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Polybia, Paraphyly, and Polistine Phylogeny

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ABSTRACT

A cladistic analysis of the subgenera of the paper wasp genus *Polybia* Lepeletier (Hymenoptera: Vespidae; Polistinae), and the other genera that construct phragmocyttarus nests, is presented. The results clearly indicate paraphyly of *Polybia* in terms of the genus *Synoecoides* Ducke. To remove the paraphyly, *Synoecoides* is reduced in rank, to a subgenus of *Polybia*, new synonymy.

INTRODUCTION

Polybia is one of the most familiar of the neotropical paper wasp genera. From Mexico to Argentina, this genus is typically the most abundantly represented by individuals (e.g., Jeanne, 1991: table 6.2). Its colonies are likewise the most commonly encountered (Jeanne, 1991: table 6.3), especially among those genera that make phragmocyttarus nests, that is, with each comb covered by an envelope and succeeding combs built upon the envelopes of those preceding. With 56

species currently recognized (and another 19 subspecies) the genus is by far the most speciose among the Epiponini, the endemic New World tribe characterized by founding new colonies by swarms. A number of these species are among the most well studied of the Polistinae (see references in Jeanne, 1991; West-Eberhard et al., 1995). The genus ranks first by the measures of "success" listed by Jeanne (1991: table 6.4), and Richards (1978: 33) stated that it "might be regarded as the most typical of the genera of South American social wasps."

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Yet if typical, *Polybia* is not characteristic. Alone among the epiponine genera, *Polybia* possesses no obvious autapomorphy—nor even an ambiguous one. The other genera that construct phragmocytarus nests are all readily characterized. In the cladistic analysis by Carpenter (1991: table 3), which did not include autapomorphies as such, the phylogenetic diagnoses for these genera were as follows: *Protonectarina* (eyes bristled); *Chartergus* (thyridium transverse and basal); *Brachygastra* (eyes bristled, pretegular carina lost, and scrobal sulcus lost); and *Synoecoides* (occipital carina lost, and tempora narrowed). Neither *Epipona* nor *Polybia* was optimized for a phylogenetically informative trait, but for *Epipona* autapomorphies are readily adduced: for example, the parallel-sided metasomal petiole, emarginate clypeus, and shiny black cuticle. Other autapomorphies can be adduced for the other genera (e.g., *Protonectarina*, posterior ocelli widely separated; *Chartergus*, propodeum dorsally carinate; *Brachygastra*, scutellum sharply angled; and *Synoecoides*, flattened mesosoma). Listing autapomorphies does not appear to be possible for *Polybia*. Nor do larvae (Kojima, 1998) or nest characters (Wenzel, 1998) provide autapomorphies for *Polybia*, with many characters showing polymorphic states in the genus.

Cladistic analysis has only recently been applied at the generic level in Polistinae (Carpenter and Wenzel, 1990; Carpenter, 1991, 1993, 1996; Wenzel, 1993; Wenzel and Carpenter, 1994; Carpenter et al., 1996; Kojima, 1997). In studies of relationships among genera, the placement of *Polybia* has fluctuated greatly. In the analysis by Carpenter (1991), based primarily on adult morphology, *Polybia* was placed in an unresolved hexatomy (!) with the other phragmocytarus-nesting genera, the genus *Protopolybia*, and the genera that make astelocytarus nests (with a single comb flat on a substrate and covered by an envelope). In the analysis of behavioral characters by Wenzel (1993), *Polybia* was placed as the sister group of the genus *Protonectarina*. In the simultaneous analysis of behavioral data with adult and larval morphology by Wenzel and Carpenter (1994), *Polybia* was placed as the sister group of *Synoecoides* + *Epipona*.

The lack of any diagnostic apomorphy for *Polybia* raises the question as to whether the instability of its placement in previous analyses might not be due, at least in part, to the genus not being monophyletic. If that is the case, progress in understanding phylogenetic relationships among the polistine genera will remain hindered. The present study therefore addresses the question of the monophyly of *Polybia*. This genus was divided into subgenera by Richards (1978). Thus, analysis at the level of subgenera, together with a sufficient number of outgroup genera, can test the monophyly of the genus, and that is what is undertaken here.

TAXONOMIC BACKGROUND

The description of the genera *Polistes* and *Epipona* by Latreille (1802) might be said to be the first recognition of the group we now treat as the subfamily Polistinae. Into these genera Latreille and other authors transferred many of the species described in the 18th century in the Linnaean genus *Vespa*. After Latreille, a few other genera were described (*Gyrostoma* Kirby, 1828; *Ropalidia* Guérin-Méneville, 1831; *Brachygastra* Perty, 1833), but it is in the work of Lepeletier de St. Fargeau (1836) that the first outlines of the modern classification are seen. Lepeletier first recognized a group Polistinae (as “Polistides”), and described the genus *Polybia*, as well as *Agelaia*, *Apoica*, *Chartergus*, and *Rhopalidia* (suppressed, International Commission on Zoological Nomenclature, 1976; =*Angiopolybia* Araujo, 1946). This work was expanded upon in the worldwide monograph by de Saussure (1853–1858). As well as describing several new genera of Polistinae and many new species, de Saussure proposed the first subdivision of *Polybia*. He divided it into two subgenera, the newly described *Clypearia* and *Polybia* “proprement dites.” The latter was, in turn, subdivided into seven “divisions”: *Alpha*, *Iota*, *Phi*, *My*, *Kappa*, *Omega*, and *Parapolybia*. Later, de Saussure (1863) added *Pseudopolybia* as a division of the genus *Polybia*, without mentioning subgenera. As detailed in Carpenter and Day (1988), the criteria of availability now in the International Code of Zoological Nomenclature make all of these names avail-

able (Carpenter and Day were referring to the third edition; the new fourth edition is the same in this case). Thus, the subgeneric classification by Richards (1978), who rejected these names as published by de Saussure, was corrected by Carpenter and Day, and that revised nomenclature is followed here.

Subsequent to the monograph of de Saussure, two of his divisions of *Polybia* came to be treated as genera (*Parapolybia* and *Pseudopolybia*), but the other infrasubgeneric names were otherwise largely ignored. The modern generic classification of Epiponini took shape in the work of Ducke (1905). Ducke treated *Clypearia* as a genus, and described several new genera (*Metapolybia*, *Monacanthocnemis*, *Protopolybia*, *Pseudochartergus*, and *Synoecoides*), in part for species previously placed in *Polybia*. Ducke (1905: 5) stated that the aim of his new classification was to be more natural than de Saussure's ("je crois avoir réussi à classer les Vespides d'une manière plus naturelle qu'on ne l'a fait jusque ici") by taking into account new observations on nesting behavior. Nevertheless, *Synoecoides*, monotypic for the new species *depressus*, was described without knowledge of its nesting behavior. It was distinguished by morphology: depressed thorax; narrow, truncate clypeus; narrow tempora; obtusely angulate metanotum; and sessile metasoma. Ducke emphasized the lack of resemblance to other social wasps, albeit naming it for resembling on first view *Synoeca*. The phragmocyttarus nest was later described by Ducke (1907: 163, pl. 3, fig. 7), but the status of the genus was not reassessed by Ducke, or by subsequent workers (e.g., Araujo, 1944; Richards, 1978).

Ducke's classification was embellished upon by subsequent workers, and Richards (1978) brought the classification of *Polybia* to its current form by removal of two species to another genus (*Occipitalia*; one included species was subsequently split off into another genus, *Asteloeca* Raw, 1985; *Occipitalia* was later synonymized with *Clypearia* by Carpenter et al., 1996). As mentioned previously, Richards (1978) also subdivided *Polybia*, into 10 subgenera: *Apopolybia*, *Cylindroeca*, *Formicicola*, *Furnariana*, *Hypopolybia*, *Myrapetra*, *Pedothoeca*, *Platypolybia*, *Polybia* s.s., and *Trichothorax*. All of these

taxa save the typical subgenus and *Myrapetra* White, 1841, were newly described. As already noted, Richards' classification has been amended (Carpenter and Day, 1988): *Hypopolybia* Richards, 1978, is a synonym of *Alpha* de Saussure, 1854, and *Trichothorax* Richards, 1978, has been replaced on account of homonymy by *Trichinothorax* Carpenter and Day, 1988.⁴ Richards' subgeneric scheme has not otherwise been re-examined.

In his monograph, Richards (1978: 33) stated of *Polybia*, "it is a well defined and almost certainly monophyletic group." He did not establish that however; as pointed out by Carpenter (1991), Richards' dendrogram is not actually based on phylogenetic analysis of the characters he adduced. For reasons enumerated above, the question of the monophyly of *Polybia* is, in fact, open and will now be addressed.

MATERIALS AND METHODS

Characters for the subgenera of *Polybia* and the outgroup genera are presented in tables 1–3. The outgroups are all the other genera that construct phragmocyttarus nests: *Protonectarina*, *Chartergus*, *Brachygastra*, *Epipona*, and *Synoecoides*. The phragmocyttarus-nesting genera were supported as a monophyletic group in the analyses by Wenzel (1993) and Wenzel and Carpenter (1994). The program DADA (Nixon, 1998a) was used for data editing. Cladistic analysis (Hennig, 1966) was implemented with the programs NONA (Goloboff, 1999a) and PIWE (Goloboff, 1999b). A posteriori character weighting included both successive weighting, as implemented in NONA, and implied weighting, as implemented in PIWE, to check the self-consistency of results under more than one weighting scheme. Character optimization and diagnoses were accomplished with the CLADOS program (Nixon, 1998b). There are three sources of character data: morphology of the adults, morphology of the larvae, and morphology of the nests. Each of these character partitions will be dis-

⁴ *Iota* is now considered a synonym of *Polybia* s.s., and *My* is a synonym of *Myrapetra*; *Phi*, *Kappa*, and *Omega* are subgenera of the genus *Mischocyttarus* de Saussure.

TABLE 1

Adult Characters for Subgenera of *Polybia* and Five Outgroup Genera

Multistate character 15 is treated as additive; multistate characters are otherwise treated as non-additive. An asterisk denotes a polymorphism showing all applicable states; a dollar sign denotes a subset polymorphism (*Myrapetra*: states 0 and 1 in character 1, 0 and 1 in character 11, and 1 and 4 in character 20; and *Trichinothorax*: states 0 and 2 in character 1, 0 and 1 in character 5, 0 and 1 in character 11, 0 and 1 in character 14, 1 and 3 in character 20, and 0 and 1 in character 23).

Taxa	Character				
	1	5	10	15	20
<i>Protonectarina</i>	200020001000020100000002				
<i>Epipona</i>	002021011011120000052000				
<i>Synoecoides</i>	011120110000102002131031				
<i>Chartergus</i>	00000000001000103260012				
<i>Brachygastra</i>	2000\$0000001000103261012				
<i>Polybia</i>	010100100020101001130013				
<i>Apopolybia</i>	010100100000111011121023				
<i>Alpha</i>	010100100000111001020013				
<i>Myrapetra</i>	\$10000**00\$01100000\$0004				
<i>Furnariana</i>	01010000010*100101011024				
<i>Cylindroeca</i>	010111011220100100001014				
<i>Trichinothorax</i>	\$10*\$10**0\$01\$01*00\$10\$4				
<i>Pedothoeca</i>	010121011010110100000024				
<i>Formicicola</i>	010100110000111101020124				
<i>Platypolybia</i>	110110110000120101010024				

cussed in turn, and the results of separate and combined analyses presented. The data were combined by splicing together the data sets with the program WINCLADA (Nixon, 1999).

ADULT CHARACTERS

The study of adult characters was made by Carpenter, who examined specimens of nearly all described species in these taxa.⁵ Morphological terminology is as in Carpenter (1991, 1996). Characters examined were drawn particularly from the subgeneric classification by Richards (1978), with new characters added as detailed below. Most of these characters have never previously been illus-

⁵ Specifically, all described species in these genera except one of *Polybia* (viz., *eberhardae* Cooper).

TABLE 2

Larval Characters for Subgenera of *Polybia*, and Five Outgroup Genera

Multistate characters are treated as nonadditive. Question marks denote missing values; the larva of the genus *Synoecoides* and of the subgenera *Furnariana* and *Platypolybia*, are unknown. An asterisk denotes a polymorphism showing all applicable states; a dollar sign denotes a subset polymorphism (*Chartergus*: states 0 and 1 in character 41; *Brachygastra*: states 0 and 1 in character 37; *Myrapetra*: states 1 and 2 in character 41; and *Trichinothorax*: states 1 and 2 in character 35, and 0 and 2 in character 37).

Taxa	Character				
	25	29	34	39	44
<i>Protonectarina</i>	0?1110???	200??0??0???			
<i>Epipona</i>	0100011-1210100010110				
<i>Synoecoides</i>	???????????????????????				
<i>Chartergus</i>	0011110102201100\$0001				
<i>Brachygastra</i>	011101*00321\$10*10000				
<i>Polybia</i>	?011?1010210000010001				
<i>Apopolybia</i>	001111???	01???	0???	???	???
<i>Alpha</i>	0011011-0100010010001				
<i>Myrapetra</i>	*011*1*1*2200*	*0\$0001			
<i>Furnariana</i>	???????????????????????				
<i>Cylindroeca</i>	?0?11???	01???	0???	???	???
<i>Trichinothorax</i>	1011111-00\$0\$00010001				
<i>Pedothoeca</i>	001111*1132101001*00*				
<i>Formicicola</i>	10110101022100001100?				
<i>Platypolybia</i>	???????????????????????				

trated, therefore 12 plates are provided, that show a range of taxa (figs. 1–48).

1. **Eyes:** without bristles (0), figs. 1–2, 5–8; few bristles (1), fig. 4; many bristles (2), fig. 3 [nonadditive]. Richards (1978: 35) used “Eyes with some hairs” as a key character for *Platypolybia*. “Eyes hairy” was also used as a key character for some species of *Trichinothorax* (Richards, 1978: 43). The condition in the species of *Platypolybia* (and some *Myrapetra*) is distinct from the densely bristled condition in *Protonectarina* (figs. 3, 9) and *Brachygastra* (fig. 11). It is intermediate, and so the character could be treated as additive. However, because it is polymorphic, it is treated as nonadditive, as is the case with most of the multistate characters in table 1. In this particular case, *Trichinothorax* has states 0 (e.g., figs. 6, 12) and 2; thus, if the character were additive, it should evi-

TABLE 3

Nest Characters for Subgenera of *Polybia*, and Five Outgroup Genera

Multistate characters are treated as nonadditive. The question mark denotes a missing value. An asterisk denotes a polymorphism showing all applicable states.

Taxa	Character	
	46	50
<i>Protonectarina</i>	031100000	
<i>Epipona</i>	000100101	
<i>Synoecoides</i>	000011101	
<i>Chartergus</i>	030100011	
<i>Brachygastra</i>	010011110	
<i>Polybia</i>	100000001	
<i>Apopolybia</i>	100010000	
<i>Alpha</i>	111001101	
<i>Furnariana</i>	020000111	
<i>Cylindroeca</i>	10001?100	
<i>Trichinothorax</i>	001210100	
<i>Pedothoeca</i>	020010100	
<i>Formicicola</i>	000100100	
<i>Myrapetra</i>	*00010***	
<i>Platypolybia</i>	000010011	

dently be interpreted as having the full range of values in the polymorphism within *Trichinothorax*, although this is not observed.

2. **Clypeus:** convex (0), figs. 9, 11; dorsally flattened in profile (1), figs. 10, 12, 14–16. New character.

3. **Clypeal apex:** rounded point (0), figs. 3–8; truncate (1), fig. 1; emarginate (2), fig. 2 [nonadditive]. *Synoecoides* and *Epipona* are characterized, respectively, by the truncate or emarginate apex of the clypeus. The clypeus also appears longer than broad in *Synoecoides*.

4. **Clypeal–eye contact:** equal to length of antennal socket (0), figs. 2–3, 7; much longer than antennal socket (1), figs. 1, 4–5, 8. A long clypeal–eye contact appeared repeatedly in the key to species of *Polybia* and subgeneric diagnoses by Richards (1978). He also distinguished a condition of “Clypeus at sides in contact with eyes for a distance equal to half the height of the antennal socket” in his couplet 6 (Richards, 1978: 36) when keying out the subgenus *Myrapetra*, however couplet 16 (p. 39) contradicted this, with *divisoria* Richards stated to have “Eyes in con-

tact with the sides of clypeus for a distance about equal to height of antennal socket.” Distinguishing more than a short versus a long state does not appear to be useful, as it is partitioning small degrees of continuous variation, and in any event offers no resolution at the level of the present study.

5. **Clypeal pubescence:** present (0); reduced (1); absent (2) [nonadditive]. By pubescence is meant the tomentum, dense over most of the clypeus in some of these taxa, restricted to a dorsal area in others (fig. 4), or even absent (most of the taxa figured, however this character does not show up well in the scanning electron micrographs). The character appeared in several places in Richards’ (1978) key and diagnoses, and is variable in some of the taxa (*Brachygastra* and *Trichinothorax*).

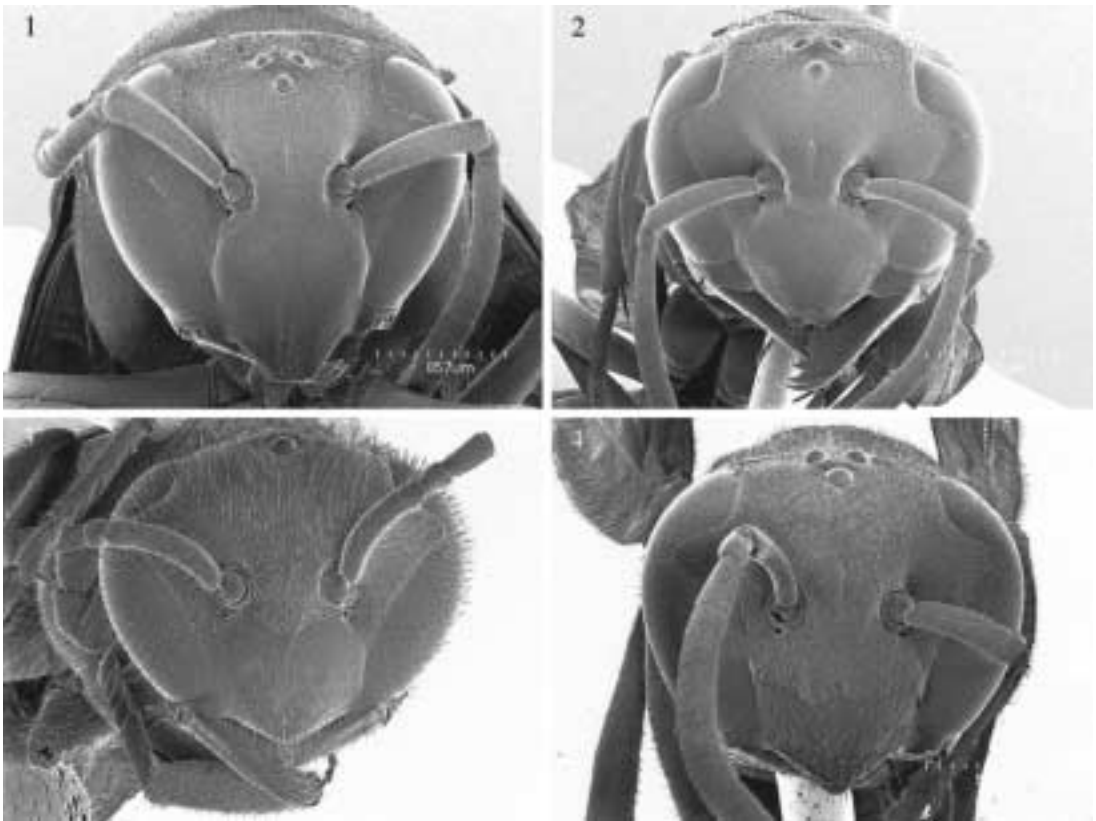
6. **Malar space:** very short (0), figs. 1, 3–4, 7–8; elongate (1), figs. 2, 5–6. Relative length of the malar space was used by Richards (1978) to distinguish among species of *Trichinothorax* and *Pedothoeca*. The elongate condition distinguished here refers to a length about half the width of the antennal socket.

7. **Tempora:** nearly as wide as eye (0), figs. 11–12; half width of eye (1), figs. 10, 13–16. This is one of the traditional diagnostic features for *Synoecoides*, but the tempora narrow was also used repeatedly as a key character in Richards’ (1978) key to species of *Polybia*.

8. **Occipital carina:** present (0), figs. 9, 11–12, 15–16; absent (1), figs. 10, 13. A traditional character, both for genera and species.

9. **Cuticle:** dull (0); shiny (1). This character appeared repeatedly in Richards’ (1978) key and descriptions. Not visible in the scanning electron micrographs, it can readily be seen with light microscopy or the naked eye.

10. **Anterior pronotal carina:** present (0), figs. 22–24, 27–28; reduced (1), fig. 26; lamellate (2), fig. 25 [nonadditive]. Richards (1978: 35) characterized *Furnariana* and *Cylindroeca*, respectively, by whether the anterior pronotal carina was reduced (“Pronotal fovea evanescent or even absent, area in front of it not raised”) or raised (“Prominence in front of pronotal fovea long and



Figs. 1–4. Head in frontal view. 1. *Synoecoides depressus* Ducke. 2. *Epipona niger* (Brèthes). 3. *Protonectarina sylveirae* (de Saussure). 4. *Polybia procellosa* Zavattari.

mostly sharp”). Although not polymorphic, these different states are not similar, hence the character is treated as nonadditive.

11. **Dorsal pronotal carina:** lamellate (0), figs. 17, 19–20, 23–24, 26, 28; absent (1), figs. 18, 27; pronotum dorsally compressed (2), fig. 22 [nonadditive]. Presence or absence of the dorsal pronotal carina is a traditional character. As Richards (1978: 99) noted in his diagnosis of *Cylindroeca*, “Pronotal keel not developed though there is an obtuse curved elevation in the relevant position” (partially visible in our fig. 25). A somewhat less pronounced condition also occurs in *Polybia* s.s. (fig. 22).

12. **Pronotal fovea:** present (0), figs. 22–28; absent (1), figs. 18–20. This character figured prominently in Richards’ (1978) key to genera.

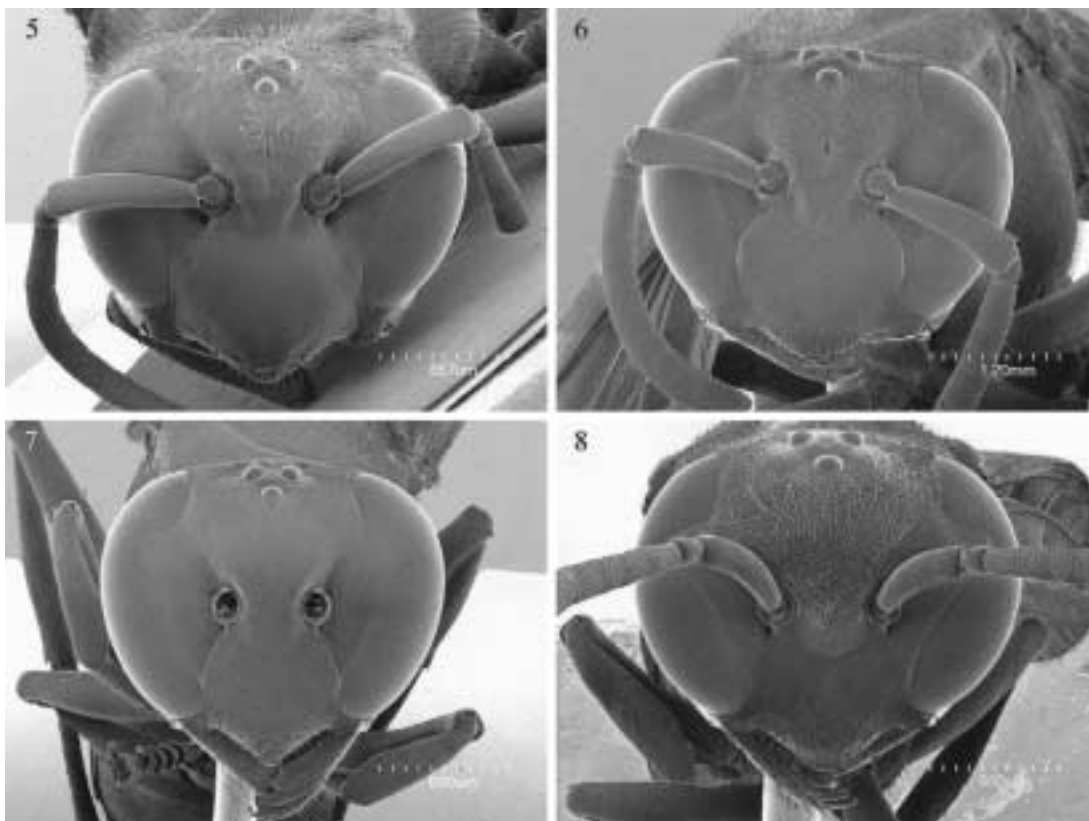
13. **Prothoracic external groove:** absent (0), fig. 37; present (1), fig. 39. New char-

acter. This groove is also found in those genera that make astelocytarus nests.

14. **Secondary spiracular entrance:** narrow (0), fig. 26; wide (1), figs. 23, 28; elongate (2), fig. 18 [nonadditive]. Richards (1978) emphasized this character, distinguishing various states having to do with curvature of the lip, etc., but those states do not appear informative at this level.

15. **Mesoscutum:** convex (0), figs. 18–19, 26–27; flattened (1), figs. 22–23; planar (2), fig. 21. This character refers to the strongly flattened scutum of *Synoecoides* (fig. 21) – but note that various subgenera of *Polybia* also have a flattened scutum (e.g., fig. 22); the state found in *Synoecoides* is simply more pronounced. Thus, three additive states are distinguished in this character.

16. **Scutal setae:** appressed (0), figs. 18, 21–23, 28; outstanding, hairlike (1), figs. 20,



Figs. 5–8. Head in frontal view. 5. *Polybia dimidiata*. 6. *Polybia chrysothorax* (Lichtenstein). 7. *Polybia nidulatrix* Bequaert. 8. *Polybia richardsi* Cooper.

25–27. This was an important subgeneric character in the key by Richards (1978).

17. **Scutal margin:** absent (0); present (1), fig. 17. A margined scutum was used to diagnose *Apopolybia* by Richards (1978), who also used it as a key character for several species of *Trichinothorax*.

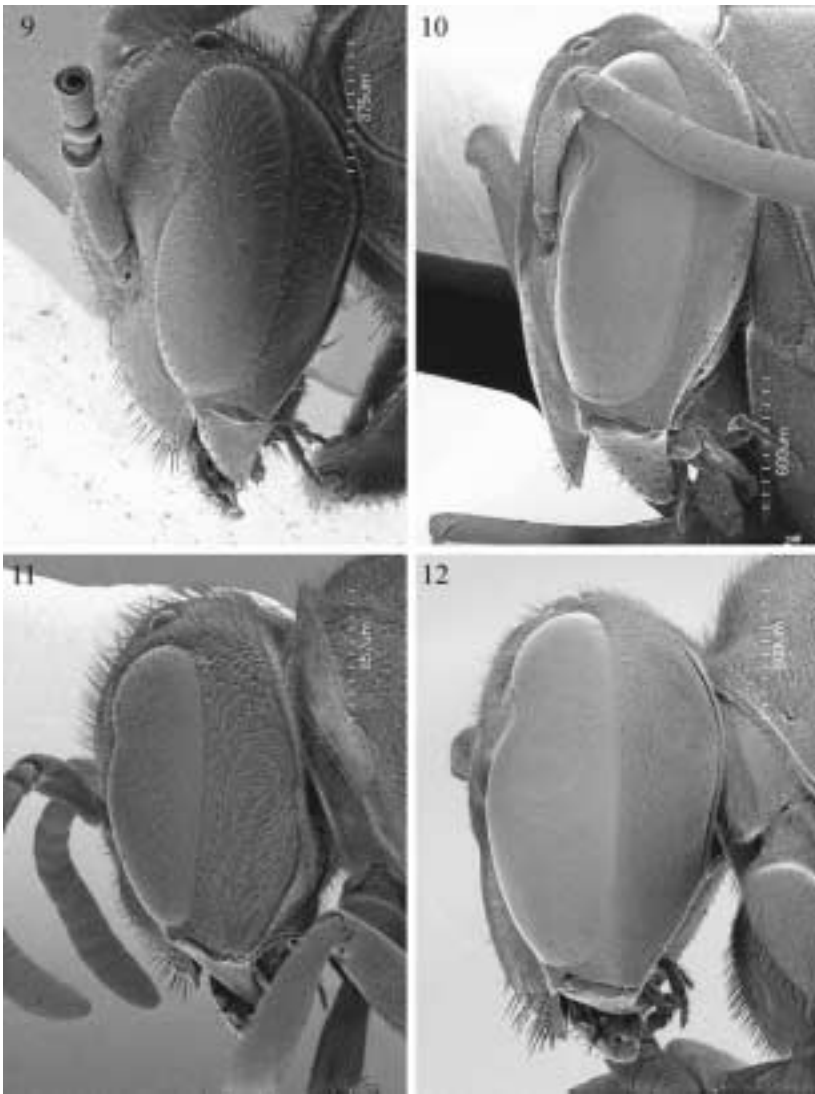
18. **Scutellum:** convex (0), figs. 18, 27; flattened (1), figs. 22, 24, 26; planar (2), fig. 21; compressed (3), fig. 20 [nonadditive]. The scutellum is strongly flattened in *Synoecoides* (fig. 21), but is also flattened, albeit less so, in various subgenera of *Polybia*. In *Chartergus* and *Brachygastra* the scutellum is compressed (sharply angled in *Brachygastra*, fig. 20, as mentioned above).

19. **Metanotum:** convex (0), figs. 18, 24, 27; vertically projecting (1), figs. 21–22; compressed in profile (2), fig. 20 [nonadditive]. The metanotum “very convex” was used as a diagnostic character for *Polybia* s.s.

by Richards (1978). His generic key stated of *Synoecoides* “Metanotum oblique throughout” (Richards, 1978: 10), but the state is similar (cf. figs. 21 and 22). In *Chartergus* and *Brachygastra* the scutellum is compressed, almost vertical in *Chartergus* (which is tuberculate) to quite vertical in *Brachygastra* (which may have a rudimentary tubercle).

20. **Propodeal concavity:** deep furrow (0), fig. 31; weak furrow (1), fig. 33; shallow (2), figs. 34–36; deep, wide (3), figs. 30, 32; absent (4); deep, basal (5); shallow, wide (6), fig. 29 [nonadditive]. The type of “posterior cavity” of the propodeum was used by Richards (1978) in both generic and subgeneric keys.

21. **Propodeal punctation:** absent in propodeal concavity (0), figs. 33, 36; present in propodeal concavity (1), figs. 30, 35; propodeum rugoso-punctate (2) [nonadditive].



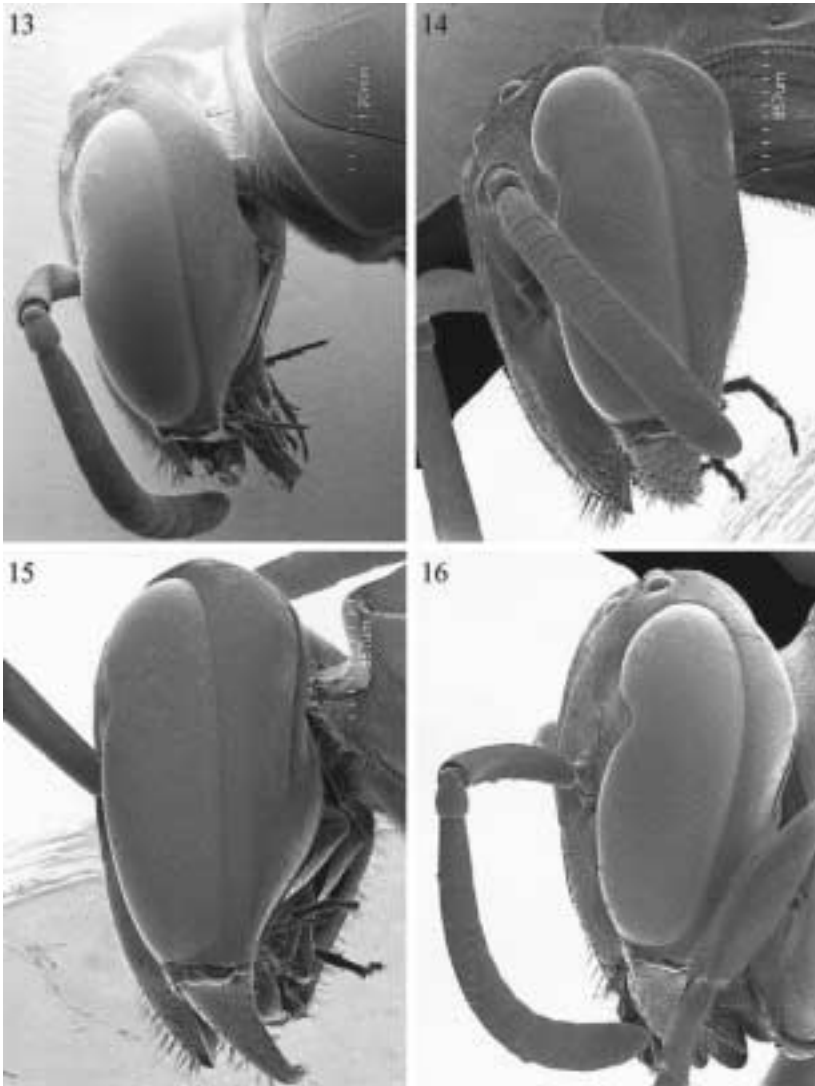
Figs. 9–12. Head in lateral view. **9.** *Protonectarina sylveirae*. **10.** *Synoecoides depressus*. **11.** *Brachygastera lecheguana* (Latreille). **12.** *Polybia chrysothorax*.

This was an important subgeneric character in the key by Richards (1978).

22. Propodeal orifice: dorsally broad (0), figs. 32–33, 35–36, 42–44; narrow (1), figs. 34, 45. A dorsally pointed propodeal orifice was used as a diagnostic feature for *Formicicola* by Richards (1978: 35, as “Propodeal muscle-slit”). As the figures show, the alternative condition subsumes a wide range of variation, and the orifice is sometimes more or less pointed above (e.g. fig. 33), albeit less narrow.

23. Propodeal valvula: smooth (0); with secondary emargination (1), fig. 22; anteriorly narrow (2), fig. 24; smooth, broad (3), fig. 21 [nonadditive]. Richards (1978) mentioned the valvula (as “valves”) in his keys and subgeneric diagnoses. Because the valvula is translucent, it is best seen under light microscopy.

24. Metasomal petiole: parallel-sided petiolate (0), fig. 41; subsessile (1), fig. 43; forming narrow cap on second segment (2), figs. 38, 40; short, broad petiole (3), figs. 42,



Figs. 13–16. Head in lateral view. **13.** *Polybia rejecta*. **14.** *Polybia jurinei*. **15.** *Polybia liliacea* (Fabricius). **16.** *Polybia bifasciata* de Saussure.

44, 47; long petiole (4), figs. 45–46, 48 [non-additive]. A traditional character.

LARVAL CHARACTERS

The study of larvae was made by Kojima. Although larval characters are often useful for phylogenetic studies of social wasps, such information is still limited. For the tribe Epiponini, Reid (1942) described mature larvae of 8 species in 5 genera and 3 subgenera in *Polybia* and Dias Filho (1975) 19 species

in 8 genera including 4 subgenera of *Polybia*. However, their descriptions did not refer to most of the microscopic structures that are often useful for phylogenetic studies (Kojima and Keeping, 1988). Richards (1978) provided a key to mature larvae of polistine genera, including 14 epiponine genera and 6 subgenera of *Polybia*; his key, however, did not provide sufficient information for phylogenetic analysis and included some errors (Kojima, 1998). Later Silveira (1994) described ma-

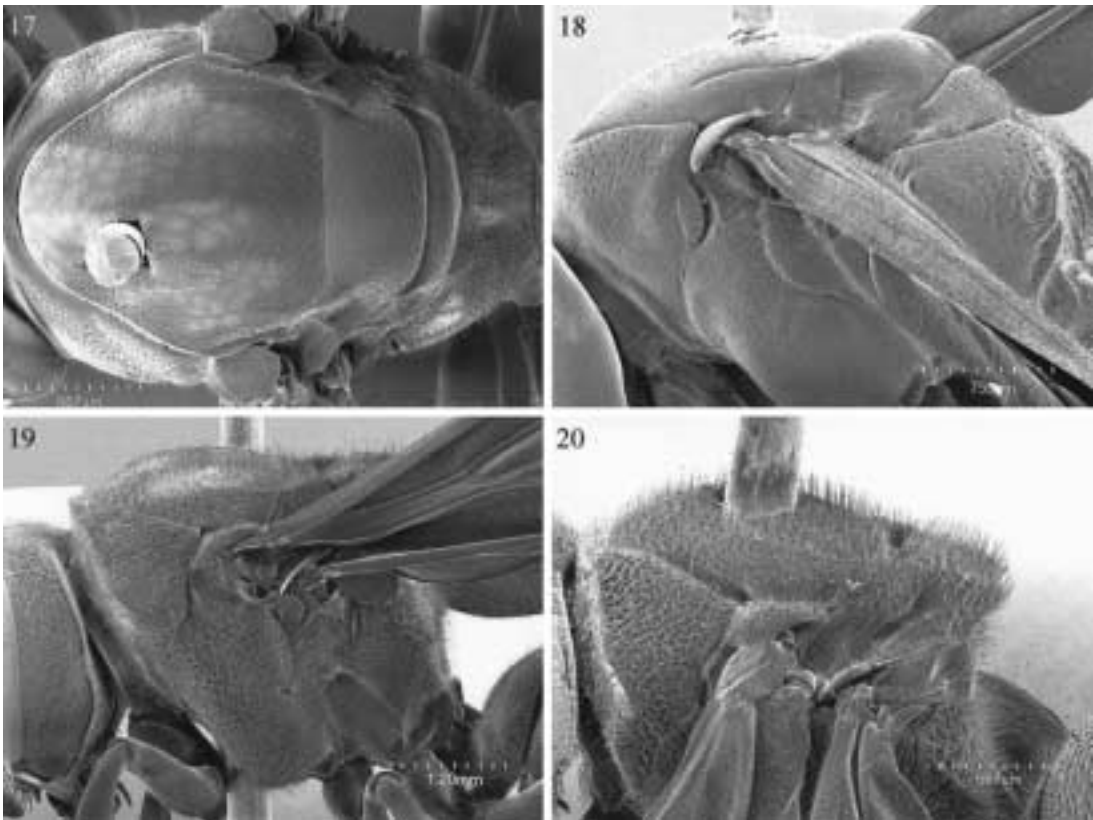


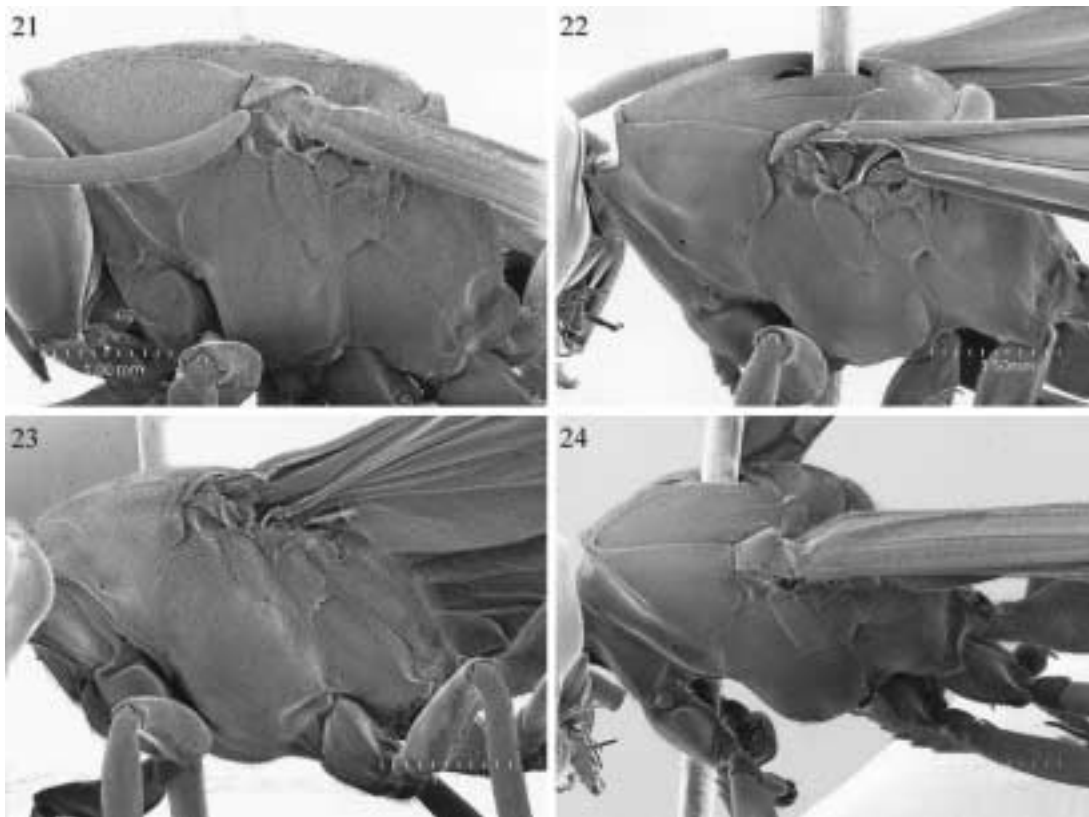
Fig. 17. *Polybia jurinei*. scutum in dorsal view. Figs. 18–19. Mesosoma in lateral view. **18.** *Epipona niger*. **19.** *Brachygastra lecheguana*. Fig. 20. *Brachygastra lecheguana*. dorsum of mesosoma in lateral view.

ture larvae of *Protopolybia chartergoides* for the first time, but did not add new information at the generic level. Kojima (1998) made a comprehensive descriptive work on social wasp larvae, and presently the only epiponine genera for which no larval information is available are *Marimbonda* Richards, 1978, and *Synoecoides* Ducke, 1905, and the only subgenera *Funariana* Richards, 1978, and *Platypolybia* Richards, 1978, of the genus *Polybia*. In the present paper, we extracted larval characters from Kojima (1998), with reference to Dias Filho (1975) for the species (also the genus *Protonectarina*, and subgenera *Apopolybia* and *Cylindroeca*) that Kojima did not examine. For a list of specimens examined, as well as illustrations of the characters, see Kojima (1998).

25. Hypostomal ridge: nearly straight (0); ventral margin produced ventrally near man-

dibular base (1). In *Trichinothorax* and *Myrapetra* the ventral margin of the hypostomal ridge is produced ventrally near the mandibular base, and thus the cranium in frontal view appears produced just below the mandibles. Two of the species of *Myrapetra* examined had a nearly straight ventral margin of the hypostomal ridge (*bistriata* (Fabricius) and *scrobalis* Richards). A similarly produced hypostomal ridge is found in *Agelaia cajennensis* (Fabricius) and *Parachartergus* (Kojima, 1998).

26. Cranial setae: short and inconspicuous (0); conspicuous, bristlelike (1). Richards (1978: 16) used this character in his key to larvae of the polistine genera; ambiguity of his definition, however, was pointed out by Kojima (1998). Among the genera treated in this study, *Epipona* and *Brachygastra* have conspicuous bristlelike setae on the cranium.



Figs. 21–24. Mesosoma in lateral view. 21. *Synoecoides depressus*. 22. *Polybia liliacea*. 23. *Polybia bifasciata*. 24. *Polybia rejecta*.

Such bristlelike setae on the cranium are also found in *Synoeca chalibea* de Saussure and *Clypearia sulcata* (de Saussure).

27. **Antenna:** small (0); large (1). In the Polistinae small antennae are found in *Polistes* and *Mischocyttarus*. In the clade Ropalidiini + Epiponini the antennae are large except in *Epipona*. The condition in *Epipona* might be secondary reduction in size, thus this character is uninformative for the analysis within the Epiponini.

28. **Antenna–anterior tentorial pit distance:** distinctly more than diameter of antenna (0); less than diameter of antenna (1). State 0 (not 1) is found in *Polistes*, *Mischocyttarus*, and *Epipona*. As with the size of the antenna, the state found in *Epipona* might have been secondarily derived.

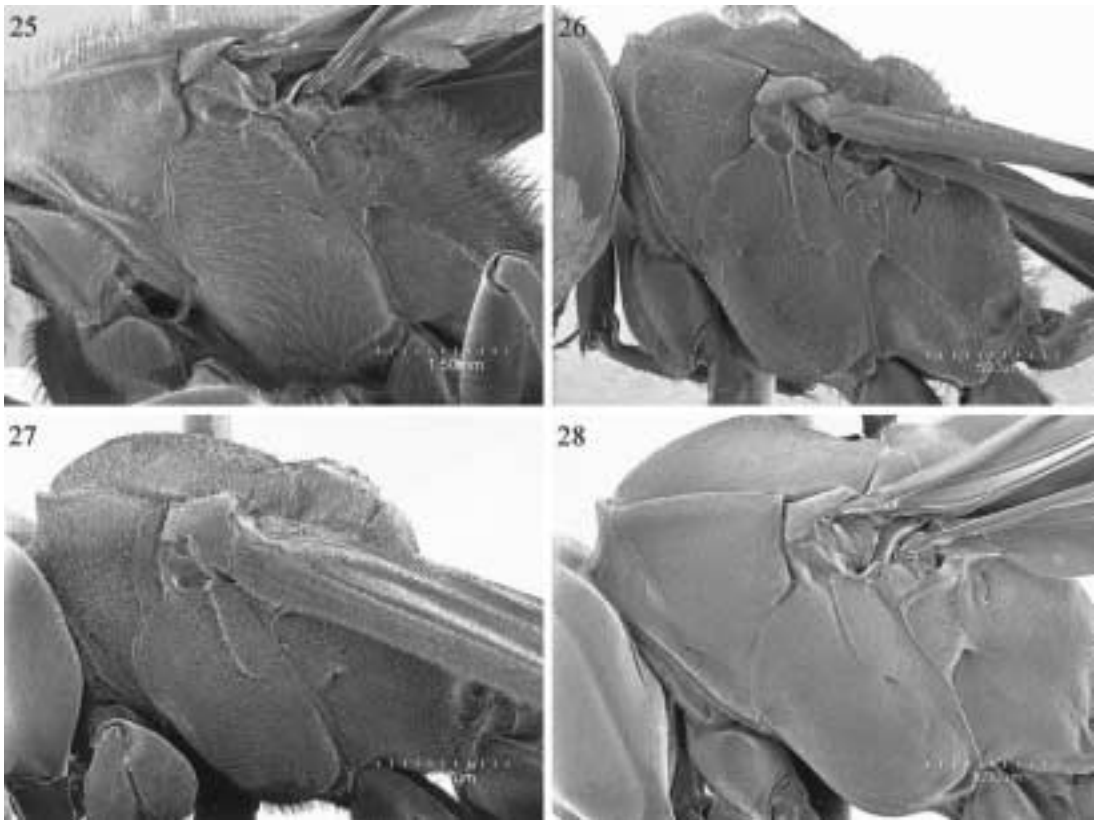
29. **Labral width:** narrower than the maximum width of the clypeus (0); nearly as wide as the maximum width of the clypeus

(1). In the Vespidae except Polistinae, the clypeus is produced and narrowed ventrally, and the dorsal width of the labrum is nearly the same as the ventral width of the clypeus. Consequently the labrum is narrower than the maximum width of the clypeus. In the Polistinae, the clypeus is hardly produced below, and thus this character is sometimes ill defined.

30. **Dorsal margin of labrum except dorsal membrane area:** narrowed where it joins clypeus (0); not narrowed where it joins clypeus (1).

31. **Spicules on palate:** present ventrally, laterally, or both (0); absent (1).

32. **Shape of palate spicules:** pointed apically (0); scalelike (1). In the clade *Pseudopolybia-Epipona* in Wenzel and Carpenter (1994), spicules on the palate are, if present, scalelike except in *Brachygastra*, of which



Figs. 25–28. Mesosoma in lateral view. 25. *Polybia dimidiata*. 26. *Polybia richardsi*. 27. *Polybia emaciata*. 28. *Polybia jurinei*.

the larvae have apically pointed spicules on the palate, if present, in very reduced form.

33. **Spicules on mandibular corium:** absent (0); present (1).

34. **Mandibles:** touching or slightly separated when closed (0); elongate, attenuate, crossed when closed (1); reduced in size, widely separated when closed, with tooth elongate (2); reduced in size, with tooth short or nearly disappearing (3) [nonadditive].

35. **Mandibular teeth:** two, nearly equal in size (0); two, one shorter (1); one (2) [nonadditive].

36. **Mandibular setae:** absent (0); present (1). One or a few setae are present on the outer surface of the mandible in *Brachygastera*, *Pedothoeca*, and *Formicicola*. Such setae are also found in some species of *Polistes* and *Charterginus*.

37. **Maxillary spicules:** present on upper surface, extending apically, or both (0); pre-

sent in basal (or lateral) half both on upper and lower surface (1); absent (2) [nonadditive].

38. **Maxillary palpus:** flat apically (0); not flat and irregular apically (1).

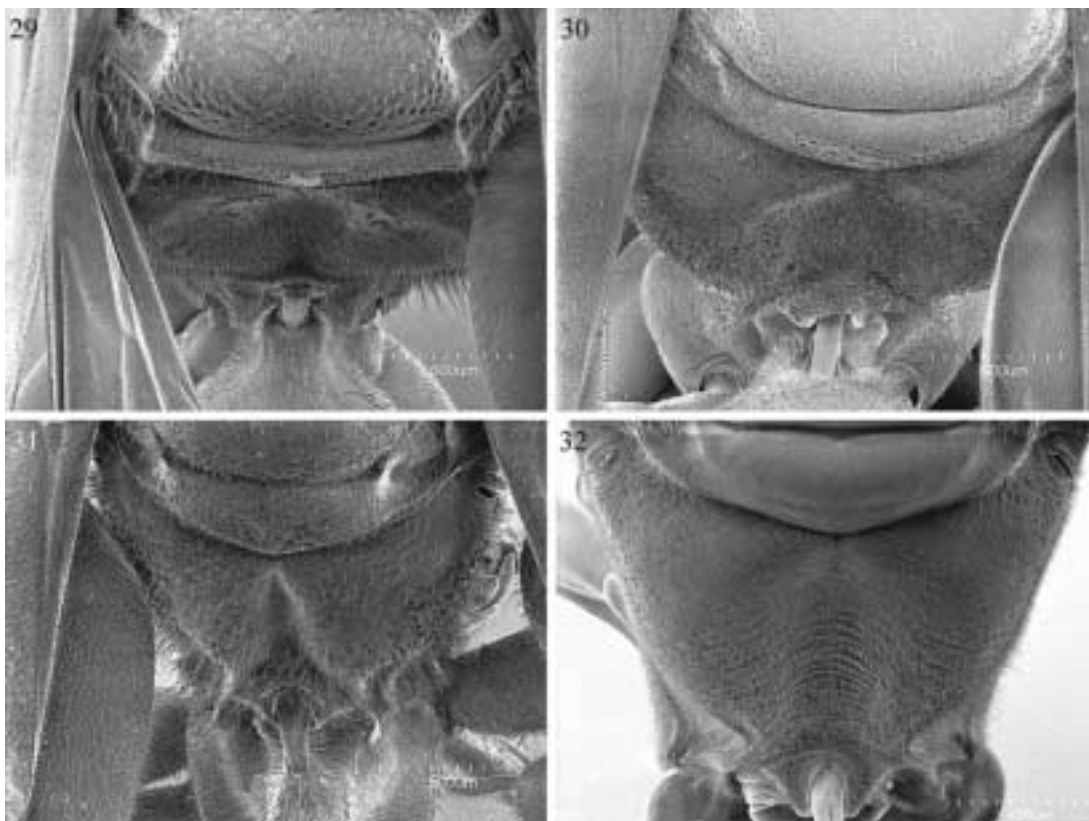
39. **Prementum:** circular or subcircular (0); rounded-quadrate (1).

40. **Labial palpus:** thick, flat apically (0); weakly bilobed apically (1).

41. **Spicules on postmentum:** absent (0); present ventrally, laterally, or both (1); dense on nearly entire surface (2) [nonadditive].

42. **First spiracle:** as large as or slightly larger than successive spiracles (0); larger, about 1.5× (1).

43. **Setae on venter of first thoracic segment:** minute or short (0); thick bristles (1). Bristles on the venter of the first thoracic segment are present in *Epipona* and *Synoeca chalibea*. Thus this character is uninformative for the present analysis.



Figs. 29–32. Propodeum in posterior view. **29.** *Chartergus globiventris*. **30.** *Synoecoides depressus*. **31.** *Polybia emaciata*. **32.** *Polybia liliacea*.

44. Setae on venter of first abdominal segment: minute or short (0); thick bristles (1). The situation for the present character is similar to that for the setae on the venter of the first thoracic segment, although bristles on the venter of the first abdominal segment are found in *Mischocyttarus*.

45. Spicules on venter of second and third thoracic segments: simple, pointed apically (0); simple, rounded apically or minutely dentate ridges (1). This character shows considerable homoplasy in the Polistinae.

NEST CHARACTERS

The study of nests was made by Wenzel (see Wenzel, 1998, for illustrations). Nest architecture has been important for recognizing groups in Polistinae, with many groups distinguished originally by their nests and sub-

sequently supported by morphological characters. The nest types formalized by de Saussure (1853–1858) were retained to greater or lesser degree over the years and sometimes augmented (Richards and Richards, 1951). The major categories are “gymnodomous” (no envelope) versus “calyptodomous” (covered by an envelope), “stelocytarus” (comb hanging on pedicels from the substrate), “astelocytarus” (combs sessile on the substrate, nest expanded primarily along the substrate) and “phragmocytarus” (primary comb without a pedicel, subsequent combs built sessile on the preceding envelope). Subcategories exist also, such as “laterinidal” versus “rectinidal” to distinguish combs built such that cells are perpendicular versus parallel to the supporting pedicel, respectively. While these terms are useful as phenetic descriptors, they are nonetheless in-



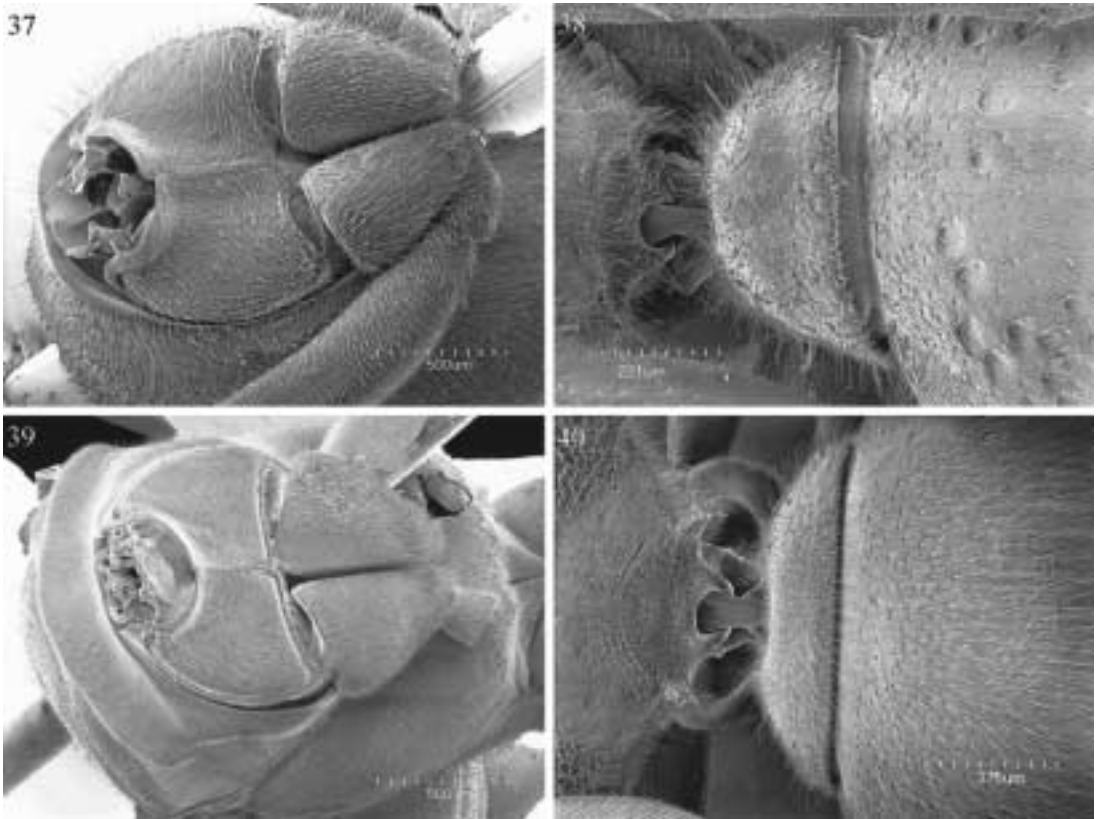
Figs. 33–36. Propodeum in posterior view. **33.** *Polybia nidulatrix*. **34.** *Polybia rejecta*. **35.** *Polybia jurinei*. **36.** *Polybia bifasciata*.

adequate to capture the variation now known in South American Polistinae (let alone the world fauna) and may not relate to homologous states that are useful in modern systematic treatments.

One shortcoming of the classical descriptions of nests is that they tended to focus on diagnosing species and exploring what may be unique aspects of a species' nest rather than describing features shared with some relatives. Many new nest characters are now available to help in the systematic context, and for the most part all genera can be distinguished easily (Wenzel, 1998) and placed in a hierarchical scheme of relationships using cladistic methods (Wenzel, 1993). As indicated above, such a hierarchy is not yet stable to the addition of new data, nor does it match exactly the pattern obtained by cladistic analysis of adult morphology, but the two forms of data frequently appear to com-

plement each other (Wenzel, 1993) even as they come in conflict (above). In the present context, the challenge is to find some synapomorphic characters among the genera that build phragmocyttarus nests. De Saussure's description of the phragmocyttarus form was based on a geometrical ideal that was supposed to represent in abstraction the perfect forms of nests built imperfectly by natural species (de Saussure 1853–1858: XLVII, and ff., pl. XXXV). Certain ideal elements seem to be true of all taxa concerned here, whether recognized by de Saussure (such as secondary combs sessile on preceding envelope) or by more recent authors (such as the envelope not being removed and expanded after closure; Wenzel, 1991), but it is nonetheless appropriate to question what, if anything else, does "phragmocyttarus" really mean?

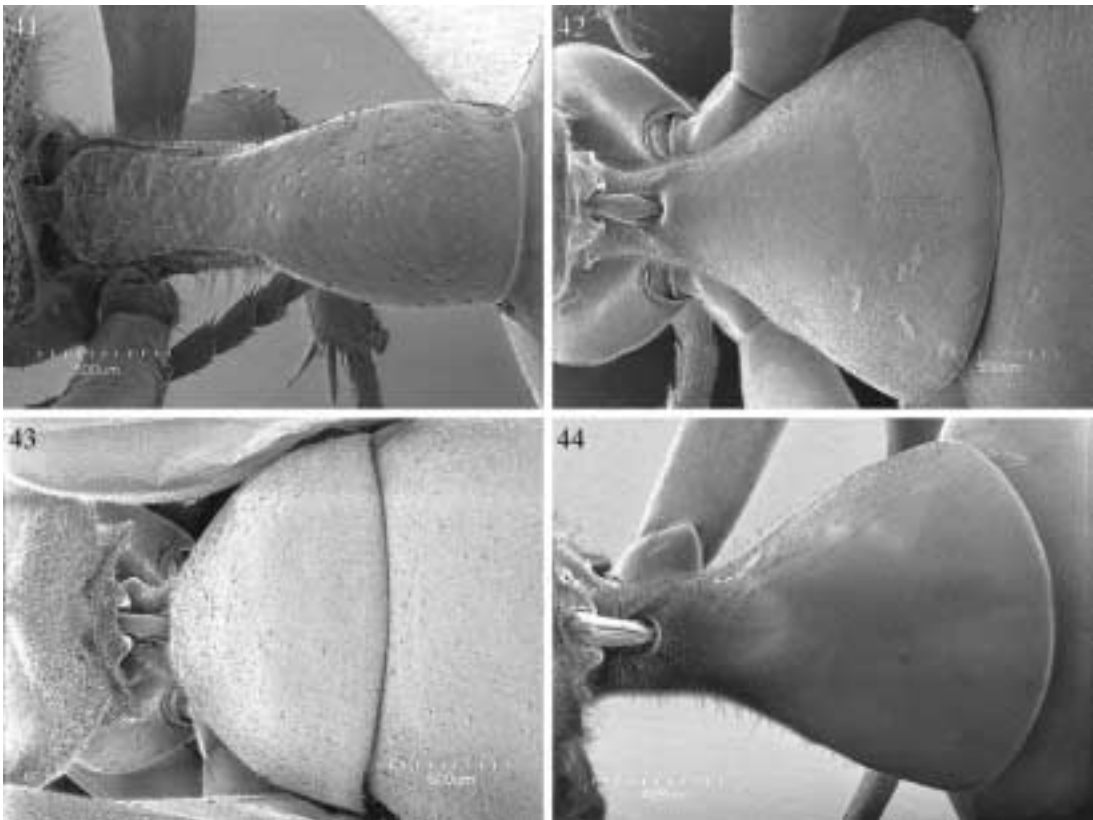
Variation among these nests does not form a neat pattern, as the characters offered be-



Figs. 37–38. *Protonectarina sylveirae*. **37.** Prothorax in frontal view. **38.** Metasomal tergum I in dorsal view. Fig. 39. *Polybia rejecta*, prothorax in frontal view. Fig. 40. *Brachygastra lecheguana*, metasomal tergum I in dorsal view.

low demonstrate (more thorough descriptions are available in earlier work such as Wenzel, 1991, 1993, 1998). But, just as important as the characters themselves is the identity of the species chosen to represent each group. Certain hypothetical ideals may be postulated (as de Saussure did), but they do not exist. Actual species should be used rather than ideals. For example, *Brachygastra* and *Polybia* cannot be separated easily because the diversity of forms in each genus is overlapping (Wenzel, 1998). For the present purposes, nests of *B. smithii* (de Saussure) were used partly because they are easy to characterize, whereas the very different nests of *B. mellifica* (Say) are not. For *Polybia*, the species used were *P. (Polybia) striata* (Fabricius), *P. (Alpha) quadricincta* de Saussure, *P. (Apopolybia) jurinei* de Saussure, *P. (Furnariana) furnaria* von Ihering, *P. (Cylindroeca) dimidiata* (Olivier), *P. (Trichinothorax) sericea* (Olivier), *P. (Pedothoeca) emaciata* Lucas, *P. (Formicicola) rejecta* (Fabricius), and *P. (Platypolybia) incerta* Ducke. The subgenus *Myrapetra* is so diverse that polymorphisms were coded because finding a “typical” species is a great challenge. For the monotypic genera *Protonectarina* and *Synoecoides*, and for *Epipona*, in which all species’ nests look very much alike, there is no problem with diversity of forms within the genus. *Chartergus globiventris* de Saussure was used as representative of that genus, because this species is best represented in both new and old nests in collections, and the mode of nest expansion is clearer.

46. Envelope reinforcement: blots of paper (0); both blots and imbricate reinforcement (1).



Figs. 41–44. Metasomal tergum I in dorsal view. 41. *Epipona niger*. 42. *Polybia bifasciata*. 43. *Synoecoides depressus*. 44. *Polybia liliacea*.

47. **Envelope material:** coarse vegetable matter (0); tiny fragments (1); mud (2); long fiber (3) [nonadditive]. States 0 and 1 divide the class of “short chips” defined elsewhere (e.g., Wenzel, 1998).

48. **Secretion:** sparse (0); common, at least on top (1).

49. **Primary comb:** initially sessile, but growing off substrate (0); entirely sessile (1); supported by a buttressed sheet (2) [nonadditive].

50. **Entrance:** ventral (0); lateral (1).

51. **Sculpture below entrance:** none (0); pair of ribs (1).

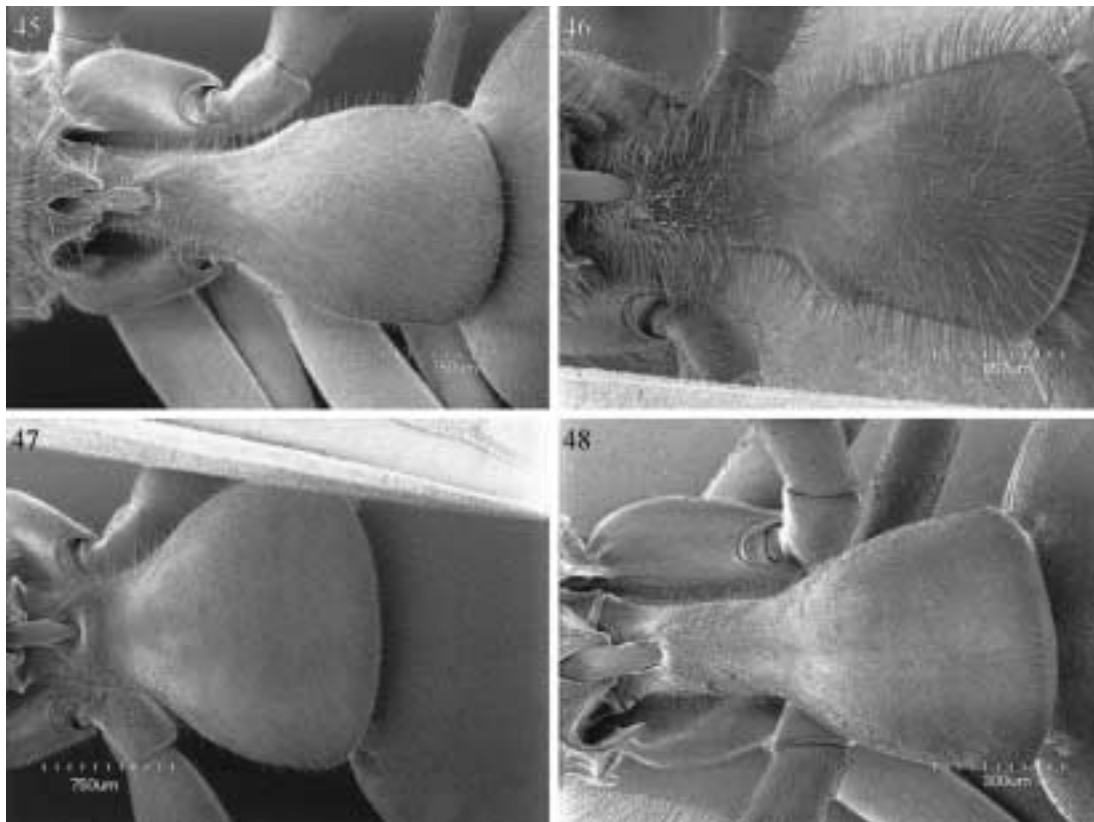
52. **Secondary envelopes:** close to preceding comb, with narrow passage (0); distant from preceding comb, deeply dished (1).

53. **Abrupt angles on upper surface of nest:** absent (0); present (1).

54. **Abrupt angles on lower surface of nest:** absent (0); present (1).

RESULTS

Analysis of the data on adult morphology (table 1) with NONA, using a variety of approximate search commands, resulted in eight cladograms of length 72, consistency index 0.61, and retention index 0.64. This result was verified with exact analysis, using the command **mswap 12**, which swapped cutting the trees in 12 places. All of the cladograms are strictly supported (sensu Nixon and Carpenter, 1996b). The consensus is shown in figure 49. Weighting with either successive weighting (using the consistency index) or implied weighting (default concavity) resulted in one cladogram, with the topology shown in figure 53; this topology is



Figs. 45–48. Metasomal tergum I in dorsal view. 45. *Polybia rejecta*. 46. *Polybia dimidiata*. 47. *Polybia jurinei*. 48. *Polybia nidulatrix*.

one of those resulting from the analysis under equal weights.

Analysis of the data on larval morphology (table 2) with NONA results in many thousands of cladograms of length 31, consistency index 0.67, and retention index 0.54, but of course this is an artifact: the three taxa unknown for the larvae, and thus scored with all missing values, function as “wildcards” in the sense of Nixon and Wheeler (1992), being placed in every possible position on the topology. The consensus of even a small number of the cladograms is thus completely unresolved. Analysis of the data excluding these three terminals results in 157 cladograms of length 31, and, of these, just 79 are strictly supported (retained after the **best** command). The consensus of this set of cladograms is shown in figure 50; it resolves one group. With successive weighting of the exclusive data 12 cladograms result, the con-

sensus of which contains this group, and also places *Brachygastra* with *Pedothoeca*. With implied weighting of the exclusive data a single cladogram results, one of those produced under equal weights, better resolved but likewise placing *Brachygastra* with *Pedothoeca*.

Analysis of the data on nest architecture (table 3) with NONA yields 1002 cladograms of length 27, consistency index 0.44, and retention index 0.53. Of these cladograms, 457 are strictly supported, but their consensus is entirely unresolved (not shown). Many of these cladograms differ in alternative placement of *Myrapetra*, which may take many positions due to the polymorphisms. If *Myrapetra* is excluded from the analysis, 186 trees of 27 steps are found, 123 being retained after filtering with the **best** command. The consensus is still unresolved, but successive weighting stabilized on four cladograms. The consensus of these four

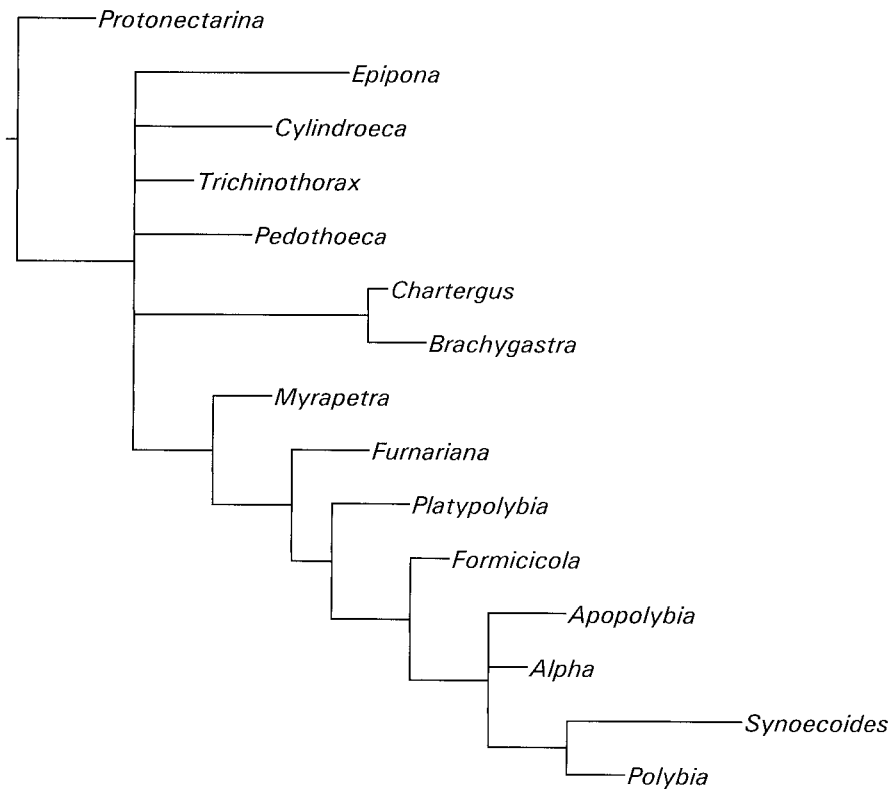


Fig. 49. Consensus tree for eight cladograms resulting from analysis of the adult character matrix in table 1.

cladograms includes *Synoecoides* among the subgenera of *Polybia*, but not near *Polybia* s.s. As might have been predicted, *Brachygastra* also falls among the subgenera of *Polybia*, and this is true even when a matrix using *B. mellifica* rather than *B. smithii* is run (not included here). Both *Synoecoides* and *Brachygastra* are similarly included among the subgenera of *Polybia* under implied weighting using the program PIWE.

The incongruence length difference (Mickey and Farris, 1981; see Farris et al., 1994) for combination of the three data sets is 17. This amount is significant, according to the test implemented in DADA (which required using the program HENNIG86 (Farris, 1988), in turn requiring that polymorphic variables be treated as missing values) at a level of $p = 0.02$ for 100 replicates. The pairwise data set combinations were each congruent, according to the test implemented in NONA; it is the three-way combination that

is incongruent. Some authors would interpret the significant incongruence as a reason not to combine the data sets, but as reviewed in Nixon and Carpenter (1996a), simultaneous analysis of combined data is the method of choice in cladistics, because it better maximizes parsimony than do separate analyses. We agree with Nixon and Carpenter (1996b) in regarding the significance test of Farris et al. (1994) simply as a means of determining whether the amount of incongruence is large or small. It is large among these three data sets; these data sets nevertheless should be combined, and we analyze them simultaneously next.

Analysis of the combined data in tables 1–3 with NONA resulted in 13 cladograms of length 147, consistency index 0.52, and retention index 0.47. This result was verified with exact analysis, using the command **mswap 12**. All of the cladograms are strictly supported; the consensus is shown in figure 51.

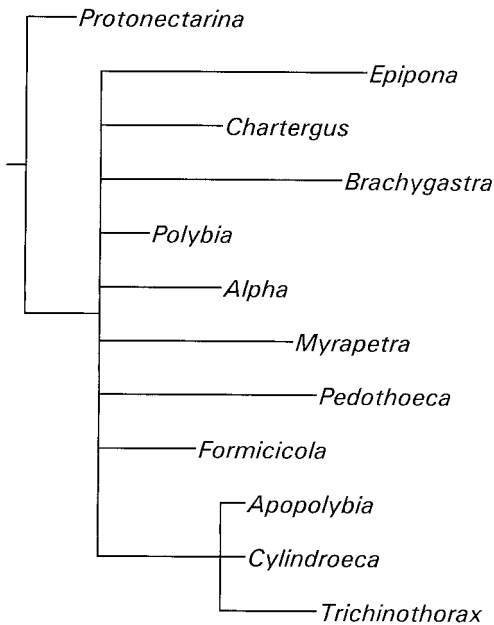


Fig. 50. Consensus tree for 79 strictly supported cladograms resulting from analysis of the larval character matrix in table 2, excluding the three terminals that have all missing values.

Successive weighting resulted in one cladogram, shown in figure 52; this is not identical to any of the cladograms resulting from the analysis under equal weights. Implied weighting resulted in a different cladogram (figure 53), also not among those resulting from analysis under equal weights. Selection of either cladogram from a posteriori weighting on the basis of the self-consistency of results (that is, most parsimonious under the weights that it implies, and so considered the best established cladogram, in the sense of being based upon the most reliable characters; Carpenter et al., 1993; Goloboff, 1993) would thus be dependent upon the particular weighting function adopted. The basis for adopting a particular weighting function is unclear. However, the weighted cladograms differ in just two respects: relative relationships of *Furnariana* and *Platypolybia*, and of *Alpha* and *Apopolybia*. Both cladograms are permitted by the relatively unresolved consensus. The discussion that follows will therefore refer to the weighted cladograms.

The combined data indicate paraphyly of *Polybia*, in terms of *Synoecoides*, which is

the sister group of the subgenus *Polybia* s.s. This relationship is also shown by the adult characters alone. It is established by the deep, wide, propodeal concavity, and the narrow secondary spiracular entrance (a homoplastic character, reversing from the wide condition).

The consensus under equal weights does not resolve that particular sister-group relationship (fig. 51), but all analyses support a clade including *Polybia* s.s., *Synoecoides*, and the subgenera *Alpha* and *Apopolybia*, based on a short, broad metasomal petiole (from which the sessile condition in *Synoecoides* is then a further derivation) and presence of an occipital carina and appressed scutal hairs (both optimized as reversals). The envelope reinforcement (both blots and imbricate reinforcement) could also be optimized as homoplastic support for this clade. The larval mandible with two teeth, one shorter, could also be optimized to support this clade on the tree resulting from successive weighting, but is unknown for *Synoecoides*.

Under implied weighting, the sister group of *Polybia* s.s. + *Synoecoides* is the subgenus *Apopolybia*, a grouping supported by the projecting metanotum. Under successive weighting the sister group is the subgenus *Alpha*, supported only by homoplasies (in the propodeal valvula and lower surface of the nest).

The sister group to the clade including these four taxa is the subgenus *Formicicola*, a relationship also supported under equal weights, based on by the flattened scutum and change of a weak furrow into a shallow propodeal concavity.

Under implied weighting, the sister group, in turn, to this clade of five taxa is the subgenus *Platypolybia*, based on narrow tempora. Under successive weighting, however, *Platypolybia* is the sister group of *Furnariana*, based on two homoplastic nest characters (abrupt angles on upper and lower surfaces). In either case, *Platypolybia* and *Furnariana* are placed with the aforementioned subgenera and *Synoecoides* based on the flattened scutellum and anteriorly narrow propodeal valvula (a homoplastic character).

Successive sister groups under both equal weighting and a posteriori weighting are, in

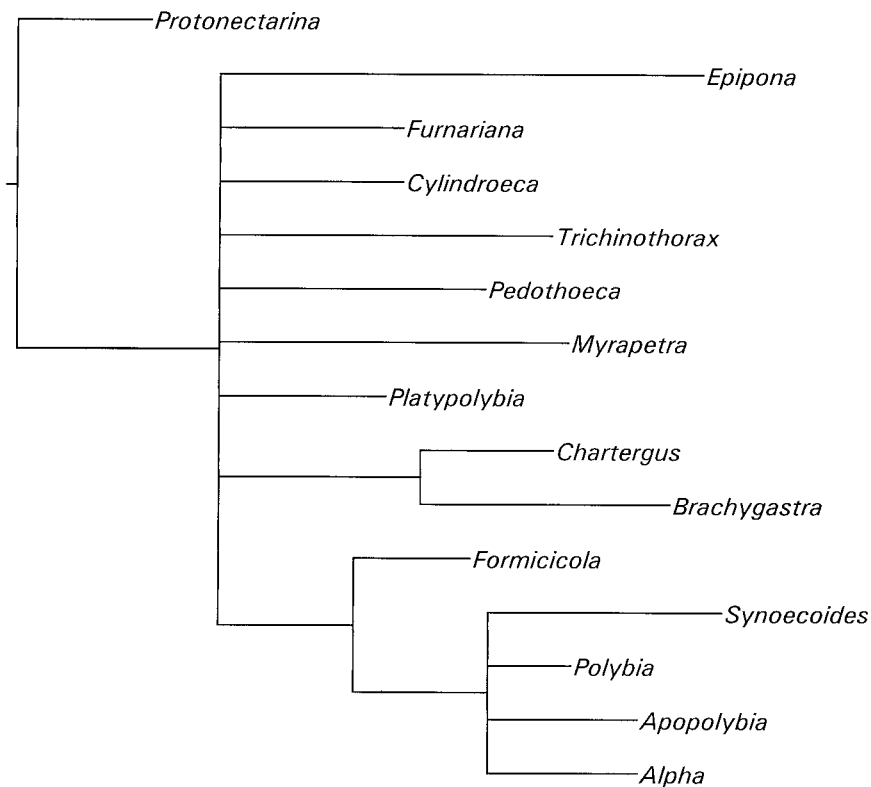


Fig. 51. Consensus tree for 13 cladograms resulting from simultaneous analysis of the combined character data in tables 1–3.

turn, *Myrapetra*, supported by a short malar space (a reversal), and *Trichinothorax*, supported by change of the propodeal concavity from a deep to a weak furrow and clypeal pubescence present (homoplastic).

Interrelationships of the subgenera *Cylindroeca* and *Pedothenoeca* are not resolved, but *Polybia* inclusive of *Synoecoides* is a monophyletic group. This is supported by the dorsally flattened clypeus and larval maxillary spicules on the upper surface (unknown for several taxa). Several other, homoplastic characters support this clade as well: the elongate clypeal–eye contact (then reversed in *Myrapetra* and polymorphic in *Trichinothorax*), the secondary spiracular entrance wide (several subsequent reversals), and nest primary support sessile and entrance lateral (both reversing subsequently).

Under weighting, *Epipona* is the sister group to *Polybia* inclusive of *Synoecoides*. The consensus under equal weights does not

resolve that relationship, because both *Epipona* and *Chartergus* + *Brachygastra* group with some of the basal subgenera of figure 51 on various of the underlying cladograms. In any case this analysis should not be regarded as addressing the question of the sister group of *Polybia* (inclusive of *Synoecoides*), as discussed below.

CONCLUSIONS

The conclusion that may be drawn for taxonomic purposes from these analyses is clear: *Synoecoides* cannot be maintained as a genus. It is closely related to the subgenus *Polybia* s.s., thus, recognition of a genus *Synoecoides* renders *Polybia* paraphyletic. Although *Synoecoides* has a number of autapomorphies, most of those by which the genus was originally diagnosed are now seen to be an extreme development of characters found in *Polybia*. This situation is most sim-

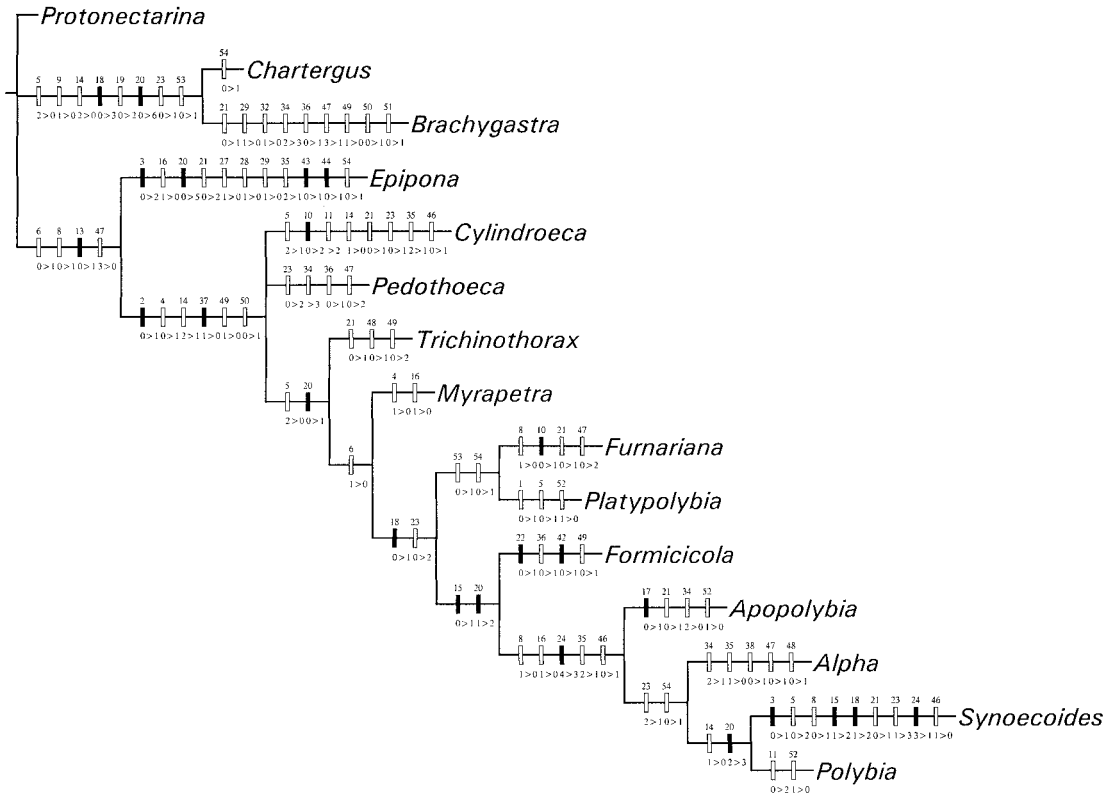


Fig. 52. Cladogram resulting from successive weighting of the combined character data. Characters have been optimized with only unambiguous changes plotted. Character numbers are above the hashmarks; state changes are shown below, with the respective primitive and derived conditions separated by a greater than sign. Filled hashmarks denote uncontroversial changes whereas open hashmarks indicate homoplasy in the character.

ply rectified by synonymizing *Synoecoides* with *Polybia*, and that is the solution we are adopting here (NEW SYNONYMY). It seems best to treat *Synoecoides* as a subgenus of *Polybia* given the unsettled status of the subgeneric taxa of *Polybia*, a topic we will next discuss.

Even if *Polybia* inclusive of *Synoecoides* is monophyletic, the need for further work on the subgenera of *Polybia*, and the relationships of *Polybia* to other epiponine genera, is also clear. Weighted or not, none of the trees is completely resolved. The weighted cladograms contain groups supported only by homoplasies, and thus do not appear to be well established. This is also the case for a number of the subgenera (*Polybia* s.s., *Alpha*, *Platypolybia*, *Myrapetra*, *Trichinothorax*, and *Pedothoeca*), and all of the rest are supported mostly by homoplasies. Two of the

subgenera are highly polymorphic (*Trichinothorax*, 12 cells in the combined matrix; *Myrapetra*, 16), and thus the course of breaking these terminals into monomorphic ones suggests itself (Nixon and Davis, 1991). That is, analysis at the species level should be pursued. In addition, the outgroup could be expanded. Although this group of phragmocytarus-nesting genera has been supported as monophyletic by analysis of behavioral data (Wenzel, 1993) and simultaneous analysis of behavior along with adult and larval morphology (Wenzel and Carpenter, 1994), it was not monophyletic in the analysis by Carpenter (1991). The instability of relationships among these genera from one analysis to another may now be seen to be, in part, the product of paraphyly of *Polybia*. Settling the relationships among these genera has not

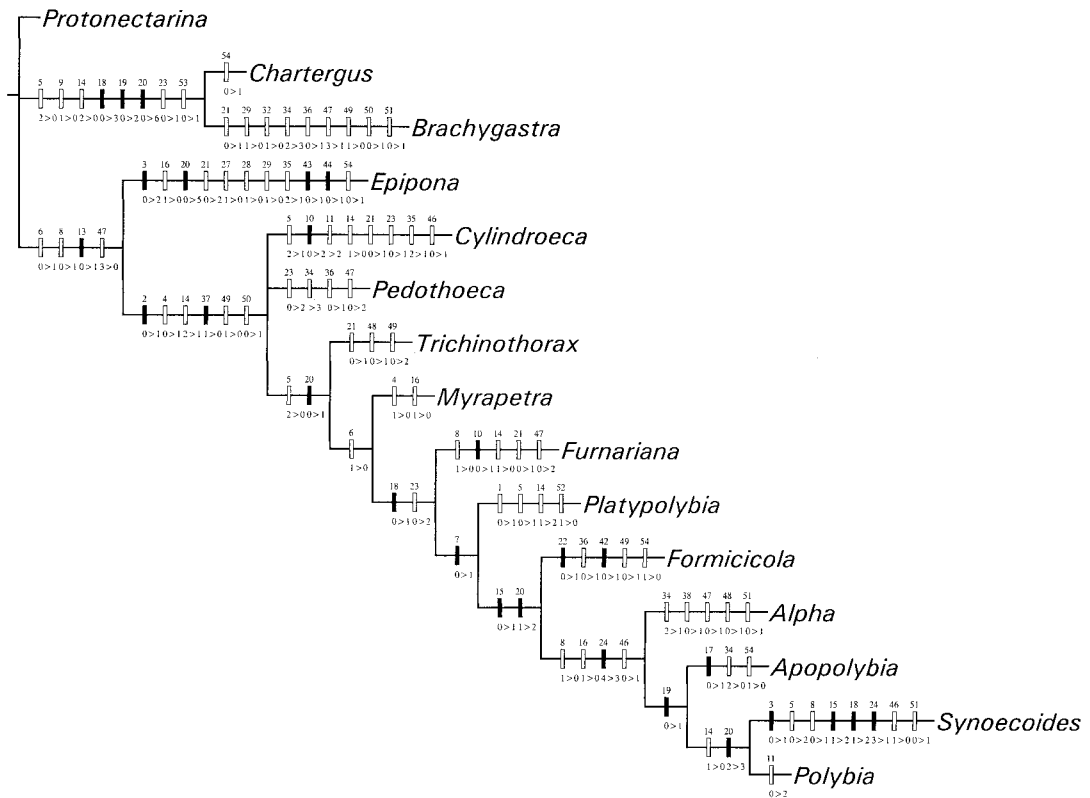


Fig. 53. Cladogram resulting from implied weighting of the combined character data. Plotting conventions as in fig. 52.

been an object of this study, and the characters listed in tables 1–3 are insufficient to do so. Addition of related genera (namely, the astelocytarus-nesting genera, *Protopolybia*, and *Charterginus*) and relevant characters are required. Both courses are necessary to advance further toward a more comprehensive picture of polistine phylogeny. In the meantime, the subgenera of *Polybia* should be maintained, now including *Synoecoides*.

ACKNOWLEDGMENTS

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REFERENCES

- Araujo, R. L.
1944. Contribuição para o conhecimento do gênero "*Synoecoides*" Ducke, 1905 (Hym., Vespidae). *Rev. Bras. Biol.* 4(3): 399–348.
- Carpenter, J. M.
1991. Phylogenetic relationships and the origin of social behavior in the Vespidae. In K. G. Ross and R. W. Matthews (eds.), *The social biology of wasps: 7–32*. Ithaca, NY: Cornell Univ. Press.
1993. Biogeographic patterns in the Vespidae (Hymenoptera): Two views of Africa and South America. In P. Goldblatt (ed.), *Biological relationships between Africa and South America: 139–155*. New Haven, CT: Yale Univ. Press.
1996. Phylogeny and biogeography of *Polistes*. In S. Turillazzi and M. J. West-Eberhard (eds.), *Natural history and*

- evolution of paper-wasps: 18–57. Oxford: Oxford Univ. Press.
- Carpenter, J. M., and M. C. Day
1988. Nomenclatural notes on Polistinae (Hymenoptera: Vespidae). *Proc. Entomol. Soc. Washington* 90: 323–328.
- Carpenter, J. M., and J. W. Wenzel
1990(1989). Synonymy of the genera *Protopolybia* and *Pseudochartergus* (Hymenoptera: Vespidae; Polistinae). *Psyche* 96: 177–186.
- Carpenter, J. M., J. E. Strassmann, S. Turillazzi, C. R. Hughes, C. R. Solís, and R. Cerovo
1993. Phylogenetic relationships among paper wasp social parasites and their hosts (Hymenoptera: Vespidae; Polistinae). *Cladistics* 9: 129–146.
- Carpenter, J. M., J. W. Wenzel, and J. Kojima
1996. Synonymy of the genus *Occipitalia* Richards, 1978, with *Clypearia* de Saussure, 1854 (Hymenoptera: Vespidae; Polistinae, Epiponini). *J. Hym. Res.* 5: 157–165.
- Dias Filho, M. M.
1975. Contribuição a morfologia de larvas de vespídeos sociais do Brasil. *Rev. Bras. Entomol.* 19: 1–36.
- Ducke, A.
1905. Nouvelles contributions à la connaissance des vespides sociales de l'Amérique du Sud. *Rev. Entomol. Caen* 24: 5–24.
1907. Novas contribuições para o conhecimento das vespas (Vespidae sociales) da região neotropical. *Bol. Mus. Emilio Goeldi Pará* 5: 152–199.
- Farris, J. S.
1988. Hennig86, ver. 1.5. Program and documentation. Port Jefferson Station, NY.
- Farris, J. S., M. Källersjö, A. G. Kluge, and C. Bult
1994. Testing significance of incongruence. *Cladistics* 10: 315–319.
- Goloboff, P. A.
1993. Estimating character weights during tree search. *Cladistics* 9: 83–91.
1999a. NONA, version 2. Program and documentation. Fundación e Instituto Miguel Lillo, Tucumán, Argentina.
1999b. PIWE, version 3. Program and documentation. *Ibid.*
- Hennig, W.
1966. *Phylogenetic systematics*. Urbana: Univ. Illinois Press.
- International Commission on Zoological Nomenclature
1976. Opinion 1051. *Rhopalidia* Lepeletier, 1836 (Insecta: Hymenoptera): Suppressed under the plenary powers. *Bull. Zool. Nomencl.* 32: 240–241.
- Jeanne, R. L.
1991. The swarm-founding Polistinae. In K. G. Ross and R. W. Matthews (eds.), *The social biology of wasps*: 191–231. Ithaca, NY: Cornell Univ. Press.
- Kojima, J.
1997. Abandonment of the subgeneric concept in the Old World polistine genus *Ropalidia* Guérin-Méneville, 1831 (Insecta: Hymenoptera: Vespidae). *Nat. Hist. Bull. Ibaraki Univ.* 1: 93–105.
1998. Larvae of social wasps (Insecta: Hymenoptera; Vespidae). *Nat. Hist. Bull. Ibaraki Univ.* 2: 7–227.
- Kojima, J., and M. G. Keeping
1988. Description of mature larva of *Belonogaster dubia* Kohl (Hymenoptera, Vespidae), with notes on the larval characters of the Polistinae. *Kontyû* 56: 817–823.
- Latreille, P. A.
1802. *Histoire naturelle, générale et particulière des crustacées et des insectes*. Paris: Sonnini's suites à Buffon.
- Lepeletier de St. Fargeau, A.L.M.
1836. *Histoire naturelle des insectes. Hyménoptères, 1*. Paris: Roret's Suites à Buffon.
- Mickevich, M. F., and J. S. Farris
1981. The implications of congruence in Menidia. *Syst. Zool.* 30: 351–370.
- Nixon, K. C.
1998a. DADA, version 1.3. Program and documentation. Ithaca, NY: Bailey Hortorium, Cornell University.
1998b. CLADOS, version 1.7. Program and documentation. *Ibid.*
1999. WINCLADA, version 0.9.95b (beta). Program and documentation at cladistics.com.
- Nixon, K. C., and J. M. Carpenter
1996a. On simultaneous analysis. *Cladistics* 12: 221–241.
1996b. On consensus, collapsibility and clade concordance. *Ibid.*: 305–321.
- Nixon, K. C., and J. I. Davis
1991. Polymorphic taxa, missing values and cladistic analysis. *Cladistics* 7: 233–241.
- Nixon, K. C., and Q. D. Wheeler
1992. Extinction and the origin of species. In Q. D. Wheeler and M. J. Novacek (eds.), *Extinction and phylogeny*: 119–143. New York: Columbia Univ. Press.

- Raw, A.
1985. *Asteloeca*, a new neotropical wasp genus (Hymenoptera, Vespidae). *Rev. Bras. Entomol.* 29: 185–188.
- Reid, J. A.
1942. On the classification of the larvae of the Vespidae. *Trans. R. Entomol. Soc. London* 92 (2):285–331.
- Richards, O. W.
1978. The social wasps of the Americas, excluding the Vespinae. London: British Museum (Natural History).
- Richards, O. W. and M. J. Richards
1951. Observations on the social wasps of South America (Hymenoptera, Vespidae). *Trans. Entomol. Soc. London* 102: 1–170.
- Saussure, H. de
1853–1858. Monographie des Guêpes Sociales ou de la Tribu des Vespiens. Paris: Masson; and Genève: J. Cherbuliez. [1–96, 1853; 97–256, 1854]
1863. Mélanges Hyménoptérologiques. II. Vespides. *Mém. Soc. Phys. Hist. Nat. Genève* 17: 171–244.
- Silveira, O. T.
1994. External morphology of the larva of *Pseudochartergus chartergoides* (Gribodo) (Hym., Vespidae, Polistinae). *Entomol. Mon. Mag.* 130: 71–75.
- Wenzel, J. W.
1991. Evolution of nest architecture in social vespids. In Ross, K. G. and R. W. Matthews (eds.), *The social biology of wasps*: 480–519. Ithaca, NY: Cornell Univ. Press.
1993. Application of the biogenetic law to behavioral ontogeny: a test using nest architecture in paper wasps. *J. Evol. Biol.* 6: 229–247.
1998. A generic key to the nests of hornets, yellowjackets, and paper wasps worldwide (Vespidae: Vespinae, Polistinae). *Am. Mus. Novitates* 3224: 39 pp.
- Wenzel, J. W., and J. M. Carpenter
1994. Comparing methods: Adaptive traits and tests of adaptation. In P. Eggleton and R. I. Vane-Wright (eds.), *Phylogenetics and ecology*: 79–101. London: Academic Press.
- West-Eberhard, M. J., J. M. Carpenter, and P. Hanson
1995. The vespid wasps (Vespidae). In P. Hanson and I. Gauld (eds.), *The Hymenoptera of Costa Rica*: 561–587. London: The Natural History Museum.
- White, A.
1841. Description of a South American wasp which collects honey. *Ann. Mag. Nat. Hist.* 7: 315–322.

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