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[1]Contribution Number 3234 from the Snow Entomological Division, Natural History Museum, and Department of Entomology, The University of Kansas.

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ABSTRACT The superfamily Apoidea is one of the three major groups of Hymenoptera Aculeata, being composed of the sphecoid wasps, the bees, and the Heterogynaidae, a small and poorly known group of wasps. The phylogenetic relationships among the major lineages of apoids were investigated using 130 characters from the morphology of the adult insects, six from larval morphology, and three characters from adult behavior. These 139 characters were analyzed under three parsimony methods: equal weighting, implied weighting, and successive weighting. Different phylogenetic hypotheses were produced by each method (55 trees under equal weighting, four trees under implied weighting, and one tree under successive weighting, for analyses including all 54 exemplar taxa). The results from implied weighting are favored over those of the other two methods and are used to propose a higher level classification for the Apoidea. Heterogynaidae and Ampulicidae constitute the most basal apoid clades; however, the position of Heterogynaidae remains ambiguous: in three implied weighting-trees, it comes out as the sister group of Ampulicidae and in the fourth as the sister group of the remaining Apoidea, excluding Ampulicidae. The remaining families recognized and their relationships are: [Sphecidae (sensu stricto) + [Apidae (sensu lato) + Crabronidae]]. Only five subfamilies of Crabronidae are recognized: Astatinae, with the tribes Astatini, Eremiasphecini and Ammoplanini; Bembicinae; Crabroninae (including the genera *Dinetus*, *Laphyragogus*, *Mellinus* and *Xenosphex*); Pemphredoninae, with the tribes Psenini (including the genera *Odontosphex* and *Entomosericus*) and Pemphredonini; and the Philanthinae.

INTRODUCTION

The superfamily Apoidea is one of the three major clades of the Aculeata Hymenoptera (Brothers 1975, Gauld and Bolton 1988, Brothers and Carpenter 1993). A peculiar difference exhibited by aculeate females in relation to the remaining Hymenoptera is their modified ovipositor, no longer used for laying eggs, but only as a sting to inject venom into the host or prey, as well as into potential attackers (defensive function). As in many groups of parasitic Hymenoptera, females of most aculeate lineages behave as idiobiont parasitoids, i.e., upon finding a suitable host, usually concealed in protected places, the female wasp paralyzes it with its venomous sting and lays an egg on the host surface (Gauld and Bolton 1988). However, several lineages of Aculeata departed from this ancestral mode of life and have evolved complex nesting and social behaviors to a degree not paralleled by any other group of insects, except termites. Several aspects of the biology and evolution of the aculeate wasps are presented and discussed by Evans and West-Eberhard (1970), Iwata (1976), Gauld and Bolton (1988) and Hanson and Gauld (1995).

The phylogeny of the major aculeate lineages was recently investigated by Brothers and Carpenter (1993). This comprehensive study mostly reevaluated Brothers' (1975) work, incorporating new characters systems proposed since 1974 and new studies, in particular Carpenter's (1986) investigation on the Chrysidoidea (= Brothers' Bethyloidea). Their results largely support the phylogenetic patterns found in these two previous works, including the three major lineages of Brothers (1975). The now widely accepted superfamilial classification for the Aculeata proposed by Brothers (1975) is based on the recognition of these three lineages, i.e. Chrysidoidea, Apoidea and Vespoidea. Chrysidoidea, the basal clade of the Aculeata, contains small wasps most of which behave as parasitoids or sometimes as cleptoparasites. Vespoidea is a large assemblage of very distinct aculeate lineages; most are parasitoids, but well-known groups like ants and social paper wasps are also included.

Classification and Phylogenetic Relationships within the Apoidea

The Apoidea is composed of the sphecoid wasps [Sphecidae sensu Bohart and Menke (1976)], the bees and the genus *Heterogyna* Nagy (the genera *Daycatinca* and *Daya* are treated here as synonyms of *Heterogyna*; see below), a small and poorly known group of wasps placed in a family of its own (Brothers and Carpenter 1993). Most apoids show derived life history traits compared to the ancestral

aculeate parasitoid behavior, with the females exhibiting a high degree of parental care. Their host, or better, the immature's provisions are now transported and concealed in a pre-existing or especially built cavity. Construction of a nest before prey capture apparently evolved only once in the Apoidea (Melo, in prep.).

The "Sphecidae" of Bohart and Menke forms a large and diverse assemblage of predatory wasps, attacking most insect orders, as well as spiders [see Iwata (1976) and Bohart and Menke (1976) for prey records]. In the monumental revisionary work of Bohart and Menke (1976), this group was divided into 11 subfamilies: Ampulicinae, Sphecinae, Pemphredoninae, Astatinae, Laphyragoginae (containing only the genus *Laphyragogus*), Larrinae, Crabroninae, Entomosericinae (containing only *Entomosericus*), Xenosphecinae (containing only *Xenosphex*), Nyssoninae (= Bembicinae; see Menke 1997) and Philanthinae. Larrinae and Crabroninae have been treated under one name in the past (e.g., Evans 1964a) and more recently, Lomholdt (1985) and Menke (1988), among others, have advocated such classification. Alternative classifications, based on a division of the aculeate wasps into several superfamilies, have recognized a superfamily Sphecoidea, with the subfamilies of Bohart and Menke treated as families (e.g., Krombein 1979). Others have used only one superfamily for bees and sphecoid wasps, but raised all sphecoid subfamilies to family level (e.g., Finnamore and Michener 1993). Bohart and Menke (1976) revised all genera of sphecoid wasps then known, providing subfamilial, tribal and generic identification keys, as well a summary of the known aspects of the biology for each genus.

Because of the distinct feeding habits of bees compared to other aculeates, including sphecoid wasps, the older Linnaean classifications for the Aculeata always had bees and sphecoid wasps in separate higher categories. The sphecoid wasps were usually among a large group of fossorial wasps (e.g., Shuckard 1837) and the bees, like the ants, were not recognized as having any clear links to a particular group. Despite relatively earlier recognition of the close relationship between bees and sphecoid wasps (Müller 1872), a formal classification placing these two groups into one superfamily was proposed much later (Handlirsch 1907). Such a classification received strong support from Michener's (1944) study on the relationships among bees. Brothers' (1975) study on the phylogenetic relationships within the Aculeata provided reliable evidence, in terms of shared derived features, for the close proximity between bees and sphecoid wasps. Based on the phylogenetic tree obtained in his study, he placed bees and sphecoid wasps in his superfamily Sphecoidea; Michener (1986) has shown, however, that Apoidea is the valid name for Brothers's Sphecoidea. Brothers (1975) also proposed an informal division of the Apoidea into two groups, the Spheciformes (= Sphecidae sensu Bohart and Menke) and the Apiformes (bees).

Heterogyna with its reduced size and particularly its very reduced forewing venation remained an enigmatic group for a relatively long time since its proposal by Nagy (1969). This author clearly had very confused ideas about its relationships with other Aculeata lineages, since he placed it in a large, heterogeneous assemblage combining 'Ampulicidae, Dryinidae and Cleptidae'. Brothers (1975) placed *Heterogyna* in his plumariid group based on Nagy (1969). Day (1984), upon gathering material of new species from Africa, provided convincing evidence that *Heterogyna* belonged in the Sphecidae sensu Bohart and Menke, placing it in a separate subfamily. Day (1984) also described for the first time the females, which are brachypterous and have a very unusual morphology compared to other sphecoid wasps. The phylogenetic analyses by Alexander (1992a) and especially by Brothers and Carpenter (1993) confirmed Day's placement of *Heterogyna*, and in the latter work, the genus was assigned to a separate family, the Heterogynaidae.

Alexander (1992a) was the first to investigate the relationships among the major lineages of the apoids using modern phylogenetic methods. His study combined two major sets of morphological characters used previously in determining relationships among sphecoid wasps: Evans' larval characters [see reviews in Evans (1959a, 1964a)] and Bohart and Menke's (1976) adult characters. One of the major problems of Evans' and Bohart and Menke's works is their assumption that the major lineages of "Sphecidae" could be properly classified without including bees among them, even after admitting that some lineages of sphecoid wasps seemed more closely related to bees than to the rest of "Sphecidae". Before Alexander's (1992a) study, Lomholdt (1982) had already proposed dividing the "Sphecidae" into two, according to him, monophyletic groups, one uniting Sphecinae + Ampulicinae and the other containing all the remaining sphecid subfamilies, forming his Larridae, which he considered the sister group of the bees. Alexander's study also provided ample evidence for the paraphyletic nature of Sphecidae sensu Bohart and Menke; however, none of his analyses specifically supported Lomholdt's phylogeny. The overall results of Alexander's analyses are inconclusive regarding the relationships among the major groups of Apoidea, especially because numerous conflicting relations are supported by one or more of his analyses. He was well aware of the preliminary status of his work and concluded that much more remained to be done.

THE PRESENT STUDY

The present study developed from an investigation of the relationships among the genera of the tribe Pemphredonini sensu Bohart and Menke (1976). Early into that study, I realized that their Pemphredonini seemed to be diphyletic, but proper evaluation of this question would require a broader investigation of the relationships among the different sphecoid lineages. Because of the poor resolution obtained by Alexander (1992a) when using mainly character systems from previous authors, I decided to repeat his study, but mostly using original characters and a representation of taxa not requiring hypotheses of monophyly above the level of genus (Alexander used the tribes recognized by Bohart and Menke). For obvious reasons, the Pemphredoninae received closer attention and better representation. Despite this bias, I am confident that results obtained here represent a fair investigation into the phylogeny of the major apoid lineages.

The preferred phylogenetic hypothesis found by this study is used to propose a higher level classification for the Apoidea. From now on, I will be using the classification proposed here, and reference to higher taxa whose previous definitions conflict with the ones proposed here will be marked as such.

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MATERIAL AND METHODS

SELECTION OF REPRESENTATIVE TAXA

Representatives of all major lineages of Apoidea were included in the present study, as well as of some basal lineages of aculeates as outgroup taxa. Two limiting factors were taken into account when selecting the specific taxa: availability of specimens (adult insects) for complete dissection and of published information on larval morphology. However, a few important taxa whose larvae are unknown were still included; also, *Laphyragogus* and *Xenosphex* were included, despite lack of material for complete dissections (only mouthparts, including oral plate, and external genitalia were dissected). In some cases, I also chose specific genera that were considered previously to have a relatively basal position within their respective lineages; this is the case for the exemplar taxa of bees, of Sphecidae (s.str.), and for most of the Crabroninae and the Bembicinae. Table 1 lists the exemplar taxa included in the formal parsimony analyses. Among the Crabronidae, I tried to include representatives of all subfamilies recognized by Bohart and Menke (1976), as well as "problem" genera, i.e. genera whose taxonomic positions in Bohart and Menke's classification were not supported by Alexander's (1992a) study. Besides the taxa listed in Table 1, material of several other taxa, in particular specimens of Apoidea deposited in the insect collection of the University of Kansas, were also examined. More relevant taxa are listed below.

Material of the following additional hymenopteran taxa not included in the analyses were also completely dissected and examined:

Crabronidae.—Astatinae: *Ammoplanops cockerelli* Pate (female), *Ammoplanellus umatilla* Pate (female), *Ammoplanellus* sp. (female), *Dryudella* sp. (female); Bembicinae: *Alysson melleus* Say (female), *Argogorytes* sp. (male); Crabroninae: *Bothynostethus* sp. (male), *Ectemnius stirpicola* (Packard) (female), *Entomognathus texanus* (Cresson) (male), *Oxybelus emarginatum* Say (female and male), *Trypoxylon frigidum* Smith (male); Pemphredoninae: *Araucastigmus masneri* Finnamore (female), *Arpactophilus* sp. (female), *Carinostigmus* sp. (female), *Diodontus atratulus*

Table 1. List of taxa used as exemplars; ingroup taxa arranged according to the classification proposed here. F = female; M = male.

OUTGROUP
Bethylidae:
1. *Epyris* sp. (from Brazil), F, M
Pompilidae:
2. *Notocyphus* sp. (from Costa Rica), M
Rhopalosomatidae:
3. *Rhopalosoma nearticum* Brues, F
Sapygidae:
4. *Eusapyga proxima* (Cresson), F
Scolebythidae:
5. *Clystopsenella longiventris* Kiefter, F
Sierolomorphidae:
6. *Sierolomorpha canadensis* Provancher, M
INGROUP
Ampulicidae:
7. *Ampulex* sp. (from Costa Rica), F
8. *Aphelotoma rufiventris* Turner, M
9. *Dolichurus* sp. (from Costa Rica), F, M
Apidae (sensu lato):
10. *Anthophorula albata* (Timberlake), F
11. *Conanthalictus nigricans* Timberlake, F
12. *Ctenocolletes smaragdinus* (Smith), F
13. *Hesperapis carinata* Stevens, F
14. *Lonchopria zonalis* (Reed), F
Crabronidae:
Astatinae:
15. *Astata nevadica* Cresson, F
16. *Eremiasphecium sahelense* (Simon-Thomas), F
17. *Ammoplanus* cfr. *apache* Pate, F
18. *Pulverro mescalero* Pate, F, M
19. *Timberlakena yucaipa* Pate, F
Bembicinae:
20. *Bembecinus quinquespinosus* (Say), F
21. *Didineis texana* (Cresson), M
22. *Heliocausus larroides* (Spinola), F
23. *Hoplisoides spilopterus* (Handlirsch), F
24. *Nysson rusticus* Cresson, F
25. *Ochleroptera bipunctata* (Say), F
Crabroninae:
26. *Dinetus pictus* (Fabricius), M
27. *Laphyragogus pictus* Kohl
28. *Mellinus alpestris* Cameron, M
29. *Xenosphex timberlakei* Williams
30. *Anacrabro ocellatus* Packard, F
31. *Lindenius columbianus* (Kohl), F
32. *Lyroda subita* (Say), F
33. *Nitela amazonica* Ducke, F
34. *Palarus latifrons* Kohl, M
35. *Plenoculus davisi* Fox, M
Pemphredoninae:
36. *Odontosphex paradoxus* Menke, M
37. *Entomosericus concinnus* Dahlbom, F
38. *Mimesa cressonii* Packard, F, M
39. *Pluto minutus* (Malloch), F, M
40. *Psenulus mayorum* Bohart & Grissell, F
41. *Arpactophilus steindachneri* Kohl, F
42. *Diodontus rugosus* Fox, F, M
43. *Parastigmus huecuvus* Finnamore, F
44. *Passaloecus areolatus* Vincent, F, M
45. *Pemphredon mornata* Say, F
46. *Spilomena catamarca* Antropov, F
47. *Stigmus temporalis* Kohl, F
Philanthinae:
48. *Aphilanthops frigidus* Smith, M
49. *Philanthus gibbosus* (Fabricius), F, M
Heterogynaidae:
50. *Heterogyna fantsilotra* Day, M
Sphecidae (sensu stricto):
51. *Chlorion aerarium* Patton, F
52. *Palmodes rufiventris* (Cresson), M
53. *Podalonia communis* (Cresson), M
54. *Stangeella cyaniventris* (Guérin-Meneville), F

Taschenberg (male), *Microstigmus nigrophthalmus* Melo (female), *Passaloecus cuspidatus* Smith (female), *Pemphredon lethifer* (Shuckard) (female), *Polemistus braunsii* (Kohl) (male), *Polemistus dickbolharti* Menke (female), *Spilomena subterranea* McCorquodale & Naumann (female), *Spilomena* sp. (female), *Stigmus fulvipes* Fox (male), *Stigmus temporalis* Kohl (female); Philanthinae: *Cerceris rufopicta* Smith (female).

Apidae (s.l.).—*Calliopsis andreniformis* Smith (female), *Callomelitta antipodes* (Smith) (female), *Hylaeus* sp. (female).

Mutillidae.—*Myrmosa unicolor* Say (male).

Pompilidae.—*Aporinellus fasciatus* (Smith) (female).

Sierolomorphidae.—*Sierolomorpha nigrescens* Evans (male).

Vespidae.—*Eumenes fraternus* Say (female).

Braconidae.—unidentified species (female).

Evaniidae.—unidentified species (male).

Trigonalidae.—unidentified species (male).

Xiphydriidae.—*Xiphydria* sp. (female).

Xyelidae.—*Macroxyela ferruginea* (Say) (male).

Undissected or only partially dissected (e.g., terminalia) specimens of the following taxa were also examined:

Ampulicidae.—*Aphelotoma fuscata* Riek (female and male), *Dolichurus corniculus* (Spinola) (female), *Paradolichurus bohartí* Kimsey (female and male), *Paradolichurus obidensis* (Ducke) (female and male), *Trirogma caerulea* Westwood (female).

Crabronidae.— *Clypeadon laticinctus* (Cresson) (male), *Entomosericus kaufmanni* Radoszkowski (female and male), *Eremiasphecium budrysi* (Kazenas) (female), *E. longiceps* (Gussakovskij) (female and male), *Laphyragogus ajjer* Beaumont (female and male), *Mellinus arvensis* (Linnaeus) (female and male), *Mellinus bimaculatus* Packard (female), *Odontosphex damara* Pulawski (female and male), *Palarus variegatus* (Fabricius) (female and male), *Paracrabro froggratti* Turner (female), *Tiguipa* cfr. *fiebrigi* (Brèthes) (male), *Timberlakena calmilla* Pate (female), *Xenosphex xerophilus* Williams (female).

Heterogynaidae.—*Heterogyna protea* Nagy (female and male) and males of all African *Heterogyna* species, except for *H. ravenala* Day.

DISSECTION OF ADULT SPECIMENS

At least one adult specimen from each of the taxa listed in Table 1 (except *Laphyragogus* and *Xenosphex*) was processed as follows before examination:

(1) Soaking in 10% KOH solution overnight;
(2) Clearing in 3% hydrogen peroxide for species with a dark integument;
(3) Transfer to 50–70% ethanol, then boiling for a few minutes, followed by slow cooling;
(4) Transfer to water and then slow addition of glycerin;
(5) Transfer to and storage in pure glycerin.

In order to avoid excessive clearing of mouthparts and terminalia, these parts were dissected before transferring to peroxide. Boiling in ethanol is important to remove, from inside the specimen, especially from the head, bubbles produced by the peroxide. Partial dismembering of the specimen was carried out before transferring to pure glycerin, since at this stage the integument is still relatively malleable from the KOH treatment.

For species in Table 1 with only one sex listed, the terminalia of the opposite sex were removed and submitted to the same procedure described above, so that sex specific characters from this part of the body could be examined; for three genera, only material of other congeneric species was available: a male of *Eusapyga* sp., a female of *Aphelotoma nigricula* Riek and a female of *Heterogyna protea* Nagy.

The heads of specimens preserved in fixative (or sometimes in alcohol) of the following species were dissected for examination of the morphology of the pharynx (see characters 13 and 14):

Ampulicidae.—*Dolichurus* sp. (Costa Rica, male).

Apidae (s.l.).—*Augochlora pura* (Say) (female).

Crabronidae.—*Alysson melleus* Say (Bembicinae, female), *Crossocerus* sp. (from USA, Crabroninae, male), *Didineis texana* (Cresson) (Bembicinae, female), *Diodontus flavitarsis* Fox (Pemphredoninae, female), *Hoplisoides* sp. (from Costa Rica, Bembicinae, female), *Nysson* spp. (female from USA, male from Costa Rica, Bembicinae), *Ochleroptera bipunctata* (Say) (Bembicinae, female), *Philanthus gibbosus* (Fabricius) (Philanthinae, female), *Psenulus* sp. (from Costa Rica, Pemphredoninae, female), *Sphecius speciosus* (Drury) (Bembicinae, male), *Spilomena alini* Antropov (Pemphredoninae, female), *Stigmus americanus* Packard (Pemphredoninae, female).

Sphecidae (s.str.).—*Isodontia* sp. (from USA, female), *Sphex ichneumoneus* (Linnaeus) (male).

Sapygidae.—*Sapyga* sp. (from USA, male).

CHARACTER SELECTION AND DELIMITATION

Most of the characters used in the present study are derived from the morphology of the exoskeleton of the adult insects, including internal processes (e.g., furca, 2nd phragma). Selection of characters was based on dry, pinned specimens, as well as on dissected specimens in glycerin, using a stereoscopic microscope Olympus SZ60 (up to 126×) and incident and transmitted light. The remaining characters were taken from the morphology of immature stages (larva) and from the behavior of adult females.

In order to confirm the glandular nature of two characters (82 and 83), female specimens of *Ammoplanus* cfr. *apache*, *Passaloecus arcolatus*, and *Stigmus americanus* preserved in Kahle's fixative were embedded in LR White resin following the procedures described by Lindley (1992) and sectioned with a Sorvall Ultra Microtome (MT 5000); the sections were slide-mounted using Euparal. The slides were observed and photographed under a Olympus BH-2 microscope with differential interference contrast optics.

It is difficult to explain or justify the process of character discovery and subsequent delimitation of those characters into states. For complex characters, i.e. characters that show a great amount of apparently important cladistic information but are not readily divisible into discrete states or expressible in a quantitative manner (e.g., Characters 58 or 68), I tried to provide detailed descriptions and illustrations, so that the states here recognized can be apprehended and more properly evaluated by other people. But the problem of making explicit the decision processes followed when delimiting the states for these complex characters still remains. In most such cases, I included a larger number of states to match more closely the condition present in the different taxa. However, if taken to an extreme and if the states are nonadditive, this procedure can make any character useless by assigning a different state for each taxon.

In some cases, to preserve the informational content of a complex character, I divided it into two characters, one of them representing presence or absence of a structure or of a particular condition and the second character representing its different states (e.g., Character pairs 70 and 71, or 77 and 78). Taxa in which the structure or condition is absent are assigned a question mark for the second character; this corresponds to treating inapplicable characters as missing data. This can be problematic under certain circumstances (e.g., Maddison 1993), but the current computer algorithms are not able to handle inapplicable characters differentially. One alternative would be to have only one character, but this is exactly what was being avoided in the first place.

Another issue that should be mentioned is the treatment given to morphometric characters (approxi-

mately 25% of the characters used here, not considering meristic characters, e.g., Character 4 or 73). In most cases, a quantitative description was adopted to express a qualitative nature not easily captured as such; most commonly, this qualitative nature involved shape of structures. For example, the labrum (Character 1) in Pemphredonini and most Ammoplanini is relatively similar in overall shape and in a few other attributes, but I tried to express this similarity mostly by the proportions of the labrum (state 1-1); characters 19 and 20 are additional examples.

Different procedures have been developed to divide morphometric characters into more or less objective states taking into consideration intra- and intertaxon variation [see reviews by Stevens (1991) and Thiele (1993)], as well as to produce characters representing shape (e.g., Zelditch et al. 1995). I did not employ any of these procedures for the quantitative characters used here. The characters selected are believed to show very little intraspecific variation, since they were chosen exactly for being stable across at least two representative taxa. However, the limits for the different states were usually arbitrary (see e.g., Characters 8, 9 or 29) and were defined to circumscribe two or more taxa thought to form a natural group. This approach has been criticized for its potential to bias the phylogenetic analyses in favor of pre-conceived ideas of relationships (e.g., Stevens 1991, Gift and Stevens 1997). Submitting these characters to the procedures mentioned above could diminish these potential biases, but I think it would represent little improvement for the quantitative characters used here [see also Farris (1990)]. In any case, I classified all 139 characters used in the analyses accordingly to their nature (see Table 4). This somewhat crude sorting can be used to identify those characters whose cladistic informational content should be viewed with more caution.

In the case of absence of one or more of the veins delimiting the forewing submarginal cells (see Characters 87–89), I used relational information to infer the putative losses. This problem of similarity assessment usually has been circumvented by considering only the number of submarginal cells present [e.g., Alexander's (1992a) Character 59, or Alexander and Michener's (1995) Character 84]. However, I think this approach can lead to loss of information, and therefore I tried to introduce a more precise assessment, especially because several lineages of Crabronidae have lost some of these veins. Here I provide more detailed justifications for the similarity assessments made in each case:

Pemphredonini.—The presence of only two submarginal cells in this group is considered here to be derived from loss of the segment of Rs separating the 1st and 2nd submarginal cells, i.e. fusion of these two cells. This assumption is based on presence among members of this tribe of a disproportional elongate 1st submarginal and the relatively wide separation between 1m-cu and the vein here interpreted as 2rs-m, especially in genera like *Diodontus* and *Pemphredon*.

Ammoplanini.—The presence of two or only one submarginal cell in this group seems at first more difficult to explain, because members of the basal lineage, *Pulverro* (and *Ammoplanops*), have a very reduced venation pattern. However, I am postulating that the ancestral lineage for this tribe had two submarginal cells as seen in some species of *Timberlakena* (and also in *Protostigmus*). This two-celled condition was created by loss of 3rs-m and M distal to 2rs-m (character 89). These postulated vein losses, instead of loss of the segment of Rs separating the 1st and 2nd submarginal cells as suggested for the Pemphredonini, are inferred from the close proximity between 1m-cu and the vein here interpreted as this segment of Rs in *Pulverro* and *Timberlakena* (see Figs. 20 and 21). Also, the venation pattern of the Ammoplanini can be easily derived by patterns similar to that of some species of *Eremiasphecium* (see Fig. 22) assuming the changes postulated here.

Dinetus.—The two-celled condition in this genus can be derived easily from a shortening of the marginal cell accompanied by loss of 3rs-m and the segment of M distal to 2rs-m. The genus *Gastrosericus* (Crabroninae, Larrini) has a similar condition, but clearly independently acquired.

Nitela, Lindenius* and *Anacrabro.—The presence of only one submarginal cell in these three genera can be derived from a pattern with two submarginal cells (in which the 2nd cell is petiolate) by loss of M distal to the segment of Rs separating the 1st and 2nd submarginal cells and loss of the segment of 2rs-m not fused with Rs. Indeed, in *Encopognathus* [see Fig. 116A in Bohart and Menke (1976)] and in some species of *Nitela*, a clear indication (or the vein remains in the case of *Nitela*) of a petiolate 2nd submarginal cell can be seen.

Hesperapis.—The two-celled condition in this genus is assumed to have occurred by loss of 2rs-m. This assumption is based on presence of a relatively long 2nd submarginal cell (i.e. 2nd and 3rd fused) and 1m-cu connected to the segment of M delimiting the 2nd cell. In bees, 1m-cu apparently almost always connects to M between the segment of Rs separating the 1st and 2nd submarginal cells and 2rs-m.

Heterogyna.—This genus has a somewhat unusual and very reduced wing venation. I use here the same interpretation given by Day (1985) for *H. protea*: first submarginal cell complete, second cell petiolate and distally open (2rs-m present, but not reaching spectral M).

I made no especial effort to include known synapomorphic characters or to look for new putative

synapormorphies for the following taxa previously found to be monophyletic: Sphecidae (sensu stricto) (Alexander 1992a), Apidae (sensu lato) (Alexander 1992a, Alexander and Michener 1995) and the Philanthinae sensu Alexander (1992b). Obviously, I paid close attention to any evidence that could contradict these previous studies. Characters found by Brothers and Carpenter (1993) to support the monophyly of Apoidea were included (however, several of them were circumscribed differently), as well as additional relevant characters providing resolution for relationships among the outgroup taxa.

The sample of characters used here is not intended to represent the result of an exhaustive search for informative characters, but only as one of the many samples of characters that could be extracted from these insects. Some areas of the body that seem to contain important characters were completely ignored. For example, the internal ridges and lamellae associated with the hypostomal bridge in the head exhibit a large amount of variation among the taxa sampled, but I was simply unable to organize this variation in any meaningful way. This region of the body and many others are worth exploring in future studies.

TERMINOLOGY

The morphological terms adopted here were mostly taken from Bohart and Menke (1976), Michener (1944) or Snodgrass (1942, 1993) and definitions for these terms can be found in those works. However, terminology for wing characters (see also Fig. 14) was taken from Day (1988); for the thoracic pleuron, from Gibson (1993); for external genitalia, from Smith (1970). Sources for a few additional morphological terms are given directly in the list of characters. For indication of direction for structures in the head, I used the convention of an insect with a prognathous head, so that the frons is in a dorsal position and the occiput, ventral. Reference is made to metasomal sclerites (Michener 1944), instead of abdominal sclerites, except for gonocoxites and gonapophyses of female's sting.

LARVAL AND BEHAVIORAL CHARACTERS

Six characters (131–136) derived from the external morphology of the larva were used. The data for all larval characters were taken from the literature (Table 2), except for *Spilomena*; I also examined larvae of a few additional taxa, like *Pemphredon*, *Psenulus*, and *Stigmus*, as well as of some taxa not included in the present study, like *Sceliphron*, *Cerceris*, and *Megachile*. There is no published information on the larvae of nine genera of the ingroup: *Aphelotoma*, *Ctenocolletes*, *Didineis*, *Eremiasphecium*, *Laphyragogus*, *Xenosphex*, *Timberlakena*, *Parastigmus*, and *Heterogyna*. These taxa have missing entries for larval characters in the character matrix, except *Didineis*, for which the states were taken from the description of the larva of *Alysson melleus* by Evans and Lin (1956b), and *Ctenocolletes*, from the description of the larva of *Stenotritus pubescens* (Smith) by Houston (1975); these pairs of genera have very similar adult morphology and nesting behavior, respectively. Information for outgroup taxa was taken at the family level from Evans et al. (1987), except for Scolebythidae and Sierolomorphidae, for which there is no available information.

These six characters were selected from a list of 10 characters considered of phylogenetic significance by Evans (1959a). Two of the 10 were omitted because of their apparent complexity (larval body shape and mandibles); I am not comfortable using them without examining the specimens. The two others (parietal bands and opening between atrium and sub-atrium of spiracles) were given less importance by Evans. Alexander's (1992a) study can be used to evaluate the significance of these four characters in a cladistic context.

Three behavioral characters were incorporated in the formal analyses: type of larval food, food relocation and nest construction. All prey records for ampulicids, crabronids, and sphecids were taken from Bohart and Menke (1976), except for *Eremiasphecium* taken from Kazenas (1991; prey records for *E. budrysi* Kazenas), *Arpactophilus* from Matthews and Naumann (1989; prey record for *A. mimi* Naumann), *Ammoplanus* from Maneval (1939; prey record for *A. perrisi* Giraud) and from Ahrens (1948; prey record for *A. handlirschi* Gussakovskij), *Laphyragogus* from Kazenas (1985; prey record for *L. turanicus* Gussakovskij), *Entomosericus* from Kazenas and Alexander (1993; prey record for *E. kaufmani* Radoszkowski) and for *Odontosphex paradoxus* from M. Prentice (pers. comm.). Biological information for the outgroup taxa was taken from Hanson and Gauld (1995).

DATA ANALYSIS

Methods incorporating parsimony have won widespread acceptance among systematists interested in producing phylogenetic hypotheses for the various groups of organisms, especially because parsimony has been considered the only criterion that implements Hennig's auxiliary principle [e.g., Hennig (1966:121)] that the most preferable tree topology is the one that minimizes the number of *ad hoc* hypotheses of homoplasy (e.g., Wiley 1981, Farris 1983). Parsimony is usually associated only with methods that do not assign different weights to the characters being used, i.e. methods in which all characters are treated equally in terms of cladistic information they provide. However, parsimony can also be applied under a weighting function. Herein, I employ two distinct methods (implied and successive weighting) that assign differential weights to the characters based on their degree of homoplasy.

Table 2. List of ingroup taxa whose larval descriptions were used for information on larval characters.

Genus	Species	Reference
Ampulex	*canaliculata* Say	Evans (1959b)
Dolichurus	*corniculus* (Spinola)	Maneval (1939)
Anthophorula	*chionura* Cockerell	Rozen (1957)
Lonchopria	*zonalis*	McGinley (1981)
Conanthalictus	*conanthi*	Rozen (1993)
Hesperapis	(eight species)[1]	Rozen and McGinley (1974)
Astata	(three species)	Evans (1958, 1959a)
Pulverro	*monticola* Eighme	Bohart and Grissell (1972)
Ammoplanus	*perrisi* Giraud	Maneval (1939)
Bembecinus	(three species)	Evans and Lin (1956b), Evans (1959a, 1964b)
Heliocausus	*larroides*	Evans (1971)
Hoplisoides	(three species)	Evans and Lin (1956b)[2], Evans (1959a)[2]
Nysson	(two species)	Evans and Lin (1956b), Evans (1959a)
Ochleroptera	*bipunctata*	Evans and Lin (1956b)
Mellinus	*arvensis* (Linnaeus)	Evans (1959a)
Dinetus	*pictus*	Asís et al. (1997b)
Anacrabro	*ocellatus*	Evans (1957)
Lindenius	*tylotis* Court and Bohart	Evans (1959a)
Lyroda	*subita*	Evans (1964b)
Nitela	*spinolae* Latreille	Janvier (1962)
Palarus	(two species)	Gayubo et al. (1992)
Plenoculus	*davisi*	Evans (1959a)
Odontosphex	*paradoxus*	M. A. Prentice (pers. comm.)
Entomosericus	*kaufmani* Radoszkowski	Kazenas and Alexander (1993)
Mimesa	*bicolor* (Jurine)	Janvier (1956)
Pluto	*albifacies* (Malloch)	Evans (1959a)
Psenulus	(four species)	Evans (1959a)[3], Asís et al. (1993, 1997a)
Arpactophilus	*steindachneri*	Evans (1964b)
Diodontus	(two species)	Evans (1958)[4]
Passaloecus	(two species)	Evans (1958, 1964b)
Pemphredon	(four species)	Evans (1958a, 1964b)
Spilomena	(several species)	pers. obs.
Stigmus	(two species)	Evans (1958), Asís et al. (1993)
Aphilanthops	*frigidus*	Evans (1957)
Philanthus	*gibbosus*	Evans (1957)
Chlorion	*aerarium*	Evans (1964b)
Palmodes	*dimidiatus* (De Geer)[5]	Evans and Lin (1956a)
Podalonia	(two species)	Evans and Lin (1956a), Evans (1964b)
Stangeella[6]	*cyanuventris*	Janvier (1928)

[1]Including *H. carinata*. [2]Cited as *Psammaecius*. [3]Cited as *Diodontus*. [4]Cited as *Xylocelia*. [5]Cited as *P. daggyi*. [6]Cited as *Sphex*.

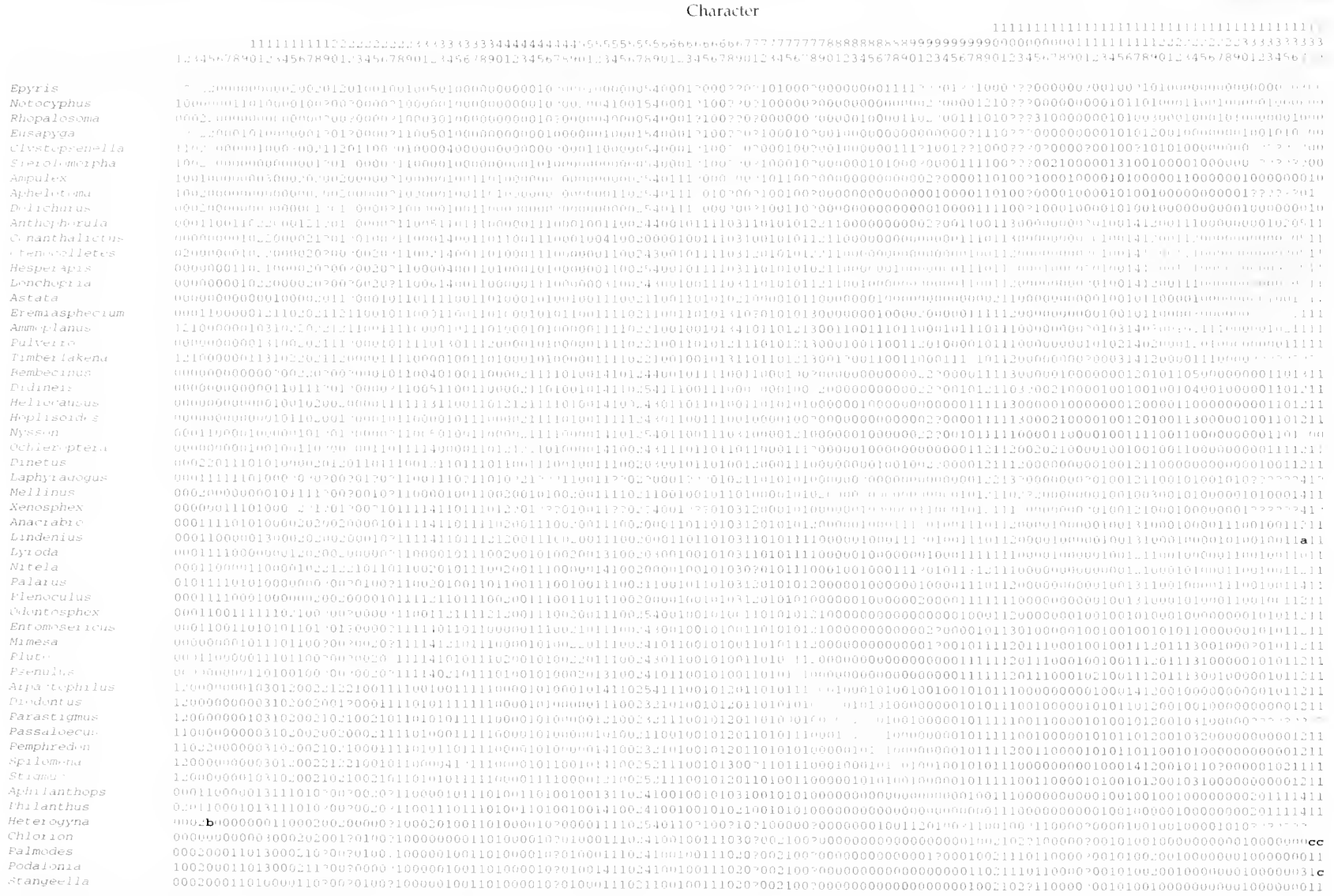
Two additional issues should be considered before discussing the analysis of the data. One of them is character ordering, i.e. prior determination of the direction, and sometimes the likelihood, of the possible transformations among the different states of a multistate character. It has been argued that transformation series should be ordered whenever possible to take into consideration the nested nature of homology. However, I opted to treat all multistate characters as unordered, because in very few of them could the hypothetical states be arranged in what seemed to be a logical linear (additive) transformation series. In some of the cases involving nested homology, two characters were used instead, one representing absence or presence of a given structure and the other, the different conditions of the structure.

The second issue refers to the effects of having taxa with missing data from one or more data sets. Lack of data from larval morphology is the main reason for most of the missing entries in the present study; however, besides having their larvae unknown, *Laphyragogus* and *Xenosphex* also have several missing entries because of lack of material for complete dissections. In order to evaluate the effects of these two taxa, two sets of analyses were carried out for each of the three parsimony methods described below: one set containing all taxa in Table 3 (complete data matrix) and the other excluding *Laphyragogus* and *Xenosphex* (partial data matrix).

Parsimony under implied weighting.—Goloboff (1993) proposed implied weighting as a method for

Table 3. Matrix of character states. Letters represent polymorphic condition (a = 2 & 4, b = 0 & 2, c = 0 & 1).

Character



weighting characters according to their degree of homoplasy. Unlike successive weighting (see below), the weights are calculated simultaneously with tree search, the different tree topologies being evaluated according to the character weights which in turn are implied by the distribution of the characters on a given topology. This method seeks trees with the maximum sum of character weights or maximum total fitness, i.e. trees which imply the characters to have, on average, as high a weight as possible. The individual character fitness (f_i) is given by the function

$$f_i = (k + 1) / (s_i + k + 1 - m_i)$$

where k is a constant of concavity introduced to regulate how strongly homoplastic characters are down-weighted (the higher its value, the lesser the down-weighting), s_i is the actual number of steps observed for character i on a given topology, and m_i is the minimum number of steps possible for character i [see Goloboff (1993) for more details]. The higher the degree of homoplasy of a character in a given topology, the lower its weight will be.

The analysis of the present data using the method of implied weighting was implemented by the computer program Pee-Wee, Version 2.8 (Goloboff 1997a). Tree search was carried out with the command *mult** adopting $k = 3$, the program's default value for the weighting constant. The following command sequence was used: *hold**; *hold/2*; *mult*300*; *max**. The command *mult** randomizes the order of the taxa in the data matrix, creates a weighted Wagner tree, and submits it to tree bisection-reconnection branch-swapping (300 replicates); the command *max** does branch-swapping on the trees found by *mult**, looking for additional trees with the same fitness. The resulting trees were examined using MacClade, Version 3.06 (Maddison and Maddison 1996); character optimizations shown on the illustrated cladograms (Figs. 1, 2, 5 and 6) were carried out also using MacClade.

Parsimony under equal weighting.—Under this procedure, the characters receive equal weight, and therefore one change in a given character has the same effect as one change in any other character (except when characters differ in their ordering status). The objective is to find the trees that minimize the total number of changes, i.e. trees of minimum length. This method was implemented by Nona, Version 1.8 (Goloboff 1997b), using the following command sequence: *hold**; *hold/2*; *mult*300*; *max**. The data matrix was submitted to heuristic search using tree bisection-reconnection swapping (*mult**), with random addition sequence (300 replicates). The resulting trees were examined using MacClade.

Parsimony under successive weighting.—Successive weighting was originally proposed by Farris (1969); more recently Carpenter (1988) has advocated applying it as a means to select among multiple equally parsimonious trees. This is an iterative procedure, in which the character weights are calculated after each run of tree search, the new weights then applied to the next run. The process is stopped when the results of a given iteration are identical to those produced in the iteration immediately preceding it. The weight for each character is calculated according to the character consistency index; this index is a function of the amount of homoplasy shown by the character in a given tree topology. This method was carried out using PAUP*, Version 4.0 b2 (Swofford 1999). The initial set of most parsimonious trees produced under equal weighting was used as the starting point. Reweighting of characters was done according to their consistency index, using the maximum value (best fit) with base weight equal to 10 (weight values not truncate). The data matrix was submitted to heuristic search using subtree pruning-regrafting swapping, with random addition sequence (100 replicates); also the parsimony settings were adjusted to have branches collapsed when their minimum length was zero, which is equivalent to *amb-* in Nona. The resulting trees were examined using MacClade.

CHARACTERS AND CODES FOR THEIR STATES

The morphological characters are listed according to their positions in the insect body, the structures of the head listed first, followed by thorax and then abdomen; the larval and behavioral characters are at the end. When necessary, I also included (after listing the character and its states) comments on the character or explanations for decisions made while assigning states to certain taxa. The 54 exemplar taxa (Table 1) were examined and scored for the 105 morphological characters. The complete data matrix, listing all taxa and the state codes assigned to them, is presented as Table 3. Morphological characters are illustrated in Figures 10–82 in the Appendix.

1. Labrum:
   (0) at least one and a half times wider than long.
   (1) less than one and a half times wider than long, very flat (Figs. 34 and 40).

Labral width measured across its base. In taxa with state (0), the labral apex usually has numerous bristles, whereas in taxa with state (1) the labrum has few or no bristles. *Podalonia* has a flat, long labrum, but with several apical bristles; *Ampulex* also has an elongate and somewhat flat labrum; both were assigned state (1). In *Epyris* and *Eusapyga*, the labrum is vestigial and these taxa were assigned (?) for characters 1–3.

2. Labral apex:
   (0) entire and broadly rounded, or at most slightly emarginate in the middle.
   (1) entire and pointed.
   (2) notched in the middle (Figs. 34 and 40).

In *Arpactophilus steindachneri* the apex has several small teeth, but the labrum is considered notched in the middle. The common condition in the genus seems to be a shallow notch in the middle and small lateral teeth.

3. A pair of rounded or oval spots on base of labrum:
   (0) absent.
   (1) present.

It is not known what those spots represent, but they do not seem to be some type of sensillum; in the cleared specimens, they look like areas where the dorsal and ventral surfaces of the labrum are fused, being similar to the margins of the labrum.

4. Female mandibular apex:
   (0) apical plus one dorsal subapical tooth.
   (1) apical tooth only, i.e., simple.
   (2) apical plus two or more dorsal subapical teeth.

Some groups, like *Psenulus* and some species of *Parastigmus*, have a small, more basal tooth along the inner margin that it is not taken into consideration here.

5. Male mandibular apex:
   (0) apical plus one dorsal subapical tooth.
   (1) apical tooth only.
   (2) apical plus two or more dorsal subapical teeth.

The number of teeth varies among species of *Heterogyna*. Males of *H. fantsilotra* have two subapical teeth, whereas in *H. protea* has only one tooth. *Heterogyna* is assigned both states, i.e., (0) and (2).

6. Subbasal cleft on inner edge of mandible (female):
   (0) absent.
   (1) present.

This cleft or incision is found in several Crabroninae. For an illustration of this character, see Fig. 2 in Pulawski (1995).

7. Outerventral margin of mandible:
   (0) simple.
   (1) notched.

This is the same as the externoventral notch of Bohart & Menke (1976).

8. Glossa:
   (0) less than twice as long as wide.
   (1) at least twice as long as wide.

9. Prementum:
   (0) less than three times as long as apical width.
   (1) at least three times as long as apical width.

10. Ventral surface of prementum:
   (0) continuous with lateral surfaces or separated by rounded angles.
   (1) separated from lateral surfaces by sharp angles or carinae.

The ventral surface of the prementum in *Podalonia* and *Eusapyga* is excavated longitudinally, forming a sulcus margined by two ridges; *Lindenius* has a similar condition (although the middle part is slightly elevated). In *Diodontus* and *Passaloecus*, the separation between ventral and lateral surfaces is quite abrupt, but there are no carinae. These are all coded as (0).

11. Basal margins of lateral arms of prementum:
   (0) approximately perpendicular to ventral surface (angle over 60º) (Figs. 10 and 11).
   (1) slanting, forming an acute angle (45º or smaller) with ventral surface (Fig. 12).
   (2) lateral arms absent.

The lateral arms of the prementum are considered absent in the bees. In this group, the basal part (articulated with the prementum) of the anterior conjunctival thickenings of Michener (1944) may be homologous to the lateral arms of the prementum that became detached from the rest of the prementum. Another possibility is that the basal portion of these thickenings could have originated from a detached part of the stipes and that the lateral arms disappeared.

12. Paramandibular process:
   (0) absent or very short, well separated from back of clypeus.
   (1) closing at least 3/4 of mandibular socket, but not reaching back of clypeus.
   (2) reaching back of clypeus, but not fused to it.
   (3) fused to clypeus.

In some taxa, for example *Philanthus*, *Aphilanthopsis*, *Palmodes* and *Podalonia*, males and females differ in the degree of development of the paramandibular process. I chose to use the state found in females, because for most taxa only female specimens were available for complete dissection. In *Ampulex* females, the mandibular socket is closed by an extension of the gena, and not of the hypostoma. In the species dissected, the hypostoma gets close to but does not reach the clypeus. In the males, however, the mandibular socket is closed by a hypostomal process. *Ampulex* is assigned state (3).

13. Posterior wall of pharynx (between arms of oral plate):
   (0) not expanded.
   (1) forming two bulging sacs (walls usually covered with numerous acanthae) (Figs. 29–33).

These structures are sometimes hard to see in specimens treated in KOH, especially when the pharyngeal walls are relatively thin. For this reason, specimens preserved in fixative were dissected and examined; due to lack of suitable specimens, most of the material dissected belongs to species (or even genera) not included in the phylogenetic analyses. Figures 31 and 33 show cross-sections of the pharyngeal sacs prepared from material of *Ammoplanus* preserved in fixative. The cleared specimen of *Bembecinus* has what seems to be small expansions on the pharyngeal wall, but no fixed material was available for dissection. It was scored as (?). The male of *Heterogyna fantsilotra* has a distinct expansion of the pharynx. The posterior wall of the pharynx is dilated, but does not form a pair of sacs, and is continuous with two short expansions on the upper part of the pharynx. It is assigned (1) despite these differences.

14. Upper part of pharynx (at the tip of the oral plate arms):
    (0) simple, not expanded.
    (1) forming a pair of elongate, sometimes very large and branched, diverticula (Fig. 33).
15. Apical inflection of clypeus:
    (0) joining epistomal ridge lateral to tentorial pit (Fig. 35).
    (1) joining at tentorial pit.
    (2) joining considerably mesal to tentorial pit (Figs. 13, 14 and 34).

The term "apical inflection" was taken from Roig-Alsina and Michener (1993); see their paper for additional illustrations. The segment of the inflection being considered here seems to be, in most taxa, internal to the membrane that connects the base of the mandible to the inflection. In *Eremiasphecium sahelense*, the joining of the inflection at the tentorial pits seems to result from an apparent outward displacement of the tentorial pits, and not from an expansion of the inflection; it is assigned state (0). In *Philanthus*, the inflection joins a lower branch of the tentorial arm which is broadly fused to a laminar epistomal ridge. In *Entomosericus* and *Mimesa*, the apical inflection joins the epistomal ridge slightly lateral to the tentorial pits, but these taxa are coded as having state (1). The male of *Heterogyna fantsilotra* has an internal longitudinal ridge connecting each internal rim of the antennal sclerite to the apical inflection of the clypeus. This peculiar condition is not treated as equivalent to state (2) above. This taxon is assigned state (0).

16. Eye–clypeus contact:
    (0) none.
    (1) extending for the diameter of one antennal socket or less.
    (2) extending for more than the diameter of one antennal socket.
17. Subantennal sutures:
    (0) absent.
    (1) present, not connected to tentorial arms.
    (2) present, connected to tentorial arms.

This character applies only to taxa assigned states (0) or (1) for characters 18 or 21. *Laphyragogus* and *Xenosphex* have subantennal sutures, but they are assigned (?) because no internal observations were made.

18. Distance between antennal socket and clypeus (female):
    (0) more than one half of socket diameter.
    (1) one half of socket diameter or less, but not nil.
    (2) nil.
19. Epistomal suture, between antennal sockets, in taxa wherein the antennal sockets are in contact with clypeus (female):
    (0) not above transverse median line across antennal sockets (Fig. 34).
    (1) above transverse median line across antennal sockets, but not reaching tangent to upper rims (Fig. 13).
    (2) extending above tangent to upper rims of antennal sockets (Fig. 14).

This character applies only to taxa with state (2) in the preceding character.

20. Tentorial pit (female):
    (0) below or level with tangent to lower rims of antennal sockets (Fig. 13).
    (1) above tangent to lower rims of antennal sockets (Fig. 14).
21. Distance between antennal socket and clypeus (male):
    (0) more than one half of socket diameter.
    (1) one half of socket diameter or less, but not nil.
    (2) nil.
22. Epistomal suture, between antennal sockets, in taxa wherein the antennal sockets are in contact with clypeus (male):
    (0) not above transverse median line across antennal sockets.
    (1) above transverse median line across antennal sockets, but not reaching tangent to upper rims.
    (2) extending above tangent to upper rims of antennal sockets.

This character applies only to taxa with state (2) in the preceding character.

23. Tentorial pit (male):
    (0) below or level with tangent to lower rims of antennal sockets.
    (1) above tangent to lower rims of antennal sockets.
24. Tentorial pit II:
    (0) situated on epistomal ridge.
    (1) distinctly placed above epistomal ridge.

25. Internal rim of antennal sclerite:
(0) level with internal surface of head or projecting only slightly (Fig. 34).
(1) expanded toward the center and covering most of the socket (portion containing antennifer not expanded) (Fig. 35).
(2) expanded and forming a short, but distinct cylinder (portion containing antennifer expanded together with rest of rim) (Figs. 36 and 37).

The term antennifer is taken from Michener (1944). In state (2), the antennifer remains at the edge of the rim.

26. Pedicel attachment:
(0) basically centric.
(1) eccentric (Figs. 38 and 39).

27. Socket on apex of scape with an eccentric pedicel:
(0) entirely membranous.
(1) sclerotized in the center (Fig. 38).

This character applies only to taxa with state (1) for the preceding character.

28. Sexual dimorphism in number of antennomeres:
(0) none.
(1) male with 13 and female with 12 antennomeres.

29. Female 2nd flagellomere:
(0) at least 3× longer than pedicel.
(1) less than 2× longer than pedicel.

This character is used to characterize the relative length of the antenna. The female of *Heterogyna protea* has an unusually long pedicel; it is assigned state (0) despite the fact that its 2nd flagellomere is not 3× longer than the pedicel.

30. Facets of compound eyes (female):
(0) approximately uniform in size.
(1) frontal facets much larger than remaining ones.

31. Facets of compound eyes (male):
(0) more or less uniform in size.
(1) frontal facets much larger than remaining ones (Fig. 39).

32. Inner orbits of compound eyes (female):
(0) straight or slightly concave, more or less parallel.
(1) concave, diverging below.
(2) more or less straight, diverging below.
(3) convex, diverging below.
(4) sinuate (upper portion concave, lower portion convex), strongly converging below.
(5) straight, converging below.
(6) concave, converging below.

33. Integument of paraocular area of female:
(0) not differentiated from more median part of frons.
1) with a specialized area, sometimes very distinct and forming a fovea (Figs. 40–43).

This specialized area represents the surface for release of the secretions of an underlying epidermal gland [see Schuberth and Schönitzer (1993)]. It differs considerably in development and position among the various taxa; I consider all different forms as homologous.

34. Preoccipital carina:
(0) complete (Fig. 44).
(1) interrupted ventrally.
(2) interrupted ventrally, but reaching hypostomal carina.
(3) interrupted dorsally.
(4) completely absent.

This is the same as occipital carina of Bohart and Menke (1976). The species of *Dolichurus* dissected does not have a preoccipital carina, but it is assigned state (1) based on a female of *D. corniculus*.

35. Periforaminal depression:
(0) absent.
(1) present (Fig. 44).

This character concerns a distinct depression on the occipital region. It is usually more developed dorsally, as well as laterally, and in some taxa, it is marked dorsally and laterally by a marginal sulcus and/or carina. The anterior dorsal portion of the pronotum seems to fit in this depression; in the taxa with a well-developed marginal sulcus, one could imagine that head and pronotum are locked together when the anterior dorsal margin of the pronotum is inside the marginal sulcus. In *Entomosericus*, the depression is weakly indicated, but this taxon is considered as having state (1).

36. Cervical sclerite:
(0) absent.
(1) present.

37. Posterolateral angle of pronotum:
(0) evenly rounded (or modified differently from state 1).
(1) reduced dorsally above and anterior to differentiated spiracular operculum.

This character corresponds to character 35 of Brothers and Carpenter (1993).

38. Ventral angle of pronotum:
(0) scarcely exceeding base of procoxa.
(1) greatly produced mesad and closely approaching its counterpart midventrally.

This character is being used to indicate the distinct condition found in all Apoidea, irrespective of the small variation found among them in how closely the two ventral halves of the pronotum approach each other. Brothers and Carpenter's (1993) assignment of a distinct state to bees is unjustified, since a similar condition to that found in bees is present in several other Apoidea.

39. Pronotal collar:
(0) anterior edge rounded, or a collar not differentiated from anterior portion of pronotum.
(1) delimited anteriorly by a transverse carina (some-

times interrupted in the middle) (Fig. 45).
(2) delimited by a carina only laterally.

40. Pronotum (internally):
(0) without lateral ridges.
(1) with a pair of lateral, oblique ridges (converging anteriorly).

Ammoplanus and *Hesperapis* have only a pair of weak carinae (very short in *Hesperapis*); both are coded as (1). In some taxa, e.g., *Astata*, *Ctenocolletes* and *Stangeella*, the ridges are continuous in the middle. The male of *Aphelotoma rufiventris* has no ridges, but the female of *A. nigricula* has a distinct external sulcus in the place where the ridge is situated; this taxon is assigned state (1). *Laphyragogus* and *Xenosphex* are also assigned (1) based only on external examination (presence of a sulcus in *Xenosphex* and a line in *Laphyragogus*).

41. Outer ventral posterior corner of prothoracic episternum:
(0) not differentiated from rest of episternum.
(1) more or less protuberant in lateral view, lateral carina of episternum not differentiated.
(2) as (1), but lateral carina of episternum, above the protuberance, forming a distinct lamella.

42. Short sulcus dorsal to outer ventral posterior corner of prothoracic episternum:
(0) absent.
(1) present (Fig. 47).

A correspondingly short segment of the anterior margin of the pronotum fits inside this sulcus, although it does not show any particular modification in relation to the remainder of the anterior margin. This sulcus is present only in *Heliocausus* and *Ochleroptera*.

43. Prothoracic basisternum:
(0) lateral segments of posterior edge oblique, converging in the middle.
(1) posterior edge basically straight, except for small medial projection, lateral corners pointed.
(2) as (1), but lateral corners rounded (basisternum very small).

This structure shows considerable variation among the taxa examined, making difficult the delimitation of discrete characters and states. This character is used to recognize what seems to be a distinct morphology found in the Bembicinae examined.

44. Medial portion of prothoracic basisternum:
(0) at same level as rest of basisternum, strongly pointed posteriorly (Fig. 46).
(1) declivous in relation to anterior portion (sometimes only slightly), rounded or weakly pointed posteriorly.

The comment for character 43 also applies here; however, the present character is being used to represent the distinct posterior reduction of the medial portion of the basisternum in Apidae s.l. and Crabronidae in relation to the other Apoidea. In *Clystopsenella* and *Eusapyga*, the medial portion is not strongly pointed, but they are assigned state (0).

45. Apophyseal arms of prothoracic endosternum:
(0) separate (Figs. 48 and 49).
(1) fused (forming a bridge) (Fig. 50)

46. Bases of apophyseal arms of prothoracic endosternum (internally):
(0) not connected by divergent plates (Fig. 48).
(1) connected by two continuous, divergent plates originating at base of furcasternum (broadening dorsally) (Fig. 49).

In *Palarus*, these plates are very broad and close half of the coxal cavity. In *Didineis* and *Ochleroptera*, the plates are apparently absent, but I assume that the plates fused completely to the furcasternum (the medial line in the furcasternum is absent, contrary to what occurs in groups where the plates are originally absent).

47. Internal divergent plates of prothoracic endosternum:
(0) separate from furcasternum by a medial ridge.
(1) partially (dorsally) or completely fused to furcasternum, medial ridge absent at least dorsally (Fig. 50)

This character applies only to taxa with state (1) for the preceding character.

48. Fore basitarsus:
(0) apex not modified, or only with a short apical lobe.
(1) with a distinct apical lobe, extending at least to half the length of second tarsomere.

The condition described in state (1) is found only in females of *Laphyragogus* and in most species of *Eremiasphecium* [see Figs. 118–123 in Marshakov (1976)].

49. Foretarsal rake (females):
(0) absent.
(1) present, bristles longer than diameter of basitarsus.
(2) present, bristles as long as or shorter than diameter of basitarsus.

50. Socket of foreleg spur:
(0) broadly connected to basitarsal socket.
(1) narrowly connected to basitarsal socket and away from tibial apex.
(2) as (1) or even farther from tibial apex and, and spur socket almost or completely closed (Fig. 51).

In *Lyroda* and *Laphyragogus*, the spur socket is somewhat closed, but it is situated near the tibial apex. Both taxa are coded (0).

51. Leg form of female:
(0) all similar, slender and generalized (or modified differently from state 1).

(1) all femora inflated and fusiform although midfemur often less so; tibiae and tarsi fairly slender.

52. Claws:
(0) with a subapical or at least one subbasal tooth.
(1) simple, without subapical or subbasal teeth.

53. Notauli:
(0) indicated externally by a sulcus and internally by a ridge.
(1) indicated externally by a line and internally by a ridge.
(2) indicated only externally by a sulcus.
(3) vestigial.
(4) no indication (absent).

Laphyragogus and *Xenosphex* are assigned (1) based on external examination only.

54. Supra-alar carina:
(0) absent or if present, not meeting tegular ridge (preaxilla open anteriorly; Fig. 25).
(1) curving down anteriorly and fused to the anterior segment of the tegular ridge (preaxilla closed off anteriorly; Fig. 26).

The terms supra-alar carina and tegular ridge were taken from Michener (1944). This carina has also been named scutal flange by Menke (1988).

55. Setal patch on anterior segment of tegular ridge:
(0) present.
(1) absent.

This setal patch seems to be a proprioreceptor field and is present in all aculeate outgroup taxa I studied. It is absent from a braconid, evaniid, trigonalyid and a xiphydriid examined. Judging from Ronquist and Nordlander (1989), it is also apparently absent from Ibaliidae. This might be a synapomorphy for Aculeata.

56. Oblique scutal carina:
(0) absent.
(1) present.

57. Prepectus:
(0) not immovably fused to the mesepisternum.
(1) immovably fused to mesepisternum, suture between them not obliterated.
(2) as (1), but suture completely obliterated.

I recognized only three states for the taxa included here, taking into consideration only the degree of fusion to the mesepisternum. Brothers (1975) assumed that the prepectus in Apoidea extended completely across the anterior margin of the mesepisternum, being fused in the midline, as well as fused to and forming the depressed anterior margin of the mesepisternum. Considering the condition in basal Chrysidoidea and Vespoidea, an alternative interpretation for the Apoidea would be a prepectus not contiguous medially and fused to the mesepisternum only along its dorsal half; the depressed anterior margin of the mesepisternum would be a modification of the mesepisternum itself in response to a modified pronotum (ventral angles greatly produced mesad). The prepectus in *Rhopalosoma* is very narrow, but it has a distinct fovea also present in *Eusapyga* and *Sierolomorpha*.

58. Mesepisternal ridge:
(0) complete, reaching anterior edge of mesepisternum away from body's midline.
(1) complete, reaching body's midline ventrally.
(2) reaching ventral portion of mesepisternum, but absent from middle of mesepisternum.
(3) restricted to ventral portion of mesepisternum (absent laterally).
(4) restricted to lateral portion of mesepisternum (absent ventrally).
(5) absent.

This is an internal ridge present laterally and/or ventrally on the mesepisternum (Fig. 52). In most cases it is marked externally by a sulcus (see next character). In *Dinetus* and *Lyroda*, the ridge is interrupted ventrally and only a small segment is present along the anterior edge of the mesepisternum; both taxa are coded as (0). In *Bembecinus*, the mesepisternal ridge is vestigial since only a very short segment is present below the subalar fossa; however, it is still coded (4).

59. Mesepisternal sulcus:
(0) complete, reaching anterior edge of mesepisternum away from body's midline.
(1) complete, reaching body's midline ventrally (Fig. 53).
(2) restricted to ventral portion of mesepisternum (absent laterally).
(3) restricted to lateral portion of mesepisternum (absent ventrally).
(4) absent.

Sometimes the sulcus is only weakly indicated ventrally. In *Ctenocolletes*, the sulcus is only weakly indicated on the upper part of the mesepisternum; it is assigned (3).

60. Omaular sulcus:
(0) absent.
(1) present (Fig. 54).

61. Omaular carina:
(0) absent.
(1) present.

This carina corresponds to the "omaulus" of Bohart and Menke (1976). Omaulus here is used to designate the area of the mesepisternum where its anterior and lateral surfaces meet. When both a carina and a sulcus are present, the carina is always anterior to the sulcus (Fig. 54).

62. Interfurcal muscle:
(0) present.
(1) absent.

Absence of this muscle is considered a synapomorphy for Apoidea by Heraty et al. (1994). Only a male of *Sierolomorpha canadensis* and of *Dolichurus* sp. were examined using the technique described by these authors. The remaining taxa were assumed to have the groundplan condition postulated by Heraty et al. (1994). The loss of this muscle is probably correlated with the ventral fusion of the meso- and metathoraces in Apoidea (condition not used here as an independent character).

63. Arms of meso- and metathoracic furca:
    (0) fused.
    (1) not fused or only weakly fused (separate in KOH cleared specimens; Figs. 15 and 16).

Together with loss of the interfurcal muscle, Heraty et al. (1994) considered fusion of the arms of the meso- and metathoracic furca a synapomorphy for the Apoidea. In two apoid groups, however, the arms are not immovably fused and become separated after KOH treatment. This condition was found in Ampulicidae and in the crabronid genera *Astata*, *Eremiasphecium* and *Pulverro* (as well as *Ammoplanops*). In the Ampulicidae, this probably represents a plesiomorphic condition, while in those crabronid genera, it is clearly a secondary derived condition. In the cleared specimen of *Astata nevadica*, the metafurcal arm has a cup-like expansion and the mesofurcal arm has a callus-like structure (finely fibrous) in the region where they are supposed to be fused (Fig. 15). The lateral arm of the metafurca has also an additional cup-like expansion on its tip and it is weakly attached to the larger cup-like expansion projecting from the endophragmal (= upper metapleural) apophysis. Dissection of a specimen of *Astata* sp. (Costa Rica) preserved in alcohol showed that the two furcal arms are firmly attached to each other and that the cup-like expansions of the metafurcal arms are covered with tendon-like material (finely fibrous and whitish). The KOH treatment probably breaks down this material, causing the separation of the furcal arms. In the cleared specimens of *Pulverro* and *Eremiasphecium sahelense*, the lateral arms of the metafurca are broad (laminar) and also separate from the mesofurcal arms (Fig. 16). Apparently the two cup-like expansions observed in *Astata* fused together and became one large expansion entirely covering each lateral arm of the metafurca in these taxa.

64. Upper margin of discriminal lamella (segment posterior to furcal arms):
    (0) narrow, as broad as remainder of lamella.
    (1) expanded, forming a horizontal lamella perpendicular to vertical portion.

This character applies only to taxa assigned state (1) for character 67.

65. Pseudophragma of second phragma:
    (0) absent (Fig. 17).
    (1) present (Fig. 18).

66. Mesepisternum and metepisternum:
    (0) not fused laterally.
    (1) fused laterally; suture mostly obliterated.

In most taxa, this fusion is restricted to the lower lateral parts of the mesepisternum and metepisternum.

67. Medial portion of mesometepisternal suture (between midcoxae):
    (0) clearly visible (Fig. 59).
    (1) mostly obliterated (Figs. 23, 24, 60–62).

In all Apoidea, the mesepisternum and metepisternum are fused ventrally. The morphology of this area is very complex and variable, making character delimitation difficult. Brothers and Carpenter (1993) consider loss of any sulcus between meso- and metepisterna, ventrally, as part of the Apoidea groundplan. However, in Ampulicidae and *Heterogyna*, the suture is clearly visible (the two lateral halves converge forward) and the midcoxal sockets are small and widely separated; also the mesal articulation is closer to the lateral articulation than to the body's midline. The coxal sockets are large and the suture is mostly obliterated only in the remaining apoids. The expansion of the coxal sockets was apparently accompanied by a posterior expansion of the mesokatepisternum, forming a broad flap covering the sockets medially (Fig. 23); concomitantly, the suture is directed posteriorly (in lateral view; Fig. 24). Brothers and Carpenter (1993) also inappropriately consider this condition as part of the Apoidea groundplan (see their Fig. 11 and state 57-2 in their Appendix IX).

Eremiasphecium and the Ammoplanini have a somewhat distinct condition. Their metepisternum is not projected in the middle as a strong keel continuous with the mesepisternum (see Fig. 62); there is a transverse line that looks like the mesometepisternal suture; this line does not seem to be homologous to the suture and it is probably a structure unique to these taxa. Despite these modifications, they are coded as having state (1).

68. Medial flap of mesokatepisternum and condyle of mesal midcoxal articulation:
    (0) flap well developed and broadly continuous in the middle; portion containing condyle not or only slightly projecting (Fig. 23 and 60).
    (1) flap well developed, interrupted in the middle by a deep cleft; condyle close to midline of body, but not situated at apex of flap projection.
    (2) flap well developed, interrupted in the middle by a deep cleft; condyle situated at apex of flap projection and close to midline of body (Fig. 61 and 62).
    (3) flap narrow, interrupted in the middle by a deep cleft; condyle situated at apex of flap projection and well separated from midline of body (Fig. 53).

This character applies only to taxa assigned state (1) for the preceding character. This region probably represents the fusion of the true katepisternum with the trochantin [see discussion in Gibson (1993)], since it seems more parsimonius to assume that the mesal articulation in the Hymenoptera is homologous to the trochantinal articulation of other insects, and not a new articulation.

69. Medial portion of metepistenum:
   (0) narrow, forming a strong keel and narrowly fused to medial portion of mesokatepisternum (anterior portion of keel extending through vertical medial portion of mesokatepisternum) (Fig. 59–61).
   (1) narrow, forming a carina, perpendicular to vertical medial portion of mesokatepisternum (anterior portion of carina not extending through vertical medial portion of mesokatepisternum) (Fig. 62).
   (2) narrow, but not forming a strong keel or carina, narrowly fused to mesokatepisternum.
   (3) wide and flat, broadly fused to mesokatepisternum (mesometepisternal suture transverse or V-shaped in ventral view) (Fig. 23).
   (4) wide and flat, broadly fused to mesokatepisternum (mesometepisternal suture indistinct) (Fig. 53).

This character applies only to taxa assigned state (1) for Character 62 (ventral fusion of meso- and metathoraces). *Xenosphex* is assigned (3) despite the fact that the medial portion of its metepisternum is mostly vertical.

70. Mesocoxal carina 1:
   (0) absent.
   (1) present (Fig. 55–57).

This carina runs from the lateral articulation obliquely across the coxa to the ventral articulation with the trochanter posteriorly (Michener 1981). In some taxa, for example *Aphilanthops* and *Philanthus*, it is present only basally, on the rest of the coxa being indicated by a rounded ridge; contrary to Alexander (1992a), I assigned state (1) to these taxa (but see next character).

Michener (1981) assumed, without further argumentation, that the basal groove on the coxa of the Apoidea represents the separation of the basicoxite from the rest of the coxa (Michener's disticoxite) and that the mesocoxal carina is present only in those taxa whose basal groove has been displaced distally, i.e. taxa in which an enlargement of the "basicoxite" and a correlated reduction of the "disticoxite" occurred. Michener's terminology and homology assessments were also adopted by Johnson (1988) for the rest of Hymenoptera. The Xyelidae examined here have a distinct basal suture, certainly homologous to the basicostal suture of other insects as defined by Snodgrass (1993), delimiting a very short basicoxite. The other Hymenoptera examined have no such basicoxite and the basicostal suture seems to correspond to the region of attachment of the membrane connecting the base of the coxa to its thoracic socket. It is assumed here that a basicoxite is absent from the Apoidea and that the mesocoxal carina, therefore, does not mark the limit between the basicoxite and a disticoxite.

71. Mesocoxal carina 2:
   (0) weak, sometimes restricted to upper half or indicated only by a ridge (Fig. 55).
   (1) well defined, more or less uniform throughout (Fig. 56).
   (2) conspicuously enlarged, becoming a lamella toward lower half (Fig. 57).

This character applies only to taxa assigned state (1) in the preceding character.

72. Basal part of mesocoxa:
   (0) more or less continuous with rest of coxa (Fig. 55–57).
   (1) forming a narrow pedicel (coxa pedunculate) (Fig. 58).

73. Number of mid tibial spurs:
   (0) two.
   (1) one.

74. Hind coxal socket:
   (0) closed by membrane only.
   (1) closed by a narrow sclerotized bridge connecting the propodeum to the metakatepisternum.
   (2) closed mostly by an enlargement of the medial portion of the metakatepisternum (Fig. 23).

75. Socket of mesal articulation on hindcoxa:
   (0) away from ventral surface of hindcoxa (distance to ventral surface at least one half of distance between socket of mesal articulation and condyle of lateral articulation).
   (1) on ventral surface of hindcoxa or very close to it (Fig. 27).

76. Hind coxal carina:
   (0) absent.
   (1) present, well developed but not forming a lamella.
   (2) present, very strong, forming a lamella (Fig. 63).

This hind coxal lamella is present in the Ammoplanini. In several taxa in this tribe, the lamella is stronger anteriorly and sometimes absent posteriorly, forming a spine-like projection.

77. Paired lobes on inner side of hind coxal apex:
   (0) subequal in size and separated by a narrow cleft.
   (1) dorsal lobe large, usually forming a spatulate process, ventral lobe small or absent (Fig. 64).

Eremiasphecium and the Ammoplanini are assigned state (1) despite the fact that their coxal apices are practically straight, without any lobes (see Fig. 63). In *Ochleroptera*, the lobes are subequal in size, but the dorsal one is spatulate; it is assigned state (1). In *Heterogyna*, *Clystopsenella* and *Sierolomorpha*, the lobes are very small

and separated by a shallow notch in the female and practically nil in the male; these taxa are assigned state (0).

78. Dorsal apical process on inner surface of hindcoxa:
(0) relatively small, trochanter without any conspicuous depression.
(1) well developed, articulating with a basal depression on inner surface of trochanter, apical edge of depression not delimited by a weak crest (Fig. 64).
(2) as (1) or even more developed, apical edge of trochanterical depression delimited by a weak crest.
(3) nil (Fig. 63).

This character applies only for taxa assigned state (1) in the preceding character. These modifications of the coxa and trochanter are probably related to the truncation of the femoral apex, since they are more developed in taxa with such modified femora (see next character), like *Entomosericus* and *Odontosphex* (also *Bothynostethus*, *Cerceris*, *Oxybelus* and a few other crabronid taxa). These structures probably allow the femur to be locked in one position.

79. Apex of hind femur (females):
(0) unmodified.
(1) broadened, truncate.
(2) with an apical spatulate process.

80. Basitibial plate (females):
(0) absent.
(1) present.

81. Hind tibial bristles:
(0) present (at least one).
(1) absent.

These bristles correspond to relatively large and spiniform setae, in contrast to the fine and usually shorter setae also present on the hind tibia. Despite the large and plumose setae on the hind tibia of bees, bristles are considered absent from this taxa; their plumose setae probably correspond only to enlarged fine setae.

82. Gland on posterior surface of hind tibia:
(0) absent.
(1) present (Figs. 65–67).

The presence of this gland was initially inferred from the distinct micropore field [term taken from Finnamore (1995)] on the posterior surface of the tibia (Figs. 65 and 66). Its presence was confirmed with histological sectioning only for *Ammoplanus* (Fig. 67). This gland possibly is absent from *Timberlakena*, because there is no micropore field on its hindtibia, except for a transverse darker area in the region where the field is situated in the other Ammoplanini. It is assigned (?), because a histological study might reveal the presence of the gland.

83. Pterostigma:
(0) flat, not conspicuously thickened.
(1) thickened dorso-ventrally (Figs. 72–74), in dry specimens postero-medial portion conspicuously convex ventrally.

A thickened pterostigma is present in members of the subtribes Pemphredonina and Stigmina of the Pemphredonini. In *Stigmus*, the pterostigma is greatly enlarged and both dorsal and ventral surfaces possess a distinct micropore field (Figs. 68–71); under these fields, there is a thick glandular epidermis (Figs. 72 and 73). This gland is probably present in all Stigmina, because most of them also have a distinct micropore field on the pterostigma. Also a somewhat diffuse micropore field is present in *Diodontus* (Fig. 75). The pterostigma of *Passaloecus* is similarly swollen, but no glandular tissue was detected (Fig. 74).

84. Width of forewing costal cell:
(0) at least as wide as width of vein C.
(1) linear, narrower than vein C.

Maximum width measured perpendicular to costal margin of wing. *Dinetus* was assigned state (0), but its condition is somewhat intermediate between the two states. *Laphyragogus* is assigned (?) because its vein C is unusually slender.

85. Pterostigma width:
(0) less than or subequal to length of prestigma (Sc + R distal to Rs).
(1) at least one and a third the length of prestigma.

Maximum width measured perpendicular to costal wing margin.

86. Marginal cell:
(0) longer than pterostigma (measured along vein C) (Fig. 19).
(1) shorter than pterostigma (Figs. 20–22).

Some species of *Astata* have a marginal cell longer than the pterostigma, but the remaining Astatini have state (1), including *A. nevadica*. Considering that *Astata* does not seem to be the most basal lineage within the tribe, the relatively long marginal cell in some of its species might represent a derived condition. A positive correlation between body size and relative length of the wing cells has been documented for the Hymenoptera (Danforth 1989). Since *Astata* contains the largest forms in the tribe, it is expected that they have longer cells as well.

87. Segment of Rs separating 1st and 2nd submarginal cells:
(0) present.
(1) absent.

The characters of forewing venation for *Eremiasphecium* were taken from *E. longiceps* and not from *E. sahelense*, because this latter species has some reductions that are probably not part of the groundplan for the genus [see also Fig. 184G in Bohart and Menke (1976) for the wing venation of *E. schmiedeknechtii* Kohl]. For *Heterogyna*, wing characters taken from male of *H. protea*.

88. Forewing 2rs-m:
(0) present.
(1) absent.

Present only as nebulous vein in *Heterogyna*.

89. Forewing M (distal to 2rs-m) and 3rs-m:
(0) present.
(1) absent.

Present only as spectral veins in *Sierolomorpha*.

90. Forewing CuA1 and 2m-cu:
(0) present.
(1) absent (discal cell 2 absent).

Present only as spectral veins in *Sierolomorpha*.

91. Forewing Rs (anterior to 2r-rs) and 2rs-m:
(0) separated by Rs (segment distal to 2r-rs) anteriorly (Fig. 19 and 21).
(1) touching anteriorly (i.e., 2nd submarginal cell pointed anteriorly).
(2) fused anteriorly (i.e., 2nd submarginal cell petiolate; Figs. 20 and 22).

Nitela, *Lindenius* and *Anacrabro* are assigned (?) for this character because some of the veins involved are absent, but there is good evidence that their reduced venation pattern is derived from lineages with a petiolate 2nd submarginal cell.

92. Forewing M and CuA:
(0) diverging distal to cu-a.
(1) diverging at cu-a.
(2) diverging basal to cu-a.

93. Forewing M + CuA (distal to cu-a):
(0) subequal to or shorther than cu-a (Fig. 21).
(1) longer than cu-a (Fig. 19 and 20).

This character applies only to taxa assigned states (0) or (1) in the preceding character.

94. Forewing M (basal to Rs):
(0) gently curved or straight (Figs. 19, 20 and 22).
(1) strongly bent (Fig. 21).

95. Forewing vein CuA2:
(0) present, reaching vein 1A.
(1) much reduced or absent, not reaching vein 1A.

96. Hindwing C:
(0) present.
(1) absent.

In *Heterogyna*, *Epyris* and *Clystopsenella*, it is not possible to determine if the vein along the costal margin of the hindwing represents only Sc+R or a fusion of C with Sc+R. They are assigned (?).

97. Hindwing M:
(0) diverging from CuA before or at cu-a (Fig. 19).
(1) diverging from CuA after cu-a.

Nitela and *Timberlakena* are assigned (?) because their hindwing venation is very reduced and parts of the veins involved are lacking.

98. Hindwing vein 2A:
(0) indicated at least as a short spur on basal portion of 1A.
(1) absent.

99. Hindwing clavus (= plical lobe):
(0) indicated posterodistally by moderate incision.
(1) indicated by short incision or only a shallow notch.
(2) not indicated posterodistally on wing margin.

100. Jugal lobe:
(0) absent.
(1) small to moderately long and indicated by distinct incision.
(2) large and not indicated by an incision on wing margin (fused to clavus).

101. Metapostnotum I:
(0) transverse, depressed and distinct mesally between metanotum and propodeum (or shortened).
(1) strongly expanded posteromesally to form "propodeal triangle."

102. Metapostnotum II (propodeal enclosure):
(0) restricted to dorsal surface of propodeum, apex rounded.
(1) extending as a narrow triangle onto posterior surface of propodeum, but for less than half the length of the posterior surface.
(2) extending as a narrow triangle for more than half the length of the posterior surface, but not reaching posterior apex of propodeum.
(3) extending as a narrow triangle to posterior apex of propodeum.

This character applies only to taxa assigned state (1) in the preceding character. It is being used to represent an apparent progressive shortening of the propodeum and a simultaneous relative elongation and posterior narrowing of the metapostnotum within Apoidea.

103. Third mesosomal phragma:
(0) forming a transverse, vertical flange, continuous or narrowly interrupted in the middle.
(1) forming only a narrow medial, transverse flap, situated at the apex of expanded metapostnotum.
(2) as (1), but flap longitudinal.
(3) as (1), but forming a spine-like projection.
(4) absent or indistinctly fused to metapostnotum (except sometimes for presence of a longitudinal carina).

104. Triangular posterior extension of metapostnotum:
(0) flat or forming a broad, shallow sulcus.
(1) forming a narrow, deep sulcus (Fig. 76).

This character applies only to taxa assigned states (1) to (3) for character 102.

105. Metasomal petiole:
(0) absent, tergum I and sternum I not immovably fused, suture between them clearly visible.
(1) present, tergum I and sternum I fused anteriorly, portion of tergum I forming petiole very reduced, suture between tergum I and sternum I along petiole mostly obliterated.
(2) present, tergum I and sternum I not fused, sclerites subequal in size, suture between them clearly visible.

Dolichurus has what looks like a very short petiole and is coded as state (1).

106. Lateral line on tergum I:
(0) present, sometimes marked as a weak carina.
(1) absent.

107. Lateral carina on base of tergum I (dorsal to lateral line):
(0) absent.
(1) present, basal portion simple.
(2) present, basal portion protuberant.

108. Medial longitudinal ridge on base of sternum I:
(0) absent.
(1) present, more developed basally.

109. Second sternum posteromedially:
(0) slightly convex to flat, basal portion more or less at same level as remainder of sclerite.
(1) strongly convex, basal portion distinctly in a different level in relation to remainder of sclerite, surface separating these two portions almost vertical (Fig. 28).

This character is used to recognize the distinct condition found in the Ampulicidae. *Palarus* and males of *Heliocausus* have sternum II modified (with transverse and thick keels), but differently from the condition found in the Ampulicidae. These two taxa are assigned state (0) to avoid creating autapomorphic states for them.

110. Basal portion of lateral gradulus of sternum II.
(0) simple, not modified, or gradulus absent.
(1) laminar and directed inward, forming a specialized articulating surface with the differentiated posterior portion of the lateral edge of sternum I (Fig. 77).

111. Anterior lateral epidermal gland on sternum II:
(0) situated mesal to lateral gradulus.
(1) situated lateral to lateral gradulus (Fig. 78).

Taxa in which the lateral gradulus is absent, as well as those in which the gland could not be detected, were coded as (?).

112. Adult female silk glands:
(0) absent.
(1) present, associated with tergum VI.
(2) present, associated with sterna IV and V.

See Melo (1997) for more details on the structure, function and taxonomic distribution of these glands.

113. Female pygidial plate (tergum VI):
(0) absent.
(1) present.

114. Sixth metasomal sternum (females):
(0) similar to other segments, except for troughlike vertical side walls.
(1) elongate, forming an exposed tapering tube through which sting is exserted.

115. Apex of female sternum VI medially:
(0) simple (truncate, slightly rounded or emarginate), more or less continuous with lateral portions of the apex.
(1) forming a medial lobe (Fig. 79).
(2) with two pointed projections separated by a deep V-emargination (Fig. 80).
(3) denticulate (Fig. 81).

116. Seventh metasomal tergum of female I:
(0) partly exposed and evenly sclerotized.
(1) hidden under tergum VI and considerably desclerotized.

117. Seventh metasomal tergum of female II:
(0) two broad, lateral plates connected anteriorly by a sclerotized bridge.
(1) as (0), but bridge displaced toward posterior margin of tergum.
(2) lateral plates narrow (not sclerotized dorsad to spiracles), connected by a narrow, but strongly sclerotized bridge.
(3) as (2), but lateral segments of bridge forming a 90° angle with dorsal segment.
(4) forming two separate lateral plates (hemitergites), connected by membrane only.

This character applies only to taxa assigned state (1) in the preceding character.

118. Female hemitergites VIII:
(0) narrowly connected dorsally by a sclerotized bridge.
(1) connected by membrane only.

119. Female gonapophyses VIII in lateral view:
(0) strongly curving downward.
(1) gently curving downward.
(2) straight.
(3) curving upward.

Ctenocolletes is assigned (?) because its sting is very reduced (gonapophyses widely separated at their bases).

120. Articulation within gonocoxite IX of female:
(0) absent.
(1) present.

121. Male tergum VII:
(0) entire.
(1) with lateral lobes.

122. Male cerci (tergum VIII):
(0) present.
(1) absent.

123. Male sternum VII:
(0) partly exposed.
(1) completely hidden under sternum VI.

124. Apex of male sternum VIII:
(0) continuous with disk or forming a broad and short medial lobe (broader than or as broad as long).
(1) forming a medial lobe or projection longer than broad, but less than 3× longer than wide, relatively broad.
(2) medial projection more than 3× longer than wide, broad, sides diverging distally.
(3) as (2), but narrow and sides parallel or converging distally.
(4) with two long, lateral spiniform projections.
(5) forming three long, spiniform projections.

125. Lateral margin of projection of male sternum VIII:
(0) entire.
(1) serrate (Fig. 82).
(2) with short, thick bristles.

126. Apical margin of male sternum VIII:
(0) entire.
(1) denticulate.

127. Posterior edge of gonobase foramen (ventrally):
(0) close to bases of gonocoxites.
(1) widely separated from bases of gonocoxites.

128. Volsellae:
(0) clearly differentiated from gonocoxites.
(1) largely fused to gonocoxites, usually small or sometimes apparently absent.

129. Gonapophyses of male genitalia dorsally:
(0) connected by membrane only or by a sclerotized bridge, but not forming a distinct tube.
(1) completely fused, forming a tube.

Various forms of sclerotized bridges are found among the taxa analyzed, making difficult the recognition of discrete states. This character is used to recognize the distinct condition found among several Crabroninae.

130. Apicoventral edge of gonapophyses of male genitalia:
(0) without teeth.
(1) with numerous short teeth.

Sometimes, these teeth are very inconspicuous, like those in *Mellinus* [see illustrations in Menke (1996)].

131. Larval integument:
(0) with minute spicules or smooth.
(1) with dense, short spicules.
(2) with dense, conspicuous seta-like acanthae.

In the descriptions of the larva of *Mimesa bicolor*, Janvier (1956) makes no reference to the integument; *Mimesa* was coded as (?).

132. Position of larval anus:
(0) terminal, directed caudad.
(1) ventral, preapical, directed ventrad.

133. Larval antennal papillae:
(0) absent (sometimes the orbits are protuberant, but there are no papillae).
(1) present, usually well developed and conspicuous.

134. Larval maxillae:
(0) directed mesad apically, closely associated with labium and hypopharynx.
(1) projecting apically as large, free lobes.

135. Larval galea:
(0) large, subequal in size to maxillary palpus.
(1) small, less than half the size of maxillary palpus.
(2) absent.

136. Larval spinneret:
(0) a transverse slit.
(1) with paired openings, each at the end of a projection.
(2) absent.

137. Provisions for larvae:
(0)Orthopteroids (Blattodea, Mantodea, Phasmatodea and Orthoptera).
(1) Thysanoptera.
(2) Hemiptera (Heteroptera and Homoptera)
(3) immature Holometabola.
(4) adult Holometabola.
(5) pollen.
(6) Araneae.

Besides preying on aphids, *Nitela* is also known to prey on Psocoptera, but this state was not included because, among the exemplar taxa, it would be present only in this genus. *Lindenius* and *Arpactophilus* are assigned more than one state. *Nysson* and *Eusapyga* are coded (?) since they are cleptoparasites.

138. Relocation of larval food:
(0) absent.
(1) present.

Chlorion is assigned both states. *Epyris* females are known to relocate their prey, but this is an exception for bethylids; it is assigned (0).

139. Construction of a nest before obtaining larval food:
(0) absent.
(1) present.

Chlorion and *Podalonia* are assigned both states.

RESULTS

Analysis of the complete data matrix resulted in four most fit cladograms when applying implied weighting. The four cladograms differ mainly in the position of *Heterogyna*: three of them have *Heterogyna* as sister group to Ampulicidae (one is shown in Fig. 1), whereas the fourth has it as the sister group of the remaining Apoidea, excluding Ampulicidae (Fig. 2). A strict consensus tree for these four cladograms is shown in Figure 3. Under equal weighting, 55 most parsimonious trees were found (one is shown in Fig. 5a), and a strict consensus tree for the 55 trees is shown in Figure 4a. Successive weighting produced only one most parsimonious tree (Fig. 6). This tree is similar to the implied weighting trees regarding the position of the main lineages.

Under implied weighting, removal of *Laphyragogus* and *Xenosphex* from the data matrix resulted in only one tree (not shown), which was identical to the tree in Figure 1 regarding the composition and relationships among the main lineages. Analysis of the partial data matrix under equal weighting produced eight trees (one is shown in Fig. 5b), and a strict consensus tree for the eight trees is shown in Figure 4b. Under successive weighting, analysis of the partial data matrix resulted in only one most parsimonious tree, which is identical to one of the trees produced under equal weighting (Fig. 5b).

The character weights implied by the topologies of implied weighting-1 tree 1 and implied weighting-2 tree, and the final weights for succesive weighting-1 and successive weighting-2 trees are listed in Table 4. The frequency distributions for the character weights determined by implied weighting-1 tree 1 and by the successive weighting-1 tree are shown in Figure 7; it can easily be perceived how stronger use of the consistency index in successive weighting down-weighs the homoplastic characters compared to the weighting function employed by implied weighting.

Table 5 presents information on length, fitness (sensu Goloboff) and some statistics (consistency, rescaled consistency and retention indices) for the resulting trees (see also Figs. 1, 2, 5 and 6). Unweighted length for trees produced under implied and successive weighting was obtained from Nona; total fitness for trees produced under equal and successive weighting were obtained by importing the trees produced by Nona and PAUP* into Pee-Wee and then executing the command *fit*. The total fitness for the 55 trees produced under equal weighting varies from 695.5 to 697.0.

Only unambiguous changes were plotted in the cladograms shown in Figures 1, 2, 5 and 6. Some of the ambiguous changes could have been resolved on a one to one basis, especially for characters with a low number of alternative optimizations, but for several characters the number of possible optimizations is so numerous that choosing any of them would be extremely arbitrary. Also, no restrictions in relation to character irreversibility were imposed; however, changes in a few characters, as for example in Characters 73 and 122, probably should have been optimized as irreversible.

DISCUSSION

CHOICE OF ANALYTICAL METHOD

Considering that the different parsimony methods produced conflicting arrangements involving the major lineages being investigated, one could manifest no preference for any of the specific results and then make use of only those components common to the different arrangements. Nevertheless, I prefer to argue in favor of using one of the parsimony methods over the others and then make use of all components present in the resulting tree (or set of trees) produced by application of this method.

The major contrast among the methods used here involves use or not of differential weights for the characters during tree search. Character weighting has always been a controversial issue (e.g., Kluge 1998), despite the frequent assumption that characters are not all equally informative (e.g., Farris 1983, Swofford et al. 1996, Goloboff 1993). Explicit *a priori* weighting of morphological characters has been strongly criticized because of its intrinsically subjective and arbitrary nature; however, characters are usually differentially weighted before reaching the stage of data analysis, although this is not always realized. The process of character selection, for example, is a form of attributing different weights to the potential characters, the ones selected receiving weight one and the ones left out receiving weight zero. Not considering cases where potential characters are overlooked, what is assumed to be random variation among the exemplar taxa is usually neglected as a source of informative characters. The problem of selecting genes showing an amount of sequence divergence "appropriate" for resolving relationships among taxa in a study using molecular data (e.g., Graybeal 1994, Simon et al. 1994) is another example of weighting equivalent to the initial differential selection of morphological characters.

The main reason why characters are assumed to be uneven regarding their phylogenetic informational content is because they can evolve at different rates. In a study involving a large number of taxa, the characters selected will certainly have changed at different rates during the

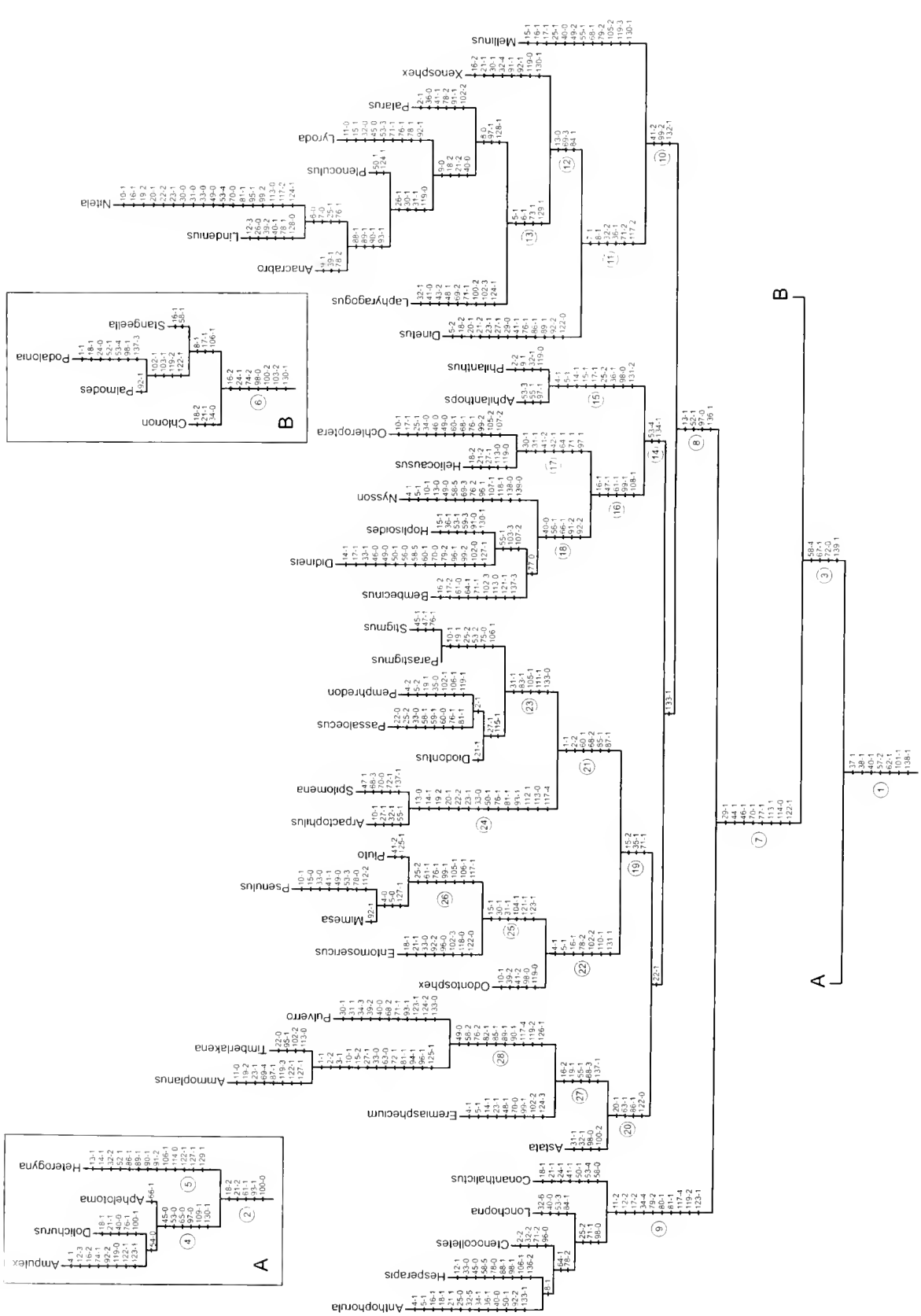


Fig. 1. One of the trees (implied weighting-1, tree 1, length of 907 steps) produced under implied weighting (complete data matrix). Only unambiguous changes and the ingroup taxa are depicted. Numbers inside circles refer to the branch closest to them.

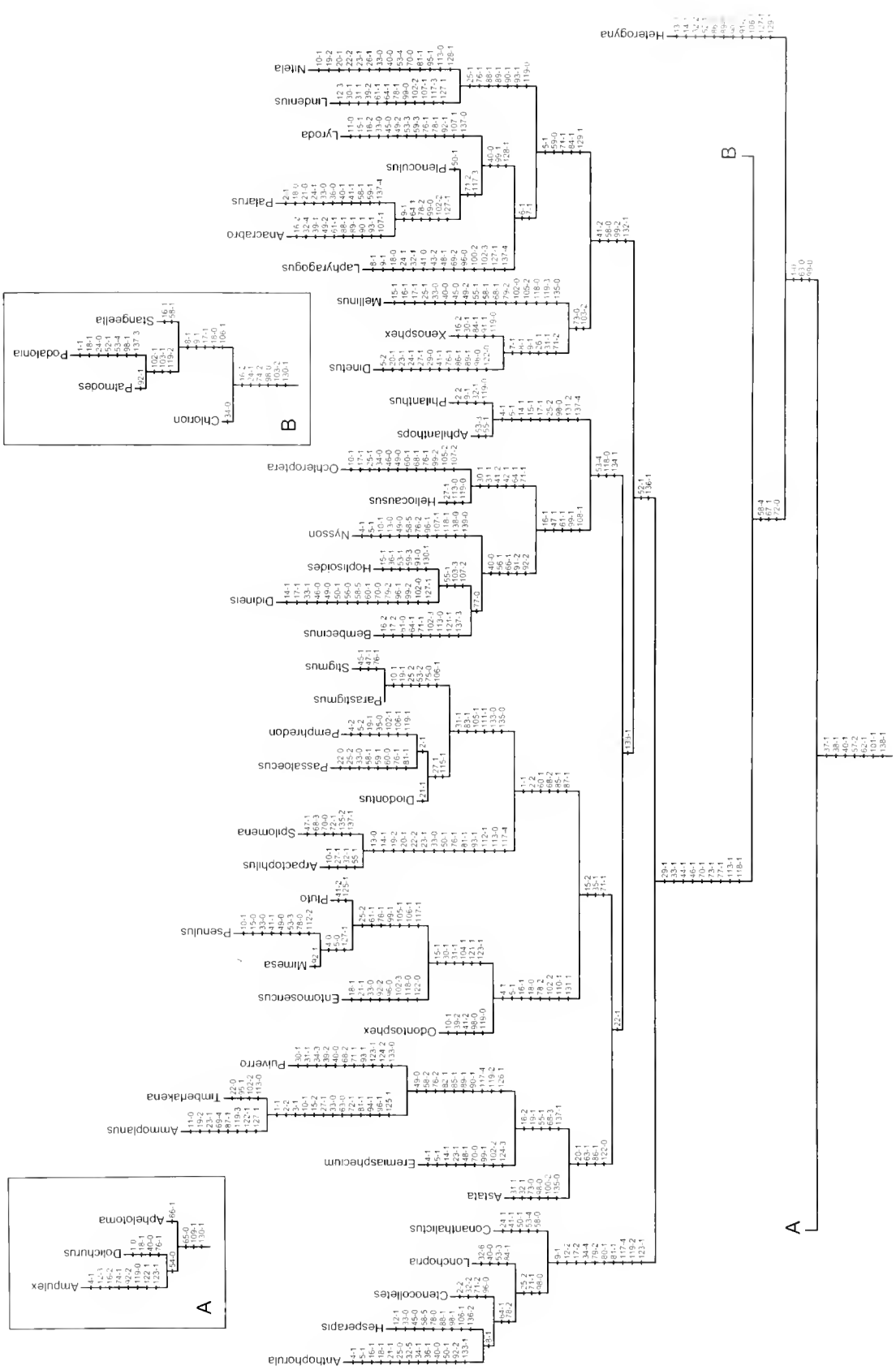


Fig. 2 One of the trees (implied weighting-1, tree 4, length of 920 steps) produced under implied weighting (complete data matrix). Only unambiguous changes and the ingroup taxa are depicted.

evolutionary history of the clades involved, and therefore will be appropriate to resolve relationships at distinct hierarchical levels. In this case, characters should not compete on an equal basis in a parsimony analysis, unless someone had a way to guarantee that the characters used were always represented proportionally to the weights they deserve. But, as this cannot be done, and because there is no way to know *a priori* what the rates of change for these characters are, one has to rely on other types of information to formulate a weighting scheme.

The amount of homoplasy exhibited by a character in a given topology has been suggested as the only type of information that can defensibly be considered an appropriate criterion for weighting characters differentially (Goloboff 1993). As already explained above, the two weighting methods employed here, implied and successive weighting, use the degree of homoplasy of the characters in their weighting functions. One fundamental difference between implied and successive weighting is that in the former method calculation of the appropriate weights is carried out simultaneously with search for the most parsimonious trees, whereas in the latter method, the weights are calculated after each search run, in an iterative process. This reliance on tree topologies obtained previously to weight computation, in particular for the starting point, makes successive weighting less desirable as a weighting method when compared to implied weighting (Goloboff 1993). The influence of the starting trees is well illustrated here by the discrepant results produced by successive weighting for the complete and partial (*Laphyragogus* and *Xenosphex* excluded) data matrices (compare Figs. 5b and 6).

One problem associated with both implied and successive weighting is that each character is assigned a fixed weight to be applied for any type of change within that character (see e.g., Horovitz and Meyer 1995), as well as for all sections of a given topology. If different types of changes within the same character occur at different rates or if the rates vary among the different clades being sampled, then these weighting procedures will be insensitive to the distinct sources of potential homoplasy. This type of problem is probably less relevant for studies using morphological characters than for those using molecular data, for example DNA sequence information.

Taking into consideration the issues discussed above, the results obtained under implied weighting (see Figs. 1–3) are being favored over the results of the other methods employed here (equal and successive weighting; see Figs. 4–6). The tree shown in Figure 1 will be used throughout the remainder of the present work as a basis to discuss the phylogenetic relationships among the taxa involved, and also to propose the classification being adopted here. The relationships among the clades given family status here are shown in Figure 8.

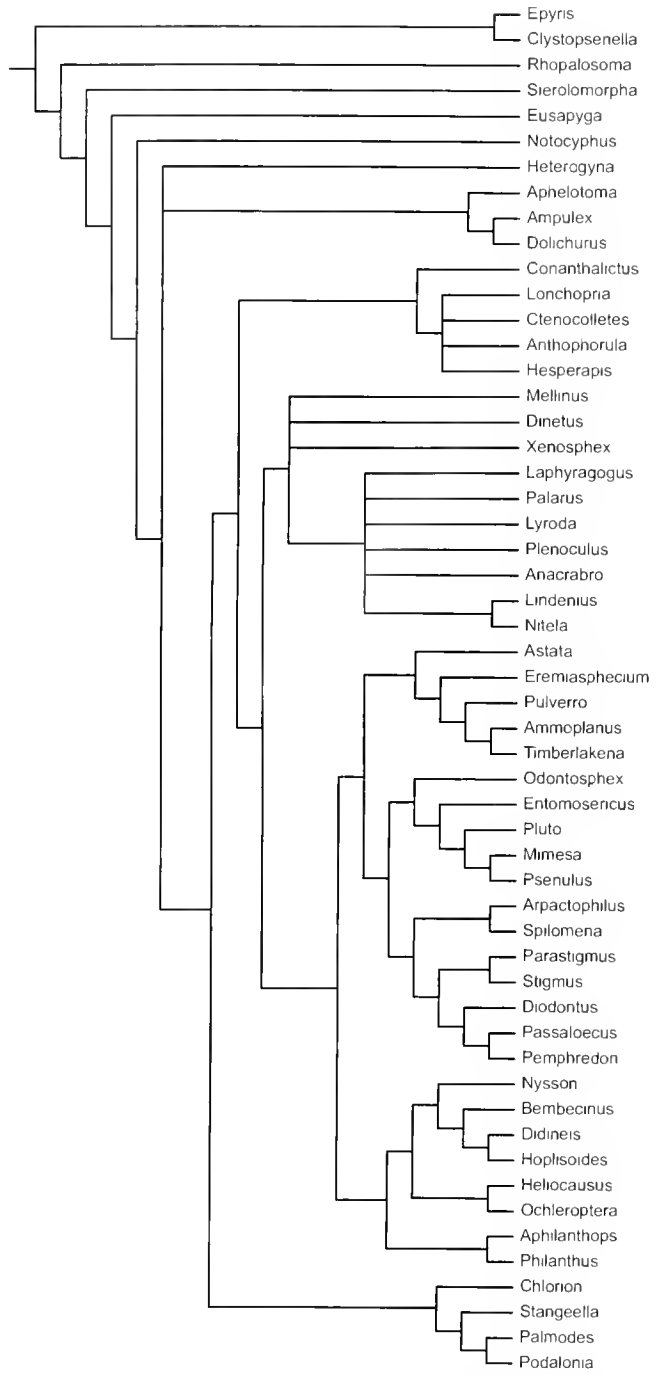


Fig. 3. Strict consensus tree of the four most fit trees produced under implied weighting (complete data matrix).

APOIDEA AND ITS BASAL CLADES

The monophyly of the Apoidea, under its present composition, was already demonstrated by Brothers and Car-

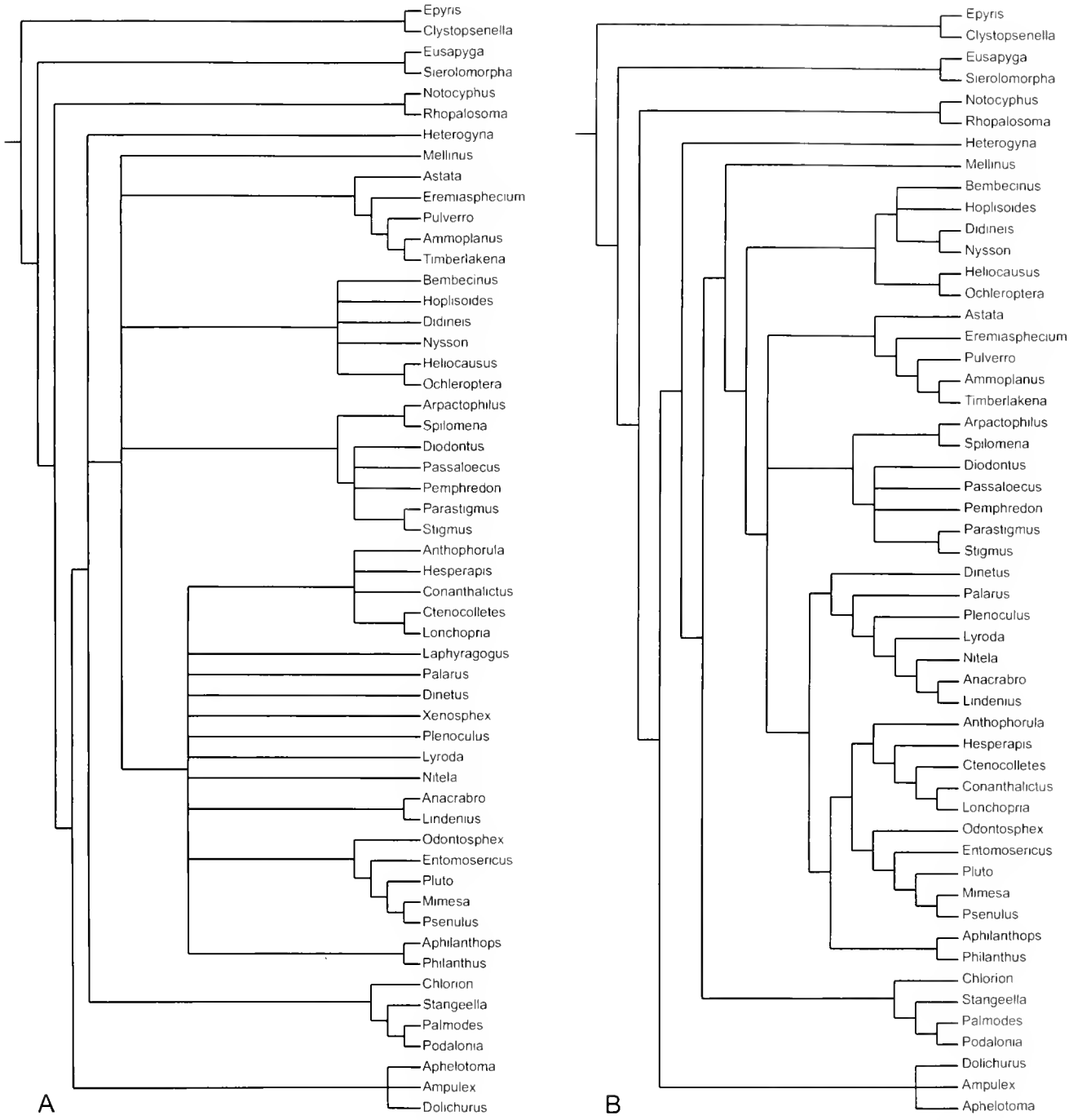


Fig. 4. A.—Strict consensus tree of the 55 most parsimonious trees produced under equal weighting (complete data matrix). B.—Strict consensus tree of the eight most parsimonious trees produced under equal weighting (partial data matrix).

penter (1993). In the present work, seven unambiguous changes support the monophyly of the Apoidea (Branch 1, Fig. 1):

(1) pronotum with posterolateral angle reduced above spiracular lobe (37-1);
(2) ventral angle of pronotum considerably produced mesad (38-1);
(3) pronotum with a pair of lateral, oblique ridges (40-1);
(4) prepectus immovably fused to mesepisternum, suture between them completely obliterated (57-2);
(5) interfurcal muscle absent (62-1);
(6) metapostnotum expanded posteromesally to form "propodeal triangle" (101-1);
(7) larval food relocated (138-1).

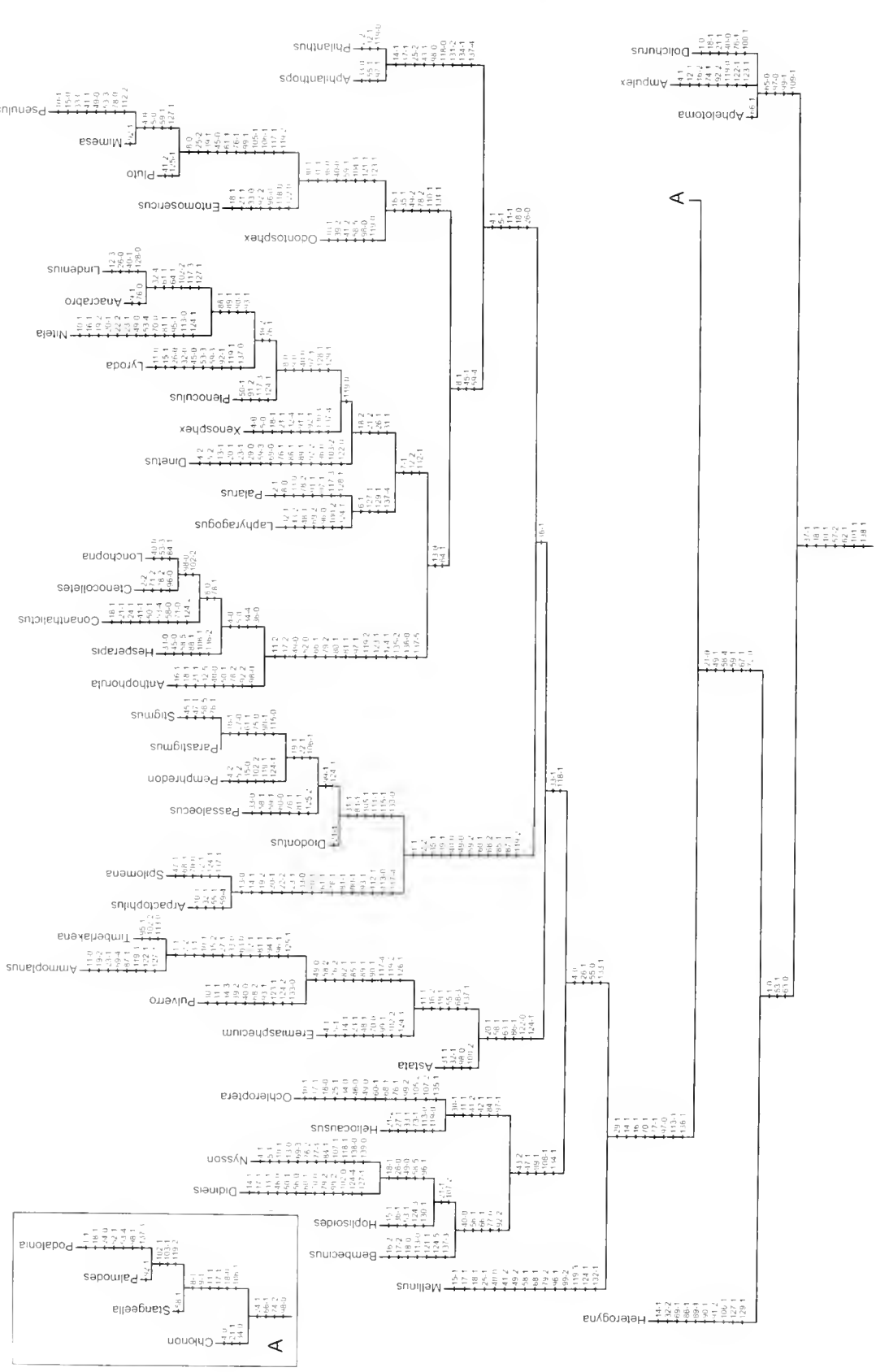


Fig. 5A One of the 45 most parsimonious trees (equal weighting-1, tree 40, length of 880 steps) produced under equal weighting (complete data matrix). Only unambiguous changes and the ingroup taxa are depicted.

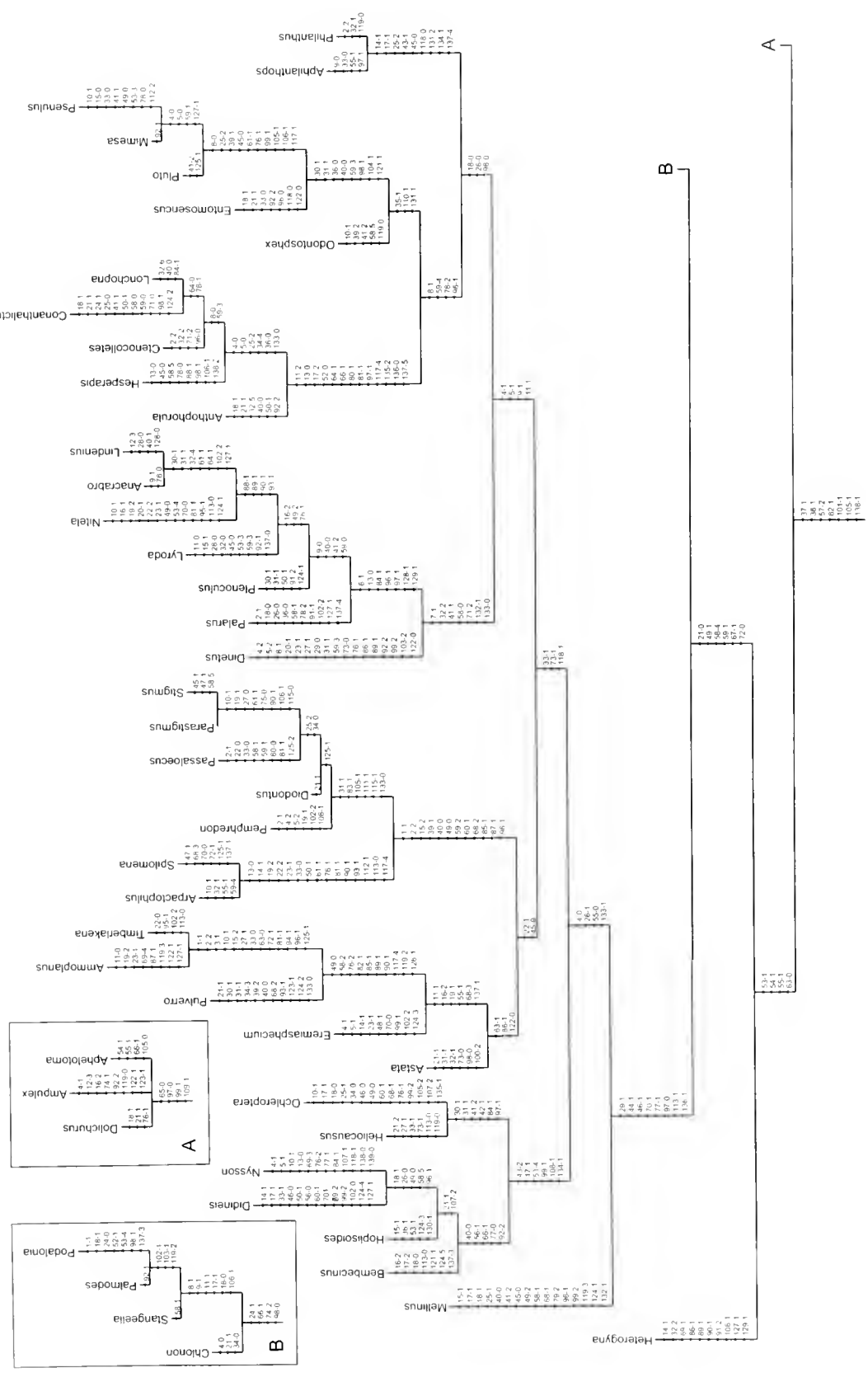


Fig. 5B. One of the eight most parsimonious trees (equal weighting-2, tree 4, length of 849 steps) produced under equal weighting (partial data matrix). Only unambiguous changes and the ingroup taxa are depicted.

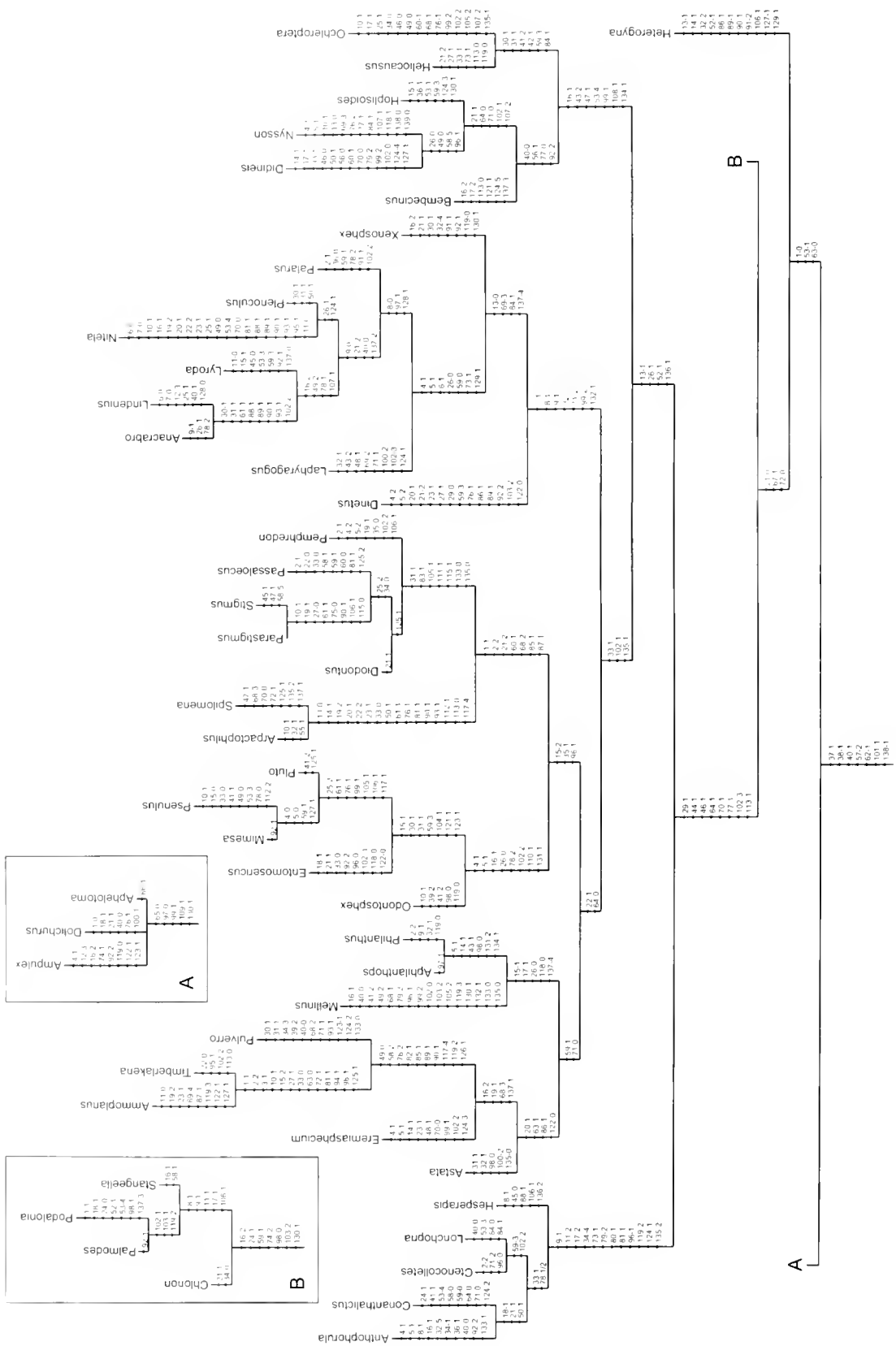


Fig. 6. Tree produced under successive weighting (length of 887 steps; complete data matrix). Only unambiguous changes and the ingroup taxa are depicted.

Table 4. Final weights for characters after implied (iw) and successive weighting analyses (sw) and their approximate classification regarding their qualitative or quantitative nature (N).

Character	iw1 tree 1	iw1 tree 4	iw2 tree	sw1 tree	sw2 tree	N
1	3.3	3.7	3.3	2	2	Qt[1]
2	3.7	3.7	3.7	3	3	CC[2]
3	10.0	10.0	10.0	10	10	Ql
4	2.0	2.0	2.1	1	2	Ql
5	2.7	2.7	2.7	2	2	Ql
6	7.5	10.0	10.0	3	3	Ql
7	7.5	7.5	7.5	3	3	Ql
8	3.3	3.3	3.7	1	2	Qt
9	2.3	2.3	2.3	1	1	Qt
10	3.0	3.0	3.0	1	1	Ql
11	2.5	2.3	2.5	2	2	Qt
12	2.3	2.3	2.3	2	2	Qt
13	4.2	3.7	4.2	2	2	Ql
14	4.2	4.2	4.2	2	2	Ql
15	3.0	3.0	3.0	3	2	Qt
16	2.0	1.8	2.0	2	2	Qt
17	3.7	3.7	3.7	3	3	Ql
18	1.4	1.3	1.5	1	1	Qt
19	3.7	3.7	3.7	3	3	Qt
20	4.2	4.2	4.2	2	2	Qt
21	1.4	1.2	1.4	1	1	Qt
22	5.0	5.0	5.0	4	4	Qt
23	3.7	3.7	3.7	2	2	Qt
24	3.3	3.3	3.7	1	2	Qt
25	3.0	3.0	2.7	2	2	Qt
26	2.5	2.5	2.7	1	1	Am[4]
27	4.2	4.2	4.2	2	2	Ql
28	10.0	10.0	10.0	10	10	Ql
29	5.0	5.0	5.0	3	3	Qt
30	3.7	3.3	3.7	2	2	Qt
31	2.7	2.7	2.7	1	1	Qt
32	1.5	1.4	1.5	3	3	CC
33	1.7	1.7	1.8	1	1	Ql
34	2.5	2.5	2.5	3	4	CC
35	7.5	7.5	7.5	5	3	Ql
36	2.7	2.5	2.5	1	1	Ql
37	10.0	10.0	10.0	10	10	Ql
38	10.0	10.0	10.0	10	10	CC
39	4.2	4.2	4.2	3	3	Ql
40	2.3	2.1	2.3	1	1	Ql
41	3.0	3.0	3.3	2	3	CC
42	10.0	10.0	10.0	10	10	Ql
43	7.5	7.5	10.0	7	10	CC
44	7.5	7.5	7.5	5	5	CC
45	2.1	2.1	2.1	1	1	Ql
46	4.2	4.2	4.2	3	3	Ql
47	6.0	6.0	6.0	3	3	Ql
48	7.5	7.5	—[3]	5	10	Qt
49	2.1	2.0	2.0	2	2	CC
50	3.3	3.3	3.3	3	3	Qt
51	10.0	10.0	10.0	10	10	Qt
52	5.0	5.0	5.0	3	2	Ql
53	1.8	1.8	1.8	2	2	CC
54	7.5	7.5	7.5	3	3	Ql
55	3.0	3.0	3.0	1	1	Ql
56	7.5	7.5	7.5	5	5	Ql
57	10.0	10.0	10.0	7	7	CC
58	2.1	2.1	2.1	3	3	CC
59	1.7	1.7	1.8	3	3	CC
60	5.0	5.0	5.0	3	3	Ql
61	3.0	2.7	3.0	1	1	Ql
62	10.0	10.0	10.0	10	10	Ql
63	5.0	6.0	5.0	3	3	Ql
64	3.3	3.7	3.3	1	1	Am
65	7.5	7.5	7.5	5	5	Ql
66	5.0	5.0	5.0	3	3	Ql
67	10.0	10.0	10.0	10	10	CC
68	5.0	5.0	5.0	5	5	CC
69	2.7	2.5	3.0	3	4	CC
70	4.2	4.2	4.2	2	2	Ql
71	2.7	3.0	2.7	2	2	CC
72	4.2	4.2	4.2	2	2	Ql
73	3.7	4.2	4.2	2	3	Ql
74	7.5	7.5	7.5	7	7	Ql
75	5.0	5.0	5.0	3	3	CC
76	2.1	2.1	2.0	2	2	CC
77	7.5	7.5	7.5	3	3	Ql
78	2.7	3.0	2.7	3	3	CC
79	5.0	5.0	5.0	4	4	Ql
80	10.0	10.0	10.0	10	10	Ql
81	3.3	3.3	3.3	1	1	Ql
82	10.0	10.0	10.0	10	10	Ql
83	10.0	10.0	10.0	10	10	CC
84	4.2	3.7	4.2	2	2	Qt
85	6.0	6.0	6.0	3	3	Qt
86	6.0	6.0	6.0	3	3	Qt
87	5.0	5.0	5.0	3	3	Ql
88	6.0	5.0	5.0	3	3	Ql
89	4.2	3.7	3.3	1	2	Ql
90	3.7	3.3	3.0	1	1	Ql
91	3.3	3.3	3.7	3	3	CC
92	2.3	2.3	2.5	2	2	Qt
93	5.0	3.7	4.2	2	2	Qt
94	10.0	10.0	10.0	10	10	CC
95	6.0	6.0	6.0	3	3	Ql
96	2.3	2.3	2.5	1	1	Ql
97	2.5	2.3	2.5	1	1	Qt
98	3.3	3.3	3.3	1	1	Ql
99	1.7	2.0	1.8	1	1	Qt
100	3.7	3.3	5.0	3	3	Qt
101	10.0	10.0	10.0	10	10	Ql
102	1.5	1.6	1.6	2	2	CC
103	6.0	7.5	7.5	5	5	CC
104	10.0	10.0	10.0	10	10	Ql
105	3.7	3.7	3.7	4	4	Ql
106	3.3	3.3	3.3	1	1	Ql
107	3.7	3.7	3.7	4	3	Ql
108	7.5	7.5	7.5	5	5	Ql
109	10.0	10.0	10.0	10	10	CC
110	10.0	10.0	10.0	10	10	Ql
111	7.5	7.5	7.5	5	5	Ql
112	10.0	10.0	10.0	10	10	Ql
113	3.7	3.7	3.7	2	2	Ql
114	7.5	7.5	7.5	5	5	Qt
115	7.5	7.5	7.5	6	6	Ql
116	10.0	10.0	10.0	10	10	Ql
117	2.5	2.5	2.5	3	3	CC
118	2.7	2.7	2.7	1	1	Ql
119	1.7	1.5	1.7	2	2	CC
120	10.0	10.0	10.0	10	10	Ql
121	7.5	7.5	7.5	5	5	Ql
122	2.5	2.5	2.5	1	1	Ql
123	2.7	2.7	2.7	1	1	Ql
124	1.6	1.6	1.7	3	3	Qt

Table 4 continued

Character	iw1 tree 1	iw1 tree 4	iw2 tree	sw1 tree	sw2 tree	N
125	4.2	4.2	4.2	4	4	Ql
126	10.0	10.0	10.0	10	10	Ql
127	2.5	2.7	2.7	1	1	Qt
128	7.5	7.5	10.0	5	5	CC
129	6.0	6.0	6.0	3	3	Ql
130	3.7	3.7	4.2	2	2	Ql
131	7.5	7.5	7.5	7	7	Ql
132	10.0	10.0	10.0	5	5	Ql
133	3.7	3.7	3.7	1	1	Qt
134	10.0	10.0	10.0	5	5	Am
135	2.5	2.5	2.5	2	2	Qt
136	7.5	7.5	7.5	7	5	Ql
137	3.0	2.7	3.3	5	5	Ql
138	7.5	7.5	7.5	3	3	Ql
139	7.5	7.5	7.5	3	3	Ql

[1]Quantitative; [2]Complex; [3]Qualitative; [4]Ambiguous; *Character uninformative.

Brothers and Carpenter's (1993) study was not intended to resolve the relationships among the major lineages of Apoidea, but they did analyze and discuss the relations among three major groups: Heterogynaidae, "sphecids," and "apids." Their "sphecids" were composed of taxa here placed in Ampulicidae, Sphecidae (sensu stricto) and Crabronidae, and their "apids" included representatives of the major lineages of bees [Apidae (sensu lato)]. Listing of the exemplar taxa can be found in Brothers (1975). Some of their analyses have Heterogynaidae as the basal lineage of Apoidea, whereas in others, the "apids" are at the base. These authors suggest that placement of Hetero-gynaidae as the basal lineage should be preferred because this is the result obtained when family groundplans are analyzed, and also because *Heterogyna* assumes a more basal position than the bees in Alexander's (1992a) study. In this latter study, the analysis including *Heterogyna* resulted in Sphecidae (sensu stricto) as sister group of Ampulicidae, and both taxa forming the basal clade of Apoidea; *Heterogyna* is at the base of a large clade containing the remaining apoids [see Fig. 10 of Alexander (1992a)].

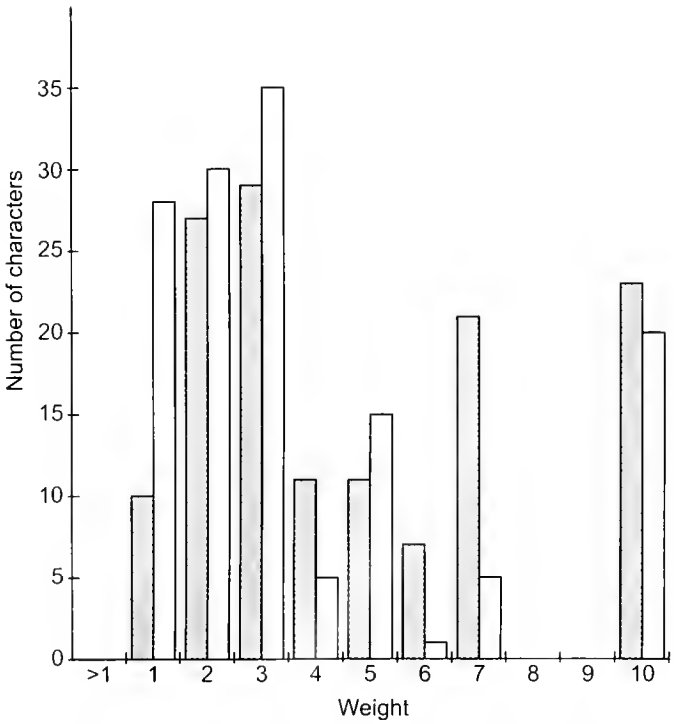


Fig. 7. Frequency distributions for the character weights determined by implied weighting for implied weighting-1 tree 1 (gray bars) and by successive weighting for the successive weighting-1 tree (open bars). See Table 4 for individual character values.

Brothers and Carpenter's (1993) preferred cladogram (their Fig. 11) indicates the following synapormophies for the Apoidea excluding Heterogynaidae, i.e. for a putative clade formed by Ampulicidae, Sphecidae s.str., Apidae s.l. and Crabronidae (numbers in square brackets refer to their character numbering; see their Appendix VI):

(1) meso- and metatibial spurs dorsally flattened and elongate with few or no teeth on margins [126-2];

(2) prey relocated, no nest construction (or nest constructed but not closed, or pre-existing cavity closed off) [180-1];

Table 5. Total fitness, length and statistics for the trees produced by the three parsimony methods. Set 1 refers to the analyses involving all 54 exemplar taxa, while Set 2 refers to the analyses in which *Laphyragogus* and *Xenosphex* were excluded. Number of resulting trees indicated in parentheses.

	Implied weighting		Equal weighting		Successive weighting	
	Set 1 (4)	Set 2 (1)	Set 1 (55)	Set 2 (8)	Set 1 (1)	Set 2 (1)
Total Fitness	711.0	714.3	695.5–697.0	701.4–702.1	700.4	702.1
Total Length	906–920	889	880	849	887	849
Consistency Index	0.23–0.24	0.24	0.25	0.25	0.24	0.25
Rescaled CI	0.13–0.14	0.14	0.15	0.15	0.14	0.15
Retention Index	0.57–0.58	0.57	0.59	0.60	0.59	0.60

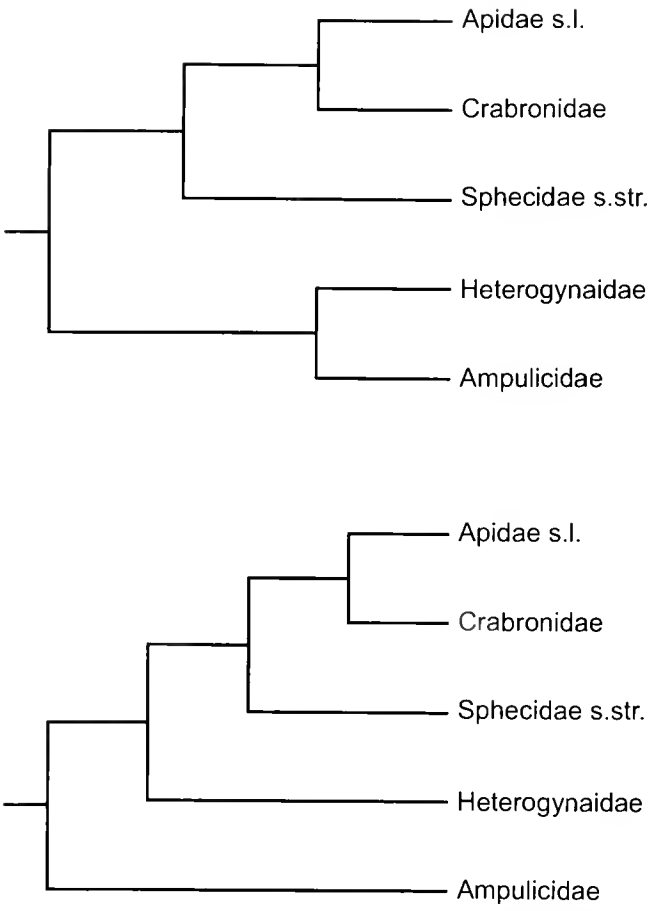


Fig. 8. Cladograms summarizing the relationships among the Apoidea clades given family status here. See Fig. 1 for component taxa. Ampulicidae corresponds to branch 4; Heterogynaidae, branch 5; Sphecidae (sensu stricto), branch 6; Crabronidae, branch 8; and Apidae (sensu lato), branch 9 in Fig. 1.

(3) mesocoxa subdivided by a broad sulcus into large basicoxite and disticoxite and mesocoxal cavities large and approximated or narrowly separated medially [193-0].

The 1st and 3rd characters above are not valid because Ampulicidae has basically the same morphology as *Heterogyna*. The second synapomorphy depends on *Heterogyna* having a parasitoid life style, with no relocation of prey; however, nothing is known of its biology. Brothers and Carpenter (1993) have suggested that because of their brachypterous condition, females in this group are unlikely to move their prey from where it is captured and paralyzed. However, considering that Ampulicidae relocate their prey on foot, instead of carrying it on flight as most of the remaining apoids do, it is possible then that *Heterogyna* behaves in the same way. Also, Day (1984) speculated that the modifications of the female's tergum VI and sting gonocoxites could be adaptations for prey transport.

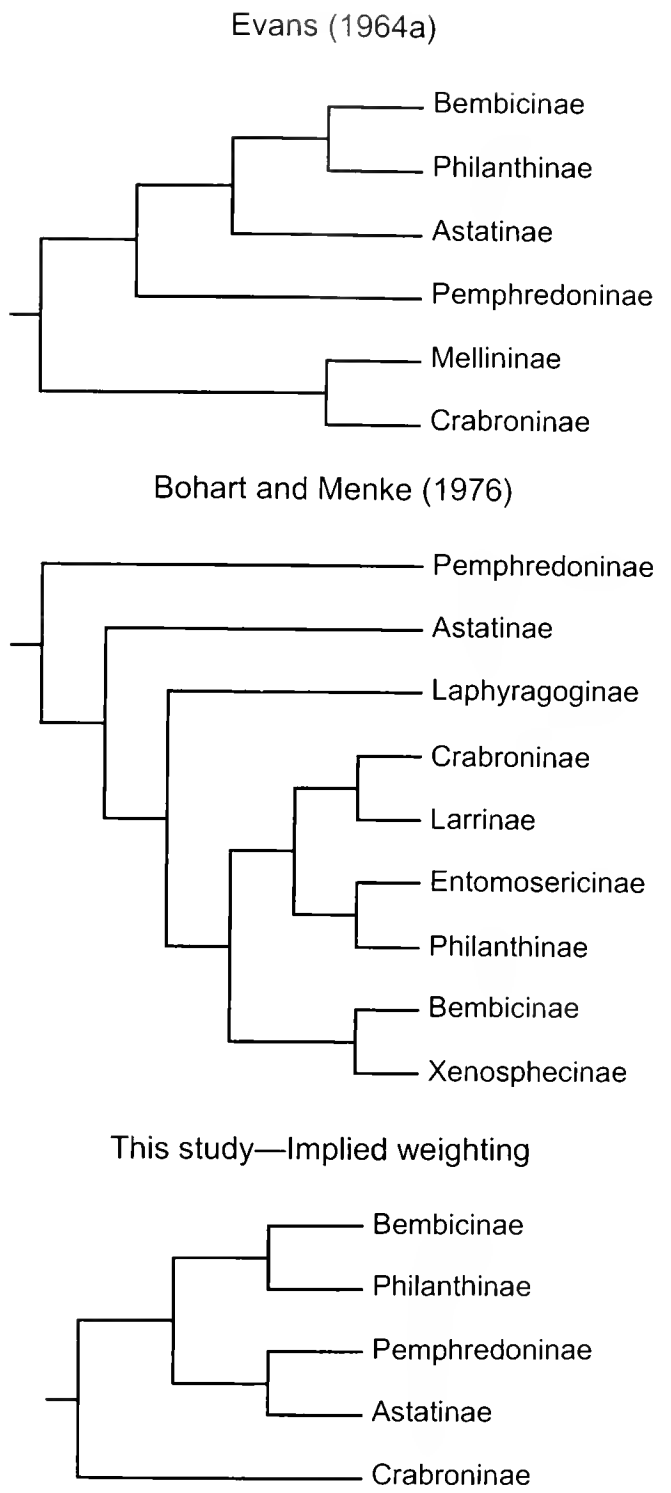


Fig. 9. Relationships among the subfamilies of Crabronidae obtained under implied weighting. Cladograms presented by previous authors are also shown for comparison.

In contrast to Brothers and Carpenter's study, the present analyses did not support placement of Heterogynaidae as the most basal clade in Apoidea, its position varying depending on the analyses. In the implied weighting cladograms, it comes out either as the sister group of Ampulicidae or as the sister group of the remaining Apoidea, excluding Ampulicidae.

Unambiguous changes supporting placement of Heterogynaidae as sister group to Ampulicidae are (branch 2, Fig. 1):

(1) distance between antennal sockets and clypeus nil (18-2 and 21-2);
(2) presence of an omaular carina (61-1);
(3) forewing M+CuA (distal to cu-a) longer than cu-a (93-1);
(4) jugal lobe absent (100-0).

Except perhaps for presence of an omaular carina, the characters supporting this relationship are relatively weak. The fourth character, jugal lobe absent, probably does not represent a synapomorphy for this putative clade, because presence of a lobe in *Dolichurus* (as well as in *Trirogma*) in the Ampulicidae can hardly be considered a true reversal.

The alternative position of Heterogynaidae as sister group of [Sphecidae (sensu stricto) + [Apidae (sensu lato) + Crabronidae]] is supported by (based on Fig. 2):

(1) labrum at least one and a half times wider than long (1-0);
(2) arms of the meso- and metathoracic furca immovably fused (63-0);
(3) hindwing clavus indicated by moderate incision (99-0).

Likewise, the evidence for this placement of *Heterogyna* is rather weak, except for Character (2) above. Even in this case, however, the fusion of the furcal arms in *Heterogyna* and in Sphecidae (sensu stricto) + [Apidae (sensu lato) + Crabronidae] might be a parallelism, because loss of the interfurcal muscle (Character 62-1) is already part of Apoidea groundplan and the reduced size, as well as female brachyptery, in *Heterogyna* could have favored this fusion.

HETEROGYNAIDAE

This family contains only seven described species, all placed here in the genus *Heterogyna* (see below). Before Day (1984), only the type species, *H. protea* Nagy from the Greek island of Rhodes, was known. Day (1984) described four new species from Africa and provided a key for identifying all five species. He also described for the first time the putative females of this genus. The type specimen of *H. protea* was redescribed by Day (1985). Argaman (1986) described a new species (based on a female specimen) from Israel and also provided a key for all species known at that time. More recently a new species from Turkmenia was described by Antropov and Gorbatovskii (1992). Nothing is known of the biology of these wasps. Large numbers of males have been taken with Malaise traps and one female specimen was collected in a yellow pan trap (Day 1984).

Argaman (1986) proposed a new genus, *Daycatinca* (type-species: *Heterogyna fautsilotra*), for the three Madagascan species. Antropov and Gorbatovsky (1992), apparently unaware of Argaman's paper, proposed the subgenus *Daya* (type-species: *Heterogyna madecassa*) for the four African species. These two genus-group names are treated here as synonyms of *Heterogyna*, especially because recognition of more than one generic name for such a small group seems completely unnecessary and also because proposal of these names was not based on phylogenetic studies. Recognition of *Daycatinca* or *Daya* would probably make *Heterogyna* (sensu stricto) paraphyletic or vice-versa.

AMPULICIDAE

This group (branch 4, Fig. 1) has usually been treated as a subfamily of "sphecid" wasps (e.g., Leclercq 1954, Evans 1964a, Bohart and Menke 1976) or sometimes as a separate family of "sphecoid" wasps (e.g., Evans 1959a). In Alexander's (1992a) study, the two tribes of Bohart and Menke's classification, Dolichurini and Ampulicini, were consistently grouped together, forming a monophyletic group. He presented the following putative synapomorphies for them (see his Table 7):

(1) pitted transverse basal sulcus on scutellum;
(2) subalar line a very prominent carina or flange;
(3) posterior margin of 'metasternum' distinctly bilobed, lobes diverging apically;
(4) metasomal sternum 2 swollen at base, with a transverse sulcus and/or carina;
(5) male with fewer than seven visible metasomal segments.

Characters (2), (3) and (5) above do not seem to be valid synapomorphies for Ampulicidae. In Sphecidae (sensu stricto), the subalar line is also a prominent flange (the outer margin of the tegula rests on it when the wings are in repose); a weaker or vestigial carina can also be seen in some Crabronidae. Also, the morphology of the ventral portion of the metepisternum posteriorly (Character 3 above) in Ampulicidae does not seem to be particularly different from that of Sphecidae (sensu stricto), of some Crabronidae, or even of *Heterogyna*. The distinct metepisternal morphology of *Ampulex* is not found in the other Ampulicidae examined. Regarding the 5th character, the condition described above seems to be restricted to males of *Ampulex*, because males of *Dolichurus* and *Aphelotoma* have seven visible metasomal segments; nevertheless, enlargement of

the first three metasomal segments and a distinct reduction of the remaining distal segments are characteristic of Ampulicidae.

In the present work, Ampulicidae always came out as a monophyletic group; it is supported by the following unambiguous changes (based on optimizations shown on Fig. 1):

(1) apophyseal arms of prothoracic endosternum separate (45-0);
(2) notauli indicated externally by a sulcus (53-0);
(3) pseudophragma of second phragma absent (65-0);
(4) hindwing M diverging from CuA before or at cu-a (97-0);
(5) second sternum strongly convex posteromedially (109-1);
(6) apicoventral edge of gonapophyses of male genitalia with short teeth (130-1).

The assignment of this condition for the notauli (Character 2 above) as a synapomorphy for Ampulicidae is probably an artifact of having Pompilidae (represented by *Notocyphus*) coming out as sister group of Apoidea in the implied weighting analysis. Notaulus indicated externally by a sulcus is plesiomorphic for apocritans; among the outgroup used here, this state is present in Bethylidae, Scolebythidae, Sierolomorphidae and Sapygidae. The condition in Ampulicidae is certainly not a reversal. The sixth character is also found in Sphecidae (sensu stricto) and a few Crabronidae (e.g., *Mellinus* and *Xenosphex*). Its optimization on the tree implies that this condition arose several times independently; however, its presence in these basal lineages suggests that it might be part of the apoid groundplan, having been lost in Heterogynaidae, Apidae (sensu lato) and in most Crabronidae.

In Bohart and Menke's (1976) tribal classification for their Ampulicinae, *Ampulex* is placed in its own tribe, whereas the remaining genera are placed together in a second tribe, the Dolichurini. The results obtained here in the implied weighting analyses contradict this classification, because *Ampulex* and *Dolichurus* form consistently a monophyletic clade. This relationship is supported by a relatively strong synapomorphy, supra-alar carina not meeting the tegular ridge (54-0). In the remaining Apoidea, including *Aphelotoma*, the supra-alar carina is fused to the anterior segment of the tegular ridge, a condition also present in Pompilidae. It seems improbable that the peculiar mesoscutal morphology seen in *Ampulex* and *Dolichurus* (as well as in *Trirogma* and *Paradolichurus*) arose twice independently.

SPHECIDAE (SENSU STRICTO) + [APIDAE (SENSU LATO) + CRABRONIDAE]

In the present study, the monophyly of this lineage (branch 3, Fig. 1) is strongly supported by the following synapomorphies:

(1) mesepisternal ridge present (58-4);
(2) medial portion of mesometepisternal suture mostly obliterated (67-1);
(3) basal part of midcoxa continuous with rest of coxa, not pedunculate (72-0);
(4) females construct a nest before obtaining larval food (139-1).

Presence of a mesepisternal sulcus (see Character 59) should also be considered a synapomorphy for this clade. As this character was divided into several states, there is no unambiguous optimization for the states used at this branch. If the character had been coded only as either absent or present, then presence of a sulcus would certainly be shown as an unambiguous change for this branch. Someone could argue that the sulcus is not independent from the internal ridge and therefore should not be used as a separate character. The only reason why this was done is because the changes in these two characters are not perfectly correlated (Table 3). Bohart and Menke (1976) considered the presence of a mesepisternal sulcus as part of the groundplan of their Sphecidae, because they assumed that a remnant of this sulcus was sometimes present in Ampulicidae. However, the small segment of a ventral sulcus present anteriorly in the mesepisternum of most Ampulicidae could be the anterior remnant of a long hypersternaulus. Such a long and continuous hypersternaulus can be seen in *Aphelotoma*.

Johnson (1988) considered a midcoxa broadly connected and open to the mesothorax as part of the groundplan for the Aculeata, but as demonstrated by Sharkey and Wahl (1992) and Brothers and Carpenter (1993), the ancestral condition for the aculeates is a midcoxa with a narrow, pedunculate basal portion, similar to that found in *Heterogyna* and Ampulicidae.

A sister-group relationship between Sphecidae (sensu stricto) and Ampulicidae has been suggested by several authors (e.g., Lomholdt 1982, Alexander 1992a, Ohl 1996a). Two of the three supposed synapomorphies presented by Lomholdt (1982) are simply plesiomorphies, as correctly interpreted by Ohl (1996a). The third one, namely presence of a "propodeal sclerite", is not valid because a sclerotized bridge closing the hindcoxal sockets is not present in the ampulicids *Aphelotoma* and *Dolichurus*, and also the condition in the others (*Ampulex* and *Trirogma*) does not seem to be homologous to that of Sphecidae (sensu stricto) (see Character 74). Of the four supposed synapomorphies presented by Alexander (1992a), only two were considered possible synapomorphies by Ohl (1996a). One of them, female metasomal sternum VI forming an exposed tapering tube (see Character 114), cannot be considered a synapomorphy because a similar condition is found in the outgroup. The second character, "penis valves" with small

teeth on ventral edges (Character 130-1), was optimized here as having arisen independently in Sphecidae (sensu stricto) and Ampulicidae. As was suggested above, this condition might be part of the groundplan for the Apoidea.

SPHECIDAE (SENSU STRICTO)

The name Sphecidae is used here in its narrow sense, corresponding to the subfamily Sphecinae of Bohart and Menke's (1976) classification. As explained in Material and Methods, no particular effort was made to include characters that potentially could support the monophyly of this group. Despite that, Sphecidae came out monophyletic in all analyses, being supported by several unambiguous changes (see branch 6, Fig. 1). Alexander (1992a) and Ohl (1996a) list several other putative synapomorphies for Sphecidae (sensu stricto). Ohl's study, however, is compromised by his assumption of a sister-group relationship between Sphecidae (sensu stricto) and Ampulicidae. Judging by his list of exemplar taxa, no representatives from Crabronidae or Apidae (sensu lato) were included in his analysis. Therefore, some of his supposed synapomorphies for Sphecidae (sensu stricto) could be plesiomorphies shared with Crabronidae + Apidae (sensu lato).

The phylogenetic relationships among the major lineages of Sphecidae (sensu stricto) were evaluated recently by Ohl (1996a). The results of his studies basically confirm the arrangement proposed by Bohart and Menke (1976), with the exception that the genus *Stangeella* Menke is removed from Sceliphrini (= their Sceliphronini) and it is placed as the sister group of the clade Sphecini + Ammophilini. In the present study, the relationships among the four exemplar genera of Sphecidae (sensu stricto) are congruent with Ohl's results. Most of the characters used by Ohl (1996a) are from the male genitalia and it is possible that detailed investigation of additional character systems could produce alternative phylogenetic arrangements. Another shortcoming of Ohl's study is that he did not submit his primary homology statements to a congruence test (e.g., parsimony) and therefore the putative synapomorphies presented by him are not derived from secondary homology statements [sensu Pinna (1991)]. The relationships among the four genera of Sceliphrini restricted to the Neotropical region were studied by Ohl (1996b). His results also confirm Bohart and Menke's arrangement for these four genera.

APIDAE (SENSU LATO) + CRABRONIDAE

Lomholdt (1982) was the first one to suggest a sister-group relationship between Apidae (sensu lato) and Crabronidae (his Larridae). Of the two putative synapomorphies he presented in support of this hypothesis, only one, a shortened propodeum with an elongated metapostnotum, seems tenable. This modification of the metapostnotum and propodeum is treated here under Character 102. In the present analysis, however, this character does not support the monophyly of Apidae (sensu lato) + Crabronidae (see branch 7, Fig. 1) because *Mellinus*, which occupies a relatively basal position in the Crabronidae, has a condition similar to that of the basal apoids and because *Palmodes* and *Podalonia* [Sphecidae (sensu stricto)] have a condition similar to that of some crabronids. In any case, this character would require further study to have its significance better evaluated.

The second synapomorphy used by Lomholdt (1982), i.e. subbasal claw tooth absent, is interpreted differently here. The subbasal tooth present in most Sphecidae (sensu stricto) is considered only a displaced, but still homologous, subapical tooth (see Character 52). A subapical tooth is part of the aculeate groundplan and its absence in *Heterogyna* represents an autapomorphy (Brothers and Carpenter 1993: see also branch 5 of Fig. 1); it is present in Ampulicidae and Apidae (sensu lato).

A close relationship between Apidae (sensu lato) and Crabronidae was also found by Alexander (1992a). Indeed, Crabronidae, as defined here, always comes out in Alexander's analyses as a paraphyletic assemblage in relation to Apidae (sensu lato) (his Apiformes) and also sometimes in relation to Ampulicidae. Taking into consideration only Alexander's analyses in which Crabronidae is not paraphyletic to Ampulicidae and also only those in which character polarization was determined by the parsimony analyses (his analyses 5A, 5B, 6B, 7A, 7B, 9B, 10), the following characters support, in at least one of these seven analyses, the monophyly of a group including all the members of Crabronidae and Apidae (sensu lato) (numbers from Alexander's list of characters): 17-1, 19-1, 25-0, 27-0, 32-1, 33-1, 38-1, 41-1, 47-1, 51-0, 67-2, 68-1, 80-1, 82-1, 83-1, 84-1, 85-1, 88-1. Characters 17, 27, 33, 68, 80, 82, 83 and 85 were not used in the present work and will not be discussed.

Alexander's Characters 32-1 [Character 70-1 here] and 51-0 [113-1] were also found here to support the monophyly of Crabronidae + Apidae (sensu lato) (see list of synapomorphies below); 25-0 [58/59] and 41-1 [49-1; ambiguous in some optimizations], however, were found to support the monophyly of Sphecidae (sensu stricto) + [Apidae (sensu lato) + Crabronidae]; 38-1 [52-1] and 88-1 [136-1] were found to support the monophyly of Crabronidae (see below); 19-1 [53-1] supports a larger group, including part of the outgroup or, in some cases, a clade containing all Apoidea excluding Ampulicidae; 84-1 [133-1] was found to support different clades within Crabronidae, depending on the analyses; 67-2 [98-1] is the condition in all outgroup taxa used, as well as in Ampulicidae and *Heterogyna*, and therefore presence of the

vein 2A was optimized as arising *de novo* in the ingroup taxa which have it; 47-1 [108-1] was treated here differently.

In all of my analyses, the bees [Apidae (sensu lato)] also consistently grouped with a large assemblage formed by all sphecid subfamilies of Bohart and Menke's classification, with the exclusion of their Ampulicinae and Sphecinae, i.e., the Crabronidae. This relationship was strongly supported by several characters, including the following unambiguous changes (based on optimizations shown on Fig. 1):

(1) female antennae shortened (29-1);
(2) medial portion of prothoracic basisternum declivous in relation to anterior portion (sometimes only slightly), rounded or weakly pointed posteriorly (44-1);
(3) base of apophyseal arms of prothoracic endosternum (internally) connected by two continuous, divergent plates originating at the base of furcasternum (46-1);
(4) mesocoxal carina present (70-1);
(5) dorsal lobe on inner side of hindcoxal apex large, usually forming a spatulate process, ventral lobe small or absent (77-1);
(6) metasomal tergum VI of female with a pygidial plate (113-1);
(7) metasomal sternum VI of female not forming an exposed tapering tube (114-0);
(8) male cerci absent (122-1).

Except for absence of male cerci, all the unambiguous changes listed above seem to represent valid synapomorphies for Apidae (sensu lato) + Crabronidae. Males in several taxa of Crabronidae possess cerci and as discussed below (see section on the Astatinae), presence of cerci in these crabronids should not be treated as a reversal, but only retention of a plesiomorphic condition. Changes for character 122 should have been optimized as irrereversible.

Contrary to Alexander's (1992a) results discussed above, most of my analyses supported a monophyletic Crabronidae (branch 8 in Fig. 1). Four unambiguous changes were found to support this clade:

(1) posterior wall of pharynx forming two bulging sacs (13-1);
(2) claws simple, without subapical or subbasal teeth (52-1);
(3) hindwing M diverging from CuA before or at cu-a (97-0);
(4) larval spinneret with paired openings, each at the end of a projection (136-1).

Except for a somewhat similar condition found in *Heterogyna*, the first character is unique to this clade; these pharyngeal expansions are well developed in several crabronids, for example *Odontosphex*, *Astata*, *Mellinus* and the Philanthinae, but they have been lost at least three times (see branches 12 and 24 and *Nysson* in the Bembicinae). These paired sacs have not been previously described and their function is unknown. Among the Apoidea, a larval spinneret with paired openings is also unique to this clade. This is the only synapomorphy provided by Lomholdt (1982) to support the monophyly of his Larridae. No case of reversal among the Crabronidae is known for the second or fourth synapomorphies, except for the presence of a small subbasal tooth (or teeth) in the female's claw in some species of Crabroninae [see genera *Liris* and *Kohliella* in Bohart and Menke (1976); in *Liris*, the unique parallel teeth seems to be derived from the parallel carinae on the ventral side of the claws].

Despite this relatively weak support, the recognition of a monophyletic Crabronidae seems well founded. Its supposed paraphyly in relation to Apidae (sensu lato) found in some of my analyses and also by Alexander (1992a) seems spurious. Alexander's results indicated a possible sister-group relationship between Apidae (sensu lato) and the Philanthinae (sensu Alexander, 1992a, b). This relationship was consistently supported by both groups sharing subantennal sutures. However, this similarity is probably superficial because in bees the subantennal suture represents the line of attachment of the dorsal sheet of the anterior tentorial arm to the frons (Roig-Alsina and Michener,1993), whereas in the Philanthinae the sutures have no connection to the tentorium. Also, subantennal sutures similar to those of the Philanthinae are present in some Bembicinae, Crabroninae and some Sphecidae (sensu stricto) (see Character 17). Some of my analyses, based on equal and successive weighting of characters, resulted in a paraphyletic Crabronidae, with bees more closely related to Crabroninae (excluding *Mellinus*; Figs. 4 and 5). Reasons for not favoring the results produced by these two parsimony methods were discussed above.

Biogeographic patterns also contribute to reinforce the hypothesis of a sister-group relationship between Apidae (sensu lato) and Crabronidae. In both these taxa, several lineages usually regarded as older basal clades are restricted to, or exhibit higher diversity, in deserts of the temperate zone [for bees, see Michener (1979); for Crabronidae, one can cite the genera *Odontosphex*, *Entomosericus*, *Dinetus*, *Xenosphex*, *Heliocausus*, *Pseudoscolia* and the Astatinae as a whole]. Such a pattern is not apparent within the Sphecidae (sensu stricto).

Apidae (sensu lato) and Crabronidae could easily be treated under only one name, because the degree of divergence between them seems comparable to that present among the subfamilies of Crabronidae. However, the bees have traditionally been considered distinct from the rest

of the Apoidea and such classification would be considered confusing and probably of little use.

APIDAE (SENSU LATO)

Despite the intentional exclusion of characters known to support the monophyly of bees, except for Character 80 and a few character states unique to bees, this clade was present in the results of all analyses and in all cases, supported by a large number of synapomorphies (branch 9, Fig. 1). These putative synapomorphies are not listed or discussed here; a discussion of the monophyly of bees and a more complete and detailed list of their synapomorphies can be found in Alexander and Michener (1995).

The various lineages of bees have been traditionally classified in several separate taxa accorded family status (e.g., Michener 1944, Roig-Alsina and Michener 1993, Alexander and Michener 1995). Such a classification was justifiable while the bees were considered the sole components of the superfamily Apoidea. However, with the inclusion of other non-bee taxa in the Apoidea and the recognition of only three superfamilies for the aculeate wasps (Brothers 1975), treating the higher groups of bees at family level would leave the whole clade without a formal name and would be inconsistent with the higher-level classification of the other aculeate clades. For these reasons, some authors have adopted a classification in which all bees are treated under one family, the Apidae (e.g., Lomholdt 1982, Gauld and Bolton 1988, Gauld and Hanson 1995, Griswold et al. 1995). The recognition of a monophyletic Crabronidae as the sister group of bees, as proposed here, strongly supports such a classification. The use of Spheciformes (= Sphecidae sensu Bohart and Menke) and Apiformes (bees), informal divisions of the Apoidea proposed by Brothers (1975), should be avoided because Spheciformes, as it has been demonstrated, is paraphyletic in relation to Apiformes.

In the present work, an investigation of the relationships among the higher-level lineages of the Apidae (sensu lato) was avoided. This problem was recently studied by Roig-Alsina and Michener (1993) and Alexander and Michener (1995). Nonetheless, the arrangements found here under implied weighting for the five bee representatives do not contradict the possible arrangements found by Alexander and Michener (1995).

CRABRONIDAE

The family Crabronidae (branch 8, Fig. 1), as defined here, includes all the taxa classified at the subfamily level by Bohart and Menke (1976), with the exception of their Ampulicinae and Sphecinae. Only five crabronid subfamilies are here recognized: Astatinae, Bembicinae, Crabroninae, Pemphredoninae and Philanthinae. This classification is very similar to that proposed by Evans (1964a), based on larval morphological characters. It is worth noting that larvae of some genera of Crabronidae (e.g., *Dinetus*, *Entomosericus*) were only recently described, and larvae are still unknown for others (e.g., *Eremiasphecium*, *Laphyragogus*, *Xenosphex*), and therefore were not included in Evans' studies. Evans' classification also differs from the one proposed here regarding the placement of the genus *Mellinus*: Evans (1964a) recognized a monotypic subfamily for *Mellinus*, the Mellininae; herein, I take a more conservative approach and include *Mellinus* in the Crabroninae. In Evans' phylogeny, Mellininae is the sister group of his Larrinae, an arrangement that corresponds exactly with the one here preferred in which *Mellinus* is the basal clade of the Crabroninae. However, the position of *Mellinus* within the Crabronidae differs considerably depending on the analysis, an indication that additional studies might reveal a different position from the one favored here.

Except perhaps for the Crabroninae, the monophyly of each of the five subfamilies recognized here seems well-supported. In contrast, the relationships among the subfamilies indicated in Figure 1 can be considered very weakly supported. Two of the internal basal branches inside the Crabronidae are each supported by only one unambiguous change. The support for the branch leading to branches 19 + 20 is even more suspicious considering that character 22 was considered inapplicable [i.e. coded (?)] for all the members of the Psenini (branch 22). At this point, the relationships indicated should be taken as very tentative and a perhaps better representation would be to consider the subfamilies forming a polytomy, except perhaps for Bembicinae and Philanthinae. Figure 9 summarizes the relationships among the subfamilies indicated by implied weighting, as well as shows cladograms previously proposed for these groups by Evans (1964a) and Bohart and Menke (1976).

In the following subsections, the monophyly and composition of the five crabronid subfamilies are discussed in detail, particular attention being given to taxa whose placements are in conflict with those proposed by Bohart and Menke (1976). Discussion of the arrangements found here for the more distal taxa within each subfamily is avoided because, in most cases, taxonomic representation is rather inadequate.

Astatinae.—The subfamily Astatinae (branch 20) is defined here to include the tribe Astatini, the genus *Eremiasphecium* and the subtribe Ammoplanina of Bohart and Menke's (1976) classification (each one of these groups is treated here as a tribe, i.e. Astatini, Eremiasphecini and Ammoplanini). The discovery of this clade was somewhat surprising because its members seem superficially distinct

and to a lesser extent because they were placed in totally separate taxa in Bohart and Menke's classification. In their classification, Astatinae contained the tribes Astatini and Dinetini (containing only the genus *Dinetus*), *Eremiasphecium* was part of the Philanthinae and Ammoplanina was part of the Pemphredonini. The monophyly of the Astatinae is supported by the following unambiguous changes:

(1) tentorial pit of female situated above tangent to lower rims of antennal sockets (20-1);
(2) lateral arms of meso- and metathoracic furca weakly fused (63-1);
(3) forewing marginal cell shorter than pterostigma (86-1);
(4) male cerci present (122-0).

Conditions (1) and (3) above are not unique to this clade; among the exemplar taxa, character state 20-1 was also found to be a synapomorphy for the Spilomenina (branch 24) and an autapomorphy for *Nitela* and *Dinetus*, whereas 86-1 is an autapomorphy for *Dinetus*. The 2nd synapormorphy is unique to the Astatinae, although it reverses within the Ammoplanini, probably as a consequence of a reduction in body size; these wasps are among the smallest Apoidea, only 2 to 3 mm in length. The fourth condition above cannot be considered as a valid synapomorphy, because it is highly unlikely that once lost the cerci would be regained. In Hymenoptera, the cerci are quite reduced and in most groups can be considered vestigial. Absence of cerci in females is a synapomorphy for the aculeate Hymenoptera (Brothers and Carpenter 1993), and no case of reversal is known. Given the vestigial condition of the cerci in males of aculeate Hymenoptera, it seems reasonable to assume that their loss is irreversible.

If *Dinetus* had not been included in the analysis, someone looking only at these synapomorphies could run the risk of arguing that this genus is easily shown to be part of the Astatinae, as originally proposed by Bohart and Menke. But the analyses carried out here clearly show that the similarities of *Dinetus* to the Astatinae are the result of convergence.

Astatini (represented by *Astata* in the cladograms) is the sister group to the rest of the Astatinae. The sister-group relationship between Eremiasphecini and Ammoplanini (branch 27) is supported by:

(1) eye-clypeus contact extending for more than one antennal socket diameter (16-2);
(2) epistomal suture, between antennal sockets, situated above median line across antennal sockets (19-1);
(3) setal patch on anterior segment of tegular ridge absent (55-1);
(4) medial flap of mesokatepisternum narrow, interrupted in the middle by a deep cleft, and condyle of mesal midcoxal articulation situated at tip of flap projection and well separated from body's midline (68-3);
(5) use of Thysanoptera as larval food (137-1).

In relation to the fourth synapomorphy, considering that *Pulverro* has a distinct state (68-2) than the one indicated above (68-3), one can suspect that the similar condition in *Eremiasphecium*, *Timberlakena* and *Ammoplanus* could have evolved independently from a condition similar to that of *Pulverro*. These two tribes also share a similar morphology for the medial portion of the metepisternum (Character 69-1) and practically lack the dorsal apical process of the hindcoxa (78-3). However, these similarities were not considered synapomorphies because of their ambiguous status; the conditions for these characters present in *Astata* and in the immediate outgroups prevent the optimization process from reaching any unambiguous statements.

A sister-group relationship between *Eremiasphecium* and the Ammoplanini was recently postulated by Kazenas (1991) when describing his new genus *Taukumia* [subjective junior synonym of *Eremiasphecium*; see Pulawski (1992)], although he assumed that Ammoplanini was part of the Pemphredonini and that *Eremiasphecium* was a member of the Philanthinae; also he does not present any list of characters that would support his hypothesis. Pulawski (1992) revised *Eremiasphecium* and considered a possible relation with Ammoplanini unfounded. The two characters mentioned by him to dismiss this relationship, however, have no bearings to this problem: absence of cerci and the 3rd submarginal cell in Ammoplanini. Presence of cerci would certainly be simply a plesiomorphy (contrary to Pulawski's assumption, males of most genera of Ammoplanini do have cerci) and loss of the 3rd submarginal cell is an autapomorphy of Ammoplanini.

The monophyly of Ammoplanini is supported by numerous unambiguous changes (see branch 28 in Fig. 1). Some of these changes (85-1 and 117-4), as well as some of the changes in the branch leading to *Timberlakena* and *Ammoplanus* (1-1, 2-2, 33-0 and 81-1) also occur as part of the groundplan of the Pemphredonini (branch 21) or only of the Spilomenina (branch 24). The similarities in wing characters, namely increase in pterostigma width (85-1), absence of the veins Cu1 and 2m-cu (90-1) and presence of only two submarginal cells, between Ammoplanini and at least some of Pemphredonini were probably important in Bohart and Menke's decision to maintain these two groups together (absence of Cu1 and 2m-cu occurs in Spilomenina and also in the branch leading to *Parastigmus* + *Stigmus*, but it is not shown because its optimization is ambiguous; I would favor the repeated loss of these two veins, instead of loss in the ancestor of Pemphredonini and then reappearance in the branch leading to *Diodontus*, *Pemphredon*

and *Passaloecus*). As shown by the analysis, these similarities between Ammoplanini and Pemphredonini are the result of convergence, probably in relation to reduction of body size in these lineages. Danforth (1989) showed that small species of Hymenoptera tend to have disproportionately large pterostigmata, but it is worth noting that the Crabroninae apparently does not follow this trend; very small species in this group, like some species of *Belomicrus*, have the pterostigma as reduced as that of its larger relatives. Also, among insects in general, loss of wing veins seems to be strongly correlated with reduction in body size, but this trend has not been properly documented.

Bembicinae.—Bohart and Menke (1976) recognized seven tribes in their subfamily Nyssoninae (= Bembicinae). I included in this study representatives of six of these seven tribes. One of them, Bohart and Menke's Mellinini (containing only *Mellinus*), is considered here the basal clade of the Crabroninae. The other five were found to form a monophyletic group (branch 16), being supported by:

(1) eye-clypeus contact extending for the diameter of one antennal socket or less (16-1);
(2) internal divergent plates of prothoracic endo-sternum partially (dorsally) or completely fused to furcasternum, medial ridge absent at least dorsally (47-1);
(3) omaular carina present (61-1);
(4) hindwing clavus indicated by short incision or only a shallow notch (99-1);
(5) medial longitudinal ridge on base of sternum I present (108-1).

The two main lineages (branches 17 and 18) found here for the six bembicine taxa do not seem to be spurious, as one could suppose because of somewhat different relationships compared to that indicated by the current classifications. The two representatives of Bohart and Menke's Gorytini, *Hoplisoides* and *Ochleroptera*, did not form a monophyletic clade. *Ochleroptera* was found to be most closely related to *Heliocausus* (branch 17), whereas *Hoplisoides* is most closely related to *Didineis*. This is not a surprising result considering that Bohart and Menke had already indicated the polyphyletic nature of their Gorytini (see their Fig. 155). Also, as Alexander's (1992a) study did not evaluate the monophyly of the tribes he used, one cannot assume that his Gorytini is monophyletic.

Nemkov and Lelej (1996) analyzed the phylogenetic relationships among the genera of Bohart and Menke's Gorytini. Despite some weaknesses in their study [e.g., assuming monophyly of the tribe, or using only characters listed in Bohart and Menke (1976)], they also found that *Ochloptera* was very weakly associated with the rest of Gorytini. However, they kept this genus (together with *Clitemnestra*) in the Gorytini, as the most basal clade. The close association of *Ochleroptera* with *Heliocausus*, supported here by a considerable number of unambiguous synapomorphies (see branch 17), seems well founded. It is interesting to note that males of some species of *Clitemnestra*, a group closely related to *Ochleroptera*, exhibit derived morphological features similar to those typical of Heliocausini males, as for example eyes large and strongly converging above, thorax somewhat spherical and metasomal sternum II with a strong, keel-like protuberance.

The close relationship found here between *Hoplisoides* and *Didineis* in the implied weighting analysis also deserves to be discussed. *Didineis* together with the genus *Alysson* has traditionally been placed in a separate tribe (or subfamily depending on the classification) distinct from the rest of the Bembicinae (e.g., Evans 1966, Bohart and Menke 1976, Krombein 1979, 1985), and usually considered a somewhat relictual and basal group (e.g., Evans 1966, Bohart and Menke 1976). [More recently Krombein (1985) described a new genus, *Analysson*, from Sri Lanka; judging from the diagnostic characters, recognition of *Analysson* probably makes *Alysson* paraphyletic, but this needs to be evaluated by a phylogenetic analysis.] However, I suspect that the often-assumed plesiomorphic appearance of the species in this group is in reality the result of several derived modifications of the Gorytini groundplan. The absence in *Alysson* and *Didineis* of the "oblique scutal carina", a feature whose presence is heavily weighted as diagnostic of the Bembicinae, could be the result of an elongation and narrowing of the whole body. *Alysson* and *Didineis* resemble four genera, *Eogorytes* (not examined), *Lestiphorus*, *Oryttus* and *Psammaletes*, assumed to form a monophyletic group within the Gorytini (Nemkov and Lelej 1996), especially *Lestiphorus*. The species in these six genera have in common females with elongated fore legs, in which the fifth tarsomere and arolia are conspicuously larger than those of the other legs, long antennae (in particular the slender and long basal flagellomeres) and no mesepisternal sulcus (at least on the upper part of the mesepisternum). Future phylogenetic studies should take into consideration these putative relationships.

Crabroninae.—The Crabroninae (branch 10) is defined here to include the genera *Mellinus*, *Dinetus*, *Laphyragogus* and *Xenosphex*, and the subfamilies Crabroninae and Larrinae of Bohart and Menke (1976). In Bohart and Menke's classification *Mellinus* was considered the basal lineage of their Nyssoninae (= Bembicinae), *Dinetus* was in their Astatinae, and *Laphyragogus* and *Xenosphex* had each its own subfamily. Bohart and Menke (1976) treated their Larrinae and Crabroninae as separate subfamilies "for practical considerations". These two taxa have been treated under one name in the past (e.g., Evans 1964a), and also in

more recent works (e.g., Lomholdt 1985, Menke 1988). The valid name for the taxon including these two groups is Crabroninae [see discussion in Menke (1993)].

Bohart and Menke (1976) suggested that the genus *Xenosphex* was remotely, but most closely, related to *Mellinus*. However, as these authors themselves acknowledged, their list of similarities between *Xenosphex* and *Mellinus* involved only shared plesiomorphies. In Alexander's (1992a) study, *Xenosphex* shows no consistent association with any other taxon. In the present study, *Xenosphex* always came out as one of the basal lineages of the Crabroninae. This position is supported by several unambiguous changes (see branches 10–12), among them a notch on the outerventral margin of the mandible (7-1), a strong, lamella-like mesocoxal carina (71-2), the loss of the paired expansions on the posterior wall of the pharynx (13-0) and a linear forewing costal cell (84-1). The morphology of the oral plate, with the lateral arms strongly converging posteriorly, is also found only among members of this lineage. The peculiar morphology, in comparison to the more distal crabronines, of the mesepisternum and metepisternum ventrally in *Xenosphex* (medial flap of mesokatespisternum narrow, anterior portion of metepisternum vertical medially, not leveled with mesepisternum) seems to have been modified in conjunction with the enlargement of the mesocoxa. The male genitalia has a generalized morphology (gonapophyses not fused dorsally and volsella clearly differentiated from the gonocoxites), like *Dinetus* and *Mellinus*, and unlike the distal crabronines. The larva of *Xenosphex* is unknown, but I would expect it to have a ventral, preapical anus (132-1), as do all other Crabroninae. One interesting modification observed in the metasoma of the male of *X. timberlakei* (the only male of *Xenosphex* examined) is the presence of lateral transverse sulci at the bases of T4–7 (each lateral sulcus extends almost to the middle of the tergum). Examination of KOH-cleared terga VI and VII showed hundreds of chitinous ducts associated with each sulcus (these are probably ducts of unicellular epidermal glands). It would be worth checking to see if males of the other two species of *Xenosphex* also possess such sulci.

Laphyragogus traditionally has been considered part of the Crabroninae (e.g., Beaumont 1959), but Bohart and Menke (1976) placed it in its own subfamily based on some wing features, the relatively generalized male genitalia, the peculiar mouthparts and the morphology of the thorax in the area adjacent to the midcoxae. They indicated a somewhat intermediate position between their Astatatinae and Larrinae. Except for the specialized mouthparts, which probably could be considered autapomorphies, the remaining features used by Bohart and Menke do seem to suggest exclusion of *Laphyragogus* from the Crabroninae. In the present analyses, however, *Laphyragogus* is unambiguously placed in the Crabroninae (see branch 13). Four synapomorphies support placement of *Laphyragogus* as the most basal branch of the distal crabronines (based on optimizations shown in Fig. 1):

(1) male mandibles with apical tooth only (5-1);
(2) female mandibles with a subbasal cleft on their inner edge (6-1);
(3) mid tibia with one spur (73-1);
(4) gonapophyses of male genitalia completely fused dorsally, forming a tube (129-1).

The subbasal cleft in the mandibles of females (as well as in males in some groups) is present in several distal crabronine taxa and is usually associated with a correspondent notch (or notches) on each side of the apical margin of the clypeus [see e.g., Fig. 8 in Lomholdt (1985); also Fig. 2 in Pulawski (1995)]. These modifications of the mandible are known to occur only in taxa traditionally considered as members of the Crabroninae (among the taxa represented here, the inner notch is present in *Lyroda*, *Palarus*, *Plenoculus* and *Anacrabro*, besides *Laphyragogus*).

The condition in *Laphyragogus* for two characters exhibiting synapomorphic change in branches 11 and 12, respectively, can be considered a derived divergence from what is present in the more distal crabronines: (1) the mesocoxal carina (Character 71) is not particularly strongly developed as in most distal crabronines, but its morphology is somewhat reminiscent of their condition, especially at the region near the ventral articulation with the trochanter; (2) the relatively broad forewing costal cell (character 84) could be considered as an artifact due to the way the character states were defined, because in *Laphyragogus*, the vein C is unusually slender. The volsellae (Character 128), although clearly differentiated from the gonocoxites, seem to possess an intermediate morphology between a more generalized condition, as found in *Dinetus* and *Xenosphex*, and the more specialized condition found in most distal crabronines, because they are largely fused to the gonocoxites.

Some changes considered ambiguous in the optimizations can be taken as additional evidence supporting placement of *Laphyragogus* in the Crabroninae. The mesepisternal sulcus in *Laphyragogus* is very similar to that of most crabronines (reaching the anterior edge of mesepisternum away from the body's midline). Although also found in other crabronid subfamilies, the elongate mouthparts and the putative use of holometabolous insects as prey (Lepidoptera; see Kazenas 1985) suggest crabronine taxa. Indeed, the somewhat specialized galeal comb, formed by numerous short, blunt bristles, is reminiscent of the condition present in *Palarus*. *Laphyragogus* seems to represent a somewhat relictual and specialized lineage that

has strongly diverged from the other distal crabronines, a hypothesis somehow supported by its possession of several unusual features, for example (1) a proepisternum almost completely sunk inside the pronotum, (2) a strongly enlarged occipital area and a correspondingly reduced pronotal collar, (3) enlarged mouthparts, in particular the broad cardines, (4) broad connection between the meso- and metasomata, and (5) apically expanded basal tarsomeres of the female foreleg, especially the basitarsus (such modifications of the tarsomeres are also found in most species of *Eremiasphecium*, probably a convergence due to nesting in sand, because these expansions bear large rake bristles).

The somewhat heterogeneous composition proposed here for the Crabroninae might be seen by some as an indication of an artificial, rather than a natural, monophyletic group, especially because of the inclusion of several, highly divergent basal lineages. However, except perhaps for *Mellinus*, this heterogeneous composition seems rather an indication of a relatively old clade, in which several of its basal lineages did not go extinct. This pattern seems also to support a basal position for the subfamily as a whole within the Crabronidae.

Pemphredoninae.—This subfamily (branch 19) is defined here to include the genera *Odontosphex* and *Entomosericus*, and the tribes Psenini and Pemphredonini of Bohart and Menke (1976), except for their Ammoplanina. Two tribes are recognized: Pemphredonini (branch 21), which corresponds to Bohart and Menke's Pemphredonini without their Ammoplanina, and Psenini (branch 22), which includes *Odontosphex*, *Entomosericus* and Bohart and Menke's Psenini. Each one of these two clades is well-supported in most analyses, but they formed together a monophyletic clade only under implied weighting and under successive weighting (analysis of the complete data matrix). Despite this relatively weak support, I opted for having both clades under one subfamily, instead of treating each as a separate subfamily, to emphasize their probable sister-group relationship and at the same time, to avoid an unnecessary disruption of the traditional classification.

The following synapomorphies were found to support unambiguously the monophyly of the Pemphredoninae:

(1) apical inflection of clypeus joining epistomal ridge considerably mesal to tentorial pit (15-2);
(2) occiput with periforaminal depression (35-1);
(3) well-defined mesocoxal carina (71-1);

The last character can barely be considered a synapomorphy for this group, because presence of a mesocoxal carina, which was probably well-defined when first originated, is part of the Apidae (sensu lato) + Crabronidae groundplan (see Character 70). The first two synapomorphies seems to provide the strongest evidence for the monophyly of this group, especially the periforaminal depression. This is a unique structure not observed in other taxa included in this study.

The monophyly of the tribe Pemphredonini is supported by several synapomorphies (see branch 21). Two main clades where found within this tribe, one represented by *Spilomena* and *Arpactophilus* [branch 24; the subtribe Spilomenina as defined in Menke (1989)] and the other containing the subtribes Stigmina, as redefined in Menke (1989) and Pemphredonina, as defined in Bohart and Menke (1976) (branch 23). The monophyly of Spilomenina is very strongly supported, with 14 unambiguous synapomorphies listed for branch 24. Some of these changes, however, should not be considered part of the subtribe groundplan, because they are not present in some of its members [e.g., a group of species restricted to Australia, with only one described species (as a *Spilomena*; see McCorquodale and Naumann 1988), does not possess silk glands (Character 112; see Melo 1997) and has a pygidial plate (Character 113); these conditions seem to be plesiomorphies for this group, and not reversals as one could suspect (Melo, in prep.)]. The clade containing Stigmina and Pemphredonina is supported by fewer, but strong synapomorphies as well. The supposed sister-group relationship between Stigmina and Spilomenina suggested by Bohart and Menke (1976) was not supported by the parsimony analyses. Stigmina is a well-defined monophyletic group [*Parastigmus* + *Stigmus*; see also Finnamore (1995)], whereas only two synapomorphies support the monophyly of Pemphredonina.

The close relationship of *Odontosphex* and *Entomosericus* to Bohart and Menke's Psenini can also be considered somewhat surprising. *Odontosphex* was in the Philanthinae and *Entomosericus* had its own subfamily in Bohart and Menke's classification. The psenine wasps with their metasomal petiole look quite distinct from the more robust and non-petiolate *Odontosphex* and *Entomosericus*. However, they share several derived characters (see synapomorphies for branch 22), including a somewhat specialized articulation between sterna I and II (Character 110). One possible subdivision for this tribe would be the recognition of three subtribes, the basal clade Odontosphecina (containing only *Odontosphex*) and the sister subtribes Entomosericina (containing only *Entomosericus*) and Psenina (= Psenini of Bohart and Menke's classification). The sister-group relationship between *Entomosericus* and Psenina, as well as the monophyly of Psenina, also are well-supported (see branches 25 and 26, respectively).

Philanthinae.—The Philanthinae (branch 15) was recently redefined by Alexander (1992a) to include only four of the six tribes attributed to it by Bohart and Menke (1976). In Alexander's study, the affinities of the two excluded

tribes, Eremiasphecini (containing only *Eremiaspheciuni*) and Odontosphecini (containing only *Odontosphex*), remained unsolved. In a subsequent paper, Alexander (1992b) analyzed the relationships within the Philanthinae and found evidence for recognition of only five monophyletic genera: *Philanthinus*, *Philanthus* (including *Trachypus*), *Pseudoscolia*, *Cerceris* (including *Eucerceris*), *Clypeadon* and *Aphilanthops*.

Alexander (1992b) indicated that the only reliable synapomorphy for the Philanthinae is the presence of a clypeal brush in the males. Although in the present study representatives of only two genera (*Philanthus* and *Aphilanthops*) were included and no effort was made to evaluate the monophyly of this subfamily, the unambiguous changes shown in figure 2 for the branch leading to the these two genera (branch 15) can be considered as putative synapomorphies for the Philanthinae.

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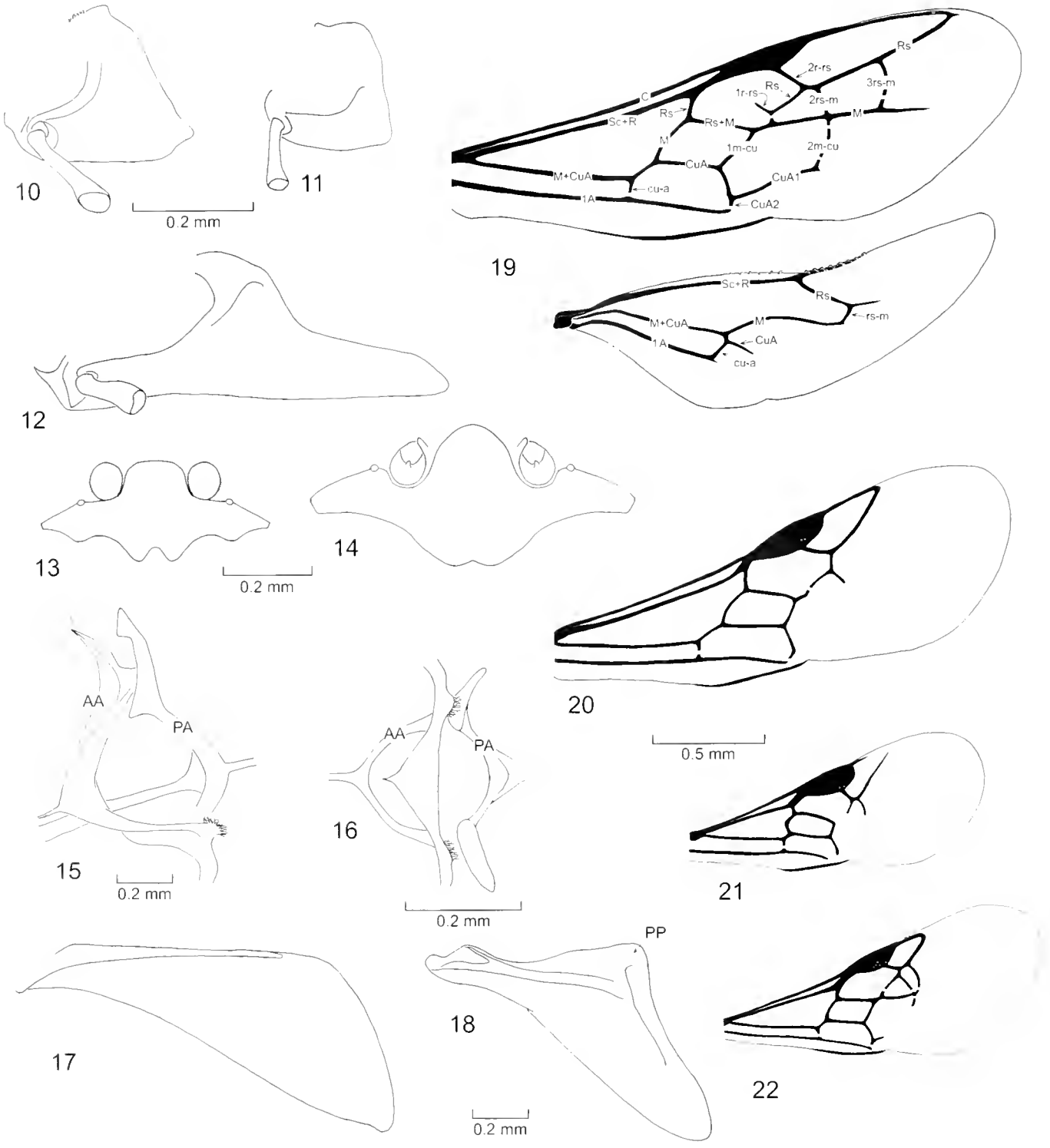
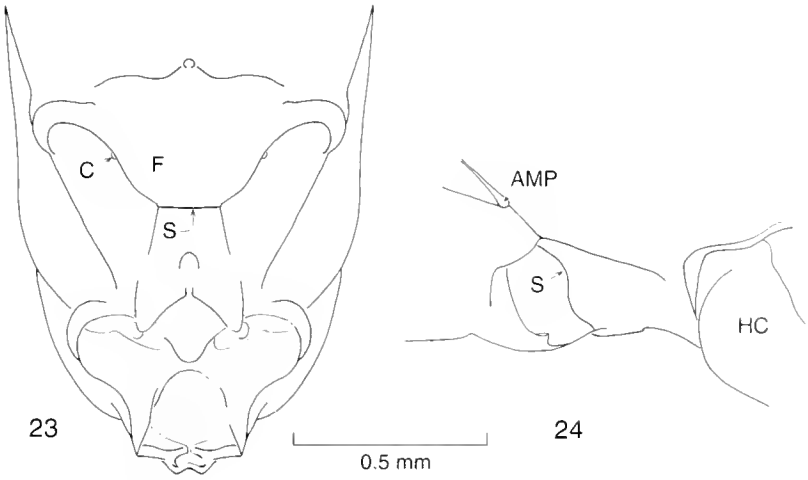
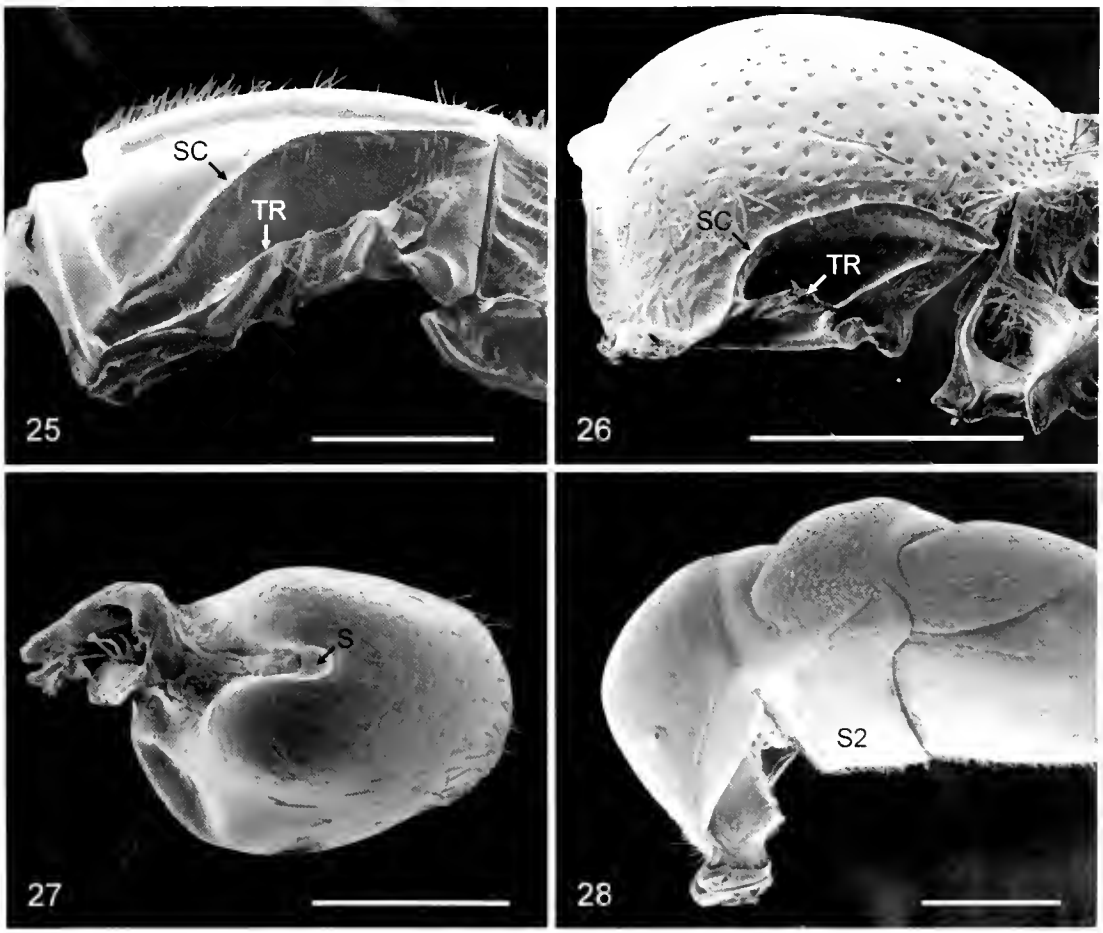


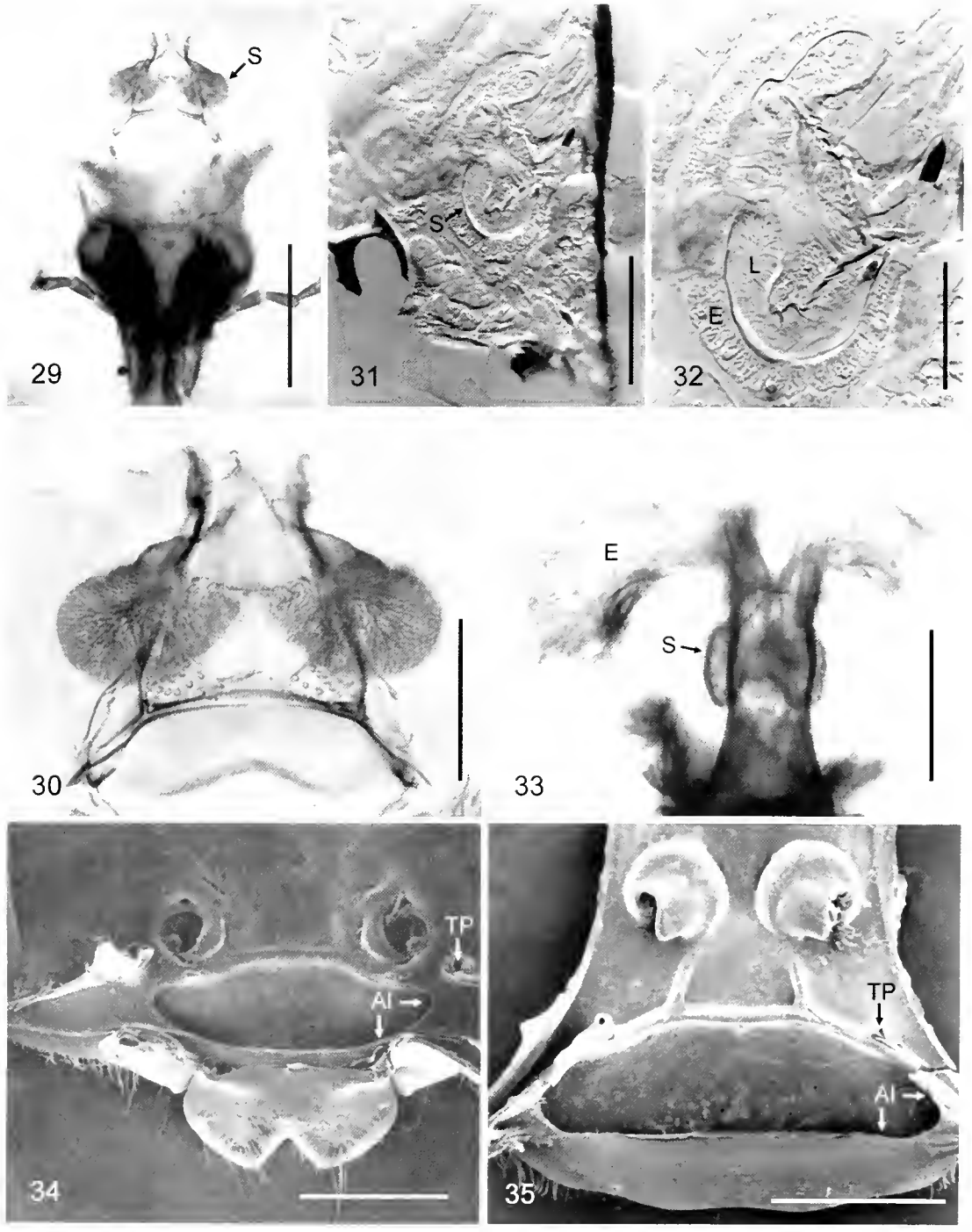
Figs. 10–22. 10.–Prementum of male of *Mellinus alpestris*, lateral view. 11.–Same, female of *Diodontus rugosus*. 12.–Same, female of *Mimesa cressoni*. 13.–Clypeus and antennal sockets of female of *Stigmus temporalis*, frontal view. 14.–Same, female of *Arpactophilus* sp. 15.–Furcal arms of female of *Astata nevadica*, dorsolateral view; abbreviations: AA = anterior arm, PA = posterior arm. 16.–Same, male of *Pulverro mescalero*, anterodorsal view. 17.–Second phragma of male of *Dolichurus* sp., lateral view. 18.–Same, female of *Mimesa cressoni*; abbreviation: PP = pseudophragma. 19.–Wings of *Aphelotoma rutiventris* showing wing venation terminology. 20.–Forewing of *Pulverro mescalero*. 21.–Same, *Timberlakena yucaipa*. 22.–Same, *Eremasphecium budrysi*.



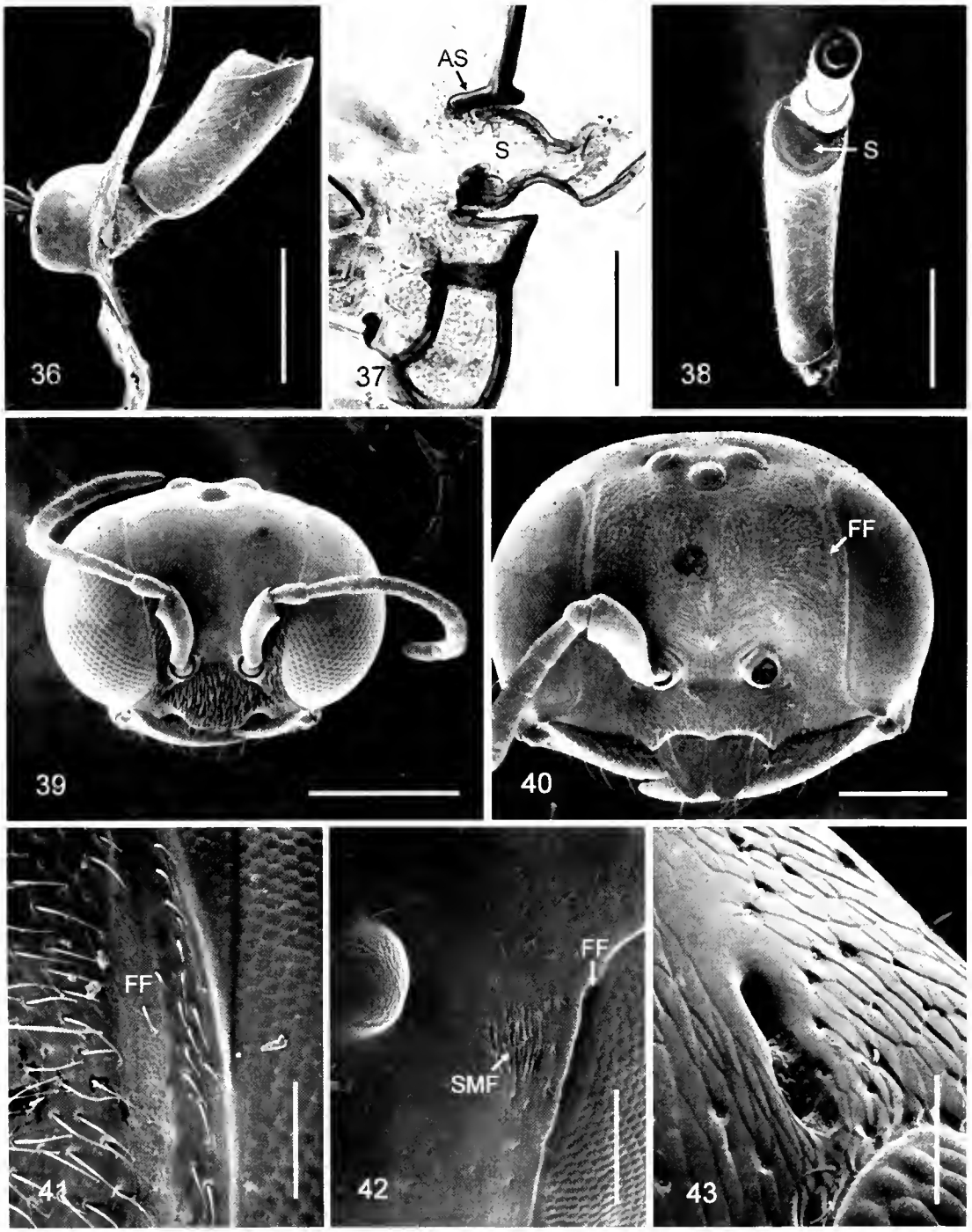
Figs. 23–24. 23.—Posterior portion of mesosoma of female of *Chlorion aerarium*, ventral view; abbreviations: C = condyle of mesal articulation of mid coxa, S = suture between mesepisternum and metepisternum, F = medial flap of mesokatepisternum. 24.—Same, lateral view; abbreviations: AMP = anteroventral metapleural pit, HC = hind coxa.



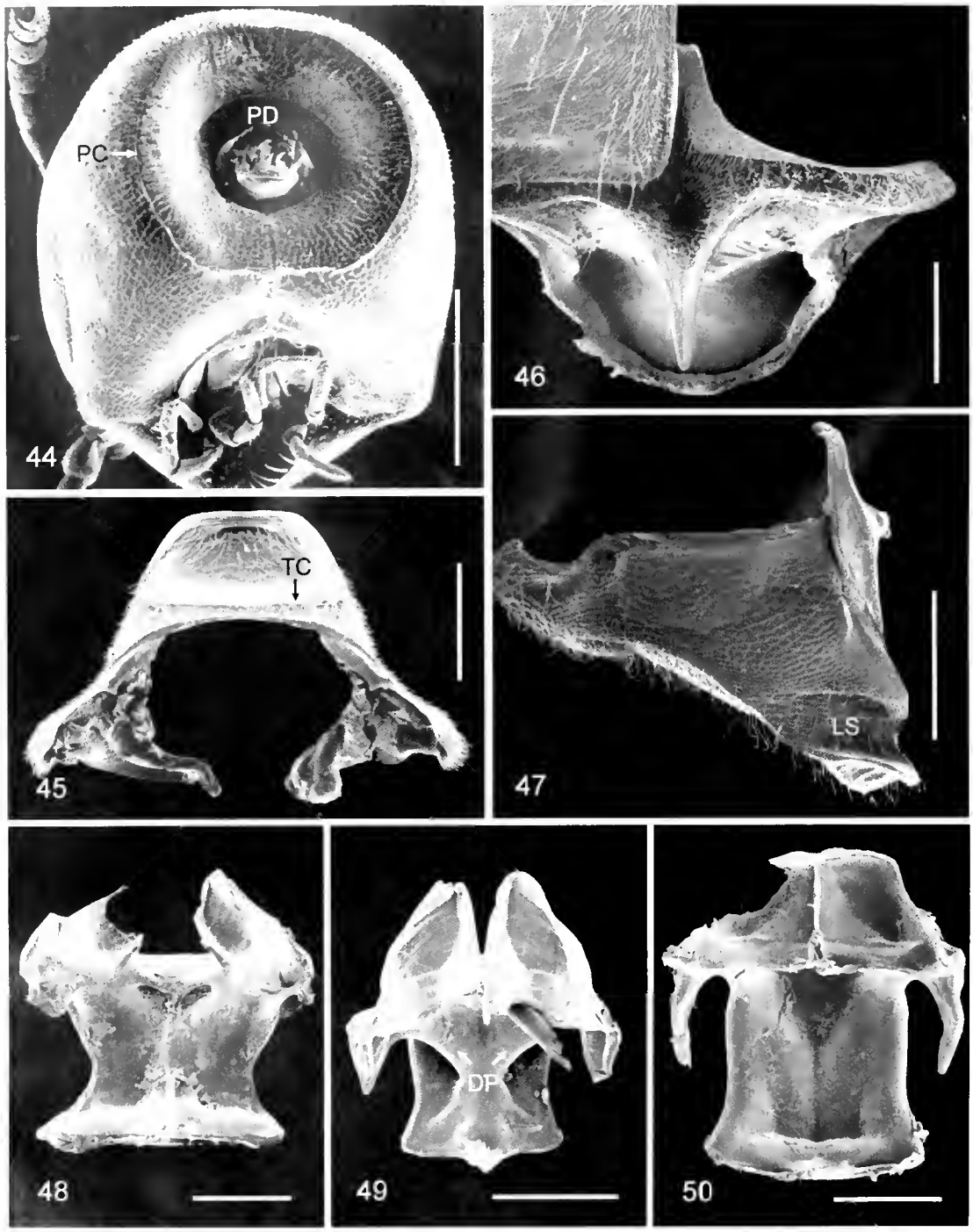
Figs. 25–28. 25.—Mesoscutum of male of *Dolichurus* sp., lateral view; abbreviations: SC = supra-alar carina, TR = tegular ridge; scale = 0.3 mm. 26.—Same, male of *Mimesa cressoni*; scale = 0.3 mm. 27.—Hind coxa of male of *Dolichurus* sp., antero-ventral view; abbreviation: S = socket of mesal articulation; scale = 0.2 mm. 28.—Metasoma of male of *Dolichurus* sp., lateral view; note modified sternum II (S2); scale = 0.5 mm.



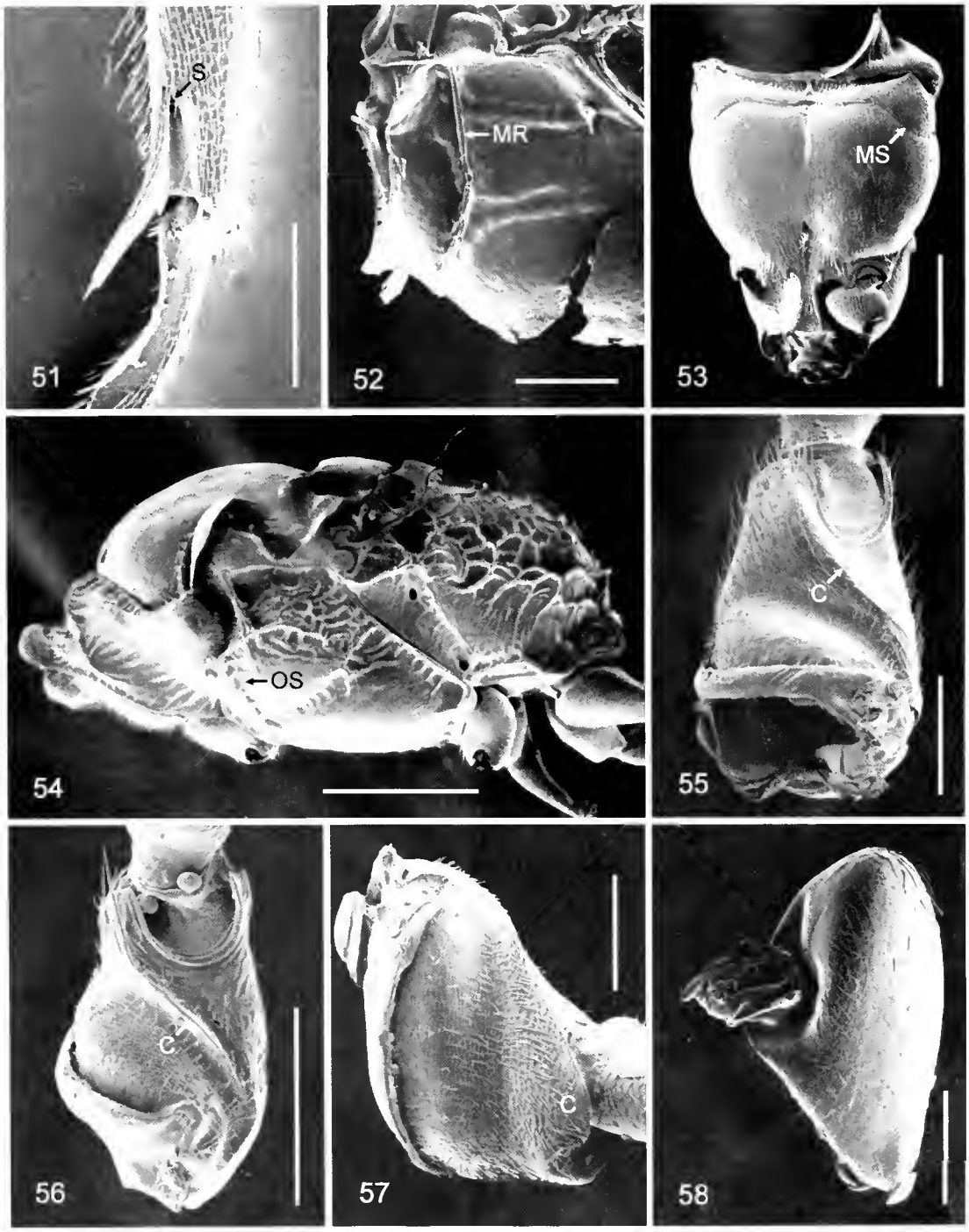
Figs. 29–35. 29.—Paired sacs (S) of the pharynx (showed attached to labio-maxillary complex) of female of *Odontosphex paradoxus* (specimen cleared in KOH), frontal view; scale = 0.5 mm. 30.—Same as Fig. 29; note numerous acanthae covering sac walls; scale = 0.2 mm. 31.–Section of head of female of *Ammoplanus* sp. (cfr. *apache*) showing pharyngeal sacs (S), oblique sectioning (anterior to the left); scale = 0.1 mm. 32.—Same as Fig. 31; note thick epidermis (E) forming the sac wall and numerous acanthae occupying lumen (L); scale = 0.05 mm. 33.—Expansions (E) of the upper pharynx of female of *Philanthus gibbosus* (material preserved in Kahle's fixative), frontal view; note also pharyngeal sacs (S); scale = 0.5 mm. 34.—Internal view of lower frons, clypeus, and labrum (soft tissues and most of tentorial arms and paramandibular processes removed) of female of *Diodontus flavitarsis*; abbreviations: AI = apical inflection of clypeus, TP = anterior tentorial pit; scale = 0.3 mm. 35.—Internal view of lower frons and clypeus (soft tissues and most of tentorial arms removed) of female of *Ochleroptera bipunctata*; abbreviations: AI = apical inflection of clypeus, TP = anterior tentorial pit; scale = 0.3 mm.



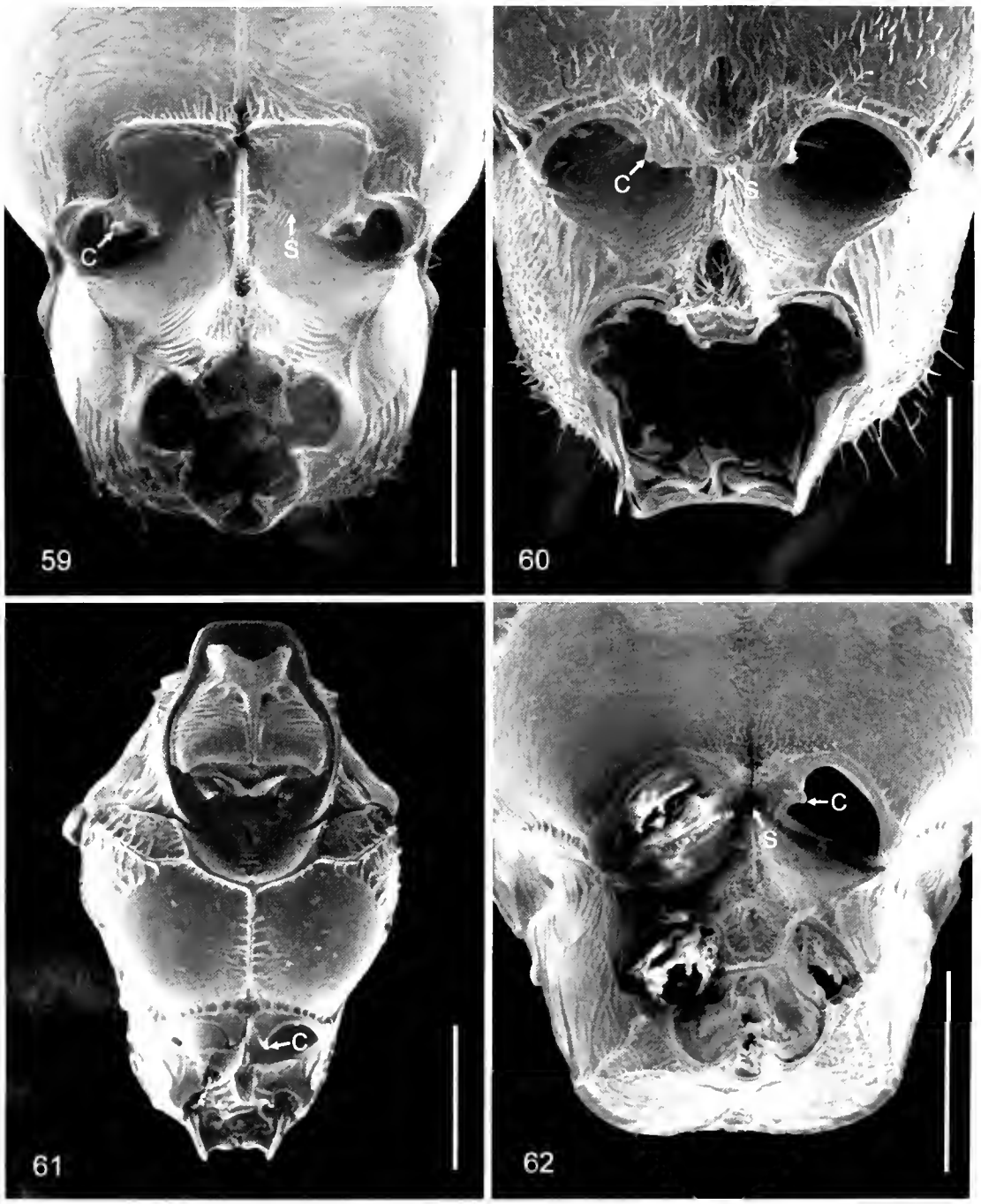
Figs. 36–43. 36.—Ventral internal view of the protruding antennal sclerite (left) of female of *Philanthus gibbosus*; scape (right) still attached to socket; scale = 0.3 mm. 37.—Sagital section of head of female of *Stigmus americanus* showing the protruding antennal sclerite (AS); base of scape (S) inserted into socket; scale = 0.1 mm. 38.—Base of antenna of female of *Diodontus flavitarsis* showing eccentric insertion of the pedicel into the socket at the apex of the scape; the central portion of the membrane covering the socket is sclerotized (S); scale = 0.3 mm. 39.—Head of male of *Stigmus americanus* showing the distinctly enlarged frontal facets of the compound eyes; scale = 0.5 mm. 40.—Head of female of *Diodontus virginianus* (Rohwer), frontal view; abbreviation: FF = facial fovea; scale = 0.5 mm. 41.—Same as Fig. 40. Close-up view of the elongate and shallow facial fovea (FF); scale = 0.1 mm. 42.—Vertex of female of *Stigmus americanus*, dorsal view; abbreviations: FF = facial fovea, SMF = secondary micropore field; scale = 0.1 mm. 43.—Close-up view of the facial fovea of female of *Pulverro mescalero*, frontal view; scale = 0.02 mm.



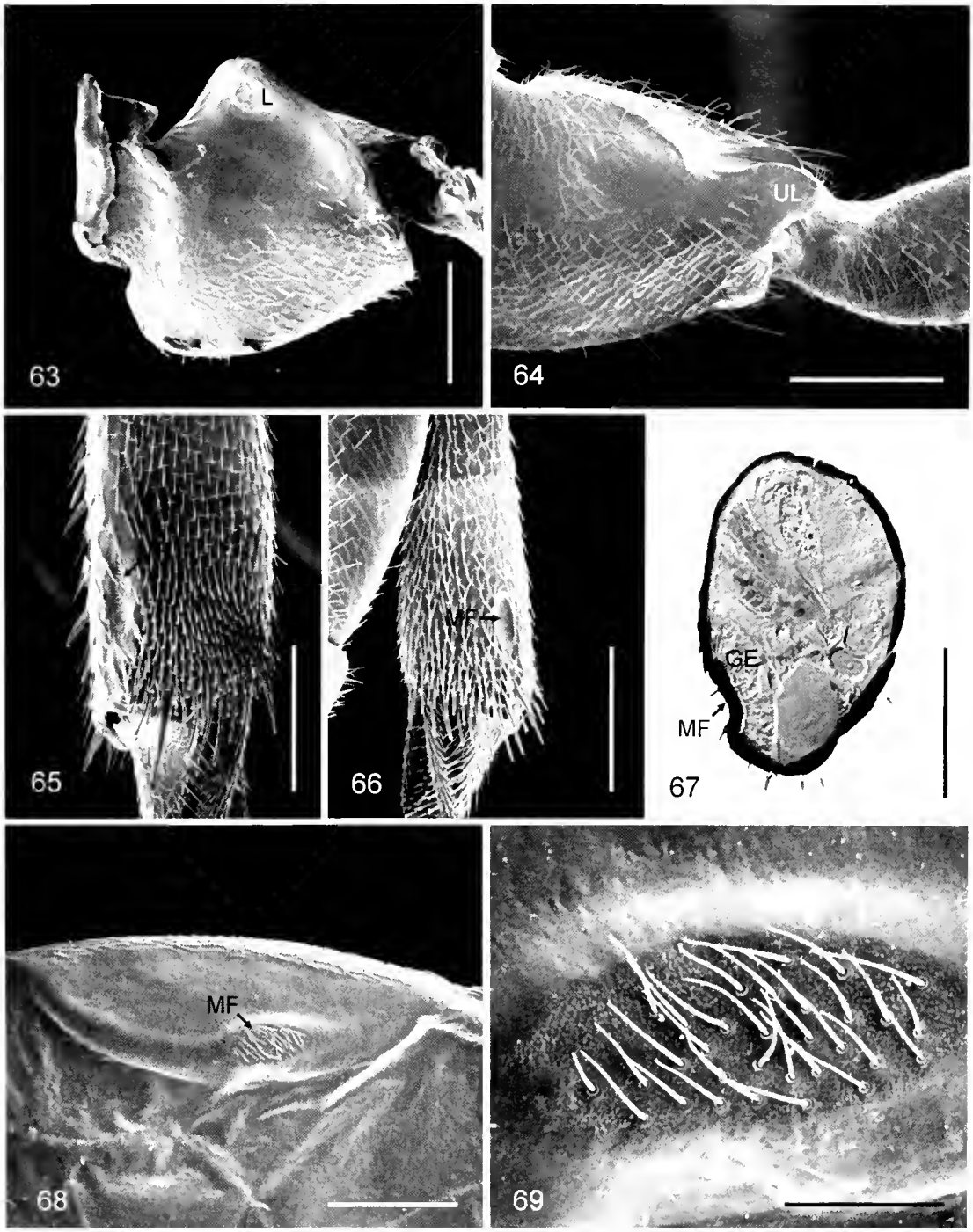
Figs. 44–50. 44. Head of female of *Passaloecus monilicornis* Dahlbom, posterior view; abbreviations: PD = perforaminal depression, PC = preoccipital carina; scale = 0.5 mm. 45.—Pronotum of female of *Passaloecus monilicornis*, dorsal view; abbreviation: TC = transverse carina; scale = 0.3 mm. 46.—Prothoracic basisternum of female of *Chlorion aerarium*, ventral view; scale = 0.5 mm. 47.—Prothoracic episternum of female of *Ochleroptera bipunctata*, lateral view; abbreviation: LS = lateral sulcus; scale = 0.2 mm. 48.—Internal view of prothoracic endosternum of male of *Dolichurus* sp., anterior view; scale = 0.2 mm. 49.—Same, male of *Minesa cressoni*; abbreviation: DP = divergent plates; scale = 0.2 mm. 50.—Same, female of *Didineis texana*; scale = 0.2 mm.



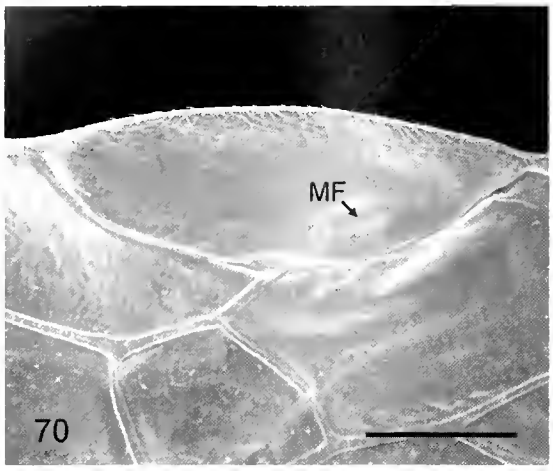
Figs. 51–58. 51.—Apex of fore tibia of male of *Mimesa cressoni* showing displaced and closed spur socket (S); scale = 0.2 mm. 52.—Internal view of the mesepisternum of female of *Passaloecus monilicornis*; abbreviation: MR = mesepisternal ridge; scale = 0.2 mm. 53.—Thorax of female of *Ammoplanus* sp. (cfr. *apache*), ventral view (legs removed, except for left mid coxa); abbreviation: MS = mesepisternal sulcus; scale = 0.3 mm. 54.—Mesosoma of male of *Stigmus americanus*, lateral view (legs removed, except for coxae); abbreviation: OS = omaular sulcus, scale = 0.5 mm. 55.—Mid coxa of male of *Mellinus crabroneus* (Thunberg), dorsolateral view; abbreviation: C = midcoxal carina; scale = 0.2 mm. 56.—Same, male of *Mimesa cressoni*, scale = 0.2 mm. 57.—Same, female of *Plenoculus davisi*, lateral view, scale = 0.2 mm. 58.—Same, male of *Dolichurus* sp., ventral view; scale = 0.2 mm.

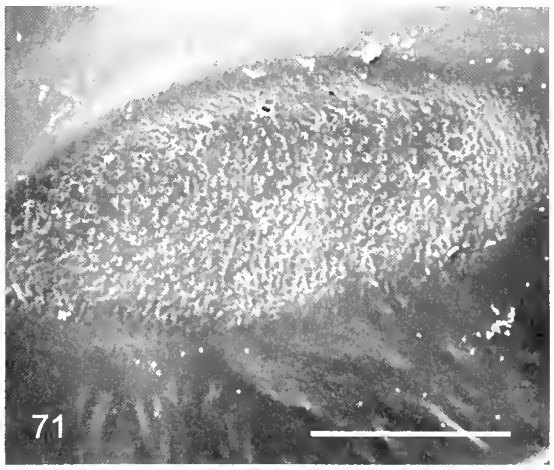


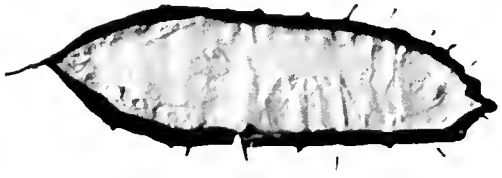
Figs. 59–62. 59.—Posterior portion of mesosoma of male of *Dolichurus* sp., postero-ventral view (legs removed); abbreviations: S = suture between mesepisternum and metepisternum; C = condyle of mesal articulation of mid coxa; scale = 0.5 mm. 60.—Same, male of *Mimesa cressoni*; scale = 0.3 mm. 61.—Mesosoma of female of *Stigmus americanus*, ventral view (legs removed, except for right mid coxa); abbreviation: C = condyle of mesal articulation of mid coxa; scale = 0.5 mm. 62.—Posterior portion of mesosoma of female of *Pulverro mescalero*, posteroventral view (legs removed); abbreviations: S = suture between mesepisternum and metepisternum; C = condyle of mesal articulation of mid coxa; scale = 0.3 mm.

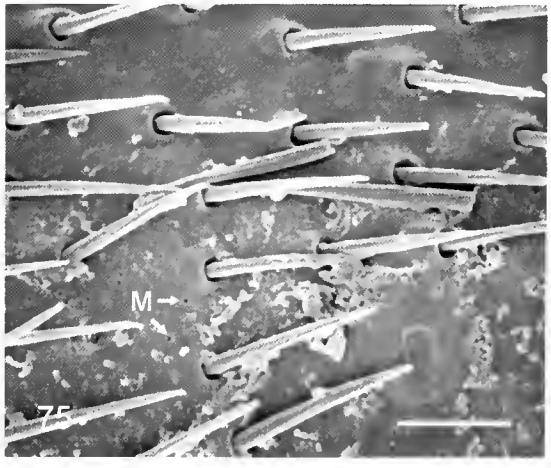


Figs. 63–69. 63.—Hind coxa of female of *Pulverro mescalero* showing dorsal, crest-like lamella (L), inner view; scale = 0.1 mm. 64.—Same, male of *Mimesa cressoni*, inner view; abbreviation: UL = upper lobe; scale = 0.2 mm. 65.—Hind tibia of female of *Pulverro mescalero*, inner view; MF = micropore field; scale = 0.1 mm. 66.—Same, female of *Ammoplanus* sp. (cfr. *apache*); scale = 0.1 mm. 67.—Cross-section of hind tibia of female of *Ammoplanus* sp. (cfr. *apache*); abbreviations: GE = glandular epidermis, MF = micropore field; scale = 0.05 mm. 68.—Pterostigma of female of *Stigmus americanus*, dorsal view; abbreviation: MF = micropore view; scale = 0.2 mm. 69.—Same as Fig. 68; close-up view of micropore field; scale = 0.05 mm.

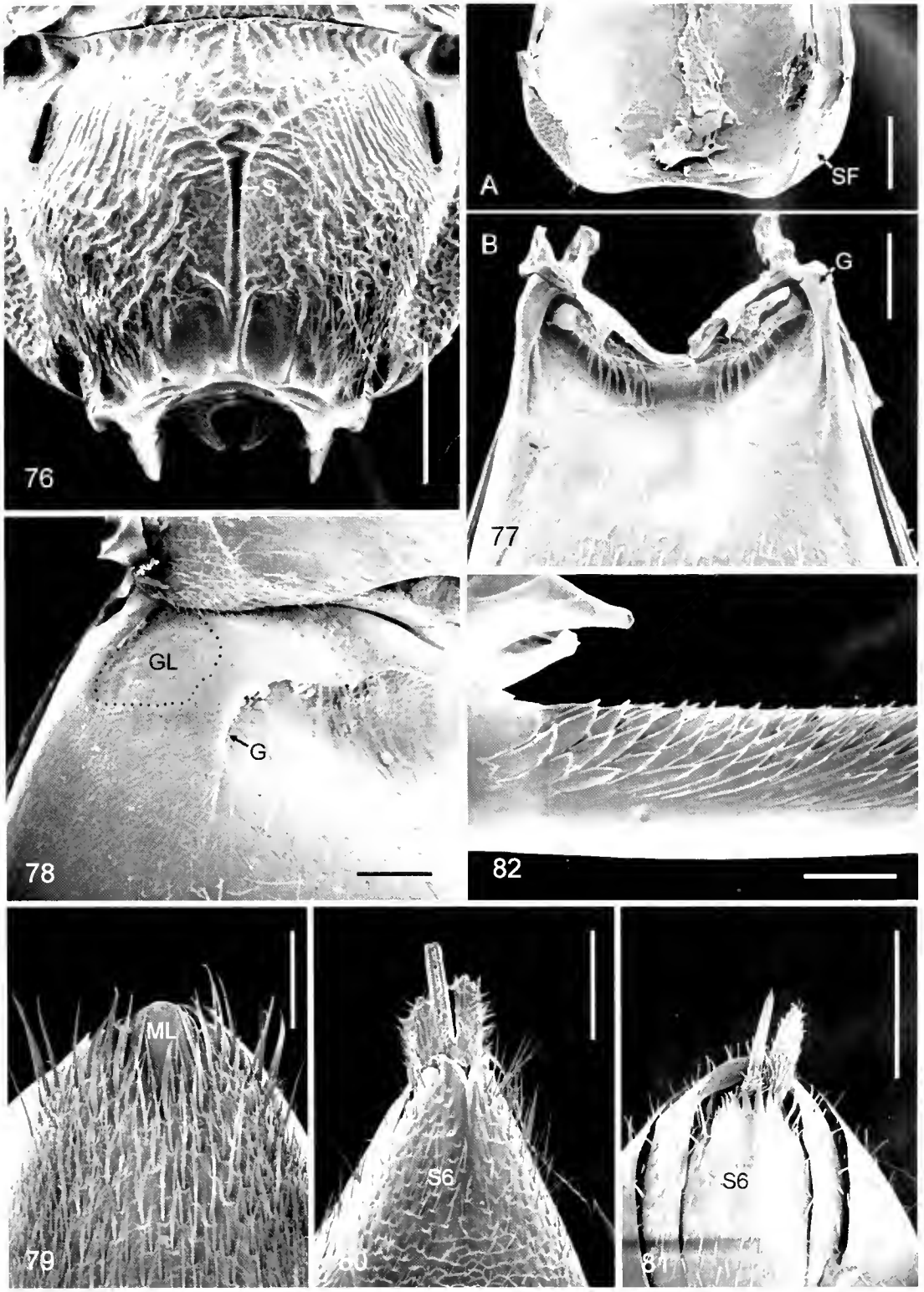








Figs. 70–75. 70.—Pterostigma of female of *Stigmus americanus*, ventral view; abbreviation: MF = micropore field; scale = 0.2 mm. 71.—Same as Fig. 70; close-up view of micropore field; scale = 0.03 mm. 72.—Cross-section of pterostigma of female of *Stigmus americanus* showing the distinctly developed epidermal glands (dorsal and ventral glands); scale = 0.1 mm. 73.—Same as Fig. 72; close-up view of glandular tissue; scale = 0.05 mm. 74.—Cross-section of pterostigma of female of *Passalocus arcolatus* (material not stained); scale = 0.05 mm. 75.—Close-up view of micropores (M) forming a diffuse micropore field on the dorsal surface of the pterostigma of the female of *Diodontus rugosus*; note absence of pores on upper half of illustration; scale = 0.01 mm.



Figs. 76–82. 76.—Mesosoma of male of *Mimesa cressoni*, posterior view; note deep sulcus (S) separating the two halves of the propodeum, scale = 0.3 mm. 77.—A. Posterior apex of sternum I of male of *Mimesa cressoni*, dorsal view; SF = specialized surface. B. Anterior apex of sternum II showing specialized portion of lateral gradulus (G), ventral view; scales = 0.1 mm. 78.—Anterior apex of sternum II of female of *Dodontus virginianus*, ventral view; G = gradulus; GL = glandular integument (contours indicated by dotted line); scale = 0.1 mm. 79.—Posterior apex of sternum VI of female of *Dodontus virginianus*, ventral view; ML = medial lobe; scale = 0.1 mm. 80.—Posterior apex of metasoma of female of *Pulvero mescalero*, ventral view; note modified apex of sternum VI (S6); scale = 0.1 mm. 81.—Same, female of *Ammoplanus* sp. (ctr. *apachei*), note denticulate apex of sternum VI (S6); scale = 0.1 mm. 82.—Base of apical projection of sternum VIII of male of *Stigmus americanus*, lateral view; scale = 0.02 mm.

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