Essay on the phylogeny of Braconidae (Hymenoptera: Ichneumonoidea)

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A cladistic analysis is given of the higher classification of the Braconidae (Hymenoptera). The analysis is based on characters of both adult and larval morphology, as well as on their general biology. The Aphidiinae are considered to be a subfamily of the Braconidae not closely related to any of the other main groups of the subfamilies. Three groups are given subfamily rank in this paper: Dirrhopinae subfam. nov. (based on the Holarctic genus *Dirrhope* Foerster, 1862), Histeromerinae Fahringer (based on the Holarctic genus *Histeromerus* Wesmael, 1838), and Trachypetinae Schulz (based on the Australian genus *Trachypetus* Guérin, 1831). The Cenocoeliinae are separated from the Helconinae, a subfamily to which they are not closely related. The Blacinae (including *Dyscoletes* Haliday, 1849) are treated as a group most closely related to the Euphorinae, and the Microtypini are included in the Homolobinae. New tribes are: Leptorhaconotini trib. nov. (position uncertain, provisionally in the Doryctinae; based on the genus *Leptorhaconotus* Granger, 1949 from Malagasy), Dyscoletini trib. nov. (included in the Blacinae and based on the Holarctic genus *Dyscoletes* Haliday, 1840), and Acampsini trib. nov. (included in the Sigalphinae, and based on the Palaearctic genus *Acampsis* Wesmael, 1835). The tribus Minangini De Saeger (based on the Afrotropical genus *Minanga* Cameron, 1906) is removed from the Cheloninae and included in the Sigalphinae.

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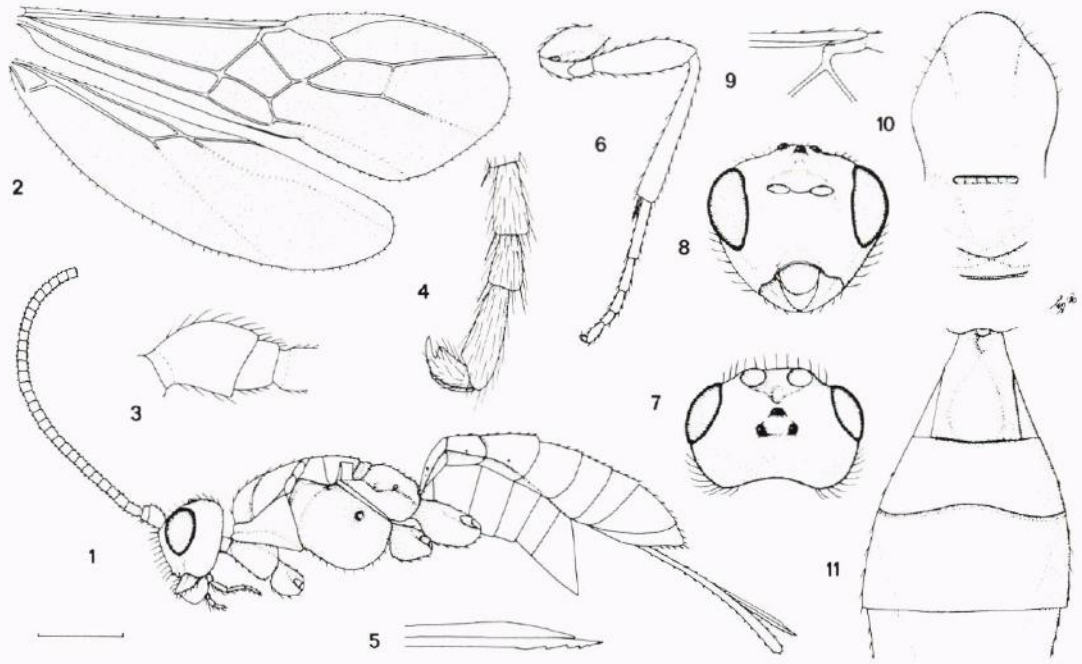
The phylogeny of the Braconidae has been the subject of only a limited number of papers. The basis was laid by Griffiths (1964, only Alysiinae-Dacnusini), Čapek (1965 & 1970), and Tobias (1967). In all these papers general biology was of importance for the construction of a final classification. Van Achterberg (1976) gave a historical review and tried to construct a division and key to the subfamilies of the Braconidae, mainly based on morphological characters of the final instar larvae and (some additional) features of the adults, especially of the 1st metasomal tergite (Van Achterberg, 1974).

The (internal) relationship of some subfamilies have been analyzed cladistically: Amicrocentrinae (Van Achterberg, 1979a), Xiphozelinae (id., 1979b), Homolobinae (id., 1979c), Helconinae (id., 1983a), Gnaptodontinae (id., 1983b), and Microgastrinae (Mason, 1981), but the majority of the groups remain untreated. A major advance was the research of Edson and Vinson (1979) on the venom apparatus of female braconids.

The main reason for the confusion in the systematics of the Braconidae is the occurrence of many parallel evolutionary trends (leading to "homeoplasies"); for a list see Van Achterberg, 1976. A good example is the formation of a metasomal carapace (Tobias & Dudarenko, 1974). Comparative morphology of the posterior side of the head (Tobias & Potapova, 1982) and grouping on base of overall similarity, result in one huge mixed group (= type H II): including part of the Agathidinae, Blacinae, Euphorinae, Neoneurinae, Macrocentrinae, Microgastrinae, Ichneutinae, part of Opiinae, Gnaptodontinae, Sigalphinae, Orgilinae, Homolobinae, Acaeliinae, Cheloninae, Helconinae, and Cenocoeliinae. Additionally a large, more homogenous group (B II with Rogadinae, some Doryctinae, Braconinae, and large part of Opiinae), a smaller



Figs. 1–11. *Bracon sabulosus* Szépligeti, holotype ♀, Braconidae-Braconinae. – 1. Habitus, lateral aspect. – 2. Wings. – 3. Scapus and pedicellus, outer aspect. – 4. Outer middle claw. – 5. Apex of ovipositor. – 6. Hind leg. – 7. Head, dorsal aspect. – 8. Head, frontal aspect. – 9. Detail of vein 1-SR of fore wing. – 10. Thorax, dorsal aspect. – 11. 1st–3rd metasomal tergites, dorsal aspect. – 1, 2, 6. Scale-line = 1 mm. – 3–5. Scale-line = 5 mm. – 7–11. Scale-line = 2 mm.

homogeneous group (B I with part of Doryctinae and Histeromerinae) and groups with specialized head morphology (A II with Alysiinae, Ag II containing part of Agathidinae with elongated head, H III with *Chrysopophthorus* and *Wesmaelia* (Euphorinae) and H IV with Cercobarconinae). Only these latter groups possess "positive apomorphous character-states" in the head morphology, opposed to "negative apomorphous character-states" or "reductional character-states" (Van Achterberg, 1983b). The latter concerns reductions, which occur rather frequently and independently in different groups; thus easily leading to incorrect conclusions. The chance of parallelism in "positive apomorphous character-states" (especially when complicated structures are involved) is less and is found only rarely in distantly related groups, but the secondary loss of a structure should be reckoned with. Another problem is the lack of synapomorphous character-states for some groups. For instance, the Doryctinae and the Rogadinae seem to be sister-groups because of overall similarity, but no synapomorphy has yet been detected. For such a group the name "interim-group" is proposed because of its provisional nature and to indicate that it is "sandwiched" between groups with autapomorphies. At least some of the interim-groups may be poly- or paraphyletic and will certainly be subdivided in the future. Candidates within e.g., the Doryctinae, are the tribes Evaniodini Fischer (Neotropics) and Leptorhaconotini **(tribus nov.**, based on *Leptorhaconotus* Granger, 1949 from Malagasy), which do not fit well within the Doryctinae; other groups assigned very provisionally to a subfamily are the Microtypini (Homolobinae) and the Aneurobraconini (Orgilinae). The only possibility for a more natural system is to find more (positive) apomorphous character-states by careful cladistic analysis of large collections. It is obvious that the cladistic analysis as summarized in Figs. 12–17 is a very provisional one to stimulate further research; e.g., larvae of too many subfamilies (22 out of 35) are not or hardly morphologically known.

New or less known characters used for the analysis

Despite the huge size of the Braconidae (± 40.000 spp. or more) this paper attempts to give an overall analysis of the subfamilies. Many characters have been reviewed in the material available and some characters found to be stable enough within genera or tribes to be used for the cladistic analysis. However, several exceptions are present, but these are usually not mentioned because they appear to be secondary developments; e.g., the few Ichneumonidae-Cryptinae with 2nd and 3rd metasomal tergites united.

1. *Venom apparatus of female* (Edson & Vinson, 1979). Group II and a majority of the Aphidiinae posses a type I venom reservoir with a wall containing many longitudinal and circular muscles. The minority of the Aphidiinae and the groups III and IV have type II venom reservoir: thin-walled with relatively few muscles. Outgroup comparison reveals that type I is the apomorphous state (as outgroup is used the sister-group of the Braconidae as depicted in Fig. 12); this state is probably lost independently in the tribe Praini of the Aphidiinae, a group with several other (not related) apomorphous character-states. The venom apparatus of the following subfamilies has not examined by Edson & Vinson: Histeromerinae, Mesostoinae, Ypsistocerinae, Gnaptodontinae, Acaeliinae, Miracinae, Dirrhopinae, Meteorideinae, Cercobarconinae, Trachypetinae, Xiphozelinae, Sigalphinae, Khoikhoiinae, Betylobraconinae, and Amicrocentrinae. Mostly small subfamilies of which no material in alcohol was available for study. I have prepared the venom apparatus of *Acaelius subfasciatus* (Haliday) (Acaeliinae); it proved to be different from the venom apparatus of the Microgastrinae, a group with which it is generally associated, and fits best the diagnosis of type I.

2. *Caudal vesicle of the first and second larval instars*. The rectum (proctodaeum) is evaginated in many young larvae of the groups III and IV. Such an evagination has been found in the Helconinae (Brachistini: Haeselbarth, 1962), Macrocentrinae (Daniel, 1932), Orgilinae (Oatman et al., 1969), Cheloninae (Vance 1932; Rosenberg, 1934), and Microgastrinae (Vance, 1931; Parker, 1935). The caudal process of the Agathidinae is not vesicle-shaped (Nickels et al., 1950), but the base of the "tail" is widened as in the Euphorinae (Euphorini: Jackson, 1928; Brindley, 1939; Centistini: Loan & Holdaway, 1962; Meteorini: Simmonds, 1947), a condition dissimilar to the (plesiomorphous) condition in early instar larvae of group II. In the Aphidiinae some Aphidiini may have a somewhat widened base of the "tail", a condition absent in the other tribes (e.g., Starý, 1966). The young larval instars of many groups still need to be investigated, especially in such controversial groups as the Acaeliinae, Miracinae, Dirrhopinae, Gnaptodontinae, Meteorideinae, Blacinae, and Sigalphinae. The function of the caudal vesicle is uncertain; it may be an accessory respiratory organ, used for the excretion or for the avoiding encapsulation by the host; an explanation is needed to account for the disappearance of the organ in later instars of the endoparasitic larva.

3. *Ecto- versus endoparasitism*. In the past confusion has arisen about the ectoparasitism of several subfamilies in the groups III and IV, because (as was discovered later) numerous endoparasites have a final (obligatorily) ectoparasitic phase. External feeding of endoparasites was observed in the Macrocentrinae (Daniel, 1932), Homolobinae (Allen, 1977), Helconinae (Brachistini: Haeselbarth, 1962), Cheloninae (Vance, 1932), and Agathidinae (Simmonds, 1947; Nickels et al., 1950). Endoparasites of group I (e.g., Alysiinae: Caudri, 1941) and the Aphidiinae, also some parasites of the groups III and IV (Microgastrinae: Vance, 1931; Cardiochilinae: Chamberlin & Tenhet, 1926; Euphorinae: Brindley, 1939; Loan and Holdaway, 1962) have no ectoparasitic final phase. It is obvious from cladistic analysis that the switch from ecto- to endoparasitism has been made at least 4 or 5 times (first in the parent population of the groups III and IV, later in the Aphidiinae, in the Ichneutinae-group (nos. 10–14), in the Alysiinae-group (nos. 8 and 9), and finally in the Rogadinae). The groups of Braconidae with the least apomorphous character-states are all parasites of Coleoptera (especially larvae of Cerambycidae) and there is little room for doubt (also considering the out-groups) that endoparasitism is a later development departing from an ectoparasitic (sometimes gregarious) "predatory" behaviour. Therefore it is assumed that the Braconidae developed from ectoparasites of concealed living coleopterous larvae. Being

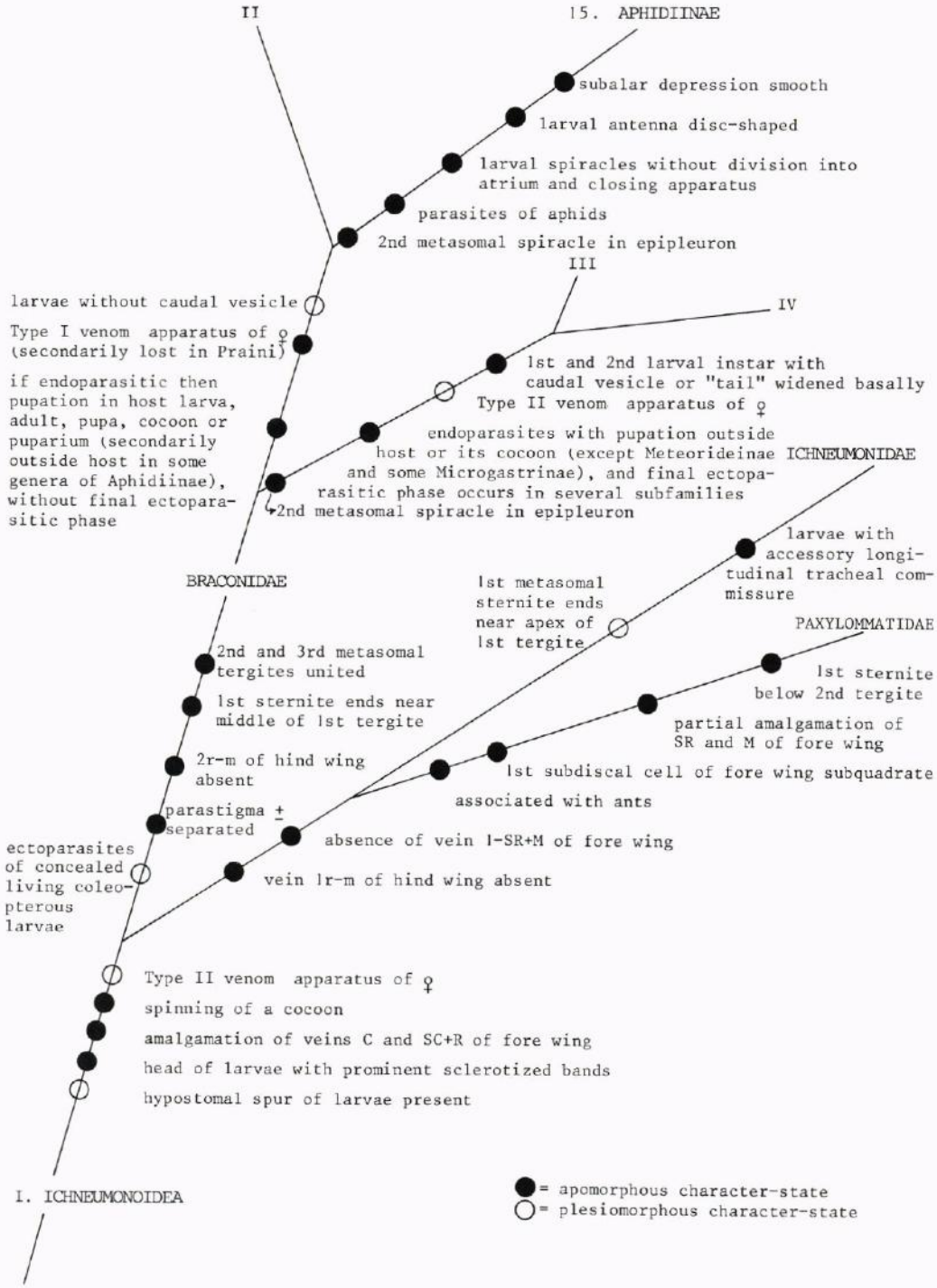


Fig. 12. Cladogram of Ichneumonoidea: families and subfamily groups within the Braconidae (Aphidiinae and groups II-IV).

an endoparasite of a (partly) concealed living host larva still allows a final ectoparasitic phase (e.g., in the Helconinae, Cheloninae, Homolobinae, and Macrocentrinae). An ectoparasitic phase of an exposed ("phanerozoic") host larva would involve a high risk for predation. This may be why the final ectoparasitic phase is absent (thus secondarily lost) in the Microgastrinae, Cardiochilinae and Euphorinae. If this is correct, then it is to be predicted that the Orgilinae have an ectoparasitic phase, although it has yet to be observed.

4. *Pupation in- or outside the host or its cocoon.* Pupation site selection is an indication of the polyphyletic origin of the endoparasitism. Most aberrant is pupation in the mummified caterpillar by the Rogadinae-Rogadini.

In the Alysiinae-group the parasite pupate inside the host-puparium (usually after the construction of a delicate cocoon) and in the Alysiinae the specialized mandibles are used to make a hole in the puparium. The subfamilies of the Ichneutinae-group (nos. 10–14) are known to make a delicate cocoon within the host-cocoon. The Aphidiinae pupate within the mummified aphid skin mounted to the surface of the plant; only three genera (with several apomorphies) are known to pupate below the aphid, viz., *Praon* Haliday (tribe Praini), *Dyscritulus* Hincks and *Protaphidius* Ashmead (both tribe Aphidiini). The remaining groups III and IV, which contain endoparasites, pupate outside the host or its cocoon. Exceptions are the genus *Deuterixys* Mason (pupation in host cocoon, parasite of Lyonetiidae, obviously a secondary development within the Microgastrinae) and the subfamily Meteorideinae (gregarious parasites of Gelechiidae and Tortricidae, spin cocoons inside the host pupa; which is almost unique for the Braconidae, independently developed only in the genus *Bucculatriplex* Viereck (Rogadinae)).

5. *Situation of the spiracle of the second metasomal tergite.* The spiracle may be dorsally situated (thus in the notum of the tergite, as usual for the Braconinae-group (nos. 1–3)) or laterally in the epipleuron, more or less separated by a lateral crease from the notum (as in most other Braconidae). The position of the spiracle in the epipleuron is considered to be the apomorphous state because in the sister-group (Fig. 12) the spiracle is situated in the notum (or nearly so). The same applies to the 1st metasomal tergite and the statement of Mason (1981:3) that the position of the 1st spiracle in the epipleuron should be considered the plesiomorphous state is, in my opinion, therefore incorrect.

6. *Development of parastigma.* The parastigma is usually much more differentiated from vein SC+R than in other Hymenoptera and seems to be an autapomorphy of the Braconidae. The vein connected to it (1-SR) is also subject to change of position in many groups (part of the Braconinae, Microgastrinae, Neoneurinae) or may be (largely) absent (Agathidinae).

7. *Development of dorsope.* The development of a dorsope (Van Achterberg, 1974) is an important apomorphous character-state. It is not known outside the Braconidae and occurs in two groups: the group with Doryctinae and Alysiinae (large parts of nos. 1, 2, 8 and 9, but absent in nos. 3–7) and in the Euphorinae-group (large part of nos. 17–19). Within these groups the dorsope may be secondarily lost or shallow. In the Blacinae a shallow dorsope is still recognizable by the curvature of the dorsal carinae basally; in the Euphorinae as well in the Doryctinae the dorsope disappears because of the petiolization of the 1st metasomal tergite.

8. *Hypoclypeal depression.* Usually referred to by the incorrect term "cyclostoma"; the real apomorphous state concerns a more or less concave and glabrous labrum and a clypeus which is partly depressed and forms part of the hypoclypeal depression. The result is not a "round mouth" (=cyclostoma), because the mouth is situated more ventrally and the depression is normally elliptical rather than round. The hypoclypeal depression may have been evolved to provide the mandibles more working space, especially to grip objects. The hypoclypeal depression is distinctly development in almost all spp. of the subfamilies nos. 1–3; the nos. 5 and 6 have the depression formed only by the backwards slanted and (rather) concave labrum and the clypeus is not depressed. The clypeus is narrowly depressed and wide in a peculiar way in the Histeromerinae and the Telengaiinae.

9. *Posterior flange of propleuron.* The propleuron usually has a somewhat differentiated posterior flange, more or less protruding over the lower posterior part of the pronotum in front of the fore coxa. Outgroup comparison indicates that the absence of the propleural flange is the apomorphous state. The flange is absent in the

Braconinae (except in a few tropical genera), Histeromerinae, Mesostoinae, Ypsistocerinae, Ichneutinae, Neoneurinae, Cardiochilinae, Khoikhoiinae, and Microgastrinae (with the exception of *Philoplitis* Nixon).

10. *Transverse posterior scutellar depression.* This is a frequently narrow, transverse depression medio-posteriorly at the scutellum and is more or less crenulate. Main character-state for group III, uniting mainly spp. with comparatively complete venation of the wings, if compared with group IV. Especially in the Microgastrinae and the Cardiochilinae the scutellum may be sculptured posteriorly, but only very rarely (e.g., *Hartemita* Cameron) is it similarly depressed as in group III. This may indicate the transverse posterior scutellar depression is secondarily lost in group IV.

11. *Separated cuspidal process.* As pointed out by Tobias (1967), an unseparated cuspidal process of the male genitalia has to be considered the plesiomorphus character-state, as present in the sister-group. A narrow cuspidal process is separated in the Homolobinae as treated in this paper (including the Microtypinae) as well as in the Euphorinae and Blacinae. A dissimilar separate cuspidal process is present in the Agathidinae. In the cladistic analysis presented here the Agathidinae are referred to a group different from the group which includes the Homolobinae and the Euphorinae; so it appears that the separation of the cuspidal process in these two groups is a parallelism. The presence of a separate cuspidal process in the Homolobinae as well as in the Blacinae and Euphorinae (p.p.) seems to be another case of parallelism, although these groups are comparatively closely related.

12. *Development of pronope.* The development of a pronope (a depression in the pronotum: Van Achterberg, 1983: 301, Fig. 55) is considered to be an important character-state of several groups av Braconidae; e.g., of the Helconinae-group (nos 16-19). Some genera of these groups may have the pronope absent, e.g., *Dyscoletes* Haliday of the Blacinae, but usually the pronope is more or less developed.

Subfamilies of the Braconidae

1. **Doryctinae** Foerster, 1862

Rather large subfamily, consisting of ectoparasites of larvae of (wood- and bark-boring) Coleoptera. Less commonly other hosts in plant tissues are attacked.

2. **Rogadinae** Foerster, 1862

Large and heterogenous group; in this subfamily an independent transition to endoparasitism has taken place. This accompanied with some peculiarities, such as the toothless mandibles of the larvae and the mummification of the host-caterpillar. Gregarious ectoparasitism occurs in several genera, e.g., *Hormius* Nees, *Oncophanes* Foerster, and *Chremylus* Haliday. Solitary endoparasitism is usual in the genus *Rogas* Nees and its allied genera, but gregarious endoparasitism is known.

3. **Braconinae** Stephens, 1829

Very large subfamily, consisting of solitary or gregarious ectoparasites of larvae of holometabolous insects. According to Čapek (1970:862) the host larva is paralyzed at egg deposition, the parasite larva feeds on the paralyzed host and forms its delicate cocoon in a sheltered place. It is the only group wherein genera occur with two fore tibial spurs (*Rhamnura* Enderlein and some new genera).

4. **Telengaiinae** Tobias, 1962

Small subfamily, containing only the South Palaearctic genus *Telengaia* Tobias. The biology is unknown. Because of the 5-segmented maxillary palp, the absence of the occipital and prepectal carinae, and of the dorsope it seems to be related to the Braconinae. However, the lack of the synapomorphies of the hind wing, as well the highly aberrant mesopleural depression seem to justify its separate position.

5. **Ypsistocerinae** Cushman, 1923

Small subfamily, which contains the genera *Ypsistocerus* Cushman and *Termitobracon* Brues. They live, probably as parasites, in the nests of termites in the Neotropical region. The numerous autapomorphous character-states (e.g., the highly inserted antennae, the very reduced palpi, the unidentate mandibles, the numerous long setae of the wing membrane, and the

submedially inserted ovipositor) makes it difficult to place this group. Because of the hypoclypeal depression, the flattened 1st metasomal tergite and reductions similar to those present in the Braconinae, it is placed near that group.

6. **Mesostoinae** Van Achterberg, 1975

Small subfamily, containing only the genus *Mesostoa* Van Achterberg from Australia. The biology is unknown; autapomorphous character-states are the absence of the precoxal and scutellar sulci, the peculiar clypeus, and the compressed legs and metasoma.

7. **Histeromerinae** Fahringer, 1930, **stat. nov.**

Small subfamily, containing the Holarctic genus *Histeromerus* Wesmael; in the Netherlands found to be a parasite of Cisidae boring in *Polyporus* sp., in the Nearctic region reared from Anobiidae and Lyctidae (Coleoptera). This group was included in the Braconinae by Van Achterberg (1976: 45) because of several synapomorphies. However, it does not fit well (as it did not in the Doryctinae before) because of the following apomorphous character-states: 2nd and 3rd metasomal spiracles in the epipleuron, peculiar shape of head and antenna, the cluster of pegs on the fore tibia, and the long hind basitarsus. Further plesiomorphus character-states (absent in the Braconinae) such as the presence of the occipital carina and the long vein M+CU of the hind wing stress the isolated position of this group.

8. **Opiinae** Foerster, 1862

Rather large subfamily, consisting of endoparasites of (especially mining) larvae cyclorraphous Diptera, exceptionally ovo-larval parasitism occurs. The pupation (as in the following subfamily) is in the puparium of the host. Frequently a shallow hypoclypeal depression has been developed, indicating the relationship with the Braconinae-group, but the labrum is flat and frequently bears some setae.

9. **Alysiinae** Stephens, 1829

One of the largest subfamilies of the Braconidae; almost all spp. are solitary endoparasites of larvae of cyclorraphous Diptera, but some are gregarious (some spp. of *Aphaereta* Foerster). Some spp. of *Aphaereta* Foerster are (facultative) hyperparasites, because they include the Tachinidae in their host-range. The egg is usually deposited in the larva, seldom in the egg (*Polemochartus* Schulz), or probably sometimes in the (pre)pupa (*Aphaereta* Foerster). The most striking autapomorphous character-state of the Alysiinae is the shape of the mandibles; the 3–7 mandible teeth are bent outwards and the mandibles do not contact each other when they are closed.

10. **Gnaptodontinae** Fischer, 1970

Small subfamily, the cosmopolitan genus *Gnaptodon* Haliday is primarily a parasite of Nepticulidae (Lepidoptera). It is still not certain if this genus contains ecto- or endoparasites (Van Achterberg, 1983b); the morphology of the venome apparatus and of the larva is unknown.

11. **Dirrhopinae subfam. nov.**

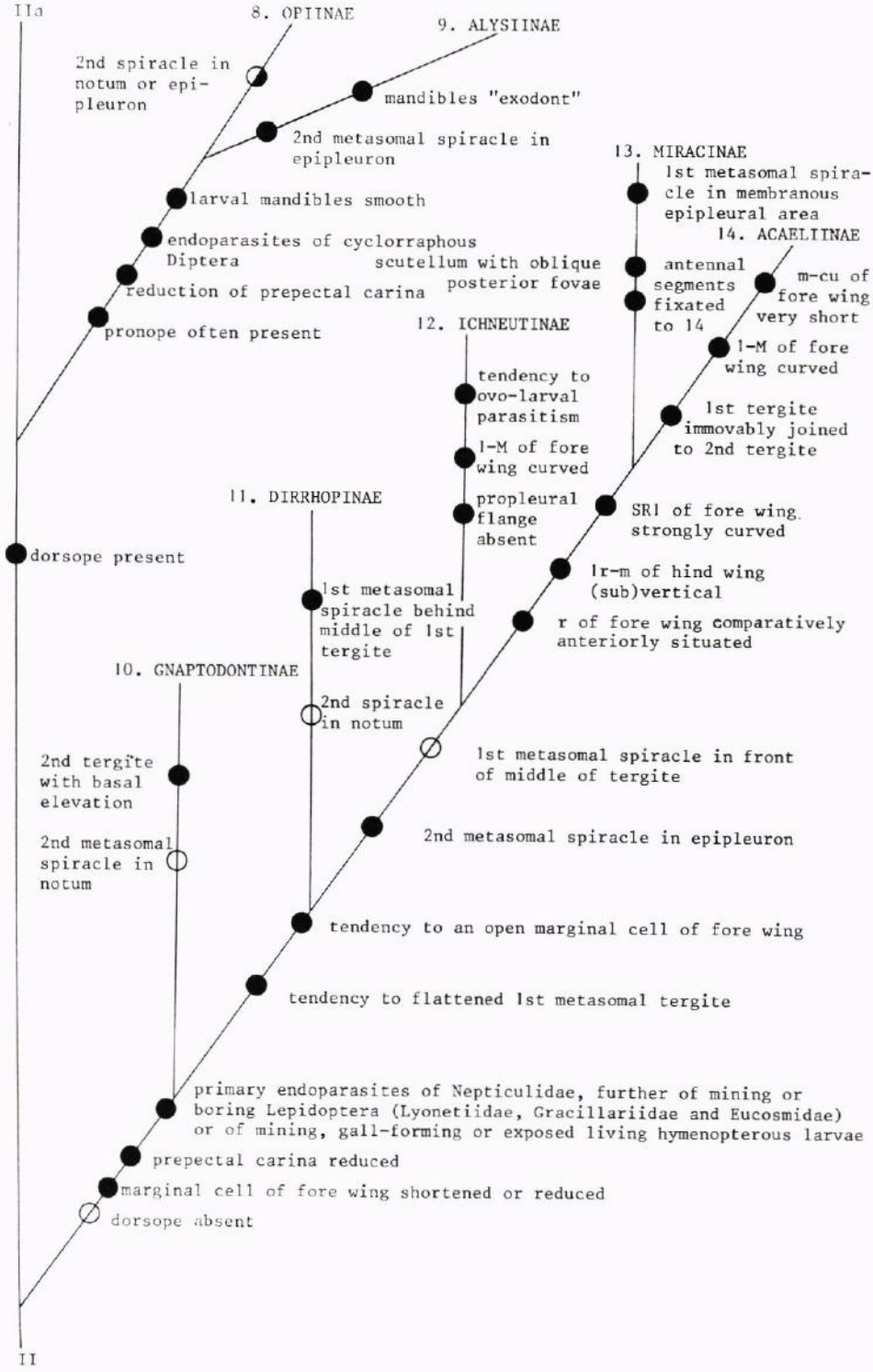
Contains only one genus, *Dirrhope* Foerster, known in the Northern Hemisphere, and a parasite of Nepticulidae. Peculiar autapomorphy is the flattened 1st metasomal tergite with the spiracle behind the middle of the tergite.

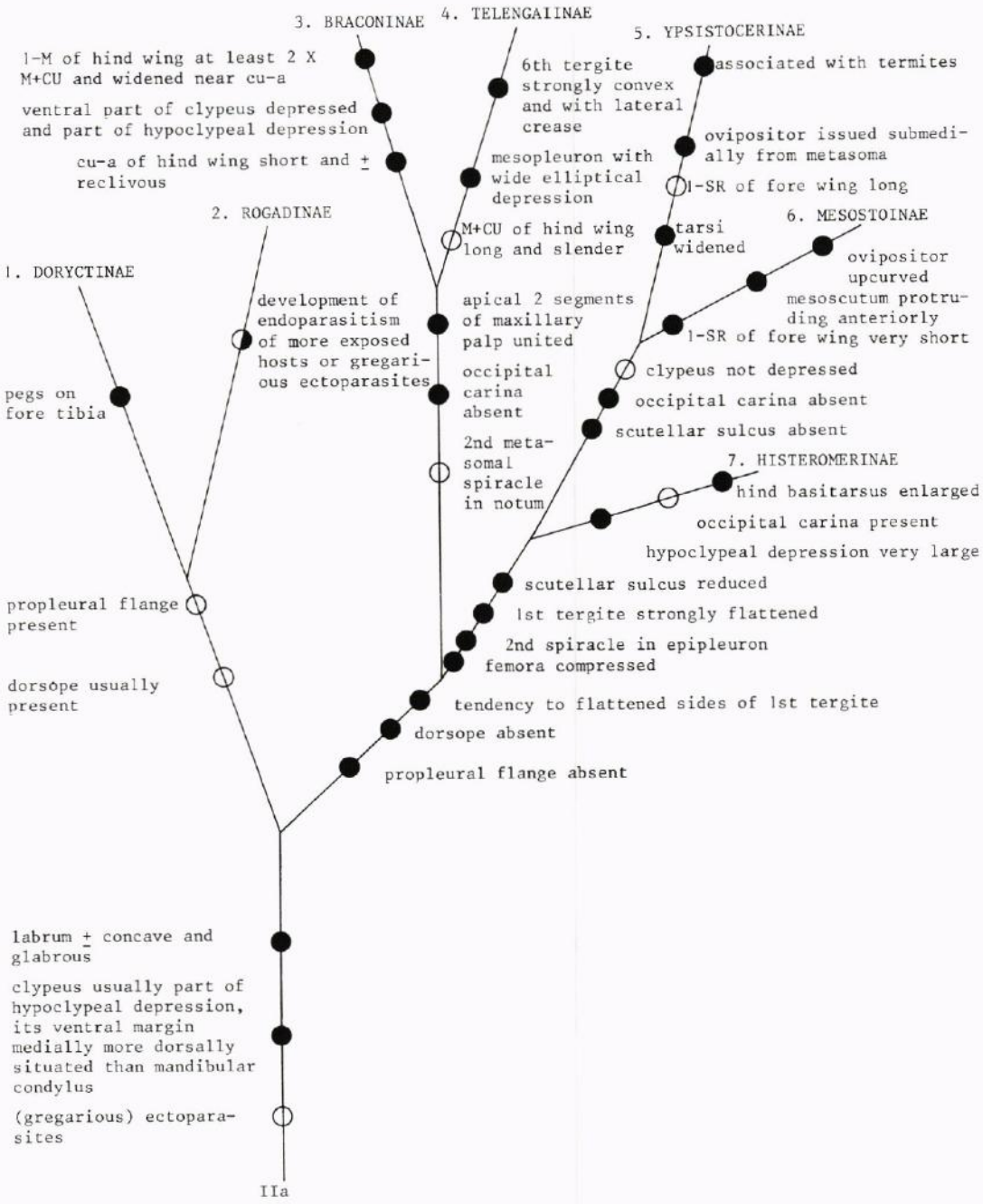
12. **Ichneutinae** Foerster, 1862

Rather small subfamily, consisting of endoparasites of larvae of sawflies (Ichneutini Foerster and Proteropini Van Achterberg, both with fairly complete fore wing venation) and of lepidopterous leaf-miners (Nepticulidae: Muesebeckiini Mason with reduced wing venation).

13. **Miracinae** Viereck, 1918

Small subfamily, parasites of Nepticulidae and Lyonetiidae, in the Palaearctic region only the genus *Mirax* Haliday. Additional apomorphous character-states are the strongly oblique vein cu-a of hind wing and the absence of the prepectal carina.


IIa
8. OPIINAE
9. ALYSIINAE
2nd spiracle in notum or epipleuron
mandibles "exodont"
2nd metasomal spiracle in epipleuron
13. MIRACINAE
1st metasomal spiracle in membranous epipleural area
14. ACAELINAE
larval mandibles smooth
endoparasites of cyclorraphous Diptera
scutellum with oblique posterior fovae
antennal segments fixated to 14
m-cu of fore wing very short
reduction of prepectal carina
pronope often present
12. ICHNEUTINAE
1-M of fore wing very short
tendency to ovo-larval parasitism
1st tergite immovably joined to 2nd tergite
1-M of fore wing curved
11. DIRRHOPINAE
propleural flange absent
SR1 of fore wing strongly curved
dorsope present
1r-m of hind wing (sub)vertical
1st metasomal spiracle behind middle of 1st tergite
r of fore wing comparatively anteriorly situated
10. GNAPTODONTINAE
2nd spiracle in notum
2nd tergite with basal elevation
1st metasomal spiracle in front of middle of tergite
2nd metasomal spiracle in notum
2nd metasomal spiracle in epipleuron
tendency to an open marginal cell of fore wing
tendency to flattened 1st metasomal tergite
primary endoparasites of Nepticulidae, further of mining or boring Lepidoptera (Lyonetiidae, Gracillariidae and Eucosmidae) or of mining, gall-forming or exposed living hymenopterous larvae
prepectal carina reduced
marginal cell of fore wing shortened or reduced
dorsope absent
II



Figs. 13–14. – 13. (left) Cladogram of subfamily group II, excluding IIa. – 14. (above) Cladogram of subfamily group IIa.

14. **Acaeliinae** Viereck, 1918

Small subfamily, sometimes incorrectly spelled as Adeliinae which is based on a "lapsus calami" in the original description. Primarily solitary endoparasites of larvae of Nepticulidae, but also reported from Gracilariidae and Eucosmidae.

15. **Aphidiinae** Haliday, 1833

Medium-sized subfamily, exclusively solitary endoparasites of aphid nymphs and adults. Frequently treated as a separate family, but it shares all the synapomorphies of the Braconidae, several ones with group II (venom apparatus!), and the cephalic structure of the final instar larva is similar to that of other Braconidae according to Čapek (1970: 848). The occurrence of two additional apomorphies: the venom apparatus type II in the Praini and the obviously original pupation within the host of most spp. indicate the correctness of the inclusion.

16. **Helconinae** Foerster, 1862

Rather large subfamily, all endoparasites of larvae of Coleoptera. The group is not well characterized by autapomorphous character-states, both larvae and adults possess many plesiomorphous character-states. This supports the hypothesis that the Braconidae evolved from ectoparasites of sheltered living larvae of Coleoptera (e.g., Cerambycidae).

17. **Meteorideinae** Čapek, 1970

Small subfamily; gregarious endoparasites of larvae of Lepidoptera and pupation inside the host pupa. Contains two genera: *Benama* Nixon and *Meteoridea* Ashmead, and is resticted to the (sub)tropics (but unknown from the Australian region).

18. **Blacinae** Foerster, 1862

Medium-sized subfamily, containing the Blacini sensu Van Achterberg, 1976 and the Dyscoletini (**tribus nov.** based on the genus *Dyscoletes* Haliday). Frequently the Blacini are included in the Helconinae or in the Euphorinae. The venation of the adults and the cephalic structure of the final instar larvae of the Blacini is similar to those of the tribe Brachistini of the Helconinae. However, the presence of a dorsope (if weakly developed still recognizable by the curvature of the basal part of the dorsal carinae) separates the Blacinae from the Helconinae. Because the similarities concern negative apomorphies (reductions) and the development of a dorsope is a positive apomorphy, I give most weight to the latter character. Therefore the Blacini and the Dyscoletini are excluded from the Helconinae and form a separate subfamily. The secondary loss of the dorsope by the Brachistini is unlikely because of the shape of the basal portion of the dorsal carinae, further they differ by the short dorsal face of the propodeum. A paper (partly dealing with the phylogeny of the Blacinae) will be published in the near future.

The Blacini are included in the Euphorinae s.l. by Tobias (1965: 502–504, translation) on basis of a negative apomorphy: the loss of vein CU1b of the fore wing, but it is also lost in the subgenus *Calyptus* of the genus *Eubazus* of the Helconinae. A further reason is the presence of a separated cuspidal process and of a supposed similar biology. The biology has not been well studied, but the best provisional conclusion is that the Blacini are parasites of coleopterous larvae. The Dyscoletini are parasites of larvae of Boreidae (Mecoptera). Further study of the larvae is necessary; study of the morphology of the 1st and 2nd larval instars, and the presence of a final ectoparasitic phase (absent in the Euphorinae, present in the Helconinae) is essential. Inclusion of the Blacini in the Euphorinae is obstructed by differences in the mandibles of the final larval instar, the biology and the morphology of the 1st metasomal tergite.

Peculiar to the Blacini is the development of nuptial swarming, starting with swarming congregation of males in the evening and followed by mainly nocturnal mating. Southwood (1957) observed two types of dance in a swarm of males, similar to a chironomid swarm: a slow vertical dance and a rapid horizontal dance leading to consolidation of the swarm, probably owing to the entry of a female.

19. **Euphorinae** Foerster, 1862

Rather large and diverse subfamily, consisting of solitary or gregarious endoparasites of lepidopterous and coleopterous larvae (Meteorini Cresson; some spp. with the cocoon hanging

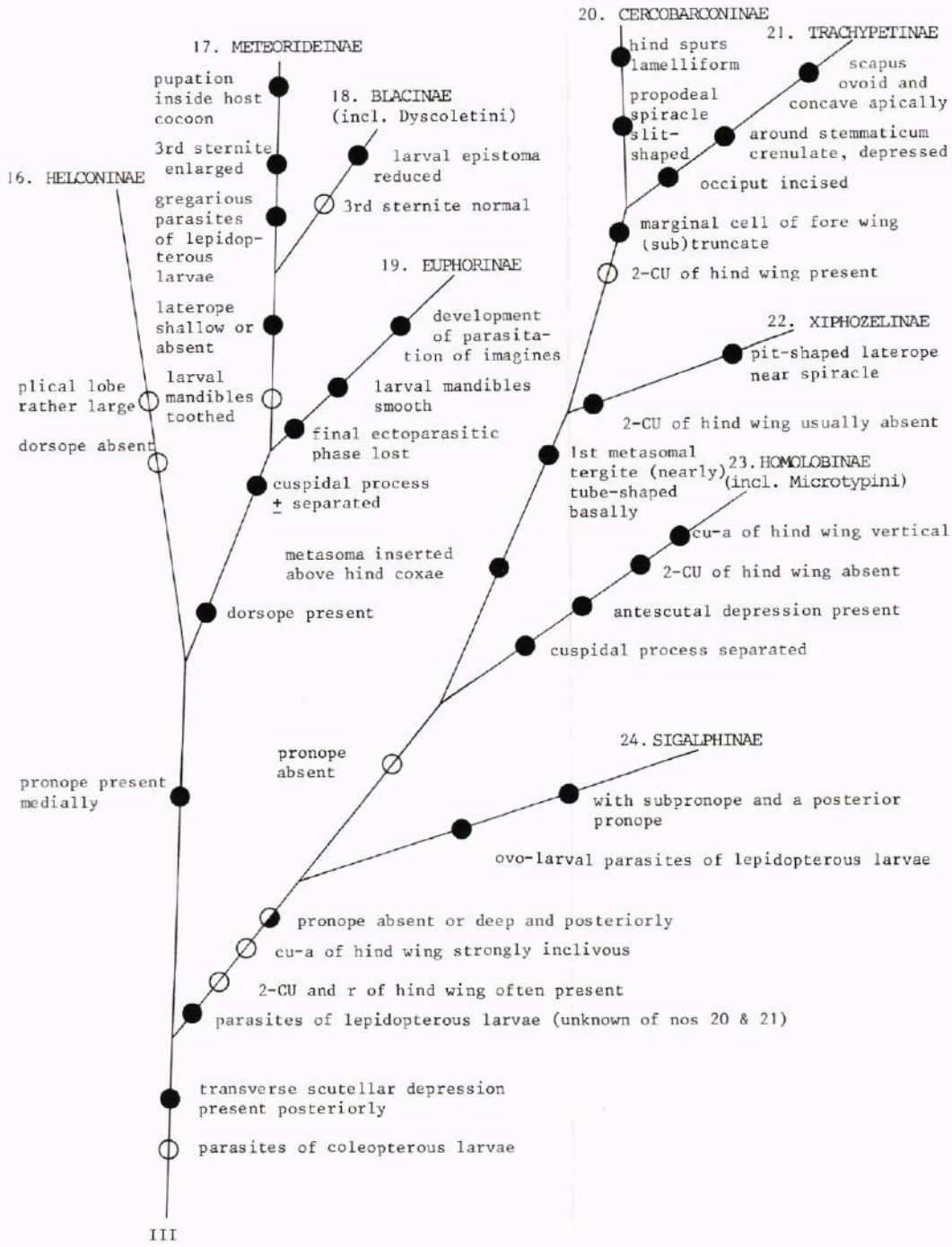


Fig. 15. Cladogram of subfamily group III.

from a thread), of solitary or gregarious endoparasites of adult Coleoptera (and more seldom of their larvae; Cosmophorini Muesebeck & Walkley, Centistini Čapek, and several genera of the Euphorini: *Perilitus*-group, *Ropalophorus* Haliday, *Cryptoxylos* Viereck, *Cryptoxiloides* Čapek & Čapecki, and *Streblocera* Westwood s.l.), of adult parasitic and aculeate Hymenoptera (*Syntretus* Foerster s.l., the only case that Braconidae are hyperparasitic on parasitic Hymenoptera), of adult Neuroptera (*Chrysopophthorus* Goidanich), of nymphal Heteroptera (emergence from adult or nymph: *Wesmaelia* Foerster, *Aridelus* Marshall, *Leiophron* Nees, and *Holdawayella* Loan), and of nymphal Psocoptera (emergence from adult or nymph: *Euphorus* Nees, and *Euphoriella* Ashmead). It is the only subfamily containing endoparasitic species that may leave the host in a fit state to resume feeding. The host caterpillar of *Meteorus ictericus* (Nees) may live up to 16 days (of which 6–10 days are of resumed feeding) after the parasite larva has emerged (Shaw, 1981: 37). The endoparasites of adult Coleoptera are known usually to cause sterility, but otherwise relatively slight damage to their hosts. Exceptionally such hosts may remain capable of reproduction or even serve as host again (Timberlake, 1916). Related to this phenomenon is the supposed loss of the ectoparasitic phase of the final larval instar, in its turn related to the smooth mandibles. Important tendencies in this subfamily are: the (extreme) reduction of venation (in the Euphorini, Cosmophorini, and Centistini), and the spiracles of the 1st metasomal tergite situated in the middle of the tergite or behind the middle (in the Meteorini and Euphorini).

20. **Cercobarconinae** Tobias, 1979

Small subfamily, restricted to the Australian region. It contains three genera: *Cercobarcon* Tobias, *Rhamphobarcon* Tobias, and *Megalohelcon* Turner, of which the biology is unknown. Conspicuous autapomorphies are present in the wing venation, the female genitalia (e.g., the curved ovipositor), the long slit-shaped propodeal spiracle, the hind spurs, and the shape of the head.

21. **Trachypetinae** Schulz, 1911

Small subfamily with only the Australian genus *Trachypetus* Guérin, of which the biology is unknown. Only the type-species, *T. clavatus* Guérin, 1831 is described and the female is unknown. *Trachypetus* was generally included in the Helconinae, however, there are many differences (e.g., in the shape of the 1st metasomal tergite) which warrant a separate status for this group.

22. **Xiphozelinae** Van Achterberg, 1979

Small genus with two genera: *Xiphozele* Cameron (S.E. Palaeartical, Oriental, and Australian) and *Distilirella* Van Achterberg (New Guinea). Parasites of (Noctuid) caterpillars. A review of the apomorphous character-states is given by Van Achterberg (1979b).

23. **Homolobinae** Van Achterberg, 1979

Medium-sized subfamily, containing endoparasites of lepidopterous larvae with a final ectoparasitic phase. With three tribes: Homolobini Van Achterberg (*Exasticolus* Van Achterberg and *Homolobus* Foerster (= *Zele* auct.), Charmontini Van Achterberg (*Charmontia* Van Achterberg and *Charmon* Haliday (= *Eubadizon* auct. p.p.)) and Microtypini Szépligeti (*Microtypus* Ratzeburg). The latter tribe is removed from the Orgilinae as a result of the phylogenetic analysis, and provisionally included in the Homolobinae, but may be better treated as separate family. Additional apomorphous character-states are listed by Van Achterberg (1979c: 254); especially the (narrow) antescutal depression and the transverse scutellar depression justify an inclusion of the Microtypini in the Homolobinae. For an analysis of the character-states of Homolobini and Charmontini as well as a discussion on the supposed relationship with *Zele* Curtis (= *Zemiotes* Foerster) of the Euphorinae-Meteorini, see Van Achterberg (1979c).

24. **Sigalphinae** Blanchard, 1845

Small subfamily, including the tribes Sigalphini Blanchard (*Sigalphus* Latreille), Minangini De Saeger (**stat. nov.**, with *Minanga* Cameron), and Acampsini **trib. nov.** (based on *Acampsis* Wesmael). The biology of the Minangini is unknown; the final instar larva of both other tribes have a distinctly transverse labial sclerite (as the

Homolobinae). According to Čapek (1970: 859) the Sigalphini and Acampsini are ovo-larval endoparasites of lepidopterous larvae.

25. **Cenocoeliinae** Szépligeti, 1901

Rather small subfamily, containing endoparasites of larvae of wood- or bark-boring Coleoptera, usually Cerambycidae, but sometimes Scolytidae or Buprestidae. Some spp. parasitize beetle larvae (Curculionidae and Cerambycidae) within herbaceous stems or fruits (Saffer, 1982). The Cenocoeliinae are included in the Helconinae by Čapek, (1970), because of the resemblance in biology and larval structures. However, the larval structures are different from the Helconinae; the labial sclerite is more transverse and the stipital sclerite is crooked (figs. 7–8 versus figs. 9–11 + 14 in Čapek, 1970). The Cenocoeliinae form an isolated group because of the extremely high inserted metasoma and the subpetiolate 1st metasomal tergites of the imagines. The absence of a transverse scutellar depression, and the more or less developed postpectal carina (respectively, present and absent in the Helconinae) are other remarkable features. The position of the Cenocoeliinae is uncertain and it is placed provisionally as an old group basally in group IV.

26. **Agathidinae** Blanchard, 1845

Rather large and homogeneous subfamily, containing solitary or gregarious endoparasites of lepidopterous larvae. Remarkable apomorphous character-states are the narrow marginal cell of fore wing of adults and the paired fleshy ventral processes in the 1st larval instar (may be modified larval legs).

27. **Macrocentrinae** Foerster, 1862

Moderately sized subfamily, containing solitary or gregarious endoparasites of lepidopterous larvae. Polyembryony is known of several spp. (even of a secondary solitary sp.) and the gregarious specimens spin a common web. The most striking apomorphy is the presence of small pegs on the trochantellus of the adults.

28. **Amicrocentrinae** Van Achterberg, 1979

Small subfamily, containing only the Afrotropical genus *Amicrocentrum* Schultz, with solitary parasites of large boring lepidopterous larvae (Cossidae and Noctuidae). Despite the large number of remarkable autapomorphous character-states as listed by Van Achterberg (1979a: 2–3), and the lack of almost any synapomorphous character-states uniting the Macrocentrinae and Amicrocentrinae, with the available set of characters both groups seem to be the most closely related subfamilies of the Braconidae, a conclusion in agreement with the morphology of the larval cephalic structures (Short in Van Achterberg, 1979a).

29. **Betylobraconinae** Tobias, 1979

Small subfamily, restricted to the Australian region and containing one genus: *Betylobracon* Tobias. The biology is unknown, but may be peculiar considering the large number of apomorphous character-states. The Betylobraconinae are associated by Tobias (1979) with the Braconinae-group, but I could not find any synapomorphous character-state to justify this placement. In the cladistic analysis the group comes near the Orgilinae, but more synapomorphies are needed to be certain of this alignment.

30. **Orgilinae** Ashmead, 1900

Rather small subfamily, containing three tribes: Orgilini Ashmead (mainly *Orgilus* Nees), Mimagathidini Enderlein (mainly *Stantonia* Ashmead), and Mesocoelini Viereck (provisionally included, contains *Mesocoelus* Schulz and *Aneurobracon* Brues). This subfamily is often included in the Agathidinae because of the rather narrow marginal cell of fore wing. As shown in the cladogram the Orgilinae are not closely related, although both belong to group IV. The reduction of the fore wing venation is most extreme in the Mesocoelini, which also have extremely long hind legs and spurs, and the scutellum possesses a hemi-circular depression medio-posteriorly. Especially the latter may indicate that the Mesocoelini does not really belong here and should be treated as a separate subfamily.

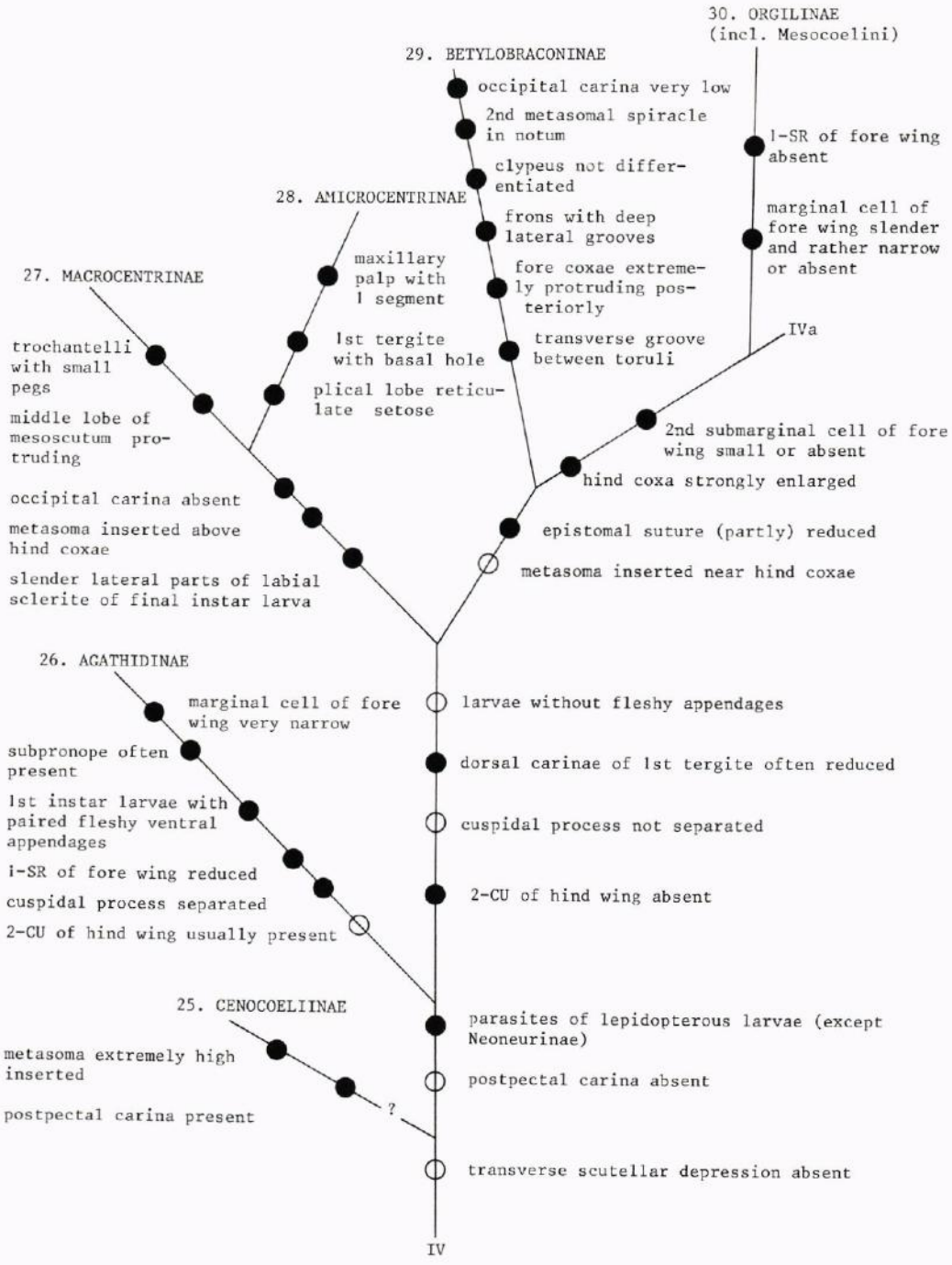


Fig. 16. Cladogram of subfamily group IV, excluding IVa.

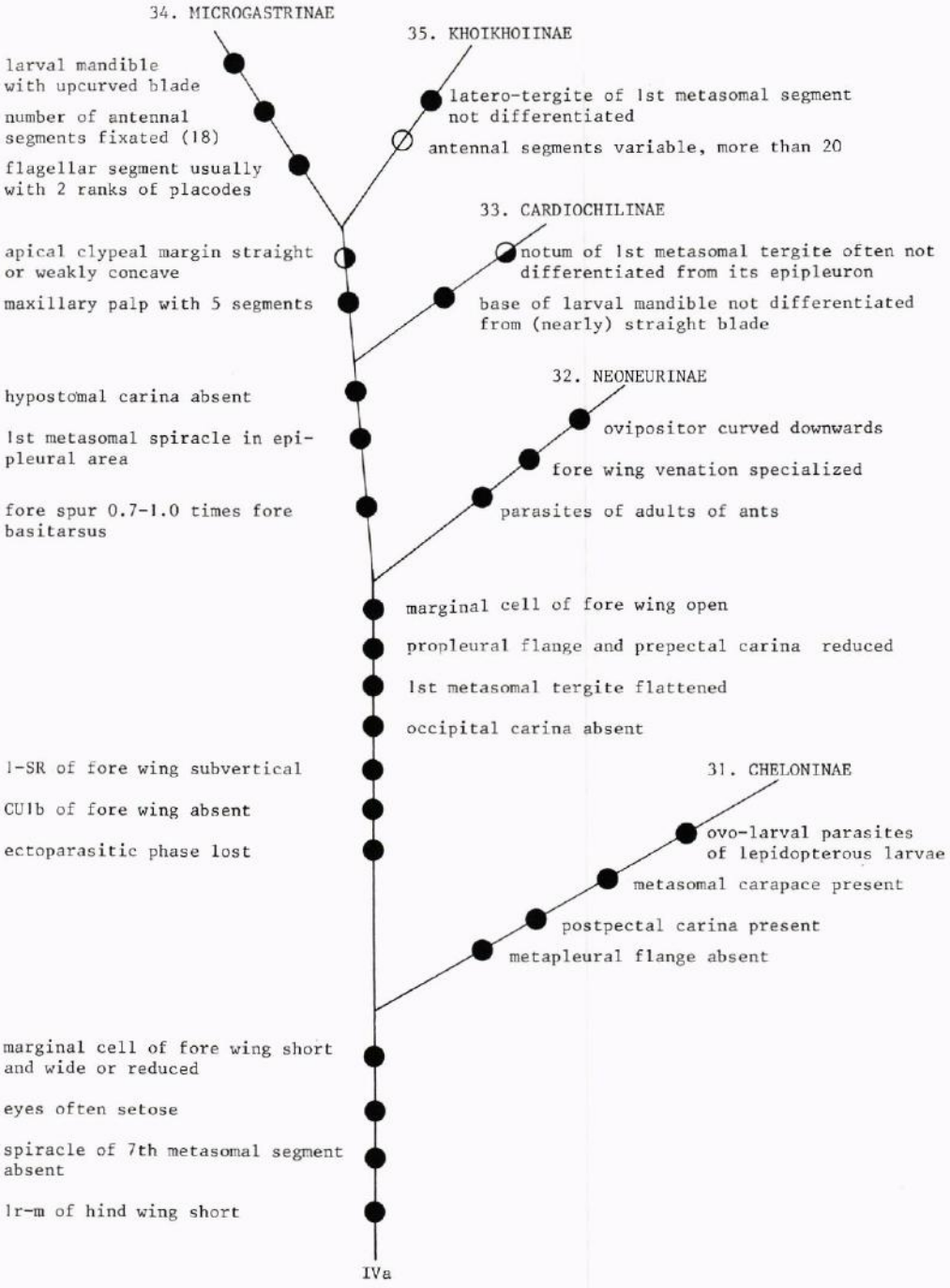


Fig. 17. Cladogram of subfamily group IVa.

31. **Cheloninae** Nees, 1816

Rather large subfamily, which consists of solitary endoparasites of lepidopterous larvae. The egg is deposited in the egg of the host; this may be an adaptation to the hosts (which live as larva at less exposed places) as well as to avoid encapsulation by the host. Easily recognizable group because of the metasomal carapace, combined with the presence of the postpectal carina.

32. **Neoneurinae** Bengtsson, 1918

Small subfamily, containing endoparasites of adults of worker ants; the development is in the metasoma of the host. Because of the biology (parasitism of adult insects) it has been inserted in the Euphorinae by Tobias (1966). According to Tobias it is unlikely that the parasitism of adult insects could develop twice within the same family (Braconidae). However, this has happened more than once, viz., in the Aphidiinae, in the Euphorinae (in three not closely related tribes), and, in my opinion, independently also in the Neoneurinae. The downwards curved ovipositor and the reduced wing venation are the only characters which might allow inclusion in the Euphorinae. In the cladistic analysis presented in this paper it was not possible to insert the Neoneurinae near or in the Euphorinae; actually numerous apomorphies allow an insertion near the Microgastrinae. The very long and slender stipital sclerite of the final larval instar is unique among the Braconidae so far as is known (fig. 25 in Čapek, 1970); the smooth mandibles is a parallelism (independently developed in the Microgastrinae as well in the Euphorinae) judging from the other larval structures.

Besides the synapomorphies with the Microgastrinae-group mentioned in the cladogram, several tendencies occur both in the Neoneurinae and in the Microgastrinae-group, e.g., antennal segments of ♀ with pseudodivision (most Microgastrinae and in the Neoneurinae: *Parelasmosoma* Tobias & Yuldashev), ♂ antenna sometimes compressed and widened, absence of the lateral carina of the mesoscutum, vein SR1 of the fore wing sometimes with ramellus (as frequently in the Cardiochilinae), vein C+SC of fore wing more or less widened distally, and vein 3-CU1 of fore wing not angled with vein 2-CU1. Striking autapomorphies of the Neoneurinae are the un- or indistinctly differentiated hind trochantellus, the usually strongly flattened and curved ovipositor, the more or less incised hypopygium medio-posteriorly, and the spiracle of the 1st tergite behind middle of the tergite.

33. **Cardiochilinae** Ashmead, 1900

Medium-sized subfamily, containing solitary endoparasites of lepidopterous larvae. The cephalic structures of the final larval instar are similar to those of several Microgastrinae, but the mandibles lack the apomorphous condition of a differentiated base. The bifid apex of the larval mandibles may be a synapomorphy with the Microgastrinae, although in the Microgastrinae several other (obviously apomorphous) conditions occur. The adults are recognizable by the vein SR1 of the fore wing strongly curved towards vein 1-R1 (straight or nearly so in nearly all Microgastrinae, rather intermediate in the Khoikhoiinae and some genera of the Microgastrinae, e.g., *Semionis* Nixon) and the large 2nd submarginal cell of the fore wing (intermediate in the Khoikhoiinae and in some genera of the Microgastrinae-Apantelini (*Semionis* Nixon and *Pelicope* Mason)).

34. **Microgastrinae** Foerster, 1862

Very large and comparatively homogenous subfamily, consisting of solitary or (frequently) gregarious endoparasites of lepidopterous larvae. Pupation is outside the host or its cocoon. Only in the small genus *Deuterixys* Mason is the pupation in the host cocoon, apparently a secondary development. The gregarious specimens spin a common web, sometimes with the cocoons very regularly arranged. A cladistic analysis is given by Mason (1981 & 1983); as treated in this paper an easily recognizable group because both sexes have antennae with 18 segments. The tribe Apantelini Viereck s.l. (including the Microgastrini sensu Mason) contains the species with the largest number of plesiomorphous character-states, e.g., the morphology of the 1st metasomal tergite, the ovipositor sheath of the adults and the mandibles of the final larval instar.

35. **Khoikhoiinae** Mason, 1983

Small subfamily, of which the biology is unknown. Known only from South Africa and difficult to differentiate from the Microgastrinae with autapomorphous character-states. The only autapomorphy seems to be the striated epipleural membrane (lacking a more or less differentiated latero-tergite as present in the Microgastrinae) of the 1st metasomal tergite. Unfortunately the latero-tergite of the 1st segment (wherein the spiracle is situated) is often scarcely differentiated in the Microgastrinae, makes it a difficult character to interprete. Nevertheless the Khoikhoiinae are easily recognizable because of the long vein 3-SR of the fore wing, the 1st tergite with a long medial groove and antennae with more than 18 segments.

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Sammanfattning

Parasitstekelfamiljen Braconidae omfattar minst ca 40 000 arter. Utseendet hos en representant för gruppen visas i figurerna 1–11. Viktiga karaktärer som skiljer familjen Braconidae från övriga Ichneumonoidea är att 2:a och 3:e bakkroppssegmentens ryggplåtar är förenade hos Braconidae och att vingnerven 1-SR+M (skrivs oftast Rs+M) finns kvar hos Braconidae men ej hos övriga Ichneumonoidea (se Fig. 12).

Arbetet presenterar en kladistisk analys av huvudgrupperna inom familjen Braconidae. Analysen resulterar i en klassificering där familjen indelas i 35 underfamiljer grupperade i fyra större avdelningar (Aphidiinae samt grupperna II–IV, se Fig. 13–17). Den kladistiska analysen kan lätt följas i figurerna 12–17. De under evolutionen nytillkomna (apomorfa) karaktärerna är markerade med fyllda cirklar, och det är dessa karaktärer som håller samman grupper på olika nivåer i kladogrammen. De utnyttjade karaktärerna är hämtade från såväl morfologin hos fullbildade steklar och larver som från allmän biologi (värddjursgrupp, yttre resp. inre parasit, förpuppning utanför eller inne i värddjuret etc).