

MONOPHYLY AND RELATIONSHIP OF THE GENUS *COELOPISTHIA* FOERSTER (CHALCIDOIDEA: PTEROMALIDAE)



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Introduction

The genus *Coelopisthia* Foerster, 1856, belongs to the subfamily Pteromalinae and is known from Europe (Askew 1980) through Middle Asia (Dzhanokmen 1978) to China (Yang 1996), and North America (Peck 1963). Twelve species are considered as valid by Noyes (1998 sub *Kranophorus* Graham) but examination of a large amount material from the Holarctic region revealed that there may be at least 15 species. Host records are rather scarce and include various Lepidoptera (Arctiidae, Geometridae, Noctuidae, Tortricidae) and Coleoptera (Curculionidae, Scolytidae) (Peck 1963; Graham 1969; Dzhanokmen 1978; Askew 1980; Yang 1996). A few species possibly attack their hosts as secondary parasitoids via other Hymenoptera (Ichneumonidae) (cf. Huber *et al.* 1996).

Species of *Coelopisthia* have been readily recognised in the past by a combination of features (Graham 1956, 1969; Bouček & Rasplus 1991; Bouček & Heydon 1997) which include a protruding face at the level of the toruli, a large head with conspicuous temples, enlarged anelli with at least the second one subquadrate, reduced wing pilosity, and an almost circular gaster. Although these characters may well be diagnostic for the genus they have proved to be critical with respect to phylogenetic considerations. There are for instance many other genera within the pteromalines with which individual features are shared, e. g. enlarged anelli (*Rhopalicus* Foerster), a protruding face (*Conomorium* Masi, *Diglochis* Foerster), a roundish gaster (*Cyclogastrella* Bukowskii, *Schizonotus* Rutzeburg). Moreover, some species, like *Coelopisthia pachycera* Masi, deviate considerably from the above pattern in that the anelli are quite strongly transverse and the face is much less protruding. In the context of a revision of Holarctic species of *Coelopisthia* these findings thus led to open questions about monophyly and relationships. In order to determine the natural limits of the genus a cladistic analysis was performed of which the results are presented here. The study concentrated on identifying synapomorphies of *Coelopisthia* whereas the cladistic structure among its species was of secondary interest. It was also not intended to solve problems of monophyly and relationship of any other genera mentioned below, as these should be addressed in a more comprehensive study of the entire subfamily. N.B. The authors for genera and species are given in Appendix 1.

Materials and Methods

The material examined in this study is deposited in the institutions listed in the Acknowledgements. Specimens were examined either under a stereo-microscope with a magnification up to 100× or a scanning electron microscope (SEM). Individual parts were mounted on slides according to the method described by Noyes (1982) but with the use of Euparal instead of Canada balsam. Morphology and terminology follow Gibson (1997).

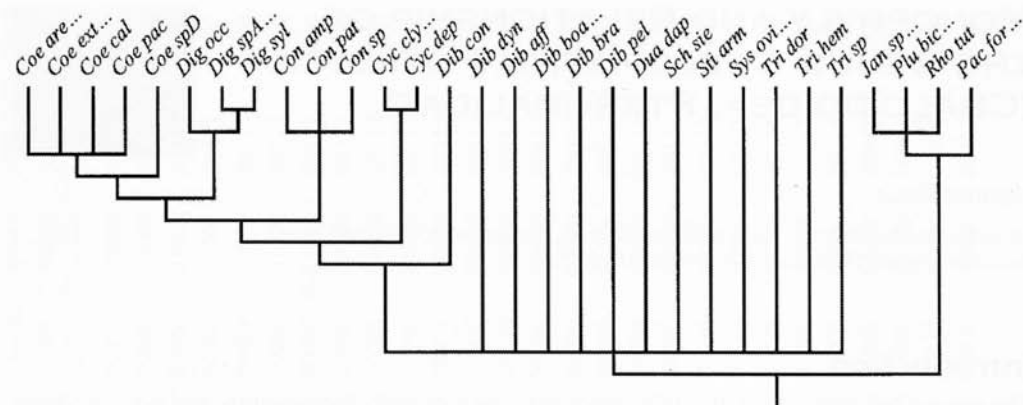


Figure 1 Strict consensus tree of 203 most parsimonious trees of a length of 67 steps (CI 0.67, RI 0.84). Taxon names abbreviated using the first three letters of genus and species name (cf. Appendix 3).

For the cladistic analysis 17 discrete morphological characters were scored for females of 44 species in 16 genera (see Appendices 1–3). These taxa could be united into 30 groups by the «search & merge» routine in MacClade (Maddison & Maddison 1992) before the analysis. Multi-state characters were not polarised and treated as unordered, and multistate taxa as polymorphic. A parsimony analysis was performed using PAUP 3.1.1 (Swofford 1993). Because of the large size of the data matrix the heuristic search method was employed using random addition sequences with 50 replicates and TBR branch swapping. The search was repeated five times and always found the same set of most parsimonious trees. Consensus trees were computed with PAUP but the final trees were edited in MacClade.

Phylogenetic Analysis

The selection of taxa for the ingroup and outgroup was difficult, since the phylogenetic relationships within and among Pteromalinae have not yet been investigated. Graham's (1969) monumental revision of the species of north-western Europe is the last comprehensive treatment of the subfamily at the species level but dates from a pre-cladistic era. Although the work offers plenty of information, and the genera are apparently arranged according to some supposed relationship, no statements can be found with regard to their particular classification. The *Dibrachys*-group of Wallace (1973) simply lumps several genera of Pteromalinae in a more or less artificial manner. Bouček's (1988) account on the Australasian fauna which I will follow here is more informative with respect to some lower levels (tribes) but covers few of the potentially useful genera. In an attempt to find a sound starting point for the analysis, exemplars of an array of genera within the tribe Pteromalini were therefore chosen for the ingroup (Appendices 1, 3). These taxa are characterised by having the postmarginal vein only about as long as the stigmal vein. Considering the rest of Pteromalinae and the probably closely related Miscogastrinae (Bouček 1988; Bouček & Rasplus 1991) as outgroups, a reduced postmarginal vein may appear as a possible synapomorphy of those genera. There are, however, some exceptions in pteromalines: species of *Meximalus* Bouček, *Ptinocida* Bouček, *Hemadas* Bouček (cf. Bouček & Heydon 1997), and certain *Mesopolobus* Westwood (e.g. *M. adrianae* Gijswijt) also have a shortened postmarginal vein but are likely to be only distantly related and were not included in the analysis.

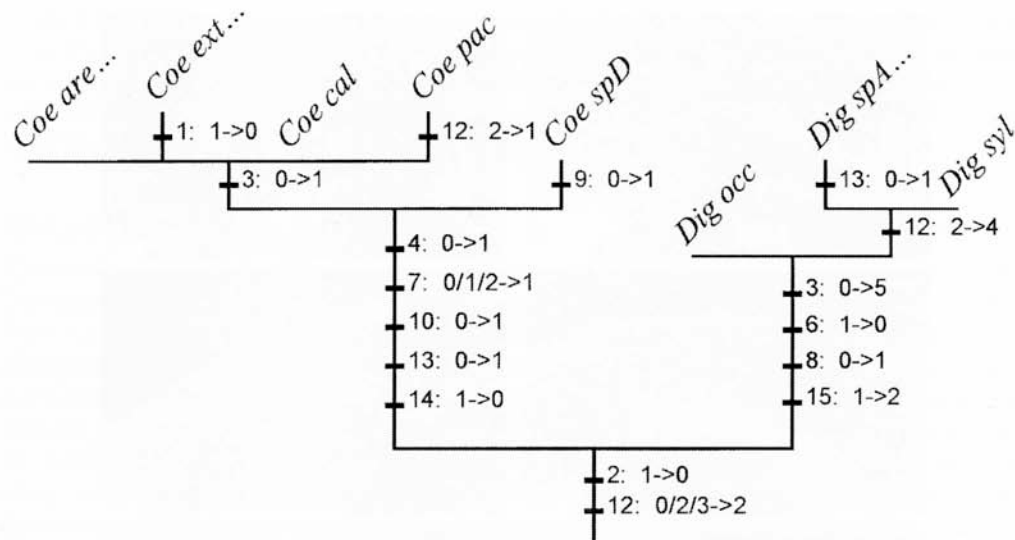
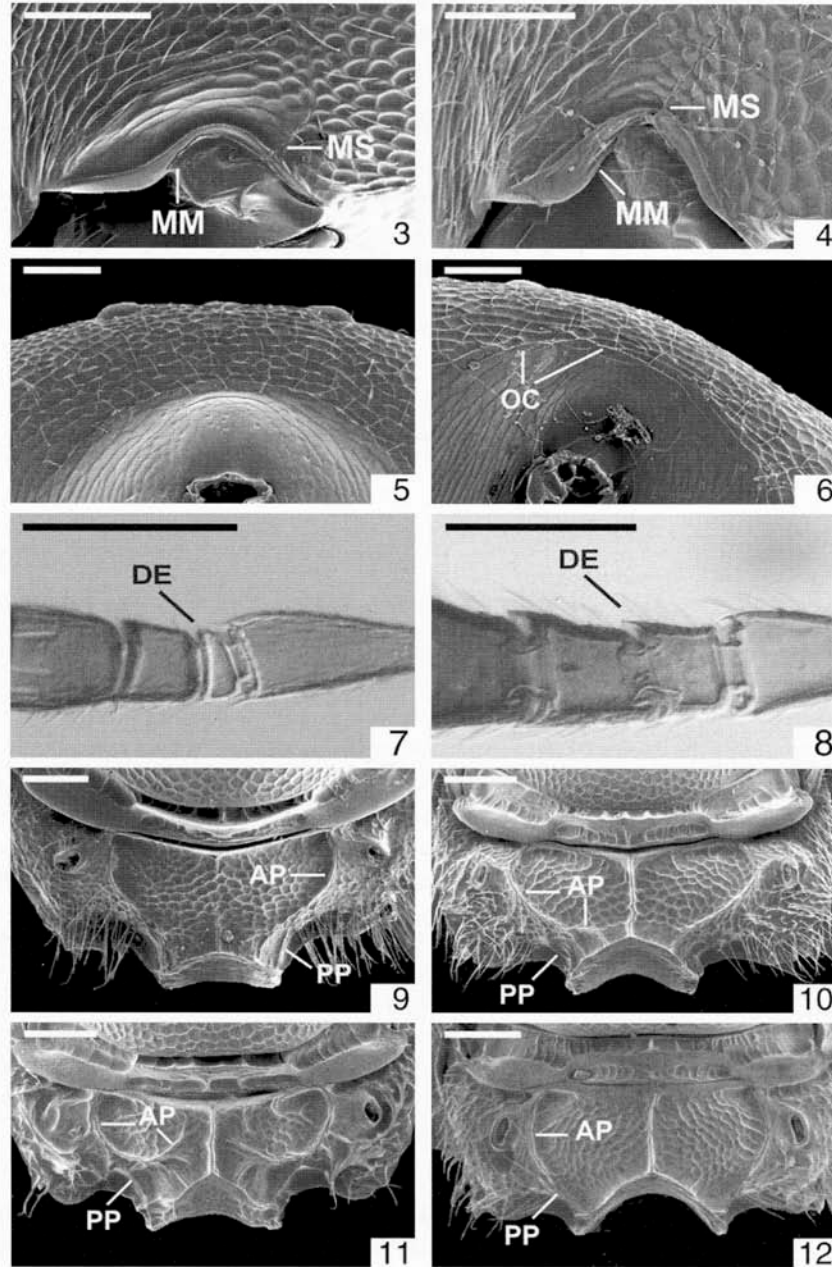


Figure 2 Section of strict consensus tree (Fig. 1) showing distribution of character state changes in *Coelopisthia s.l.* and *Diglochis*.

Coelopisthia s.l. (cf. Appendix 1) comprised 12 species of which *C. pachycera*, *C. sp. D*, and *C. sp. F* were tentatively placed in the genus. The latter deviate more or less from the general pattern of *Coelopisthia* and their position on the tree was therefore subjected to a test in the analysis. Following Yeates (1995) the choice of representatives for the other large genera consisted of a mixed sample of supposed basal and derived taxa. The same applied to the outgroup taxa with respect to the ingroup. *Pachyneuron* is possibly close to the ingroup and shows many derived traits, while *Rhopalicus* would be expected to split off at the base of Pteromalini. *Janssoniella* and *Plutothrix* are currently classified in the tribe Trigonoderini, while *Rhincocoelia* belongs to the Miscogastrinae.

Adult females of each species (see Appendix 1) were examined for discrete morphological characters. Males were not available for many species and were therefore excluded from the analysis. For some of the features it was not possible to define discrete states, since the underlying structure varied continuously. This led to the exclusion of much potentially useful information, sometimes to fusion of states. Some of these characters were nevertheless retained for the analysis and were broken arbitrarily into different states (marked with *). Furthermore, where characters appeared to be correlated they were treated as one character with a number of states (e. g. characters 4, 12). Eventually, a total of 17 characters were scored and are described in Appendix 2.

Analysis of the reduced data matrix yielded more than 200 most parsimonious trees. This large number was probably caused by insufficient data available to resolve some of the taxa. These groups show numerous polytomies, some of them with many branches, in the strict consensus tree (Fig. 1). However, the latter is most revealing with regard to the initial questions about monophyly and relationship of *Coelopisthia* (Fig. 2). *Diglochis* appeared as the sister group of *Coelopisthia s.l.* based on the mouth margin being straight before its junction with the malar sulcus (2.0, Fig. 4), and the anterior part of the plicae strongly bent inwards (12.2, Fig. 10). Both character states appeared only once on the tree. It should be noted, however, that these states are independently derived in *C. pachycera* (12.1, Fig. 9) and some species of *Diglochis* (12.4, Fig. 11).



Figures 3–12 3) mouth margin (MM) and malar sulcus (MS) of *Conomorium amplum*; 4) mouth margin (MM) and malar sulcus (MS) of *Coelopisthia pachycera*; 5) occipital carina absent in *Conomorium amplum*; 6) occipital carina (OC) present in *Coelopisthia extenta*; 7, 8) distal edge (DE) of first left antennal anellus: 7) *Dibrachys cavus*; 8) *Coelopisthia* sp. L.; 9) anterior plica (AP) and posterior plica (PP) of *Coelopisthia pachycera*; 10) anterior plica and posterior plica of *Coelopisthia extenta*; 11) anterior plica and posterior plica of *Diglochis sylvicola*; 12) anterior plica and posterior plica of *Cyclogastrella clypealis*. Scale lines = 0.1 mm.

Coelopisthia s.l. (i. e. the above mentioned doubtfully placed species *C. pachycera*, *C. sp. D*, and *C. sp. F* plus the rest of the genus) is characterised by the presence of a laminate edge at the distal end of the first anellus (4.1, Fig. 8) and the particular shape of the third flagellar segment (7.1), both uniquely derived. The latter species except *C. sp. D*, finally shows a laterally weakly developed and medially almost effaced occipital carina (Fig. 6) as a synapomorphy.

Discussion

The above results confirm to some extent the works of earlier studies (Bouček & Rasplus 1991, Graham 1956, 1969). On the other hand there are some differences which may reflect a shift in focus. One aim of this study was then to transform earlier claims into some precise hypothesis on character state distribution and sister group relationship using cladistic methodology. This is particularly illuminating with regard to characters and the formulation of separate states. For instance Graham's (1969) mentioning of the anelli being large is certainly true as these are larger in *Coelopisthia* than in many other genera and somehow 'different'. But as discussed above, size alone was not the decisive criterion, since other and sometimes similar species shared this feature, too. What matters was the laminate edge on the distal end of the first anellus, evidently a synapomorphy of those species. Moreover, some important characters have also gone unnoticed in the past. One of them concerns the occipital carina, an autapomorphy of *Coelopisthia s.str.* According to Graham (1956) those species show no carina but only a slight edge due to the abrupt angle by which the vertex turns into the occiput. Close examination nevertheless revealed that a weak carina was always indicated laterally below the transition from the vertex to the occiput (Fig. 6). The condition described by Graham is present in species of *Conomorium* where no carina was discernible (Fig. 5).

The species which were initially regarded as doubtfully placed in the genus must now be considered differently. *C. pachycera* and *C. sp. F* were unified in a polytomy with *Coelopisthia s.str.* and therefore caused no problem. On the other hand, *C. sp. D*, an undescribed North African species, was shown to be the single sister taxon of the latter clade. That species differed considerably from all other species and showed many highly derived features. It might therefore be considered as belonging to a separate genus by many workers. However, it still shared two synapomorphies (4.1, 7.1) and was equally supported as the sister group on all of the trees. This and a certain discomfort with the creation of a generic name for a single species, particularly in a group where according to Grissell & Schauff (1990) about half of the Nearctic genera alone were monotypic, led to the inclusion of *C. sp. D* in *Coelopisthia*. Based on this broader concept the genus is thus characterised as follows: body generally squat; head large with conspicuous temples, more or less protuberant at level of toruli; antenna with both anelli enlarged, also the first anellus with a laminate edge at the distal end, third flagellar segment with one row of longitudinal sensilla confined to distal half; fore wing broad, wing disk slightly to very distinctly vaulted, sometimes darkened, sparsely pilose, without marginal setae; marginal and postmarginal vein slightly removed from wing margin, postmarginal vein from slightly shorter than to as long as stigmal vein; plica of propodeum with anterior part often strongly bent inwards and sometimes reaching adpetiolar strip, posterior part distinct and sometimes reaching anterior part or spiracles; median carina of propodeum effaced in the middle or irregular; gaster almost circular, broader than mesosoma.

Finally, the sister group relationship of *Coelopisthia* and *Diglochis* is most interesting concerning their hosts. Species of *Coelopisthia*, *Conomorium* and *Cyclogastrella* are known to attack mostly

Lepidoptera (occasionally Coleoptera in some *Coelopisthia*) while *Diglochis* was reared exclusively from tabanid flies (Noyes 1998). The strict consensus tree suggests that there was a host switch from Lepidoptera to Diptera in the ancestor of *Diglochis*. How this different preferences came into existence can not be the subject of this study but probably led to the apparent differentiation of many features in those taxa (cf. Graham 1969).

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Appendix 1

List of material used in the analysis. Information on each species is arranged as follows: species, number of females, distribution, depository (N = Nearctic, P = Palearctic; see acknowledgements for abbreviation of acronyms).

Coelopisthia Foerster

- areolata* Askew [>10; P – Austria, Czech Rep., Switzerland; MHNG, NMBE, NMW, ZB]
 sp. B = sp. indet. [>10; N – Arkansas, Tennessee; CNCI, USNM]
bicarinata Girault [3; N – Maryland, Montana; USNM]
 sp. C = sp. indet. [3; N – Florida, Virginia; USNM]
caledonica Askew [>10; P – Scotland, Switzerland; BMNH, NMBE]
 sp. D = sp. indet. [2; P – Algeria; MHNG]
extenta (Walker) [>10; P – Germany, England, Switzerland; BMNH, NMBE, NMW]
 sp. F = sp. indet. [3; P – Nepal, China; CNCI, IZAS]
fumosipennis Gahan [10; N – Ontario, Florida, Montana; CNCI, USNM, ZB]
 sp. L = sp. indet. [6; P – Japan; SEHU]
pachycera Masi [>10; P – England, Italy, Switzerland; BMNH, MHNG, NMBE]
suborbicularis (Provancher) [>10; N – Canada, USA; CNCI, USNM, ZB]

Conomorium Masi

- amplum* (Walker) [10; P – Italy, Switzerland; MHNG, NMBE]
patulum (Walker) [9; P – Sweden, Switzerland; NMBE, NRS]
 sp. indet. [2; P – Morocco; MHNG]

Cyclogastrella Bukowskii

- clypealis* Bouček [>10; P – France, Morocco, Switzerland; NMBE]
simplex (Walker) [= *deplanata* (Nees)] [8; P – Switzerland; NMBE]
flavius (Walker) [4; P – Switzerland; NMBE]

Dibrachoides Kurdjumov

- dynastes* (Foerster) [9; P – Morocco, Sweden; NMBE, NRS]

Dibrachys Foerster

- affinis* Masi [4; P – Serbia; MHNG]
boarmiae (Walker) [6; P – Switzerland; NMBE]
 cf. *braconidis* (Ferrière & Faure) [7; P – Switzerland; NMBE]
cavus (Walker) [6; Cosmopolitan; Switzerland; NMBE]
confusus (Girault) [2; N – Wisconsin; USNM]
pelos Grissell [2; N – Connecticut; USNM]

Diglochis Foerster

- sp. A = sp. indet. [1; P – Hungary; HNHM]
 sp. B = sp. indet. [1; P – Hungary; HNHM]
occidentalis (Ashmead) [2; N – Colorado; USNM]
sylvicola (Walker) [8; P – Switzerland, Hungary; HNHM, MHNG, NMBE]

Duarteia Bouček

daphne (Girault) [3; N – California; BMNH, USNM]

Janssoniella Kerrich

sp. indet [1; P – Switzerland; NMBE]

Pachyneuron Walker

formosum (Walker) [>10; P – England, Switzerland; MHNG, NMBE]

muscarum (L.) [5; P – Switzerland; NMBE]

Plutothrix Foerster

bicolorata (Spinola) [2; P – Switzerland; NMBE]

obtusiclava Graham [1; P – Switzerland; NMBE]

Rhinocelesia Graham

constans (Walker) [8; P – Switzerland; NMBE]

Rhopalicus Foerster

tutela (Walker) [>10; P – Switzerland; NMBE]

Schizonotus Ratzeburg

sieboldi Ratzeburg [6; P – Hungary, Switzerland; HNHM, NMBE]

Stichocrepis Foerster

armata Foerster [3; P – Hungary; HNHM]

Systemlogaster Gahan

gahani Wallace [2; N – Montana; USNM]

ovivora Gahan [3; N – USA, Vienna, Va; USNM]

Tritneptis Girault

doris Burks [4; N – Arizona; USNM]

hemerocampae Girault [3; N – New Jersey, Connecticut; USNM]

sp. indet = ?*klugii* (Ratzeburg) [6; P – Switzerland; NMBE]

Appendix 2

Characters and character states († and †† refer to SEM micrographs published in Bouček & Rasplus (1991) and Huber *et al.* (1996), respectively; see comments in text for asterisks).

1. *Level of toruli (frontal view with lower edge of median ocellus and of toruli equidistant to the objective): upper edge below (0); upper edge at or above (1); lower edge at or above ocular line (2).
2. Mouth margin before conjunction with malar sulcus: straight with weak fovea above (0) (Fig. 4); curving with weak fovea above (1) (Fig. 3); curving with fovea reaching halfway along malar sulcus (2).
3. Occipital carina: absent (0) (Fig. 5); weakly developed laterally, more or less effaced medially, curving, high (1) (Fig. 6); distinct throughout, curving, high (2) (Fig. †29); distinct throughout, straight, low (3) (Fig. †30); weakly developed medially along edge formed by vertex and occiput (4); as 1 but traceable medially, longer, and more curving (5); absent but distinct edge in the middle quarter formed by vertex and occiput (6); distinct throughout, curving, low (7).
4. First anellus: laminate edge on distal end absent (0) (Fig. 7); laminate edge on distal end present (1) (Fig. 8).
5. Third flagellar segment, shape: conical (0); cylindrical (1); with constricted neck at base (2).
6. Third flagellar segment, arrangement of longitudinal sensilla: absent (0); in one row (1); in two or more rows (2).
7. Third flagellar segment, distribution of longitudinal sensilla: distributed over distal two thirds to base (0); confined to distal half (1); confined to distal quarter (2).
8. Micropilosity on clava: present on third segment only (0); present on all segments (1); present on second and third segment (2).
9. Pronotal collar: bluntly ridged medially (0); sharply carinate medially (1); evenly rounded (2).
10. Position of marginal and postmarginal vein: right along wing margin (0); slightly removed from wing margin (1).
11. *Length of postmarginal vein: about as long as stigmal vein (0); distinctly longer than stigmal vein (1).
12. Plica, anterior (AP) and posterior part (PP): AP sharp, moderately curving, reaching halfway along propodeum (PPD), PP hardly traceable (0); like 0 but PP distinctly developed (Fig. 9) (1); AP sharp, strongly curving, often reaching adpetiolar strip, PP distinct, sometimes reaching AP or spiracles (Fig. 10, ††20) (2); AP and PP sharp and smoothly joining to form a moderately sinuate edge, AP sometimes forming a costula (3) (Fig. 12); like 2 but AP pointing backwards (4) (Fig. 11); AP blunt, weakly curving, PP distinct (5) (Fig. ††21); AP hardly developed, PP distinct (6); like 6 but PP almost reaching spiracles (7); AP sharp, strongly bent inwards and joining median carina at base, PP distinct (8). The above anterior and posterior parts of plica are collectively referred to as one 'plica' or 'plical carina' in all major textbooks (e. g. Graham 1969; Bouček 1988; Gibson 1997). However, close examina-

tions revealed that it consists of an anterior and a posterior part. Even where both parts form a seemingly continuous edge (Fig. 12), a small break was always detectable. On the other hand, where a cross carina known as 'costula' was indicated, that was formed by the anterior part of plica curving inwards.

13. Median carina of PPD: straight, distinct throughout (0) (Figs 11, 12); irregular and/or effaced medially (1) (Figs 9, 10).
14. Pilosity on callus of PPD: reaching below spiracles (0); not reaching below spiracles (1).
15. Petiole surface structure: alutaceous to weakly reticulate without median carina (0); smooth with indistinct median carina (1); smooth with strong median carina (2).
16. Proximal edge of gastral tergum one: lateral laminate borders fused medially (0); borders just touching medially (1); borders separate (2).
17. Placement of cerci on metasomal tergum eight: ventro-laterally (0); dorsally (1).

Appendix 3

Data matrix of character states for 44 species of 16 genera. Taxa arranged according to their appearance on the strict consensus tree (Fig. 1).

<i>Coelopisthia areolata</i>	1	0	1	1	0	1	1	0	0	1	0	2	1	0	1	0	0
<i>C. sp. B</i>	1	0	1	1	0	1	1	0	0	1	0	2	1	0	1	0	0
<i>C. sp. F</i>	1	0	1	1	0	1	1	0	0	1	0	2	1	0	1	0	0
<i>C. extenta</i>	0	0	1	1	0	1	1	0	0	1	0	2	1	0	1	0	0
<i>C. bicarinata</i>	0	0	1	1	0	1	1	0	0	1	0	2	1	0	1	0	0
<i>C. sp. C</i>	0	0	1	1	0	1	1	0	0	1	0	2	1	0	1	?	0
<i>C. fumosipennis</i>	0	0	1	1	0	1	1	0	0	1	0	2	1	0	1	0	0
<i>C. sp. L</i>	0	0	1	1	0	1	1	0	0	1	0	2	1	0	1	0	0
<i>C. suborbicularis</i>	0	0	1	1	0	1	1	0	0	1	0	2	1	0	1	0	0
<i>C. caledonica</i>	0	0	1	1	0	1	1	0	0	1	0	2	1	0	1	0	0
	1																
<i>C. pachycera</i>	1	0	1	1	0	1	1	0	0	1	0	1	1	0	1	0	0
<i>C. sp. D</i>	1	0	0	1	0	1	1	0	1	1	0	2	1	0	1	0	0
<i>Diglochis occidentalis</i>	1	0	5	0	0	0	?	1	0	0	0	2	0	1	2	0	0
<i>D. sp. A</i>	1	0	5	0	0	0	?	1	0	0	0	4	1	1	2	0	0
<i>D. sp. B</i>	1	0	5	0	0	0	?	1	0	0	0	4	1	1	2	0	0
<i>D. sylvicola</i>	1	0	5	0	0	0	?	1	0	0	0	4	0	1	2	0	0
<i>Conomorium amplum</i>	1	1	0	0	2	1	2	0	0	0	0	0	0	1	0	0	0
<i>C. patulum</i>	2	1	0	0	2	1	2	0	0	0	0	0	0	1	0	0	0
<i>C. sp.</i>	1	1	0	0	2	1	2	0	0	0	0	0	0	1	0	0	0
	2												1				
<i>Cyclogastrella clypealis</i>	2	1	0	0	0	0	?	0	2	0	0	3	0	0	1	0	0
													1				
<i>C. flavius</i>	2	1	0	0	0	0	?	0	2	0	0	3	0	0	1	0	0
													1				
<i>C. simplex</i>	1	1	0	0	0	0	?	0	2	0	0	3	0	0	1	0	0
													1				
<i>Dibrachys confusus</i>	1	1	2	0	1	1	0	0	2	0	0	3	0	1	1	2	0
<i>Dibrachoides dynastes</i>	2	2	4	0	1	1	0	0	1	0	0	5	1	1	1	1	0
<i>Dibrachys affinis</i>	2	1	3	0	1	1	0	0	0	1	0	3	1	1	1	2	0
<i>D. boarmiae</i>	2	1	2	0	1	1	0	0	2	1	0	5	1	1	1	2	0
<i>D. cavus</i>	2	1	2	0	1	1	0	0	2	1	0	5	1	1	1	2	0
<i>D. braconidis</i>	2	1	2	0	1	1	0	0	2	0	0	5	1	1	1	2	0
<i>D. pelos</i>	1	1	2	0	1	1	0	0	2	1	0	5	1	1	1	2	0
<i>Duarte daphne</i>	2	2	7	0	1	1	0	2	2	0	0	5	1	1	1	2	0
<i>Schizonotus sieboldi</i>	2	2	0	0	1	1	0	0	2	1	0	3	0	1	1	1	1
													1				
<i>Stichocrepis armata</i>	0	1	0	0	1	1	0	0	2	1	0	8	1	1	1	0	0
<i>Systellogaster ovivora</i>	2	1	6	0	1	1	0	0	2	1	0	5	1	1	1	2	0
<i>S. gahani</i>	2	1	6	0	1	1	0	0	2	1	0	5	1	1	1	2	0
<i>Tritneptis doris</i>	0	1	0	0	1	1	0	0	2	1	0	3	1	1	1	2	0

<i>T. hemerocampae</i>	1	1	0	0	1	1	0	0	2	1	0	5	1	1	1	2	0
<i>T. sp.</i>	1	1	0	0	1	1	0	0	2	1	0	3	1	1	1	2	0
<i>Janssoniella sp.</i>	2	1	0	0	1	2	0	0	2	0	1	7	0	1	1	2	0
<i>Rhcnocoelia constans</i>	2	1	0	0	1	2	0	0	2	0	1	7	0	1	1	? 0	
<i>Plutothrix bicolorata</i>	2	1	0	0	1	2	0	0	1	0	1	7	0	1	1	2	0
<i>P. obtusiclava</i>	2	1	0	0	1	2	0	0	1	0	1	7	0	1	1	2	0
<i>Rhopalicus tutela</i>	2	1	0	0	1	2	0	0	2	0	1	6	0	1	1	2	0
<i>Pachyneuron formosum</i>	2	1	0	0	1	1	0	0	1	0	1	5	1	1	0	2	1
<i>P. muscarum</i>	2	1	0	0	1	1	0	0	1	0	1	5	1	1	0	2	1

Source

Baur, H. 2000. Monophyly and relationship of the genus *Coelopisthia* Förster (Chalcidoidea, Pteromalidae). Pp. 165–177 in Austin, A. D. & Downton, M. (eds): Hymenoptera: Evolution, biodiversity and biological control. CSIRO, Collingwood, Australia xi + 468 pp.