VOLUME 59
1972

ANNALS OF THE
Missouri Botanical Garden

Published by the Missouri Botanical Garden Press
St. Louis, Missouri 63110

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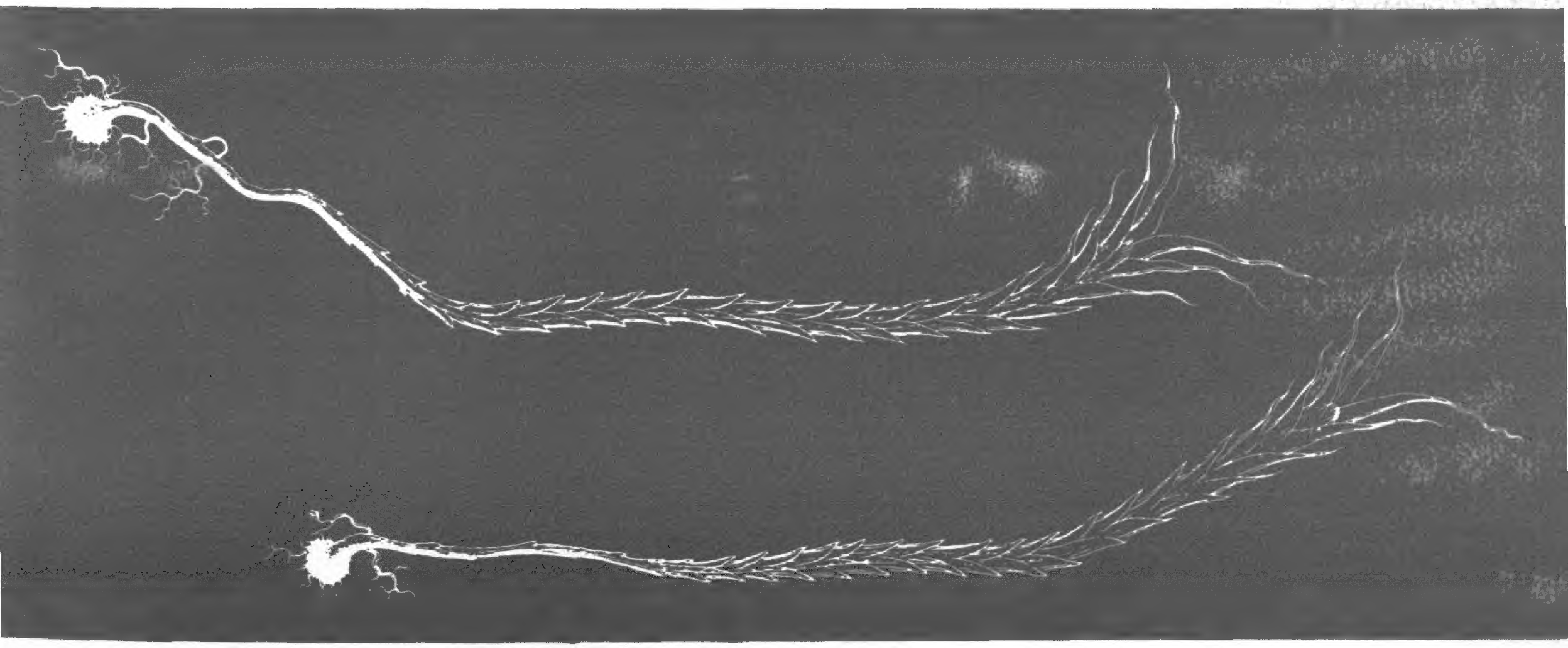

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Published by the Missouri Botanical Garden Press, St. Louis, Missouri 63110.

ALLEN PRESS, INC. PRINTED IN U.S.A. LAWRENCE, KANSAS

VOLUME 59
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MOSSES OF THE INTERIOR HIGHLANDS OF NORTH AMERICA

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ABSTRACT

A manual of the mosses of the Interior Highlands of North America that include diagnostic keys to the families, genera, and species.

The Interior Highlands of North America includes several diverse physiographic regions (Figure 1) that generally coincide with the boundaries of the oak-hickory forest region as outlined by Braun (1950). The northern portion of this region includes two extensive plateaus, the Salem and the Springfield. Upland forest associations include both oak-hickory forests and sugar maple-white oak forests. Along north slopes and in narrow ravines more mesic forests, such as the sugar maple-red oak association, may be present. Along flood plains mature forests are often dominated by sugar maple and bitternut hickory. Local relief is frequently rugged and consequently extensive rock outcrops and bluffs, composed chiefly of limestone and dolomite, are common. On the thin soils of the summits of ridges and drier south-facing slopes, cedar glades and rocky barrens are often encountered. Springs are also a common feature of these plateaus. Some exposures of sandstone may be encountered, particularly along the western border of the Springfield Plateau adjacent to the Prairie Plains and in the eastern part of the Salem Plateau. Within the Salem Plateau there is a residual upland area of rugged relief, the St. Francois Mountains, where crystalline rocks, mainly felsite and granite, are extensively exposed. In such areas open, rocky barrens commonly develop, particularly on the steeper slopes near and on the summits of the ridges. Oak-hickory forests are very well developed in this region.

To the south of the northern plateau region lie the Boston Mountains or Boston Plateau, a peneplained area dissected by numerous narrow, deep ravines, particularly along the Buffalo River drainage system. Sandstone is commonly exposed at the higher elevations, while shale and limestone occur at the lower elevations. On the ridges oak-pine or oak-hickory forests are usually well developed. Narrow ravines and north-facing slopes are frequently occupied by rich,

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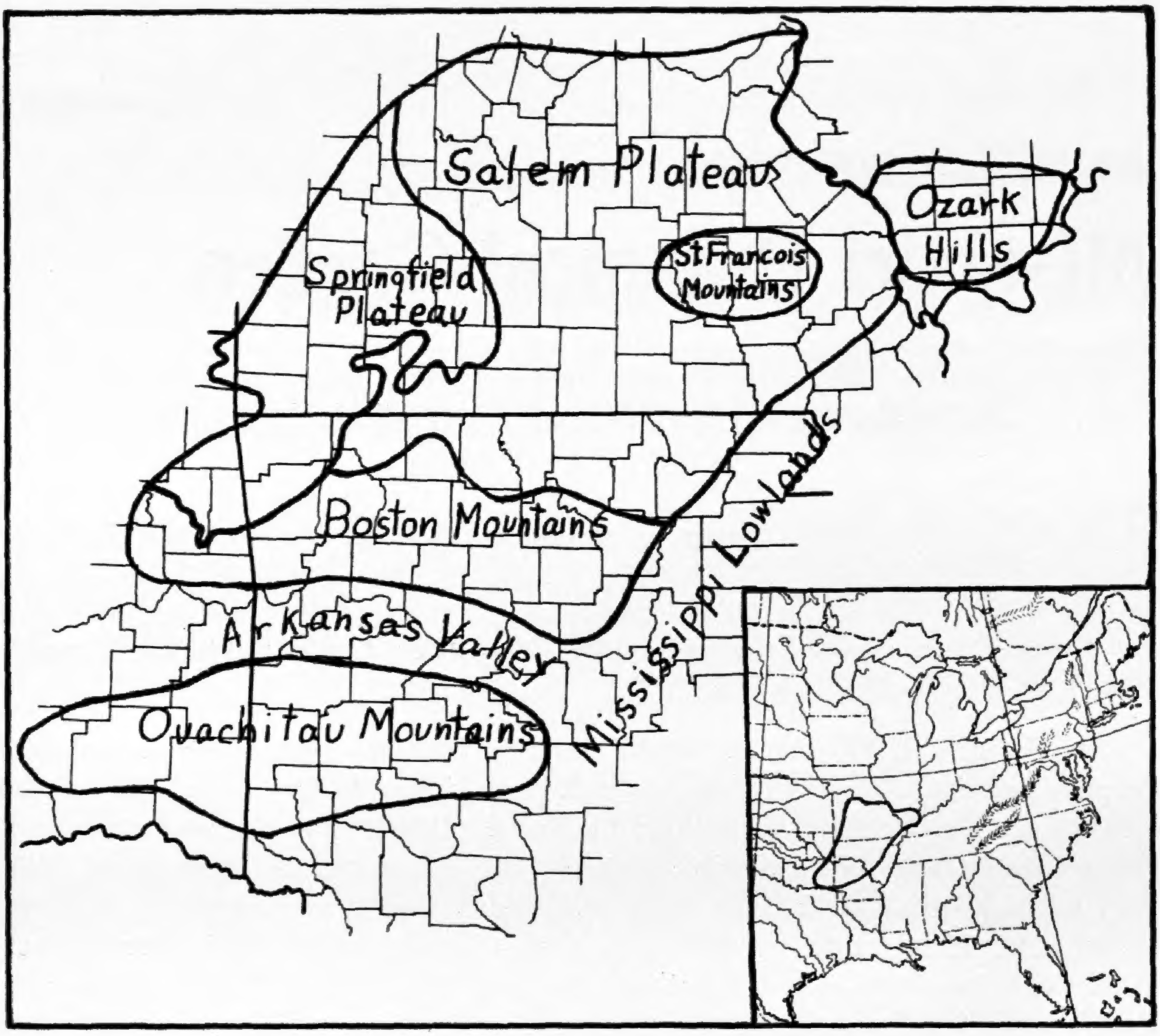

FIGURE 1. Physiographic regions of the Interior Highlands of North America. Inset shows location of the Interior Highlands in Eastern North America. Boundaries approximate.

mesophytic forests that often contain a large percentage of beech and umbrella magnolia.

The southern border of the Interior Highlands is represented by the Ouachita Mountains. The eastern region of the mountains in Arkansas is characterized by a series of low hills separated by narrow, rocky valleys where shale, sandstone, quartzite, and chert are exposed. Pine-oak forests are common, although on deeper soils, oaks and hickories may completely replace pine. The western region of the Ouachita Mountains lies in western Arkansas and southeastern Oklahoma. The valleys separating the mountains are relatively high and broad. Mesophytic forests are common in the ravines which indent the lower and middle slopes. Extensive erosion has exposed shale, sandstone, chert, limestone, and norvaculite.

The Arkansas Valley separates the Boston and Ouachita Mountains. This valley, while of generally low relief, contains numerous synclinal mountains that have the appearance of steep-sided buttes. Most of the slopes are covered with a mesophytic forest. The rocks most commonly exposed are sandstone and shale. On the benches and flat summits, drainage is often poor enough to produce small

Sphagnum bogs. Along the smaller streams of the valley the sandy soils are occupied by forests that include both pine and sweetgum.

The Ozark Hills of southern Illinois contain two basic types of escarpments (Voight & Mohlenbrock, 1964): Those composed of sandstone and extending in an east-west direction, and those composed of limestone running in a north-south direction paralleling the Mississippi River. The forests near the summits of ridges are xerophytic, oak-hickory type, while the forests of ravines and lower slopes are of the mesophytic type. Along ledges and ravines, extensive exposures of sandstone or limestone are common and support a diverse rock ledge vegetation.

In the development of the diagnostic keys and the arrangement of the families no originality is claimed. Previously published treatises, particularly by Grout (1928–1940) and Welch (1957), have been particularly useful although extensive modification was often required. Recent monographs and revisions have also been consulted and are cited wherever appropriate. Nomenclature has been updated so as to be consistent with not only the most recent monographs and revisions, but also in general accord with "A list of the mosses of North America" by Crum, Steere, and Anderson (1965) and "Index Muscorum" (Wijk *et al.*, 1959–1969). The arrangement of the families follows the sequence given by Brotherus (1924–1925).

Descriptions are limited to the families and genera and have been synthesized from only the taxa occurring within the Interior Highlands. Consequently, these descriptions may not always include features of the family or genus in their broadest sense. Synonymy is not meant to be complete, but is included only for those taxa where recent changes may result in some confusion when compared with earlier works. The distribution of each taxon is based primarily on material collected during this study or examined in herbaria of the University of Missouri, the University of Arkansas, the Missouri Botanical Garden, and the Field Museum of Natural History. Literature reports, particularly by Gier (1955*a*) for Missouri, have also been considered. The commonness of each species refers to its distribution in expected habitats (Gleason & Cronquist, 1964) and is, of course, a judgement based upon my own field experience. The terms used to express commonness—rare, uncommon, common, and very common—must be considered purely subjective.

Support for the field and herbarium studies was made possible not only by my own institution, Southwest Missouri State College, but also by a series of research grants from the Society of Sigma Xi and the National Science Foundation (NSF Grants G-9059, GB-67, and GB-4095). Their support is gratefully acknowledged.

Voucher specimens of all species collected in this study are deposited in the herbarium of Southwest Missouri State College (SMS). All collection numbers cited are mine unless otherwise indicated.

One final caution on the use of the keys. There is an old adage that "keys are made by people who don't need them for people who can't use them." There is a certain amount of truth in such a statement, but the fact that keys may often function poorly may be due to the complex and dynamic nature of the species being keyed out and that a particular collection may not possess all the stages that make identification relatively sure. Therefore, one should develop the habit, particularly if experience with mosses is limited, of comparing carefully each collection identified with its description and with a herbarium specimen that has been named by someone more experienced with mosses. If such collections are not available, any number of bryologists, including the author, are usually more than willing to examine unidentified or identified collections, provided the specimens are supplied in good condition and with adequate collection data. Ideally, such data should include the type of substrate (soil type, rock type, or species of tree and location on tree) upon which the moss was growing, general habitat of the species, exact location, date of collection, and collector. You should send enough material so that the person identifying the collection may retain a duplicate for his records.

To aid in the use of the keys, a glossary of the more common bryological terms is included in Appendix I. An index to families and genera follows in Appendix II.

KEY TO THE MOSSES OF THE INTERIOR HIGHLANDS OF NORTH AMERICA[2]

1\. Leaves composed of a single layer of two kinds of cells, narrow linear chlorophyllose-cells forming the meshes of a network enclosing large rhomboidal hyaline cells .... SPHAGNACEAE (1)
1\. Leaves not as above 2
  2\. Plants large, erect, dendroid (tree-like) in growth form 3
  2\. Plants not dendroid 4
3\. Leaves irregularly serrate near apex .... *Thamnobryum* (29)
3\. Leaves serrate, often coarsely so, but not irregularly serrate .... *Climacium* (25)
  4\. Leaves composed almost entirely of costa made up of 2–3 layers of hyaline cells whose walls are perforated with circular pores and enclose a central layer of narrow chlorophyllose cells; plants in cushion-like tufts, whitish green .. *Leucobryum* (8)
  4\. Plants not as above 5
5\. Plants acrocarpous, generally but not always erect in habit 6
5\. Plants pleurocarpous, generally but not always creeping in habit 12
  6\. Leaves in two ranks or if in three ranks, leaves of some branches complanate .... SECTION A
  6\. Leaves in three ranks, not appearing complanate 7
7\. Leaves ecostate .... SECTION B
7\. Leaves costate 8
  8\. Leaves with lamellae on upper surface of costa .... POLYTRICHACEAE (43)
  8\. Leaves without lamellae 9
9\. Gemmae bearing structures conspicuous .... SECTION C
9\. Gemmae bearing structures not conspicuous; gemmae, if present, on leaves or in axils of leaves 10
  10\. Leaves with hyaline apices or excurrent costae .... SECTION D
  10\. Leaves not as above 11
11\. Leaves papillose or mammillose .... SECTION E
11\. Leaves smooth .... SECTION F
  12\. Leaves costate 13
  12\. Leaves ecostate .... SECTION G
13\. Costa short and double (may be absent in some leaves) .... SECTION H
13\. Costa reaching the middle of the leaf or beyond 14
  14\. Leaves not papillose .... SECTION I
  14\. Leaves papillose .... SECTION J

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[2] Number in parenthesis is the number of the family or the family in which the taxon may be found.

Section A

Plants acrocarpous: leaves distichous or in three ranks and complanate.

1. Leaves distichous 2
1. Leaves only appearing distichous, in three ranks and complanate .... *Mnium* (17)
    2. Leaves split at base and clasping stem .... *Fissidens* (2)
    2. Leaves not split at base .... *Bryoxiphium* (5)

Section B

Plants acrocarpous (though often with the growth form of a pleurocarp); leaves three-ranked, not complanate, ecostate.

1. Leaf cells smooth .... *Venturiella sinensis* (21)
1. Leaf cells papillose .... *Hedwigia ciliata* (26)

Section C

Plants acrocarpous; leaves three-ranked, costate; gemmae bearing structures conspicuous.

1. Leaves ovate to ovate-lanceolate; many sterile stems bearing a gemmae-bearing cup composed of small leaves; peristome single, composed of 4 teeth ... *Tetraphis pellucida* (15)
1. Leaves long-lanceolate; some stems bearing pseudopodia that are naked or bearing minute leaf-like gemmae in a cluster at upper end; peristome double, teeth 16 .... *Aulacomnium* (18)

Section D

Plants acrocarpous; leaves three-ranked, costate, apices or excurrent costa hyaline; gemmae not present on special structures.

1. Plants dark green, blackish green, or golden green in color 2
1. Plants light green to whitish green in color .... *Bryum argenteum* (16)
    2. Leaves mostly lanceolate-subulate; alar cells inflated .... *Campylopus introflexus* (7)
    2. Leaves not as above 3
3. Leaves obtuse, emarginate to truncate at apex; cells papillose; basal cells hyaline, rectangular to long 5
3. Leaves not possessing the above combination of characters 4
    4. Costa subpercurrent to shortly excurrent; septate brood bodies absent ... *Grimmia* (12)
    4. Costa ending below apex; septate brood bodies present ... *Orthotrichum diaphanum* (23)
5. Plants small, 2–5 mm high; awn smooth .... *Desmatodon plinthobius* (11)
5. Plants larger, 5–15 mm high; awn smooth or serrate; if plants small, growing on trees .... *Tortula* (11)

Section E

Plants acrocarpous; leaves three ranked, costate, apices or excurrent costa not hyaline, cells papillose or mammillose; gemmae not present on special structures.

1. Plants minute, usually growing in wet, sandy sites .... *Ephemerum* (13)
1. Plants small to large 2
    2. Leaves strongly serrate, bordered from base to apex by hyaline, elongated cells; the inner cells of sheathing base, thin-walled and hyaline .... *Syrrhopodon texanus* (9)
    2. Leaves not as above 3
3. Hyaline cells extending up the margin of the leaf base further than along the costa, forming a V; leaves oblong-lanceolate to broadly lanceolate-acuminate 4
3. Hyaline cells absent along the leaf base, or if present, only faintly showing a V-shaped arrangement; leaves narrowly lanceolate to linear-lanceolate 5
    4. Margins of leaf entire; basal hyaline cells extending to the costa ... *Tortella humilis* (11)
    4. Margins of leaf minutely serrate near apex; basal hyaline cells not extending to the costa .... *Pleurochaete squarrosa* (11)
5. Leaves bordered with bands of 2–3 rows of light-colored cells .... *Desmatodon* (11)
5. Leaves not so bordered 6
    6. Papillae formed by projecting end walls of cells, evident at least on lower cells if not on upper cells .... BARTRAMIACEAE (19)
    6. Papillae centered over the lumen of all cells 7

7. Leaves with a hyaline or yellowish basal sheath; margins strongly serrate from sheathing base to apex .... *Timmia* (20)
7. Leaves not as above 8
  8. Apices of leaves channelled, acuminate or acute; costa percurrent to short-excurrent; alar cells usually inflated .... *Dicranum* (7)
  8. Leaves not as above 9
9. Costa excurrent 10
9. Costa percurrent or ending below apex 15
  10. Costa excurrent as a short, yellow or pellucid, rounded mucro; cells strongly papillose on back; leaves oblong to lingulate from ovate base, apices usually obtuse .... *Barbula* (11)
  10. Leaves not as above 11
11. Costa excurrent into a long awn 12
11. Costa not excurrent as a long awn, leaves often ending in a small, short, sharp, nearly hyaline to hyaline point; margins plane or strongly involute above .... POTTIACEAE (11)
  12. Awn smooth or nearly so 13
  12. Awn spinose or sharply serrate 14
13. Leaves obovate, lingulate or panduriform; apices rounded or truncate; propagula often present at apex of stem, in axils of upper leaves, or on upper surface of leaves .... *Tortula* (11)
13. Leaves ovate to oblong-lanceolate; apices acuminate; propagula absent .... *Phascum* (11)
  14. Plants small; leaves nearly linear, subulate-lanceolate; apices mostly acuminate or subulate .... *Bruchia* (7)
  14. Plants moderately large; leaves oblong-spatulate; apices obtuse or truncate .... *Tortula* (11)
15. Costa ending below the apex 16
15. Costa ending in the apex or excurrent 18
  16. Leaves lingulate; apices obtuse; capsule oblique-pointed and immersed in hair-like perichaetial leaves .... *Diphyscium* (42)
  16. Leaves and capsule not as above 17
17. Leaves elongate-ovate; apices usually obtuse and apiculate; margins coarsely toothed in upper ½–⅔ .... *Aulacomnium* (18)
17. Leaves lanceolate to lingulate; apices subacute, acuminate, or obtuse .... POTTIACEAE (11)
  18. Leaves lingulate, subspatulate; apices obtuse; margins plane and coarsely serrate above; propagula present in axils of upper leaves; plants usually growing on rocks in or along streams .... *Hyophila involuta* (11)
  18. Plants not as above 19
19. Leaves lanceolate to ovate-lanceolate or oblong-lanceolate 20
19. Leaves oblong-lingulate to lingulate .... *Desmatodon* (11)
  20. Costa with elongated cells on upper surface; capsules exserted .... *Barbula* (11)
  20. Costa without elongated cells on upper surface; capsules immersed to emergent .... ORTHOTRICHACEAE (23)

SECTION F

Plants acrocarpous; leaves three-ranked, costate, apices or excurrent costae not hyaline, cells smooth; gemmae not present on special structures.

1. Leaves distinctly bordered, at least in part, by 1 to several rows of narrow, hyaline cells 16
1. Leaves not distinctly bordered by narrow, hyaline cells 2
  2. Alar cells clearly differentiated, usually enlarged and inflated; leaves broadly to narrowly lanceolate .... DICRANACEAE (7)
  2. Leaves not as above 3
3. Plants dark green, brownish green, or blackish green 4
3. Plants green, light green, whitish green, or reddish green 7
  4. Plants minute, leaves subulate, growing on limestone .... *Seligeria* (6)
  4. Plants not as above 5
5. Plants with primary stems prostrate and bearing numerous erect, crowded, and densely foliate branches .... *Drummondia* (23)
5. Plants not as above 6

  6. Leaves crisped when dry, linear from a lanceolate base; margins plane, entire or serrate above; apices obtuse to almost blunt .... *Ptychomitrium* (22)
  6. Leaves usually imbricate when dry, ovate-lanceolate to linear-lanceolate; margins plane to narrowly or strongly recurved; apices muticous to subobtuse .. *Grimmia* (12)
7. Leaves crispate when dry 8
7. Leaves not crispate when dry 9
  8. Plants very small, stems usually less than 1 mm long; calyptra mitrate; seta arcuate .... *Campylostelium saxicolum* (22)
  8. Plants larger, stems 2–10 mm long; calyptra cucullate; seta not distinctly arcuate .... DICRANACEAE (7)
9. Leaves secund, frequently falcate .... DICRANACEAE (7)
9. Leaves not secund or falcate 10
  10. Plants small, stems usually averaging less than 4 mm in height 11
  10. Plants larger, stems usually averaging greater than 5 mm in height 12
11. Capsules immersed, globular, dehiscing at equatorial line .... *Aphanorhegma* (14)
11. Capsules not as above 15
  12. Plants densely tufted; leaves oval, ovate, ovate-lanceolate to narrowly lanceolate 13
  12. Plants loosely gregarious; leaves oblong-lanceolate, obovate-lanceolate to obovate .... FUNARIACEAE (14)
13. Median leaf-cells thick-walled, quadrate to hexagonal or roundish-quadrate, 6–10 μ in diameter 14
13. Median leaf-cells thin- or thick-walled, prosenchymatous, rhomboidal-hexagonal to linear, 14–100 μ in longest direction .... BRYACEAE (16)
  14. Margins entire; median leaf-cells rounded quadrate .... *Didymodon trifarius* (11)
  14. Margins denticulate to serrate near apex; median leaf-cells quadrate, hexagonal-quadrate or irregular .... *Ceratodon purpureus* (4)
15. Capsules ovoid, cylindric, or pyriform 19
15. Capsules sphaerical, indehiscent and immersed 18
  16. Plants with large terminal rosette of leaves .... *Rhodobryum roseum* (16)
  16. Plants not as above 17
17. Median leaf-cells parenchymatous, mostly hexagonal or rounded .... *Mnium* (17)
17. Median leaf-cells prosenchymatous, rhomboidal, rhomboid-hexagonal to linear .... BRYACEAE (16)
  18. Leaves lanceolate-subulate; spores few (*ca.* 24), large, 145–174 μ in diameter, angular or tetrahedral, deep yellow or orange .... *Archidium ohioense* (3)
  18. Leaves broadly ovate; spores smaller, 40–50 μ in diameter .... *Acaulon muticum* var. *rufescens* (11)
19. Capsules ovoid or cylindric 20
19. Capsules pyriform .... *Bruchia* (7)
  20. Plants minute; capsules inoperculate .... *Ephemerum* (13)
  20. Plants larger; capsules operculate .... DITRICHACEAE (4)

SECTION G

Plants pleurocarpous; leaves three-ranked, ecostate.

1. Plants large and normally aquatic .... *Fontinalis* (24)
1. Plants small or large, not aquatic 2
  2. Leaves papillose 3
  2. Leaves smooth 4
3. Plants slender; leaves ovate to ovate-lanceolate; alar cells abruptly quadrate to short rectangular .... *Schwetschkeopsis fabronia* (32)
3. Plants more or less robust; leaves ovate-elliptical; alar cells roundish-quadrate; secondary stems sparingly branched, branches curved outward and upward from substratum .... *Leucodon* (28)
  4. Branches and stems complanate-foliate at least in part 5
  4. Branches and stems not at all complanate-foliate 6
5. Leaves oblong-ovate, soft, thin, light-green; median leaf cells 50–60 μ wide .... *Hookeria acutifolia* (30)
5. Leaves ovate-lanceolate, lingulate, or cultriform, green to yellow-green or brownish green; leaf cells 10 μ or less wide .... NECKERACEAE (29)

6. Secondary stems not to sparingly branched, branches curved outward and upward from substratum; leaves ovate to ovate-lanceolate; alar cells numerous, roundish-quadrate .... *Leucodon* (28)
6. Secondary stems and leaves not as above 7
7. Leaves squarrose-spreading, triangular-cordate .... *Campylium* (35)
7. Leaves not both squarrose-spreading and triangular-cordate 8
8. Plants very small; leaves to 0.6 mm long; alar cells not inflated .... *Platydictya* (35)
8. Plants larger; leaves to 2.5 mm long; alar cells inflated .... SEMATOPHYLLACEAE (39)

SECTION H

Plants pleurocarpous; leaves three-ranked, costa short and double.

1. Leaves papillose 14
1. Leaves not papillose 2
2. Branches complanate-foliate 3
2. Branches not complanate-foliate 5
3. Leaves falcate-secund .... HYPNACEAE (40)
3. Leaves not falcate-secund 4
4. Numerous quadrate alar cells extending 8–10 rows up margin .... *Entodon* (37)
4. Alar cells not as above .... PLAGIOTHECIACEAE (38)
5. Foliated stems and branches julaceous 6
5. Foliated stems and branches not julaceous 10
6. Stems conspicuously red; leaves broadly ovate-elliptic; alar cells enlarged and somewhat inflated .... *Pleurozium* (37)
6. Plants not as above 7
7. Secondary stems curved outward and upward from substratum; apices of leaves abruptly short-acuminate; alar cells numerous, roundish quadrate .... *Leucodon* (28)
7. Plants not as above 8
8. Quadrate alar cells numerous, extending 10–20 rows along the margin .... *Entodon* (37)
8. Alar cells not as above 9
9. Alar cells composed of 3–8 conspicuously large, inflated, hyaline or colored cells .... *Sematophyllum* (39)
9. Alar cells not as above .... PLAGIOTHECIACEAE (38)
10. Tips of shoot frequently crowded with bud-like axillary gemmae; one inflated cell at extreme basal angle of leaf .... *Platygyrium* (40)
10. Plants not as above 11
11. Branches erect; leaves ovate to oblong-ovate, abruptly and broadly short-acuminate, concave; margins entire; alar cells numerous and quadrate or transversely elongate and extending upward ⅓ length of margin .... *Homomallium adnatum* (40)
11. Plants not as above 12
12. Secondary stems numerous, abundantly subpinnately branched, often bending outward and upward from substratum .... *Forsstroemia* (27)
12. Secondary stems not as above 13
13. Alar cells distinctly enlarged .... SEMATOPHYLLACEAE (39)
13. Alar cells numerous, quadrate .... *Pylaisiella* (40)
14. Plants light to bluish green .... *Myurella sibirica* (31)
14. Plants green to dark green .... *Pterigynandrum filiforme* (37)

SECTION I

Plants pleurocarpous; leaves three-ranked, costa single or double and reaching the middle of the leaf or beyond, cells not papillose.

1. Plants dendroid from creeping stems 2
1. Plants not dendroid 3
2. Leaves irregularly serrate near apex .... *Thamnobryum* (29)
2. Leaves serrate, often coarsely so, but not irregularly serrate .... *Climacium* (25)
3. Plants aquatic to subaquatic; leaves carinate-conduplicate .... FONTINALACEAE (24)
3. Plants not aquatic; if aquatic, not carinate-conduplicate 4
4. Plants glossy, golden yellow to brownish yellow; branches turgid, terete-foliate, julaceous; branch leaves very concave, ovate, acumination of rounded apices twisted ½ turn .... *Bryoandersonia* (36)
4. Plants not as above 5

5. Plants complanate-foliate; leaves oblong-cultriform, rounded obtuse .... NECKERACEAE (29)
5. Plants not as above 6
   6. Plants possessing conspicuous paraphyllia .... *Cratoneuron* (35)
   6. Paraphyllia absent or inconspicuous 7
7. Branches and stems falcate-secund; leaves with distinct, hyaline, enlarged and inflated alar cells that form distinct auricles .... *Drepanocladus* (35)
7. Plants not as above 8
   8. Leaves with a distinct border of elongated, thick-walled cells .... *Sciaromium* (35)
   8. Leaves not as above 9
9. Leaves squarrose to erect-spreading .... *Campylium* (35)
9. Leaves not as above 10
   10. Plants small and slender, in soft, thin mats; quadrate alar cells filling entire base and extending 12–20 rows up margin; margins entire to laciniate-dentate or serrate-dentate .... *Fabronia* (32)
   10. Plants not as above 11
11. Plants slender; quadrate basal cells numerous, distinctly different in shape from median leaf-cells 12
11. Plants not both slender and with numerous quadrate basal cells that differ markedly from median leaf cells 13
   12. Leaves distinctly serrate; costa of branch leaves usually reaching middle of leaf or beyond .... BRACHYTHECIACEAE (36)
   12. Leaves entire to obscurely serrulate .... *Clasmatodon* (32)
13. Branch leaves ovate-lanceolate; median leaf-cells rhombic-hexagonal; alar cells few, thin-walled, quadrate to rectangular; capsule erect, strongly contracted beneath mouth when dry .... *Anacamptodon* (32)
13. Plants not as above 14
   14. Median leaf-cells short, rounded-ovate to isodiametric; if long, alar cells very numerous, rounded-quadrate to transversely oblong and capsule on a short seta .... CRYPHAEACEAE (27)
   14. Median leaf-cells long; alar cells not as above 15
15. Leaves ovate-lanceolate or ovate, apices long and slenderly acuminate, usually not plicate; margins entire to slightly serrulate; costa reaching middle of leaf to percurrent or excurrent; median leaf-cells oblong-hexagonal, rhomboidal, to linear, 5–15 : 1; capsule curved and inclined, strongly contracted beneath mouth when dry .... AMBLYSTEGIACEAE (35)
15. Leaves ovate-lanceolate, ovate, ovate-cordate to triangular-cordate, often plicate; margins serrate to serrulate; costa usually ending near middle of leaf in a dorsal spine; median leaf-cells linear, linear-flexuose, oblong-rhomboidal to elongate-rhomboidal, 5–12 : 1; capsule erect to inclined, symmetrical to asymmetrical, not strongly contracted beneath mouth when dry .... BRACHYTHECEACAE (36)

SECTION J

Plants pleurocarpous; leaves three-ranked, costa reaching middle of leaf or beyond, cells papillose.

1. Costa long and double .... *Rhytidiadelphus triquetrus* (41)
1. Costa single 2
   2. Plants robust; leaves secund and strongly rugose; papillae dorsal, extending from angle of cell and strongly directed forward .... *Rhytidium rugosum* (41)
   2. Plants not as above 3
3. Leaves papillose because of thickened cell angles 4
3. Papillae developed over lumen of cells 5
   4. Plants slender, julaceous; cells strongly papillose .... *Pterygynandrum filiforme* (37)
   4. Plants not as above; leaves of stem loosely imbricate .... *Bryhnia* (36)
5. Plants glaucous-green, branches julaceous .... THELIACEAE (31)
5. Plants not as above 6
   6. Apex of leaf hyaline; costa ending near middle of leaf .... *Lindbergia brachyptera* (33)
   6. Apex of leaf not hyaline; if hyaline, costa ending near apex 7
7. Paraphyllia inconspicuous or entirely absent 8

7. Paraphyllia numerous, often branching .... THUIDIACEAE (34)
  8. Capsules usually numerous, immersed in perichaetial leaves; secondary stems sparingly branched; costa protruding on dorsal side of leaf .... *Cryphaea* (27)
  8. Plants not as above 9
9. Leaf bases not clasping the stem .... *Leskea* (33)
9. Leaf bases subclasping to clasping .... THUIDIACEAE (34)

1. SPHAGNACEAE

1. *Sphagnum* L.

The following treatment is adapted from a monograph by Andrews (1913).

Plants primarily of bogs, wet rock ledges and sandy creek banks, erect, whitish green to bright green, often tinged with purple, pink, red, or brown, extensively branching in fascicles disposed spirally about stem, near apex branches often densely crowded; stems without central strand, central portion composed of thin-walled parenchymatous cells, passing gradually into thick-walled, pigmented prosenchymatous cells, these latter cells enclosed by one or more layers of thin-walled parenchymatous cortical cells that may be dimorphic and porose, and have spiral fibril-bands reinforcing walls inwardly; leaves of stems and branches of two kinds of cells, narrow, linear chlorophyllose-cells forming the meshes of a network enclosing large rhomboidal hyaline cells, the latter being porose and with their walls reinforced inwardly by ring-shaped or spiral fibril-bands, pores round to elliptic in shape; sporophytes exserted on a pseudopodium; seta short; capsule globose, dark brown to black; operculum smooth; annulus and peristome absent.

a. Cortical cells of stems and branches reinforced by spiral fibril-bands .... b
a. Cortical cells of stems and branches without spiral fibril-bands c
  b. Chlorophyllose-cells of branch leaves usually isosceles-triangular in section .... 1. *S. palustre*
  b. Chlorophyllose-cells of branch leaves equilateral-triangular in section .... 2. *S. imbricatum*
c. Cortical cells of branches uniform, each with a pore at upper end; chlorophyllose-cells of branch leaves included .... 3. *S. compactum*
c. Cortical cells of branches dimorphic, the large retort-cells with a neck and a pore in the axils of leaves; chlorophyllose-cells of branch leaves not completely included .... d
  d. Chlorophyllose-cells of branch leaves exposed exclusively or more broadly on outer surface .... e
  d. Chlorophyllose-cells of branch leaves equally exposed on both surfaces or exposed exclusively or more broadly on inner surface .... f
e. Cortical cells of stem small and thick-walled .... 4. *S. recurvum*
e. Cortical cells of stem large, thin-walled, in 1–3 layers .... 5. *S. cuspidatum*
  f. Chlorophyllose-cells of branch leaves equally exposed on both surfaces .... 6. *S. subsecundum*
  f. Chlorophyllose-cells of branch leaves exposed exclusively or more broadly on inner surface .... g
g. The free convexity on the outer surface of hyaline cells of stem leaves mostly less than ½ their diameter .... 7a. *Sphagnum capillaceum* var. *capillaceum*
g. The free convexity on the outer surface of hyaline cells of stem leaves usually more than ½ their diameter .... 7b. *S. capillaceum* var. *tenerum*

1. *Sphagnum palustre* L.

Rare, Boston and Ouachita Mtns., Salem and Springfield Plateaus; on sandy soil, edges of streams and creeks.

2. *Sphagnum imbricatum* Hornsch. *ex* Russ. var. *imbricatum*

Rare, Ozark Hills; around seepage areas of springs.

3. *Sphagnum compactum* Lam. & DC.

Uncommon, Boston and Ouachita Mtns., Ozark Hills, eastern Salem Plateau; on moist sandstone ledges of bluffs.

4. *Sphagnum recurvum* P. Beauv.

a. Branch leaves undulate .... 4a. *S. recurvum* var. *recurvum*
a. Branch leaves hardly undulate because of reduced size .... 4b. *S. recurvum* var. *tenue*

4a. *Sphagnum recurvum* var. *recurvum*

Uncommon, Ouachita Mtns.; on sandy moist soil at bases of bluffs.

4b. *Sphagnum recurvum* var. *tenue* Klinggr.

Rare, western Salem Plateau; on moist sandy soil along narrow gully.

5. *Sphagnum cuspidatum* Ehrh. *ex* Hoffm. var. *cuspidatum*

Rare, Ouachita Mtns., Ozark Hills, Prairie Plains; in moist areas beneath sandstone ledges, bluffs, along creeks, and in strip mine pits (Waller & Bass, 1967).

6. *Sphagnum subsecundum* Nees *ex* Strum

Common, Boston and Ouachita Mtns., Salem Plateau; on soil, edges of creeks and streams.

7a. *Sphagnum capillaceum* (Weiss) Schrank var. *capillaceum*

Reported from Boston Mtns., in Franklin County, Arkansas, by Wittlake (1950).

7b. *Sphagnum capillaceum* var. *tenerum* (Sull. & Lesq. *ex* Sull.) Crum (1971)

Rare, Ozark Hills, eastern Salem Plateau; on moist shaded sandy soil of slopes and rock ledges.

2. Fissidentaceae

Members of this family are easily recognized by two features. First, leaves are arranged in two vertical rows in a single plane (distichous) and, second, each leaf consists of a "boat-like" portion (the vaginant or sheathing laminae), which clasps the stem, a dorsal (lower) lamina, and a terminal (apical) lamina. Both the dorsal and apical laminae may be absent in dwarf male plants. Only *Bryoxiphium norvegicum* has a similar arrangement of leaves, but this species is bulb-like at its base, whereas members of the Fissidentaceae are not.

1. *Fissidens* Hedw.

a. Leaves rigid, opaque, several cell layers in thickness .... 15. *F. grandifrons*

a. Plants not as above .... b

b. Plants aquatic; apical lamina 2–3 times as long as the vaginant lamina .... 16. *F. fontanus*

b. Plants not aquatic; apical lamina as long as the vaginant lamina or shorter; if longer, not 2–3 times c

c. Leaves obtuse, entire .... 4. *F. obtusifolius*

c. Leaves acute to acuminate .... d

d. Leaves distinctly bordered with a row of elongate cells that extends to the apex or subapical region of the apical and dorsal laminae .... e

d. Leaves not distinctly bordered; if bordered, the border confined to the vaginant lamina or border not composed of elongated cells .... g

e. Leaves widely spreading, forming an angle of 45° or more with the stem .... 3. *F. viridulus*

e. Leaves not widely spreading, forming an angle of 30–45° with the stem .... f

f. Leaf cells 6–10.0 μ in diameter, obscure; leaves narrowly lanceolate to oblong lanceolate; apex acute to acuminate .... 1. *F. minutulus*

f. Leaf cells 10–13 μ in diameter, pellucid; leaves lanceolate to ligulate; apex acute to obtuse .... 2. *F. pusillus*

g. Leaves bordered by elongated cells, border confined to the vaginant laminae, at times indistinct, absent or confined to perichaetial leaves, often intramarginal; if absent plants less than 5 mm tall[3] .... h

g. Leaves not bordered by elongated cells, plants 5 mm or more tall .... k

h. Leaf cell papillose i

h. Leaf cells smooth or bulging .... j

i. Costa ending 2–several cells below apex .... 8. *F. garberi*

i. Costa percurrent to excurrent .... 7. *F. ravenelii*

j. Leaf margins entire except near apex .... 5. *F. exiguus*

j. Leaf margins sub-entire to irregularly crenate; margins of the vaginant laminae strongly crenate-dentate .... 6. *F. exilis*

k. Leaves coarsely and irregularly crenulate-serrate l

k. Leaves finely and evenly crenulate by projecting cell angles .... n

l. Costa ending several cells below apex and covered with low mammillose cells .... 14. *F. subbasilaris*

l. Costa percurrent and not covered with mammillose cells .... m

m. Leaf cells obscure, enlarged and elevated tumid cells appearing singly or in groups in surface view of apical lamina; leaf cells 7–9 μ in diameter; border of paler or thicker-walled cells distinct; leaves crowded on stem, rolled inward from tips when dry .... 11. *F. cristatus*

m. Leaf cells clear, tumid cells absent or few; leaf cells 13–16 μ in diameter; border of differentiated cells often indistinct; leaves distant on stem, curving underneath stem and with upper ¼ wrinkled and distorted when dry .... 13. *F. adianthoides*

n. Costa ending several cells below apex; sporophyte terminal .... 10. *F. osmundioides*

n. Costa percurrent to shortly excurrent; sporophyte lateral .... o

o. Costa stout, usually filling apiculus, short-excurrent; cells of apical lamina conically papillose or mammillose .... 9. *F. taxifolius*

o. Costa slender, not filling apiculus, percurrent; cells of apical lamina pluripapillose .... 10. *F. bushii*

1. *Fissidens minutulus* Sull. var. *minutulus*

Common throughout Interior Highlands; often abundant on moist, shaded rocks.

The bordered groups (Sections *Bryoidium* and *Semilimbidium*) of this genus are not well understood. Many workers, notably Crum (1964), consider not only *Fissidens minutulus* but *F. viridulus* var. *viridulus* and *F. exiguus* to be forms of

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[3] Occasionally smaller forms of *Fissidens taxifolius* or *F. osmundioides* may key out here.

F. bryoides Hedw. Other workers do not even recognize *F. pusillus*. Grout (1936) considers it a synonym of *F. minutulus*, and Wijk and Margadant (1960) consider it a subspecies of *F. minutulus*. However, this work follows the treatment by Pursell (1957) that recognizes not only *F. minutulus*, but also *F. pusillus* and *F. viridulus* var. *viridulus*. Since *F. exiguus* also seems distinct in Ozark material, it is also retained. For the present, such an arrangement best expresses the situation.

2. *Fissidens pusillus* (Wils.) Mild.

Fissidens minutulus Sull. subsp. *pusillus* (Wils.) Wijk & Marg.

Uncommon, Boston Mtns., Prairie Plains, Salem and Springfield Plateaus; on shaded rocks that are usually in or near creeks and streams.

This species is undoubtedly closely related to the previous one. In *Fissidens minutulus*, leaves are narrowly lanceolate to oblong-lanceolate with an acute apex, and the cells of the apical lamina are small (6–10 μ in diameter) and consequently appear obscure. In contrast, the leaves of *F. pusillus* are broader, lanceolate to ligulate with an acute to obtuse apex; the cells of the apical lamina are relatively large (10–13 μ in diameter) and appear pellucid.

3. *Fissidens viridulus* (Sw.) Wahlenb. var. *viridulus*

Fissidens bryoides Hedw. var. *viridulus* (Sw.) Kindb.

Common throughout the Interior Highlands; on rocks and soil, particularly of moist and well shaded forests.

In addition to the character mentioned in the key, this species may be recognized in the field by its unusually distinct margins, relatively robust size (stems 3–8 mm in length), and the lustrous dark to light green color of the plants.

4. *Fissidens obtusifolius* Wils. var. *obtusifolius*

Common, Boston Mtns., Prairie Plains, Salem and Springfield Plateaus; on limestone or sandstone rocks in or along the edge of creeks and streams. Locally, this species may be very abundant.

A species easily recognized in the field because of its obtuse leaves and the pale green, at times almost glaucous, color of the colonies.

5. *Fissidens exiguus* Sull. subsp. *exiguus*

Uncommon, Boston Mtns., Prairie Plains, Salem and Springfield Plateaus; on rocks rarely soil along banks of creeks and streams.

This species is of doubtful validity. As noted previously, Crum (1964) considers it to be a form of *Fissidens minutulus*.

6. *Fissidens exilis* Hedw.

Reported from northern Salem Plateau by Gier (1955*a*:34) from collections made by N. L. T. Nelson. The location of Nelson's collection is unknown.

7. *Fissidens ravenelii* Sull.

Uncommon, Boston and Ouachita Mtns., Ozark Hills, Salem and Springfield Plateaus; restricted to moist shaded crevices of sandstone.

Superficially this species resembles *Fissidens garberi*; the presence of a percurrent to excurrent costa in *F. ravenelii*, however, is usually a reliable distinguishing character.

8. *Fissidens garberi* Lesq. & James

Common, Boston and Ouachita Mtns., Prairie Plains, Salem Plateau; on sandy dolomite and sandstone along streams and creeks. Occasionally plants occur deep within rock crevices.

The presence of this species in the Interior Highlands was first noted by Ireland from a collection made in Cedar County, Missouri (see Redfearn, 1961).

The border of the vaginant lamina is often difficult to demonstrate. Breen (1963:7) notes that the border is usually restricted to the uppermost pair of leaves (perichaetial). In the Interior Highlands, the separation of this species from *Fissidens ravenelii* is not always easy. However, in *F. garberi* the costa in most leaves is not percurrent and ceases 2–several cells below the apex.

Florschütz (1964) places both this species and *Fissidens ravenelii* in synonymy under *F. guianensis* Mont. Considering the difficulty encountered in separating *F. ravenelii* and *F. garberi* in the Interior Highlands, he may be correct.

9. *Fissidens taxifolius* Hedw. var. *taxifolius*

Very common throughout the Interior Highlands; on shaded soil, rock ledges and crevices, bases of trees, and decaying wood.

10. *Fissidens osmundioides* Hedw. var. *osmundioides*

Uncommon, Boston and Ouachita Mtns., Ozark Hills, Salem Plateau; on shaded sandstone ledges and soil banks along creeks and streams.

Sterile forms of this species may be confused with *Fissidens taxifolius* or poorly developed forms of *F. cristatus*. However, a costa which distinctly ends 2 to several cells below the apex will serve to separate it from *F. taxifolius*, and the even and finely serrulate to crenulate margins will distinguish it from *F. cristatus*.

11. *Fissidens cristatus* Wils. *ex* Mitt. var. *cristatus*

Very common throughout the Interior Highlands; occurring in nearly every conceivable type of habitat—soil, limestone, sandstone, granite and felsite rocks, trees, decaying wood.

This species may be confused with the next, however the distinctions noted in the key have been demonstrated by Anderson and Bryan (1956) to be quite reliable.

12. *Fissidens bushii* (Card. & Thér.) Card. & Thér.

Uncommon, Boston and Ouachita Mtns., Ozark Hills, Salem and Springfield Plateaus; on shaded soil and decaying wood.

13. *Fissidens adianthoides* Hedw. var. *adianthoides*

Uncommon, Boston and Ouachita Mtns., Salem and Springfield Plateaus; on moist shaded soil along creeks and streams, occasionally on rocks along seepage areas.

14. *Fissidens subbasilaris* Hedw.

Common throughout the Interior Highlands; on moist soil, shaded rocks, bases and trunks of trees, and decaying wood.

15. *Fissidens grandifrons* Brid. var. *grandifrons*

Uncommon, Boston Mtns., Salem Plateau, St. Francois Mtns.; on submerged stones, usually near the emergence of swiftly flowing springs.

The stiff, dark leaves are very distinctive. It is not unusual for this species to be locally very abundant. At Big Springs in Carter County, Missouri, rocks near the spring outlet are densely covered with this species, a condition not unusual at other large springs.

16. *Fissidens fontanus* (B. Pyl.) Steud.

Fissidens debilis Schwaegr.

Common throughout Interior Highlands; on stones, roots, and branches in streams and creeks.

3. ARCHIDIACEAE

1. *Archidium* Brid.

Plants erect, small, terrestrial; leaves narrow, lanceolate to subulate; margins entire to serrulate; costa excurrent to ending in a subulate awn; cells smooth; perichaetial leaves long-pointed, to 2.25 mm, 3–4 times as long as the capsule; capsule cleistocarpous, sessile, ovoid, thin walled and containing about 12–24 very large (120–160 μ in diameter), yellow to orange spores clearly visible through the thin wall of the capsule; oil bodies conspicuous in spores.

Sterile plants of this genus are difficult, if not impossible, to separate from *Pleuridium* and *Bruchia*. When fertile, the ovoid, sessile, cleistocarpous capsule containing the largest spores found in the mosses will at once separate this genus from all other mosses in our area.

1. *Archidium ohioense* Schimp. *ex* C. Müll.

Rare, known only on the Springfield Plateau from Dade County, Missouri, *ca.* 1 mile W of Bona along Highway H, SW ¼ Sect. 33, R. 25 W., T. 33 N. On sandy soil of open oak forest.

Probably more common but overlooked when sterile because of its small size and the tendency of plants to be half buried in sand.

4. DITRICHACEAE

Plants dark green to yellow-green, erect, small to moderate in size, usually less than 2 cm tall, gregarious to scattered; leaves lanceolate to lanceolate-subulate from a broader base, not distinctly secund, occasionally contorted when dry; costa percurrent to excurrent and occupying the larger part of the awn; leaf-cells smooth to faintly papillose; alar cells not inflated; capsule immersed to exserted on a long seta, spherical, ovoid, or cylindrical, cleistocarpous or dehiscing regularly; peristome, when present, of 16 teeth split to base or nearly so into 32 filiform divisions.

Three genera of this family are represented in the Interior Highlands. When sterile, identification is difficult and dubious. Consequently the following key is based primarily upon sporophytic characters. This is not to say that generic identification of sterile material is not possible in some cases, but should only be undertaken after complete familiarity with fertile plants.

a. Plants small, usually less than 2 mm high; capsule cleistocarpous; peristome absent .... 1. *Pleuridium*
a. Plants usually larger; capsule dehiscing regularly; peristome present .... b
  b. Leaves ovate-lanceolate to narrowly-lanceolate, green to dark-green, often contorted; margins conspicuously revolute, rarely to apex; upper leaf-cells quadrate to short-rectangular .... 2. *Ceratodon*
  b. Leaves lanceolate-subulate, light green to yellowish green, often slightly secund; median leaf-cells rectangular to linear .... 3. *Ditrichum*

1. *Pleuridium* Brid.

Plants small, green to yellowish green; leaves erect-spreading, mucronate to subulate from an ovate to lanceolate base; margins entire to minutely serrate; costa sub-percurrent, to percurrent, to excurrent; cells mostly elongate-rectangular, smooth; alar cells not enlarged or inflated; capsule erect on short seta, ovoid to subglobose, apiculate, immersed in perichaetial leaves; peristome absent.

a. Broad base of perichaetial leaves short, scarcely reaching the base of capsule .... 1. *P. subulatum*
a. Broad base of perichaetial leaves longer, nearly reaching the end of the capsule .... 2. *P. acuminatum*

1. *Pleuridium subulatum* (Hedw.) Rabenh.

Common, Arkansas Valley, Boston Mtns., Mississippi Valley, Ozark Hills, Salem and Springfield Plateaus; on soil of pastures, fields, and rocky ridges. Capsules present from early spring to summer.

Because of the small size of this species, it is likely to be overlooked; however, when fruiting it is easily identified by its yellow-green appearance, subulate leaves, and immersed, small, subglobose, cleistocarpous capsule. *Pleuridium subulatum* is difficult to separate from *P. acuminatum*. In addition to the distinctions used in the key to the species that have been suggested by Nyholm (1954), Bryan (1956) reports cytological differences: *P. subulatum* is a diploid ($n = 13$) and *P. acuminatum* is a tetraploid ($n = 26$).

2. *Pleuridium acuminatum* Lindb.

Common, Prairie Plains, Salem Plateau; on moist soil of open forests, in fields and pastures.

Like the preceding species, this one is frequently overlooked, but when fruiting may be separated from *P. subulatum* by the characters noted above.

2. *Ceratodon* Brid.

1. *Ceratodon purpureus* (Hedw.) Brid.

Caespitose plants, green when young, often becoming reddish when old; leaves ovate-lanceolate to narrowly lanceolate, twisted and contorted when dry; margins revolute from apex nearly to base, usually serrate above; median leaf-cells rectangular to square, weakly collenchymatous; seta dark red to purplish, 1–2.5 cm long; capsule oblong, deeply grooved, more or less curved and unsymmetric; peristome with 16 bifid, dark red teeth.

Common, Arkansas Valley, Boston and Ouachita Mtns., Ozark Hills, Prairie Plains, Salem and Springfield Plateaus; on various types of substrates—bases of tree, sandy soil, soil pockets of sandstone, dolomite, granite, and rhyolite boulders. In urban areas very common on cedar shingle roofs.

This species is often anomalous particularly when sterile. Amateur and professional alike have been fooled by its many forms. However, the intersections of the collenchymatous median leaf-cells are characteristic when viewed under low magnification (*ca.* 100 ×) in that they usually appear as a row of small four-pointed stars due to refraction of light.

3. *Ditrichum* Hampe

Small caespitose mosses; leaves loosely spreading to erect, green to light green or yellowish; costa broad, percurrent to excurrent; upper leaf-cells subquadrate to long rectangular, smooth; seta slender, long; capsule oblong, cylindric to ovoid, erect to inclined.

a. Leaves long, linear-subulate, more or less erect to loosely spreading; awn slender, as long as to much longer than broad base; apex acute .... b
a. Leaves not long, linear-subulate, appressed; awn shorter than broad base; apex obtuse .... 2. *D. lineare*
  b. Seta red; upper leaves 2–3 mm long; costa in awn clearly distinct .... 1. *D. pusillum*
  b. Seta yellow; upper leaves often more or less secund, 3–5 mm long; costa in awn indistinct .... 3. *D. pallidum*

1. *Ditrichum pusillum* (Hedw.) Hampe

Uncommon, Ozark Hills, Prairie Plains, Salem Plateau; on soil, especially along creeks and gullies.

2. *Ditrichum lineare* (Sw.) Lindb.

Apparently rare, eastern Salem Plateau; in crevices of moist sandstone and rhyolite rocks.

3. *Ditrichum pallidum* (Hedw.) Hampe

Very common throughout Interior Highlands; on bare soil of woods and fields, occasionally in moist rock crevices.

Sterile plants may be confused with *Dicranella heteromalla*; however, in that species the leaves are more consistently secund and the plants are usually much taller (0.5–4 cm).

5. Bryoxiphiaceae

1. *Bryoxiphium* Mitt.

Slender plants similar to *Fissidens*; leaves conduplicate, not clasping the stem at base; stem with a bulb-like base.

Many authors place the genus *Bryoxiphium* in the Fissidentaceae. However, Löve and Löve (1953) have concluded from their rather exhaustive study of this genus that it should be placed in a separate family.

1. *Bryoxiphium norvegicum* (Brid.) Mitt. subsp. *norvegicum* var. *norvegicum*

Rare, Boston and Ouachita Mtns., Prairie Plains, eastern Salem Plateau, where plants may be abundant on moist, shaded vertical sandstone bluffs beneath overhanging ledges.

6. Seligeriaceae

Plants very small, less than 1 mm tall, gregarious, green to dark brownish-green; leaves subulate from a broader, sheathing, ovate-lanceolate base, costate; margins entire to serrulate; alar cells enlarged to undifferentiated; seta straight, longer than perichaetial leaves; capsule small, pyriform; peristome of 16 teeth or absent.

In the Interior Highlands this family is represented by a single genus, *Seligeria*, whose alar cells are undifferentiated. *Seligeria* is commonly found growing on calcareous rocks, especially on the overhanging ledges.

1. *Seligeria* B.S.G.

a. Peristome lacking .... 1. *S. donniana*
a. Peristome present .... b
  b. Awn short and thick, usually developing abruptly from the sheathing base .. 2. *S. calcarea*
  b. Awn not short and thick, usually slender, gradually tapering from a lanceolate base .... 3. *S. pusilla*

1. *Seligeria donniana* (Sm.) C. Müll.

Sterile forms of this taxon cannot be adequately distinguished from the next taxon. Although not yet reported from the Interior Highlands, there is no phytogeographic reason for its absence. Further field studies may yet reveal its presence in our area.

2. *Seligeria calcarea* (Hedw.) B.S.G.

Uncommon, Boston Mtns., Salem and Springfield Plateaus; in crevices and pockets of shaded calcareous rocks. Probably more common in the Interior

Highlands than distribution records indicate as it is seldom collected if not carefully searched for.

3. *Seligeria pusilla* (Hedw.) B.S.G.

Reported from eastern Salem Plateau in Franklin County, Missouri (Gier, 1955*a*: 38).

7. DICRANACEAE

Plants erect, variable in size, usually growing in mats or tufts, pale, to yellowish, to dark green; stems often branching, densely foliate and tomentose; leaves costate, variable in outline, straight, often curved, secund, sometimes crispate or subulate; leaf-cells smooth or papillose, variable in shape from rectangular near the base to shorter, often irregular or isodiametric near the apex; alar cells frequently clearly differentiated into distinct auricles; capsule short to long exserted, curved or erect, pyriform to cylindrical; peristome absent or of 16 teeth, each divided ½ or more into 2 slender divisions.

Cytological evidence presented by Bryan (1956) indicates that the genera *Bruchia* and *Trematodon* should be included in this family as it was originally conceived by Brotherus (1924:172–214) and not in the Ditrichaceae.

a. Plants small; leaves subulate to ovate-lanceolate, not secund; capsule obovoid to pyriform, inoperculate .... 1. *Bruchia*
a. Plants small to large; leaves narrowly to broadly lanceolate or subulate, often secund; capsule cylindrical, often curved, operculate .... b
  b. Capsule with a long, slender neck .... 2. *Trematodon*
  b. Capsule without a long, slender neck c
c. Alar cells conspicuously inflated or enlarged .... f
c. Alar cells not conspicuously inflated or enlarged .... d
  d. Leaves crisped when dry .... 4. *Rhabdoweisia*
  d. Leaves not crisped when dry .... e
e. Costa at least ¾ the width of the leaf base; plants pale green; numerous rudimentary branchlets often present in the axils of upper leaves .... 7. *Brothera*
e. Costa less than ⅓ the width of the leaf at base; plants darker green; rudimentary branchlets absent .... 3. *Dicranella*
  f. Costa less than ½ the width of the leaf at base .... 5. *Dicranum*
  f. Costa ½–¾ the width of the leaf at base .... 6. *Campylopus*

1. *Bruchia* Schwaegr.

Small gregarious plants of moist soil in open fields and pastures; leaves subulate to abruptly acuminate from an ovate to lanceolate base; seta shorter than to barely as long as perichaetial leaves; capsule pyriform, inoperculate.

A difficult genus for which mature fruiting material is generally required for identification of the species. Although *Bruchia donnellii* and *B. texana* have been reported from the Interior Highlands, they have been excluded for lack of reliable material to study.

a. Leaves short acuminate, imbricate-appressed .... 2. *B. hallii*
a. Leaves subulate-lanceolate, not imbricate-appressed .... 1. *B. flexuosa*

1. *Bruchia flexuosa* (Sw. *ex* Schwaegr.) C. Müll.

Bruchia sullivantii Aust.

Rare, Boston and Ouachita Mtns., Ozark Hills, and Salem Plateau; on damp soil of open fields and pastures. Sporophytes maturing in late spring or early summer.

2. *Bruchia hallii* Aust.

Rare, Springfield Plateau; on open sandy soil.

2. *Trematodon* Michx.

1. *Trematodon longicollis* Michx.

Plants gregarious to scattered, yellowish green in color; leaves more or less crisped when dry, gradually tapering from a broad, clasping base to a lanceolate or subulate apex; margins more or less revolute; costa percurrent; leaf-cells smooth, thin-walled, elongate hexagonal above, rectangular below; seta 2–3 cm long; capsule very distinctive, operculate, yellow to yellow-orange with a neck about twice as long as urn; operculum long rostrate.

Uncommon, Boston Mtns., Ozark Hills, Springfield Plateau; on open sandy soil along creek and river bottoms and in open woods.

3. *Dicranella* (C. Müll.) Schimp.

Plants small, gregarious or forming open to dense tufts or mats, bright green to yellowish green; leaves ovate-lanceolate to narrowly lanceolate from a sheathing base, often falcate secund; costa less than ⅓ the width of the leaf at base; alar cells not differentiated; seta red to yellow, 5–30 mm long; capsule erect to inclined and curved, smooth to furrowed when dry and empty; operculum rostrate; peristome of 16 single teeth divided to near the middle into 2–3 papillose divisions.

Key to Fruiting Plants

a. Mature capsules erect, symmetric or nearly so, seta red-brown .... 1. *D. rufescens*
a. Mature capsule inclined, unsymmetric; if erect then distinctly furrowed when dry .... b
  b. Capsule plicate or furrowed when dry and empty; seta yellow .... 3. *D. heteromalla*
  b. Capsule smooth or only slightly furrowed when dry and empty; seta reddish .... 2. *D. varia*

Key to Sterile Plants (Less Reliable)

a. Margins of leaves recurved, entire .... 2. *D. varia*
a. Margins of leaves plane, entire to serrulate .... b
  b. Margins of leaves entire except at apex; leaves erect-spreading to slightly secund; mostly of moist, open soil along streams and ditches .... 1. *D. rufescens*
  b. Margins of leaves serrulate nearly to base; leaves usually clearly falcate-secund; habitat various .... 3. *D. heteromalla*

1. *Dicranella rufescens* (With.) Schimp.

Rare, Salem Plateau; on moist soil, chiefly bare of other plants.

2. *Dicranella varia* (Hedw.) Schimp.

Uncommon, Ozark Hills, Springfield and Salem Plateaus; on moist soil and rocks, chiefly along streams and ditches.

3. *Dicranella heteromalla* (Hedw.) Schimp.

a. Capsule erect and symmetric, urn coarsely furrowed when dry and empty .... 3b. *D. heteromalla* var. *orthocarpa*
a. Capsule inclined and asymmetric, capsule plicate when dry and empty .... 3a. *D. heteromalla* var. *heteromalla*

3a. *Dicranella heteromalla* var. *heteromalla*

Very common throughout the Interior Highlands; on apparently all types of soil or rock substrates.

3b. *Dicranella heteromalla* var. *orthocarpa* (Hedw.) Jaegr. & Sauerb.

Rare, Ozark Hills; on sandstone.

4. *Rhabdoweisia* B.S.G.

1. *Rhabdoweisia denticulata* (Brid.) B.S.G.

Plants small, tufted, yellowish to dark green; leaves oblong to linear-lanceolate, crisped when dry, finely serrulate above, teeth often few and distant, apex acute; costa stout, ending just below apex; upper leaf-cells mostly round-quadrate, obscurely papillose; seta erect, 2–5 mm long, yellow; capsule ovoid, 8-plicate; peristome teeth 16, undivided.

Rare, Boston and Ouachita Mtns., eastern Salem Plateau; on vertical sandstone.

5. *Dicranum* Hedw.

Plants small to large, in loose to dense tufts, yellowish to dark green, usually radiculose below; leaves lanceolate to ovate-lanceolate, erect-spreading, crisped, or falcate-secund, narrowly costate with distinctly enlarged alar cells; basal leaf-cells rectangular to elongate, walls often pitted; upper leaf-cells rectangular, oblong-rhomboidal, or irregularly shaped, walls plain to pitted, often papillose on the lower surface; seta erect; capsule cylindrical and symmetrical to inclined, curved and asymmetrical; operculum long rostrate; peristome teeth red, single, 16, divided to near the middle into 2–3 divisions.

a. Walls of lower leaf cells not pitted .... b
a. Walls of lower leaf cells pitted .... d
  b. Costa broad, ⅓ or more the width of the leaf base .... 3. *D. fulvum*
  b. Costa narrower, ⅐–⅕ the width of the leaf base c
c. Leaves strongly crisped when dry, margins irregularly serrate to serrulate; flagelliform branches absent .... 1. *D. montanum*
c. Leaves crisped, erect-spreading to secund when dry, margins essentially entire; flagelliform branches usually present .... 2. *D. flagellare*
  d. Upper leaf-cells elongate, more or less pitted .... f
  d. Upper leaf-cells 1–2 : 1 .... e
e. Leaves widest some distance above base; upper leaf-cells irregular in shape, highly mammillose lower surface .... 5. *D. spurium*

e. Leaves widest near the base; upper leaf cells more or less uniform in shape, smooth or slightly papillose on lower surface .... 4. *D. sabuletorum*
  f. Leaves distinctly transversely undulate .... 6. *D. polysetum*
  f. Leaves not transversely undulate .... 7. *D. scoparium*

1. *Dicranum montanum* Hedw.

Uncommon, Boston and Ouachita Mtns., Ozark Hills, Prairie Plains, Salem Plateau; on shaded dolomite, rhyolite, sandstone, and bases of trees.

2. *Dicranum flagellare* Hedw.

Common, Boston and Ouachita Mtns., Ozark Hills, Salem Plateau, St. Francois Mtns.; mostly on decaying wood, occasionally on shaded sandstone.

3. *Dicranum fulvum* Hook.

Common throughout the Interior Highlands; on vertical, shaded, non-calcareous rocks.

4. *Dicranum sabuletorum* Ren. & Card.

Common throughout the Interior Highlands; on rocky soil, decaying wood, crevices and ledges of rocks. Often mixed with *Dicranum scoparium.*

5. *Dicranum spurium* Hedw.

Uncommon, Boston and Ouachita Mtns., Ozark Hills, Salem Plateau, St. Francois Mtns.; on rock ledges, especially granite, sandstone and dolomite, occasionally on rocky, acid soil of ridges.

6. *Dicranum polysetum* Sw.

Dicranum rugosum (Funck) Hoffm. *ex* Brid.
Dicranum undulatum Ehrh. *ex* Web & Mohr

Rare, known only from the Springfield Plateau in Barry Co., Missouri, where it occurred on soil in a mixed oak-cedar forest along a ridge *ca.* ½ mile east of Roaring River State Park.

7. *Dicranum scoparium* Hedw.

Very common throughout the Interior Highlands; on soil of ridges, wooded slopes, and rock ledges. Occasionally on decaying wood and bases of trees.

6. *Campylopus* Brid.

Plants dark to yellowish green, in loose to compact tufts; leaves erect spreading to secund, narrowly lanceolate-subulate; costa often to ¾ width of the leaf base, in cross section showing stereid cells above and below guide cells, upper surface cells larger than guide cells; seta 5–10 mm long; capsule ovoid, cylindric to pyriform elliptic; peristome of 16 teeth divided to near the middle into papillose divisions; apparently fruiting infrequently.

a. Leaves, particularly older ones, ending in a hyaline hair point; narrow rectangular hyaline cells extending up the margin from base as in *Tortella* .... 2. *C. introflexus*
a. Leaves without hyaline hair points; no hyaline cells extending up margin .. 1. *C. flexuosus*

1. *Campylopus flexuosus* (Hedw.) Brid.

Campylopus tallulensis Sull. & Lesq.

Uncommon, Boston and Ouachita Mtns., eastern Salem Plateau; on shaded sandstone.

2. *Campylopus introflexus* (Hedw.) Brid.

Uncommon, Boston and Ouachita Mtns.; on open flat (occasionally vertical) exposures of sandstone and novaculite. Often forming extensive cushions.

Excluded species:

Campylopus fragilis (Brid.) B. S. G.—The collection cited by Lowe (1919) is *C. flexuosus.*

7. *Brothera* C. Müll.

1. *Brothera leana* (Sull.) C. Müll.

Common, Boston Mtns., Ozark Hills, Salem and Springfield Plateaus; usually in crevices of dolomite or sandstone of bluffs, particularly along the upper reaches of bluffs and cliffs.

Excluded taxa:

Dicranoweisia cirrata (Hedw.) Lindb. *ex* Milde and *D. crispula* (Hedw.) Lindb. *ex* Milde—Collections from Arkansas determined as these species are *Weissia controversa.*

8. LEUCOBRYACEAE

1. *Leucobryum* Hampe

Plants in whitish to glaucous, dense, spongy, cushion-like tufts, often to one foot in diameter; stems erect, to 15 cm or more high; leaves thick, lanceolate, the base composed almost entirely of a broad costa composed of 2 or more layers of large, empty, hyaline cells surrounding a layer of small chlorophyllose-cells; seta erect; capsule erect and symmetric to inclined and asymmetric; peristome single, composed of 8 or 16 teeth, entire or split to the middle into two sections.

a. Leaves in cross section near the base at the middle of the costa 4–5 layers of cells thick (2 layers of hyaline cells above and 1–2 layers below a single layer of chlorophyllose cells); leaves 5–8 mm long .... 1. *L. glaucum*
a. Leaves in cross section near the base at the middle of the costa 3 layers of cells thick (1 layer of hyaline cells above and below a single layer of chlorophyllose cells); leaves 2–4.5 mm long .... 2. *L. albidum*

1. *Leucobryum glaucum* (Hedw.) Ångstr. *in* Fr.

Very common throughout the Interior Highlands; on acid soil of ridges, on rock ledges, particularly granite, rhyolite, felsite, sandstone, and dolomite. Often mixed with *Polytrichum* and *Dicranum.*

Plants growing under dry conditions, particularly along oak-hickory ridges, are difficult to separate from the next species. However, structural differences of the lower costa as well as examination of older stem leaves will usually prove the key characters to be reliable.

2. *Leucobryum albidum* (Brid. *ex* P. Beauv.) Lindb.

Common throughout the Interior Highlands; on soil, bases of trees, and rock ledges.

9. CALYMPERACEAE

1. *Syrrhopodon texanus* Sull.

Plants tufted, often forming extensive dark green or brown cushions, 1–4 cm high; leaves crisped when dry, linear to lingulate, often appearing whitish near tips; marginal cells elongated, hyaline, and coarsely toothed; costa rough on both surfaces; upper leaf-cells papillose; basal cells hyaline, forming acute angles above; sporophytes unknown in material from the Interior Highlands.

Rare, Boston Mtns., Ozark Hills, and eastern Salem Plateau; on vertical shaded sandstone and shaded soil.

10. ENCALYPTACEAE

1. *Encalypta procera* Bruch

Encalypta streptocarpa Hedw. (*sensu* Flowers).

Plants in loose, brownish green tufts; leaves crisped when dry, broad, lingulate; costa single; upper leaf-cells short, densely papillose; basal leaf-cells hyaline, oblong, smooth; filamentous brood bodies arising from leaf axils.

Rare, Salem Plateau; on exposed soil of ridge. Known only from Ozark County, Missouri, from a NW facing cherty slope *ca.* 3 miles SE of Dora, SW ¼ Sect. 14, T. 24 N., R. 11 W. When dry, colonies may be mistaken for *Atrichum angustatum.*

11. POTTIACEAE

Plants variable in size, erect to decumbent, in loose to dense tufts, yellowish to dark green to blackish in color; leaves variable in shape, frequently contorted when dry; costa strong, often long excurrent; basal leaf-cells usually thin walled and hyaline; upper leaf-cells small, isodiametric, thick-walled and more or less papillose; alar cells not differentiated; capsule usually erect, sessile to long exserted on a straight seta; peristome when present composed of 16 teeth, often divided and spirally twisted.

a. Plants small, bulbiform; upper leaves broadly ovate; cells smooth; capsule immersed .... 13. *Acaulon*
a. Plants not as above .... b
  b. hyaline cells of leaf-base extending up the margin further than along the costa, forming a V; leaves oblong-lanceolate to broadly lanceolate-acuminate c
  b. Hyaline cells of leaf base not as above; if faintly showing V-shaped arrangement of hyaline basal cells, then leaves narrowly lanceolate to linear-lanceolate .... d

c. Hyaline cells of leaf base not reaching the costa .... 8. *Pleurochaete*

c. Hyaline cells of leaf base reaching the costa .... 7. *Tortella*

d. Margins of the upper half of leaf involute .... e

d. Margins of the upper half of leaf plane or reflexed .... f

e. Peristome present, inserted at the mouth of the capsule; costa 60 μ or more wide at base; leaves linear-lanceolate from a broadly oblong to oblong-lanceolate base .... 6. *Trichostomum*

e. Peristome absent; if present, inserted below the mouth of the capsule; costa 50 μ or less wide at base, if wider, then leaves narrowly oblong-lanceolate .... 2. *Weissia*

f. Leaves erect-spreading, tips usually curled, very narrowly linear .... 6. *Trichostomum*

f. Leaves not possessing this combination of characters .... g

g. Leaves bordered by a band of 2–3 rows of slightly elongated, lighter colored cells .... 15. *Desmatodon*

g. Leaves not bordered as above .... h

h. Leaves strongly papillose with many of the papillae c-shaped i

h. Leaves smooth; if papillose, papillae not c-shaped .... j

i. Leaves without excurrent costa; if costa excurrent, upper hyaline basal cells with distinct trigones; plant small, usually less than 5 mm tall .... 15. *Desmatodon*

i. Leaves with excurrent costa (may be short); upper hyaline basal cells without distinct trigones; plant taller, 0.5 cm or more tall; if shorter, plants bearing propagula .... 16. *Tortula*

j. Leaf margins in upper half reflexed; if plane, then leaves either torn and broken, or plants growing on trees .... k

j. Leaf margins plane; leaves not torn or broken; plants not growing on trees .... s

k. Costa with a single dorsal stereid band l

k. Costa with two stereid bands .... n

l. Costa ending below the apex, spurred above .... 4. *Husnotiella*

l. Costa excurrent, not spurred above .... m

m. Leaves ovate to oblong-lanceolate; apex acuminate; growing on soil .... 14. *Phascum*

m. Leaves obovate, lingulate or spatulate, ovate-lanceolate to oblong; apices acute, obtuse, emarginate, truncate or blunt; plants on rocks and trees .... 16. *Tortula*

n. Leaf margins 2–3-stratose .... 10. *Didymodon*

n. Leaf margins not bistratose .... o

o. Upper leaf cells not to only weakly papillose .... p

o. Upper leaf cells distinctly papillose .... q

p. Basal leaf-cells hardly different from upper leaf-cells .... 10. *Didymodon*

p. Basal leaf-cells thin-walled, clearly different from upper-leaf cells .... 12. *Barbula*

q. Peristome teeth twisted .... 12. *Barbula*

q. Peristome teeth erect, not twisted .... r

r. Leaves entire throughout .... 10. *Didymodon*

r. Leaves denticulate to strongly dentate at apex .... 11. *Bryoerythrophyllum*

s. At least some of the leaves broadly lingulate .... y

s. Leaves not broadly ligulate .... t

t. Leaves toothed just above the base at the upper margin of the hyaline cells .... 5. *Eucladium*

t. Leaves not as above .... u

u. Costa ending somewhat below apex; plants growing on vertical calcareous rocks .... z

u. Costa percurrent to excurrent; if ending below apex, plants growing on soil v

v. Leaf apex obtuse .... 12. *Barbula*

v. Leaf apex acute .... w

w. Leaves closely imbricate when dry .... 12. *Barbula*

w. Leaves crisped or curled when dry x

x. Leaf cells pluripapillose; the cells of basal ¼ of leaves rectangular, elongated, hyaline; plants yellowish green .... 6. *Trichostomum*

x. Leaf cells bipapillose; the basal ¼ of leaves with few and inconspicuously elongate cells; plants bluish green .... 1. *Anoectangium*

y. Plants with numerous polymorphous gemmae in axils of upper leaves .... 9. *Hyophila*

y. Plants without gemmae .... 17. *Scopelophila*

z. Leaves bistratose in patches; archegonial inflorescences laterial .... 1. *Anoectangium*

z. Leaves not bistratose; archegonial inflorescences terminal .... 3. *Gymnostomum*

1. *Anoectangium* Schwaegr.

Plants tufted, whitish to bluish green; leaves contorted when dry, linear-ligulate to linear-lanceolate, apex obtuse to acute; margins plain, entire; costa ending below apex; upper leaf-cells papillose; basal leaf-cells hyaline and rectangular; archegonial and antheridial inflorescences lateral.

a. Leaves acute, bluish green .... 1. *A. sendtnerianum*
a. Leaves obtuse, whitish .... 1. *A. obtusifolium*

1. *Anoectangium sendtnerianum* B.S.G.

Molendoa sendtneriana (B.S.G.) Limpr.

Rare, Boston Mtns.; on moist calcareous rocks.

This species may be confused with *Trichostomum cylindricum.* Iwatsuki and Sharp (1958) have observed that the latter taxon differs from *A. sendtnerianum* by having 3 or more papillae per cell and large, rectangular, elongated, and hyaline cells in the basal quarter of the leaf.

2. *Anoectangium obtusifolium* (Broth. & Par. *ex* Card.) Grout

Rare, Boston Mtns.; on sandstone. May grow mixed with *Eucladium verticillatum.*

2. *Weissia* Hedw.

Small, densely tufted, yellowish to bluish green plants; leaves narrowly lanceolate, costate; margins strongly involute to plane above, erect-spreading when moist, crispate when dry; upper leaf-cells strongly papillose; capsule immersed or exserted; operculum functional to non-functional; peristome absent or of 16 teeth inserted below the mouth of the capsule.

a. Capsules immersed in perichaetial leaves .... b
a. Capsules exserted beyond perichaetial leaves c
  b. Setae often clustered; leaf margins both plane and involute above .... 2. *W. ludoviciana*
  b. Setae solitary; leaf margins strongly involute above .... 1. *W. muehlenbergiana*
c. Costa 70 μ or more in width at base of leaf .... 4. *W. tortilis*
c. Costa less than 60 μ in width at base of leaf .... 3. *W. controversa*

1. *Weissia muehlenbergiana* (Sw.) Reese & Lemmon (1965).

Astomum muehlenbergianum (Sw.) Grout

Common throughout the Interior Highlands; on open soil of fields, road banks, paths, and lawns. Sporangia produced in late winter and early spring.

2. *Weissia ludoviciana* (Sull.) Reese & Lemmon (1965).

Astomum ludovicianum (Sull.) Sull.

Very rare, Arkansas River Valley; on open soil.

3. *Weissia controversa* Hedw.

Weissia viridula Hedw.

Plants gregarious, small; leaves lanceolate; costate; cells very papillose above; leaf margins entire, strongly involute above; capsule cylindrical, smooth or plicate when dry, exserted on a yellow seta; operculum functional; peristome of 16 teeth.

Two varieties are represented in the Interior Highlands and may be separated as follows:

a. Seta 3–8 mm long .... 3a. *W. controversa* var. *controversa*
a. Seta 10–15 mm long .... 3b. *W. controversa* var. *longiseta*

3a. *Weissia controversa* var. *controversa*

Very common throughout the Interior Highlands; on soil and rocks of open areas such as lawns, pastures, roadways.

3b. *Weissia controversa* var. *longiseta* (Lesq. & James) Crum, Steere & Anderson (1964).

Weissia viridula Hedw. var. *australis* Aust.

Reported from eastern Salem Plateau in Franklin, St. Louis, and Ste. Genevieve Counties, Missouri, by Gier (1955*a*:38).

4. *Weissia tortilis* (Schwaegr.) C. Müll.

Rare, known only from a collection by Moore (1965) from Conway Co., Arkansas, in the eastern Boston Mtns.

When sterile this species may be confused with *Trichostomum jamaicensis.* However, the linear-lanceolate leaves with oblong-ovate base easily separate this species from *Weissia tortilis.* May be a tetraploid of *W. controversa* (L. E. Anderson, personal communication).

3. *Gymnostomum* Nees, Hornsch. & Sturm

Densely tufted mosses, usually growing on moist, vertical limestone, often forming dense cushions several centimeters deep, dull to bright green in color; leaves erect-spreading when moist, little contorted to suppressed, incurved, and contorted when dry, oblong- to linear-lanceolate, keeled, apex acutely obtuse to acute; costa strong, vanishing below apex; upper leaf-cells papillose; seta long exserted, erect; capsule erect, symmetric, oval to oblong, glossy at maturity; operculum long rostrate; peristome absent.

a. One or both margins recurved below; leaves little contorted when dry; upper leaf-cells clear, 12–15 μ wide; operculum usually remaining attached to exserted columella .... 2. *G. recurvirostrum*
a. Leaf margins not recurved; leaves usually crispate when dry; upper leaf-cells obscure, 7–12 μ wide, densely papillose; operculum not persistent .... 1. *G. aeruginosum*

1. *Gymnostomum aeruginosum* Sm.

Common, Boston Mtns., Ozark Hills, Prairie Plains, Salem and Springfield Plateaus; on vertical, moist limestone and sandstone especially at bases of bluffs.

Confusion between this species and *Gymnostomum calcareum* Nees & Hornsch. is, as noted by Crum and Anderson (1956), quite common in this country. These authors have come to the conclusion that nearly all specimens called *G. calcareum* in the United States are forms of *G. aeruginosum.* Only from California have they seen specimens which they felt could essentially be assigned to *G. calcareum*. There is apparently a taxonomic problem involved here which can only be resolved by a careful world-wide monographic study. Until this is done a conservative position is followed, and all the material from the Interior Highlands is assigned to *G. aeruginosum*.

2. *Gymnostomum recurvirostrum* Hedw.

a. Papillae of leaf-cells comparatively few; stems not papillose .... 2a. *G. recurvirostrum* var. *recurvirostrum*
a. Leaf-cells densely papillose; stems papillose .... 2b. *G. recurvirostrum* var. *latifolium*

2a. *Gymnostomum recurvirostrum* var. *recurvirostrum*

Common, Boston Mtns., Salem and Springfield Plateaus; on moist, vertical limestone and dolomite. Occasionally on sandstone.

2b. *Gymnostomum recurvirostrum* var. *latifolium* (Zett.) Flow. *ex* Crum

Gymnostomum recurvirostrum Hedw. var. *scabrum* (Lindb.) Grout

Uncommon, Boston Mtns., Salem Plateau; on limestone and occasionally on sandstone.

4. *Husnotiella* Card.

1. *Husnotiella revoluta* Card. var. *palmeri* (Card.) Bartr.

Plants small, 4–6 mm tall, in dense, light green tufts; leaves erect spreading when moist, contorted when dry, linear-lingulate, acute to apiculate; margins entire, revolute above; costa strong, ending abruptly below the apex, wider and spurred on dorsal surface; leaf-cells small, 7–10 μ in diameter, obscure, rounded and more or less papillose.

Rare, known only from a collection made by W. B. Drew (*67*) from the Salem Plateau at Alley Spring State Park, Shannon Co., Missouri, on soil of limestone ledge.

May be confused with *Didymodon tophaceus* from which it may be distinguished by the possession of a spurred costa and absence of strongly decurrent leaves.

5. *Eucladium* B.S.G.

1. *Eucladium verticillatum* (Brid.) B.S.G.

Plants in dense, light to dark green tufts, 1–3 cm tall, frequently white below due to encrustations of lime; leaves appressed to spreading when dry, erect to widely spreading when moist, linear-lanceolate to linear-subulate, acute; costa strong, usually excurrent; margins plane, toothed at base just above hyaline basal cells; upper leaf-cells clear, papillose, rectangular to quadrate, thick-walled; lower leaf-cells hyaline and larger than upper cells.

Common, Boston Mtns., Ozark Hills, Salem and Springfield Plateaus; on vertical to underside of overhanging limestone (rarely sandstone) subject to seepage.

6. *Trichostomum* Bruch

Plants small to moderate in size, 5–30 mm tall, yellowish green to dark green, in loose to dense tufts; leaves linear-lanceolate, to 8 mm long, strongly contorted when dry, involute to nearly plane above; costa strong, usually excurrent; leaf-cells small and densely papillose; capsule cylindrical, exserted upon an erect seta 8–15 mm long; peristome teeth 16, inserted at the mouth of the capsule.

a. Margin of upper leaf plane or involute only near apex .... b
a. Margin of upper leaf strongly involute .... 1. *T. jamaicense*
  b. Leaves distinctly curled from tip when dry, very narrowly linear, plane to apex .... 3. *T. mollissimum*
  b. Leaves twisted but not curled from tip when dry, linear-lanceolate to ligulate, often involute near apex .... 2. *T. tenuirostre*

1. *Trichostomum jamaicense* (Mitt.) Jaeg. & Sauerb.

Weissia jamaicense (Mitt.) Grout

Uncommon, Boston Mtns., Salem and Springfield Plateaus; on limestone, dolomite, felsite and sandstone.

When sterile this species may be confused with *Weissia controversa* and *W. tortilis*. Generally plants of *W. controversa* are shorter, their leaves are tightly crispate, and the costa is less than 50 μ wide near the base. In contrast, plants of *W. jamaicensis* are taller, and their leaves are more loosely crispate with the leaves curled mainly at the tips. The costa usually exceeds 65 μ in width near the base.

2. *Trichostomum tenuirostre* (Hook. & Tayl.) Lindb.

Trichostomum cylindricum (Bruch) C. Müll.

Rare, Boston Mtns., Salem Plateau; on rocks. Reported from Taney County, Missouri, by Gier (1955*a*: 38) and Missouri (no County given) by Crum and Anderson (1958). This latter paper should be consulted for an excellent discussion of the variability of this taxon.

3. *Trichostomum mollissimum* (Broth. *ex* Bartr.) Crum

Tortella mollissima Broth. *ex* Bartr.

Rare, SW-Salem Plateau in Douglas County, Missouri; on sandy, vertical shaded dolomite, growing with *Myurella sibirica*.

The status of this taxon leaves much to be desired. L. E. Anderson (personal communication) believes that the plants from Douglas County are *T. tenuirostre*.

7. *Tortella* (C. Müll.) Limpr.

1. *Tortella humilis* (Hedw.) Jenn.

Plants in erect, loose to dense yellowish green to green tufts; leaves crisped when dry, oblong-lanceolate, apex acute to obtuse; margins plane, entire, sometimes undulate; costa shortly excurrent in a mucro-point; upper leaf-cells small, densely papillose; lower leaf-cells hyaline, rectangular, extending obliquely higher up the margin than the costa, abruptly becoming small and chlorophyllose; capsule oblong, exserted on a seta about 1.5 cm long; peristome teeth 32, twisted 2–3 times.

Very common throughout the Interior Highlands; on decaying wood, bases of trees, and soil; occasionally on rocks.

Excluded species:

Tortella tortuosa (Hedw.) Limpr.—Reports from Taney County, Missouri, by Gier (1955*a*: 38) are based upon collection by H. S. Conard (Nov. 30, 1940) and Paul Rissens (Aug. 29, 1931) deposited in the Herbarium of the State University of Iowa. Both of these collections have been examined and are *Tortella humilis.*

8. *Pleurochaete* Lindb.

1. *Pleurochaete squarrosa* (Brid.) Lindb.

Plants in loose tufts, 1–10 cm tall, often decumbent, yellow-green in color; leaves flexuose when dry, squarrose when moist, lanceolate-acuminate from a wide, sheathing base; margins finely serrate, undulate; costa strong, excurrent to percurrent; upper leaf-cells quadrate, papillose; marginal basal cells rectangular, hyaline for 5–7 cells in towards the costa below, decreasing to 1–2 cells above; median basal cells rectangular, colored; plants usually not fruiting.

Common, Boston Mtns., Salem and Springfield Plateaus; on soil in glades when limestone or sandstone rocks are close to the surface. Usually forms very loose mat-like growths, especially beneath cedar trees.

9. *Hyophila* Brid.

1. *Hyophila involuta* (Hook.) Jaeg. & Sauerb.

Hyophila tortula (Schwaegr.) Hampe

Plants in dark green tufts; leaves inrolled and curled when dry, lingulate, obtuse, nearly entire to coarsely serrate above; margins plane above, recurved below; costa strong, ending below apex to slightly excurrent; upper leaf-cells quadrate, slightly papillose to smooth; basal leaf-cells rectangular; polymorphic gemmae in axils of upper leaves; sporophytes absent.

Common throughout the Interior Highlands; on shaded rocks in and along edges of creeks and streams.

10. *Didymodon* Hedw.

Plants in short to tall, light to dark green tufts; leaves ovate-lanceolate to lingulate from a broader base, twisted to only incurved when dry, erect-spreading when moist, apices acute to obtuse; margins entire, revolute to plane above, recurved below, one to 2–3 stratose; costa strong, percurrent to sub-percurrent, both dorsal and ventral rows of stereids present in cross section; upper leaf-cells small, round, smooth or papillose, slightly elongated at base; capsule erect, cylindric, exserted upon a short, 1–1.5 cm long, red seta; peristome teeth 16, variously divided, straight to slightly twisted.

a. Margin of leaves 2–3 stratose in upper part .... 1. *D. rigidulus*
a. Margin of leaves unistratose, recurved in upper part .... b
  b. Leaves strongly decurrent; leaf-cells papillose .... 2. *D. tophaceus*
  b. Leaves not strongly decurrent; leaf-cells smooth to only weakly papillose .... 3. *D. trifarius*

1. *Didymodon rigidulus* Hedw.

Rare, known only from the southern Springfield Plateau from a collection by R. R. Ireland, Jr. (*3520*, US) from Roaring River State Park, Barry Co., Missouri; on limestone rock outcrop.

2. *Didymodon tophaceus* (Brid.) Lisa

Uncommon, Salem and Springfield Plateaus; on moist, shaded calcareous rocks, especially where seepage occurs, rarely on soil.

3. *Didymodon trifarius* (Hedw.) Röhl.

Reported from the Salem Plateau in Camden and Dallus Counties, Missouri, by Gier (1955*a*: 34).

11. *Bryoerythrophyllum* Chen

1. *Bryoerythrophyllum recurvirostrum* (Hedw.) Chen

Didymodon recurvirostris (Hedw.) Jenn.

Plants in loose green tufts, tending to be reddish brown below; leaves erect-spreading when moist, crisped, flexuous, and curled when dry, lanceolate from a broad base; margins revolute, dentate (often obscurely so) at apex; costa strong, excurrent in a pellucid apiculus; upper cells quadrate, densely papillose; lower cells rectangular, hyaline to reddish brown; capsule oblong-cylindric upon an erect, reddish seta; peristome teeth 16.

Uncommon, Boston Mtns., Salem and Springfield Plateaus; usually on calcareous rocks, occasionally on soil.

12. *Barbula* Hedw.

Plants small to moderate in size, 1–20 mm tall, in dense to loose tufts, dark green to yellowish green; leaves linear-lanceolate to ovate-lingulate, contorted or crisped when dry; margins entire, plane or revolute; costa strong, ending just below the apex to excurrent; upper leaf-cells small, thick-walled, papillose; basal cells larger, thin-walled and smooth; propagula often present; capsule exserted, cylindric; peristome teeth divided into 32 thread-like segments, usually strongly twisted.

a. Leaves oblong, lingulate or ligulate .... b
a. Leaves lanceolate or subulate, tapering gradually from an ovate base .... e
  b. Seta yellow; perichaetial leaves convolute .... 1. *B. convoluta*
  b. Seta red; perichaetial leaves not convolute c

c. Upper leaf-cells smooth to slightly papillose .... 4. *B. ehrenbergii*
c. Upper leaf-cells densely papillose .... d
  d. Propagula present .... 3. *B. cruegeri*
  d. Propagula absent .... 2. *B. unguiculata*
e. Cells of upper surface of costa linear .... 5. *B. fallax*
e. Cells of upper surface of costa quadrate .... 6. *B. acuta*

1. *Barbula convoluta* Hedw.

Uncommon, Boston Mtns., Salem Plateau; on shaded to open soil.

2. *Barbula unguiculata* Hedw.

Common, throughout the Interior Highlands; on calcareous soil and rock ledges, old fields, waste places, edges of creek and streams.

3. *Barbula cruegeri* Sond. *ex* C. Müll.

Common, Ouachita Mtns., Ozark Hills, Prairie Plains, Salem and Springfield Plateaus; on moist, calcareous rocks and rock crevices.

The status of this taxon in relation to *Barbula unguiculata* is confused especially in the Interior Highlands where both taxa occur. Gier (1955*a*: 32) calls attention to this problem and suggests controlled experiments might help resolve this problem.

4. *Barbula ehrenbergii* (Lor.) Fleisch.

Uncommon, Salem Plateau; on moist, shaded calcareous rocks. Plants are often encrusted with lime.

5. *Barbula fallax* Hedw.

Uncommon, Salem and Springfield Plateaus; on soil of crevices and ledges of limestone.

6. *Barbula acuta* (Brid.) Brid.

Two varieties are encountered in the Interior Highlands and may be separated as follows:

a. Plants in short dense tufts .... 6a. *B. acuta* var. *acuta*
a. Plants in loose, elongate tufts .... 6b. *B. acuta* var. *bescherellei*

6a. *Barbula acuta* var. *acuta*

Reported from the eastern Salem Plateau in St. Louis County, Missouri, by Gier (1955*a*: 32).

6b. *Barbula acuta* var. *bescherellei* (Sauerb. *ex* Jaeg. & Sauerb.) Crum (1969).

Rare, Springfield Plateau; on flat exposed limestone along dry creek bed in small ravine *ca.* 4 miles south of Springfield, on Mo. Hwy. 160.

13. *Acaulon* C. Müll.

1. ***Acaulon muticum*** (Hedw.) C. Müll. var. ***rufescens*** (Jaeg. & Sauerb.) Crum (1969).

Acaulon rufescens Jaeg. & Sauerb.

Plants sub-globose, bulbiform, small, less than 2 mm tall, yellowish green; leaves broadly ovate, concave; margins plane below, sharply serrate and reflexed above; costa strong, percurrent to excurrent; lower cells smooth, hyaline, rectangular, to 100 μ long; upper cells smooth, smaller, rhomboid-hexagonal; capsule erect, immersed, globose; spores smooth, 40–50 μ in diameter.

Rare, Boston Mtns., Ozark Hills, eastern Salem Plateau, Prairie Plains; on sandy soil.

14. *Phascum* Hedw.

1. ***Phascum cuspidatum*** Hedw.

Plants in dense light to yellow-green tufts; upper leaves largest, ovate to oblong-lanceolate, acuminate; margins entire and revolute in the middle; costa short to long excurrent; lower cells rectangular and hyaline below; upper cells quadrate to hexagonal, papillose; capsule ovoid-globose, immersed to slightly emergent, cleistocarpous.

Two varieties are present in the Interior Highlands and may be separated as follows:

a. Costa excurrent .... 1a. *P. cuspidatum* var. *cuspidatum*
a. Costa long excurrent .... 1b. *P. cuspidatum* var. *americanum*

1a. ***Phascum cuspidatum*** var. ***cuspidatum***

Uncommon Prairie Plains, Springfield Plateau; on soil, often sandy, of old fields, pastures, and waste places.

1b. ***Phascum cuspidatum*** var. ***americanum*** Ren. & Card. *ex* Ren. & Thér.

Uncommon, Salem and Springfield Plateaus; habitats similar to var. *cuspidatum.*

15. *Desmatodon* Brid.

Plants small, usually less than 6 mm tall, in compact to loose, yellowish to dark green tufts; leaves closely appressed, often contorted when dry, obovate, oblong-lanceolate to oblong-lingulate, apex obtuse to acute; margins entire, plane to revolute nearly to apex; costa strong, sub-percurrent to excurrent in a smooth hair-point; upper cells irregularly quadrate, densely papillose with many c-shaped papillae; lower cells rectangular to elongate-hexagonal, smooth, pale; capsule oblong to cylindric, exserted upon an erect seta; peristome teeth 16, cleft to base, at times poorly developed.

a. Leaves bordered by a band of lighter-colored cells .... 1. *D. porteri*
a. Leaves not bordered .... b
  b. Upper leaves awned or hair-pointed .... 2. *D. plinthobius*
  b. Upper leaves not awned or hair-pointed .... 3. *D. obtusifolius*

1. *Desmatodon porteri* James *ex* Aust.

Uncommon, Boston Mtns., Ozark Hills, Salem and Springfield Plateaus; on dolomite and limestone.

2. *Desmatodon plinthobius* Sull. & Lesq. *ex* Sull.

Common, Boston and Ouachita Mtns., Prairie Plains, Salem and Springfield Plateaus; on limestone, dolomite, and sandstone.

3. *Desmatodon obtusifolius* (Schwaegr.) Schimp.

Common throughout the Interior Highlands; on sandy soil and sandstone, rarely dolomite and limestone.

16. *Tortula* Hedw.

Plants small to large, in dense to loose mats or rocks, soil or trees; leaves oblanceolate, obovate, spatulate, elongate-ligulate to elongate-spatulate, often forming a crowded rosette near the stem apex, twisted and appressed when dry, widely spreading when moist, apex obtuse, rounded, truncate or emarginate; margins plane to revolute; costa strong, excurrent as an awn; upper cells small, strongly papillose, basal cells much larger, smooth, hyaline, often appearing suddenly differentiated on each side of costa; brood-leaves (propagula) often present on surface of leaf or in the upper leaf axils.

a. Costate brood-leaves found in axils of upper stem leaves; upper leaves often torn and broken in various ways; costa shortly excurrent .... 2. *T. fragilis*

a. Plants not possessing the above combination of characteristics .... b

b. Ecostate brood-leaves present in axils of upper leaves or on upper side of leaf costa c

b. Brood-leaves absent .... d

c. Brood-leaves borne in axils of leaves at apex of stem .... 4. *T. pagorum*

c. Brood-leaves borne on upper surface of leaves .... 3. *T. papillosa*

d. Awn smooth .... 1. *T. muralis*

d. Awn sharply serrate .... 5. *T. ruralis*

1. *Tortula muralis* Hedw.

Reported from the Ouachita Mtns., McCurtain Co., Oklahoma, by Sharp (1930: 49).

2. *Tortula fragilis* Tayl.

Rare, Southwestern Springfield Plateau; on dry, vertical south-facing sandstone. Known only from Cherokee Co., Oklahoma.

3. *Tortula papillosa* Wils. *ex* Spruce

Rare, southern Springfield Plateau; on oak and cedar; probably also occurs on other trees.

4. *Tortula pagorum* (Milde.) De Not.

Common throughout the Interior Highlands; mainly on trees, but occasionally vertical calcareous and sandstone rocks.

5. *Tortula ruralis* (Hedw.) Gaertn., Meyer & Schreb.

Uncommon, Springfield Plateau; on open calcareous soil and rocks, especially along bluffs.

17. *Scopelophila* (Mitt.) Lindb.

1. *Scopelophila ligulata* (Spruce) Spruce

Merceya ligulata (Spruce) Schimp.

Plants in loose to compact tufts; leaves light to bright green in color above, often reddish to brown below; stems radiculose; leaves broadly spatulate to ligulate, broadest near apex, bluntly pointed on obtuse; margins entire and plane (may be slightly recurved below); costa ending in the apex; upper leaf-cells quadrate, oblong, to irregular; basal cells larger, thin-walled and often inflated, marginal basal cells narrower.

Rare, Ouachita Mtns., Ozark Hills; on sandy soil.

Considerable variation in morphology related to moisture has been reported by Noguchi (1956) and confirmed by Zander (1967). Both the loosely pulvinate, flaccid "hydric" form and the more densely pulvinate "montane" form occur in the Interior Highlands.

12. GRIMMIACEAE

1. *Grimmia* Hedw.

Plants in green to blackish or brownish green cushions, mats, or dense tufts, often appearing whitish because of hyaline leaf apices; leaves crowded, usually imbricate when dry, erect-ascending, spreading, or recurved when moist, lanceolate, often from an oblong to ovate base, plane, concave, carinate, or caniculate; margins plane or revolute; costa sub-percurrent to excurrent, flat or terete in cross section, often terminating in a hyaline, smooth to spinulose hair-point; upper leaf-cells rounded-quadrate, unistratose to bistratose, papillose; lower leaf-cells smooth, quadrate to rectangular; cell walls thin and smooth to thick and sinuose; capsule symmetric, immersed to exserted upon a straight to arcuate seta; peristome single, composed of 16 perforate or cleft teeth; calyptra cucullate or mitrate; with rare exceptions all taxa grow on rocks.

A difficult genus in need of critical revision. The following key is based upon a key to North American species of *Grimmia* by Sayre (1952).

a. Upper leaves (excluding perichaetial) without hair-points .... b
a. Upper leaves with hair-points (may be inconspicuous or absent in some leaves) .... e
  b. Apex of some or all of the upper leaves obtuse or rounded .... 2. *G. alpicola*
  b. Apex of upper leaves acuminate or acute c
c. Leaves less than 1.5 mm long .... 1. *G. apocarpa*
c. Leaves 1.5–3.0 mm long .... d
  d. Peristome teeth red, pointed; capsule ovate; most leaves ovate-lanceolate .... 2. *G. alpicola*
  d. Peristome teeth pale, truncated; capsule oblong; most leaves linear-lanceolate .... 1. *G. apocarpa*
e. Margins of leaves inrolled in some part of the leaf; apex often drawn out to a channeled acumen .... f

e. Margin of leaves plane or erect, or one or both recurved; apex not channeled .... g
  f. Seta curved; costa terete, hair-point spinose .... 11. *G. olneyi*
  f. Seta straight; costa mostly flat, hair-point nearly smooth .... 9. *G. ovalis*
g. Leaves broader above the middle or oblong, abruptly acuminate; hair-point 1½ times the length of upper leaves .... 3. *G. wrightii*
g. Leaves broader below the middle, gradually acuminate or acute; hair-point shorter .... h
  h. Leaf-cells mostly unistatose, large and clear .... 4. *G. rauei*
  h. Leaf-cells mostly bistratose, small and obscure i
i. Costa flat; leaf apex usually acute; capsule exserted .... 5. *G. laevigata*
i. Costa terete; apex usually acuminate; capsule immersed .... j
  j. Leaves almost lingulate, ending in a long denticulate hair-point to ¾ the length of leaf .... 10. *G. pulvinata*
  j. Leaves lanceolate to ovate-lanceolate, hair-point shorter, less than ⅓ the length of leaf .... k
k. Most mature leaves 2 mm long or longer l
k. Most mature leaves 1–1.5 mm long .... n
  l. Both margins equally and distinctly revolute .... m
  l. Margins plane or only one revolute and the other slightly recurved below .. 8. *G. arizonae*
m. Leaves narrowly acuminate from ovate base; costa forming about ¼ of the leaf base; basal leaf-cells rectangular, thick-walled and sinuose; alar cells hyaline .... 7. *G. pilifera*
m. Leaves lanceolate, some acute; lower leaf-cells 2:1; alar cells not hyaline .. 1. *G. apocarpa*
  n. Plants not filiform; alar cells not differentiated; most leaves with both margins revolute .... 1. *G. apocarpa*
  n. Plants filiform; alar cells differentiated, usually hyaline; some or all leaves with one revolute margin and the other incurved .... 6. *G. teretinervis*

1. *Grimmia apocarpa* Hedw.

Schistidium apocarpum (Hedw.) B.S.G.

This is a highly polymorphic taxon, and there is a great deal of confusion regarding not only the status of subspecific taxa but with the next taxon. Varieties have been described that may be local or general environmental modifications. Nyholm (1956: 145) has suggested what is perhaps the only answer to this perplexing group, cultivation experiments. Five varieties are known, reported from, or may occur in the Interior Highlands and can be separated by the following differences.

a. Upper leaves (excluding the perichaetial) not piliferous .... b
a. Upper leaves piliferous c
  b. Leaves under 1.5 mm long .... 1b. *G. apocarpa* var. *dupretii*
  b. Leaves 1.5–3 mm long .... 1e. *G. apocarpa* var. *obscuriviridis*
c. Mature leaves 2 mm long or longer .... 1c. *G. apocarpa* var. *stricta*
c. Mature leaves 1–1.5 mm long .... d
  d. Plants dark green or black; capsule oblong .... 1a. *G. apocarpa* var. *apocarpa*
  d. Plants bright green; capsule globose .... 1d. *G. apocarpa* var. *conferta*

1a. *Grimmia apocarpa* var. *apocarpa*

Common throughout the Interior Highlands; on dry, exposed rocks, usually on but not limited to calcareous types.

1b. *Grimmia apocarpa* var. *dupretii* (Thér.) Sayre

Rare, Springfield Plateau; on flat exposed limestone.

Known only from Roaring River State Park, Barry Co., Missouri. This variety has recently been placed in the species *Grimmia alpicola* by Crum (1971: 168).

1c. *Grimmia apocarpa* var. *stricta* (Turn.) Hook. & Tayl.

Grimmia apocarpa Hedw. var. *gracilis* (Schleich.) Web. & Mohr

Reported from Shannon Co., Missouri, by Gier (1955*a*: 35).

1d. *Grimmia apocarpa* var. *conferta* (Funck) Spreng.

Uncommon, Boston Mtns.; on rocks.

1e. *Grimmia apocarpa* var. *obscuriviridis* Crum

Not known from Interior Highlands, but Sayre (personal communication) believes that it should be.

2. *Grimmia alpicola* Sw. *ex* Hedw.

Grimmia apocarpa var. *alpicola* (Hedw.) Hartm.
Schistidium alpicola (Hedw.) Limpr.

Common throughout the Interior Highlands; on exposed rocks, especially limestone, along edges of creeks and gullies.

May be confused with the preceding taxa. However, when fertile they may be separated by the shape of the capsule. *Grimmia alpicola* has a more or less globular capsule, while the capsule of *G. apocarpa* is more distinctly ovoid to ellipsoid.

3. *Grimmia wrightii* (Sull.) Aust.

Reported from Missouri by Sayre (personal communication).

4. *Grimmia raui* Aust.

Reported from Missouri by Sayre (personal communication).

5. *Grimmia laevigata* (Brid.) Brid.

Very common throughout Interior Highlands; as a pioneer on exposed rocks. Often locally abundant.

May be recognized by its decurrent, flat, spinulose, hyaline apex.

6. *Grimmia teretinervis* Limpr.

Rare, Springfield Plateau; on open limestone.

Known only from Greene Co., Missouri, on bluffs above James River just below Lake Springfield Dam.

7. *Grimmia pilifera* P. Beauv.

Common throughout the Interior Highlands; as a pioneer species on exposed to shaded rocks of all types, rarely on decaying wood. Often locally abundant.

8. *Grimmia arizonae* Ren. & Card.

Sayre (personal communication) reports that this species occurs in Oklahoma. It may, therefore, be present in the Interior Highlands.

9. *Grimmia ovalis* (Hedw.) Lindb.

Rare, Salem Plateau; on rocks.

10. *Grimmia pulvinata* (Hedw.) Sm. *ex* Sm. & Sowerby

Uncommon, Ouachita Mtns., Prairie Plains, Springfield Plateau; on dry, open flat sandstone exposures and occasionally on brick walls. Apparently most frequent in the Prairie-border regions of the Interior Highlands.

11. *Grimmia olneyi* Sull.

Rare, St. Francois Mtns.; on non-calcareous rocks in exposed sunny places.

Excluded taxa:
Rhacomitrium aciculare (Hedw.) Brid.—The collection from McCurtain County by Sharp (1930) is *Grimmia alpicola.*

13. Ephemeraceae

1. *Ephemerum* Hampe

Small inconspicuous plants, stems almost absent, growing from persistent protonema; leaves costate or ecostate, lanceolate; margins strongly toothed to serrate; capsule cleistocarpous, ovoid, apiculate; calyptra campanulate, 0.2 mm or more in over-all length.

The following treatment is based upon a study of this family by Bryan and Anderson (1957).

a. Cells in the middle third of leaf lamina smooth, in distinct diagonal rows from costa to margin .... 3. *E. cohaerens*
a. Cells of the leaf lamina papillose above, usually conspicuously so; if smooth, not in diagonal rows .... b
  b. Spines of upper leaves mostly recurved at an angle of 45° or more; leaves usually narrowly linear-lanceolate; lamina papillose or smooth above; leaf-cells at middle of leaf about 4–8:1 .... 2. *E. spinulosum*
  b. Upper leaves almost entire to strongly toothed; most of the teeth extending at an angle of less than 45°; lamina conspicuously papillose above; leaf-cells at middle of leaf less than 4:1 c
c. Upper leaves lanceolate, without shoulder .... 1a. *E. crassinervium* var. *crassinervium*
c. Upper leaves broadly lanceolate-subulate, with slight to prominent shoulder .... 1b. *E. crassinervium* var. *texanum*

1a. *Ephemerum crassinervium* (Schwaegr.) Hampe var. *crassinervium*

Rare, eastern Salem Plateau; on sandstone. Known only by a single collection from Jefferson Co., Missouri, made by Barkley, Oct. 23, 1936.

The distinguishing characters of this taxon are its long-lanceolate upper leaves that reach 1.5 mm in length and 0.2 mm in maximum width, margins serrate in upper ⅔, dense areolation in upper half, and a strong costa running from base to apex (Bryan & Anderson, 1957).

1b. *Ephemerum crassinervium* var. *texanum* (Grout) Bryan & Anderson.

Reported from Boston Mtns., Conway Co., Arkansas, by Moore (1965).

2. *Ephemerum spinulosum* Bruch & Schimp. *ex* Schimp.

Rare, western Springfield Plateau; on soil, edge of creek. Known only from vicinity of Horse Creek, 2 miles south of Olympia on County Rd. A, Cedar Co., Missouri, *Ireland 3273* (US).

Plants of this taxon may be distinguished from the preceding taxa by the presence of unusually abundant and persistent protonema at the time leafy gametophytes mature (Bryan & Anderson, 1957).

3. *Ephemerum cohaerens* (Hedw.) Hampe

Rare, Salem Plateau; on moist, shaded, sandy soil. Known only from vicinity of Blue Springs, edge of Jack's Fork River, Shannon Co., Sect. 31-32, T. 28 N., R. 6 W., *Redfearn 7736.*

14. FUNARIACEAE

Plants annual, sometimes biennial, in low, light green, loose to clustered tufts, characteristically growing in open areas on bare soil or soil sparcely covered by other plants; stems erect; upper leaves closely clustered, concave, costate, often serrate above; leaf-cells large, parenchymatous, *ca.* 20–30 μ in width, rhombic- to oblong-hexagonal to rectangular, lax, border weakly defined; capsules immersed to exserted on long setae, globose to pyriform, symmetric to strongly inclined and asymmetric; peristome when present composed of an outer row of 16 reddish to brownish red teeth and an inner row of 16 yellowish, often rudimentary segments.

a. Capsules immersed; peristome absent .... b
a. Capsules emergent to exserted; peristome present or absent c
  b. Capsule functionally inoperculate; exothecial cells not strongly collenchymatous .... 1. *Physcomitriella*
  b. Capsule operculate, dehiscing along the equatorial line; exothecial cells strongly collenchymatous .... 2. *Aphagnorhegma*
c. Capsule unsymmetric and curved .... 5. *Funaria*
c. Capsule symmetric, straight .... d
  d. Seta short, about length of capsule; calyptra 4-angled .... 4. *Pyramidula*
  d. Seta longer than capsule; calyptra symmetrically rostrate .... 3. *Physcomitrium*

1. *Physcomitriella* B.S.G.

1. *Physcomitriella patens* (Hedw.) B.S.G.

Aphanorhegma patens (Hedw.) Lindb.

Small, inconspicuous plants with immersed, inoperculate capsules; leaves erect-spreading, lanceolate, costate; margins serrate; median leaf-cells oblong-rectangular, 3–4 : 1; marginal cells longer.

Rare, Salem Plateau; on open soil. Matures in fall and, because of small size, commonly overlooked.

This taxon is closely related to the next from which it may be separated by its inoperculate capsules with exothecial cells not conspicuously collenchymatous. Hybrids with *Physcomitrium pyriforme* have been reported by Bryan (1957).

2. *Aphanorhegma* Sull.

1. *Aphanorhegma serratum* (Hook. *f.* & Wils. *ex* Drumm.) Sull.

Similar to *Physcomitriella patens* except that capsule is dehiscent along equatorial line and exothecial cells are strongly collenchymatous.

Uncommon, Salem and Springfield Plateaus; on open to shaded moist soil. Plants with mature capsules may be found from late fall to early winter.

3. *Physcomitrium* (Brid.) Fürnr.

1. *Physcomitrium pyriforme* (Brid.) De Not.

Small, light green, tufted plants; leaves oblong-oblanceolate to oblong-lanceolate, contorted when dry, spreading when moist; margins serrate above; capsules erect, globose-pyriform when fresh, turbinate and constricted below mouth when dry, exserted on setae 5–15 mm long.

Very common through the Interior Highlands; on soil in pastures, lawns, and waste places.

Physcomitrium collenchymatum Gier has been reported from Clay County, Missouri, just north of the Missouri River (Gier, 1955*b*: 330). This taxon may be collected in the Interior Highlands and may be distinguished from *P. pyriforme* by its smaller size and the extremely flared condition of the capsule when dry and empty (Crum & Anderson, 1964).

4. *Pyramidula* Brid.

1. *Pyramidula tetragona* (Brid.) Brid.

Small, loosely tufted, short-stemmed plants; capsule erect, symmetric, globose-pyriform, barely exserted; calyptra 4-angled, entirely covering the capsule.

Rare, southwestern edge of Interior Highlands; on sandstone. Known only from Muskogee Co., Oklahoma, from a collection reported by Little (1936: 12).

5. *Funaria* Hedw.

Plants in loose to dense tufts, upper leaves often forming bud-like clusters; leaves entire or serrate; setae long; capsule with conspicuous neck, elongated-pyriform, strongly unsymmetric to arcuate; annulus present or absent; peristome in two rows of 16 teeth each, outer row reddish to brownish red and somewhat twisted to right, inner row yellowish, often rudimentary.

a. Annulus present, conspicuous .... b
a. Annulus absent .... d
  b. Segments of inner peristome obtuse, less than ½ length of outer teeth; spores 20–30 μ in diameter .... 2. *F. flavicans*
  b. Segments of inner peristome lanceolate, slenderly pointed, at least ¾ length of outer teeth; spores 12–18 μ in diameter c
c. Capsules horizontal to pendent, turgid, strongly arcuate .... 1a. *F. hygrometrica* var. *hygrometrica*
c. Capsule slender, merely inclined, less arcuate .... 1b. *F. hygrometrica* var. *calvescens*
  d. Leaves entire, costa excurrent .... 3. *F. americana*
  d. Leaves serrate, costa ending below apex in most leaves .... 4. *F. serrata*

1a. *Funaria hygrometrica* Hedw. var. *hygrometrica*

Common throughout Interior Highlands; on bare soil of waste places, limestone glades, around areas of recently burned trash.

1b. *Funaria hygrometrica* var. *calvescens* (Schwaegr.) Mont.

Rare, eastern Salem Plateau; on moist soil.

2. *Funaria flavicans* Michx.

Common throughout Interior Highlands; on moist, shaded to exposed soil and limestone, piles of ashes, and on rocks along edges of creeks.

3. *Funaria americana* Lindb.

Rare, Springfield Plateau; on bare soil.

4. *Funaria serrata* Brid.

Rare, Boston and Ouachita Mtns.; on moist bare soil.

15. TETRAPHIDACEAE

1. *Tetraphis pellucida* Hedw.

Plants small to medium in size, scattered to tufted, bright green to brownish green; stems erect, simple or sparingly branched; leaves ovate to ovate-lanceolate, apex acute; margins plane, entire; costa ending in apex or below; median leaf-cells isodiametric, rounded-hexagonal, incrassate, capsule erect, symmetrical, ovoid to cylindrical; operculum conic; peristome single, teeth 4; shoots frequently bearing terminal gemmiferous cups, formed of 4–5 broadly cordate bracts, containing lenticular gemmae.

Common, Boston and Ouachita Mtns., Ozark Hills, Prairie Plains, Salem and Springfield Plateaus; on moist shaded sandstone, rarely on soil at bases of sandstone boulders and bluffs.

When sporophytes are present, a peristome composed of only four teeth is distinctive. Sterile forms may be confused with *Mnium stellare*; however, that species has serrate leaf margins.

16. BRYACEAE

Plants in loose to dense tufts, dark green, yellow-green to silvery, often tinged with red; leaves ovate-lanceolate, obovate-spatulate, to narrowly linear-setaceous, frequently larger and crowded into a rosette at the stem apex; margins smooth to serrate, often bordered with elongated cells; costa strong, ending below apex to percurrent or excurrent; cells smooth, thin- to thick-walled, hexagonal, rhomboidal, or linear near the apex; sporophyte terminal; capsule ovate to cylindrical with short or long neck, erect, inclined to pendulous, exserted upon a long seta; peristome double, teeth 16, segments alternating with teeth, often with cilia.

a. Plants whitish-green to silvery in color .... b
a. Plants green, yellow-green, to reddish green c

- b. Plants whitish green, growing in moist habitats; leaves loosely imbricate, lanceolate to linear lanceolate .... 1. *Pohlia*
- b. Plants silvery, growing in drier habitats; leaves closely imbricate, broadly ovate to obovate .... 3. *Bryum*

c. Erect shoots with terminal rosette of large, obovate-spatulate, serrate leaves; shoots rising from stolons .... 4. *Rhodobryum*

c. Plants not as above .... d

- d. Leaves very narrowly linear-setaceous; costa broad and occupying most of the terminal end of leaf .... 2. *Leptobryum*
- d. Leaves wider, ovate, ovate-lanceolate to obovate; costa narrower and not filling the upper part of the leaf .... e

e. Margins serrate in upper ¼ of leaf, if denticulate, upper leaf cells 8–12 : 1 and leaves clearly imbricate on stem; border of elongated cells not well developed; costa sub-percurrent to excurrent .... 1. *Pohlia*

e. Margins entire to only denticulate in upper ¼ of leaf; border of elongate cells often well developed; costa sub-percurrent to excurrent .... 3. *Bryum*

1. *Pohlia* Hedw.

Loosely to densely tufted plants, yellow-green to whitish green in color; leaves closely imbricate to distant on stem, narrowly lanceolate to ovate-lanceolate, denticulate to serrate near apex; costa ending below apex to percurrent; median leaf-cells rhomboidal-linear or rhombic-hexagonal, smooth.

a. Leaves closely imbricate c

a. Leaves distant on stem .... b

- b. Elongate, twisted-vermiform gemmae present .... 1. *P. annotina* var. *loeskei*
- b. Gemmae absent .... 4. *P. wahlenbergii*

c. Leaves denticulate near apex; upper leaf-cells 8–12 : 1; branches filiform .. 2. *P. filiformis*

c. Leaves serrate near apex; upper leaf-cells shorter, 5–7 : 1; branches not filiform .. 3. *P. nutans*

1. *Pohlia annotina* (Hedw.) Lindb. var. *loeskei* Crum, Steere & Anderson

Rare, Springfield Plateau; on moist shaded sandstone or sandy soil, along creeks and streams.

The presence of elongated, twisted-vermiform gemmae distinguishes this taxon from other Pohlias in the Interior Highlands.

2. *Pohlia filiformis* (Dicks.) Andr. var. *filiformis*

Rare, Springfield Plateau of western Missouri; on sandstone outcrops, near Cedar Springs in Cedar County (*Ireland 3462*) and at Lichen Glade in St. Clair County (*Redfearn 27333*).

3. *Pohlia nutans* (Hedw.) Lindb. var. *nutans*

Very common throughout the Interior Highlands; a weedy species growing on rocky soil, rock ledges and crevices, and occasionally around bases of trees. Frequently mixed with other bryophytes.

Forms having three cilia have been given varietal status as *Pohlia nutans* var. *tricilata* (Jenn.) Jenn. by some authors. However, this practice is not followed in this treatment because the three-ciliate forms appear to be randomly dispersed among the two-ciliate forms.

4. *Pohlia wahlenbergii* (Web. & Mohr) Andr.

Common throughout the Interior Highlands; on moist soil and rocks, edges of creeks and streams.

2. *Leptobryum* (B.S.G.) Wils.

1. *Leptobryum pyriforme* (Hedw.) Wils.

Plants in loose to dense, yellow-green tufts; leaves narrowly linear-setaceous; costa broad; capsule cylindrical, inclined to pendent, with pronounced neck, exserted upon a long seta, light to dark brown, lustrous.

Uncommon, Prairie Plains, Salem and Springfield Plateaus; on moist substrates, especially sandstone or sandy soil, occasionally on decaying logs or stumps near water.

Sterile collections may be confused with *Ditrichum* or *Dicranella.* The broad costa and long linear-rectangular to fusiform basal leaf-cells serve to distinguish *L. pyriforme* from these taxa.

3. *Bryum* Hedw.

Plants loose to densely tufted, silvery, yellow to dark or reddish green in color; leaves ovate, obovate, to lanceolate, often distinctly bordered by elongated cells; margins entire to denticulate near apex, plane or recurved; costa ending below apex to strongly excurrent; upper leaf-cells short-rhomboidal to rhomboidal-hexagonal; lower cells rectangular; capsule exserted on a short to long seta, cylindrical, clavate, pyriform to oval, neck often well differentiated, inclined to pendulous.

a.	Plants silvery in color	2. *B. argenteum*
a.	Plant not silvery in color	b
b.	Leaves obtuse, rounded-obtuse, to sub-acute; costa not excurrent	c
b.	Leaves acute to acuminate; costa often excurrent	e
c.	Leaves decurrent	d
c.	Leaves not decurrent	9. *B. mniatum*
d.	Leaf cells thin-walled	12. *B. tortifolium*
d.	Leaf cells thick-walled, at least at corners	7. *B. gemmiparum*
e.	Plants small with regularly to irregularly sphaerical gemmae attached to rhizoids	f
e.	Gemmae not present on rhizoids	g
f.	Rhizoids usually deep violet in color	11. *B. ruderale*
f.	Rhizoids pale yellowish to brownish, but not violet in color	8. *B. klinggraefii*
g.	Costa percurrent to slightly excurrent	h
g.	Costa long-excurrent or upper cells forming a cuspidate apex	i
h.	Leaves to 2.5 mm[4] or more long, strongly bordered; plants often dark reddish purple in color	10. *B. pseudotriquetrum*
h.	Leaves 1 mm or less long, not distinctly bordered	3. *B. bicolor*
i.	Leaves obovate to obovate-spatulate, usually spirally twisted around stem	5. *B. capillare*
i.	Leaves ovate to long-lanceolate, not spirally twisted about stem	j
j.	Inner peristome with rudimentary, imperfectly developed cilia	k
j.	Inner peristome with well developed cilia	l
k.	Inner peristome adherent to outer peristome by transverse ridges	1. *B. angustirete*

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[4] Occasional aquatic forms may have much smaller leaves with the border less well developed.

k. Inner peristome not adherent to outer peristome .... 13. *B. uliginosum*
  l. Inflorescense synoicous; upper leaf-cells 3–5 : 1 .... 6. *B. creberrimum*
  l. Inflorescense dioicous; upper leaf-cells 6–7 : 1 .... 4. *B. caespiticium*

1. *Bryum angustirete* Kindb. *ex* Mac.

Bryum pendulum (Hornsch.) Schimp.

Rare, Salem Plateau; on soil.

Without capsules, separation of this taxon from other taxa of *Bryum* is not possible. However, when capsules are present, the lack of well developed cilia on the inner peristome and the adherence of the inner peristome to the outer by transverse ridges is distinctive.

2. *Bryum argenteum* Hedw.

Two varieties may be encountered in the Interior Highlands and may be separated as follows:

Costa ending below apex .... 2a. *B. argenteum* var. *argenteum*
Costa percurrent to excurrent .... 2b. *B. argenteum* var. *lanatum*

2a. *Bryum argenteum* var. *argenteum*

Common throughout the Interior Highlands; on soil of disturbed habitats, crevices of sidewalks, cedar shingle roofs, rarely bases of trees or on rocks.

2b. *Bryum argenteum* var. *lanatum* (P. Beauv.) Hampe

Reported from Greene and St. Louis Counties, Missouri, by Gier (1955*a*: 32). This variety is not recognized by many authors (Nyholm, 1958: 252).

3. *Bryum bicolor* Dicks.

Uncommon, throughout the Interior Highlands; on soil.

This species is quite small, usually less than 0.5 mm tall, gregarious, and frequently mixed with other mosses. Axillary bulbiform gemmae, when present, are distinctive.

4. *Bryum caespiticium* Hedw.

Uncommon, Salem and Springfield Plateaus; on sterile soil, occasionally on rocks.

Sterile plants are difficult to identify. Various authors have attempted to distinguish this taxon on the basis of leaf border and shape of leaf cells. However, these characters are notoriously variable in *Bryum* and may be misleading rather than definitive.

5. *Bryum capillare* Hedw.

Common, throughout the Interior Highlands; on soil, wooded areas, rocks, ledges, pastures, and waste places. Occasionally abundant in crevices of vertical rock exposures.

The soft, ovate-obovate leaves that are spirally twisted about the stem serve to distinguish this species from other taxa of *Bryum* in the Interior Highlands.

6. *Bryum creberrimum* Tayl.

Bryum cuspidatum (B.S.G.) Schimp.

Common, Salem and Springfield Plateaus; on open to shaded soil and rocks.

Sterile collections are difficult to identify with certainty. When fertile, the synoicous inflorescence, lanceolate leaves with short (3–5:1) upper cells, and excurrent costa, and peristome with well developed cilia are distinctive for this taxon.

7. *Bryum gemmiparum* De Not.

Uncommon, Boston Mtns., Salem and Springfield Plateaus; forming dense cushions on calcareous rocks subject to inundation or seepage.

The calciphile nature of this species combined with its obtuse to sub-acute leaves serve to separate it from all taxa except *Bryum tortifolium*. The latter species may be distinguished by the presence of distinctly rounded leaf apices and thin-walled upper leaf-cells.

8. *Bryum klinggraefii* Schimp. *in* Klinggr.

Apparently rare, eastern Salem Plateau; on bare or disturbed soil, often associated with *Physcomitrium, Bryum ruderale* or *Physcomitriella patens*, on mud at margins of ponds and reservoirs.

Reported by Crundwell and Nyholm (1964: 615) from St. Louis County, Missouri, near Creve Coeur Lake from a collection by N.L.T. Nelson, 1906 (as *Physcomitrium rostellatum* Kindb.)

9. *Bryum miniatum* Lesq.

Rare, St. Francois Mtns.; in crevice of felsite rocks, edge of creek. Known only from Johnson Shut-In State Park, Reynold County, Missouri (*Redfearn 13884*).

The taxonomic status of this species is open to question. It is very similar to and may be conspecific with *Bryum muehlenbeckii* B.S.G.

10. *Bryum pseudotriquetrum* (Hedw.) Gaertn., Meyer & Schreb.

Bryum bimum Schreb.

Very common throughout the Interior Highlands; on soil and rock exposures, particularly abundant in areas subject to seepage, occasionally around bases of trees.

11. *Bryum ruderale* Crundw. & Nyh.

Apparently rare; mixed with *Physcomitrium rostellatum* and *Bryum klinggraefii* (see discussion under latter species).

12. *Bryum tortifolium* Funck *ex* Brid.

Rare, Salem and Springfield Plateaus; on rocks in swiftly flowing creeks.

This species can be confused with *Bryum gemmiparum* (see discussion under that species).

13. *Bryum uliginosum* (Brid.) B.S.G.

Bryum cernum (Hedw.) B.S.G.

Rare, eastern Salem Plateau; on rocky soil of wooded slopes.

4. *Rhodobryum* (Schimp.) Hampe

1. *Rhodobryum roseum* (Hedw.) Limpr.

Large plants with erect branches arising from a stolon; leaves in a large terminal rosette, loosely imbricate when dry, widely spreading when moist, obovate-spatulate, serrate; upper cells regularly oblong-hexagonal, walls thick and pitted; not observed fruiting in the Interior Highlands.

Common throughout the Interior Highlands; on calcareous soil of rock ledges, rarely at the bases of trees.

17. MNIACEAE

1. *Mnium* Hedw.

Plants light to dark green, loosely to densely tufted, sterile stems often prostrate; leaves complanate, ovate, rounded-ovate, obovate to ovate-lanceolate, frequently decurrent, entire to serrate, usually with a border of elongated cells, costate, frequently crisped when dry; leaf-cells hexagonal, often collenchymatous; inflorescence terminal, synoicous or dioicous; capsule ovate to cylindrical, horizontal to pendulous, exserted upon a long seta; peristome double.

a. Leaves distinctly bordered by elongated cells .... b

a. Leaves not distinctly bordered by elongated cells .... 1. *M. stellare*

  b. Margins of leaves serrate; if entire, bases not cuneate c

  b. Margins of leaf entire, bases cuneate .... 8. *M. punctatum*

c. Marginal teeth double .... d

c. Marginal teeth single .... g

  d. Leaves narrowly elliptic-ovate to ovate-lanceolate; costa toothed on back near apex, not reaching apex of leaves .... 2. *M. hornum*

  d. Leaves ovate lanceolate; costa not toothed on back, reaching apex in most leaves .... f

f. Leaf-cells averaging 25 μ in diameter, collenchymatous, tending to be arranged in longitudinal rows; synoicous or paroicous .... 4. *M. marginatum*

f. Leaf-cells averaging less than 20 μ in diameter, walls uniformly thickened; dioicous .... 3. *M. orthorrhynchum*

  g. Leaves serrate nearly to base .... h

  g. Leaves serrate only in upper ½ or ⅔ .... 5. *M. cuspidatum*

h. Teeth of leaves 1–3-cells-long; apex obtuse or mucronate; dioicous .... 7. *M. affine*

h. Teeth of leaves one-cell-long, rarely more; apex acute to acuminate; synoicous .. 6. *M. medium*

1. *Mnium stellare* Hedw.

Uncommon, Boston Mtns., Ozark Hills, Salem and Springfield Plateaus; on shaded soil and rocks, rarely at bases of trees or on decaying wood.

The serrations along the border of the leaf are often obscure and a faint border of elongated cells may be occasionally noted. Sterile forms of *Tetraphis pellucida* may be confused with this taxon. However, *T. pellucida* has rounded leaf cells and entire leaf margins.

2. *Mnium hornum* Hedw.

Reported from St. Louis County, Missouri, by Andrews (*in* Grout, 1933). The report from Jackson County, Illinois, by Redfearn (1966: 507) is an error as the collection (*Redfearn 18789*) is *Mnium marginatum.*

3. *Mnium orthorrhynchum* Brid.

Uncommon, Boston Mtns., Salem Plateau; on shaded moist limestone and sandstone exposures.

Plants of this species are quite small and easily overlooked. Consequently, its distribution is probably wider than collection records indicate. This taxon may be confused with the next. When fertile, its dioicous condition serves to distinguish it from *Mnium marginatum.* Sterile plants are more difficult to separate. However, the leaf cells of *M. marginatum* are generally larger (<25 μ in diameter) and collenchymatous, while the cells of *M. orthorrhynchum* are smaller (some do average <20 μ in diameter) and thin-walled with little thickening at the corners.

4. *Mnium marginatum* (With.) Brid. *ex* P. Beauv.

Mnium serratum Schrad. *ex* Brid.

Common, Boston Mtns., Ozark Hills, Salem and Springfield Plateaus; on shaded, moist rocks, particularly in crevices and undersides of overhanging ledges, occasionally on soil or bases of shrubs or trees.

For distinctions from *Mnium orthorrhynchum,* see notes under that taxon.

5. *Mnium cuspidatum* Hedw.

Very common throughout the Interior Highlands; on moist, shaded soil and rocks.

An easily recognizable taxon with rounded, ovate to obovate leaves that are strongly decurrent and serrate only in the upper ½–⅔.

6. *Mnium medium* B.S.G.

Reported from Conway County, Arkansas, by Moore (1965: 32).

7. *Mnium affine* Bland. *ex* Funck

This taxon shows considerable variability and several varieties have been suggested. Of these, only the variety *rugicum* seems worthy of recognition in the Interior Highlands.

a. Leaves decurrent; leaf cells to 50 μ in length .... 7a. *M. affine* var. *affine*
a. Leaves not decurrent; leaf cells often exceeding 70 μ in length .. 7b. *M. affine* var. *rugicum*

7a. *Mnium affine* var. *affine*

Very common throughout the Interior Highlands; on shaded soil and rocks.

May be confused only with *Mnium medium* from which it may be separated by the features noted in the key above.

7b. *Mnium affine* var. *rugicum* (Lour.) B.S.G.

Mnium rugicum Laur.

Rare, Salem and Springfield Plateaus; on shaded rocks and soil beside creeks and streams.

The taxonomic validity of this taxon is questioned by many. However, it is distinct in its size and form and should be recognized, especially since there is not any evidence as to the basis of its remarkable differences. These differences may be due to environmntal or cytological factors, or both. Clearly, further study is needed.

8. *Mnium punctatum* Hedw.

Common throughout the Interior Highlands; on rocks and decaying wood in moist, shaded areas, particularly in rock crevices and beside streams and gullies.

18. AULACOMNIACEAE

1. *Aulacomnium* Schwaegr.

Plants in dense to loose tufts, pale to blackish green in color, often tomentose at base; leaves ovate to lanceolate, coarsely toothed to denticulate above; costa stout at base, ending below the apex; upper leaf-cells small (7–18 μ), collenchymatous with single papillae on both surfaces; lower leaf-cells larger, elongate, to 30 μ long, walls incrassate; fusiform brood-bodies often present on pseudopodia; capsules on twisted seta, 1–1.5 cm long, suberect, longitudinally striate; operculum beaked; peristome double.

a. Leaves ovate, coarsely serrate above .... 1. *A. heterostichum*
a. Leaves lanceolate, denticulate above .... 2. *A. palustre*

1. *Aulacomnium heterostichum* (Hedw.) B.S.G.

Common throughout the Interior Highlands; on moist, shaded soil banks and rock ledges. Often mixed with *Mnium affine*, *M. cuspidatum*, or *Bartramia pomiformis*.

2. *Aulacomnium palustre* (Hedw.) Schwaegr.

Uncommon throughout the Interior Highlands; often very abundant on moist, dripping sandstone ledges and at bases of bluffs or on soil subject to a great deal of seepage. Not infrequently mixed with *Sphagnum* in bogs.

19. BARTRAMIACEAE

Plants yellowish green to bright green, in loose to dense tufts, densely tomentose below; leaves linear-lanceolate to ovate-lanceolate, costate; cells papillose by projection of end-walls; capsule subglobose to ovoid, furrowed when dry, inclined or cernuous, exserted upon a long seta; peristome double.

a. Plants in large, soft tufts; leaves 5–6 mm long, linear- to elongate-lanceolate, subulate, flexuous from an ovate, more or less clasping base; margins usually strongly denticulate to sharply serrate above .... 1. *Bartramia*
a. Plants in coarse, dense tufts; leaves 1.5–2 mm long, linear-lanceolate to ovate-lanceolate, not flexuous; serrate but not denticulate above .... 2. *Philonotis*

1. *Bartramia* Hedw.

1. *Bartramia pomiformis* Hedw.

Soft tufted mosses, bright green to bluish green; leaves 5–6 mm long, elongate-lanceolate, subulate, flexuous from an ovate, more or less clasping base; margins revolute to apex, strongly denticulate to sharply serrate above, bistratose distally; upper leaf-cells thick-walled and short-rectangular, papillose on both surfaces; basal cells linear to oblong, smooth; capsule exserted on seta 1–2 cm long, inclined or cernuous, globose to ovoid, deeply furrowed when dry, reddish to dark chestnut brown; peristome double.

Common throughout the Interior Highlands; on moist, shaded soil banks and rock ledges. Often mixed with *Aulacomnium heterostichum.*

2. *Philonotis* Brid.

Plants usually densely tufted, bright to light green, occasionally pale or glaucous, branches whorled and subtending perigonia, stems densely tomentose below; leaves to 2 mm long, narrowly triangular-lanceolate to ovate-lanceolate, apex acuminate; margins plane or revolute, singly or doubly serrate; costa percurrent to long-excurrent; upper leaf-cells oblong to linear, papillose at upper or lower ends or both; basal leaf cells larger, smooth or papillose; autoicous or dioicous, perigonia gemmiform or discoid; seta long; capsule subglobose to ovoid, inclined to cernuous, reddish-brown, longitudinally furrowed; peristome double.

a. Costa percurrent to slightly excurrent; leaves distinctly papillose; apex acuminate to acute .... b
a. Costa ending below apex; leaves weakly papillose; apex blunt or obtuse .... 1. *P. gracillima*
  b. Papillae at lower end of cells .... e
  b. Papillae at upper end of cells, occasionally at both ends c
c. Perigonia gemmiform; leaves narrowly lanceolate to triangular-lanceolate; leaf-cells linear to rectangular; basal cells not noticeably shorter and wider .... 2. *P. longiseta*
c. Perigonia discoid; leaves ovate-lanceolate to triangular-lanceolate; leaf-cells linear to oblong; basal cells distinctly larger and broader than median leaf-cells .... d
  d. Leaves ovate-lanceolate; median leaf-cells oblong to linear, weakly papillose, papillae occasionally at both ends of cells, not forming noticeable parallel rows; basal cells tending to be smooth .... 4. *P. muehlenbergii*
  d. Leaves ovate-lanceolate to triangular-lanceolate; median leaf-cells mostly linear, distinctly papillose and arranged in parallel rows; basal cells usually papillose .... f
e. Margins of leaves singly serrate, not recurved .... 6. *P. caespitosa*
e. Margins of leaves doubly serrate, recurved above .... 7. *P. fontana*
  f. Costa percurrent or shortly excurrent; leaves ovate-lanceolate to triangular-lanceolate .... 3. *P. marchica*
  f. Costa long and slenderly excurrent; leaves often slenderly lanceolate .... 5. *P. capillaris*

1. *Philonotis gracillima* Ångstr.

Rare, Ouachita Mtns., eastern Salem Plateau; on shale and sandstone.

2. *Philonotis longiseta* (Michx.) Britt. var. *longiseta*

Uncommon, Boston and Ouachita Mtns., Salem and Springfield Plateaus; on shaded sandy soil, sandstone, dolomite, or shale, usually near flowing water.

3. *Philonotis marchica* (Hedw.) Brid.

Common throughout the Interior Highlands; on rocks and soil, mostly calcareous, along banks of gullies and streams.

This taxon is difficult to distinguish from the next. Transitional forms may be encountered making assignment to either difficult if not impossible. Further research is needed to resolve the difficulties in this and related taxa.

4. *Philonotis muehlenbergii* (Schwaegr.) Brid.

Uncommon throughout the Interior Highlands; on moist soil and rocks along gullies, creeks, and streams. Easily confused with *Philonotis marchica.*

5. *Philonotis capillaris* Lindb.

Rare, eastern Salem Plateau, known only from Pickle Springs in Ste. Genevieve County, Missouri; on shaded sandstone ledge.

6. *Philonotis caespitosa* Jur. var. *caespitosa*

Reported from Conway County, Arkansas, by Moore (1965).

7. *Philonotis fontana* (Hedw.) Brid. var. *fontana*

Common throughout the Interior Highlands; on moist soil and rock ledges along flowing water or standing surface water in glades.

20. TIMMIACEAE

1. *Timmia megapolitana* Hedw.

Plants in loose to dense tufts, green above, brown to yellow-green below, 3–5 cm tall; leaves crisped with inrolled margins when dry, spreading and margins plane when moist, 4–10 mm long and 1–1.5 mm wide, lanceolate to linear-lanceolate, apex gradually narrowing, base sheathing, concave to keeled; margins strongly toothed from just above the sheathing base to the apex with multicellular teeth; costa strong, papillose above, sub-percurrent to percurrent; leaf-cells rounded-hexagonal and collenchymatous above, thin-walled and linear in the sheathing base; autoicous; capsule erect to horizontal; seta red, 2–2.5 cm long; operculum rounded, apiculate; outer peristome teeth 16, yellowish, pellucid and slightly papillose below, longitudinally striate and often perforate above; inner peristome arising from a basal membrane about ½ length of outer teeth and ending in 64 cilia united into groups of 4; calyptra erect from seta behind the capsule.

Uncommon, Boston Mtns., Ozark Hills, Salem Plateau; on moist, shaded calcareous rocks and soil along banks of streams and gullies and on ledges.

When young sporophytes are present, the peculiar position of the calyptra is diagnostic for this taxon. Sterile plants may be recognized by the rather large size of the plants and the long leaves that have inrolled margins and are crispate when dry, and are strongly serrate with multicellular teeth and have thin-walled linear cells in the sheathing base.

21. Erpodiaceae

1. *Venturiella sinensis* (Vent. *ex* Rabenh.) C. Müll.

Small plants in creeping, flattened mats with terete, erect branches, 2–4 mm long; leaves ovate, imbricate-appressed, widely spreading when moist, dark green with hyaline, denticulate tips; upper leaf-cells hexagonal, smooth, quadrate at margins, elongated and becoming linear in hyaline acumination; seta short; capsule pale yellow, oval-cylindric, 1.5 mm long, immersed to emergent.

Rare, south-western Boston Mtns.; on vertical, south facing sandstone. Known only from Cherokee Co., Oklahoma, on bluff along Terapin Creek near Hwy. 82, Sect. 24, T. 14 N., R. 22 W.

22. Ptychomitriaceae

Small to minute plants in yellowish to brownish or blackish green tufts; leaves crispate when dry, erect-spreading when moist, linear-subulate to linear-lanceolate, not plicate; costa percurrent to sub-percurrent; upper cells smooth, rounded to quadrate; capsule cylindrical to ovoid, exserted; peristome teeth 16, variously split; calyptra mitrate to campanulate-mitrate.

a. Leaves linear-subulate; seta arcuate when moist .... 1. *Campylostelium*
a. Leaves linear from a lanceolate base; seta straight when moist .... 2. *Ptychomitrium*

1. *Campylostelium* B.S.G.

1. *Campylostelium saxicolum* (Web. & Mohr) B.S.G.

Plants minute, in loose, yellow-green tufts; leaves subulate from a narrow, ovate base, crisped when dry, keeled; margins entire; median cells green and rectangular; basal cells thin-walled, elongate-rectangular, hyaline; capsule exserted on an arcuate seta, cylindrical, sulcate with age; operculum long subulate.

Rare, Boston Mtns.; on shaded, moist vertical sandstone.

2. *Ptychomitrium* Fürnr.

Plants in small, brownish to blackish green tufts; leaves crispate when dry, linear-lanceolate; margins entire to serrate in upper half; costa single, percurrent to sub-percurrent; seta short, 2–3 mm long, not arcuate; capsule ovoid; operculum subulate; calyptra mitrate to campanulate-mitrate.

a. Leaves entire or nearly so; plants growing on rocks .... b
a. Leaves serrate in upper half; plants growing on trees .... 3. *P. drummondii*
  b. Leaves 1.2–2.0 mm long; seta 2.0–2.5 mm long .... 1. *P. incurvum*
  b. Leaves 3.0–4.0 mm long; seta 4–5 mm long .... 2. *P. leibergii*

1. *Ptychomitrium incurvum* (Schwaegr.) Sull.

Common throughout the Interior Highlands; on exposed to shaded rocks.

This species characteristically grows in pockets of boulders. Colonies are seldom large, although they may be quite frequent.

2. *Ptychomitrium leibergii* Best

Rare, southern Salem Plateau; on limestone in cedar glade. A distinctive species known only from a cedar glade above the west bank of Norfork Lake, ca. ¼ mile west of Tecumseh, Sect. 16, T. 22, R. 12 W.

The leaves of this species are remarkably similar to the Asiatic species *P. sinense* Jaeg. However, the latter species has a longer seta and a more cylindrical capsule.

3. *Ptychomitrium drummondii* (Wils.) Sull.

Uncommon, Ouachita Mtns., Ozark Hills, St. Francois Mtns., Springfield Plateau; on trees.

This species may be more common than collection records indicate as sterile plants are likely to be mistaken for sterile species of *Orthotrichum.*

23. ORTHOTRICHACEAE

Dark, tufted plants, growing on trees and rocks; stems erect or creeping; leaves crowded, appressed or crispate when moist, keeled above, lanceolate; margins entire; costa strong; upper leaf-cells small, irregularly rounded, papillose; capsule immersed to exserted, erect and symmetric, often plicate; peristome double; calyptra mitrate, hairy or smooth.

a. Primary stems long and creeping .... 3. *Drummondia*
a. Plants erect, stems not creeping .... b
  b. Gemmae present in upper leaf axils .... 4. *Zygodon*
  b. Gemmae absent c
c. Capsule long exserted .... 2. *Ulota*
c. Capsule immersed to emergent .... 1. *Orthotrichum*

1. *Orthotrichum* Hedw.

Small, dark to brownish green tufted plants; stems erect, branched above; leaves lanceolate to ovate-lanceolate; costa strong; upper leaf-cells small, irregularly rounded, papillose on both surfaces; basal cells rectangular, rhomboidal to linear; capsules immersed to emergent, often ribbed and strangulate when dry; stomata scattered and immersed in our species; outer peristome teeth 16, often united in pairs and reflexed when dry; inner peristome when present of 8–16 narrow segments; calyptra usually campanulate, covering most of the urn, plicate, hairy.

A difficult genus where identification depends on the presence of old, mature capsules. The following key is based in part on the treatment of *Orthotricha straminea* by Crum and Anderson (1956) and on suggestions by Dr. Dale Vitt (personal communication).

a. Upper leaves with hyaline points .... 7. *O. diaphanum*
a. Upper leaves without hyaline points .... b
  b. Plants growing on rocks c
  b. Plants growing on trees .... d
c. Peristome papillose .... 2. *O. strangulatum*

c. Peristome striate .... 1. *O. cupulatum*
d. Exostome teeth recurved .... e
d. Exostome teeth reflexed .... f
e. Exothecial cells poorly differentiated .... 4. *O. pusillum*
e. Exothecial cells clearly differentiated .... 5. *O. pumilum*
f. Capsule constricted below mouth; exothecial cells different in color from rest of capsule .... 6. *O. stellatum*
f. Capsule not constricted below mouth .... 3. *O. ohioense*

1. *Orthotrichum cupulatum* Brid.

Rare, on rocks. Reported from McCurtain Co., Oklahoma, by Sharp (1930: 53).

2. *Orthotrichum strangulatum* P. Beauv.

Common, Boston Mtns., Prairie Plains, Salem and Springfield Plateaus; on open to shaded rocks.

3. *Orthotrichum ohioense* Sull. & Lesq. *ex* Aust.

Common, Boston and Ouachita Mtns., Salem and Springfield Plateaus; on tree trunks.

Plants often mixed with the next taxon. Capsules frequently strangulate with age.

4. *Orthotrichum pusillum* Mitt.

Common throughout the Interior Highlands; on tree trunks, rarely on sandstone.

5. *Orthotrichum pumilum* Sw.

Uncommon, Prairie Plains, Salem and Springfield Plateaus; on tree trunks.

6. *Orthotrichum stellatum* Brid.

Common, Boston and Ouachita Mtns., Salem and Springfield Plateaus; on tree trunks.

7. *Orthotrichum diaphanum* Brid.

Uncommon, Boston Mtns., Salem and Springfield Plateaus; on tree trunks and rarely acidic rocks.

2. *Ulota* Mohr *ex* Web.

1. *Ulota hutchinsiae* (Sm. *ex* Sowerby) Hammar

Ulota americana (P. Beauv.) Limpr.

Erect, dark green tufted plants; leaves closely imbricated when dry, concave-carinate, lanceolate to ovate-lanceolate, obtuse to obtusely acute; margins recurved; costa strong; upper leaf-cells thick-walled, circular to elliptic, papillose; capsule exserted, oblong-ovoid with long neck, 8-ribbed; peristome teeth 16, united in pairs; calyptra very hairy.

Uncommon, Boston and Ouachita Mtns.; on vertical shaded dolomite and sandstone. Locally abundant.

3. *Drummondia* Hook. *ex* Drumm.

1. *Drummondia prorepens* (Hedw.) Britt.

Primary stems creeping with numerous erect, short, dark green to blackish, densely foliate branches; leaves closely appressed when dry, oblong- to ovate-lanceolate, concave, carinate, acute to narrowly obtuse; margins plane or widely inrolled; upper leaf-cells small, rounded, thick-walled, smooth; capsule exserted, erect, on seta 2–3 mm long, symmetric, ovoid-globose; peristome teeth 16; calyptra conic, without hairs.

Common throughout the Interior Highlands; on trees, rarely on shaded acidic rocks.

4. *Zygodon* Hook. & Tayl.

1. *Zygodon apiculatus* Redfearn (1967).

Plants very small, 1–4 mm high, dark green, erect; leaves when dry erect, when moist widely spreading, crowded, keeled, oblong-lanceolate or oblong-ovate, acute, rather abruptly short apiculate, terminal cells of apiculus little elongated, yellowish-brown or concolorous; margins plane or slightly wavy; costa conspicuous, ending below apex and papillose near tip; upper leaf-cells green, hexagonal, thin-walled, pluripapillose on both surfaces; gemmae abundant in leaf axils, subcylindric to fusiform, composed of 3–4 (rarely 5) uniserrate cells.

Rare, Salem Plateau; on oak trees.

24. FONTINALACEAE

The following treatment follows the comprehensive monograph of this family by Winona Welch (1960).

Plants aquatic, filiform to robust, yellowish green, olive-green, brownish green, blackish green, golden brown, or reddish brown; stems flaccid to rigid, short to 90 cm long, often denuded near base, regularly to irregularly branched; leaves erect-spreading or spreading, distant to close, costate or ecostate, plane, concave to keeled, lanceolate, oblong-lanceolate, ovate-lanceolate, subovate, ovate, apices short to long acuminate, subacute, acute to obtuse; margins entire to serrate; median leaf-cells subrhombic, linear-rhomboidal, linear-rhombic to linear; alar cells not enlarged to enlarged, subquadrate, suboval or subhexagonal; auricles distinct or none; capsules usually erect, sessile or on a short seta, completely immersed to completely emergent; peristome double, teeth 16.

a. Leaves ecostate .... 1. *Fontinalis*
a. Leaves costate .... b
  b. Ends of foliated stems and branches conspicuously three-angled, not curved or uncinate; leaves not secund; capsule completely immersed; costa percurrent to ending below apex .... 2. *Brachelyma*
  b. End of foliated stems and branches not conspicuously three-angled, commonly slightly to distinctly curved, frequently uncinate; capsule emergent; leaves secund and falcate; costa long-excurrent .... 3. *Dichelyma*

1. *Fontinalis* Hedw.

Plants aquatic, floating or submerged; leaves tristichous, plane, subconcave, concave to canaliculate, subtubular, convolute-tubulose, subcarinate or carinate-conduplicate, ecostate, sublanceolate, lanceolate, oblong-lanceolate, ovate-lanceolate, ovate; margins plane to narrowly or broadly involute; apices short to long-acuminate, subacute, subobtuse or obtuse; median leaf-cells subrhomboidal, rhomboidal, linear-rhomboidal, linear; alar cells enlarged, subquadrate, subrectangular, or subhexagonal; capsule sessile or subsessile, immersed in perichaetial leaves or emergent.

a. Leaves usually plane .... b

a. Leaves usually concave .... d

  b. Leaves broadly ovate-lanceolate or oval-lanceolate; margins tapering from approximately middle into apex; apices short and broadly acuminate .... 7. *F. duriaei*

  b. Leaves generally narrowly ovate-lanceolate or lanceolate; margins tapering from basal ¼ or ½ into apex; apices long, acuminate c

c. Apices gradually narrowed, tips commonly acute and entire; auricles usually none .... 6. *F. hypnoides*

c. Apices often abruptly narrowed, tips commonly obtuse to truncate and serrulate; auricles very conspicuous .... 8. *F. flaccida*

  d. Margins usually involute .... e

  d. Margins not involute .... g

e. Margins near apex commonly narrowly involute .... 1. *F. novae-angliae*

e. Margins near apex commonly broadly involute .... f

  f. Apices long acuminate; apical cells rhombic, rhomboidal, quadrate, rectangular, or hexagonal .... 3. *F. biformis*

  f. Apices obtuse to truncate; apical cells linear or linear-rhomboidal .... 1b. *F. novae-angliae* var. *cymbifolia*

g. Apical cells rhomboidal, rhombic, quadrate, rectangular, or hexagonal .... 3. *F. biformis*

g. Apical cells linear or linear-rhomboidal .... h

  h. Stems flaccid; leaves usually subflaccid, lanceolate to ovate-lanceolate .. 2. *F. missourica*

  h. Stems rigid, leaves firm, narrowly lanceolate i

i. Leaves 0.75–1.5 mm wide .... 4. *F. disticha*

i. Leaves 0.35–0.5 mm wide .... 5. *F. filiformis*

1. *Fontinalis novae-angliae* Sull.

a. Margins commonly narrowly involute in apical portion .... b

a. Margins commonly broadly involute in apical portion .... 1b. *F. novae-angliae* var. *cymbifolia*

  b. Blades usually firm, ovate-lanceolate, 1–2 mm wide .... 1a. *F. novae-angliae* var. *novae-angliae*

  b. Blades usually flaccid, broadly ovate-lanceolate, 1.5–3.5 mm wide .... 1c. *F. novae-angliae* var. *latifolia*

1a. *Fontinalis novae-angliae* var. *novae-angliae*

Common throughout the Interior Highlands; on boulders, tree limbs and roots, in intermittently flowing streams, creeks and shallow gullies.

1b. *Fontinalis novae-angliae* var. *cymbifolia* (Aust.) Welch

Rare, reported from eastern Salem Plateau in Ste. Genevieve County, Missouri, by Gier (1955*a*).

1c. *Fontinalis novae-angliae* var. *latifolia* Card. *ex* Nichols

Rare, throughout the Interior Highlands (absent Ozark Hills); on sandstone in creeks and gullies.

2. *Fontinalis missourica* Card.

Common throughout the Interior Highlands; on noncalcareous rocks in streams and creeks.

3. *Fontinalis biformis* Sull.

Apparently rare, Salem Plateau; on limestone in creeks.

The collection (*Redfearn* 9889) from Taney County, Missouri, was distributed as *F. disticha*. The correct identification of this collection was made by Dr. Howard Crum.

4. *Fontinalis disticha* Hook. & Wils. *ex* Drumm.

Rare, Ouachita Mtns.; on rocks in intermittently flowing streams.

5. *Fontinalis filiformis* Sull. & Lesq. *ex* Aust.

Uncommon, Ouachita Mtns., Ozarks Hills, Salem Plateau; attached to stones and tree bases in swiftly flowing streams and creeks.

6. *Fontinalis hypnoides* C. J. Hartm.

Rare, Salem Plateau; attached to stone in spring branches.

7. *Fontinalis duriaei* Schimp.

Common, Salem and Springfield Plateaus; on tree bases and roots, and stones in swiftly flowing creeks, streams, and spring branches.

8. *Fontinalis flaccida* Ren. & Card.

Uncommon, Ouachita Mtns., eastern Salem Plateau; attached to rocks in gullies and in swampy areas.

2. *Brachelyma* Schimp. *ex* Card.

1. *Brachelyma subulatum* (P. Beauv.) Schimp. *ex* Card.

Plants slender, yellowish green, green to brown, youngest portion of stems conspicuously three-angled, regularly or irregularly pinnately branched; median cauline leaves 2–4 mm long and 0.5–1 mm wide, imbricate, firm, erect-spreading, carinate-conduplicate, subulate, oblong-lanceolate, sublanceolate, or lanceolate, apices obtuse or acute, keel straight to moderately curved, frequently abruptly curved near apex, leaf tips serrulate, occasionally entire; costa percurrent or ending a short distance below apex; median leaf-cells subrhombic, subrhomboidal or subhexagonal, 2–4 : 1; marginal cells linear with attenuate ends forming a border of 4–5 rows of cells; alar cells subquadrate or subrectangular; auricles slight or none, bases immersed in perichaetial leaves.

Rare, lowland regions of eastern Boston Mtns., southwestern Ouachita Mtns., eastern Salem Plateau; on bases of tupelo gum, cypress, and other lowland hardwoods, occasionally on sandstone boulders, edge of rivers, streams, and creeks.

3. *Dichelyma* Myr.

1. *Dichelyma capillaceum* (With.) Myr.

Plants relatively slender, yellowish green, green or brownish green with subrigid to rigid, irregularly divided stems; branches few to numerous; median cauline leaves close to distant, 4.5–7 mm long and 0.4–0.8 mm wide, firm, erect-ascending to occasionally erect-spreading, carinate-conduplicate, straight to moderately curved along keel or subfalcate to falcate, generally subsecund to secund, narrowly lanceolate, width gradually decreasing from base to apex; margins entire below to subserrulate above; apices subulate or acuminate; costa long excurrent, serrate or entire at end; median leaf-cells linear with attenuate ends, 10–20 : 1; alar cells indistinct, slightly enlarged, usually quadrate or rectangular; bases not decurrent; capsule at first immersed in perichaetial leaves, later laterally emergent.

Rare, Ouachita Mtns., Mississippi lowlands; attached to tree roots and sandstone in intermittently flowing creeks and gullies.

25. CLIMACIACEAE

1. *Climacium americanum* Brid.

Large plants with upright branches, 5–8 cm tall, usually tree-like, arising from an underground creeping stem; aerial branches usually tapering; leaves of main aerial stem large, 2.5–3.5 mm long and 1.5–2.0 mm wide, ovate, apex acuminate, base clasping; branch leaves of aerial stems smaller, 2.0–2.5 mm long and 1.0–1.5 mm wide, ovate-elliptic to oblong-lanceolate, auriculate, apex acute to obtuse, serrate; costa stout, reaching nearly the apex; median leaf-cells oblong-hexagonal, ends rounded to truncate, 2–7 : 1; alar cells short-rectangular to quadrate; paraphyllia filiform, numerous on branches and secondary stems; fruiting infrequently, capsule erect, cylindric, 5–6 : 1, symmetric, on long seta; peristome double, teeth 16, reddish-brown.

This species may be separated into two rather indistinct varieties based on the following key.

a. Median leaf cells of branch leaves 5–7 : 1 .... 1a. *C. americanum* var. *americanum*
a. Median leaf cells of branch leaves 2–3 : 1 .... 1a. *C. americanum* var. *kindbergii*

1a. *Climacium americanum* var. *americanum*

Common throughout the Interior Highlands; on moist shaded soil, particularly of ledges and bases of bluffs. Often very abundant.

The striking, tree-like growth habit of this plant is distinctive and not likely to be confused with any other species except perhaps *Thamnobryum alleghaniense* which is a smaller plant with a more coarsely serrate apex composed of distinctly rhomboidal cells.

1b. *Climacium americanum* var. *kindbergii* Ren. & Card.

Climacium kindbergii (Ren. & Card.) Grout

Less common than the preceding variety throughout the Interior Highlands; usually, but not necessarily, confined to substrates along shallow, rocky streams.

The distinction between these two varieties is poor and not consistent, and intergrading forms are encountered. One suspects that they may be no more than environmental forms. However, until such time as this is demonstrated, these varieties are retained.

26. HEDWIGIACEAE

A family of uncertain affinities represented in our area by a single taxon.

1. *Hedwigia ciliata* (Hedw.) P. Beauv.

Plants in loose, gray-green tufts, branching freely; leaves ecostate, broadly ovate-lanceolate, apex hyaline, serrate (occasionally absent); cells of leaf incrassate with branching papillae, rounded to oblong above, elongate below and becoming reddish along mid-line near base; capsule erect, immersed, symmetrical; peristome absent.

Very common throughout the Interior Highlands; on exposed to shaded rocks, rarely around the bases of trees. Often locally abundant.

Several forms have been described for this species. However, variability is erratic and often variation in ciliation of the perichaetial leaves or development of the hyaline point on stem leaves occurs within the same colony or clump. Anderson (1958: 291) is quite correct in not applying form names to such variations.

27. CRYPHAEACEAE

Plants small to moderately large, yellowish to dark green, in loose tufts or mats; secondary stems profusely to sparingly branched, densely foliate; leaves appressed-imbricate to julaceous when dry, more or less spreading when moist, concave, ovate, ovate-elliptical to ovate-lanceolate, apices acute or short acuminate; margins slightly recurved, entire or slightly serrulate near apex; costa single, strong or thin and reaching the middle of the leaf to double and almost lacking; median leaf-cells smooth or papillose, oblong-fusiform, rounded-oval to isodiametric, thick-walled; marginal cells rounded-quadrate, oval; capsule short-oblong to ovoid-cylindric, immersed to extending beyond perichaetial leaves; peristome double, teeth 16; calyptra more or less hairy.

a. Secondary stems profusely branched; if sparingly branched, seta long and capsule exserted beyond perichaetial leaves .... 2. *Forsstroemia*

a. Secondary stems sparingly branched; seta very short and capsule immersed in perichaetial leaves .... 1. *Cryphaea*

1. *Cryphaea* Mohr *ex* Web.[5]

1. *Cryphaea glomerata* B.S.G. *ex* Sull. var. *glomerata*

Plants small, slender, light to brownish green; secondary stems sparingly branched with leaves closely imbricated and julaceous when dry; leaves concave,

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[5] See "Note Added in Proof," p. 103.

ovate to ovate-elliptical, apices acute to short-acuminate; margins slightly reflexed below, entire or serrulate at apex; costa strong, reaching the middle of the leaf and projecting on the dorsal side; median leaf-cells papillose on dorsal surface, thick-walled, subcircular to oval; perichaetial leaves as long as or longer than capsule; seta very short; capsule short-oblong to ovoid; operculum conic; calyptra conical.

Common in Boston and Ouachita Mtns., uncommon in Salem and Springfield Plateaus; on hardwoods and shrubs, particularly along creeks and streams. Occasionally very abundant.

2. *Forsstroemia* Lindb.

Plants moderately large to slender, yellowish to dark green, in dense to loose tufts; secondary branches profusely to sparingly branched, densely foliate; leaves plicate or smooth, appressed-imbricate when dry, spreading when moist, concave, ovate to ovate-lanceolate, apices acute to abruptly short-acuminate; margins entire or nearly so; costa reaching middle of leaf and strong, strongly protruding on dorsal side of leaf to thin, reaching middle of leaf or short and double to almost wanting; median leaf-cells smooth or slightly papillose, oblong-fusiform to rounded-oval; capsule ovoid to oblong, exserted or immersed in perichaetial leaves; calyptra hairy.

a. Secondary stems sparingly branched; leaves not plicate; costa strong and protruding on dorsal side .... 1. *F. ohioensis*
a. Secondary stems profusely branched; leaves plicate; costa thin, reaching middle of leaf to short and double .... 2. *F. trichomitria*

1. *Forsstroemia ohioensis* (Sull.) Lindb.

Leptodon ohioensis Sull.

Rare, known only from the vicinity of Gladden Creek in Shannon County, Missouri, on the Salem Plateau and along Roaring River Spring branch at Roaring River State Park, Barry County, Missouri, on the Springfield Plateau; on hardwoods and red cedar. May be more common as it is easily overlooked.

2. *Forsstroemia trichomitria* (Hedw.) Lindb.

Forsstroemia trichomitria var. *immersa* (Sull. & Lesq.) Lindb.
Leptodon trichomitrion (Hedw.) Mohr.

Common throughout the Interior Highlands; on hardwoods and red cedar and on shaded vertical rocks. Often very common.

The varieties established by earlier authors are not recognized in this study, a procedure in agreement with a recent treatment by Breen (1963: 108–109).

28. LEUCONDONTACEAE

1. *Leucodon* Schwaegr.

Plants green to dark green above and brownish below, with numerous moderately large, julaceous secondary stems that are suberect or pendent and curved outward from the substratum; secondary branches few; stem leaves crowded, appressed and imbricate when dry, spreading when moist, smooth or plicate when dry, straight to secund, concave, ecostate, ovate-elliptical to ovate or ovate-lanceolate, apices abruptly short-acuminate to gradually long-acuminate; margins plane or reflexed at base, entire to serrulate near apex; median leaf-cells smooth, rhomboidal, 3–5 : 1; apical cells similar, smooth or roughened-mammillose on back; cells near base and margin roundish quadrate; lower median cells linear-fusiform; capsule immergent or exserted, oblong-ovoid, erect and symmetrical; operculum conic-rostrate; peristome simple.

a. Leaves ovate-elliptical, abruptly short acuminate, scarcely plicate when dry; apical cells mammillose-roughened on back .... 2. *L. julaceus*
a. Leaves ovate to ovate-acuminate, not abruptly acuminate, plicate when dry; apical cells scarcely mammillose-roughened on back .... 1. *L. brachypus*

1. *Leucodon brachypus* Brid.

Rare, Boston and Ouachita Mtns., Salem plateau; on shaded rocks and trees.

2. *Leucodon julaceus* (Hedw.) Sull. fo. *julaceus*

Leucodontella julacea (Hedw.) Noguchi

Very common throughout the Interior Highlands; on shaded to open rocks, trees, stumps, and logs. Often very abundant.

Leucodon julaceus fo. *flagelliferous* Grout is occasionally encountered on tree trunks. It is distinguished from fo. *julaceus* by the presence of numerous long, slender, flagelliform branches bearing small lanceolate leaves.

29. Neckeraceae

Plants small to robust, in loose mats, trailing, or dendroid, shining yellow-green, brownish green, to pale or dark green; branches complanate-foliate to terete; flagelliform or stoloniform branches often present; branch leaves symmetric to asymmetric, lingulate, spatulate, broadly ovate, to ovate, elliptic-oblong or oblong lanceolate, apices acute, abruptly acuminate to rounded-obtuse; margins plane, entire, slightly crenulate, serrate to coarsely and irregularly serrate above; costa present or absent; median leaf-cells smooth, quadrate to hexagonal or rhombic to linear-fusiform; capsule oblong-ovoid to oblong-cylindric, erect to cernuous.

a. Plants dendroid, branches terete-foliate; leaves strongly costate, coarsely and irregularly serrate above .... 4. *Thamnobryum*
a. Plants loosely tufted, at least some branches complanate-foliate; leaves ecostate or costa slender, not coarsely serrate above .... b
  b. Leaves with small lobes at adaxial base, ecostate .... 3. *Homaliadelphus*
  b. Leaves without small lobes at adaxial base, costate or ecostate c
c. Leaves with distinct but thin costa reaching middle of leaf .... 2. *Homalia*
c. Leaves ecostate .... 1. *Neckera*

1. *Neckera* Hedw.

1. *Neckera complanata* (Hedw.) Hüb.

Plants in green to pale green, glossy, loose mats; branches complanate-foliate; leaves lingulate or spatulate with short to elongated point, decurrent; margins plane, entire to denticulate above; median leaf-cells smooth, fusiform to linear-flexuose, 5–10 : 1; apical cells shorter; alar cells quadrate; vegetative propagation by means of elongated, stoloniform branches and numerous flagelliform branchlets.

Very rare, Boston Mtns.; on shaded vertical sandstone below overhanging ledges. Known only from Cleburne County, Arkansas, near Greer's Ferry Reservoir Dam.

2. *Homalia* (Brid.) B.S.G.

1. *Homalia trichomanoides* (Hedw.) B.S.G. fo. *gracilis* (James *ex* Peck) Crum

Homalia gracilis James *ex* Peck
Homalia jamesii var. *gracilis* (James *ex* Peck) Wagn.

Plants in green to dark green, glossy mats; shoots complanate-foliate, often ending in slender, terete-foliate branches; leaves asymmetrical, spatulate, shortly obtuse to rounded-obtuse; margins plane above, one side incurved at base, more or less entire; costa thin, reaching middle of leaf; median leaf-cells smooth, hexagonal; cells of upper part of leaf rhomboidal; basal cells quadrate to rectangular.

Rare, Boston Mtns., Salem Plateau; on shaded, vertical limestone, dolomite or sandstone, especially beneath overhanging ledges.

The nomenclature of this taxon follows the suggestion of Crum (1969: 243–244).

3. *Homaliadelphus* Dix. & P. de la Varde

1. *Homaliadelphus sharpii* (Williams) Sharp var. *sharpii*

Plants prostrate, in glossy, yellow- to brownish green patches; branches densely complanate-foliate; leaves broadly ovate, ecostate, with small lobes at adaxial base; margins entire or slightly crenulate; median leaf-cells smooth, short, rounded-hexagonal, thick-walled.

Very rare, known only from the Salem Plateau; on vertical, dry dolomite of bluffs along Jacks Fork River near Bay Creek, Shannon County, Missouri.

4. *Thamnobryum* Nieuwl.

1. *Thamnobryum alleghaniense* (C. Müll.) Nieuwl.

Plants robust, conspicuously dendroid, light to dark green; branches stout, terete-foliate; leaves loosely erect-spreading when dry, concave, ovate to elliptical-oblong or oblong-lanceolate, acute and coarsely irregularly serrate above; costa stout, toothed on back; median leaf-cells smooth, quadrate to hexagonal; basal cells longer, oblong to oblong-rectangular.

Uncommon, Boston Mtns., Ozark Hills, eastern Salem Plateau; on shaded, moist, vertical to flat sandstone exposures in narrow crevices and ledges, or on sandy soil along edges of creeks.

30. Hookeriaceae

1. *Hookeria acutifolia* Hook. & Grev.

Plants soft, glossy, whitish green to yellowish green, in soft mats; leaves closely imbricate and complanate, translucent, plane, ovate, ovate-lanceolate or oblong-ovate, ecostate, apices acute; margins entire; median leaf-cells oblong-hexagonal or oval-hexagonal, large and thin-walled; rhizoid-like filaments occasionally arise from leaf-cells.

Uncommon, Boston Mtns.; on sandstone and shale, usually of moist, shaded crevices or ledges.

31. THELIACEAE

Plants in slender, densely caespitose to closely interwoven, glaucous green to bluish green mats; stems creeping, more or less pinnately branching; branches short, erect to ascending, paraphyllia present or absent; leaves loosely imbricate to erect-open and distant to closely julaceous, round-ovate, concave, abruptly subulate or apiculate to slenderly acuminate, narrowed to insertion, slightly decurrent; margins plane, spinose-dentate, ciliate-serrulate to ciliate-laciniate below; costa short or lacking to reaching the middle of leaf; median leaf-cells with branched or unbranched papillae on dorsal surface, short, rounded-rhombic to fusiform; basal and apical cells longer and often smooth; seta 5–15 mm long; capsule erect and symmetric; operculum conic-rostrate; peristome double, teeth 16 and whitish.

a. Paraphyllia absent; leaves loosely imbricate to erect open; costa short or lacking .... 2. *Myurella*
a. Paraphyllia present; leaves closely julaceous; costa reaching middle of leaf, only occasionally short and double .... 1. *Thelia*

1. *Thelia* Sull.

Plants in slender, densely caespitose to closely interwoven, glaucous white mats; branches numerous, ascending, strongly julaceous; paraphyllia present, polymorphous, laciniate or ciliate; leaves very concave, abruptly subulate-acuminate, decurrent; margins plane, ciliate-laciniate, ciliate to laciniate below; costa single, reaching the middle of leaf to rarely short and double; median leaf-cells rhombic to fusiform with large forked or unforked papillae on the dorsal surface.

The following key to the species of this genus is adapted from one proposed by Crum (1966).

a. Dorsal papillae single .... 1. *T. hirtella*
a. Dorsal papillae forked, with two or more branches .... b
  b. Stems creeping, radiculose, once pinnately branched; leaves not particularly crowded; margins ciliate-papillose above, long-ciliate below; apex acute or obtuse, long-apiculate or piliform-apiculate .... 2. *T. asprella*
  b. Stems crowded and ascending, not or only slightly radiculose, irregularly branched; leaves crowded; margins not to somewhat ciliate-papillose, not long ciliate below; apex obtuse, short-apiculate .... 3. *T. lescurii*

1. *Thelia hirtella* (Hedw.) Sull.

Common throughout the Interior Highlands; on bark of hardwoods and red cedars, rarely on rocks.

Generally recognized in the field by its many erect-ascending branches that are all pointed to the same side of the stem.

2. *Thelia asprella* Sull.

Very common throughout the Interior Highlands; on bark of hardwoods, logs, rocks, and sterile soil, in dry open woods.

3. *Thelia lescurii* Sull. *in* Gray

Common throughout the Interior Highlands; on open dry soil, especially of oak-hickory woods, open cedar glades, and rocky barrens.

Gier and Kennedy (1955) consider this species to be an environmental form of *Thelia asprella.* However, Crum (1966) chooses for various reasons to retain *T. lescurii* as a valid species, which seems to be a reasonable decision.

2. *Myurella* B.S.G.

1. *Myurella sibirica* (C. Müll.) Reim. var. *sibirica*

Myurella careyana Sull.

Slender, small, glaucous green plants with stems erect to ascending; branches julaceous, numerous, often flagelliform at ends; paraphyllia absent; leaves very concave, loosely imbricate to erect-open and distant, broadly round-ovate to subcircular, abruptly apiculate to slenderly acuminate; margins spinose-dentate from base to apex; costa short or lacking; median leaf-cells rounded-rhombic, 1.5–2 : 1, pellucid, with a single large dorsal papilla over lumen.

Rare, Boston Mtns., Salem Plateau; in crevices of shaded, calcareous rocks.

32. FABRONIACEAE

Plants small and slender, in thin, glossy light to dark green mats or tufts; stems freely branching, densely foliate, imbricate when dry, erect-spreading when moist; leaves ovate to ovate-lanceolate, acuminate; margins entire or toothed; ecostate or costate; median leaf-cells thin-walled, oblong-rhombic to narrowly oblong-hexagonal, smooth or papillose on dorsal side; alar cells numerous to few, quadrate to short-rectangular; capsules exserted, erect, cylindric and symmetrical, often contracted strongly beneath mouth; operculum short-conic to long rostrate; peristome single or double.

a. Leaves ecostate; cells papillose on dorsal side; margins slightly denticulate .... 3. *Schwetschkeopsis*
a. Leaves costate; cells smooth; margins entire, toothed or laciniate-dentate .... b
  b. Leaves toothed or laciniate-dentate .... 1. *Fabronia*
  b. Leaves entire c
c. Peristome double; alar cells few, thin-walled, quadrate to rectangular, not extending 12–16 rows along margin .... 2. *Anacamptodon*
c. Peristome single; alar cells numerous, thick-walled, quadrate, forming large triangular area and extending along margin for 12–16 rows .... 4. *Clasmatodon*

1. *Fabronia* Raddi

Plants small and slender, in soft, thin, glossy, light green patches; stems irregularly branched, julaceous; leaves closely imbricate when dry, erect-spreading when moist, ovate-lanceolate, long acuminate; margins entire to dentate or dentate-laciniate; costate; median leaf-cells smooth, elongate-rhomboidal to elongate-hexagonal; alar cells quadrate, filling entire base and extending 12–20 rows up margin.

a. Leaves laciniate-dentate with teeth often of more than one cell .... 2. *F. gymnostoma*
a. Leaves entire to dentate with large projecting marginal cells .... b
  b. Leaves entire or nearly so .... 3. *F. ravenelii*
  b. Leaves irregularly serrate-dentate .... 1. *F. ciliaris*

1. *Fabronia ciliaris* (Brid.) Brid. var. *ciliaris*

Common throughout the Interior Highlands (except Ozark Hills); on trunks of hardwoods and red cedar and in crevices and vertical surface exposures of rocky bluffs.

Fabronia ciliaris var. *imperfecta* Sharp has been reported from the Salem and Springfield Plateaus by Gier (1955*a*: 34), who considers it to be a drought form of var. *ciliaris.*

2. *Fabronia gymnostoma* Sull. & Lesq. *ex* Sull.

Reported from the extreme western edge of the Arkansas Valley in Muskogee County, Oklahoma, by Little (1936).

3. *Fabronia ravenelii* Sull.

Rare, known only from Petit Jean Mountain, Conway County, Arkansas (Moore, 1965).

2. *Anacamptodon* Brid.

1. *Anacamptodon splachnoides* (F. Froel. *ex* Brid.) Brid.

Plants in dark, glossy, green mats; stems irregularly branching; leaves close, loosely spreading when dry, concave, ovate-lanceolate; margins entire; costa reaching middle of leaf; median leaf-cells smooth, rhombic-hexagonal, 2–3 : 1; upper leaf-cells longer, 4–6 : 1; basal cells thin-walled, rectangular to quadrate; capsule conspicuously contracted beneath mouth when dry.

Rare, known only from Ozark Hills, near Belle Smythe Springs, Pope County, Illinois, collected by R. Hatcher (*1239*); on tree trunk.

Anacamptodon splachnoides var. *tayloriae* is reported from Lafayette Co., Missouri, by Chamberlain (1919).

3. *Schwetschkeopsis* Broth.

1. *Schwetschkeopsis fabronia* (Schwaegr.) Broth.

Schwetschkeopsis denticulata (Sull.) Broth.

Plants in light olive- to yellow-green, glossy, crowded mats; stems slender, julaceous; leaves, concave, ovate-lanceolate, short-acuminate; margins slightly denticulate; ecostate; median leaf-cells oblong-oval to oblong-linear, 2–4 : 1, unipapillose on dorsal surface; basal cells quadrate to irregularly rectangular.

Common to uncommon throughout the Interior Highlands; on smooth-barked hardwood tree trunks and on shaded, moist dolomite, sandstone, and novaculite.

4. *Clasmatodon* Hook. & Wils. *ex* Wils.

1. *Clasmatodon parvulus* (Hampe) Hook. & Wils. *ex* Sull. var. *parvulus*

Plants in thin, light to dark green mats; branches short, irregularly divided, more or less julaceous; leaves crowded, concave, ovate to broadly ovate-lanceolate, slenderly acuminate to abruptly short-acuminate, acute or obtuse in branch leaves; margins plane and entire; costate; median leaf-cells smooth, rhomboidal, 1–3 : 1; alar cells numerous, quadrate, forming across the base to near costa and extending 12–16 rows along margin; seta short, erect; capsule exserted cylindric and symmetric; operculum with a curved beak.

Common throughout the Interior Highlands; on trunks of hardwood trees and on shaded vertical surfaces of rocky bluffs.

Clasmatodon parvulus var. *rupestris* Sull. & Lesq. *ex* Lesq. & James occurs scattered throughout the Boston Mtns. and the Salem and Springfield Plateaus, on shaded, vertical surfaces of rocky bluffs. It may be distinguished from var. *parvulus* by its more densely tufted habit and broadly ovate and obtuse to obtusely acute branch leaves.

33. LESKEACEAE

Plants slender to moderate in size, forming green to light or dark green mats or loose spreading tufts; stems prostrate, subpinnately to pinnately divided; branches erect and ascending; paraphyllia few or none; leaves imbricate when dry, concave to subconcave, ovate to ovate-lanceolate, not to slightly decurrent, apices rounded, obtuse to narrowly acuminate; margins plane to one or both margins revolute, usually entire; costa present, usually ending at middle of leaf or beyond; median leaf-cells papillose, quadrate-hexagonal to oval or elliptic-rhomboid; capsule oval, oblong-cylindric, erect to curved and inclined; peristome double, teeth 16.

a. Apices of leaves hyaline .... 1. *Lindbergia*
a. Apices of leaves green .... 2. *Leskea*

1. *Lindbergia* Kindb.

1. *Lindbergia brachyptera* (Mitt.) Kindb.

Plants procumbent, irregularly branched, in loose tufts; leaves imbricate when dry, broadly deltoid-ovate, acuminate, concave; margins plane, entire or nearly so; costa extending to middle of leaf or beyond; median leaf-cells distinctly papillose, rounded to short-oval or rhombic-hexagonal, longer and hyaline at apex; capsule ovoid-cylindric, erect and symmetric; operculum short-conic.

Common, Boston Mtns., Salem and Springfield Plateaus, unaccountably rare in the Ouachita Mtns., and absent in the Ozark Hills; on bark of hardwoods, never in great abundance.

2. *Leskea* Hedw.

Small to medium-sized plants growing in yellow- to dark green or reddish brown mats or tufts; stems prostrate, pinnately to subpinnately or sparingly branched; branches simple, erect or ascending; paraphyllia few; leaves loosely appressed to subjulaceous when dry, ovate to ovate-lanceolate, apices acute, acuminate, or obtuse; costate; margins plane or revolute, entire to serrulate; median leaf-cells papillose, isodiametric, quadrate-hexagonal; capsule oval to subcylindric, erect or curved; operculum mammillate to long conic.

a. Leaves small, averaging less than 0.6 mm long; median leaf-cells 5–7 μ wide .... 2. *L. australis*
a. Leaves larger, averaging more than 0.7 mm long; median leaf-cells 7–10 μ wide .... b
  b. Capsules curved .... 1. *L. arenicola*
  b. Capsules straight c
c. Stem leaves asymmetric, not plicate, margins not revolute, apices rounded-obtuse to sub-acute .... 4. *L. obscura*
c. Stem leaves symmetric, biplicate, one or both margins usually recurved, apices gradually acute, obtuse, or blunt-pointed .... d
  d. Stem leaves averaging more than twice as long as wide .... 5. *L. polycarpa*
  d. Stem leaves averaging less than twice as long as wide .... 3. *L. gracilescens*

1. *Leskea arenicola* Best

Rare, known only from the western edge of Springfield Plateau near Lamar, Barton County, Missouri; on trunks and logs of hardwoods.

2. *Leskea australis* Sharp

Rare, eastern Ouachita Mtns., Mississippi lowlands, Salem Plateau; on bases of hardwoods and cypress.

3. *Leskea gracilescens* Hedw.

Very common throughout the Interior Highlands; on trunks and bases of hardwoods and shaded rocks, especially along streams.

4. *Leskea obscura* Hedw.

Common throughout the Interior Highlands; on trunks and bases of hardwoods and shaded rocks, especially along streams.

5. *Leskea polycarpa* Hedw. var. *polycarpa*

Uncommon, reported from Ozark Hills (Hauge, 1934), Salem, and Springfield Plateaus (Gier, 1955*a*: 36).

Leskea polycarpa var. *paludosa* (Hedw.) Schimp. has been reported from the Ouachita Mtns., in McCurtain County, Oklahoma, by Sharp (1930). It may be distinguished from var. *polycarpa* by its more robust form and diffuse branches.

34. Thuidiaceae

Plants minute to robust, in bright to dark green mats; main stems creeping; branches simple, pinnate, bipinnate to irregular, ascending; paraphyllia present or absent; leaves erect-spreading, plane or plicate, ovate, ovate-lanceolate to lingulate, apices acuminate to rounded-obtuse; margins plane or recurved, denticulate, serrate, rarely entire; median leaf-cells usually papillose, mostly short and rounded, but occasionally oblong to linear-rhomboidal; branch leaves often different from larger stem leaves; capsule erect and symmetric to inclined and asymmetric; peristome double, teeth 16.

a. Paraphyllia lacking .... b
a. Paraphyllia present c
b. Leaves strongly and irregularly serrate above .... 3. *Herpetineuron*
b. Leaves not strongly and irregularly serrate above .... e
c. Median leaf-cells linear-rhomboidal, 8–15 : 1 .... 6. *Helodium*
c. Median leaf-cells rounded quadrate to short-rectangular .... d
d. Apical cells of branch leaves unipapillate .... 4. *Haplocladium*
d. Apical cells of branch leaves pluripapillate .... 5. *Thuidium*
e. Plants slender; leaf tips green, brittle with many older tips broken off .. 1. *Haplohymenium*
e. Plants robust; if slender, leaf tips hyaline .... 2. *Anomodon*

1. *Haplohymenium* Dozy & Molk.

1. *Haplohymenium triste* (Ces. *ex* De Not.) Kindb.

Anomodon tristis (Ces.) Sull. & Lesq.

Plants in slender, dull green, interwoven mats; stems prostrate, irregularly to subpinnately branching; ultimate branches erect to ascending; leaves appressed when dry, brittle, with tips of older leaves often broken off, ovate-lanceolate, broadly acute to slender at apex; margins crenulate, apices rounded to apiculate; costa ending near middle of leaf; median leaf-cells rounded to polygonal, more or less isodiametric, turgid, pluripapillate on both surfaces; basal cells near costa smooth and elongated.

Very common throughout the Interior Highlands; on hardwoods and cedars and shaded vertical rock surfaces.

2. *Anomodon* Hook. & Tayl.

Plants in yellow to dark green, dense mats or cushions; primary stems creeping, nearly leafless, secondary stems numerous, erect or ascending, sometimes flagelliform; paraphyllia absent; leaves brittle, close, acuminate or lingulate from ovate base; margins plane and entire; costa strong and usually ending below apex; median leaf-cells small, rounded-hexagonal, densely papillose on both surfaces; basal cells smooth and elongated; capsules erect and symmetric; operculum conic or rostrate.

a. Plants slender; leaves acuminate, ending in hair point .... 3. *A. rostratus*
a. Plants coarse; leaves lingulate, not ending in hair point .... b
b. Secondary stems much branched, many attenuate to flagelliform branches evident; leaves often apiculate or toothed at apex .... 1. *A. attenuatus*
b. Secondary stems sparingly branched, attenuate or flagelliform branches absent c
c. Upper portion of leaves lingulate-lanceolate, conspicuously tapering to the apex, somewhat contorted and crisped when dry, often secund; usually growing on rocks .... 5. *A. viticulosus*
c. Upper portion of leaves lingulate, not conspicuously tapering, not secund; usually growing on trees, stumps, or logs .... d
d. Leaves not decurrent, often apiculate, fimbriate-papillose auricles present, somewhat crisped when dry .... 4. *A. rugelii*
d. Leaves decurrent, not apiculate, without auricles, scarcely contorted when dry .... 2. *A. minor*

1. *Anomodon attenuatus* (Hedw.) Hüb.

Very common throughout the Interior Highands; on hardwood tree trunk and bases, stumps, and logs, on shaded rocks and soil.

2. *Anomodon minor* (Hedw.) Fürnr.

Very common throughout the Interior Highlands; on hardwood tree trunks and bases, stumps, and logs, on shaded rocks and soil.

3. *Anomodon rostratus* (Hedw.) Schimp.

Very common throughout the Interior Highlands; on hardwood and cedar tree trunks and bases, stumps, and logs, on shaded, moist rocks. Often extremely abundant with mats covering large areas.

4. *Anomodon rugelii* (C. Müll.) Keissl.

Reported from the Ozark Hills by Hauge (1934).

5. *Anomodon viticulosus* (Hedw.) Hook. & Tayl.

Uncommon, Boston Mtns., Salem and Springfield Plateaus; on shaded vertical limestone and dolomite exposures.

3. *Herpetineuron* (C. Müll.) Card.

1. *Herpetineuron toccoae* (Sull. & Lesq. *ex* Sull.) Card.

Plants loosely caespitose, moderately robust and dark green; secondary stems simple, little divided, densely foliate, often subcircinate; paraphyllia absent; leaves irregularly imbricate when dry, ovate-lanceolate, concave, plicate below, plane above; margins reflexed at base, plane and strongly and irregularly serrate above; costa strong, ending in or near apex; median leaf-cells very small, uniform, rounded-quadrate, thick-walled, smooth; capsule erect and symmetric.

Uncommon, Boston and Ouachita Mtns., Ozark Hills; on moist, shaded, vertical sandstone and novaculite, occasionally on logs.

4. *Haplocladium* (C. Müll.) C. Müll.

Plants in loose yellowish to dark green mats, regularly to pinnately divided; paraphyllia numerous, multiform; stem leaves broadly rounded-ovate to ovate-lanceolate, gradually to abruptly acuminate, rounded at base and narrowed to insertion, scarcely plicate to biplicate; margins plane or revolute, entire or serrate to erose-dentate; costa almost percurrent; branch leaves smaller, less slenderly acuminate; median leaf-cells quadrate-oblong to oval-rhombic or hexagonal, unipapillate; apical cell of branch leaves unipapillate; capsule oblong, curved and inclined to drooping.

a. Stem leaves roundish-ovate, scarcely plicate, abruptly acuminate to a broad, oblong point; margins erose-serrate .... 2. *H. virginianum*
a. Stem leaves gradually long-acuminate, biplicate; margins crenulate-serrate or entire .... 1. *H. microphyllum*

1. *Haplocladium microphyllum* (Hedw.) Broth.

Uncommon throughout the Interior Highlands; on shaded, moist, tree bases, rocks, and soil.

2. *Haplocladium virginianum* (Brid.) Broth.

Very common throughout the Interior Highlands; on shaded rocky soil, tree bases, and rock ledges, particularly of open, upland hardwood forests.

5. *Thuidium* B.S.G.

Minute to robust plants in yellowish, greenish or brownish mats; stems creeping, ascending or erect, pinnately branched, often regularly and in one plane; branches simple, pinnate or bipinnate; paraphyllia numerous, simple or branched; stem leaves ovate-triangular to oblong-lanceolate, acuminate, cordate, strongly costate, papillose on one or both surfaces; branch leaves smaller, ovate to ovate-lanceolate; apical cell pluripapillate; capsule oblong-cylindric, unsymmetric, suberect to pendulous; operculum short-conic to long-rostrate.

a. Plants small to minute; paraphyllia few, small, mostly 2–6 cells long .... b
a. Plants large; paraphyllia many, more or less branched c
  b. Branches papillose .... 4. *T. pygmaeum*
  b. Branches smooth .... 3. *T. minutulum*
c. Stem leaves spreading-recurved, abruptly narrowed to a long acumen; costa ending below apex but continued by a series of long, narrow cells that fill the apex; papillae of paraphyllia located close to forward septum; perichaetial leaves not ciliate .... 2. *T. recognitum*
c. Stem leaves erect-spreading, gradually acuminate; costa ending below apex, cells of acumen never long, similar to those of rest of leaf; papillae of paraphyllia borne medianly; perichaetial leaves ciliate .... 1. *T. delicatulum* var. *delicatulum*

1. *Thuidium delicatulum* (Hedw.) B.S.G. var. *delicatulum*

Common throughout the Interior Highlands; on moist, shaded soil, humus, and rock ledges. Often very abundant.

Thuidium delicatulum var. *radicans* Crum, Steere & Anderson has been reported from the Salem Plateau by Gier (1955*a*: 38). It may be distinguished from var. *delicatulum* by the long, slender and hyaline apex of its stem leaves.

2. *Thuidium recognitum* (Hedw.) Lindb.

Very common throughout the Interior Highlands; on dry, open, rock, calcareous soil, particularly of upland hardwood and hardwood-pine forests. Often very abundant.

3. *Thuidium minutulum* (Hedw.) B.S.G.

Uncommon throughout the Interior Highlands; on shaded logs and tree bases, occasionally on stones.

4. *Thuidium pygmaeum* B.S.G.

Common throughout the Interior Highlands; on moist, shaded rocks along creeks and gullies.

6. *Helodium* (Sull.) Warnst.

1. *Helodium paludosum* (Sull.) Aust.

Plants in green to yellowish green deep, soft, tufts, branching irregularly pinnate; paraphyllia dense, filamentous and branched; stem leaves erect spreading when moist, plicate-striate, oblong- to ovate-lanceolate, narrowly to scarcely decurrent at base; margins revolute below, sinuate-serrulate above; costa nearly percurrent; median leaf-cells long, 8–15 : 1, oblong to linear-rhomboidal, smooth or only slightly papillose at distal ends of dorsal surface; branch leaves narrower and smaller, less slenderly acuminate; capsule oblong-cylindric, curved, inclined to horizontal.

Rare, known only from Ozark Hills in Pope County, Illinois, at Azotus Spring, on open wet soil of a seep spring.

35. AMBLYSTEGIACEAE

Plants creeping and irregularly to pinnately branching; leaves straight to secund, imbricate, erect-spreading to squarrose-spreading, oblong-ovate, ovate-lanceolate to triangular, cordate, acuminate to rounded or obtuse; margins entire to serrulate, plane or recurved, sometimes composed of elongated cells; costa single, short to percurrent or excurrent, sometimes short and double or absent; median leaf-cells smooth, hexagonal, rhomboidal to narrowly linear; alar cells often enlarged and inflated, colored or hyaline, often decurrent; seta usually tall, reddish or red, smooth; capsule usually curved, unsymmetric, cernuous, often contracted below mouth when dry; peristome double.

a. Paraphyllia present on stem .... 1. *Cratoneuron*
a. Paraphyllia absent .... b
  b. Leaves with a distinct border of elongated, thick-walled cells .... 3. *Sciaromium*
  b. Leaves without a distinct border of elongated, thick-walled cells c
c. Leaves falcate-secund; alar cells large, inflated and markedly decurrent .... 6. *Drepanocladus*
c. Leaves not falcate-secund; if falcate secund, alar cells not large, inflated, and decurrent .... d
  d. Plants small, very slender; leaves averaging less than 0.6 mm long .... 5. *Platydictya*
  d. Plants not small and very slender; leaves averaging more than 0.6 mm long; if smaller, widely spreading to squarrose .... e
e. Alar cells in distinct, more or less well defined group; leaves widely spreading, recurved .... 2. *Campylium*
e. Alar cells not in a distinct group; leaves erect spreading to widely spreading, not recurved .... 4. *Amblystegium*

1. *Cratoneuron* (Sull.) Spruce

1. *Cratoneuron filicinum* (Hedw.) Spruce var. *filicinum*

Plants green, yellowish green, or golden yellow, mostly irregularly to pinnately branched; branches slender, short, stiff, usually hooked at apex; paraphyllia oval to lanceolate, divided, numerous to few on stem; stem leaves erect-spreading to slightly falcate, oval to triangular, apices acuminate, bases decurrent, cordate; margins serrulate to denticulate; costa single, percurrent or excurrent; median leaf-cells smooth, elliptic-hexagonal, rectangular to oblong-linear; alar cells hyaline or colored, abruptly inflated, rectangular, extending from margin to costa or nearly so; capsule cylindrical, curved; peristome double.

Uncommon, Boston Mtns., Salem Plateau; in wet, usually calcareous habitats. This species is highly variable and small slender forms may be confused with *Amblystegium varium*, particularly if paraphyllia are few; however, inflated alar cells are lacking in *A. varium*. Some confusion with *Drepanocladus aduncus* is also possible; however, that species always lacks paraphyllia, its leaves are falcate-secund, and its inflated alar cells do not usually reach the costa.

2. *Campylium* (Sull.) Mitt.

Plants slender or robust, in yellowish to golden brownish mats, branching irregularly from prostrate stem; leaves squarrose, ovate, ovate-lanceolate to triangular-cordate, apices long to abruptly acuminate, bases often decurrent; margins entire to serrulate; costa single and reaching middle of leaf, or short and double, or absent; median leaf-cells smooth, oblong-linear, prosenchymatous, 3–10 : 1; alar cells in distinct group, quadrate, subrectangular, often thick-walled and slightly inflated; seta long; capsule oblong-cylindric, curved, contracted beneath mouth when dry and empty; peristome double, teeth 16.

a. Leaves 1–1.5 mm long; costa single, reaching middle of leaf or beyond .. 2. *C. chrysophyllum*
a. Leaves 0.8 mm or less long; costa short and double, or absent .... 1. *C. hispidulum*

1. *Campylium hispidulum* (Brid.) Mitt.

Two varieties of this species are recognized, and although their differences are not striking, they can be separated on the basis of the following key (for extensive discussion see: Andrews, 1957: 129–133).

a. Leaves squarrose, abruptly acuminate; alar cells well differentiated .... 1a. *C. hispidulum* var. *hispidulum*
a. Leaves erect-spreading, slenderly acuminate; alar cells poorly differentiated .... 1b. *C. hispidulum* var. *sommerfeltii*

1a. *Campylium hispidulum* var. *hispidulum*

Very common throughout the Interior Highlands; particularly around bases of hardwood trees, on decaying wood and on calcareous soil, occasionally on rocks.

1b. *Campylium hispidulum* var. *sommerfeltii* (Myr.) Lindb.

Reported from the western Salem Plateau and the Springfield Plateau by Gier (1955*a*: 33).

2. *Campylium chrysophyllum* (Brid.) J. Lange

Two varieties are recognized in the Interior Highlands and may be separated as follows:

a. Plants very robust; leaves more or less falcate, apex usually serrate .... 2b. *C. chrysophyllum* var. *brevifolium*
a. Plants large; leaves not falcate, apex entire .... 2a. *C. chrysophyllum* var. *chrysophyllum*

2a. *Campylium chrysophyllum* var. *chrysophyllum*

Very common throughout the Interior Highlands; on open to shaded soil, rocks, tree bases. Often very abundant.

2b. *Campylium chrysophyllum* var. *brevifolium* (Ren. & Card.) Grout

Uncommon, Salem and Springfield Plateaus; on moist, shaded soil and rocks.

3. *Sciaromium* Mitt.

1. *Sciaromium lescurii* (Sull.) Broth.

Platylomella lescurii (Sull.) Andrews

Plants in loose, dark green mats, branching irregularly; stem leaves loosely spreading, broadly cordate-ovate to oblong-ovate, abruptly acuminate to subobtuse, serrulate at apex, bordered by rows of thick-walled, elongated cells; costa thick, reaching apex where confluent with border; median leaf-cells, smooth, oblong-hexagonal to short-rhomboidal, 1–3 : 1; basal cells and alar cells more or less rectangular; branch leaves narrower, ovate-lanceolate to lingulate, often obtuse, border of thick-walled cells indistinct; capsule cylindrical, curved and cernuous.

Common, Boston and Ouachita Mtns., uncommon Ozark Hills, Salem and Springfield Plateaus; on acidic rocks in and along edge of gullies, creeks, and streams.

As has been suggested earlier (Grout, 1931: 75), this species resembles the *Hygroamblystegium* complex of the genus *Amblystegium*. It should probably be assigned to that genus.

4. *Amblystegium* B.S.G.

The treatment of this very complicated genus follows the suggestion by Conard (1959) in that it includes the genera *Leptodictyum* and *Hygroamblystegium*, a procedure also followed by Nyholm (1965: 482–493). As noted by Conard, this is a return to the broad concept of the genus *Amblystegium* used by the authors of *Bryologia Europaea*, 1853. Considering the continuum of variation from *Leptodictyum* to *Hygroamblystegium* to *Amblystegium* (*sensu stricto*), this procedure seems entirely reasonable.

Plants slender to robust, light to dark green, mostly irregularly divided; leaves erect-spreading to widely spreading, sometimes almost complanate, triangular-ovate, ovate-lanceolate to lanceolate, apices short acuminate to long acuminate, tips acute to occasionally obtuse, bases narrowed, rounded or almost cordate to insertion; margins plane, entire to serrulate; costa extending to middle of leaf, percurrent or excurrent; median leaf-cells smooth, elongate-hexagonal to linear, 2–16 : 1; alar cells usually indistinctly limited, short-rectangular to rectangular, sometimes a few inflated; seta long, smooth, often twisted, reddish; capsule subcylindric, unsymmetric to arcuate, inclined to horizontal, contracted below mouth when dry; operculum conic, obtuse to apiculate; peristome double, teeth 16.

There is probably no other genus of mosses in the Interior Highlands where the characters separating species are so unclear. This may be due to environmental effects on growth, it may be genetical, or it may be a combination of both. The latter seems highly probable. The following key is an attempt to segregate the numerous perplexing forms into groups that correspond to currently recognized taxa. It may well be that many of the varieties should be species, although it is also possible that they are only forms. It is also a distinct possibility that some species are only varieties or even just forms. A careful monograph of this genus is long overdue, and until such time as this can be done, the parameters of the taxa included in this key should be considered tentative.

a. Median leaf-cells averaging 8–16 : 1 .... 1. *A. riparium*
a. Median leaf-cells averaging 3–8 : 1 .... b
    b. Costa of stem leaves subpercurrent, percurrent, or excurrent c
    b. Costa of stem leaves ending near middle of leaf .... g
c. Plants not aquatic; leaves broadly ovate-lanceolate, abruptly narrowed into a long, narrow acumen .... d
c. Plants aquatic; leaves cordate-ovate, triangular-ovate, oblong-lanceolate, oblong-ovate, not abruptly narrowed into long, narrow acumen .... e
    d. Leaves widely spreading; costa extending 6/7 length of leaf .... 3. *A. trichopodium*
    d. Leaves erect-spreading; costa percurrent or nearly so .... 8. *A. varium*
e. Leaves narrowed to base .... 9. *A. tenax*
e. Leaves rounded to base .... f
    f. Many leaves with very strong, excurrent costa .... 11. *A. noterophilum*
    f. Costa percurrent in most leaves .... 10. *A. fluviatile*
g. Plants robust, somewhat complanate, distinctly aquatic, usually growing in swiftly flowing water .... 5. *A. laxirete*
g. Plants smaller, growing on moist substrates, but not aquatic .... h
    h. Leaves erect-spreading; basal cells quadrate to tranversely elongate i
    h. Leaves widely spreading; basal cells oblong to rectangular .... j
i. Leaves short acuminate .... 2. *A. brevipes*
i. Leaves long acuminate .... 6. *A. serpens*
    j. Leaf margins almost entire .... 4. *A. kochii*
    j. Leaf margins serrulate .... 7. *A. juratzkanum*

1. *Amblystegium riparium* (Hedw.) B.S.G.

Leptodictyum riparium (Hedw.) Warnst.

A number of poorly defined forms of this species are recognized and may be separated by the following characters suggested by Conard (1959: 102–103).

a. Apex of leaf acute, ending in mostly 2 cells .... 1e. *A. riparium* fo. *obtusum*
a. Apex acuminate to slenderly acuminate, ending mostly in 1 cell .... b
    b. Plants of wet habitats, but not floating or submerged .... 1a. *A. riparium* fo. *riparium*
    b. Plants floating or submerged c
c. Plants usually floating; leaves 3.5–5 mm long, acumination very long filiform .... d
c. Plants submerged-floating; apices long and filiform .... 1c. *A. riparium* fo. *fluitans*
    d. Leaves crowded, imbricate .... 1b. *A. riparium* fo. *elongatum*
    d. Leaves distant .... 1d. *A. riparium* fo. *longifolium*

1a. *Amblystegium riparium* fo. *riparium*

Common throughout the Interior Highlands; on wet soil, decaying wood, and rocks.

1b. *Amblystegium riparium* fo. *elongatum* (B.S.G.) Moenk.

Leptodictyum riparium var. *elongatum* (B.S.G.) Warnst.

Uncommon, Salem and Springfield Plateaus; on rock in creeks and streams.

1c. *Amblystegium riparium* fo. *fluitans* (Lesq. & James) Grout

Reported from the northern Salem Plateau (Hickory Co., Missouri) by Gier (1955*a*: 36).

1d. *Amblystegium riparium* fo. *longifolium* (Schultz) Warnst.

Rare, Boston and Ouachita Mtns., eastern Salem Plateau; on rocks in streams and creeks.

1e. *Amblystegium riparium* fo. *obtusum* (Grout) Grout

Common, Boston Mtns., Salem and Springfield Plateaus; on rocks (mostly calcareous) in swiftly flowing water.

2. *Amblystegium brevipes* Card. & Thér.

Leptodictyum brevipes (Card. & Thér. *ex* Holz.) Broth.

Rare, eastern Salem Plateaus; on moist shaded soil.

3. *Amblystegium trichopodium* (Schultz) Hartm.

Leptodictyum trichopodium (Schultz) Warnst.

Uncommon, Salem and Springfield Plateaus; on moist rocks and soil.

4. *Amblystegium kochii* B.S.G.

Leptodictyum trichopodium var. *kochii* Lindb.

Common, Salem and Springfield Plateaus; on moist rocks, decaying wood, and soil.

Large forms of *Amblystegium juratzkanum* may easily be confused with this species. Some forms can be confused with *A. varium* or *A. tenax*. Certainly the relation between these taxa is perplexing and in crying need of biosystematic study.

5. *Amblystegium laxirete* Card. & Thér.

Uncommon, Boston and Ouachita Mtns., Salem and Springfield Plateaus; usually on calcareous rocks in swiftly flowing water.

6. *Amblystegium serpens* (Hedw.) B.S.G.

Common throughout the Interior Highlands; on moist shaded rocks, woods, and soil. Occasionally on the bases of trees.

7. *Amblystegium juratzkanum* Schimp.

Uncommon, Boston Mtns., Ozark Hills, Prairies, Plains, Salem and Springfield Plateaus; on shaded moist rocks, rotten wood, and soil.

Nyholm (1965: 484–485) treats this species as a variety of *Amblystegium serpens.*

8. *Amblystegium varium* (Hedw.) Lindb.

Two varieties may be recognized in the Interior Highlands and may be separated as follows:

a. Leaves concave, round-ovate; median leaf-cells 2 : 1 .... 8b. *A. varium* var. *ovatum*
a. Leaves slightly concave, ovate-lanceolate; median leaf-cells 2–5 : 1 .... 8a. *A. varium* var. *varium*

8a. *Amblystegium varium* var. *varium*

Common throughout the Interior Highlands; on moist, shaded soil, rocks, logs, and tree bases.

May be confused with *Amblystegium kochii* or *A. tenax*, see note under first species.

8b. *Amblystegium varium* var. *ovatum* (Grout) Grout

Rare, Salem and Springfield Plateaus; on tree bases.

9. *Amblystegium tenax* (Hedw.) C. Jens.

Amblystegium irriguum B.S.G.
Hygroamblystegium irriguum (Wils.) Loeske
Hygroamblystegium tenax (Hedw.) Jenn.

Two varieties of this species are recognized in the Interior Highlands and may be separated as follows:

a. Costa very thick, wide, percurrent to long often ending diffusely in apex, excurrent .... 9b. *A. tenax* var. *spinifolium*
a. Costa thick, extending ¾ length of blade to percurrent, not ending diffusely in apex .... 9a. *A. tenax* var. *tenax*

9a. *Amblystegium tenax* var. *tenax*

Very common throughout the Interior Highlands; on rocks, decaying wood, and tree bases in creeks, streams and seepage areas.

9b. *Amblystegium tenax* var. *spinifolium* (Schimp.) Jenn.

Common, Boston Mtns., Salem and Springfield Plateaus; on rocks in swiftly flowing streams, creeks, and spring branches, rarely where seepage occurs.

10. *Amblystegium fluviatile* (Hedw.) B.S.G.

A highly variable taxon in which three varieties and one form have been recognized in the Interior Highlands. These may be separated as follows:

a. Leaves broadly cordate-ovate; costa narrowing from base to apex .... 10b. *A. fluviatile* var. *orthocladon*
a. Leaves ovate, ovate-lanceolate; costa not narrowing noticeably from base to apex .... b
  b. Leaves broadly ovate, apices broadly obtuse .... 10c. *A. fluviatile* var. *ovatum*
  b. Leaves oblong-lanceolate to oblong-ovate, apices subobtuse c
c. Leaves oblong-lanceolate; costa ending below apex .... 10a(1). *A. fluviatile* var. *fluviatile* fo. *fluviatile*
c. Leaves ovate-lanceolate, costa ending diffusely in apex .... 10a(2). *A. fluviatile* var. *fluviatile* fo. *brevifolium*

10a(1). *Amblystegium fluviatile* var. *fluviatile* fo. *fluviatile*

Common throughout the Interior Highlands; on moist shaded soil, rocks, and decaying wood, often submerged in streams and creeks.

10a(2). *Amblystegium fluviatile* var. *fluviatile* fo. *brevifolium* Moenk.

Uncommon, Boston Mtns., Salem and Springfield Plateaus; on submerged rocks, especially of spring branches.

10b. *Amblystegium fluviatile* var. *orthocladon* (P. Beauv.) Crum, Steere & Anderson

Common throughout the Interior Highlands; on rocks in creeks and streams.

10c. *Amblystegium fluviatile* var. *ovatum* Grout

Uncommon, Boston Mtns., Salem and Springfield Plateaus; on moist rocks along or in creeks and streams.

11. *Amblystegium noterophilum* (Sull. & Lesq.) Holz.

Uncommon, Salem and Springfield Plateaus; on rocks in stream and spring branches.

5. *Platydictya* Berk.

Plants quite small and very slender, irregularly branching, creeping, light to dark green; leaves small, 0.1–0.6 mm, erect-spreading, narrowly triangulate, ovate-lanceolate, to linear-lanceolate, apex acute slenderly acuminate; margins plane, entire or serrulate; costa short or absent; median leaf-cells oblong-hexagonal to rhomboidal, 2–4 : 1, smooth; alar cells usually quadrate but sometimes rectangular, often numerous and extending 5–10 cells up the margin; seta short, about 5 mm long; capsule erect to horizontal, symmetric to curved; peristome double.

a. Plants growing on trees; leaves with a short, single costa .... 2. *P. subtile*
a. Plants growing on rocks; leaves ecostate or nearly so .... b
  b. Leaves usually serrate to denticulate .... 3. *P. jungermannioides*
  b. Leaves, entire or nearly so c
c. Leaves scarcely narrowed to insertion; alar cells rectangular .... 4. *P. minutissimum*
c. Leaves narrowed to insertion; alar cells quadrate .... 1. *P. confervoides*

1. *Platydictya confervoides* (Brid.) Crum
Amblystegiella confervoides (Brid.) Loeske

Common, Boston Mtns., Ozark Hills, Prairie Plains, Salem and Springfield Plateaus; on open to shaded calcareous rocks.

The extreme smallness of this species, leaves usually less than 0.2 mm long, its epilithic habitat, and entire leaves that are narrowed to insertion serve to distinguish it from other species in the Interior Highlands.

2. *Platydictya subtile* (Hedw.) Crum
Amblystegiella subtilis (Brid.) B.S.G.

Uncommon, Boston and Ouachita Mtns., Salem and Springfield Plateaus; on trunks and bases of trees.

This species is the largest of the genus. Leaves may be up to 0.6 mm long, are ovate-lanceolate with a short single costa, and numerous quadrate alar cells.

3. *Platydictya jungermannioides* (Brid.) Crum

Amblystegiella sprucei (Bruch) Loeske

Reported from Conway County, Arkansas, by Moore (1965).

4. *Platydictya minutissimum* (Sull. & Lesq. *ex* Sull.) Crum

Amblystegiella minutissima (Sull. & Lesq.) Nickols

Rare, Boston Mtns., in crevices of moist sandstone.

Crum (1969: 244) concludes that this species deserves recognition because of its small size, linear-lanceolate leaves that are scarcely narrowed to the insertion, and median leaf-cells that are up to 3–6 : 1.

6. *Drepanocladus* (C. Müll.) Roth

1. *Drepanocladus aduncus* (Hedw.) Warnst.

Plants in dark to yellowish green, loosely intertangled mats or dense tufts; stems irregularly to pinnately branched; stem leaves usually secund and often falcate, broadly triangular-ovate, acute to slenderly acuminate, long-lanceolate to filiform-acuminate in aquatic forms; costate to middle of leaf; margins entire; auricles large, decurrent and composed of strongly inflated, usually hyaline cells that may reach the costa; median leaf-cells smooth, linear-flexuose to oblong-hexagonal; branch leaves smaller, different in shape and often more falcate; seta ca. 2.5 cm long; capsules oblong, curved and cernuous.

a. Lower leaf-cells linear .... 1a. *D. aduncus* var. *aduncus*
a. Lower leaf-cells oblong-hexagonal .... 1b. *D. aduncus* var. *polycarpus*

1a. *Drepanocladus aduncus* var. *aduncus*

Uncommon, Salem and Springfield Plateaus; on shaded moist rocks and soil along wet ledges of limestone bluffs or cedar glades.

1b. *Drepanocladus aduncus* var. *polycarpus* (Bland. *ex* Voit) Roth

Uncommon, Salem and Springfield Plateaus; habitats same as var. *aduncus*.

36. BRACHYTHECIACEAE

The following treatment is based, in part, on the recent generic revision of this family by Robinson (1962) and his later taxonomic changes (Robinson, 1965: 319; 1967: 38).

Plants prostrate, branches terete-foliate to complanate-foliate, creeping to ascending or erect and densely caespitose, irregularly to pinnately divided, green to yellowish green; leaves loosely to closely imbricated to julaceous, often heterophyllous, in some taxa plicate, lanceolate, ovate-lanceolate, ovate, to broadly triangular, apex acuminate, acute, short acuminate to obtuse, often twisted, bases often decurrent or cordate-auriculate; margins subserrulate to sharply serrate, often revolute; costa single, well developed, often spinose on back; median leaf-cells elongate, smooth or papillose on back by projecting cell ends; alar cells often numerous, quadrate to rectangular, lax to inflated; seta reddish, elongate, smooth or rough; capsule inclined to rarely erect; peristome double; calyptra cucullate, smooth or rarely hairy.

a. Plants slender and small, often with elongate gemmae or rhizoids present on back of costa, growing on rocks .... 6. *Rhynchostegiella*
a. Plants not slender and small, no gemmae or rhizoids on back of costa; if plants small and slender, leaves abruptly acuminate, and usually growing on trees .... b
  b. Leaves broadly ovate, very concave, cordate-auriculate and clasping the stem .... 5. *Bryoandersonia*
  b. Leaves not broadly ovate, concave, or cordate-auriculate and clasping the stem c
c. Leaves papillose on back by projecting cell ends .... 4. *Bryhnia*
c. Leaves not papillose .... d
  d. Leaves distinctly plicate .... 3. *Brachythecium*
  d. Leaves not distinctly plicate .... e
e. Alar cells usually small and quadrate, never lax or inflated .... f
e. Alar cells lax or inflated .... g
  f. Leaves lanceolate, small quadrate alar cells numerous, sharply serrate from base to apex .... 1. *Homalothecium*
  f. Leaves ovate or ovate-lanceolate, small alar cells not numerous; if leaves lanceolate or quadrate alar cells numerous, not sharply serrate from base to apex .... h
g. Calyptra with hairs; leaves rather abruptly acuminate; median leaf-cells less than 5 times as long as wide .... 2. *Homalotheciella*
g. Calyptra not hairy; leaves not abruptly acuminate; median leaf-cells more than 5 times as long as wide .... h
  h. Branch leaves blunt or acute, tips filled with cells distinctly shorter than median cells, usually sharply serrate .... 7. *Rhynchostegium*
  h. Branch leaves acuminate to long-acuminate, tips not filled with cells distinctly shorter than median leaf cells .... 3. *Brachythecium*

1. *Homalothecium* B.S.G.

1. *Homalothecium leskeoides* (Hook.) Robins.

Palamocladium leskeoides (Hook.) Britt.

Plants robust, irregularly branched, yellowish green; leaves not plicate, lanceolate; margins coarsely serrate; costa extending about ⅔ length of blade; median leaf-cells smooth, linear-fusiform, 6–8 : 1; alar cells quadrate; sporophytes rather erect and unsymmetric.

Rare, southwestern Springfield Plateau; on vertical limestone. Known only from Cherokee Co., Oklahoma, along Terapin Creek near Hwy. 82, Sect. 24, T. 14 N., R. 22 W.

2. *Homalotheciella* (Card.) Broth.

1. *Homalotheciella subcapillata* (Hedw.) Broth.

Plants in thin glossy, yellowish mats, creeping, irregularly to subpinnately branching; leaves not plicate, imbricate, ovate to elliptical-oblong, abruptly acuminate, more or less serrate above, concave; costa extending to middle of leaf or beyond; median cells smooth, linear-fusiform 8–9 : 1; quadrate alar cells numerous, bordering lower ¼ of leaf; capsule sub-erect to nearly horizontal, brown, oblong and slightly curved, swollen on one side; operculum convex-conic, short rostrate; peristome double, teeth 16, brownish yellow to dark red; calyptra cucullate, hairy.

Common throughout the Interior Highlands; on trees or rarely on calcareous rocks.

This species often grows mixed with other corticolous species. When sporophytes are present, the hairy calyptra is distinctive since such a condition is found in only one other corticolous moss in the Interior Highlands, *Forsstroemia*, which is a much more robust plant with julaceous branches.

3. *Brachythecium* B.S.G.

Plants terete-foliate, sometimes prostrate and complanate-foliate; branches often densely caespitose, irregularly to pinnately divided; leaves lanceolate to ovate-lanceolate, acuminate, sometimes plicate and decurrent; margins plane, rarely entire; costa single, from ½–¾ the length of the blade; median leaf-cells fusiform to rhomboid-fusiform, 4–8 : 1 to 8–12 : 1; alar cells small and quadrate to short rectangular, lax or inflated, often forming a distinct area extending from margin to costa; autoicous or dioicous; seta smooth or rough; capsule erect and symmetrical to horizontal and unsymmetrical; peristome double, teeth 16; calyptra cucullate, smooth.

a. Alar cells numerous, quadrate to short-rectangular, forming a distinct triangular area from margin to costa .... 1. *B. acuminatum*
a. Alar cells not as above, lax or inflated, if quadrate to subquadrate, not forming a distinct triangular area from margin to costa .... b
  b. Alar cells, enlarged, lax or inflated c
  b. Alar cells quadrate to subquadrate, little enlarged, not lax or inflated .... f
c. Leaves broadly decurrent; alar cells inflated; plants generally aquatic .... 7. *B. rivulare*
c. Leaves not broadly decurrent; alar cells enlarged, lax, but not inflated; plants not aquatic .... d
  d. Branch leaves plicate .... 2. *B. salebrosum*
  d. Branch leaves not plicate .... e
e. Seta rough; operculum conic; plants generally terete-foliate .... 6. *B. rutabulum*
e. Seta smooth; operculum long rostrate; plants generally complanate-foliate .... 9. *B. serrulatum*
  f. Leaves not plicate .... 8. *B. plumosum*
  f. Leaves plicate .... g
g. Capsule nearly erect .... 3. *B. oxycladon*
g. Capsule inclined to horizontal .... h
  h. Seta minutely roughened; main stem leaves with serrate margins .... 5. *B. campestre*
  h. Seta smooth; stem leaves with margins entire or nearly so .... 4. *B. calcareum*

1. *Brachythecium acuminatum* (Hedw.) Rau & Herv.

Chamberlania acuminatum (Hedw.) Grout

Common throughout the Interior Highlands; on tree bases, logs, and soil around trees.

Two varieties are often recognized. They may be distinguished as follows (Welch, 1957):

a. Stem leaves deeply concave, ovate to ovate-lanceolate; apices acute to short acuminate; median leaf-cells 4–8 : 1 .... *B. acuminatum* var. *cyrtophylla*
a. Stem leaves slightly concave, lanceolate to ovate-lanceolate; apices acuminate; median leaf-cells 5–10 : 1 .... *B. acuminatum* var. *acuminatum*

2. *Brachythecium salebrosum* (Web. & Mohr) B.S.G.

   Brachythecium acutum (Mitt.) Sull.
   Chamberlania salebrosa (Web. & Mohr) Robins.

Common throughout the Interior Highlands; on rocks or thin soil over rocks.

Robinson (1962) considers *Brachythecium acutum* to be only a variation of *B. salebrosum* with non-plicate leaves.

3. *Brachythecium oxycladon* (Brid.) Jaeg. & Sauerb.

   Chamberlania oxyclada (Brid.) Robins.

Very common throughout the Interior Highlands; on various types of substrate from thin soil over rocks to open rocky soil or in pastures.

4. *Brachythecium calcareum* Kindb.

   Brachythecium flexicaule Ren. & Card.
   Chamberlania calcarea (Kindb.) Robins.

Uncommon throughout the Interior Highlands; on soil, particularly around the bases of trees.

This species is distinctive in that it has both mostly entire leaves and a smooth seta.

5. *Brachythecium campestre* (C. Müll.) B.S.G.

   Chamberlania campestris (B.S.G.) Robins.

Reported from Hot Springs, Garland County, Arkansas, in the Ouachita Mtns., by Scully (1941).

6. *Brachythecium rutabulum* (Hedw.) B.S.G.

Uncommon throughout the Interior Highlands; on shaded soil.

This species differs from *Brachythecium serrulatum* by usually being terete-foliate and having a rough seta and rostrate operculum. Robinson (1962) feels that gametophytic characters are unreliable and consequently sterile plants cannot be determined with certainty. Consequently, when sterile plants that are complanate-foliate are assigned to *B. serrulatum* and terete-foliate plants to *B. rutabulum*, the chance for error is obviously great.

7. *Brachythecium rivulare* B.S.G.

Common throughout the Interior Highlands; on logs or rocks in aquatic habitats. Often very abundant in spring branches.

The strikingly decurrent leaves with alar cell both inflated and with thick, often porous walls sets this species apart from all other *Brachythecia* in the Interior Highlands.

8. *Brachythecium plumosum* (Hedw.) B.S.G.

   Brachythecium flagellare (Hedw.) Jenn.

Uncommon throughout the Interior Highlands; on thin soils overlying acidic rocks.

9. *Brachythecium serrulatum* (Hedw.) Robins.

Eurhynchium serrulatum (Hedw.) Kindb.
Rhynchostegium serrulatum (Hedw.) Jaeg. & Sauerb.

Very common throughout the Interior Highlands; on open to shaded soil and rocks.

Easily confused with *Brachythecium rutabulum* (see discussion under that species).

4. *Bryhnia* Kaur.

Plants slender, in prostrate mats, bright green, pale green to yellowish green, irregularly divided; branches erect-ascending, terete-foliate, often subjulaceous; leaves of branches loosely imbricate when dry, erect-spreading when moist, ovate, broadly ovate to ovate-lanceolate, decurrent, apex acuminate, sometimes twisted; margins serrulate to sharply serrate; costa extending to near middle of leaf, often ending in spine on back; median leaf-cells oblong-hexagonal to linear-oblong and flexuose, 4–8 : 1, papillose on back by angles of cell wall; alar cells slightly enlarged; seta 8–15 mm long, red, very rough; capsule cernuous to horizontal, oval to oblong-cylindric; operculum conic; peristome double, teeth 16.

a. Branch leaves broadly to ovate-lanceolate, broadly decurrent, apices twisted one-half turn to right; costa not ending in a well developed spine; papillae often obscure .... 1. *B. novae-angliae*
a. Branch leaves narrowly ovate-lanceolate, narrowly decurrent, apices not twisted; costa ending in a well developed spine; strongly papillose .... 2. *B. graminicolor*

1. *Bryhnia novae-angliae* (Sull. & Lesq. *ex* Sull.) Grout

Rare, Ozark Hills, eastern Salem Plateau, Springfield Plateau; on moist shaded sandstone.

2. *Bryhnia graminicolor* (Brid.) Grout var. *graminicolor*

Common throughout the Interior Highlands; on soil and rocks in moist shaded areas.

Bryhnia graminicolor var. *holzingeri* (Ren. & Card.) Grout has been reported from the Salem and Springfield Plateaus by Gier (1955*a*: 32). It may be separated from var. *graminicolor* by its more densely caespitose, shorter branches with leaves that are broader and shorter acuminate. This is probably not a good variety.

5. *Bryoandersonia* Robins.

1. *Bryoandersonia illecebra* (Hedw.) Robins.

Cirriphyllum boscii (Schwaegr.) Grout
Cirriphyllum illecebrum (Hedw.) L. Koch

Plants creeping or with julaceous branches in erect, dense tufts, robust, light to golden or brownish green; leaves closely imbricate, concave, broadly ovate, cordate-auriculate bases clasping the stem, short-acuminate apexes, often twisted; costa extending ⅓–⅔ the length of leaf; median leaf-cells linear, 10–15 : 1; basal cells shorter, often strongly porose; seta elongate; capsule inclined, oval to oblong-oval; operculum long-rostrate; peristome double; calyptra cucullate.

Very common throughout the Interior Highlands; on open to shaded dry rocky soil to moist, shaded rock ledges, and soil banks. Frequently very abundant with mats covering large areas.

6. *Rhynchostegiella* (B.S.G.) Limpr.

1. *Rhynchostegiella compacta* (C. Müll.) Loeske subsp. *compacta*

Amblystegium compactum (C. Müll.) Aust.

Plants small and slender in yellowish green, dense tufts; stems irregularly branching, radiculose, rhizoids often minutely scabrous; leaves erect-open, narrowly decurrent, ovate-lanceolate, ca. 1 mm long, lanceolate and smaller on branches, gradually and evenly acuminate; margins finely denticulate, teeth at base frequently recurved or double by the protruding angles of two adjacent cells; costa percurrent, frequently with rhizoids or delicate elongated gemmae present on back; leaf-cells linear-rhomboidal, thin-walled, 4–10:1; basal cells shortly rectangular to quadrate; seta 1–3 cm long; capsule oblong, erect or nearly so; symmetric, operculum conic-apiculate; peristome double.

Uncommon, Ozark Hills and Salem Plateau; on shaded, moist limestone or sandstone, usually forming extensive loose mats.

Robinson (1965: 318) does not agree with the placement of this species in the genus *Rhynchostegiella*, but retains it in the genus *Amblystegium*.

7. *Rhynchostegium* B.S.G.
(*sensu* Robinson, Bryologist 70:38. 1967)

Plants with irregularly divided branches erect to ascending from prostrate stems, dark green to yellowish green, often slightly glossy; branch leaves loosely to closely imbricate, often dimorphic, sometimes slightly plicate, broadly triangular to orbicular, apex acute in stem leaves, obtuse in branch leaves, leaf bases not to slightly decurrent; margins plane, serrate; costate from ½ to more than ¾ the length; median cells 5–15 : 1, linear-oblong; apical cells distinctly shorter; capsules inclined to horizontal, ovoid to oblong-cylindric; operculum long-rostrate; peristome double.

a. Plants aquatic or subaquatic, robust, stems woody or wiry; seta smooth .... 3. *R. riparioides*
a. Plants not aquatic, not robust, stems not woody or wiry; seta rough or smooth .... b
  b. Seta rough; branch leaves broadest ⅓ above base; stem leaves obtusely acute, not decurrent .... 2. *R. hians*
  b. Seta smooth; branch leaves broadest at base; stem leaves acuminate, slightly decurrent .... 1. *R. pulchellum*

1. *Rhynchostegium pulchellum* (Hedw.) Robins.

Eurhynchium pulchellum (Hedw.) Jenn.

Two varieties are present in the Interior Highlands and may be separated as follows:

a. Branch leaves loosely imbricate; branch ends attenuate .... 1a. *R. pulchellum* var. *pulchellum*
a. Branch leaves closely imbricate; branches julaceous, ends blunt .... 1b. *R. pulchellum* var. *praecox*

1a. *Rhynchostegium pulchellum* var. *pulchellum*

Common throughout the Interior Highlands; on shaded soil and rocks. Occasionally on tree trunks and bases.

1b. *Rhynchostegium pulchellum* var. *praecox* (Hedw.) Dix.

Very common throughout the Interior Highlands; on open to shaded soil, rocks, and tree bases.

Crum, Steere, and Anderson (1965: 421) consider this variety merely a form.

2. *Rhynchostegium hians* (Hedw.) Delogn.

Eurhynchium hians (Hedw.) Sande Lac.
Oxyrhynchium hians (Hedw.) Jenn.

Common throughout the Interior Highlands; on moist soil, rocks, and logs.

3. *Rhynchostegium riparioides* (Hedw.) Card. *in* Tourret

Eurhynchium rusciforme Milde.
Oxyrhynchium riparioides (Hedw.) Jenn.

Common, Boston Mtns., Salem and Springfield Plateaus; on wet or submerged rocks in stream and spring branches. Often very abundant.

37. ENTODONTACEAE

The genera included here in this family are those included by Brotherus in the 2nd edition of *Die natürlichen Pflanzenfamilien* (1925), a procedure also adopted by Crum, Steere, and Anderson (1965: 395–396).

Plants slender to moderately large, in loose to dense, glossy, yellowish green to dark green mats, sparingly to subpinnately branched, prostrate to suberect; leaves loosely imbricate, julaceous, to strongly complanate-foliate, concave, oblong-ovate, ovate, to obovate with acuminate, apiculate, to rounded or obtuse tips, gradually narrowed to base, sometimes slightly decurrent; margins plane to narrowly recurved near base and strongly infolded near apex, entire to denticulate above; costa absent or short and double; median leaf-cells smooth or papillose by projecting cell ends, linear to narrowly rhomboidal; apical cells shorter; basal cells numerous in several rows, quadrate to subrectangular; alar cells often enlarged and colored; capsule subcylindric, arcuate and cernuous to cylindric and erect; peristome double, teeth 16; propagula present in *Pterigynandrum*.

a. Stems red; leaves strongly infolded near apex .... 3. *Pleurozium*
a. Stems not red; leaves not strongly infolded near apex .... b
  b. Leaf cells smooth .... 2. *Entodon*
  b. Leaf cells papillose .... 3. *Pterigynandrum*

1. *Pterigynandrum* Hedw.

1. *Pterigynandrum filiforme* Hedw. var. *filiforme*

Plants slender, in thin mats, branches irregularly spaced, often ascending and flagelliform, julaceous, with small, filiform to much branched paraphyllia; leaves obovate to ovate-oblong, obtusely pointed to shortly acuminate or acute, secund or closely appressed when dry; margins slightly denticulate or entire above, reflexed below, slightly decurrent; costa absent or short and double; median leaf-cells papillose by projecting angles, short linear-vermicular to narrowly rhombic, 3–5 : 1; cells of apex broader or shorter; basal cells irregularly quadrate to short-rectangular in 2–8 rows; propagula often present, golden-brown, ovoid, smooth, consisting of 2–3 cells borne on hyaline stalk; capsule erect and usually symmetric.

Reported from Salem and Springfield Plateaus by Gier (1955*a*: 37).

2. *Entodon* C. Müll.

Plants in glossy yellow-green to dark green mats, stems julaceous to complanate-foliate, subpinnately branched; leaves oblong-ovate, oblong-elliptical to oblong- or ovate-lanceolate, abruptly acute, short apiculate to narrowly acuminate, narrowed to insertion, concave; margins entire to denticulate at apex, often narrowly recurved below; costa absent to short and double; median leaf-cells smooth, linear-fusiform to linear-flexuose, 8–15 : 1, cells of apex shorter; basal cells numerous in several rows, quadrate and enlarged; seta red or yellow; capsules erect and cylindric.

a. Leaves narrowly acuminate	1. *E. brevisetus*
a. Leaves acute to apiculate	b
b. Branches julaceous, scarcely complanate-foliate	5. *E. seductrix*
b. Branches complanate-foliate	c
c. Plants slender, branches 1 mm wide or less	3. *E. compressus*
c. Plants moderately robust, branches more than 1 mm wide	d
d. Seta yellow	4. *E. macropodus*
d. Seta reddish brown	2. *E. cladorrhizans*

1. *Entodon brevisetus* (Hook. & Wils. *ex* Wils.) Lindb.

Reported from vicinity of St. Louis by Wilson (1842).

2. *Entodon cladorrhizans* (Hedw.) C. Müll.

Common throughout the Interior Highlands; on shaded rocks, soil, tree bases, and logs.

3. *Entodon compressus* C. Müll.

Entodon challengeri (Par.) Card. (See Mizushima, 1967.)

Uncommon, Prairie Plains, Salem and Springfield Plateaus; on shaded rocks, decaying wood, and tree bases.

The small size and complanate leaves slanting towards the substratum from the middle of the stem and thus resembling the roof of a house distinguish this species from all others in the genus.

4. *Entodon macropodus* (Hedw.) C. Müll.

Entodon drummondii (B.S.G.) Jaeg. & Sauerb.

Common, Boston and Ouachita Mtns., Ozark Hills; on moist shaded noncalcareous rocks, tree bases, and humus.

5. *Entodon seductrix* (Hedw.) C. Müll. var. *seductrix*

Very common throughout the Interior Highlands; on moist shaded rocks, soil, logs, tree bases and trunks.

Entodon seductrix var. *minor* Aust. *ex* Grout has been reported from the Ouachita Mtns. in Garland County, Arkansas, by Scully (1941). This is apparently a poorly segregated variety that is much smaller than var. *seductrix*.

3. *Pleurozium* Mitt.

1. *Pleurozium schreberi* (Brid.) Mitt. var. *schreberi*

Calliergonella schreberi (B.S.G.) Grout

Plants in large, loose, shining yellow-green mats, stems red, rather closely pinnate to irregularly branched, branches terete, loosely julaceous; leaves elliptic or oblong-ovate; margins entire or crenulate-serrate above, strongly infolded above, reflexed below, apex rounded-obtuse; costa faint, short and double or lacking; median leaf-cells smooth, linear-flexuose, 8–15 : 1; apical cells shorter; basal cells short, broader, incrassate and porose, often colored; alar cells enlarged, subrectangular and often colored, forming a triangular patch; capsule subcylindric, arcuate, and cernuous.

Uncommon throughout the Interior Highlands; on moist, shaded rocks and soil, especially of stream banks. Often forming mats that cover extensive areas.

A striking species that may be easily recognized by its large yellow-green loose mats and its red stem.

38. PLAGIOTHECIACEAE

This treatment of this family essentially follows the recent revision of the genus *Plagiothecium* by Ireland (1969*b*).

Plants small to medium in size, irregularly to sparingly branched, prostrate; pseudoparaphyllia present or absent; leaves erect-spreading, imbricate, complanate, though sometimes julaceous, ovate, oblong-ovate, or triangular, straight or secund, acute to acuminate, rarely obtuse, bases not to strongly decurrent; margins plane or narrowly recurved, entire to serrate; costa short, double, or absent; median leaf-cells smooth or dorsally papillose, shortly elliptic, rhomboid-elongate, elongate-linear, to linear-flexuose; alar cells quadrate to rectangular, incrassate or thin walled and enlarged; capsule cylindric, mostly inclined and asymmetric, contracted below mouth when dry; operculum conic to long-rostrate; peristome double, teeth 16.

a. Leaves decurrent .... 1. *Plagiothecium*
a. Leaves not decurrent .... b
  b. Pseudoparaphyllia present, leaf-like .... 3. *Taxiphyllum*
  b. Pseudoparaphyllia absent; if present, filamentous .... 2. *Isopterygium*

1. *Plagiothecium* B.S.G.

Plants medium in size, dull to glossy green, in loose mats; pseudoparaphyllia absent; stems complanate-foliate or julaceous, irregularly branched; leaves imbricate, oblong-ovate, ovate, acute or slenderly acuminate; margins plane or recurved near apex, entire or serrate near apex; costa short and double; median leaf-cells smooth, linear to linear-rhomboidal; alar cells oval, quadrate to rectangular, forming a decurrent region auriculate oval to triangular in outline; brood bodies consisting of 2–7 cells often present; capsule erect to inclined, straight or arcuate; operculum rostrate.

a. Plants usually julaceous with symmetric, concave leaves, decurrent portion of leaf composed of mostly rectangular cells in 1–5 vertical rows, triangular in outline .... 2. *P. roeseanum*

a. Plants complanate-foliate with asymmetric, flat leaves, decurrent portion of leaf composed of many inflated sphaerical, oval, or elongate cells in 2–8 vertical rows .... 1. *P. denticulatum*

1. *Plagiothecium denticulatum* (Hedw.) B.S.G.

Reported from Jackson Co., Illinois, in the Ozark Hills by Hatcher (1952).

2. *Plagiothecium roeseanum* B.S.G.

Common throughout the Interior Highlands; on thin soil or humus overlying rocks.

2. *Isopterygium* Mitt.

Plants in flat, glossy, dark to light green to yellowish green mats; stems and branches usually complanate-foliate, sparingly and irregularly branched; pseudoparaphyllia lacking or present; leaves imbricate to distant, erect-spreading to secund or squarrose, symmetric or asymmetric, not decurrent, ovate, ovate-lanceolate to oblong-lanceolate, acute but more often acuminate; margins plane or recurved, serrate to entire below or throughout; costa short and double or sometimes lacking; median leaf-cells smooth, linear or linear-flexuose; apical cells often shorter and rhomboidal; alar cells not differentiated or differentiated and forming a small area of quadrate to rectangular cells; propagula usually present; capsule oblong or ovoid, straight or arcuate, inclined to cernuous; operculum conic to short-rostrate.

a. Pseudoparaphyllia present, filamentous, of 1–2 rows of cells; alar cells often over 12 μ wide, marginal row usually quadrate or transversely elongate; asexual reproductive bodies with papillose cells .... 1. *I. tenerum*

a. Pseudoparaphyllia absent; alar cells usually less than 12 μ wide (except in *I. muellerianum*), marginal row rectangular, seldom quadrate; asexual reproductive bodies with smooth cells .... b

  b. Outer layer of stem cells large and thin-walled in cross-section; leaves usually abruptly short-acuminate, entire or minutely serrulate .... 2. *I. muellerianum*

  b. Outer layer of stem cells small and thick-walled in cross section; leaves not abruptly short-acuminate; serrulate to strongly serrate in upper half c

c. Leaves mostly cultriform and undulate; propagula twisted-vermiform with 1–5 teeth at apex .... 3. *I. distichaceum*

c. Leaves rarely cultriform, mostly symmetric, seldom undulate; propagula resembling parent plant but smaller .... 4. *I. elegans*

1. *Isopterygium tenerum* (Sw.) Mitt.

Isopterygium micans (Sw.) Kindb.
Plagiothecium micans (Sw.) Par.
Plagiothecium micans var. *fulvum* (Hook. & Wils.) Par.

Common throughout the Interior Highlands; on decaying logs and stumps, tree bases, sandy soil, less rarely on rocks.

2. *Isopterygium muellerianum* (Schimp.) Jaeg. & Sauerb.

Plagiothecium muellerianum Schimp.

Rare, Boston Mtns., eastern Salem Plateau, Ozark Hills; on moist shaded noncalcareous rock crevices and ledges.

3. *Isopterygium distichaceum* (Mitt.) Jaeg. & Sauerb.

Plagiothecium subfalcatum Aust.

Rare, Boston Mtns., eastern Salem Plateau, Ozark Hills; on moist, shaded sandstone or humus, in crevices or on ledges.

Closely related to and considered a variety of the next species by some authors.

4. *Isopterygium elegans* (Brid.) Lindb.

Isopterygium borrerianum (C. Müll.) Lindb.
Plagiothecium elegans (Brid.) Schimp.

Common, Boston and Ouachita Mtns., Prairie Plains, Ozark Hills, and eastern Salem Plateau; on shaded, moist noncalcareous rocks, tree bases and humus.

3. *Taxiphyllum* Fleisch.

Plants in glossy, dark to golden green mats; stems branched, often sparingly, complanate-foliate; pseudophyllia always present, large, foliate; leaves appressed-imbricate, close or distant, appearing distichous, symmetric to somewhat asymmetric, smooth or plicate, broadly ovate to ovate- or oblong-lanceolate, acuminate or abruptly narrowed to an acute, filiform, or rarely subobtuse apex; margins plane or narrowly recurved, serrulate to strongly serrate above; costa lacking or short and double; median leaf-cells smooth or papillose dorsally by projecting cell ends, linear-flexuose; apical cells shorter and rhomboidal; alar cells quadrate to short rectangular in 1– several rows with 1–8 in marginal row; capsule oblong or ovoid, cernuous, straight or arcuate; operculum obliquely rostrate.

a. Leaves usually close, appressed-imbricate; median leaf-cells smooth ...... 1. *T. deplanatum*
a. Leaves distant, not appressed-imbricate; median leaf-cells often papillose .. 2. *T. taxirameum*

1. *Taxiphyllum deplanatum* (C. Müll.) Fleisch.

Isopterygium deplanatum (C. Müll.) Mitt.
Plagiothecium deplanatum (C. Müll.) Spruce

Common throughout the Interior Highland except for the Ouachita Mtns.; on shaded calcareous rocks and soil, occasionally on bases of trees and rotten logs.

2. *Taxiphyllum taxirameum* (Mitt.) Fleisch.

Isopterygium geophilum (Aust.) Jaeg. & Sauerb.
Isopterygium taxirameum (Mitt.) Jaeg. & Saeurb.
Plagiothecium geophilum (Aust.) Grout
Taxiphyllum geophilum (Aust.) Fleisch.

Very common throughout the Interior Highlands; on shaded rocks or soil.

39. SEMATOPHYLLACEAE

Plants slender to moderately large, creeping; branches prostrate to erect and curved, irregular to subpinnate; paraphyllia absent or present; leaves erect-spreading to almost julaceus or complanate, often secund to falcate-secund, ovate-lanceolate to narrowly oblong-lanceolate, slenderly acuminate to short-acuminate; margins plane or revolute below, entire to serrate; costa short and double or absent; median leaf-cells smooth, linear-flexuose, long-rhomboidal or fusiform; alar cells quadrate to rectangular with 2–several large, pellucid, hyaline or colored cells conspicuous at basal angles; capsule erect and symmetric to more or less inclined and asymmetric; operculum rostrate; peristome double, teeth 16.

a. Leaves distinctly serrate above .... 2. *Brotherella*
a. Leaves entire .... b
  b. Paraphyllia large and multiform .... 1. *Callicladium*
  b. Paraphyllia absent .... 3. *Sematophyllum*

1. *Callicladium* Crum

1. *Callicladium haldanianum* (Grev.) Crum (1971)

Heterophyllium haldanianum (Grev.) Kindb.

Plants in loose, irregularly branching, dark to brownish green mats; paraphyllia large and multiform; leaves loosely imbricate, ovate- to oblong-lanceolate, narrowed to a short acumination, concave; margins plane and entire; costa short and double or absent; median leaf-cells linear rhomboidal, 12–18 : 1; basal cells rectangular to quadrate, thin-walled, enlarged and inflated near extreme angles, forming distinct auricles; capsule suberect or inclined, somewhat curved.

Rare, Ozark Hills, Prairie Plains, and eastern Salem Plateau; on shaded sandstone.

2. *Brotherella* Loeske *ex* Fleisch.

1. *Brotherella tenuirostris* (Bruch & Schimp. *ex* Sull.) Broth.

Plants in thin, glossy, green- to yellow-green mats; branches slender, creeping, pinnate or nearly so; leaves slightly curved to secund with apices turned ventrally, loosely imbricate when dry, oblong-lanceolate and slenderly acuminate; margins reflexed below and usually sharply serrate above; costa absent or short and double; median leaf-cells broadly linear, 7–10 : 1; basal cells shorter, quadrate to subquadrate with angular cells inflated, hyaline or slightly colored; capsule erect and symmetric.

Uncommon, Boston and Ouachita Mtns., Ozark Hills, Salem Plateau; on shaded moist acidic rocks, decaying logs and tree bases.

This species may be confused with *Hypnum pallescens*, but the presence of distinctly inflated alar cells distinguishes it from that species.

3. *Sematophyllum* Mitt.

Slender to moderately large plants; branches spreading to erect and curved upward, irregular or pinnate, green to yellowish green; leaves often secund, closely imbricate when dry, concave, oblong-lanceolate to oblong-ovate, gradually acuminate to short-acuminate or acute; margins reflexed to plane, entire; costa absent or short and double; median leaf-cells smooth, fusiform to linear-fusiform or linear-flexuose, 6–12 : 1; apical cells shorter; alar cells oblong to rectangular, often incrassate and colored with 2–6 inflated and enlarged cells at the basal angles; capsule oblong, erect and symmetric to curved and asymmetric, contracted below mouth when dry; operculum rostrate.

a. Plants growing on bark of trees; capsule erect and symmetric .... 1. *S. adnatum*
a. Plants growing on rocks; capsule inclined and asymmetric .... b
  b. Plants moderately large; leaves 1.2–1.8 mm long; median leaf-cells 8–12 : 1 .... 3. *S. marylandicum*
  b. Plants slender; leaves averaging less than 1.2 mm long; median leaf cells 6–8 : 1 .... 2. *S. carolinianum*

1. *Sematophyllum adnatum* (Michx.) Britt.

Uncommon, Boston and Ouachita Mtns., Prairie Plains, Salem and Springfield Plateaus; on decaying logs and tree bases.

2. *Sematophyllum carolinianum* (C. Müll.) Britt. var. *carolinianum*

Common throughout the Interior Highlands; on moist shaded acidic rocks, occasionally on calcareous rocks.

3. *Sematophyllum marylandicum* (C. Müll.) Britt.

Rare, Ouachita Mtns., Ozark Hills, eastern Salem Plateau; on moist shaded norvaculite and sandstone.

40. HYPNACEAE

Plants usually prostrate, irregularly to regularly pinnate; leaves straight to curved, secund, or falcate-secund, concave, ovate-lanceolate to triangular, erect-spreading, apex acuminate, bases cordate, slightly oriculate or ovate; margins entire to serrate or dentate; costa short and double or absent; median leaf-cells smooth or rarely slightly papillose on back, narrow to elongate-elliptic or fusiform, 4–8 : 1; basal cells short-rectangular to quadrate, incrassate, sometimes slightly inflated, often very numerous and extending up margin 8–10 rows, hyaline or colored; seta tall; capsule asymmetric and curved or symmetric and straight; operculum conic to rostrate; peristome double, teeth 16; gemmae rare except in *Platygyrium*.

a. Leaves sharply serrate from base to apex .... 5. *Ctenidium*
a. Leaves entire or only slightly denticulate or serrulate, mostly in upper part .... b
  b. Most leaves clearly curved, sometimes falcate or secund .... 4. *Hypnum*
  b. Most leaves straight with only terminal branch leaves being curved or secund c

c. Terminal branch leaves secund; plants usually growing on tree trunks; capsule erect and symmetric .... 2. *Pylaisiella*
c. Terminal branch leaves not secund; plants growing on rocks or tree trunks and logs; capsule straight or curved .... d
  d. Numerous small deciduous branchlets in clusters in upper leaf axils; leaf-margin narrowly recurved; median leaf-cells 8 : 1; capsule straight and symmetric; usually growing on trees or decaying wood .... 1. *Platygyrium*
  d. Small deciduous branchlets absent; leaf-margins plane; median leaf-cells 4–8 : 1; capsule curved and asymmetric; usually growing on rocks .... 3. *Homomallium*

1. *Platygyrium* B.S.G.

1. *Platygyrium repens* (Brid.) B.S.G. var. *repens*

Plants glossy, usually dark green, in prostrate mats; leaves erect-spreading to loosely imbricate, oblong-ovate to oblong-lanceolate, acute to acuminate; margins entire, narrowly revolute; costa absent or short and double; median leaf-cells smooth, elongate, elliptic to linear-rhomboidal 8 : 1; apical cells rhomboidal; basal cells quadrate, numerous, extending up margin of leaf for 8–10 rows; seta 1–2 cm long; capsule erect, ovate-cylindric, symmetric, gemmae, shaped like small deciduous branchlets, abundant in upper leaf axils.

Very common throughout the Interior Highlands; on decaying tree trunks, stumps, occasionally on acidic rocks.

This species is not likely to be confused with other species, especially when gemmae are present, which is almost always the case. When it grows on rocks it may be confused with *Homomallium adnatum,* particularly if gemmae are few and not well developed. It differs from *H. adnatum* species in that its median leaf-cells are 8 : 1 and its capsule is erect or nearly erect and symmetrical. In *H. adnatum* the median leaf-cells are 4–8 : 1 and the capsule is inclined and asymmetrical.

2. *Pylaisiella* Kindb.

Plants glossy, green to yellow-green, growing creeping over substrate, branching pinnately; branches erect or ascending, strongly recurved at tips because of secund apical leaves; leaves ovate-lanceolate, long-acuminate, entire or nearly so; margins plane or involute; costa absent or short and double; median leaf-cells linear-fusiform, 7–12 : 1, alar cells numerous, quadrate, extending up margin for up to 20 rows; seta 1–2 cm long; capsule erect and symmetrical, oval to oblong-cylindric; peristome double.

a. Segments of inner peristome longer than and only partially adherent to teeth; quadrate alar cells numerous, extending to 15–20 rows along margin .... 1. *P. selwynii*
a. Segments of inner peristome about same length as and wholly adherent to teeth; quadrate alar cells fewer, extending only to about 10 rows along margin .... 2. *P. intricata*

1. *Pylaisiella selwynii* (Kindb.) Crum, Steere & Anderson

Pylaisia selwynii Kindb.

Very common throughout the Interior Highlands; on tree trunks, decaying stumps and logs, rarely on sandstone.

2. *Pylaisiella intricata* (Hedw.) Grout

Pylaisia intricata (Hedw.) Schimp.

Reported from Prairie Plains and eastern Salem Plateau by Gier (1955*a*: 37).

3. *Homomallium* (Schimp.) Loeske

1. *Homomallium adnatum* (Hedw.) Broth.

Plants in dark to light green, closely adherent patches with irregular, short, erect branches; leaves crowded, loosely appressed when dry, concave, ovate to oblong-ovate, abruptly short-acuminate; margins plane and entire; costa short and double or rarely single, often absent; median leaf-cells, smooth, short, linear-hexagonal to subrhomboidal, 4–8:1; alar cell quadrate, numerous, often extending up ⅓ length of leaf on margin; seta 0.5–1.0 cm long, purplish below; capsule oblong to oblong-cylindric, inclined and asymmetric; operculum conic to long-conic and apiculate; peristome double, teeth 16.

Very common throughout the Interior Highlands; on boulders and small stones in shaded places, occasionally on tree bases.

May be confused with *Platygyrium repens*. See notes under that species.

4. *Hypnum* Hedw.

Plants prostrate, light yellow, green, to brownish green, loosely to closely pinnately branched; paraphyllia often present; leaves concave, ovate-lanceolate, decurrent, acuminate to a long, fine point, almost straight, secund, to falcate-secund, often slightly complanate; margins plane, smooth to denticulate; costa short and double; median leaf-cells linear-flexuose, smooth; alar cells distinct, small and quadrate to inflated and hyaline; capsule asymmetric, inclined to horizontal, oblong to cylindric; peristome double, teeth 16.

a. Stems surrounded by thin-walled, hyaline cells; alar cells conspicuously inflated .... 5. *H. lindbergii*
a. Stems surrounded by incrassate cells; alar cells not to only slightly inflated .... b
  b. Quadrate to short-rectangular alar cells numerous, 6–10 in the marginal row c
  b. Quadrate to short-rectangular alar cells few, 4–6 along margin, inflated cells often present, alar group distinct, often colored .... d
c. Leaf margins entire .... 2. *H. cupressiforme* var. *resupinatum*
c. Leaf margins serrate .... 4. *H. pallescens*
  d. Leaves usually abruptly narrowed to a subcordate to cordate base; paraphyllia few; capsule curved, plicate when dry and empty .... 3. *H. curvifolium*
  d. Leaves usually tapering to insertion; paraphyllia numerous, broad, often ciliate; capsules suberect, not plicate when dry and empty .... 1. *H. imponens*

1. *Hypnum imponens* Hedw.

Uncommon, Boston Mtns., Prairie Plains, Salem Plateau; on sandstone of shaded habitats.

2. *Hypnum cupressiforme* Hedw. var. *resupinatum* (Wils.) Schimp.

Common, Boston and Ouachita Mtns.; on shaded, vertical norvaculite and sandstone rocks, sometimes on rock ledges.

3. *Hypnum curvifolium* Hedw.

Common throughout the Interior Highlands; on shaded, rocky soil, rock ledges, and logs. Often extremely abundant and forming extensive mats.

4. *Hypnum pallescens* (Hedw.) P. Beauv.

(Includes *Hypnum reptile* Michx.)

Uncommon, Salem Plateau; on shaded, decaying logs and sandstone. Also reported from McCurtain Co., Oklahoma, in the Ouachita Mtns., by Sharp (1930). This species may be confused with *Brotherella tenuirostris* (see remarks under that species).

5. *Hypnum lindbergii* Mitt. var. *lindbergii*

Hypnum arcuatum Lindb.
Hypnum patientiae Lindb.

Very common throughout the Interior Highlands; on shaded to open rocks, soil, and decaying wood beside creeks and streams.

Hypnum lindbergii var. *demissum* (Schimp.) Loeske has been reported from the Salem Plateau by Gier (1955*a*: 36). This seems to be a poorly distinguished variety separated from var. *lindbergii* by being in thin, light to yellow-green mats.

5. *Ctenidium* (Schimp.) Mitt.

1. *Ctenidium molluscum* (Hedw.) Mitt.

Hypnum molluscum Hedw.

Plants regularly pinnate and plumose, golden-green to yellowish, to occasionally bright-green; leaves crowded, when dry falcate-secund, plicate, slenderly acuminate from an auriculate, cordate-triangular base; margins plane, serrate or dentate; costa short, double, or absent; median leaf-cells linear, 8–12 : 1, slightly papillose at upper ends of cells on back of leaf; alar cells shorter, quadrate-rectangular, not inflated or colored; seta smooth, 1–2 cm long, capsule ovate, curved, inclined to horizontal.

Common throughout the Interior Highlands; on shaded rocky soil, especially of steep slopes and ridges. Occasionally on tree bases.

41. RHYTIDIACEAE

Large, robust, irregularly to sparcely divided plants in loose, intertangled, yellow- to gray-green mats; stems to 15 cm or more long with pseudoparaphyllia sparingly found in branch axils; leaves crowded on stem, imbricate, often strongly secund, to squarrose-spreading, ovate-lanceolate to triangularly cordate, slenderly acute to acuminate, plicate, often rugose; margins sharply dentate to denticulate and revolute; costa single or double; median leaf-cells linear, smooth or papillose; alar cells rounded-quadrate and numerous to few and hexagonal-oblong; sporophytes not known in material from Interior Highlands.

a. Leaves secund and strongly rugose; costa single .... 1. *Rhytidium*
a. Leaves spreading to squarrose, plicate, but not rugose; costa double .... 2. *Rhytidiadelphus*

1. *Rhytidium* (Sull.) Kindb.

1. *Rhytidium rugosum* (Hedw.) Lindb.

Large, robust plants; leaves crowded-imbricate, ovate-lanceolate, strongly rugose and secund; costa single reaching middle of leaf or beyond; median leaf-cells linear; basal cells rounded quadrate, numerous.

Rare, central Salem Plateau; on open to shaded rocky soil near edges of high, north-facing bluffs along Jacks Fork River in Texas and Shannon Counties, Missouri.

2. *Rhytidiadelphus* (Lindb.) Warnst.

1. *Rhytidiadelphus triquetrus* (Hedw.) Warnst. var. *triquetrus*

Large, robust plants; leaves widely spreading to squarrose, cordate-triangular, plicate; margins sharply dentate above, denticulate below; costa double; median leaf-cells linear, spinose-papillose on back by projecting cell angles; basal cells hexagonal-oblong, thick-walled and pitted.

Rare, central Salem Plateau and Boston Mtns.; on open to shaded rocky soil along edges of high, north-facing bluffs or rarely on shaded soil, bases of bluffs.

42. Diphysciaceae

1. *Diphyscium* Mohr

1. *Diphyscium foliosum* (Hedw.) Mohr

Small, dark green plants in large dense mats; leaves crisped when dry, lingulate, obtuse; costa broad and flattened, often indistinct, ending below apex; upper leaf-cells obscure, rounded-quadrate, strongly papillose on both surfaces; lower leaf-cells rectangular, hyaline and smooth; perichaetial leaves large, ovate-lanceolate, costa ending in a long setaeous point; capsule sessile, shorter than awns of perichaetial leaves, resembling a grain of wheat, golden brown when mature; peristome double, outer rudimentary or lacking, inner whitish, 16-plicate.

Common throughout the Interior Highlands; on shaded, rocky soil, vertical rock exposures, and undersides of overhanging ledges, particularly sandstone.

43. Polytrichaceae

Plants erect, small to robust, growing in green to brownish or reddish green, open, short to tall tufts; leaves stiff, coarse, with or without a sheathing base, lamellae usually present on upper surface of costa; capsule erect to inclined, terete or angled, exserted; peristome of 32 or 64 short teeth attached by their tips to a thin membrane.

a. Leaves with 0–8 rows of lamellae, bordered by a row of elongated cells, without a sheathing base; capsule terete, peristome of 32 teeth; calyptra smooth .... 1. *Atrichum*
a. Leaves with 10–70 rows of lamellae, not bordered by a row of elongated cells, sheathing base present; capsule terete or angled, peristome of 32 or 64 teeth; calyptra hairy .... b
  b. Plants small, 2–8 mm tall, forming open, short tufts; leaves 3–4 mm long; capsule terete; peristome of 32 teeth .... 2. *Pogonatum*

b. Plants large, 2–20 cm tall, usually forming dense tall tufts; leaves 2–12 mm long; capsule angled; peristome of 64 teeth .... 3. *Polytrichum*

1. *Atrichum* P. Beauv.

Plants erect, small to robust, forming green to brownish green tufts; leaves ovate to lingulate or lanceolate, lamellae few (0–8); margins distinctly bordered by elongated cells; capsules erect to inclined, elongated, terete; peristome of 32 teeth; calyptra smooth.

a. Leaves elliptical to obovate, lamellae 0–3 cells high .... 1. *A. crispum*
a. Leaves lingulate to lanceolate, lamellae 2–14 cells high .... b
  b. Leaves 1–1.3 mm wide, lingulate, lamellae obscuring ⅕ or less of the leaf width at the midpoint of leaf length .... 2. *A. undulatum*
  b. Leaves 0.5–1.0 mm wide, linear-lanceolate, lamellae obscuring ¼–⅔ of the leaf width at the midpoint of leaf length .... 2. *A. angustatum*

1. *Atrichum crispum* (James) Sull. & Lesq. var. *crispum*

Rare, Boston Mtns., Salem Plateau; on soil banks of ditches and gullies.

2. *Atrichum undulatum* (Hedw.) P. Beauv.

This species is generally very robust with leaves that are strongly crispate when dry and markedly undulate when moist. Three varieties are represented in the Interior Highlands and may be separated as follows:

a. Lamellae obscuring ⅐–⅕ of the width of the leaf at midpoint of its length .... 2b. *A. undulatum* var. *minus*
a. Lamellae obscuring 1⁄11–⅐ of the width of the leaf at midpoint of its length .... b
  b. Lamellae 6, 2–6 cells high; plants autoicous .... 2c. *A. undulatum* var. *alte-cristatum*
  b. Lamellae 2–5, rarely 6, 6–8 cells high; plants monoicous .... 2a. *A. undulatum* var. *undulatum*

2a. *Atrichum undulatum* var. *undulatum*

Common and locally abundant throughout the Interior Highlands; on shaded sandy or calcareous soils along gullies, ditches, and, especially, shaded ravines.

2b. *Atrichum undulatum* var. *minus* (Hedw.) Par.

Uncommon, Boston and Ouachita Mtns., Prairie Plains, Salem and Springfield Plateaus; on shaded rocky soil in ravines.

2c. *Atrichum undulatum* var. *alte-cristatum* Ren. & Card.

Reported from the Salem Plateau by Gier (1955*a*: 32). Frye (1949) considers this variety a poor one, not always distinct from *A. undulatum* var. *undulatum*, although Ireland (1969*a*: 363) considers it a distinct species.

3. *Atrichum angustatum* (Brid.) B.S.G. var. *angustatum*

Atrichum xanthopelma (C. Müll.) Jaeg.
Atrichum macmillanii (Holz.) Frye
Atrichum papillosum (Jenn.) Frye

Very common throughout the Interior Highlands; on poor soil of ditches, gullies, lawns, and on bare soil and soil mounds in forests.

Forms with papillose leaves are occasionally encountered. Such forms have been considered as a separate species, *Atrichum xanthopelma*, by Frye (1949). Thomas (1953) considers such papillose forms to be *A. angustatum*, a judgement followed in this treatment.

2. *Pogonatum* P. Beauv.

Plants small, erect, scattered or forming open tufts; green to dark green; leaves lanceolate to lanceolate-subulate from a sheathing base, 3–4 mm long, lamellae 10–35; margins of leaves not bordered by elongated cells; capsules erect, terete; peristome of 32 teeth; calyptra hairy; protonema persistent.

a. Leaves with 10–15 lamellae, serrate in upper half; plants usually scattered .... 1. *P. pensilvanicum*
a. Leaves with 20–70 lamellae, entire; plants usually forming dense tufts .. 2. *P. brachyphyllum*

1. *Pogonatum pensilvanicum* (Hedw.) Par. var. *pensilvanicum*

Pogonatum brevicaule P. Beauv.

Common throughout the Interior Highlands; on shaded, sandy soil banks. Plants usually scattered on a mat of dense, green protonema.

Male plants are usually smaller than the female plants.

2. *Pogonatum brachyphyllum* (Michx.) P. Beauv.

Common throughout the Interior Highlands; on shaded, sandy soil, especially along road cuts and ditches. Plants usually form dense mats.

This species is easily recognized by its short, thick, entire leaves and is usually restricted to soil of weathered dolomite and sandstone.

3. *Polytrichum* Hedw.

Plants usually 2–20 cm tall, forming open to dense tufts; leaves 2–15 mm long, rigid, lanceolate, linear-lanceolate, to linear-subulate; margins entire or toothed, plane or involute; lamellae numerous along upper surface; capsule angled, usually inclined; peristome of 64 teeth; calyptra densely hairy.

a. Leaves entire c
a. Leaves toothed .... b
  b. Terminal cells of lamellae flat, not appearing notched in cross section .... 1. *P. ohioense*
  b. Terminal cells of lamellae notched in cross section .... 2. *P. commune*
c. Awn of leaf reddish .... 3. *P. juniperinum*
c. Awn of leaf white or hyaline .... 4. *P. piliferum*

1. *Polytrichum ohioense* Ren. & Card.

Very common throughout the Interior Highlands; on open to shaded rocky soil of ridges, ledges, rock crevices, and around the edges of glades. In this last area this species often forms dense carpets along the edges of flat rock exposures of both sandstone and limestone where it is interdispersed with equally well-developed colonies of *Leucobryum glaucum*, *Philonotis fontana*, and *Climacium americanum*.

2. *Polytrichum commune* Hedw.

a. Perichaetial leaves distinctly longer than the upper stem leaves, forming an erect tuft about the seta .... 2b. *P. commune* var. *perigoniale*
a. Perichaetial leaves similar to the upper stem leaves, not forming an erect tuft about the seta .... 2a. *P. commune* var. *commune*

2a. *Polytrichum commune* var. *commune*

Common throughout the Interior Highlands; on open soil around the bases of boulders, on rock ledges, or on soil pockets of large flat rock exposures, particularly felsite and granite. Tufts are usually very tall, 10–20 cm.

Small plants may be confused with *P. ohioense,* but may be separated by the features noted in the key to species.

2b. *Polytrichum commune* var. *perigoniale* (Michx.) B.S.G.

Apparently uncommon, Arkansas Valley, Boston Mtns., Salem and Springfield Plateaus; on soil of rocky woodlands, creek banks, and moist rock ledges.

3. *Polytrichum juniperinum* Hedw. var. *juniperinum*

Very common throughout the Interior Highlands; on open, dry soil of oak-hickory and oak-pine forests along ridges, and on thin soil over flat rock exposures of sandstone, granite, and felsite.

4. *Polytrichum piliferum* Hedw.

Rare, Prairie Plains and Springfield Plateau; on thin soil over sandstone, especially along open bluffs. Often mixed with *Polytrichum juniperinum.*

Appendix I

Glossary

Acrocarpous: archegonia located at tip of branch, plants usually, but not always, of erect habit.
Acumen: the slenderly tapering point of leaf.
Acuminate: slender point of leaf that is gradually tapering.
Alar cells: cells at the basal angles of leaves.
Annulus: ring of specialized cells between rim of capsule and the operculum.
Antheridium: multicellular male gametangium.
Apiculate: leaf ending in a short, abrupt, sharp point.
Apophysis: swelling of seta just beneath capsule.
Appressed: leaves lying flat on an erect stem.
Archegonium: multicellular female gametangium.
Arcuate: bent like a bow.
Areolation: network formed by cell walls of leaf as seen in surface view.
Aristate: with a bristle-shaped or awn-like point.
Astomous: capsule not opening by a regularly dehiscent lid or operculum.
Attenuate: tapered or long drawn out leaves.
Auriculate: ear-like lobes more or less developed at basal angles of leaves.
Bicostate: leaves having two mid-ribs.
Brood-bodies: vegetative reproductive cells; also called gemmae.
Calcicolous: growing on calcareous substrates.
Calyptra: cap or hood covering capsule, derived from upper portion of archegonium.

Campanulate: calyptras shaped like a bell.
Canaliculate: leaves channelled in upper portion.
Capsule: enlarged spore producing portion of sporophyte.
Carinate: leaves folded sharply along midrib and thus forming a keel.
Caulescent: possessing a stem.
Cernuous: capsule drooping, nodding, or slightly inclined.
Caespitose: growing in tufts or mats.
Chlorophyllose: containing chloroplasts.
Cilia: delicate hair-like structures between segments of inner peristome.
Circinate: leaves coiled or bent into partial or complete circle.
Clavate: club-shaped.
Cleistocarpous: capsule opening irregularly.
Collenchymatous: cell walls thickened at angles or corners.
Complanate: leaves flattened or compressed along stem.
Conduplicate: leaves folded lengthwise along costa.
Convolute: leaves with rolled margins.
Cordate: broadest portion of leaf near base.
Crenate: teeth of leaf rounded or convex.
Crenulate: leaf margins with small, rounded projections.
Crispate: leaves curled or twisted.
Cucullate: calyptra hood-like, usually split along one side.
Cuneate: wedge shaped.
Cuspidate: tip of leaf with sharp or rigid point.
Decurrent: lower margin of leaf extending down the stem below place of attachment.
Dehiscent: splitting open.
Deltoid: triangular.
Dendroid: tree-like in growth form.
Dentate: teeth of leaf extending outward.
Denticulate: teeth of leaf minute.
Dioicous: antheridia and archegonia on separate plants.
Distichous: leaves arranged on stem in two vertical ranks.
Dorsal: surface of leaf away from stem axis.
Ecostate: leaves without costa.
Elliptic: oblong with rounded ends.
Elongate: considerably longer than wide.
Emarginate: leaf notched at apex.
Emergent: capsule extending slightly beyond perichaetial leaves.
Endostome: inner peristome.
Entire: margin of leaf smooth.
Erect-ascending: leaves almost erect, extending upwards or forward.
Excurrent: costa extending beyond tip of leaf.
Exostome: outer row of peristome.
Exothecial: outer layer of cells of the capsule wall.
Exserted: capsule extending beyond the perichaetial leaves.
Falcate: leaves curved like a sickle.
Falcate-secund: leaf curved like a sickle and all leaves extending in the same direction or turning to one side of the stem.
Fasciculate: branches clustered, arranged more or less in bundles.
Fibrils: spiral thickenings of the walls of hyaline cells in *Sphagnum*.
Filament: thread-like structure.
Fimbriate: fringed with cilia.
Flaccid: soft in texture.
Flagelliform: slender, string-like branchlets.
Flexuous: irregularly wavy.
Foliose: leaf-like.
Fruit: referring to sporophyte.
Fulvous: yellow, tawny, or dull brownish yellow.
Fuscous: dull brown.
Fusiform: spindle-shaped; narrowly oval with narrow, tapering ends.
Gemma: cell or cluster of cells of gametophyte capable of reproducing the plant vegetatively.

Gemmiform: bud-like.

Geniculate: bent like a knee.

Gibbous: capsule swollen more on one side than another.

Glabrous: smooth, neither hairy or papillose.

Glaucous: bluish-gray or bluish-white; whitened with a bloom.

Globose: rounded like a ball, sphaerical.

Gregarious: plants growing near each other or clustered.

Guard cells: cells surrounding the stoma.

Guide cells: large parenchymatous cells seen in cross-section of costa.

Gymnostomous: failing to produce peristome.

Habit: general appearance or aspect of a plant.

Hair-point: leaf tip which differs from rest of leaf in appearance.

Heteroicous: more than one form of inflorescence in the same species.

Homomallous: leaves or branches all pointing in same direction.

Imbricate: leaves closely overlapping.

Immersed: capsule hidden with perichaetial leaves.

Incrassate: thickened cell-walls.

Inflated: cells of alar region enlarged much beyond size of neighboring cells.

Inflorescence: cluster of antheridia and/or archegonia.

Insertion: attachment of leaves to stem.

Involute: margins of leaves inrolled.

Isodiametric: cells having equal diameter in all directions.

Julaceous: smooth, slender, and cylindrical; leaves uniformly erect or appressed.

Keel: sharp ridge formed by longitudinal folding of leaves.

Laciniate: jagged or torn.

Lamellae: longitudinal strips of tissue in the form of thin blades standing on edge and extending parallel with one another along the costa.

Lamina: blade of leaf.

Lanceolate: shaped like a point, broadest at base and tapering to a point.

Leucocysts: cells without chlorophyll.

Ligulate: strap-shaped.

Linear: very narrow with nearly parallel margins.

Linear-rhomboidal: narrow, somewhat elongate rhomboid.

Lingulate: tongue-shaped.

Lumen: cavity or space within a cell.

Mammillate: operculum with a short point; or large, rounded papilla covering a cell.

Median: pertaining to cells of leaf in the middle between the costa and margins.

Mitrate: calyptra shaped like a peaked cap with margins undivided or with several equal clefts.

Monoicous: antheridia and archegonia on same plant.

Mucro: very short, small, abrupt point, usually stout.

Muticous: not pointed; awnless.

Oblong: elliptic, obtuse at each end, with the length 3–4 times the width.

Obovate: inversely ovate, narrowed towards the base and broadest at the distal end.

Obtuse: blunt or rounded at the apex.

Ochraceous: yellowish-brown.

Operculum: lid covering the mouth of the capsule.

Orbicular: almost circular.

Oval: broadly elliptical.

Ovate: egg shaped with broader end downward.

Panduriform: shape of a fiddle.

Papillae: minute, nipple-shaped, rounded, or acute projections.

Paraphyllia: thread-like structures or minute leaf-like structures growing among the leaves.

Paraphyses: jointed, hyaline hairs or minute threads among the antheridia and archegonia.

Parenchymatous: cells joined with broad ends, walls thin and intercellular spaces often conspicuous.

Paroicous: antheridia and archegonia on same plant but not mixed.

Patulous: leaves spreading from the stem at an angle of 46–90°.

Pellucid: completely or partially transparent.

Pendent: hanging down from its support.

Percurrent: costa extending through the entire leaf, but not beyond.

Perichaetial: leaves that enclose archegonia.
Perigonal: leaves that enclose antheridia.
Peristome: fringe of teeth and segments surrounding the mouth of the capsule.
Peristome perfect: complete with teeth and segments.
Peristome single: consisting of teeth only.
Piliferous: with hair-like projections at tips of leaves.
Pinnate: branches spreading in a feather-like fashion.
Pleurocarpous: archegonia located on a short, lateral branch, plants usually of a creeping habit.
Plicate: folded lengthwise into pleats and furrows.
Plumose: regularly and closely pinnate.
Porose: cell walls perforated by pores.
Procumbent: trailing along the ground.
Propagula: small structures capable of reproducing the plants vegetatively.
Prosenchymatous: narrow cells with ends dove-tailed into each other.
Pseudopodium: leafless, branch-like extension of gametophyte resembling a seta.
Pulvinate: shaped like a cushion.
Pyriform: pear-shaped.
Quadrate: square, or nearly so, in surface view.
Radiculose: covered with rhizoids.
Reflexed: bent backwards.
Reniform: kidney shaped.
Reticulate: forming a net.
Retort cells: enlarged, cuticular cells of branches of *Sphagnum*.
Retuse: shallow notch in a rounded apex.
Revolute: margins rolled backward.
Rhizoids: simple or branched, reddish-brown, multicellular outgrowths of stems and sometimes leaves.
Rosette: terminal leaves so arranged as to resemble a rose.
Rostellate: operculum having a short beak.
Rostrate: operculum having a long beak.
Rupestral: growing on rocks.
Secund: leaves all turned to one side.
Segments: projections of the inner row of peristome.
Serrate: toothed.
Serrulate: minutely serrate.
Sessile: not stalked.
Seta: stalk of sporophyte.
Setaceous: tip of leaf bristle-like.
Sinuate: margin deep-wavy.
Sinuose: cells wavy.
Spatulate: narrowly obovate and attenuate downwards.
Spinose: with small spines.
Squarrose: extending from stem at an angle greater than 45°.
Sterid cells: small, thick-walled cells seen in cross-section of costa.
Strumose: goiter-like on one side.
Subulate: leaves with a very fine point, needle-like or awl-like.
Sulcate: longitudinally grooved capsule.
Synoicous: archegonia and antheridia mingled in same inflorescence.
Teeth: projections of outer peristome.
Terete: cylindrical, round in cross-section.
Tomentose: covered with matted hairs.
Trigones: the thickening in the angles of the cells of leaves.
Triquetrous: sharply three-angled.
Tristichous: arranged in three rows or ranks.
Truncate: ending abruptly.
Tubulose: leaves with strongly inrolled margins that meet.
Tumid: swollen, inflated, or distended.
Turbinate: top-shaped.
Turgid: swollen or inflated.
Uncinate: hook-shaped.

UNDULATE: surface or margin wavy.
UNIPAPILLATE: one papilla per cell.
VAGINANT: sheathing.
VENTRAL: surface of leaf facing the stem when parallel with the axis.
VERMIFORM: worm-shaped.
WHORLED: branches arranged in a ring or circle about stem.
XERIC: dry habitat.

APPENDIX II

INDEX TO FAMILY NUMBERS FOR FAMILIES AND GENERA

The number after each entry is the number of the family or the family in which the genus may be found. Families are indicated in large and small caps, accepted genera in *italic*, and genera cited only as synonyms in roman.

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NOTE ADDED IN PROOF

Monte G. Manuel has discovered that a collection determined as *Cryphaea glomerata* from Pike County, Arkansas, (*Redfearn 20214*) is *Cryphaea ravenelii* Aust. This latter species may be distinguished from *C. glomerata* by its rounded-obtuse leaves and single peristome.—*PLR.*

Editor's Note

The moss *Bryoxiphium norvegicum* (Brid.) Mitt. is a rare member of the flora of the Interior Highlands. Julian A. Steyermark first discovered *Bryoxiphium* in the Interior Highlands at Pickle Spring, Ste. Genevieve Co., Missouri, one of the State's most interesting botanical localities, in 1934. This locality, which fortunately remains largely undisturbed, harbors many other interesting plants, both cryptogams and phanerogams.

Askell and Doris Löve's "Studies on *Bryoxiphium*" (The Bryologist 56: 73–94; 183–203. 1953) presents a detailed investigation of the history, taxonomy, and distribution of the genus. Since Steyermark's discovery and the Löves' study, several additional localities for this species have been discovered in the Interior Highlands; these are summarized by Paul L. Redfearn, Jr. in "Mosses of the Interior Highlands of North America" in this issue of the Annals.

The illustration of *Bryoxiphium norvegicum* on the cover banner is taken from W. S. Sullivant's plate in his "Contributions to the bryology and hepaticology of North America" (Mem. Amer. Acad. Arts 3: 57–66 + 5 pl. 1848). Sullivant was the first to collect the moss in North America, in Ohio and Kentucky. *Bryoxiphium norvegicum* has never been found in Norway, indeed it is not known from Europe at all. According to the Löves' "Studies," the Dane Axel Mörch first collected it—in Iceland in 1820. Mörch sent his moss collections to the German bryologist C. F. Hornschuch, who apparently determined the specimen as *Weissia volcanica* P. Beauv., a moss of Madagascar and Réunion Island. Hornschuch seems to have wondered if the Icelandic moss could be conspecific with the one known from off eastern Africa and sent some material to Augustin Desvaux in Paris for further study. Desvaux realized that Mörch's collection had been misdetermined and sent the specimen on to S. E. Bridel. Although Desvaux was correct in his determination, he noted on the specimen that it had been collected in Norway. Bridel published the name *Phyllogonium norvegicum* in his *Bryologia Universa* (1827) based on this collection, and Mitten (*Musci Austro-Americani*, 1869) made the combination *Bryoxiphium norvegicum*, the name by which it is known today.—*Editor.*

The previous two issues of the Annals of the Missouri Botanical Garden, Vol. 58, No. 2, pp. 99–266, and Vol. 58, no. 3, pp. 267–369, were published on 21 January 1972 and 25 May 1972, respectively.

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A brief Latin diagnosis for each new taxon is preferred to a complete Latin description. A complete description should be given in English.

The citation of specimens should be concise. Geographic names are put in order of decreasing political magnitude. Only the barest essential data concerning each specific locality should be given. Collectors are cited by family name and collection number. If there is no collection number, the year of collection should be given. Herbaria are designated according to the current edition of *Index Herbariorum.*

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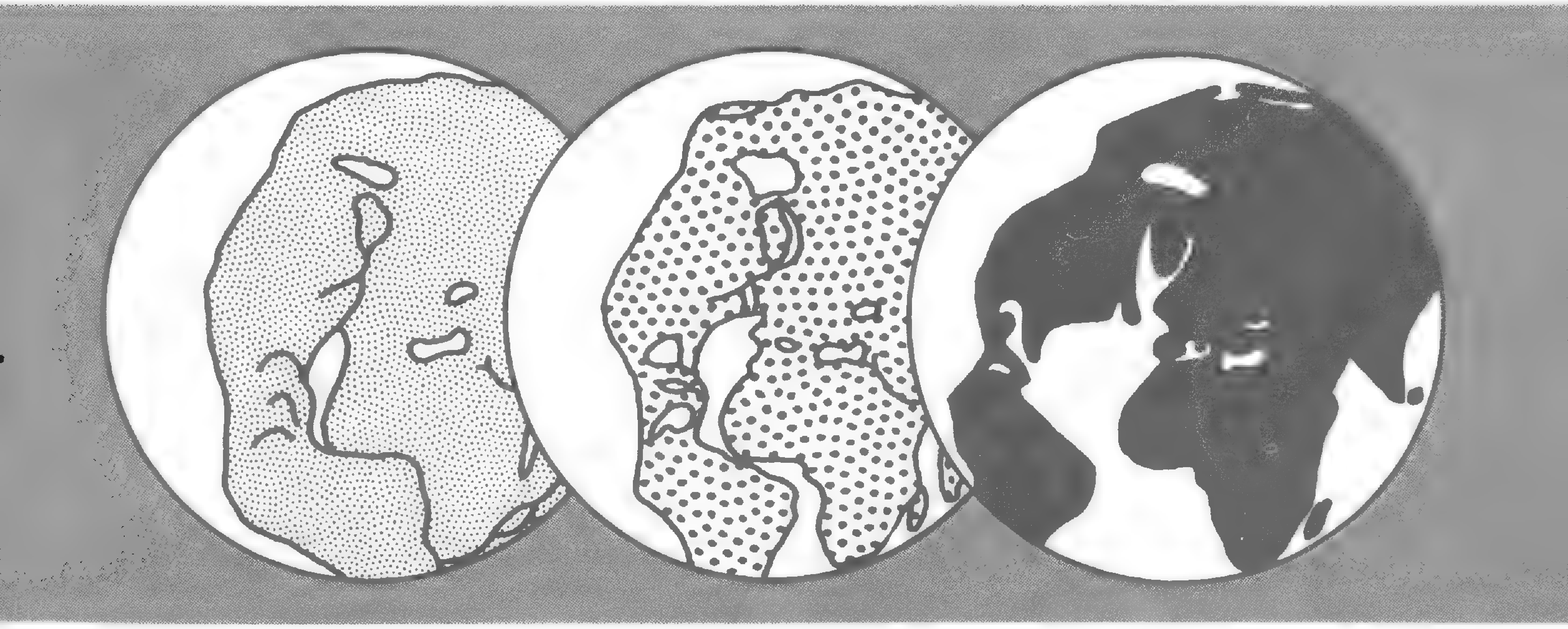
VOLUME 59
1972
NUMBER 2

ANNALS OF THE
Missouri Botanical Garden



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ANNALS OF THE
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Published by the Missouri Botanical Garden Press, St. Louis, Missouri 63110.

ALLEN PRESS, INC. PRINTED IN U.S.A. LAWRENCE, KANSAS

VOLUME 59
1972
NUMBER 2

ANNALS OF THE
Missouri Botanical Garden

DISJUNCTIONS IN PLANTS: A SYMPOSIUM

Otto T. Solbrig[1]

The following pages present all but one of the papers presented at a symposium held in Edmonton, Canada, during the joint meetings of the Canadian and American Botanical Societies. The symposium was jointly sponsored by the American Fern Society, The American Society of Plant Taxonomists, the Botanical Society of America and the Bryological Society. Dr. Warren H. Wagner and myself were charged by these associations with the task of organization.

All species of plants, with the exception of a few relicts now restricted to one population, have disjunct distributions in the strictest sense of the word. However, the botanist uses the term in a more restricted way. Range disjunctions refer usually to large discontinuities in the distribution of the populations of a species. There is no rigorous criterion however as to what magnitude of discontinuity qualifies as a "range disjunction," and consequently we see the term applied equally to relatively small discontinuities in the order of 100 miles, and large bipolar ones involving thousands of miles.

The interruption in the range of a species can have two origins: (1) the range was once continuous and the intermediate populations have become extinct, or (2) the range was never continuous and the disjunct populations have become established with the aid of some event that carried the propagules over the inhospitable area. To these two possible origins, recognized since the problem of range disjunctions was identified, a third explanation has been added lately: the movement of continents that has physically moved apart populations that once were contiguous. This applies particularly to amphiatlantic disjunctions.

The study of disjunctions of single species is fraught with all the problems involved in trying to reconstruct what was a unique event. When the disjunction is the result of extinction of intermediate populations of a once continuous range, fossil evidence if available can help solve the problem in an unmistakable way. Such is the case with the many disjunctions involving southeastern North America and southeastern Asia, an example of which is the genus *Nyssa*. Where once a

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continuous range from southeastern Asia to the southeastern United States via the lands bordering the Bering Straits was proposed, we know now that the continuity existed in the opposite direction, across Europe and Asia. In this respect the new evidence regarding continental drift has both simplified and complexed the problem: simplified in that the position of the land masses in the past can now be assessed using independently obtained, non-biological criteria; complexed because the relative position of continents throughout geological time in relation to each other and to the poles and equator has to be taken into account. Both ancient and modern amphiatlantic disjunctions can be understood when the wandering of the continents are taken into account, from the tree ferns of the upper Carboniferous, to many angiosperms on both sides of the Atlantic.

Evidence for the establishment of disjunctions as a result of long-range dispersal of propagules cannot be obtained directly, and therefore the study of such disjunctions is less satisfying intellectually. Given the spotty fossil record of the past, and its bias toward certain types of plants, it is not possible to state that absence of a fossil record in an area indicates that a plant has never grown there. What is needed is a set of additional criteria that will allow us to recognize unmistakably a relict disjunction due to long range dispersal. To produce reliable criteria, if indeed it is ever possible, we need to make use of all the tools that modern biology has to offer. The objective of the symposium was to gather together a number of researchers who were working on these problems in order to discuss these problems.

The symposium—and the papers here presented—was divided into two sessions. A morning session aimed at assessing the possible contributions of various techniques and approaches: morphology and phytogeography (C. Wood); palynology (D. Whitehead); genetics and cytology (E. Klekowski) and chemistry (B. Turner). The afternoon session was devoted to assessing the biological peculiarities of diverse phyletic groups: Lichens (W. Culberson); bryophytes (W. Schofield and H. Crum); ferns (W. Wagner) and angiosperms (O. T. Solbrig, J. H. Hunziker, and T. Mosquin). The meeting was summarized by P. Raven. The presentations and the discussion showed that a great deal of progress has been made towards setting up criteria to assess disjunctions; that the new disciplines have new insights to offer; and that different phyletic groups have different probabilities of long-range dispersal and establishment. It also showed however that more work is needed and that it is an interesting and rewarding area of research.

In closing I would like to thank Dr. Soper and Dr. Taylor for chairing the sessions; all the contributors for their work; and our hosts, the Canadian Botanical Societies and the University of Alberta, for their hospitality. Finally, I would like to thank Dr. Peter Raven and the Missouri Botanical Garden that made publication of this work possible.

MORPHOLOGY AND PHYTOGEOGRAPHY: THE CLASSICAL APPROACH TO THE STUDY OF DISJUNCTIONS

CARROLL E. WOOD, JR.[1]

Disjunctions are evident in the distribution of almost every species of plant, for it is obvious that no species is composed of completely continuous populations. Discontinuities, however, range from small to very large. Although formerly widely distributed, the giant redwoods or big trees (*Sequoiadendron giganteum*) now occur in groves (populations) of varying size scattered over a distance of 250 miles along the western slopes of the Sierra Nevada of California. The gaps between groves may be insignificant or up to 50 miles wide, but disjunctions of this size do not draw particular attention, except as showing that the intervening habitats presumably are now unfavorable for the establishment and growth of *Sequoiadendron*. If, however, a grove of big trees were to be found in some part of the world as remote from California as the Himalayas of Nepal or the Smoky Mountains of North Carolina and Tennessee, the find might be more exciting than the discovery of living *Metasequoia* in central China. To the inquisitive mind such a large gap in distribution would demand explanation, and, unsurprisingly, disjunctions of this size are the ones that have most intrigued biologists.

A disjunction in the distribution of a single species or genus, even a very wide one as in the hypothetical example above, may make one wonder, but when numerous species in the flora of a given region show the same general disjunction, the curious scientist who realizes that there is a common pattern can hardly resist searching for the circumstances behind it. Patterns of disjunction between eastern North America and eastern Asia, between Europe and North America, between eastern and western North America, and between North and South America are among those that have proved to be especially intriguing (at least to biologists of the continents involved). Almost from Linnaeus onward, botanists have sought and advanced explanations as diverse as double creation of species, long-distance dispersal, disruption (by a variety of factors) of formerly continuous ranges, drifting of continents, and the either conscious or unintentional activities of man.

A great deal of effort has gone into the study of disjunct distributions, and in all of the published material that has resulted, it is evident that comparative morphology is basic. Morphology is basic to the study of disjunctions (and to all of phytogeography, for that matter), because it is basic to taxonomy. Without a taxonomic frame of reference for each disjunct taxon comparisons of almost any sort become meaningless. As taxonomic ideas about a taxon change, so must conclusions based upon the earlier taxonomy. The new data brought into taxonomy by biosystematics have not upset the fundamental taxonomic framework built on morphology but have generally confirmed its soundness. The new data have, moreover, served to broaden the parameters of taxonomy, at the same time

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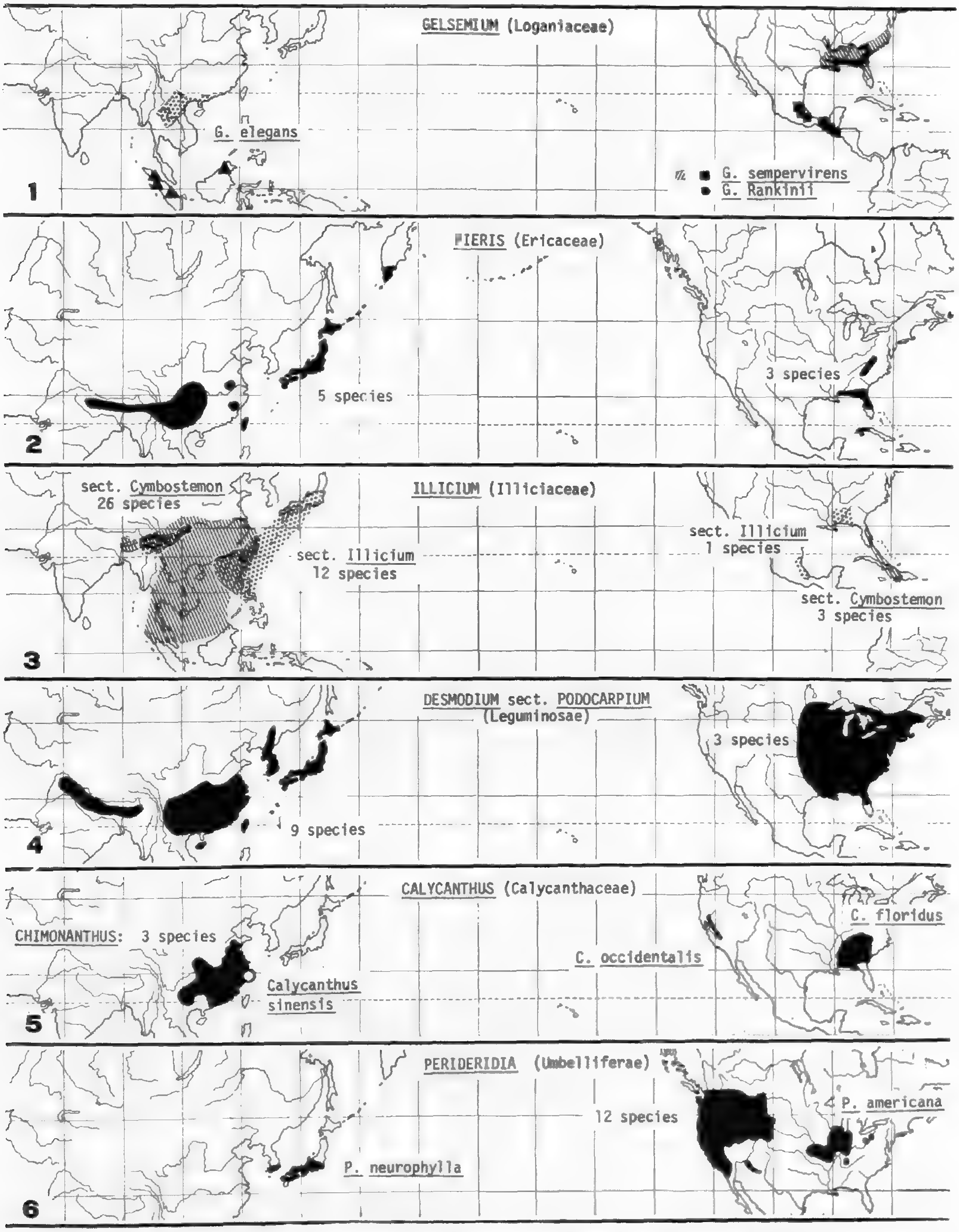
strengthening its framework and providing new clues that help to untangle knotty evolutionary problems. Similarly, in the study of disjunctions new techniques are providing new clues that comparative morphology alone cannot. Modern botanists are using data from geology, palaeobotany, ecology, palynology, cytology, genetics, physiology, and chemistry in their search for further evidence that will help to explain the fascinating patterns of disjunction in the distribution of plants.

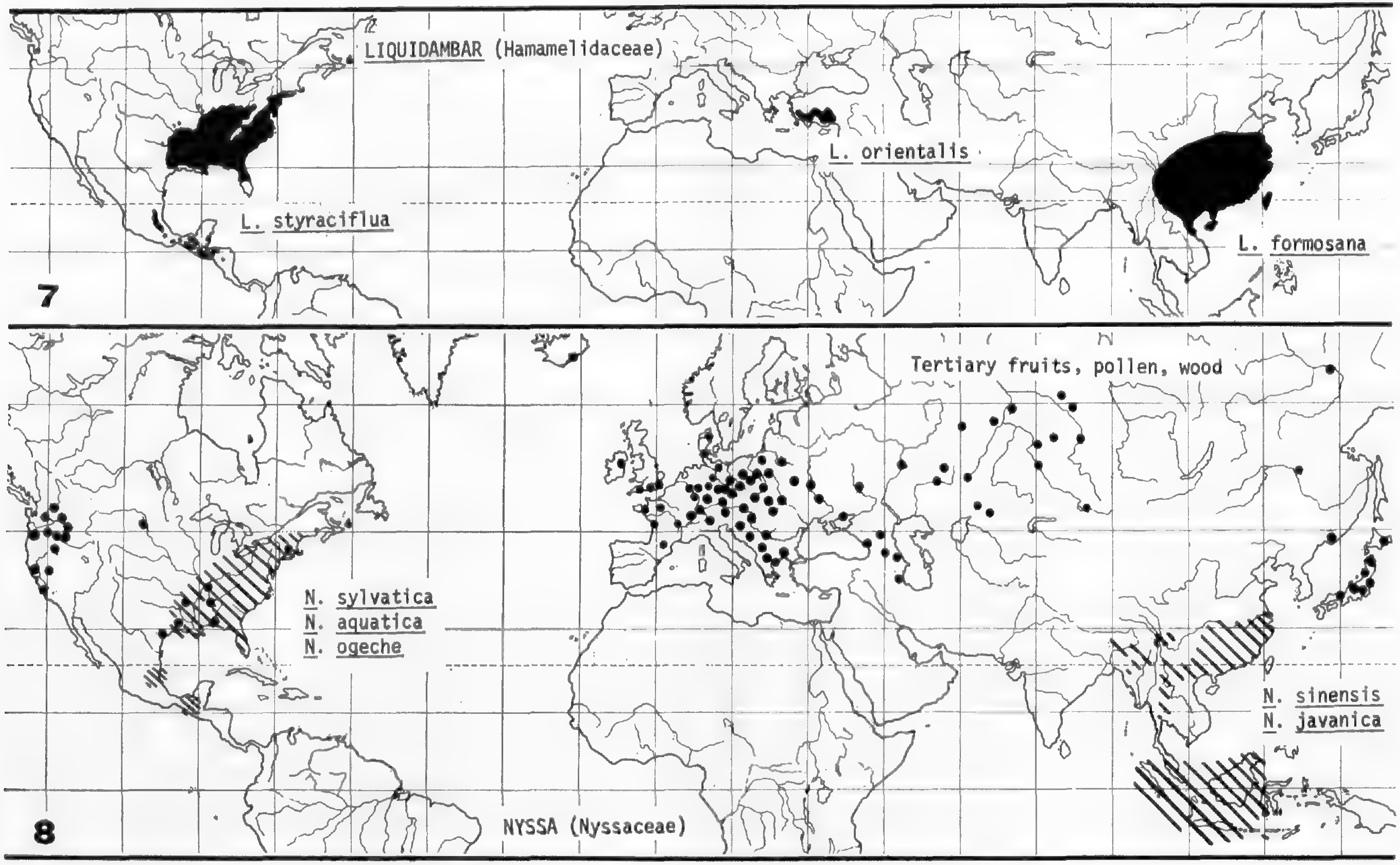
Before considering various aspects of morphology and taxonomy involved in the study of disjunctions in the ranges of plants, it may be useful to look more or less briefly at three of the patterns of disjunction in the distribution of North American plants: Tertiary relict disjunctions; eastern North American–western North American disjunctions; and North American–South American disjunctions.

Tertiary Relict Disjunctions (Maps 1–11).—This pattern of disjunction is an extension of the spectacular and long-known eastern North American–eastern Asian floristic relationship (Maps 1–3, 8) that was first commented on by Linnaeus (1750; *cf.* Graham, 1966), later recognized independently by Thunberg (1784) and Castiglioni (1790; *cf.* Li, 1955), but really brought to the attention of American and European scientists by Asa Gray through a series of papers published between 1840 and 1878 (Gray, 1840–1878). In the most important paper of the series Gray (1859) showed that there are numerous similarities between the floras of eastern North America and Japan, similarities so marked in many instances that it appeared to him that the same species occurred in both regions. Surprisingly, similarities between the floras of Japan and western North America were fewer, and many of the "identical species" common to the eastern parts of both continents were missing. To explain the presence of the same species in both Japan and eastern America Gray advanced an hypothesis involving migration and interchange of species of Asia and America across the region of the Bering Strait followed by disruption of the continuous ranges by the Pleistocene glaciations, ideas that have played a fundamental role in the development of plant geography. Subsequent discoveries, especially in China, have revealed even stronger floristic ties between eastern and southeastern Asia and eastern North America. At present, the two areas are known to share at least seven pairs of closely related genera, 62 genera that now occur nowhere else, and at least 24 more widely distributed genera that have closely related species or groups of species in the two regions (Maps 1–4, 8). It has also become evident that most of Gray's (1859) original "identical species" are morphologically distinguishable in the two areas, and, in most instances, are quite distinct (*cf.* Li, 1952), with the exception of circumboreal species and a few others. There seem to be only relatively few identical species that are disjunct between the two areas (*e.g. Tipularia discolor, Cypripedium arietinum*, both of which may possibly be examples of long-distance dispersal, and *Alnus maritima* [*A. japonica*] with its truly amazing disjunctions between Asia, Oklahoma, and Delaware), although there are a number of species that are treated by various authors as distinct at the varietal, subspecific, or specific level (*e.g. Adlumia fungosa, Penthorum sedoides, Gaultheria hispidula, Phryma leptostachya*).

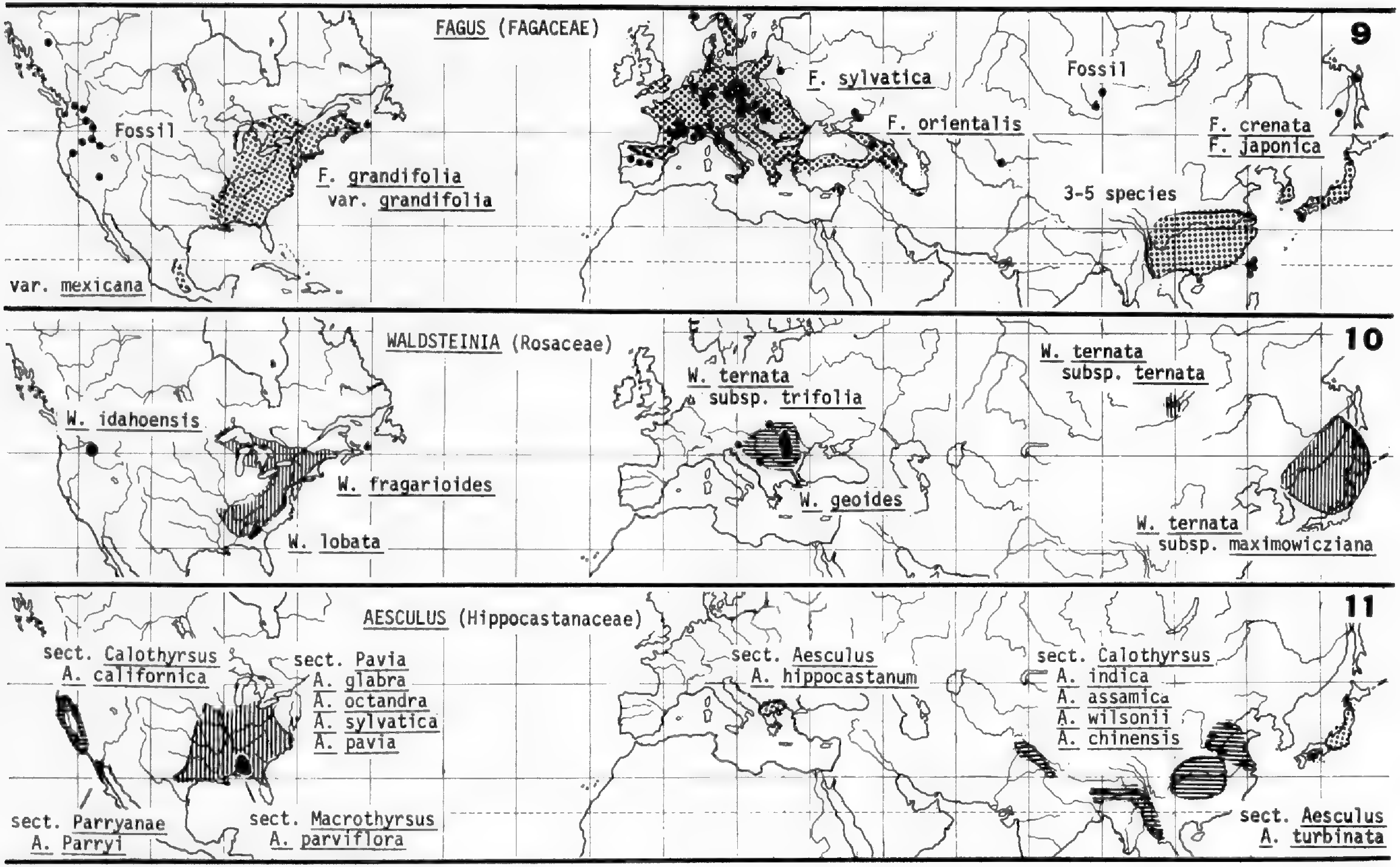
Beyond this bicentric distribution there are also at least ten genera that have



MAPS 1–6.—1–4. Some taxa restricted to eastern Asia and eastern North America.—1. *Gelsemium* (after Ornduff, 1970).—2. *Pieris*.—3. *Illicium* (after Smith, 1947).—4. *Desmodium* section *Podocarpium* (after Isley, 1951).—5–6. Two examples of taxa restricted to eastern Asia, western North America, and eastern North America.—5. *Calycanthus* (largely after Nicely, 1965).—6. *Perideridia* (after Chuang & Constance, 1969).



Maps 7–8. Two relict Tertiary genera.—7. Extant species of *Liquidambar* (courtesy of A. L. Bogle; *L. styraciflua* after Little, 1971).—8. *Nyssa*, hatched areas, extant species; dots, Tertiary occurrences (after Eyde, 1963, and Eyde & Barghoorn, 1963).



MAPS 9–11. Three genera with relict Tertiary distribution.—9. *Fagus,* stipples, extant species; dots, records from Tertiary deposits (after Tralau, 1962; Little, 1971).—10. Extant species of *Waldsteinia* (after Teppner, 1968).—11. Extant species of *Aesculus,* note distribution of sections *Aesculus* and *Calothyrsus* (after Hardin, 1957, 1960).

related taxa in eastern North America, eastern Asia, and southeastern Europe–Asia Minor (*e.g. Liquidambar* [Map 7], *Fagus* [Map 9], *Carpinus, Epigaea*) and 30 genera that have disjunct related taxa in eastern North America, western North America, and eastern Asia. At least a dozen genera (*e.g. Erythronium, Ostrya, Hepatica, Platanus, Waldsteinia* [Map 10], *Cercis*, and *Aesculus* [Map 11] occur only in all four areas, and at least six more wide-spread genera have related species distributed in this pattern. In all, at least 146 genera of eastern North America (13 per cent of the indigenous genera of seed plants) are involved; almost half of these (67 genera) are woody plants.

Over the years paleobotanical findings have confirmed the widespread occurrence of many of these same genera, mainly the woody ones, in Eurasia and North America in broad areas from which they are now missing, and it is clear that the extant representatives of the same widely distributed woody genera are the survivors of the gradual climatic deterioration, volcanism, orogenic movements, and the glaciations that followed.

Wolfe (1969) has pointed out that the representatives of some lineages that were present in the Tertiary in Pacific Northwestern America were able to adapt to changing climatic conditions (especially the switch from wet summer to dry summer) and now survive in different associations, others became extinct, and others survive in what are essentially relict habitats (especially in the Klamath Range of northern California and southern Oregon). The same undoubtedly was true in other regions of the Northern Hemisphere. The four disjunct areas, though, are the present more or less mesic refugia for many of the surviving descendants of formerly more widespread genera. The largest, and ecologically most complex, of the relict areas are eastern Asia and eastern North America; those of western North America and Europe-Asia Minor are smaller, and many genera that formerly occurred in them have disappeared (*e.g. Ulmus* and *Liquidambar* [Map 7] from western North America; *Tsuga* from Europe; *Liriodendron, Magnolia*, and *Nyssa* [Map 8] from both).

The general pattern of formerly wide boreal distributions that were fragmented by orogenic movements, gradual climatic cooling, volcanism, and the Pleistocene glaciations seems to be well established, but much is unknown. The majority of the plants involved are as yet unknown as fossils (but palynologists might well look routinely for their pollen grains, even though many are not wind pollinated). The taxonomic interrelationships in many of the genera need much more study; it is not certain that all of the disjunctions are of the same age; their areas of survival during the Pleistocene are for the most part unknown; and the accumulating

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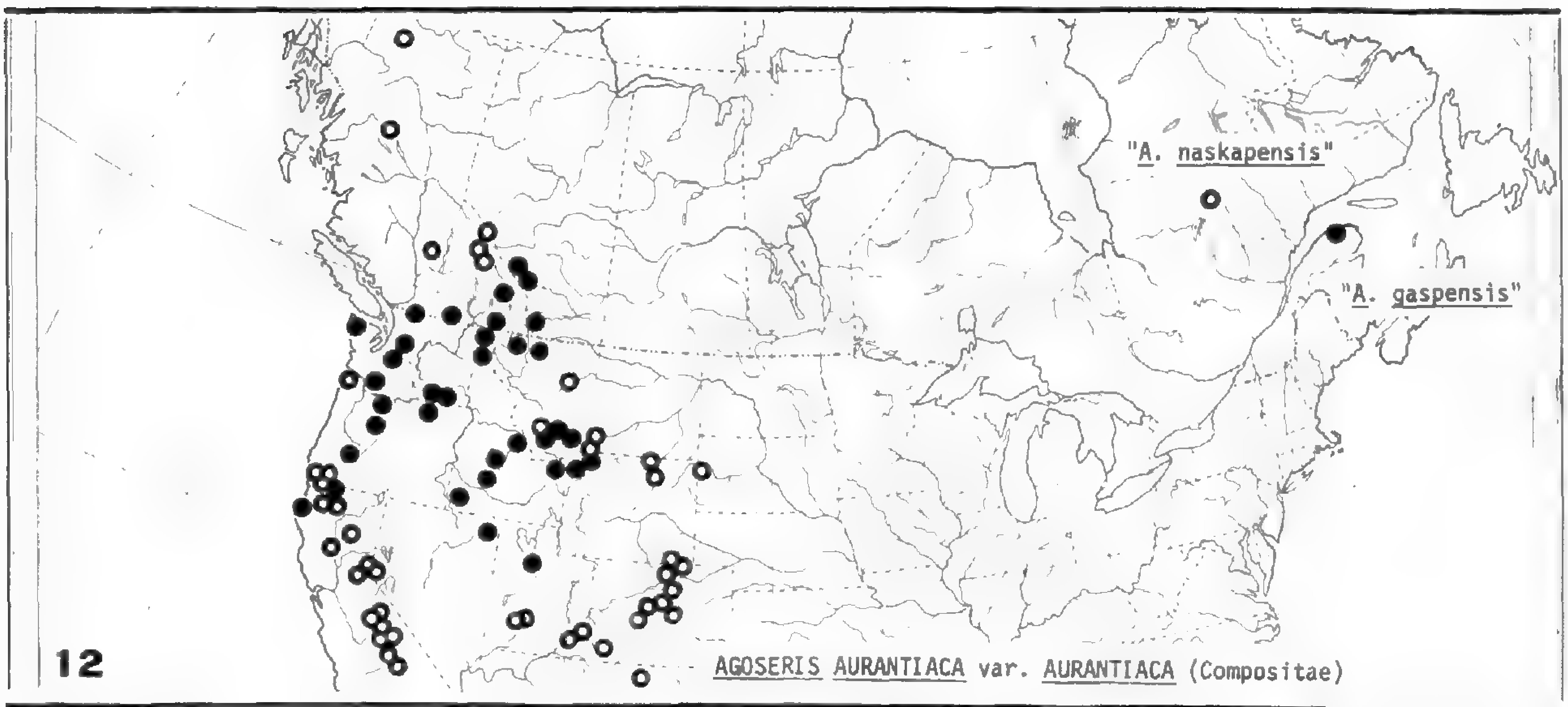
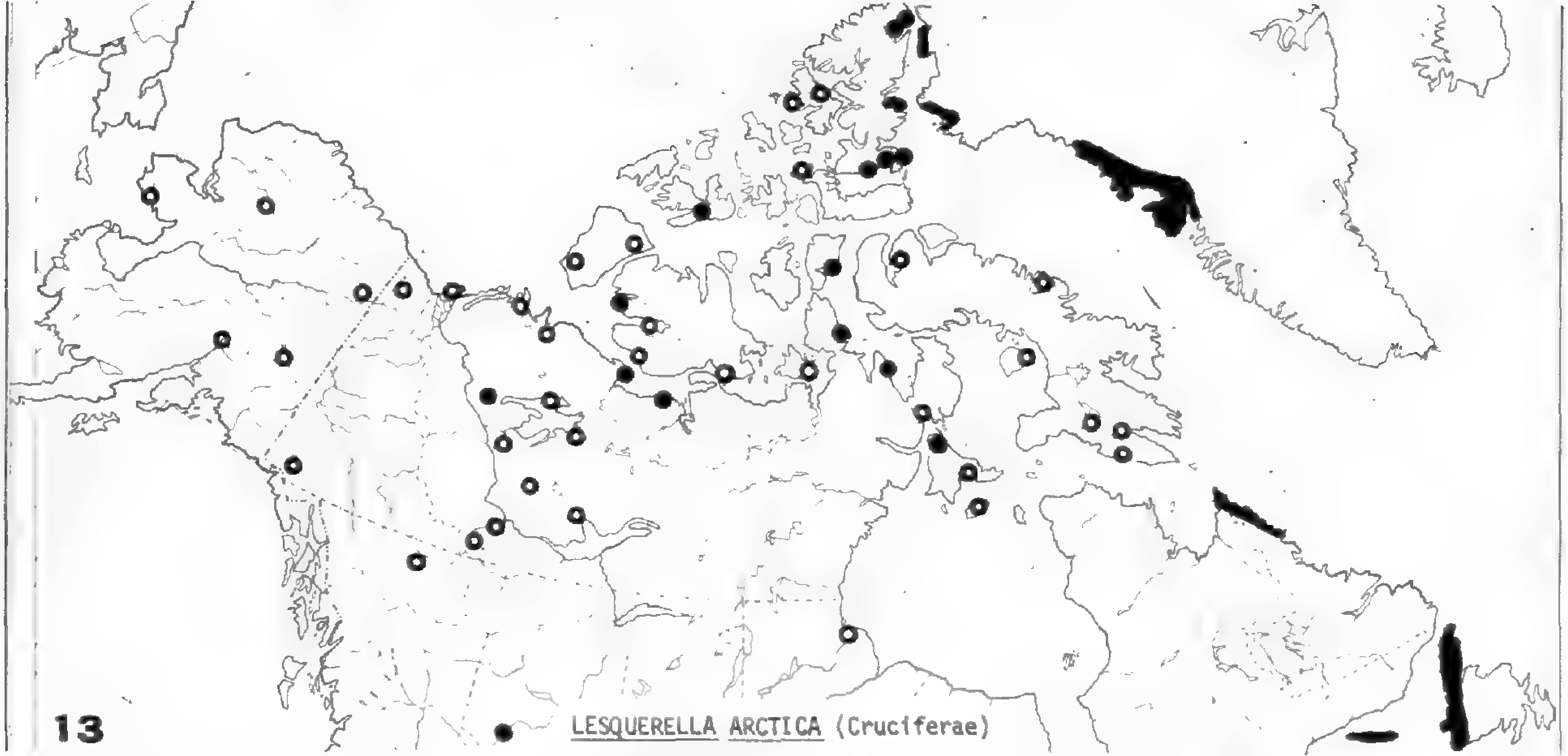
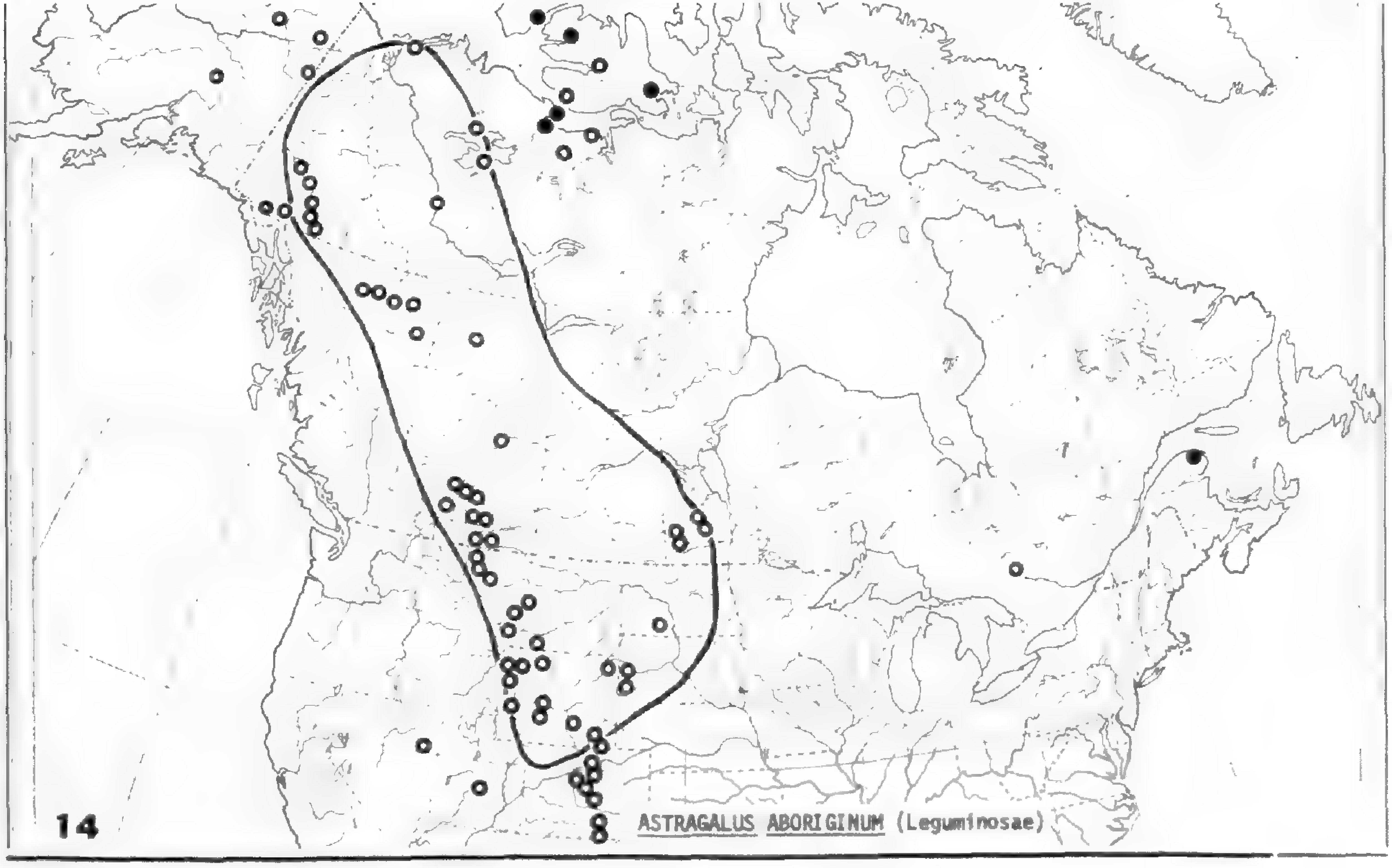
MAPS 12–14. Western North American or arctic taxa with disjunctions in eastern North America.—12. *Agoseris aurantiaca* var. *aurantiaca*, dots, localities mapped by Fernald (1925) for *A. gaspensis* and *A. gracilens*; circles, additional collections mapped by Quentin Jones; see text.—13. *Lesquerella arctica*, black areas and dots, localities mapped by Fernald (1925); circles, additional localities mapped by Rollins and Shaw (1973); stations in northeastern Greenland and Siberia not shown.—14. *Astragalus aboriginum*, dots and outlined area as mapped by Fernald (1925); circles, localities mapped by Barneby (1964), three Alaskan stations not shown.



12 AGOSERIS AURANTIACA var. AURANTIACA (Compositae)



13 LESQUERELLA ARCTICA (Cruciferae)



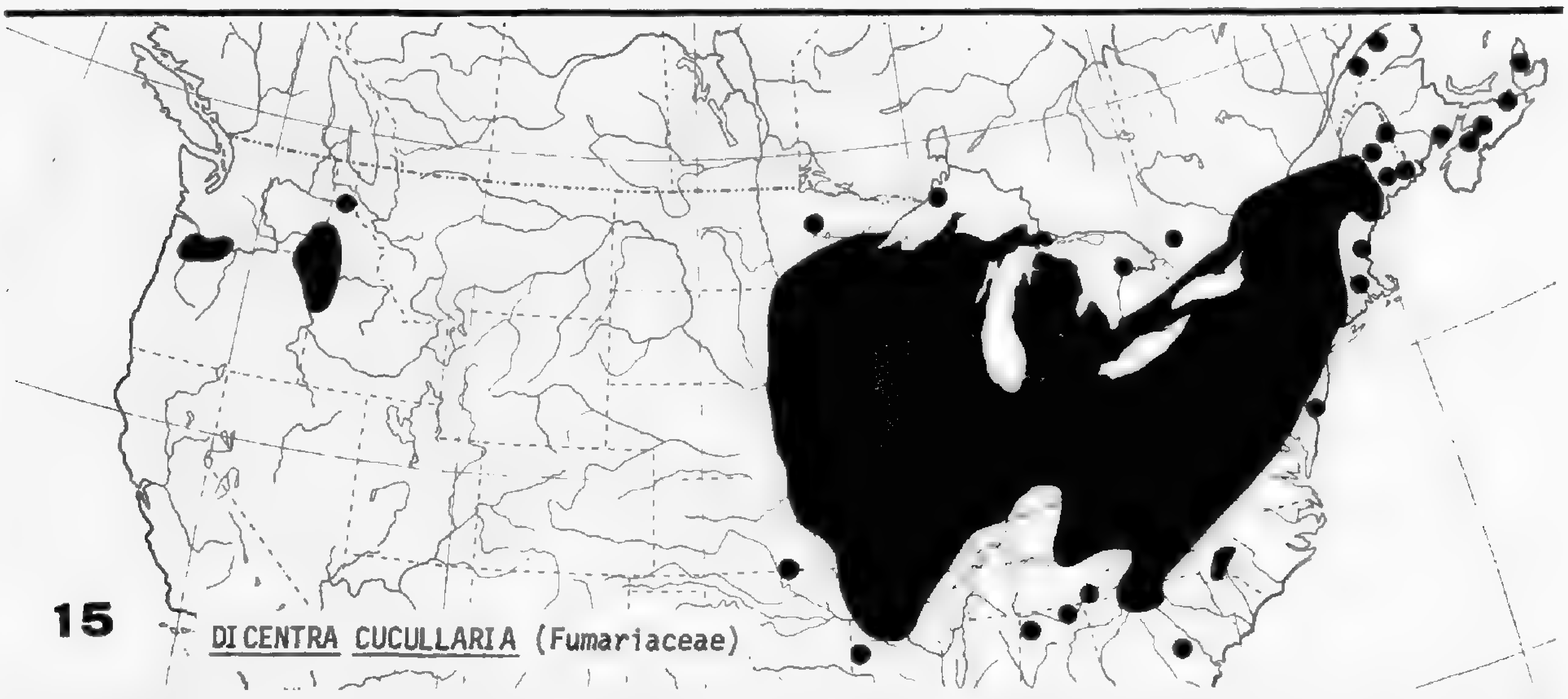
14 ASTRAGALUS ABORIGINUM (Leguminosae)

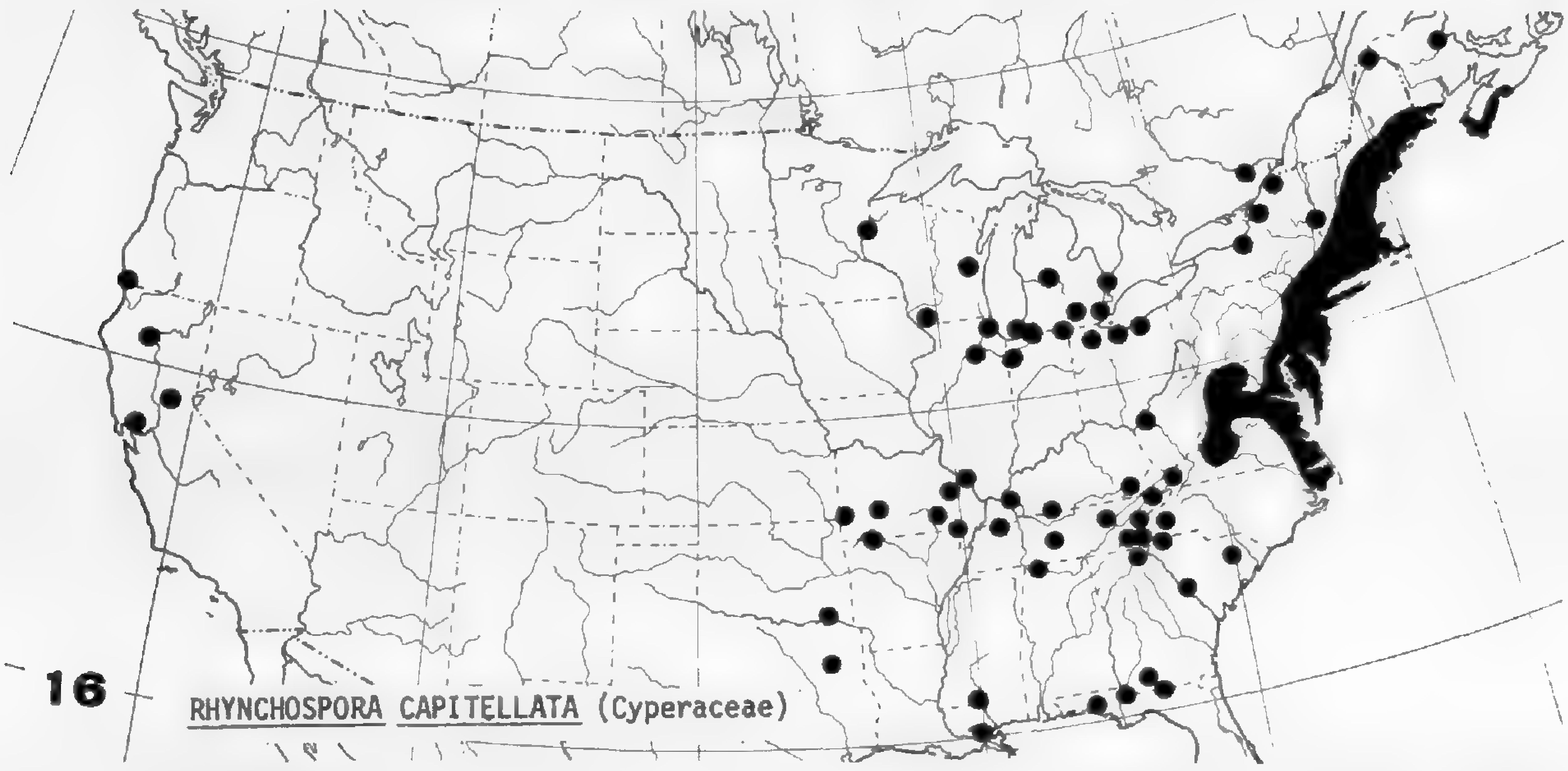
proof of continental drift introduces new spatial relationships that must be considered in connection with the migrations of plants.

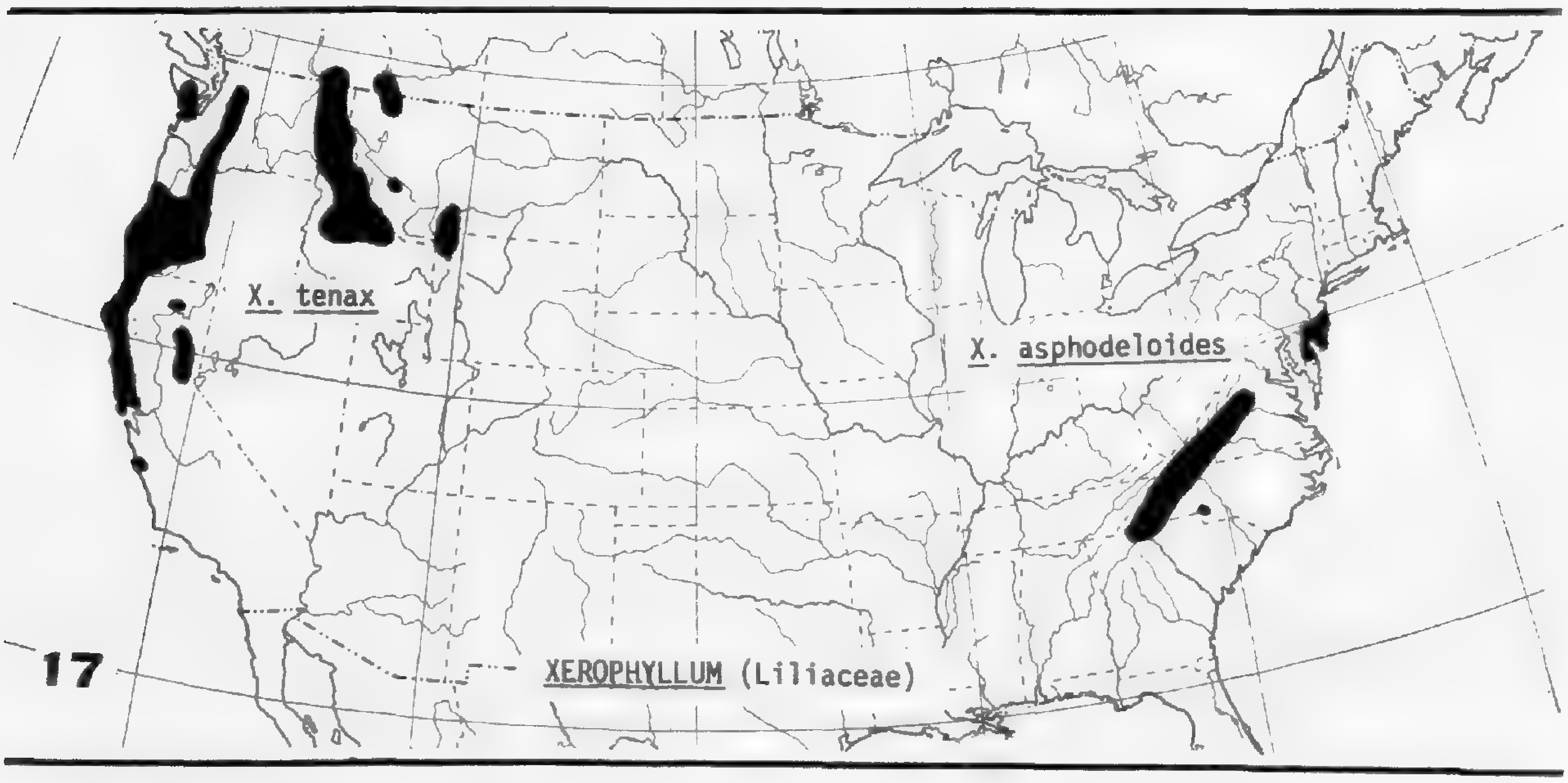
Eastern North American–Western North American Disjuncts.—The now familiar pattern of species of the high arctic and of the cordillera of western North America disjunct in the glaciated area of northeastern North America (see Maps 12–14, 21) has received much attention, largely as a result of Fernald's stimulating hypothesis (1925–1935) that western and arctic plants were able to survive in unglaciated *nunatak* areas around Lake Superior, on the Gaspé Peninsula, on the tablelands of the Long Range of Newfoundland, and in the Torngat Mountains of Labrador, and that the surviving populations of these "old species" were unable to spread from these areas. "This failure of the plants of the unglaciated spots to extend their ranges into closely adjacent areas which, upon the melting of the Labrador sheet, became open territory ready for invasion, is interpreted as a further evidence of the antiquity of these plants; at the close of the Pleistocene they were already too old and conservative to pioneer, although they are able to linger as localized relics in their special undisturbed crannies and pockets" (Fernald, 1925: 243). He provided a list of some 295 species and varieties that either show this disjunction or are endemics (about 80 species or varieties) related to species of western North America and showed that these occur in areas that were thought by many geologists of the time to have escaped glaciation. However, subsequent work has shown that all of the areas involved were indeed glaciated, and further field work has filled in some of the disjunctions in places that undoubtedly were glaciated (*cf.* Maps 12, 14, 21). Monographic work has changed the taxonomic status of many of the supposed endemics, suggesting a shorter period of isolation. The work of a number of ecologists, too, has shown that the arctic plants are restricted to high altitudes or to river canyons or other places where their requirements for cold are met, and that many of the other relicts or endemics are plants of unstable habitats (cliffs, talus slopes, serpentine barrens) where they can grow but are removed from competition with the dominant eastern boreal plants (*cf.* Rune, 1954). In this last respect they apparently are similar to the endemic species of ultramafic soils studied by Kruckeberg (1951, 1967, 1969) and to the shale-barren endemics of Virginia and West Virginia studied by Platt (1951).

In reviewing the disjuncts from northwestern North America, Schofield (1969) summarizes, "The most plausible explanation of their disjunction is that the eastern representatives are remnants of a more widespread flora of the past, possibly of pre-Pleistocene arctic-alpine distribution in North America. The Pleistocene glaciations can be assumed to have eliminated the north-central portion of the range, but since habitats were available in north-eastern and western North America the species survived, probably south of the glacial boundary, but possibly in nunataks or coastal refuges, moving to their present sites following retreat of the ice sheet but being eliminated from their Pleistocene refugium by the encroaching vegetation and by a succession toward more mesophytic temperate vegetation. Evidence for nunataks and refugia in eastern North America has been disputed."

Much less attention has been focused on East-West disjuncts to the south of





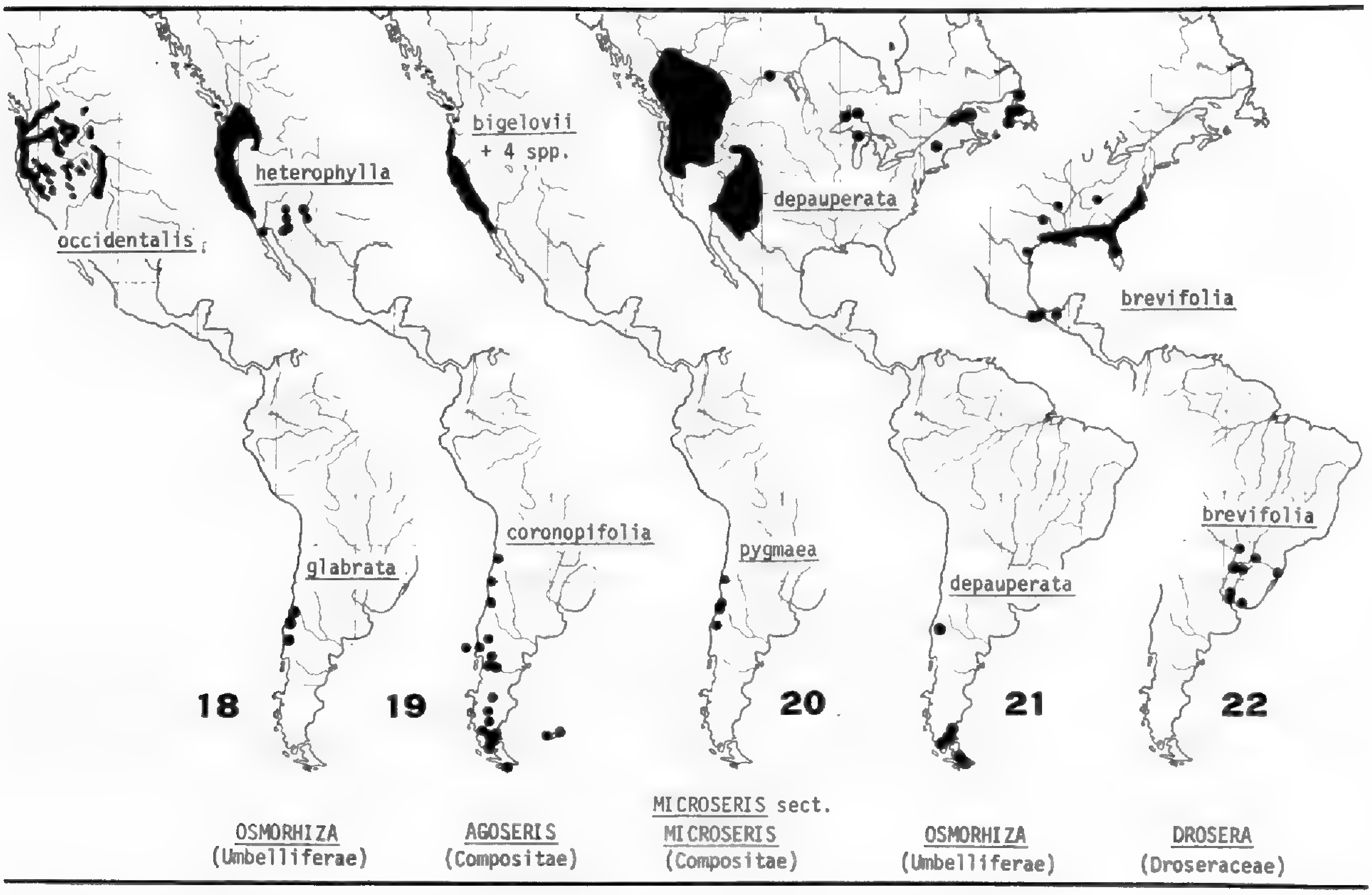


MAPS 15–17. Some taxa of unglaciated eastern North America with a disjunction to western North America.—15. *Dicentra cucullaria* (after Stern, 1961).—16. *Rhynchospora capitellata* (from Wood, 1971).—17. *Xerophyllum* (from Wood, 1971).

the maximum extent of the Pleistocene ice, although some vicarious pairs of species (*e.g. Pinus strobus–P. monticola, Thuja occidentalis–T. plicata, Dirca palustris–D. occidentalis, Calycanthus floridus–C. occidentalis* [Map 5], *Xerophyllum asphodeloides–X. tenax* [Map 17]) have often been cited. Wood (1971) has sorted out over 150 genera with taxa showing disjunct relationships between the part of the Appalachian mountain system south of the area of glaciation and western North America. This group includes some 50 genera with one or more species that appear to be disjunctly distributed (*e.g. Dulichium arundinaceum* [Map 23], *Rynchospora capitellata* [Map 16], *R. globularis, Ranunculus pusillus, Sibara virginica, Dicentra cucullaria* [Map 15], *Viola canadensis* vars. *canadensis* and *corymbosa*, and *Trichostema brachiatum*) and 112 genera with related taxa of the same rank on both sides of the continent. Among the latter group are 20 genera that are restricted (or nearly so) to North America and 46 with distributions that suggest the Arcto-Tertiary relict pattern (*cf.* Maps 5–6, 10). In all, at least 158 genera (14 per cent of the indigenous genera of seed plants of eastern North America) have disjunctions between the southern Appalachians and western North America either within the same taxon or between related taxa.

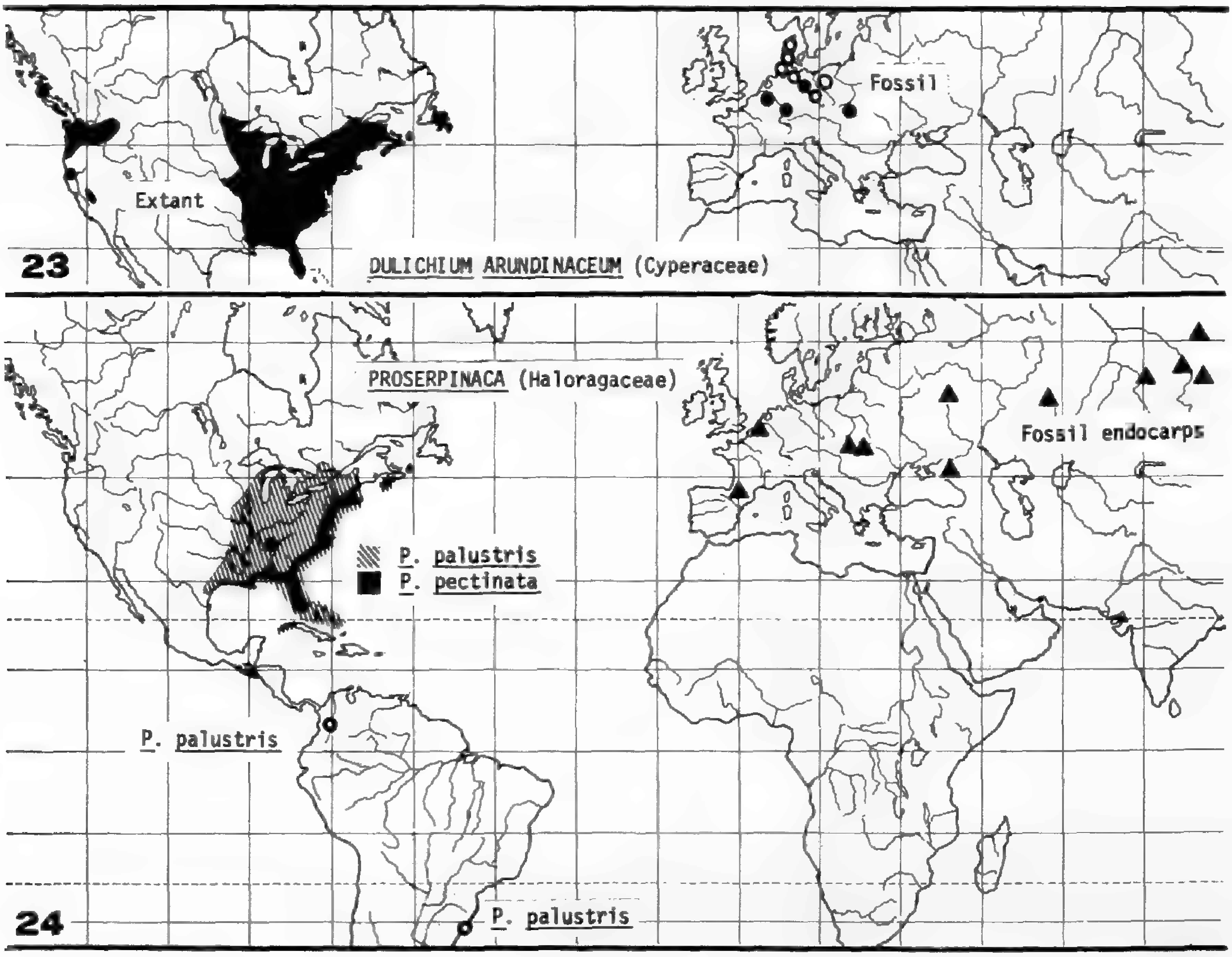
Most of the taxa involved have not been studied in great detail, and the distributional history of most is unknown. It seems likely that the disjunctions may be of different ages, since various taxonomic ranks are involved. Some fit the relict Tertiary pattern, others probably are the result of the disruption of formerly more continuous ranges by the Pleistocene glaciations, and still others may possibly be examples of long-distance dispersal. In some instances there may have been several disruptions, such as those postulated by Russell (1956) to account for the East-West disjunction of *Viola macloskeyi* subsp. *pallens* and the occurrence of both subsp. *pallens* and subsp. *macloskeyi* in the West. Whatever the causes of disruption, one of the key issues is the question of how much of a vegetational shift southward was brought about by the Pleistocene glaciations (*cf.* Whitehead, this symposium).

Amphitropical Disjunctions between North and South America.—Monographers and floristic workers over a period of many years have pointed out examples of disjunctions from both boreal and temperate North America to corresponding climatic parts of South America, mostly on the western side of both continents (Maps 18–22, 24) and disjunctions from the Sonoran and Chihuahuan desert regions of North America to deserts of northern Argentina and northern Chile. In summarizing a symposium on the amphitropical relationships in the herbaceous flora of the Pacific coast of North and South America (Quart. Rev. Biol. 38: 109–177. 1963), Raven (1963) brought together the most comprehensive catalog to date of the herbaceous examples and thoroughly discussed the possible ways in which such disjunctions could have come about. The amphitropical disjunctions fall into three groups: "bipolar or high-latitude, with about 30 species; temperate, with about 130 species; and desert, with a substantial number." In the herbaceous plants of all three groups (the first two are entirely herbaceous), the disjunction involves either the same species or closely related subspecific taxa in both areas. In the bipolar examples, the northern taxon is also either circumboreal



MAPS 18–22. Some taxa with an amphitropical disjunction between North and South America.—18. *Osmorhiza occidentalis* and *O. glabrata*, a species-pair (after Constance & Shan, 1948).—19. *Agoseris heterophylla* and *A. coronopifolia*, another species-pair (after Jones, 1954, and Chambers, 1963).—20. *Microseris* section *Microseris*, with five species in western North America and *M. pygmaea* in South America (after Chambers, 1955, 1963).—21. *Osmorhiza depauperata* (after Constance & Shan, 1948).—22. *Drosera brevifolia* (in part after Wynne, 1944).

in distribution or (in a few cases) belongs to a circumboreal group. Of the examples of temperate disjuncts brought together by Raven, in 111 instances the North American taxon is a species of western North America, in 13 is wide-spread in North America, and in 6 is a species of eastern North America. The desert disjuncts include both woody plants (with no species common to the two areas and with few common genera) and herbaceous ones (with either the same or closely related species in both areas). Some of the amphitropical disjuncts in all three categories have been studied in considerable detail, others have been recognized from herbarium materials on purely morphological grounds. In summary, "Pertinent general considerations are that: (1) the North and South American populations are closely related; (2) the plants are almost without exception self-compatible and often autogamous; (3) they constitute an unbalanced assemblage entirely unrepresentative of the two extratropical areas; (4) they grow almost exclusively in open communities, not in woodland or scrub associations; (5) there are no corresponding cases among terrestrial vertebrates and very few among the insects; and (6) the floras of the two areas have been distinct since at least the middle Cretaceous and are still very different at present. The only explanation that accounts for all of these facts seems to be that at least the great majority of the plants reached their disjunct areas by long-distance dispersal relatively re-



MAPS 23–24. Two genera formerly distributed in the Eastern but now restricted to the Western Hemisphere.—23. *Dulichium*, the single species disjunct between east and west in North America; dots, Tertiary; circles, interglacial records (after Tralau, 1959); black, extant distribution, generalized (after Wood, 1971).—24. *Proserpinaca, P. palustris* disjunct in Central America, Colombia, and Brazil; *P. pectinata* disjunct in Tennessee (both after Fassett, 1953); triangles, Tertiary occurrences (after Dorofeev, 1958).

cently. For the bipolar species, the Pleistocene seems the most likely time of dispersal; for the temperate species, the late Pliocene or Pleistocene; and for the desert species, excluding those that may have differentiated from common ancestors that spanned the tropics, no time has probably been more likely than the recent past. Both bipolar and temperate disjuncts have come mostly from the north . . . and are almost entirely herbaceous. The desert disjuncts, on the other hand, often appear to have originated in the south . . . or to have diverged from a common tropical ancestor. Many of them are woody" (Raven, 1963).

Throughout all three of these examples of general patterns of distribution it is apparent how crucial taxonomic relationships and comparative morphology are in the study of disjunctions. Gray's "identical species" in eastern America and Japan have already been mentioned, as has the status of some of Fernald's Gaspé endemics that have been shown to be a part of the variation in more widespread western species. As one example of the latter, both *Agoseris gaspensis* and the later-described *A. naskapensis* (from Chicoutimi County, Quebec), along with the western *A. gracilens* (from which Fernald differentiated his *A. gaspensis*), have been included by Quentin Jones (1954) in the western American *A. aurantiaca* var. *aurantiaca* (Map 12). Jones notes that both of the eastern disjuncts fall well within the range of variability in the polymorphic var. *aurantiaca* and that if the source of the collection were unknown it would be impossible to refer it with any assurance either to the disjunct eastern populations or to the Rocky Mountain ones. This changed taxonomy not only merges *A. gaspensis* and *A. gracilens* with *A. aurantiaca*, but includes an eastern population (*A. naskapensis*) from an area that undoubtedly was glaciated, producing a rather different problem in disjunction from that seen by Fernald (1925).

Similarly, the enlargement of *Perideridia* (Umbelliferae) by Chuang and Constance (1969) to include the Asiatic *Pterygopleurum neurophyllum* produces a different phytogeographical problem. *Perideridia* has been regarded as an entirely American genus with most of the species in the western United States and *P. americana* disjunct in the east-central United States (Map 6). However, Chuang and Constance showed that *Pterygopleurum neurophyllum*, which is distributed in southern Japan and Korea, has corky fruit ribs like those of *Perideridia howellii*, has foliage closely similar to that of *Perideridia gairdneri* subsp. *borealis*, and, most decisively, has "exactly the type of polystelic tuberous root found in most species of *Perideridia* (except *P. Howellii* and *P. Kellogii*), a feature unknown in *Cenolophium*, *Ligusticum*, or *Sium*," the other possible genera to which it might be related. Accordingly they included the species in *Perideridia* as *P. neurophylla*. "The confirmation of the close similarity and probable affinity of this Asiatic species to the taxa of *Perideridia* inhabiting Pacific Northwest America suggests that the genus may once have been considerably more widely distributed in the northern hemisphere, perhaps before Pleistocene glaciation."

At a different taxonomic level, disjunct relationships between the species of a genus may be seen to be very different when the taxonomic framework is overhauled. The genus *Aesculus* (revised by Hardin, 1957, 1960) has an interrupted distribution in Asia, southeastern Europe, eastern North America, and western North America (Map 11). The four species of the Himalayas and China, however, belong to a different section of the genus from the geographically adjacent *A. turbinata* of Japan, which, with *A. hippocastanum*, of the Balkan Peninsula, constitutes section *Aesculus*. The Himalayan and Chinese species find their closest relative in the North American *A. californica*, the five comprising section *Calothyrsus*! The remaining American species constitute three sections (two monotypic) without disjunctions between their species.

Osmorhiza (Umbelliferae), *Amsonia* (Apocynaceae), *Gaultheria* (Ericaceae), and *Styrax* (Styracaceae) all have representatives in eastern North America, as well as in the western part of the continent. However, in each genus the species of the eastern United States belong to a different alliance from their western congeners, and, in each instance, they are morphologically closer to species of eastern Asia than to the much nearer western ones (*cf.* Wood, 1971: 378). In *Gaultheria*, for example, the two eastern American representatives, *G. procumbens* and *G. hispidula* var. *hispidula*, both members of section *Gaultheria*, are respectively most closely related to *G. pyroloides* (of section *Leucothoides*) and *G.*

hispidula var. *japonica*, of Japan. Of the three quite different western American species, *G. ovatifolia* and *G. humifusa* belong to section *Amblyandra*, and *G. shallon* belongs to section *Brossaeopsis*, which also includes two species of the West Indies and those of Mexico (*cf.* Shaw, 1940). Consequently, although the genus is of disjunct distribution in North America, the proper phytogeographic comparison of the eastern species is not with those in western North America but with species of Asia.

It is obvious, too, that as the state of knowledge of a flora changes, as it becomes better known, and as floras of other areas become better known, new discoveries may greatly alter phytogeographical relationships. At the time Gray (1859) wrote his important paper on the relationships between the floras of Japan and North America, he had rather scant Japanese material and little or nothing from China. Continued exploration, particularly of China and adjacent Indochina and Burma, has brought in new collections that have made possible better taxonomic decisions, and many new examples of close relationships between the floras of China and Japan and of China and eastern North America have been found. Even relatively recently, the discovery in eastern China of a white-flowered species of *Calycanthus* (described as *C. sinensis* in 1963, and raised to generic rank as *Sinocalycanthus* by Cheng and Chang, 1964) added a new morphological dimension to the genus and confirmed the relict relationship suggested by the occurrence of *Chimonanthus* (the only other genus of the family) in China and of species of *Calycanthus* in the eastern United States and in California (Map 5).

As a result of his studies of Asiatic plants Gray suggested that relatives of "monotypes" of eastern North America should be sought in Asia, and, with the continuing botanical exploration of Asia, numerous examples of this relationship have been found (*e.g.* in *Saururus*, *Decumaria*, *Itea*, *Berchemia*, and *Gordonia*, to name only a few). One of the more recently recognized instances of this relationship is that of the monotypic endemic genus *Anemonella* (Ranunculaceae). *Anemonella thalictroides*, of wide distribution in open deciduous woods over much of the eastern United States, is a low, herbaceous, tuberous-rooted plant with *Thalictrum*-like foliage and a reduced inflorescence of *Anemone*-like flowers with a perianth of five to ten conspicuous white or pinkish tepals. Although usually treated as a distinct genus, it has occasionally been referred to *Anemone*. Boivin (1957), however, prompted by comments of A. J. Eames that *Anemonella* and *Thalictrum* are the only genera of the Ranunculaceae with multiple carpellary traces, found that *Anemonella* should be referred to *Thalictrum* section *Physocarpum*. Aside from *T. clavatum*, of the southern Appalachians, and the very similar *T. mirabile*, of Kentucky and Alabama, both of which seem to be more closely related to Asian taxa than to *Anemonella*, this section is composed of twelve species of eastern Asia. The tuberous roots, the compound leaves, and the tepals, stamens, carpels, and fruits of *Anemonella* fit well with those of species of this section. A number of the species have subopposite or opposite leaves; *T. tubiferum* and *T. filamentosum* have two opposite leaves, as in *Anemonella*; and *T. coraneum* and *T. chiaonis* have reduced inflorescences. The tendencies toward reduction in leaves and inflorescences seem only to have been carried somewhat further in *Anemonella*, and the plant fits well in *Thalictrum* (but not at all in *Anemone*, from which it differs fundamentally in leaves, inflorescences, and carpels). Accordingly, *Anemonella* became, rather redundantly, *Thalictrum thalictroides*, and a further disjunct relationship between eastern North America and eastern Asia became evident.

Discoveries that alter the distributional patterns that led Fernald to think in terms of nunataks have already been mentioned, and a few of these are seen in the maps of *Agoseris aurantiaca, Lesquerella arctica*, and *Astragalus aboriginum* (Maps 12–14). In another geographic direction, work on the flora of the State of Santa Catarina, Brazil, has added species such as *Arenaria groenlandica, Xyris brevifolia, Hypericum gentianoides*, and *Proserpinaca palustris* (Map 24) to the list of plants that are disjunct in Brazil from the main body of their distribution in the eastern United States (*cf.* Raven, 1963); and other examples of this disjunction have been found.

Beyond these considerations, one of the principal problems in understanding disjunctions is our meager knowledge of the past distributions, the expansions and contractions in the ranges, of most plants. The fragmentary palaeobotanical record will always leave much to be desired, and the usefulness of palaeobotanical data is further impaired by misidentifications made by uncritical workers. Many of these misidentifications are based upon fossil leaves that it may or may not be possible to identify on the basis of detailed studies, and many of the reports based on fossils of this type must be discounted, at least for the present. The comments of Tralau (1963: 40) in his review of Eurasian fossils attributable to *Magnolia kobus* are pertinent: "It is, nevertheless, uncertain and can not be decided here whether all these finds [of leaves] really belong to the genus *Magnolia* or not. On the other hand fossil foliar specimens referred to the genera *Juglans, Ficus, Anona, Persea, Lindera, Laurus, Eriobotrya, Evodia, Rhododendron, Ardisia, Solandra*, and possibly even others actually may be remains belonging to *Magnolia*. Because of this obvious uncertainty the prospect of unravelling the problems associated with these remains and reconstructing the Tertiary history of *M. Kobus* with them is most unattractive."

Some groups, however, have been reviewed carefully and now have relatively well-documented fossil records based on wood, fruits, and pollen (*e.g. Nyssa*, Map 8, after Eyde & Barghoorn, 1963; *Fagus*, Map 9, after Tralau, 1962) that show that the present disjunctions are the remnants of formerly broad ranges. Fossil pollen, in particular, is proving to be helpful in showing the presence of various genera of flowering plants in areas where they no longer occur (*e.g.* the well-documented pollen record of *Liquidambar* in Eurasia, and the growing pollen record of *Pachysandra* in western North America).

Contrary to the assertions of many plant geographers, present distributions do not necessarily indicate where a group of plants has occurred in the past, although there are exceptions. On the basis of similarities in the modern distributions of plants that are restricted in their occurrence to the four areas where Tertiary relicts occur it can be inferred that genera such as *Narthecium, Erythro-*

nium, *Asarum*, *Aesculus*, and *Waldsteinia* (see Maps 10–11) were formerly distributed around the Northern Hemisphere as *Nyssa* and *Fagus* were. However, the modern distributions of most plants may not show where they have occurred in the past, and many speculations about origins, migrations, and disjunctions can be nothing more than speculations unless other evidence can be found.

For example, the sedge *Dulichium arundinaceum* is widely distributed in the eastern United States and occurs quite disjunctly in the Pacific Northwest and in a few localities in California. One cannot suspect from its extant range that it formerly occurred in western Europe, where fossil remains of it are known from a number of localities (*cf.* Map 23, after Tralau, 1959). Further, in the aquatic genus *Proserpinaca* (Haloragaceae), *P. pectinata* is mostly confined to the Coastal Plain of the southeastern United States, while the other species of the genus, *P. palustris*, is more widely distributed in eastern North America and has disjunct occurrences in Central America, Colombia, and southern Brazil (Map 24). Certainly there is nothing in this distribution to suggest that *Proserpinaca* formerly occurred in Europe and Asia, but Dorofeev (1958) has illustrated fossil endocarps that he assigns to two species analogous to the living ones. Although on the basis of morphology of the all too similar endocarps, the recognition of two extinct species hardly seems justified, these endocarps certainly represent *Proserpinaca* and document a formerly wide Eurasian range for the genus. These two examples, to which many others can be added, show that distributions of individual species have changed in the past—and undoubtedly are still changing—and strongly suggest that in dealing with disjunctions the phytogeographer must be wary of interpretations based only on extant distributions.

Morphology, then, is basic to the taxonomy of both extant and extinct plants, and, consequently, to the study of disjunctions. As in taxonomy, however, there are questions that cannot be answered by morphology alone, and evidence from other disciplines must be sought. For most species of living plants it is unlikely that we shall ever have any sort of fossil record that will show where their ancestors grew, but detailed studies involving morphology coupled with ecology, cytology, genetics, physiology, and other disciplines will undoubtedly provide many clues that will be of great importance in explaining the many patterns of disjunction. Some data will provide answers, some will only be suggestive, and some will raise still further questions. The other papers in this symposium show some of the varied ways of approaching these problems, but in all of them morphology, the foundation of taxonomy and plant geography, is always the corner stone, no matter how elaborate the structure it supports.

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APPROACHES TO DISJUNCT POPULATIONS: THE CONTRIBUTION OF PALYNOLOGY

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ABSTRACT

An examination of the palynological (and other paleoecological) literature provides interesting perspectives on a number of North American disjunction problems. A great body of paleoecological data demonstrates that significant southward displacement of biota took place during glacial maxima. Thus necessary conditions for a southward movement of "northern" disjuncts can be verified. In a few cases we have direct evidence of the disjuncts being displaced into or beyond regions where they now occur as isolated populations. In other cases we have indirect evidence in the form of modern associates of the disjuncts. The data suggest the probability of arrival of the disjuncts during the full-glacial and late-glacial with survival until the present. The same body of information suggests that components of the mixed-mesophytic forest (often considered as a disjunct community) were displaced some distance south and that the present community is a function of reimmigration and reassociation during the late-glacial and postglacial. The relict populations in the Gulf of St. Lawrence are probably not glacial survivors; some probably dispersed eastward in a discontinuous zone of instability south of the ice margin during full-glacial and late-glacial time. Such an eastward dispersal is known for many vertebrates. The evidence suggests that the prairie disjuncts could have arrived either during the late-glacial when boreal woodland and/or tundra bordered the retreating ice or during the hypsithermal when there was a pronounced eastward movement of the prairie-forest border (at least in the upper Midwest (Minnesota)). Many explanations are possible for the Atlantic Coastal Plain disjuncts, some of which would have found favorable sites for inland dispersal during full-glacial times, others of which, notably the strand and dune plants, may have dispersed inland along the shores of the Champlain sea during the early late-glacial. Paleoecological approaches are clearly essential to illuminate the historical environmental context of the disjunction, but must be used in conjunction with other disciplines to provide definitive insights.

Discontinuous distributions of species and communities have long fascinated both ecologists and evolutionary biologists. This fascination has led to an enormous literature and much speculation. A multitude of intriguing questions can be posed concerning such disjunct occurrences; for example: Do the disjuncts represent relict populations (or communities)? If so, at what time and under what conditions did the disjunction develop? Have the disjuncts always been where we find them? How similar are the disjuncts (genetically and otherwise) to the presumed parent populations? Alternatively, are the disjuncts instead indicative of relatively recent dispersal from some distant source? If so, when and under what conditions did they arrive? What changes have taken place in the populations (or communities) since arrival?

It is readily apparent that a great many factors may have contributed to the development and maintenance of any disjunction. It is equally apparent that an adequate understanding of such biogeographic phenomena will require a broadly interdisciplinary approach. For example, it is imperative that we understand the structure and historical evolution of the environmental "stage" on which this biogeographic "play" has been enacted. Such an understanding can be derived, at

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ANN. MISSOURI BOT. GARD. 59: 125–137. 1972.

least in part, from application of a variety of paleoecological techniques, notably palynology. In this manner a number of the questions posed above can be dealt with a little less speculatively.

Similarly, many of the insights of mathematical ecology will be essential to develop an understanding of the dynamics of disjunction. For example, can disjuncts be thought of as occupying "islands" within a complex environmental mosaic? (See Levins, 1968.) Can we think of disjunct populations in equilibrium terms—as involving an interaction between definable immigration and extinction rates (*e.g.* MacArthur & Wilson, 1967; Wilson, 1969; Whitehead & Jones, 1969). Much potentially valuable information could derive from such approaches to discontinuous distributions.

In this paper I will limit myself to the potentialities of paleoecological investigations and consider the extent to which the information available from such studies can enhance our understanding of several intriguing eastern North American disjunction questions. The issues we will approach include: (1) isolated populations of northern or boreal species south of their region of continuous distribution; (2) "relict" populations in the region of the Gulf of St. Lawrence; (3) occurrence of prairie species east of the forest-prairie boundary; (4) presence of "coastal plain" species in the interior; and (5) the mixed-mesophytic forest as a disjunct community.

"NORTHERN" DISJUNCTS

One of the most common forms of disjunction in North America involves "northern" or "boreal" disjuncts—outlying populations some distance south of the area of continuous distribution. An alternative form of the same pattern is the presence of populations of essentially "montane" species at lower elevations or at some distance from the mountains.

Examples of this pattern are provided by hemlock (*Tsuga canadensis*) and curly-grass fern (*Schizaea pusilla*). Hemlock occurs as a constituent of the "northern hardwoods" forest complex (Braun, 1950) throughout much of northeastern United States and occurs throughout the Appalachian complex reaching as far south as northern Georgia and northern Alabama (Munns, 1938). A great many outlying populations occur farther south and at lower elevations. Such populations have been described in North Carolina, Georgia, Alabama, Kentucky, and Indiana (*e.g.* Bormann & Platt, 1958; Segars *et al.*, 1951; Oosting & Hess, 1956; Braun, 1950; Hardin & Cooper, 1967). Such disjunct populations usually occur in specialized situations, such as north-facing bluffs or ravines, often in association with other similar "disjuncts."

The curly-grass fern presents a more spectacular case of disjunction. This highly restricted and rare species occurs in Nova Scotia, Newfoundland, and Bruce County, Ontario and much farther south in isolated populations in the Pine Barrens of New Jersey (Fernald, 1950; Gleason, 1952). More recently an additional disjunct population has been discovered on Long Island (Moldenke, 1960).

Many other "northern" or montane species show analogous distribution patterns. Particularly well described is the mountain-eastern Piedmont disjunction in North Carolina (Hardin & Cooper, 1967). Some sixty species are involved in this relationship—species that occur primarily in the mountain counties or farther to the north, but which are represented as disjuncts near the eastern border of the Piedmont. Similar is the arctic-alpine element in the Lake Superior region (Soper & Maycock, 1963), and in the "driftless area" of Wisconsin (Cushing, 1965; Rosendahl & Moore, 1947).

It has long been assumed that such populations or communities represent "glacial relicts," that is remnants of populations established at some point during the late Pleistocene when cooler conditions led to a southward (or downward) displacement of many northern species. At such times it is supposed that boreal forest communities were well developed in areas now occupied by a variety of more southern forest types. Postglacial climatic changes resulted in the establishment of the present patterns and the elimination of all northern species and communities save for the disjuncts. The disjuncts presumably survived, despite the climatic amelioration of the hypsithermal, in particularly protected habitats.

Although there is a body of opinion to the contrary (*e.g.* Braun, 1955), there is now considerable evidence that significant vegetational displacement took place during times of glacial advance. The work of Terasmae (Harrison *et al.*, 1965), Craig (1969), Frey (1951, 1953, 1955), Whitehead (1963, 1964, 1965, 1967, 1968), and Watts (1970) in the region extending from Virginia to northern Georgia has provided a reasonably cohesive picture. The full-glacial pollen assemblages bear absolutely no resemblance to modern pollen assemblages from the same regions; components of the modern flora are not represented; and pollen, spores, seeds, and other remains of northern species are well represented. For example, the full-glacial pollen spectra from Virginia and northeastern North Carolina are dominated by northern pines (jack and/or red pine), spruce (up to 30% spruce pollen); full-glacial spectra from southeastern North Carolina and northern Georgia are dominated by pine (jack and/or red pine) with spruce present in low percentages. In addition, a number of northern species occur—these include: *Abies*, *Larix*, *Arceuthobium*, *Schizaea pusilla*, *Isoëtes macrospora*, *Lycopodium annotinum*, *L. clavatum*, *L. lucidulum*, *L. obscurum*, *Sanguisorba canadensis*, etc.). The full-glacial spectra are more or less similar to those presently produced in various forest regions in northern New England, the northern Mid-west, and southern Canada. For example, the spectra from the Bladen Lakes region are quite similar to modern spectra from areas of jack pine forest in central Manitoba (Lichti-Federovich & Ritchie, 1968). The pollen data from these several sites and Watts' (1970) seed data from northern Georgia are consistent with a vegetational displacement of *at least* 1000 kilometers and a temperature some 7° C cooler than the present.

Thus it is apparent that a basic prerequisite for validating the "glacial relict" hypothesis is verifiable from the palynological record—significant southward displacement of biota took place during times of glacial advance. The magnitude of the displacement for various species is as yet unclear, as critical information is lacking from regions still farther south. However, it does appear as if the displacement was essentially azonal, as no exact modern counterparts can be found for the fossil spectra. In addition, the spectra show admixtures of types from a number of northern communities.

The paleoecological record may be used to ask further questions concerning the hypothetical glacial relicts; for example: do the data provide direct evidence of the displacement of the disjunct species? Can we determine the time span during the late Pleistocene (or postglacial) when the disjuncts appeared in the regions in question? Is there evidence that the disjuncts have persisted since the time of arrival?

Satisfactory evidence cannot be provided for all of these questions. Obviously not all of the species are likely to be well-represented in the palynological record. Insect pollinated taxa will be represented only rarely, and even wind pollinated species might not be represented if they are rare and occur as constituents of a forest type dominated by prolific pollinators. Furthermore, very few pollen accumulating basins occur close to the disjunct localities, hence much speculative extrapolation will be required.

It is significant that a number of the most interesting northern disjuncts are known from Pleistocene and postglacial horizons in the Southeast. This list includes hemlock, white pine, the curly-grass fern, and several species of *Lycopodium*. Seed data from the Midwest indicate that one of Lake Superior disjuncts, *Dryas integrifolia*, was widespread in Minnesota during the late-glacial (Baker, 1965; Watts, 1967). Similarly, two of the arctic-alpine elements from the driftless area, *Rhododendron lapponicum* and *Sedum* cf. *rosea*, are known from the late-glacial of northeastern Minnesota (Baker, 1965). Hence it seems apparent that a number of the disjuncts did occur extensively in the region south of their present range. Of these taxa *Schizaea pusilla* is perhaps the most interesting. As mentioned previously, its present distribution includes specialized habitats in Nova Scotia, Newfoundland, and Ontario and disjunct populations on Long Island and the Pine Barrens of New Jersey. It is now apparent that this unique and fascinating fern was widespread in the Southeast during the Pleistocene. It was first discovered in organic horizons in the western Piedmont of both North Carolina and South Carolina by Whitehead and Barghoorn (1962) and has since been found in a number of localities on the coastal plain of both states (Whitehead, 1963, 1965). Regrettably, nothing is known of its fossil history in the region of the Pine Barrens or Long Island.

What can be said concerning the time at which the disjuncts arrived in the regions in question? The sequence of vegetational changes recorded in the sediments of the Carolina Bays in southeastern and northeastern North Carolina spans at least 40,000 years including the mid-Wisconsin Plum Point and Port Talbot interstadials (see Dreimanis, 1969), the full-glacial, the late-glacial, and the entire postglacial. Some of the disjuncts and many of the species with which they presently occur in northern regions were present in eastern North Carolina during the Plum Point and Port Talbot interstadials (50,000–23,000 B.P.), but many of them were apparently eliminated during the full-glacial when conditions became too harsh. This applies to both white pine and hemlock, both of which occur during the major interstadial, but are at best infrequently represented during the full-glacial, and reappear in the fossil record during the late glacial (this occurred about 11,000 years ago in southeastern North Carolina, 10,000 years ago in northeastern North Carolina, and 9500 years ago in eastern and western Virginia) (Frey, 1955; Whitehead, 1967; Craig, 1969). This suggests that these taxa were displaced farther to the south during full-glacial time and that their reappearance during the late-glacial was a function of reimmigration from the south in response to climatic amelioration. Thus many of the northern disjuncts represent remnants of populations established during the late-glacial, while others (such as *Lycopodium lucidulum*) represent remnants of populations established during the full-glacial (or even earlier).

Much evidence from both glaciated and unglaciated regions throughout North America suggests that a portion of the postglacial was characterized by higher temperatures and/or lower rainfall than the present. This has been defined as the hypsithermal interval by Deevey and Flint (1957). Evidence from Minnesota (*e.g.* Wright, 1968; Cushing, 1965, 1967) indicates that a significant eastward displacement of the prairie-forest border took place during this interval. Similarly, pollen data from Ohio (Ogden, 1966) and New England (Davis, 1965, 1967, 1969; Whitehead *et al.*, 1967) show evidence of hypsithermal environmental changes, albeit more subdued than in Minnesota.

If such a climatic amelioration affected the entire continent, then questions arise concerning whether the disjuncts could have survived *in situ*. The present disjunct stations might thus indicate a post-hypsithermal reimmigration to favorable sites. Such a hypothesis has in fact been proposed to explain the disjunct stands of hemlock and white pine in Indiana (*e.g.* Braun, 1951).

Evidence for hypsithermal climatic amelioration in the southeast is meagre—there is little indication of warmer (or drier) conditions in the diagrams from Georgia, North Carolina, and Virginia. Furthermore, recent work from the Prairie peninsula region of Indiana (R. E. Bailey, unpublished) indicates relatively little vegetational change during the last 8000 years. This might suggest that hypsithermal climatic changes were felt primarily in the west and higher latitudes in the east (upper Midwest and New England) and that if the disjuncts had arrived prior to the hypsithermal their chances of survival to the present would be excellent. However, critical evidence on this point is lacking in both the Southeast and Indiana. We know that in both regions some of the disjuncts and species with which they are now associated farther to the north arrived during the late-glacial and early postglacial and that the populations subsequently underwent a decline as the present vegetational types became established during the postglacial; but little can be said concerning the survival of relict populations as most of the depositional sites are too far removed from the areas of disjunction. Occasional grains of hemlock and white pine occur sporadically throughout the postglacial in both Indiana and the Southeast, but that is hardly proof of survival.

In summary, palynological work provides us with some fascinating insights concerning the hypothetical glacial relicts, indicating that the required displacements of boreal elements did take place during times of glacial maximum, suggesting that some of the relict populations may have become established during the full-glacial, that others may have immigrated from the south during the late-glacial, and that in both the lower Midwest and Southeast hypsithermal climatic changes may not have been severe enough to cause temporary elimination of the relict populations. Further work in both the Midwest and Southeast will doubtless shed additional light on the subject.

DISJUNCTS IN THE GULF OF ST. LAWRENCE

Many years ago Fernald (1925) demonstrated that many unique species occurred in isolated populations in specialized habitats near the mouth of the Gulf of St. Lawrence. The biogeographic and geological data then available led Fernald to the conclusion that portions of this region had not been glaciated during the Pleistocene and that many of the disjunct populations had survived *in situ* on the unglaciated areas ("nunataks"). Much subsequent work has been critical of this hypothesis (*e.g.* Wynne-Edwards, 1937, 1939; Livingstone & Livingstone, 1958; Drury, 1969), but innumerable questions remain unanswered. It is now apparent that a number of the species thought by Fernald to occur as disjuncts only in the Gulf of St. Lawrence region have a number of other stations in Canada and that the region in question has been glaciated, albeit not intensively (Drury, 1969). Drury's careful analysis of the biogeographic data has reduced the once sizeable list of disjuncts to about 40 for which some special interpretation may be necessary. Within this group (and among Fernald's much larger list) are a number of taxa with biogeographic affinities in the Cordilleran region. Many of these have their nearest stations many hundreds of kilometers to the west. It is perhaps significant that many of the disjuncts are restricted to highly specialized, often unstable habitats (talus slopes, serpentine, etc.).

Although the palynological data do not yet permit us to make definite comments concerning this disjunction problem, a combination of paleoecological approaches does shed additional light on past conditions which may have contributed. For example, the Pleistocene vertebrate record indicates that a number of characteristic western species occurred at various places in the East. This list includes the magpie, sharp-tailed grouse, thirteen-lined ground squirrel, and pika, plus a number of taxa from the arctic west of Hudson Bay (*e.g.* Guilday *et al.*, 1964). The environmental changes which permitted such range extensions for various vertebrates may have affected a number of plant taxa as well. In fact, the palynological data from New England, the Maritimes, and the Midwest (*e.g.* Davis, 1965, 1967, 1969; Cushing, 1965, 1967) suggest a rather broad, time and space transgressive zone south of the ice margin which was characterized by instability (frost action) and an open structured vegetation (boreal woodland and/or tundra). Although little is known concerning full-glacial and late-glacial conditions west of the Appalachian complex, such a zone may have extended for varying distances south of the ice margin. Within such an environmental complex one might imagine the dispersal of a number of taxa adapted for survival in disturbed habitats but unable to withstand competition in more stable situations. Given the dispersal capacities of most species, one need not conceive of a broad, continuous zone flanking the ice—a highly discontinuous, patchy, tundra-like zone would be adequate.

It is thus quite possible that a number of the Cordilleran elements now found isolated near the Gulf of St. Lawrence were capable of establishing several ephemeral populations to the East during times of relative glacial expansion—such populations might have developed in the more open, unstable environments marginal to the ice. As the climate ameliorated and ice underwent an oscillating retreat, one can imagine several things happening to the isolated populations of western species. Many of the populations were eliminated through competitive interactions with newly immigrated species which were better adapted to the increasingly stable environments. There might have been a northward dispersal of western taxa within the northward moving zone of instability. The relicts of the Gulf of St. Lawrence could then be thought of as the last remnants of this late-Pleistocene and early–postglacial eastward and then northward dispersal of Cordilleran species. For some of these western taxa a number of scattered northern populations remain on the Canadian shield and the Gulf of St. Lawrence, while for others all intervening populations were eliminated during the postglacial and only the Gulf relicts survive.

It is important to note that the palynological data indicate the feasibility of such a pattern of dispersal and survival, but do not constitute proof. We have no direct evidence of the relicts within the supposed tundra and boreal woodland zone—nor do we have evidence of either persistence or time of arrival of the relicts within the Gulf of St. Lawrence region.

Prairie Disjuncts

Within the category of prairie disjuncts we will consider stations of prairie species or prairie communities east of the prairie-forest boundary and occurrences of prairie plants on the dune complexes along the shores of the Great Lakes. It has been traditional to interpret these populations as indicative of the eastward expansion of prairies and in particular of the prairie peninsula during the hypsithermal interval and the subsequent isolation of the populations by post-hypsithermal climatic deterioration.

As mentioned previously, there is convincing evidence for an eastward movement of the forest-prairie boundary in the upper Midwest, most notably in Minnesota. In this region the boundary was displaced eastward by as much as 100–200 kilometers during the hypsithermal interval (McAndrews, 1966; Wright, 1968*a*, 1968*b*). During the same period of time there was a northward movement of the arctic tree-line (Ritchie & Hare, 1971). Less convincing evidence is available elsewhere in the Midwest (*e.g.* Ogden, 1966) and New England (Davis, 1965, 1967, 1969; Whitehead & Bentley, 1963; Whitehead *et al.*, 1967). Until recently no detailed studies had been carried out in northern Indiana. This would be quite crucial, as the northeastern extension of the prairie peninsula occurs in northwestern Indiana. The work of R. E. Bailey (unpublished) on two small lakes within the prairie peninsula has helped to fill this void. The diagrams from the two lakes are gratifyingly similar and postglacial portions of both are remarkably monotonous—there is little indication of any significant vegetational and climatic changes during the past 8500 years. In other words, if there were appreciable changes within the prairie peninsula during the hypsithermal, the pollen profiles do not record it. It may be that different air masses have affected the upper Midwest and lower Midwest and that, as a consequence, the hypsithermal climatic changes were much more appreciable farther west and at higher latitudes. Further work east of the eastern edge of the prairie peninsula in Indiana may help to clarify this situation.

The pollen records indicate that a number of "prairie" species were represented in the Midwest during the late-glacial and early postglacial (*e.g. Artemisia* and short-spine composites). The present general vegetational patterns were established by 8500 years ago. Hence prairie species could have arrived during the late glacial and persisted on dune habitats along lake shores and on the coarse outwash that characterizes the prairie peninsula of Indiana. The eastward expansion of prairies in Minnesota and the postglacial development of the prairie peninsula would have provided conditions facilitating further eastward dispersal of prairie taxa during the postglacial. Thus prairie disjuncts may have arrived at a number of different times during the late Pleistocene and early postglacial.

Much additional light may be cast on this problem, as a number of detailed studies are currently in progress in northern Indiana. These studies are designed to deal with the question of the history of the disjuncts and the developmental history of the prairie peninsula.

"COASTAL PLAIN" SPECIES IN INLAND REGIONS

Braun (1950, 1955) summarizes the evidence concerning supposed "coastal plain" species that occur in isolated populations in inland areas. Some of these involve taxa with specific adaptations to dune and shore environments which are known from the shores of the Great Lakes, notably the southeastern shore of Lake Michigan; others are plants of wet or boggy habitats which occur in such situations in the Southern Appalachians (Braun, 1937; Fernald, 1931; McLaughlin, 1932; Peattie, 1922). The explanations for these disjunctions are various, generally involving historical factors of some antiquity. Although palynology *per se* can provide little insight concerning either of the disjunctions mentioned above, a variety of geological and paleoecological studies has suggested possible explanations for the relationships.

The disjuncts occurring on the Lake Michigan shores are a case in point. It is now apparent from much geological and paleontological work in the Northeast that during the late-glacial and early–postglacial there was a significant extension of the sea which involved the St. Lawrence Valley, the Champlain lowland, and Lake Ontario (Flint, 1957). This ephemeral marine transgression was a function of two factors; (1) the land, deeply depressed by the weight of ice, had not yet begun significant rebound following removal of ice load, and (2) the sea had begun a significant rise due to ice melt. The result of this was a rapid incursion of the sea into the still depressed St. Lawrence and Champlain lowland. The net result of this temporary transgression was the production of a variety of shore and dune habitats permitting the westward dispersal of a number of plants of the Atlantic Coast.

Geomorphological and palynological work on the Piedmont (Whitehead & Barghoorn, 1962; Parizek & Woodruff, 1956, 1957) has provided further information concerning the occurrence of Coastal Plain bog taxa (such as *Sarracenia*, *Drosera*, *Eriocaulon*, etc.) in the mountains. This work has demonstrated the presence of a number of buried organic horizons of Pleistocene age in the western Piedmont of North Carolina and South Carolina. The organic horizons indicate that bog-like habitats were present in the Piedmont during the late-Pleistocene.

This in itself is significant, as such habitats are extremely rare in that region at present. In addition, the pollen profiles from these horizons indicate the presence of a number of bog species such as *Lycopodium carolinianum*, *L. inundatum* and/or *L. alopecuroides*, *Sanguisorba canadensis*, *Schizaea pusilla*, *Sarracenia*, *Drosera*, *Eriocaulon*, etc.).

In this context Watts' (1970) work on the Bartow County ponds in northern Georgia is of interest. Coastal Plain disjuncts occur near the ponds, hence a direct approach to the disjunction problem is possible. Watts' data show that for these ponds the disjuncts (*Psilocarya nitens*, *Carex virens*) have arrived in the late post-glacial.

Work in the Midwest suggests that present ranges of some of the Coastal Plain disjuncts must be interpreted with care, as both *Juncus balticus* and *Hemicarpha micrantha* are known from the late-glacial of Minnesota and South Dakota (Baker, 1965; Cushing, 1965).

Thus we have evidence of both bog habitats and bog taxa on the Piedmont during the Pleistocene and post-glacial. Consequently it is possible to suggest that the physical environmental changes of the Pleistocene brought about changes in geomorphic processes which in turn created bog habitats in a region where they are presently very uncommon. This, in turn, created conditions favorable for the dispersal of bog species and the establishment of transient populations in inland regions. This does not prove that such Coastal Plain species reached the mountains during times of glacial maximum, but it does indicate that such species were more widespread at those times and that interchange between the mountains and the Coastal Plain would have been facilitated.

The Mixed-Mesophytic Forest; a Survivor from the Tertiary?

One of the major debates concerning environmental changes in unglaciated regions has centered around the mixed-mesophytic forest—an enormously diverse forest complex which Gray (Braun, 1950, 1955) and others consider as a disjunct community—the parent community being the deciduous forest communities of southeast Asia. Braun (1950, 1955) contends that the mixed-mesophytic forest and its various outliers have existed essentially in place since the mid-Tertiary. This would require an ability to withstand the climatic changes of the Pleistocene. In contrast to this are the views of Deevey (1949), Martin (1958), Whitehead (1965, 1967), and others who suggest that significant displacement of vegetation, including forest types in unglaciated regions, accompanied glaciation. According to the latter view, components of the mixed-mesophytic forest would have been displaced by some hundreds of kilometers. Boreal communities presumably occupied the area in which the mixed-mesophytic forest now occurs.

Although critical evidence is lacking from within the area now occupied by the mixed-mesophytic forest, there is now a wealth of information concerning Pleistocene conditions from other areas south of the drift border. This includes the profiles from Virginia, North Carolina, South Carolina, and Georgia that have been discussed previously, information from the area of Illinoian drift in Illinois (Grüger, 1970), and data from the Southwest (Martin & Mehringer, 1965). In all of these regions the full-glacial spectra bear no resemblance to modern from the same regions, temperate forest components are not represented, and the pollen assemblages are dominated by species that have been displaced by some 1000–1500 kilometers.

Geomorphological evidence suggests intensive frost processes in the mountains as far south as southern Virginia (Clark, 1968). This indicates the probability that the higher elevations in the mountains were essentially treeless, which in turn requires a significant downward displacement of species and communities. As mentioned previously, these changes are consistent with an average temperature some 7°C cooler than the present. It is hard to imagine the Cumberland Plateau and its vegetation remaining relatively unaffected while lower elevations in Virginia and northeastern North Carolina were covered by a spruce-northern pine forest and regions farther to the south (extending at least as far as northern Georgia) were vegetated by decidedly boreal forests dominated by northern pines with some spruce and other "northern" elements (Terasmae (Harrison *et al.*, 1956); Craig, 1969; Whitehead, 1963, 1964, 1965, 1967, 1968; Watts, 1970).

The palynological, seed, and vertebrate data suggest significant displacement with virtually no temperate elements surviving. Furthermore, it appears as if the displacement was essentially azonal—as there are interesting admixtures of species from different boreal communities and as there are no perfect modern analogues for the fossil pollen assemblages. Thus species were displaced according to their own ecological tolerances and dispersal capabilities.

The logical extension of this is to assume an analogous displacement of components of the mixed-mesophytic forest and to suggest that the mixed-mesophytic as we now see it represents the last shuffling of the ecological cards—a shuffling that brought about a reasonable approximation of the present forest structure by the early postglacial. This would require that the mixed-mesophytic components were displaced to more southern "refugia" (about which we have no evidence as critical studies are lacking from more southerly regions) and that they reimmigrated into Cumberland Plateau and other regions from the south in response to the postglacial climatic amelioration.

It is unlikely that significant evidence bearing upon this will ever be obtained from within the mixed-mesophytic forest itself, but studies currently in progress in Florida and the Gulf Coast may well provide invaluable evidence bearing on the extent to which temperate forest species were displaced.

CONCLUSIONS

It is apparent that paleoecological investigations can contribute significantly to our understanding of disjunction problems. However, the extent of the contribution is variable, depending upon the species, community, and geographic region in question. As for the discontinuous distributions touched upon in the present paper, some insight can be gained concerning each issue, but no definitive conclusions can be reached. It is apparent that palynology has contributed quite significantly to our interpretations of both the northern disjuncts and the Pleistocene history of the mixed-mesophytic forest complex. It is also apparent that the contribution in each case would have been more significant had the disjunction been of prime interest to Pleistocene investigators. This same generalization applies to the other biogeographic problems that I have discussed—in no case has an extensive paleoecological investigation been undertaken for the sole purpose of dealing with a disjunction problem. The contributions are thus fortuitous. However, it is quite likely that the studies currently in progress both in the unglaciated region (principally Florida) and the Midwest (notably Indiana) will contribute significant information.

The weakness of these studies (*vis-a-vis* disjunction problems) is that they represent a unidisciplinary approach to a problem that can only be dealt with from an interdisciplinary point of view. It is imperative that we encourage a collaborative approach to these truly fascinating biological problems.

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GENETICAL FEATURES OF FERNS AS CONTRASTED TO SEED PLANTS[1]

EDWARD J. KLEKOWSKI, JR.[2]

Many disjunct populations of plants are the result of the dispersal and germination of a single propagule; the seed in seed plants; the spore in homosporous ferns. Although both of these propagules are generally an aspect of sexual reproduction in these organisms, populations established from either a single spore or seed are genetically very distinct. Populations which differ genetically may be expected to exhibit different evolutionary prospects. This paper will attempt to elucidate these genetic differences and speculate upon their evolutionary prospects.

As Figure 1 shows, an angiosperm seed is a propagule which develops after meiosis and syngamy have occurred. This propagule contains the results of double fertilization; endosperm tissue and an embryo. Upon seed germination this embryo will develop into a mature sporophyte. The genotype of this sporophyte does not reflect its current isolation but rather is related to the breeding system of the parental sporophyte population. Thus it may be homozygous or very heterozygous.

In contrast, an homosporous fern spore is a propagule that develops after meiosis but prior to syngamy. In this case only a single haploid cell is dispersed and upon germination undergoes a series of mitotic cell divisions leading to the development of a haploid, generally autotrophic plant, the gametophyte. This organism is functionally hermaphroditic, simultaneously developing male and female gametangia at some point during its life. Self-fertilization (intragametophytic selfing) results in a single diploid cell, the zygote, which is completely homozygous. This homozygous cell undergoes mitotic cell divisions leading to the development of an embryo and eventually a mature sporophyte. Thus the establishment of a sporophyte from a single propagule in an homosporous fern results in a completely homozygous individual, whereas in a seed plant the sporophyte genotype may be heterozygous.

Because of the above genetic distinctions between a seed and a spore, the evolutionary future of disjunct populations of homosporous ferns and angiosperms might predictably be very different. The angiosperm sporophyte, if it is perennial and dioecious, may live long enough to encounter a sporophyte of the opposite sex, outcross, and form progeny. These resulting progeny in all likelihood would be heterozygous to some degree.

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[1] This work was supported by National Science Foundation GB-8721. I should like to extend my thanks to Mr. Steve Garanin for technical assistance; to Dr. Roger Perry of the Charles Darwin Research Station for the collections of Galapagos *Pteridium*; to Dr. R. M. Lloyd for the collections of Hawaiian *Pteridium*. I should especially like to extend my thanks to Dr. R. M. Tryon and Mr. Leslie Hickok for many useful and stimulating discussions.

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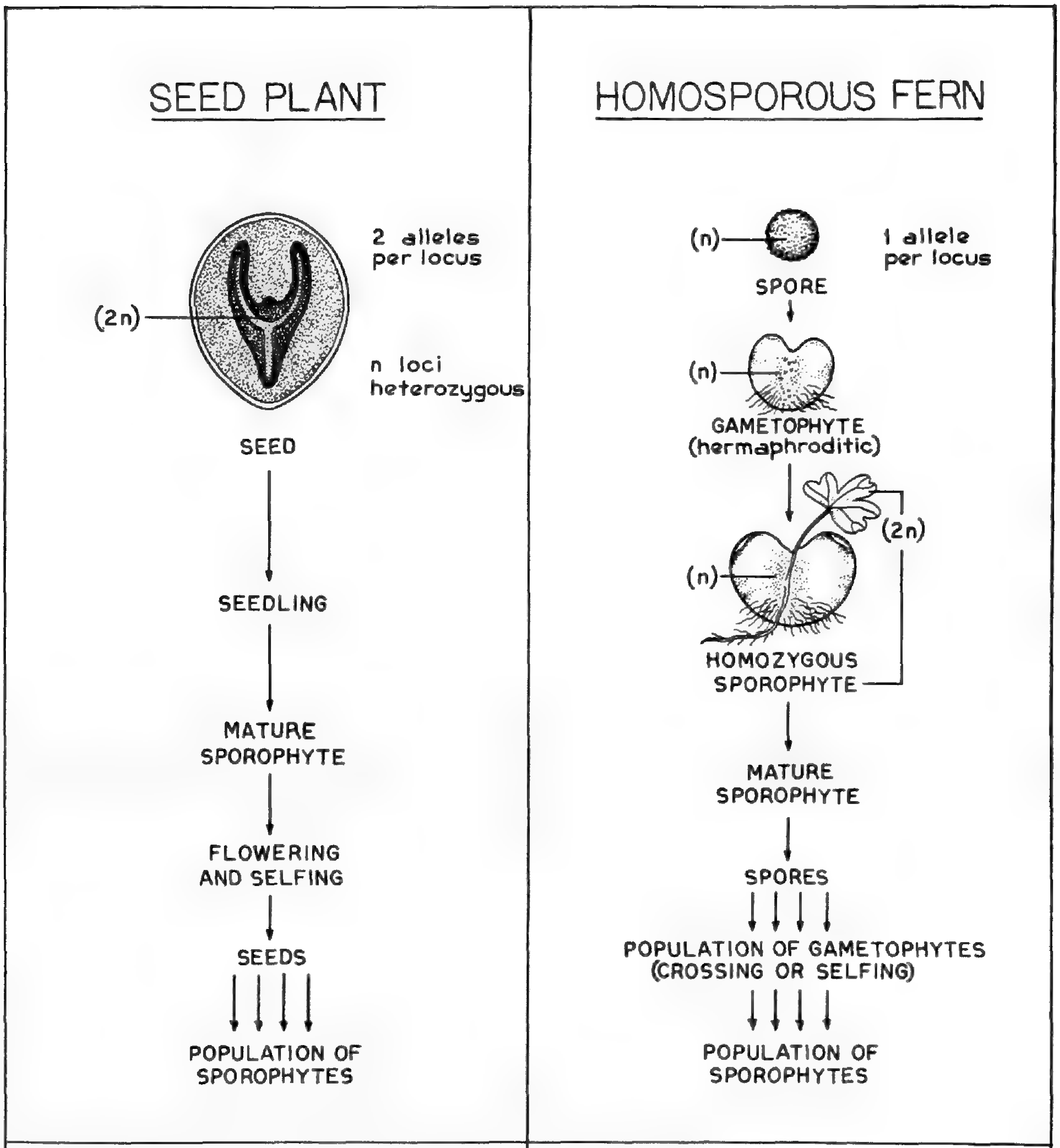
ANN. MISSOURI BOT. GARD. 59: 138–151. 1972.



3^n	NUMBER OF POSSIBLE GENOTYPES	1
$\frac{1}{2}$	PROBABILITY OF A LOCUS BEING HOMOZYGOUS	1
$(\frac{1}{2})^n$	PROBABILITY OF A COMPLETELY HOMOZYGOUS SPOROPHYTE	1

FIGURE 1. Genetic comparison of sporophyte populations established from a single seed or a single spore.

TABLE 1. Statistics of the gametic chromosome numbers of the Pteridophyta (only sexual taxa).[a]

	Heterosporous	Homosporous
Overall mean	13	54
Mean base number[b]	12.7	37.5
Number of taxa with base number[b]	81	1027
Number of polyploid taxa	11	682
Percent polyploid	12%	40%
Total number of taxa tabulated	92	1709

[a] Gametic chromosome numbers greater than 100 tabulated as 100.

[b] Base numbers are usually the lowest gametic numbers reported in a genus.

If the angiosperm sporophyte is monoecious or bears hermaphroditic flowers, self-pollination would probably occur. The resulting progeny would be more homozygous than the parent, but the family of progeny would be a heterogeneous array of genotypes related to the number of loci at which the parental sporophyte was heterozygous. Figure 1 illustrates these relationships.

In contrast, the fern sporophyte established from a single propagule is necessarily completely homozygous. Thus all the genetic material has been exposed to selection in the homozygous condition. The progeny of this plant are completely homozygous whether intragametophytic mating or intergametophytic mating occurs (see Klekowski, 1970*c*, for a discussion of this terminology). The only possible source of variability in this population of progeny is mutation, since all normal recombinations result in genotypes which are identical to the parental sporophyte. Therefore, populations of homosporous ferns which were established by a single propagule will have only one allele per locus present, whereas populations of angiosperms established from a single propagule potentially could have two alleles per locus present. Since evolution is dependent upon inherited variability in populations, one might assume the evolutionary prospects of disjunct populations of angiosperms to be greater than that of homosporous ferns.

The above conclusions are based upon the premise that a homozygous fern sporophyte resulting from intragametophytic selfing will breed true; that is, its progeny will be genetically equivalent. Recent experiments conducted in my laboratory in Amherst indicate that this premise does not hold in all cases. In order to fully understand the nature and meaning of these experiments, some knowledge of the kind of genetic systems present in these organisms is necessary.

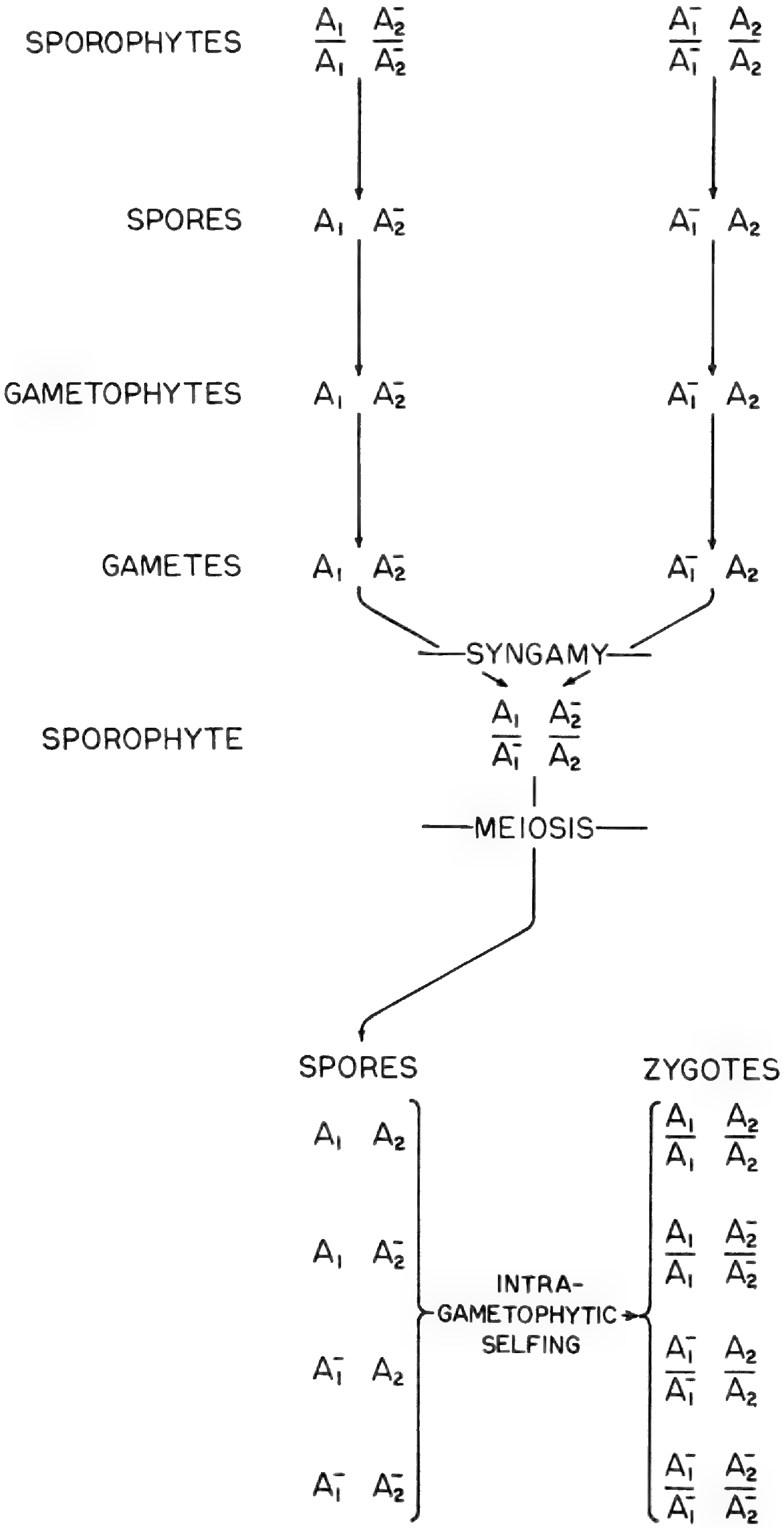
Klekowski and Baker (1966) pointed out the correlation that the homosporous pteridophyta are characterized by higher chromosome numbers than the heterosporous pteridophyta. Table 1 shows an analysis of the chromosome numbers in the homosporous and heterosporous pteridophyta. It is obvious that there is an excellent correlation between the utilization of polyploidy and the evolution of taxa in the homosporous pteridophyta. A model causally relating polyploidy and the capacity for intragametophytic selfing with its consequent homozygosity has been proposed to explain this correlation (Klekowski & Baker, 1966). A key point in this model is the idea that a plant genetic system must fulfill at least two roles; that is, the storage of genetic variability and its release. If intragametophytic selfing occurs in a diploid organism these two roles are negated. A genetic system which could tolerate intragametophytic selfing and still store and release genetic variability is one based upon unlinked duplicated loci. Such a genetic system is the product of polyploidy.

Intragametophytic selfing in this genetic system would result in sporophyte genotypes which are homozygous within homologous chromosomes but potentially heterozygous between the sets of homoeologous chromosomes. Given the phenomenon of dominance, such a genetic system could readily shelter from selection recessive alleles in sporophytes originating from intragametophytic selfing. As Figure 2 indicates, occasional hybridization between sporophytes followed by intragametophytic selfing would result in the generation of new genotypes and phenotypes. A polyploid genetic system, therefore, allows the storage and release of genetic variability in spite of intragametophytic selfing.

Recent experiments by my student, Mr. Leslie Hickok, and myself suggest the possibility of another means of releasing the genetic variability stored in duplicated loci in homosporous ferns. Sporophytes of *Ceratopteris pteridoides* and *C. thalictroides* were chosen as experimental material because of their ease of culture and short life cycles (Klekowski, 1970*a*). Both of these species are of polyploid origin, as the base number in the genus $x = 40$, is of polyploid origin. Genetic and cytogenetic studies utilizing x-ray induced and naturally occurring chromosomal aberrations (translocations and an inversion) support the hypothesis that the chromosomes regularly pair within homoeologous sets rather than with the same homologous partner at meiosis. The evidence for this interpretation of meiosis in *Ceratopteris* is based upon the cytological expression of chromosomal aberrations during meiosis in completely homozygous sporophytes.

Generalizing from these experiments with *Ceratopteris* to all of the homosporous ferns, it is possible to formulate an hypothesis whereby completely homozygous homosporous fern sporophytes can store and release genetic variability. It is hypothesized that homosporous ferns have evolved a genetic system based upon homoeologous heterozygosity and homoeologous recombination. Figure 3 graphically illustrates this means of recombination. It is assumed that the cytological mechanism whereby the homoeologous recombination occurs is via occasional homoeologous pairing at meiosis. Although bivalent formation at meiosis is the rule in polyploid ferns, it is hypothesized that these pairs are not limited to homologous chromosomes but involve members of homoeologous sets. This kind of meiotic pairing would allow the perpetuation of functionally duplicated loci. The phenomenon of diploidization would be retarded in a manner similar to a situation where multivalents are the rule. (See Ohno, 1970, and Mackey, 1970, for further discussion of diploidization in polyploids.)

Given homoeologous recombination, the genetic comparison of a seed and a spore presented in Figure 1 must be modified. Obviously some spore genotypes can establish a sporophyte which will produce genetically variable progeny. The main criterion of these spore genotypes is that they must be interlocus heterozygotes (Fig. 3). Whether a spore genotype fulfills this criterion is a reflection of the genotype of its parental sporophyte, which in turn is related to the taxon's mating system. Klekowski (1969*b*) has classified fern reproductive systems into


SPOROPHYTES
$\frac{A_1}{A_1}\ \frac{A_2^-}{A_2^-}$
$\frac{A_1^-}{A_1^-}\ \frac{A_2}{A_2}$
SPORES
$A_1\ A_2^-$
$A_1^-\ A_2$
GAMETOPHYTES
$A_1\ A_2^-$
$A_1^-\ A_2$
GAMETES
$A_1\ A_2^-$
$A_1^-\ A_2$
SYNGAMY
SPOROPHYTE
$\frac{A_1}{A_1^-}\ \frac{A_2^-}{A_2}$
MEIOSIS
SPORES
$A_1\ A_2$
$A_1\ A_2^-$
$A_1^-\ A_2$
$A_1^-\ A_2^-$
INTRA-
GAMETOPHYTIC
SELFING
ZYGOTES
$\frac{A_1}{A_1}\ \frac{A_2}{A_2}$
$\frac{A_1}{A_1}\ \frac{A_2^-}{A_2^-}$
$\frac{A_1^-}{A_1^-}\ \frac{A_2}{A_2}$
$\frac{A_1^-}{A_1^-}\ \frac{A_2^-}{A_2^-}$

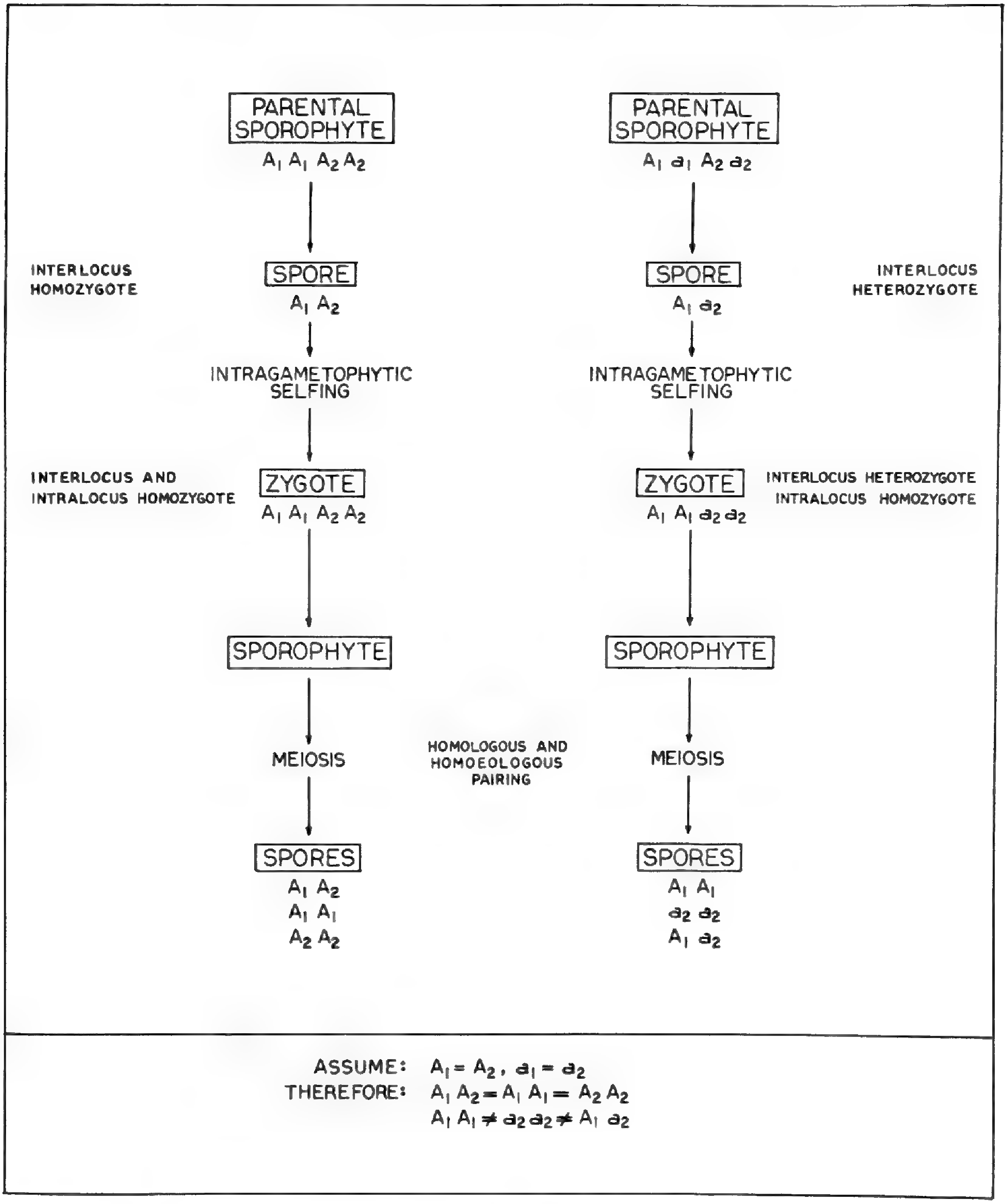


FIGURE 3. Homoeologous recombination model.

three categories; apogamy, intragametophytic mating, and intergametophytic mating. Only the latter two categories are sexual modes of reproduction. Taxa characterized by intragametophytic mating systems (fusion of gametes from the same gametophyte) generally have sporophyte genotypes with high levels of

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FIGURE 2. Storage of genetic heterozygosity in duplicated loci and its release via hybridization.

homozygosity (both intralocus and interlocus). Heterozygous sporophytes are more frequent in populations where intergametophytic mating (fusion of gametes from different gametophytes) occurs. Thus the mating system of the parental sporophyte is related to the spore genotype, intragametophytic mating being associated with interlocus homozygotes and intergametophytic mating with interlocus heterozygotes.

Spores which are interlocus heterozygotes have two implications in the biology of disjunct fern populations. Such a spore can develop into a gametophyte, which upon intragametophytic selfing, will form a sporophyte with unusual genetic properties. Although this sporophyte is the result of the fusion of two identical gametes, meiosis will result in a population of genetically variable spores. (See Figure 3). Thus spores which are interlocus heterozygotes will not follow the pattern outlined in Figure 1; a disjunct population of sporophytes established from such a spore will have a source of genetic variability other than mutation. The genetic relationship between a seed and a homosporous fern spore in Figure 1 applies only to situations in which the spore is an interlocus homozygote or the cytological mechanism for homologous recombination is absent. In the latter situation, spore genotypes which are interlocus heterozygotes are still advantageous from an evolutionary viewpoint. Genetic variability may be stored and sheltered from selection in such homozygous sporophytes. After a number of genetically different homozygous sporophytes are established, hybridization will release this variability, as is shown in Figure 2. Thus the evolutionary future of a disjunct population of ferns established by single spores is dependent upon the genotypes of those propagules. In the case where a population is established by a single spore, the genotype of that cell determines the sources of genetic variability available for subsequent evolution. If it is an interlocus homozygote, the main source of genetic variability in subsequent generations will be mutation, but where this propagule is an interlocus heterozygote, the sources of genetic variability will be recombination as well as mutation. In situations where a population has its origin in a number of independent spore entries and hybridization between new immigrants and indigenous individuals occurs, the genetic variability in the resultant population will be greater if the spore genotypes were interlocus heterozygotes.

Any discussion of the establishment and evolution of disjunct homosporous fern populations must start with an assessment of the kinds of spores most likely to establish sporophytes. Because of their size, there is no doubt that most fern spores can be dispersed great distances by the wind (Tryon, 1970). Lloyd (personal communication) reports that a *Nephrolepis* spore collected 2,000 feet above the ocean in the vicinity of Hawaii germinated readily and formed a normal gametophyte. A number of homosporous fern taxa have green spores with short viabilities in contrast to long viabilities in non-green spores such as *Nephrolepis* (Lloyd & Klekowski, 1970); therefore the dispersal capabilities of taxa with green spores might be expected to be less than non-green spores. However, since the majority of ferns have non-green spores, dispersal would not seem to be a great problem in the majority of these (Tryon, 1970).

Actual establishment of a disjunct population is dependent upon the establishment and survival of the gametophyte and the formation and maturation of a sporophyte. Since the subsequent evolutionary future of a disjunct population is dependent upon the genotype of this sporophyte, it is important to determine the probability for interlocus heterozygosity in this genotype. Two arguments will be advanced which suggest that the long distance establishment of such a genotype is less likely in homosporous ferns than an interlocus homozygote.

With reference to the establishment of a sporophyte from a single propagule, the length of the gametophyte generation is shortest in apogamous and intragametophytic mating systems and the longest in intergametophytic mating systems (Klekowski, 1969*b*; Whittier, 1970). Ferns with intergametophytic mating systems produce spores which have a higher probability of being interlocus heterozygotes. Since the mating system and the degree of interlocus heterozygosity are related, the ecology of the disjunct area has an influence on the kinds of spore genotypes which successfully establish sporophytes. Where ecological conditions are adverse to prolonged gametophyte growth, sporophytes with apogamous or intragametophytic mating systems will become established. Where ecological conditions are more conducive to prolonged gametophyte growth, taxa with apogamous, intragametophytic, and intergametophytic mating systems will be established. Figure 4 graphically illustrates this relationship between mating systems, ecology, and genetics in homosporous ferns.

Another factor decreasing the frequency of establishment of taxa with intergametophytic mating systems is the phenomenon of genetic load. Klekowski (1970*a*, *b*, 1971) has shown that many sporophytes in nature are heterozygous for recessive zygotic or early embryonic lethals. Such sporophytes produce many spore genotypes capable of developing into normal gametophytes which will not give rise to viable sporophytes when intragametophytic selfing occurs. The frequency of sporophytes heterozygous for such lethals might be expected to be higher in taxa with intergametophytic mating systems in comparison to taxa with intragametophytic mating systems. Thus in a given sample of spores entering a disjunct area, the gametophytes which have the capability of giving rise in isolation to a sporophyte will be predominantly from taxa with apogamous and intragametophytic mating systems. Another characteristic of genetic load in ferns is the phenomenon of "leaky lethality" (Klekowski, 1970*b*). Gametophyte genotypes vary in ability to form viable sporophytes. Experiments have shown (Klekowski, unpublished) that some gametophyte genotypes form sporophytes very readily whereas others do so only after repeated self-fertilizations (simple polyembryony). Gametophytes from heterozygous sporophytes exhibit "leaky lethality" to a greater degree than gametophytes from homozygous sporophytes. When a gametophyte exhibits this phenomenon of "leaky lethality," the formation of a viable sporophyte via intragametophytic selfing requires a longer period of gametophyte survival. Therefore the establishment of a disjunct population of a fern taxon with an intergametophytic mating is less probable on both ecological and genetic grounds.

Recent research on the genus *Lygodium* has revealed data which illustrate these points. *Lygodium volubile* forms sporophytes apogamously, and *L. heterodoxum* is a sexual taxon with an intergametophytic mating system. In the latter

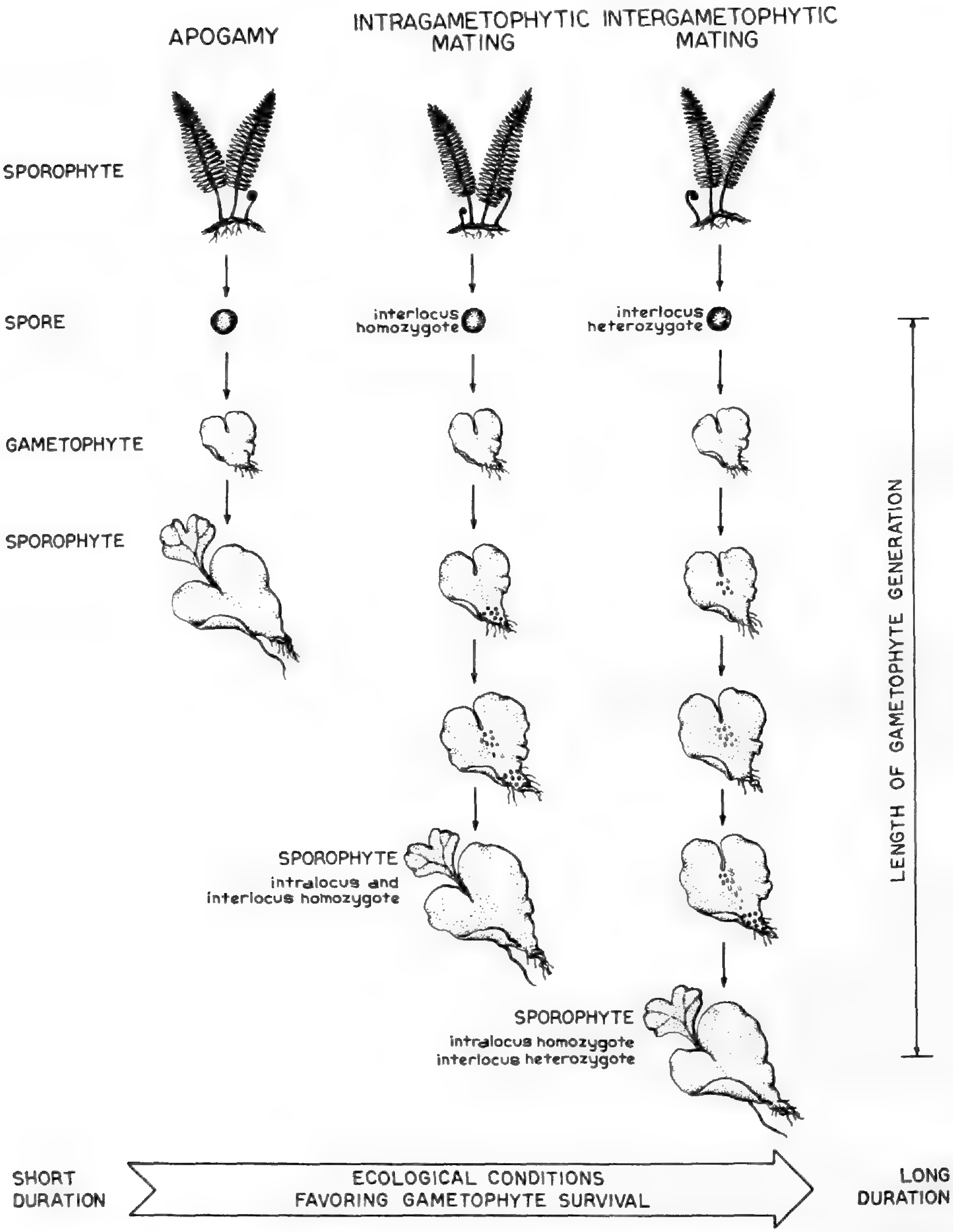

Figure 4. Relationship between reproductive systems, genetics, and ecology in homosporous ferns.

species, in composite cultures only male and female gametophytes are initially present, whereas if gametophytes are grown singly they are initially female and later become hermaphroditic (as do those in composite culture). These results are compatible with a mating system based upon antheridogen. Voeller (1971) has documented the positive response of members of this genus to antheridogen B.

Under laboratory culture conditions (see Klekowski, 1969*a*, for description), *Lygodium volubile* forms sporophytes (first leaf) 30 days after spore sowing, whereas isolated gametophytes of *L. heterodoxum* begin to form sporophytes after 51 days from sowing. A sample of spores of *L. volubile* obtained from the Royal Botanic Gardens, Kew, was used in a breeding test; of the ten gametophytes isolated, all formed sporophytes that exhibited similar and apparently normal ontogeny. Thus in *L. volubile*, the apogamous taxon, all of the spore genotypes tested could function as a single propagule in sporophyte establishment.

Spores of *Lygodium heterodoxum* were obtained from a single sporophyte growing near Tela, Honduras. In the breeding test, 50 gametophytes were isolated and allowed to undergo intragametophytic selfing. Forty-eight of these gametophytes formed what appeared to be normal sporophytes. Two (4%) of the isolated gametophytes formed sporophytes which terminated their development prior to the elongation of the first root and leaf. Both gametophytes underwent simple polyembryony and each had a number of such inhibited embryos. Thus at least 4% of the spore genotypes could not function as a single propagule in the establishment of a sporophyte. Of the 48 homozygous sporophytes, 25 were transplanted into the greenhouse and allowed to undergo further development. Three months later these sporophytes were examined morphologically. Twenty-four of these plants exhibited abnormal patterns of growth. These abnormalities included differences in plant size, organ (leaf and root) development, and coloration with respect to chlorophyll development. These results are compatible with the hypothesis that the parental sporophyte was heterozygous for recessive detrimental alleles distributed throughout the genotype. During the ontogeny of these homozygous sporophytes, genes not expressed during the embryonic stages were "turned-on" as the plants grew older and more complex. As more of the genotype was utilized, new deleterious homozygous combinations became evident. Thus in *L. heterodoxum* approximately 4% of the spore genotypes could function as a single propagule and lead to the establishment of a viable sporophyte, whereas in the apomict *L. volubile* 100% of the spore genotypes tested fulfilled this criterion. Thus from both the genetic and ecological points of view the apogamous species (*L. volubile*) would establish disjunct populations more readily than the outbreeding species (*L. heterodoxum*). In contrast, disjunct populations of the latter species would more readily evolve into endemic taxa than the former.

Given these ecological and genetic relationships, the comparison of the evolutionary prospects of disjunct populations in homosporous ferns and seed plants reveals some novel differences. Without doubt the dispersibility of spores is greater than seeds. This has led to the hypothesis that the principal limiting factor in the evolution of island endemics in ferns is the regressive effects of gene flow from source areas into these disjunct areas (Tryon, 1970). The foregoing discussions have indicated that because of the peculiar interactions between genetics and ecology in homosporous ferns, a hypothesis can be formulated that in certain disjunct populations the principal limiting factor in the evolution of endemic taxa is the genetically depauperate nature of these populations.

There is a limited amount of experimental evidence to support this latter

Table 2. Genetic load studies in Galapagos and Hawaiian *Pteridium*.

GALAPAGOS ISLANDS				HAWAIIAN ISLANDS			
Spore Collection	Isolates	Sporophytes	%	Spore Collection	Isolates	Sporophytes	%
G1	20	20	100	4672	49	46	94
G6	50	50	100	4677	50	46	92
G3	49	45	92	BL-2	45	40	89
G7	49	45	92	4671	49	37	76
G5	49	43	88	4657	46	31	67
G8	48	39	81	4375	40	13	33
				4666	50	14	28

hypothesis. Contrasting the degree of endemism in the floras of the Hawaiian and Galapagos Islands reveals some interesting relationships. The Hawaiian Islands are more isolated geographically from continental source areas than the Galapagos Islands. Carlquist (1967) has indicated that in the Hawaiian flora 94.4% of the angiosperm species are endemic in contrast to 60–70% of the fern species. The 1400–2000 contemporary species and varieties of angiosperms probably evolved from 168 immigrants (Carlquist, 1967), whereas 142 contemporary species and varieties of ferns probably evolved from 97 immigrants (Wagner, personal communication). In contrast, in the Galapagos flora, of the 59 taxa of ferns present, 5% are endemic, whereas of the 531 seed plants, 44.7% are endemic (Wiggins, 1966). These data appear interpretable upon the basis that the differences in fern endemism are related to the differences in geographical isolation of these two groups of islands. One might assume that greater geographical isolation results in greater genetic isolation and that in the ferns this is reflected in the greater degree of endemism in the Hawaiian Islands as contrasted to the Galapagos Islands.

Recent studies on the genetics of the cosmopolitan fern species *Pteridium aquilinum* (Klekowski, 1972) indicates that this interpretation may be too simple. Spore samples from individual sporophytes in both island groups were screened for embryonic recessive lethals. A gametophyte culture was generated and populations of paired and isolated gametophytes were established from the spores of each sporophyte sampled. If the parental sporophyte were heterozygous for recessive lethals, a portion of the hermaphroditic gametophytes in both populations failed to form sporophytes. Evidence that the failure of hermaphroditic gametophytes to form sporophytes is due to genetic causes is shown by the consistently higher frequencies of sporophytes in the paired populations. Table 2 compares the response of Hawaiian and Galapagos spore samples. From the isolation hypothesis one might predict the Hawaiian plants to show greater genetic uniformity and less heterozygosity for lethals than the Galapagos plants. Actually the data indicate the converse. The Galapagos *Pteridium* is more homogeneous and exhibits less heterozygosity for lethals than the Hawaiian *Pteridium*. In the former, 9% of the spore genotypes tested evidenced the presence of recessive sporophytic lethals whereas in the latter, 31% of the spore genotypes exhibited this phenomenon. The Hawaiian *Pteridium* populations seem more heterozygous than the Galapagos *Pteridium* populations. This is correlated with the fact that the Hawaiian *Pterid-*

ium has evolved into an endemic taxon (Tryon, 1941), whereas the Galapagos *Pteridium* is similar taxonomically to the South American form. Thus in *Pteridium,* evolution of an endemic taxon is correlated with the presence of greater genetic variability in the disjunct population. Conversely, the lack of evolution may be attributed to the genetically depauperate nature of the disjunct Galapagos populations rather than gene flow from neighboring South America.

To explain this paradoxical relationship between apparent geographical isolation and increased genetic heterozygosity, the ecology of these two groups of islands must be considered. Contrasting the Hawaiian Islands to the Galapagos Islands, the former would probably offer more habitats for prolonged gametophyte growth and survival than the latter. Such a situation would allow the establishment of taxa with intergametophytic mating systems and, with reference to *Pteridium,* sporophytes which are interlocus heterozygotes. In the more xeric Galapagos Islands one would expect a preponderance of taxa which are apogamous or have intragametophytic mating systems to become established. With reference to the Galapagos *Pteridium,* gametophytes originating from spores of inbred mainland sporophytes would form sporophytes more readily, and these probably would be interlocus homozygotes (see previous discussion on leaky lethality and ecology).

This relationship is supported by recent research on the Hawaiian fern genus *Sadleria.* This genus is endemic to Hawaii and comprises four species. Holbrook (1971) has found that three of the four species have intergametophytic mating systems and that heterozygosity for recessive sporophytic lethals is present in the populations. In this case endemism is correlated with the presence of intergametophytic mating and heterozygosity. Thus the differences between the frequency of fern endemics on the Hawaiian and the Galapagos Islands are explicable in terms of the differences in the ecologies of these two groups of islands. In all the above discussions the differences in ages of these two groups of islands has not been considered, it has been assumed that both groups of islands have been in existence sufficient periods of time to discount their age differences.

CONCLUSIONS

The high dispersability of the spores and the determination of the zygote genotype after migration are pivotal characteristics in any discussions of the genetics and evolution of disjunct fern populations. An independent consideration of either characteristic can result in two distinct, and somewhat antithetic, hypotheses concerning the nature of evolutionary processes in disjunct fern populations. In his study of island fern floras, Tryon (1970), considered gene flow from source areas (because of the ease of spore dispersability) to be an important agent in retarding the evolution of island fern endemics. For convenience this will be called the "reproductive isolation hypothesis." In this communication the author has considered the second characteristic (determination of the zygote genotype after migration) at great length. Because of the relationship of the fern mating system to its ecology and genetics, it has been argued that the primary phenomenon retarding the evolution of fern endemics is the absence of inherited variability in disjunct populations. For convenience this is called the "genetic depauperization hypothesis."

The relationship between these two hypotheses is illustrated by the following example. Assume an island is populated by a number of fern species, a few of which are endemic. The acceptance of either hypothesis for this hypothetical situation will result in a separate and distinct set of predictions concerning the biology of the endemic and non-endemic ferns present on the island. Assuming the validity of the "reproductive isolation hypothesis," one would expect the levels of heterozygosity in the populations of non-endemics to approximate those of their respective source areas, whereas the endemics would be characterized by lower levels of heterozygosity than populations of closely related taxa in source areas. One also would predict the absence of any correlation between mating system and endemism.

The "genetic depauperization hypothesis" would predict lower levels of heterozygosity in the non-endemic taxa in comparison to populations in their respective source areas. The populations of the endemics would be characterized by higher levels of heterozygosity than those of the non-endemics. The degree of heterozygosity of the endemics would approach that of populations of related taxa in source areas. Intergametophytic mating systems would predominate in endemic taxa whereas non-endemics could be apogamous or have either intergametophytic or intragametophytic mating systems.

Both the "reproductive isolation hypothesis" and the "genetic depauperization hypothesis" represent extreme interpretations based upon very restricted amounts of real data. The usefulness of these hypotheses lies in the predictions which can be formulated because of their extreme positions. As data are gathered on the taxonomy, gametophyte biology and genetics of island fern floras and other disjunct populations of ferns, these predictions can be tested. The outcome of these researches probably will indicate that both of these views are too simplistic and that the biology of disjunct fern populations represents an integration of both hypotheses with as yet unsuspected parameters of fern biology.

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CHEMOSYSTEMATIC DATA: THEIR USE IN THE STUDY OF DISJUNCTIONS[1]

B. L. Turner[2]

Cain (1944) in his excellent text, *Foundations of Plant Geography,* does not use the term disjunct to describe those taxa having discontinuous distributions; rather, he uses the term vicariads (sometimes spelled vicariants), which he defines as "closely related allopatric species derived from a common ancestral population." Closely related allopatric species are usually only peripherally allopatric and hence are not the same as the term disjunct as used in this paper. Other workers, however, such as Setchell (1935) have defined vicariads as any two species only slightly discontinuous morphologically but widely discontinuous geographically. This, of course, is the meaning which most of the present contributors assign to the term disjunction. However, as indicated by Good (1953) the term vicariad has been loosely applied to almost any pair of related taxa showing almost any degress of disjunction. Löve (1954) refers to disjunct taxa as corresponding taxa, using this term to cover all vicariads with unknown origins.

Disjunctions or discontinuous distributions (the term used by both Cain, 1944, and Good, 1953) may refer to the spatial conditions holding for taxa at any hierarchical level; thus one may speak of disjunctions at the varietal or specific level or at the generic level or higher. Because of the lax use of these terms and the fact that *all* populations and/or taxonomic categories possess some degree of discontinuity with respect to their aerial distribution, I would like to define disjuncts yet further in this particular contribution. Distinction, however, should be made between at least two kinds of disjuncts, depending upon the origin and phyletic status of the populations concerned.

Heretofore, plant geographers have mainly been responsible for the terminology pertaining to disjuncts, and many bizarre explanations have been given for their occurrence (*e.g.* Croizat, 1952). Most workers have been content, however, to merely catalog or describe their occurrence, with only brief schrift given to their probable origins. This perhaps reflects the obvious difficulty in assembling any data other than the geographical and morphological, although much interesting work bearing on disjuncts has been proposed from cytogenetical data (Löve, 1954).

In any case, I am of the opinion that the terms autojuncts and allojuncts (proposed below) will prove useful in future efforts to communicate on this subject.

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[1] I am grateful to Professor James Hanover of Michigan State University for personally providing plates from his interesting work with *Picea glauca* and to my colleague Professor Robert Flake for providing me with unpublished data regarding the clustering of disjunct populations within that species. Special gratitude is due my graduate student, Mr. Stewart Sanderson, who made available to me preliminary results of his most interesting work on *Hymenoxys odorata* and *H. anthemoides.* Parts of the original research referred to in this paper were supported by grants (GB-5548X) from the National Science Foundation.

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Further, use of these terms should suggest to the interested worker that some effort should be extended in determining the likely origin of a given disjunct, and *this* I believe will inevitably involve the worker with chemosystematic approaches to the problem. At least, chemical methods provide a large spectrum of new approaches to such problems, especially where convergent evolution has obscured what appears to be relatively simple cases of autojunction (*e.g.* with *Larrea divaricata*, as discussed below).

KINDS OF DISJUNCT POPULATIONS

Autodisjunctions (autojuncts): These may be defined as two or more morphologically similar populations that are widely separated spatially, the more remote elements having become isolated through the dissemination of appropriate colonizers from some *extant* population or gene pool. Except for those very few cases which have been studied in great detail, most autojuncts will of necessity be at the species level or below, that is to say the isolated population will be very similar to the parental population and is likely to be treated as a species by most taxonomists. Autojuncts may arise in a number of ways (see below), but most, very remote, populations of the same species are likely to have arisen through long distance dispersal from some much larger parental population. Where formidable barriers to the migration of species are lacking, autojuncts might arise as a result of the distributional expansion of a given population with subsequent regression so that the autojuncts are left as relict populations. The latter are likely to be quite similar to the more widespread parental populations. Given time, however, such autojuncts may diverge from the parental (extant) populations so that they may come to be recognized as subspecies or even closely related species. Lacking fossil data, however, convincing evidence for the wide morphological divergence of an autojunct from some extant populational source would be difficult to assemble.

Allodisjunctions (allojuncts): These may be defined as two or more closely related populations (*i.e.* more closely related to each other than either is to yet some other taxon) that are widely separated spatially, the various elements of which have been derived through phyletic divergence from populations now *extinct*. As indicated above, most allojuncts will be recognized in the first place by morphological criteria, the term being reasonably applicable to nearly all species, genera, families, etc., whose members have remote spatial disjunctions not explicable through origins from extant populations or taxa.

FORMATION OF DISJUNCTS

Disjunct populations or taxa are usually formed through any of the following:

1) long-range dispersal of seeds or propagules with the subsequent establishment of reproducing populations;

2) extinction of once intervening populations and subsequent survival (relict) of the more remote populational elements;

3) parallel divergence from ancestral populations, the latter becoming extinct;

4) "convergence" from phyletically remote populations;

5) remote isolation by purely tectonic forces (*e.g.* continental drift);

6) differential migration of whole populations following events, either physical or biological, leading to populational fragmentation.

If the parental populations or gene pool from which the original disjuncts arose persist, then disjunct populations might properly be referred to as autojuncts. This would be so whether or not the disjunct element diverged considerably or remained essentially like that of the parental population. Of course, the greater the genetic divergence of the disjunct populations from the more stabilized parental population, the more difficult it becomes to establish autojunction or allojunction, but it seems reasonable to assume that *most* cases involving 1) and 2) are likely autojunctional, while those involving 3) and 4) are allojunctional. Categories 5) and 6) may be either autojunctional or allojunctional depending upon the degree of adaptational divergence encountered in the gene pool following their initial isolation.

In any case, chemical data and their treatment by numerical methods already developed should make it possible to choose at least between some of these alternatives. Selected examples of the use of chemical data in such studies will be presented in the discussion that follows.

Chemical Approaches in the Study of Disjuncts

The study of disjuncts is essentially a systematic enterprise, and reasonable insight into the nature of such phenomena can only come as a result of detailed monographic study of the taxa involved. This would include the study of taxa related to, but not part of, the disjunct populations under consideration; consequently, if one contemplates the study of disjunct genera, he must consider the morphology and distribution of related genera; if at the species level, those species related to the disjuncts must be considered; and at the infraspecific level, a wide knowledge of the probably allojunct populations must be had, preferably from material drawn from throughout the range of both the parental population and its disjunctive body.

As indicated in previous reviews (Turner, 1967, 1969) chemical approaches to systematic problems can be broadly categorized as being either micromolecular or macromolecular. The latter involves work with very large molecules or polymeric compounds, while the former is concerned with compounds of small molecular weight, usually monomeric in nature.

Macromolecular approaches: There are four principal macromolecular approaches available for the study of disjuncts at the present time, these being 1) amino acid sequence analysis of proteins, 2) DNA/RNA hybridization, 3) serology, and 4) protein band and isozyme studies. The merits, shortcomings, and systematic potential of these various approaches have been considered in general detail elsewhere (Turner, 1967, 1969, 1971), and it need only be noted here that approaches 1), 2), and 3) are perhaps most applicable at the higher categorical levels while 4) is more applicable at the lower categorical levels.

Instrumental and technological advances are not available to permit the rapid acquisition of sufficient data from sequence analysis of proteins and DNA hybridization studies to make them especially useful in the study of disjuncts at present. The same may be said for serology, for the imposition of an antibody-producing organism in the methodological approach introduces serious constraints with respect to the breadth and number of samples which may be taken.

Protein-band and isozyme techniques, however, permit relatively rapid and extensive surveys among populations. In this respect, they are like micromolecular approaches, for a good technician using relatively simple procedures and instrumentation can accumulate considerable data of this sort. Unfortunately, there are serious problems in the interpretation of mere protein band data, especially when attempting to make comparative correlations among taxa at the species level or higher (Turner, 1967, 1969). Isozyme data are somewhat useful in that band homologies for comparative purposes can be reasonably assumed, but because of the considerable polymorphism found in most isozymes in natural plant populations (Marshall & Allard, 1970; Scogin, 1968), their application to the study of disjuncts becomes difficult (in that extensive surveys are needed to establish even *statistical* estimates of the variability occurring).

Nevertheless, isozymes should prove most useful in determining the origin of what appear to be clear cases of autojunction. In fact, I suspect that most examples of relatively recent (say within the last 500 years), long-range dispersal will be best documented by this approach, for introduction of a single autogamous plant into a new habitat far removed from its parental source is not likely to build up, in such rapid order, a variable gene pool for isozymes such as is likely to be possessed by the parental population from which it arose. Thus, while the disjunct element might colonize its new habitat quite rapidly, it will not be able to concomitantly build up a store of gene variability without some considerable time factor. Of course, if the disjunct population arose through the establishment of *several* outcrossing individuals, then the population will have a much better base for the accumulation of variability at the various loci concerned, but not nearly so great a variability as might exist in the parental populations.

Micromolecular approaches: Micromolecular approaches involve the study of chemical components of relatively small molecular weight compounds such as flavonoids, terpenoids, alkaloids, free amino acids, etc. Normally, they do not occur as other than mono- or bi-molecular units, and consequently, they are readily isolated and structurally identified by relatively simple techniques and instrumentation (*i.e.* isolation by chromatography and identification by spectroscopy). Because of their ease in identification they are perhaps more useful in the study of disjunction than mere protein-band data, for the establishment of character homology in disjuncts is critical. Their use in systematics has been soundly criticized by several workers, especially where the investigators concerned have made sweeping taxonomic generalizations from data taken from only a few individuals or populations.

It has been pointed out also that micromolecular compounds are likely to be much more ubiquitous than is generally conceded, as indicated by Professor W. L. Fowden of London Univ. (personal communication), who has identified several previously unreported (indeed unsuspected!) compounds in commercial quantities of sugar beet syrup, simply by having access to exceptionally large samples from industrial sources. That is, these compounds occurred in such small quantities that they could not be detected by ordinary procedures.

Finally, it should be noted that micromolecular components of any one class are limited in number. Further, some of the more common types occur across a wide spectrum of plant taxa. This has been adequately emphasized by Alston (1967), and because of this, I feel that the primary application of micromolecular data to the study of discontinuous distributions should be to those situations involving autojunction. There are rare instances, however, where these data might prove quite convincing in the establishment of allojunction, even those at the familial level or higher. Perhaps the best example of this type reported to date is that involving the yellow and red pigments of the betalain type found in the order Chenopodiales (discussed below).

The extensive application of micromolecular data to systematic problems across a wide spectrum of plant taxa can be said to have begun only in the late 1950's and early 1960's (Alston & Turner, 1963). Because of this, relatively few chemical studies have been directed toward the study of disjuncts. Chemosystematic investigations, however, as judged by the publication and research currently going on, now appear to be in an early stage of exponential growth, and unquestionably such studies will be applied to problems of disjunction with increasing frequency.

The remainder of this paper, then, will concern itself with the consideration of a few selected examples in which micromolecular data have contributed toward the solution of both allo- and autojunction. By their nature, allojuncts are difficult to detect, but as already indicated (Turner, 1971) micromolecular data can prove very incisive in the study of populational problems at the infraspecific level.

Chemical Studies Bearing on Allojuncts

Cactaceae—Aizoaceae: According to Vierhapper (1919), these two families are vicariads or allojuncts (in my terminology). They are both very large, distinct categories, the members of which are apparently more closely related one to the other than either is to yet another taxon. The Aizoaceae is predominantly succulent, occurring mostly in the arid regions of the Old World, especially South Africa. The Cactaceae likewise is predominantly succulent, occurring mostly in the arid regions of the New World. Vierhapper's suggestion as to their allojunct nature is most extraordinary considering that he proposed this at a time when many experts thought the families to belong to quite different orders, and without knowledge of the recent evidence bearing on continental drift, to say nothing of the chemical data of the betalain type discussed here.

The close relationship of the Cactaceae and Aizoaceae is now widely accepted by most phyletic taxonomists. Much of the convincing evidence for this relationship rests on the fact that both families possess betalain pigments, a group of nitrogenous micromolecules restricted to the Chenopodiales (Wohlpart & Mabry, 1968).

My own speculations regarding the origin of this pair of allojuncts are as follows: It is probable that the ancestral populations from which these two families arose occupied xeric or at least halophytic habitats of the Southern Hemisphere, probably on the ancient continent of Gondwanaland, presumably where southwestern Africa and southeastern South America were once connected. Subsequent gradual drift of these continents isolated some fraction of this primordial population, the South American fraction developing into the Cactaceae, the Old World elements developing into the Aizoaceae. Ancestral prototypic members no longer exist, but both families have retained their red and yellow betalain pigments (neither possess pigments of the anthocyanin type), and both still possess their peculiar sieve tube plastids, which are found in all members of the Chenopodiales (and Caryophyllales) but are absent in other plant families (Behnke & Turner, 1971).

Equally interesting is the occurrence of betalains in the small xerophytic family Didieraceae, which is restricted to Madagascar. The phyletic position of this family was long in dispute, but the discovery of betalain pigments in this family has convinced most workers that it belongs to the Chenopodiales. It will be interesting to consider possible allojuncts with this family, for Madagascar is believed to have been contiguous with India (McElhinny & Luck, 1970), and it might prove fruitful to examine those betalain families centered in India or Australia as possible disjuncts.

The more temperate, mostly mesophytic, Caryophyllaceae, which is often placed within the betalain-containing order (Behnke & Turner, 1971), does not contain betalain but *does* contain the peculiar sieve tube plastids characteristic of that order. It appears, therefore, that the Caryophyllaceae is a parallel offshoot of the ancestral phyletic line leading to the Chenopodiales. Interestingly, the Caryophyllaceae is mostly Northern Hemisphere in its distribution, while the Chenopodiales is either centered in the Southern Hemisphere or else is highly adapted to saline habitats or xeric conditions. This is particularly true of the latter order in the Southern Hemisphere where the group presumably had its origin. This point is emphasized here, for plant geographers and especially ecologists have tended to ignore phyletic adaptational trends, at least within higher plant categories, as especially significant in their studies of plant communities and their origin.[3]

CHEMICAL STUDIES BEARING ON AUTOJUNCTS

In the case of disjuncts at the higher categorical level, their characterization as possible autojuncts will undoubtedly prove difficult if not impossible. At the

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[3] I refer specifically to the suggestions of Axelrod (1950) and others as to the time of origin of the warm desert communities on the various continents. To assign an age of only one million years or so for most extant deserts does injustice to the considerable floristic evidence available. For example, the Cactaceae, Aizoaceae, Didieraceae, and presumably most of the families of the Chenopodiales were probably already xerophytically disposed even before the development of forces leading to continental drift, or else these betalain-containing families would not so often dominate such habitats on these widely separated continents today. This is to say nothing of the obviously xerophytic families Fouquieriaceae, Koeberliniaceae, Krameriaceae, Welwitschiaceae, etc., which are desert groups without close peripheral mesophytic relatives. That is, these families have probably been a feature of the deserts in which they occur for many millions of years, or else one must assume that nature is selectively capricious in her destruction of the presumably more stable, mesic relatives from which they have had to arise; lacking this, one must assume a degree of adaptational divergence from some once closely related ancestor, the like of which baffles the imagination.

generic or familial level recognition will depend heavily upon amino acid sequence studies of proteins or else must await the development of more sophisticated methods for the study of nucleotide sequences in DNA. Until such a time, morphological features will probably continue to serve as the primary criteria for their recognition.

At the species level or below, the establishment of disjunct populations as autojunctional will probably rely quite heavily upon microchemical data, for it is difficult to believe that purely morphological data might do more than provide a model against which to test the chemical data. Of the various microchemical components which have been used for systematic purposes, the most common have been flavonoids and volatile oils. The former are relatively easy to isolate and identify, but since they are usually detected on a presence or absence basis only, they are not particularly useful in the study of disjuncts, especially in those cases which appear to be autojunctional.

Ideally, chemical characters used in the study of putative autojuncts should be

1) rapidly and easily surveyed for, preferably by tests on a single individual or plant part;

2) readily quantified, preferably by automatic methods;

3) under genetic control so that they might respond to adaptational changes under selective influences.

At present, the group of compounds which best fills all three criteria are those which are easily identified by gas liquid chromatography (GLC), for example, terpenes. In fact, using combined GLC-mass spectroscopy and appropriate computer methods, it is possible to identify and quantitate up to 100 volatile components within a 60 minute period. All of this is done by the hardware, of course, leaving little, if anything, to procedural bias, except for the collection of the specimens from which the compounds are obtained, that itself being a kind of intuitive bias since one cannot observe chemical constituents in the field.

Further, the information, once assembled, lends itself to appropriate algorithms which purport to do for the chemical data what the taxonomist does for the morphological, with the exception that use of the former permits the objective (numerical) presentation of data along with statistical tests as to significance (Flake, von Rudloff & Turner, 1969). This is not generally true for the morphological data, and as indicated above, this cannot be done with chemical compounds such as flavonoids where quantitation is not so readily obtained.

In my consideration of the examples that follow, I would like to emphasize that their selection has been due primarily to their hueristic value in presenting the potential of such techniques, or else they have been selected for their enigmatic nature, inquiry into which must require ultimately some knowledge of the volatile constituents of the plants themselves.

Autojunct populations in Picea glauca: Wilkinson *et al.* (1971) have studied in considerable detail the monoterpene composition from 16 localities of *Picea glauca* (White Spruce) in North America (Fig. 1). While the study was confined to the analysis of only nine monoterpenes from ten trees from any one locality, it is remarkable in that all of the trees sampled were taken from nature and grown

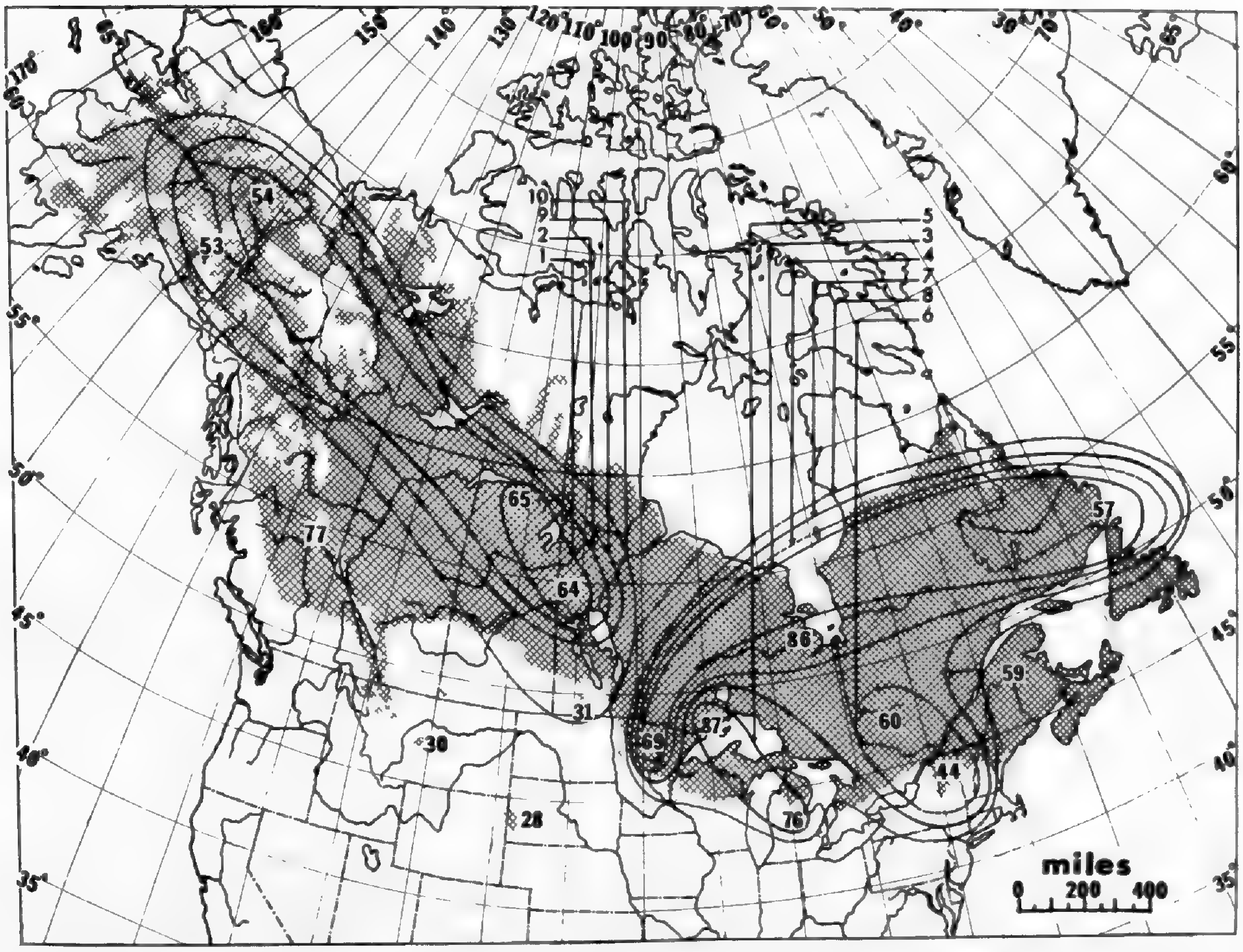

FIGURE 1. Aggregation contours of populations of white spruce (*Picea glauca*) using weighted chemical characters (Wilkinson *et al.*, 1971). The disjunct populations 30 and 28 clustered at a level below those for which contours are drawn and are discussed in more detail in the text.

in an experimental garden so that environmental factors affecting the variation were presumably minimal.

The study also pertains to this symposium, for it illustrates nicely the potential of chemical approaches to problems involving disjunction. *Picea glauca* exists in relatively extensive populations from northwestern North America to Alaska, south to the Great Lakes region of northern Minnesota and Illinois. There are, however, at least two well-defined disjunct populations, one in central Montana and the other in southwestern South Dakota. The latter, in particular, is isolated from the main populational mass by approximately 400 miles. Using replicated data and a character-weighting algorithm developed around the assumption that those characters showing the least variance from population to population ought to be given more weight in cluster analysis, Wilkinson *et al.* (1971) were able to show that the species consisted of two divergent chemical clines: one extending from the Lake States north-westward to Alaska, and the other north-eastward into Labrador. Furthermore, they suggested that these clines perhaps resulted from the migration of *P. glauca* both north-eastward and north-westward from populations to the south of the ice following glacial recession during post-Wisconsin time.

With knowledge of the chemical structure of the main populational mass, it was possible to consider the status of the disjunct populations 28 and 30 (Fig. 1).

It is interesting to note that these two populations entered the aggregations at a level below that for most of the more northern populations, but when the South Dakota population (28) entered the aggregation, it did so with a set of the typical "western" populations 54, 64, and 65 (R. H. Flake, personal communication). This knowledge permits several interpretations, the most reasonable being that of the authors themselves:

> "The divergence of the South Dakota source could possibly be related to its isolation and perhaps unique evolutionary history in that the source is often considered to be a remnant from Pleistocene glaciation."

The autojunctional population 28 is presumably a relict stand of *Picea glauca* whose origin goes back to a time when the main populational mass had a much more extensive distribution to the south; that is, its isolation does not appear to relate to the more northern populations, the latter presumably having dispersed from populations arranged along the front of the most recently glaciated regions. At least, there is no evidence that population 28 has been established through *recent* long-range dispersal from its more northern neighbors.

Surprisingly, the Montana disjunct population 30 entered the aggregation at a slightly lower level than did population 28, clustering instead with a large set of "eastern" populations (44, 57, 60, 69, 76, 86, and 87)! This is anomalous in that population 30 is northwest of 28 and would be expected to cluster with the western set. However, this is believed to be readily explicable in that the Montana population occurs in a region of sympatry with *Picea engelmannii*, and chemical examination of populations in this area suggests that they are involved in hybridization (Habeck & Weaver, 1969). In short, the relationship of population 30 to the more eastern population seems to be spurious, resulting from peripheral perturbations in the gene pool of *P. glauca* as a result of hybridization with *P. engelmannii*. In fact, it was shown by Wilkinson *et al.* (1971) that hybridization between these two taxa should result in the kind of chemical variation actually found in the Montana population.

In my opinion, it would have been difficult, if not impossible, to assemble morphological evidence bearing on the origin of these two autojunctional populations without the use of chemical data. Differences among the various populations of *Picea glauca* are simply not sufficiently distinctive to permit any sort of objective structuring of the populations using morphological characters.

Hymenoxys odorata–Hymenoxys anthemoides: According to Parker (1962), these two species are thought to be disjuncts, *H. odorata* occurring in the desert regions of North America; *H. anthemoides* occurring in the drier regions of Argentina.

The genus *Hymenoxys* is centered in North America where two well-defined subgenera are recognized: *Hymenoxys* and *Tetraneuris*, some workers preferring to treat them as distinct genera. Both *H. odorata* and *H. anthemoides* belong to the subgenus *Hymenoxys*; the somewhat larger subgenus, *Tetraneuris*, is not represented in South America, while *Hymenoxys* is represented by four species.

The suggestion that *Hymenoxys anthemoides* is most closely related, on morphological grounds, to *H. odorata* is interesting because it bears upon the origin of a whole group of interior arid land disjuncts with amphi-tropical distributions in the New World. In fact, this group of plants constitutes one of the most enigmatic assemblages of floristic disjunctions known to me, and there have been a number of hypotheses put forward to explain their occurrence (Bray, 1900; Johnston, 1940; Raven, this symposium).

The case for the disjunctive nature of *Hymenoxys odorata* and *H. anthemoides* received impetus with the preliminarily cytological findings that *H. odorata* was dibasic with chromosome numbers of $n = 11$ and 15, while *H. anthemoides* was monobasic with $x = 15$. This suggested that the South America populations were derived from those populations in North America with $x = 15$ or vice versa.

This is about where the problem stood until about a year ago at which time Mr. Stewart Sanderson, graduate student at the University of Texas, began an intensive chemosystematic study of the subgenus *Hymenoxys* using terpenoid characters. His preliminary data bearing on the possible disjunctive nature of *Hymenoxys anthemoides* and *H. odorata* are quite interesting. The two species together possess over 40 volatile components, and examination of populations of both species grown in the same experimental garden has shown that only a few of these compounds are shared. In fact, by terpenoid chemistry, *H. anthemoides* is more closely related to some of the more restricted, mountainous species of North America than it is to *H. odorata.* Finally, the North American cytological races ($n = 11$ and 15) were clearly quite closely related by their terpenoid chemistry (and morphology), thereby denying any likely relationship between the races of *H. odorata* with $n = 15$ and *H. anthemoides* with $n = 15$.

Of course, the subgenus *Hymenoxys* must still be counted as a disjunctional element, but it seems clear from the chemical evidence available that the South American *H. anthemoides* is not particularly close to *H. odorata*, and the two species could scarcely be termed an autojunctional pair. A more likely explanation for their disjunction, if the taxonomic suggestions put forth by Parker are valid, is that they are allojuncts, the South American populations having reached the arid regions of the Southern Hemisphere via long-range dispersal at some distant time and that subsequent divergence of the North American parental population has occurred. The reason for asserting that North America is the ultimate place of origin for *Hymenoxys* is that this genus *and related genera* are far and away best developed on that continent (Bierner, 1971).

Other interpretations of these preliminary data are possible, of course, but it appears likely that a more comprehensive chemical study of the numerous species of *Hymenoxys* on both continents will do much to clarify the nature of these interesting disjuncts. In fact, taken together, a series of such studies on a wide spectrum of plant groups might do much to resolve the particular problem of whence came these amphi-tropical patterns and how. Indeed, such a collaborative study is already underway, and it will be most interesting to consider the impact of data assembled from these studies.

Larrea divaricata–Larrea tridentata: Of the numerous disjunct taxa worthy of chemosystematic study, the genus *Larrea* (Zygophyllaceae) seems unusually qualified for detailed investigation, since it is a dominant element of the desert vegetation in both North and South America; and at least one species, *L. divari-*

cata, is so similar to its southern hemisphere counterpart, *L. tridentata,* that some authors have considered them to be the same species. In fact, this is the best known example of an amphi-tropical autojunct. Since its distribution and ecological position in the deserts of both North America and South America are treated in detail by Solbrig (this symposium) and Hunziker *et al.* (this symposium), I will confine my remarks here to the potential contribution that comparative biochemistry might hold for the study of disjuncts.

On the surface, *Larrea* would seem to be an "ideal" genus to study chemosystematically. It possesses a large number of volatile compounds which are readily detected by gas chromatography. The plants occur in very large populations, and a single leafy branch will suffice for distillation purposes. Thus, one can sample individual shrubs over a large region, marking the plants with permanent tags so that re-samples might be made, if needed.

However, there are many problems, foremost of which is the quantitative variability likely to be induced in the volatile constituents by environmental factors. It has been amply demonstrated that the volatile fraction of a plant will vary significantly from month to month depending on the metabolic stage of the organism, which in turn presumably depends upon moisture and temperature conditions affecting the populational site itself. Much of this plant-to-plant variation can be "smoothed out" by statistical treatment of the populational data but, except for trees growing under conditions of reduced metabolism in the field (*e.g. Juniperus virginiana* and presumably other conifers which show little or no growth activity during the winter months; Flake, von Rudloff & Turner, 1969), chemical analyses should come from plants grown in a uniform garden. This is particularly important with a desert shrub such as *Larrea,* for preliminary work on field populations of *L. divaricata* has shown quite extraordinary quantitative variation from individual to individual at a given site, and from population to population, presumably depending upon the amount of ground water available to the plants. Such variation might be due to the extraordinary sensitivity of the volatile compounds themselves, most of which are guanilides, a group of peculiar constituents unrelated to the terpenes. Since *Larrea* is an evergreen shrub, more or less restricted to temperate regions, it might prove feasible to sample populations in the winter, much as in *Juniperus,* but this is an aspect of the problem which has not been investigated.

Finally, I cannot help but note that three views prevail as to the origin of the more xeric amphi-tropical elements found on the North and South American continents. These are:

1) that the species (and deserts) are ancient (60 million years or more) having a common origin;

2) that the floras evolved separately through parallel selective influences from the surrounding vegetation, *i.e.* the floras have no historical connections as such; or

3) that the species (and deserts) are of relatively recent origin, the disjuncts having reached the two desert areas via long-distance dispersal.

If the latter view (3) is held, then one would expect a very close similarity in the secondary compounds of the various disjunct taxa. On the other hand, if very similar species have very different secondary compounds this might indicate a long-time isolation or different phyletic history of the taxa concerned, the morphological traits (*e.g.* habit and vegetative features), through parallel selective influences, remaining at least superficially similar; the secondary compounds, inasmuch as they are presumably under weak selective pressures probably reacted differently to the different parasitic and grazing fauna of the South American region. In other words the secondary compounds, being under quite different selective forces, should have diverged considerably from their disjunct counterparts in spite of the quite similar climatic regimes in which they presently occur (Turner, 1969).

As yet we do not know the origin of the apparently autojunct *Larrea divaricata.* Hunziker (personal communication, this symposium) interprets his preliminary protein-band data as suggestive of a South American origin for the group as a whole. I am more cautious, for while I recognize the better development of *Larrea* (as to number of species) in South America, I am also aware that the North American element is made up of diploid, tetraploid, and hexaploid populations, all of which show considerable variation, indicative of a species with some considerable tenure in the North American deserts. I suggest, therefore, that it is equally likely that *L. divaricata* developed as a diploid population in North America millions of years ago, and that subsequently it was established in South America through long-range dispersal. The fact that there are two other species of *Larrea* in South America implies little, for *L. divaricata* may be only remotely related to these. Of course, it is also possible that the genus itself, and *L. divaricata* specifically, has existed since early Tertiary time, such as suggested by Bray (1900) and Johnston (1940). But this would seem to raise serious problems as to the origin of the desert areas themselves, for it seems unlikely that the desert areas were ever connected such that *Larrea divaricata* achieved its disjunct status from a once intact gene pool with only subsequent physical events responsible for its isolation. Or does it?

I tend to believe that the disjuncts making up the various amphi-tropical elements have a multiplicity of origins. They may be allojunctional, as appears to be the case with *Hymenoxys odorata-H. anthemoides*, or they may be autojunctional, as appears to be the case with *Larrea divaricata.* Further, I tend to believe that the desert areas on the two continents developed early enough (at least beginning with Miocene) to have permitted the establishment of many kinds of disjuncts. Some of these are relatively old, and some relatively new, but presumably all have passed over the tropics as long-distance dispersants in one direction or the other.

Clearly, more data of every sort will be needed before these abominable amphi-tropical disjunctions can be explained or understood. No doubt comparative chemistry will make up an important part of this information.

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DISJUNCTIVE DISTRIBUTIONS IN THE LICHEN-FORMING FUNGI[1]

William Louis Culberson[2]

There is a widespread notion among botanists that the nonvascular cryptogams are easily disseminated, ubiquitous plants without well defined geographic ranges. Certainly for many groups, such as the fresh-water algae and the nonpathogenic or nonsubstrate-specific microfungi, this view seems to be justified, for few meaningful geographic-to-taxonomic correlations among these organisms have been perceived. In other groups, for example the higher Basidiomycetes, our ignorance of phytogeographically significant ranges may reflect only the magnitude of the problems inherent in the study of organisms known only from ephemeral sporocarps. There are, however, two large groups of cryptogams in which species and taxa of higher than specific rank show well marked geographic distributions, including disjunctive ones, like those known in the vascular plants. These are the bryophytes and the lichens, the only major groups of terrestrial nonvascular cryptogams in which the vegetative plant body is exposed and perennating. The aim of this paper is to examine disjunction as it is known with regard to the second group, the lichen-forming fungi.

Reliable distribution maps have been published for few (only hundreds) of the approximately 20,000 recognized species of lichen fungi. Most of the best substantiated distributions are for conspicuous foliose or fruticose species from temperate regions of the northern hemisphere. To underline the point that lichen fungi may have geographic ranges comparable to those of vascular plants, Table 1 gives eight pairs of common, locally abundant, native North American plants, in each case a lichen fungus and a tree, for which the total geographic ranges are almost congruent or very highly comparable. It should be pointed out that although all but one of the lichen examples are epiphytes, none is ecologically restricted to the bark of the tree species to which its range is compared. Many more such examples could be given from the flora of North America and the floras of Europe and the Far East. So similar in fact are the well documented ranges of lichens to the ranges of vascular plants that the conclusion that both result from the same physioecological and historical factors is inescapable.

TYPES OF DISJUNCTIVE DISTRIBUTIONS IN LICHEN FUNGI

Most plant species can be said to have disjunctive ranges if the concept of what continuity of distribution consists of is sufficiently narrowed. The types of disjunctions that I shall discuss, however, are major ones in which centers of modern ranges are on different continents. Disjunction could as well be discussed in a more restricted framework for the examples of North American and European

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[1] This paper was prepared under the tenure of National Science Foundation grant GB-8359.

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Ann. Missouri Bot. Gard. 59: 165–173. 1972.

TABLE 1. Eight pairs of common, native North American species, a lichen and a tree, in which the total geographic ranges are nearly congruent or highly similar. [Ranges of trees from Little (1971); ranges of lichens from various authors.]

Lichen Species	Tree Species
Actinogyra muehlenbergii (Ach.) Schol.	*Tsuga canadensis* (L.) Carr.
Anzia colpodes (Ach.) Stizenb.	*Quercus palustris* Muenchh.
Dermatocarpon tuckermanii (Rav.) Zahlbr.	*Carya ovata* (Mill.) K. Koch
Parmelia caroliniana Nyl.	*Diospyros virginiana* L.
Parmelia livida Tayl.	*Cornus florida* L.
Physcia millegrana Degel.	*Juniperus virginiana* L.
Platismatia herrei (Imsh.) Culb. & Culb.	*Picea sitchensis* (Bong.) Carr.
Pseudevernia cladonia (Tuck.) Hale & Culb.	*Picea rubens* Sarg.

lichen species disjunctive in their own native continent are numerous. I have selected my examples of disjunctive ranges from those species with distributions including the New World in the hope that comparisons to species of other plant groups discussed in this symposium may become apparent. I have attempted to minimize the inaccuracies that accompany insensitive taxonomies by restricting my examples to taxa *1*) that are well-known systematically (even if their taxonomic rank is in dispute), *2*) that have been recently studied, *3*) that are common in at least part of their range, and *4*) that are large enough to be conspicuous (and consequently often collected). Some of my examples may not satisfy all these criteria, but most of them do.

1. Widespread disjunctions.—Many taxonomically well-defined species have extremely broad ranges and are represented on most continents. This is often pointed to as evidence that evolution in the lichens is (or has become) very slow. The following species occur on at least four continents:

Cladonia merochlorophaea Asah.
Heterodermia leucomelaena (L.) Poelt
Menegazzia terebrata (Hoffm.) Mass.
Normandina pulchella (Borr.) Nyl.
Parmelia crinita Ach.
Peltigera polydactyla (Neck.) Hoffm.
Sphaerophorus melanocarpus (Sw.) DC.
Thamnolia vermicularis (Sw.) Ach. *ex* Schaer.

There are also large numbers of pantropical species, for example:

Baeomyces absolutus Tuck.
Cladonia aggregata (Sw.) Ach.
Cladonia balfourii Del.
Dirinaria aegialita (Ach.) B. Moore
Heterodermia tremulans (Müll. Arg.) Culb.
Graphis afzelii Ach.
Parmelia cristifera Tayl.
Parmelia tinctorum Del. *ex* Nyl.

The two lists above include some species that reproduce by sexual means through ascospores that must find an appropriate algal partner and others that reproduce primarily by asexual propagules—soredia or isidia, structures that are composed of both hyphal fragments and algal cells and constitute a prolific source of "instant" lichens. But among the widely distributed species, the production of asexual propagules is doubtless more common than among the lichens as a whole. The recently monographed *Parmelia* subgen. *Amphigymnia* (Hale, 1965) provides data that may well prove to be typical for many widely distributed genera of lichen fungi: There are 26 pantropical species of *Parmelia* subgen. *Amphigymnia* of which only 5 (19%) lack soredia or isidia. Although circumstantial evidence confirms the great importance of soredia and isidia as effective propagules, direct observation of the dissemination of these bodies is infrequent. It has been shown experimentally that soredia are indeed detached and carried by wind (Bailey, 1966). Soredia have also been recovered from samples of air-borne plant fragments (Rudolph, 1970), but most soredia in samplings from the air are probably recorded as algae and not recognized for what they are.

In the category of widespread disjunctions one might include very large numbers of lichen species with enigmatic disjunctive ranges—for example *Parmelia latissima* Fée, which occurs in tropical America and India. Are such distributions the result of long-distance dispersal or are they the relicts of earlier and broader ranges? Definitive explanations of such ranges are simply not possible in groups such as the lichen fungi that lack a fossil record.

2. *Circumboreal disjunctions.*—The following arctic and north-temperate species have circumboreal, disjunctive ranges:

Alectoria nidulifera Norrl.
Cetraria halei Culb. & Culb.
Cetrelia cetrarioides (Del. *ex* Duby) Culb. & Culb.
Evernia mesomorpha Nyl.
Lobaria linita (Ach.) Rabenh.
Nephroma arcticum (L.) Torss.
Parmeliopsis ambigua (Wulf.) Nyl.
Peltigera horizontalis (Huds.) Baumg.
Solorina saccata (L.) Ach.
Umbilicaria arctica (Ach.) Nyl.
Xanthoria fallax (Hepp) Arn.

The disjunctions of some circumboreal species are maintained by narrow amplitudes of ecologic tolerance. For example, the extremely oceanic species *Platismatia norvegica* (Lynge) Culb. & Culb. occurs in the oceanic parts of Scandinavia (main European range), in Scotland, in Newfoundland, and along the North American West Coast from Oregon to southern Alaska (main American range). However, no obvious ecological factors limit the distribution of the tundra lichen *Asahinea chrysantha* (Tuck.) Culb. & Culb., which occurs continuously over large parts of Siberia and Alaska (main range) and locally on Baffin Island and in northern Scandinavia. The main range of this species would seem to have developed from gradual spread from a center of origin with the outliers the result of long-distance dispersal. Unlike *Platismatia norvegica*, *Asahinea chrysantha* does not seem to be limited to a specialized environment by a restrictive physiology.

3. *Bipolar disjunctions.*—Although some of the examples of lichens with bipolar disjunctive distributions pointed out by Du Rietz 30 years ago are perhaps to be challenged upon faulty taxonomy, the fact that this distribution type exists among the lichens is irrefutable. The best documented example is in the recently monographed genus *Platismatia* (Culberson & Culberson, 1968). The temperate species *P. glauca* (L.) Culb. & Culb. is locally very abundant in northern and western Europe, in northern North America, and in extreme southern Argentina

and Chile. The species is apparently absent from the high mountains of western South America. Long-distance dispersal of this sorediate species would seem to have been the origin of the antipodal population. This explanation is supported by the occurrence of *P. glauca* on Mt. Aberdare, Kenya, and Mt. Kilimanjaro, Tanzania, localities in east-central Africa about 5,000 km south of the southern limit of the European range of the species. Curiously, this widespread species does not occur in Himalaya, Japan, or Southeast Asia but is replaced there by a very distinctive vicariad, *P. erosa* Culb. & Culb.

4. *Europe-North America disjunctions.*—Some species occur in Europe and North America but are unknown elsewhere. Good examples are *Parmelia quercina* (Willd.) Vain. (widespread in southwestern Europe, locally common in California), *P. hypoleucina* J. Stein. (occasional in the Mediterranean Basin, common in the North American Atlantic Coastal Plain, rare in southern California), and *Letharia vulpina* (L.) Hue (locally common in the mountains of Central Europe, Morocco, and western North America). It is never possible to exclude long-distance dispersal as the explanation, but it is tempting to see these present ranges as the relicts of more extensive distributions before the separation of the continents.

5. *Eastern North America-Japan disjunctions.*—The early appreciated and now classic affinities between the floras of eastern Asia and eastern North America are well represented among the lichen fungi. In the vascular plants the floristic affinities are usually revealed through vicarism, but in the lichens some species are common to both regions. The following are all lichens known to me to be restricted to the regions in question and to be so uniform that both the eastern Asiatic and the eastern North American representatives are considered to be conspecific:

Anaptychia palmulata (Michx.) Vain.
Anzia ornata (Zahlbr.) Asah.
Candelaria fibrosa (Fr.) Müll. Arg.
Cladonia submitis Evans
Cladonia clavulifera Vain.
Lobaria erosa (Eschw.) Nyl.
Lobaria quercizans (Michx.) Vain.
Parmelia aurulenta Tuck.
Parmelia formosana Zahlbr.
Parmelia galbina Ach.
Pyxine sorediata (Ach.) Mont.
Stereocaulon tennesseense Magn.

It will be noted that all twelve of the above species are either foliose or fruticose. Surely as the crustose lichens become better known, the number of examples of this distribution type will be multiplied.

A relatively large number of other species have their main distributions in Japan and eastern North America but are also known elsewhere. *Actinogyra muehlenbergii* (Ach.) Schol. and *Heterodermia hypoleuca* (Ach.) Trev. are examples, the former occurring additionally in Siberia and the latter occurring additionally in Himalaya. *Umbilicaria caroliniana* Tuck. occurs on the highest peaks of the Southern Appalachians and in the mountains of Honshu and is known additionally from unglaciated parts of Alaska and from one locality in Siberia. *Cetrelia chicitae* (Culb.) Culb. & Culb. is one of the commonest lichens in the mountains of the eastern United States and of central Japan. It is also known

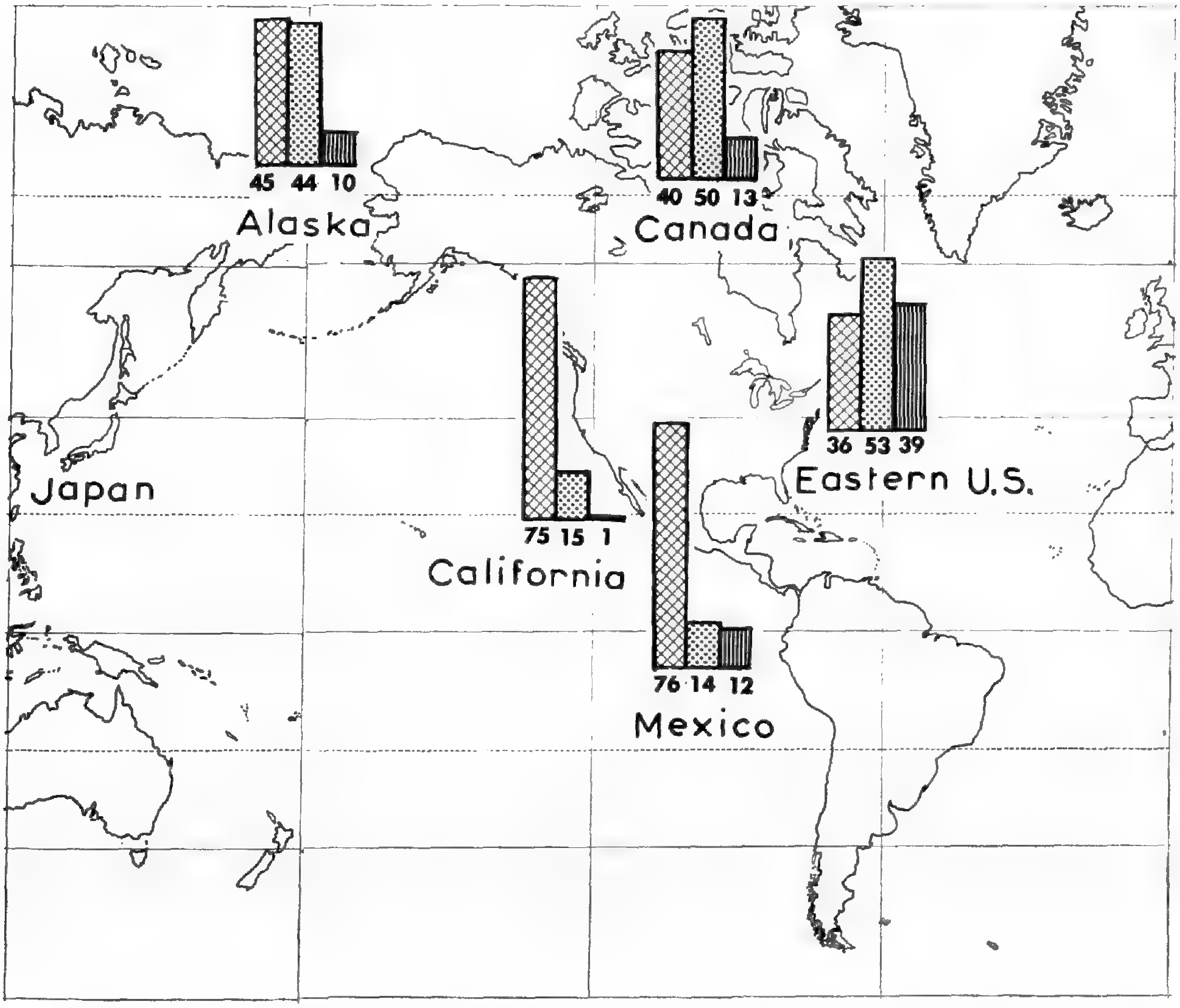

FIGURE 1. Comparison of the *Cladonia* flora of Japan (90 species) with that in various parts of North America. From left to right the columns refer to the number of species present in Japan but absent from the indicated region (cross hatched), the number of species common to Japan and the indicated region (stipple), and the number of species absent from Japan but present in the indicated region (vertical lines). Redrawn from Yoshimura (1968).

from a single locality in Europe (in the Vosges) and from a few mountain stations in Southeast Asia.

The large and diverse genus *Cladonia* is well represented in Japan and North America and is better known there than elsewhere for having attracted the attention of perceptive chemotaxonomists in both countries. Summarizing our present knowledge of the genus, Yoshimura (1968) showed that the number of species common to floras in various parts of North America and to the flora of Japan varies greatly. The number of species shared is greater in Alaska, Canada, and the East and smaller in California and Mexico, underlining the classic relationship among the species of an entire genus (Fig. 1).

The explanation of the origin of the eastern Asiatic-eastern North American vicarism is surely the same as that for the vicarism seen in the vascular plants of these regions—namely, that a richly diverse and once continuous Tertiary vegetation that extended from North America through the then adjoining continent of Europe and across Asia to Japan was subsequently reduced to widely separated relictual populations by wholesale extinctions. The role of glaciation in eliminating from Europe the Tertiary lichen species now shared by Japan and eastern North America has been well discussed by Poelt (1963).

DISJUNCTION WITH DIFFERENTIATION: THE ORIGIN OF VICARIADS

Divergent evolution in populations that have become disjunct for whatever reason leads to speciation if the process goes far enough. It must always be borne in mind however, that apparent vicariads might owe their origin to the extinction in the disjunct populations of reciprocal members of a once sympatric species pair.

1. *Vicariads in Japan (and/or eastern Asia) and eastern North America.*—The most striking example of vicarism in lichen fungi comes again from the relationships of the eastern Asiatic and eastern North American floras. Such vicarious species may be differentiated by morphology or by chemistry of secondary natural products or by both.

Morphologically differentiated:

Anzia colpodes (Ach.) Stizenb. in eastern North America; *A. colpota* Vain. in Japan.
Cladonia caroliniana (Schwein.) Tuck. in eastern North America; *C. nipponica* Asah. in Japan.
Parmelia rudecta Ach. in eastern North America; *P. ruderata* Vain. in Japan.
Umbilicaria mammulata (Ach.) Llano in eastern North America; *U. esculenta* (Miyoshi) Minks in Japan.

Chemically (and in some also morphologically) differentiated:

Cladonia evansii Abb. (atranorin and accessory usnic acid) in eastern North America; *C. pseudevansii* Asah. (usnic acid) in Japan.
Cladonia atlantica Evans (baeomycesic and squamatic acids) in eastern North America; *C. hondoensis* Asah. (barbatic acid) in Japan.
Cladonia cristatella Tuck. (barbatic and didymic acids) in eastern North America; *C. pseudomacilenta* Asah. (squamatic acid) in Japan.
Cladonia uncialis (L.) Wigg. (accessory squamatic acid) in eastern North America; *C. pseudostellata* Asah. (hypothamnolic acid) in Japan and Alaska.
Cladonia cylindrica (Evans) Evans (grayanic acid) in eastern North America; *C. norikurensis* Asah. (merochlorophaeic acid) in Japan.
Cladonia didyma (Fée) Vain. (barbatic acid) in eastern North America; *C. pseudodidyma* Asah. (accessory bellidiflorin) in Japan.

The title of this section implies that the divergence that produced the ten species pairs listed above took place after rather than before isolation by disjunction. It could be argued, however, that all these species were present throughout the extent of the Tertiary forest and that in each pair, *A* and *B*, *A* became extinct in Asia and *B* became extinct in North America. This explanation cannot be categorically ruled out for some of the vicariad pairs. But it makes an unconvincing explanation for the whole list, because one would not expect every pair of micro- or sibling species to have followed such a pattern of reciprocal extinctions. There should be at least a few pairs of microspecies still present in both places but not found elsewhere—yet I know not a single example.

2. *Ubiquitous collective species.*—Disjunctions in wide-spread collective species may lead to sufficient differentiation of the isolated populations that the regional elements are recognized taxonomically. Morphological (as opposed to chemical) differentiation can be seen in the common reindeer lichen, *Cladonia rangiferina* (L.) Web. subsp. *rangiferina* (circumboreal), and its regional derivatives subsp. *grisea* Ahti (eastern Asia), var. *abbayesii* Ahti (Mexico, Central America), and var. *vicaria* (Sant.) Ahti (Patagonia, Antarctica). Three common, closely related umbilicate lichens appear to owe their differentiation to past disjunction: *Lasallia pustulata* (L.) Mér. is common in Europe and rare in northern North America, *L. papulosa* (Ach.) Llano is common in subboreal and higher-elevation temperate eastern North America, and *L. asiae-orientalis* Asah. represents the complex in Japan.

The most enigmatic differentiations to be seen in widely distributed collective species are chemical ones. The already mentioned *Parmelia hypoleucina* J. Stein. occurs in the Mediterranean Basin and southern California and very abundantly on the Atlantic Coastal Plain from Cape Cod to Mississippi. But throughout the east-central section, from central Texas to southern New York and northern Georgia, the morphologically indistinguishable *P. hypotropa* Nyl. abounds and is one of the commonest of all eastern North American lichens outside the Coastal Plain. Phenotypically *P. hypotropa* differs from *P. hypoleucina* in being unable to convert its most abundant secondary natural product, norstictic acid, to stictic acid as *P. hypoleucina* does. Although this chemical change is a minor one—a one-step methylation that could conceivably be mediated by a single enzyme controlled by a single gene—the demonstrable but small chemical difference in the two populations must be linked to factors governing prodigious differences in physiological potential. *Parmelia hypotropa*, the dominant North American representation of the complex, seems to have been derived from the much older and (on a world-wide scale) still more widely distributed one.

An even more enigmatic case of chemical differentiation perhaps related to disjunction can be seen in the genus *Thamnolia*, which is monotypic or ditypic depending upon the weight assigned to chemistry. In spite of being totally asexual, *Thamnolia* is one of the most successful of all lichen genera, occurring abundantly on bare soil and among herbs throughout the arctic and alpine regions of the world. Individuals belong to one or the other of two chemical types: they produce either a pair of β-orcinol-type *para*-depsides (baeomycesic and squamatic acids) or a β-orcinol-type *meta*-depside (thamnolic acid). The constituent(s) of a given specimen can be determined only by appropriate chemical analysis, and consequently the abundant representation of the genus in herbaria constitutes a world-wide random sample of the chemical variation. By testing herbarium specimens Sato (1968) demonstrated that the *para*-depsides are produced exclusively or more commonly in populations in the northern hemisphere while the *meta*-depside is produced exclusively or more commonly in populations in the southern hemisphere, even though most populations in both

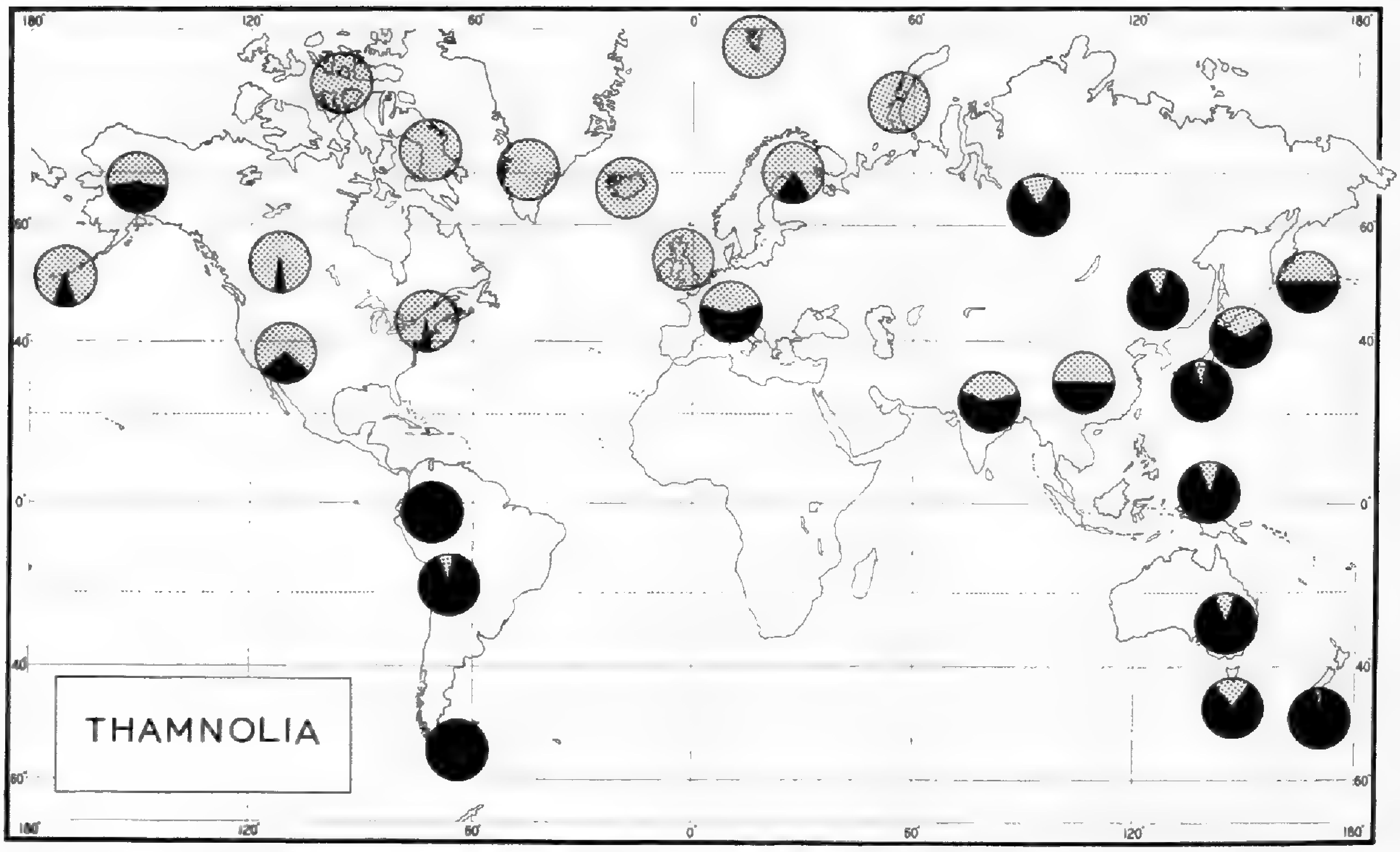

FIGURE 2. The proportion of the *Thamnolia* vegetation in various parts of the world consisting of *para*-depside producers (stipple) [= *T. subuliformis* (Ehrh.) Culb.] and *meta*-depside producers (black) [= *T. vermicularis* (Sw.) Ach. *ex* Schaer.]. Redrawn from Sato (1968).

hemispheres contain both chemical types (Fig. 2). Are these differences to be interpreted as coming from an allopatric differentiation in populations that have subsequently become extensively sympatric? The chemical differences involved are sufficiently complex that they would seem to reflect more than a superficial genetic modification and to require more than a simplistic explanation.

DISJUNCTION AND CONTINENTAL DRIFT

Although certain Old World-New World lichen distributions may owe their origin to the ancient connection of these land masses, long-distance dispersal usually seems a more reasonable explanation. One body of information, however, can be interpreted only in relation to the now known geological events that produced the Atlantic Ocean.

Parmelia subgen. *Amphigymnia* is a natural, well defined taxon of 106 species. Its botany and chemistry are well known thanks to Hale's (1965) recent monograph, and the plants are so large and conspicuous that they are well represented in herbaria. Figure 3 shows the number of species that occur in various parts of the world and the number of species endemic there. It will be noted that most of the species occur in Africa (64 species: 60% of the total), South America (51; 48%), Central America and Mexico (47; 44%), and North America (25; 24%). Thirty (28%) of the species are endemic to the New World, 22 (21%) are endemic to Africa, and 7 species are found only in tropical America and Africa. Fewer species occur in Europe (8; 8%) and Australia-New Zealand (17; 16%), and none of these are endemic. Most of the southern Asiatic and Pacific representation is drawn from the group of 26 pantropical species. Significantly 21 (81%) of the pantropical

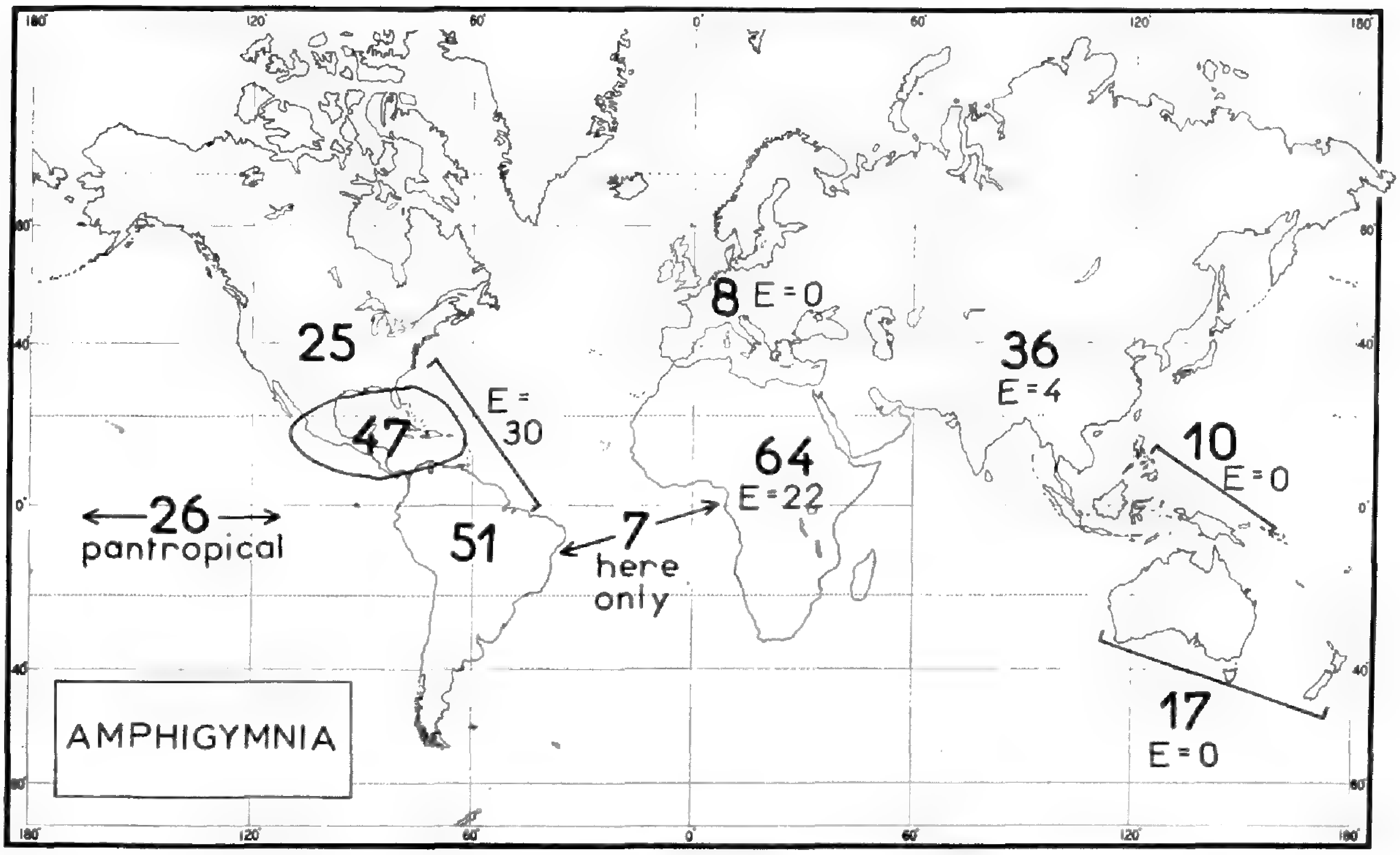

FIGURE 3. The numbers of species of *Parmelia* subgen. *Amphigymnia* in various parts of the world (larger-size numbers) and the number of endemic (*E*) species in each region (smaller-size numbers). Seven species are found only in Africa and South America. Data taken from Hale (1965).

species produce asexual propagules. *Parmelia* subgen. *Amphigymnia* must have been well differentiated before the New World separated from the Old some 100 million (?) years ago and its present disjunctive distribution is due primarily to historical events and secondarily to long-distance dispersal.

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DISJUNCTIONS IN BRYOPHYTES

W. B. Schofield[1] and H. A. Crum[2]

Abstract

In spite of the more general distribution of many bryophytes, dramatic disjunctions exist, many of them similar to those shown by vascular plants. Various explanations have been offered to explain these disjunctions including continental drift, long-distance dispersal, and the fragmentation of a once more continuous distribution. No single hypothesis is sufficient to accommodate all species within any disjunctive pattern. The most serious difficulty is the inadequacy of exploration of considerable areas of the globe.

Various bryophyte disjunctions are mapped in 51 distribution maps, and details of sexual patterns and dispersal mechanisms are assessed.

Most bryophytes are widely distributed. In the Northern Hemisphere more than 60% of the flora of arctic and boreal regions is made up of the same species. Within this wide range, however, each species has highly specific requirements and some are exceedingly local.

Because bryophytes have air-borne diaspores their means of dissemination would appear to guarantee a wide distribution of all species. That disjunctions exist at all would seem somewhat anomalous, yet such disjunctions do exist, some of them very dramatic. The explanation of these disjunctions has led to numerous intriguing hypotheses, many of which have been derived from similar studies of flowering plant disjunctions.

In North America the disjunctions that have received the greatest attention are eastern American–East Asian disjuncts (Iwatsuki, 1958*a*, 1958*b*, 1958*c*; Iwatsuki & Sharp, 1967, 1968; Sharp & Iwatsuki, 1965. See Maps 1–7); tropical and subtropical taxa in the Southern Appalachians (Anderson, 1951; Andrews, 1920; Billings & Anderson, 1966; Crum, 1966; Sharp, 1936, 1938, 1939, 1941. See Maps 8–9); amphi-Pacific taxa (Ando, 1966; Ando, Persson & Sherrard, 1957; Crum, 1965; Hattori, 1952, 1963, 1966*b*; Hattori & Sharp, 1968; Hattori *et al.*, 1968; Horikawa & Ando, 1957; Lazarenko, 1957; Noguchi & Saito, 1970; Persson, 1946*a*, 1946*b*, 1947, 1949, 1952, 1958, 1962, 1968; Persson & Gjaervoll, 1957; Schofield, 1962, 1965, 1966*a*, 1966*b*, 1966*c*, 1968*a*, 1968*b*, 1969; Sharp & Hattori, 1967; Steere, 1969; Steere & Schofield, 1956; Steere & Schuster, 1960. See Maps 10–20); bipolar disjuncts (Martin, 1946, 1949, 1952*a*, 1952*b*; Du Rietz, 1940; Sainsbury, 1942; Schuster, 1969. See Maps 21–22); taxa disjunctive between Europe and western North America (Abramova & Dildarin, 1969; Evans, 1914; Harvill, 1950; Haynes, 1915; Koch, 1956; Paton, 1966; Schofield, 1968*a*, 1968*b*, 1969; Whitehouse, 1961, 1963. See Maps 23–33); amphi-Atlantic taxa (Andrews, 1938, 1961; Maass, 1965, 1966*a*, 1966*b*; Schuster, 1962; Sharp, 1941. See Maps 34–37); and arctic-alpine taxa, that have received surprisingly little attention (Gams, 1955; Schuster, 1958*a*, 1958*b*; Steere, 1937, 1938, 1953, 1965. See Maps 38–40).

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Ann. Missouri Bot. Gard. 59: 174–202. 1972.

Irmscher (1929) studied moss disjunctions particularly in their contribution to an insight reflecting plant distributions as influenced by continental drift. Herzog (1926) in his monumental *Geographie der Moose* treats bryophyte disjunctions briefly. Details from other areas are treated by Abramova & Abramov (1969), Bowers (1970), Croizat (1962, 1966), Crum (1966), Crum & Anderson (1964), Fulford (1951), Greig-Smith (1950), Horikawa (1955), Koch (1954), Lazarenko (1957), Müller (1916, 1954), Schelpe (1969), Schofield (1969), and Schuster (1967, 1968, 1969).

Hypotheses explaining these disjunctions have been based mainly on historical factors. In most cases the opinion is that these various disjunct populations represent remnants of a more continuous distribution of the past, always placed preceding the Pleistocene glaciations and usually suggested to be as early as the Tertiary. Information from fossil bryophyte material is generally sparse; thus the assumption is made that bryophytes were associated with a vascular vegetation which exhibited a more continuous distribution during the Tertiary.

One bryophyte showing disjunctive European–western North American distribution is *Claopodium whippleanum* (Noguchi, 1952. See Map 33). The species is also present in the Hawaiian Islands. Abramova and Abramov (1969) indicate that they discovered it as fossil material from Middle Pliocene deposits in the Caucasus region. In Europe the species is presently restricted to a number of localities in Portugal and Spain. Another species of similar distribution, but with the Caucasus showing the only extant European population, is *Crumia latifolia* (see Map 26). This is discussed by Abramova and Dildarin (1969). These distributions strongly suggest a more continuous distribution of the past.

Remarkable features of a high proportion of disjunctive species is that they are dioicous and in many cases produce no specialized propagula that would make them readily disseminated. This complete reliance on asexual reproduction by simple fragmentation leads to a paucity of biotypes. These combined features mean that the disjuncts tend to be, within their disjunctive areas, highly localized as relatively small populations with very specific environmental requirements. In most cases they are very poor competitors with the more generally distributed flora and are often confined to sites that are continually undergoing ecesis (Lye, 1967).

Areas particularly rich in disjunctive taxa often have hyperoceanic climates. This subject has been treated thoroughly by Ratcliffe (1968) and Størmer (1969) in particular, but also discussed by Amann (1929), Billings and Anderson (1966), Courtejaire (1962), Gaume (1952–1954), Iwatsuki (1958*a*), Lye (1967), Nicholson (1930), Persson (1949), Schuster (1962), and Touffet (1964).

The areas richest in disjunctive species confined largely to hyperoceanic climates are: Britain and Norway, the Faeroes, the Alps, the Himalayas, high mountains of Japan and Taiwan, North Pacific North America, and to a certain degree, high mountain slopes in the Hawaiian Islands. In some cases identical disjunctive species are found in many of these widely separated areas, for example: *Geheebia gigantea* (Map 41), *Mastigophora woodsii* (Map 42), *Scapania ornithopodioides* (Map 43), *Anastrepta orcadensis* (Map 44), *Anastrophyllum donianum* (Map 45), *Pleurozia purpurea* (Map 46), *Bazzania pearsonii*, *Cephaloziella pear-*

sonii, Campylopus atrovirens, and others. Species of the East Asian–eastern American disjunction, the European–western American disjunction and amphi-Pacific disjunction are also largely of oceanic climates.

In the Southern Hemisphere disjunctions are also richly represented in hyperoceanic climates: the southern Australasian–southern South American disjunction is the most pertinent example, shown in Maps 47–48 (see especially Schuster, 1969).

Disjuncts of more arid climates are equally dramatic: thus the isolation in Australasia and South Africa represented by *Carrpos sphaerocarpos* (Map 49) of arid salt pans and *Pottia maritima* (Map 50) of sandy sites. These species, however, are either very rare or are overlooked because of their inconspicuousness. As Schelpe (1969) has shown, the number of bryophytes of this disjunctive pattern may increase as both areas become better collected.

Species of mediterranean climates exemplify yet another type of disjunction. *Neckera menziesii, Antitrichia californica* (Map 32), *Funaria muehlenbergii,* and *Bartramia stricta* are particularly good examples. The *Neckera* is largely mediterranean in Eurasia and North Africa but in western North America is both in mediterranean and more humid climates, but in the more humid climates is confined largely to edaphically dry calcareous rock; it is rare in Japan. *Antitrichia* shows a similar pattern but is absent from Japan.

As has been noted (Sharp, 1938; Schornherst, 1943), many bryophytes of tropical affinity disjunctive in more northern areas tend to be calcicoles. Considering the Florida moss flora, Schornherst (1943) suggests that this may be the result of the frequency of this habitat in the tropics, thus the selection favoring bryophytes of this specificity.

In spore-producing plants there is an obvious temptation to state that long-distance dispersal is especially important. Spore size enhances wind-dispersal and air transport of spores is necessary even in short-distance dissemination of most spore-bearing plants.

In bryophytes it is apparent that long-distance dispersal is not only possible, but in some cases probable. Certainly the taxa of volcanic oceanic islands reached their present sites via long-distance dispersal. Although published analyses of the Hawaiian bryoflora are lacking, this archipelago could serve as a particularly important source of information concerning long-distance dispersal in bryophytes. The archipelago is relatively youthful, emerging no earlier than the Late Tertiary, thus has been available for colonization for approximately ten million years. A number of disjunctive bryophytes are of particular interest: *Cyrtopus setosus* (Map 48) is otherwise a species of the Southern Hemisphere. Dixon (1922) has established the authenticity of the Hawaiian collection of the species, but it has not been recollected recently. The hyperoceanic taxa *Scapania ornithopodioides* (Map 43) and *Anastrepta orcadensis* (Map 44), in particular, are of considerable significance. These are both dioicous and sporophytes are rare or unknown. Gemmae are present in only the *Anastrepta,* and the *Scapania* has no specialized vegetative disseminules. It must be assumed that the species did produce sporophytes in the past, and it would be reasonable to assume that the species were then more widespread. If rare, even in the past, their chances of establishing their many widely disjunct populations would be so greatly reduced as to be unreasonable. The added problems of disseminules taken from the parental population of a humid environment, drawn into updraughts of air and then carried to a favourable site (which for these species is highly specialized) make the chances of long-distance dispersal even more unlikely. Yet the species are present in areas that they could not have reached except by wind-dispersal from sources a considerable distance away.

Størmer (1969) has outlined a clear instance of long-distance dispersal in the moss *Orthodontium lineare*. Although not so spectacular as the Hawaiian disjunction, this case is well documented. *Orthodontium lineare* was inadvertently introduced to the Liverpool district of Great Britain around 1911. The species has spread rapidly through Britain, by 1963 being present in most vice counties in England and reported also in Scotland and Ireland. In 1952 the species was reported from Holland, where "the spores must have been carried 300 km or more before they found suitable habitation" (Størmer, 1969). In 1939 the species was discovered in Germany, presumably derived from the British populations. In many cases, at least, the expansion of the range of this species must be ascribed to wind dispersal of the spores.

Considerable discussion was elicited by the paper of Petterson (1940) concerning the long-distance dispersal of the mosses *Aloina brevirostris* and *A. rigida* from Siberia to southwestern Finland, where he had recovered numerous spores of the species in rainwater. Persson (1944) and Bergeron (1944) have demonstrated the greater likelihood that the spores originated from nearby Scandinavian populations. The fact that moss spores serve as nuclei for rain drops is of particular importance, however, and should not be overlooked. The discussions of both Bergeron (1944) and Gregory (1945) are especially rich in information concerning dispersion of air borne spores.

In a few cases bryophytes are disjunctive because they have been introduced to their widely separated localities through man's activities. The hepatics *Lunularia cruciata* and *Marchantia polymorpha* are common greenhouse weeds and are widely dispersed throughout the world because of this. More precisely documented cases are those for *Tortula stanfordensis* (Map 31) and *Pseudoscleropodium purum* (Map 51). The *Tortula* was described by Steere (1951) from the San Francisco Bay Region of California where it is widely distributed on hard clayey soil both near habitations and in the native vegetation. Paton (1966) reported this species from southern Britain. More recently further details have appeared concerning its British distribution (Whitehouse, 1961; Whitehouse & Paton, 1963). In the latter publication the authors state "since both Mousehole and Gulval are centres for the horticultural and market gardening industries, it seems possible that *Tortula stanfordensis* may have been accidentally introduced to one or both of these areas from California." It is suggested that it might have been introduced in soil of planted trees originating from a Californian nursery.

For *Pseudoscleropodium* the disjunctions are equally interesting and are discussed by Dickson (1967); details for the western American localities are given by Lawton (1960) and Schofield (1965), while the New Zealand populations are discussed by Sainsbury (1935, 1955). Dickson states that the species was probably

TABLE 1. Sexuality of disjunct bryophyte taxa. A plus sign (+) indicates that most disjunctive species are sterile. An asterisk (*) indicates that the species is consistently or usually sterile.

Monoicous	Dioicous
Desmatodon randii	*Pterogonium gracile*
Pottia maritima	*Echinodium* (the genus)
Sphagnum junghuhnianum (also dioicous)	+ *Myurium* (the genus)
Grimmia olympica	*Phyllogonium* (the genus)
Aulacomnium heterostichum	*Drepanocladus uncinatus*
Buxbaumia minakatae	*Hylocomium splendens*
Hookeria lucens	*Cyrtopus setosus*
Cephaloziella turneri (also dioicous)	* *Tortula caroliniana*
* *Pleurozia purpurea*	* *Leptodontium orcuttii*
	* *Gollania turgens*
	Sphagnum junghuhnianum (also monoicous)
	+ *Acanthocladium* (sect. *Tanythrix*)
	Oligotrichum hercynicum
	* *Geheebia gigantea*
	Drummondia prorepens
	* *Homaliadelphus sharpii*
	* *Schwetschkeopsis fabronia*
	Atrichum crispum
	Sphagnum angermanicum
	* *S. pylaesii*
	* *Ditrichum zonatum*
	Plagiothecium undulatum
	* *Crumia latifolia*
	* *Leptodontium recurvifolium*
	Antitrichia californica
	Polytrichum sphaerothecium
	* *Acrobolbus ciliatus*
	* *Mastigophora woodsii*
	* *Anastrepta orcadensis*
	* *Scapania ornithopodioides*
	Bucegia romanica
	Porella cordaeana
	Cephaloziella turneri (also monoicous)
	* *Plagiochila japonica*
	* *Radula auriculata*
	Carrpos sphaerocarpos
	* *Ascidota blepharophylla*
	* *Anastrophyllum donianum*
	Haplomitrium hookeri
	* *Takakia ceratophylla*
	* *Macrodiplophyllum plicatum*
	* *Plagiochila carringtonii*

introduced to the south Atlantic islands of St. Helena and Tristan da Cunha as packing material of young trees. In western North America the species is a lawn weed and is always associated with human habitation, thus a probable introduction with nursery stock from Europe. The case for New Zealand is less clear, most populations being confined to areas near human habitation, but "the Tasman finding was in *Leptospermum* scrub and would be more likely to indicate an indigenous moss" (Sainsbury, 1955).

As mentioned earlier, a high proportion of disjunct bryophytes are dioicous. In some cases, the male plant is in one of the areas of disjunction and the female plant in another: *Acrobolbus ciliatus* (Map 7) is male in Japan, female in the Southern Appalachians. In such cases the only reasonable explanation for the disjunction is to assume that both arose from an originally continuous population. Why one sex should survive in one region and the other in the second is not readily explained. *Homaliadelphus sharpii* (Map 2) would appear to be sterile in North America but fertile in eastern Asia. However, dwarf male plants have been found in two North American populations, and therefore it is obvious that spores have been produced there, though indeed rarely.

In dioicous species of mosses specialized means of asexual production are no more frequent than in monoicous species whose ranges tend to be wider (Gemmell, 1952). The wider range of the monoicous species is presumably more a reflection of their spore dispersal than their greatly increased variability. As Gemmell (1950) has noted, it appears that many of the monoicous species are self-fertilized, greatly decreasing the possible variability that would be available through cross fertilization.

For species occupying open areas and in which either spores or gemmae are produced, the chances of wind dispersal are greatly improved, and in areas of relatively dry climates, the possibility of getting propagula air-borne is even greater. As Persson (1944) and Petterson (1940) have shown, such spores are air transported and can come to earth in rainfall some distance from their place of origin. The problem if their germination and survival in the place where they are deposited is much more uncertain. Since most bryophytes are ecologically restricted and conditions favoring germination and survival of propagula are highly critical, the chances that many air-transported propagula survive to establish a colony are very remote. The factors severely limiting the effectiveness of distance dispersal are discussed by Crum (1966, 1972).

A further complication is the fact that many disjunctive taxa are in hyperoceanic climates. This further decreases the opportunities for propagula to become air-borne in the rare cases when they are produced. Added to this is their restrictive ecology. Lye (1966) has emphasized that oceanic bryophytes are commonest "in localities where topography prevents both wind and sunshine from reaching high intensities."

It might be suggested that some bryophytes appear to be disjunctively distributed merely because collections have been inadequate in the intervening areas. Although this may prove to be true for a number of species now considered disjunctive, it is not likely to greatly decrease the number. In areas relatively thoroughly explored as for example, Europe, the disjunctive patterns have been maintained even after increased knowledge of the area. The absence of suitable habitats in the intervening areas also makes their possible presence in them very doubtful.

A knowledge of the details concerning continental drift is unlikely to be helpful in explaining most disjunctions in the Northern Hemisphere. In the Southern Hemisphere, however, Schuster (1969) suggests that the disjunctions are readily accommodated by the notion of a large Gondwanaland continent. It is also believed that many of the disjunctive taxa are extremely ancient, perhaps dating back to these earliest times. As frequently emphasized, bryophytes appear to be extremely conservative, controlled both by their inbreeding and by infrequency of sexual reproduction in many.

No single hypothesis can explain all disjunctions. Each hypothesis when applied to all disjuncts raises a number of serious questions.

First, assuming that long-distance dispersal is the answer:

1. Why has dispersal been so selective for taxa that now possess such inefficient means of dissemination and are presumably poor in biotypes?
2. Why should so many disjuncts be confined to oceanic environments?
3. Two areas possessing disjunctive species also have many species endemic to them that are widespread there, ecologically diverse and have ready means of air-dissemination, yet in both cases these species have not reached the other disjunctive area. The problem is: why not?

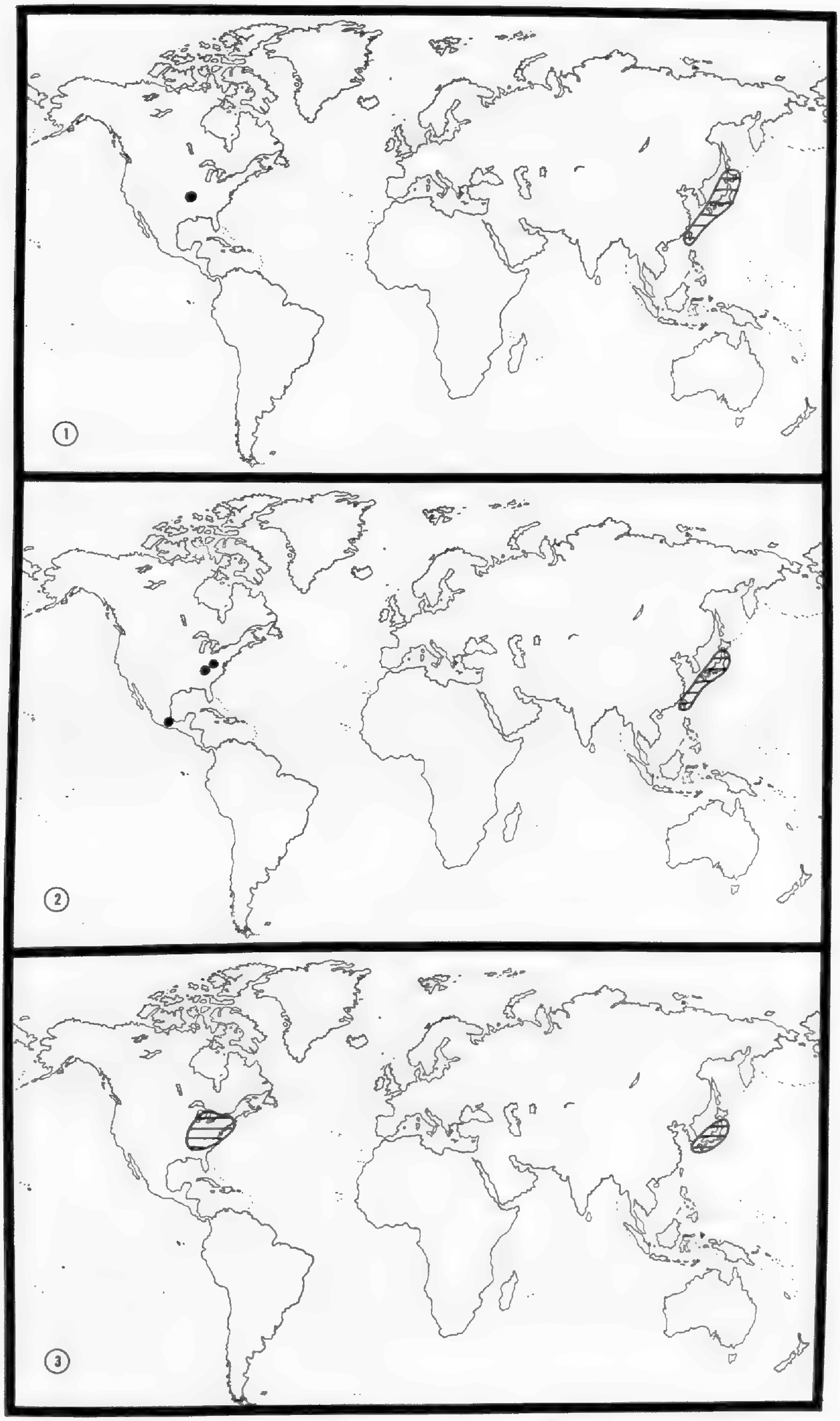
Second, assuming that the disjunctive bryophytes represent remnants of an ancient flora that has persisted in or near the present location of the disjunctive population:

1. Why should some of the disjunctive species now exist in areas that have been available for only the time since the Pleistocene glaciations?
2. Since a number of disjuncts that presently lack any diaspores that are readily air-transported are now present on oceanic islands where they must have arrived by air, why could not other disjuncts have reached their sites in the same manner?

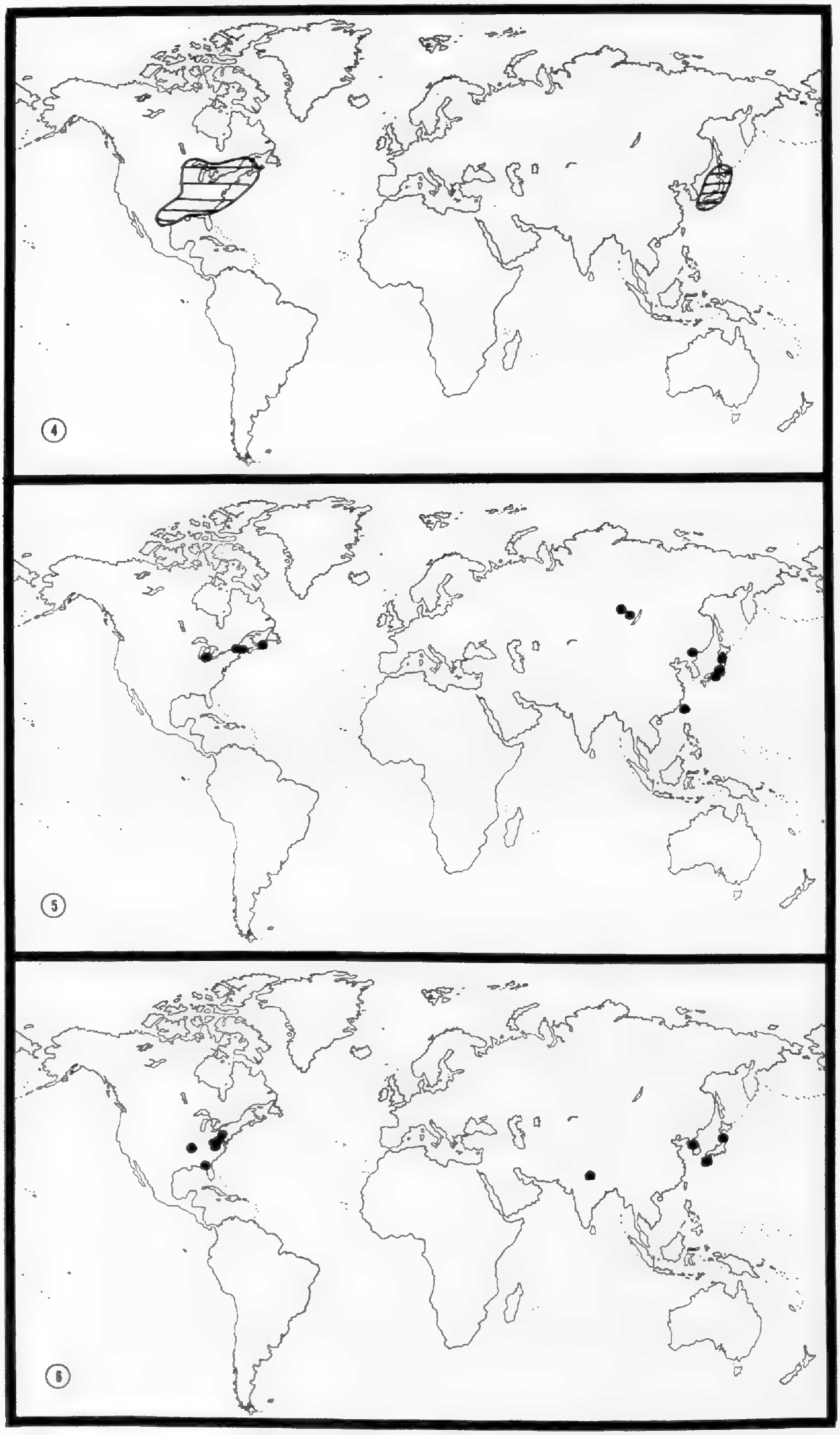
Third, assuming that continental drift has led to the establishment of the disjunctions:

Although this would be satisfactory for the amphi-Atlantic species, it creates further difficulties in attempting to explain the western North American–western European disjunction and the eastern North American–eastern Asian disjunction. It also poses serious problems in explaining the amphi-Pacific taxa, since preceding continental drift, these continental masses would have been even more distant.

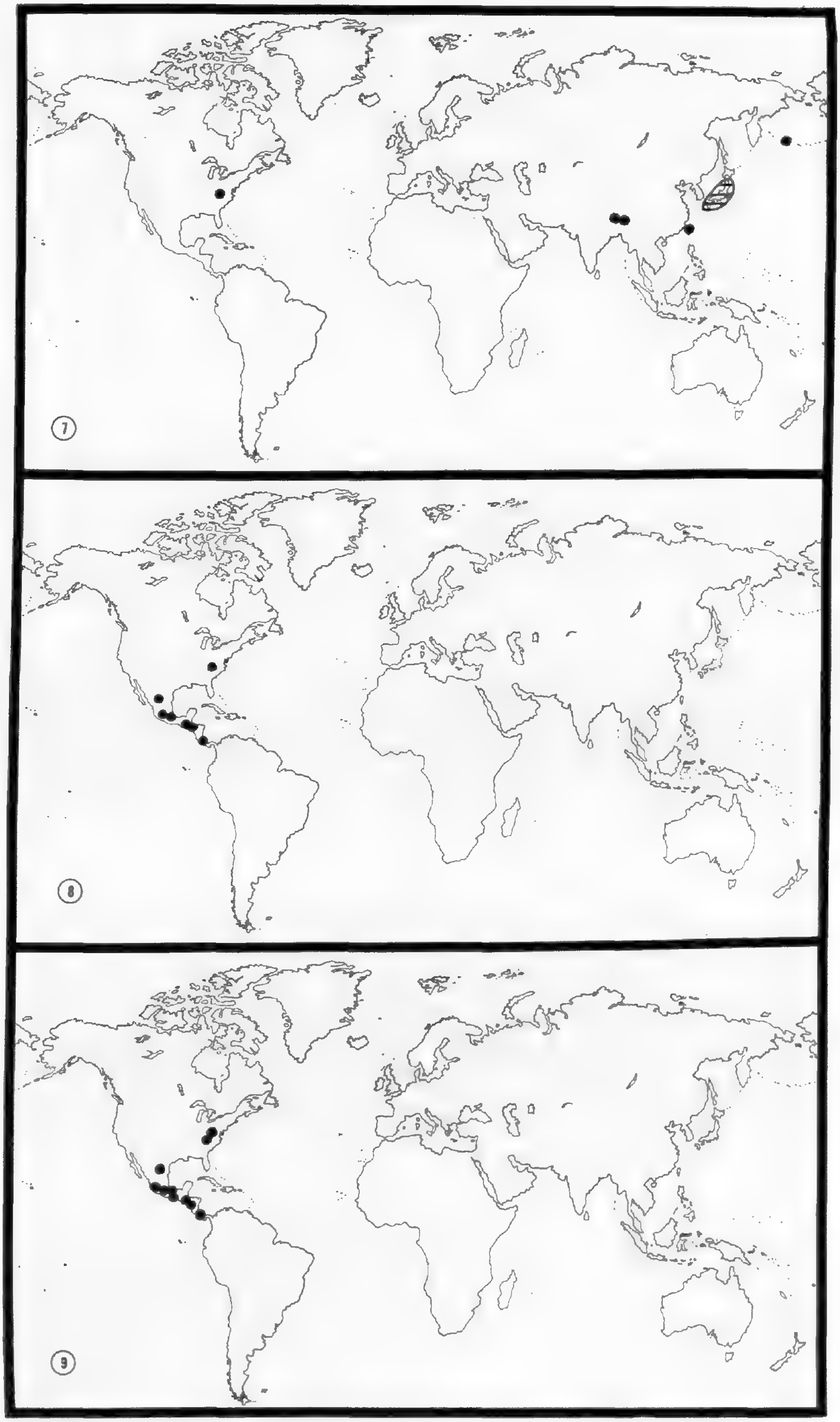
At present, then, there is no conclusive hypothesis that will explain all disjunctive distributions.



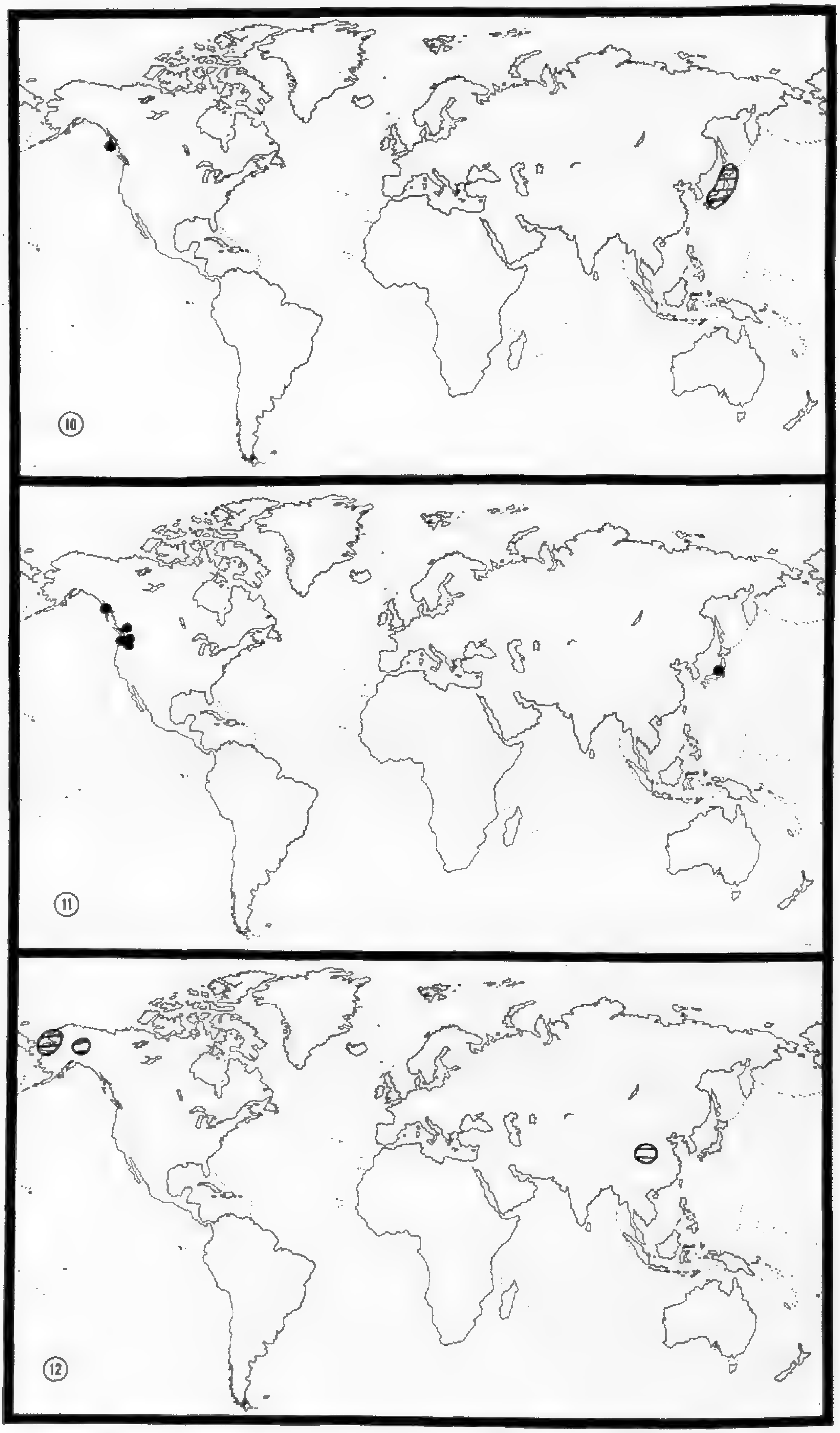
Maps 1–3.—Distribution of *Plagiochila japonica* Sande Lac. *ex* Miquel.—2. Distribution of *Homaliadelphus sharpii* (Williams) Sharp.—3. Distribution of *Drummondia prorepens* (Hedw.) Brid. (after Iwatsuki, 1958, in part).



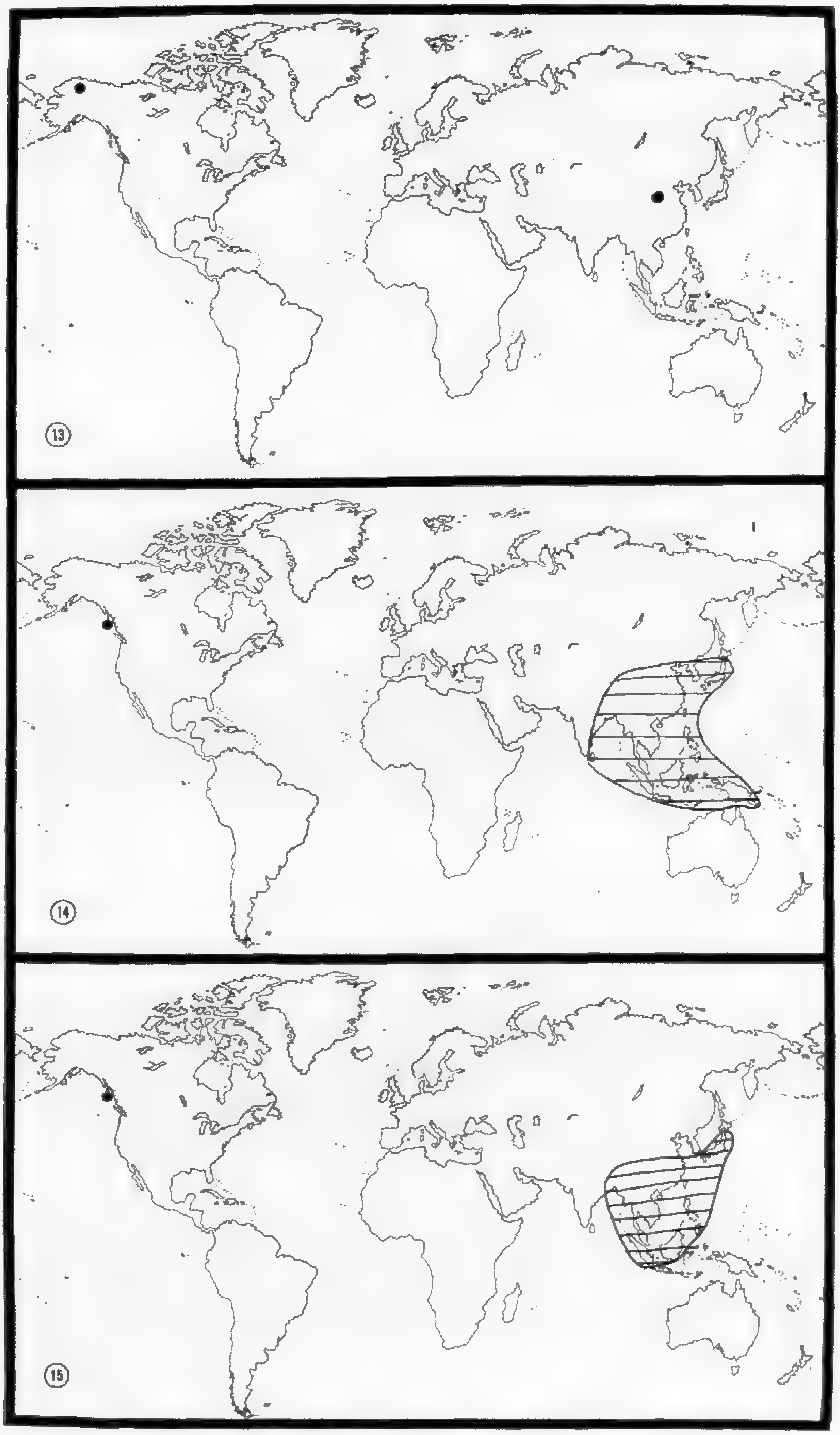
MAPS 4–6.—4. Distribution of *Aulacomnium heterostichum* (Hedw.) B.S.G. (after Iwatsuki, 1958, expanded).—5. Distribution of *Buxbaumia minakatae* O. Okam. (after Iwatsuki & Sharp, 1967).—6. Distribution of *Schwetschkeopsis fabronia* (Schwaegr.) Broth. (after Iwatsuki & Sharp, 1967).



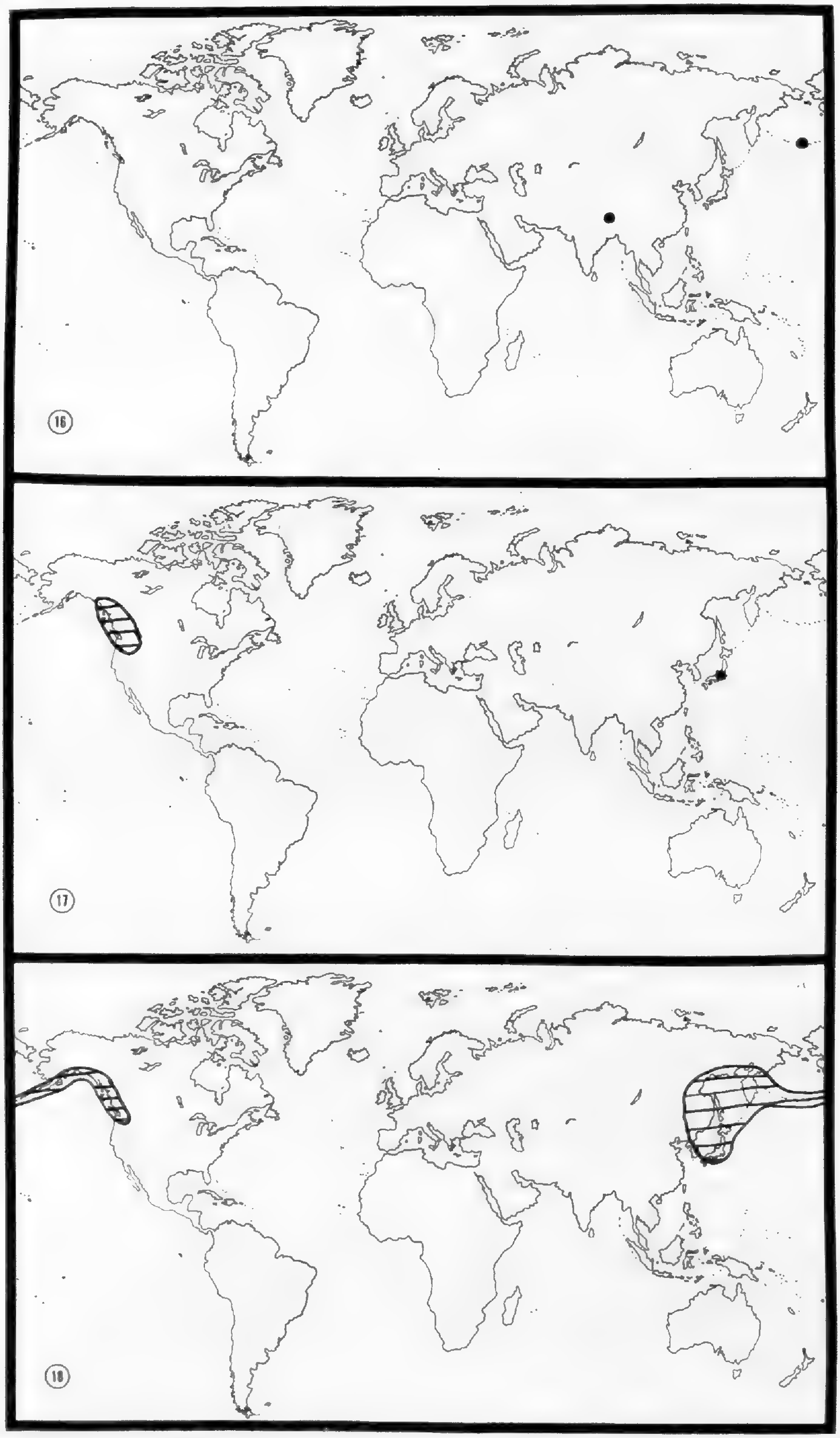
MAPS 7–9.—7. Distribution of *Acrobolbus ciliatus* (Mitt.) Schiffn. (from information in Sharp & Hattori, 1968).—8. Distribution of *Leptodontium orcuttii* Bartr.—9. Distribution of *Tortula caroliniana* Andr.



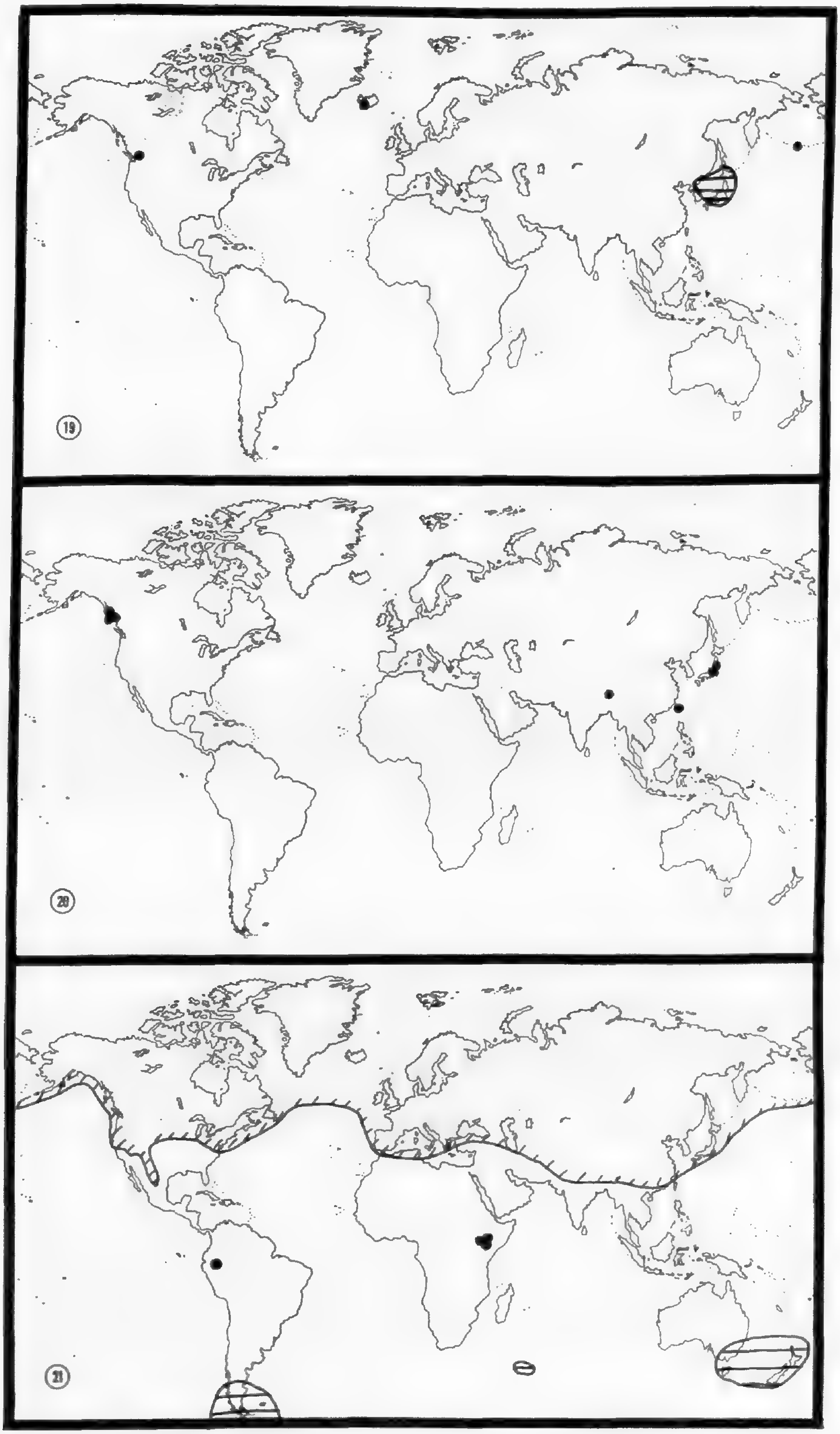
Maps 10–12.—10. Distribution of *Radula auriculata* Steph.—11. Distribution of *Grimmia olympica* Britt. *ex* Frye.—12. Distribution of *Gollania turgens* (C. Müll.) Ando (after Ando, Persson & Sherrard, 1957; Ando & Gjaervoll, 1961).



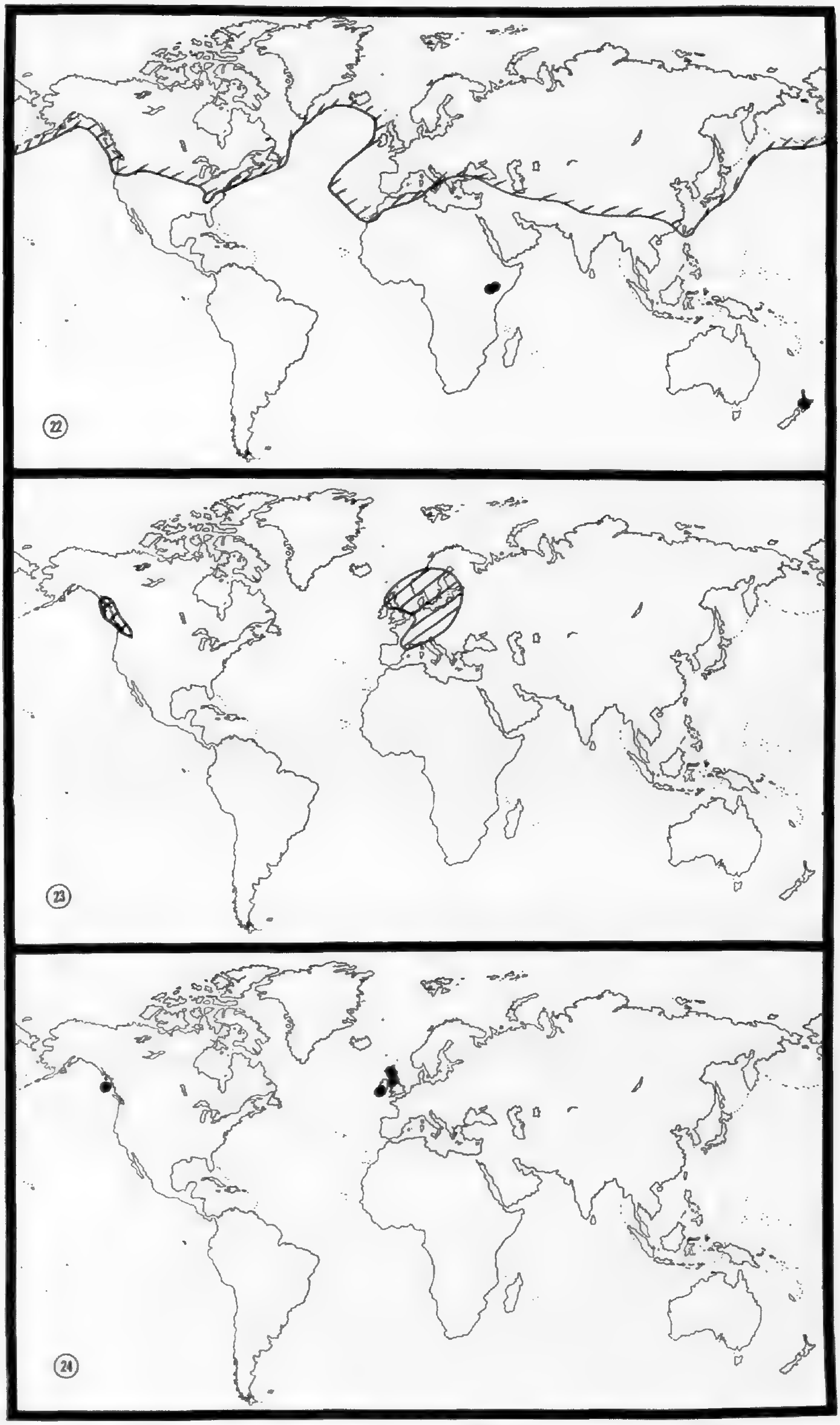
MAPS 13–15.—13. Distribution of *Ascidota blepharophylla* Mass.—14. Distribution of *Acanthocladium* (Sect. *Tanythrix*).—15. Distribution of *Sphagnum junghuhnianum* Dozy. & Molk.



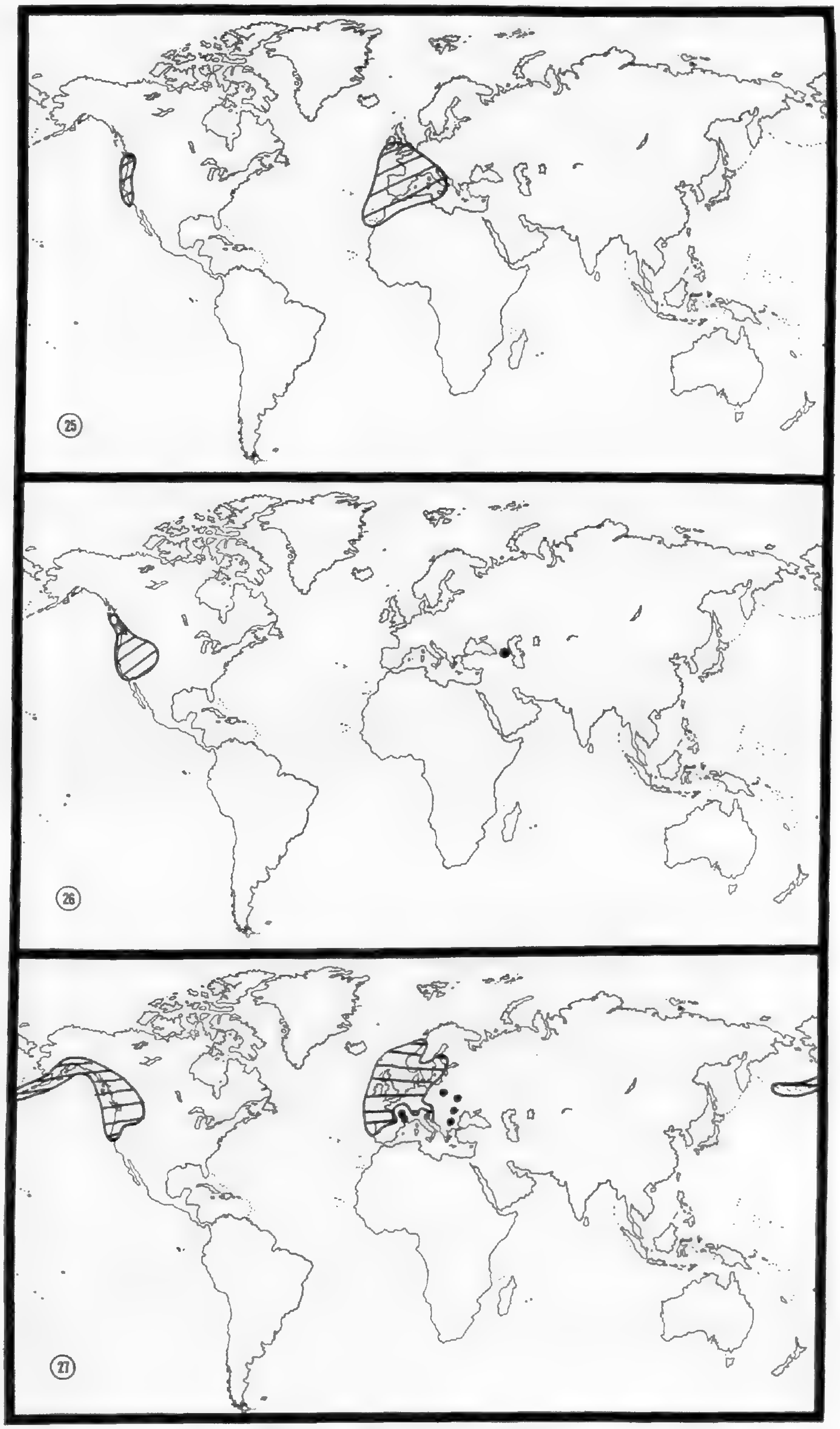
MAPS 16–18.—16. Distribution of *Takakia ceratophylla* (Mitt.) Grolle (after Hattori *et al.*, 1968).—17. Distribution of *Rhizomnium nudum* (Williams *ex* Britt. & Williams) Koponen.—18. Distribution of *Macrodiplophyllum plicatum* (after Horikawa, 1955, expanded).



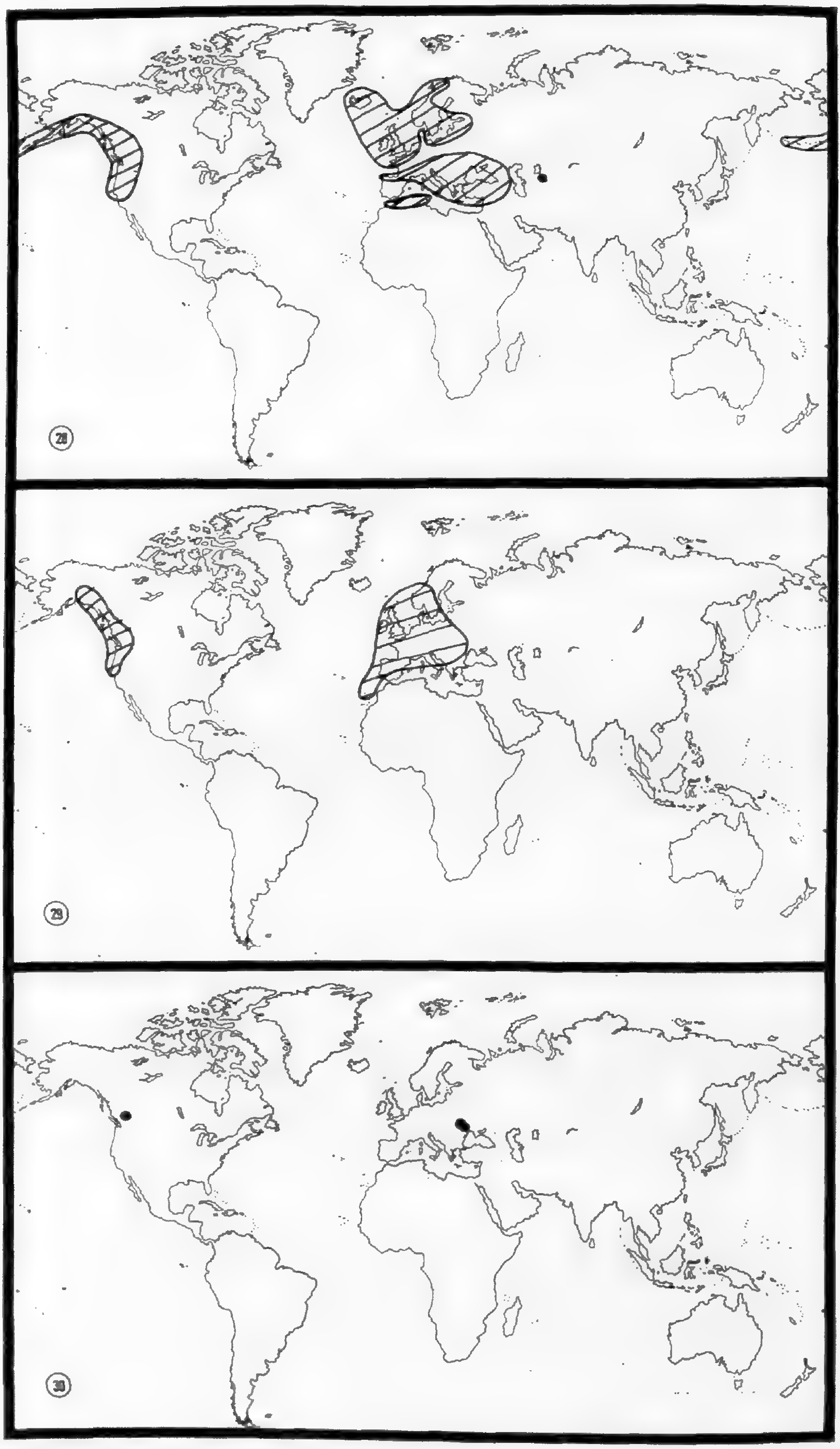
Maps 19–21.—19. Distribution of *Polytrichum sphaerothecium* (Besch.) Broth.—20. Distribution of *Treubia nana* Hatt. & Inoue (after Hattori *et al.*, 1966, expanded).—21. Distribution of *Drepanocladus uncinatus* (Hedw.) Warnst. (after Irmscher, 1929, expanded).



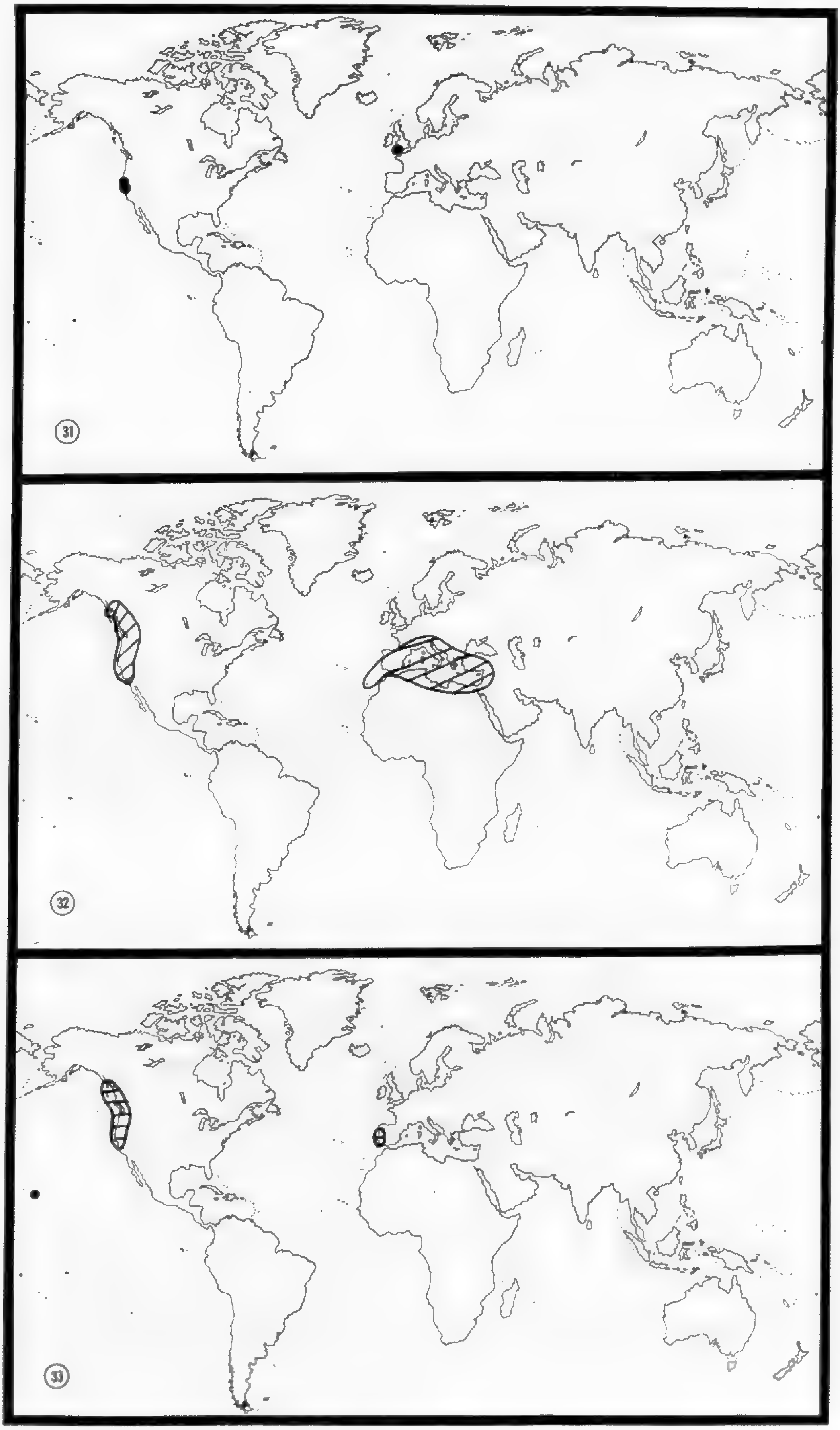
MAPS 22–24.—22. Distribution of *Hylocomium splendens* (Hedw.) B.S.G.—23. Distribution of *Ditrichum zonatum* (Brid.) Kindb.—24. Distribution of *Leptodontium recurvifolium* (Tayl.) Lindb.



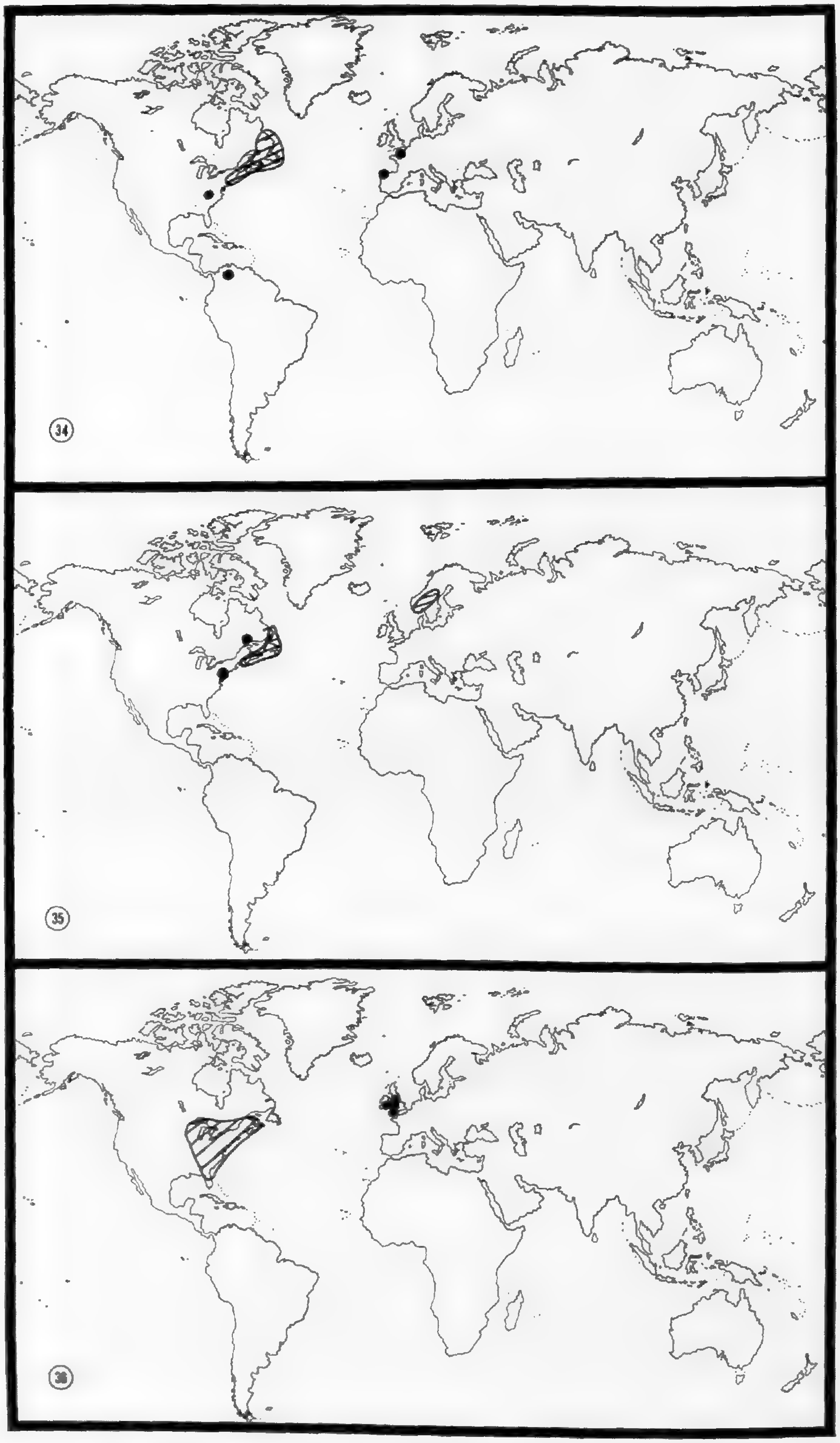
Maps 25–27.—25. Distribution of *Cephaloziella turneri* (Hook.) Müll.—26. Distribution of *Crumia latifolia* (Kindb. *ex* Mac.) Schof. (after Abramova & Dildarin, 1969).—27. Distribution of *Plagiothecium undulatum* (Hedw.) B.S.G. (after Ireland, 1969, Størmer, 1969).



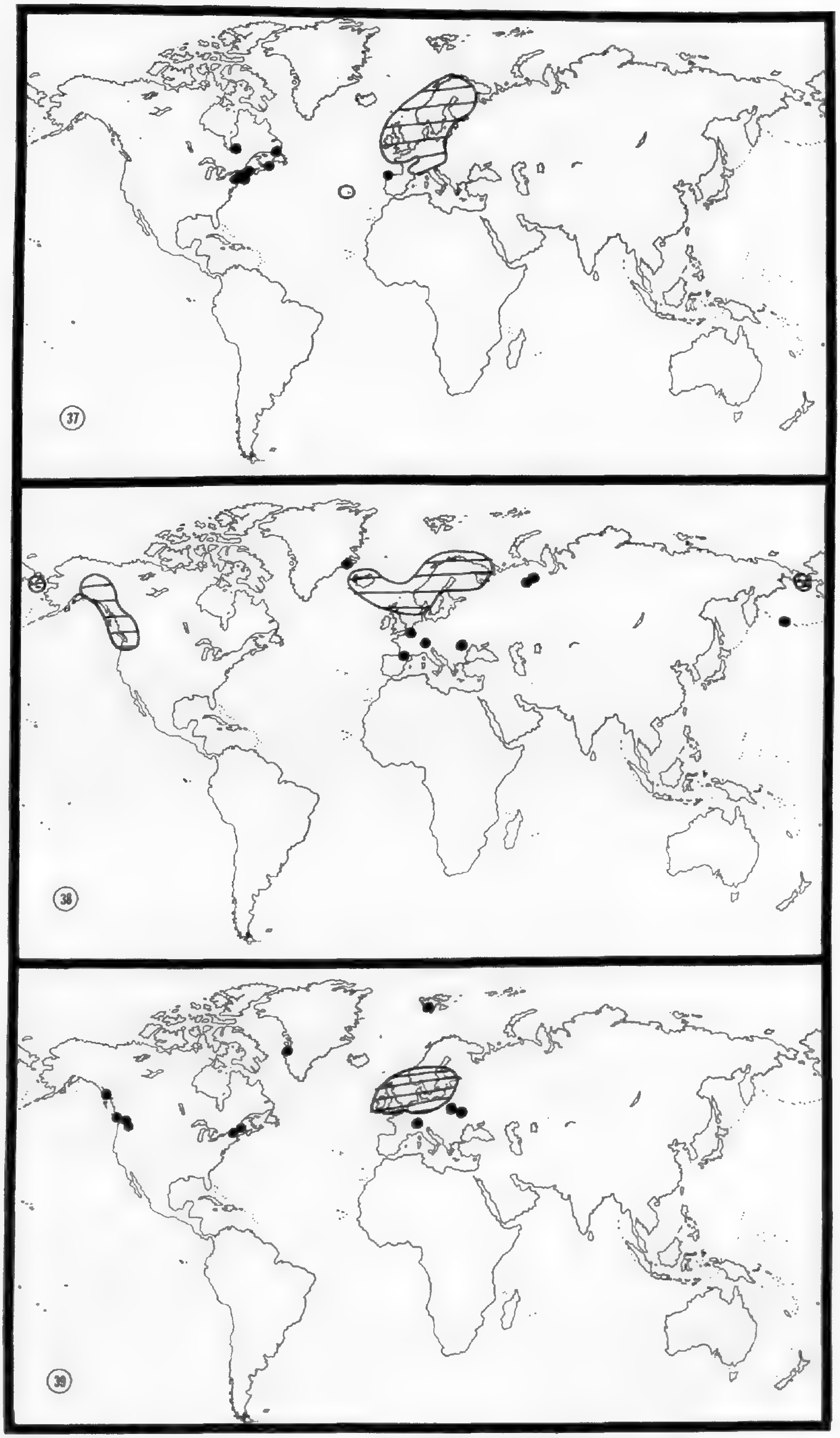
MAPS 28–30.—28. Distribution of *Porella cordaeana* (Hueb.) Evans (after Szwekowski, 1962).—29. Distribution of *Hookeria lucens* (Hedw.) Sm. (after Irmscher, 1929, modified; Størmer, 1969).—30. Distribution of *Bucegia romanica* Radian (after Szwekowski, 1964).



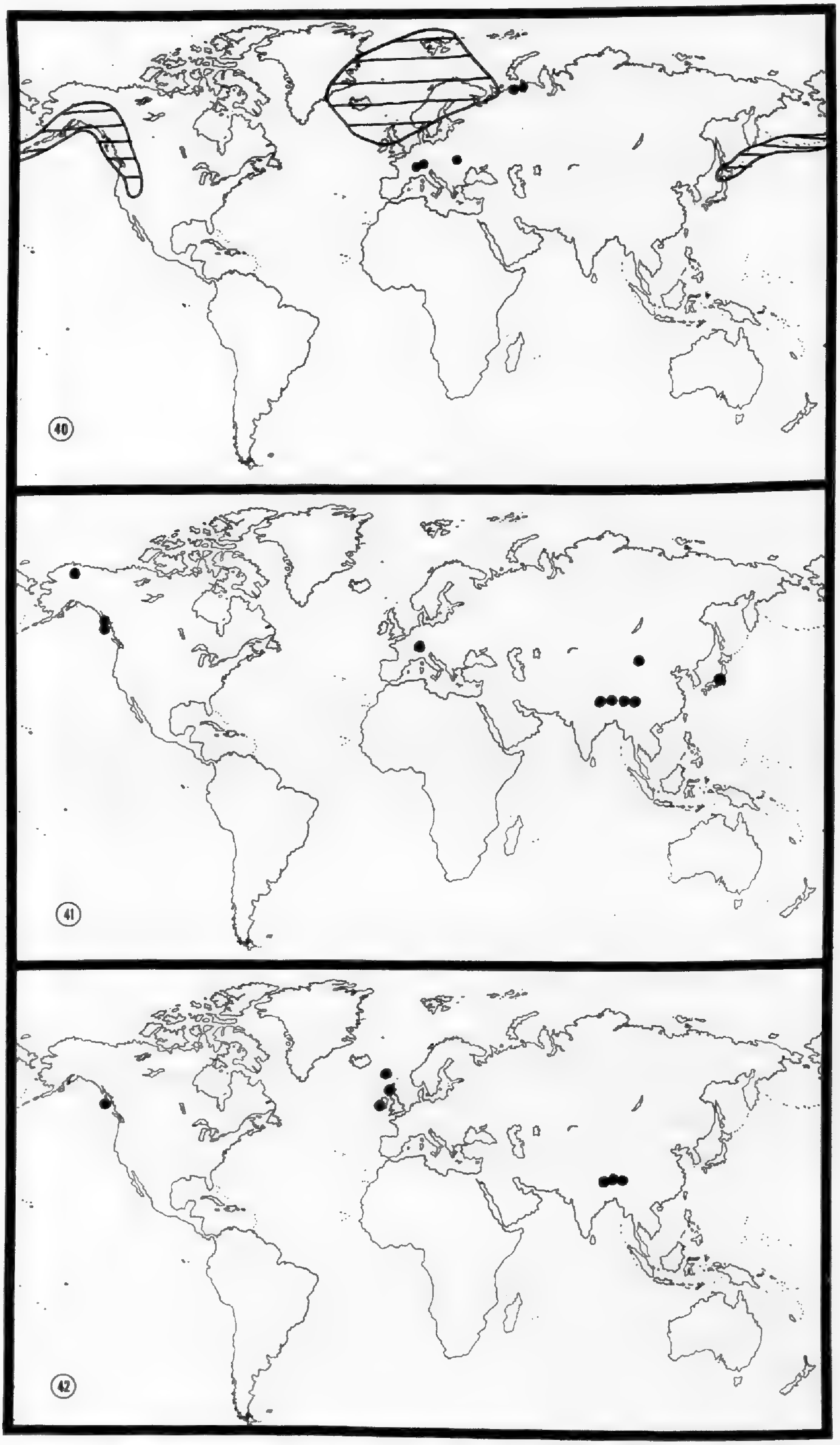
MAPS 31–33.—31. Distribution of *Tortula standfordensis* Steere.—32. Distribution of *Antitrichia californica* Sull. *ex* Lesq.—33. Distribution of *Claopodium whippleanum* (Sull.) Ren. & Card. (from Noguchi, 1952, expanded).



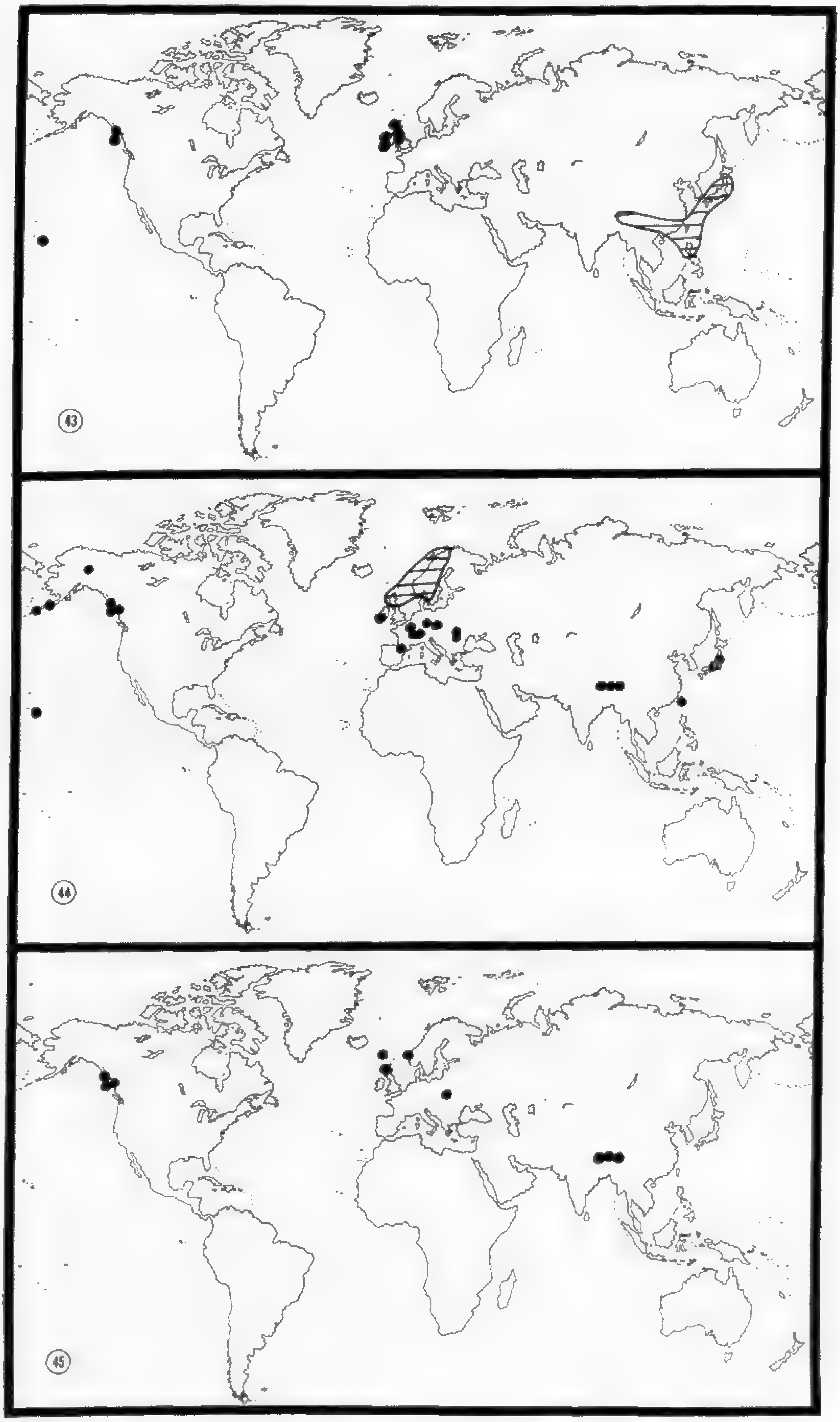
MAPS 34–36.—34. Distribution of *Sphagnum pylaesii* Brid. (from Maass, 1966*a*, 1966*b*). —35. Distribution of *Sphagnum angermanicum* Melin (supplied by W.S.G. Maass).—36. Distribution of *Atrichum crispum* (James) Sull. & Lesq. (after information in Ireland, 1969; Smith, 1966).



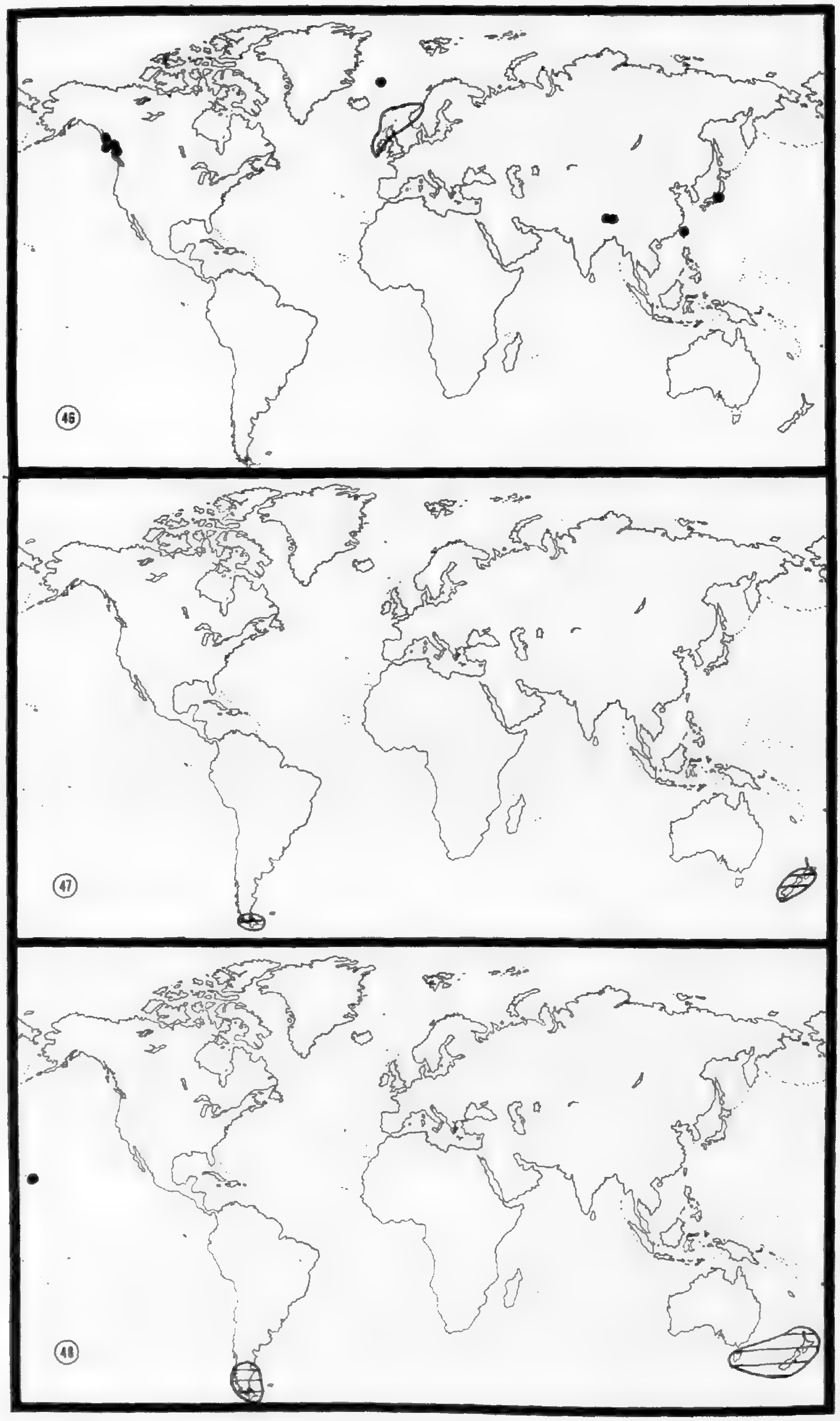
MAPS 37–39—37. Distribution of *Cladopodiella francisci* (Hook.) Dum. (after Szweykowski, 1964, expanded).—38. Distribution of *Oligotrichum hercynicum* (Hedw.) Lam. & DC.—39. Distribution of *Haplomitrium hookeri* (Sm.) Nees (after Szweykowski, 1966, expanded; Corely, 1970).



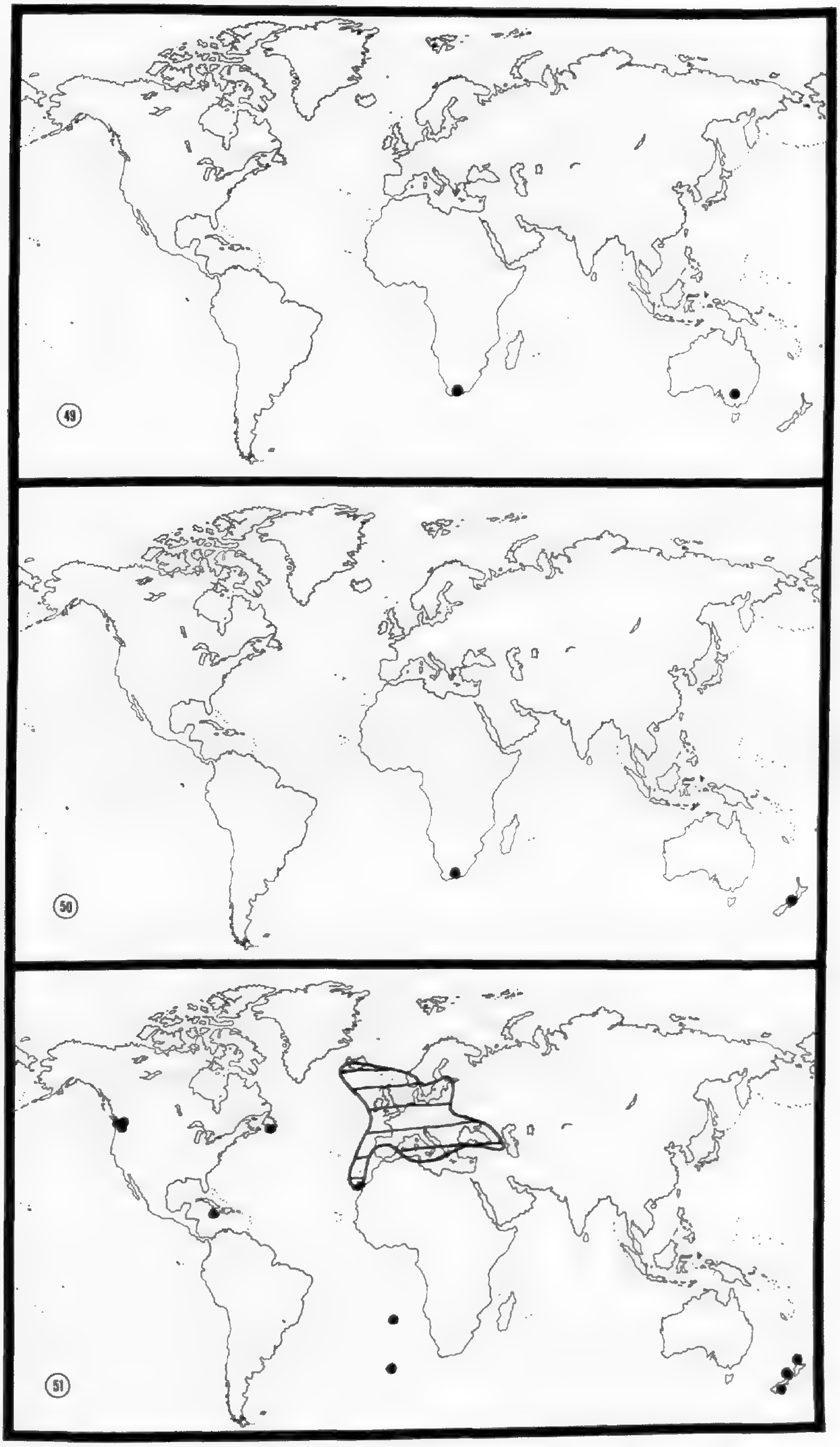
MAPS 40–42.—40. Distribution of *Pleuroclada albescens* (Hook.) Spr. (after Szweykowski, 1966).—41. Distribution of *Geheebia gigantea* (Funck.) Boul.—42. Distribution of *Mastigophora woodsii* (after Ratcliffe, 1963, in part).



Maps 43–45.—43. Distribution of *Scapania ornithopodioides* (With.) Pears. (after Ratcliffe, 1965, in part).—44. Distribution of *Anastrepta orcadensis* (Hook.) Schiffn. (after Szweykowski, 1964, expanded).—45. Distribution of *Anastrophyllum donianum* (Hook.) Spr. (after Szweykowski, 1966, emended; Ratcliffe, 1965, in part).



MAPS 46–48.—46. Distribution of *Pleurozia purpurea* (Lightf.) Lindb. (after Ratcliffe, 1969, in part).—47. Distribution of the genus *Phyllothallia* Hodgs. (after Schuster, 1969).—48. Distribution of *Cyrtopus setosus* (Hedw.) Hook.



Maps 49–51.—49. Distribution of *Carrpos sphaerocarpos* (Carr) Prosk.—50. Distribution of *Pottia maritima* (R. Br.) Broth. (after information in Schelpe, 1969).—51. Distribution of *Pseudoscleropodium purum* (Hedw.) Fleisch. (after Størmer, 1969, in part; Dickson, 1967).

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DISJUNCTIONS IN HOMOSPOROUS VASCULAR PLANTS[1]

W. H. Wagner, Jr.[2]

Pteridophyte geography has been examined from a number of standpoints (*cf.* Christ, 1910; Winkler, 1938; Tryon, 1969, 1970). A complete assessment of the significance of their geographical disjunctions would be difficult to make because of the numerous factors involved. The following discussion will concentrate upon special problems and the examples will have a strongly North American bias. Homosporous vascular plants are pteridophytes which lack micro-megaspore differentiation; all of the spores are presumably bipotential and capable of producing gametophytes with both sex organs. These pteridophytes include some of the widest ranging of all vascular plants, such as *Lycopodium clavatum, Osmunda regalis, Cystopteris fragilis,* and *Asplenium trichomanes.* The distribution patterns of pteridophytes in general are basically like those of seed plants: Narrow endemism is common, and long distance disjunctions frequently occur. One of our major concerns is whether a given disjunction may not be the result of a casual spore introduction. As Klekowski (this symposium) has pointed out, there are significant contrasts between ferns and seed plants, not only in means of dispersal but in their genetic apparatus as well. Some patterns of distribution, *e.g.* eastern Asia–North America and the amphitropical ones, may be related to major events in earth history. Others may be merely recent occurrences resulting from chance spores that traveled long distances.

Their popularity with researchers and field botanists has caused the pteridophytes to be well collected and represented in herbaria. In the eastern United States, for example, we know the ranges of these plants so well that finding a disjunct population only 100 miles from previously known stations is considered an event. As to what we may call a disjunction, there is, of course, no set definition. As Erickson (1945) showed in a species of *Clematis,* the range is made up of thousands of spatially separated populations. Ehrlich and Raven (1969) assert that distances of only a few miles or less may suffice to isolate plant populations from gene flow. Here I give as examples of disjunctions separations in range of as little as 100 miles.

Most of my examples (Table 1) deal with situations in which there is a large center of population and a small strongly disconnected population or group of populations. The principal seat or center will here be designated the "*metropolis*" and the small disjunct stand the "*outlier.*" Although the metropolis was not necessarily the ancestral area, in some cases it probably was. Some taxa, as we go away from their centers of abundance, simply "fade out," their occurrences becoming

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[1] Written under National Science Foundation grant GB-8113, "The Evolutionary Characters of the Ferns." Among those who helped I wish to thank especially C. E. Delchamps, Thomas Duncan, Hugh Iltis, David B. Lellinger, T. Lawrence Mellichamp, Dale J. Hagenah, Elbert L. Little, Ronald L. Stuckey, and Florence S. Wagner.

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Ann. Missouri Bot. Gard. 59: 203–217. 1972.

more and more scattered, but lacking extreme peripheral disjunctions. The best example of transition from common to rare or sporadic in eastern United States is probably among the species of woodferns, *Dryopteris*, *e.g.* Crested woodfern, *D. cristata*; Spinulose woodfern, *D. spinulosa*, as we proceed down the Appalachian mountain chain. Common in the north, frequent in the middle range, and rare in the south, these species probably have no large gaps of 100 or more miles. Really large gaps are expectedly much more common in the western mountains because of their more xeric conditions and their more precipitous and isolated peaks.

The eastern North American–eastern Asiatic pattern of disjunction, first promulgated by Asa Gray, is illustrated by such examples as Shining clubmoss, *Lycopodium lucidulum*; the "Japanese grapefern," *Botrychium ternatum* (but see below); Interrupted fern, *Osmunda claytoniana*; and Sensitive fern, *Onoclea sensibilis*—all of which appear in more or less identical form in the eastern parts of the two continents (*cf.* Broun, 1938; Fernald, 1950; Wherry, 1961). Amphitropical distributions have been discussed by Raven (1963), who lists several pteridophytes. Probably the best example involving western North America and southern South America is *Polystichum mohrioides* (syn. *P. lemmonii;* also confused with *P.* × *scopulinum*; see Taylor, 1970: 172–187). The plants from Washington, Oregon, and northern California are closely similar to those from the Andes of South America and certain of the antarctic islands, and they are evidently conspecific.

An apparent near relative of the circumboreal and familiar Moonwort fern, *Botrychium lunaria*, is also amphitropical. The plant in question, which ranges from Los Angeles Co., California, far to the north in British Columbia and Alberta, is evidently the same as the species distinguished by A. H. G. Alston as *B. dusenii*, heretofore known only from Argentina (*cf.* Alston, 1960; Wagner & Lord, 1956). In at least some North American localities, *B. dusenii* grows sympatrically with *B. lunaria* (*e.g.* Snohomish Co., Washington). Probably all of the plants from western North America which were formerly identified as *B. minganense* are actually *B. dusenii.*

Although there is much interest in disjunctions of pteridophytes over water (*e.g.* Hawaii, Fiji, Samoa, Canary Islands, Galapagos—*cf.* Tryon, 1970), overland disjunctions across continents are equally intriguing, and they present different problems. Many intracontinental disjunctions are vexing because of seemingly suitable habitats in intervening areas where one would expect to find the plants in question. Oceanic disjunctions cause no problems from this standpoint because pteridophytes cannot grow upon the high seas or on intervening wind-swept atolls. Disjunctions of continental nature call forth all of the profound mysteries of plant distribution conjured up by the familiar phrase "rare and local."

SOME MAJOR DISJUNCTIVE TRENDS

In Table 1, I have listed a number of disjunctive "trends" in North American pteridophytes, giving the metropolis, estimated distance of the disjunction, ploidal level, and references. The following discussion refers to that table.

A. *North to South Trend.* In this the southernmost occurrences become widely separated, either "fading out" as they go southward, finally appearing only on the highest peaks, or forming more or less large disjunctions. Climate seems to be the major controlling factor, but often a given species is found upon one peak and then skips a number of others that would seem to be appropriate. When this happens we get disjunctions like those in Table 1. The Slender rock brake, *Cryptogramma stelleri,* was known only as far south as the ravines of northern Pennsylvania until Wherry (1961) found it in West Virginia: "Unexpectedly, there in a crevice so sheltered that the sun's rays never entered, and kept cool by evaporating moisture, was a colony of this tiny rock fern; its known range was thus extended some 200 miles southward."

The most peculiar north-south pattern is that of American Hart's-tongue, *Phyllitis scolopendrium* var. *americanum.* This fern has a strongly disrupted range except on the Niagara Escarpment of Bruce and Grey counties in Ontario (Soper, 1954), the center of its metropolis. All other stations are much further separated, and especially those far to the south in Tennessee. As early as 1878, Hart's-tongue plants were encountered in cool, damp limesinks there (Shaver, 1954). (The Mexican and Caribbean plants assigned to this species apparently represent a distinct subspecies.)

In connection with investigations of the spontaneous floras of pine plantations, a curious north-south disjunction was recently discovered involving the Braun's holly fern, *Polystichum braunii.* The "Marshall Tract" near the town of Ann Arbor, Michigan, was planted with species of spruce and pine on an old pasture during the 1920's and since, as in practically all similar plantations of the region, a distinctive, though small, spontaneous flora has arisen, including Running pine, *Lycopodium flabelliforme*; Spinulose woodfern, *Dryopterus spinulosa*; Sensitive fern, *Onoclea sensibilis*; and Ebony spleenwort, *Asplenium platyneuron.* A solitary plant of Braun's holly fern was discovered here in June, 1971, by Florence S. Wagner, growing in a deeply shaded valley with the foregoing pteridophytes. This constitutes a range extension of over 200 miles from the nearest locality to the north on South Manitou Island.

Hagenah (1955: 75–76) reported a disjunction of the sterile woodfern hybrid, *Dryopteris filix-mas* × *marginalis* in southern Lower Michigan—a single collection, some 200 miles south of the nearest localities to the north. Perhaps, in this case, certain "sterile" hybrids are able to produce occasional viable spores (Morzenti, 1967). Such spores are unreduced and capable of forming apogamous sporophytes.

Another example in Michigan which fits this pattern is the Mingan moonwort, *Botrychium minganense*, which I discovered south of Detroit in 1962. Commenting on this occurrence, Hagenah (1966: 159) wrote as follows: "The most unusual locality for this species in Michigan is that in Wayne County . . . far to the south of all other stations. Although only one plant was found here originally, it was observed for several years and now there are two." Since 1966 both plants, probably offsets of the same one, have disappeared. It probably represents an unsuccessful single spore introduction, the site being too far south for continued survival.

B. *South to North Trend.* Examples in which the metropolis is southern rather than northern are very few in homosporous pteridophytes. A prominent south-

TABLE 1. Some examples of outlying North American over-land pteridophytic disjunctions with rough estimates of mileages away from their metropolises. * = polyploid (level given if known). † = outliers suspected of being casual spore establishments rather than relicts of past floras.

	TAXON	METROPOLIS	ESTIMATED DISJUNCTION	PLOIDY	OUTLIER & REFERENCE
			A. NORTH TO SOUTH TREND		
	Botrychium multifidum	n. N. Amer.	100 mi.	2x	Madison Co., Va. (Wagner, 1946)
	Woodsia ilvensis	n. N. Amer.	100	2x	Ashe Co., N.C. (Bozeman, 1968)
	Botrychium lanceolatum var. *angustisegmentum*	n. e. N. Amer.	150	2x	Macon Co., N.C. (Wagner *et al.*, 1970)
	Gymnocarpium dryopteris	n. N. Amer.	150	4x*	Ashe Co., N.C. (Bozeman, 1968)
	Thelypteris phegopteris	n. N. Amer.	150	3x*	Macon Co., N.C. (Wagner *et al.*, 1970)
	Botrychium simplex	n. N. Amer.	200	2x	Giles Co., Va. (Wagner, 1963)
	Cryptogramma stelleri	n. N. Amer.	200	2x	Pendleton Co., W. Va. (Wherry, 1939)
†	*Dryopteris filix-mas* × *marginalis*	n. e. N. Amer.	200	3x*	Barry Co., Mich. (Hagenah, 1955)
†	*Polystichum braunii* var. *purshii*	n. N. Amer.	200	4x*	Washtenaw Co., Mich. (Wagner, unpubl.)
	Botrychium minganense	n. e. N. Amer.	200	4x*	Wayne Co., Mich. (Hagenah, 1966)
	Polystichum × *scopulinum*	n. w. N. Amer.	450	4x*	Cochise Co., Ariz. (Wagner, unpubl.)
	Phyllitis scolopendrium var. *americanum*	Bruce Peninsula, Ontario	650	4x*	Marion Co., Tenn. (Shaver, 1954; Fernald, 1935)
			B. SOUTH TO NORTH TREND		
	Ophioglossum vulgatum "var. *pycnostichum*"	s. e. U.S.	100	*	Lenawee Co., Mich. (Wagner, 1971)
†	*Dennstaedtia punctilobula*	s. e. U.S.	150	2x	Jackson, Shiawassee Cos., Mich. (Wagner, unpubl.)
†	*Adiantum capillus-veneris*	s. U.S.	700	2x, 4x	Fairmont, B.C. (Taylor, 1970)
			C. TREND TO SOUTHWESTERN MICHIGAN		
†	*Lygodium palmatum*	s. e. U.S.	300	2x	Kalamazoo Co., Mich. (Pippen, 1966)
†	*Woodwardia areolata*	s. e. U.S.	300	2x	Van Buren Co., Mich. (Billington, 1952)
	Dryopteris × *celsa*	s. e. U.S.	400	4x*	Kalamazoo Co., Mich. (Wagner *et al.*, 1969)
	Lycopodium appressum	e. Coastal Plain	600	2x?	Van Buren Co., Mich. (Wagner & Hagenah, unpubl.)
			D. TREND TO "DRIFTLESS AREA"		
	Asplenium × *pinnatifidum*	s. highlands	300	4x*	Iowa Co., Wisc. (H. Iltis, pers. comm.)
	Lycopodium porophilum	s. highlands	350	*	Grant Co., Wisc. (Hartley, 1966)
	Thelypteris simulata	e. Coastal Plain	700	4x*	Jackson Co., Wisc. (Hartley, 1965)

TABLE 1. (*Continued*)

	TAXON	METROPOLIS	ESTIMATED DISJUNCTION	PLOIDY	OUTLIER & REFERENCE
			E. EAST TO WEST TREND		
	Cystopteris bulbifera	n. e. N. Amer.	650	2x	Guadalupe Mts., N. Mex. (Blasdell, 1963)
	Ophioglossum vulgatum "var. *pseudopodum*"	n. e. N. Amer.	1300	*	Kittatas Co., Wash. (Taylor, 1970)
			F. WEST TO EAST TREND		
†	*Cystopteris* × *tennesseensis*	Cumberland Plateau	400	4x*	Jones, Craig Cos., N.C. (Wagner, 1965)
†	*Polystichum munitum*	w. N. Amer.	550	2x	Pennington Co., S.D. (Brooks, 1968)
†	*Gymnocarpium* × *heterosporum*	Lake Superior	650	3x*	Blair Co., Pa. (Wagner, 1965)
†	*Cryptogramma crispa* var. *acrostichoides*	w. N. Amer.	900	2x	Isle Royale, Mich. (Soper, 1963; Fernald, 1950)
†	*Cheilanthes castanea*	w. N. Amer.	1000	3x*	Montgomery Co., Va.; additional localities in Va., W. Va. (Knobloch & Lellinger, 1969)
†	*Pellaea* × *wrightiana*	s. w. N. Amer.	1000	4x*	Alexander Co., N.C. (Wagner, 1965)
†	*Asplenium septentrionale*	w. N. Amer.	1200	4x*	Monroe Co., W. Va. (Emory, 1971)
†	*Aspidotis densa*	w. N. Amer.	2200	2x	Megantic Co., Quebec (Fernald, 1950)
†	*Polystichum* × *scopulinum*	n. w. N. Amer.	2400	4x*	Gaspé Co., Quebec (Fernald, 1950)
			G. SPOROPHYTE TO GAMETOPHYTE TREND (Outliers all or mostly gametophytes)		
	Vittaria sp.	Tropics	250	?	Rabun Co., Ga. (Farrar, 1971)
†	*Grammitis nimbata*	Cuba, Jamaica	800	?	Macon Co., N.C. (Farrar, 1971)
†	*Hymenophyllum wrightii*	S. Japan	4500	?	Queen Charlotte I., B.C., Biorka I., Alaska (Taylor, 1970)

north disjunction is that of Southern maidenhair fern, *Adiantum capillus-veneris*, growing in Fairmont, British Columbia (Taylor, 1970), many hundreds of miles north of its normal latitudinal limit. This south-temperate to subtropical fern is flourishing in the runnels of a system of hot springs, an obviously unusual site.

Limitations of north extensions of many species into the Great Lakes area are probably due to cold winters and short growing seasons. Hay-scented fern, *Dennstaedtia punctilobula*, of the southern and eastern United States has been taken in Michigan on only two occasions, these widely separated in time. (A third collection, allegedly from the Keweenaw Peninsula of the Upper Peninsula, by O. A. Farwell, is under question.) In 1889, G. H. Hicks recorded a collection from Shiawassee Co. (specimen in University of Michigan Herbarium), and in 1954 I discovered it in Jackson Co. Of special interest for our subject is the fact that the latter collection comprised two juvenile plants, probably offsets from a single plant, found growing in the depression made by the overturning of a large tree—a transient habitat ideal for the growth of fern prothallia. In the loose, exposed sand there we found hundreds of gametophytes and young sporophytes of other fern species. One of the offsets of the Hay-scented fern was left *in situ*, but was gone the following year, having failed to survive the winter.

Our best example of "fading out" of species going northward is Ebony spleenwort, *Asplenium platyneuron*. Among the most abundant of ferns in southern and eastern United States, it decreases rapidly in numbers north of the Wisconsin glaciation in Ohio, Indiana, and Illinois (well illustrated in the last state by Mohlenbrock, 1967: 157). By the time we reach Michigan and Wisconsin, the plant becomes very sporadic. Some "colonies" are but a single plant. Of 21 counties in which Ebony spleenwort has been found in Michigan, only two are north of Saginaw Co. It was taken once at the University of Michigan Biological Station, Cheboygan Co., and has been found twice in crevices of limestone "pavements" in Chippewa Co. The suggestion seems plausible that this fern may be constantly re-established from wind-blown spores coming from the south. Single plants or small colonies may survive for a while and then perish.

C. *Eastern U. S. to Southwestern Michigan Trend.* In the Upper Great Lakes area, two regions have special interest for their pteridophytic disjunctions, the area along the southeastern shores of Lake Michigan and the "Driftless Area" of Wisconsin. The former is the region involving the counties of three states running from approximately Chicago, Illinois, to Muskegon, Michigan. From the standpoint of plant geography, this locality is famous for the most spectacular disjunction in the United States—*Thismia americana* (Burmanniaceae) which once grew near Lake Calumet, Illinois, separated from its nearest relatives in New Zealand and Tasmania (Swink, 1969: 411).

Of disjunct pteridophytes, several have been detected only during the past few years, *viz.* American climbing fern, *Lygodium palmatum*; the Log fern, *Dryopteris × celsa*; and the Southern clubmoss, *Lycopodium appressum*. All are at least several hundred miles from their metropolises. The clubmoss has only recently been distinguished, because it grows together with the closely similar Bog clubmoss, *Lycopodium inundatum*, with which it is readily confused.

D. *Eastern U. S. to "Driftless Area" Trend.* This well known focus of phytogeographical interest boasts three outstanding examples of pteridophyte disjuncts, namely the Massachusetts fern, *Thelypteris simulata,* a plant of low, sandy woods (Hartley, 1965); the Rock clubmoss, *Lycopodium porophilum* (also known as *L. selago* var. *patens,* but probably not the same; *cf.* Hartley, 1966; Wherry, 1961); and Lobed spleenwort, *Asplenium* × *pinnatifidum* (Iltis, personal communication)—both of the latter plants of sandstone cliffs.

E. *East to West Trend.* Very few pteridophytes show this pattern, in which the outliers are western. Most species which occur in both the East and West tend to skip the Great Plains and are actually "bimetropolitan" in that the eastern and western populations are more or less equivalent, neither being obviously the outlier of the other. Of bimetropolitan taxa I include such plants as Leather grapefern, *Botrychium multifidum*; Moonwort, *B. lunaria*; Least moonwort, *B. simplex*; Five-fingers or "American" maidenhair, *Adiantum pedatum*; Fragile fern, *Cystopteris fragilis*; Crested fern, *Dryopteris cristata*; Spinulosa woodfern, *D. spinulosa*; Spreading woodfern, *D. assimilis*; and Maidenhair spleenwort, *Asplenium trichomanes.* Some of these are undoubtedly connected in the forested areas at the north of the Great Plains. All of them are wide-ranging and are known also in Europe and (or) Asia. They are probably disjunctive due to past historical events.

Two examples which seem clearly to involve a metropolis in the East with outliers in the West may be cited. One is the Northern Adder's-tongue, *Ophioglossum vulgatum* var. *pseudopodum,* which is a frequent and widespread plant north of the line of maximum Wisconsin glaciation from the eastern coast (New Jersey to Quebec and Nova Scotia) west to Minnesota and western Ontario. This Adder's-tongue reappears in the Northwest, where it is exceedingly rare and local. Although it is possible that the western plants may represent a distinct variety, I doubt it. A second example, the familiar eastern Bulblet fern, *Cystopteris bulbifera,* occurs in a few very widely scattered localities in southwestern United States, the outlying stations hundreds of miles from each other. Bulblet fern is enabled to produce enormous colonies by forming gemmae, subspherical structures, along the costae, which abscise and roll, and will germinate into new sporophytes if they reach suitable sites. The Adder's-tongue, on the other hand, forms extensive colonies by root proliferation. Thus both of these plants are capable of developing large stands without sexual processes.

F. *West to East Trend.* In terms of number of examples and distances, this pattern of metropolis to outlier is the most striking of the directional trends. Some reach 2,000 or more miles in length of disjunction. Over half of those listed in Table 1 have been recognized only during the past 20 years, the outliers being so rare and local that they were overlooked. Wright's cliffbrake, *Pellaea* × *wrightiana,* is known from a single granite outcrop in North Carolina. The solitary locality in Pennsylvania for the Hybrid oakfern, *Gymnocarpium* × *heterosporum,* no longer supports a population, the limestone upon which it grew being now destroyed in the excavation of a quarry. The Forked spleenwort, *Asplenium septentrionale,* is so far represented in the eastern United States on only two rock cliffs in Virginia one-fifth of a mile apart. In view of the present incidence of populations in the outlying eastern region of these and others of those listed, the conclusion seems inescapable that at least some of them may not represent relicts of former floras in which the taxa were once more abundant and widespread. Rather they have arisen by long-distance spore dispersal following the prevalent winds from the west. Alternatively, some may have originated from spores on nursery or garden stock transferred from one part of the country to another, or escapes of western plants cultivated in the east.

G. *Sporophyte to Gametophyte Trend.* Surely the strangest disjunctions of homosporous vascular plants are those ferns that show dominant sporophytes in the metropolis and dominant gametophytes in the outliers. All of the examples discovered thus far are from North America (Wagner & Sharp, 1964; Farrar, 1967; Taylor, 1967), but we may expect additional examples to turn up in other parts of the world, especially in temperate rock outcropping regions. The examples involve tropical rainforest fern genera with gemmiferous gametophytes capable of dispersal by few-celled bodies which abscise and germinate, if deposited in appropriate sites. The gametophytes exist as disjuncts far into temperate latitudes, but their sporophytes form sporadically if at all, according to the researches of Farrar at Iowa State University (personal communication) involving examples of several groups of Filmy-ferns (Hymenophyllaceae), Shoestring ferns (Vittarioideae), and Dwarf polypodies (Grammitidoideae). In the wild these gametophytes are almost totally overlooked by vascular plant field botanists. Even bryologists, assuming presumably that the plants were algae, tended to disregard them in the past. Phycologists, upon encountering them, probably treated them as bryophytes. In view of our present knowledge, field botanists of all persuasions are urged to look out for these "ferns without sporophytes." They differ from "standard" cordate fern prothallia in being narrower and more profusely branched. Some are mere branching filaments. All produce more or less specialized gemmae, and even if they form tiny sporophytes, they usually do not complete the alternation of generations. The classical generalization that homosporous pteridophytes have dominance of the sporophyte generation does not apply in the outlying populations, and the plants behave more or less as do algae or bryophytes, occupying similar microhabitats on shaded cliffs and on damp tree bark. In the outlying populations the gametophytes no longer seem to "need" their sporophytes and spores, being able to propagate and spread entirely by their gametophytic gemmae.

H. *Indigenous to Naturalized Trend.* More and more pteridophytic disjunctions are being reported in which the populations of the metropolis are indigenous members of the flora and the outlying populations have resulted from man's activities. Two illustrative areas of such disjunctions in the United States are given in Table 2 listing the suspected artificial introductions in the states of Florida and Hawaii. Some of the taxa included, *e.g.* Ladder brake, *Pteris vittata*; and so-called "Garden maidenhair fern," *Adiantum hispidulum*, are now being naturalized in many places from cultivated garden and greenhouse plants. Some are conservatory and hothouse weeds. In some cases the same species may be both native and naturalized.

TABLE 2. Artificial pteridophyte outliers in Florida and Hawaii. Species listed in parentheses probably native in that state. Metropolises: O = Old World tropics, N = New World tropics, X = Pantropics.

	FLORIDA[a]	HAWAII	METROPOLIS
SELAGINELLACEAE		*Selaginella krausiana*	O
OPHIOGLOSSACEAE	*Ophioglossum petiolatum* (May be introduced in part.)	*O. petiolatum* (May be introduced in part.)	X
MARATTIACEAE		*Angiopteris evecta*	(?)O
POLYPODIACEAE	*Phymatodes scolopendria*	*P. scolopendria*	O
	(*Phlebodium aureum.*)	*P. aureum*	N
SCHIZAEACEAE	*Lygodium japonicum*	*L. japonicum*	O
	L. scandens (syn. *L. microphyllum.*)		O
ADIANTACEAE	*Adiantum hispidulum*	*A. hispidulum*	O
	Pellaea viridis (Volunteer in orchid houses.)	*P. viridis*	O
	Pityrogramma calomelanos (Probably introduced.)	*P. calomelanos*	N
	Pteris cretica	(*P. cretica*)	X
	P. ensiformis		O
	P. multifida		O
	P. vittata	*P. vittata*	O
	P. tripartita		O
		Ceratopteris thalictroides	O
ASPLENIACEAE	*Athyrium esculentum* (In and near gardens.)	*A. esculentum* (In and near gardens?)	O
	A. japonicum	*A. japonicum*	O
	Cyrtomium falcatum	*C. falcatum*	O
	Thelypteris torresiana	*T. torresiana*	O
	T. dentata	*T. dentata*	O
		T. parasitica	O
	(*Blechnum occidentale*)	*B. occidentale*	N
	Nephrolepis hirsutula (s.l.)	*N. hirsutula* (s.l.)	O
	N. cordifolia (Introduced in part?)	*N. cordifolia* (Introduced in part.)	X
		N. biserrata cv. "Furcans"	?
AZOLLACEAE		*Azolla filiculoides*	N

[a] Records from C. E. Delchamps in part.

It is remarkable that many naturalized ferns seem now to be fully "at home" in their newly adopted countries. In Hawaii particularly certain introduced species are spreading well into the native forest, especially along the foot trails, and some appear as if they were native (Wagner, 1950). To analyze the phytogeography of Hawaiian pteridophytes it is essential that we recognize which species are adventive through man's commerce and which indigenous. Failure to do so has given strange results: For example, MacCaughey (1918) listed six species as native (including one he called "endemic"!) which were actually brought in by man.

Although ferns and other pteridophytes have not been especially popular garden plants in temperate zones, they flourish in tropical plantings. Greenhouse gardeners are familiar with the experience of receiving specimens of some

TABLE 3. Considerations to determine whether disjunctive populations arose by (A) natural means or by (B) actions of man.

STANDPOINT	A. NATURAL	B. ARTIFICIAL
1. Documentation	Data confirmed and dependable	Data unconfirmable and probably erroneous
2. Transport	Unlikely to be carried by man	Likely to be carried by man
3. Flora	Area in question poorly known	Area in question well known
4. Prominence	Plant easily overlooked or confused	Plant difficult to overlook or confuse
5. Abundance	Plants numerous and in more than one colony	Plants solitary or in only one colony
6. Taxonomy	Population showing divergence	Population showing no divergence
7. Remoteness	Disjunction only a short distance	Disjunction over a long distance
8. Dispersal	Propagules capable of wide dispersal	Propagules incapable of wide dispersal
9. Pattern	Distribution pattern fits in with other, similar ones	Distribution pattern entirely peculiar
10. Habitat	Physical environment typical for taxon	Physical environment atypical
11. Associates	Adjacent species native ones	Adjacent species adventive exotic ones
12. Genetics	Reproductively self-compatible or apomictic	Reproductively self-incompatible and sexual

rare orchid or exotic gesneriad, for example, and losing the seedplant only to have it replaced by a foreign fern arising from spores in the soil. Tropical situations are probably more conducive to artificial introductions than temperate. However, in northern United States and southern Canada the Ostrich fern, *Matteuccia*, is the most popular garden fern. I wonder how many of the presumed "native" populations of Ostrich fern are actually escapes from cultivation, from either broken rhizome fragments or wind-blown spores of nearby plantings. Even some of the disjunctions listed in Table 1 may actually have resulted from man's activities.

In this connection, Fosberg (1967) repeats a wonderful story of a disjunct population of an Asiatic water lily found in a lake in Idaho: "It was assumed that here was a remarkable instance of a wide disjunction in range until someone pointed out that some years earlier there had been a Chinese laundry on the shore of this lake." What tests can we apply to evaluate whether a given disjunction was the result of artificial introduction or not? In Table 3 I have listed a number of considerations that must be applied in each case. Even mere carelessness or inadvertent error in documentation (improper labeling especially) can lead to statements of range disjunctions that never existed and create serious problems in phytogeography. The data in herbarium or publication may be erroneous but nevertheless perpetuated in the literature of botany forever. In Michigan, for example, several reports of Oliver A. Farwell are under question, these involving very large disjunctions in the Keweenaw Peninsula.

Our knowledge of disjunctions is going to be more and more concerned with artificial introductions with increasing commerce of the future. Table 3 can be used as a sort of "Index of Autochthonism" for the expanding problems of artificial disjunction in the study of plant distribution. As Fosberg (1967) points out, however, "it is frequently difficult to prove conclusively that a species was brought by man in the absence of documentary evidence directly involving the introduction."

INTRINSIC FACTORS BEARING UPON PTERIDOPHYTE DISJUNCTIONS

Thus far we have considered mainly extrinsic factors bearing upon disjunctions. Geological history and floristic changes account for some patterns; climatic conditions for others; and human intervention for others. Prevailing winds may have produced the outliers of taxa with primarily western metropolises. Cold temperate conditions may have influenced primarily tropical rainforest species to change from the dominantly sporophytic expression of the metropolis to the dominantly gametophytic expression of the northern outposts. What of intrinsic factors such as chemical differentiation? Chromosomes? Examples of a few of these will be enumerated below.

Chemistry. Comparison of chemical aspects of disjunct populations in pteridophytes is still in its infancy. The case of the rare "Japanese grapefern," *Botrychium ternatum*, in the region of the St. Lawrence Seaway poses a number of questions. I had interpreted plants of the outlying American populations to be the same taxonomically as those of the metropolis in Japan, China, and India (Wagner, 1959; Wherry, 1961). I am still unable to separate them morphologically. My student, David M. Smith (1967), however, has shown that the American taxon differs in presence or absence of six phenolic compounds from the Japanese. In spite of these chemical contrasts I am inclined to continue treating the American plant as only varietally distinct at best. Will we find similar chemical differentiation in such disjunctive plants as *Lycopodium lucidulum, Osmunda claytoniana,* and *Onoclea sensibilis*? Should we treat separated populations which are morphologically alike but chemically unlike as distinct varieties?

Cytology. In Table 1, the current knowledge of level of polyploidy is indicated for the various patterns of disjunction. Most disjunctive taxa have the same chromosome number in their outliers as in their metropolis, but our knowledge is still limited and some of the examples in Table 1 may be shown to have different polyploid levels represented. One of the best known examples of polyploid differentiation is the Hart's-tongue, *Phyllitis scolopendrium.* Its metropolis in eastern Eurasia and north Africa comprises diploids (*cf.* Tryon, 1969: map 4), but its outliers in Japan and northern North America are tetraploids. The western variety of the Oak fern, *Gymnocarpium dryopteris* var. *disjunctum* is practically indistinguishable morphologically from the eastern American plant, but the former possesses $2x = 80$, the latter $2x = 160$. The Hawaiian Palaa, *Sphenomeris chinensis* (*S. chusana* of authors) is a diploid with $n = 47$, but all those populations of this taxon so far studied in India, Ceylon, and Japan are polyploid with $n = 94$ or near that number.

There are two important facets of polyploidy to consider in relation to disjunction, namely the effect it would have on the fate of the resulting population if the arriving spore were polyploid, and what causes arriving populations to remain diploid or change to polyploid. Tryon (1970) noted that Hawaii constitutes the only notable exception to the rule that ferns, in general, do not develop endemic "species flocks" on islands. He concluded that in fern floras of oceanic islands adaptability of the genotype-phenotype of the single spore to a new environment and sensitivity to selection are characteristics that dominate success in migration and evolutionary potential under geographic isolation. Our data on Hawaii seem to fit this conclusion: the incidence of polyploidy is approximately twice as great among the non-endemic taxa as it is among the endemic (Wagner & Wagner, unpubl.). According to our present evidence of *ca.* 85 percent of the fern taxa (exclusive of Ophioglossaceae and Gleicheniaceae), over 60 per cent of the non-endemic indigenous species are polyploid (3*x*, 4*x*, 6*x*, and 8*x*), but less than 30 per cent of the endemics are polyploid. Also, not one of the members of the endemic "species flocks" in Hawaii displays polyploidy (namely *Cibotium* with 5 species, *Sadleria* with 4, *Diellia* with 5, and *Adenophorus* with 8). In contrast, however, among the solitary endemics, including some of Hawaii's most distinctive taxa, there are several (*Pteris lidgatii*, *Thelypteris* (*"Toppingia"*) *keraudreniana*, and *Microsorium spectrum*) which are tetraploids. These may constitute last remnants of earlier "species flocks" which evolved high levels of differentiation from their ancestors and are now senescent, being represented by isolated vestigial species.

Hybridity. Seven of the disjuncts discussed in this paper are interpreted as interspecific hybrids rather than normal, divergent species. They show metropolis-to-outlier disjunctions ranging from *ca.* 200 to over 2,000 miles. The outliers may be separated from one or both presumed parents. Five of the intermediates are sexual allotetraploids, and two are "sterile" allotriploids. There is no problem of accounting for long distance disjunction in the sexual hybrids, as they can spread by spores in the same manner as normal species. Our present interpretations of their origins are as follows:

Polystichum × *scopulinum* = *P. mohrioides* × *munitum*
Dryopteris × *celsa* = *D. goldiana* × *ludoviciana*
Asplenium × *pinnatifidum* = *A. montanum* × *rhizophyllum*
Pellaea × *wrightiana* = *P. longimucronata* × *ternifolia*
Cystopteris × *tennesseensis* = *C. bulbifera* × *protrusa*

The widest transcontinental disjunction of these is shown by *Polystichum* × *scopulinum*, the outlier skipping 2,400 miles of intervening country and confined to Gaspé Co., Quebec. This hybrid is a well known western American holly fern in its extensive metropolis where it occurs in both sterile diploid and fertile tetraploid forms. It is intermediate between the two species with which it most commonly grows—the amphitropical montane *P. mohrioides* and the extremely abundant and widespread endemic North American *P. munitum*. The former, *P. mohrioides*, has apparently produced no outliers east of Washington, Oregon, and California. However, the latter, *P. munitum*, which is vastly more abundant in its metropolis, has recently had an outlier reported as far east as South Dakota.

A much greater problem lies in the explanation of disjunctions of sterile triploids. *Dryopteris filix-mas* × *marginalis*, despite its abnormal spores, forms remarkably large local populations in certain localities in its metropolis, *e.g.* Bruce

Peninsula of Ontario and a few offshore islands of Lake Superior. It normally occurs with the parents near by. *Gymnocarpium* × *heterosporum* combines the characters of *G. dryopteris* ($n = 40$, 80) and *G. robertianum* ($n = 80$). None of the populations of the intermediate Oak fern has yet been discovered with normal spores. How such plants can spread if at all we can only guess. Perhaps it is by dispersion of unreduced spores (*cf.* Morzenti, 1967).

Morphology. More or less subtle anatomical differences are likely to be found between separated populations. These differences may be sufficient to designate them as different varieties or subspecies. For example, the Asiatic counterpart of *Osmunda claytoniana* differs from its eastern American representative in its hairiness (it has been separated as "var. *vestitum.*")

A particularly interesting taxonomic-geographic situation arises when we discover a disjunction of one variety in the area of another. No better example can be found than the situation in Bracken ferns, *Pteridium aquilinum* sensu lato. Most of the so-called "varieties" are allopatric and some are widely separated from the others, such as "var. *decompositum*" in the Hawaiian islands, an obviously highly disjunctive taxon. Brackens have been lumped by many authors into one species—"the only species of the monotypic genus *Pteridium* . . . ." (Tryon, 1941). However, a real question exists here, for two of the so-called "varieties" may also grow sympatrically. In March, 1970, I observed taxon *arachnoideum* intergrowing in abundance with taxon *caudatum* over a very large area of the Blue Mountains of Jamaica. The clones of these ferns differ respectively from each other in many obvious characters and they produce mixed tangles which are almost impenetrable, but which afford an excellent opportunity to compare under like site conditions. The metropolis for *arachnoideum* is mainly South American, while that for *caudatum* is southern North America and Central America. However, both coincide over a very large area of the islands of the Caribbean and the land mass of Central America.

SIGNIFICANCE OF DISJUNCTIONS IN HOMOSPORUS PTERIDOPHYTES

Do long-distance disjunctions in homosporous pteridophytes necessarily give evidence of major geological and biological events in floristic history? If the disjunctions are between large and broadly distributed populations, they may indeed be highly significant as indicators of past events and relict floras. On the contrary, where the disjunctions exist between a large population center or metropolis and one or a few widely separated small populations or outliers, the significance may be less. Perhaps some of these are actually mere casual and short-lived introductions, such as those occasionally noted, say, among the butterflies, which establish themselves in a given area for a few years only to disappear. Spores of the homosporus pteridophytes are capable of long-distance dispersal by wind (Ewan, 1945; Tryon, 1970). Even though the statistical chances of a given spore reaching a given point rapidly become smaller the farther away we go from the source point, at least some spores must be able to reach highly isolated positions—as in Hawaii where the nearest sources over perhaps millions of years have been well over 2,000 miles away. The question of whether a single spore, by itself, can initiate and establish a population now seems to be satisfactorily answered in the work of Klekowski and Baker (1966, bibliography; present symposium), who find that ferns indeed are capable of intragametophytic selfing and that thus a single spore *can* start a colony.

Many of the disjunctions cited in this paper (those marked with daggers in Table 1) may be casual introductions in fairly recent times rather than "relicts" in the sense of persistent remains of ancient floras. Stanley A. Cain (1944) wrote, "Minor discontinuities of areas probably frequently result from recent migrations, but major disjunctions seem almost exclusively to have resulted from historical causes which have produced the disjunctions, in a once more nearly continuous area, through destruction or divergent migrations caused by climatic or some other changes." However, in homosporous pteridophytes, if it is true that spores can be carried long distances and produce self-fertilizing gametophytes, then we must be cautions not to read too much into long-distance disjunctions, especially those with well marked metropolis and outliers.

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THE FLORISTIC DISJUNCTIONS BETWEEN THE "MONTE" IN ARGENTINA AND THE "SONORAN DESERT" IN MEXICO AND THE UNITED STATES[1]

OTTO T. SOLBRIG[2]

One of the best known but most puzzling disjunctions is that between the temperate regions of South America and the temperate regions of North America. It is puzzling because it involves a large number of floristic elements, and because it is evident from the geological data available that the two regions have never been closer to each other than they are today (Dietz, 1961).

Raven (1963, 1971) has addressed himself to this problem and has very accurately pointed out that we are dealing with more than one type of disjunction. There is the disjunction involving elements that grow in the cold regions of South and North America; the disjunctions involving plants that grow in areas with a Mediterranean type of climate in both continents; the disjunctions between areas with a mesic hydric and temperature regimes; and finally the disjunctions between the so-called "desert areas." In his reviews, Raven presents evidence that indicates that these disjunctions are relatively recent and that they probably have arisen almost exclusively by long-range dispersal.

However, Raven did not discuss in detail the disjunction involving the desert areas. This is the best known one (Bray, 1898, 1900; Campbell, 1944) and probably the most controversial. It also involves the largest percentage of the flora. In this paper I want to present data that lead me to believe that we are dealing with patterns of distribution that have been established over a long period of time and that no one single explanation can encompass them all. In order to clarify the discussion, only plants that grow in the phytogeographical province of the "Monte" in Argentina and the "Sonoran Desert" in Mexico and the southwestern United States will be discussed.

DESCRIPTION OF THE TWO REGIONS

The Monte and the Sonoran Desert are remarkably alike in their physical characteristics (Hauman, 1947; Morello, 1958; Shreve, 1951; Shreve & Wiggins, 1964; Solbrig, 1972). Basically they are ecological semideserts with mild winters and hot summers, rainfall that rarely exceeds 300 mm, and negative evapotranspiration throughout most of the year. The rainfall regime varies within both areas. Each region has areas of winter rainfall, winter and summer rainfall, and only summer rainfall.

Physiognomically both areas can be described as xerophytic scrubs with a predominance of perennial shrubs. These show a series of adaptations to a deficient water economy such as small leaves, sunken stomata, thick cuticles with

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[1] Work done under a National Science Foundation grant, which is gratefully acknowledged.

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ANN. MISSOURI BOT. GARD. 59: 218–223. 1972.

waxy and resinous exudates, etc. In addition to the shrubs, other conspicuous elements are succulents, particularly Cactaceae, Bromeliaceae, Agavaceae, and Fouquieraceae. A third element is the annual flora, which grows in conjunction with the rains and consequently, both winter and summer annuals can be identified.

In areas that span such latitudinal and altitudinal ranges as the Monte and the Sonoran Desert, by necessity variations in all kinds of physical and biological parameters will be encountered. There will be truly "desert" elements as well as riparian elements that because of their ability to tap underground water are able to escape to a degree the limitations that lack of water impose on plant growth. This should be borne in mind when the disjunctions are discussed in detail. It also applies to the density of the vegetation and total coverture that one is likely to find. Although basically both regions are characterized by less than 100% coverture, this is not always so, particularly in those areas where more humidity is locally available for one reason or another.

The Floristic Similarities

The flora of the Sonoran Desert has been recently studied by Shreve and Wiggins (1964). Although they give no exact figures, a rough estimate is that it is formed by approximately 3,000 species. No comparable work exists for the Monte, the closest being Morello's (1958) study of the vegetation, which cites 307 species in a list that does not wont to be complete. The exact figure is probably closer to 3,000. Of this total of roughly 5,000 species growing in both areas, only some 100 to 150 are disjunct or pairs of closely related species, roughly 2 per cent. The number of genera in common is much higher, the regions sharing approximately 50 of the roughly 500 genera growing in both areas, that is approximately 10 per cent. On a purely numerical basis the common elements are not very great. What is impressive is that among the elements that are shared by both areas are some of the most important species of both areas.

First in importance is the creosote bush, gobernadora or jarilla, *Larrea divaricata,* the most important perennial shrub in the Sonoran Desert and in the Monte. In both areas *Larrea divaricata* occupies hundreds of square miles with an abundance of 90% or more. In the Monte two other species of *Larrea, L. cuneifolia* and *L. nitida,* often replace *L. divaricata,* but the latter is still the most important species.

The second most important element with a disjunct distribution is the genus *Prosopis,* sect. *Algarrobia,* the "mesquite" and "algarrobos." Although there are no common species between South and North America, *P. chilensis* from South America and *P. juliflora* from North America are very closely related and were considered conspecific at one time. These trees are the principal riparian element in both the Monte, where they have speciated extensively, and in the North American deserts.

A number of other floristically abundant shrubs and trees also show disjunct distributions or have pairs of closely related species at the northern and southern sites. Among them are the genus *Celtis* in the family Ulmaceae, represented in South America by *C. spinosa* and in North America by *C. pallida* and *C. laevigata;*

the genus *Condalia* in the Rhamnaceae, represented in the Sonoran Desert by *Condalia lascioides* and *C. spathulata* and in the Monte by *C. microphylla*; also in the Rhamnaceae the genus *Ziziphus*, represented by *Z. mistol* in the Monte and by *Z. sonoriensis* in the Sonoran Desert; in the Leguminosae we find among others *Caesalpinia gillesii* with a disjunct distribution and the genus *Cercidium* with closely related species at both sites; and finally in the Capparaceae, the species *Atamisquea emarginata* is a very conspicuous element of the flora of both the Monte and the Sonoran Desert. All these species are important elements of their respective vegetations, being widespread and abundant.

Members of the family Cactaceae are very conspicuous elements of the flora of the Monte and the Sonoran Desert. Although several genera are shared by both regions, notably *Opuntia* and *Cereus*, no close relationship at the specific level is known that can not be traced to a recent introduction by man (such as the "choya" cactus *Opuntia fulgida*, introduced into Argentina in historic times). There is however a great ecological and morphological similarity, notably among the giant "saguaro" and "organ" type cacti.

In addition to the species and genera mentioned, a great number of species and genera which occupy a much less conspicuous role in the vegetation have species in common, or pairs of closely related species. Although some of these genera are woody, most notably some of the compositae, the majority are herbaceous.

THE DISTRIBUTIONAL PATTERNS

There are three main explanations that can be brought forward to explain the floristic similarities between North and South America. They are as follows: that the disjunction has arisen as a result: (1) of long-distance dispersal; (2) of a once continuous distribution; or (3) of parallel convergent evolution. All three explanations have been brought forward, and there are reasons to believe that all three are applicable in some instances.

Long-range dispersal. It will never be possible to say conclusively that a certain pattern of distribution is due to long-range dispersal. However, with a judicious use of Okam's razor, circumstantial evidence may point to long range dispersal as the most likely explanation.

For the Monte-Sonoran disjunction, long-range dispersal is obviously the simplest explanation if the dispersal agent is not considered. However, it becomes much more difficult to see how long-range dispersal can be effected if the possible dispersal agents are considered. Wind as a dispersal agent can be discarded from the onset. The flow of air, both at the surface and in the upper atmosphere, at every time of the year is such that it is impossible for seeds to be carried from one area to the other by wind across the equator. Neither is there any evidence that the flow of air masses was different in the past. We can therefore safely discard wind as an agent of long-range dispersal between the Monte and the Sonoran Desert.

This leaves only animals as possible agents of dispersal. Obviously more knowledge is needed, and particularly experimental work to determine the effectiveness of birds as agents of dispersal. Species of birds are known that fly from the United States to Argentina in their migration flights. None of these intercontinental migrators are birds of the desert areas, however. To consider them as agents of dispersal it must be hypothesized that either regularly or occasionally they stop at the periphery or the center of the areas under consideration. A further complication is the well-known behavior trait of migrating birds of flying with an empty gut. Seeds still could be carried on feet or plumage. In any case, birds as agents of migration can not be ruled out, but neither are they a very likely source.

What makes long-range dispersal attractive as an explanation in certain cases is the pattern of distribution of certain species. Axelrod (1950) has shown that the vegetation of the North American desert areas has two main sources: one is the so-called Arcto-Tertiary element, a northern, cold-temperate source; the other is the so-called Madro-Tertiary element from a warm-tropical source. Raven (1971) has pointed out that because of its geographical situation the southern hemisphere has not produced an equivalent of the Arcto-Tertiary flora. Although this interpretation is open to discussion and more work on the fossil floras of the southern hemisphere is needed to shed light on this point, it is undoubtedly true that most of the elements of the flora of the dry temperate areas of South America have a tropical origin as Raven (1971) has pointed out. This is also true of the Monte, where Leguminosae, Zygophyllaceae, Rhamnaceae, Cactaceae, etc. are the dominant elements.

If this line of reasoning is accepted, then it is tempting to assume that disjunct species belonging to northern genera not represented in the tropics have been dispersed by long-range dispersal. Particularly some grasses such as *Bephlaridagne benthammianae*, *Andropogon saccharoides*, *Stipa speciosa*; Compositae such as *Verbesina encelioides*, *Encelia farinosa*, etc. that possess small seeds, are herbaceous, either annual or short-lived perennials, might have dispersed this way. In some cases such as *Leptochloa uniflora* the pattern of dispersal involves a series of steps across the equator.

In summary, although it is hard to envision how exactly seeds are carried across the equator, certain patterns of distribution are easiest to explain assuming long-range dispersal in recent times.

Continuous distribution across the tropics. The greatest intellectual block in accepting this explanation is the existence of a tropical belt between the Monte and the Sonoran Desert. It is well known that plants are good dispersers across physical gaps such as water barriers or mountain ranges, but poor dispersers across climatic barriers.

Although this is an undeniable fact, it might not be as formidable a consideration as it appears. Plants are capable of tolerating a greater set of environmental conditions than those to which they are exposed, as witnessed by the variety of ambients where species can grow under cultivation. What usually happens is that although plants are able to grow, they are not able to compete under the warmer climatic regimes.

At present, desert conditions exist scattered across the tropics of South America, and what evidence exists points to the existence of such areas also in the past (Harrington, 1962; Vuilleumier, 1971). Such dry areas exist mostly in the lee of mountains in the western parts of the continent. Competition in such areas is mostly for water, and it is possible that plants from more mesic, but dry areas, such as the Monte and the Sonoran Desert, could have used these areas as stepping stones in moving from North to South or vice versa.

Indirect evidence for such an explanation is found in the present distribution of certain characteristic shrubs and trees. *Cercidium* is a genus of seven species. Two of these are found in the Monte and adjacent areas; four in the Sonoran and Chihuahuan Deserts; and the last, *C. praecox*, has an almost continuous distribution from Mexico to Peru, through the Antilles. *Cercidium praecox* is so closely related to the Monte species that it is considered conspecific by some botanists, and although the North American species are more distinct, it appears very likely that the genus spread from North America to South America or vice versa through the intervening dry tropical areas.

The genus *Bulnesia* in the family Zygophyllaceae is formed by seven species. It is obviously of tropical origin and speciated in the Chaco and adjacent areas of South America. The species *Bulnesia retama* is a conspicuous element of the flora of the Monte. This is the most xeric species of the genus. The distribution of *Bulnesia retama* is of interest because it extends from Argentina to Venezuela, again hopping through the dry areas. Although *Bulnesia* is not found in the Sonoran Desert, it conceivably could get there in the future if populations can become established in the Antilles. Also in the Zygophyllaceae, the distribution of *Larrea divaricata* is of interest. This dominant element of the Monte and Sonoran Desert has a few intermediate stations in Bolivia and Peru. It is tempting to postulate that the species once had a broader range of distribution in the tropical areas.

In brief, there are patterns of distribution particularly among the shrubs and trees that point to a more continuous distribution across the islands of xeric climate in the American tropics, and this explanation at least for cases such as *Cercidium* can not be ruled out.

Convergent evolution. The final alternative explanation for the disjunct distribution says that we are not dealing with a disjunction at all, but with a case of convergent evolution. The proponents of this hypothesis (Barbour, 1969) state that those elements that are tropical in nature might have produced, under the selection of the similar climates of the desert region of the Monte and the Sonoran Desert, similar or identical types through convergence. The major problem with this hypothesis is to find an independent criterion to discriminate between it and the other two. Nevertheless, the distribution of the genus *Prosopis* is suggestive of the validity of the idea of convergence, at least in some cases.

Prosopis is one of the most primitive genera of the Mimiosoid-Legumes. Species of *Prosopis* grow in the Old World (Asia Minor and East Africa) as well as in the Americas, where they are found from the southern United States to northern Argentina. The distribution suggests an early Tertiary or even Cretaceous origin for the genus, since at that time Africa and South America were joined together. It also suggests a tropical origin. This idea is reinforced by the distribution of the sections, with the primitive section *Algarrobia* being both tropical and subtropical in distribution, while all the other more specialized American sections are either found in the mountains or temperate regions.

If we look at the various species of *Prosopis*, sect. *Algarrobia*, we find that the less specialized species are found in the more mesic areas both in the tropics and in the temperate zones, while the more specialized species are found in the Monte and the Sonoran Desert. This is accompanied by the development of similar morphological specializations in leaf structure and habit. The convergence is, however, not so great as to put any doubt on the separate origin of the North and South American desert species. However, presumably the process could proceed to the point where the species may become identical morphologically. If this were accompanied by the extinction of the parental species, the resulting distributional pattern would be suggestive of long-range dispersal.

Summary and Conclusions

The American tropics are flanked by areas with semidesert climate. These xeric belts possess some floristic elements in common. Since they are separated by some 6,000 miles across tropical climate, this presents a formidable problem. Three hypotheses to explain those disjunctions have been proposed: (1) long-range dispersal; (2) continuous distribution across the tropics in the past; and (3) convergent evolution from tropical ancestors. There is circumstantial evidence in favor of the possible correctness of each of the three hypotheses in special cases. What is now needed is careful, detailed work with the species involved in order to obtain more insights into their genetics, cytology, chemistry, and ecological relationships.

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SPECIES DISJUNCTIONS IN *LARREA*: EVIDENCE FROM MORPHOLOGY, CYTOGENETICS, PHENOLIC COMPOUNDS, AND SEED ALBUMINS[1]

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and Lidia Poggio[2]

Larrea divaricata, the "creosote bush," is often regarded as the most drought tolerant higher plant in North America (Barbour, 1969; Morello, 1955). It is probably a single species having an enormous disjunct distribution. In North America it extends from the State of Nevada to the State of Hidalgo in Mexico, where it is called "gobernadora" on account of its dominance in the natural vegetation (Fig. 1). In South America it occurs in several isolated places in Peru (Ica, Nazca, Chuquibamba, Moquegua), in Bolivia (Tarija), and in Chile (Atacama, Concepción). In Argentina it is called "jarilla," and it extends from Salta in the North to North Patagonia (Chubut) (Fig. 2). As pointed out by Barbour the disjunction reaches 36 degrees latitude, that is, nearly 4,000 km (Barbour, 1969).

The question that immediately arises, when considering such an extense distribution is whether we are dealing with a single species or at least two vicariant species: *Larrea tridentata* (North America) and *L. divaricata* (South America).

How much have these populations diverged since they became separated? Typical *Larrea divaricata* was described from Mendoza, Argentina, South America, and the North American taxon has been named *L. tridentata*. Morphologically, they can easily be separated by the form of the stipules, the North American populations having acute while the South American ones have obtuse stipules. They could be distinguished, therefore, as different subspecies as done recently by Felger and Lowe (1970) who recognize *L. divaricata* Cav. subsp. *divaricata* for the South American subspecies and its ecotypes and subsp. *tridentata* (Sesse & Moc. *ex* DC.) Felger & Lowe for the North American subspecies and its ecotypes.

Biosystematics of the Genus *Larrea*

A brief consideration of the biosystematics of the genus will help us to have an idea of the degree of morphological diversity and the genomic differentiation of

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[1] The authors wish to express their gratitude to several persons that in one way or another helped their research. Mrs. Vilma B. de Fernández performed the protein electrophoresis experiments; Miss Aída De Gregorio made part of the cytological preparations; Dr. J. Morello gave us some data on the present day distribution of *L. divaricata* in Santiago del Estero, Argentina, Dr. J. Rzedowski and Dr. Otto T. Solbrig collected seed samples in the field; Dr. Tien Wei Yang very generously supplied us with many seed samples identified insofar as chromosome number is concerned. Financial support through a National Science Foundation (U.S.A.) grant to Dr. O. T. Solbrig and two grants from the Consejo Nacional de Investigaciones Científicas y Técnicas to the senior author is acknowledged.

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Ann. Missouri Bot. Gard. 59: 224–233. 1972.

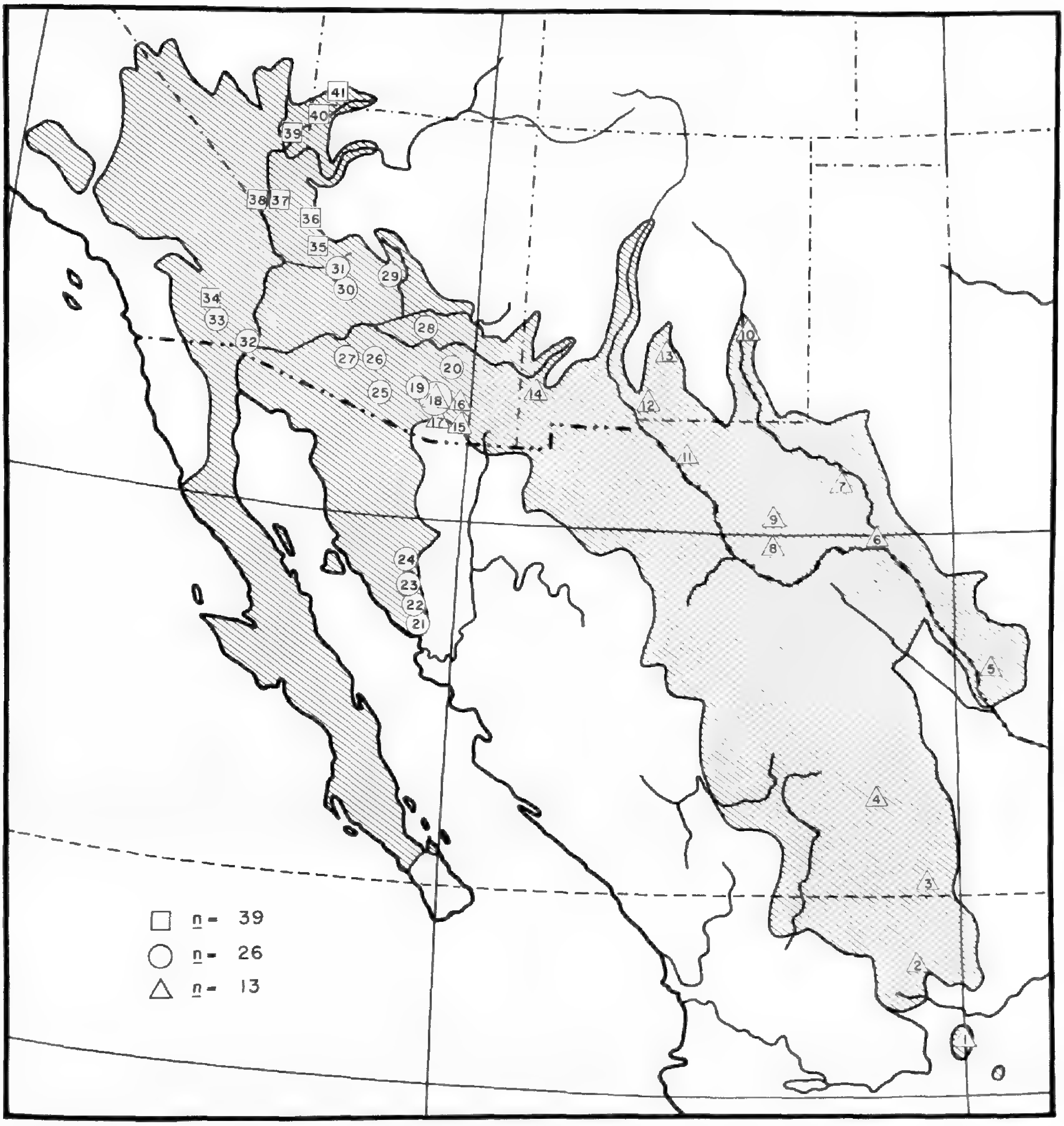

FIGURE 1. Chromosome numbers of creosote bush populations in North America (*Larrea divaricata* subsp. *tridentata*). Diploid populations 1–17 occur in the Chihuahuan Desert and adjacent desert grassland. Tetraploid populations 19–33 are situated in the Sonoran Desert. Hexaploid populations 35–41 are located in the Mojave Desert. Shaded area shows the contemporary distribution of *Larrea divaricata* subsp. *tridentata* in North America. Reproduced from Yang (1970) by kind permission of the author.

the species, the center of species diversity, the age of some species, and the possible patterns of migration.

Table 1 summarizes some of the characteristics of the five taxa of the genus *Larrea* and their geographic distribution. The multifoliolate species having small petals and many leaflets are supposed to be representatives of a more primitive group, since most species of the other genera in the family Zygophyllaceae are multifoliolate. The bifoliolate species would represent a more specialized and recent group. All species have acute (or nearly so) stipules except South American *L.*

FIGURE 2. Distribution of diploid *Larrea divaricata* subsp. *divaricata* in South America. The triangles indicate localities where chromosome counts ($n = 13$ II) have been made. (Base map copyright University of Chicago.)

divaricata subsp. *divaricata* which has obtuse stipules. North American *L. divaricata* subsp. *tridentata* has acute stipules (Fig. 3) as has been pointed out by Porter (1963). Figure 4 shows the leaf morphology, the growth habit, and the phenolic patterns of the four South American species of *Larrea* and of their five natural interspecific hybrids (Hunziker, Palacios, Valesi & Poggio, in preparation). Each species has at least one characteristic marker phenolic compound which is shown by a different type of drawing. These genome marker compounds have been found in the hybrids showing that there is addition of the markers in the hybrids. They have been very helpful for the identification of the parental species of the hybrids (Hunziker *et al.*, in preparation).

All South American species are diploid except *Larrea cuneifolia* which is a tetraploid forming nearly 23 closed bivalents with at least one chiasma at each

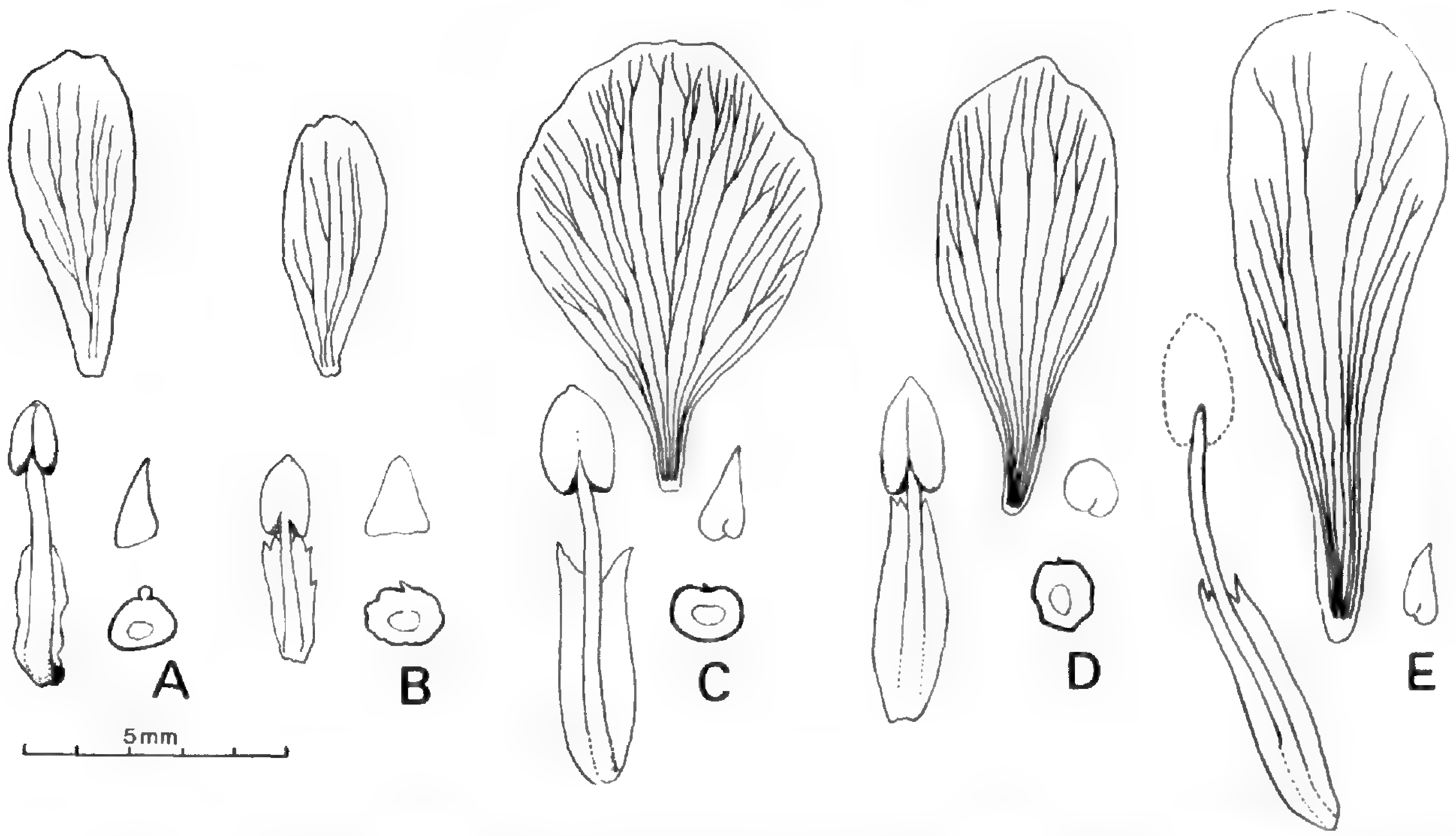

FIGURE 3. Petals, stamens, staminal scales, stipules, and seed cross sections of the five taxa of the genus *Larrea*. A = *L. nitida*, B = *L. ameghinoi*, C = *L. cuneifolia*, D = *L. divaricata* subsp. *divaricata*, E = *L. divaricata* subsp. *tridentata*.

side of the centromere. The diploid South American species form 10.4–12.6 closed bivalents. As the diagram of Fig. 5 indicates, the hybrid *L. ameghinoi* × *L. nitida* is highly fertile and forms nearly 13 bivalents. This points out the close relationship of *L. ameghinoi* to *L. nitida*. It is possible that introgression has occurred between some populations of these two taxa, especially of genes from *L. ameghinoi* to *L. nitida* (Hunziker *et al.*, in preparation).

The triploid hybrid between tetraploid *Larrea cuneifolia* and diploid *L. divaricata*, on the other hand, forms 13 bivalents + 13 univalents in nearly 50% of the

TABLE 1. Leaflet characteristics, chromosome numbers, and geographic distribution of the five taxa of the genus *Larrea*.

Group	Morphological characteristics	Taxon	Leaflet number	Habit	Chromosomes (n)	Distribution
Multifoliolate	Flowers small, mericarps puberulous	*L. nitida* Cav.	8–16	Erect	13	Argentina and Chile
		L. ameghinoi Speg.	3–7	Prostrate	13	Argentina (Patagonia)
Bifoliolate	Flowers larger, mericarps hairy	*L. divaricata* Cav. subsp. *divaricata*	2	Erect	13	Peru, Bolivia Argentina Chile
		L. divaricata Cav. subsp. *tridentata* (Sesse. & Moc. *ex* DC.) Felg. & Lowe	2	Erect	13 26 39	Chihuahuan Desert Sonoran Desert Mohave Desert
		L. cuneifolia Cav	2	Erect	26	Argentina

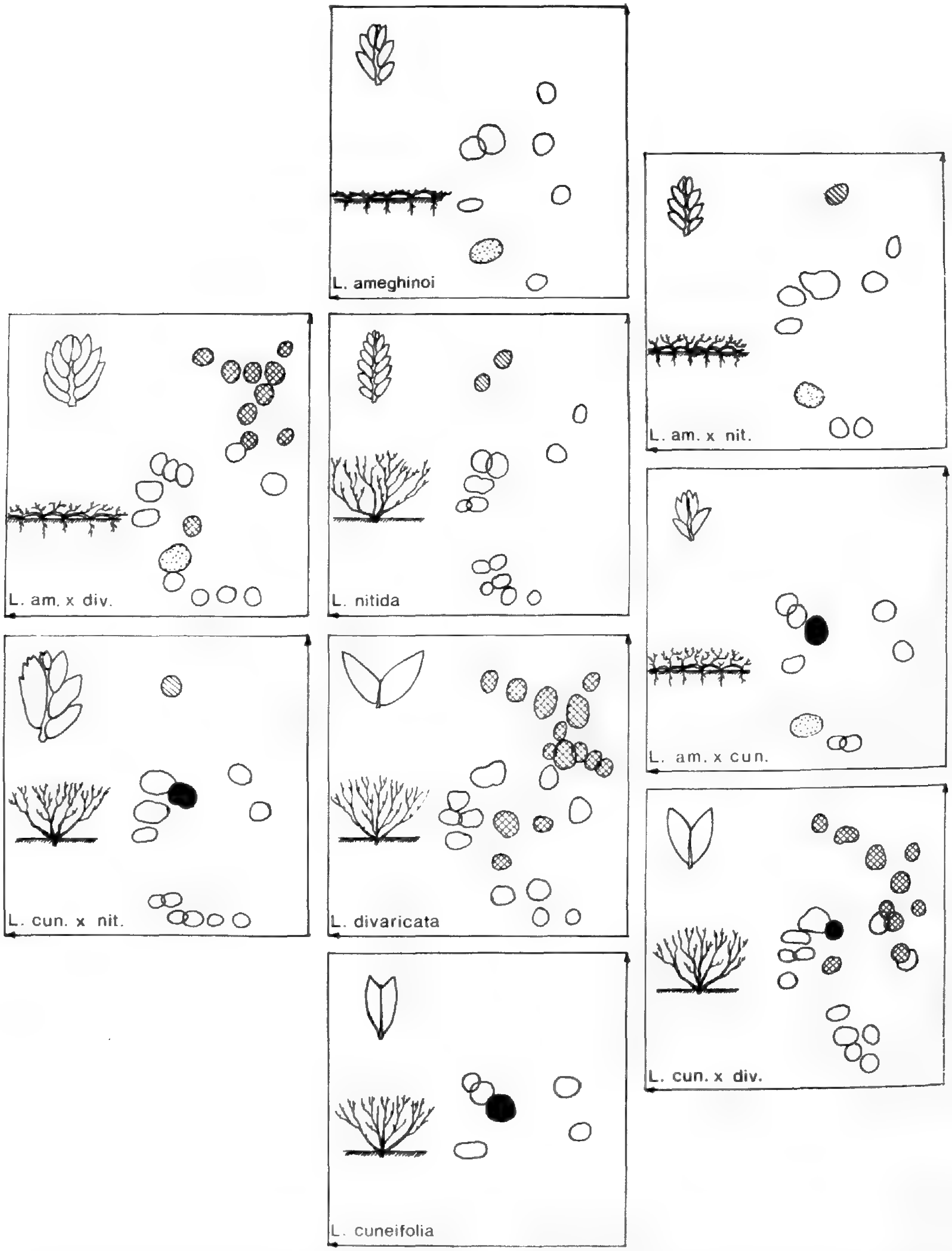

FIGURE 4. Leaves, growth habit, and phenolic compounds of North Patagonian species and hybrids of *Larrea*.

cells (Hunziker *et al.*, in preparation). *Larrea divaricata* is, therefore, one of the parental species of tetraploid *L. cuneifolia* or very closely related to one of the ancestral progenitors. The other hybrids are highly sterile (*L. ameghinoi* × *L. cuneifolia*), completely sterile (*L. cuneifolia* × *L. divaricata*), or flower rarely and

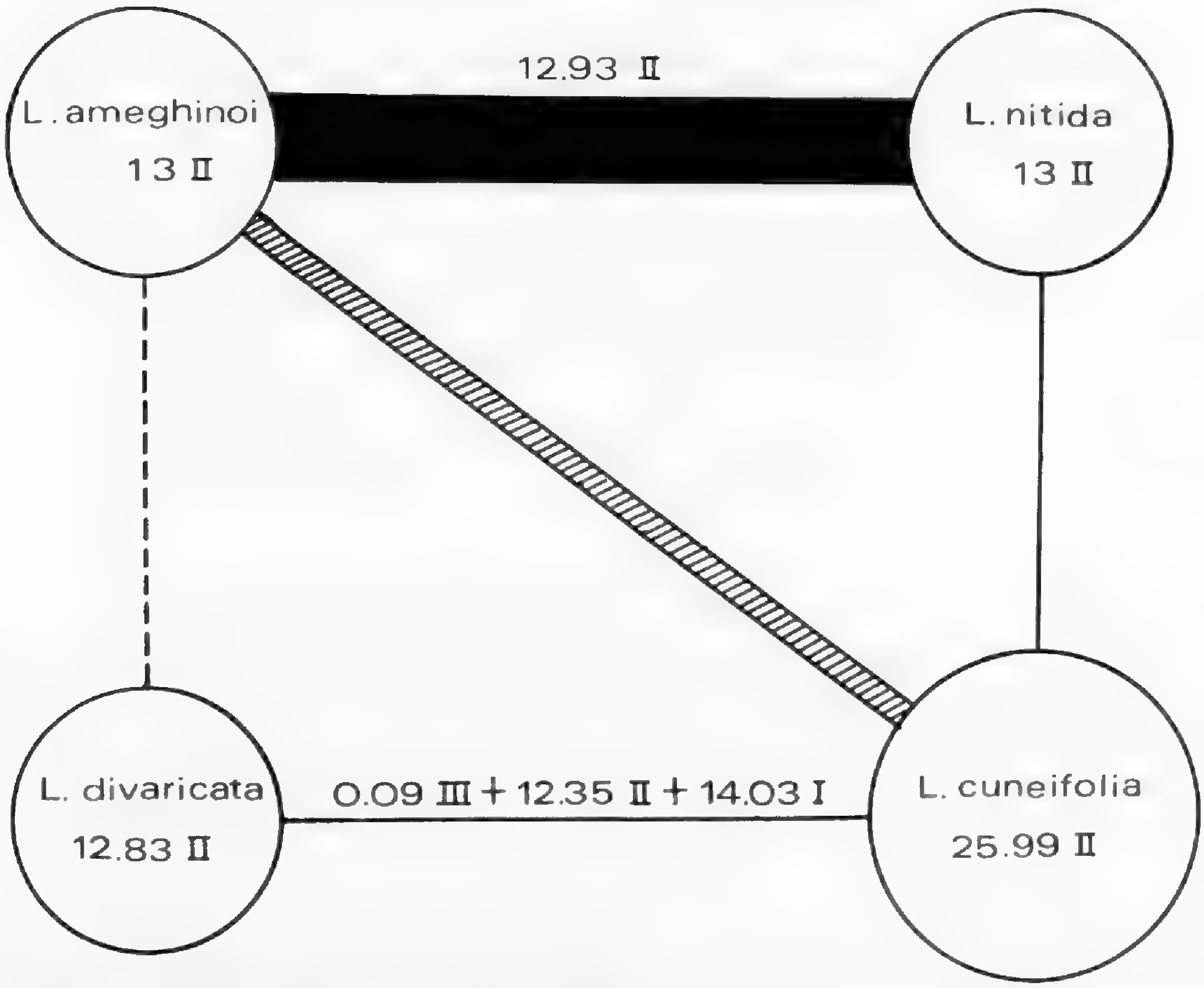

FIGURE 5. Putative crossing relationships of the four species of *Larrea* and their five natural hybrids. Mean chromosome associations are indicated for species and hybrids. The connections between circles give an idea of fertility as measured by the percent of seed-bearing mericarps: black, > 70%; hatched, partially fertile (15–19%); solid line, sterile; broken line, flowering sporadical, almost sterile.

are highly sterile (*L. ameghinoi* × *L. divaricata*). Analysis of chromosome associations in these hybrids could not be studied with success due to the occurrence of cytomixis, which produced cells with very different chromosome numbers and associations.

There is evidence that *L. divaricata* subsp. *tridentata* from California and *L. nitida* or *L. ameghinoi* are self compatible species (Twisselmann, 1956; Raven, 1963; Hunziker *et al.*, in preparation).

Larrea cuneifolia is possibly a relatively old species having a fairly wide distribution in Argentina. As we have seen, it shares a genome with *L. divaricata*, which would be one of its diploid progenitors. However, *L. cuneifolia* has lost many of the abundant phenolic markers produced by the South and North American *divaricata* genomes (Figs. 4, 6). The other diploid has apparently become extinct and perhaps was responsible for the two most remarkable morphological characteristics of *L. cuneifolia*: a) the fusion of the leaflets, and b) the orientation of the epiphylls towards the east.

It is probably this last characteristic, which enables the plant to avoid the full exposure of the leaves to noon sunrays, that makes *Larrea cuneifolia* more drought tolerant than *L. divaricata*. Since the *divaricata* diploid genome seems, therefore,

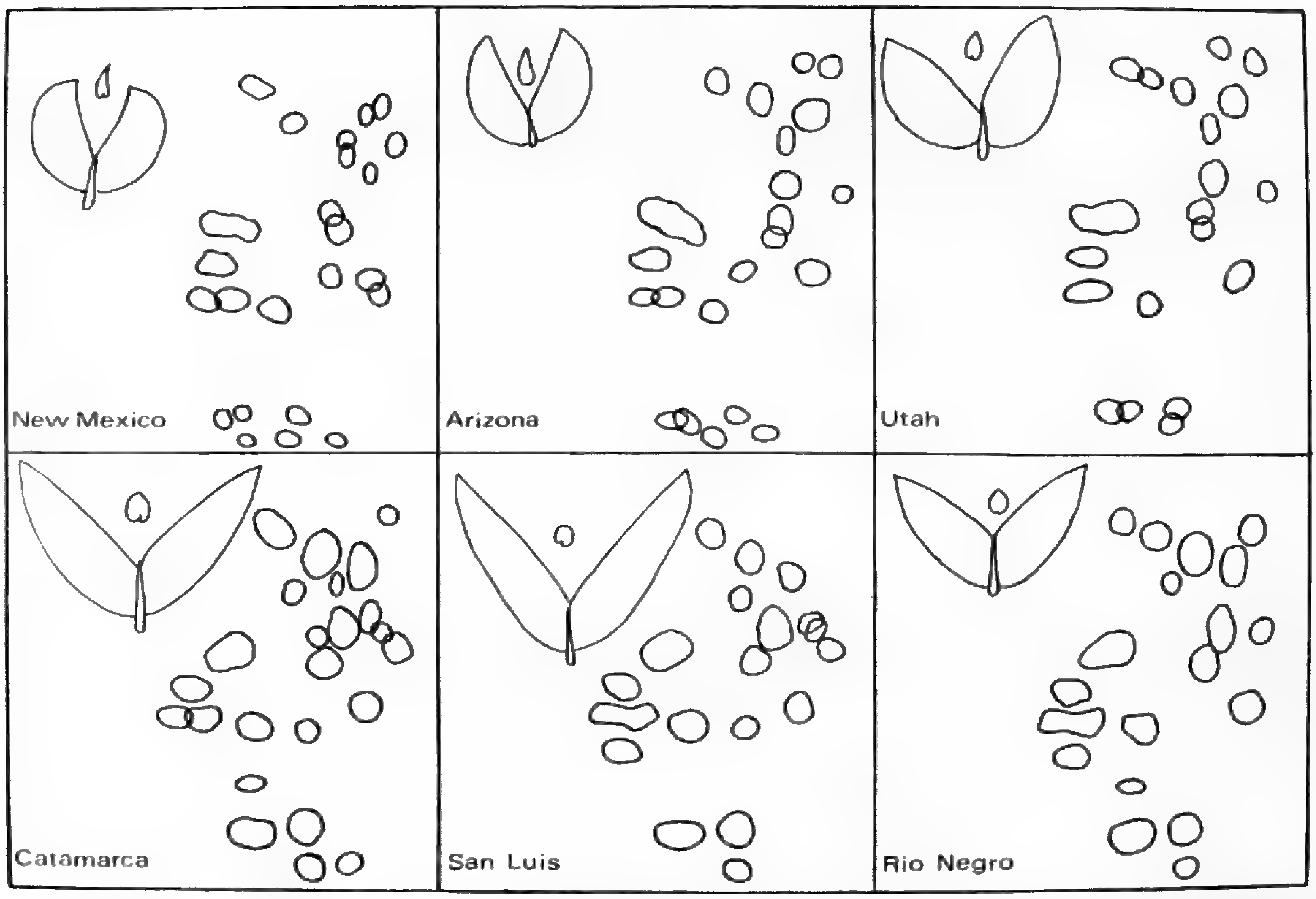

FIGURE 6. Chromatograms and leaf and stipule forms of three populations each of *Larrea divaricata* subsp. *tridentata* (upper row) and *L. divaricata* subsp. *divaricata* (lower row). New Mexico, Eddy Co., diploid (NME); Arizona, Tucson, tetraploid (AP, WA); Utah, near Toquerville, hexaploid (UW). All three collected by Dr. T. W. Yang, who also has determined the chromosome numbers. The samples of *L. divaricata* subsp. *divaricata* are from the northwest (Catamarca Prov., Dep. Belén, near Hualfin), center (San Luis Prov., Luján) and south (Río Negro, Dep. San Antonio, Mina Gonzalito) of Argentina.

to be quite an ancient one in South America it is possible that *L. divaricata* in South America is older than in North America.

THE DISJUNCTION OF *LARREA DIVARICATA* AND ITS DIFFERENTIATION IN NORTH AMERICA

The studies of Yang (1970) and Barbour (1969) have shown that *Larrea divaricata* subsp. *tridentata* in North America is composed of 3 races: diploid in the Chihuahuan Desert (Mexico, Texas, New Mexico, Arizona), tetraploid in the Sonoran Desert (Arizona, western Mexico, southeastern California) and hexaploid in the Mohave Desert (California, western Arizona, Nevada, Utah). With a few exceptions, these chromosome races are allopatric.

Yang (1970) studied 41 local races of *Larrea divaricata* subsp. *tridentata* regarding chromosome number. His detailed geographic chromosome survey shows (Fig. 1):

1) There appears to be some sympatric contact in limiting areas of diploids and tetraploids (southeastern Arizona). In some places diploids and tetraploids are living together (Population 18). Also in west-central Arizona and southeastern California hexa- and tetraploid plants occur together.

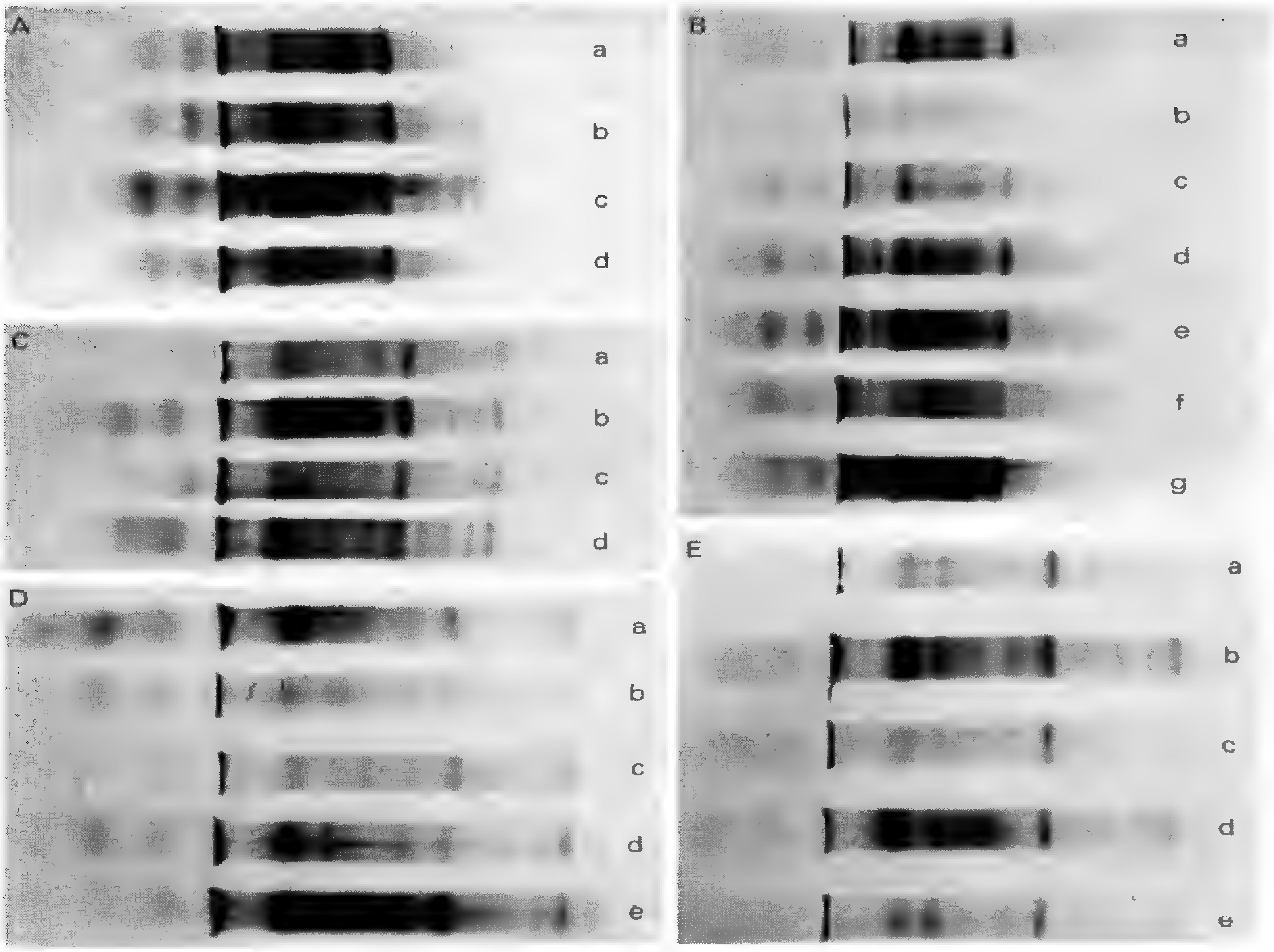

FIGURE 7. Polyacrylamide gel electrophoresis of seed albumins of South and North American *Larrea* species. Anode to the right.—A. Diploid *L. divaricata* from South and North America; a and b = subsp. *divaricata*; c and d = subsp. *tridentata*. [a = Dep. San Antonio, Río Negro, Argentina; b = Dep. Valcheta, 73 km W. of Sa. Grande; c = Hidalgo Co., New Mexico; d = Vizarrón, Querétaro, México.]—B. Diploid *L. divaricata* subsp. *tridentata* from different localities in the U.S.A.; a = Arizona, Pima Co.; b = ídem; c = New Mexico, Eddy Co.; d = New Mexico, Luna Co.; e = N. Mexico, Chaves Co.; f = Texas, Maverick Co.; g = Texas, Crockett Co.—C. Tetraploid *L. divaricata* subsp. *tridentata* from different localities in the U.S.A. a, b, and c = Arizona, Tucson or vicinity; d = Arizona, Pima Co.—D. Hexaploid *L. divaricata* subsp. *tridentata* from different localities in the U.S.A. a, b = Nevada; c = Nevada, Hoover Dam; d, e = Arizona, Mohave Co.—E. Different polyploid races of *L. divaricata* subsp. *tridentata*. a = diploid, Arizona, Pima Co.; b = tetraploid, Arizona, Pima Co.; c = tetraploid, Arizona, Yuma Co.; d = diploid, New Mexico, Eddy Co.; e = hexaploid, Nevada, Nye Co.

2) In these areas, so far no natural triploids and pentaploids have been found on the basis of actual chromosome counts. This is in fact surprising considering the amount of cross pollination that probably occurs due to insects, and to the fact that in South America hybridization among four different species is frequent and five out of the six possible hybrid combinations have been found. It may be a consequence of the difficulty in distinguishing the parents on morphological grounds. Therefore, the hybrids, if existing, might not be easily detected.

3) Yang (1970) has also found a disjunct diploid in Central Arizona (30 miles north-northeast of population 29, which is tetraploid). It is isolated from tetra-, hexa- and other diploid populations. (The nearest diploids are approximately 100 miles to the southeast.)

4) Diploid and tetraploid populations can be recognized in the field on the

basis of habit, height and other morphological features. Tetra- and hexaploid individuals are more difficult as already mentioned.

On the other hand, several chromosome counts made along a stretch of 2,500 km from individuals collected in the provinces of Salta, Tucumán, Mendoza, and Río Negro (from the northern, western and southern part of the area) indicate that subsp. *divaricata* is uniformly diploid in South America (Fig. 2).

The chromatographic pattern of the phenolics of North and South American specimens of *Larrea divaricata* present some slight differences but on the whole are strikingly similar (Fig. 6).

Electrophoresis of seed albumins has been found to support the arrangement of species within the genus made on morphological grounds (Hunziker, 1971; Hunziker *et al.*, in preparation). Moreover, the electrophoregrams show that there are few differences among diploids of *Larrea divaricata* growing in distant places as northern Patagonia (subsp. *divaricata*) and New Mexico (subsp. *tridentata*); compare *b* and *c* from Fig. 7A, which are separated by 74° latitude or nearly 7,000 km.

Within *Larrea divaricata* subsp. *tridentata* there are not marked differences in the protein patterns of the different chromosomal races. The diploid patterns present some slight differences among themselves (Fig. 7B). There are no obvious differences in the presence or absence of bands among the tetraploids except concentration of certain fractions (Fig. 7C). The hexaploids also show slight variation; they are almost identical except *e*, which shows an extra fast band on the extreme right (Fig. 7D).

As shown in Fig. 7E there are no major differences among di-, tetra- and hexaploid patterns. This strongly suggests that autoploidy is involved in the origin of tetra- and hexaploid populations of *Larrea divaricata* subsp. *tridentata.*

If alloploidy were involved, the tetra- and hexaploid patterns would be more complex than the diploids because in amphiploids generally there is at least some addition of protein fractions from the original diploids (Hall, 1959; Hall & Johnson, 1962; Johnson & Hall, 1965; Smith *et al.*, 1971).

CONCLUSIONS

On the basis of morphological, phenolic, and protein data it is likely that both diploid *Larrea divaricata* from South and North America should be regarded as conspecific, but the final answer to this question should come from the analysis of the hybrid between both populations (chromosome behavior, fertility).

The evidence from morphology, phenolic patterns, and albumin electrophoresis suggests that intervarietal autoploidy is involved in the origin, differentiation, and northwest migration of the chromosome races in North America. The entire distribution of the genus, with species diversity in northern Patagonia (primitive and more recent species) and the role played by diploid South American *Larrea divaricata* subsp. *divaricata* in the origin of a relatively old species such as *L. cuneifolia* suggests a South-to-North America pattern of migration. Since *L. divaricata* appears to be self compatible, this characteristic might have helped in the expansion of its range as suggested by Baker (1955).

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PLANT SPECIES DISJUNCTIONS: A SUMMARY[1]

PETER H. RAVEN[2]

Disjunctions in the ranges of plant species have fascinated biologists ever since they were first detected; their interpretation has long been regarded as one of the central problems of plant geography. It seems intuitively reasonable that following its origin, a species should migrate to occupy a more or less continuous range; but when we find it occupying two or more areas separated by hundreds or even thousands of miles, we wonder how this pattern could possibly have originated. If the disjunction is expressed at a higher level—for instance, generic or familial—the problem remains the same, but its solution may be even more difficult.

Other papers in this symposium have touched on the major classes of disjunctions which have concerned biologists in the past. Before reviewing these, it is appropriate first to consider some general points that pertain to the study of all disjunctions and to consider some of the new and important kinds of evidence that have been brought into play in recent years.

GENERAL CONSIDERATIONS

In the study of disjunctions, as in all other questions of plant geography, an accurate taxonomic framework is a prerequisite, as stressed by Wood (this symposium). For example, the moss *Macromitrium sullivantii* C. Müll., thought to be an endemic of a small area of the southeastern Blue Ridge escarpment of the United States, has recently been shown to be identical with *Macrocoma hymenostomum* (Mont.) Grout, a well known species that occurs throughout the American tropics and South America (Anderson, 1970). The range as now understood becomes a striking example of a disjunct distribution. On the other hand, the genus *Boisduvalia* (Onagraceae), comprising six species of semiarid western North and South America, was until recently thought to include a species of the mountains of southeastern Australia and Tasmania, *B. tasmanica* (Hook. f.) Munz. With the demonstration that this species is actually an *Epilobium*, now known as *E. curtisiae* Raven, which forms natural hybrid populations with closely related Australian species (Raven, 1963*a*, and unpubl.), the situation demands a very different interpretation. In efforts to clarify the relationships between disjunct populations, the methods of chemosystematics (Hunziker *et al.*, Wagner, Turner, this symposium), biosystematics (*e.g.* Moore & Raven, 1970; Wagner, this symposium), and other modern techniques often have proven useful adjuncts to the more traditional morphological approaches (Wood, this symposium).

If one considers the distributions of plants throughout the world, one will be able to find examples of almost any conceivable sort of disjunct range. Thus very

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[1] Support received from the U. S. National Science Foundation, most recently through Grant GB-29905, is gratefully acknowledged. D. I. Axelrod has kindly reviewed this manuscript.

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ANN. MISSOURI BOT. GARD. 59: 234–246. 1972.

few genera of semiarid habitats are common to Australia and South America, but *Plagiobothrys* (Boraginaceae), *Calandrinia* (Portulacaceae), and *Nicotiana* (Solanaceae) exhibit this sort of range. The fact that *Nicotiana* also occurs on some Pacific islands (van Steenis & van Balgooy, 1966: 78–9) may provide a clue to its pathway of dispersal, but hardly justifies the construction of a landbridge across the tropical Pacific, as proposed for example by Corner (1963). Similarly, the occurrence of *Sibthorpia* (Rosaceae), *Hypochoeris* (Asteraceae), and *Deschampsia setacea* (Huds.) Hack. (Poaceae) in Europe and South America, but not in North America, must be taken as special cases and not used as the basis for postulating vast geological rearrangements.

Nevertheless, when considerable numbers of ranges coincide in their disjunctions, we are justified in looking for some collective reason. The recurrent disjunction between eastern Asia and eastern North America has been treated elegantly by Wood in the present volume; that between semiarid North and South America by Solbrig and by Turner; and the famous disjunction in range between some of the plants and animals of temperate South America and temperate Australasia has been mentioned by Culberson and by Schofield and Crum. For these and other equally impressive patterns, some historical explanation must be sought, but it must always be kept in mind that most patterns have been affected, sometimes profoundly, by Pleistocene events (Whitehead, this symposium).

At its simplest, a disjunction in range shows that there is some similarity between the habitats in the two disjunct areas. This fact in itself should serve as a warning when attempting to make summary judgments, for when two habitats are similar, there is always some probability of additional plants achieving the disjunction, regardless of its original historical basis (Simpson, 1952). For example, the disjunctions in range between *Nothofagus* (Fagaceae) and Proteaceae in temperate South America and Australasia are certainly related to Eocene geography, as we shall discuss below. On the other hand, to assert, as Melville (1966) does, that *Juncus scheuchzerioides* Gaud. (Juncaceae) achieved its range at such a remote time, is incredible. This species has dust-like seeds easily carried in the mud adhering to the feet of birds, and it occurs on many subantarctic islands known to have been completely glaciated in the Pleistocene. It is often possible to assign a maximum, but not a minimum, age to any particular example of disjunction, unless there is a fossil record (Whitehead, this symposium). Whenever two habitats are similar, they may have similar plants and animals, regardless of how far apart they may be, and additional ones may be added at a rate consistent with their powers of dispersal subsequently. Many plants have achieved striking disjunctions in range as weeds since the initiation of human activities on a global scale (Wagner, this symposium), and this is an indication of the sort of process that went on continuously before.

As in every human question, the explanation of disjunction may be strongly colored by the expectations and desires of the explainer. It is tempting to adduce only certain fractions of the evidence in the espousal of particular explanations, but it is unreasonable to expect these explanations to be correct for the whole. Each disjunction has its own explanation, and the reasons can be verified convincingly for the particular case only if there is a fossil record.

LONG-DISTANCE DISPERSAL

Islands such as Hawaii, Tahiti, and Samoa have never been connected with any continental area, and yet they have acquired significant numbers of plants and animals as a result of long-distance dispersal. In the case of Hawaii, the pattern of dispersal has been particularly well documented (Fosberg, 1948; Gemmell, 1954; Carlquist, 1967, 1970). South American bryophytes have spread to Tristan da Cunha, a million-year-old island in the middle of the South Atlantic (Schuster, 1969). On Marion and Prince Edward Islands, which lie in the Antarctic Ocean south of Africa and are no more than 276,000 years old, there occurs a flora of at least 80 species of mosses (van Zanten, 1971) and 36 liverworts (Grolle, 1971), including many "Antarctic relicts" that are often taken as evidence of continental drift. On these same islands, a pollen grain of *Nothofagus* that must have come about 7,500 km from South America was collected from snow (Schalke & van Zinderen Bakker, 1971). Similar patterns are evident in both the Arctic and the Antarctic (*e.g.* Young & Kläy, 1971), where recolonization of areas glaciated in the Pleistocene has taken place rapidly and recently.

In the face of these observations, it is clear that long-distance dispersal must also take place with a certain frequency in continental areas, despite the attempts of authors such as Crum (1972) to minimize its importance. If islands that have never been connected to continents have acquired certain animals and plants, then animals and plants with similar characteristics must be dispersed between areas on the mainland also. The characteristics of seed plants that are dispersed to islands have been discussed in an elegant essay by Carlquist (1967). The question is whether they will, once they have reached new areas, become established.

One of the most important aspects in the establishment and subsequent fate of a plant in a new locality is the breeding system of the population in question. Thus Baker (1955) pointed out the connection between self-compatibility and establishment following long-distance dispersal. In the present symposium, Schofield and Crum have considered the effect of dioicism upon establishment by moss species, while Klekowski has stressed the genetic constitution of the sporophyte as related to the characteristics of the gametophyte in ferns. In both bryophytes (Crum, 1972) and ferns (Tryon, 1970), the spores are light and easily airborne for great distances; despite this, and also in the lichens (Culberson, this symposium), patterns of distribution, while perhaps somewhat broader on the whole, are strikingly like those observed in the flowering plants. In bryophytes and ferns, the gametophytes and sporophytes may demand different conditions for survival; and in both, gametophytes may occur far beyond the range in which sporophytes are normally produced in nature (Schofield & Crum, Wagner, this symposium). This is especially likely in dioicous mosses, for obvious reasons.

SEA-FLOOR SPREADING

During the past five years, the earth sciences have been the subject of a major revolution, as theories of plate tectonics have provided for the first time a basis sufficient to account for the kinds of movements of the continents first postulated in 1915 by Wegener (Hammond, 1971*a*, 1971*b*). Since much of the information now generally accepted about the late Mesozoic and early Tertiary positions of the continents is of direct application to problems of disjunction in the ranges of plant taxa, it will be summarized briefly here.

Among the salient points that are emerging from this new synthesis are the early Cretaceous (110 m.y. BP) separation of South America from Africa, the middle Cretaceous (~ 90 m.y. BP) separation of Africa from Antarctica, the early to middle Eocene (55–47 m.y. BP) separation of Europe from North America, and the upper Eocene (45–49 m.y. BP) separation of South America and Australia from Antarctica (Dietz & Holden, 1970; Tarling, 1971; Raven & Axelrod, 1972). Some of the progressive climatic change that has taken place through the course of the Tertiary has been associated with sea floor spreading and changes in the position of the continents. For example, North America, Africa, and Australia have moved northward some 15° of latitude during the Cretaceous and Tertiary, and India some 50°, colliding with the mainland of Asia and throwing up the Himalayas in the process. All of these changes have had profound effects upon the disjunct distributions we observe at the present, as will be discussed below.

AGE OF TAXA INVOLVED IN DISJUNCTIONS

Increasing study of the fossil record has begun to provide valuable information on the probable age of angiosperm taxa, which can be brought to bear on problems of the age of particular disjunct ranges. For example, despite worldwide study and the common use of their pollen as indicators of particular strata, Asteraceae have not been identified in the fossil record before the lower Miocene, some 25 m.y. BP (Muller, 1970), and the tribe Cichorieae of this family not until the upper Miocene, about 10 m.y. BP (Couper, 1960). Too much evidence is available now to continue ignoring this fact, and it is scientifically inadmissible to continue attributing "antarctic" distributions of members of this family to dispersal across Antarctica during the Cretaceous or Eocene, more than 40 m.y. BP. Indeed, it is doubtful that *any* living sympetalous genus, with advanced pollination systems, existed early enough to have taken advantage of such a route of dispersal. The species of *Microseris* (Asteraceae—Cichorieae) that occur in western North America, western South America, and temperate Australasia can *only* have achieved their present ranges by long-distance dispersal, regardless of how improbable this may seem.

It is worth noting in passing that we have very little hard evidence about the rates of evolution of particular taxa, and it is extremely dangerous to reason from a given degree of morphological divergence to a length of time thought necessary to produce that divergence. If the Hawaiian honeycreepers (Drepanididae) could have differentiated from a common ancestor within a million years (Bock, 1970), why should we assume that the Hawaiian silverswords and their relatives (Asteraceae—Madiinae) have taken longer? On the other hand, certain plant species in Europe and western North America have scarcely changed since the late Eocene, some 40 m.y. (Axelrod, 1958, 1973)—much longer than the entire history of the family Asteraceae, in all likelihood. It is simply not justified to state that a certain degree of differentiation must have required a certain length of time, unless there is a fossil record, yet arguments of this sort are commonplace in the literature on disjunct distributions.

Major Patterns of Disjunction

Five major patterns of disjunction have been discussed repeatedly in the literature and mentioned frequently in the papers of this symposium. In addition, smaller disjunctions have been considered in other papers of this symposium and very often in the literature. The five major patterns distinguished here are treated in the sections that follow.

1. North Temperate Disjunctions

It has long been noted that many of the forest plants of the north temperate region have disjunct ranges, commonly between eastern Asia and eastern North America, but also involving western North America, southeastern Europe-Asia Minor and the mountains of eastern and southern Mexico. In the light of recent geological information, the long-standing explanation first proposed by Asa Gray, that of migration through the Bering Straits in times of milder climate, must be regarded as highly questionable. About 47–55 m.y. BP, in the early to middle Eocene, North America was still broadly joined to Europe from about 50°N latitude northward (Dietz & Holden, 1970). At this time Arcto-Tertiary forest vegetation was continuous across northern Europe and in much of western North America (Axelrod, 1973), and it is clear that the main migration path between Eurasia and North America was *via* Europe and the eastern United States (McKenna, 1972). By the start of the Tertiary (63 m.y. BP), the relationship between Asia and North America approached that of the present day (Pitman & Talwani, 1972; Churkin, 1972), so that migration into and out of North America was possible both from the east and from the west. The Bering Straits seem to have functioned as an important migration route between North America and Eurasia throughout the Tertiary (Simpson, 1947; Hopkins, 1967), although the geological history of Beringia needs further consideration in the light of plate tectonics.

If these relationships are as assumed above, the close similarity of Miocene floras in Japan, Alaska, and Oregon (Wolfe & Leopold, 1967) is not surprising. In the Cretaceous, there seems to have been a greater similarity between the pollen floras of eastern Asia and eastern North America than to any other part of the north Temperate zone; Muller (1970) has recognized an East Siberian-North Pacific pollen province and a North Atlantic-European one, reviewing the pertinent palynological literature. Smiley (1967) has considered Cretaceous leaf floras of Alaska to be closely similar to those of northeastern Siberia, although he later (Smiley, 1969) has stressed the homogeneity of the floras of the entire northern portion of Eurasia and North America at this time. These observations are consistent with the hypothesis of Churkin (1972), which places the west boundary of the North American continental plate in Yakutia, east Siberia. This suture is believed to have closed in early Cretaceous time. Nonetheless, direct migration *via* Europe apparently was feasible between Eurasia and North America into the early to middle Eocene (55–47 m.y.).

Disjunct ranges in the north temperate forest, excepting the rapid expansion of Arctic species into formerly glaciated areas, are mainly Eocene in origin. For the boreal conifers, a more recent disjunction is implied. These relationships are interesting from an evolutionary point of view, because they imply that the related species of eastern Asia and the eastern United States have been evolving in isolation for approximately 47–55 m.y. As pointed out by Wood (this symposium), there are genera common to these two regions but very few species, a good indication of evolutionary rate in the groups concerned. Plants that are now found in various favorable areas of the north temperate zone have, in general, been separated by the deterioration of the climate in intervening areas; in this process, Pleistocene glaciation in Europe, with its east-west trending mountains, and the uplift of the Sierra Nevada-Cascade system in western North America have been important.

In evaluating such relationships, however, it is important to remember that for most of the Tertiary, the North Atlantic has been much narrower than at present, and probably was also dotted with islands. For many million years after the definitive separation of Europe and North America, birds probably flew back and forth regularly, and the probabilities of dispersal were very different from those obtaining at present. Some of the common species might have attained their disjunct ranges even more recently, as stressed by Wood (this symposium), as a result of long-distance dispersal; but it must be borne in mind that these are "closed" communities, where the chance of establishment may be relatively low, even if a seed does reach the disjunct area occasionally. For such entities as orchids, *Phryma leptostachya* L. (Verbenaceae), and *Circaea* (Onagraceae), all of which have readily dispersed seeds or fruits, it is difficult to imagine that they attained their disjunct ranges as early as the Eocene, and it would be dangerous to use their distributions to argue for or against such an antiquity for these plants.

One special disjunct pattern in the north temperate zone involves persistence in areas of mild oceanic climate, documented in this symposium by Culberson (for lichens), Schofield and Crum (for mosses), and Wagner (for ferns). Such ecological requirements have resulted in disjunctions between western North America and Europe, both onshore from warm oceanic currents. Patterns of this sort are rare or absent among the flowering plants.

2. East-west Desert and Mediterranean Disjuncts

Although there has always been a belt of reduced precipitation flanking the tropics, areas of desert and mediterranean climate in their present continental scale are a phenomenon of the past five million years (Axelrod, 1958, 1973; Raven & Axelrod, 1972). Some plant families that are restricted to semiarid or subhumid habitats have certainly been in existence since the Cretaceous, as pointed out by Rzedowski (1962) and others, but many species and genera confined to these areas have had a much more recent origin. In general, there is very little evidence for contact between the plants of the desert and mediterranean areas of North America and Eurasia (Raven, 1971, 1973*a*), despite the fact that these continents were broadly joined in the Eocene (Dietz & Holden, 1970; Tarling, 1971). This implies strongly that the plant associations involved were not in existence at the time, and also probably reflects the fact that the continents were joined only at the north. It also suggests that the few genera and even fewer species common to the deserts and areas of mediterranean climate in the Old and New Worlds must have attained their present ranges by long-distance dispersal, a contention supported by the almost complete faunistic dissimilarity of the two areas. The several mosses (Schofield and Crum, this symposium) with this disjunction in range were almost certainly spread from one area to the other by long-distance dispersal.

3. Tropical Disjuncts

As reviewed by Axelrod (1970), there are many genera and infrafamilial taxa common to Africa and South America. Most of these presumably were present in the tropical vegetation of the two areas when they were contiguous in the early Cretaceous, or evolved in one or the other when the two continents were relatively near and partially connected by islands. Primary freshwater characoid fishes certainly spread overland between Africa and South America (Myers, 1967). On the other hand, present patterns of distribution suggest strongly that Cactaceae and Bromeliaceae evolved in South America subsequently, one genus of each having reached Africa, perhaps quite recently, by long-distance dispersal. If Bromeliaceae had been in existence in the Cretaceous, for example, it would be virtually unimaginable that they would not be represented in Africa at present. This strongly implies that the entire evolution of the family has taken place in the past 110 m.y. or less, a useful landmark in the fossil-poor monocots.

Many other plants have been dispersed between Africa and South America during the Tertiary, and they are doubtless still being dispersed at present. This possibility has been stressed recently by Iltis (1967) and others, and it would be a serious error to relate every disjunction between the continents to Cretaceous geography. In the lichen *Parmelia* subgen. *Amphigymnia*, discussed by Culberson (this symposium), it is especially difficult to date the time of dispersal between South America and Africa, in view of the presence of wind-dispersed soredia or isidia in many species; they may have been lost in others in the course of evolution.

Prior to the middle Tertiary, migration between subtropical areas in southeast Asia, India, and Africa has been simple and direct. Only with the late Tertiary development of the deserts of Arabia and the Near East has this communication been interrupted, and it is therefore not surprising to find many links between the floras of the Indo-Malaysian region and Africa. Madagascar, now known to have been separated from the coast of Somalia in the Cretaceous or more recently (Heirtzler & Burroughs, 1971), is the home of many relict plants and animals that have become extinct on the African mainland subsequently. Such survival accounts for the otherwise inexplicable similarities between the flora and fauna of Madagascar and the West Indies (Stearn, 1971) and between Madagascar and New Caledonia (Good, 1950).

Australasia, moving northward some 15° of latitude during the past 45–49 m.y., has approached tropical latitudes only within the past 10 million years, particularly with the emergence of New Guinea (Oligocene and subsequently; Raven & Axelrod, 1972). It has acquired its tropical flora during this period of time from the Indo-Malaysian region and as a result of the evolution of tropical representatives of archaic, austral groups of plants and animals as it moved northward.

4. Southern Hemisphere Temperate Disjunctions

Biologists have long been fascinated by the group of plants and animals that occupy disjunct ranges in the far-flung disjunct lands of the southern hemisphere. Many of these are related to the position of Australia and South America at the close of the Eocene, some 45–49 m.y. BP; both were directly connected with Antarctica (Dietz & Holden, 1970; Tarling, 1971; Raven & Axelrod, 1972). All three continents were occupied by a continuous cool temperate forest of gymnosperms and evergreen angiosperms that existed under equable conditions; in this forest were such plants as Podocarpaceae, Araucariaceae, Proteaceae, Winteraceae, Atherospermataceae, Epacridaceae, Loranthaceae, Myrtaceae, *Nothofagus*, and *Gunnera*, as well as many groups of lower plants and invertebrate animals that now have disjunct distributions in the south, including marsupials, hylid and leptodactylid frogs, and chelyid turtles, which crossed from South America to Australia by this route (review in Raven & Axelrod, 1972).

The gradual disruption of this once continuous forest by the movements of the continents was provided a predominant theme in southern hemisphere distributions. Some distributions, however, may be related to the earlier connection of Africa and India with Antarctica, broken during the middle Cretaceous. The austral gymnosperms (Florin, 1963), side-neck turtles, ratite birds, and galaxiid fishes (Darlington, 1948; Evans, 1958) seem to have reached Africa by this route, as did some leafy liverworts (Fulford, 1963). Among the angiosperms, there are a few patterns of distribution that suggest dispersal prior to the separation of Africa from Antarctica. Proteaceae, best developed in Australia, with closely related lines in South America and Asia and three very distinct lines in Africa, are suggestive of such a history (Johnson & Briggs, 1963); Xyridaceae and Restionaceae are also possible candidates (Cutler, 1972). It seems purely fanciful to relate the distributions of such living genera as *Gossypium* and *Solanum* (Hawkes & Smith, 1965), which provide no hint of such antiquity, to Cretaceous geography. Both genera have native species in Hawaii. The suggestion of Turner (this symposium) that the Centrospermae differentiated in a Gondwanaland that included Africa (= early Cretaceous) is almost ruled out by the Eocene origin of most families in this group (Muller, 1970). On the other hand, the families he discusses may well have differentiated in the south, after the separation of Africa, and subsequently spread to the northern hemisphere.

Many disjunct distributions involving southern lands, in contrast, are recent in origin (Moore, 1972); the case of *Juncus scheuchzerioides* and some other examples have already been mentioned. A number of plants that are easily dispersed by wind have doubtless been spread by the prevailing westerlies, seasonally four times as powerful as the corresponding winds in the northern hemisphere (Lamb, 1959). There is a great deal of evidence of such dispersal of small animals and seeds; recently data have been published which show that a balloon released at Christchurch, New Zealand, and held at approximately 40,000 feet elevation, made eight complete circuits of the southern hemisphere during 102 days (Mason, 1971). Other plants have been carried in the ocean currents (Sykes & Godley, 1968) or by birds (review in Raven & Axelrod, 1972; Raven, 1973*b*; see also Carlquist, 1970, Chapter 4). Like all other disjunct distributions, ones between the southern lands must be taken with caution as indications of the age of the groups involved.

A single concrete example involves *Fuchsia* (Onagraceae), with more than 50 species in South America (northward to Mexico and the West Indies) and one section of four species in the Old World, three in New Zealand and one in Tahiti. It might at first be supposed that *Fuchsia* was a member of the Antarcto-Tertiary Geoflora and reached its disjunct stations overland via Antarctica, but four lines of evidence suggest that this was not the case: 1) the family Onagraceae may be no older than the middle Eocene (Muller, 1970); 2) *Fuchsia* first appears in the fossil record in New Zealand in the middle Miocene, fully 25 million years after the separation of Australasia from Antarctica, and it is not known from the fossil record in either Australia or Antarctica; 3) *Fuchsia* is bird-pollinated, both in the Old World and the New, and it is most unlikely that the specialized lines of birds that regularly visit and pollinate flowers were in existence much, if at all, before the Miocene; and 4) *Fuchsia* occurs on Tahiti, which stands in the middle of the Pacific and has never been connected to any land, a station it must have achieved by long-distance dispersal. In summary, the weight of evidence suggests strongly that *Fuchsia*, despite its occurrence in cool-temperate forest in both South America and New Zealand, attained its present disjunct distribution long after Antarctica was no longer available as a migration route, by means of long-distance dispersal across the Pacific.

5. Trans-Tropical Disjunctions

Disjunct distributions that span the tropics are not as likely to be remnants of formerly continuous distributions as the sorts of east-west disjunctions we have just discussed. Nevertheless, as Solbrig (this symposium) has indicated, there are opportunities for plants and animals of semiarid habitats to achieve only slightly interrupted ranges through the tropics even at the present day. Certain plants of temperate regions must also have passed through the tropics along elevated regions in the distant past, as suggested for example by the presence of *Nothofagus* as the only genus of Fagaceae in the southern hemisphere.

There are relatively few trans-tropical disjunctions involving Europe and Africa, presumably because the temperate area of South Africa is so limited. More disjunctions are known involving Asia and Australasia, and most of these seem quite recent in origin. Australasia has come into contact with Asia only in the upper Miocene, some 10 million years ago, and the mountains of Malaysia, New Guinea, Australia, and New Zealand were all uplifted in the Pliocene and later. Consequently, the migration paths visualized by van Steenis (1934*a*, 1934*b*, 1936) through Malaysia are no more than a few million years old, and the plants found on these mountains reached their disjunct stations mainly during the late Pliocene and Pleistocene by long-distance dispersal. Many north-temperate groups of plants reached Australia and New Zealand only at this time, and some have evolved rapidly in the newly opened subalpine and alpine habitats, particularly in New Zealand (Raven, 1972).

The best studied and most numerous transtropical disjuncts are those between North and South America, which have been in approximately their same relative positions since at least the Cretaceous (Raven 1963*b*; Moore, 1972). Many of these involve identical or very closely related species of annual herbs in areas of mediterranean climate that were set up only in the late Pleistocene and subsequently (Moore & Raven, 1970; Raven, 1973*a*; Axelrod, 1973); there seems no doubt that most of these have achieved their disjunct ranges by direct, long-distance dispersal within the past several hundred thousand years. Each year during this time millions of individuals of the semipalmated plover, *Charadrius vulgaris*, have migrated between the areas that have disjunct plant species on the two continents, and these birds have provided at least one obvious means for direct long-distance dispersal (Cruden, 1966). Carlquist (1967) has convincingly demonstrated the probability of dispersal by birds as a means for achieving many of the disjunct distributions between North and South America, comparing these patterns with those involving dispersal to the Pacific Islands. Other plants have moved between North and South America by shorter jumps along the Andean chain, presumably in the main following its Pliocene uplift (Raven, 1973*a*).

Disjunctions on range between the plants of desert and other semiarid areas of North and South America have received considerable attention in this symposium (papers by Hunziker *et al.*, Solbrig, Turner). Even though areas of reduced precipitation have existed on the margins of the tropics since the beginnings of angiosperm evolution, and provided the initial site of evolution of many of the plant groups that occur in these deserts at the present time, the deserts themselves, in their present continental scale, are a phenomenon of the latest Tertiary (Axelrod, 1958). In other words, chances for dispersal between these areas, across the tropics or from east to west, are greater now than they have ever been at any time in the past (Axelrod, 1952). Solbrig has rightly re-emphasized the various times of dispersal that must have led to the many different patterns of disjunction at the present time. Some of the woody plants common to the deserts of North and South America have differentiated from tropical ancestors, whereas others extend more or less continuously through the tropics in "islands" of subhumid vegetation.

In general, the dissimilarity of the vegetation of semiarid areas in the Old and New World is a strong indication that many of the groups now involved in disjunctions in the New World were rare or not in existence in the Eocene. At any time subsequently, they may have become dispersed between North and South America, almost certainly in a series of steps. Drier sites in the tropics may have provided stepping stones by which such plants may have become dispersed throughout the Tertiary, but the fact that less than 2% of the desert floras of Argentina and the southwestern United States and adjacent Mexico are common to both areas makes it quite impossible to imagine a direct and simple pathway through the tropics, also not possible on climatic grounds. In addition, the insects and other animals of the two areas are almost entirely different, something that would not be true were there direct communication. The level of similarity that is actually observed is consistent with a sporadic, stepwise migration, operating at different times throughout the Tertiary and by different pathways, and resulting in a limited exchange of plant species and genera between North and South America. Detailed studies, such as that of Hunziker *et al.* (this symposium) on *Larrea* (Zygophyllaceae), will be necessary to clarify individual cases.

Concerning trans-tropical disjunctions, however, Florin's (1963) insistence on the long-sustained separation of north and south temperate floras still provides the most cogent generality. The uplift of mountains in the tropics of Africa, Malaysia, and America has facilitated movement between northern and southern hemisphere temperate areas, but such movement has apparently never been particularly easy, despite indications (*e.g.*, the origin of *Nothofagus*; podocarps and araucariads in the Tertiary of Europe) that it has continued throughout the entire history of angiosperms. During Pleistocene and Recent time, the great expansion of open semiarid habitats on both sides of the tropics has apparently provided conditions especially favorable for the establishment of some plants following long-distance dispersal, but the only appreciable exchange of this sort seems to have been that between North and South America, perhaps because these areas lie on regular migration paths of birds. There has been almost no corresponding exchange between semiarid regions of the Old and New Worlds except that brought about as a result of human activities. There is a considerable amount of bird migration between Eurasia and South Africa, but almost none that crosses Wallace's line into Australasia (McClure, 1971). Could this possibly be attributable to the relatively recent (15 m.y. BP) juxtaposition of Asia and Australia?

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NOTES ON PANAMANIAN TREES AND SHRUBS COLLECTED IN 1971 BY L. R. HOLDRIDGE AND OTHERS

John D. Dwyer[1]

The following is a list of trees and shrubs collected by L. R. Holdridge, E. A. Lao, L. Maasola, and A. Gentry during the spring and summer of 1971 in the Republic of Panama. All the collections were made at approximately sealevel; the few collected at or above 100 meters will be noted in the list. No collection was made above 650 meters. Collections of the following families seem especially important: Humariaceae, Lauraceae, Myristicaceae, and Sapotaceae. Some material was identified in the sterile state by Dr. Holdridge and possibly by his colleagues; the sterile collections are recognized in the list by the asterisk (*) placed before the collector's name. The author identified approximately one half of the collections which are in flower and fruit. The collections of the Burseraceae and Rutaceae were identified by Dr. Duncan Porter; the Boraginaceae were identified by Dr. Joan Nowicke. Dr. Thomas Croat gave valuable assistance in the critical identification of several species. Miss Mireya Correa A. of Panama University deserves a special note of thanks for forwarding some of the collections. Mr. Yow-Yuh Chen of the Department of Biology, St Louis University, prepared the figure of the *Sacoglottis* fruit.

Among the more than 180 collections in the list one encounters 47 localities in Panama. For the sake of convenience the localities have been segregated along provincial lines and listed below, with each locality being given a number. The number is placed in parentheses following the collector and his collection number.

Bocas del Toro
1. Isla Colón; 2. La Gruta, Isla Colón; 3. El Chumical.
Canal Zone
4. Albrook; 5. Ancón; 6. Balboa; 7. Pipe Line Road; 8. Summit Garden.
Colón
9. Between Colón and Portobelo; 10. Buena Vista; 11. Entrada a Sabanitas; 12. Gatún; 13. María Chiquita; 14. Playa Langosta; 15. Portobelo; 16. Río Indio; 17. Río Piedras; 18. Río Santa Izabel; 19. Río Trapiche; 20. Road to Portobelo; 21. Salud; 22. Santa Rita; 23. Santa Rita Arriba; 24. Villa Alondra, road to Portobelo; 25. West of Canal Zone.
Herrera
26. Menchacha, Ocú; 27. Llaño de Las Minas; 28. La Cabuya, Las Minas; 29. Cerro Colorado de Las Minas; 30. El Chumal; 31. Los Hatillos, Pesé; 32. Quebrada El Cammaron; 33. Divisa.
Los Santos
34. El Ejido de Los Santos.
Panamá
35. Arraíjan, Cerro Silvestre; 36. Calzada Larga; 37. Canitos de Chepo; 38. Capira; 39. Cerro Azul; 40. Chichebre, Chepo; 41. Chiltepe; 42. La Chorrera; 43. La Cresta; 44. Nuevo Guararé; 45. Panamá; 46. Río Indio; 47. Sajalices, Capira.

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Ann. Missouri Bot. Gard. 59: 247–261. 1972.

In citing the collections the following format has been used. The families are arranged alphabetically. In parentheses, following the name of the family, one finds the author, the part, the volume, pagination, and year of publication of the specific family as found in the *Flora of Panama*, published periodically in the ANNALS OF THE MISSOURI BOTANICAL GARDEN. Some families have not been treated in the ANNALS, *e.g.* Rubiaceae.

Following the binomial name and its author, the collectors are abbreviated as follows: *G*—Gentry; *H*—Holdridge; *L*—Lao; *M*—Maasola. The collection site of each collection is indicated by the number in parentheses following the collection number. The DBH of the tree or shrub is given in centimeters and the height in meters, as for example 8 cm × 6 m. Common names, supplied by collectors, are appended. The notes which accompany many of the species in the list are those of the author, unless otherwise indicated. Special stress is placed upon range extensions within the Republic of Panama. Families recently treated in the *Flora of Panama* may be considered reliable in determining geographical ranges of species in the Republic. All determinations made by the author were checked in the herbarium of the Missouri Botanical Garden. Dr. L. R. Holdridge also checked much of the material at the same institution.

It is appropriate to point out that many species of trees and shrubs from Panama are poorly represented in herbaria. The arboreal vegetation, and for that matter, all kinds of vegetation, along the Atlantic face of the Isthmus, is poorly known. This is especially true of the area extending from the Province of Bocas del Toro, especially its eastern part, to the western side of the Panama Canal and into the Province of Colón. More than a quarter of the collections cited in this paper are from Salud, Province of Colón, immediately adjacent to the western part of Gatun Lake in the Canal Zone. These collections serve to support the need for intensive collecting in Colón. Equally significant are the collections in the list, though fewer in number, made in Colón on the eastern side of the Canal. The Santa Rita area in Colón, which is currently attracting a large number of collectors, has yielded several new species and has proven important in extending the geographical ranges of many others. While our collectors did not extend their efforts to the Province of Darién, it is appropriate to point out that there are few collections from the mountains of Darién. This makes it difficult to trace the geographical distribution of montane species at the eastern end of the Republic and in neighboring Colombia. By the same token the few specimens available from the Atlantic side of the western end of the Isthmus present a problem in defining phytogeographical relationships between Costa Rica and Panama. The reader is referred to my remarks concerning areas poorly collected in Panama (Dwyer, 1964: 115).

ANNONACEAE (Fries—Part 4. Vol. 49: 491–525. 1962).

Annona glabra L.—*L & H 234* (21), 10 cm × 8 cm. This species grows in southern Florida, tropical America, and West Africa. It is common in Panama.

A. spraguei Saff.—*L & H 179* (25), 9 m. A strictly Panamanian species with wide distribution in the Republic.

Malmea depressa (Baill.) Fries—*L 96* (1), 30 cm × 20 m, "Yaya." This species is not listed in Fries' recent treatment but was collected by Bristan (*360* (MO)) near Río Ganglon, Darien. The species extends from Mexico to Panama.

Stelechocarpus burahol (Hook. f.) Thoms.—*H 6518* (8), 20 cm × 6 m. This exotic species, native of Malaya, was identified by Dr. Croat. The flowers are cauliflorous.

Unoniopsis floribunda Diels—*L 91* (1), 20 cm × 16 cm, "Yaya Amarilla."

U. panamensis Fries—*L & H 161* (20), 4 cm × 7 m. This species heretofore has been known only in Panama from Cerro Campana, Province of Panamá.

U. pittieri Saff.—*L & H 50* (16), 3 cm × 6 m. This species has been previously collected in the Canal Zone and in the Province of Colón. It has been reported from British Honduras, Honduras, and Panama.

Xylopia macrantha Tr. & P.—*L & H 51* (16). The fruits only were collected. The aggregate fruits are as large as a tennis ball. Dr. Croat reports that he has collected fruits twice this size on Barro Colorado Island, Canal Zone; the follicles, on splitting become brick-red within.

ANACARDIACEAE (Blackwell & Dodson—Part 6. Vol. 54: 351–379. 1969).

Spondias mombin L.—*L 62* (47),—18 cm × 10 m. A common tree in Panama.

APOCYNACEAE (Nowicke—Part 8. Vol. 57: 59–130. 1970).

Himatanthus sp.—*L & H 188* (21), "Calacuchillo," collected at 100 m. This sterile specimen is probably *H. articulata* (Vahl) Woodson. It is known in Panama only from the Provinces of Darién and San Blas. Nowicke (p. 81) erroneously cites *Williams 823* (NY), collected in Cana, Darién, as having been collected in the Province of Colón.

Malouetia tamaguarina (Aubl.) DC—*L 159* (20), 6 cm × 5 m. This species has not been reported north of the Guianas. Holdridge identified this collection. I note, however, that the fruits are not elongate and linear but rather measure about 1½ cm in diameter. The leaves of the Lao collection, on the other hand, certainly suggest *M. tamaguarina*.

AQUIFOLIACEAE (Edwin—Part 6. Vol. 54: 381. 1967).

Ilex guianensis (Aubl.)Ktze—*L & H 229* (21), 10 cm × 8 m. This species has heretofore been reported from Bocas del Toro, Chiriquí, and Panama, this being the initial collection from Colón.

ARALIACEAE

Dendropanax arboreus (L.) Dcne. & Planch.—*L, H & G 15* (7), 15 cm × 10 m, collected at 350 m elevation. This species has been reported from practically all Provinces of Panama.

BOMBACACEAE (Robyns—Part 6. Vol. 51: 37–68. 1964).

Theobroma bernoullii Cuatr.—*L & H 213* (21), 15 cm. The sole representative of this species is the type *Pittier 4105* (US). It was also collected from the Province of Colón. The flowers are cauliforous.

BORAGINACEAE (Nowicke—Part 9. Vol. 56: 33–69. 1969).

Cordia dentata Poir—*L 45* (30), 30 cm × 10 m, "Cuguaro" and "Billulo." This is common on the Pacific slope, having been collected in the Provinces of Herrera, Los Santos, and Veraguas.

C. panamensis Riley—*H 6444B* (10), 30 cm × 10 m. A common species much in need of study for intraspecific variation. It ranges from El Salvador to Panama.

C. porcata Nowicke—*L, H & G 7* (22), shrub or treelet, collected at 100 m. Nowicke reports *Dwyer & Lallathin 8586* (MO) incorrectly as collected in the Province of Los Santos.

BURSERACEAE (Porter—Part 6. Vol. 57: 5–27. 1970).

Protium costaricense (Rose) Engl.—*L, H & G 16* (7), 20 cm × 10 m. This species is known from seven collections in the Province of Panamá and one in the Canal Zone (Barro Colorado Island).

P. glabrum (Rose) Engl.—*L & H 172* (21), 3 cm × 6 m. While there are four collections of this species from the Province of Colón, *Pittier 3949, 4190, 4191* (all US), and *Tyson et al. 450* (MO), the present collection from Salud represents the most westward collection of the taxon in Panama.

P. tenuifolium subsp. *sessiliflora* (Rox.) Porter—*L 123* (37), 15 cm × 6 m. A well collected species, known from numerous collections in the Canal Zone, as well as from the Provinces of Chiriquí, Darién, and Panamá.

CELASTRACEAE

Maytenus jamaicensis Kr. & Urb.—*L & H 23* (21), 25 cm × 10 m. This species, according to Dr. Croat, is present on Barro Colorado Island, Canal Zone. I suspect that it is common in the Provinces of Panamá and Colón. *Lao & Holdridge 23* is in fruit and flower, a combination rarely observed on herbarium specimens. The collectors describe the fruit as orange.

Zinowiewia costaricensis Lundell—*L & H 49* (36).—This species, known from Costa Rica and from a solitary collection in Panama, *Maxon 5109* (F), from El Boquete, Province of Chiriquí, has its range extended considerably eastward in the Republic.

COCHLOSPERMACEAE (Robyns—Part 6. Vol. 54: 61–64. 1967).

Cochlospermum williamsii Macbride—* *L & H 178* (10), 15 cm × 9 m. While the collection is sterile, Holdridge has identified it as to species. This taxon, originally described from Peru, was not reported from Panama in Robyns' recent treatment.

COMBRETACEAE (Exell—Part 7. Vol. 45: 143–164. 1958).

Terminalia bucioides Standley & Williams—*L & H 15* (24), 25 cm × 15 m; *H & M 6530* (13), 10 cm × 7 m. This species is not listed in the relatively recent treatment of the family in the *Flora of Panama.*

T. edulis Blanco—*H 6521* (8), 20 cm × 6 m. An exotic tree growing in Summit Garden. It is native to the Philippines.

DILLENIACEAE (Hunter—Part 6. Vol. 52: 579–598. 1965).

Saurauia laevigata Tr. & Pl.—*H & M 6528* (13), 25 cm × 8 m, collected at 150 m; *L & H 182* (21), 10 cm × 7 m. This species is common in Panama.

ERYTHROXYLONACEAE

Erythroxylum amplum Benth.—*L & H 226* (21), 8 cm × 6 m. I have seen three sheets of this species in the Herbarium of the Missouri Botanical Garden; all of these are from Barro Colorado Island, Canal Zone: *Shattuck 1022* and *Croat 8265, 12679.*

EUPHORBIACEAE (Webster & Burch—Part 6. Vol. 54: 211–350. 1967).

Acalypha diversifolia Jacq.—*H 6446* (19), 3 m. This shrub is common in Central America.

Croton sp.—*L & H 224* (21), "Algodoncillo." This may be a new species. This collection has 3-lobed leaves resembling in shape and size those of *Gossypium barbardense* L. I have been unable to match it with any of our identified Central American crotons. Among the undetermined crotons I discovered a recent collection (*Kirkbride & Duke 1665* (MO)) from nearby Cerro Trinidad, Province of Panama, with the same vernacular name, "Algodoncillo." It compares favorably with the Lao and Holdridge collection. The field notes on the Kirkbride and Duke sheet are illuminating: "Tree without red latex, 20 m tall; bark whitish; wood malodorous, rank smelling; flowers scurfy, greenish; stamens greenish-yellow. Second growth and culled forest, SE slopes of Cerro Trinidad."

C. billbergianus Muell.-Arg.—*L 148* (30); *L & H 170* (21), 6 cm × 5 m; *L & H 202* (21), 8 m, "Vaguero." A common species in Panama.

C. panamensis (Kl.) Muell.-Arg.—*L 148* (30), 15 cm × 7 m, collected at 140 m, "Sangrillo." A common species in Panama.

Mabea occidentalis Benth.—*L, H & G 2* (22), 6 m, collected at 100 m. A common species, collected on several occasions by the author on Cerro Azul and Cerro Jefe, Province of Panamá. It is rather common around the Canal Zone and adjacent Provinces, although readily confused with *M. montana* Muell.-Arg., the latter with leaves only subacuminate at the apex. *Mabea occidentalis* also occurs in Costa Rica.

Margaritaria nobilis L. f.—*L & H 236* (21), 15 cm × 8 m. This has been widely collected in Panama but heretofore has not been reported for the Province of Colón.

Pera arborea Mutis—*L, H & G 12* (23), 15 cm × 10 m. Known from previous collections in the Canal Zone and the Provinces of Colón, Darién and Panamá. It also occurs in Colombia.

Phyllanthus acuminatus Vahl—*H 6525* (13). A common species ranging from Mexico to Argentina.

Sapium caudatum Pittier—*L 113* (44), 20 cm × 10 m, "Olivo."

Tetrorchidium gorgonae Croizat subsp. *robledoanum* (Cuatr.) Webster—*L & H 13* (23), 50 cm × 10 m; *L & H 33* (39), 16 cm × 10 m, collected at 600 m. This species heretofore has been known only from Cerro Jefe, Province of Panamá, and west of Gatun Locks in the Canal Zone. The present collections were made only a few miles from Cerro Jefe.

FLACOURTIACEAE (Robyns—Part 6. Vol. 55: 145–169. 1968).

Casearia javitensis HBK—*L & H 230* (21), 15 cm × 6 m. Common in Panama.

C. sylvestris Sw.—*H 6458* (40), 10 cm × 7 m. Common in Panama. It ranges from Mexico to Panama.

Laetia thalmia L.—*L & H 228* (21), 15 cm × 10 m, collected at 600 m elevation. It is common in the Canal Zone and in adjacent Provinces.

Ryania speciosa var. *panamensis* Monachino—*H & M 6532* (13), 5 m, collected at 100 m. This species is known from the Provinces of Bocas del Toro, Canal Zone, Colón, and San Blas. The Holdridge collection was made only a few miles from Santa Rita Ridge, Province of Colón, where Dressler and Correa (*647* (MO)) recently collected material of this species.

Zuelania guidonia (Sw.) Britt. & Millsp.—*H 6445* (19), 20 cm × 10 m. This species, with a wide range from southern Texas to Panama, has heretofore been reported from Panama only once, *Pittier 2710* from "the hills between Rio Grande and Pedro Vidal, Canal Zone." Dr. Croat has collected it several times on Barro Colorado Island, Canal Zone (*Croat 4962, 4973, 7187, 8393* (all MO). Other collections from Barro Colorado Island, deposited in the Missouri Botanical Garden are *Woodworth & Vestal 719*; *Zetek 3343, 3463*).

GUTTIFERAE

Calophyllum brasiliense Camb.—*H & M 6534* (13), 75 cm × 30 m. This large tree was identified from dried leaves. The material matches well a fruiting collection of the author (*Dwyer et al. 7301* (MO)) from the summit of Cerro Jefe, Province of Panamá, a well-known collecting spot, less than 20 miles from María Chiquita, the location of the Holdridge and Maasola collection. This species ranges from southern Mexico to Panama.

Marila verapazensis Donn. Sm.—*L, H & G 17* (7). This species is known from several collections in Panama. Holdridge notes that "this species grew in La Selva, Costa Rica." It ranges from British Honduras to Colombia.

Rheedia madruno (HBK) Tt. & Pl.—*L & H 190* (21), 40 cm × 20 m, "Satro." As this species has been collected on Barro Colorado Island (*Croat 10840* (MO)), its collection in nearby Salud, Province of Colón, is not surprising.

HUMARIACEAE

Sacoglottis ovicarpa Cuatr.—*L, H & G 5* (22), "Conocillo"; * *L & H 193* (21), 19 cm × 18 m, collected at 120 meters elevation; *L & H 195* (21), 60 cm × 25 m, "Corotu." L. R. Holdridge identified the three collections and in deference to his field experience with *Sacoglottis* I am giving his identifications priority. As the discussion which follows indicates, however, I am prepared to challenge them.

Of the three collections listed here, the one designated by an asterisk is sterile, while the others are in fruit. All three collections were made on the Atlantic side of the Isthmus.

The fruits of *Lao & Holdridge 195* are oblong, measuring 3–4 cm in length and 2.2–2.8 cm in width. One drupe measuring 4 cm in length, was sectioned transversely with a bandsaw. The surface (exocarp) is smooth and deep purple-red in color in the dry state. The exocarp and mesocarp are evident on the cut face, the mesocarp appearing as a thin line. In softening a slice of the fruit in aerosol and boiling in glycerine the mesocarp became even more evident. The exocarp is thin, measuring 0.1–0.2 cm in width; the ligneous endocarp is studded with resinous subrotund cysts which measure 1–4 (–6) mm in diameter. There is no separation of the resinous cysts into large and small groups. The septal lines are faint on the cut face.

The fruit of *Lao, Holdridge & Gentry 5* is oblong, measuring 3 cm in

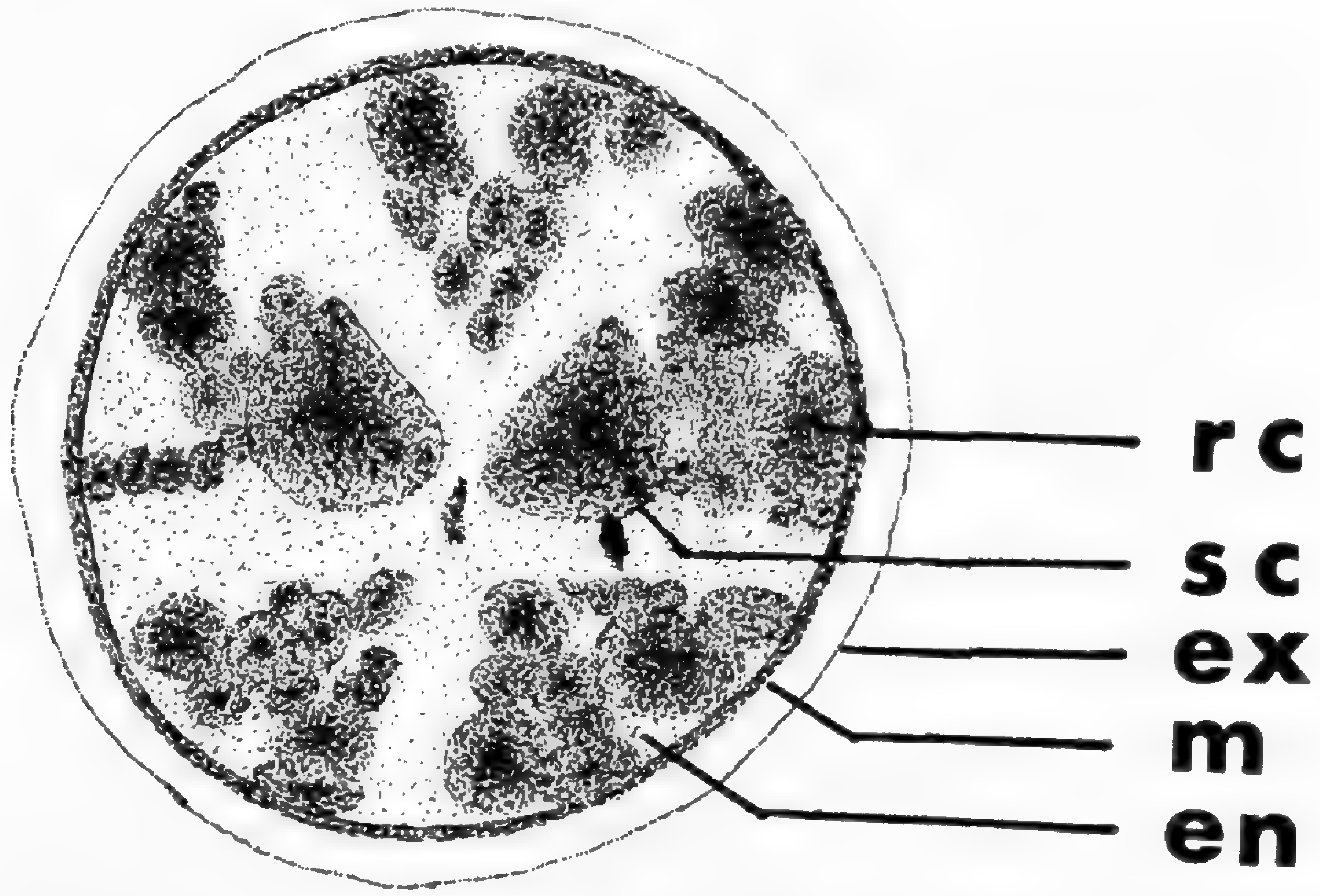

FIGURE 1. Cross section of fruit of *Sacoglottis* sp. (or *Schistostemon*) showing cut surface natural size. En—endocarp; ex—exocarp; m—mesocarp; rc—resinous cyst; sc—seminal cavity. Based on *Lao & Holdridge 195* (MO). ×2.

length and 2 cm in width. The surface is rugose and pitted (resinous cysts), the exocarp presumably having rotted away. The superficial pits of the endocarp are more or less circular, measuring 1–1.5 mm in diameter (*cf.* Fig. 1).

On being cut transversely with a band-saw, the ligneous endocarp of *Lao, Holdridge & Gentry 5* exhibited great resistance. Most noticeable on the cut surface are 3 large seminal cavities, measuring ± 6 mm in diameter. The resinous cysts, scattered throughout the valves of the endocarp, are small, with a diameter measurement of 0.5–1.5 mm and averaging about 6 per valve. The cut faces of the valves appear cuneiform. On cutting the fruit, the 5 parts (which I regard as valves) of the endocarp easily separated themselves (or if they remained in position, could be pried loose with a fingernail) from 5 radially disposed septa of about equal length (*cf.* Fig. 2). These septa may contain occasional resinous cysts or canals. Each arm of the "star" measures about 0.2 cm in diameter on the cut surface. Viewed laterally, the septum extends almost the full length of the endocarp (Fig. 1). The remnants of the disintegrated seeds are evident.

From a study of the illustrated fruits in Cuatrecasas (1961) revision of the Humariaceae, especially Fig. 31, n–p I decided that *Lao, Holdridge & Gentry 5* either belongs to the genus *Schistostemon*, known from the Guianas and parts of the Amazon Basin, or is to be referred to *Sacoglottis mattogrossensis* Malme, found in Colombia, Venezuela, the Guianas, and Brazil. The genus *Sacoglottis* has been reported from Panama by Johnston (1949; 161) as occurring in the drift on the beaches of San José Island, Province of Panamá, and by Holdridge (1970: 260). Holdridge in his manual does not designate the species of *Sacoglottis* which occurs in Panama, however. At the same time he indicates that *Sacoglottis* occurs in

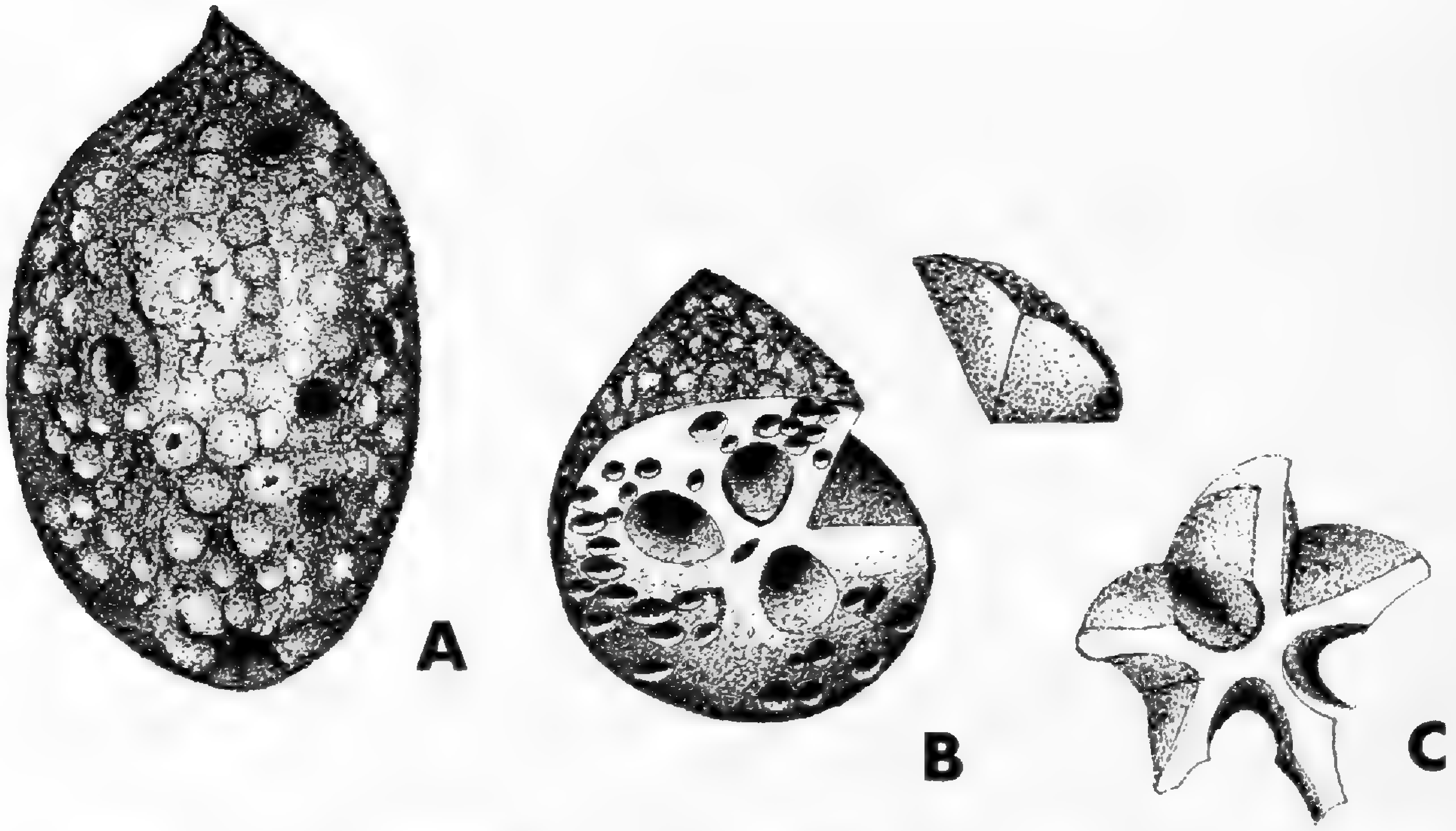

FIGURE 2. Fruit of *Sacoglottis* sp. (or *Schistostemon* sp.), endocarp only shown natural size.—A. External view, the resinous cysts visible as holes of varying diameter.—B. Endocarp shown in hemisection, one displaced valve shown to right; the seminal cavities are large, the resinous cysts smaller.—C. Lignified septa with all valves absent. Based on *Lao, Holdridge & Gentry 5* (MO). ×1⅔.

Costa Rica. Dr. Holdridge says (personal communication) that S. *ovicarpa* Cuatr. is the forest dominant on Cocos Island, Costa Rica.

In conclusion, one speculates whether *Sacoglottis* and *Schistostemon* may not be congeneric. The floral differences separating the two genera do not appear to be strong, judging from Cuatrecasas' work. What is especially needed is intensive collection of the Humariaceae, particularly the fruits in various stages of development.

LACISTEMACEAE (Nevling—Part 4. Vol. 47: 124–127. 1960).

Lacistema aggregatum (Berg.) Rusby—*H 6451* (19), 8 cm × 6 m. A common tree in the Republic.

Lozania pedicellata (Standley) L. B. Smith—*H 6484* (15), 6 m. There are only three collections of *L. pedicellata* from Panama, *von Wedel 2121* (MO) from Old Bank Island, Province of Bocas del Toro, *Ebinger 348* (MO) from Cerro Campana, Province of Panamá, and *Shattuck 972* from Barro Colorado Island, Canal Zone.

LAURACEAE (Allen—Part 5. Vol. 35: 1–68. 1948).

Nectandra fuscobarbata (Mez) Allen—*H 6403* (15), 40 cm × 15 m. Known previously from two widely separated localities in Panama: Isla Colón, Province of Bocas del Toro, and Pinas Bay, Province of Darién.

N. gentlei Lundell—*H 6407* (6), 30 cm × 10 m. Known in Panama from the lowlands of Chiriquí Province and from the Canal Zone.

N. globosa (Aubl.) Mez—*L & H 52* (36), 20 cm × 10 m, collected at 100 meters elevation; *H 6447* (18), 35 cm × 13 m. This species ranges from

Guatemala to Panama; it has been reported in Panama from the Province of Panamá and the Canal Zone.

N. martinicensis Mez—*H 6508* (21), 22 cm × 10 m. Our material in the Missouri Botanical Garden is from Tobago, Trinidad, and Granada in the West Indies.

N. standleyi Allen—*L 102* (2), 15 cm × 10 m, "Sigua Amarillo"; *L 103* (2), "Sigua Blanco." This species is known from Bocas del Toro and possibly from the Province of Panamá, especially from Juan Diaz (*Allen 942* (MO)).

Persea caerulea (R. & P.) Mez—*L 46* (27), 30 cm × 15 m, collected at 350 m elevation. There is a single collection of this well-known species in the Missouri Botanical Garden, *Allen 1015* from Boqueté, Province of Chiriquí.

Phoebe johnstonii Allen—*H 6433B* (45), 10 cm × 5 m; *H 6518* (5), 20 cm × 8 m. This has been previously reported from San Jose Island, Province of Panamá (*Johnston 697* (MO, the type collection)) and from the Province of Chiriquí (*Stern et al. 1143* (MO)).

P. mexicana Meisn.—*H. 6475* (40), 8 m. This species is well distributed in Mexico and Central America. This is probably the first report of the species in Panama, although Dr. Croat informs me that he has undistributed material of the species from Barro Colorado Island, Canal Zone.

LECYTHIDACEAE (Woodson—Part 7. Vol. 45: 115–136. 1958).

Grias fendleri Seem.—*L & H 232* (21), 25 cm × 8 m. This species is known from the Provinces of Bocas del Toro, Canal Zone, and Colón. Dr. Croat reports its presence on Barro Colorado Island, Canal Zone.

Eschweilera calyculata Pittier—*L & H 158* (20), 12 cm × 10 m. This is the first report of the species in the Province of Colón. It has been previously reported from the Provinces of Bocas del Toro and the Canal Zone.

E. pittieri R. Kunth—*L, H & G 12* (7), 40 cm × 25 m, collected at 100 meters elevation; *L & H 191* (21), 18 cm × 15 m, collected at 100 meters elevation, "Ollito." This species, heretofore reported only from the Provinces of Chiriquí and the Province of Darién, is common along the Pipe Line Road in the Canal Zone.

LEGUMINOSAE

Andira inermis (Sw.) H.B.K.—*H 6496* (40), 20 cm × 8 m. Known from collections in Bocas del Toro, Canal Zone, Coclé, Darién, and Panamá.

Bauhinia monandra Kurz—*H 6348* (42), 6 m. This is an ornamental species widely grown in tropical regions. It is native to India. Mr. R. Wunderlin, a specialist on *Bauhinia*, indicates (personal communication) that it occasionally escapes from cultivation in Panama and that it is becoming naturalized in parts of Central America and the West Indies.

Cassia siamea Lam.—*L 86* (35), 22 cm × 5 m.

Copaifera panamensis (Britt.) Standley—*L 44* (31), 50 cm × 5 m, "Cabimo"; *L 43* (31), 30 cm × 10 m, "Cabimo." Rather common near streams in the lowlands of Veraguas and Coclé Provinces in Panama.

Coumarouna oleifera (Benth.) Taub.—*L & H 177* (10), 60 cm × 25 m, collected at 150 meters elevation. Heretofore, this species was reported only from the Provinces of Darién and Panamá.

Cynometra bauhiniaefolia Benth.—*L & H 17* (24), 70 cm × 20 m; *L & H 168* (16), 50 cm × 15 m. This species, ranging from Guatemala to Chile, has been rarely collected in Panama.

Erythrina berteroana Urb.—*L 112* (44), 15 cm × 5 m, "Pito."

Hymenaea courbaril L.—*H 6434* (45), 50 cm × 12 m. This species is common in the dry lowlands of the Azuero Peninsula, Panama.

Inga edulis Willd.—*L 59* (45), 15 cm × 8 m, "Guabo." A common tree.

I. thibaudiana DC.—*L & H 187* (21), a small tree.

Lonchocarpus peninsularis (Smith) Pittier—*L & H 253* (13), 10 cm × 6 m, "Gallito."

L. pentaphyllus (Poir.) DC. (*P. latifolius* H.B.K.)—*L & H 242* (21), 25 cm × 25 m; *L & H 153* (20), 6 cm × 6 m. This species is common in Central America, the West Indies, and northern South America.

Machaerium arboreum (Jacq.) Vogel—*L & H 186* (21), 3 m. It ranges from Mexico to Panama. It is known from two collections in the Canal Zone.

Ormosia coccinea (Aubl.) Jacq.—*L 114* (42). This will probably prove to be a new variety of *O. coccinea*. According to Dr. Croat it is common on Barro Colorado Island, Canal Zone.

Platymiscium polystachum Benth. *ex* Seem.—*L 142* (32), 60 cm × 20 m, collected at 100 meters elevation, "Guyacan." It is known in Panama from the Provinces of Canal Zone, Coclé, Darién, Los Santos, and Panamá.

Pithecellobium dulce (Roxb.) Benth.—*L 60* (42), 45 cm × 10 m.

P. latifolium (L.) Benth.—* *L & H 238* (21) 5 m.

P. rufescens Benth.—* *H 6391* (10), collected at 100 meters elevation; * *H 6404* (15), 30 cm × 10 m. This species, restricted to Panama, is common throughout the Republic.

Swartzia panamensis Benth.—*H 6450* (19), 25 cm × 10 m.

MALPIGHIACEAE

Brysonima spicata (Cav.) H.B.K.—*L & H 251* (21), 12 m, "Nancillo." The species has heretofore been known only from Barro Colorado Island, Canal Zone. Dr. Croat reports that it reaches a height of 20 meters on the Island.

MELASTOMACEAE (Gleason—Part 7. Vol. 45: 203–304. 1958).

Conostegia xalapensis (Bonpl.) Don—*H 6442* (19), 6 m. This species is very common in Panama.

Leandra consimilis Gleason—*L & H 220* (21), 6 cm × 5 m.

Miconia borealis Gleason—*L & H 171* (11), 4 cm × 3 m; *H 6420* (4), 5 m tall. This species is common in the lowlands.

M. lacera (Bonpl.) Naud.—*L & H 184* (21), 5 cm × 4 m. Very common.

M. aff. *macrophylla* Tr.—*L & H 215* (21), small tree.

M. pteropoda Benth.—*L 78* (29), 5 cm × 5 m, collected at 400 meters elevation, "Canillo."

MELIACEAE (Smith—Part 6. Vol. 52: 55–79. 1965).

Carapa guianensis Aubl.—*L & H 239* (21), 35 cm × 20 m. There are no collections of this species from Panama in the Herbarium of the Missouri Botanical Garden.

Cedrela fissilis Vell.—*L 104* (45), 32 cm × 13 m, "Cedro Amargo." This species has a wide range extending from Costa Rica through Panama, southward to Brazil.

Guarea glabra Vahl—*H 6444* (19), 30 cm × 10 m. It is common throughout Panama.

Trichilia cipo (Juss.) C. DC.—* *H 6501* (40), 20 cm × 14 m; *H 6394* (10), 15 cm × 10 m; *L & H 204* (21).

T. tomentosa H.B.K.—*L & H 189* (21), collected at 100 meters elevation; *H 6498* (40), 15 cm × 10 m; * *H 6499* (10), a small tree, collected at 100 meters elevation. This species has been previously reported in the Provinces of Bocas del Toro, Chiriquí, Darién, and Panamá.

MONINIACEAE (Duke—Part 4. Vol. 49: 537–551. 1963).

Siparuna guianensis Aubl.—*L & H 180* (21), 4 m. This species is widely distributed in Panama, with most collections at lower elevations but a few extending to 800 meters elevation.

S. pauciflora (Beurl.) DC.—*L & H 208* (21), "Pasmo." This species is widely distributed in Panama.

MORACEAE (Woodson *et al.*—Part 4. Vol. 47: 114–165. 1960).

Brosimum guianense (Aubl.) Huber—*H & M 6533* (5). This is presumably the second collection of this species in the Republic; the one collection was that of Pittier (*4336*) from Puerto Obaldía, Province of San Blas.

Cecropia eximia Cuatr.—*L & H 211* (21), 20 cm × 10 m, "Guarumo Blanco." Dr. Holdridge says that this is conspecific with *Cecropia insignis* Liebm. The species has been collected on the Atlantic side of the Canal Zone by Johnston (*1758*) and is reported to attain a height of 125 feet on Barro Colorado Island, Canal Zone (*fide* Dr. Croat).

C. longipes Pittier—*L 120* (21), 10 cm × 8 m, "Guarumo." This collection is noteworthy for having well-developed male inflorescences. Three recent collections are noteworthy: *Croat 10115* (MO) from Barro Colorado Island, Canal Zone; *Blum 2241* (MO) from Albrook, Canal Zone; *Lazor & Correa 3440* (MO) from the Airport at El Real, Province of Darién. The species is probably more widely distributed in the Republic than collections suggest.

C. maxonii Pittier—*L & H 181* (21), 12 cm × 8 m, "Guarumo Peludo." There is a single collection of this species in the Herbarium of the Missouri Botanical Garden: *Davidson 862* (MO) from Boqueté, Province of Chiriquí.

C. obtusifolia Bertol.—*L & H 169* (21). This is the first report of this species in the Province of Colón, although it is known from the Provinces of Bocas del Toro, Canal Zone, Darién, and Veraguas.

C. peltata L.—*L & H 203* (21). This is very common in Panama.

Coussapoa panamensis Pittier—*L & H 21* (24), 20 cm × 20 m. This species, extending from Guatemala to Panama, is known in Panama from the Provinces of Bocas del Toro, Canal Zone, Colón, and Panamá.

Ficus colubrinae Standley—*H 6441* (19), 25 cm × 7 m.

F. perforata L.—*L & H 235* (21)), 10 cm × 8 m. This is described on the herbarium label as an epiphyte.

F. radula Willd.—*H 6461* (41). The only sheet which I have seen labelled *F.*

radula is *Standley 26722* (MO). In his treatment of *Ficus* in the *Flora of Panama* (p. 189), DeWolf regards this species as a synonym of the well collected *F. maxima* Mill., extending from Mexico to the Amazon Basin.

Perebea xanthochyma Karst.—*H 6483* (15), 15 cm × 8 m. This species is known from the Provinces of the Canal Zone and Bocas del Toro; its overall range is from Costa Rica to Colombia. Johnston (*1692* (MO)) notes are helpful: "Understory tree, 10–30 ft. tall, in shady forest, no latex but a honey-like resinous sap that turns brown after exposure to air . . ."

MYRTACEAE (Amshoff—Part 7. Vol. 45: 165–201. 1958).

Eugenia aff. *salamancana* Standley—*L & H 237* (21), 25 cm × 10 m; *L & H 194* (21), 25 cm × 20 m, collected at 100 meters elevation. This species is known only from the type collection, *Woodson, Allen & Seibert 1570* (MO), collected at the Salamanca Hydrographic Station in the Canal Zone, adjacent to the site of the present collection. The type, described as having white flowers, is flowerless. While the type collection and the Lao and Holdridge collections agree in having coriaceous leaves, they differ in that the latter collection has glabrous twiglets. The fruits, heretofore undescribed for *E. salamancana*, are axillary, sessile, conglomerate, with each fruit measuring to 1½ cm in length; the sepals are 4, persistent, erect, and ⅓–½ the length of the body of the fruit.

E. zeketiana Standley—*L & H 214* (21), 3 cm × 3 m. This species was first described by Paul Standley in 1925 from two collections in the Canal Zone: *Standley 27503* (US, type collection) and *27192* (US). While the inflorescence is described in detail, the flowers are referred to merely as "subsessile." It is true that the calycine lobes, as found in the fruit, are described in detail. Johnston collected the plant (*1606* (MO)) on "the road to Battery VII" in the Canal Zone, noting its abundance in the "high shady forests." He has illuminating notes on the herbarium sheet: "Stamens white or cream; petals rose on outer face; fruit globose, 20 mm diam., one-seeded, seed with fleshy watery coat; fruiting calyx inflexed, persistent." The recent collection of *E. zeketiana* by *Duke & Elias* (*13761* (MO)) from Cerro Pirre, Province of Darién, Panama, extends the range almost to the Colombian border. The vernacular name is "Gasparillo."

Myrcia aff. *costaricensis* Berg.—*L 138* (20), 12 cm × 6 m, collected at 350 meters elevation. The fruits are described as edible.

M. costaricensis Berg.—*L & H 155* (20), 15 cm × 11 m. This species is known from Costa Rica to Panama.

M. fallax (Rich.) DC.—*L & H 223* (21), 15 cm × 6 m. This species is not listed in the relatively recent treatment of the family in the *Flora of Panama*.

M. splendens (Sw.) DC.—*L 144* (28), 5 cm × 3–4 m, collected at 350 meters elevation. It extends from southern Mexico to South America; it also occurs in the West Indies. To my knowledge this is the first report for Panama.

Psidium sp.—*H 6459* (40), 6 cm × 7 m. This tree is probably a new species. The leaves, borne on wiry branchlets, have petioles to 5 mm long and stiffly chartaceous glabrous blades which measure to 10.5 cm long and 4 cm wide; the acumen of the blade measures to 1.5 cm long; the calycine lobes spread radiately with each lobe to 1 cm long and obtuse to deltoid at the apex; the petals, described on the label as red or white, measure to 2 cm in length.

MYRISTICACEAE (Duke—Part 4. Vol. 49: 214–225. 1963).

Dialyanthera parvifolia Markg.—* *L & H 209* (21), collected at 100 meters elevation. This species is not listed in the relatively recent treatment of the family Myristicaceae in the *Flora of Panama.*

Virola koschyni Warb.—* *L & H 205* (21), "Miguelario." This species, ranging from Guatemala to Panama, has been reported previously as collected in the Provinces of Chiriquí and Darién in Panama.

V. surinamensis (Rol.) Ward.—*L & M 201* (21), 6 m, "Velario." This species has not been reported from Panama, although it occurs in the Lesser Antilles, the Guianas, and in parts of Brazil.

MYRSINACEAE (Lundell—Part 8. Vol. 58: 285–353. 1971).

Rapanea pellucido-punctata (Oerst.) Mez—*L 74* (29), 10 cm × 6 m, "Manglillo."

NYCTAGINACEAE (Woodson—Part 4. Vol. 48: 393–407. 1961).

Guapira costaricana (Standley) Woodson—*H 6413* (6), 5 m. Very common in Panama.

OLACACEAE (Nevling—Part 4. Vol. 47: 293–302. 1961).

Heisteria concinna Standley—*H 6468* (41), 10 cm × 8 m. This species is known from five provinces of Panama: Canal Zone, Darién, Herrera, Los Santos, and Veraguas.

H. longipes Standley—*L 165* (18), 8 cm × 8 m, "Sierrito." This is common throughout Panama.

Ximenia americana L.—*H 6481* (14), 20 cm × 7 m. This coastal species is widely distributed in Panama.

PALMAE (Bailey—Part 2. Vol. 30: 231–396. 1943).

Attalea allenii H. E. Moore—*L & H 197* (21). "Palm without trunk, racemes of fruits apparently rising from the ground" is recorded on the collection. The common name is "Bangue." The type collection is *Allen 4103* (MO).

PIPERACEAE (Yuncker—Part 4. Vol. 37: 1–120. 1960).

Piper aduncum L.—*L & H 219* (21), 4 m; *L & H 200* (21), 4 m, "Pasmo."

P. arboreum Aubl.—*L 22* (24), shrub or small tree. This collection was made at 600 meters elevation. Although this species is poorly represented in the herbarium of the Missouri Botanical Garden, it has been widely collected in the Republic, particularly at elevations between 300 and 800 meters.

P. reticulatum L.—*H 6443* (19), 10 cm × 6 m. This is a common species in Panama.

POLYGONACEAE (Howard (*Coccoloba* only)—Part 4. Vol. 47: 340–353. 1961).

Coccoloba caracasana Meissn.—*H 6379* (45), 13 m tall; *H 6453* (40), 20 cm × 8 m. This is common throughout the Republic.

RHIZOPHORACEAE

Cassipourea elliptica (Sw.) Poir.—*L 167* (18), 15 cm × 8 m; *L & H 196* (21), 8 cm × 9 m. This species is widely distributed in Central America and the West Indies.

ROSACEAE (McVaugh—Part 5. Vol. 37: 147–178. 1950).

Hirtella americana L.—*L 68* (38), 45 cm × 15 m, collected at 110 meters elevation. It extends through most of Middle America to northern South America.

H. latifolia Prance—*H & M 6526* (13), 20 cm × 8 m, collected at 100 meters elevation. This matches well the type collection, *Duke 8012* (MO), from Cerro Jefe, Province of Panamá.

H. triandra Sw.—*H 6392* (10), 20 cm × 12 m, collected at 100 meters elevation.

Licania platypus (Hemsley) Frit.—*H 6457* (40), 30 cm × 12 m. This species occurs throughout Middle America, extending to Colombia. It also occurs in the West Indies.

RUBIACEAE

Alibertia edulis (Rich.) Rich.—*L & M 224* (21), 3 m. This species is common throughout tropical America.

Amaioua corymbosa Benth.—*L & M 225* (21), 12 cm × 6 m. This species is found sporadically in some countries of Middle America, extending to the Guianas and Brazil. It also occurs in Trinidad and Cuba. In Panama it is common in the woods at Cerro Azul, Province of Panamá, at about 650 meters elevation.

Chomelia spinosa Jacq.—*H 6536* (5), 20 cm × 10 m.

Coutarea hexandra (Jacq.) Schum.—*H 6534B* (5). This species is sporadic in Panama. I have collected it several times at Farfan Beach, Canal Zone.

Guettarda odorata (Jacq.) Lam.—*L 139* (28), 4 cm × 8 m, collected at 350 meters elevation.

Isertia hypoleuca Benth.—*L 127* (4), 15 cm × 8 m; *L, H & G 10* (23), 25–30 cm × 8 m. This species is readily collected on the Atlantic side of the Isthmus at Mariá Chiquita, Province of Colón.

Machaonia acuminata HBK—*L 146* (26), shrub or small tree. This was collected, the herbarium label tells us, between wet and dry woods at 130 meters elevation. This species is readily accessible at the military airstrip, in the adjacent thickets, at Río Hato, Province of Coclé, Panama.

Macronemum glabrescens Benth.—*L 233* (21), 20 cm × 10 m.

Morinda citrifolia L.—*H 6507* (21), 20 cm × 10 m. This species has been frequently collected in the Province of Colón, Panama.

Pentagonia macrophylla Benth.—*L 93* (1), 20 cm × 18 m, "Indian Ink." I suspect that Lao may be in error when he notes that this tree reaches almost 60 feet in height.

Psychotria umbelliformis Dwyer & Hayden—*L 164* (18), 10 cm × 10 m, "Palo de Agua," collected at 200 meters elevation. There are at least three collections of this species: *Duke 12154* (MO) from Cerro Pilón, Province of Coclé; *Duke 15219* (MO, the type collection), from Cerro Jefe, Province of Panamá; *Kirkbride & Duke 1641* (MO) from Cerro Trinidad, Province of Panamá.

Randia aculeata L.—*L & H 248* (21), 3 m.

Tocoyena pittieri (Standley) Standley—*H 6514* (43), 30 cm × 10 m. This species was known previously in Panama from Barro Colorado Island, Canal Zone, and from Darién Province. For a discussion of the genus *Tocoyena* see Dwyer (1968).

RUTACEAE

Zanthoxylum setulosum P. Wilson—*L 137* (28), 10 cm × 5 m. This species is common throughout Panama.

SAPINDACEAE

Cupania costaricensis Radkl.—*L & H 162* (20), 20 cm × 10 m.

C. papillosa (= *C. latifolia*)—*H 6388* (10), 40 cm × 8 m.

C. scrobiculata L.—*H 6416* (4), 3 m tall.

SAPOTACEAE (Blackwell—Part 8. Vol. 55: 145–169. 1968).

Pouteria campechiana (HBK) Baehni—*H 6497* (40), 10 cm × 10 m. This species ranges from southern Mexico to Panama. It also occurs in Cuba and the Florida Keys. In Panama it has been reported in the Canal Zone and in the Provinces of Coclé, Colón, and Panamá.

P. durlandii (Standley) Baehni—*L & H 192* (21), 20 cm × 10 m. This species ranges from Mexico to Costa Rica, and now has its range extended into Panama.

P. engleri Eyma—* *H 6524* (13), 50 cm × 20 m.

P. neglecta Cronquist—*L & H 198* (21), 6 m; *H 199* (21), 25 cm × 20 m. This species, now reported for the first time in Panama, ranges from Guatemala to Panama. Dr. Croat recently collected this tall tree at the Río Frijoles in the Canal Zone (*Croat 16619* (MO)).

P. sapota (Jacq.) Moore & Stearn—*L 108* (44), 29 cm × 17 m, "Mamey." This species is widely distributed in the tropics.

P. stylosa (Pierre) Dubard—* *H 6466* (41), 25 cm × 8 m. This species is known from the Provinces of Bocas del Toro, Canal Zone, and Panamá.

STAPHYLEACEAE

Turpinia paniculata Vent.—*L & H 14* (7), small tree.

URTICACEAE (Killip—Part 4. Vol. 47: 179–198. 1960).

Myriocarpa yzabalensis (Donn. Sm.) Killip—*H 6449* (19), 5 m. This species is common throughout the Republic.

VERBENACEAE

Cornutia grandifolia (Schl. & Cham.) Schauer—*H 6454* (40), 5 m.

Lippia urticoides Steud.—*L 175* (33), 3 m.

VIOLACEAE (Robyns—Part 6. Vol. 54: 65–84. 1967).

Rinorea brachythrix Blake—*H 6472* (41), 4 m. This is the second collection of this species in Panama. The type, *Pittier 6601* (US), is from the vicinity of La Palma, Province of Darién, Panama.

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SOLANACEAE STUDIES II: TYPIFICATION OF SUBDIVISIONS OF *SOLANUM*

W. G. D'Arcy[1]

A useful step in the study and identification of plants is the assembling of species into infrageneric groups, and this is especially so in the genus *Solanum.* In this genus the great number and diversity of species discourages study, yet many groups can readily be assembled within the genus which have every appearance of being natural and distinct from one another. In the past, many groups were formally recognised with a considerable redundance of names. To bring some order to the surfeit of names, names of subdivisions of the genus are reviewed here with respect to their rank, validity of publication and typification; and to clarify the relationships of taxa to one another, a provisional conspectus is presented, not as a reworking of the taxonomy of the genus so much as a framework from which nomenclatural values can be seen. The desirable sequel, designation of the limits of taxa and keys to distinguish them, must await later efforts. The present paper is one necessary step in making the parts of this important genus more accessible to study. The literature search was careful and perhaps exhaustive, but there is the usual possibility of unexpected discoveries altering the nomenclature presented here, and in the future, especially when the flora of South America is better understood, there will be additions to the generic subdivisions noted here.

Help was sought from other workers: Susan M. Coles, University of Birmingham, chose the lectotype for section *Cryptocarpum*; R. M. Polhill, Royal Botanic Gardens, Kew, chose lectotypes for African taxa, and Don Ugent, University of Southern Illinois, Carbondale, chose the lectotype for *Regmandra.* Roger Polhill also helped in checking bibliographic references, and R. K. Brummit, Royal Botanic Gardens, Kew, uncovered several names overlooked by the writer. In addition to the above who helped directly in the study, the late C. V. Morton, Smithsonian Institution, Washington, and W. D. Margadant, Biohistorisch Institut der Rijksuniversiteit, Utrecht, provided advice on particular aspects of the project. Assistance from these people is gratefully acknowledged: the writer at the same time takes full responsibility for all choices and decisions not clearly attributed to others.

The alphabetical listing of names indicates the first rank, place, and date of publication as well as the validity of each name published in the genus *Solanum* between the ranks of genus and species. This is followed by subsequent changes of rank and finally by the type species. Holotypes and automatic choices under Art. 22 of the *Code* are indicated as "Type species." Other choices are "Lectotype species," and if the choice is not first made here by the writer, source of the choice follows in square brackets.

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Ann. Missouri Bot. Gard. 59: 262–278. 1972.

In the provisional conspectus of the genus, synonymy based on the same type species is indicated by an equals sign (=). The nearly equals sign (≈) is used to indicate taxonomic affinity which may in fact be taxonomic synonymy, but this paper does not present any new decisions as to taxonomic synonymy. The nearly equals sign and placement in the hierarchy either reflect a decision by a previous worker or merely suggest a close affinity. In most cases, taxa of equal rank are listed in alphabetical order. Names without clear indication of rank (gradi ambigui) are placed in the conspectus to reflect their presumed position in the taxonomic hierarchy without intention of assigning them to rank at this time.

Changes in Art. 22 (on autonyms) in the 1972 *Code* require some different names from those called for under the 1966 *Code*. Thus section *Herposolanum* is now correct instead of the autonym *Bassovia* and sect. *Acanthophora* is correct instead of sect. *Leptostemonum*. This brings to mind a remark of Wm. T. Stearn (British Museum, N. H.) that there are more changes of names because of legislation than for any other cause.

The ranks of names published by some authors are only indirectly evident. Dunal in 1813 (*Hist. Sol.*) used twelve names for groups of *Solanum* species, and in 1816 (*Sol. Syn.*) he added two more. On page 43 of the 1813 work he referred to section *Pteroidea*. On page 172 he suggested that several species might be grouped into a distinct section, and in 1816 he gave these same species the name *Leiodendra*. As all names used by Dunal in these two publications are of apparent equal rank, they are all treated as sections. More than 35 years later in the Solanaceae of the De Candolle *Prodromus* (Prodr. 13(1): 1–690. 1852), Dunal paid little attention to earlier names and erected a completely new framework for the genus. A host of categories between the rank of subsection and species were given names and diagnoses, and a few of these gradi ambigui have been assigned to rank by later workers. Lowe in 1868 (*Man. Fl. Madeira*) used new names for several infrageneric taxa in *Solanum*. Because he attributed two names (*Morella* and *Tuberarium*) to Dunal without comment, it is presumed he was accepting the names at Dunal's rank of subsection. Lowe's names are all of apparent equal rank. The same rationale is used in accepting names in *Solanum* in Dumortier's *Florula Belgica* (1827), even though Dumortier changed the orthography of Dunal's *Maurella* to *Morella*. In 1913, Georg Bitter (Fedde Rep. 11: 381) equated the German word "Reihe" with the Latin "sectio," so his use of Reihe in subsequent places is interpreted to mean section. Wessely (1961), in commenting on Pojarkova's (1955) series, also used the term Reihe in this sense. Bitter's "Grossart" (*Dunaliana*) and Pojarkova's "Cycle" (*Alata* and *Nigra*) are considered to be gradi ambigui.

The treatment of names published without clear indication of rank has long been the subject of debate, but all proposals to amend Art. 35 of the *Code*, which deals with this matter, were defeated at the Seattle Congress. Changes in Art. 22 (on autonyms) effected at the Seattle Congress do reduce the possibilities for negating the priority of names by assigning gradi ambigui to higher (*e.g.* subgeneric) rank and thus substituting an autonym for a name of lower rank (*e.g.*

section), but the situation is by no means clear. An example is the taxon *Lasiocarpa* Dun. The present writer wishes to recognise a section with *Solanum lasiocarpum* Dun. as the type species. Introduction of a completely new name would leave open the possibility that another writer might at some time assign *Lasiocarpa* Dun. to the rank of section and claim it had priority as a section from 1852 when first published by Dunal. The Dunal name is chosen for use here, and it appears in the form section *Lasiocarpa* (Dun.) D'Arcy. But two other interpretations are possible: first that because the publication of the name by Dunal indicated no rank, it has no priority in any rank and the section should be treated as newly published, *i.e.* sect. *Lasiocarpa* D'Arcy; while a second alternative interpretation might be drawn from Art. 22 of the *Code* to say that because the section takes its name from its type species, prior use of the name at any rank other than section is immaterial and the name at sectional rank is sect. *Lasiocarpa* D'Arcy. Fortunately most of the early names for subdivisions of *Solanum* are assignable to rank. The question of treatment of gradi ambigui has been left for future disputation; but such names in *Solanum* have been assigned type species, and they have been placed in the generic conspectus in likely positions.

Establishment of type species for many infrageneric taxa in *Solanum* is automatic, either because the author included only one species in his original protologue (holotype species), or by application of Art. 22 of the *Code* which in part provides:

> "When the epithet of a subdivision of a genus is identical with or derived from the epithet of one of its constituent species, this species is the type of the name of the subdivision of the genus unless the original author of that name designated another type."

This rule was not part of the *Code* when Seithe (1962) selected *S. swartzianum* rather than *S. lepidotum* as the lectotype of sect. *Lepidotum.* Fortunately these two names are from a taxonomic viewpoint very similar if not synonymous. By application of the above cited portion of Art. 22, all but one of the series in sect. *Petota* and most series in subgenus *Leptostemonum* are automatically typified. A future Botanical Congress might well consider a recommendation that new names for series and subseries be formed from the stem of the epithet of a constituent species.

Lectotypes for a number of sections in *Solanum* were selected earlier by Seithe (1962), and a type for *Lycianthes* was indicated by D'Arcy (1972). The writer's choices of lectotypes in the present paper follow study of herbarium specimens and living material of most taxa. In those few cases where material was not available, study of the literature and in one case of a type photograph preceded selection of the lectotype species. Lectotypes for three series, *Borealia, Glabrescentia,* and *Transaequatorialia,* were not selected, leaving the choice to someone more familiar with these groups than the present writer.

Without some structure, nomenclatural relationships cannot be understood, much less taxonomic relationships. The conspectus of the genus presented here is derived for the most part directly from the schemes of other workers, and the new elements of taxonomy are few. At the sectional level, the scheme used is roughly that of Seithe (1962) with corrections in nomenclature and the addition of several sections. The infrasectional arrangement in sect. *Potatoe* is adjusted from that of Hawkes (1963), that in sect. *Basarthrum* is taken from Correll (1962) and that for sect. *Solanum* from Pojarkova (1955). Infrasectional treatment for most sections in subgenus *Leptostemonum* are taken from various papers of Bitter (1911–1923; summarised by Seithe, 1962). Working mainly with the African species, Bitter distinguished several sections which may be considered taxonomically synonymous when a full range of the genus in the New World is taken into account. In particular, sect. *Melongena* should probably include sects. *Lathyrocarpum, Leprophora, Oliganthes,* and *Torva* and perhaps also sects. *Micracantha* and *Eriophyllum.* The new sections *Lasiocarpa* and *Extensum* are proposed largely as a result of the author's recent studies of Central American Solanaceae.

Dunal (1813, 1852), Bitter (1911–23) and Seithe (1962), among others, have tried to recognise a fundamental dichotomy on the genus which separates species with stellate hairs, tapering anthers, and spines from those species with simple hairs, stout anthers, and no spines. This simplistic approach has led to disagreement over placement of a number of groups. Rather than two lines of evolution, it would appear that there are several distinct lines of evolution in the genus. Seven subgenera are recognised here: subgenus *Archaesolanum* includes South Pacific species with distinctive leaf shape, axillary inflorescences, and sometimes aneuploidy; subgenus *Bassovia* includes groups with stout anthers, simple hairs, no spines, pinnate leaves without interstitial leaflets, and in many cases, axillary inflorescences and pointed fruits; subgenus *Brevantherum* includes groups with stout anthers, entire leaves, and dendritic or stellate hairs; subgenus *Leptostemonum* includes groups with tapering anthers, stellate hairs, and often spines; subgenus *Lyciosolanum* was recognised by Bitter and Seithe on the basis of the elongate filaments and local distribution (South Africa) of its sole species, *S. aggregatum* Jacq. (≈ *S. guienënse* L.), but its distinctiveness at the subgeneric level is not apparent to this writer and perhaps it should be considered a section of subgenus *Solanum*; subgenus *Potatoe* includes groups with scandent species, pinnate leaves often with interstitial leaflets, lateral pendulous inflorescences, and articulation of the pedicels above the base (sometimes only slightly so), which may indicate the site of an ancestral bracteole; and subgenus *Solanum* which includes groups with stout anthers, simple hairs and no spines. Section *Aculeigerum* may also represent a distinctive line of evolution from the common ancestral *Solanum* stock and warrant recognition at the subgeneric level. For present purposes it is placed as a section of subgenus *Potatoe*.

It is important that any omissions or errors in the following listing be brought to early notice so that nomenclature in the genus may soon achieve a good measure of stability.

NAMES FOR SUBDIVISIONS OF THE GENUS *SOLANUM*

Acanthocalyx Series Bitt., Fedde Rep. Beih. 16: 175. 1923.
  Lectotype species: *S. richardii* Dun.
Acanthophora Section Dun., Hist. Sol. 131, 218. 1813.
    Subsection G. Don, Gen. Syst. 4: 434. 1838.
    Grad. ambig. Dun. *in* DC., Prodr. 13(1): 30, 235. 1852.
  Lectotype species: *S. mammosum* L.

Acaulia Series Juz. *ex* Buk. & Kameraz, Princ. Potato Breed. 21. 1959.
  Type species: S. *acaule* Bitt.
Aculeastrum Series Bitt., Fedde Rep. Beih. 16: 165. 1923.
  Type species: S. *aculeastrum* Dun.
Aculeata Grad. ambig. [?subgenus] Dun., Hist. Sol. 125. 1813. *Nomen nudum.*
    Section G. Don, Gen. Syst. 4: 423. 1838.
    Grad. ambig. ['Division'] Walp., Rep. Bot. Syst. 3: 67. 1844.
  Lectotype species: S. *mammosum* L.
Aculeigerum Section Seithe, Bot. Jahrb. 81: 291. 1962.
  Type species: S. *wendlandii* Hook. f.
Aethiopica Series Bitt., Fedde Rep. Beih. 16: 43. 1923.
  Type species: S. *aethiopicum* L.
Afrodecumbens Series Bitt., Fedde Rep. 16: 163. 1923.
  Type species: S. *nigriviolaceum* Bitt.
Afroindica Series Bitt., Fedde Rep. Beih. 16: 4. 1923.
  Lectotype species: S. *indicum* L.
Afrosolanum Section Bitt., Bot. Jahrb. 54: 420–1, 440. 1917.
  Lectotype species: S. *terminale* Forsk. [Seithe, 1962].
Alata Series Pojark., Not. Syst. 17: 336. 1955.
    Grad. ambig. ['Cycle'] Pojark., Fl. URSS. 22: 32. 1955.
  Type species: S. *alata* Mill.
Albicaule Series Bitt., Fedde Rep. Beih. 16: 100. 1923.
  Type species: S. *albicaule* Dun.
Alticola Series Buk., Prob. Bot. 2: 319. 1955. *Nomen invalidum* [no Latin description].
  Type species: S. *alticola* Bitt.
Anarrhichomenum Section Bitt., Fedde Rep. 11: 247. 1912.
  Lectotype species: S. *sodiroi* Bitt. [Seithe, 1962].
Andigena Series Buk. *in* Buk. & Kameraz, Princ. Potato Breed. 24. 1959.
  Type species: S. *andigenum* Juz. & Buk.
Andreana Series Hawkes, Bull. Imp. Bur. Pl. Breed. 2: 50. 1944. *Nomen nudum.*
  Type species: S. *andreanum* Baker.
Androceras Genus Nutt., Gen. Amer. 1: 129. 1818.
    Section Marzell *in* Hegi, Fl. Mitt. Eur. 2585. 1927.
  Type species: A. *lobata* Nutt. (= S. *rostratum* Dun.).
Andromonoecum Section Bitt., Fedde Rep. Beih. 16: 142, 157. 1923.
    (Based on *Mogenoplum* and *Melongena* Dun.)
  Lectotype species: S. *melongena* L.
Angustisegmentata Grad. ambig. Buk., Prob. Bot. 2: 325. 1955. *Nomen invalidum* [no Latin description].
  Lectotype species: S. *canasense* Hawkes.
Anisantherum Section Bitt., Bot. Jahrb. 54: 420, 503. 1917.
  Lectotype species: S. *pubescens* Willd. [Seithe, 1962].
Anomalum Series Bitt., Bot. Jahrb. 57: 276. 1922.
  Type species: S. *anomalum* Thonn.
Anthopleuris Grad. ambig. Dun. *in* DC., Prodr. 13(1): 29, 123. 1852.
    Section Bitt., Fedde Rep. 16: 10. 1920.
  Lectotype species: S. *nudum* H. & B. *ex* Dun.
Anthoresis Grad. ambig. Dun. *in* DC., Prodr. 13(1): 29, 95. 1852.
    Section Bitt., Bot. Jahrb. 54: 489. 1917; 55: 66. 1919; Fedde Rep. 16: 79. 1919.
  Lectotype species: S. *pulverulentum* Pers.
Appendiculata Grad. ambig. Rydb., Bull. Torrey Bot. Club 51: 146, 174. 1924. *Nomen nudum.*
    Series Corr., Potato & Wild Rel. 62. 1962.
  Type species: S. *appendiculatum* H. & B. *ex* Dun.
Aquartia Genus Jacq., Enum. Pl. Carib. 1: 12. 1760.
    Grad. ambig. Dun. *in* DC., Prodr. 13(1): 30, 193. 1852.
    Section D'Arcy, stat. nov.
  Type species: A. *aculeatum* Jacq. (= S. *aquartia* Dun.).
Aracciana Grad. ambig. Buk., Prob. Bot. 2: 320. 1955. *Nomen invalidum* [no Latin description].

Type species: S. *aracc-papa* Juz.
Archaesolanum Subgenus Bitt. *ex* Marzell, Fl. Mitt. Eur. 2583. 1927.
Type species: S. *aviculare* Forst. f.
Armatae Grad. ambig. [?subgenus] C. H. Wright, Fl. Trop. Africa 4(2:2): 209. 1906.
Lectotype species: S. *aculeatissimum* Jacq. (≈ S. *capsicoides* All.).
Articulata Series Corr., Potato & Wild Rel. 62. 1962.
Type species: S. *sanctae-marthae* Bitt.
Asterochlaena Subsection Lowe, Man. Fl. Madeira 2(1): 80. 1868.
Type species: S. *auriculatum* Ait.
Asterotrichotum Subsection Dun. *in* DC., Prodr. 13(1): 30, 282. 1852.
Lectotype species: S. *carolinense* L.
Austroafricana Series Bitt., Fedde Rep. Beih. 16: 71. 1923.
Lectotype species: S. *tomentosum* L. [Polhill].
Avicularia Series Herasim., Nov. Syst. Pl. Vasc. 7: 270. 1970.
Type species: S. *aviculare* Forst. f.
Basarthrum Subsection Bitt., Fedde Rep. 11: 350. 1912.
Section Bitt., Fedde Rep. 13: 101. 1913.
Lectotype species: S. *suaveolens* Kunth & Bouché [Seithe, 1962].
Bassovia Genus Aubl., Pl. Guiane 1: 217, t. 85. 1775.
Subgenus Bitt., Fedde Rep. 17: 329. 1920.
Type species: *B. sylvatica* Aubl. (= S. sp.).
Bassovioides Grad. ambig. Dun *in* DC., Prodr. 13(1): 29, 154. 1852.
Lectotype species: S. *anceps* R. & P.
Benderanum Section Bitt., Bot. Jahrb. 54: 487. 1917.
Type species: S. *benderanum* Schimp. *ex* C. H. Wright.
Bifurca Series ['Reihe'] Bitt., Bot. Jahrb. 54: 436, 452. 1917.
Lectotype species: S. *bifurcum* Hochst. *ex* Dun. (≈ S. *terminale* Forsk.).
Borealia Series Buk., Prob. Bot. 2: 323. 1955. *Nomen invalidum* [no Latin description].
Series Corr., Potato & Wild Rel. 388. 1962.
Type species: Not selected.
Brachylobus Grad. ambig. Dun. *in* DC., Prodr. 13(1): 31, 353. 1852.
Lectotype species: S. *esculentum* Dun. (= S. *melongena* L.).
Brevantherum Section Seithe, Bot. Jahrb. 81: 297. 1962.
Subgenus D'Arcy, stat. nov.
Type species: S. *verbascifolium* sensu Seithe (= S. *erianthum* D. Don) non L.
Bulbocastana Grad. ambig. Rydb., Bull. Torrey Bot. Club 51: 172. 1924. *Nomen nudum.*
Series Corr., Potato & Wild Rel. 254. 1962. *Nomen nudum.*
Type species: S. *bulbocastanum* Dun.
Campanulisolanum Section Bitt., Fedde Rep. 11: 234. 1912.
Lectotype species: S. *fiebrigii* Bitt. [Seithe, 1962].
Campylacantha Subseries Bitt., Fedde Rep. Beih. 16: 202, 207. 1923.
Type species: S. *campylacanthum* Hochst.
Canensa Series Corr., Potato & Wild Rel. 99. 1962.
Type species: S. *canense* Rydb.
Capensiformia Series Bitt., Fedde Rep. Beih. 16: 62. 1923.
Type species: S. *capense* L.
Cardiophylla Series Buk. *in* Buk. & Kameraz, Princ. Potato Breed. 26. 1959.
Type species: S. *cardiophyllum* Lindl.
Caripensa Series Corr., Potato & Wild Rel. 50. 1962.
Type species: S. *caripense* H. & B. *ex* Dun.
Cerasocarpum Subsection Lowe, Man. Fl. Madeira 2(1): 79. 1868.
Type species: S. *pseudocapsicum* L.
Chamaesarachidium Section Bitt., Fedde Rep. 15: 93. 1917.
Type species: S. *chamaesarachidium* Bitt.
Circaeifolia Series Hawkes, Ann. Mag. Nat. Hist. ser. 12(7): 702. 1954.
Series Corr., Potato & Wild Rel. 245. 1962.
Type species: S. *circaeifolium* Bitt.
Clara Series Grah. & Dion. *in* Corr., Potato & Wild Rel. 243. 1962.
Type species: S. *clarum* Corr.

Commersoniana Series Buk. *in* Buk. & Kameraz, Princ. Potato Breed. 19. 1959.
Type species: S. *commersonii* Lam.
Conicibaccata Series ['Reihe'] Bitt., Fedde Rep. 11: 381. 1912.
Lectotype species: S. *oxycarpum* Schiede.
Cuneolata Series Hawkes, Bull. Imp. Bur. Pl. Breed. 118. 1944.
Type species: S. *infundibuliforme* Phil. [Hawkes & Hjerting, 1969].
Cyphomandropsis Section Bitt., Fedde Rep. 12: 461. 1913.
Lectotype species: S. *stuckertii* Bitt. [Seithe, 1962]. (= *Cyphomandra stuckertii* (Bitt.)) D'Arcy, comb. nov., based on S. *stuckertii* Bitt., Fedde Rep. 12: 461. 1913. Lectotype specimen: Argentina, *Stuckert 21589* (?B, not seen; photo NY)).
Cryptocarpum Section Dun., Hist. Sol. 134, 232. 1813.
Subsection G. Don, Gen. Syst. 4: 438. 1838.
Grad. ambig. Dun. *in* DC., Prodr. 13(1): 30, 325. 1852.
Lectotype species: S. *balbisii* Dun. [Coles].
Cypellocalyx Section Bitt., Bot. Jahrb. 55: 91. 1919.
Lectotype species: S. sp. (= *Lycianthes* sp.).
Demissa Series Buk. *in* Buk. & Kameraz, Princ. Potato Breed. 27. 1959.
Type species: S. *demissum* Lindl.
Dulcamara Genus Moench., Meth. 514. 1794.
Section Dumort., Fl. Belg. 39. 1827.
Subsection Dun. *in* DC., Prodr. 13(1): 28, 60. 1852.
Grad. ambig. Dun. *in* DC., Prodr. 13(1): 28, 68. 1852.
Section Bitt., Bot. Jahrb. 54: 428. 1917.
Type species: *D. flexuosa* Moench. (= S. *dulcamara* L.).
Dunaliana Grad. ambig. ['Grossart'] Bitt., Bot. Jahrb. 55: 70. 1919.
Type species: S. *dunalianum* Gaud.
Durigibbosa Series Bitt., Fedde Rep. 16: 79. 1920.
Lectotype species: S. *cladotrichum* Vandas [Polhill].
Endotricha Series Bitt., Fedde Rep. 16: 83. 1920.
Type species: S. *endotrichum* Bitt.
Eoafra Series Bitt., Fedde Rep. Beih. 16: 102. 1923.
Lectotype species: S. *zanzibarense* Vatke [Polhill].
Episarcophyllum Section Bitt., Fedde Rep. 11: 241. 1912.
Lectotype species: S. *sinuatirecurvum* Bitt. [Seithe, 1962].
Eriophylla Section Dun., Hist. Sol. 127, 189. 1813.
Grad. ambig. G. Don, Gen. Syst. 4: 426. 1838.
Lectotype species: S. *jamaicense* Mill.
Erythracanthum Subseries Bitt., Fedde Rep. Beih. 16: 105, 122. 1923.
Type species: S. *erythracanthum* Boj.
Etuberosa Series Juz. *ex* Buk. & Kameraz, Princ. Potato Breed. 18. 1959.
Type species: S. *etuberosum* Lindl.
Euincana Subseries Bitt., Fedde Rep. Beih. 16: 206, 270. 1923.
Type species: S. *incanum* L.
Euleptostemonum Subsection Dun. *in* DC., Prodr. 13(1): 29, 183. 1852.
Lectotype species: S. *mammosum* L.
Eulycianthes Grad. ambig. Dun. *in* DC., Prodr. 13(1): 29, 161. 1852.
Lectotype species: S. *lycioides* L. (= *Lycianthes lycioides* (L.) Hassl.).
Eumelongena Grad. ambig. Dun. *in* DC., Prodr. 13(1): 31, 355. 1852.
Lectotype species: S. *esculentum* Dun. (= S. *melongena* L.).
Eusolanum Subgenus Bitt., Bot. Jahrb. 55: 62. 1919.
Lectotype species: S. *nigrum* L. [Hitchcock & Green, 1929].
Eutorvum Series Bitt., Bot. Jahrb. 57: 251. 1922.
Type species: S. *torvum* Sw.
Extensum Section D'Arcy, sect. nov. Arbores v. frutices scandentes, inermes, folia tirones interdum adsunt; pilis stellatis porrectis gerentibus; calyce interdum accrescenti, foliaceo; floribus parvis; antheris aequalibus, crassis, poris terminalibus magnis aperientibus; acino globoso glabro v. pubescenti.
Type species: S. *extensum* Bitt.
Geminata Subsection G. Don, Gen. Syst. 4: 418. 1838.
Section Walp., Rep. Bot. Syst. 3: 58. 1844.

Lectotype species: S. *nudum* H. & B. *ex* Dun.

Giganteiformia Series Bitt., Bot. Jahrb. 57: 255. 1922.
Type species: S. *giganteum* Jacq.

Glabrescentia Series Buk., Prob. Bot. 2: 318. 1955. *Nomen invalidum* [no Latin description].
Series Buk. *ex* Buk. *in* Buk. & Kameraz, Princ. Potato Breed. 19. 1959.
Type species: Not selected.

Gonatotrichum Section Bitt., Fedde Rep. 11: 230. 1912.
Type species: S. *gonatotrichum* Bitt.

Gonianthes Grad. ambig. Dun. *in* DC., Prodr. 13(1): 29, 163. 1852.
Lectotype species: S. *stellatum* Jacq. (= *Lycianthes stellata* (Jacq.) Bitt.).

Graciliflora Grad. ambig. Dun. *in* DC., Prodr. 13(1): 29, 183. 1852.
Section Seithe, Bot. Jahrb. 81: 302. 1962.
Type species: S. *graciliflorum* Dun.

Grandiflorae Grad. ambig. (?subsection) C. H. Wright, Fl. Trop. Africa 4(2: 2): 210. 1906.
Lectotype species: S. *melongena* L.

Herposolanum Section Bitt., Fedde Rep. 11: 250. 1912.
Type species: S. *reptans* Bunb.

Herpystichum Section Bitt., Fedde Rep. 17: 331. 1920.
Lectotype species: S. *trifolium* Dun. [Seithe, 1962].

Heteracantha Grad. ambig. Dun. *in* DC., Prodr. 13(1): 30, 197. 1852.
Lectotype species: S. *jamaicense* Mill.

Holochlaina Subsection G. Don, Gen. Syst. 4: 422. 1838.
Section Walp., Rep. Bot. Syst. 3: 62. 1844.
Lectotype species: S. *bigeminatum* Nees (= *Lycianthes bigeminata* (Nees) Bitt.).

Holophylla Subsection G. Don, Gen. Syst. 4: 414. 1838.
Section Walp., Rep. Bot. Syst. 3: 51. 1844.
Lectotype species: S. *pulverulentum* Pers.

Hyperbasarthrum Subsection Bitt., Fedde Rep. 11: 359. 1912.
Lectotype species: S. *tuberosum* L.

Incaniformia Series Bitt., Fedde Rep. Beih. 16: 201. 1923.
Lectotype species: S. *incanum* L.

Indubitaria Grad. ambig. Dun. *in* DC., Prodr. 13(1): 29, 123. 1852.
Subsection Seithe, Bot. Jahrb. 81: 289. 1962.
Lectotype species: S. *brachystachys* Dun. [Seithe, 1962].

Inermia Grad. ambig. [?subgenus] L., Sp. Pl. 184. 1753. *Nomen nudum.*
Grad. ambig. ['Division'] Walp., Rep. Bot. Syst. 3: 1844.
Lectotype species: S. *nigrum* L.

Inermes Grad. ambig. (?subgenus) C. H. Wright, Fl. Trop. Africa 4(2: 2): 208. 1906.
Lectotype species: S. *nigrum* L.

Inermis Section G. Don, Gen. Syst. 4: 400. 1838.
Lectotype species: S. *nigrum* L.

Ingaefolia Series Ochoa *in* Corr., Potato & Wild Rel. 129. 1962.
Type species: S. *ingaefolium* Ochoa.

Irenosolanum Section Seithe, Bot. Jahrb. 81: 301. 1962.
Type species: S. *woahense* Dun.

Ischyracanthum Section Bitt., Fedde Rep. Beih. 16: 142. 1923.
Lectotype species: S. *ogadense* Bitt. [Seithe, 1962].

Jasminosolanum Section Bitt., Fedde Rep. 17: 330. 1920. *Nomen nudum.*
Section Seithe, Bot. Jahrb. 81: 291. 1962.
Type species: S. *jasminoides* Paxt.

Juciri Subsection Marzell *in* Hegi, Fl. Mitt. Eur. 2584. 1927.
Type species: S. *wendlandii* Hook. f.

Juglandifolia Grad. ambig. Rydb., Bull. Torrey Bot. Club 51: 173. 1924. *Nomen nudum.*
Series Corr., Potato & Wild Rel. 102. 1962. *Nomen invalidum* [no Latin description].
Series D'Arcy, ser. nov. Frutices v. labruscae, stolones tuberaque carentes, caulibus lignosis, floribus aureis.
Type species: S. *juglandifolia* Bitt.

Juripeba Grad. ambig. Dun. *in* DC., Prodr. 13(1): 30, 197. 1852.
Type species: S. *juripeba* Rich.

Kieseritzkiana Grad. ambig. Pojark., Fl. URSS. 22: 10. 1955. *Nomen invalidum* [no Latin description].
Type species: S. *kieseritzkii* C. A. Mey.
Laciniata Series Herasim., Nov. Syst. Pl. Vasc. 7: 273. 1970.
Type species: S. *laciniatum* Ait.
Lasiocarpa Grad. ambig. Dun. *in* DC., Prodr. 13(1): 30, 252. 1852.
Section D'Arcy, stat. nov.
Type species: S. *lasiocarpum* Dun.
Lathyrocarpum Subsection G. Don, Gen. Syst. 4: 436. 1838.
Section Walp., Rep. Bot. Syst. 3: 88. 1844.
Lectotype species: S. *carolinense* L.
Leiodendra Section Dun., Sol. Syn. 20. 1816.
Grad. ambig. Dun. *in* DC., Prodr. 13(1): 29, 137. 1852.
Lectotype species: S. *nudum* H. & B. *ex* Dun.
Lemurisolanum Section Bitt., Bot. Jahrb. 54: 422, 436. 1917.
Lectotype species: S. *madagascariense* Dun. [Seithe, 1962].
Lepidota Grad. ambig. Dun. *in* DC., Prodr. 13(1): 29, 131. 1852.
Series ['Reihe'] Bitt., Fedde Rep. 16: 404. 1920.
Section Seithe, Bot. Jahrb. 81: 298. 1962.
Type species: S. *lepidotum* H. & B. *ex* Dun [S. *swartzianum* R. & S. design. err. Seithe].
Leprophora Section Dun., Hist. Sol. 125, 181. 1813.
Grad. ambig. G. Don, Gen. Syst. 4: 423. 1838.
Lectotype species: S. *elaeagnifolium* Cav.
Leptostemonum Section Dun. *in* DC., Prodr. 13(1): 29, 183. 1852.
Subgenus Bitt., Bot. Jahrb. 55: 68. 1919; Fedde Rep. 16: 395, 405. 1920.
Subgenus Marzell *in* Hegi, Fl. Mitt. Eur. 2584. 1927.
Lectotype species: S. *mammosum* L.
Lobanthes Grad. ambig. Dun. *in* DC., Prodr. 13(1): 29, 174. 1852.
Lectotype species: S. *bigeminatum* Nees (= *Lycianthes bigeminata* (Nees) Bitt.).
Longipedicellata Series Buk. *in* Buk. & Kameraz, Princ. Potato Breed. 27. 1959.
Type species: S. *longipedicellatum* Bitt.
Lycianthes Subsection Dun. *in* DC., Prodr. 13(1): 29, 156. 1852.
Section Wettst. *in* Engl. & Prantl, Nat. Pflanzenf. 4(3b): 22. 1895.
Subgenus Bitt., Bot. Jahrb. 54: 424. 1917.
Genus Hassl., Ann. Conserve. Jard. Genève 20: 173. 1917.
Lectotype species: S. *lycioides* L. [D'Arcy, 1972] (= *Lycianthes lycioides* (L.) Hassl.).
Lycioides Section Walp., Rep. Bot. Syst. 3: 61. 1844.
Type species: S. *lycioides* L. (= *Lycianthes lycioides* (L.) Hassl.)
Lyciosolanum Subgenus Bitt., Bot. Jahrb. 54: 421, 428. 1917.
Type species: S. *aggregatum* Jacq. (≈ S. *guineënse* L.).
Lycopersicarpon Grad. ambig. Dun. *in* DC., Prodr. 13(1): 31, 350. 1852.
Lectotype species: S. *aethiopicum* L.
Lycopersicon Genus Mill., Gard. Dict. ed. 4 abr. 1754.
Section Wettst. *in* Engl. & Prantl, Nat. Pflanzenf. 4(3b): 24. 1895.
Section Bitt., Bot. Jahrb. 54: 500. 1917.
Subgenus Seithe, Bot. Jahrb. 81: 204. 1962.
Type species: L. *esculentum* Mill. (= S. *lycopersicum* L.)
Lysiphellos Subsection Bitt., Fedde Rep. 16: 90. 1919.
Section Seithe, Bot. Jahrb. 81: 288. 1962.
Type species: S. *decorticans* Sendt. *in* Mart.
Macracanthum Series Bitt., Fedde Rep. Beih. 16: 99. 1923.
Type species: S. *macracanthum* A. Rich.
Macrocarpon Grad. ambig. Dun. *in* DC., Prodr. 13(1): 31, 353. 1852.
Series Bitt., Fedde Rep. Beih. 16: 186. 1923.
Type species: S. *macrocarpon* L. f.
Macronesiotes Section Bitt., Bot. Jahrb. 54: 422, 432. 1917.
Lectotype species: S. *imamense* Dun. [Seithe, 1962].
Macrophyllae Grad. ambig. (?section) C. H. Wright, Fl. Trop. Africa 4(2: 2): 210. 1906.
Lectotype species: S. *aculeatissimum* Jacq. (≈ S. *capsicoides* All.).

Madagascariensia Subseries Bitt., Fedde Rep. Beih. 16: 105, 124. 1923.
  Lectotype species: S. *nossibeënse* Vatke [Polhill].
Maglia Series ['Reihe'] Bitt., Fedde Rep. 11: 360. 1912.
  Type species: S. *maglia* Schlecht.
Maurella Section Dun., Hist. Sol. 119, 151. 1813.
  Lectotype species: S. *nigrum* L.
Megistacroloba Series Cárd. & Hawkes, Jour. Linn. Soc. Bot. 53: 93. 1945.
  Type species: S. *megistacrolobum* Bitt.
Meiomeris Grad. ambig. Dun. *in* DC., Prodr. 13(1): 29, 156. 1852.
  Lectotype species: S. *lycioides* L. (= *Lycianthes lycioides* (L.) Hassl.)
Melongena Genus Mill., Gard. Dict. ed. 4 abr. 1754.
    Section Dun., Hist. Sol. 130, 208. 1813.
    Subsection G. Don, Gen. Syst. 4: 432. 1838.
    Grad. ambig. Dun. *in* DC., Prodr. 13(1): 31, 350. 1852.
    Subseries Bitt., Fedde Rep. Beih. 16: 206, 292. 1923.
  Lectotype species: *M. ovata* Mill. (≈ S. *melongena* L.).
Micracantha Section Dun., Hist. Sol. 128, 193. 1813.
    Grad. ambig. G. Don, Gen. Syst. 4: 426. 1838.
    Grad. ambig. Dun. *in* DC., Prodr. 13(1): 30, 216. 1852.
  Type species: S. *micracanthos* Lam.
Micranthes Subsection Dun. *in* DC., Prodr. 13(1): 28, 95. 1852.
    [Section Marzell *in* Hegi, Fl. Mitt. Eur. 2584. 1927. err. = sect. *Macracantha* Dun.].
  Type species: S. *micranthum* Willd. *ex* R. & S. *in* L.
Microphyllae Grad. ambig. (?section) C. H. Wright, Fl. Trop. Africa 4(2: 2): 209. 1906.
  Lectotype species: S. *macracanthum* A. Rich.
Minutifoliola Series Corr., Potato & Wild Rel. 216. 1962.
  Type species: S. *minutifoliolum* Corr.
Mogenoplum Grad. ambig. Dun. *in* DC., Prodr. 13(1): 30, 335. 1852.
  Lectotype species: S. *lanceolatum* Cav.
Monadelphoidea Series Bitt., Fedde Rep. 16: 87. 1920.
  Lectotype species: S. *monodelphum* Heurck & Muell.-Arg.
Monodolichopus Section Bitt., Fedde Rep. 15: 94 nota. 1917. *Nomen nudum.*
    Section Bitt., Fedde Rep. Beih. 16: 297. 1923.
  Lectotype species: S. *dubium* Fresen non Dun. (≈ S. *thruppii* C. H. Wright) [Seithe, 1962].
Morella Section Dumort., Fl. Belg. 39. 1827. [Spelling changed from *Maurella* Dun.]
    Grad. ambig. G. Don, Gen. Syst. 4: 411. 1838.
    Subsection Dun. *in* DC., Prodr. 13(1): 28, 44. 1852.
    Section Bitt., Bot. Jahrb. 54: 416, 493. 1917.
  Lectotype species: S. *nigrum* L.
Morelliformia Series Hawkes, Scott. Pl. Breed. Sta. Ann. Rep. 156. 1956.
  Type species: S. *morelliformia* Bitt. & Muench.
Muricata Series Corr., USDA Agr. Monogr. 11: 49. 1952.
  Type species: S. *muricatum* Ait.
Nakurensia Series Bitt., Bot. Jahrb. 54: 447. 1917.
Neolycopersicon Section Corr., Potato & Wild Rel. 39. 1962.
  Type species: S. *pennellii* Corr.
Nigra Grad. ambig. ['Cycle'] Pojark., Fl. URSS 22: 25. 1955. *Nomen invalidum* [no Latin description].
  Type species: S. *nigrum* L.
Normania Genus Lowe, Man. Fl. Madeira 2: 70. 1868.
    Section Bitt., Fedde Rep. 11: 251. 1912.
  Type species: *N. triphylla* Lowe (= S. *trisectum* Dun., fide Bitt., loc. cit.).
Nycterium Genus Vent., Jard. Malm. t. 85. 1803.
    Section Dun., Sol. Syn. 35. 1816.
    Subsection G. Don, Gen. Syst. 4: 439. 1838.
    Grad. ambig. Dun. *in* DC., Prodr. 13(1): 30, 331. 1852.
    Section Bitt., Fedde Rep. 16: 307. 1923.
  Type species: *N. cordifolium* Vent. (= S. *vespertillio* Ait.)

Oliganthes Grad. ambig. Dun. *in* DC., Prodr. 13(1): 30, 282. 1852.
Section Bitt., Fedde Rep. Beih. 16: 1. 1923.
Lectotype species: *S. indicum* L. [Seithe, 1962].
Oppositifolia Grad. ambig. Dun. *in* DC., Prodr. 13(1): 29, 123. 1852.
Section Seithe, Bot. Jahrb. 81: 288. 1962.
Subsection Seithe, Bot. Jahrb. 81: 289. 1962.
Lectotype species: *S. nudum* H. & B. *ex* Dun. [Seithe, 1962].
Oxycarpa Grad. ambig. Rydb., Bull. Torrey Bot. Club 51: 172. 1924. *Nomen nudum.*
Type species: *S. oxycarpum* Schiede.
Pachyphylla Section Dun., Hist. Sol. 122, 168. 1813.
Lectotype species: *S. betaceum* Cav. (= *Cyphomandra betacea* (Cav.) Sendt.).
Pachystemonum Section Dun. *in* DC., Prodr. 13(1): 28, 31. 1852.
Lectotype species: *S. nigrum* L.
Parviflorae Grad. ambig. (?subsection) C. H. Wright, Fl. Trop. Africa 4(2: 2): 210. 1906.
Lectotype species: *S. aculeatissimum* Jacq. (≈ *S. capsicoides* All.)
Parvifolia Subseries Bitt., Fedde Rep. Beih. 16: 106, 129. 1923.
Lectotype species: *S. hastifolium* Hochst. *ex* Dun. [Polhill].
Persicaefolia Grad. ambig. Dun. *in* DC., Prodr. 13(10): 30, 183. 1852.
Type species: *S. persicaeifolium* Dun.
Persicariae Section Dun., Hist. Sol. 126, 183. 1813.
Type species: *S. persicaeifolium* Dun.
Petota Section Dumort., Fl. Belg. 39. 1827.
Type species: *S. tuberosum* L.
Pinnatisecta Grad. ambig. Rydb., Bull. Torrey Bot. Club 51: 146, 167. 1924. *Nomen nudum.*
Series Corr., Potato & Wild Rel. 268. 1962. *Nomen invalidum* [no Latin description].
Type species: *S. pinnatisectum* Dun.
Piurana Series Hawkes, Ann. Mag. Nat. Hist. ser. 12. 7: 693. 1954.
Type species: *S. piurae* Bitt.
Polyadenia Series Buk. *in* Buk. & Kameraz, Princ. Potato Breed. 26. 1959.
Type species: *S. polyadenium* Greenm.
Polybotryon Grad. ambig. G. Don, Gen. Syst. 4: 425. 1838.
Section Bitt., Fedde Rep. 11: 469, 564. 1912, 1913.
Lectotype species: *S. mite* R. & P.
Polygama Grad. ambig. G. Don, Gen. Syst. 4: 425. 1838.
Grad. ambig. Dun. *in* DC., Prodr. 13(1): 30, 196. 1852.
Type species: *S. polygamum* Vahl.
Polymeris Section Dun., Hist. Sol. 123, 174. 1813.
Grad. ambig. G. Don, Gen. Syst. 4: 420. 1838.
Lectotype species: *S. stellatum* Jacq. (= *Lycianthes stellata* (Jacq.) Bitt.).
Potatoe Subsection G. Don, Gen. Syst. 4: 400. 1838.
Section Walp., Rep. Bot. Syst. 3: 38. 1844.
Grad. ambig. Dun. *in* DC., Prodr. 13(1): 28, 31. 1852.
Subgenus D'Arcy, stat. nov.
Lectotype species: *S. tuberosum* L.
Protocryptocarpum Section Marzell *in* Hegi, Fl. Mitt. Eur. 2585. 1927.
Type species: *S. sisymbriifolium* Lam.
Pseudo-capsica Genus Moench., Meth. 476. 1794.
Grad. ambig. G. Don, Gen Syst. 4: 410. 1838.
Section Bitt., Bot. Jahrb. 54: 497. 1917.
Type species: *P. undulatifolium* Moench. (= *S. pseudocapsicum* L.).
Pseudoflava Series Pojark., Not. Syst. 17: 338. 1955.
Type species: *S. pseudoflavum* Pojark.
Pseudolycianthes Grad. ambig. Dun. *in* DC., Prodr. 13(1): 29, 156. 1852.
Lectotype species: *S. aggregatum* Jacq. (≈ *S. guineënse* L.).
Psilocarpa Grad. ambig. Dun. *in* DC., Prodr. 13 (1): 30, 216. 1852.
Lectotype species: *S. lancaeifolium* Jacq.
Pterophyllum Grad. ambig. Dun. *in* DC., Prodr. 13(1): 28, 38. 1852.
Lectotype species: *S. fraxinifolium* Dun.
Pteroidea Section Dun., Hist. Sol. 43, 117, 136. 1813.
Lectotype species: *S. mite* R. & P.

Pyracanthum Series Bitt., Fedde Rep. Beih. 16: 139. 1923.
Type species: S. *pyracanthos* Lam.
Quadrangulare Section Bitt., Bot. Jahrb. 54: 421, 428. 1917.
Type species: S. *quadrangulare* Thunb.
Regmandra Grad. ambig. Dun. *in* DC., Prodr. 13(1): 28, 60. 1852.
Section Ugent, stat. nov.
Lectotype species: S. *montanum* L. [Ugent].
Rhodacanthum Series Bitt., Fedde Rep. Beih. 16: 184. 1923.
Type species: S. *eickii* Damm.
Rhynchantherum Section Bitt., Fedde Rep. 12: 61. 1913.
Type species: S. *graveolens* Bunb.
Septemloba Series Pojark., Fl. URSS 20: 11. 1955. *Nomen invalidum* [no Latin description].
Type species: S. *septemlobum* Bunge.
Silicisolanum Subsection Bitt., Fedde Rep. 16: 10. 1919.
Type species: S. *trachytrichum* Bitt.
Similia Series Herasim, Nov. Syst. Pl. Vasc. 7: 274. 1970.
Type species: S. *simile* F. Muell.
Simplicipilum Section Bitt., Fedde Rep. 18: 309. 1922. *Nomen nudum.*
Section Bitt., Fedde Rep. Beih. 16: 147. 1923.
Lectotype species: S. *aculeatissimum* Jacq. (≈ S. *capsicoides* All.) [Seithe, 1962].
Sodomela Subsection Lowe, Man. Fl. Madeira 2(1): 81. 1868.
Series Bitt., Fedde Rep. Beih. 16: 158. 1923.
Type species: S. *sodomeum* L.
Solanum Genus L., Sp. Pl. 184. 1753.
Subgenus Seithe, Bot. Jahrb. 81: 285. 1962.
Section Seithe, Bot. Jahrb. 81: 286. 1962.
'Chorus subgenerum' Seithe, Bot. Jahrb. 81: 285. 1962.
Lectotype species: S. *nigrum* L. [Hitchcock & Green, 1929].
Somalanum Section Bitt., Bot. Jahrb. 54: 500. 1917.
Lectotype species: S. *jubae* Bitt. [Seithe, 1962].
Spinosa Grad. ambig. [?subgenus] L., Sp. Pl. 186. 1753. *Nomen nudum.*
Stellatipilum Subgenus Seithe, Bot. Jahrb. 81: 296. 1962.
Section Seithe, Bot. Jahrb. 81: 297. 1962.
'Chorus subgenerum' Seithe, Bot. Jahrb. 81: 285. 1962.
Type species: S. *melongena* L.
Suaveolentia Grad. ambig. Rydb., Bull. Torrey Bot. Club 51: 173. 1924. *Nomen nudum.*
Series Corr., Potato & Wild Rel. 89. 1962.
Type species: S. *suaveolens* Kunth & Bouché.
Subcontinentalia Subseries Bitt., Fedde Rep. Beih. 16: 104, 107. 1923.
Lectotype species: S. *zanzibarense* Vatke [Polhill].
Subdulcamara Grad. ambig. Dun. *in* DC., Prodr. 13(1): 28, 84. 1852.
Lectotype species: S. *ipomoea* Sendt.
Subinermia Section Dun., Hist. Sol. 128, 198. 1813.
Subsection G. Don, Gen. Syst. 4: 428. 1838.
Type species: S. *subinerme* Jacq.
Tarijensa Series Corr., Potato & Wild Rel. 233. 1962.
Type species: S. *tarijense* Hawkes.
Torva Section Nees, Trans. Linn. Soc. London 17: 51. 1834.
Subsection G. Don, Gen. Syst. 4: 430. 1838.
Type species: S. *torvum* Sw.
Torvaria Subsection Dun. *in* DC., Prodr. 13(1): 30, 258. 1852.
Section Bitt., Bot. Jahrb. 57: 248, 250. 1922.
Type species: S. *torvum* Sw.
Transaequatorialia Series Buk. *in* Buk. & Kameraz, Princ. Potato Breed. 21. 1959.
Type species: Not selected.
Transcaucasica Series Pojark., Not. Syst. 17: 332. 1955.
Type species: S. *transcaucasicum* Pojark.
Trifida Series Corr., Texas Res. Found. Contr. 1: 12. 1950.
Type species: S. *trifidum* Corr.

Tuberarium Subsection Dun. *in* DC., Prodr. 13(1): 28, 31. 1852.
Section Bitt., Fedde Rep. 11: 349. 1912.
Type species: S. *tuberosum* L.
Tuberosa Grad. ambig. Rydb., Bull. Torrey Bot. Club 51: 146, 147. 1924. *Nomen nudum.*
Series Rydb. *ex* Buk. & Kameraz, Princ. Potato Breed. 18. 1959.
Type species: S. *tuberosum* L.
Vaviloviana Series Buk. *in* Buk. & Kameraz, Princ. Potato Breed. 18. 1959.
Type species: S. *vavilovii* Juz. & Buk.
Yungasensa Series Corr., Potato & Wild Rel. 220. 1962.
Type species: S. *yungasense* Hawkes.

A Provisional Conspectus

Genus *Solanum* L. Lectotype species: S. *nigrum* L.
Chorus subgenerum *Solanum* (L.) Seithe Type species: S. *nigrum* L.
Subgenus *Solanum*
= Subgenus *Eusolanum* Bitt. Lectotype species: S. *nigrum* L.
≈ *Inermes* C. H. Wright Lectotype species: S. *nigrum* L.
Section *Solanum*
= Sect. *Inermis* G. Don Lectotype species: S. *nigrum* L.
= Sect. *Maurella* Dun. Lectotype species: S. *nigrum* L.
= Sect. *Morella* Dumort. Lectotype species: S. *nigrum* L.
= Sect. *Pachystemonum* Dun. Lectotype species: S. *nigrum* L.
≈ Sect. *Campanulisolanum* Bitt. Lectotype species: S. *fiebrigii* Bitt.
Nigra Pojark. Type species: S. *nigrum* L.
Series *Transcaucasica* Pojark. Type species: S. *transcaucasicum* Pojark.
Alata Pojark. Type species: S. *lutea* Mill.
Series *Lutea* Pojark. Type species: S. *luteum* Mill.
Series *Pseudoflava* Pojark. Type species: S. *pseudoflavum* Pojark.
Section *Afrosolanum* Bitt. Type species: S. *terminale* Forsk.
Series *Bifurca* Bitt. Type species: S. *bifurcum* Dun.
Series *Nakurensia* Bitt. Type species: S. *nakurense* C. H. Wright
Section *Benderanum* Bitt. Type species: S. *benderanum* C. H. Wright
Section *Chamaesarachidium* Bitt. Type species: S. *chamaesarachidium* Bitt.
Section *Episarcophyllum* Bitt. Type species: S. *sinuatirecurvum* Bitt.
Section *Gonatotrichum* Bitt. Type species: S. *gonatotrichum* Bitt.
Section *Leiodendra* Dun. Lectotype species: S. *nudum* Dun.
= Sect. *Anthopleuris* (Dun.) Bitt. Lectotype species: S. *nudum* Dun.
= Sect. *Geminata* (G. Don) Walp. Lectotype species: S. *nudum* Dun.
= Sect. *Oppositifolia* (Dun.) Seithe Lectotype species: S. *nudum* Dun.
Subsection *Micranthes* Dun. Type species: S. *micranthum* R. & S.
Subsection *Silicisolanum* Bitt. Type species: S. *trachytrichum* Bitt.
Section *Lemurisolanum* Bitt. Lectotype species: S. *madagascariense* Dun.
Section *Lysiphellos* (Bitt.) Seithe Type species: S. *decorticans* Sendt.
Section *Macronesiotes* Bitt. Lectotype species: S. *imamense* Dun.
Section *Quadrangulare* Bitt. Type species: S. *quadrangulare* L. f.
Subgenus *Archaesolanum* Marzell Type species: S. *aviculare* Forst. f.
Series *Avicularia* Herasim. Type species: S. *aviculare* Forst. f.
Series *Laciniata* Herasim. Type species: S. *laciniatum* Ait.
Series *Similia* Herasim. Type species: S. *simile* F. Muell.
Subgenus *Bassovia* (Aubl.) Bitt. Type species: B. *sylvatica* Aubl. (= S. sp.)
Section *Herposolanum* Bitt. Type species: S. *reptans* Bunb.
Section *Herpystichum* Bitt. Lectotype species: S. *trifolium* Dun.
Section *Pteroidea* Dun. Lectotype species: S. *mite* R. & P.
= Sect. *Polybotryon* (Dun.) Bitt. Lectotype species: S. *mite* R. & P.
≈ *Bassovioides* Dun. Lectotype species: S. *anceps* R. & P.
Subgenus *Brevantherum* (Seithe) D'Arcy
Section *Brevantherum* Seithe Type species: S. *verbascifolium* auct. non L.
Subsection *Asterochlaena* Lowe Type species: S. *auriculatum* Ait.
Section *Extensum* D'Arcy Type species: S. *extensum* Bitt.

Section *Holophylla* (G. Don) Walp. Lectotype species: *S. pulverulentum* Pers.

= Sect. *Anthoresis* Bitt. Lectotype species: *S. pulverulentum* Pers.

Series *Durigibbosa* Bitt. Lectotype species: *S. cladotrichum* Vandas

Series *Endotricha* Bitt. Type species: *S. endotrichum* Bitt.

Series *Monadelphoidea* Bitt. Type species: *S. monadelphum* Heurck. & Muell.-Arg.

Subsection *Indubitaria* (Dun.) Seithe Lectotype species: *S. brachystachys* Dun.

Section *Lepidotum* Seithe Type species: *S. lepidotum* Dun.

Section *Pseudocapsicum* Bitt. Type species: *S. pseudocapsicum* L.

Subsection *Cerasocarpum* Lowe Type species: *S. pseudocapsicum* L.

Subgenus *Leptostemonum* (Dun.) Bitt. Lectotype species: *S. mammosum* L.

≈ *Armatae* C. H. Wright Lectotype species: *S. aculeatissimum* Jacq. (≈ *S. capsicoides* All.).

Section *Acanthophora* Dun. Lectotype species: *S. mammosum* L.

= Sect. *Aculeata* G. Don Lectotype species: *S. mammosum* L.

≈ *Leptostemonum* Dun. Lectotype species: *S. mammosum* L.

≈ *Parviflorae* C. H. Wright Lectotype species: *S. aculeatissimum* Jacq. (≈ *S. capsicoides* All.).

≈ *Simplicipilum* Bitt. Lectotype species: *S. aculeatissimum* Jacq. (≈ *S. capsicoides* All.).

Subsection *Euleptostemonum* Dun. Lectotype species: *S. mammosum* L.

Section *Aculeigerum* Seithe Type species: *S. wendlandii* Hook. f.

Subsection *Juciri* Marzell Type species: *S. wendlandii* Hook. f.

Section *Androceras* (Nutt.) Marzell Type species: *A. lobata* Nutt. (= *S. rostratum* Dun.)

Section *Anisantherum* Bitt. Lectotype species: *S. pubescens* Willd.

Section *Aquartia* (Jacq.) D'Arcy Type species: *A. aculeatum* Jacq. (= *S. aquartia* Dun.)

Aquartia (Jacq.) Dun. Type species: *A. aculeatum* Jacq. (= *S. aquartia* Dun.)

Polygama G. Don Type species: *S. polygamum* Vahl

Section *Cryptocarpum* Dun. Lectotype species: *S. balbisii* Dun.

≈ Sect. *Protocryptocarpum* Marzell Type species: *S. sisymbriifolium* Lam.

Section *Eriophyllum* Dun. Lectotype species: *S. jamaicense* Mill.

Heteracantha Dun. Lectotype species: *S. jamaicense* Mill.

Section *Graciliflorum* (Dun.) Seithe Type species: *S. graciliflorum* Dun.

Section *Irenosolanum* Seithe Type species: *S. woahense* Dun.

Section *Ischyracanthum* Bitt. Lectotype species: *S. ogadense* Bitt.

Section *Lasiocarpum* (Dun.) D'Arcy Type species: *S. lasiocarpum* Dun.

Section *Lathyrocarpum* (G. Don) Walp. Lectotype species: *S. carolinense* L.

Asterotrichotum Dun. Lectotype species: *S. carolinense* L.

Section *Leprophora* Dun. Lectotype species: *S. elaeagnifolium* Cav.

Section *Melongena* Dun. Lectotype species: *M. ovata* Mill. (= *S. melongena* L.).

= Sect. *Andromonoecum* Bitt. Lectotype species: *S. melongena* L.

= Sect. *Stellatipilum* Seithe Lectotype species: *S. melongena* L.

≈ *Grandiflorae* C. H. Wright Lectotype species: *S. melongena* L.

Series *Acanthocalyx* Bitt. Lectotype species: *S. richardii* Dun.

Series *Aculeastrum* Bitt. Type species: *S. aculeastrum* Dun.

Series *Afrodecumbens* Bitt. Type species: *S. nigriviolaceum* Bitt.

Series *Incaniformia* Bitt. Type species: *S. incanum* L.

Subseries *Campylacantha* Bitt. Type species: *S. campylacanthum* Hochst.

Subseries *Euincana* Bitt. Type species: *S. incanum* L.

Series *Macrocarpon* Dun. Type species: *S. macrocarpon* L. f.

Series *Rhodacanthum* Bitt. Type species: *S. eickii* Damm.

Series *Sodomela* (Lowe) Bitt. Type species: *S. sodomeum* L.

Brachylobus Dun. Lectotype species: *S. esculentum* Dun. (= *S. melongena* L.)

Eumelongena Dun. Lectotype species: *S. esculentum* Dun. (= *S. melongena* L.)

Mogenoplum Dun. Lectotype species: *S. lanceolatum* Cav.

Section *Micracantha* Dun. Type species: *S. micracanthos* Lam.

Psilocarpa Dun. Lectotype species: *S. lancaeifolium* Jacq.

Section *Monodolichopus* Bitt. Type species: *S. dubium* Fresen

Section *Nycterium* (Vent.) Dun. Type species: *N. cordifolium* Vent. (= *S. vespertillio* Ait.).

- Section *Oliganthes* (Dun.) Bitt. Lectotype species: *S. indicum* L.
  - ≈ *Microphyllae* C. H. Wright Lectotype species: *S. macracanthum* A. Rich.
  - Series *Aethiopica* Bitt. Type species: *S. aethiopicum* L.
    - *Lycopersicarpon* Dun. Lectotype species: *S. aethiopicum* L.
  - Series *Afroindica* Bitt. Type species: *S. indicum* L.
  - Series *Albicaule* Bitt. Type species: *S. albicaule* Dun.
  - Series *Austroafricana* Bitt. Lectotype species: *S. tomentosum* L.
  - Series *Capensiformia* Bitt. Type species: *S. capense* L.
  - Series *Eoafra* Bitt. Lectotype species: *S. zanzibarense* Vatke
    - Subseries *Erythracanthum* Bitt. Type species: *S. erythracanthum* Boj.
    - Subseries *Madagascariensia* Bitt. Lectotype species: *S. nossibeënse* Vatke
    - Subseries *Parvifolia* Bitt. Lectotype species: *S. hastifolium* Dun.
    - Subseries *Subcontinentalia* Bitt. Lectotype species: *S. zanzibarense* Vatke
  - Series *Macracanthum* Bitt. Type species: *S. macracanthum* A. Rich.
  - Series *Pyracanthum* Bitt. Type species: *S. pyracanthos* Lam.
- Section *Persicariae* Dun. Type species: *S. persicaeifolium* Dun.
  - *Persicaefolia* Dun. Type species: *S. persicaeifolium* Dun.
- Section *Subinermia* Dun. Type species: *S. subinerme* Jacq.
  - *Juripeba* Dun. Type species: *S. juripeba* Rich.
- Section *Somalanum* Bitt. Lectotype species: *S. jubae* Bitt.
- Section *Torva* Nees Type species: *S. torvum* Sw.
  - = Sect. *Torvaria* (Dun.) Bitt. Type species: *S. torvum* Sw.
  - Series *Anomalum* Bitt. Type species: *S. anomalum* Thonn.
  - Series *Eutorvum* Bitt. Type species: *S. torvum* Sw.
  - Series *Giganteiformia* Bitt. Type species: *S. giganteum* Jacq.
    - *Dunaliana* Bitt. Type species: *S. dunalianum* Gaud.

Subgenus *Lyciosolanum* Bitt. Type species: *S. aggregatum* Jacq. (≈ *S. guineënse* L.).

- *Pseudolycianthes* Dun. Lectotype species: *S. aggregatum* Jacq. (≈ *S. guineënse* L.)

Subgenus *Potatoe* (G. Don) D'Arcy

- Section *Petota* Dumort.
  - = Section *Potatoe* (G. Don) Walp. Lectotype species: *S. tuberosum* L.
  - = Sect. *Tuberarium* (Dun.) Bitt. Type species: *S. tuberosum* L.
  - Subsection *Potatoe* G. Don Lectotype species: *S. tuberosum* L.
    - = Subsection *Hyperbasarthrum* Bitt. Lectotype species: *S. tuberosum* L.
    - = Subsection *Tuberarium* Dun. Type species: *S. tuberosum* L.
    - Series *Acaulia* Buk. & Kameraz Type species: *S. acaule* Bitt.
    - Series *Circaeifolia* Hawkes Type species: *S. circaeifolium* Bitt.
    - Series *Clara* Grah. & Dion. Type species: *S. clarum* Corr.
      - ≈ Series *Bulbocastanum* Corr. Lectotype species: *S. bulbocastanum* Dun.
    - Series *Conicibaccata* Bitt. Lectotype species: *S. oxycarpum* Schiede
      - ≈ *Oxycarpa* Rydb. Type species: *S. oxycarpum* Schiede
    - Series *Commersoniana* Buk. Type species: *S. commersonii* Lam.
      - ≈ Series *Glabrescentia* Buk. Type species: Not selected.
      - ≈ Series *Tarijensa* Corr. Type species: *S. tarijense* Hawkes
      - ≈ Series *Yungasensa* Corr. Type species: *S. yungasense* Hawkes
    - Series *Cuneolata* Hawkes Type species: *S. infundibuliforme* Phil.
    - Series *Demissa* Buk. Type species: *S. demissum* Lindl.
    - Series *Etuberosa* Buk. & Kameraz Type species: *S. etuberosum* Lindl.
    - Series *Ingaefolia* Ochoa Type species: *S. ingaefolium* Bitt.
    - Series *Juglandifolia* D'Arcy Type species: *S. juglandifolium* Bitt.
    - Series *Longipedicellata* Buk. Type species: *S. longipedicellatum* Bitt.
      - ≈ Series *Borealia* Corr. Type species: Not selected.
    - Series *Maglia* Bitt. Type species: *S. maglia* Schlecht.
      - ≈ Series *Andigena* Buk. Type species: *S. andigenum* Juz. & Buk.
      - ≈ Series *Andreana* Hawkes Type species: *S. andreanum* Baker
      - ≈ Series *Minutifoliola* Corr. Type species: *S. minutifoliolum* Corr.
      - ≈ Series *Transaequatorialia* Buk. Type species: Not selected.
      - ≈ *Vaviloviana* Buk. Type species: *S. vavilovii* Juz. & Buk.

Series *Megistacroloba* Cárd. & Hawkes Type species: *S. megistacrolobum* Bitt.
≈ Series *Alticola* Buk. Type species: *S. alticola* Bitt.
Series *Morelliformia* Hawkes Type species: *S. morelliforme* Bitt. & Muench.
Series *Piurana* Hawkes Type species: *S. piurae* Bitt.
Series *Polyadenia* Corr. Type species: *S. polyadenium* Greenm.
Series *Trifida* Corr. Type species: *S. trifidum* Corr.
≈ Series *Cardiophylla* Corr. Type species: *S. cardiophyllum* Lindl.
≈ Series *Pinnatisecta* Corr. Type species: *S. pinnatisectum* Dun.
Series *Tuberosa* Buk. & Kameraz Type species: *S. tuberosum* L.
Angustisegmentata Buk. Lectotype species: *S. canasense* Hawkes
Aracciana Buk. Lectotype species: *S. aracc-papa* Juz.
Section *Anarrhichomenum* Bitt. Lectotype species: *S. sodiroi* Bitt.
Section *Basarthrum* (Bitt.) Bitt. Lectotype species: *S. suaveolens* Kunth & Bouché
Series *Appendiculata* Corr. Type species: *S. appendiculatum* Dun.
Series *Articulata* Corr. Type species: *S. sanctae-marthae* Bitt.
Series *Canensa* Corr. Type species: *S. canense* Rydb.
Series *Caripensa* Corr. Type species: *S. caripense* Dun.
Series *Muricata* Corr. Type species: *S. muricatum* Ait.
Series *Suaveolentia* Corr. Type species: *S. suaveolens* Kunth & Bouché
≈ *Pterophyllum* Dun. Lectotype species: *S. fraxinifolium* Dun.
Section *Dulcamara* Dumort. Type species: *S. dulcamara* L.
Kieseritzkiana Pojark. Type species: *S. kieseritzkii* C. A. Mey.
Septemloba Pojark. Type species: *S. septemlobum* Bunge
Subdulcamara Dun. Lectotype species: *S. ipomoea* Sendt.
Section *Jasminosolanum* Seithe Type species: *S. jasminoides* Paxt.
Section *Neolycopersicon* Corr. Type species: *S. pennellii* Corr.
Section *Normania* (Lowe) Bitt. Type species: *N. triphylla* Lowe (= *S. trisectum* Dun.).
Section *Regmandra* (Dun.) Ugent Lectotype species: *S. montanum* L.
Section *Rhynchantherum* Bitt. Type species: *S. graveolens* Bunb.

Nomina *Solano* Excludenda

Ad *Cyphomandra* Sendt.
Section *Cyphomandropsis* Bitt. Lectotype species: *C. stuckertii* (Bitt.) D'Arcy
Section *Pachyphylla* Dun. Lectotype species: *Cyphomandra betacea* (Cav.) Sendt.

Ad *Lycianthes* (Dun.) Hassl.
Section *Cypellocalyx* Bitt. Lectotype species: *Lycianthes* sp.
Subsection *Holochlaina* G. Don Lectotype species: *L. bigeminata* (Nees) Bitt.
Lobanthes Dun. Lectotype species: *L. bigeminata* (Nees) Bitt.
Section *Lycioides* Walp. Type species: *L. lycioides* (L.) Hassl.
Subgenus *Lycianthes* (Dun.) Bitt. Type species: *L. lycioides* (L.) Hassl.
Section *Lycianthes* (Dun.) Wettst. Type species: *L. lycioides* (L.) Hassl.
Subsection *Lycianthes* Dun. Lectotype species: *L. lycioides* (L.) Hassl.
Eulycianthes Dun. Lectotype species: *L. lycioides* (L.) Hassl.
Meiomeris Dun. Lectotype species: *L. lycioides* (L.) Hassl.
Section *Polymeris* Dun. Lectotype species: *L. stellata* (Jacq.) Bitt.
Gonianthes Dun. Lectotype species: *L. stellata* (Jacq.) Bitt.

Ad *Lycopersicon* Mill.
Subgenus *Lycopersicon* (Mill.) Wettst. Type species: *L. esculentum* Mill.
Section *Lycopersicon* (Mill.) Bitt. Type species: *L. esculentum* Mill.

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NEW TAXA AND RECOMBINATIONS IN *LOPEZIA* (ONAGRACEAE)

Uzi Plitmann,[1] Peter H. Raven,[2] and D. E. Breedlove[3]

Studies of the 22 species of Lopezieae, one of the six tribes of Onagraceae, have led to the conclusion that these are best treated as a single genus. In the course of our investigations, three new taxa have been discovered and several new combinations have become necessary. These are published here so that they may be available for one or more papers on the group that will appear before our monograph, to be published in the *Annals of the Missouri Botanical Garden* in 1973.

This work has been supported by a series of grants from the U.S. National Science Foundation to Peter H. Raven.

New Taxa

Lopezia ciliatula Plitmann, Raven & Breedlove, sp. nov.

Herbae annuae hirtellae, pilis rectis vel crispis. Rami 40–80 cm alti, erecti, plerumque ramosi; ramulosi tenues, teretes ad angulares. Folia 1–9 × 0.5–5 cm, alternantia ad raro opposita, ovata vel oblongo-ovata ad lanceolata, membranacea, longipetiolata, basi plerumque obliquo vel inaequale subcordata ad obtusa vel late cuneata, apice acuta ad acuminata, serrata vel serrulata, in quoque latere costae venulis 4–8 praedita, hispidula, pilis paucis strigulosis admixta, ciliata; petioli 0.3–6.5 cm longa, angustissime alati, pubescentes. Inflorescentia terminalis delicata infra foliosa; bracteae 0.3–2.5 × 0.05–0.7 cm, lanceolatae ad lineares vel subulatae, basi subcuneatae, apice acuminatae, subserrulatae vel integrae, petiolatae vel subsessiles; pedicelli 0.8–1.5 cm longi, subascendentes, filiformes atque angulares vel alati, dense et breviter hirsuti. Sepala 0.3–0.45 × 0.07–0.1 cm, plerumque lineаro-lanceolata, acuta, subglabra, viridia ad purpurascentia. Petala inferiora 0.25–0.4 × 0.15–0.2 cm, oblongo-ovata, in unquem brevem producta, subcrenulata, ad basin plus minusve breviter ciliata, rubescentes vel albescentes; petala superiora 0.25–0.4 × 0.05–0.09 cm, anguste lineаro-spatulata, ad basin parum angustata demum late obtriangularo-obovata auriculis alatis glandis 2 viridibus, sessilia, apice obtusa, ciliata, rubescentia ad purpurascentia. Stamen 0.3–0.4 cm; filamentum alato-dilatum apice excepto; anthera 0.1–0.13 × 0.07 cm, plantis locarum umbrosarum pallidior. Staminodium 0.25–0.4 × 0.15–0.2 cm, suborbiculare vel obovato-spatulatum, apice subemarginatum, in unguem longum productum, reubescente. Stylus 0.25–0.35 cm longus; stigma parvum, capitato-obconideum; ovarium globosum ad ellipsoideum, pilosum. Capsula 0.15–0.35 × 0.15–0.35 cm, subglobosa, strigulosa. Semina ca 0.08 × 0.05 mm, oblongo-ovoidea,

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Ann. Missouri Bot. Gard. 59: 279–281. 1972.

parum falcata, distincto papilloso-tuberculata, atrobrunnea. Numerus chromosomaticus gameticus, $n = 9$.

Type: MEXICO. SINALOA: Sierra Surutato, Cañon de Tarahumares between Arroyo Verde and Rancho Tarahumares, steep north-facing slope, 27 February 1968, *D. E. Breedlove 15921* (DS, holotype).

Distribution: Known only from a single population on a steep-walled canyon with *Bursera* and *Ipomoea* in the Cañon de Tarahumares of the Sierra Surutato, elevation ca. 1100 m.

Lopezia ciliatula is easily distinguishable from the related species with two glands on each of the upper petals, by its small flowers, sessile and basally auriculate-winged upper petals, ciliation of the petals, pubescence of the petioles, pedicels, capsules, and inflorescence. It may have been derived from *L. miniata* Lag., which it resembles most closely.

Lopezia laciniata (Rose) Jones subsp. **ovata** Plitmann, Raven & Breedlove, subsp. nov.

Rami flexuosi, decumbentes vel ascendentes, interdum tenues, subglabra. Folia quam in subsp. *laciniata* plerumque latiora (ad 2.2 cm lata), ovata vel lanceolata, basi subcordata ad subacuto-cuneata, apice acuta, superiora distincte petiolata. Numerus chromosomaticus gameticus, $n = 10$.

Type: MEXICO. DURANGO: 20 miles west of La Cicudad, steep moist cliff on edge of barranca, elevation 7,600 feet, 3 October 1966, *D. E. Breedlove 15552* (DS, holotype).

Distribution: Moist places, usually on wet cliffs and slopes, in rock crevices or near streams; altitude (800–) 1300–2800 m. In Durango and Sinaloa.

Lopezia laciniata subsp. *laciniata* is found in similar habitats in the Sierra Madre Occidental of Jalisco.

Lopezia nuevo-leonis Plitmann, Raven & Breedlove, sp. nov.

Herbae annuae vel biennes sparse strigulosae ad glabrae. Rami 25–70 cm alti, erecti, ramosi, basi sublignosi (ad 1 cm crassi), angulares, viridescentes ad purpureo-rubescentes. Folia 0.6–4 × 0.2–2.5 cm, oblongo-ovata ad lanceolata, basi rotundata ad late cuneata, apice subacuta vel acuminata, acute serrata, subcrassa, subglabra, quoque lateris costae venulis 2–6, basi opposita alia plerumque alternantia; petioli 0.1–3.8 × 0.05–0.2 cm, sparsissime strigulosi ad glabri, viridescentes vel rubrescentes; stipulae ca. 1 mm longae, acicularo-subulatae, deciduae. Inflorescentia aperte paniculata interdum racemosa terminalis; bracteae 0.3–1.3 × 0.1–0.4 cm, lanceolatae vel lineares, subsessilia, subserratae vel serrulatae, subglabrae; pedicelli 0.8–2.1 cm longi, ascendentes, appressi et breve pubescentes ad lateram unam, subglabri ad lateram alteram, viridescentes ad purpurei. Sepala 0.45–0.7 × ca. 0.1 cm, linearia ad anguste lanceolata vel oblanceolata, acuta, viridescentes ad purpurascentes, glabra. Petala rubrescentes, inferiora 0.5–0.8 × 0.2–0.35 cm, obovata, subasymmetrice in unguem longum producta, apice rotundata, interdum subcrenulata ad subretusa, superiora 0.5–0.85 × 0.1–0.15 cm, oblanceolata-linearia, subobtusa, unguiculata, breviter obtuseque auriculata, glandis adjaceis 2 praedita. Stamen 0.4–0.5 cm; anthera 0.15–0.2 × 0.07–

0.13 cm, caeruleo-cinerea. Staminodium 0.35–0.45 × 0.2–0.3 cm, late obovatum, abrupte unguiculatum, apice emarginatum, rubescente atque infra pallidiore. Stylus 0.3–0.4 cm longus, filiformis; stigma 0.5–1.1 mm diam., capitatum; ovarium glabrum atque infra breviter strigulosum. Capsula 0.3–0.5 × 0.2–0.4 cm, oblonga vel ovoidea-ellipsoidea, subglabra, nonnullam apice aperta. Semina 0.9–1.1 × 0.6–0.8 mm, oblongo-ovoidea, incurvata, crasse rugoso-tuberculata, subatrae. Numerus chromosomaticus gameticus, $n = 8$.

Type: MEXICO. NUEVO LEÓN: Sierra Madre Oriental, Santa Rosa Canyon, 21 miles west of Linares, cool north-facing talus and rock edges, elevation 2100 feet, 28 October 1964, *H. D. Ripley and R. C. Barneby 13569* (DS, holotype; NY, isotype).

Distribution: Rocky slopes in the Sierra Madre Oriental in Nuevo León and San Luis Potosí; rare and local.

Lopezia nuevo-leonis differs from *L. racemosa* in its long, glabrescent stems, two (not one) glands on each upper petal, more or less oblong capsules, and other features. From *L. miniata* it can be distinguished by its angular reddish stems; acutely serrate leaves (generally glabrous, fleshy and with fewer veins); pinkish-red flowers; shortly and obtusely auricled upper petals; oblong or ovoid-ellipsoid and somewhat longer capsules; coarsely rugose-tubercled, blackish and slightly larger seeds. It likewise differs from both of these species, which have $n = 10$ ($n = 20$ in some populations of *L. racemosa*) in chromosome number.

NEW COMBINATIONS

Lopezia gentryi (Munz) Plitmann, Raven & Breedlove, comb. nov.

Lopezia laciniata (Rose) M. E. Jones subsp. *gentryi* Munz, Brittonia 13: 84. 1961.

Lopezia grandiflora Zuccar. subsp. **macrophylla** (Benth.) Plitmann, Raven & Breedlove, comb. nov.

Lopezia macrophylla Benth., Pl. Hartw. 83, 92. 1841.

Lopezia lopezioides (Hook. & Arn.) Plitmann, Raven & Breedlove, comb. nov.

Diplandra lopezioides Hook. & Arn., Bot. Beech. Voy. 292, *pl. 60.* 1838.

Lopezia riesenbachia Plitmann, Raven & Breedlove, nom. nov.

Riesenbachia racemosa Presl, Rel. Haenk. 2: 36, *t. 54.* 1831.

Lopezia semeiandra Plitmann, Raven & Breedlove, nom. nov.

Semeiandra grandiflora Hook. & Arn., Bot. Beech. Voy. 291, *pl. 59.* 1838.

THE COMPARATIVE MORPHOLOGY OF THE COCHLOSPERMACEAE. III. THE FLOWER AND POLLEN[1]

RICHARD C. KEATING[2]

ABSTRACT

The flowers and pollen of *Amoreuxia* and *Cochlospermum* have been studied anatomically to contribute to determining trends of specialization and relationships of the Cochlospermaceae. Perianth vascularization consists of 10 traces in some species of *Cochlospermum* but is reduced to 6 or 5 in other species. Androecial development is centrifugal with the vascularization consisting of 5 or more trunk bundles. The ovary has a single, 3–5 carpellate, ramified locule in all species examined. Pollen is mostly intectate to semitectate and tricolporoidate. Floral morphology of *Bixa* is more specialized in some ways and less specialized in others and its placement in a separate family from *Amoreuxia* and *Cochlospermum* can be justified. While the Cochlospermaceae show similarities to many parietalian families, the floral anatomy is also compatible with that found in the Malvales.

Previous papers in this series (Keating, 1968, 1970), discussed the relationships of the Cochlospermaceae using the evidence from vegetative anatomy. Although floral and pollen morphology have demonstrated value in systematics, there is no complete treatment of the flower of even a single species of *Cochlospermum*. The genus *Amoreuxia* is not known to have been anatomically investigated at all. Schnarf (1931) investigated the development of the seed of *C. orinocense*. His comments on the nature of the septa of the gynoecium made no mention of its vascular anatomy. In illustrating the vasculature of the perianth and androecium of *C. vitifolium*, Wilson (1937) pointed out that more species would have to be investigated before drawing conclusions regarding the basic nature of the vasculature in this genus. The numerous stamens and reported parietal placentation have placed the family in the Bixales-Flacourtiaceae alliance (Cronquist, 1968; Takhtajan, 1969), while vegetative anatomy (Keating, 1968, 1970) indicates malvalian affinities.

Erdtman (1952) briefly described the pollen of three species of *Cochlospermum* and noted their resemblance to pollen of *Bixa*. Nair (1962) briefly described the pollen of *C. religiosum*. Floral anatomy and pollen of *Rhopalocarpus*, previously assigned to the Cochlospermaceae, has been investigated by Huard (1965*a*, *b*, *c*).

My present purpose is to examine the floral anatomy and pollen of many species of Cochlospermaceae in order to determine more accurately the relationships of the family.

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[1] I am grateful to the office of Research and Projects, Southern Illinois University, for its support of this work. Valuable assistance was given by the staffs of the herbaria of the Field Museum of Natural History, Harvard University, Missouri Botanical Garden, New York Botanical Garden, and the Smithsonian Institution. Also, my thanks go to collectors and curators in many nations for their generous response to my requests for specimens.

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ANN. MISSOURI BOT. GARD. 59: 282–296. 1972.

TABLE 1. Specimens examined[a].

Name	Collector, source[b]	Material
Amoreuxia wrightii A. Gray	*von Rozynski s.n.* (1932), F	Bud
	Webster & Miller 13137, PUL	Bud
	Wooten s.n. (1919), US	Bud
	Axtell F-03484, SIUE	Pollen
A. palmatifida Mocino & Sesse	*Niles 425*, ARIZ	Bud
Bixa orellana L.	*Tate 32*, NY	Bud
	Keating 360, 414, SIUE	Bud, pollen
Cochlospermum fraseri Planch.	*Specht s.n.* (1948), US	Bud
	Perry s.n. (1949), US	Bud
C. gillivraei Benth.	*Sprecht s.n.* (1948), US	Bud
C. gregorii F. Muell.	*Perry s.n.* (1948), US	Bud, pollen
C. orinocense Steud.	*Kuhlmann & Jimbo 387*, SP	Bud, pollen
	Holt & Gehringer s.n. (1930), US	Bud, pollen
	Piras s.n. (1947), US	Bud, pollen
C. parkeri Planch.	*Klug s.n.* (1933), US	Bud
C. planchonii Hook. f. *ex* Planch.	*Wimbush s.n.* (1962), SIUE	Bud
	Chevalier s.n. (1910), P	Bud
	Ibem s.n. (1963), SIUE	Pollen
C. regium (Mart & Shrank) Pilger	*Hoehne s.n.* (1931), SP	Bud
	Hassler s.n. (1907–8), US	Bud
	Dahlgren s.n. (1935), F	Pollen
C. religiosum (L.) Alston *ex* Trimen	*Subba Rao s.n.* (1963), CAL	Bud
	Bole s.n. (1963), BLAT	Bud, pollen
	Yongboonkird s.n. (1963), BK	Bud
C. tetraporum H. Hallier	*Pflanz 4034*, US	Bud
C. tinctorium A. Rich	*Chevalier 94*, P	Bud
	Le Testu s.n. (1922), P	Pollen
C. vitifolium (Willd.) Spreng.	*Stern, Eyde & Ayensu 1694*, US	Bud
	Rowlee & Mixter s.n. (1921), US	Bud
	Jack s.n. (1930), US	Bud
	Schipp 49, NY	Pollen
C. williamsii Macbride	*Williams* (1929), F	Bud

[a] Specimens cited according to the procedure recommended by Stern and Chambers (1960).
[b] Southern Illinois University, Edwardsville, designated as SIUE.

MATERIALS AND METHODS

Flowers and buds of *Amoreuxia* and *Cochlospermum* from a geographically diverse sampling of each genus were obtained for study (Table 1). Specimens of *Bixa* were available for comparison. Floral anatomy was studied from microtomed serial sections and from cleared thick sections of both dried and FPA preserved material. Thick sections were cleared using the NaOH-Chloral hydrate method of Arnott (1959) or the peroxide-lactic acid technique of Sporne (1948). Occasionally 5% sodium hypochlorite (straight household bleach) was needed to remove dark deposits from the floral receptacle. Vascular structure of the clearings was readily visible without staining and drawings were made with the aid of a 50× dissecting microscope. Serial microtomed sections of most species were prepared using paraffin techniques from preserved material or from dried herbarium specimens. Staining was accomplished using Safranin O and Fast Green FCF for the preserved material while Methyl Violet 2B and Bismarck Brown Y proved to be the best combination for the restored material.

Pollen was prepared by KOH-acetolysis (Faegri & Iversen, 1964) and mounted in glycerin jelly containing safranin. Sections of some samples were made at 1 μ thickness with an ultramicrotome after embedding in Epon-Araldite. Measurements of polar and equatorial axes were based on at least 20 grains per sample from acetolyzed specimens.

Descriptions of floral anatomy emphasize vascularization because of its demonstrated value in determining relationships (Moseley, 1967). Descriptions of vascular "events" in the observations section are topographical and are designed for comparisons of the anatomy of mature flowers. Such terms as "diverge from the stele" refer to the appearance of vascular bundles viewed in successively higher (more distal) serial sections and yield the most efficient graphic descriptions. It should be understood that developmental interpretations of these terms will produce nonsense.

OBSERVATIONS

General floral morphology and histology is similar for both *Cochlospermum* and *Amoreuxia.* The perianth is composed of five quincuncially imbricate sepals alternating with five rotate petals. Both genera show a tendency toward zygomorphy, the condition being more pronounced in *Amoreuxia.* The bright orange-yellow petals in both genera have red glide ways on four of the five petals. These are only slightly visible on fresh flowers of *C. vitifolium.* Short unbranched trichomes range from dense to nearly absent on the receptacle and sepals. Vascularization enters the receptacle as a siphonostele and extraxylary fibers are absent at anthesis. In some specimens of *Cochlospermum* and *Amoreuxia,* vertical lysigenous canals are present in the ground tissue.

Vascularization of the perianth is most discrete in *Cochlospermum orinocense, C. gregorii,* and *C. regium.* In these species the vasculature of the calyx consists of five vascular bundles which diverge from successively higher serial sections in a $2/5$ phyllotactic sequence. Each sepal is vascularized by one of these bundles (Fig. 29). At higher levels they trifurcate with the lateral branches fusing to form a ring (Fig. 10). At the base of the sepals, this ring of vasculature is used up in producing a series of parallel veinlets in each sepal. Alternating with the five sepal traces, five petal traces leave the siphonostele above them (Figs. 10, 29). At higher levels, the petal traces also appear to branch to form numerous parallel bundles in the petals. In *Amoreuxia, C. vitifolium,* and in most other species of *Cochlospermum* examined, the perianth traces are five to six instead of 10 in number. The traces diverge from the siphonostele in no discernible phyllotactic pattern. In higher sections, where the receptacle is considerably broadened, the traces trifurcate with the lateral branches fusing with neighboring laterals to form a circular vascular plexus (Figs. 2–3, 9, 31). Vascular bundles continue upward from the original traces and vascularize the sepals. Traces originating from the plexus between the original sepal traces vascularize the petals.

The androecium.—The stamens have basifixed anthers which are four loculed. Pollen is shed through single introrse apical pores and a pair of lateral basal pores in most species of *Cochlospermum* (Figs. 4–6). In *Amoreuxia,* the anthers have a

FIGURE 1.—Longisection of flower of *Cochlospermum vitifolium*, × 6.5. Cut was made along plane of bilateral symmetry. Note differences in length of anther filaments, the recurved style, the curved peduncle.

pair of obliquely arranged apical slits across the tops of lateral pairs of locules (Fig. 7). Septa between the pairs of locules become thin and may disintegrate when pollen is shed. The elongate filaments have a single vascular trace which enters the base of the anthers and continues between the locules to the apex.

Vascularization of the stamens originates above the origin of the perianth vasculature with 5–6 traces alternating with the previous series of bundles (Figs. 2–3). As many as 8–10 stamen bundles appear in some species due to early bi- or trifurcation, but five gaps in the stele are common even in these cases. These trunk bundles branch at higher levels to form a broken circle of vasculature which develops in a centrifugal pattern (Fig. 11). A broad zone of stamen traces is formed which at the surface of the receptacle appears to be a complete circle of 3–6 concentric ranks of bundles. In *Cochlospermum gregorii* the most obscure pattern of vascularization is found. From the lowest level where perianth traces diverge from the stele, there is an indistinct number of vascular traces, bifurcations, and fusions forming a discontinuous plexus which vascularizes all segments of the perianth. The remaining, slightly contracted, siphonostele provides androecial traces at a higher level. There are no distinct trunk bundles; a circular band of vasculature moves out centrifugally as higher sections are examined. Rows of stamen traces mature first nearest the center of the receptacle, the outermost being the most recently formed.

The gynoecium.—The pistil of Cochlospermaceae consists of a globose ovary surmounted by an elongate, linear style, recurved at the summit in the plane of bilateral symmetry (Fig. 1). The ovary is three, four, or five carpellate, and all specimens showed the same anatomy with minor modifications. Transections through the lower or upper parts of the ovary give the appearance of axile placentation while, transections through the middle part show parietal placenta-

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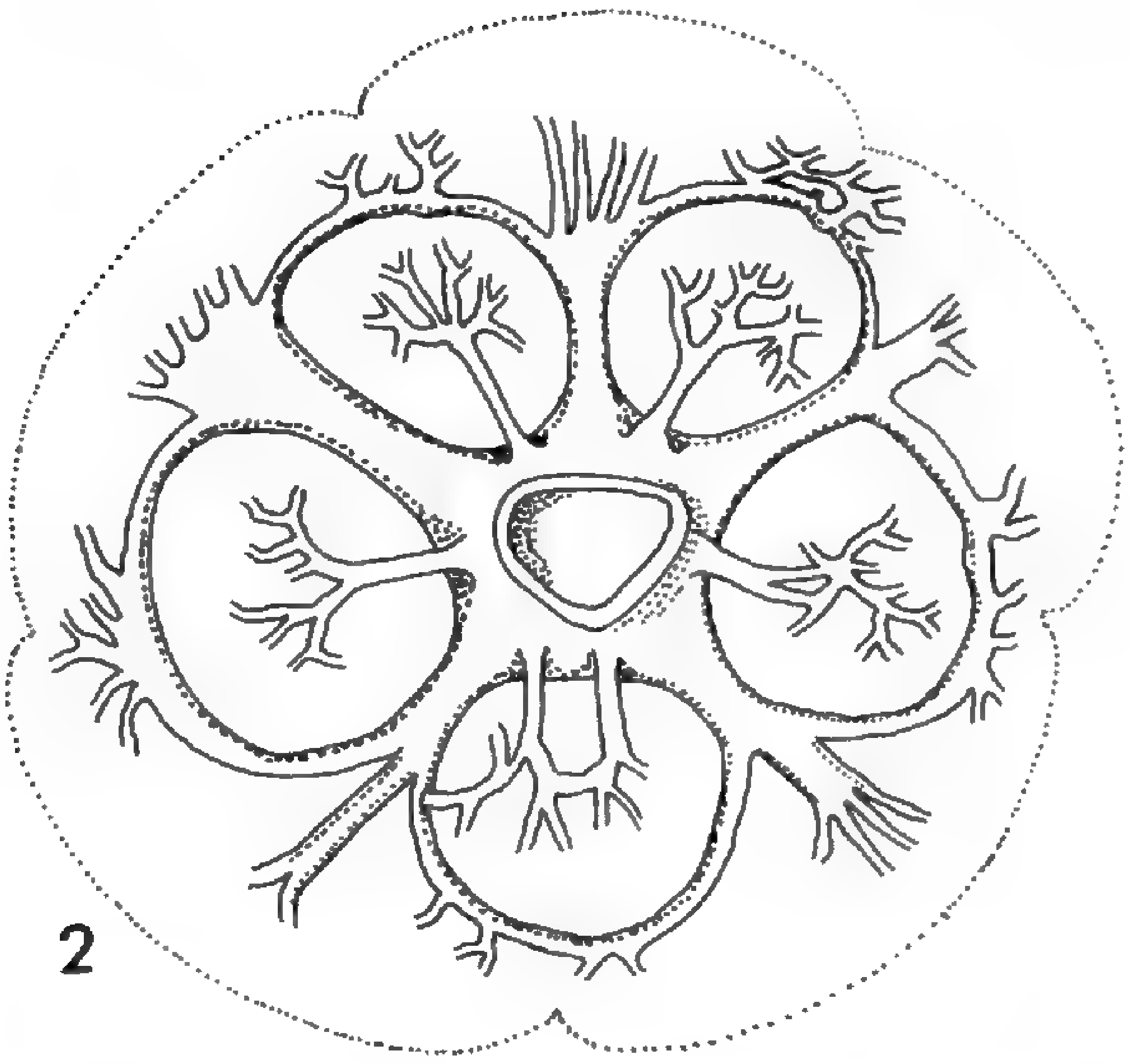
FIGURES 2–18.—Floral anatomy of Cochlospermaceae.—2–3. Cleared transverse thick sections through floral receptacle.—2. *Amoreuxia palmatifida*, × 10. Note five perianth traces and six stamen trunk bundles.—3. *Cochlospermum vitifolium*, × 5. Note six perianth traces and five stamen trunk bundles.—4–7. Cleared whole anthers, × 6.—4. *Cochlospermum vitifolium*, adaxial view. Note small apical pore.—5. *Cochlospermum religiosum*, lateral and adaxial views. Note basal pore in lateral view and elongate apical pore in adaxial view.—6. *Cochlospermum religiosum*, adaxial view. Note large apical pore.—7. *Amoreuxia palmatifida*, lateral and adaxial views. Note pair of elongate apical slits.—8. *Cochlospermum religiosum*, × 7. Longisection of ovary showing placental ridges.—9–10. Diagrammatic composite longisections showing perianth vasculature types.—9. Perianth traces trifurcate with lateral branches fusing to form a plexus from which petal traces and lateral sepal traces arise, *e.g. Amoreuxia, Cochlospermum vitifolium.*—10. Perianth vascularized by separate petal and sepal traces, *e.g. Cochlospermum orinocense.*—11. *Cochlospermum religiosum*, ×9. Stamen trunk bundles and anastomosing branches which produce stamen traces.—12–18. *Cochlospermum regium*, × 7. Serial transections through the pistil.—12. View at level of receptacle. Note three dorsal bundles and three ventral bundles.—13. View of ovary above the receptacle, appears trilocular.—14. View of ovary cut equidistant between base and upper surface. Note parietal placentation with pairs of ventral bundles in placental ridges.—15. View above center of ovary.—16. View at juncture of placentae to form a trilocular configuration.—17. View at base of style. Note stylar canal at center surrounded by pairs of ventral traces.—18. View through center of style. Note stylar canal, three dorsal traces and three ventral traces.



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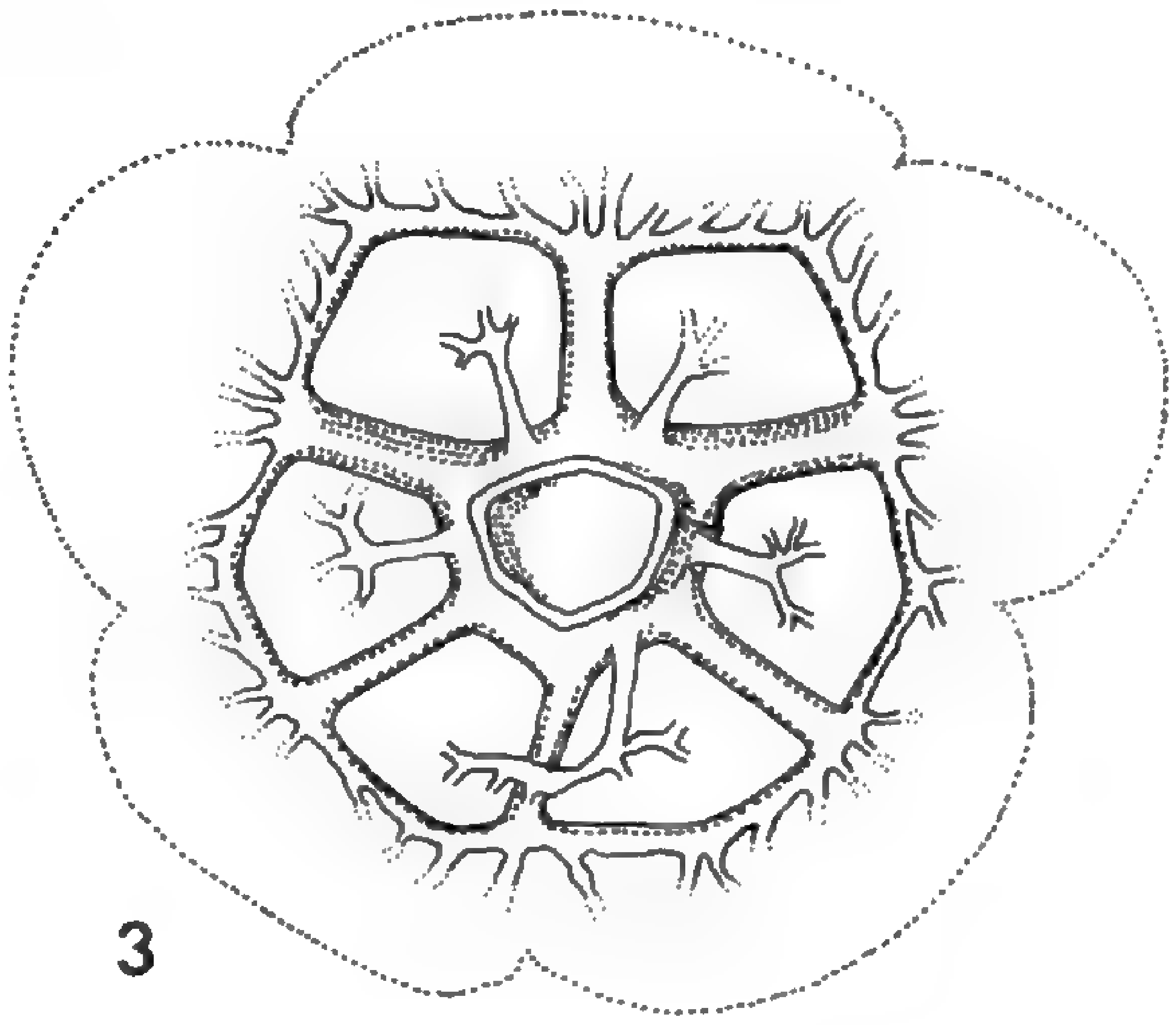

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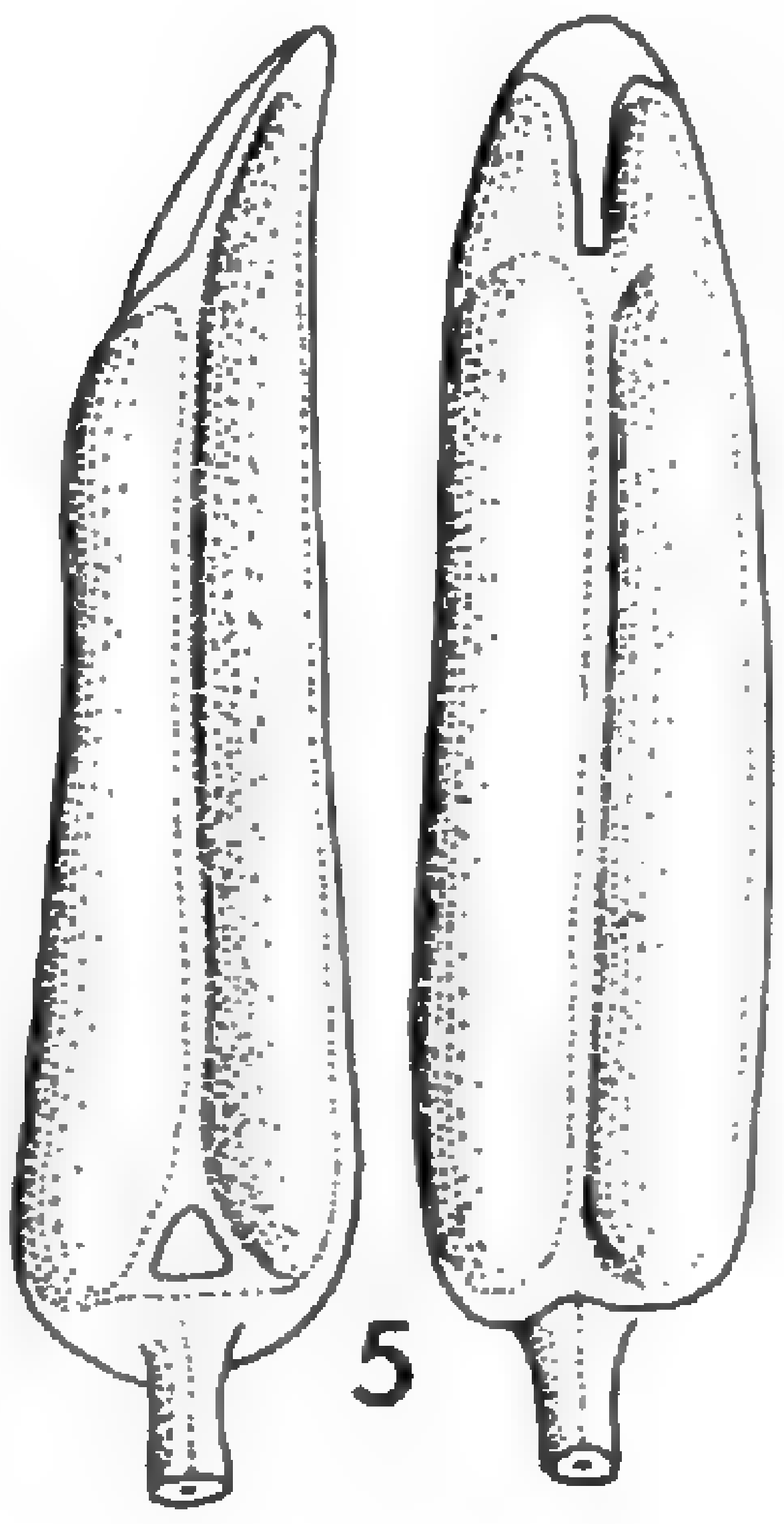

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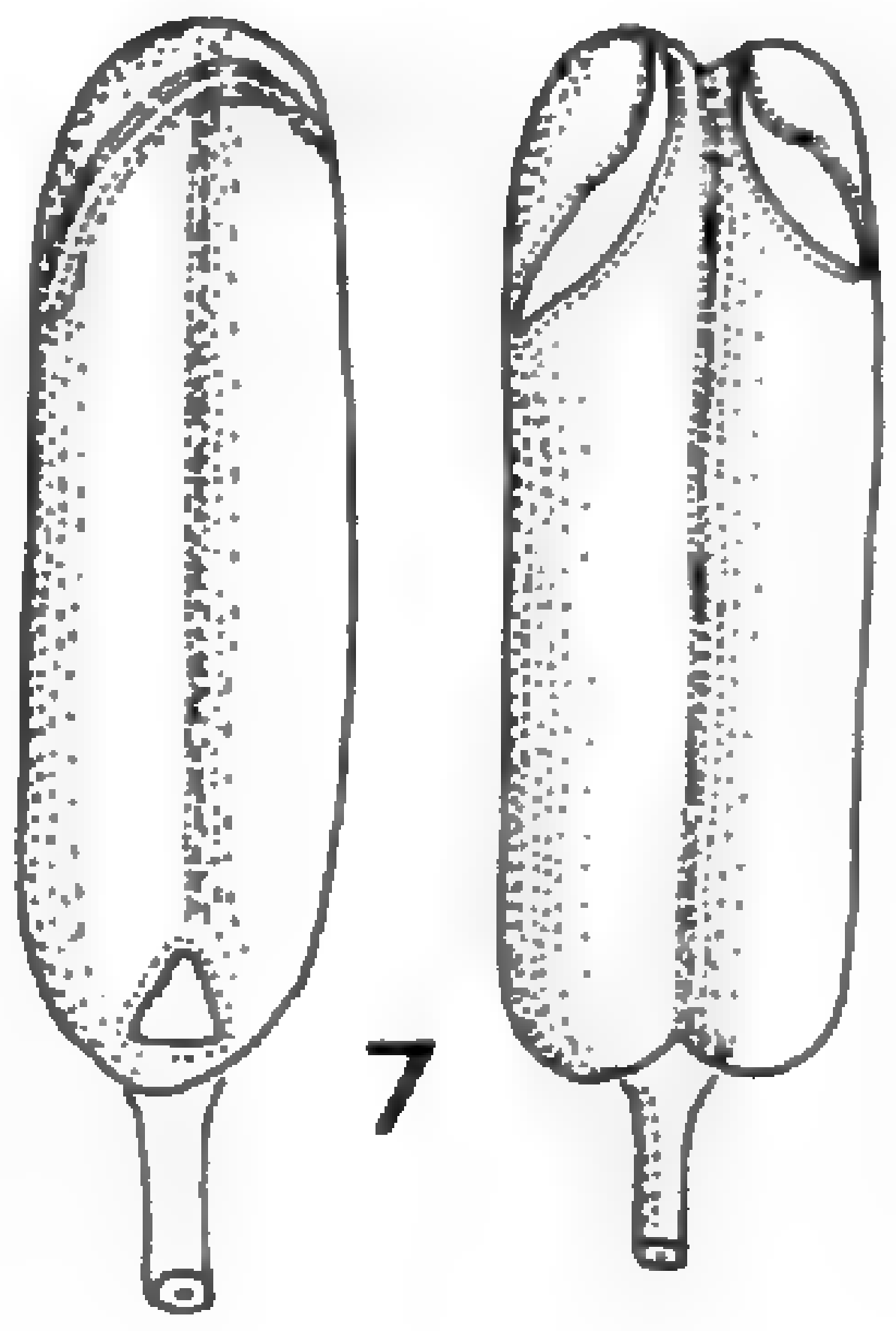

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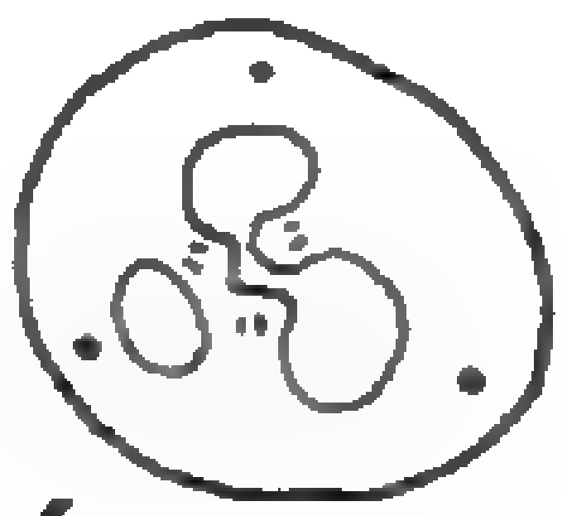

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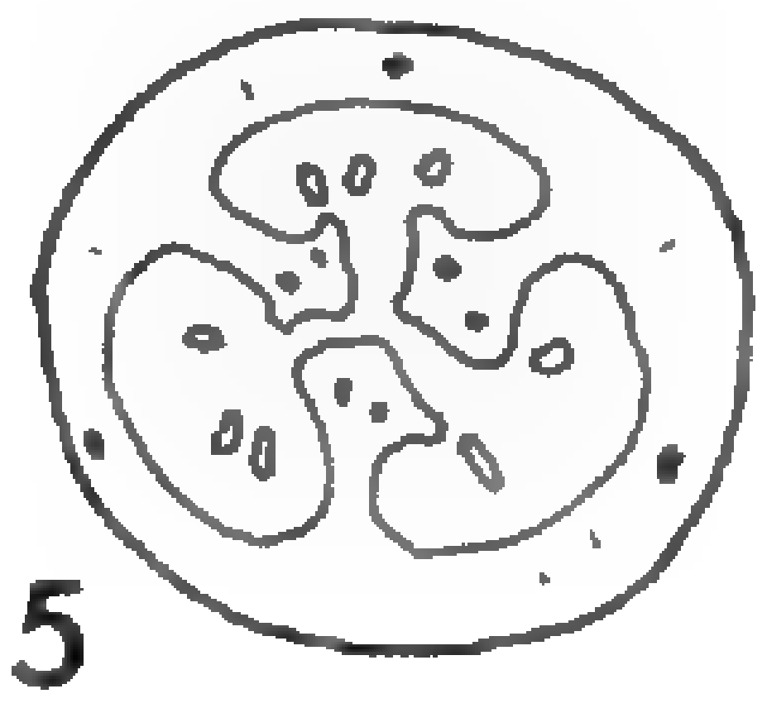

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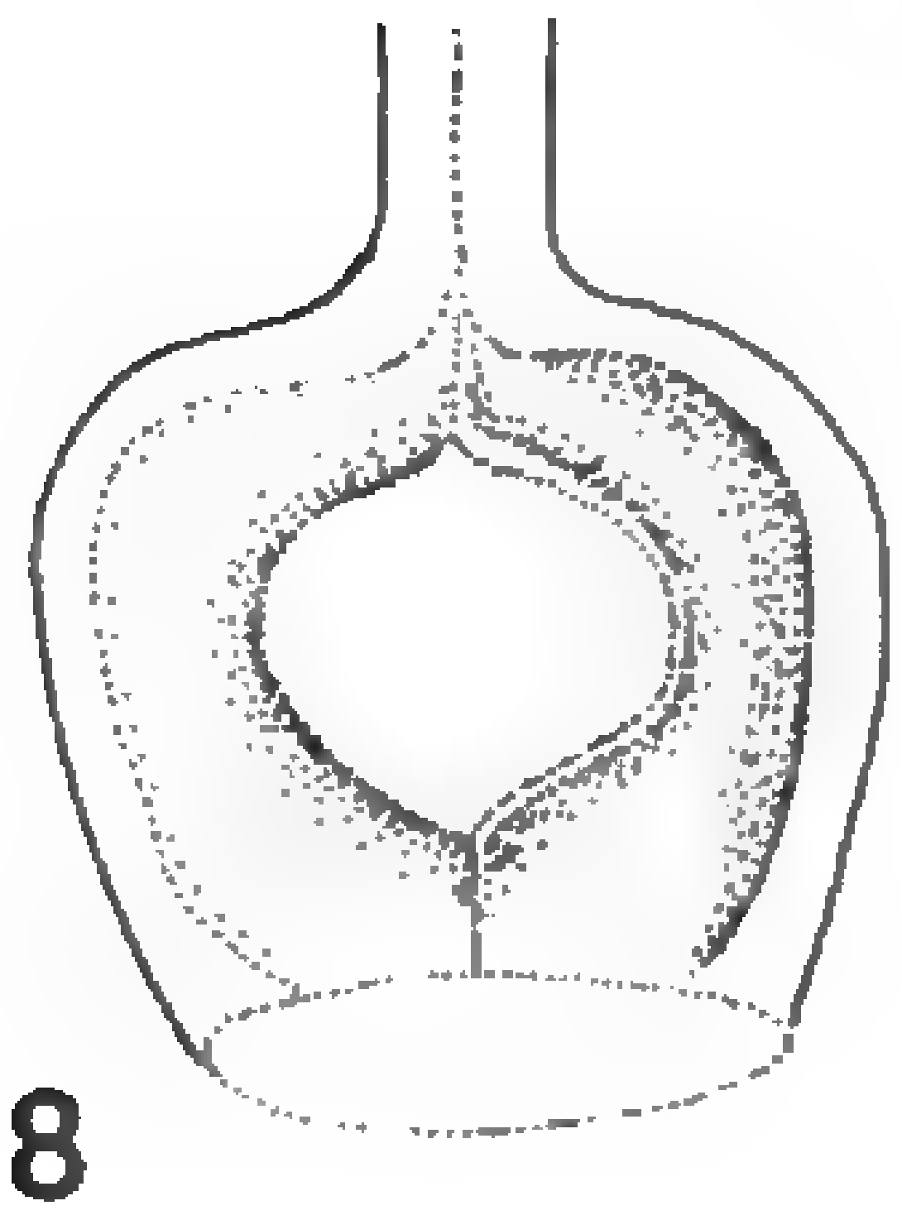

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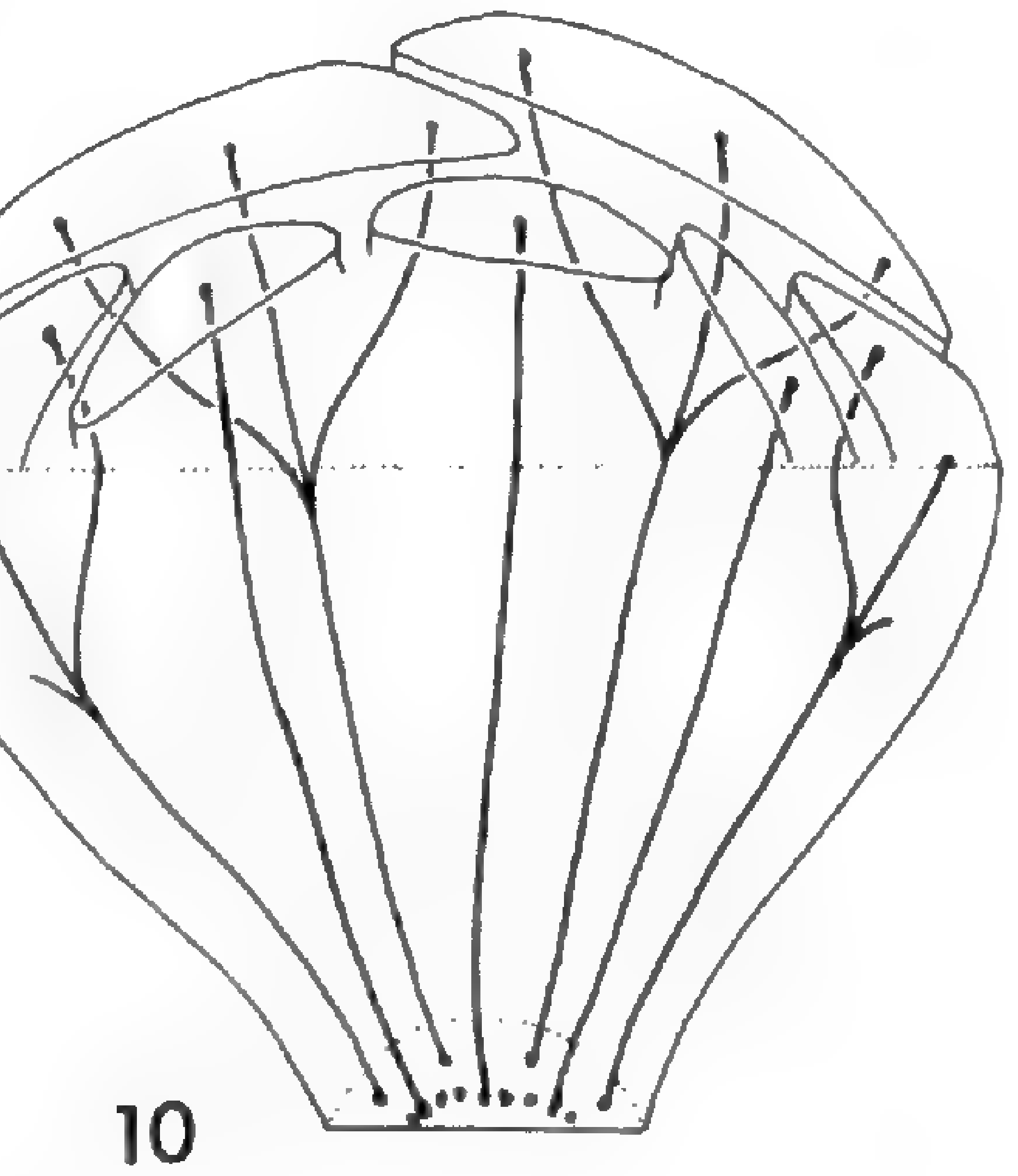

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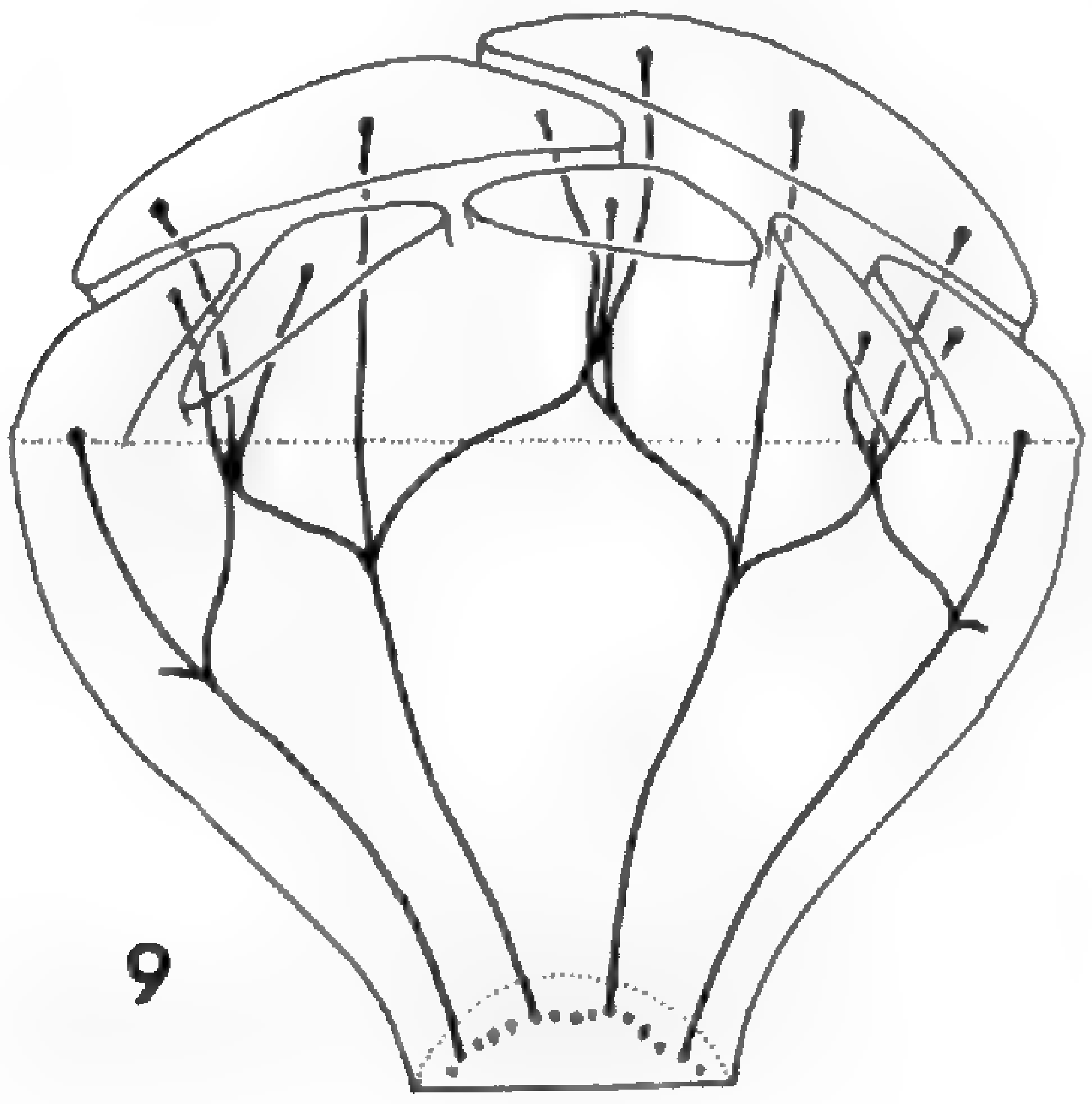

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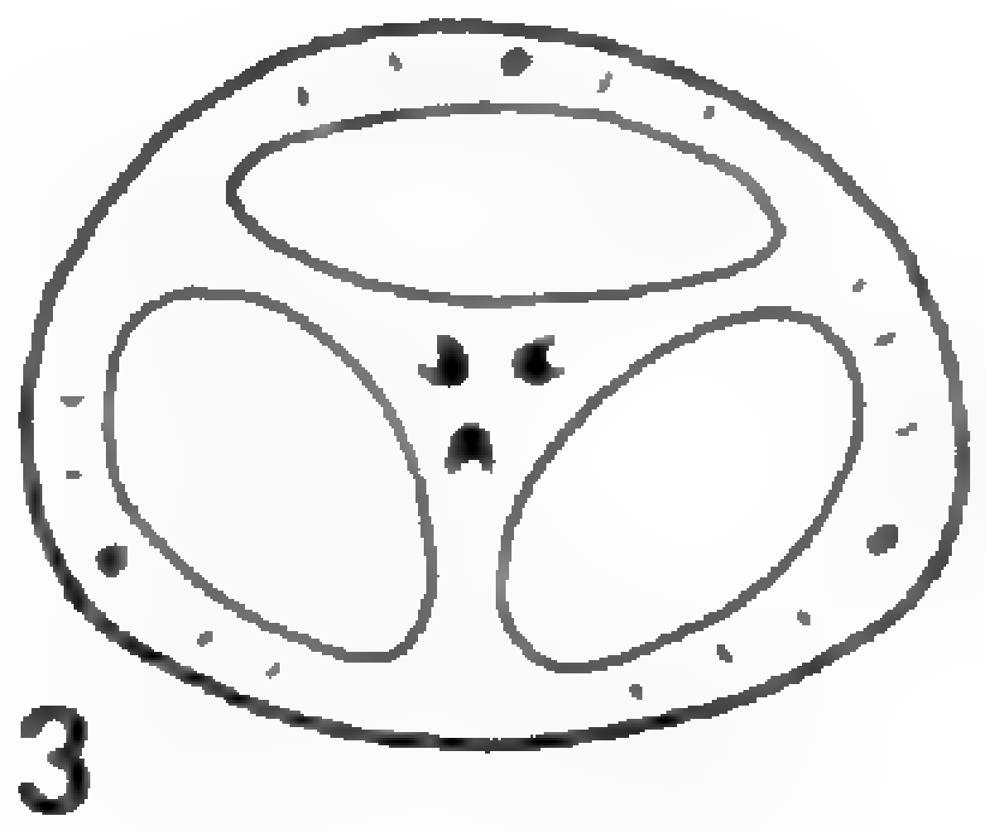

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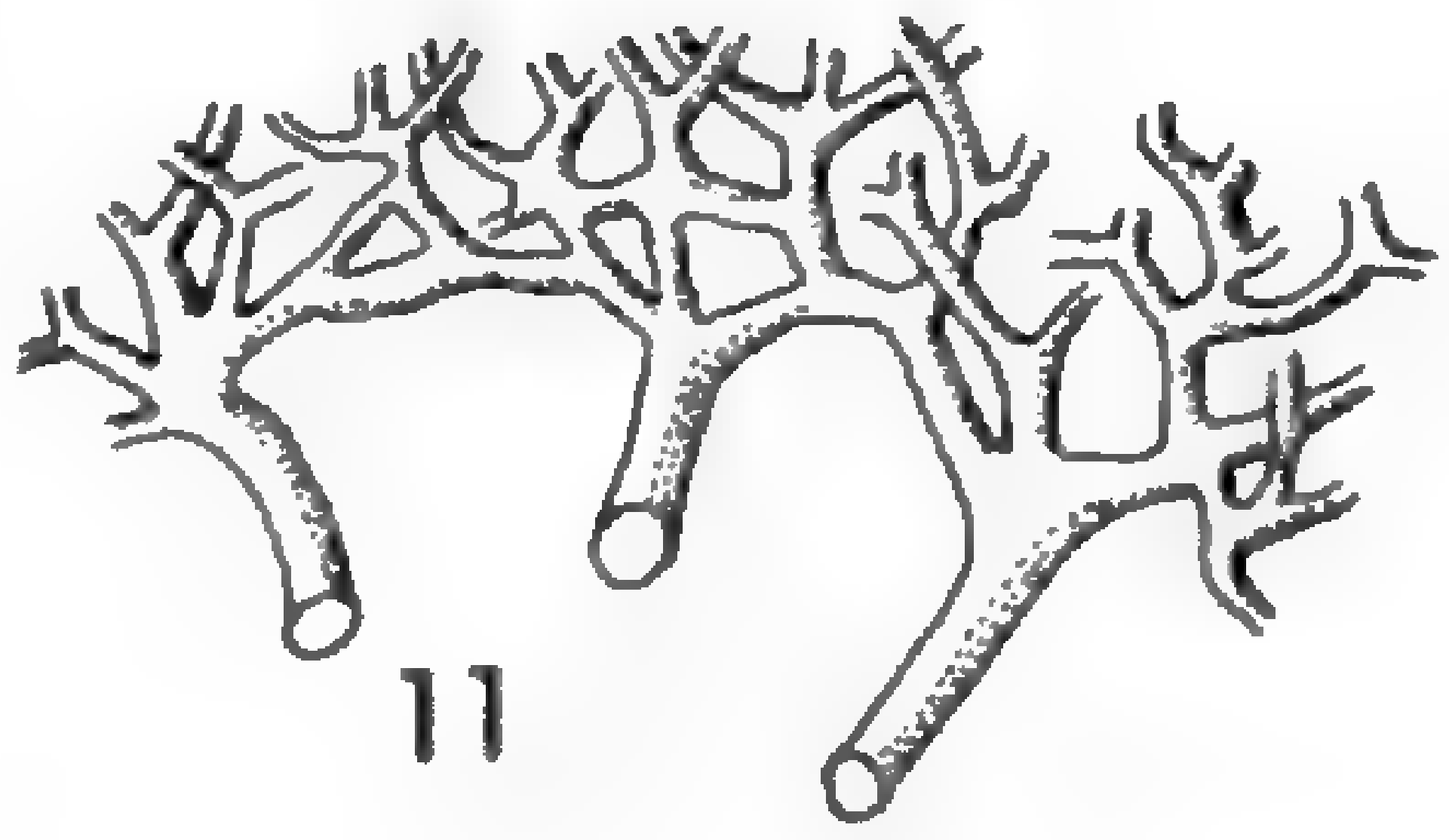

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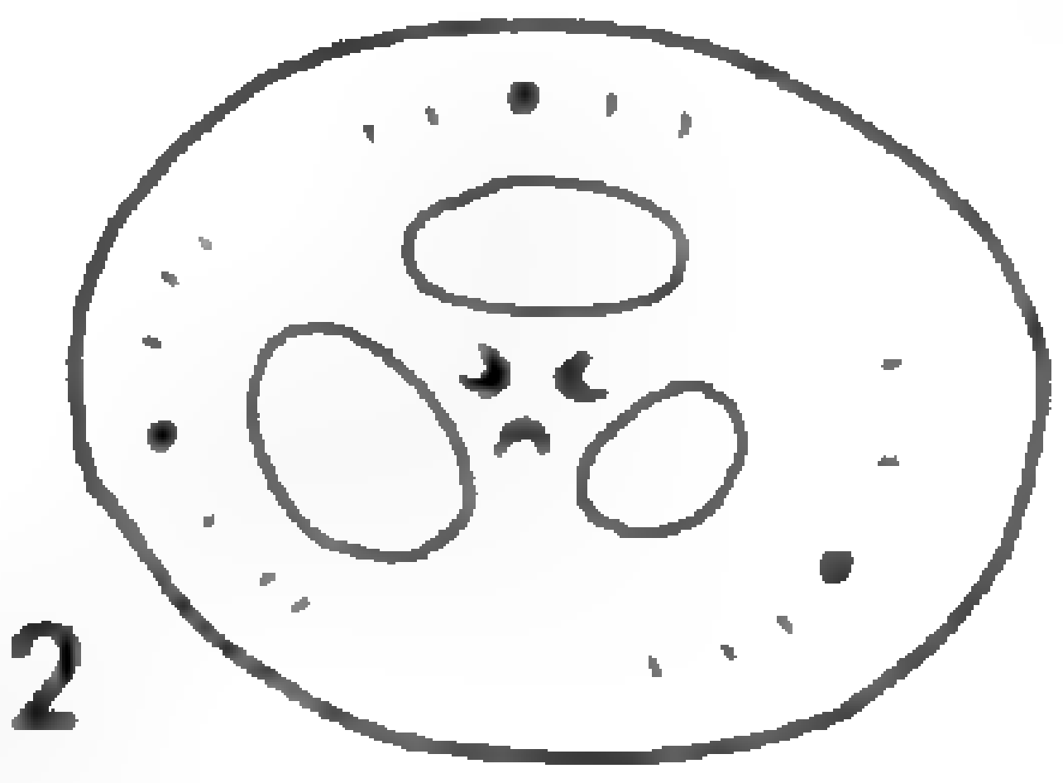

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tion (Figs. 8, 12–18). The ovary therefore has a single ramified locule with three, four, or five lobes corresponding to the number of carpels. The style is usually hollow and is lined with a glandular surface. The stylar canal is not usually continuous with the locule of the ovary. The pistil is vascularized by what remains of the stele above the perianth and androecial vascularization. In *Cochlospermum gregorii*, *C. fraseri*, *C. religiosum*, and *C. vitifolium*, the pistil is five carpellate. The stele divides into ten segments with five outer segments alternating with five inner segments. The five inner bundles represent fused lateral pairs of carpellary bundles each of which may divide into pairs at higher levels. The five inner bundles are inverted with the phloem on the adaxial side of the xylem (Fig. 30). The outer five bundles represent the dorsal carpellary traces.

In other specimens of *Cochlospermum orinocense*, *C. parkeri*, *C. regium*, *C. tetraporum*, *C. tinctorium*, *C. williamsii*, and *A. wrightii*, the pistil is three-carpellate. Vascularization is as described above except that there are three dorsal and three pairs of ventral traces. Specimens of *C. planchonii* examined were four carpellate, and one specimen of *C. religiosum* had only four sets of ventral bundles but five carpels.

The connate carpel walls are vascularized by pairs of bundles which supply traces to the placental ridges and ovules. The dorsal bundles may disappear at lower levels of the ovary wall by dividing into a number of minor parallel ovary wall bundles.

In a specimen of *Cochlospermum regium*, the ventral bundles are quite distinct in the base of the ovary with the phloem on the adaxial side of the three bundle pairs (Figs. 12–13). The dorsal bundles at that level branch into numerous traces to the ovary wall but are not used up in the process. At the top of the ovary, the three fused pairs of ventral bundles and the three dorsal bundles vascularize the length of the style as six evenly distributed traces (Fig. 18). The ventral bundles appear as free pairs only in the central portion of the ovary (Figs. 14–16).

Pollen.—Grains of *Amoreuxia* and *Cochlospermum* are quite similar. Shape: mostly spheroidal to subprolate, occasionally suboblate. Structure: mostly semi-

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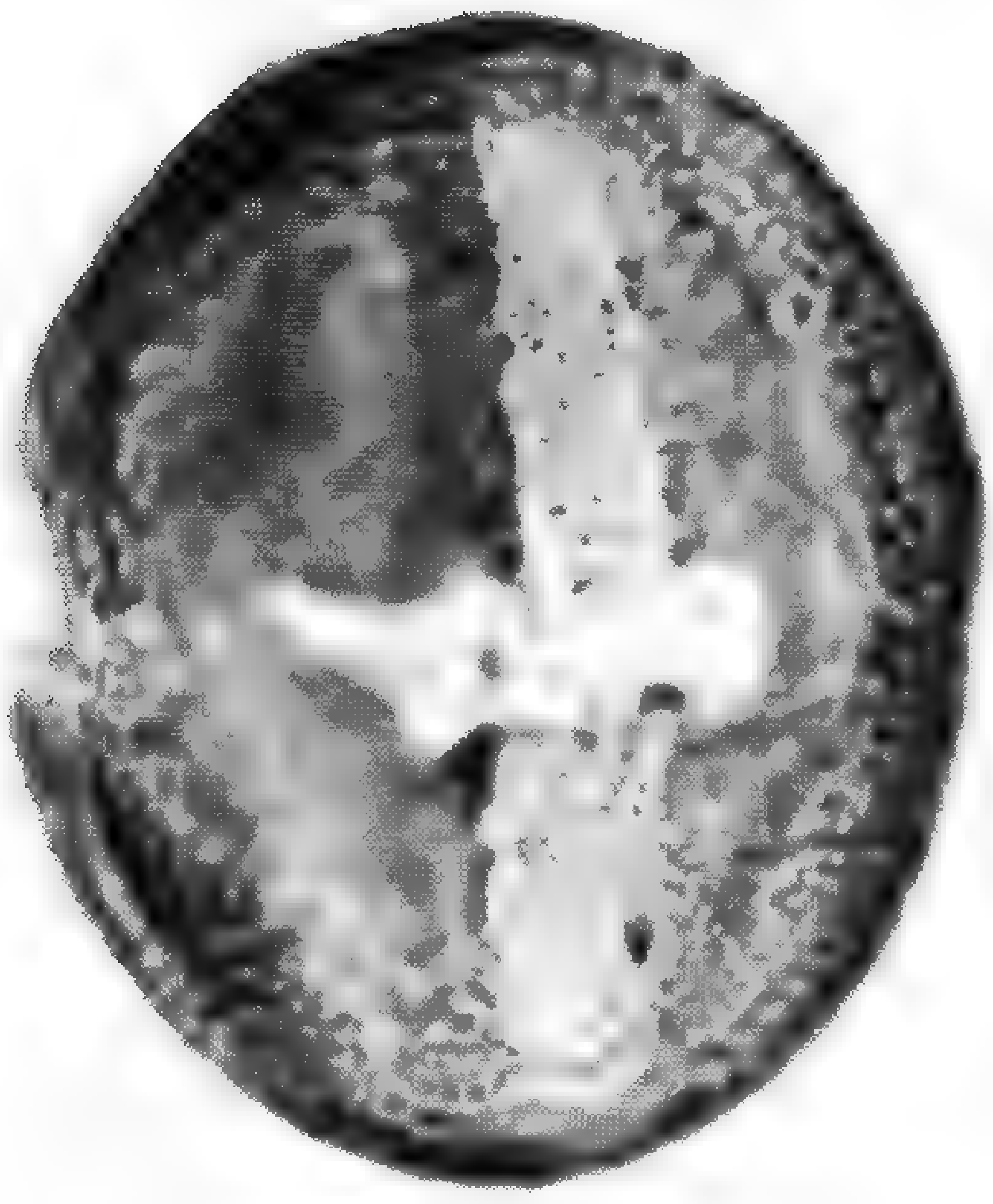
FIGURES 19–31.—Photomicrographs of pollen and floral anatomy.—19–28. Pollen grains of Bixaceae, Cochlospermaceae, × 1000.—19–20. *Bixa orellana.*—19. Equatorial view. Note reticulate ektexine, sculpturing elements on colpus, pore with constricted lateral extensions.—20. Equatorial view. Note oval pore.—21–22. *Cochlospermum religiosum.*—21. Equatorial view. No visible pore.—22. Polar view, note finely reticulate ektexine.—23–24. *Cochlospermum tinctorium.*—23. Equatorial view. Note equatorial constriction in colpus.—24. Polar view. Note intectate, rugulate sculpturing.—25. *Amoreuxia wrightii*, equatorial view. Note constriction in colpus at equator.—26. *Cochlospermum parkeri*, equatorial view. No pore is visible in colpus.—27–28. *Cochlospermum gregorii.*—27. Equatorial view. Note constricted colpus.—28. Polar view. Note reticulate ektexine, sharply defined ends of colpi.—29–31. Transections through the floral receptacle showing vasculature.—29. *Cochlospermum orinocense*, × 10. Note five large sepal traces and five petal traces (arrows).—30–31. *Cochlospermum vitifolium.*—30. Gynoecium vasculature below surface of the receptacle, × 45. Note dorsal bundles (arrows) and fused ventral bundles (Vb) with xylem on the abaxial side.—31. Section cut above level of origin of androecial vascularization, × 10. Note perianth traces; note three simple and two branched stamen trunk bundles (arrows).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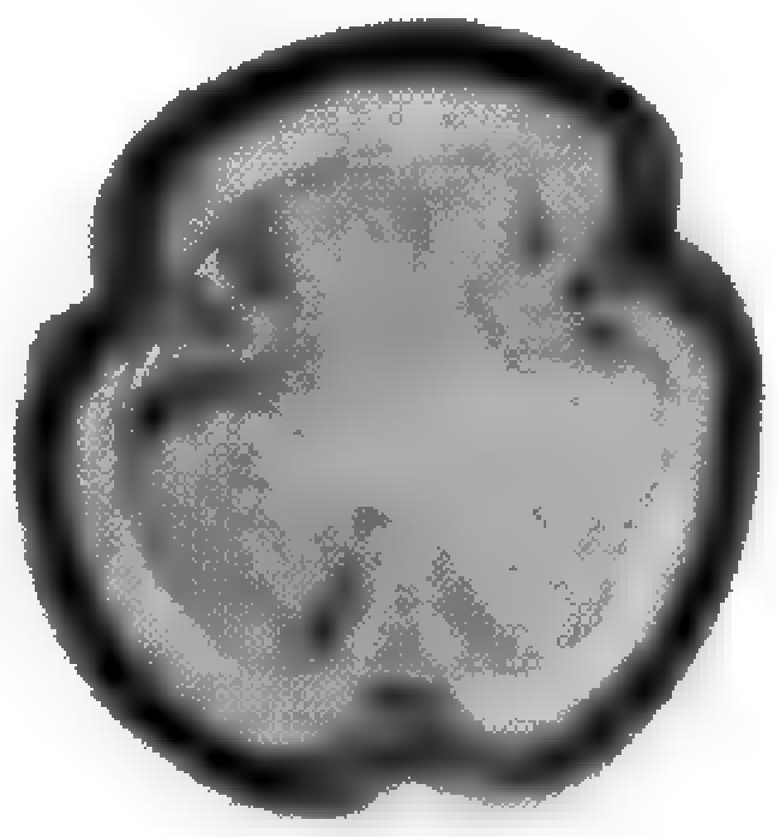
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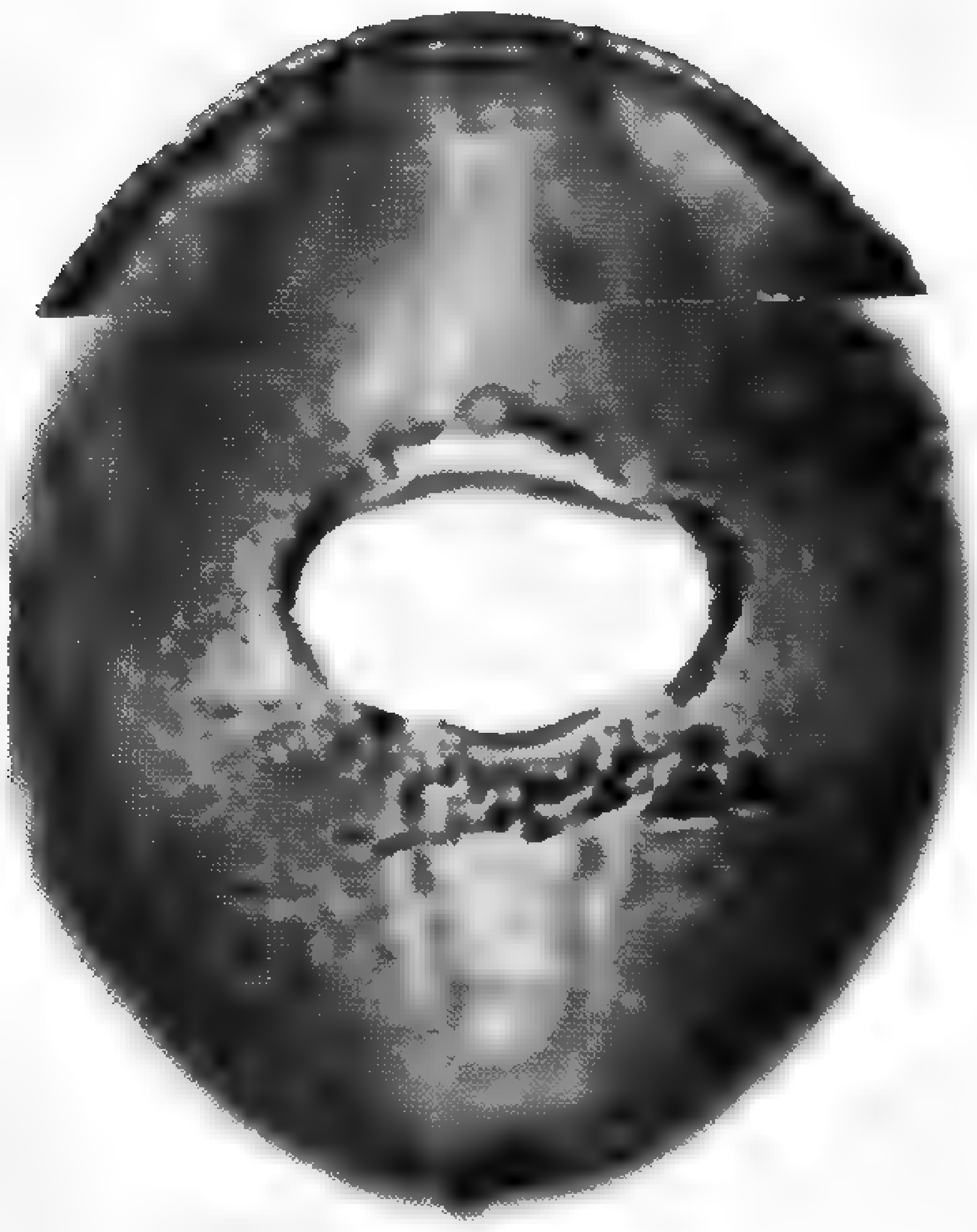
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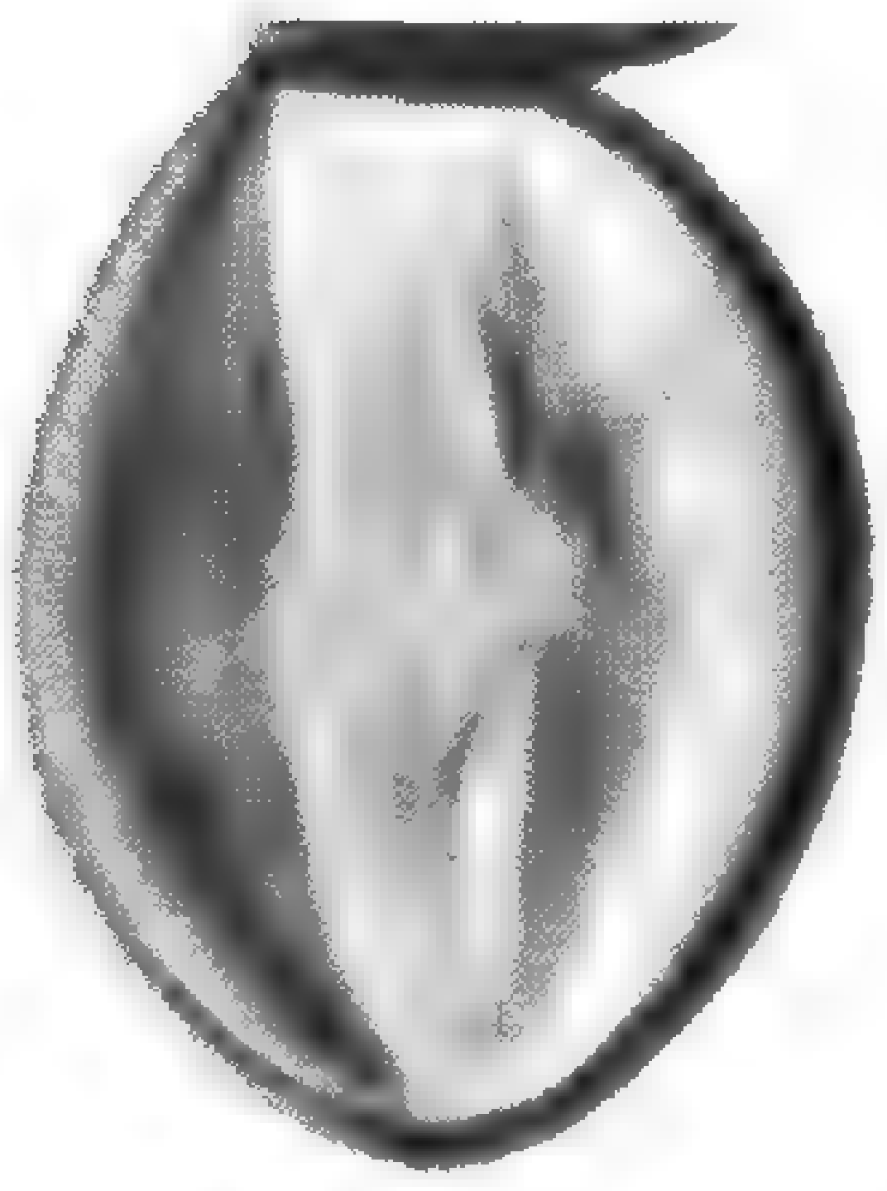
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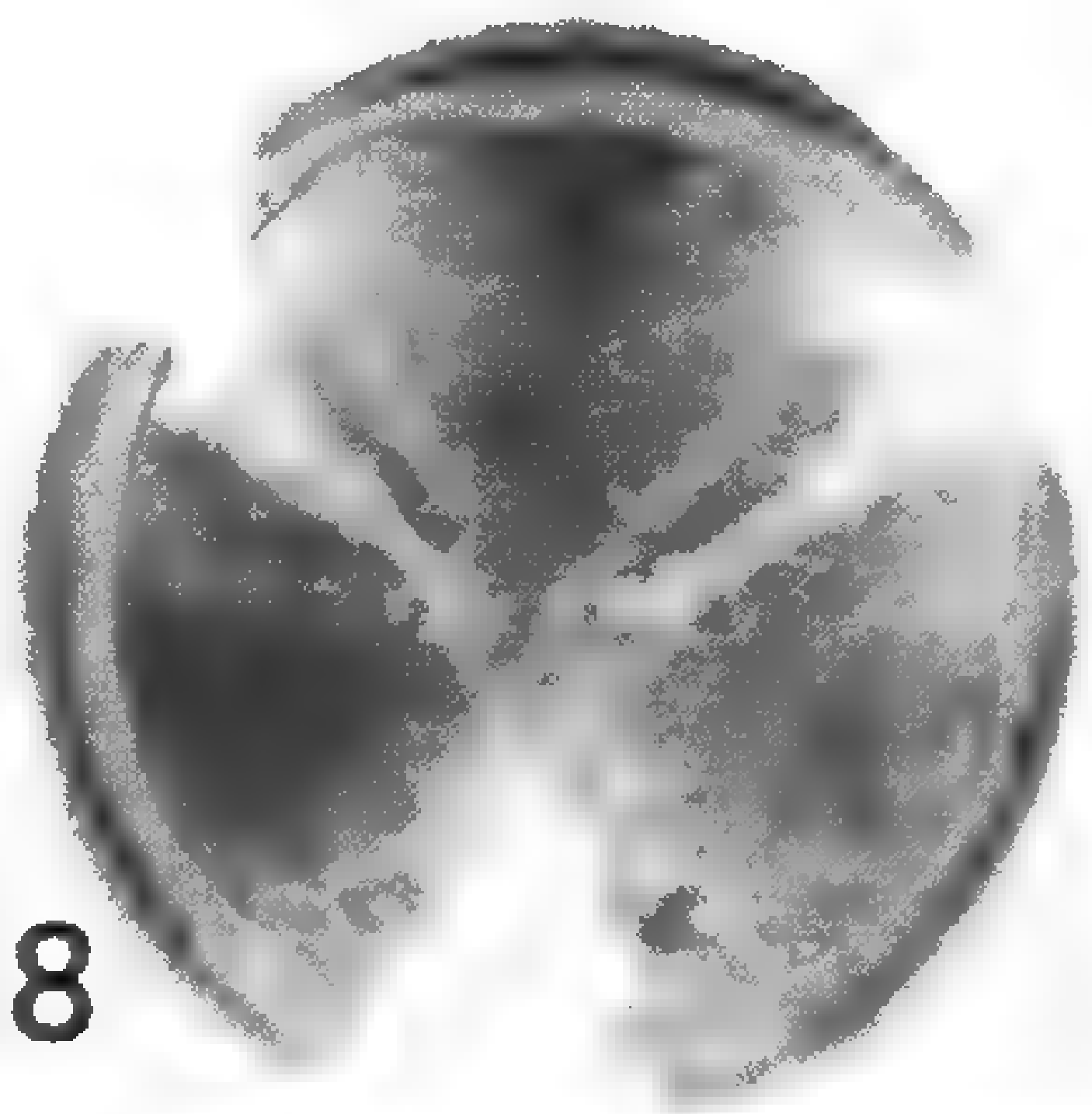
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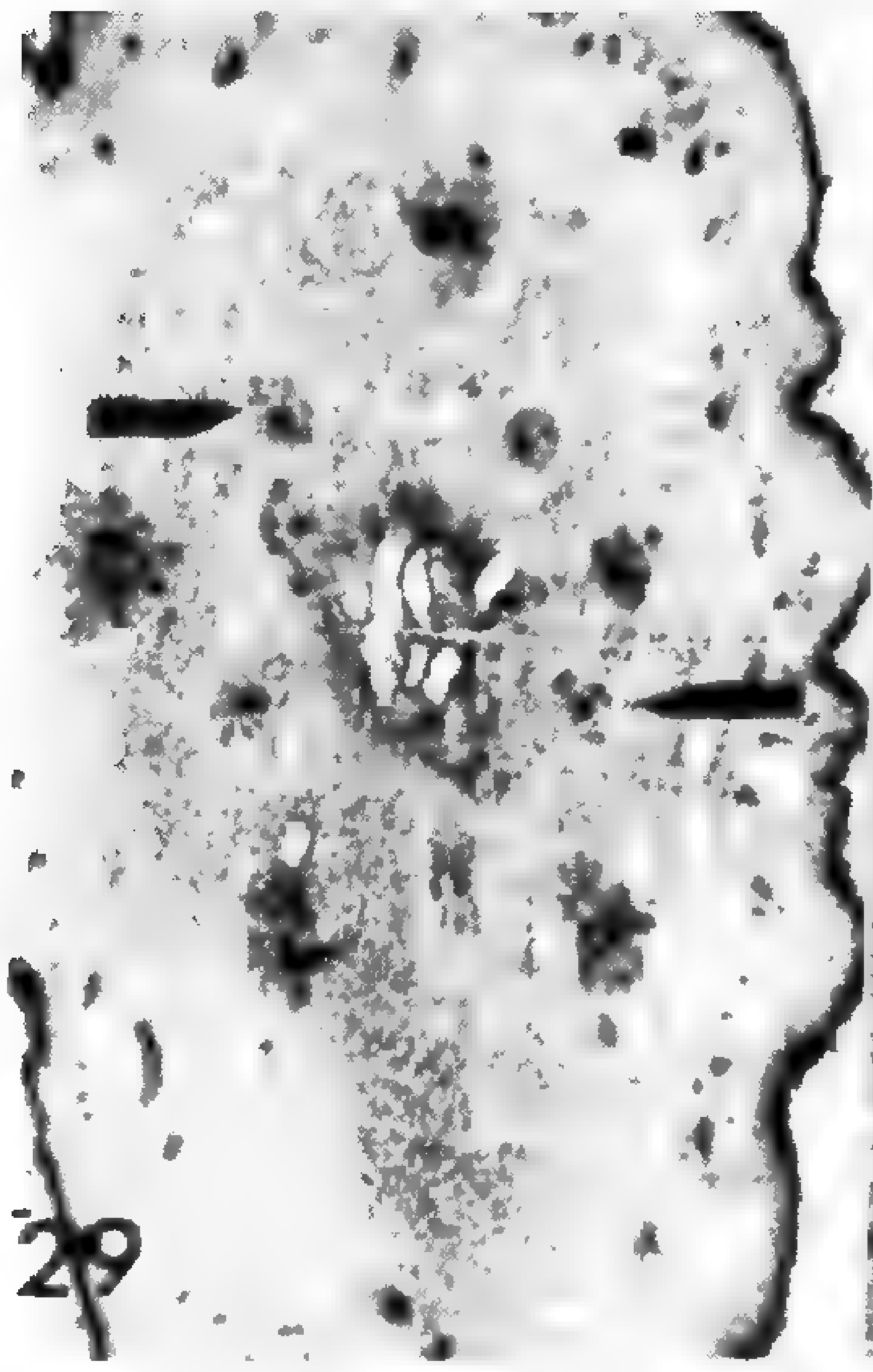
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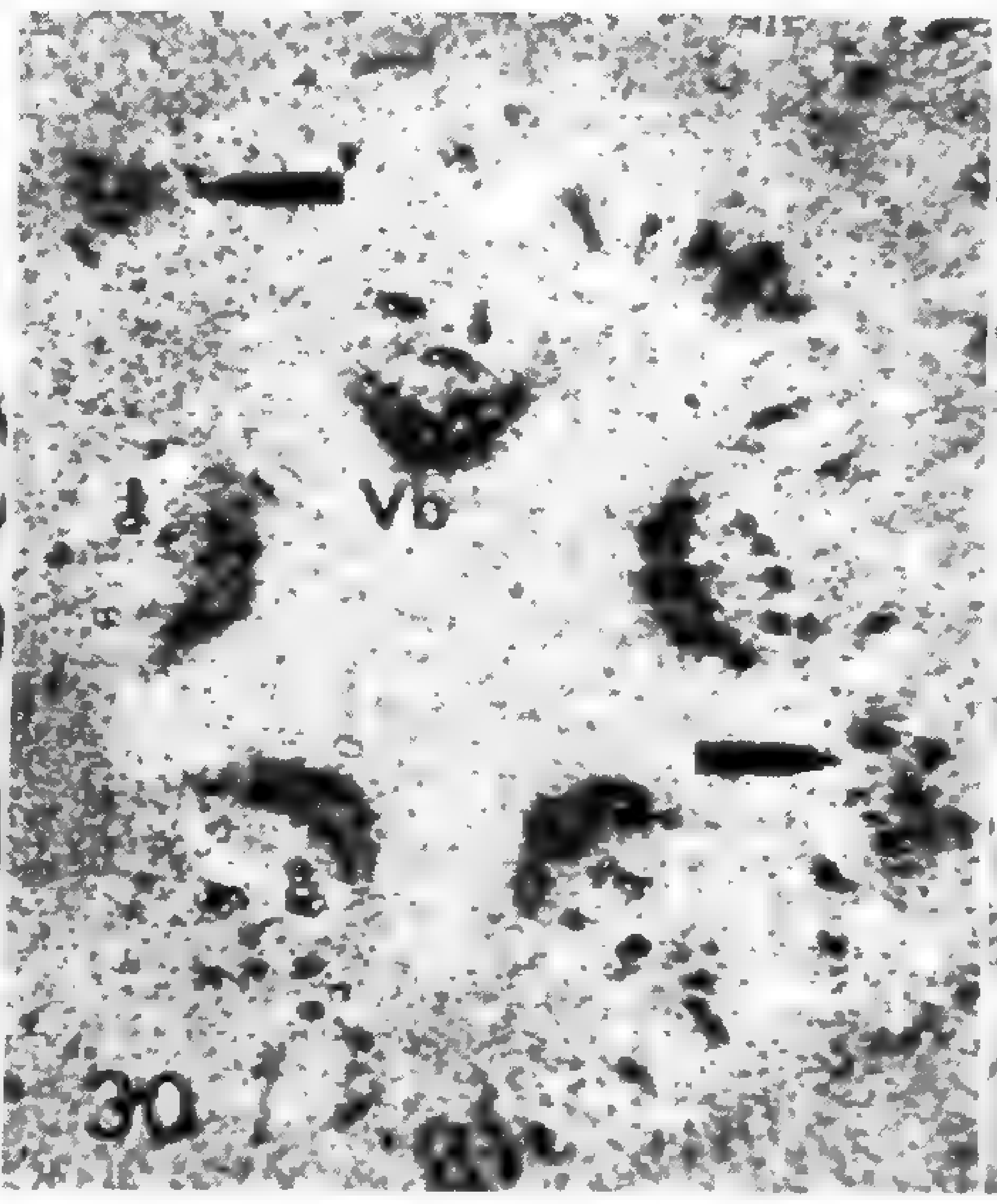

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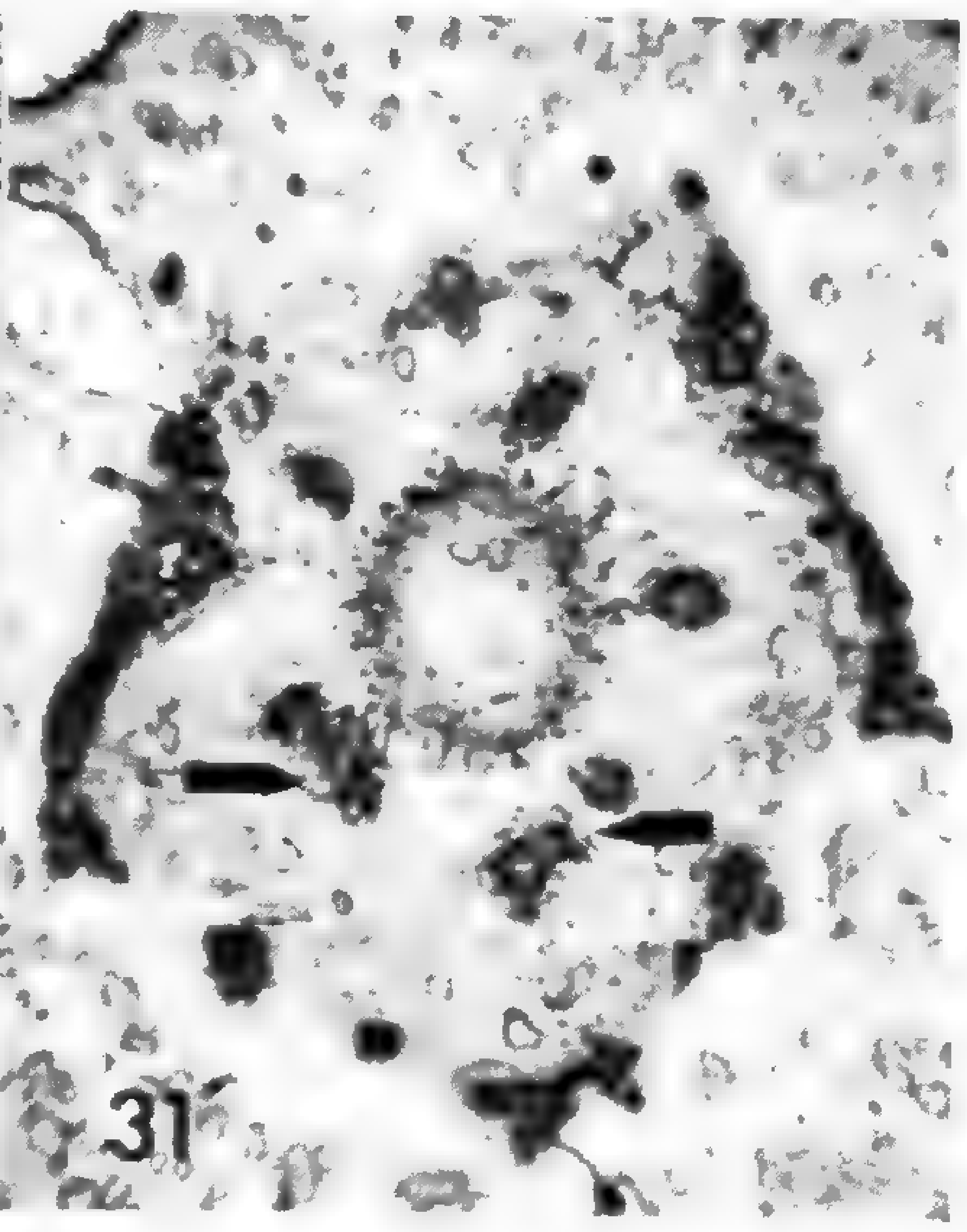
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tectate or intectate. Exine thickness 1–1.5 μ. Ektexine equal to or greater than the endexine in thickness. Sculpture: psilate, scabrate, finely reticulate (Fig. 22) to rugulate (Fig. 24). Apertures: zoniaperturate, tricolporoidate, tricolporate, or tricolpate. Colpi are costate. Colpi often appear constricted at the equator or they may be divided in half by an equatorial bridge in the ektexine (Fig. 23). Pore zone often indistinct, appearing as a thin area in the endexine. When present, porae are usually lalongate. Delimitation of the porae is usually diffuse. Size: *Cochlospermum* averages for most species P = 17–23 μ; E = 16–27 μ (*C. gregorii* P = 25 μ; E = 34 μ). *Amoreuxia* P = 33–34 μ; E =32–35 μ (reported as 22 × 19.5 μ by Erdtman, 1952). (Figs. 21–28.)

Pollen grains of *Bixa* examined in this study are easily distinguished from those of *Cochlospermum* and *Amoreuxia*. They are tectate, reticulate, tricolporate with ektexine elements on the colpi membranes (Fig. 19) or around the porae (Fig. 20). The porae are oval, lalongate occasionally with ragged, indeterminate ends. *Bixa* pollen is considerably larger with the longest axis extending to over 40 μ.

Discussion

The flower has been subject to a greater variety of interpretation as to its basic nature than any other structure of the plant. The basic assumption is made here that the flower is a modified shoot, *i.e.* a short stem with specialized lateral appendages. Lengthy evidence has been presented (Eames, 1931, 1961; Moseley, 1961) that the vasculature of the receptacle is homologous with that of the vegetative shoot. Ontogenetic studies by Tepfer (1953) uphold this view. Perianth parts, stamens, and carpels do not appear to be fundamentally different than the leaves of the shoot (Sporne, 1958; Joshi, 1947).

Perianth.—The most primitive perianth vasculature is seen in *Cochlospermum orinocense* and *C. regium* in which five sepal traces alternate with five petal traces in the base of the receptacle. Quincuncial initiation is not usually apparent due to the lack of internodal elongation of the receptacle. Other species of *Cochlospermum* and all those of *Amoreuxia* examined show only five to six perianth traces which branch to form a plexus from which the traces are produced for the calyx and corolla. In all specimens examined, the outermost perianth traces trifurcate and form a plexus whether or not the petals may be supplied separately. The fusion of these traces is probably a natural result of the phylogenetic shortening of the axis to where the phyllotactic spiral disappears completely.

Wilson (1937) accurately illustrated the perianth vasculature for *Cochlospermum vitifolium* as containing six perianth traces for its pentamerous perianth. It is difficult to understand the function of the sixth trace. It is possible that the basic number of perianth traces in the family is 10 and reduction to 5 may be a result of contracted space in the receptacle. Bilateral symmetry of the vasculature is well developed and the sixth trace is probably a vestige of separate petal vascularization. The sixth trace is produced on a side of the receptacle where perianth vasculature is least strongly developed.

Androecium.—In his discussion of the phylogeny of the stamen, Wilson (1937) used several lines of circumstantial evidence to support the hypothesis that stamens are derived from branching systems. He stressed that the Parietales and Malvales provide evidence upholding the telome theory. These two orders contain a number of families which have fascicled stamens or branched stamen trunk bundles in the receptacle, and the Cochlospermaceae were cited as an example. Wilson believed stamen trunk bundles to be relicts of highly branched clusters of sporangium-bearing branches or fertile telomes. In *Cochlospermum vitifolium* five gaps in the stele produce three single trunks, one double trunk, and one triple trunk (Fig. 31). The precocious branching in the latter two cases cannot be considered dichotomous branching, a condition cited as the anatomical basis for primitive telome formation.

Eames (1961) agreed that the existence of trunk vascular supplies would seem to support the view that the fascicle is a unit organ but that actually the formation of fascicles is probably an early step in androecium reduction. Basing his views on comparative anatomy of Dilleniaceae and Paeoniaceae, Eames held that the fascicle is an aggregation of simple stamens.

Neither concept adequately explains the nature of stamen trunk bundles nor do they consider developmental data. In many families, floral vasculature reflects a history of separateness for many presently fused parts. Wilson's concept would require regarding malvalian genera with visible fascicles as primitive, those with numerous stamens and vascular trunk bundles in the receptacle (Cochlospermaceae, Bixaceae, Cistaceae) as intermediate, and laminar stamens with separate traces (Magnoliaceae, Degeneriaceae) as most specialized. Clearly, this concept does not agree with other lines of comparative anatomical evidence (Bailey, 1944, 1951; Bailey & Swamy, 1951; Canright, 1952). Wilson (1965) concluded that reduction in the number of stamens per trunk bundle and reduction in the number of trunk bundles has been the case in *Hibbertia* (Dilleniaceae). While this is probably the case for that genus, there is no reason to regard this as a unidirectional sequence. Selection pressure on the pollination system could prolong the activity of the androecial meristem. The genus *Bixa*, many ways more specialized than Cochlospermaceae, including its anther morphology, has nearly twice as many stamens as any species of *Amoreuxia* or *Cochlospermum.*

There is as great a difficulty in explaining the stamens as aggregates as there is with telomes. To consider the stamens as aggregates, it must be assumed that vascular fusion preceded the aggregation of anthers. Presently accepted tenets of floral evolution agree that fusion of parts is a specialized condition, and such specialization is almost universally reported to precede vascular fusion. The stamen trunks are related to single gaps and show no evidence of any major reorganization at the stele of the receptacle. The genera showing stamen trunks (*cf.* Corner, 1946; Sporne, 1958) all have a shortened receptacle with a laterally expanded torus, a condition which removes the space where spiral phyllotaxis might otherwise occur. When shortening of the floral axis occurs in strobiloid flowers, crowding of the vasculature produces a complicated plexus of anastomosing traces as in *Nymphaea* (Moseley, 1961) and *Nuphar* (Moseley, 1965).

Vascular fusion in these genera is quite different from those in which stamen trunk bundles are found.

Difficulties presented by the telome and aggregation theories are eliminated by the centrifugal stamen concept as revived by Corner (1946) from original observations by Payer (1857). Corner accumulated developmental evidence showing that the broad disc from which the stamens arise is the last portion of the floral apex to develop. Using the genera *Wormia*, *Tetracera*, and *Bixa*, Corner showed that the stamen primordia arise radially from the base of the gynoecium separating it from the already well-developed perianth primordia. This disc interposes tissue in a centrifugal direction (basipetal with reference to the gynoecium). A provascular zone, beginning as five traces, branches regularly to produce well spaced rows of traces and stamen primordia. One implication of this developmental pattern is that numerous stamens may be specialized over few, a trend opposite to that in strobiloid flowers. Centrifugal development probably arose early in angiosperm evolution, but it is not known if it developed out of or concomitant with the strobiloid androecium. No indication of the origin of centrifugal stamens has appeared in genera thus far shown to have the condition. However, an intensive investigation from a developmental standpoint might prove to be highly informative.

Gynoecium.—The ovary structure of Cochlospermaceae has been subject to misinterpretations of important systematic consequence which could have been avoided by serial sectioning. Eichler (1871) described the ovary of *Cochlospermum* as having three to five placentae with a septum dividing the ovary from base to apex into three to five locules. Pulle (1906) described a three-chambered ovary in *C. wentii*. On the other hand, Pilger (1925) and Hutchinson (1967) separated *Cochlospermum* and *Amoreuxia* by the presence of a single chambered ovary in the former in contrast to a multichambered one in the latter. All material I examined had a single ramified locule in the ovary. Transections cut low or high appear axile while those at the center appear parietal. Both genera are identical in this respect.

Description of the gynoecium of *Cochlospermum orinocense* by Schnarf (1931) was based on serial sections, but he made no mention of the position of vascular bundles. In speculating on the nature of the gynoecium, he felt that his material provided no evidence as to whether the septa were laminal outgrowths of the ovary wall or the united walls of carpels. He concluded that we can probably assume they are not united carpel walls. Hutchinson (1959) illustrated the gynoecium of *C. tinctorium* as having marginally joined carpels with a single circular locule. No specimen studied here approximated his drawing. If we assume that the presence of pairs of vascular bundles running up the lamina of the ovary are ventral carpel bundles, then certainly the laminae are fused carpel walls and not secondary proliferations or septae.

Several authors have discussed the evolutionary status of axile versus parietal placentation (Parkin, 1955; Puri, 1952; Eames, 1961). Arguments distinguishing between primitive parietal and advanced parietal placentation seem unconvincing. All such discussions seem to assume that carpels were completely closed or completely open when syncarpy took place. Gundersen (1939) has pointed out that *Hypericum*, *Theobroma*, *Shortia*, *Feijoa*, and *Myrtus* have ovaries which have axile placentation in the base of the ovary and parietal placentation in the upper part. There is no basis to assume that those ovaries were originally all closed or all open before syncarpy took place. Gundersen noted that wherever there is a change in placentation in ontogeny, it is always from parietal to axile. His opinion on the primitiveness of parietal placentation is thus based on recapitulationary arguments. There is no evidence for determining whether the partially parietal placentation in the Cochlospermaceae is primitively axile or primitively parietal or whether the carpels were partially sealed at syncarpy. In Puri's (1952) comprehensive review of the nature of the placenta, he is not sure that the primitively parietal condition actually exists. The condition is held by him to be derived from axile placentation in a number of families. In descriptive work, the terms axile and parietal should be used topographically without trends of specialization being necessarily implied.

Level of specialization in the flower.—In both genera, primitive features include hypogenous structure, separate perianth parts, separate stamens, numerous ovules. Of intermediate specialization can be included open racemose inflorescence, centrifugal stamen maturation, numerous stamens, expanded receptacle, incipient bilateral symmetry, poricidal dehiscence of the anther, and the syncarpous gynoecium. The flowers of the family can be best characterized as between primitive and moderately specialized.

Relationships among the Parietales and Malvales.—*Bixa* is undoubtedly related to the Cochlospermaceae but is more specialized in many ways including the more numerous stamens, folded anthers with apical (morphologically lateral) dehiscence (Venkatsh, 1956), and reduction of the gynoecium to two carpels. *Bixa* is more primitive in having no detectable bilateral symmetry and in having separate calyx and corolla vasculature. Trichomes on the ovary wall are vascularized by the dorsal wall vasculature. *Bixa* has been separated biologically from *Amoreuxia* and *Cochlospermum* for a very long time, and its placement in a separate family seems justified. The evidence from vegetative anatomy supports this view.

Flowers of *Rhopalocarpus* are readily distinguishable from the above genera by the four-merous perianth, fewer and larger ovules, an androgynophore, as well as numerous gross differences in vegetative anatomy. Its inclusion with *Dialyceras* in the Rhopalocarpaceae by Capuron (1962) is upheld by the studies of Huard (1965*a*, *b*, *c*).

The Flacourtiaceae, thought to be the basal stock from which the Bixales (Cistales) series arose, are poorly known at present. Evolutionary tendencies in this family have produced perigyny, epigyny, loss of petals, unisexual flowers, reduction in stamen number, and reduction in carpel number (Cronquist, 1968). The genera of flacourts with which the Cochlospermaceae show closest affinities is yet to be identified.

Many features found in the flowers of the Cochlospermaceae seem to be widespread in both parietalian and malvalian families. Trifurcating sepal traces with separate petal bundles are common in many families including the Cistaceae

(Saunders, 1936), the Sterculiaceae (Rao, 1949), Tamaricaceae (Murty, 1954), and the Bixaceae. The Rhopalocarpaceae (Huard, 1965*a*) have separate petal and sepal traces with an indefinite number of parallel traces arising from a single gap for each appendage. The formation of a plexus or ring from which the petal traces arise is also found in the Onagraceae (Baehni & Bonner, 1948) and the Dilleniaceae (Wilson, 1965).

Corner (1946), Sporne (1958), and Wilson (1937) have listed the families which have stamen trunk bundles as follows: Actinidiaceae, Aizoaceae, Bixaceae, Bombacaceae, Cactaceae, Capparidaceae, Crossosomataceae, Cochlospermaceae, Dilleniaceae, Flacourtiaceae, Hypericaceae, Lecythidaceae, Malvaceae, Onagraceae, Loasaceae, Paeoniaceae, Theaceae, and Tiliaceae. A characteristic of this type of stamen vasculature is almost complete separation of androecial and perianth vasculature. This is well illustrated by *Sparmannia* (Tiliaceae) figured by Sporne (1948).

Of the families listed above, malvalian flowers have the most highly advanced centrifugal stamens with their clusters above the receptacle, staminal tubes, or fusions to the style. Cochlospermaceae have not reached that level nor have many other genera associated with malvalian families. The imbricate calyx of the Cochlospermaceae and Bixaceae might seem to preclude inclusion in the Malvales, but the valvate condition is easily derived from the imbricate. *Ryania* (Flacourtiaceae) shows the transition from an imbricate to a valvate calyx in each flower. Nor does parietal placentation really present a difficulty. In the Tiliaceae, the genera *Belotia*, *Christiania*, *Colona*, *Entelia*, *Goethalsia*, *Mollia*, *Nettoa*, *Sparmannia*, *Tilia*, and *Triumfetta* all have parietal placentation appearing in at least some sections of the ovary (Weibel, 1945; Baehni, 1934). Several of the genera have ovary morphology almost identical to that of *Amoreuxia* and *Cochlospermum*.

A comparison of pollen characters demonstrated that almost all families of the Bixales, Theales, and Malvales include tricolpor(oid)ate, zoniaperturate pollen. Their grains have mostly thin exines, psilate to reticulate sculpturing, range from oblate to prolate, and are intectate to tectate (Erdtman, 1952, 1969). Elaborations occur as in the highly sculptured large grains of many genera in the Malvales.

Pollen of the Cochlospermaceae does not closely resemble that of *Bixa* but is distinguished by smaller size and less distinct porae. Many genera of the Flacourtiaceae, Aizoaceae, Ochnaceae, Loasaceae, Tiliaceae, Sterculiaceae, and Theaceae have pollen close to that of the Cochlospermaceae, when all characters are considered.

None of the other families in the Bixales or Theales have more than a few random characters in common with the Cochlospermaceae and Bixaceae. I suggest that the Cochlospermaceae and Bixaceae are transitional families. Their level of specialization would be considered primitive for the Malvales, yet they seem unquestionably allied to them. We can agree with Meeuse (1965), who placed the Flacourtiaceae and Dilleniaceae as basal families of this taxonomic plexus, that the relationships of the many families will be difficult to clarify.

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NEW WORLD JUGLANDACEAE, III. A NEW PERSPECTIVE OF THE TROPICAL MEMBERS WITH WINGED FRUITS[1]

DONALD E. STONE[2]

ABSTRACT

Morphological and anatomical evidence is presented for recognizing the generic status of the two American species of Juglandaceae with winged fruits. *Oreomunnea pterocarpa* is endemic to Costa Rica, while *O. mexicana* ranges from Mexico to Costa Rica. *Engelhardia nicaraguensis* Molina is reduced to synonymy under *O. mexicana* subsp. *mexicana*, and *O. mexicana* subsp. *costaricensis* is described as new. Information is provided on the geographic range, general ecology, morphology, and taxonomy of the American taxa. The somatic count of $2n = 32$ for *O. mexicana* subsp. *mexicana* is the first report for the genus.

The New World species of Juglandaceae with winged fruits form an alliance that is recognized by some as the genus *Oreomunnea* (Hjelmqvist, 1948; Leroy, 1951, 1955) and by others as a section of the predominantly Old World genus *Engelhardia* (Candolle, 1914; Nagel, 1914; Standley, 1927*a*; Manning, 1949, 1959). While four Central American species have been described to date, the paucity of collections, particularly fertile ones, has handicapped critical taxonomic evaluations. *Oreomunnea pterocarpa* Oersted (1856), for example, is represented today by fewer than fifteen flowering and fruiting specimens. And until recently no fruits of *Engelhardia mexicana* Standley (1927*a*) had been collected since Rovirosa roamed Chiapas, Mexico, in 1891. *Engelhardia nicaraguensis* Molina (1968) is based on two fruiting specimens, but again no information was made available on the important floral characteristics. The fourth species was described by Standley (1940) as *E. guatemalensis* on the basis of several sterile collections, but as Manning (1959) has since pointed out some of the specimens have proved to be *E. mexicana* and *Alfaroa costaricensis.* The residue of Standley's *E. guatemalensis* is by no means well understood. According to Manning (1959) it ". . . might not be distinct from *Alfaroa manningii*, *A. hondurensis*, or *Engelhardtia pterocarpa*." Fortunately, this puzzle now seems to have been resolved by the discovery of fruiting material at the type locality. *Engelhardtia guatemalensis* Standley is in reality an *Alfaroa*, apparently related most closely to *A. hondurensis* (Williams & Molina, 1970).

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[1] Supported by National Science Foundation grants GB-5233X and GB-28525X. The line drawings are the artistry of Susan Carlton Smith and were sponsored by the Duke University Council on Research. I am indebted to several biologists for their information and support in locating trees in the hinterlands of Mexico and Central America: Drs. Arturo Gomez Pompa and Ramón Riba, Mexico; Mr. Antonio Molina R., Nicaragua; and Drs. William H. Hatheway and Lester R. Holdridge, Costa Rica. The initial fieldwork that was conducted in the spring of 1966 was outstandingly successful, due in large part to the support of my research assistant, Mr. Louis F. Conde, and travelling companions, Drs. Marshall R. Crosby and James W. Walker. Appreciation is also noted for services rendered by the curators of the many herbaria that have played such an important part in this study: A, CR, DUKE, EAP, F, GH, IICA, NO, NY, PH, US. Professor William Louis Culberson has kindly provided the Latin diagnosis, and Drs. R. L. Wilbur, B. G. Schubert, and W. E. Manning have been most helpful in suggesting improvements in the manuscript in form and content.

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ANN. MISSOURI BOT. GARD. 59: 297–321. 1972.

Since Manning's last report (1959) on the status of the New World Engelhardias, several critical collections have become available for study. The purpose of this paper is to reassess the evidence for recognizing the genus *Oreomunnea*, detail new information on the cytology, morphology and distribution of the American species, and discuss the patterns of variation in light of proposed taxonomic changes.

GENERIC CONSIDERATIONS

Oreomunnea Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 3: 33–34. 1856.

Engelhardtia sect. *Oreomunea* (Oersted) DC., Ann. Sci. Nat. Bot. IV. 18: 36. 1862.
Engelhardtia sect. *Oreomunnea* (Oersted) DC., Podr. 16: 142. 1864.
Oreamunoa Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1870: 166. 1870.

Trees, or rarely large shrubs; bark scaly or tight; pith solid; buds naked; leaves opposite, evergreen; leaflets 4–12, opposite to subopposite, symmetrical to asymmetrical at base, revolute on one or both margins, with or without auricles, with or without serrations on young trees and stump sprouts, entire on mature trees, adaxial surface glabrous, abaxial surface dotted with peltate scales; monoecious, with both staminate and androgynous panicles, in the latter case female spike flanked by 1–3 decussate pairs of staminate catkins; staminate flowers numerous, alternately arranged, abaxial 3-lobed bract cupped or long and slender, receptacle round or elongate, inner floral envelope of 2 bracteoles and 2–4 sepals, stamens 8 in one series to 18 or so in two series, pollen tectate with fine scabrate sculpturing, diameter *ca.* 20μ; pistillate flowers numerous, alternately arranged, subtended by 3-lobed abaxial bract and adaxial bracteolar rim, calyx tube fused to bract-bracteole cup at base, forming distinct tube above, deeply parted, with 4 narrow or broad sepal lobes extending to summit of stigma or beyond, style short or long tapering, deep cleft separating two stylar arms, stigmas horseshoe shaped, carinal, capping the ends of the stylar arms; fruit 3-winged, medium to large (5–13 cm), adaxial bracteoles expanded to cover pistil, nut 8-celled at equator; germination hypogeal, first two aerial leaves opposite and simple or compound, succeeding several leaves alternate and simple or compound, shifting to opposite, compound leaves at maturity.

When Oersted described *Oreomunnea*[3] (1856) as a new endemic genus from Costa Rica, he was quite aware of its close kinship to the Old World Engelhardias. However, he stressed particularly basic differences in the stigmas, fruit, and seed. With little additional information de Candolle (1862) saw fit to reduce the New World taxon to sectional rank in the genus *Engelhardia*. Thus started the long-standing debate on the merits of *Engelhardia* sect. *Oreomunnea* versus *Oreomunnea*. Once the lines were drawn more opinions were added without shedding much additional light. Oersted (1870*a*, 1870*b*) restated the case for recognizing the genus *Oreomunnea* and was later given support by Hjelmqvist (1948) and

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[3] The name has been spelled in various ways since the genus was first described in honor of don Francisco María Oreamuno. Manning (1949: 200) discussed the tortured history of the spelling in a footnote.

Leroy (1951, 1955); however, de Candolle (1864, 1914), Standley (1927*a*), and Manning (1949, 1959) continued to classify New World Juglandaceae with winged fruits as a section of *Engelhardia*. As Manning (1949) has so aptly pointed out, the decision on what to call the New World group depends on which of many similarities and differences are emphasized.

The issue took on new dimensions as a result of Standley's report (1927*b*) of another new genus, *Alfaroa*, from Costa Rica. Though Standley mistook the superficial similarity of the fruit as a basis for close relationship with *Juglans*, Manning (1938, 1940, 1948), Hjelmqvist (1948), and Leroy (1955) have since established that *Alfaroa* has its closest affinities with *Oreomunnea*. This appears to be a most remarkable assertion, because *Alfaroa* has a wingless fruit, whereas both *Oreomunnea* and *Engelhardia* have a conspicuous 3-winged bract. Manning (1949, 1959) summarized the many similarities of the New World members and presented substantial evidence that the fruit is about the only reliable basis for distinguishing between *Alfaroa* and *Oreomunnea*. The question then becomes one of assessing the relationship of *Alfaroa* and *Oreomunnea* as well as *Oreomunnea* and *Engelhardia*. On the basis "that the only reliable features are the position in flower and the condition in fruit of the bract and bracteoles (prophylls) . . ." Manning (1949) concluded that *Oreomunnea* is best considered a section of *Engelhardia* and that *Alfaroa* should be recognized as a weak generic segregate. Since the last reappraisal, however, new data on leaf crystals (Stone, unpublished) and seedlings (Conde & Stone, 1970; Stone, 1970), when combined with previous findings on phyllotaxy, venation patterns, and fruit morphology, provide, in my view, persuasive evidence for conferring generic rank on *Alfaroa*, *Oreomunnea*, and *Engelhardia*. The essence of these findings is summarized in Table 1 and discussed below.

Five characters shared by *Alfaroa* and *Oreomunnea* seem particularly significant in focusing on the close relationship of these New World members of the family. (1) Phyllotaxy is opposite at maturity (Figs. 2A, 7A; Stone, 1968: Fig. 1), though both genera pass through the seedling stage with alternate leaves (Figs. 4F, 9G; Stone, 1968). Occasionally, however, the phyllotaxy may vary between alternate, opposite, and whorled in rapidly growing shoots of *Alfaroa*. Members of both Old World sections of *Engelhardia* (§ *Engelhardia* and § *Psilocarpeae*) possess alternate phyllotaxy throughout their life span (Jacobs, 1960; Manning, 1966). (2) The intercostal and marginal leaf-venation patterns which permitted Wolfe (1957) to make generic identification of extant and fossil Juglandaceae are useful in recognizing two groups. *Alfaroa* and *Oreomunnea* form part of one group which is characterized by an intercostal network of closed veinlets. The second group, in which *Engelhardia* is a member, has an intercostal mesh that forms a network of free-ending veinlets. (3) Leaf crystals also serve to identify the Old World and New World components. As Nagel (1914) and Metcalfe and Chalk (1950) have pointed out, calcium oxalate crystals are common in various tissues of the juglandaceous plant. Leaf crystals in particular are common in certain genera and are often quite conspicuous. In hickories (*Carya*), for example, the adaxial leaflet surface may show minute bumps which are caused by druse crystals in the palisade parenchyma. A survey of leaf crystals indicates that druses are

TABLE 1. Diagnostic features of *Alfaroa*, *Oreomunnea*, and *Engelhardia*.

			Engelhardia	
CHARACTER	*Alfaroa*	*Oreomunnea*	§ *Psilocarpeae*	§ *Engelhardia*
Phyllotaxy	opposite	opposite	alternate	alternate
Leaflet venation, intercostal mesh	closed veinlets	closed veinlets	free-ending veinlets	free-ending veinlets
Leaflet crystals, large rhombic	present	present	absent	absent
Fruit size	large	medium	small	small
Fruit partitions	8-celled	8-celled	4-celled	2(–4)-celled
Position of cotyledons in fruit	separate	separate	tangled	tangled
Testa of cotyledons	tight	tight	loose	loose
Seedling germination	hypogeal	hypogeal	epigeal	epigeal
Cotyledonary node	1-gap, 3-trace	1-gap, 3-trace	1-gap, 2-trace	1-gap, 2-trace
Pollen diameter (μ)	24 (19–29)	21 (19–23)	15 (13–17)	19 (15–25)
Pollen, polar view	subtriangular	subtriangular	triangular	subtriangular
Pollen, equatorial view	suboblate	suboblate	oblate	oblate-spher.
Pollen nexine	thick	thick	thick	thin
Stigma orientation	carinal	carinal	split-carinal	commissural
Stigma shape	subglobose	subglobose	subglobose	elongate
Inflorescence	terminal and lateral	terminal and lateral	terminal and lateral	lateral
Fruit bract	very small	3-winged	3-winged	3-winged
Fruit bracteoles	very small	large	small	small
Fruit wing venation	absent	triveined	pinnate	pinnate

common in *Carya*, *Juglans*, *Pterocarya*, and *Platycarya*, but not in *Alfaroa*, *Oreomunnea*, or *Engelhardia*. Instead, *Alfaroa* and *Oreomunnea* have numerous small crystals in the leaf struts formed by the bundle-sheath extensions and large rhombic crystals localized primarily in the palisade. Large rhombic crystals have not been detected in *Engelhardia*. (4) The internal anatomy of the fruit of *Alfaroa* and *Oreomunnea* is also distinctive. A median cross section of the fruit exposes eight chambers in these New World genera (Figs. 4E, 9F; Stone, 1968: Fig. 13) but only two or four in *Engelhardia* (Leroy, 1955; Manning, 1966). The basic partitioning of the fruit into two chambers is effected by the primary septum. Primary and secondary septa intersect to form the 4-chambered fruit, while the 8-chambered condition is the result of the elaboration of tertiary septa which bisect each of the four basic chambers. Leroy (1951, 1955) also discovered that the vascularization of the fruit is identical in *Alfaroa* and *Oreomunnea*. Four placental strands fuse into one bundle in the plane of the primary partition prior to entering the funiculus. In *Engelhardia*, on the other hand, there are only two placental strands present to unite into a single vascular bundle. (5) The morphology of junglandaceous seeds and seedlings is a subject of considerable import and has been detailed elsewhere (Conde & Stone, 1970; Stone, 1970). The main findings confirm the separation of *Oreomunnea* from *Engelhardia* and its alliance with *Alfaroa*. *Engelhardia* has epigeal germination and one-gap, two-trace cotyledonary nodes. *Oreomunnea pterocarpa* (Conde & Stone, 1970: Fig. 7) and *O.*

mexicana (Fig. 9G) are hypogeal and have a one-gap, three-trace cotyledonary node as in *Alfaroa* (Conde & Stone, 1970: Fig. 20). While I was surprised to discover that the New World taxa with winged fruits have hypogeal germination, Hjelmqvist (1948: 58) shrewdly observed that the testa "attaches itself to all irregularities of the cotyledons, while in *Engelhardtia* it forms an even covering. *Oreomunnea* in this respect approaches the type that is found in *Juglans* and *Carya*, the character possibly being connected with the fact that the germination is hypogeal as in these; the germination of *Oreomunnea* is, however, not described."

The similarities of *Alfaroa* and *Oreomunnea* as discussed above are subtle but quite substantial. The similarities of *Oreomunnea* and *Engelhardia* are more apparent than real. By this I mean that the conspicuous 3-winged fruits that are common to both taxa are, on closer examination, quite distinctive. As the paleontologists have long recognized and MacGinitie (1969) recently commented, *Oreomunnea* fruits have a 4-lobed involucre consisting of 3 wings (bract) and a well developed adaxial or basal lobe (bracteoles) that covers the pistil. *Engelhardia* on the other hand has a 3-winged involucre with a highly reduced fourth lobe. Furthermore, the wings are triveined with looping laterals in *Oreomunnea*, whereas *Engelhardia* wings have pinnate venation. The closest ties of *Oreomunnea* to *Engelhardia* are through *E. roxburghiana* (Leroy, 1955; Stone, 1970), a monotypic representative of sect. *Psilocarpeae*. Whitehead (1965), for example, viewed the small, triangular pollen grains of *E. roxburghiana* as similar to an ancestral type from which were derived the larger subtriangular grains of *Alfaroa*, *Oreomunnea*, and *Engelhardia* sect. *Engelhardia*. The intermediate status of *E. roxburghiana* is further supported by similarities to *Oreomunnea* in inflorescence position, stigma orientation, fruit anatomy, and staminate flower morphology. Both taxa, as well as *Alfaroa*, have terminal androgynous panicles from which specialized lateral inflorescences were derived (i.e. *E.* sect. *Engelhardia*; Manning, 1938). Stigma development and orientation, a feature that has undergone considerable change in the evolution of the family (Manning, 1940), also characterizes *E. roxburghiana*, *Oreomunnea*, and *Alfaroa*. The short style and stigma are bifurcate with the primary separation oriented parallel to the line of carpel fusion, i.e. carinal stigma (Manning, 1940; Leroy, 1955: Fig. 75). The secondary or minor separation that is oriented at right angles to the primary separation is quite pronounced in *E. roxburghiana* and effectively separates the stigma into four lobes, hence giving rise to the term split-carinal. The more specialized members of *Engelhardia* have commissural stigmas with the elongate stigma halves positioned at right angles to the line of carpel fusion. As mentioned previously, *Alfaroa* and *Oreomunnea* have 8-celled flowers and fruits, whereas those of *Engelhardia* are either 2- or 4-celled. The fruits of *E.* sect. *Engelhardia* are 2-celled at the equator, although a weakly developed secondary partition is frequently present at the base. *Engelhardia roxburghiana* flowers are fundamentally similar to *Oreomunnea* but have a much more simple organization (Leroy, 1955). They lack the tertiary partition altogether, and the secondary partition is only moderately well developed. In addition, however, Leroy notes that the development of a *excroissance tabulaire* at the plane of insertion of the ovule in *E. roxburghiana* (Leroy, 1955: Fig. 72) establishes a relationship with *Oreomunnea* (and *Alfaroa*), as well as with *Pterocarya* (and *Platycarya*). The staminate flowers are somewhat less revealing of relationship, although *E. roxburghiana* and *Oreomunnea mexicana* (Figs. 7D, E) are the only members of the complex with a regularly arranged floral envelope. Manning (1948) notes, for example, that "In all species of the genus except *E. chrysolepis* [*E. roxburghiana* Wall.] the bracteoles and lateral sepals may be irregularly arranged so that it is often difficult to determine the exact identity of a given organ." The male flowers of *Oreomunnea pterocarpa* more closely approximate the irregular floral envelope arrangement found in *E.* sect. *Engelhardia.*

Even after the last character is assessed in the evaluation of relationships, the decision as to the appropriate taxonomic rank to assign a particular taxon remains in the subjective hands of the taxonomist. The evidence presented here leads me to conclude that the ties between *Alfaroa* and *Oreomunnea* are just as strong as those between *Oreomunnea* and *Engelhardia.* Consequently, it would seem logical that the three taxa should be given coordinate rank; whether it be at the sectional or generic level depends, of course, on their standing in relation to the other members in the family. In this regard Manning (1949) has stated that *Alfaroa* is as distinct from *Engelhardia* as *Juglans* is from *Pterocarya.* Accepting this opinion I must conclude that *Alfaroa, Oreomunnea,* and *Engelhardia* deserve generic rank. The dilemma posed by these three taxa reflects a close and what appears to be almost linear relationship. *Engelhardia* sect. *Psilocarpeae* has intermediate characters linking the wind-dispersed members of *E.* sect. *Engelhardia* and *Oreomunnea.* A shift in adaptive zones from wind to animal dispersed seeds, with the concomitant loss of wings and enlargement of seed, seems like a plausible explanation for the evolution of *Alfaroa* from *Oreomunnea*-like ancestors (Stone, 1970).

SPECIES CONSIDERATIONS

Three taxa of New World Juglandaceae with winged fruits are herein recognized. *Oreomunnea pterocarpa* is endemic to mid-elevations in the central cordilleras of Costa Rica. *Oreomunnea mexicana* (*Engelhardtia mexicana* Standley) is a premontane rainforest element ranging from southern Mexico to Costa Rica. The trees from Mexico, Guatemala, and Nicaragua (*E. nicaraguensis* Molina) are treated as *O. mexicana* subsp. *mexicana,* while the Costa Rican plants are placed in a new subspecies, *O. mexicana* subsp. *costaricensis.* The following section is devoted to a taxonomic appraisal of these taxa.

KEY TO SPECIES OF *OREOMUNNEA*

Bark tight; shoot tip glaucous; petioles long (3.5–6 cm), hairy at base; petiolules long (5–15 mm); leaflets long (8.5–16 cm), and wide (3–6 cm), sometimes revolute at base but not auriculate, the secondary veins not conspicuously forking; female flowers with elongate style and deep cleft separating stylar halves; male flowers with elongate receptacles bearing 16–19 stamens in two disorganized series; fruits large, the lateral wing span wide (to 13 cm); first pair of aerial seedling leaves simple ..... 1. *O. pterocarpa*

Bark exfoliating; shoot tip bronzy-yellow; petioles short (1.3–3.3 cm), glabrous at base; petiolules short (to 3 mm); leaflets long (6–10 cm), and narrow (1.5–2.5 cm), revolute and at least some auriculate at base, the secondary veins conspicuously forking; female flowers with short, nearly obsolete style, and shallow cleft demarcating

FIGURE 1. Tree of *Oreomunnea pterocarpa* with 27 in dbh at *Stone 2684* location east of Tuís, Costa Rica.

stylar arms; male flowers with small oval to rectangular receptacles bearing 8–12 stamens in one or two series; fruits medium, the lateral wing span narrow (to 5 cm); first pair of aerial seedling leaves compound .... 2. *O. mexicana*

1. **Oreomunnea pterocarpa** Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 3: 33–34. 1856. (Tree: Figs. 1, 2A–C. Inflorescence: Fig. 3;

Manning, 1938: Figs. 9, 20; Hjelmqvist, 1948: Fig. 8C. Staminate flower: Figs. 4A–C; Candolle, 1914: Fig. I; Manning, 1948: Figs. 38–41, 64, 68, 72. Pistillate flower and fruit: Figs. 3, 4D–E; Candolle, 1862: Fig. 50; Oersted, 1870*a*: Plate II, Figs. 1–11; Eichler, 1878: Fig. 15M; Candolle, 1914: Fig. II 1–3; Manning, 1940: Figs. 32, 33, 61, 78, 102, 103; Hjelmqvist, 1948: Fig. 21a; Pittier, 1957: Fig. 20. Seedling: Fig. 4F; Conde & Stone, 1970: Fig. 7).

Engelhardtia pterocarpa (Oersted) Standley, Trop. Woods 12: 15. 1927.

Tree to 46 m tall, 73 cm dbh (*Stone 2222*), buttresses well developed; bark tight, outer surface grayish to reddish and verrucose, inner bark yellowish-orange; wood white throughout, with definite growth rings (Heimsch & Wetmore, 1939), diffuse porous, the vessel members from trunk averaging $221\mu \times 937\mu$; pith solid; buds naked, protected by closely appressed, paired leaf-primordia, studded with butter-yellow peltate scales, without hairs, the axillary buds superposed; leaves decussate; petioles 3.5–6.0 cm, hairy at base in sapling and sucker sprouts; raches 7.0–10.0 cm; leaflets 6–8, opposite to subopposite; petiolules 5–15 mm; blades of leaflets 2.5–3 times longer than wide, 8.5–16.0 cm × 3.0–6.0 cm, symmetrical to asymmetrical at base, most revolute on one or both margins, most pronounced on basiscopic side, the margins entire, the secondary veins not conspicuously forked; young leaflets pink to greenish yellow; mature leaflets corriaceous, the adaxial surface dark green and essentially glabrous, the abaxial surface light green to glaucous, dotted with peltate scales of two sizes, moderate number of large butter-yellow scales and numerous small transparent or brownish scales, no hairs. *Inflorescences* borne laterally on old wood or occasionally at junction of old and new wood; "androgynous panicle . . . , with usually four to six opposite staminate catkins, the inflorescence terminated by a fifteen- to twenty-flowered pistillate catkin" (Manning, 1938; diagrammed as terminal in Hjelmqvist, 1948: Fig. 8c). *Staminate flowers* alternately arranged; abaxial bract 3-lobed, long and narrow; mature flower with elongate receptacle; inner floral envelope of two bracteoles and 3–4 sepals; stamens ca. 19, in two disorganized series, filaments essentially obsolete, anthers glabrous, dehiscing by longitudinal slits; pollen tectate with fine scabrate sculpturing, suboblate, subtriangular in polar view, pores equatorial, averaging 21μ in diameter. *Pistillate flowers* small (6–7 mm), highly reduced, lacking petals; subtending hand-like cup formed from 3-lobed abaxial bract and adaxial bracteole rim; calyx tube tightly fused to bract and bracteoles, the four narrow sepal lobes appearing as distinct outgrowths of ovary, seemingly not united into calyx tube; ovary inferior, elongate tapering style extending to same height as divergent sepal lobes, with deep cleft separating two stylar arms; stigmas carinal, subglobose or horseshoe shaped, capping ends of stylar arms, verrucose

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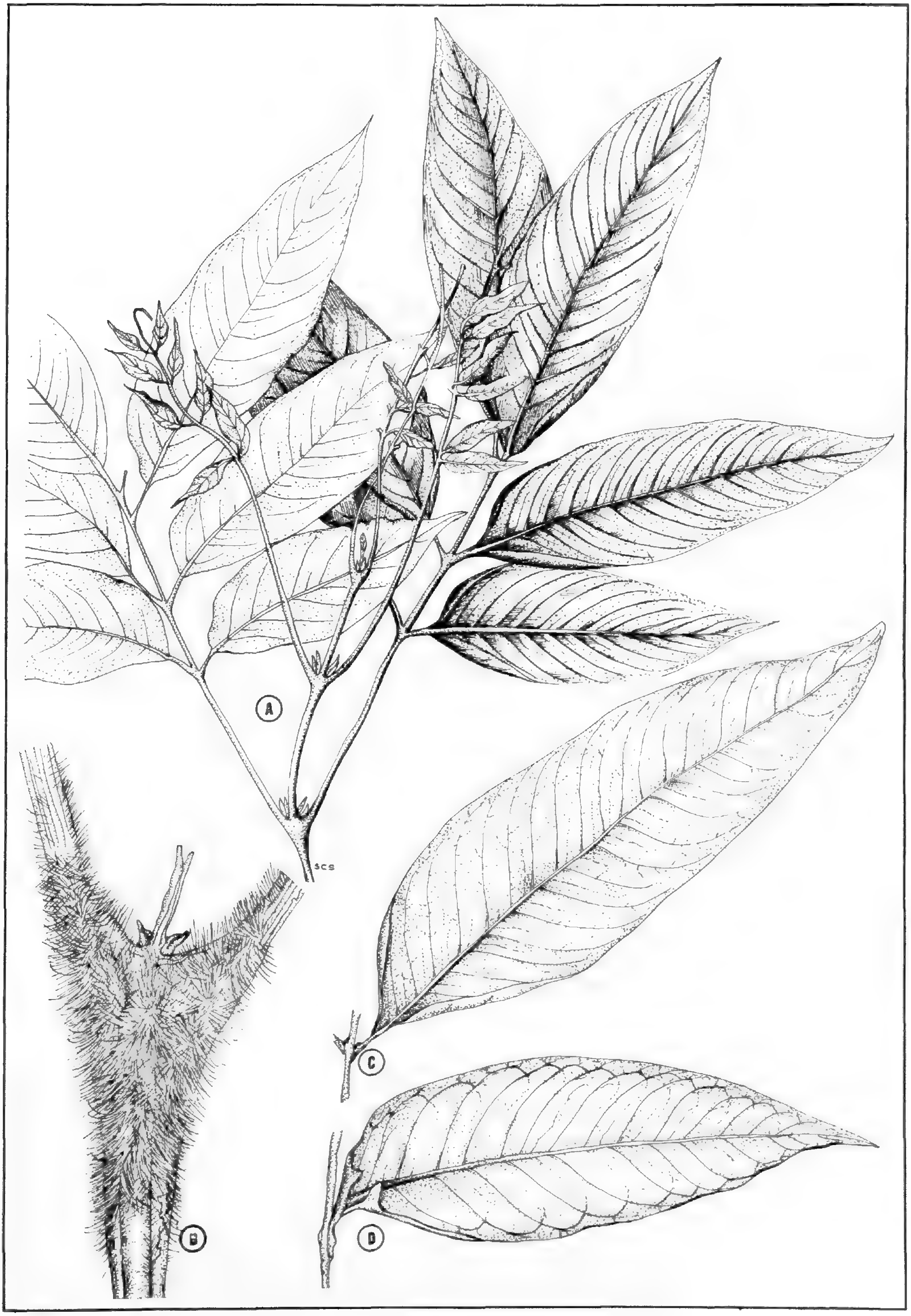
FIGURE 2. Vegetative aspects of *Oreomunnea*.—A. Shoot of *O. pterocarpa* displaying decussate phyllotaxy (*Stone 1907*), × 0.4.—B. Pubescent node of sapling of *O. pterocarpa* (*Stone 2169*), × 1.7.—C. Leaflet of *O. pterocarpa* (*Stone 1907*) with secondary veins that curve upward toward tip and end without conspicuous branching, × 0.6.—D. Leaflet of *O. mexicana* subsp. *costaricensis* (*Stone 2680*) with auricles at base and secondary veins that curve upward toward tip, branch and then fuse near margin, × 0.8.


A
SCS
B
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D

stigmatic surface confined to rim and outer surface. *Fruits* large, 3-winged, lateral wing spread to 13 cm, central wing to 11 cm long, strong central primary vein flanked by two subordinate primaries and interconnected by looping laterals; adaxial pair of fused bracteoles enclosing globose nut and stylar-stigma region; nut 8-celled at equator, 4-celled near poles; fruit splitting loculicidally along secondary partition on germination. *Seedling* with long, slender tap root; germination hypogeal; first two aerial leaves opposite and simple, succeeding several leaves alternate and simple, followed by transition to compound, and later abrupt shift to opposite phyllotaxy; shoots pale to vivid pink; simple leaves with long petioles (20–30 mm) and large blades (40–80 × 75–250 mm), with conspicuous midrib and secondaries; transitional compound leaves (3-, 5-, and 7-foliolate) with extremely long petioles (30–60 mm), near-sessile lateral leaflets (to 2 mm), and an extended petiolule (15–20 mm) supporting large terminal leaflet (50–100 × 100–200 mm); leaves with more than five leaflets have even-pinnate pattern characteristic of those of mature tree; simple leaves and leaflets of compound leaves entire, no evidence of inrolling of basal margins; adaxial leaflet surface dark green, glabrous; abaxial leaf surface glaucous, free of hairs, dotted with large butter-yellow peltate scales and numerous brown peltate scales.

Oersted's original description (1856) and subsequent discussions (1870*a*, 1870*b*) were based on fruiting material only. It was nearly sixty years before collections by Adolfo Tonduz made vegetative and flowering specimens available for study (Candolle, 1914). The paucity of collections is as much a function of the difficulty of collecting specimens from these forest giants as it is locating them along the steep ravines of the valley and tributaries of the Río Reventazón. Trees in the virgin rainforest around Platanillo and Tuís commonly have plank buttresses extending eight feet in diameter at the base and tapering to a 2 to 3 foot trunk at head height (Fig. 1). The bark is smooth and tight, and the trunk is often without branches for the first 40 to 50 feet. The mature trees may reach 46 m (Tonduz *in* de Candolle, 1914) to become upper story emergents. Young shoots are usually vivid pink, while mature leaves are dark green above and glaucous below. Perceptive native guides are remarkably accurate in spotting the broad crowns from distant hillsides. In the Platanillo area woodsmen readily differentiate between *gavilán blanco* (*Oreomunnea pterocarpa*) and *gavilán colorado* (*Alfaroa manningii* León).

One of the most intriguing aspects about *Oreomunnea pterocarpa* is its highly restricted range. As both Standley (1927*a*, 1937) and Manning (1959) have pointed out, it is known only from the low to middle elevations on the Atlantic drainage of Costa Rica. All of the verified specimens are from the Río Reventazón valley in Cartago Province, although Mr. Charles Lankester presented me with typical *O. pterocarpa* fruits, ostensibly collected at Laguna Hule in Alalueja Province. Collection data from herbarium sheets indicate that *O. pterocarpa* ranges from 200 m (Manning, 1959: locality not cited nor known to me) to 1500 m elevation (Tonduz *in* Candolle, 1914: Rincón del Indio). The large tree on the grounds of the IICA at Turrialba (*Stone 1346*) is situated at 550 m, while León's topotype collection from La Gloria (*León 1523*) was located at 820 m. There is,

FIGURE 3. Inflorescence of *Oreomunnea pterocarpa* (*Stone 1346*) with laterally borne fruits, × 0.54.

in addition, a cultivated tree in the Botanic Garden of the Universidad de Costa Rica in San José (1168 m) that appears to be doing quite well. Manning (1959) suggested that a specimen from Baja Verapaz, Guatemala (*Standley 90967*, GH) might be *O. pterocarpa*. However, the specimen is sterile and lacks the glaucous shoot tip and long petiolules characteristic of *O. pterocarpa*; it appears to be a member of the genus *Alfaroa*, probably *A. guatemalensis* (Standley) Williams & Molina.

Oreomunnea pterocarpa, like so many of the tropical forest trees, may be locally abundant but not common. This is one of the puzzling aspects of tropical diversity that has led to speculation that many tropical plants are self pollinated (Baker, 1959, 1963). *Oreomunnea* has typical amentiferous catkins, and the large 3-winged fruits of *O. pterocarpa* (Fig. 3) show obvious adaptations to wind dispersal. Furthermore, the tree crown is favorably situated in the upper canopy. Fruit production on the tree in San José (*Stone 1016*) offers affirmative evidence for self pollination in *O. pterocarpa*. No other trees are known to occur within 20 miles of this specimen and yet fruit and seedlings are produced at least occasionally (Jan 1962, Nov 1967).

COSTA RICA. ALAJUELA: Edge of Laguna Hule, ca. 12 km N of V. Poás, no date, *Lankester* (DUKE). CARTAGO: Juan Viñas, no date, *Calvert 57* (PH); Cachí, Jun 1910, 4 Jul 1914, *Lankester* (NY); La Gloria, bordes del Río Chiz, 820 m, 23 Apr 1949, *León 1523* (EAP, IICA); La Gloria, 700–800 m, 29 Apr 1914, *Tonduz 18000* (A, CR, EAP, F, GH, NY, PH, US); Peralta, 13 Jul 1923, *Stevens 468a* (US); grounds of Inst. Interamericano Ciencias Agricolas (IICA) near Río Turrialba, 550 m, 7 Sep 1949, *León 1819* (IICA); slope behind IICA station overlooking Río Reventazón, 550 m, 22 Jan 1963, 28 Mar 1966, 26 Jan 1968, *Stone 1346* (DUKE, NO), 8 Jul 1965, *Stone 1908* (DUKE); on peninsula between Molina Quebrada and Río Reventazón near Turrialba, 10 Jul 1965, *Stone 1919, 1920, 1921* (DUKE), 23 Apr 1966, *Stone 2169* (DUKE); Pejibaye, 2000 ft., 3 Jul 1928, *Stork 2808* (F); hills S of Platanillo, 22 Jan 1963, *Stone 1347, 1348* (DUKE); midslopes SE of Platanillo, 25 Mar 1967, *Stone 2222* (DUKE); Montaña Baja Coronó, E of Tuís and N of Platanillo, 2 Sep 1968, *Stone 2684* (DUKE); no locality, 1927 and 1964, *Lankester* (F, US). SAN JOSE: Botanic Garden, Universidad de Costa Rica, San José, 3800 ft., 19 Jan 1962, 7 Jul 1965, *Stone 1016* (Duke), 10 Nov 1967, *Stone 1016 A, B, C* (DUKE).

2. **Oreomunnea mexicana** (Standley) Leroy, Bull. Mus. Hist. Nat. (Paris) Sér. 2. 23: 127. 1951. (Tree: Figs. 5, 6A–C, 7A, 8. Inflorescence: Figs. 7B, 7C, 9A, 11. Staminate flower: Figs. 7D, 7E, 10A, 10B. Pistillate flower and fruit: Figs. 9A–F, 10C–J; Manning, 1940: Figs. 34, 35, 106. Seedling: 9G.)

Engelhardtia mexicana Standley, Trop. Woods 12: 15. 1927.
Engelhardtia nicaraguensis Molina, Fieldiana Bot. 31: 358. 1968.

Tree to 32 m tall (*Stone 2177B*) or more, 150 cm dbh (*Stone 2807* locality), buttresses developed on both downhill and uphill sides of trunk, occasionally extending to height of 3 m; bark exfoliating, outer surface reddish brown, inner bright orange; wood white throughout or heartwood sometimes pink, diffuse porous, the vessel members from trunk averaging $160\mu \times 693\mu$; pith solid; buds naked, protected by closely appressed paired leaf-primordia, studded with bronzy-yellow peltate scales, without hairs, axillary buds superposed; leaves decussate, petioles 1.3–3.3 cm, with dense covering of short hairs (.04 mm) on young trees, raches 1.8–11.8 cm, with dense covering of short hairs on young trees; leaflets 4–12, opposite to subopposite; petiolules 0–3 mm; blades of leaflets 4–5 times longer than wide, 6.0–10.0 × 1.5–2.5 cm, symmetrical to asymmetrical at base, revolute on one or both margins, most pronounced on basiscopic side, auricles often present on one or both margins, the margins mainly entire, with coarse serrations on distal half of stump sprouts and some shoots, the secondary veins conspicuously forked; young leaflets pink; mature leaflets coriaceous, the adaxial surface dark green and essentially glabrous, the abaxial surface light green to glaucous, dotted with peltate scales of two sizes, moderate number of large bronze scales and numerous small brownish scales, short hairs on basal portion of midrib

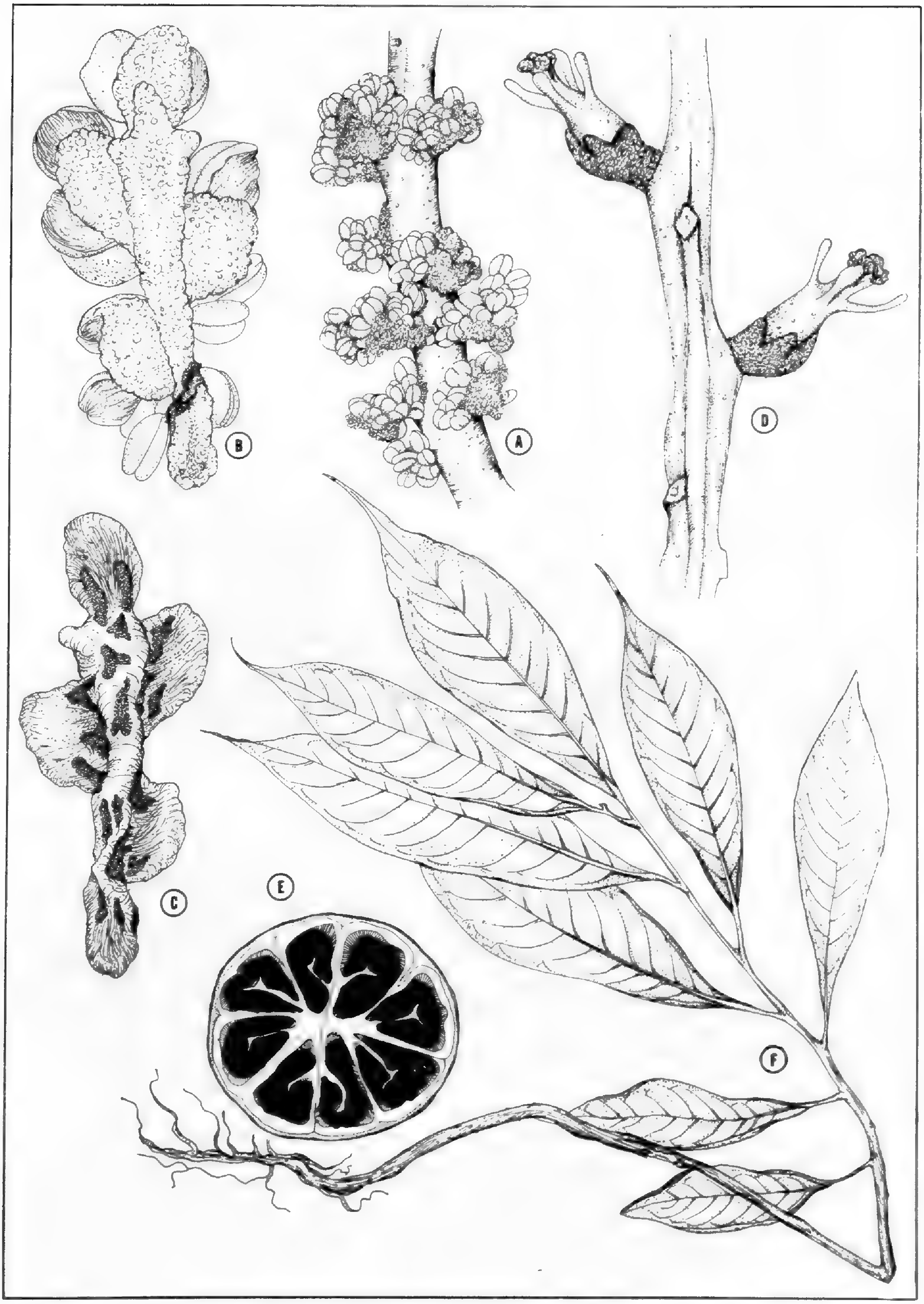

FIGURE 4. Flowers, fruit, and seedling of *Oreomunnea pterocarpa*.—A. Portion of staminate catkin (*Stone 1346*), × 4.3.—B. Abaxial view of staminate flower with 5 floral segments (*Stone 1346*), × 10.4.—C. Adaxial view of same flower as in C, exposing attachment points of 19 stamens, × 10.4.—D. Pistillate flowers (*Stone 1346*), × 3.4.—E. Transverse section of fruit at equator, oriented with primary partition in east-west direction: 8-celled, thin husk and thin cartilaginous shell (*Stone 1346*), × 2.1.—F. Seedling with alternately arranged leaves, hypogeous cotyledons shed (*Stone 2684*), × 0.4.

FIGURE 5. *Oreomunnea mexicana* (*Stone 2718*), 30.5 in. dbh, Tapantí, Costa Rica.

and long hairs tucked in fold of auricle on young trees. *Inflorescences* initiated terminally with flush of new growth or occasionally laterally, of three types: androgynous panicle with central female spike flanked at base by 1 to 3 decussate pairs of staminate catkins (Fig. 11); staminate panicle consisting of 1 to 3 de-

FIGURE 6. Habit and habitat of *Oreomunnea mexicana.*—A. Moderate development of buttresses, *Stone 2177B* location.—B. Bark separating into long platelets on 14 in. dbh trunk, *Stone 2181.*—C. Fog-shrouded mountains south of Muñeco, Costa Rica, ca. 1500 m elev., June 1970.

cussate pairs of catkins; pistillate panicle of one to several catkins, fruiting spikes elongate but fruits congested. *Staminate flowers* alternately arranged, small (2–3 mm), sessile or essentially so, outer surface sprinkled with butter-yellow and transparent peltate scales; abaxial 3-lobed bract cupped; mature flower with rounded receptacle; inner floral envelope of two lateral bracteoles and two (rarely three) sepals; stamens 8 in one series, ranging to 12 in two series, filaments essentially obsolete, anthers glabrous, dehiscing by longitudinal slits; pollen tectate with fine scabrate sculpturing, suboblate, subtriangular in polar view, pores equatorial, averaging 19μ (*Stone 2144*) to 23μ (*Stone 2181*) in diameter. *Pistillate flowers* small (3–5 mm), highly reduced, lacking petals; subtending hand-like cup formed from 3-lobed abaxial bract and adaxial bacteole rim; calyx tube fused to bract and bracteoles at base, forming distinct calyx tube above, four broad sepal lobes incurved or spread, extending well beyond stigma; style short tapering, with deep cleft separating two stylar arms; stigmas carinal, subglobose or horseshoe shaped, capping the ends of stylar arms, the verrucose stigmatic surface confined to rim and outer surface. *Fruit* medium-sized, 3-winged, with lateral wing spread to 5 cm, central wing to 4 cm long, with three primary veins and looping laterals; adaxial bracteoles enclosing globose nut and stylar-stigma region, to 12 mm long; nut 8-celled at equator, 4-celled near poles; fruit splitting loculicidally along secondary partition on germination. *Seedling* with long, slender tap root; germination hypogeal; first two aerial leaves opposite and pinnately compound, succeeding several leaves alternate and compound, abrupt shift to opposite phyllotaxy in young sapling stage, 1–2 feet tall (*Stone 1872*); shoots pale to vivid pink; most leaves odd-pinnate, the 18–20 (14–22) leaflets coarsely serrate; petiole short (to 7 mm) in first formed leaves, longer (to 25 mm) in later ones; leaflets essentially sessile with petiolules rarely 2 mm long; later formed leaflets becoming entire, the last formed leaves of 3–4 foot saplings with entire margins on basal half of leaflets, coarse serrations on distal half; leaflet bases often asymmetrical, auricles usually present on leaflets of larger saplings; a coating of short (.04 mm) hairs on stem tip, petiole, and rachis and a cluster of longer hairs (.6 mm) at junction of petiole and stem; adaxial leaflet surface dark green, with butter-yellow scales scarce; abaxial leaflet surface light green to glaucous, occasionally with a few long hairs at base, dotted with large butter-yellow peltate scales. *Chromosome number*, $2n = 32$, based on counts from roottips of seedlings, greenhouse progeny of *Stone 2141* (DUKE).

Oreomunnea mexicana as here recognized constitutes a very natural assemblage. The range from Oaxaca, Mexico, to Cartago, Costa Rica, may at first appear to be rather exceptional, but not when viewed in light of the similarity in environmental conditions at each locality. All trees that I have seen, including ones from Mexico, Guatemala, Nicaragua, and Costa Rica, are invariably situated on steep hillsides and fog-shrouded ridges. Miranda (1946) vividly described this type of habitat for the Orizaba population: ". . . emergian de la sombra de la neblina y cuyas altas copas volvian a perderse en ella." Present records indicate that the species ranges from 900 to 2600 m. There is reason to believe that the plants at higher elevations may not fare nearly so well as those growing in the 1000–1700 m

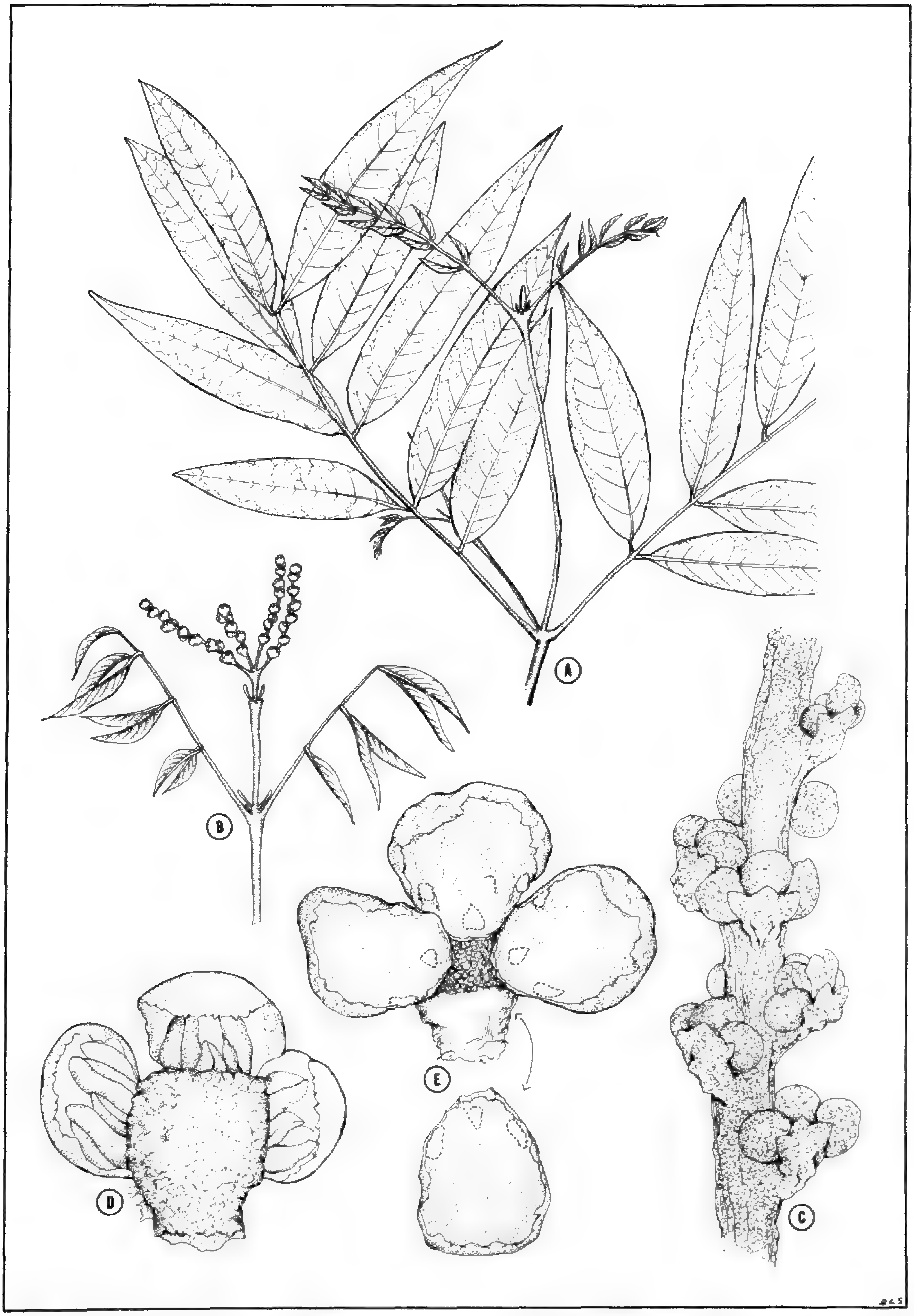

FIGURE 7. Vegetative and flowering features of *Oreomunnea mexicana* subsp. *mexicana*. —A. Shoot displaying decussate phyllotaxy (*Stone 2141*), × 0.4.—B. Terminal staminate inflorescence (*Stone 2141*), × 0.4.—C. Portion of staminate catkin (*Stone 2144*), × 6.5.—D. Adaxial view of staminate flower (*Stone 2144*) with proximal sepal obscuring view of 3 stamens and receptacle, × 13.—E. Adaxial view of staminate flower exposing attachment points of 12 stamens in two series (*Stone 2144*), × 13.

FIGURE 8. Holotype of *Oreomunnea mexicana* subsp. *mexicana* (*Rovirosa 1006*, PH).

belt. Out of ten or so locations known for *O. mexicana* subsp. *mexicana*, only four have yielded flowering or fruiting specimens. These include: Rovirosa's type collection (fruits) from Chiapas (900–1000 m); Martinez (fruits) and Stone (male and female flowers and fruits) specimens from Oaxaca (1700 m); female flowers by Stone from Alta Verapaz, Guatemala (1300–1500 m); collections by Salas and Taylor (fruits) and Stone (flowers and fruits) from Jinotega and Matagalpa, Nicaragua (1450 m). A notation by Ross (*Ross 55*, US) that *O. mexicana* is a "shrub in elfin forest" at 1500 m suggests that unfavorable exposures at even moderate altitudes may handicap growth and reproduction. Perhaps marginal populations are maintained through asexual means. I have observed, for example, that saplings of *O. mexicana* are capable of vegetative propagation. If the stem is prostrated on the ground, adventitious shoots may be stimulated. Also, it is quite likely that stump sprouts arise here as in *Alfaroa* (personal observation).

The geographical range of *Oreomunnea mexicana* has, to be sure, promoted varying degrees of population divergence, but the differences are subtle. Miranda (1946) thought he perceived a difference in the more numerous and sessile leaflets in the Orizaba specimens and indicated that he would later describe this element as a new species. However, no formal recognition was ever proposed, and, except for Molina's *Engelhardtia nicaraguensis* (1968), no other segregate or close relative has been recognized. The field characteristics of seedlings, saplings, and adult trees of *Oreomunnea mexicana* are remarkably distinctive and as far as I am aware uniform in all of the Middle American populations. Foliage of younger plants and sucker shoots on trees are typically reddish; the leaves are opposite, pinnately compound, and the leaflets are serrate. The larger trees can usually be spotted by the exfoliating bark that peels off in large strips (Fig. 6B). The leaflets on mature trees are mostly entire, but some serrate leaflets can always be found. *Alfaroa costaricensis* sensu lato (including *A. williamsii* Molina) is the only other species of tropical American Juglandaceae that approaches *O. mexicana* in this respect. The leaflets and terminal shoots of *O. mexicana* tend to be more slender than those of *O. pterocarpa* and the Alfaroas. This combination of characters unites the Mexican, Guatemalan, Nicaraguan, and Costa Rican populations of *O. mexicana*. Only in flower characters has it been possible to discern any significant differences. The following key emphasizes these differences in recognizing two subspecies.

KEY TO SUBSPECIES OF *OREOMUNNEA MEXICANA*

Female flowers and fruits with conspicuous pedicels to 3 mm long; pistil oriented parallel to axis of catkin, sepals incurved; Mexico to Nicaragua .... 2a. subsp. *mexicana*
Female flowers and fruits sessile or nearly so; pistil oriented at a 45° angle to axis of catkin, sepals spread; Costa Rica .... 2b. subsp. *costaricensis*

2a. Subspecies **mexicana**

Holotype: MEXICO. CHIAPAS: Hab. regione temperata locis humidis Andium Chiapensium, 900–1000 m, *Rovirosa 1006* (PH; photograph with two leaflets and several fruits, US).
Engelhardtia nicaraguensis Molina, Fieldiana Bot. 31: 358. 1968.
Type: NICARAGUA. MATAGALPA: Bosque nebulosa vecindades de Santa María de Ostuma, 1300 m, *Salas 2967* (F; isotype, EAP).

There are no vegetative features that I have found that can be used to recognize the subspecies. Thus, when the sterile specimens are cited it should be noted that provisional identification was based solely on geographic location. The female flowers of *Oreomunnea mexicana* have the only reliable diagnostic features. Subspecies *mexicana* has flowers with long pedicels and a bract-bracteole cup that curves to orient the pistil parallel to the axis of the catkin (Fig. 10H); in this respect it is reminiscent of the female flower of *Engelhardia roxburghiana* (see Manning, 1940).

After careful examination of the type specimen of *Engelhardtia nicaraguensis* and a few subsequent collections, I can find no basis for recognizing this taxon. The female flowers (Fig. 10H) are indistinguishable from those of the Mexican (*Stone 2807*) and Guatemalan (*Stone 3003*) specimens. In the original description Molina (1968) did not single out any diagnostic features, but rather relied on a host of meristic differences between the type specimens:

	E. mexicana	*E. nicaraguensis*
Pairs of leaflets	3–4	4–6
Petiole length (cm)	1.5–2	2.5–3.5
Rachis length (cm)	2–6	4–9
Petiolule length (mm)	2–3	1–2
Leaflet length (cm)	5–8.5	3–8.5
Nut length (mm)	6–7	6–8

The inclusion of additional samples in this comparison completely blurs the distinctions noted above (see diagnostic descriptions under *O. mexicana*).

Fertile specimens: MEXICO. CHIAPAS: Hab. regione temperata locis humidis Andium Chiapensium, 900–1000 m, 24 Jul 1891, *Rovirosa 1006* (PH, holotype; US). OAXACA: Highway 175, 102.5 km S Valle Nacionál, 1700 m, 7 Nov 1962, *Martinez 13–39* (MEXU, DUKE); highway 175, 42.1 km S Valle Nacionál, 4900 feet, 16 Mar 1966, *Stone 2141* (DUKE); highway 175, 38.8 mi N Ixtlán de Juarez, 2 Feb 1971, *Stone 2807* (DUKE).

NICARAGUA. MATAGALPA: Bosque nebuloso vecindades de Santa María de Ostuma, 1300 m, May 1957, Salas 2967 (F, holotype; EAP). JINOTEGA: Cerca de Aranjuez, 1160 m, Aug 1957, *Salas & Taylor 2967A* (EAP); near Santa María de Ostuma, on road to Aranjuez, 0.9 mi E of highway 3, 1450 m, 6 May 1966, *Stone 2181* (DUKE).

GUATEMALA. ALTA VERAPAZ: On highway 7E, 1.3 mi SE of highway 5 intersec. near Tactic, 25 May 1971, *Stone 3003* (DUKE).

Sterile specimens: MEXICO: VERACRUZ: Cerro de San Cristobal, near Orizaba, 4200–5000 feet, 3 Aug 1953, *Manning & Manning 53746* (A), 4 Aug 1953, *Manning & Manning 53770* (NY, PH), *Manning & Manning 53775* (DUKE), 8 Mar 1966, *Stone 2518, 2119, 2120, 2121, 2122, 2123, 2124* (DUKE); Santa Marta, 5000 feet, Los Tuxtlas range, 17 Jun 1963, *Ross 55* (US); near Ocotal Chico, 3000 feet, Los Tuxtlas, 24 Mar 1965, *Ross 120* (US); Ejido San Fernando, vertiente SW Sierra de Santa Marta, 1000 m, 14 Mar 1968, *Sousa 3551* (DUKE). OAXACA: Highway 175, 42.1 km S Valle Nacionál, 4900 feet, 28 Jan 1965, *Stone 1872, 1873, 1875* (DUKE); highway 175, 42.1 km S Valle Nacionál, 4900 feet, 2 Feb 1971, *Stone 2808, 2809, 2810, 2811, 2812* (DUKE).

GUATEMALA: ALTA VERAPAZ: Region of Chelac, NE of Carchá, 1500 m, 2 Apr 1939, *Standley 70379* (A, F); ridge SE of Tactic, 9 Nov 1969, *Stone 2697* (DUKE); highway 7E SE of Tactic, 2 km from junction with highway 5, 10 Nov 1969, *Stone 2703, 2704, 2705* (DUKE). BAJA VERAPAZ: Sierra de las Minas, E of Chilascó, 28 May 1950, *Lamb 113* (F, EAP). EL PROGRESSO: Montaña Canahui, between Finca San Miguel and summit, 1600–2300 m, 10 Feb 1942, *Steyermark 43810* (A, F). GUATEMALA: No locality or date, *Aguilar 616* (F). HUEHUETENANGO: Cerro Huitz, Sierra de los Cuchumatanes, between Mimanjuitz and Yulhuitz, 1500–2600 m, 14 Jul 1942, *Steyermark 48619* (F).

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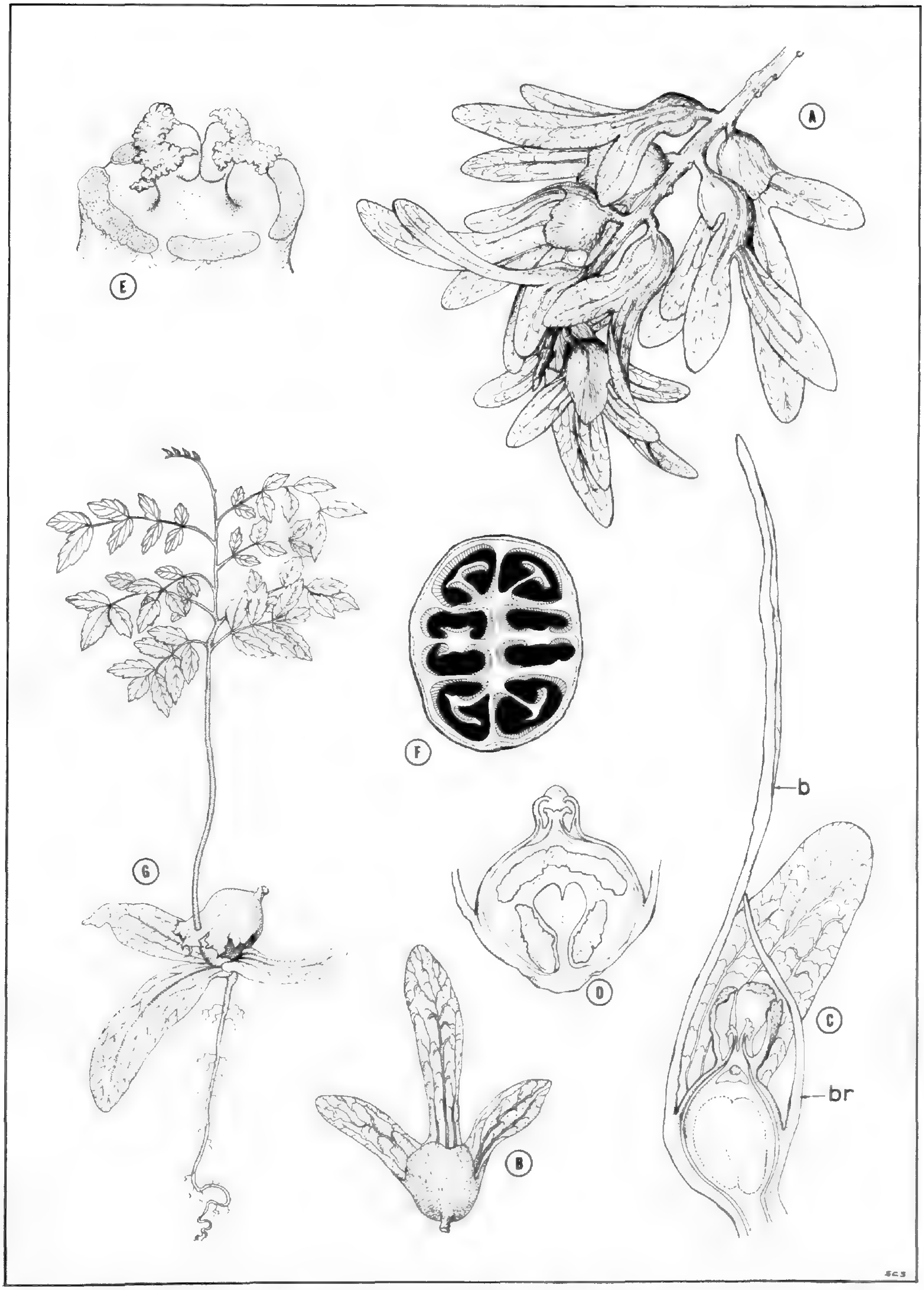
FIGURE 9. Fruits and seedling of *Oreomunnea mexicana* subsp. *mexicana*.—A. Inflorescence with terminally-borne fruits (*Stone 2141*), × 0.8.—B. Adaxial view of mature fruit (*Stone 2141*) showing triveined wings and well-developed basal lobe, × 0.8.—C. Radial section of fruit along secondary partition exposing two stylar arms separated by major groove and enclosed by abaxial bract (b) and adaxial bracteoles (br) or basal lobe (*Stone 2141*), × 3.4.—D. Radial section of fruit along primary partition exposing bifurcation of one stylar



arm by minor groove (*Stone 2141*), × 3.4.—E. Polar view of horseshoe-shaped stigma on fruit, major groove oriented in north-south direction (*Stone 2141*), × 8.7.—F. Transverse section of fruit at equator, oriented with primary partition in north-south direction: 8-celled, thin husk (outer dark band) and thin cartilaginous shell (stippled zone) (*Stone 2141*), × 3.4. —G. Seedling displaying hypogeal germination, first aerial leaves opposite and compound, succeeding leaves alternate (*Stone 2142*), × 0.8.

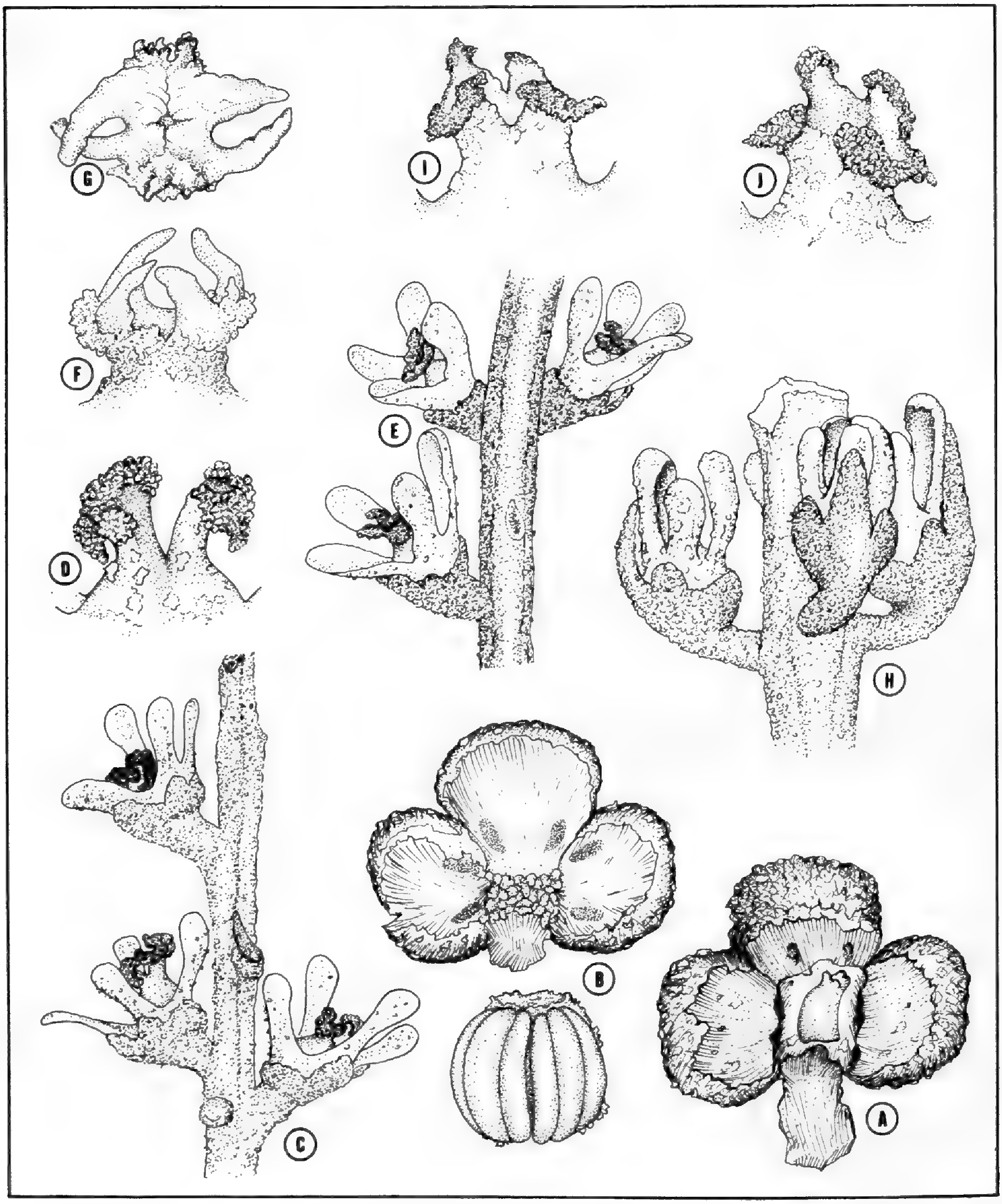


FIGURE 10. Inflorescence and flowers of *Oreomunnea mexicana*: A, C–G, subsp. *costaricensis*; B, H–J, subsp. *mexicana* (Nicaragua).—A. Adaxial view of staminate flower with 8 stamens and aborted pistil (*Stone 2680*), × 15.—B. Adaxial view of staminate flower with 8 stamens in one series (*Stone 2181*), × 15.—C. Pistillate flowers with spreading sepals and moderately-developed stigma (*Stone 2177B*), × 6.5—D. Carinal stigma (*Stone 2177B*), × 18.—E. Pistillate flowers with spreading sepals and well-developed stigma (*Stone 2680*), × 6.5.—F. Side view of stigma sighting along major groove (*Stone 2680*), × 18.—G. Polar view of stigma (*Stone 2680*), × 18.—H. Pistillate flowers with incurved sepals (*Stone 2181*), × 5.1.—I–J. Side view of carinal stigma (*Stone 2181*), × 18.

Figure 11. Androgynous panicle of *Oreomunnea mexicana* subsp. *costaricensis* (*Stone 2680*), × 2.1.

2b. Subspecies **costaricensis** Stone, subsp. nov.

Flores feminei pedicellis brevibus et calycum lobis reflexis.

Type: Costa Rica. cartago: 4 km S of Muñeco, ridge between Río Patarrá and Río Sombrero, *Stone 2680* (DUKE).

This new subspecies is known only from Cartago Province, Costa Rica. While it grows in the same general areas as *Oreomunnea pterocarpa*, *Alfaroa costaricensis*, and *A. manningii*, *O. mexicana* subsp. *costaricensis* is usually situated above the protected ravines on fog-shrouded mountain ridges in a premontane rainforest (*sensu* Holdridge, 1964). No good fruiting material has been collected, although remnants of the winged bracts were found attached to young seedlings. The female flowers are somewhat smaller than those of *O. mexicana* subsp. *mexicana*, in addition to the fact that the pedicel is short, the pistil is oriented at a 45° angle to the axis of the catkin, and the sepal lobes are spread and rather flat. There appears to be some variation in the extent of elaboration of the stylar arms. The material from Valle Escondido (*Stone 2177B*) has a deep stylar cleft, but only moderately developed minor grooves on the stigma lobes (Figs. 10C–D). Specimens from Muñeco (*Stone 2680*) have deep minor grooves that give the stigma a pronounced 4-pronged appearance (Figs. 10E–G). The significance of these differences cannot be evaluated until more collections are available.

Fertile specimens: Costa Rica. cartago: Ridge above Valle Escondido, ca. 14 km NE of Tuís, 1100 m, 29 Apr 1966, *Stone 2177B* (DUKE); 4 km S of Muñeco, ridge between Río Patarrá and Río Sombrero, 29 Aug 1968, *Stone 2680* (DUKE, holotype).

Sterile specimens: Costa Rica: cartago: Valle Escondido, ca. 14 km NE Tuís, 1100 m, 1966, *Hatheway* (DUKE), 29 Apr 1966, *Stone 2177A* (DUKE); Tapantí, 1300 m, 2 Sep 1966, *Hatheway* (DUKE), 6 Nov 1967, *Stone 2316, 2317, 2318* (DUKE), 20 Jan 1968, *Stone 2334A, 2335* (DUKE); ridge above Tapantí on precipitous road to Tausito, 4500 feet, 23 Mar 1968, *Stone 2342, 2343* (DUKE), 13 Nov 1969, *Stone 2718, 2718A* (DUKE), 8 Jun 1970, *Stone 2745, 2746* (DUKE); Muñeco on Río Navarro, 1400–1500 m, 6–7 Mar 1926, *Standley & Torres 50969* (US); La Estrella, 26–27 Mar 1924, *Standley 39446* (US); 4 km S of Muñeco on knoll between Río Patarrá and Río Sombrero, 24 Mar 1968, *Stone 2351* (DUKE); ca. 5 km S of Muñeco, above Río Sombrero, 9 Jun 1970, *Stone 2750* (DUKE).

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Editor's Note

The first eleven papers in this issue of the Annals were presented at the symposium "Plant Species Disjunctions, their Significance and Methodological Approaches." The symposium was co-sponsored by the American Bryological and Lichenological Society, the American Fern Society, the Pteridological and Systematic Sections of the Botanical Society of America, and the American Society of Plant Taxonomists. It was held at the joint meeting of the Canadian Botanical Society and the American Institute of Biological Sciences at Edmonton, Alberta, in June 1971.

The revolution in geological sciences brought about in the past few years by theory of plate tectonics affects the interpretation of many plant disjunctions. Biologists must constantly keep in mind not only past positions of continents when studying disjunctions, but factors affected by the position of continents, such as climate, must also be considered. The cover banner on this issue of the Annals is simplified from one of Alfred Wegener's reconstructions in the fourth edition of his *Die Entstehung der Kontinente und Ozeane* (an English translation by John Biram is available from Dover Publications). The three views show, from left to right, the Americas, Africa, and Europe in the Upper Carboniferous, Eocene, and Lower Quaternary.—*Editor.*

The Fifth Annual Jesse M. Greenman Award

The 1972 Greenman Award was presented at the Annual Banquet of the Botanical Society of America to William T. Gillis, Arnold Arboretum. The award winning publication is an exhaustive, broadly systematic study of two sections of *Toxicodendron*, "The systematics and ecology of poison-ivy and the poison-oaks (*Toxicodendron*, Anacardiaceae)" (Rhodora 73: 72–159; 161–237; 370–443; 465–540. 1971).

The Award of $250 is presented each year by the Alumni Association of the Missouri Botanical Garden. It recognizes the best paper in plant systematics based on a doctoral dissertation published during the *previous* year. Papers published in *1972* are now being considered. Reprints of such papers should be sent to Peter H. Raven, Director, Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110, before 1 May 1973.—*Editor.*

The previous issue of the Annals of the Missouri Botanical Garden, Vol. 59, No. 1, pp. 1–104, was published on 27 July 1972.

PREPARATION OF MANUSCRIPT

The ANNALS publishes original manuscripts in systematic botany and related fields. There is a charge of $25 per printed page to help defray costs of publication. Authors are asked to follow the suggestions below in order to expedite editing and publication. If an author feels that his manuscript presents special problems, he should write the editor concerning the best way to handle these before submitting the manuscript.

Manuscripts must be typewritten on one side of substantial weight paper, 8½ × 11 in. The manuscript should have wide margins and be double spaced throughout, including the abstract, footnotes, legends, tables, lists of specimens, and the bibliography. Tables should be typed separately and placed at the end of the text. Authors should indicate in the margins the approximate places for illustrations and tables. Submission of the original and one carbon or xerographic copy of the manuscript is desirable, and the author should also retain a copy of the final, typed draft.

Acknowledgements to granting agencies, herbaria, illustrators, and technical assistants may be conveniently placed as a footnote on page one. The author's full mailing address should appear as a second footnote.

An abstract must accompany each paper other than "Notes." The abstract should succinctly summarize the findings and conclusions of the paper and should be completely comprehensible itself.

A brief Latin diagnosis for each new taxon is preferred to a complete Latin description. A complete description should be given in English.

The citation of specimens should be concise. Geographic names are put in order of decreasing political magnitude. Only the barest essential data concerning each specific locality should be given. Collectors are cited by family name and collection number. If there is no collection number, the year of collection should be given. Herbaria are designated according to the current edition of *Index Herbariorum.*

Abbreviations should be checked for consistency and to make sure they are unambiguous. Periods are used after all abbreviations except metric measures, compass directions, and herbarium designations.

All illustrative material should be mounted on stiff cardboard. If the originals are too large to be conveniently mailed, photographic reductions should be submitted. The maximum size of a printed illustration is 5 × 7¾ in., and therefore, the height of an illustration must not exceed about 1.5 its width. Figures are numbered consecutively, since they are not printed as "plates." Numbering must be done with a mechanical device or with dry-transfer lettering and never by hand. The amount of reduction should be noted on the back of each illustration, together with the figure numbers, author's name and title of the paper. Photographs should be sharp, glossy prints. Numbering should be applied directly to the surface of the photograph. Several photographs may be assembled to form a composite block, and each photograph should be numbered separately. The individual photographs should be mounted with the interior edges flush. Line drawings are prepared with India ink and must never be placed in the same block with photographs. Authors wishing to have original illustrations returned must notify the editor when proofs are returned.

The bibliography should be compiled with care. The author should check to make sure each entry in the bibliography is referred to in the text and each reference to a paper in the text is entered in the bibliography. Citations of periodical literature should appear as follows: Author's last name, initial(s). Year. Full title of article. Name of journal. Volume: inclusive pagination. Names of journals are abbreviated according to *Botanico-Periodicum-Huntianum,* except *Journal* should be abbreviated *Jour.* and *Zeitschrift, Zeitschr.* Citations of books should appear as follows: Author's last name, initial(s). Year. Full title. Edition, if applicable. Place of publication.

Author will receive page proof. Since changes in proof are expensive, authors should not make revisions at this stage. Authors will be charged for alterations other than corrections of printer's errors.

Reprints may be purchased at cost plus postage. An order blank for reprints will be enclosed with proofs. A reprint price list is available from the editor.

All manuscripts should be addressed to the Editor, Marshall R. Crosby, Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

Publications of the

Missouri Botanical Garden

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The Annals of the Missouri Botanical Garden contains contributions mainly in plant systematics. The Annals appears three times a year, and three numbers, totaling about 400 pages, constitute a volume. Many back issues are available, and out-of-print numbers will be reprinted as required. All subscriptions to the Annals must be placed through Allen Press, Inc., 1041 New Hampshire, Lawrence, Kansas 66044. Allen Press also handles all claims for missing numbers and all orders for back issues. The prices below are strictly net; there is no discount to agents.

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NUMBER 3

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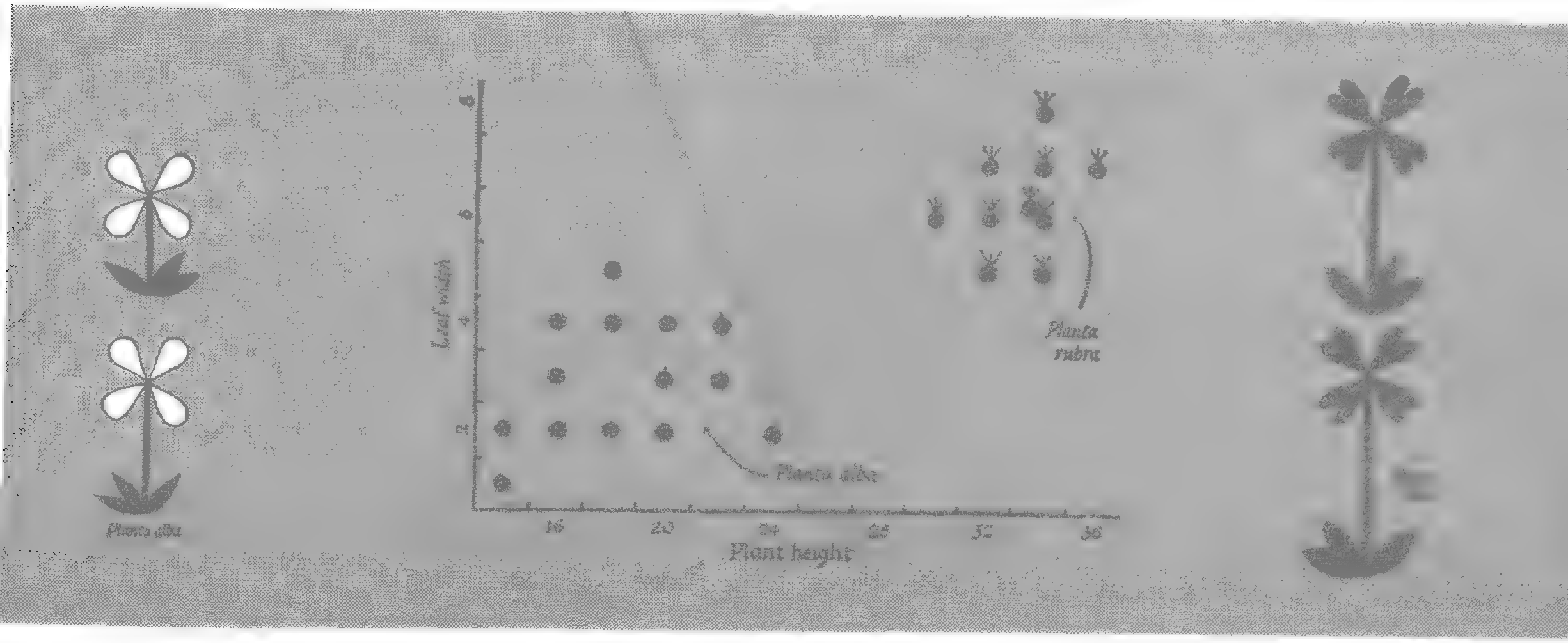
Missouri Botanical Garden



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The ANNALS contains papers, primarily in systematic botany, contributed from the Missouri Botanical Garden and the Department of Biology of Washington University. Papers originating outside the Garden or University will also be accepted. For information on preparation of manuscripts, see the inside back cover.

The ANNALS appears three times a year, and three numbers, totaling about 400 pages, constitute a volume. For information concerning *subscriptions*, see the back cover. Matters regarding *exchange of publications* are handled by the Library, Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

Published by the Missouri Botanical Garden Press, St. Louis, Missouri 63110.

ALLEN PRESS, INC. PRINTED IN U.S.A. LAWRENCE, KANSAS

This publication is dedicated to the memory of Edgar Anderson (November 9, 1897–June 18, 1969), lover of natural beauty and order; great scientist; good and gentle man.

This photograph was taken in 1966.

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I REJOICE IN WHAT HE AFFIRMED[1]

Several weeks ago we asked Edgar Anderson to write an article on conservation along the lines of the address, "Our Home for Generations," he gave at Illinois Yearly Meeting in 1965.

He accepted promptly and started to write it. He did not finish it. The beginning and some rough, penciled notes he apparently meant to incorporate were sent us by a colleague of his at the Missouri Botanical Garden with this note: "These were on Dr. Anderson's desk. He died June 18 of a heart attack."

So we have our own bequest from Edgar Anderson, the last words he put on paper, but the first (and therefore the most important) that came to his mind and heart as he began his testament of devotion:

"I began to attend Friends Meetings when I was a graduate student at Harvard right after World War I. Since my lodgings were at Jamaica Plain, I attended the Dorchester Meetings not far away. It had a pastor and a piano but long periods of silence. I was greatly moved by the long group silences with which the Meeting began and by the handshaking and kindly interests of the old people who sat next to us. One Sunday I persuaded a fellow graduate student to accompany me. When meeting was over, the old lady nearest to him shook his hand and said, 'Is thee a Friend?' He cordially answered, 'Not exactly; just a roommate.' I joined the Cambridge Meeting shortly before it moved to the Brattle Street location. The oldest member was Sarah Hallowell who attended regularly and sat well towards the front. The meeting was changing its character rapidly, and there were students of the social sciences who sometimes talked at length about burning issues of the day. One beautiful spring morning we had a completely silent meeting. Immediately after all had shaken hands, Sarah Hallowell rose tall and dignified and faced all of us, saying, 'This morning we have had the privilege, *the very rare privilege*, of a completely silent meeting. I have enjoyed it greatly and"

How Edgar Anderson meant to continue we shall never know, but we learned more about the wellspring of the article, its source, in the words Theodore H. von Laue wrote in The Saint Louis Newsletter of the St. Louis Meeting:

"The last time Edgar Anderson and I talked together—on Dorothy Nash's screen porch—we talked about trees, flowers, and weeds and about the tradi-

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[1] From the *Friends Journal* for August 1, 1969, page 419.

tional association of botany with Quakerism. Maybe it is easier to find 'that of God' in trees and plants than in human beings (Edgar, so Phoebe told me, took care of his plants every morning before he turned to human beings); maybe there is a secret affinity between all living things that men tuned to God become aware of. Nature and man's 'natureliness' have always been an inspiration for godliness; God's work happens at the still waters and in the well-nurtured order of gardens.

"Many a Sunday Edgar brought this source of worship with him into meeting, speaking of simple things, the blooming of a shrub in early spring, the loess soils at the confluence of the Missouri and Mississippi, or the effect of temperature on grasses. He also knew the folklore of roots and leaves and how to make Sassafras tea or lemonade from Sumac berries.

"It was a joy for young and old to go with him on nature walks. He was always brimming over with useful knowledge of all growing things; he was so on the day I last talked to him. The explanations attached to trees and plants in the Missouri Botanical Garden convey, with characteristic economy of words, his deep pleasure in imparting botanical knowledge.

"He was also unusually knowledgeable in the ways of the human spirit, with a fine awareness of the need for constant care and nurture. He was a complex man, fiercely ambitious as a scientist and sometimes sharp in his judgment, his spirit buffeted between rival impulses. But from meeting for worship, which he diligently attended, he had learned the arts of spiritual gardening.

"He knew from experience how to assist by deft controls the natural powers of growth, of peace, of silence, of God—in himself and in the men and women around him. In this manner he converted his remarkable intellectual powers into a spiritual gift as well—against considerable odds if my insight into his condition serves me right.

"As a scientist he has written his name legibly and visibly into the textbooks of advancing knowledge about the ways of nature. As a human being he has, through all who came to know him, woven himself into the cloth of immortality that shelters the passing generations from loneliness and despair. As I mourn his death I rejoice in what he affirmed."

EDGAR ANDERSON
1897–1969

JOHN J. FINAN[1]

Edgar Anderson's contributions as teacher and scientist were so great that a brief biography such as this cannot begin to do justice to the man who was as multi-faceted as he was outstanding. Here is presented merely a sketch of him that some later biographer, with longer time to research and write, with more documentation as Anderson's letters and other manuscripts are collected, and with the perspective of time, can fill out.

He was born November 9, 1897 in Forestville, New York. His father, A. Crosby Anderson, was administrator of a private school and his mother, Inez Evora Shannon Anderson, also from New York State, was the daughter of a general store proprietor and state legislator who had the distinction of introducing the earliest legislation requiring that Indians be counted in the census as whole persons. She had been trained in piano at the Boston Conservatory of Music, but because of early arthritis was not able to fulfill the promise of her talent and training. Her extensive record collection was to introduce the young Edgar to the music which was close to him for all of his life.

The Anderson family moved to East Lansing, Michigan, when Edgar was three years old. His father obtained a post in the Michigan Agricultural College as an instructor and later professor of dairy husbandry. Edgar's exceptionally high intelligence seemed to have been recognized early but not taken into special account in his rearing. His being able to describe in detail, from infantile observation, their home in New York must have made clear to his parents the prodigy he was. Later in life, during informal conversations with his students, he recalled his parents as stern and unbending and attributed to this apparent lack of understanding in the home some of the later insecurity he manifested. The wife of a colleague of his father's at Michigan State, Maude Marshall, "recalled young Edgar as a beloved boy who had very few friends indeed. His judgments were too sharp, and his tongue far from still."

His interest in botany was early. He told Anne Roe, who wrote of him as "Henry" in her volume *The Making of a Scientist* (Roe, 1952, p. 94–96):

> When I was 4 I was given some beans to play with, weevils got into them. I lived in an enormous Dutch house and in the spring when the frost was going out of the ground the man who came to deliver the wood left wheel tracks all over. So I planted the beans in the wheel tracks and then it rained. I may have patted down the dirt. Anyway I went away on a vacation and while I was gone the beans came up. At first no one could imagine what had happened in the front yard, and then mother remembered giving me the beans. They were all gone by the time I came home.
>
> When I was a child a brook ran in back of our house and a sandy beach, and I had a sandpile down there and when I was about 6, I was fascinated by the way people made geranium cuttings. I snipped off some of my mother's geranium shoots when she wasn't looking and carried them to my place by the creek and rooted them. I expected to be punished for doing it. I can still remember how astonished I was that I wasn't punished but mother was proud I had pulled off something like that.

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[1] School of International Service, The American University, Washington, D. C.

ANN. MISSOURI BOT. GARD. 59: 325–345.

> The next experiment I remember I was 8. I was always thrilled every spring with the things planted in the garden and always helped. Every year father had planted morning glories and nasturtiums. I had heard about hybridizing plants, and I decided I would hybridize nasturtiums and morning glories. I started out with typical and superb self-confidence. I took the morning glory seeds and pushed them into the seeds of the nasturtiums. I had no doubt that they would grow. I planted them in the edge of my wild flower garden. The morning glories didn't come up but some of the nasturtiums did, but even they looked a little sick. I expected either they would be morning glory flowers on nasturtium vines, or nasturtium flowers on morning glory vines, but I wasn't sure which they would be and that was one reason why I was so fascinated.

From the diary he kept during his last year of high school, he appears to have been limited in social life but dutiful in tasks, carrying on regular after-school jobs (emptying ashes, chopping wood, working in the college dairy), studying diligently (with special attention to Latin and physics), playing chess, taking private singing lessons, attending church regularly, and participating in church activities. His sports were tennis and swimming. Only rarely is there a mention in the diary of plants:

> [May 6, 1914] Went for greens and transplanted violets, ferns, etc. from woods.
> [June 3, 1915] Mr. Woodcock carried flowers to Botany Bldg for me. Got 100 on Botany test.

He entered Michigan Agricultural College (now Michigan State University) in the Fall of 1914, about two months before his seventeenth birthday. The high school pattern of regular outside work, diligent application to studies, dedication to church but only limited participation in student social activities, continued. Concerning these years, he told Anne Roe (1952, p. 98–99):

> I went through high school in 3 years at the principal's request. He asked Father. Father knew there would be problems when my emotional age was behind. I went to college at 16 and had great trouble because I was really emotionally a child. It was an agricultural college and had lots of boys from small towns and the entrance age was higher than now. I had all this terrific energy and a great interest in people and these things. It has prevented me from having any nostalgia for old college days. I didn't get into any fraternity so I founded one which became a stinking political influence in my alma mater. When I went to college I already knew I wanted to be a botanist, but I'm one in spite of my undergraduate work. It was sound stuff but not very attractively taught.
>
> My chief problem in college had been social adjustment. In an ordinary family it would not have been so hard but the rest were socially brilliant. Everyone adored Father, my mother was the reigning dowager and my brother was always president of his class and all that. But here was I, very calfish, especially seen against the background of my family. I tried to do things the way they did, that was just it. I'm like my father in some ways and like my mother in some so I couldn't do things the way either of them did. It's just experience that has taught me I'm different. I didn't feel different. An old lady I met when I was in the navy taught me to just go ahead and be myself.
>
> At college I would have rated below 100 in popularity in a class of 150, but in graduate school I was very happy most of the time. My thesis was not particu-

> larly interesting; the topic was largely a question of what was available. I don't think it did me any harm and it did give me an insight into a certain field. The main thing was that they left me alone.

The yearbook of his senior year, *1918 Wolverine*, lists him as a horticulture major. He was Associate Editor of the College newspaper *Holcad*, active in the Horticulture Society, and elected to Sem-Bot, the honorary Botanical Society. His college nickname "Theda Bara" was given him perhaps in early recognition of the theatricality (or "showmanship" as some of his colleagues termed it) which he frequently manifested to color the unconquerable shyness only intimates perceived.

Following graduation from college, he entered the Naval Reserve and, not long afterwards while still a reserve Gunner's Mate Second Class, was admitted to a new and remarkable graduate school at Harvard, the Bussey Institution. Located in the University's Arnold Arboretum, which was away from Cambridge in the Jamaica Plain section of Boston, it offered a doctoral (Sc. D.) program in Applied Biology. The Bussey was an institution where, as Reed C. Rollins, the present director of the Gray Herbarium at Harvard, recently noted:[2] "independence of mind and action were the hallmark of the faculty and students alike. Every person there was put on his mettle from morning 'til night with the result that nearly every person trained at the Bussey was an individualist first and anything else he might be afterwards." Anderson (1940), himself, in writing about the institution later in an obituary essay on his mentor there, Edward Murray East, called the Bussey "one of the most successful experiments in higher education which has yet been undertaken in this country. A few brilliant biologists, East, Castle, Wheeler, Brues, Ames, and Bailey, were associated informally with a small group of students in an antiquated building far enough removed from the rest of the university to permit the development of group individuality. There was little expensive equipment; when apparatus was needed it was constructed insofar as possible from the materials in the ancient stock room, but there were ample opportunities for growing experimental plants and animals and a rather complete freedom from institutional red tape."

In the same essay, Anderson tells of meeting East, who had been trained as a chemist and shifted to corn breeding:

> I have a very vivid memory of my first meeting with him when I came east to begin graduate work in the spring of 1919 . . . . I knocked and there was a sharp, clear "come in!" Facing me across the desk was a neatly dressed middle-aged man of average size, whose strong features threw into high relief his direct, determined, impersonal stare. He welcomed me pleasantly and in a quick, business-like fashion arranged details of residence, instruction and research. He was curt but considerate, and increased my confusion by treating me as an equal.

Some typical diary entries from his years at the Bussey are these:

> Tues. Jan. 20, 1920. Spent most of the day in greenhouse and Dr. East's office going over the seeds and seedlings with him. Seminar in the afternoon. Dr. Castle spoke on linkage and seems to have come around almost completely to Morgan's view. Grand free for all discussion—Dean Wheeler vs. Everybody Else.

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[2] Letter to author from Reed C. Rollins.

Richard Anderson, Edgar Anderson's brother, in ROTC wartime uniform; A. Crosby Anderson, his father; and Edgar Anderson, just released from the U. S. Navy as a Gunner's Mate, Second Class. Photograph taken in 1919.

Friday, Jan. 23, 1920. Went over to the Arboretum in the morning to see Prof. Jack about reversion. Spent so long going through the herbarium that I was late for dinner.

Thursday, Feb. 12, 1920. Early to breakfast for a wonder. Early at work in the greenhouse getting plants ready to pollinize. Brot in tulip to Miss Moore. Talked over several matters with Dr. East. Sent out cards for Experiment Station Bulletins. Made list of crosses to try. . . .

> Thursday, July 8, 1920. . . . Richard Crook stopped here on his way home and after a shower we took our lunch out in the open fields and combined supper and Gray's Manual. I came back, identified a plant or two and talked with Jenkins.

> Sunday, Dec. 5, 1920. I wonder if I ever will reach that desired perfection when I shall rise on time each morning, take my cold shower unflinchingly, eat no more than is good for me, and keep my house in order. If I were to do that now there would be little effort left for anything else.

Only rarely was he given in his diary-writing to broad philosophizing, such as in the following very polished entry which perceptively sensed the arrival of the "Roaring Twenties":

> Sunday, Nov. 14, 1920. Our progress is not a steady march but we are swung along in mighty surges, til the great mean is overbalanced and we come thundering back with such momentum that the center is again over-reached and the reaction sets up its counter reaction. Thus we find disgust in the excesses of Victorianism awakening a healthy cynicism that has waxed so great that I begin to recognize about me the awakening protest that shall carry us back the other way.

As noted in an earlier quote (page 326), graduate school was a fairly happy time of life for him. What is very clear from his graduate school diaries is his love of the countryside. Perhaps it is in the incessant walks and hikes, mentions of which abound in the diaries, that some clues are offered to his later articulated conviction that the entire natural environment—rather than laboratory genetics or herbarium taxonomy—provides the most fruitful context for the study of plant variation. Whenever he could get away from Bussey graduate research tasks or from his teaching assistantship in botany at Harvard College, he took to the fields. In March 1921, a year before he obtained his doctorate, he confided to his diary:

> March 19, 1921. What a guilty feeling always comes over me when I have to confess that I am walking for the fun of it—because I enjoy walking. I occasionally take refuge as today by saying that I am a scientist doing some field work, but even at that I feel like a child caught in the jam pot.

His account of one of these hiking trips, taken in June 1921, just after the end of the school year and before he was off as a Counselor at a boys' camp in Maine, has been preserved. The following excerpts communicate liltingly his Thoreau-like joy in the out-of-doors.

> South Station, Boston, Midnight, June 2, 1921. My train leaves in four hours and I sit alone in the great waiting room, feeling like a very small little boy setting out alone into a very large, cold cruel world. This will pass, I know, when the sun comes up and afoot and light-hearted I take to the open road.

> Friday afternoon, June 3rd, 1921. Between Great Barrington and Sheffield. Below me flows the placid Hausatonic, almost as dirty as own Red Cedar; across the wide and fertile valley rises the grey blue dome of Mt. Everett; and in the distance, faintly outlined against the sky, rises Bear Mountain, climbed last September. I left the train at Becket and utilized the cool morning hours to good advantage,

> making three miles an hour across hills via roads that were seldom more than cat tracks. Mountain laurel, fragrant pink azaleas, and a pair of oxen plowing, made the walk more interesting. At East Lea a truck picked me up for the short mile but at South Lea a benevolent, but slow-moving meat truck took me in and carried me thru the beautiful summer towns of Stockbridge etc. to Great Barrington where I turned off from the main road to follow this river road. I took a three-minute dip in a forest-girt pool this morning and bathed my feet this afternoon. These rock out crops are interesting to me. I wish I knew the language in which they are written (Idea for boys' talk-diary).
>
> Saturday, June 4th 1921. 7:30 A.M. Canaan, Conn. After writing you [diary] the other afternoon I sauntered on a mile or two, passing pleasant comfortable farm houses where the cattle were first being brot up to be milked. I picked out a trim little house with a neat lawn and asked if I might sleep in their barn and if they would sell me some supper; that I was "sane and respectable" in spite of my get up. Permission being granted I helped Mr. Cahill and his high-school boy son to put the cattle in the barn (note for father—they were grade Holsteins and the stable shone with white whitewash.) . . . . After supper I milked two cows, played mumble-ty-peg with Harold, and sat on the piazza until dusk. Harold, finding that I was guilty of an Agricultural College education, in a mildly kidding way asked me what new farming wrinkles I had picked up in college. I told him we learned to plant potatoes and onions in alternate rows; this made the potatoes' eyes water and irrigated the potatoes. His Dad seemed to think I had the laugh on Harold and chaffed him about it. I departed for "bed" at nine, in spite of earnest entreaty to use a real bed in the house. . . It thunderstormed during the night but started to clear up when I started at 5 and the air is now fresh and cool and the mountains in their new spring duds, are a bright light green. . . .

Although he was especially devoted, in graduate school, to his principal professor, Dr. East, he seems to have been fascinated by, but at the time not fully appreciative of, the Economic Botany course at the Bussey given by Oakes Ames, director of the Harvard Botanical Museum. It was only much later, as Anderson acknowledged in *Plants, Man and Life* (1952), that he gave importance to Ames's provocative questions about the origins of cultivated plants—questions that Anderson 20 years later was to seek to find answers to in his own research on maize and in that of many of his students on sunflowers, amaranth, tomatoes, rubber, beans etc.

The person at the Bussey who turned out ultimately to be the most important to him was a young laboratory assistant to Dr. East, Dorothy Moore. She had been trained at Wellesley, and was completing Master's work in botany there while assisting at the Bussey. Edgar met Dorothy, as their daughter remembers the story, when Dorothy berated him for leaving a microscope dirty from staining. He courted her for two years, bringing her flowers (see diary entry of Feb. 12, 1920 above) and taking her on hikes. They were married in 1923. Totally uncontrived, of quiet but keen intelligence, and always glowing with absolute inner goodness, Dorothy Anderson provided unfailing support in a union that was to last 46 years.

After his degree completion at Harvard, Anderson was invited to join the staff of the Missouri Botanical Garden, which had, through the Henry Shaw School of Botany, a tie with Washington University. His adjustment to life in St. Louis seems to have been quick not only because he was reared a mid-Westerner but because St. Louis, like Boston, maintained cosmopolitan intellectual and cultural values, while not foregoing provincial charm. The director of the Garden, George T. Moore, who was responsible for Anderson's going to St. Louis, had, like Anderson, been trained at Harvard. George H. Pring, for many years superintendent of the Garden, has recalled Anderson's arrival in St. Louis:[3]

> Dr. Moore said to me that he was bringing a young geneticist from Boston for an interview. He asked me to show him about the Garden and to acquaint him with the city. After doing this, I took him to Ruggeri's for a meal. After eating, I asked if he had ever tasted our famous German cheesecake in St. Louis, and he said he hadn't. So he ordered a large piece of cheesecake and consumed it with gusto. Ever after he made reference to his first impressions of St. Louis centered around that cheesecake.

Anderson held three posts during those first years in St. Louis: an assistant (later associate) professorship in Botany at Washington University, geneticist to the Garden, and director of its School of Gardening. Emmet Layton, now in landscape architecture at the University of Wisconsin, Green Bay, who was studying at the Garden in this period, recalls:[4]

> Even in the somewhat alien field of the Henry Shaw School of Gardening, [Anderson] contributed as much to his students as did the more appropriate Landscape Architect John Noyes. Where John taught techniques, Edgar taught scholarship and the love of learning, along with an empathy with the earth itself.
>
> He also had a genius for giving succor in serious situations which might otherwise have demolished the individual. He could rescue a failing student by sheer force of his own vast energy and a determination to teach. He also made sure there was no exaggerated sense of obligation. Where his gift was beyond price, he always found a way for the recipient to contribute something, in return for which Edgar would express sincere gratitude. When I found advanced mathematics as impossible to learn as Sanscrit, Edgar not only resorted to absolutely Herculean methods to teach me so thoroughly that mathematics became a lifelong part of my personal vocabulary . . . but he arranged for me to drive him home to Webster Groves after those long night sessions and thanked me profusely for a performance I naturally regarded as a privilege.
>
> For Edgar opened the entire future for me, and led me through doors I could never have entered without him. Without his help I would never have been able to enter the School of Architecture at Washington University, since I would have found the entrance examinations quite beyond my capacity. In turn, Edgar was careful to explain how much he appreciated my own skill in graphics presentations, in producing and interpreting plans which he always claimed he could never understand without a model—though he could take any blueprint and read it like a book, provided it applied to something in which he took a special interest.

From the point of view of the history of science, these first years of Anderson in St. Louis are important because it was during them that there was developing the interest in "biosystematics," as it came to be called, which was to provide the framework for most of his later research. Unfortunately he did not keep diaries during most of this period, and it was a time when he published very little.

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[3] Letter to author from George H. Pring.

[4] Letter to author from Emmet Layton.

He once said to me, although I did not realize the full significance of his words until the preparation of this biographical essay, that it was during this period he very consciously decided not to publish but to *think*. Out of those months and years of reflection, and frequent visits, as Layton remembers, to "the vast fields of wild iris beyond the city of Saint Charles, in the Missouri River flood plain," emerged his now classic papers on speciation in *Iris*.

The development of Anderson's thought leading to his discovery of the important role of backcrossing ("introgressive hybridization" as he termed it) in the evolution of natural populations and cultivated plants and his devising of means to analyze and measure it, can be traced only superficially here. His going in 1922 from the Bussey Institution, where he had majored in genetics, to the Missouri Botanical Garden, which had an historic strength and distinction in taxonomy, probably was fortuitously influential in stimulating his interest in the rich but largely unexplored area between the two fields. Too, his mentality was conducive to such a research direction; he frequently referred to his "summarizing mind" which was indeed highly classificatory but was at the same time distrustful of "labels" and was provoked by the analytical preclusions which he felt they often imposed. Also, his natural bent for turning associations with colleagues and students into mutually creative experiences must be taken into account.

The Garden staff and students whom he came to know in the years 1922 to 1931, when he returned to Harvard, contributed significantly to his scientific growth. The Director of the Garden, George Moore, administered the institution urbanely with a great tolerance for creative individuality. Anderson consulted with Moore frequently, as attested in the diaries, about professional and personal problems and always found understanding. The Curator of the Garden Herbarium, Jesse Greenman, austere and reserved but receptive to all serious inquiry, counseled Anderson as he explored the genetic significance of taxonomic groupings. His debt to Greenman is acknowledged in a survey article published shortly before Anderson's death (Anderson, 1969):

> This review is dedicated to Dr. J. M. Greenman, former Curator of the Missouri Botanical Garden Herbarium and my colleague during much of the time these studies got underway. In answering my naive questions about the species problem, he frequently quoted to me the statement "Species are but judgments." It was due to him that I became fascinated with the problem of finding factual evidence as to the ways in which such judgments are formed.

Among the students of this period who proved to be especially influential on Anderson's thinking was a graduate student at the Garden, Robert Woodson, who had majored as an undergraduate at Washington University in Romance Languages but shifted to Botany after taking courses with Greenman and Anderson. Only about six years Anderson's junior, and like him, finding joy in nature and the out-of-doors, Woodson established a friendship with Anderson which was more that of peer than student as they went on countless field trips together. Both intensely sensitive as well as highly intelligent, they were nevertheless in many ways unlike; and their association, which was to continue for four decades after Woodson joined the Garden staff, was, while mutually creative, often turbulent. It was perhaps only to be expected that the perfectionism which was characteristic of Woodson and the individualism which was a strong trait of Anderson would create explosive tensions. Anderson records one such clash in his diary for February 22, 1929:

> Today I started in earnest to work out the taxonomy of the spongy-seeded Irises. A good part of the day was spent copying references out of Dykes and getting them smoothed out and on to a systematic arrangement of cards. Bob [Woodson] and I performed petulantly at lunch. He ended by washing my face in my lettuce salad—a most disgusting sight.

Two days later all had blown over and they were off again on a trip to the field. Out of these trips and collaborative research was produced their monograph on the United States species of *Tradescantia* (Anderson & Woodson, 1935). More importantly, it was as a result of work with Woodson that Anderson made his discovery of introgressive hybridization, as he has acknowledged (Anderson, 1969):

> In his Doctor's thesis my colleague Dr. Robert E. Woodson published an interpretation of the phylogeny of the genus *Apocynum* which was decades ahead of its time. He envisaged it as a genus in which inter-specific hybridization has been so important that its evolutionary pattern is more like an anastomosing network than a branching tree. To me his ideas though stimulating and interesting, seemed rather in need of experimental confirmation by other than purely morphological criteria. After much friendly argument an experiment was planned, a simple progeny test of two common American species, *Apocynum cannabinum* and *A. androsaemifolium*, strikingly different plants, and their putative hybrid. It confirmed all his hypotheses, including some I had been skeptical about. . . . [It] also presents evidence for a phenomenon that I do not remember having talked, read or thought about up to that time, the various restrictions to free recombination of multiple-factor characters which operate in hybrid germ plasms. . . . It was these experiments with *Apocynum* which led me to examine the general restrictions to recombination in multiple factor characters and eventually to describe, define and diagram introgressive hybridization.

After the mid-1930's, the research interests of each became distinct and their relations, especially after Anderson became Director of the Garden in the 1950's, very strained. To the end, however, Anderson always spoke of his former student with affection and respect.

Crucial to the development of Anderson's thought leading to his hypothesis of introgressive hybridization and to the establishment of its importance in evolution were the methods he worked out to note and quantify character variation and associations in plants. Mildred E. Mathias, who was a student at the Garden in the late 1920's and is now Professor of Botany and Director of the Botanical Gardens-Herbarium, University of California, Los Angeles, recalls Anderson's early measurement techniques:[5]

> Edgar was my genetics teacher and at that time was completing the field studies on his treatment of *Iris versicolor* and *I. virginica*. The four of us in the class did many of the measurements of the flowers and night after night I carried home a quart jar of iris flowers in formalin. From these measurements he developed the "ideograms" and I can remember his delight at finally finding the right word

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[5] Letter to author from Mildred E. Mathias.

> to describe the stylized iris flower parts. It was this same fertile mind which led to the many other pictorial methods which he devised to illustrate variation in plant populations, methods which are now so commonly used that many do not realize that it was Anderson who started it all.

The "ideograms" or ideographs were introduced in Anderson's seminal paper, "The problem of species in the northern blue flags" (Anderson, 1928). These early methods were later elaborated to his "whiskers" technique which allowed for measurements and depiction of four characters in a scatter diagram, as Anderson (1952, p. 93–94) himself explained:

> By the time Dr. Woodson and I had finished monographing the American species of *Tradescantia*, it was evident to both of us that hybridization between the various species might well be of evolutionary importance in that group of plants. In those days there was a good deal of argument going on about this subject, much of it merely the voicing of opinions by biologists who had been studying other matters but had had some opportunity to observe hybridization or the lack of it. It seemed to me that instead of just arguing it would be better to set up some kind of a method for measuring the effects of hybridization. Postponing the fascinating question of whether or not hybridization was generally important in evolution as a whole, I began to work out ways for measuring what it was and was not doing in our spiderworts. . . . Eventually a simple and generally applicable technique was worked out. . . . One of my assistants always referred to it as "whiskers" . . . and that term is still used informally around the laboratory. However, such sprightliness is not considered good form among scientists so when it was finally formally published it was described under the mouthfilling phrase of "pictorialized scatter diagrams."

Fundamental, of course, to Anderson's success with these measuring techniques, however ingenious, was what David M. Gates, who became director of the Garden in the 1960's, called Anderson's "unique perception." As William Brown, Anderson's student and close associate for almost three decades in corn research, has noted:[6]

> One of the things I admired most about Edgar's scientific approach was his emphasis on what was biologically important. He had an excellent grasp of statistics and its use, yet his unique ability to search out critical traits with which to work and his emphasis upon the kinds of differences that delimit species and varieties, usually precluded the use of statistical methods to measure significance. . . .

In Anderson's paper "The species problem in *Iris*" (1936) and the aforementioned "Hybridization in *Tradescantia* III" (Anderson & Hubricht, 1938) are the fruitful hypotheses which are his greatest contributions to science and which guided almost all of his later research. As he summarized his work in a draft inventory of his professional interests written about 1957 and fortunately preserved among his papers:

> . . . . My basic professional discovery has been how to measure evolution in progress by analyzing variation between individuals so effectively that one could pre-

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[6] Letter to author from William L. Brown.

> cisely determine its source. From work on the species problem I have moved on to the classification and the origin of agriculture. This has led to studies on the importance of hybridization in evolution, particularly in a cryptic way through successive back-cross (introgression) to the original species. Gradually I learned to depart from conventional statistical methods, to analyze species differences exhaustively at a morphological level before taking up quantitation of these differences.

Thus it was that during Anderson's first years at the Missouri Botanical Garden—in the 1920's— the scientific interests which became the basis for all his later major contributions were firmly formed. At the end of the decade, he received a National Research Fellowship for study in England. He worked during the academic year 1929–30 under the guidance of J. B. S. Haldane and studied cytology with C. D. Darlington at the John Innes Institution and statistics with R. A. Fisher at Rothampstead. There is recorded in his diary his first impressions of Haldane and Fisher:

> Oct. 16, 1929. . . . After dinner, I wrote letters to all the people suggested by Murrill, and a couple others stationed at Lake Baikal, begging for seed of *Aquilegia.* I was just finishing up on this job when J. B. Haldane came. We had a long conference and he was most encouraging in regard to the possibilities of my data and suggested extending them by something of the sort on *Primula sinensis.* Dr. East had said he was large—but I had failed to anticipate. He reminds me of a large St. Bernard or Newfoundland. Big and bulky, rough tweedy clothes, scrizzly hair (such as there is) & general air of being difficult to comb. At tea Miss Pellow remarked that she wanted someone meek and industrious to score plants for her. J. B. S. H. said to apply to some Catholic father for a Catholic Botanist who needed to do penance.
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> Nov. 5, 1929: Out to Rothamstead on the ten o'clock train to see Dr. Fisher. At the lab there had been some mix-up and I had to cool my heels for two hours in the marble entrance hall. At length he appeared, short, slight, with greying hair, and a full beard of silky brown. All this one notices as he comes in and as quickly forgets as soon as talk has started. He took me home to dinner. . . . In criticizing *Martin Arrowsmith* he said that S. Lewis had exaggerated the artist, in Martin the scientist—that a real scientist would have had more effect upon his assistant's habit of thought and habit of work. In the afternoon I went over my data with him and made plans to come up in February for the whole month. Until then I shall work on Calculus and get my data into shape.

He returned to the Missouri Botanical Garden in 1930 and remained there for one year when he accepted an appointment as Arborist at the Arnold Arboretum, where he remained on the staff until 1935. These were, on the whole, frustrating years for him because, as his daughter recalls, the large number of speaking and other public service obligations at the Arboretum did not allow him to pursue his research interests. Indeed, the press of duties became so great that, as Dorothy Anderson's diary records, he suffered severe exhaustion in the Spring of 1934. He went with his family to England in July, 1934 and he spent August and September on a collecting trip to the Balkans.

His interest in the Balkans stemmed from his belief that the U. S. climate is duplicated there more approximately than anywhere else in Europe. He brought back rooted cuttings of Balkan strains of ivy, yew, and boxwood, expressing the hope, in a report to the U. S. Department of Agriculture, "that these strains, coming from a climate so similar to our own, will prove more adaptable to American conditions than have those already imported from northern Europe." His hope was fulfilled far beyond expectations by the popular acceptance of his introductions, especially the Balkan ivy, in many shady gardens in the United States. For this work in international botanical cooperation, he was awarded the Order of the Yugoslavian Crown in 1937.

With his return in 1935 to the Missouri Botanical Garden, he continued, as mentioned above, his earlier work with *Iris* and from his studies of *Apocynum* enunciated his hypothesis concerning introgressive hybridization. In 1939, from studies of character recombination in the second generation of a semi-fertile cross between two very different species of flowering tobacco, he demonstrated the importance of linkage and the partial association in the progeny of all the multiple factor characters going into the cross (Anderson, 1939). This study of hybridization of two very dissimilar species of *Nicotiana* coincided with the publication, by his old Bussey roommate, Paul C. Mangelsdorf, and R. G. Reeves (1939), of a demonstration of another wide cross, *Zea mays* × *Tripsacum*. Their resulting hypothesis that *teosinte*, rather than being, as widely believed, the putative ancestor of Indian corn, was in fact a hybrid of maize and tripsacum, stimulated Anderson's interest in variation in these plants.

A new focus of research thus began. For the next decade and a half, Anderson launched a series of studies toward a natural classification of maize. While he drew upon the important hypotheses and measuring techniques he had developed earlier, he knew relatively little about the corn plant when he started this research. With typical lucidity and simplicity, he has described how he began his study of maize (Anderson, 1952, p. 211):

> . . . to understand maize one would have to know something about grasses in general. I knew next to nothing about them technically, so I began in the simplest, most fundamental ways I could put my hands on. The English morphologist, Mrs. Agnes Arber, had just published a general volume on grasses. I read it from cover to cover. It seemed so simple that I wondered at her writing so elementary a book, but as the months went on I began to realize that like a good sonnet the book had more than just words—it transmitted an attitude, and with new attitude one could look down whole new vistas of experience, and old facts took on new significance.
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> After these new ideas had seasoned for a few months I acquired another book, also deceptively simple . . . Mrs. Agnes Chase's *First Book of Grasses*. . . . With this remarkable little book and a hand microscope I retired to the country for the summer and learned how to identify all the wild grasses of a small area. I found, to my joy, that though most botanists consider grasses difficult to understand they are really quite simple. The trouble springs merely from the fact that they are specialized. Their leaves look rather like the leaves of other plants and their roots are obviously roots but the rest of the plant, including the tassels, is so very peculiar that a familiarity with ordinary plants is not much help in understanding it. With Mrs. Chase to guide me these troubles disappeared and by the end of the first summer I could see that I was getting real insight into these curiously specialized plants, many of which man has used for so many thousands of years.

Recognizing thus the close relation of maize to man, Anderson sought to broaden his knowledge and understanding of ethnobotany and historical geog-

Edgar Anderson in 1948, in the laboratory where he accomplished much of his important work on plant evolution and variation.

raphy by using a Rockefeller grant in 1943 to study with Carl Sauer, the distinguished geographer at the University of California. This grant was followed by a Guggenheim award which allowed him to make a preliminary survey of maize in Mexico. It was typical of the man that he sought to undertake, essentially alone, the enormous task of a natural classification of maize in Mexico. That this goal could not be attained by any one man but ultimately by a team using the extensive resources at the disposal of the Rockerfeller Foundation is significant only to the extent that if Anderson had not begun the task, its completion would have been considerably delayed. His experiences in Mexico are touched upon in *Plants, Man and Life.* What is notable about them is that he manifested the same respect for and search for understanding of Indian behavior as he did for plant variation; his analysis of the logic behind an Indian garden, for example, is an ethnobotanical classic.

The breadth of his concern in following years with almost all aspects of maize can be noted in the wide range of specialists with whom he collaborated: archaeologists, anthropologists, geographers. It can also be noted in the very large number of articles on maize which he produced by himself and with collaborators, as cited in the bibliographical article included with this issue of the ANNALS. He was aided in his corn research by his informal association with the Pioneer Hi-Bred Corn Co. of Des Moines, Iowa. He spent parts of many summers at the Pioneer research center in Johnston, Iowa, where, with his former student, William Brown, now Pioneer's vice-president for research, he carried on a great part of his investigations. He summarized, on a scrap of paper—perhaps for Garden public relations requirements—the results of his research:

> He discovered that corn is made up of hundreds (but not thousands) of intergrading races and worked out most of the methods for classifying them. He worked closely with professional hybrid corn companies in demonstrating the value of these methods and discoveries in the continuing improvement of hybrid corn. . . .

In a larger sense his research on maize reiterated the validity, through his interdisciplinary breadth of focus, and through his humanistic concern for showing the mutually influential relation of plants and man, of his oft-stated conviction that knowledge is all of a piece.

Equaling his distinction and achievements in scientific research was his great talent in teaching. His fundamental educational philosophy was the ancient, Socratic one in which the teacher's role is maieutic. He loved to arouse and draw out latent creative intelligence, whether that of doctoral students or of garden club women; and his permissiveness (an excellent example is cited in Charles Heiser's essay in this issue of the ANNALS) must have frequently shocked colleagues and irritated administrators. He gave particular attention to bright "undisciplinables"—persons whose interest or curiosity had never been whetted enough or whose intelligence never appropriately challenged for creative achievement. It seems to have mattered little to him whether a learner had much formal education or not; the formal degree-granting system he frequently characterized as "red tape" and having little to do with real learning. It is significant in this regard that one of his most important papers, "Hybridization in *Tradescantia* III. The evidence for introgressive hybridization" (Anderson & Hubricht, 1938), was prepared in collaboration with a gifted young man without formal university training.

Many of the comments which Anderson made about E. M. East's teaching abilities apply to himself. "All of his students," he wrote of East, "learned to judge scientific theories on their merits and without reference to the eminence of their sponsors." Further, ". . .like any great teacher he treated his students as individuals. The work of some was closely supervised; others were left largely to their own devices, even when they produced no immediate results" (Anderson, 1940).

Anderson manifested the vigor of a Renaissance scientist battling the scholastics in his determination to remove any unexamined theory that interposed between the student and observable nature. As Harold J. Kidd, who studied with Anderson in the 1950's remembers:[7] "A frequent remark made (by Anderson) when I would mention someone's opinion supporting one of my own: Is that necessary to feel sure you are right?" One teaching technique of Anderson's—perhaps learned from W. J. Beall at Michigan State—was to ask students to write up their observations immediately without recourse to relevant literature. For some of his classes he would distribute at the first meeting "free textbooks" in the form of twigs. It was exhilarating for the neophyte to have Anderson's confidence-inspiring comments on what had been observed. However myopic they might have been, he stimulated all of his students toward keen and independent "eye-mindedness," and, ever after, their view of the world was sharper and more clearly their own. As expressed by Russell J. Seibert, who studied at the Garden in the late 1940's:[8]

> I can think of no one who ever caused me to open my powers of observation, both to look and to think, more than he. Plants to me became animate objects capable of communication, of telling a lot about themselves only after he made me realize that the answers to many of my taxonomic problems were there shown by the very plants I studied, if only I would take a new look and analyze their characteristics with an open and uncluttered mind.

Anderson's relations with students were mutually creative, as Seibert further remarks:

> Any achievements which he accomplished in research were motivated by his association with his students. His enthusiasm was easily caught up by his students who in turn further motivated his very active mind. He was never happier than when with his students or with a responsive audience with whom he could sound out his thoughts and stimulate discussion.

Anderson delighted in taking students to the field and asking them to reconstruct the natural history of an area. He described his approach (Anderson, 1956):

> . . . . I hit upon an exercise so effective that I used it year after year. . . . I selected a big white oak tree and, leaning against it, addressed the class somewhat as follows: "It is just over a hundred years since this hillside was first taken title to by pioneers from Virginia. In that time many things have happened on this site. . . . Now your assignment for the next hour is to find what were the main steps in vegetational change on this site in the last century. You can solve the problem with no more technical equipment and no more botanical training than you now have. . . . What has happened here in a century? Don't neglect any kind of evidence, just because it seems trivial. The world is full of easy keys to important problems; only once in a while does a genius come along and label these trivial keys as significant evidence. . . ." . . . .In twenty years I have had just two students who had the wit to notice that all the time I was talking to them my left hand was playing

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[7] Letter to author from Harold J. Kidd.

[8] Letter to author from Russell J. Seibert.

> idly with a scrap of barbed wire which sticks out an inch or so from a scar on the big oak. Off to the left about thirty feet is another tree with a similar scar, though without any barbed wire, and way off to the right in more or less of the same straight line, is another oak with two such horizontal scars, one about a foot above the other. There had, you see, been a wire fence strung through the woods, using the trees as posts. When the land on both sides of it was acquired for an arboretum, the barbed wire was most removed but it had stayed in place so long that some of the trees had buried it in their bark. This was more than just a fence row; it was a section line, the boundary between two farms which had been differently managed. One had been cut-over and fairly heavily grazed; the other family had taken out a tree here and there. . . .One was almost as certain as if he had been present that this was indeed an old fence line between two fields one of which had been cut over and the other not. One's mind and eye worked back and forth from data to hypotheses, then back again to data. Inductive and deductive reasoning tripped so closely on one another's heels that they were one simultaneous process. . .The properly trained scholar looks around for significant repeatable patterns in the data and reasons back and forth from observation to hypothesis until he has found his way into it. The finicky pointer-reading data, single-sense impressions, lengths, widths, weights, so useful for precise analysis, are best deferred until we know what kind of a problem we are up against.

His teaching methods and philosophy lent themselves more effectively to work with individual students or with small groups. The experience of Emanuel Rudolph, who was a student at the Garden in the early 1950's, is typical:[9]

> I am sure that others have had the experience I did when working on a joint paper with him. While I was doing my thesis he came to me one day with a proposal for an introgression paper on lichens. After getting started, I would work a week on the data and take the results to him. In a few minutes he would have ideas for at least two more weeks of work and notions for several other related projects. Andy was an idea man and I cannot count the number of his ideas that I have incorporated into my thinking.

Stories are legion of Anderson's generosity to students—kindnesses carried out in a way that tried not to let the right hand know what the left was doing. Henry Andrews, Anderson's colleague, recalls:[10]

> This happened quite a few years ago when we had a young man. . .who was working at the Garden and was a Master's degree candidate as I recall it. He lived in the Boston area and had planned to go home for Christmas but a day or two before his departure date (on the train) he came down with a very bad cold. He had little in the way of funds and had a coach ticket; Andy knew this and knew that a 30-hour train ride sitting in a coach is not the most pleasant experience. Andy gave me a $10 bill (or maybe a $20) and told me to go to the RR station in St. Louis and get the student a first class ticket and berth, take him to the train and put him on, all of which I did. The student was so sick that I don't think he cared for much of anything but getting home for Christmas, and I don't know whether he ever knew what Andy had done. I rather think Andy did many things like this.

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[9] Letter to author from Emanuel Rudolph.

[10] Letter to author from Henry Andrews.

Dr. and Mrs. Anderson on the patio of their home, the Cleveland Avenue Gatehouse in the Missouri Botanical Garden, in the early 1950's. Here students, colleagues, and friends received a uniformly warm reception and hours of stimulating conversation.

Emanuel Rudolph remembers another example of Anderson's generosity:[11]

> Andy was a person who could be embarrassingly generous. Although I was not his student, he took me under his wing as he did so many students. I remember talking with him about my desire to take a particular course at the Scripps Oceanographic Institute if I could afford to do so. He immediately insisted on giving me the money to take this summer course. I tried to refuse his offer to no avail. Fortunately for me, the course was filled and I did not have to make a decision about accepting his offer.

He took special delight in working with those who loved plants but who had no specialized or professional training. While at the Arnold Arboretum in the early 1930's, he founded in Boston the Herb Society of America, "with a small group of Boston Back Bay dowagers" as he referred to them. He became the Society's president in 1935. He organized, with Mary E. Baer, a St. Louis branch in 1941. "He called us all his herb ladies," she remembers,[12] "and dispensed his doses of herbal knowledge to his would-be herb savants." Another recollection is that of Mary A. Gamble, who joined the St. Louis group in the 1950's:[13]

> Dr. Anderson was simply tremendous with volunteers and amateurs. He credited any reasonably intelligent and energetic person with the ability to do some pretty intricate work. . . . He kept a sharp eye on the herb garden given to the Missouri Botanical Garden by the Herb Society and it was not unusual to get a call from him saying that such and such a plant was labeled incorrectly. . . . He was pragmatic and inventive. I remember one spring, when as always, our savory and hyssop plants reached that point in their growth when they look like identical twins. We took one of each plant to two botanists; the first sent for herbarium sheets; Dr. Anderson bit first into one plant and then the other. "This is winter savory," he said, handing us the one. . . . There were times when he was too busy to attend a meeting but he invariably came down the steps in time to join us in the kitchen back of the meeting room. He liked unusual foods and was an enthusiastic participant in the Herb Society's regular food tasting and testing session held in the kitchen after the regular meetings. He could always identify every herb in every dish.

Religion played a very important role throughout his life. Reared as a Methodist, he turned while in Graduate School to Quakerism, a faith he maintained thereafter. Among the last of his writings is an account of his early Quaker experience (Stefferud, 1969, p. 419):

> I began to attend Friends Meetings when I was a graduate student at Harvard right after World War I. Since my lodgings were at Jamaica Plain, I attended the Dorchester Meeting not far away. It had a pastor and a piano but long periods of silence. I was greatly moved by the long group silences with which the Meeting began and by the handshaking and kindly interest of the old people who sat next to us. One Sunday I persuaded a fellow graduate student to accompany me. When meeting was over, the old lady nearest to him shook his hand and said, "Is thee a Friend?" He cordially answered, "Not exactly; just a room-mate." I joined the Cambridge Meeting shortly before it moved to the Brattle Street location. . . .

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[11] Letter to author from Emanuel Rudolph.

[12] Letter of Mary E. Baer to author.

[13] Letter of Mary A. Gamble to author.

His faith was such an integral part of his life that he seems to have been spared those tensions in dealing with the trans-rational which afflict many intellectuals. I once attended with him the Friends Meeting in Washington and saw him genuinely overcome with emotion when a member reported a dying son's last words: "God is love." He told me afterwards, "You can't overestimate the power of love; it really makes the world go round." At the same time, he could be coolly detached. In reply to a question I later posed concerning the role of religion, he said quite matter-of-factly, "It helps us to endure the disintegration of the body."

In late 1959, during a visit to Chicago, he had an illuminating religious experience which he described later to his daughter as similar to that of the conversion of St. Paul. Mrs. Anderson affirmed in her diary the impact of the experience upon him:

> Nov 30, 1959. Edgar so very exhilarated from his trip to Chicago he really frightens me. He talks continually, mostly about "his religious experience." He's one of those rare geniuses—a twice born man. He has suddenly become more integrated.

Whatever the significance of this experience his religion, in the broadest and most meaningful sense, was his firm belief in an orderly universe, his uncompromising commitment to intellectual honesty, and a lifestyle that paid quiet but clear respect to the Sermon on the Mount.

An article like this would be incomplete without some mention of Anderson's distinguished prose style. He seemed to find great creative fulfillment in writing, and the volume of his output was so large as to give some credence to the suggestion of colleagues that as a writer he was "compulsive." His writings—even the most technical—are without exception models of clarity and readability. Despite an appearance of ready facility, he rewrote his material frequently until his pieces attained that succinctness and personally-informed simplicity which are as real a mark of his genius as his scientific achievements. Some of his "rewriting" took place in his mind, while walking or driving, as he tested the appropriateness of words against his keen ear. He very consciously selected words of Anglo-Saxon derivation over those from the Latin, and he delighted in emphasizing to students the few words of Latin derivation in the Lord's Prayer and the oft-quoted psalms of the King James Bible. I once asked him who influenced him most in his writing style and he replied, "It's the utter transparency of Hazlitt that has been my model and should be a model for us all." The *Missouri Botanical Garden Bulletin*, intended for a popular readership, became an important vehicle for many essays which articulate his extraordinary perceptions. Beginning the 1950's, he prepared several pieces for *Landscape* which also show his unusual ability to communicate to a wider audience.

The last decade and a half of Anderson's life were years of mixed blessings. When he assumed in 1954 the directorship of the Missouri Botanical Garden, he confronted the enormous postponed challenges of an institution which had been under one administration for four decades. While seeking to turn the Garden in new directions, he found full-time administration frustrating and creatively defeating and resigned in 1957, resuming his teaching and research.

These were also years when many important honors were conferred upon him. In 1954 he was elected to the National Academy of Sciences, and especially close to his heart was a letter of tribute sent him on the occasion by a group of his students who wrote:

> We take pride that we were led through the fundamentals of our craft by a craftsman of excellence, and we hope that we carry along with us, from our years with you, something of your great devotion to the search for truth, your intellectual honesty, magnanimity and very warm human understanding.

Among other esteemed awards, he received the Darwin-Wallace Medal of the Linnean Society, London, and a Golden Jubilee Award of Merit from the Botanical Society of America.

In the last years, he suffered severe illness, but the "grandeur of the man," to use Emmet Layton's words, never faltered. He left as his legacy not only many fundamental contributions to our understanding of plant evolution but a whole generation of students who because of him are looking at the world about them in a sharper, clearer way and, following in his path, seeking to teach others to do the same.[14]

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[14] Letters were received from the following persons with information concerning Edgar Anderson. All correspondence is being deposited in the Missouri Botanical Garden.

Henry N. Andrews, University of Connecticut; Mary E. Baer, St. Louis, Missouri; Clarence Barbre, Webster Groves, Missouri; Robert W. Baxter, University of Kansas, Lawrence; William L. Brown, Pioneer Hi-Bred Corn Company, Des Moines, Iowa; E. G. Cherbonnier, St. Louis; Mary Chomeau, St. Louis; Robert B. Clark, Department of Parks, County of Monroe, New York; Hugh C. Cutler, Missouri Botanical Garden, St. Louis; Gilbert S. Daniels, Hunt Botanical Library, Carnegie-Mellon University; Donald N. Duvick, Pioneer Hi-Bred Corn Company, Johnston, Iowa; F. Ehrendorfer, University of Vienna; Mary A. Gamble, St. Louis; Verne Grant, University of Texas, Austin; Charles B. Heiser, Jr., Indiana University, Bloomington; William M. Hiesey, Camino, California; Nell Horner, St. Louis; Harold J. Kidd, Pioneer Hi-Bred Corn Company, Plainview, Texas; Emmet Layton, University of Wisconsin, Green Bay; Mildred E. Mathias, University of California, Los Angeles; Frank L. Mercer, St. Louis College of Pharmacy; Lily N. Perry, Arnold Arboretum, Harvard University; George H. Pring, former Superintendent, Missouri Botanical Garden; Howard C. Reynolds, Fort Hays Kansas State College, Hays, Kansas; David J. Rogers, Gulf Universities Research Consortium, Bay St. Louis, Mississippi; Reed C. Rollins, Harvard University; Emanuel Rudolph, Ohio State University; Robert W. Schery, The Lawn Institute, Marysville, Ohio; Wellington F. Scott, Jr., St. Louis; Russell J. Seibert, Longwood Gardens, Kennett Square, Pennsylvania; Julian Steyermark, Instituto Botánico, Caracas, Venezuela; Yutaka Suda, University of Iwate, Ueda, Morioka, Japan; Thomas W. Whitaker, U. S. Horticultural Field Station, La Jolla, California; Louis O. Williams, Field Museum of Natural History, Chicago.

Dr. Peter H. Raven and his staff at the Missouri Botanical Garden put at my disposal important archival material relating to Dr. Anderson. Their help in all aspects of the preparation of this article was unfailing. Miss Phoebe Anderson was also especially helpful to me in my work.

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THE PUBLICATIONS OF EDGAR ANDERSON

Erna R. Eisendrath[1]

Although Edgar Anderson was born in New York State, November 9, 1897, a good deal of his life was spent in the Middle West. He graduated, in 1918, from Michigan State University, where his father was Professor of Dairy Husbandry, with a B.S. degree. Four years later he had received Master's and Doctor's degrees from Harvard, where he had served as an assistant in genetics. Immediately after completing his studies, Dr. Anderson came to St. Louis, with the titles Geneticist at the Missouri Botanical Garden, Assistant Professor at the Henry Shaw School of Botany, Washington University.

In 1923 Dr. Anderson married Dorothy Moore, who had a degree in Botany from Wellesley College. Dr. and Mrs. Anderson remained in St. Louis until 1931; during this period Dr. Anderson was also Director of the School of Gardening run by the Missouri Botanical Garden, and travelled a good deal in connection with his research on the genus *Iris*. During the year 1929–30 he served, also, as a Fellow of the National Research Council (British), working at the John Inness Horticultural Institute, near London. During the last year of this first stay in St. Louis, Dr. Anderson was promoted to an Associate Professorship at the University.

There are relatively few bibliographical listings from this period, probably because Dr. Anderson signed only a small number of the articles he wrote during that time for the *Missouri Botanical Garden Bulletin*; although the style of a number of unlisted *Bulletin* articles is very like his, there is no way of corroborating his authorship; consequently I have included only those to which he did at least append his initials.[2]

As is quite clear from the listings, Dr. Anderson's activities shifted back to Harvard, in 1931, when he was appointed Arborist at the Arnold Arboretum. Four years later, however, he returned to St. Louis, appointed once again Geneticist at the Botanical Garden and, this time, a full Professor at the University. In the same year, 1935, appeared one of his most important publications. In conjunction with Dr. Robert E. Woodson, Jr., Dr. Anderson had carried out extensive research on the American Tradescantias, much of it cytological. As a result, their monograph on this group of plants led him on to further experimental study of the role of interspecific hybridization in the evolution of both weeds and cultivated plants.

During the first year after his return to St. Louis Dr. Anderson was elected to the presidency of the Herb Society of America, which he had helped establish. The following year, 1936, he was awarded the Order of the Yugoslavian Crown,

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[2] I have, on the other hand, included some signed materials so slight as to raise the question whether they should not have been forgotten. I have listed them primarily because they demonstate, often far more vividly than does his serious work, a very important aspect of Dr. Anderson's many-faceted personality.

Ann. Missouri Bot. Gard. 59: 346–361.

in recognition of his introduction to this country of the hardy, vigorous Bulgarian ivy, since 1934 increasingly popular in shady gardens. Further honors came his way as well: in 1937, the distinguished Engelmann Professorship at Washington University; in 1941, membership on the editorial board of the *American Journal of Botany*. And, in the same year, Dr. Anderson participated with Dr. Ernst Mayr in presenting the Jessup lectures at Columbia University.

At about the same time, Dr. Anderson began to narrow his interest in genetics to a study of *Zea mays* and its relatives; this interest as well as his close association with Dr. Hugh Cutler in working out the problems of maize genetics, over a long period of years, are both evidenced by many entries in the bibliography. In 1943, a Rockefeller grant made it possible for Dr. Anderson to work with Dr. Carl Sauer at the University of California, Berkeley; a Guggenheim Fellowship permitted further study of the races of maize in the southwestern States and Mexico. In June of that year Dr. Anderson participated, as a member of its Committee on Common Problems of Genetics and Paleontology, in deliberations held by the National Research Council at Berkeley. His interest in Indian corn was further broadened when the Pioneer Hi-Bred Corn Company offered him an opportunity to experiment with corn breeding on a scale prohibitive at the Missouri Botanical Garden. This association continued until his death.

The many references to various aspects of his maize studies during subsequent years reflect not only Dr. Anderson's concentration in this area, but also the geographical spread of his visits elsewhere, to study living plants and herbaria. Dr. Anderson remained widely interested in all sorts of other subjects, as is made abundantly clear from the variety of topics listed in the bibliography. For still further evidence of the breadth of his study and activity one can find in the Annual Reports of the Garden references to a great number of lectures, travel in many parts of the world, and participation in institutes of various sorts. These include, for instance, the development of an experimental garden, devoted to growing tropical strains of important economic plants, in Honduras; a visit to India as the American delegate to a UNESCO symposium; the winning of an alumni award, for distinguished service, from his college—all in 1951. In the following year Dr. Anderson was appointed Assistant Director of the Missouri Botanical Garden, but his important publications during that year prove that the added administrative duties in no way slowed his other work. He even managed to teach at Stanford University, during the spring quarter, and to serve, in 1952, as President of the Botanical Society of America.

During the years 1954–56, Dr. Anderson was Director of the Garden, but again his productive activity was not slowed down. In the first of these years he was also elected to the National Academy of Sciences. As a member also of the American Academy of Arts and Sciences, he was one of the very few scientists ever to achieve both honors.

In 1957 Dr. Anderson gave over his heavy administrative duties to assume the title at the Garden, Curator of Useful Plants. This title, however, belied the continued breadth of his activities: He served as Visiting Fellow in Mathematics at Princeton, as Visiting Fellow at the Center for Advanced Studies in the Behavioral Sciences at Stanford, as Senior Fellow of the Guggenheim Foundation, and as Visiting Fellow at the Center for Advanced Studies at Wesleyan, as well as President of the Society for the Study of Evolution, in 1959. It is no wonder that, at about the same time, Dr. Anderson received a number of distinguished awards: a Certificate of Merit from the Botanical Society of America; the silver Darwin-Wallace medal of the Linnean Society (London); and gold medals from both the Men's Garden Clubs of America and the National Council of State Garden Clubs. In 1965–66 Dr. Anderson demonstrated his continued interest in the origin and evolution of cultivated plants by accepting the Presidency of the Society for Economic Botany; at the same time he continued to edit, as he had since 1963, the Garden's popular publication, the *Bulletin.*

When Edgar Anderson retired, in 1967, after a number of bouts of serious illness, he retained the University title, Engelmann Professor of Botany, emeritus; but at the Garden he was listed until the time of his death (June 18, 1969) simply as "Botanist." This was at his own request because, as he wrote to the editor of *The Herb Grower*, "I am one, never wanted to be anything else, and (the title) covers all of my activities."

Note: In the bibliography titles followed by an asterisk (*) were signed "E.A."

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1927

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1928

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1929

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1931

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STUDENT DAYS WITH EDGAR ANDERSON
OR
HOW I CAME TO STUDY SUNFLOWERS[1]

Charles B. Heiser, Jr.[2]

When Dr. Porter invited me to give this address in a symposium honoring Dr. Edgar Anderson, I was, of course, delighted to accept. In my reply to him I suggested several possible topics—the origin of *Solanum quitoense*, the current status of introgression, variation in the bottle gourd, why did man plant seeds, and the title that he selected. I really didn't expect him to choose the one he did, for at the time I suggested it I thought it a rather clever title, but I did not have the vaguest idea as to what I would say, whereas for most of the others I did have some hard data. In a sense it is a most appropriate title, and Dr. Anderson would have enjoyed seeing that I still get into the kind of predicaments I did 30 years ago. It is also appropriate, for after a day of data and hypotheses, something different is called for, and I promise you that this will be different—if nothing else.

I hesitate to give this talk for two reasons. First, I do not feel that I am old enough to give a talk of reminiscences. But the other day my son said to me, "Dad, do you realize that you are a half century old." Somehow when put this way it makes me seem old enough. Secondly, I hesitate giving this talk since it involves talking a lot about myself and exposing a brash young student still wet behind the ears, and it becomes necessary to say a lot about him to develop the theme that the title implies. By way of background I should say that I was a student at Washington University and that sunflowers have been my principal research interest for a number of years.

In a sense the story began in a room in Rebstock Hall in 1939 when I took Bob Woodson's Botany 101 course. I took it as my science requirement, for at the time I had listed myself as an English major. Before the course was over I had changed my mind. However at Bob's suggestion I took no botany the next year, for he thought that I shouldn't change my major too rapidly. So I didn't really become acquainted with Edgar Anderson until my senior year and that was somewhat of an accident.

That year I had planned to take an advanced taxonomy course with Woodson, but that was all changed when he was asked to give a geography course for students the Army had sent to campus. Anderson volunteered to give Woodson's course. That in itself now appears unusual to me. How many of you have colleagues who will volunteer to give your courses? There were two students in Botany 550 that year—myself and another botany major, Dorothy Gaebler (I wonder what became of her?). We soon found that this

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[1] Banquet address presented at Seventeenth Annual Symposium on Systematics of the Missouri Botanical Garden.

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Ann. Missouri Bot. Gard. 59: 362–372.

FIGURE 1. Dr. Anderson with Ada Hayden, Richard Holm, Lillian Nagel, and Dorothy Gaebler Heiser. — Edgar was way ahead of his time in many ways, including fashion as this photograph of a field trip to the Arboretum shows (about 1945). I don't think he was ever happier than when he was conducting students on field trips.

was no ordinary course. At the time I assumed it was because of the small number of students, but I was later to learn that Anderson never taught an ordinary course. He was a most unorthodox but a most effective teacher. I don't think that anyone else should try to teach a course the way he did, for only an Edgar Anderson could do it that way. One thing, I remember, was that I wanted to look up answers in books. This he did not encourage—one looked at plants.

The plants that fall were composites, and the entire semester was devoted to them. We started with sunflowers and then proceeded to Asters, Solidagos, and many others. Weedy composites occupied most of our time. Gas rationing limited our trips outside of St. Louis, and, of course, as is well known, Anderson had a special affection for weeds. Of these, none held a greater fascination for him than the common sunflower, and these plants served as the primary basis for his classes' studies year after year. St. Louis with all of its slums, railroad yards, and dump heaps had plenty of sunflowers in those days. Edgar knew all the places where sunflowers grew. In fact, when he met visitors at Union Station he took great delight in taking them to the Garden on one of his "short-cuts." The visitor would see nothing but slums and factories and lots of sunflowers. In addition to the beautiful scenery the short cut afforded, it didn't take more than 10 minutes longer than the normal route. Edgar would also delight in telling about the time he was in the hospital and some of his students brought him a bouquet of weedy sunflowers. It was on that occasion he told me that he first understood the marvelous events that took place from hour to hour in a sunflower head.

I recall that it was on one of the field trips to Dago Hill with his class of two students that he said, "Charley, I think that if someone looked into sunflowers carefully, he would discover something very significant." That remark stuck with me. He had a singular ability to make even the most insignificant plant a thing of great interest. He always conveyed the impression that there was something very mysterious going on in plants about which scientists knew very little and, moreover, that they didn't realize how little they knew. One had to look at plants in a new way. One way for people to do this was to use a ruler and to look at populations, not single plants. This, of course, we now take for granted.

It was also at this time that I became aware that he could see things in plants that others couldn't, or a least that I couldn't. Some years later I had my doubts and decided that maybe this was partly an act, for there is no doubt about it, he was a showman! But he was a natural showman not an intentional one, and I now realize that he could look at a field of plants and actually see things that escaped others. In trying to analyze this ability I have decided that it involved two things: an ability to correlate a large number of independent observations in a very short time—he was a numerical taxonomist with his own built-in computer—and an ability to analyze patterns. For example, inflorescences of plants which meant little to the ordinary taxonomist revealed a great deal to him.

But back to our course. I recall that he had us get some colored modeling clay and asked us to make models of disk flowers. There were no regular lectures, although he would frequently come into the lab and pick up some plant or our clay model and ask what we had learned. He would listen a while (and for a great talker one of the amazing things about him was that he was also a good listener) and then he might turn around and walk—maybe stalk is a better word—out of the room, or he might hold forth on some subject for 15 minutes or so. I don't recall taking any notes—maybe because I knew there was to be no exam. Our grade was to be based on two term papers which the students were to do jointly.

It takes great courage—or perhaps foolishness—on my part but I am going to read you some from the first term paper. I ask your indulgence and patience but I assure you that I shall not read it all to you, for which you should be thankful.

THE SEX LIFE OF COMPOSITES AND OTHER INTERESTING FACTS GLEANED FROM BOTANY 550

by dorothy m. gaebler and charles b. heiser, jr.

> "To name all of the species of *Solidago* or the asters at sight is a feat probably no one living can perform."—*Nature's Garden*
> (It's also hard to do with *Gray's Manual*—Heiser)

In the Ode, "Intimations of Immortality from Recollections of Early Childhood," Wordsworth says:

> "To me the meanest flower that blows can give
> Thoughts that do often lie too deep for tears."

The Romanticists all found depth of meaning, beauty, and expression in the flowers, but Peter Bell in another poem by Wordsworth didn't find any such meanings.

> "A primrose by a river's brim
> A yellow primrose was to him,
> And it was nothing more."

Well, it was that way with us until recently—to us a sunflower was nothing but a sunflower. Then for a brief period it became "that damn thing," and now what it is is simply amazing!

> "A fool sees not the same tree that a wise man sees."—Blake.

This article seems very useless in that we won't tell Dr. Anderson very much about the composite family that he doesn't already know, but the point of this is that we get something out of writing the article and that poor Dr. Anderson has to read it. But we're going to try to tell him some things that he doesn't know; for instance, how if he had entered the morphology lab late on a certain afternoon last fall he would have had a wad of clay thrown in his face, pappus and all.

At the beginning of our course we were given several sunflowers. We were told to examine them, which we did. There was nothing extraordinary about them—or so we thought—but we learned fast as the result of some very embarrassing questions asked us about the sex life of *Helianthus.* Our next line of study consisted of making a clay model of a disc flower of *Helianthus*, an assignment that sounded ludicrous at the time and was even called worse things before we finished the model.

> "Wee, modest, crimson-tipped flow'r,
> Thou's met me in an evil hour."—
> *To a Mountain Daisy*, Burns

A very great friendship was almost broken up over the question of whether to put hairs on the stigma or not to put hairs on the stigma. However, at last we finished and we decided that it really hadn't been so bad, that it was rather fun, and that we did know the disc flower inside out—and we do mean inside out.

That was done. We would start on the other composites next time. We were through with the clay (we thought). So imagine our surprise and consternation when our professor told us that he wanted us to make models of the pappi of as many different composites as we could obtain. We considered hiring some first grade pupil who had some experience with modeling clay, but as we couldn't afford paying union rates we decided to do the things ourselves. The arguments about the hairs on the stigma were now forgotten for far greater and more important controversies. In fact, when Heiser took Gaebler's model of *Gaillardia* and finished it to his satisfaction, sparks flew; but when he criticised and tried to change her model of the marigold pappus, it was practically the last pappus straw. No more work was accomplished that day. A long and beautiful friendship was tottering on the brink, but alas, love conquers all and finally the models were finished. We really began to learn things now.

We learned that one tenth of all of the flowering plants of the world belong to the composite family. In Missouri according to Palmer and Steyermark there are 65 native and 15 introduced genera, 243 native and 71 introduced species, five native forms and two introduced ones, and 15 hybrids of composites. . . .

From here on it begins to sound a little more like an ordinary term paper. I don't recall that I ever saw that paper again until 1960, when it arrived by mail along with a letter from Edgar. After a first paragraph dealing with variation in *Claytonia*, he went on to write:

> Topic No. 2. *Helianthus annuus*. I am returning herewith the paper by Heiser and Gaebler. You will note that it is still in its original cover. The writing on it is Dr. Moore's [G. T. Moore, then Director of the Garden]. I told Dr. Moore what I was doing in the course and that I had leaned over backwards farther, in giving a good mark to this term paper than I ever had before. His eyes twinkled and he said he would like to see the paper, so I turned it over to him. He took it home and read it at his leisure and spoke to me about it some days afterwards. He handed it back with the remark "Anderson, I must say in this case I doubt your judgement. You have had a number of unusual students and have done well with them, but in this case it seems to me that this young man ought to have his ears boxed." However, you will notice that it still bears the pencilled grade of "A" which I put on at that time. I hope you will have the courage and the intelligence to keep this paper. If I thought you would destroy it, I would not let you have it back again, but it is a personal thing and therefore it belongs to you and your wife. However, it has a scientific career of its own and is a demonstration of something which precious few teachers of elementary students seem to get into their heads. One is not turning out finished botanists at the end of the first or second or third course in botany. One is leading students on to become better and better botanists. I still refer to the year (when I just had the two of you) as the most successful year my class ever had, and I feel that very deeply. I hope someday you will have the courage and intelligence to show this to young teachers of botany in mingled pride and humility. It might help them to understand the lengths to which I was willing to go in following William James Beal's method of having promising students write up their own discoveries from every-day examination of plants brought in for them to study.

Here perhaps is a missed opportunity, for this would be a good stopping place, but I agreed to tell why I came to study sunflowers so I must return once more to the forties. Our course in composites was supposed to be followed by one in grasses, but Dr. Anderson had the opportunity to go to Mexico the next semester so the course wasn't given. I wasn't particularly enthusiastic about studying grasses at the time, but I now look upon it as a great opportunity missed.

After receiving my A.B. I continued on at Washington for a Master's under Dr. Greenman's direction. I suggested to him that sunflowers would make a good problem, but he discouraged me. However, since by now I was most interested in composites he suggested another genus in the family, *Psilostrophe*. The thesis was eventually published and forgotten. At the same time, however, my interest in sunflowers continued, probably largely because Edgar gave me little pep talks from time to time. I began to assemble various varieties of cultivated sunflowers which I grew in the greenhouse. I made morphological comparisons and had little thought of doing anything more until Edgar asked if I minded if he attempted to make hybrids between some of the varieties. I said, "No, of course not," but he didn't get around to it immediately so I started making hybrids—which I am sure is exactly what he had hoped I would do.

Edgar decided that I should go to Arizona the next summer to learn about the Hopi sunflower. He managed to get $50 from the Garden for the trip and arranged with the Museum of Northern Arizona for me to spend a week there. I went by Greyhound bus—and I had a wonderful week although I had to live

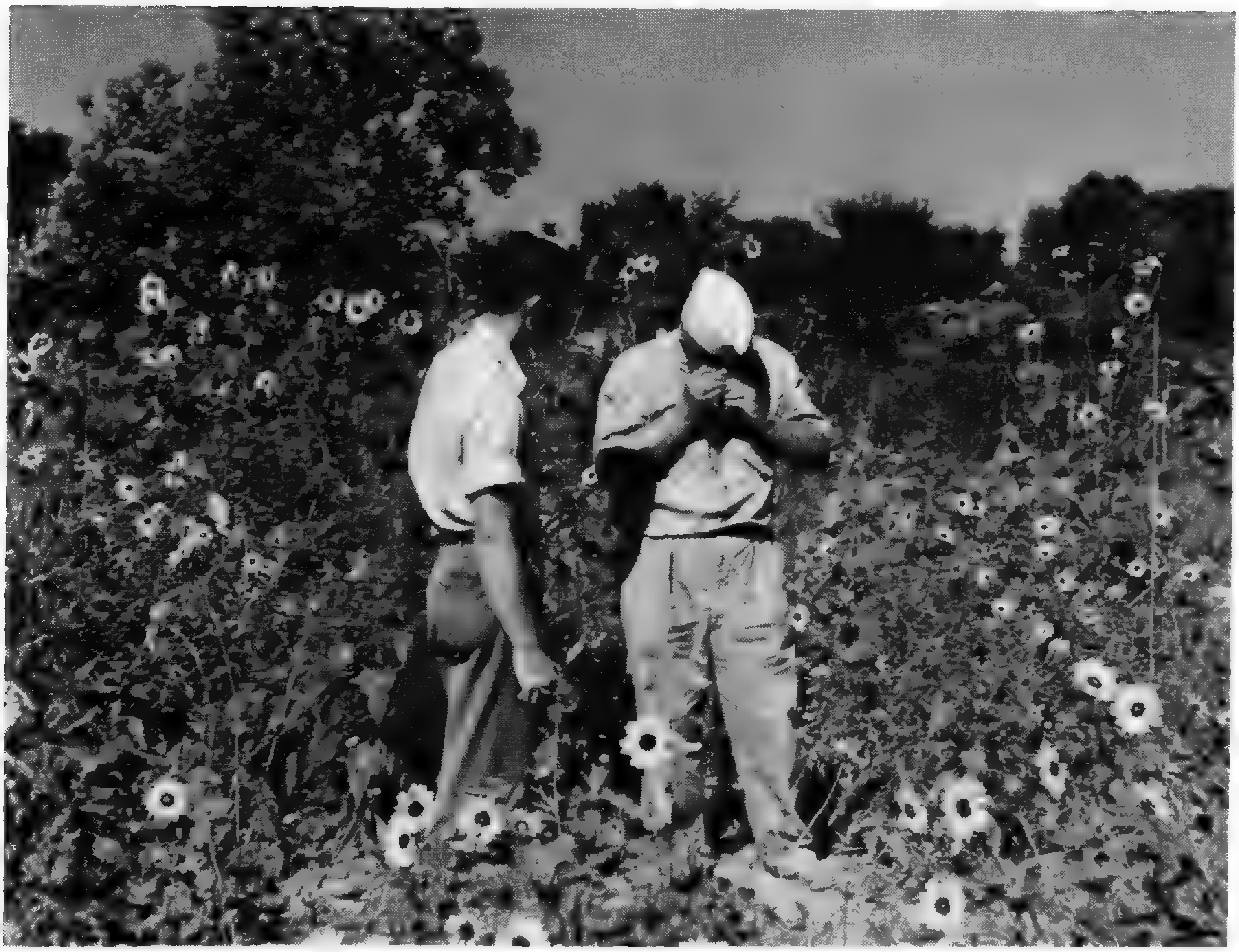

FIGURE 2. Dale Smith and Dr. Anderson. — Edgar examining a sunflower on a visit to the Experimental Garden at Indiana University (about 1955). He was very fond of his "Nehru hat" which he had obtained on a visit to India.

on cheese, since I had forgotten to bring any meat rationing coupons with me. It was my first contact with a flora outside of the Middle West and, as a good taxonomist should, I spent a lot of time filling presses with plants—or bailing hay as it is known to the non-taxonomist. I didn't learn very much about the Hopi sunflower. Because of gas rationing I never did get to the Reservation, although I did get to talk to the Hopis at the Museum about its uses. But fortunately weedy sunflowers—both the common sunflower, *Helianthus annuus*, and *H. petiolaris*—grew near the Museum. I was struck by some unusual variants, but I didn't analyze them fully at the time. When I returned to St. Louis, I decided to take a closer look at *H. petiolaris*—a population of which grew at the streetcar stop next to the University. On the same day I looked at some plants of *H. annuus* which were growing about a quarter of a mile away where the streetcar tracks crossed Skinker Blvd. My attention was drawn to three very depauperate plants which grew a few yards away. The more I examined them the more excited I became, but I decided to look at them again the next day before telling Edgar that I had found some sunflower hybrids. Needless to say, he was delighted, and so was I, for the first time I had discovered something about sunflowers that he didn't already know. I then recalled the unusual plants that I had seen in Arizona and pulling out my dried specimens I realized that they included plants that were probably both F_1's and backcrosses of *H. annuus* and *H. petiolaris*. Today the finding of another hybrid

FIGURE 3. Robert McClary, Vernita Neher, Jack Humbles, Emma Fraysur, Ralph Jacqmain, A. Isabelle Hamilton, Dr. Anderson, Jane Haskett. — A botany class visits the Arboretum in 1959. Photograph taken in front of "Woodson's cabin."

is hardly cause for a celebration, but this was more than a quarter of a century ago when many taxonomists were still very skeptical about Anderson's claims for hybrids. I remember one saying that calling a plant a hybrid was an excuse for not being able to identify it.

After receiving my Master's I stayed on the next year at Washington University as an instructor, as a replacement for Bob Schery, who had gone to Brazil in the wartime rubber program. At the same time I was asked to coach the basketball team at the University. I was offered $100 for the season. I accepted immediately, for I thought of it as pure gravy, for after all, I was already being paid $1500 for the year as a botany instructor, and I thought of myself as well off. I won't dwell at length on my career as a basketball coach which lasted only the one season. I kept losing players to the draft and I ended up the season with two war veterans, a couple of 4-F's and some 17 year old boys. In fact, the player situation became so desperate that the manager, Mas Yamada,[3] who may be here tonight, had to suit up for the final games. As I recall, Mas distinguished himself by picking up two personal fouls in one minute's playing time in our final game. The reason for the inclusion of basketball here is that it leads up to one of Edgar's

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[3] Mas, who is still employed in the Department of Biology, was brought to Washington University by Dr. Anderson.

favorite stories, or if not his favorite, one that I heard him tell on numerous occasions.

My office in Rebstock Hall had the only phone for the Department of Botany; and since most of the staff members spent most of their time at the Garden, it fell upon me to handle incoming calls at certain times of the day. Edgar delighted to say that I would always answer, "Botany Department, Coach Heiser speaking." I don't recall that it ever happened and I never thought it particularly funny, but I do know that both Edgar and Bob Woodson were quite pleased that a botany instructor was also a basketball coach, for they thought that it gave a new image to botany.

It was in the spring of the year 1945 that I learned that I was going to the University of California. Actually it wasn't my decision, for I had no particular desire to leave Washington University. But both Edgar and Bob decided that I should go away for a year of seasoning and that Berkeley would be the appropriate place. Bob arranged an assistantship, and Edgar called me in to tell me about the people that I should see immediately—these were W. L. Jepson, whom I never did meet, Carl O. Sauer, and G. Ledyard Stebbins, Jr. I was then quite excited about making chromosome smears, and he told me that Ledyard had a dropper bottle of aceto-carmine within arm's reach anyplace in his lab. Shortly after my arrival I presented myself to Ledyard. I recall noting that there was only one bottle of aceto-carmine in his lab, but that was my only disappointment. I believe that we discussed possible Ph.D. problems for me on this first meeting. I brought up the possibilities of *Stephanomeria*, a composite that I had become acquainted with in the herbarium of the Missouri Botanical Garden, and sunflowers. *Helianthus annuus*, of course, was common in California, and I knew that a closely related annual, *H. bolanderi*, also grew in California. Ledyard told me he knew where it grew—I was later to learn that he knew where nearly everything grew in California—and we set up a field trip for a couple of weeks later.

In the meantime I wrote Anderson about my reception in Berkeley and about the possibilities for my research topic. He wrote back almost immediately (Oct. 16, 1945):

> Personally, I have a very different opinion about the *Stephanomeria* problem. It is a very nice problem, you already have your teeth into it and so does Stebbins, and working under his direction you would finish it in record time. It would be a good piece of work and widely acclaimed, BUT it would be just another monograph done in cyto-taxonomy. You wouldn't have learned very much, merely practiced.
>
> On the *Helianthus* problem you are not merely working out a problem, you are uncovering an entire new field of work. There is no question in my mind that for your eventual growth and development you would get the most out of the sunflowers.
>
> Up to the present, you have worked on the problem largely with me, and my ideas are pretty violently warped. It would be very helpful to you to work on *Helianthus* under Stebbins, who has another set of ideas and who undoubtedly is not mad about the genus.
>
> It is your decision, however, and not mine and I shall continue to vote for you even though you do nothing but *Stephanomeria*.

I won't go into detail concerning the trip I made with Ledyard except to say that we found *Helianthus annuus* and *H. bolanderi* growing together in several places and there were hybrids in nearly every mixed population. I was excited and so was Dr. Stebbins. My research problem for my Ph.D. was determined that day.

I wrote back to Anderson to tell him that I had decided to work on *Helianthus* which delighted him, of course. I also took the opportunity to ask him to explain a remark in his previous letter.

> If I am uncovering an entirely new field of work in *Helianthus* I wish you would let me in on what it is. Is it . . . tracing the origin of the cultivated sunflower or the hybrid work? Stebbins, I think, thinks you mean the latter. He is very interested in the hint that I dropped that California *annuus* may be a new subspecies . . . derived from hybridization.

To which he replied:

> The taxonomy of cultivated plants is an unsolved and neglected problem. It will require new attitudes, new techniques, and new horizons. What you are doing with *Helianthus annuus* as a prehuman and post human weed, and as a series of cultivated entities is a contribution to a discipline which is yet a-borning. Having read this much go and talk the whole biss over with COS and see if he doesn't agree with me. It is a field which abuts upon the following fields: Genetics, Taxonomy, Agronomy, History, Archaeology, Anthropology. Its major techniques I imagine have still to be invented though one or two are suggested in Anderson and Cutler and in Carter and Anderson. After seeing COS and thinking this over please write me about it again. I can go into horribly complete details if necessary.
>
> Have you been to Davis and seen Beetle? Try to find out everything you can about what Agronomists are like and what they know and don't know.
>
> My best to you both. Don't kill yourselves just because U. of C. will give you the chance. There is no-one there to be an old mother hen on the sidelines to cluck at you when you are not sitting back calmly from time to time to enjoy life. The days I shamelessly played hookey when I was a Graduate Student have paid better dividends than the times I worked too late in the lab. Of course there are limits.

And then on Nov. 12 I wrote:

> Stebbins is quite excited (hardly a strong enough word) by sunflowers by now. If you are an authority on taxonomists I am becoming one on geneticists. I see what you mean when you say it would never do for Stebbins and me to work in the same lab. Dot [Dorothy Gaebler Heiser] says that we literally become mad when we see a plant, and Constance thinks our influence on each other will make us both nervous wrecks.

I should add here that although I had been sent to California for a year and was expected to return I never did so. I took my degree there in Botany, not Genetics, so although Stebbins was not my major adviser in name, he was in spirit and deed.

I continued to exchange letters with Edgar while I was in Berkeley and in fact, ever since. I have a file of correspondence with him over 2 inches thick. At the time it didn't seem unusual to receive a two page letter from him, but looking back I realize that it is something that an ordinary professor doesn't find time for. Over the years there was no telling from where I would get a postcard from him with some observations about a sunflower he had seen in his travels. This past summer I spent a most delightful afternoon reading all his letters, and I would like to quote just a few comments from some of them.

FIGURE 4. Dr. Anderson with potatoes. — Here we are spending a nice quiet evening with potatoes in 1959. Edgar's essay, "How to spend a Nice Quiet Evening with a Potato" (Missouri Botanical Garden Bulletin 43: 50–53. 1955), is my favorite among the many delightful popular articles he wrote. The table where many a student and visitor has eaten is situated behind the "Barn" at the Arboretum. Edgar and Mrs. Anderson used to live at the "Barn" during the summer in his earlier years at the Garden, while he grew his experimental plants in nearby fields.

On February 6, 1946—on being frustrated at not finding something he wanted in the herbarium—he wrote,

> Oh God, oh stamp collecting, when will taxonomists ever take any interest in being biologists. Once when I traveled with E. J. Palmer I went to a good deal of trouble to get a whole sheet of Lily pods and he threw it away because it made such a nasty looking specimen and he wasn't certain what species it belonged to anyway.

Later the same year (Nov. 18):

> Jon Sauer is starting in on several minor cultivated plants. I've learned a lot as usual. What an incredible gift good students are.

In 1950 (Feb. 2) when I wrote him that I was looking for some new research problems,

> Butt. What's this about ditching *Helianthus*? I suspect you have been traveling with Job's comforters. If you are tired of the damned weeds and don't want to look at em any more for a while, why by all means put them aside. Don't let anybody's advice, including mine, keep you from what you are happiest doing.

This was followed by some compelling reasons why I should continue.

Once I obtained roots of a hybrid of *Helianthus grosseserratus* × *maximiliani* which he grew as an ornamental in his backyard but I failed to get information on its parentage. So I wrote him and he sent back this very brief message (May 26, 1960):

> The hybrid plants came up in my garden where I was growing both parent plants. I ask you, Mr. Taxonomist, is this a natural or an artificial hybrid?

After I came to Indiana University in 1947 he continued to be not only my teacher, but my students' teacher as well. For many years I used to take my class to the Missouri Botanical Garden's Arboretum at Gray Summit for a weekend field trip. Whenever possible he would come out to join us. He delighted in telling my students stories about me when I was a student and loved to try to embarrass the proper young professor. He also came to Bloomington frequently to see my sunflower garden.

It's time to stop and I haven't told you anything about his music sessions He played the recorder. Nor about the square dances at the "Barn." Nor about his cooking. I think one of the worst dishes I have ever eaten was his spam covered with bread crumbs soaked in loganberry juice—perhaps because he raved so about it. I have talked way too much about myself, but I hope by doing so it has given you some insight into the character of Edgar Anderson, teacher and botanist. The latter is the title he chose for himself in his later years at the Garden.

EDGAR ANDERSON: RECOLLECTIONS OF A LONG FRIENDSHIP

G. LEDYARD STEBBINS[1]

Edgar Anderson was one of the most extraordinary men whom I or anyone else has ever known. As a scientist, he was remarkable for the precision with which he recorded what he saw, as well as his distaste for excessive detail, which sometimes led him to gloss over valid objections to his theories as he stated them. Long before other geneticists, he perceived almost intuitively the enormous complexity of genetic variation in natural populations. Most of his scientific career was devoted to a search for techniques by which this complexity could be expressed in such a way that any biologist, regardless of his mathematical background, could understand and appreciate it. In achieving this goal, he was largely successful. He was a true naturalist—a keen, analytical observer of plants in their natural surroundings. Perhaps his interpretations were sometimes too facile. Nevertheless, no plant scientist known to me was more able than Edgar Anderson to compare in their natural habitat the leaves, flowers, and wonderfully symmetrical architecture of plants, and to express their interrelationships in a meaningful way.

In his personality as in his scientific achievements, Edgar was a man of almost unbelievable contrasts. He could be rudely abrupt, if the occasion arose, with either his scientific opponents, his acquaintances, or even his closest friends. On the other hand, he could never hold a grudge, or hurt people intentionally. He could be equally warm and friendly to scientific colleagues, older scientists whose opinions he respected, to the grandes dames of Philadelphia's main line, or the high society of St. Louis; as well as to his subordinates in the Garden, and to the country people of Missouri, California, Mexico, or any other country that he might be visiting. His warmth, friendliness, and encouragement was, above all, showered lavishly upon younger scientists and students who, in his opinion, were sufficiently intelligent and ambitious to warrant his attention. He set great store by his unconventionality. He could never resist the temptation of exercising his keen wit at someone else's expense. Nevertheless, he was even more concerned with improving his ability to understand the needs and motives of others. In this, he was usually successful.

In these pages I shall illustrate the above remarks as well as I can by telling a few anecdotes about my 38-year friendship with Edgar Anderson.

In the summer of 1930, as a graduate student on my first trip to Europe, I looked forward with particular anticipation to the International Botanical Congress in Cambridge, England. In many ways, the Congress lived up to expectations. I had a chance to meet, even if only casually, the renowned botanists whose works I had been reading: A. C. Seward, Otto Rosenberg, Georg Tischler, Agnes Arber, and many others. At other times, however, the

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sessions were long, tiring, and, to me, excessively occupied with meaningless trivia. At the end of one of these sessions an expansive young man, in his broad Michigan accent, gave a clear, incisive description of differences between species of *Iris* that had been well known to me already in my childhood spent on the coast of Maine. Tying his account to chromosome numbers and to the probable evolution of the species with relation to the Pleistocene glaciation, Dr. Anderson immediately set going in my mind a train of thoughts about plant evolution that have been with me ever since. With some trepidation, I went up to him after the session and asked a question about his talk. His response was immediate, cordial, and enthusiastic. In a long session in his room that evening, we discussed his research on *Iris*, *Aquilegia* and *Tradescantia*, my own Ph.D. problem in *Antennaria*, and many other items, relevant and irrelevant. During the rest of the Congress, I spent as much time with him as I could. I gained a new insight into our field of common interest and learned to look at botanists in a new light. "Look at Edith Saunders in her square hat, doesn't she look just like a female bishop?" "There's that bore Ruggles Gates, trying to hide his Canadian origin by being more British than the British." "The trouble with C. D. Darlington is that after Newton's death, he came up too fast. He doesn't realize that to write intelligently about plant chromosomes, you at least ought to know what the plants look like that they came from." "There's Agnes Arber; why don't you go up and talk to her about plant anatomy and evolution. I'm sure she'll give you some good ideas."

A few years later, when I was a young instructor at Colgate University, Edgar paid me his first visit at my home. His visit was only partly on my account. He had also been attracted by the incomparable collection of peony species and hybrids being grown by a Professor of Chemistry, A. P. Saunders, at nearby Hamilton College. His letter to Professor Saunders included a characteristic question: "Do you have in your garden any peonies except those big puffy ones that aren't good for anything except a horse's funeral?" We assured him that he had, and the visit went off most successfully. Among other things we had a musical session at which Professor Saunders displayed his superb artistry on the violin, and I was persuaded, I don't know why, to present a sample of my woefully inadequate piano playing. Its sequel came a few weeks later when I had an occasion to visit Harvard and the Bussey Institution. After dinner at his home, Edgar addressed a characteristic remark to Mrs. Anderson: "Dorothy, I want you to hear Ledyard play 'Joshua fit de battle of Jericho,' not hitting any note right, but getting the spirit of it better than you do!" That was the best compliment on my piano playing that I have ever received!

After going to California in 1935 I saw less of Edgar, but we renewed our friendship at the A.A.A.S. meetings in Dallas at the end of December 1941. Three weeks after Pearl Harbor, these meetings were noted chiefly for the difficulty that all of us had in paying attention to science. At one session, a paper was presented by the father of hybrid vigor in plants, G. H. Shull. Although all of us revered Dr. Shull, his current research was rather hard to take. It consisted of a detailed account of gene transmission in shepherd's purse, for which he used the then current generic name *Bursa*, and was illustrated by an endless succession of impossibly detailed typewritten charts. In the middle of this performance I felt a hand on my shoulder, took a note from Edgar, who was sitting behind me, and opened it up. It read: "Times are bad and getting worsa, But G. H. Shull still diddles with *Bursa*."

At the end of the talk, I turned around and remarked: "You ought to be made poet laureate of this session." At which, Edgar leaned back in his chair, spread out his arms, and let out a characteristic, resounding guffaw. It coincided exactly with the end of the modest applause that Dr. Shull received for his paper. Nearly everyone looked around at us, and I could only imagine what they were thinking. The Chairman, Dr. Castetter, a tall man with impressive dignity and enormous bushy eyebrows, transfixed me with a stare that made me feel like crawling out of the room under the seats. After the session, I went up to Dr. Shull to apologize and explain, but found him more interested in discussing with me our mutual interest in genetics. A few years later, when I gave lectures on plant evolution at Columbia University in New York, Dr. Shull came up from Princeton to hear me, and we developed a most pleasant acquaintance.

The longest continuous association that I had with Edgar Anderson was in 1943, when he came to Berkeley on a Guggenheim Fellowship, in order to be associated with my then chief, Professor E. B. Babcock, as well as with C. O. Sauer in the Geography Department.

One incident that occurred during this period is best related in Edgar's words, as I heard him tell it many times to mutual acquaintances.

"When I was in Berkeley during the war, Ledyard and I used to have lunch together in the warm sunny alcove outside of his laboratory on the top floor of Hilgard Hall. We had many good talks together, but I'll never forget his reaction to something that I did a little while after I arrived in California. You see, almost all of the men were gone, and I had heard that the sororities were having trouble in finding help. So I went to one of them, offered my services, and they hired me as a waiter. When I told Ledyard this, he looked at me, all of the blood of his strict New England ancestors curdled in his veins, and he blurted out: 'Edgar, you'd do *anything* to be bizarre, wouldn't you?'"

Evening seminars with Edgar, Professor Sauer, and the few students who were around during that period were memorable occasions. I learned to look for and find evidences of man's impact upon his environment far greater than I had previously suspected. Theories about the conditions under which agriculture developed were new to me, and although I could not accept all of these that Anderson and Sauer suggested, they stimulated all of us to a lot of careful thinking. The same can be said about their theories regarding pre-Columbian exchanges of crop plants between the Old World and the New.

That spring, we had a day together in the field that remains as a high point in my long experience of plant hunting excursions. Our objective was to obtain precise data on variation in the flowers of *Iris longipetala*, an endemic of the San Francisco Bay Region, which at that time was abundant on the lower slopes of San Bruno Ridge, on the outskirts of South San Francisco. The March sun was warm and inviting, and the green hills were flushed with the pale blue of hundreds of *Iris* flowers. We sat down in the middle of one of the larger patches, and Edgar inspected carefully the delicate, fragile petals of the nearest flowers. He could see immediately that flowers on each plant had their own intricate and distinctive design of lines and spots on the outer petals and asked for my help in reducing the patterns to a diagrammatic order that could be expressed in quantitative terms. Then in the middle of the most intense observation and recording of data, he leaned back, spread himself out on the soft grass, looked up at the blue sky and remarked: "Aren't we just the two luckiest people on earth to be out here in this gorgeous sunshine, looking at the incredible beauty of design in these flowers, and calling it 'Work.'"

After the war, in the summer of 1946, I made a tour of several Middle Western and Eastern university campuses before settling down to my Jesup Lectureship at Columbia. Not unnaturally, the tour began when I left my westbound family at St. Louis, and visited for several days with Edgar, who was then occupying the home on Flora Place that was his before he became Director of the Garden. We spent evenings in his garden, looking at the native perennial species of sunflower that he was cultivating there, and discussing the origin of temperate North America's most distinctive cultigens, the Annual Sunflower and the Jerusalem Artichoke (*Helianthus tuberosus*). A memorable trip to Gray Summit, including my first introduction to the fascinating vegetation of limestone glades, was a high point of this visit.

Another interesting conversation occurred when he showed me paintings done by an artist friend of his, who had been captivated by the beauty of design that one can see in histological, sectioned and stained preparations of human viscera. "You know," said Edgar, "she came to me before she put together a one-woman show of these paintings, asking permission to borrow a portrait that she had made of me the previous year. Here it is. You see, I was working out at Gray Summit on a warm summer day, and had taken off my shirt and undershirt so that I would be more comfortable. She thought that the people who came to see the exhibit, and who might be repelled by nothing but human viscera, would feel better if a more conventional portrait were included. But the result turned out to be exactly the opposite. When she asked her friends how they liked the exhibit they replied: 'Well, the livers and kidneys were all right and rather fascinating, but why did you have to include that huge, monstrous bare torso!'"

At the end of this visit, Edgar drove me to Urbana for my next visit, at the University of Illinois. "You know," he said, "that your host in the Herbarium will be George Neville Jones. I have known Jones for a long time. He first came from the state of Washington, where he was rather a lone wolf and little known. He went to Harvard, where he worked under Elmer Merrill at the Arnold Arboretum. He was very much under Merrill's thumb, shy and very subdued. But then he came to Illinois, where he was the only taxonomist, could pose as an authority from Harvard, and had the job of building up the

Herbarium. In this connection, he built himself up, too. Every time I have visited him he has displayed a little more self confidence, until now, he greets me as one African potentate to another." The simile was so apt when we actually arrived that I had difficulty in restraining my laughter.

A few years later, in 1951, Edgar came out to the meeting of the Society for the Study of Evolution in Berkeley. Both of us were on the Executive Council of this Society, which had its annual meeting at the home of Vice President Ralph Chaney. The meeting was preceded by a lunch in the patio, but before we sat down we were given a tour of Dr. Chaney's unique garden. As a paleontologist, he had assembled all that he could of the "living fossil" plants that are now relics of past geological periods and had arranged them into assemblages representing the forest communities that dominated past geological epochs. As we were shown the distinctive characteristics of each species, I lingered behind the group in order to inspect more carefully a shrub with which I had been previously unacquainted. In doing so, I failed to notice that the branch that was closest to me for inspection contained at its other end a paper wasps' nest. The wasps, however, did notice me, and I was impelled to make the most rapid trip through the Eocene, Oligocene, Pliocene, and Pleistocene up to the recent security of the lunch table that any traveller has ever made. As soon as I had related my troubles, Edgar came out with one of his immortal couplets:

"The day was hot, our host was gracious,
But Ledyard got stung in the early Cretaceous."

The following year, Edgar was elected President of the Botanical Society of America. This honor led to his being upstaged in the deftest manner possible. Professor Katherine Esau is not only one of America's most eminent botanists: she also has a dry, rapier-sharp wit. At the annual banquet, the President has, among his other duties, that of introducing the speaker of the evening, who is always the Society's President for the previous year. This was Edgar's task for Dr. Esau at the banquet held at Cornell. As might have been expected, he was not thoroughly at ease before such a large gathering, and he showed this self consciousness by preceding his introduction with a long peroration about his being confused with Dr. E. G. Anderson of Cal Tech, about his aversion to college deans, of which the one at Cornell was a happy exception, and various other irrelevant matters. When he finally called attention to Dr. Esau and her botanical eminence, his audience had become somewhat fidgety and impatient. She got up, and in her quiet, matter-of-fact tone of voice replied with this succinct remark: "I have read in a book of etiquette that the function of the master of ceremonies is to draw attention away from himself and toward the speaker of the evening."

During the same year, I received a copy of his new book, *Plants, Man and Life*, characteristically inscribed: "To Ledyard from Edgar with many thanks." I, of course, felt that the thanks should go in the other direction. Rarely has the first reading of a new book given me such delight. It is Edgar Anderson, through and through. His chief technical contribution to science, the pictorialized scatter diagram, appears there in its final and most useable form, in a chapter, entitled characteristically, "How to Measure an Avocado." Another gem is his diagrammatic map of an orchard-garden in Guatemala, showing how a community of cultivated plants can be made compact and harmonious. His devotion to the lore of the origin of cultivated plants, and his appreciation of the complexity that apparently simple problems concerning them may present, is set forth in his chapter on sunflowers. Sprinkled through the book are thumbnail sketches of personalities, living, historical, and partly fictional or anonymous, like the field taxonomist who rushes past the fascinating, unsolved problems of tropical crop plants and their associated weeds, in order to concentrate on the "tiny patches of cloud forest" that cover the remote ridges rising above the plains. Then oblivious of the awe-inspiring beauty and solemnity of the scene, he "rushes about with a great excess of energy, throwing the plants into presses, searching here and there for something yet uncollected." The characterization that appealed to me the most, however, was that of the medieval herbalist, Leonhard Fuchs, whom he visualizes as "a big, broad-shouldered Henry-the-Eighth sort of man, with handsome clothes and a general air of getting things done." Couldn't there be something of a self portrait included, either consciously or unconsciously, in this characterization?

When Edgar came to Berkeley in 1953 for his second year in Sauer's Department, I was already in Davis, and we saw each other only occasionally. He did, however, come out to Davis to give a seminar to the Agronomy Department about his work with corn and preceded it with one of his favorite stories. According to him, in an unnamed agronomy department of a Middle Western university, an unimaginative professor assigned to an equally unimaginative student the task of distinguishing between oranges and apples. Both of them were first rate statisticians, and so they went about their task in a businesslike, objective, and thoroughly scientific fashion. The student measured heights, diameters, and circumferences. He obtained weights and specific gravities. Then he used chi square tests, t-tests, correlation coefficients, and all of the other accepted statistical methods for combining data. At the end of six months' work, the student reached the firm, statistically irrefutable conclusion that, while one could always distinguish populations of oranges from populations of apples, it is impossible to distinguish a single orange from a single apple!

The story impressed me in two ways. First, Edgar had the nerve to tell it to an audience of agronomists, and he got away with it. Second, the kernel of truth that it illustrates impressed me then and still impresses me. If one is to use statistical methods with biological material, one cannot succumb to the temptation to select parameters of measurement because they are the easiest ones to handle statistically. Usually, the best distinctions between two different kinds of objects involve such subtle non-metric characters as (in oranges and apples) shades of color, roughness *versus* smoothness of surface, chemical content, etc. My personal experience has been many published statements to the effect that, for instance, a particular chromosomal race cannot be distinguished from another are based only upon an inadequate survey of a few easily measured characters.

During his visit of 1953, Edgar and I decided to record in print the outcome of our numerous discussions on the subject of hybridization between plants in nature. We agreed that the important fact about this phenomenon is not its taxonomic but its ecological and evolutionary consequences. Our observations of many plant groups had convinced us that, almost regardless of the degree of fertility of an F_1 hybrid, the chances that such a hybrid will contribute significantly to future gene pools and so to evolutionary change depends almost entirely upon the environment in which the hybrid is growing. If this environment presents an array of new and unoccupied or poorly filled ecological niches, some of the hybrid progeny are likely to be capable of filling them. On the other hand, if the hybrid is formed in a closed habitat, which presents no ecological opportunities for the establishment and spread of its descendants, it will have no effect on evolution, regardless of its vigor or fertility. The purpose of our sole joint contribution, published in the *American Naturalist* in 1954, was to point out that man's disturbance of natural habitats, although it is at present the chief source of evolutionary opportunity, is by no means the only kind of significant disturbance that exists and has existed in the past. Glaciations, volcanic eruptions, advance and retreat of epicontinental seas, the rise and extinction of large herbivorous animals: all of these, at one time or another, have favored the evolutionary success of hybrid progeny. Neither he nor I have seen any reason since then for deviating from this belief.

My last extensive visits with Edgar were during 1958, when he was a Fellow of the Center for Advanced Studies in the Behavioral Sciences at Stanford. Our discussions during this time were largely reminiscences and reviews of ground that we had already covered. After he left Stanford, I saw him only a few times. He had made his impression upon me and had given me a great deal to live by.

Not all of our discussions consisted of science and witticisms. I cannot conclude without referring to Edgar Anderson's great faith in mankind, which led him to adopt and follow zealously the Quaker religion and way of life. He accepted family tragedies calmly and resolutely. His inner conflict with himself was never wholly resolved, but he never wavered in his belief that he could make life better for others by his kindness toward them, and his ability to share with them his extraordinary perception of the wonders of plant life, and what plants could mean to people.

HYBRIDIZATION, EVOLUTION, AND SYSTEMATICS

Duncan M. Porter[1]

It was appropriate that the Missouri Botanical Garden's Seventeenth Annual Systematics Symposium be dedicated to the late Dr. Edgar Anderson, who was associated with the Garden for almost 45 years.[2] Dr. Anderson's long series of researches on certain aspects of hybridization, and especially his book *Introgressive Hybridization* (Wiley, New York. 1949), have profoundly influenced studies in the field. Until he began field studies of hybridization under natural conditions in the 1930's, most investigations of the phenomenon were made in the garden and the greenhouse. Anderson took the investigator out of the laboratory and into the field, successfully integrating ecology and genetics. He also pioneered in using simple methods to solve complex infraspecific variation, and the effects of hybridization thereon.

The Symposium was held in the Museum building of the Missouri Botanical Garden on Friday and Saturday, 16–17 October 1970. About 225 botanical and zoological systematists, representing 65 institutions in the United States and Canada, attended. The theme of the Symposium was the importance of hybridization in evolution and its effects on systematics.

Six papers were presented at the Symposium, with the resulting discussion directed by the Symposium moderator, Dr. G. Ledyard Stebbins, University of California, Davis. Speakers and their topics were Dr. Lewis E. Anderson, Duke University, "Population cytology, hybridization, and systematic relationships in mosses"; Dr. Leslie D. Gottlieb, University of California, Davis, "Levels of confidence in the analysis of hybridization in plants"; Dr. Norton Nickerson, Tufts University, "Introgression in *Hudsonia* (Cistaceae)"; Dr. Sarah B. Pipkin, Howard University, "Introgression between *Drosophila* sibling species in Panama"; Dr. Robert K. Selander, University of Texas, "Biochemical genetics of hybridization in European house mice"; and Dr. Lester L. Short, American Museum of Natural History, "The significance of hybridization in avian evolution and systematics." In addition, Dr. Charles B. Heiser, Jr., Indiana University, presented a colorful evening talk on "Student days with Edgar Anderson —Or how I came to study sunflowers" at Wilson Auditorium, Washington University. The papers of Drs. Anderson, Gottlieb, Nickerson, Pipkin, and Short, plus the talk of Dr. Heiser, and reminiscences of Edgar Anderson by Dr. Stebbins follow in this issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN. All contributed to a successful Symposium.

Dr. John Finan, The American University, and Erna R. Eisendrath, Washington University, have contributed, respectively, a biography and bibliography

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[2] The Symposium was supported by National Science Foundation Grant GB-22057.

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of Dr. Anderson. These two papers, truly labors of love, have been added to those from the Symposium to complete the section of this issue of the ANNALS dedicated to Edgar Anderson.

My acquaintance with Edgar Anderson was all too short. I was struck by his eager willingness to help others to understand problems of variation. His ability to quickly grasp a complex problem and to explain it clearly to others is sorely missed.

CYTOLOGICAL STUDIES OF NATURAL INTERGENERIC HYBRIDS AND THEIR PARENTAL SPECIES IN THE MOSS GENERA, *ASTOMUM* AND *WEISSIA*[1]

Lewis E. Anderson[2] and Betty E. Lemmon[3]

The relationships of a complex of species within or near the moss genus, *Weissia* Hedw., have puzzled bryologists for more than a hundred years. The main problem is the uncertain status of two segregate genera, *Hymenostomum* R. Br. and *Astomum* Hampe. Recurring reports of intergeneric hybrids between species of all three genera have tended to weaken the case for maintaining separate genera, yet the segregate genera are based on characters which usually are considered strong. An opportunity to study meiosis in two natural intergeneric hybrids, *Astomum ludovicianum* Sull. × *Weissia controversa* Hedw. and *A. muhlenbergianum* (Sw.) Grout × *W. controversa*, initially prompted this study.

Taxonomic relationships within the *Weissia* complex and arguments for and against maintaining one or more of the segregate genera have been discussed by Lindberg (1879), Andrews (1920, 1922, 1924, 1933), Hilpert (1933), Grout (1938), Jensen (1939), Chen (1941), Steere, Anderson and Bryan (1954), Podpěra (1954), Nyholm (1956), Demaret and Castagne (1964), Reese and Lemmon (1965), and Williams (1966). The distinguishing characters of the three genera, as presently understood, are summarized in Table 1.

Astomum includes species with immersed capsules in which an operculum is lacking or very poorly differentiated and non-functional. Capsules are cleistocarpous, breaking open irregularly at maturity. Peristome is lacking, and there is no membranous covering or "hymenium" at the mouth of the capsule.

Hymenostomum embraces species with exserted capsules, a functional operculum, and a thin membrane which covers all or a portion of the mouth of the capsule. Annulus and peristome are lacking.

Weissia contains species with exserted capsules, a differentiated operculum, annulus, and peristome, although the latter is sometimes much reduced in size, or rarely absent.

Distinguishing gametophytic characters are lacking, if all species are considered. Gametophytes of the two North American species of *Astomum*, how-

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[1] A grant by the National Science Foundation to Duke University (GB-6394), which provided partial support for the work, is gratefully acknowledged. We thank the following colleagues for assistance in collecting material: Fred Anliot, Marshall Crosby, Howard Crum, Fred Hermann, Ardith Johnsen, Norton Miller, Paul Redfearn, William Reese, Wilfred Schofield, Jack Sharp, and Richard Zander. Jerry Snider's invaluable help in photography, techniques, and in countless discussions is acknowledged. We owe a special debt to the late Claire Williams, who went to extraordinary lengths to locate, collect, and ship meiotic material of hybrids in southern Ontario. Her untimely death, terminating her important researches in that area, is a great loss to bryology.

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Ann. Missouri Bot. Gard. 59: 382–416.

TABLE 1. Distribution of sporophytic characters in the three genera of the *Weissia* complex.

	ASTOMUM	*HYMENOSTOMUM*	*WEISSIA*
Seta	short, capsule immersed	short to long, capsule emergent to exserted	short, capsule exserted
Capsule shape	subglobose to oblong-cylindric	rounded-ovate to long-cylindric	rounded-ovate to long-cylindric
Operculum	absent to slightly differentiated	present	present
Annulus	absent	absent	present
Oral membrane	absent	present	absent
Peristome	absent	absent	present

ever, are distinctive and are generically recognizable, although *A. ludovicianum* and *A. muhlenbergianum* can scarcely be told apart without sporophytes. Compared with the North American species of *Weissia* and *Hymenostomum*, the leaves of *A. ludovicianum* and *A. muhlenbergianum* are larger, they have longer and broader leaf bases, the acuminations are longer and more sharply pointed, and the costae are more longly excurrent.

As many investigators have pointed out, especially Andrews (1920), in *Weissia*, *Astomum* and *Hymenostomum*, generic distinctions are not always sharp, and the genera are connected by species which with about equal logic could be placed in either genus. For example, *W. controversa* and *W. wimmeriana* (Sendtn.) BSG. sometimes lack even rudiments of a peristome. *Astomum ludovicianum* often produces capsules with a row of differentiated cells, forming a line of demarcation between a possible urn and operculum, although the latter apparently is never functional. Also the setae, normally short and bearing immersed capsules, are sometimes exserted beyond the perichaetium. An oral membrane is only partially developed in *H. tortile* (Schwaegr.) BSG., and usually disappears by the time the capsule is mature. Finally, *H. rostellatum* (Brid.) Schimp., which is gymnostomous and has an oral membrane, is cleistocarpous and has immersed capsules, suggesting a relationship with *Astomum*. Loeske (1910) resurrected even another genus to accommodate the latter species, *Kleioweissia* Bahrh., which, as Andrews (1920) stated, makes matters worse rather than better.

Nicholson (1905) published the first account of hybrids in the *Weissia* complex. He described hybrid sporophytes from southern England, which he attributed to natural crosses between *Astomum crispum* (Hedw.) Hampe (as *Weissia*) ♀ and *Weissia fallax* Schlm. (as *W. crispata* Lindb.) ♂, and between *W. fallax* ♀ and *A. crispum* ♂. Although there were minor differences between the reciprocals, sporophytes from both crosses were intermediate between the parents. Spores from the *A. crispum* ♀ × *W. fallax* ♂ capsules were abortive and produced in small numbers, or they were brownish red, which suggests they may have been non-viable. Viable spores are generally greenish. The reciprocal hybrid, according to Nicholson, produced no spores or at most a few undeveloped hyaline cells clustered around the columella.

A year later, Nicholson (1906) found plants in a rough, stony field near Lewes, Sussex, which, he concluded, were hybrids between *Astomum crispum* ♀ and *Hymenostomum microstomum* (Hedw.) R. Br. ♂. The hybrid sporophytes had short setae, a differentiated operculum, no peristome and portions of a membrane over the mouth. The spores were described as reddish brown, again, suggesting sterility, but attempts at germination were not mentioned. The reciprocal was not found.

An even more remarkable hybrid was reported a few years later by Nicholson (1910). On the Sussex coast, between Seaford and Eastbourne, he found capsules on plants of *Tortella flavovirens* (Bruch) Broth. (as *Trichostomum*), which he regarded as hybrids between *Tortella flavovirens* ♀ and *Astomum crispum* ♂. The capsules were stout, on very short setae, and had calyptrae which appeared too large for the capsules. Capsules were partially cleistocarpous, and the peristomes were imperfectly developed. According to Nicholson, gametophytes were clearly *T. flavovirens*, a determination he claimed was confirmed by Levier. Nicholson's account of this extraordinary hybrid caused Andrews (1920) to wonder if generic lines in this complex should be drawn even broader and possibly involve *Tortella* (C. Müll.) Limpr. and *Trichostomum* Bruch. In practice, however, Andrews never went this far.

In a later paper, Andrews (1922) himself, now aware of the possibility of hybrids in the complex, speculated that the type specimen of *Astomum nitidulum* BSG. might have been a hybrid involving *A. muhlenbergianum* (Sw.) Grout ♀ × *Weissia controversa* ♂. Apparently, the type of *A. nitidulum* consisted of a single plant, or, at most, a few plants, which were intermixed in the type collection of *A. sullivantii* BSG. (= *A. muhlenbergianum*). Unfortunately, when Schimper returned the type specimen, Sullivant lost the contents in opening the packet. Andrews based his speculation of hybridity on drawings found in the Sullivant herbarium at Harvard University and upon presumed duplicate material collected by Sullivant.

Khanna (1960*a*, *b*) found the chromosome number, $n = 26$, in *Astomum exserta* Broth. (as *Weissia*), from the Siwalik Range, India, and concluded that it is an amphidiploid. He claimed that *A. exserta* capsules are intermediate in all respects between *A. crispum* and *W. controversa*, and must have arisen through hybridization of these two species, followed by chromosome doubling. Meiosis in *A. exserta* was normal in all respects. He found no multivalents, disjunction was normal, and the chromosomes were distributed equally to the four nuclei. Khanna assumed that lack of irregularities in meiosis ruled out any possibility of autotetraploidy, but this is not correct (Stebbins, 1950, 1958; Lewis & John, 1963).

Reese and Lemmon (1965) described natural hybrid capsules which were discovered near Pont Brule, Lafayette Parish, Louisiana, intermixed in populations of *Astomum muhlenbergianum* (as *Weissia*), *A. ludovicianum* (as *Weissia*), and *W. controversa*. The hybrid capsules were intermediate between *A. ludovicianum* and *W. controversa*. No evidence could be found of *A.*

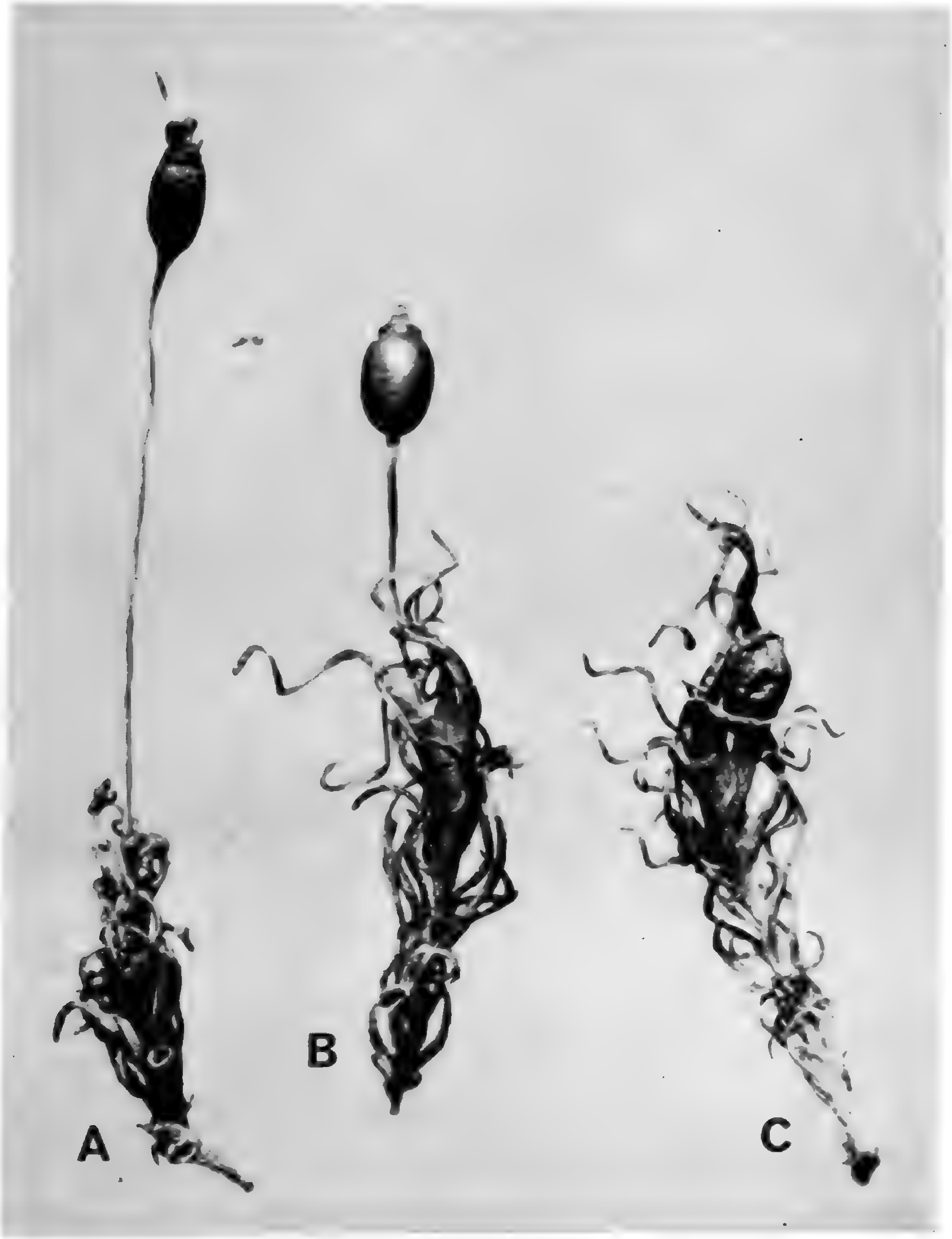

FIGURE 1. B. Hybrid sporophyte borne by female plant of *Astomum ludovicianum*. — C. Nearby plant of *A. ludovicianum*, with normal sporophyte. — A. Nearby plant of *Weissia controversa*, the paternal species. × 15.

muhlenbergianum parentage in any of the hybrids. Stating that "no authors have yet been able to demonstrate any significant or convincing differences between the gametophytes of *W. controversa* and *A. ludovicianum*," Reese and Lemmon felt that "either species may serve as male or female parent." All of the hybrid sporophytes that we have examined in herbarium specimens (*Reese* 7925; LAF, DUKE), however, are on *Astomum* gametophytes (Fig. 1). It seems probable, therefore, that the Louisiana hybrids all resulted from *A. ludovicianum* ♀ × *W. controversa* ♂.

Reese and Lemmon found that most of the hybrid capsules they examined contained spores, but in some capsules the spores had obviously aborted and were shrunken, collapsed, or arrested in tetrads. A few hybrid capsules contained no spores or only an amorphous mass of tissue around the columella. Spores from seven capsules of the hybrid were tested for viability by sowing on Benecke's nutrient agar. Viability ranged from 0 to 2%; two capsules contained all non-viable spores, while the remaining five yielded 7, 8, 8, 15, and 22 germinating spores, respectively. Attempts to grow leafy gametophytes from the protonemata of these viable hybrid spores failed (personal communication), but the failure could have resulted from less than optimum cultural conditions.

Claire Williams (1966) reported hybrid sporophytes which she attributed to *Astomum muhlenbergianum* ♀ × *Weissia controversa* ♂. They were generously intermixed with normal sporophytes of the two parents on heavy clay soils in well-established permanent pastures near Thedford, Lambton County, in southern Ontario. The hybrids were clearly intermediate between the two parents. Hybrid capsules contained spores about 22μ, but many were described as "imperfect." Attempts to germinate the hybrid spores were unsuccessful.

Among the genera, *Astomum*, *Hymenostomum* and *Weissia*, thirteen species have been investigated cytologically (Table 2). Of these, ten species have populations with the number, $n = 13$; three species have populations with the number, $n = 13 + m$; three species have polyploid populations, $n = 26$. Populations with and without the m-chromosome have been reported in *A. crispum* and *W. controversa*. Diploid and tetraploid populations, $n = 13$ and 26, are known in *H. microstomum*. These numbers are in close accord with those reported for other members of subfamily Trichostomoideae (Pottiaceae).

Chromosome numbers, based on North American populations, have been published for the three species reported to be involved in the formation of natural hybrids. Steere, Anderson, and Bryan (1954) recorded the number, $n = 13$, for two Californian populations of *W. controversa* (as *W. viridula* Hedw.), and the same number has since been found in four populations in North Carolina (Bryan, 1956; Al-Aish & Anderson, 1961) including a single population identified as var. *longiseta* (Lesq. & James) Crum, Steere & Anderson (as var. *australis*), and in single populations in Ohio (Anderson & Lemmon, 1967) and Iowa (Messmer & Lersten, 1968). The number, $n = 13 + m$, has not heretofore been recorded for North American populations of *W. controversa*.

Bryan (1956) has published the only chromosome numbers for North American species of *Astomum*. She found the number, $n = 13$, in a single population of *A. ludovicianum* and the number, $n = 26$, in two populations of *A. muhlenbergianum*; each collection came from North Carolina. She found the chromosome morphology in each species similar to *Weissia controversa*, except for the doubled number in *A. muhlenbergianum*. Meiosis was completely normal in the tetraploid, however. She observed no multivalents, and she mentioned no secondary associations of bivalents. A large bivalent, which has been described as characteristic of nearly all the species of this complex which have

TABLE 2. Summary of chromosome numbers reported for the three genera, *Astomum*, *Hymenostomum* and *Weissia*.

	Haploid number n =	Location	Reference
Astomum			
A. crispum	13	Japan	Sannomiya, 1958
	13	India	Khanna, 1959*a*, *b*; 1960*a*, *b*
	13	Hungary	Györffy, 1964
	13 + m	India	Khanna, 1960*a*, *b*
A. exserta	26	India	Khanna, 1960*a*, *b*
A. ludovicianum	13	USA	Bryan, 1956
A. muhlenbergianum	26	USA	Bryan, 1956
Hymenostomum			
H. krassavinii	13 + m	USSR	Lazarenko *et al.*, 1968
H. microstomum	13	Hungary	Györffy, 1964
	13	USSR	Visotskaya, 1967
	13	England	Smith & Newton, 1968
	13	USSR	Lazarenko *et al.*, 1969
	26	USSR	Visotskaya, 1967
H. papillosissima	13	USSR	Lazarenko, 1967
	13	USSR	Lazarenko *et al.*, 1970
H. tortile	13	USSR	Visotskaya, 1967
	13	USSR	Lazarenko *et al.*, 1969
Weissia			
W. controversa	13 + m	Finland	Vaarama, 1950
	13	USA	Steere *et al.*, 1954
	13	Japan	Sannomiya, 1955
	13	USA	Bryan, 1956
	13	India	Khanna, 1960*a*, *b*
	13	USA	Al-Aish & Anderson, 1961
	13	Hungary	Györffy, 1964
	13	USA	Anderson & Lemmon, 1967
	13	USSR	Visotskaya, 1967
	13	USSR	Lazarenko *et al.*, 1967
	13	England	Smith & Newton, 1967
	13	USA	Messmer & Lerston, 1968
	13	USSR	Lazarenko *et al.*, 1968, 1969
	13	Wales	Ramsay, 1969
var. *longiseta*	13	USA	Anderson & Bryan, 1958
var. *densifolia*	13	England	Smith & Newton, 1967
var. *edentula*	8	India	Gangulee & Chatterjee, 1960
W. fallax	13	Wales	Smith & Newton, 1967
W. longidens	13	Japan	Sannomiya, 1955
W. occidentalis	13	England	Smith & Newton, 1968
W. rutilans	13	USSR	Visotskaya, 1967

been investigated (Table 2), was noted by Bryan to be present in *A. muhlenbergianum*, but she did not indicate if it was present in duplicate, as might be expected if autopolyploidy is involved.

There are no published accounts of meiotic or other chromosome studies

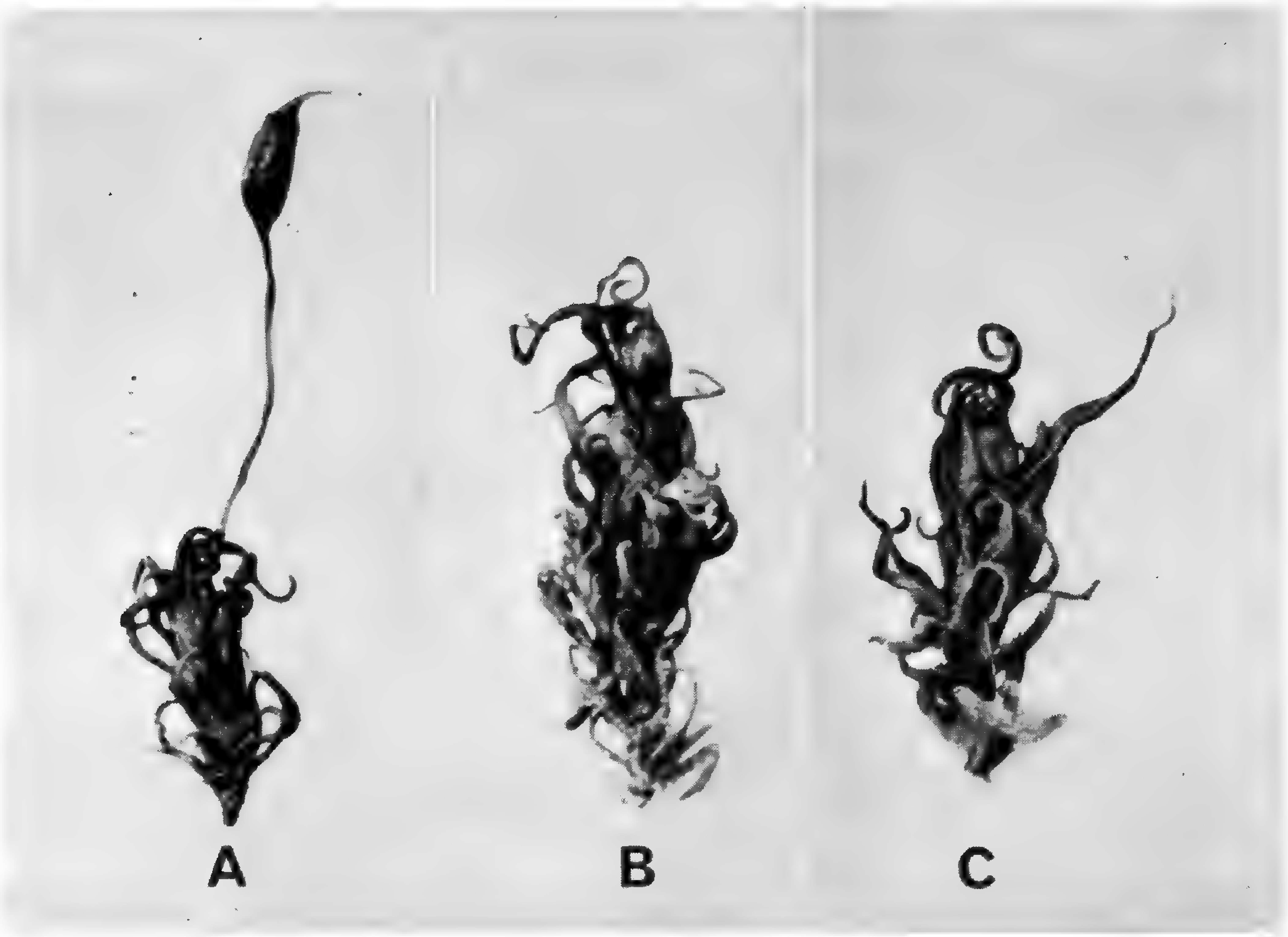

FIGURE 2. B. Hybrid sporophyte borne by female plant of *Astomum muhlenbergianum.* — C. Nearby plant of *A. muhlenbergianum,* with normal sporophyte. — A. Nearby plant of *Weissia controversa,* the paternal species. × 15.

of the *Astomum* × *Weissia* or other hybrids in this species complex. If Khanna (1960*a*, *b*) has made the correct interpretation that *A. exserta* is an amphidiploid, involving *A. crispum* × *W. controversa,* his studies include the first cytological analysis of a natural hybrid.

The present study was begun in 1966, as a joint undertaking, to investigate meiotic chromosome behavior in available natural intergeneric hybrids in *Weissia* and *Astomum,* and to examine meiosis and variations in chromosome number among different populations of the parental species. This paper presents the results of meiotic studies of two natural hybrids, *A. ludovicianum* ♀ × *W. controversa* ♂ and *A. muhlenbergianum* ♀ × *W. controversa* ♂, and a preliminary report on intraspecific chromosome variations in the species involved. Possible applications of the results to the taxonomy of the complex, specifically the status of the genus *Astomum,* and to problems of reproductive isolation are discussed.

MATERIALS AND METHODS

Weissia controversa occurs throughout North America. It is semi-weedy and is often found in disturbed areas. It is most abundant in the southern United States, becoming less and less common to the north and to the west. Tolerant of full shade to full sunlight, it is restricted to bare soils and rocks. It is never epiphytic or epixylic. Road banks, pastures, lawns, and waste places that are sparsely vegetated are favored sites, but it is also found on bare patches of soil in woods. The species is not tolerant of high moisture, apparently, preferring xeric or mesic situations.

Astomum muhlenbergianum is confined to eastern North America, where it ranges from southern Canada to the Gulf of Mexico. *Astomum ludovicianum* is restricted to southern United States, extending north to Kentucky, West Virginia, and Maryland. The two species of *Astomum* share identical habitats with *W. controversa*, and occasionally the three species are found together.

Phenological development is approximately the same in all three species. In Florida and the Gulf States, meiosis begins in some capsules in November and continues into March, when most capsules are mature. The largest number of capsules in meiosis was found in January in the Gulf area. In the Middle Atlantic States, capsules can be found in meiosis more or less continuously from early September to June. The largest number of capsules in meiosis was found in November and in March, decreasing markedly during the colder months of December, January, and February. Across the northern United States and in the West, the meiotic season apparently lasts from March to August, being later at more northern latitudes and higher altitudes. We have few observations, however, for northern and western regions.

All of the spore mother cells of a single capsule undergo meiosis at about the same time, but there is usually considerable spacing of stages among different capsules of the same clump. In a single clump a succession of meiotic capsules may extend over a period of two months. Occasionally in the Southeast, some of the capsules in a clump will undergo meiosis in the fall, while the remaining capsules delay meiosis until spring.

There is a prodigious production of sporophytes in *Weissia controversa* and in both species of *Astomum*. Partly, this is due to the large number of archegonia, up to eight in each perichaetium, and antheridia, up to twenty in each perigonium. Only about 10% of the archegonial plants produce perigonia, but nearly every plant produces archegonia. Also, both archegonia and antheridia develop sequentially over a period of several months. During the fertile period, at any one time a perichaetium will contain from one to three receptive archegonia, and a perigonium will have usually one or sometimes two ripe antheridia.

All of the chromosome studies described here were obtained from living capsules brought into the laboratory, where the preparations were made and studied immediately. Permanent slides were not made. Mitotic preparations were not attempted.

Samples for cytological examination were collected in polyethylene bags and labeled with locality, habitat, and date of collection. They were then sealed and usually placed in an ice chest until taken to the laboratory, where they were stored at about 5°C. until they were studied. As noted by Anderson and Crum (1958), we found no effects of low temperature on meiosis except that its rate is decreased. If proper humidity conditions are maintained in the plastic containers, and if there is sufficient number of properly spaced stages of younger capsules, a succession of meiotic capsules can be maintained in a clump for six weeks or longer. If plants are kept too moist, they will be overrun with molds and bacteria. If they are too dry, capsules shrivel and meiosis stops or becomes aberrant.

Meiosis occurs in all of the species studied after the capsule has reached its full size, and while it is still green. Capsules which have developed a slight yellowish hue and a characteristic translucence are apt to be in meiosis. Usually, when capsules become distinctly yellow and begin to look opaque, meiosis is complete. When growing in full sun, walls of the urn and rarely the beak develop considerable reddish coloration before the onset of meiosis. This obscures all external clues, making it necessary to resort to chance and trial and error.

The cytological techniques used were essentially the same as those described by Steere, Anderson and Bryan (1954) with some of the modifications added that were outlined by Anderson and Crum (1958), especially those pertaining to the handling and storing of living material. Only a brief outline of the procedures will be given here.

Promising capsules were selected, the contents squeezed out in a drop of Carnoy's solution (3:1), a drop of water, or directly into a drop of dye on a clean slide. The sporocytes were freed from the columella and any extra debris removed. If the dissection was carried out in water, as soon as the sporocytes were free, the water was removed with a piece of absorbent paper, and the fixative or dye was then applied. Dissections in the fixative were allowed to stand until most of the fixative evaporated, and then the dye was applied. Any one of these three procedures is entirely satisfactory. The dye used was acetic orcein (synthetic orcein saturated in 45% acetic acid and filtered). After applying a cover glass, the slide was heated almost to boiling several times in succession. The chromosomes were then spread and flattened by repeated tapping and by pressing on the cover glass. The progress of this operation was checked at intervals under the microscope. When the preparation was completed, the cover glass was sealed by ringing with petroleum jelly. Occasional slides were allowed to stand overnight to improve the staining.

A complete series of voucher specimens was deposited either in the herbarium of Duke University (DUKE) or the University of Southwestern Louisiana (LAF).

OBSERVATIONS

1. Polymorphism for Chromosome Numbers

Early in this study the chromosome numbers, $n = 13$ and $n = 13 + m$, were discovered in *Weissia controversa*[4], and $n = 13$, $n = 13 + m$, and $n = 26$, in both *Astomum ludovicianum* and *A. muhlenbergianum*. We addressed our-

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[4] The number, $n = 26$, was discovered in a few populations in Tennessee, Missouri, and Arkansas. These plants had previously been identified as *Weissia controversa*, but they possess morphological and habitat distinctions which we think may justify separating them taxonomically. We are currently examining this question.

selves first to the question, how are the different chromosome numbers distributed within or among populations?

As Stebbins (1950) points out, the term population has no precise meaning, but it generally denotes a group of interbreeding individuals. Almost nothing is known about breeding systems in mosses. Gene flow distances are completely unknown. We can only make inferences based on knowledge of where the sex organs are produced, how they are distributed among the leafy plants, and specific growth habits of the species involved. There is even less information concerning spore dispersal and how local populations spread.

Weissia and *Astomum* are caespitose and, with few exceptions, grow in distinct, clearly delimited clumps, consisting of hundreds of more or less tightly compacted leafy gametophytes. Plants are autoicous, but only about 10% of the archegonial plants bear antheridia, a device that increases cross-fertilization within the clump. It is not known whether the clump is clonal, whether it originates from a single spore or from a vegetative propagule, whether it comes from more than one spore from the same capsule or from different capsules. These are important questions that require study.

The clump itself, however, would appear to be the interbreeding unit in these species. It is not easy to visualize movement of sperm from one clump to another, unless the clumps are contiguous. Perhaps, the moss clump corresponds to the "local population" or "deme," which Mayr (1970) defines as "a group of individuals so situated that any two of them have equal probability of mating with each other and producing offspring." At any rate, we have chosen to use the clump as the population unit, and we shall use the terms clump and population interchangeably. We realize this is a narrow application of the term population. Some might wish to use sub-population or an even lesser designation. But, if we expand the meaning of population beyond the individual clump, we have no notion where to stop. The clump comprises a discrete group of interbreeding individuals and, until we know in mosses how much comprises what Mayr (1970) terms "the community of potentially interbreeding individuals at a locality," it is a practical unit for study. If two or more clumps were found overlapping, they were regarded as a single population in this study.

To determine whether individual clumps contained plants with different chromosome numbers, a series of sampling studies were carried out with *Weissia controversa*, with populations from four areas. At each locality, from four to six individual clumps were taken from an area of approximately 100 m × 10 m. All of the habitats were road banks, along which clumps were distributed, usually scattered in bare spots among grasses. Originally, the intent was to sample 20 capsules from each clump. The number was soon dropped to 10, because of the work involved and because not every clump yielded 20 capsules in meiosis. Even a goal of 10 was unattainable in several clumps. The results are shown in Table 3.

The data in Table 3 indicate there is a high degree of uniformity in chromosome number within individual populations. This inference is strengthened by the fact that we have also examined from 3 to 5 capsules from hundreds of

TABLE 3. Chromosome numbers of sampled capsules from individual populations from four different areas. Collection numbers are those of Lewis E. Anderson, and specimens are on file in the Duke Herbarium.

Locality	Date	Collection Number	No. Capsules Examined	Chromosome Number n = 13	Chromosome Number n = 13 + m
Durham, N. C.	12/'67	20,212	12	12	
		20,213	15		15
		20,214	19	19	
		20,215	11	11	
		20,216	20	20	
		20,217	11		11
Washington,	12/'68	20,457	8	8	
Alabama	12/'68	20,458	10	10	
		20,459	10	10	
		20,460	6	6	
		20,461	10	10	
		20,462	4	4	
Live Oak,	1/'70	20,763	10	10	
Florida		20,767	10		10
		20,768	8	8	
		20,769	9	9	
Mayo,	1/'71	21,009	10		10
Florida		21,010	10	10	
		21,011	10	10	
		21,012	9		9
		21,013	6	6	

populations of *Weissia controversa*, distributed over an even wider geographical area, and we have not encountered a single polymorphic population. Nothing short of determining the chromosome number of every plant in a clump can establish beyond doubt that a population contains only a single number, but if mixed populations exist they are either rare or the frequencies of plants with supernumerary chromosomes are so low they are difficult to demonstrate through sampling.

The question of whether individual populations are clonal is still not answered. This will have to be studied experimentally, hopefully in the field under natural conditions. The data do indicate, however, that there is limited mixing of propagules during dispersal or else protonema from a single propagule gains dominance and crowds out competitors. The former seems more likely.

2. Non-random Distribution of Supernumerary m-chromosome Populations

Preliminary observations indicated that populations of *Weissia controversa* with m-chromosomes are not distributed at random. This prompted us to expand the studies geographically and to sample as many populations as practicable over as large an area as we could manage. Between 1966 and 1969, we obtained counts from 460 populations of *W. controversa*, 17 of *Astomum ludovicianum*, and 10 of *A. muhlenbergianum*. The scarcity of collections of the two species of *Astomum* reflect not only their infrequent occurrences,

TABLE 4. Distribution of cytological collections of *Weissia controversa*, by states, and the number and percentages of n = 13 populations and 13 + m populations in each state.

		Chromosome Number			
		n = 13		n = 13 + m	
State	Total Number of Collections	Number of Collections	%	Number of Collections	%
Alabama	58	47	82	11	18
Arkansas	16	14	87	2	13
Florida	33	27	82	6	18
Georgia	72	67	93	5	7
Louisiana	70	59	80	11	20
Mississippi	39	30	77	9	23
North Carolina	78	59	76	19	24
South Carolina	35	25	72	10	28
Tennessee	29	29	100	0	0
Virginia	12	12	100	0	0
Others	18	17	–	1	–
Totals	460	386	84	74	16

but their camouflaged habits, as well. Collections of the three species were distributed over 17 states and 2 provinces of Canada, but the collections were mainly centered in 10 southern and southeastern states. Much of the collecting was carried out fortuitously while both of us were travelling on other business, and some collections were shipped to us by colleagues. Sampling, therefore, was not always by design, and much of it was carried out along road banks of arterial highways.

Since the bulk of the data referring to the distribution of chromosome numbers involve populations of *Weissia controversa*, we have segregated the data for this species. The results are compiled in Table 4, arranged by states, and include frequencies of chromosome numbers for each state. States for which we have fewer than 10 collections are combined.

The 13-chromosome populations comprised 386 or about 84% of the clumps examined, while populations with the number, n = 13 + m, totalled 74 or about 16%. Excepting Georgia, whose low m-frequency is due to a strong bias in collecting in mountains and Piedmont, the differences in frequencies of the m-chromosome-populations from state to state are not very striking.

If the population samples are grouped according to physiographic province, however, a strong non-random pattern is revealed. The results are shown in Table 5. Ozarks, Cumberlands, and Appalachians are grouped together as Mountains.

The m-chromosome frequency is approximately 23% in the Atlantic Coastal Plain, in contrast to only 12% in the Piedmont Plateau and less than 3% in the Mountain Provinces. It should be pointed out that we have not studied any populations in the Coastal Plain north of North Carolina.

Not enough populations of either species of *Astomum* were studied to

TABLE 5. Distribution of m-chromosome populations according to physiographic province.

Physiographic Province	Total Number of Collections	Chromosome Number			
		n = 13		n = 13 + m	
		Number of Collections	%	Number of Collections	%
Coastal Plain	254	197	77	57	23
Piedmont	118	104	88	14	12
Mountains	75	73	97	2	3

establish reliable frequencies for the different chromosome populations. Seventeen populations of *A. ludovicianum* were studied. Eleven had the number, n = 13 (6 in Louisiana, 3 in North Carolina, 1 in Florida, and 1 in Kentucky), while three had the number, n = 13 + m (all from Louisiana). In addition, two populations (one each from Mississippi and Georgia) were tetraploid, n = 26.

Ten populations of *Astomum muhlenbergianum* were studied. Seven had the number, n = 13 (3 in North Carolina, 2 in Louisiana, and 1 each in Kentucky and Tennessee). A single population with the number, n = 13 + m, was discovered in Louisiana, while two tetraploid populations, n = 26, were found in North Carolina. Bryan (1956) also found two tetraploid populations of this species in North Carolina.

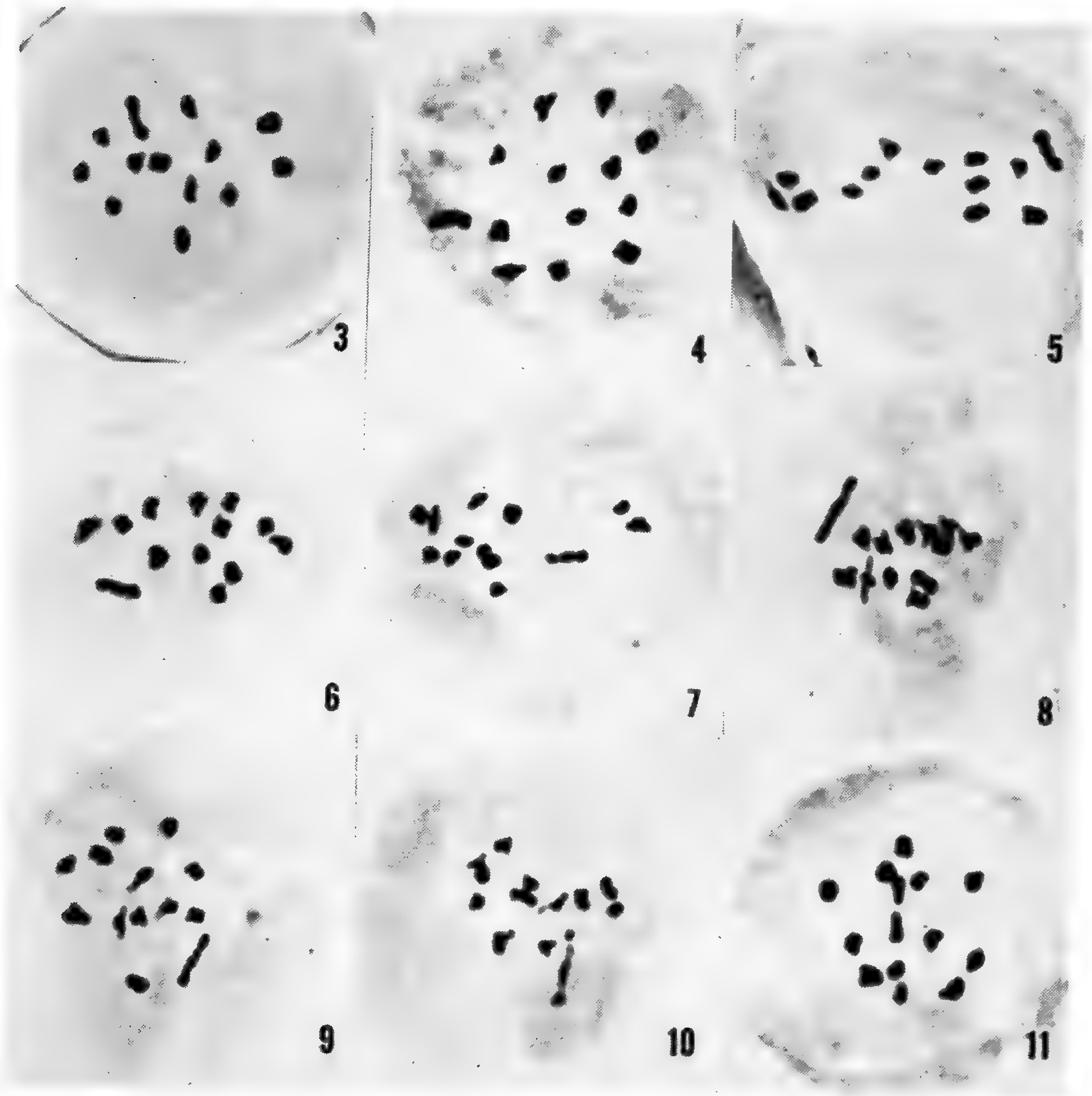
3. The Standard Meiotic Complement

The standard chromosome complement is similar, if not identical, in the three species, *Weissia controversa* (Figs. 3–11), *Astomum ludovicianum* (Figs. 21–23), and *A. muhlenbergianum* (Figs. 30–32). The number, n = 13, is regarded as the standard complement, not only in this complex, but probably in all of the sub-family Trichostomoideae.

The complement is characterized by the presence of a conspicuous, rod-shaped bivalent (Figs. 3–10, 21–22), which is about 2 μ long when completely condensed. It is held together by a single terminal chiasma, and has a primary sub-median kinetochore and a sub-terminal secondary constriction (Fig. 10). During prometaphase the large rod-shaped bivalent undergoes pronounced stretching (Figs. 8–10), and nearly always disjoins earlier than the other bivalents.

The remainder of the complement consists of twelve even-sized bivalents, averaging about 1 μ long. None of the individuals in this group of small bivalents could be recognized from cell to cell. Kinetochore positions were not established.

Except for the large bivalent, it was not possible to estimate chiasma frequencies. Diplotene and diakinesis are rarely observed in any moss, and *Weissia* and *Astomum* are not exceptional. When a rare sporocyte was encountered in diplotene or diakinesis, the chromosomes were so clumped and so poorly delineated that it was not possible to analyze the configurations.



FIGURES 3–11. Meiotic chromosomes of *Weissia controversa*, n = 13, the standard complement. — 3–7. Polar views of prometaphase figures from North Carolina, Louisiana, Kentucky, Ohio, and British Columbia, respectively, showing uniformity in meiotic complements. — 8–10. Prometaphase, showing degrees of stretching of the large, rod-shaped bivalent. — 11. Prometaphase, showing early disjunction of the largest chromosome. × 1905.

Of possible significance, were the observations in occasional sporocytes of *Weissia controversa*, and in a single sporocyte of *Astomum ludovicianum*, in which there was obvious secondary pairing among ten of the twelve smaller bivalents. In Figure 23, from a population of *A. ludovicianum*, from North Carolina, five pairs of bivalents are secondarily associated. Three pairs are in tight association, while two pairs are more loosely paired. The large, rod-shaped bivalent and two of the smaller bivalents are unassociated. In each observed instance of secondary pairing, ten bivalents, forming five secondary pairs, were always involved. Whether they are the same bivalents in each case could not be determined, since the smaller bivalents are unidentifiable.

These observations are pertinent if a lower basic chromosome number for the complex is considered. Gangulee and Chatterjee (1960) reported the number, n = 8, in a population of *Weissia controversa* var. *edentula* (Mitt.) Chen, from India, which, although the count needs reconfirming, is indicative of a lower basic number. If the five secondary pairs which we observed in *W. controversa* are duplications, then five of these bivalents added to the three unassociated bivalents makes a total of 8, which is the number reported by Gangulee and Chatterjee in the Indian variety. This is a tantalizing parallel, which may not be coincidental.

4. The Supernumerary m-chromosome

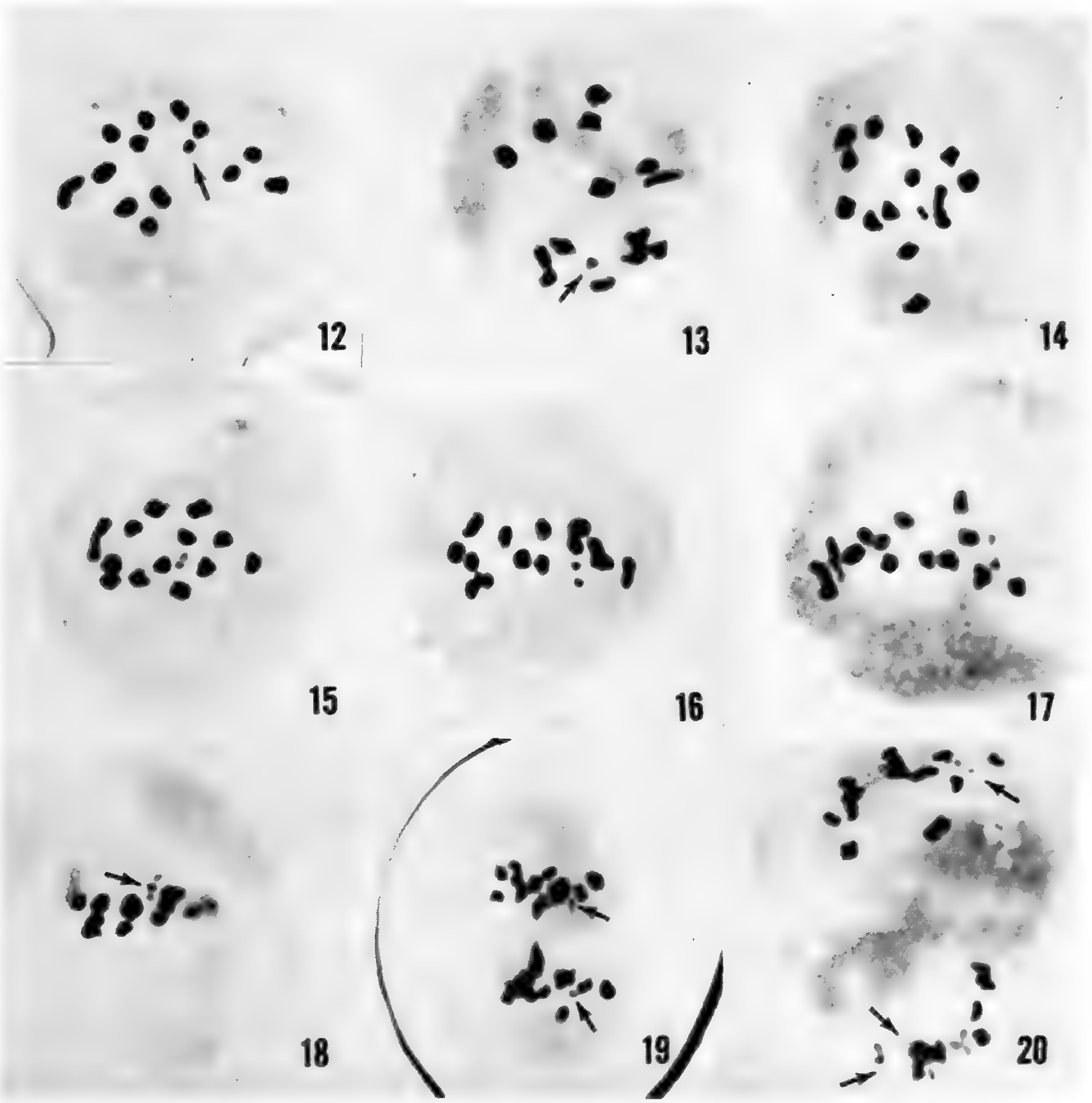
We discovered m-chromosome populations in all three species, *Weissia controversa* (Figs. 12–20), *Astomum ludovicianum* (Figs. 24–26), *A. muhlenbergianum* (Figs. 33–35), and in the natural hybrid *A. ludovicianum* ♀ × *W. controversa* ♂ (Figs. 39–42). No differences in form or behavior could be detected among the m-chromosomes of the three species or the hybrid. The descriptions that follow, therefore, apply equally to the three species, and references will be made interchangeably to figures of all the species and the hybrid.

The supernumerary chromosome observed matches the m-chromosomes which have been described in the literature for a broad range of moss species (Heitz, 1927; Vaarama, 1950, 1953; Steere, Anderson & Bryan, 1954; Bryan, 1955; Yano, 1957*a–c*, as h-chromosomes; Anderson & Bryan, 1958; Anderson, 1964; Smith & Newton, 1967; and others). From the descriptions of these investigators, m-chromosomes can be characterized as follows: They are heteropycnotic in mitotic and meiotic interphases and during prophase I of meiosis; they are largely heterochromatic; they often stain less intensely with orcein and carmine at metaphase I; rarely, they are negatively heteropycnotic; they assume a complex variety of configurations and numbers at prometaphase and early metaphase I in different sporocytes of the same capsule.

Yano (1957*a–c*) and Inoue (1968, 1969), among others, have established that the usual m-chromosome complement in gametophytic tissues of mosses consists of one small, heteropycnotic chromosome. The complement for sporophytic tissue has been shown by many investigators to consist of two m-chromosomes. Both *Weissia* and *Astomum* are autoicous, and the populations or clumps are probably mostly clonal. Thus, inbreeding is the rule. These facts, coupled with observations that m-chromosomes are stable in populations that have been watched over a period of years, strongly indicate that the diploid sporophytic m-pairs are homologous. They pair physically during meiosis, forming bivalents. Being heteropycnotic during prophase I, however, would preclude the formation of chiasmata. The bivalent configurations, therefore, are assumed to be achiasmic.

Within a single capsule, four different numbers and configurations of m-chromosomes were observed at prometaphase or early metaphase I. They will be described separately.

(1) The m-chromosomes are united into a single, more or less tightly



FIGURES 12–20. Meiotic chromosomes of *Weissia controversa*, n = 13 + m, the supernumerary complement. — 12–13. Prometaphases, each showing 13 bivalents plus the tightly associated achiasmic, m-chromosome. — 14–17. Prometaphase figures, showing distance association of the two homologous m-chromosomes. — 18. Early metaphase I, with tripartite configuration of m-chromosome, composed of a half-bivalent and two chromatids. — 19. Anaphase I, showing a single m-half-bivalent near each pole. — 20. Late anaphase I, showing two m-chromatids at each pole. × 1905.

associated bivalent (Figs. 12–13, 24, 33–34, 39). Sporophytes with this configuration present a straightforward appearance of 13 regular bivalents plus the m-bivalent. This basic configuration, which is repeated in nearly all mosses with m-chromosomes, has provided the rationale for the customary notation, n = 13 + m.

(2) The two m-chromosomes are not physically paired (Figs. 14–17, 19, 35). The two presumed homologs may be almost touching (Fig. 14) or they may be separated by varying distances (Figs. 15–17, 35). A distance-pairing relationship, however, is always evident. At anaphase I, the two homologous

elements move to opposite poles (Fig. 19), each chromosome divides during second division, and the four m-chromosomes are distributed one to each of the tetrad nuclei.

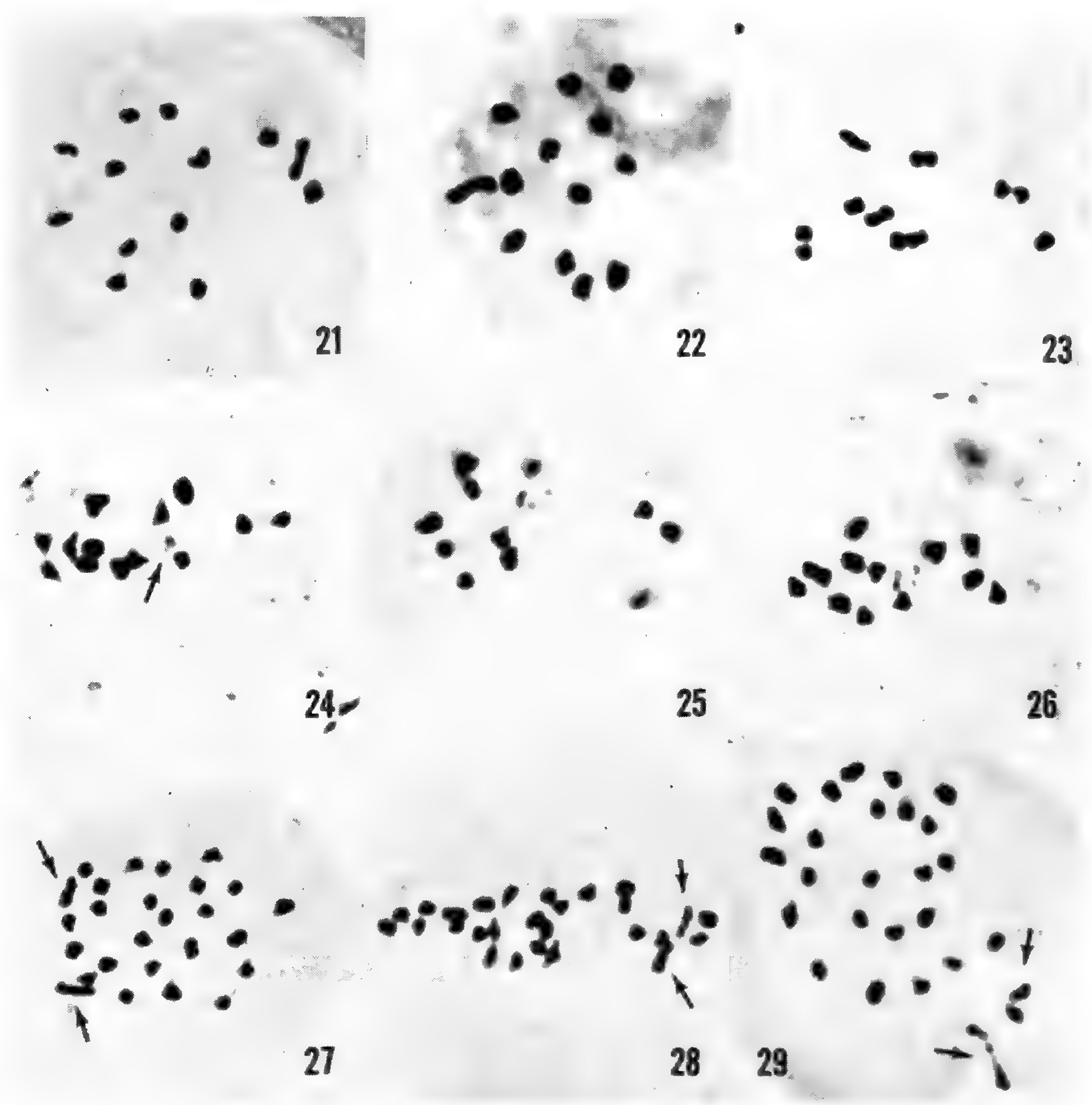
(3) The m-chromosomes are in a heteromorphic, tripartite configuration (Figs. 18, 25, 40). One of the three chromosomal elements is approximately twice as large as the two smaller elements. This is especially evident in Figure 25. Obviously, this configuration results from the division of one of the two distantly associated chromosomes described in (2). Tripartite associations were observed as early as prometaphase. During anaphase I, the single undivided m-chromosome moves to one pole, and the divided chromatids move independently but synchronously to the opposite pole (Fig. 42). In the latter figure, the two divided chromatids are at the lower pole; the undivided single chromosome is at the upper pole, where unfortunately it is somewhat obscured because it lies over another chromosome.

(4) The m-chromosomes are in a quadripartite configuration (Figs. 26, 41). This configuration was least commonly observed. It results from the division of both of the distantly associated chromosomes described in (2). Thus, the four chromosomal elements of the quadripartite association are chromatids, one of which is destined for each of the eventual tetrad nuclei. In Figure 41, which is a prometaphase sporocyte, at 9 o'clock there are four chromatids arranged in two's. The lower pair is slightly out of focus. Usually, each pair of chromatids is separated by fine chromosomal fibers (Fig. 26). During metaphase I and anaphase I, each of the four chromatids orients independently but as pairs, one pair moving to one pole the other pair to the opposite pole. In Figure 20, a pair of separated chromatids can be seen at each pole (arrows). The chromatids in the lower anaphase group of the photograph are slightly out of focus, which explains why they appear lighter in color.

At least three interpretations can be invoked to explain the variability in m-chromosome configurations described above.

The first interpretation assumes that the achiasmic m-bivalent, as seen, for example in Figures 12 and 13, undergoes desynapsis (Fig. 14) during prometaphase, forming two homologous half-bivalents (Figs. 15–17). According to this interpretation, each half-bivalent orients syntelically at metaphase I, or di-syntelically (co-orientation) with respect to each other, and moves to opposite poles during anaphase I (Fig. 19). Each half-bivalent then orients amphitelically (auto-orients), and an m-chromatid is distributed to each tetrad nucleus.

Based on this interpretation, variations in numbers of m-chromosome elements are explained in the following ways. Tripartite configurations represent desynapsed half-bivalents in which one of the half-bivalents has divided into its two sister chromatids and the homologous half-bivalent remains undivided, which explains the larger size of the latter (see Fig. 25). The undivided half-bivalent then orients syntelically, and the distantly associated sister chromatids orient independently and syntelically with respect to each other. The divided sisters and the undivided half-bivalent, however, orient di-syntelically with respect to each other, and in anaphase I, the undivided half-bivalent moves to



FIGURES 21–29. Prometaphase and metaphase meiotic figures of *Astomum ludovicianum*, showing different chromosome numbers. — 21–22. The standard complement, n = 13. — 23. Prometaphase of the standard complement, in which ten bivalents are secondarily paired. — 24–26. The supernumerary complement, n = 13 + m, showing respectively a bivalent m-configuration, a tripartite and a quadripartite m-chromosome association. — 27–29. Tetraploid meiotic figures, showing the duplicated long chromosome (arrows), and in Fig. 29, one of the long chromosomes is undergoing prometaphase stretching. × 1905

one pole, and the two sisters move together to the opposite pole (Fig. 42). Quadripartite configurations originate similarly, except that both half-bivalents divide into their respective sister chromatids (Figs. 26, 41). Thus, the two pairs of distantly associated sister chromatids move independently to the equator and the two pairs of sister chromatids orient di-syntelically, and move to opposite poles. The various configurations according to this interpretation therefore represent different degrees of disassociation of an achiasmic bivalent into two half-bivalents, one half-bivalent and two sister chromatids, or four sister chromatids.

A second interpretation assumes that both asynapsis and synapsis occur in different sporocytes. Thus, in configurations with distantly associated m-chromosomes (Figs. 16, 17, 35, for example), the latter could be half-bivalents or univalents, depending upon whether they had previously synapsed and have since desynapsed or whether they originally paired distantly and have never been in contact. This can not be determined with fixed preparations.

A third interpretation which cannot be ruled out is that in some or all sporocytes, post-reduction takes place. This interpretation assumes that an m-bivalent divides into half-bivalents, each of which is composed of non-sister chromatids. Segregation is postponed until second division. If post-reduction occurs, tripartite configurations (Figs. 18, 25, 40, 42) consist of a half-bivalent and two non-sister chromatids, while quadripartites (Figs. 20, 26) comprise two pairs of non-sister chromatids.

In summary, since m-bivalents are present throughout all of the material studied, many of the distantly associated m-chromosomes observed at prometaphase and metaphase I must comprise two desynapsed half-bivalents. It cannot be proved, however, that some are not distantly associated univalents. The designation, $n = 13 + 1mII/2mI$, might be more appropriate for populations containing the m-chromosomes. It says the population contains 13 regular bivalents plus 1 m-bivalent or 2 m-univalents.

5. The Tetraploid Complement

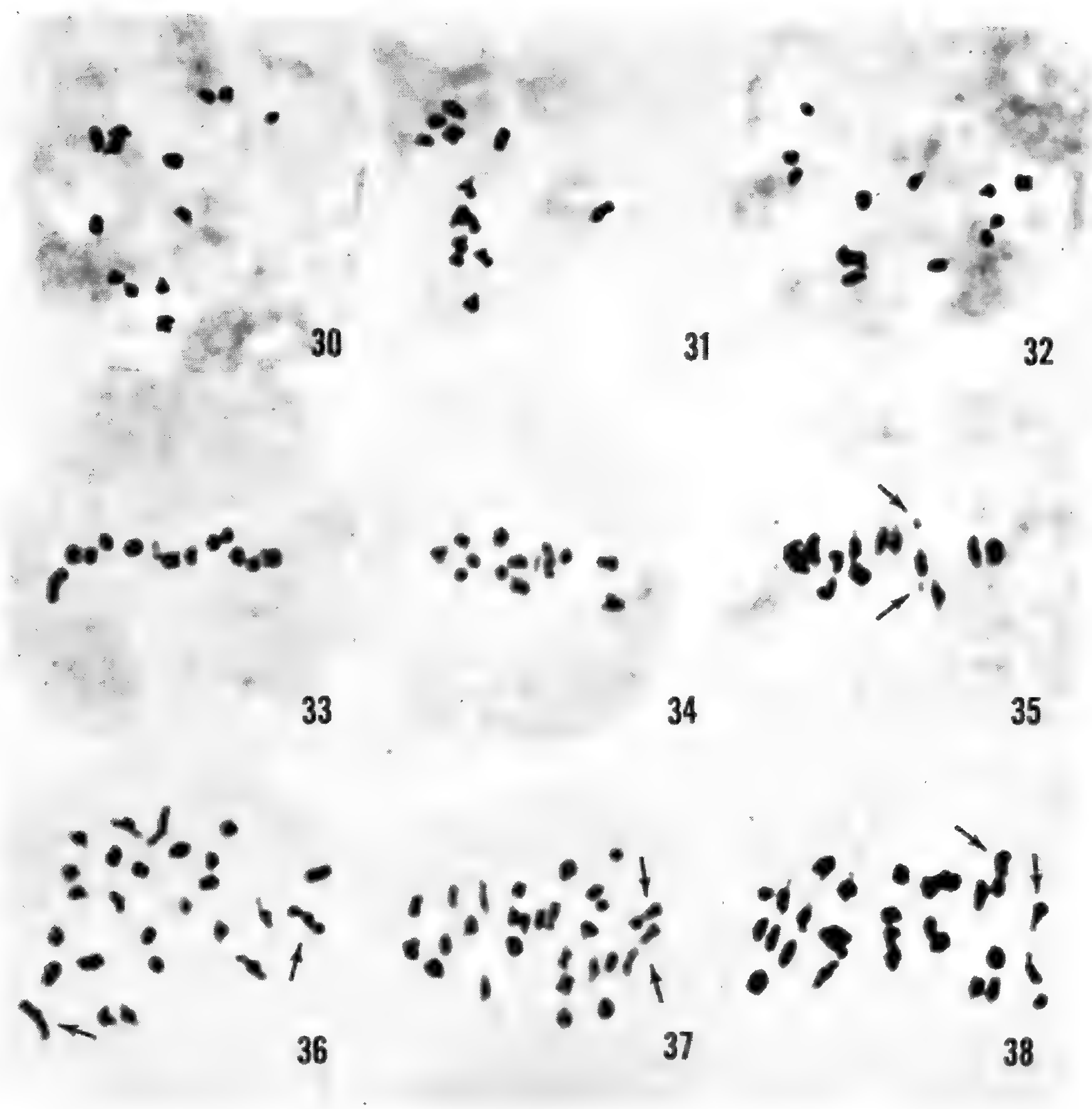
Single tetraploid populations of *Astomum ludovicianum* were encountered in Georgia and Louisiana. These are the first records of tetraploids in this species. Figures 27 to 29 are from the Georgia population. Two tetraploid populations of *A. muhlenbergianum* (Figs. 36–38) were found in North Carolina, where Bryan (1956) also found two tetraploid populations of the same species.

As in the diploids, the tetraploid complement is outwardly identical in the two species. As expected, the large rod-shaped bivalent described in the diploids, is in duplicate (Figs. 27–28, 36–37), as are the 12 indistinguishable, smaller bivalents. Respective sizes of bivalents are about the same in diploids and tetraploids. The large bivalents average about 2 μ in the tetraploids and the smaller about 1 μ.

At least one of the large bivalents undergoes prometaphase stretching (Fig. 29). In all of the tetraploid sporocytes observed, the two large bivalents disjoined asynchronously. In Figure 37, one of the large bivalents has almost separated, while its duplicate has scarcely begun anaphasic stretching. Similarly, in Figure 38, one of the large rods has completely disjoined, while the other is still tightly condensed.

Meiotic divisions in the tetraploids are completely regular, as far as we could determine. We observed no multivalents, no increase in lagging anaphase chromosomes over that observed in the diploids, no chromatin bridges, and the incidence of chromosomes which failed to get included in nuclei was no higher in the tetraploids than in the diploids.

Dr. Richard Zander kindly tested the viabilities of spores from three capsules from a tetraploid population of *Astomum muhlenbergianum*, from North Carolina,



FIGURES 30–38. Meiotic chromosomes of *Astomum muhlenbergianum.* — 30–32. The standard complement, n = 13. — 33–35. The supernumerary complement, n = 13 + m. — 36–38. The tetraploid complement, n = 26; note prometaphase stretching of the large bivalent in Fig. 37, and early disjunction of a similar bivalent in Fig. 38. × 1905

by sowing them on separate agar plates (Benecke's). He obtained 92%, 94%, and 89% germination from the three capsules. Spores from a diploid population similarly sown were, unfortunately, overrun by molds. Reese and Lemmon (1965), however, obtained 93% germination in a diploid population of *A. ludovicianum,* from Louisiana.

6. Morphological Comparisons of Populations with Different Chromosome Numbers

To determine if phenotypic differences are associated with different chromosome numbers, morphological comparisons were made. Randomly selected plants from each population were selected, washed in water and mounted on a slide in Hoyer's mounting medium. Each plant was scored for the following: total length of plant (gametophyte and sporophyte), length of old gametophyte, length of previous years gametophyte, length of leaf, width of leaf, length of the flattened leaf base, average cell size near the leaf tip, shape of leaf apex, degree of involution of leaf margin, total length of sporophyte, length of seta, length of vaginula, total length of capsule, length of urn, width of urn, length of operculum, annulus, peristome teeth, average size of exothecial cells, degree of thickening of exothecial cells, and size of mature spores.

Weissia controversa: Forty populations each with the number, $n = 13 + m$ and $n = 13$, were sampled. Attempts were made to select one population with each chromosome number from the same site, or at least from the same general area. The forty paired populations were distributed from Louisiana to North Carolina.

The same extremes of variations for all twenty characters were found in both chromosome populations. All characters were assigned quantitative values, and each character was plotted on graph paper to show numbers of populations with and without m-chromosomes for each value. The curves for the two chromosome numbers matched almost exactly, in all 20 characters. Morphological variations between the two chromosome populations are not significant.

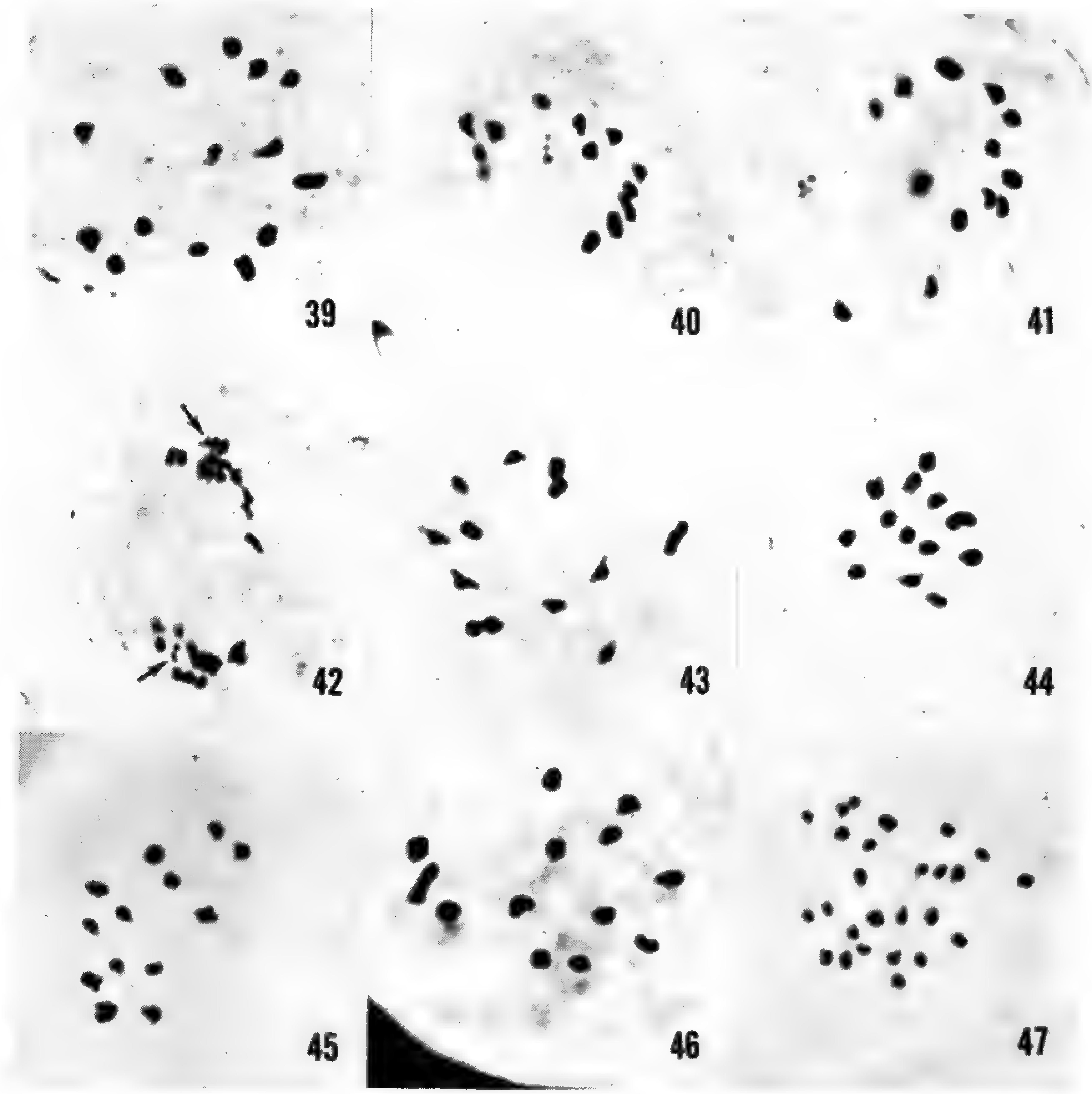
Similarly, the three chromosome races of both *Astomum ludovicianum* and *A. muhlenbergianum* were analyzed, using the same 20 morphological characters. No differences could be found between the three chromosome numbers of either species. Cell sizes and spore measurements did not average larger in the tetraploids than in the diploids, as might have been expected.

7. *Astomum ludovicianum* ♀ × *Weissia controversa* ♂

A swarm of hybrid sporophytes of this cross was discovered on clayey, poorly drained soil on a land fill about five years old on the east bank of the Vermilion River, near Lafayette, Lafayette Parish, Louisiana, on February 15, 1966 (*Betty E. Lemmon 1340*, LAF, DUKE). Meiotic stages were plentiful in hybrid capsules and in intermixed capsules of both parental species.

Plants of the parental species and hybrid sporophyte, which were growing together in a small clump, are illustrated in Figure 1. The photograph shows the male parental species, *Weissia controversa* (A), the female parental species, *Astomum ludovicianum* (C), and the hybrid sporophyte attached to a gametophyte of *A. ludovicianum* (B). These hybrids are identical, as far as we can determine, with those described by Reese and Lemmon (1965). The two hybrid localities are only 8 miles apart.

The contrasting gametophytes of *Weissia controversa* and *Astomum ludovicianum* are shown in Figure 1A and 1C. The latter has long spirally twisted leaves, with a broad, long, semi-sheathing base, and long attenuated leaf tips, while the former has leaves which are shorter, the bases are scarcely sheathing, and the leaf tips are shorter and more tightly crisped. The plants were photographed in a dried condition. It is apparent from the photograph, without having to resort to microscopic characters, that the gametophyte supporting the hybrid capsule in Figure 1B is *Astomum*, and not *Weissia*.



FIGURES 39–47. — 39–42. Meiotic chromosomes of the hybrid, *A. ludovicianum* × *W. controversa*; note absence of univalents in the standard complement. — 39. Prometaphase, with 13 tightly associated regular bivalents and one m-bivalent. — 40. Tripartite m-configuration. — 41. Quadripartite m-configuration. — 42. Late anaphase I, showing two m-chromatids at the lower pole and an undivided half-bivalent at the upper pole. — 43. Meiotic complement of *A. muhlenbergianum*, n = 13, maternal species of the Ontario hybrids. — 44. Meiotic complement of *W. controversa*, n = 13, paternal species of the Ontario hybrids. — 45–47. Meiotic chromosomes of the hybrid, *A. muhlenbergianum* × *W. controversa*, from southern Ontario. — 45–46. Prometaphase figures, showing 13 tightly associated bivalents. — 47. Early anaphase I, showing 13 half-bivalents during poleward movement; note regularity of separation. × 1905.

As can be seen in Figure 1A, the seta of *Weissia controversa* is long; the capsule is more or less cylindrical; the operculum is dehiscent; and the lid has a long, rostrate beak. In the photograph, the operculum is partially detached, revealing a well-developed peristome. The seta of the female parent, *Astomum ludovicianum* (Fig. 1C), is short, so that the capsule is immersed within the perichaetial leaves; the capsule is ovoid, the operculum is poorly differentiated and indehiscent; there is no peristome; and the beak is short and somewhat obtuse. The hybrid capsule, as seen in Figure 1B, is partially raised on a short seta (in this respect, there is considerable variation from hybrid to hybrid; the seta pictured is slightly longer than average); the capsule is oval-cylindrical; the operculum is differentiated, but still indehiscent; there is a rudimentary peristome inside; and the beak is longer than in *A. ludovicianum* but much shorter and less pointed than in *W. controversa.* The hybrid is described in more detail by Reese and Lemmon (1965).

Hybrid capsules contained few or no spores, which Reese and Lemmon (1965) also noted, but unlike the latter authors, who were able to obtain 2% viability of spores in some capsules, we obtained no spore germinations in viability tests of four capsules.

The chromosome number, $n = 13 + m$, was observed in all of the hybrid capsules examined (Fig. 39), which corresponded with the numbers found in capsules of adjacent parent species (*Weissia controversa*, Fig. 12; *Astomum ludovicianum*, Fig. 24). Surprisingly, in view of the high abortion rates and the almost complete sterility of the spores in the hybrid capsules, meiosis was observed to be completely regular. The thirteen regular chromosomes are totally compatible and formed tight, apparently chiasmic bivalents in all of the hybrid sporocytes examined. The m-chromosomes exhibited the same variable configurations that have already been described. In Figure 39, the m-chromosomes are closely associated as a bivalent; in Figure 40, one m-half-bivalent has divided into two chromatids and the homologous half-bivalent is undivided, forming a tripartite configuration, which has already been described. In Figure 41, a quadripartite configuration of four chromatids is apparent. Disjunction is regular in the bivalents, and anaphase separation is no different in the hybrid than in the parents. Figure 42 is a late anaphase of a hybrid sporocyte. Thirteen chromosomes plus the m-chromosome (arrow) are visible at the upper pole.

Second division of meiosis is also regular in the hybrids. Occasional tetrad cells were observed in which one or more chromosomes failed to get included in nuclei, but with no higher frequency than in the parents. Cytokinesis is regular, and secondary walls form around the potential spores.

Up to the formation of tetrads, meiotic events in the hybrids are without irregularities. There is total chromosomal compatibility, including the m-pair. No univalents were observed among the regular chromosomes.

Abnormal development in the hybrids begins with spore maturation and differentiation. Some tetrads are arrested in development and abort immediately, while others develop abnormally thickened walls and remain in that condition. Other tetrads break up, and the spores shrivel and disappear, or they may develop a more or less normal wall covering, but fail to enlarge. These may shrivel and disappear; or they may fail to develop chlorophyll, become reddish, and persist in this condition. About half the capsules reach maturity and contain no greenish spores, and about half contain from 2 to 10 spores (Reese & Lemmon, 1965, found as many as 22 green spores in a capsule).

In summary, the high sterility in the spores of the hybrid, *Astomum ludovicianum* × *Weissia controversa*, is not due to meiotic irregularities but is caused by failure of spores to develop and mature properly following tetrad formation. This would suggest genetic imbalance rather than chromosome imbalance.

8. *Astomum muhlenbergianum* ♀ × *Weissia controversa* ♂

This hybrid was discovered by the late Claire Williams, in heavy clay soil, in a field seeded to permanent pasture, near Thedford, Bosanquet Twp., Lambton County, Ontario, in 1966, and described in detail in a paper published that same year (Williams, 1966). She kindly sent some of this material to us for study, but it was too old for meiotic stages. A second batch of material, sent in 1967, arrived in poor condition, and was overrun with bacteria and molds. Finally, in 1968, material in perfect condition arrived, from which we were able to observe meiosis in the hybrid capsules and in both parental species. The material studied was collected from the same pasture described above (*C. Williams 1555*, March 20, 1968).

The parents and the hybrid are shown in dried condition in Figure 2. The female parent, *Astomum muhlenbergianum*, is at the right (Fig. 2C). It has long, sharply tapering leaves, which are less inrolled than in *Weissia controversa*, and its capsule is completely immersed within the perichaetial leaves. The seta length is less than 0.2 mm; the capsule is subglobose, although this is hard to see in the photograph, because it is so well-hidden in the perichaetium; the capsule is indehiscent; there is no peristome; the exothecial cells are thin-walled; and the spores average 26 μ.

The male parent, *Weissia controversa*, has shorter, mucronate leaves; the capsule is exserted on a seta, which averages 3.5 mm long. The capsule is cylindric, dehiscent; there is a well-developed peristome; the exothecial cells are thick-walled; and the spores average 20 μ.

The hybrid sporophytes are attached to gametophytes which obviously belong to *Astomum muhlenbergianum* (compare Fig. 2B with 2C). The hybrid capsule (Fig. 2B) is on a short seta, averaging 1.2 mm (the hybrid pictured in Fig. 2B, has a seta somewhat shorter than average). Capsules are subglobose and immersed to emergent. Exothecial cells are slightly to moderately thickened. A well-differentiated operculum is present, but it is nonfunctional: it does not dehisce. There is a rudimentary peristome of 16 teeth, each containing one to four articulations. Spores average 22 μ.

The meiotic chromosomes of the two parents are shown in Figures 43 (*Astomum muhlenbergianum*) and 44 (*Weissia controversa*), and each has the number, $n = 13$. The m-chromosome is lacking in both. Meiotic cells of the hybrid are shown in Figures 45 to 47. As in the previous hybrid, meiosis is regular, there are no univalents, and there is an even distribution of chromosomes to the four tetrad nuclei. Figure 47 shows a sporocyte of the hybrid, in anaphase I. Thirteen chromosomes can be seen clearly in both anaphase groups. In prometaphase figures (Figs. 45 & 46), the 13 bivalents are well separated and are all in tight bivalent configurations.

Williams (1966) was unsuccessful in attempts to germinate spores of the hybrid. She obtained no germinations. Only a few spores are produced in each hybrid capsule, and they are mostly small and reddish. As in the previous hybrid, spore infertility is not due to meiotic irregularities but to failure of the spores to mature and develop normally, following tetrad formation. Again, genetic imbalance is suggested.

DISCUSSION

1. The Nature and Significance of m-chromosomes

It is now well established in many species of mosses that there is polymorphism with respect to the presence or absence of m-chromosomes in different populations. This is contrary to earlier indications and predictions by a number of workers, who based their generalizations upon chromosome counts from a few populations, sometimes on only a single population. In a summary of m-chromosome studies up to that time, Anderson (1964) concluded that diminutive chromosomes (including m-chromosomes) in mosses are not variable in number from individual to individual, but are of constant occurrence with the species. This generalization is completely wrong, as investigations have since shown (Inoue, 1968, 1969; Visotskaya, 1967, 1970; Smith & Newton, 1966, 1967, 1968; Lazarenko & Visotskaya, 1965). The list of species of mosses which have been demonstrated to have populations with different chromosome numbers is long and impressive.

In the three species of *Astomum* and *Weissia* with which we worked, all the plants in an individual population either uniformly contained m-chromosomes or uniformly lacked them, although low frequencies of m-chromosomes in a population might be difficult to detect. The uniformity of chromosome number within a population, even when populations containing the supernumerary were nearby, suggests a very low percentage of outcrossings. It also suggests that clumps of mosses are either clonal or they arise from spores from a single capsule. That these mosses are highly inbred is indicated by these data.

The present studies are the first to indicate that m-chromosome populations are not randomly distributed. Approximately 23% of the populations of *Weissia controversa* in the Atlantic Coastal Plain, of the U.S., contain m-chromosomes; about 12% of the populations in the Piedmont Plateau, and only 2% of populations in the Mountains contain m-chromosomes. These differences are highly significant, and indicate that the presence of m-chromosomes in a higher frequency in the Coastal Plain has selective significance or that m-chromosomes are originating spontaneously and that their rate of origin is higher in the Coastal Plain. Their mode of origin is unknown. We have made yearly checks on a number of populations with and without m-chromosomes in North Carolina and Florida, for a period of four years, and we have found no year to year changes in the chromosomes. We have no evidence that they are accumulating, nor do we have any evidence that they are being eliminated. We can only conclude that they are stable within a population from year to year.

Although we lack quantitative data, there is no question in our minds, after several years of field work, that *Weissia controversa* is more abundant on the

Coastal Plain than in the Piedmont. It is least abundant in the Mountains. Thus, m-chromosome populations are more abundant in the physiographic province in which the species is most abundant. The climatic conditions which seem to favor the moss are mild winter temperatures, high summer temperatures, and possibly open, exposed habitats. Favorable edaphic conditions include sandy, well-drained soils. Sites which favor the most abundant colonization of the moss are sandy soils near the sea coast or sandy banks in the Sand Hills regions of the Coastal Plain. Piedmont soils are composed mainly of heavy, compact clays. Sandy, alluvial soils in the Piedmont are mainly confined to bottomlands and flood plains, where there is too much shade to support *W. controversa* in quantity. In the Mountains, *W. controversa* is uncommon to rare, and the habitats are more likely to be rock crevices, or thin soil over rocks. Temperatures are lower, rainfall is higher, and in general, the sites are more mesic.

A remarkable parallel to m-chromosome distribution in *Weissia controversa* is found in the grasshopper, *Myrmeleotettix maculatus* (Thunb.), in Great Britain, which was investigated by John and Hewitt (1965*a*, *b*) and by Hewitt and John (1967). They found that the number of populations of the grasshopper which contained B-chromosomes decreased from southern to northern Britain, although some populations in the south also lack B-chromosomes. In other words B-chromosomes were found preferentially in populations of *M. maculatus* occupying warm, dry habitats. They were present in reduced frequency or absent altogther in habitats which are either colder or wetter or both. This is precisely the situation in m-chromosome distributions in *W. controversa* in southern and southeastern United States, although our data lack the elegant statistical sophistication provided by the British authors.

Hewitt and John (1967) found that pronounced increase in chiasma frequency accompanied the presence of B-chromosomes in *Myrmeleotettix maculatus*. They argued, therefore, that the value of these supernumerary chromosomes "lies in their capacity to produce increased variability through the development of novel and experimental genotypes under optimal or near optimal environments." These workers are careful to point out, however, that B-chromosomes add to the range of variability of the population rather than providing an improvement in the form of immediate variation of the individual. We are unable to determine chiasma frequencies in *Weissia controversa*, so it is not known whether m-chromosomes influence chiasma frequencies. Any device, however, that would increase genetic variability, even slightly, in a moss like *W. controversa*, which appears to have such low outbreeding capabilities and that propagates vegetatively with such ease, should be selective. We need to know more about population dynamics in mosses and especially the mode of spread of populations, the degree of spread by spores *vs.* vegetative propagation, and some of the elements in short and long range dispersal.

As the m-chromosomes of more and more species of mosses are found to be supernumerary, the question arises, are they different from B-chromosomes? Inoue (1968) has recently adopted the term B-chromosome for m-chromosome in mosses (or for h-chromosomes, as the Japanese have rather uniformly labelled them), without any discussion of reasons for or against. A large number of species of mosses remains in which m-chromosomes have been observed in all the populations that have been studied. Mehra and Khanna (1961) attempted to distinguish between m-chromosomes and accessory chromosomes, a term introduced by Håkansson (1945) and Müntzing (1945), to more or less substitute for the term B-chromosome. Mehra and Khanna would restrict the term m-chromosome to those species in which it is a regular member of the complement, that is, when it is not a supernumerary. This distinction was also suggested by Lewis (1961), who realized there may be two types of diminutive chromosomes in mosses. Until more thorough studies have been made of these small chromosomes, however, it seems best to retain the term m-chromosome until more precise characterizations can be found.

Not enough populations of either species of *Astomum* were studied to determine whether populations with m-chromosomes are distributed randomly or non-randomly. Similarly, it was not possible to determine whether all of the individuals in each population have the same chromosome number. As already noted, relatively large numbers of individuals must be sampled from a population to detect a low frequency of plants with the supernumerary. If plants with m-chromosomes comprise 10% of the population, it requires a sample of 45 to detect m-chromosomes in the populations with even a 5% significance level. Since we studied only ten collections of *A. muhlenbergianum*, it is remarkable that three different chromsome numbers were discovered.

2. Polyploidy

Polyploid populations were found in all three species investigated. The polyploid populations of *Weissia controversa*, as we have already stated, have morphological distinctions and even habit characteristics that we think may merit specific rank. Furthermore, all of these polyploids were restricted to a unique habitat, namely limestone and dolomitic cedar (*Juniperus virginiana*) outcrops in the Blue Ridge, Valley, Cumberland, and Ozarkian Provinces. We are currently studying these populations.

Of the 460 populations of typical *Weissia controversa*, not a single tetraploid was found. From this, we conclude that ploidy is not recurring frequently, or if so, the plants are not becoming established.

The tetraploids in *Astomum ludovicianum* and *A. muhlenbergianum* are indistinguishable from the diploids. Tetraploids in both species possess the same range of leaf cell sizes and spore sizes, and no differences could be found in their relative vigor. Löve claims that "types with different euploid chromosome numbers can always be separated by an unbiased student." As Lewis and John (1963) point out, however, this may be true for experimental material, but there are many exceptions among natural polyploids, even allopolyploids. Stebbins (1950) lists several examples of extreme allopolyploids which may resemble one or the other of their parental species so closely that they have not been recognized as distinct by systematists. Dozens of species of mosses can be cited in which there are indistinguishable tetraploid and diploid populations. Among these are *Distichium capillaceum*, n = 14 and 28

(Visotskaya, 1967; Anderson & Crum, 1958); *Ditrichum pallidum*, n = 13, 26 (Al-Aish & Anderson, 1961); *Dicranum fuscescens*, n = 12, 24 (Anderson & Crum, 1958); *Octoblepharum albidum*, n = 13, 26 (Khanna, 1960*c*); *Hypoptergium rotulatum*, n = 9, 18, 27, 36 (Ramsay, 1967), *etc.* (see Anderson, 1964).

Autopolyploids in higher plants tend to be highly sterile, usually because of multivalent associations of chromosomes in meiosis, although many exceptions to this have been listed by Stebbins (1950), Lewis and John (1963), and others. Unfortunately, no one has carried out germination tests of tetraploid populations in mosses, but thus far, all of the natural tetraploid populations studied have been found to undergo normal meiosis. Bivalent formation is the rule, and, at most, secondary associations of bivalents have been described. Even in an experimentally produced autotetraploid, Wettstein and Straub (1942) reported normal bivalent formation. This is also the case in both *Astomum muhlenbergianum* and *A. ludovicianum.* It seems probable that somehow mosses have adjusted their meiotic mechanism in such a way that the duplicated bivalents do not form multivalents. Lewis and John (1963) call attention to the fact that larger chromosomes tend to form multivalents more than smaller ones and that multivalents are formed more often where there is a high frequency of distributed chiasmata. No data are available on chiasma frequency in mosses. It is probably low, judging from bivalent configurations observed at prometaphase and metaphase I. Also, the amount of heterochromatin in moss chromosomes appears to be high, compared to many plants, and there may be more achiasmic bivalents than is suspected. The smallness of moss chromosomes has been repeatedly mentioned. In addition to these physical factors, however, there are probably intrinsic genetic influences that operate against multivalent formation.

3. Hybridization and Sterility Barriers

Several natural intergeneric hybrids have been described in mosses that parallel features of the *Astomum* × *Weissia* hybrids. The most notable, perhaps, are between cleistocarpous and stegocarpous genera in the Funariaceae, which were first described by Britton (1895) and Andrews (1918), both of whom reported finding natural hybrids between *Physcomitrella patens* × *Physcomitrium turbinatum.* Wettstein (1924) produced comparable hybrids experimentally, by crossing *Physcomitrella patens* × *Physcomitrium euryostomum*, and *Physcomitrella patens* × *Funaria hygrometrica.* The latter two hybirds have also, from time to time, been observed in nature. More recently, Andrews and Hermann (1959), reported natural hybrids between *Pleuridium acuminatum*, also a cleistocarpous moss, and *Ditrichum pallidum*, which has an operculum and a well-developed peristome.

Represented by these intergeneric hybrids are three families of mosses that are relatively unrelated, *Ditrichaceae*, *Pottiaceae* and *Funariaceae*, although the former two families are more closely related to each other than to the latter. Yet, each of the hybrid combinations shares the following characteristics: (1) one parent is cleistocarpous, the other is stegocarpous; (2) reciprocal hybrids have not been found in nature; (3) each hybrid capsule produced few or no spores, and the few spores produced are highly sterile; (4) meiosis is regular in the hybrids, pairing of chromosomes is complete, and no univalents are present (*Pleuridium-Ditrichum* hybrid has not been studied cytologically); and (5) despite production of a few fertile spores by each hybrid, no F_2 plants have ever been found in nature, and there is no evidence of introgression among the genera and species involved.

The fact that the chromosome complements among species of closely related genera are similar in number and apparent morphology, and that they pair with ease when brought together in a hybrid combination probably indicates a minimum of major structural changes and rearrangements in the complement during evolution. The imbalance in hybrids is intrinsically genic, rather than chromosomal. The hybrid chromsomes pair and segregate with no difficulty, but the new genic combinations brought together in the respective cells of the tetrads create an imbalance that leads to sterility in nearly all of them. Even the so-called fertile spores which are produced and are able to germinate apparently do not grow into mature plants. At least they are never found in nature. Thus, in spite of the ease with which F_1 hybrid sporophytes are produced, the sterility barrier appears to be total.

Wettstein (1924), who found complete chromosome compatibility in hybrid sporophytes, *Physcomitrella patens* × *Physcomitrium turbinatum*, and nearly complete sterility, found occasional tetrads in which two of the spores were viable, and the other two were sterile. He was able to grow the two viable spores to maturity, but found that the two plants they produced were identical with the maternal parent. Wettstein hypothesized that the two viable spores contained a complete set of maternal chromosomes, which had been segregated at meiosis as a complete maternal genome. The two spores which received the paternal set were sterile, according to Wettstein, because the paternal set of chromsomes can not function in maternal cytoplasm.

If Wettstein's hypothesis is correct, namely, that the few viable spores which are produced by these hybrids contain a complete set of maternal chromosomes, then this would explain the lack of F_2 plants in natural populations. Viable spores from the hybrids would always grow into plants indistinguishable from the maternal species. However, this hypothesis requires an explanation to account for the preferential segregation of complete sets of parental genomes. There are 27 pairs of chromosomes in the *Physcomitrella-Physcomitrium* hybrids, and 13 pairs in the *Astomum-Weissia* and *Pleuridium-Ditrichum* hybrids. The probability of segregation of complete parental sets by chance is too low to account for even a few tetrads per capsule. Some mechanism must be postulated to provide a slight preference for segregation of whole sets.

Another explanation that has been advanced to explain sterility in hybrids which have normal meioses is that sterility is caused by structural hybridity involving small chromosomal segments. Originally suggested by Sax (1933), Stebbins (1950) has proposed the term cryptic structural hybridity for this type of sterility, and Stebbins lists a number of higher plants in which this explanation might apply. Sterility is presumably caused by heterozygosity for structural differences so small as not to influence materially chromosome pairing. The origin of such tiny structural differences involves a series of inverted chromsome segments followed by re-inversions in which the breaks are almost but not quite at the same places on the chromosome (Müntzing, 1930; Sturtevant, 1938).

Stebbins (1958) has stressed the difficulties involved in distinguishing between genic and chromosomal sterility, especially when the latter involves such small structural differences that chromosomes pair normally at meiosis. The only reliable criterion for distinguishing between them is that furnished by chromosome doubling. If an *Astomum-Weissia* hybrid can be found with the number, $n = 26$, and if its sterility is significantly reduced in comparison with the diploid hybrids, then sterility in the latter is due to chromosomal imbalance. If, on the other hand, doubling does not produce increased fertility, genic imbalance is indicated.

4. Isolating Mechanisms and Generic Limits

There is a set of remarkable parallelisms surrounding the *Astomum-Weissia, Pleuridium-Ditrichum, Physcomitrium-Physcomitrella-Funaria* hybrids that have been referred to above. These parallels are discussed below.

First, within each complex, the gametophytes of the hybridizing species are closely alike, morphologically. In each cross, one parent is cleistocarpous, the other parent is stegocarpous, and is either peristomate or gymnostomous. In the evolution of mosses, capsule reduction has taken place independently in a number of diverse families. The reduction sequence is presumed to be: operculate and peristomate → operculate and gymnostomous → operculate, but non-functional → cleistocarpous. In the three complexes, the sequence is represented by the following genera: *Weissia* → *Hymenostomum* → *Astomum*; *Ditrichum* → *Pringleella*, et al. → *Pleuridium*; *Funaria* → *Physcomitrium* → *Aphanorrhegma* → *Physcomitrella.*

Second, the regular chromosome complement of the species of each complex is identical, except in the *Funaria* complex. Most species of *Funaria* have the number $n = 28$ (14), instead of $n = 27$, as in *Physcomitrium* and *Physcomitrella.* There is complete pairing of chromosome sets in each of the hybrids which has been studied (*Pleuridium-Ditrichum* hybrids are unstudied), and meiosis in each hybrid is apparently regular.

Third, although meiosis in the hybrid capsules is regular and produces normal-appearing tetrads, in nearly all of the latter, spore development is arrested or the spores abort, and the capsules produce few or no spores.

Fourth, although the species within each of the three complexes hybridize with seeming ease, neither F_2 nor backcrosses have been observed in nature. Nearly all of the parental species involved are notoriously variable, morphologically, but they are taxonomically distinct, and intergradations in the field are unknown. They are not "problem" species, except, perhaps, at subspecific levels. The lack of apparent introgression indicates the effectiveness of the sterility barriers.

These parallels suggest that the same isolating mechanisms may be operating in each of the complexes. Whether genic or chromosomal imbalances or a combination of the two are responsible for the high degree of haplontic sterility cannot be determined at this point. The role of spatial isolation in these organisms is almost entirely unknown. The caespitose or clump habit of *Astomum* and *Weissia*, and doubtless other genera, may provide a major isolating device by forcing interbreeding among plants within the clump. Until the origin or origins of clumps are known, the degree of spatial isolation it provides cannot be estimated. Local and wide-range dispersal patterns and the incidences of asexual *vs.* sexual reproduction are in need of study.

The fact that intergeneric hybridization occurs between species of *Astomum* and *Weissia*, and because the gametophytes of species in the two genera are almost indistinguishable, Reese and Lemmon (1965) merged *Astomum* with *Weissia*, taxonomically, and made the necessary nomenclatural transfers. Claire Williams (1966), after finding intergeneric hybrids between species of the same genera, arrived at the same conclusion.

The close similarities of chromosome complements and the regular pairing of chromosomes in hybrid meioses indicate that *Weissia controversa*, *Astomum ludovicianum*, and *A. muhlenbergianum* are closely related species. The close relationship between the species which have been placed in the two genera is also borne out by the resemblances of the gametophytes. It should be kept in mind, however, that gametophytic resemblances, in somewhat lesser degree, extend to *Trichostomum*, *Tortella*, and to an even lesser extent to *Timmiella*. A putative hybrid between *Tortella flavovirens* and *Astomum crispum*, described by Nicholson (1910), should be recalled.

Despite the similarities in chromosome complements and in morphological characteristics of the gametophytes, however, the isolation barriers between the two species of *Astomum* and *Weissia controversa* are highly effective. Equally effective barriers may exist between *A. ludovicianum* and *A. muhlenbergianum*, although we have no information. Hybrids between the latter have not been reported.

Cleistocarpy, as a taxonomic character, should carry considerable weight, especially since it represents a rather significant evolutionary step in capsule reduction. Also, its development involved more than a few trivial genic alterations, since it has been accompanied by a high degree of genetic isolation. Stebbins (1950) cites many examples in which two species may differ in a very large number of gene differences or even by as many as 30 to 50 translocated or inverted chromosomal segments, yet, when hybridized, the offspring have regular pairing and a high degree of haplontic sterility.

The final judgment, therefore, as to whether *Astomum* is worthy of generic rank, must be made primarily upon morphological assessments. Detailed morphological analyses of all of the described taxa in the complex should be made. A competent evaluation of generic groupings can then be made in the light of cyto-genetical information which we have presented in this paper. In the meantime, attempts at experimental hybridization and analyses of population dynamics in mosses are long overdue.

SUMMARY

1. Cytogeographical studies were carried out on 460 populations of *Weissia controversa,* 17 populations of *Astomum ludovicianum,* and 10 populations of *A. muhlenbergianum.* Polymorphism as to chromosome number was found in all three species: *W. controversa,* $n = 13$ and $n = 13 + m$; *A. ludovicianum* and *A. muhlenbergianum,* $n = 13$, $n = 13 + m$, and $n = 26$.

2. Populations of *Weissia controversa* containing m-chromosomes are nonrandomly distributed. In the Atlantic Coastal Plain, the m-chromosome frequency is approximately 23%. In the Piedmont Plateau, the m-frequency is 12%, and in the Mountains it is less than 3%. The over-all frequency of m-chromosome populations is 16%.

3. Morphological analyses were carried out on selected plants from populations with each of the chromosome numbers. No correlations exist between chromosome number and morphology. Any effects that m-chromosomes exert must be endophenotypic.

4. The varying configurations that m-chromosomes display during prometaphase and metaphase I of meiosis can be explained by assuming they are achiasmic, and they thus reveal various degrees of pairing and desynapsis, including configurations of bivalents, univalents, half-bivalents, chromatids, and their derivative combinations.

5. Meiosis was studied in two intergeneric hybrids, *Astomum ludovicianum* ♀ × *Weissia controversa* ♂, and *A. muhlenbergianum* ♀ × *W. controversa* ♂. In both hybrids meiosis was regular and there was complete pairing of chromosomes. No univalents or other irregularities sometimes associated with hybrids were observed.

6. Hybrid sporophytes in both crosses produced few spores. Fertility among the few spores produced is very low, from 0 to 2%, and no leafy plants were produced, although failure of the latter may have been due to poor cultural conditions.

7. Normal-appearing tetrads are produced by the hybrids, but spores fail to develop or they develop partially and abort. Sterility results from either chromosome imbalances brought about by very small structural differences that do not impair synapses or by genic imbalances in the segregated haploid sets. It was not possible to determine which of these imbalances produces the haplontic sterility.

8. The close resemblances of the standard chromosome complements and their close compatibility in hybrid meioses suggest a close relationship among the three species, but the high degree of sterility of the hybrids and the absence of introgression suggest highly effective isolation barriers. It is suggested therefore, that a taxonomic evaluation of *Astomum* await a world-wide systematic revision of the entire complex.

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CYTOLOGICAL EVIDENCE OF INTROGRESSION BETWEEN *DROSOPHILA* SPECIES IN PANAMA[1]

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Abstract

Cytological evidence of introgression in the classical sense of Anderson (1949) and Stebbins (1950) has been presented for the sibling species *Drosophila metzii* and *Drosophila pellewae* in a population of the Isthmus of Darien, Panama. Salivary chromosome karyotypes of hybrids between the two species show multiple translocations involving the four large autosomes. A strain of *D. metzii* collected from a mixed population of the two species near El Real, Darien, Panama, displays both heterozygous and homozygous translocation figures and regions of asynapsis in salivary chromosomes of third instar larvae. A heterozygous translocation figure is seen in some salivary gland cells of larvae of the Darien strain of *D. pellewae.* Observations of variations in length of chromosomes in different individuals of the Darien *D. metzii* strain suggest restructuring arising presumably from crossing over in progenitors heterozygous for multiple translocations.

The requirements necessary for introgressive hybridization outlined by Anderson (1949) and Stebbins (1950: 251–297) are fulfilled by the relationship between the sibling species *Drosophila metzii* and *Drosophila pellewae.* Each species has a characteristic range with a region of overlap in the Isthmus of Darien. *Drosophila pellewae* has been collected from Barro Colorado Island, Canal Zone, where it is extremely rare, to Río Raposo, Colombia, where it is moderately common (Pipkin & Heed, 1964). In the north, *D. metzii* has been collected at Sonte Comapun (near Vera Cruz, Mexico) by Fabergé (personal communication), at Turrialba, Costa Rica (Pipkin, 1965), and San Salvador, El Salvador (Heed & Wheeler, 1957), and to the south as far as Santa Marta on the northern coast of Colombia (Heed, personal communication). Mixed populations of these siblings occur in forests, feeding over the same fallen fruit or flowers. Pipkin (1968*a*) has presented evidence that the species do cross in nature and that a specific character, white carina color, has been transferred from *D. metzii* into populations of *D. pellewae,* where an obscure carina color polymorphism is seen both in the Darien and Río Raposo populations. Although 280 individuals consisting of 60% *D. pellewae,* 40% *D. metzii* were collected from a single unusually large population in the Darien in 1961, gene exchange between the two species is greatly reduced, owing partly to translocations involving the four major autosomes (Pipkin, 1968*a*). A primitive karyotype consisting of five pairs of rod-shaped and one pair of dot-shaped chromosomes, characterizes both species according to analysis of larval ganglionic cells of strains originating

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[1] Supported by NSF Grant GB-8770 and NIH Grant 1R 101 GM 18409-01.

The author is deeply indebted to Mr. Eric Schabtach, formerly of The Johns Hopkins University, now of The University of Oregon, Eugene, Oregon, not only for making the photographs used in this paper but also many other study photographs; to Dr. H. Ursprung, formerly of The Johns Hopkins University, for his generous permission to use the Zeiss photomicroscope; to Mr. L. M. Powers, for culturing *Drosophila metzii* and *Drosophila pellewae.*

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Ann. Missouri Bot. Gard. 59: 417–434.

Figure 1. Photograph of salivary chromosomes of *Drosophila metzii/D. pellewae* hybrid. — A. Upper half of cell 1. — B. Lower half of cell 1. — One of the paired homologs of the distal end of chromosome 5 in Fig. 1B is joined to the unpaired homolog of another chromosome. Homologs of chromosome 4 are largely unpaired. The hybrid is heterozygous for a large paracentric inversion in chromosome 3.

outside the region of overlap (Pipkin & Heed, 1964). Salivary chromosome maps of nine members of the *tripunctata* species group, including the Barro Colorado Island strain of *D. metzii* have been made by Kastritsis (1966). The present paper will offer cytological evidence of introgression both from *pellewae* into *metzii* and from *metzii* into *pellewae* and evidence from octanol dehydrogenase isozyme patterns that the two species have nevertheless remained distinct in the Isthmus of Darien, Panama.

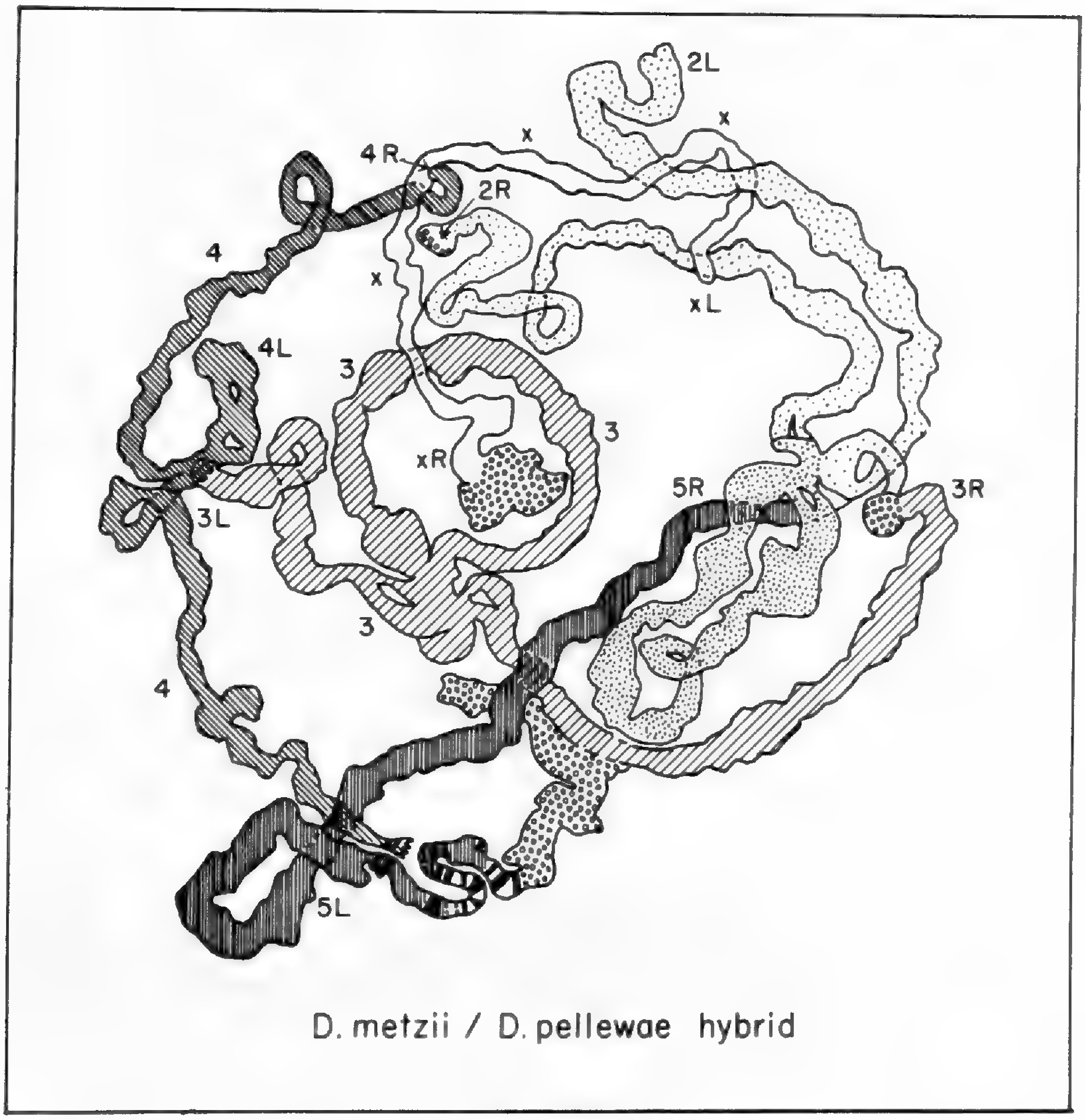

FIGURE 2. Diagram of chromosomes shown in Fig. 1.

MATERIALS AND METHODS

A description of the collection localities and numbers of founders of *Drosophila pellewae* from Barro Colorado Island, and Darien, Panama; Río Raposo (near Buenaventura), Colombia; and of the strains of *D. metzii* from Barro Colorado Island, Darien, and Almirante, Panama, and from Trinidad, West Indies, has been given by Pipkin (1968*a*). Temporary aceto-orcein lactic acid smears of third instar larvae were prepared according to a modified method of Wasserman (1954) described by Pipkin (1968*a*). Photographs of salivary gland chromosomes were made at varying focal depths using a Zeiss photomicroscope with phase contrast lighting at The Johns Hopkins University by Eric Schabtach, now of the Department of Biology, The University of Oregon.

RESULTS

1. Somatic pairing between homologs of salivary gland chromosomes of *D. metzii/D. pellewae* hybrids.

Pairing is usually close between homologous chromosomes of salivary gland cells of hybrids between *Drosophila metzii* and *D. pellewae*, affording an idea of the gross differences in banding sequence which distinguish these species. In hybrids using any of several strains of each species, complex translocation figures involving chromosomes 2, 3, 4, and 5 are seen (Pipkin, 1968*a*). The X chromo-

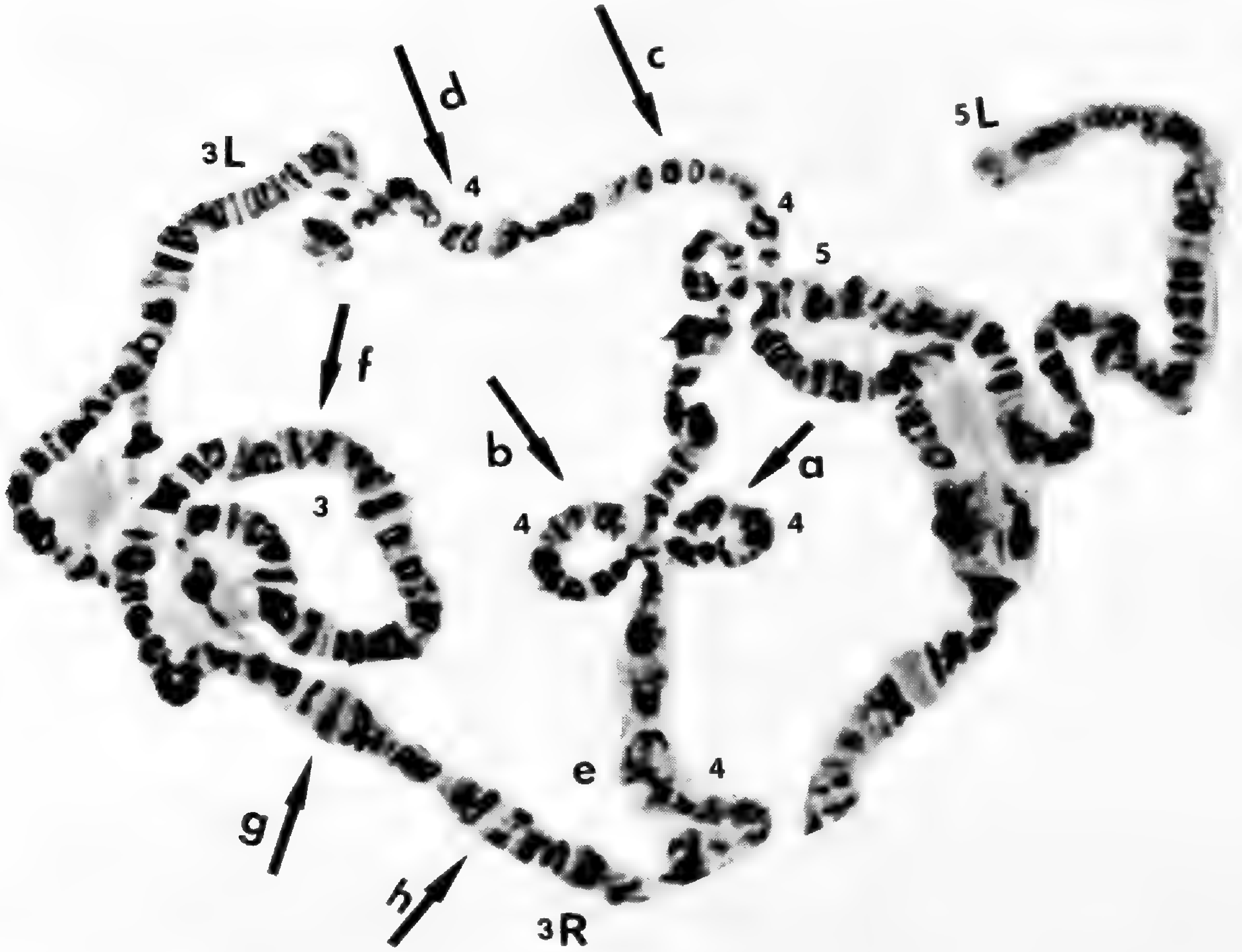

FIGURE 3. Photograph of part of cell 2 of a *Drosophila metzii/D. pellewae* hybrid showing at a and b heterozygous overlapping inversions figure in chromosome 4; c and d unpaired homolog of chromosome 4; e region of chromosome 4 where homologs are poorly paired; f a large heterozygous inversion figure in chromosome 3; g and h a region of poor pairing of chromosome 3.

some and short chromosome 6 are always free from the translocations. Most cytological work on species hybrids has been done using offspring of females of the Almirante strain of *metzii* and males of the Barro Colorado Island strain of *pellewae*. Photographs of the two halves of the cell of such a species hybrid appear in Figure 1A and B, together with an explanatory diagram of the entire cell in Figure 2. The X chromosome is free from the translocations involving the autosomes; its banding sequence resembles that of the X chromosome of *D. metzii* strain of Barro Colorado Island according to the map of Kastritsis. The banding sequences of the ends only of autosomes have been completely identified; these are indicated in the photographs (Fig. 1A,B) and diagram (Fig. 2). Some of the translocation interchanges have been broken in the cell shown in Fig. 1A and B, but certain features demonstrate prominent differences in banding patterns of the two species. The species hybrid is heterozygous for a large paracentric inversion in chromosome 3 which appears to be associated with the other chromosomes only at its heterochromatic end. Other cells of the same hybrid examined suggest that an interchange connecting

FIGURE 4. Chromosomes of *Drosophila metzii/D. pellewae* hybrid. — A. Distal ends of paired chromosome 5 homologs, with one end broken during squashing. — B. Poorly paired distal tips of chromosome 2 homologs.

chromosome 3 to the unidentified chromosome loop, which is heavily stippled in the diagram of Figure 2, has been broken by squashing the cell. The homologs of chromosome 4 are largely unpaired in Figure 1A,B, although at least a portion of the banding sequence of the two homologs is homosequential. More complete synapsis of the chromosome 4 homologs can be seen in another cell (Fig. 3) where an overlapping inversions figure is apparent. Even in the cell shown in Figure 3, the homologs of a portion of the distal region of chromosome 4 remain unpaired (indicated on the photograph by arrows at c, d), and homologs of the proximal end of this chromosome at e are poorly paired. In the *metzii/pellewae* hybrid of Figure 1B, the distal end of chromosome 5 is attached to the proximal part of another chromosome in one of the homologs. In another preparation (Fig. 4a) this interchange has been broken by squashing so that the distal end of one of the paired chromosome 5 homologs appears a little shorter than its partner. In the karyotype of a *metzii/pellewae* hybrid shown in Figure 5, chromosome 2 shows a short heterozygous inversion figure marked with an arrow at a and overlapping inversions at b before it enters a translocation cross-shaped figure at c. These inversion and translocation interchanges have been broken in the cell shown in Figure 1A and in the diagram, Figure 2. In hybrids between *metzii* and *pellewae*, homologs of the distal tip of chromosome 2 are often unpaired or poorly so, as in Figures 1A, 4B and 5.

FIGURE 5. Photograph of part of cell 3 of a *Drosophila metzii/D. pellewae* hybrid showing a short inversion, a, in chromosome 2; b, a heterozygous overlapping inversions figure; c, an interchange of a heterozygous translocation figure.

2. Evidence of transfer of portions of the *Drosophila pellewae* genome into that of *D. metzii* in the Darien population.

A number of cells prepared from the Darien strain of *Drosophila metzii* showed six paired homologs of lengths similar to those observed by Kastritsis (1966) in the Barro Colorado Island strain of *D. metzii*, as in the photograph (Fig. 6) and diagram (Fig. 7). A large mass of heterochromatin usually present at the proximal portion of the X chromosome has broken away in this cell. The karyotype of this cell, where the relative lengths of homologs may be represented as $2 > 3 \sim X > 4 > 5 > 6$, is arbitrarily designated as standard. Several different heterozygous translocation figures appearing to involve two non-homologous chromosomes only have been seen in larvae of the Darien strain of *metzii*. For example, Figure 8 shows a photograph of a cell of a larva heterozygous for a translocation involving chromosomes 2 and 4. The banding pattern of the portion of the chromosomes outside the region of inversions is closely similar to that of parts of chromosomes 2 and 4 of the *D. metzii* map of Kastritsis (1966). The overlapping inversions observed in the *metzii/pellewae* hybrid of Figure 4 resemble those of Figure 8 and suggest that

FIGURE 6. Photograph of a cell of an individual of the Darien strain of *Drosophila metzii* with a standard karyotype in which the relative chromosome lengths are $2 > X \sim 3 > 4 > 5$.

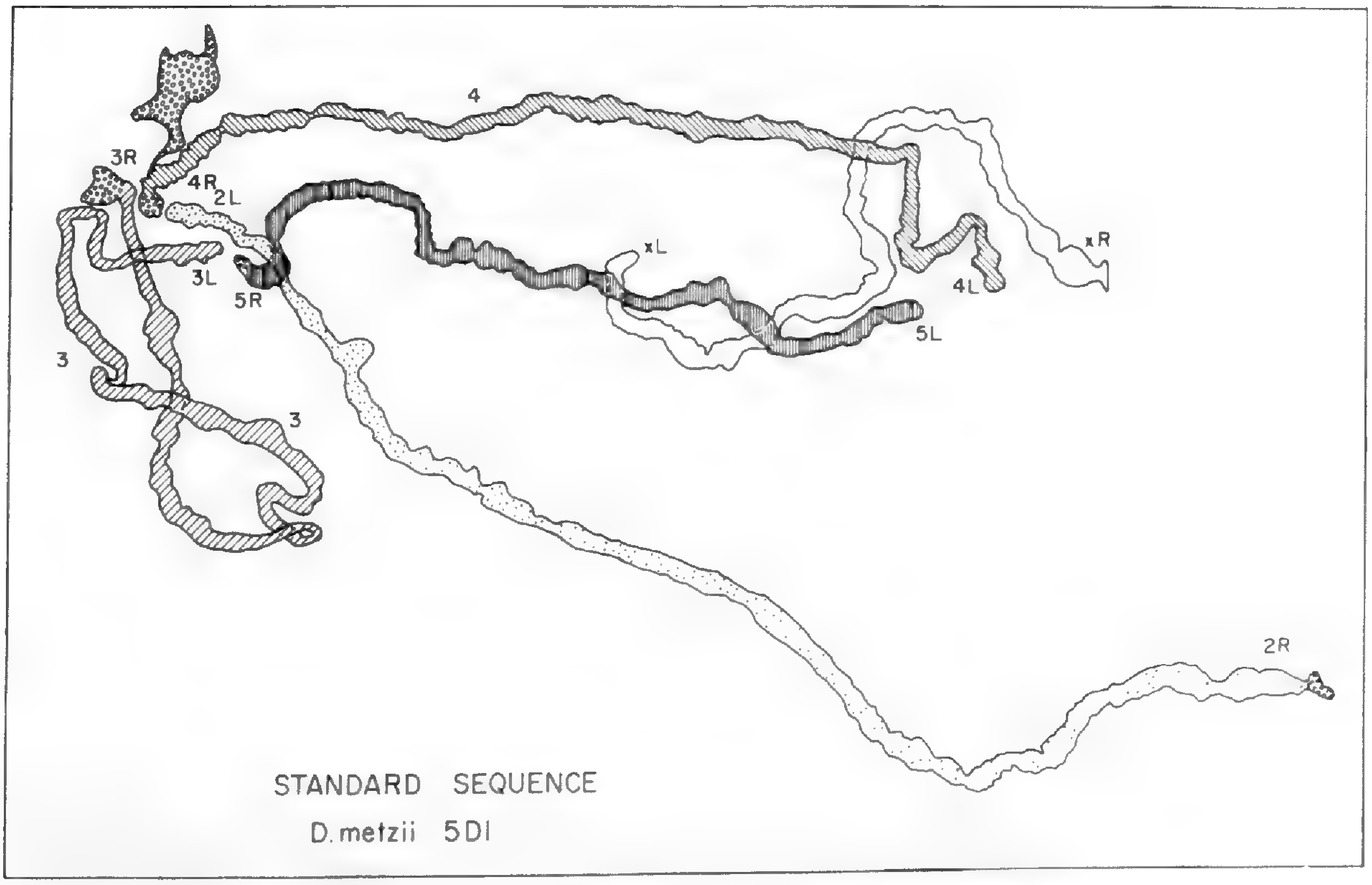

FIGURE 7. Diagram of chromosomes shown in Fig. 6.

FIGURE 8. Photograph of a heterozygous translocation figure taken from an individual of the Darien strain of *Drosophila metzii*. A heterozygous overlapping inversions figure is near the interchange of the heterozygous translocation figure.

a transfer of *D. pellewae* genome covered by the inversions and adjacent to the translocation interchange has entered the gene pool of *D. metzii* causing a polymorphism. The finding in another preparation of one of the homologs of the distal portion of chromosome 5 slightly shorter than the other as in the *metzii/pellewae* hybrid of Figure 4a suggests that a translocation involving chromosome 5 is still heterozygous in the Darien *metzii* strain. In two other preparations chromosomes 2 and 5 were part of a heterozygous translocation figure involving interior regions of both chromosomes, but these cells were only sketched and not photographed. A homozygous transposition involving chromosomes 2 and 4 has been found in cells of different individuals of the Darien strain of *D. metzii* (Fig. 9A and B, with an explanatory diagram in Fig.

FIGURE 9. — A. Photograph of a cell of an individual of the Darien strain of *Drosophila metzii* homozygous for a 2,4 transposition with a very long "chromosome 2" and a very short "chromosome 4." — B. The long "chromosome 2" of another cell.

10). A large segment of the middle part of chromosome 4 has been inserted into the middle part of chromosome 2, with the result that the karyotype of an individual homozygous for the transposition displays an exceptionally long "chromosome 2" and a correspondingly short "chromosome 4."

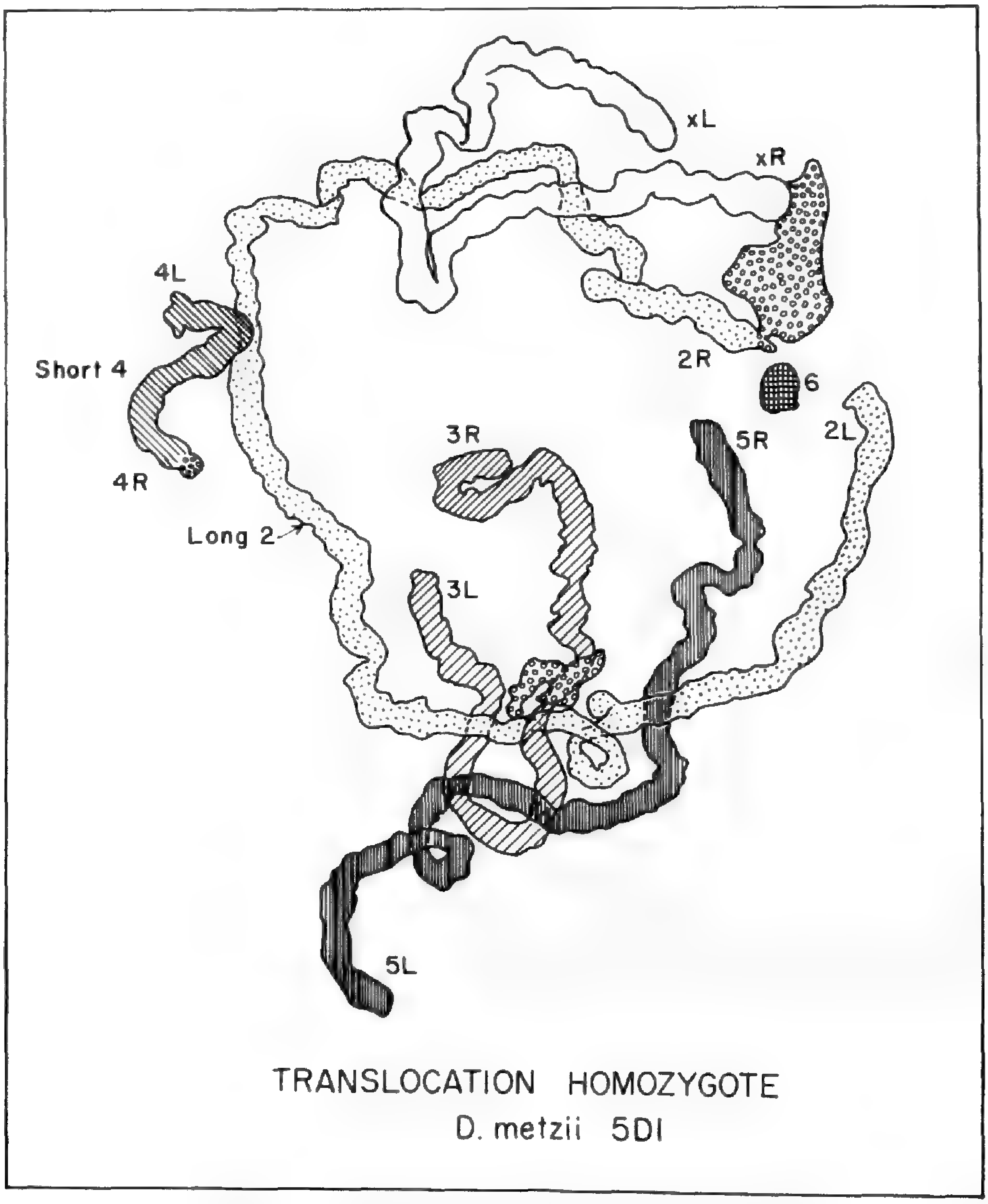

FIGURE 10. Diagram of the cell shown in Fig. 9A.

Finally introgression of a portion of *pellewae* genome into that of *metzii* is evidenced by asynapsis of certain of those homologs which failed to pair also in the species hybrid. Lack of pairing of the two homologs of the proximal part of chromosome 4 of the species hybrid shown in Figure 11A often occurs in the same region of this chromosome in the Darien *metzii* strain (Fig. 11B). Failure of pairing of the medial portion of chromosome 4 is seen in the Darien *metzii* strain occasionally (Fig. 11C). The chromosome 4 of Figure 11C is distinctly shorter than that of the standard karyotype, indicating restructuring. Asynapsis of portions of chromosome 4 in Figure 11A and B is not due to rearrangement since the banding patterns are homosequential. Even when homologs are paired, the proximal end of chromosome 4 is sometimes exceptionally broad, indicating looseness of pairing. The proximal end of the paired homologs of chromosome 2 in the Darien *metzii* strain also is sometimes broad (Fig. 11D), or even forked, indicating a slight asynapsis similar to that observed in Figures 1A, 4B, and 5 of the *metzii/pellewae* hybrid.

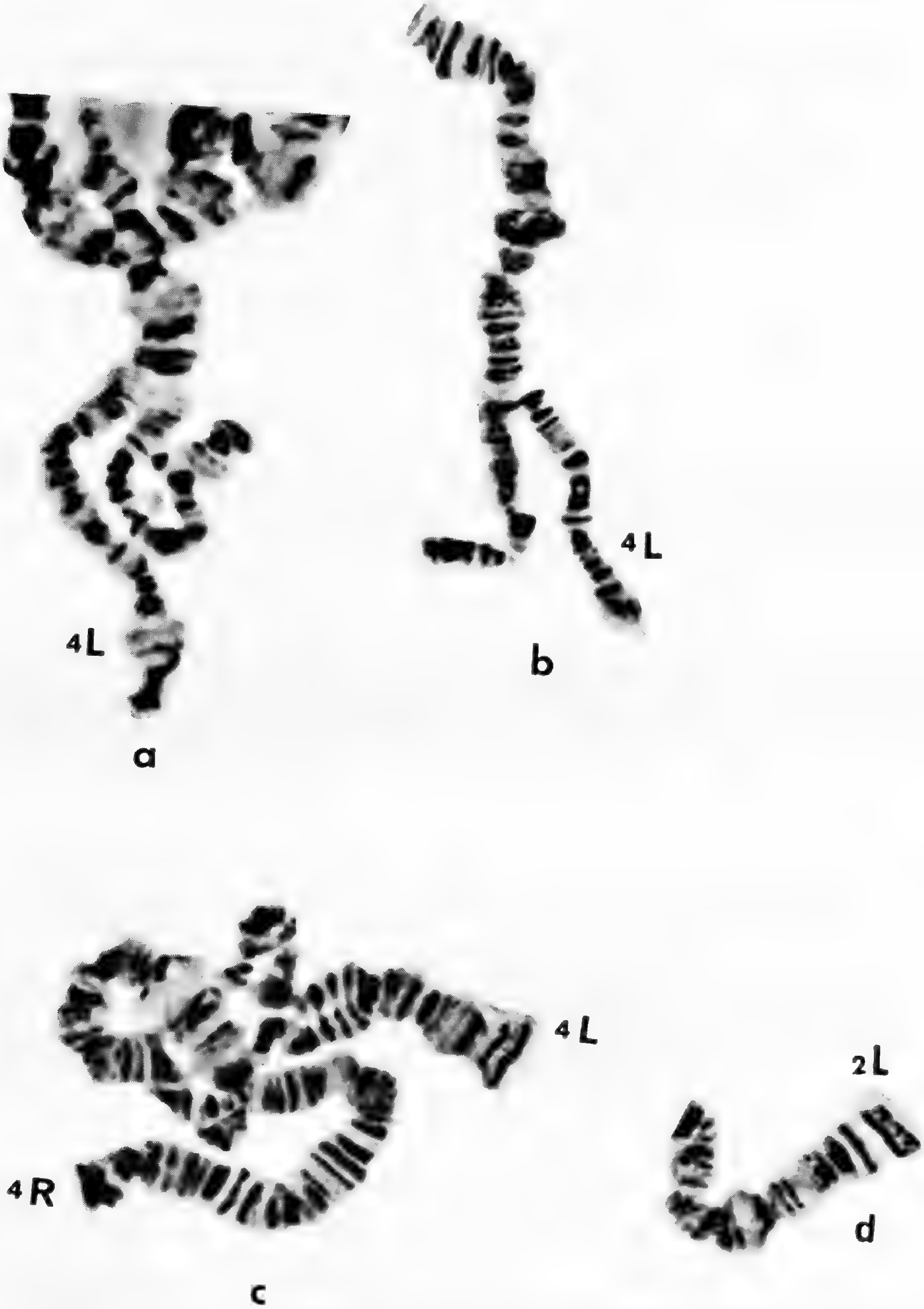

FIGURE 11. — A. Asynapsis of the same distal portion of chromosome 4 in a cell of a *Drosophila metzii/D. pellewae* hybrid. — B. Asynapsis of the same distal portion of chromosome 4 in a cell of the Darien strain of *D. metzii.* — C. Asynapsis of the medial portion of chromosome 4 in an individual of the Darien strain of *D. metzii;* here chromosome 4 is shorter than in the standard karyotype. — D. Broad proximal end of paired homologs of chromosome 2 in the Darien strain of *D. metzii.*

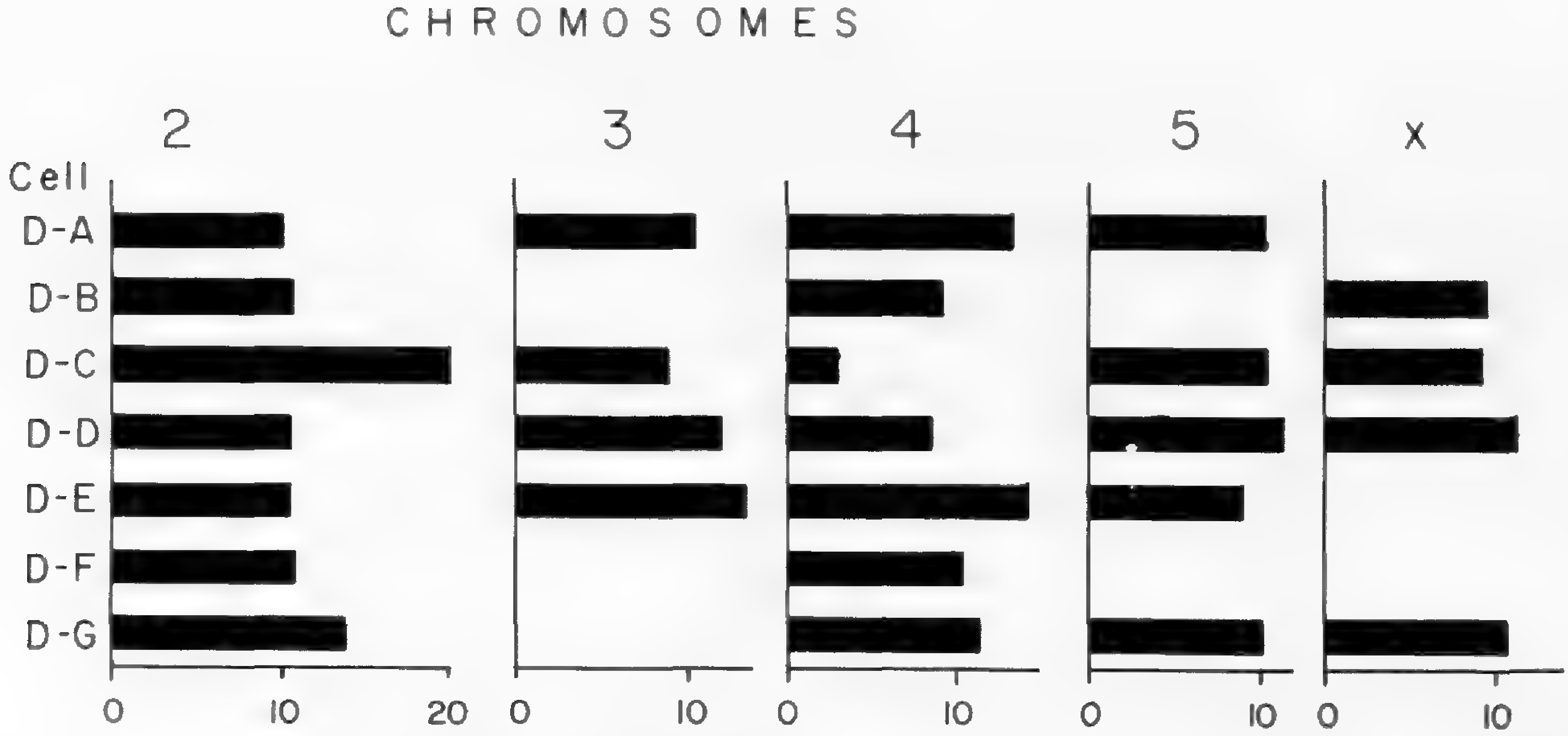

FIGURE 12. Diagram of chromosome lengths in cells of seven individuals of the Darien strain of *Drosophila metzii* showing relative lengths differing from those of the standard karyotype in which $2 > X \sim 3 > 4 > 5$. The restructuring of chromosomes is hypothesized to depend on crossing over in a *D. metzii/D. pellewae* progenitor which was heterozygous for autosomal translocations.

Further restructuring of chromosomes 2, 3, 4, and 5 of individuals taken from the Darien strain of *Drosophila metzii* is deduced from a comparison of lengths of these chromosomes obtained by measuring photographs of the chromosomes taken at similar magnifications. Some variation in such lengths can be explained as due to relative stretching of the chromosomes during squashing. To avoid this error as much as possible, cells were chosen in which the widths of paired chromosomes were similar. Figure 12 shows that except for the chromosomes of cell D-C with the homozygous 2,4 transposition, the length of chromosome 2 varied little. Variations in chromosomes 4 and 5 appeared to be inversely correlated as indicated by a comparison of the sums of the lengths of these chromosomes in the respective cells given in Table 1. Variation in the length of chromosome 3 suggests that this chromosome also has undergone restructuring.

TABLE 1. Restructuring of karyotypes suggested by comparison of lengths of respective salivary chromosomes of cells of different individuals of the Darien strain of *D. metzii*. Photographs taken at similar magnifications were used for measuring chromosomes in inches.

Chromosome(s)	2	3	4	5	X	2+4	2+4 +5	3+4 +5	2+3 +4+5
Cell D-A	10.0	10.6	13.3	10.3	—	23.3	33.6	34.2	44.2
Cell D-B	10.5	—	9.1	—	9.5	19.6	—	—	—
Cell D-C	20.0	9.1	3.0	10.5	9.2	23.0	33.5	22.6	42.6
Cell D-D	10.5	12.0	8.5	11.6	11.3	19.0	30.6	32.1	42.6
Cell D-E	10.4	13.5	14.1	9.0	—	23.9	32.9	36.6	47.0
Cell D-F	10.8	—	10.5	—	—	21.3	—	—	—
Cell D-G	13.8	—	11.3	10.1	9.8	25.1	35.2	—	—

FIGURE 13. — A. Photograph of a heterozygous translocation figure taken from an individual of the Darien strain of *Drosophila pellewae*. — B. An enlargement of the region of translocation interchange showing overlapping inversions.

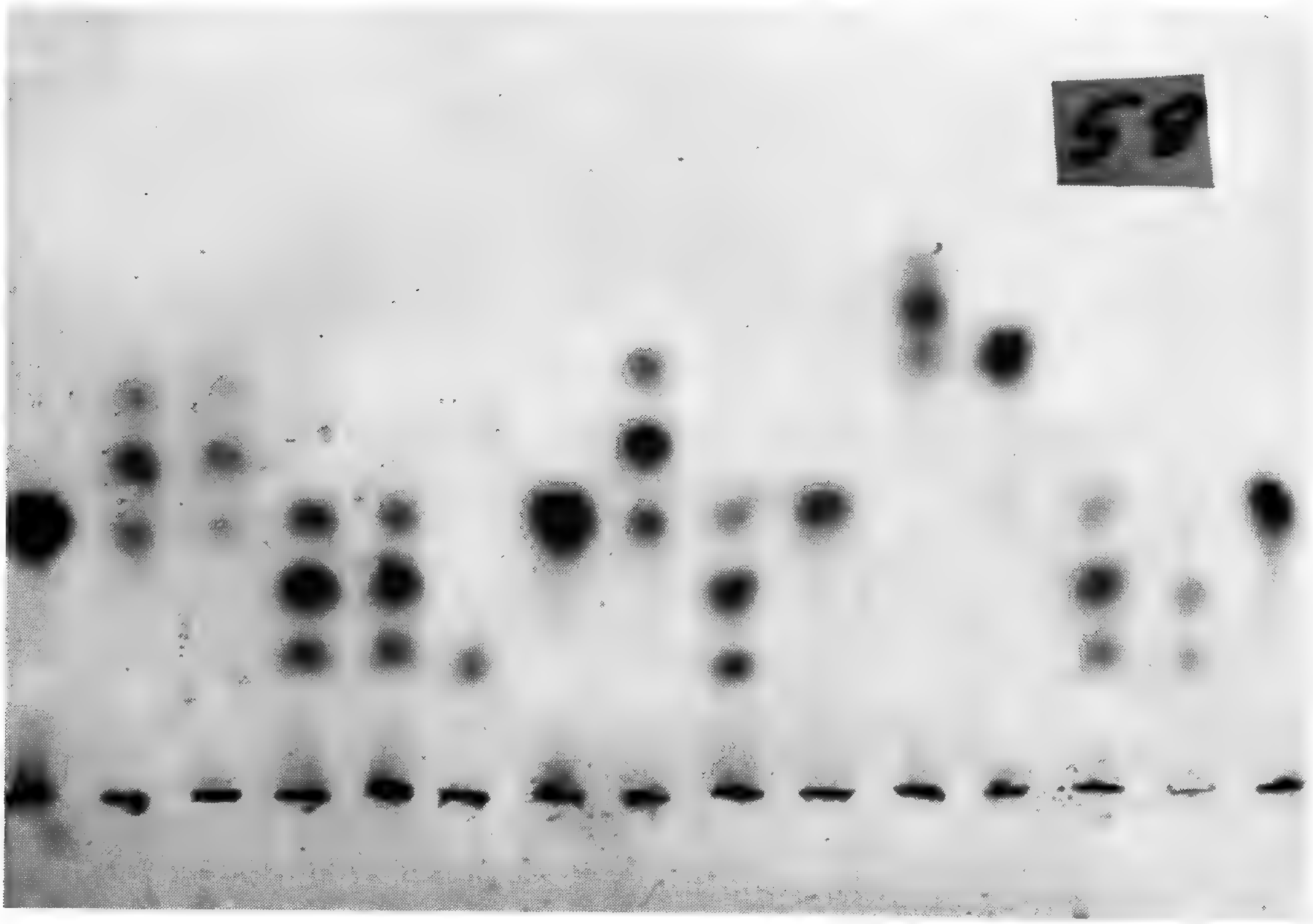

Figure 14. Zymograms obtained using agar gel electrophoresis and formazan staining of octanol dehydrogenase isoenzyme patterns of single adult females, 4–6 days old, taken from the unselected strain of the Darien strain of *Drosophila pellewae.*

3. Evidence of transfer of portions of the *Drosophila metzii* genome into that of *D. pellewae* of the Darien strain.

Although the salivary chromosomes of *Drosophila pellewae* are poorer material for cytological study than those of *D. metzii,* a cross-shaped heterozygous translocation figure involving chromosomes 2 and 4 (Fig. 13A) has been observed in several cells of different preparations. Two complex inversions are present at the junction of the translocation interchange shown in the enlargement of this region in Fig. 13B. The heterozygous 2,4 translocation figure found in *D. pellewae* (Fig. 13A) shows a general resemblance to that of *D. metzii* (Fig. 8), suggesting that similar portions of chromosomes 2 and 4 of each foreign species have been introgressed into the respective siblings. However, the *D. pellewae* inversion figure (Fig. 13B) indicates more extensive restructuring than in the corresponding part of the *D. metzii* heterozygous inversions near the point of translocation interchange (Fig. 8). No other heterozygous translocation figure, or asynapsis, or the large paracentric inversion of chromosome 3 has been observed in the Darien *pellewae* strain.

4. Evidence that in spite of some gene exchange, the Darien strains of *Drosophila metzii* and *D. pellewae* have remained distinct species.

An examination of the octanol dehydrogenase (ODH) isozyme patterns of the sympatric Darien strains of *Drosophila metzii* (Fig. 14) and *D. pellewae*

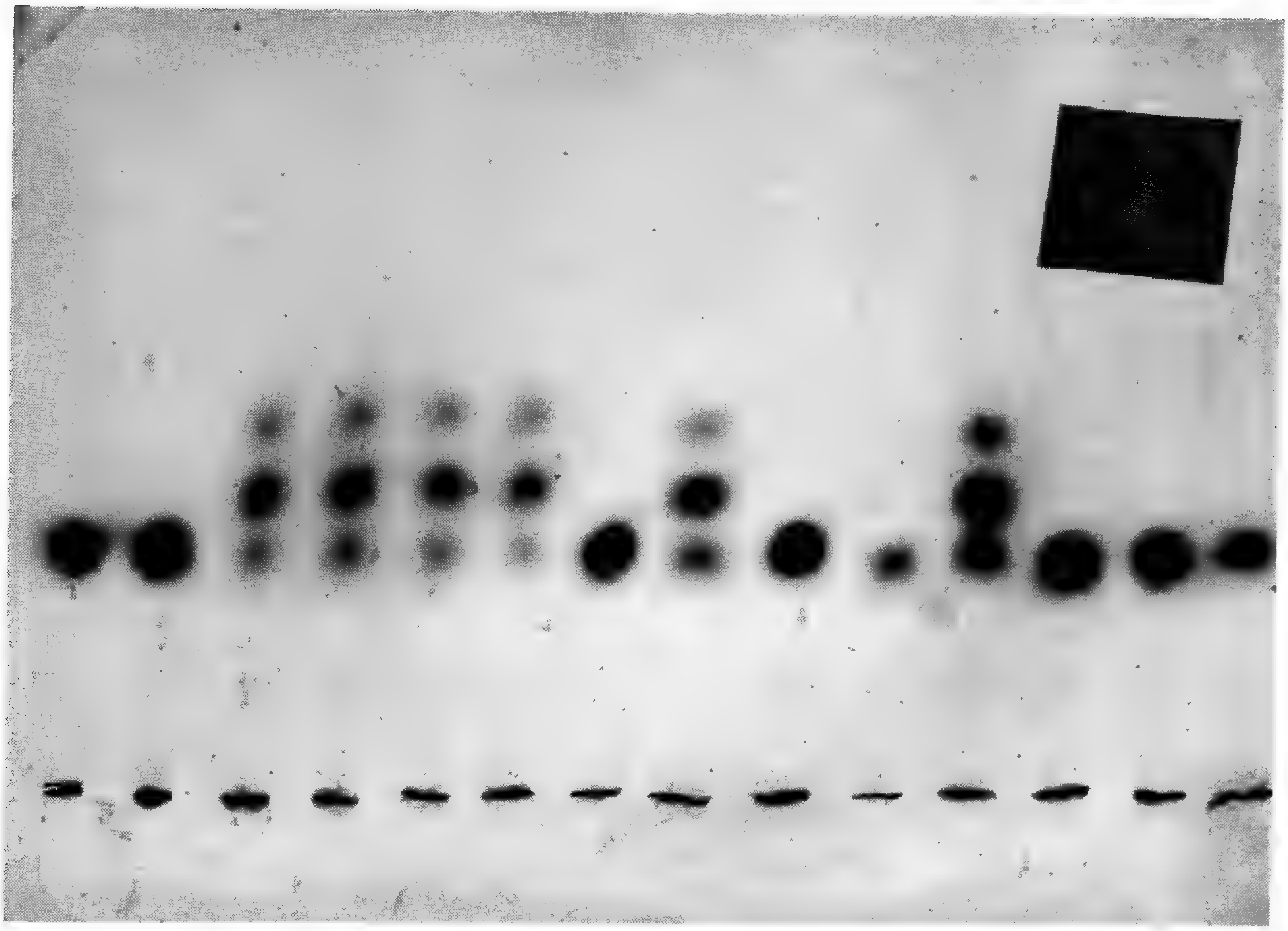

FIGURE 15. Zymograms obtained using agar gel electrophoresis and formazan staining of octanol dehydrogenase isozyme patterns of single adult females, 4–6 days old, of the unselected Darien strain of *Drosophila metzii.*

(Fig. 15) shows striking differences indicating that the genes controlling these patterns differ in the two siblings. The genetics of true breeding ODH variants isolated from these polymorphic strains has been reported by Pipkin (1968*b*, 1969). At least three structural genes coding subunits for the ODH molecule have been hypothesized by Pipkin and Bremner (1970). Homozygous variants differ in the level of certain ODH isozymes. The zymogram of mass homogenates of a strain true breeding for a given ODH pattern shows more isozymes than that of a single female of the same strain. However, breeding experiments demonstrate that all the ODH isozymes belong to the same enzyme system (Pipkin, 1968*b*, 1969). Homozygous ODH variants differ in genes regulating the synthesis of subunits coded by structural genes (or the degradation of certain isozymes). Clearly, slowly migrating isozymes can be seen in zymograms of some individuals of the Darien *pellewae* stain (Fig. 14) which cannot be detected in members of the Darien *metzii* strain (Fig. 15). Previous work has shown that the slowly migrating isozymes can be detected with formazan staining in the Darien *metzii* strain if mass homogenates are used (Pipkin & Bremner, 1970). Sympatric strains of the two sibling species thus differ in genes regulating the level of ODH isozymes.

Drosophila metzii and *D. pellewae* also differ in sexual isolation both with respect to one another and to a third sibling, *D. leticiae* (Pipkin, 1968*a*). Polygenes account for differences in sexual isolation between *D. persimilis* and *D. pseudoobscura* (Tan, 1946); between strains of *D. melanogaster* (Mather & Harrison, 1949; Petit, 1958); between members of the *D. paulistorum* complex (Ehrman, 1961); between *D. l. lebanonensis* and *D. l. casteeli* (Pipkin, 1963).

Further evidence that *Drosophila pellewae* and *D. metzii* remain distinct in the Darien Isthmus is the fact that the species can be separated by a morphological character, carina color (Pipkin & Heed, 1964). Males of *D. metzii* have a chalk white carina and face; females, a whitish carina. Males of the Barro Colorado Island strain of *D. pellewae* and females of all strains have a brown carina and face. The carina is either brown or whitish in males of the Darien *pellewae* strain. This obscure carina color polymorphism first suggested to Pipkin (1968*a*) that introgression between the two siblings was occurring. In laboratory experiments a similar obscure polymorphism was observed in progeny of *metzii/pellewae* female hybrids backcrossed with *pellewae* males. Pipkin (1968*a*) concluded that dominance modifiers which extend and intensify the white area on face and carina of *metzii* males are not present in *D. pellewae*.

DISCUSSION

Stone (1962) pointed out that restructuring of karyotypes of closely related *Drosophila* species has come about chiefly owing to inversions rather than translocations. The latter are strongly selected against because of the deleterious effect on viability of aneuploidy found among progeny of an individual heterozygous for a translocation. Three cases of translocations fixed in species were cited by Stone (1962): in *D. miranda* and *D. pseudoobscura* (Dobzhansky & Tan, 1936), in *D. ananassae* (Kaufman, 1932; Kikkawai, 1938), and in *D. tumiditarsus* (Hsiang, 1949). Translocations in the last two species and those inferred by Clayton (1969, 1971) among the Hawaiian Drosophilidae have affected mainly the amount and distribution of heterochromatin. In *D. albomicans* of the *nasuta* subgroup of the *immigrans* group, Wilson *et al.* (1969) described a fusion combining three of the five primitive rod-shaped elements characteristic of the genus *Drosophila* into one long chromosome, indicating a result of multiple translocations.

A comparison of the relative lengths of respective salivary chromosomes in nine species of the neotropical *tripunctata* species group, taken from the data of Kastritsis (1966) suggests that translocations involving *euchromatin* have played a role in restructuring the karyotypes of members of this group. The ends of chromosomes in nine species show similar banding patterns in salivary gland chromosomes, but interior parts of chromosomes are highly reorganized and cannot be homologized from species to species (Kastritsis, 1966). Measurements of chromosome maps of Kastritsis show variations in chromosome lengths among the species examined. If chromosomes are identified by the terminal banding sequences, chromosome 2 is the longest in all species except *D. mediopunctata* where it is equal in length to that of the X chromosome. Either chromosome 3 or the X is the second longest in six species, but chromosome 4 is second longest in three other species. Although chromosome 5 is the shortest in five of the nine species, it is third longest in *D. mediopictoides*. Nearly all of the *tripunctata* species possess the primitive karyotype of five pairs of rod-shaped and one pair of dot-shaped chromosomes, but fusion of chromosomes 2 and 5 and of chromosomes 3 and 4, respectively, occurs in *D. unipunctata* (Kastritsis, 1966).

A mechanism whereby a translocation, disadvantageous when heterozygous, may be maintained long enough to become homozygous, lies in the selective advantage of coadapted polygenic complexes present in the chromosomes involved in the translocation. The sparse distribution of individual *Drosophila* species in neotropical forests (Pipkin, 1965) must contribute to the isolation and thus persistence of populations in which translocations become fixed. Isolation by translocation homozygosity could contribute ultimately to a sympatric differentiation of species. The importance of coadapted polygenic complexes in the maintenance of inversion heterozygosity has been discussed by Levitan (1958), Kastritsis (1966), and Carson (1969). The present study on Darien populations of *D. metzii* and *D. pellewae* suggests that individuals homozygous for a transposition arise as recombinants in descendants of a *metzii/pellewae* hybrid, similar to the crossover products described by McDonald and Rai (1970) in the progeny of double translocation heterozygotes of *Aedes aegypti*. Even when *D. metzii/D. pellewae* hybrids are produced occasionally in nature, coadaptation of the entire chromosome set of each species leads usually to the continued isolation of these sibling species. However, an opportunity for limited gene exchange due to crossing over is afforded. Since *metzii/pellewae* hybrid males are sterile, gene exchange must occur through backcrossing rare hybrid females with males of either parental species, *i.e.* through introgression.

Although *Drosophila metzii* and *D. pellewae* are difficult cytological material, they present a challenge for the future to discover the extent of karyotype restructuring in each species resulting from introgression in the Darien overlap zone.

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LEVELS OF CONFIDENCE IN THE ANALYSIS OF HYBRIDIZATION IN PLANTS[1]

L. D. Gottlieb[2]

Criteria of Hybridization

One of the hypotheses often used to explain many present-day variation patterns in plants is that they result from interspecific hybridization followed by stabilization of hybrid derivatives. To test this hypothesis we make use of several criteria. Our level of confidence depends on the adequacy of the criteria and the extent to which they are satisfied. This, in turn, depends on various features of the biology of the plants under study. For example, several criteria are employed at the polyploid level which cannot be applied at the diploid level. These criteria have to do with chromosome number, chromosome pairing in experimental inter-ploidal hybrids, tetrasomic inheritance, and the colchicine-synthesis of artificial polyploids from F_1 hybrids between the progenitors. The use of these additional criteria provides a stronger test of hybridity at the polyploid level than can be made at the diploid level.

At the diploid level, the number of criteria are fewer, and they are equivocal. As a result it is more difficult to recognize stabilized diploid hybrid entities, and the literature contains only a small number of examples relative to the number of examples of allopolyploids. The putative diploid hybrids include Corn Belt Dent corns (Anderson & Brown, 1952), *Potentilla glandulosa* subsp. *hansenii* (Clausen, Keck & Hiesey, 1940), *Achilea rosea-alba* (Ehrendorfer, 1959), several subspecies of *Gilia capitata* (Grant, 1950), *Gilia achilleaefolia* (Grant, 1954), *Gilia ochroleuca* subsp. *vivida* and *G. cana* (Grant & Grant, 1960), *Phlox maculata* subsp. *pyramidalis* (Levin, 1966; Hadley & Levin, 1969), *Phlox pilosa* subsp. *deamii* and *P. amoena* subsp. *lighthipei* (Levin & Smith, 1966), *Delphinium gypsophilum* (Lewis & Epling, 1959), *Clarkia deflexa* (Lewis & Lewis, 1955), *Lasthenia ferrisiae* (Ornduff, 1966), the "Abbeville Red" Iris (Randolph, Nelson & Plaisted, 1967), *Penstemon spectabilis* and *P. clevelandii* (Straw, 1955), and *Purshia glandulosa* (Stutz & Thomas, 1964).

The primary criterion of hybridity is morphological intermediacy in several characters; in fact, in the absence of this condition, a hybrid origin would not be suspected. Other criteria include:

1) An additive profile for biochemical characters such as flavanoids or seed proteins that are present in each parent but not in both of them.

2) Unusual amounts of interpopulation morphological variability presumably resulting from continued segregation of parental differences.

3) Distribution in the zone of geographical overlap of the parents.

4) Occurrence in more recent geological formations than the parents.

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[1] Slightly condensed from a talk presented at the Seventeenth Systematics Symposium of the Missouri Botanical Garden.

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Ann. Missouri Bot. Gard. 59: 435–446.

5) Occurrence in ecologically intermediate habitats and intermediacy for physiological characters.

6) Existence of at least partial fertility in F_1 hybrids between the parents to permit the possibility of the production of segregant genotypes.

7) Experimental synthesis of individuals resembling the hybrid taxon in segregants of hybrids between the parents (at least partially achieved by Ehrendorfer, 1959; Grant, 1950; Lewis & Epling, 1959; Ornduff, 1966; Stebbins, 1957).

With the exception of experimental synthesis, none of these criteria are strong, because they do not rigorously distinguish between the hypothesis of interspecific hybridization and alternative hypotheses. Thus, morphological intermediacy and biochemical additivity may reflect ancestral and not derivative status, or selection of mutants that occurred independently in the gene pool rather than having been introduced by hybridization. An unusual amount of inter-populational morphological variability may reflect differences in breeding system, environmental heterogeneity, or founder effect. The occurrence of the taxon on recent or ecologically intermediate formations may also indicate the result of selection of genetic variants already present in the gene pool. Partial fertility of F_1 hybrids does not provide information about the likelihood of forming F_2 and backcross progeny and whether they would survive in nature. Where experimental studies have been done, for example, in *Gilia* (Grant, 1966), most segregating hybrid progeny were inviable and highly sterile and were kept alive only by the most careful greenhouse practices. Consequently, we see that the individual criteria do not provide a rigorous and unequivocal means of testing the hypothesis that a particular diploid entity has a hybrid origin. The criteria should be more accurately considered a series of questions; the more of them that are answered positively, the higher is the level of confidence that our hypothesis is correct.

INTRODUCTION TO *STEPHANOMERIA*

I would like to illustrate the problems of using these criteria by examining the variation patterns and reproductive relationships of the annual species of the western North American genus *Stephanomeria*, a member of the Chicory tribe of the Compositae. The annual Stephanomerias are closely related species widely distributed in a number of habitats in California and adjacent regions. They have long been known for their complex morphological intergradation which has stymied taxonomic efforts to separate the taxa one from another (Ferris, 1960: 574). They constitute both a polyploid complex and a homogamic complex in which the same divergent diploid species are connected by morphologically intermediate tetraploid and diploid taxa. They are now known to include nine diploid and two tetraploid entities (Gottlieb, 1969; unpublished). A formal taxonomic classification of the annual Stephanomerias has not yet been set forth, because certain additional field studies are required before taxonomic rank can be determined. Eight of the diploid taxa are divided into two distinct clusters on the basis of morphology, cytology, breeding system, crossability, hybrid fertility, and homology of chromosome structure (*ibid.*):

The Exigua Cluster contains Exigua (*Stephanomeria exigua* Nutt.), Deanei (*S. exigua* var. *deanei* MacBride), Coronaria (*S. coronaria* Greene), Carotifera (*S. carotifera* Hoover), Paniculata (*S. paniculata* Nutt.), and Macrocarpa, a newly discovered and undescribed taxon.

The Virgata Cluster contains Virgata (*S. virgata* Benth.) and Pleurocarpa (*Ptiloria pleurocarpa* Greene).

The morphological features of the two clusters are combined in an additional diploid species Diegensis (*S. diegensis* Gottlieb, in manuscript), and two different tetraploid taxa. Carotifera also varies morphologically in the direction of Virgata.

The grouping of taxa into two clusters is the result of experimental and observational analyses. Problems of phylogenetic interest develop when we try to analyze the relationships of the morphologically intermediate Diegensis, Carotifera, and the two tetraploids. To illustrate these problems we will make the initial hypothesis that these entities have a hybrid origin between the clusters.

THE TETRAPLOIDS

We have a high degree of confidence that the tetraploids are allotetraploids, and I will treat them briefly. Their chromosome number is $2n = 32$, an addition of the diploid number of $2n = 16$ common to all the diploid Stephanomerias. They show normal meiosis with bivalent chromosome pairing. They either resemble one or the other diploid cluster or are morphologically intermediate; neither one has any unique morphological features. One of them is found within the zone of geographical overlap of the diploid clusters in central and southern California; the other is found partially within the overlap zone but also to the north of it in the North Coast Ranges and the western foothills of the Sierra Nevada. Both are commonly encountered in disturbed areas along roadsides and freeways and in open habitats such as coastal sand dunes, chaparral openings, oak savannah, and grassy meadows. Triploid F_1 hybrids between different diploids from both clusters and the tetraploids show *Drosera* chromosome pairing with the essential absence of multivalents. Artificial tetraploids synthesized with colchicine from sterile F_1 hybrids between different members of the two clusters had fully restored fertility and exhibited regular meiosis. Consequently, it is possible to satisfy most of the criteria that the tetraploids have arisen as a result of chromosome doubling following interspecific hybridization between species in the Exigua and Virgata Clusters.

THE PARENTAL DIPLOID STEPHANOMERIAS

The hypothesis that Diegensis and Carotifera also result from interspecific hybridization between the clusters is more difficult to deal with, and the level of confidence regarding their phylogeny is correspondingly weaker. In order to convey some of the problems in the limited time available I will summarize the relevant evidence and then discuss the possible interpretations.

Virgata and Pleurocarpa are distributed primarily in California (Fig. 1) in oak savannah and chaparral openings; Virgata is also abundant on roadsides and freeway embankments in southern California. The taxa resemble each

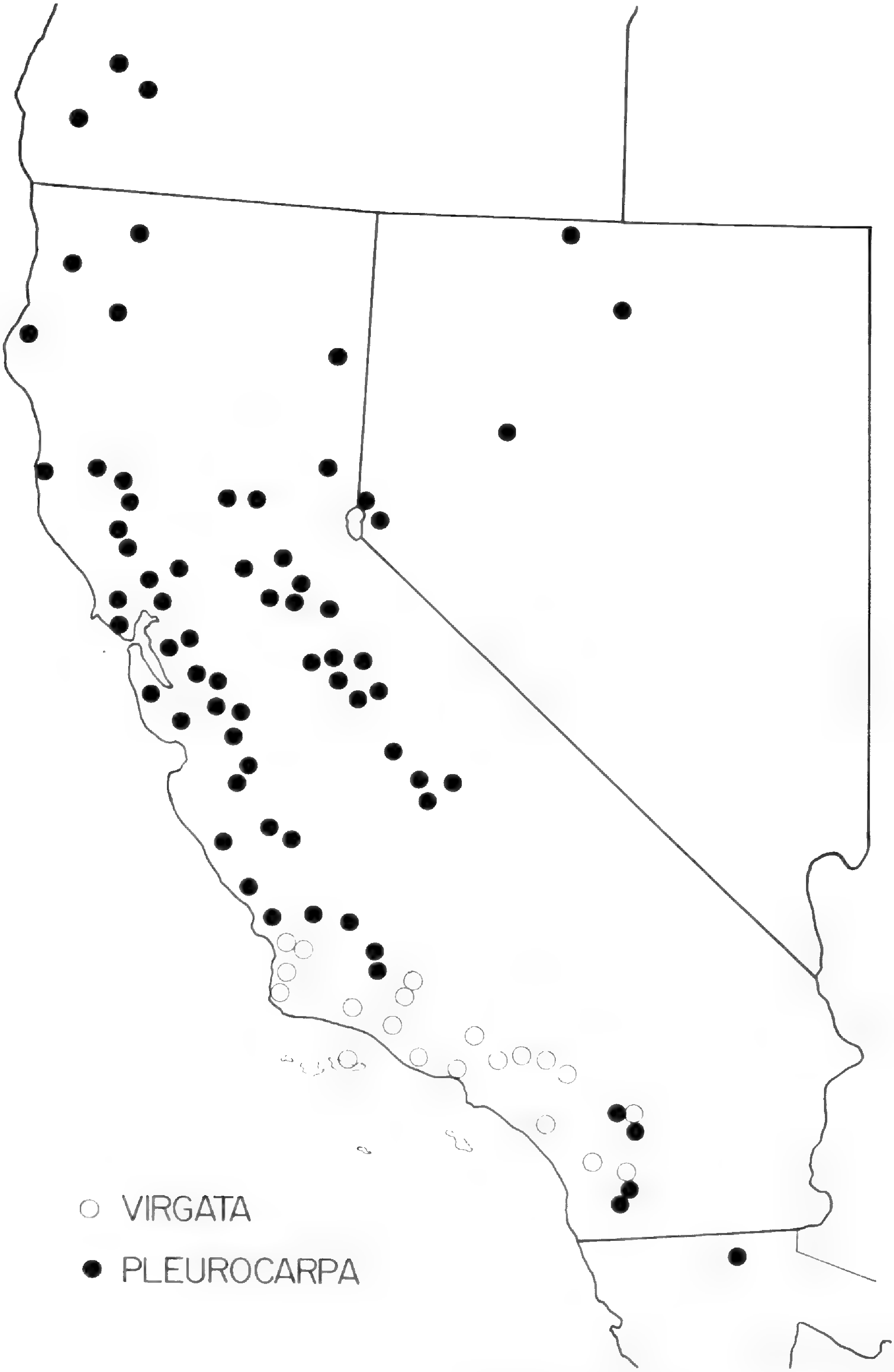

FIGURE 1. Distributions of Virgata and Pleurocarpa.

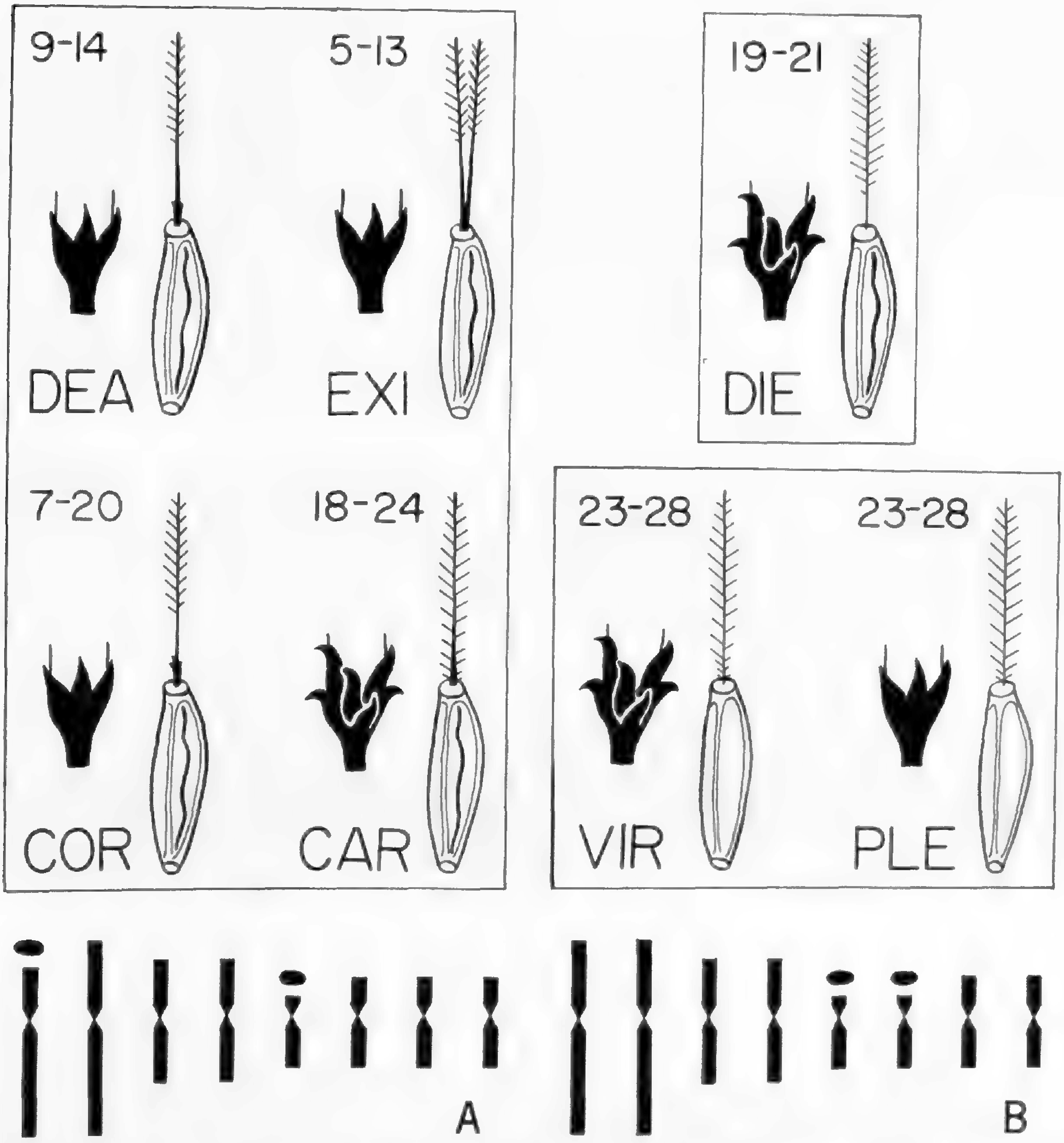

FIGURE 2. Diagram of the karyotypes and morphological characteristics of the achenes, pappus bristles (including number per achene), and basal involucral bracts of different taxa of *Stephanomeria*. Karyotype A is found in Deanei, Exigua, Coronaria, and Carotifera. Karyotype B is found in Diegensis, Virgata, and Pleurocarpa.

other in many features of their achenes and pappus bristles, but differ in the condition of the basal involucral bracts which are reflexed in Virgata and appressed in Pleurocarpa (Fig. 2). F_1 hybrids between them are highly fertile and have mean pollen stainabilities ranging from 78% to 90%, with an overall mean of 84% (Fig. 3). Their chromosomes pair extremely well, and an average of 95% of the PMC's in their F_1 hybrids have eight bivalents.

In the Exigua Cluster, Exigua and Coronaria are widespread in California, the Southwest, and the Great Basin (Fig. 4). Exigua is distributed in sandy soils in sagebrush and creosote bush desert communities. Coronaria occupies a wide variety of habitats from the maritime Channel Islands to the eastern

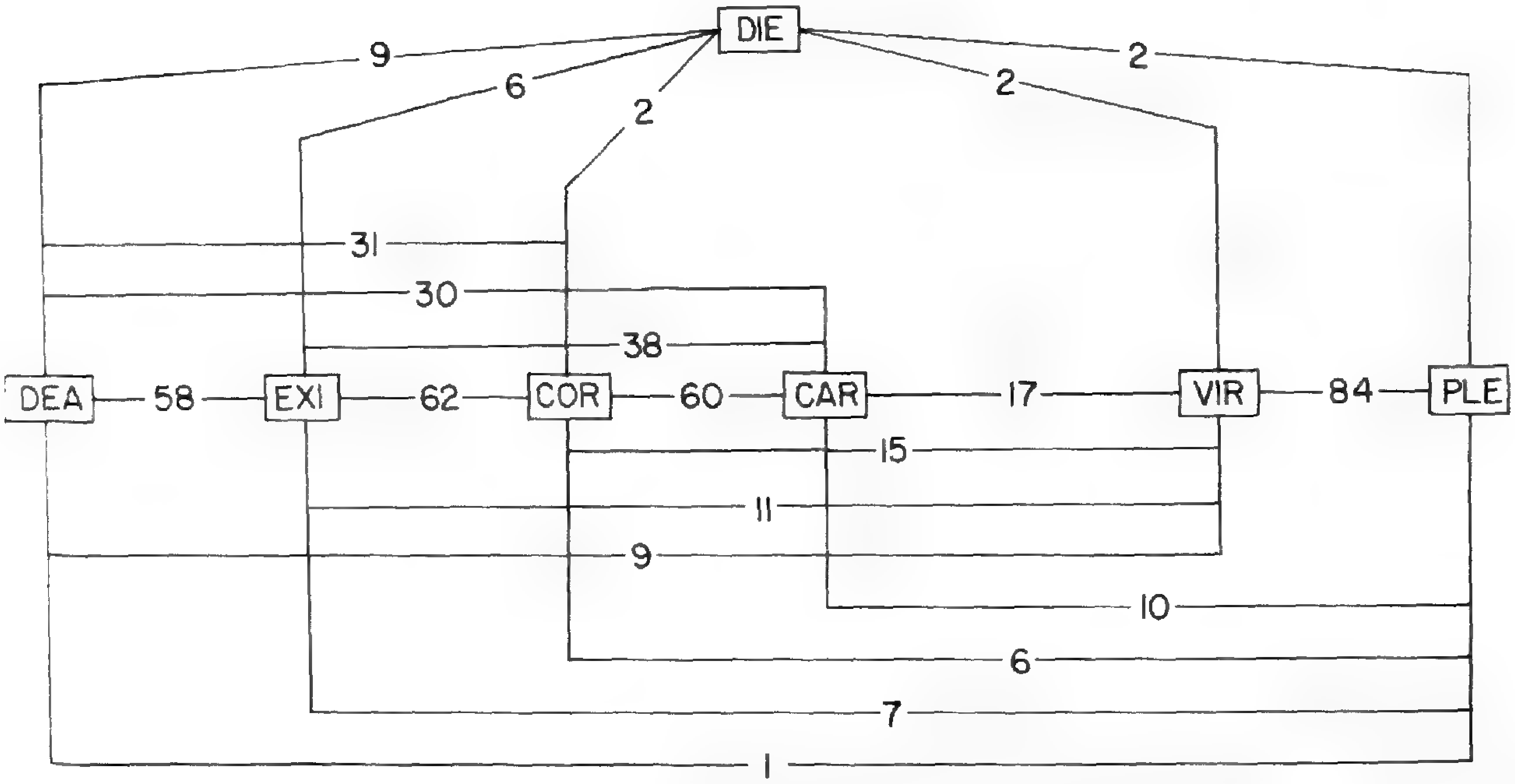

FIGURE 3. Summary of the pollen fertilities (in percent) of F_1 hybrid progenies between different taxa of *Stephanomeria*.

Sierra Nevadas and the cold desert of eastern Oregon and Idaho. Deanei is distributed in sandy fields and chaparral in southern coastal California, and Carotifera on sand dunes and marine shales and arid inland sites in south central California (Fig. 4). The distributions of Coronaria, Deanei, and Carotifera partially overlap those of Virgata and Pleurocarpa.

These four members of the Exigua Cluster as well as both members of the Virgata Cluster have a sporophytic self-incompatibility system and are consequently obligate outcrossers. Paniculata and Macrocarpa are self-compatible and are self-pollinated in the greenhouse. They are most likely derived from different outcrossing members of the Exigua Cluster and do not concern us further here.

The members of the Exigua Cluster share many morphological features but each of them is set off by particular characters or combinations of characters. As a group they exhibit a number of morphological characters which differentiate them from the Virgata Cluster (Fig. 2). The achenes of the Exigua Cluster are grooved longitudinally, and the pappus bristles are less numerous, at least slightly thickened at the base, often connate in groups of two to four, and, with the exception of the fully plumose Carotifera, are 40% to 75% plumose. In contrast, the achenes of the Virgata Cluster lack grooves, and its pappus bristles are more numerous, not thickened, separate at the base, and densely plumose for their entire length. The involucral bracts of Exigua, Deanei, and Coronaria are appressed like those of Pleurocarpa, whereas those of Carotifera are reflexed like those of Virgata. The two clusters also differ morphologically in several other characters of pubescence and inflorescence branchlet length.

The karyotypes of both clusters are similar in relative chromosome lengths and centromere positions. They differ in that in the Exigua Cluster a satellite is borne on the short arm of one long and one short chromosome, whereas in the Virgata Cluster a satellite is found on the short arm of two short chromosomes (Fig. 2).

Forty F_1 hybrid progenies were grown from crosses within the Exigua Cluster. Within-taxon progenies were highly fertile with an overall mean of 85% pollen stainability. Between-taxon progenies had means ranging from 30% to 62%, with an overall mean of more than 40% (Fig. 3). Cytogenetic studies of 14 hybrid progenies reveal a high degree of homology in chromosome structure within the cluster. The percentage of PMC's with regular bivalent pairing ranged from 65% to 100%, with an overall mean of 86%. The number of unpaired chromosomes was less than 0.2 per PMC. However, most hybrids had a single quadrivalent suggesting the presence of a reciprocal translocation; and single bridge and fragment configurations, suggestive of a paracentric inversion, were also observed.

Although the members of the Exigua Cluster have diverged from one another to a moderate degree both morphologically and reproductively, they remain similar in many respects. They are probably best considered a group of semispecies in which strong discontinuities have not yet developed.

The reproductive relationships of the clusters with each other were tested by growing out twenty different F_1 hybrid progenies. The mean pollen fertility of these hybrids was sharply reduced compared to that of the hybrids within each cluster. Between Virgata and different members of the Exigua Cluster, the mean hybrid pollen stainability ranged from 9% to 17%; between Pleurocarpa and the Exigua Cluster the range was 1% to 10% (Fig. 3). The reductions in hybrid fertilities were accompanied by increases in the proportion of PMC's with meiotic abnormalities. For example, for the nine hybrids analyzed cytogenetically, the mean percentage of PMC's with regular bivalent chromosome pairing dropped to 42%. The number of multivalents was high, and each of the F_1 hybrids examined had high percentages of cells with at least one quadrivalent and several of the hybrids had additional and/or larger multivalents. The reduced fertility of these hybrids is most likely the result of differences in chromosome structure between the two clusters. This suggestion is strengthened by the fact that artificially doubling the chomosome number of two between-cluster F_1 hybrids by using colchicine increased their pollen stainability from 16% to 94% and from 6% to 98%. Both artificial tetraploids showed preferential bivalent pairing and no multivalents were observed.

In addition to reductions in hybrid fertility, the two clusters are separated by crossability barriers such that only 5–10% of experimental cross-pollinations between them yielded seed. Within the clusters, 50–75% of the between-taxa cross-pollinations yielded seed. No barriers reducing crossability were detected between populations of the same taxon.

A number of between-cluster natural hybrids have been found where populations of the clusters are sympatric. Like the experimental hybrids, these individuals are vigorous and retain partial fertility. Consequently, they satisfy the criterion that the putative parents can hybridize in nature to produce at least partially fertile offspring. The opportunity for sympatry is high in

California where their distributions widely overlap and where they occupy habitats which are often juxtaposed.

The differences between the Exigua and Virgata Clusters in morphology, karyotype, chromosomal structural arrangement, crossability, and hybrid fertility are believed to reflect a fundamental phylogenetic divergence within the annual Stephanomerias. The hypothesis of hybridity of the morphologically intermediate entities requires that the parental taxa be phylogenetically older than the derivative taxa. Although there is no fossil evidence, the great age of the clusters is attested to by their wide distributions, and broad ecological amplitudes. In addition, they are the progenitors of two different tetraploid entities. The Exigua Cluster contains morphologically and reproductively divergent taxa and also includes two derivative self-compatible entities, one of which (Paniculata) is widespread.

THE PUTATIVE HYBRID DIPLOID STEPHANOMERIAS

Having reviewed the characteristics and relationships of the two clusters, we can examine more closely the evidence that Carotifera and Diegensis result from their hybridization.

Let us look first at Carotifera. The available evidence satisfies many of the criteria for its having a hybrid origin. In overall morphology, karyotype, and chromosomal homology, it resembles other members of the Exigua Cluster. However, in several morphological features, it varies in the direction of Virgata. For example, it has reflexed involucral bracts and fully plumose pappus bristles, and it has an intermediate number of bristles and an intermediate degree of bristle base thickening. Despite the geographically restricted distribution of Carotifera, it shows a high degree of inter-populational morphological variability in a number of characters such as ligule color, floret number and length, rosette leaf width, and degree of bristle base thickening.

The bristle base character is particularly interesting, because it divides Carotifera into two groups of populations. Inland populations have markedly thickened bases like other taxa in the cluster, while coastal populations have very slightly thickened bases, varying toward those of Virgata. Colinear with this morphological difference, the inland populations are reproductively closer to Coronaria than are the coastal populations. Hybrids between the inland populations and Coronaria are 75% fertile, whereas those between the coastal populations and Coronaria are only 45% fertile. The inland and coastal populations are fully interfertile. This difference in reproductive compatibility is not shown towards the geographically more remote Exigua and Deanei.

Carotifera is distributed where other members of the Exigua Cluster and Virgata and Pleurocarpa are sympatric in the South Coast Ranges. Hybrids between the two clusters have been found in this region. Inland populations of Carotifera are also presently sympatric in several localities with both Virgata and Pleurocarpa, and hybrid individuals have been observed in these sites. Seeds taken from a natural hybrid between the inland form of Carotifera and Pleurocarpa were grown in a progeny test. Three seedlings matured. They were similar morphologically to Carotifera in some characters and intermediate in

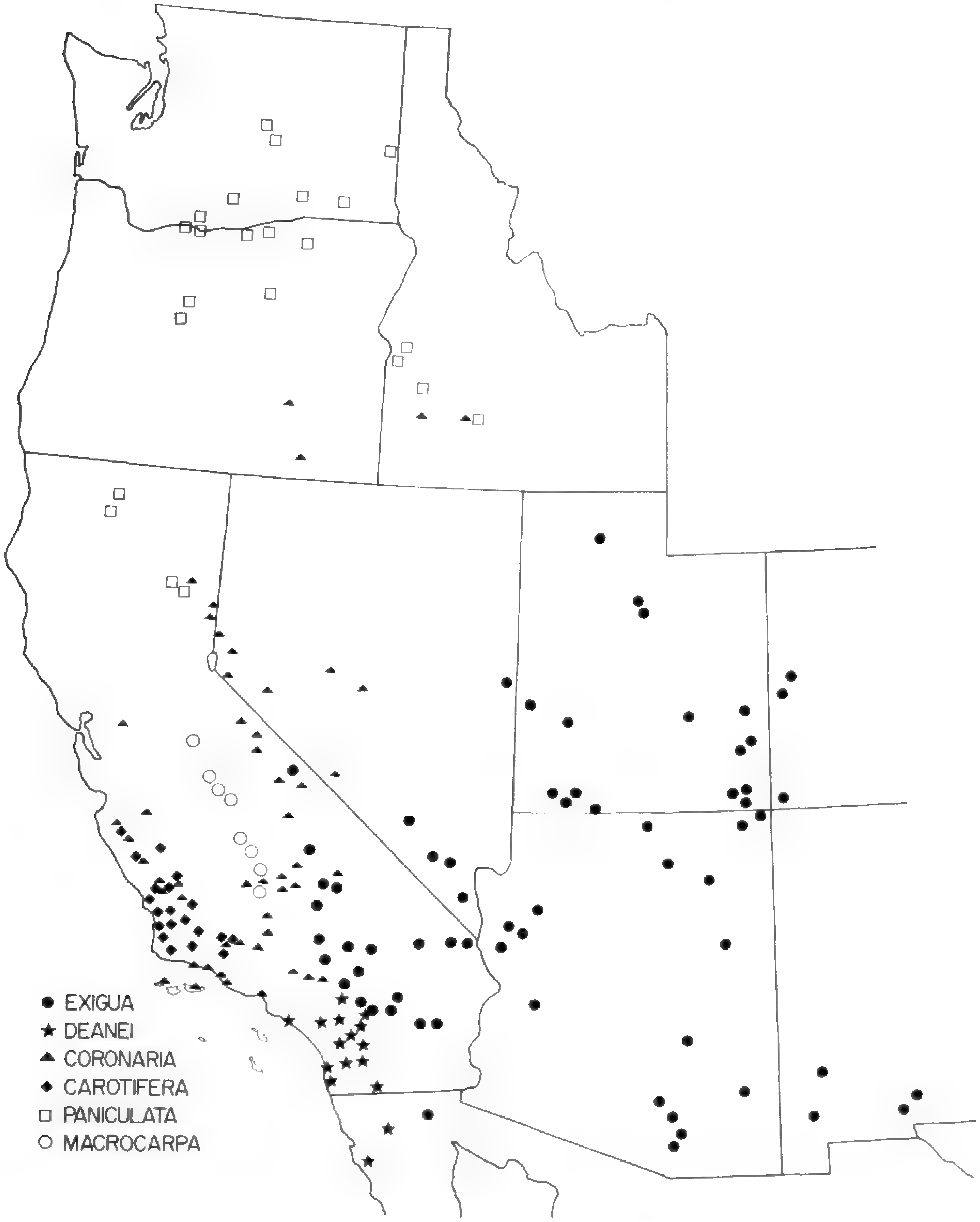

FIGURE 4. Distributions of Exigua, Cornaria, Deanei, Carotifera, Paniculata, and Macrocarpa.

others. Their pollen stainabilities were 23%, 23%, and 55%, whereas the mother plant had only 11% stainable pollen. The seedlings were apparently backcrosses to Carotifera, and the increase in their fertility indicates that selection can be expected to operate rapidly for this trait.

The ecological preferences of Carotifera are open, temporary, and pioneer habitats. Coastal populations are found on sand dunes and shales; the inland populations favor sandy sites in grasslands and oak savannah in the arid inner South Coast Ranges.

With the exception of an experimental synthesis and biochemical studies, the criteria for the hybrid origin of Carotifera are reasonably satisfied. However, it would be well to try to rule out several alternative hypotheses. First, Carotifera may be a remnant of an ancient entity from which the two clusters diverged. This suggestion does not seem likely because of the recency of its habitats and preferences for temporary sites, features not generally associated with ancient relics. In addition, the close relationships of Carotifera to Coronaria and Exigua suggest it is not ancient. Another hypothesis is that the resemblance of Carotifera to Virgata may result from mutation within the gene pool of Carotifera followed by selection for the morphological traits in question. This is a difficult hypothesis to prove because we would have to know the number of genes involved in the characters, their linkage relationships, their regulation, and their selective advantages. In the absence of this information as well as information on the amount of genetic variability for these characters in the gene pool of Carotifera at some time in the past, we have no reason to favor such an hypothesis.

In summary, the evidence we have suggests that the morphological characters of Carotifera that cause it to resemble Virgata are the result of hybridization between Coronaria or Exigua and Virgata followed by backcrossing to the Exigua Cluster parent accompanied by selection for a new balance of adaptation. The level of confidence in this hypothesis is high, but it is not as high as with the tetraploids where additional criteria are satisfied.

The other putative hybrid diploid *Stephanomeria* is Diegensis which is found in southern coastal California and northern Baja California (Fig. 5). It also occupies pioneer habitats such as old clearings, the landward sides of coastal sand dunes, chaparral openings, and sandy roadsides and freeway embankments. Diegensis has a different combination of the morphological characters of the clusters. It has grooved achenes, but its pappus bristles are separate, not thickened at the base, and intermediate in number and plumosity (Fig. 2). In the southern part of its range, the involucral bracts are strongly reflexed, but in northern populations they are less reflexed. Diegensis also combines pubescence and inflorescence branchlet length characteristics of the two clusters. The only unique morphological features of Diegensis are its higher number of florets per head and the longer lateral pinnae along the pappus bristles. Its karyotype is similar to that of the Virgata Cluster in having satellites borne on the short arms of two short chromosomes (Fig. 2).

Diegensis is the most reproductively isolated taxon of all the outcrossing diploid Stephanomerias. Twelve different F_1 hybrid progenies between it and the other taxa had mean pollen stainabilities ranging from 2% to 9% (Fig. 3). The reduction in fertility of these hybrids is accounted for by the finding that the chromosomes of Diegensis are extensively repatterned from those of the other taxa. In the five different F_1 hybrids studied cytogenetically, the percentages of PMC's with regular bivalent pairing ranged from 1% to 29%, and the number of unpaired chromosomes was substantial, ranging from 2.3 to 6.6 per PMC. Multivalents and bridge and fragment configurations were

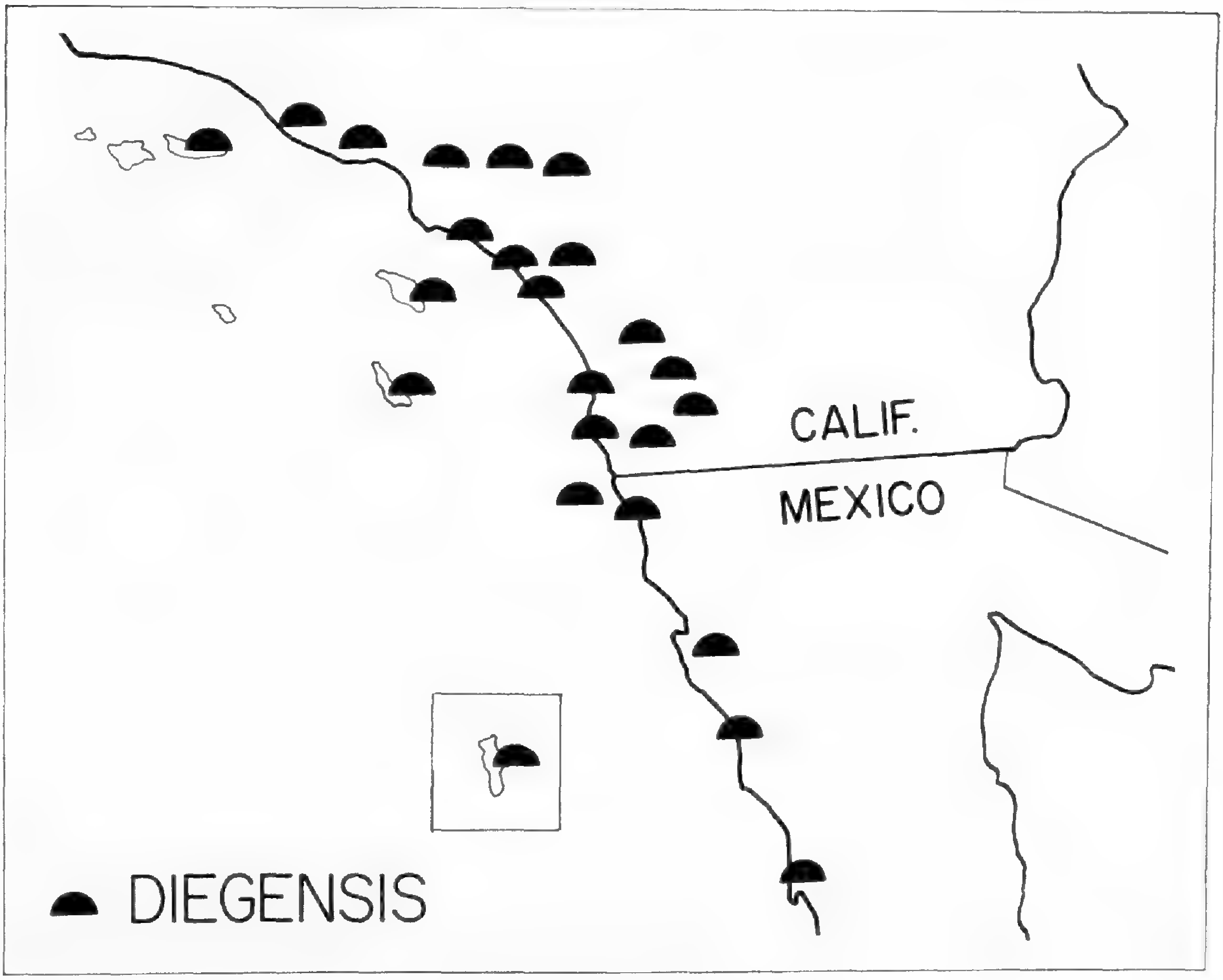

Figure 5. Distribution of Diegensis.

common. Not only is hybrid fertility reduced, but crossability barriers are also present since it was difficult to obtain hybrids with Diegensis as a parent.

The strong reproductive isolation of Diegensis increases the complexity of evaluating its phylogenetic relationships. Three hypotheses can be suggested. First, Diegensis may be an ancient relic and is a morphological composite of the two clusters, because they differentiated from it or from a similar taxon. The problem with this hypothesis is that it cannot explain why members of the two clusters diverged in morphology, karyotypes, and ecological adaptations, and yet failed to diverge reproductively to the same extent, remaining more compatible with each other than with their supposed progenitor. Also it seems unlikely that Diegensis is an ancient relic, because it is found on temporary and often disturbed sites. A second hypothesis assumes that the Exigua Cluster, the Virgata Cluster, and Diegensis are each derived from a different perennial *Stephanomeria* and consequently show different degrees of reproductive isolation. This hypothesis requires that the perennial species that gave rise to Diegensis was morphologically intermediate, which simply removes the problem of explaining the intermediacy to an earlier time. Also, the extant perennial species of *Stephanomeria* are distinct from each other, and none of them exhibit morphological intermediacy. The third hypothesis is that Diegensis also results from hybridization between the Exigua and Virgata Clusters but one that occurred independently of the hybridization that led to the formation of Carotifera. The third hypothesis satisfactorily accounts for the morphological intermediacy of Diegensis and presumes that its reproductive isolation which results from extensive chromosomal repatterning does not reflect an ancient lineage. It has frequently been suggested (Lewis & Raven, 1958; Lewis, 1966) that hybrid sterility in annual plants often results from differences in chromosome structure and that these differences can accumulate in a relatively small number of generations. The level of confidence in the inference that Diegensis has a hybrid origin is not as high as with Carotifera or the tetraploids. This is because fewer criteria are satisfied and an additional assumption is necessary to explain its sharp reproductive isolation.

In summary, *Stephanomeria* illustrates the problems of attempting to deal with past events. Depending on the available evidence and the adequacy of the criteria satisfied, the best we can do is establish levels of confidence for the inferences we make.

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HYBRIDIZATION, TAXONOMY AND AVIAN EVOLUTION

Lester L. Short[1]

This report treats mainly the taxonomic significance of avian hybridization. I will take care of my impression of its evolutionary significance very briefly—(1) hybridization is insignificant in terms of hybrid origin of avian species, and (2) it is quite significant in terms of variation potential.

My approach to the investigation of hybridization is that of an evolutionary biologist, trained in taxonomy and with special interests in zoogeography, ethology, ecology, and genetics.

Birds offer various advantages for studies of hybridization and several disadvantages. Among the advantages are: (1) Birds are higher vertebrates whose primary senses, like ours, are visual and auditory. Sounds and sights are important to them, and they are employed behaviorally, including use as isolating mechanisms. Hence, we can appreciate the signals of birds more easily than signals used by most animals. (2) Birds are mainly diurnal, conspicuous and common. (3) Their geographic distribution is exceptionally well known. And (4) their systematics is relatively better known at the species level than that of other animals. Disadvantages are that: (1) Birds are difficult to maintain and are very difficult to breed in captivity in significant numbers. (2) They are hence rather poorly known genetically. And (3) they are highly mobile, that is they fly rapidly, they are very active, and often they are migratory. It might be noted also that their fossil record is poor, and hence we must largely base our knowledge of their relationships upon studies of modern birds.

My remarks deal mainly with hybridization in secondary contact and sympatric hybridization in nature. Following Anderson (1949), Stebbins (1959) and others, I include both intra- and interspecific hybridization, but bear in mind that all the interbreeding forms I shall mention are considered species by some ornithologists, even today.

Natural hybrids have been reported involving many avian species. I estimate that perhaps 40% of bird species ultimately will be shown to hybridize rarely to commonly. Our present knowledge of this phenomenon is uneven because of emphasis on game and other large species, on very distinctively marked species, and on species handled frequently by bird banders. Because many birds are sexually dimorphic, and males usually have brighter plumages than females, most reported hybrids are males, whereas less colorful female hybrids pass undetected. Many of the latter doubtless will be found eventually in present museum collections.

Only a few points will be noted here (see Short, 1969) concerning the significance of rare and unusual hybrids. Interspecific hybrids in this category can be evaluated taxonomically only after allowance is made for: (1) the

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Ann. Missouri Bot. Gard. 59: 447–453.

TABLE 1. Analysis of avian hybrid situations in North America.[a]

Situation	Number of Superspecies involved	 Species involved	 Cases[b] involved	Extent of Zone[c] Great	 Small
Hybrid zones	—	16	19	10	9
Zones of overlap and hybridization	17	35	—	12	6
Hybrid swarms	3	5	4	0	4

[a] Data from Mayr and Short (1970); *only* the better documented cases are included (see text).
[b] Differs from "species involved" only intraspecifically for hybrid zones and hybrid swarms; a "case" is *one* pair of forms, and several different pairs of forms (subspecies or subspecies groups) may hybridize within a species, yielding several "cases."
[c] "Great" is 25 miles or more in extent (*not* width; see text), and "small" is less than 25 miles in extent.

relative opportunity for hybridization, that is the degree of actual sympatry within the group considered; and (2) the opportunity to recover hybrids. If there is much opportunity for interbreeding and for the recovery of hybrids within a particular group (*e.g.*, a family or a genus), then relative hybridization may provide useful taxonomic information.

Most hybrid birds are adults that often have undergone extensive migrations. The great number of avian hybrids (Gray, 1958) is puzzling in relation to the general view that animal hybrids encounter more severe homeostatic problems than do plant hybrids. The frequent survival to maturity in nature of hybrid birds, sometimes representing crosses between distantly related species, suggests that their physiology is not disrupted to the extent that has been thought. The occurrence of these hybrids indicates a great genetic similarity within many bird families. Crosses between species of different avian families are rare. Since an obvious correlation exists between the potential for hybridization and the degree of relationship, the occurrence and survival to adulthood of *any* hybrid, even in the aviary, is an indication of considerable genetic compatibility and resemblance.

More important are interspecific and intraspecific hybridization and backcrossing in secondary contacts (see Table 1). Among 517 extant species and superspecies of birds nesting in North America, 35 or 7% hybridize in this manner (Mayr & Short, 1970). Each of these 35 situations involves at least two (sometimes three) forms that have been considered separate species in the past and may be so considered by an extreme taxonomic "splitter" today. These cases denote a critical stage of speciation—the test of the degree of divergence of two populations. Although the number of species affected is not very great it is significant because: (1) The species involved are not rare, local species, but are common, widespread, hence biologically successful species; examples are the mallard ducks (*Anas* [*platyrhynchos*][2]), flickers (*Colaptes auratus*), house wrens (*Troglodytes aedon*), orioles (*Icterus galbula*), towhees (*Pipilo erythrophthalmus*), juncos (*Junco hyemalis*), and others. And (2) allowing an average life of say 1,000,000 years for species, it is evident

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[2] Brackets indicate superspecies; see Amadon (1966) and Mayr and Short (1970).

that hybridization could have played a role in the evolution of many or possibly even most avian species. This possibility is reinforced by the occurrence of limited sympatric hybridization in overlap zones involving 17 other species and superspecies (these include over 34 distinct forms). Thus, an additional 3% of North American species may have hybridized more extensively in the recent past. Furthermore, additional Nearctic species hybridize outside North America (Mayr & Short, 1970). It is probably safe to say that hybridization has been a significant factor in the recent evolution of at least 15% of the Nearctic avifauna.

I suspect that hybridizing species have been favored in the Pleistocene, that is, more rapidly speciating avian species may have suffered a greater rate of extinction than have those speciating more slowly. In this view hybridization is assigned an important role as a source of recombination under the rapidly shifting environmental conditions of the Pleistocene. Although radically different in its effects from glaciation, the impact of European civilization on North America may be likened to that of a new glacial period. Hybridizing avian species, survivors of the Pleistocene, not surprisingly seem to be doing well in man-modified environments.

I have endeavored (Short, 1969) to utilize field data in evaluating the taxonomic status of hybridizing forms. When two populations come into contact and interbreed to any extent, one of two situations commonly results. In one case a "hybrid zone" develops. This zone, however extensive, is inhabited by a population comprised entirely of hybrids (and diverse recombinants). Gene exchange is free, breeding is random, and the taxa are considered conspecific (they represent subspecies, often of different subspecies groups). Such a hybrid zone is interposed between the parental populations and effectively *both* connects *and* separates them. Thus, the parental forms are *not* sympatric. The distance across the zone from one to the other parental population, here called its width, of course is determined by natural selection. Its "actual" width is not determinable from field data, for its "apparent" width varies depending upon the nature and the number of characters used. Biochemical characters, for example, often extend the area of a hybrid zone previously determined by external morphological features. The depth or extent of the zone (perpendicular to its width) is determined by diverse factors such as topography and vegetation. An example of an extensive hybrid zone is shown in Figure 1 (see also Table 1).

A second type of situation is one in which there is overlap of the parental forms with hybridization occurring within the area of overlap which is termed a "zone of overlap and hybridization." Thus, the hybridizing forms, considered species (allospecies comprising a superspecies; see Amadon, 1966), are sympatric. One must ascertain that the parental phenotypes are sufficiently frequent and regular to insure that they are not extreme recombinants. I use the arbitrary value of 5% or more of *each* parental phenotype (or phenotypes), but in practice no problems occur because substantial numbers of both parental phenotypes (usually totaling some 30 to 90% or more of the population in the zone) are present in most reported cases. At each edge of the zone one parental

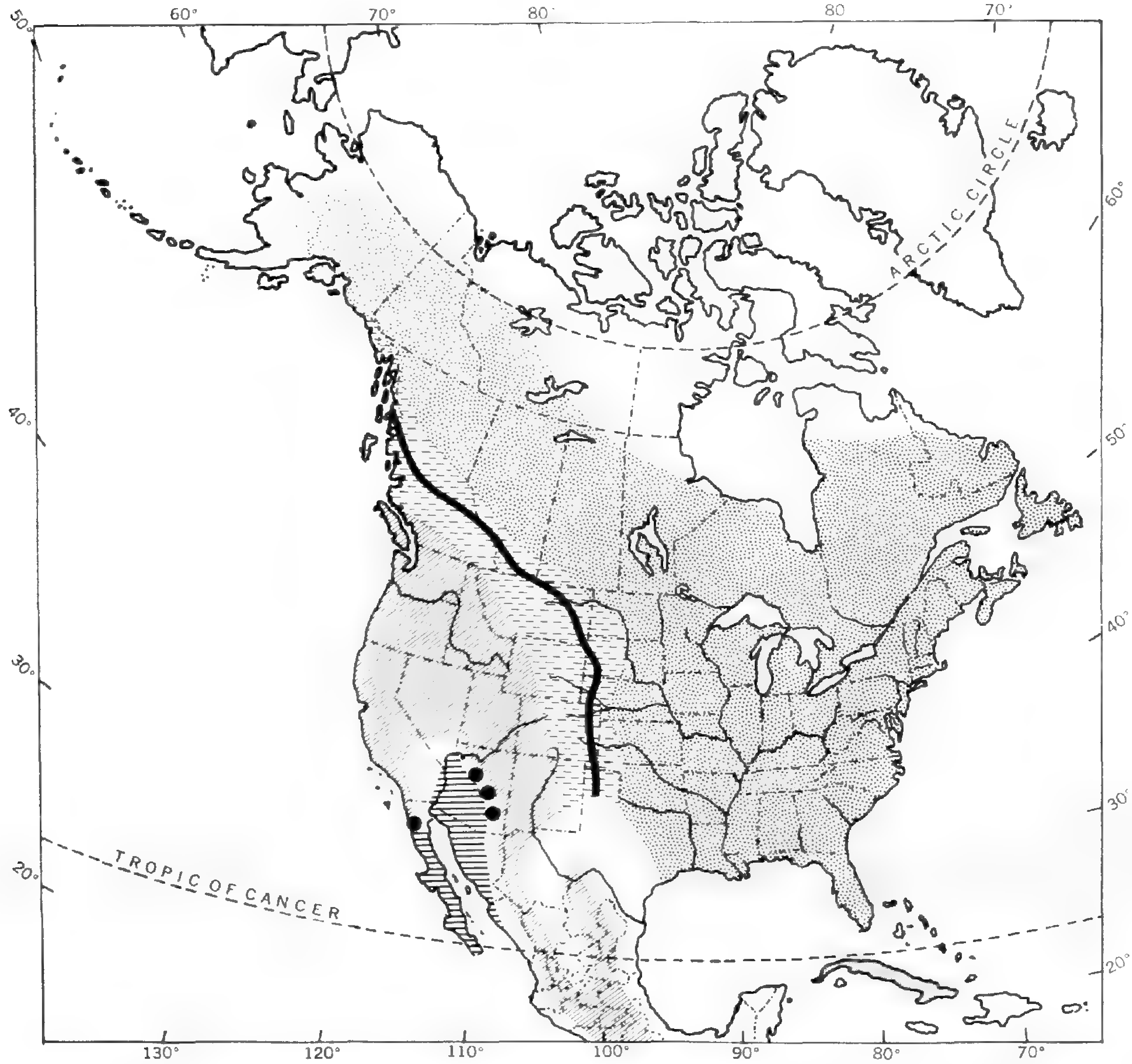

FIGURE 1. — The distribution of subspecies groups and hybrid zones in the North American flicker (*Colaptes auratus*). The groups are: *auratus* group—stippled; *chrysocaulosus* group—gray (Cuba); *cafer* group—diagonal lines; and *chrysoides* group—horizontal lines. A fifth group occurs allopatrically in highland Middle America. The *cafer* and *auratus* groups interbreed in an extensive hybrid zone, shown by dashed lines. The center of the hybrid zone is indicated by a heavy line. Note that the hybrid zone is broader to the west and south. Introgression affects populations of these groups as far as the West Coast and the East Coast, with stronger introgression (based on a 6-character analysis) to the west. Local hybridization in narrow (habitat-limited) hybrid zones and isolated hybrid swarms occur in the Southwest between the *cafer* and *chrysoides* groups, as shown by large black circles. (Adapted from map in Short (1965).)

species reaches the limit of its range and drops out, leaving the other species in allopatry. Figure 2 illustrates a zone of overlap and hybridization (see also Table 1).

Hybrid swarms are hybrid populations out of genetic contact with parental forms. While they present evidence that the parental forms are so closely related that hybrids and backcross products are viable (or even that recombinant genotypes can be selectively emphasized in the case of *stabilized* hybrid swarms), they do not permit full testing of the parental populations in

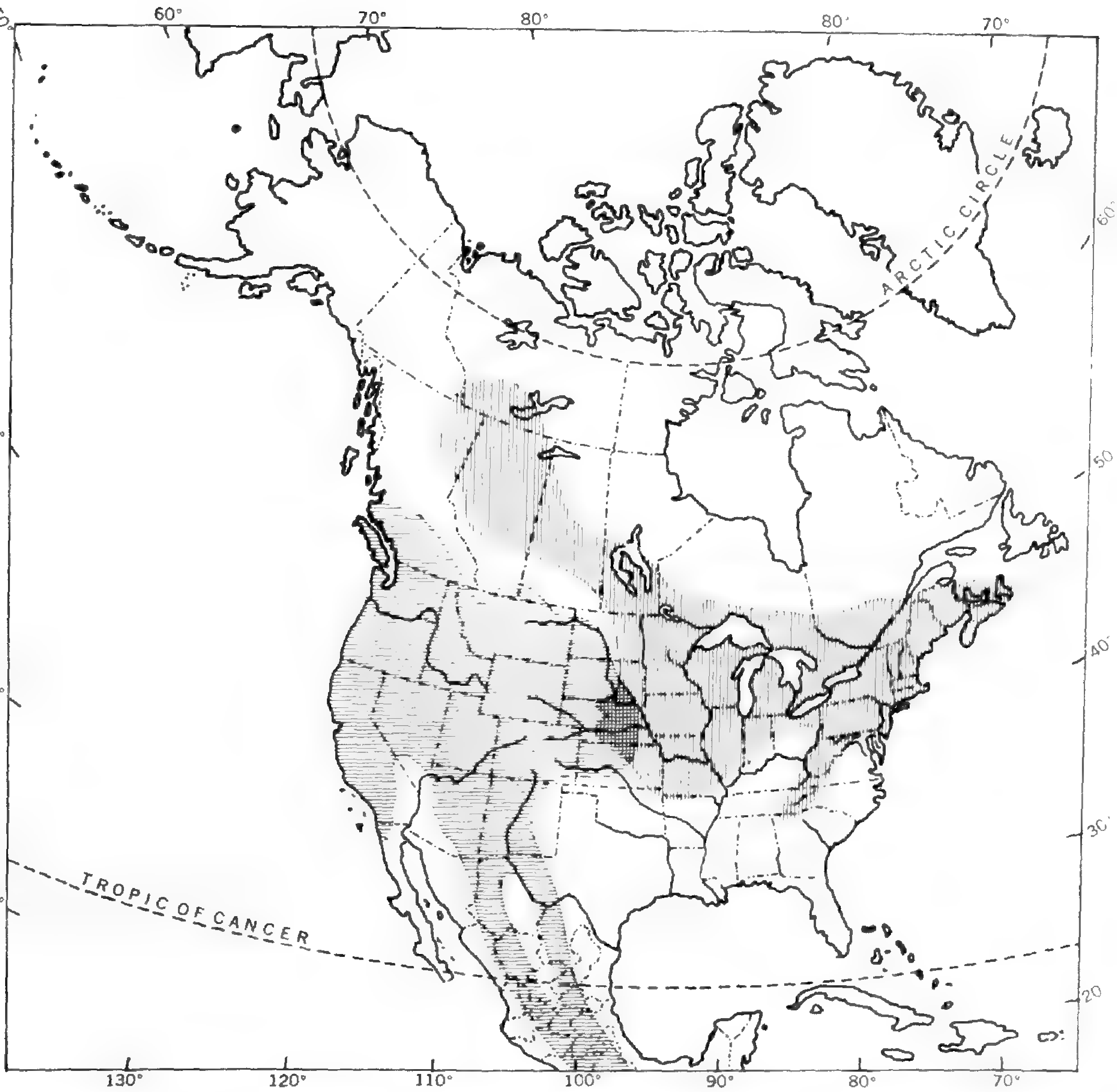

FIGURE 2. — The distribution of North American grosbeaks (*Pheucticus ludovicianus* superspecies) and their zone of overlap and hybridization. The eastern *P. ludovicianus* (vertical lines) meets and overlaps with western *P. melanocephalus* (horizontal lines) in the Great Plains. The zone of overlap and hybridization is shown by cross-hatching. Within this zone occur *both* parental species and numerous, diverse, hybrid phenotypes. Individuals of the parental species are about as numerous as are the hybrids in the center of the zone of overlap and hybridization. (Modified from map in West (1962) on the basis of studies by Short (unpublished).)

continuous contact. Rather their isolation renders local selection of paramount importance. I have previously (Short, 1969) discussed the taxonomic treatment of various types of hybrid swarms (see Table 1). Essentially I look to the situations involving the two forms elsewhere—that is, are they otherwise sympatric? Do adjacent populations show introgression? And, do other such swarms exist?—in order to render tentative decisions.

The various supposed and the few demonstrated cases of circular overlap, the famous "rings of races," are also discussed in Short (1969). If the intervening populations are connected by "true" hybrid zones and zones of primary intergradation, I considered the end forms to be conspecific despite their usually small area of overlap. Not more than five to 10 such cases are known in birds, and none has been shown conclusively to exemplify a true "ring."

There is a small number of cases involving differential interactions—combinations of various sorts involving the same two forms. Most such cases can be resolved taxonomically by emphasizing that interaction which is of major occurrence, or that affecting the major portion of the populations involved. At one extreme are cases in which broadly sympatric and reproductively isolated species hybridize extensively in a single area—some examples are the Indian bulbuls *Pycnonotus cafer* and *P. leucogenys* (Sibley & Short, 1959), and the Herring-Glaucous gulls (*Larus argentatus*, *L. hyperboreus*) in Iceland (Ingolfsson, 1970). At the other extreme are cases in which two forms interbreed whereever they meet, but the extent of hybridization varies—as between the *chrysoides* and *cafer* groups of the flicker *Colaptes auratus* (Short, 1965). The first extreme involves species, and the other extreme involves conspecific populations. Some of the very few, taxonomically difficult intermediate situations are discussed in Short (1969).

Finally, I would like to mention briefly several points concerning the persistence of hybrid zones and of zones of overlap and hybridization. Hybrids very much less viable either in the F_1 or in backcross generations ought to be strongly selected against. A recent computer simulation study by Crosby (1970) demonstrates that reinforcement of isolating mechanisms will occur rapidly, and suggests that it will even spread beyond the overlap area when hybrids are of low viability. Hybridization of long duration indicates that hybrids are about as viable as the parental genotypes. Any genetic factors tending to lessen their viability are balanced by heterosis, or by recombinations superior to parental genes in the zone of contact. That this should be true is suggested by the fact that the parental populations are at the limit of their ranges where they meet and hybridize. Under the pressure of local selection at their range limit, and often in tenuous genetic contact in but one direction with the main parental populations, it is not surprising that hybrids or some of their recombinants may be favored, perhaps strongly. This may retard or even halt the reinforcement of partly effective isolating mechanisms present when the secondary contact was formed. As a last point, there is evidence (citations are in Short, 1970) that many hybrid zones are ancient. Long-enduring hybrid zones suggest that hybrid genotypes are at a selective advantage within the zone, but that strong selection against at least some alien genes is occurring in the parental populations adjacent to the hybrid zone.[3]

In conclusion, the application of criteria based upon the biological species concept allows the taxonomic solution of most cases of avian hybridization. This serving of a taxonomic purpose, of course, is but a prelude to more detailed analyses, which may provide insight into the ecology, behavior, and genetics of such situations. As more data are obtained we can progress toward the eventual solution of such fundamental problems as the role of factors influencing

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[3] This action of natural selection differs in no way from that occurring adjacent to zones of primary intergradation between subspecies that have not been geographically isolated.

the *extent* of hybrid zones, and of introgression, and the functional relation to hybridization of morphological features, such as those used in hybrid indexes.

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VARIATION AND SPECIATION IN THE GENUS *HUDSONIA*[1]

Judith Troop Skog[2] and Norton H. Nickerson[3]

Abstract

Study of herbarium specimens and of living populations of *Hudsonia* plants over several seasons showed a wider range of variation than could be accommodated by the present nomenclature of the genus. Four characters (leaf length, pedicel length, leaf hairiness, and ovary hairiness) were found to form distinct associations on a scatter diagram. Ecological conditions showed correlations with these morphological associations. The associations are designated as five subspecies of *Hudsonia ericoides* L. Linnaeus' type specimen of the genus is a taxon intermediate between subsp. *tomentosa* and an unnamed clearly distinct taxon now apparently confined to Nova Scotia but formerly more widespread southward along the coast. This latter heretofore unrecognized taxon is here described as *H. ericoides* subsp. *andersonii.* Evidence is presented which indicates that this subspecies is headed toward oblivion by man's use of its habitat.

Representatives of the genus *Hudsonia* collected from 1963 to 1965 at many stations along the coast of New England were found to vary from the descriptions given in *Gray's Manual of Botany, 8th Edition* (Fernald, 1950) for either *H. ericoides* L. or *H. tomentosa* Nutt. Inclusion of these specimens in *H. tomentosa* var. *intermedia* Peck made the morphogical limits of that taxon extremely wide. Fernald further noted that this variety "needs critical study," and that it "resembles a hybrid between *H. ericoides* and *H. tomentosa.*" Hall (1956) concluded that the var. *intermedia* Peck was a backcross from hybridization or is an introgressant. This study presents evidence for a much wider range of character variation and proposes the nomenclatorial changes demanded.

Methods

Both herbarium specimens and living populations of the genus *Hudsonia* were studied. Voucher specimens of these populations are deposited in the Tufts University Herbarium, Medford, Massachusetts. Collections were examined from the following herbaria: ACAD, BH, CONN, DAO, FLAS, GH, MO, NCU, NEBC, NHA, NY, US, and Tufts University. Population samples from Massachusetts, New Hampshire, Maine, and Nova Scotia were measured for five morphological characters: degree of hirsuteness of leaves, degree of hirsuteness of ovaries, lengths of leaves, lengths of pedicels, and number of seeds per fruit. A scale of increasing hairiness from 1 to 5 was used for the first two measurements; lengths to the nearest 0.5 mm were measured with a standard laboratory ruler for the next two. For individual plants, an average of 10 values for each measurement was taken. These values, from both living and preserved specimens, were plotted on a pictorialized scatter diagram

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[1] This work was originally supported by NSF grant #GY847, an Undergraduate Research Participation Grant in Biology made to Tufts University.

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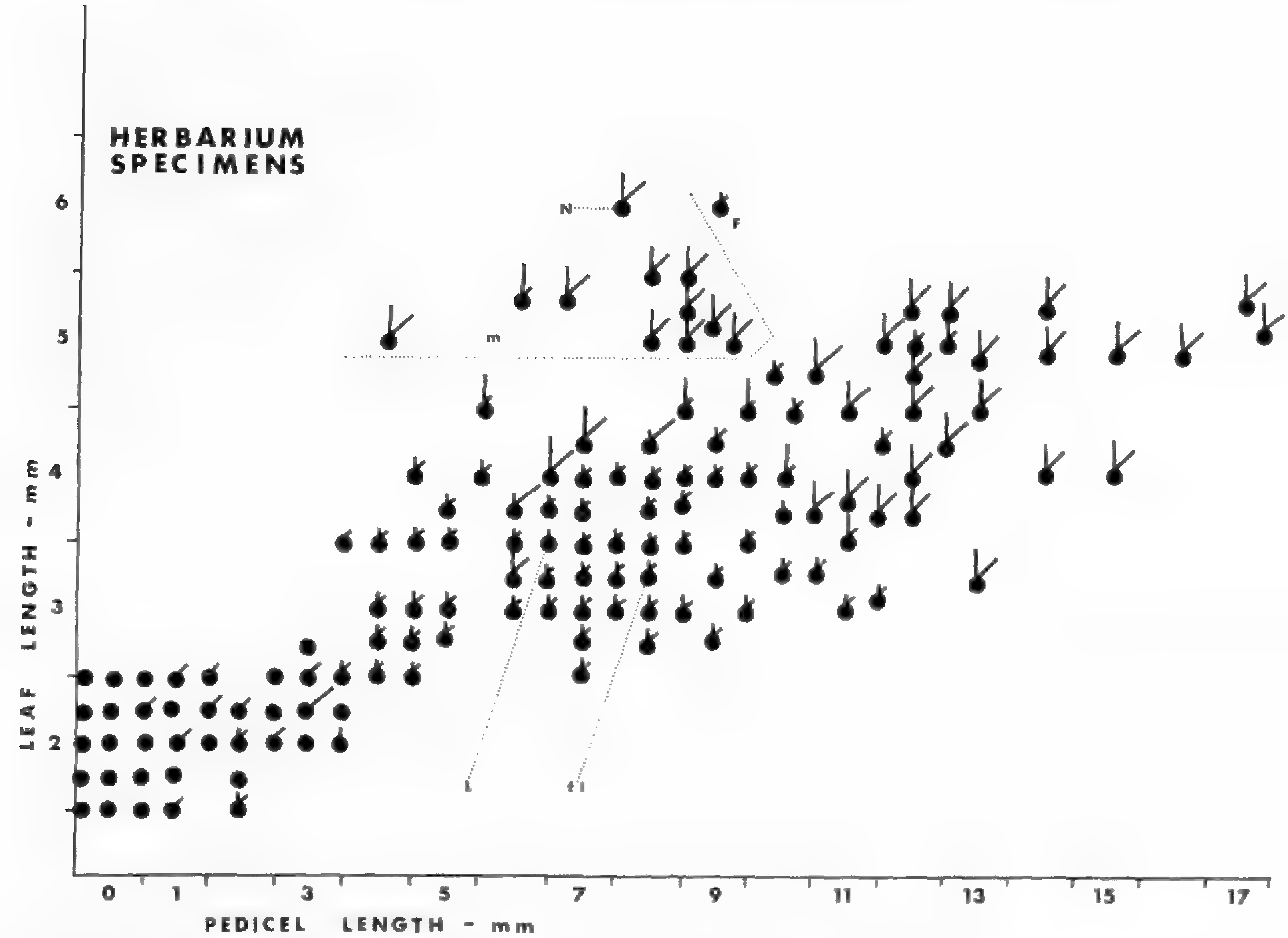

FIGURE 1. — Scatter diagram of four measurements of *Hudsonia* plants from representative herbarium specimens. See upper right of Fig. 2 for explanation of both vertically-oriented and angled bars and half-bars. Glyphs set apart with dotted lines and indicated "m" represent individual subsp. *montana* plants. Single individual marked "N" represents Nuttall's type specimen for his *H. montana*. Individual marked "F" represents plants typical of extant population at Freedom, New Hampshire. Individual marked "L" represents Linnaeus' type specimen of his *H. ericoides*. No data on ovary hairiness were obtained for this specimen. Individual marked "fl" represents Fernald's type specimen of his forma *leucantha*. Glyphs at lower left, with pedicel lengths from 0 to 3 mm and leaf lengths of 2 and 3 mm represent 25 individuals each; all other glyphs represent separate individuals, but were replicated an average of 5 times among the various collections studied. Further explanation in the text.

(Anderson, 1949), here presented as Figure 1. Seed number values were not utilized because of absence of fruiting material on many specimens. The width of the spindle in Figure 1, according to the statistical methods of Kendall (1962) and Goodman (1966) measured within the 99% level of significance. Five extant Massachusetts populations were studied in detail. These populations were located as follows: Plum Island, Crane's Beach, Ipswich, a beach area and an inland area along Cove Road, Wellfleet, and one inland dry, open area near Pine Hill Cemetery, North Truro (Table 3 and Fig. 2). The life histories of these populations were followed over a five-month period (April–August, 1966), and specimens were collected at various intervals. Field plot diagrams were made for comparison of percent cover and plant density. Observable ecological conditions and soils of these and several other populations in Maryland, Massachusetts, New Hampshire, Maine, and Nova Scotia were compared.

TABLE 1. Taxonomic treatment of the genus *Hudsonia*. The genus *Hudsonia* as established by Linnaeus (Mant. Plant., 1767) is based upon his *Hudsonia ericoides*.

Hudsonia ericoides L.

subsp. *ericoides*
(H. *ericoides* L. forma *leucantha* Fernald)

subsp. *tomentosa* (Nutt.) Nickerson & J. Skog comb. et stat. nov.
(*H. tomentosa* Nutt., Gen. N. Amer. Pl. 2: 5. 1818.

subsp. *intermedia* (Peck) Nickerson & J. Skog comb. et stat. nov.
(*H. tomentosa* var. *intermedia* Peck, New York St. Mus. Rep. 45: 86. 1893.

ssp. *montana* (Nutt.) Nickerson & J. Skog comb. et stat. nov.
(*H. montana* Nutt., Gen. N. Amer. Pl. 2: 5. 1818

ssp. *andersonii* Nickerson & J. Skog subsp. nov.

Fruticulus globosus dumosus sempervirens, ad 2 dm altus. *Folia* viridula linearia 3–5.5 mm longa glabrata vel glabra. *Flores* axillares lutei; pedicelli graciles 11–16 mm longi. *Calyx* persistens. *Ovarium* hirtellum vel hirsutum. *Capsula* plerumque trisperma.

Small globose, bushy-branched, evergreen shrub, to 2 dm tall. Leaves greenish, linear, 3–5.5 mm long, glabrate to glabrous. Flowers axillary, yellow; pedicels slender, 11–16 mm long. Calyx persistent. Ovary hirtellus to hirsute. Capsule usually 3-seeded.

Ecological preferences: Shade tolerant; argillaceous shallow soil not subject to sea spray. Known extant population on headlands 30 m above sea level, south shore of Purcell's Cove, Nova Scotia.

Type collection: *Troop 85*, Purcell's Cove, Nova Scotia, August 1966 (GH). Paratype collections: *Nickerson 2908, 2909*, Purcell's Cove, Nova Scotia, August 1968; *Donley 1320*, Queens Co., Nova Scotia, 1958 (ACAD, BH, CONN, DAO, FLAS, MO, NCU, NEBC, NHA, NY, US, and Tufts University). Paratypes from areas with no apparent extant populations: *Redfield 11695*, Martha's Vineyard, Massachusetts, 1885. *10004*, Nantucket Island, Massachusetts, 1885. *Fernald*, Cape Popham, Maine, 1894. *Fernald & Long 9946* (in part) Wareham, Massachusetts, 1913.

RESULTS AND DISCUSSION

The pattern data fall into a spindle which, when measured statistically, is uniform and narrow, indicating that the measured characters are consistently related. Symbols at the left corner of Figure 1 each represent 25 plants, whereas those in the upper right corner represent single plants. These results are interpreted to mean that the measured values for a specific plant are predictable and that influence of one extreme (*Hudsonia ericoides* subsp. *tomentosa*) is predominant in extant seaside populations. Table 1 summarizes the taxonomic treatments for each of the overlapping sub-groups of ecologically and/or geographically distinct major populations.

Measurements from specimens of *Hudsonia montana* Nutt. (here considered as *H. ericoides* subsp. *montana*) were included in the graph (Fig. 1) and marked m, although the living members of this taxon on Table Mountain, North Carolina, now appear to be extinct (personal correspondence, A. E. Radford). Since representatives of this taxon can be plotted almost midway from the extremes found, they may represent a relict population derived from a cross of subsp. *andersonii* (see below) and subsp. *tomentosa*. Possibly because of post-glacial isolation, the Table Mountain population has remained an intermediate entity in which little selection for the presumably less well-adapted extreme parental types can be detected. Its ecological requirements appear similar to many of the present populations of intermediate forms (Table 2). While these facts indicate that subsp. *montana* can logically be included among subsp. *ericoides*, it is here maintained as a separate taxon because of its probable extinction, its present herbarium documentation, and its prior isolated occurrence. Lewis E. Anderson (personal communication, 1970) has stated to the second author that subsp. *montana* also occurs on a few neighboring hills in the vicinity of Table Mountain.

Measurements of a photograph of Linnaeus' type species, as well as the description he gave in the *Mantissa Plantarum* (1767), indicate that he also was dealing with an intermediate form when he named *Hudsonia ericoides*. This specimen has been seen by the first author in London. According to the 8th Edition of *Gray's Manual* (Fernald, 1950), all similar specimens must be included with *H. ericoides* L., while those tending toward *H. tomentosa* Nutt. must be called *Hudsonia tomentosa* var. *intermedia* Peck. This study presents evidence that a gradation of measurable characters between, among, and beyond these taxa exists and that ecological requirements strengthen our suggested taxonomic separations. The proposed taxonomic revision in Table 1 is consistent with the data discussed below.

Hudsonia ericoides subsp. *tomentosa* (Nutt.) Nickerson & J. Skog is a common and clearly identifiable taxon. It may be regarded as one parental extreme that may have contributed to hybrid populations which have been variously and somewhat arbitrarily set off and designated as separate species.

Hudsonia tomentosa var. *intermedia* Peck must be refined in concept, as must *H. ericoides* L., since these two as well as *H. montana* Nutt. represent intermediate forms. The taxon *H. ericoides* f. *leucantha* Fernald has no valid standing, as we have found single plants with some branches all white-flowered and others all yellow-flowered. The plants now growing at Purcell's Cove, Nova Scotia, and present as at least one specimen from Prince Edward Island, emerge as another taxon as yet unnamed. It is here designated *H. ericoides* L. subsp. *andersonii*, Nickerson & J. Skog in honor of Edgar Anderson, 1896–1969, originator of the method of extrapolated correlates by which the characters of this taxon were first predicted and later verified, first through herbarium records and later in the field (see Anderson, 1949, 1952).

Ecological notes are summarized in Tables 2 and 3. *Hudsonia ericoides* subsp. *tomentosa* requires fine open sand and full sun for optimum growth. The plant is spreading in habit. Well-established individuals are 0.5–2 dm high and 2–6 dm in diameter, but form is influenced by wind, shade, and soil movement onto the site. Along the seashore these plants are first encountered behind the crests of front dunes, sheltered from the brunt of salt and whipped sand, but nonetheless in a habitat to which sand is being intermittently added. The plants may grow close together forming a closed mat over the rolling dune surface (as at Plum Island, Massachusetts), or they may be scattered from 0.5 to 1 meter apart singly over the sand (as at Assateague Island, Maryland).

TABLE 2. Comparison of characters of the subspecies of *Hudsonia ericoides* L.

Taxonomic designation	Pedicel length (mm)	Leaf length (mm)	Leaf hair condition	Ovary condition	Average number of full-formed seeds per fruit	Habit	Shade tolerance	Soil preference
subsp. *tomentosa* (Nutt.) Nickerson & J. Skog	0–1	1.5–2.5	hirsute	glabrous to glabrate	1	spreading	none	dry sandy reaches
subsp. *intermedia* (Peck) Nickerson & J. Skog	1.5–7	2–3.5	hirsutulous to hirsute	glabrate to hirtellous	1 with 2 partially developed	spreading	none to slight	dry sandy reaches
subsp. *ericoides*	4–10	3–4.5	hirtellous to hirsutulous	hirtellous to hirsutulous	1, sometimes 2; with 2 or 1 partially developed	subglobose	none to considerable	dry sand-clay mixtures
subsp. *montana* (Nutt.) Nickerson & J. Skog	4–7	5–6	glabrate	hirsute	(undetermined) reported by Nuttall as 1	subglobose	(unknown)	weathered rock soils
subsp. *andersonii* Nickerson & J. Skog	11–16	3.–5.5	glabrate to glabrous	hirtellous to hirsute	3	globose	high	argillaceous soils

TABLE 3. Comparison of development in three subspecies of *Hudsonia tomentosa* from several localities in eastern Massachusetts, 1966 growing season. (Pattern verified again by N. H. N. in 1970, but flowering periods 5 days later).

Date	subsp. *tomentosa*	subsp. *intermedia*	subsp. *ericoides*
May 4	no growth noted	no growth noted	few early flowers open
May 25	no growth noted	few early flowers open	peak of flowering
June 1	few early flowers open	peak of flowering	end of flowering
June 2–3	peak of flowering	end of flowering	maturing fruits
June 4	end of flowering	maturing fruits	active vegetative growth
June 20	maturing fruits, active vegetative growth	active vegetative growth	fruits falling
July 4	maturing fruits, active vegetative growth	fruits falling	new growth, hardening[a]
July 20	fruits falling	new growth, hardening[a]	
August 10	new growth, hardening[a]		

[a] Vegetative growth may cease in midsummer or may apparently continue slowly into October, depending on rainfall pattern and Indian summer weather.

This distribution may be a reflection of the age of the stand, older plants apparently being more scattered. Subspecies *tomentosa* is gradually invaded by other sand-dune species and is spoken of as "growing in open association" with beach plum (*Prunus maritima*), bayberry (*Myrica pennsylvanica*), beach grass (*Ammophila breviligulata*), pine (*Pinus rigida* or *P. taeda* southward), poison ivy (*Toxicodendron radicans*), seaside goldenrod (*Solidago sempervirens*), several species of *Lechea*, and beach pea (*Lathyrus japonica*). It apparently does not thrive nor long persist in the shade of other plants. Blowing sand may cover most of a plant; however, if the tips remain above ground, they will both flower and continue vegetative growth. These extensive root and branch systems apparently contribute to dune stabilization. This subspecies follows beach grass on the dunes in succession; however, it is not as resistant to abrasion and does not colonize the foot paths or vehicle tracks of man. The plants also do not grow on dry narrow dune crests nor in the low, wet, and boggy ("black water") areas often found among dunes. It is this subspecies which ranges along the coast from the tip of the Gaspé peninsula to the Outer Banks of North Carolina, westward on sandy blowouts to West Virginia and the Great Lakes region in the United States, and as far west as Alberta in Canada. It is least variable at its extremities, based on our studies of both living plants and preserved specimens.

Hudsonia ericoides subsp. *andersonii* was found only in shallow argillaceous soils (those with a noticeable percentage of clay). These soils occur over acidic rock bases, and as a stable product of weathering, they are rather different from the constantly shifting sandy soils of dunes. Typical plants of subsp. *andersonii* are 1–2 dm high, densely branched, spherical, and upright, rather than open, low, spreading, and sprawling as are those of subsp. *tomentosa*. In the barren rocky fields along Purcell's Cove, Nova Scotia, subsp. *andersonii*

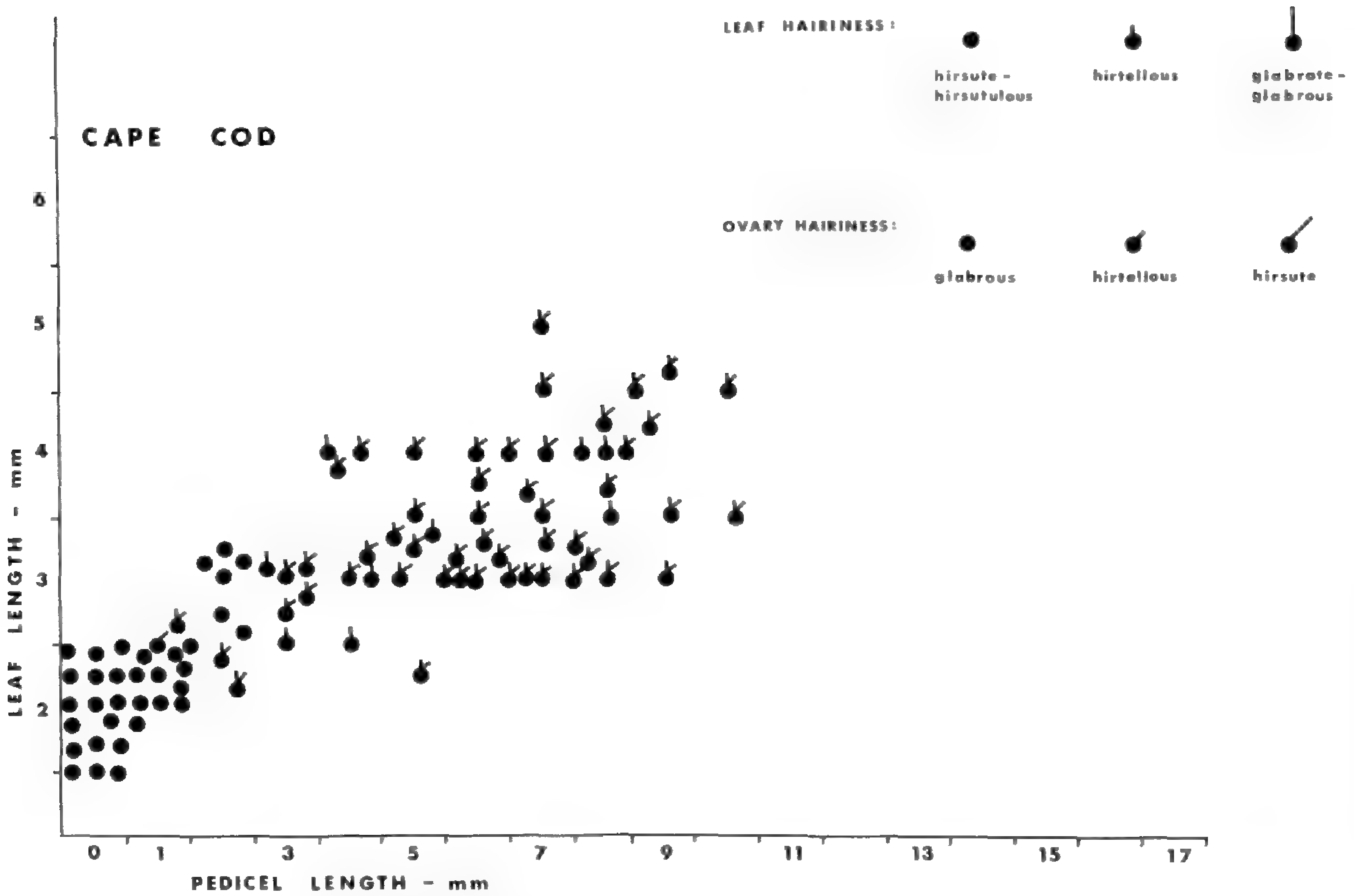

FIGURE 2. — Scatter diagram of four measurements of *Hudsonia* plants collected for study from representative extant populations on Cape Cod. Explanation of both vertically-oriented and angled half-bars in upper right. Glyphs at lower left, with leaf lengths of 2 and 3 mm and pedicel lengths from 0 and 3 mm represent 25 individuals each; all other glyphs represent separate plants whose frequency of occurrence on the peninsula as a whole is much lower. Note that glyphs clearly indicating either subspecies *andersonii* or *montana* are lacking. Further explanation in the text.

individuals dot the landscape and are in association with mosses, lichens, lycopods, several species of *Vaccinium*, and pine sprouts. Root systems are not as extensive nor as deep as those of subsp. *tomentosa*. Subspecies *andersonii* apparently can persist in partial shade; in the areas where it is now found, many of the plants are shaded for several hours of each day. While at least one individual from Prince Edward Island occurred among the herbarium specimens, it is not known if that population is extant.

Intermediate forms (subsp. *intermedia* and subsp. *ericoides*) may grow in fine sand, in clay and gravel, or most commonly in mixtures of sand, clay and gravel (*cf.* Anderson, 1949). The plants have either a rounded or spreading form with extensive root systems, but not quite as extensive as those characteristics of subsp. *tomentosa*. Bushy intermediate plants (those resembling subsp. *andersonii* most strongly) can stand partial shade and on Cape Cod grow in association with blueberry (*Vaccinium angustifolium*), broom crowberry (*Corema conradii*), bearberry (*Arctostaphylos uva-ursi*), and pitch pine (*Pinus rigida*). Certain observations of developmental histories of the three plant taxa common to Massachusetts are summarized in Table 3. The dates of flowering show that cross pollination between taxa can occur, but that they tend to remain intra- rather than inter-fertile.

Distribution of *Hudsonia* subspecies on the outer part of Cape Cod was carefully noted. A local Wellfleet resident informed us that some areas of the high plains of Truro and Wellfleet, originally forested, were logged and used for pasture and agriculture. Now pitch pines are taking over these fields. Subspecies *intermedia* is present over much of the Cape in sandy seaside areas, but there is a noticeable lack of all *Hudsonia* plants along the beaches of the heavily-used south shore from Falmouth to Chatham. An exception occurs at West Dennis, where several dozen plants of subsp. *tomentosa* have appeared in a dune area fenced off for four years. Subspecies *andersonii* is no longer found on Cape Cod; the intermediate forms closest to it occur sporadically inward from the shore on the almost untraveled, sparsely forested, rolling hills of the lower Cape from Wellfleet to Provincetown. These intermediate forms range from "good" subsp. *ericoides* inland to "good" subsp. *intermedia* nearer the outer dunes. Vegetation at the Marconi Beach and Headquarters areas of the Cape Cod National Seashore is particularly rich in such forms and shows the gradation clearly in both flowering dates and vegetative characters. When a new area is opened, such as the open sandy barrens beside modern stores on Route 6 in Wellfleet and the banks of the highway rotary at the terminus of U. S. Route 6 in Provincetown, variable forms resembling either one of both extremes appear, in about equal proportions, perhaps because stray deposits of sand-clay road base soil lie in close proximity with dune sand (*cf.* Anderson, 1948). In mixed populations of this type there is much variation, consistent within each plant, in lengths of all four characters used in Figure 1 and in general plant form. These groups are here regarded as intermediates, and all may be separated out as either subsp. *intermedia* or subsp. *ericoides*, as defined in Table 2.

Geographical distribution in the United States and Canada from north to south and east to west is presented in Table 4, which summarizes information from field work and from herbarium specimens.

These data indicate that the intermediate forms which are here treated taxonomically as subsp. *intermedia* and subsp. *ericoides* are far more common than the extreme subsp. *tomentosa* and subsp. *andersonii*, most probably because disturbed habitats formed and maintained by man's activities abound. Examples of such are mowed and brushed roadsides, fields, railroad embankments and rights of way, abandoned sand pits, and new sandy road cuts and fills. Individuals of subsp. *tomentosa* seem to be confined to undisturbed open dunes and sand banks. This subspecies is not highly variable, but a greater number of intermediate individuals more closely resemble this parental type, possibly because they have derived from it a greater tolerance to open, dry, dune-like areas where competition from other vegetation is at a minimum and where the more than occasional passage of man contributes to continued habitat disturbance. The higher headlands and open savanna-like evergreen tree-shrub habitats which have some clay in their soils were apparently the original habitats of subsp. *andersonii*. These areas, since the advent of man, have become much more severely altered in their vegetational cover than have the dunes. They were utilized by man successively for timber cutting, pastures, and farmlands,

TABLE 4. Geographical distribution (from collections and annotated herbarium specimens).

Location by state or province	subsp. *tomentosa*	subsp. *intermedia*	subsp. *ericoides*	subsp. *montana*	subsp. *andersonii*
Nova Scotia	×	×	×		×
Newfoundland	×	×			
New Brunswick	×				
Prince Edward Island	×	×	×		×[a]
Quebec	×	×	×		
Maine	×	×	×		×[a]
New Hampshire	×	×	×		
Vermont	×				
Massachusetts	×	×	×		×[a]
Rhode Island	×				
Connecticut	×	×			
New York	×	×			
New Jersey	×	×	×		
Maryland	×				
Delaware	×	×			
Virginia	×				
North Carolina	×			×	
West Virginia	×				
Ohio	×				
Indiana	×				
Illinois	×				
Michigan	×				
Iowa	×				
Wisconsin	×				
Minnesota	×				
Ontario	×				
Manitoba	×				
Saskatchewan	×				
Alberta	×				

[a] Population probably not extant.

and they now are being cut up for building lots. Because of man's unchecked uses of this habitat in Nova Scotia, we conclude that subsp. *andersonii* is disappearing there, and intermediates which resemble it, confined as they are by selection to the same areas desired by man for other uses, will become far less frequent in the total population of *Hudsonia.* We presume that this situation is being intensified because subsp. *ericoides* is no longer as wide-spread as herbarium specimens indicate it once was. Indeed, Nuttall (1818) stated "*ericoides*" to be along the "Virginia, New Jersey and North Carolina coasts."

Our evidence is strengthened by recent collections of subsp. *andersonii* having been made only from an active subdivision area at Purcell's Cove, Nova Scotia, and intermediate plants resembling it being markedly less frequent in occurrence, both now and in herbaria, than those resembling subsp. *tomentosa.*

In some areas (the beach at Ogunquit, Maine; Plum Island, and Crane's Beach, north of Boston, beaches at Sagamore and at Chapin Memorial Beach in Dennis, on Cape Cod, all in Massachusetts) no subsp. *andersonii*-like forms (here considered as subsp. *ericoides*) exist at all, yet there are herbarium records of their collection from these locations. A "rare find" (personal communication, Frank McKeever) collected in New Jersey in 1966 and sent to the second author turned out to be an intermediate form which would be classified here as subsp. *ericoides.* There is a 1960 collection of one plant from New Jersey which also is so classified. Subspecies *ericoides* also presently exists on Nantucket, Martha's Vineyard, in Provincetown, Truro, Wellfleet, the south side of Dennis, and Plymouth, Massachusetts, as well as in isolated coastal areas of Maine, Prince Edward Island, Nova Scotia, and New Brunswick, and inland at Freedom, New Hampshire (see Fig. 1).

Hall (1956) stated that his data indicated perhaps a considerable time period had been involved in the production of all these intermediates (referred by him to var. *intermedia* Peck). It has been certainly implied in our data that this spread of characters represents the development of hybrids from two parental types and may indeed be leading to introgression in the sense often proposed by Anderson (1949), which is that variation in the parental types is gradually increasing by backcrosses with the presumptive hybrid swarms. In view of the evidence recently presented by Randolph *et al.* (1967) that the original species of *Iris* studied by Anderson and Riley (Anderson, 1949) are still very much extant and seem to be unchanged, and of Rudloff *et al.* (1967) and of Flake *et al.* (1969) regarding the apparent lack of introgression in *Juniperus*, it may be premature to indicate that introgression in any sense has occurred in *Hudsonia.* It seems reasonable to interpret our data as meaning that two new complexes of characters, clustering around subsp. *intermedia* and around subsp. *ericoides-montana* as herein defined, are emerging from a much broader spectrum in the genus *Hudsonia*, and that the extremes of this spectrum, represented by subsp. *tomentosa* and subsp. *andersonii*, may be facing extinction because of subtle but relentless pressures imposed by increased populations of man. However, two further interpretations are possible. We may be dealing with a single clinal variation, as has been proposed in *Juniperus virginiana* (Rudloff *et al.*, 1967; Flake *et al.*, 1969). Alternatively, we may be dealing with two clinal variations, one *tomentosa-intermedia*, the other *ericoides-montana-andersonii*, neither one particularly involved in gene exchange with the other. To help resolve these questions, a study of biochemical constituents of extreme plants and several of their intermediates is now being conducted in another laboratory, utilizing modern chemotaxonomic methods. These results will be presented in a subsequent paper.

Pollen studies made with the light microscope do not reveal any easily-discernible consistent morphological differences. Pollen from both fresh and preserved specimens were compared. Electron scanning microscope studies are currently underway by John Semple, Missouri Botanical Garden, to confirm or deny this sameness.

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C-4 AND C-3 CARBOXYLATION CHARACTERISTICS IN THE GENUS *ZYGOPHYLLUM* (ZYGOPHYLLACEAE)[1]

R. Kent Crookston[2] and Dale N. Moss[3]

Abstract

Higher plants can be placed into two separate groups according to their pathways of photosynthetic CO_2 fixation. One group initially fix CO_2 into the 3-carbon acid 3-phosphoglycerate and are thus called C-3 plants. The others first fix CO_2 into one of three 4-carbon acids: aspartate, malate, and oxaloacetate and are therefore called C-4 plants. Several anatomical and physiological characteristics are correlated with the respective pathways. It has been suggested that the occurrence of these two different groups of plants may be taxonomically useful as each type is restricted to distinct plant taxa. Both types have been reported in at least four genera, but in each of these cases, species association is uncertain and taxonomic revision has been recommended. We found both C-4 and C-3 species in the genus *Zygophyllum* (Zygophyllaceae). This suggests that portions of the genus may have been misclassified. Our results also support the concept that some easily measured anatomical and physiological traits associated with the C-4 system can be used to clarify relationships in certain families. Use of these traits may be particularly useful in removing some uncertainties in classification of the Zygophyllaceae.

Plant species that form C-4 dicarboxylic acids as first products of photosynthesis (C-4 plants) have in common several anatomical and physiological characteristics that differ from plants with Calvin cycle photosynthesis (C-3 plants). Among these are carbon dioxide compensation points near 0 μl CO_2/liter of air and prominent chlorenchymatous vascular bundle sheaths. Downton and Tregunna (1968) suggested that C-4 traits could be taxonomically useful, as they are easily and experimentally discernible and they occur only in distinct taxa. Although a few genera do contain both C-4 and C-3 species, this has been reported only where species association is not certain and where revision has been recommended—*Panicum, Cyperus, Euphorbia*, and *Atriplex* (Downton *et al.*, 1969; Moss *et al.*, 1969; Tregunna & Downton, 1967).

We report here another genus which contains both C-4 and C-3 species, *Zygophyllum* (Zygophyllaceae). Our determination is based on leaf anatomy studies and CO_2 compensation point measurements.

Materials and Methods

For this report we studied seven species of the genus *Zygophyllum*: *Z. aurantiacum* F. Muell, *Z. coccineum* L., *Z. dumosum* Boiss, *Z. fabago* L., *Z. howittii* F. Muell, *Z. iodocarpum* F. Muell, and *Z. simplex* L. All plants were

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[1] Minnesota Agricultural Experiment Station Journal Series Paper Number 7778.

We wish to thank the following institutions for supplying seeds: Botanic Garden, Adelaide, Australia; Botanical Garden "Mikveh-Israel," Holon, Israel; Botanic Gardens, Department of Botany, The Hebrew University of Jerusalem, Israel; The Herbarium, Botany Department, Cairo University, Giza, Egypt, U.A.R.; Missouri Botanical Garden, St. Louis, Missouri. This work was supported in part by Rockefeller Foundation Grant GA Agr. 6972.

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Ann. Missouri Bot. Gard. 59: 465–470.

grown from seed sown in a 2:1 mixture of loam and peatmoss in 5-inch clay pots. These were placed in growth chambers with either 21-16° or 27-21°C day-night temperatures, a 16-hour daylength and a light intensity of 0.1 cal. cm^{-2} min^{-1} (400–700 nm). We made CO_2 compensation measurements with branches of plants that were approximately 40 days old. This consisted of measuring the equilibrium CO_2 concentration in a closed system containing an illuminated branch. The system consisted of a large stoppered glass test tube (leaf chamber) with two copper tubes extending through its rubber stopper. The chamber was immersed vertically in a water bath maintained at 29°C. Excised branches were placed in the leaf chamber with their stems resting in about 3 ml of water and were illuminated by two 150-watt incandescent lamps through a 10 cm water filter (light intensity of 2,400 ft-c). The copper tubes connected the leaf chamber to a pump which circulated the air in the system through an infrared gas analyser (Beckman model 215) and back to the chamber. The output from the analyser was recorded with a Sargent model SR recording potentiometer.

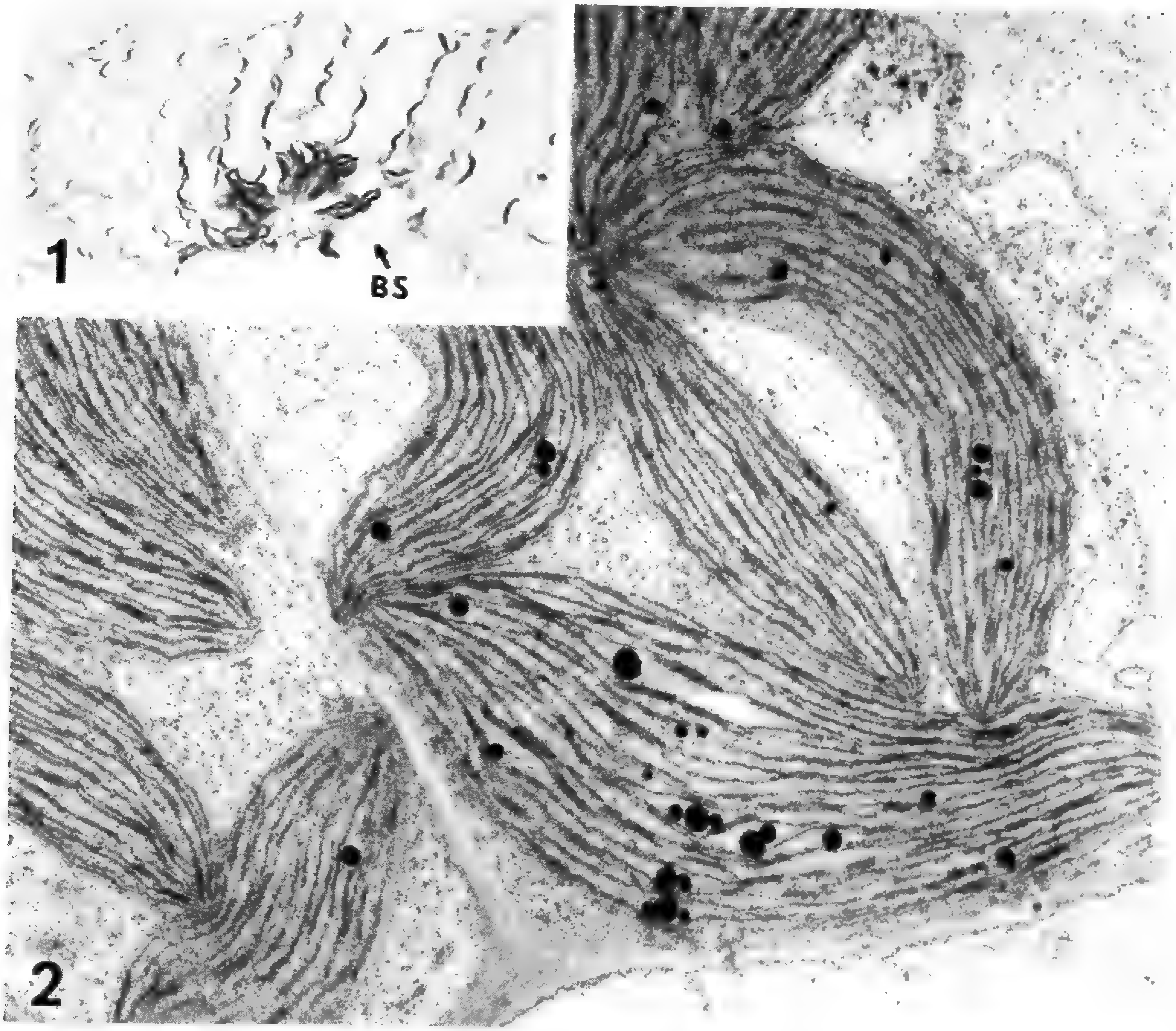
Freshly cut cross-sections of leaves of all species were examined with a light microscope for the presence or absence of C-4 type leaf anatomy. This included staining the sections with I_2-KI so that starch-storage patterns could be observed. I_2-KI solution was placed near one edge of the cover slip and drawn underneath by placing filter paper at the opposite side.

In addition, leaves of *Zygophyllum simplex*, which had a low CO_2 compensation point, were examined with the electron microscope. Leaf tissue was cut into segments approximately 1 mm square and fixed for two hours in a 2.5% glutaraldehyde solution freshly treated with $BaCO_3$ and buffered with 0.05 M $NaPO_4$ buffer (*p*H 6.8). It was then washed in buffer, post-fixed in OsO_4 (1% aqueous solution) for one hour, taken through a water-acetone dehydration series ending in dry acetone, and embedded in Spurr's embedding mixture (Spurr, 1969). Silver sections (approximately 800 Å thick) were cut using a glass knife on a Sorvall MT-2 ultramicrotome. These were mounted on uncoated # 400-mesh grids, post-stained in uranyl acetate (ten minutes) and lead citrate (five minutes), and viewed with a Hitachi HU-11-C electron microscope operated at 75 kV. Approximately 2μ-thick sections of this same material were also cut and mounted in immersion oil on glass slides to obtain photomicrographs.

RESULTS AND DISCUSSION

Of the seven *Zygophyllum* species which we studied, one, *Zygophyllum simplex*, had a low CO_2 compensation point (less than 5 μl CO_2/liter of air). It had leaves with prominent thick-walled vascular bundle sheaths. The cells of the bundle sheaths contained large chloroplasts (Fig. 1) which stained intensely with I_2-KI indicating abundant starch. These associated traits suggest that *Zygophyllum simplex* is a C-4 species.

Electron microscopy showed that *Zygophyllum simplex* also had ultrastructural characteristics of C-4 plants. The bundle sheath cells contained numerous large chloroplasts which exhibited little grana formation (Fig. 2).



FIGURES 1–2.—1. Cross section of a leaf of *Zygophyllum simplex*. The area shown is from the outer portion of the cylindrical leaf. The cells of the bundle sheath (BS) contain large chloroplasts. The bundle sheath is located at the inner edge of a layer of palisade cells. Epidermal cells are outside (above in figure), and large non-green parenchyma cells are inside (below in figure) this pallisade layer. × 88.—2. Electron micrograph of chloroplasts in the vascular bundle sheath cells of a *Zygophyllum simplex* leaf. The chloroplasts are relatively starch free as the leaf was fixed in the early morning. × 9,360.

These chloroplasts lacked an extensive peripheral reticulum, which is different from many C-4 species, although traces of a reticulum could be detected in some chloroplasts. These bundle sheath cells also contained numerous mitochondria grouped in large clusters near the cell walls (Fig. 3). Such groups of mitochondria were not found in central portions of the cells where there was a more uniform distribution of single mitochondria, or very small groups. All mitochondria had well-developed tubular cristae.

The species *Zygophyllum aurantiacum*, *Z. coccineum*, *Z. dumosum*, *Z. fabago*, *Z. howittii*, and *Z. iodocarpum* had high CO_2 compensation points (greater than 40 μl CO_2/liter of air). One of these high CO_2 compensating species, *Z. coccineum*, had leaves similar to the low CO_2 compensating species, *Z. simplex* (cylindrical, with chlorenchyma only around the outer edge), but without vascular bundle sheaths (Fig. 4). The other five species had oval or flattened

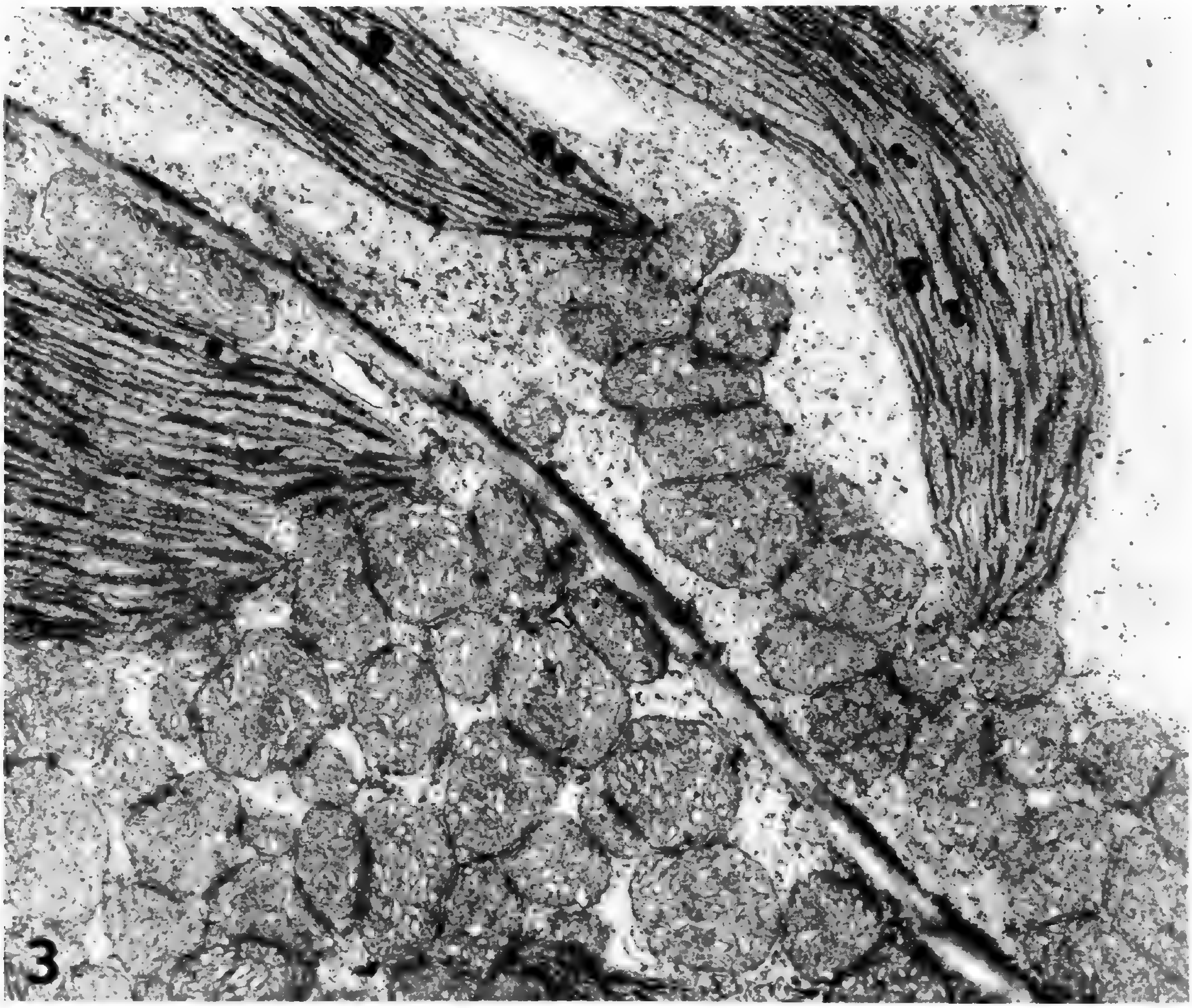


FIGURE 3. Electron micrograph showing the numerous and closely grouped mitochondria found within *Zygophyllum simplex* bundle sheath cells. Such groups of mitochondria were found only next to cell walls. × 6,320.

leaves composed of green palisade tissue and also lacking vascular bundle sheaths. I_2-KI staining indicated that there were no specialized areas of starch formation in leaves of any of the high CO_2 compensating species. These six species were therefore determined to be C-3 type.

The fact that the genus *Zygophyllum* contains both C-4 and C-3 species suggests that portions of it may have been misclassified. Porter (1963, 1969) has dealt with taxonomic problems of certain genera of the Zygophyllaceae and has referred to several workers who recommend reclassification of much of the family. He states that cytological and genetical data are needed before one can knowingly discuss natural relationships. Since C-4 characteristics are cytologically prominent, we suggest that they could be used to assist in classification of *Zygophyllum*.

In addition to *Zygophyllum*, two other genera of the Zygophyllaceae have also been found to contain C-4 traits. We reported earlier that *Tribulus terrestris* L. had a low CO_2 compensation point and chlorenchymatous vascular bundle sheaths (Crookston & Moss, 1970). We have also observed these traits in *Tribulus cistoides* L., *T. hystrix* R. Br., *Kallstroemia maxima* L., *K. pubescens*

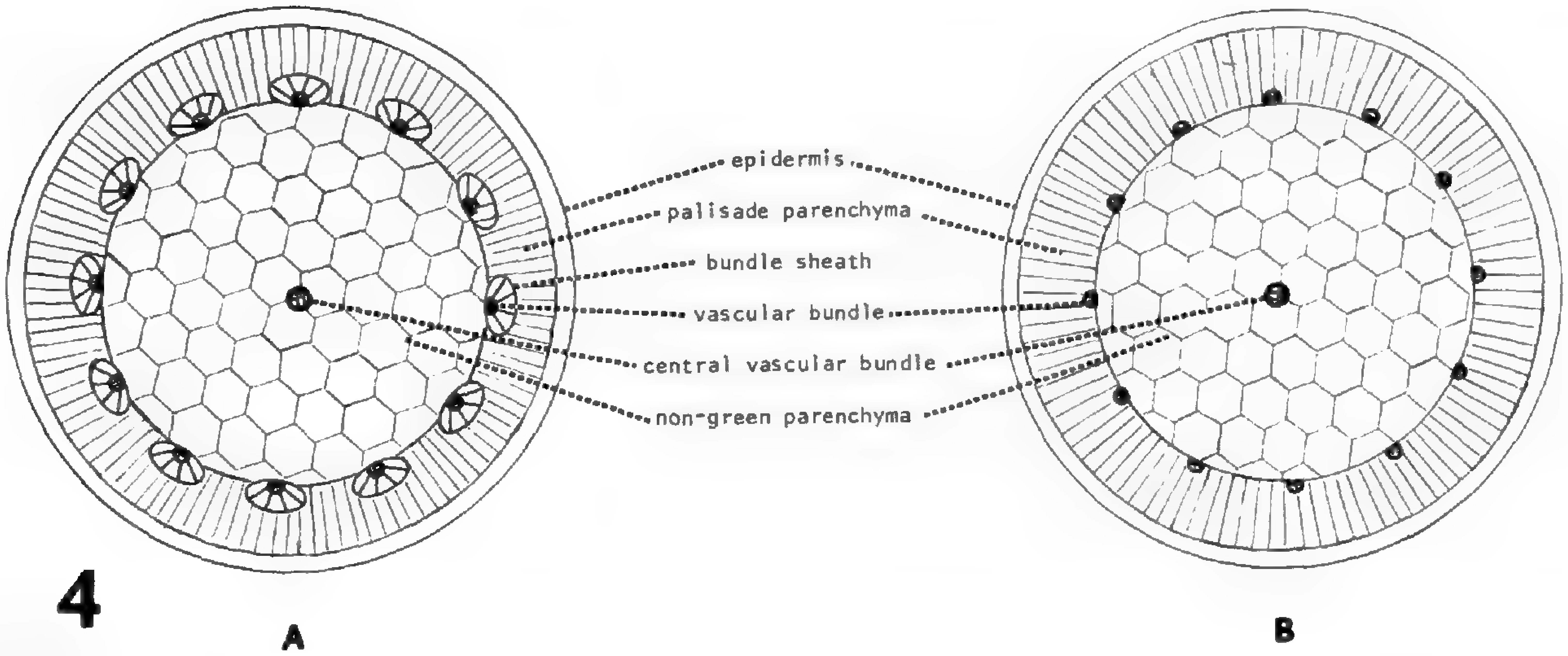


FIGURE 4. Diagrams of cross sections of two different *Zygophyllum* leaves: *Z. simplex*, A; and *Z. coccineum*, B. Both of these leaves are cylindrical in shape. Note the presence of vascular bundle sheaths in *Z. simplex*.

(G. Don) Dandy, and *K. rosei* Rydb. In contrast to *Zygophyllum* however, we have no indication that any C-3 species exist in *Tribulus* or *Kallstroemia*.

Porter (1969) suggests that *Tribulus* and *Kallstroemia*, along with *Kelleronia* and *Tribulopis*, "constitute a natural group deserving recognition as a major subdivision of the family [Zygophyllaceae]." Engler (1931) believed *Neoluederitzia* and *Sisyndite* also to be closely related to these four genera and said that they had all arisen from a "single primitive stock." Porter indicates that *Neoluederitzia* and *Sisyndite* have kinship elsewhere in the family, however, and do not belong in the group. Consideration of the presence or lack of C-4 traits by these genera should be helpful in confirming assumed relationships based, to present, on such characteristics as pollen type, leaf arrangement, and flower and fruit details.

An advantage of monitoring C-4 traits is that one can determine species type at almost any stage of growth and with certainty. There are numerous ways of making such determinations. According to Black and Mollenhauer (1971) the number and concentration of organelles in the bundle sheath, such as chloroplasts and mitochondria (Fig. 3–4), is the "most reliable anatomical criterion presently available for determining the photosynthetic capacity of a given plant" (C-4 or C-3 type). Electron microscopy is time consuming however, and we have found that when freshly cut cross-sections of leaves are viewed with a light microscope, C-4 sheaths appear very prominent and can be easily distinguished, even from the chlorenchymatous vascular bundle sheaths found in some C-3 species (Crookston & Moss, 1970). Since C-4 plants store starch primarily in their vascular bundle sheaths, staining cross sections of leaves with I_2-KI is often useful in confirming plant type determinations. Leaves of some C-4 species may be completely free of starch in early morning however, and they may contain considerable starch outside the sheath by late afternoon. Staining to detect starch storage patterns is therefore generally helpful, but it is not a completely reliable method of determination.

In addition to anatomical methods, we have found that measuring CO_2 compensation points is both a reliable and rapid method of determining whether a plant is C-4 or C-3 type. Individual measurements take approximately ten minutes and, thus far, low CO_2 compensation points have been found only in C-4 species. We therefore agree with Downton and Tregunna (1968) that examining plants for C-4 characteristics should, in many cases, be taxonomically useful.

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NEW COMBINATIONS IN COMPOSITAE[1]

R. P. Wunderlin[2]

While preparing the Compositae for R. H. Mohlenbrock's forthcoming *Guide to the Illinois Flora*, it became evident that a number of new nomenclatural combinations would have to be made to better align certain taxa. It is deemed better to publish these separately as a note rather than to include them in a flora. Thus, the following combinations in *Heterotheca, Bidens*, and *Eupatorium* are proposed.

Heterotheca villosa (Pursh) Shinners var. **camporum** (Greene) Wunderlin, *comb. nov.*

Chrysopsis camporum Greene, Pittonia 3: 88. 1896.
Chrysopsis villosa (Pursh) Nutt. var. *camporum* (Greene) Cronq., Bull. Torrey Bot. Club 74: 150. 1947.
Heterotheca camporum (Greene) Shinners, Field & Lab. 19: 71. 1951.

Shinners (1951) proposed that *Chrysopsis* was congeneric with *Heterotheca*. This was founded on the fact that the traditional segregation based on the absence of a pappus in the ray-florets of *Heterotheca* was weakened by the occurrence of a vestigial pappus on some species and by a reduction of the ray-floret pappus in some species of *Chrysopsis*. Wagenknecht (1960) provided additional morphological data and Harms (1965) cytogenetic evidence to further substantiate this merger. In the author's opinion *Chrysopsis camporum* is best treated as a variety of *Chrysopsis villosa* as proposed by Cronquist (1947), but due to the merger of *Chrysopsis* with *Heterotheca* a new combination under *Heterotheca* must be made.

Bidens aristosa (Michx.) Britt. var. **aristosa** f. **fritcheyi** (Fern.) Wunderlin, *comb. et stat. nov.*

Bidens aristosa (Michx.) Britt. var. *fritcheyi* Fern., Rhodora 15: 78. 1913.

In the author's opinion this taxon is best treated as a forma rather than a variety, because of the occurrence of retrorse barbs on the awns of achenes in other taxa of *Bidens* which normally possess antrorsely barbed awns (*i.e. B. connata, B. eatonii*, and *B. frondosa*).

Bidens aristosa (Michx.) Britt. var. **aristosa** f. **mutica** (Gray) Wunderlin, *comb. et stat. nov.*

Coreopsis aristosa Michx. var. *mutica* Gray, Man. Bot. Ed. 5. 260. 1867.
Bidens aristosa (Michx.) Britt. var. *mutica* (Gray) Gattinger *ex* Fern., Rhodora 15: 78. 1913.

In the author's opinion this taxon is best treated as a forma rather than a

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[1] Supported in part by grants from the Society of the Sigma Xi and the Illinois State Academy of Science.

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Ann. Missouri Bot. Gard. 59: 471–473.

variety, because of the variability of the length of the awns in this and other species of *Bidens*.

Bidens aristosa (Michx.) Britt. var. **retrorsa** (Sherff) Wunderlin, *comb. nov.*

Bidens polylepis Blake var. *retrorsa* Sherff, Bot. Gaz. 80: 386. 1925.

The number of outer involucral bracts, their length, and the condition of their margins (serrate-ciliate *vs.* smooth to ciliate) separates *Bidens polylepis* from *B. aristosa.* These characters overlap, and certain intermediate specimens are difficult to place. Thus, in the author's opinion, this taxon does not warrant specific recognition and is best reduced to a variety. It has been stated by various other workers (*i.e.* Cronquist, 1952, 1963; Steyermark, 1963) that *B. polylepis* is probably a variety of *B. aristosa*, but no new combinations have been made to this effect by these workers.

Bidens aristosa (Michx.) Britt. var. **retrorsa** (Sherff) Wunderlin f. **involucrata** (Nutt.) Wunderlin, *comb. et stat. nov.*

Coreopsis involucrata Nutt., Jour. Acad. Phila. 7: 74. 1834.
Diodonta involucrata (Nutt.) Nutt., Trans. Amer. Phil. Soc. n.s. 7: 360. 1841.
Bidens involucrata (Nutt.) Britt., Bull. Torrey Bot. Club 20: 281. 1893, *non* Sch.-Bip., 1846, *nec* Phil., 1891.
Bidens polylepis Blake, Proc. Biol. Soc. Wash. 35: 78. 1922.
Bidens polylepis Blake var. *typica* Sherff, Brittonia 6: 339. 1948.

In the author's opinion this taxon is best treated as a forma, because of the frequent occurrence of antrorsely and retrorsely barbed awns in other species of *Bidens* (see *B. aristosa* var. *aristosa* f. *fritcheyi* above).

Further new nomenclatural combinations are undoubtedly needed in *Bidens* but, this would require extensive study of the genus which is beyond the scope of a flora.

Eupatorium × polyneuron (F. J. Herm.) Wunderlin, *comb. et stat. nov.*

Eupatorium perfoliatum L. var. δ T. & G., Fl. N. Amer. 2: 88. 1841.
Eupatorium cuneatum Engelm. *ex* T. & G., Fl. N. Amer. 2: 88. 1841, *pro syn., non* DC., 1836.
Eupatorium perfoliatum L. var. *cuneatum* (Engelm. *ex* T. & G.) Engelm. *ex* Gray, Syn. Fl. N. Amer. 1: 100. 1884.
Uncasia cuneata (Engelm. *ex* T. & G.) Greene, Leafl. Bot. Obs. & Crit. 1: 13. 1903.
Eupatorium serotinum Michx. var. *polyneuron* F. J. Herm., Rhodora 40: 86. 1938.

This plant is a frequently occurring hybrid between *Eupatorium perfoliatum* and *E. serotinum* found in Arkansas, Illinois, Indiana, Louisiana, and Missouri. A more detailed analysis of the hybrid nature of this plant is currently under investigation by the author.

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NOTES

CAPPARIS HYPOLEUCA PRESL: A SYNONYM OF *SOLANUM SCHLECHTENDALIANUM* WALP.

Among the rich *Capparis* collections in the Czech National Herbarium (PR), once kept in Prague but now housed in the romantic setting of the castle at Pruhonice, there resides the type specimen of *Capparis hypoleuca* Presl from Guayaquil, Ecuador. It was collected on the voyage round the world by the Bohemian merchant Thaddaeus Haenke and published in Presl's *Reliquiae Haenkeanae* 2: 87. 1835. The species has never been recognized since, and its nature has remained an enigma.

When looking at this specimen in 1965, I was struck by an uneasy feeling that, while it did resemble some stellate-tomentose species of *Capparis* such as *C. crotonoides* (a species which Presl thought closely related and which Haenke in fact did collect in Ecuador), I had seen this plant some place else, and not in *Capparis*. The very tiny buds were no help in identification, yet looked different than those of *Capparis*.

Fortunately, my interests do not lie only in New World Capparidaceae: several of my students have worked and are working in the genus *Solanum*. Thus upon my return to Madison, and a re-examination of a leaf fragment of *Capparis hypoleuca*, it became immediately apparent that the specimen the name is based on belongs to *Solanum schlechtendalianum* Walpers (*Solanum salviifolium* Lam.), a well-known species widely distributed from Mexico to northern South America. Fate has been on the side of nomenclatural stability here, because a *Solanum hypoleucum* (Standl.) Morton of 1940 (based on *Lycianthes hypoleuca* Standl., 1927) already exists. Thus, in conformity with Article 55 of the *International Code of Botanical Nomenclature* (1961), that combination must stand, since a new combination of Presl's name under *Solanum* would create a superfluous homonym. *Capparis hypoleuca* must be considered simply a synonym of *Solanum schlechtendalianum*.

I wish to thank authorities at the Czech National Herbarium at Prague for permission to examine the specimen and to take a leaf fragment and the Research Committee of the University of Wisconsin Graduate School for travel support to Pruhonice. — *Hugh H. Iltis, Department of Botany, University of Wisconsin, Madison 53706.*

THE CHROMOSOME NUMBER OF *UTRICULARIA DENTICULATA* BENJAMIN

Utricularia denticulata which grows in Mexico was reduced to a synonym of *U. livida* E. Meyer by Taylor (Kew Bull. 18: 1–245. 1964). *Utricularia livida* (*sensu lato*) is widely distributed, occurring in Africa, Madagascar, and Mexico.

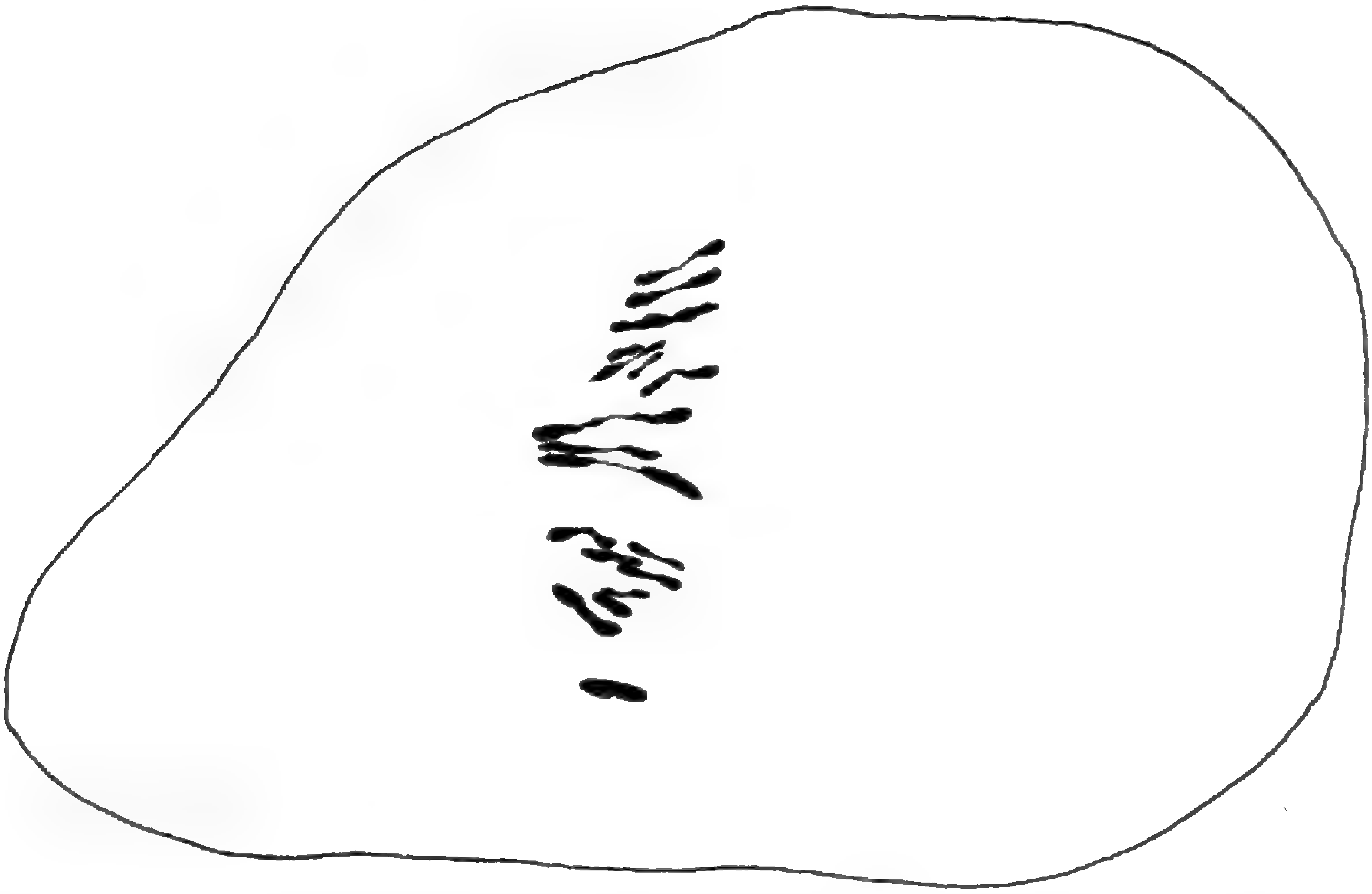

FIGURE 1. — Chromosomes (× 2400) in pollen mother-cells of *Utricularia denticulata* Benjamin ($n = 18$).

According to Kamienski's Lentibulariaceae in *Die natürlichen Pflanzenfamilien*, *Utricularia denticulata* should be placed in sect. *Oligocista* DC. Barnhart (Mem. New York Bot. Gard. 6: 39–64. 1915) placed *U. denticulata* in *Calpidisca* in his original treatment of the genus. Since Barnhart's segregation of genera in the Lentibulariaceae has been questioned, chromosomal relationships between these genera should be investigated. Some of Barnhart's genera, *Lecticula, Orchyllium, Pleiochasia, Setiscapella, Stomoisia,* and *Utricularia,* have already had their chromosome numbers recorded and discussed by Kondo (Chromosome Inform. Serv. 13: in press). The chromosome number of Mexican *U. denticulata* which is in Barnhart's segregated genus *Calpidisca* is, however, reported here for the first time.

The material for this study was collected by T. Hamada in Oaxaca, Mexico, (exactly locality unknown) in 1959 and determined as *Utricularia denticulata* by S. Komiya. The flower bud of the species used was obtained under cultivation in the greenhouse of the Kondo Collection in Nagoya, Japan. Observations were made after preparation by the aceto-carmine squash method.

Eighteen bivalent chromosomes at metaphase I of meiosis in PMC's were observed for this species (Fig. 1). The same chromosome number ($n = 18$) was previously counted (Kondo, Jour. Jap. Bot. 46: 26–29. 1971) in *Utricularia resupinata* B. D. Greene which was placed in the genus *Lecticula* by Barnhart (Mem. New York Bot. Gard. 6: 39–64. 1915). Both *Utricularia resupinata* and *U. denticulata* are indigenous to the New World. This and previous observations (Kondo, Jour. Jap. Bot.: in press) indicate that the basic chromosome number $x = 9$ for *Utricularia* may be found only in the New World species.

Chromosome number data known for Barnhart's segregated genera in the Lentibulariaceae still do not clarify relationships between them. — *Katsuhiko Kondo, Department of Botany, The University of North Carolina, Chapel Hill, North Carolina* 27514.

EDITOR'S NOTE

Publication of the papers presented in this Edgar Anderson memorial number of the ANNALS OF THE MISSOURI BOTANICAL GARDEN has been aided by funds from two sources. Pioneer Hi-Bred International, Des Moines, Iowa, has presented a grant to help subsidize publication of these papers. Pioneer Hi-Bred has generously supported various activities at the Garden for many years, and this support is gratefully acknowledged.

The Edgar Anderson Memorial Fund, created by Dr. Anderson's friends and students, has also contributed to the publication of these papers. The Fund has also made possible the dedication of a staff office in the Garden's new John S. Lehmann Building to the memory of Dr. Anderson. In addition, the Boxwood Study Group of the St. Louis Herb Society is planting a wonderful boxwood garden in his memory to the southwest of the Climatron. The Garden is most grateful to the many contributors to the Fund.

The cover illustration for this issue of the ANNALS is adapted from Edgar Anderson's study of two populations of *Planta alba* and *P. rubra.* The population of *P. alba* was growing in a meadow, while that of *P. rubra* was from a nearby woodland. Five characters are represented in the scatter diagram—leaf width and plant height by the axes of the graph, and stem hairiness, flower color, and petal notching by the glyphs on the dots. For a complete discussion of this complex see pages 94–101 of Anderson's *Plants, Man and Life* (1952, reprinted 1967).—*Editor.*

XII INTERNATIONAL BOTANICAL CONGRESS
JUNE 23–30, 1975

The Closing Plenary Session of the XI International Botanical Congress held at Seattle, U.S.A., in 1969, accepted an invitation issued by the Academy of Sciences of the U.S.S.R. to convene the XII International Botanical Congress in the City of Leningrad in 1975. In 1971 the Organizing Committee was appointed consisting of a chairman (A. L. Takhtajan); four vice-chairmen (A. A. Prokofiev, A. A. Theodorov, N. V. Tsitsin, A. A. Yatsenko-Khmelevsky); a secretary-general (O. V. Zalensky); a scientific secretary (N. S. Snigirevskaya); and a number of members at large. The XII International Botanical Congress is intended to facilitate interdisciplinary communication among botanists as well as an informal exchange of ideas. A number of sections are planned, including special ones to accommodate mycologists (also lichenologists), phycologists, and bryologists.

The Congress will be divided between organized half-day symposia and half-day contributed paper sessions. In addition to the opening and closing plenary sessions, two evening lectures are being scheduled. All special interest groups wishing to apply for space and time during the Congress should do so by writing as soon as possible to the secretary-general, Dr. Oleg Zalensky, Komarov Botanical Institute of the Academy of Sciences of the U.S.S.R., 2, Prof. Popov Street, Leningrad 197022, U.S.S.R.

The sessions of the Nomenclature Section will take place, as usual, immediately before the opening of the Congress—on June 20–23. Four days are set aside in order to enable the Section to convene for six to eight sessions of two to four hours each.

A meeting of the International Association of Botanic Gardens (President Academician N. V. Tsitsin) will be held in Moscow at the Main Botanical Garden of the Academy of Sciences of the U.S.S.R. on June 20.

A tentative schedule of scientific field trips has been planned for the immediate pre-Congress and post-Congress periods. The principal purpose of these trips is to acquaint visiting botanists with as many interesting and unique features of the flora and vegetation of various regions of the U.S.S.R. as possible. Some specialized trips for phycologists, lichenologists, bryologists, and palaeobotanists are also planned.

Double postcards announcing the XII International Botanical Congress were mailed during the last months of 1972. Those who wish to receive further information on the Congress should return their interest cards by March 1, 1973, so that they will be placed on the mailing list for the First Information Circular expected to be published June–July 1973.—*A. Takhtajan, Chairman, Organizing Committee*

The previous issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, VOL. 59, NO. 2, pp. 105–322, was published on 28 March 1973.

PREPARATION OF MANUSCRIPT

The ANNALS publishes original manuscripts in systematic botany and related fields. There is a charge of $25 per printed page to help defray costs of publication. Authors are asked to follow the suggestions below in order to expedite editing and publication. If an author feels that his manuscript presents special problems, he should write the editor concerning the best way to handle these before submitting the manuscript.

Manuscripts must be typewritten on one side of substantial weight paper, 8½ × 11 in. The manuscript should have wide margins and be double spaced throughout, including the abstract, footnotes, legends, tables, lists of specimens, and the bibliography. Tables should be typed separately and placed at the end of the text. Authors should indicate in the margins the approximate places for illustrations and tables. Submission of the original and one carbon or xerographic copy of the manuscript is desirable, and the author should also retain a copy of the final, typed draft.

Acknowledgements to granting agencies, herbaria, illustrators, and technical assistants may be conveniently placed as a footnote on page one. The author's full mailing address should appear as a second footnote.

An abstract must accompany each paper other than "Notes." The abstract should succinctly summarize the findings and conclusions of the paper and should be completely comprehensible itself.

A brief Latin diagnosis for each new taxon is preferred to a complete Latin description. A complete description should be given in English.

The citation of specimens should be concise. Geographic names are put in order of decreasing political magnitude. Only the barest essential data concerning each specific locality should be given. Collectors are cited by family name and collection number. If there is no collection number, the year of collection should be given. Herbaria are designated according to the current edition of *Index Herbariorum*.

Abbreviations should be checked for consistency and to make sure they are unambiguous. Periods are used after all abbreviations except metric measures, compass directions, and herbarium designations.

All illustrative material should be mounted on stiff cardboard. If the originals are too large to be conveniently mailed, photographic reductions should be submitted. The maximum size of a printed illustration is 5 × 7¾ in., and therefore, the height of an illustration must not exceed about 1.5 its width. Figures are numbered consecutively, since they are not printed as "plates." Numbering must be done with a mechanical device or with dry-transfer lettering and never by hand. The amount of reduction should be noted on the back of each illustration, together with the figure numbers, author's name and title of the paper. Photographs should be sharp, glossy prints. Numbering should be applied directly to the surface of the photograph. Several photographs may be assembled to form a composite block, and each photograph should be numbered separately. The individual photographs should be mounted with the interior edges flush. Line drawings are prepared with India ink and must never be placed in the same block with photographs. Authors wishing to have original illustrations returned must notify the editor when proofs are returned.

The bibliography should be compiled with care. The author should check to make sure each entry in the bibliography is referred to in the text and each reference to a paper in the text is entered in the bibliography. Citations of periodical literature should appear as follows: Author's last name, initial(s). Year. Full title of article. Name of journal. Volume: inclusive pagination. Names of journals are abbreviated according to *Botanico-Periodicum-Huntianum*, except *Journal* should be abbreviated *Jour.* and *Zeitschrift*, *Zeitschr.* Citations of books should appear as follows: Author's last name, initial(s). Year. Full title. Edition, if applicable. Place of publication.

Author will receive page proof. Since changes in proof are expensive, authors should not make revisions at this stage. Authors will be charged for alterations other than corrections of printer's errors.

Reprints may be purchased at cost plus postage. An order blank for reprints will be enclosed with proofs. A reprint price list is available from the editor.

All manuscripts should be addressed to the Editor, Marshall R. Crosby, Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

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