of the style.

Distribution. This species has been collected in only two areas of Madagascar (Fig. 5). It occurs in the wet, central and eastern littoral and sublittoral forests in the northern part of Toamasina province, in the vicinity of Fénérive-Est.

Additional specimens examined. MADAGASCAR. **Toamasina:** Tampolo, 10 km from N of Fénérive-Est, road to Soanieran'Ivongo, just at the intersection with the road to Rantolava, over the bridge, *Randrianasolo 244* (K, MO, P, TAN); Botanical garden #21, Tampolo, Fénérive, *SF 16455, 19176, 19228* (P, TEF); littoral forests on sand, in Antetezana, N of Tamatave, *SF 18089* (P, TEF); sublittoral forests on sand in Mahambo, S of Fénérive, *SF 18147, 18149* (P, TEF).

5. **Sarcolaena humbertiana** Cavaco, Bull. Soc. Bot. France, Actual. Bot. 97: 96. 1950. TYPE: Madagascar. Toliara: Manampanihy basin (Sud-Est), Mont Vohimavo N of Ampasimena, 830 m, 27–28 Mar. 1947 (fl, young fr), *Humbert 20705* (holotype, P!).

Trees, 3–4 m tall; twigs brown sericeous, glabrate. Leaf blades lanceolate to narrowly elliptic-oblong, 5.5–9.3 cm long, 1.9–3 cm wide, apex acute to attenuate or slightly acuminate, base obtuse; adaxial blade surfaces glabrous, occasionally with a few appressed hairs on midrib, abaxial blade surfaces sparsely brown sericeous, with one induplicate prefoliation trace on either side of midrib; petiole 6–7 mm long, adaxially canaliculate, brown sericeous. Flowers solitary, axillary or terminal. Involucre ± 12 mm long, exterior surface sericeous,

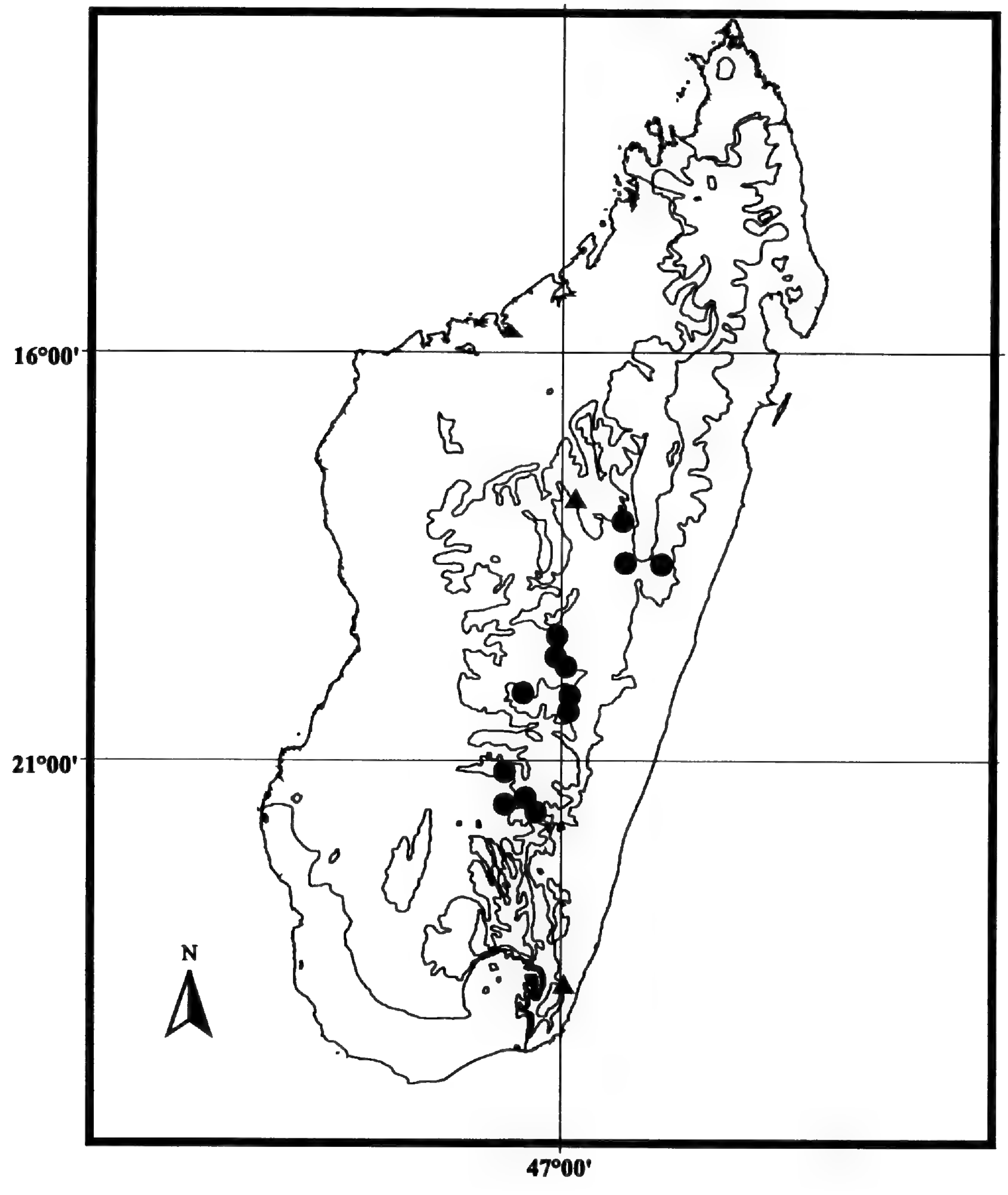


Figure 6. Geographic distribution of *Sarcolaena humbertiana* (triangles) and *S. oblongifolia* (circles).

interior surface pubescent; calyx 5-merous, with 2 exterior and 3 interior sepals, exterior sepals ovate, 2 mm long and 1.5 mm wide, with few hairs at the apex, inner sepals widely to very widely ovate, 4 mm long and 3.5–4 mm wide, sparsely sericeous with an apical tuft of hairs; corolla 5-merous; stamens about 40; ovary hairy. Fruit unknown.

Despite the fact that few collections have been made for *Sarcolaena humbertiana,* it appears that the involucre not divided into two parts separates it from the rest of the species in the genus. According to Cavaco (1952), the character of solitary flowers bearing 5 instead of 3 sepals is unique in the genus. However, the number of specimens is not sufficient to confirm whether Cavaco's description was accurate.

Distribution. This species has been collected only twice, at Ambohitantely at 1600 m, north of Ankazobe, in the province of Antananarivo; and distantly in southeastern Madagascar, to the north of the Fort-Dauphin region, at the Vohimavo peak at 830 m (Fig. 6).

Additional specimen examined. MADAGASCAR. **Antananarivo:** Tamponketsa au Nord d'Ankazobe (centre), forêt d'Ambohitantely et restes de forêts aux alentours, 1600 m, *Humbert 11098 bis* (P).

6. **Sarcolaena isaloensis** A. Randrianasolo & J. S. Mill., Novon 4: 292–294. 1994. TYPE: Madagascar. Fianarantsoa: plateau and valleys of Isalo, W of Ranohira, 800–1250 m, 29 Jan.–2 Feb. & 8–10 Apr. 1955 (young buds), *Humbert 28695* (holotype, P!).

Trees, 6–10 m tall; young twigs sericeous, glabrate. Leaves alternate, simple, entire, coriaceous; leaf blades narrowly ovate to narrowly elliptic, 3–5.3 cm long, 0.5–1.1 cm wide, apex acute, mucronate, base obtuse; adaxial blade surfaces glabrous, abaxial blade surfaces sparsely brown sericeous, lacking induplicate prefoliation traces; petiole 4–8 mm, canaliculate, abaxially brown sericeous. Inflorescence terminal, flowers solitary or paired. Young involucre surrounded by a brown sericeous caducous spathe. Involucre with long, spreading, stiff hairs, peduncle brown sericeous, 2–6 mm long. Flowers and fruits unknown.

This species is distinctive in its very narrow leaves that lack the induplicate prefoliation traces present elsewhere in *Sarcolaena*, and in the long, stiff, spreading hairs on the young involucre.

Distribution and ecology. This species occurs in Isalo, west of Ranohira, the southern limit of the central domain (Fig. 7).

Specimens examined. MADAGASCAR. **Fianarantsoa:** Isalo massif, Betanimanga, 1000–1300 m, 18–20 Nov. 1960, *Leandri 3951* (P); Isalo, tapia woodland, 900 m, 24 Nov. 1932, *Perrier de la Bâthie 16688* (P); Isalo massif nearby the sign of Isalo Sud, W of Ranohira, *SF 11.675* (P).

7. **Sarcolaena multiflora** Thouars, Hist. Veg. Isles. Austral. Afriq. 40. 1806. TYPE: Madagascar. Without exact locality, *Thouars s.n.* (lectotype, here designated, P!; isolectotype, P!).

Sarcochlaena multiflora var. *latifolia* Hochr., in Annuaire Conserv. Jard. Bot. Genève, 12: 73. 1908. TYPE: Madagascar. District of Vatomandry, en sol sabloneux, arbre de taille moyenne, 25 Oct. 1903, *Guillot 52* (G).

Trees, 4–15 m tall; young twigs brown sericeous to glabrate with white lenticels. Leaf blades lanceolate to ovate or narrowly elliptic to elliptic, (5.5–)8.5–15.5(–19.7) × (2.5–)3–6.5(–8.5) cm, apex acute to obtuse, sometimes rounded and abruptly acuminate, mucronate or retuse, base obtuse, rounded or subcordate; adaxial blade surfaces generally glabrous but occasionally with a few long, appressed hairs along the midrib, more so on young leaves, the abaxial surface sparsely sericeous, very often on the midrib only, with 1 to 3 induplicate prefoliation traces on either side of midvein; petiole (9–)10–15(–20) mm long, adaxially canaliculate, sericeous. Inflorescence terminal, usually 20- or more-flowered, but sometimes less. Involucre widely to very widely obovate, 5–7 mm long and 5–6 mm wide, exterior with short hairs, inside surface sericeous; sepals very widely to very depressed ovate, 2.5–3 mm long and 3–4 mm wide, with a few long, appressed hairs on the abaxial surface and with an apical tuft of hairs; petals obovate, 12–18 mm long and 6–10 mm wide, glabrous, white or yellow; stamens 32 to 39, 11–13 mm long, anthers 1 mm long; ovary hairy, 1.5–1.8 mm long, style 10–14 mm long, basally pubescent. Fruit very widely ovoid, 6–7 mm long and 6–7 mm broad, completely included in mature involucre 7–9 mm long and 6–11 mm wide.

Sarcolaena multiflora shares many morphological characters with *S. grandiflora* and can also be confused with *S. oblongifolia*. However, it is easily distinguished from these two species by its small involucres, its large leaves up to 20 cm long, inflorescences usually with 20 or more flowers, each with 32 to 39 stamens (Figs. 2C, 3A).

Distribution and ecology. This species is the most widespread in the genus. It ranges from the northeast to Fort-Dauphin in both rainforest and littoral forests of the eastern domain (Fig. 7).

Additional specimens examined. MADAGASCAR. **Antsiranana:** Sambava, Forêt d'Atiala, 100 m, *Deroin et al. 138* (MO, P); Environs de Sambava, massif rhyolitique d'Ambatobiribiry, 50–345 m, *Humbert et al. 24429* (P); Antalaha Ambohitralanana, *RN 3385* (P); Antalaha, *RN 4928* (P); Antalaha Ambohitralanana, *RN 5719, 6794, 8054, 10098, 10740* (all P); Antalaha, *SF 1646* (TAN); Sambava, eastern forests, remnant forests in SW Sambava vicinity, *SF 9244* (P); Manampona Tsaratanana, *SF 9477* (P); Anovoka Sambava, *SF 13285* (P). **Fianarantsoa:** Mananjary, *Geay 8087* (MO); Ambalavonika Mananjary, *Geay 8088, 8089* (P); Anefitrala Vangaindrano, *SF 4091* (P); Mananjary, *SF 5629* (P); Andrianabo-Amparibe Vangaindrano, *SF 7109* (P); Nosiala-Efatsy Farafangana, *SF 7297* (P); Pangalana Sud, Mananjary, *SF 9504* (P); Nosiala-Efatsy Farafangana, *SF 12212* (P); Fitiamito ambahy Nosy Varika, *SF 13457* (P); Amborondamba Nosy Varika, *SF 15478* (P); Farafangana, Bema Evato, *SF 15242* (P); Tohakandra Ihorombe Farafangana, *SF 16154* (P); Marohita Mananjary, *SF 16176, 21001* (P). **Toamasina:** Vatomandry, *Bernard 1903* (P); Ile Sainte Marie, *Bernier 191* (P); Ambila Lemaitso, *Boiteau 457* (P), *Boivin s.n.* (P); Foulpointe, *Bojer s.n.* (P); Ambila Lemaitso, derrière la lagune, 3–5 m, *Cours 2940* (P); along the route #5, S of Fénérive-Est between PK 80–PK 100, mostly sandy soil, more than 50 m, *Croat 32592* (MO); road to Analalava, W of Foulpointe, *Dorr & Barnett 3317* (MO, P), *4459* (MO); littoral forest at Reserve of Mahatsara Foulpointe,

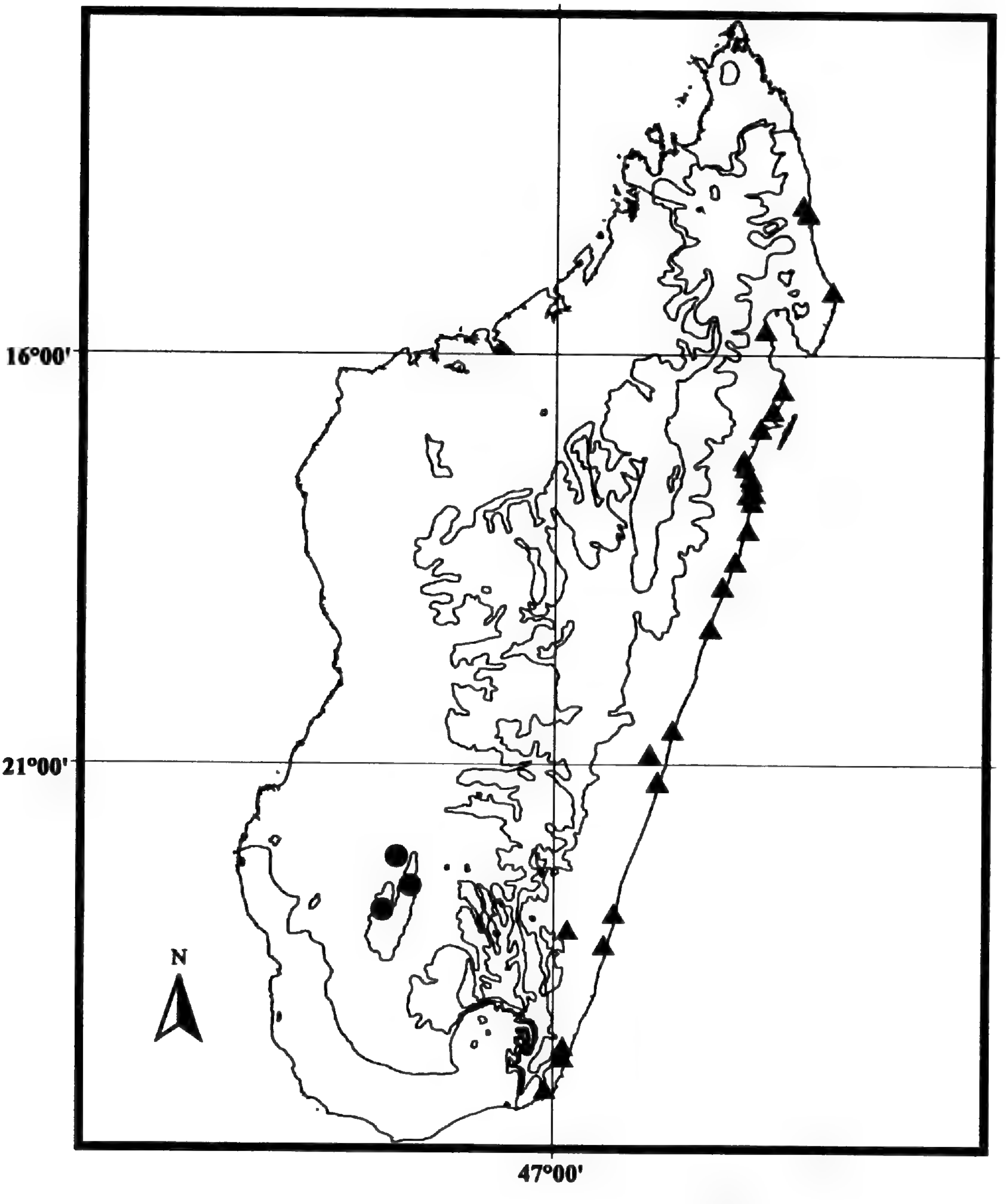


Figure 7. Geographic distribution of *Sarcolaena isaloensis* (circles) and *S. multiflora* (triangles).

Evrard 11267 (MO); Circa Tamatave, *Goudot s.n.* (P); Vatomandry, *Guillot 52* (G, MO); Soanieran'Ivongo, *Humbert 3160* (TAN); 1 km W of Ambila Lemaitso, *Keating & Miller 2249* (MO, P, TAN); Soanierana, *Lam & Meeuse 5579* (K, P); Environs d'Ambila Lemaitso, *Le Thomas 124* (P); about 2 km W of town on road toward Rantabe (RN5), partially cleared coastal forest along road on sandy soil, *Lowry II et al. 3994* (MO); Tampina, *Martine D8* (P); 1 km NW of Ambila Lemaitso, *Miller & Schatz 3637* (MO, P, TAN); Antanambe Mananara, *Morat et al. 8626* (P); Foulpointe, *Peltier 3364* (P); Fénérive-Est, *Perrier de la Bâthie 3001* (P); Tampina, *Perrier de la Bâthie 13265, 15873* (P); Mahanoro, *Perrier de la Bâthie 18118* (P); Antanambe Mananara, *Raharimalala 137, 259* (P); Manompana, route de Mananara, *Rakotozafy 1318* (TAN); Ambila Lemaitso, close to the ferry, 5 km S of the Ambila Lemaitso village, *Randrianasolo 223* (K, MO, P, TAN); vicinity of Foulpointe, along the road RN 5, *Randrianasolo 245* (K, MO, P, TAN); Eastern domain, Ambila Lemaitso, 10 km E of Brickaville, coastal dune forest and taller forest behind lagoon, *Schatz & D'Arcy 1484* (MO); Ambila Lemaitso, coastal dune forest just N of railroad bridge, W of Pangalane (canal), *Schatz et al. 3442* (MO, P); Ambila Lemaitso, *SF 1107* (P, TAN), *1618* (MO, P, TAN), *5868, 8310* (P); Antetezana Tamatave, *SF 1324, 14496* (P); Soanierana Ivongo, *SF 2415* (P); Antananala Ambila Lemaitso, *SF 3221* (P, TAN); Ambodisira Rantabe Maroantsetra, *SF 6250* (P); Tampolo Fénérive Est, *SF 10054, 10834, 15162, 15337, 16456, 17803* (P); Iamboala Mahanoro, *SF 11108* (P); Sahavolamena Soanierana Ivongo, *SF 12417* (P); sublittoral forests on sand in Mahambo, S of Fénérive Est., *SF 18148* (P); vicinity of Antongil Bay, littoral and sublittoral forests on sand in Antoraka, *SF 18279* (P); Tampina, *Ursch 118* (P); vicinity of Tamatave, *Viguier & Humbert 282* (P). **Toliara:** Fort-Dauphin, *Cloisel 143* (P); forestry station of Mandena, 7 km N of Fort-Dauphin, forest on white sand, elev. 10 m, *D'Arcy & Rakotozafy 15383* (MO); littoral forest, Fort-Dauphin, *Decary 10144* (P); forest glade, Evatra cap Fort-Dauphin, *Decary 10889* (P); Ebakika, ancient dunes Fort-Dauphin, *Decary 11077* (P); Mandena Fort-Dauphin, forest on sand, *Dorr 3996* (MO), *Dumetz 706* (MO, P); St. Luce forest Fort-Dauphin, *Dumetz et al. 746* (MO); Mandena station 9 km NE of Fort-Dauphin and less than 1 km W of Lac Ambavarana, *Gereau & Dumetz 3266* (MO); 5.5 km E of Fort-Dauphin–Manantenina road, on road to Manafiafy, in dense coastal forest, *Gereau 3422* (MO); Mandena, *Johnson s.n.* (MO, P); between St. Louis Peak and the sea, Fort-Dauphin vicinity, *Humbert 5996* (P, TAN); region of Fort-Dauphin, on QIT concession, Mandena site, low forest on sand, *McPherson et al. 14136* (MO); St Luce (Manafiafy), 44 km N of Fort-Dauphin on road to St Luce, dense coastal forest on flat sandy substrate, 50 m, *Phillipson et al. 3959* (MO); Mandena, in the Botanical garden, *Randrianasolo 251, 253* (K, MO, P, TAN); Mandena, *SF 394* (P), *1547* (P, TAN), *3385* (TAN), *4046* (P, TAN), *6250, 7009, 7815, 14535, 15621* (P); Bemangidy Manantenina Fort-Dauphin, *SF 21446* (P); about 10 km NNE of Fort-Dauphin, Mandena region, coastal low forest on sand, *Zarucchi et al. 7505* (MO, TAN). **Province unknown:** central Madagascar, specimens without exact locality, *Baron 4650* (P); *Baron s.n.* (P); *Boivin s.n.* (P); *Chapelier s.n.* (P); *Commerson s.n.* (P); *Cours 2940* (P); *Humblot 163, 165* (P), *169* (TAN), *365* (P); *Goudot s.n.* (P); *Lantz 7* (P); *Perrotet s.n.* (P); *Richard s.n.* (P); *Waterlot s.n.* (P).

8. Sarcolaena oblongifolia F. Gérard, Ann. Inst. Bot. Geol. Colon. Marseille, ser. 3, 7: 26–28. 1919. TYPE: Madagascar. Fianarantsoa: Tapia woodland, rocky (quartzitic), between Ambatomainty and Itremo, Ambositra, 1400 m, June 1912 (fl), *Perrier de la Bâthie 3006* (holotype, P!).

Trees, 3–12 m tall; young twigs sericeous, glabrate. Leaf blades narrowly ovate, elliptic or oblong to ovate or elliptic, (3.2–)4.6–7.4(–9.2) cm long, apex acute, sometimes obtuse, mucronate or retuse, occasionally acuminate, base ± obtuse; adaxial blade surfaces glabrous, occasionally with a few long appressed hairs, more so when young, with 1 or 2 induplicate prefoliation traces on either side of midrib; petiole (5–)7–10(–11) mm long, adaxially canaliculate, brown sericeous. Inflorescence terminal, reduced dichotomous cymes of 1 to 2 or 4 flowers. Involucre widely obovate, 10–13 mm long and 9–10 mm wide, exterior surface brown with short hairs, interior sericeous; sepals widely ovate, 6–8 mm long and 4.5–5 mm wide, abaxial surface with few appressed long hairs and an apical tuft of hairs at the apex; corolla obovate to widely obovate, 20–23 mm long and about 13 mm wide, white to slightly yellow, glabrous; stamens 45 to 50, filaments ca. 16–18 mm, anthers 1–1.1 mm long; ovary oblong, 2–2.2 mm long, style 18–24 mm long, pubescent from the base to ca. ⅔ of its length. Fruits completely included in the involucre, which is 13–15 mm long and 13.5–24 mm wide.

Sarcolaena oblongifolia is one of the most distinctive species of the genus. It can be easily recognized by its large flowers having sepals 6–8 mm long and petals 20–23 mm long (Figs. 2D, 3C$_2$).

Distribution and ecology. This species occurs mainly on the central and southwestern slopes of the central domain where it is one of the main components of the sclerophyllous forests from Antsirabe, south to Ihosy, and west to the Itremo chain (Fig. 6). Its distribution extends also to the eastern escarpment (from ca. 800 m), a transitional zone between the central and eastern domains.

Additional specimens examined. MADAGASCAR. **Antananarivo:** 5 km of Antilarisona N of Antsirabe, 1250–1300 m, *Croat 29205, 29228* (MO, P); rocky hillside along route #35, 54 km E of Finandrohana, area very dry with occasional springs, 1300 m, *Croat 29652* (MO); Parc Tsimbazaza, Antanananrivo city, cultivated, *Dorr 2746* (MO); Anjozorobe, ca. 2 km E of Primary and Secondary Antsahabe School at Anjozorobe, primary mountain top, mesic forest, slightly disturbed, 1410 m, roadside, *Harder et al. 1542* (MO, P); 7 km E of Anjozorobe, transitional zone between plateau and eastern domain, slightly disturbed wet forest, 1450 m, *Lowry II et al. 4389* (MO, P, TAN); 8 road-km along track W of Anjozorobe, 3.4 km past school near Antsahabe, Mt. Hafatrapeo, disturbed remnant forest, 1270 m, *Zarucchi et al. 7371, 7546* (MO, P, TAN). **Fianarantsoa:** Col d'Itremo, 2 km of Vodiharana, 1600 m, *Baum 29* (MO); Col de tapia, patches of the western slope forests, *Boiteau 332* (P); Col des Tapias, route d'Ambositra, *Boiteau 332 B* (P); between Antsirabe and Ambositra, PK 202, 1400 m, *Bosser 9958* (P, TAN), *Service forestier 231P* (P); PK 12 road Ivato to Ambatofinandrahana, *Bosser 9959* (P, TAN); Mont Ibity (W slope), SW of Antsirabe, 1900 m, *Cremers 2036* (MO, TAN); Ambositra district, Andina Ihadilalana county, Ambatonanahary montane, 1400–1800 m, *Cours 5737* (P); vicinity of Ambatofinandrahana, 1600–1800 m, *Decary 13208* (P); Faliarivo Ambositra, western forest, *Decary 14026* (P); Ambositra in the tapia woodland, *Decary 17250* (P); Ambatofinandrahana, tapia woodland forest, *Decary 17416* (P); between Antsirabe and Ambositra, PK 202, 1400 m, *Dorr 3840* (MO); Itremo, 1800 m, *Guillaumet 4257* (P, TAN); vicinity of Ambositra, rest of western slope woodland in Faliarivo, 1600 m, *Humbert 14485* (P); montanes W of Itremo, 1500–1700 m, *Humbert 28271, 30022* (P); Itremo, Massif d'Itremo, W of Ambositra, dry rocky slopes with scattered trees, 1500 m, *McPherson et al. 16464* (MO); Itremo, *Morat 899* (P, TAN); Ingaro forest, western slope formation, *Morat 3172* (TAN), *3323* (MO, P, TAN); district Ambositra, near Anjoma, tapia woodland forest, *Peltier 2191* (P); Fiadanana, Ilaka centre, *Peltier 2163* (P); tapia woodland forest, 1600 m, *Perrier de la Bâthie 9339* (P); western slope formation, S of Antsirabe, 1500 m, *Perrier de la Bâthie 13095* (P); Mont Ibity, 2000 m, *Perrier de la Bâthie 13575* (P); Andringitra chain, 1500 m, *Perrier de la Bâthie 13915* (P); tapia woodland, S of Ibity, 1200 m, *Perrier de la Bâthie* (P, TAN); half way Antsirabe–Ambositra, RN 7, PK 45, Col de tapia, *Randrianasolo 226* (K, MO, P, TAN); road to Ambatofinandrahana, 12 km from Ivato, *Randrianasolo 231* (K, MO, P, TAN); road to Morondava, 8.7 km SW of Ambatofinandrahana, *Randrianasolo 233* (K, MO, P, TAN); Itremo chain, 43 km from Ambatofinandrahana, along the road to Morondava, *Randrianasolo 236* (K, MO, P, TAN); Ambatofinandrahana–Mandrosonoro, Pk 19.3, *Randrianasolo 238* (K, MO, P, TAN); between Antsirabe and Ambositra, Pk 202, 1400 m, *SF 231* (P); Ankaramena Ambalavao, *SF 1918* (P); Antanimena forest, *SF 4724* (P); Amboandrozana forest, Ambalavao Ankaramena, *SF 10528* (P); rest of forest of western slope, forest of Faliarivo, SW of Ambositra, *SF 11544* (P); Ankijoma-Ambohimahazo-Ambositra *SF 13471, 14767* (P); Centre, granitic massif of Ifandana, between Ankaramena and Ihosy, 1300–1400 m, *SF 23507* (P). **Toamasina:** Antatabe, 20 km E of Mandraka on the road to Moramanga, 900 m, disturbed premontane forest, *Miller et al. 6275* (MO, P, TAN); Analamazaotra, forest N of Andasibe, 860 m, along the railroad tracks, *Miller et al. 8745* (MO, P, TAN); Ambatovy, 11 km NE of Moramanga, *Morat 3223* (MO, P).

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RELATIONSHIPS AND MORPHOLOGICAL CHARACTER CHANGE AMONG GENERA OF CELASTRACEAE SENSU LATO (INCLUDING HIPPOCRATEACEAE)[1]

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ABSTRACT

A cladistic analysis of Celastraceae sensu lato (including Hippocrateaceae) was conducted using 69 informative morphological characters representing variation in gross morphology, seed anatomy, seedling development, leaf anatomy, wood anatomy, pollen morphology, and karyotype. The 82 taxa sampled included 31 genera of Celastraceae sensu stricto, 22 genera of Hippocrateaceae, 7 genera that have been associated with Celastraceae (*Brexia, Canotia, Forsellesia, Goupia, Lophopyxis, Plagiopteron,* and *Siphonodon*), and outgroups from Corynocarpaceae, Crossosomataceae, Euphorbiaceae, Geissolomataceae, Huaceae, Saxifragaceae, and Stackhousiaceae. Character state changes mapped onto the phylogenetic hypotheses were generated to infer patterns of evolution of characters, including the aril in Celastraceae s.l. Based on this analysis, the inclusion of *Bhesa* and *Goupia* within Celastraceae s.l. is ambiguous, and *Siphonodon* should be excluded from Celastraceae s.l. *Forsellesia* (= *Glossopetalon*) is supported as closely related to Crossosomataceae. *Lophopyxis* is supported as a member of Euphorbiaceae. *Canotia* is resolved as the sister group of *Acanthothamnus,* included within Celastraceae sensu stricto. *Brexia* is resolved as the sister group of Celastraceae s.l. Theodor Loesener's subfamilies and tribes of Celastraceae s. str. are generally not supported. The Hippocrateaceae are resolved as having a single origin, and as nested within a paraphyletic Celastraceae s. str. with *Brassiantha, Dicarpellum,* and *Sarawakodendron* as "transitional" genera between the groups. *Campylostemon* appears as a derived group within Hippocrateaceae, not as a "transitional" genus. Nicolas Hallé's subfamilies of Hippocrateaceae are supported, but his tribes generally are not, with Campylostemoneae and Helictonemateae nested within Hippocrateeae. *Plagiopteron* is resolved as nested within tribe Hipocrateeae.

The Celastraceae sensu lato (including Hippocrateaceae) are a primarily pantropical family of woody lianas, shrubs, and trees with several subtropical and fewer temperate members. Members of the family exhibit substantial variation in stamen, fruit, and seed characters, which have been used to subdivide the family taxonomically. Economically important taxa within Celastraceae include: "khat," *Catha edulis,* used socially as a stimulant in northeastern Africa, the Arabian Peninsula, and Madagascar (Krikorian, 1985); *Euonymus, Celastrus,* and *Paxistima,* which are widely cultivated as ornamentals; *Kokoona zeylandica,* as a source of oil; fruits of *Salacia* from which the pulp is eaten; and various species of *Euonymus,* used for latex, medicines, and dyes (Hou, 1962; Heywood, 1993). This large family (850 to 1300 species) has not been the subject of a comprehensive taxonomic treatment since Loesener's monograph (1942a, 1942b), and a phylogenetic analysis of intergeneric relationships in the family is not available.

The Celastraceae s.l. have been estimated to include about 55 genera and 850 species (Hallé, 1986; Thorne, 1992; Heywood, 1993), 60–70 genera (Robson et al., 1994), 78 genera and 1150 species (Scholz, 1964), 85 genera (Brummitt, 1992), 85–90 genera and 860 species (Takhtajan, 1997), 90 genera and over 1000 species (Hou, 1962), 1100 species (Cronquist, 1981), or up to 94 genera and 1300 species (Mabberley, 1993). Estimates vary in part because relatively little taxonomic work has been done on the family, and because of dis-

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agreements regarding generic delimitations. Also, questions concerning the recognition of Celastraceae and Hippocrateaceae as distinct families have existed since the initial description of Celastraceae (as the order "Celastrinae") by Robert Brown in 1814. Brown (1814: 555) stated that Celastrinae "in many respects so nearly approaches to the Hippocraticeae of Jussieu, that it may be doubted whether they ought not to be united." Diagnostic characters that have been used to distinguish Hippocrateaceae from Celastraceae are: stamens 3 (rarely 2 or 5) versus 4 or 5 (rarely 10), filaments inserted inside the disk versus at or below the margin of the disk, filaments connate at the base and recurved versus distinct and often incurved, and seeds not albuminous versus albuminous (Bentham & Hooker, 1862; Cronquist, 1981).

Since the original family descriptions (de Jussieu, 1811; Brown, 1814), Hippocrateaceae and Celastraceae have been recognized either as two distinct families (de Candolle, 1825; Lindley, 1853; Miers, 1872; Loesener, 1892a, 1892b, 1942a, 1942b; Smith, 1940; Perrier de la Bâthie, 1946; Hallé, 1962; Hutchinson, 1969; Cronquist, 1981) or as a single family (Bentham & Hooker, 1862 [as separate tribes of the order Celastrineae]; Baillon, 1880 [as 2 of 7 separate series of Celastraceae]; Hou, 1962, 1964; Robson, 1965; Hallé, 1978; Takhtajan, 1980, 1997; Dahlgren, 1983; Thorne, 1992; Robson et al., 1994). For the unified family, Celastraceae have been conserved over Hippocrateaceae (Bullock, 1958). Excellent taxonomic histories of Hippocrateaceae are provided by Miers (1872) and Smith (1940).

Miers (1872) cited 11 characters differentiating Hippocrateaceae from Celastraceae s. str. However, Hou (1964: 389) noted, "Many new genera and species have been described since 1873 [sic] which have obliterated many of Miers's arguments, and recent specialists agree that, if any, only few characters do hold." Lindley (1853) and Loesener (1942b) recognized Hippocrateaceae as distinct from Celastraceae s. str. based on one character—stamen number 4 or 5 in Celastraceae s. str., versus 3 (rarely 2) in Hippocrateaceae. This was the sole basis for Loesener's (1942a) transfer of two genera (*Campylostemon* and *Cheiloclinium*), which earlier workers included within Hippocrateaceae (Miers, 1872; Baillon, 1880; Loesener, 1892b; Smith, 1940), to Celastraceae s. str. Recently, on the basis of the very different fruits and seeds of *Hippocratea* s.l. relative to those of *Salacia* s.l., it has been suggested that taxa assigned to Hippocrateaceae have been derived from different parts of Celastraceae s. str. such that the Hippocrateaceae are a polyphyletic group (Robson, 1965; Robson et al., 1994).

Hallé's taxonomic treatments of Hippocrateaceae. Hallé (1962) recognized Hippocrateaceae as a family, separate from Celastraceae. He described two subfamilies (Hippocrateoideae, Salacioideae) and three tribes (Campylostemonae [sic] and Hippocrateae [sic] of subfamily Hippocrateoideae; Salaciae [sic] of subfamily Salacioideae). In later publications, Hallé (1978, 1981, 1983, 1984) recognized Hippocrateaceae as a tribe ("Hippocrateae") of Celastraceae. In two later floras, Hallé (1986, 1990) cited Celastraceae as composed of two subfamilies—Celastroideae and Hippocrateoideae. Subfamily Hippocrateoideae was composed of four tribes—Salacieae (as "Salaciae" in 1986: 12), Helictonemeae [sic] ("Helictonemae" in 1986: 12), Hippocrateae, and Campylostemoneae. Following the *Code* (Greuter et al., 1994), Hallé's tribe "Helictonemeae" is properly Helictonemateae and Hallé's tribe "Hippocrateae" is properly Hippocrateeae (Richard Korf, pers. comm. 1998; note: we do not validly propose these names here).

In the classification of Hallé (1986, 1990), in which subfamily Hippocrateoideae is divided into four tribes, the hierarchical information of the classification of Hallé (1962), in which Hippocrateaceae are divided into subfamilies and tribes, is lost. It is unclear if this was intentional. In Hallé's most recent publication (Robson et al., 1994), in which he was a co-author, no subfamilial classification was provided.

Cronquist's five "aberrant genera." Apart from the question of including Hippocrateaceae in Celastraceae, there is an additional set of problems in delimiting Celastraceae. Cronquist (1981: 714) stated, "[Celastraceae] is rather diversified and loosely knit," and he segregated "five of the more aberrant genera. . ." as separate families. These five genera are *Canotia, Chingithamnus, Goupia, Lophopyxis,* and *Siphonodon. Chingithamnus* has been recognized by Handel-Mazzetti (1933) and Merrill and Freeman (1940) as a member of *Microtropis* (Celastraceae). We know of no additional work on *Chingithamnus* other than the original description by Handel-Mazzetti (1932) and the later treatment of the species as a member of *Microtropis* by Handel-Mazzetti (1933) and Merrill and Freeman (1940). The remaining four genera are more problematic. Each genus has one or more character states that are unique within Celastraceae s.l. if considered a member of the family.

Canotia has been variously referred to Rutaceae (Gray 1877), Koeberliniaceae (Barnhart, 1910), and

Celastraceae (Hutchinson, 1969), as an anomalous genus (Loesener 1942a), or as closely related to *Acanthothamnus* (Johnston, 1975). Inclusion of *Canotia* within Celastraceae (and its close relation to *Acanthothamnus*) was later supported by Tobe and Raven (1993) on the basis of embryology. The unique character state of *Canotia* is its septicidally dehiscent capsules.

Goupia has been recognized as unusual relative to other members of Celastraceae by the vascular structure of its petiole (Metcalfe & Chalk, 1950), gross morphology (T. A. Sprague, in Metcalfe & Chalk, 1950), and wood anatomy (Loesener, 1942a), but not on the basis of leaf anatomy (Den Hartog née Van Ter Tholen & Baas, 1978). Hutchinson (1969: 357) discussed the taxonomic history of *Goupia*, which has also been assigned to Araliaceae and Rhamnaceae, and concluded, "If only on account of these diverse views it seems better to regard it as a separate family, following Miers (Contrib. Bot. 2, 134, t. 74 (1860–69))." *Goupia* has been suggested to be more closely related to Euphorbiaceae than to Celastraceae based on a chloroplast *rbc*L 5′ flanking sequence gene tree (Savolainen et al., 1997). Unique character states of *Goupia* are its umbellate inflorescences and bilobed extended anther connectives with brush-hairy tips.

Lophopyxis, when described by Hooker (1887–1888; 1888), was tentatively assigned to Euphorbiaceae. Pfeiffer (1951) recognized the genus as the only member of its own family, Lophopyxidaceae. This treatment was followed by Willis (1966), Dahlgren (1983), Thorne (1992), and Takhtajan (1997). Scholz (1964) included *Lophopyxis* within Celastraceae subfamily Tripterygioideae. The unique character states of *Lophopyxis* relative to Celastraceae s.l. are its tendrils, tomentose ovaries, and obturators.

Siphonodon has been recognized as unusual relative to other genera in Celastraceae based on structure of the gynoecium (Croizat, 1947), wood anatomy (Metcalfe & Chalk, 1950), and pollen morphology (Erdtman, 1952). *Siphonodon* has been retained in close relationship to Celastraceae s. str. (Loesener, 1892a, 1942a; Croizat, 1947), Hippocrateaceae (Bentham & Hooker, 1862; Hutchinson, 1969), or Celastraceae s.l. (Hou, 1963). This recognition of *Siphonodon* as unusual, but closely related to other members of Celastraceae s.l., was supported by an *rbc*L 5′ flanking sequence gene tree (Savolainen et al., 1997) in which *Siphonodon* was resolved as sister group of the five Celastraceae s.l. (including *Brexia*) sampled. A thorough summary of the varied taxonomic history of *Siphonodon* is given by Hou (1963). Unique character states of *Siphonodon* are the presence of staminodes and stamens in a single flower (see Berkeley, 1953, in which the disk of Celastraceae is suggested to be composed of suppressed stamens), an apical hollow in the center of the ovary, and many irregularly superposed locules in the ovary.

Relationships of Celastraceae. Cronquist (1981) included Celastraceae s. str. and Hippocrateaceae as 2 of 11 families in the order Celastrales. The other families included were Aextoxicaceae, Aquifoliaceae, Cardiopteridaceae, Corynocarpaceae, Dichapetalaceae, Geissolomataceae, Icacinaceae, Salvadoraceae, and Stackhousiaceae. Cronquist recognized the Dichapetalaceae as anomalous and the inclusion of Aextoxicaceae, Cardiopteridaceae, Corynocarpaceae, and Geissolomataceae as debatable.

Dahlgren (1983) recognized the order Celastrales as including Celastraceae s.l., Lophopyxidaceae, Stackhousiaceae, Cardiopteridaceae, and Corynocarpaceae (the last two as "uncertain"). Thorne (1992) cited the order Celastrales as including all the families Dahlgren did, except Cardiopteridaceae and Corynocarpaceae. Takhtajan (1980) described the order Celastrales as including all the families included by Cronquist, Dahlgren, and Thorne (except Aextoxicaceae and Dichapetalaceae), plus Medusandraceae, Paracryphiaceae, and Sphenostemonaceae. Takhtajan (1997) narrowed his circumscription of Celastrales to include only Celastraceae s.l., Goupiaceae, Lophopyxidaceae, and Stackhousiaceae. *Siphonodon* has been treated as a separate family (Takhtajan, 1980; Cronquist, 1981) or included within Celastraceae (Dahlgren, 1983; Thorne, 1992; Takhtajan, 1997). Likewise, *Goupia* has been treated as a separate family (Takhtajan, 1980, 1997; Cronquist, 1981; Thorne, 1992) or included within Celastraceae (Dahlgren, 1983).

Recent evidence has suggested that the Celastrales, as defined by Cronquist, Dahlgren, Takhtajan, and Thorne, are an unnatural group. Aquifoliaceae and Icacinaceae have been recognized as not closely related to Celastraceae s.l. by Savolainen et al. (1994, 1997) and Spichiger et al. (1993), using cpDNA sequence from the 5′ flanking region of *rbc*L. Likewise, the gene tree presented by Savolainen et al. (1997) suggested that Aextoxicaceae, Corynocarpaceae, Dichapetalaceae, Salvadoraceae, and Stackhousiaceae are all more closely related to families not included in Cronquist's Celastrales than to Celastraceae. In the gene tree, only Geissolomataceae were resolved as closely related to Celastraceae s.l. Salvadoraceae have been shown to be included within the order Capparales based on morphology (Rodman, 1991) and *rbc*L sequence data (Rodman et al., 1996).

In the *rbc*L gene trees presented by Chase et al. (1993) and Morgan and Soltis (1993), *Brexia* (Brexiaceae) was resolved as the sister group of *Euonymus* (Celastraceae). The sister group of this clade was *Lepuropetalon* and *Parnassia* (Saxifragaceae). The same resolution of these taxa was found in the 18S nrDNA gene tree presented by Soltis et al. (1997). In the combined analysis of *rbc*L and many non-molecular characters presented by Nandi et al. (1998), Huaceae were resolved as the sister group of Plagiopteraceae plus "Celastrales s. str." (= Goupiaceae, Celastraceae, Stackhousiaceae). Four taxa within Celastraceae s.l. (one species each of *Hippocratea* and *Salacia*, two species of *Euonymus*) were sampled by Savolainen et al. (1994) and Spichiger et al. (1993). In the 5′ flanking region of the *rbc*L gene tree, *Salacia* was resolved as the sister group of *Euonymus* and *Hippocratea*, and Euphorbiaceae were resolved as the sister group of Celastraceae s.l. Savolainen et al. (1997) sampled the Celastrales more extensively. In their gene tree, the two species of *Euonymus* were resolved as the sister group of the clade that consists of *Hippocratea* and *Salacia*. *Brexia* was resolved as most closely related to this clade, followed by *Siphonodon* (Celastraceae/Siphonodontaceae), *Parnassia*, and *Geissoloma* (Geissolomataceae) as more distantly related.

The purpose of this study is to investigate patterns of structural character change and phylogenetic relationships within Celastraceae s.l. Based on these patterns, we attempt to: determine relationships among genera placed within Celastraceae s.l., determine if Cronquist's "aberrant genera" should be recognized as separate families or included within Celastraceae s.l., determine if Loesener's (1942a) subfamilies and tribes of Celastraceae s. str. are natural groups, and determine if Hallé's (1962, 1986, 1990) subfamilies and tribes are natural groups.

MATERIALS AND METHODS

Taxon sampling. The taxa included in the analysis are listed in Appendix 1. Members of Celastraceae s. str. are approximately arranged according to Loesener (1942a); members of Hippocrateaceae are arranged by the classification of Hallé (1986, 1990). Two modifications to Loesener's nomenclature are that tribe Eucassineae is recognized as tribe Cassineae, and tribe Eucelastreae is recognized as tribe Celastreae. The reason for this is that names of tribes are based on legitimate generic names (Greuter et al., 1994), and there are no genera "*Eucassine*" or "*Eucelastrus*" (Loesener, 1942a; Royal Botanic Gardens, Kew, 1997). Therefore, Eucassineae and Eucelastreae are not valid tribes (Richard Korf, pers. comm. 1998).

Thirty-five (of about 65 currently recognized) genera of Celastraceae s. str. were sampled in addition to four genera that have been associated with Celastraceae (*Canotia*, *Goupia*, *Lophopyxis*, and *Siphonodon*), but recognized by Cronquist (1981) as separate families. *Chingithamnus*, the fifth genus that Cronquist (1981) recognized as a separate family, is not included in the analysis because Handel-Mazzetti (1933) and Merrill and Freeman (1940) have already reduced it to synonymy within *Microtropis* (Celastraceae). Twenty (of about 26 currently recognized) genera of Hippocrateaceae were sampled. *Brexia* was included in the analysis based on morphological (Perrier de la Bâthie, 1933), embryological (Kamelina, 1988; Tobe & Raven, 1993), and molecular (Chase et al., 1993; Morgan & Soltis, 1993; Savolainen et al., 1997; Soltis et al., 1997) studies that suggest it is closely related to Celastraceae. *Plagiopteron* was included in the analysis based on anatomical (Baas et al., 1979), embryological (Tang, 1994), and molecular (Nandi et al., 1998) studies that suggest it is closely related to Celastraceae.

Genera were selected for inclusion in the analysis based on four criteria. We wanted to include at least two representatives of every subfamily and tribe proposed by Loesener (1942a) and Hallé (1962, 1986, 1990) that include more than one genus, as well as those genera with unusual character states relative to other members of Celastraceae s.l. For character coding, we chose genera that are well described in the literature and/or represented by herbarium specimens at the herbaria visited (see below under "character coding"). Finally, we excluded "wildcard taxa" (terminals resolved in many different locations on most-parsimonious cladograms due to their many missing values; Nixon & Wheeler, 1991) in preliminary analyses. Missing values in these terminals were usually due to poorly detailed published descriptions, coupled with paucity of herbarium specimens available (e.g., many Australian endemics). Also omitted were genera that lack pertinent structures and which were therefore coded as inapplicable for those features (e.g., *Psammomoya*, in which the leaves are reduced to cataphylls).

The decision to use genera instead of representative species in the analysis was based on two factors. First, some publications do not list the individual species examined, only the genera (e.g., Metcalfe & Chalk, 1950). Other publications list the species examined but describe only the genus, even when the genus is polymorphic for some of the characters described (e.g., Solereder, 1908). Furthermore, if only one species of a genus was selected, and a different species of that genus had been described for a given character, we would not have been able to include that information in our data matrix. This problem is magnified with each successive character scored from the literature as, for example, Erdtman (1952) in describing pollen morphology for a given genus probably did not look at the same species as Mennega (1997) in describing wood anatomy, or as Den Hartog née Van Ter Tholen and Baas (1978) in describing leaf anatomy. Second, many genera were represented by only a few sheets in the herbaria visited. In such cases, some species were only represented by flowering specimens, while other species were only represented by fruiting specimens. If only a single species was used, there would be that much more missing data for the flower or fruit characters, respectively. In our coding, flower characters may have been taken from one species and fruit characters taken from another. These compromises were made to avoid excessive missing values in the data matrix that would result in complete lack of resolution.

The problems with this approach to coding "composite terminals" have been discussed by Nixon and Davis (1991). These problems are: underestimating the cladogram length and overestimating the consistency indices, the most-parsimonious cladogram(s) using composite terminals may differ from the most-parsimonious cladogram(s) when the composite terminals are divided into all naturally occurring combinations of character states, and that the composite terminals are assumed to be monophyletic when they may not be. These factors should be taken into account in interpreting the cladograms presented.

Genera were initially planned to be the terminals in this analysis, but selected genera that were extremely variable in the characters scored were divided into subgenera (when available) or individual species (when subgenera were not available) to partition the variation into separate terminals. The division of *Celastrus* into subgenera follows Hou (1955). The division of *Cheiloclinium* into species groups follows Smith (1940). Note that the terminal "*Cheiloclinium* except species-group *Anomala*" represents members of Smith's other three species groups—*Cognata, Hippocrateoides,* and *Serrata.* The division of *Salacia* into subgenera follows Loesener (1942b). *Cassine* is recognized as distinct from *Elaeodendron* following Archer and van Wyk (1997). The recognition of *Gymnosporia* as distinct from *Maytenus* follows Jordaan and van Wyk (in press). *Quetzalia* is recognized as distinct from *Microtropis* based on Lundell (1970). *Tricerma* is recognized as distinct from *Maytenus* following Lundell (1971). *Catha* is restricted to *Catha edulis* following Robson (1965) and the assertion by van Wyk and Prins (1987) that the other two species that have been assigned to *Catha* are not closely related to *Catha edulis.* When individual species were used as terminals (as in *Cassine, Elaeodendron, Euonymus,* and *Maytenus* s.l. [including *Gymnosporia* and *Tricerma*]), at least two representative species of each genus were included to represent some breadth of the character state variation and to test the monophyly of that genus. Individual species were selected based on how divergent they are relative to one another in terms of character states scored in this analysis (we tried to maximize the variation to test monophyly of the genus), and based on our ability to code character states for them (i.e., herbarium specimensand/or thorough literature descriptions available).

Outgroup selection. Outgroup terminals were selected from seven families: Corynocarpaceae, Crossosomataceae, Euphorbiaceae, Geissolomataceae, Huaceae, Saxifragaceae, and Stackhousiaceae. Morphological (Takhtajan, 1980, 1997; Cronquist, 1981; Dahlgren, 1983; Thorne, 1992) and molecular (Chase et al., 1993; Morgan & Soltis, 1993; Savolainen et al., 1994, 1997; Soltis et al., 1997; Nandi et al., 1998) studies have variously suggested that members of these outgroup families are closely related to Celastraceae s.l. Crossosomataceae were included because *Forsellesia* (= *Glossopetalon* A. Gray) has been transferred from Celastraceae to Crossosomataceae (Thorne & Scogin, 1978). Based on this transfer, *Crossosoma* and *Forsellesia* are expected to be resolved as sister groups. The specific genera of the seven outgroup families were chosen based on literature and/or herbarium specimens available describing character states in these genera, possession of structures that could be scored for the characters included in the analysis, and genera that were not too variable for the characters included in the analysis. We did not include *Euphorbia* (Euphorbiaceae) because of extreme reduction in its flowers. The cladogram was rooted with genera from Euphorbiaceae.

Character coding. Seventy-nine characters representing gross morphology, leaf and stem anatomy, pollen morphology, and karyotype characters were scored. Of these 79 characters, 10 are uninformative. These 10 uninformative characters were in-

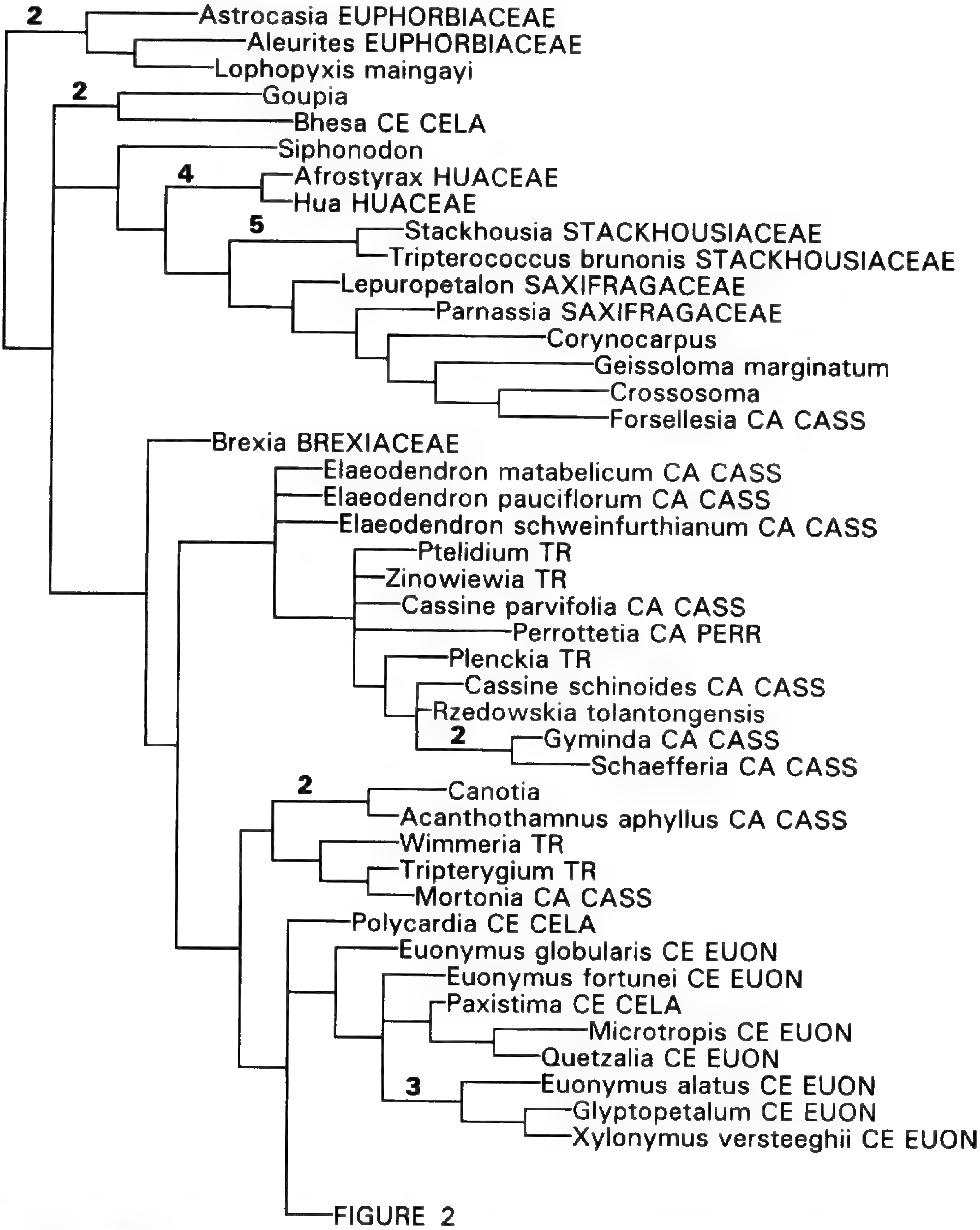


Figure 1. "Basal" portion of strict consensus of 115 most-parsimonious cladograms (309 steps, CI = 0.36, RI = 0.72, excluding uninformative characters; 321 steps including uninformative characters) for 82 taxa of Celastraceae and related families, obtained by equal-weighted analysis of 69 informative characters (Appendices 1, 2). Bremer-support values (Bremer, 1988) greater than 1 are plotted above branches.

cluded in this paper (but not in cladogram searches or cladogram statistics) for their information content in delimiting genera. The "unique" character states are not autapomorphies (unless the genus is monotypic); they are synapomorphies for individual genera. Characters were initially taken from original taxon descriptions, monographs of individual genera and entire families, e.g., Loesener (1942a,

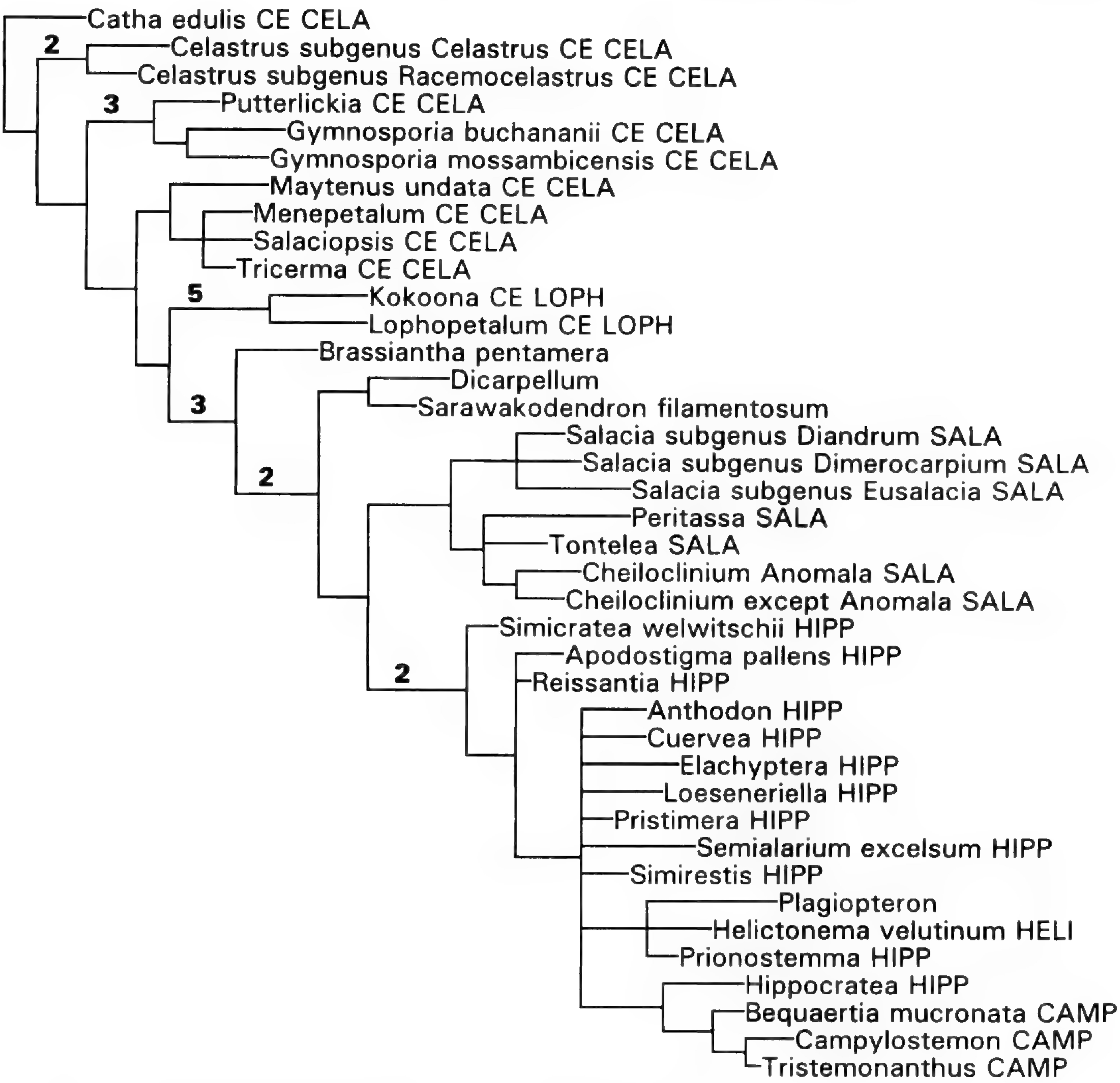


Figure 2. "Distal" portion of strict consensus of 115 most-parsimonious cladograms (309 steps, CI = 0.36, RI = 0.72, excluding uninformative characters; 321 steps including uninformative characters) for 82 taxa of Celastraceae and related families, obtained by equal-weighted analysis of 69 informative characters (Appendices 1, 2). Bremer-support values (Bremer, 1988) greater than 1 are plotted above branches.

1942b), floras, surveys for specific characters, e.g., "Les pollens des Celastrales" by Lobreau-Callen (1977), large-scale taxonomic treatments, e.g., Cronquist (1981), and large-scale anatomical treatments, e.g., Metcalfe and Chalk (1950). The 151 initial potential characters were examined for feasibility of scoring, errors in the literature, independence of characters, distinctness of character states, and constancy of character states within taxa. Material permitting, characters of gross morphology were then examined on herbarium specimens at BH, MO, NY, P, and US. The 79 final characters are described in Appendix 2, which includes comments on distribution of character states, literature sources used, how character states were delimited, and how questionable character states were scored. The characters that were rejected for inclusion in the cladistic analysis, and the reason(s) for rejection are listed in Appendix 3. The data matrix is in Appendix 4. Literature sources used to code gross-morphological characters are listed in Appendix 1. Herbarium specimens used to code gross-morphological characters are listed in Appendix 5.

If observation of properly annotated herbarium specimens contradicted literature entries, the observations were used instead of the literature entries (e.g., *Elaeodendron* for character 39). However, if the literature described a more general condition than observed in the specimens (e.g., observed only cymose inflorescences, literature describes the genus as having cymose or paniculate inflorescences), the literature entry was used.

For anatomical characters taken from Solereder (1908), Record (1943), Metcalfe and Chalk (1950), and Den Hartog née Van Ter Tholen and Baas (1978) where multiple taxa are listed as having been studied, but an unusual character state was described for only some of the taxa, the other taxa that were cited as being studied, but which were not described for the unusual character state, were coded as having the "normal" character state. For example, Record (1943) described Celastraceae as having generally simple perforation plates, but cited 2 of the 13 genera he examined as having scalariform perforation plates. Based on this information, the other 11 genera he examined were coded as having simple perforation plates.

Where an older paper described a character state for a given species, the species was referenced in *Index Kewensis* ver. 2.0 (Royal Botanic Gardens, Kew, 1997) to determine if the species has been assigned to a different genus since the publication. An example is Solereder (1908) in which *Salacia calypso* was described for character 70. However, the species has been transferred to *Tontelea*. Therefore, *Tontelea* was coded for this character based on the description, not *Salacia*.

If a character state was described for only one species from a genus that is not monotypic, the entire genus was coded as having that character state. Furthermore, if a genus was divided into subgenera (*Celastrus, Salacia*), species groups (*Cheiloclinium*), or individual species (*Cassine, Elaeodendron, Euonymus, Gymnosporia, Maytenus*), each of these terminals was coded identically for that character state. An example is *Elaeodendron*, which is represented in this study by three species. *Elaeodendron roxburghii* was described in *Index to Plant Chromosome Numbers 1975–1978* (Goldblatt, 1981: 182) as having 17 chromosomes in the gametophyte stage. Based on this, which is the only report of chromosome numbers we know of in *Elaeodendron*, all three species of *Elaeodendron* that were included in the analysis were coded as having a base chromosome number of 17.

Data analysis. The character data matrix (Appendix 4) was created using *Dada* ver. 1.7 (Nixon, 1998b). Cladistic analysis was performed using *Nona* ver. 1.6 (Goloboff, 1993). The analysis was performed through 10,000 searches, each consisting of cladogram construction using a random-taxon entry sequence followed by tree-bisection-reconnection branch swapping with up to 50 most-parsimonious cladograms retained (*hold/50 mult*10000*). The most-parsimonious cladograms retained were then swapped to completion using tree-bisection reconnection (*max**). The strict-consensus cladogram (Schuh & Polhemus, 1980; Sokal & Rohlf, 1981) was calculated by *Nona* (*nelsen*). The most-parsimonious cladograms and the strict-consensus cladogram were examined in and printed from *Clados* version 1.7 (Nixon, 1998a). Bremer-support values (Bremer, 1988) were estimated using *Nona* with 10,000 cladograms retained up to five steps longer than the most-parsimonious cladograms (*hold 10000 bs 5*).

RESULTS

Seventy-nine characters were coded for 82 taxa. Of 6478 cells in the data matrix (Appendix 4), 12.1% of the cells were scored missing (unobserved), 13.2% of the cells were scored as inapplicable (the character is not present in a given taxon), 1.6% of the cells were scored as polymorphic (complete or subset), and 73.1% of the cells were scored with single character states.

Cladistic analysis resulted in 115 most-parsimonious cladograms of length 321 (309 excluding uninformative characters), ensemble consistency index (CI; Kluge & Farris, 1969) of 0.36 (excluding uninformative characters), and ensemble retention index (RI; Farris, 1989) of 0.72. One of the 115 most-parsimonious cladograms was arbitrarily selected and is presented in Figures 3–5 with character state changes mapped on it. Fifty-nine clades are resolved in the strict consensus cladogram (Figs. 1, 2). *Lophopyxis* and the two genera of Euphorbiaceae form a clade. *Bhesa* and *Goupia* are sister groups. *Siphonodon* is the sister group of the clade that consists of the outgroup taxa (except Euphorbiaceae) and *Forsellesia*. Huaceae (*Afrostyrax* and *Hua*) and Stackhousiaceae (*Stackhousia* and *Tripterococcus brunonis*) are monophyletic groups. *Forsellesia* is the sister group of *Crossosoma* (Crossosomataceae). *Brexia* is sister to the clade that consists of Celastraceae s. str. (except *Bhesa* and *Forsellesia*) and Hippocrateaceae.

Subfamily Celastroideae and the Hippocrateaceae are nested within a paraphyletic (Hennig, 1966; Farris, 1974) assemblage of subfamilies Cassinoideae and Tripterygioideae. Genera assigned to subfamily Tripterygioideae are nested among members of subfamily Cassinoideae. *Perrottetia* (subfamily Cassinoideae tribe Perrottetieae) is nested among members of subfamily Cassinoideae tribe Cassineae. Subfamily Celastroideae is a paraphyletic group, in which the Hippocrateaceae are nested. Subfamily Celastroideae tribe Euonymeae is a

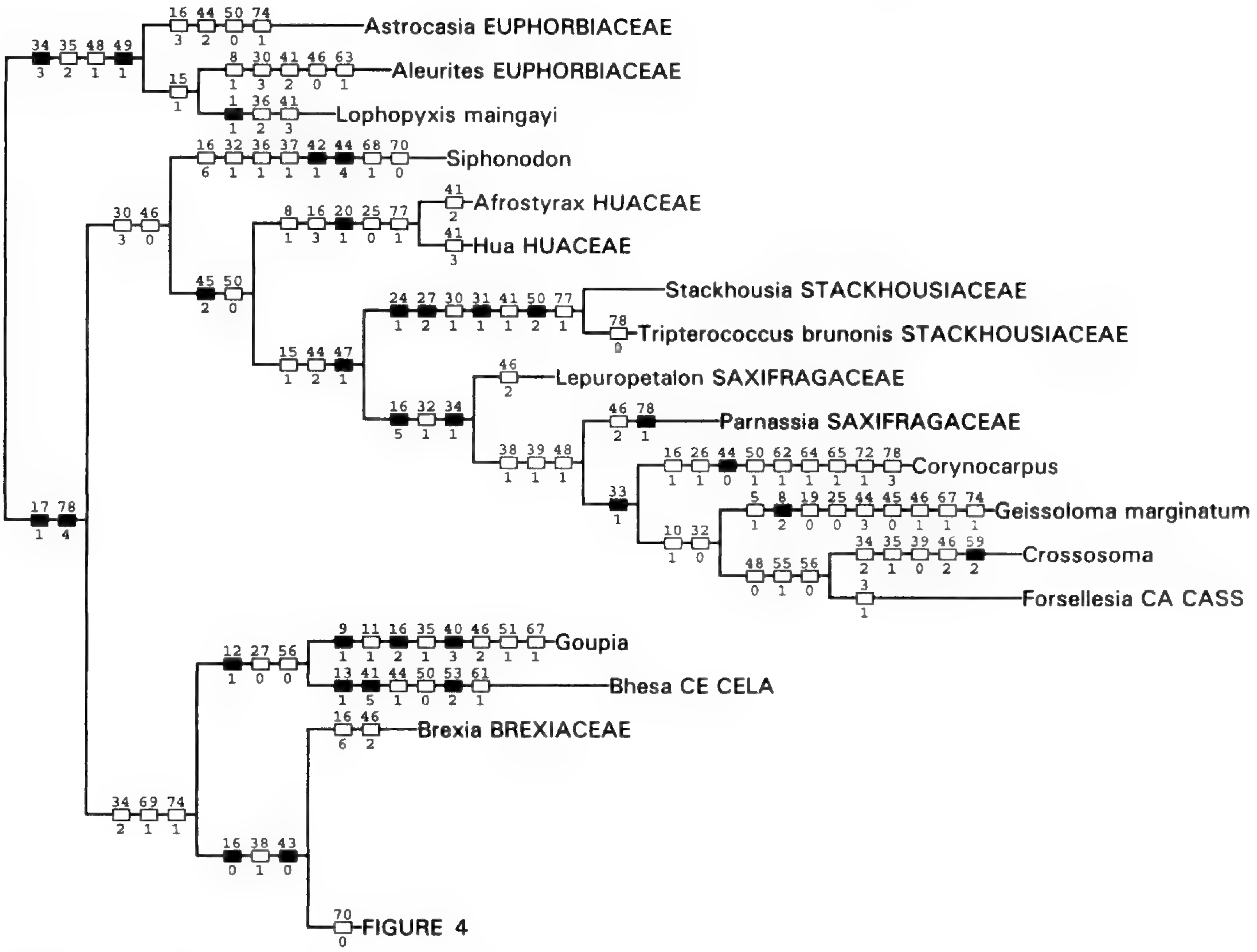


Figure 3. "Basal" portion of one of 115 most-parsimonious cladograms (309 steps, CI = 0.36, RI = 0.72, excluding uninformative characters; 321 steps including uninformative characters as shown) for 82 taxa of Celastraceae and related families, obtained by equal-weighted analysis of 69 informative (79 including uninformative) characters (Appendices 1, 2). Character-state changes, as mapped using slow (DELTRAN) optimization, are marked as bars on internodes, with the number above each bar indicating the character number, and the number below each bar indicating the change to the apomorphic character state (Appendix 2). Solid bars indicate unique origins of character states (regardless of whether or not a reversal occurs) and unshaded bars indicate parallel origins and reversals of character states.

paraphyletic group that includes *Paxistima* of subfamily Celastroideae tribe Celastreae.

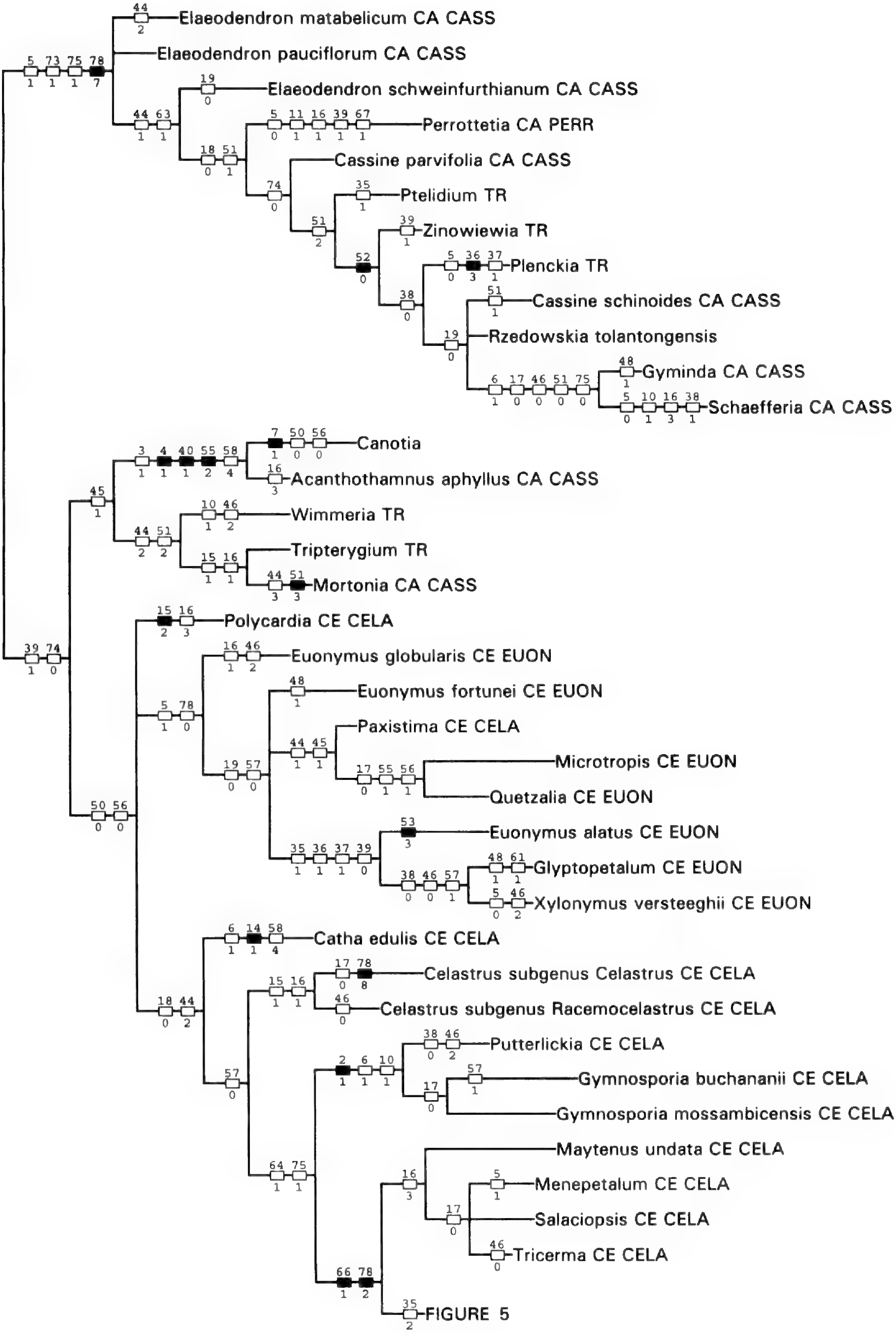
Tribe Lophopetaleae is a monophyletic group (Hennig, 1966). The Hippocrateaceae are a monophyletic group (that includes *Plagiopteron*) sister to the clade that consists of *Dicarpellum* and *Sarawakodendron*. Tribe Salacieae is a monophyletic group sister to the clade that consists of tribe Campylostemoneae, tribe Helictonemateae, and tribe Hippocrateeae. Tribe Hippocrateeae is a paraphyletic group with tribe Helictonemateae, tribe Campylostemoneae, and *Plagiopteron* nested within it. Tribe Campylostemoneae is monophyletic.

DISCUSSION

"Basal" groups. *Lophopyxis* is resolved as nested within Euphorbiaceae. Character states grouping *Lophopyxis* with Euphorbiaceae are unisexual flowers, pendulous ovule attachment, and obturators (only present in this clade). This resolution of *Lophopyxis* is consistent with its placement by Hooker (1887–1888; 1888).

Forsellesia is resolved as the sister group of *Crossosoma* (Crossosomataceae) by two synapomorphies: capsule dehiscence by one side laterally splitting and aril presence. This resolution is consistent with the transfer of *Forsellesia* from Celastraceae to Crossosomataceae by Thorne and Scogin (1978). This transfer has also been supported by leaf and wood anatomy (DeBuhr, 1978).

Bhesa and *Goupia* are resolved as sister groups. Synapomorphies of this clade are distinct crossbar tertiary leaf veins (only present in this clade) and a cupular disk. *Bhesa* has been recognized as unusual, relative to other Celastraceae, based on its gross morphology (Pierre, 1893) and wood anatomy (Metcalfe & Chalk, 1950; Xinying et al., 1990). Xinying et al. (1990: 60) stated, "Significantly,


44 2
Elaeodendron matabelicum CA CASS
5 73 75 78 1 1 1 7
Elaeodendron pauciflorum CA CASS
19 0
Elaeodendron schweinfurthianum CA CASS
44 63 1 1
5 11 16 39 67 0 1 1 1 1
Perrottetia CA PERR
18 51 0 1
Cassine parvifolia CA CASS
74 0
35 1
Ptelidium TR
51 2
39 1
Zinowiewia TR
52 0
5 36 37 0 3 1
Plenckia TR
38 0
51 1
Cassine schinoides CA CASS
Rzedowskia tolantongensis
19 0
48 1
Gyminda CA CASS
6 17 46 51 75 1 0 0 0 0
5 10 16 38 0 1 3 1
Schaefferia CA CASS
7 50 56 1 0 0
Canotia
3 4 40 55 58 1 1 1 2 4
16 3
Acanthothamnus aphyllus CA CASS
45 1
10 46 1 2
Wimmeria TR
44 51 2 2
Tripterygium TR
15 16 1 1
44 51 3 3
Mortonia CA CASS
15 16 2 3
Polycardia CE CELA
39 74 1 0
16 46 1 2
Euonymus globularis CE EUON
48 1
Euonymus fortunei CE EUON
5 78 1 0
Paxistima CE CELA
44 45 1 1
19 57 0 0
17 55 56 0 1 1
Microtropis CE EUON
Quetzalia CE EUON
53 3
Euonymus alatus CE EUON
50 56 0 0
35 36 37 39 1 1 1 0
48 61 1 1
Glyptopetalum CE EUON
38 46 57 0 0 1
5 46 0 2
Xylonymus versteeghii CE EUON
6 14 58 1 1 4
Catha edulis CE CELA
17 78 0 8
Celastrus subgenus Celastrus CE CELA
15 16 1 1
18 44 0 2
46 0
Celastrus subgenus Racemocelastrus CE CELA
38 46 0 2
Putterlickia CE CELA
2 6 10 1 1 1
57 0
57 1
Gymnosporia buchananii CE CELA
17 0
Gymnosporia mossambicensis CE CELA
Maytenus undata CE CELA
64 75 1 1
16 3
5 1
Menepetalum CE CELA
17 0
Salaciopsis CE CELA
46 0
Tricerma CE CELA
66 78 1 2
35 2
FIGURE 5

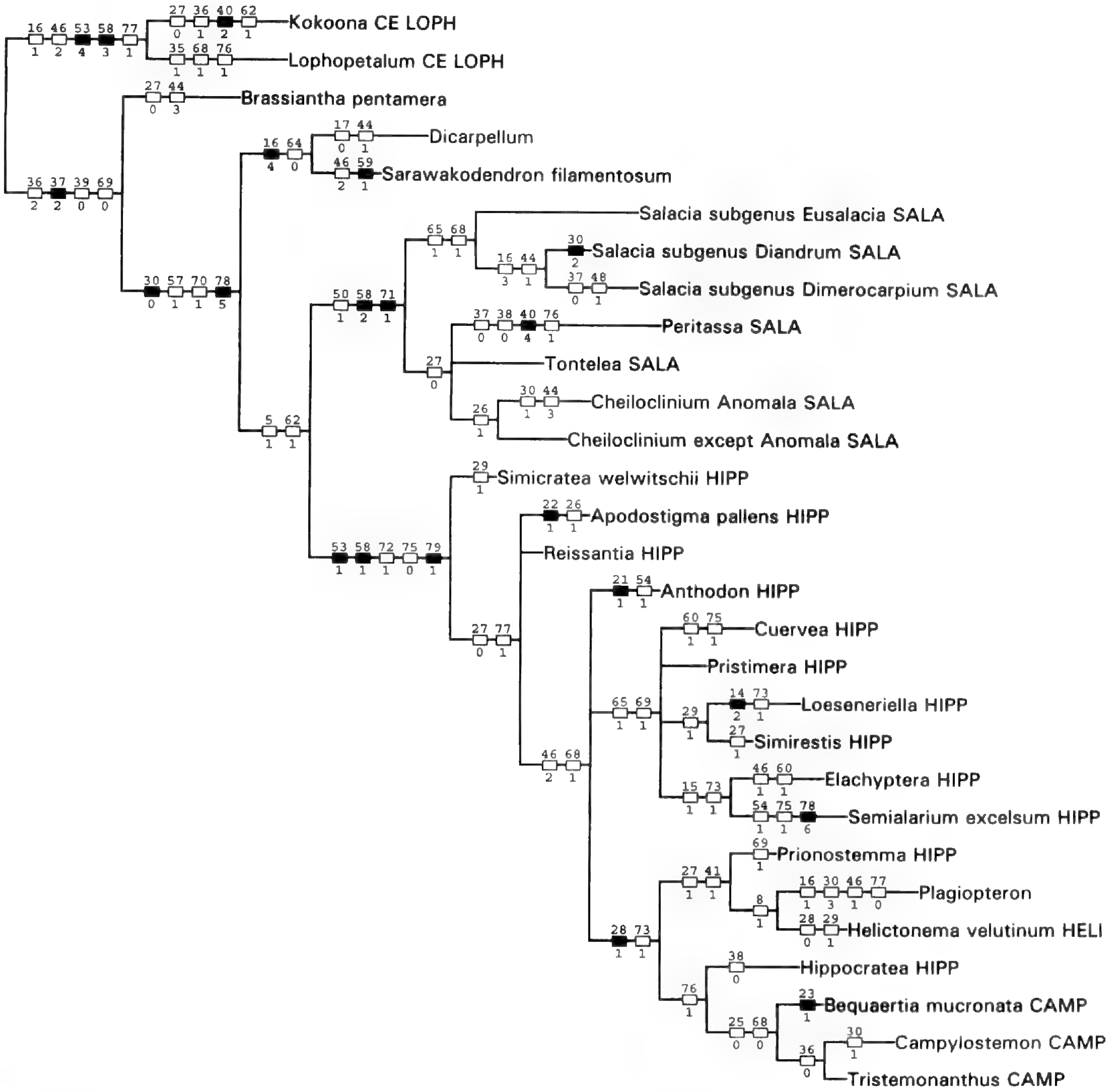


Figure 5. Second "distal" portion of one of 115 most-parsimonious cladograms (309 steps, CI = 0.36, RI = 0.72, excluding uninformative characters; 321 steps including uninformative characters as shown) for 82 taxa of Celastraceae and related families, obtained by equal-weighted analysis of 69 informative (79 including uninformative) characters (Appendices 1–4). See legend of Figure 3 for further information.

none of the other genera in [tribe Eucelastreae] bear any wood anatomical resemblance to *Bhesa*." To our knowledge, *Bhesa* and *Goupia* have never been associated with one another in the literature.

Brexia is resolved as sister group of the remaining Celastraceae s.l. (i.e., all other taxa sampled). Synapomorphies for *Brexia* and Celastraceae are dorsifixed anthers and connate styles. Synapomorphies for Celastraceae (not including *Brexia*) are an uninterrupted vascular strand through the petiole and cymose inflorescences. *Brexia* has been variously assigned to Escalloniaceae (Hutchinson, 1967), Brexiaceae (Verdcourt, 1968), and Grossulariaceae (Cronquist, 1981). Close relationship between *Brexia* and Celastraceae was first proposed by Perrier de la Bâthie (1933), rejected by Loese-

←

Figure 4. First "distal" portion of one of 115 most-parsimonious cladograms (309 steps, CI = 0.36, RI = 0.72, excluding uninformative characters; 321 steps including uninformative characters as shown) for 82 taxa of Celastraceae and related families, obtained by equal-weighted analysis of 69 informative (79 including uninformative) characters (Appendices 1–4). See legend of Figure 3 for further information.

ner (1937), and then retracted, based on Loesener's criticism, by Perrier de la Bâthie (1942). On the basis of embryology, Kamelina (1988) disputed the inclusion of *Brexia* within Escalloniaceae and suggested it be recognized as a separate family, Brexiaceae, in the order Saxifragales. On the basis of embryology and other characters, Tobe and Raven (1993) suggested including Brexiaceae within the order Celastrales, not the order Saxifragales. Based on *rbc*L gene trees (Chase et al., 1993; Morgan & Soltis, 1993), 18S rDNA (Soltis et al., 1997), and *rbc*L 5′ flanking sequence gene tree (Savolainen et al., 1997), *Brexia* was resolved as sister group of Celastraceae (when only one taxon of Celastraceae was sampled) or included within Celastraceae (when more than one taxon was sampled; Savolainen et al., 1997) as an early-derived lineage. Based on the resolution of our analysis, *Brexia* may be included within Celastraceae or retained as a separate family.

Celastraceae sensu stricto. The results of this cladistic analysis generally do not support Loesener's (1942a) classification of subfamilies and tribes of Celastraceae. None of the three subfamilies and only one of the four tribes that include more than one genus are resolved as monophyletic. Only tribe Lophopetaleae, represented by two genera in this study, is resolved as monophyletic. Loesener's (1942a) subfamilies and tribes have been found to be heterogeneous based on wood anatomy (Metcalfe & Chalk, 1950), pollen structure (Lobreau-Callen, 1977), and leaf anatomy (Den Hartog née Van Ter Tholen & Baas, 1978). However, all members of Loesener's subfamily Celastroideae (composed of the tribes Celastreae, Euonymeae, and Lophopetaleae) included in the analysis are resolved as a paraphyletic assemblage that includes Hippocrateaceae. Synapomorphies of this group are dehiscent fruits and arillate seeds. The clade of Celastroideae plus Hippocrateaceae is nested within a paraphyletic assemblage of genera Loesener (1942a) assigned to subfamily Cassinoideae and Tripterygioideae.

Two genera (*Campylostemon* and *Cheiloclinium*) that Loesener (1942a) included in Celastraceae are resolved as members of Hippocrateaceae. Loesener (1892b) originally recognized *Campylostemon* as a member of Hippocrateaceae, but transferred the genus to Celastraceae in his 1942 classification, placing it in its own subfamily, Campylostemonoideae. In spite of recognizing the Hippocrateaceae-like growth form of *Campylostemon*, Loesener made this transfer based on its five-merous androecium. All members of Hippocrateaceae, as delimited by Loesener (1942b), have either two or three stamens. Loesener did not have fruits of *Campylostemon* available for examination. Finally, Loesener noted that this genus is transitional between Celastraceae and Hippocrateaceae, which is not supported in this analysis.

Loesener (1942a) transferred Mier's (1872) genus *Cheiloclinium* to Celastraceae, also based on the number of stamens. However, Loesener did have fruit and seed descriptions that described the mucilaginous pulp and lack of albumen, characteristic of Hippocrateaceae. Loesener transferred the genus, then consisting of *C. anomalum* J. Miers and *C. schwackeanum* L. E. T. Loesener, to Celastraceae based on its five-merous androecium.

Due to the lack of resolution at the "basal" node in this analysis, we cannot support or refute Loesener's (1942a) recognition of subfamily Goupioideae as a member of Celastraceae (if *Brexia* is included within Celastraceae). Loesener (1942a) described two genera, *Canotia* and *Siphonodon*, as doubtfully associated with Celastraceae based on the septicidally dehiscent capsules of *Canotia* and the unusual structure of the gynoecium in *Siphonodon*. In this analysis, *Canotia* is supported as a member of Celastraceae. In contrast, *Siphonodon* is resolved among the outgroup taxa, though closely related to Celastraceae. Based on this resolution, *Siphonodon* should be excluded from Celastraceae s.l.

The two tribes and three subtribes proposed by Bentham and Hooker (1862) are no better supported than the subfamilies and tribes delimited by Loesener (1942a). The naturalness of the tribes and subtribes as defined by Bentham and Hooker (1862) is evaluated here. Tribe Hippocrateae is resolved as nested within tribe Celastreae. Tribe Hippocrateae (composed of *Hippocratea* s.l., *Salacia* s.l., *Siphonodon*, and *Llavea*) is not monophyletic though; *Siphonodon* is resolved as not closely related to *Hippocratea* s.l. and *Salacia* s.l. Celastreae subtribe Euonymeae is not a natural group, with genera assigned to this subtribe resolved in many different regions of Celastraceae s. str. Celastreae subtribe Celastreae is not a natural group, as *Kurrimia* (= *Bhesa*) is not resolved as closely related to the other members. Celastreae subtribe Elaeodendreae is not a natural group, as *Forsellesia* (= *Glossopetalon*) and *Goupia* are not resolved as closely related to the other members, among other problems. In contrast to Loesener (1942a), Bentham and Hooker (1862) and Baillon (1880) recognized *Paxistima* as closely related to *Microtropis*. This assertion is supported in our analysis, as *Pax-*

istima is resolved as the sister group of *Microtropis* and *Quetzalia*.

Perrottetia is resolved as a derived member of Loesener's (1942a) subfamily Cassinoideae in our analysis (also among genera assigned to subfamily Tripterygioideae). Loesener recognized the anomalous position of *Perrottetia* by assigning it to its own tribe, Perrottetieae. *Perrottetia* has been recognized as unusual relative to other Celastraceae based on its wood anatomy (Metcalfe & Chalk, 1950) with scalariform perforation plates, paratracheal parenchyma, and lack of fiber tracheids; its seed structure (Corner, 1976) with an exotegmic palisade of lignified malpighian cells; and its leaf anatomy (Den Hartog née Van Ter Tholen & Baas, 1978) with predominately anomocytic stomates, pubescence, and domatia. In our analysis, these characters are generally shared with outgroup taxa. However, synapomorphies of *Perrottetia* and genera that are resolved as closely related to *Perrottetia* include: dioecy, dorsifixed anthers, 2-carpellate ovaries, baccate indehiscent fruits, and presence of parenchyma-like bands of thin-walled septate wood fibers.

Glyptopetalum and *Xylonymus versteeghii* have been described as closely related to *Euonymus* (Hou, 1962). *Glyptopetalum* has also been included within *Euonymus* (Baillon, 1880). Hou described *Xylonymus versteeghii* as closely related to *Euonymus* (Hou, 1962) and *Sarawakodendron* (Hou, 1969). In our analysis, *Glyptopetalum* and *Xylonymus versteeghii* are resolved as sister groups. This clade is nested within a paraphyletic *Euonymus* (represented by three species). This resolution is consistent with Hou (1962), but not Hou (1969); *Sarawakodendron* appears only very distantly related to *Xylonymus versteeghii*. Furthermore, this resolution suggests that the circumscription of *Euonymus* needs to be redefined.

The recognition or reduction of *Cassine* and *Elaeodendron* has been widely debated in the literature. Davison (1927), Hou (1962), Kostermans (1986), and Bornstein (1989) reduced *Elaeodendron* to *Cassine*, whereas Loesener (1942a), Robson (1965), Proctor (1984), Robson et al. (1994), and Archer and van Wyk (1997) recognized *Cassine* as distinct from *Elaeodendron*. A succinct taxonomic history is provided by Hou (1962). Characters distinguishing the genera (to various degrees) have been described from pollen (Archer & van Wyk, 1992), bark (Archer & van Wyk, 1993a), and wood anatomy (Archer & van Wyk, 1993b). Robson et al. (1994) suggested that *Elaeodendron* is derived from *Euonymus*, and that *Elaeodendron* is not closely related to *Cassine* s. str. (as treated by Archer & van Wyk, 1997). In our analysis, neither *Cassine* (two representative species) nor *Elaeodendron* (three representative species) is resolved as a monophyletic group. However, the two genera are supported as closely related (in contrast to Robson et al., 1994). This result is dependent on sampling; not all the genera Robson et al. (1994) treated are included in this analysis.

Canotia is resolved within Celastraceae, as sister group to *Acanthothamnus aphyllus*. This resolution supports the placement of *Canotia* as a member of Celastraceae by Hutchinson (1969) and Johnston (1975). Synapomorphies that group *Canotia* and *Acanthothamnus aphyllus* are stem apices terminating in sharp points, presence of glands on stems (only present in this clade), and triangular-extended connectives (only present in this clade). Johnston (1975: 119) noted, "In the minutest details of epidermis, bracts, calyx, petals, stamens, gynophore, ovaries, and ovules, *Acanthothamnus* is a diminutive replica of *Canotia*."

Gymnosporia has been treated either as distinct from *Maytenus* (Hou, 1955; Jordaan & van Wyk, in press), or included within it (Exell, 1953; Hou, 1962; Sebsebe, 1985). Loesener (1942a) recognized both genera, but considered the distinction as a stopgap measure with little difference to distinguish between the genera. Jordaan and van Wyk (in press) reinstated *Gymnosporia* to include all "spiny" species of *Maytenus* s.l. (but excluding *Moya*). A thorough taxonomic history of *Gymnosporia* and *Maytenus* is given by Sebsebe (1985). In our analysis, *Putterlickia* is resolved as sister group to two representative species of *Gymnosporia*. This resolution supports the assertion by Jordaan and van Wyk (1998) that *Gymnosporia* and *Putterlickia* (and *Gloveria*) are a natural group. The three synapomorphies supporting this clade are presence of thorns, phyllotaxy alternate on vegetative shoots and opposite on flowering shoots or thorns, and leaves fascicled on short branches. The two species of *Gymnosporia* are recognized as distinct from *Putterlickia* by having unisexual instead of bisexual flowers.

Maytenus, not including *Gymnosporia*, is resolved as a clade separate from the clade of *Gymnosporia* and *Putterlickia*. This resolution supports the recognition of *Gymnosporia* as distinct from *Maytenus*. The two elements of *Maytenus* included in this analysis (*Maytenus undata* and *Tricerma*) are not resolved as sister groups. *Maytenus undata* is resolved as sister group of the clade composed of *Menepetalum*, *Salaciopsis*, and *Tricerma*. This suggests that *Tricerma* should be recognized as distinct from *Maytenus* following Lundell (1971). *Maytenus* is a large and variable genus; further sampling needs to be conducted to test the resolution found here.

"Transitional" genera between Celastraceae and Hippocrateaceae. Many authors have commented on "transitional" genera and/or characters between Celastraceae and Hippocrateaceae (Smith, 1940; Smith & Bailey, 1941; Loesener, 1942a; Hou, 1962, 1964; Robson, 1965; Robson et al., 1994; Den Hartog née Van Ter Tholen & Baas, 1978; Görts-van Rijn & Mennega, 1994; Mennega, 1997). *Brassiantha* (Den Hartog née Van Ter Tholen & Baas, 1978; Görts-van Rijn & Mennega, 1994), *Campylostemon* (Loesener, 1942a; Hou, 1964), *Elaeodendron* and *Crocoxylon* (Robson, 1965), *Kokoona* (Hou, 1964), *Lophopetalum* (Robson, 1965), and *Sarawakodendron* (Hou, 1967) have been proposed as transitional genera. The bases given for recognizing these genera as transitional have been: 5 stamens with an extrastaminal disk (*Brassiantha, Campylostemon,* and *Kokoona*); an extrastaminal disk and a drupaceous fruit with 3 locules (*Elaeodendron/Crocoxylon*); opposite leaves, 5 stamens located on the disk, a 3-locular ovary, and winged seeds (*Lophopetalum*); or an erect habit, 3 stamens, capsular fruit with 3 locules, and albuminous arillate seeds (*Sarawakodendron*).

Our analysis supports *Kokoona, Lophopetalum, Brassiantha, Dicarpellum,* and *Sarawakodendron* as closely related to the most recent common ancestor of the genera traditionally referred to Hippocrateaceae (*Hippocratea* s.l. and *Salacia* s.l.). In contrast, *Campylostemon* is resolved as a derived genus within Hippocrateaceae (supporting Robson, 1965, in his disagreement with Hou, 1964), and *Elaeodendron* is not resolved as closely related to Hippocrateaceae.

Robson (1965: 43) suggested, "The so-called *Hippocrateaceae* comprise two groups of genera that have independently evolved a 3-merous androecium arising inside the disk" such that "the *Hippocratea* group (with dehiscent mericarps and winged seeds) and the *Salacia* group (with indehiscent drupaceous fruits) have been derived from different parts of the *Celastraceae*" (Robson et al., 1994: 1). Our analysis supports Hippocrateaceae as a monophyletic group (including *Plagiopteron*), in contrast to Robson's assertion. However, the *Salacia* group and the *Hippocratea* group (including *Plagiopteron*) are each monophyletic, such that the indehiscent drupaceous fruits of the *Salacia* group apparently did not evolve from the dehiscent mericarps and winged seeds of the *Hippocratea* group, or vice versa. The derivation of these fruit types from a capsular fruit, which was not lobed or parted, appears to have been independent of one another.

Kokoona and *Lophopetalum*, the only two representatives of Loesener's (1942a) tribe Lophopetaleae, are resolved as a natural group. The five synapomorphies for this clade are: paniculate to racemose inflorescences, variable number and more than four ovules per locule, capsular fruit flattened along each locule but not parted (only present in this clade), aril modified into a wing surrounding the seed (only present in this clade), and absence of the pollen annulus. *Lophopetalum* has been treated as a section of *Euonymus* (Baillon, 1880); this is not supported by our analysis. *Kokoona* was originally described as a member of Hippocrateaceae by Thwaites (1853). Thwaites (1853: 380) noted, "In habit and general appearance [*Kokoona*] resembles the *Celastraceae*, though it would seem to differ almost as much from members of that natural family as do the *Hippocrateaceae*, from all the genera of which latter Order it differs in having five stamens." It seems that Thwaites was uncertain whether to assign *Kokoona* to Celastraceae or Hippocrateaceae. Based on the resolution of our analysis in which Hippocrateaceae are nested within Celastraceae and *Kokoona* is one of the "transitional" genera, this uncertainty was well justified; the "natural family" Celastraceae does not appear natural at all, if Hippocrateaceae are recognized as distinct. The synapomorphy that groups the clade that consists of *Kokoona* and *Lophopetalum* with Hippocrateaceae is the insertion of filaments inside the inner edge of the disk (only present in this clade [except *Kokoona* in which the filaments are inserted on the disk] and in Euphorbiaceae). Also, of the eight genera scored, only in *Lophopetalum* and *Salacia* do seedlings not become free from all envelopments during growth.

Smith and Bailey (1941: 393), in the original description of *Brassiantha*, noted:

> "To summarize, the genus *Brassiantha* appears to have no characters which can be used to exclude it from the Hippocrateaceae. On the other hand, it is so distinct from known genera, in the characters of its disk, stamens, ovary, and fruit, as to make comparison superfluous. It appears to be rigidly excluded from the Celastraceae, as that family is presently constituted, by the position of the stamens within the disk. This, indeed, may be the only fixed character by which the families Hippocrateaceae and Celastraceae may be separated. If so, one must consider the families quite artificial. . . ."

One may interpret this to mean that Smith and Bailey recognized the character states that *Brassiantha* shares with other members of Hippocrateaceae are plesiomorphic, but apomorphic relative to members of Celastraceae. Indeed, *Brassiantha* is resolved as sister group of the rest of Hippocrateaceae, and nested within Celastraceae. Synapomorphies for *Brassiantha* and the rest of Hippocrateaceae are three anther characters: anthers not versatile, and transversely dehiscent in the extrorse direction. Extrorsely dehiscent anthers are only present in this clade (though introrse dehiscence occurs in *Campylostemon* and *Tristemonanthus*) and in *Lophopyxis.* Based on this resolution, the distinction between Celastraceae and Hippocrateaceae is indeed artificial.

The first species of *Dicarpellum* was described as *Salacia pancheri* by Baillon (1872). Loesener (1907) named three more species and placed them, and *Salacia pancheri,* into *Salacia* subg. *Dicarpellum.* Smith (1941: 442) elevated subgenus *Dicarpellum* to the generic level and stated, "The genus is not closely related to *Salacia.*" Smith distinguished *Dicarpellum* from *Salacia* based on disk shape and anther dehiscence plane; but neither of these characters excludes *Dicarpellum* from the variable *Salacia* subg. *Eusalacia.* However, based on our analysis, Smith correctly observed that *Dicarpellum* is not closely related to *Salacia. Salacia* is resolved as more closely related to *Peritassa, Tontelea,* and *Cheiloclinium* than it is to *Dicarpellum,* which is resolved as sister group of *Sarawakodendron.* The synapomorphy for the clade that consists of *Dicarpellum* and *Sarawakodendron* is the inflorescence modified into a condensed bracteate raceme.

Hou (1967: 142–143) described *Sarawakodendron* as "closely allied to *Kokoona* and *Lophopetalum* of the *Celastraceae*" and "one of the transitional links between the two very closely related families, *Hippocrateaceae* and *Celastraceae.*" Both of Hou's assessments are supported by our analysis.

Hippocrateaceae. Our analysis supports the inclusion of Hippocrateaceae within Celastraceae. Traditionally defined members of Hippocrateaceae (*Hippocratea* s.l. and *Salacia* s.l.) are resolved as a clade by two synapomorphies: opposite leaves and loss of albumen (also lost in *Kokoona* and *Corynocarpus* [Corynocarpaceae]). Two other characters supporting this clade (though not unambiguously optimized on the supporting branch) are interrupted vascular strand through petiole in cross section (within Hippocrateaceae, only described in *Salacia, Tontelea,* and *Hippocratea*), and base chromosome number of 14 (occurs only in Hippocrateaceae [although the base chromosome number of *Semialarium excelsum* is 15], but only known in *Cuervea, Salacia, Campylostemon, Hippocratea,* and *Loeseneriella*).

Hallé's division of Hippocrateaceae variously into subfamilies and tribes (1962) and only tribes (1986, 1990) is partially supported by this analysis. Subfamily Salacioideae (= tribe Salacieae) is resolved as a monophyletic group (excluding *Dicarpellum*), sister to subfamily Hippocrateoideae, which includes the tribes Campylostemoneae, Helictonemateae, and Hippocrateeae. The synapomorphies for subfamily Salacioideae are the indehiscent fruit, aril modified into mucilaginous pulp (only present in this clade), and the presence of included phloem (also only present in this clade). This supports Hallé's recognition of the two subfamilies, Hippocrateoideae and Salacioideae. Two synapomorphies for subfamily Hippocrateoideae are some rays greater than ten cells wide (only present in this clade and *Corynocarpus* [Corynocarpaceae]) and loss of parenchyma-like bands of thin-walled septate wood fibers. Three other characters supporting this clade (though not unambiguously optimized on the supporting branch) are capsules strongly parted among locules ("mericarps"; only present in this clade), aril modified into a basal wing with the vasculature of the funiculus along the wing (only present in this clade), and presence of pollen annulus (except in *Simicratea;* also present in *Kokoona* and *Lophopetalum*). However, as Hippocrateaceae are nested within Celastraceae, these subfamilies may not be formally recognized. Tribes Campylostemoneae and Helictonemateae are nested within the paraphyletic tribe Hippocrateeae. Tribe Helictonemateae is monotypic, and tribe Campylostemoneae is monophyletic. Because recognition of tribes Campylostemoneae and Helictonemateae renders tribe Hippocrateeae paraphyletic, recognition of these tribes is not supported.

Note that Hallé (1962: 42) apparently did not interpret his subfamilies or tribes to be monophyletic as indicated in his "Tableau des liaisons intergénériques." In this diagram, which he described as an entirely hypothetical tracing of the evolution of the Hippocrateaceae, the monophyly of the subfamilies is ambiguous, as is the recognition of tribe Helictonemateae as separate from tribe Hippocrateeae. Tribe Campylostemoneae is clearly nested within tribe Hippocrateeae. The synapomorphy for tribe Campylostemoneae is the loss of the disk (which occurs only in this clade).

In this same table (Hallé, 1962: 42), *Simirestis, Bequaertia,* and *Tristemonanthus* are illustrated as transitional genera, with *Simirestis* directly giving rise to six different genera independently. These

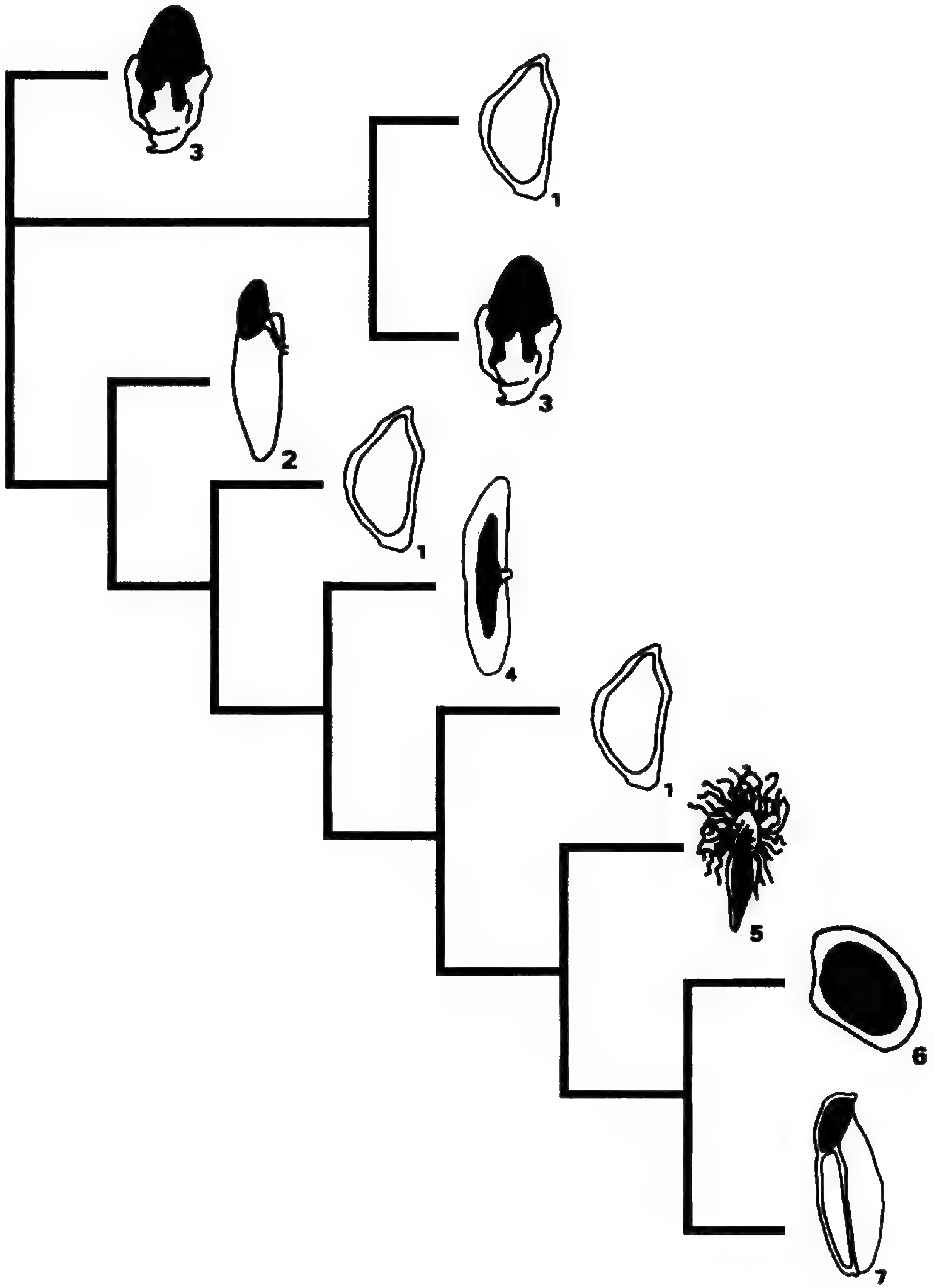


Figure 6. The pattern of aril modification in the clade composed of the most recent common ancestor of *Catha edulis*, *Euonymus*, and *Polycardia*, and their descendents, mapped onto part of a simplified strict-consensus tree from Figures 1 and 2. Embryoniferous portion of seed, when not enveloped by the aril, is shaded. Aril and vasculature of the funiculus are not shaded. —1. Aril entirely enveloping seed (redrawn from Smith & Bailey, 1941). —2. Aril modified into a basal wing with the vasculature of the funiculus attached above the wing (redrawn from Robson et al., 1994). —3. Aril partially enveloping the seed (redrawn from Mueller, 1995). —4. Aril modified into a wing surrounding

transitional genera and narrowly defined segregate genera that Hallé recognized have been criticized by Robson (1965). If Hallé's and Robson's assertion that some of the genera of tribe Hippocrateeae are not monophyletic groups is correct, this would help explain the large polytomy in tribe Hippocrateeae in our analysis. This polytomy reflects character conflict.

Plagiopteron (Plagiopteraceae) is resolved as a derived member of tribe Hippocrateeae, closely related to *Helictonema velutinum* and *Prionostemma*. Characters supporting inclusion of *Plagiopteron* within Hippocrateaceae include: opposite leaves, stellate leaf pubescence, not versatile, transversally dehiscent, extrorse anthers, filaments inserted inside the disk, pilose ovary pubescence, capsular fruit strongly parted among locules, and presence of crystals in leaf epidermal cells.

Evolution of the aril. Characters 56 (aril presence), 57 (aril position on seed), and 58 (aril form) are all coded based on the assertion that the aril may be fleshy (typical of most arils; in *Euonymus*, *Maytenus*, etc.), modified into a basal wing with the vasculature of the funiculus along the wing (in members of *Hippocratea* s.l.), modified into a basal wing with the vasculature of the funiculus attached above the wing (in *Canotia* and *Catha edulis*), modified into a wing surrounding the seed (in *Kokoona*, *Lophopetalum*, and *Peripterygia*), or modified into mucilaginous pulp (in *Salacia* s.l.). This assertion is based on descriptions from the literature and personal observations and inferences. See Appendix 2 for further information on character coding. A brief review of the relevant literature and the basis for the coding follows.

Miers (1872: 323) described the basal wing of the seed in *Hippocratea* as a "very membranous, wing-like support, which is a laminiform expansion of its outer integument: this wing has been supposed to be an expanded funicle; but this I much doubt: one of its margins, that furthest from the sutural line of the cell, is thickened into a narrow coriaceous tube, enclosing a simple chord of numerous spiral threads (the raphe)." We believe that Miers misused the term "raphe." A raphe is defined as a "longitudinal ridge on the outer integument or seed coat in anatropous ovules where the funiculus becomes fused with the integument" (Blackmore & Tootill, 1984: 307). Based on this definition and the description by Miers, what he described as the raphe is the vasculature of the funiculus. Therefore, there is no basis to conclude that the "laminiform expansion" is not an expanded funicle (i.e., an aril). Hallé (1962) described the wing of *Hippocratea* s.l. as a membranous testa.

The small, thin, flat, basal structures with the vasculature of the funiculus attached above the wing, which occur in *Canotia* and *Catha edulis*, have variously been described as arils or as wings. Loesener (1942a) described the structure in *Catha edulis* as a well-developed white wing-like aril, whereas he described a very similar structure in *Canotia* as a triangular wing, without reference to it being a modified aril. Johnston (1975: 121) described the wing of *Canotia* as a "winglike structure" without further elaboration. Relative to the basal wings found in *Hippocratea* s.l., the basal wings of *Canotia* and *Catha edulis* are much smaller (about the same size as the embryoniferous portion of the seed), and the wing is located immediately below the point of attachment—the vasculature of the funiculus does not run along the wing. No basis was found to code the basal wings of *Canotia* and *Catha edulis* as separate character states.

The vasculature of the funiculus is also medially attached in *Lophopetalum* and *Peripterygia* (basally attached in *Kokoona*), except that the wing surrounds the seed. Loesener (1942a) stated that he was unsure if the wing of *Kokoona* represented a modified aril or a further development of the testa.

The mucilaginous pulp found only in fruits of *Salacia* s.l. was described by Miers (1872: 324) as follows: "In some cases this testa is covered with a white fleshy coating, like that which I formerly described as an *arilline**, and which ultimately forms a sparse pulp in which the seeds are embedded." Miers (1856: 89) defined arilline as an aril "in which the vessels of the raphe are always imbedded." Again, we interpret what Miers described as the "vessels of the raphe" to be the vasculature of the funiculus. Baillon (1880: 15) described the seeds of Salaceae as "nude, or partially enveloped in an aril springing from the umbilicum." Loesener (1942b), in describing the mucilaginous pulp, noted that it is not derived from the ovary walls, but is rather a de novo structure or an outgrowth of the seeds.

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the seed (redrawn from Hou, 1962). —5. Aril partially enveloping the seed with filamentous extensions from base (redrawn from Hou, 1967). —6. Aril modified into mucilaginous pulp (cross section; redrawn from Hallé 1962). —7. Aril modified into a basal wing with the vasculature of the funiculus along the wing (redrawn from Hallé, 1986).

All four character states described above (character 58, states 1–4) have been associated with arils (i.e., modified funiculi) in the literature, as cited above. In all cases, the structures are located at the base of the seed or surrounding the seed, thus establishing positional similarity, which is a basis for a hypothesis of primary homology (de Pinna, 1991). Furthermore, in no case is there an additional structure present in taxa with one of these four character states that could be interpreted as an aril. Therefore, the homology assessment passes Patterson's (1982) test of conjunction.

The following statements are based on the resolution and optimization of unordered character states (Fitch, 1971) on the strict consensus of the most-parsimonious cladograms (Figs. 1, 2), and are applicable only to the taxa included in the analysis. The presence of arils is a derived character state that arose three times in Celastraceae (and once in Crossosomataceae, including *Forsellesia*): once in *Bhesa*, once in *Canotia*, and once in the most recent common ancestor of *Catha edulis*, *Euonymus*, and *Polycardia*. In this latter clade, the aril has been lost only once (although presence/absence of the aril is unknown in *Plagiopteron*), in the clade of *Microtropis* and *Quetzalia*. This suggests that the "thick testa" of *Microtropis* seeds described by Corner (1976: 94) is actually homologous to an aril as cited by Hou (1962). See character 56 in Appendix 2 for further discussion.

In the clade composed of the most recent common ancestor of *Catha edulis*, *Euonymus*, and *Polycardia*, and their descendents, the aril underwent modification from a typical fleshy form (primitive state) to the four above-mentioned forms (derived states). The aril as a basal wing with the vasculature of the funiculus attached above the wing has arisen independently in two terminals, *Canotia* and *Catha edulis*. Each of the three other derived states has arisen only once, and in no case has the derived state been lost (i.e., shown a reversal in the cladogram). Finally, each of the four derived states has arisen independently from the others. The pattern of aril modification in the clade composed of the most recent common ancestor of *Catha edulis*, *Euonymus*, and *Polycardia*, and their descendents is diagrammed in Figure 6. In this cladistic analysis, the aril-homology assessments were tested against homology assessments of other characters (that is to say, tested by congruence; Wiley, 1975; Patterson, 1982). Based on the resolution of this cladogram, in which there is a unique origin for three of the four derived aril character states, these three original homology assessments are supported.

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Appendix 1. Taxa sampled for cladistic analysis.

Literature surveyed for gross-morphological characters in parentheses.

Canotia, *Goupia*, *Lophopyxis*, and *Siphonodon* are arranged as separate families following Cronquist (1981). Genera within Celastraceae s. str. are arranged by subfamily and tribe according to Loesener (1942a), except *Campylostemon* and *Cheiloclinium* are arranged in Hippocrateaceae following Hallé (1962, 1986, 1990) and Smith (1940), respectively. Genera within Hippocrateaceae are arranged by tribe according to Hallé (1986, 1990). Capitalized, bold-faced, two- and four-letter abbreviations following subfamilies and tribes, respectively, are used to indicate terminals belonging to these taxa in the strict consensus of 115 most-parsimonious cladograms (Figs. 1, 2). Sixty-two gross-morphological characters were scored for 82 taxa based on literature and/or herbarium specimens. Following the taxon name and author are the literature source(s) examined when coding that taxon.

CORYNOCARPACEAE
(1) *Cornynocarpus* J. R. Forster & G. Forster (Cronquist, 1981; Guymer, 1984; Philipson, 1987)
CROSSOSOMATACEAE
(2) *Crossosoma* Nuttall (Nuttall, 1848; Cronquist, 1981)
EUPHORBIACEAE
(3) *Aleurites* J. R. Forster & G. Forster (Forster, 1996)
(4) *Astrocasia* B. L. Robinson & Millspaugh (Webster, 1992)
GEISSOLOMATACEAE
(5) *Geissoloma marginatum* J. Lindley ex K. S. Kunth (Dahlgren & Rao, 1969; Cronquist, 1981)
HUACEAE
(6) *Afrostyrax* J. R. Perkins & E. F. Gilg (Chevalier, 1947; Baas, 1972)

(7) *Hua* J. B. L. Pierre ex É. A. J. De Wildeman (Chevalier, 1947; Germain, 1963; Willis, 1966; Baas, 1972)

SAXIFRAGACEAE

(8) *Lepuropetalon* C. Elliott (Spongberg, 1972)

(9) *Parnassia* L. (Spongberg, 1972)

STACKHOUSIACEAE

(10) *Stackhousia* J. E. Smith (Barker, 1977, 1984)

(11) *Tripterococcus brunonis* S. F. L. Endlicher (Barker, 1984)

BREXIACEAE

(12) *Brexia* F. Noroña ex L. M. A. P. Thouars (Hutchinson, 1967; Verdcourt, 1968)

CANOTIACEAE

(13) *Canotia* J. Torrey (Johnston, 1975)

GOUPIACEAE

(14) *Goupia* J. B. C. F. Aublet (Aublet, 1775)

LOPHOPYXIDACEAE

(15) *Lophopyxis maingayi* J. D. Hooker (Hooker, 1887–1888, 1888; Willis, 1966)

PLAGIOPTERACEAE

(16) *Plagiopteron* W. Griffith (Airy Shaw, 1965; Willis, 1966; Baas et al., 1979)

SIPHONODONTACEAE

(17) *Siphonodon* W. Griffith (Hou, 1964)

CELASTRACEAE

subfamily Celastroideae L. E. T. Loesener **CE**

tribe Euonymeae L. E. T. Loesener **EUON**

(18) *Euonymus alatus* (C. P. Thunberg) P. F. von Siebold (Ka, 1965)

(19) *Euonymus fortunei* (P. K. N. S. Turczaninow) H. R. E. Handel-Mazzetti (Turczaninoff, 1863; Bailey, 1951)

(20) *Euonymus globularis* Ding Hou (Hou, 1975)

(21) *Glyptopetalum* G. K. Thwaites (Hou, 1962)

(22) *Microtropis* N. Wallich ex C. D. F. Meisner (Hou, 1962; Merrill & Freeman, 1940)

(23) *Quetzalia* C. L. Lundell (Lundell, 1939)

(24) *Xylonymus versteeghii* C. Kalkman ex Ding Hou (Hou, 1962)

tribe Celastreae **CELA**

(25) *Bhesa* F. Buchanan-Hamilton ex G. A. W. Arnott (Hou, 1962)

(26) *Catha edulis* (M. Vahl) S. F. L. Endlicher (Robson et al., 1994)

(27) *Celastrus* L. subg. *Celastrus* (Hou, 1955)

(28) *Celastrus* L. subg. *Racemocelastrus* Ding Hou (Hou, 1955)

(29) *Gymnosporia buchananii* L. E. T. Loesener (Robson et al., 1994)

(30) *Gymnosporia mossambicensis* L. E. T. Loesener (Robson et al., 1994)

(31) *Maytenus undata* (C. P. Thunberg) R. A. Blakelock (Sebsebe, 1985)

(32) *Menepetalum* L. E. T. Loesener (Mueller, 1995)

(33) *Paxistima* C. S. Rafinesque (Navaro & Blackwell, 1990)

(34) *Polycardia* A. L. de Jussieu (Perrier de la Bâthie, 1946)

(35) *Putterlickia* S. F. L. Endlicher (Robson, 1966; Jordaan & van Wyk, 1998)

(36) *Salaciopsis* E. G. Baker (Mueller, 1995)

(37) *Tricerma* F. M. Liebmann (Lundell, 1969, 1971; Correll & Johnston, 1970)

tribe Lophopetaleae L. E. T. Loesener **LOPH**

(38) *Kokoona* G. H. K. Thwaites (Hou, 1962)

(39) *Lophopetalum* R. Wight ex G. A. W. Arnott (Hou, 1962)

subfamily Triperygioideae L. E. T. Loesener **TR**

(40) *Plenckia* S. Reissek (Lourteig & O'Donnell, 1955)

(41) *Ptelidium* L. M. A. P. Thouars (Perrier de la Bâthie, 1946)

(42) *Tripterygium* J. D. Hooker (Ka, 1965)

(43) *Wimmeria* D. F. L. von Schlechtendal & L. K. A. von Chamisso (Lundell, 1939)

(44) *Zinowiewia* P. K. N. S. Turczaninow (Lundell, 1939)

subfamily Cassinoideae L. E. T. Loesener **CA**

tribe Cassineae **CASS**

(45) *Acanthothamnus aphyllus* (F. R. R. Schlechter) P. C. Standley (Brandegee, 1909; Standley, 1923; Loesener, 1942a; Johnston, 1975)

(46) *Cassine parvifolia* O. W. Sonder (Archer & van Wyk, 1997)

(47) *Cassine schinoides* (C. P. J. Sprengel) R. H. Archer (Archer & van Wyk, 1997)

(48) *Elaeodendron matabelicum* L. E. T. Loesener (Robson & Sousa, 1969)

(49) *Elaeodendron pauciflorum* L. R. Tulasne (Perrier de la Bâthie, 1946)

(50) *Elaeodendron schweinfurthianum* L. E. T. Loesener (Robson et al., 1994)

(51) *Forsellesia* E. L. Greene (Ensign, 1942; Thorne & Scogin, 1978)

(52) *Gyminda* C. S. Sargent (Bornstein, 1989)

(53) *Mortonia* A. Gray (Gray, 1852, 1853)

(54) *Schaefferia* N. J. von Jacqin (Bornstein, 1989)

tribe Perrottetieae **PERR**

(55) *Perrottetia* K. S. Kunth (Hou, 1962)

NOT ASSIGNED TO SUBFAMILY OR TRIBE

(56) *Brassiantha pentamera* A. C. Smith (Hippocrateaceae) (Hou, 1964)

(57) *Dicarpellum* (L. E. T. Loesener) A. C. Smith (Hippocrateaceae) (Smith, 1941; Simmons, in press)

(58) *Rzedowskia tolantonguensis* F. G. Medrano (Gonzalez-Medrano, 1981)

(59) *Sarawakodendron filamentosum* Ding Hou (Hou, 1967, 1969; Corner, 1976)

HIPPOCRATEACEAE

tribe Campylostemoneae N. Hallé **CAMP**

(60) *Bequaertia mucronata* (M. A. Exell) R. Wilczek (Hallé, 1986; Robson et al., 1994)

(61) *Campylostemon* F. M. J. Welwitsch (Hallé, 1986; Robson et al., 1994)

(62) *Tristemonanthus* L. E. T. Loesener (Hallé, 1986; Robson et al., 1994)

tribe Helictonemateae N. Hallé **HELI**

(63) *Helictonema velutinum* (A. Afzelius) J. P. L. Pierre (Hallé, 1986; Robson et al., 1994)

tribe Hippocrateeae N. Hallé **HIPP**

(64) *Anthodon* H. Ruíz López & J. A. Pávon (Smith, 1940; Görts-van Rijn & Mennega, 1994)

(65) *Apodostigma pallens* (J. É. Planchon ex D. Oliver) R. Wilczek (Hallé, 1986; Robson et al., 1994)

(66) *Cuervea* Triana ex Miers (Smith, 1940; Hallé, 1986; Robson et al., 1994)

(67) *Elachyptera* A. C. Sm., Smith, 1940; Görts-van Rijn & Mennega, 1994)

(68) *Hippocratea* L. (Smith, 1940; Görts-van Rijn & Mennega, 1994)

(69) *Loeseneriella* A. C. Sm. (Hallé, 1986; Robson et al., 1994)

(70) *Prionostemma* Miers (Smith, 1940; Görts-van Rijn & Mennega, 1994)

(71) *Pristimera* Miers (Smith, 1940)

(72) *Reissantia* N. Hallé (Hallé, 1986; Robson et al., 1994)

(73) *Semialarium excelsum* (HBK) A. C. Smith (Smith, 1940)

(74) *Simicratea welwitschii* (D. Oliver) N. Hallé (Hallé, 1986; Robson et al., 1994)

(75) *Simirestis* N. Hallé (Hallé, 1986; Robson et al., 1994)

tribe Salacieae N. Hallé **SALA**

(76) *Cheiloclinium* Miers species-group *Anomala* (Smith, 1940)

(77) *Cheiloclinium* Miers except species-group *Anomala* (Smith, 1940)

(78) *Peritassa* J. Miers (Hallé, 1986)

(79) *Salacia* L. subg. *Diandrum* L. E. T. Loesener (Loesener, 1942b; Hou, 1964)

(80) *Salacia* L. subg. *Dimerocarpium* L. E. T. Loesener (Loesener, 1942b)

(81) *Salacia* L. subg. *Eusalacia* L. E. T. Loesener (Loesener, 1942b; Hallé, 1986)

(82) *Tontelea* J. P. C. F. Aublet (Smith, 1940; Görts-van Rijn & Mennega, 1994)

APPENDIX 2. Characters and character states.

Seventy-nine characters were scored for 82 taxa of Celastraceae and related families (Appendix 1). Notes on character coding are given in cases where observations and codings conflict with descriptions in the literature, and when different publications described the taxon scored as having different character states. Also included are discussions of questionable character-state codings, and literature sources (if any) that were used to code each character and/or individual character states. Independence of characters and division of characters into character states are also discussed, and taxa with unusual or infrequent character states are noted. All multistate characters were scored as unordered. The four numbers (or ranges) following each informative character description represent optimization of the character on the 115 most-parsimonious cladograms. The four numbers are: number of steps on most-parsimonious cladograms, number of extra steps beyond minimum required if the character was consistent on the cladograms, consistency index, and retention index. Additional steps implied by polymorphism within terminals are not included in the calculation of steps or consistency indices. Uninformative characters (alternative character state[s] only present in single terminal[s]) are indicated by "UNINF" in place of the four numbers.

STEM AND LEAF

1. *Tendril presence*: absent (0); present (1). Uninformative [UNINF].

Within Celastraceae s.l., tendrils are only present in *Lophopyxis*. Described by Willis (1966: 668) as "watch-spring tendrils (modif. infl.)."

2. *Thorn presence*: absent (0); present (1). 1, 0, 1.00, 1.00.

Within Celastraceae s.l., thorns are present in *Gloveria*, *Gymnosporia*, *Moya*, and *Putterlickia*. In the literature (e.g., Robson et al., 1994; Jordaan & van Wyk, 1998), the thorns are generally described as spines. However, we interpret these structures to be modified stems, not modified leaves. Sebsebe (1985) also interpreted these structures to be modified axillary shoots, but incorrectly cited them as spines. Spines are modified leaves (or parts of leaves), thorns are modified stems (Blackmore & Tootill, 1984). Loesener (1942a) also described these structures as modified shoots, though the German word "Dorn" can be interpreted as either thorn or spine (Artschwager & Smiley, 1925). Evidence favoring the interpretation of the structures (what we term "thorns") in *Gymnosporia* as modified shoots includes leaves generally subtending the structures, and inflorescences and leaves often borne on the structures.

The protuberances on older stems (prickles?) of *Simirestis klaineana* do not appear similar to the thorns of *Gymnosporia*. To our knowledge, these "prickles" only occur in this one species (Hallé, 1962, 1986; Robson et al., 1994).

3. *Stem apices*: not terminating in sharp points (0); terminating in sharp points (1). 2, 1, 0.50, 0.50.

Within Celastraceae s.l., stem apices terminating in sharp points are only present in *Acanthothamnus aphyllus*, *Canotia*, and *Forsellesia*.

4. *Presence of glands on stems*: absent (0); present (1). 1, 0, 1.00, 1.00.

Within Celastraceae s.l., glandular stems are only present in *Acanthothamnus aphyllus* and *Canotia*.

5. *Phyllotaxy on vegetative shoots*: alternate (0); opposite or whorled (1). 9, 8, 0.11, 0.78.

Elaeodendron, which is described as having "leaves all opposite or subopposite to alternate towards the base of the shoot" (Robson et al., 1994: 29), was coded as having opposite or whorled phyllotaxy. No species of *Elaeodendron* we know of has strictly alternate leaves. Specimens we have seen almost always have nodes with opposite leaves and a small minority of nodes that bear subopposite or alternate leaves.

Within Celastraceae s.l., we know of whorled leaves only in *Brexiella*, *Crossopetalum*, and *Evonymopsis*.

6. *Phyllotaxy on plants with alternate leaves*: strictly alternate (0); alternate on vegetative shoots, opposite on thorns or flowering shoots (1). 3, 2, 0.33, 0.50.

Within Celastraceae s.l., phyllotaxy alternate on vegetative shoots and opposite on thorns or flowering shoots occurs in *Catha edulis*, *Gymnosporia*, *Putterlickia*, and *Schaefferia*. Sebsebe (1985: 9) noted, "The leaves are normally alternate in all species [of *Maytenus*, in which *Gymnosporia* was treated], but may be opposite when growing on thorns. These are often seen in *M. obbiadensis*, *M. putterlickioides* and *M. senegalensis*, and more rarely in *M. arbutifolia* and *M. heterophylla*. When growing on short lateral branches the leaves are often clustered." Inflorescences are often, but by no means always, located on the thorns of *Gymnosporia*. Krikorian (1985) made no mention of the similarity between *Catha edulis* and *Gymnosporia*, nor have we found reference to this in any other publication.

7. *Leaf form*: planar (0); sessile delta-shaped scales (1). UNINF.

Within Celastraceae s.l., leaves reduced to sessile delta-shaped scales are present in *Canotia*. The reduced leaves of *Psammomoya* do not appear similar to the reduced leaves of *Canotia*.

8. *Leaf pubescence*: without stellate hairs (0); with stellate hairs (1). 4–5, 3–4, 0.40–0.50, 0.25–0.50.

Most genera of Celastraceae are essentially glabrous. The stellate hairs of *Aleurites* are less dense, smaller, and weaker than the stellate hairs of *Helictonema velutinum*, but were coded as homologous. *Plagiopteron* is the only other taxon in Celastraceae s.l. with stellate hairs.

9. *Leaf venation*: pinnate (0); acrodromous (1). UNINF.

Within Celastraceae s.l., acrodromous leaf venation occurs only in *Goupia* and *Pottingeria acuminata.*

10. *Leaf position*: not fascicled on short branches (0); often fascicled on short branches (1). 4, 3, 0.25, 0.57.

Within Celastraceae s.l., leaves often fascicled on short branches occur in *Forsellesia, Gymnosporia, Putterlickia, Schaefferia,* and *Wimmeria.* The short branches we refer to in *Gymnosporia* and *Putterlickia* are in addition to the thorns, not the thorns themselves. Short branches are also described for *Mystroxylon* (Robson et al., 1994) and occur on *M. burkeanum* O. W. Sonder (A. E. van Wyk, pers. comm. 1998), but not on specimens of *M. aethopicum* (C. P. Thunberg) L. E. T. Loesener that the senior author has examined at NY.

11. *Domatia in axils of midrib and secondary veins*: absent (0); sometimes present (1). 2, 1, 0.50, 0.00.

Within Celastraceae s.l., domatia occur only in *Goupia* and *Perrottetia.* Domatia were described by Hou (1962) for *Perrottetia,* and confirmed on herbarium specimens. The domatia are scattered. They are not present in the axils of the midrib and all secondary veins. Lundell (1985: 239) cited domatia in *Goupia guatemalensis* and stated, "The pitted and barbate domatia are similar to those found in some species of *Perrottetia,* a genus remotely related." We have not examined specimens of *Goupia guatemalensis.*

12. *Distinct-crossbar tertiary leaf veins*: absent (0); present (1). 1, 0, 1.00, 1.00.

Within Celastraceae s.l., distinct-crossbar tertiary leaf veins are only present in *Bhesa* and *Goupia.* The crossbar tertiary leaf veins are not perpendicular to the secondary veins, but rather are perpendicular to the midrib. This character state is most pronounced in *Bhesa* and is a bit less uniform in *Goupia.*

13. *Upper petiole angle*: not geniculate (0); thickened, geniculate (1). UNINF.

Within Celastraceae, thickened, geniculate upper petioles are only present in *Bhesa.*

14. *Stipule morphology on opposite leaves*: intrapetiolar (0); intra- or interpetiolar with tuft of hairs (1); intra- or interpetiolar without tuft of hairs (2). UNINF.

This character was coded as inapplicable for taxa with strictly alternate leaves. Stipules intra- or interpetiolar with a tuft of hairs are present in *Catha edulis.* Stipules intra- or interpetiolar without a tuft of hairs are present in *Loeseneriella.*

INFLORESCENCE AND FLOWER

15. *Inflorescence position*: axillary (0); at least some inflorescences terminal (1); epiphyllous or rarely axillary (2). 6–7, 4–5, 0.28–0.33, 0.66–0.73.

Within Celastraceae s.l., epiphyllous inflorescences are only present in *Polycardia.*

16. *Inflorescence type*: cymose (0); paniculate to racemose (1); umbellate (2); fasciculate (3); condensed bracteate racemose (4); flowers solitary (5); irregularly cymose-umbellate (6). 20, 14, 0.30, 0.53.

Within Celastraceae s.l., umbellate inflorescences are only present in *Goupia.* Condensed bracteate racemose inflorescences are present in *Dicarpellum, Sarawakodendron,* and *Maytenus abbottii* A. E. van Wyk. Irregularly cymose-umbellate inflorescences are present in *Brexia* and *Siphonodon. Siphonodon* is described as cymose (e.g., Hou, 1964; Jessup, 1984). The cymes are generally condensed, contorted, and woody. A similar pattern occurs in inflorescences of *Brexia,* which appear almost umbellate, except the pedicels generally diverge from three areas of the peduncle apex, appearing as reduced cymes.

Fasciculate inflorescences often appear to be sessile cymes (e.g., *Maytenus* has both fasciculate and cymose inflorescences). Through dissections, the second author has found fasciculate inflorescences of *Maytenus* and *Salacia* to be reduced cymes.

17. *Flower sexuality*: unisexual (0); bisexual (1). 7, 6, 0.14, 0.50.

18. *Unisexual-flowered plants*: dioecious (0); monoecious (1). 2, 1, 0.50, 0.83.

19. *Perianth merosity*: four-merous (0); five-merous (1); three-merous (2). 4, 3, 0.25, 0.70.

Within Celastraceae s.l., no taxa have strictly three-merous perianths. However, *Plagiopteron* has a variously three- to five-merous perianth.

20. *Sepal gland presence*: absent (0); present (1). 1, 0, 1.00, 1.00.

Glandular sepals are present in the outgroups *Afrostyrax* and *Hua* (Huaceae).

21. *Petal margins*: entire, ciliate, or irregularly toothed (0); regularly toothed (1). UNINF.

Regularly toothed petal margins occur in *Anthodon.* Initially, attempts were made to code entire, ciliate, irregularly toothed, and regularly toothed petals as separate character states. However, several taxa have two or more of these character states present and also have intermediate states. The only character state that stood out, and was therefore retained, was the regularly toothed petals of *Anthodon.*

22. *Corolla symmetry*: actinomorphic (0); zygomorphic with four of five petals arched (1). UNINF.

Within Celastraceae s.l., zygomorphic corollas with four of five petals arched are only present in *Apodostigma.* This is well illustrated by Hallé (1986). The character state is less obvious in herbarium specimens. The irregularly sized petals (three larger, two smaller) of *Bequaertia mucronata* also make the flower zygomorphic. However, this is not similar to the five equally sized, variously curved petals of *Apodostigma.*

23. *Petal fleshiness*: not fleshy (0); fleshy and irregularly sized (1). UNINF.

Within Celastraceae s.l., fleshy and irregularly sized (three larger, two smaller) petals are only present in *Bequaertia mucronata.* The character state is well illustrated by Hallé (1986) and is obvious on herbarium specimens.

24. *Petal connation*: free (0); free at base, connate above (1). 1, 0, 1.00, 1.00.

Stackhousia and *Tripterococcus brunonis* (Stackhousiaceae) have petals that are free at the base and connate above.

25. *Disk presence*: absent (0); present (1). 3, 2, 0.33, 0.60.

The disk is absent in *Bequaertia mucronata, Campylostemon,* and *Tristemonanthus.* All disk descriptive characters were coded as inapplicable for these three genera. What appears to be a disk in *Campylostemon* and *Tristemonanthus,* we interpret (as do Hallé, 1986, 1990; Robson et al., 1994) as flared filament bases.

The disk is inconspicuous, though still present, in some genera (e.g., *Lepuropetalon* [Saxifragaceae], *Microtropis,* and *Schaefferia*). The five nectaries present in *Corynocarpus* (Corynocarpaceae) are interpreted as a discontinuous disk (see discussion by Philipson, 1987).

26. *Disk division*: continuous (0); discontinuous (1). 3, 2, 0.33, 0.33.

A discontinuous disk is present in *Apodostigma* and

Cheiloclinium. The disk in these genera may actually be very deeply lobed, not divided. Smith (1940: 525) described the disk of *Cheiloclinium* as "forming 3 (5 in group *Anomala*) (rarely 4) saccate carnose staminiferous lips." These "staminiferous lips" surround the stamens, with the disk divided between stamens. This is in contrast to some Celastraceae s. str. in which the disk is notched at the point of filament insertion on the disk.

27. *Disk shape*: cupular, not adnate to sepals (0); annular, flat, or margins upturned (1); cupular, adnate to sepals (2). 7–8, 5–6, 0.25–0.28, 0.62–0.68.

A cupular disk that is not adnate to sepals primarily occurs in genera of Hippocrateaceae. Many genera of Celastraceae s. str. have flat disks with the margins upturned, whereas cupular disks do not have a flat inner region.

Cupular disks that are adnate to sepals are present in *Stackhousia* and *Tripterococcus brunonis* (Stackhousiaceae).

28. *Disk pubescence*: glabrous (0); conspicuously puberulent (1). 2, 1, 0.50, 0.50.

The disk is pubescent in *Hippocratea*, *Plagiopteron*, and *Prionostemma*.

29. *Androgynophore presence*: absent (0); present (1). 3–4, 2–3, 0.25–0.33, 0.00–0.33.

This character was scored as inapplicable for taxa that have strictly unisexual flowers. Within Celastraceae s.l., an androgynophore is only present in *Helictonema velutinum*, *Loeseneriella*, *Simicratea*, and *Simirestis*.

30. *Stamen plus staminode number*: three or generally three (0); same as petal number (1); two (2); twice or more than twice petal number (3). 8, 5, 0.37, 0.83.

31. *Fertile stamen length*: equal (0); unequal and monomorphic (1). 1, 0, 1.00, 1.00.

Unequal length monomorphic stamens occur in *Stackhousia* and *Tripterococcus brunonis* (Stackhousiaceae) in addition to some species of *Forsellesia*.

32. *Staminode presence in same flower with functional stamens*: absent (0); present (1). 3, 2, 0.33, 0.33.

Staminodes in the same flower with functional stamens occur in *Corynocarpus* (Corynocarpaceae), *Lepuropetalon* and *Parnassia* (Saxifragaceae), and *Siphonodon*. In all of these genera, five functional stamens alternate individually with five staminodes.

33. *Stamen-petal arrangement*: alternate (0); opposite (1). 1, 0, 1.00, 1.00.

Opposite stamen-petal arrangement occurs in *Corynocarpus* (Corynocarpaceae) and *Forsellesia*.

34. *Numerous stamen arrangement*: unicyclic and twice petal number (0); bicyclic and twice petal number (1); bicyclic and more than twice petal number (2); clustered or connate in center of flower (3). 4, 1, 0.75, 0.75.

35. *Filament insertion relative to disk*: at outer disk margin (0); on disk (1); inside inner edge of disk (2). 7, 5, 0.28, 0.84.

36. *Anther dehiscence direction*: introrse to introrse-latrorse (0); strictly latrorse (1); extrorse (2); apical (3). 7, 4, 0.42, 0.86.

Most Celastraceae s. str. are introrse to introrse-latrorse. Most Hippocrateaceae are extrorse.

Apical dehiscence occurs in *Plenckia* and *Crossopetalum*. *Plenckia* was coded as having apical oblique dehiscence, whereas other obliquely dehiscent genera (e.g., *Glyptopetalum*, *Euonymus alatus*) were coded as strictly latrorse. The difference between *Plenckia* and the other taxa is that *Plenckia* does not have a thick triangular connective that makes the anthers latrorse, while the others do.

37. *Anther dehiscence plane*: longitudinal (0); oblique (1); transverse (2). 6, 4, 0.33, 0.84.

This character may seem to be non-independent with character 29, as longitudinal dehiscent anthers are introrse while transversely dehiscent anthers are extrorse. However, *Campylostemon* and *Tristemonanthus* have transversely dehiscent introrse anthers. *Kokoona* is the only genus with strictly latrorse longitudinally dehiscent anthers.

38. *Anther attachment*: basifixed (0); dorsifixed (1). 8, 7, 0.12, 0.61.

The transversely dehiscent anthers of Hippocrateaceae were scored as dorsifixed, not basifixed. This coding is not immediately obvious as these anthers appear basifixed. However, if the anther locules were folded downward, as occurs in some longitudinally dehiscent species in *Salacia* subg. *Eusalacia*, the anthers would be easily recognized as dorsifixed.

39. *Anther versatility*: not versatile (0); versatile (1). 6–7, 5–6, 0.14–0.16, 0.77–0.81.

Taxa were scored as versatile if, on herbarium specimens, a probe may be used to easily twist the anther on the filament. Stamens with thin, tapered connectives generally have versatile anthers. *Elaeodendron* is described as having versatile anthers (Hou, 1962, as *Cassine*; Robson et al., 1994). However, none of the herbarium specimens of *Elaeodendron* the senior author has examined (in species other than the three included in the analysis) have versatile anthers. This may be due to a difference in versatility in fresh versus dried flowers.

40. *Connective extension shape*: absent or apiculate (0); triangular (1); large ornamented extension (2); bilobed with brush-hairy tip (3); bilobed without brush-hairy tip (4). 4, 0, 1.00, 1.00.

Apiculate extended connectives were not distinguished from connectives without extensions. The presence or absence of an apiculum may vary among flowers of a single specimen. Within Celastraceae s.l., triangular connective extensions are only present in *Acanthothamnus aphyllus* and *Canotia*; large ornamented connective extensions are only present in *Kokoona*; bilobed connective extensions with brush-hairy tips are only present in *Goupia*; bilobed connective extensions without brush-hairy tips are only present in *Peritassa*. These various forms of connective extensions are not coded as homologous because of their striking differences in shape or pubescence.

41. *Ovary pubescence*: glabrous (0); completely pilose (1); stellate (2); tomentose (3); densely hirsute (4); apex pilose (5); stellate (6). 7, 2, 0.57, 0.50.

42. *Apical hollow in ovary center*: absent (0); present (1). UNINF.

With Celastraceae s.l., an apical hollow in the center of the ovary occurs only in *Siphonodon* (see Croizat, 1947, for discussion of this structure). This structure is not the same as found in *Brassiantha*, which is described by Smith and Bailey (1941: 393) as ". . . the stigmas are obscure, apparently reduced to minute radiating lines in the hollow of the ovary-summit." *Siphonodon*, in contrast, has a deep circular cavity with a narrow column arising from the base.

43. *Style connation*: connate (0); not connate (1). 1, 0, 1.00, 1.00.

Bhesa, in which the two styles are free or connate only at the very base, was coded as uncertain. This character was coded as inapplicable for taxa without styles (e.g., *Brassiantha*). For *Siphonodon*, we follow Croizat (1947) in which the narrow column in the apical cavity is not interpreted as a style; rather, the styles are around the margin of the cavity (see his fig. 4). *Lophopyxis* was coded based on Hooker's (1888) description "stigmas 5, sessile, subulate, recurved," in conjunction with the illustration of Hooker (1887–1888) plate 1714 numbers 8 and 9 where stigmas (or styles?) are obviously distinct from one another.

44. *Ovary carpel number*: one (0); two or modifications thereof (1); three (2); equals perianth merosity (3); many irregularly superposed (4); four, when not equaling perianth merosity (5). 16, 11, 0.25, 0.61.

Within Celastraceae s.l., many irregularly superposed carpels occur only in *Siphonodon*, which is very different from all other taxa sampled.

45. *Ovary septa walls*: complete (0); incomplete (1); absent (2). 4, 2, 0.50, 0.77.

This character is based on whether or not ovary septa walls meet in the center of the ovary (complete) or not (incomplete). *Stackhousia* and *Tripterococcus brunonis* (Stackhousiaceae), in which the carpels are basically separate from one another, were coded as inapplicable for this character.

Brexia was coded as polymorphic based on the description by Verdcourt (1968: 1) in which the genus was described as ". . .completely or imperfectly 5–7 locular."

46. *Ovule number per locule*: one (0); two or four (1); variable and more than four (2). 21, 19, 0.09, 0.42.

47. *Placentation*: axile (0); parietal (1). 1, 0, 1.00, 1.00.

Parietal placentation occurs in *Lepuropetalon* and *Parnassia* (Saxifragaceae).

48. *Axile ovule attachment*: basal to axile, erect or horizontal (0); pendulous (1). 7, 6, 0.14, 0.25.

49. *Obturator presence*: absent (0); present (1). 1, 0, 1.00, 1.00.

Obturators are present in *Aleurites*, *Astrocasia* (Euphorbiaceae), and *Lophopyxis*. *Lophopyxis* was scored based on Willis (1966: 668), who described ovules of Lophopyxidaceae as ". . .each surmounted by an obturator-like appendage." Pfeiffer (1951: 6) also cited this as an "anomalous appendage." However, note that Hooker (1888) cited *Lophopyxis* as "obturator 0." Hooker (1887–1888) also cited "obturatore 0." We are making the assumption that Pfeiffer and Willis saw something Hooker did not, which does in fact exist. Willis (1966) cited no other taxa included in this study (outside of Euphorbiaceae) as having an obturator.

FRUIT

50. *Fruit type*: dehiscent (0); indehiscent (1); cocci (2). 8, 6, 0.25, 0.79.

51. *Indehiscent fruit type*: drupaceous (0); baccate (1); samara (2); nut (3). 7–8, 4–5, 0.37–0.42, 0.37–0.50.

All samaroid indehiscent fruits were coded as homologous, regardless of wing position. This assertion is based on the observation that in fruits with apical wings (see character 52), the wing begins at the base along the side of the fruit; the wing is not confined to the apex of the seed.

52. *Fruit wing form*: at apex (0); at side along each locule (1). 2, 1, 0.50, 0.50.

This character was coded as inapplicable for taxa without winged fruits to avoid non-independence among characters. Within Celastraceae s.l., an apical fruit wing occurs only in *Plenckia*, *Rzedowskia tolantonguensis*, and *Zinowiewia*. A wing along the side of each locule occurs in *Ptelidium*, *Tripterygium*, *Wimmeria*, and also *Platypterocarpus* and some *Euonymus*.

53. *Capsular fruit shape*: not lobed or parted (0); strongly parted among locules (1); lobed but not parted among locules (2); lobed to base but not parted among locules (3); flattened along each locule but not parted (4). 4, 0, 1.00, 1.00.

Within Celastraceae s.l., capsular fruits that are strongly parted among locules occur only in *Hippocratea* s.l. Each of these three-parted segments is generally termed a mericarp in the literature. A capsular fruit that is lobed but not parted among locules occurs in *Bhesa*. A capsular fruit that is lobed to the base but is not parted among locules occurs in *Euonymus alatus* and several other *Euonymus* species. A capsular fruit that is flattened along each locule but is not parted occurs in *Kokoona*, *Lophopetalum*, and *Peripterygia*. States two, three, and four are quite distinct from state one.

54. *Mericarp connation*: separate (0); connate (1). 2, 1, 0.50, 0.00.

This character was coded only for taxa with state one (capsules strongly parted among locules) in character 53. The character was scored as inapplicable for all other taxa. Within Celastraceae s.l., connate mericarps are only present in *Anthodon* and *Semialarium excelsum*.

55. *Capsular fruit dehiscence*: loculicidal (0); one side laterally split (1); septicidal (2). 3, 2, 0.66, 0.66.

This character was scored only for taxa with dehiscent fruit (character 50 state 0). The character was scored as inapplicable for all other taxa. Capsular fruits that split laterally along one side occur in *Crossosoma* (Crossosomataceae), *Forsellesia*, *Microtropis*, and *Quetzalia*. Within Celastraceae s.l., septicidal capsule dehiscence is only present in *Canotia*. Note that the fruit of *Canotia* also splits, although less strongly, loculicidally (there are twice as many splits as there are locules).

Sarawakodendron was described by Corner (1976) as having capsules with septicidal dehiscence. However, in the original generic description by Hou (1967), *Sarawakodendron* was described and illustrated as having capsules with loculicidal dehiscence. We followed Hou (1967) in our coding.

SEED

56. *Aril presence*: absent (0); present (1). 5, 4, 0.20, 0.86.

The small wings of *Canotia* and *Catha edulis* seeds are interpreted as modified arils. The large apical and circular wings of *Kokoona* and *Lophopetalum* (also present in *Peripterygia*) are interpreted as modified arils. The large basal wings (or flanges) of *Hippocratea* s.l. are also interpreted as modified arils. Finally, the mucilaginous pulp surrounding seeds of *Salacia* s.l. (Salacieae) is also interpreted as a modified aril.

Helictonema velutinum was described by Robson et al. (1994: 43) as having "no pocket-like structure at the point of attachment (such as occur in *Simirestis* and *Pristimera*) but sometimes with the vestiges of arils." However, in examining the well-preserved mature fruiting holotype specimen (*R. P. Klaine 1316*), the senior author found no evidence of any such "vestiges of arils." He did, however, note a "pocket-like structure" at the point of seed attachment. Therefore, based on these observations, this "vestiges of arils" character was not coded into the matrix.

Corner (1976) contradicted Hou (1962) in describing seeds of *Microtropis* and *Perrottetia* as exarillate. For *Microtropis*, Corner (1976: 94) stated, "It appears that the thick testa has been mistaken for an aril (Hou, 1962)." Lundell (1970) described *Quetzalia*, which he segregated from *Microtropis*, as exarillate. However, in observing

Breedlove 55604 (NY) the senior author thought he observed an aril, apparently making the same mistake Hou did, in misinterpreting the orangish red fleshy seed coat. We followed Corner (1976) in coding *Microtropis* and *Perrottetia* as exarillate.

57. *Aril position on seed*: entirely enveloping seed (0); partly enveloping seed (1). 5, 4, 0.20, 0.55.

The wings (modified arils) of *Kokoona* and *Lophopetalum* are interpreted as entirely enveloping the seed. This coding was based on the descriptions and illustrations of Hou (1962) in which the primarily apical wing of *Kokoona* also extends around the base of the seed, and the circular wing of *Lophopetalum* completely encircles the seed. The basal wings of *Canotia, Catha edulis,* and *Hippocratea* s.l. were coded as partly enveloping the seed. The mucilaginous pulp (modified aril) of *Salacia* s.l. (Salacieae) was coded as entirely enveloping the seed.

58. *Aril form*: fleshy (0); basal wing with vasculature of the funiculus along wing (1); mucilaginous pulp (2); wing surrounding seed with medial or basal attachment of the vasculature of the funiculus (3); basal wing with vasculature of the funiculus attached above wing (4). 5, 1, 0.80, 0.95.

Within Celastraceae s.l., a basal wing with vasculature of the funiculus along the wing occurs only in *Hippocratea* s.l. Mucilaginous pulp occurs only in *Salacia* s.l. (Salacieae).

An aril modified to be a wing surrounding the seed with medial (or basal in *Kokoona*) attachment of the vasculature of the funiculus occurs only in *Kokoona, Lophopetalum,* and *Peripterygia.* A basal wing with vasculature of the funiculus attached above the wing occurs in *Canotia* and *Catha edulis.*

59. *Fleshy aril form*: without filamentous extensions (0); with filamentous extensions from base (1); with filamentous extensions from apex. UNINF.

This character was only coded for taxa with fleshy arils (character 58 state 0). *Sarawakodendron filamentosum* has fleshy arils with filamentous extensions from the base. *Crossosoma* (Crossosomataceae) has fleshy arils with filamentous extensions from the apex. Taxa with laciniate arils (e.g., *Maytenus abbottii* van Wyk) were not interpreted as having filamentous extensions from the apex of the aril.

60. *Basal seed wing form*: membranous, papyraceous, or thin coriaceous (0); membranous or a flange (1). 2, 1, 0.50, 0.00.

This character was only coded for those taxa with a basal seed wing with the vasculature of the funiculus along the wing (Campylostemonae, Helictonemateae, and Hippocrateeae). A membranous or flange-like basal seed wing occurs in *Cuervea* and *Elachyptera.* Both genera have species with a large membranous wing and other species in which the wing is a flange. A similar state also occurs in *Hylenaea.*

61. *Raphe branching*: unbranched (0); branched (1). 2, 1, 0.50, 0.00.

A branched raphe (postchalazal vascular branches) is present in *Bhesa* and *Glyptopetalum.* A branched raphe also occurs in *Brexiella.* All three genera with branched raphes were observed by the senior author; the branched raphes of *Bhesa* and *Glyptopetalum* are also described by Corner (1976).

62. *Endosperm presence*: present (0); absent (1). 3, 2, 0.33, 0.85.

Many codings were taken from Miers (1872), Hou (1962, 1964), and Robson et al. (1994). The coding for *Dicarpellum* was taken from Baillon (1872) and observations by the senior author. The coding for *Sarawakodendron* was taken from Hou (1967) and Corner (1976).

63. *Exotegmic palisade of lignified malpighian cells presence on seed*: absent (0); present (1). 2, 1, 0.50, 0.00.

An exotegmic palisade of lignified malpighian cells occurs in *Aleurites* (Euphorbiaceae) and *Perrottetia.* This character was coded from Corner (1976).

64. *Seed tegmen composition*: fibrous (0); not fibrous (1). 3, 2, 0.33, 0.71.

This character was coded from Corner (1976) and Tobe and Raven (1993).

65. *Seed germination type*: epigeal (0); hypogeal (1). 4, 3, 0.25, 0.50.

Codings were taken from Hallé (1962, 1986) and de Vogel (1980).

66. *Seedling growth*: becoming free from all envelopments (0); not becoming free from all envelopments (1). 1, 0, 1.00, 1.00.

Codings were taken from de Vogel (1980). This character appears independent from character 57, as *Lophopetalum* has epigeal germination with the seed not becoming free from all envelopments, whereas *Salacia* has hypogeal germination with the seed not becoming free from all envelopments.

LEAF ANATOMY

67. *Mucilaginous leaf epidermal cells*: absent (0); present (1). 3, 2, 0.33, 0.00.

This character was coded from Solereder (1908). Solereder (1908: 875) stated, "Mucilaginous epidermal cells have only been recorded in *Goupia glabra,* Aubl., *Perrottetia alpestris,* Loes. and *P. sandwicensis,* Gray." Metcalfe and Chalk (1950) did not note mucilaginous cells in any Celastraceae s.l. Mucilaginous leaf epidermal cells are also present in *Geissoloma marginatum.*

68. *Presence of crystals in leaf epidermal cells*: absent (0); present (1). 5, 4, 0.20, 0.73.

Codings for this character and character 69 were taken from Den Hartog née Van Ter Tholen and Baas (1978).

69. *Crystal type*: druses (0); solitary rhomboidal crystals (1). 5, 4, 0.20, 0.33.

Only taxa that were coded as having crystals in leaf epidermal cells present (character 68) were coded for this character. This character was coded as inapplicable for all other taxa to avoid non-independence among characters.

70. *Vascular strand through petiole in cross section*: uninterrupted (0); interrupted (1). 3, 2, 0.33, 0.85.

Codings were taken from Solereder (1908), Metcalfe and Chalk (1950), Baas et al. (1979), and Mueller (1995). *Aleurites* and *Astrocasia* (Euphorbiaceae) were coded as interrupted based on Metcalfe and Chalk (1950: 1213) who stated, "Petiole examined in 125 genera by Dehay (557), according to whom 3 leaf-traces enter the base in most species, although higher numbers (up to 8 in *Ricinus*) were observed in a few instances." *Lepuropetalon* is coded as interrupted based on Metcalfe and Chalk (1950), in which all Saxifragaceae were described and illustrated as having an interrupted vascular strand through the petiole in cross section. *Lepuropetalon* was one of the genera of Saxifragaceae cited as examined by Metcalfe and Chalk (1950).

WOOD ANATOMY

71. *Included phloem presence*: absent (0); present (1). 1, 0, 1.00, 1.00.

Character-state codings were taken from Brown (1922), Record (1943), and Mennega (1994, 1997). Mennega (1997: 335) stated, "Included phloem is restricted to the Salacieae where it is found in all genera, though not in all species, as it is usually not present in trees, *Cheiloclinium cognatum* excepted." Therefore, this character was only coded for taxa in which some members are scandent or are lianas, unless they are found to have included phloem in the trees (which has not been reported except in *Cheiloclinium cognatum*). For taxa in which some species are lianas and have included phloem, whereas other species in the taxon are erect shrubs or trees and do not have included phloem, this character was coded as included phloem present, not as polymorphic, because only scandents or lianas are being coded. It is expected that Record (1943) would have described any Celastraceae he examined as having included phloem, were it present. He did not describe included phloem in any of the Celastraceae examined. Therefore, those taxa that he studied which include scandent members were coded as included phloem not present.

72. *Ray width*: one to six cells (0); some greater than ten cells (1). 2, 1, 0.50, 0.93.

Within Celastraceae s.l., very wide rays are only present in *Hippocratea* s.l. Most taxa coded as having narrow rays have only uniseriate and biseriate rays. Most codings were taken from Record (1943) and Mennega (1972, 1997). *Bhesa* was coded based on Xinying et al. (1990), and *Stackhousia* was coded based on Carlquist (1987). Solereder (1908: 884) cited "the absence of medullary rays in the wood" in Stackhousiaceae. However, Carlquist (1987) described rays as one to three cells wide in *Stackhousia*. We followed Carlquist (1987) in our coding of *Stackhousia*.

73. *Unlignified ray cells on the growth ring border presence*: present (0); absent (1). 3–5, 2–4, 0.20–0.33, 0.20–0.60.

Codings were taken from Mennega (1997). This character was only coded for taxa with state one in character 72. This is based on Mennega (1997: 335): "A striking feature of the wide rays in certain genera of the Hippocrateae (Table 2 [sic]) is constituted by the rows of unlignified cells forming a V-shaped figure at the growth ring margins (Fig. 21, 24)." As Salacieae (Mennega only examined genera of Hippocrateaceae) do not have wide rays, they were coded as inapplicable for this character. *Reissantia* was coded as uncertain because Mennega (1997: 366) cited unlignified ray cells at the growth ring border in *Reissantia* as "only noticed as rare cells in *R. indica* var. *loeseneriana*." This may be due to growth rings being inconspicuous or absent in the genus (Mennega, 1997).

74. *Perforation plate type*: simple (0); scalariform (1). 5, 4, 0.20, 0.50.

Codings were taken from Record (1943), Metcalfe and Chalk (1950), Den Hartog née Van Ter Tholen and Baas (1978), Xinying et al. (1990), Archer and van Wyk (1993b, 1997), and Mennega (1994). *Aleurites* and *Astrocasia* (Euphorbiaceae) were coded from Metcalfe and Chalk (1950) where they cited Crotonoideae as having simple perforation plates and Phyllanthoideae as having scalariform (their group A) or simple perforation plates (their group B). *Aleurites* is a member of Crotonoideae, and *Astrocasia* is a member of Phyllanthoideae (Webster, 1975). As we do not know if *Astrocasia* would be included in Metcalfe and Chalk's group A or B, the genus was coded as uncertain for this character.

75. *Parenchyma-like bands of thin-walled septate wood fibers presence*: absent (0); present (1). 5–6, 4–5, 0.16–0.20, 0.33–0.78.

Codings were taken from Brown (1922), Smith and Bailey (1941), Record (1943), Xinying et al. (1990), Archer and van Wyk (1993b), and Mennega (1994, 1997). *Elaeodendron* was coded as polymorphic following Archer and van Wyk (1993b).

POLLEN MORPHOLOGY

76. *Pollen aggregation*: monads (0); tetrads or polyads (1). 3, 2, 0.33, 0.60.

This character was scored primarily from Lobreau-Callen (1977). *Sarawakodendron* was scored from Hou (1967); *Corynocarpus* (Corynocarpaceae) was scored from Nowicke and Skvarla (1983); *Lophopyxis* and Euphorbiaceae were scored from Erdtman (1952); and *Plagiopteron* was scored from Baas et al. (1979). All genera scored as having "tetrads or polyads" have tetrads, though *Hippocratea* and *Lophopetalum* also sometimes have polyads.

77. *Pollen annulus presence*: absent (0); present (1). 5, 4, 0.20, 0.78.

This character was scored from Lobreau-Callen (1977). *Plagiopteron* was scored from Baas et al. (1979), and *Sarawakodendron* was scored from Hou (1967). The annulus is a thickening on the interior of the pore (Lobreau-Callen, 1977, plate 14 number 10).

KARYOTYPE

78. *Base chromosome number*: 8 (0); 9 (1); 10 (2); 11 (3); 12 (4); 14 (5); 15 (6); 17 (7); 23 (8). 10, 2, 0.80, 0.85.

Chromosome numbers are quite variable within Celastraceae s. str. Within Hippocrateaceae, however, the base chromosome number stabilizes at 14 (15 for *Semialarium excelsum*). This character was coded from Bolkhovskikh et al. (1969) and *Index to Plant Chromosome Numbers* (Cave, 1958, 1961, 1964; Ornduff, 1967, 1968; Moore, 1971, 1973, 1977; Goldblatt, 1981, 1984, 1985, 1988; Goldblatt & Johnson, 1990, 1991, 1994).

79. *Haploid chromosome number of plants with base chromosome number of 14*: 14 (0); 28 (1). 1, 0, 1.00, 1.00.

This character was coded only for those taxa with a base chromosome number of 14 in character 78. All other taxa were coded as inapplicable (if their chromosome numbers are known).

APPENDIX 3. Rejected characters for cladistic analysis. List of 80 characters rejected for inclusion in cladistic analysis and reason(s) for rejection. "1" = unable to score from herbarium specimens; "2" = unable to confirm description from literature with observations from herbarium specimens; "3" = unable to distinguish distinct character states; "4" = lack of independence from other character(s); "5" = developmental stage that may or may not appear present on herbarium specimens depending on when collected or where on plant specimen was collected; "6" = invariant.

Character	Reason for rejection
Plant habit: herbaceous, woody	3
Woody plant habit: scandent, erect	3
Presence of buttressed trunks	1
Presence of thin, papery orange layer on older bark	2
Presence of deep furrows filled with parenchyma on old stems	2
Presence of swollen and/or slightly flattened nodes	3
Presence of branchlets drying blackish	3
Presence of darkened branchlets	3
Presence of zigzag branchlets	4
Presence of striate branchlets	3
Presence of subpersistent bracts at terminal node	5
Presence of elastic or resinous threads	4
Vegetative plant pubescence	3
Opposite leaf arrangement: opposite, opposite or subopposite	5
Opposite leaf arrangement: decussate, distichous	3
Alternate leaves: spiral, distichous	5
Presence of convex midrib so blades fold in herbarium specimens	2
Presence of heteromorphic leaf sizes	5
Presence of decurrent leaves	2
Presence of shiny adaxial leaf blades	3
Presence of black dots on abaxial surface of leaf blade	1
Leaf margin: entire, toothed or crenate, dentate-thorned	3
Presence of stipules	6
Stipule persistence	3
Stipule margin: simple, laciniate, or fimbriate	3
Structure subtending inflorescence: leaves, leaves or only bracts	5
Presence of cauliflorous inflorescences	1
Presence of accessory branches in axils of leaves subtending inflorescences	2
Presence of quadrangular internodes	3
Presence of bracts in inflorescence	6
Color of bracts in inflorescence	3
Inflorescence bract persistence	3
Pedicel bract number at articulation	5
Inflorescence flower number	3
Flower pubescence	4
Petal color	3
Corolla aestivation: imbricate, valvate	3
Presence of irregularly cleft inner petals	2
Size of inner relative to outer calyx lobes	3
Sepal margin: entire, fringed, ciliate	3
Sepal connation	2
Petal connation	2
Presence of contorted petals	2
Presence of petals with two longitudinal grooves	1
Presence of clawed petals	3
Petal margin: entire, erose, ciliate, denticulate	3
Petal adnation to staminal disk	3
Disk conspicuousness	3
Disk texture: fleshy, membranous	3
Presence of notch in disk opposite stamens	3
Disk margin: entire, lobed, or angular	3
Disk surface: smooth, rugose, or papillate	3
Stamen position relative to disk lobes: between, within	6
Stamen position at anthesis: inflexed, erect, reflexed	3, 5
Stamen persistence	3, 5
Stamens ± connivent around ovary	2
Presence of pappillae on filaments	2, 5
Presence of thick dorsal connective on stamens	3, 4
Pollen surface	6
Pollen aperture type	2
Ovary position relative to disk	3
Ovary adnation to disk	3
Style shape: obscure, short and stout, long and slender	3
Stigma division: lobed, unlobed	3
Stigma with central depression	3
Position of stigmas relative to stamens: alternate, opposite	1
Presence of disk subtending fruit	6
Perianth subtending fruit: none, calyx, calyx and corolla	5
Inner capsule pubescence: glabrous, densely pubescent	4
Columella persistent after capsule dehiscence	2
Seed color: black, red or red-brown, brown	3
Testa surface texture: smooth, wrinkled	5
Seed pubescence: glabrous, pubescent	4
Presence of angular seeds	3
Presence of elongated funiculus	3
Presence of elevated bilobed structure subtending seeds	4
Aril color: white, orange, or red	3
Cotyledon connation	1
Radicle prominence: prominent, very reduced	3
Leaf gap number: unilacunar, trilacunar	4

Appendix 4. Character data matrix. Data matrix for 79 characters (Appendix 2) scored for 82 taxa of Celastraceae and related families (Appendix 1). Complete and subset polymorphisms are indicated as signified as: A = [0,1]; B = [0,1,2]; C = [0,2]; D = [0,1,3]; E = [0,1,2,3]; F = [1,2]; G = [1,3]; H = [1,4]; I = [1,2,4]; J = [2,3]; K = [2,5]. "-" = character inapplicable for a taxon; "?" = character state unobserved for a taxon.

	Character number							
		1 1	2 2	3 3	4 4	5 5	6 6	7 7
Taxon	1 5	1 5	1 5	1 5	1 5	1 5	1 5	1 5
(1)	0000000000	000-111-10	0000111003	?111-00110	00-0-0-101	0----1----	01011?0??1	-1?000?3-
(2)	0000000001	000-151-10	0000101003	00-2100100	0012-2--00	--0-10102-	?000??0???	-0?A00?4-
(3)	0000000100	000-110?10	00001010-3	00-3200000	201E000111	0----1----	?01000???1	-??0?0?3-
(4)	0000000000	000-030A10	000010A0-A	00-32?0000	0012010110	--0-01----	00000????1	-??1?00?-
(5)	00001-0201	0000151-00	00000---03	00-1-00110	001301-100	--0-01----	?0????1???	-0?100???
(6)	0000000100	000-031-11	00000---03	00-0-?00?0	20?320-00?	?-0-?1----	?0????00-1	-??0?0???
(7)	0000000100	000-031-11	00000---03	00-0-?0000	30-320-000	--0-?1----	?0????00-1	-??0?01??
(8)	0000000000	000-151-10	---010-003	0101000000	0012221-00	--0-01----	?000?????1	-????00H-
(9)	00000000?0	000-151-10	000010-003	0101-00110	001K221-00	--0-01----	?A??0?????	-????0?1-
(10)	0000000000	000-111-10	0001102001	100-000000	101J-0-002	-----1----	?00???0???	-0?0?01I-
(11)	0000000000	000-111-10	0001102001	100-000000	1012-0-002	-----1----	?00???0???	-0?0?010-
(12)	0000000000	000-061-10	0000101001	000-000100	0003A20001	0----1----	?000?????1	-0?1?????
(13)	0011001000	0---001-10	0000101001	000-000111	00031F0000	----2014-0	?000??????	-???0????
(14)	0000000010	110-021-10	0000100001	000-100003	0013?20001	1----????-	?0????10-1	-0?1000??
(15)	1000000?00	???-1A0110	0000101?-1	000-?2???0	3013?10111	??---????-	?0????????	?????0???
(16)	00001-0100	0000011-B0	0000101103	00-2222100	1002010000	--10??????	??????01?1	0??0?00??
(17)	0000000000	000-061-10	0000101003	0100011000	0114?00A01	0----1----	?0??000100	-??0?00??
(18)	00001-0000	000000A100	0000101001	000-111100	000J010000	--3-00000-	000A?000-0	-0?00000-
(19)	00001-0000	000000A100	0000101001	000-000110	0003010100	--0-00000-	000A?000-0	00?00000-
(20)	00001-0000	0000011-10	0000101001	000-0001?0	0003020000	--0-00100-	000A?000-0	-0?00000-
(21)	00001-0000	0000001-00	0000101001	000-111000	0003000100	--0-00100-	1?0????0-0	-????00??
(22)	00001-0000	000000A1A0	000010A001	000-0C0110	0001A10000	--0-11----	?000??00-0	-??0?00??
(23)	00001-0000	00000001A0	0000101001	000-000110	00011A0000	--0-11----	?0?????0-?	-??0?00??
(24)	0000000000	000-001-00	0000101001	000-111000	00-3020000	--0-00100-	?0?????0-?	-????00??
(25)	0000000000	011-011-A0	0000100001	000-0C0000	50?1?10000	--2-A0A00-	10000000-1	-0-1?00??
(26)	0000010000	0001001-10	0000101001	000-000110	00?2A10000	--0-0014-0	00?0??00-0	-??0?00??
(27)	0000000000	0000110010	000010A0-1	000-000110	0002A10000	--0-00000-	0000?000-0	00?00008-
(28)	0000000000	0000111-10	0000101001	000-000110	0002A00000	--0-00000-	0000?000-0	00?0000?-
(29)	0100010001	000-000A10	0000101001	000-000110	0002A10000	--0-00100-	0A01??00-0	-??0100H-
(30)	0100010001	000-000A10	0000101001	000-000110	0002A10000	--0-00000-	0A01??00-0	-??0100H-
(31)	0000000000	000-031-10	0000101001	000-000110	0002A10000	--0-00A00-	0A????00-0	-??A100I-

Appendix 4. Character data matrix. Continued.

Taxon	Character number							
		1 1	2 2	3 3	4 4	5 5	6 6	7 7
	1 5	1 5	1 5	1 5	1 5	1 5	1 5	1 5
(32)	00001-0000	0000030010	00001010-1	000-000110	0002010000	--0-00A00-	00???????0	-????00??
(33)	00001-0000	0000001-00	0000101001	000-000110	0001110000	--0-00?00-	?0????0???	00?00000-
(34)	0000000000	000-231-10	0000101001	000-000110	0003010000	--0-00100-	?A????0???	-????00??
(35)	0100010001	000-001-A0	0000101001	000-000010	0002?20000	--0-00000-	00????0???	-????????
(36)	0000000000	000-030010	00001010-1	000-000110	0002010000	--0-00A00-	00???????A	-????00??
(37)	0000000000	000-030010	00001010-1	000-000110	0002?00000	--0-00000-	?0?????0-?	-??????2?
(38)	0000A-0000	0000011-10	0000100001	000-210112	00-2020000	--4-0003--	?101??00-?	-??0?01??
(39)	0000A-0000	0000011-10	0000101001	000-100110	0002020000	--4-0003--	0A01010110	-??0?112-
(40)	0000000000	000-001-10	0000101001	000-031000	0001?10001	20---1----	00????00-?	-0?0100??
(41)	00001-0000	0000001-A0	0000101001	000-100100	0001010001	21---1----	?0????????	-????00??
(42)	0000000000	000-11A110	0000101001	000-000110	0002110001	21---1----	0?????0??0	?????004?
(43)	0000000001	000-001-A0	0000101001	000-000110	000F120001	21---1----	00????00-?	-0?0000??
(44)	00001-0000	0000001-10	0000101001	000-000110	0001010001	20---1----	00????????	-????00??
(45)	0011000000	000-031-10	0000101001	000-000111	0003?10001	0----1----	?000??????	-????????
(46)	00001-0000	0000001-10	0000101001	000-000100	0001?10001	1----1----	?0????0A10	-010100??
(47)	00001-0000	0000001-00	0000101001	000-000000	0001?10001	1----1----	?0????0A10	-010100??
(48)	0000100000	0000001-10	0000101001	000-000100	0002010001	0----1----	00????0A10	-0111007-
(49)	0000100000	0000001-10	0000101001	000-000100	0003010001	0----1----	00????0A10	-0111007-
(50)	0000100000	000000A100	0000101001	000-000100	0001010001	0----1----	00????0A10	-0111007-
(51)	0010000001	000-151-A0	000010100G	A011000110	00-B2A-000	--0-10100-	00????0???	-??0?0???
(52)	00001-0000	0000000000	00001010-1	000-000000	0001000101	0----1----	?0????????	-????00??
(53)	0000000000	000-111-10	0000101001	000-000110	0003110001	3----1----	00????0???	-0?0000??
(54)	0000010001	000-030000	00001010-1	000-000100	0001000001	0----1----	?0????0???	-0?0000??
(55)	0000000000	100-01A0A0	0000101001	000-000110	0001010001	1-0--1----	0010??1??0	-0?1100??
(56)	0000000000	000-0A1-10	0000100001	000-222100	00-30F0000	--0-00000-	?0?????0-?	-???100??
(57)	0000000000	000-040010	000010A000	00--22C100	0001010000	--0--0100-	00????????	-?-??0???
(58)	00001-0000	0000001-00	00001010?1	000-??00?0	0001?10001	20---1----	00????????	-????????
(59)	0000000000	0?0-041-10	0000101000	00--222100	0002020000	--0-00101-	0000???0-?	-????00??
(60)	00001-0000	0000001-10	00100---00	00---22100	00-2020000	--100011-0	0?????????	0110011??
(61)	00001-0000	00000A1-10	00000---01	000--02100	00-2020000	--100011-0	0???0??0-?	011001151
(62)	00001-0000	0000001-10	00000---00	00---02100	0002020000	--100011-0	0?????????	0110011??
(63)	00001-0100	0000001-10	0000101010	00--222100	1002020000	--100011-0	0??????10?	0110001??
(64)	00001-0000	0000001-10	1000100000	00--222100	0002020000	--110011-0	0??????10?	0100001??
(65)	00001-0000	0000001-10	0100110000	00--222100	00-2010000	--100011-0	0???0??0-?	0100001??

Appendix 4. Character data matrix. Continued.

Taxon	Character number							
	1 5	11 15	21 25	31 35	41 45	51 55	61 65	71 75
(66)	00001-0000	0000001-10	0000100000	00--222100	00020F0000	--100011-1	01??1??11?	010010151
(67)	00001-0000	00001A1-10	0000100000	00--222100	0002010000	--100011-1	0???????11?	0110001??
(68)	00001-0000	00000A1-10	0000100100	00--222000	0002020000	--100011-0	010????101	01100115A
(69)	00001-0000	0002001-10	0000100010	00--222100	0002020000	--100011-0	01??1??11?	01100015A
(70)	00001-0000	0000001-10	0000101100	00--222100	1002020000	--100011-0	01?????11?	0110001??
(71)	00001-0000	0000001-10	000010A000	00--222100	0002020000	--100011-0	0??????11?	0100001??
(72)	00001-0000	0000001-10	0000100000	00--222100	0002010000	--100011-0	01??0??0-?	01?0001??
(73)	00001-0000	00001A1-10	0000100000	00--222100	0002020000	--110011-0	01?????11?	01101016-
(74)	00001-0000	0000001-10	0000101010	00--222100	0002010000	--100011-0	0?????????	0100000??
(75)	00001-0000	0000001-10	0000101010	00--222100	0002020000	--100011-0	0???1??11?	0100001??
(76)	00001-0000	0000001-A0	0000110001	00--222100	00-3010001	0----0?2--	?1?????0-?	10-0100??
(77)	00001-0000	00000A1-A0	0000110000	00--222100	00-2010001	0----0?2--	?1?????0-?	10-0100??
(78)	0000A00000	00000A1-10	0000100000	00--220004	00020A0A01	0----0?2--	?1?????0-?	10-0110??
(79)	00001-0000	0000031-10	0000101002	00--222100	0001010001	0----0?2--	?10111?101	10-010050
(80)	00001-0000	0000031-10	0000101000	00--220?00	000F010101	0----0?2--	?10111?101	10-010050
(81)	0000A00000	00000D1-10	000010A0A0	00--22C100	00020F0001	0----0?2--	?10111?101	10-010050
(82)	0000A00000	0000001-A0	0000100000	00--222100	00020F0001	0----0?2--	?1?????0-1	10-0100??

APPENDIX 5. Specimens examined for gross-morphological characters.

Sixty-two gross-morphological characters were scored for 82 taxa based on literature and/or herbarium specimens. The numbering of taxa follows that of Appendix 1. Following the taxon name and author are the specimens examined, if any (some taxa were scored entirely based on the literature). If the taxon entered in the data matrix is a genus or subgenus, the species of each herbarium specimen examined is listed. Herbarium specimens were examined at BH, NY, P, and US (Holmgren et al., 1990).

(1) *Cornynocarpus laevigata* J. R. Forst. & G. Forst., *Hitchcock 15173* (US). (2) *Crossosoma bigelovii* Wats., *Dearing 4022* (BH), United States. (3) *Aleurites moluccana* (L.) Willd., *Bailey 604* (BH), Panama; *De Winter 2931* (BH), South Africa (Cultivated); *Zanoni 18848* (BH), Dominican Republic. (4) None examined. (5) *Geissoloma marginatum* Lindl. ex Kunth, *Carlquist 4558* (BH), South Africa. (6) None examined. (7) None examined. (8) *Lepuropetalon spathulatum* Ell., *Blake s.n.* (NY). (9) *Parnassia fimbriata*, *Jones 23924* (BH), Canada; *Perkins s.n.* (BH), Canada. (10) *Stackhousia monogyna* Labill., *Conn 2282* (NY). (11) *Tripterococcus brunonis* Endl., *Morrison s.n.* (US). (12) *Brexia madagascariensis* Thouars ex Ker-Gawl., *Degener 36588* (BH), United States (Cultivated); *Houghton 1104* (BH), United States (Cultivated); *Wikoff 1390* (BH), United States (Cultivated). (13) *Canotia holacantha* Torr., *Collom s.n.* (NY); *Landrum 6151* (NY). (14) *Goupia glabra* Aubl., *Silva 2401* (NY); *Wurdack 40961* (NY); *Zanderij 73* (NY). (15) None examined. (16) None examined. (17) *Siphonodon celastrineus* Griff., *Kostermans 9647* (NY); *Poilane 3054* (P); *Wenzel 3255* (NY). (18) *Euonymus alatus* (Thunb.) Siebold, *Unknown s.n. 8 May 1921* (BH), United States (Cultivated); *Unknown s.n. October 1933* (BH), United Kingdom (Cultivated); *Simmons 1772* (BH), United States (Cultivated). (19) *Euonymus fortunei* (Turcz.) Hand.-Mazz., *Simmons 1778* (BH), United States (Cultivated). (20) None examined. (21) *Glyptopetalum feddei* (Lév.) Ding Hou, *Esquirol 4007* (P); *G. gracilipes* Pierre, *Kerr 20323* (P); *G. poilanei* Tardieu, *Petelot 6874* (P). (22) *Microtropis fokiensis* Dunn., *Kanehira 3067* (US); *Rock 7536* (US); *M. japonica* Hallier f., *Murata 21451* (US); *Sonohara 44* (US); *Wilson 8194* (US); *Yokoyama 1152* (US); *M. wallichiana* Wight. ex Thwaites, *Waas 883* (US). (23) *Quetzalia occidentalis* (Loes. ex Donn.) Lundell, *Magana 5343* (US); *Smith P3299* (US); *Standley 48169* (US). (24) None examined. (25) *Bhesa* Buch.-Ham. ex Arn.; *B. archboldiana* (Merr. & Perry) Ding Hou, *Brass 25551, 28105* (US); *B. paniculata* Arn., *Beaman 9527* (US); *Boeea 7215* (US); *Toroes 3923* (US). (26) *Catha edulis* (Vahl) Endl., *Bailey 9036* (BH), United States (Cultivated); *Gander A321* (BH), United States (Cultivated); *Moran 2410, 7172* (BH), United States (Cultivated). (27) *Celastrus scandens* L., *Fernald 13973* (US); *Knowlton s.n.* (US); *Lix 569* (US); *Moiser s.n.* (US); *Smith 882* (US); *Waugh 129* (US). (28) *Celastrus pringlei* Rose, *Hinton 3506, 9020* (US); *King 5040* (US); *McVaugh 10308* (US); *Smith 4437* (US); *C. racemosus* Turcz., *Silva 1609* (US). (29) None examined. (30) None examined. (31) None examined. (32) *Menepetalum salicifolium* Loes., *Compton 1476* (BH), New Caledonia; *M. schlechteri* Loes., *McPherson 4821* (BH), New Caledonia; *Schlechter 15630* (BH), New Caledonia. (33) *Paxistima myrsinites* (Pursh) Raf., *Dress 4273* (BH), United States (Cultivated); *Muenscher 910, 17016* (BH), United States (Cultivated). (34) *Polycardia aquifolium* Tul., *Harder 1700* (P), Madagascar; *Villiers 4952* (P), Madagascar; *P. lateralis* O. Hoffm., *Dorr 3031* (P), Madagascar. (35) None examined. (36) *Salaciopsis eocaledonica* Baker F., *Compton 1692, 1944* (BH), New Caledonia; *S. sparsiflora* Hürl., *Guillaumin & Baumann-Bodenheim 8948* (A), New Caledonia. (37) None examined. (38) *Kokoona ochracea* Merr., *Soejarto 7021* (NY). (39) *Lophopetalum beccarianum* Pierre, *Jacobs 5546* (BH), Borneo; *L. javanum* Turcz., *Kostermans 5894* (BH), Borneo; *L. rigidum* Ridl., *Jacobs 5519* (BH), Borneo. (40) *Plenckia populnea* Reissek, *Anderson 10036* (NY); *Heringer 5678* (NY); *Ratter et al. 2582, 3794* (NY). (41) *Ptelidium ovatum* Poir., *Caprun 22742* (P), Madagascar; *P. scandens* H. Perrier, *Leandri 2193* (P), Madagascar. (42) *Tripterygium regelii* Sprague & Takeda, *Davis 80–220* (BH), United States (Cultivated); *Elsik 3290* (BH), United States (Cultivated); *Michener 4682* (BH), United States (Cultivated). (43) *Wimmeria persicifolia* Radlk., *Conralli 4273* (US); *Kirkby 2795* (US); *Pringle 6210* (US). (44) *Zinowiewia costaricensis* Lundell, *Skutch 4028* (US); *Jiménez 1538* (US); *Z. integerrima* Turcz., *Calzada 01799* (US); *Nee 29403* (US); *Purpus 2386* (US). (45) *Acanthothamnus aphyllus* (Schltr.) Standl., *Lundell 12520* (US), Mexico. (46) *Cassine parvifolia* Sond., *Burchell 5769* (P). (47) *Cassine schinoides* (Spreng.) R. H. Archer (none examined). (48) None examined. (49) None examined. (50) None examined. (51) *Forsellesia spinescens* Gray, *Clokey 8514* (BH), United States; *Constance 1002* (BH), United States; *Duran 548* (BH), United States. (52) *Gyminda latifolia* Urb., *Correll 47427, 47672* (NY); *Zanoni 39340* (NY). (53) *Mortonia scabrella* A. Gray, *Powers s.n.* (BH), United States; *Wentworth 118* (BH), United States; *Wolf 2495* (BH), United States; *M. utahensis* A. Nelson, *Thorne 44536* (BH), United States. (54) *Schaefferia cuneifolia* A. Gray, *Chiang 10136* (US); *S. frutescens* Jacq., *Acevedo-Rdgz. 5357* (US); *Britton 3328, 5972* (US); *Crosby 1026* (US); *Ekman 10605* (US); *Jak 6938* (US). (55) *Perrottetia longistylis* Rose, *Breedlove s.n.* (NY); *Calderón 486* (NY); *Utley 3082* (NY); *P. ovata* Hemsl., *Fernandez 4076* (NY). (56) None examined. (57) *Dicarpellum pancheri* (Loes.), A. C. Sm., *Balansa 1354* (BH), New Caledonia; *Bamps 5927* (BH), New Caledonia; *Compton 1664* (BH), New Caledonia. (58) *Rzedowskia tolantonguensis* Medrano, *Rzedowski 38344* (US), Mexico. (59) None examined. (60) *Bequaertia mucronata* (Exell) R. Wilczek, *Andoh 5494* (P); *Chevalier 19055* (P); *Tisserant 1197* (P). (61) *Campylostemon angolense* Welw. ex Oliver, *Asonganyi 293* (P); *C. laurentii* W. J. de Wilde, *Louis 10273* (NY); *Tisserant 1189* (P); *C. warneckeanum* Loes. ex Fritsch, *Troupin 6308* (NY). (62) None examined. (63) *Helictonema velutinum* (Afzel.) Pierre, *Benoît 455* (P); *Letouzey 5531* (P); *Reitsma 2271* (P); *Rlaine 1316* (P). (64) *Anthodon panamense* A. C. Sm., *Croat 8426, 11734, 12622* (NY); *Hayden 139* (NY); *A. decussatum* Ruíz & Pav., *Liesner 5400* (NY). (65) *Apodostigma pallens* (Planch. ex Oliv.) R. Wilczek, *Heudelot 341* (P); *Jansen 1662* (P); *Pobéguin 815* (P). (66) *Cuervea kappleriana* (Miq.) A. C. Sm., *Cid 1110* (NY); *Oliveira 4772* (NY); *Rabelo 3699* (NY). (67) *Elachyptera bipendensis* (Loes.) R. Wilczek, *Bos 3581* (P); *Rlaine 1505* (P); *Sita 1526* (P); *E. holtzii* (Loes. ex Harms) R. Wilczek, *Fleury 26299* (P); *E. parvifolia* (Oliver) N. Hallé, *Dubois 202* (P). (68) *Hippocratea volubilis* L., *Goodland 946* (US); *Henkel 2441, 4586* (US); *Jansen-Jacobs 3203* (US). (69) *Loeseneriella clematoides* (Loes.) R. Wilczek, *Louis 13499* (NY); *L. apiculata* (Welw. ex Oliv.) R. Wilczek, *Reitsma 2276* (NY); *L. concinna* A. C. Sm., *Tsang 21743* (NY). (70) *Prionostemma aspera* Miers, *Davidson 10645* (NY); *Ek 770* (NY); *Steyermark 107744*

(NY). (71) *Pristimera andongensis* (Welw. ex Oliv.) N. Hallé, *Hladik 2854* (P); *Wild 6611* (P). (72) *Reissantia indica* (Willd.) N. Hallé, *Corbisier-Baland 1637* (NY); *R. angustipetala* (H. Perrier) N. Hallé, *Keraudren 438* (P). (73) *Semialarium excelsum* (HBK) A. C. Sm., *Ayala 730* (NY); *Molina 13698* (NY); *Walker 422* (NY). (74) *Simicratea welwitschii* (Oliv.) N. Hallé, *Klaine 177, 1001* (P); *Lock 46710* (P). (75) *Simirestis dewildemaniana* N. Hallé, *Tisserant 938, 2125* (P). (76) *Cheiloclinium anomalum* Miers, *Ferreira 6309* (NY); *Wurdack 2379* (NY). (77) *Cheiloclinium belizense* (Standl.) A. C. Sm., *Ferreira 7374* (NY); *C. cognatum* (Miers) A. C. Sm., *Dionizia 37* (NY); *Irwin 10935, 17633* (NY); *Maguire 56441* (NY). (78) *Peritassa campestris* (Cambess.) A. C. Sm., *Eiten 1628* (NY); *Irwin 7010, 16847* (NY); *Mimura 427* (NY); *P. laevigata* (Hoffmg.) A. C. Sm., *Irwin 17468*; *Maguire 56092* (NY). (79) *Salacia erythrocarpa* K. Schum., *Schlechter 18864, 47003* (NY). (80) None examined. (81) *Salacia prinoides* DC, *Merrill 371, 2044* (NY); *Ramos 44109* (NY). (82) *Tontelea attenuata* Miers, *Cid 748* (NY); *Little 9535* (NY); *Vásquez 2950* (NY); *T. brachypoda* Miers, *Goodland 886* (NY); *Harley 10138* (NY); *Hassler 5030, 9667* (NY); *Ratter 390* (NY).

THE LONG-PROBOSCID FLY POLLINATION SYSTEM IN *GLADIOLUS* (IRIDACEAE)[1]

Peter Goldblatt[2] *and John C. Manning*[3]

ABSTRACT

Pollination strategies of *Gladiolus*, one of the largest genera of the monocot family Iridaceae, are unusually diverse and involve various bee species, foraging either for nectar or for pollen, or moths, a large butterfly, passerine birds, and long-proboscid flies foraging for nectar. The latter system has been demonstrated for 16 species of *Gladiolus* of diverse taxonomic affinities. These species are primarily or exclusively pollinated by flies with elongate mouthparts. All have similar flowers with a slender, elongate perianth tube, mostly 25–50 mm long, a white to cream or pink perianth, usually marked with pink or red nectar guides on the lower tepals, and lack floral odor. The flowers produce ample quantities of sucrose-rich to sucrose-dominant nectar of moderate sugar concentration. Each of these species is pollinated by one or two species of flies of the families Tabanidae or Nemestrinidae, which have mouthparts usually 20–60 mm long, exceptionally to 80 mm in *Moegistorhynchus longirostris*. An important aspect of long-proboscid fly-pollination systems is the formation of guilds in which a number of species of plants of different genera and families have similar flowers and utilize the same pollinator. In these guilds pollen placement on the pollinator's body is fairly precise, and different members of a guild at any site use different parts of the pollinator's body for pollen transport. An additional 13 species of southern African *Gladiolus* have flowers conforming to those pollinated by long-proboscid flies and are thus inferred to have this pollination strategy. These species extend from the southern African winter-rainfall zone in the southwest to the Drakensberg Mountains of the eastern half of the subcontinent and flower at precisely the times that long-proboscid flies are on the wing, mostly late spring in the west (mid September to November) or late summer in the east (February to April). An autumn-flowering guild using a different fly species occurs in the southern part of the winter-rainfall zone. The taxonomic relationships of *Gladiolus* species pollinated by long-proboscid flies are diverse, with these 29 species falling in six of the seven sections of the genus occurring in southern Africa, and the pollination system appears to have evolved independently in each section.

Pollination by flies in the Nemestrinidae and Tabanidae with elongate mouthparts exceeding 15 mm and usually 25–60 mm long comprises a pollination strategy quite distinct from any described in the standard source works on pollination biology (Manning & Goldblatt, 1996, 1997; Johnson & Steiner, 1995, 1997). Yet the biological importance of the system in the African flora has only begun to be explored. Floral visits by long-proboscid flies were first noted by Marloth (1908) in South Africa, and long-proboscid fly pollination now appears to be significant only in the flora of southern Africa, although it has also been reported in northern India (Fletcher & Son, 1931). Reports of so-called long-tongued fly pollination in California (Grant & Grant, 1965) refer to pollination by bombyliid flies with probosces less than 15 mm long and are not comparable with long-proboscid fly pollination described here. The Iridaceae and Geraniaceae predominate among several guilds of long-tubed flowers pollinated by long-proboscid flies in the flora of the southern African winter-rainfall zone (Goldblatt et al., 1995; Manning & Goldblatt, 1996, 1997). Among the species of several genera of Iridaceae pollinated by long-proboscid flies studied by Goldblatt et al. (1995) and Manning and Goldblatt (1997) were four species of the African and Eurasian genus *Gladiolus*. Inferring from the distinctive morphology of flowers adapted for this pollination strategy, it seemed likely that many more species of *Gladiolus* have flowers specifically adapted for long-proboscid fly pollination.

As part of a broad-ranging study of *Gladiolus*, including both taxonomy and pollination ecology, we have established that this predominantly sub-Saharan African genus of some 255 species (Goldblatt, 1996; Goldblatt & Manning, 1998) is remarkably diverse in its pollination biology. Pollination by long-tongued bees is most common and is probably ancestral (Goldblatt & Manning, 1998; Goldblatt et al., 1998), but the several other pollination strategies in the genus include those us-

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ing short-tongued bees (Goldblatt et al., 1998), the satyrid butterfly *Aeropetes* (Johnson & Bond, 1994), night-flying moths (Goldblatt & Manning, 1998, and in prep.), passerine birds (still poorly documented and largely anecdotal), and several species of long-proboscid flies. Here we explore the importance of long-proboscid fly pollination in *Gladiolus* and document the strategy in 16 southern African species of the genus. We describe in detail the features that characterize this pollination system in *Gladiolus*, and that, in general, contribute to the understanding of this pollination system, evidently developed extensively only in southern Africa.

MATERIALS AND METHODS

Species examined. Observations made during the years 1993 to 1999 in the field in southern Africa and in living collections at the Missouri Botanical Garden, St. Louis, and Kirstenbosch Botanic Gardens, Cape Town, on aspects of the floral biology of southern African *Gladiolus* showed many species have flowers that appeared to be adapted for long-proboscid fly pollination. From our research on the systematics of the genus (Goldblatt & Manning, 1998; Manning et al., 1999), we identified 29 species that have flowers closely matching those known to be pollinated by long-proboscid flies out of a total 165 species of *Gladiolus* that occur south of the Limpopo–Cunene River axis. The 29 species fall in six of the seven sections recognized in the genus in southern Africa. They were recognized by their elongate, tubular flowers, exserted unilateral stamens, pink, cream, or whitish pigmentation with longitudinal, red tepal markings (we use the term tepal for perianth lobe here). Observations on the floral biology of 16 of these species show that their flowers are pollinated primarily or, more often, exclusively by flies of the Nemestrinidae and/or Tabanidae having mouthparts exceeding 15 mm and mostly more than 20–60 mm long. The remaining 136 species in southern Africa either have short-tubed zygomorphic or actinomorphic flowers, or flowers with elongate floral tubes, but then with floral features different from those pollinated by long-proboscid flies.

Seasonality, floral phenology and longevity, and floral presentation. Direct phenological observations are presented on 16 species of *Gladiolus* made during the years 1993 to 1998 in the field (Table 1) and in living collections at Kirstenbosch Botanic Gardens, Cape Town. Observations include mode and timing of anthesis (i.e., opening of individual buds), anther dehiscence, expansion of stigmatic lobes, followed by withering of the perianth. Data on seasonality are taken from Goldblatt and Manning (1998). Plant vouchers (Table 1) are deposited at the Missouri Botanical Garden Herbarium (MO) and/or the Compton Herbarium (NBG).

Presence or absence of floral scent was noted in the field and in cultivated plants. Scents were recorded after individual flowers were picked and placed in clean, lidded glass jars and stored in a warm place. The contents of each jar was sniffed after a minimum of 60 minutes (Buchmann, 1983).

Nectar analysis. Nectar volume measurements were taken from unbagged flowers in the field, reflecting both rates of secretion and depletion, and from plants maintained in the laboratory and not visited by insects. Experience with Iridaceae has shown that nectar characteristics gradually change in species retained in water for periods greater than 24 hours (Goldblatt et al., 1995). Nectar from cut flowers in the laboratory maintained in water was therefore sampled within 18 hours. To collect nectar, whole flowers were picked and nectar was withdrawn from the base of the perianth tube with 3-μl capillary tubes after separating the ovary from the perianth base. The percentage of sucrose equivalents in fresh nectar was measured in the field or laboratory on a Bellingham and Stanley hand-held refractometer (0–50%) from five or more individuals per population, unless fewer individuals were available. Additional nectar samples were dried on Whatman's filter paper no. 1 and sent to B.-E. van Wyk, Rand Afrikaans University, Johannesburg, for HPTLC sugar analysis.

Compatibility. Compatibility relationships were examined for two species, *Gladiolus angustus* and *G. undulatus*, maintained in cultivation and isolated from possible pollinators. Fruit and seed set were compared in five hand-selfed flowers and five flowers crossed with pollen of another genotype of the same species.

Pollination mechanisms and pollen load analyses. Observations of insects on *Gladiolus* flowers involved 4–8 hours per species. These included mode of foraging and whether insects contacted anthers and stigmas during visits to flowers. Insects observed to probe the floral tube or to brush the anthers or stigmas were netted and then immobilized in a jar using ethyl acetate fumes. To prevent contamination of the body of an insect with pollen carried by another in the same jar, the bodies of insect specimens were isolated from each other by wrapping them in tissue prior to pinning. Body length and proboscis length of insects were recorded from captured specimens. Body length was mea-

Table 1. Study sites and voucher information for species studied. Vouchers are housed at MO (Goldblatt) or at NBG (other collectors). All study sites are in South Africa.

Species	Study site and voucher
GLADIOLUS SECTION *DENSIFLORUS*	
series *Densiflorus*	
G. varius F. Bolus	Mpumalanga, Long Tom Pass, Feb., *Goldblatt & Manning 9832*
series *Calcaratus*	
G. calcaratus G. J. Lewis	Mpumalanga, Mt. Sheba road, Feb., *Goldblatt & Manning 10479*
G. macneilii Oberm.	Mpumalanga, Abel Erasmus Pass, Apr., *Goldblatt & Manning 10638*
series *Scabridus*	
G. microcarpus G. J. Lewis	Free State, Witzieshoek, Feb., *Goldblatt & Manning 9860*
G. mortonius Herb.	Eastern Cape, near Cathcart, Feb., *Batten s.n.*
GLADIOLUS SECTION *OPHIOLYZA*	
series *Oppositiflorus*	
G. oppositiflorus Baker	Eastern Cape, Naude's Nek, Feb., *Goldblatt & Manning 9549*
GLADIOLUS SECTION *BLANDUS*	
series *Blandus*	
G. angustus L.	W Cape, near Darling, Oct., *Goldblatt & Manning 10052*
G. bilineatus G. J. Lewis	W Cape, near Albertinia, Mar., *Manning 2014*
G. carneus D. Delaroche	W Cape, Cape Peninsula, Devil's Peak, Oct., no voucher W Cape, Silvermine plateau, Oct., *Compton 15455*
G. undulatus L.	W Cape, Bain's Kloof, Oct., *Goldblatt & Manning 10118A* N Cape, Nieuwoudtville Waterfall, Nov., *Goldblatt & Manning 10116*
series *Floribundus*	
G. floribundus Jacq.	W Cape, near Robertson, Oct., no voucher
GLADIOLUS SECTION *LINEARIFOLIUS*	
series *Linearifolius*	
G. monticola G. Lewis ex Goldblatt & J. C. Manning	W Cape, near Simonstown, Nov., *Goldblatt & Manning 10460* W Cape, Table Mountain, Jan., *Roux 264*
G. rhodanthus J. C. Manning & Goldblatt	W Cape, Stettyn's Peak, Jan., *Manning & Paterson Jones, 2207*
GLADIOLUS SECTION *HOMOGLOSSUM*	
series *Gracilis*	
G. vigilans Oberm.	W Cape, Cape Point Reserve, Nov., *Taylor 6553*
G. virgatus Goldblatt & J. C. Manning	W Cape, Helderberg Reserve, Nov., *Manning 2010*
series *Teretifolius*	
G. engysiphon G. J. Lewis	W Cape, near Albertinia, Mar., *Manning 1055*

Additional species with similar flowers, assumed to be adapted for pollination by long-tongued flies: section *Densiflorus*: *G. cataractarum* Oberm., *G. lithicola* Goldblatt & J. C. Manning, *G. scabridus* Goldblatt & J. C. Manning; section *Blandus*: *G. pappei* Klatt, *G. geardii* L. Bolus, *G. aquamontanus* Goldblatt & Vlok; section *Hebea*: *G. leptosiphon* G. Bolus, *G. lapeirousioides* Goldblatt; section *Homoglossum*: *G. cylindraceus* G. J. Lewis, *G. debilis* Sims, *G. roseovenosus* Goldblatt & J. C. Manning, and *G. variegatus* (G. J. Lewis) Goldblatt & J. C. Manning.

sured from the base of the labrum to the tip of the abdomen. Mouthpart length was measured from the base of the labrum to the tip of the proboscis. After identification, insect voucher specimens were deposited with the Natal Museum, Pietermaritzburg, or the Snow Entomological Museum, Lawrence, Kansas.

Capturing a fly at any site appeared to reduce the insect population significantly. We therefore killed as few insects as necessary to obtain specimens for identification. Identification of pollen on insect bodies was done in one of two ways. The first involved direct recognition, when pollen was of a distinctive color or in a specific position. In flies, which are comparatively large insects, sites of pollen deposition are quite discrete and the identity

Figure 1. Inflorescences and flowers of southern African *Gladiolus* pollinated by long-proboscid flies, with longitudinal sections of flowers of some species. —A. *G. angustus.* —B. *G. pappei.* —C. *G. monticola.* Scale bar 10 mm.

of pollen can often be determined without using a microscope because of its distinctive color. Thus, the sites and identity of pollen loads can often readily be identified without killing the fly. Alternatively, pollen was gently removed from the body surface with a dissecting needle. The residue from needle probes was collected on glass slides and mounted in 1–2 drops of Calberla's fluid (Ogden et al., 1974). Pollen grains were identified microscopically by comparison with reference to pollen grain preparations made from plants flowering at study sites. *Gladiolus* pollen grains are recognized by their large size, monosulcate aperture with prominent 2-banded operculum, and perforate-scabrate exine.

RESULTS

Seasonality, floral phenology and longevity, and floral presentation. Flowering time in the *Gladiolus* species of southern Africa that are pollinated by long-proboscid flies is correlated with their geographic ranges in one of two separate rainfall zones (Goldblatt & Manning, 1998). Species of the winter-rainfall zone mostly flower in late spring (September to November), whereas species of the summer-rainfall zone flower in late summer (late January to April) (Table 2; Fig. 3). This coincides with the end of the period of optimal plant growth, during or soon after the main rainy period. Flowering out of phase with the flowering peak occurs in four species of the winter-rainfall zone, *G. bilineatus, G. engysiphon, G. monticola* (Goldblatt & Manning, 1998), and *G. rhodanthus* (Manning et al., 1999), which flower from January to April although vegetative growth occurs in the winter and spring.

Population density appears to be moderately diffuse, and plants form extended populations with

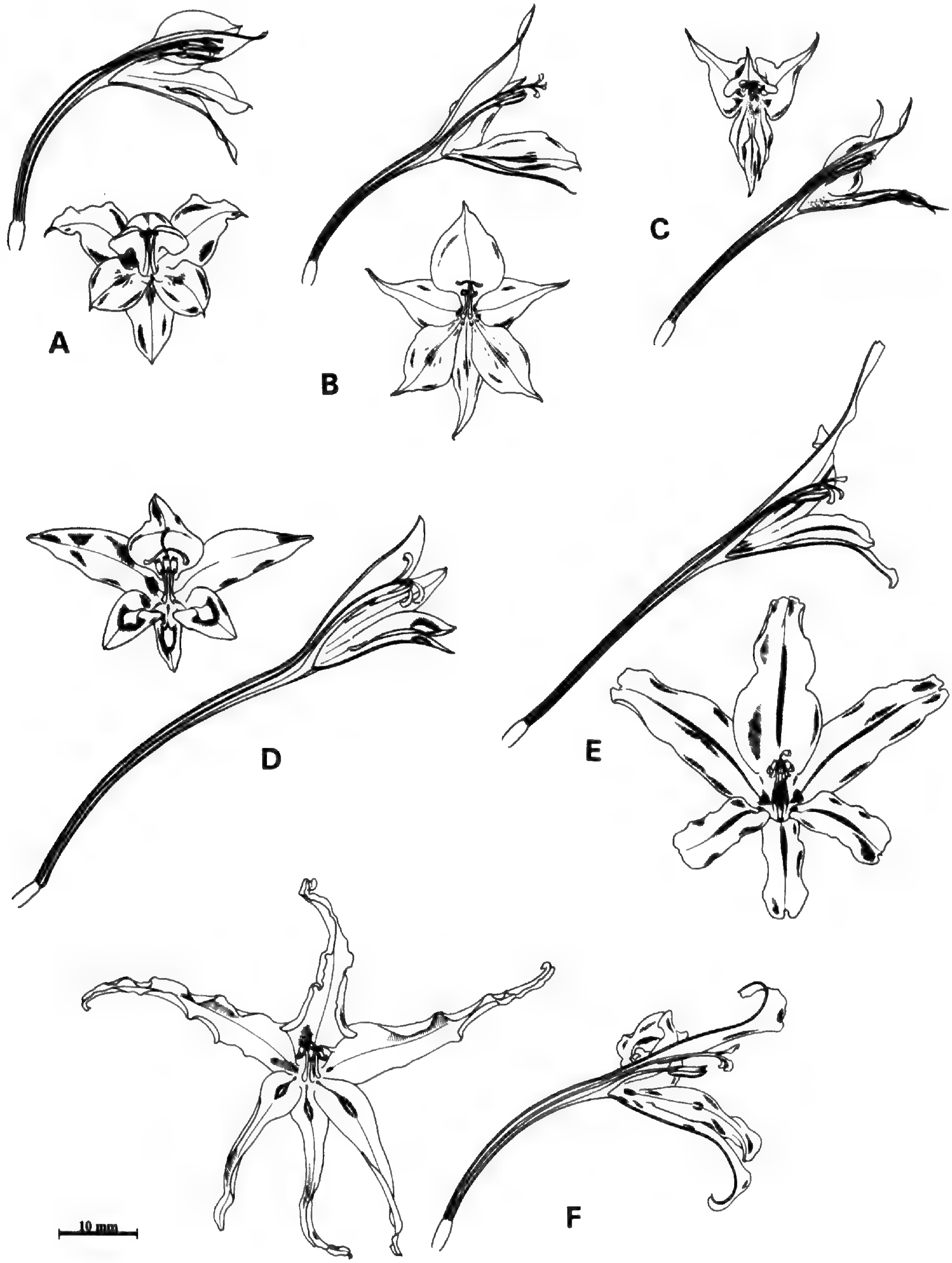


Figure 2. Front view and longitudinal section of flowers of selected species of *Gladiolus* pollinated by long-proboscid flies. —A. *G. varius* (sect. *Densiflorus*). —B. *G. microcarpus* (sect. *Densiflorus*). —C. *G. macneilii* (sect. *Densiflorus*). —D. *G. angustus* (sect. *Blandus*). —E. *G. floribundus* (sect. *Blandus*). —F. *G. undulatus* (sect. *Blandus*). Scale bar 10 mm.

Table 2. Floral and phenological data for southern African *Gladiolus* species with flowers adapted for pollination by long-tongued flies. Species are arranged taxonomically according to Goldblatt and Manning (1998). Perianth tube length was recorded at study sites and may not represent the range for the species. An asterisk (*) indicates species of the winter-rainfall zone flowering out of phase with the region, in the summer and autumn.

Species	Flower color	Perianth tube mm	Main flowering time	Rainfall zone
GLADIOLUS SECTION *DENSIFLORUS*				
G. calcaratus	white	25–37	Feb.–Mar.	summer
G. macneilii	pink	40–45	Mar.–Apr.	summer
G. microcarpus	pink	35–40	Jan.–Feb.	summer
G. mortonius	pink	30–45	Mar.–Apr.	summer
G. varius	pink	45–48	Feb.–Mar.	summer
GLADIOLUS SECTION *OPHIOLYZA*				
G. oppositiflorus	pink	40–50	Feb.–Mar.	summer
GLADIOLUS SECTION *BLANDUS*				
G. angustus	cream	70–100	Mar.–Apr.	summer
G. bilineatus	pink	50–65	Mar.–Apr.	winter*
G. carneus	cream	28–35	Oct.–Nov.	winter
G. floribundus	cream	45–60	Oct.	winter
G. undulatus	cream	52–60	Nov.–Dec.	winter
GLADIOLUS SECTION *LINEARIFOLIUS*				
G. monticola	cream	22–30	Dec.–Jan.	winter*
G. rhodanthus	pink	25–36	Dec.–Jan.	winter*
GLADIOLUS SECTION *HOMOGLOSSUM*				
G. engysiphon	cream	40–60	Mar.–Apr.	winter*
G. vigilans	pink	35–40	Nov.	winter
G. virgatus	pink	24–27	Sep.–Nov.	winter

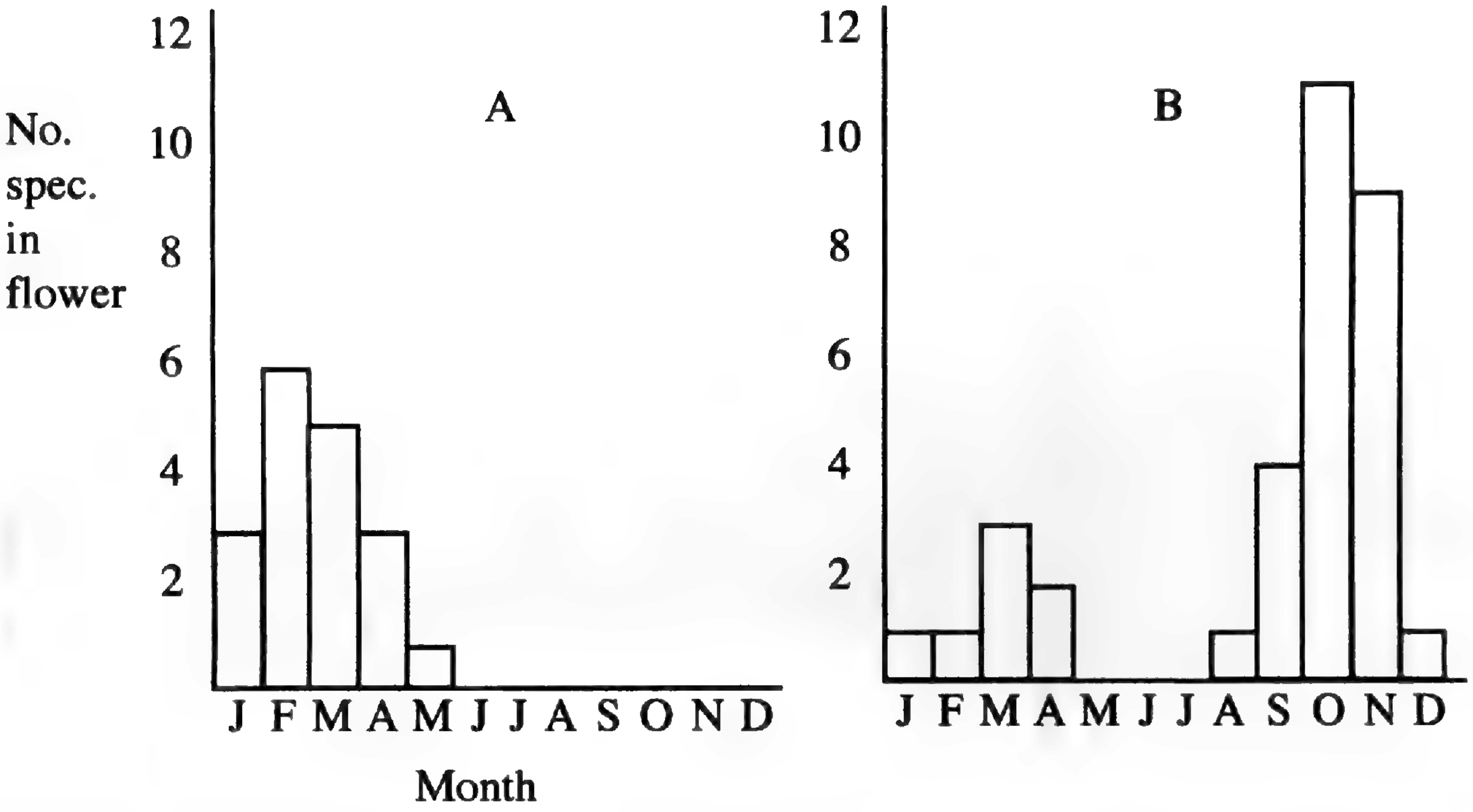


Figure 3. Seasonality of flowering in southern African *Gladiolus* species with flowers adapted for long-proboscid fly pollination. —A. Summer-rainfall zone. —B. Winter-rainfall zone.

flowering individuals standing 1–3 m apart. After artificial disturbance such as partial vegetation clearing or a wildfire, populations may be more dense, and then reproductive success for a species with a specialized pollination strategy may be compromised due to an excess of flowering plants relative to available pollinators.

The pattern of flower buds opening on an inflorescence is acropetal. In all species, a mature bud expands in the early to mid morning, and the open flower typically lasts four (occasionally three or five) days. Flowers usually open one to two days apart, hence there are often three or four flowers open at any time on an inflorescence (Fig. 1). At sunset, the flowers of most species partly close, loosely enclosing the exserted anthers and stigmas.

Flowers of many *Gladiolus* species have been shown to exhibit mechanical protandry (Scott Elliot, 1891; Goldblatt et al., 1998), and the species studied here conform to this pattern. The anthers dehisce longitudinally one to four hours after the tepals first unfold. This depends to some extent on ambient temperature and humidity; anthers dehisce later in wet, cool conditions. Pollen grains are clumped together and pollen remains in the anther thecae until removed by an insect. The three style branches, the distal adaxial surfaces of which comprise the stigmas, are loosely held together for the first three (or four) days that the flower is open and lie laxly over on the dorsal surface of the anthers. On the fourth (or fifth) day of anthesis, the style elongates and the style branches diverge, arching outward beyond the anthers. At the same time, the conduplicate margins of the distal half of each style branch unfold, exposing the moist, sticky stigmatic surfaces of the now spathulate style branches. Only then are the stigmas of a flower accessible to pollen deposition. Pollen adheres to these areas following hand-pollination.

Thus of the four (or five) days that a flower is open, it typically has three days in an exclusively male phase during which time pollen is usually removed from the anthers by insects. Anthers can be seen with the naked eye to lack pollen after three days if flowers were actively visited. By the time the stigma lobes unfold the flower is then in an exclusively female phase that lasts for the final one (or two) days that it is open. Mechanical self-pollination cannot readily occur, even if pollen remains in the anthers by the time the receptive stigmatic areas are exposed, because of the spatial separation of the pollen-bearing anthers and the stigmatic surfaces. We have no data on the biochemistry of stigmatic receptivity.

Species of *Gladiolus* are medium-sized, corm-bearing geophytes, typically 45–120 cm high (Fig. 1). Individuals produce a single, simple or few-branched flowering stem annually. Flowering in a population is synchronous and lasts two to four weeks. Inflorescences of species with flowers adapted for pollination by long-proboscid flies are secund spikes with the flowers facing to the side and with the floral tube in an ascending position (Figs. 1, 2). In *G. oppositiflorus* the spikes are distichous or nearly so.

Floral morphology is fairly uniform, irrespective of sectional affinity (Figs. 1, 2). The perianth is relatively large, mostly 45–80 mm long, but up to 140 mm in *Gladiolus angustus*. The perianth tube in these species is slightly longer than, to as much as 2.5 times as long as the tepals (Fig. 2). The perianth tube consists of a long, slender basal portion ca. 2 mm in diameter, either fairly straight or gently curved, and typically from 16 to 65 mm long, but up to 100 mm in *G. angustus* (Table 2; Fig. 2D). The tube is expanded and flared for the distal 5–15 mm. Flowers are zygomorphic and the dorsal tepal is usually largest and typically inclined, while the upper lateral tepals spread outward. The lower tepals are usually slightly smaller than the upper three and are held loosely together and directed forward. The style and stamens are unilateral and arch to lie close to and just beneath the dorsal tepal and are thus contained within the cup formed by the ascending tepals. The filaments are exserted from the tube, and the anthers are parallel to one another with the lines of dehiscence facing toward the center of the flower and the lower tepals.

Flowers are predominantly shades of white to cream or pale pink to salmon (Table 2; Fig. 4). Each of the lower tepals typically has a contrasting, dark pink to red longitudinal marking in the form of a linear stripe, a broader streak, or a spear- to diamond-shaped mark with a pale center (Figs. 1A, B, 2, 4). The lower tepal markings are often collectively referred to as a nectar guide, and we follow this practice. Collectively, the bases of the tepals and the distal part of the tube form a wide throat leading to the narrow, proximal part of the tube. The tapering throat (Fig. 2) accommodates the head and thorax of a large fly fairly snugly. In the sense of Faegri and van der Pijl (1979), these are gullet flowers but with a particularly elongated floral tube. The flowers of all species lack detectable odor.

The color of the anthers and pollen is unusual in three species. Although either conventionally colored yellow (*Gladiolus angustus*) or more often the same shade as the tepals, cream to light pink, the anthers and pollen are dark purple in *G. flori-*

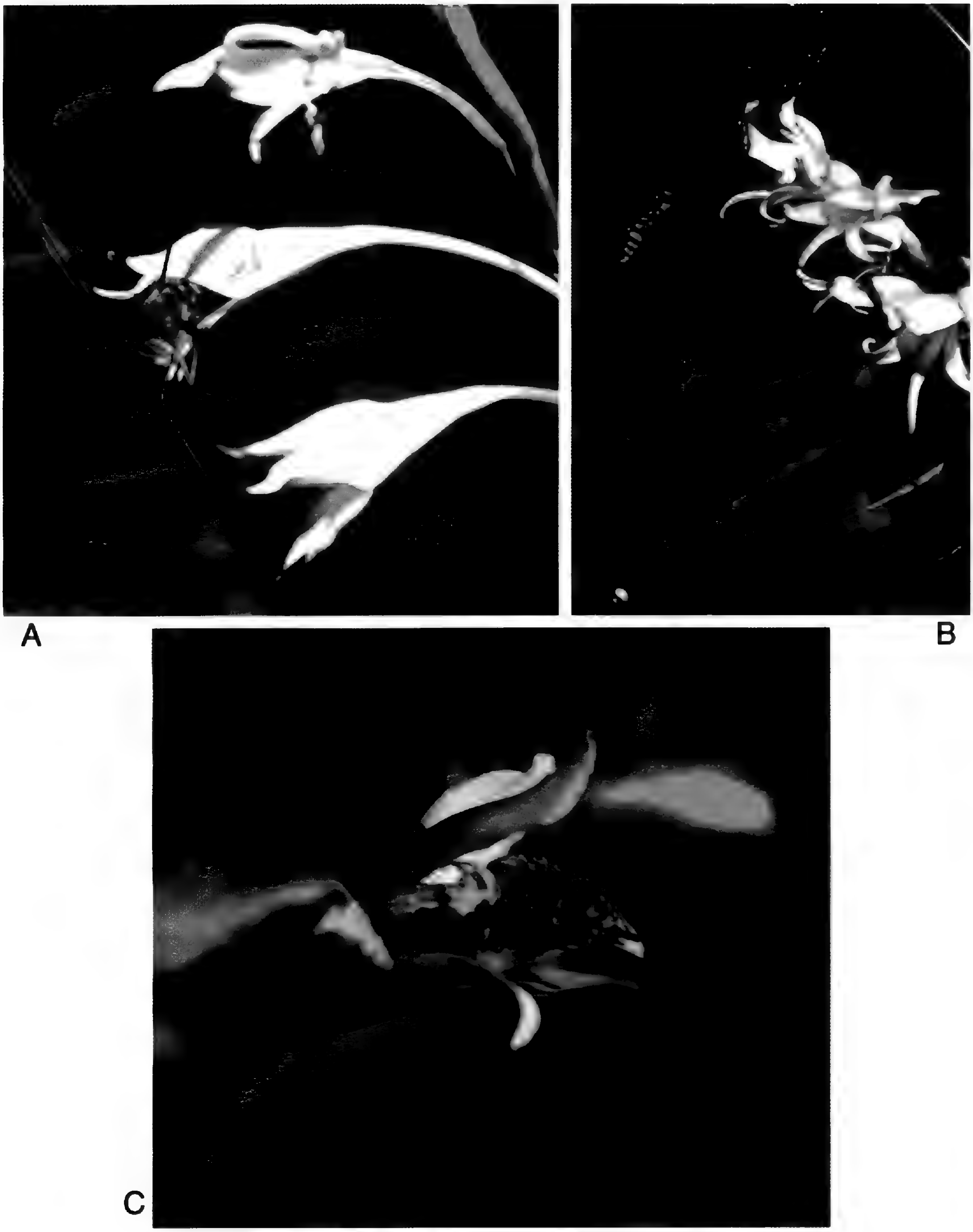


Figure 4. Floral foraging in southern African *Gladiolus* pollinated by long-proboscid flies. —A. *Stenobasipteron wiedmannii* grasping the tepals of *G. macneilii* while foraging. —B. *Philoliche rostrata* approaching a flower of *G. undulatus*, the anthers of which are concealed under the dorsal tepal. —C. *Moegistorhynchus longirostris* entering a flower of *G. angustus*. Arrows indicate position of colored pollen on the dorsal surface of the thorax of a fly.

Table 3. Available nectar characteristics of species of southern African *Gladiolus* pollinated by long-tongued flies. Nectar analyses were provided by B.-E. van Wyk, Rand Afrikaans University, Johannesburg, South Africa. Number of samples (n) is the same for volume and concentration columns.

Gladiolus species	Nectar volume μl (n)	% Nectar concentation (±SD)	% Range of sugars			Sugar ratio S/F + G (n)
			Fructose	Glucose	Sucrose	
G. angustus	3.9–9.6 (5)	27.8 (2.2)	1–2	6–11	87–93	9.00 (2)
G. bilineatus	4.7–5.6 (3)	27.2 (1.4)	4	11	85	5.67 (1)
G. calcaratus	2.6–5.1 (6)	26.0 (3.5)	4–11	10–18	71–86	3.65 (2)
G. carneus	—	—	2–3	12	85–86	5.90 (2)
(Devil's Peak)	1.6–2.4 (2)	29.0–31.0	0–7	9–13	80–91	5.89 (2)
G. engysiphon	2.8–4.3 (5)	26.8 (1.4)	0	16	84	5.25 (1)
G. floribundus	2.8–3.7 (2)	28.0–29.5	—	—	—	—
G. macneilii	4.5–5.8 (5)	26.8 (1.9)	—	—	—	—
G. microcarpus	3.8–4.5 (5)	26.0 (1.1)	—	—	—	—
G. monticola	2.4–4.2 (10)	33.2 (3.6)	3–5	10–14	81–85	5.12 (3)
G. mortonius	4.4–5.7 (10)	27.7 (1.6)	5–11	16–19	70–79	2.85 (3)
G. oppositiflorus	6.4–12.8 (6)	27.3 (1.3)	6–8	14–28	74–78	3.17 (2)
G. undulatus						
(Bain's Kloof)	1.8–4.1 (8)	24.8 (5.1)	12–19	7–16	65–81	2.70 (2)
(Nieuwoudtville)	6.6–10.6 (3)	25.3 (2.6)	2–3	12	85–86	5.90 (2)
G. varius	6.5–8.9 (7)	30.3 (2.4)	2–6	10–18	76–88	4.80 (4)
G. virgatus	2.8–4.2 (4)	29.9 (0.8)	0–5	4–8	87–96	9.71 (3)

***bundus*, *G. macneilii*, and *G. undulatus*.** The bases of the anthers of *G. calcaratus* and *G. macneilii* (sect. *Densiflorus*: series *Calcaratus*) form hard, elongate, sterile appendages. These appendages extend downward across the floral throat, effectively closing off entry to the proximal part of the floral tube. As a large-bodied insect pushes its head and thorax into the flower, the appendages are raised and the anthers are pulled downward swabbing the dorsal surface of the thorax with pollen.

Nectar. Nectar glands are septal in *Gladiolus* species, as they are in the entire subfamily Ixioideae (Goldblatt, 1990, 1991; Manning & Goldblatt, in prep.). Nectar is secreted from the top of the ovary directly into the base of the perianth tube and is retained in the proximal part of the tube. Nectar typically fills the proximal fourth to half of the narrow portion of the tube. The nectar may reach to between 10 and 30 mm below the mouth of the narrow part of the tube (40–50 mm in *G. angustus*) before a flower has been visited by a nectarivorous insect. It is thus accessible only to insects with narrow, tubular mouthparts at least exceeding 15 mm and up to 70 mm. All species examined for this character were observed to secrete nectar. Nectar volumes are modest to fairly large (Table 3), mostly 2.5–5.8 μl and in *G. angustus* and *G. undulatus* more than 9 μl in flowers that have not received visits from pollinators (Table 3). Nectars are sucrose-rich to sucrose-dominant with sugar solute making up 25–33% of the total volume of fluid (Table 3).

Compatibility. At least *Gladiolus angustus* and *G. undulatus* have been shown experimentally to be self-incompatible, and in this they appear to conform to the common pattern in the genus (Goldblatt et al., 1998). Observations in the field confirm that *G. angustus* and *G. undulatus* are obligate outcrossing plants. At sites where pollinators seemed to be absent (none seen on two separate days of observation) the numerous individuals (over 25 examined) of both species set no fruit. At sites where flies were found to be active, plants produced capsules containing large numbers of well-formed seeds. The compatibility relationships of other species in the genus pollinated by long-proboscid flies are unknown.

Pollination mechanisms and pollen load analysis. *Gladiolus* species pollinated by long-proboscid flies extend almost throughout southern Africa, from the winter-rainfall zone in the southwest to the summer-rainfall zone in the northeast of the subcontinent. The identities of pollinators differ with geography and the flowering times of the species visited (Tables 2, 4). In the late spring and early to mid summer in the southern African winter-rainfall zone, flies captured on *Gladiolus* species included the nemestrinids, *Moegistorhynchus longirostris*, *M.* sp. nov., and *Prosoeca nitidula*, and the tabanids,

Table 4. Perianth tube length of *Gladiolus* species and length of mouth parts of fly species captured on each species. Measurement of perianth tube length and fly mouth-parts are ranges for the populations studied.

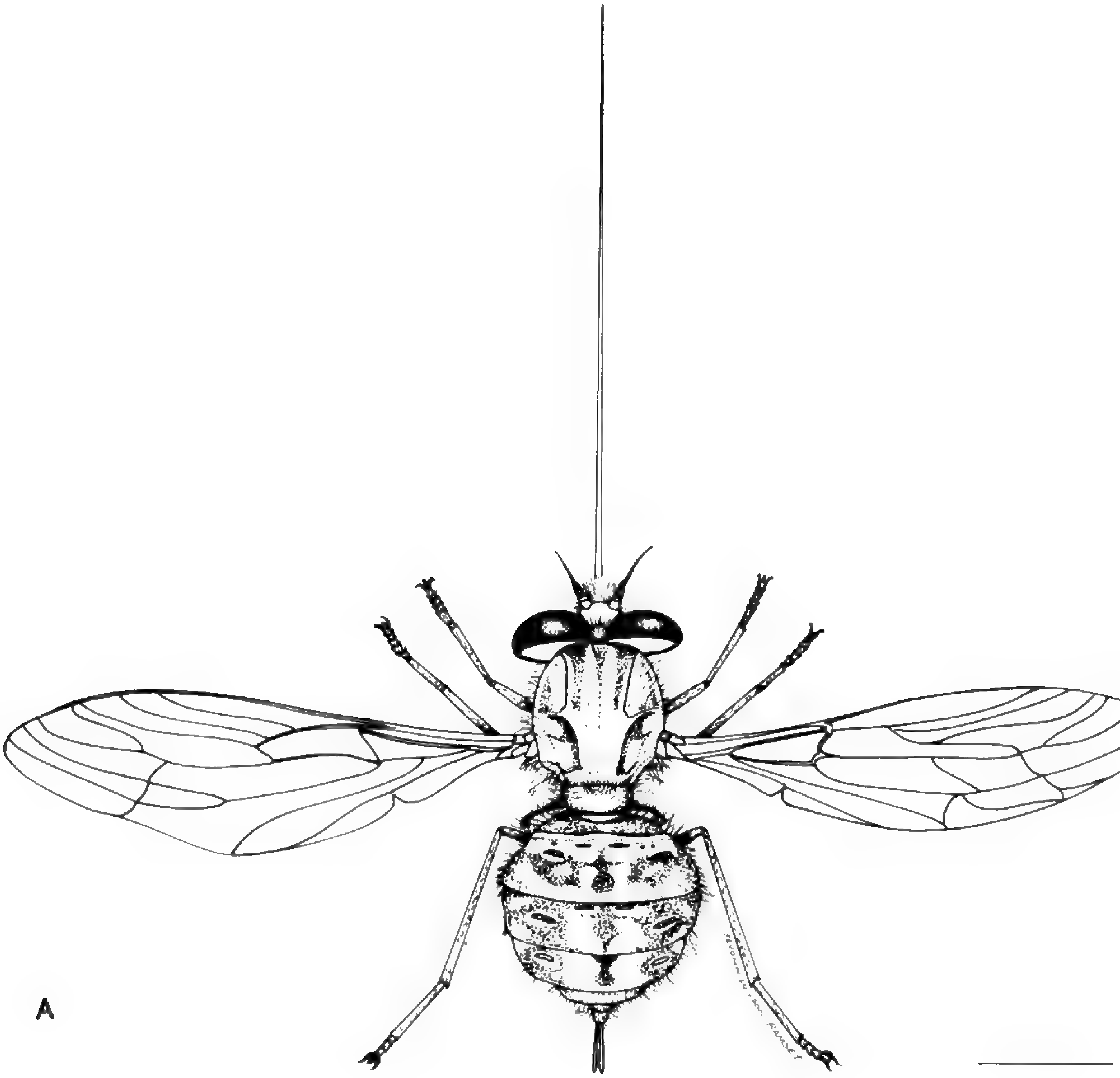
	Perianth tube			Mouth part	
Plant species	Proximal mm	Distal mm	Fly species	mm	(n)
Summer-rainfall zone					
GLADIOLUS SECTION *DENSIFLORUS*					
G. calcaratus	20–32	ca. 8	*Prosoeca robusta*	20–23	3
G. macneilii	32–37	ca. 8	*Stenobasipteron wiedmannii*	23–29	4
G. microcarpus	30–35	ca. 5	*Prosoeca ganglbaueri*	27–30	4
G. mortonius	30–45	6–8	*Prosoeca ganglbaueri*	31–42	4
G. varius	35–38	ca. 10	*Prosoeca ganglbaueri*	33–35	4
GLADIOLUS SECTION *OPHIOLYZA*					
G. oppositiflorus	30–40	ca. 10	*Prosoeca ganglbaueri*	28–32	4
Winter-rainfall zone					
GLADIOLUS SECTION *BLANDUS*					
G. angustus	60–90	ca. 10	*Moegistorhynchus longirostris*	67–70	4
G. bilineatus	40–50	ca. 12	*Prosoeca longipennis*	38–40	2
G. carneus	24–29	ca. 8	*Philoliche rostrata* (Devil's Peak)	22–24	3
			Prosoeca nitidula (Silvermine)	18–24	2
			Philoliche rostrata	24	1
G. floribundus	30–45	ca. 15	*Philoliche rostrata*	30–34	1
			Philoliche gulosa	17–19	2
G. undulatus	44–55	ca. 8	*Philoliche rostrata*	25–27	4
GLADIOLUS SECTION *LINEARIFOLIUS*					
G. monticola	16–18	ca. 7	*Philoliche rostrata* (Simonstown)	18–22	3
	20–22	ca. 7	*Prosoeca nitidula* (Table Mt.)	18–20	2
G. rhodanthus	20–27	5–7	*Moegistorhynchus* sp. nov.	ca. 20	1
GLADIOLUS SECTION *HOMOGLOSSUM*					
G. engysiphon	35–52	5–8	*Prosoeca longipennis*	38–40	2
G. vigilans	30–35	ca. 5	*Philoliche rostrata*	23–25	2
G. virgatus	18–22	ca. 5	*Philoliche rostrata*	18–20	2

Philoliche gulosa and *P. rostrata*. In the same rainfall zone *Prosoeca longipennis* is on the wing in the autumn (Manning & Goldblatt, 1995).

In the summer-rainfall zone flies were captured in the late summer to early autumn and included *Prosoeca ganglbaueri*, *P. robusta*, and *Stenobasipteron wiedmannii* (Fig. 5A, B). In all flies the proboscis length was slightly shorter to about as long as the floral tube of the *Gladiolus* species on which they were captured (Table 4). The fly with the longest proboscis is *M. longirostris* (67–70 mm in our study population), and individuals at other sites have probosces up to 80 mm long and as little as 40 mm (Goldblatt et al., 1995; Manning & Goldblatt, 1997).

Very occasionally, in a few species other potential pollinators were observed visiting the flowers. These included the anthophorine bees *Amegilla spilostoma* (Apidae) on *G. carneus* and *G. monticola*, and *A. capensis* on *G. calcaratus*. The tongues of these bees are only 10–12 mm long (Goldblatt et al., 1998), thus too short to allow them to reach the nectar, and they usually did not actively collect pollen. The bees do, however, carry loads of *Gladiolus* pollen, and we suspect that they sometimes accomplish pollen transfer and cross pollination. Nevertheless, their visits appear to be infrequent and their behavior undirected, and we consider them to be no more than occasional, opportunistic visitors to these flowers. Female *A. spilostoma* bees were seen to collect pollen from anthers of *G. carneus* while clinging upside down to the anthers. This activity invariably followed unsuccessful attempts to probe the floral tube, presumably in search of nectar.

Irrespective of geography and plant species visited, foraging behavior of long-proboscid flies was similar. Flies were most active on warm days in the morning between 0800 and 1200 hours. *Moegisto-*



rhynchus longirostris was exceptional in being active at one of our study sites between 0700 and 0900 hours and was not seen there at other times of the day. In Namaqualand (Goldblatt et al., 1995) *M. longirostris* was seen to be most active in the late afternoon, 1600 to 1800 hours. When not foraging, tabanid flies hold their mouthparts extended forward, while the mouthparts of nemestrids hang loosely downward (the mouthparts are not retractable). When approaching a flower, nemestrid flies may raise their mouthparts depending on the orientation of the flower, while keeping their bodies horizontal. At the beginning of a foraging bout, flies attempted to insert their mouthparts into the tube, not always with immediate success. When the proboscis encountered the floral tube, the fly moved toward the flower and grasped the tepals as soon as these were within reach (Fig. 4A). Flies usually forced their bodies into the wide throat of the flower, continuing to move their wings rapidly throughout foraging.

During the foraging process, anthers, which are located below the dorsal tepal in *Gladiolus* species, brushed against the dorsal thorax of the fly, and pollen (when present) was deposited on the bristly body. Pollen deposition was usually so liberal that pollen could be seen streaked across the thorax of a fly. Since flies, unlike bees, do not groom their bodies to remove pollen to specific sites on their bodies, the dorsal thorax of flies that had visited *Gladiolus* flowers could be seen with the naked eye to be covered with pollen of a particular color. In flies that had visited *G. floribundus*, *G. macneilii*, or *G. undulatus*, which have dark purple pollen, the dorsal surface of the thorax was visibly purple, the result of a heavy covering of pollen (Fig. 4). Likewise, flies that had visited *G. oppositiflorus* can often be seen to have a prominent pale blotch on the dorsal part of the thorax, due to the heavy load of the pale mauve pollen of the species.

The same flies foraging on flowers with the stigmatic surfaces unfolded accomplished passive pol-

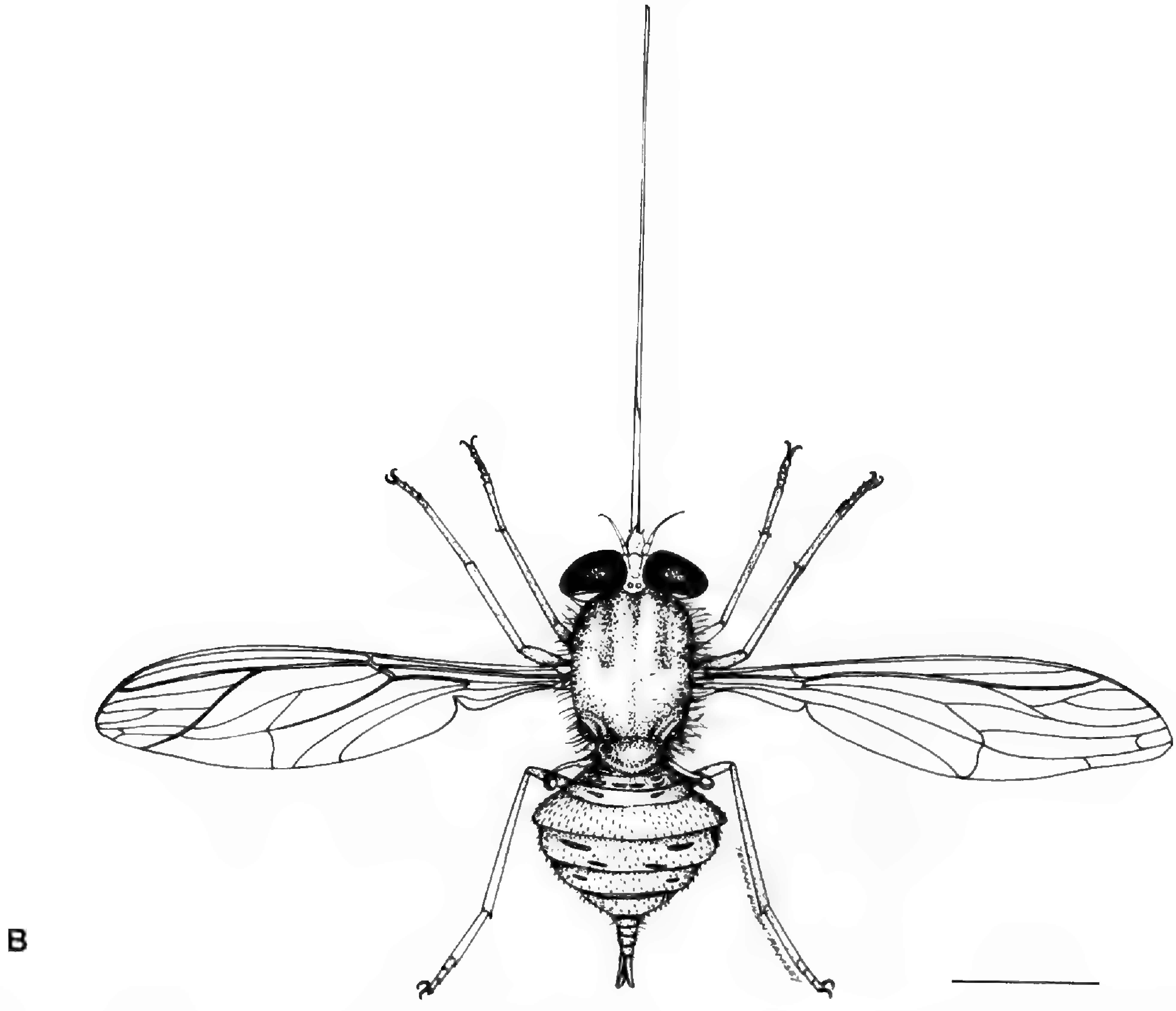


Figure 5. Representative long-proboscid flies captured on flowers of *Gladiolus* showing proboscis length relative to body size. —A (facing page). *Stenobasipteron wiedmannii.* —B. *Prosoeca ganglbaueri.* Scale bar 5 mm.

len transfer. As a fly forced its body into the tube of a flower, pollen was brushed onto the moist stigmatic surfaces of the outspread style branches. Again, because of the distinctive color of pollen in some species, pollinated flowers could usually be immediately identified by the presence of appropriately colored pollen on the stigmas.

Foraging by long-proboscid flies was occasionally constant, with an insect visiting flowers of a particular species consecutively, or foraging was non-constant, a fly visiting flowers of a range of plant species in a random pattern, thus shifting its attention to flowers of different species, one after another. Very often this was also a long-tubed flower of similar color and shape, and with a nectar supply held within a long floral tube. The species at a particular site that were pollinated by a particular fly usually broadly resembled one another in the general size, shape, and color of their flowers. They may thus be considered to comprise guilds, that is, a group of species utilizing a particular resource in a similar way (Root, 1967). In this case, the flowers of several plant species have converged and resemble one another in general shape, color, and marking in order to make use of a specialized pollinator.

Flowers of the various species in guilds associated with *Gladiolus* species pollinated by long-proboscid flies consistently show a precise placement of pollen on a different part of the body of a fly (Table 5). Thus, pollen of one species is not normally mixed with that of any other, and species-pure pollen loads are delivered to stigmas, avoiding clogging of stigmas by foreign pollen, an important consideration for species pollinated by semi-constant or non-constant pollinators (Waser, 1978).

There are at least five main sites of pollen deposition available to a plant (Manning & Goldblatt, 1996, 1997): the dorsal surface of the thorax; the dorsal part of the head; the frons and top of the proboscis; the proximal surface of the ventral thorax; and the distal ventral surface of the thorax and abdomen. Pollen scraped from captured flies confirmed the presence of pure loads of a particular pollen species from these different parts of a fly's body. Among the guilds observed in the course of this study (Table 5), no two species were found to

Table 5. Pollen (pollinaria) load analysis and pollen (pollinaria) loading sites of flies (and other insects) captured on *Gladiolus* species. Taxonomic associations of insects are as follows: Apoidea (bees): *Amegilla* (Anthophoridae); Muscoidea (flies): *Moegistorhynchus, Prosoeca, Stenobasipteron* (Nemestrinidae); *Philoliche* (Tabanidae). Families of plant taxa: *Brunsvigia* (Amaryllidaceae); *Erica* (Ericaceae); *Babiana, Geissorhiza, Hesperantha, Ixia, Lapeirousia, Watsonia* (Iridaceae); *Hemizygia, Orthosiphon* (Lamiaceae); *Brownleea, Disa* (Orchidaceae); *Pelargonium* (Geraniaceae); *Zaluzianskya* (Scrophulariaceae).

Plant and [insect taxon]	Insects carrying *Gladiolus* pollen	Insects carrying pollen other spp.	Other species carried (pollen loading site)
SUMMER-RAINFALL ZONE			
G. calcaratus			
[*Prosoeca robusta*]	3	2	*Hemizygia* sp. (frons), *Watsonia wilmsii* (dorsal abdomen)
[*Amegilla capensis*]	1	1	*Hemizygia* sp., unidentified dicot
G. macneilii			
[*Stenobasipteron wiedmannii*]	4	4	*Orthosiphon tubiformis* (frons)
G. microcarpus			
[*Prosoeca ganglbaueri*]	4	4	*Hesperantha rupicola* (head, frons), *Zaluzianskya microsiphon* (base of proboscis)
G. mortonius			
[*Prosoeca ganglbaueri*]	4	3	*Brunsvigia grandiflora* (upper and lower abdomen)
G. oppositiflorus			
[*Prosoeca ganglbaueri*]	4	2	*Brownleea macroceras* (pollinaria on proboscis and ventral thorax)
G. varius			
[*Prosoeca ganglbaueri*]	4	2	*Disa amoena* (upper proboscis)
WINTER-RAINFALL ZONE			
G. angustus			
[*M. longirostris*]	4	4	*Pelargonium longicaule* (ventral abdomen), *Geissorhiza exscapa* (ventral thorax), *Ixia paniculata* (base of proboscis), *Disa draconis* (proximal proboscis)
G. bilineatus			
[*Prosoeca longipennis*]	2	2	*Pelargonium dipetalum* (ventral thorax), *P. pinnatum* (ventral abdomen)
G. carneus			
[*Philoliche rostrata*]			
(Devil's Peak)	3	3	*Pelargonium elongatum* (frons, base of proboscis)
(Silvermine)	2	2	*Pelargonium myrrhifolium* (ventral thorax), *Watsonia borbonica* (ventral abdomen)
[*Prosoeca nitidula*]	2	4	*Geissorhiza bonaspei* (ventral abdomen), *Pelargonium myrrhifolium* (ventral thorax)
[*Amegilla spilostoma*]	2	2	undetermined dicots
G. engysiphon			
[*Prosoeca longipennis*]	2	2	*Pelargonium dipetalum* (ventral thorax), *P. pinnatum* (ventral abdomen)
G. floribundus			
[*Philoliche rostrata*]	1	2	*Pelargonium* spp. (ventral thorax, abdomen), Asteraceae (scattered, trace amounts)
[*Philoliche gulosa*]	1	2	*Pelargonium peltatum* (lower head and ventral thorax)
G. monticola			
[*Philoliche rostrata*]	3	3	*Pelargonium myrrhifolium* (ventral thorax)
[*Prosoeca nitidula*]	2	0	none
[*Amegilla spilostoma*]	2	2	undetermined dicots
G. rhodanthus			
[*M.* sp. nov.]	1	1	*Pelargonium radiatum* (ventral thorax), *Erica praecox* (frons)

Table 5. Continued.

Plant and [insect taxon]	Insects carrying *Gladiolus* pollen	Insects carrying pollen other spp.	Other species carried (pollen loading site)
G. undulatus [*Philoliche rostrata*]	4	4	*Pelargonium patulum* (ventral head and thorax), *Disa harveiana* (proximal proboscis), *Geissorhiza confusa* (ventral abdomen)
G. vigilans [*Philoliche rostrata*]	2	2	*Pelargonium* sp. (ventral thorax)
G. virgatus [*Philoliche rostrata*]	3	3	*Watsonia borbonica* (ventral abdomen), *Pelargonium myrrhifolium* (ventral thorax)
Totals	60	56	

use the same pollen deposition site. In *Gladiolus* species pollinated by long-proboscid flies, pollen is consistently placed on the dorsal thorax, sometimes extending onto the dorsal abdomen.

DISCUSSION

Long-proboscid flies have now been captured on 16 species of *Gladiolus* in southern Africa, and according to our results they are the primary and usually the only large-bodied insect visitors and effective pollinators of these species, all of which have a similar floral morphology. A further 13 species have the same floral morphology and are inferred to have the same pollinator. Thus, 29 (17%) of the 165 species of southern African *Gladiolus*, belonging to six of the seven sections of the genus, may be considered to have flowers adapted for long-proboscid fly pollination. Long-proboscid flies are not currently known across the remainder of the range of *Gladiolus*, that is, through tropical Africa and Arabia to Eurasia. Hence, the pollination system occurs in only some 10% of the entire genus. Long-proboscid fly pollination is the second most common pollination strategy in the southern African species of *Gladiolus*, but for the entire genus it is marginally less important than pollination by sunbirds, which may occur in as many as 20 species in southern Africa (Goldblatt et al., 1999) and, as inferred from floral morphology (Goldblatt, 1996), in about 10 more in tropical Africa.

Flowers adapted for pollination by long-proboscid flies are zygomorphic, bilabiate, and white, cream, or pink with reddish linear, spear- or diamond-shaped markings on the lower tepals. The floral tube is elongate, exceeding the length of the tepals, and at least 22 mm long with the narrow, proximal part of the tube more than 15 mm long. They also lack a floral odor in marked contrast to the flowers of *Gladiolus* species adapted for pollination by moths or bees. Flowers of moth-pollinated *Gladiolus* species are consistently fragrant (Goldblatt & Manning, 1998), as are bee-pollinated species of the genus occurring in the southern African winter-rainfall zone; flowers of bee-pollinated *Gladiolus* in the southern African summer-rainfall zone are unscented (Goldblatt et al., 1998).

The 29 species with flowers adapted for pollination by long-proboscid flies are all endemic in southern Africa. Their range in the subcontinent extends from the southwest through the southern and eastern Cape to the Drakensberg of eastern southern Africa. This range largely corresponds with that of long-proboscid flies except for the semi-arid northwest coast and near interior of South Africa and southern Namibia, where several species of long-proboscid flies occur (Manning & Goldblatt, 1996, 1997) but *Gladiolus* species adapted for their pollination do not.

Long-proboscid fly pollination in *Gladiolus* is thus established across a large part of southern Africa and involves different fly species in different parts of the subcontinent or at different times of the year. To the list of nemestrinids, *Moegistorhynchus longirostris* and *Prosoeca longipennis*, and the tabanid, *Philoliche gulosa*, already known to pollinate *Gladiolus* species in the winter-rainfall zone of southern Africa (Manning & Goldblatt, 1995, 1997), we can now add *Moegistorhynchus* sp., *Prosoeca nitidula*, and *Philoliche rostrata*. Long-proboscid fly pollination, not previously known in eastern southern African *Gladiolus* species, is now demonstrated to involve the nemestrinids *Prosoeca* *ganglbaueri*, *P. robusta*, and *Stenobasipteron wiedmannii*. *Prosoeca ganglbaueri* has already been reported to be the specialist pollinator of long-tubed *Nivenia stenosiphon* Goldblatt (Iridaceae) (Goldblatt & Bernhardt, 1990) and species of Orchidaceae: Disinae in the Drakensberg Mountains (Johnson & Steiner, 1995). The long-proboscid fly pollination system described here has been characterized by Struck (1997) as "long-proboscid hovering fly pollination." In *Gladiolus*, nemestrinid flies do not hover while foraging. They grasp the tepals firmly while continuing to vibrate their wings. Thus, hovering is not an essential part of the strategy as it is, for example, in hummingbirds.

Relatively few plant species are specialized for a single pollinator (Feinsinger, 1983), but it is clear that the species of *Gladiolus* pollinated by long-proboscid flies fall into this category. These flowers are specifically adapted for pollination by flies with elongate mouthparts exceeding 15 mm. Most of these *Gladiolus* species are, moreover, pollinated by just one fly species at a particular site and, so far as known, at most two over their entire range. We have occasionally captured two long-proboscid fly species at a study site. Dependence on a single pollinator places a plant at risk, because its long-term survival hinges on the survival of the pollinator. Long-proboscid flies have complex life cycles, the phases of which may be completed at sites distant from their food plants and often in different habitats. Tabanid fly larvae are aquatic and carnivorous, whereas nemestrinid fly larvae are most likely endoparasitic (Scholz & Holm, 1985), but this is unknown for the nemestrinid flies in southern Africa. Conservation of *Gladiolus* species must accommodate this aspect of their reproductive biology. It is particularly worrying that we have encountered sites where *Gladiolus* species with long-proboscid fly flowers are consistently not pollinated (observations for up to three successive years for *G. undulatus* at Nieuwoudtville, two for *G. angustus* at Mud River, Darling). At these sites plants did not set seed.

At Robertson, *Philoliche gulosa* had mouthparts 17–19 mm long, whereas *P. rostrata* had mouthparts 30–34 mm long (Table 4). *Philoliche gulosa* was barely able to reach the nectar in the tubes of *Gladiolus floribundus* that had received no visitors, and once the nectar levels had diminished, it could no longer successfully forage on this species. Individuals of *P. rostrata* were at no such disadvantage, and they must be regarded as the main pollinator of *G. floribundus* at this site. Since the length of the mouthparts of both tabanid and nemestrinid flies varies moderately within populations (e.g., Johnson & Steiner, 1995) and considerably across populations (Table 4; also Goldblatt et al., 1995; Johnson & Steiner, 1997), the situation at the Robertson site does not necessarily hold for other populations of *G. floribundus*. In the Drakensberg of Mpumalanga we encountered *Prosoeca ganglbaueri* and *P. robusta* together. The latter usually had shorter mouthparts, 20–23 mm long, and could forage successfully on *G. calcaratus* but could not reach the nectar of longer-tubed *G. varius*, on which it rarely foraged. *Prosoeca ganglbaueri* (mouthparts 33–35 mm) foraged on both *G. varius* and *G. calcaratus*, but because of its long mouthparts it did not contact the anthers of that species while foraging and in effect "robbed" the nectar of *G. calcaratus*. The only other study site where two fly species were encountered was at Silvermine, Cape Peninsula, where *G. carneus* received visits from the widespread and common *Philoliche rostrata* and the rare, evidently Cape Peninsula endemic, *Prosoeca nitidula*. The mouthparts in these two species were of comparable length, and the two fly species may be in direct competition for the same food resource. In a related study at Ysterfontein, Clanwilliam, *Moegistorhynchus longirostris* and *Philoliche gulosa* were recorded visiting the same suite of species (Manning & Goldblatt, 1997). These two flies had mouthparts of quite different lengths, 60–70 mm vs. 26–30 mm, and as at the Robertson site, the fly with the longer proboscis appeared to be at a competitive advantage. Pollination by a single species at a particular site is, however, the most common situation in long-proboscid-fly-pollinated *Gladiolus* species (Table 5).

These pollinator species generally fit the pattern outlined by Thompson (1981) in which pollinators tend to travel long distances between flowers and include visits to intervening plants when they recognize the cues presented. Convergence in floral form and the development of a mimicry ring (or guild) are thus striking features of plants using this pollination strategy. Mimicry can result in the increase in the number of visits to the flowers of a particular species, but pollen may be lost to stigmas by clogging with foreign pollen (Waser, 1978). In the guilds using long-proboscid flies as the main or sole pollinator, delivery of mixed pollen loads to stigmas is effectively prevented by divergence in the placement of their floral parts and thus in the deposition of pollen on the insect's body, a condition predicted by Waser (1983) and shown to be a constant feature of long-proboscid fly pollination (Manning & Goldblatt, 1996, 1997). In these studies on southern African pollination guilds, no two species have been found to use the same pollen deposition site at any study area.

Nectar volume in *Gladiolus* species with flowers adapted for long-proboscid fly pollination is generally higher than in species pollinated by anthophorine bees (see Goldblatt et al., 1998). This is likely to be related to the comparatively large size of these flies (and their presumably large dietary requirements) compared with substantially smaller bees. The high volume of nectar produced per flower may also be part of the long-proboscid fly pollination system. Flies have relatively few plant species on which they alone can forage, and an ample reward may ensure that flies forage on *Gladiolus* flowers even when other nectar sources are available. Nectar volume in *Gladiolus* species pollinated by long-proboscid flies is consistently higher than in any other species flowering at our study sites. Thus, during their comparatively short flowering time, the relatively few flowers produced per *Gladiolus* plant constitute a particularly rewarding source of nectar (Manning & Goldblatt, 1997, and in prep.). Obviously, long-proboscid flies can forage on flowers of species with shorter tubes (and are sometimes seen foraging on short-tubed flowers) but must then compete with a large nectarivorous fauna including bees, wasps, bombyliid flies, and shorter-proboscid nemestrinids and tabanids. By virtue of their size, smaller flowers offer smaller quantities of nectar. Moreover, other species with long-tubed flowers belonging to long-proboscid fly guilds that include *Gladiolus*, e.g., *Orthosiphon* (Lamiaceae) and *Pelargonium*, also usually have less nectar than *Gladiolus* flowers (Manning & Goldblatt, 1997, and in prep.). In some *Disa* and *Hesperantha* species (Manning & Goldblatt, 1997, and in prep.) no nectar is produced, and the pollination of these species depends on the close resemblance of their flowers to those of *Gladiolus* and other members of these guilds.

Nectar sugar composition is sucrose dominant in nearly all the *Gladiolus* species examined for the character (including all fly-pollinated species), but this is evidently not related to taste preferences or energy requirements of long-proboscid flies. Flowers of most ixioid Iridaceae have sucrose-dominant nectar (Goldblatt et al., 1995; Manning & Goldblatt, 1996, 1997; B.-E. van Wyk, pers. comm.) except for some that are adapted for bird pollination (Goldblatt et al., in prep.). Species of some other plant families with long-proboscid-fly flowers, notably *Pelargonium* species, often have hexose-dominant nectar (Manning & Goldblatt, 1997, and in prep.).

The evolution of pollination systems in African Iridaceae has been demonstrated to be fairly labile in some genera. For example, in *Lapeirousia*, with some 40 species, flowers of different species are adapted for generalist pollination by bees, wasps, and butterflies, two quite independent long-proboscid fly systems, as well as hawk moths (Goldblatt et al., 1995). Comparing pollination systems to the phylogeny of subgenus *Lapeirousia*, the two types of long-proboscid fly systems appear to have each evolved independently at least twice from an ancestral generalist system, while long-tongued bee pollination appears to have evolved in two lineages from ancestors pollinated by long-proboscid flies (Goldblatt et al., 1995; Goldblatt & Manning, 1996). Such labile floral evolution likewise appears characteristic of *Gladiolus*. Pollination by nectarivorous long-tongued bees appears ancestral in the genus (Goldblatt & Manning, 1998; Goldblatt et al., 1998). Long-proboscid fly pollination occurs in six of the seven southern African sections of the genus (it does not occur in sect. *Heterocolon*). Long-proboscid fly pollination has now been confirmed in species of five of these sections (Table 1), and species with long-proboscid-fly-type flowers also occur in section *Hebea* (inferred for 2 spp.).

Except in section *Blandus*, the pollination system is represented by just a few specialized species of the section. However, in series *Blandus* it is the dominant pollination strategy, and speciation within the long-proboscid fly pollination system appears to have occurred within this series. Radiation in series *Blandus* must have involved geographic, edaphic, and microclimatic factors as well as pollinator shifts in some species (Goldblatt & Manning, 1998).

At a conservative estimate, long-proboscid fly pollination may have evolved some ten times within *Gladiolus*, once within each of three series of section *Densiflorus*, twice in section *Linearifolius*, once in section *Ophiolyza*, and at least once in each of three series of sections *Hebea* and *Homoglossum*. In total, 29 species of southern African *Gladiolus*, 17% of the species in the region, have flowers putatively or known to be adapted for pollination by long-proboscid flies. By comparison, in *Pelargonium* some 25% of 208 taxa (species and subspecies) in southern Africa have flowers adapted for pollination by long-proboscid flies (Struck, 1997), making *Pelargonium* the genus in which long-proboscid fly pollination is most common. In *Pelargonium*, there is a similar pattern of repeated evolution of the pollination strategy from the ancestral bee pollination that occurs in most of the sections of that genus (Struck, 1997).

We may speculate on the reasons for the shift in pollination system. A feature of the long-proboscid fly pollination in *Gladiolus* is that species utilizing the system flower after the middle of the main flowering season in both the summer- and winter-rainfall zones of southern Africa. Species also bloom close to the time when long-proboscid flies emerge. Populations of bee fauna in both climate zones are in decline at this time of the year, as most bee species have completed their life cycles and have provisioned nests. Pollinators may thus be a limiting factor at such times. Under such conditions, selection for long-proboscid fly pollination would presumably be favored. Whatever the initial stimulus, the multiple evolution of the strategy suggests the existence of strong selective pressures favoring long-proboscid fly pollination at certain times of the year. Except for reports of long-proboscid fly activity in the Himalayas (Dierl, 1968), long-proboscid fly pollination as understood here is unknown outside southern Africa. The strategy evidently does not occur in tropical Africa, where no *Gladiolus* species exhibit the adaptations that are associated with long-proboscid fly pollination in southern Africa.

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BOOK REVIEW

Polhill, Roger & Delbert Wiens. 1998. Mistletoes of Africa. Royal Botanic Gardens, Kew. ISBN 1 900347 56 3. v + 370 pp., illustrated, hardbound.

This beautifully produced book provides a thorough and entirely novel synthesis of the biology, geographic distribution, morphology, and taxonomy of the Loranthaceae and Viscaceae of continental Africa. Copiously illustrated with 139 color photographs, 43 line drawings, and 162 maps, it is visually a pleasure to use. The opening chapter on the parasitic habit puts these remarkable plants in their biological context and prepares the reader for the excellent and detailed studies of haustorial morphology in the chapter by Clyde Calvin and Carol Wilson, and pollination mechanisms in the chapter by Donald Kirkup. The presentation of host ranges for each genus in Table 1 was particularly welcome, and helped to clarify trends that I had noted but never attempted to quantify by field observations. The short chapter on the origins and evolution of the families is a competent summary from studies in embryology, cytology, anatomy, morphology, DNA sequences, and phytogeography, but would be more satisfactory if the putative phylogeny of all of the families of Santalales were presented as one or more cladograms. A chapter on biogeography summarizes trends apparent in distribution maps of individual species within the context of the main chorological divisions of Africa, and a brief chapter touches on the (mostly negative) economic importance of these parasites.

The authors set the stage for the systematic core of the book in the chapter "Generic Classification of African Loranthaceae" (pp. 61–66). For one who has struggled with great difficulty to find acceptable modern generic placements for countless basionyms in *Loranthus,* the comparison of various authors' generic arrangements in Table 6 was particularly revealing. The separation of the genera into two major lines of evolution, the Tapinanthoid and Taxilloid groups, is a genuine advance in phylogenetic understanding, but here as at the family level, presentation of generic relationships as a cladogram, however tentative, would make the conclusions much more accessible. In particular, more explicit support for the separate recognition of *Actinanthella, Agelanthus, Englerina, Oliverella, Oncocalyx,* and *Spragueanella* in the Tapinanthoid group would be highly desirable. In the Taxilloid group, the segregation of *Taxillus* and *Vanwykia* must be seen as questionable pending inclusion of *Bakerella* and *Socratina* from Madagascar and the Indian Ocean islands in the analysis.

The systematic part of the book (pp. 76–359) is meticulously well organized and clearly presented. Running titles in a colored bar on the right margin relieve the user of the tedium of searching through the text after using the key to genera. I experienced few problems in using the keys to genera and species to identify herbarium specimens. Although the distinctions between the sections of *Agelanthus* (p. 138) seem a bit vague, and specimens of dioecious species of *Viscum* can present problems in a key (pp. 280–282) that in places relies on characters of only staminate or pistillate flowers, these are minor problems that can readily be addressed with reduced numbers of species in the regional flora treatments for which this volume is stated to be a precursor. Descriptions of genera and species are beautifully parallel throughout, greatly facilitating comparison of taxa when any doubt remains from the keys. The line drawings by Christine Grey-Wilson and Marguerite Scott are of excellent quality and highly diagnostic, complemented by numerous, mostly excellent color photographs that underline the need for careful recording of flower color patterns in collectors' field notes. The inclusion of distribution maps for all species contributes greatly to the usefulness of the book, but at least this user finds the semitopographic, gray-colored maps somewhat difficult to scan visually and would prefer black-and-white outline maps. Bibliographic citations and synonymy are thorough and accurate, and the decision to apply lectotypification rather sparingly (p. 76) has been most judiciously applied. Although very few specimens other than types are cited in the text, the list of specimens on pp. 317–359 is unusually extensive and an invaluable aid to herbarium curation. Inevitably, a few discrepancies between stated geographic distributions and listed specimens have crept in (e.g., *Breteler 654* from Gabon cited on p. 321 as *Globimetula elegantiflora,* stated on p. 217 as only "possibly in Gabon"), but these are editorial details that detract nothing from the overall quality of the work. In short, this is a magnificent volume that belongs on the shelf of anyone concerned with the biology and systematics of parasitic plants, and I commend the authors on this culmination of many years of dedicated endeavor.—Roy E. Gereau, *Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A.*

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Cover illustration. *Barnadesia corymbosa* (Ruiz & Pavón) D. Don, by Iona Nieva.

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REVISION OF *BERBERIS* (BERBERIDACEAE) IN CHILE AND ADJACENT SOUTHERN ARGENTINA[1]

Leslie R. Landrum[2]

ABSTRACT

Twenty species of *Berberis* are recognized in continental Chile, the Juan Fernández Islands, and adjacent southern Argentina, comprising a considerable reduction in species number from the works of earlier authors. Hybridization between species is common. Each species is described, and all are distinguished with a dichotomous key. Maps are provided for all species and photographs for all continental species. Notes on phenology, habitat, distribution, and distinguishing characters are included. One new combination, *B. chilensis* var. *brachybotria* (Gay) Landrum, is made. The following taxa are lectotypified: *B. brachyacantha* Phil. ex Reiche, *B. buxifolia* var. *antarctica* C. K. Schneid., *B. congestiflora* Gay, *B. crispa* Gay, *B. ferox* Gay, *B. brachybotria* Gay, *B. empetrifolia* var. *magellanica* C. K. Schneid., *B. florida* Phil., *B. horrida* Gay, *B. linearifolia* Phil., *B. montana* var. *chillanensis* C. K. Schneid., *B. mutabilis* Phil., *B. polymorpha* Phil., *B. variiflora* C. K. Schneid., *B. wawrana* C. K. Schneid., and *B. zahlbruckneriana* C. K. Schneid.

This paper is a more complete version of my treatment of *Berberis* for the Flora de Chile project being coordinated by the Universidad de Concepción, Concepción, Chile. For the sake of brevity, many things, namely nomenclatural citations and synonymy, lists of representative specimens, illustrations, an index to collectors, and numbers and discussion of systematic criteria and geography,

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[1] This study was made possible in part by funding from the National Geographic Society. While in Chile I was kindly supported by the Departamento de Botánica of the Universidad de Concepción (and through that institution by the Andrew Mellon Foundation and National Science Foundation), and the Sección Botánica of the Museo Nacional de Historia Natural in Santiago. I especially thank Clodomiro Marticorena, Roberto Rodríguez, Eduardo Ruiz, Max Quezada, and Mélica Muñoz for their help with field studies and in the preparation of this manuscript. The Corporación Nacional Forestal (CONAF) provided a collecting permit and logistic support. CONAF employees G. Gutiérrez, A. Morales, and J. Flores were especially helpful in relocating *Berberis* species near Paposo. I thank my wife, Sonia, for her cheerful companionship and help in the field. Generous relatives have provided us with lodging. We thank the families of Bárbara Cubillos and Esmeralda Cubillos of Santiago, Alejandro Suanes of Concepción, Armando Carrasco of Valdivia, and Ricardo Suanes in Paris, France, for their kind hospitality. Charlotte Taylor, Jorge S. Marroquí, and Clodomiro Marticorena reviewed and Victoria C. Hollowell edited this manuscript. They have all kindly offered many helpful suggestions. The following herbaria were consulted for this study and the curators are thanked: ASU, BM, BR, CAS, CONC, CORD, F, G, HIP, LP, LY, MERL, MO, NA, NY, OS, P, RSA, SGO, SI, TEX, US, and W.

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could not be included in the *Flora de Chile* but are provided here. I have also expanded coverage to follow phytogeography rather than political boundaries, including adjacent southern Argentina where many of the Chilean species grow. Many plants of the humid forests of southern South America grow on both sides of the Andes, but distributions are much less extensive in Argentina because of the Andean rain shadow. This is the case with seven species of *Berberis* (*B. darwinii*, *B. empetrifolia*, *B. ilicifolia*, *B. microphylla*, *B. montana*, *B. serratodentata*, and *B. trigona*). Two additional endemics of western Argentina have also been included, *Berberis comberi* and *B. grevilleana*. The major purpose of this paper is to make identification of *Berberis* as simple as possible for southwestern South America. A map of the regions of Chile is provided (Fig. 1).

The Berberidaceae are a family of about 15 genera and 650 species, widespread in the Northern Hemisphere and with a single genus, *Berberis*, extending into temperate and Andean South America.

In the most recent worldwide study of *Berberis*, Ahrendt (1961) recognized about 500 species with simple leaves (true *Berberis*) and approximately 200 species in the Northern Hemisphere genus *Mahonia* Nuttall with compound leaves; the latter genus is now commonly combined with *Berberis*. Thus, *Berberis* s. str. is a huge group, and if it is combined with *Mahonia*, the genus is even more vast. Such large groups are "taxonomic black holes," because no one can understand them in a reasonable number of years, or even a lifetime. It becomes extremely difficult to define useful taxonomic entities (e.g., subgenera or sections) because it is impossible to know more than a subset of the species well.

The simple-leaved species of *Berberis* have two important centers of diversity corresponding to the informal subgeneric groups first given names by Schneider (1908): the *Septentrionales* of Eurasia with ca. 300 species, and the *Australes* of South America with ca. 200 species (Ahrendt, 1961), most of which are Andean. The actual number may be much less, considering that Ahrendt recognized ca. 60 species in Chile and adjacent southern Argentina and I accept only 20.

Division between *Septentrionales* and *Australes* appears mainly to be geographically based. Red berries and deciduous leaves, found in many *Septentrionales*, are rare in South American species; foliaceous spines, dentate stamens, and deep orange flowers found in many *Australes* are rare or do not exist in *Septentrionales* (Ahrendt, 1961). Evaluation of the validity of *Septentrionales* and *Australes*, requiring a broad knowledge of both groups, is beyond the scope of the present study.

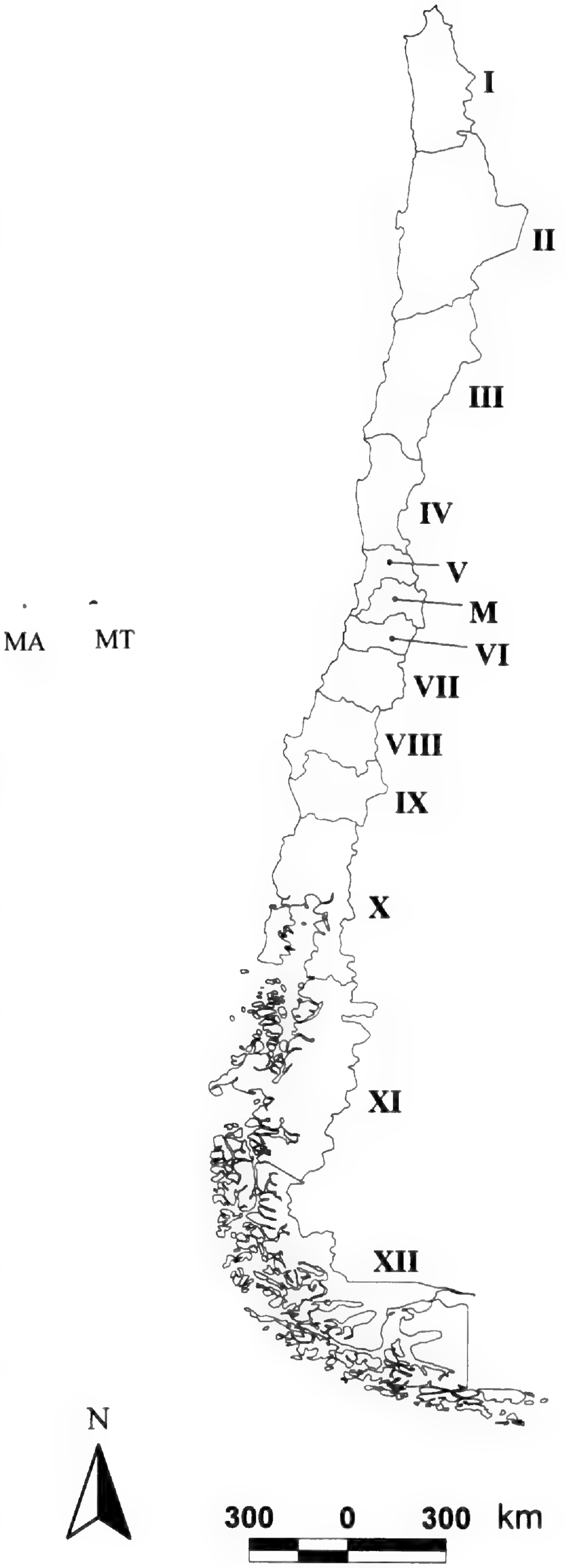

Figure 1. Regions of Chile. Más Afuera (MA) and Más a Tierra (MT) of the Juan Fernández Archipelago correspond to Región V. Made in Arizona State University Library Map Collection with data from ESRI (Environmental Systems Research, Inc.).

Prior to Ahrendt's treatment, Schneider (1905) divided *Berberis* s. str. into 21 sections, 6 of which occur in southwestern South America. Ahrendt (1961) divided *Berberis* s. str. into 29 sections, 8 of which are found in southwestern South America. Both authors often subdivided these sections into subsections. Their groups often conform to what I believe to be closely related species or even single species. In general, I recognize fewer species than they do. I differ from both authors in joining under one name *B. microphylla, B. buxifolia,* and *B. heterophylla*; they place each of these taxa in separate sections. I also differ with Ahrendt in submerging *B. pearcei* within *B. serratodentata,* species he placed in different sections.

SYSTEMATIC CRITERIA

Leaves of *Berberis* vary greatly in size and shape and in the toothing of the margin (Fig. 2). Infraspecific variation is great, and leaves of plants that have been browsed or cut over can be quite different from typical leaves. In spite of this variation, leaf morphology is of great taxonomic importance. The texture varies from membranous (e.g., *B. rotundifolia*) to stiffly coriaceous (e.g., *B. comberi*). Shape varies from subacicular to suborbicular, and leaf size is, of course, important. Venation may be of a reticulate-actinodromous type (Fig. 2A) with the midvein and some secondary veins of about equal importance, or a mixed craspedodromous type (Fig. 2D) with dominant midvein, or even an intermediate type (Fig. 2H). Leaves of a single plant may vary from type to type, but tendencies in venation are of taxonomic importance. The veins in both types tend to form loops, and some veins reach the margins. The leaf surfaces vary from smooth to papillose. The petioles often have a noticeable "joint" someplace between the blade and the twig. The portion below the "joint" often persists after the rest of the leaf has fallen.

Spines are the reduced leaves of long shoots and are variable in their morphology (Fig. 3), being foliaceous (Fig. 3A, D), star-like (Fig. 3B), palmate (Fig. 3C), or trifid (Fig. 3F, G). The leaves of short shoots are more or less normal in their morphology and occur as clusters in the axils of the spines. In *Berberis valdiviana* a nearly perfect intermediate between an elliptic leaf and a trifid spine occasionally can be found. Some species or individuals (or even particular branches) never develop spines, the leaves of the long shoots developing into typical leaves. Sometimes the spines are so similar to true leaves that they can easily be confused with them (Fig. 3A).

Flowers and fruits may be borne singly (Fig. 12B), in sessile umbels (13C), in pedunculate umbels (Fig. 13A), or racemes (13D). A pedunculate dense raceme to umbel is also possible (Figs. 4F, 10B). Paniculate inflorescences are normally found only in *B. corymbosa,* among the species treated here, but are common farther north in the Andes.

Flowers may be yellow, orange, to red-orange and are usually uniform in color, but in *B. montana* the inner tepals are darker than the outer and the flower looks superficially like a miniature daffodil. The perianth typically has 5 or 6 whorls of 3 tepals, the inner 2 whorls with 2 nectariferous glands on the lower inner surface. The next whorl or two whorls toward the outside are somewhat larger, and the more exterior whorls decrease in size, the outermost being bract-like.

Six stamens are located opposite the inner two whorls of tepals. Two tooth-like projections just below the anther (Fig. 4H) can be found in some species, but are absent in others.

The pistils are mostly of two types, those with an elongate style (Fig. 4D) and those with little or no style (Fig. 4G). Species of the Juan Fernández Archipelago seem to be intermediate. Ovule number is sometimes important.

Fruits are always dark purple, bluish, or black, but are sometimes covered with a waxy bloom. The seeds are usually separate at maturity, but in *B. comberi* and *B. grevilleana* they are fused together in a mass.

In general, *Berberis* is known for possessing a rich array of alkaloids, and the species of Chile have been particularly well studied (see summary of Fajardo, 1992). I have not attempted to analyze the results of these studies from a taxonomic perspective, but perhaps this can be done in the future.

SPECIES GROUPS

I am opposed to accepting formal sections or subsections at present because I think it is still impossible to know whether they have any phylogenetic basis. Geography seems to have played an important role in Schneider's and Ahrendt's subgeneric classifications, their sections generally being confined to a geographic area. However, species from widely separated places in South America can look very similar, and even species from other continents can closely resemble some Chilean species. Certainly, homoplasy has been pervasive in *Berberis.* The best approach for future studies of the genus probably will be regional revisions. Nonetheless, two clusters appear among the southwestern South

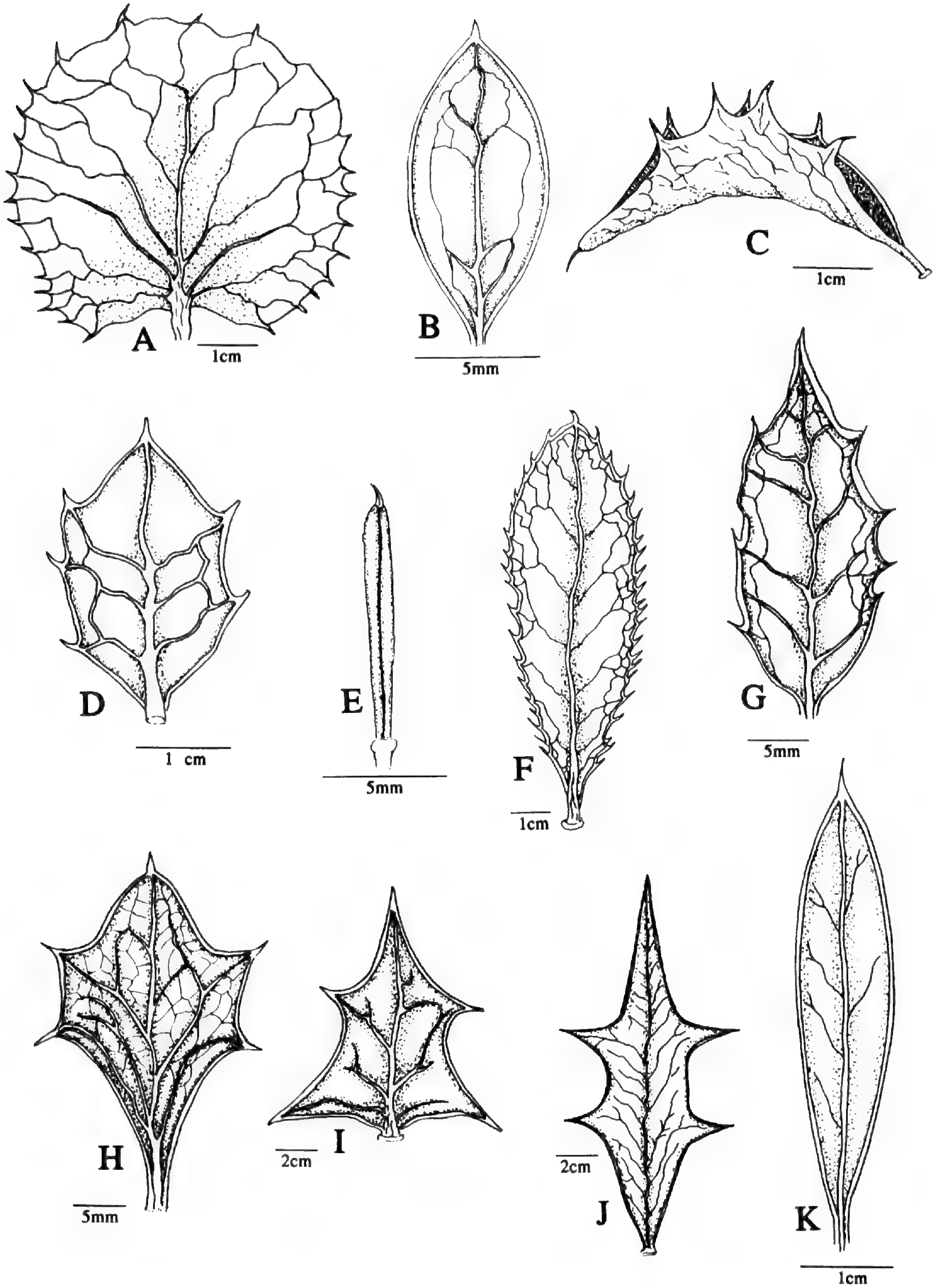

Figure 2. Leaves of various species of *Berberis*. —A. *B. actinacantha*, southern form (*7952*). —B. *B. microphylla* (*8153*). —C. *B. chilensis* var. *chilensis* (*7907*). —D. *B. darwinii* (*8148*). —E. *B. empetrifolia* (*8182*). —F. *B. serrato-dentata* (*8112*). —G. *B. chilensis* var. *brachybotria* (*Bricker 186*). —H. *B. grevilleana* (*8340*). —I. *B. comberi* (*8353*). —J. *B. comberi* (*8379*). —K. *B. trigona* (*8007*). All collections by Landrum except for G.

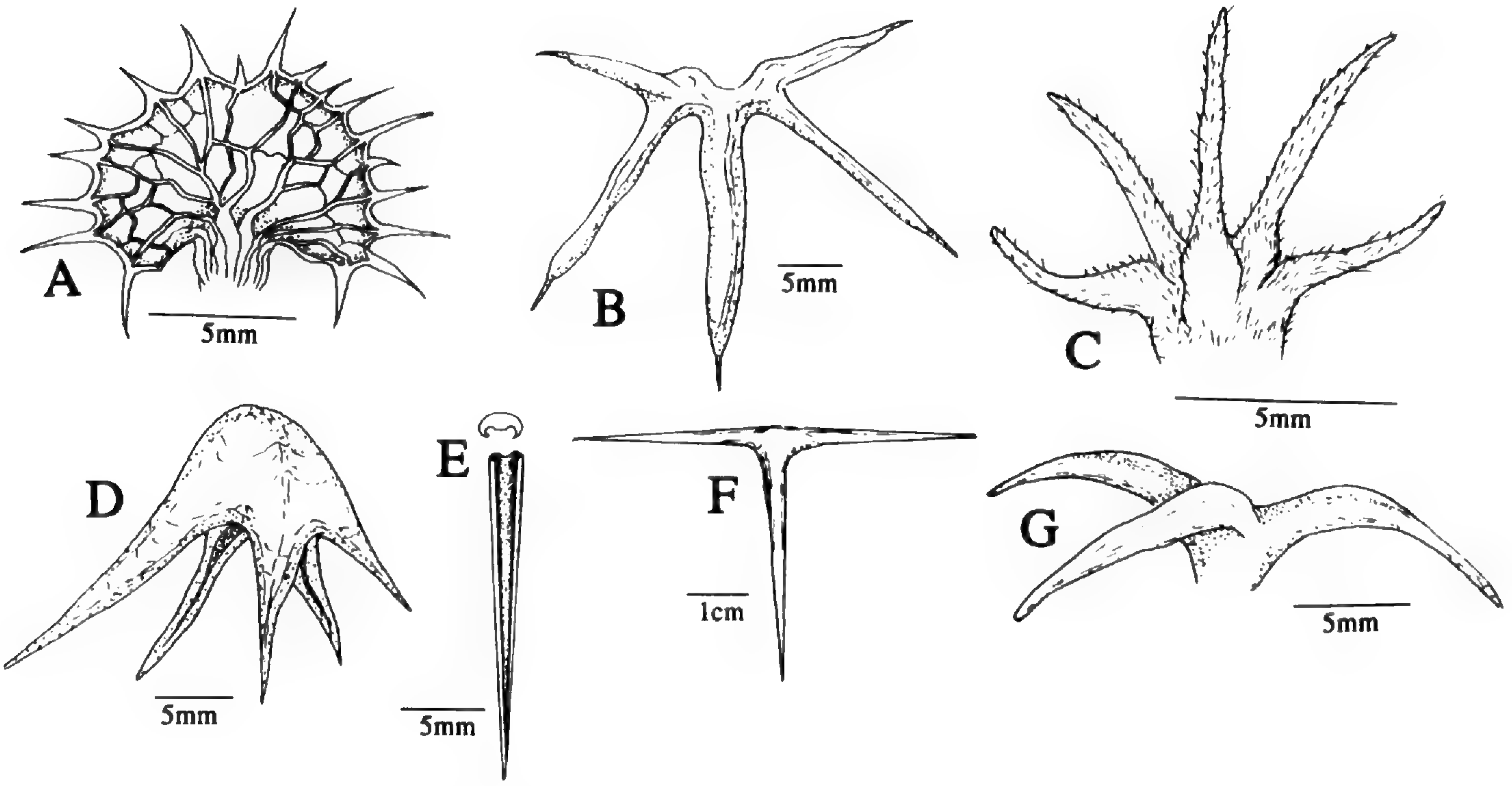

Figure 3. Spines of various species of *Berberis*. —A. *B. actinacantha*, foliaceous spine (*7548*). —B. *B. actinacantha*, star-like spine (*7887*). —C. *B. darwinii*, palmate spine (*Burkhardt 57[3]*). —D. *B. rotundifolia*, foliaceous spine (*7951*). —E. *B. microphylla*, one arm of a trifid spine from below and in section (*8153*). —F. *B. grevilleana* (*8340*), straight trifid spine. —G. *B. trigona*, recurved trifid spine (*8007*). All collections by Landrum except for C.

American species that seem to have some phylogenetic basis. Using these as a start, one might try to discover more members in other areas.

The first group generally has umbellate inflorescences, foliaceous spines, predominantly reticulate-actinodromous venation, short styles, and stamens with lateral teeth just below the anther. It includes at least *B. actinacantha*, *B. congestiflora*, *B. rotundifolia*, and *B. horrida*. Species that are perhaps similar, but that lack one or more characters typical of this group, are *B. empetrifolia*, *B. microphylla*, *B. glomerata*, *B. grevilleana*, and *B. comberi*.

A second group shares racemose inflorescences, relatively large 3-parted spines, predominantly mixed craspedodromous venation, long styles, and stamens without lateral teeth. It includes *B. chilensis*, *B. litoralis*, and *B. valdiviana*. Other species that seem to be related but lack one or more typical characters are *B. darwinii*, *B. ilicifolia*, *B. trigona*, *B. serratodentata*, and *B. negeriana*. *Berberis laurina* Billbg. of Brazil and Uruguay probably belongs to this group, being quite similar to *B. litoralis* and *B. valdiviana*.

Berberis montana, *B. corymbosa*, and *B. masafuerana* do not clearly belong to either group. In *B. corymbosa* the inflorescence and style are similar to *B. jobii* Orsi and *B. jujuyensis* Job, both of northwestern Argentina.

GEOGRAPHY

Stuessy and Taylor (1995) have provided an extensive synthesis of numerous phytogeographic studies of the Chilean flora. The following discussion is, of course, much shorter and restricted in scope.

The sclerophyllous mediterranean matorral of central Chile and the wet temperate forests of southern Chile and adjacent southern Argentina with rainfalls sometimes exceeding 4 m (Cabrera, 1971) together comprise an island of relatively abundant plant growth surrounded by ocean on the west and south, the Atacama Desert in the north, and the Patagonian Desert in the east. It is an area of high endemism. For instance, among the dominant woody plant groups, all species of Fagaceae, Monimiaceae, Lauraceae, Cunoniaceae, Flacourtiaceae, Eucryphiaceae, Araliaceae, Celastraceae, Elaeocarpaceae, Podocarpaceae, Cupressaceae, Araucariaceae, and nearly all species of Cornaceae, Proteaceae, and Myrtaceae are endemic. Many genera are endemic, including the following woody plants and epiphytes: *Jubaea*, *Myoschilos*, *Boquila*, *Lardizabala*, *Peumus*, *Pitavia*, *Valenzuelia*, *Bridgesia*, *Berberidopsis*, *Sarmienta*, *Mitraria*, *Asteranthera*, *Saxegothaea*, *Fitzroya*, *Pilgerodendron*, *Amomyrtus*, *Tepualia*, and *Legrandia*. Three angiosperm families are endemic: Aextoxicaceae, Gomortega-

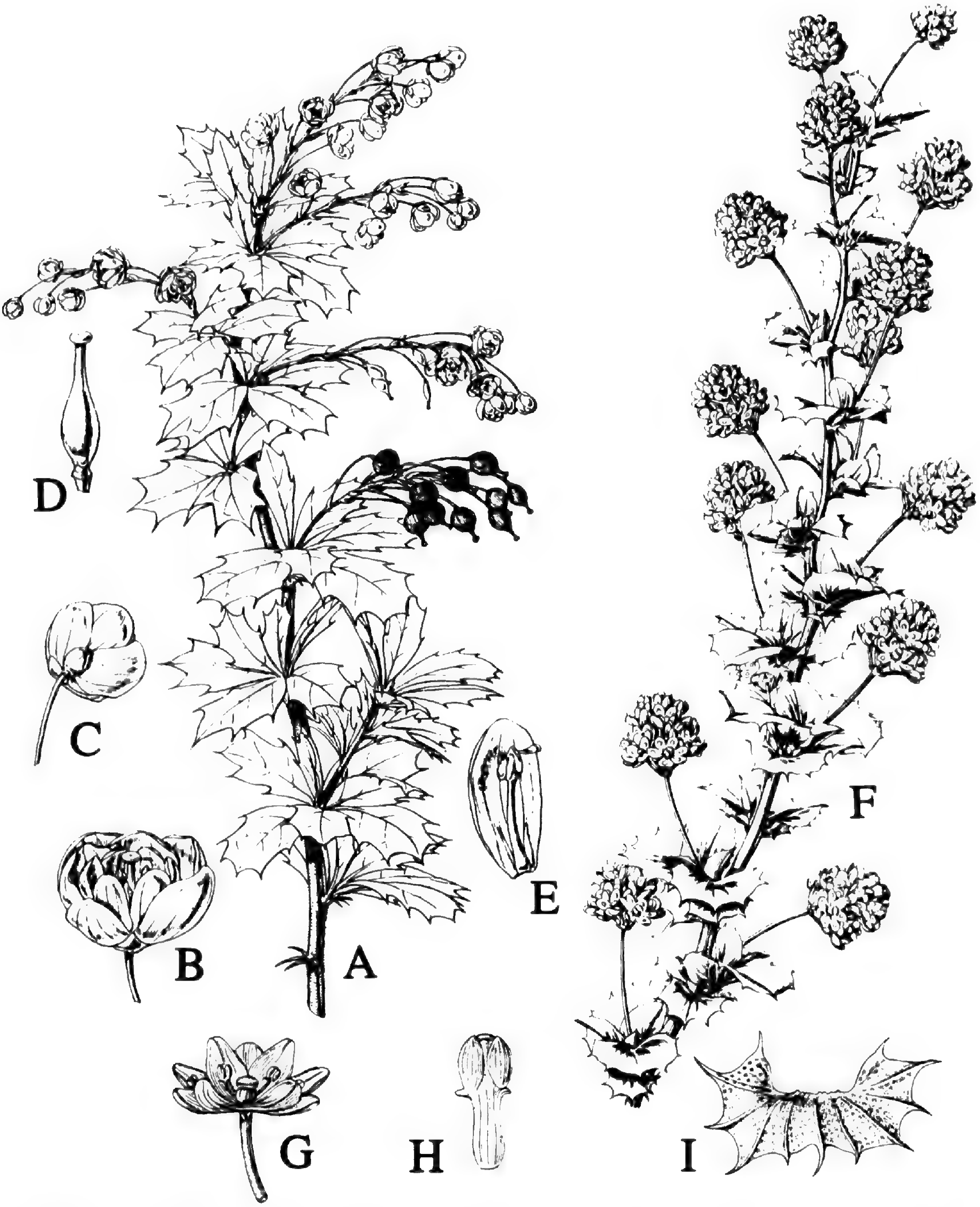

Figure 4. A–E. *Berberis darwinii.* —A. Branch with fruits and flowers. —B. Open flower from above. —C. Open flower from below. —D. Pistil with elongate style. —E. Single tepal with stamen. Reproduced from W. J. Hooker, Icon. Pl. 7, t. 672. 1844. F–I. *B. congestiflora.* —F. Flowering branch. —G. Open flower (note essentially sessile stigma). —H. Stamen with tooth-like appendages. —I. Foliaceous spine. Reproduced from lámina 3 of the *Atlas of C. Gay's Historia física y política de Chile 1845–1854* and a copy of the same in C. Muñoz (1966), *Sinopsis de la flora chilena,* fig. 36.

ceae, and Misodendraceae (Cronquist, 1981). Such a high degree of endemism, especially at the higher taxonomic levels, generally indicates long isolation. Various factors have contributed to the isolation of the flora of southwestern South America: continental drift, desertification of northern Chile and Patagonia, and the rise of the Andes (Stuessy & Taylor, 1995).

Berberis is diverse in southwestern South America. If the two species of the Juan Fernández Islands and the two species of the adjacent Patagonian Desert (*B. comberi* and *B. grevilleana*) are excluded, then there are still 16 species of *Berberis*, sometimes quite dissimilar, in continental Chile and adjacent Argentina in this southwestern South American "island" of vegetation. Thus, it is unlikely that *Berberis* is a recent introduction, for if that were the case, only several introductions or rapid divergent evolution could account for the diversity. But if *Berberis* is a long-time resident of southern South America, the diversity is more understandable. In fact, leaf fossils that are apparently of *Berberis* have been found in the early Tertiary of Neuquén and Santa Cruz, Argentina (Berry, 1938; Fergulio, 1949; Orsi, 1976).

Disjunct genera with some species in other parts of South America or in Australasia are another notable feature of the southwestern South American flora. For instance, *Myrceugenia, Azara, Escallonia, Crinodedron, Quillaja, Lithrea, Blepharocalyx,* and *Myrcianthes* have disjunct species in southeastern Brazil. *Berberis* has the same disjunct geography in South America. Other genera are disjunct in Australasia, e.g., *Nothofagus, Laurelia, Gevuina, Lomatia,* and *Eucryphia.*

I have hypothesized (Landrum, 1981) that much of the flora of temperate South America can be divided into two groups based on modern patterns of distribution and that these correspond to two ancestral floras that merged in southern South America in the Tertiary. I believe one group was living in southern South America since at least the early Tertiary, and members of this flora are often disjunct in eastern temperate South America. *Berberis* belongs to that group. I believe another group entered southern South America from Antarctica, and these are often disjunct in Australasia, *Nothofagus* being the most well-known example. *Nothofagus* appeared first in the fossil record of southernmost South America as pollen in the late Cretaceous and slowly migrated northward to its approximate present distribution by the Miocene (Tanai, 1986). The Antarctic Peninsula was very near, or in contact with, southernmost South America from the late Cretaceous to about the mid-Oligocene, the best connection probably being early (Cunningham et al., 1995). Therefore, *Nothofagus* and associated plant groups may have entered South America early but have not migrated rapidly northward. Warmer climates and meeting with a resident South American vegetation may have been factors slowing that migration.

Genera of southwestern South America are sometimes disjunct in the central and northern Andes. My explanation for this pattern is that the uplift of the Andes, which caused drying in Argentina, cutting off migration to eastern South America, also provided a pathway to the north for temperate genera. They were in fact pre-adapted to the cold mountainous habitats where sufficient rainfall was available. The southern tip of this pathway still exists in northwestern Argentina, where moisture-laden winds from the northeast support the Yunga (subtropical forest) vegetation (Cabrera, 1971) and where, for instance, *Blepharocalyx, Myrcianthes, Azara, Escallonia,* and *Crinodendron* grow. All are disjunct in eastern temperate South America and southwestern South America. Yunga vegetation is now separated by hundreds of kilometers of mountains and desert from similar vegetation in southwestern South America. The Andes have provided a pathway south for northern genera such as *Alnus* and *Juglands* (Digilio & Legname, 1966) that reach the Yunga vegetation but go no farther.

Between 27 and 19 million years ago there was a major tectonic episode in Bolivia (Sempere et al., 1990) and presumably farther south in the Andes. The uplift of the Andes caused climatic drying that changed warm woodlands to grassland in southern Argentina, as indicated by the appearance of grazing mammals (Marshall & Sempere, 1993: 349) in six different lineages (Patterson & Pascual, 1972: 282). As the Andes continued to rise a more severe rain shadow was created by 15 million years ago. The desertification of northern Chile occurred in late Oligocene-Miocene time, or about the same time as the desertification of Patagonia, being caused also by the uplift of the Andes that cut off the subtropical winds from the east and by the development of the cold Humboldt Current from Antarctica (Marshall & Sempere, 1993: 340; Galli-Olivier, 1967). In Antarctica, the source of the Humboldt Current, glaciers were reaching sea level in the late Oligocene and an ice sheet developed in East Antarctica in the Miocene (Shackelton & Kennett, 1975). Pitman et al. (1993) calculated that the separation of South America and Antarctica was complete by 30 million years ago. Thus, the southwestern South

American "island" of vegetation became increasingly isolated from 30 to 15 million years ago and probably has not been in contact with other similar vegetations since.

One might speculate that since the Berberidaceae are mainly a Northern Hemisphere group, the South American *Berberis* must have migrated from North America. Direct migration would be relatively recent, since the union of North and South America occurred ca. 2.5 million years ago (Goldblatt, 1993). Island hopping between continents has been hypothesized for some mammal groups as early as the late Oligocene (Marshall & Sempere, 1993: 330) and could be hypothesized for *Berberis* as well. Even if *Berberis* reached northern South America early, somehow it would have had to migrate to temperate southern South America rapidly to appear in the fossil record there and to reach the now isolated flora of southwestern South America. *Juglands* and *Alnus*, obvious arrivals for North America, never reached southwestern South America. I believe it is more probable that *Berberis* was already diverse in southern South America before North and South America united and that migration has subsequently been northward.

When and how did *Berberis* s. str. (simple-leaved species), which has an additional center of diversity in Asia, reach South America? The answer is beyond the scope of this paper, but the best connection between northern and southern continents in the late Cretaceous would have been through Africa (Raven & Axelrod, 1974) and *Berberis* s. str. does grow in Africa (Ahrendt, 1961). Raven and Axelrod have hypothesized this same African route for the related family Lardizabalaceae with about 30 species, most of which are Asian, but with 2 endemic monotypic genera in southwestern South America.

TAXONOMY

Berberis L., Sp. Pl. 330. 1753. TYPE: *Berberis vulgaris* L. (lectotype, designated by Britton & Brown (1913)).

Shrubs or small trees, often spiny; spines the reduced leaves of long shoots, palmate to leafy, or 3-parted, rarely simple; bracts present at the bases of new vegetative growth or inflorescences, ovate to lanceolate. Leaves alternate, simple in South America, sometimes compound in North America and Asia, evergreen or deciduous, arranged singly along the stems or more frequently in rosettes (short shoots) in the axils of spines; margins entire or spinescently toothed. Inflorescence a solitary flower, a sessile or pedunculate umbel, or a raceme. Flowers yellow, orange, to red-orange, the perianth typically with 5 or 6 whorls of 3 tepals; tepals of inner 2 whorls with 2 nectariferous glands on the lower inner surface; middle whorl (or sometimes 2 whorls) with somewhat larger tepals; outer whorls of gradually smaller tepals, the outermost bract-like; stamens 6, the anthers about equaling the filaments in length, sometimes with tooth-like appendages just below the anthers; pistil barrel-shaped to urceolate, 1-celled, the ovules up to 10, the style pronounced or not; stigma peltate; placenta basal to lateral; fruit a berry; seeds one to a few.

The common names "calafate" and "michay" are applied to many species of Chilean *Berberis*. They are probably not consistently used for particular species.

Key to the Species of *Berberis* in Chile and Adjacent Southern Argentina

1a. Spines foliaceous or star-like, with (3–)5 or more pointed arms radiating from a ± foliaceous blade (Fig. 3A, B, D).
2a. Lower leaf surface with raised, reticulate veins, covered with stiff, erect hairs .... *B. horrida*
2b. Lower leaf surface smooth, the veins only slightly raised if at all.
3a. Leaf blades at anthesis submembranous; leaf margins nearly all entire, with only a few teeth sometimes present; peduncle plus rachis (if any) of inflorescence 1–4 cm long .... *B. rotundifolia*
3b. At least some leaf blades at anthesis coriaceous; some leaf margins toothed; peduncle and rachis of inflorescence 0–5 cm long.
4a. New leaves appearing on flowering branches with entire margins, glaucous beneath; inflorescence with the peduncle plus rachis 2–5 cm long; flowers per inflorescence up to 25; pedicels 2–4 mm long .... *B. congestiflora*
4b. New leaves appearing on flowering branches with toothed margins, not notably glaucous beneath; inflorescence with the peduncle plus rachis 0–3 cm long; flowers per inflorescence up to 14; pedicels 3–20 mm long .... *B. actinacantha*
1b. Spines lacking, or if present without a foliaceous blade, with (1–)3–5 arms (Fig. 3C, F, G).
5a. Inflorescence a panicle or umbel; spines lacking or insignificant; leaves mostly entire; fruit with a style ca. 1 mm long and stigma 1.5–2 mm wide; endemic to Más a Tierra Island, Juan Fernández Archipelago .... *B. corymbosa*
5b. Inflorescence a raceme, umbel, or solitary flower; spines often present and robust; fruit often with a

style less than 1 mm long and stigma often less than 1.5 mm across; continental or growing on Más Afuera Island, Juan Fernández Archipelago.

6a. Leaves entire, subacicular to linear, up to ca. 1 cm wide, mainly 3 or more times as long as wide.

7a. Leaves subacicular, 1–1.2 mm wide; flowers generally solitary .... *B. empetrifolia*

7b. Leaves linear, 4–10 mm wide; flowers in umbels.

8a. Style 1.5–3 mm long; spines 3–18 mm long .... *B. trigona*

8b. Style less than 0.5 mm long; spines 7–33(–40) mm long .... *B. microphylla*

6b. Leaves toothed or entire, variously shaped, often over 1 cm wide, often less than 3 times as long as wide.

9a. Leaves mainly oblong to narrowly elliptic, 2.3–10 cm long, the margin often with 10 or more teeth per side.

10a. Leaves lustrous below; marginal and secondary veins slightly raised above; margins coarsely serrate (rarely entire) with 6–16 spine-tipped teeth per side; peduncle plus rachis 2–8 cm long; endemic near Concepción, Chile, at elevations of ca. 300 m .... *B. negeriana*

10b. Leaves dull below; marginal and secondary veins slightly impressed above; margins usually serrate with 10–32 spine-tipped teeth per side; peduncle plus rachis 0.5–1.5 cm long; from Arauco to Aisén, Chile, and Río Negro, Argentina, usually at elevations above 1000 m .... *B. serratodentata*

9b. Leaves variously shaped, often all less than 5 cm long, the margins entire or with fewer than 10 teeth per side.

11a. Inflorescence a raceme; style on fruit 1–3 mm long; continental species.

12a. Young twigs densely pubescent; spines pubescent, mainly with 5 arms 2–7 mm long, the arms ± ascending (Fig. 3C) .... *B. darwinii*

12b. Young twigs glabrous or papillate-puberulent; spines not pubescent, with 3 (rarely more) arms 4–38 mm long, the laterals often perpendicular to the central.

13a. Flowers 5–10 mm long, 3–7 per inflorescence; leaves with impressed marginal and secondary veins above, usually lustrous above, the margins minutely papillate; year-old twigs with distinct longitudinal ridges and grooves .... *B. ilicifolia*

13b. Flowers up to ca. 5 mm long, 6–30 per inflorescence; leaves with flat or slightly raised marginal and secondary veins above, lustrous or not above, the margins not papillate; year-old twigs ± terete.

14a. Leaf apex obtuse to broadly rounded; small veins between secondary veins usually clearly visible below; pedicels 6–15 mm long; spines 0.5–2.3 cm long; inflorescence with up to ca. 20 orange flowers; ovules 5–6; Región II .... *B. litoralis*

14b. Leaf apex usually acute; small veins between the secondary veins indistinct below; pedicels 3–10 mm long; spines 1–3.8 cm long; inflorescence with up to ca. 30 yellow flowers; ovules 1–4; Regions IV–X.

15a. Leaf margin commonly entire; midvein impressed above; leaves commonly over 5 cm long and 2.5 cm wide, not glaucous below; tree or shrub of forest habitats .... *B. valdiviana*

15b. Leaf margin rarely entire; midvein not impressed above; leaves rarely over 5 cm long and 2.5 cm wide, usually glaucous below; shrub of sclerophyllous scrub .... *B. chilensis*

11b. Inflorescence an umbel or solitary flower; style on fruit in continental species less than 1 mm long or up to 2 or 3 mm long in *B. montana* and *B. comberi*; style on fruits of Juan Fernández Island species ca. 1 mm long.

16a. Leaf margins generally entire; leaves mostly oblanceolate to obovate; spines insignificant or if present those near the tips of twigs often simple (i.e., without lateral arms); flowers mainly over 3 mm long.

17a. Spines absent or insignificant; Juan Fernández Archipelago.

18a. Inflorescence multiflorous; leaves often over 1.5 cm wide; Más a Tierra Island .... *B. corymbosa*

18b. Inflorescence probably of solitary flowers or few-flowered sessile umbels; leaves rarely over 1.5 cm wide; Más Afuera Island .... *B. masafuerana*

17b. Spines normally present; continental species.

19a. Mature leaves submembranous; apex rarely mucronate; style 1–2 mm long; usually near the upper limit of woody vegetation; from Cerro Caqui near Valparaíso (Región V) to Volcán Osorno (Región X) .... *B. montana*

19b. Mature leaves coriaceous; apex usually mucronate; style less than 0.5 mm long; from near sea level to the upper limit of woody vegetation;

from the Andes of Curicó (Región VI) to the Strait of Magellan (Región XII) .... *B. microphylla*

16b. Leaf margins generally spinescent-toothed; leaves variously shaped; spines normally present (except in *B. comberi*), those near the tips of twigs with 3–5 subequal arms; flowers mainly under 3 mm long.
  20a. Mature seeds fused into a mass; style 0.5–3 mm long; leaves mostly over 1 cm wide; Mendoza and deserts of Neuquén, Argentina.
    21a. Plants spineless; style ca. 3 mm long; Neuquén and Mendoza up to ca. 1100 m .... *B. comberi*
    21b. Plants with 3-parted spines up to 4.5 cm long; style ca. 0.5 mm long; Mendoza at about 2000 m .... *B. grevilleana*
  20b. Matures seeds free from each other; style 0–0.5 mm long; leaves mainly less than 1 cm wide; Chile and lake district of Neuquén, Argentina, and farther south.
    22a. Leaves up to ca. 2 cm long, angularly obovate to oblanceolate to rhomboid, usually arcuate; margin usually with 1–2 spine-tipped teeth per side; Coquimbo .... *B. glomerata*
    22b. Leaves usually over 2 cm long, variously shaped, usually about flat; margins often with more than 2 spine-tipped teeth per side.
      23a. Leaf blades mostly not more than 2 times as long as wide; leaf margin often with more than 3 teeth per side, these usually ascending or radiating; inflorescence often with a noticeable peduncle and/or rachis .... *B. actinacantha*
      23b. Leaf blades 2–7 times as long as wide; teeth of leaf margin often less than 3 per side, usually perpendicular; inflorescence a solitary flower or a sessile umbel.
        24a. Flower solitary or in pairs, 4–5 mm long; spine arms normally over 5 mm long .... *B. microphylla*
        24b. Flowers in umbels of 7–11, ca. 3 mm long; spine arms 1–4 mm long .... *B. actinacantha*

1. **Berberis actinacantha** Mart., in Schult. & J. H. Schult., Syst. veg. 7: 12. 1829. TYPE: Chile. "Baths of Collina," *Macrae s.n.* (holotype, BR!, = ASU photo!; isotype, G!).

Berberis crispa Gay, Fl. chil. 1: 86. 1845. *Berberis actinacantha* var. *crispa* (Gay) Reiche, Anales Univ. Chile 88: 95. 1894. TYPE: Chile. Santiago, Valparaíso, San Fernando, *Gay s.n.* (lectotype, designated here, P["TYPE"]!, = ASU photo!; isolectotype, P!).

Berberis florida Phil., Linnaea 33: 5. 1864. TYPE: Chile. Andes of Colchagua, ca. 6000 ft., *Landbeck s.n.* (lectotype, designated here pro parte [non *B. valdiviana* at right], SGO-063345!, = ASU photo!).

Berberis congestiflora var. *hakeoides* Hook. f., Bot. Mag. t. 6770. 1884. *Berberis hakeoides* (Hook. f.) C. K. Schneid., Bull. Herb. Boissier, ser. 2, 5: 146. 1905. TYPE: cultivated in England, seeds from "Arguihue," Chile (holotype, K!, = ASU photo!).

Berberis brachyacantha Phil. ex Reiche, Anales Univ. Chile 88: 96. 1894. TYPE: Chile. Constitución, *Philippi s.n.* (lectotype, designated here, SGO-063352!, = ASU photo!; isolectotype, SGO!, = ASU photo!).

Berberis variiflora C. K. Schneid., Bull. Herb. Boissier, ser. 2, 5: 147. 1905. TYPE: Chile. Villarrica, *Neger s.n.* (lectotype, designated here, M [Schneider's hand]!; isolectotype, M!).

Berberis coquimbensis Muñoz, Agric. Técn. (Chile) 8: 79. 1948. TYPE: Chile. Coquimbo, Fray Jorge, *Jiles s.n.* (holotype, SGO-57575!, = ASU photo!; isotype, CONC-27637 not seen).

Shrub ca. 1 m high, glabrous or with young twigs, leaf bases, bracts, and/or petioles puberulent; young twigs green to light gray or reddish brown, glabrous or puberulent, the older twigs with longitudinal cracks and ridges, often covered with numerous small black dots; spines foliaceous or star-like, the blade (the central portion) 1–3 mm long in star-like spines and 1–6 mm long in foliaceous spines, the arms 3–18, 1–24 mm long, often with two grooves below; bracts ovate to lanceolate, 1.5–4 mm long. Leaves suborbicular, reniform, elliptic, ovate, obovate, or oblanceolate, the blade 1.3–5.5 cm long, 0.4–4.5 cm wide, 0.7–2.5(–5) times as long as wide, coriaceous, drying gray-green to light brown, sometimes glaucous below, the margin with (0–)2–20 spinescent teeth per side; apex round to acute or truncate, usually with a spinescent tip; base truncate, cordate, cuneate, or acuminate; petiole 0–5 cm long, 0.5–1 mm thick, puberulent to glabrous; venation predominantly reticulate-actinodromous, the tertiary veins forming a distinct to obscure reticulate pattern between the larger veins. Inflorescence a sessile, or less often a pedunculate, umbel or raceme, with (1–)2–14 flowers, the peduncle plus rachis up to 3 cm long; pedicels 3–20 mm long; flowers 2–3(–5) mm long; tepals usually 14, the 6 innermost elliptic to obovate, clasping the stamens, somewhat smaller than the next 3; stamens 1.5–2.5(–3) mm long, with 2 minute tooth-like lateral appendages below the anther, the anther ⅓ to ½ the length of the stamen; pistil barrel-shaped to urceolate, 1.5–2.5 mm long, the stigma 0.5–1 mm wide, essentially sessile; ovules

(2–)5(–7), basal. Fruit subglobose, 5–6 mm long; seeds (1–)4–5, 3–5 mm long. Figures 2A, 3A & B, 6A, 9A & B. [Figs. 6–13 pp. 823–830.]

Distinguishing features. Stigma essentially sessile; stamens with tooth-like appendages; spines star-like or foliaceous; inflorescence a several-flowered umbel; leaves with toothed margins, smooth below, usually not glaucous below.

Phenology. Flowering mainly from August to November. Fruiting mainly from November to December.

Distribution and habitat. Endemic to Chile, from near Paposo (Región II) to Temuco (Región IX); from ca. 100 to 1900 m. A shrub of the sclerophyllous scrub vegetation of central Chile; locally common; apparently thriving with limited disturbance.

Common name. Michay (Gay, 1845; Navas, 1976).

Selected specimens. CHILE. **Región II:** Antofagasta, Cachinales, 39 km S of Paposo (25°09′S, 70°26′W), ca. 600 m, 16 Sep. 1991 (fl), *Landrum 7493* (ASU). **Región IV:** Coquimbo, Illapel, Monte Redondo (31°03′S, 71°35′W), 400 m, 17 Nov. 1947 (st), *Jiles 481* (CONC-103493); Coquimbo, Parque Nacional Fray Jorge, along "sendero" in forest (ca. 30°45′S, 71°45′W), high hills next to coast, 22 Sep. 1991 (st), *Landrum 7547* (ASU); Coquimbo, Pichidangui, Cerro Silla del Gobernador (32°08′S, 71°30′W), 530 m, 12 Aug. 1961 (fl), *Schlegel 3796* (CONC-47208). **Región V:** Isla Negra, road to Totoral, ca. 5.5 km from coast, ca. 0.5 km before junction with road to Huellilemu (33°21′S, 71°40′W), ca. 300 m, 28 Sep. 1993 (fl), *Landrum 7885* (ASU); Cuesta La Dormida between Limache and Tiltil, at high point of road and ca. 1.4 km towards N on side road to *Nothofagus* forest, ca. 1400 m, 29 Sep. 1993, *Landrum 7895* (ASU); El Tabo, Quebrada de Córdoba, 30 Dec. 1980 (fr), *Meza & Villagrán 878* (SGO); near Quilpué, Hacienda Las Palmas, 17 June 1973 (fl), *Zöllner 6726* (NA). **Región Metropolitana:** Rancagua, prope La Leona, 1828 (fl), *Bertero s.n.* (SGO); región montañosa de Aculeo, Nov. 1968 (fl), *Castillo G. s.n.* (CONC-108097); Santiago, Los Domínicos, Camino El Alba, Quebrada San Ramón, between "La Cascada" and ca. 1 km W (ca. 33°25′S, 70°30′W), ca. 1200 m, 3 Oct. 1991 (st), *Landrum 7562* (ASU); Santiago, Rinconada de Lo Cerda, Quebrada de La Plata, al final de la Quebrada Los Maquis (33°39′S, 70°56′W), 800 m, 25 Sep. 1960 (fl), *Schlegel 2947* (CONC-42129). **Región VI:** Colchagua, Pichilemu (34°23′S, 72°00′W), Sep. 1929 (fr), *Montero 1526* (CONC-84027). **Región VII:** Constitución, montañas Placilla, 28 Sep. 1939 (fl), *Alberti s.n.* (SGO-133541); Linares, Llancanao, a orillas del Ancoa (35°5′S, 71°31′W), 6 Sep. 1953 (fl), *Ansoleaga s.n.* (CONC-14215); Linares, Parral, Termas de Catillo (36°17′S, 71°38′W), 320 m, 5 Jan. 1961 (st), *Montero 6278* (CONC-84098); Linares, La Mina, camino al Melado, 1500 m, 17 Dec. 1953 (fr), *Ricardi 2781* (CONC-14609). **Región VIII:** Arauco, at the N limit of Cañete along highway to Concepción (ca. 37°47′S, 73°25′W), < 200 m, 23 Oct. 1993 (fl), *Landrum 7970* (ASU); Arauco, camino de Curanilahue a Cañete, entre río Curanilahue y estero Paso Hondo (37°28′S, 73°23′W), 200 m, 6 Jan. 1977 (fr), *Marticorena 1145* (CONC-88866); Arauco, Cordillera de Nahuelbuta, orillas del río Caramávida (37°41′S, 73°11′W), 850 m, 19 Dec. 1978 (fr), *Marticorena et al. 1621* (CONC-88847); Ñuble, Atacalco, faldas del Caracol (36°53′S, 71°38′W), 700 m, 19 Sep. 1944 (fl), *Pfister 6323* (CONC-6323). **Región IX:** Cautín, Cunco, 200 m, Sep. 1943 (fl), *Gunckel 72950* (CONC-108066); Cautín, Padre Las Casas, 250 m, Dec. 1948 (fl), *Gunckel 72960* (CONC-108040); Malleco, ca. 1.5 km W of Purén on road to Contulmo (ca. 38°3′S, 73°7′W), ca. 100 m, 24 Oct. 1993 (fl), *Landrum 7978* (ASU); Cautín, Temuco, Cerro Ñielol, ca. 150 m, 27 Nov. 1947 (fr), *Sparre 3237* (SGO).

Three varieties may be suggested within this variable species: a typical one in the area of Santiago and Valparaíso with mainly star-like spines (Fig. 3B); a second from the coastal region from Concón north to Paposo with leafy spines and relatively small leaves (Fig. 3A); and a third from Arauco to Cautín with leafy spines and relatively large leaves (Fig. 2A). Although these characters generally hold up for the areas mentioned, so many specimens do not conform that varietal names cannot consistently be assigned to these entities.

Some forms of this species and *B. microphylla* can be confused in their area of overlap (Curicó to Temuco). *Berberis actinacantha* is best distinguished from *B. microphylla* by having several-flowered inflorescences, in contrast to *B. microphylla* with only one or two (rarely three) flowers per inflorescence. *Berberis actinacantha* generally grows at lower elevations than *B. microphylla*. *Berberis actinacantha* is also similar to *B. congestiflora* (see lead 4 in key).

In the protologue of *Berberis variiflora* Schneider stated, "im Herb. München mit echter *congestiflora* gemischt" [in the Munich herbarium mixed with true *congestiflora*]. Of two possible specimens at M, the one selected as lectotype is an unmixed sheet: each piece is marked with "b" and the sheet has a long note by Schneider attached.

2. **Berberis chilensis** Gillies ex Hook., Bot. Misc. 3: 135. 1833. TYPE: Chile. Talca, *Gillies s.n.* (syntype, E-GL not seen; = SGO photo!); Valparaíso, *Bridges s.n.* (syntype, E-GL? not seen).

Shrub up to 2 m high, glabrous; young twigs smooth, reddish brown, often glaucous, the older twigs gray, with ± fibrous bark; spines (1–)3-parted, the arms (0.5–)1–4(–5.5) cm long, about equal in length, or central somewhat longer, the laterals perpendicular to the central; bracts ± triangular, gray-brown, ca. 1–2 mm long. Leaves elliptic to oblanceolate, either arched along the midvein with the margins turned upward (Fig. 2C), or nearly flat with margins revolute (Fig. 2G), 0.5–5 cm long, 0.7–2.5 cm wide, 1.2–4.7 times as long as wide, the lower surface strongly glaucous or less often gray-green, the upper surface usually lustrous, gray-green, the margins usually with 1–5 coarse spine-tipped teeth per side; apex acute, spine-tipped; base cuneate, usually blending into petiole or the petiole distinct and up to 8 mm long; venation mixed craspedodromous, the midvein nearly flat above, moderately prominent below, the secondary veins up to ca. 5 pairs faint to distinct, the tertiary veins faint to distinct; blades stiffly coriaceous. Inflorescence a raceme (sometimes with minor side branches) ca. 1–5 cm long, with 10–30 flowers; pedicels 3–5 mm long, subtended by narrowly triangular, boat-shaped bracts 2–3 mm long; flowers lemon-yellow, 3–5 mm long; tepals (11–)12(–14), the inner six obovate, 2.5–5 mm long; stamens 2–3 mm long, without lateral appendages, the anther ca. ⅓ the length; pistil 2–4 mm long, the style ca. ½ the length; ovules (2–)3(–4), basal. Fruit subglobose, 5–7 mm long, terminating in a persistent style ca. 1–2 mm long; seeds 1–3, 4–5 mm long.

Distinguishing features. Style long; stamens without tooth-like appendages; spines 3-armed, usually large; inflorescence a several-flowered raceme; leaves with toothed margins, acute apices, flat midvein above, and often glaucous.

Common names. Michay (Navas, 1976), richa, palo amarillo (Hoffmann, 1978), espino maulino (Muñoz, 1966).

Berberis chilensis is most likely to be confused with *B. valdiviana* (see lead 15 in key).

KEY TO VARIETIES OF *BERBERIS*

1a. Leaves recurved, the margins directed upward (Fig. 2C); marginal teeth 2–7 mm long; pre-cordillera of the Andes .... *B. chilensis* var. *chilensis*
1b. Leaves nearly flat, not recurved, the margins not directed upward (Fig. 2G); marginal teeth 1–2 mm long; coastal cordillera and coast .... *B. chilensis* var. *brachybotria*

2a. Berberis chilensis var. chilensis

Berberis ferox Gay, Fl. chil. 1: 80. 1845. TYPE: Chile. Santiago, *Gay s.n.* (lectotype, designated here, P!, = F-34519!; isolectotype, P!).

Berberis diffusa Gay, Fl. chil. 1: 80. 1845. *Berberis chilensis* var. *diffusa* (Gay) Reiche, Anales Univ. Chile 88: 92. 1894. TYPE: Chile. Santiago, *Gay s.n.* (holotype, P!, = F-34516!).

Berberis fragrans Phil. ex Reiche, Anales Univ. Chile 88: 92. 1894. TYPE: Chile. Curicó, Vichuquén, *Philippi? s.n.* (holotype, SGO-063348!, = ASU photo!).

Leaves recurved with the margins directed upward, gray-green below; margins not revolute; marginal teeth 2–7 mm long; spines 1–5(–5.5) cm long. Figures 2C, 6B, 9C.

Phenology. Flowering mainly in September and October. Fruiting mainly from November to March.

Distribution and habitat. Endemic to Chile, from Coquimbo (Región IV) to Malleco (Región IX), mainly in the pre-cordillera of the Andes. A shrub of sclerophyllous scrub vegetation, usually in fairly open habitats, from 370 to 1600 m.

Selected specimens. CHILE. **Región IV:** Coquimbo, Ovalle, Las Palmas (32°03′S, 71°25′W), 600 m, 6 May 1967 (fl), *Jiles 5029* (M); Coquimbo, Combarbalá, sector La Fraguita (31°07′S, 70°34′W), 1100 m, 10 Jan. 1978 (fr), *Jiles 6352* (CONC-108048). **Región Metropolitana:** Barnechea in Las Condes, hills near Nido de Aguilas (ca. 33°30′S, 70°30′W), ca. 550 m, 21 Jan. 1978 (fr), *Landrum 3074* (ASU); Los Domínicos, Camino El Alba, Quebrada San Ramón, between "La Cascada" and ca. 1 km W (33°25′S, 70°30′W), ca. 1200 m, 3 Oct. 1991 (fl), *Landrum 7558* (ASU); Cajón de Maipo, El Melocotón, near school on river terrace, ca. 1000 m, Oct. 1993 (st), *Landrum 8215* (ASU); Quebrada de la Plata (33°29′S, 70°54′W), 620 m, 30 Aug. 1956 (fl), *Schlegel 1135* (CONC-47209). **Región V:** Aconcagua, Los Andes, camino a Portillo, km 13 (32°51′S, 70°28′W), 1200 m, 15 Nov. 1970 (fr), *Marticorena & Weldt 551* (CONC-34740, OS); Aconcagua, Los Andes, Río Colorado (32°52′S, 70°15′W), 1000 m, 24 Apr. 1943 (st), *Schlegel 36* (CONC-47211); Aconcagua, Resguardo Los Patos near Putaendo, 1000 m, 5 Oct. 1975 (fl), *Zöllner 7323* (NA); Valle del Colliguay (33°12′S, 71°15′W), Jan. 1918 (st), *Jaffuel s.n.* (CONC-47445). **Región VI:** Cachapoal, La Leona, 1830 (fl), *Bertero 93* (F, G); Colchagua, San Fernando, Cerro Centinela, 460 m, 30 Sep. 1927 (fl), *Montero 190* (F); Rancagua, Termas de Cauquenes, ca. 1 km beyond Termas on road to CONAF reserve (ca. 34°15′S, 70°30′W), ca. 800 m, 26 Sep. 1993 (st), *Landrum 7880* (ASU); Rancagua, Coya, ca. 7 km E of bridge at Coya on road to Sierra Nevada (ca. 34°14′S, 70°31′W), ca. 800 m, 6 Oct. 1993 (yfr), *Landrum 7907* (ASU). **Región VII:** Talca, Sep. 1926 (fl), *Claude-Joseph 4328* (US); Linares, El Colo, altos de los Rabones (35°50′S, 71°24′W), 300 m, 14 Mar. 1988 (fr), *Rodríguez & Baeza 2301* (CONC-113069); Talca, road to Vilches, at turn off of main road to Laguna del Maule, ca. 800 m, 12 Jan. 1988 (fr), *Bricker 195* (ASU); Talca, Espinal de Los Llanos (35°20′S, 71°17′W), 300 m, 27 Nov. 1990 (fr), *Matthei & Quezada 1175* (CONC-110703). **Región VIII:** Bío Bío, Millantú (37°24′S, 72°36′W), 2 Oct. 1955 (fl), *Junge s.n.* (CONC-18838); Bío Bío, San Rosendo, cerros, 23 Dec. 1957 (st), *Montero 5554* (CONC-84083); Bío Bío, Arenales de Canteras (37°22′S, 71°53′W), 370 m, 6 Dec. 1977 (fr), *Oehrens s.n.* (CONC-47614). **Región IX:** Malleco, Angol, cerros, 13 Oct. 1957 (fl), *Montero 5279* (CONC-84088); Malleco, Mininco, 187 m, 8 Jan. 1967 (st), *Montero 7833* (CONC-84094); Malleco, Deuco, lado sur, camino a Angol (37°52′S, 72°45′W), 6 Nov. 1977 (st), *Montero 10690* (CONC-84085).

2b. Berberis chilensis var. **brachybotria** (Gay) Landrum, comb. nov. Basionym: *Berberis brachybotria* [*brachybodria*] Gay, Fl. Chil. 1: 81. 1845. TYPE: Chile. Valparaíso, *Gaudichaud* (*212*) (lectotype, designated here, P["TYPE"]!, = ASU photo!; isolectotype, P!, = F-34508!, = ASU photo!).

Berberis brachybotria var. *brevispina* Reiche, Anales Univ. Chile 88: 92. 1894. TYPE: Chile. Cuesta de Zapata, entre Santiago y Valparaíso, *Philippi?* (holotype, SGO-063367!, = ASU photo!).

Leaves nearly flat, not recurved, gray-green or yellow-green below; margins slightly revolute; marginal teeth ca. 1–2 mm long; spines 1–2.5 cm long. Figures 2G, 6C, 9D.

Phenology. Flowering mainly in August and September. Fruiting mainly from October to January.

Distribution and habitat. Endemic to Chile, from Coquimbo (Región IV) to Colchagua (Región VI) in the coastal cordillera and on the coast. A shrub of sclerophyllous, sometimes dense, scrub.

Selected specimens. **Región IV:** Coquimbo, Illapel, parte S de la cuesta Los Hornos, 1500 m, 22 Sep. 1960 (fl), *Jiles 3740* (CONC-41671); Coquimbo, Combarbalá, El Churque (30°26′S, 70°50′W), 11 Oct. 1971 (fl), *Jiles 5725* (CONC-108047). **Región V:** Algarrobo, 3–4 km de la costa por el camino a Casablanca, 19 Aug. 1978 (fl), *Cassels 142* (SGO); Colliguay (33°10′S, 71°09′W), 470 m, 9 Sep. 1956 (fl), *Garaventa 6624* (CONC-70275, OS); Marga Marga, Estero de las Piedras (33°11′S, 71°17′W), Jan. 1932 (fr), *Jaffuel 3255* (CONC-47446); Isla Negra, road to Totoral, ca. 6 km E of Isla Negra, at junction with road to Huellilemu (33°25′S, 71°40′W), ca. 300 m, 28 Sep. 1993 (fl), *Landrum 7893* (ASU). **Región VI:** Colchagua, Hacienda Mallermo, 2 Dec. 1924 (fr), *Fuentes s.n.* (G); O'Higgins, Cachapoal, Palmas de Cocalán (34°11′S, 71°14′W), 450 m, 27 Nov. 1970 (fr), *Oehrens 933* (CONC-41823); Rancagua, Loncha, ca. 23 km W of entrance to Codelco property, ca. 400 m, Oct. 1993 (st), *Landrum 8212* (ASU).

The name *Berberis gayi* K. Koch (Hort. Dendr. 19, number 66. 1853) is apparently a new (superfluous) name for *Berberis brachybotria.*

3. Berberis comberi Sprague & Sandwith, Kew Bull. 1927: 175. 1927. TYPE: Argentina. Neuquén: Cerro Lotena, 3000 ft., 24 Sep. 1925, *Comber 49* (holotype, K not seen, = K photo-13717 at SGO!).

Shrub to ca. 1 m high; young twigs yellowish brown, the mature twigs gray, obscurely striate, gradually tapering from point of attachment to tip without branching for up to ca. 18 cm; spines none; bracts broadly ovate, 0.8–2 mm long. Leaves rhombic, oblong-elliptic, or subpalmate, 2–4.5 cm long, 1.7–4.6 cm wide, 0.9–1.4 times as long as wide, solitary or in clusters of 2 or 3 on short shoots; blade stiffly coriaceous, drying yellow-brown, slightly lustrous above and below, or dull below; margin with 1–2 subtriangular spinescent teeth per side; base narrowly acute to acuminate, or hastate to truncate; apex acute to acuminate, spinescent; petiole none or up to ca. 2 mm long, blending with base; venation reticulate-actinodromous to mixed craspedodromous, not impressed, generally faint to indistinguishable. Inflorescence uniflorous or an umbel of 2 or 3 flowers; pedicels 2–4 mm long; flowers ca. 1 cm long, yellow-orange; tepals probably about 12–14, the innermost 7–9 mm long; stamens 4.5–5 mm long, the anther ca. ½ the length; pistil vase-shaped, ca. 8 mm long; style ca. 3 mm long, the stigma ca. 1 mm diam.; ovules 8–10, basal. Fruit subglobose, ca. 1–1.3 mm long, the persistent style ca. 3 mm long, the peltate stigma 1.5–2 mm diam., the fruit wall papery when dry; seeds 4–11, fused into a stone-like mass ca. 10 mm long at maturity. Figures 2I & J, 6B, 10A.

Distinguishing features. Style long; stamens without tooth-like appendages; spines none; inflorescence a solitary flower or 2–3-flowered umbel; leaves stiff, the margins spiny; twigs spur-like; mature seeds fused in a mass.

Phenology. Flowering probably in September and October. Fruiting in November and December.

Distribution and habitat. Endemic to central western Argentina, found only in Mendoza and Neuquén provinces. A shrub of desert scrub in the rain shadow of the Andes.

Selected specimens. ARGENTINA. **Mendoza:** Depto. Malalhue, Ranquil de Lirkai, 1100 m, 9 Dec. 1960 (fr), *Ruiz Leal 21446* (ASU, MERL). **Neuquén:** 38 km N of Zapala on ruta 40 (ca. 38°40′S, 70°W), ca. 865 m, 9 Dec. 1994 (st), *Landrum 8352* (ASU, MERL); near ruta 40 and Río Picun Leufu, 2 km along road to Bajada Los Molles from ruta (ca. 39°15′S, 70°W), ca. 750 m, 11 Dec. 1994 (fr), *Landrum 8377* (ASU, MERL); más o menos 2 km antes de la bifurcación del camino de Huitrin y Chosmalal, 13 Jan. 1963, *Roig et al. 4423* (MERL); 20 km al N de Zapala, 25 Feb. 1993, *Roig et al. 14716* (MERL).

Berberis comberi is an extraordinary species. It is known only from a few localities in the Patagonian deserts of Neuquén and Mendoza, Argentina, that have dramatic seasonal changes. It forms dense shrubs with stiff, spur-like branches up to ca. 18 cm long. The leaves are stiffly coriaceous and spinose, but the twigs lack spines. The flowers were reported to be 5-merous (Sandwith, 1927), which would be quite unusual in *Berberis*: I have seen no flowering specimens to verify this. The floral characters in this description are based on reports of

Sprague and Sandwith (1927) and Job (1942), all of whom had only the flowering type specimen to examine. Ruiz Leal (1965) was first to describe fruiting specimens. The seeds agglutinate together to form a "stone-like" mass.

Berberis comberi is not clearly closely related to any other species of *Berberis* in southern South America except perhaps *B. grevilleana.* They share the unusual characteristic of having seeds that fuse together in a mass in the mature fruit.

4. Berberis congestiflora Gay, Fl. chil. 1: 75, t. 3. of Atlas. 1845. TYPE: Chile. Valdivia, *Gay s.n.* (lectotype, designated here, P["TYPE"]!, = ASU photo!; 2 isolectotypes, P!, = ASU photos!; isolectotype, G!, = F-27406!).

Shrub to 3 m high, glabrous or the young petioles, bracts, and twigs minutely puberulent; young twigs light gray, often shiny, becoming dull, the bark sometimes fibrous with age; spines star-like to broadly foliaceous, the arms 5–12(–15), 2–5 mm long, the central blade portion about as long as or longer than the arms, the margin revolute; bracts ovate, 1–3 mm long. Leaves elliptic, ovate, or suborbicular, the blade 0.9–3.5 cm long, 0.6–2.5 cm wide, 1–1.7(–2.4) times as long as wide, subcoriaceous, glaucous below, the margin entire or with up to 7 spinescent teeth per side; apex acute to rounded; base cordate, truncate, or rounded; petiole 0–1.5 cm long, normally much shorter than the blade; venation predominantly reticulate-actinodromous, weak to prominent. Inflorescence an umbel or raceme with up to 25 flowers, the rachis, if present, up to 2 cm long, the peduncle plus rachis 2–5 cm long; pedicels 2–4 mm long, subtended by triangular bracts 1–2 mm long. Flowers ca. 2.5–3 mm long; tepals 14, the six innermost elliptic to obovate, 2–2.5 mm long, clasping the stamens, somewhat smaller than the next three; stamens 1.5–2 mm long, with two minute, tooth-like lateral appendages below the anther, the anther ca. ½ the length of the stamen; pistil barrel-shaped to urceolate, ca. 1.5 mm long, the stigma ca. 0.8 mm wide, essentially sessile; ovules (4–)5, basal. Fruit subglobose, ca. 6 mm long; seeds 4–5, ca. 4 mm long, lustrous. Figures 4F–H, 6C, 10B.

Distinguishing features. Style short; stamens with tooth-like appendages; spines star-like or foliaceous; inflorescence a several-flowered umbel or raceme; leaves subcoriaceous, usually glaucous below, the margins often entire.

Phenology. Flowering mainly from October to December. Fruiting mainly in January.

Distribution and habitat. Endemic to the Central Valley of Chile, Regions IX and X, at elevations of less than 500 m. This species seems to thrive (especially along fences) in open areas of the Central Valley that are now largely converted to agriculture. Gay stated that it grows in "prados naturales . . . entre Villarica y Guanegue," which now must be quite rare or nonexistent.

Common name. Michai (Rodriguez et al., 1995).

Selected specimens. CHILE. **Región IX:** Cautín, Vilcún (38°40'S, 72°13'W), 200 m, 24 Nov. 1920 (fl), *Hollermayer 329* (CONC-108103); Malleco, road from Traiguén to Victoria, ca. 9 km W of Highway 5 (ca. 38°15'S, 72°25'W), < 200 m, 24 Oct. 1993 (fl), *Landrum 7983* (ASU, SGO); Cautín, ca. 9 km E of highway 5 on road to Vilcún, ca. 200 m E of road to El Natre (ca. 38°40'S, 72°22'W), ca. 250 m, 29 Oct. 1993 (fl), *Landrum 8050* (ASU); Cautín, Lautaro, camino entre Lautaro y Curacautín, km 15, 1 km antes de Santa Ana (38°29'S, 72°17'W), 270 m, 19 Jan. 1976 (fr), *Marticorena et al. 700* (CONC-45000). **Región X:** Valdivia, La Unión, Catamutún, 150 m, 26 Oct. 1928 (fl), *Behn 23299* (CONC-23299); Valdivia, Cordillera de Ranco, summis cacum, Dec. 1854 (fl), *Lechler 2990* (CONC-73583); Valdivia, río Traiguén, entre La Unión y río Bueno, 9 Feb. 1931 (fl), *Rudolph 26* (SGO); Valdivia, Fundo San Antonio, 5 km S de La Unión, río Lollehue, 3 Jan. 1967 (fr), *Zollitsch 156* (M).

Berberis congestiflora is similar to *B. actinacantha,* overlapping with it in Malleco and Cautín (see lead 4 in key). Field studies of these species would be useful to see whether they hybridize and if they show some habitat and phenology differences.

I found one hybrid between *B. congestiflora* and *B. darwinii* (*Landrum 8012*) near Victoria.

5. Berberis corymbosa Hook. & Arn., Bot. Misc. 3: 135. 1833. TYPE: Chile. Juan Fernández [Archipelago, Más a Tierra Island], *Graham s.n.*, *Douglas s.n.*, and *Cuming 1338* (syntypes, not seen, = SGO photo [*Cuming 1338, E–GL*]!).

Berberis paniculata Phil., Anal. Univ. Santiago 1872: 664. 1872. TYPE: Chile. Juan Fernández [Archipelago, Más a Tierra Island], *Philippi s.n.* (holotype, SGO!, = ASU photo!; isotype, CONC!, = ASU photo!).

Shrub or tree to ca. 5 m high, glabrous; young twigs reddish brown to yellowish brown, smooth, ± terete, becoming gray to light brown, slightly rough; spines usually few or lacking, 3-parted, weak, the arms 2–5 mm long, the laterals ascending slightly; bracts ovate, ca. 2 mm long. Leaves elliptic, oblanceolate, obovate, or orbicular, the blade 2–4.2 cm long, 0.8–4 cm wide, 1–3 times as long as wide, submembranous, the margin entire, rarely with a few spinescent teeth; apex obtuse, rounded, or acute, rarely apiculate; base attenuate; petiole 3–

22 mm long, the persistent base after leaf fall usually slightly flattened, usually truncate, ca. 2 mm long; venation prominent to weak, basal, reticulate, actinodromous. Inflorescence a panicle or umbel with up to ca. 10 flowers, the main axis and peduncle 1.5–7 cm long; pedicels (2–)10–20 mm long; flowers ca. 5–6 mm long; tepals ca. 14, those of the innermost whorl ca. 4.5 mm long, shorter than the immediately adjacent outer whorls; stamens ca. 3.5 mm long, the anther less than ½ the length; pistil urceolate, ca. 3.5 mm long, the style ca. ⅓ the length, the stigma ca. 1 mm wide; ovules ca. 4, basal. Fruit subglobose, ca. 9 mm long, the persistent style ca. 1 mm long, the stigma 1.5–2 mm wide; seeds few, ca. 5–6 mm long. Figure 6A.

Distinguishing features. Style and stigma prominent; stamens without tooth-like appendages; spines none or insignificant; inflorescence a panicle or umbel; leaves usually submembranous, the margins usually entire.

Phenology. Flowering in November and December. Fruiting in January and February.

Distribution and habitat. Endemic to Más a Tierra Island of the Juan Fernández Archipelago (Región V), Chile. Apparently a relatively rare species of humid forest or scrub.

Selected specimens. CHILE. **Región V:** Juan Fernández Archipelago, Más a Tierra Island, Cerro Pascua, Quebrada Michay, 300 m, 8 Feb. 1980 (fr), *Marticorena et al. 9157* (CONC-52650, M, NA); near Selkirk tablet on Quebrada Villagra side of Portezuelo, 1800 ft., 9 Dec. 1965 (fl, yfr), *Meyer 9486* (CONC-122685, MO, NA, RSA); on ridge between La Vaquería and Valle Inglés, 480 m, 5 Feb. 1990 (fr), *Stuessy & López 11394* (CONC-116590); path to Salsipuedes, 350 m, 15 Jan. 1991 (st), *Stuessy et al. 11734* (CONC-121541).

Berberis corymbosa, endemic to Más a Tierra Island, is the only species of the genus growing there and thus should not be confused with any other. Its true affinities are not clear. The leaves are similar to *B. microphylla, B. masafuerana,* and *B. rotundifolia* of Chile, and the inflorescence and style are similar to *B. jobii* Orsi and *B. jujuyensis* Job, both of northwestern Argentina. More detailed studies would be useful.

6. **Berberis darwinii** Hook., Icon. Pl. 7, t. 672. 1844. TYPE: Chile. Valdivia and Osorno, *Bridges 585* (lectotype, designated by Porter (1986), K not seen); *Bridges 582* (syntype, K not seen); & Chiloé, *Darwin s.n.* (syntypes, CGE not seen, K not seen).

Berberis costulata Gand., Bull. Soc. Bot. Fr. 59: 705. 1913. TYPE: Chile. Chiloé, Quellón, *Skottsberg 310* (holotype, LY!, = ASU photo!).

Shrub up to ca. 1.5 m high, glabrous except for pubescent twigs and spines; twigs initially reddish brown, densely pubescent, the hairs reddish brown to whitish, to ca. 0.5 mm long, the bark of older twigs gray, longitudinally cracked; spines ± palmate, not foliaceous, with 5(–7) arms 2–7 mm long, pubescent; bracts ovate to lanceolate, 2–4 mm long. Leaves obovate, oblanceolate, or elliptic, 1.4–3 cm long, 0.5–1.4 cm wide, 1.2–4 times as long as wide, glabrous, the margin somewhat revolute, with 1–4(–6) pairs of spines; apex acute to subtruncate, terminating in a spine ca. 1 mm long; base acute, cuneate, or obtuse; petiole 0.5–1 mm long, 1–2 mm wide, glabrous; venation mixed craspedodromous, the midvein usually impressed above and prominent below, the secondary veins 2–4 pairs; blades coriaceous, lustrous above, dull beneath. Inflorescence a raceme 2–5 cm long with ca. 10 flowers; pedicels 5–12 mm long, 0.3–0.5 mm wide; flowers 4.5–7 mm long, orange; tepals 10–16, the smallest ovate, 2–3 mm long, the largest obovate, 4–6.5 mm long; stamens 2.5–5 mm long, without lateral appendages, the anther 1–1.5 mm long; pistil urceolate, 3–5.5 mm long, the style about ½ the length; ovules 4–8, attached laterally to sublaterally near base of ovary. Fruit subglobose, 7–8 mm long, dark blue, terminating in a persistent style 1.5–3 mm long; seeds 3–6 per fruit, 3–4 mm long. Figures 2D, 3C, 4A–E, 6D, 10C.

Distinguishing features. Styles long; stamens without tooth-like appendages; spines small, palmate, pubescent; inflorescence, a several-flowered raceme; leaves with toothed margins, relatively small; twigs pubescent; flowers orange.

Phenology. Flowering in two peaks, from September to November and from February to March. Fruiting mainly from December to March.

Distribution and habitat. Endemic to southwestern South America. Found in Chile from the pre-cordillera of Curicó (Región VII) to near Lago Carrera (Región XI) and in Argentina in western Río Negro and Neuquén, Argentina. A species of disturbed forest habitats, it is now a common roadside shrub in south-central Chile and adjacent Argentina, much appreciated for its attractive flowers, and sometimes cultivated in California, New Zealand, and England.

Common names. Michai, quelung (Rodriguez et al., 1995).

Selected specimens. CHILE. **Región VII:** Curicó, Potrero Grande, Fundo El Pangal, río de las Islas, 700 m, 31 Oct. 1954 (fl), *Kausel 4048* (F); Curicó, Upeo, 1000 m, 7 Dec. 1975 (yfr), *Zöllner 8977* (MO, NA). **Región VIII:** Cordillera de Nahuelbuta bei Pino Huacho, ca. 800 m, 5 Nov. 1981 (fl), *Bayer & Rodríguez 175* (M); 22 km

SE of Mulchen, Fundo Fresia, 1500 ft., 29 Oct. 1961 (yfr), *Greer 22* (OS); Antuco, El Toro, río Polcura, above recinto of Endesa (ca. 37°15′S, 71°28′W), ca. 900 m, 19 Oct. 1993 (fl), *Landrum 7956* (ASU); Arauco, camino de Quidico a Relún, cerca de Paillaco (38°16′S, 73°22′W), 450 m, 6 Jan. 1977 (fr), *Marticorena et al. 1177* (CONC-45650). **Región IX:** Temuco, road to Cunco, ca. 40 km E of Temuco, ca. 2.2 km E of Faja 18 road (ca. 38°55′S, 72°10′W), ca. 300 m, 25 Oct. 1993 (fl), *Landrum 7992* (ASU, SGO); road from Lautaro to Curacautín, ca. 17 km E of Lautaro, ca. 2 km W of Puente Peu Peu (ca. 38°28′S, 72°15′W), ca. 300 m, 28 Oct. 1993 (yfr), *Landrum 8029* (ASU); camino entre Curacautín y laguna Conguillío, a orillas del estero Quinchillama (38°31′S, 71°48′W), 600 m, 19 Jan. 1976 (fr), *Marticorena et al. 708* (CONC-44173); Volcán Llaima, ca. 1000 m, Feb. 1927 (fr), *Werdermann 1216* (CAS, F, G, K, M, MO, NY). **Región X:** Parque Nacional Puyehue, road to Antillanca, ca. 8 km above Administration at Aguas Calientes (ca. 40°45′S, 72°20′W), ca. 650 m, 9 Nov. 1993 (fl), *Landrum 8054* (ASU, SGO); Chiloé, Isla Talcán, Las Cuevas (42°46′S, 72°56′W), 22 Feb. 1961 (fl), *Marticorena 1734* (CONC-26391); Panguipulli, camino entre Coñaripe y Liquiñe, km 16, a orilla del río Llancahue (39°36′S, 71°54′W), 400 m, 16 Jan. 1976 (fr), *Marticorena et al. 476* (CONC-44347); camino El Mirador–Las Trancas, Cordillera Pelada (40°10′S, 73°29′W), 1000–1300 m, 2 Feb. 1961 (fr), *Ricardi 5283* (CONC-26515). **Región XI:** Aisén, Isla Carmen (43°02′S, 72°48′W), 17 Oct. 1947 (fl), *Behn 11* (CONC-8241); Aisén, carretera austral, Villa Santa Lucía, km 339, 150 m, 9 Feb. 1985 (fr), *Billiet 3854* (BR); Cerro Divisadero SE of Coihaique, road to centro de ski El Fraile, ca. 4.2 km from beginning of road, 16 Oct. 1993 (fl), *Landrum 8109* (ASU); Carretera Austral, ca. 20 km S of Puerto Tranquilo (ca. 72°35′W, 46°40′S), 19 Oct. 1993 (yfr), *Landrum 8152* (ASU). ARGENTINA. **Neuquén:** Lago Trapil, 21 Mar. 1939 (fl), *Cabrera 5085* (CAS); al NW del Lago Falkner, Feb. 1975 (fr), *Cassels s.n.* (SGO); Lago Mascardi, Mar. 1959 (fl), *Dawson 3282* (CONC-37568); Depto. Lacar (Parque Lanín), Lago Lacar, Pucará, 9 Nov. 1956 (fl), *Roig 1960* (MERL). **Río Negro:** región del Lago Nahuel Huapi, Lago Correntoso, 10 Jan. 1953 (fr), *Cabrera & Job 222* (NY); Alrededores de Bariloche, 13/21 Oct. 1975 (fl), *Roig & E. Méndez 8797* (MERL).

Berberis darwinii is most similar to *B. ilicifolia,* which differs in having glabrous spines with usually 3 arms and thicker, larger leaves. *Berberis darwinii* has been observed to hybridize with *B. trigona, B. valdiviana,* and *B. congestiflora.*

Although I have not seen the type of *Berberis darwinii,* the description and the illustration leave no doubt as to its identity.

The type of *Berberis knightii* (Lindl.) K. Koch (see excluded taxa), a plant cultivated in England in the mid-19th century, has not been located. Lindley's description indicates that the plant might have been *B. darwinii.*

7. **Berberis empetrifolia** Lam., Tabl. encycl., 2: 391, t. 253, fig. 4. 1792. TYPE: Detroit de Magellan, *Commerson s.n.* (holotype, P not seen, = F-34517!; isotypes, P!, CONC!, G!, W!).

Berberis mutabilis Phil., Anal. Univ. Santiago, 1872: 665. 1872. TYPE: Chile. Cordillera de Aculeo, collector? *s.n.* (lectotype, designated here, SGO-049024!; isolectotypes, BM!, SGO-063353!, = ASU photo!, W!).

Berberis empetrifolia var. *magellanica* C. K. Schneid., Bull. Herb. Boissier, ser. 2, 5: 140. 1905. TYPE: Chile. Sandy point, *[Lechler] Hohenacker 1065* (lectotype, designated here, W! ["Acqu. 1889 No.8378"], = ASU photo!; isolectotypes, BR!, G!, M!, NY!, W!); Feuerland, Magellan, *Commerson s.n.* (syntypes, G!, W!).

Berberis wawrana C. K. Schneid., Bull. Herb. Boissier, ser. 2, 5: 140. 1905. TYPE: Chile. Without locality, *Seibold-Wawra n. 3039* (lectotype, designated here, W!, = F-30140!, = ASU photo!); Cordillera de Colchagua, *Philippi s.n.* (syntype, W!).

Low-spreading shrub up to ca. 0.5 m high; twigs at first angular, yellowish to reddish, often glaucous, becoming terete, gray, the older bark slightly flaky; spines 3-armed (less often simple), the central arm 3–18 mm long, the laterals ascending slightly or perpendicular to the central, equaling it or somewhat shorter, the dilated spine base to ca. 3 mm long; bracts ovate, 1–2 mm long, light brown to reddish, often glaucous. Leaves subacicular, often falcate, the blade 5–18 mm long, 1–1.2 mm wide, in cross section rounded above, with a deep groove below, the margin strongly revolute; apex acute, often apiculate; base acute, sometimes glaucous; petiole 1–2.5 mm long, often glaucous, persisting as a peg-like structure after blade falls; venation indistinct, the midvein visible only as a faint impressed line above. Inflorescence a solitary flower; pedicels 2–14 mm long; flowers 3–5 mm long; tepals 12–17, the outermost oblong, the central ones obovate, the innermost obovate, 2–3 mm long, somewhat shorter than the adjacent outer tepals; stamens 2–2.5 mm long, with 2 minute tooth-like lateral appendages below the anther, the anther ca. ½ the length; pistil ca. 1.5 mm long, ± barrel-shaped, the stigma sessile; ovules 3–10, basal; fruit subglobose, 4–7 mm long, the stigma sessile; seeds (1–)3–7(–9), 3–4 mm long. Figures 2E, 7A, 10D.

Distinguishing features. Leaves subacicular, short; flowers solitary; style short; stamens with tooth-like appendages.

Phenology. Flowering mainly from November to January. Fruiting mainly from December to March.

Distribution and habitat. Endemic to southwestern South America. Found in Chile from the Andes of Coquimbo (Región IV) and in Argentina from the Andes of Mendoza at elevations around 3000 m to Tierra del Fuego in both countries at about sea level. This is a species well adapted to harsh, cold habitats, e.g., rocky slopes in the high

Andes, wind-blown pampa in Aisén, and sandy beaches along the Strait of Magellan.

Common names. Zarcilla, monte negro (Rodriguez et al., 1995), uva de la cordillera (Hoffmann, 1980).

Selected specimens. CHILE. **Región IV:** Ovalle, Cordillera del río Hurtado, 3000 m, Jan. 1933 (fl), *Iribarren s.n.* (G); Cordillera de Ovalle, río Torca (31°08′S, 70°43′W), 3000 m, 12 Feb. 1961 (fr), *Jiles 3772* (CONC-102224); Cordillera de Combarbalá, Potrero Grande (31°18′S, 70°50′W), 3000 m, 18 Feb. 1968 (fr), *Jiles 4533* (M); Illapel, Quebrada La Vega Escondida, 3 hours by horse due E of Cuncumén, 2700 m, 18 Nov. 1938 (fl), *Worth & Morrison 16553* (G, MO, NA). **Región V:** Los Andes, Laguna del Inca, Portillo (32°49′S, 70°11′W), 2900–3150 m, 12 Jan. 1981 (fl), *Arroyo 81242* (CONC-53335); ca. 3 km SW of Caracoles along road from Portillos, 3000 m, 11 Dec. 1951 (fl), *Hutchinson 155* (F, G, US); Estación Portillo, 2800 m, 14–16 Apr. 1933 (st), *Looser s.n.* (G); Aconcagua, camino Internacional entre Caracoles y Cristo Redentor, 3500 m, 15 Jan. 1964 (fl), *Marticorena & Matthei 565* (CONC-30501, OS). **Región Metropolitana:** Cajón de Maipo, ca. 22 km above San Gabriel, ca. 1 km below Embalse del Yeso, ca. 3000 m, 14 Dec. 1993 (fr), *Landrum 8224* (ASU, SGO); Valle del río Volcán, Refugio Lo Valdés, 1950 m, Feb.–Mar. 1944 (fl), *Looser s.n.* (G); San Ramón, cumbre Pirámide (33°30′S, 70°28′W), 3000 m, 5 Apr. 1959 (fr), *Schlegel 2489* (CONC-46716); Perez Caldera (33°12′S, 70°14′W), 2800 m, 27 Jan. 1954 (fr), *Sparre 10619* (CONC-17550, OS). **Región VI:** Sewell, río Coya, 2100–2600 m, 10 Feb. 1942 (fl), *Jiles s.n.* (G); Termas del Flaco (34°56′S, 70°25′W), 1900 m, 3 Feb. 1989 (st), *Niemeyer & Fernández 8904* (CONC-100031); junta del río Tinguiririca y río del Azufre (34°49′S, 70°34′W), 1220 m, 9 Mar. 1979 (fl), *Villagrán & Arroyo 55920* (CONC-55920). **Región VII:** alrededores de la Laguna del Teno (35°10′S, 70°33′W), 2560 m, 29 Mar. 1973 (fl), *Marticorena 20* (CONC-39325); Laguna del Maule (36°0′S, 70°30′W), 2200 m, 3 Apr. 1975 (fr), *Parra & Rodríguez 198* (CONC-43613). **Región VIII:** Laguna del Laja (37°27′S, 71°27′W), ca. 1300 m, 29 Nov. 1959 (fl), *Montero 6132* (CONC-83988); camino a Termas de Chillán, pasado Puente Torrealba (36°54′S, 71°27′W), 1250 m, 18 Nov. 1976 (fl), *Oehrens s.n.* (CONC-45393); Volcán Antuco, 2.9 km al SE del Refugio (37°22′S, 71°19′W), 1380 m, 19 Feb. 1988 (fr), *Stuessy & Baeza 11045* (CONC-110419); Baños de Chillán, Aguas Calientes, 2200 m, Mar. 1927 (fr), *Werdermann 1301* (BM, CAS, CONC-64750, F, G, K, M, MO). **Región IX:** 20.7 km W of Paso Pino Hachado, 3800 ft., 9 Mar. 1962 (st), *Greer 1380* (OS); pasado la confluencia de los ríos Lolco y Lancú (38°16′S, 71°28′W), 1050 m, 9 Jan. 1977 (fl), *Marticorena et al. 1369* (CONC-45760); Termas del río Blanco, Piedra El Sapo (38°35′S, 71°37′W), 1900 m, 31 Jan. 1938 (st), *Montero 3386* (CONC-83993, OS); Volcán Llaima, refugio, 1800 m, 10 Dec. 1939 (st), *Montero 3820* (OS). **Región XI:** Aisén, Balmaceda, along road to Portezuelo, 13.6 km W of junction with road to Coihaique (ca. 45°50′S, 71°40′W), ca. 500 m, 17 Oct. 1993 (fl), *Landrum 8133* (ASU); Aisén, Coihaique, Puente Pedregoso, ca. 4.5 km W of Coihaique Alto (ca. 45°25′S, 71°35′W), 20 Nov. 1993 (fl), *Landrum 8204* (ASU); Chile Chico, Ventisquero Soler (46°52′S, 73°08′W), 150 m, 24 Mar. 1967 (st), *Seki 577* (CONC-37238); La Tapera, just W of village, 650 m, 20 Mar. 1985 (fr), *Stuessy 7547* (OS). **Región XII:** NW face of Mt. Aymond, route 255-N (52°9–10′S, 69°25–29′W), 9 Oct. 1971 (st), *Dudley et al. 114* (NA); Puerto Williams, Isla Navarino, 8 Feb. 1959 (fr), *Godley 1172* (K); Parque Nacional Torres del Paine, ca. 11 km beyond Posada río Serrano on road to Lago Grey (ca. 51°10′S, 73°5′W), ca. 150 m, 24 Dec. 1994 (fl), *Landrum 8411* (ASU); Punta Steinman, ca. 35 km along road to Punta Canelo from main highway (ca. 53°10′S, 71°25′W), ca. 3 m, 31 Dec. 1994 (fr), *Landrum 8452* (ASU). ARGENTINA. **Chubut:** Esquel, La Hoya, 1000 m, 18 Jan. 1972 (fl), *Cabrera 21958* (CONC-37604); 21.3 km W of río Pico on road to Lago Vinter, 1000 m, 7 Dec. 1984 (fl), *Stuessy 6883* (OS); ca. 3 km E of Lago Vinter on road to río Pico, 930 m, 7 Dec. 1984 (st), *Stuessy et al. 6891* (OS). **Mendoza:** Malargue, Las Leñas (35°07′S, 70°06′W), 14 Jan. 1987 (fr), *Del Vitto 1435* (MERL); Santa Rosa de los Andes to Uspallata Pass, *Moseley s.n.* (BM); Luján, Agua de la Pampa, en la Pampa de la Polcura, 28 Jan. 1962 (st), *Roig 4208* (MERL); Las Heras, alto de los Manantiales, 3000 m, 19 Feb. 1965 (fr), *Roig 5283* (MERL). **Neuquén:** Aluminé, 16 Nov. 1967 (fl), *Cabrera 18699* (CONC-37594); Moquehue, 1230 m, 5 Jan. 1968 (fr), *Ruiz Leal 25798* (MERL); Copahue, 14 Jan. 1963 (fl, fr), *Ruiz Leal & F. A. Roig 22482* (MERL). **Santa Cruz:** a 4 km al E del Lago Burmeister, 1000 m, 8 Dec. 1980 (fl, fr), *Cei & S. S. de Cei s.n.* (MERL); a 14 km de Puente Blanco, 60 m, 20 Jan. 1970 (fr), *Ruiz Leal 27076* (MERL). **Tierra del Fuego:** Ushuaia en la península a 6–8 km de la población, 9 Jan. 1950 (fr), *Ruiz Leal & Carretero 12955* (MERL).

Berberis empetrifolia seems to hybridize with at least *B. montana* and *B. grevilleana.* Population samples of hybrid populations would be useful.

Lamarck did not mention a locality or collector for *Berberis empetrifolia,* but the specimen that has been taken as the holotype was collected by Commerson in the area of the Strait of Magellan.

The type specimens of *Berberis mutabilis* seem to represent a hybrid population of *B. empetrifolia* and some other species, perhaps *B. montana.* A specimen most similar to *B. empetrifolia* has been selected as the lectotype.

The original material of *Berberis wawrana* probably represents *B. empetrifolia* hybridized with another uncertain species.

8. Berberis glomerata Hook. & Arn., Bot. Beech. Voy. 5. 1830. TYPE: Chile. Coquimbo, *Macrae s.n.* (holotype, not seen, E-GL?, K?; isotype, G not seen; = F-27409!).

Berberis zahlbruckneriana C. K. Schneid., Bull. Herb. Boissier, ser. 2, 5: 145. 1905. *Berberis glomerata* var. *zahlbruckneriana* (C. K. Schneid.) Ahrendt, J. Linn. Soc., Bot. 57: 232. 1961. TYPE: Chile. Coquimbo, Illapel, *Philippi s.n.* (lectotype, designated here, W!, = F-30129!, = ASU photo!; isolectotype, W!, = ASU photo!).

Shrub up to ca. 2 m high, the stems often erect, wand-like, with few lateral branches; young twigs dark reddish brown, becoming gray with age, minutely puberulent-papillate; spines with 3 nearly equal arms (central arm perpendicular to laterals) or palmate with ca. 5 arms, the arms 3–11 mm long; bracts broadly ovate, less than 1 mm long. Leaves angularly obovate, oblanceolate to rhomboid, usually arcuate, the blade 8–20 mm long, 2–10 mm wide, 1.5–4 times as long as wide, stiffly coriaceous, drying gray-green to olive-green, nearly concolorous, sometimes slightly lustrous, the margin with 0–2 spine-tipped teeth per side, the marginal spines ca. 1 mm long, the tooth plus spine often wing-like and directed upward, contrasting with the downwardly directed apex; apex acute, tipped by a spine ca. 1 mm long; base cuneate, often narrowly so; petiole less than 0.5 mm long; venation mixed craspedodromous, the midvein flat above, moderately prominent below, up to ca. 3 pairs of secondary veins visible. Inflorescence an umbel or raceme with the rachis scarcely elongate with 3–8 flowers, the peduncle plus rachis about 1–2 cm long; pedicels 3–7 mm long, the subtending bracts 1.5–2 mm long; flowers probably yellow, ca. 2.5 mm long; tepals 11, the innermost suborbicular to obovate, 1.5–3 mm long; stamens ca. 2 mm long, with two tooth-like lateral appendages below the anther, the anther about half the stamen's length; pistil subglobose, 1.5–2 mm long, the stigma subsessile, ca. 1 mm wide; ovules 2–5, basal. Fruit globose, purple, 6–7 mm long; seeds ca. 4 mm long. Figures 7B, 11A.

Distinguishing features. Style short; stamens with tooth-like appendages; spines small, with 3–5 arms; inflorescence an umbel or short raceme of up to 8 flowers; leaves small, angular, with wing-like marginal teeth, smooth below, not glaucous.

Phenology. Flowering from July to September. Fruiting from September to November.

Distribution and habitat. Endemic to Región IV of Chile. A species of sparse to dense sclerophyllous scrub.

Selected specimens. CHILE. **Región IV:** Ovalle, entre El Toro y Cuesta Punitaqui (30°52′S, 71°12′W), 28 Oct. 1950 (fr), *Jiles 1929* (CONC-32283, M); Coquimbo, Combarbalá, Manquehue (30°57′S, 71°11′W), 620 m, 21 Aug. 1951 (fl), *Jiles 2010* (CONC-32210, M); road to Andacollo, 17.8 km SE of La Serena–Ovalle highway (30°15′S, 71°05′W), ca. 600 m, 22 Sep. 1991 (st), *Landrum 7544* (ASU, SGO); Coquimbo, Pichasca, ca. 750 m, 2 May 1980 (st), *Troncoso A. s.n.* (SGO).

Berberis glomerata is probably most closely related to *B. actinacantha*, sharing with that species a short style, stamens with tooth-like appendages, and a generally umbellate inflorescence.

9. **Berberis grevilleana** Gillies ex Hook. & Arn., Bot. Misc. 3: 136. 1833. *Berberis actinacantha* var. *grevilleana* (Gillies ex Hook.) C. K. Schneid., Bull. Herb. Boissier, ser. 2, 5: 145. 1905. TYPE: Argentina. Andes of Mendoza, *Gillies s.n.* (holotype, E-GL!, = ASU photo!; isotype, K not seen, = SGO photo!).

Shrub to ca. 2 m high, glabrous or minutely papillose on young growth; young twigs smooth to minutely papillose, gray-green to light yellow-brown, the older twigs gray, with longitudinal cracks, with numerous black dots, the bark eventually somewhat stringy; spines with 3(–4) arms, the arms 1.2–4.5 cm long, ca. 2–3 mm wide, each with 2 parallel grooves beneath (rarely somewhat foliaceous); bracts broadly ovate, ca. 1.5 mm long. Leaves elliptic, oblanceolate, rhombic, obovate, or suborbicular, 1.5–3 cm long, 0.5–2.6 cm wide, 1.1–3 times as long as wide, the blade coriaceous, drying gray-green; margin entire or with 1–3(–4) teeth per side; base acuminate; apex acute with a spinescent tip up to 1.5 mm long; petiole ca. 0.5 mm long, blending with base; venation mixed craspedodromous to reticulate-actinodromous, the midvein prominent, the tertiary veins forming an elongate reticulate pattern between the larger veins, or obscure. Inflorescence an umbel with 1–5 flowers; pedicels 0.4–0.7(–1.1) cm long; flowers ca. 5 mm long; tepals ca. 14, the innermost obovate to elliptic, slightly fleshy, somewhat smaller than the next 3; stamens 2.5–3 mm long, usually with 2 minute tooth-like lateral appendages below the anther, the anther ca. ½ the length of the stamen; pistil ovoid to urceolate, 2.5–3 mm long, the stigma 1–1.2 mm wide, elevated on a short style; ovules 3–5, basal. Fruit ca. 1 cm long, the style ca. 0.5 mm long, the stigma ca. 1.5 mm wide; seeds 3–4 mm long, fused together in a stone-like mass at maturity. Figures 2H, 3F, 7B, 11B.

Distinguishing features. Style short, but evident; stamens usually with tooth-like appendages; spines large, usually 3-parted; inflorescence a few-flowered umbel; leaves with toothed margins, coriaceous, gray-green; mature seeds fused in a mass.

Phenology. Flowering mainly in October and November. Fruiting mainly in January and February.

Distribution and habitat. Endemic to central western Argentina: most abundant in Mendoza from 1800 to 2800 m, but also rarely found in the provinces of San Juan and Córdoba (Orsi, 1976). Rocky slopes in shrubby desert vegetation.

Common name. Crucero.

Selected specimens. ARGENTINA. **Mendoza:** San

Carlos, Refugio General Alvarado, 2400 m, 27 Jan. 1950 (fr), *Cuezzo & Barkley s.n.* (TEX); road from Termas Villavicencio to Uspallata, ca. 6 km beyond the Termas (ca. 69°W, 32°30′S), ca. 2000 m, 4 Dec. 1994 (yfr), *Landrum 8329* (ASU, MERL); Potrerillos, Las Vegas, 5 km beyond road to Vallecitos (ca. 69°5′W, 33°S), ca. 2000 m, 4 Dec. 1994 (yfr), *Landrum 8347* (ASU, MERL); Las Heras, Quebrada de la Casa de Piedra, en laderas de los cerros, 16 Jan. 1938 (fr), *Ruiz Leal 4781* (MERL).

Berberis grevilleana is superficially similar to both *B. chilensis* and *B. actinacantha,* but it lacks the racemose inflorescence of *B. chilensis* and has large 3-parted spines unlike those of *B. actinacantha.* It is separated geographically from both of them by the Andes. It hybridizes with *B. empetrifolia.* It is perhaps most closely related to *B. comberi,* because both share the unusual character of seeds that are tightly fused together in the mature fruit.

Lechler (1857) and subsequent authors have reported *B. grevilleana* in Chile. In Lechler's time this was probably due to travelers crossing the Andes between Mendoza and Santiago not clearly specifying where specimens were collected. In later years there seems to have been a confusion with *B. chilensis.*

10. Berberis horrida Gay, Fl. chil. 1: 84. 1845. *Berberis actinacantha* var. *horrida* (Gay) Reiche, Anales Univ. Chile 88: 96. 1894. TYPE: Chile. Provincias centrales, *Gay s.n.* (lectotype, designated here, P! [sheet a mixed collection, lefthand portion lectotype; righthand portion *B. actinacantha,* excluded], = ASU photo!; isolectotype, P! [mixed collection, as in previous, lefthand portion isolectotype], = F-34526!).

Berberis actinacantha var. *mollis* Reiche, Anales Univ. Chile 88: 96. 1894. TYPE: Chile. Rancagua, San Fernando (holotype, SGO not seen).

Berberis pilosifolia Ahrendt, J. Linn. Soc., Bot. 57: 235. 1961. TYPE: Chile. [Termas de?] Cauquenes, 3000–4000 ft., Dec. 1927, *Clarence Elliott 114* (holotype, K!, = ASU photo!).

Shrub up to ca. 2 m high; young twigs yellowish to glaucous gray or reddish gray, glabrous to minutely hirsute (but not densely so), sometimes with numerous black dots, the older twigs with somewhat stringy, gray bark; spines foliaceous or star-like, the blade (central portion) 2–6 mm long, the arms 2–7 mm long; bracts ovate, 1–3 mm long, the apex obtuse to sharply acuminate. Leaves elliptic to orbicular, sometimes palmately lobed, the blade 1–4 cm long, 0.5–2.2 cm wide, 1–3.3 times as long as wide, stiffly coriaceous, drying light gray-green to brown, the upper surface smooth or nearly so, dull or lustrous, the lower surface prominently reticulate, shortly hirsute-papillose, the margin with 2–4 spinescent teeth per side, or in broader leaves the teeth becoming lobes; apex acuminate, spine-tipped; base cuneate to rounded; petiole 1–20 mm long; venation reticulate-actinodromous, the midvein prominent, the secondary and tertiary veins forming a raised pattern below. Inflorescence a sessile umbel (rarely a panicle), with 3–10 flowers; pedicels 5–10 mm long; flowers yellow, 3–5 mm long; tepals usually 14, the six innermost elliptic, ca. 3 mm long, clasping the stamens, somewhat smaller than the next three; stamens ca. 2 mm, with 2 tooth-like lateral appendages below the anther, the anther ½ the length of the stamen; pistil barrel-shaped, ca. 2 mm long, the stigma ca. 1 mm wide, essentially sessile; ovules 3–9, basal. Fruit 4–6 mm long; seeds 2–3, 3–4 mm long. Figures 7C, 11C.

Distinguishing features. Style short; stamens with tooth-like appendages; spines star-like or foliaceous; inflorescence an umbel of up to ca. 10 flowers; leaves with toothed margins, reticulate, hirsute-papillose below.

Phenology. Flowering mainly in September and October. Fruiting mainly in December and January.

Distribution and habitat. Endemic to central Chile from Cerro La Campana (Región V) to the cordillera of San Fernando (Región VI). I have found this species growing in sclerophyllous scrub along rocky river terraces in the pre-cordillera of the Andes at about 800 to 1000 m. These habitats have often been converted to agriculture, and the species is now rather rare.

Common name. Michai (Gay, 1845; Navas, 1976).

Selected specimens. CHILE. **Región Metropolitana:** Cerro Manquehue, 25 Oct. 1891 (fl), *collector unkown s.n.* (SGO); Huinganes, 50 mi. SE of Santiago, 16 Nov. 1901 (fr), *Hastings 369* (US). **Región V:** Cerro de La Campana, Nov. 1979 (st), *Martínez s.n.* (CONC-108042). **Región VI:** San Fernando, road to Termas del Flaco, 6.4 km E of La Rufina Hostería, 10.4 km beyond road to Bellavista, ca. 800 m, 7 Oct. 1993 (fl), *Landrum 7915* (ASU); Rancagua, road from Coya to Mina La Juanita, ca. 7–8 km above Coya (34°14′S, 70°31′W), ca. 900 m, 18 Jan. 1995 (fr), *Landrum 8491* (ASU, SGO); Baños de Cauquenes, May 1956 (st), *Richter s.n.* (CONC-108011).

Berberis horrida is one of the rarest species of *Berberis* in Chile. It is probably most closely related to *B. actinacantha.* They share all the features mentioned above under "distinguishing features" except the reticulate, hirsute-papillose lower leaf surface of *B. horrida.*

11. Berberis ilicifolia L. f., Suppl. pl. 210. 1782. TYPE: *Sparrmann s.n.* (holotype, LINN not seen).

Berberis lagenaria Poir., Encycl. Meth. 8: 619. 1808. TYPE: Detroit de Magellan, *Commerson s.n.* (holotype, P not seen; isotype, P!, = ASU photo!).

Berberis subantarctica Gand., Bull. Soc. Bot. Fr. 59: 705. 1913. TYPE: Argentina. Patagonia, Pt. Grappler, *Skottsberg 293* (holotype, LY!, = ASU photo!).

Shrub 1–4 m high; young twigs dark reddish brown, longitudinally ridged, minutely papillate-puberulent, with age becoming more nearly terete, gray to yellowish, the leaf scars persisting as semicircular, often corky, protuberances; spines normally 3-parted, smooth or minutely papillate, the arms ca. 0.4–1.2 cm long, often slightly curved, the lateral arms perpendicular or forming an acute angle with the central arm; bracts narrowly triangular, to ca. 10 mm long. Leaves obovate, oblong-lanceolate, elliptic, oblanceolate, the blade 2–5 cm long, 1.2–2.2 cm wide, 1.6–2.8 times as long as wide, stiffly coriaceous, drying lustrous or dull gray-green to brownish above, usually lighter below, the upper surface minutely papillate along the margin, the margin with (0–)1–6 spine-tipped teeth, the marginal spines 1–4 mm long; apex acute to subtruncate, spine-tipped; base acute to rounded, blending with petiole or petiole distinct and up to 4 mm long; venation mixed craspedodromous, the midvein impressed above, prominent below, the secondary veins 3–5 pairs, impressed or nearly flat above, about flat below, the tertiary veins impressed to flat above, indistinct or faint below. Inflorescence a raceme with 3–7 flowers, the peduncle plus rachis 0.7–2(–3.5) cm long, usually shorter than the pedicels; pedicels 0.7–2 cm long; flowers orange, 0.5–1 cm long; tepals ca. 14, the innermost suborbicular to obovate; stamens ca. 3 mm long, without lateral appendages, the anther slightly over half the length; pistil nearly cylindric at anthesis, 3–7 mm long; stigma ca. 1.5 mm across; ovules (4?–)5–6, basal. Fruit subglobose, to ca. 10 mm long, with a persistent style ca. 2–3 mm long; seeds 4–6, 5–6 mm long. Figures 7C, 11D.

Distinguishing features. Style long; stamens without tooth-like appendages; spines usually 3-parted; inflorescence a raceme of 3–7 flowers; leaves with toothed margins, with impressed veins above, often lustrous; young twigs longitudinally ridged.

Phenology. Flowering mainly from August to December. Fruiting mainly from November to March.

Distribution and habitat. Endemic to southwestern South America. Found in Chile from the Cordillera Pelada and Puyehue (Región X) to Cabo de Hornos (Región XII) and in Argentina from Chubut, Santa Cruz, and Tierra del Fuego (Orsi, 1976). An understory shrub in *Nothofagus* forests.

Common name. Chelia (C. Muñoz, 1966).

Selected specimens. CHILE. **Región X:** Valdivia, Monumento Natural Alerce Costero (40°11'S, 73°31'W), 1000 m, 12 Feb. 1988 (fr), *Gardner & Knees 4171* (K); Chiloé, Cordillera San Pedro, 8 Oct. 1958 (fl), *Godley 416* (BM); Osorno, Parque Nacional Puyehue, road to Antillanca, ca. 8 km above Administration at Aguas Calientes (ca. 40°45'S, 72°20'W), ca. 650 m, 9 Nov. 1993 (fl), *Landrum 8058* (ASU); Chiloé, Cordillera de Pichihué, Feb. 1983 (fr), *Villagrán 4916* (SGO). **Región XI:** Aisén, Carretera Austral, 58 km S and W of Villa Castillo towards Puerto Murta, near Lago Cofré (ca. 46°15'S, 72°30'W), 18 Oct. 1993 (fl), *Landrum 8150* (ASU); Aisén, Carretera Austral, ca. 177.9 km S of Coihaique, a few km N of entrance to Puerto Murta (ca. 72°45'W, 46°25'S), 19 Oct. 1993 (st), *Landrum 8169* (ASU). **Región XII:** Fiordo Contralmirante Martínez Brazo S-E (54°33'S, 70°36'W), 19 Mar. 1991 (fr), *Henríquez & Palma 63* (HIP); Fuerte Bulnes ca. 50 km S of Punta Arenas, ca. 3.7 km E of main road to Punta Arenas (ca. 53°40'S, 70°55'W), ca. 100 m, 22 Dec. 1994 (fl), *Landrum 8399* (ASU); ca. 30 km SW of Punta Arenas, ca. 1.5 km E of Laguna Parrillar (ca. 53°30'S, 71°15'W), ca. 320 m, 22 Dec. 1994 (yfr), *Landrum 8400* (ASU); Isla Noir, Tierra del Fuego (54°29'S, 73°05'W), 26 Dec. 1983 (fr), *Venegas s.n.* (HIP). ARGENTINA. **Tierra del Fuego:** Ushuaia, 22 Dec. 1949 (fr), *Ruiz Leal 12838* (MERL); Estancia Fique, a orillas del río Olivia, 16 Feb. 1953 (fr), *Ruiz Leal & Roig 14995* (MERL).

The ranges of *Berberis ilicifolia* and *B. serratodentata* overlap from Región XI (near Coihaique) to Región X (at Puyehue and the Cordillera Pelada). In this large area of overlap, which is still poorly collected, the lines between these two species are sometimes not clear. *Berberis ilicifolia* extends farther south to the tip of South America, and *B. serratodentata* grows as far north as the Cordillera de Nahuelbuta. Beyond the region of overlap, the species are quite distinct; the differences are summarized in the key below.

KEY TO *BERBERIS ILICIFOLIA* AND *B. SERRATODENTATA*

1a. Leaves about 1.5–2.5× as long as wide; leaf margins usually with 1–4 teeth per side; lower leaf surface smooth; margins of upper leaf surface papillate; spines common .... *B. ilicifolia*
1b. Leaves about 2.5–4× as long as wide; leaf margins usually with 10 or more teeth per side; lower leaf surface papillate; margins of upper leaf surface smooth; spines uncommon .... *B. serratodentata*

In the area of overlap I have not found any specimens that match typical *B. ilicifolia* from farther south, but I do find plants representative of typical *B. serratodentata.* This suggests that *B. ilicifolia* from Aisén northward is introgressed with *B. serratodentata.* Most of these plants I have identified as *B. ilicifolia,* realizing that they are not quite pure.

In 1914, Skottsberg described *Berberis pseudoilicifolia* from the area of overlap and proposed that it might be a hybrid between *B. ilicifolia* and *B. serratodentata.* I concur with his opinion (see excluded taxa).

Berberis ilicifolia is also similar to *B. darwinii;* the differences are discussed under the latter.

12. **Berberis litoralis** Phil., Fl. atacam., 7. 1860. TYPE: Chile. Quebrada Miguel Diaz, coast of Atacama Desert, *Philippi s.n.* (holotype, SGO-063351!, = ASU photo!; isotype, W!; isotype, B lost, = F-14298!).

Shrub up to ca. 5 m high, glabrous; young twigs dark reddish brown, soon becoming gray and longitudinally ridged; spines usually 3-parted, the arms about equal in length, 0.5–1.4(–2.3) cm long, the laterals perpendicular to the central; bracts ovate-triangular to lanceolate-triangular, 1.5–8 mm long, ca. 1.5 mm wide, gray to dark brown. Leaves elliptic to obovate, the blade (2–)3.3–5.8 cm long, (0.8–)1.5–3.2 cm wide, 1.5–2.2 times as long as wide, coriaceous, drying dull to slightly lustrous, gray-green, darker above than below, the margin slightly revolute, usually spinescent-serrate (rarely entire), the teeth 1–10 per side, 1–2 mm long; apex usually broadly rounded to obtuse, spine-tipped; base acuminate to acute, merging with petiole or the petiole distinct and up to ca. 3 mm long; venation mixed craspedodromous, the midvein impressed slightly above, prominent below, the secondary veins about 4–7 pairs, the tertiary veins forming a usually distinct reticulate pattern within the larger veins. Inflorescence a raceme 2–5 cm long, with 6–17 flowers, sometimes terminating leafy branchlets; pedicels 6–15 mm long, subtended by narrowly triangular, keeled bracts ca. 3 mm long; flowers ca. 5 mm long, orange; tepals 14, the innermost suborbicular to obovate, 5–6 mm long; stamens ca. 4 mm long, without lateral appendages, the anther ca. 1.5 mm long; pistil ca. 5 mm long, the style ca. ½ the length or less; stigma ca. 2 mm wide; ovules 5–6, basal; fruit subglobose, ca. 7 mm long, terminating in a style ca. 1 mm long; seeds ca. 5, ca. 5 mm long. Figures 7C, 12A.

Distinguishing features. Style long; stamens without tooth-like appendages; spines 3-parted; inflorescence a raceme of 6–17 flowers; leaves usually serrate, usually with a rounded apex.

Phenology. Flowering mainly in September and October.

Distribution and habitat. Endemic to the coast of northern Chile: restricted to coastal hills near Paposo (Región II) at elevations of 500 to 1000 m. A species of local foggy habitats that support some of the northernmost patches of sclerophyllous vegetation in Chile.

Selected specimens. CHILE. **Región II:** Paposo, Quebrada de Miguel Díaz, 550 m, 4–5 Sep. 1989 (fl), *Flores et al. s.n.* (SGO-109958); 10.5 km N of Paposo, La Rinconada (ca. 24°54′S, 70°30′W), ca. 850 m, 15 Sep. 1991 (fl), *Landrum & Gutiérrez 7460* (ASU); 39 km S of Paposo, Cachinales (ca. 25°09′S, 70°26′W), ca. 600 m, 16 Sep. 1991 (fl), *Landrum & Morales 7492* (ASU); Quebrada Sepultura (24°55′S, 70°30′W), 840 m, 3 Oct. 1991 (fl), *Quezada & Ruiz 171* (CONC-121406).

Berberis litoralis is most similar to *B. valdiviana,* and they are in fact sometimes difficult to distinguish based solely on morphology. They share racemose inflorescences, pronounced styles, large trifid spines, and relatively large, mainly elliptic leaves. Fortunately, they have widely disjunct distributions: *Berberis litoralis* is restricted to a few coastal populations near Paposo in the Atacama Desert at ca. 25°S latitude, and *B. valdiviana* is found no farther north than ca. 35°S latitude. The most consistent characters distinguishing these species are found in lead 14 of the key.

13. **Berberis masafuerana** Skottsb., Nat. Hist. Juan Fernández 2: 125, species no. 57, fig. 9 a–b. 1921. TYPE: Chile. Más Afuera, Quebrada de las Casas, Quebrada de la Lobería, *Skottsberg s.n.* (holotype, S? not seen).

Shrub or small tree to 2 m high, glabrous or the young growth sometimes minutely puberulent; twigs smooth, subterete, light or dark reddish brown when young, becoming gray, slightly rough with age; spines lacking, insignificant or weak, awl-shaped to 3–5-armed, the arms unequal to equal, to 4 mm long; bracts ovate, 1.5–2 mm long. Leaves obovate, oblanceolate, elliptic, or rarely suborbicular, the blade 1.6–3 cm long, 0.5–1.5 cm wide, (1.2–)2–3.6 times as long as wide, drying gray-green to brownish green, darker above than below, subcoriaceous to submembranous; apex rounded, often mucronate; base acute to cuneate; petiole 2–3 mm long, ca. 0.5 mm wide, the persistent base ca. 1–3 mm long; venation reticulate-actinodromous, the midvein raised slightly to impressed proximally above, moderately prominent below, the secondary veins usually 1–2 pairs. Inflorescence a solitary flower or perhaps a few-flowered umbel;

flowers unknown; fruit 6–8 mm diam., the persistent style ca. 0.5 mm long. Figure 6A.

Distinguishing features. Style short; spines lacking or insignificant; leaves usually obovate or oblanceolate, with entire margins.

Phenology. Probably flowering mainly from September to November and fruiting mainly from December to January. Fertile specimens practically unknown.

Distribution and habitat. Endemic to Más Afuera of the Juan Fernández Islands (Región V), Chile. Skottsberg reported that the species grows on inaccessible canyon walls. Perhaps it grew in other habitats before goats were introduced to Más Afuera.

Selected specimens. CHILE. **Región V:** Juan Fernández Islands, Más Afuera: Quebrada del Tongo, 280–320 m, 14 Feb. 1986 (st), *Landero & Gaete 8479* (CONC-112201, RSA); Cuchillo de Imán, N side of island, down from Cerro Verde, 880 m, 20 Jan. 1986 (st), *Landero & Gaete 9148* (CONC-111574); Quebrada Guatón on W side of island, 1100 m, 26 Jan. 1986 (st), *Landero & Ruiz 9313* (CONC-112172, RSA); Quebrada Larga, 550 m, 5 Feb. 1986 (st), *Ruiz et al. 8299* (CONC-111819).

Berberis masafuerana is a poorly known and rather uniform entity endemic to Más Afuera. It is similar to *Berberis microphylla* and *B. montana*, but differs from them in having weak spines that are occasionally 5-armed. The style of *B. masafuerana* is about 0.5 mm long on the mature fruit, shorter than in *B. montana* and longer than in *B. microphylla*. It is also possible that *B. masafuerana* is related to *B. corymbosa* of Más a Tierra Island. When more collections have been made the situation should be evaluated again.

14. Berberis microphylla G. Forst., Commentat. Soc. Regiae Sci. Gott. 9: 29. 1787. TYPE: Chile or Argentina. Tierra del Fuego, *Forster s.n.* (holotype, BM? not seen; isotype, W!, = ASU photo!).

Berberis buxifolia Lam., Tabl. encycl., 2: 391, t. 253, fig. 3. 1792. TYPE: Chile or Argentina. Strait of Magellan, *Commerson s.n.* (holotype, P not seen, = F-34509!; isotypes [4 sheets] P!, = ASU photos!).

Berberis inermis Pers., Syn. pl. 387. 1805. TYPE: Chile or Argentina. Strait of Magellan, *Commerson s.n.* (apparent holotype, P not seen, = F-34527!; isotypes [2 sheets], P!, = ASU photos!).

Berberis heterophylla Juss. ex Poir., Encycl. 8: 622. 1809. TYPE: Chile or Argentina. Strait of Magellan, *Commerson s.n.* (holotype, P not seen, = F-34525!; isotype, G not seen, = F-27413!).

Berberis cuneata DC., Syst. nat., 2: 16. 1821. TYPE: Argentina. Puerto Deseado (holotype, BM? not seen).

Berberis dulcis Sweet, Brit. fl. gard. 4, plate 100. 1831. TYPE: England. Cultivated, from Strait of Magellan (holotype, not seen, CGE?, MW?).

Berberis marginata Gay, Fl. chil. 1: 88. 1845. TYPE: Chile. Lago Llanquihue, *Gay s.n.* (holotype, P!, = F-34528!).

Berberis buxifolia var. *spinosissima* Reiche, Fl. Chile 1: 39. 1895. *Berberis spinosissima* (Reiche) Ahrendt, J. Linn. Soc., Bot. 57: 241. 1961. TYPE: Chile. Cordillera de Chillán, Collector unknown, s.n. (holotype, SGO-049057!, = ASU photo!).

?*Berberis heterophylla* var. *pluriflora* Reiche, Anales Univ. Chile 88: 97. 1894. TYPE: Chile. Cordillera de Cauquenes (holotype, SGO not seen).

Berberis buxifolia Lam. var. *gracilior* Albov, Revista Mus. La Plata 7: 361. 1896. TYPE: Argentina. Ushuaia, *Albov 1896–83* (holotype, LP? not seen; isotype, SI not seen, = ASU photocopy!).

Berberis buxifolia var. *papillosa* C. K. Schneid., Ill. Handb. Laubh. 1: 302. 1904. TYPE: Chile. Villarrica, *Neger s.n.* (apparent holotype, M!, = ASU photo!).

Berberis buxifolia var. *nuda* C. K. Schneid., Bull. Herb. Boissier, ser. 2, 5: 142. 1905. TYPE: Chile. Villarrica, *Neger s.n.* (holotype, M! [excluding "a"], = ASU photo!).

Berberis buxifolia var. *antarctica* C. K. Schneid., Bull. Herb. Boissier, ser. 2, 5: 142. 1905. TYPE: Chile. Cape Horn, *Hooker 1098* (lectotype, designated here, M!, = ASU photo!; isolectoypes, B lost, G not seen, W!, = ASU photo!).

Berberis antucoana C. K. Schneid., Bull. Herb. Boissier, ser. (2), 5: 144. 1905. *Berberis buxifolia* var. *antucoana* (C. K. Schneid.) Orsi, in Correa, Flora Patagónica pt. IVa: 331. 1984. TYPE: Chile. Cordillera de Antuco, *Poeppig s.n.* (syntype, W not seen; isosyntype, M!, = F-19121!; Sierra Velludo, *Philippi s.n.* (syntype, W not seen).

Berberis parodii Job, Darwiniana 5: 184, fig. 1. 1941. TYPE: Argentina. Cerro Otto, San Carlos de Bariloche, *Cabrera & Job LP 127* (holotype, LP-26389!).

Berberis michay Job, Revista Mus. La Plata, Secc. Bot. 5: 55. 1942. TYPE: Argentina. Santa Cruz: Dpto. Lago Argentino, Arroyo del Bote, Mar. 1914, Comis, Iter Patagonicum 354 (holotype, SI not seen, = ASU photocopy!; isotype, SI not seen, = ASU photocopy!).

Berberis barilochensis Job, Revista Mus. La Plata, Secc. Bot. 5: 50. 1942. TYPE: Argentina. Río Negro: San Carlos de Bariloche, 5 Jan. 1935, *Cabrera & Job 33* (holotype, LP-26118!, = ASU photo!).

Shrub up to 3 m high, glabrous or the twigs and young growth pubescent to puberulent; twigs reddish brown, light brown, yellowish, or gray, with longitudinal ridges, often with numerous black spots, the bark smooth, with age slightly fibrous or flaky; spines 3-parted, the arms (3–)5–45 mm long, about equal in length or the lateral arms shorter or absent (especially near the branch tips); bracts ovate to suborbicular, 1–2 mm long, light green to reddish brown, becoming gray with age. Leaves usually obovate to oblanceolate, less often elliptic to nearly linear, the blade 6–40 mm long, 2–14 mm wide, 1.4–7 times as long as wide, coriaceous to subcoriaceous, drying olive-green, dull to slightly lustrous above, the margin entire or with 1–2 perpendicular spinescent teeth per side; apex acute to obtuse, often with a terminal spine-like apiculum to ca. 1–1.5 mm long; base cuneate to acute; petiole to 1.5(–5) mm long, often persisting as a peg-like structure after the blade falls, with a broadened base; venation reticulate-actinodromous, the midvein weak to prominent below, weak to indistinct above, the secondary veins prominent to indistinct, usually 2–3 pairs. Inflorescence a solitary flower (rarely an umbel of 2 or 3); pedicels 5–24 mm long; flowers 4–5 mm long, yellow; tepals about 12–15, those of the innermost whorl 2.5–4 mm long, shorter than the immediately adjacent outer whorls; stamens 2.5–3 mm long, with or without two tooth-like lateral appendages below the anther, the anther ca. ½ or less the length; pistil ca. 3 mm long, ovoid to barrel-shaped, the style insignificant, the stigma 1–1.5 mm wide; ovules usually ca. 7, basal. Fruit subglobose, 7–11 mm diam., the style essentially none; seeds (1–)6–10, ca. 4–6 mm long, dark black to brown. Figures 2B, 3E, 7B, 12B.

Distinguishing features. Style short; stamens with or without tooth-like appendages; spines 3-parted or simple; inflorescence usually a solitary flower; leaves obovate to oblanceolate, usually with entire margins; flowers yellow.

Phenology. Flowering from August to March, with the peak being from October to January. Fruiting mainly from December to March.

Distribution and habitat. Endemic to southwestern South America from the Andes of Curicó (Región VI) in central Chile at 2500 m to sea level in Tierra del Fuego in both Chile and Argentina. A shrub of disturbed habitats, doing especially well in pastures and along roads.

Common names. Michai, mulun, calafate (Gay, 1845; Rodriguez et al., 1995).

Selected specimens. CHILE. **Región VI:** orillas de la Laguna de Teno (35°10′S, 70°35′W), 2500 m, 10 Mar. 1967 (fl), *Marticorena & Matthei 916* (CONC-70278, OS); interior of valley Teno, 2000 m, 30 Dec. 1971 (fl), *Zöllner 5095* (NA); Laguna Planchón, 2500 m, 30 Dec. 1971 (fl), *Zöllner 6347* (CONC-108020, NA). **Región VII:** Altos de Vilches (35°36′S, 71°12′W), 25 Nov. 1970 (fr), *Oehrens 925* (CONC-41821); Cajón de los Helados (34°50′S, 70°33′W), 7 Jan. 1951 (fr), *Ricardi s.n.* (CONC-10172); Laguna Dial (36°25′S, 70°55′W), 1520 m, 26 Jan. 1961 (fr), *Schlegel 3683* (CONC-88848). **Región VIII:** Reducción Pitracuicui (37°47′S, 73°30′W), 110 m, 8 Aug. 1979 (fl), *Cuevas 8* (CONC-88745); Refugio Garganta del Diablo (36°54′S, 71°24′W), 1800 m, 31 Dec. 1964 (fl), *Gleisner 168* (CONC-88852); road between Pemuco and Yungay, ca. 8 km N of Yungay (ca. 37°5′S, 71°55′W), ca. 200 m, 18 Oct. 1993 (st), *Landrum 7954* (ASU); Lago Lanalhue, road on W side of lago to Hostería, ca. 2 km from main highway (37°53′S, 73°20′W), 23 Oct. 1993 (fl), *Landrum 7972* (ASU). **Región IX:** 9.4 km al oeste del Paso Pino Hachado, Mar. 1962 (fl), *Greer 26* (CONC-27391); Volcán Lonquimay, near gate and house of guardaparque (ca. 38°25′S, 71°30′W), ca. 1500 m, 26 Oct. 1993 (fl), *Landrum 8001* (ASU, SGO); Licanray, 210 m, 18 Sep. 1974 (fl), *Montero O. 9336* (CONC-84025); 6 km S de Curacautín, 23 Mar. 1954 (st), *Sparre & Constance 10857* (CONC-17566). **Región X:** Parque Nacional Puyehue, road to Antillanca, ca. 8 km above Administration at Aguas Calientes (ca. 40°45′S, 72°20′W), ca. 650 m, 9 Nov. 1993 (fl), *Landrum 8059* (ASU, SGO); Chiloé, camino de Chacao a Ancud, 1 km antes de la entrada del camino a Caulin (41°51′S, 73°37′W), 45 m, 10 Jan. 1975 (fr), *Marticorena et al. 4* (CONC-42826); Niebla, Playa Grande, 27 Sep. 1975 (fl), *Montero 9739* (CONC-84024); Isla Gran Guaiteca, Puerto Low in Bahía Low (43°51′S, 73°55′W), 7–15 Jan. 1984 (fr), *Patterson s.n.* (F, NY). **Región XI:** Puerto San Andrés, N side, Taitao Península (46°33′S, 75°26′W), 23 May 1973 (st), *Goodall 47* (NA); Cerro Divisadero SE of Coihaique, road to centro de ski El Fraile (ca. 45°37′S, 70°00′W), 16 Nov. 1993 (fr), *Landrum 8108* (ASU); río Exploradores, entre río Verde y río Teresa, Parque Nacional Laguna San Rafael, Sector Hotel (46°37′S, 73°33′W), 25 Jan. 1988 (fr), *Pisano V. 6201* (CONC-104598); junta del río Soler y río Romero (47°00′S, 73°05′W), 700 m, 29 Mar. 1962 (st), *Seki 608* (CONC-88750). **Región XII:** Puerto Inútil, Isla Navarino (54°59′S, 67°50′W), below 50 ft., 6 Dec. 1968 (st), *Barret & Norris 58-10* (NA); Puerto Hambre ca. 50 km S of Punta Arenas (ca. 53°40′S, 70°55′W), 0–10 m, 22 Dec. 1994 (fr), *Landrum 8393* (ASU); Punta Steinman, ca. 35 km along road to Punta Canelo from main highway (ca. 53°10′S, 71°25′W), ca. 3 m, 31 Dec. 1994 (fr), *Landrum 8462* (ASU); Fiordo Peel, río Murtillar (50°27′S, 73°37′W), 17 Nov. 1985 (fl, yfr), *Pisano V. 5912* (CONC-73141). ARGENTINA. **Chubut:** proximo del desvío de Ruta 40 a Alto río Senguer, 720 m, 13 Jan. 1978 (fr), *Ambrosetti & Méndez 27523* (MERL); Tehuelches, cerca río Pico, 7–26 Feb. 1993 (fr), *Roig 14300* (MERL); entre río Mayo y Alto Seuguer (ruta 40), 560 m, 11–12 Dec. 1986 (fr), *Roig Junent 12903* (MERL); 35 km E of Esquel on route 25 (2.9 km SE of the junction of routes 40 and 25), 670 m, 4 Dec. 1984 (fr), *Stuessy et al. 6828* (OS). **Neuquén:** Lacar, Lago Lacar (Parque Lanín), Pucará, 9 Nov. 1956 (fr), *Roig 1950* (MERL); al NW del Lago Falkner, Feb. 1975 (fr), *Cassels s.n.* (SGO); entre Zapala y Laguna Miranda, 1180 m, 7 Dec. 1990 (fr), *Roig et al. 12967* (MERL). **Río Negro:** Dep. Bariloche, Cerro Catedral, 13 Nov. 1968 (yfr), *Cabrera et al. 19496* (CONC-42805); Valle El Bolsón, 10 Feb. 1983 (fr), *Roig 13342* (MERL); Meseta de Somuncura, Laguna Raimunda, 1440 m, 20 Feb. 1967 (fr), *Ruiz Leal 25575* (MERL); 3.3 km S of Foyel on route 258, 750 m, 3 Dec. 1984 (fr), *Stuessy et al. 6792* (OS). **Santa Cruz:** valle superior del río Turbio, 23 Jan. 1978 (st), *Ambrosetti & Méndez s.n.* (MERL); 4 m al E del Lago Burmeister, 1000 m, 8 Dec. 1980 (fl), *Cei & de Cei s.n.* (MERL); Güer Aike cerca de La Esperanza, 14 Feb. 1993 (fr), *Roig et al. 14378* (MERL); río Chico, cerca de Riera, 20 Feb. 1993 (fr), *Roig et al. 14597* (MERL). **Tierra del Fuego:** Lapataia National Park above Ushuaia, 16 Feb. 1976 (fr), *Barclay s.n.* (US); Ushuaia, 6–8 km de la población, márgen derecha río Olivia, 22 Dec. 1949 (fl, fr), *Ruiz Leal & Carretero 12815* (MERL); Valle de Tierra Mayor, 24 Feb. 1956 (fr), *Ruiz Leal & Roig 15081* (MERL).

The name *Berberis buxifolia* has long been the name most commonly used for this species, but an older, less frequently used name, *B. microphylla*, exists and should be used in accordance with the rules of nomenclature.

This is a variable and widespread species that has benefitted from human disturbance. Other authors have subdivided it into numerous entities, but after field and herbarium studies I find that I cannot erect any satisfactory subspecific division.

Leaf shape variation in *B. microphylla* is illustrated in Figure 5. Plants of wetter habitats are near the top, whereas those of drier habitats are near the bottom of this figure.

In more humid areas leaves tend to be broader and entire and the spines shorter; in drier areas the leaves tend to be narrower and are often toothed and the spines longer. The plants of the Patagonian steppe that have long been called *B. heterophylla* combine relatively narrow leaves, long spines, and leaves with toothed margins, but where I have seen these growing the characters are not consistent within local populations, so recognizing even a variety at this point seems unwarranted. If extensive populations can be found that are uniform in a particular set of character states, then a Patagonian variety might be accepted. It would be better not to use the epithet *heterophylla* because the type of *B. heterophylla* does not have exceptionally narrow leaves or long spines, nor are the leaf margins especially toothed.

Berberis microphylla is most likely to be confused with *B. montana*. They are contrasted directly in lead 19 of the key. It perhaps hybridizes with *B. valdiviana* (*Landrum 8032*) and *B. trigona* (*Landrum 8018*).

Berberis dulcis Sweet was described and illustrated from a cultivated plant, so perhaps no specimens exist. The illustration and origin clearly indicate its identity.

Some authors have taken Paxton's description of *Berberis dulcis* (Paxton's Mag. Bot. 10: 171. 1843) as a new species description. I do not believe that was Paxton's intention because he mentioned that the plant had been growing in England for about 13 years, or about the number of years since it was described by Sweet. In any case, it would be an illegitimate later homonym.

Usteri (Mitt. Deutsch. Dendrol. Ges. 8: 94. 1899) introduced three names into the *Berberis* literature: *Berberis buxifolia* var. *nana* Hort. ex A. Usteri, *Berberis buxifolia* var. *pygmaea* Hort. ex A. Usteri, and *Berberis buxifolia* var. *macrantha* Phil. ex A. Usteri. There was only incidental mention of these taxa in a key, and it was probably not the intention of the author to establish new names. Thus, I believe these were not validly published.

The type of *Berberis brevifolia* Phil. ex. Reiche (see excluded taxa) is sterile but appears to be *B. microphylla*, although it comes from outside the known range of that species. It might also be a form of *B. actinacantha*.

15. Berberis montana Gay, Fl. chil. 1: 90. 1845. TYPE: Chile. Montañas de Cauquenes y de Talcaregue, *Gay s.n.* (holotype, P!, = F-34529!).

Berberis coletioides Lechler, Berberid. Amer. austral., 38. 1857. *Berberis montana* var. *coletioides* (Lechler) C. K. Schneid., Bull. Herb. Boissier, ser. 2, 5: 395. 1905. TYPE: Chile. Cordillera de Santiago, *Philippi s.n.* (syntypes, SGO not seen, Lechler hb. 3135 [at MB?] not seen).

Berberis polypetala Phil., Anal. Univ. Santiago 1872: 666. 1872. TYPE: Chile. Volcán Calbuco, *Juliet s.n.* (holotype, SGO-063370!, = ASU photo!).

Berberis montana var. *gracilis* C. K. Schneid., Bull. Herb. Boissier, ser. 2, 5: 395. 1905. *Berberis coletioides* var. *gracilis* (C. K. Schneid.) Ahrendt, J. Linn. Soc., Bot. 57: 247. 1961. TYPE: Chile. Villarrica, *Neger s.n.* (holotype, M not seen; isotype, G!).

Berberis montana var. *chillanensis* C. K. Schneid., Bull. Herb. Boissier, ser. 2, 5: 395. 1905. *Berberis chillanensis* (C. K. Schneid.) Sprague, Kew Bull. 9: 455. 1932. TYPE: Chile. Cordillera de Chillán, *Germain s.n.* (lectotype, designated here, W!, = ASU photo!; isolectotypes, CONC!, F!, G!); *Philippi s.n.*, 1855 (syntype, W!).

Berberis chillanensis var. *hirsutipes* Sprague, Kew Bull. 9: 456. 1932. TYPE: Argentina. Suangulo, 1950 m, 16 Jan. 1926 (fl), *Comber 479* (holotype, K!, = ASU photo!).

Berberis cabrerae Job, Revista Mus. La Plata, Secc. Bot. 5: 60. 1942. TYPE: Argentina. Río Negro: Bariloche, Cerro López, 1500 m, 15 Jan. 1935, *Cabrera & Job 325* (holotype, LP-26065 not seen; isotype, LP-24657!, = ASU photo!).

Shrub up to ca. 2 m high, glabrous or the twigs and young growth pubescent to minutely papillate-puberulent; twigs reddish brown, tan, or gray, with longitudinal ridges, the bark smooth, with age slightly fibrous; spines 3-parted, the arms 3–12(–15) mm long, or often the lateral arms absent or insignificant, especially near the branch tips; bracts ovate to broadly rounded, 1–2 mm long, membranous to submembranous, reddish brown to yellowish tan. Leaves obovate, oblanceolate, or oblong, the blade 5–18 mm long, 1.5–9 mm wide, 2–3.3(–4.7) times as long as wide, membranous to submembranous, drying gray-green, dull to slightly lustrous above, the margin normally entire; apex acute to rounded, usually without an apiculum; base acute to acuminate; petiole in living leaves usually insignificant, but often present as persistent leaf bases, these 2–3 mm long, with a broad clasping base and narrow neck-like apex, borne in the

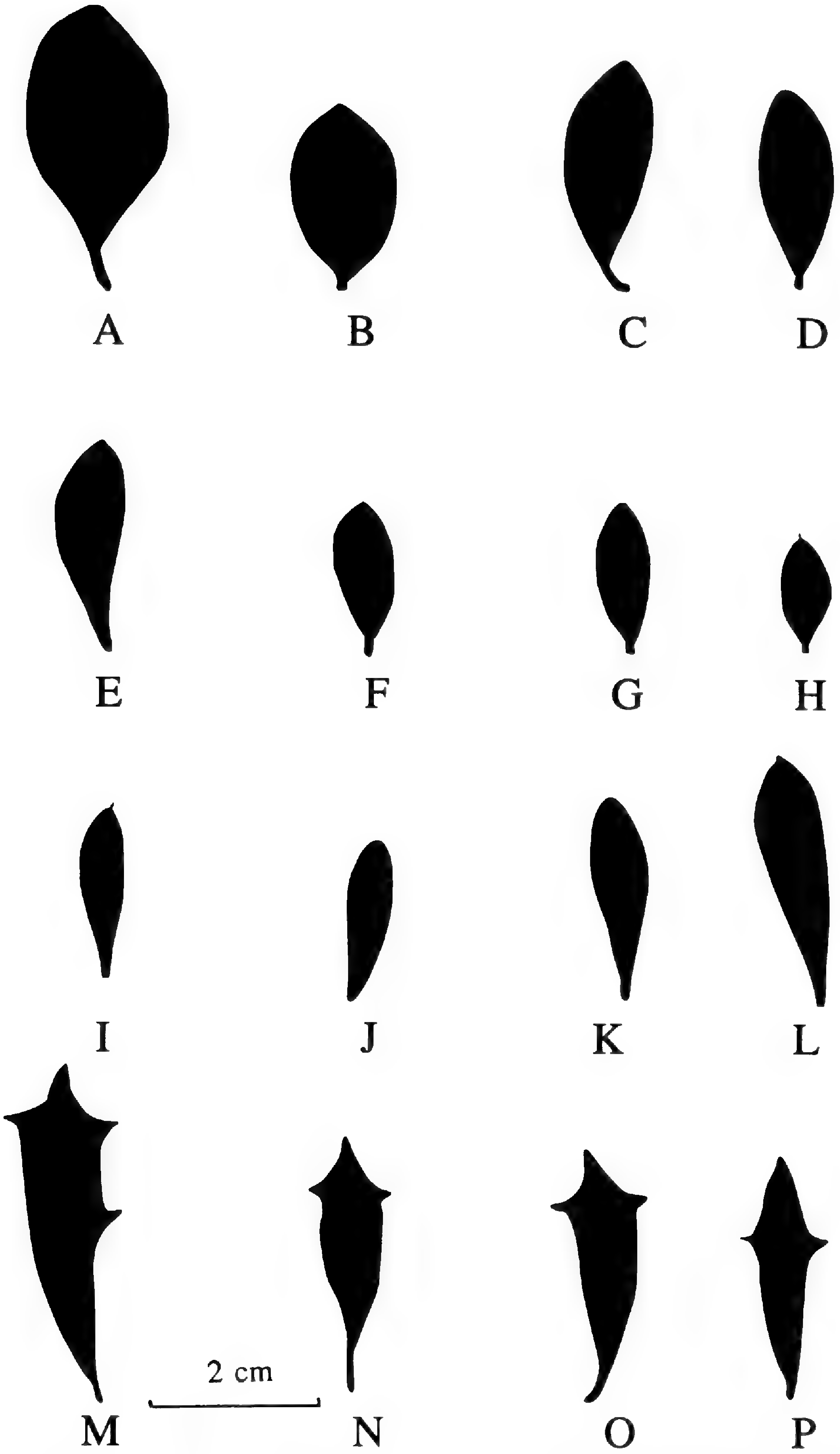

Figure 5. Leaf variation in *Berberis microphylla*. In general, the leaves at the top come from wetter localities and those at the bottom come from drier localities. Each leaf is from a separate collection, each made by the author. General locality and Region are indicated for each collection. —A. *8059*, Puyehue (X). —B. *8067*, Puyehue (X). —C. *8000*, road to Volcán Lonquimay (IX). —D. *7972*, Lanalhue (VIII). —E. *7607*, Volcán Villarrica (IX). —F. *7945*, Termas de Chillan (VIII). —G. *7592*, Valdivia (X). —H. *7613*, Huerquehue (IX). —I. *8434*, Cullen (XII). —J. *7941*, Recinto (VIII). —K. *8418*, Cerro Guido (XII). —L. *8146g*, Puerto Ibañez (XI). —M. *8141*, Puerto Ibanez (XI). —N. *8425*, San Gregorio (XII). —O. *8146h*, Puerto Ibañez (XI). —P. *8406*, Lago Sarmiento (XII).

axils of spines and subtending leaf clusters; venation reticulate-actinodromous, the midvein weak to prominent below, the veins otherwise weak to indistinct. Inflorescence a solitary flower or a sessile umbel-like cluster of 2–3; pedicels 0.6–1.2 cm long; flowers 3.5–6 mm long; tepals about 15, the innermost 6, 2–4 mm long, darker yellow-orange than the other tepals, shorter than the immediately adjacent outer whorls; stamens 3–3.5 mm long, with very small appendages just below the anther, the anther ca. ½ the length; pistil 3–4 mm long, elongate urceolate, the style ca. ½ the length; ovules 4–7, basal. Fruit subglobose, ca. 8 mm diam., the style 1–2 mm long; seeds up to about 7, ca. 4 mm long. Figures 7D, 12C.

Distinguishing features. Style long; stamens with tooth-like appendages; spines 3-parted or simple; inflorescence a solitary flower or 2–3-flowered umbel; leaves mostly obovate to oblanceolate, with entire margins; flowers yellow-orange, the innermost 6 tepals darker than others.

Phenology. Flowering mainly from November to January. Fruiting mainly from January to March.

Distribution and habitat. Endemic to southwestern South America. Found in Chile from Cerro Caqui (Región V) to Volcán Osorno (Región X) and in Argentina only in the vicinity of Lago Nahuelhuapi and probably near Baños de Copahue. A shrub of forests and open areas, usually near the upper limit of woody vegetation.

Common name. Palo amarillo (Gay, 1845).

Selected specimens. CHILE. **Región V:** Valparaíso, La Calera, Cerro Caqui (32°43′S, 71°03′W), 1800 m, 12 Oct. 1966 (fl), *Zöllner 1650* (CONC-108058). **Región Metropolitana:** San Gabriel (33°26′S, 70°14′W), ca. 2500 m, Dec. 1951 (fr), *Gunckel 21744* (CONC-108062); Quebrada Jorquera, cerca del Refugio de Farellones, 2200 m, 9–12 Feb. 1957 (fr), *Looser 5707* (G); Melipilla, Las Vizcachas, ca. 10 km from La Dormida, 1860 m, 8 Dec. 1938 (fl), *Morrison 16811* (G, MO, NA); Cerro San Ramón, Paso del Inca (33°28′S, 70°25′W), 2700 m, 21 Nov. 1955 (fl), *Schlegel 938* (CONC-88844). **Región VI:** Colchagua, San Fernando, Vegas del Flaco (34°56′S, 70°25′W), 1800 m, 7 Feb. 1955 (fr), *Ricardi 3155* (CONC-18846). **Región VII:** Talca, El Picazo (35°32′S, 71°00′W), 28 Dec. 1936 (fl), *Barros 320* (CONC-108094); Linares, Valle Botacura (36°05′S, 70°40′W), 2000 m, 21 Jan. 1961 (fr), *Schlegel 3570* (CONC-88867). **Región VIII:** Chillán, Termas de Chillán, ca. 1 km below Puente Aserradero (ca. 36°55′S, 71°27′W), ca. 1300 m, 17 Oct. 1993 (fl), *Landrum 7943* (ASU); Bío Bío, alrededores de Termas de Copahue, Feb. 1942, *Muñoz & Montandón 3016* (SGO); Bío Bío, Las Cuevas, Laguna del Laja (37°28′S, 71°19′W), 1300 m, 2 Nov. 1952 (fl), *Ricardi 2343* (CONC-13183, OS). **Región IX:** P. N. Nahuelbuta, Piedra del Aguila (37°49′S, 72°59′W), 1350 m, 24 Nov. 1987 (fl), *Baeza 5* (CONC-110170); road from Curacautín to Lonquimay, ca. 1.5 km before turnoff to road to Volcán Lonquimay (ca. 38°25′S, 71°30′W), ca. 1300 m, 26 Oct. 1993 (fl), *Landrum 7997* (ASU); Temuco, camino desde la Laguna Conguillío, 2 km antes de la Laguna Captrén (38°39′S, 71°40′W), 1300 m, 20 Jan. 1976 (fl), *Marticorena et al. 820* (CONC-44201); Los Pinos, 6 km antes de Paso Pino Hachado (38°39′S, 70°56′W), 1600 m, 10 Jan. 1977 (fr), *Marticorena et al. 1382* (CONC-88851). **Región X:** Volcán Osorno, La Picada, El Lomón (41°05′S, 72°25′W), 950–1500 m, 28–30 Nov. 1939 (fl), *Gunckel 9365* (CONC-108105); Parque Nacional Puyehue, road to Antillanca, ca. 14.4 km above Park Administration (ca. 40°45′S, 72°20′W), ca. 800 m, 10 Nov. 1993 (fl), *Landrum 8066* (ASU, SGO); Lago Pirihueico (39°54′S, 71°52′W), 1060 m, 7 Dec. 1976 (fl), *Veblen 507* (CONC-88863); río Pilmaiquén, La Poza (40°33′S, 72°50′W), 110 m, Mar. 1967 (fl), *Zollitsch 99* (CONC-41835). ARGENTINA. **Neuquén:** Cerro Chapelco, 1400 m, 12 Jan. 1972 (fl), *Cabrera 21913* (CONC-37550); Neuquén, Pino Hachado, 18 Nov. 1969, *Ruiz Leal 26757* (MERL).

Sprague's new combination and variety (*Berberis chillanensis* (Schneider) Sprague var. *hirsutipes* Sprague) published in 1932 were also reported informally by Bean in the same year in *New Flora and Silva* 5: 49–51. It was clearly the intention of Bean to report on the activities of Sprague as they were being published in the *Kew Bulletin,* so I assume Sprague's publication was first to appear.

Berberis montana is most likely to be confused with *B. microphylla;* the two are compared directly in lead 19 of the key.

Berberis montana probably hybridizes with *B. empetrifolia.* Both grow at high elevations, and the harsh habitat of exposed volcanic soils and cold winds may have locally favored hybrids.

Cortella and Orsi (1986) found that *B. copahuensis* Job (see excluded taxa), which they considered to be a species, intergrades with *B. empetrifolia.* I hypothesize that *B. copahuensis* is a hybrid between *B. empetrifolia* and *B. montana* and that it is back-crossing with *B. empetrifolia* in the population they studied.

16. **Berberis negeriana** Tischler, Bot. Jahrb. Syst. 31: 640. 1902. TYPE: Chile. Concepción, *Neger s.n.* (holotype, M!, = ASU photo!, = F neg. 19123!).

Shrub up to ca. 1 m high; young twigs light brown to gray, minutely papillate, the older bark gray, with longitudinal cracks and ridges; spines absent; bracts triangular to narrowly triangular, up to 9 mm long. Leaves oblong-elliptic, the blade 4.8–10 cm long, 1.3–4.2 cm wide, 2.3–3.7 times as long as wide, coriaceous, drying dark green to brown, somewhat lighter below than above, lustrous on both surfaces, the margin coarsely serrate (rarely entire), with 6–16 spine-tipped teeth, the marginal spines 1–3 mm long, the teeth (not including spine) 0.5–3 mm long, sometimes every other tooth directed downward; apex acute; base acuminate to broadly cuneate; petiole 0–3 mm long; venation mixed craspedodromous, the midvein impressed slightly to nearly flat above, prominent below, the secondary veins distinct, raised above and below, 7–13 pairs, the tertiary veins distinct. Inflorescence a raceme with the peduncle plus rachis 2–8 cm long, with few to ca. 12 flowers; pedicels 10–16 mm long, the subtending bracts 2–3 mm long; flowers yellow, ca. 5–8 mm long; tepals 14, the innermost elliptic to obovate, ca. 6 mm long; stamens ca. 5 mm long, without lateral appendages, the anther ca. ½ the length; pistil ca. 6 mm long, the style ca. 2 mm long, elongating to ca. 4 mm long soon after anthesis; ovules 2–3, basal. Fruit (perhaps only seen immature) oblong, ca. 7 mm long by ca. 4 mm wide, the persistent style ca. 3 mm long. Figures 7D, 12D.

Distinguishing features. Style long; stamens without tooth-like appendages; spines none; inflorescence a raceme of up to ca. 12 flowers; leaves oblong-elliptic with serrate margins, the lower surface lustrous.

Phenology. Flowering from September to November. Fruiting in December and January.

Distribution and habitat. Endemic to the area just east of Concepción (Región VIII), Chile. Reports of specimens from Villarrica seem to be based on confused labels. An understory shrub of *Nothofagus* forest.

Selected specimens. CHILE. **Región VIII:** Concepción, Bosque Fisco at Nonguén, SE of Concepción (36°50′S, 73°2′W), ca. 200–300 m above houses, 4 Sep. 1991 (fl), *Landrum & Ruiz 7434* (ASU); Concepción, Chiguayante, hills N of town following a path beginning at San Pablo and San Marcos streets, climbing ca. 1 hour, 30 Nov. 1993 (st), *Landrum & Ruiz 8210* (ASU); Concepción, Chiguayante, Cerro Manquimávida (36°55′S, 73°01′W), Oct. 1936 (fl), *Pfister s.n.* (CONC-7724, OS).

Orsi (1976) placed *Berberis negeriana* in synonymy under *B. serratodentata,* but they differ in various ways outlined in lead 10 of the key. It may also be confused with *B. valdiviana*; the differences are discussed under that species.

This is the rarest and most endangered species of *Berberis* in Chile. Only a few individuals are known, growing in a remnant *Nothofagus* forest, vulnerable to being completely destroyed.

17. Berberis rotundifolia Poepp. & Endl., Nov. gen. sp. pl. 2: 63. 1838. TYPE: Chile. Pico de Pilque, *Poeppig s.n.* (holotype, W not seen, = F-30137!; isotypes, G!, M!, = ASU photo!, W!, = ASU photo!).

Berberis polymorpha Phil., Linnaea 28: 664. 1856. TYPE: Chile. Cordillera near Chillán, *Germain s.n.* (lectotype, designated here, SGO-063364! [lower left portion only, the right and upper portions excluded], = ASU photo!; isolectotype B, lost, = F-14307!).

Berberis umbellata Phil., Anal. Univ. Santiago 663. 1872. *Berberis philippii* Ahrendt, J. Linn. Soc., Bot. 57: 232. 1961, = *B. umbellata* Phil. 1872, non Wall. ex G. Don, Gen. hist. 1: 116. 1831. TYPE: Chile. Río Bueno, Valdivia, *Krause s.n.* (holotype, SGO-063372!, = ASU photo!).

Shrub to ca. 1.5 m high, glabrous; young twigs smooth, light reddish brown to yellowish, becoming gray; spines star-like, the arms (3–)5–7, 2–15 mm long, the central blade portion about as long as or shorter than the arms, the margin revolute; bracts broadly ovate, ca. 2 mm long. Leaves suborbicular, elliptic, ovate, or obovate, the blade 1.5–5 cm long, 0.6–4 cm wide, 0.9–2(–2.7) times as long as wide, submembranous, drying light brown to gray-green, darker above than below, sometimes glaucous below, the margin entire or with a few weak teeth, especially near the base; apex acute to rounded; base acuminate to rounded or truncate; petiole 0–4.5 cm long, ca. 0.5 mm wide; venation reticulate-actinodromous, the midvein narrow, ca. 0.1–0.2 mm wide, the tertiary veins distinct. Inflorescence an umbel or raceme with 7–12 flowers, the rachis if present short, the peduncle plus rachis 1–4 cm long; pedicels 4–12 mm long, subtended by triangular bracts 1–2 mm long. Flowers ca. 4 mm long; tepals 11–14, the innermost elliptic to obovate; stamens 2–2.5 mm long, with two minute, tooth-like lateral appendages below the anther, the anther ca. ½ the length; pistil barrel-shaped, ca. 2 mm long, the stigma subsessile, ca. 1 mm wide; ovules (3–)5, basal. Fruit subglobose, 6–7 mm long, blue-purple; seeds usually 5, ca. 4 mm long, dark, shiny. Figures 3D, 8A, 13A.

Distinguishing features. Style short; stamens with tooth-like appendages; spines star-like or foliaceous; inflorescence a several-flowered, pedunculate umbel or short raceme; leaves submembranous, mostly with entire margins.

Phenology. Flowering from November to January. Fruiting from January to March.

Distribution and habitat. Endemic to central and southern Chile, from Curicó (Región VII) to at least Temuco (Región IX), and perhaps to río Bueno (Región X) where the type of *B. umbellata* is reported to have been collected. A shrub of *Nothofagus* forest understory and regeneration.

Selected specimens. CHILE. **Región VII:** Cordillera de Talca, El Picazo (35°32′S, 71°00′W), 2320 m, 28 Dec. 1936 (yfr), *Barros 318* (CONC-103559); Curicó, Los Quenes (35°05′S, 70°30′W), 1500 m, Jan. 1933 (st), *Grandjot s.n.* (CONC-23279); Curicó, Molina, Area de Protección, Radal Siete Tazas, Parque Inglés, Cajón de los Bueyes, 28 Dec. 1989 (fl, fr), *Muñoz S. 2508* (SGO). **Región VIII:** Pemehue, 1370 m, 19 Jan. 1946 (st), *Kuschel s.n.* (SGO); Termas de Chillán, ca. 200 m above Puente Aserradero (ca. 36°55'S, 71°27'W), ca. 1300 m, 17 Oct. 1993 (fl), *Landrum 7951* (ASU); Termas de Chillán, camino de bajada por la lavandería, 1700 m, 9 Jan. 1945 (fl), *Pfister 964* (CONC-6322, OS); cordillera del río Manso, 1000–1200 m, Feb. 1896, *Reiche s.n.* (SGO). **Región IX:** 11.3 km W of Lonquimay, 5200 ft., 20 Dec. 1960 (st), *Greer 1126* (OS); 10 km WNW of Lonquimay, 5100 ft., 4 Feb. 1962 (st), *Greer 1215* (OS); Toltén, Jan. 1917 (fr), *Gusinde 633* (W); Temuco, road to Cunco, ca. 40 km E of Temuco, ca. 2.2 km E of Faja 18 road (ca. 38°55'S, 72°10'W), ca. 300 m, 25 Oct. 1993 (fl), *Landrum 7995* (ASU, SGO).

Berberis rotundifolia is part of a complex of species related to *B. actinacantha* and is distinguished from them in leads 2 and 3 of the key. Some forms of *B. corymbosa* of Más a Tierra Island are similar in leaf shape and texture to *B. rotundifolia*, and the possibility of a relationship must be considered.

18. Berberis serratodentata Lechler, Berberid. Amer. austral., 16. 1857. TYPE: Chile. Cordillera de Valdivia, tierra de los Pehuenches, *Lechler 2985* (holotype, MB? not seen; isotype, P!, = F-34538!).

Berberis pearcei Phil., Linnaea 33: 4. 1864. TYPE: Chile. Boquete de Ranco, Andes de Valdivia, *Pearce s.n.* (holotype, SGO!, = ASU photo!).

Shrub to ca. 1.5 m high, glabrous; young twigs smooth (sometimes shiny), yellow-brown, the older bark becoming gray, fibrous; spines usually absent or less often a few present, 3-parted to palmate with the arms to ca. 4 mm long; bracts oblong-truncate, ovate-triangular to narrowly acuminate-triangular, 3–12 mm long. Leaves oblong, elliptic, narrowly elliptic, ovate, lanceolate, or oblanceolate, the blade 2.3–9.3 cm long, 1.1–2.4 cm wide, 2–4.3 times as long as wide, coriaceous, drying gray-green to yellow-green, dull to lustrous above, dull, papillate below, the margin often revolute, usually serrate with 10–32 spine-tipped teeth per side, the marginal spines 1–2.5 mm long, the teeth (not including spine) to ca. 1 mm long; apex acute to rounded; base acuminate, acute, decurrent along the petiole, the petiole to ca. 7 mm long; venation mixed craspedodromous, the midvein impressed above, prominent below, the secondary veins faint to prominent, impressed slightly to flat above, 7–12 pairs, the tertiary veins faint to indistinct. Inflorescence a raceme, with 8–15 flowers, the peduncle plus rachis 0.5–1.5 cm long; pedicels 6–13 mm long; flowers orange, 5–7 mm long; tepals 14, the innermost obovate; stamens 4–5 mm long, without lateral appendages, the anther ½ or less the length; pistil ca. 5 mm long; stigma ca. 1.5 mm across; ovules 4–6, basal. Fruit subglobose, ca. 7 mm long, the style ca. 2 mm long; seeds 4–6, ca. 5 mm long. Figures 2F, 8B, 13B.

Distinguishing features. Style long; stamens without tooth-like appendages; spines usually none; inflorescence a raceme of 8–15 flowers; leaves mainly oblong, with serrate margins, the lower surface dull, papillate.

Phenology. Flowering in November and December. Fruiting from January to March.

Distribution and habitat. Endemic to southwestern South America. Found in Chile from the Cordillera of Nahuelbuta (Región VIII) to Coihaique (Región XI) and in Argentina in western Río Negro, Neuquén, and Santa Cruz (Orsi, 1984). An understory shrub of *Nothofagus* and *Araucaria* forests.

Common name. Saloll (Muñoz, 1966).

Selected specimens. CHILE. **Región IX:** road from Curacautín to Lonquimay over mountain, ca. 5 km after turnoff to road to Volcán Lonquimay (ca. 38°25'S, 71°30'W), ca. 1600 m, 26 Oct. 1993 (st), *Landrum 8015* (ASU); Melipeuco, China Muerta (38°42'S, 71°31'W), ca. 1800 m, 23 Jan. 1958 (st), *Montero 5805* (CONC-84040, OS); Volcán Mocho (39°56'S, 72°04'W), 1300 m, 19 Feb. 1956 (st), *Montero 4996a* (CONC-84092); Angol, Parque Nacional de Nahuelbuta, Piedra de Aguila (37°49'S, 72°59'W), 1350 m, 9 Jan. 1968 (fr), *Ricardi et al. 1971* (CONC-41833, F). **Región X:** Chiloé, Piruquina (42°24'S, 73°48'W), 400 m, 20 Feb. 1932 (st), *Junge 325* (CONC-2225); Llanquihue, Cerro Vichadero, Casa Pangue (41°04'S, 71°51'W), 1200 m, 14 Jan. 1953 (fr), *Pfister s.n.* (CONC-13561); Parque Nacional Puyehue, road to Antillanca, ca. 15.5 km above Park administration (40°45'S, 72°20'W), 1100 m, 10 Nov. 1993 (fl), *Landrum 8070* (CONC-47918). **Región XI:** Cerro Divisadero SE of Coihaique, road to centro de ski El Fraile, ca. 12.2 km from beginning of road (ca. 45°37'S, 70°00'W), 16 Oct. 1993 (fl), *Landrum 8118* (ASU). ARGENTINA. **Río Negro:** ca. 2 km down from top of Cerro Otto towards San Carlos de Bariloche, ca. 1250 m, 2 Dec. 1984 (fl), *Stuessy et al. 6758* (OS).

Berberis serratodentata is similar to *B. negeriana;* the two are contrasted in lead 10 of the key. *Berberis serratodentata* hybridizes with *B. ilicifolia*, and this problem is discussed under that species.

19. Berberis trigona Kunze ex Poepp. & Endl., Nov. gen. sp. pl. 2: 63, t. 187. 1838. TYPE: Chile. Antuco, *Poeppig s.n.* (holotype, W not seen; isotype, M!).

Berberis linearifolia Phil., Linnaea 28: 663. 1857. TYPE: Chile. Strait of Magellan [probable error], *Lechler s.n.* (lectotype, designated here, SGO-049022!, = ASU photo!); Volcán Osorno, *Philippi s.n.* (SGO not seen).

Berberis grisebachii Lechler, Berberid. Amer. Austral. 34. 1857. TYPE: Chile. Laguna de Ranco, *Lechler 823* (holotype, MA? not seen; isotypes, BR!, G!, = F-27415!, M not seen, = F-19122!, W!).

Berberis trigona var. *longifolia* Reiche, Fl. Chile 1: 36. 1895. *Berberis linearifolia* var. *longifolia* (Reiche) Ahrendt, J. Linn. Soc., Bot. 57: 256. 1961. TYPE: Chile. Valle del estero de Chillán, Collector unknown, s.n. (holotype, SGO!, = ASU photo!).

Shrub up to 2 m high, glabrous; twigs usually light gray to tan (rarely dark reddish brown), with longitudinal ridges, the bark of older twigs becoming fibrous; spines 3-parted, not foliaceous, the arms nearly equal, 3–18 mm long, curved slightly downward; bracts ovate to ovate-oblong, dark brown, ca. 3 mm long. Leaves elliptic, narrowly elliptic, oblanceolate, or linear, the blade 1.7–5.4 cm long, 0.4–1(–1.5) cm wide, (2–)2.6–8 times as long as wide, stiffly coriaceous, drying olive-green, lustrous above, dull below, the margins revolute; apex acute to rounded, ending in a sharp spine up to 2 mm long; base acute to acuminate; petiole 0.5–1.5 mm long and thick; venation mixed craspedodromous, the midvein impressed above, prominent below, the other veins indistinct. Inflorescence an umbel-like cluster of 2–4 flowers; pedicels 1–2.7 cm long, 0.3–0.5 mm wide; flowers orange to reddish orange, ca. 9 mm long; tepals 15–21, the smallest linear to oblong, ca. 3 mm long, the largest obovate to elliptic, 7–10 mm long; stamens ca. 5 mm long, without lateral appendages, the anther less than ½ the length; pistil 4.5–7 mm long; style 1.5–3 mm long; stigma peltate, ca. 1.5 mm wide; ovules 4–9. Fruit subglobose, 7–10 mm long, terminating in a persistent style ca. 3–4 mm long; seeds 5–9, 3.5–4 mm long. Figures 2K, 3G, 8C, 13C.

Distinguishing features. Style long; stamens without tooth-like appendages; spines 3-parted, up to 18 mm long, slightly recurved; inflorescence an umbel-like cluster of 2–4 flowers; leaves mostly over 3 times as long as wide, the margins entire; flowers orange to reddish orange.

Phenology. Flowering mainly from November to February. Fruiting mainly in January and February.

Distribution and habitat. Endemic to southwestern South America. Found in Chile from Antuco (Región VIII) to Volcán Osorno (Región X) and in Argentina only in western Neuquén and Río Negro. An understory shrub of *Nothofagus* forests.

Common names. Calafate (Rodriguez et al., 1995), michai (M. Muñoz et al., 1981).

Selected specimens. CHILE. **Región VIII:** Bío-Bío, Los Angeles, Antuco, El Canelo (37°20'S, 71°41'W), 650 m, 15 Jan. 1982, *Montero 12178* (CONC-84006). **Región IX:** Malleco, road from Curacautín to Lonquimay over mountain, ca. 3 km after turnoff to road to Volcán Lonquimay (ca. 38°25'S, 71°30'W), ca. 1500 m, 26 Oct. 1993 (fl), *Landrum 8004* (ASU, SGO); road from Victoria to Curacautín, at Puente Collihuanqui, ca. 38 km E of Victoria (ca. 38°22'S, 71°57'W), ca. 800 m, 26 Oct. 1993 (fr), *Landrum 8020* (ASU); Melipeuco, China Muerta (38°42'S, 71°31'W), ca. 1800 m, 23 Jan. 1958 (fl), *Montero 5793* (CONC-84001); Termas de Tolhuaca, 950–1180 m, 12 Mar. 1939 (fl), *Morrison & Wagenknecht 17487* (G, MO, NA). **Región X:** San Juan de la Costa, 500–600 m, 6 Feb. 1958 (fr), *Eyerdam 10610* (F, NY, US); Parque Nacional Puyehue, road to Antillanca, ca. 13.7 km above Park Administration (ca. 40°45'S, 72°20'W), ca. 800 m, 10 Nov. 1993 (fl), *Landrum 8064* (ASU, SGO); Cordillera Pelada, camino a Hueicolla (40°10'S, 73°29'W), 1100 m, 21 Jan. 1964 (st), *Montero 6733* (CONC-84007); Llancacura, Alerzal de Huenchucona (40°18'S, 73°24'W), 10 Jan. 1963 (fr), *Schlegel 4527* (CONC-46742). ARGENTINA. **Neuquén:** al NW del Lago Falkner, cerca del camino, Feb. 1975 (fl), *Cassels s.n.* (SGO); San Carlos de Bariloche, Cerro Tronador, ca. 900 m, 29 Oct. 1983 (fl), *Charpin 18483* (G); Lago Lacar, Pucará, 9 Nov. 1956 (yfr), *Roig & A. Ruiz Leal 1968* (MERL). **Río Negro:** Laguna Frías, 29 Jan. 1975, *Ambrosetti 2331* (MERL-47027); Lago Nahuel Huapi, Puerto Meyer, 8 June 1939 (fr), *Cabrera & Job 207* (NY); camino del Lago Mascardi a Lago Hess, 28 Nov. 1946 (fl), *Teague s.n.* (K); arriba del río Guillermo, 28 Nov. 1946 (fl), *Teague s.n.* (K).

Berberis trigona has more commonly been called *B. linearifolia*, but the first is the older name. It hybridizes with at least *B. darwinii* (*Landrum 8041* and *8046* from near Vilcún) and, perhaps, also with *B. microphylla.*

Berberis lologensis is a hybrid between *B. trigona* and *B. darwinii* (see excluded taxa). I have not seen a type of *B. bidentata* (see excluded taxa), but it seems to be a hybrid between the same species.

20. **Berberis valdiviana** Phil., Linnaea 28: 609. 1856. TYPE: Chile. Dagli pulli, Valdivia, *Philippi s.n.* (holotype, SGO-063359!, = ASU photo!).

Berberis valdiviana var. *gracilifolia* Ahrendt, J. Linn. Soc., Bot. 57: 261. 1961. TYPE: Chile. Valdivia, Malalhue, 650 ft., Sep. 1924 (fl), Jan. 1925 (fr), *Hollermayer (Werdermann) 682* (holotype, K not seen; isotypes, BM!, G!, M!, MO!, = ASU photo!, NY!).

Shrub to ca. 3 m high, glabrous; young twigs reddish brown, soon becoming gray and eventually longitudinally ridged; spines 3-parted, the arms about equal in length, or the central somewhat longer, 1–3.8 cm long, the laterals perpendicular to the central; bracts ovate to lanceolate, 2 to 6 mm long, gray to brown. Leaves elliptic, oblanceolate or less often ovate, occasionally a few trilobed leaves present (leaf-spine intermediates), the blade 1.8–8 cm long, 1–3.4 cm wide, 1.6–4.6 times as long as wide, stiffly coriaceous, drying gray-green to yellow-brown, usually lustrous above, somewhat lighter and not as lustrous below, the margin flat to slightly revolute, entire or with up to 8 small, spine-tipped teeth per side, the teeth 1–2(–4) mm long; apex acute to obtuse, spine-tipped; base acuminate to rounded, gradually merging with petiole or the petiole distinct and up to 7 mm long; venation mixed craspedodromous, the midvein impressed above, prominent below, the secondary veins 4–6 pairs, connected by an equally strong marginal vein 2–3 mm within the margin (a weaker exterior marginal vein sometimes present), the tertiary veins faint to distinct. Inflorescence a raceme 3.5–9 cm long, with 10–30 flowers; pedicels 4–6 mm long, subtended by narrowly triangular, keeled bracts 2–3 mm long; flowers 3–5 mm long, yellow; tepals 14, the innermost obovate, 3–4 mm long; stamens 2–3 mm long, without lateral appendages, the anther ca. 1 mm long; pistil 2–3 mm long, the stigma 1.2–1.5 mm wide; style about half the length; ovules 1–4, basal. Fruit subglobose, ca. 6 mm long, terminating in a style ca. 1 mm long; seeds 1–2(–4?), ca. 4 mm long. Figures 8D, 13D.

Distinguishing features. Style long; stamens without tooth-like appendages; spines 3-parted; inflorescence a many-flowered raceme; leaves mostly elliptic, lustrous above and below, the margins usually entire; flowers yellow.

Phenology. Flowering mainly from September to November. Fruiting mainly from November to January.

Distribution and habitat. Endemic to southern central Chile, from Colchagua (Región VI) to La Unión (Región X). An understory shrub or small tree of *Nothofagus* forests. Often regenerating along roads and in pastures, probably from root sprouts.

Common names. Clen (Rodriguez et al., 1995); espina en cruz (pers. obs.)

Selected specimens. CHILE. **Región VI:** Colchagua, Tanumé (34°12'S, 71°57'W), Nov. 1920 (fl), *Aspillaga s.n.* (CONC-46447); Colchagua, Lolol, Cerro Robles, 650 m, 19 Feb. 1946 (st), *Kausel 1898* (SGO-059728). **Región VII:** Parral, cerca Estación Quella del ramal a Cauquenes en lugar Titinvilo, 3 Nov. 1964 (fr), *Aravena 50L* (SGO). **Región VIII:** Atacalco, la subida del Cerro Castillo (36°53'S, 71°38'W), 960 m, Oct. 1944 (fl), *Heck 6319* (OS); road from Florida to Penco ca. 4 km NW of Florida (ca. 36°47'S, 72°37'W), ca. 230 m, 16 Oct. 1993 (yfr), *Landrum 7936* (ASU); Concepción, Agua de la Gloria (36°49'S, 72°52'W), Sep. 1933 (fl), *Pfister s.n.* (CONC-654); camino de Concepción a Cabrero, Fundo El Queule (36°53'S, 72°56'W), 340 m, 8 Oct. 1986 (fl), *Rodríguez 2156* (CONC-125990). **Región IX:** entre los ríos Toltén y Allipén (39°01'S, 72°29'W), 22 Sep. 1935 (st), *Junge s.n.* (CONC-3821); road from Victoria to Curacautín, ca. 30 km E of Victoria, ca. 5 km E of easternmost road to Selva Oscura (ca. 38°20'S, 72°5'W), ca. 800 m, 26 Oct. 1993 (fl), *Landrum 8010* (ASU, SGO); road from Lautaro to Curacautín, ca. 8–9 km E of Lautaro, vicinity of Estero Ñirca (ca. 38°30'S, 71°29'W), ca. 250 m, 28 Oct. 1993 (yfr), *Landrum 8028* (ASU); Temuco, Cerro Ñielol, ca. 175 m, 3 Oct. 1935 (fl), *Montero 2463* (CONC-84042, OS). **Región X:** Valdivia (fl), *Philippi 534* (G); Malalhue, 1925 (fl), *Werdermann 682* (BM, CAS, G, M, NY); La Unión, Fundo San Antonio, río Lollelhue (40°16'S, 73°04'W), 60 m, Mar. 1967 (fr), *Zollitsch 150* (CONC-38510, M).

Berberis valdiviana is most likely to be confused with *B. chilensis* (see lead 15 of the key for distinguishing characteristics) and *B. litoralis* (see discussion under that species). When specimens lack spines and the leaves have serrate margins, which is common in stump sprouts, *B. valdiviana* can look very similar to *B. negeriana*. However, in *B. valdiviana* the leaves tend to be smaller, and less lustrous beneath, and there are many more flowers in the inflorescence. To date, I have only found specimens of *B. negeriana* near Concepción, whereas *B. valdiviana* occurs from Colchagua to La Unión.

Berberis valdiviana forms a vigorous and attractive hybrid with *Berberis darwinii* (*Landrum 8009* from near Victoria).

EXCLUDED OR UNCERTAIN TAXA

Berberis bidentata Lechler, Berberid. Amer. austral. 11. 1857. TYPE: Chile. Laguna de Maihue, Cordillera de Ranco, *Lechler 3133* (holotype, MA? not seen). A probable hybrid between *B. trigona* and *B. darwinii.* See discussion under *B. trigona.*

Berberis brevifolia Phil. ex Reiche, Anales Univ. Chile 88: 96. 1894. TYPE: Chile. Colchagua, Cáhuil (holotype, SGO!, = ASU photo!). See discussion under *B. microphylla.*

Berberis buxifolia Lam. var. *gracilis* Albov, Revista Mus. La Plata 7: 300. 1896. [Orthographic variant of *gracilior.*]

Berberis copahuensis Job, Notas Prelim. Mus. La Plata, Bot. 16: 146. 1953. TYPE: Argentina. Baños de Copahue, *Kurtz s.n.* (holotype, CORD not seen, = ASU photo!). Hybrid between *B. empetrifolia* and *B. montana*; see discussion under *B. montana.*

Berberis knightii (Lindl.) K. Koch, Dendrologie 1: 413. 1869. *Mahonia knightii* Hort. ex Lindl., J. Hort. Soc. London 5: 20. 1850. TYPE: Unknown. See discussion under *B. darwinii.*

Berberis lologensis Sandwith, Kew Bull. 3: 108. 1928. TYPE: Argentina. Neuquén: Lago Lolog, 20 Feb. 1927 (fr), *Comber 1061* (holotype, K!, = ASU photo!). Hybrid between *B. trigona* and *B. darwini*; see discussion under *B. trigona.*

Berberis morenonis Kuntze, Rev. Gen. Plant. 3(2): 3. 1898. TYPE: Argentina. Patagonia, 50°–

[Continued on page 831]

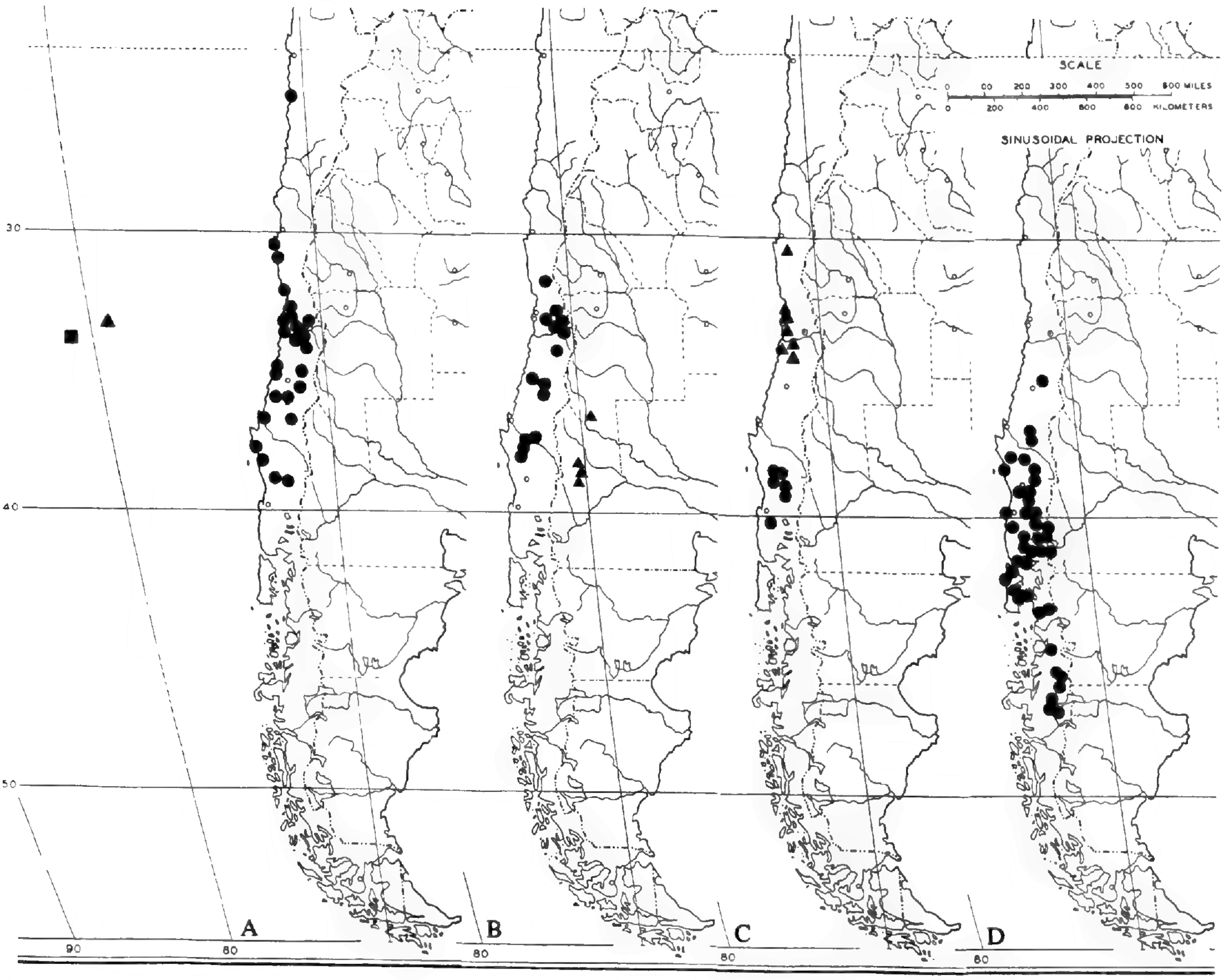

Figure 6. Distribution of selected species of *Berberis*. —A. *B. actinacantha* (dots), *B. corymbosa* (triangle), and *B. masafuerana* (square). —B. *B. chilensis* var. *chilensis* (dots) and *B. comberi* (triangles). —C. *B. chilensis* var. *brachybotria* (triangles) and *B. congestiflora* (dots). —D. *B. darwinii*.

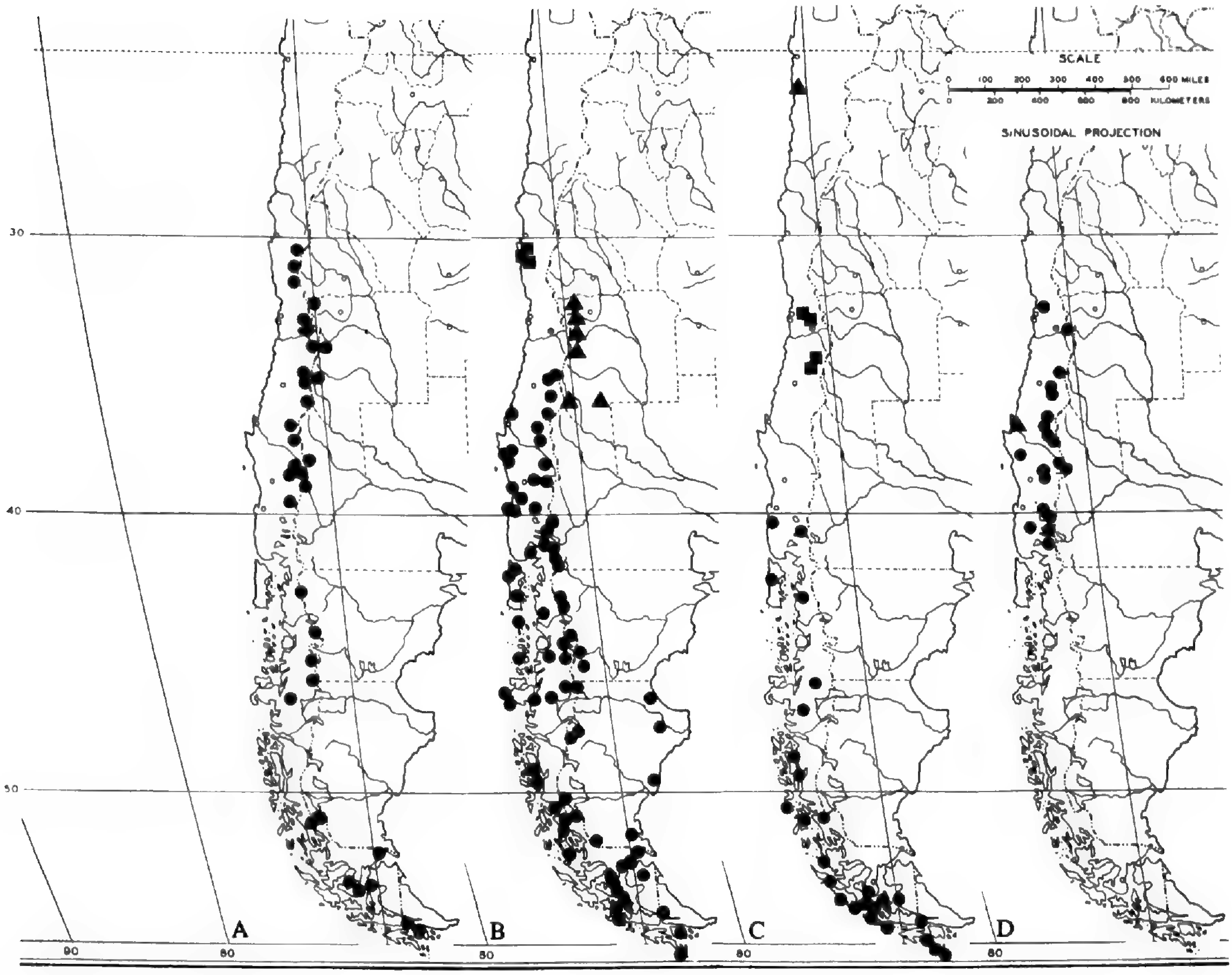

Figure 7. Distribution of selected species of *Berberis*. —A. *B. empetrifolia*.—B. *B. glomerata* (squares), *B. grevilleana* (triangles), and *B. microphylla* (dots). —C. *B. horrida* (squares), *B. ilicifolia* (dots), and *B. litoralis* (triangle). —D. *B. montana* (dots), and *B. negeriana* (triangle).

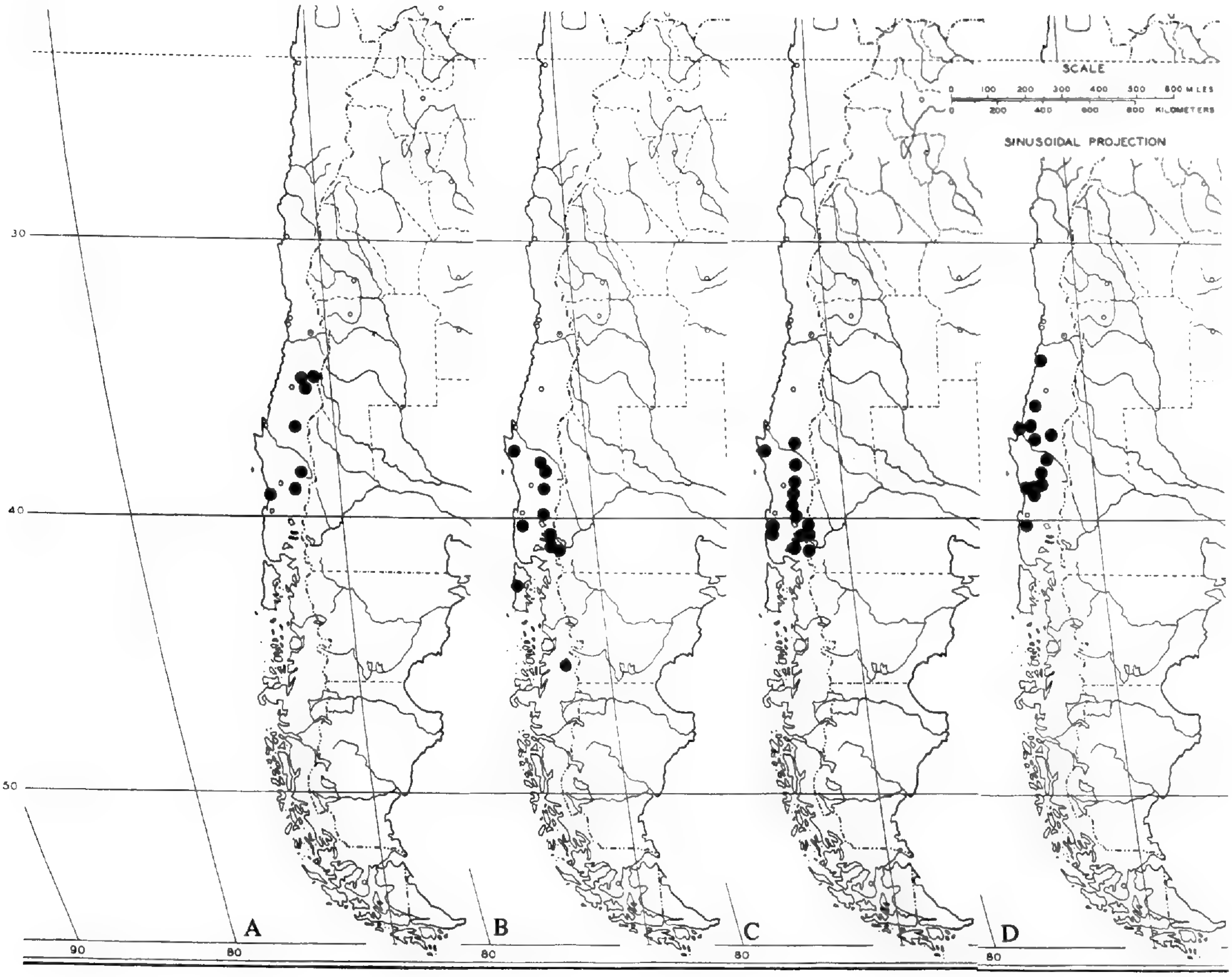

Figure 8. Distribution of selected species of *Berberis*. —A. *B. rotundifolia*. —B. *B. serratodentata*. —C. *B. trigona*. —D. *B. valdiviana*.

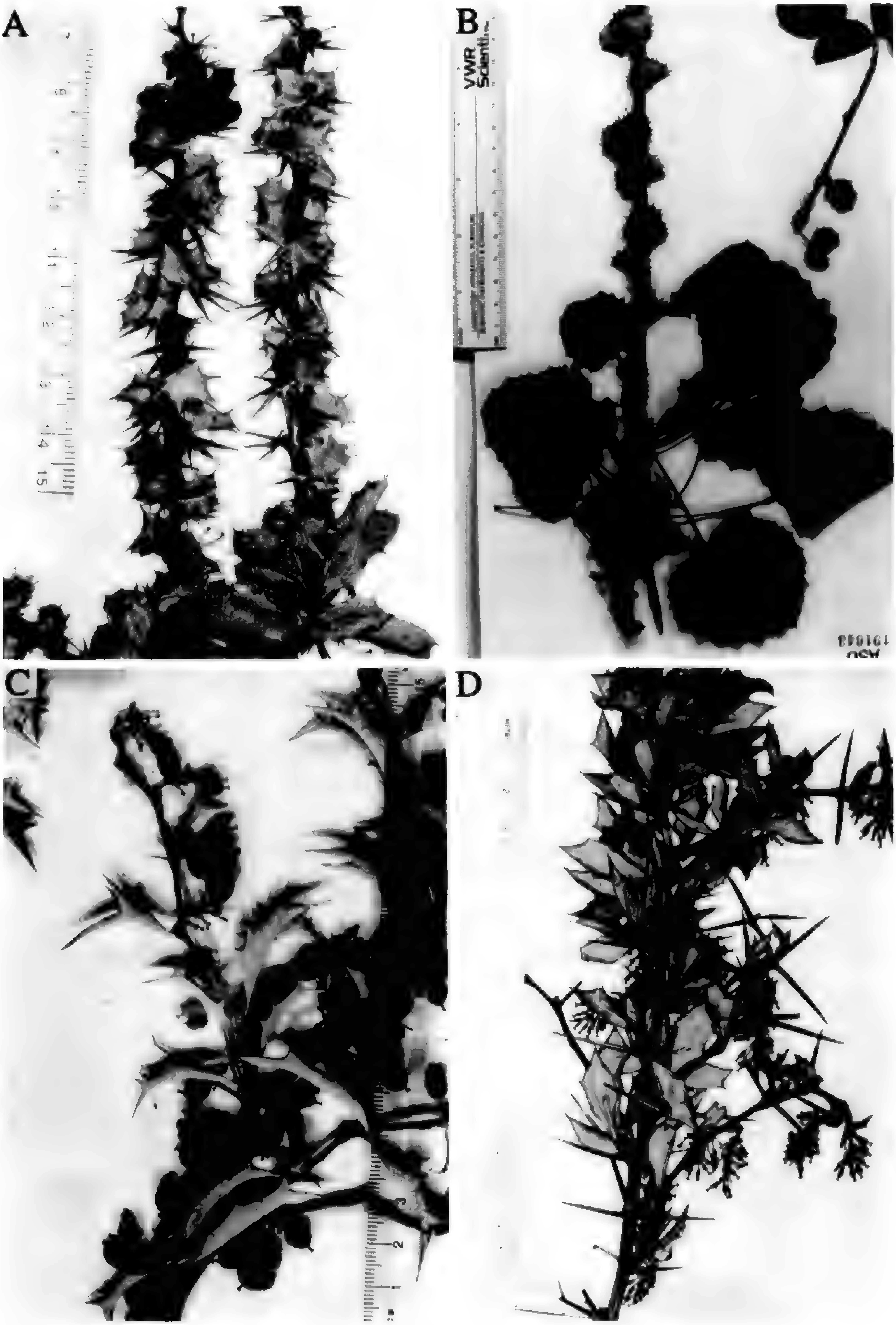

Figure 9. Photos of selected specimens of *Berberis* collected by the author. —A. *B. actinacantha* from northern part of range (*7885*). —B. *B. actinacantha* from southern part of range (*7952*). —C. *B. chilensis* var. *chilensis* (*8492*). —D. *B. chilensis* var. *brachybotria* with immature fruits (*7894*).

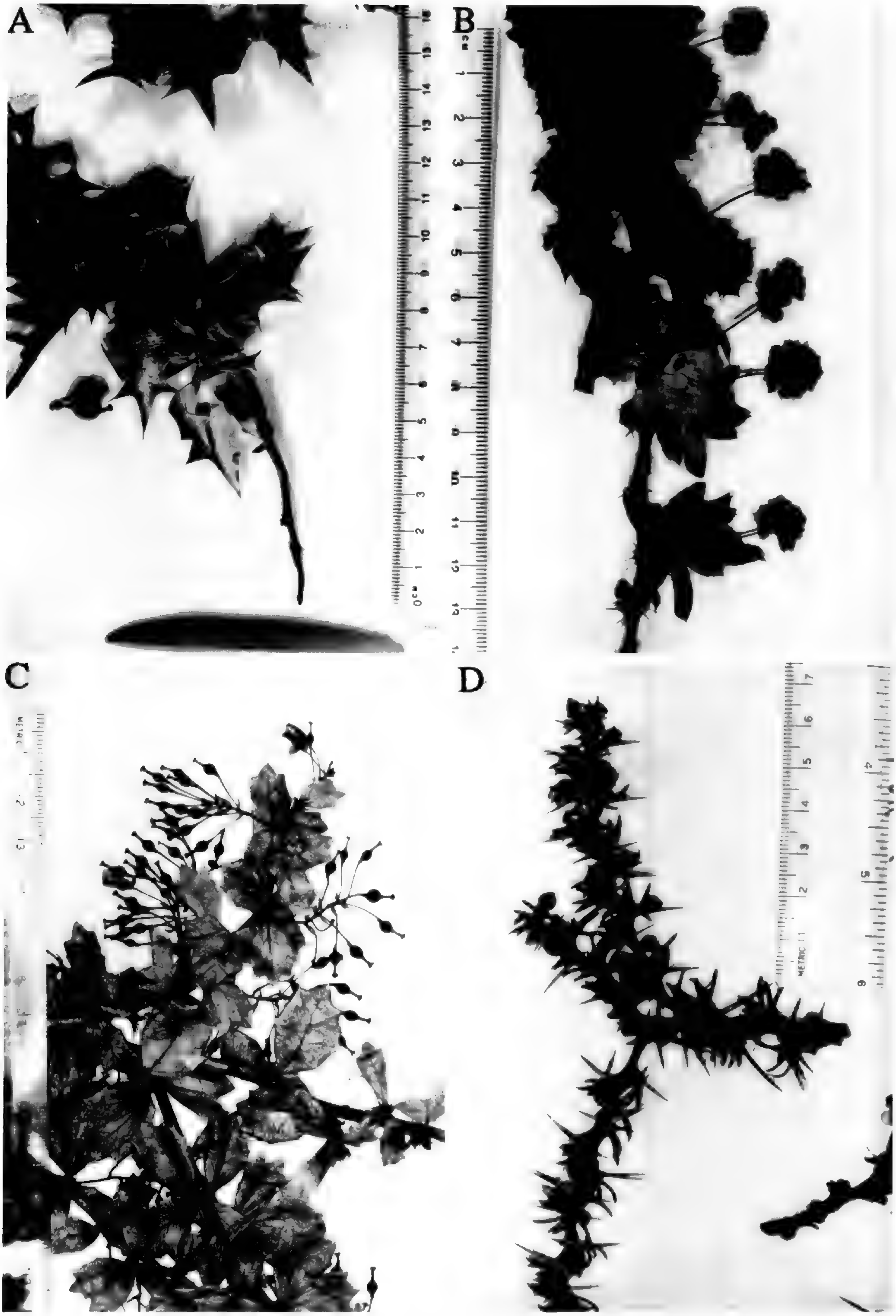

Figure 10. Photos of selected specimens of *Berberis* collected by the author. —A. *B. comberi* (*8379*). —B. *B. congestiflora* (*7988*). —C. *B. darwinii* with immature fruits (*8148*). —D. *B. empetrifolia* (*8344*).

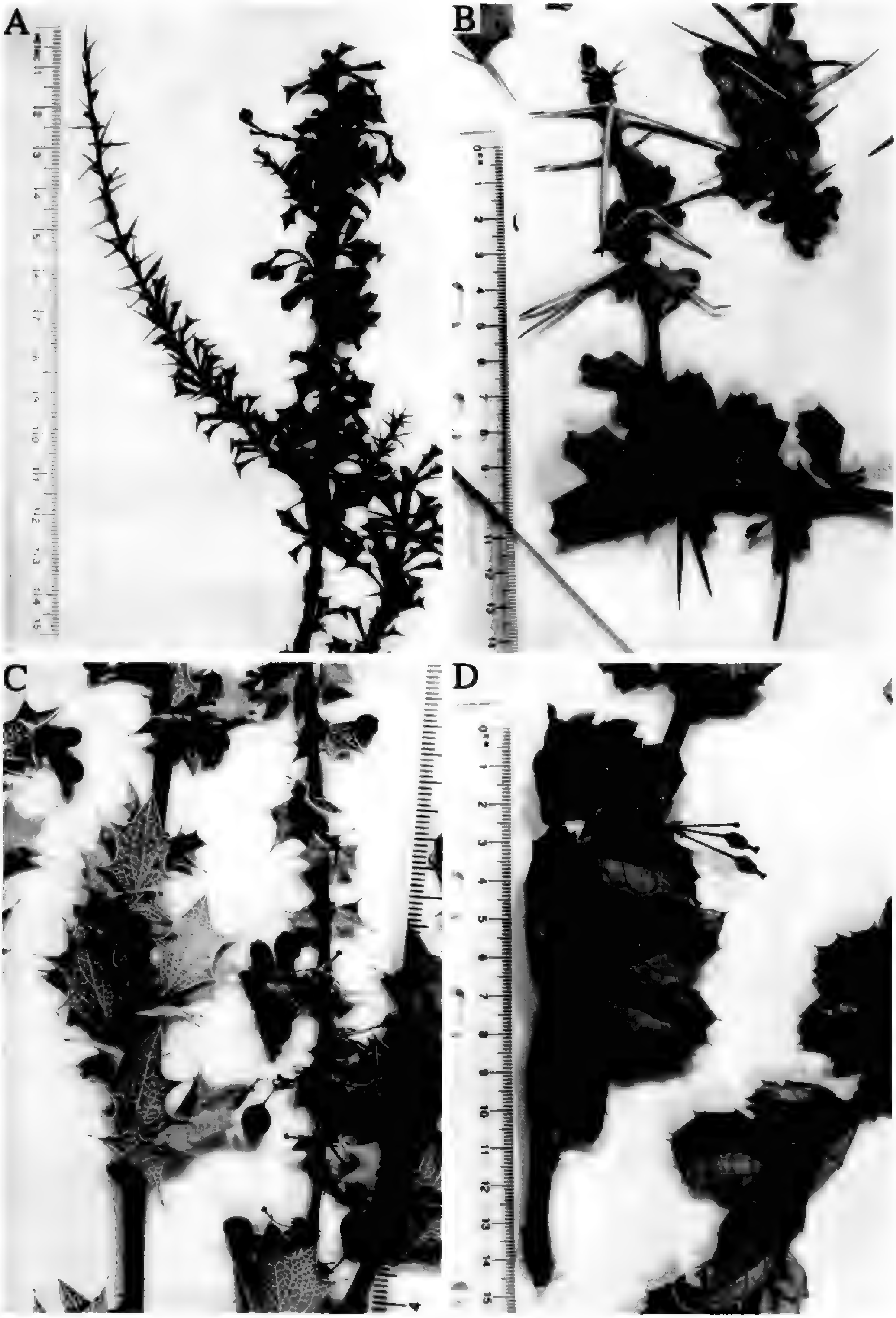

Figure 11. Photos of selected specimens of *Berberis* collected by the author. —A. *B. glomerata* (*7525*). —B. *B. grevilleana* (*8332*). —C. *B. horrida* (*7903*). —D. *B. ilicifolia* with immature fruits (*8394*).

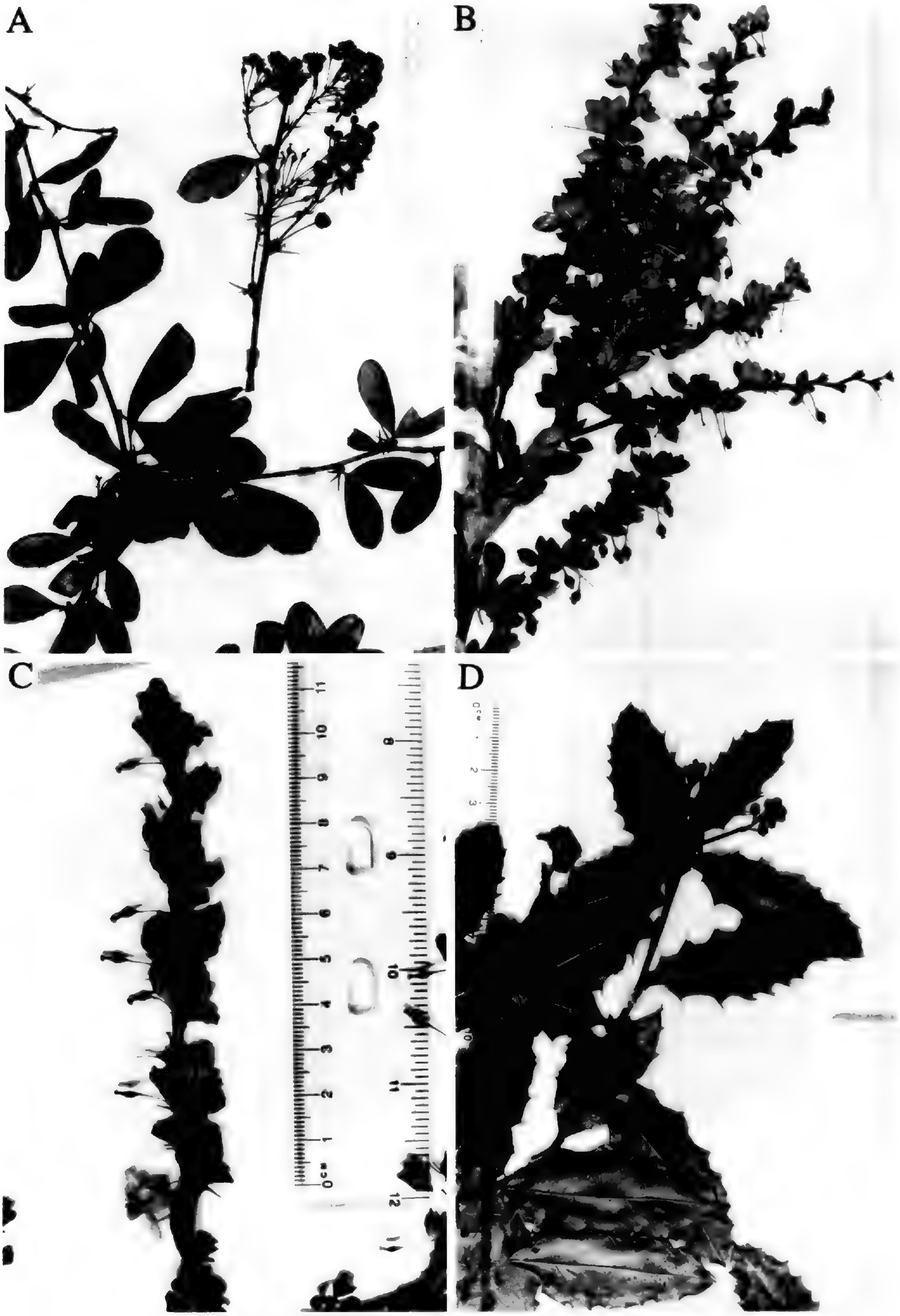

Figure 12. Photos of selected specimens of *Berberis* collected by the author or C. M. Taylor. —A. *B. litoralis* (*Landrum 7492*). —B. *B. microphylla* (*Landrum 7607*). —C. *B. montana* with immature fruits (*Taylor 10313*). —D. *B. negeriana* with buds (*Landrum 7436*).

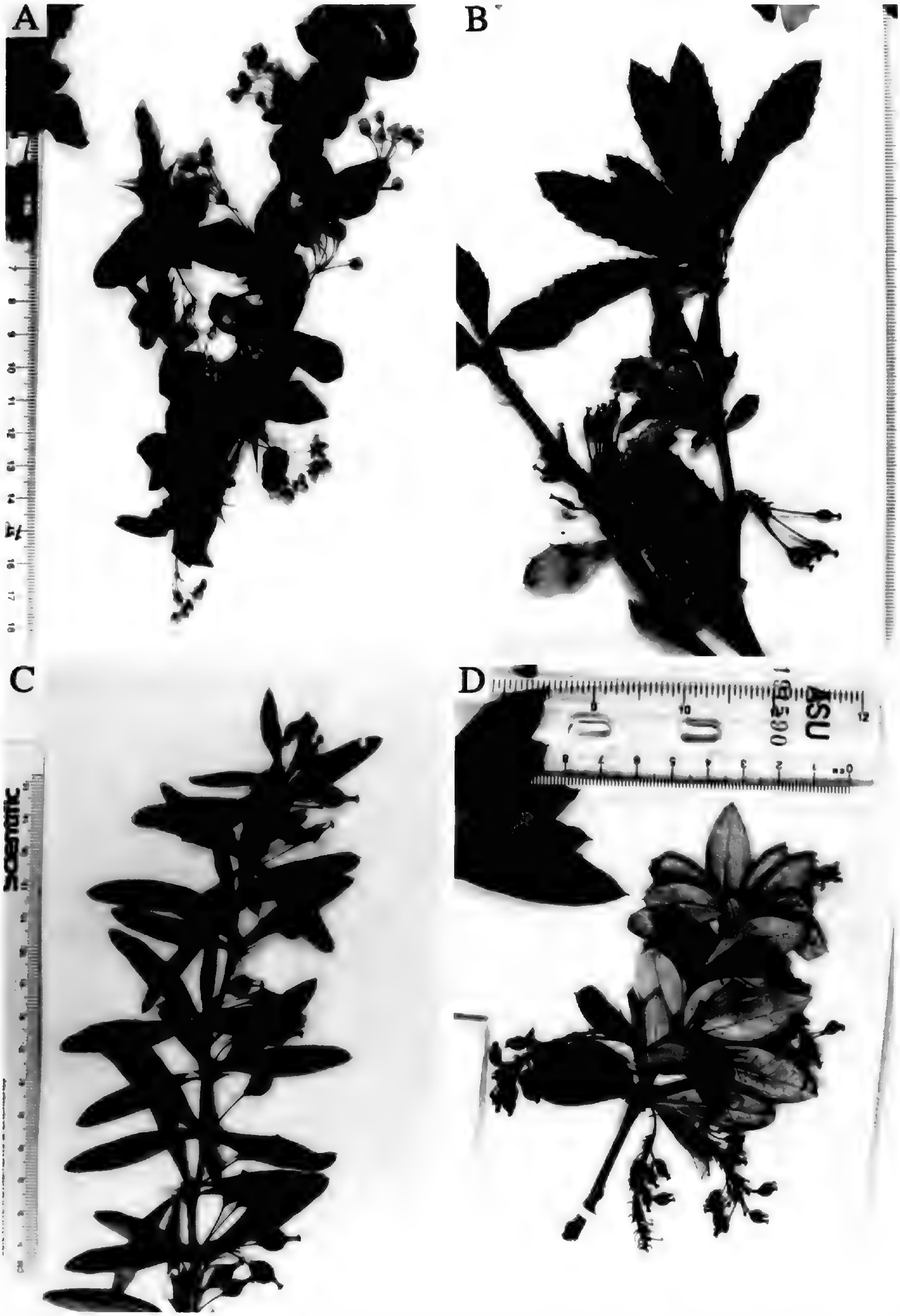

Figure 13. Photos of selected specimens of *Berberis* collected by the author. —A. *B. rotundifolia* (*7951*). —B. *B. serratodentata* (*8111*). —C. *B. trigona* (*8020*). —D. *B. valdiviana* (*7931*).

53°, *Moreno 768*. Possible type, LP!, = ASU photo! [seedlings only].

Berberis pseudoilicifolia Skottsb., Kongl. Svenska Vetenskapsakad. Handl. 56(5): 226. 1914. TYPE: Chile. Cordillera Pelada, *Philippi s.n.* (syntype, B lost; possible isosyntypes, G!, = ASU photo!, SGO-039418!, SGO-063349!); Volcán Osorno, *Reiche s.n.* (syntype, B lost). Hybrid between *B. ilicifolia* and *B. serratodentata*; see discussion under *B. ilicifolia*.

Berberis setigrifolia Ahrendt, J. Linn. Soc., Bot. 57: 237. 1961. TYPE: Chile [probably in error]. *Pearce s.n.* (holotype, K!, = ASU photo!). [Apparently a species of Peru or Bolivia.]

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List of Recognized Taxa

1. *B. actinacantha* Mart.
2. *B. chilensis* Gillies ex Hook.
   2a. *B. chilensis* var. *chilensis*
   2b. *B. chilensis* var. *brachybotria* (Gay) Landrum
3. *B. comberi* Sprague & Sandwith
4. *B. congestiflora* Gay
5. *B. corymbosa* Hook. & Arn.
6. *B. darwinii* Hook.
7. *B. empetrifolia* Lam.
8. *B. glomerata* Hook. & Arn.
9. *B. grevilleana* Gillies ex Hook. & Arn.
10. *B. horrida* Gay
11. *B. ilicifolia* L. f.
12. *B. litoralis* Phil.
13. *B. masafuerana* Skottsb.
14. *B. microphylla* G. Forst.
15. *B. montana* Gay
16. *B. negeriana* Tischler
17. *B. rotundifolia* Poepp. & Endl.
18. *B. serratodentata* Lechler
19. *B. trigona* Kunze ex Poepp. & Endl.
20. *B. valdiviana* Phil.

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PHYLOGENY OF POACEAE INFERRED FROM *mat*K SEQUENCES[1]

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ABSTRACT

Complete sequences of the plastid gene *mat*K were determined for 62 species of Poaceae from 60 genera, 26 tribes, and nine subfamilies to infer phylogenetic relationships. *Restio tetraphyllus* (Restionaceae) and *Joinvillea ascendens* (Joinvilleaceae) were used as outgroups. Cladistic analysis using PAUP yielded 39 most parsimonious trees with several well-supported major lineages. The strict consensus tree shows *Streptochaeta* and *Anomochloa* forming the two most basal lineages in grasses, followed by *Pharus* being sister to the remaining species. The other grasses divide into three clades: (1) subfamily Bambusoideae (excluding *Brachyelytrum*) plus Pooideae; (2) Oryzoideae; and (3) subfamilies Panicoideae, Arundinoideae, Centothecoideae, and Chloridoideae (termed PACC). Except for Arundinoideae, monophyly of each PACC subfamily is generally well supported; however, relationships among subfamilies are unresolved or weakly supported. Results obtained using *mat*K sequences are largely consistent with other phylogenies based on molecular and structural data, particularly in that relationships among subfamilies remain unclear.

Interest in the evolution of grasses began early in this century with proposed hypotheses based on assessment of existing knowledge of the family (e.g., Bew, 1929; Hubbard, 1948; Stebbins, 1956, 1982; Prat, 1960; Clayton, 1981; Tsvelev, 1983). Empirical approaches to phylogenetic reconstruction of the Poaceae followed those initial hypotheses, starting with cladistic analyses of morphological and anatomical characters (Baum, 1987; Kellogg & Campbell, 1987; Kellogg & Watson, 1993). Recently, molecular data have provided the grounds for phylogenetic hypotheses in grasses at the subfamilial and tribal levels. These studies were based on information from chloroplast DNA (cpDNA) restriction sites and DNA sequencing of the *rbc*L, *ndh*F, *rps*4, *rpo*C2, *mat*K, nuclear ribosomal DNA (nrDNA) 18S and 26S, phytochrome, and granule-bound starch synthase genes, as well as the noncoding nrDNA Internal Transcribed Spacer (ITS) region (Hamby & Zimmer, 1988; Doebley et al., 1990; Davis & Soreng, 1993; Cummings et al., 1994; Hsiao et al., 1994; Nadot et al., 1994; Barker et al., 1995, 1999; Clark et al., 1995; Duvall & Morton, 1996; Liang & Hilu, 1996; Mathews & Sharrock, 1996; Mason-Gamer et al., 1998; Soreng & Davis, 1998; Hsiao et al., 1999).

Although these studies have refined our understanding of grass evolution at the subfamilial level and, to a certain degree, at the tribal level, major questions remain to be resolved. Although the basal positions of Anomochloeae, Phareae, and Streptochaeteae have been established, their relative placement and taxonomic status are debatable. Uncertainties also exist concerning the phylogenetic affinities among subfamilies and the taxonomic rank of others such as the Oryzoideae.

In this study, the chloroplast *mat*K gene was chosen to address these and other questions pertaining to higher-level grass systematics. The *mat*K gene is ~1515 base pairs (bp) in most angiosperms, located within the *trn*K intron, and functionally may be involved in splicing group II introns (Neuhaus & Link, 1987; Ems et al., 1995; Hilu & Alice, in press a). The effective application of this gene in plant systematics (e.g., Johnson & Soltis, 1994, 1995; Hilu & Liang, 1997; Kron, 1997) and grasses (Liang & Hilu, 1996; Hilu & Alice, in press a, b) has already been documented. *mat*K is known to have relatively high rates of substitution compared to other chloroplast genes (see Olmstead & Palmer, 1994; Johnson & Soltis, 1995). This gene exhibits a relatively high proportion of transversions, and the 3′ region of its open reading frame (ORF) has

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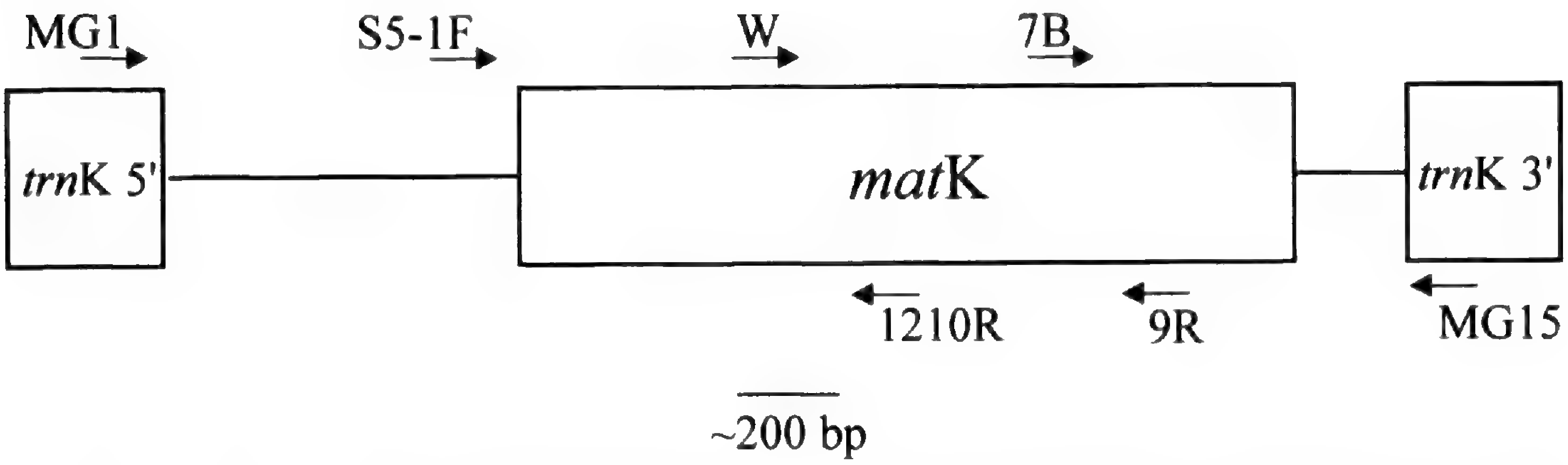

Figure 1. Diagram of the *trn*K region including the *mat*K gene. PCR and sequencing primers are indicated with arrows. Primer sequences are: MG1 = CTACTGCAGAACTAGTCGGATGGAGTAGAT; MG15 = ATCTGGGTTGCTAACTCAATG; S5–1F = ACCCTGTTCTGACCATATTG; 1210R = GTAGTTGAGAAAGAATCGC; W = TACCCTATCCTATCCAT; 7B = GATTTATCA/GGATTGGGAT; and 9R = TACGAGCTAAAGTTCTAGC. *trn*K exons and primers are not drawn to scale.

been demonstrated to be quite useful in resolving subfamilial, and to a certain degree, tribal relationships in Poaceae (Liang & Hilu, 1996).

MATERIALS AND METHODS

PLANT SAMPLES

We sequenced the entire *mat*K gene of 62 Poaceae species representing 60 genera, 26 tribes, and nine subfamilies (Appendix 1). Subfamilial and tribal classification generally follows Clayton and Renvoize (1986). ***Restio tetraphyllus*** (Restionaceae) and ***Joinvillea ascendens*** (Joinvilleaceae) were used as outgroups because recent studies have demonstrated that these two families are closely related to grasses (Doyle et al., 1992; Kellogg & Linder, 1995; Soreng & Davis, 1998, and references therein).

DNA ISOLATION, POLYMERASE CHAIN REACTION (PCR) AMPLIFICATION, AND SEQUENCING

Leaf tissue was harvested from either greenhouse-grown plants, field-collected plants, or herbarium specimens. Total cellular DNA was isolated following M'Ribu and Hilu (1996). Because the *mat*K gene is part of the *trn*K intron, we used two primers (MG1 or *trn*K3914 and MG15), located in the *trn*K 5′ and 3′ exons, respectively, for PCR amplification. For sequencing, *trn*K region PCR products were electrophoresed in 0.8% agarose gels and DNA fragments of appropriate size excised and purified using a QIAquick gel extraction kit (QIAGEN, Inc., Valencia, California). For each accession, the entire *mat*K coding region was sequenced, utilizing three to six primers (Fig. 1). Sequencing reactions were carried out using two different ABI Prism™ Dye Terminator Cycle Sequencing Kits (Perkin Elmer, Norwalk, Connecticut). Most samples were electrophoresed in an ABI 373A automated DNA sequencer with a stretch gel or in an ABI 310 Genetic Analyzer (Applied Biosystems, Inc., Foster City, California). Resulting chromatograms were manually edited using Sequence Navigator 1.0 software (Applied Biosystems Inc., Foster City, California). Sequences were deposited in GenBank (see Appendix 1).

SEQUENCE ALIGNMENT AND PHYLOGENETIC ANALYSIS

Alignment of complete *mat*K sequences was unambiguous and, thus, done manually. Twelve gaps varying in length from 1 to 9 bp were required to align sequences (Table 1). Non-random structure in the data was tested by using the random trees option in PAUP*4.0b2a (Swofford, 1998). The g_1 value for the distribution of tree lengths of 100,000 random trees was compared using the critical value (at $\alpha = 0.05$) for 500 variable characters and 25 taxa. Beyond 15 taxa, g_1 critical values change only slightly, allowing them to be used in a conservative test with more taxa (Hillis & Huelsenbeck, 1992).

Phylogenies were generated using Fitch parsimony as implemented in PAUP, employing heuristic searches consisting of 1000 replicates of random stepwise addition of taxa with MULPARS on and tree-bisection-reconnection (TBR) branch swapping. Gaps were treated as missing data. Sets of equally parsimonious trees were summarized by strict consensus. Parsimony-informative gaps are mapped onto the strict consensus cladogram (Fig. 2). Because the transition/transversion ratio (ns/nv) in this *mat*K data set is 1.33 : 1.0, all characters were equally weighted. The ns/nv was calculated with MacClade 3.01 (Maddison & Maddison, 1992) and based on the strict consensus tree. To explore the effects of positional weighting, third positions of codons were downweighted to one-half that of

Table 1. List of 12 gaps required for alignment of *mat*K sequences of the outgroups *Restio tetraphyllus* and *Joinvillea ascendens*, and 62 Poaceae species. Gap codes (a–l) are used in the text and Figure 2. Each gap was determined to be an insertion (I) or a deletion (D) based on the strict consensus phylogeny (Fig. 2). Position (5′ → 3′) is based on the overall number of aligned nucleotides (1576). * indicates parsimony-informative indels.

Code	Taxa	Gap	Length (bp)	Position
a	*Pharus*	I	6	4–9
*b	All Poaceae	D	9	127–135
*c	*Leymus, Triticum*	I	3	154–156
d	*Joinvillea*, all Poaceae	I	3	163–165
e	*Echinochloa*	I	3	166–168
f	*Lithachne*	D	3	283–285
g	*Zizania*	I	6	829–834
*h	*Hyparrhenia, Sorghum*	I	6	1471–1476
i	*Ehrharta*	D	1	1552
*j	All Poaceae except *Anomochloa, Streptochaeta*	D	1	1559
k	*Restio*	D	3	1561–1563
*l	PACC	I	6	1564–1569

first and second positions. Decay indices (Bremer, 1988; Donoghue et al., 1992) and bootstrap values (Felsenstein, 1985), based on 100 replicates, were calculated as measures of support for individual clades. Decay analyses were performed with AutoDecay (Eriksson & Wikstrom, 1996), using the reverse constraint option in PAUP. The data set was also analyzed with a Neighbor-Joining (NJ) approach utilizing Jukes-Cantor (1969) and Kimura 2-parameter (1980) distance estimates.

RESULTS

*MAT*K LENGTH, GC CONTENT, SEQUENCE DIVERGENCE, AND NUCLEOTIDE SITE VARIATION

The *mat*K ORF in the species examined ranges in length from 1521 bp (*Ehrharta*) to 1548 bp (*Hyparrhenia* and *Sorghum*). However, most species have an ORF of 1536–1542 bp. Mean guanine + cytosine (G + C) content is ~32%. Pairwise divergence of sequences ranges from 7.3 to 22.3% between the outgroups and Poaceae and 0.46 to 11.9% within Poaceae. Of the overall 1576 aligned characters, 836 (53.0%) are variable and 520 (33.0%) are parsimony informative. In Poaceae 764 (48.8%) characters are variable and 473 (30.0%) are parsimony informative. The first, second, and third positions of codons comprise 30.7, 25.6, and 43.7% of the variable sites, respectively, and account for 28.5, 23.1, and 48.4% of the parsimony-informative sites.

PHYLOGENY OF POACEAE

Evidence of non-random structure in the Poaceae *mat*K data set is significant ($P < 0.01$) based on the g_1 value (−0.376). Cladistic analysis with gaps coded as missing data yielded 39 equally parsimonious trees 2163 steps in length (strict consensus in Fig. 2). The Consistency Index (CI) and Retention Index (RI), excluding uninformative characters, are 0.453 and 0.700, respectively. Based on the polynomial regression of Sanderson and Donoghue (1989), the estimated CI for 64 taxa is 0.364; therefore, levels of homoplasy in our data set are lower than predicted. Their regression is limited to 60 or fewer taxa, and expected CIs for 44 and 60 taxa are virtually identical (0.344 and 0.347, respectively). Thus, the expected CI value for 64 taxa according to Sanderson and Donoghue's (1989) regression may be inflated.

The strict consensus tree (Fig. 2) shows *Streptochaeta* and *Anomochloa* to be the two most basal lineages, followed by *Pharus* as sister to the other grasses. The remaining species assort into three well-supported lineages. One clade includes members of Bambusoideae and Pooideae (including *Brachyelytrum*; Bambusoideae), another contains Oryzoideae (including *Ehrharta*, Ehrharteae), and a third clade comprises subfamilies Panicoideae, Arundinoideae, Centothecoideae, and Chloridoideae (PACC). Among the three clades, the PACC group has the greatest support with a bootstrap value of 100% and a decay index of 13.

The bambusoid-pooid clade is well supported (88% bootstrap and decay of 4) and divided into two lineages: one corresponding to the Bambusoideae and the other to *Brachyelytrum* + *Nardus* and other Pooideae. Within the Bambusoideae, *Sasa* and *Phyllostachys* (both Bambuseae) form a strongly supported subclade (100% bootstrap) as do *Par-*

iana (Parianeae) and *Lithachne* + *Olyra* (both Olyreae). However, *Chusquea* (Bambuseae) emerges as an unresolved lineage. *Brachyelytrum* (Bambusoideae, Brachyelytreae; sensu Clayton & Renvoize, 1986) and *Nardus* (Pooideae; Nardeae) form a clade that is sister to the remaining Pooideae; this clade is supported with an 81% bootstrap value and a decay index of 3. The other pooids appear in a trichotomy including: *Stipa* + *Nassella* (Stipeae); *Melica* (Meliceae); and a large, well-supported clade comprising Bromeae (*Bromus*) + Triticeae (*Hordeum*, *Leymus*, and *Triticum*) in one subclade and Poeae (*Poa* and *Vulpia*) + Aveneae (*Avena* and *Phalaris*) in another subclade. The positions of *Briza* (Poeae) and *Phleum* (Aveneae) are unusual in that *Briza* clusters with the Aveneae and *Phleum* with the Poeae. Subfamily Oryzoideae appears monophyletic (100% bootstrap and decay 10) with *Ehrharta* sister to *Oryza* + *Zizania*. The Oryzoideae lie sister to the PACC clade, although bootstrap (<50%) and decay (1) support is low.

In a strongly supported PACC clade, *Aristida* appears basal, but bootstrap and decay support is low (Fig. 2). Following this group are four unresolved lineages: (1) *Arundo*, (2) *Phragmites* + *Molinia*, (3) subfamilies Centothecoideae and Panicoideae, and (4) *Danthonia*, *Centropodia*, + subfamily Chloridoideae. Monophyly of the Centothecoideae is not well supported (74% bootstrap and decay of 1), yet support for the *Zeugites-Lophatherum-Orthoclada* subclade is very strong (bootstrap value of 100% with a decay index of 15). The Panicoideae do not appear monophyletic because *Loudetiopsis* (Arundinelleae) appears as an unresolved lineage separate from the Centothecoideae and Panicoideae. Aside from *Loudetiopsis*, the panicoid grasses are strongly supported with a bootstrap value of 95% and a decay index of 4. The Panicoideae divide into two subclades: (1) Paniceae (*Digitaria*, *Panicum*, and *Echinochloa*); and (2) the apparently paraphyletic Andropogoneae (*Zea*, *Sorghum*, *Hyparrhenia*, and *Andropogon*), with *Tristachya* (Arundinelleae) sister to the latter three genera. Support for the monophyly of, and relationships among, the Centothecoideae, Panicoideae, and *Loudetiopsis* is low.

The association of *Danthonia* and *Centropodia* (both Arundinoideae) with subfamily Chloridoideae has reasonable support (bootstrap value of 62% and a decay index of 2) based on *mat*K data. The Chloridoideae are very strongly supported (100% bootstrap and decay of 10) as a monophyletic lineage. Within the chloridoid clade are three well-defined subclades, including *Uniola*, *Pappophorum*, and *Eragrostis* as sister to the other species, *Sporobolus* + *Zoysia*, and a third subclade containing the remaining members of the Chlorideae, Eragrostideae, and Orcuttieae. The only well-supported structure within this latter group is a clade including *Astrebla*, *Chloris*, and *Microchloa* (97% bootstrap and decay 5).

When third positions of codons are downweighted (tree not shown) there is a general loss of resolution among the Arundinoideae taxa at the base of the PACC clade, *Loudetiopsis* emerges unresolved and separate from the centothecoid-panicoid clade, and the Oryzoideae occupy an intermediate position between the Bambusoideae-Pooideae clade and PACC. The NJ analysis based on Jukes-Cantor and Kimura 2-parameter distances yielded trees identical in topology to each other (Fig. 3) and that are largely consistent with the parsimony phylogeny (Fig. 2). Most differences are matters of increased resolution, such as the relationships among PACC subfamilies, and the positions of *Chusquea* and *Melica*. Topological disagreement does exist concerning the positions of *Orcuttia* and *Tristachya*. In the parsimony tree *Orcuttia* is weakly supported (bootstrap <50% and decay 2) as sister to *Bouteloua*; however, in the NJ tree *Orcuttia* clusters with *Kengia*. The difference in the position of *Tristachya* between the parsimony and NJ analyses is minor, involving only a switch with the adjacent *Sorghum* concerning the sister relationship to *Andropogon* + *Hyparrhenia*.

INSERTIONS AND DELETIONS (INDELS) IN *MATK*

The incorporation of 12 gaps was necessary to align the *mat*K sequences of *Restio*, *Joinvillea*, and Poaceae. From the strict consensus tree (gaps coded as missing data), seven insertions and four deletions were determined (Table 1). Another 3-bp gap (k) in *Restio* was identified as a deletion based on a broader sampling of *mat*K sequences (Hilu & Alice, in press a). Five of these indels are parsimony-informative (three insertions and two deletions), of which four are synapomorphic. These synapomorphic indels include the 9-bp deletion (b) uniting the Poaceae, the 1-bp deletion (j) distinguishing *Streptochaeta* and *Anomochloa* from all other grasses, the 6-bp insertion (l) characterizing the PACC clade, and the 3-bp insertion (c) present in *Leymus* and *Triticum*. The 6-bp insertion (h) found in *Hyparrhenia* and *Sorghum* is homoplasious. The two indels that are not a multiple of three (i and j; both are single base deletions) occur near the 3′ end of the *mat*K gene and, thus, do not have a major impact on protein composition (Hilu & Alice, in press a). Among the remaining indels, six (a–f) are located within the first 285 nucleotide sites of the 5′ region, one (g) is found at sites 829–834, and three indels (h, k, and l) occur within ~100 sites of the 3′ end of the gene.

DISCUSSION

Analyses of the *mat*K sequences for the 62 grass species demonstrate again the high rate of substitution in this gene. The 764 (48.8%) variable and 473 (30.0%) parsimony-informative positions contribute a considerable number of characters for resolving the phylogeny of the Poaceae. This data set is considerably larger than the one used in the exploratory *mat*K study of Liang and Hilu (1996) in which 17 species were analyzed with 583 nucleotides, of which 87 were parsimony-informative. The overall ns/nv is 1.33 for the whole *mat*K gene. This ns/nv ratio is lower than the 1.79 value obtained by Liang and Hilu (1996) from the 3′ region, but is in line with the 1.01 ns/nv ratio calculated by Hilu and Liang (1997) for the whole *mat*K gene of various plant taxa. The relatively large number of transversion mutations detected in the whole *mat*K gene of Poaceae appears to be a reflection of differential rates of transversion mutations in different sectors of the gene (K. Hilu, unpublished data).

BASAL LINEAGES IN POACEAE

The Bambusoideae were traditionally considered the most ancestral group of grasses, but the presence of derived anatomical, vegetative, and some reproductive characters led Soderstrom (1981) to state that the Bambusoideae are a specialized group. Soderstrom (1981) also stated that among Bambusoideae the herbaceous *Streptochaeta* has long been regarded as the most primitive grass. Kellogg and Campbell (1987) raised the possibility of a most basal position for the "herbaceous bambusoids," while Kellogg and Watson (1993) maintained that the Bambusoideae cannot be both basal and monophyletic.

Using data from *ndh*F sequences and cpDNA restriction sites alone or in combination with structural (anatomy, gross morphology, physiology, and chloroplast genome structural mutations) characters, *Streptochaeta* + *Anomochloa*, and *Pharus* (traditionally considered as herbaceous bamboos) emerged as basal lineages with *Pharus* sister to other grasses (Clark et al., 1995; Soreng & Davis, 1998). Duvall and Morton (1996) also cited support for a basal position of *Anomochloa* based on *rbc*L sequences (*Streptochaeta* and *Pharus* were not sampled). Additionally, the ITS study by Hsiao et al. (1999) supports the basal positions of *Streptochaeta* and *Pharus* (*Anomochloa* was not sampled). Clark and Judziewicz (1996) placed *Anomochloa* (Anomochloeae) and *Streptochaeta* (Streptochaeteae) in subfamily Anomochlooideae and established subfamily Pharoideae to encompass the Phareae.

Although this study shows *Streptochaeta* as the most basal genus in Poaceae, it does not support the monophyly of *Anomochloa* and *Streptochaeta* as shown by Clark et al. (1995) and in Soreng and Davis's (1998) molecular and combined analyses. Cladistic analysis of 42 structural characters is consistent with our *mat*K results (Soreng & Davis, 1998). Support for the separation of these two genera as distinct lineages based on *mat*K sequences is reasonable (bootstrap value of 78% and a decay index of 3) and, therefore, these data argue against monophyly of the Anomochlooideae sensu Clark and Judziewicz (1996). Clark and Judziewicz asserted that it is not easy to find anatomical and morphological synapomorphies to define this clade. The position of *Pharus* in the *mat*K phylogeny is in agreement with all studies that have included this taxon. However, in Soreng and Davis's (1998) analysis of structural characters, *Pharus* was unresolved with *Eremitis* and these appear as sister to other grasses. *Pharus* also appeared distinct from all 215 grass genera (including the Bambusoideae) in the numerical study of Hilu and Wright (1982) that was based on 85 structural characters.

DEEP BIFURCATION IN GRASS PHYLOGENY

When *Streptochaeta*, *Anomochloa*, and *Pharus* are excluded from consideration, a split of grasses into two lineages is evident, yet the composition of the groups varied (Davis & Soreng, 1993; Cummings et al., 1994; Clark et al., 1995). The phylogeny based on cpDNA restriction sites (Davis & Soreng, 1993) depicted two lineages, one corresponding to the Pooideae and the other including all remaining grass taxa. The alliance of the Bambusoideae-Oryzoideae clade with the PACC group in the second major lineage was unstable, and the overall topology of the tree changed considerably after the exclusion of one restriction site (Davis & Soreng, 1993, figs. 2, 3). In a subsequent cpDNA and structural data study, a bifurcation was not evident (Soreng & Davis, 1998). Cummings et al. (1994) reported a phylogeny based on the *rpo*C2 gene, showing two major grass lineages: (1) Pooideae + *Zea* (Panicoideae) and (2) Oryzoideae-Panicoideae-Arundinoideae-Chloridoideae. The tree was rooted with spinach and tobacco, two very distant taxa.

Clark et al. (1995) resolved a bifurcation in the family following *Streptochaeta* + *Anomochloa* and

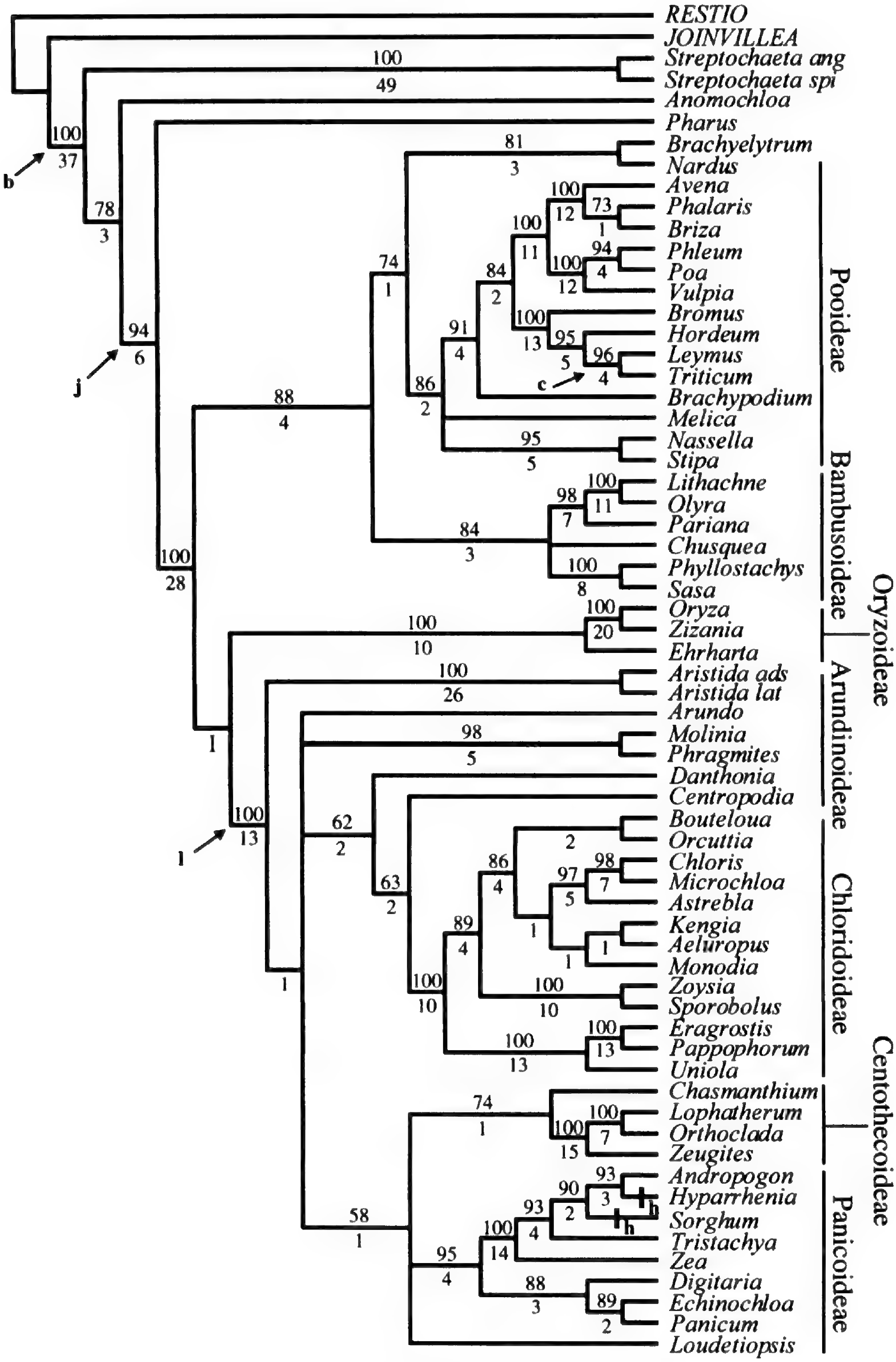

Figure 2. Strict consensus of 39 equally parsimonious trees including 62 Poaceae species and the two outgroups *Restio tetraphyllus* and *Joinvillea ascendens* (shown in uppercase). *Aristida ads* = *A. adscensionis*, *Aristida lat* = *A. latifolia*, *Streptochaeta ang* = *S. angustifolia*, and *Streptochaeta spi* = *S. spicata*. Parsimony-informative indels are indicated with bold, lowercase letters: b = 9-bp deletion, c = 3-bp insertion, h = 6-bp insertion, j = 1-bp deletion, and l = 6-bp insertion (see Table 1). For indels, arrows symbolize synapomorphies and bars indicate autapomorphies. Numbers above branches are bootstrap values > 50% and numbers below branches are decay indices.

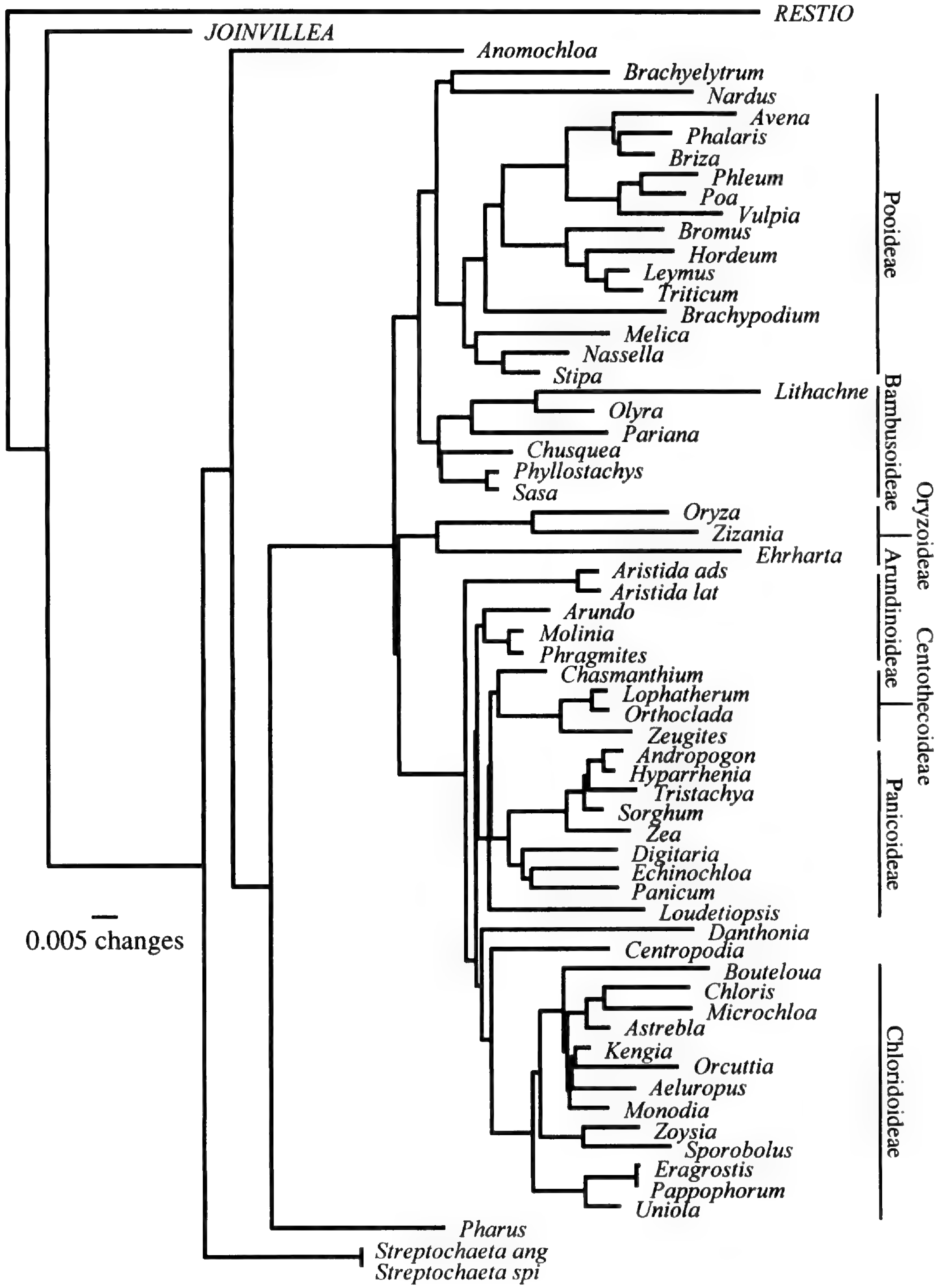

Figure 3. Neighbor-Joining phylogram based on Juke-Cantor and Kimura 2-parameter distance models. For abbreviations of species, see Figure 2 caption.

Pharus that corresponded to: (1) Bambusoideae, Oryzoideae, and Pooideae; and (2) PACC. This split led them to coin the term BOP for the first group, although the clade was weakly supported. Mathews and Sharrock (1996) reported a similar bifurcation based on 174 informative sites from combined phytochrome gene sequence data. However, the Bambusoideae and Oryzoideae were represented only by *Bambusa* and *Oryza*, respectively.

The appearance of subfamilies Panicoideae, Arundinoideae, Centothecoideae, and Chloridoideae in one major group was first demonstrated by Hilu and Wright (1982) on the basis of a phenetic analysis of morphological-anatomical characters. Further support for this grouping was provided by the protein and immunological studies of Hilu and Esen (1988) and Esen and Hilu (1989). This assemblage, which they named PACC, was also evident in the cpDNA restriction site study of Davis and Soreng (1993). The monophyly of the group has since been substantiated by overwhelming molecular and structural data (Davis & Soreng, 1993; Barker et al., 1995; Clark et al., 1995; Duvall & Morton, 1996; Liang & Hilu, 1996; Soreng & Davis, 1998; Hsiao et al., 1999). Additional support for the monophyly of the PACC group is evident from the 6-bp insertion at the 3′ end of *mat*K that is lacking in other grasses and outside the Poaceae (Hilu & Alice, in press a).

The *mat*K data also show a bifurcation in the evolution of the Poaceae. Following the sequential divergence of *Streptochaeta, Anomochloa*, and *Pharus*, the Bambusoideae and Pooideae form a clade supported by an 88% bootstrap and decay of 4, and the Oryzoideae appear sister to PACC. Support for the latter relationship is very low (<50% bootstrap and decay of 1). Therefore, the BOP clade does not gain support from this study, nor is it strongly contradicted. However, the sister-group relationship between Pooideae and PACC is not substantiated by these *mat*K data. In contrast with the well-defined monophyletic PACC lineage, available evidence is inconclusive concerning the phylogenetic affinities among the Bambusoideae, Pooideae, and Oryzoideae.

SYSTEMATICS OF GRASS SUBFAMILIES

Bambusoideae. The emergence of *Streptochaeta, Anomochloa*, and *Pharus* as basal lineages in the *mat*K phylogeny provides further evidence for the polyphyly of the Bambusoideae as previously suspected by Kellogg and Watson (1993) and demonstrated by other researchers (Barker et al., 1995; Clark et al., 1995; Duvall & Morton, 1996; Soreng & Davis, 1998; Hsiao et al., 1999). The clade containing Bambusoideae (excluding *Brachyelytrum*) shows strong support for the monophyly of the herbaceous genera (98% bootstrap and 7 decay). Within this clade the olyroid genera, *Olyra* and *Lithachne*, form a well-supported lineage sister to *Pariana* (Parianeae). However, the woody bambusoids (Bambuseae) do not segregate into their respective subtribes sensu Clayton and Renvoize (1986). *Sasa* and *Chusquea* of the Arundinariinae do not appear monophyletic; instead, *Sasa* forms a strongly supported clade with *Phyllostachys* (Bambusinae), and *Chusquea* is unresolved. The lack of support for the monophyly of these two subtribes is also apparent in other studies (Clark et al., 1995; Soreng & Davis, 1998; Hsiao et al., 1999). These studies also indicate a position for *Brachyelytrum* at or near the base of the Pooideae clade.

Pooideae. The Pooideae clade (excluding *Nardus*) has good support and includes the Stipeae that emerge as a basal lineage along with the unresolved *Melica* (Meliceae). The Stipeae have been inconsistently treated in the Bambusoideae, Pooideae, Arundinoideae, and as a distinct subfamily with affiliation to the Bambusoideae (discussed in Barkworth & Everett, 1987). The basal or near-basal position of the Stipeae in the Pooideae is in agreement with other molecular data (Barker et al., 1995; Clark et al., 1995; Mathews & Sharrock, 1996; Catalán et al., 1997; Soreng & Davis, 1998).

The remaining pooid genera form two major lineages with *Brachypodium* as the sister taxon. The Triticeae and Bromeae form one subclade, and the Aveneae and Poeae comprise the other. This phylogenetic position for *Brachypodium* is in agreement with Catalán et al.'s (1997) results and does not differ greatly from that in Soreng and Davis (1998) where the genus was sister to the Meliceae and basal to most of the Pooideae. *Brachypodium* has been placed in the Triticeae, Bromeae, and Brachypodieae (Bor, 1970; Harz, 1980; Hilu & Wright, 1982; Clayton & Renvoize, 1986; Macfarlane, 1987). The taxonomic uncertainties regarding *Brachypodium* are due to its floret characteristics that are intermediate between the Triticeae and Bromeae, possession of smaller chromosomes than those found in the Triticeae, and occurrence of base chromosome numbers of 7, 9, and 10 (see Hilu & Wright, 1982). The *mat*K-based phylogeny herein supports the tribal rank of *Brachypodium*.

The position of *Bromus* as sister to the Triticeae underscores the phylogenetic affinities between these taxa. *Bromus* is generally placed in its own tribe, and Clayton (1978) considered it a link between the Poeae and Triticeae. The sister relationship between the Bromeae and Triticeae is congruent with the study of Soreng and Davis (1998) and Catalán et al. (1997). The three genera of Triticeae sampled seem monophyletic, and *Leymus* and *Triticum* appear more closely related to each other than either is to *Hordeum,* as evidenced by a synapomorphic 3-bp insertion (Table 1, Fig. 2). The remaining six pooid genera form two lineages: (1) the *Poa-Vulpia-Phleum* clade, and (2) the *Avena-Phalaris-Briza* clade. *Poa* and *Vulpia* belong to the Poeae and *Avena* and *Phalaris* to the Aveneae (Clayton & Renvoize, 1986). The positions of *Briza* (Poeae) and *Phleum* (Aveneae) in this analysis are anomalous. Yet, other studies that have included *Briza* (Soreng et al., 1990; Hsiao et al., 1999) resolve it within the Aveneae.

The placement of *Melica* as an unresolved lineage at or near the base of the Pooideae is congruent with other molecular phylogenies and supports its treatment as a separate tribe. In the NJ tree, *Melica* is sister to the Stipeae (Fig. 3). *Brachyelytrum,* traditionally classified in the Bambusoideae, emerges in a clade with *Nardus* (Pooideae; Nardeae) as sister group to the remaining Pooideae. Although this relationship may be inconsistent with traditional classifications based largely on morphology, it is in close agreement with recent phylogenetic studies (Clark et al., 1995; Catalán et al., 1997; Soreng & Davis, 1998; Hsiao et al., 1999). Each of these studies presents alternative relationships for *Brachyelytrum* and *Nardus,* but all indicate that one or both genera are basal in an expanded definition of Pooideae. The overall morphological and anatomical affinity between *Nardus* and the Pooideae has been demonstrated by Hilu and Wright (1982). Clayton and Renvoize (1986) asserted that the unusual spikelet of the Nardeae gives no clue to its origin, but proposed that it would be better treated as an early departure from the pooid line before the loss of microhairs. The taxa identified as basal to the Pooideae could fit Clayton and Renvoize's notion of odd genera in an evolutionary transition. A number of them have one floret per spikelet, a mixture of pooid and non-pooid characters, and currently appear as relics having different geographic distributions. This information may point to an early evolution of a pre-pooid group and considerable subsequent diversification and geographic radiation.

Oryzoideae. The association of *Ehrharta* (Ehrharteae) with the Oryzoideae (bootstrap 100% and decay index 10, Fig. 2) provides strong evidence for an expanded concept of this subfamily. Historically, the taxonomic position of *Ehrharta* (Ehrharteae) has been disputed. The taxon has been placed within the Bambusoideae (Renvoize, 1986; Watson & Dallwitz, 1992), Arundinoideae (Ellis, 1987), and Oryzoideae (see Hilu & Wright, 1982). In a review of the Ehrharteae, Tateoka (1963) concluded that the tribe could be placed in or near the Oryzoideae or near the "arundiform" grasses. An arundinoid affinity of the Ehrharteae is dismissed because of its lack of a 6-bp deletion synapomorphic to the PACC clade that includes this subfamily (Hilu & Alice, in press a). An oryzoid alliance of *Ehrharta* was evident in the numerical analysis of Hilu and Wright (1982). In contrast, Soreng and Davis's (1998) cladistic analysis of structural characters does not support the inclusion of *Ehrharta* in the Oryzoideae. The strong support for the *Ehrharta-Oryza-Zizania* clade using *mat*K sequences clearly demonstrates the phylogenetic affinity of *Ehrharta* to the oryzoid grasses. This phylogenetic position for *Ehrharta* is in agreement with the *ndh*F-based phylogeny of Clark et al. (1995), the combined cpDNA restriction site and structural data analysis of Soreng and Davis (1998), and the ITS-based phylogeny of Hsiao et al. (1999).

The sister relationship of the oryzoid lineage to the PACC clade in this *mat*K parsimony tree (Fig. 2) is not congruent with studies using other data. Those studies have variably placed the Oryzoideae in an unresolved trichotomy with the Bambusoideae and Pooideae (Clark et al., 1995), sister to the Bambusoideae (Barker et al., 1995; Hsiao et al., 1999), or elsewhere (Duvall & Morton, 1996; Mathews & Sharrock, 1996; Soreng & Davis, 1998). However, this sister position of the oryzoids to PACC is not well supported (bootstrap <50% and decay index 1), and the bootstrap 50% majority-rule tree shows subfamily Oryzoideae sister to the bambusoid-pooid clade. Differential weighting of the codon positions also places the oryzoids in a trichotomy with PACC and bambusoid + pooid lineages (tree not shown).

The oryzoid grasses have either been recognized as a distinct subfamily or included in the Bambusoideae. Analyses of structural data have been inconsistent in terms of taxonomic rank of the oryzoids (Hilu & Wright, 1982; Baum, 1987; Campbell & Kellogg, 1987; Kellogg & Watson, 1993; Soreng & Davis, 1998). The presence of 10–18 kDa (kilodalton) prolamins endorses the affinities between oryzoid and bambusoid taxa (Hilu & Esen, 1988), but the low immunological cross-reactivities clearly demonstrate a high divergence (Esen & Hilu, 1989). DNA data have shown the oryzoids as a distinct entity (Hamby & Zimmer, 1988; Duvall & Morton, 1996; Barker et al., 1995, NJ tree; Clark et al., 1995; Soreng & Davis, 1998). In this study, the monophyletic oryzoid clade (including *Ehrharta*) is strongly supported by a 94% bootstrap and a decay index of 10. This molecular information thus strongly supports the treatment of the Oryzoideae as a distinct subfamily, although its phylogenetic position is unclear.

Aristideae. This tribe is represented only by *Aristida* in this study. The basal position of the genus in the PACC clade is weakly supported (bootstrap <50% and decay index 1). The taxonomic position of the Aristideae in the Poaceae is disputable because of unique anatomical features. The tribe has been placed either in the Chloridoideae or Arundinoideae (reviewed in Hilu & Wright, 1982). Caroline and Jacobs (cf. Jacobs, 1987) found differing differentiation for the two Kranz sheaths in *Aristida* species from different ecological habitats, leading Jacobs (1987) to believe that *Aristida* is not distantly related to the chloridoid grasses. Based on prolamin polypeptide size and immunological similarities, *Aristida* appeared intermediate between the Chloridoideae and Arundinoideae (Hilu & Esen, 1990, 1993; Esen & Hilu, 1991). The prolamin profile of *Stipagrostis* differs from that of *Aristida*, and the former shows low immunological affinities to *Aristida*, grouping with the Chloridoideae (Esen & Hilu, 1991). Sequence data from *rbc*L show *Aristida* and *Stipagrostis* to be monophyletic and sister to the Chloridoideae (Barker et al., 1995). The chloridoid affinity of *Aristida* was also apparent in the *ndh*F-based phylogeny (Clark et al., 1995). Although the distinctness of *Aristida* in the PACC clade is not in question, the phylogenetic position of the Aristideae remains unsettled, especially given that the tribe has been represented by only the type genus in the majority of recent studies. Good representation of the tribe and increased resolution are essential before a conclusive assessment of its taxonomic status and phylogenetic position can be determined. The group represents a heterogeneous assemblage particularly from anatomical and physiological perspectives; *Stipagrostis* has a Kranz anatomy that differs from the unique Kranz pattern of *Aristida*; *Sartidia* lacks Kranz anatomy.

Panicoideae. The Panicoideae do not appear monophyletic in our study because the position of *Loudetiopsis* (Arundinelleae) is unresolved in the parsimony tree (Fig. 2) and is sister to the Centothecoideae-Panicoideae in the NJ tree (Fig. 3). However, the remaining eight genera sampled do form a strongly supported clade divided into two lineages: one corresponding to the Paniceae (*Digitaria, Echinochloa,* and *Panicum*); and the other representing an apparently paraphyletic Andropogoneae due to the inclusion of *Tristachya* (Arundinelleae). Support for the monophyly of the Panicoideae, excluding *Loudetiopsis,* is very convincing (95% bootstrap and a decay index of 4). Similar results were evident in Clark et al.'s (1995) study that showed *Danthoniopsis* (Arundinelleae) nested in a clade comprised of Centothecoideae + *Thysanolaena* (Thysanolaeneae; Arundinoideae). This clade was sister to the Pancoideae.

Tristachya (Arundinelleae) is strongly nested (100% bootstrap and 14 decay) within the Andropogoneae clade of *Zea, Sorghum, Andropogon,* and *Hyparrhenia* (Fig. 2). The presence of spikelets in triads characteristic of the Arundinelleae breaks down in *Tristachya,* where paired spikelets of the andropogonoid type are found in some species. *Tristachya* also emerged within the Andropogoneae in the *rbc*L and *rpo*C2 (data set II) studies of Barker et al. (1995, 1999). Hsiao et al.'s (1999) ITS phylogeny is the only other study that included an Arundinelleae representative. In their analysis, *Arundinella* was sister to the Andropogoneae. Thus, it seems that the Arundinelleae are not a monophyletic tribe, but perhaps distributed among at least three lineages. This postulate gains support from the molecular study of Mason-Gamer et al. (1998) in which the Arundinelleae were not monophyletic. The Arundinelleae share some spikelet features with the Andropogoneae and are thought to have given rise to the latter tribe (Clayton, 1981). The alliance of *Tristachya* with the Andropogoneae is supported by this *matK* study but not its ancestral position.

Centothecoideae. The Centothecoideae were segregated from the Arundinoideae by Clayton (1978); however, their phylogenetic position remains unresolved. Based on the *rbc*L study of Barker et al. (1995), the centothecoid *Chasmanthium* occurred in a clade with *Thysanolaena* (Arundinoideae; Thysanolaeneae) and was separated from the Panicoideae by the arundinoid *Gynerium.* However, the position of *Gynerium* was described as "equivocal." In the *ndh*F study of Clark et al. (1995), the centothecoid genera *Zeugites* and *Chasmanthium* appeared in a clade containing *Danthoniopsis* (Panicoideae; Arundinelleae) and *Thysanolaena.* In this *mat*K study, the Centothecoideae appear monophyletic and related to the Panicoideae, although support is low and neither *Danthoniopsis* nor *Thysanolaena* were sampled. Apart from *Chasmanthium,* the remaining Centothecoideae (*Zeugites, Lophatherum,* and *Orthoclada*) are very closely related (Fig. 2; 100% bootstrap and decay 15), raising the question about the position of *Chasmanthium.* The centothecoids cannot be included in the Bambusoideae as treated by Watson and

Dallwitz (1992) because they possess the 6-bp insertion unique to PACC (Hilu & Alice, in press a), and based on their phylogenetic position in this and other molecular studies. A more comprehensive sampling of the Centothecoideae, including potentially related genera such as *Danthoniopsis, Gynerium,* and *Thysanolaena,* are important prerequisites for accurately assessing the monophyly of this group and its relationships within PACC. Nevertheless, the studies that have included centothecoid representatives, including this one, demonstrate a greater alliance with the Panicoideae than with either the Arundinoideae or Chloridoideae.

Arundinoideae. The Arundinoideae are known to be a taxonomically problematic group. The polyphyletic or paraphyletic nature of the arundinoid grasses has been proposed on the basis of morpho-anatomical characters (Campbell & Kellogg, 1987) and *rbc*L, *rpo*C2, and *ndh*F sequence data (Barker et al., 1995, 1999; Clark et al., 1995). The Arundinoideae sample in Barker et al. (1995, 1999) is one of the largest among these studies. They presented one of 26 most-parsimonious trees that showed the arundinoids split between two major clades that are supported by bootstrap values of only 33% and 47%. The number of most parsimonious trees and the low bootstrap values make it difficult to assess the relationships of the arundinoid taxa. A more recent study based on the *rbc*L gene (Duvall & Morton, 1996) implied monophyly of the arundinoids; however, the study included only *Arundo* and *Phragmites.*

Our study does not substantiate a monophyletic Arundinoideae. The positions of *Arundo* and *Molinia* + *Phragmites* are unresolved, whereas *Danthonia* and *Centropodia* are closely related to the Chloridoideae. The *Phragmites-Molinia* clade is strongly supported with a 98% bootstrap and a decay index of 5 (Fig. 2). The affinity between *Molinia* and *Phragmites* is apparent in Clayton and Renvoize's (1986: fig. 14) diagram of relationships of the Arundineae and is congruent with the results of Barker et al. (1995, 1999; used syn. *Moliniopsis*) and the combined analysis of Soreng and Davis (1998).

Chloridoideae. The monophyly of the Chloridoideae, which is often disputed, is strongly supported by these *mat*K sequence data (Fig. 2) and a more comprehensive *mat*K study (Hilu & Alice, in press b). The association of *Centropodia* and *Danthonia* with the chloridoid clade is quite intriguing. The sister relationship of *Centropodia* to the Chloridoideae is in agreement with the *rbc*L-based phylogeny of Barker et al. (1995), as is the position of *Danthonia. Centropodia* is traditionally placed in the Arundineae (Clayton & Renvoize, 1986) or considered as a danthonoid (see Barker et al., 1995). The genus has a well-developed Kranz anatomy (Ellis, 1984) that separates it from the Arundineae and allies it with the Chloridoideae. Barker et al. (1995) indicated that the lack of haustorial synergids supports its exclusion from the danthonoid grasses. The multinerved glumes and lemmas of *Centropodia* represent traits shared with the Pappophoreae and Uniolinae, members of a basal chloridoid lineage.

The major tribes Eragrostideae and Chlorideae do not appear to be monophyletic. The lack of support for the Chlorideae and Eragrostideae as distinct lineages was also reflected in the morphological-anatomical study of the subfamily (Van den Borre & Watson, 1997) and the *mat*K-based study of Hilu and Alice (in press b). The emergence of the Pappophoreae, Uniolinae, and *Eragrostis* in a basal clade is congruent with Hilu and Alice (in press b). Clayton and Renvoize (1986) placed the Uniolinae as a basal group in the Chloridoideae, and Van den Borre and Watson (1997) demonstrated a near-basal position of the Pappophoreae in their phylogeny.

Another noteworthy group includes *Sporobolus* and *Zoysia* in a well-supported clade that is consistent with Soreng and Davis (1998) and Clark et al. (1995). The presence of the Chlorideae genera *Astrebla, Chloris,* and *Microchloa* in a strongly supported clade is taxonomically sound. A similar assemblage was also apparent in Van den Borre and Watson's (1997) morphological study. A comprehensive systematic study of the Chloridoideae is in progress (K. Hilu & L. Alice, unpublished data).

The *mat*K gene provides sequence information sufficient for elucidating evolutionary relationships among grass lineages. The results of this study identify several well-supported clades that are in agreement with other recent molecular studies. Most evidence points to *Streptochaeta* and *Anomochloa* as representing the most basal grass lineages. However, the question of whether these two genera constitute a monophyletic subfamily or two distinct lineages remains unanswered due to conflict among data sets. *Pharus* has an intriguing position. Although *Pharus* corresponds with *Streptochaeta* and *Anomochloa* by its own distinct lineage, the genus is strongly separated from most other grasses supporting its subfamilial status as proposed by Clark and Judziewicz (1996). Yet, *Pharus* shares with other grasses the synapomorphic 1-bp deletion that is not found in *Streptochaeta* and *Anomochloa* (Hilu & Alice, in press a). Subfamilies

Bambusoideae, Oryzoideae, and Pooideae can be considered monophyletic with individual modification. As others have demonstrated, the Bambusoideae should exclude *Streptochaeta, Anomochloa, Pharus,* and possibly *Brachyelytrum,* the last mentioned being allied with *Nardus* and other Pooideae. Oryzoid taxa, including *Ehrharta,* resolve well from the Bambusoideae and are strongly supported as a monophyletic unit deserving subfamilial rank. The Pooideae are also well supported with their definition expanded to include *Brachyelytrum.* Based on existing phylogenetic evidence, there is no consensus with regard to the relationships among Bambusoideae, Oryzoideae, and Pooideae or to their affinities with the firmly established PACC clade.

Within PACC, the best supported subfamily is the Chloridoideae. The Panicoideae (excluding *Loudetiopsis*) and the Centothecoideae are also taxonomically sound groups, although support is low for the relationship between *Chasmanthium* and other centothecoid members. However, the Centothecoideae may be paraphyletic due to the inclusion of such genera as *Danthoniopsis, Gynerium,* and *Thysanolaena* nesting within the centothecoid clades in other studies. Finally, the Arundinoideae are clearly polyphyletic with some elements at or near the base of the PACC clade (*Aristida*), and others (*Danthonia* and *Centropodia*) closely related to the Chloridoideae.

Most molecular phylogenies of the Poaceae have been inferred from chloroplast genome data and, thus, may not be considered truly independent. To further resolve the systematic relationships in Poaceae and to test existing hypotheses, robust, nuclear-based phylogenetic analyses are warranted.

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Appendix 1. Accessions used along with their classification, which generally follows Clayton and Renvoize (1986), and sources of material. Subfamilial classification of *Anomochloa, Pharus,* and *Streptochaeta* follows Clark and Judziewicz (1996). Cultivars are indicated by quotation marks following species' names. BBG = University of Bonn Botanical Garden, MBG = Missouri Botanical Garden living collections, NIAR = National Institute of Agrobiological Resources, PBG = Pretoria Botanical Gardens, VTDPP = Virginia Tech Department of Plant Pathology. PI and W6 numbers = U.S. Department of Agriculture-National Plant Germplasm System accessions. Herbarium codes follow Holmgren et al. (1990). * = accession of *Brachypodium sylvaticum* either PI 325218 (ex USSR) or PI 268222 (Iran).

Taxon	Origin	Source/Voucher	GenBank
RESTIONACEAE			
Restio tetraphyllus Labill.	unknown	BBG 00700-90/*T. Borsch 3319,* VPI	AF164379
JOINVILLEACEAE			
Joinvillea ascendens Gaud. ex Brongn. & Gris.	unknown	*J. Davis s.n.* (DNA)/*H. Moore 10438,* BH	AF164380
POACEAE			
Anomochlooideae			
Anomochloeae			
Anomochloa marantoidea Brongn.	Brazil	*L. Clark 1299,* ISC	AF164381
Streptochaeteae			
Streptochaeta angustifolia Soderstr.	Brazil	*L. Clark 1304,* ISC	AF164382
Streptochaeta spicata Schrad. ex Nees	Brazil	MBG 93091/*K. Hilu 0001,* VPI	AF164383
Arundinoideae			
Aristideae			
Aristida adscensionis L.	Pakistan	PI 269867/*K. Hilu 5516,* VPI	AF164412
Aristida latifolia Domin	Australia	*J. Dalby 97/12,* NSW	AF164413
Arundineae			
Arundo donax L.	unknown	*K. Hilu 5546,* VPI	AF164408
Centropodia glauca (Nees) Cope	Namibia	*N. Barker 967,* BOL	AF164410
Danthonia spicata (L.) P. Beauv. ex Roem. & Schult.	VA-USA	J. Randall (seed)/*K. Hilu 5505,* VPI	AF164409
Molinia caerulea (L.) Moench	Germany	BBG 13977/*T. Borsch 3320,* VPI	AF164411
Phragmites australis (Cav.) Trin. ex Steud.	VA-USA	*G. Fleming s.n.,* VPI	AF144575
Bambusoideae			
Bambuseae			
Chusquea coronalis Soderstr. & C. E. Calderón	unknown	MBG 896581/*K. Hilu 0002,* VPI	AF164389
Phyllostachys aurea Rivière & C. Rivière	unknown	*K. Hilu 9418,* VPI	AF164390
Sasa kurilensis (Rupr.) Makino & Shibata	Japan	A. Nishiwaki (seed)/*K. Hilu 5774,* VPI	AF164391
Brachyelytreae			
Brachyelytrum erectum (Schreb.) P. Beauv.	VA-USA	*T. Wieboldt s.n.,* VPI	AF164384
Olyreae			
Lithachne pauciflora (Sw.) P. Beauv.	Costa Rica?	L. Clark 1297, ISC	AF164385
Olyra latifolia L.	Brazil	*L. Clark 1191,* ISC	AF164386

Appendix 1. Continued.

Taxon	Origin	Source/Voucher	GenBank
Parianeae			
Pariana radiciflora Sagot ex Döll	Brazil?	*MBG 931696/K. Hilu 0003*, VPI	AF164387
Centothecoideae			
Centotheceae			
Chasmanthium laxum (L.) H. O. Yates	VA-USA	G. Fleming (seed)/*K. Hilu 5716*, VPI	AF164414
Lophatherum gracile Brongn.	Japan	*Nishimura 277*, MO	AF164415
Orthoclada laxa (Rich.) P. Beauv.	Ecuador	MBG 930596/*K. Hilu 0004*, VPI	AF164416
Zeugites pittieri Hack.	Costa Rica	*L. Clark 1171*, ISC	AF144576
Chloridoideae			
Chlorideae			
Astrebla lappacea (Lindl.) Domin	Australia	PI 284733/*K. Hilu 5639*, VPI	AF144589
Bouteloua curtipendula (Michx.) Torr.	TX-USA	PI 216213/*K. Hilu 5717*, VPI	AF144578
Chloris gayana Kunth	South Africa	PI 207542/*K. Hilu 5726*, VPI	AF164424
Microchloa caffra Nees	South Africa	PI 300028/*K. Hilu 5635*, VPI	AF164425
Zoysia macrostachya Franch. & Sav.	China	PI 553020/*K. Hilu 5751*, VPI	AF164426
Eragrostideae			
Aeluropus littoralis (Gouan) Parl.	ex USSR	PI 392332/*K. Hilu 5685*, VPI	AF144597
Eragrostis airoides Nees	Brazil	PI 204184/*K. Hilu 5538*, VPI	AF164427
Kengia songorica (Roshev.) Packer	Mongolia	W6 18025/*K. Hilu 5760*, VPI	AF164428
Monodia stipoides S. Jacobs	Australia	*S. Jacobs 8032*, NSW	AF144602
Sporobolus heterolepis (A. Gray) A. Gray	USA	MBG 951706/*K. Hilu 0005*, VPI	AF164429
Uniola paniculata L.	VA-USA	*D. Knepper s.n.*, VPI	AF144607
Orcuttieae			
Orcuttia californica Vasey	CA-USA	*O. Mistretta s.n.*, RSA	AF144599
Pappophoreae			
Pappophorum bicolor E. Fourn.	Mexico	PI 216526/*K. Hilu 5542*, VPI	AF144604
Oryzoideae			
Ehrharteae			
Ehrharta longifolia Schrad.	South Africa	PI 270493/*K. Hilu 5728*, VPI	AF164392
Oryzeae			
Oryza sativa L. "Nipponbare"			X15901
Zizania aquatica L.	VA-USA	*K. Hilu 9423*, VPI	AF164393
Panicoideae			
Andropogoneae			
Andropogon gerardii Vitman	SD-USA	PI 315661/*K. Hilu 5554*, VPI	AF144577
Hyparrhenia hirta (L.) Stapf	South Africa	Kirstenbosh Gardens/*N. Barker 1134*	AF164417

Appendix 1. Continued.

Taxon	Origin	Source/Voucher	GenBank
Sorghum bicolor (L.) Moench	unknown	VTDPP (seed)/*K. Hilu 9408*, VPI	AF164418
Zea mays L.			X86563
Arundinelleae			
Loudetiopsis chrysothrix (Nees) Conert	Brazil	T. Filgueiras (seed)/*K. Hilu 5748*, VPI	AF164419
Tristachya biseriata Stapf	South Africa	PBG/*N. Barker 1126*	AF164420
Paniceae			
Digitaria sanguinalis (L.) Scop.	unknown	Sharp Bros. Seed Co./*K. Hilu 6*, VPI	AF164421
Echinochloa utilis Ohwi & Yabuno	Japan	NIAR (seed)/*K. Hilu 3091*, VPI	AF164422
Panicum capillare L.	Afghanistan	PI 220025/*K. Hilu 3120*, VPI	AF164423
Pharoideae			
Phareae			
Pharus latifolius L.	unknown	*L. Clark 1302*, ISC	AF164388
Pooideae			
Aveneae			
Avena sativa L.	unknown	Southern States Co. (seed)/*K. Hilu 9406*, VPI	AF164395
Phalaris arundinacea L.	unknown	PI 578797/*K. Hilu 5606*, VPI	AF164396
Phleum pratense L.	unknown	PI 303130/*K. Hilu 3318*, VPI	AF164397
Bromeae			
Bromus inermis Leyss	unknown	Wetsel Seed Co. (seed)/K. Hilu 8, VPI	AF164398
Meliceae			
Melica altissima L.	ex USSR	PI 325418/*K. Hilu 5576*, VPI	AF164399
Nardeae			
Nardus stricta L.	Germany	BBG 14504/*T. Borsch 3321*, VPI	AF164394
Poeae			
Briza erecta Lam.	Uruguay	PI 282880/*K. Hilu 5590*, VPI	AF164401
Poa pratensis L.	unknown	Southern States Co. (seed)/*K. Hilu 7*, VPI	AF164402
Vulpia myuros (L.) C. C. Gmel.	India	PI 217618/*K. Hilu 5666*, VPI	AF164403
Stipeae			
Nassella tenuis (Phil.) Barkworth	Argentina	PI 282897/*K. Hilu 5663*, VPI	AF164406
Stipa offneri Breistr.	unknown	PI 287941/*K. Hilu 5640*, VPI	AF164407
Triticeae			
Brachypodium sylvaticum (Huds.) P. Beauv.		*USDA collection	AF164400
Hordeum vulgare L.			X64129
Leymus angustus (Trin.) Pilg.	China	PI 547357/*K. Hilu 5574*, VPI	AF164404
Triticum aestivum L. "Massey"	unknown	Starling s. n. (seed)/*K. Hilu 5*, VPI	AF164405

PHYLOGENETICS OF HYACINTHACEAE BASED ON PLASTID DNA SEQUENCES[1]

Martin Pfosser[2] *and Franz Speta*[3]

ABSTRACT

Hyacinthaceae presently consist of approximately 70 genera and 1000 species. To investigate the monophyly of the family and the generic relationships, we sequenced the *trn*L intron and the *trn*L-*trn*F intergenic spacer region of chloroplast DNA for 105 taxa in Hyacinthaceae and 18 species of related families. By testing different outgroup compositions, we provide evidence for the monophyly of the family if the North American genera *Camassia* and *Chlorogalum*, which are more closely related to *Agave* and *Hosta*, are excluded from Hyacinthaceae sensu Dahlgren. Several generic implications can be deduced from the analysis, the most prominent one of which is the polyphyletic origin of the Linnaean genera *Scilla*, *Ornithogalum*, and *Hyacinthus*. Especially members of the genera *Scilla* and *Hyacinthus* are extensively intermixed with each other. According to the DNA sequence data, the only true *Scilla* species are found in the Mediterranean region and appear as a monophyletic clade. A tetrapartition of the family into (1) the monotypic subfamily Oziroëoideae Speta, accommodating the South American Hyacinthaceae; (2) the subfamily Urgineoideae Speta, housing relatives of the squills; (3) the subfamily Ornithogaloideae Speta, including the tribes Ornithogaleae Rouy and Dipcadieae Rouy; and (4) the largest and most advanced subfamily, Hyacinthoideae Link, consisting of the tribe Massonieae Baker (including species from Africa south of the Sahara and from India) and the Mediterranean/Asian tribe Hyacintheae Dumort., is proposed. Previously included in Hyacinthaceae sensu Dahlgren, the North American genera *Chlorogalum* and *Camassia* show affinities to Agavaceae and Funkiaceae and appear as a distinct clade together with Anthericaceae. Furthermore, the occurrence of taxa from southern Africa at basal positions in all subfamilies points to the origin of evolution of the Hyacinthaceae in this region.

For many systematists the bulbous plants represent the very center of Liliaceae (Cronquist, 1981). Therefore, it was a big surprise when Dahlgren et al. (1982, 1985) emphasized that these bulbous plants are members of two families, the Liliaceae sensu stricto and the Hyacinthaceae, which moreover belong to the different orders Liliales and Asparagales, respectively. However, the process of arriving at this systematic decision was not straightforward: The first circumscription of an independent plant family Hyacinthaceae by Batsch (1786) was not widely utilized by the scientific community. Batsch combined in this family rather heterogeneous liliaceous plants possessing flowers with a fused perianth. Among the 17 genera included within Hyacinthaceae sensu Batsch, only two (*Hyacinthus*, *Lachenalia*) are considered as belonging to the present circumscription of this plant family (Speta, 1998a, b). The genera *Ornithogalum*, *Scilla*, and *Albuca* Batsch placed within Alliaceae. In 1836 familial status was reduced to tribal level by Endlicher, who included species irrespective of the degree of perianth fusion. Interestingly, he also included the American genus *Camassia* in Hyacintheae. In his 1866 posthumously published fragment "The genera of plants," Salisbury re-evaluated the Linnaean genera *Hyacinthus*, *Scilla*, and *Ornithogalum* and redistributed often new genera into the families Eucomaceae, Lachenaliaceae, Hyacinthaceae, and Ornithogalaceae. Adopting a broader circumscription of Liliaceae, Baker, who obviously knew Salisbury's publication, refused to follow his ideas although he used tribes for his Liliaceae sensu lato. Hyacintheae and Scilleae were created in 1870, followed by Massonieae (1871) and Chlorogaleae (1873). Genera with floral fusion were placed in Hyacintheae, whereas those with more or less free tepals were accommodated within Scilleae. Later, Engler (1887) would separate bulbous Liliaceae, for him central to the family, into tribes Lilieae and Scilleae but considered these groups to be closely related. *Bowiea* and *Schizobasis* were included within Eriosperminae (Asphodeloideae–Asphodeleae) by Engler, whereas *Schoenolirion*, *Chlorogalum*, and *Hemiphylacus* were coalesced within Chlorogalinae with *Camassia* directly related to *Scilla* (Engler, 1887). His student Schulze (1893) simi-

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[1] We are grateful to M. W. Chase for supplying us with DNA of *Fortunatia biflora* and to M. W. Chase and A. V. Cox for permission to use their unpublished sequence data of the outgroup species *Aspidistra elatior*, *Disporopsis pernyi*, *Polygonatum hookeri*, *Liriope platyphylla*, *Peliosanthes* sp., *Eustrephus latifolius*, *Leucocrinum montanum*, *Milla magnifica*, *Bessera elegans*, *Brodiaea jolonensis*, and *Dichelostemma pulchellum* included in our analysis. We thank all botanical gardens and private collectors who supplied us with living plant material.

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larly concluded that distinctions between Tulipeae and Scilleae were not morphologically warranted. It was early this century when Fritsch in Graz, together with his Ph.D. students, investigated Liliaceae sensu lato. Not only did their comparative anatomical studies substantiate the distinction of the Lilioideae into Tulipeae and Scilleae (Fuchsig, 1911), but they also arrived at the conclusion that *Bowiea* is rather isolated within Asphodeleae (Bouvier, 1915). Based on these results, Fritsch (1932) proposed the recognition of several smaller and more homogeneous families rather than keeping the conservative concept of a large and heterogeneous family Liliaceae.

A more profound contribution to the classification of Liliaceae was provided by Schnarf and students in Vienna (Schnarf, 1929; Wunderlich, 1937; Schmid, 1938; Buchner, 1949), utilizing comparative embryology. Building from them, Krause (1930) elevated Scilleae and Lilieae tribes to subfamilial status. Wunderlich (1937) moreover questioned, based on embryological characters, the retention of obviously different groups like Lilioideae and Scilloideae in the same family, with Scilloideae further shown as embryologically heterogenous. Two groups were distinguished: (1) an *Ornithogalum*-group consisting of genera *Ornithogalum, Muscari,* and *Puschkinia* with helobial endosperm and (2) a second group (*Scilla, Hyacinthus, Camassia, Galtonia*) with nuclear endosperm and more variation in embryo sac development. Further, Schmid (1938) divided Scilloideae on differences in pistil anatomy and pollen-tube leading tissue: (1) *Albuca, Galtonia*; (2) *Scilla, Camassia, Ornithogalum, Hyacinthus, Puschkinia, Muscari*; (3) *Ledebouria* (*Drimia* in her thesis), *Eucomis,* and *Veltheimia.* Later, Buchner (1949) supported Schmid's second group embryologically, grouping *Ornithogalum, Muscari,* and *Puschkinia,* then *Scilla* and *Hyacinthus* together. The status of *Camassia, Drimiopsis,* and *Urginea* remained unresolved.

In contrast to other families, Hyacinthaceae proved to be karyologically variable (as reviewed in Speta, 1998b). Nevertheless, chromosome numbers are usually constant at the genus level in Hyacinthaceae, irrespective of the genus size (*Scilla* sensu stricto: $x = 9$; *Muscari*: $x = 9$; *Bellevalia*: $x = 4$; *Albuca*: $x = 9$). However, the occurrence of dysploid series again complicated the situation (*Prospero*: $x = 4, 5, 6, 7$; *Barnardia*: $x = 8, 9$; *Hyacinthella*: $x = 9, 10, 11, 12$; *Stellarioides*: $x = 2, 3, 4, 5, 6, 7, 8, 9$; *Schnarfia*: $x = 9, 10$). Nevertheless, Huber (1969) accepted Wunderlich's (1937) proposal, independently recognizing Scilloideae as family Hyacinthaceae. Species were divided according to seed characters into tribes Chlorogaleae (*Chlorogalum, Schoenolirion,* and probably *Hemiphylacus*), Bowieae (*Bowiea, Schizobasis*), and Scilleae. For tribe Scilleae, Huber (1969) noted *Camassia* and *Ornithogalum* to be the basal genera. *Camassia* was the most basal genus of the blue-flowering group and was closely related to *Endymion* Dumort. [= *Hyacinthoides* Medicus] and *Scilla. Puschkinia* and *Chionodoxa* were closely related to *Scilla.* Another blue-flowering group includes *Hyacinthus* and *Muscari* sensu lato with *Lachenalia* and *Massonia* closely related to *Hyacinthus.* In contrast to blue-flowering Scilleae, which all show affinities to each other, Scilleae with non-blue flowers isolate into several groups. Some showed distant relationship to blue-flowering lines like *Lachenalia* and *Massonia.* For other genera (*Drimiopsis, Eucomis,* and *Veltheimia*) a more likely relationship to *Ornithogalum* was proposed. Close relationship was drawn between *Drimia* and *Galtonia, Dipcadi* and *Pseudogaltonia, Albuca* and *Urginea* (Huber, 1969).

Pollen features can be systematically valuable but not for Hyacinthaceae. Therefore, Schulze (1980) was reluctant to recognize the family status of Hyacinthaceae based on pollen characters. He only recognized the tribes Scilleae and Massonieae sensu Huber but did not include Chlorogaleae and Bowieae in Hyacinthaceae. Tribes Chlorogaleae and Bowieae were later included within Anthericaceae (Schulze, 1982).

As reviewed here, traditional methodologies have not resolved subfamilial relationships within Hyacinthaceae. Certain characters like perianth features are clearly non-informative. For example, *Chionodoxa* with its fused tepals was shown to be closely related with generitype *Scilla bifolia* L., which has more or less free tepals. *Chionodoxa* was therefore synonymized under *Scilla* (Speta, 1971, 1976).

Splitting of the large Linnaean genus *Hyacinthus* into a series of more homogeneous genera is now widely accepted. Conversely, the distribution of species of the Linnaean genus *Scilla* into distinct genera has not achieved a broad consensus. The broad circumscription of the genus *Scilla* by Linnaeus (1753), a name that was previously exclusively reserved for the squills, apparently had an adverse effect on the necessary dissection of this genus into more natural genera. Consequently, a new name had to be found for the relationship of the squills. In fact, a whole squill subfamily (Urgineoideae) is encapsulated within an obviously heterogeneous *Squilla* and an equally heterogeneous genus *Drimia* (Jessop, 1977; Stearn, 1978; Stedje, 1987). Only Jessop (1970) acknowledged an independent genus *Ledebouria* within African/Indian *Scilla* sensu lato. This was later substantiated by molecular data (Stedje, 1998), whereas other *Scilla* sensu lato relationships remained untouched.

The Hyacinthaceae have been long recalcitrant to a natural classification into subfamilies and tribes. One reason is the classification of most species into three highly heterogeneous genera, *Scilla, Hyacinthus*, and *Ornithogalum*, by Linnaeus. Efforts to find characters to discriminate at higher hierarchical levels within Hyacinthaceae have revealed the obsoleteness of most characters, which otherwise have been shown to be useful for classification in other families. Characters useful at higher taxonomic levels in other families often reveal a high variability among closely related species within Hyacinthaceae. For example, the type of the embryo sac or endosperm can be variable even within closely related species of *Scilla* sensu stricto (Svoma, 1981) or *Prospero* (Ebert, 1993). Likewise, chromosome numbers can be constant within certain genera but highly variable in other genera, resulting in aneuploid series difficult to interpret. Pollen grains of many genera in Hyacinthaceae do not show significantly different morphologies and are only of limited taxonomic value (Schulze, 1980). Chromosome counts and morphology have been phylogenetically useful at the species level but higher-order taxa remain problematic (Speta, 1979). Improvement of cytological techniques (chromosome banding, nuclear DNA amounts, etc.) has aided in the advancement of classification at species level but contributes little to higher-level systematics.

Chemotaxonomic features have been shown to be useful to distinguish genera within Hyacinthaceae and to group them at higher hierarchical levels. Cardiac-active steroids occur in several genera. One group, the bufadienolids, have been found only in species clearly related to *Charybdis maritima* (L.) Speta (Krenn, 1990, 1994) and thus delineate the subfamily Urgineoideae. A second group of cardiac-active compounds, cardenolids, have been found in several allies to *Ornithogalum* (subfamily Ornithogaloideae). However, investigation of species within Ornithogaloideae is not yet completed, and several members lack these compounds. It cannot be excluded therefore, that this subfamily may still contain additional characteristic compounds. *Zahariadia saundersiae* (Baker) Speta and *Eliokarmos thyrsoides* (Jacq.) Raf. are characterized by cholestan steroids (Kubo et al., 1992a, b). Furthermore, most species in *Ornithogalum* and allies exhibit protein crystals in their nuclei, a feature absent from other Hyacinthaceae (Speta, unpublished). An unrelated group of phenolic compounds (homoisoflavanoles) (Heller & Tamm, 1981) discriminate a third group of genera (subfamily Hyacinthoideae) from *Urginea*- and *Ornithogalum*-affined taxa. Interesting in this respect are serological investigations placing North American *Camassia* near Agavaceae (Cupov & Kutjavina, 1981), although they alternatively could be included in Hyacinthaceae due to chemotaxonomic and karyological features. An independent family Camassiaceae, sister to Agavaceae and Hesperocallidaceae, has even been proposed (Cupov, 1994). When Fay and Chase (1996) circumscribed the new family Themidaceae, they also sequenced the *rbc*L locus of a few genera in Hyacinthaceae. Again, *Camassia* and *Chlorogalum* showed affinities to Agavaceae.

At present the Hyacinthaceae accommodate approximately 1000 species distributed into roughly 70 genera (Speta, 1998a, 1998b). To evaluate generic relationships within the family Hyacinthaceae, we sequenced the *trn*L-intron and the intergenic spacer (IGS) between the *trn*L-(UAA)-3′-exon and *trn*F-(GAA) chloroplast gene, two DNA regions where sequence divergence is useful to resolve generic and subgeneric relationships (Fangan et al., 1994; Stedje, 1998). In total, we sequenced 123 accessions comprising 105 species and 51 genera of Hyacinthaceae, as well as four accessions of North American *Camassia* and *Chlorogalum* species, and 14 selected outgroup species from the lilioid families Agavaceae, Amaryllidaceae, Anthericaceae, Blandfordiaceae, Doryanthaceae, Funkiaceae, Hemerocallidaceae, Lomandraceae, and Nolinaceae. Furthermore, we included DNA sequence data from 12 published species of Hyacinthaceae, as well as unpublished sequences of 11 outgroup species, in our analysis. We interpret our results with reference to well-established morphological and cytogenetic data. From this phylogenetic perspective, we discuss the generic limitations within Hyacinthaceae as well as the monophyly of most genera as recognized by Speta (1998a, b).

MATERIALS AND METHODS

PLANT MATERIAL AND DNA EXTRACTION

Genetic accessions and herbarium vouchers of all plant materials are listed in Appendix 1. Nomenclature of taxa included in the study follows that of Speta (1998a, b).

DNA was extracted from 5–50 mg of plant material obtained either from fresh leaves or bulb scales or from herbarium specimens (*Whiteheadia etesionamibensis* Müller-Doblies, *Zagrosia persica* (Hausskn.) Speta acc. 1, *Scilla* cf. *bulgarica* Speta, and *Urginavia micrantha* (A. Rich.) Speta) following the single tube isolation protocol of Steiner et al. (1995) with minor modifications. Lyophilized and powdered material was extracted with 400 μl ROSE buffer (10 mM Tris-HCl pH 8.0; 312.5 mM EDTA, pH 8.0; 1% sodium lauryl sarkosyl; and 1% polyvinylpolypyrrolidone) at 90°C for 10 minutes. After centrifugation, 10 μl of the supernatant were diluted 100-fold with TE buffer pH 8.0 and stored at 4°C. Two μl of the diluted DNA were used as a template in a 50 μl PCR reaction.

DNA AMPLIFICATION

Two noncoding regions of the chloroplast genome were sequenced. The *trn*L(UAA)-intron and the intergenic spacer (IGS) between *trn*L-(UAA)-3′-intron and *trn*F-(GAA) gene were amplified together in a single PCR reaction using the C- and F-primers as published by Fangan et al. (1994). The thermal cycling protocol comprised 30 cycles of 10 sec at 94°C, 10 sec at 45°C, and 20 sec at 72°C in a TouchDown thermal cycler (HYBAID), operated in tube-control mode. Amplified, double-stranded DNA fragments were purified using the Wizard DNA purification system from Promega.

DNA SEQUENCING

Purified PCR products were directly sequenced on an A.L.F. automated sequencer (Pharmacia) using 5′-fluorescein-labeled nested primers (two primers 5′-CTACGGACTTAATTGGATTGAGC-3′ and 5′-GGGGATAGAGGGACTTGAAC-3′ for the *trn*L-intron and two primers 5′-GGTTCAAGTCCCTCTATCCC-3′ and 5′-AGGATTTTCAGTCCTCTGCTC-3′ for the intergenic spacer) following the cycle sequencing protocol of the manufacturer (AutoCycle sequencing kit, Pharmacia). Both strands were sequenced, and in cases where ambiguities could not be resolved by comparison with the sequence of the complementary strand, additional PCR reactions were performed to generate new templates for sequencing. Ambiguities resulting from compressions were resolved by using the Thermo Sequenase fluorescent labeled primer cycle sequencing kit with 7-deaza-dGTP (Amersham).

DATA ANALYSIS

Sequence manipulations and phylogenetic analyses were performed on a Digital Alpha 1000A 5/400 server under the operating system Digital Unix V.4.0D. DNA sequences were prealigned by using the PileUp program of the GCG software Package (Genetics Computer Group, 1994). Final alignment of DNA sequences was done by eye. *Aspidistra elatior* was designated as the outgroup in phylogenetic reconstructions using test version 4.0d64 of PAUP* written by David L. Swofford. Using the gapcode = missing parameter the data matrix was subjected to 1000 replicates of random sequence additions using tree bisection-reconnection (TBR) branch-swapping under the Fitch criterion (unordered states and equal weights: Fitch, 1971). At each step only ten trees were permitted to be held to minimize the time the algorithms spent for searching for trees on sub-optimal islands.

Successive weighting was applied and new heuristic searches were performed using the trees of the previous analysis as starting trees until tree lengths remained the same in two successive rounds. Finally, 10,000 fast bootstrap (Felsenstein, 1985) replicates, as well as 10,000 replicates using the jackknife algorithm, were performed to assess confidence limits for tree topology using the final weight set from successive weighting. During all analyses the maximum number of trees in memory was limited to 10,000. Indels in the data matrix were coded as additional characters, and tree searches were performed using the nucleotide data alone or together with the indel data. Tree manipulations were performed using MacClade version 3.06 (Maddison & Maddison, 1992).

The DNA sequence data consisting of the *trn*L intron and the *trn*L-*trn*F intergenic spacer have been deposited in the EMBL data library (accession numbers, see Appendix 1). An aligned DNA matrix is available via electronic mail from MP upon request (email: martin@gem.univie.ac.at).

RESULTS

SEQUENCE VARIATION OF *TRN*L-INTRON AND *TRN*L-*TRN*F IGS REGIONS

In total, the combined and aligned intron+IGS sequences yielded 1297 characters with 452 parsimony-informative positions. Thirty indels, which mainly consisted of simple 4–5-bp-long sequence repeats and thus were easy to align, were coded and added to the data matrix. The lengths of the intron sequences varied between 515 and 592 nucleotides except for *Eliokarmos graminifolius* (Thunb.) Speta, which shows a large deletion in this region and therefore only contains 273 nucleotides, as well as the *Anthericum* and *Leucocrinum* sequences, which are likewise shorter (472–480 nt). The lengths of the IGS sequences ranged from 342 to 408 nucleotides with the exception of *Eustrephus latifolius* (265 nt), *Thysanotus virgatus* Brittan (324 nt), *Leucocrinum montanum* (267 nt), *Anthericum*

(296–299 nt), *Chlorogalum* (306 nt), *Albuca nelsonii* N. E. Br. (247 nt), *Whiteheadia etesionamibensis* Müller-Doblies (268 nt), *Hyacinthella* (271 nt), and *Pfosseria bithynica* (Boiss.) Speta (282 nt), which again exhibit deletions in this region. From nucleotide position 433 to 480 within the intron, a hypervariable AT-rich region occurred, evolving presumably from a di-nucleotide microsatellite. A similar hypervariable poly-T microsatellite was also found in the IGS region from nucleotide position 827 to 835. Since in both cases it was difficult to find unequivocal alignments, and different alignments in these regions always resulted in high homoplasy indices, both regions have been excluded from phylogenetic analyses.

PHYLOGENETIC ANALYSIS

Cladistic analysis of the combined nucleotide plus indel data set yielded more than 10,000 equally parsimonious trees of 1415 steps with a CI of 0.597 and RI of 0.862. Examination of approximately 50 randomly chosen trees revealed only minor differences in the placement of closely related taxa among different trees. One of the most parsimonious trees calculated from the combined nucleotide-indel data set is presented in Figures 1 and 2. Percent support from bootstrap analysis is shown above each branch. Statistical support for branching information using the jackknife procedure is indicated graphically by marking strongly supported clades (node score > 0.63) with closed circles and moderately supported clades (node score < 0.63 but > 0.5) with open circles. Phylogenetic analysis of the same data set but excluding indel data resulted in similar tree topology with only minor changes in bootstrap values (data not shown). Trees constructed using distance matrix analysis using neighbor joining did not deviate significantly from parsimony analysis but showed the tendency to misplace taxa with larger deletions in their sequences (data not shown).

RELATIONSHIPS

The ingroup relationships of all species representing Hyacinthaceae analyzed in this study are depicted in Figure 1, whereas the second part of the tree presenting the outgroup relationships is shown in Figure 2. There is a strong bootstrap support (100%) for the monophyly of the family, if the North American genera *Camassia* and *Chlorogalum* are excluded from Hyacinthaceae, but the monotypic South American genus *Oziroë* Raf. is included. Monophyly of most genera is also supported by bootstrap values: *Fessia* (76%), *Prospero* (87%), *Hyacinthella* (94%), *Scilla* (99%), *Muscari* (97%), *Bellevalia* (100%), *Hyacinthoides* (99%), *Tractema* (96%), *Oncostema* (100%), *Autonoë* (100%), *Drimiopsis* (84%), *Ornithogalum* (53%), *Albuca* (72%), *Dipcadi* (98%), *Charybdis* (<50%), *Rhadamanthus* (92%), *Oziroë* (100%). No single most recent ancestor for all analyzed species of the genera *Ledebouria, Lachenalia, Merwilla, Eliokarmos, Galtonia, Stellarioides,* and *Urginavia* can be found. The remaining genera are represented by a single species only, and therefore no information about the generic delineations can be deduced from the sequence data.

The classification of the Hyacinthaceae into the subfamilies Hyacinthoideae, Ornithogaloideae, Urgineoideae, and Oziroëoideae based on chemotaxonomic characters according to Speta (1998a, b) is also reflected in the cladogram. The monotypic South American subfamily Oziroëoideae Speta is the basal group (100%), followed by the Urgineoideae Speta (100%), a group of species that contains bufadienolids, the Ornithogaloideae Speta (100%), which are characterized by cardenolids and/or the presence of protein crystals in the nucleus, and the less strongly supported clade of Hyacinthoideae Link (56%), a group of species that contains phenolic substances (homoisoflavanoles).

In addition to the classification in four subfamilies, a further species distribution of the subfamilies Hyacinthoideae and Ornithogaloideae into tribes is reflected in the cladogram. Within Hyacinthoideae two clearly separated branches are formed (Figs. 1, 3). The basal branch combines all Indian and African genera south of the Sahara and coincides with the delineation of the tribe Massonieae Baker (67%). The second and more advanced monophyletic clade includes the Mediterranean and Asian genera [= tribe Hyacintheae Dumort.] and is also supported by bootstrap values (78%). Sister to the Hyacinthoideae is the subfamily Ornithogaloideae, which can be further divided into the tribes Dipcadieae Rouy and Ornithogaleae Rouy. However, the relationships are less pronounced in the gene trees (Figs. 1, 4). The Dipcadieae comprise the genera *Pseudogaltonia, Dipcadi, Galtonia, Stellarioides,* and *Albuca* and appear paraphyletic in the analysis, whereas the remaining, mainly Mediterranean genera belong to the tribe Ornithogaleae. If South African *Zahariadia,* which shows affinities to members of *Galtonia,* is excluded from Ornithogaleae, monophyly in this tribe is strongly supported (97%).

The most basal and isolated position in Hyacintheae is occupied by *Barnardia,* a genus with a huge geographical distribution ranging from North

Africa to Japan (Fig. 1). The adjacent clade with *Brimeura, Oncostema, Tractema, Autonoë,* and *Hyacinthoides* is sister to a more advanced clade containing the *Scilla* and *Hyacinthus* alliances. Within *Hyacinthoides,* a division into subgenus *Somera* (Salisb.) Speta consisting of *H. italica* (L.) Rothm., *H. lingulata* (Poir.) Rothm., and *H. aristidis* (Coss.) Rothm. (94%) and subgenus *Hyacinthoides* consisting of *H. nonscripta* (L.) Chouard ex Rothm., *H. hispanica* (Mill.) Rothm., *H. vincentina* (Hoffmanns. & Link) Rothm., and *H. reverchonii* (Degen & Hervier) Speta (85%) is visible (Fig. 3). These two subgenera are characterized by differences in flower morphology, consisting either of a stellate or a campanulate perianth, respectively (Speta, 1987). Furthermore, a well-supported clade with *Hyacinthella, Prospero, Puschkinia, Othocallis, Pfosseria, Hyacinthus, Fessia,* and *Zagrosia* (95%) and a clade with *Chouardia, Nectaroscilla, Schnarfia, Muscari, Bellevalia,* and *Scilla* (84%) are resolved (Fig. 1). There is no bootstrap support for a genus *Chionodoxa.* On the contrary, members of this obsolete genus (*S. nana* (J. A. & J. H. Schultes) Speta, *S. siehei* (Stapf) Speta, *S. albescens* Speta) are intermixed with species of *Scilla* (Fig. 1).

Within Massonieae, a close relationship between *Drimiopsis* and *Ledebouria* is evident (100% bootstrap support), as well as a relationship between *Lachenalia* and *Polyxena* (100%). However, both *Ledebouria* and *Lachenalia* are genera with huge numbers of species, the examination of which still can lead to further differentiation.

Sister to Hyacinthoideae is a clade combining members of the subfamily Ornithogaloideae (Fig. 4). Basal in Ornithogaloideae are members of the tribe Dipcadieae, which accommodates mainly South African genera (*Galtonia, Albuca, Stellarioides, Pseudogaltonia, Dipcadi*). Interestingly, *Galtonia candicans* (Baker) Decne. groups with *Stellarioides* and *Albuca* (86%), whereas *G. viridiflora* Verdoorn and *G. princeps* (Baker) Decne. are combined in one clade with *Zahariadia* (98%) (Fig. 1). Basal in the tribe Ornithogaleae are African species (*Eliokarmos*) followed by the Mediterranean genera *Melomphis* and *Cathissa,* whereas the remaining Mediterranean species are clearly separated (97%) and occur at a more advanced position (e.g., *Loncomelos, Honorius,* and the *Ornithogalum umbellatum* L. and affines).

The next major clade contains species belonging to the subfamily Urgineoideae (Fig. 1). Clearly included in Urgineoideae is the rather peculiar genus *Bowiea* (100%), which lacks leaves as an adult plant except for the bulb scales, and assimilates energy by an intricately branched inflorescence. In this subfamily the basal positions are again occupied by genera from South Africa and Madagascar (*Bowiea, Rhadamanthus, Thuranthos, Ebertia, Urginavia, Karoophila*), and are sister to a clade combining the Mediterranean genera *Urginea* and *Charybdis* (100%).

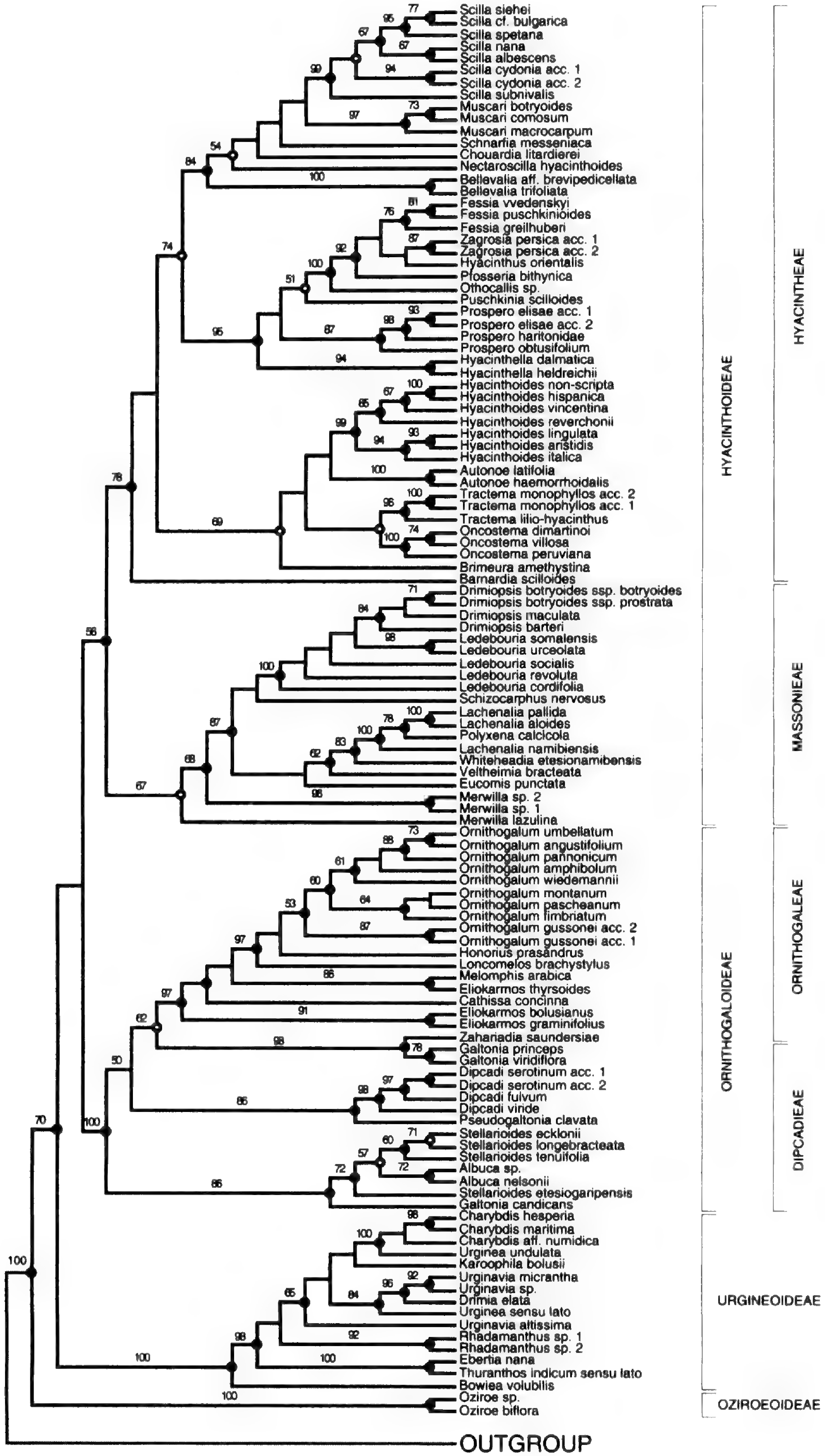
Sister to all Old World Hyacinthaceae is the South American subfamily Oziroëoideae, with the only genus *Oziroë* [= *Fortunatia* Macbr.] (Fig. 1).

Clearly distinct from Hyacinthaceae are the North American bulbous genera *Chlorogalum* and *Camassia,* which form a monophyletic clade (97%) (Figs. 2, 5). Instead, these genera show affinities to the North American family Agavaceae, the East Asian Funkiaceae, and Anthericaceae, which show a worldwide distribution even in the narrow circumscription of Conran (1998a) but with major centers of diversity in Africa, Southeast Asia, and Central and South America. Between this *Chlorogalum–Camassia* clade and Hyacinthaceae, the family Themidaceae, which is endemic to North America, is inserted, although this tree topology is not supported by bootstrap values. More distantly related to Hyacinthaceae are members of the Australian families Lomandraceae, Doryanthaceae, Blandfordiaceae, members of the Asian family Hemerocallidaceae, and of the African, South American, and Laurasian family Amaryllidaceae. Interestingly, *trn*L and *trn*F sequence data place Blandfordiaceae and Doryanthaceae (100%) in close association (Fig. 2). More distantly related are other asparagoid Lilianae like the Laurasian family Convallariaceae, and the North American Nolinaceae. A possible relationship to Alliaceae could not be evaluated since their sequences are too divergent due to extensive deletions and rearrangements in the *trn*L and *trn*F region (data not considered here).

Discussion

Phylogenetic analysis of about 53 genera in Hyacinthaceae and 24 outgroup genera (including *Camassia* and *Chlorogalum*) provides additional data to readdress several critical systematic questions of this controversial plant family.

Scilla clade. Our data strongly support a narrow concept of the genus *Scilla,* as already evident from karyological and morphological data (Speta, 1979, 1986, 1987, 1998a, b). According to our sequence data, the only true *Scilla* species are found in the European and Southwest Asian Mediterranean region, and no direct relatives exist in Africa south of the Sahara (Speta, 1998a). Inclusion of sequence data of the species *S. lazulina* Wild and *S. nervosa* Burch. in a recently published study on


Scilla siehei
Scilla cf. bulgarica
Scilla spetana
Scilla nana
Scilla albescens
Scilla cydonia acc. 1
Scilla cydonia acc. 2
Scilla subnivalis
Muscari botryoides
Muscari comosum
Muscari macrocarpum
Schnarfia messeniaca
Chouardia litardierei
Nectaroscilla hyacinthoides
Bellevalia aff. brevipedicellata
Bellevalia trifoliata
Fessia vvedenskyi
Fessia puschkinioides
Fessia greilhuberi
Zagrosia persica acc. 1
Zagrosia persica acc. 2
Hyacinthus orientalis
Pfosseria bithynica
Othocallis sp.
Puschkinia scilloides
Prospero elisae acc. 1
Prospero elisae acc. 2
Prospero haritonidae
Prospero obtusifolium
Hyacinthella dalmatica
Hyacinthella heldreichii
Hyacinthoides non-scripta
Hyacinthoides hispanica
Hyacinthoides vincentina
Hyacinthoides reverchonii
Hyacinthoides lingulata
Hyacinthoides aristidis
Hyacinthoides italica
Autonoe latifolia
Autonoe haemorrhoidalis
Tractema monophyllos acc. 2
Tractema monophyllos acc. 1
Tractema lilio-hyacinthus
Oncostema dimartinoi
Oncostema villosa
Oncostema peruviana
Brimeura amethystina
Barnardia scilloides
Drimiopsis botryoides ssp. botryoides
Drimiopsis botryoides ssp. prostrata
Drimiopsis maculata
Drimiopsis barteri
Ledebouria somalensis
Ledebouria urceolata
Ledebouria socialis
Ledebouria revoluta
Ledebouria cordifolia
Schizocarphus nervosus
Lachenalia pallida
Lachenalia aloides
Polyxena calcicola
Lachenalia namibiensis
Whiteheadia etesionamibensis
Veltheimia bracteata
Eucomis punctata
Merwilla sp. 2
Merwilla sp. 1
Merwilla lazulina
Ornithogalum umbellatum
Ornithogalum angustifolium
Ornithogalum pannonicum
Ornithogalum amphibolum
Ornithogalum wiedemannii
Ornithogalum montanum
Ornithogalum pascheanum
Ornithogalum fimbriatum
Ornithogalum gussonei acc. 2
Ornithogalum gussonei acc. 1
Honorius prasandrus
Loncomelos brachystylus
Melomphis arabica
Eliokarmos thyrsoides
Cathissa concinna
Eliokarmos bolusianus
Eliokarmos graminifolius
Zahariadia saundersiae
Galtonia princeps
Galtonia viridiflora
Dipcadi serotinum acc. 1
Dipcadi serotinum acc. 2
Dipcadi fulvum
Dipcadi viride
Pseudogaltonia clavata
Stellarioides ecklonii
Stellarioides longebracteata
Stellarioides tenuifolia
Albuca sp.
Albuca nelsonii
Stellarioides etesiogaripensis
Galtonia candicans
Charybdis hesperia
Charybdis maritima
Charybdis aff. numidica
Urginea undulata
Karoophila bolusii
Urginavia micrantha
Urginavia sp.
Drimia elata
Urginea sensu lato
Urginavia altissima
Rhadamanthus sp. 1
Rhadamanthus sp. 2
Ebertia nana
Thuranthos indicum sensu lato
Bowiea volubilis
Oziroe sp.
Oziroe biflora
OUTGROUP
HYACINTHOIDEAE
HYACINTHEAE
MASSONIEAE
ORNITHOGALOIDEAE
ORNITHOGALEAE
DIPCADIEAE
URGINEOIDEAE
OZIROEOIDEAE

sub-Saharan *Scilla* relationships (Stedje, 1998) clearly supports this view. Both species group within the Massonieae clade and show no relationship to *Scilla* sensu stricto and therefore have been named *Merwilla lazulina* (Wild) Speta and *Schizocarphus nervosus* (Burch.) Speta, respectively (Speta, 1998a). Although *Chionodoxa* can be easily discriminated from *Scilla* due to the basal fusion of the tepals and a broadening of the filaments, these morphological characters are overestimated as useful phylogenetic markers. Instead, in phylogenetic reconstructions this character appears to be paraphyletic and seems to have evolved in several lines within the family. Moreover, *Chionodoxa* species can give rise to hybrids when crossed with members of the *Scilla bifolia* L. complex. It has been proposed to include them in *Scilla*, whereas *Puschkinia*, similar to *Chionodoxa* in habit, evidently has other affinities (Speta, 1971, 1976). DNA sequence data place *Puschkinia* in a clade with *Hyacinthella*, *Prospero*, *Othocallis*, *Pfosseria*, *Hyacinthus*, *Zagrosia*, and *Fessia*, clearly different from the *Scilla* relationship (95%) (Fig. 1). However, the phylogenetic signal within the *Scilla* clade is not very strong. Branch lengths differ in only 1 to 4 steps in this clade (Fig. 3). The two accessions of *S. cydonia* Speta even have exactly the same DNA sequences, although they are collected from geographically distant regions (Crete and Karpathos). Re-examination of this relationship with additional molecular data sets could increase the resolution in this clade.

The genus *Muscari* is monophyletic and represents an example of how in Hyacinthaceae even karyotype differences can be overestimated (Garbari & Greuter, 1970). Monophyly in this clade could support the idea of a broader genus concept in *Muscari* (Speta, 1982, 1989) instead of dividing this genus into the genera *Muscari*, *Leopoldia*, and *Muscarimia*, represented in our analysis by *Muscari botryoides* (L.) Mill., *M. comosum* (L.) Mill., and *M. macrocarpum* Sweet, respectively (Fig. 1). Whereas Garbari recognized these genera as distinct from each other due to karyotypic differences, Speta (1982, 1989), Bentzer (1973), and Davis and Stuart (1984) found transitions in character expression between different species and therefore suggested they be treated only as subgenera.

Fessia clade. Similarities in the karyotypes of *Chouardia* Speta [= *Scilla litardierei* Breistr.] and *Hyacinthella* as well as morphologies (locules with two ovules side by side, terete scape, dense raceme) have led to the speculation of a closer relationship (Speta, 1981). However, Persson and Wendelbo (1982) supported the view that the similarity in the karyotypes is probably only secondary, constituting a case of convergent evolution within the *Scilla* sensu lato lineage as well as the lineage to present *Hyacinthella* species. In our analysis, *Hyacinthella* clearly belongs to the clade *Fessia–Zagrosia–Hyacinthus–Pfosseria–Othocallis–Puschkinia–Prospero* (95%), and not to the *Scilla* relationship (Fig. 1). However, the relative position of *Hyacinthella* within this clade is not stable due to a basal polytomy in this group (Fig. 3). Unfortunately, *Alrawia*, a genus that could show affinities to *Hyacinthella* and therefore could shed light on this relationship, was not available for this study. The IGS sequences of the two *Hyacinthella* species contain a characteristic 5 bp deletion, which they share with Oziroëoideae, Ornithogaloideae, the African genera *Eucomis*, *Veltheimia*, and the *Lachenalia/Polyxena* clade: this may suggest the motif represents an ancient element. The existence of ancient elements in DNA sequences of species belonging to different groups sometimes results in weakly supported tree topologies. This is also the case with the position of *Hyacinthella*, which in some trees showed a different position within this clade (data not shown). Although the habit of problematic *Puschkinia* closely resembles that of *Scilla bifolia*, phylogenetic reconstructions position it clearly distinct from *Scilla* sensu stricto. Additionally, a suite of morphological characters also clearly separates *Puschkinia* from *Scilla*. The corolla and corona, the *Fessia*-like ovary, seeds with a sarcotesta, bulbs with vaginate scales, and chromosome number ($2n = 10$) are all characters discriminating *Puschkinia* from *Scilla*. A similar chromosome number in *Fessia* ($2n = 10$) suggests a possible relationship, but Greilhuber and Speta (1976) demonstrated karyological differences. A closer relationship with *Muscari* (Wunderlich, 1937) is refuted by our DNA sequence data. In *Fessia*, two species complexes have been proposed: (1) the *S. hohenackeri* group and (2) the *S. bisotunensis* relationship (Speta, 1981). Sev-

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Figure 1. One of the most parsimonious successively weighted trees showing the relationships within Hyacinthaceae. Bootstrap percentages are indicated above the branches. Subfamilial and tribal limits sensu Speta (1998a, b) are indicated on the right border. Nodes strongly supported by the jackknife algorithm (node score > 0.63) are indicated by solid circles. Open circles indicate nodes that are weakly supported (node score > 0.5 but < 0.63).

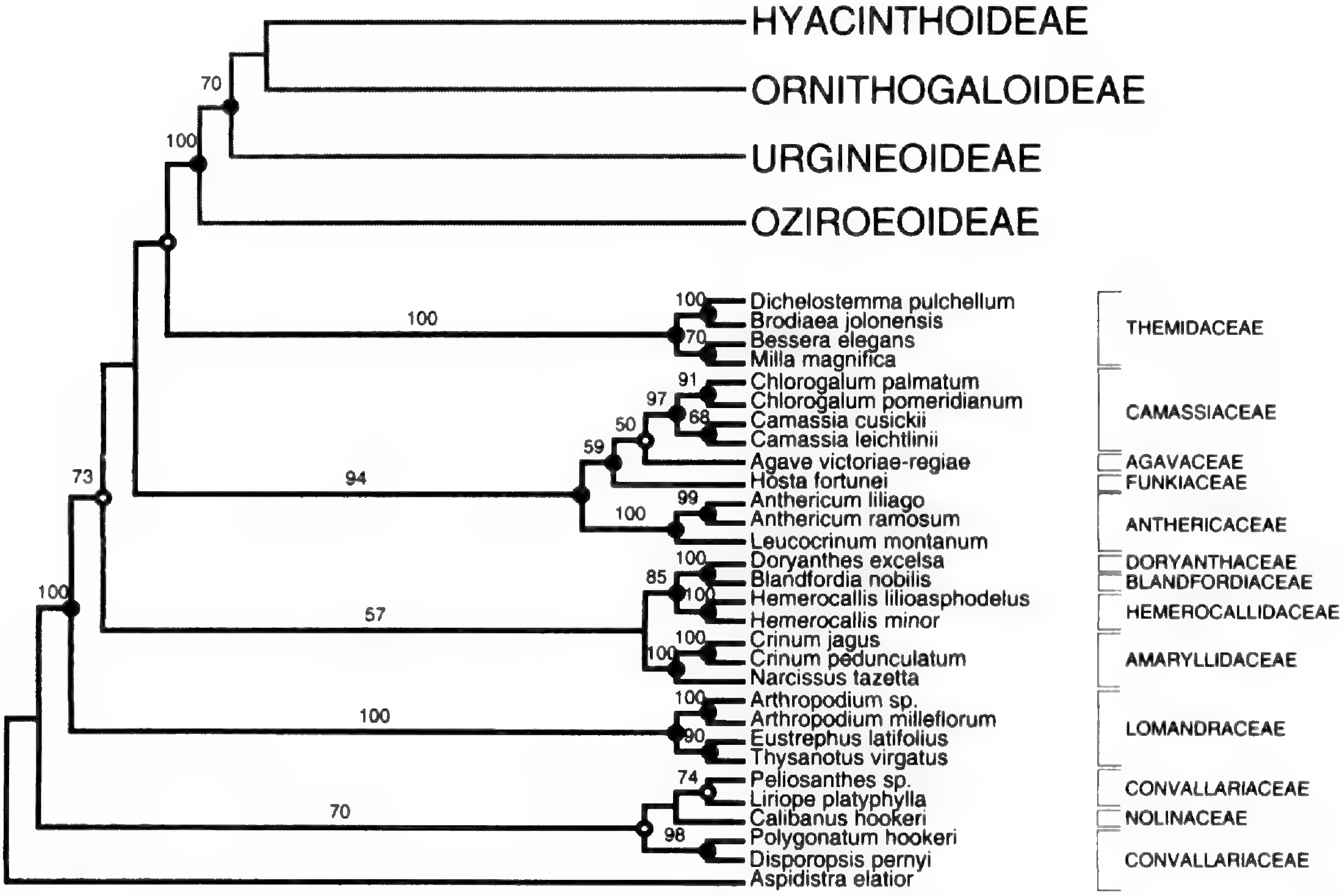

Figure 2. Second part of one of the most parsimonious successively weighted trees showing the outgroup relationships. Bootstrap percentages are indicated above the branches. Nodes strongly supported by the jackknife algorithm (node score > 0.63) are indicated by solid circles. Open circles indicate nodes that are weakly supported (node score > 0.5 but < 0.63).

eral character anomalies exist such as hypogeous cotyledons in *F. greilhuberi* (Speta) Speta but epigeous ones in all other species examined, or a karyotype in *F. gorganica* (Speta) Speta of $2n = 18$ rather than the typical $2n = 10$: these warrant further research in this clade. The close nesting of *Zagrosia* and *Hyacinthus* is particularly unexpected. DNA sequence data of two other *Hyacinthus* species, *H. litwinowii* E. Czern. and *H. transcaspicus* Litw. from Turkmenistan and northeast Iran, respectively, could address the position of *Hyacinthus* in this clade. Similarities in the karyotypes of *Zagrosia* and *Bellevalia* (large chromosomes; $x = 4$; Speta, 1974, 1981: 169) suggest a possible relationship, but no indication of such emerges from the molecular data. The strong separation of *Othocallis* and *Scilla* sensu stricto is somewhat surprising, indicating that morphological and karyological differences may have been underestimated so far.

Hyacinthoides clade. Morphological and karyological evidence do not support a relationship between *Autonoë* and *Hyacinthoides* as suggested by their close association in the cladogram (Figs. 1, 3). Although combined in a separate branch in the molecular analysis, there is no bootstrap support for a possible direct relationship (Fig. 1). Basal to this clade is a cluster with *Brimeura, Oncostema,* and *Tractema*, a relationship already suggested on morphological and karyological grounds (Speta, 1987). Although bootstrap support for this relationship is not very high, closer affinity is likely, since trees constructed from *mat*K sequences directly connect *Brimeura* with *Tractema* (Pfosser, unpublished data). Tree topology clearly corroborates the division of *Hyacinthoides* into subgenera *Somera* and *Hyacinthoides*, a position not shared by Ortiz and Rodríguez-Oubiña (1996).

As in *Hyacinthella, Barnardia,* the most basal member of Hyacinthoideae, also contains sequence elements shared by different groups like *Lachenalia, Polyxena,* and *Dipcadi*, again indicating an ancient origin for *Barnardia*. Evidence relating *Barnardia* to *Prospero* Speta (1986, 1993) is based on the dysploid series of chromosome numbers (*Prospero*, $x = 4, 5, 6, 7$, and *Barnardia*, $x = 8, 9$), and that both are autumn-flowering genera with similar habit. This relationship is not supported by the molecular data.

Massonieae clade. All South African genera cluster together in tribe Massonieae. This is surprising since they appear morphologically hetero-

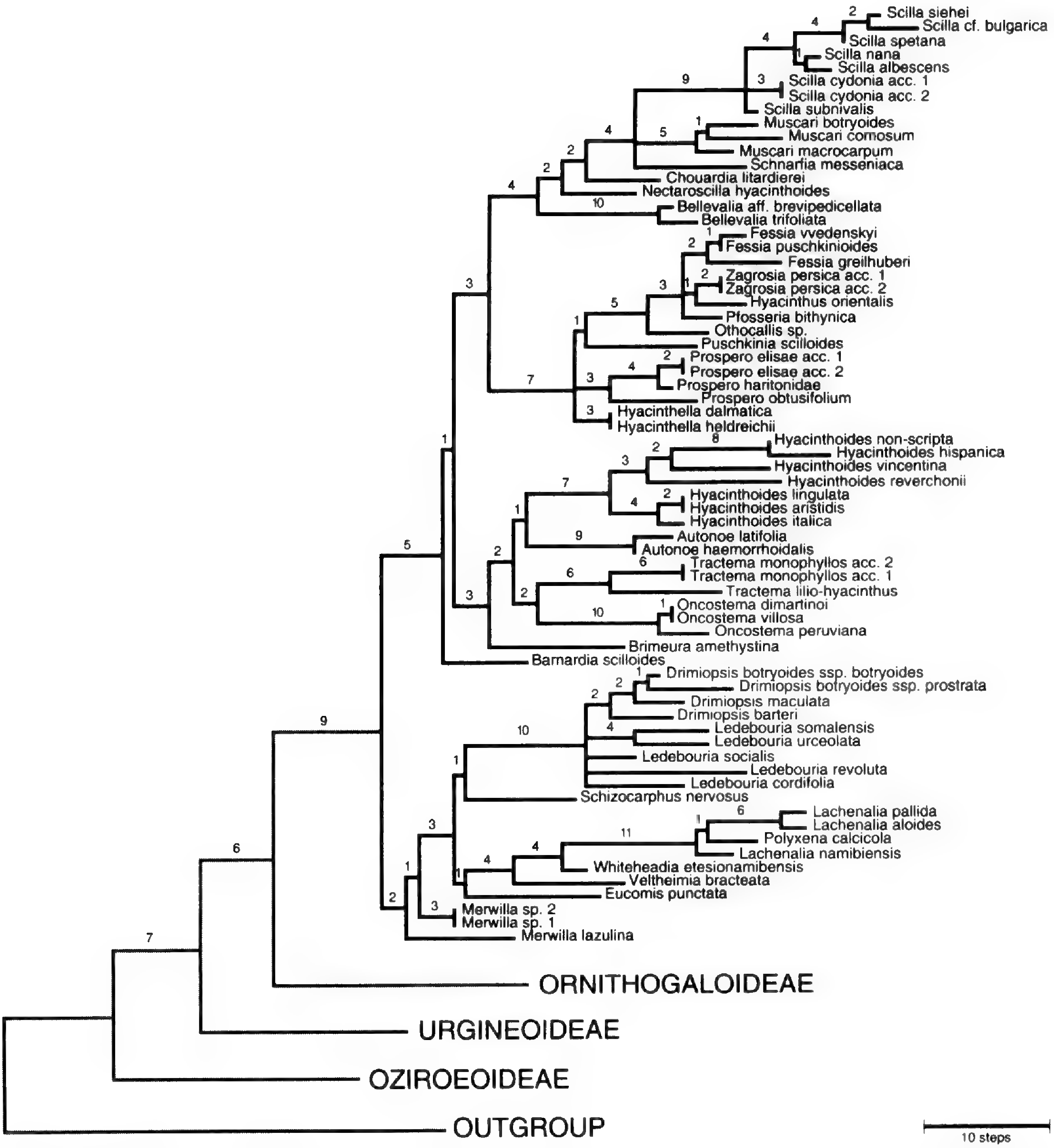

Figure 3. Phylogram showing the relationships within subfamily Hyacinthoideae. Fitch branch lengths are indicated above the branches. For bootstrap percentages compare with Figure 1.

geneous when considering *Eucomis*, *Veltheimia*, *Lachenalia*, *Ledebouria*, and *Merwilla*. It would be interesting to more thoroughly investigate the genera *Lachenalia* and *Polyxena*. *Lachenalia* with almost 100 species was split into several genera by Salisbury (1866). Although only three species were analyzed by us, our data at least suggest that there might be enough variability to warrant further splitting of this genus. If the generic status of *Polyxena* is maintained, then at least two relationships are indicated: the *Lachenalia namibiensis* W. F. Barker and the *L. aloides* (L. f.) Engl./*L. pallida* Aiton relationships. In contrast to our evidence for close relationship between *Lachenalia* and *Polyxena*, Müller-Doblies and Müller-Doblies (1997) placed these two genera in the different subtribes Lachenaliinae and Massoniinae, respectively. In their classification, *Lachenalia* and *Veltheimia* belong to the subtribe Lachenaliinae, whereas *Whiteheadia*, which in our analysis inserts between these two genera, belongs to subtribe Massoniinae. A close relationship between *Ledebouria* and *Drimiopsis* [= subtribe Ledebouriinae sensu U. & D. Müller-Doblies] is supported by our molecular data (100%

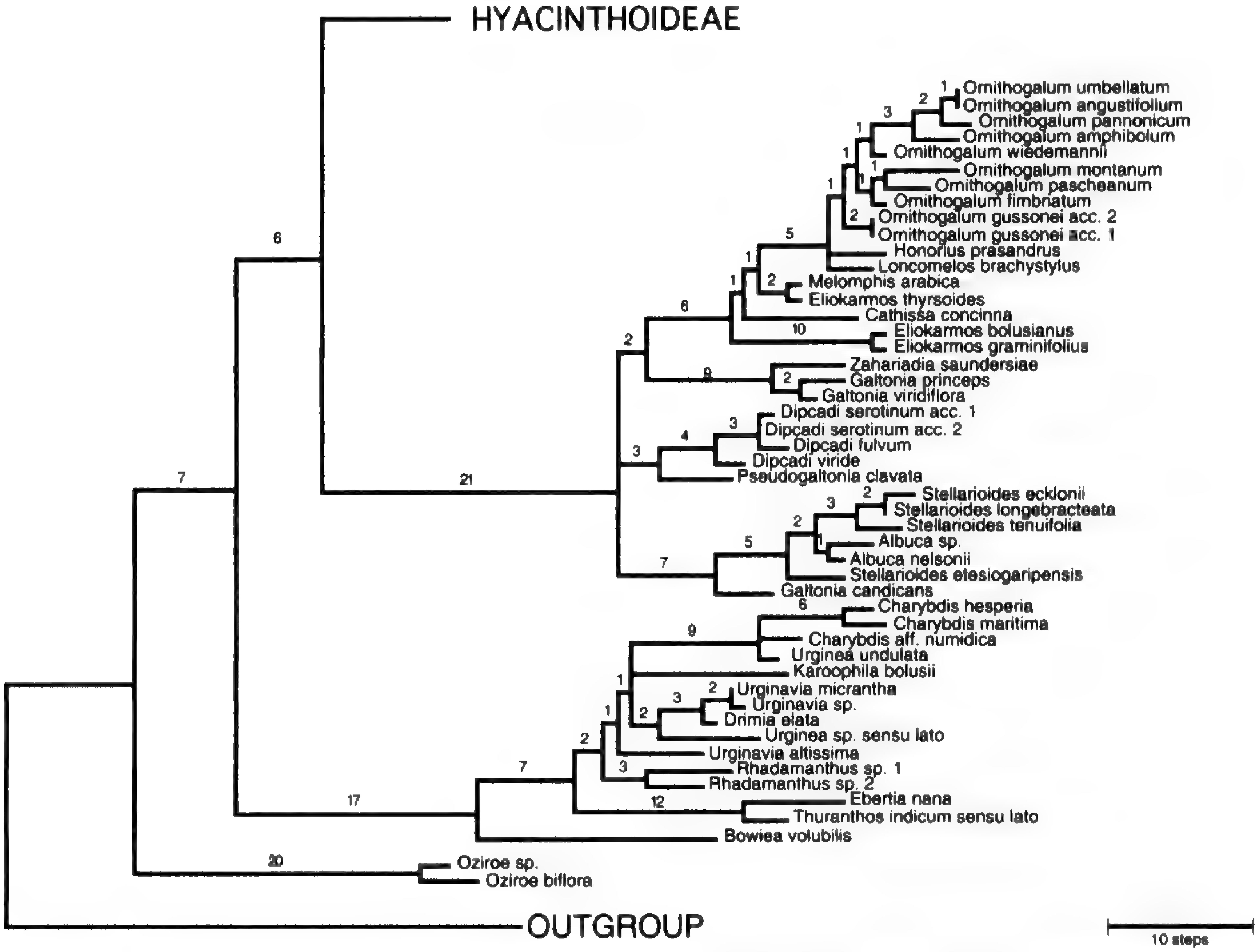

Figure 4. Phylogram showing the relationships within the subfamilies Ornithogaloideae, Urgineoideae, and Oziroëoideae. Fitch branch lengths are indicated above the branches. For bootstrap percentages compare with Figure 1.

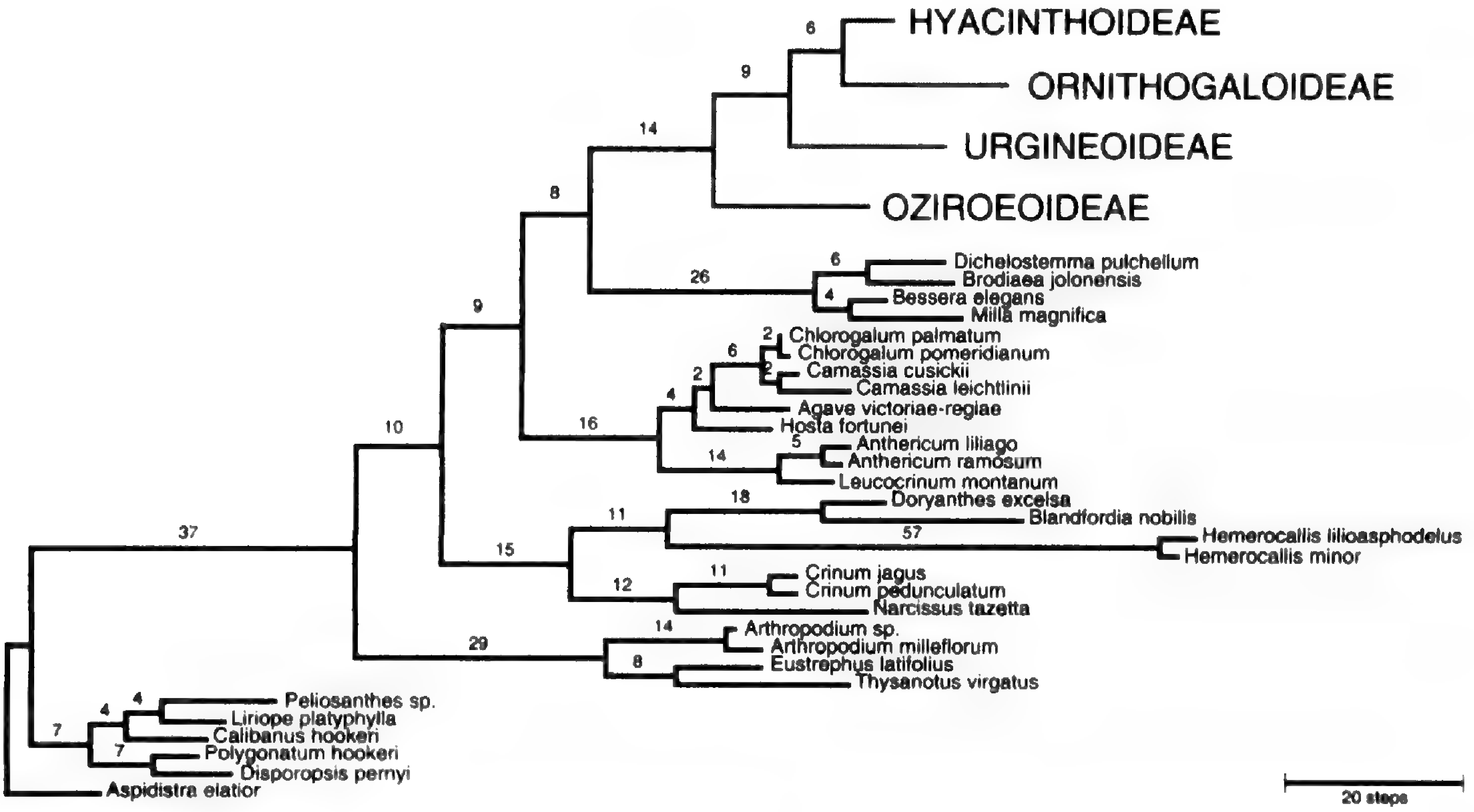

Figure 5. Phylogram showing the outgroup relationships. Fitch branch lengths are indicated above the branches. For bootstrap percentages compare with Figure 2.

bootstrap support in Fig. 1). However, *Resnova*, a third genus included in Ledebouriinae, was not available for sequencing. How far the generic combinations of Jessop (1975) within Massonieae are paralleled by molecular data remains to be seen, especially since *Polyxena* and *Lachenalia* are in close neighborhood in our analysis. *Daubenya*, *Androsiphon*, and *Amphisiphon* share many characters with *Whiteheadia* and therefore would no doubt insert in the same branch. However, their individual positions as distinct genera should probably be reevaluated since various prominent features of corolla and filaments might have been overestimated so far. Stedje (1998) published a study examining the relationships of sub-Saharan *Scilla* sensu lato species, which revealed a close relationship between *Ledebouria* and *Drimiopsis*, whereas the generic status of other members of *Scilla* sensu lato was not resolved. Inclusion of her DNA sequence data in our analysis clearly demonstrated a close relationship of the South African species to *Ledebouria* and *Drimiopsis*, but no affinity to the Mediterranean species.

Less clear are the generic relationships within the two major branches consisting of the subfamilies Ornithogaloideae and Urgineoideae.

Ornithogaloideae clade. The old Linnaean genus *Ornithogalum*, a heterogeneous assemblage of numerous species, represents a big taxonomic problem and still awaits its distribution into more natural genera. This unsatisfactory situation may partly inflate the analysis, since taxon sampling in Ornithogaloideae is less complete than in Hyacinthoideae. Nevertheless, the 30 species investigated in this study form a monophyletic group (100% bootstrap support in Fig. 1). Taxon sampling should be further increased as soon as a clearer view of this large genus is available. One distinct branch, combining *Stellarioides* and *Albuca*, one with *Dipcadi* and *Pseudogaltonia*, and one with the rest of the subfamily are visible (Fig. 1). In the phylogram, a polytomy is indicated with these three clades arising from a single node (Fig. 4). Within Ornithogaleae, *Cathissa* from the southwest Mediterranean and *Eliokarmos* from South Africa appear as basal genera, while the generitype *O. umbellatum* L. occupies a rather derived position (Fig. 4). Based on DNA sequence data, a proposed relationship between the *Ornithogalum longebracteatum* Jacq. group [= *Stellarioides*] and *Ornithogalum* subg. *Beryllis* [= *Loncomelos*] (Baker, 1873) can be clearly refuted. The first group of species is in close vicinity to *Albuca* and belongs to *Stellarioides*. Originally included under *Ornithogalum*, a closer relationship of this genus with *Albuca* was noticed by Obermeyer (1978). Once again, only a few indications of a direct relationship between Mediterranean and South African genera are recognizable. Similar to the *Scilla* clade, only short branches separate *Ornithogalum* species from each other. Again, molecular data sets with higher variability could probably increase the resolution within this *Ornithogalum* clade. Preliminary *trn*L and *trn*F sequence data of the *Ornithogalum montanum* Ten. sensu lato relationship does suggest that sequence variation in this region may suffice to describe different geographical races as they occur in the Aegean region (Pfosser, unpublished data).

Urgineoideae clade. Obscure relationships similar to those in Ornithogaloideae also exist in the large subfamily Urgineoideae, with *Bowiea* providing a historic example. Takhtajan (1997) questioned its position in Hyacinthaceae, concluding that this genus probably should be included somewhere else. However, it appears clear now from Figure 1 that *Bowiea* has to be included in subfamily Urgineoideae after misplacement in Asphodeloideae–Eriosperminae (Engler, 1887) and in Liliaceae–Bowieae (Hutchinson, 1934). Even more problematic is the taxonomic history of Mediterranean squill. This old medicinal plant was first treated as *Scilla maritima* (Linnaeus, 1753), then as *Urginea maritima* aggregate (Steinheil, 1834), later separated from *Urginea* as *Squilla* (Steinheil, 1836). It has even been included in *Drimia* (Jessop, 1977; Stearn, 1978; Stedje, 1987). Both Speta (1998a) and Steinheil (1836) were convinced of an independent status of the *Urginea maritima* relationship, which consequently led to the introduction of the genus *Charybdis* (Speta, 1998a). In Figure 1, the Mediterranean squills are at least in the vicinity of a true member of *Urginea* (*U. undulata* (Desf.) Steinh.). The number of species investigated in this clade is not sufficient to lead to an adequate description of this subfamily; however, the results thus obtained do provide valuable anchor points for additional sampling.

Oziroeoideae clade. The last subfamily in Hyacinthoideae contains the South American genus *Oziroë* [= *Fortunatia*] and occupies an isolated basal position in Hyacinthaceae. This indicates an ancient split between Old World and New World taxa, resulting in two independent evolutionary lineages. If there are direct relatives to *Oziroë* existing somewhere in Africa, they remain to be found.

Outgroup. Enough evidence has accumulated to demonstrate that the North American genera *Camassia* and *Chlorogalum* can no longer be included in Hyacinthaceae (Figs. 2, 5). Our *trn*L and *trn*F sequence data, *rbc*L sequence data (Fay & Chase, 1996; Chase et al., 1995), as well as serological data (Cupov & Kutjavina, 1981), all point to a relationship of these genera to Agavaceae, Funkiaceae, and Anthericaceae and not to Hyacinthaceae. Recognizing these genera as a separate family Camassiaceae as proposed by Cupov (1994) should await evaluation of all available data. For now we concur, since this proposal offers the most appropriate perspective on these genera. At least *Hosta, Camassia,* and *Chlorogalum* share a bimodal karyotype typical for Agavaceae. However, Agavaceae represent a paraphyletic assemblage in their present circumscription as suggested by nuclear ITS sequence data (Bogler & Simpson, 1996). Recently, now that increasing *rbc*L data has accumulated and been phylogenetically evaluated, major rearrangements among the Liliaceae sensu lato, Anthericaceae, and other monocot families have been attempted. Kubitzki (1998) tried to incorporate molecular information in his treatment of monocots in volume III of his *The Families and Genera of Vascular Plants.* Chase et al. (1996) previously noted that Amaryllidaceae, Alliaceae, and Lomandraceae are probably sister families to Hyacinthaceae. Moreover, Themidaceae have been shown to be in close vicinity to the Hyacinthaceae (Fay & Chase, 1996), a view supported also from *trn*L and *trn*F data (Fig. 2). Since the position of *Chlorogalum* and *Camassia* also had to be investigated, we included a few less well-known potential relatives in our analysis. Somewhat surprising in our analysis is the position of the family Amaryllidaceae, which is sister to a clade combining *Hemerocallis* and *Doryanthes* and *Blandfordia.* Since an affinity of Doryanthaceae to Phormiaceae was suggested (Dahlgren et al., 1985), and the Hemerocallidaceae were recently coalesced with Phormiaceae and are no longer monogeneric (Clifford et al., 1998), this clade becomes more understandable. Although bound by relatively long branches (Fig. 5), *Doryanthes* and *Blandfordia,* both monotypic for their respective families (Dahlgren et al., 1985), combine in one clade (100% bootstrap support in Fig. 2). Adjacent to this clade, *Arthropodium, Thysanotus,* and *Eustrephus* also combine (100% bootstrap support in Fig. 2). Support for this comes from *rbc*L sequence data (Chase et al., 1996; Conran, 1998b), with these species combined under Lomandraceae.

Deep branching points of all subfamilies except Hyacinthoideae are characterized by long branches of 21 steps (Ornithogaloideae), 17 steps (Urgineoideae), and 20 steps (Oziroeoideae), indicating a high number of nucleotide changes before speciation within the subfamilies occurred (Fig. 4). This could either suggest that the nucleotide substitution rate in this family was higher during a primary radiation than subsequent ones, or that sampling bias occurred because of extinction events, or that primary radiation occurred slowly. The presence of a few isolated genera like *Brimeura, Barnardia, Merwilla,* and *Bowiea* at basal positions in some subfamilies, however, could suggest extinction events. If other basal genera still exist, then they probably will be found among the Urgineoideae or Ornithogaloideae in South Africa or Madagascar.

Most genera in this analysis grouping together also show a sympatric occurrence. While true for Hyacintheae or Massonieae in general, *Galtonia* and *Zahariadia* from eastern South Africa are also sympatric (Obermeyer, 1978; Hilliard & Burtt, 1988), as are *Tractema, Oncostema, Brimeura,* and *Hyacinthoides* from the western Mediterranean, as well as outgroup genera like *Blandfordia* and *Doryanthes.* Similarly, that molecular data reflect sympatric relationships was already noted for *Crinum* species (Fangan & Nordal, 1993). This in turn suggests that environmental influences leading to convergent evolution or reversals of morphological characters after species migration should be cautiously re-examined with respect to systematic research. To address this, it would be necessary to evaluate morphological characters that are not or only to a small extent influenced by environmental constraints. It is still not clear if molecular data, especially noncoding DNA regions, are absolutely free of biases resulting from convergent evolution, which could inflate the significance of the analysis. Recently, it has been shown that even noncoding DNA, free of functional constraints, still can show convergent evolution due to specific sequence motifs, which can lead to preferred sites of mutations (Morton, 1995). It should also be noted that the most advanced positions in each clade are generally occupied by genera containing numerous species (*Fessia, Scilla, Hyacinthoides, Drimiopsis* and *Ledebouria, Ornithogalum, Dipcadi, Charybdis*), indicating a process of active evolution. Conversely, basal positions of clades usually contain genera with only a few species in relic areas like *Bowiea* in southern and eastern Africa, *Galtonia* and *Zahariadia* in eastern South Africa, *Pseudogaltonia* in western South Africa, *Merwilla* in South Africa, *Chouardia* in the Dalmatian region, *Nectaroscilla* in the eastern Mediterranean, and *Brimeura* in the western Mediterranean. Exceptions to this trend are: (1) the large genus *Lachenalia,* with a rather confined radiation south of the Sahara; and (2) *Barnardia,* a basal genus with a huge disjunct distribution extending from northwest Africa to southeast Asia. Alternately, *Barnardia* could be viewed as the only extant genus of a largely extinct clade, as indicated by its isolated basal position in subfamily Hyacinthoideae.

Involvement of species from South Africa, South America, and Madagascar in the basal branchings of subfamilies and tribes is indicative of southern, Gondwanic, origin of the Hyacinthaceae. Direct migration between South America, Africa, Madagascar, and India was possible until the mid Cretaceous (ca. 100 m.y. BP). Similar radiation patterns are known elsewhere, such as fossil evidence for sauropods in the Upper Cretaceous of Madagascar, with the genus *Laplatasaurus* reported in India and Madagascar, as well as South America (Charig, 1973). Since there is no evident relationship of North American *Chlorogalum* and *Camassia* species to the Hyacinthaceae, species diversification or migration to different continents perhaps did not start before Laurasia and Gondwanaland were separated in early Cretaceous. At this time, South America was still connected to Africa, but no land bridge existed between South and North America. Species distribution within Massonieae in Africa only south of the Sahara, and in the Indian subcontinent (*Ledebouria, Drimiopsis*), further suggests that diversification occurred when India was still connected to southern Africa, not only via species migration to northern Africa and Eurasia. The distribution pattern of members of the tribe Hyacintheae in the Mediterranean region and in Eurasia, but not in North America, suggests that diversification in this tribe began later, when North America was already clearly separated from Eurasia. The appearance of *Barnardia* at the most basal position of Hyacintheae indicates an early origin of evolution for this genus, making it a candidate for first colonization of the Mediterranean region. Its continental distribution from north Africa to east Asia, even to Japan, is a typical radiation pattern for an old taxon. This would explain why no members of the Hyacinthaceae are found in North America, although climatic conditions are suitable. An unrelated origin of the Camassiaceae apart from the Hyacinthaceae moreover avoids such an unusual disjunction between the Camassiaceae, endemic to North America, and monotypic *Oziroë* in Chile. Similarily, the paradox of range disjunction between Alliaceae and Brodiaeae in North America, yet the rest of the Alliaceae being mainly South American, was recently elucidated by the phylogenetic positioning of Brodiaeae apart from Alliaceae. To retain a monophyletic Alliaceae, the family Themidaceae was resurrected for this tribe (Fay & Chase, 1996). For the entire order Asparagales, West Gondwanaland most likely was the primary site of evolution. Family members close to Asphodelaceae and Phormiaceae seem to have reached Australasia early, whereas elements related to Asparagaceae, Asphodelaceae, and Amaryllidaceae–Hemerocallidaceae suggest old connections between Africa and South America. The Agavaceae alliance of subhumid and arid regions of North America presumably represent an ancient Laurasian group (Raven & Axelrod, 1974). Similar interfamilial relationships have already been proposed by Fay and Chase (1996). The Alliaceae alliance, which in their study shows affinities to Amaryllidaceae, has been excluded in our analysis since their sequences are too divergent due to massive deletions and rearrangements in the *trn*L and *trn*F regions: their inclusion would have inflated the phylogenetic signal in the calculations (data not shown).

For no plant family is it more true than for Hyacinthaceae that the interpretation of single morphological characters resulted in highly erratic classifications when delineating tribal and subfamilial relationships. No character, from bulb morphology to pistils or seeds, or even karyological data, has proved to be reliable. Therefore, it was necessary to assemble all available information for proper classification. Four subfamilies were best distinguished by their secondary metabolites and by the presence or absence of nuclear protein crystals. Assessment of relationships based on molecular data offers the considerable advantage that a priori biases of relative character value are largely avoided. Comparing groups at generic and higher hierarchical levels as classified by Speta (1998a, b) with cladistic analysis of molecular data was clearly warranted. It was more than a surprise when sequence data confirmed not only the higher-level classification but also most generic groupings. Outside of Scilleae, only *Bowiea* and *Schizobasis* had to be included in Hyacinthaceae, and exclusion of Camassiaceae finally resulted in a monophyletic family Hyacinthaceae. The Hyacinthaceae obviously represent the final products of a lineage showing affinities to Themidaceae, Anthericaceae, and Amaryllidaceae. This cladistic analysis results in significant progress in the splitting of the Linnaean genera *Scilla* and *Hyacinthus* into more homogeneous genera. *Ornithogalum* and some complexes within Urgineoideae still await further taxonomic resolution. However, the molecular data presented here serve as valuable starting points toward identifying critical taxa or for the evaluation of additional nonmolecular characters.

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Appendix 1. Species analyzed, arranged alphabetically by families, including collector's data and EMBL data library accession numbers. ° Vouchers for all species sequenced in this study are deposited in LI unless other herbarium designations are given. * Species, for which DNA sequences have been produced directly from herbarium specimens. § Publication, in which trnL/trnF sequences for this taxon were first cited.

Species	Family	Locality	Voucher°	EMBL acc. no.		Literature citation§
				Intron	IGS	
Agave victoriae-regiae T. Moore	Agavaceae	Mexico: Nueva Leon, Huasteca Canyon	Schatzl AG02	AJ232447	AJ232570	this paper
Crinum jagus (Thomson) Dandy	Amaryllidaceae	Cameroon: 3 km E of Ngaoundere	I. Nordal 952 (O)	X74729	X74580	Fangan et al., 1994
Crinum pedunculatum R. Br.	Amaryllidaceae	Australia: N.S.W., Highway btw. Coopernook and Taree, 20 m	Speta H422	AJ232438	AJ232561	this paper
Narcissus tazetta L.	Amaryllidaceae	Italy: Capri, below Villa Javi	Kiehn AM01	AJ232439	AJ232562	this paper
Anthericum liliago L.	Anthericaceae	Austria: Niederösterreich	Pfosser LI04	AJ232444	AJ232567	this paper
Anthericum ramosum L.	Anthericaceae	Austria: Burgenland	Pfosser LI05	AJ232445	AJ232568	this paper
Leucocrinum montanum Nutt. ex A. Gray	Anthericaceae	USA: Colorado	Chase 795 (K)	AF117003	AF117031	Meerow et al., 1999
Blandfordia nobilis Sm.	Blandfordiaceae	Australia: N.S.W., Royal N.P. near Heathcote, 180 m	Speta H416	AJ232441	AJ232564	this paper
Camassia cusickii Lindl.	Camassiaceae	cult. B. G. Linz	Speta H223	AJ232450	AJ232573	this paper
Camassia leichtlinii S. Wats.	Camassiaceae	cult. ex B. G. Marburg (69/84)	Pfosser H231	AJ232451	AJ232574	this paper
Chlorogalum palmatum (Lindl.) Kunth	Camassiaceae	USA: California, Highway 128, 300 m	Quibell H260	AJ232448	AJ232571	this paper
Chlorogalum pomeridianum (Lindl.) Kunth	Camassiaceae	USA: California, Rohnert Park	Quibell H012	AJ232449	AJ232572	this paper
Aspidistra elatior Blume	Convallariaceae	cult., origin unknown	Chase 833 (K)	AF117016	AF117044	Meerow et al., 1999
Disporopsis pernyi (Hua) Diels	Convallariaceae	China: Jiangsu Province	Chase 493 (K)	—	—	Chase, unpublished
Liriope platyphylla F.T. Wang & T. Tang	Convallariaceae	cult., origin unknown	Chase 131 (NCU)	AF117009	AF117038	Meerow et al., 1999
Peliosanthes sp.	Convallariaceae	Indonesia: Borneo	Chase 847 (K)	AF117006	AF117034	Meerow et al., 1999
Polygonatum hookeri Baker	Convallariaceae	Nepal	Chase 492 (K)	AF117010	AF117036	Meerow et al., 1999
Doryanthes excelsa Correa	Doryanthaceae	Australia: N.S.W., Brisbane Water N. P., near Mt. White, 150 m	Speta H415	AJ232440	AJ232563	this paper
Hosta fortunei L.H. Bailey	Funkiaceae	cult. ex B. G. Nantes (1168/97)	Pfosser H433	AJ232446	AJ232569	this paper
Hemerocallis lilioasphodelus L.	Hemerocallidaceae	cult. ex B. G. Bonn (410/97)	Pfosser H435	AJ232442	AJ232565	this paper
Hemerocallis minor Mill.	Hemerocallidaceae	cult. ex B. G. Bonn (8411/97)	Pfosser H434	AJ232443	AJ232566	this paper
Albuca nelsonii N.E. Br.	Hyacinthaceae	cult. B. G. Vienna	Pfosser H062	AJ232468	AJ232591	this paper

Appendix 1. Continued.

Species	Family	Locality	Voucher°	EMBL acc. no.		Literature citation§
				Intron	IGS	
Albuca sp.	Hyacinthaceae	Guinea: Moyenne Guinée, NW of Timbo	Ebert & Bangoura H204	AJ232467	AJ232590	this paper
Autonoe haemorrhoidalis (Webb & Berth.) Speta	Hyacinthaceae	Spain: Teneriffa	Klenner H160	AJ232518	AJ232641	this paper
Autonoe latifolia (Willd.) Speta	Hyacinthaceae	Morocco: Agadir	Ehrendorfer H015	AJ232517	AJ232640	this paper
Barnardia scilloides Lindl.	Hyacinthaceae	Japan, ex B. G. Kanagawa (214/94)	Pfosser H025	AJ232509	AJ232632	this paper
Bellevalia aff. brevipedicellata Turrill	Hyacinthaceae	Greece: Crete, Ep. Selinou, Gavdos	Jahn H214	AJ232547	AJ232670	this paper
Bellevalia trifoliata Kunth	Hyacinthaceae	Greece: Rhodos, Faliraki	Speta H052	AJ232548	AJ232671	this paper
Bowiea volubilis Harvey ex J.D. Hooker	Hyacinthaceae	S Africa, cult. B. G. Vienna	Pfosser H222	AJ232454	AJ232577	this paper
Brimeura amethystina (L.) Chouard	Hyacinthaceae	cult. ex B. G. Tallinn (237/80)	Pfosser H225	AJ232510	AJ232633	this paper
Cathissa concinna (Salisb.) Speta	Hyacinathaceae	Spain: Càceres, Las Hurdes	Raus H047	AJ232481	AJ232604	this paper
Charybdis aff. numidica (Jord.) Speta	Hyacinthaceae	Greece: Crete, Moni Gouvernetou	Weigl H003	AJ232464	AJ232587	this paper
Charybdis hesperia (Webb & Berth.) Speta	Hyacinthaceae	Spain: Fuerteventura, Betancuria, 500 m	Skala H069	AJ232465	AJ232588	this paper
Charybdis maritima (L.) Speta sensu stricto	Hyacinthaceae	Spain: central Spain	Speta H319	AJ232466	AJ232589	this paper
Chouardia litardierei (Breistr.) Speta	Hyacinthaceae	Croatia: Dalmatia, cult. B. G. Vienna	Pfosser H230	AJ232541	AJ232664	this paper
Dipcadi fulvum (Cav.) Webb. & Berth.	Hyacinthaceae	Spain: Canar. Island, Lanzarote, NW of Orzola, Playa de la Canteria	Tod H207	AJ232479	AJ232602	this paper
Dipcadi serotinum (L.) Medicus acc. 1	Hyacinthaceae	Spain: Mini Hollywood, N of Almeria	Stech H061	AJ232477	AJ232600	this paper
Dipcadi serotinum (L.) Medicus acc. 2	Hyacinthaceae	Portugal: Nazaré	Scheiblreiter H336	AJ232478	AJ232601	this paper
Dipcadi viride (L.) Moench sensu lato	Hyacinthaceae	Senegal: Région de Fatick, Mbam, 4 km E of Foundiougne	Ebert & Bangoura H365	AJ232476	AJ232599	this paper
Drimia elata Jacq.	Hyacinthaceae	Zimbabwe: 19 km E of Chevy	Nordal 2501	Z99135	Z99136	Stedje, 1998
Drimiopsis barteri Baker	Hyacinthaceae	Tanzania: Iringa District, Ruaha Natl. Park, 3.5 km N of Msembe	A. Bjornstad 1158	Z99137	Z99138	Stedje, 1998

Appendix 1. Continued.

Species	Family	Locality	Voucher°	EMBL acc. no.		Literature citation§
				Intron	IGS	
Drimiopsis botryoides Baker subsp. *botryoides*	Hyacinthaceae	Tanzania: Uzaramo District, Mbudya Island	Nordal 1600	Z99139	Z99140	Stedje, 1998
Drimiopsis botryoides Baker subsp. *prostrata* B. Stedje	Hyacinthaceae	Tanzania: Iringa District, at the foot of Image Mt.	I. Bjornstad 780	Z99141	Z99142	Stedje, 1998
Drimiopsis maculata Lindley	Hyacinthaceae	cult. LI	Speta H002	AJ232502	AJ232625	this paper
Ebertia nana (Oyewole) Speta	Hyacinthaceae	Guinea: Moyenne Guinée, SW of Labé	Ebert & Bangoura H406	AJ232456	AJ232579	this paper
Eliokarmos bolusianus (Baker) Speta	Hyacinthaceae	R. South Africa: Graaff-Reinet, 3–4 km from Murragsburg road, 950 m	Müller-Doblies H183	AJ232484	AJ232607	this paper
Eliokarmos graminifolius (Thunb.) Speta sensu lato	Hyacinthaceae	R. South Africa	Müller-Doblies H141	AJ232485	AJ232608	this paper
Eliokarmos thyrsoides (Jacq.) Raf.	Hyacinthaceae	R. South Africa, cult. B. G. Vienna (ex B. G. Kirstenbosch)	Pfosser H404	AJ232483	AJ232606	this paper
Eucomis punctata (Thunb.) L'Herit.	Hyacinthaceae	cult. LI	Speta H221	AJ232500	AJ232623	this paper
Fessia greilhuberi (Speta) Speta	Hyacinthaceae	cult. B. G. Vienna	Pfosser H013	JA232534	AJ232657	this paper
Fessia puschkinioides (E. Regel) Speta	Hyacinthaceae	Tadschikistan: Hissar Mts., 60 km E of Duschanbe	Fritsch H211	AJ232536	AJ232659	this paper
Fessia vvedenskyi (Pazij) Speta	Hyacinthaceae	Uzbekistan: 20 km NE of Schargun	Speta H234	AJ232535	AJ232658	this paper
Galtonia candicans (Baker) Decne.	Hyacinthaceae	cult. LI	Speta H233	AJ232472	AJ232595	this paper
Galtonia princeps (Baker) Decne.	Hyacinthaceae	South Africa, ex B. G. Harrogate (499/97)	Pfosser H379	AJ232474	AF232597	this paper
Galtonia viridiflora Verdoorn	Hyacinthaceae	South Africa, ex B. G. Harrogate (500/97)	Pfosser H378	AJ232473	AJ232596	this paper
Honorius prasandrus (Griseb.) Holub	Hyacinthaceae	Turkey: Uludag	Mertens H048	AJ232486	AJ232609	this paper
Hyacinthella dalmatica (Baker) Chouard	Hyacinthaceae	Croatia: Dalmatia	Gutermann H297	AJ232526	AJ232649	this paper
Hyacinthella heldreichii (Boiss.) Chouard	Hyacinthaceae	Turkey: Sertavul Pass	Markus H210	AJ232527	AJ232650	this paper

Appendix 1. Continued.

Species	Family	Locality	Voucher°	EMBL acc. no.		Literature citation§
				Intron	IGS	
Hyacinthoides aristidis (Coss.) Rothm.	Hyacinthaceae	Algeria: near Yakouren, Djurdjura	Schneider H065	AJ232521	AJ232644	this paper
Hyacinthoides hispanica (Mill.) Rothm.	Hyacinthaceae	Spain: Provincia de Cádiz, 6 km S of Ubrique	Voglmayr H338	AJ232525	AJ232648	this paper
Hyacinthoides italica (L.) Rothm.	Hyacinthaceae	France: Alpes Maritimes (ex B. G. Neuchatel 71/84)	Pfosser H300	AJ232519	AJ232642	this paper
Hyacinthoides lingulata (Poir.) Rothm.	Hyacinthaceae	Tunisia: btw. Nefza and Ain Sebaa	Koenen H066	AJ232520	AJ232643	this paper
Hyacinthoides non-scripta (L.) Chouard ex Rothm.	Hyacinthaceae	France: Maquere sur la route N-823 a 12 km du Man (ex B. G. Neuchatel 145/83)	Pfosser H235	AJ232524	AJ232647	this paper
Hyacinthoides reverchonii (Degen & Hervier) Speta	Hyacinthaceae	Spain: Provincia de Jaén, Parque Nacional Sierra de Cazorla	Voglmayr H307	AJ232523	AJ232646	this paper
Hyacinthoides vincentina (Hoffmanns. & Link) Rothm.	Hyacinthaceae	Portugal: Cabo de Sao Vincente (Vila do Bispo)	Scheiblreiter H305	AJ232522	AJ232645	this paper
Hyacinthus orientalis L.	Hyacinthaceae	Romania: Greci cult.	Speta H067	AJ232539	AF232662	this paper
Karoophila bolusii Müller-Doblies ined.	Hyacinthaceae	—	Müller-Doblies H182	AJ232462	AJ232585	this paper
Lachenalia aloides (L. f.) Engl.	Hyacinthaceae	cult. B. G. Vienna	Pfosser H159	AJ23508	AJ232631	this paper
Lachenalia namibiensis W.F. Barker	Hyacinthaceae	Namibia	Müller-Doblies H059	AJ232505	AJ232628	this paper
Lachenalia pallida Aiton	Hyacinthaceae	cult. B. G. Vienna	Pfosser H021	AJ232507	AJ232630	this paper
Ledebouria cordifolia (Baker) Stedje & Thulin	Hyacinthaceae	Malawi: Nyika plateau, Kongolo hills	Nordal & Stedje 2409	Z99143	Z99144	Stedje, 1998
Ledebouria revoluta (L. f.) Jessop	Hyacinthaceae	Zimbabwe: 8 km SW of Selous	Nordal 2082	Z99146	Z99147	Stedje, 1998
Ledebouria socialis (Baker) Jessop	Hyacinthaceae	cult. B. G. Vienna	Pfosser H014	AJ232501	AJ232624	this paper
Ledebouria somaliensis (Baker) Stedje & Thulin	Hyacinthaceae	Ethiopia: Bale region, 3.6 km S of Ginir	Nordal 2296	Z99150	Z99151	Stedje, 1998
Ledebouria urceolata Stedje in Stedje & Thulin	Hyacinthaceae	Ethiopia: Bale region, 8.4 km W of Goro	Nordal 2297	Z99148	Z99149	Stedje, 1998

Appendix 1. Continued.

Species	Family	Locality	Voucher°	EMBL acc. no.		Literature citation§
				Intron	IGS	
Loncomelos brachystylus (Zahar.) Speta	Hyacinthaceae	Greece: Rhodos, Attaviros from Embona	Speta H008	AJ232487	AJ232610	this paper
Melomphis arabica (L.) Raf.	Hyacinthaceae	cult. B. G. Linz	Speta H004	AJ232482	JA232605	this paper
Merwilla lazulina (Wild) Speta	Hyacinthaceae	Zimbabwe: 40 km NE of Rusape on road to Nyanga	Nordal 2491	Z99155	Z99156	Stedje, 1998
Merwilla sp. 1	Hyacinthaceae	cult. B. G. Vienna	Puff H219	AJ232499	AJ232622	this paper
Merwilla sp. 2	Hyacinthaceae	cult. B. G. Vienna	Puff H218	AJ232498	AJ232621	this paper
Muscari botryoides (L.) Mill.	Hyacinthaceae	Austria: Hasenufer near Pucking	Kleesadl H011	AJ232545	AJ232668	this paper
Muscari comosum (L.) Mill.	Hyacinthaceae	Italia: Monte	Neuner H056	AJ232546	AJ232669	this paper
Muscari macrocarpum Sweet	Hyacinthaceae	Turkey: Konya, 3 km outside of Göktepe, 1400 m	Fritsch H212	AJ232544	AJ232667	this paper
Nectaroscilla hyacinthoides (L.) Parl.	Hyacinthaceae	Portugal: Sierra da Amabina, close to Aleia de Irmaos (road to N. P.)	Scheiblreiter H016	AJ232542	AJ232665	this paper
Oncostema dimartinoi Raf.	Hyacinthaceae	Italia: Isola Marettimo, Egadi I., in colle Falcone, 400 m	Vezda H178	AJ232514	AJ232637	this paper
Oncostema peruviana (L.) Speta	Hyacinthaceae	Portugal: Algarve, Vila do Bispo sul de Portugal (ex B. G. Lisboa 231/88)	Pfosser H198	AJ232516	AJ232639	this paper
Oncostema villosa (Desf.) Raf.	Hyacinthaceae	Tunisia: peninsula Bon, btw. Korbous and Douela, 90 m	Gruber H217	AJ232515	AJ232638	this paper
Ornithogalum amphibolum Zahar.	Hyacinthaceae	Romania: btw. Cochirlen and Rasova, 70 m	Speta H173	AJ232493	AJ232616	this paper
Ornithogalum angustifolium Bor. ($2n = 27$)	Hyacinthaceae	Poland: Krakow, Batowice (ex B. G. Amsterdam)	Raamsdonk H020	AJ232497	AJ232620	this paper
Ornithogalum fimbriatum Willd.	Hyacinthaceae	Romania: btw. Babadag and Enisala	Speta H139	AJ232491	AJ232614	this paper
Ornithogalum gussonei Ten. acc. 1	Hyacinthaceae	Greece: Rhodos, Prof. Ilias, 770 m	Speta H164	AJ232489	AJ232612	this paper
Ornithogalum gussonei Ten. acc. 2	Hyacinthaceae	Greece: NW Peloponnes, pine forest near Araxos	Speta H166	AJ232488	AJ232611	this paper
Ornithogalum montanum Ten	Hyacinthaceae	Greece: Lafkas, Soulaki from Ajos Ilias, 600–1150 m	Speta H007	AJ232490	AJ232613	this paper
Ornithogalum pannonicum Vill.	Hyacinthaceae	Austria: Mödling, 200 m	Brandstätter H006	AJ232496	AJ232619	this paper

Appendix 1. Continued.

Species	Family	Locality	Voucher°	EMBL acc. no.		Literature citation§
				Intron	IGS	
Ornithogalum pascheanum Speta	Hyacinthaceae	Turkey: Bolu, Abantsee, 1400–1600 m	Vasak H022	AJ232492	AJ232615	this paper
Ornithogalum umbellatum L. *aggr.* (2n = 45)	Hyacinthaceae	Slovakia: Bratislava, Kalinkovo, 80 m	Vasak H005	AJ232495	AJ232618	this paper
Ornithogalum wiedemannii Boiss.	Hyacinthaceae	Turkey: Yedi-Göller area, 30 km N of Bolu, 1850 m	Pasche H018	AJ232494	AJ232617	this paper
Othocallis sp.	Hyacinthaceae	Turkey: Nigde, Kamirkazik Dag, 1600 m	Pasche H179	AJ232533	AJ232656	this paper
Oziroe biflora (Ruiz & Pavon) Speta	Hyacinthaceae	Chile	MWC 793 (K)	AJ232453	AJ232576	this paper
Oziroe sp.	Hyacinthaceae	Chile: Prov. Copiapo, 1 km on Panamericana N of turnoff to Bahia Inglesa and Caldera, 100–160 m	Eggli & Leuenberger H362	AJ232452	AJ232575	this paper
Pfosseria bithynica (Boiss.) Speta	Hyacinthaceae	Bulgaria: Burgas, Aitoska Planina, Gorica, 300–400 m	Vasak H232	AJ232540	AJ232663	this paper
Polyxena calcicola U. & D. Müller-Doblies	Hyacinthaceae	South Africa	Müller-Doblies H216	AJ232506	AJ232629	this paper
Prospero elisae Speta acc. 1	Hyacinthaceae	Greece: Lefkas, Soulaki from Ajos Ilias, 1150 m	Speta H068	AJ232530	AJ232653	this paper
Prospero elisae Speta acc. 2	Hyacinthaceae	Greece: Parnass 1100 m	Ehrendorfer H155	AJ232531	AJ232654	this paper
Prospero haritonidae Speta	Hyacinthaceae	Greece: near Mikrothivae	Speta H027	AJ232528	AJ232651	this paper
Prospero obtusifolium (Poiret) Speta	Hyacinthaceae	Morocco: Beni-el Quidane, 1300 m	HC H053	AJ232529	AJ232652	this paper
Pseudogaltonia clavata (Masters) Phillips	Hyacinthaceae	cult. B. G. Vienna	Speta H220	AJ232475	AJ232598	this paper
Puschkinia scilloides Adams	Hyacinthaceae	cult. B. G. Linz	Speta H224	AJ232532	AJ232655	this paper
Rhadamanthus sp. 1	Hyacinthaceae	Madagascar: Antsalova region	Rafamantanantsoa H409	AJ232457	AJ232580	this paper
Rhadamanthus sp. 2	Hyacinthaceae	Madagascar: Antsalova region	Rafamantanantsoa H410	AJ232458	AJ232581	this paper
Schizocarphus nervosus (Burch.) Merwe	Hyacinthaceae	Zimbabwe: Chimanimani Mts.	Stedje 94/15	Z99157	Z99158	Stedje, 1998
Schnarfia messeniaca (Boiss.) Speta	Hyacinthaceae	Greece: 3 km NW of Kalamata, Mons Velalidis, 200 m	Vasak H177	AJ232543	AJ232666	this paper
Scilla albescens Speta	Hyacinthaceae	Greece: Crete, Psiloritis, Ida cave	Speta H237	AJ232553	AJ232676	this paper
Scilla cf. bulgarica * Speta	Hyacinthaceae	Romania: SE of Greci	Speta H158	AJ232555	AJ232678	this paper

Appendix 1. Continued.

Species	Family	Locality	Voucher°	EMBL acc. no.		Literature citation§
				Intron	IGS	
Scilla cydonia Speta acc. 1	Hyacinthaceae	Greece: Crete, btw. Nea Roumata and Papadiana	Jahn et al. H215	AJ232549	AJ232672	this paper
Scilla cydonia Speta acc. 2	Hyacinthaceae	Greece: Karpathos: Kali'Limni, ca. 1200 m	Speta H489	AJ232550	AJ232673	this paper
Scilla nana (J.A. & J.H. Schultes) Speta	Hyacinthaceae	Greece: Crete, Levka Ori, E. Kallergi, 1600 m	Speta H238	AJ232552	AJ232675	this paper
Scilla siehei (Stapf) Speta cv. "Pink Giant"	Hyacinthaceae	cult. LI	Speta H010	AJ232551	AJ232674	this paper
Scilla spetana Kereszty	Hyacinthaceae	Austria: Kreuttal near Unterolberndorf	Speta H227	AJ232556	AJ232679	this paper
Scilla subnivalis (Halacsy) Speta	Hyacinthaceae	Greece: Kephalonia, Änos, 1080–1630 m	Speta H240	AJ232554	AJ232677	this paper
Stellarioides ecklonii (Fisch. & Mey.) Speta	Hyacinthaceae	cult. B. G. Graz	Speta H289	AJ232470	AJ232593	this paper
Stellarioides etesiogaripensis (U. & D. Müller-Doblies) Speta	Hyacinthaceae	Namibia: farm Klein-Kubub, 1.5 km W of Rosh Pinah road	Müller-Doblies H138	AJ232469	AJ232592	this paper
Stellarioides longebracteata (Jacq.) Speta	Hyacinthaceae	cult. B. G. Vienna	Pfosser H407	AJ232471	AJ232594	this paper
Stellarioides tenuifolia (F. Delaroche) Speta	Hyacinthaceae	Uganda: Toro Distr., Queen Elizabeth Natl. Park, Mweya Peninsula	A. Bjornstad 548	Z99152	Z99153	Stedje, 1998
Thuranthos indicum (Roxb.) Speta sensu lato	Hyacinthaceae	Senegal: Région de Thiès, 2 km N of Mbour, near Sali Portugal	Ebert & Bangoura H202	AJ232455	AJ232578	this paper
Tractema lilio-hyacinthus (L.) Speta	Hyacinthaceae	Spain: Picos de Europa, at about 1450 m alt.	Hoog & Hoog H298	AJ232511	AJ232634	this paper
Tractema monophyllos (Link) Speta acc. 1	Hyacinthaceae	Spain: Cáceres, Salorino	Raus H049	AJ232513	AJ232636	this paper
Tractema monophyllos (Link) Speta acc. 2	Hyacinthaceae	Spain: Andalucia, Sierra de Cazorla 1200 m	W. & S. Till H306	AJ232512	AJ232635	this paper
Urginavia altissima (L. f.) Speta	Hyacinthaceae	Zimbabwe: 40 km NE of Gokwe	Nordal 2302	Z99133	Z99134	Stedje, 1998
Urginavia micrantha * (A. Rich.) Speta	Hyacinthaceae	Ethiopia: W-Schoa, Guder	Hildebrandt H439	AJ232460	AJ232583	this paper

Appendix 1. Continued.

Species	Family	Locality	Voucher°	EMBL acc. no.		Literature citation§
				Intron	IGS	
Urginavia sp.	Hyacinthaceae	Guinea: Région de Moyenne Guinée, NW of Timbo	Ebert & Bangoura H357	AJ232461	AJ232584	this paper
Urginea sensu lato	Hyacinthaceae	Guinea: Moyenne Guinée, N of Pita, road to Hafia	Ebert & Bangoura H405	AJ232459	AJ232582	this paper
Urginea undulata (DESF.) STEINH.	Hyacinthaceae	Tunisia: Hammamet	Teppner H454	AJ232463	AJ232586	this paper
Veltheimia bracteata HARV. EX BAKER	Hyacinthaceae	cult. LI	Speta H060	AJ232503	AJ232626	this paper
Whiteheadia etesionamibensis * MÜLLER-DOBLIES	Hyacinthaceae	Namibia: Namuskluft	Lavranos & Pehlemann H444	AJ232504	AJ232627	this paper
Zagrosia persica * (HAUSSKN.) SPETA acc. 1	Hyacinthaceae	Turkey: btw. Siirt and Bitlis	Leep H440	AJ232537	AJ232660	this paper
Zagrosia persica (HAUSSKN.) SPETA acc. 2	Hyacinthaceae	Turkey: Beyez Dag, 1400 m	Stevens H500	AJ232538	AJ232661	this paper
Zahariadia saundersiae (BAKER) SPETA	Hyacinthaceae	South Africa (ex B. G. Berlin)	Speta H024	AJ232480	AJ232603	this paper
Arthropodium milleflorum (DC.) J.F. MACBR.	Lomandraceae	Australia: N.S.W., Barrington TOPS N. P., 1100–1400 m	Speta H418	AJ232436	AJ232559	this paper
Arthropodium sp.	Lomandraceae	Australia: N.S.W., Chichester State Forest, Jerusalem Creek, 380–490 m	Speta H423	AJ232435	AJ232558	this paper
Eustrephus latifolius R. BR.	Lomandraceae	Australia: NSW	Chase 193 (NCU)	AF117004	AF117032	Meerow et al., 1999
Thysanotus virgatus BRITTAN	Lomandraceae	Australia: NSW, Marley Track, Royal N. P.	Speta H413	AJ232437	AJ232560	this paper
Calibanus hookeri TREL.	Nolinaceae	Mexico: San Luis Potosi: Mts. near Balneario de Lourdes	Schatzl AG01	AJ232434	AJ232557	this paper
Bessera elegans SCHULT. f.	Themidaceae	Mexico: Sinaloa	Chase 626 (K)	AF117015	AF117040	Meerow et al., 1999
Brodiaea jolonensis EASTW.	Themidaceae	USA: California	Chase 1831 (K)	AF 117017	AF117046	Meerow et al., 1999
Dichelostemma pulchellum A. HELLER	Themidaceae	cult. ex U of California, Irvine, Arboretum	—	—	—	Chase, unpublished
Milla magnifica H.E. MOORE jr.	Themidaceae	—	Meerow 2309 (FLAS)	AF117011	AF117041	Meerow et al., 1999

THE EVOLUTION OF PARASITISM IN SCROPHULARIACEAE/ OROBANCHACEAE: PLASTID GENE SEQUENCES REFUTE AN EVOLUTIONARY TRANSITION SERIES[1]

Nelson D. Young,[2] Kim E. Steiner,[3] and Claude W. dePamphilis[4]

ABSTRACT

Parasitic plants in Scrophulariaceae and Orobanchaceae have been traditionally depicted as forming a linear evolutionary series beginning with hemiparasitism and ending with holoparasitism. The genera *Lathraea, Harveya,* and *Hyobanche* have been viewed as transitional links between the parasitic members of Scrophulariaceae and the strictly holoparasitic habit of the traditional Orobanchaceae. Phylogenetic analyses of plastid *rps*2 and *mat*K sequences were performed. The transitional genera are not transitional to the traditional Orobanchaceae, but represent multiple independent origins of holoparasitism. Within Scrophulariaceae, the two traditional subfamilies Rhinanthoideae and Antirrhinoideae are defined by the arrangement of the corolla lobes during aestivation. However, neither of the two subfamilies is monophyletic in our analyses, suggesting that corolla lobe position is a homoplastic character. While the traditional Orobanchaceae are monophyletic, tribes Buchnereae and Rhinantheae are clearly not, and genus *Orobanche* probably is not. Clades of parasitic genera correspond well with biogeographic provinces. One strongly supported clade contains the parasitic Scrophulariaceae, the traditional Orobanchaceae, and *Lindenbergia.* It is proposed that this clade be defined as the Orobanchaceae.

Parasitic angiosperms are found in 16 families and live in diverse habitats, ranging from tropical forests to arctic islands (Musselman & Press, 1995). Recent work on several parasitic groups has explored their anatomy, physiology, ecology, and molecular biology and the control of economically significant parasites (Press & Graves, 1995). Parasites exhibit dramatic adaptations. Some lack leaves, stems, roots, and the ability to photosynthesize. For many lineages of non-photosynthetic parasites, study of their evolution is impeded by the very fact that they are so specialized and so different from their nearest photosynthetic relatives. In many cases the identity of those relatives remains unknown (Nickrent & Duff, 1996; Nickrent et al., 1998). The evolution of parasitism can best be studied in a group where near relatives are known, and different degrees of parasitic specialization are encountered. The group with the greatest range in parasitic specialization is found within the Scrophulariaceae/Orobanchaceae. This family pair includes nonparasites, both facultative and obligate hemiparasites (photosynthetic plants that obtain water, nutrients, or photosynthates from their host), and holoparasites (non-photosynthetic, obtaining all photosynthates from their host). Much has been learned about the anatomy and physiology of parasitism in this group, especially in *Striga* Loureiro and *Orobanche* L., which are important pests of crop plants (Press & Graves, 1995). Reliable information on phylogenetic relationships among the various nonparasites, hemiparasites, and holoparasites would enable us to better understand the anatomical, physiological, and genetic changes that occur during the evolution of parasitism and the loss of photosynthetic ability.

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Boeshore (1920: 171) argued for a close relationship between the Scrophulariaceae (figworts) and the traditional Orobanchaceae (broomrapes), describing in detail an evolutionary transition series:

> "All macroscopic and microscopic details suggest that the parasitic Scrophulariaceae and Orobanchaceae form a continuous and parasitically degrading morphological series that show transitional steps from green nearly autotrophic plants like *Melampyrum, Rhinanthus*, and *Euphrasia* to increasingly condensed and degraded genera like *Bartsia* and *Harveya*, on to *Lathraea*, that has been shown to be placed by some botanists in Scrophulariaceae, by others in Orobanchaceae, thence through species of *Orobanche* to *Epiphegus*, and finally *Aphyllon* and *Conopholis*."

According to Boeshore, the evolutionary series among parasitic figworts and broomrapes involved progressive enlargement and consolidation of haustoria (the connection to the host), shortening of the vegetative stem, reduction of leaves, simplification of the inflorescence, change from few, large seeds to numerous, small seeds, and a reduction in the ovary from two locules to one. Weber constructed a different evolutionary series based on haustorial anatomy (Weber, 1980), but otherwise, Boeshore's depiction of the group's evolution has endured remarkably well to the present. Later authors have cited Boeshore and reiterated his ideas. The parasitic Scrophulariaceae were viewed as "a pointer to . . . Orobanchaceae" (Hutchinson, 1969: 630); Kuijt (1969: 95) observed, "Many features of Orobanchaceae appear to be already foreshadowed in their figwort relatives," and Cronquist (1981: 940) stated, "The evolutionary journey toward parasitism obviously begins in Scrophulariaceae; the Orobanchaceae merely occupy the house at the end of the road."

Recent results from DNA sequencing show a more complicated history for the group. Phylogenies based on the plastid genes *rps*2 and *rbc*L (dePamphilis et al., 1997; Wolfe & dePamphilis, 1998; Nickrent et al., 1998) show that parasitism evolved a single time in the figwort/broomrape family pair. Thus all the hemi- and holoparasites, taken together, form a monophyletic group. This agrees with Boeshore, whose evolutionary series also contains a single origin of parasitism. Within this parasitic clade, however, evolution has not proceeded as Boeshore envisioned. The *rps*2 phylogeny also shows that the transitional genera (*Lathraea, Harveya, Hyobanche*) are not transitional at all, but occupy their own branches among the parasitic figworts, representing separate losses of photosynthesis, independent of the broomrapes (dePamphilis et al., 1997). It is not surprising that Boeshore had developed a different view of the group's evolution based on morphology. Many of the morphological characters that bear on phylogeny are probably adaptations to the parasitic lifestyle, and most involve reduction or loss of structures. This makes it difficult to interpret relationships within the group. It seems that, as the separate lineages independently specialized as parasites, they converged (sensu Eldredge & Cracraft, 1980) on similar morphologies. This paper includes additional DNA sequence data, enabling us to more rigorously test whether the parasites form a monophyletic group and whether the holoparasites form multiple groups. Because the five basal branches of the parasitic clade were left unresolved in the *rps*2 study (dePamphilis et al., 1997), we have, in this study, included a wider sample of taxa for *rps*2 and added characters from another plastid gene, *mat*K. This gives us the increase in resolution needed to provide a more detailed phylogeny.

A new definition of Orobanchaceae will be presented. For that reason, the common name "broomrapes" will be used for the traditional Orobanchaceae.

Throughout this paper we will use the classification system of Wettstein (1897), which, although dated (Thieret, 1967), is the best worldwide treatment of Scrophulariaceae. There are two minor exceptions to our use of Wettstein's system. We have included his subfamily Pseudosolaneae in the Antirrhinoideae (Thieret, 1967), and we use the name Buchnereae Benth. for his tribe Gerardieae Benth., following Pennell's (1935: 379) "desire that the tribal designation be based on a generic name unquestionably applying to a member of this group." Scrophulariaceae are divided into two subfamilies, Antirrhinoideae and Rhinanthoideae, "which differ fundamentally in the single character of the former having the posterior (corolla) lobes, and the latter the anterior lobes external in aestivation." (Pennell, 1935: 40). This corolla aestivation character has been studied throughout floral development for a number of figwort genera (Armstrong & Douglas, 1989), and the ontogenetic patterns were consistent within each subfamily. However, a study of *rbc*L and *ndh*F sequences (Olmstead & Reeves, 1995) found the Antirrhinoideae to be polyphyletic. In that study, the Rhinanthoideae, which consist of two nonparasitic tribes (Digitaleae and Veroniceae) and two parasitic tribes [Buchnereae and Rhinantheae Benth. (= Euphrasiae Benth.)], were represented only by two nonparasites, *Digitalis* and *Veronica*. Thus, neither the position of the parasites nor the monophyly of the Rhinanthoideae could be addressed. Phylogenies of *rps*2 (dePamphilis et al., 1997, and unpublished) and *rbc*L (Wolfe & dePamphilis, 1998) indicate that the parasitic and nonparasitic Rhinanthoideae each form a clade, and the two clades are separated by many other taxa including Bignoniaceae and Lamiaceae. Corolla aestivation pattern is also used to separate the two parasitic tribes of subfamily Rhinanthoideae. Of the three abaxial lobes, the center one folds over the two outer ones in the Buchnereae, and the outer two fold over the center one in the Rhinantheae (Armstrong & Douglas, 1989). The membership of these tribes has been stable since their inception.

The broomrapes or traditional Orobanchaceae (Beck von Mannagetta, 1930) consist entirely of holoparasites and have long been hypothesized to have affinities either with Scrophulariaceae or the Gesneriaceae. Gesneriaceae have been considered the closest relatives of the broomrapes by some authors (Baillon, 1891; Fritsch, 1895; Wettstein, 1897; Beck von Mannagetta, 1930), emphasizing the unilocular placentation of both families. Hallier (1903) and Bellini (1907) both proposed formal inclusion of the broomrapes in subfamily Rhinanthoideae of Scrophulariaceae. Boeshore (1920) also found the broomrapes to be similar to the parasitic figworts, not only in the parasitic habit and the presence of haustoria, but in many other features, such as: (1) plants similarly reduced, with very short vegetative axes and linear inflorescence axes; (2) leaves reduced to tooth-like scales; (3) sepals and stamens with tapered, multicellular hairs interspersed with capitate-glandular hairs; (4) parallel anther lobes growing downward into stiff, awn-like horns; and (5) nectary often a median knob in line with the floral axis. Cronquist (1981) referred to the Orobanchaceae as "... derived from Scrophulariaceae," but, due to its parasitic habit and parietal placentation, retained it as a separate family. Finally, a cladistic analysis of DNA sequences from the plastid gene *rps*2 showed the Orobanchaceae to be firmly ensconced within the parasitic figworts, which are not monophyletic (dePamphilis et al., 1997). Despite the lack of monophyly, we use the name Scrophulariaceae and its common name, figworts, as they have been traditionally used, until a reclassification is published.

This study assessed the monophyly of three groups: genus *Orobanche*, the broomrapes, and the broomrapes plus parasitic figworts. If monophyletic, the study also sought the sister group of each clade. The position of *Schwalbea* was also examined. *Schwalbea* was thought to be among the most "primitive" of parasitic figworts, based on its fifth (posterior) sepal, septicidal dehiscence of the capsule, and two bractlets subtending the flower (Pennell, 1935).

These questions were addressed using two plastid genes: *rps*2 and *mat*K. These are two of the small set of plastid genes that are found intact in all of the taxa in this group, even in the holoparasites. Although the ribosomal protein gene *rps*2 is new to plant phylogenetic analysis (dePamphilis et al., 1997), *mat*K has become widely used and has many advantages for use in phylogenetic studies (Hilu & Liang, 1997). It is large (~ 1500 bp) and rapidly evolving (Wolfe et al., 1992; Olmstead & Palmer, 1994), changing 2 or 3 times as fast as *rbc*L (Steele & Vilgalys, 1994; Johnson & Soltis, 1995), thus providing many substitution characters. The changes in *mat*K are distributed more evenly among the three codon positions and throughout its length than in other, more conserved genes (Johnson & Soltis, 1994; Hilu & Liang, 1997). As a coding region, *mat*K is easier to align than non-coding regions, yet most data sets have a few small indels (insertions or deletions) of 3 to 15 bp, providing additional characters. Interestingly, although the *trn*K locus is absent from *Epifagus* (Morden et al., 1991), and possibly several other Orobanchaceae taxa (N. D. Young & C. W. dePamphilis, unpublished), we found an intact *mat*K gene in all Orobanchaceae and Scrophulariaceae tested, including holoparasites such as *Epifagus* (dePamphilis & Palmer, 1990; Wolfe et al., 1992) and *Conopholis* (Colwell, 1994).

MATERIALS AND METHODS

SAMPLING

Multiple taxa were chosen from each of the five major lineages of parasitic figworts and broomrapes found previously (dePamphilis et al., 1997). We also included *Schwalbea*, a monotypic genus that may represent a sixth parasitic lineage (Pennell, 1935). Both parasitic figwort tribes, Rhinantheae and Buchnereae, were well sampled. From the broomrapes, we sampled *Epifagus*, *Conopholis*, *Boschniakia*, *Cistanche*, and all four sections of *Orobanche*: *Gymnocaulis* (*O. uniflora* and *O. fasciculata*), *Nothophyllon* (*O. corymbosa*), *Orobanche* (*O. caryophyllaceae*, *O. cernua*, and *O. hederae*), and *Trionychon* (*O. ramosa*).

*rps*2 phylogeny showed that the nearest relatives to the parasites are clearly not the Digitaleae (dePamphilis et al., 1997), as was previously thought. We therefore sampled members of all of Wettstein's (1897) figwort tribes except two small ones, Aptosimeae and Manuleae, for which material was not available. Additional sampling outside the figworts was based on previous *rps*2 phylogenies (dePamphilis et al., 1997, and unpublished), and emphasized lineages that appeared to be closely related to the parasites. We also included *Lindenbergia,* which, although not parasitic, shares some floral similarities with the parasitic figworts (Brühl, 1920). Trees were rooted with *Ligustrum* (Oleaceae) and *Nicotiana* (Solanaceae). The taxa used are listed, along with collection information and the GenBank accession numbers of the sequences, in Table 1.

DNA ISOLATION, AMPLIFICATION, AND SEQUENCING

The CTAB method (Doyle & Doyle, 1987) was used to isolate total DNA from plant leaf or stem tissue. Amplification of *rps*2 followed dePamphilis et al. (1997), and *mat*K sequences were amplified using 1X Taq Extender buffer (Stratagene), 0.2 mM each dATP, dCTP, dGTP, and dTTP (Pharmacia), 3.6 mM $MgCl_2$, 0.32 μM each primer (see Fig. 1), 0.25 unit of Taq DNA polymerase, 0.25 unit of Taq Extender coenzyme (Stratagene), and ~ 500 ng of total DNA in a 50 μL volume. Figure 1 shows the primary *mat*K primers (Genosys) used. Additional species-specific primers were occasionally needed, especially for *Orobanche.* PCR products were purified in 1% agarose gels using Qiaquick columns according to the manufacturer's instructions (Qiagen). Sequences were generated by two methods: with the ABI 377 autosequencer (P. E. Biosystems) according to the manufacturer's instructions (with the exception that reactions were done in 10 μL, rather than the standard 20 μL volume) and manually, with the Sequenase (U.S. Biochemicals) double-stranded method (dePamphilis et al., 1997). Both strands were sequenced, and all ambiguities clarified by individual examination using Sequencher 3.0 software (GeneCodes, Ann Arbor, MI). Sequences were translated to verify that the protein-coding regions contained no internal stop codons, which would signify a possible sequencing error or pseudogene sequence.

ALIGNMENT

The *rps*2 alignment was simple, requiring only two small indels. The *mat*K alignment was more complicated, requiring 14 locations with indels ranging from 3 to 21 bp, some of which varied among taxa in length and exact position. Initially 22 alignments were produced, using Clustal W 1.4 (Thompson et al., 1994) and the following variations: gap opening penalties (GOP) ranging from 5 to 30, gap extension penalties (GEP) from 1 to 10, with and without transition/transversion weighting, with the NJ guide tree replaced by a "conservative" parsimony tree (derived from a data set with length-variable regions removed), with complex length-variable regions coded as multistate characters, as in Baum et al. (1994), or with length variation divided into characters based on the longest possible independently varying units (Young, 1998), and, finally, protein translations were aligned and the DNA alignments altered to match.

The 22 alignments thus produced were evaluated according to the consistency among characters [the rescaled consistency (RC) index of Farris (1989)] on the resulting maximum parsimony (MP) trees (Wheeler, 1995). This provided an objective optimality criterion: whichever alignment yielded the MP tree(s) with the highest RC was considered the best alignment.

PHYLOGENETIC ANALYSIS

We used two methods of phylogenetic analysis in the program PAUP: maximum parsimony (MP) and maximum likelihood (ML). For *rps*2, positions homologous to positions 48–660 of the *Nicotiana* gene were used [*Nicotiana* plastid genome positions 16275–16887 (Shinozaki et al., 1986)], and for *mat*K, *Nicotiana* gene positions 297–1286 were used (*Nicotiana* plastid genome positions 2425–3414). Because there were more than twice as many taxa sampled for *rps*2 than for *mat*K, we analyzed each gene alone and in two different combined analyses: one with only those taxa sequenced for both genes, and one with all the taxa. In analyses of the *mat*K-only and small-merger matrices, heuristic searches were performed with 100 random addition orders and TBR branch swapping. The *rps*2-only and large-merger matrices were too large for a full heuristic search, so we used a search strategy designed to sample tree space thoroughly in large data sets (Catalan et al., 1997). In the *mat*K-only analysis, the effect of the two regions with overlapping gaps was investigated by repeating the analysis with the gaps removed. Bootstrap support (Felsenstein, 1985) was estimated from the *mat*K-only and small-merger matrices, using the same parameters as the heuristic search (Fig. 3), and at least 500 replicates (Figs. 2, 4). For the *rps*2-only and large-merger matrices, each bootstrap replicate was limited to five random addition orders and five fully swapped trees each (Figs. 2, 4). Bremer support values (Bremer, 1988) were calculated for all four matrices. Topological constraints were used to find the number of extra steps that would be added to the MP trees under specific hypotheses (Table 2). Maximum-likelihood analyses were conducted on the *mat*K-only and small-merger matrices; the *rps*2-only and large-merger matrices had too many taxa. The substitution model included a transition/transversion ratio of 2.0 and base frequencies estimated from the data (Hasegawa et al., 1985). Analyses were conducted using test version 4.0d54 of PAUP*, with permission of the program's author, David L. Swofford. The aligned data can be obtained from TreeBASE (study accession number S402) at http://www.herbaria.harvard.edu/treebase/.

RESULTS

Although a cpDNA phylogeny cannot be assumed identical to the organismal phylogeny (e.g., Doyle, 1992), introgression or lineage sorting are not likely to be problems above the level of genera, so we expect close correspondence between the cpDNA phylogenies and the organismal phylogeny. The four data matrices used in the phylogenetic analyses are detailed in Table 2. The first, referred to as "*rps*2-only," contains *rps*2 gene sequences from 63 taxa. The second matrix (*mat*K-only) contains *mat*K sequences from 26 of those taxa (plus *Cistanche*, just recently obtained). The third matrix (small-merger) combines sequences for the 26 taxa that have data from both genes (all of the taxa in the *mat*K analysis except *Cistanche*, which had only two-thirds of its *mat*K gene sequenced, due to technical difficulties). This type of analysis (many characters, few taxa) is expected to provide the strongest support for clades on trees (Sanderson, 1989). The fourth matrix (large-merger) also excludes *Cistanche*, but contains all 63 remaining taxa; about 39% of the data are missing. This type of analysis (many taxa, fewer characters per taxon) can be expected to have lower support for clades on trees, but can give at least a preliminary indication of relationships for all the taxa.

The strict consensus tree resulting from the *rps*2-only MP analysis (Fig. 2) supports the monophyly of the parasitic figworts and broomrapes and indicates that *Lindenbergia* is the nearest relative to the parasites, among those plants sampled. Within the parasites, early branching events are unresolved, but the transitional genera (*Lathraea*, *Harveya*, and *Hyobanche*) clearly do not group with the broomrapes. Constraining them to do so adds 14 steps to the tree (Table 2).

The best alignment of the *mat*K sequences, resulting in MP trees with a RC = 0.380, was generated with Clustal W alignment parameters GOP = 15, GEP = 5, transition/transversion weighting on, and the seven resulting indel characters were coded as in Baum et al. (1994). The indels, all in multiples of three bases, were distributed throughout the gene, but were more common near the ends. Because it had the highest RC, this alignment was chosen for the *mat*K-only, small-merger, and large-merger analyses. Similar alignment parameters produced RC values only slightly lower and yielded the same phylogenetic trees. However, parameters that differed substantially (such as GOP < 5 or GOP > 25) produced RC values less than 0.375 and led to less resolved consensus trees.

The *mat*K-only MP analysis resulted in six shortest trees, which differ only in the placement of *Schwalbea* and *Cistanche*. The strict consensus tree (Fig. 3) resolves the basal branches of the parasitic clade better than the *rps*2-only analysis. The *mat*K-only analysis supports the monophyly of traditional Orobanchaceae, whose sister group is the *Striga-Harveya* clade (though support measures are not high). It also indicates that the genus *Orobanche* is diphyletic (polyphyletic, forming two clades), with moderately high support. It also resolves the *Castilleja* clade as sister to the *Melampyrum* clade. The ML (maximum likelihood) tree differs only in that *Antirrhinum* and *Veronica* form a monophyletic group rather than a paraphyletic one. This indicates that the parsimony algorithm may have allowed *Veronica* and *Nicotiana* to be attracted to each other due to their long branches (Felsenstein, 1978). That *Antirrhinum* belongs with *Veronica* is supported by both the *rps*2-only and large-merger analyses, which break up these branches with the addition of more taxa (Figs. 2, 4). When the two regions containing overlapping gaps were removed from the analysis, as well as the gap characters generated by these regions, the strict consensus MP tree differed by a single feature: the sister relationship of two of the outgroups, *Hemimeris* and *Verbascum*, becomes unresolved.

The small-merger analysis (Fig. 3) gives additional support to the findings of the previous two analyses. *Cistanche* has been removed, but otherwise the resulting MP trees have exactly the same topologies. Again, the ML analysis conflicts only in the placement of *Veronica*. The monophyly of the parasites (hemi- plus holo-) is strongly supported, as is the position of *Lindenbergia* as sister group to the parasites. The holoparasites are clearly polyphyletic. Although the broomrapes (as sampled) are monophyletic, *Harveya* and *Lathraea* do not form a clade with them. Instead, each of these holoparasites is revealed as a close relative of green hemiparasites. *Harveya* is related to *Alectra* and *Striga* (and others of tribe Buchnereae; Fig. 4). *Lathraea* is in a clade with *Tozzia* and *Melampyrum* (and oth-

Table 1. Specimens used for DNA sequencing, with family (and subfamily and tribe for Scrophulariaceae) according to Wettstein (1897), DNA number, voucher numbers (in parentheses), localities (in quotes), herbarium of deposition in square brackets, and GenBank accession numbers for *rps*2 and *mat*K sequences.

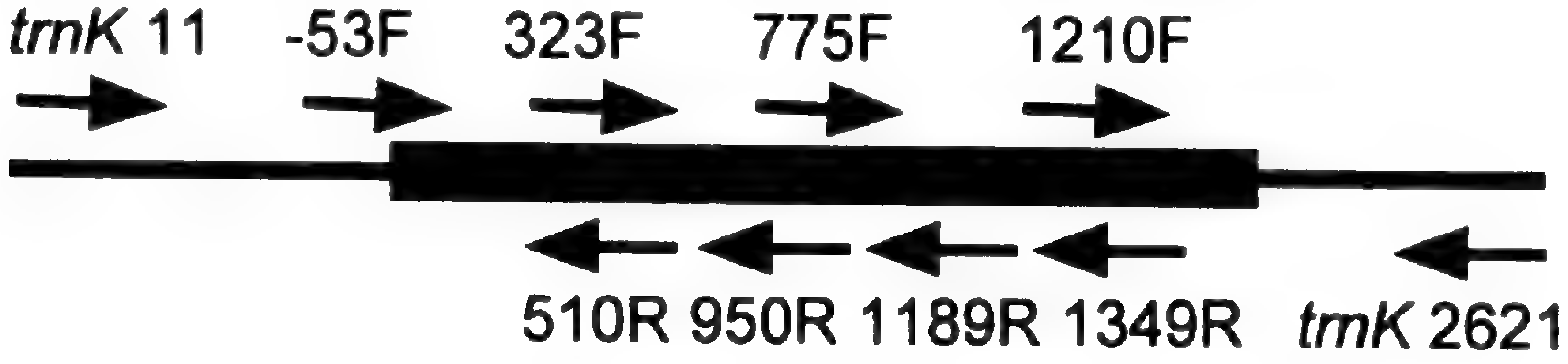
Family/subfamily/tribe	Species	DNA number/voucher	*rps*2	*mat*K
Scrophulariaceae				
Pseudosolaneae				
(we include in Antirrhinoideae)				
Verbasceae	*Verbascum blattaria* L.	CWD 90.117 "Davidson Co., Tennessee, USA" [PSU]	VBU48763	
	Verbascum thapsis L.	CWD 89.201 "Washtenaw Co., Michigan, USA" [PSU]		AFO52002
	Leucophyllum frutescens I. M. Johnston	CWD 95.21 "Austin Co., Texas, USA" [PSU]	AFO55156	
Antirrhinoideae				
Hemimeridae	*Hemimeris sabulosa* L.	(*K. E. Steiner 2387*) "Cape Province, S. Africa" [PSU]	HSU48765	AFO51985
Calceolarieae	*Calceolaria* sp.	CWD 90.203 "ex hort., Indiana U., USA" [PSU]	AFO55162	
Antirrhineae	*Antirrhinum majus* L.	CWD 90.204 "ex hort., U. Michigan, USA" [PSU]	AMU48766	AFO51978
Cheloneae	*Scrophularia californica* Cham. & Schlect.	CWD SS20 "Foster, California, USA" [PSU]	SCU48762	
	Chelone obliqua L.	CWD SS15 (*C. W. Morden 853*) "ex hort., Indiana U., USA" [PSU]	COU48770	
	Paulownia tomentosa Steud.	CWD SS24 "cultivated, Indiana U., USA" [PSU]	AFO55255	AFO51997
Gratioleae	*Mimulus aurantiacus* Renjifo	CWD 90.11 "cultivated, UC Berkeley, USA" [PSU]	AFO55154	
	Lindenbergia phillipinensis Benth.	CWD 98.01 (*J. G. Armstrong 1163*) "cult., Vanderbilt U., USA" [PSU]	AFO55151	AFO51990
	Gratiola pilosa Michx.	CWD 90.34 (no voucher)	AFO55163	
Selagineae	*Selago thunbergii* Choisy	CWD 90.21 "ex hort., UC Berkeley #62.1022, USA" [PSU]	AFO55158	
Rhinanthoideae				
Digitaleae	*Hemiphragma heterophyllum* Wall.	CWD 90.118 "ex hort., UC Berkeley #74.1009, USA" [PSU]	AFO55161	
	Veronica arvensis L.	CWD 92.201 "Davidson Co., Tennessee, USA" [PSU]	VAU48768	AFO52003
	Digitalis purpurea L.	CWD 93.41 "ex hort., Vanderbilt U., USA" [PSU]	DPU48767	
Gerardieae Benth.				
(we use Buchnereae Benth.)				
	Melasma scabrum Berg.	(*K. E. Steiner 2250*) "Farm Huisrivier, Cape Province, S. Africa" [PSU]	MSU48743	
	Alectra orobanchoides Benth.	(*K. E. Steiner 2278*) "Hhluhluwe, Natal, R. S. Africa" [PSU]	AOU48741	
	Alectra sessiliflora var. *sessiliflora* (Vahl.) O. Kunze	(*K. E. Steiner 2446*) "Ysterklip, Cape, R. S. Africa" [PSU]	ASU48742	AFO51977
	Macranthera flammea Pennell	CWD 90.140 (*J. R. Allison & A. K. Gohlson 5053*) "Liberty Co., FL, USA" [UGA]	AFO55139	

Table 1. Continued.

Family/subfamily/tribe	Species	DNA number/voucher	*rps*2	*mat*K
	Seymeria pectinata Pursh	CWD 94.142 (*J. R. Allison 4260b*) "Head Co., Georgia, USA" [UGA]	AF055141	AF051999
	Agalinis tenuifolia (M. Vahl.) Rafin.	CWD 90.129 "Monroe Co., Indiana, USA" [PSU]	ASU48738	
	Sopubia cana Harv.	CWD 94.152 (*K. E. Steiner 2473*) "Sani Pass, Natal Province, S. Africa" [PSU]	SCU48748	
	Buchnera floridana Gandoger	CWD 90.13 (*J. R. Allison & A. K. Gohlson 4452*) "Jackson Co., Florida, USA" [UGA]	BFU48744	
	Cycnium racemosum Benth.	(*A. Batten 1121*) "Mt. Kemp, Cape Province, S. Africa" [A. Batten]	CRU48745	
	Striga asiatica (L.) Kuntze	CWD 94.98 (no voucher) "cultivated, Whiteville, North Carolina, USA"	SAU48746	AF052000
	Striga gesnerioides (Willd.) Vatke ex Engl.	(*G. Sallé 13D*) "Mali, parasitic on cow pea" [PSU]	SGU48747	
	Harveya capensis Hook.	(*K. E. Steiner 2432*) "Onderboskloof, S. Africa" [PSU]	AF055142	
	Harveya purpurea Harv.	(*K. E. Steiner 2433*) "Cape Province, S. Africa" [PSU]	HPU48749	AF051984
	Hyobanche sanguinea L.	(*K. E. Steiner 2536*) "20.5 km E of turnoff to Daskop, Cape Province, S. Africa" [NBG]	HSU48750	
Rhinantheae	*Castilleja leariifolia* Benth.	CWD 90.93 (*Heckard & Chuang 6743*) [UCB]	CLU48739	AF051981
	Orthocarpus bracteosus Benth.	(*Heckard & Chuang 6757*) "California, USA" [UCB]	AF055140	
	Triphysaria versicolor Fisch. & Mey.	CWD 90.17 [PSU]	AF055137	
	Melampyrum sylvaticum L.	(*W. Wetschnig 2 Aug. 1992*) "Styria, E. Alps, Austria" [PSU]	AF055148	AF051991
	Tozzia alpina L.	CWD 93.38 (*W. Wetschnig 2 Aug. 1992*) "Styria, E. Alps, Austria" [PSU]	TAU48754	AF052001
	Lathraea clandestina L.	(*M. W. Chase 2605*) "ex hort., Kew R.B.G." [KEW]	LCU48755	AF051989
	Euphrasia spectabilis Phil.	CWD 93.39 (*W. Wetschnig 2 Aug 1992*) "Styria, E. Alps, Austria" [PSU]	ESU48752	
	Parentucellia viscosa L.	(*C. W. dePamphilis, L. Heckard & T. I. Chuang 90.89*) "Marin Co., California, USA" [PSU]	PVU48753	
	Bartsia alpina L.	CWD 93.37 (*W. Wetschnig 2 Aug. 1992*) "Styria, E. Alps, Austria" [PSU]	BAU48751	
	Pedicularis attolens A. Gray	(*W. Wetschnig s.n. 2 Aug. 1992*) "Styria, E. Alps, Austria" [PSU]	AF055149	
	Pedicularis foliosa L.	(*W. Wetschnig s.n. 2 Aug. 1992*) "Styria, E. Alps, Austria" [PSU]	PFU48740	
	Rhinanthus aristatus Čelak.	(*W. Wetschnig s.n. 2 Aug. 1992*) "Styria, E. Alps, Austria" [PSU]	RCU48756	

Table 1. Continued.

Family/subfamily/tribe	Species	DNA number/voucher	*rps*2	*mat*K
	Lamourouxia viscosa	CWD SS16 (*R. Ornduff 9660*) "cultivated, UC Berkeley, USA" [UCB]	AFO55138	
	Schwalbea americana L.	CWD 95.22 (*K. Kirkman s.n.*) "Albany, Georgia, USA" [PSU]	AFO55150	AFO51998
Orobanchaceae	*Cistanche phelypaea* L.	CWD 96.501 (*J. A. Hoder 1996*) "Coutino, Spain" [PSU]	AFO56149	
	Conopholis americana Wallr.	CWD 90.231 "Monroe Co., Indiana, USA" [PSU]	CAU48759	
	Epifagus virginiana Barton	CWD 88.01 "Washtenaw Co., Michigan, USA" [PSU]	EPFCPCG	EPFCPCG, AFO51982
	Boschniakia hookeri Walp.	CWD 94.61 "Marin Co., California, USA" [PSU]	BHU48757	AFO51979
	Boschniakia strobilacea A. Gray	CWD 94.153 (*G. Cohn s.n.*) [PSU]	BSU 48758	AFO51980
	Orobanche caryophyllaceae Sm.	(*M. W. Chase 2769*) "cultivated, KEW R.B.G., London" [KEW]	AFO55145	AFO51992
	Orobanche cernua Loefl.	CWD s.n. (*L. J. Musselman s.n.*) "Valdulapalli, India" [PSU]	AFO55147	AFO56147
	Orobanche corymbosa (Rydb.) Ferris	(*Heckard & Chuang 6751*) "Mono Co., California, USA" [PSU]	OCU48760	AFO51993
	Orobanche fasciculata Nutt.	CWD 94.151 (*Heckard 6754*) "Inyo Co., California, USA" [PSU]	AFO55143	AFO51994
	Orobanche hederae Duby	(KEW 2836) "cultivated, KEW R.B.G., London" [KEW]	AFO55146	AFO51995
	Orobanche ramosa L.	CWD 94.149 (*K. E. Steiner s.n.*) "Kirstenbosch, Capetown, S. Africa" [PSU]	ORU48761	AFO56148
	Orobanche uniflora L.	(*C. W. dePamphilis, L. Heckard & T. I. Chuang 94.15*) "Mt Tamalpais, California, USA" [PSU]	AFO55144	AFO51996
Bignoniaceae	*Kigelia pinnata* DC.	CWD 90.78 "ex hort., Missouri Botanical Garden #897541, USA" [PSU]	KSU48764	AFO51988
	Schlegelia parviflora (Oerst.) Monachino	CWD 90.41 (*A. Gentry #14221*) "cultivated, Missouri Botanical Garden, USA" [PSU]	AFO55152	
Callitrichaceae	*Callitriche hermaphrodita* L.	(*C. T. Philbrick 3022*)	AFO55159	
Gesneriaceae	*Kohleria digitiflora*	CWD 90.57 "ex hort., Missouri Botanical Garden 894763, USA" [PSU]	AFO55164	
Hippuriaceae	*Hippuris vulgaris* L.	(*C. T. Philbrick 305A*) [CA]	AFO55160	
Myoporiaceae	*Myoporum parvifolium* R. Br.	CWD 90.43 "ex hort., Missouri Botanical Garden #896655, USA" [PSU]	AFO55157	
Oleaceae	*Ligustrum japonicum* Buch.-Ham. ex D. Don	CWD SS69 (*J. D. Palmer CPS704*) "ex hort."	LJU48769	
Solanaceae	*Nicotiana tabacum* L.	CWD s.n. "cultivated, Vanderbilt U., USA" [PSU]	CHNTXX	CHNTXX
Verbenaceae	*Verbena bonariensis* L.	*R. G. Olmstead* 464	AFO55153	



trnK 11	CTCAACGGTAGAGTACTCG
trnK 2621	AACTAGTCGGATGGAGTAG
matK -53F	CTTGTTTTGRCTNTATCGCACTATG
matK 323F	TATTCTCAAATCATATCRGAGGG
matK 775F	TCTTGAACGAATCTATTTCTRYGG
matK 1210F	GGGCATCCCATTAGTAAGNC
matK 1349R	CTTTTGTGTTTCCGAGCYAAAGTTC
matK 1189R	CGGTTACTAATGGGATGCCC
matK 950R	CCACARCGAAAAATRMCATTGCC
matK 510R	GAAGAGTTTGAACCAAKAYTTCC

Figure 1. Map of the *mat*K gene (thick line) and flanking regions (thin line) with primer sites indicated. Primer sequences are listed 5′ to 3′; some contain IUPAC ambiguity codes. *trn*K 11 was designed by G. Learn; *trn*K 2621 was designed by K. Steele (Steele & Vilgalys, 1994).

ers of tribe Rhinantheae). *Tozzia* is therefore not an evolutionary transition to *Lathraea*, though they are fairly close relatives. The genus *Orobanche* is diphyletic (Fig. 3). Two New World species group with *Boschniakia*, and four Old World species group with *Epifagus*. The *rbc*L phylogeny also supports *Orobanche* diphyly (Wolfe & dePamphilis, 1998). However, the support values for the New World clade are low, so this result must be regarded as preliminary.

The strict consensus tree resulting from the large-merger analysis (Fig. 4) is more resolved and generally better supported than that from the *rps*2-only analysis, but is otherwise completely congruent with it. The relationships at poorly supported nodes, especially among the outgroups, should be regarded as very preliminary. Neither subfamily of Scrophulariaceae is monophyletic, and this is not only because the broomrapes, mints, and other families derive from within the subfamilies. The tribe Digitaleae sensu Wettstein, which includes *Veronica* and *Hemiphragma*, forms a clade with the tribe Antirrhineae and its relatives rather than with the rest of the subfamily Rhinanthoideae. Likewise neither parasitic tribe is monophyletic. Constraint analyses show that many extra steps would have to be added to make the subfamilies and parasitic tribes monophyletic (Table 2). Surprisingly, there is strong support for a clade that includes members of both the Rhinantheae and the Buchnereae. All of the genera in this clade have their center of distribution in North America (Mabberley, 1997).

DISCUSSION

These analyses of *rps*2 and *mat*K gene sequences allow us to better understand the phylogeny and thus the evolution of parasitism within the figworts and broomrapes. The number of characters and taxa we have utilized exceeds that of previous studies. Out of the 27 taxa contained in the *rps*2 tree and the *mat*K tree, there are only two conflicts. The combination of the data sets is therefore supported (Mason-Gamer & Kellogg, 1996). The monophyly of the parasitic figworts and broomrapes is strongly supported in all four analyses. The monophyly of the parasites also indicates a single origin of parasitism. It is not yet clear how many times haustorial parasitism has evolved in other groups, but an estimate of at least 11 times (Nickrent et al., 1998) suggests that the habit may be relatively uncommon in flowering plants. However, once hemiparasitism has been established, the loss of photosynthesis (and evolution of holoparasitism) may be more common.

Holoparasitism has arisen five independent times in the figwort/broomrape clade. In addition to the *Harveya*, *Lathraea*, and broomrape lineages, it has also occurred once within the genus *Alectra* and once within the genus *Striga* (dePamphilis et al.,

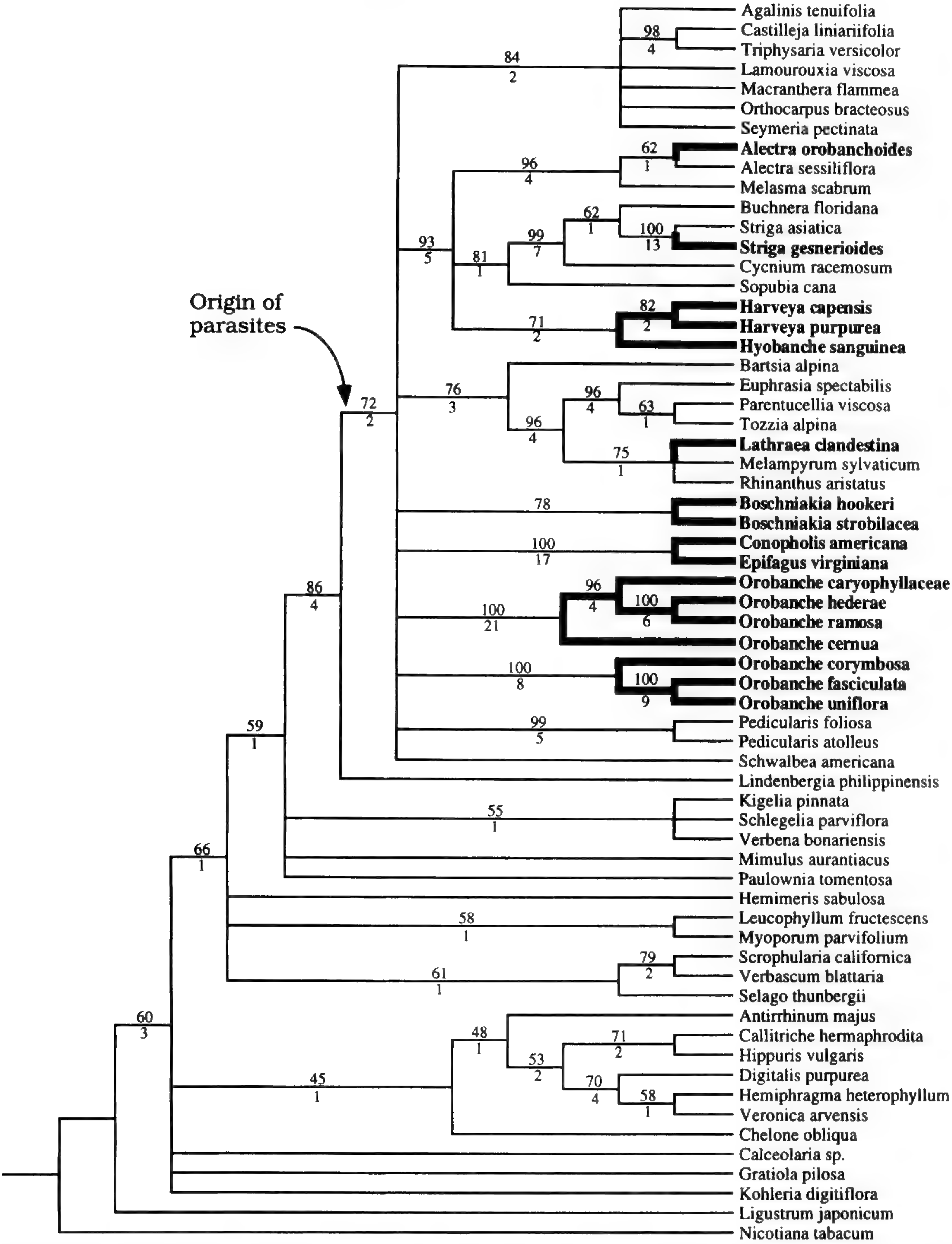


Figure 2. Phylogeny of figworts and broomrapes based on *rps*2 gene sequences. The strict consensus tree is shown, with bootstrap values (above branch) based on 500 replicates and Bremer support values (below branch). Bold font typeface and bold font branch segments indicate holoparasitic taxa.

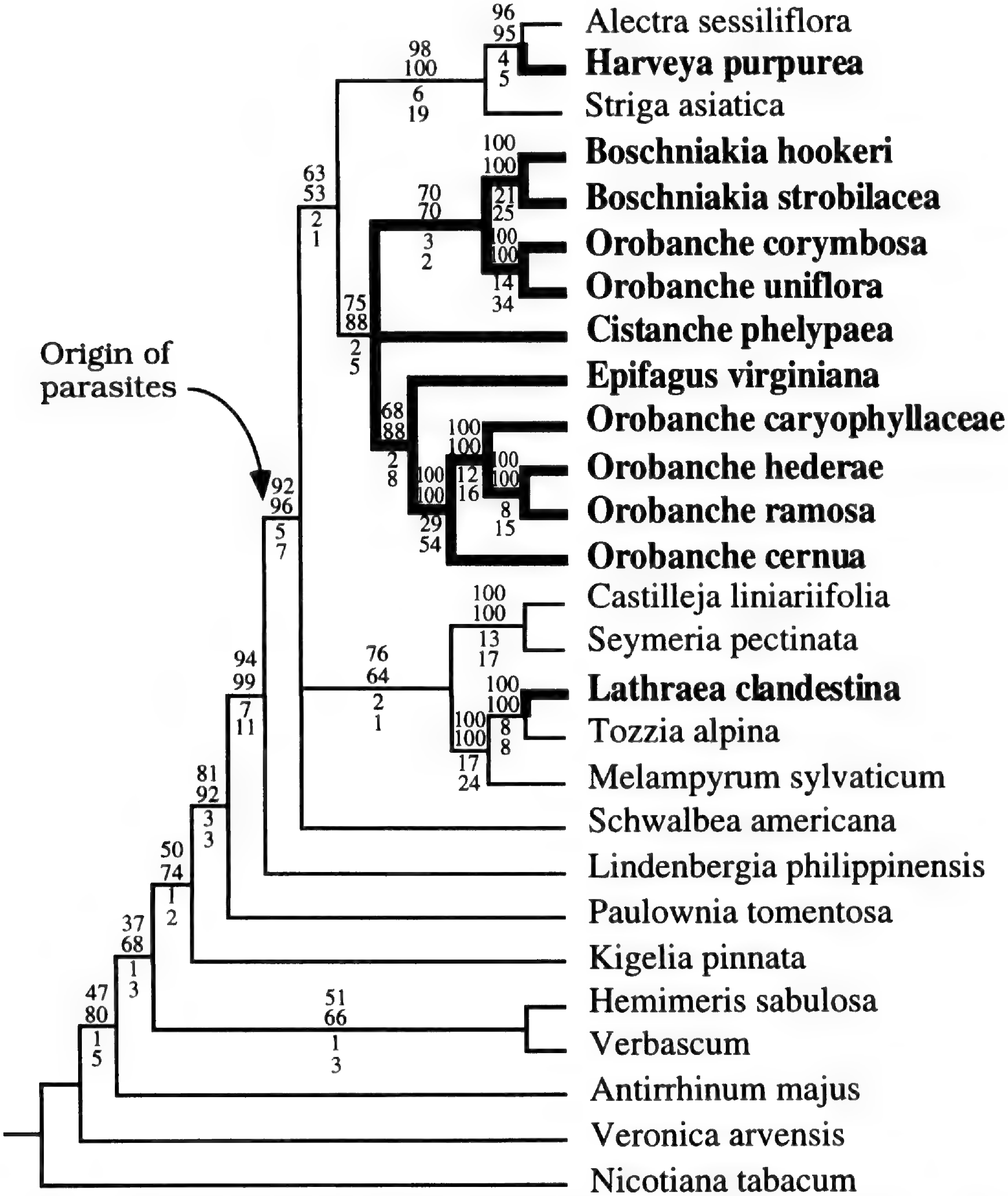


Figure 3. Results of both the *mat*K-only analysis and the small-merger analysis. The topology shown is the strict consensus tree from the *mat*K-only analysis. *Cistanche* and *Schwalbea* have unresolved placements; when these taxa are removed, a single, fully resolved tree is found. The small-merger combined analysis of *rps*2 and *mat*K yielded a strict consensus tree with this same topology, except that *Cistanche* was not included in that analysis. The four numbers displayed at each node represent, top to bottom, the *mat*K bootstrap value (based on 1500 replicates), the small-merger bootstrap value (based on 838 replicates), the *mat*K Bremer support value, and the small-merger Bremer support value. In one case, different species were used to represent a genus: *Verbascum blattaria* was sequenced for *rps2*; *V. thapsis* was sequenced for *mat*K. Bold font typeface and bold font branch segments indicate holoparasitic taxa.

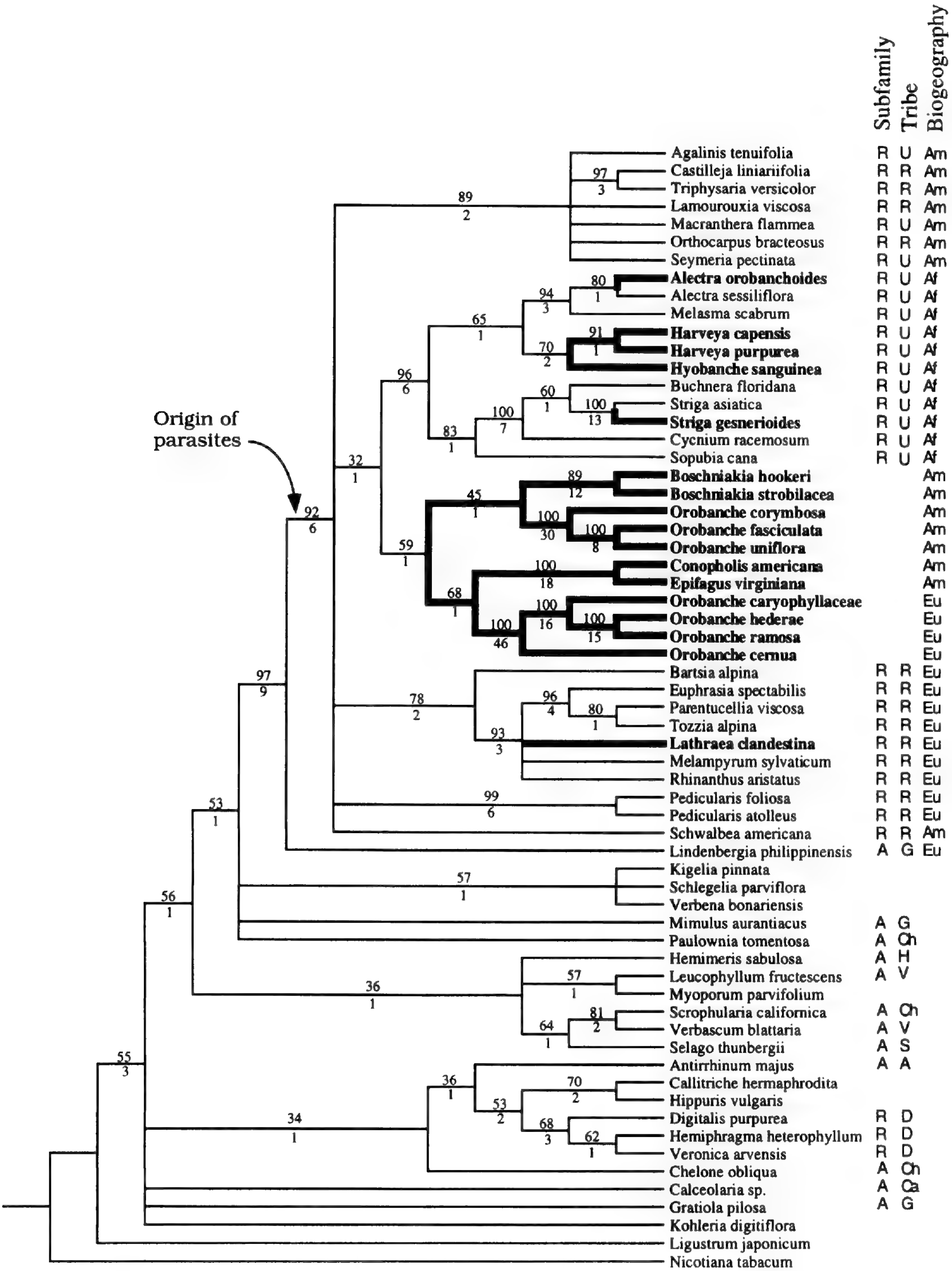


Figure 4. Strict consensus tree from the large-merger analysis. Bootstrap values (above) based on 500 replicates and Bremer support values below. Bold font typeface and bold font branch segments indicate holoparasitic taxa. Subfamily codes: A = Antirrhinoideae, R = Rhinanthoideae. Codes for Wettstein's tribes: U = Buchnereae, R = Rhinantheae, G = Gratioleae, Ch = Cheloneae, H = Hemimeridae, V = Verbasceae, S = Selagineae, A = Antirrhineae, D = Digitaleae, Ca = Calceolarieae. Biogeography codes—taxa have their centers of distribution in the following province: Am = Americas, Af = Africa, Eu = Eurasia.

Table 2. Descriptive measures from parsimony analyses and results of monophyly constraint analyses. Small = small merger, Large = large merger, MP = maximum parsimony.

	*rps*2	*mat*K	Small	Large
No. of taxa	63	27	26	63
No. of characters	617	1205	1822	1822
No. of MP trees	15000	6	3	13941
Tree length	727	1421	1823	2137
CI	0.552	0.669	0.677	0.627
RC	0.370	0.380	0.398	0.381
Constraints[1]:				
F-S	20	21	34	36
SF-A	15	15	22	29
SF-R	19	23	37	38
T-B	6	17	22	25
T-R	6	17	22	22
G-O	0	9	8	7
B&TG	14	54	67	67

[1] The number of extra steps added when the following groups are constrained to be monophyletic (Swofford, 1993): F-S = family Scrophulariaceae (excluding broomrapes), SF-A = subfamily Antirrhinoideae, SF-R = subfamily Rhinanthoideae, T-B = tribe Buchnereae, T-R = tribe Rhinantheae, G-O = genus *Orobanche*, B&TG = broomrapes with the transitional genera *Harveya*, *Lathraea*, and *Hyobanche* (if present on tree).

1997). In all cases, holoparasitic taxa have been derived from hemiparasitic ancestors. This suggests that the loss of photosynthesis may only occur subsequent to the evolutionary origin of the haustorium, the key character defining a parasitic strategy.

THE EVOLUTIONARY SERIES IS NOT SUPPORTED

The transitional genera *Lathraea*, *Harveya*, and *Hyobanche* are each more closely related to green hemiparasitic lineages than they are to the broomrapes. The placement of *Lathraea* with the *Melampyrum* group is found in 100% of bootstrap replicates and all trees up to 23 steps longer (Fig. 3). The grouping of *Harveya* (and presumably *Hyobanche*, based on Fig. 4) with hemiparasites of the *Striga* group is also extremely well supported (bootstrap value = 100, Bremer support value = 19). This reveals that the characters used previously to group these taxa with the broomrapes (e.g., loss of green color, reduction of leaves, the condensation of the vegetative axis, and reduction of cell number in the ovary) are all homoplastic and may be correlated with holoparasitism. The past practice of grouping the transitional genera with the broomrapes may be due to the fact that their specialization involves the loss or reduction of many features, and convergently reduced or lacking features will seem to be homologies due to common ancestry.

OTHER SYSTEMATIC CONCLUSIONS

Olmstead and Reeves (1995; Reeves & Olmstead, 1998) began the disintegration of the Scrophulariaceae by reporting that there are at least two major lineages of figworts. In studies of the chloroplast genes *ndh*F and *rbc*L, they identified the fact that *Antirrhinum*, *Digitalis*, and *Veronica* form a clade distinct from *Scrophularia*, *Verbascum*, and *Selago*. We have identified five additional clades of nonparasitic figworts. *Leucophyllum* represents a clade sister to the Myoporaceae. *Mimulus* and *Paulownia* represent clades that are not in the parasitic figwort clade, but are closer to it, Verbenaceae, and Bignoniaceae than they are to the *Scrophularia* clade. Finally, *Calceolaria* and *Gratiola* represent two clades whose positions are unresolved. Each of these lineages may end up as a family of its own or may be included with one of the other families, depending on its position on future, more resolved, phylogenies. A combined analysis is being conducted, using *rps*2, *ndh*F, and *rbc*L and extensive sampling of nonparasitic Scrophulariaceae and related lineages (R. G. Olmstead, C. W. dePamphilis, A. D. Wolfe, N. D. Young, W. J. Elisens & P. A. Reeves, unpublished).

Based on Figure 4, we can see that neither of the traditional subfamilies (Antirrhinoideae, Rhinanthoideae) are monophyletic. When trees are constrained to contain a monophyletic subfamily, they are at least 15 steps longer (Table 2). In order to circumscribe monophyletic groups, the subfamilies must be broken up, and their members placed into at least five new or re-defined families, separated by other existing families (R. G. Olmstead, C. W. dePamphilis, A. D. Wolfe, N. D. Young, W. J. Elisens & P. A. Reeves, unpublished). One redefined family will combine taxa out of both subfamilies.

Digitalis and *Veronica,* classified by Wettstein (1897) in the Rhinanthoideae, are herein (Fig. 3) more closely related to *Antirrhinum* than to the remainder of Rhinanthoideae. This implies that the floral aestivation character used to distinguish Rhinanthoideae from the other subfamily, Antirrhinoideae (Bentham, 1846; Bentham & Hooker, 1876; Wettstein, 1897; Armstrong & Douglas, 1989), has changed more than once in the evolution of the group: *Digitalis, Veronica,* and their relatives probably represent an independent origin of the rhinanthoid corolla aestivation type: the traditional Rhinanthoideae are clearly polyphyletic. This placement of *Digitalis* and *Veronica* agrees not only with *ndh*F/*rbc*L phylogeny (Olmstead & Reeves, 1995) but also with pollen morphology. Pollen exine structure is tectate with reticulate sculpturing in *Digitalis, Veronica, Antirrhinum,* and *Chelone,* a structure that is otherwise rare in the family (Minkin & Eshbaugh, 1989).

The nearest relative to the parasitic figworts and broomrapes is the figwort genus *Lindenbergia,* not Gesneriaceae. Gesneriaceae (here represented by *Kohleria*) must therefore have derived unilocular placentation independently from Orobanchaceae. *Lindenbergia,* a southeast Asian genus, has traditionally been placed in the tribe Gratioleae in subfamily Antirrhinoideae (Bentham & Hooker, 1876) despite corolla aestivation similar to parasitic figworts and broomrapes (Cooke, 1903; Duthie, 1903–1920; Brühl, 1920; J. E. Armstrong, unpublished). Brühl (1920) has suggested that *Lindenbergia* shares a closer relationship with the parasitic figworts than with the Gratioleae, which agrees with our analysis (Figs. 2–4). *Lindenbergia* is here shown to be the sister group to the parasites, confirming its floral similarity. The clade containing all parasitic figworts, broomrapes, and *Lindenbergia* is strongly supported. In the small-merger analysis, it has a bootstrap value of 99 and a Bremer support value of 11. In addition, this clade has a defining (though not unique) morphological synapomorphy: anterior lobes external in corolla aestivation. This group warrants family status, and the appropriate name is Orobanchaceae, a conserved name (Greuter et al., 1994). We recommend expanding the Orobanchaceae and suggest the following clade definition:

> Orobanchaceae are the least inclusive clade that contains *Orobanche uniflora, Schwalbea americana,* and *Lindenbergia philippinensis.*

This definition, along with the changes suggested in Olmstead et al. (R. G. Olmstead, C. W. dePamphilis, A. D. Wolfe, N. D. Young, W. J. Elisens & P. A. Reeves, unpublished), forms a new taxonomic system, which is compared to Wettstein's (Wettstein, 1897) in Table 3. Orobanchaceae now include hemiparasites and nonparasites, as well as holoparasites.

Within the parasites, *Schwalbea* is among the basal lineages, as suggested by its morphology (Pennell, 1935), but its exact position remains unresolved. The two parasitic tribes Buchnereae and Rhinantheae are each not monophyletic (Fig. 4). *Agalinis* (= *Gerardia), Macranthera,* and *Seymeria,* the New World representatives of Buchnereae Benth. 1846 (= Gerardieae Benth. & Hook., 1846), are part of a clade that is otherwise made up of genera of Rhinantheae with centers of distribution in North America. This clade is an example of the strong biogeographic pattern seen in this phylogeny (Fig. 4). Clades on the parasitic part of the phylogeny tend to be made up of genera with their centers of distribution (Mabberley, 1997) in the same biogeographic province (Fig. 4). There are large clades of taxa centered in Africa and Eurasia that include both hemiparasites and holoparasites. Even within the broomrapes a pattern emerges, with two clades of taxa centered in the Americas and one in Eurasia.

In Figures 3 and 4, the broomrapes are monophyletic. Their sister group (Fig. 3) is the *Striga-Harveya* group. However, this is not as well supported as our other conclusions and must be regarded as preliminary. The other potential sister groups are the *Tozzia-Lathraea* and *Castilleja-Seymeria* groups. Moderately well supported is the finding that *Orobanche* comprises at least two groups: one allied with *Boschniakia,* the other allied with *Epifagus* and *Conopholis* (Fig. 4). In the small-merger analysis (Fig. 3), these two new groupings are supported by bootstrap values of 70 and 88, respectively. The current classification of *Orobanche* (Beck von Mannagetta, 1930; Collins, 1973; Heckard & Chuang, 1975) contains two Old World sections and two New World sections. Beck von Mannagetta (1890) united the two New World sections into one branch of the genus, and the two Old World sections to form the other. Cytology indicates that one of the Old World sections, section *Orobanche,* has chromosome numbers that are generally $2n = 38$, while the other three sections have chromosome numbers that are nearly always $2n = 24, 48, 72,$ or 96 (Heckard & Chuang, 1975). To be consistent with Beck von Mannagetta's scheme, the cytology suggests that section *Orobanche* might be monophyletic and derived from the other Old World section, *Trionychon* (including *O. ramosa,* $2n$

Table 3. Genera of the Scrophulariaceae/Orobanchaceae complex used in this study, deposited according to the taxonomic systems of Wettstein (1897), and Olmstead et al. (R. G. Olmstead, C. W. dePamphilis, A. D. Wolfe, N. D. Young, W. J. Elisens & P. A. Reeves, unpublished).

Wettstein	Olmstead et al.
Schrophulariaceae	Scrophulariaceae
Pseudosolaneae	*Verbascum*
Verbasceae	*Leucophyllum*
Verbascum	*Scrophularia*
Leucophyllum	*Selago*
Antirrhinoideae	
Hemimeridae	Antirrhinaceae
Hemimeris	*Antirrhinum*
Calceolarieae	*Chelone*
Calceolaria	*Gratiola*
Antirrhineae	*Hemiphragma*
Antirrhinum	*Veronica*
Cheloneae	*Digitalis*
Scrophularia	*Callitriche*
Chelone	*Hippuris*
Paulownia	
Gratioleae	Calceolariaceae
Mimulus	*Calceolaria*
Lindenbergia	
Gratiola	Orobanchaceae
Selagineae	*Lindenbergia*
Selago	*Melasma*
Rhinanthoideae	*Alectra*
Digitaleae	*Macranthera*
Hemiphragma	*Seymeria*
Veronica	*Agalinis*
Digitalis	*Sopubia*
Gerardieae	*Buchnera*
Melasma	*Cycnium*
Alectra	*Striga*
Macranthera	*Harveya*
Seymeria	*Hyobanche*
Agalinis	*Castilleja*
Sopubia	*Orthocarpus*
Buchnera	*Triphysaria*
Cycnium	*Melampyrum*
Striga	*Tozzia*
Harveya	*Lathraea*
Hyobanche	*Euphrasia*
Rhinantheae	*Parentucellia*
Castilleja	*Bartsia*
Orthocarpus	*Pedicularis*
Triphysaria	*Rhinanthus*
Melampyrum	*Lamourouxia*
Tozzia	*Schwalbea*
Lathraea	*Cistanche*
Euphrasia	*Conopholis*
Parentucellia	*Epifagus*
Bartsia	*Boschniakia*

Table 3. Continued.

Wettstein	Olmstead et al.
Pedicularis	*Orobanche*
Rhinanthus	
Lamourouxia	No family designation, near Orobanchaceae
Schwalbea	*Mimulus*
Orobanchacae	*Paulownia*
Cistanche	
Conopholis	Bignoniaceae
Epifagus	*Kigelia*
Boschniakia	
Orobanche	No family designation, near Bignoniaceae
Bignoniaceae	*Schlegelia*
Kigelia	
Schlegelia	Verbenaceae
Callitrichaceae	*Verbena*
Callitriche	
Gesneriaceae	Gesneriaceae
Kohleria	*Kohleria*
Hippuriaceae	
Hippuris	
Myoporiaceae	
Myoporum	
Verbenaceae	
Verbena	

= 24). Our plastid phylogeny (Fig. 4) supports the Old World–New World division, but finds a paraphyletic relationship of section *Orobanche* (*O. caryophyllaceae, O. hederae,* and *O. cernua,* all $2n = 38$) to section *Trionychon* ($2n = 24$). This indicates that the Old World branch of the genus may have begun with $2n = 38$ and later experienced a reduction in section *Trionychon* to $2n = 24$. No counts have been reported for *Epifagus, Conopholis,* or *Boschniakia. Cistanche* has $2n = 40$ (Hambler, 1956).

Having a classification that reflects monophyletic relationships will be a great advantage, especially to comparative biologists. These phylogenetically defined groups may even be easier to identify based on morphological characters, compared to the traditional family Scrophulariaceae, which is recognized by symplesiomorphies such as the presence of endosperm, capsular fruit, and strongly zygomorphic flowers. Furthermore, *Antirrhinum majus* serves as a model organism in the field of developmental biology (Coen & Nugent, 1994; Bradley et al., 1996). Such work can be placed in an illuminating context by the study of its relatives and their phylogeny (Reeves & Olmstead, 1998).

Knowing that photosynthesis has been lost multiple times in Orobanchaceae opens up many opportunities for comparative analysis. It allows for the comparison of rates of DNA base substitution (dePamphilis et al., 1997), plastid genome structural evolution (dePamphilis, 1995), as well as rates of loss of particular photosynthetic genes (Wolfe & dePamphilis, 1997). Haustorial anatomy and physiology, host plant use, morphology, as well as the genetic changes that have accompanied parasitism, can all be investigated using the phylogeny for reference. Awareness of the multiple, independent origins of holoparasitism provides us with a powerful comparative framework in which to study the process of parasitic evolution.

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PHYLOGENETIC CONSIDERATIONS OF EUPHORBIACEAE TRIBE ALEURITIDEAE[1]

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ABSTRACT

A phylogenetic analysis based on morphological characters of Euphorbiaceae tribe Aleuritideae was performed, examining the monophyly of subtribe Aleuritinae and its delimitation into three genera. The subtribe was supported as monophyletic and its current classification justified. Differences between the genera, though small, are based on apomorphies, and the genera are monophyletic. Within subtribe Aleuritinae, *Aleurites* (2 species) is sister to both monotypic *Reutealis* and *Vernicia* (3 species). Monophyly was not confirmed for tribe Aleuritideae. One of the selected outgroups for Aleuritideae *(Paracroton,* formerly *Fahrenheitia)* appeared within the ingroup in the most parsimonious cladograms. For the other subtribes, monophyly was tentatively supported for only subtribe Garciinae (monogeneric), Crotonogyninae (3 genera), and Neoboutoninae (2 genera). The largest subtribe, Grosserinae (7 genera), is probably paraphyletic, because *Domohinea* (recently placed in synonymy of *Tannodia* by Radcliffe-Smith) and *Tannodia* group with subtribe Aleuritinae.

Nowadays subtribe Aleuritinae comprises three small genera: *Aleurites* (2 species), *Reutealis* (1 species), and *Vernicia* (3 species). Müller (1866) had formerly united the three genera within a broader *Aleurites*. Airy Shaw (1967) subdivided *Aleurites* s.l. because of three new genera, *Deutzianthus, Loerzingia,* and *Tapoides,* thought to be closely related to *Aleurites* s.l. Recently, *Tapoides* was placed in subtribe Grosserinae (tribe Aleuritideae) by Webster (1994b). He considered *Deutzianthus* (with *Loerzingia* as synonym) to belong to tribe Jatropheae and not tribe Aleuritideae.

Revision of subtribe Aleuritinae for *Flora Malesiana* suggests differences between the genera to be narrow and reticulate. It is therefore reasonable to ask whether this taxonomic division is justified and whether the split genera and subtribe Aleuritinae are monophyletic. The phylogenetic analysis herein for all genera of tribe Aleuritideae (Table 1) will address these questions.

For tribe Aleuritideae, the four subtribes Garciinae, Grosserinae, Crotonogyninae, and Neoboutoninae show various degrees of homogeneity (see Table 1 for classification). American subtribe Garciinae is monogeneric and almost by definition homogenous; however, the two species of *Garcia* differ considerably in the stamen number (29 versus 63 to 160). The two genera of subtribe Neoboutoninae share the absence of petals and leaves with small glandular hairs; however, they differ in leaf venation, presence of a caruncle, and persistence of stipules. African *Manniophyton* (subtribe Crotonogyninae) is distinguished by its vining habit, palmate venation, and stinging hairs; the other two genera, *Crotonogyne* and *Cyrtogonone,* are quite similar and share characters such as dioecy and fused petals. The mainly African Grosserinae is the largest subtribe, with seven genera, all dioecious and with free petals. The morphological variability among these genera is great and their distributions (Table 1) disparate (South America, Africa, Southeast Asia), indicative perhaps of a paraphyletic group.

MATERIALS AND METHODS

CHARACTER SELECTION

The characters used in the cladistic analysis are explained in Appendix 1; the data matrix is presented in Table 2. The character states were obtained from herbarium specimens (Appendix 2) and literature (Table 1).

The following characters were not included in the cladistic analysis because they are typical for single taxa and, therefore, are presumably autapomorphies: whorled leaves; ovary 2-locular (*Borneodendron*); amplexicaul stipules; bracts forming a

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Table 1. Webster's classification (1994b) for the taxa mentioned in this study. References were sources of information for character states.

Tribe Aleuritideae		
Subtribe Aleuritinae		
Aleurites	2 species, Malesia, Australia, Pacific	Stuppy et al. (1999)
Reutealis	1 species, Philippines	Stuppy et al. (1999)
Vernicia	3 species, China, Indochina, Japan	Stuppy et al. (1999)
Subtribe Garciinae		
Garcia	2 species, Central America	Lundell (1945)
Subtribe Grosserinae		
Anomalocalyx	1 species, Brazil	Ducke (1934)
Cavacoa	3 species, African	Elffers & Taylor (1956)
Domohinea	1 species, Madagascar	Leandri (1940)
Grossera	7 species, African	Pax & Hoffmann (1912)
Sandwithia	2 species, Neotropics	Lanjouw (1932)
Tannodia	ca. 4 species, E. Africa, Comoros	Pax & Hoffmann (1912)
Tapoides	1 species, Borneo	Airy Shaw (1971)
Subtribe Crotonogyninae		
Crotonogyne	15 species, Africa	Pax & Hoffmann (1912)
Cyrtogonone	1 species, Africa	Pax & Hoffmann (1912)
Manniophyton	1 species, Africa	Pax & Hoffmann (1912)
Subtribe Neoboutoninae		
Benoistia	3 species, Madagascar	Radcliffe-Smith (1988)
Neoboutonia	3 species, Madagascar	Pax & Hoffmann (1914)
Tribe Crotoneae		
Paracroton	4 species, tropical Asia	
Tribe Jatropheae		
Deutzianthus	2 species, Indochina, Sumatra	
Tribe Ricinocarpeae		
Subtribe Bertyinae		
Borneodendron	1 species, Borneo	

cone (*Cavacoa*); submarginal abaxial glands present, crater-like; stigmas bifid to multifid (*Crotonogyne*); staminate receptacle with disc-like glands (*Cyrtogonone*); pilose receptacle (*Domohinea*, now a synonym of *Tannodia*, see Radcliffe-Smith, 1998); thick sepals (*Grossera*); liana; stinging hairs; raised glands on abaxial surface of leaves (*Manniophyton*); lobed stipules; seeds caruncululate (*Neoboutonia*); branches 5-angular; stigmas bifid to multifid (*Reutealis*); hair tuft domatia on lower leaf surface (*Tannodia*); glands at apex of petiole slenderly stalked [*Vernicia cordata* (Thunb.) Airy Shaw]; clavately stalked (*Vernicia montana* Lour.).

Some characters, including several used in Webster's (1994b) keys, were not included in the phylogenetic analysis, partly because they were too variable to permit the discrimination of states (e.g., inflorescence position; inflorescence type; flower size; fruit and inflorescence pubescence), or because the states could not be scored for many taxa [e.g., anther dehiscence; ovary tapering gradually vs. abruptly into the style (important within *Vernicia*), petal venation].

OUTGROUP SELECTION

The choice of an outgroup was difficult, because there is no obvious sister group to tribe Aleuritideae. The presence of a sister group is not a requisite (Nixon & Carpenter, 1993), but may facilitate character polarization. *Deutzianthus*, considered by Airy Shaw (1967) to be a close relative of *Aleurites*, probably has other affinities. Webster (1994b) placed it in a relatively distant tribe, Jatropheae. *Deutzianthus* was not selected as outgroup, because if Webster is correct, many homoplasious parallel developments would exist between *Deutzianthus* and subtribe Aleuritinae, and these would likely complicate the cladogram. Testing Airy Shaw's hypothesis would require that many more genera be included in the analysis, and that is beyond the scope of this article. Although Webster's classification was not based on phylogenetic analyses, the sequence of taxa shows an increase in apomorphies (for a list of synapomorphies, see Webster, 1994a). Therefore, it is logical to look for an outgroup in the tribes treated before the Aleuritideae. *Borneo-*

Table 2. Morphological data matrix for the cladistic analysis. The characters are explained in Appendix 1. Absence of a character is never noted as 0 to avoid any suggestion of primitiveness. Unknown characters due to insufficient material are marked as missing (—). *Borneodendron* and *Paracroton* are the outgroups.

Taxon	Character number																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Borneodendron	2	2	2	1	1	1	2	1	1	1	1	1	1	1	?	2	3	1	1	1	—	1	1	1	1
Paracroton	2	2	2	1	2	1	2	2	1	1	1	1	3	2	1	2	2	2&3	1	1	1	2	2	1	1
Aleurites	2	1	2	2	2	2	2	1	1	1	3	2	2	2	1	2	2	3	1	1	1	1	3	2	1
Reutealis	2	1	2	2	2	1	1	1	1	1	3	2	2	2	1	1	2	2	1	1	—	1	3	1	1
Vernicia	2	1	1	1	2	2	1	3	1	1	3	2	2	2	1	1	2	2	1	1	—	1	3	1	2
Garcia	2	1	1	1&2	1	1	2	1	1	1	1	2	2	3	1	3	1	1	1	1	1	1	2	1	1
Anomalocalyx	1	1	1	1	1	1	2	1	1	1	1	2	2	2	1	2	1	1	1	1	1	2	2	1	1
Cavacoa	1	1	1	1	1	1	2	1	2	1	1	2	2	2	1	2	3	1	1	1	1	2	2	1	1
Domohinea	1	1	1	1	1	1	2	1	1	1	2	2	2	2	1	1	2	2	1	1	2	1	2	1	1
Grossera	1	1	1	1	2	1	2	2	2	1	1	2	2	2	1	2	3	1	1	1	1	2	2	1	1
Sandwithia	1	1	1	1	1	1	2	1	1	1	1	2	2	2	1	2	1	1	1	1	1	2	2	1	1
Tannodia	1	1	1	1	1	1	2	1	1	1	2	2	2&3	2	1	1	2	2	1	1	2	2	2	1	1
Tapoides	1	1	1	1	1	1	2	1	1	1	1	2	2	2	1	1	2	2	1	1	1	2	2	1	1
Crotonogyne	1	1	3	1&2	2	1	1&2	1	1	1	1	2	2	2	2	1&2	1	1	3	1	1	2	2	1	1
Cyrtogonone	1	1	3	2	2	1	2	1	1	1	1	2	2	2	1	2	1	1	—	1	1	—	—	—	—
Manniophyton	1	1	3	2	2	2	1	1	1	1	3	2	2	2	2	1&2	1	1	3	1	1	2	2	1	1
Benoistia	1	1	1	1	1	1	2	1	1	2	1	2	2	1	?	2	1	1	2	2	1	3	2	1	1
Neoboutonia	1	1	2	1&2	2	1	1	1	1	2	3	2	2	1	?	2	1	1	2	2	1	2	2	1	1

dendron (tribe Ricinocarpeae, subtribe Bertyinae) and *Paracroton* [tribe Crotoneae; formerly and better known as *Fahrenheitia* (Balakrishnan & Chakrabarty, 1995)] are outgroup candidates, because they have been well described in the literature and abundant material was available to check characters.

CLADISTIC ANALYSIS

The cladistic analysis was performed with PAUP version 3.1.1 (Swofford, 1993). A Branch and Bound search was performed with furthest addition of taxa, and Mulpars invoked. Statistical significance of the results was evaluated with the aid of a Bootstrap Analysis, Decay Indices up to the level D = 6 (retaining all trees five steps longer than the most parsimonious trees), and a Permutation Tail Probability (PTP) test (Siddall, 1993). The Bootstrap (200 replicates) and Decay analyses were also performed with PAUP 3.1.1 (Swofford, 1993), with settings for: Heuristic search, TBR, Furthest, Mulpars. Siddall's PTP test was performed in conjunction with Hennig86 (Farris, 1988), with settings: characters unordered, mh*; bb*. Character optimizations were studied with MacClade version 3 (Maddison & Maddison, 1992).

RESULTS

Seven most parsimonious cladograms were found and are summarized in the strict consensus tree (Fig. 1): length 66, Consistency Index (CI) = 0.67, Retention Index (RI) = 0.67, RC = 0.45. All cladograms comprise the monophyletic subtribes Aleuritinae, Crotonogyninae, Garciinae, and Neoboutoninae. Subtribe Aleuritinae is sister group to the outgroup *Paracroton,* and these together form a clade with part of subtribe Grosserinae (the monophyletic group *Domohinea, Tannodia,* and *Tapoides*). Subtribe Neoboutoninae is sister group to the three former subtribes (Aleuritinae, Grosserinae, Crotonogyninae), and subtribe Garciinae is sister group to all other subtribes in tribe Aleuritideae.

The Probability Tail Permutation test (Faith & Cranston, 1991; Källersjö et al., 1992) indicated that the data matrix contains a significant amount of cladistic information (P = 0.001001; a* = 0.000376).

A strict consensus tree of all cladograms up to 69 steps, Decay Index 4, only resulted in a polytomy for all groups. A strict consensus of the 4446 trees of up to 68 steps, Decay Index 3, showed subtribe Aleuritinae as a clade, and the strict consensus of 308 trees of up to 67 steps, Decay Index 2, also showed the clade taxa *Domohinea* and *Tannodia* (Fig. 1).

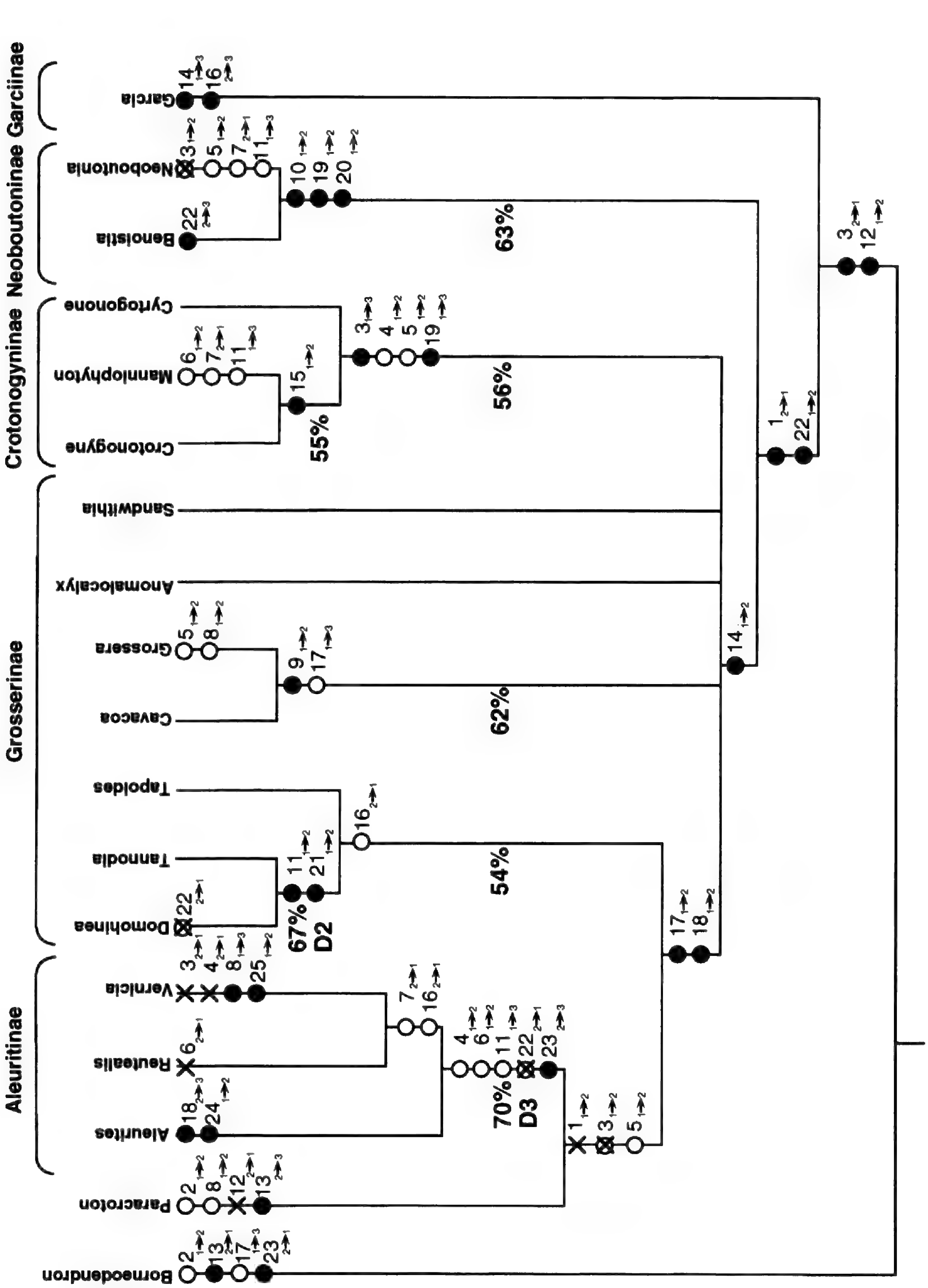
DISCUSSION

The matrix comprised several polymorphic taxa. MacClade provides the most parsimonious optimization for the polytypic characters by choosing one state. The other state is considered to be an autapomorphy and is counted as a step. The following optimizations are suggested:

Character 4 (pubescence of abaxial leaf surface): (sub)glabrous (state 1) for *Garcia* (subtribe Garciinae) and *Neoboutonia* (subtribe Neoboutoninae); densely hairy (state 2) for *Crotonogyne* (subtribe Crotonogyninae).
Character 7 (shape of leaf blade base): cuneate (state 2) for *Crotonogyne* (subtribe Crotonogyninae).
Character 13 (number of staminate sepals): 2 to 4 sepals (state 2) for *Tannodia* (subtribe Grosserinae).
Character 16 (number of stamens): 12 to 40 (state 2) for *Crotonogyne* and *Manniophyton* (subtribe Crotonogyninae).
Character 18 (arrangement of stamens): ordered in two series (state 2) for *Paracroton.*

Several of the optimizations (Fig. 1) can be interpreted differently. The characters at the root are now interpreted as either typical for the outgroup *Borneodendron* (2, 13, 17, 23) or for the ingroup (3, 12); see below. Characters 4 and 6 are regarded as synapomorphies for subtribe Aleuritinae with a reversal for *Vernicia* (ACCTRAN optimization); these characters can also be optimized as two parallel developments for *Aleurites* and *Reutealis* (DELTRAN optimization). DELTRAN optimization is used for character 2, a parallel development for *Borneodendron* and *Paracroton* (the alternative is a synapomorphy for the ingroup with a reversal for *Paracroton*). The state of character 19 is unknown for *Cyrtogonone* (subtribe Crotonogyninae); however, this character is still regarded as a synapomorphy for subtribe Crotonogyninae, thus an apiculate connective is presumed for *Cyrtogonone.*

The strict consensus cladogram (Fig. 1) is supported by a relatively high CI (0.67) and RI (0.67). Other statistical support is rather poor. Only two clades obtained a somewhat higher Decay Index (see Results). Bootstraps in this study were never 95% or higher; therefore, no clades appeared to have statistically significant support (Felsenstein, 1985). Recently, Hillis and Bull (1993, confirmed by Felsenstein & Kishino, 1993) empirically dem-


Garciinae
Neoboutoninae
Crotonogyninae
Grosserinae
Aleuritinae
Garcia
Neoboutonia
Benoistia
Cyrtogonone
Manniophyton
Crotonogyne
Sandwithia
Anomalocalyx
Grossera
Cavacoa
Tapoides
Tannodia
Domohinea
Vernicia
Reutealis
Aleurites
Paracroton
Borneodendron
63%
56%
55%
62%
54%
67%
D2
70%
D3

onstrated that bootstrap values of 70% or higher correspond to a probability of 95% or more that a clade is real. In this interpretation subtribe Aleuritinae (bootstrap 70%) has significant support (Fig. 1), and none of the other clades do. A bootstrap limit of 95% is very high, because it corresponds to three apomorphies for a clade without any homoplasy (Felsenstein, 1985). Morphological data matrices usually do not include many characters, and, therefore, high bootstrap support cannot be expected for all clades. The bootstrap method is purely statistical; it does not interpret the phylogenetic significance of the characters. We think that a clade with a unique character combined with a bootstrap of 60% is phylogenetically acceptable (a 60% bootstrap level corresponds to one non-homoplasious character per clade). Unique characters are considered to constitute useful characters for recognition in classifications, being reliable apomorphies.

It may appear curious that subtribe Neoboutoninae has a bootstrap of just 63%, even though it is supported by three apomorphies; this is probably due to the many homoplasious changes in *Neoboutonia* (characters 3, hairs stellate; 5, basal blade glands; 7, cordate leaf base; and 11, palmate venation). All three apomorphies (10, abaxial glandular leaf hairs; 19, connective with gland; and 20, anthers elongate) are unique; therefore, this clade is considered to be phylogenetically acceptable.

The group *Domohinea*, *Tannodia*, and *Tapoides* (54%) has no significant phylogenetic value, because character 16 (6 to 12 stamens) is not unique within tribe Aleuritideae.

Our purpose was to test the monophyly of subtribe Aleuritinae and to determine which generic classification of subtribe Aleuritinae is supported cladistically. We conclude that subtribe Aleuritinae is monophyletic: the bootstrap is high enough, the clade has a Decay Index of 3, and it possesses a divided pistillate disc as a unique character state (character 23). Airy Shaw's (1967) division of subtribe Aleuritinae into three genera is supported; at least, *Aleurites* and *Vernicia* each have two unique characters (*Aleurites*: 18, stamens in 4 series; 24, drupaceous fruit; *Vernicia*: 8, glands in leaf margin crenations; 25, seeds dorsally warty). *Reutealis* is seemingly untypically characterized by a single reversal (16, stamens 6 to 12); however, it possesses two unique autapomorphies: branches 5-angular, and stigmas bifid or multifid. The sister-group relationship between *Reutealis* and *Vernicia* is only supported by two parallel developments (though unique within subtribe Aleuritinae): 7 (leaf base cordate) and 16 (stamens 6 to 12).

Monophyly of subtribes Crotonogyninae and Neoboutoninae is supported in terms of unique characters, though not by significant bootstrap values or decay indices. Subtribe Garciinae is monogeneric, and, therefore, no bootstrap values or decay indices are available. *Garcia* seemingly has two unique character states (14, staminate petals 6 to 13; 16, 63 to 160 stamens); however, character 16 applies only to one of the two species in the genus, leaving only the higher number of staminate sepals as a unique character.

Subtribe Grosserinae is not supported at all; the relationships of the American genera, *Anomalocalyx* and *Sandwithia*, are still especially obscure (both genera, due to several non-included autapomorphies, received the same coding). Within subtribe Grosserinae, *Cavacoa* and *Grossera*, both African, constitute a distinct group (supported by the unique character 9, pellucid dots in leaves; and the non-unique 17, all stamens connate). The supposed relationship between *Tannodia* (including *Domohinea)* and *Tapoides* (Africa, Madagascar, Comores, Borneo) is weak (see discussion above).

The relationships between all distinct groups (lower branches in Fig. 1) are not supported by bootstrap values or Decay Indices. Characters 1 (monoecious plants) and 22 (5 pistillate sepals) are not unique; they reverse in several taxa. Characters 14 (3 to 5 staminate petals) and 22 (5 pistillate sepals), unique in this group, are not unique in the Euphorbiaceae, nor are the inner connate stamens, 17, and biseriate stamens, 18.

One of the outgroups, *Paracroton*, could not be placed parsimoniously at the base of the cladogram, because it shares various apomorphies with subtribe Aleuritinae. This suggests that tribe Aleuritideae is not monophyletic and that *Paracroton* is part of the ingroup. The major synapomorphy for tribe Aleuritideae (character 12, rupturing, connate

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Figure 1. Strict consensus cladogram for Euphorbiaceae tribe Aleuritideae (length 66 steps, including 8 steps for polymorphic taxa, CI = 0.667, RI = 0.676). Outgroups used were *Borneodendron* (tribe Ricinocarpeae subtribe Bertyinae) and *Paracroton* (tribe Crotoneae). ● = apomorphies, ○ = parallel developments, × = reversals, and ⊗ = parallel reversals. The character state change is indicated for every character. Decay Indices higher than 1 and bootstraps of 50% and higher are shown.

sepals) is perhaps overvalued (sepals are free in *Paracroton*).

Another synapomorphy for tribe Aleuritideae (including *Paracroton*) is character 3 (stellate indumentum), but this character reverses several times in the cladogram and does not provide strong support. Character states 2 (red exudate), 13 (staminate sepals absent), 17 (stamens all connate), and 23 (pistillate disc absent) are considered apomorphies for the outgroup, *Borneodendron,* because these states are exceptional and their opposites, present in subtribe Aleuritideae, are common. However, more taxa have to be added to the analysis for a better evaluation of these optimizations, and that is beyond the scope of this study.

This cladistic analysis, based on morphological characters, does not reveal whether or not tribe Aleuritideae is monophyletic. The addition of more taxa is warranted for that goal.

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Appendix 1.

The following characters and their states (state numbers in parentheses) are included in the analysis:

1. Sexuality: dioecious (1) vs. monoecious (2).

Monoecy is often difficult to diagnose because the flowers of different sexes may open at different times, yielding functionally unisexual inflorescences. For this reason, Stuppy et al. (in press) recorded all three species in *Vernicia* to be occasionally dioecious. However, in this analysis monoecy was regarded as being typical for these species, and the occasional unisexual specimen was ignored.

2. Red exudate: absent (1) or present (2).

3. Hair type: simple only (1), simple and stellate (2), or simple and lepidote (3).

All taxa have simple hairs, though sometimes only on the very young parts. Several taxa also have stellate hairs or lepidote hairs. Subtribe Crotonogyninae all have lepidote hairs, though those of the only liana in tribe Aleuritideae, *Manniophyton,* are somewhat different: lepidote with an added upright stinging filament (inflated trichome of Webster, 1994b), giving a stellate appearance. However, the presence of stinging filaments, in this study an autapomorphy for *Manniophyton,* is perhaps typical for lianas, because they are present in all other, unrelated, Malesian lianas. Once the stinging filaments have broken off, the remaining part is perfectly scale-like and, therefore, the hairs have been coded as lepidote. Radcliffe-Smith (1988) recorded lepidote hairs for *Benoistia*; however, we have seen only simple hairs.

4. Pubescence of abaxial leaf surface: (sub)glabrous (1) or densely hairy (2).

This character was added because it may provide a synapomorphy for *Aleurites* and *Reutealis.* The character states can usually be established quite easily, especially in the young parts. Only a few genera, *Crotonogyne* (subtribe Crotonogyninae), *Garcia* (subtribe Garciinae), and *Neoboutonia* (subtribe Neoboutoninae), have some species with glabrous leaves and others with densely hairy leaves; these genera are coded as polymorphic in the analysis.

5. Glands on the petiole-leaf blade transition: absent (1) or present (2).

Quite a few genera, the outgroup *Paracroton,* subtribe Aleuritinae, *Grossera* (subtribe Grosserinae), subtribe Crotonogyninae, and *Neoboutonia* (subtribe Neoboutoninae), show big glands on top of the petiole. Most taxa possess sessile glands, but a few species have stalked ones. The shape of the latter ones may vary, but this information could not be used in the analysis because the different shapes are typical for single species and, therefore, only provide autapomorphies.

6. Leaf margin: unlobed (1) or often/always lobed (2).

Lobed leaves may present a synapomorphy for *Aleurites* and *Vernicia* in subtribe Aleuritinae. Of all the other genera, only *Manniophyton* (subtribe Crotonogyninae) and *Neoboutonia* (subtribe Neoboutoninae) have lobed leaves.

7. Leaf base: cordate (1) or rounded to cuneate, attenuate, or acute (2).

Leaf bases are always cordate or cuneate within subtribe Aleuritinae. State 1 is also unambiguous within the other genera of tribe Aleuritideae, but state 2 is variable and shows overlap among the species.

8. Marginal leaf glands: absent (1), or abaxially on the teeth (2), at teeth apices (3), or in teeth sinuses or crenations.

Most taxa of tribe Aleuritideae have no glands along the leaf margins. *Paracroton* (outgroup) and *Grossera* (subtribe Grosserinae) have glands on the abaxial side of the teeth, but it is not clear if these are homologous. *Vernicia* (subtribe Aleuritinae) is the only genus of tribe Aleuritideae with glands in the sinuses of the leaf margin.

9. Pellucid dots in leaves: absent (1) or present (2).

Punctation is only found in *Cavacoa* and *Grossera* of subtribe Grosserinae.

10. Abaxial sessile glandular hairs: absent (1) or present (2).

Small, one-celled sessile glandular hairs are found only in subtribe Neoboutoninae.

11. Venation: pinnate (1), triplinerved (2), or palmate (3).

All members of subtribe Aleuritinae have palmate venation, as do *Manniophyton* (subtribe Crotonogyninae) and *Neoboutonia* (subtribe Neoboutoninae). Palmate venation is associated with but not completely dependent on the presence of leaf lobes (character 6); leaves of *Reutealis* are never lobed, but have palmate venation. Triplinerved leaves, a special case of pinnate venation, are found only in *Domohinea* (now *Tannodia*) and *Grossera* of subtribe Grosserinae.

12. Fusion of staminate sepals: free or absent (1) or fused, rupturing spathaceously (2).

Staminate sepals connate in bud and rupturing during anthesis are typical of all members of tribe Aleuritideae. The staminate sepals are free in *Paracroton* and absent in *Blumeodendron.*

13. Number of staminate sepals: absent (1), 2–4 (2), or 5 or 6 (3).

Sepals are absent in one of the outgroups, i.e., *Borneodendron.* All other genera of tribe Aleuritideae show 2 to 4 sepals except *Tannodia* (subtribe Grosserinae) with up to 6 sepals; the other outgroup, *Paracroton,* has 5 or 6 sepals. *Tannodia* has been coded as polymorphic.

14. Number of staminate petals: absent (1), 3–5 (or 6) (2), or 6–13 (3).

Petals are absent in the staminate flowers of *Borneodendron* and subtribe Neoboutoninae. *Garcia* (subtribe Garciinae) is the only genus with many (6–13) petals. There is a slight overlap in character states, because some genera that usually have 5 petals can sometimes exhibit variation from 5 to 6 petals within a particular inflorescence, specimen, or species.

15. Fusion of staminate petals: free (1) or connate (2).

Fusion of the staminate petals is considered typical for subtribe Crotonogyninae. However, of this group only *Manniophyton* consistently has connate petals, while *Crotonogyne* is dimorphic for this character (though coded as always present, see discussion), and *Cyrtogonone* has free petals. This character is dependent on the former one; therefore, the outgroup *Borneodendron* is coded with a question mark because the petals are lacking.

16. Number of stamens: 6–12(–14) (1), 12–40 (2), or 63–160 (3).

The coding of the states is difficult due to some overlap in states 1 and 2 and the fact that *Crotonogyne* and *Manniophyton* (subtribe Crotonogyninae) are dimorphic for states 1 and 2 and *Garcia* (subtribe Garciinae) for states 2 and 3 (though coded as possessing state 3 only to prevent too much polymorphism in the matrix): *G. nutans* Vahl has 63–160 stamens, *G. parviflora* Lundell ca. 29 stamens. This character is probably not of great importance, but it was added because it often provides an important key character in Webster's (1994b) classification.

17. Fusion of stamens: all free (1), only the inner whorl connate (2), all connate (3).

Reutealis (subtribe Aleuritinae) is the only taxon that was difficult to code: its inner stamens are connate, and the outer stamens possibly also, but this may only appear to be the case, because the outer stamens also adhere to the petals as in the other two genera of subtribe Aleuritinae. However, the other two genera, *Aleurites* and *Vernicia,* have only the inner stamens distinctly connate. Therefore, *Reutealis* has been coded also as possessing state 2.

18. Arrangement of stamens: unordered (1), ordered in 2 series (2), or ordered in (3 or) 4 series (3).

This character is dependent on the foregoing one. Taxa with free filaments always have unordered stamens. Those with (partly) connate filaments may have the stamens unordered, or ordered in 2 or 4 series. *Paracroton* is the only genus that is polymorphic for states 2 and 3.

19. Apex of connective: unmodified (1), with a gland (2), or prolonged and apiculate (3).

These three states may not be homologous. Prolongation of the connective (apiculate; present in subtribe Crotonogyninae) may be different from the presence of a gland (subtribe Neoboutoninae). However, dividing these states over one or two characters does not influence the results of the analysis.

20. Shape of anthers: short, relatively thick (1) or elongate, vermiform (2).

Anthers with a short shape (1.5–2 times as long as wide) are the more common state. The very long and thin, vermiform anthers are found only in subtribe Neoboutoninae.

21. Tubercles of pollen exine: blunt (1) or sharp (2).

Sharp exine tubercles are found only in *Tannodia* (including *Domohinea;* subtribe Grosserinae). The tubercles of all other taxa are blunt (Punt, 1962), or the state is unknown.

22. Number of pistillate sepals: 2–4 (1), 5 (or 6) (2), or 6 (3).

There is a slight overlap in states; some taxa with 5 pistillate sepals occasionally have flowers with 6 sepals.

23. Pistillate disc: absent (1), annular (2), or divided into free lobes (3).

The staminate disc, when present, is always divided into free lobes. The pistillate disc shows more variation: it is absent in *Borneodendron*, divided into lobes in subtribe Aleuritinae, and annular in all other taxa.

24. Fruit type: capsular (1) or drupaceous (2).

Only the genus *Aleurites* (subtribe Aleuritinae) shows drupaceous fruits; all other genera are capsular.

25. Seeds: smooth (1) or dorsally warty (2).

All genera have smooth seeds except *Vernicia* (subtribe Aleuritinae; however, the seeds of *V. cordata* are still unknown).

APPENDIX 2.

Specimens examined. For some genera, of which hundreds of sheets were studied, only representative specimens covering the distribution are mentioned.

Aleurites moluccana (L.) Willd. (representative specimens): AUSTRAL ISLANDS. **Raivavae:** Raiurua, *H. St. John & F. R. Fosberg 15683* (BISH, L). AUSTRALIA. **Queensland:** Lankelly, *B. Hyland 5406* (L). BRUNEI. Berakas, *BRUN (H. Pukol) 5419* (L). CAROLINE ISLANDS. **Ponape:** Tolomail, *M. Takamatsu 984* (BISH). CHINA. **Guangdong:** Guangzhou, *H. G. Yip 279* (L). **Guangxi:** Lungchow, *H. B. Morse 646* (US). **Hainan:** Yeichow, *F. C. How 70593* (L, NY). **Yunnan:** Xishuangbanna, *K. S. Chow & P. P. Wan 80111* (BISH, NY). COOK ISLANDS. **Rarotonga:** Muriavai Valley, *W. R. Philipson 10136* (L). FIJI. **Vanua Levu:** Thakaundrove, Mbalanga, *O. Degener & E. Ordonez 14502* (NY). **Viti Levu:** Rewa, Nasinu, *J. W. Gillespie 3609* (BISH). FRENCH POLYNESIA. **Moorea:** Morioahu, Opunohu, *H. M. Smith 98* (BISH). HAITI. Petionville, *E. C. Leonard 4831* (NY). HORNE ISLANDS. **Futuna:** Vaisei, *M. MacKee 19772* (BISH). INDONESIA. **Kalimantan Timur:** Wanariset, *Ramlanto 62* (L). **Jawa Barat:** Banjumas, *S. H. Koorders 26890* (L). **Nusa Tenggara Timur:** Ndeki, *A. Kostermans & N. Wirawan 132* (L). **Maluku:** Otimmer, *P. Buwalda 4377* (L, NY). **Irian Jaya:** Warsamson, *BW (F. A. W. Schram) 12493* (L). **Sulawesi Tenggara:** Opa Swamp, *S. Prawiroatmodjo & S. Soewoko 1823* (L). **Sumatera Utara:** Tuktuk, *J. F. Veldkamp 7185* (L). JAPAN. **Ryukyu:** Okinawa, Shimajiri, *E. H. Walker 7750* (US). LAOS. Dok Nanh, *Spire 1190* (BM). MALAYSIA. **Selangor:** Batu Caves, *K. Ogata 10241a* (L). **Sabah:** Tenom, Kulam Ayer, *SAN (Arumpad) 15316* (L). **Sarawak:** 1st Division, Telok Pinang, *S (B. Lee) 41942* (L). MANGAREVA. Duff, *F. R. Fosberg 11360* (BISH). MARIANA ISLANDS. **Guam:** Yigo, *F. R. Fosberg 35533* (BISH). MARQUESAS. Uahuka, *E. H. Quayle 1816* (BISH). MYANMAR (BURMA). Hoho, *F. G. Dickason 9394* (L). PAPUA NEW GUINEA. **Central:** Laloki, *L. J. Brass 3644* (NY). PHILIPPINES. **Luzon:** Laguna, Los Baños, *A. D. E. Elmer 17679* (L, MO, NY). PHOENIX ISLANDS. Canton, *O. Degener 24627* (L). PITCAIRN. Parlver Valley, *H. St. John 14980* (BISH). SAMOA. **Ofu:** *T. G. Yuncker 9540* (BISH, NY). SINGAPORE. Pulau Dumat Laut, *J. Sinclair 5291* (US). SOCIETY ISLANDS. **Huahine:** Tevairahi, *F. R. Fosberg 61154* (BISH). SOLOMON ISLANDS. **New Georgia:** Tetemara, *BSIP (Maenu'u) 6099* (L). TAIWAN. **Taitung:** Tamali-hsiang, Tamali, *Y. Endo 2181* (MO). THAILAND. **Central:** Bangkok, *A. F. G. Kerr 19563* (BM). TONGA. **Eua:** Pangai, *H. E. Parks 16077* (BISH). U.S.A. **Hawaii:** Kauai, Hanapepe River, *A. A. Heller 2431* (L, MEL, NY). VANUATU. **Malekula:** Tisbel, *W. L. Chew 307* (L). VIETNAM. Cochinchine, Bien Hoa, *C. Thorel 671* (NY, W).

Aleurites rockinghamensis (Baill.) P. I. Forst. (representative specimens): AUSTRALIA. **Queensland:** Alexandra, *B. Hyland 6726* (L). PAPUA NEW GUINEA. **Morobe:** Boana, *M. S. Clemens 8119* (L). **Northern:** Isurava, *C. E. Carr 15757* (L).

Benoistia perrieri Leandri: MADAGASCAR. Moramanga, Dec. 1908, *C. d'Alleizette s.n.* (L).

Borneodendron aenigmaticum Airy Shaw (representative specimens): MALAYSIA/SABAH. **Lahad Datu:** Pulau Sakar, *SAN (H. S. Martyn) 21605* (L); Mt. Silam, *SAN (W. Meijer) 37836* (L), *SAN (Tarmiji) 72898* (L); Tembawan Island, *KEP (J. Wyatt-Smith) 80510* (L), *SAN (P. F. Burgess) 27558* (L). **Ranau:** Bukit Hampuan, Kinabalu, *SAN (A. Gibot) 61836* (L).

Cavacoa quintasii (Pax & K. Hoffm.) J. Léonard: CONGO (ZAIRE). **Kasai:** Mweka Territ., Kahenga, *R. Dechamps 208* (L). **Orientale:** Isangi Territ., Yangambi, *J. Louis 2559* (L), *4177* (L), *9676* (L).

Crotonogyne argentea Pax: CAMEROON. Bipinde: *G. Zenker 2029* (L), *2359* (L), *3078* (L), *3668 (L)*, *3893* (L).

Crotonogyne gabunense Pax: GABON. Libreville, *Courtet 6485* (L).

Crotonogyne giorgii De Wild.: CONGO (ZAIRE). **Equateur:** Ingende Territ., Bolima, Luwa, *Hulstaert 1091* (L). **Léopoldville**: Inongo Territ., Lac Léopold II, *G. Gilbert 14063* (L).

Crotonogyne parviflora Prain: CONGO (ZAIRE). Ogoané, *Karmann 6485* (L).

Crotonogyne poggei Pax: CONGO (ZAIRE). **Orientale:** Isangi Terr., Yangambi, *J. Louis 6815* (L).

Crotonogyne preussii Pax: CAMEROON. Bipinde, *G. Zenker 4666* (L).

Crotonogyne zenkeri Pax: CAMEROON. Lolodorf, June 1913, *Rouyer s.n.* (L); Bipinde, *G. Zenker 822* (L). GABON. Libreville, 18 Dec. 1900, *R. P. Klaine s.n.* (L).

Domohinea perrieri Leandri: MADAGASCAR. Analamazaoho, *C. d'Alleizette 6479* (L).

Garcia nutans Rohr: FRENCH GUYANA. Cayenne, *C. d'Alleizette 6459* (L). MARTINIQUE. St. Pierre, Feb. 1868, *L. Hahn s.n.* (L).

Grossera macrantha Pax: CONGO (ZAIRE). **Léopoldville:** Moyen-Kwilu Terr., Koiyaka, Kewango, *R. Devred 2769* (L).

Grossera major Pax: CAMEROON. Lolodorf, June 1919, *C. d'Alleizette s.n.* (L); Bipinde, *G. Zenker 1805* (L), *4227* (L).

Grossera multinervis J. Léonard: CONGO (ZAIRE). **Kivu:** Kalehe Terr., vers km 110 route Kavumu-Walikale, Irangi, reserve IRSAC, *G. Troupin 4529* (L), *4700* (L).

Grossera paniculata Pax: CAMEROON. Bipinde, *G.*

Zenker 1741 (L), *1760* (L), *2070* (L), *3050* (L), *3088* (L), *3125* (L), *3231* (L), *3372* (L), *3377* (L), *3460* (L), *3532* (L), *4920* (L).

Manniophyton africanum Müll. Arg.: CAMEROON. 10 km N of Ndemba II, 30 km N of km 29 of road Bertona–Nanga Eboke, *A. J. M. Leeuwenberg 5846* (L); Yaunde, *G. Zenker 1404* (L); Bipinde, *G. Zenker 4690* (L). CONGO (ZAIRE). **Orientale:** Isangi Territ., Yangambi, Plateau Isalewi, *J. Louis 14553* (L). GABON. Nyanga, *C. d'Alleizette 6460* (L).

Neoboutonia africana Müll. Arg.: CAMEROON. Bipinde, *G. Zenker 1527* (L), *3202a* (L), *4246* (L); Yaunde, *G. Zenker 1430* (L). GABON. Libreville, *C. d'Alleizette* 6517 (L).

Neoboutonia macrocalyx Pax: MALAWI. Nyassa Hochland, Station Kyimbila, *A. Stolz 2043* (L). TANZANIA. Uhehe, *W. Goetze 758* (L).

Neoboutonia melleri Prain: MALAWI. Nyassa Hochland, Station Kyimbila, *A. Stolz 444* (L), *590* (L).

Paracroton pendula (Hassk.) Miq. (representative specimens): BRUNEI. Andulau Forest Reserve, *BRUN (P. S. Ashton) 3255* (L). INDONESIA. **Jawa Barat:** Bantam, *S. H. Koorders 2604* (L). **Kalimantan Barat:** Gunung Palung Nature Reserve, on Air Putih River, 20 km SE of Talukmelano, *S. A. Mori & J. D. Mitchell 17848* (L). **Kalimantan Selatan:** Pleihari, Asam-Asam, *bb 9494* (L). **Kalimantan Tengah:** headwaters of Sungai Kehayan, 5 km NW of Tumbang Sian Logging Camp, *J. S. Burley, Tukirin et al. 820* (L). **Kalimantan Timur:** E. Kutei, Sungai Kerajaan, N of Sangkulirang, *A. Kostermans 5782* (L). **Sumatera Selatang:** Bangka, Lobok-besar, Gunung Pading, *A. Kostermans & Anta 927* (L). MALAYSIA. **Pahang:** S of Kuala Lompat, Krau Game Reserve, *KEP FRI (T. C. Whitmore) 3580* (L). **Sabah:** Labag Dist., Lokan Forest Reserve, Kinabatangan, *SAN (J. Ampuria) 36385* (L). **Sarawak:** Miri, Ulu Luak, Sungai Setap, *S (O. Haron) 21312* (L). PHILIPPINES. **Luzon:** Laguna Prov., San Antonio, *BS (A. Ramos) 23828* (L). **Mindanao:** Agusan Prov., Tungao, *PNH (D. R. Mendoza) 41965* (L). **Palawan:** Pagdanan Range, road E from San Vicente, *SHI (C. E. Ridsdale) 1511* (L). THAILAND. Peninsular, Phatthalung Prov., Tamote Falls Nature Park, *J. F. Maxwell 86–547* (L).

Paracroton zeylanicus (Müll. Arg.) Balakr. & T. Chakrab. (representative specimens): INDIA. **Kerala:** Cardamon Hills, Puliyar, Munnar–Alwaye Road, ca. 15 km from Munnar, *C. E. Ridsdale 767* (L). SRI LANKA. Galle Distr., Hinidunma, *A. Kostermans 26608* (L).

Reutealis trisperma (Blanco) Airy Shaw (representative specimens): INDONESIA. **Jawa Barat:** Tjiomas, *C. A. Backer 36081* (L). PHILIPPINES. **Guimaras:** Iloilo, Miagao. **Luzon:** Batangas, *M. Ramos 1923* (L, MO); Cavite, Maragondong, *BS (E. Fénix) 5160* (NY); Laguna, *BS (R. C. McGregor) 22912* (BM, K); Rizal, *FB (Ahern's collector) 2440* (K, L). **Mindanao:** Agusan, Butaan, *PNH (D. R. Mendoza) 42223* (L); Davao, Santa Cruz, *R. S. Williams 2852* (NY).

Tannodia cordifolia Baill.: COMORES. Mutsamdra?, *C. d'Alleizette 6484* (L).

Tapoides villamilii (Merr.) Airy Shaw: MALAYSIA. **Johore:** Mersing, Tenggaroh Forest Reserve, Compt. 101, *KEP (K. Ogata) 105167* (L). **Sabah:** Sepilok Forest Reserve, *SAN (G. H. S. Wood) 16532* (L), *(W. Meijer & Aban) 128772* (L), *(W. Meijer) 27676* (L); Jalan Trig, Leila Forest Reserve, *SAN (P. Lasan) 62527* (L).

Vernicia cordata (Hemsl.) Airy Shaw (representative specimens): INDONESIA. **Java:** *H. Zollinger 3576* (MEL). JAPAN. Hondo, *E. H. Wilson 7138* (US); Kyoto, *Tagawa-Motozi 2091* (C); Kyushu, Isso-Rindo, *K. Deguchi 5014* (NY); Nomo Saki, *Pierot 925* (L). VIETNAM. **Tonkin:** Hanoi, *C. d'Alleizette 6458a* (L).

Vernicia fordii (Hemsl.) Airy Shaw (representative specimens): CHINA. **Fujian:** Yenping, Buongkang, *H. H. Chung 3344* (BO). **Geizhou:** Tsunyi Hsien, Liang Feng Yah, *A. N. Steward et al. 256* (NY). **Guangdong:** Lung Tou Shan, *S. P. Ko 50228* (K, NY). **Guangxi:** Yung Hsien, Ta Te Tauen, *A. N. Steward & K. C. Cheo 1059* (NY). **Hubei:** Patung Hsien, *H. C. Chow 147* (NY). **Hunan:** P'ing T'ou Shan, *W. T. Tsang 23509* (US). **Jiangsu:** Nanking, Drum Tower, *Y. C. Chiao 11993* (BO). **Jiangxi:** Lingchuan, *Y. Tsiang 9822* (NY). **Sichuan:** Yulei, *D. E. Boufford et al. 24035* (NY). **Yunnan:** Likiang, *J. F. Rock 5066* (NY, US). **Zhejiang:** Hangchow, *C. Y. Chiao 7969* (NY). INDIA. **Assam:** Burnihat, *W. N. Koelz 22834* (K). **Utah Pradesh:** Dehra Dun, *U. Singh 131* (NY). INDONESIA. **Jawa Barat:** Bangkelan, *J. G. B. Beumée A 913* (BO). JAPAN. **Ryukyu:** Okinawa, Yabu, *E. H. Walker et al. 6356* (L, US). SOUTH KOREA. Yongtung, *B. R. Yinger et al. 3791* (K). TAIWAN. **Chiayi Hsien:** Fanlu Hsiang, Pantienyen, *Y. R. Lin 515* (MO).

Vernicia montana Lour. (representative specimens): CHINA. **Guangdong:** Shiu Hing, *H. O. Chan 13904* (L). **Guangxi:** Won Bin, *R. C. Chin 6354* (NY). **Hainan:** Chiang Mai, Ku Tung, *C. I. Lei 495* (BO, L, NY, US). **Hong Kong:** Taipo, *S. Y. Hu 10435* (K). **Jiangxi:** Wu Yuan, *R. C. Ching 3275* (K). INDIA. **Assam:** Hmuntha, *T. R. Chand 4329* (L). INDONESIA. **Jawa Tengah:** Pengalengan, *S. M. Popta 1295* (L). **Jawa Timur:** Djembu, *B. Kruyne 1* (L). MYANMAR (BURMA). **Wa States:** Pansan, *Maung Po Khant 15329* (K). PHILIPPINES. **Luzon:** Laguna, Los Baños, *FB (N. Catalan) 26923* (BO). THAILAND. **Northern:** Chiang Mai, Doi Sutep, *J. F. Maxwell 88–350* (AAU, L). VIETNAM. **Tonkin:** Taai Wong Mo Shan, *W. T. Tsang 28987* (B, C, K).

Managing Editor's Note

If you've been watching the inside covers of the *Annals* and *Novon* this year, you may have noticed a couple of significant changes. Beginning with the *Annals* 86(1) and *Novon* 9(1), a new editor's name has appeared, that of Victoria C. Hollowell, who became the Scientific Editor and Head of MBG Press at the end of 1998. Dr. Hollowell is the Garden's first full-time Scientific Editor, and she is responsible for overseeing the scientific content of both journals, the *Monographs in Systematic Botany from the Missouri Botanical Garden,* and other book titles produced by the Press, as well as overseeing the overall Press operations. It would be a daunting job for even the most enthusiastic botanist interested in the dissemination of accurate, clearly presented botanical information, but Victoria has proven herself to be more than up for the challenge. She brings botanical and editorial expertise and diligence, computer skills and knowledge, as well as a healthy sense of humor, for which she is already well known and appreciated. She came to the Garden most recently from the University of South Carolina, and has research interests in the origin and evolution of Poaceae, particularly bamboo grasses (*Pariana* and *Eremitis*). Victoria takes the *Annals*' editorial pen from Dr. Michael H. Grayum, who served as Editor from 1997 to 1999 (beginning with *Annals* 84(2) and concluding with co-editorship of *Annals* 86(1)), at the same time continuing his work as editor on the *Manual to the Plants of Costa Rica* project. He brought considerable botanical knowledge and editorial and analytical skills to the job. Mike is a perfectionist, and his high standards served the journal and its readers well during his tenure. Victoria succeeds Dr. Marshall R. Crosby as the editor of *Novon.* He was the founder and Editor of this nomenclatural journal, which made its debut in 1991 and has since filled a real niche for publishing novelties in both vascular plants and bryophytes. Marshall, a bryologist wearing several different hats during his 30+-year tenure at the Garden, is a born editor and an excellent nomenclaturalist. The Garden's Research Division, and in particular the editorial staff of MGB Press, is grateful for the contributions of the past editors and looks forward to a long and fruitful association with the new editor.

Amy Scheuler McPherson
Managing Editor
17 November 1999

ANNALS OF THE MISSOURI BOTANICAL GARDEN: CHECKLIST FOR AUTHORS

1. General Instructions

☐ Text is in English or Spanish on numbered pages.
☐ Manuscript is typed on one side of nonglossy 8½ × 11 in. paper.
☐ At least 1 in. is left as margin all around, except on the first page, which has 3 in. left blank at the top.
☐ Three copies of double- or triple-spaced printed manuscript, including abstract, legends, tables, specimen lists, Literature Cited, and footnotes, are enclosed.
☐ Manuscript is also submitted on MS-DOS/WINDOWS 3½ in. diskette, as Microsoft Word7 [preferable] file.
☐ Right-hand margin is not justified, and words are not broken there.
☐ Special typefaces are not used. Common Latin words or phrases are not italicized (e.g., et al., i.e., sensu, etc.).
☐ Only names at the rank of genus and below are italicized.
☐ Correct accents, umlauts, and other diacritical marks have been included.
☐ All figures and tables are cited in the text and are numbered in the order in which they are to appear.
☐ Photocopies of the figures are included with each copy of the manuscript.
☐ Authorities, abbreviated according to Brummit & Powell's *Authors of Plant Names,* are provided for species' names the first time they are mentioned in the text; OR they are provided in a table that includes names of species.

2. Style

☐ Recent issue of the *Annals* is used as a model.
☐ *Chicago Manual of Style,* latest edition, is used as a reference.

3. First Page

☐ Footnotes are typed as double-spaced paragraphs on the first page. The first footnote contains acknowledgments, including information on granting agencies, herbaria that loaned specimens, and the name of the artist. The second footnote is the author's address. Addresses for additional authors are each separate footnotes. No other footnotes occur, except in tables, where unavoidable.

4. Abstract

☐ A one-paragraph abstract precedes text. Papers in Spanish have an English abstract in addition to a Spanish resumen.
☐ The abstract is concise (1 paragraph) and includes brief statements about the paper's intent, materials and methods, results, and significance of findings.

5. Tables

☐ Tables are neat, double-spaced, and easily understood rather than long and complex.
☐ Tables do not contain vertical or horizontal lines. [Editor and/or printer will add them as needed.]
☐ Captions are typed double-spaced as paragraphs at the tops of the tables.
☐ Each table starts on a separate sheet.

6. Abbreviations

☐ Periods are used after all abbreviations (which are minimized) except metric measures, compass directions, and herbarium designations.
☐ When dates are given as part of collection information, three-letter month abbreviations are used, except for months with four letters, which are spelled out in full.
☐ States are not abbreviated, and cities are spelled out. [St., as in St. Louis, is acceptable.]
☐ Periodicals are abbreviated according to *B-P-H (Botanico-Periodicum-Huntianum)* and to *B-P-H/S (Botanico-Periodicum-Huntianum/Supplementum).*
☐ Authors' names are abbreviated according to Brummit & Powell's *Authors of Plant Names.*
☐ Book titles are abbreviated according to *Taxonomic Literature,* edition 2, but with initial letters capitalized. Book titles are spelled out in the Literature Cited.
☐ Herbaria are abbreviated according to *Index Herbariorum,* edition eight (8).

7. Taxonomic Treatment

☐ Species entries are organized as follows: Heading, vernacular name(s), Latin diagnosis (if necessary), description, distribution, summary, specimens examined, discussion. The discussions are parallel and follow the same order, e.g., diagnostic characteristics, distinction from similar species, variation, distribution and ecology, nomenclature and typification, uses.
☐ One paragraph per basionym is used as follows: *Taxon* author, literature citation, type citation, e.g., *Pleurothyrium amplifolium* (Mez) Rohwer, Mitt. Inst. Allg. Bot. Hamburg 20: 43. 1986. *Nectandra amplifolia* Mez, Arbeiten Königl. Bot. Gart. Breslau 1: 131. 1892. TYPE: Brazil. Rio de Janeiro: Alto Macahé, *Glaziou 17731* (holotype, B; isotypes, B, G, K, NY, P).
☐ Lectotype designations are included together with an indication of where they were designated, the year, and the author. This reference is listed in the Literature Cited. If the author of the paper submitted is making the lectotypification, the phrase "here designated" is used.
☐ Exclamation points are used for specimens examined, and types not seen are indicated as such (e.g., MO!, US not seen).
☐ A brief Latin diagnosis for each new taxon is provided rather than a complete Latin description.
☐ For species with infraspecific taxa: Description and discussion are composite (incorporating all infraspecific taxa) and parallel with other species descriptions. Descriptions of infraspecific taxa are parallel with one another (in the same species). All synonyms are listed under the appropriate infraspecific taxon.

☐ Descriptions: Descriptions are parallel, within a given rank. All measurements are metric. Hyphens are used for parenthetical extremes: "peduncle (8.2–)14.3–28.0(–31.9) cm long," unless intermediate values are not expected: ovary with (2)4(6) locules. Length × width are given in the following manner: lamina 36.4–82.8 × 9.1–16.8 cm.

☐ When relevant, nomina nuda, misapplied names and excluded names are included in the discussion following the description, or at the end of the paper, but are not part of the formal synonymy.

8. Specimens Examined

☐ If many specimens were examined, those cited in the text are limited to ca. 1½ manuscript pages.

☐ An index to specimens examined is placed at the end of the paper, following the Literature Cited. It is arranged alphabetically by collector, followed by collection number, followed by the number of the taxon in the text. Names (including initial(s) of first and second collector are provided, "et al." if three or more.

☐ Specimens are cited in the text as follows: *Additional specimens examined (or Selected specimens examined).* MEXICO. **Oaxaca**: Sierra San Pedro Nolesco, Talea, 12°37′N, 85°14′W, 950–1100 m, 3 Feb. 1987 (fl), *Jergensen 865* (BM, G, K, US). [Dates and reproductive status are optional but are omitted from longer lists.] Countries are run together in the same paragraph, e.g., COUNTRY A. **Major political division:** . . . COUNTRY B. **Major political division:** . . . . Separate paragraphs are used for major continental regions within major political divisions.

9. Specimen Vouchers and Genetic Sequences

☐ If paper presents original data, associated herbarium vouchers are cited. [Vouchers for seed and/or other collections should be included where pertinent. Dependent on the paper, reference to the original wild source may be required.] Vouchers are also cited from common names and uses taken from specimen labels.

☐ Herbarium vouchers state the collector and number, herbarium in which the voucher is located, and a clear annotation that the material represents the voucher for the study in question.

☐ Nucleic acid or protein sequences corresponding to equal or greater than 50 nucleotides are entered into an appropriate data bank, e.g., GenBank/EMBL. The accession numbers are provided before publication. [Long sequences (exceeding two pages) will not be routinely published.]

☐ Author accepts responsibility for establishing the accuracy of information provided.

10. Keys

☐ Keys are clear and have been checked carefully for consistency with the descriptions. Leads of each couplet are parallel.

☐ Dichotomous keys are indented.

☐ Infraspecific taxa are keyed separately, not in species keys.

11. Literature Cited

☐ The Literature Cited contains all references cited in the text.

☐ All entries in the Literature Cited are cited in the text.

☐ Spelling of author(s) name(s) and years of publication have been double-checked.

☐ All entries have been verified against original sources, especially journal titles, accents, diacritical marks, and spelling in languages other than English.

☐ Periodicals are listed as follows: author's last name, initial(s). Year. Full title of article. Journal abbreviated as in *B-P-H/S.* Volume: pages. No parenthetical part numbers after volume numbers are given unless each part is paginated separately.

☐ For more than one author, this style is followed: author's last name, initial(s), second author's initial(s), last name & third author's initial(s), last name.

☐ Books appear as follows: author's last name, initial(s). Year. Full Unabbreviated Title (edited by Editor), 3rd ed., Vol. 2. Publisher, City of Publication.

☐ Citations of work "in prep.," unpublished theses and dissertations, and similar references to inaccessible sources have been eliminated or kept to a minimum. They are not included in the Literature Cited.

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