

ORIGINAL ARTICLE

# Cladistic analysis of morphological characters in the eulophine tribe Cirrospilini (Hymenoptera: Eulophidae)

Rosichon UBAIDILLAH,<sup>1</sup> John LASALLE,<sup>2,3,4†</sup> Donald L. J. QUICKE<sup>3</sup>  
and Jun-ichi KOJIMA<sup>5</sup>

<sup>1</sup>Museum Zoologicum Bogoriense, Research Center for Biology, Indonesian Institute of Sciences – LIPI, Cibinong, Bogor, Indonesia; <sup>2</sup>Unit of Parasitoid Systematics, CABI Biosciences UK Center (Ascot), <sup>3</sup>Department of Biological Sciences, Imperial College London, Silwood Park Campus, Ascot, Berkshire and <sup>4</sup>Department of Entomology, The Natural History Museum, London, UK; and <sup>5</sup>Natural History Laboratory, Faculty of Science, Ibaraki University, Mito, Japan

## Abstract

A total of 56 morphological characters were analyzed for 53 cirrospiline species that represent all of the 17 described genera of the tribe. The other taxa of the Eulophinae included in the analysis were six species of six representative genera in the tribe Eulophini, a species of *Elasmus* (the only genus comprising the tribe Elasmini), and a species of *Trichospilus* (unplaced). *Trichospilus* and two of the six genera of Eulophini examined were placed within Cirrospilini. Monophyly of Cirrospilini (when these two genera of Eulophini and *Trichospilus* are included) and of the cirrospiline genera for which more than one species were examined was supported, but the relationships between the genera were poorly resolved. An exception was *Cirrospilus*, the largest genus in the Cirrospilini, monophyly of which was not supported to any extent.

**Key words:** Chalcidoidea, monophyly, parasitic wasp, parsimony analysis.

## INTRODUCTION

Within the superfamily Chalcidoidea Latreille, 1817, the Eulophidae Westwood, 1828 is one of the largest families in terms of the numbers of species and genera, with approximately 4300 species in 294 genera. The family is present and common in all geographic regions (Noyes 2002). Most eulophids are entomophagous, attacking insects and other arthropods such as spiders and mites. Parasitoid forms are considerably divergent: they can be endoparasitoids or ectoparasitoids, primary parasitoids or hyperparasitoids, specialists or generalists in their host selection, and they can have a gregarious or solitary

larval development. A few genera are known to be phytophagous, but the species of these phytophagous genera again display various lifestyles (Gauthier *et al.* 2000; Noyes 2002).

Since Ashmead (1904) formally classified the Eulophidae into subfamilies and tribes, their concepts have been changed greatly (Domenichini 1953; Bouček 1958, 1988; Peck *et al.* 1964; Riek 1967; Bouček & Askew 1968; Burks 1979; Yoshimoto 1984; Coote 1997; Gibson 1999). Ranks and even nested patterns of the family group taxa in the Eulophidae and its related ‘families’ have frequently been changed, and sometimes in a rather arbitrary manner (Domenichini 1953; Riek 1967; Burks 1979; Bouček 1988).

Bouček (1988) extensively studied the Eulophidae and recognized four subfamilies: Eulophinae Westwood, 1828; Entedoninae Förster, 1856; Tetrastichinae Förster, 1856; and Euderinae Erdős, 1956. Graham (1987) and Bouček (1988) re-examined the characters that formed the basis by which the Elachertinae Förster, 1856 had been treated as distinct from the Eulophinae (Ashmead 1904; Riek 1970), and independently reached the

*Correspondence:* Dr Jun-ichi Kojima, Natural History Laboratory, Faculty of Science, Ibaraki University, Mito, 310-8512 Japan. Email: jkrte@mx.ibaraki.ac.jp

<sup>†</sup>*Present address:* Australian National Insect Collection, Division of Entomology, CSIRO, Canberra, ACT 2601, Australia.

Received 1 November 2002; accepted 12 May 2003.

conclusion that these characters (notaulus and male antennal funicle) were not sufficiently consistent to distinguish the two groups at the subfamily level. Bouček (1988) then arranged the eulophine genera into six tribes (Eulophini; Anselmellini Bouček, 1988; Keryini Bouček, 1988; Ophelimini Ashmead, 1904; Elachertini; and Euplectrini Ashmead, 1904). Bouček's (1988) classification at the subfamilial and tribal levels has been generally followed by subsequent authors (LaSalle & Schauff 1992; Schauff & LaSalle 1993; Schauff *et al.* 1997). Finally, Gauthier *et al.* (2000) proposed a new classification based on molecular and morphological data. They recognized the same four subfamilies in the Eulophidae as Graham and Bouček had previously (Eulophinae, Entedoninae, Tetrastichinae and Euderinae), synonymized Elachertini and Euplectrini under Eulophini, removed the Keryini from the Eulophidae, removed the Anselmellini and Ophelimini from the Eulophinae, and moved the Elasmidae Walker, 1871 into the Eulophinae at the tribal rank. One of the authors (J. L.) proposed a new tribe, Cirrospilini, in the Eulophinae. Consequently, Gauthier *et al.* (2000) recognized three tribes in the Eulophinae: Eulophini, Elasmmini and Cirrospilini.

The monophyly of the Cirrospilini was assumed based on the molecular data of the 28S rDNA D2 region (Gauthier *et al.* 2000). The subsequent morphological comparisons of Gauthier *et al.* (2000) suggested that synapomorphies for Cirrospilini were the presence of transverse grooves on the frons, the antenna with two or three funicles, and the scutellum having a distinct submedian groove and two pairs of setae. Included in the Cirrospilini by Gauthier *et al.* (2000) were most genera of the Ophelimini in the sense of Bouček (1988), some genera that Bouček (1988) placed in the Elachertini, as well as a few genera not treated by Bouček (1988), such as *Danuviella* Erdős, 1958 and *Oxycantha* Surekha and Ubaidillah, 1996. The genera *Aulogymnus* Förster, 1851 and *Dichatomus* Förster, 1878 were tentatively placed in the Cirrospilini, although Gauthier *et al.* (2000) themselves expressed some doubt about this placement: all species of these two genera lack either the transverse groove on the face or the submedian groove on the scutellum. Gauthier *et al.* (2000) failed to assign *Trichospilus* Ferrière, 1930 to a tribe and treated it as 'unplaced' in the Eulophinae.

The Cirrospilini are a group of moderate size in terms of number of species, with approximately 300 described species in 17 genera. The species of the Cirrospilini are known from all geographic regions, being most abundant in the Australasian Region. Most genera contain a

relatively small number of species; that is, approximately two-thirds of the genera include fewer than 10 species. The tribe is dominated by a single genus, *Cirrospilus* Westwood, 1832, which consists of approximately 135 described species and is cosmopolitan. Certain other genera are restricted to a single region, such as *Pseudiglyphus* Girault, 1915 and *Semiellacher* Bouček, 1988 to the Australo-Pacific and *Danuviella* Erdős, 1958 to the Palearctic.

As outlined above, the Cirrospilini have not yet been defined by robust morphological characters, and the relationships between the genera within the tribe are still poorly understood. In the present study, we analyze the morphological characters of the Cirrospilini to test whether any of the characters so far used in the taxonomy of Eulophinae and those newly introduced in the present study support the monophyly of the tribe and included genera.

## MATERIALS AND METHODS

For the subfamilial and tribal classification in the subsequent parts of the present paper, we followed the system of Gauthier *et al.* (2000).

A total of 53 species representing all of the 17 cirrospiline genera were used for the analysis (Table 1). They include species (i) encompassing the morphological diversity within the tribe as exhaustively as possible; (ii) of as many type species of the cirrospiline genera as possible; and (iii) from throughout the world. Twenty of these species were from the genus *Cirrospilus*, the largest cirrospiline genus.

Representatives of the other two tribes in the Eulophinae, Eulophini (six species) and Elasmmini (one species), and a species of *Trichospilus* were included in the analysis, and also included for rooting were representative taxa from the other three subfamilies of the Eulophidae (Table 1).

Observation on the morphology was carried out by R. U. on specimens deposited in the Australian National Insect Collection, CSIRO (Canberra), The Natural History Museum (London), Bernice P. Bishop Museum (Honolulu), Museum Zoologicum Bogoriense (Cibinong), Canadian National Collection of Insects, Arachnids and Nematodes (Ottawa), and the US National Museum of Natural History (Washington, DC).

A total of 56 characters discussed in the next section were subjected to the cladistic analysis. Most parsimonious trees were found using PAUP\* (Swofford 1999). Initially, 30 000 random additions were carried out, followed by TBR branch swapping, but holding only

**Table 1** Eulophid species used in the present analysis, with subfamilial and tribal classification following Gauthier *et al.* (2000)

<b>Eulophinae</b> Westwood, 1828	Genus <i>Meruana</i> Delucchi, 1962
<b>Cirrospilini</b> LaSalle, 2000	<i>M. cameronounensis</i> Risbec, 1955
Genus <i>Ascotolinx</i> Girault, 1913	<i>M. cuprata</i> Ferriere, 1950
<i>A. funeralis</i> Girault, 1913 <sup>†</sup>	<i>M. liriomyza</i> Bouček, 1962
<i>A. reticoxa</i> Bouček, 1988	Genus <i>Naumanniola</i> Bouček (1988)
Genus <i>Aulogymnus</i> Förster, 1851	<i>N. ramosa</i> Bouček, 1988
<i>A. aceris</i> Förster, 1851 <sup>†</sup>	<i>N. varians</i> Bouček, 1988 <sup>†</sup>
<i>A. pulchra</i> (Mayr, 1877)	Genus <i>Oxycantha</i> Surekha & Ubaidillah, 1996
<i>A. skianeuros</i> Ratzeburg, 1844	<i>O. darwini</i> Surekha & Ubaidillah, 1996
<i>A. trilineata</i> (Mayr, 1877)	Genus <i>Pseudiglyphus</i> Girault, 1915
<i>A. californica</i> Gordh, 1977	<i>P. grotiusi</i> Girault, 1915 <sup>†</sup>
Genus <i>Cirrospiloidelleus</i> Girault, 1913	Genus <i>Semielacher</i> Bouček, 1988
<i>Cirrospiloidelleus</i> sp.	<i>S. petiolata</i> (Girault, 1915)
Genus <i>Cirrospilus</i> Westwood, 1832	<i>S. silvicola</i> Bouček, 1988 <sup>†</sup>
<i>C. afer</i> (Silvestri, 1914)	Genus <i>Zagrammosoma</i> Ashmead, 1904
<i>C. ambiguus</i> Hansson & LaSalle, 1996	<i>Z. buselus</i> Walker, 1839
<i>C. argei</i> Crawford, 1911	<i>Z. centralineatum</i> Crawford, 1913
<i>C. atripropodeum</i> (Girault, 1926)	<i>Z. latilineatum</i> Ubaidillah, 2000
<i>C. curvineurus</i> Askew, 1965	<i>Z. lineaticeps</i> (Girault, 1915)
<i>C. diallus</i> Walker, 1838	<i>Z. talitzkii</i> Bouček, 1961
<i>C. elegantissimus</i> Westwood, 1832 <sup>†</sup>	<b>Eulophini</b> Westwood, 1828
<i>C. festivus</i> (Girault, 1915)	Genus <i>Colpoclypeus</i> Lucchese, 1941
<i>C. flavitibia</i> (Girault, 1928)	<i>C. florus</i> (Walker, 1839)
<i>C. fuscus</i> (Girault, 1913)	Genus <i>Di cladocerus</i> Westwood, 1832
<i>C. lyncus</i> Walker, 1839	<i>D. westwoodii</i> Thomson, 1878
<i>C. margiscutellum</i> (Girault, 1939)	Genus <i>Euplectrus</i> Westwood, 1832
<i>C. occipitis</i> Girault, 1928	<i>E. bicolor</i> (Swederus, 1795)
<i>C. pictus</i> (Nees, 1834)	Genus <i>Hyssopus</i> Girault, 1916
<i>C. pulcher</i> (Girault, 1913)	<i>H. nigrifulus</i> Zetterstedt, 1838
<i>C. staryi</i> Bouček, 1958	Genus <i>Paraolinx</i> Ashmead, 1894
<i>C. tau</i> (Girault, 1913)	<i>P. typica</i> Howard, 1895
<i>C. variegatus</i> (Masi, 1907)	Genus <i>Sympiesis</i> Förster, 1856
<i>C. viticola</i> (Rondani, 1877)	<i>S. dolichogaster</i> Ashmead, 1988
<i>C. vittatus</i> Walker, 1838	<b>Elasmini</b> Walker, 1871
Genus <i>Danuviella</i> Erdős, 1958	Genus <i>Elasmus</i> Westwood, 1833
<i>D. sublana</i> Erdős, 1958 <sup>†</sup>	<i>E. steffani</i> Vigiani, 1967
Genus <i>Diaulinopsis</i> Crawford, 1912	Unplaced
<i>D. arenaria</i> Erdős, 1915	Genus <i>Trichospilus</i> Ferrière, 1930
<i>D. callichroma</i> Crawford, 1912 <sup>†</sup>	<i>T. diatraeae</i> Cherian & Margabandhu, 1942
Genus <i>Dichatomus</i> Förster, 1878	
<i>D. acerinus</i> , Förster, 1878	<b>Euderinae</b> Erdős, 1956
Genus <i>Diglyphus</i> Walker, 1848	Genus <i>Euderus</i> Haliday, 1844
<i>D. isaea</i> (Walker, 1838)	<i>E. albitarsis</i> Zetterstedt, 1838
<i>D. guptai</i> (Subba Rao, 1957)	<b>Entedoninae</b> Förster, 1856
<i>D. bulbosus</i> Ubaidillah & Yefremova, 2001	Genus <i>Closterocerus</i> Westwood, 1833
Genus <i>Gallowayia</i> Bouček, 1988	<i>C. coffeellae</i> Ihering, 1914
<i>G. picta</i> Bouček, 1988 <sup>†</sup>	<b>Tetrastichinae</b> Förster, 1856
Genus <i>Gattonia</i> Bouček, 1988	Genus <i>Aprostocetus</i> Westwood, 1833
<i>G. basirufa</i> Bouček, 1988 <sup>†</sup>	<i>A. fidius</i> Girault, 1917
<i>G. nigra</i> Bouček, 1988	Genus <i>Nesolynx</i> Ashmead, 1905
Genus <i>Melittobiopsis</i> Timberlake, 1926	<i>N. thymus</i> (Girault, 1916)
<i>M. ereunetiphila</i> Timberlake, 1926	

<sup>†</sup>Type species.

one tree at any one time. This strategy enables a large 'area' of tree space to be sampled (Quicke *et al.* 2001), and increases the chance of finding multiple islands of most parsimonious trees (Maddison 1991). Each of the most parsimonious trees found by this method were then used as starting trees for further TBR searching with 'maxtrees' unlimited. Successive approximations weighting (Farris 1989; Carpenter 1994) was used to try to narrow down the number of most parsimonious trees to provide a preferred subset of trees. As the weighting functions for successive approximations weighting, we used both the maximum and minimum values of the retention index (Quicke *et al.* 1999;

Gauthier *et al.* 2000; Basibuyuk *et al.* 2002). Data decisiveness (Goloboff 1991) was calculated using 100 000 equiprobable trees generated by PAUP\*.

Because polarities of most characters were not determined by outgroup comparisons, all characters were treated as unordered.

## CHARACTERS

In this section, the morphological characters in the Cirrospilini are discussed. The characters used in the analysis are numbered and the coding adopted for each character is described.

**Table 2** Character matrix for Eulophinae (Cirrospilini, Eulophini, Elasmini, *Trichospilus*) and four outgroups (= first four)

	1.....5.....10.....15.....20.....25.....30.....35.....40.....45.....50.....55
	..... ..... ..... ..... ..... ..... ..... ..... ..... ..... ..... .....
<i>Closterocerus coffeellae</i>	000010000100201????00000010000000000200002220000011000000
<i>Euderus albitarsis</i>	0000100000001011000000110000000000200000010001-00011001
<i>Aprostocetus fidius</i>	002010001000111200000000101002-0021200000010110000011011
<i>Nesolynx thymus</i>	0010000001001000100000001011000000100000000110000010011
<i>Colpocypeus florus</i>	00001100101011112201000000102-2100020200011100000011000
<i>Di cladocerus westwoodii</i>	000010000010011211010000110102-2120020200001100000010001
<i>Hyssopus nigrifolius</i>	10000000000011120000100000010002120000200001110000010001
<i>Euplectrus bicolor</i>	00010000100011110011210000010002000001200001110000110011
<i>Paraolinx typica</i>	20000000000001120001010000010102100020110001110001010000
<i>Sympiesis dolichogaster</i>	001000000000102300102100000102-2100100210001101-00010010
<i>Elasmus steffani</i>	000001000100112210000000100102-2000200000011110000010?01
<i>Trichospilus diatraeae</i>	20000000100011212200000000200011000?0010100111-01001?10
<i>Ascotolinx funeralis</i>	010000031000111121010100000102-1030020100001011-00101001
<i>Ascotolinx reticoxa</i>	01100003100011112110100000102-1030020100001010000101001
<i>Aulogymnus aceris</i>	12200000100111101100010100010002100010200011111-11010011
<i>Aulogymnus californica</i>	10101001110010122101000101010002100200200011110011011011
<i>Aulogymnus pulchra</i>	02100000100111101100000100010002100000200011101-11010111
<i>Aulogymnus skianeuros</i>	0210000010011111111000100010002000000200011110010010011
<i>Aulogymnus trilineata</i>	021000000001111111110001000100020?0000200011101-10010011
<i>Cirrospilus afer</i>	1000001?100021112200010000011000020200000011110011001011
<i>Cirrospilus ambiguus</i>	10000000000021112200000000010101120200000011110010001001
<i>Cirrospilus argei</i>	1000000?100021112200010000000001120000000021110000001001
<i>Cirrospilus atripropodeum</i>	1000000?100021112200000100010000010001000?1110010001001
<i>Cirrospilus curvineurus</i>	10000001100021112200010000010001020000200021110100001001
<i>Cirrospilus diallus</i>	10100001100021112200010100010001120020200021110000001001
<i>Cirrospilus elegantissimus</i>	10100001100021112200010100010001110000100011010000001011
<i>Cirrospilus festivus</i>	001000011000211122000?0000010001120200000011111-00011001
<i>Cirrospilus flavitibia</i>	00100001100021112200000000000001120200000011111-00001001
<i>Cirrospilus fuscus</i>	10100000100021112200000000001000000020200011110000001201
<i>Cirrospilus lyncus</i>	10100001100021112200000100011002120000100011110000001001
<i>Cirrospilus margiscutellum</i>	10100000100021112200000100011002120200200011110001001001
<i>Cirrospilus occipitis</i>	00100001110021112200000100011002120200200011111000001001
<i>Cirrospilus pictus</i>	10100001110021112200010000011001120000100011110000001001
<i>Cirrospilus pulchellus</i>	10100001110021122?0?0101?00110010200002000111100000010?1
<i>Cirrospilus staryi</i>	001000011000211122000100010110010102002000211100000?1001
<i>Cirrospilus tau</i>	00100001100021112200010000011001020200200011111-000?1011

Table 2 Continued

	1.....5.....10.....15.....20.....25.....30.....35.....40.....45.....50.....55
	..... ..... ..... ..... ..... ..... ..... ..... ..... ..... .....
<i>Cirrospilus variegatus</i>	1010001?1000211122000100000110021202000000111100010010?1
<i>Cirrospilus viticola</i>	1010000111002111220001010001?001020000200021110000001001
<i>Cirrospilus vittatus</i>	00100001110021112200010100011002120200100011110100001001
<i>Cirropiloidelleus</i> sp.	1010000011002111220?010100010000020020000011110000001001
<i>Danuviella subplana</i>	10001000110021112200010101010100120020000011110000001001
<i>Diaulinopsis arenaria</i>	10001001110021112200011001010000020200001011110000001001
<i>Diaulinopsis callichroma</i>	10001001110021112200011001010002120200001011110000001001
<i>Dichatomus acerinus</i>	10001000100011112101010101010001100000100011111-00011001
<i>Diglyphus isaea</i>	10001001000011112100000001010101120100200011110100011001
<i>Diglyphus guptai</i>	10001001000011112200000001010101120200200011110100011001
<i>Diglyphus bulbosus</i>	10001001000011112200001001011001120100200011111-00011001
<i>Gallowayia picta</i>	10100101010011222200100101020012120001100010110001001201
<i>Gattonia basirufa</i>	010110000100111121000100010102-1020021300000110000011001
<i>Gattonia nigra</i>	010110000000111122000100010102-1020021300000110000011001
<i>Meruana cameronouns</i>	100000000000111122000100010102-1120010200011110000001201
<i>Meruana cuprata</i>	100000000000111122000100010102-1120010200011110000001101
<i>Meruana liriomyzae</i>	100000000000111122000100010102-11200102000111100000?1201
<i>Melittobiopsis ereunetiphila</i>	10000000000011222200010000010001100200002011100000001001
<i>Naumanniola ramosa</i>	10000001110011?112?0210101020101020001100011110000000001
<i>Naumanniola varians</i>	1000000111101111110110101020101020001100011110000000001
<i>Oxycantha darwini</i>	00010000111021?2?1?0010100010101100020000010111-0000?001
<i>Pseudiglyphus grotiusi</i>	001011010010111122000?0000010111120020200011101-00001001
<i>Semiellacher petiolata</i>	00100002010121112200000001010001120010100011110000001201
<i>Semiellacher silvicola</i>	001000020101211?220?00001010001120010100011110000001201
<i>Zagrammosoma buselus</i>	101000111000211222000000010111021?0000000011110001011001
<i>Zagrammosoma centrolineatum</i>	10100011100021222200000001021100010000100011010011011001
<i>Zagrammosoma lineaticeps</i>	001000101000212222000000?1021100010000000011000001011001
<i>Zagrammosoma talitzkii</i>	0010001?1000212222000000?10211000100000000110000010?1001
<i>Zagrammosoma latilineatum</i>	101000111000212?2?0?000??20100000000000011010001001001

Characters indicated with question marks were those of which states were not observed due to the bad condition of the specimens examined.

## Head

Terminology for subdivisions of the head follows Bouček (1988) and Gibson (1997).

1. Compound eye setose: *absent*, 0; *scattered*, 1; *dense*, 2.

There are two character states in the Cirrospilini: setae absent (Figs 1–3,6) or scattered (setae always short, interspaced by at least a few facets; Figs 5,7,8). In *Paracolinx* (Eulophini) and *Trichospilus*, the compound eyes have dense setae (nearly all facets armed with a seta).

2. Clypeal apical margin: *linear*, 0; *produced medially*, 1; *bilobed*, 2.

This character is modified from Schauff (1991) and Heraty (1994). Heraty (1994) considered the linear apical margin of the clypeus to be a plesiomorphic state in

the Chalcidoidea. The clypeus with linear apical margin is found in most members of the Cirrospilini (Figs 1–8), but *Aulogymnus* has a clypeus with bilobed apical margin (Fig. 9), and the clypeus of *Ascotolinx* (Fig. 10) and *Gattonia* (Fig. 11) is ventrally produced medially. Among other eulophid genera, the apically bilobed clypeus is found in several genera not included in the present study, such as *Dimmockia* Ashmead, 1904 (Eulophini) and *Ceratoneura* Ashmead, 1894 (Tetrastichinae).

3. Frontoclypeal suture: *absent*, 0; *present only laterally*, 1; *present laterally and dorsally*, 2.

Heraty (1994) treated this character in combination with the shape of the clypeal apical margin. There is, however, no ground to combine these two characters. Three conditions are recognized: suture absent, thus the



clypeus barely delimited (Figs 3,7,8,11); sutures present along the lateral margins of the clypeus ventrally to the tentorial pits (Figs 1,2,6,9,10); and the clypeus delimited by both lateral sutures and dorsal suture running between the tentorial pits.

4. Malar sulcus: *present, 0; absent, 1.*

This character is adopted from Graham (1987) and Schauff (1991). The malar sulcus is present in all eulophine species examined (Figs 1,2,6,9,19), except species of *Gattonia* (Fig. 11), *Oxycantha* (Fig. 3) and *Euplectrus*.

5. Frontal suture: *absent, 0; present, 1.*

A transverse frontal suture is situated just ventral to the anterior ocellus in most eulophids (Figs 4,5). Bouček (1988) and Schauff (1991), who called this suture 'frontal groove', recognized the migration of this suture ventrally to approximately halfway between the anterior ocellus and the torulus in the Entedoninae, but it is different from the 'transverse grooves on frons' as discussed later.

6. Occipital carina: *absent, 0; present, 1.*

This character that has not been referred to in the taxonomy of the Cirrospilini occurs in *Pseudiglyphus* and *Gallowayia* and some outgroups.

7. Vertex: *flat, 0; vaulted, 1.*

In *Zagrammosoma*, the vertex is strongly swollen dorsally distinctly beyond the level of the upper margin of compound eyes (Figs 19,20), that Gordh (1978) considered an apomorphy for the genus. Bouček (1988) and LaSalle (1989) followed Gordh (1978), but the condition is found also in some *Cirrospilus* species (Fig. 21).

8. Transverse grooves on frons: *absent, 0; straight, 1; curved, 2; angled, 3.*

Gauthier *et al.* (2000) referred to the presence of a transverse groove in each lateral side of the frons approximately midway between the anterior ocellus and the torulus (= basal socket of the antenna), which occurs in addition to the frontal suture, and is independent of the presence of the frontal suture. Gauthier *et al.* (2000) considered this a defining character for the tribe Cirrospilini, but as they themselves pointed out, these grooves are absent in several genera that they placed in the Cirrospilini, and the conditions vary even within a single genus. When they are present, the grooves may be straight or only slightly curved (Figs 1,4–6), distinctly

curved dorsally to form an acute angle where they meet (Fig. 2) or angled submedially (Fig. 10).

9. Scrobal groove: *present, 0; absent, 1.*

Schauff (1991) treated this character in combination with the frontal suture. This groove, however, may occur independently of the presence or absence of the frontal suture. In the present study, we treat this character separately from the frontal suture. Most cirrospiline wasps have a depressed scrobe without a distinct groove. A distinct groove is, however, found in several genera (Figs 1,2,4,6,7).

10. Paired large setae on vertex: *absent, 0; present, 1.*

11. Short, scattered setae on vertex: *present, 0; absent, 1.*

Two distinctly different types of setae on the vertex are recognized: large setae that are always paired (Figs 3,22) and might be sensory setae, and short and scattered setae. They are treated as separate characters. In the cirrospilines examined in the present study, small and scattered setae on the vertex are absent only in *Naumanniola varians*, *Oxycantha darwini* and *Pseudiglyphus grotiusi*.

12. Tentorial pits: *invisible, 0; distinct, 1.*

In most species of the Cirrospilini and outgroups in the present study, the tentorial pits are indistinct and barely visible, even under a compound microscope. They are distinct and very deep in *Semielaecher* (Fig. 2), and shallow but distinct in most species of *Aulogymnus* (Fig. 9).

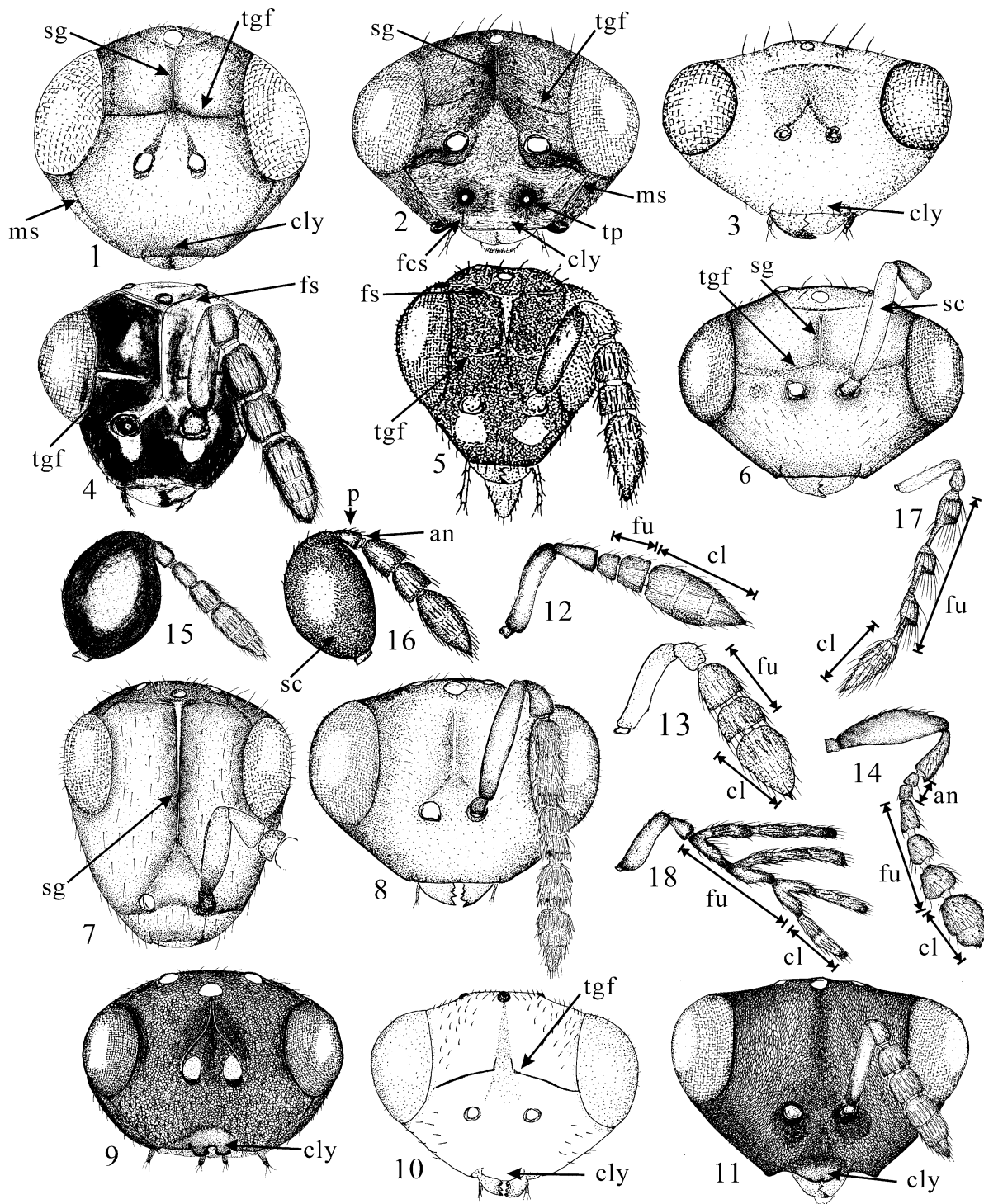
13. Maxillary palp: *three-segmented, 0; two-segmented, 1; single-segmented, 2.*

14. Labial palp: *three-segmented, 0; two-segmented, 1.*

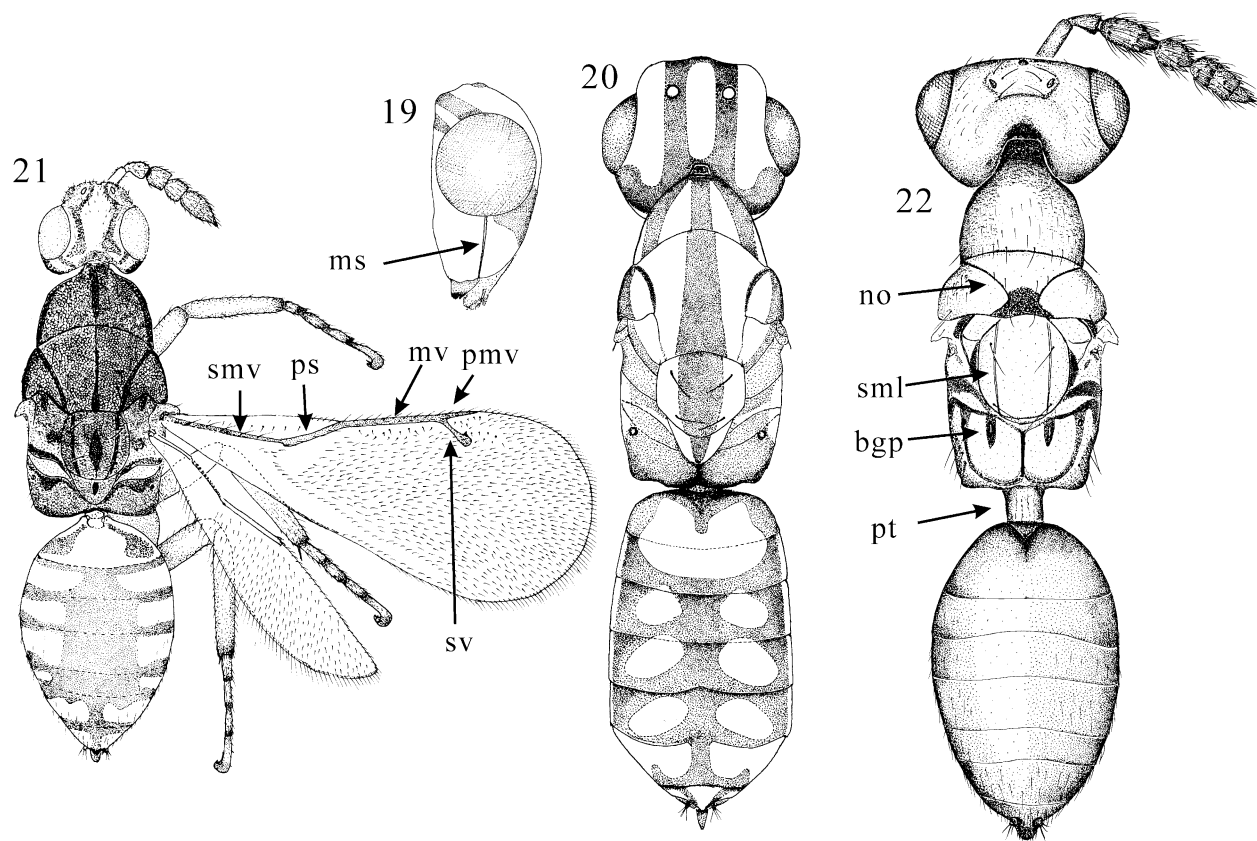
In the Hymenoptera in general, reduction of the numbers of segments of the maxillary and labial palps is considered to be a derived state (Gauld 1985). In Cirrospilini, the maxillary palp composed of one or two segments, and a three-segmented maxillary palp, was observed only in two outgroup species, *Paraolinx typica* and *Di cladocerus westwoodii*.

## Antennae

Characters relating to sensory organs on the antennae, such as sensilla and setae, are probably of importance in phylogenetic as well as behavioral studies in



Figures 1–18 Heads and antennae in Cirrospilini. 1–11 Female head in front (1–3,9,10 antennae removed; 4,5,8,11 right antenna removed; and 6,7 right antenna removed, only basal articles of left antenna drawn); 12–18 left antenna (12–14 female; 15–18 male). 1 *Pseudiglyphus grotiusi*; 2 *Semiolacher silvicola*; 3 *Oxycantha darwini*; 4,15 *Diglyphus bulbis*; 5,16 *Diaulinopsis callichroma*; 6,17 *Gallowayia picta*; 7,12 *Melittobiopsis ereunetiphila*; 8,18 *Naumanniola ramosa*; 9 *Aulogymnus trilineata*; 10,13 *Ascotolinx reticosa*; 11 *Gattonia nigra*; and 14 *Dichatomus acerinus*. an, anellus; cl, club; cly, clypeus; fcs, frontoclypeal sulcus; fu, funicle; ms, malar sulcus; p, pedicel; sc, scape; sg, scrobal groove; tgf, transverse groove on frons; tp, tentorial pit.



Figures 19–22 Cirrospiline wasps. 19 Head in profile; 20–22 dorsal view. 19,20 *Zagrammosoma latilineatum*; 21 *Cirrospilus variegatus*; and 22 *Gallowayia picta*. bgp, basal groove on propodeum; ms, malar sulcus; mv, marginal vein; no, notaulus; pmv, postmarginal vein; ps, parastigma; pt, petiole of first metasomal segment; sml, submarginal line on scutum; smv, submarginal vein; sv, stigmal vein.

Eulophidae. However, information on the sensory organs in the Eulophidae is still very limited. In the present study, presence or absence of large setae on the pedicel was the only antennal sensory organ character included in the analysis.

15. Number of female anelli: *three*, 0; *two*, 1; *one*, 2.

16. Number of male anelli: *three*, 0; *two*, 1; *one*, 2; *anelli absent*, 3.

Lack of the anelli is the plesiomorphic state in the Hymenoptera as a whole (Gibson 1989), and their presence is a character defining the Chalcidoidea. Anelli are usually very short and ring like, but sometimes they are larger and more distinct (Fig. 14). The number of anelli may or may not be the same in both sexes. Graham

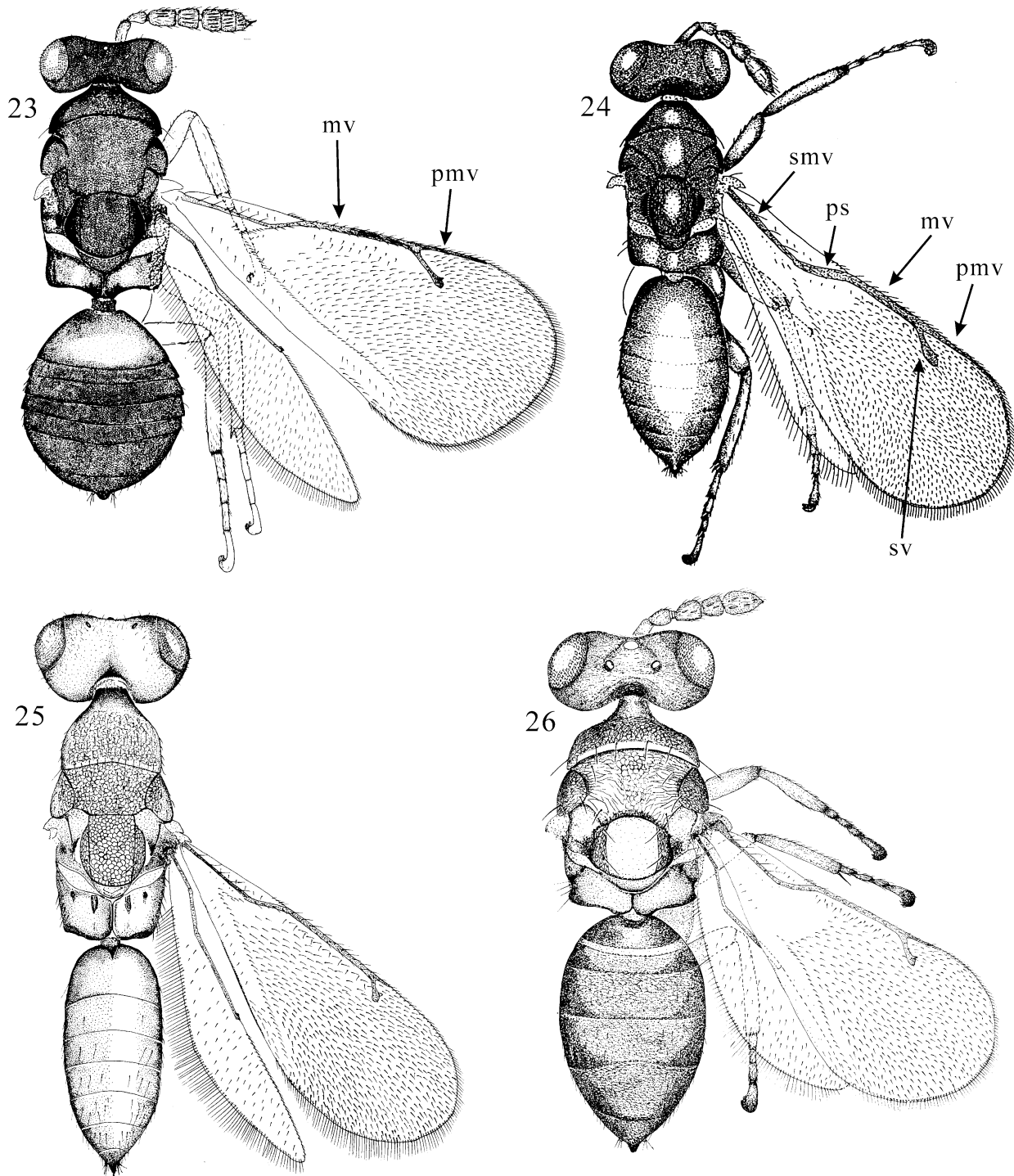
(1987) mentioned that the presence of three anelli is plesiomorphic for the Eulophidae, and assumed that reduction in the number of anelli was a secondarily derived condition (see also Storozheva 1991).

17. Number of female funicles: *four*, 0; *three*, 1; *two*, 2.

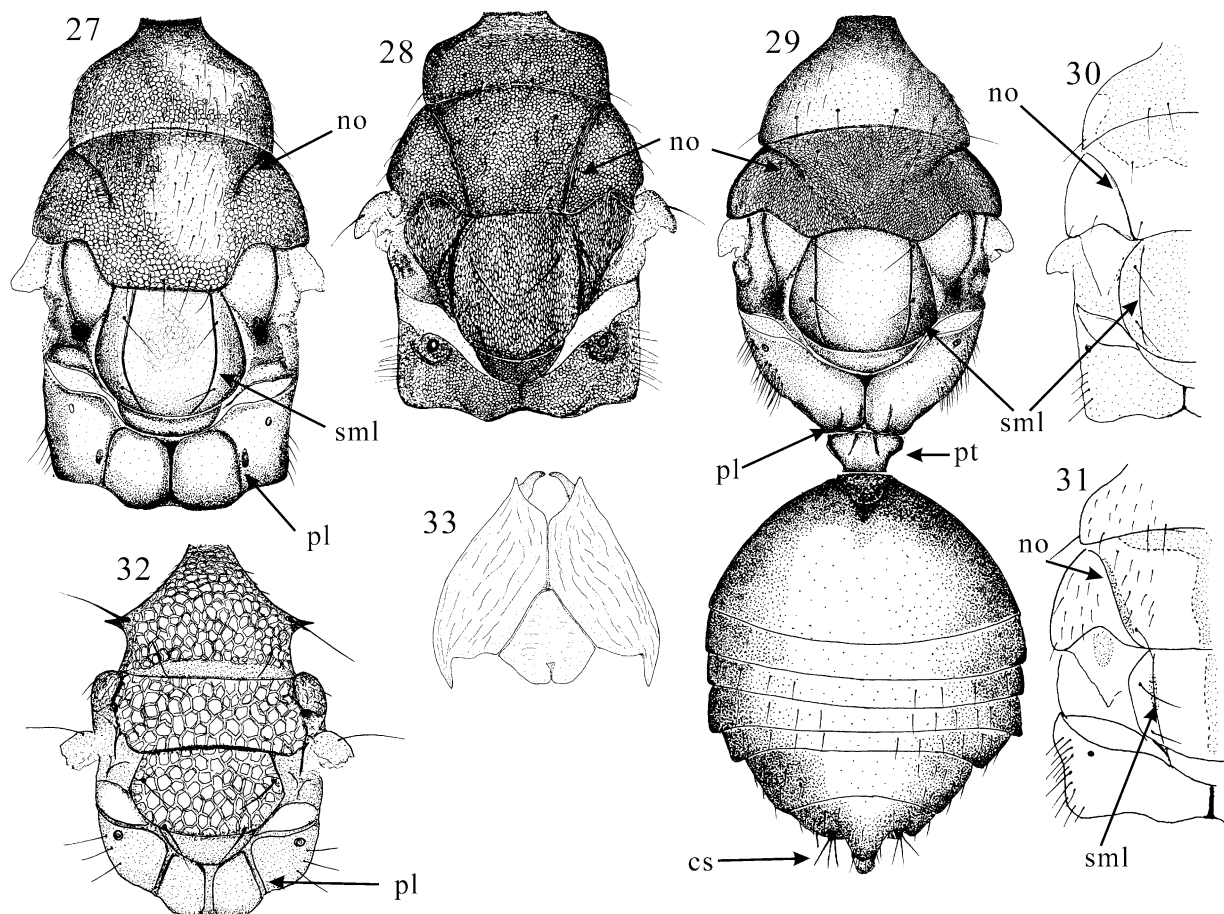
18. Number of male funicles: *four*, 0; *three*, 1; *two*, 2.

Graham (1987) and Bouček (1988) mentioned that the reduced number of funicles is apomorphic in the Eulophidae, with four or five funicles as the most primitive condition for both sexes (Bouček 1988). In most genera of the Cirrospilini, the number of funicles is the same in both sexes (three or two) (*Diglyphus bulbosus*: Figs 4,15; *Diaulinopsis callichroma*: Figs 5,16;





Figures 23–26 Cirrospiline wasps in dorsal view. 23 *Danuviella subplana*; 24 *Diaulinopsis callichroma*; 25 *Naumanniola ramosa*; and 26 *Pseudiglyphus gratiusi*. mv, marginal vein; pmv, postmarginal vein; ps, parastigma; smv, submarginal vein; sv, stigmal vein.



Figures 27–33 Characters in Cirrospilini. 27,28,30–32 Mesosoma in dorsal view; 29 mesosoma and metasoma in dorsal view; and 33 proplura. 27 *Ascotolinx reticosa*; 28 *Aulogygnus trilineata*; 29 *Meruana liryomyzae*; 30 *Cirrospilus viticola*; 31 *Cirrospilus atripropodeum*; 32 *Oxycantha darwini*; and 33 *Pseudiglyphus grotiusi*. cs, cercal seta; no, notaulus; pl, plica; pt, petiole; sml, submarginal line on scutum.

*Naumanniola ramosa*: Figs 8,18) but in *Ascotolinx* and *Gallowayia*, females have two funicles (Fig. 22) while males have three (Fig. 17).

19. Number of female club articles: *three*, 0; *two*, 1.

20. Number of male club articles: *three*, 0; *two*, 1. As for the anelli and funicles, reduction in the number of club articles (Figs 13,18) has been considered to be apomorphic in the Eulophinae (Storozheva 1991). Although some authors have used this character in combination with the funicles (Graham 1987; Heraty 1994), they could be treated as independent characters in a phylogenetic analysis.

21. Shape of male funicles: *cylindrical*, 0; *humped*, 1; *branched*, 2.

Sexual dimorphism in the shape of the funicles is considered to be apomorphic (Heraty 1994). The cirrospiline males generally have unmodified funicles, while the funicles are humped in *Gallowayia picta* (Fig. 17) and *Naumanniola varians*, and branched in *Naumanniola ramosa* (Fig. 18).

22. Large setae on pedicel: *absent*, 0; *present*, 1.

Large and suberect setae on the pedicel, probably sensory setae, are found in many cirrospiline genera.

23. Male scape: *not swollen, 0; strongly swollen, bulbous 1.*

Bouček (1988) used a male scape that is strongly swollen or bulbous to distinguish *Diaulinopsis* (Fig. 16) from other eulophine genera. The same condition, however, occurs in some species of *Diglyphus* (Fig. 15) (see also Zhu *et al.* 2000).

24. Female scape: *short, apex not reaching level of vertex, 0; long, apex extended beyond level of vertex, 1.*

This character was taken from Heraty (1994). The female scape in some genera such as *Gallowayia* (Fig. 6) and *Naumanniola* (Fig. 8) is elongated beyond the level of the vertex, while in most cirrospilines it is short and does not reach the level of the vertex (Figs 4,5,7,11). *Cirrospilus* is also heterogeneous in this character.

25. Whorled setae on male funicle: *absent, 0; present, 1.*

Graham (1987) suggested the presence of whorled setae is apomorphic in the Tetrastichinae. No species of the Cirrospilini examined had such whorled setae.

26. Placoid sensilla on funicle: *scattered, 0; arranged in rows, 1.*

Schauff (1991) used the placoid sensilla in a phylogenetic study of the Entedoninae, and regarded this character as uninformative. In contrast, Barlin and Vinson (1981) showed that the states of antennal sensilla are informative in Chalcidoidea. Those sensilla are scattered (Fig. 12) or arranged in rows (Figs 4,5,8,11).

27. Ventral plaque of male antennal scape: *absent, 0; present, 1.*

This character was adopted by Graham (1987), who regarded the presence of the putative sensory plaque is apomorphic in the Tetrastichinae. In the present study, the character was found only in the two species of Tetrastichinae examined.

## Mesosoma

28. Pronotum: *transverse, truncate anteriorly, 0; bell shaped, 1; elongate, 2.*

This character is based on Bouček (1988). In Cirrospilini, a few *Cirrospilus* species have such a transverse pronotum that is very short and truncate anteriorly. In other *Cirrospilus* species and other genera of Cirrospilini, the pronotum is produced anteriorly to be bell shaped (Figs 21,23,26–29,32) or further elongated (Figs 20,22,25).

29. Elongate grooves on lateral side of pronotum: *absent, 0; present, 1.*

These grooves, which are generally situated in paired longitudinal black stripes, were found in most species of *Zagrammosoma*, some *Cirrospilus* species and *Diglyphus bulbosus*.

30. Mesoscutal notaulus: *complete to posterior margin of mesoscutum, 0; ending at axilla, 1; incomplete, 2.*

Several authors have used this character to differentiate subfamilies, tribes and genera within the Eulophidae (Graham 1987; Bouček 1988; Schauff 1991; Schauff *et al.* 1997). The notauli occur in most species of Cirrospilini: they are either complete to the hind margin of the mesoscutum (Figs 21,22,24,28,30,31), or complete but curved to meet the axilla (Figs 20,25,32). The notauli are sometimes reduced, being present only anteriorly (Figs 27,29), or completely absent in a few species.

31. Notaulus shape: *straight or slightly curved, 0; sinuate, converging medially, 1.*

The majority of genera have straight notauli (Figs 20,21,23–25,28,30,31), although they may be curved to meet the axilla as in *Pseudiglyphus* (Fig. 26). Notauli that are complete, but sinuate and strongly converging to each other, are found only in *Gallowayia* (Fig. 22).

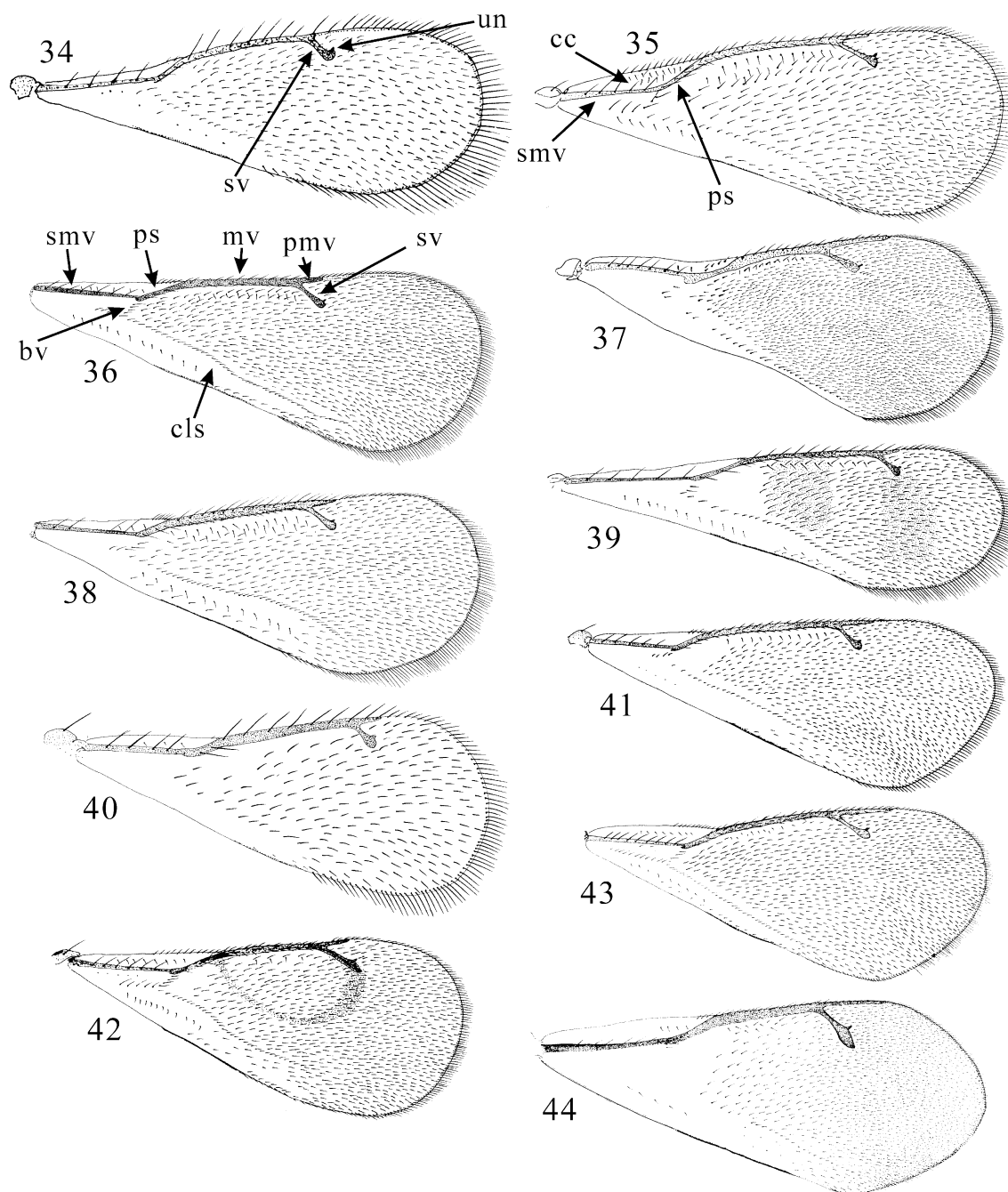
32. Large setae on mesoscutum: *one pair, 0; two pairs, 1; three or more pairs, 2.*

33. Small, scattered setae on mesoscutum: *present, 0; absent, 1.*

Two different types of setae are observed on the mesoscutum. One type is the large setae, which are rather sparse; the presence or absence of this kind of setae has been referred to by Bouček (1988), Schauff (1991) and LaSalle and Schauff (1994). The other type is the small but dense setae, which may or may not cover the mesoscutum regardless of the presence or absence of the large setae.

34. Scutellar submedian lines: *absent, 0; indicated by sculpture change, 1; distinct, straight medially, 2; distinct, curved posteriorly and meeting medially, 3.*

This character was taken from Graham (1987), Bouček (1988), Schauff (1991) and Schauff *et al.* (1997). Graham (1987) considered the presence of the scutellar



Figures 34–44 Right forewings of Cirrospilini. 34 *Melittobiopsis ereunetiphila*; 35 *Ascotolinx reticoxa*; 36 *Meruana liryomyzae*; 37 *Dichatomus acerinus*; 38 *Semielacher silvicola*; 39 *Gallowayia picta*; 40 *Oxycantha darwini*; 41 *Cirrospilus tau*; 42 *Cirrospilus afer*; 43 *Cirrospilus viticola*; and 44 *Aulogygmus trilineata*. bv, basal vein setae; cc, costal cell; cls, cubital line of setae; mv, marginal vein; pmv, postmarginal vein; ps, parastigma; smv, submarginal vein; sv, stigma vein; un, uncus.



submedian lines as plesiomorphic in the Tetrastichinae. In the Cirrospilini, the lines are absent (Figs 20,28,32), indicated by sculpture change (Fig. 31), distinct in straight lines (Figs 22,25,26,29,30) or curved inward posteriorly (Fig. 27).

35. Scutellar sublateral lines: *absent, 0; present, 1.*

Several authors have used this character to define Tetrastichinae (Graham 1987; Bouček 1988; Schauff 1991; Schauff *et al.* 1997). These lines were not found in any of the cirrospilinae species examined.

36. Propodeal median carina: *complete, 0; anteriorly only, 1; absent, 2.*

Bouček (1988) used this character in his key to the genera of the Eulophidae, specifically referring to the presence of two submedian carinae in *Ceratoneuronella* Girault, 1913 (Tetrastichinae) and some entedonine genera. In the Cirrospilini and outgroup taxa here examined, the propodeum has a single median carina, which is in most species complete (Figs 20,22,23,25–32), but obliterated posteriorly in two *Diglyphus* species, and entirely lacking in some genera such as *Diaulinopsis* (Fig. 24) and some species of *Cirrospilus* (Fig. 21).

37. Plica on propodeum: *absent, 0; posteriorly only, 1; complete, 2.*

This character was taken from Graham (1987), Bouček (1988) and Schauff (1991). A complete plica occurs only in a few genera such as *Ascotolinx* (Fig. 27) and *Oxycantha* (Fig. 32). Plicae present only posteriorly are found in *Aulogymnus aceris*, *Meruana* (Fig. 29) and *Semielacher*.

38. Paired basal grooves on propodeum: *absent, 0; present, 1.*

In *Gattonia*, *Gallowayia* (Fig. 22) and *Naumanniola* (Fig. 25), the propodeum has paired, short, longitudinal grooves in the anterior part: such grooves are absent in other cirrospilinae genera and outgroups.

39. Pilosity on propodeal callus: *a few setae, arranged in a single row, 0; more than six setae, arranged in a row, 1; setae arranged in two or more rows, 2; setae dense, not arranged in rows, 3.*

The condition that the callus is extremely pilose, with the pilosity not arranged in rows, is one of the characters to diagnose *Gattonia* (Bouček 1988). When setae are arranged in row(s), the propodeum has a few setae arranged in a single row on each lateral side (Figs 21,32),

more than six setae in a single row (Figs 22,27) or setae arranged in two or more rows (Figs 28,29).

40. Propleura: *separated posteriorly, 0; connected along entire medial margins, 1.*

The propleura meet along their entire medial margins in the Eulophini and Elasmmini (but are separated in *Elasmus steffani* examined in the present study), and are posteriorly separated in the Cirrospilini (Gauthier *et al.* 2000) (Fig. 33).

## Wings

41. Postmarginal vein: *0.5–1.5× stigmal vein, 0; elongate, more than 2× stigmal vein, 1; very short or absent, 2.*

This character has been used by several authors to differentiate genera within the Eulophidae (Graham 1987; Bouček 1988; Schauff 1991). However, conditions vary more or less continuously among cirrospilinae genera: the postmarginal vein is as long as, somewhat longer than or shorter than the stigmal vein (Figs 21,23,25,26,35–44), while the former is absent in *Melittobiopsis* (Fig. 34) or is very elongated (more than twice as long as the stigmal vein) in *Diaulinopsis* (Fig. 24).

42. Number of setae on submarginal vein: *three or more, 0; two, 1; one, 2.*

Graham (1987) concluded that reduction in the number of setae on the submarginal vein was a derived condition, which has been followed by Bouček (1988), Schauff (1991) and Schauff *et al.* (1997). In the cirrospilinae genera, the submarginal vein always has three or more setae.

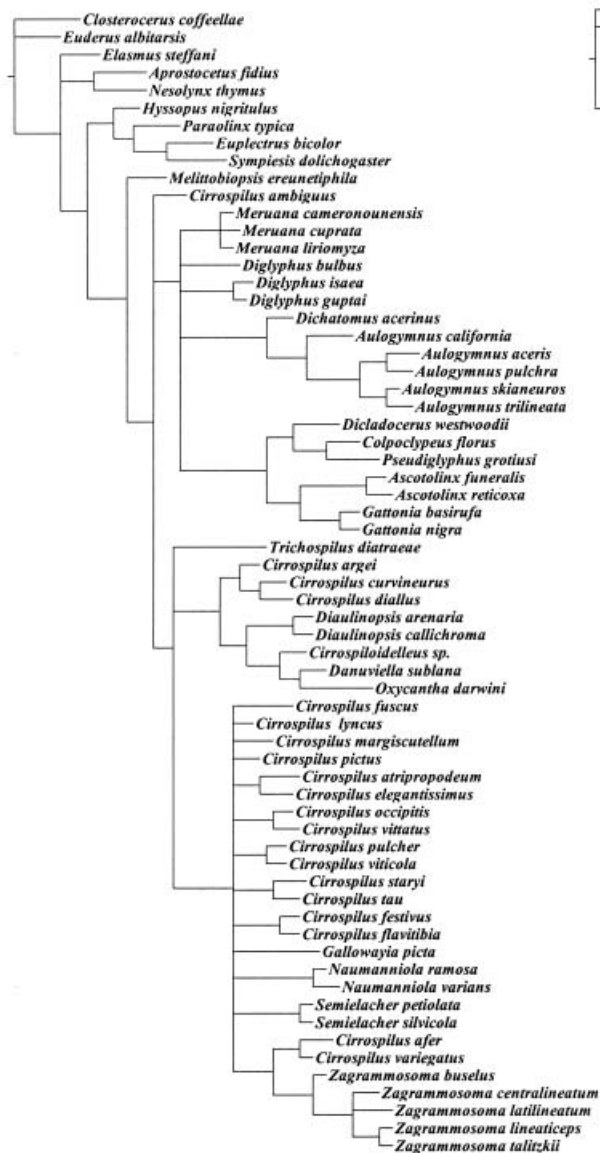
43. Submarginal vein: *smoothly joining parastigma, 0; tapering apically, continuous to parastigma, 1; tapering apically, not continuous to parastigma, 2.*

The submarginal vein joining the parastigma smoothly (Fig. 35) has been used for more than 40 years to separate the Eulophinae from the Tetrastichinae, Entedoninae and Euderinae (Graham 1959; Graham 1987; Bouček 1988; Schauff 1991). In the Cirrospilini, however, the submarginal vein often tapers apically before joining the parastigma (Figs 21,23,24–26,34,36–42,44) or is very narrowly separated from the latter (Fig. 43).

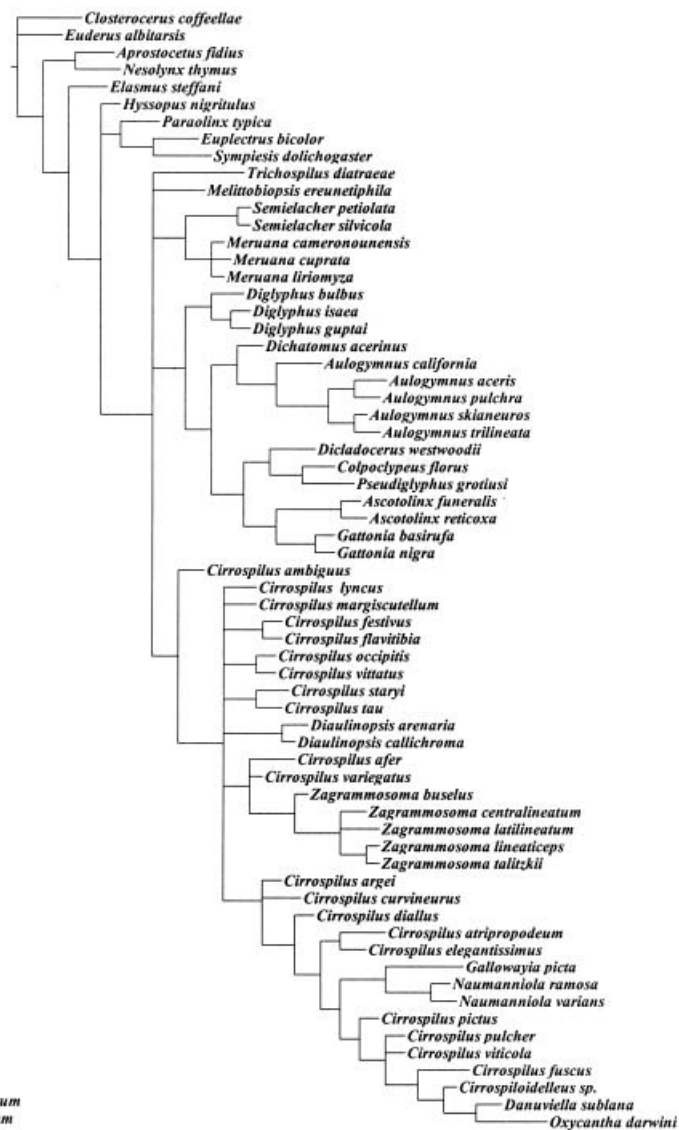
44. Marginal setae on costal cell: *absent, 0; present, 1.*

The marginal setae are arranged in a row running from the junction between the anterior margin of the costal

45



46



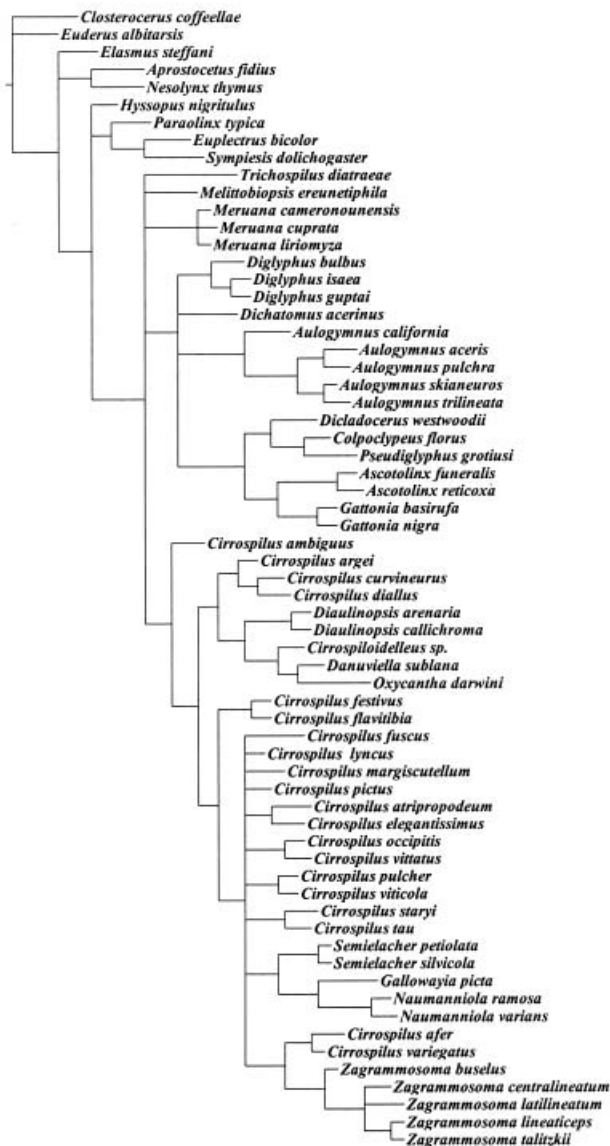
Figures 45,46 Strict consensus trees of islands of most parsimonious trees of length 367 with eight (45) and 20 (46) component trees.

cell and the end of the parastigma toward the base of the forewing. Most cirrospilines have the setae in varying numbers (Figs 21,23–26,34–38,41–44), but the setae are absent in some outgroups and in *Gallowayia* (Fig. 39), *Gattonia* and *Oxycantha* (Fig. 40).

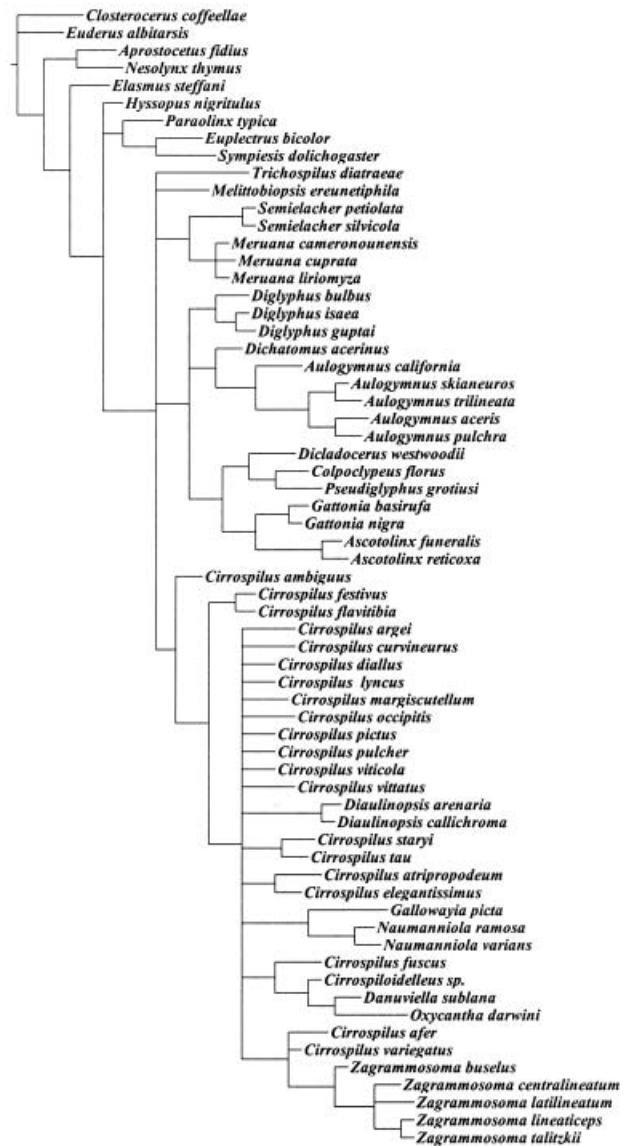
45. Admarginal setae: *one row, 0; two or more rows, 1.*

This character is taken from Graham (1959) and Miller (1970). In most cirrospilines and outgroups, setae posterior to the marginal vein on the underside of the

47



48



Figures 47,48 Strict consensus trees of islands of most parsimonious trees of length 367 with 36 (47) and 40 (48) component trees.

forewing are arranged in two or three rows. Setae arranged in a single row are found in *Ascotolinx*, *Zagrammosoma* and a few *Cirrospilus* species, and in two outgroup species.

46. Basal vein setae: *absent*, 0; *present*, 1.

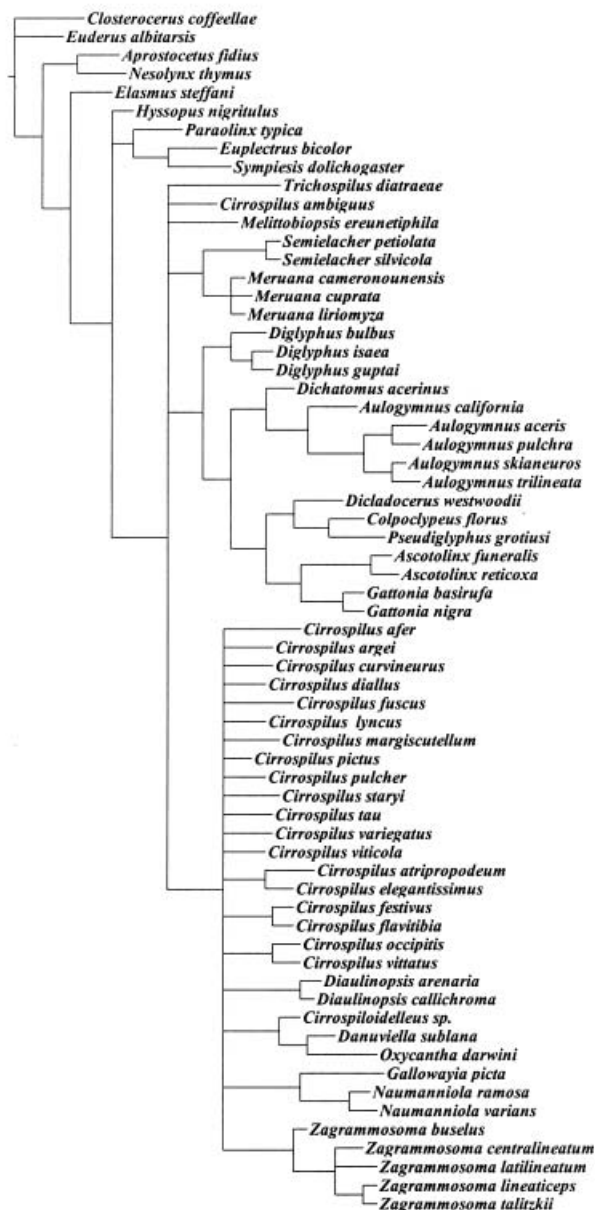
This character is based on Graham (1959). In most cirrospilines, setae are arranged in a row on the basal vein (Figs 21–25,35–43); the setae lacking in some spe-

cies of *Aulogymnus*, *Melittobiopsis*, *Pseudiglyphus* and some species of *Zagrammosoma* (Figs 26,34,44).

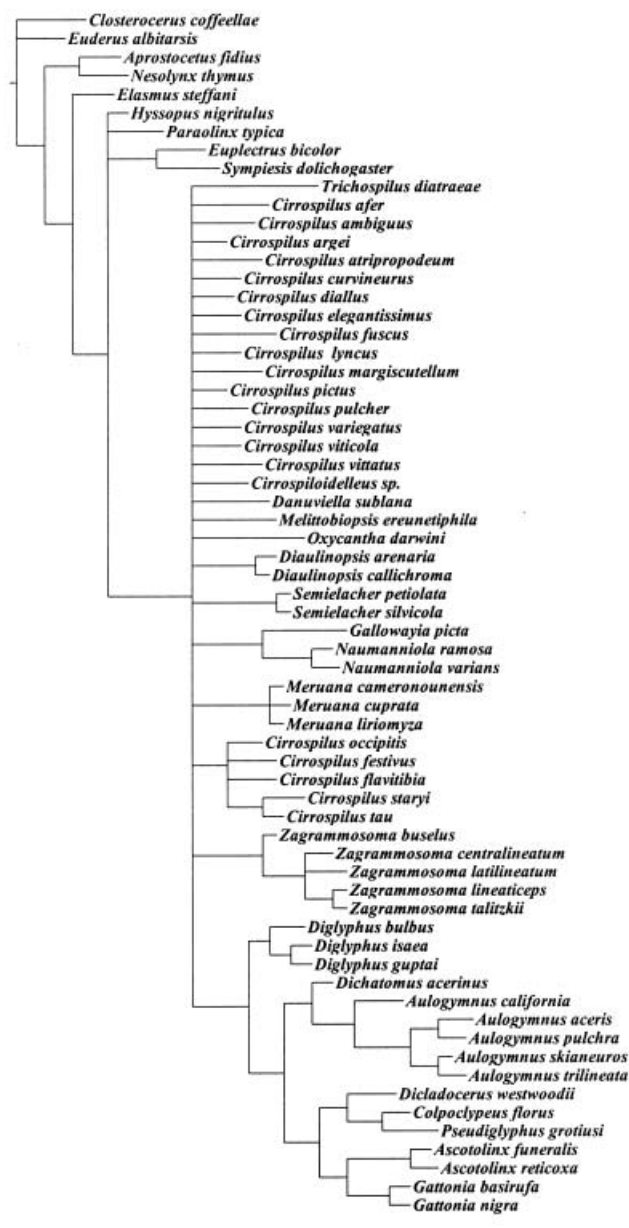
47. Cubital line of setae: *complete at least to basal vein (speculum closed)*, 0; *incomplete, not reaching basal vein (speculum open)*, 1.

This character was referred to by Graham (1959) and Miller (1970). The most primitive state in the

49



50



Figures 49,50 Strict consensus trees of islands of most parsimonious trees of length 367 with 228 (49) and 696 (50) component trees.

Eulophidae may be the line of setae being complete and reaching near the base of the forewing. However, the states in the Cirrospilini are variable, and then we recognized two distinct states in the tribe: the cubital line of the setae is complete at least to the basal vein (in other words, the speculum is closed) (Figs 21,23–25,34–36,38,39,42,43); and the cubital line of the setae ends

well before the basal vein (speculum open) (Figs 26,37,40,41,44).

48. Cubital vein: *nearly straight, 0; strongly curved anteriorly near basal vein, 1.*

This character is taken from Graham (1959). In most cases, the cubital vein, when it reaches the basal vein, is



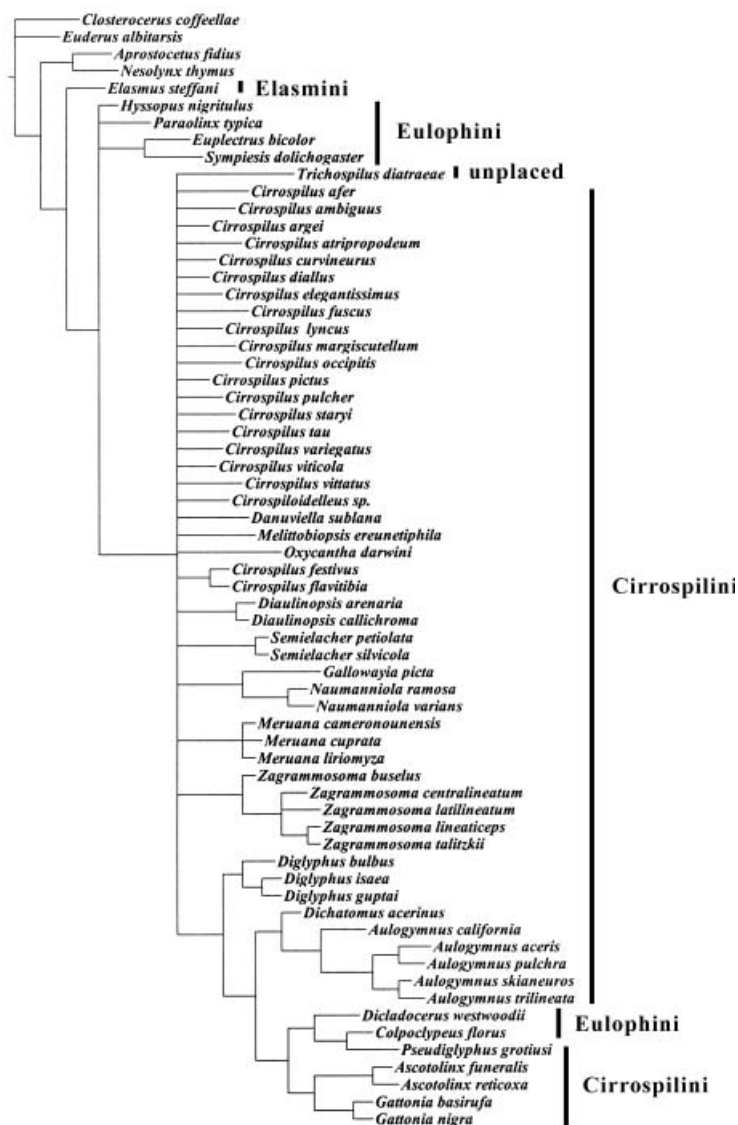


Figure 51 Strict consensus tree of all most parsimonious trees, with the delimitations of the eulophine tribes in the sense of Gauthier *et al.* (2000) indicated on the left side.

straight in its basal part, while in *Diglyphus* and a few species of *Cirrospilus*, the cubital vein is strongly curved anteriorly near the basal vein.

49. Uncus position: *at apex of stigma*, 0; *shifted basally*, 1.

In most species of the Cirrospilini, the uncus is located at or near the apex of the stigma (Figs 21,23–26,34–41,43), while it is distinctly shifted basally in *Aulogymnus* (Fig. 44) and some species of *Zagrammosoma* and *Cirrospilus* (Fig. 42).

50. Forewing disc coloration: *without markings, hyaline*, 0; *with distinct darkened pattern*, 1.

Compared with the body color, the presence of a darkened pattern of the forewing (Figs 39,42) is stable and could be informative in a phylogenetic study.

## Legs

51. Hind tibial spur: *shorter than first tarsomere*, 0; *longer than first tarsomere*, 1.

The hind tibial spur longer than the first tarsomere is characteristic of the *Euplectrus* (namely of the

Eulophini). A similar condition is, however, found in *Ascotolinx*.

52. Hind basitarsus: *shorter than second tarsomere, 0; longer than second tarsomere, 1.*

In most cirrospiline genera, the hind basitarsus is proportionally short; that is, it is distinctly shorter than the second tarsomere. The hind basitarsus is elongated in *Aulogygnus*, *Dichatomus*, *Diglyphus*, *Gattonia* and most species of *Zagrammosoma*. Most *Cirrospilus* species have short hind basitarsi, but that of *Cirrospilus festivus* is elongated.

53. Tibial spur formula: *one + one + two, 0; one + one + one, 1.*

Hind tibia with two spurs are found in most outgroups included in the present study. Conditions are stable within a single genus, but vary in *Aulogygnus*.

### Metasoma

54. Petiole: *very small, nearly absent, 0; long, sculptured, without dorsal ridges, 1; long, sculptured, with dorsal ridges, 2.*

In most Eulophinae, the petiole is very short, strongly transverse and almost concealed in dorsal view (Figs 20,21,23–26). In the Cirrospilini, the petiole is conspicuous and sculptured in *Gallowayia*, *Meruana*, *Semielacher*, and is usually armed with dorsal ridges (Figs 22,29). The condition varies in *Aulogygnus* and *Cirrospilus*.

55. Female cercal setae: *equal in length, 0; one seta thicker, longer and darker than others, 1.*

Graham (1987) discussed this character. Cercal setae all in equal length (Fig. 29) is the state in most species examined. The condition in which one seta is longer, thicker and darker than the others is found in *Aulogygnus* and some *Cirrospilus* species, and in some outgroups.

56. Spiracle on seventh tergum: *invisible, 0; visible, 1.*

This character is taken from Graham (1987). In all cirrospiline genera, however, the spiracle is visible, and thus the character is not informative for an analysis of the relationships between genera within the Cirrospilini.

## RESULTS OF CLADISTIC ANALYSIS

The initial tree search strategy yielded 92 trees of length 368 steps (retention index = 0.60; consistency

index = 0.22). Subsequent swapping on each yielded six separate islands of most parsimonious trees of length 367 with eight, 20, 36, 40, 228 and 696 component trees. The strict consensus tree of each of these islands is shown in Figures 45, 46, 47, 48, 49 and 50, respectively, and the strict consensus of all of them is shown in Figure 51. Stability was reached after one round of successive approximations weighting using all 1028 most parsimonious trees as input trees, and the maximum value of the retention index as the reweighting function, with four optimal trees. These four trees were a subset of the island of 40 trees. When the minimum value of the retention index was used, five trees were obtained at stability after three iterations, and these were a subset of the island of 36 trees. As using the minimum retention index will only give high weight to characters that performed well on all of the input trees, successive approximations trees obtained using this may be considered as the most conservative.

The strict consensus tree of all most parsimonious trees (Fig. 50) shows that (i) *Dicladocerus* and *Colpoclypeus*, which Gauthier *et al.* (2000) placed in the Eulophini, were placed in the Cirrospilini to form a clade with *Pseudiglyphus*, which is the sister group of (*Gattonia* + *Ascotolinx*); (ii) monophyly of Cirrospilini, including two eulophine genera (*Colpoclypeus* and *Dicladocerus*) in the sense of Gauthier *et al.* (2000) and *Trichospilus*, is suggested; (iii) except *Cirrospilus*, all cirrospiline genera for which more than one species was examined appear to be monophyletic; and (iv) a clade (*Diglyphus* + ((*Dichatomus* + *Aulogygnus*) + ((*Dicladocerus* + (*Colpoclypeus* + *Pseudiglyphus*)) + (*Gattonia* + *Ascotolinx*)))) is recognized.

*Cirrospilus afer* + *C. variegatus* + *Zagrammosoma* is supported by the vaulted vertex (no. 7) in the first four islands (Figs 45–48).

## DISCUSSION

Although most characters we examined were homoplastic, requiring several steps on the most parsimonious trees, the relatively high retention index (0.60) indicates that they are not random, but still carry a reasonable amount of phylogenetic signal. Monophyly of the Cirrospilini was supported in the present study by several characters, which included three of the six characters used by Gauthier *et al.* (2000) to define it. These included the antenna with two or three funicle segments in both sexes (no.s 17 and 18 in the present study), but an antenna with three funicle segments was also found

in *Di cladocerus* (Eulophini; but placed within the Cirrospilini in the present study), as well as in female *Nesolynx thymus* (and almost all other female Tetrastichinae) and female *Elasmus steffani* (Elasmini). *Colpoclypeus florus*, with two funicle segments, was placed in the Eulophini by Gauthier *et al.* (2000), but was placed within the Cirrospilini in the consensus tree in the present work. The presence of transverse grooves on the frons (no. 8) also supported monophyly of the Cirrospilini. However, the grooves are absent not only in *Aulogygnus* and *Dichatomus* but also in several other genera, and the condition of this character often varies within a given genus.

The condition of the propleura (no. 40) and the setae on the submarginal vein (no. 42) appear plesiomorphic and were not included in the characters supporting monophyly of the Cirrospilini: the same conditions are also found in members of most of the outgroup taxa. The condition of the postmarginal vein (no. 41) in the outgroups is also found in some members of the Cirrospilini, while *Melittobiopsis* lacks this vein.

The following seven characters also supported monophyly of the Cirrospilini in our analyses: fronto-clypeal suture present laterally (no. 3), scrobal groove absent (no. 9), maxillary palp with a single segment (no. 13), male antenna with two anelli (no. 16), two pairs of large setae on the mesoscutum (no. 32), hind basitarsus short (no. 52) and the hind tibia with one spur (no. 53). However, all of these show considerable homoplasy. In conclusion, the present study shows that the Cirrospilini in the sense of Gauthier *et al.* (2000) is essentially monophyletic except that a few changes in the included genera are required. However, all characters supporting monophyly of the Cirrospilini are relatively homoplastic, and therefore we have difficulties, at least at the moment, in defining the tribe with diagnostic morphological characters.

All of the cirrospilinae genera for which we examined more than one species, except for *Cirrospilus*, seemed to be monophyletic; but again, characters supporting their monophyly are not robust, showing considerable homoplasies, and relationships between the genera are poorly resolved. Monophyly of *Zagrammosoma* was supported by a distinctive character, the vaulted vertex (no. 7), although the same condition was also found in two *Cirrospilus* species. *Cirrospilus*, the largest genus in the tribe, can hardly be diagnosed by morphological characters, as pointed out earlier by Bouček (1988), and here it was shown to be paraphyletic with respect to a number of other taxa. Species relationships within this genus were also poorly resolved. Monophyly of *Cir-*

*rospilus* was not supported to any extent in the molecular analysis of Gauthier *et al.* (2000), either.

The results presented here should be considered as preliminary. There are still many unresolved differences between the relationships suggested by the present study and those presented in Gauthier *et al.* (2000) which was based mainly on molecular data. These differences strongly suggest that a phylogenetic analysis combining more comprehensive morphological and molecular data for a wider range of taxa in the Eulophinae will be necessary to come to a firmer conclusion. Only such a study can provide a more robust phylogenetic framework that serves as a reference system to test hypotheses of the evolution of the diverse life histories seen in the Eulophinae.

## ACKNOWLEDGMENTS

This study was supported by the grant from the GEF-Indonesian Biodiversity and Collection Project (no. TF028657) to R. U. We thank J. Noyes and S. Lewis of the Natural History Museum (London) for the arrangement of the access and the loan of specimens, and J. Huber of the Canadian National Collection of Insects (Ottawa), J. Cardale of the Australian National Insect Collection (Canberra), G. Nishida of the Bernice P. Bishop Museum (Honolulu) and Pudji Aswari of the Museum Zoologicum Bogoriense (Bogor) for the loan of specimens.

## REFERENCES

- Ashmead WH (1904) Classification of the chalcid flies of the superfamily Chalcidoidea, with descriptions of new species in the Carnegie Museum, collected in South America by Herbert H. Smith. *Memoirs of the Carnegie Museum* 1, 225–551.
- Barlin MR, Vinson SB (1981) Multiporous plate sensilla in antennae of the Chalcidoidea (Hymenoptera). *International Journal of Insect Morphology and Embryology* 10, 29–42.
- Basibuyuk HH, Rasnitsyn AP, Fitton MG, Quicke DLJ (2002) The limits of the family Evaniidae (Insecta: Hymenoptera) and a new genus from Lebanese amber. *Insect Systematics and Evolution* 33, 23–34.
- Bouček Z (1958) A study of central European Eulophidae, I: Eulophinae (Hymenoptera). *Acta Entomologica Musei Nationalis Pragae* 33, 117–170.
- Bouček Z (1988) *Australasian Chalcidoidea (Hymenoptera). A Biosystematic Revision of Genera of Fourteen Families, with a Reclassification of Species*. CAB International, Wallingford, UK.

- Bouček Z, Askew RR (1968) *Index of Palearctic Eulophidae (Excl. Tetrastichinae). Index of Entomophagous Insects* 3. Le François, Paris.
- Burks BD (1979) Family Eulophidae. In: Krombein KV, Hurd PD Jr, Smith DR, Burks BD (eds) *Catalog of Hymenoptera in America North of Mexico*, Vol. I. *Symphyta and Apocrita (Parasitica)*, pp 967–1022. Smithsonian Institution Press, Washington, DC.
- Carpenter JM (1994) Successive weighting, reliability and evidence. *Cladistics* 10, 215–220.
- Coote LD (1997) Elasmidae. In: Gibson GAP, Huber JT, Woolley JB (eds) *Annotated Keys to the Genera of Nearctic Chalcidoidea (Hymenoptera)*, pp 165–169. NRC Research Press, Ottawa.
- Domenichini G (1953) Studio sulla morfologia dell'addome degli Hymenoptera Chalcidoidea. *Bollettino Di Zoologia Agraria E Bachicoltura*, Milano 19, 183–298.
- Farris JS (1989) The retention index and the rescaled consistency index. *Cladistics* 5, 417–419.
- Gauld ID (1985) The phylogeny, classification and evolution of parasitic wasps of the subfamily Ophioninae (Ichneumonidae). *Bulletin of the British Museum (Natural History), Entomology Series* 51, 61–185.
- Gauthier N, LaSalle J, Quicke DLJ, Godfray HCJ (2000) Phylogeny of the Eulophidae (Hymenoptera, Chalcidoidea), with a reclassification of the Eulophinae and the recognition that the elasmidae are derived eulophids. *Systematic Entomology* 25, 521–539.
- Gibson GAP (1989) Phylogeny and classification of Eupelmidae, with a revision of the world genera of Calosotinae and Metapelmatinae (Hymenoptera: Chalcidoidea). *Memoirs of the Entomological Society of Canada* 149, 1–121.
- Gibson GAP (1997) Eupelmidae. In: Gibson GAP, Huber JT, Woolley JB (eds) *Annotated Keys to the Genera of Nearctic Chalcidoidea (Hymenoptera)*, pp 430–476. NRC Research Press, Ottawa.
- Gibson GAP (1999) Sister group relationships of the Platygastroidea and Chalcidoidea (Hymenoptera) – an alternate hypothesis to Rasnitsyn (1988). *Zoologica Scripta* 28, 125–138.
- Goloboff PA (1991) Random data, homoplasy and information. *Cladistics* 7, 395–406.
- Gordh G (1978) Taxonomic notes on *Zagrammosoma*, a key to the Nearctic species and descriptions of new species from California (Hymenoptera: Eulophidae). *Proceedings of the Entomological Society of Washington* 80, 344–359.
- Graham MWR de V (1959) Keys to the British genera and species of Elachertinae, Eulophinae, Entedontinae and Euderinae (Hym., Chalcidoidea). *Transactions of the Society for British Entomology* 13, 169–204.
- Graham MWR de V (1987) A reclassification of the European Tetrastichinae (Hymenoptera: Eulophidae), with a revision of certain genera. *Bulletin of the British Museum (Natural History) (Entomology Series)* 55, 1–392.
- Heraty JM (1994) Classification and evolution of the Oaseminae in the Old World, including revisions of two closely related genera of Eucharitinae (Hymenoptera: Eucharitidae). *Life Sciences Contributions, Royal Ontario Museum* 157, 1–174.
- LaSalle J (1989) Notes on the genus *Zagrammosoma* (Hymenoptera: Eulophidae) with description of a new species. *Proceedings of the Entomological Society of Washington* 91, 230–236.
- LaSalle J, Schauff ME (1992) Preliminary studies on neotropical Eulophidae (Hymenoptera: Chalcidoidea): Ashmead, Cameron, Howard and Walker species. *Contributions of the American Entomological Institute* 27, 1–47.
- LaSalle J, Schauff ME (1994) Systematics of the tribe Euderomphalini (Hymenoptera: Eulophidae): parasitoids of whiteflies (Homoptera: Aleyrodidae). *Systematic Entomology* 19, 235–258.
- Maddison DR (1991) The discovery and importance of multiple islands of most-parsimonious trees. *Systematic Zoology* 43, 315–328.
- Miller CD (1970) The Nearctic species of *Pnigalio* and *Sympiesis* (Hym. Eulophidae). *Memoirs of the Entomological Society of Canada* 68, 1–121.
- Noyes JS (2002) *Interactive Catalogue of World Chalcidoidea* (2001, 2nd edn). (CD-ROM). Taxapad, Vancouver and The Natural History Museum, London.
- Peck O, Bouček Z, Hoffer A (1964) Keys to the Chalcidoidea of Czechoslovakia (Insecta: Hymenoptera). *Memoirs of the Entomological Society of Canada* 34, 1–120.
- Quicke DLJ, Basibuyuk HH, Fitton MG, Rasnitsyn AP (1999) Morphological, palaeontological and molecular aspects of ichneumonoid phylogeny (Hymenoptera, Insecta). *Zoologica Scripta* 28, 175–202.
- Quicke DLJ, Taylor J, Purvis A (2001) Changing the landscape: a new strategy for estimating large phylogenies. *Systematic Biology* 50, 60–66.
- Riek EF (1967) Australian Hymenoptera Chalcidoidea family Eulophidae, subfamily Elasmidae. *Australian Journal of Zoology* 15, 145–199.
- Riek EF (1970) Hymenoptera (wasps, bees, ants). In: Division of Entomology, Commonwealth Scientific and Industrial Research Organisation (eds) *The Insects of Australia*, pp 867–959. Melbourne University Press, Carlton.
- Schauff ME (1991) The Holarctic genera of Entedoninae (Hymenoptera: Eulophidae). *Contributions of the American Entomological Institute* 26, 1–109.
- Schauff ME, LaSalle J (1993) Nomenclatural notes on genera of North American Eulophidae (Hymenoptera: Chalcidoidea). *Proceedings of the Entomological Society of Washington* 95, 488–503.
- Schauff ME, LaSalle J, Coote L (1997) Eulophidae. In: Gibson GAP, Huber JT, Woolley JB (eds) *Annotated Keys to the Genera of Nearctic Chalcidoidea (Hymenoptera)*, pp 325–429. NRC Research Press, Ottawa.



- Storozheva NA (1991) Morphology and evolution transformation on antennae of Eulophinae (Hymenoptera, Eulophidae). *Entomologicheskoe Obozrenie* **70**, 168–182, 262. (In Russian.) English translation appears in *Entomological Review, Washington* **70**, 16–30.
- Swofford DL (1999) *paup\**, *Phylogenetic Analysis Using Parsimony, version 4.0b4a*. Laboratory of Molecular Systematics, Smithsonian Institution, Washington, DC.
- Yoshimoto CM (1984) *The Families and Subfamilies of Canadian Chalcidoid Wasps. The Insects and Arachnid of Canada. Part 12*. Agriculture Canada Publication 1760. Agriculture Canada, Ottawa.
- Zhu C, LaSalle J, Huang DW (2000) A review of the Chinese *Diglyphus* Walker (Hymenoptera: Eulophidae). *Oriental Insects* **34**, 263–288.