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Phylogeny of the Eucoilinae (Hymenoptera: Cynipoidea: Figitidae)

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The Eucoilinae are a diverse and important group of parasitoids of Diptera, particularly in the tropics, but they are poorly known systematically and their generic classification is partly chaotic. Here, we present the first comprehensive cladistic analysis of higher eucoiline relationships. The analysis is based on 148 skeletal characters of adults documented in more than 1100 digital images available in an Internet-accessible database. The characters were coded for 45 taxa representing 35 eucoiline genera, spanning the entire diversity of the group, and 7 outgroup genera. Relationships were partly difficult to resolve and parsimony analysis under implied weights performed considerably better than analysis under uniform weights. The results support the monophyly of the Eucoilinae and show that eucoilines are most closely related to the figitid subfamilies Emargininae and Pycnostigminae, but are ambiguous concerning the exact relationships among these three lineages. Of the 6 eucoiline genus groups recognized by Nordlander in 1982 (*Entomol. Scand.* 13, 269–292), only 2 are supported as monophyletic: the *Trybliographa* and *Kleidotoma* groups. The *Gronotoma* group is a paraphyletic assemblage of two different basal clades of eucoilines. The *Rhoptromeris* group is unnatural and only the 2 core genera, *Rhoptromeris* and *Trichoplasta*, form a monophyletic lineage. The data are ambiguous concerning the *Ganaspis* group, which appears to be paraphyletic, and the *Chrestosema* group, which may be a good clade. Based on the results we propose a modified system of informal genus groups in the Eucoilinae and discuss putative synapomorphies supporting each genus group. The proposed relationships imply that the first eucoilines were parasitoids of leaf-mining agromyzids. The earliest split in the group was apparently between an Afrotropical and a Neotropical lineage, and much of the early radiation of the group occurred in these regions, particularly in the Neotropics.

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INTRODUCTION

Recent phylogenetic analyses suggest that about 90% of the insect-parasitic cynipoids, particularly those of small body size, belong to a single monophyletic lineage conveniently recognized as a single family, the Figitidae (*sensu lato*) (Rasnitsyn, 1980, 1988; Ronquist, 1994, 1995b, 1999). With this broad circumscription, the Figitidae include some taxa that have previously been treated as separate families by many workers, namely, the Charipidae, Eucoilidae, and Anacharitidae. However, these lineages are phylogenetically nested among taxa traditionally regarded as figitid subfamilies and, for this reason and others, they are best treated as subfamilies in the Figitidae (Ronquist, 1999). All figitids develop as internal parasites in larvae of endopterygote insects belonging to the orders Hymenoptera, Neuroptera, or Diptera (Ronquist, 1994, 1995b, 1999).

The Eucoilinae are, by far, the most species-rich figitid subfamily (Ronquist, 1995b). Currently, nearly 1000 eucoiline species placed in 82 genera have been described (Ronquist, 1999) but it is estimated that this constitutes only 5–20% of the true diversity of the group (Nordlander, 1984). The highest eucoiline diversity is found in the tropics, particularly in the Neotropics (Fergusson and Hanson, 1995; Nieves-Aldrey and Fontal-Cazalla 1997a, b; Fontal-Cazalla and Nieves-Aldrey 1999), but the subfamily is recorded from all biogeographic regions (Nordlander, 1984).

Eucoilines are nicely identified as a natural group by the presence of an elevated plate dorsally on the scutellum, referred to as the scutellar plate or cup. On the dorsal surface, the plate has a glandular pit, the function of which is unknown (cf. 77:2, Figs. 7E and 7F). The scutellar plate is present in all eucoilines and is unique to them among parasitic wasps.

The Eucoilinae are small insects, with adults usually ranging in size from 1 to 5 mm, most often fully winged but occasionally brachypterous. The majority of species are shining black to brown in color and the body is largely polished, without distinct surface sculpture. The female antenna typically has 13 articles and the flagellum is often swollen distally to form a more or less distinct club but it is never geniculate. The male antenna is 15-segmented and usually has the third or fourth segment, which carries the antennal sex glands, modified. Many genera possess a patent hairy ring anteriorly on the metasoma, situated at the base of the third abdominal tergum.

All eucoilines are solitary koinobiont endoparasitoids that attack the first-instar larvae of cyclorrhaphous Diptera in various microhabitats, emerging from the pupa of their hosts by biting an irregular hole through the puparium. The adults frequent the sites where their hosts develop, such as fungi, bird nests, cow manure, rotten wood, rotting vegetation, rotting carcasses, or leaves and others parts of plants infested by dipteran larvae.

Because of their habits, eucoilines are important in the study of forensic entomology and parasitoid ecology and in the biological control of serious dipterous pests affecting crops (food and ornamentals), livestock, or commercial fungi. A few species have become popular model organisms in studies of parasitic wasp biology (Ronquist, 1999, and references cited therein). Several species have been examined for their potential usefulness as natural enemies of pest Diptera and some have been used in biological control programs (Baloch *et al.*, 1967; Baranowski *et al.*, 1993; Clauson *et. al.*, 1965; Hertlein, 1986; Ihering, 1905; Johnson, 1993; Matrangolo *et al.*, 1997; Menezes *et al.*, 1997; Nakao and Funasaki, 1979; Ovruski and Fidalgo, 1994; Pickens and Miller, 1980; Rathman *et.*

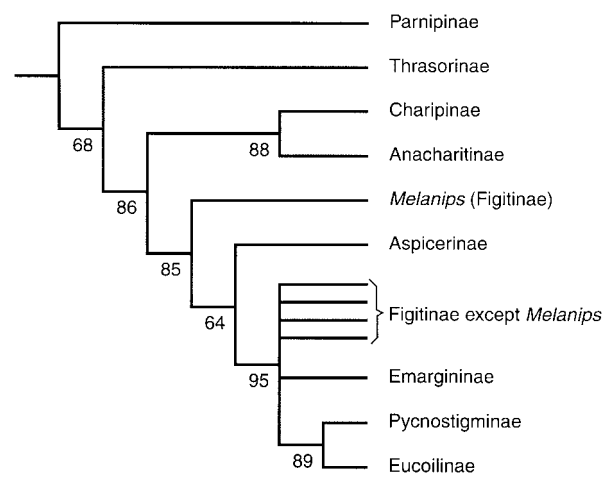

FIG. 1. Figitid relationships according to the preliminary analysis of Ronquist (1999). Numbers on branches are bootstrap support values.

al., 1991; Rozova, 1991; Turica, 1968, Villeneuve and Trottin Caudal, 1997; Wharton *et al.*, 1998).

Eucoilines were originally treated as members of the Cynipidae (Kieffer, 1901, 1902; Dalla Torre and Kieffer, 1910; Weld, 1952) but later papers place them either in the Figitidae (Riek, 1971; Rasnitsyn, 1980, 1988; Fergusson and Hanson, 1995; Ronquist, 1995b, 1999) or as a separate family in the Cynipoidea (Quinlan, 1978; Nordlander, 1982b; Kovalev, 1995). Recent phylogenetic analyses of morphological data convincingly show that eucoilines are deeply nested within the Figitidae and cannot be treated as a separate cynipoid family without far-reaching consequences for the classification of the rest of the parasitic superfamily (Ronquist, 1995b, 1999). Specifically, eucoilines appear to belong to the "core figitids," a clade including the Pycnostigminae, Emargininae, Aspicerinae, and Figitinae, in addition to the Eucoilinae (Fig. 1) (Ronquist, 1999). All subfamilies of this assemblage are likely to be monophyletic except the heterogeneous Figitinae (Ronquist, 1999). As far as is known, the core figitids are exclusively dipteran parasitoids.

The exact relationships among the core figitids are still uncertain but there is some evidence to suggest that the pycnostigmines may be the sister group of eucoilines (Fig. 1), Rasnitsyn (1980) was the first to note that pycnostigmines and eucoilines share a unique modification of the female metasoma. Abdominal terga 3 to 5 are fused to form a large syntergum (cf. Fig. 12B), which is usually articulated with the anterior margin of abdominal tergum 6. The latter is positioned at some angle to the syntergum and covers most of the remaining terga, giving the metasoma a squarish, box-like appearance with only two large terga being visible. Based on this abdominal modification, Ronquist (1995b) proposed that pycnostigmines and eucoilines form sister groups. In his preliminary analysis of higher figitid relationships, Ronquist (1999) found additional support for this grouping in the absence of the submedian petiolar pits, universally present in other cynipoids (compare 133:0, Fig. 12A with 133:1, Fig. 12B). Ronquist (1999) also speculated that pycnostigmines might be derived eucoilines, since some pycnostigmines have a polished scutellar area (cf. 76:1, Fig. 7C) that could be the remnant of a eucoiline-like scutellar plate, and pointed out that further study was needed to convincingly demonstrate the monophyly of eucoilines exclusive of pycnostigmines.

Among other figitids, eucoilines are particularly similar to the Emargininae and to *Lonchidia* (Figitinae), although neither of these taxa has been tied to eucoilines by explicit synapomorphies. Members of the genus *Lonchidia* are similar to most eucoilines in being small, polished insects with a club-shaped antenna in the female. They also have a dense pubescent patch located anteriorly on the third abdominal tergum reminiscent of the hairy ring of most eucoilines. However, like emarginines they have abdominal terga 3 to 5 free (cf. Fig. 12A), the primitive figitid state, rather than fused into a syntergum as in eucoilines and pycnostigmines (cf. Fig. 12B). Furthermore, the submedian petiolar pits are distinct and the scutellum has no indication of a specialized dorsal area. The biology of *Lonchidia* is unknown.

The subfamily Emargininae was recently recognized as a separate taxon (Kovalev, 1994; Ronquist, 1999) and currently includes five genera: *Thoreauella*, *Emargo*, *Bothriocynips*, *Weldiola*, and *Quinlania*. These genera have previously been placed in the Figitinae (*Thoreauella*, Weld, 1952; *Emargo*, Weld, 1960), in the Charipinae (*Bothriocynips*, Díaz, 1978), or in the Eucoilinae (*Emargo*, Quinlan, 1988; Lin, 1988). Despite the earlier classificatory confusion, the Emargininae form a morphologically homogeneous and undoubtedly monophyletic group (Ronquist, 1999). They are parasitoids of dipteran larvae living in ant nests or in ant refuse deposits. Like members of *Lonchidia*, emarginines are similar to many eucoilines in their small body size, polished aspect, and dense pubescence anteriorly on the metasoma. Furthermore, they have a narrow, rhomboid or elongate area dorsally on the scutellum defined by prominent lateral carinae (cf. Fig. 7C). Quinlan (1988) interpreted this as a reduced scutellar plate, leading him to treat emarginines as members of the Eucoilinae. Lin (1988) also placed emarginines in the Eucoilinae. However, Ronquist (1999) pointed out several differences between the scutellar prominences of emarginines and those of eucoilines and questioned the homology of these structures.

The higher classification of the eucoilines is currently chaotic, mostly because higher relationships are unknown. This, in turn, presumably reflects the

fact that eucoilines are a "difficult" group with few if any obvious higher clades being identified by easily detected, striking apomorphies. Eucoiline taxonomic works of the first 60 years of the 20th century resulted mostly in artificial groupings and many of the taxa accepted by Kieffer (1901) and Weld (1952) are likely to be polyphyletic (Nordlander, 1976, 1982b). Since the last published global revision by Weld (1952), 43 new eucoiline genera have been described (Fontal-Cazalla *et al.*, submitted for publication) with virtually no progress concerning the higher classification. Nordlander's studies (1976, 1978, 1980, 1981, 1982a, 1982b) were the first revisions of many eucoiline genera that were based on a broad assessment of the primary types and that dealt explicitly with the circumscription of the genera. Nordlander also studied the phylogenetic relationships of several genèra, pioneering the use of cladistic techniques in eucoiline systematics (Nordlander, 1982a, b). Furthermore, he provisionally separated most eucoilines into six informal groups of genera (Nordlander, 1982b; Table 1) but, although some of the groups were loosely characterized (Nordlander, 1982a), autapomorphies or diagnoses defining them were never given. After Nordlander's studies, there have been only a few cladistic analyses of eucoilines, all dealing with intrageneric relationships (Díaz 1990; Nordlander and Grijpma, 1991; Schilthuizen *et al.*, 1998; Van Alphen *et al.*, 1991). Although Nordlander's genus groups have been used by several other workers (e.g., Quinlan, 1986; Lin, 1988), their monophyly has still not been tested in an explicit phylogenetic analysis, a comprehensive list of putative apomorphies supporting them has not been given, and the relationships among them remain unclear. In addition, many eucoiline genera have never been placed in any of the genus groups.

The eucoilines have previously been subdivided also into formal taxa at the subfamily and tribal levels (Belizin, 1961; Kovalev, 1989). However, the resulting classification is a poor starting point for further exploration of eucoiline higher relationships because it is based mainly on a few homoplastic key characters. For instance, Belizin (1961) established the tribe Glauraspidini for brachypterous eucoilines, although such a group is obviously polyphyletic. Furthermore, Belizin (1961) erected the subfamily Cothonaspinae (within Eucoilidae) for eucoilines lacking the hairy ring on the base of the metasoma, thereby uniting such disparate groups as the genus *Cothonaspis* and the *Gronotoma* group of genera (Nordlander, 1976). Because of the problematic nature of the proposed formal taxa at the subfamily and tribal levels, we consider informal genus groups a better framework for exploring eucoiline relationships at the moment and suggest that the introduction of a formal higher classification be delayed until the phylogeny is better known.

In this paper we present the first cladistic analysis of higher eucoiline relationships, based on 148 skeletal characters of adults, coded for 38 ingroup and 7 outgroup taxa (Table 1). The ingroup taxa represent all of the genus groups identified by Nordlander, as well as several eucoiline genera of uncertain affinities. The outgroups include representatives of Emargininae, Pycnostigminae, and *Lonchidia* (Figitinae) as well as morphologically archaic representatives of the Figitinae and Aspicerinae. With respect to eucoiline systematics, the aims of the study are twofold. First, we wanted to clarify the relationships between eucoilines and potential outgroups, addressing problems such as whether eucoilines form a monophyletic group exclusive of pycnostigmines and whether *Lonchidia* or Emargininae may be close relatives of eucoilines. Second, we wanted to critically assess the monophyly of the eucoiline genus groups defined by Nordlander (1982b) and elucidate the relationships among them to provide a sound basis for the further study of eucoiline systematics and evolution. In a broader context, we wanted to demonstrate the power and utility of digital image databases in biodiversity research on poorly known groups. We also used eucoilines as a test case for comparing the performance of parsimony analysis under uniform weights and under implied weights in resolving difficult phylogenetic problems.

MATERIALS AND METHODS

Terminology

The terminology for skeletal features is based on Richards (1977), Ronquist and Nordlander (1989), Ronquist (1995a), and Pujade-Villar and Arnedo (1997). The terms for surface sculpture follow Harris (1979).

TABLE 1
Ingroup (IG) and Outgroup (OG) Taxa Studied

Higher Taxon	Species	Material	Preparation	Source
'Figitinae'[a](OG)				
	Melanips opacus	4♀♀/1♂	SEM/LM/SMD	PRC
	Lonchidia sp.	7♀♀/7♂♂	SEM/LM/SMD	RLC
Aspicerinae (OG)				
	Aspicera scutellata	1♀/1♂	SEM/LM	PRC
Emargininae (OG)				
	Thoreauella sp1 (from Kenya)[b]	4♀♀	SEM/LM/SMD	RLC
	Thoreauella sp2 (from Belize)[b]	4♂♂	SEM/LM/SMD	RLC
Pycnostigminae (OG)				
	Pycnostigmus sp.	2♀♀	SEM/LM/SMD	MSC
	Tylosema nigerrimum	(1♂)	SM	MNHN
	Trjapitziniola popovi	(1♂)	SM	ZMAS
Eucoilinae (IG)				
Gronotoma group	*Gronotoma* sp.	6♀♀/4♂♂	SEM/LM/SMD	NFC
Gronotoma group	*Disorygma depile*	7♀♀/7♂♂	SEM/LM/SMD	RLC
Gronotoma group	*Zaeucoila* sp.	7♀♀/7♂♂	SEM/LM/SMD	MBC
Gronotoma group	*Rhabdeucoela* sp.	7♀♀/7♂♂	SEM/LM/SMD	NFC
Trybliographa group	*Eucoila crassinerva*	7♀♀/7♂♂	SEM/LM/SMD	GNC and MSC
Trybliographa group	*Trybliographa rapae*	7♀♀/7♂♂	SEM/LM/SMD	GNC
Rhoptromeris group	*Rhoptromeris heptoma*	7♀♀/7♂♂	SEM/LM/SMD	GNC
Rhoptromeris group	*Trichoplasta* sp.	5♀♀/5♂♂	SEM/LM/SMD	GNC
Rhoptromeris group	*Leptopilina longipes*	7♀♀/6♂♂	SEM/LM/SMD	GNC
Rhoptromeris group	*Cothonaspis longula*	7♀♀/7♂♂	SEM/LM/SMD	NFC
Chrestosema group	*Chrestosema erythropum*	7♀♀/7♂♂	SEM/LM/SMD	GNC
Chrestosema group	*Odonteucoila* sp.	2♀♀	SEM/LM/SMD	CNCI
Chrestosema group	*Dieucoila* sp.	7♀♀	SEM/LM/SMD	CNCI
Chrestosema group	*Mirandicola* sp.[c]	4♀♀/5♂♂	SEM/LM/SMD	NFC
Chrestosema group	*Glauraspidia microptera*	4♀♀/5♂♂	SEM/LM/SMD	NFC
Ganaspis group	*Ganaspis xanthopoda*	7♀♀/7♂♂	SEM/LM/SMD	GNC
Ganaspis group[d]	*Ganaspis neotropica*	7♀♀/7♂♂	SEM/LM/SMD	NFC
Ganaspis group	*Ganaspis* sp.	7♀♀/7♂♂	SEM/LM/SMD	NFC
Ganaspis group	*Hexacola hexatoma*	7♀♀/7♂♂	SEM/LM/SMD	NFC
Ganaspis group	*Didyctium nigriclava*	7♀♀/7♂♂	SEM/LM/SMD	GNC
Kleidotoma group	*Kleidotoma dolichocera*	7♀♀/7♂♂	SEM/LM/SMD	GNC
Kleidotoma group	*Kleidotoma nigra*	7♀♀/7♂♂	SEM/LM/SMD	NFC
Kleidotoma group	*Eutrias tritoma*	6♀♀/7♂♂	SEM/LM/SMD	GNC
—	*Tropideucoila* sp.	7♀♀/7♂♂	SEM/LM/SMD	NFC
—	*Dettmeria* sp.	(3♀♀/1♂)	SM	CNCI
—	*Lopheucoila anastrephae*	(1♀)	SM	NFC
—	*Steleucoela* sp.	(1♀/1♂)	SM	CNCI
—	*Odontosema anastrephae*	7♀♀/7♂♂	SEM/LM/SMD	IEX
—	*Acantheucoela* sp.	3♀♀	SEM/LM/SMD	CNCI
—	*Caleucoela* sp.	(2♀♀)	SM	CNCI
—	*Perischus* sp. 1[b]	(2♀♀)	SM	CNCI
—	*Perischus* sp. 2[b]	(3♀♀)	SM	CNCI
—	*Zamischus brasiliensis*[b]	(3♀♀)	SM	CNCI
—	*Zamischus elongatus*[b]	(3♀♀)	SM	CNCI
—	*Zamischus* n. sp.[b]	(3♀♀/4♂♂)	SM	CNCI and NMS
—	*Aganaspis pelleranoi*	7♀♀/5♂♂	SEM/LM/SMD	IEX

TABLE I—*Continued*

Higher Taxon	Species	Material	Preparation	Source
—[e]	*'Eucoila' erythropa*	4♀♀/1♂	SEM/LM/SMD	GNC and KSC
—	*Epicoela* sp.	3♀♀	SEM/LM/SMD	CNCI
—	*Nordlandiella abdominalis*	7♀♀	SEM/LM/SMD	NFC
—	*Paraganaspis* sp.	7♀♀	SEM/LM/SMD	USNM
—	*Triplasta* sp.	7♀♀	SEM/LM/SMD	USNM

Note. Assignments of eucoiline taxa to informal generic groups are exclusively those proposed by Nordlander (1982b). SM, specimens studied with stereomicroscopy without dissection; SEM, specimens dissected and studied with scanning electron microscopy; LM, specimens dissected and studied with compound microscopy; SMD, specimens dissected and studied with stereomicroscopy; CNCI, Canadian National Collection of Insects, Ottawa, Ontario, Canada; MBC, M. Buffington's Collection (Texas A&M, College Station, TX); GNC, Göran Nordlander's Collection (Swedish University of Agricultural Sciences, Uppsala, Sweden); IEX, Laboratorio del Instituto de Ecología de Xalapa, Veracruz, Mexico; KSC, Kathy Schick's Collection (private collection, Stockton, CA); MNHN, Museum National d'Histoire Naturelle, Paris, France, MSC, Michel Sporrong's Collection (Zoological Museum, University of Lund, Lund, Sweden); NFC, J. L. Nieves and F. Fontal's Collection (Museo Nacional de Ciencias Naturales, Madrid, Spain); NMS, National Museum of Scotland, Edinburgh, Scotland; PRC, J. Pujade and P. Ros's Collection (Universidad Autónoma de Barcelona, Spain); RLC, F. Ronquist and J. Liljeblad's collection (Uppsala University, Uppsala, Sweden); USNM, U.S. National Museum of Natural History, Washington, DC; ZMAS, Zoological Museum, Academy of Sciences, St. Petersburg, Russia.

[a] The 'Figitinae' are paraphyletic (Ronquist, 1995b, 1999).

[b] Multiple representatives of *Thoreauella, Zamischus,* and *Perischus* were used not because these genera are structurally heterogeneous but merely to allow coding of more characters. These genera were treated as single terminal taxa in the analysis.

[c] *Mirandicola* Belizin, 1968 is a senior synonym of *Pseudopsichacra* Quinlan, 1976 (types of the type species examined by G. Nordlander) **new synonymy.**

[d] *Ganaspis neotropica* Diaz, 1974 is a representative of the *neotropica* subgroup within the *Ganaspis* group (Nordlander, 1982a).

[e] *'Eucoila' erythropa* is a false *Eucoila* and does not belong to the *Trybliographa* group (Nordlander, 1981).

Selection of Taxa

We studied 45 taxa, corresponding mostly to single species, belonging to 42 genera, of which 35 were eucoilines and 7 were other figitids (Table 1). Eucoiline taxa were chosen to represent diverse samples of the six eucoiline genus groups recognized by Nordlander (1982b). In addition, we included a fair number of unplaced genera of uncertain affinities (Table 1). The sample included the vast majority of the large and well-known eucoiline genera and about 40% of the valid genera. Morphologically diverse genera, such as *Ganaspis* and *Kleidotoma,* were represented by several species from morphologically distinct species groups. Within the genus *Eucoila,* Nordlander (1981, 1982b) discovered two unrelated species groups, which are not congeneric: (1) the *nudipennis* group, or false *Eucoila,* belonging to an undescribed genus, and (2) the *crassinerva* group, or true *Eucoila,* including the type species of the genus. Here, we will distinguish the false *Eucoila* or *nudipennis* group by simply using quotation marks around the genus name; it is represented in our analysis by *'Eucoila' erythropa* (Table 1).

Outgroups were selected among the core figitids (Fig. 1; Ronquist, 1999). *Melanips opacus* (Hartig) was chosen as a representative of a morphologically generalized, basal core figitid (Fig. 1; Ronquist, 1999; Ros-Farré *et al.*, 2000) and was used for rooting purposes. *Aspicera scutellata* Villers was chosen to represent a generalized aspicerine. *Lonchidia* ('Figitinae'), emarginines, and pycnostigmines were included in the analysis because these figitid taxa are all potential sister groups or close relatives of eucoilines. In the Pycnostigminae, we studied representatives of all three described genera (*Pycnostigmus, Tylosema,* and *Trjapitziniola*). The subfamily Emarginae is characterized by a long series of autapomorphies but the subfamily itself is morphologically rather homogeneous (Ronquist, 1999). The subfamily as a whole has never been revised and the generic circumscriptions are therefore unclear. Here, we studied material of two undescribed species, which were

provisionally classified as belonging to *Thoreauella*, the oldest generic name in the subfamily.

Voucher specimens have been deposited in the Collection of the Museo Nacional de Ciencias Naturales (Madrid, Spain).

Preparation of Specimens

Specimens were studied using stereomicroscopy, light microscopy, and scanning electron microscopy (Table 1). When possible, the specimens were dissected to allow study of potentially informative morphological character systems, which are otherwise concealed (Table 2). Dried specimens were transferred to 70% ethanol at least 1 week prior to the dissections. The complete specimen was cleaned with a 10% dilution of *Mercryl Laurylé*, a soap of which mercurobutol is the principal component. The soap was washed away with water, after which the specimens were dehydrated by transferring them through increasing concentrations of ethanol up to absolute ethanol. All dissections were carried out in absolute ethanol. The dissected parts

TABLE 2
Body Regions Examined and Views Imaged in the Search for Phylogenetically Informative Characters

No.	Body part	View	Specimen	Technique
1	Head	Dorsal view	1st♀	SEM
2	Head	Anterior view, antennae removed	2nd♀ / 4th♀	SEM / SM
3	Head	Posterior view, with mouthparts	3rd♀ / 5th♀	SEM / SM
4	Head	Posterior view, detail of gula	3rd♀	SEM
5	Labium	Lateral view (left side)	1st♀	LM
6	Maxillary palp	Apical segment, posterior view	3rd♀	SEM
7	Left maxilla	Lateral view (left side)	1st♀	LM
8 / 9	Right mandible	Anterior view	1st♀ / 6th♀	SEM / SM
10 / 11	Left mandible	Posterior view	1st♀ / 6th♀	SEM / SM
12 / 13	Left antenna	Dorsal view	1st♀ / 2nd♀	SEM / SM
14	Right antenna	Ventral view	2nd♀	SM
15	Most modified flagellomere (male)	Ventroposterior view	1st♂	SEM
16 / 17	Mesosoma (with coxae)	Lateral view (left side)	1st♀ / 4th♀	SEM / SM
18 / 19	Mesosoma	Dorsal view	2nd♀ / 5th♀	SEM / SM
20 / 21	Mesosoma	Ventral view	3rd♀ / 6th♀	SEM / SM
22	Mesosoma	Anterodorsal view	2nd♀	SEM
23	Mesosoma	Posterodorsal view (entire metanotum visible)	2nd♀	SEM
24 / 25	Left forewing	Dorsal view	1st♀ / 2nd♀	LM / SM
26 / 27	Right forewing	Ventral view	1st♀ / 2nd♀	LM / SM
28 / 29	Left foreleg	Posterior view	2nd♀ / 3rd♀	SEM / / SM
	Right foreleg	Anterior view	2nd♀ / 3rd♀	SEM / / SM
30 / 31	Left midleg	Posterior view	2nd♀ / 3rd♀	SEM / SM
	Right midleg	Anterior view	2nd♀ / 3rd♀	SEM / SM
32 / 33	Left hindleg	Posterior view	2nd♀ / 3rd♀	SEM / SM
	Right hindleg	Anterior view	2nd♀ / 3rd♀	SEM / SM
34	Posterior claw of left metatarsus	Posterior view	1st♀	SEM
35 / 36	Metasoma	Lateral view (left side)	1st♀ / 3rd♀	SEM / SM
37 / 38	Petiole	Anteroventral view	1st♀ / 3rd♀	SEM / SM
39	Hypopygium	Ventral view	2nd♀	SEM
40 / 41	Metasoma (male)	Lateral view (left side)	1st♂ / 2nd♂	SEM / SM
42	Ovipositor	Lateral view (left side)	4th♀	LM
43	Phallus (anterior 1 / 3)	Lateral view (left side)	3rd♂	SEM
44 / 45	Phallus (without basal ring)	Dorsal view	4th♂ / 5th♂	SEM / LM
46	Phallus (without basal ring)	Ventral view	6th♂	SEM
47	Phallus (anterior 1 / 3)	Ventral view	6th♂	SEM

Note. Females were used unless otherwise noted. SEM, body parts studied with scanning electron microscopy; LM, body parts studied with compound microscopy; SM, body parts studied with stereomicroscopy. Digital SEM and LM images of these views are available at http://morphbank.ebc.uu.se.

TABLE 3
Observed Character States

Taxon	Character 1	11	21
Melanips opacus	0001000100	100–000000	1234567890
Aspicera scutellata	0000100000	210–000000	0120000000
Lonchidia sp.	0000111000	200–000000	1001000100
Thoreauella sp1/2	001110?000	200–100000	?000000110
Pycnostigmus sp.	0000110000	100–000000	0000001100
Tylosema nigerrimum	0000110000	200–100000	0?000?????
Trjapitziniola popovi	0000110000	200–100000	0?000?????
Gronotoma sp.	0000100000	000–100111	1100000110
Disorygma depile	0010100000	200–100111	1000000010
Zaeucoila sp.	0001100110	1111100110	012–000110
Tropideucoila sp.	0001100000	1111110100	0120000110
Rhabdeucoela sp.	0001100110	0112110100	0120000110
Dettmeria sp.	0001100000	0110110100	0?????????
Lopheucoila anastrephae	0001100000	0111110100	0?????????
Steleucoela sp.	0101000000	010–100100	0?????????
Odontosema anastrephae	0101110000	110–101100	0110000010
Perischus sp.	0001100010	010–100100	1?????????
Zamischus sp.	0001100010	110–100101	1?????????
Caleucoela sp.	0111100000	1112110100	1?????????
Acantheucoela sp.	0101000000	0110101100	0110000010
Aganaspis pelleranoi	0101000000	0110100100	0100100110
Epicoela sp.	0101000000	110–101100	0100200010
'Eucoila' erythropa	0101000000	210–101100	0100200010
Nordlandiella abdominalis	0100100000	210–101100	1002000110
Paraganaspis sp.	0100100000	210–100100	1002000110
Ganaspis xanthopoda	0101000000	210–100100	1000000110
Ganaspis neotropica	0001100000	010–100100	1001000110
Ganaspis sp.	0100101000	110–100100	1000000110
Hexacola hexatoma	0000101000	210–100100	1002000110
Didyctium nigriclava	0110101000	210–100100	1000000110
Chrestosema erythropum	1101000001	212–100100	1002000110
Dieucoila sp.	1100100000	012–100100	1002000110
Odonteucoila sp.	1101000000	1110101100	0000000110
Mirandicola sp.	1100101001	012–100100	1002000110
Glauraspidia microptera	0100101000	010–100100	1000000110
Trybliographa rapae	0100100010	210–100100	1000000011
Eucoila crassinerva	0101000010	010–101100	1000000011
Leptopilina longipes	0101000000	210–101100	1000000110
Rhoptromeris heptoma	0100101000	210–100100	1000000110
Trichoplasta sp.	0100100000	210–100100	1000000110
Cothonaspis longula	0110111000	210–100100	1000011110
Triplasta sp.	0110111000	210–100100	1002011110
Eutrias tritoma	0110101001	212–100100	1002011110
Kleidotoma dolichocera	0110101001	210–100100	1002011110
Kleidotoma nigra	0110101001	210–100100	1002011110

were treated differently depending on the technique with which they were being examined. Parts prepared for scanning electron microscopy (SEM) were air-dried and mounted on stubs by means of carbon tape and coated with gold. Parts prepared for bright-field light microscopy (LM) were macerated in 10% KOH, washed in 95% ethanol, and mounted in euparal on microscope slides. Parts prepared for stereomicroscopy (SM) were air-dried and glued onto cardboard tabs. Each dissected body part was mounted at a specific orientation, allowing examination of a wide range of character systems with appropriate techniques (Table

TABLE 3—*Continued*

Taxon	Character 31	41	51
Melanips opacus	0000000000	0000000000	000000000–
Aspicera scutellata	0000000000	0??1?00?0?	000000000–
Lonchidia	0110000000	0010?00?0?	000100000–
Thoreauella sp1/2	0110000000	0010?00?01	02–0000010
Pycnostigmus sp.	0110000100	0???000000	010000000–
Tylosema nigerrimum	????1011?0	?????00100	0??000000–
Trjapitziniola popovi	????2011?0	?????00100	0??000000–
Gronotoma sp.	1110100100	0100100012	1100000010
Disorygma depile	1110100100	0000100012	1100000010
Zaeucoila sp.	0110101170	?110100112	1210000110
Tropideucoila sp.	0110100110	1100110012	1100000111
Rhabdeucoela sp.	0110100110	1000100012	1101000111
Dettmeria sp.	?11010????	????1??1??	???0100111
Lopheucoila anastrephae	?1101?????	????1??0??	???0100111
Steleucoela sp.	?21010????	????1??0??	???1100110
Odontosema anastrephae	0110100000	0010111012	1101000111
Perischus sp.	?210??????	????1??0??	???1000011
Zamischus sp.	?21010????	????1??0??	?1?1000011
Caleucoela sp.	?110??????	????1??1??	???1000011
Acantheucoela sp.	01101??000	0010110112	1101000011
Aganaspis pelleranoi	0110100000	0010111112	1101000011
Epicoela sp.	01101??000	0010111112	1101100011
'Eucoila' erythropa	0110101000	0010111212	1101000011
Nordlandiella abdominalis	01101??000	0010111112	1101000010
Paraganaspis sp.	01101??000	0010111112	1101000010
Ganaspis xanthopoda	0110101000	0010111012	1101000010
Ganaspis neotropica	0110101000	0010111012	1101000010
Ganaspis sp.	0110100000	0010111012	1101000010
Hexacola hexatoma	0110100000	0010111112	1101000010
Didyctium nigriclava	0110100000	0010111112	1101000010
Chrestosema erythropum	0110100000	0010111112	1101000010
Dieucoila sp.	01101??001	0010111112	1101000010
Odonteucoila sp.	0110101001	0010111112	1101000010
Mirandicola sp.	011010?001	0010111112	1101100010
Glauraspidia microptera	0110100000	0010111112	1101000010
Trybliographa rapae	0110111000	0010110212	0111000010
Eucoila crassinerva	0110111000	0010110212	0111000010
Leptopilina longipes	0110111000	0010111112	1101000010
Rhoptromeris heptoma	0110121000	0010111112	1101011010
Trichoplasta sp.	0110121000	0012110112	1101011010
Cothonaspis longula	0110121000	0012111112	1101100010
Triplasta sp.	01111??000	0012111112	1101100011
Eutrias tritoma	0111100000	0012111112	1101100010
Kleidotoma dolichocera	0110100000	001?111112	1101100010
Kleidotoma nigra	0111100000	0010111112	1101100010

2). Some taxa were not numerous enough in our collection to allow full dissection and preparation for all techniques; these taxa were studied with stereomicroscopy only (cf. Table 1).

Character Coding

All SEM and LM preparations were digitally imaged (1166 total images, 899 from SEM and 267 from LM)

TABLE 3—*Continued*

Taxon	Character 61	Character 71	Character 81
Melanips opacus	--00000000	001000----	--00010000
Aspicera scutellata	--00011010	010000----	--00?31010
Lonchidia sp.	--01000000	011000----	--00010000
Thoreauella sp1/2	1011100000	0000011---	--00121?01
Pycnostigmus sp.	--11110000	0100010---	--00111000
Tylosema nigerrimum	--010??000	0100010---	--00111010
Trjapitziniola popovi	--010?0000	0100010---	--00011010
Gronotoma sp.	0011000000	0011112000	0000111001
Disorygma depile	0011100000	0010012000	0000110001
Zaeucoila sp.	1111110021	0011112000	0000110101
Tropideucoila sp.	2211110020	0011012100	1000101101
Rhabdeucoela sp.	2211110021	0011012000	0000110101
Dettmeria sp.	22111??020	0111012100	0000100101
Lopheucoila anastrephae	22111??020	0111012102	?020100101
Steleucoela sp.	22111??001	0110112111	1100110101
Odontosema anastrephae	2211110001	0110112111	2000100101
Perischus sp.	20011??001	0110112111	?000110111
Zamischus sp.	20011??001	0110112112	?000110111
Caleucoela sp.	21111??001	0110112112	2000100101
Acantheucoela sp.	2211110001	0110012112	202010010?
Aganaspis pelleranoi	2111100001	0010012010	2000110101
Epicoela sp.	2111100001	0110112101	100011010?
'Eucoila' erythropa	2111100001	0010112112	2000110101
Nordlandiella abdominalis	2111100001	0110112112	1100111101
Paraganaspis sp.	2211100001	0110112112	2000111101
Ganaspis xanthopoda	1111100001	1010012111	2000111101
Ganaspis neotropica	1011100001	0010012111	2000110101
Ganaspis sp.	1011100001	0010112111	2000110101
Hexacola hexatoma	1011100001	0010112112	2001111101
Didyctium nigriclava	1011100001	0010112111	100011?101
Chrestosema erythropum	1111100101	0010112111	1000110101
Dieucoila sp.	1011100001	0010112112	2010110101
Odonteucoila sp.	1211100101	0110112112	200013010?
Mirandicola sp.	1111100101	0110212112	200111110?
Glauraspidia microptera	1011100001	0110112112	200011110?
Trybliographa rapae	1211100001	0010112112	1000111101
Eucoila crassinerva	1211100001	0110112112	1000110101
Leptopilina longipes	1111100001	0110112111	1000111101
Rhoptromeris heptoma	1111100001	1110012110	1000111101
Trichoplasta sp.	1111100001	1110112110	1000121101
Cothonaspis longula	1211100001	0110012212	2000111101
Triplasta sp.	1211100001	0110212111	2000110101
Eutrias tritoma	1211100001	1210212211	2001121101
Kleidotoma dolichocera	1211100001	0210212212	2001111101
Kleidotoma nigra	1211100001	0210212211	2001121101

and printed using an ink-jet color printer. The images are available from a Web-based image databank (http://morphbank.ebc.uu.se). The search for phylogenetically informative characters was based on comparison of the printed images, complemented by examination of the same characters using stereomicroscopy.

All potentially informative characters, which fell into a limited number of well-separated character states, were coded for analysis. To minimize obvious noise in the character matrix we omitted a few characters known to vary considerably within most eucoiline genera. Multistate characters were ordered only if the

TABLE 3—*Continued*

Taxon	Character		
	91	101	111
Melanips opacus	00–0000000	0200000000	000000000–
Aspicera scutellata	00–0000000	0000000000	000002000–
Lonchidia sp.	01–0000010	0000000000	100000000–
Thoreauella sp1/2	2––2122110	0200000000	–????0002–
Pycnostigmus sp.	01–1100000	0000101000	000012010–
Tylosema nigerrimum	00–1110000	0??01?0?00	011012?0–
Trjapitziniola popovi	00–2110000	00?01?0?00	001012?0–
Gronotoma sp.	0202110010	0100100000	01101000?–
Disorygma depile	0202100010	0100100000	011010000–
Zaeucoila sp.	120210001?	1110110000	001122020–
Tropideucoila sp.	1202120010	1110110000	001122010–
Rhabdeucoela sp.	1202110010	1110110000	001122010–
Dettmeria sp.	0202?10011	01?0??0?00	0010??0?0–
Lopheucoila anastrephae	1202?00011	01?0??0?00	0010????0–
Steleucoela sp.	1?02?20110	01?0??0?00	00111?1?10
Odontosema anastrephae	2202120110	0110110000	0011220110
Perischus sp.	0202?20110	0?????0?11	00001?0?10
Zamischus sp.	0202?20110	0?????0?10	00000?0?10
Caleucoela sp.	1?02?20110	01?0??0?00	00101???11
Acantheucoela sp.	2202120110	0110110000	0010220110
Aganaspis pelleranoi	3202120110	0110100000	0010220110
Epicoela sp.	3202120110	0110110000	0010220110
'Eucoila' erythropa	3202120110	0110110000	1010220110
Nordlandiella abdominalis	3202120110	0110110000	0010220110
Paraganaspis sp.	3202120110	0110110000	0010211010
Ganaspis xanthopoda	3202120110	0110110000	0001210010
Ganaspis neotropica	2202120110	0110110000	0001211010
Ganaspis sp.	3202120110	0110110000	1010210010
Hexacola hexatoma	3202120110	0110110000	1000211010
Didyctium nigriclava	3202120110	0110110000	001?211010
Chrestosema erythropum	3202120110	0110110000	0010221011
Dieucoila sp.	3202121110	0110110000	0010220010
Odonteucoila sp.	3202120110	0110110000	0010221010
Mirandicola sp.	3302121110	0110110001	0000211011
Glauraspidia microptera	3302121110	0110110001	0000211011
Trybliographa rapae	1202120110	0110111000	1010220010
Eucoila crassinerva	1202120110	0110111000	0010220010
Leptopilina longipes	3202120110	0110111000	0000220010
Rhoptromeris heptoma	3202120110	0110110000	1001210010
Trichoplasta sp.	3202120110	0110110000	0001210010
Cothonaspis longula	3212120110	0110110000	100122002–
Triplasta sp.	3212120110	0110110100	100021002–
Eutrias tritoma	3212120110	0111110100	100021002–
Kleidotoma dolichocera	3212120110	0111110100	100121002–
Kleidotoma nigra	3212120110	0111110100	100021002–

states appeared to form a linear transformation series. Characters were coded from female specimens unless otherwise noted. However, only males were available for *Tylosema* and *Trjapitziniola* (Table 1). To reduce missing information in the matrix we coded characters that are usually sexually monomorphic in the Cynipoidea based on males of these taxa instead of females.

Phylogenetic Analysis

We analyzed the data set using both unweighted standard parsimony and parsimony analysis under implied weights (Goloboff, 1993a). Analysis under implied weights is superior to successive weighting (Farris, 1969), primarily because of the logical self-consistency of the former approach (every tree is evaluated

TABLE 3—*Continued*

Taxon	Character		
	121	131	141
Melanips opacus	0000000100	00000?0-00	00000000
Aspicera scutellata	0????01002	010?0?0-10	00000000
Lonchidia sp.	0101000100	0100000-10	00000000
Thoreauella sp1/2	0101010100	010?1?0-11	000?????
Pycnostigmus sp.	00?000101-	-1100?11?0	120?????
Tylosema nigerrimum	01????101-	-1???????0	?2???????
Trjapitziniola popovi	01????101-	-1???????0	?2???????
Gronotoma sp.	0001100100	0111001?1	11000111
Disorygma depile	0101100100	0111001?1	11000111
Zaeucoila sp.	0001000100	0111001111	11000100
Tropideucoila sp.	0001100100	0111001111	11000111
Rhabdeucoela sp.	0001100100	0111001111	11001111
Dettmeria sp.	0????01100	01????10?1	11??????
Lopheucoila anastrephae	0????01002	01????11?1	11??????
Steleucoela sp.	0????00100	01????11?1	11??????
Odontosema anastrephae	0011101100	011?011011	01000111
Perischus sp.	0????00100	011?1?10?1	01??????
Zamischus sp.	0????01103	-11?1?10?0	01??????
Caleucoela sp.	0????00100	01????10?1	01??????
Acantheucoela sp.	0111100100	0111111011	0?1?????
Aganaspis pelleranoi	0011000100	01111?10?1	01101111
Epicoela sp.	0111001100	0111111011	0?1?????
'Eucoila' erythropa	0111001000	0111111011	011?????
Nordlandiella abdominalis	0111001100	0111111011	0?1?????
Paraganaspis sp.	0111000100	0111001011	0?1?????
Ganaspis xanthopoda	0111000100	0111011011	01111111
Ganaspis neotropica	0111000100	0111011011	01111111
Ganaspis sp.	0111010100	01111?1011	01111111
Hexacola hexatoma	0111000100	0111111?0?1	011??111
Didyctium nigriclava	0?11100100	0111111011	01111111
Chrestosema erythropum	0111000100	0111111011	01111111
Dieucoila sp.	0111000100	0111111011	0?1?????
Odonteucoila sp.	0111000100	0111111011	0?1?????
Mirandicola sp.	0011000100	0111111011	01???1?1
Glauraspidia microptera	0111000100	0111111011	011??1?1
Trybliographa rapae	0111000100	011?111011	01111111
Eucoila crassinerva	0111001000	0111111011	01111111
Leptopilina longipes	0111000100	0111001011	01111111
Rhoptromeris heptoma	0011000100	0111111011	01111111
Trichoplasta sp.	0011000100	0111111011	011?????
Cothonaspis longula	0111001100	0111001011	0111111?
Triplasta sp.	1111001001	1111001010	0?1?????
Eutrias tritoma	1111001101	1111111?1	01111111
Kleidotoma dolichocera	1111011101	1111111011	01111111
Kleidotoma nigra	1111011101	1111111011	01111111

Note. The multistate characters 11, 14, 23, 24, 25, 32, 35, 36, 48, 50, 52, 61, 62, 72, 75, 78, 80, 81, 86, 91, 92, 96, 115, 116, 130, and 142 were ordered in the sequence 012(3), whereas the multistate characters 13, 44, 69, 77, 83, 94, 97, 102, and 119 were treated as unordered. 0, 1, 2, 3, observed monomorphic states; ?, state unknown or uncertain; − character not applicable.

using the character weights it implies). Implied-weights analysis often produces results that are more resolved and in better accord with intuitive evaluation of character data than standard unweighted parsimony, particularly for difficult phylogenetic problems (Goloboff, 1997; Ronquist *et al.*, 1999).

All ingroup and outgroup relationships were unconstrained in the analyses and trees were rooted *a posteriori* on *M. opacus*. Phylogenetic analyses were performed using PAUP 4.0b4a (Swofford, 1998), NONA 2.0 (Goloboff, 2000), Pee-Wee 2.5.1 (Goloboff, 1993b), and WinClada 0.9.99m24 (Nixon, 2000). Unless otherwise noted, all PAUP searches used multiple random addition sequences followed by TBR swapping with branches of maximum length zero collapsed and steepest descent off. For bootstrap runs we employed a simple addition sequence with *Melanips* as the reference taxon, followed by TBR swapping. State changes (Appendix 2) were listed using PAUP, and MacClade 3.05 (Maddison and Maddison, 1992) was used for calculating the average branch lengths of the phylogram.

RESULTS

The morphological study resulted in a set of 148 characters (cf. Appendix 1, Table 3) with an unweighted parsimony length theoretically spanning between 187 and 1240. Heuristic searches of the uniformly weighted data set using PAUP 4.0b4a (100 random addition sequences) produced three islands of equally parsimonious trees with 144, 18, and 12 trees which were hit 46, 23, and 30 times, respectively. These 174 trees had a length of 540, a CI (ensemble consistency index) of 0.347, an RI (ensemble retention index) of 0.666, and an RC (rescaled consistency index) of 0.231. The strict consensus is shown in Fig. 2 together with clade support values (bootstrap proportions).

The same data matrix (Table 3) was run in NONA 2.0 (Goloboff, 2000) (options: amb-, mult * 200). In 138 of these 200 searches, NONA found trees of length 540, that is, the same length as the shortest trees found with PAUP. In total, NONA found 136 trees of this length, the consensus of which was identical to that of the 174 trees found by PAUP. Condensing the PAUP trees by collapsing branches when their minimum length was zero, corresponding to the amb- option in NONA, resulted in 138 trees producing the same strict consensus as the original 174 more resolved PAUP trees. PAUP arrived at the same 138 trees when branches of minimum length zero were collapsed during searches (100 searches found three islands of 108, 18, and 12 trees, corresponding exactly to the three islands found initially). The 136 trees found by NONA were a subset of the 138 condensed PAUP trees. Import of the PAUP trees to NONA confirmed that all PAUP trees are unique under amb- and have length 540. The two condensed trees that NONA missed both belonged to the largest tree island found by PAUP. The reason that NONA missed these trees is apparently that the program only swaps on one dichotomous tree for each collapsed tree, and this may cause incomplete exploration of some tree islands.

To check for undiscovered tree islands, we used the parsimony ratchet (Nixon, 1999) as implemented in WinClada (Nixon, 2000). We ran 30 ratchet searches, each with 200 iterations (options: 1 tree kept in each iteration, 22 characters (15%) reweighted, 10% of clades constrained). These searches found 135 of the 138 condensed PAUP trees but no additional trees. Thus, it is unlikely that there are additional tree islands of length 540 that we have not discovered.

Under implied weights (options: $k = 2$, uninformative characters excluded, fits rounded as in Pee-Wee, other options as for unweighted analyses) PAUP found two trees of fit 979.4, representing two separate islands hit 26 and 4 times out of 100 searches. Analyses with Pee-Wee ($k = 2$, mult * 100) found the same two trees, which were together hit 30 times out of 100 searches, and reported the same fit values as PAUP did. Ten independent ratchet searches using batch files created with WinClada under the options given above and run with Pee-Wee also found the same two trees. The consensus of the two fittest trees is shown in Fig. 3 together with clade support values. We used Pee-Wee-emulated fits in PAUP rather than exact fits because we wanted to be able to compare the results with those obtained with Pee-Wee and because excessive precision may force hill-climbing algorithms to stop before reaching the most optimal trees (e.g., Ronquist *et al.*, 1999).

Although weighted and unweighted trees were quite similar, the weighted trees provided additional resolution and fit intuitive ideas about relationships better. For instance, the weighted trees grouped all genera in Nordlander's (1982b) *Chrestosema* group except *Glaurospidia*, whereas the unweighted trees split the *Chrestosema* group into three or more lineages. One of the trees found under implied weights fit Nordlander's notions about intergeneric relationships particularly

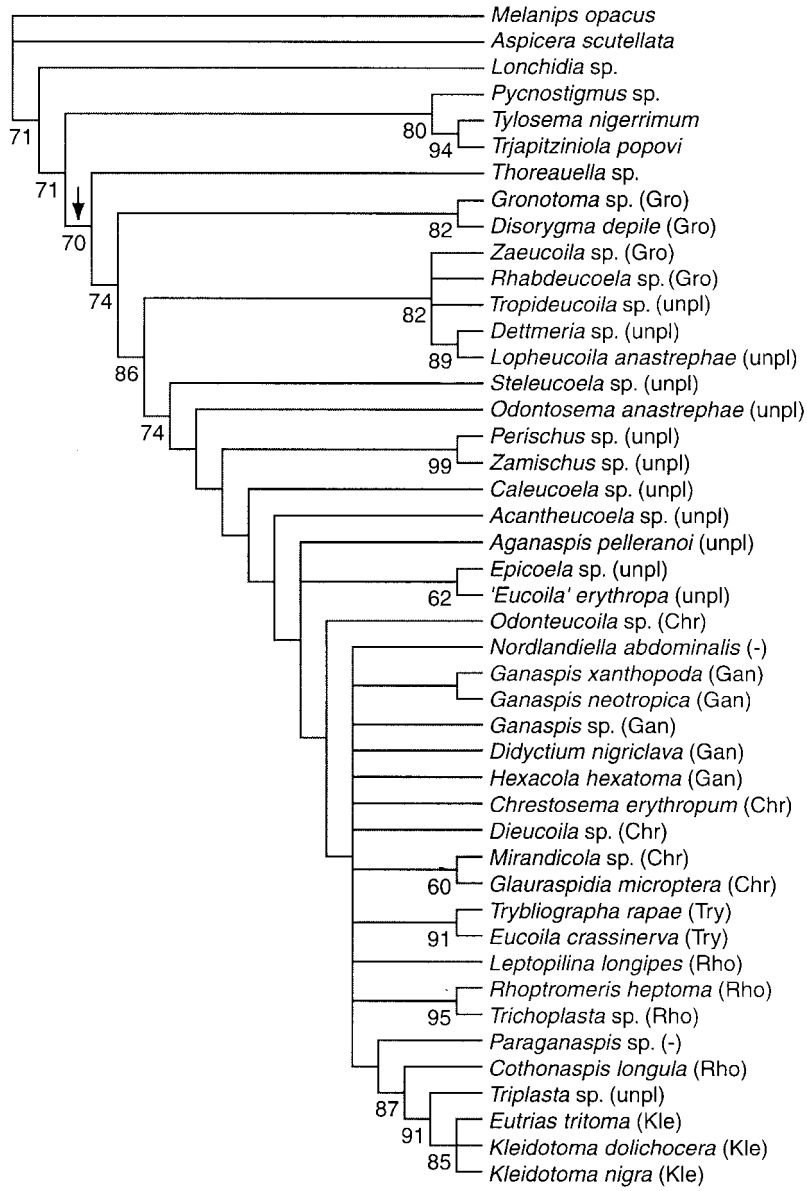

FIG. 2. Strict consensus of the 174 best trees found by heuristic analysis of the complete data set under equal weights. The numbers on the branches indicate bootstrap support (based on 500 replications). The arrow points to a branch that did not occur in the strict consensus but received bootstrap support above 50%. The placement of eucoiline genera into genus groups suggested by Nordlander (1982b) is indicated by a three-letter code following each genus name (Gro, *Gronotoma* group; Try, *Trybliographa* group; Rho, *Rhoptromeris* group; Chr, *Chrestosema* group; Kle, *Kleidotoma* group; Gan, *Ganaspis* group; unpl, unplaced; described after 1982).

well (Fig. 4). This tree had the *Trybliographa* genus group plus the genera *Rhoptromeris* and *Trichoplasta* as a monophyletic clade, largely in accord with previous ideas (cf. Nordlander, 1982a), whereas the other tree rather unexpectedly nested *Ganaspis xanthopoda* inside this clade. Therefore, the former tree was chosen for mapping unambiguous character changes (Appendix 2) and will be referred to subsequently as "the preferred tree."

The trees resulting from our unweighted searches show a CI (0.347) approximately equal to that expected for a data set of 48 taxa according to the polynomial regression analysis of empirical data by Sanderson and Donoghue (1989; expected value 0.335). The high CI

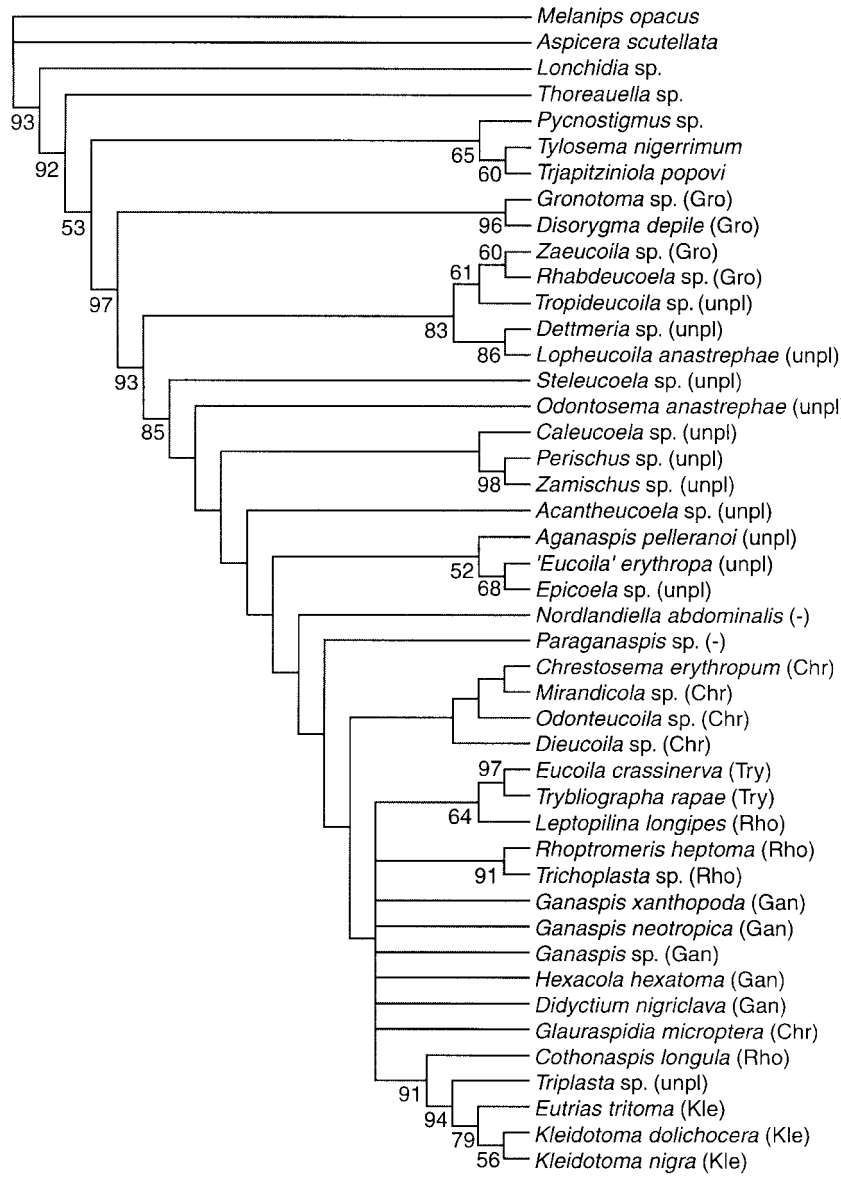

FIG. 3. Strict consensus of the two best trees (fit: 979.4) resulting from heuristic analysis of the complete data set using Goloboff fits (k = 2). Numbers on branches indicate bootstrap support (100 replications). Placement into genus groups suggested by Nordlander (1982b) is indicated by three-letter codes as in Fig. 2.

value relative to randomized or permutated data sets (Archie, 1989; Klassen *et al.*, 1991) and the high bootstrap proportions for many groups in both unweighted and weighted analyses (Figs. 2 and 3) clearly show that the data set exhibits strong phylogenetic signal despite the nominally low CI value for the best trees.

The mean number of changes among alternative character optimizations was calculated for each branch in the preferred tree (Fig. 4) using MacClade (Fig. 5). When interpreting this phylogram, it is important to note that autapomorphies of terminal taxa were generally not included in the analysis, resulting in terminal branch lengths being underestimated. Furthermore, branch lengths may also have been underestimated for branches leading to taxa with a large proportion of unknown states (*Tylosema*, *Trjapitziniola*, *Dettmeria*, *Lopheucoila*, *Zamischus*, *Perischus*, *Caleucoela*, and *Steleucoela*). In general, longer branches tend to correspond

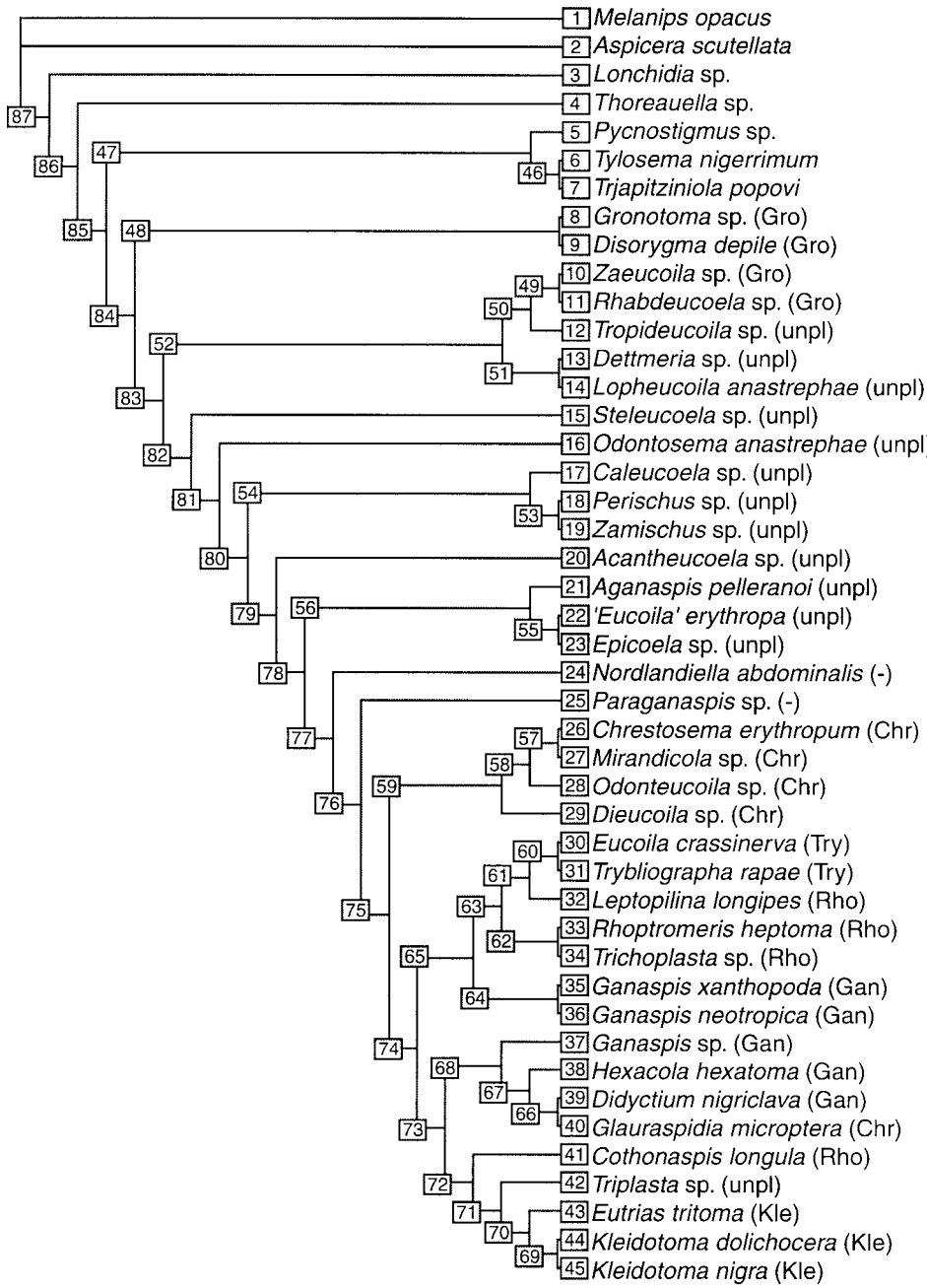

FIG. 4. The preferred tree, equivalent to one of the optimal trees from the implied-weights search (Fig. 3). This tree fit our initial hypotheses about higher eucoiline relationships particularly well and was used for mapping characters (Appendix 2). Placement into genus groups suggested by Nordlander (1982b) is indicated by three-letter codes as in Fig. 2.

to well-supported clades (compare Fig. 5 with Figs. 2 and 3).

To examine the influence of missing data on phylogenetic resolution, the studied taxa for which there was not a complete dissection (taxa labeled SM in Table 1) were excluded. The culled data set, including 37 of the original 45 taxa, was analyzed both under standard and under implied weights using the same heuristic search options as previously with PAUP, NONA, Pee-Wee, and the ratchet (10 independent runs). Under

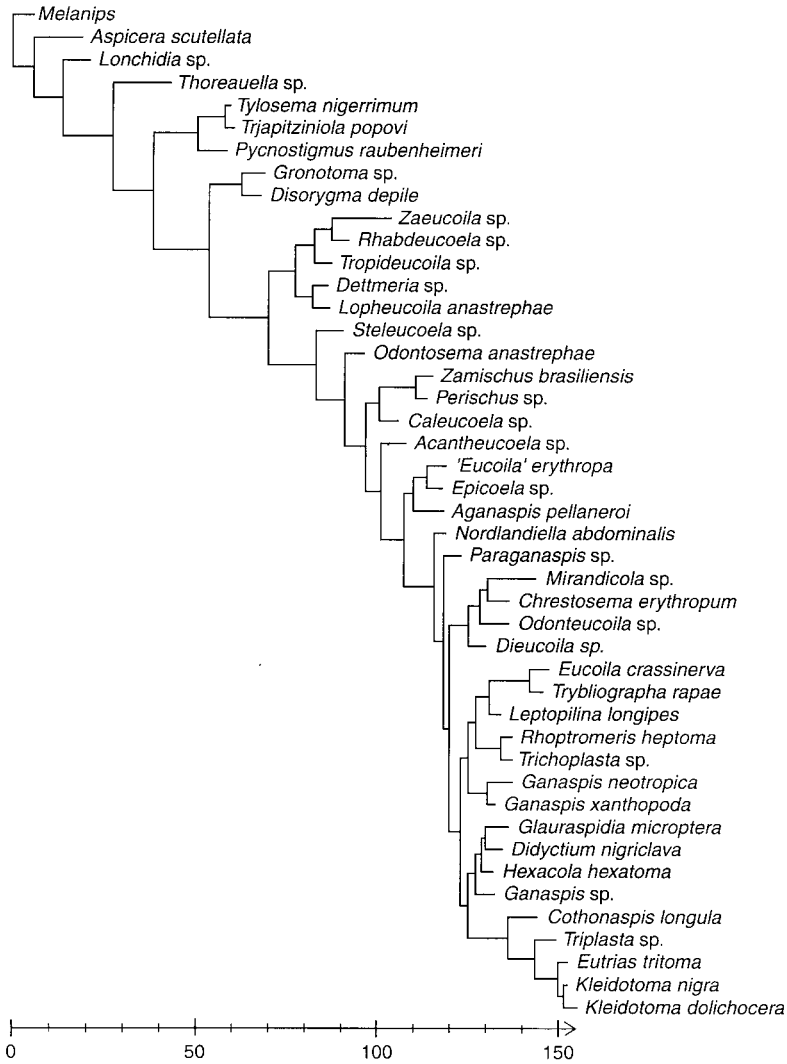

FIG. 5. Phylogram showing branch lengths, measured as the mean of changes among alternative character reconstructions, in the preferred tree. Since autapomorphies were excluded in the analysis, terminal branch lengths are underestimated.

standard uniform character weights, 266 trees of length 468 were found with PAUP. The shortest trees fell into three islands with 164, 92, and 10 trees, hit 43, 34, and 16 times, respectively, in 100 searches. NONA hit trees of the same length in 173 of 200 searches. The PAUP trees corresponded to 226 condensed trees, of which 222 were found by NONA. Ten ratchet runs with WinClada and NONA found 207 of the 226 condensed PAUP trees.

In the implied-weights analysis, PAUP found one island with three trees of fit 980.5, hit 15 times in 100 searches. The island collapsed to a single tree when branches of minimum length zero were deleted. This single fittest tree was found 19 times in 100 searches with Pee-Wee. Ten ratchet searches with Pee-Wee did not produce additional trees.

Both the standard-weights and implied-weights analyses suggested that emarginines were the sister group of eucoilines, with pycnostigmines being more basal. The bootstrap support for the emarginine + eucoiline clade was 77% in the standard-weights analysis (not shown) and 63% in the implied-weights analysis (Fig. 6). Eucoiline relationships were largely resolved in agreement with the complete analyses. The strict

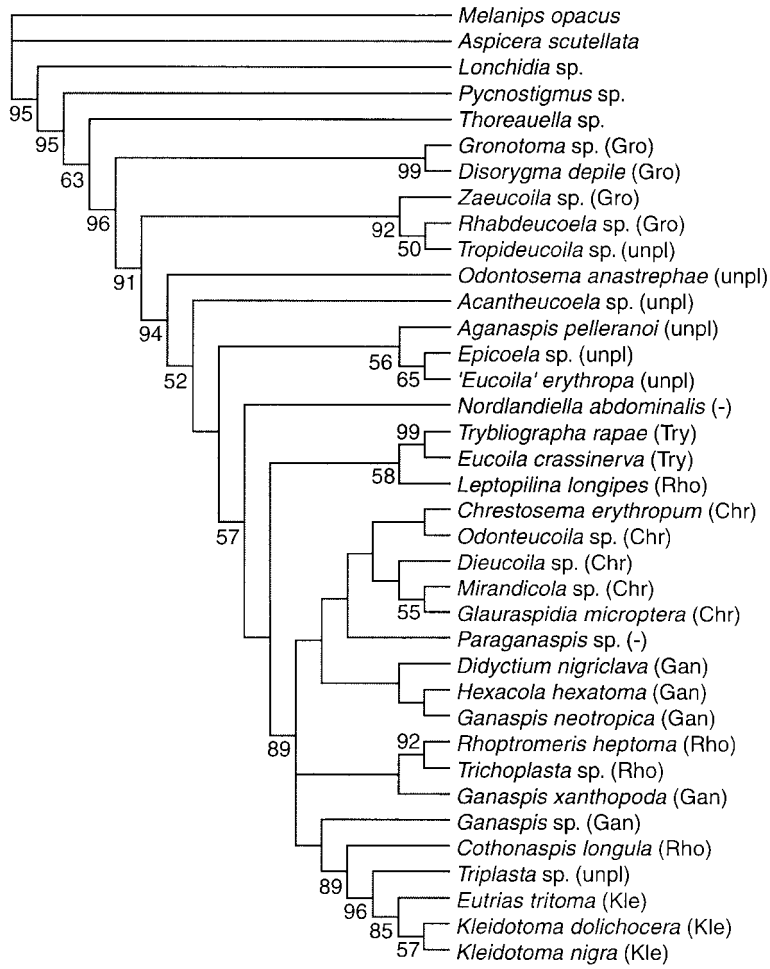

FIG. 6. Strict consensus of three trees (fit: 980.5) resulting from analysis under implied weights of a data matrix from which incompletely coded taxa were removed. Numbers on branches indicate bootstrap support levels (100 replications). Placement into genus groups suggested by Nordlander (1982b) is indicated by three-letter codes as in Fig. 2.

consensus from the standard-weights analysis was slightly less resolved than the corresponding consensus from the complete data set, suggesting that the culled taxa added critical phylogenetic information despite not being coded for all characters. However, all eucoiline clades supported by bootstrap values above 50% in the complete analysis (Fig. 2) had similar support values in the analysis of the culled matrix, with the exception of *Rhabdeucoela* + *Tropideucoila* and *Kleidotoma dolichocera* + *K. nigra* (both were unsupported in the complete analysis, but had bootstrap support of 56% and 52%, respectively, in the analysis of the culled matrix). Eucoiline relationships suggested by the implied-weights consensus (Fig. 6) differed slightly from those suggested in the consensus tree from the analysis of the complete data set (Fig. 3). In particular, the former had a monophyletic *Chrestosema* group, including *Glauraspidia* (Fig. 6). However, the strongly supported clades were the same in the analyses of the complete and the culled data sets (Figs. 3 and 6).

The putative monophyly of the six genus groups originally proposed by Nordlander (1982b) was further examined by constrained searches under standard and implied weights. The terminal taxa assigned to genus groups by Nordlander (1982b) were first included in backbone constraint trees. In each constraint tree, the genera assigned to the group of interest were specified to be monophyletic relative to the genera assigned to

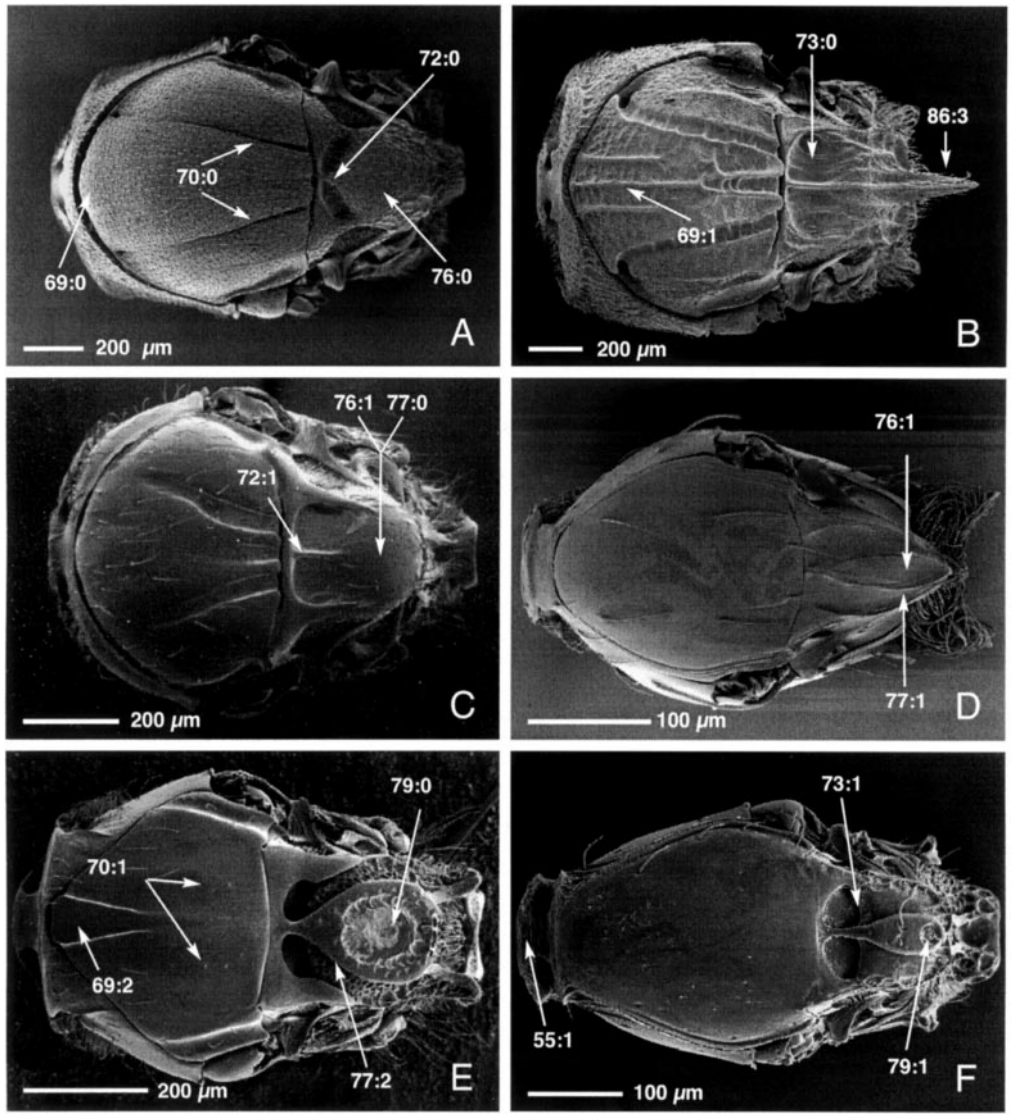

FIG. 7. Mesosoma of female, dorsal view. (A) *Melanips opacus* (Figitinae). (B) *Aspicera scutellata* (Aspicerinae). (C) *Pycnostigmus* sp. (Pycnostigminae). (D) *Thoreauella* sp. (Emargininae). (E) *Rhabdeucoela* sp. (*Zaeucoila* group). (F) *Triplasta* sp. (*Kleidotoma* group). Numbers refer to characters and character states. The placement of taxa follows our suggested division of eucoilines into informal groups (Fig. 13) and not Nordlander's original genus groups.

other groups, while the unplaced genera and outgroups were omitted. Each of these backbone constraints was enforced onto a set of 10 PAUP searches starting from random addition sequences. NONA and Pee-Wee were not used for these searches because they do not handle backbone constraints. The number of tree islands, the frequency with which these islands were hit, and the number of extra steps or the amount of added cost were recorded (Table 4). Only the *Trybliographa* and *Kleidotoma* groups appeared as monophyletic in the best trees (Figs. 2, 3, and 6; Table 4). There was fairly strong evidence against the monophyly of the *Gronotoma* and *Rhoptromeris* groups, whereas the data were only weakly incompatible with the monophyly of the *Ganaspis* and *Chrestosema* groups (Table 4).

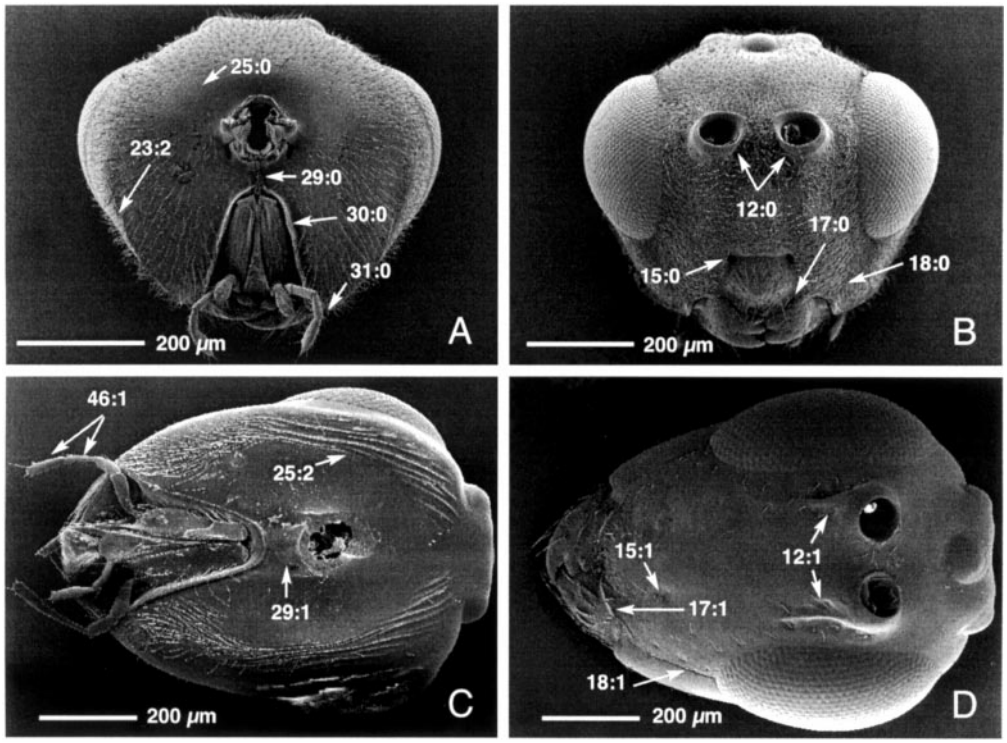

FIG. 8. Head of female, SEM. (A) *Melanips opacus* (Figitinae), posterior view. (B) *M. opacus* (Figitinae), anterior view. (C) *Epicoela* sp. ("Neotropical grade"), posterior view. (D) *Epicoela* sp. ("Neotropical grade"), anterior view. Numbers refer to characters and character states. The placement of taxa follows our suggested division of eucoilines into informal groups (Fig. 13) and not Nordlander's original genus groups.

DISCUSSION

Digital Image Databases

In molecular studies of phylogenetic relationships, it is common practice to make raw data widely available by depositing gene (or protein) sequences in public databases. Morphological systematists, however, often rely on museums to hold the specimens and preparations from which their data have been derived; only the character matrices are included in publications and public databases. Much of the raw data in morphological systematics is thus difficult for other workers to access, typically requiring museum visits and handling of invaluable specimens. This is unfortunate for many reasons. For instance, morphological analyses of relationships become difficult to evaluate because critical reexamination of the character analyses typically requires access to appropriate preparations of the relevant taxa. Furthermore, the work leading to a morphological character matrix often reveals a wealth of information about relationships at both lower and higher levels than the one in focus. Not making this information readily available to others is a waste of time and effort.

We have found that the most efficient way of producing a large morphological matrix is to code characters and states from photographic prints of the appropriate preparations in standard views. These prints can be spread out next to one another such that all taxa can be compared easily and simultaneously. The raw data used in the analysis are documented in far more detail in these pictures than in the resulting character matrix or the few illustrations that can be included in a standard scientific paper. Previously it has not been possible to make the information contained in the raw pictures easily available to other workers. However, the advent of digital imaging techniques has changed this and we here

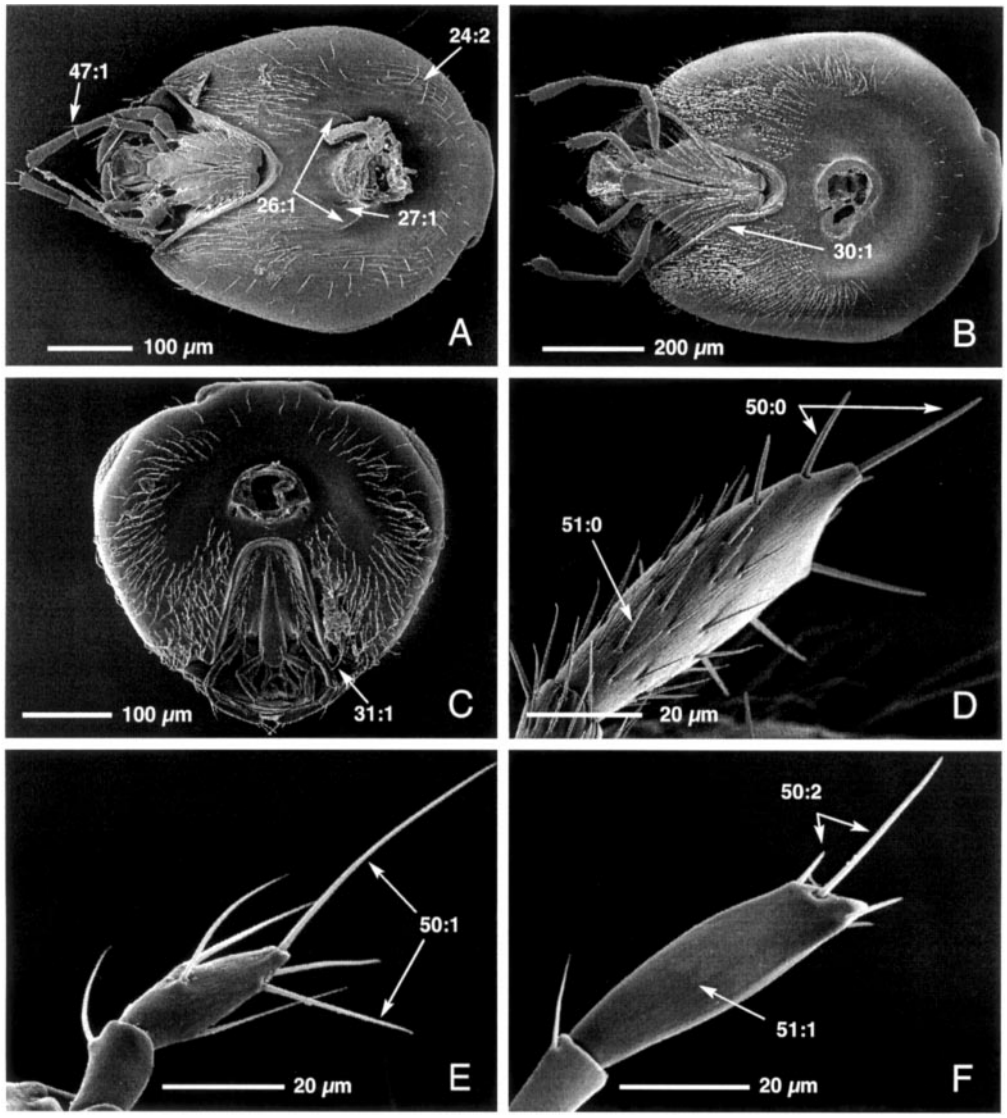

FIG. 9. (A–C) Head of female, SEM. (A) *Eutrias tritoma* (*Kleidotoma* group), posterior view. (B) *Trybliographa rapae* (*Trybliographa* group), posterior view. (C) *Disorygma depile* (*Gronotoma* group), posterior view. (D–F) Apical segment of maxillary palp of female, SEM. (D) *Melanips opacus* (Figitinae). (E) *Thoreauella* sp. (Emargininae). (F) *Kleidotoma dolichocera* (*Kleidotoma* group). Numbers refer to characters and character states. The placement of taxa follows our suggested division of eucoilines into informal groups (Fig. 13) and not Nordlander's original genus groups.

take the step to make the more than 1100 high-resolution digital images, mostly scanning electron micrographs, on which this study is based available through a searchable Web database (http://morphbank.ebc.uu.se). To our knowledge, this is the first morphological phylogenetic study to have made detailed documentation of the raw data publicly available in this fashion.

Our image database will not only be a powerful tool for morphological phylogeneticists interested in cynipoid wasps and related groups, it also represents a virtual reference collection of correctly determined eucoilines that will be valuable to workers all over the world interested in this diverse and difficult group of parasitic wasps. In the future, we foresee that similar image databases will become an indispensable tool not only in morphological phylogenetics but also in taxonomic ex-

TABLE 4
Nordlander's Genus Groups and the Number of Extra Steps or the Decrease in Goloboff Fit Induced by Forcing Them to Be Monophyletic

Genus group	Extra steps	No. islands[a]	Times hit[b]	Fit loss	No. islands[a]	Times hit[b]
Gronotoma group	8	1	3/10	9.7	1	1/10
Trybliographa group	0	2	10/10	0.0	2	3/10
Rhoptromeris group	9	3	10/10	8.4	1	3/10
Chrestosema group	3	2	6/10	0.6	1	2/10
Ganaspis group	2	1	8/10	1.3	1	4/10
Kleidotoma group	0	3	10/10	0.0	2	2/10

Note. The values are based on PAUP searches of the complete data set under backbone constraints defined by Nordlander's (1982b) assignment of genera to genus groups (cf. Table 1). Searches used standard unweighted parsimony as the fit criterion and 10 random additional sequences for each analysis followed by TBR swapping. The *Trybliographa* and *Kleidotoma* groups appear as monophyletic in the most parsimonious trees (Fig. 3) and therefore have no extra steps.

[a] Number of islands of shortest trees found in these searches.

[b] Total number of hits on any island of shortest trees / total number of searches.

ploration and documentation of the biodiversity on earth. This would be particularly true if the systematics community decided that deposition of critical high-resolution images in such databases would be a requirement for valid descriptions of new taxa.

Implied versus Uniform Weights

As is well known, characters that are uniform within terminal taxa also tend to be more informative about relationships among taxa (Farris, 1966). This information can be used to improve phylogenetic inference by weighting characters according to their homoplasy. The more homoplastic characters are, the less they should influence the results of a phylogenetic analysis. Homoplasy weighting was initially achieved through an iterative, successive reweighting protocol (Farris, 1969), but it is now possible to weight characters during tree searches, evaluating each tree according to the weights implied by that tree (Goloboff, 1993a, b).

Compared to analysis under uniform weights, implied weighting should retrieve more information about relationships from a given data set. Therefore, analysis under implied weights should produce better-supported phylogenetic results. Under difficult conditions, we might also expect more consistent results across analyses and better agreement with intuitively constructed hypotheses, given that the latter rely on differential weighting of characters according to their apparent reliability. Several studies now document both improved congruence among analyses (Goloboff, 1997: Table 1) and better agreement with intuitive results (Ronquist *et al.*, 1999), in addition to improved phylogenetic resolution. Our present analysis again documents increased resolution and better agreement with intuitive results under implied weights, as will be detailed below. Considering these facts, we think that implied weights should be used more widely than today in parsimony inference of phylogeny, particularly for difficult data sets.

Our conclusion is not necessarily in conflict with the recent observation that rapidly evolving third-codon positions provide more phylogenetic resolution, as indicated by support values, than the slower first or second positions (Källersjö *et al.*, 1999). Support levels are strongly influenced by the number of character changes and because conservative characters have fewer changes they will tend to contain less information than more homoplastic characters. The critical question is whether the conservative characters provide more information *per character change*. The results reported by Källersjö *et al.* (1999) do not address this question since, in all their comparisons, the third-codon positions taken together are likely to account for many more changes than the first and second positions combined.

Monophyly of Eucoilines

The only substantial evidence for eucoiline monophyly cited in the literature is the presence of the scutellar plate or cup (Quinlan, 1978, 1988; Nordlander,

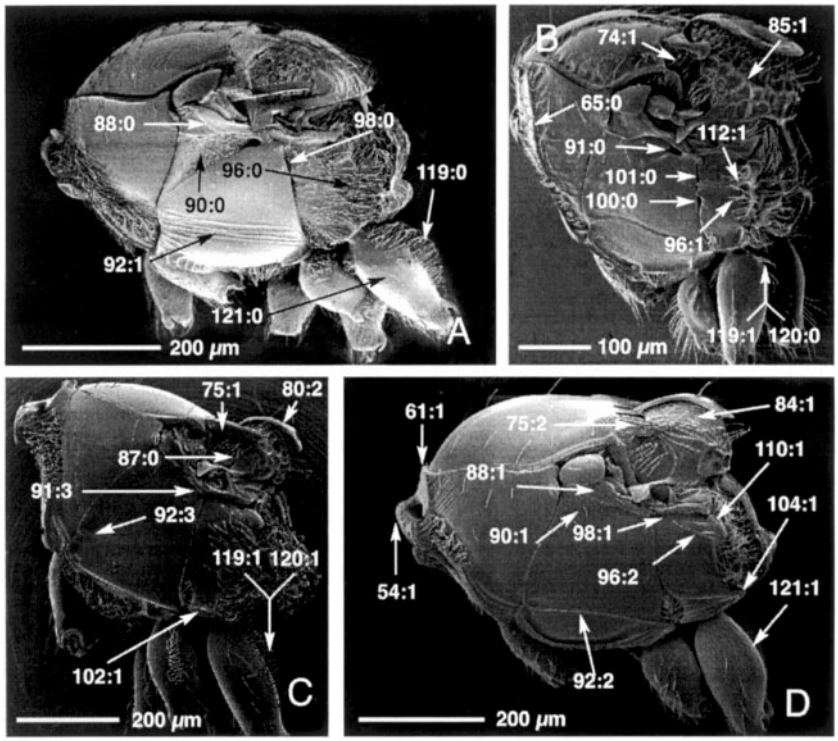

FIG. 10. Mesosoma of female, lateral view, SEM. (A) *Lonchidia* sp. (Figitinae). (B) *Gronotoma* sp. (*Gronotoma* group). (C) *Glauraspidia microptera* (*Chrestosema* group). (D) *Kleidotoma dolichocera* (*Kleidotoma* group). Numbers refer to characters and character states. The placement of taxa follows our suggested division of eucoilines into informal groups (Fig. 13) and not Nordlander's original genus groups.

1982b; Ronquist, 1999). This plate is a conspicuously raised and distinctly margined, circular to elongate-oval, median dorsal structure on the scutellum (character 77:2, Figs. 7E and 7F). The dorsal surface is equipped with a deep glandular pit (79:0, 1, Figs. 7E and 7F). The plate is present in all eucoilines but there is considerable variation in its structure. The size and shape of the plate vary, the size and position of the pit are different (compare Figs. 7E and 7F), and the plate may be flat and polished, be distinctly sculptured, or bear prominent projections dorsally.

Although the eucoiline scutellar plate is unique among parasitic wasps, some uncertainty has arisen lately concerning its value as an indicator of eucoiline monophyly because close scrutiny of some figitids has revealed scutellar features reminiscent of the eucoiline plate, particularly in emarginines. Quinlan (1988) considered the genus *Emargo* to have a narrow scutellar plate and concluded that it is a eucoiline, despite the obvious differences between eucoilines and emarginines in abdominal morphology. Lin (1988) reached the same conclusion and specifically placed *Emargo* in the *Chrestosema* group, apparently because of the long and dense pubescence located posteriorly on the mesosoma in both emarginines and some genera of the *Chrestosema* group.

Our SEM pictures reveal that the plate-like scutellar structure in the emarginines examined consists of two curved longitudinal carinae defining an oblong–oval median dorsal area on the scutellum (Fig. 7D). The median area is not raised anteriorly and only slightly so posteriorly, and it lacks any glandular pit. Thus, the emarginine structure is distinct from the eucoiline scutellar plate. Of course, it is still possible that the two states form part of the same transformation series, particularly since emarginines and eucoilines are morphologically similar in other respects.

Ronquist (1999) pointed out that some pycnostigmines have a polished area dorsally on the scutellum, which might possibly be the remnant of a eucoiline-like scutellar plate. The polished area is present in some

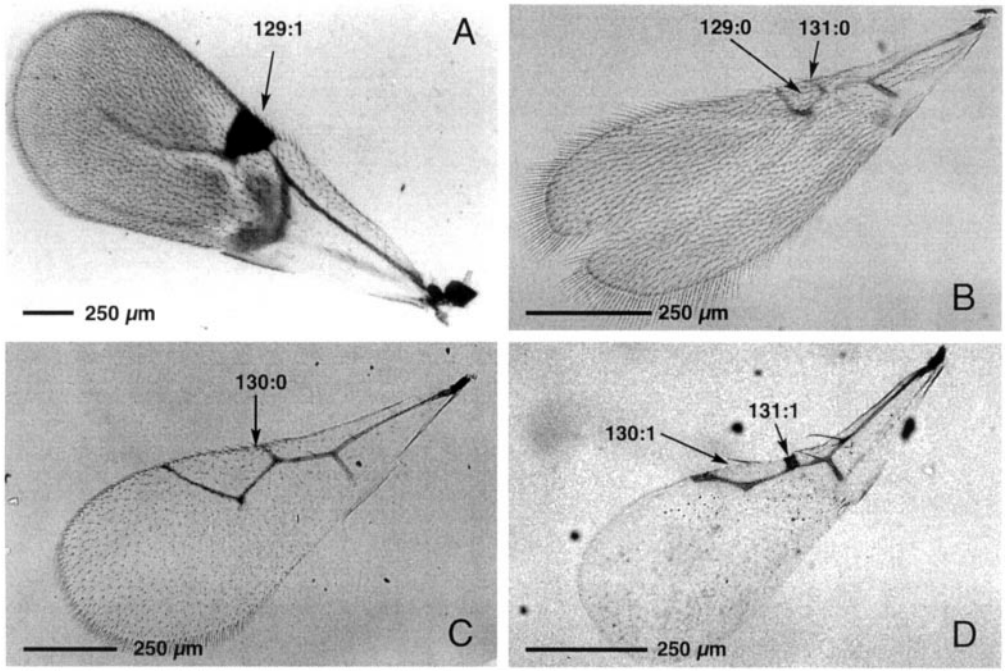

FIG. 11. Left forewing of female. (A) *Pycnostigmus* sp. (Pycnostigminae). (B) *Thoreauella* sp. (Emargininae). (C) *Nordlandiella abdominalis* (unplaced). (D) *Triplasta* sp. (*Kleidotoma* group). Numbers refer to characters and character states. The placement of taxa follows our suggested division of eucoilines into informal groups (Fig. 13) and not Nordlander's original genus groups.

species of *Pycnostigmus* (Fig. 7C) as well as in *Trjapitziniola* (Kovalev, 1994). It is never raised, nor is it defined by marginal carinae, and it never bears a glandular pit like the eucoiline scutellar plate. Nevertheless, the hypothesis that the polished area represents the remnant of a scutellar plate cannot be completely dismissed. The situation is further complicated by the fact that pycnostigmines appear to share two unique morphological apomorphies with eucoilines: fusion of abdominal terga 3–5 in females and absence of submedian pits on the articular bulb of the petiole (Ronquist, 1999). While these characters clearly suggest that pycnostigmines and eucoilines form a monophyletic group, they also raise the possibility that pycnostigmines, if they were derived from forms with a scutellar plate, are nested within the Eucoilinae (Ronquist, 1999).

In view of the uncertainty concerning the scutellar plate as a eucoiline autapomorphy, it is reassuring that our analyses provide convincing support for the monophyly of Eucoilinae excluding both the Pycnostigminae and the Emargininae (Figs. 2, 3, and 6). The support comes from several characters from different body parts. The unique synapomorphies are (for a complete list of supporting characters, see node 84 in Appendix 2): malar sulcus present (character 18:1, Fig. 8D), maxillary palp with four segments (basal two segments fused) (45:1; cf. Figs. 8C and 9A), distal segment of maxillary palp without pubescence (49:1, Fig. 9F), mesopleuron with a single, straight carina (92:2, Figs. 10B and 10D), and mechanosensory hair patch of articular bulb of petiole situated medioventrally (134:1). Thus, it appears likely that the eucoiline scutellar plate, after all, is a good synapomorphy and that the scutellar features of emarginines and pycnostigmines are not reduced eucoiline plates but either independently derived structures or intermediate states in a transformation series leading to the eucoiline plate. In either case, the glandular release pit is a unique feature of the eucoiline scutellar plate, completely absent in emarginines and pycnostigmines.

Relationships between Eucoilines and Other Figitids

Our analyses consistently suggest that emarginines, pycnostigmines, and eucoilines together form a monophyletic clade (Figs. 2, 3, and 6). The support was

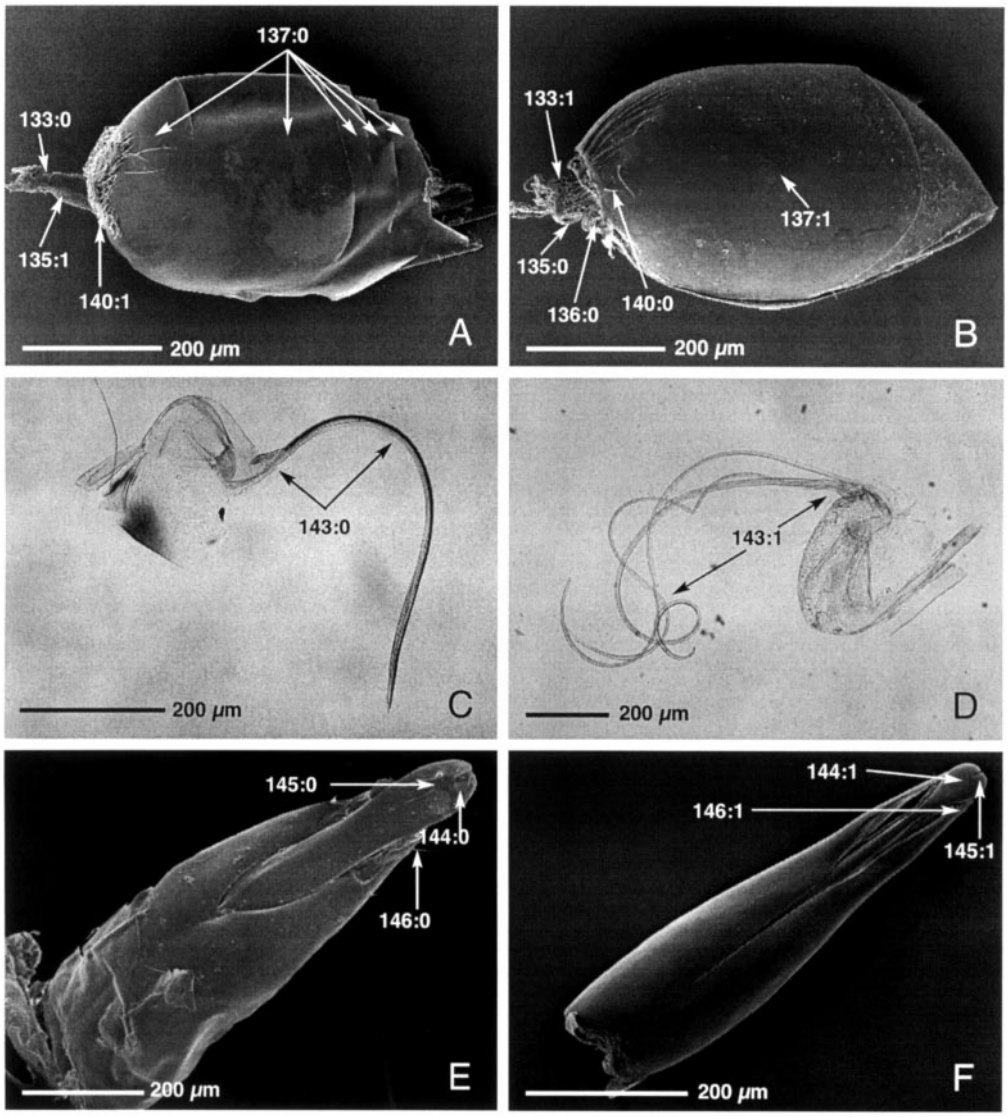

FIG. 12. (A, B) Metasoma of female, lateral view, SEM. (A) *Thoreauella* sp. (Emargininae). (B) *Triplasta* sp. (*Kleidotoma* group). (C, D) Female ovipositor, lateral view. (C) *Thoreauella* sp. (Emargininae). (D) *Hexacola hexatoma* (*Ganaspis* group). (E, F) Male phallus, dorsal view, SEM. (E) *Melanips opacus* (Figitinae). (F) *Eucoila crassinerva* (*Trybliographa* group). Numbers refer to characters and character states. The placement of taxa follows our suggested division of eucoilines into informal groups (Fig. 13) and not Nordlander's original genus groups.

strong in the weighted analyses but weaker in the unweighted analyses. The unique synapomorphies defining this clade (node 86, Appendix 2) include a reduction in the number of labial palp segments from 3 to 2 (52:1, Figs. 8C and 9A–9C), the presence of a modified dorsomedian part of the scutellum (76:1, Figs. 7C–7F), and the posterolaterally extended mesocoxal rim (95:1). The three pycnostigmine genera were convincingly supported as a monophyletic clade, sharing two unique apomorphies (node 47, Appendix 2): fusion of abdominal terga 3–5 in males (142:1) and a secondarily sclerotized, small marginal cell (129:1, Fig. 11A). There was also strong support for a sister-group relationship between *Tylosema* and *Trjapitziniola*, which is not surprising considering that the only species in the latter genus was originally placed in *Tylosema* (Kovalev, 1994).

Unfortunately, our analyses do not convincingly show whether the emarginines or the pycnostigmines, or possibly both of them together, form the sister group

of eucoilines. Among the shortest trees resulting from the unweighted analysis, there was support for both the pycnostigmine and the emarginine alternatives but not for the emarginine + pycnostigmine solution. Bootstrap analysis of the unweighted data slightly preferred the emarginine alternative (Fig. 2) but analysis under implied weights instead favored the pycnostigmine alternative (Figs. 3 and 4). This indicates that the emarginine alternative is supported by a larger number of relatively more homoplastic characters, whereas fewer but more reliable (less homoplastic) characters favor the pycnostigmine alternative. When incompletely coded taxa were removed from the analysis, both weighted and unweighted analyses preferred the emarginine alternative, albeit not with convincing bootstrap support values (Fig. 6). This effect was probably due to the reduction in the number of pycnostigmine exemplars. Thus, a fair representation of pycnostigmine diversity was essential in providing the implied-weights support for the monophyly of Pycnostigminae + Eucoilinae.

Detailed consideration of the conflicting characters suggests that the emarginine + eucoiline signal may be due at least partly to parallel modifications associated with adaptation to parasitism of small hosts in confined, dirty places. Furthermore, there are no emarginine + eucoiline synapomorphies that are unique within the Figitidae, whereas a sister-group relationship between pycnostigmines and eucoilines is supported by at least two synapomorphies that are unique within the Cynipoidea: (1) the peculiar abdominal modifications involving, among other things, fusion of abdominal terga 3–5 in the female metasoma (character 137:1), and (2) the disappearance of the submedian pits of the articular bulb of the petiole (131:1, Fig. 12B). Two additional synapomorphies are unique to pycnostigmines and eucoilines in the context of the current analysis (see node 85, Appedix 2, for a complete list of supporting characters). Thus, although the question is not yet convincingly resolved, we believe that the current evidence favors the Pycnostigminae as the sister group of Eucoilinae, particularly when the reliability of the character evidence is evaluated in a larger phylogenetic perspective. Further study of the morphological diversity of the figitid lineages surrounding the root of the eucoiline tree might be able to shed additional light on this problem.

Although our analyses consistently place *Lonchidia* as the sister group of pygnostigmines + emarginines + eucoilines, and *Lonchidia* is perhaps the figitid genus that is superficially most similar to eucoilines and emarginines, it must be borne in mind that our study included only representatives of the genera *Lonchidia* and *Melanips* from the heterogeneous Figitinae assemblage (cf. Fig. 2). Thus, the putative sister-group relationship between *Lonchidia* and eucoilines + emarginines + pycnostigmines must be tested by further analyses encompassing a more comprehensive sample of Figitinae genera before it can be regarded as well established.

Higher Phylogeny and Classification of Eucoilines

Although our analyses provide important insights into the higher-level relationships of eucoilines, many questions remain to be answered. We studied only some 40% of the described genera, and our analyses could not resolve all relationships even among the included genera. Therefore, we consider it premature to propose a formal, comprehensive higher classification for the Eucoilinae. Instead we prefer, for the time being, to work with informal genus groups. Thus, in the following detailed discussion of the results and their implications concerning eucoiline relationships, we propose modifications to Nordlander's original genus group concepts when this is warranted by our results and leave genera unplaced when there is no firm basis for placing them in larger genus groups. Our modified system of eucoiline genus groups is presented in Fig. 13, together with the original assignments by Nordlander (1982b).

Relationships among Basal Eucoilines

The basal branchings within the Eucoilinae are convincingly resolved by our data (Figs. 2, 3, and 6). The genera placed by Nordlander (1982b) in the *Gronotoma* group fall into two distinct basal clades. One consists of *Gronotoma* and *Disorygma* among the studied genera and forms the sister group of all other eucoilines. The other lineage contains *Rhabdeucoela* as well as *Zaeucoila*, *Tropideucoila*, *Dettmeria*, and *Lopheucoila*. This clade is the sister group of the remaining eucoilines, excluding *Gronotoma* and *Disorygma*. The basal branchings are well supported in all analyses (Figs. 2, 3, and 6). Furthermore, it takes eight extra steps or decreases the

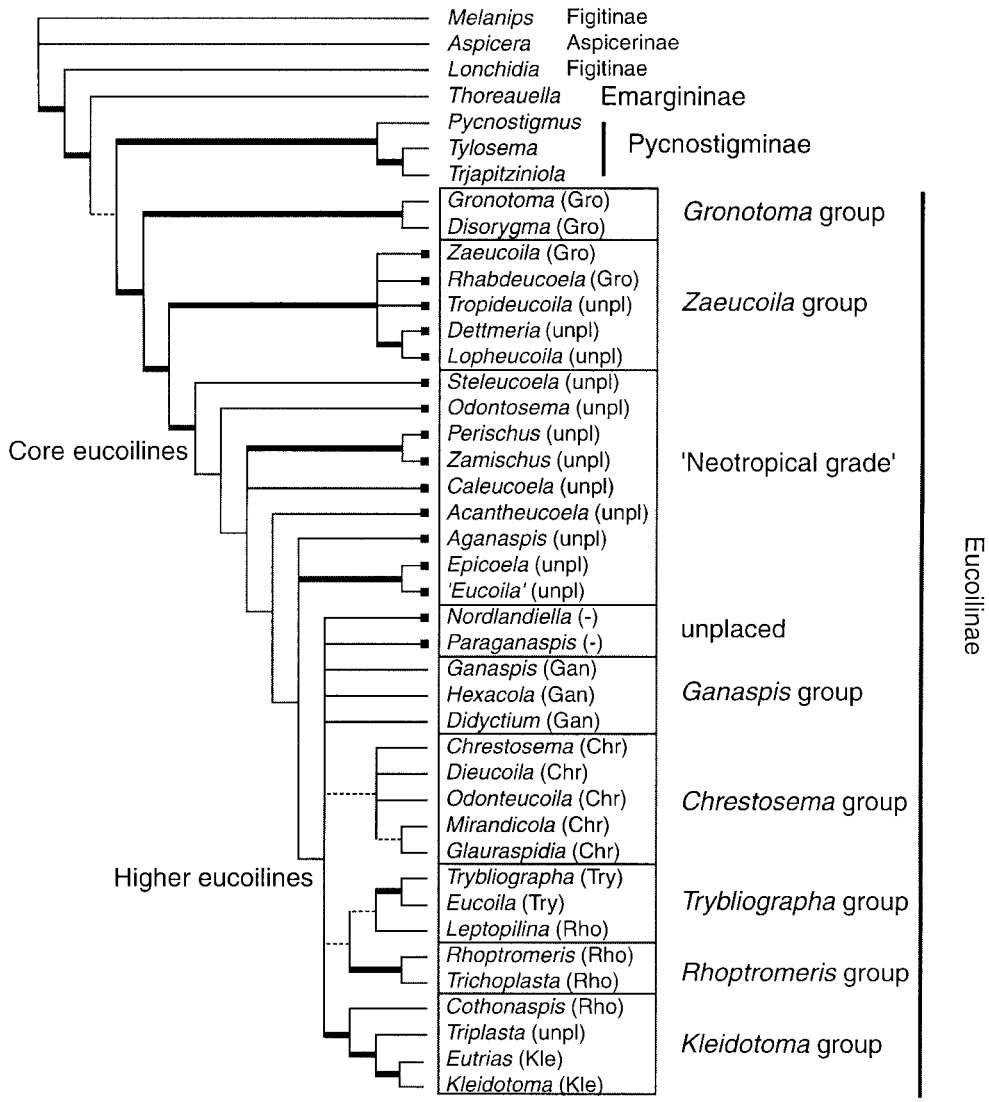

FIG. 13. Tree summarizing the results from the present analysis. Thick lines indicate well-supported clades, thin branches indicate clades that appeared in all or almost all analyses but which did not receive convincing bootstrap support, and dashed lines indicate tentative clades that appeared in only some analyses. Exclusively Neotropical eucoiline genera are marked by a black box on the corresponding terminal branch. The original placement of a genus into a genus group suggested by Nordlander (1982b) is indicated in parentheses after the genus name (see Fig. 2). The modified system of genus groups we propose is indicated to the right, together with informal names of grades and names of higher taxa.

Goloboff fit by 9.7 (10%) to retain the monophyly of the *Gronotoma* group of Nordlander (1982b) (Table 4), providing strong evidence against the monophyly of this group as originally circumscribed.

To accommodate our results, we suggest that the *Gronotoma* group be restricted to *Gronotoma*, *Disorygma*, and allied genera not included in our analysis (Fig. 13). For the other basal eucoiline lineage, we suggest the name *Zaeucoila* group (Fig. 13). This name is already in use to circumscribe the genera included in this analysis and their allies (Díaz and Gallardo, 1997, 1998; see also Gallardo and Díaz, 1999). However, this is the first study to identify actual synapomorphies supporting the *Zaeucoila* group (*sensu* Díaz and Gallardo).

The unique synapomorphies characterizing the *Gronotoma* group (*sensu stricto*) (node 48, Appendix 2) are

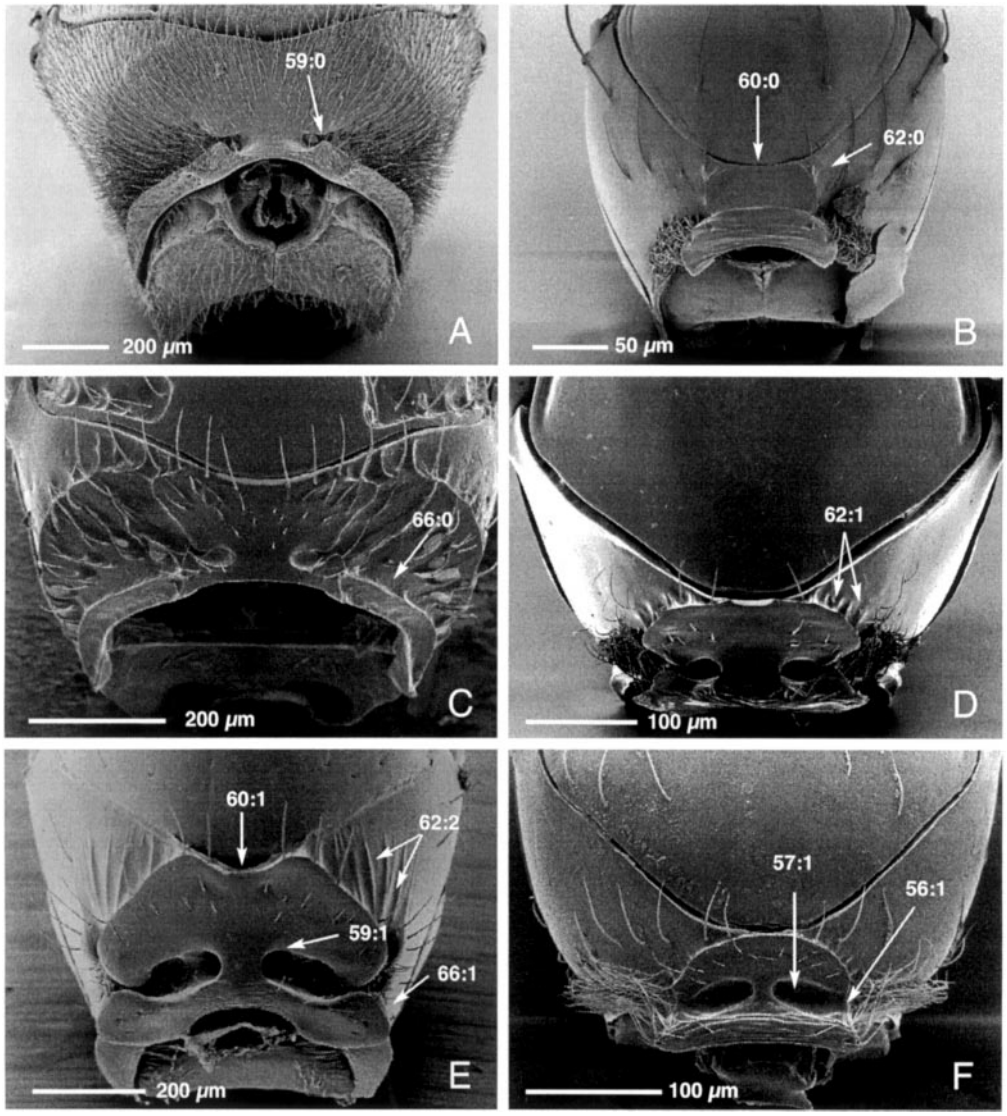

FIG. 14. Pronotum of female, anterodorsal view, SEM. (A) *Melanips opacus* (Figitinae). (B) *Thoreauella* sp. (Emargininae). (C) *Gronotoma* sp. (*Gronotoma* group). (D) *Leptopilina longipes* (*Trybliographa* group). (E) *Odontosema anastrephae* ("Neotropical grade"). (F) *Rhoptromeris heptoma* (*Rhoptromeris* group). Numbers refer to characters and character states. The placement of taxa follows our suggested division of eucoilines into informal groups (Fig. 13) and not Nordlander's original genus groups.

the projecting hypostomal carina (31:1, Fig. 9C) and the nonprojecting lateral parts of the pronotal plate (61:0, Figs. 10A and 10B). However, the polarity of the latter character is based solely on the state in emarginines and is therefore somewhat uncertain. The unambiguous but not unique synapomorphies for the group include the presence of a pyramidal prominence (19:1) and parallel sculpture (20:1) on the malar space adjacent to the mandible, long gena (21:1), a short septum separating the scutellar foveae (72:0, Figs. 7A, 7D, and 7E), and a horizontal carina anterior to the lateral propodeal carina (112:1, Fig. 11B). Quinlan (1986) considered the Afrotropical genera *Ealata* and *Nordlanderia* members of the *Gronotoma* group *sensu lato*. Examination of representatives of these genera reveals that they belong to the *Gronotoma* group *sensu stricto* (M.L.B.,

unpublished data). Other genera that belong in the *Gronotoma* group *sensu stricto* are *Diglyphosema*, *Microstilba*, and *Ganaspidium* (M.L.B., unpublished data).

The monophyly of the Eucoilinae excluding the *Gronotoma* group (*sensu stricto*) is supported by a long series of synapomorphies (node 83, Appendix 2). The two unique synapomorphies are the small subalar area of the mesopleuron (88:1, Figs. 10C and 10D) and the broad metasubpleural depression anterior to the metacoxal foramen (character 103:1). Some unambiguous synapomorphies (see Appendix 2 for a complete list) include the presence of a short vertical carina issuing from the ventral margin of the antennal socket (12:1, Fig. 8D; secondarily present in *Aspicera*, otherwise unique), a reduced subalar pit (91:1–3, Figs. 10C and 10D; also in emarginines), and an elongate metacoxal foramen (106:1; exception only in *Aganaspis*).

The *Zaeucoila* group (node 52, Appendix 2) is supported as a monophyletic group by unambiguous synapomorphies such as a single lateral carina or ledge on the lower face (13:1), a triangularly projecting clypeus (16:1), a narrow or broad median mesoscutal carina (69:1–2, Fig. 7E), and a conspicuous ventral expansion of the lateral bar (74:1, apparently independently derived in *Gronotoma*, cf. Fig. 10B). Of these synapomorphies, it is only the median mesoscutal carina (69:1–2) that is entirely unique for the *Zaeucoila* group. The sharp occipital carina (23:2) may also be autapomorphic for the group but we were not able to ascertain its presence in all *Zaeucoila* group members because of the lack of suitable material. Beyond the genera included in our analysis, the *Zaeucoila* group is likely to include *Moneucoela*, *Penteucoila*, and *Agrostocynips* (Díaz and Gallardo, 1997, 1998) as well as *Diceratapsis* (M.L.B., unpublished data).

More work is needed to clarify the relationships among the genera of the *Zaeucoila* group. Even though these South American eucoilines are rich in striking morphological features, our analyses did not manage to resolve relationships within the group, except that

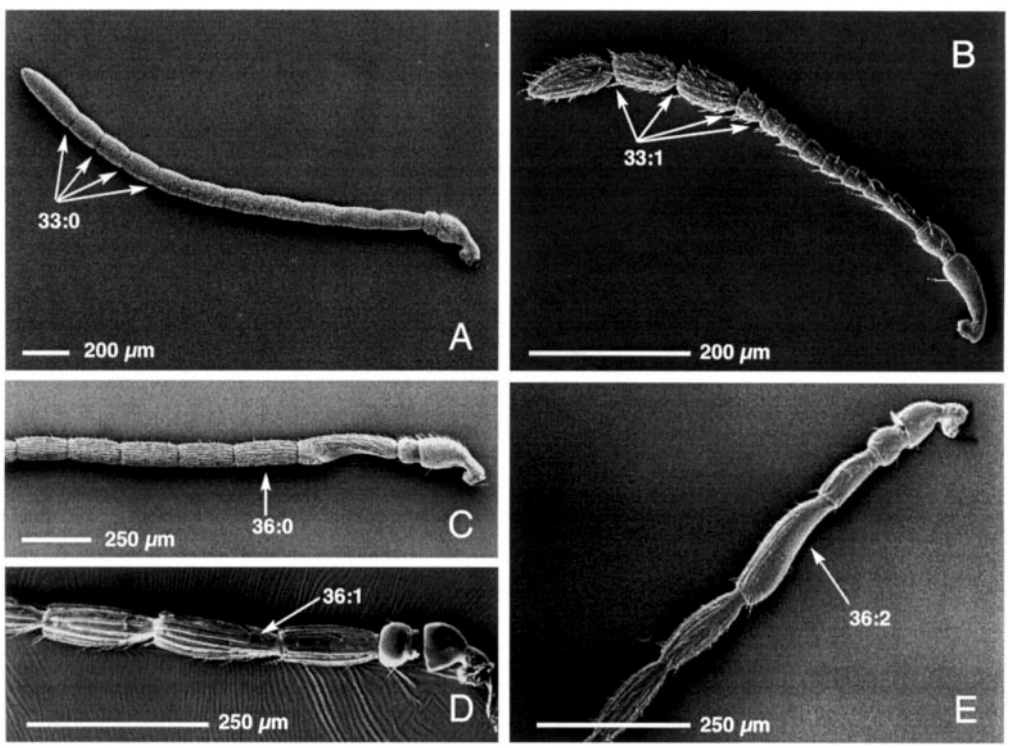

FIG. 15. Left antenna, dorsal view, SEM. (A) *Aspicera scutellata* (Aspicerinae), female. (B) *Triplasta* sp. (*Kleidotoma* group), female. (C) *Melanips opacus* (Figitinae), male. (D) *Leptopilina longipes* (*Trybliographa* group), male. (E) *Trichoplasta* sp. (*Rhoptromeris* group), male. Numbers refer to characters and character states. The placement of taxa follows our suggested division of eucoilines into informal groups (Fig. 13) and not Nordlander's original genus groups.

Dettmeria and *Lopheucoila* are closely related (Figs. 2, 3, and 6). This pattern could possibly be due to rapid early radiation in this old lineage.

The monophyly of the eucoilines excluding the *Gronotoma* and *Zaeucoila* groups (node 82, Appendix 2) is supported by a long series of characters, among which one might mention the following unambiguous synapomorphies: the elongate head (2:1, Figs. 8C, 8D, 9A and 9B; exceptions in some higher eucoilines), the anteriorly protruding anterior flange of the pronotal plate (54:1, Figs. 10A, 10C, and 10D; also in *Lonchidia* in the Figitinae), the completely absent notauli (70:1, Figs. 7D–7F; also in some *Zaeucoila* group members), the posteriorly situated glandular release pit of the scutellar plate (79:1, Fig. 7F; secondarily more anterior in *Epicoela*), the lack of the anterior metepimeral impression (98:1, Figs. 10C and 10D; also in emarginines), and the dense hair patch located posterobasally on the metacoxa (119:1, Fig. 10C; the only unique synapomorphy in the present analysis). We suggest that this clade be referred to as the "core eucoilines."

The Neotropical Grade Eucoilines

Many of the relationships among the core eucoilines were poorly resolved by our data. However, most of the familiar Northern Hemisphere eucoilines consistently grouped together in a large, apical clade. We suggest the name "higher eucoilines" for this tentative clade (Fig. 13). The higher eucoilines include all taxa assigned to genus groups by Nordlander (1982b) except those placed in the *Gronotoma* group (*sensu lato*). It also includes two previously unplaced genera, *Nordlandiella* and *Paraganaspis* (Fig. 13). The higher eucoilines consistently appeared as monophyletic in the best trees (Figs. 2, 3, and 6) and monophyly was supported by a bootstrap proportion of 57% in the implied-weights analysis of the culled data set (Fig. 6). In the phylogram (Fig. 5), the branch supporting this clade was longer than most deep branches, indicating that the higher eucoilines are distinct from other eucoilines. The unambiguous synapomorphies supporting the higher eucoilines (node 77, Appendix 2) include the small ocelli (4:0), the low position of the antennal sockets (11:2), the long gena (21:1), the impression surrounding the postocciput (22:0; Figs. 8A and 9A–9C), the costulae along the lateral margin of the occiput (24:2; Fig. 9A), the absence of a dorsal emargination in the pronotal plate (60:0, Figs. 14A–14D and 14F), and the superficially impressed axillula (87:1). However, there are moderate to large amounts of homoplasy in all of these characters. The best character is perhaps the length of the gena (character retention index 0.75). All the higher eucoilines studied by us have a long gena except *Odonteucoila*. Outside of the higher eucoilines, a long gena has evolved secondarily only three times among the taxa studied: in the *Gronotoma* group (see above), in the *Caleucoela* + *Perischus* + *Zamischus* clade, and in *Lonchidia* (Figitinae).

Between the *Zaeucoila* group and the higher eucoilines there is a partly unresolved grade of previously unplaced, exclusively Neotropical taxa, forming a morphological transition between the *Gronotoma* and *Zaeucoila* groups on one hand and the higher eucoilines on the other. In this "Neotropical grade" (Fig. 13), only two groupings are convincingly supported in our analyses: *Zamischus* + *Perischus* and *Epicoela* + '*Eucoila*' (the *nudipennis* group or false *Eucoila*). Because each of these groupings comprises few named species, and their relationships with other Neotropical grade taxa remain uncertain, we do not consider it useful at this stage to introduce new genus group names for them.

In general, the Neotropical grade taxa are rich in morphological autapomorphies but have few characters providing reliable indications of their affinities to other eucoilines. A good example of this is the *Zamischus* + *Perischus* lineage, which is characterized by a series of striking autapomorphies (node 53, Appendix 2), such as the widened and laterally compressed female antennae (32:2; also in *Steleucoela*) and the posteriorly extended propodeum (109:1; unique to *Zamischus* and *Perischus*). Our analyses did not manage to resolve their relationships with other eucoilines, although the weighted analysis of the complete data set indicated a possible link with *Caleucoela* (Figs. 3 and 4). Possibly, the poor resolution of the Neotropical grade may be due to our species sample of this assemblage being too restricted. However, it is also possible that many of the Neotropical grade taxa, such as *Perischus* + *Zamischus*, represent relictual, morphologically isolated South American lineages and that many of the intermediate taxa are now extinct, making it difficult to resolve relationships correctly.

Our analyses clearly show that the so-called "false *Eucoila*" (the *nudipennis* group) belong to the Neotropical grade eucoilines, whereas the true *Eucoila* are

deeply nested within the higher eucoilines, confirming that these taxa are unrelated as originally suggested by Nordlander (1981). Eventually, a new genus name will have to be created for the *nudipennis* group but this is deferred until a thorough revision of the species belonging to this group and related lineages indicates how this genus should best be circumscribed.

Relationships among Higher Eucoilines

Among the five genus groups of higher eucoilines recognized by Nordlander (1982b), only the *Trybliographa* and *Kleidotoma* groups appear to be monophyletic as originally circumscribed. Both these groups were strongly supported in all analyses (Figs. 2, 3, and 6). Our data provide strong evidence against the monophyly of the *Rhoptromeris* group but are only weakly incompatible with the monophyly of the *Chrestosema* and *Ganaspis* groups (Table 4).

The *Rhoptromeris* group originally included the genera *Rhoptromeris*, *Trichoplasta*, *Leptopilina*, and *Cothonaspis* (Nordlander, 1982b) and it was suggested that the *Rhoptromeris* group was the sister clade of the *Trybliographa* group (Nordlander, 1982a). Our data provide strong evidence against the monophyly of the *Rhoptromeris* group as originally circumscribed (9 extra steps (2% increase) or a fit decrease of 8.4 (0.9%); Table 4) and this is due mainly to the genus *Cothonaspis*, which does not fit well in the group. Thus, the similarities between *Cothonaspis* and other genera in the *Rhoptromeris* group, particularly the genus *Rhoptromeris* itself, appear to be homoplastic. Our data place *Cothonaspis* in a strongly supported clade together with *Triplasta* and the *Kleidotoma* group (Figs. 2, 3, and 6). Because this clade is so distinctive and because the *Kleidotoma* group, as originally circumscribed, is so small that it is of limited use in indicating higher eucoiline relationships, we propose that the *Kleidotoma* group be expanded to include both *Cothonaspis* and *Triplasta* (Fig. 13). Inclusion of *Triplasta* in the *Kleidotoma* group has already been suggested by Lin (1988). The expanded *Kleidotoma* group (node 72, Appendix 2) is characterized by two unique synapomorphies: a curved carina issuing from the lateral margin of the postocciput (26:1, Fig. 9A) and a mesopleural carina ending anteriorly closer to the venter than in other eucoilines (93:1, Fig. 10D). Some additional unambiguous synapomorphies include the oblique posterior tentorial pits (27:1, Fig. 9A), a transversely strigate anterior flange of the pronotal plate (55:1, Fig. 7F), a completely nude metacoxa (119:2, Fig. 10D), and reduced pubescence on the forewing (127:1, Fig. 11D).

In agreement with Nordlander (1982a), the remaining *Rhoptromeris* group genera did form a monophyletic clade with the *Trybliographa* group, both in our unweighted analysis (Fig. 2) and in one of the best-fit trees resulting from the weighted analysis (Fig. 4). However, the bootstrap support values were below 50% and the clade did not appear in the best trees from the analyses restricted to completely coded taxa (Fig. 6). Actually, the only character that lends some credibility to this clade (node 63, Appendix 2) in our analysis is the modification of the second male flagellomere (36:1–2, Figs. 15D and 15E), a character that is present only in *Cothonaspis* among the other eucoilines we studied. As noted above, many other characters suggest that *Cothonaspis* is not related to the *Trybliographa* and *Rhoptromeris* groups, so the flagellar modification of *Cothonaspis* is likely to be independently derived. The only other unambiguous synapomorphy for the group concerns the shape of the dorsal surface of the scutellar plate (character 81), a character that is highly plastic in higher eucoilines.

Whereas Nordlander (1982a, b) included *Leptopilina* in the *Rhoptromeris* group, our data suggest that *Leptopilina* may be more closely related to the *Trybliographa* group than to *Rhoptromeris* + *Trichoplasta* (Figs. 2, 4, and 8). The *Leptopilina* + *Trybliographa* + *Eucoila* clade (node 61, Appendix 2) is supported primarily by having a smooth, triangular projection from the posterolateral part of the metacoxal rim (107:1; independently also in *Pycnostigmus*, otherwise unique). The only other unambiguous synapomorphy of the clade is in a highly homoplastic character (116, structure of petiolar foramen). Rather than leaving *Leptopilina* unplaced, we suggest that *Leptopilina* be transferred from the *Rhoptromeris* to the *Trybliographa* group (Fig. 13), even though the expanded *Trybliographa* group is less distinct than the original group (*Trybliographa* + *Eucoila*) (Figs. 2, 3, and 6). Restricted to the genera *Rhoptromeris* and *Trichoplasta*, there is no doubt that the *Rhoptromeris* group is monophyletic (Figs. 2, 3, and 6). Pertinent unambiguous synapomorphies for this clade (see node 62, Appendix 2 for a complete list) include a strongly modified second flagellomere in the male antenna (36:2, Fig. 15E), as well as laterally closed (56:1, Fig.

14F) and shallow (57:1, Fig. 14F) submedian pronotal depressions, the latter two characters being unique for the clade among the taxa studied.

Our data neither supported nor strongly refuted the monophyly of the *Chrestosema* group (*Glauraspidia*, *Mirandicola*, *Dieucoila*, *Odonteucoila*, and *Chrestosema*). The unweighted analysis grouped *Glauraspidia* and *Mirandicola* with some bootstrap support but split the rest of the *Chrestosema* group. The implied-weights analysis grouped all genera in the *Chrestosema* group except *Glauraspidia* (Figs. 3 and 4). However, the evidence against the monophyly of the *Chrestosema* group was weak or very weak (Table 4), and the weighted analysis restricted to the completely coded taxa did have the entire *Chrestosema* group monophyletic (Fig. 6).

The uncertainty concerning the monophyly of the *Chrestosema* group arises because there are no synapomorphies of the entire group present in all genera. There are many characters which are unique to the *Chrestosema* group among eucoilines and which are present in many but not all of the genera in the group (Table 5). Since the apomorphic states of these characters have a mosaic distribution within the *Chrestosema* group, they tend to support the monophyly of the entire group when considered together. It is quite possible that more extensive taxon sampling within the *Chrestosema* group will show that several of the exceptions to putative *Chrestosema* group synapomorphies are due to secondary loss. In our analysis, we suspect that the chosen representative of *Glauraspidia* may have been particularly problematic since it was a brachypterous species, which may have secondarily lost important characters present in fully winged members of the genus. This may be the reason that the implied-weights analysis of the complete data set did not include *Glauraspidia* in the *Chrestosema* group (Fig. 3). Nevertheless, *Glauraspidia* shares five characters with other *Chrestosema* group genera (Table 5). One particularly distinct similarity is the presence of unique setal patterns (most clearly seen in *Glauraspidia*, *Mirandicola*, and *Dieucoila*; character 97:1, Fig. 10C). Taking all the available evidence into account, we consider it likely that the *Chrestosema* group, including *Glauraspidia*, is monophyletic and we retain it as originally circumscribed.

Our data do not support Nordlander's (1982b) *Ganaspis* group (Figs. 2, 3, and 6) nor do they provide strong evidence against it (Table 4) or resolve the constituent taxa consistently into other monophyletic clades. Because of the uncertainty concerning *Ganaspis* group relationships, we prefer to leave the group as originally circumscribed, that is, restricted to *Hexacola*, *Didyctium*, *Ganaspis* (Fig. 13), and *Tetramerocera*, *Paramiomoea*, *Pentamerocera*, *Hypodiranchis*, and *Coneucoela* (Nordlander, 1982b). This means that two of the higher eucoiline genera in our study (*Paraganaspis* and *Nordlandiella*) remain unplaced because their relationships are uncertain (Fig. 13). Clearly, further work is needed to clarify the relationships among these genera, which may form a paraphyletic assemblage of basal lineages of higher eucoilines.

Evolutionary Implications

The phylogenetic results presented here have important implications concerning the geographic origin

TABLE 5

Character States Unique (or Almost Unique) to the *Chrestosema* Group *sensu* Nordlander (1982b) among Eucoilines and Present in at Least Two of the Genera of this Group (the Unique States Are State 3 for Character 92 and State 1 for All Other Characters)

Character	Genus				
	Chrestosema	*Odonteucoila*	*Dieucoila*	*Mirandicola*	*Glauraspidia*
1. Body sculpture	1	1	1	1	0
40. Mandible sculpture	0	1	1	1	0
68. Mesoscutum curvature	1	1	0	1	0
92. Mesopleural carina	2	2	2	3	3
97. Mesosomal pubescence	0	0	1	1	1
110. Calyptra shape	0	0	0	1	1
120. Metacoxal hair patch	1	0	0	1	1

Note. The characters are defined in Appendix 1, and the character state distribution in other taxa is shown in Table 3 (Appendix 1).

of eucoiline diversity. The *Gronotoma* group (*sensu stricto*) has its center of diversity, and presumably also its center of origin, in the Afrotropics. The genera *Ealata* and *Nordlanderia* (Quinlan, 1986, 1988), nearly half of all described *Gronotoma* species, and at least two *Diglyphosema* species are endemic to this region. The *Zaeucoila* group, on the other hand, is almost exclusively restricted to the Neotropics (M.L.B., unpublished data), like the Neotropical-grade eucoilines (Fig. 13). This phylogenetic and distribution information suggests that there was an early split in the evolution of the Eucoilinae between an Afrotropical (*Gronotoma* group) and a Neotropical (*Zaeucoila* and core eucoilines) lineage. This split could possibly correspond to the separation of the tropical parts of Africa and South America about 100 million years ago. The ancestral stock presumably did not reach the southernmost parts of Gondwana, explaining the absence of basal eucoiline lineages in Australia and New Zealand today (only one *Gronotoma* species, *G. micromorpha* Perkins, is known from Australia and this species is likely to have been introduced recently; M. L. B., unpublished data). The split between African and American lineages was followed by extensive diversification in the Neotropics, eventually producing the higher eucoilines familiar to most workers in the Northern Hemisphere and occurring around the globe. Independently, some members of the *Gronotoma* lineage managed to disperse to the Northern Hemisphere and to other regions, but they never became successful in the Neotropics and are poorly represented there today.

Our results also have important implications concerning the hosts of the earliest eucoilines. Both the *Gronotoma* group (*Disorygma* and *Gronotoma*) and most members of the *Zaeucoila* group (*Zaeucoila, Rhabdeucoela,* and *Tropideucoila*) attack leaf-mining agromyzids (Lewis and Whitefoord, unpublished data). In the *Zaeucoila* group we also find *Dettmeria,* members of which attack otitid flies in fruit, and *Lopheucoila,* members of which attack lonchaeid and tephritid flies in fruit. Given that *Dettmeria* and *Lopheucoila* appear to be sister lineages (Figs. 2 and 3), it seems likely that their host ranges resulted from a shift away from leaf-mining agromyzid hosts to hosts living within fruits. It is not known at the present time whether *Dettmeria* and *Lopheucoila* preferentially attack flies in fruit while the fruit is still on the tree or after the fruit has fallen onto the ground. In conclusion, although the hosts of the Neotropical-grade eucoilines are still unknown, it appears likely, based on the hosts of the *Gronotoma* and *Zaeucoila* groups and their basal phylogenetic position, that the first eucoilines were parasites of leaf-mining agromyzid larvae.

CONCLUSIONS

Phylogenetic studies into the relationships between eucoilines and other figitids, as well as the relationships between higher eucoiline genera, are important for progress in eucoiline systematics, which has been chaotic for such a long time. This work is the first step toward a phylogenetically based higher classification of the Eucoilinae (Fig. 13). Although further work is needed before a formal classification can be introduced, our genus groups provide a good starting point for lower-level work on eucoiline systematics and for the placement of new taxa. Future phylogenetic work will require more comprehensive samples of the genus groups and grades whose exact relationships remain uncertain. The *Ganaspis* group is one of the assemblages for which additional phylogenetic work would be particularly valuable, since species in *Ganaspis* and related genera could be of great importance to biological control practitioners and parasitoid ecologists alike.

One of the most interesting results of this study is the discovery of the Afrotropical and Neotropical origins of the Eucoilinae. One implication of this is that, if we want to reach a solid evolutionary and phylogenetic knowledge of the eucoilines, studies of these tropical faunas are essential. As was noted almost 20 years ago ". . . these diversified Neotropical taxa present a great challenge for future systematic and evolutionary research. Unfortunately, man's wholesale destruction of entire tropical forest biotas continues unabated and threatens to eliminate taxa indispensable for our understanding of phylogenetic relationships. We therefore need to intensify our collecting efforts, particularly in threatened native forest biotypes of unique character. In order to enhance collecting efficiency and to achieve maximum scientific value from the collected material, further increased international co-operation amongst biologists is necessary. Naturally, we should not only collect specimens of endangered faunas, but we should also use our influence, in all possible ways,

in order to prevent the destructive exploitation of these areas" (Nordlander, 1982b).

APPENDIX 1: CHARACTERS USED FOR PHYLOGENETIC ANALYSIS

Unless otherwise indicated, terminology follows Ronquist (1995a) and Ronquist and Nordlander (1989). Transformation series hypotheses are given for multistate characters. Following each character is the character's consistency index and retention index on the preferred tree (Fig. 4). Observed character states are given in Table 3.

General Body Sculpture

1. Microsculpture on vertex, lateral surface of pronotum and mesoscutum: (0) absent, surface not dull (Figs. 9A–9D and 10A–10C); (1) present, linear, making the surface dull (not illustrated); (CI =1.00, RI = 1.00, goodness of fit (G-fit) = 10).

Head

2. Shape of head in anterior view: (0) rounded, approximately as high as broad (Figs. 8A, 8B, and 9C); (1) elongate, higher than broad (Figs. 8C, 8D, 9A, and 9B); (CI =0.25, RI = 0.82, G-fit = 5).

3. Relative position of eye: (0) close to ocelli, ratio of distance between compound eye and posterior mandibular articulation to distance between posterior ocellus and compound eye $\geq$ 1.18 (Figs. 8B and 8C); (1) removed from ocelli, ratio $\leq$ 1.13 (not illustrated); (CI = 0.20, RI = 0.50, G-fit = 4.3).

4. Size of ocelli: (0) small, ratio of maximum diameter of a lateral ocellus to shortest distance between lateral ocelli 0.22–0.40 (not illustrated); (1) large, ratio 0.44–0.65 (Figs. 8B and 8D); (CI = 0.11, RI = 0.62, G-fit = 2.7).

5. Relative position of anterior ocellus: (0) placed close to posterior ocelli, posterior margin of anterior ocellus behind or subcontiguous with a transverse line running through anterior margins of posterior ocelli (Figs. 8B and 8D); (1) placed farther from posterior ocelli, clearly anterior to the anterior margins of posterior ocelli (not illustrated); (CI = 0.11, RI = 0.20, G-fit = 2.7).

6. Pubescence on compound eyes: (0) short or absent (Figs. 8B and 8D); (1) long (not illustrated); (CI = 0.20, RI = 0.33, G-fit = 4.3).

7. Shape of compound eyes in dorsal view: (0) rounded, distinctly protruding from the surface of the head, particularly anteriorly (Figs. 8B and 8D); (1) less rounded, not distinctly protruding from the surface of the head (not illustrated); (CI = 0.25, RI = 0.73, G-fit = 5).

8. Lateral frontal carina: (0) absent (Fig. 8D); (1) present (Fig. 8B, more easily seen in dorsal view); (CI = 0.50, RI = 0.50, G-fit = 7.5).

9. Hair punctures on lateral part of vertex: (0) indistinct or absent (Figs. 8B and 8D); (1) present, distinctly enlarged (not illustrated); (CI = 0.33, RI = 0.60, G-fit = 6).

10. Sculpture on posterior part of vertex (seen in dorsal view, not illustrated): (0) smooth or punctate, without linear component; (1) with parallel or slightly radiating, transverse strigae; (CI = 0.50, RI = 0.75, G-fit = 7.5).

11. Relative position of antennal sockets: (0) close to ocelli; ratio of vertical distance between inner margin of antennal foramen and ventral margin of clypeus to vertical distance between anterior ocellus and antennal rim $<$ 2.0 (not illustrated); (1) intermediate, ratio 2.25–4.1 (Figs. 8B and 8D); (2) far from ocelli, ratio $>$ 4.4 (not illustrated). Ordered 012; (CI = 0.08, RI = 0.33, G-fit = 1.2).

12. Vertical carina adjacent to ventral margin of antennal socket: (0) absent (Fig. 8B); (1) present (Fig. 8D); (CI = 0.50, RI = 0.86, G-fit = 7.5).

13. Vertical delineations on lower face: (0) absent (Figs. 8B and 8D); (1) single carina or ledge (not illustrated); (2) several parallel or subparallel carinae (not illustrated). Unordered; (CI = 0.29, RI = 0.54, G-fit = 3.8).

14. (Subdivision of 13:1) Shape of single vertical delineation of lower face (not illustrated): (0) rounded divergent ledges running from antennal sockets to dorsal end of malar sulcus; (1) sharp divergent carinae running from antennal sockets to dorsal end of malar sulcus; (2) sharp convergent carinae running from antennal sockets to clypeus. Ordered 012; (CI = 0.50, RI = 0.50, G-fit = 6).

15. Size of anterior tentorial pits: (0) large (Fig. 9B); (1) small (Fig. 8D); (CI = 0.50, RI = 0.67, G-fit = 7.5).

16. Shape of ventral clypeal margin medially: (0) emarginate or straight (Figs. 8B and 8D); (1) triangularly projecting (not illustrated); (CI = 0.33, RI = 0.50, G-fit = 6).

17. Shape of ventral clypeal margin laterally, close to anterior mandibular articulation: (0) straight (Fig. 9B); (1) distinctly angled (Fig. 8D); (CI = 0.14, RI = 0.14, G-fit = 3.3).

18. Malar sulcus: (0) absent (Fig. 9B); (1) present (Fig. 8D); (CI = 1.00, RI = 1.00, G-fit = 10).

19. Small submarginal pyramidal prominence of malar space, adjacent to anterior articulation of mandible: (0) absent (Figs. 8B and 8D); (1) present (not illustrated); (CI = 0.50, RI = 0.50, G-fit = 7.5).

20. Sculpture of malar space posterior to anterior mandibular articulation: (0) without linear sculpture (Figs. 8B and 8D); (1) with a series of parallel strigae (not illustrated); (CI = 0.50, RI = 0.50, G-fit = 7.5).

21. Length of gena (from compound eye to posterolateral margin of head) (in dorsal view, not illustrated): (0) short, ratio of length of gena to length of compound eye in dorsal view smaller than 0.33; (1) long, ratio larger than 0.38; (CI = 0.20, RI = 0.75, G-fit = 4.3).

22. Shape of posterior surface of head: (0) deeply impressed around postocciput (Figs. 8A, and 9A–9C); (1) almost flat, not deeply impressed (Fig. 8C); (CI = 0.25, RI = 0.67, G-fit = 5).

23. Lateral margin of occiput: (0) not well defined (Figs. 8C, and 9A–9C); (1) defined by a raised, blunt carina (not illustrated); (2) defined by a raised, sharp carina (Fig. 8A). Ordered 012; (CI = 0.40, RI = 0.70, G-fit = 5).

24. Sculpture along lateral margin of occiput (except for raised carina, if present): (0) linear sculpture absent (Figs. 8A, 8C, 9B, and 9C); (1) one costula; (2) many costulae (Fig. 9A). Ordered 012; (CI = 0.17, RI = 0.50, G-fit = 2.3).

25. Sculpture on occiput (except extreme lateral margin): (0) without linear sculpture, at most with a few weak strigae along the peripheral margin (Figs. 8A and 9A–9C); (1) with some weak subvertical, irregular strigae (not illustrated); (2) with distinct subvertical, slightly and evenly curved costulae (Fig. 8C). Ordered 012; (CI = 1.00, RI = 1.00, G-fit = 10).

26. Carina issuing from lateral margin of postocciput, proximally horizontal but distally bending ventrally: (0) absent, at most vaguely indicated basally (Figs. 8A, 8C, 9B, and 9C); (1) present, distinct (Fig. 9A); (CI = 1.00, RI = 1.00, G-fit = 10).

27. Direction of longitudinal axis of posterior tentorial pits: (0) vertical (Figs. 8A, 8C, 9B, and 9C); (1) oblique (Fig. 9A); (CI = 0.50, RI = 0.80, G-fit = 7.5).

28. Length of gula: (0) short (Figs. 8A, 8C, 9B, and 9C); (1) long (Fig. 9A); (CI = 0.17, RI = 0.37, G-fit = 3.8).

29. Median hairy strip of gula: (0) present (Fig. 8A); (1) absent (Figs. 8C, and 9A–9C); (CI = 0.50, RI = 0.67, G-fit = 7.5).

30. Shape of hypostomal carina medially: (0) straight (Figs. 8A, 8C, 9A, and 9C); (1) distinctly angled laterally about 1/3 from proximal end (Fig. 9B); (CI = 1.00, RI = 1.00, G-fit = 10).

31. Shape of hypostomal carina ventrally: (0) ends at ventral head margin close to posterior mandibular articulation, not projecting beyond head margin (Figs. 9A and 9B); (1) ending in a distinct process some distance posterior to the mandibular articulation (Fig. 9C); (CI = 1.00, RI = 1.00, G-fit = 10).

Antennae

32. Shape of female antenna: (0) cylindrical, not widened toward apex (Fig. 15A); (1) cylindrical, distinctly widened towards apex (Fig. 15B); (2) distinctly widened and laterally compressed toward apex (not illustrated). Ordered 012; (CI = 0.67, RI = 0.67, G-fit = 7.5).

33. Articulation between flagellomeres in female antenna: (0) connate with the segments broadly joined (Fig. 15A); (1) at least distally moniliform with the segments distinctly separated by a narrow neck-like articulation (Fig. 15B); (CI = 1.00, RI = 1.00, G-fit = 10).

34. Shape of the three last antennal flagellomeres of female antenna: (0) of normal width or widened but not conspicuously enlarged (Fig. 15A); (1) conspicuously enlarged compared to adjacent flagellomeres (Fig. 15B); (CI = 0.50, RI = 0.50, G-fit = 7.5).

35. Number of articles of male antenna (not illustrated): (0) 14; (1) 15; (2) more than 15. Ordered 012; (CI = 0.67, RI = 0.75, G-fit = 7.5).

36. Shape of second flagellomere of male antenna: (0) not modified, cylindrical (Fig. 15C); (1) slightly asymmetric basally (Fig. 15D); (2) strongly asymmetric,

excavated laterally (Fig. 15E). Ordered 012; (CI = 0.50, RI = 0.71, G-fit = 6).

37. Length of second flagellomere of male antenna: (0) shorter than first flagellomere (Fig. 15C); (1) longer than first flagellomere (Figs. 15D and 15E); (CI = 0.17, RI = 0.58, G-fit = 3.8).

Mandibles

38. Shape of right mandible (not illustrated): (0) subquadratic, first and second teeth not conspicuously long; (1) elongate to triangular, first and second teeth conspicuously long; (CI = 0.50, RI = 0.86, G-fit = 7.5).

39. Basal height of right mandible (not illustrated): (0) short; (1) long; (CI =1.00, RI = 1.00, G-fit = 10).

40. Sculpture on basal third of right mandible (not illustrated): (0) smooth or punctate; (1) weakly irregularly striate; (CI = 0.50, RI = 0.50, G-fit = 7.5).

41. Third tooth of right mandible (not illustrated): (0) present; (1) absent; (CI = 1.00, RI = 1.00, G-fit = 10).

42. Submarginal ridge interiorly along dorsal margin of left mandible (not illustrated): (0) absent; (1) present; (CI = 0.33, RI = 0.00, G-fit = 6).

43. Number of setae on interior side of left mandible, close to dorsal margin (not illustrated): (0) five or more; (1) two or three, occasionally up to four; (CI = 0.25, RI = 0.25, G-fit = 5).

44. Shape of posterior mandibular process of left mandible in posterior view (not illustrated): (0) evenly rounded, not conspicuously projecting; (1) forming a small, distinctly set off, rounded projection; (2) forming a large semitriangular projection. Unordered; (CI = 0.50, RI = 0.33, G-fit = 6).

Labio-Maxillary Complex

45. Number of segments of maxillary palp (not illustrated): (0) five; (1) four (basal two segments fused); (CI = 1.00, RI = 1.00, G-fit = 10).

46. Relative position of the two last segments of maxillary palp in normal repose: (0) curved inward (Figs. 8A and 9C); (1) straight (Figs. 8C, 9A, and 9B); (CI = 0.50, RI = 0.90, G-fit = 7.5).

47. Angle of the distal margin of the subapical segment of the maxillary palp and movement of apical segment: (0) margin slants inward, apical segment bends inward (Figs. 8C and 9A); (1) margin is straight or slants distinctly outward, apical segment bends outward (Figs. 8A, 9B, and 9C); (CI = 0.25, RI = 0.80, G-fit = 5).

48. Relative length of the apical segment of maxillary palp: (0) more than 1.5 times as long as the preceding segment (Figs. 8A and 9C); (1) 1–1.5 times as long (Fig. 8C and 9A); (2) shorter than the preceding segment (Fig. 9B). Ordered 012; (CI = 0.22, RI = 0.53, G-fit = 3).

49. Pubescence on apical segment of maxillary palp: (0) consisting of a small number of erect setae and more appressed setae (Fig. 9D); (1) consisting only of erect setae (Fig. 9F); (CI = 1.00, RI = 1.00, G-fit = 10).

50. Apical seta on apical segment of maxillary palp: (0) relatively short, much shorter than twice the length of the second longest apical seta (Fig. 9D); (1) long, only slightly shorter than twice the length of the second longest apical seta (Fig. 9E); (2) conspicuously long, longer or much longer than twice the length of the second longest apical seta (Fig. 9F). Ordered 012; (CI = 0.67, RI = 0.86, G-fit = 7.5).

51. Erect setae medially on apical segment of maxillary palp: (0) present (Fig. 9D); (1) absent (Fig. 9F); (CI = 0.50, RI = 0.87, G-fit = 7.5).

52. Number of segments of labial palp: (0) three (Fig. 8A); (1) two (Figs. 8C and 9A–9C); (2) one (not illustrated). Ordered 012; (CI = 0.67, RI = 0.67, G-fit = 7.5).

53. Shape of first segment of labial palp: (0) short, shorter than or equal to apical segment (Fig. 8A, 8C, 9A, and 9C); (1) long, longer than apical segment (Fig. 9B); (CI = 0.50, RI = 0.50, G-fit = 7.5).

Pronotum

54. Shape of anterior flange of pronotal plate: (0) subvertical, not protruding (Fig. 10B); (1) distinctly protruding anteriorly (Figs. 10A, 10C, and 10D); (CI = 0.33, RI = 0.82, G-fit = 6).

55. Sculpture of anterior flange of pronotal plate: (0) smooth or punctate (Figs. 7A–7E); (1) transversely strigate (Fig. 7F); (CI = 0.20, RI = 0.56, G-fit = 4.3).

56. Shape of submedian pronotal depressions laterally: (0) open (Figs. 14A and 14C–14E); (1) closed (Fig. 14F); (CI = 1.00, RI = 1.00, G-fit = 10).

57. Depth of submedian pronotal depressions medially: (0) deep (Figs. 14A, 14D, and 14E); (1) shallow (Fig. 14F); (CI = 1.00, RI = 1.00, G-fit = 10).

58. Width of pronotal plate: (0) narrow (Figs. 14A–

14D and 14F); (1) wide, almost as wide as mesonotum (Fig. 14E); (CI = 0.50, RI = 0.83, G-fit = 7.5).

59. Lateral margin of pronotal plate: (0) defined only anteriorly (Fig. 14A); (1) defined all the way to the dorsal margin of the pronotum (Figs. 14B–14F); (CI = 0.50, RI = 0.80, G-fit = 7.5).

60. Shape of dorsal margin of pronotal plate in anterior view: (0) rounded, straight, or occasionally slightly emarginate (Figs. 14A–14D and 14F); (1) distinctly emarginate (Fig. 14E); (CI = 0.20, RI = 0.67, G-fit = 4.3).

61. Lateral part of dorsal margin of pronotal plate: (0) not raised into a crest (Figs. 10A and 10B); (1) raised into a distinct crest but not projecting above the dorsoposterior margin of pronotum (Fig. 10D); (2) raised into a distinct process projecting above the dorsoposterior margin of the pronotum (not illustrated). Ordered 012; (CI = 0.50, RI = 0.87, G-fit = 6).

62. Ridges extending posteriorly from lateral margin of pronotal plate: (0) absent or merely indicated (Figs. 14A–14C); (1) distinct but short, not extending to the dorsal margin of pronotum (Fig. 14D and 14F); (2) long, extending to the dorsal margin of pronotum (Fig. 14E). Ordered 012; (CI = 0.15, RI = 0.56, G-fit = 2.1).

63. Macrosculpture on lateral surface of pronotum: (0) present (Fig. 10A; see also Figs. 14A and 14B); (1) absent (Figs. 10B–10D); (CI = 0.33, RI = 0.67, G-fit = 6).

64. Pubescence on lateral surface of pronotum: (0) short and dense (not illustrated); (1) consisting of a few long hairs or absent (Figs. 10A–10D); (CI = 1.00, RI = 1.00, G-fit = 10).

65. Lateral pronotal carina: (0) present (Figs. 10A and 10B); (1) absent (Figs. 10C and 10D); (CI = 0.33, RI = 0.60, G-fit = 6).

66. Anteroventral inflection of pronotum: (0) narrow (Figs. 14A–14C); (1) broad, particularly adjacent to anterior part of pronotal plate (Fig. 14E); (CI = 0.25, RI = 0.50, G-fit = 5).

67. Ventral margin of pronotum: (0) not distinctly raised midlaterally (occasionally raised adjacent to pronotal plate) (Figs. 10A–10D); (1) distinctly raised midlaterally (not illustrated); (CI = 1.00, RI = 0.00, G-fit = 10).

Mesoscutum

68. Curvature of mesoscutal surface (not illustrated): (0) scutum convex and evenly curved (except for notauli, if present); (1) lateral thirds of scutum flat, depressed mesally, median third raised; (CI = 1.00, RI = 1.00, G-fit = 10).

69. Median mesoscutal carina: (0) absent (Figs. 7A, 7C, 7D, and 7F); (1) present as a narrow, distinctly defined carina (Fig. 7B); (2) present as an anteriorly broad elevation narrowing posteriorly (Fig. 7E). Unordered; (CI = 1.00, RI = 1.00, G-fit = 10).

70. Notauli: (0) present as a deep furrow or series of deep subcontiguous pits (Figs. 7A–7D); (1) completely absent or merely indicated by a series of isolated, small punctures (Figs. 7C–7F); (CI = 0.50, RI = 0.91, G-fit = 7.5).

71. Parascutal carina: (0) distinctly sinuate, posteriorly ends in a posteroventrally directed slight projection (Figs. 10A–10D); (1) less sinuate, posteriorly curved mesally, not drawn out to a posteroventrally directed projection (not illustrated); (CI = 0.33, RI = 0.33, G-fit = 6).

Scutellar–Axillar Complex

72. Length of longitudinal carina or septum separating scutellar foveae and continuing posteriorly in scutellar plate, if present: (0) short (Figs. 7A, 7D, and 7E); (1) medium (Figs. 7B, 7C, and 7F); (2) long (not illustrated). Ordered 012; (CI = 0.15, IR = 0.39, G-fit = 2.1).

73. Scutellar fovea: (0) not margined posteriorly (Figs. 7B–7D); (1) distinctly margined posteriorly (Figs. 7A, 7E, and 7F); (CI = 0.33, RI = 0.50, G-fit = 6).

74. Shape of lateral bar: (0) relatively narrow, not conspicuously widened ventrally (Figs. 10A, 10C, and 10D); (1) conspicuously widened by a large ventral lobe (Fig. 10B); (CI = 0.50, RI = 0.80, G-fit = 7.5).

75. Strigate sculpture on lateral bar: (0) absent (Fig. 10A); (1) weak (Figs. 10B and 10C); (2) strong (Fig. 10D). Ordered 012; (CI = 0.20, RI = 0.62, G-fit = 2.7).

76. Structure of the dorsal part of the scutellum: (0) without any clearly differentiated median part (Figs. 7A and 7B); (1) with a differentiated median part (Figs. 7C–7F); (CI = 1.00, RI = 1.00, G-fit = 10).

77. (Subdivision of 76:1) Structure of the modified median part of the scutellum: (0) separated by different sculpture (Fig. 7C); (1) separated by marginal carinae

(Fig. 7D); (2) raised to form an elevated scutellar plate (Figs. 7E and 7F). Unordered; (CI = 1.00, RI = 1.00, G-fit = 10).

78. (Subdivision of 77:2) Size of scutellar plate: (0) very large and rounded, almost circular, covering most of scutellum (Fig. 7E); (1) medium-sized, exposing a large part of scutellum (Fig. 7F); (2) small and narrow, exposing most of scutellum (not illustrated). Ordered 012; (CI = 0.40, RI = 0.57, G-fit = 5).

79. (Subdivision of 77:2) Position of the glandular release pit of the scutellar plate: (0) distinctly removed from the posterior margin of the plate (Fig. 7E); (1) close to the posterior margin of the plate (Fig. 7F); (CI = 0.50, RI = 0.86, G-fit = 7.5).

80. (Subdivision of 77:2) Shape of rim of scutellar plate in lateral view: (0) flat (Fig. 10B); (1) only very slightly convex; (2) distinctly convex (Figs. 10C and 10D). Ordered 012; (CI = 0.12, RI = 0.39, G-fit = 1.8).

81. (Subdivision of 77:2) Shape of dorsal surface of scutellar plate: (0) almost entire surface concave, with a clear border along the concavity (Figs. 7E and 10B); (1) smaller part of the surface concave, clear border present only anteriorly or absent; (2) flat or slightly convex (Figs. 7F, 10C, and 10D). Ordered 012; (CI = 0.25, RI = 0.68, G-fit = 3.3).

82. (Subdivision of 77:2) Transverse median carina on scutellar plate: (0) absent (Figs. 7E and 7F); (1) present (not illustrated); (CI = 0.50, RI = 0.00, G-fit = 7.5).

83. Projection from the dorsal surface of scutellar plate or homologous region of the scutellum (not illustrated): (0) absent; (1) present as a blunt, tooth-like projection; (2) present as a distinct spine. Unordered; (CI = 0.67, RI = 0.00, G-fit = 7.5).

84. Longitudinally strigate sculpture on dorsal surface of scutellum: (0) absent (Figs. 7A–7F and 10A–10C); (1) present, at least on part of dorsal surface (Fig. 10D); (CI = 0.33, RI = 0.50, G-fit = 6).

85. Carina along scutellar margin, separating the dorsal and ventral scutellar surfaces: (0) absent (Figs. 7A and 10A); (1) present, at least anteriorly (Figs. 7E, 7F, and 10B–10D); (CI = 0.50, RI = 0.50, G-fit = 7.5).

86. Shape of dorsoposterior part of scutellum in dorsal view: (0) broadly and distinctly emarginate (not illustrated); (1) rounded or truncate, occasionally slightly incised medially (Figs. 7A, 7C, 7E, and 7F); (2) produced posteriorly (Fig. 7D); (3) with delimited projection (spine) posteriorly (Fig. 7B). Ordered 0123; (CI = 0.23, RI = 0.09, G-fit = 2.3).

87. Posterior margin of axillula: (0) marked by a distinct ledge, axillula distinctly impressed adjacent to ledge (Figs. 10A–10D); (1) axillula only superficially impressed posteriorly or continuous with scutellum (not illustrated); (CI = 0.08, RI = 0.45, G-fit = 2.1).

Mesopectus (Mesopleuron and Mesosubpleuron)

88. Subalar area: (0) abruptly broadened anteriorly, with an indicated longitudinal division (Figs. 10A and 10B); (1) only slightly broadened anteriorly, without longitudinal division indicated (Figs. 10C and 10D); (CI = 1.00, RI = 1.00, G-fit = 10).

89. Sculpture of mesopleuron: (0) smooth, occasionally partly punctate (Figs. 10A–10D); (1) horizontally strigulate (not illustrated); (CI = 0.33, RI = 0.50, G-fit = 6).

90. Mesopleural triangle: (0) distinctly impressed with a marked ventral border continuing into subalar pit (Fig. 10A); (1) absent or slightly impressed but without a distinct ventral border (Figs. 10B–10D); (CI = 0.50, RI = 0.80, G-fit = 7.5).

91. Subalar pit: (0) large and well defined, lying in the posterior end of the mesopleural triangle (Figs. 10A and 10B); (1) somewhat smaller but well defined, lying in a distinct, more or less narrow subalar groove (not illustrated); (2) reduced in size, usually elongate, subalar groove narrow or absent (not illustrated); (3) absent, subalar groove indistinct or absent (Figs. 10C and 10D). Ordered 0123; (CI = 0.27, RI = 0.84, G-fit = 2.7).

92. Mesopleural carina / carinae: (0) several long, irregular, curved carinae (not illustrated); (1) several long, parallel, straight carinae (Fig. 10A); (2) one complete, straight main carina, occasionally one or a few weak or short subordinate carinae (Figs. 10B and 10D); (3) one straight carina indicated anteriorly, otherwise smooth (Fig. 10C). Ordered 0123; (CI = 0.60, RI = 0.78 G-fit = 6).

93. (Subdivision of 92:2–3) Position of anterior end of single mesopleural carina: (0) high, above notch in anterior margin of mesopleuron (Figs. 10B and 10C); (1) low, at or below notch in anterior margin of mesopleuron (Fig. 10D); (CI = 1.00, RI = 1.00, G-fit = 10).

94. Lateroventral mesopleural carina (extending along entire mesopleuron) (not illustrated): (0) absent; (1) present but not marking an abrupt change of slope of the mesopectus; (2) present and marking abrupt

change of slope. Unordered; (CI = 0.67, RI = 0.67, G-fit = 7.5).

95. Posterior part of mesocoxal rim (not illustrated): (0) rounded or only slightly extended posterolaterally; (1) conspicuously extended laterally and posterolaterally, projecting beyond margin of mesopectus; (CI = 1.00, RI = 1.00, G-fit = 10).

Metapectal–Propodeal Complex

96. Pubescence on lateral surface of metapectal–propodeal complex (excluding possible presence of felt-like or woolly pubescence located posteriorly): (0) evenly covering surface (Fig. 10A); (1) present only in posterior half (Fig. 10B); (2) consisting of a few scattered hairs located posteriorly (Fig. 10D). Ordered 012; (CI = 0.25, RI = 0.65, G-fit = 3.3).

97. Pubescence on posterior part of metapectal–propodeal complex: (0) not extremely dense (Figs. 10A, 10B, and 10D); (1) extremely dense and felt-like on posterior part of metapleuron and lateral part of propodeum (Fig. 10C); (2) extremely dense and long on entire propodeum but not on metapleuron, only slightly curled and not felt-like in appearance (Fig. 7D). Unordered; (CI = 0.50, RI = 0.00, G-fit = 6).

98. Anterior impression of metepimeron: (0) triangular with the broadest part being ventral (Figs. 10A and 10B); (1) absent or present as a narrow, linear impression which is not broadened ventrally (Figs. 10C and 10D); (CI = 0.50, RI = 0.92, G-fit = 7.5).

99. Posterior margin of metepimeron: (0) distinctly marked (not illustrated); (1) not marked, metepimeron continuous posteriorly with propodeum (Figs. 10A–10D); (CI = 0.50, RI = 0.75, G-fit = 7.5).

100. Anterior impression of metepisternum (immediately beneath anterior end of metapleural carina): (0) absent or small and narrow (Figs. 10A–10D); (1) large and wide (not illustrated); (CI = 1.00, RI = 1.00, G-fit = 10).

101. Anterior margin of metapectal–propodeal complex: (0) meeting or almost meeting the mesopleuron at the same level at least at a point corresponding to the anterior end of the metapleural carina (Figs. 10A–10D); (1) separated from the mesopleuron by a deep and broad, uninterrupted marginal impression (not illustrated); (CI = 1.00, RI = 1.00, G-fit = 10).

102. Structure of metapectus anterodorsal to metacoxal base: (0) with an ill-defined cavity (Fig. 10A); (1) with a well-defined cavity (Figs. 10C and 10D); (2) without a cavity. Unordered; (CI = 0.67, RI = 0.75, G-fit = 7.5).

103. Depression located anterolaterally on metasubpleuron, anterior to metacoxal foramen (not illustrated): (0) narrow or absent; (1) broad; (CI = 1.00, RI = 1.00, G-fit = 10).

104. Shape of posteroventral corner of metapleuron in lateral view: (0) rounded, not drawn out posteriorly (Figs. 10A–10C); (1) extended posteriorly (Fig. 10D); (CI = 1.00, RI = 1.00, G-fit = 10).

105. Anterior part of metacoxal rim (not illustrated): (0) rounded, not extended anteriorly; (1) extended anteriorly into a distinct process; (CI = 1.00, RI = 1.00, G-fit = 10).

106. Shape of metacoxal foramen (not illustrated): (0) round; (1) elongate; (CI = 0.50, RI= 0.86, G-fit = 7.5).

107. Lateral part of metacoxal rim (not illustrated): (0) narrow and not projecting, or forming a posteriorly or posterolaterally facing, rounded projection which is usually pubescent; (1) forming a smooth and nude triangular projection having its surface directed more laterally; (CI = 0.50, RI = 0.67, G-fit = 7.5).

108. Posterior part of metacoxal rim (not illustrated): (0) rounded or extended into a small posterolateral process; (1) extended into a large posterior process; (CI = 1.00, RI = 1.00, G-fit = 10).

109. Shape of propodeum: (0) normal shape, not drawn out posteriorly (Figs. 10A–10D); (1) drawn out posteriorly (not illustrated); (CI = 1.00, RI = 1.00, G-fit = 10).

110. Shape of calyptra in lateral view: (0) rounded (Figs. 10A–10C); (1) elongate (Fig. 10D); (CI = 0.33, RI = 0.00, G-fit = 6).

111. Shape of calyptra in posterior view (not illustrated): (0) rounded; (1) dorsoventrally elongate; (CI = 0.17, RI = 0.50, G-fit = 3.8).

112. Horizontal carina running anteriorly from lateral propodeal carina: (0) absent (Figs. 10A, 10C, and 10D); (1) present (Fig. 10B); (CI = 0.50, RI = 0.50, G-fit = 7.5).

113. Shape of lateral propodeal carina (not illustrated): (0) straight; (1) distinctly angled; (CI = 0.12, RI = 0.61, G-fit = 3).

114. Dorsal extent of lateral propodeal carinae: (0) not reaching scutellum (Figs. 10A–10C); (1) projecting beyond metanotum to reach scutellum (Fig. 10D); (CI = 0.14, RI = 0.40, G-fit = 3.3).

115. Shape of ventral end of lateral propodeal carina and dorsal part of nucha (not illustrated): (0) lateral propodeal carinae ending before reaching nucha; (1) lateral propodeal carinae reaching nucha but separated from each other; (2) lateral propodeal carinae reaching nucha and joined with each other along the dorsal margin of the nucha. Ordered 012; (CI = 0.40, RI = 0.79, G-fit = 5).

116. Structure of petiolar foramen (not illustrated): (0) anteriorly situated, close to metacoxae, foramen directed ventrally; (1) removed from metacoxae, foramen directed ventrally; (2) removed from metacoxae, foramen directed posteriorly. Ordered 012; (CI = 0.18, RI = 0.59, G-fit = 2.5).

117. Dorsal part of petiolar rim (not illustrated): (0) narrow, about the same width as the rest of the petiolar rim; (1) wide, distinctly wider than the rest of the rim; (CI = 0.20, RI = 0.50, G-fit = 4.3).

118. Ventral and lateral parts of petiolar rim (not illustrated): (0) narrow; (1) broad; (CI = 0.50, RI = 0.75, G-fit = 6).

Legs

119. Pubescence posterolaterally on metacoxa: (0) sparse to moderately dense but never with confined dense hair patch originating basally (Fig. 10A); (1) with a confined, dense hair patch or hair band originating basally, other pubescence usually lacking (Fig. 10C); (2) metacoxa completely nude (Fig. 10D). Unordered; (CI = 0.67, RI = 0.94, G-fit = 7.5).

120. (Subdivision of 119:1) Shape of dense hair patch basally on the posterolateral surface of the metacoxa: (0) small, circular (not illustrated); (1) elongate; (CI = 0.33, RI = 0.33, G-fit = 6).

121. Microsculpture on hind coxa: (0) absent; (1) present (Fig. 10D); (CI = 1.00, RI = 1.00, G-fit = 10).

122. Shape of metatarsal claw (not illustrated): (0) base strongly expanded and apex strongly bent, ratio width of base to length of apex >0.6; (1) base weakly expanded and apex slightly bent, ratio <0.6; (CI = 0.12, RI = 0.30, G-fit = 3).

123. Microsculpture on outer surface of metatarsal claw (not illustrated): (0) microcarinate; (1) entirely or almost entirely smooth; (CI = 1.00, RI = 1.00, G-fit = 10).

124. Pubescence on outer surface of metatarsal claw (not illustrated): (0) denser, consisting of a considerable number of setae; (1) sparser, consisting of only a few setae; (CI = 0.50, RI = 0.00, G-fit = 7.5).

125. Position of the apical seta of the metatarsal claw (not illustrated): (0) situated on outer surface of claw below dorsal margin; (1) situated on dorsal margin of claw; (CI = 0.25, RI = 0.50, G-fit = 5).

Wings

126. Shape of the apical margin of female forewing: (0) rounded (Figs. 11A, 11C, and 11D); (1) emarginate (Fig. 11B); (CI = 0.33, RI = 0.33, G-fit = 6).

127. Pubescence of forewing: (0) long and dense on most of the surface (Fig. 11B); (1) shorter, scattered or absent on basal half of wing (Figs. 11A, 11C, and 11D); (CI = 0.11, RI = 0.50, G-fit = 2.7).

128. Hair fringe along apical margin of forewing: (0) very short or absent (Fig. 11D); (1) present, long or very long (Figs. 11B and 11C); (CI = 0.17, RI = 0.29, G-fit = 3.8).

129. Marginal cell of forewing: (0) membranous, similar to other wing cells (Figs. 11B–11D); (1) sclerotized to form a pseudopterostigma (Fig. 12A); (CI = 1.00, RI = 1.00, G-fit = 10).

130. Extent of R_1: (0) tubular along at least basal part of anterior margin of marginal cell (Figs. 11B and 11C); (1) ending at anterior margin (marginal cell open anteriorly) (Fig. 11D); (2) not reaching anterior margin (marginal cell open anteriorly and basally) but at least partly present beyond 2r (not illustrated); (3) completely absent beyond 2r (not illustrated). Ordered 0123; (CI = 0.38, RI = 0.37, G-fit = 3.8).

131. Basal abscissa of R_1 (the abscissa between 2r and the wing margin) of forewing: (0) as broad as adjacent wing veins (Figs. 11B and 11C); (1) clearly broader than adjacent wing veins (Fig. 11D); (CI = 1.00, RI = 1.00, G-fit = 10).

132. Areolet of forewing: (0) present (not illustrated); (1) absent (Figs. 11A–11D); (CI = 1.00, RI = 0.00, G-fit = 10).

Metasoma

133. Submedian dorsal depressions of the articular bulb of female petiole: (0) present, large and distinct, articular bulb raised to a median ridge or keel between

them (Fig. 12A); (1) absent or merely indicated, articular bulb not raised into a median keel (Fig. 12B); (CI = 1.00, RI = 1.00, G-fit = 10).

134. Position of patches of mechanosensory hairs on articular bulb of female petiole (seen only at high magnification; not illustrated): (0) situated more laterally, not delimited by a raised central area; (1) situated more ventromedially, delimited by a slightly raised smooth central area; (CI = 1.00, RI = 1.00, G-fit = 10).

135. Shape of the posterior part of female petiole: (0) abruptly widened (Fig. 12B); (1) not abruptly widened (Fig. 12A); (CI = 0.14, RI = 0.60, G-fit = 3.3).

136. Ventral flange of annulus of female petiole: (0) large and broad, its anterior margin projecting and partially covering the articular bulb of the petiole (Fig. 12B); (1) absent or small and narrow, only slightly projecting anteriorly (Fig. 12A); (CI = 0.20, RI = 0.56, G-fit = 4.3).

137. Fusion of terga in female metasoma: (0) all postpetiolar terga free (Fig. 12A); (1) terga 3 to 5 fused to a large syntergum (Fig. 12B); (CI = 1.00, RI = 1.00, G-fit = 10).

138. (Subdivision of 136:1) Shape of syntergum (or terga 3 to 5) of female metasoma: (0) not extending ventrally beneath sterna, not folded inward, ventral margin rounded (Fig. 12B); (1) extending ventrally and folded inward beneath sterna, forming a straight ventral margin (not illustrated); (CI = 0.50, RI = 0.86, G-fit = 7.5).

139. Size of third abdominal tergum of female metasoma: (0) about as large as fourth tergum (not illustrated); (1) distinctly smaller than fourth tergum (Fig. 12A); (CI = 1.00, RI = 0.00, G-fit = 10).

140. Pubescence on third abdominal tergum of female metasoma: (0) not extending ventrally (Fig. 12B); (1) extending ventrally to ventral margin of third tergum, beneath the petiole (Fig. 12A); (CI = 0.25, RI = 0.57, G-fit = 5).

141. Relation between fifth and sixth abdominal terga of female metasoma: (0) telescoping into each other (Figs. 12A and 12B); (1) anterior margin of sixth tergum abutting and articulating with posterior margin of syntergum (tergum 5) (not illustrated); (CI = 0.50, RI = 0.87, G-fit = 7.5).

142. Fusion of terga in male metasoma (not illustrated): (0) all terga free; (1) terga 3 and 4 fused; (2) terga 3–5 fused. Ordered 012; (CI = 1.00, RI = 1.00, G-fit = 10).

Ovipositor

143. Length of terebra: (0) short, basal part of ovipositor not bent posteriorly, basal articulation of terebra curved less than 180° (Fig. 12C); (1) long, basal part of ovipositor distinctly curved posteriorly, basal articulation of terebra curved 180° or more (Fig. 12D); (CI = 1.00, RI = 1.00, G-fit = 10).

Phallus

144. Shape of apical part of aedeagus: (0) only slightly expanded subapically (Fig. 12E); (1) distinctly and abruptly expanded subapically (Fig. 12F); (CI = 1.00, RI = 1.00, G-fit = 10).

145. Dorsal suture of apical part of aedeagus: (0) long, reaching at least 0.5 times the length of the expanded part of the aedeagus (Fig. 12E); (1) short, not reaching 0.5 times the length of the expanded aedeagus (Fig. 12F); (CI = 0.50, RI = 0.86, G-fit = 7.5).

146. Length of paramere: (0) short, the paramere never reaches the apex of the penis valve (Fig. 12E); (1) long, the paramere almost reaches the apex of the penis valve (Fig. 12F); (CI = 1.00, RI = 1.00, G-fit = 10).

147. Lateroapical setae of paramere (best seen in lateral or ventral view): (0) present; (1) absent; (CI = 0.50, RI = 0.67, G-fit = 7.5).

148. Erect ventroapical seta or pair of setae of paramere (not illustrated): (0) present; (1) absent; (CI = 0.50, RI = 0.67, G-fit = 7.5).

APPENDIX 2: LIST OF CHARACTER CHANGES

All character changes on the branches of the preferred tree (Fig. 4) are listed below. The branch numbers (in boldface type) correspond to the numbers in squares in Fig. 4. Each branch number is followed by a list of character numbers and state changes. Ambiguous character changes were mapped on the tree using ACCTRAN. These changes are given in parentheses, whereas the unambiguous changes are given without parentheses. Unique synapomorphies on the preferred tree are underlined.

1. 4:0 → 1, 5:1 → 0, 8:0 → 1, 11:2 → 1, 72:1 → 0, (73:0 → 1), 102:0 → 2, <u>132:1 → 0</u>, <u>139:1 → 0</u>.

2. 12:0 → 1, 22:0 → 1, 44:0 → 1, 66:0 → 1, 67:0 → 1, 69:0 → 1, 86:1 → 3, (87:0 → 1), 89:0 → 1, 116:0 → 2, 127:0 → 1, 128:1 → 0, 130:0 → 2.

3. 6:0 → 1, 7:0 → 1, 21:0 → 1, 24:0 → 1, 54:0 → 1, (73:0 → 1), 111:0 → 1.

4. 3:0 → 1, 4:0 → 1, 52:1 → 2, 72:1 → 0, (77:0 → 1), 86:1 → 2, 91:0 → 2, 96:1 → 2, 97:0 → 2, 98:0 → 1, 102:0 → 2, 119:0 → 2, 126:0 → 1, 135:0 → 1.

5. 15:1 → 0, (35:1 → 0), 96:1 → 0, 107:0 → 1, (113:1 → 0).

6. 112:0 → 1.

7. 35:1 → 2, 85:1 → 0, (94:1 → 2).

8. 11:1 → 0, 42:0 → 1, 65:1 → 0, 74:0 → 1, 75:0 → 1, (87:0 → 1).

9. 3:0 → 1, (11:1 → 2), (22:1 → 0), 28:1 → 0, 96:1 → 0, (122:0 → 1).

10. 16:1 → 0, 19:0 → 1, 37:0 → 1, (43:0 → 1), 48:0 → 1, 52:1 → 2, 53:0 → 1, 60:1 → 0, 61:2 → 1, 62:2 → 1, 75:0 → 1, 96:1 → 0, 118:1 → 2, 125:1 → 0, 147:1 → 0, 148:1 → 0.

11. 11:1 → 0, 14:1 → 2, (42:1 → 0), 54:0 → 1, 145:0 → 1.

12. 81:0 → 1, 87:0 → 1, 96:1 → 2.

13. 14:1 → 0, 48:0 → 1, 91:1 → 0, 138:1 → 0.

14. 80:0 → 2, 83:0 → 2, 96:1 → 0, 128:1 → 0, 130:0 → 2.

15. 5:1 → 0, 11:1 → 0, 32:1 → 2, 55:0 → 1, (60:1 → 0), 82:0 → 1, (86:0 → 1), (115:2 → 1), 117:0 → 1.

16. 6:0 → 1, 127:0 → 1.

17. 3:0 → 1, 13:0 → 1, 16:0 → 1, 120:0 → 1.

18. 11:1 → 0, 80:2 → 1, 110:0 → 1.

19. 20:0 → 1, 115:1 → 0, 127:0 → 1, 130:0 → 3, 140:1 → 0.

20. 11:1 → 0, 13:0 → 1, (47:1 → 0), (62:1 → 2), 75:1 → 0, 83:0 → 2.

21. 11:1 → 0, 13:0 → 1, (17:1 → 0), 75:1 → 0, 78:1 → 0, 80:1 → 0, 106:1 → 0, 122:1 → 0.

22. 11:1 → 2, 48:1 → 2, (80:1 → 2), 111:0 → 1, 128:1 → 0.

23. 55:0 → 1, (72:0 → 1), 79:1 → 0, 81:2 → 1.

24. 81:2 → 1, 82:0 → 1, 127:0 → 1.

25. 62:1 → 2, 117:0 → 1, 135:1 → 0, 136:1 → 0.

26. 11:1 → 2, 40:1 → 0, 72:1 → 0, 80:2 → 1, 81:2 → 1.

27. (4:1 → 0), (5:0 → 1), 7:0 → 1, 11:1 → 0, 55:0 → 1, 75:1 → 2, 84:0 → 1, 87:0 → 1, 92:2 → 3, 97:0 → 1, 110:0 → 1, 113:1 → 0, 116:2 → 1, 122:1 → 0.

28. 13:2 → 1, 17:0 → 1, 21:1 → 0, 24:2 → 0, 37:0 → 1, 62:1 → 2, 86:1 → 3.

29. 11:1 → 0, 62:1 → 0, 72:1 → 0, 83:0 → 1, 97:0 → 1.

30. 11:2 → 0, 87:1 → 0, 127:0 → 1, 128:1 → 0.

31. (4:1 → 0), (5:0 → 1), (17:1 → 0), 72:1 → 0, 111:0 → 1.

32. 135:1 → 0, 136:1 → 0.

33. 7:0 → 1, 75:1 → 0, 111:0 → 1.

34. 44:0 → 2, 47:1 → 0, 86:1 → 2.

35. 5:1 → 0, 71:0 → 1.

36. 2:1 → 0, 11:2 → 0, 24:0 → 1, 62:1 → 0, 87:1 → 0, 91:3 → 2, 117:0 → 1.

37. 11:2 → 1, 48:1 → 0, 87:1 → 0, 113:0 → 1, 126:0 → 1.

38. 2:1 → 0, 24:0 → 2, 84:0 → 1.

39. 3:0 → 1, (80:2 → 1), 81:2 → 1, 113:0 → 1, 125:0 → 1.

40. 11:2 → 0, 72:0 → 1, 92:2 → 3, 97:0 → 1, 110:0 → 1, 120:0 → 1.

41. 36:0 → 2, 37:0 → 1, 75:1 → 0, (80:1 → 2), 114:0 → 1, 116:1 → 2.

42. 60:0 → 1, (78:2 → 1), 87:1 → 0, 128:1 → 0, 140:1 → 0.

43. 13:0 → 2, 71:0 → 1.

44. 34:1 → 0, 80:1 → 2, (86:2 → 1), 114:0 → 1.

45. No changes.

46. (11:1 → 2), 37:0 → 1, 48:0 → 1, 63:1 → 0, 65:1 → 0, 89:0 → 1, 92:1 → 0, (122:0 → 1).

47. 6:0 → 1, (27:0 → 1), (29:1 → 0), (50:1 → 0), (59:1 → 0), (90:1 → 0), (94:2 → 1), 99:1 → 0, (124:1 → 0), 127:0 → 1, 128:1 → 0, 129:0 → 1, (140:1 → 0), 142:1 → 2.

48. 19:0 → 1, 20:0 → 1, 21:0 → 1, 31:0 → 1, 61:1 → 0, (66:1 → 0), 72:1 → 0, 112:0 → 1, (116:2 → 0), (118:1 → 0).

49. 8:0 → 1, 9:0 → 1, (46:1 → 0), 70:0 → 1, 78:1 → 0, (86:0 → 1).

50. 72:1 → 0, 101:0 → 1.

51. 11:1 → 0, 55:0 → 1, 100:0 → 1, (114:1 → 0), 127:0 → 1.

52. 13:0 → 1, 16:0 → 1, (23:1 → 2), (39:0 → 1), (41:0 → 1), (42:0 → 1), 69:0 → 2, 74:0 → 1.

53. 2:1 → 0, 9:0 → 1, 32:1 → 2, (48:1 → 0), 62:1 → 0, 63:1 → 0, (86:0 → 1), 89:0 → 1, 91:1 → 0, 109:0 → 1, 113:1 → 0.

54. (14:1 → 2), (17:1 → 0), 21:0 → 1, (91:2 → 1), (115:2 → 1).

55. 25:1 → 2, (28:1 → 0), (37:0 → 1), 127:0 → 1.

56. 25:0 → 1, (72:1 → 0), (80:2 → 1).

57. 10:0 → 1, 120:0 → 1.

58. (4:0 → 1), (5:1 → 0), 68:0 → 1, 117:0 → 1.

59. 1:0 → 1, 11:2 → 1, 13:0 → 2, 40:0 → 1, 87:1 → 0, (116:1 → 2).

60. 9:0 → 1, 28:1 → 0, 30:0 → 1, 47:1 → 0, 48:1 → 2, 51:1 → 0, 53:0 → 1, 62:1 → 2, 80:1 → 2, 91:3 → 1, 113:0 → 1.

61. (5:1 → 0), (17:0 → 1), 107:0 → 1, (114:1 → 0), 116:1 → 2.

62. (4:1 → 0), 36:1 → 2, 56:0 → 1, 57:0 → 1, 71:0 → 1, 80:1 → 0, 122:1 → 0.

63. 36:0 → 1, 81:2 → 1.

64. 48:1 → 0, 72:1 → 0, 75:1 → 0, 135:1 → 0.

65. (4:0 → 1), 37:0 → 1, (114:0 → 1).

66. 111:1 → 0.

67. (80:1 → 2), 117:0 → 1.

68. 62:1 → 0, 72:1 → 0.

69. (44:2 → 0), 126:0 → 1.

70. (6:1 → 0), 10:0 → 1, 72:1 → 2, 84:0 → 1, (86:1 → 2), 104:0 → 1, (135:0 → 1), (136:0 → 1).

71. 24:0 → 2, 34:0 → 1, 75:1 → 2, 108:0 → 1, 121:0 → 1, 130:0 → 1, 131:0 → 1.

72. 3:0 → 1, (6:0 → 1), 26:0 → 1, 27:0 → 1, 44:0 → 2, 55:0 → 1, 62:1 → 2, (78:1 → 2), 93:0 → 1, 119:1 → 2, 127:0 → 1, (135:1 → 0), (136:1 → 0).

73. 7:0 → 1, 111:0 → 1.

74. 24:2 → 0, (80:2 → 1), 113:1 → 0.

75. 61:2 → 1.

76. (17:1 → 0), (116:2 → 1), 118:1 → 0.

77. 4:1 → 0, (5:0 → 1), 11:1 → 2, 21:0 → 1, 22:1 → 0, 24:0 → 2, 60:1 → 0, 87:0 → 1, (144:0 → 1).

78. 23:1 → 0, (28:0 → 1), 66:1 → 0, (86:0 → 1), 91:2 → 3, 125:1 → 0.

79. (5:1 → 0), 14:1 → 0.

80. (48:0 → 1), 58:1 → 0, (62:2 → 1), 80:1 → 2, (114:1 → 0), (122:0 → 1), 135:0 → 1, (143:0 → 1), (145:0 → 1).

81. (17:0 → 1), 81:1 → 2, (91:1 → 2), 138:1 → 0, 141:1 → 0.

82. 2:0 → 1, (28:1 → 0), (38:1 → 0), (43:0 → 1), (47:0 → 1), 54:0 → 1, 70:0 → 1, 75:0 → 1, 79:0 → 1, 80:0 → 1, 81:0 → 1, 96:1 → 2, 98:0 → 1, 119:0 → 1, (123:0 → 1), (136:0 → 1).

83. 4:0 → 1, 12:0 → 1, 23:0 → 1, (46:0 → 1), 58:0 → 1, (60:0 → 1), 61:1 → 2, 62:0 → 2, (78:0 → 1), (86:1 → 0), 88:0 → 1, 91:0 → 1, 103:0 → 1, 106:0 → 1, (114:0 → 1), (115:1 → 2).

84. 18:0 → 1, (22:0 → 1), 45:0 → 1, 49:0 → 1, (50:1 → 2), 51:0 → 1, (73:0 → 1), (77:0 → 2), (87:1 → 0), 92:1 → 2, 102:0 → 1, 125:0 → 1, 134:0 → 1.

85. (11:2 → 1), (35:0 → 1), 38:0 → 1, (43:1 → 0), (66:0 → 1), 105:0 → 1, (116:0 → 2), (118:0 → 1), (122:1 → 0), 133:0 → 1, 137:0 → 1, 141:0 → 1, 142:0 → 1.

86. 15:0 → 1, (29:0 → 1), 52:0 → 1, (59:0 → 1), 63:0 → 1, 65:0 → 1, 76:0 → 1, 85:0 → 1, (87:0 → 1), (90:0 → 1), 94:0 → 2, 95:0 → 1, 96:0 → 1, (113:0 → 1), (115:0 → 1), (140:0 → 1), (146:0 → 1), (147:0 → 1), (148:0 → 1).

87. 23:2 → 0, 28:0 → 1, 32:0 → 1, 33:0 → 1, (43:0 → 1), (50:0 → 1), 64:0 → 1, 92:0 → 1, 99:0 → 1, (122:0 → 1), (124:0 → 1).

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