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Cladistics and tribal classification of the Agathidinae (Hymenoptera: Braconidae)

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Five tribes of the braconid subfamily Agathidinae are recognized, *viz.* Agathidini (Blanchard), Cremnoptini (new tribe), Disophrini (new tribe), Earinini (new tribe), and Microdini (Ashmead). Phylogenetic relationships of the tribes are proposed and the phylogenetic placement of the Agathidinae within the Braconidae is discussed. Keys to, and diagnoses of, the tribes are presented.

KEYWORDS: Agathidinae, Braconidae, cladistics, classification, Hymenoptera, phylogeny, systematics.

Introduction

The Agathidinae is a moderately large subfamily in which I recognize 54 genera. It is cosmopolitan in distribution and members are found in most habitats, e.g. desert, tropical rainforest, temperate forest, savannah, alpine and subarctic habitats.

Generally, agathidines are more diverse in tropical regions but some genera such as *Agathis* and *Earinus* are exceptional, being more speciose in temperate regions. All agathidines are koinobiont endoparasitoids of larval Lepidoptera. Most host larvae are leaf rollers or stem borers, though about 20% of the hosts are free-living foragers and usually crepuscular or nocturnal. Eggs usually are laid in first- or second-instar larvae and the adult parasitoid emerges after the final instar of the host has spun its cocoon (Nickels *et al.*, 1950; Dondale, 1954; Odebiyi and Ottman, 1972, 1977).

Few detailed studies of the biology of species of Agathidinae have been conducted. Dondale (1954) described the life history of *Bassus dimidiator* Nees (as *Agathis laticinctus* Cresson) which attacks the eye-spotted bud moth *Spilonota ocellana* (D.&S.), an orchart pest. Simmonds (1947) described the biology of *Cremnops vulgaris* (Cresson) (as *Agathis vulgaris*), a parasite of the sugarbeet web-worm (*Loxostege sticticalis* L.). Hummelen (1974) studied the life history of *Alabagrus stigma* Brullé (as *Agathis stigmaterus*) a parasite of *Diatraea saccharalis* (F.). Odebiyi and Oatman (1972, 1977), recorded the biology of *Agathis gibbosa* (Say) and *Bassus unicolor* (as *Agathis unicolor*), parasites of the potato tuberworm *Phtorimaea operculella* (Zeller). Each of the works mentioned above gives a detailed account of the immature stages and assesses the value of the parasites as natural control agents.

Many members of the Agathidinae are important in the natural control of pest species of Lepidoptera. Some have been used in classical biological control programmes, e.g. *Agathis pumila* (Ratz.) and *Coleophora laricella* (Hübner) (Ryan, 1990) for

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the larch case-bearer, and *Alabagrus stigma* (Brullé) against the sugarcane borer, *Diatraea saccharalis* (F.) (Hummelen, 1974). Shaw and Huddleston (1991) provide a more thorough review of the biology of the Agathidinae.

It is the purpose of this paper to provide a cladistic classification of the Agathidinae at the tribal level. This will serve as a template for future revisionary research at the generic level.

Historical review

Muesebeck (1927) and Bhat and Gupta (1977) reviewed the higher classification of the Agathidinae, and their presentations are revised and updated here. Förster (1862) divided the subfamily into two families, the Agathoidae and the Eumacrodoidae, based on the shape of the head. Marshall (1885) did not follow this arrangement and combined the groups into one family, the Agathidides. Cresson (1887) renamed the subfamily Agathidinae, and Ashmead (1900) reintroduced Förster's concepts as the tribes Agathidini and Microdini. Szépligeti (1904) did not recognize these tribes, and used the subfamily name Agathinae for the entire assemblage. Viereck (1914) showed that *Cremnops* Förster (1862) shared the same type (*Ichneumon desertor* Linnaeus) as *Bracon* Fabricius (1804). Consequently, Gahan (1917) replaced Agathidinae of authors with the subfamily name Braconinae. This usage was followed until Hincks (1943) suggested the reinstatement of the historical concepts of Braconinae and Agathidinae.

Bhat and Gupta (1977) divided the Agathidinae into two informal groups, the *Agathis* and *Cremnops* groups. Nixon (1986) revised the European species of Agathidinae and made reference to the *Agathis–Microdus* and *Cremnops–Disophrys* genus groups, which are equivalent to those groups proposed by Bhat and Gupta (1977). Achterberg (1985) included the genus *Pselaphanus* in the Agathidinae and proposed the monotypic tribe Pselaphanini. Later Achterberg (1990) transferred the genus to its own subfamily and considered this to be the sister group of the Agathidinae.

Mesocoelus Schultz has been included in the Agathidinae, the Microgastrinae, the Orgilinae, and placed in its own monotypic subfamily twice, i.e. Mesocoelinae (Viereck, 1918) and Aneurobraconinae (Fahringer, 1936). Achterberg (1984) employed Aneurobraconini (p. 42) and Mesocoelini Viereck (p. 53) to include both *Mesocoelus* and *Aneurobracon*, and tentatively placed this single group (with two distinct tribal names employed in the same paper) in the Orgilinae. Later Achterberg (1987) treated the assemblage as a separate subfamily. Most recently Achterberg (1990) proposed the genus *Plesiocoelus* and treated the three genera (*Aneurobracon*, *Mesocoelus* and *Plesiocoelus*) as the Mesocoelina, which, together with his new subtribe Agathidina, constituted the Agathidini. Agathidini *sensu* Achterberg is the same concept as the *Agathis* group proposed by Bhat and Gupta (1977). In the same publication Achterberg (1990) recognized the tribe Vipionini Gahan (1917) to include all agathidines with 'the fore claw bifurcate, the area between the antennal sockets with a pair of protuberances and outer face of middle tibia without pegs above apical pegs'.

Gahan's concept of Vipionini applied to *Vipio* auct., which is a cyclostome braconid in the subfamily Braconinae. Achterberg's (1990) concept is the same as that of the *Cremnops* group of Bhat and Gupta (1977). This introduces a rather complicated problem concerning the genera *Vipio* and *Cremnops*.

Vipio Latreille and *Cremnops* Förster share the same type species, *Ichneumon desertor* Linnaeus. However, traditionally *Ichneumon desertor* Linnaeus and *Ichneumon desertor sensu* Fabricius have been regarded as separate species, and the genera based on them, *Vipio* and *Cremnops*, have been maintained in separate

subfamilies for over 100 years. The International Code of Zoological Nomenclature (Article 70b, 1985) clearly states, 'If, however, a type species is considered to have been misidentified, the case is to be [doit être] referred to the Commission to designate as the type species whichever nominal species will in its judgement best serve stability and universality of nomenclature, either the nominal species named in the fixation, regardless of the misidentification; or, by the use of the plenary power [Art. 79a]'.

Achterberg's (1982, 1990) use of *Vipio* violates this article of the code. Article 23b of the Code further states that 'The principle of priority is used to promote stability and is not intended to be used to upset a long accepted name in its accustomed meaning through the introduction of an unused name that is its senior synonym. An author who considers that the application of the Principle of Priority would disturb stability or universality or cause confusion is to maintain existing usage and refer the case to the Commission for a ruling.' This makes it rather clear to me that *Cremnops* and *Vipio* should be used in their traditional senses. To this effect, Drs Wharton and Mason have petitioned the Commission of Zoological Nomenclature (Wharton and Mason, 1991) to maintain the traditional usage of *Cremnops* and *Vipio*. The Code clearly states 'When a case is under consideration by the Commission, existing usage is to be maintained until the ruling of the Commission is published by the commission.' Regardless of how the Commission rules, the correct current name for the agathidine taxon is *Cremnops*.

Major revisional studies on the Agathidinae include the following: Achterberg (1990), species of *Mesocoelus*, *Aneurobracon*, and *Plesiocoelus*: Bhat and Gupta (1977), species of most genera of the Oriental region: Bhat (1979), Oriental species of *Cremnops*, Gupta and Bhat (1972, 1974), Oriental species of *Zelomorpha*, *Earinus* and *Camptothlipsis*; Nixon (1986), species of Agathidinae of northwestern Europe; Muesebeck (1927), species of Agathidinae in America north of Mexico: Sharkey (1986), species of *Alabagrus*: Tobias (1986), species of Agathidinae in European parts of the USSR. Other revisional works of note are Bhat (1978), Simbolotti and Achterberg (1990), Tobias (1963, 1976). Areas with agathidine fauna that are especially poorly known are the Neotropical, Ethiopian and Australian regions.

Monophyly of the Agathidinae

The monophyly of the Agathidinae is supported by three synapomorphies. The first and perhaps the most convincing of these is the presence of specialized male tergal glands (Fig. 9) on metasomal segments six and seven (Buckingham and Sharkey, 1988). Each of these terga has dorsolateral lobes that extend below the following tergum, and between these lobes there are one or more transverse rows of setae. Buckingham and Sharkey (1988) postulated that the lobes contain chemicals and the setal brushes are used to disperse these. Dissections of dozens of species in diverse lineages of the Agathidinae suggest that the glands are universal within the subfamily, through in one species of *Alabagrus* dissected the associated setal brushes are lost. These glands, modified with brushes, are not known to occur in any other braconids.

The second synapomorphy, the presence of a wing fold between the prestigma and medial vein of the fore wing, is universal within the Agathidinae. Usually (95%) this fold (Fig. 1) is indicated by a distinct bulla (fenestra, break) (Sharkey, 1986). This fold has not been found elsewhere in the Ichneumonoidea.

The third synapomorphy is that the radial sector (Rs) vein of the fore wing terminates on the fore margin well anterior to the wing apex such that the R1 cell is very narrow (Figs 1–8). This feature does appear in other clades within the Braconidae, e.g. some Euphorinae, but the distribution suggests that they are convergent features.

Other characters, some of which are mentioned by Achterberg (1990), such as the descleritization the basal portion of the media (M) vein (Figs 1–8) may also be synapomorphies for the Agathidinae. However, because of the widespread distribution of these characters, and a lack of knowledge about the placement of the Agathidinae within the Braconidae, it is difficult to determine if the characters diagnose a larger group or whether there are convergent occurrences of the character.

Outgroup analysis

Although the monophyly of the subfamily is well documented, the phylogenetic position of the Agathidinae within the Braconidae is problematic. Achterberg (1990) suggested a sister group relationship with Pselaphaninae, a monogeneric subfamily he proposed for the genus *Pselaphanus*, 'because it has also the veins m – cu and 1 – M of the fore wing diverging posteriorly, the hind trochanter rather widened, the scutellum without depression, and vein M + Cu1 of fore wing largely unsclerotized'. It is not clear if these characters are considered synapomorphies for the Agathidinae plus Pselaphaninae, because Achterberg goes on to say that many of these characters are found in the Sigalphinae as well, which he considered to be the sister group of Agathidinae plus Pselaphaninae. Quicke and Achterberg (1990) proposed the same relationship, i.e. Pselaphaninae and Agathidinae as sister groups; the sister group of this clade, however, is ambiguous in their analysis.

All six of the characters that Quicke and Achterberg (1990: 29, couplet 44) cite as synapomorphies for the Agathidinae plus *Pselaphanus* are problematic. These six putative synapomorphies are criticized in the following paragraphs.

Unlike the Agathidinae, and contrary to Achterberg (1985), members of *Pselaphanus* have vein M + Cu of the fore wing tubular, as do members of the Sigalphinae.

Although the posterior transverse depression of the scutellum is present in members of the Sigalphinae and absent in *Pselaphanus*, the character is variable in the Agathidinae (Sharkey, 1986). My opinion is that *Pselaphanus* and many members of the Agathidinae have convergently lost the transverse posterior depression of the scutellum. A detailed character analysis is necessary. Based on my observations, a posterior scutellar depression appears to be a synapomorphy of the Apocrita plus Orussidae. It is widespread within the Apocrita but absent in all of the Ichneumonidae that I investigated. Its polarity within the Braconidae is therefore rather difficult to determine.

The putative synapomorphy 'hind wing plical cell small' (Quicke and Achterberg, 1990) is also unsupported according to my observations. Following the terminology of Whootton (1979), Quicke and Achterberg are referring to the clavus of the hind wing. Exactly what constitutes the class of cells deemed small by Quicke and Achterberg remains uncertain; however, the clavi of agathidines are quite small relative to those of most sigalphines, whereas those of *Pselaphanus* are large and of the same magnitude as a typical sigalphine.

'Occipital carina reduced' (Quicke and Achterberg, 1990), is another supposed synapomorphy for *Pselaphanus* and Agathidinae. All agathidines lack any trace of a true occipital carina. Members of the genus *Pselaphanus* have the occipital carina absent dorsally, as do all sigalphines that I have examined, e.g. *Sigalphus bicolor*, *S. irrorator*, *Acampsis alternipes* and *Minanga spinifrons*. The loss of the occipital carina dorsally is most parsimoniously explained as a synapomorphy of the Sigalphinae including *Pselaphanus* rather than a synapomorphy of *Pselaphanus* and Agathidinae.

The 'hindwing r present' and 'prepectal carina absent' are also used by Quicke and Achterberg (1990) as synapomorphies for *Pselaphanus* and Agathidinae. The r crossvein is present in many members of the Sigalphinae and is more common in this group than in the Agathidinae. The prepectal carina (=epicnemial carina) is present in members of *Pselaphanus*, other members of Sigalphinae, and almost all members of the Agathidinae.

In summary, I am not inclined to agree with Achterberg (1990) and Quicke and Achterberg (1990). *Pselaphanus* is, in my opinion, a member of the Sigalphinae differing from other members of the subfamily only in the lack of a distinct transverse depression on the scutellum, a character that shows considerable variation in the Agathidinae and other Braconidae.

That the Sigalphinae s.l. (including *Pselaphanus*) is the sister group of the Agathidinae has some support. Of the four characters mentioned by Quicke and Achterberg (1990: 29, couplet 43), two appear to be wrong; the hind coxa is not large in members of the Sigalphine except *Pselaphanus*, also fore wing m – cu with fenestra, is not found in *Pselaphanus* or any other Sigalphinae. In this respect the drawing of the fore wing of *Pselaphanus troigoides* Szépligeti by Achterberg (1985: 343) is correct. The other two characters may be synapomorphies. The presence of the subpronope is found only in the Agathidinae and many Ichneutinae and Sigalphinae s.l. The character could be a synapomorphy for the entire group but convergences and losses must be considered in the context of all Braconidae. The other potentially useful character, 1M and m – cu of the fore wing diverging posteriorly, is poorly defined and may be a composite character involving several veins. Nonetheless, sigalphines and agathidines do have a similar shape to cell 1 – M and a search for characters in this area of the fore wing may give fruitful results. Taken as a whole the evidence for a sister group relationship between Sigalphinae s.l. and Agathidinae is poorly supported.

The outgroup for the Agathidinae remains an enigma. For the purposes of this analysis the non-cyclostome braconids as a whole are considered as the outgroup. The cyclostome braconids and the Ichneumonidae are used as secondary outgroups to verify preliminary polarities.

Cladistic analysis

Characters

(0 = plesiomorphic, 1 = apomorphic)

1. Labial palpi:
   0; palpomere 3 not reduced (Fig. 25)
   1; palpomere 3 reduced (Fig. 24)
2. Labio-maxillary complex:
   0; of normal proportions, galea shorter than mandible
   1; elongate, galea longer than mandible
3. Notauli:
   0; present
   1; absent
4. Propodeal sculpture:
   0; areolate (Fig. 14)
   1; with one to three median longitudinal carinae (Fig. 15)

5. Hind coxal cavities:
   0: sharing common foramen with metasoma (Fig. 11)
   1: separated from metasomal foramen by scleritized bridge (Figs 10, 12)
6. Tarsal claws:
   0: simple or with rounded basal tooth (Figs 17, 18, 20)
   1: bifid (Figs 16, 19)
7. Tarsal claws:
   0: smooth basally (Figs 17–20)
   1: pectinate basally (Fig. 16)
8. Hind basitarsomere:
   0: serrate ridge absent
   1: serrate ridge present (Figs 28, 29)
9. Fore wing vein 1 – Rs + M:
   0: complete (Fig. 2)
   1: incomplete (Figs 1, 3–8)
10. Metasomal tergum one:
   0: two longitudinal carinae present
   1: longitudinal carinae absent
11. Ovipositor:
   0: long and straight (concealed hosts)
   1: short and curved ventrally (exposed hosts) (Fig. 23)
12. Preapical spines on mid-tibia:
   0: absent
   1: present

Taxonomic units

The most recent tribal classification of the Agathidinae was proposed by Achterberg (1990). He recognized two tribes, the Agathidini and the Vipionini. He divided the Agathidini further into the subtribes Mesocoelina and Agathidina. As pointed out earlier in this paper, the two tribes are the same concepts as the *Agathis* and *Cremnops* species groups of Bhat and Gupta (1977). Achterberg's rationale for proposing the subtribe Mesocoelina is: 'the group seems distinct enough ... because of the slender hind trochanter, the reduced fore wing venation and the long hind legs' (Achterberg, 1990: 32). Indeed the Mesocoelina appears to be monophyletic. The problem with its status as a subtribe is that it renders the other subtribe of the Agathidini paraphyletic. The members of Mesocoelina and a subgroup of Agathidina *sensu* Achterberg have the third labial palpomere reduced to less than half the length of the fourth. Furthermore this group has the hind coxal cavities separated from the metasomal foramen of the propodeum. These two characters demonstrate that the Agathidina as defined by Achterberg (1990) is paraphyletic with respect to the Mesocoelina.

Justification for the two tribes suggested by Achterberg is also weak. Achterberg (1990: 33) presented numerous character states which describe the Agathidini and the Vipionini but did not suggest which are apomorphic and which are plesiomorphic. The character states he used to define his concept of the Agathidini are mostly plesiomorphic, i.e. 'fore claw simple or with a lobe, area between antennal sockets flat, ... outer face of middle tibia with pegs above apical pegs and occurring predominantly in temperate regions' (Achterberg, 1990: 33). Only one character state

presence of preapical pegs on the mid-tibia may be an apomorphic character but three of the four cladograms that result from my analysis (presented later) suggest that it is ground state for the Agathidinae. Monophyly of the Agathidini *sensu* Achterberg is therefore suspect.

For the phylogenetic analysis of the Agathidinae I employ five tribes. These are chosen because they are well-supported monophyletic taxa that divide the Agathidinae into distinct groups of a practical size that appear to be meaningful biologically.

The Agathidini may be the sister group to the Earinini (cladograms (A) and (D) of Fig. 30) and if so the elongate mouthparts of its members may be considered a synapomorphy (character 2). If the Agathidini is considered the sister group of ((Microdini + (Cremnoptini + Disophrini)) as in cladogram (B) of Fig. 30 then the elongate mouthparts (character 2) and the sculpture of the propodeum (character 4) are considered autapomorphies for the tribe, albeit with convergent occurrences. Finally if the Agathidini is the sister group of the (Cremnoptini + Disophrini) (cladogram (C) of Fig. 30) then only the modified propodeal sculpture (character 4) is considered an autapomorphy.

The monophyly of each of the remaining tribes is less ambiguous. An unequivocal autapomorphy of the Cremnoptini is the presence of pectinate tarsal claws (character 7). Elongate mouthparts (character 2) may also be an autapomorphy if cladogram (B) or (D) (Fig. 30) is accepted.

The Disophrini are diagnosed by two unequivocal autapomorphies, hind basitarsomere with a serrate ridge (character 8), and ovipositor short and ventrally curved (character 11).

The Earinini have one autapomorphy that is shared without exception by all known members of the taxon, the lack of notauli (character 3), and cladograms (A) and (B) of Fig. 30 suggest that the modified propodeal sculpture (character 4) may also be an autapomorphy convergently derived in the ancestor of the Agathidini.

The Microdini have one non-homoplastic autapomorphy, the third labial palpomere is reduced (character 1). If cladogram (C) or (D) (Fig. 30) is accepted then the separation of the hind coxal cavities from the metasomal foramen is also an autopomorphy for the taxon.

Results

The data set (Table 1) was run on Hennig86 (Farris, 1988) using the ie (implicit enumeration) option. The four resulting cladograms with 15 steps and consistency indices of 0·7 are those of Fig. 30. Five characters show homoplasy in these reconstructions, characters 2, 4, 5, 9 and 12. In order to select from among the four

Table 1. Data matrix of the tribes of the Agathidinae.

	Characters											
Taxa	1	2	3	4	5	6	7	8	9	10	11	12
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0
Earinini	0	0	1	1	0	0	0	0	0	0	0	1
Agathidini	0	1	0	1	0	0	0	0	1	0	0	1
Microdoni	1	0	0	0	1	0	0	0	1	0	0	1
Cremnoptini	0	1	0	0	1	1	1	0	1	1	0	0
Disophrini	0	?	0	0	1	1	0	1	1	1	1	0

cladograms one must weight these characters. I prefer to weight on the basis of character consistency (compatibility) (Sharkey, 1989). The more consistent a character is with other characters in taxa included in the analysis, and the more consistent it is with characters within these taxa, the more I am inclined to suspect that it is a synapomorphy. None of the characters are perfectly consistent within the taxa under study: however, character 4 is somewhat more consistent than characters 2, 5, 9 and 12, and on the basis of this observation, cladograms (A) and (D) of Fig. 30 are preferred. I favour cladogram (A) over cladogram (D) because I have some doubts as to the polarity of character 12 (preapical spines on the mid-tibia), despite the fact that the polarity is based on strict outgroup criteria. All agathidines have spines on the mid-tibia, some have only apical spines and some have apical and preapical spines. The absence of preapical spines is treated as plesiomorphic: however, it is just as likely that the full complement of spines is part of the agathidine ground plan. This polarity is supported by cladograms A, B and C (Fig. 30). Consequently, cladogram (A) (Fig. 30) is marginally preferred. The only unequivocal relationship, common to all cladograms, is that the Cremnoptini and Disophrini are sister groups.

Key to the tribes of the Agathidinae of the world

1 Fore tarsal claws cleft (Figs 16, 19) 2
1′ Fore tarsal claws simple or with basal lobe (Figs 17, 18, 20) 3

2 Ovipositor sheaths longer than 0·5 length of metasoma; base of fore tarsal claw usually (85%) pectinate (Fig. 16). . . . . *Cremnoptini*
2′ Ovipositor sheaths shorter than 0·5 length of metasoma (Fig. 23); base of fore tarsal claw not pectinate (Fig. 19); (rarely some thick setae may make the base appear somewhat pectinate) . . . . . *Disophrini*

3 1 − Rs + M vein of fore wing complete (Fig. 2) . . . . . *Earinini* (pt.)
3′ 1 − Rs + M vein of fore wing incomplete (Figs 1, 3, 4, 8) 4

4 Propodeum areolate (Fig. 14) . . . . . *Microdini* (pt.)
4′ Propodeum not areolate (e.g. Fig. 15). 5

5 Notauli absent 6
5′ Notauli present 9

6 Labio-maxillary complex elongate (galea longer than mandible). 7
6′ Labio-maxillary complex of normal dimensions (galea shorter than mandible . . 8

7 Strong transverse carina between hind coxae absent (Figs 11, 13); hind coxa and metasoma sharing common foramen, *or* foramina separated by narrow sclerite (Figs 11, 13) . . . . . *Agathidini* (pt.)
7′ Strong transverse carina between hind coxae present (Fig. 10); hind coxa and metasoma separated by wide sclerite (Fig. 10). . . . . *Microdini* (pt.)

8 Labial palpomere 3 reduced, less than 0·5 length of palpomere 4 (Fig. 24). *Microdini* (pt.)
8′ Labial palpomere 3 not reduced, more than 0·5 length of palpomere 4 (Fig. 25) *Earinini* (pt.)

9 With the following combination: labio-maxillary complex elongate (galea longer than mandible); hind coxa and metasoma sharing common foramen (Fig. 11), *or* foramina separated by narrow sclerite (Fig. 13); fore tarsal claws elongate with basal lobe small (Fig. 18) or absent (Fig. 20) . . . . . *Agathidini* (pt.)
9′ Without the above combination: labio-maxillary complex usually (95%) of normal dimensions (galea shorter than mandible); hind coxa and metasoma usually (85%) separated by wide sclerite (Figs 10, 12); fore tarsal claws with large basal lobe and usually (95%) not elongate (Fig. 17) . . . . . *Microdini* (pt.)

Descriptive section

Agathidinae Blanchard

Agathites Blanchard, 1845: 157, 164.
Agathidoidae Förster, 1862: 228.
Eumicrodoidae Förster, 1862: 246.
Eumicrodidae Kirchner, 1867: 113.
Agathididae Kirchner, 1867: 123.
Agathidides Marshall, 1872: 108.
Agathides Marshall, 1885: 10.
Agathidinae Cresson, 1887: 59.
Agathinae Cameron, 1990a: 397.
Agathidini Ashmead, 1990: 127.
Agathini de Gaulle, 1907: 186.
Braconinae Gahan, 1917: 97.
Bassinae Viereck, 1918: 70.
Agathidae Lyle, 1920: 177.
Agathiinae Fahringer, 1925: 20.
Agathidinen Hellén, 1957: 116.

Diagnosis

Head. Occipital carina absent; labio-maxillary complex sometimes (25%) elongate (galea longer than mandible); antennal flagellum usually (99%) with more than 18 articles; maxillary palpi 5-segmented; labial palpi 4-segmented, labial palpomere 3 often reduced and rarely absent in members of Microdini.

Wings. (Figs 1–8). 1 – Rs + M vein of fore wing often (85%) incomplete or absent; Rs vein of fore wing meeting wing margin near apex of stigma, thus cell 2 – R1 narrow; cell 1 – Rs of fore wing small or rarely (5%) absent; wing fold between prestigma and 1 – Rs + M present and often (90%) evidenced by bulla in 1 – Rs vein; M + Cu vein of fore wing not tubular in basal half; crossvein m – cu of fore wing with bulla; 2cu – a crossvein of fore wing absent, thus cell 2 – Cu open posteriorly; vein 2 – Rs2′ of fore wing sometimes (15%) present (Fig. 6) (not present in other Braconidae) vein 2 – Cu of hind wing sometimes (50%) present; crossvein 2r – m′ of hind wing sometimes (20%) indicated as spectral or nebulous vein (Fig. 7). (Note: I use the abbreviations 2r – m′ and 2 – Rs2′ to differentiate these adventitious veins from 2r – m and 2 – Rs2 respectively, with which they are not homologous.)

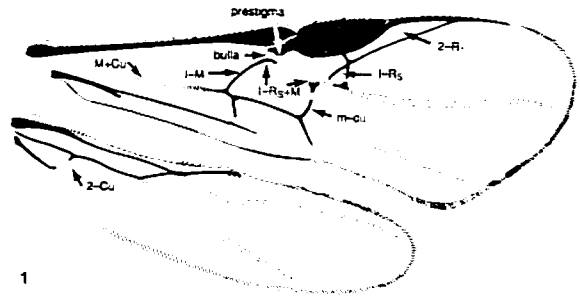
Mesosoma. Pronotum with subpronope (dorsolateral depression) (Fig. 22); mid and hind tibia with spines (Figs 26, 27); transscutal articulation not functional; posterior transverse scutellar depression usually (90%) absent; epicnemial carina present; longitudinal carina of propleuron complete; hind coxal cavity open (20%) (Fig. 11) or closed by sclerite (Figs 10, 12, 13); tarsal claws simple or cleft, with or without a basal lobe (Figs 16–20); hind coxa large, in lateral aspect as large as head; medial spur of hind tarsus more than quarter length of basitarsomere.

Metasoma. Segments two and three with spiracles on laterotergites; males with tergal glands and modified setal brushes on metasomal terga six and seven (Fig. 9); ovipositor variable in length, from barely exerted to longer than body.

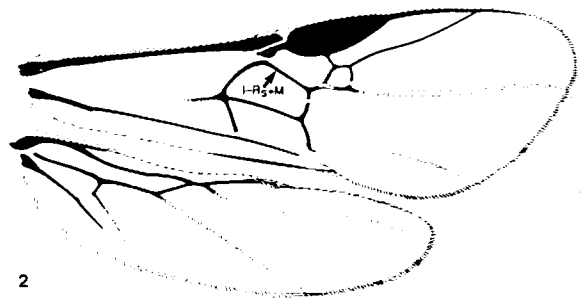
Agathidini Blanchard

Agathites Blanchard, 1845: 157, 164.
Agathidina: Achterberg, 1990: 32.

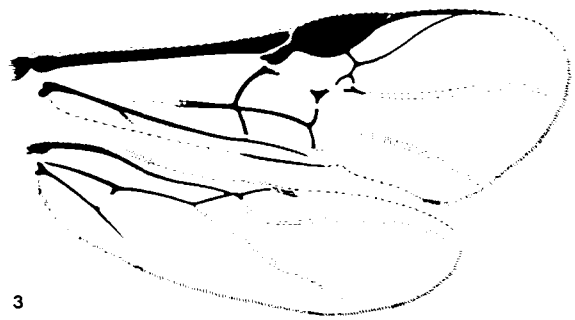
Diagnosis. Labio-maxillary complex elongate (galea longer than mandible); labial palpomere 3 not reduced, more than 0·5 length of palpomere 4 (cf. Fig. 25); tarsal claws



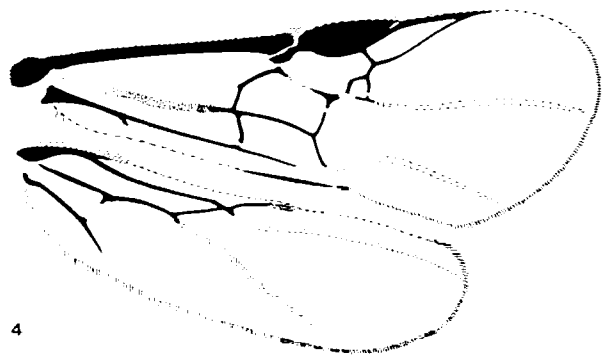
1



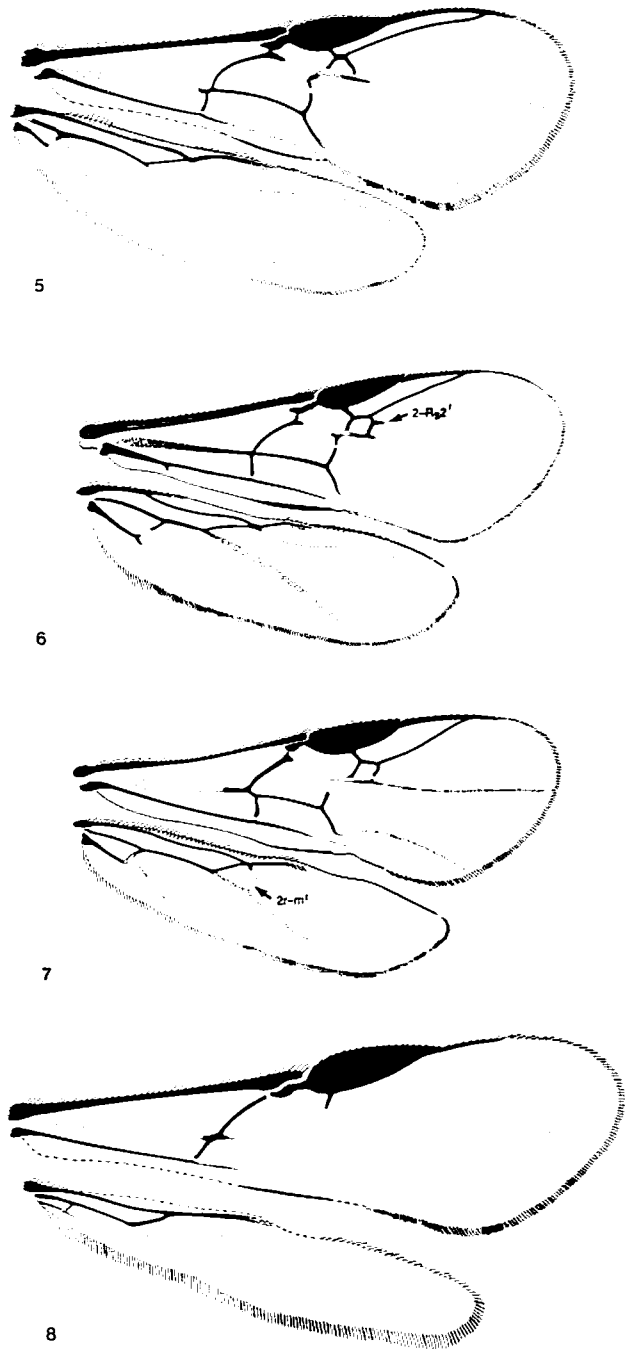
2



3



4



FIGS 1–8. Wings of *Bassus annulipes* (Cresson); (2), *Earinus limitaris* (Say); (3), *Agathirsia testacea* Muesebeck; (4), *Crassomicrodus divisus* (Cresson); (5), *Coccygidium luteum* Saussure; (6), *Disophrys inculcator* Linnaeus; (7), *Cremnops desertor* (Linnaeus); (8), *Mesocoelus philippinensis* Muesebeck.

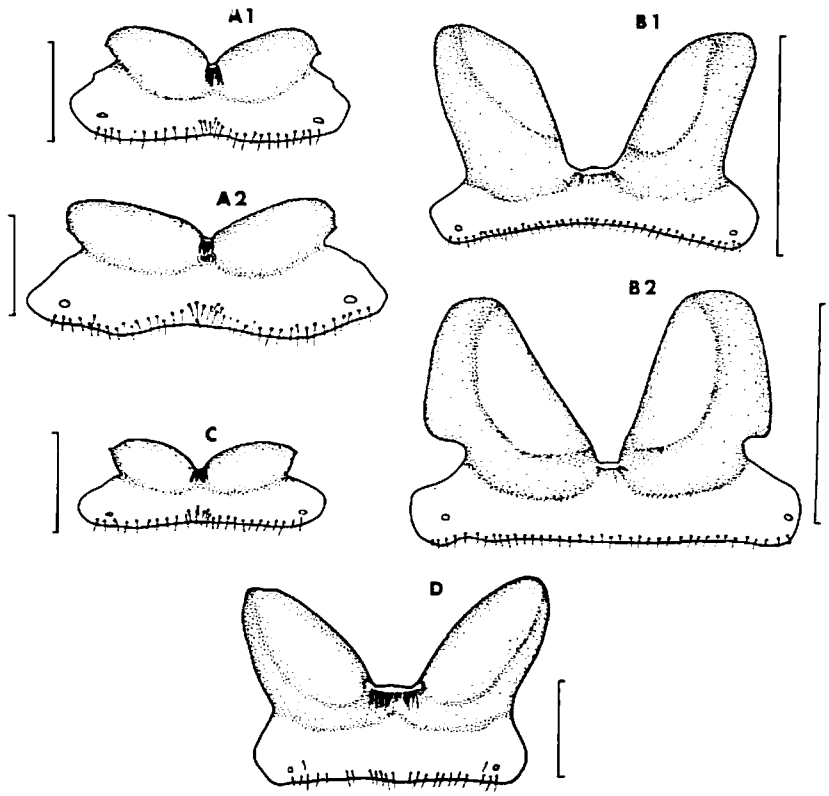
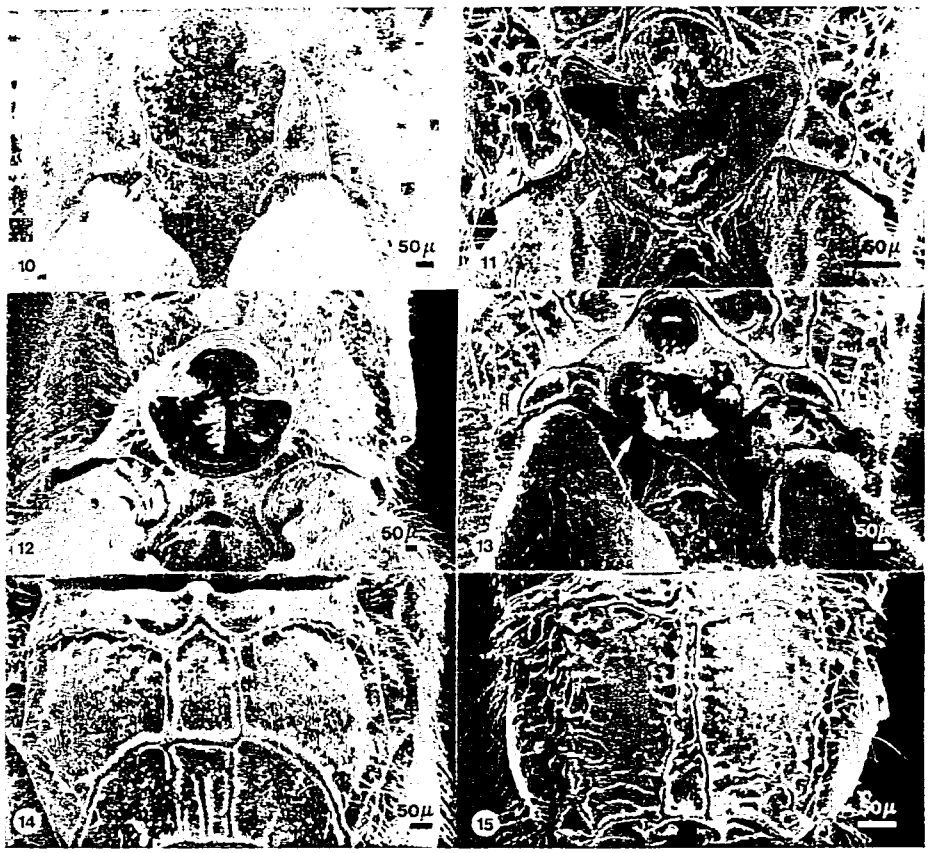


FIG. 9. Scale bars = 0·1 mm. A1, *Agathirsia nigricauda* (Viereck), tergal gland of metasomal segment seven; A2, *Agathirsia nigricauda* (Viereck), tergal gland of metasomal segment six; B1, *Agathis gibbosa* (Say), tergal gland of metasomal segment seven; B2, *Agathis gibbosa* (Say), tergal gland of metasomal segment six; C, *Agathirsia tesacea* (Muesebeck), tergal gland of metasomal segment six; D, *Cremnops vulgaris* (Cresson), tergal gland of metasomal segment six.

usually (90%) with weak basal tooth (Fig. 18) or simple (10%) (Fig. 20); mid tibia usually (95%) with preapical spines (cf. Fig. 26); hind basal tarsomere without longitudinal serrate ridge; trochantellus of hind leg without longitudinal carina; 1 – Rs + M vein of fore wing incomplete (Figs 3, 4); 1 – Rs cell of fore wing quadrate, triangular, or absent; hind coxal cavity usually (80%) not separated from metasomal foramen (Fig. 11), sometimes (20%) separated by narrow sclerite (Fig. 13); notauli usually (85%) present; propodeum with two or three median longitudinal carinae (Fig. 15), anterior transverse carina often (40%) present (Fig. 15), posterior transverse carina absent; median tergite of first metasomal segment usually (90%) with two weak longitudinal carinae, sculpture variable; ovipositor sheaths usually (98%) more than half length of metasoma and not strongly curved ventrally.

Generic Checklist of Agathidini

Agathis Latreille, 1804: 175. (*Aenigmostomus* Ashmead, 1990: 128).
Agathirsia Westwood, 1882: 20. (*Agathona* Westwood, 1882: 22; *Paragathis* Ashmead, 1889: 638).
Rhamphagathis Tobias, 1962: 1195.
Crassomicrodus Ashmead, 1900: 128. (*Epimicrodus* Ashmead, 1990: 129).
Cerostomus trichiosoma



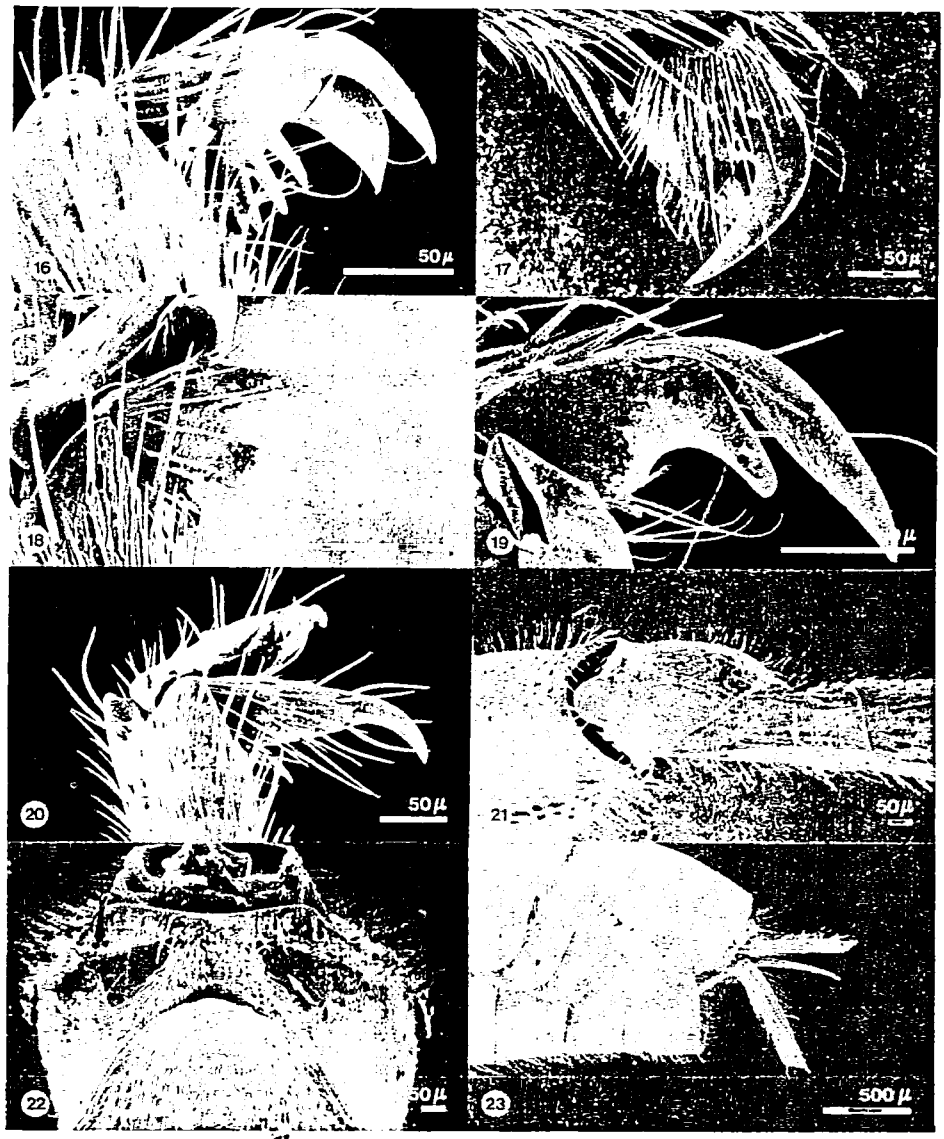
FIGS 10–15. *Bassus calcaratus* (Cresson), metasomal foramen and hind coxae: (11), *Agathis gibbosa* (Say), metasomal foramen and hind coxae; (12). *Alabagrus imitatus* (Cresson), metasomal foramen and hind coxae; (13), *Crassomicrodus* sp., metasomal foramen and hind coxae; (14), *Bassus calcaratus* (Cresson), propodeum; (15), *Agathis gibbosa* (Say), propodeum.

Cremnoptini new tribe

Diagnosis. Labio-maxillary complex elongate (galea longer than mandible); labial palpomere 3 not reduced, more than 0·5 length of palpomere 4 (cf. Fig. 25): tarsal claws cleft, and usually (98%) with basal pectination (Fig. 16); mid-tibia without preapical spines: hind basal tarsomere without longitudinal serrate ridge: trochantellus of hind leg rarely (5%) with longitudinal carina (cf. Fig. 21): 1−Rs+M vein of fore wing incomplete (Fig. 7); 1−Rs cell of fore wing quadrate (Fig. 7) or rarely (5%) triangular: notauli usually (80%) present: hind coxal cavity usually (98%) separated from metasomal foramen by wide sclerite: propodeum usually (80%) areolate (cf. Fig. 14); median tergite of first metasomal segment smooth, lacking sculpture and lacking pair of longitudinal carina; ovipositor sheaths usually (98%) less than half length of metasoma and not strongly curved ventrally.

Generic Checklist of Cremnoptini

Biroia Szépligeti, 1900: 62.



FIGS 16–23. *Cremnops vulgaris* (Cresson), fore claw; (17). *Alabagrus imitatus* (Cresson), mid claw; (18), *Agathis* sp., fore claw; (19), *Coccygidium luteum* Saussure, fore claw; (20), *Crassomicrodus fulvescens* (Cresson), fore claw; (21), *Coccygidium luteum* Saussure, ridge of hind trochantellus; (22), *Coccygidium luteum* Saussure, pronotum illustrating subpronope (lateral pit); (23), *Coccygidium luteum* Saussure, lateral spect of metasoma showing short ovipositor

Cremnops Förster, 1862: 246.
Hyrtanommatidium Enderlein, 1920: 165.
Isoptronotum Enderlein, 1920: 193.
Labagathis Enderlein, 1920: 168.
Megagathis Kriechbaumer, 1894: 311.
Mesoagathis Cameron, 1904c: 174.
Zacremnops Sharkey and Wharton, 1985: 600.

Disophrini new tribe

Diagnosis. Labio-maxillary complex sometimes (20%) elongate (galea longer than mandible): labial palpomere 3 not reduced, more than 0·5 length of palpomere 4 (cf. Fig. 25); tarsal claws cleft, and usually (98%) without basal pectination (Fig. 19); rarely (10%) hind tarsal claw simple with rounded basal lobe (cf. Fig. 17); mid-tibia without preapical spines: hind basal tarsomere with longitudinal serrate ridge (Figs 28, 29): trochantellus of hind leg usually (90%) with longitudinal carina (Fig. 21): 1 – Rs + M

FIGS 24–29. *Alabagrus imitatus* (Cresson), labial palpus; (25), *Earinus limitatus* (Say), labial palpus; (26). *Earinus zeiripherinae* Walley, preapical spines of mid tibia; (27), *Earinus zeiripherinae* Walley, apical spines of hind tibia; (28), *Coccygidium luteum* Saussure. serrate ridge of hind basitarsomere; (29), *Coccygidium luteum* Saussure, detail of serrate ridge of hind basitarsomere.

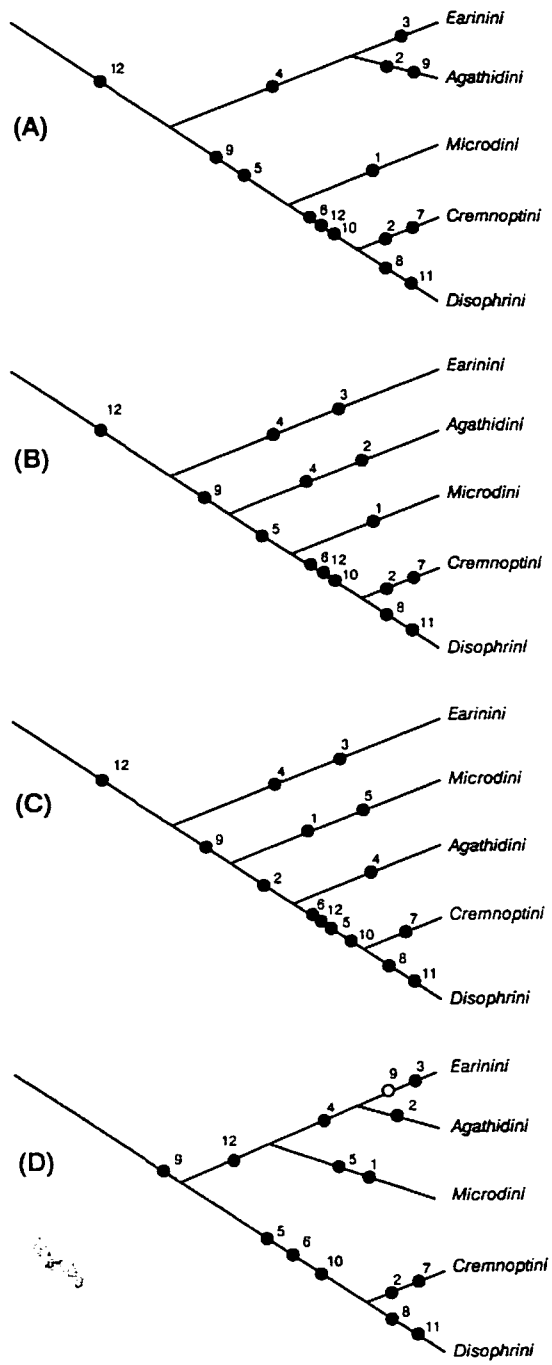


FIG. 30. Four minimum length cladograms based on the data set of Table 1.

vein of fore wing incomplete (Figs 5, 6); 1 – Rs cell of fore wing quadrate (Fig. 6) or triangular (Fig. 5); notauli usually (90%) present; hind coxal cavity separated from metasomal foramen by wide sclerite (cf. Fig. 12); propodeum often areolate (cf. Fig. 15), but variable; median tergite of first metasomal segment smooth, lacking sculpture and usually (90%) lacking pair of longitudinal carina; ovipositor sheaths less than half length of metasoma and curved ventrally (Fig. 23).

Generic Checklist of Disophrini

Balcemena Cameron, 1903: 129.
Coccygidium Saussure, 1892: pl. 15, fig. 27. (*Ahngeria* Kokujev, 1902: 6; *Brachyropalum* Kriechbaumer, 1894: 312; *Caenophylax* Schulz, 1911: 88; *Lisitheria* Cameron, 1904a: 306; *Neophylax* Ashmead, 1900: 119; *Spilomicrodus* Cameron, 1911a: 323; *Xanthomicrodus* Cameron, 1904b: 157; *Zelomorpha* Ashmead, 1900: 129; *Zelomorphidea* Viereck, 1912b: 630).
Dichelosus Szépligeti, 1902: 71.
Disophrys Förster, 1862: 246. (*Pseudagathis* Kriechbaumer, 1894: 65).
Euagathis Szépligeti, 1900: 62. (*Chromomicrodus* Ashmead, 1900: 129).
Gryochus Enderlein, 1920: 182.
Hemichroma Enderlein, 1920: 183.
Holcotroticus Cameron, 1902: 41.
Hypsostypos Baltazar, 1963: 3.
Liopsia Enderlein, 1920: 182.
Macroagathis Szépligeti, 1908: 418.
Marjoriella Sharkey, 1983: 94.
Monophrys Achterberg, 1988: 47.
Oreba Cameron, 1900b: 94.
Pelmagathis Enderlein, 1920: 168.
Platyagathis Turner, 1918: 113.
Protroticus Achterberg, 1988: 50.
Pseudocremnops Szépligeti, 1915: 152.
Troticus Brullé, 1846: 508.

Earinini new tribe

Diagnosis. Labio-maxillary complex not elongate (galea shorter than mandible); labial palpomere 3 not reduced, more than 0·5 length of palpomere 4 (Fig. 25); tarsal claws usually (80%) with weak basal tooth (cf. Fig. 18) or (20%) simple (cf. Fig. 20); mid-tibia usually (95%) with preapical spines; hind basal tarsomere without longitudinal serrate ridge; trochantellus of hind leg without longitudinal carina; 1 – Rs + M vein of fore wing usually (90%) complete (Fig. 2); 1 – Rs cell of fore wing usually (70%) quadrate (Fig. 2) or (30%) triangular; hind coxal cavity usually (90%) contiguous with metasomal foramen (cf. Fig. 11), rarely (10%) separated by narrow sclerite (cf. Fig. 13) and exceptionally (two species of an undescribed genus) separated by a wide sclerite (cf. Fig. 12); notauli absent; propodeum with two or three median longitudinal carinae (Fig. 15), anterior transverse carinae often (40%) present (Fig. 15), posterior transverse carina absent; median tergite of first metasomal segment often (50%) with two weak longitudinal carinae, and often (50%) sculptured; ovipositor sheaths usually (99%) more than half length of metasoma and not strongly curved ventrally.

Generic Checklist of Earinini

Earinus Wesmael, 1837: 246.
Sesioctonus Viereck, 1912a: 1.

Microdini Ashmead

Microdini Ashmead, 1900: 128.
Mesocoelini Viereck, 1918: 69.
Aneurobraconinae Fahringer, 1936: 587.
Mesocoelina: Achterberg, 1990: 33, 47.

Diagnosis. Labio-maxillary complex usually (95%) not elongate (usually galea shorter than mandible); labial palpomere 3 usually (95%) reduced (Fig. 24), less than 0·5 length of palpomere 4; tarsal claws usually (95%) with strong basal tooth (Fig. 17) or (5%) weak basal tooth (Fig. 18); mid-tibia usually (95%) with preapical spines (cf. Fig. 26); hind basal tarsomere without longitudinal serrate ridge; trochantellus of hind leg without longitudinal carina; 1 – Rs + M vein of fore wing incomplete or nebulous at mid-length (Figs 1, 8); 1 – Rs cell of fore wing quadrate, triangular, or absent; hind coxal cavity usually (98%) separated from metasomal foramen (Figs 10, 12), and usually (90%) separated by wide sclerite; notauli usually (85%) present; propodeum often (50%) areolate (Fig. 14), but variable; median tergite of first metasomal segment usually (85%) with two weak longitudinal carina, and usually (70%) sculptured; ovipositor sheaths usually (98%) more than half length of metasoma and not strongly curved ventrally.

Note. The subtribe Mesocoelina Viereck, employed by Achterberg (1990) renders the Microdini paraphyletic if accepted. As detailed in Sharkey (1986) members of *Mesocoelus* s.l., i.e. *Aneurobracon* Brues, *Mesocoelus* Schultz, and *Plesiocoelus* Achterberg, are aberrant agathidines with many reduced venational features. That they are members of the Microdini is evidenced by the presence of a small labial palpomere 3. The Microdini exclusive of *Mesocoelus* s.l. is paraphyletic, lacking diagnostic, synapomorphic character states.

Achterberg (1990: 32, 33) implies that the loss of fore wing vein 1 – Rs and the loss of the hemispherical depression on the scutellum posteriorly may be synapomorphies for the Agathidini + Earinini + Microdini (his subtribe Agathidina) the inferred sister group of the Mesocoelina. This is despite the fact that these characters occur in numerous lineages throughout these groups. I would rather assume independent losses in each lineage rather than independent reappearances of the ground state. Achterberg (1990: 33) suggests: 'Further research on the Agathidini may even show that the subtribe Agathidina is made paraphyletic by the separation of the subtribe Mesocoelina. Until further data becomes available it seems convenient to unite the three genera treated in this paper as the subtribe Mesocoelina Viereck.' To avoid paraphyly, or at least to avoid the use of a taxon unsupported by synapomorphies, I include *Mesocoelus* and allies in the Microdini. That this group may be the sister group of the Microdini or the clade Agathidini + Earinini + Microdini, is unsupported and contradicted by other evidence (presented earlier in the section 'Taxonomic units'). It is my belief that this group of genera is a derived lineage within the large genus *Bassus*, but further discussion is beyond the scope of this paper.

Generic Checklist of Microdini

Aerophiliodes Strand, 1911: 131.
Aerophilus Szépligeti, 1902: 73. (*Hormagathis* Brues, 1926: 287).
Alabagrus Enderlein, 1920: 203. (*Astiria* Enderlein, 1920: 207; *Craspedobothrus* Enderlein, 1920: 206; *Liyptia* Enderlein, 1920: 210).
Aneurobracon Brues, 1930: 1002.

Bassus Fabricius, 1804: 93. (*Aerophilina* Enderlein, 1920: 205. *Aerophilopsis* Vierick, 1913a: 555; *Agathellina* Enderlein 1920: 211; *Agathiella* Szépligeti, 1902: 73; *Cenostomus* Förster, 1862: 246. *Ditropia* Enderlein, 1920: 210; *Eumicrodus* Förstet, 1862: 247; *Ioxia* Enderlein, 1920: 219; *Lytophylus* Viereck, 1905; 267; *Microdus* Nees von Esenbeck, 1814: 184; *Neomicrodus* Szépligeti, 1908: 421; *Therophilus* Wesmael, 1837: 15).
Braunsia Kriechbaumer, 1894: 63.
Baeognatha Kokujev, 1903: 243.
Camptothlipsis Enderlein, 1920: 166.
Hemiogaster Enderlein, 1920: 200.
Ischnagathis Cameron, 1909: 148.
Laccagathis Watanabe, 1934: 121.
Lissagathis Cameron, 1911: 245.
Mesocoelus Schultz, 1911: 88. (*Coelothorax* Ashmead, 1898: 165).
Metriosoma Szépligeti, 1902: 74.
Obesomicrodus Papp, 1971: 338.
Orgiloneura Ashmead, 1900: 129.
Pharpa Sharkey, 1986: 1232.
Pholeocephala Achterberg, 1988: 44.
Plesiocoelus Achterberg, 1990: 44.
Trachagathis Viereck, 1913b: 366.
Zamicrodus Viereck, 1912b: 630.

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