A PRELIMINARY KEY TO THE SUBFAMILIES OF THE BRACONIDAE (HYMENOPTERA)

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With 123 figures

Abstract

A preliminary key to the subfamilies of the Braconidae is given. The subfamilies are redefined in the key and in a short description. Especially the apomorphous characters, which may be used to define the subfamilies, are discussed.

INTRODUCTION

The family Braconidae can be separated from its sister-group, the Ichneumonidae, by at least two synapomorphous characters. The most important is the rigidly joined 2nd and 3rd tergites of the metasoma and, secondly, the absence of the second recurrent vein. The rigid plate formed by the 2nd and 3rd tergites may be weakly sclerotized (as in the Aphidiinae) or may be completely fused, e.g., in the Hybrizontinae and Acaeliinae.

The first worker, who tried to give a classification of higher groups was Wesmael (1835), whose classification concerned only the Palaearctic region. The Braconidae were divided into two divisions by Wesmael (p. 11): the "braconides endodontes" and the "braconides exodontes". The latter group is what is now called the Alysiinae. The "endodont"-Braconidae were divided into four sub-divisions (p. 14): (1) the "polymorphes", (2) the "cryptogastres", (3) the "areolaires", and (4) the "cyclostomes". The "polymorphes" contain the Aphidiinae, Euphorinae, Helconinae, Ichneutinae and Opiinae. The "cryptogastres" are an aggregate of Cheloninae and convergent groups, belonging to the Helconinae and Meteorideinae. The "areolaires" embrace the convergent groups Microgasterinae, Acaeliinae, Orgilinae and Agathidinae. Finally the "cyclostomes" contains the Doryctinae, Rogadinae and Braconinae, as treated in the present paper. The first reviser of this system was Foerster (1862), who gave a very elaborate sub-division and defined 26 "subfamilies", to which he added the suffix "-oidae". The following systems were based more or less on the Foerster-system, but several "subfamilies" were given tribal rank in one large subfamily. E.g., the Braconoidae, Euspathioidae, Hecaboloidae, Doryctoidae, Hormioidae, Rogadoidae and Rhyssaloidae became in Fahringer (1925) the tribes Braconini, Spathiini, Hecabolini, Doryctini, Hormiini, Rhogadini, Exothecini and Pambolini in one subfamily Braconinae, in effect the old "cyclostomes" of Wesmael. The "Sigalphoidae" became a part of the Helconinae, while the "Chelonoidae" are the

present Cheloninae and Meteorideinae. The "Microgasteroidae" contain the Microgasterinae and Acaeliinae, and the Agathidinae were divided by Foerster in the "Agathidoidae" and the "Eumicrodoidae", while the last mentioned also contains the Orgilinae p.p. The "Pachylommatoidae" and "Aphidioidae" are called Hybrizontinae and Aphidiinae, respectively, in the present paper. The "Euphoroidae" and "Perilitoidae" form the Euphorinae, from which quite recently *Zemiotes* Foerster was excluded and added to the Zelinae (Mason, 1973). The "Brachistoidae" of Foerster are of composite nature, they belong partly to the Helconinae and partly to the Zelinae (as defined in the present paper). The "Liophronoidae", together with *Pygostolus* Haliday from the "Blacoidae", form the tribe Centistini in the Euphorinae. The remainder of the "Blacoidae" belongs to the Helconinae. The "Ichneutoidae" and "Helconoidae" became the Ichneutinae and Helconinae p.p., respectively. Foerster's "Macrocentroidae" contain the Macrocentrinae and *Zele* Curtis of the Zelinae; this grouping is still widely used, e.g., by Eady & Clark (1964) and Čapek (1970). The "Diospiloidae" belong to the Helconinae and Orgilinae. Except for *Gnaptodon* Haliday (which is included in the Rogadinae), his "Opioidae" are fully comparable with the Opiinae. Ultimately his "Alysioidae" and "Dacnusoidae" are united by Griffiths (1964: 831) in the subfamily Alysiinae; this was confirmed through the study of the larvae by Čapek (1970: 861).

The system used by Marshall (1885: 9) is essentially that of Wesmael, but he added as a sixth division the "Flexiliventres" for the Aphidiinae, because of their flexible and weakly sclerotized metasoma. In 1891 he added as a seventh division the "Pachylommatidae", now called Hybrizontinae. These mainly large groups were subdivided according to the system of Foerster with some modifications, but also resulting in 26 "subfamilies" (for which Marshall used the suffix "-ides") for the Palaearctic region.

The key by Ashmead (1900: 111) to the subfamilies of the Braconidae is the first general key, intended to be used in more than one region. Ashmead separated the Alysiinae as a family Alysiidae, while the remaining genera were divided among 17 subfamilies. His division and interpretation of the genera was often incorrect, because he used a modification of the Foerster system without examining the types of many genera.

The second and latest general key to the subfamilies, which was used more extensively, is the key published by Szépligeti in 1904. It divides the Braconidae into 31 subfamilies, one of which (the Lysiognathinae) belongs in the Ichneumonidae. From the remaining 30 subfamilies the following are removed and reduced to lower rank in the subfamilies mentioned in parentheses: Cenocoelininae (Helconinae), Gnathobraconinae (Rogadinae), Aphrastobraconinae (Braconinae); Exothecinae (Rogadinae), Spathiinae (Doryctinae), Hecabolinae (Doryctinae), Pambolinae (Rogadinae), Hormiinae (Rogadinae), Sigalphinae (Helconinae), Calyptinae (Helconinae), Liophroninae (Euphorinae), Blacinae (Helconinae), Cardiochilinae (Microgasterinae), Diospilinae (Helconinae), Meteorinae (Euphorinae) and Dacnusinae (Alysiinae). The remainder, 14 subfamilies, are augmented to 22 in the present paper, because of three newly described subfamilies (Ypsistocerinae Cushman, 1923; Telengainae Tobias, 1962; Mesostoinae Van Achter-

berg, 1975) and a rearrangement of five groups according to Čapek (1970 and 1973) and Tobias (1967). These five subfamilies are the Acaeliinae and Zelinae (according to Tobias), the Orgilinae, Meteorideinae and Neoneurinae (modified after Čapek).

The two subfamilies erected by Fahringer (1936: 586) in his fairly general (but rather confusing) key are not accepted in the present paper. His Aneurobraconinae (containing the genus *Aneurobracon* Brues) is provisionally treated in this paper as a tribe of the Agathidinae, while the Pseudodicrogeniinae (containing only the genus *Pseudodicrogenium* Fahringer) is included as a tribe in the Braconinae. The morphology of both types examined clearly justify this transfer (Fig. 120—122).

After Szépligeti, several others have given subfamily-keys for the Palaearctic region (e.g., Fahringer, 1925; Tobias, 1971), while Marsh (1963: 522) gave a key for the Nearctic region. This key was disregarded in his later key to the Nearctic genera (1971: 841), because "there is some disagreement as to the limits of the various subfamilies in the Braconidae, ...".

For the terminology used, see Van Achterberg, 1976.

Discussion

The main reason for the confusion in the systematics of the Braconidae is formed by the many convergent evolutionary trends, occurring in this group. Some of the most important trends are the following:

1. The reduction of the veins of the wing, e.g., the Blacini in the Helconinae versus the Centistini in the Euphorinae.

2. The forming of rows of setae, usually one row per tergite. In this respect I disagree with Griffiths (1964: 842), who stated that "the arrangement of hairs in single rows on the gastral segments, being found in almost all other Alysiinae and many other Braconidae is beyond doubt plesiomorph". I am convinced that the opposite is true: many species with many plesiomorphous character-states have the tergites evenly setose. Still more convincing is the fact that most Ichneumonidae (the sister-group, in most aspects clearly less evolved) have the metasomal tergites evenly setose.

3. The formation of a carapace, formed by the three basal tergites of the metasoma, e.g., in the Helconinae (Brachistini), Cheloninae, Microgasterinae (*Fornicia* Brullé), and Rogadinae (Tobias & Dudarenko, 1974).

4. The ovipositor becomes shorter, sometimes more or less curved, and its sheaths become often wider.

5. The reduction of the segments of the palpi; the plesiomorphous condition of the maxillary and labial palp is 6 and 4 segments, respectively. Lower numbers occur in e.g., the Braconinae, Alysiinae, Helconinae, Neoneurinae and Hybrizontinae.

6. The selection of hosts other than Coleoptera larvae, especially Lepidoptera and Diptera.

7. The development of endoparasitism.

8. The parasitism of adult insects by the Neoneurinae, Aphidiinae and Euphorinae.

9. The reduction of the number of antennal segments occurs in almost all groups.

10. The development of a petiolus at the basis of the first metasomal tergite: e.g., Doryctinae (Spathiini), Euphorinae (Meteorini) and Zelinae (Zemiotini).

11. The forming of a hypoclypeal depression and a more or less concave clypeus: e.g., Braconinae, Opiinae, and Euphorinae (Cosmophorini).

12. The twisting of the mandible: e.g., Macrocentrinae, Braconinae and, very extremely, in the Alysiinae.

13. The formation of a dorsope and/or a laterope, while often also the dorsal carinae become more developed, until beyond the middle of the first tergite: e.g., Helconinae, Rogadinae, Alysiinae and Euphorinae.

14. The spiracle of the first metasomal tergite becomes situated near the middle of the tergite: e.g., Euphorinae and Zelinae (Zemiotini).

15. The radial cell becomes short and/or narrow, a tendency occurring in almost all subfamilies.

16. The first metasomal tergite becomes depressed, especially laterally: e.g., Mesostoinae, Braconinae, Microgasterinae, Acaeliinae and the tribe Proteropini of the Ichneutinae.

17. The convergent development of an "ophionoid facies" (Gauld & Huddleston, 1976) an adaption for nocturnal activity, occurring in the Zelinae, Euphorinae, Macrocentrinae and Rogadinae.

18. The mandibles of the larvae become slender and toothless: e.g., Euphorinae, Neoneurinae, Aphidiinae, Alysiinae, Opiinae, Microgasterinae p.p., and Rogadinae p.p.

19. The reduction of the cephalic structures of the larvae, especially of the hypostoma: e.g., Euphorinae, Orgilinae, Helconinae (Blacini & Brachistini), Neoneurinae, Ichneutinae (Muesebeckiini), Opiinae, and Doryctinae.

20. The labial and stipital sclerites of the larvae become long and slender: e.g., Euphorinae, Helconinae, Zelinae, and Opiinae.

Mainly owing to the research by Čapek upon the cephalic structures of the final instar larvae, I have tried to construct a key to the subfamilies proposed by Čapek and Tobias. Some changes seem inevitable to me, e.g., the fusion of the subfamilies Rogadinae and Exothecinae. There are too many genera in these groups, that connect the groups in more than one character. The mummification of caterpillars by *Rogas* and closely allied genera is not sufficient (however peculiar it may be) to separate them as a subfamily. The Centistinae of Čapek (1970) are included in the Euphorinae, according to Čapek (1973). The Adeliini s.l., a tribe of the Microgasterinae in Čapek (1970), are redefined and partly maintained as the tribus Miracini in the Microgasterinae; the other part is treated as a separate subfamily, the Acaeliinae, according to Tobias (1967 and 1971, who used the name Adeliinae). The Orgilinae (the tribe Orgilini of the Agathidinae in Čapek, 1970) and the Braconinae (the tribe Braconini of the Braconinae in Čapek, l.c.) are treated as separate subfamilies. The three other tribes (Exothecini, Hormiini and Pambolini) of the Braconinae in Čapek are included in the Rogadinae. The Spathiinae of Čapek (1970) is at most a tribe of the Doryctinae, as pointed out by Čapek (1973: 267).

More problematic is the position of the genera *Zele* (and *Zemiotes*), *Charmon* (= *Eubadizon* of Čapek), *Acampsis* and *Sigalphus*. Čapek (1970) included *Zele* and *Macrocentrus* in his Macrocentrinae following, for example, Nixon (1938) and Eady & Clark (1964). But Watanabe (1969: 319) considered the most adequate location to be in a tribe Zelini of the subfamily Helconinae; also Čapek (1973) gave them a tribal rank. The larvae are distinct from the larvae of the Helconinae: the labial sclerite is pentagonal, while it is transverse (Cenocoeliini) or longitudinal (height larger than width in other tribes) in the Helconinae; they are endoparasites of Lepidoptera, while Helconinae are almost exclusively endoparasites of Coleoptera; and the imagines of *Zele* and its relatives have several synapomorphous characters in respect to the Helconinae as treated in the present paper. It is therefore that I follow Tobias (1967, 1971), who gave this group subfamily rank, and I also include *Charmon* and *Zemiotes*.

The adult morphology of *Charmon* (e.g. the genitalia of the male, cf. Fig. 36, 40 in Tobias, 1967), its biology (also endoparasites of Lepidoptera) and the regular shape of the emergence opening from the cocoon (irregular in the Orgilinae, its near relatives) indicate the relationship with *Zele*. The cephalic structures of the final instar larvae of *Charmon* (Fig. 15 in Čapek, 1970) are different from *Zele*, because of the absence of the hypostomal spur, but the slender shape of the hypostomal parts and of the stipital sclerite make a relationship with the Zelinae more likely than with the Orgilinae (cf. Fig. 16, 17 in Čapek, 1970) as treated in this paper.

Still more complicated is the placement of *Acampsis*, *Sigalphus* and *Meteoridea*. The larvae of *Acampsis* and *Sigalphus* have slender mandibles with a very wide base (Fig. 34, 35 in Čapek, 1970), unlike the basally slender mandibles of the Cheloninae (Fig. 36, l.c.). Čapek overlooked this difference, because he included them in the Cheloninae (1970: 871), even in his key to the larvae (1973: 261) where he mentioned as the key factor for the Cheloninae ". . . (mandibles) without or only with a small base". Thus owing to the shape of some cephalic structures of the larvae and because of many differences in the adult morphology (e.g., nervellus broken, postpectal carina absent), I agree with Tobias (1967: 659), who gave this group subfamily rank. Unfortunately Tobias (l.c.) used the name "Sigalphinae", a name for a long time (incorrectly) used for a group now included in the tribus Brachistini of the Helconinae. Čapek (1970: 871) erected the subfamily Meteorideinae for *Meteoridea*, because the biology of this genus is rather peculiar. It is (at least partly) comprised of gregarious endoparasites of Lepidoptera-larvae, which let pupate the host larva and thereafter the parasites spin their cocoons inside the host cocoon. The stout stipital sclerite, the very wide base of the mandible of the larvae with its apical half slender and toothed (cf. Fig. 12, 34, 35 in Čapek, l.c.), combined with similarities in the morphology of the adults (e.g., nervellus broken, rather short radial cell, first discoidal cell petiolate and ovipositor sheath wide) give some indications about its relationship with the "Sigalphinae" of Tobias. Of the characters mentioned at least the slender apical half of the mandibles of the larvae, the stout ovipositor sheath of the adults and the rather short radial cell are synapomorphous. Therefore I propose to unite the Meteorideinae of Čapek and the Sigalphinae of Tobias into the Meteorideinae s.l.

Table 1. Divisions of the Braconidae given by some authors compared with the division proposed in the present paper

Wesmael, 1835	Foerster, 1862	Ashmead, 1900	Szépligeti, 1904	Muesebeck & Walkley, 1951	present paper
---	---	---	---	---	Ypsistocerinae
"Cyclostomes"	Doryctoidae (Histeromerus Wesmael included), Euspathioidae, and Hecaboloidae	tribes Doryctini (Histeromerus Wesmael included), and Hecabolini of the Rhogadinae and the tribe Spathiini of the Spathiinae	Doryctinae (Histeromerus Wesmael included), and Spathiinae	Doryctinae (Histeromerus Wesmael included), and Spathiinae	Doryctinae (Histeromerus Wesmael excluded)
	Rogadoidae, Braconoidae p.p., Hormioidae, and Rhyssaloidae	tribes Exothecini, Rhyssalini, and Rhogadini in the Rhogadinae and the tribes Pambolini and Hormiini of the Spathiinae	Rhogadinae, Horminnae, Pambolinae, Exothecinae, and Gnathobraconinae	Rogadinae	Rogadinae (Gnaptodon Haliday included)
	Braconoidae p.p.	Braconinae	Braconinae and Aphrastobraconinae	Braconinae	Braconinae (Histeromerus Wesmael included)
	---	---	---	---	Telengainae
	---	---	---	---	Mesostoinae
"Polymorphes" p.p.	Opioidae (Gnaptodon Haliday included)	Opiinae (Gnaptodon Haliday included)	Opiinae (Gnaptodon Haliday included)	Opiinae (Gnaptodon Haliday included)	Opiinae (Gnaptodon Haliday excluded)
"Exodontes"	Alysioidae, and Dacnusoidae	the Subfamilies Alysiinae and Dacnusinae of the Alysiidae	Alysiinae and Dacnusinae	Alysiinae and Dacnusinae	Alysiinae
"Aréolaires" p.p.	Microgasteroidae p.p.	Microgasterinae p.p.	Microgasterinae p.p.	Microgasterinae p.p.	Acaeliinae
	Microgasteroidae p.p.	Microgasterinae p.p., Agathinae p.p., Sigalphinae p.p., and Cardiochilinae	Microgasterinae p.p., Agathinae p.p., Sigalphinae p.p., and Cardiochilinae	Microgasterinae p.p. (Paroligoneurus Muesebeck included), and Cardiochilinae	Microgasterinae (Paroligoneurus Muesebeck excluded)

Cheloninae	Cheloninae p.p.	Cheloninae p.p.	Cheloninae p.p.	Chelonoidae p.p.	"Cryptogastres" p.p.
Ichneutinae (*Parotigoneurus* Muesebeck included)	Ichneutinae	Ichneutinae	Ichneutinae	Ichneutoidae	"Polymorphes" p.p.
Meteorideinae	Helconinae p.p. and Cheloninae p.p.	Agathinae p.p., and Cheloninae p.p.	Agathidinae p.p., and Cheloninae p.p.	Chelonoidae p.p.	"Crypogastres" p.p.
Agathidinae	Agathidinae	Agathidinae p.p.	Agathidinae p.p.	Agathidoidae, and Eumicrodoidae p.p.	"Aréolaires" p.p.
Macrocentrinae	Macrocentrinae	Macrocentrinae p.p.	Macrocentrinae p.p.	Macrocentroidae p.p.	"Polymorphes" p.p.
Helconinae	Helconinae p.p. and Blacinae p.p.	Helconinae, Cenocoelinae, Diospilinae p.p., Calyptinae p.p., Blacinae p.p., Sigalphinae, and Cheloninae p.p.	Helconinae, Blacinae p.p., Sigalphinae p.p., and Cheloninae p.p.	Helconoidae, Brachistoidae p.p., Blacoidae p.p., Diospiloidae p.p., and Sigalphoidae	"Polymorphes" p.p. and "Cryptogastres"
Zelinae	Helconinae p.p., Blacinae p.p., and Euphorinae p.p.	Macrocentrinae p.p., Calyptinae p.p., and Meteorinae p.p.	Macrocentrinae p.p., Meteorinae p.p., Dacnusinae p.p., and Blacinae p.p.	Macrocentroidea p.p., Perilitoidea p.p., and Brachistoidae p.p.	"Polymorphes" p.p.
Orgilinae	Blacinae p.p.	Agathinae p.p., and Diospilinae p.p.	Agathinae p.p., and Blacinae p.p.	Diospiloidae p.p., and Eumicrodoidae p.p.	"Aréolaires" p.p.
Euphorinae	Euphorinae p.p. and Cosmophorinae	Euphorinae, Meteorinae p.p., Blacinae p.p., and Liophroninae	Euphorinae, Meteorinae p.p., Blacinae p.p.	Perilitoidea p.p., Euphoroidae, Blacoidae p.p., and Liophronoidae	"Polymorphes" p.p.
Neoneurinae	Neoneurinae	Neoneurinae	Microgasterinae p.p.	Microgasteroidae p.p.	– –
Aphidiinae	Aphidiinae	Aphidiinae	Aphidiinae	Aphidioidae	– –
Hybrizontinae	Paxylommatinae	Paxylommatinae	Paxylommatinae	Pachylommatoidea	"Polymorphes" p.p.

The division of the Braconidae given by Wesmael (1835), Foerster (1862), Ashmead (1900), Szépligeti (1904), and Muesebeck & Walkley (1951) are compared with the division given in the present paper in Table 1.

KEY TO THE SUBFAMILIES OF THE BRACONIDAE S.L.

1. Mandible unidentate (Fig. 10); antenna inserted on the top of the head (Fig. 8, 9); ovipositor issuing near middle of metasoma (Fig. 8); whole body densely setose (Fig. 8); associated with termites ...... `Ypsistocerinae (p. 44)
— Mandible with 2—7 teeth; antenna inserted below top of head, at height of the eyes (Fig. 5, 11, 25); ovipositor issuing near apex of metasoma (Fig. 11, 68, 72, 89, 95, 108, 109); body less setose; associated with other groups 2
2. Mesoscutum protruding above pronotum (Fig. 11); epistomal (medially) and scutellar sutures absent (Fig. 12, 15); ovipositor bent upwards (Fig. 11); clypeus straight medially, above an indistinct hypoclypeal depression (Fig. 12) ......
.... Mesostoinae (p. 44)
— Mesoscutum not strongly protruding above pronotum, if exceptionally slightly protruding, then ovipositor straight or bent downwards; epistomal and clypeal sutures almost always complete; hypoclypeal depression absent, if present, then clypeus more or less concave and differently shaped (Fig. 27, 37) 3
3. Hypoclypeal depression comparatively wide, deep and more or less round dorsally (Fig. 27, 28, 35, 37, 41), exceptionally the face takes part in the hypoclypeal depression (tribe Pseudodicrogeniini), resulting in a concave face and a flat clypeus (Fig. 121, 122); metasoma rather often sculptured, sometimes its second tergite with a semi-circular suture (Fig. 38) 4
— Hypoclypeal depression absent, if present (Fig. 5, 52), then more or less shallow, narrower and straight dorsally or nearly so; face and clypeus more or less convex, not concave (Fig. 85, 86); metasoma (if intermediate) often smooth behind the first tergite (Fig. 63), its second tergite without semi-circular suture, at most with a more or less chevron-shaped impression (Fig. 63) 8
4. Antenna situated at a protuberance, in front of the eyes (Fig. 97—99); venation of wings reduced (Fig. 105); maxillary palp with 4 segments; parasites of adult Coleoptera .... tribe Cosmophorini of the Euphorinae
— Antenna more or less situated between the eyes (Fig. 25, 27, 34, 42), without distinctly developed protuberance; venation usually more complete (Fig. 19, 23, 31, 36, 43, 44); maxillary palp with 5 or 6 segments; parasites of larvae of various groups of insects 5
5. First metasomal tergite strongly flattened basally and laterally (Fig. 22, 26); dorsope absent or nearly so, if present, then dorsal carinae are situated laterally, above the spiracles; prepectal carina absent; occipital carina absent dorsally; maxillary palpus with 5 segments, if with 6 segments (tribe Histeromerini, Fig. 25) then hind femur strongly compressed, disk-shaped (cf. Fig. 20) and fore tibia with a cluster of spines on two-third of its outer surface (Fig. 21);

nervulus interstitial or nearly so (Fig. 23) or antefurcal (Fig. 19), very excep-
tionally postfurcal (Fig. 120) .... Braconinae (p. 45)
— First tergite not or slightly flattened, usually with dorsope and/or dorsal
carinae (Fig. 33, 38, 40, 46); dorsal carinae are removed from the spiracles;
occipital carina usually (partly) present dorsally; prepectal carina variable;
maxillary palp with 6 segments; hind femur not disk-shaped, at most weakly
compressed; fore tibia with a row of spines (Fig. 32) or without spines (Fig.
39); nervulus usually postfurcal (Fig. 31, 36, 43, 44) or absent, exceptionally
interstitial 6
6. First metasomal tergite immovably joined to the second tergite, without dorsal
carinae (Fig. 29, 30); three basal tergites about as long as half of metasoma ..
.... Telengainae (p. 45)
— First tergite flexibly joined to the second tergite, almost always with dorsal
carinae, at least basally (Fig. 40); if exceptionally the first tergite is immovably
joined to the second tergite, then the formed carapace is about as long as the
metasoma 7
7. Fore tibia with short, often rather thick spines (Fig. 32), if intermediate, then
occipital and prepectal carinae complete; hind coxa usually with an anterio-
ventral tubercle; if nervulus is present, then sides of first brachial cell parallel
(Fig. 36) .... Doryctinae (p. 45)
— Fore tibia without spines (Fig. 39); occipital carina often partly, or com-
pletely absent; prepectal carina variable; hind coxa without tubercle; if
intermediate then first brachial cell widened apicad (Fig. 43) and nervulus
present .... Rogadinae (p. 45)
8. Mandibles with inner side out, their tips not touching when closed (Fig. 48,
50); mandibles usually with 3—7 teeth or lobes (Fig. 49, 51), seldom with
medial tooth large and both lateral teeth small .... Alysiinae (p. 46)
— Mandibles normal, their tips touching when closed (Fig. 5, 52, 85, 86, 90);
mandibles with two teeth, exceptionally with three teeth 9
9. Spiracles of first metasomal segment on its weakly sclerotized pleuron
(Fig. 56, 59); prepectal and occipital carinae completely absent ....
.... Microgasterinae (p. 46)
— Spiracle of the first segment on its strongly sclerotized tergite (Fig. 61, 63,
77, 80, 82, 83); prepectal and occipital carinae variable 10
10. Subdiscoidella present, often consisting of a more or less disconnected and
yellowish or brownish stripe; nervellus often weakly pigmented posteriorly
in respect to its anterior half (Fig. 65, 67, 73); if intermediate, then nervellus
broken (Fig. 64) 11
— Subdiscoidella absent (Fig. 74, 75, 79, 81, 84, 92); nervellus not broken,
seldom its posterior half weakly pigmented in respect to the anterior half
(Fig. 74, 92, 101) 12
11. First discoidal cell sessile or subsessile (Fig. 65); cu 1 often absent; occipital
carina completely absent; second tergite often with a chevron-shaped impres-
sion (Fig. 63); fore side of radial cel shorter than the pterostigma (Fig. 65) ...

.... Agathidinae (p. 47)

— First discoidal cell distinctly petiolate and cu 1 always present (Fig. 64, 67, 73); second tergite without chevron-shaped impression; fore side of radial cell equal in length to the length of pterostigma or somewhat longer (Fig. 64, 67, 73); occipital carina present, at least laterally ..... Meteorideinae (p. 47)

12. Postpectal and prepectal carinae completely present (Fig. 71); first metasomal tergite immovably joined to the second tergite, forming with the third tergite a rigid carapace (Fig. 72) .... Cheloninae (p. 47)

— Postpectal carina absent (Fig. 87, 91), exceptionally a ventral remnant present; prepectal carina variable; first tergite usually movably joined to the second tergite (Fig. 78) 13

13. First metasomal tergite flattened laterally and concave medially, almost invisible and immovably joined to the second tergite, forming with the third tergite a shield that covers slightly less than the basal half of the metasoma (Fig. 61); cuqu 1 from the pterostigma, usually far from r 1 (Fig. 62); transverse carina of propodeum strongly developed; occipital carina completely present .... Acaeliinae (p. 47)

— First tergite distinctly convex (Fig. 53, 80, 83), if seldom somewhat flattened, then occipital carina absent; first tergite usually flexibly joined to the second tergite; if the first tergite is immovably connected, then the three basal tergites cover almost the complete length of the metasoma; cuqu 1 from the radius (Fig. 75, 79, 118); transverse carina of propodeum less developed 14

14. Metasoma inserted above the hind coxae (Fig. 77, 78) 15

— Metasoma inserted between the hind coxae, at least partly (Fig. 87, 91, 103, 106, 109) 18

15. Metasoma inserted far above hind coxae (Fig. 78); occipital carina present dorsally .... tribe Cenocoeliini of the Helconinae

— Metasoma inserted near hind coxae (Fig. 77); occipital carina absent dorsally 16

16. Trochantellus with apical teeth externally (Fig. 77); submediellan cell large (Fig. 75, 81); middle lobe of mesoscutum more or less protruding (Fig. 76) .... Macrocentrinae (p. 48)

— Trochantellus without apical teeth; submediellan cell small (cf. Fig. 23); middle lobe of mesoscutum not protruding 17

17. Metapleural flange absent but with a rather wide and thin carina (cf. Fig. 91); radial cell comparatively wide (cf. Fig. 101); occipital carina present laterally .... Orgilinae (p. 50)

— Metapleural flange present (cf. Fig. 78, 87); radial cell very narrow (cf. Fig. 65); occipital carina absent .... Agathidinae (p. 47)

18. Maxillary palp short, with 2 or 3 segments (Fig. 3, 5); first brachial cell almost square (Fig. 4) or rqu present (Fig. 7); parasites of ants 19

— Maxillary palp usually longer, with 4—6 segments; first brachial cell elongate and rqu absent; parasites of other groups 20

19. First brachial cell almost square (Fig. 4); fore basitarsus very slender (Fig. 2);

clypeus very narrow, longer than wide (Fig. 3); ovipositor straight; malar space concave posteriorly . . . . Hybrizontinae (p. 48)

— First brachial cell elongate (Fig. 7); fore basitarsus stout (Fig. 6); clypeus wide, wider than long (Fig. 5); ovipositor strongly curved ventrad; malar space without concavity posteriorly . . . . Neoneurinae (p. 49)

20. Nervellus absent and radial cell (so far present) moderately long (Fig. 93, 96); first brachial cell comparatively narrow (Fig. 93, 96); metasomal tergites weakly sclerotized (Fig. 95); first metasomal tergite usually slightly or not widened apicad; clypeus comparatively small (Fig. 94); pleural suture weakly developed; occipital carina present, at least laterally; parasites of aphids . . . . Aphidiinae (p. 49)

— Nervellus present, if indistinctly developed or absent, then radial cell very short (Fig. 118), first brachial cell and clypeus wider; tergites distinctly sclerotized; first tergite and occipital carina variable; pleural suture usually wide and crenulate; parasites of other groups 21

21. Basal vein strongly curved at its anterior end (Fig. 88); occipital carina completely absent . . . . Ichneutinae (p. 49)

— Basal vein scarcely or not curved anteriorly (Fig. 92); occipital carina usually present laterally 22

22. First tergite of metasoma flattened basally and laterally, without dorsal carinae (Fig. 82); occipital carina absent; anterior tentorial pits very large (Fig. 90); radial cell short and comparatively high (Fig. 92); basal vein more or less evenly bent; parasites of saw-flies . . . . tribe Proteropini of the Ichneutinae (p. 49)

— First tergite scarcely or not flattened (Fig. 53, 83); occipital carina and/or dorsal carinae present; anterior tentorial pits much smaller (Fig. 52, 115); radial cell longer, if short, then narrow (Fig. 118); parasites of other groups 23

23. Prepectal carina absent and metasoma short, oval (Fig. 53), its first tergite flexibly joined to the second tergite; hypoclypeal depression present or absent; notauli and precoxal suture more or less reduced; parasites of Diptera . . . . Opiinae (p. 46)

— Prepectal carina almost always present; metasoma usually more slender (Fig. 111—113), sometimes tergite immovably joined to the second tergite; notauli and precoxal suture usually less reduced; almost always parasites of other groups 24

24. First metasomal tergite petiolate (Fig. 111, 113), sometimes petiolus rather short (Fig. 112) or length more than 3.2 times its apical width (Fig. 114, 116); spiracle of first tergite usually situated medially or behind the middle of the tergite (Fig. 111, 114, 116) 25

— First tergite sessile (Fig. 80, 83), shorter than 3.2 times its apical width; spiracle usually situated in front of the middle of first tergite (Fig. 80, 83) 26

25. Radiellan cell widened distad (Fig. 107), sometimes with an interradiella; whole surface of 4th and 5th tergites of metasoma densely setose (Fig. 111);

cuqu 2 present . . . . tribe Zemiotini of the Zelinae (p. 50)
— Radiellan cell narrowed or scarcely widened distad, without interradiella (Fig. 117—119); if cuqu 2 present, then 4th and 5th tergites with one row of setae per tergite (Fig. 112, 113) . . . . Euphorinae (p. 50)
26. Laterope deep (Fig. 109) and cuqu 2 absent, if intermediate, then ovipositor sheaths wide, shorter than three times its maximum width (Fig. 109) . . . .
. . . . tribe Centistini of the Euphorinae (p. 50)
— Laterope shallow (Fig. 87) or absent, if present then cuqu 2 present and/or ovipositor sheaths very slender, much longer than three times its maximal width 27
27. Dorsal carinae of first tergite present, at least basally (Fig. 80, 83); if cuqu 2 absent and dorsal carinae of first tergite weakly developed, then dorsal surface of propodeum distinctly shorter than its posterior surface (Fig. 87) and radial cell comparatively wide (Fig. 84); mainly parasites of larvae of Coleoptera . . . . Helconinae (p. 48)
— Dorsal carinae absent (Fig. 91, 103, 106), if present then cuqu 2 absent, dorsal surface of propodeum scarcely separated from its posterior surface and of more or less equal length (Fig. 91, 103, 106) and radial cell narrow (Fig. 101); parasites of Lepidoptera-larvae 28
28. Anal lobe of hind wing distinctly developed and usually with a more or less developed aqu'(Fig. 100, 104), if aqu' absent, then metapleuron with a thin, more or less protruding carina (Fig. 103); distal abscissa of radius more or less curved (Fig. 100, 104) . . . . Zelinae (p. 50)
— Anal lobe of hind wing comparatively narrow, without aqu' (Fig. 101, 102); if anal lobe is intermediate, then metapleuron without a thin carina, at most with a small flange (Fig. 106); distal abscissa of radius straight (Fig. 101, 102) . . . . Orgilinae (p. 50)

SHORT DESCRIPTIONS OF THE SUBFAMILIES

Ypsistocerinae (Fig. 8—10)

Small subfamily, which contains the two genera *Ypsistocerus* Cushman and *Termitobracon* Brues. They live probably as parasites in the nests of termites in the Neotropical region. This group possesses many apomorphous characters, e.g., the unidentate mandibles (Fig. 10); the far retracted hypopygium (Fig. 8); the densely setose body (Fig. 8); the highly inserted antenna (Fig. 9) and the strongly reduced palpi and eyes (Fig. 9, 10).

Mesostoinae (Fig. 11—18)

Small subfamily, containing only the genus *Mesostoa* Van Achterberg from the Australian region, of which the biology is unknown. As pointed out by Van Achterberg (1975: 158) almost all characters are apomorphous, e.g., the absence of the occipital and prepectal carinae (Fig. 11); the absence of the precoxal and scutellar sutures (Fig. 11, 15); the flattened first metasomal tergite without carinae

(Fig. 14); the smooth propodeum; the concave frons (Fig. 18); the upcurved ovipositor and the compressed legs (Fig. 16).

Braconinae (Fig. 19—27; 120—122)

Large subfamily, consisting of solitary or gregarious ectoparasites of larvae of holometabolous insects. The less evolved species often parasitize Coleoptera, the more evolved species also Lepidoptera, Hymenoptera-Symphyta and Diptera. According to Čapek (1970: 862) the host larva is paralysed at egg-deposition, the parasite-larva feeds on the paralysed host and forms its delicate cocoon at a sheltered place. The cephalic structures of the larvae are remarkably homogeneous. For the most parts none is reduced except for the mandibles, as in the main part of the Rogadinae as defined in the present paper. Therefore Čapek enlarged the concept of the Braconinae, in my opinion incorrectly because it is based on an aggregate of plesiomorphous characters. It only indicates that this group is less evolved than could be expected from the morphology of the adults. The adults have several apomorphous characters, e.g., the flattened first tergite (Fig. 22, 26); the reduction of the occipital and prepectal carinae and the maxillary palp consisting of 5 segments (except for the Histeromerini).

Telengainae (Fig. 28—30)

Small subfamily containing only the Palaearctic genus *Telengaia* Tobias. The biology is unknown. The shape of the metasoma is peculiar (Fig. 29, 30), but I am not sure about its position; it may be only a member of the Rogadinae.

Doryctinae (Fig. 31—36)

Rather large subfamily, consisting of ectoparasites of larvae of (wood-boring and bark-mining) Coleoptera. Less common also other hosts in plant tissues are attacked. The host-larva is paralysed before egg-deposition. The cephalic structures of the larvae are similar to those of the Braconinae. The morphology of the adults and their biology indicate their comparatively close relationship to the ancestral stem of the Braconidae. Some of the few apomorphous characters are the spines of the fore tibia (Fig. 32); the often large hypoclypeal depression (Fig. 35) and the usually distinctly developed dorsope (Fig. 33).

Rogadinae (Fig. 37—44, 46)

As treated in the present paper a large group and rather heterogeneous because in this group the transition to endoparasitism has taken place. This is accompanied with some pecularities as the tooth-less mandibles of the larvae (but already in the Braconinae occur larvae with only a few teeth on their mandibles) and the mummification of the host-caterpillar. In at least one genus closely related to *Rogas* Nees (viz., *Bucculatriplex* Viereck) the pupation takes place in the host-pupa in stead of in the mummified host-larva. Some species are solitary or

gregarious ectoparasites of larvae of Lepidoptera (*Hormius* Nees and its relatives; also *Oncophanes* Foerster, but *O. campsolechiae* Watanabe (probably belonging to *Clinocentrus* Haliday) is reported to be a gregarious endoparasite of larvae of Lepidopterous leaf-rollers; their woolly cocoon is formed outside the host). Others are solitary ectoparasites of Hymenoptera-Symphyta (*Phanomeris* Foerster s.l.) or solitary endoparasites of mining larvae of holometabolous insects (*Colastes* Haliday), while *Rogas* Nees and its allied genera are mainly solitary or gregarious endoparasites of larvae of Lepidoptera, which pupate within the mummified larva or in the pupa. Some apomorphous characters are the often deep hypoclypeal depression; the reduction of the occipital carina in several genera; the endoparasitism of the main part of the subfamily and the often distinctly developed dorsope of the first metasomal tergite.

Alysiinae (Fig. 45, 47—51)

One of the largest subfamilies of the Braconidae of which the larval cephalic structures, e.g., the simple and smooth mandibles, resemble those of the larvae of the Opiinae. Almost all species are solitary endoparasites of larvae of Diptera, but some are gregarious (*Aphaereta* Foerster). The egg is usually deposited in the larva, seldom in the egg (*Polemochartus* Schulz) or probably sometimes in the (pre-)pupa (*Aphaereta* Foerster). The delicate cocoon is made in the puparium of the host. The most striking apomorphous character of this group is the rotation of the mandibles of the adults in a way that the outer side becomes the inner side. Other apomorphous characters are the absence of the prepectal and the occipital carinae, together with the development of additional teeth on the mandible and of dorsope.

Opiinae (Fig. 52, 53)

Rather large subfamily, consisting of endoparasites of larvae of Diptera; pupation in the puparium of the host. Closely related to the Alysiinae but the mandibles are normally attached (but more or less twisted) and the occipital carina is almost always present laterally. Some of its apomorphous characters are the smooth mandibles of the final instar larvae, the absence of the prepectal carina, the comparatively short and stout metasoma, the more or less reduced notauli, precoxal and pleural suturae and the tendency to develop a hypoclypeal depression.

Microgasterinae (Fig. 54—60)

Large subfamily, consisting of endoparasites of larvae of Lepidoptera. Often gregarious; the eggs are deposited in the egg of the host or in the early instar larvae. In the Microgasterini and Cardiochilini the larvae pupate outside the host; the gregarious species often spin together in a common web. In the Miracini (which are endoparasites of leaf-mining Lepidoptera) the larvae pupate in the host-cocoon. The wing venation is often strongly reduced (Microgasterini, Mira-

cini), but the most important apomorphous characters are the position of the spiracle of the first metasomal segment and the absence of the prepectal and of the occipital carinae.

Agathidinae (Fig. 64—66)

Rather large subfamily containing solitary or gregarious endoparasites of larvae of Lepidoptera. The egg is deposited in the early instar larva, the parasites pupate outside the host larva. The presence of a more or less distinct subdiscoidella (Fig. 65) and the sometimes comparatively high insertion of the metasoma are remarkable, but are probably old plesiomorphous characters; also the larvae are in several aspects (e.g., the shape of the mandibles) rather slightly derived. Some apomorphous characters are the small second cubital cell (or cuqu 2 absent), posterior half of nervellus more or less weakly pigmented; the absence of the occipital carina; the short radial cell (Fig. 65); and the second metasomal tergite often has a more or less chevron-shaped impression (Fig. 63).

Meteorideinae (Fig. 63, 67, 68, 70, 73)

Small subfamily, solitary or gregarious endoparasites of larvae of Lepidoptera. According to Čapek (1970: 859) *Acampsis* Wesmael and *Sigalphus* Latreille may deposite their eggs in the egg of the host and pupate outside the host larva, while *Meteoridea* Ashmead pupates inside their host pupa. This group shows many plesiomorphous characters in both the larval and the adult morphology. Some of the few apomorphous characters are its endoparasitism, the comparatively wide ovipositor sheaths, the more or less developed dorsal carinae and deep laterope of the first metasomal tergite.

Cheloninae (Fig. 69, 71, 72, 74)

Rather large subfamily, which consists of solitary endoparasites of larvae of Lepidoptera. The egg is deposited in the egg of the host. The delicate cocoon is attached to the remains of the host larva. This group possesses many apomorphous characters, e.g., the metasomal carapace, the short and high radial cell, the presence of the postpectal carina, the often densely setose eyes, the basally slender mandibles of the final instar larvae and the often indistinct hypostomal suture. The deposition of the egg in the host egg is clearly an adaptation to the habits of its hosts, which live at more or less hidden places.

Acaeliinae (Fig. 61, 62)

Small subfamily, its members closely resemble the Miracini of the Microgasterinae (cf. Fig. 62 with Fig. 55). They share also their hosts, viz., both are endoparasites of larvae of leaf-mining Lepidoptera, also the pupation is in the cocoon of the host; this may account for their resemblance. The larvae are distinguishable from the larvae of the Microgasterinae by the presence of a mandibular base (cf.

Fig. 27, 28 in Čapek, 1970). The flattened shield formed by the three basal tergites of the metasoma is peculiar, they are fused almost invisibly (Fig. 61). Some other apomorphous characters are the strongly developed transverse carina of the propodeum, the position of the cuqu 1 and r 1 and the reduction of several other veins, e.g. the nervellus (Fig. 62).

Macrocentrinae (Fig. 75—77, 81, 86)

Subfamily of moderate size, containing solitary or gregarious endoparasites of larvae of Lepidoptera. The parasite pupates outside the host. Polyembryony is known of the gregarious species, of which the specimens spin together in a common web. The most strikingly apomorphous character of this group is the toothed trochantellus (Fig. 77), others are the specialized depressed area at the second tergite laterally; the high attachment of the metasoma, the reduction of the occipital carina, the more or less protruding middle lobe of mesoscutum (Fig. 76) and the usually absent dorsal carinae of the first metasomal tergite (Fig. 77).

Hybrizontinae (Fig. 1—4)

Small subfamily with one genus, *Hybrizon* Fallen, which contains endoparasites of larvae of several ant-genera. The naked pupae remain in the host nest. Possesses many apomorphous characters, e.g., the short palpi (Fig. 3), the concavity behind the malar space, the slender legs, the peculiar venation of the wings (Fig. 4), the slender clypeus and probably completely grown together 2nd and 3rd tergites (Fig. 1).

Helconinae (Fig. 78—80, 83—85, 87)

Large subfamily of which almost all species are endoparasites of larvae of Coleoptera. The few exceptions may be *Blacus* Nees (some derived species have been bred from larvae of Diptera) and *Dyscoletes* Haliday (bred from larvae of Mecoptera). This subfamily is difficult to characterize by apomorphous characters, except for the endoparasitism. Formerly this name often served for a heterogeneous group, clearly used as a rest group of remaining genera. Actually the group of genera included in this paper can be characterized by several more or less "reticulate" occurring apomorphous characters. The most important apomorphous characters in the Cenocoeliini are the highly inserted metasoma (Fig. 78), the concave frons, as occurs also in the Helconini and less distinctly in the Brachistini. The Helconini (Fig. 83) have usually the dorsal carinae distinctly developed, often reaching behind the middle of the first tergite as in the Blacini (Fig. 80) and Brachistini. A dorsope is present in the Blacini (Fig. 80) and Cenocoeliini (Fig. 78), and less commonly in the Helconini (Fig. 83). The first discoidal cell is (sub-)sessile in the Helconini (p.p.), Brachistini (Fig. 84) and Blacini (but seldom shortly petiolate). The reduction of the veins aqu 1 + 2 and aqu' occurs in the Helconini, Brachistini and Blacini, as also the reduction of the sculpture on the metasoma and of the precoxal suture. The reduction of veins leads to the loss

of the cuqu 2 in the Brachistini (Fig. 84) and Blacini. In this subfamily the tribe Helconini is clearly less derived than other tribes; it possesses many plesiomorphous character-states. The final instar larvae have also many plesiomorphous characters (Fig. 9 in Čapek, 1970), which supports the hypothesis about the evolution of the Braconidae from exoparasites of sheltered living larvae of Coleoptera.

Ichneutinae (Fig. 82, 85, 88—90, 92)

Rather small subfamily, consisting of endoparasites of larvae of sawflies (Ichneutini, Proteropini) and of lepidopterous leafminers (Muesebeckiini). The egg is deposited in the egg of the host but the larva developes after pupation of the host. The cocoon is formed inside the cocoon of the host. Rather heterogeneous group, e.g., the final instar larvae of the Muesebeckiini have (at least in one genus) slender and smooth mandibles, stipital sclerite robust and hypostoma absent, while the Ichneutini have robust and toothed mandibles (as the Proteropini) and the cephalic sclerites present and robust (Fig. 33 in Čapek, 1970). The cephalic sclerites are also present in the Proteropini but are very slender (Fig. 32, l.c.). Also the imagines differ considerably, but with the information available it seems better to unite the three tribes in one subfamily. The most important apomorphous characters are the absence of the occipital carina, and also more or less of the prepectal carina in the Muesebeckiini and Proteropini; the short and comparatively high radial cell in the Ichneutini and Proteropini (Fig. 88, 92) (which resembles the Cheloninae), the short ovipositor with its more or less widened sheaths (Fig. 89), the more or less strongly curved basal vein and the absence of aqu' (Fig. 88, 92).

Neoneurinae (Fig. 5—7)

Small subfamily, consisting of endoparasites of adults of worker ants; the development is in the gaster of the host. The cocoon is attached to the remains of the host. The most important apomorphous characters are the short palpi (Fig. 5), the peculiar venation of the wings (Fig. 7), the concave coxae dorsoapically and the strongly bent ovipositor.

Aphidiinae (Fig. 93—96)

Rather large subfamily, containing solitary endoparasites of aphid nymphs and adults. *Praon* Haliday and *Dyscritulus* Hincks emerge from their host and spin their cocoon directly beneath the aphid, whereas all other genera pupate within the mummified host skin, mounted on the surface of the plant. The cephalic structures of the larvae are like those of other Braconidae, according to Čapek (1970, p. 848). The apomorphous characters of this subfamily are especially distinct in the larvae, because of the long and funnel-shaped spiracles without a division into atrium and closing apparatus, of the simple and smooth mandibles

and of the disk-shaped antennae. The apomorphous characters of the adults are the reduction of the wing venation (Fig. 93, 96), the specialized female genitalia and the weakly sclerotized metasoma (Fig. 95).

Zelinae (Fig. 91, 100, 103, 104, 107, 111)

Small subfamily, which contains solitary endoparasites of larvae of Lepidoptera. The pupation is outside the host larva. The apomorphous character of the larvae in respect to the Orgilinae is the slender stipital sclerite; *Zemiotes* Foerster has also smooth mandibles and *Zele* Curtis has the hypostomal spur absent. The adults have few apomorphous characters, e.g., the first metasomal tergite is slender and without dorsal carinae (Fig. 103), even petiolate in *Zemiotes* Foerster (Fig. 111).

Orgilinae (Fig. 101, 102, 106)

Small subfamily containing species with often many apomorphous characters. They are endoparasites of larvae of Lepidoptera, which pupate outside the host larva; the emergence opening of the cocoon is irregular. The larvae are characterized by the absence of the hypostoma (Fig. 16, 17 in Čapek, 1970). Apomorphous characters of the adult parasites are the absence of the aqu' (Fig. 101, 102); the more or less reduced metapleural flange (Fig. 106) and occipital carina dorsally; the more or less small radial cell of fore wing and anal lobe of the hind wing (Fig. 101, 102); cuqu 2 absent (Fig. 101) or if present, forming a small second cubital cell (Fig. 102).

Euphorinae (Fig. 97, 99, 105, 108—110, 112—119)

Large and diverse subfamily, consisting of solitary or gregarious endoparasites of larvae of Lepidoptera and Coleoptera (*Meteorus* Haliday), of solitary or gregarious endoparasites of adult Coleoptera (and more seldom of their larvae), (e.g., *Perilitus* Nees s.l., *Ropalophorus* Haliday in Curtis, *Cryptoxilos* Viereck, *Streblocera* Westwood), of adult parastic and aculeate Hymenoptera (*Syntretus* Foerster, the only exception to the rule that Braconidae are primary parasites), of adult Neuroptera (*Chrysopophthorus* Goidanich), of nymphal and adult Heteroptera (*Wesmaelia* Foerster, *Aridelus* Marshall, *Leiophron* Nees, *Holdawayella* Loan) and of nymphal and adult Psocoptera (*Leiophron* Nees). In *Meteorus* Haliday the cocoon of some species hangs from a long thread. The most important apomorphous character of the larvae are the smooth and short mandibles. The apomorphous characters of the adults are rather "reticulate" as in the Helconinae, e.g., the wing venation is reduced in the Cosmophorini (Fig. 105), the Euphorini (Fig. 118, 117, 119) and to a lesser degree in the Centistini, the parasitism of adult insects also occurs in these tribes; a dorsope occurs in the Centistini (p.p.), Euphorini (p.p.) (Fig. 110) and in the Meteorini (p.p.) (Fig. 112, 113); the notauli and the precoxal suture are reduced in the Centistini and in the Euphorini; the comparatively wide ovipositor sheaths, together with a more or less robust and bent ovipositor in the Centistini (Fig. 109) and Euphorini (p.p.; Fig. 108), and the

spiracles of the first metasomal tergite are situated in the middle of the tergite or behind the middle in the Euphorini (Fig. 110, 114, 116) and in the Meteorini (p.p.; Fig. 112, 113).

The possible relations between the subfamilies are depicted in Fig. 123. The following groups may be recognized:

Group A: The old "cyclostomes" of Wesmael, together with the later formed subfamilies Telengainae and Mesostoinae. They share the hypoclypeal depression, the apically more or less concave clypeus (Fig. 27, 28, 35, 41, 12, 37, 121) and the more or less flattened first metasomal tergite (Fig. 14, 22, 26, 30, 33, 38, 40).

Group B: Specialized endoparasites of larvae of Diptera with the pupation in the host-puparium. The larvae have smooth, sickle-shaped mandibles and the labial sclerite absent or at least broadly interrupted ventrally. The adults have the prepectal carina absent and a more or less oval metasoma (Fig. 53).

Group C: Specialized endoparasites of larvae of Lepidoptera; the egg is deposited in the eggs of the host or in the early instar larvae. The larvae of the Acaeliinae and of the Microgasterinae-Cardiochilini have the tips of the mandibles bifid; the larvae of the Microgasterinae and of the Cheloninae have mandibles without or only with a small, scarcely differentiated base. The adults often have the eyes densely setose, the radial vein is often shortened (Fig. 54, 55, 57, 58, 62, 74) and the first metasomal tergite is more or less flattened in the Microgasterinae and Acaeliinae (Fig. 56—61).

Group D: Specialized endoparasites of larvae of Lepidoptera; the larvae share the robust mandibles with a long, toothed blade (but the blade is intermediate in *Meteoridea* Ashmead). The imagines have the radial cell rather small (Fig. 65, 67, 73) and the laterope deep and usually large (Fig. 68, 70).

Group E: Specialized endoparasites of larvae of Lepidoptera; the larvae have the labial sclerite transverse and the epistomal arch and hypostoma are absent. The adults share the tendency to loose the dorsal carinae of the first metasomal tergite.

Group F: Generally very specialized endoparsites, especially of adult insects. The larvae have toothless, more or less wedge-shaped mandibles. The adults share the tendency to have the spiracle of the first metasomal tergite situated near the middle (Fig. 95, 109, 110, 112—114, 116); the wing venation is often very specialized (Fig. 7, 93, 96, 105, 117—119).

The position of the Hybrizontinae within the Braconidae is rather uncertain, the situation of the spiracle near the middle of the tergite (Fig. 1) it shares with group F, but this may be a convergential development.

The Ichneutinae, Macrocentrinae, and Helconinae form separate groups on their own. The larvae of the Ichneutinae show some similarity with the larvae in Group D, but the mandibles have a more or less developed triangular base. The adults also show some similarity, e.g., the reduction of the wing venation and the flattened first metasomal tergite in several groups.

The larvae of the Macrocentrinae have a transverse labial sclerite with two processes ventrally, and polyembryony occurs in the genus *Macrocentrus* Curtis. The adults differ from the Helconinae by the shape of the trochantellus (Fig. 77),

of the first and second metasomal tergites of the mesosoma (Fig. 76), and of the head (Fig. 86).

Finally the Helconinae; both in biology and morphology a slightly derived group. The larvae have wedge-shaped and toothed mandibles with a more or less distinctly differentiated base and the adults show the tendency to develop long dorsal carinae and distinct dorsope (Fig. 78, 80, 83).

ACKNOWLEDGEMENTS

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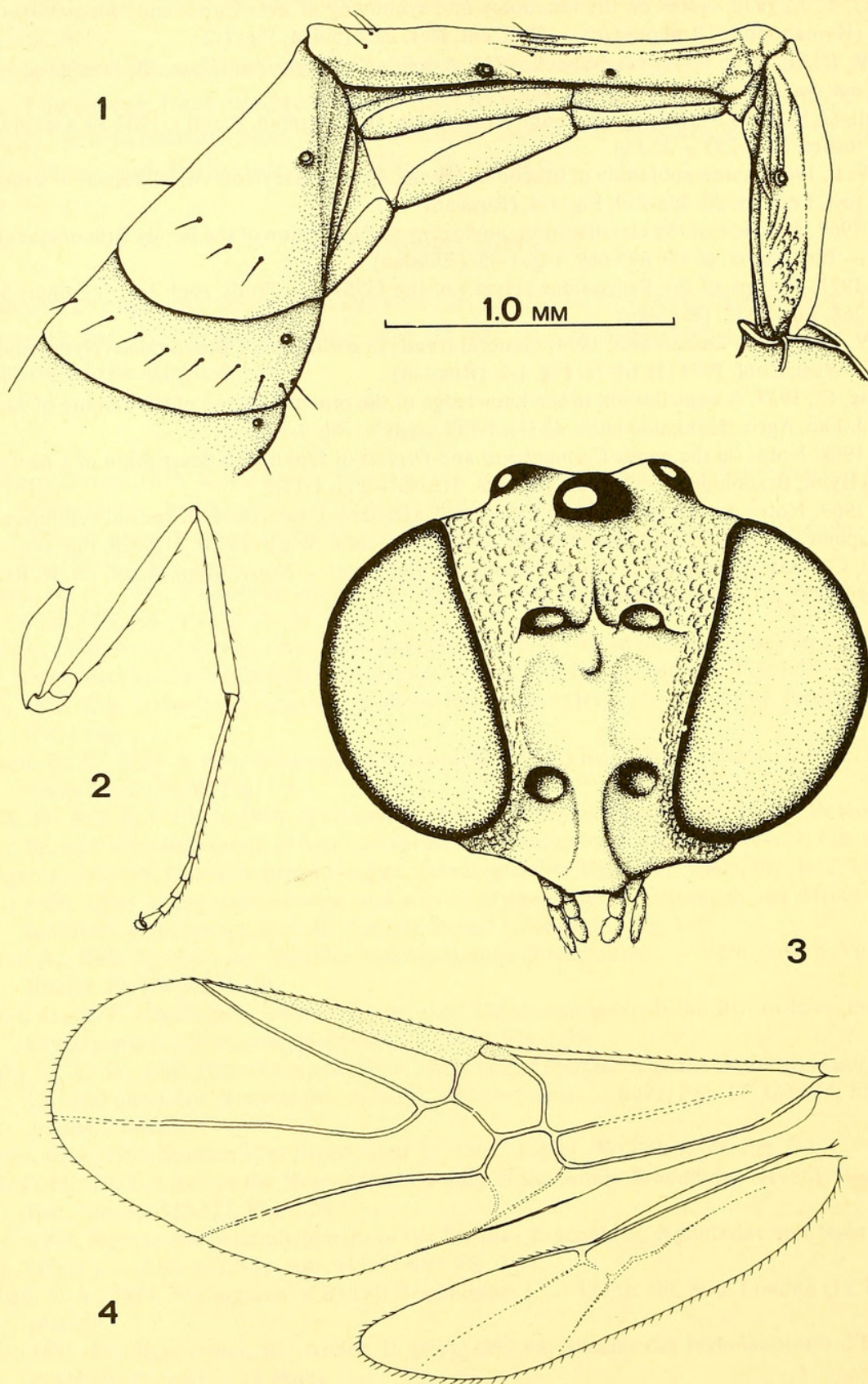
Fig. 1—4, *Hybrizon buccata* (de Brébisson), ♀, Netherlands, Meijendel. 1, basal half of metasoma, lateral aspect; 2, fore leg, lateral aspect; 3, head, frontal aspect; 4, wings. Fig. 1, 3: 2.1 times scaleline; Fig. 2, 4: scale-line
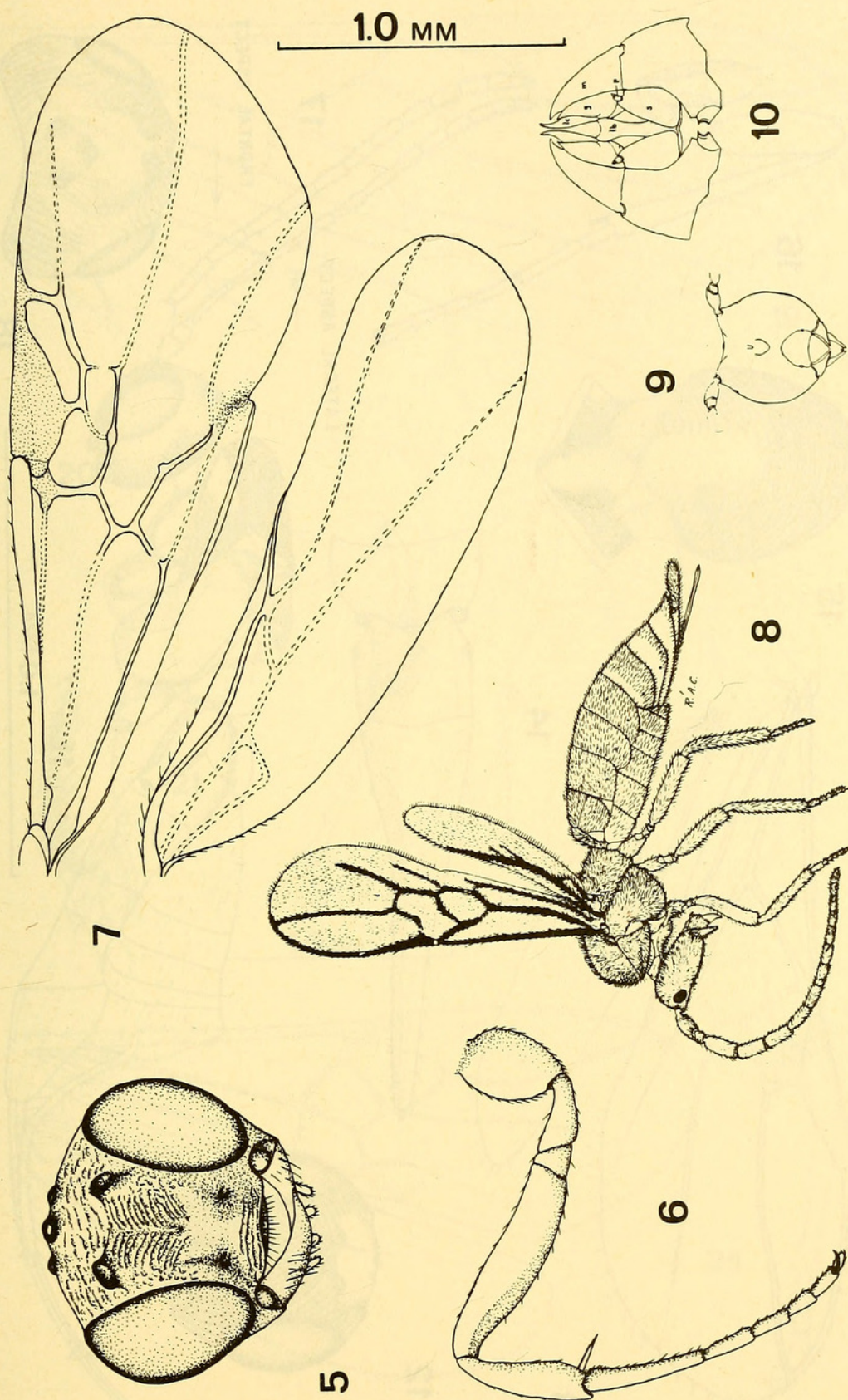
Fig. 5—7, *Neoneurus auctus* (Thomson), ♀, Lappland, Enontekiö. 5, head, frontal aspect; 6, fore leg, lateral aspect; 7, wings. Fig. 8, *Ypsistocerus manni* Cushman, ♀; habitus, lateral aspect. Fig. 9, 10, *Ypsistocerus vestigialis* Cushman. 9, head, frontal aspect; 10, mouth parts, ventral aspect. Fig. 5: scale-line; Fig. 6, 7: 1.2 times scale-line; Fig. 8: 0.5 times scale-line. Fig. 8-10 after Cushman, 1923
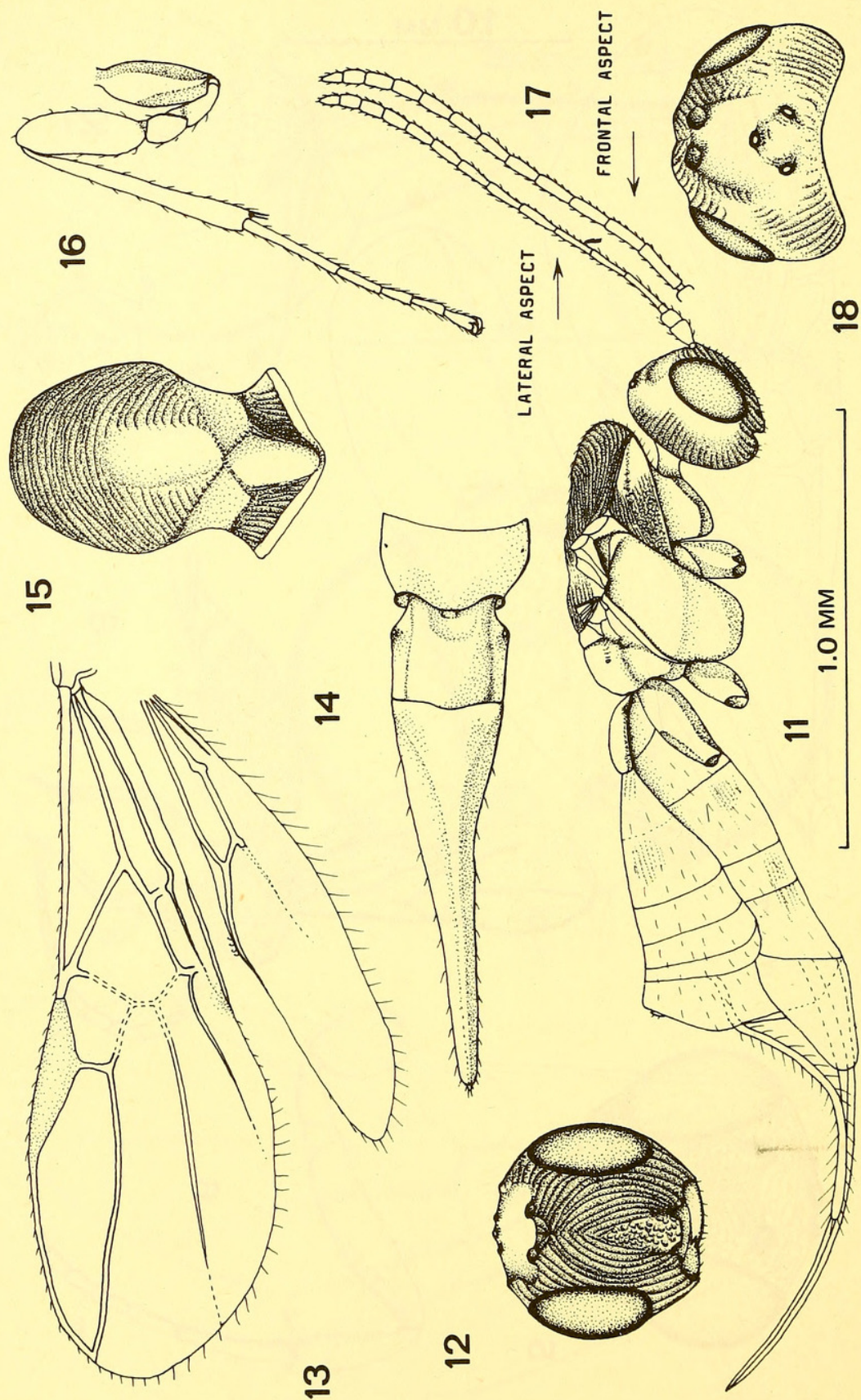
Fig. 11—18, *Mesostoa compressa* Van Achterberg, ♀, holotype. 11, habitus, lateral aspect; 12, head, frontal aspect; 13, wings; 14, abdomen, dorsal aspect; 15, mesonotum, dorsal aspect; 16, hind leg, lateral aspect; 17, antenna, frontal aspect; 18, head, dorsal aspect. Fig. 11, 13, 16, 17: scale-line; Fig. 12, 14, 15, 18: 1.5 times scale-line
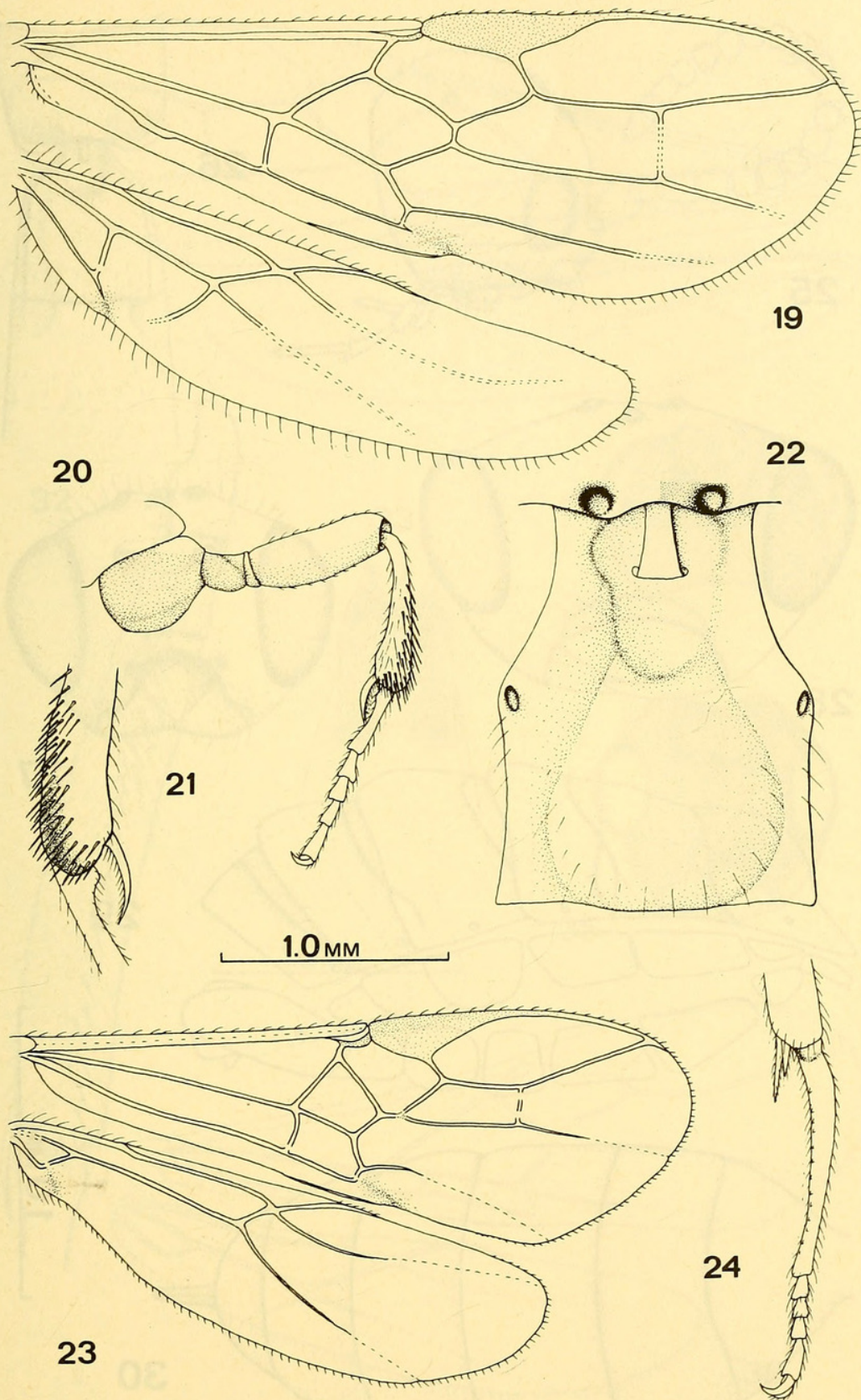
Fig. 19—21, 24, *Histeromerus mystacinus* Wesmael, ♀, Netherlands, Asperen. 19, wings; 20, fore leg, anterio-lateral aspect; 21, detail of fore tibia, posterio-lateral aspect; 24, hind tarsus, lateral aspect. Fig. 22, 23, *Bracon urinator* Fabricius, ♀, Switzerland, Saas-Fee. 22, first metasomal tergite, dorsal aspect; 23, wings. Fig. 19: scale-line; Fig. 20, 24: 1.2 times scale-line; Fig. 21, 22: 2.5 times scale-line; Fig. 23: 0.6 times scale-line
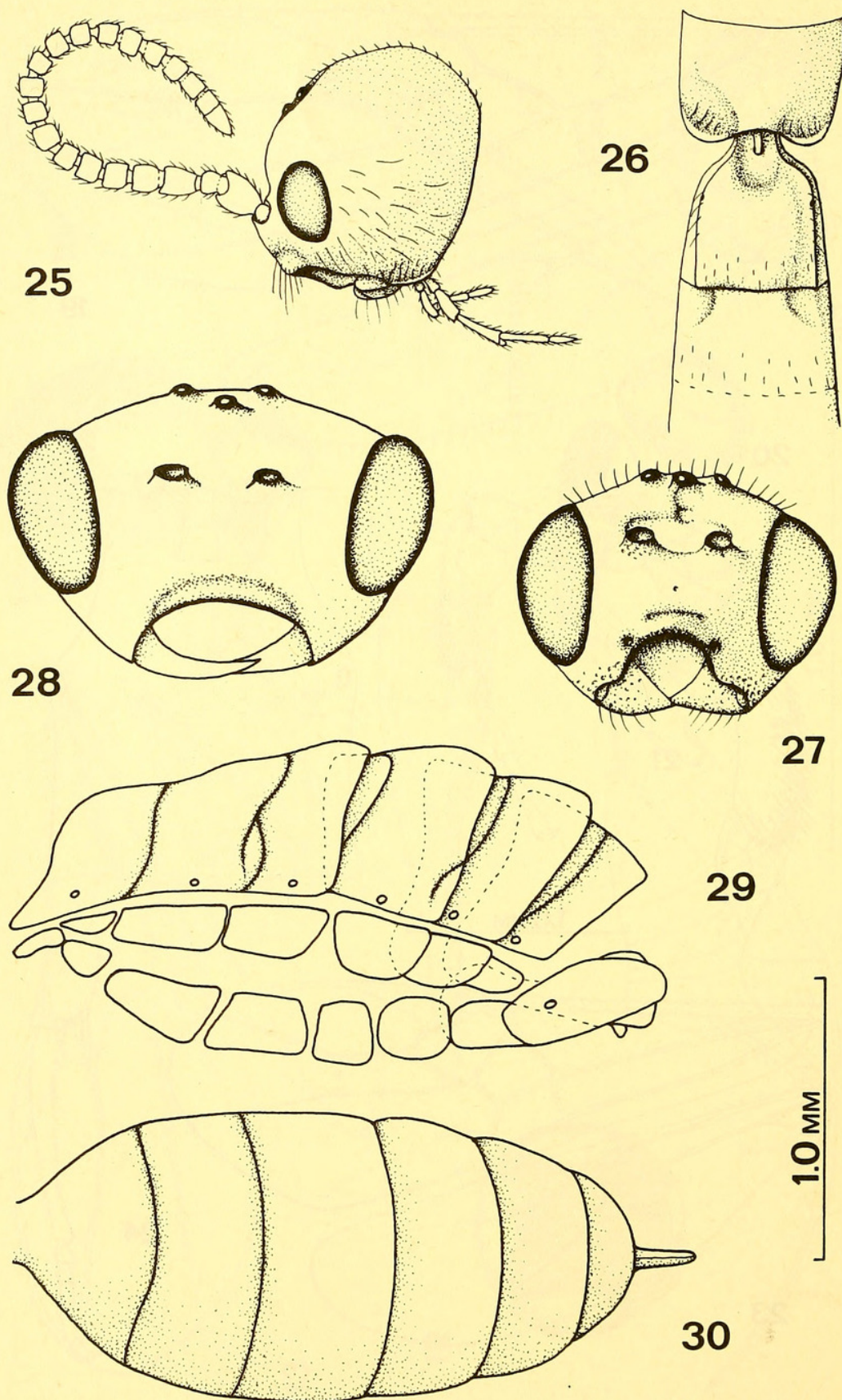
Fig. 25, 26, *Histeromerus mystacinus* Wesmael, ♀, Netherlands, Asperen. 25, head, lateral aspect; 26, propodeum, first and second metasomal tergites, dorsal aspect. Fig. 27, *Bracon urinator* Fabricius, ♀, Switzerland, Saas-Fee; head, frontal aspect. Fig. 28-30, *Telengaia ventralis* Tobias. 28, head, frontal aspect; 29, metasoma, lateral aspect; 30, metasoma, dorsal aspect. Fig. 25-27: scale-line; Fig. 28, 30: after Tobias, 1962; Fig. 29: after Tobias & Dudarenko, 1974

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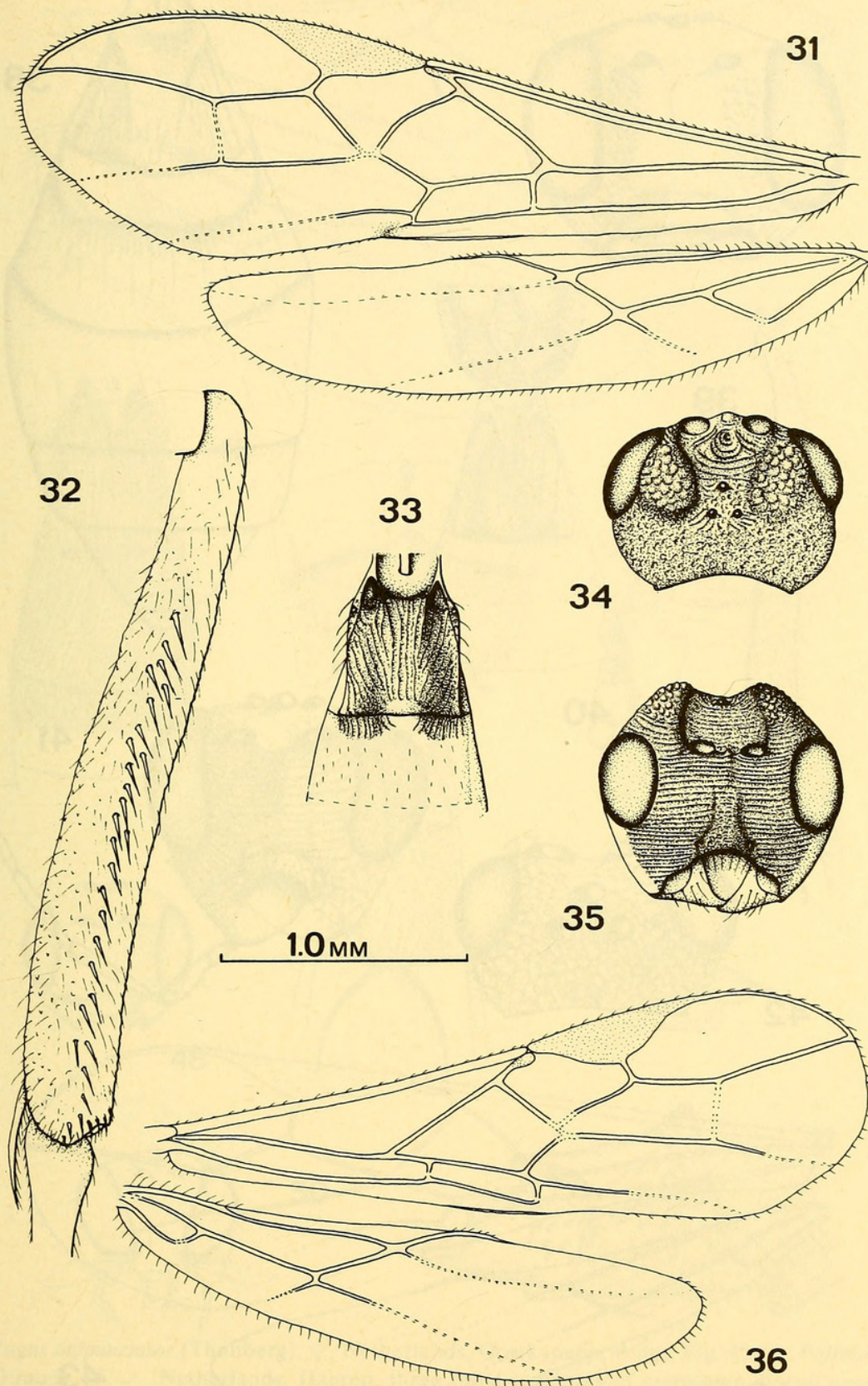
Fig. 31—33, *Doryctodes imperator* (Haliday), ♀, Netherlands, Cadier. 31, wings; 32, fore tibia, anterio-lateral aspect; 33, first and second metasomal tergites, dorsal aspect. Fig. 34-36, *Dendrosoter protuberans* (Nees), ♀, Netherlands, Best. 34, head, dorsal aspect; 35, head, frontal aspect; 36, wings. Fig. 31, 33: 0.6 times scale-line; Fig. 32: 2.5 times scale-line; Fig. 34-36: scale-line
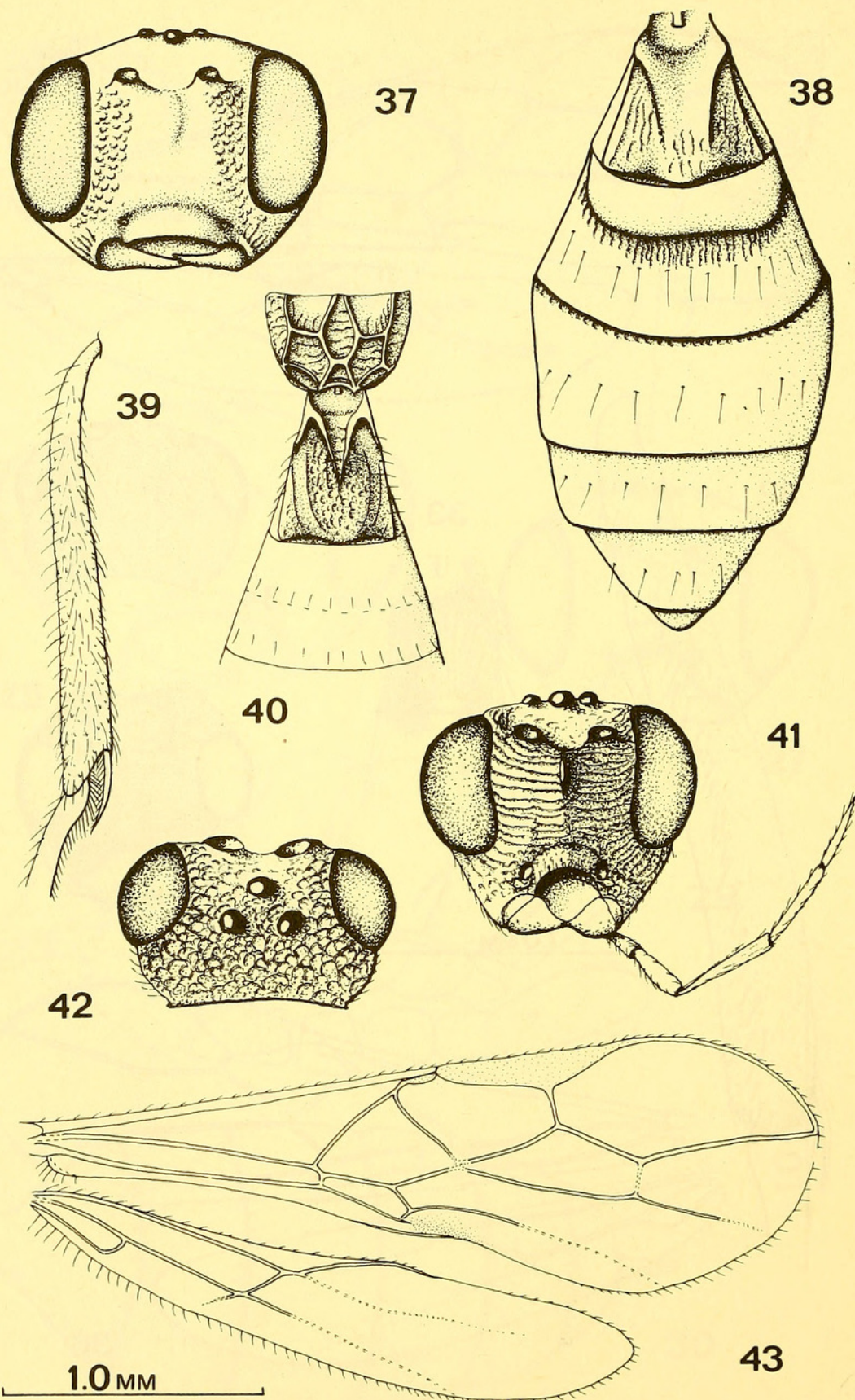
Fig. 37, 38, *Gnaptodon pumilio* (Nees), ♀, Netherlands, Waarder. 37, head, frontal aspect; 38, meta-soma, dorsal aspect. Fig. 39, 40, 43, *Rhyssalus clavator* Haliday, ♀, Netherlands, Wijster. 39, fore tibia, posterio-lateral aspect; 40, basal half of abdomen, dorsal aspect; 43, wings. Fig. 41, 42, *Rogas excavatus* (Telenga), ♂, Italy, Riva s. Garda. 41, head, frontal aspect; 42, head, dorsal aspect. Fig. 37-39: 2.5 times scale-line; Fig. 40-42: 1.2 times scale-line; Fig. 43: scale-line
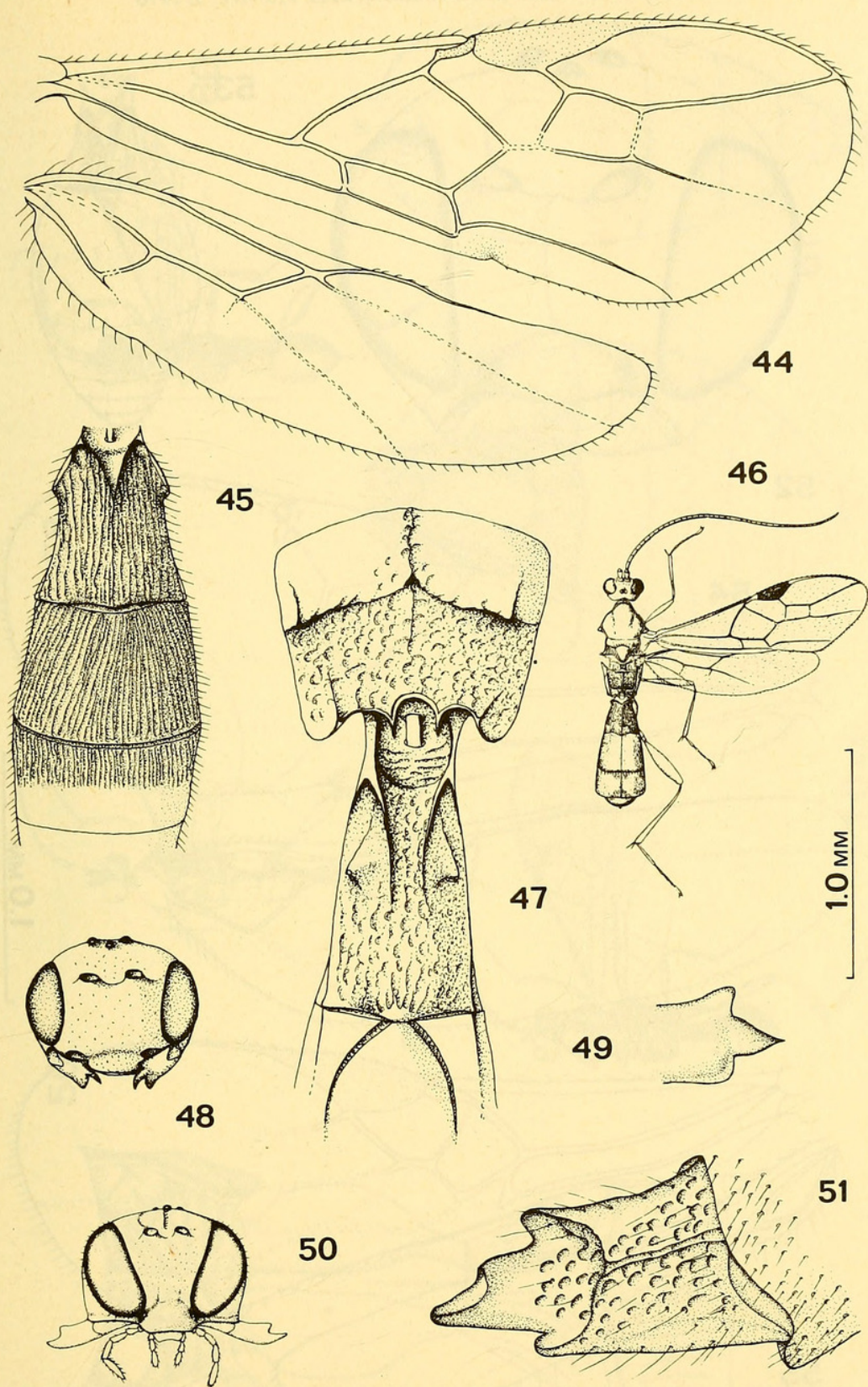
Fig. 44, *Rogas unipunctator* (Thunberg), ♀, Netherlands, Oostkapelle; wings. Fig. 45, 51, *Polemochartus liparae* (Giraud). 45, ♂, Netherlands, Haaren, three basal segments of metasoma, dorsal aspect; 51, ♀, Netherlands, Eindhoven, mandible, ventro-lateral aspect. Fig. 46, *Rogas drymoniae* Watanabe, 1937; habitus, dorsal aspect. Fig. 47-49, *Tanycarpa punctata* Van Achterberg, ♀, holotype. 47, propodeum, first and second metasomal tergites, dorsal aspect; 48, head, frontal aspect; 49, detail of mandible, lateral aspect. Fig. 50, *Chaenusa bergi* (Riegel), ♀, paratype; head, frontal aspect. Fig. 44, 45: 0.5 times scale-line; Fig. 46: 0.1 times scale-line; Fig. 47, 51: 2.5 times scale-line; Fig. 48: 1.2 times scale-line; Fig. 50: 1.8 times scale-line; Fig. 49: 3.2 times scale-line
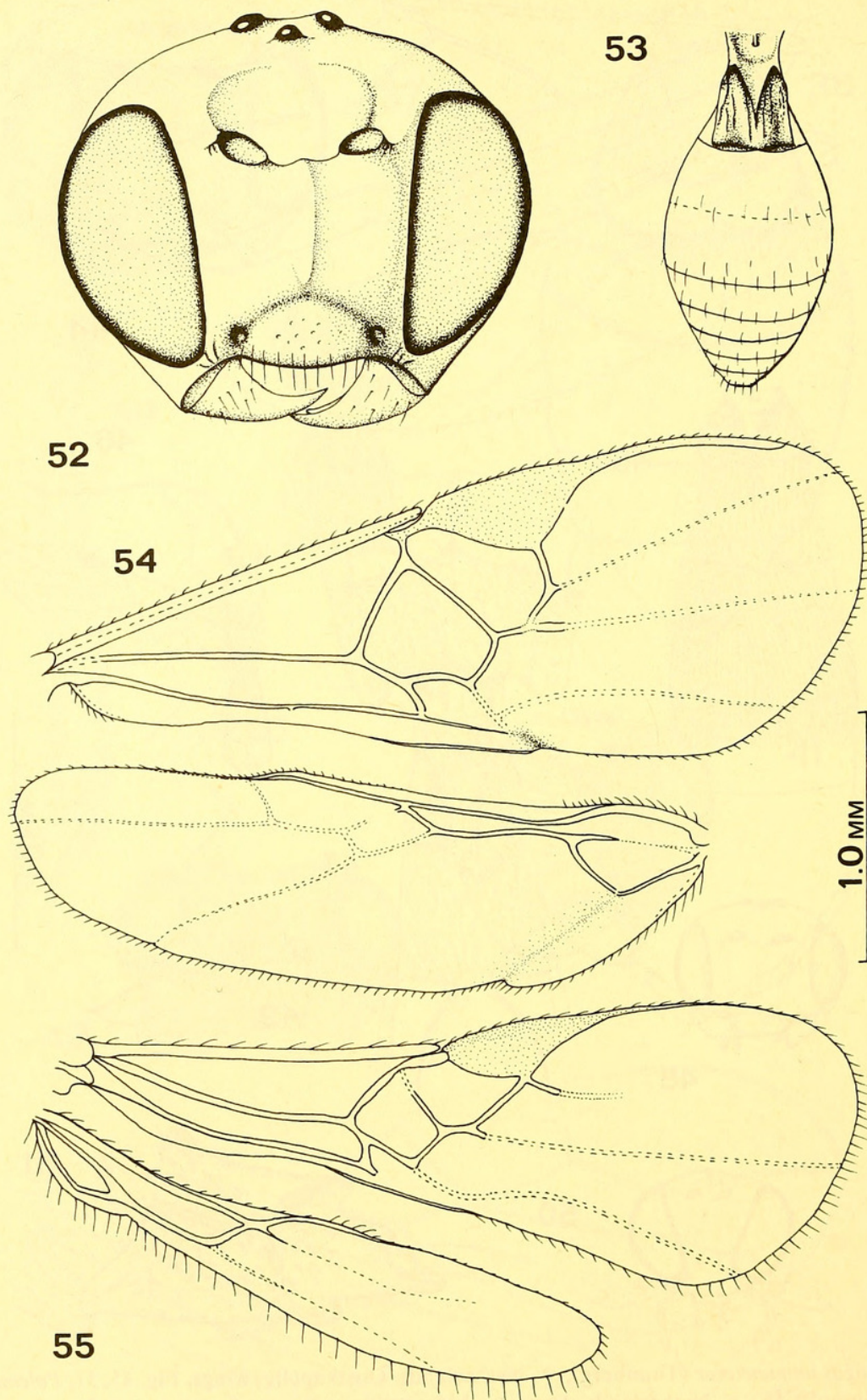
Fig. 52, 53, *Opius (Apodesmia) polyzonius* Wesmael, ♀, Netherlands, Asperen. 53, head, frontal aspect; 54, metasoma, dorsal aspect. Fig. 54, *Apanteles falcator* (Ratzeburg), ♀, Netherlands, Waarder; wings. Fig. 55, *Mirax cremastobombyciae* (Fullaway), ♀, holotype; wings. Fig. 52: 2.5 times scale-line; Fig. 53, 54: scale-line; Fig. 55: 1.7 times scale-line
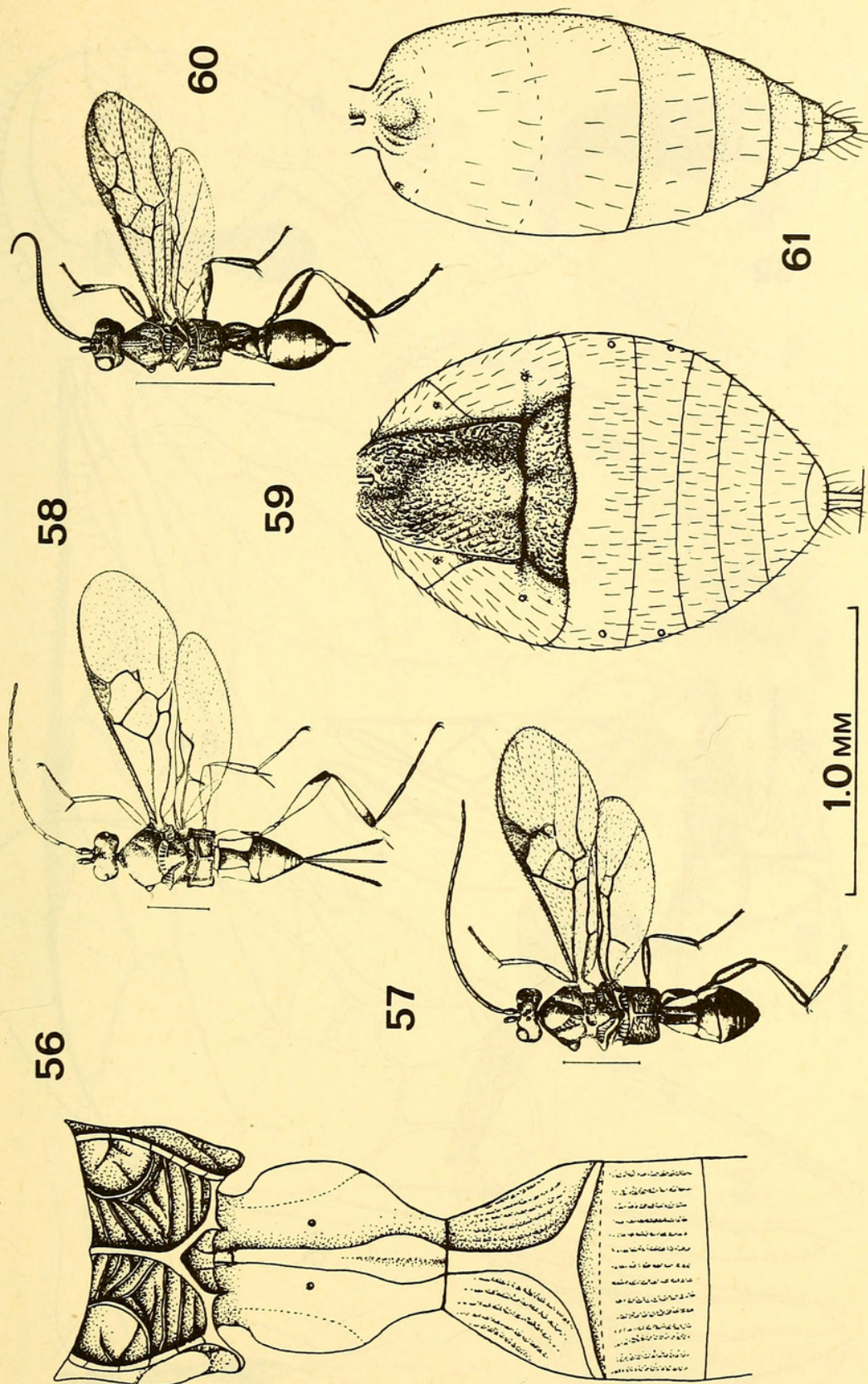
Fig. 56, *Mirax cremastobombyciae* (Fullaway), ♀, holotype; basal half of abdomen, dorsal aspect. Fig. 57, *Microplitis theretrae* Watanabe, after Watanabe, 1937; habitus, dorsal aspect. Fig. 58, *Microgaster takeuchii* Watanabe, after Watanabe, 1937; habitus, dorsal aspect. Fig. 59, *Apanteles falcator* (Ratzeburg), ♀, Netherlands, Waarder; metasoma, dorsal aspect. Fig. 60, *Cardiochiles japonicus* Watanabe, after Watanabe, 1937; habitus, dorsal aspect. Fig. 61, *Acaelius* spec., ♀, Netherlands, Oostvoorne; metasoma, dorsal aspect. Fig. 56, 61: 2.5 times scale-line; Fig. 59: scale-line; Fig. 57, 58: 0.2 times scale-line; Fig. 60: 0.1 times scale-line
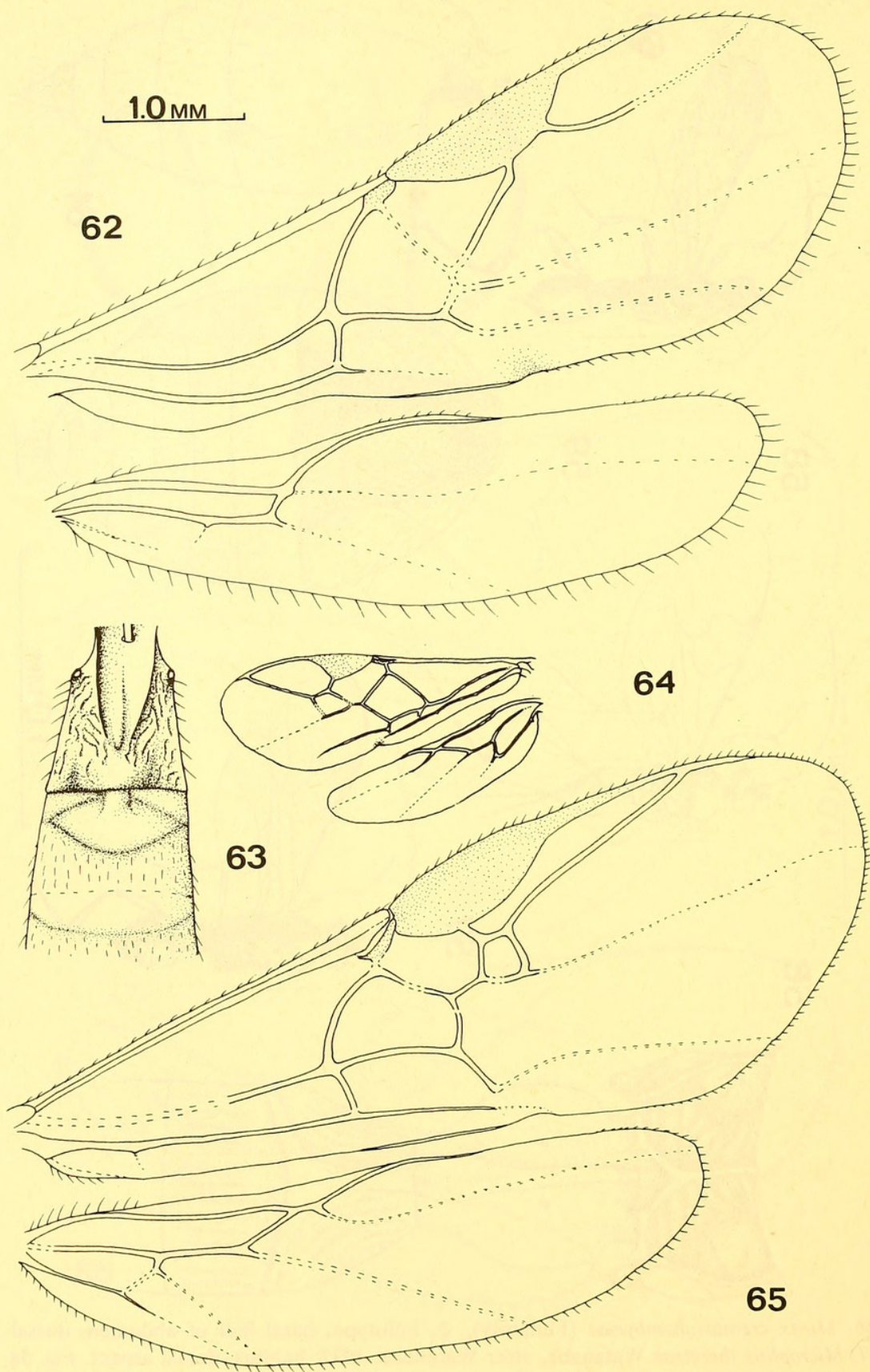
Fig. 62, *Acaelius* spec., ♀, Netherlands, Oostvoorne; wings. Fig. 63, 65, *Earinus nitidulus* (Nees), ♀, Netherlands, Schaarsbergen. 63, first and second metasomal tergites, dorsal aspect; 65, wings. Fig. 64, *Meteoridea japonensis* Shenefelt & Muesebeck, after Shenefelt & Muesebeck, 1957; wings. Fig. 62: 4.0 times scale-line; Fig. 63, 65: scale-line
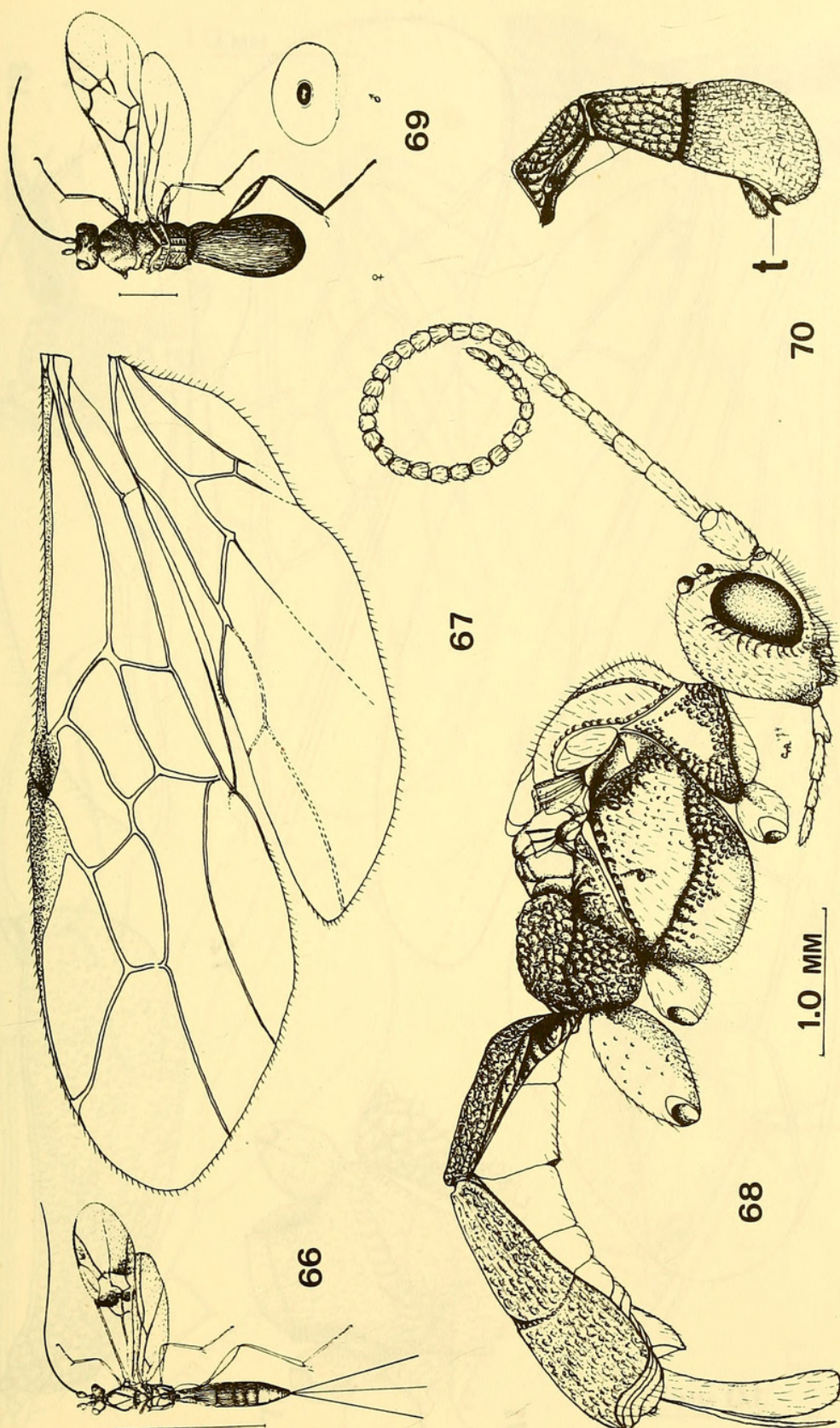
Fig. 66, *Braunsia matsumurai* Watanabe, ♀, after Watanabe, 1937; habitus, dorsal aspect. Fig. 67, 68, *Acampsis alternipes* (Nees), ♀, Netherlands, Den Haag. 67, wings; 68, habitus, lateral aspect. Fig. 69, *Chelonus* (*Microchelonus*) *tosensis* Watanabe, after Watanabe, 1937; ♀, habitus dorsal aspect; ♂, apex of metasoma, apical aspect. Fig. 70, *Sigalphus irrorator* (Fabricius), ♀, Netherlands, Naaldwijk; metasoma, lateral aspect. Fig. 66, 0.1 times scale-line. Fig 67, 68, scale-line. Fig. 69, 0.4 times scale-line. Fig. 70, 0.6 times scale-line; t = tooth
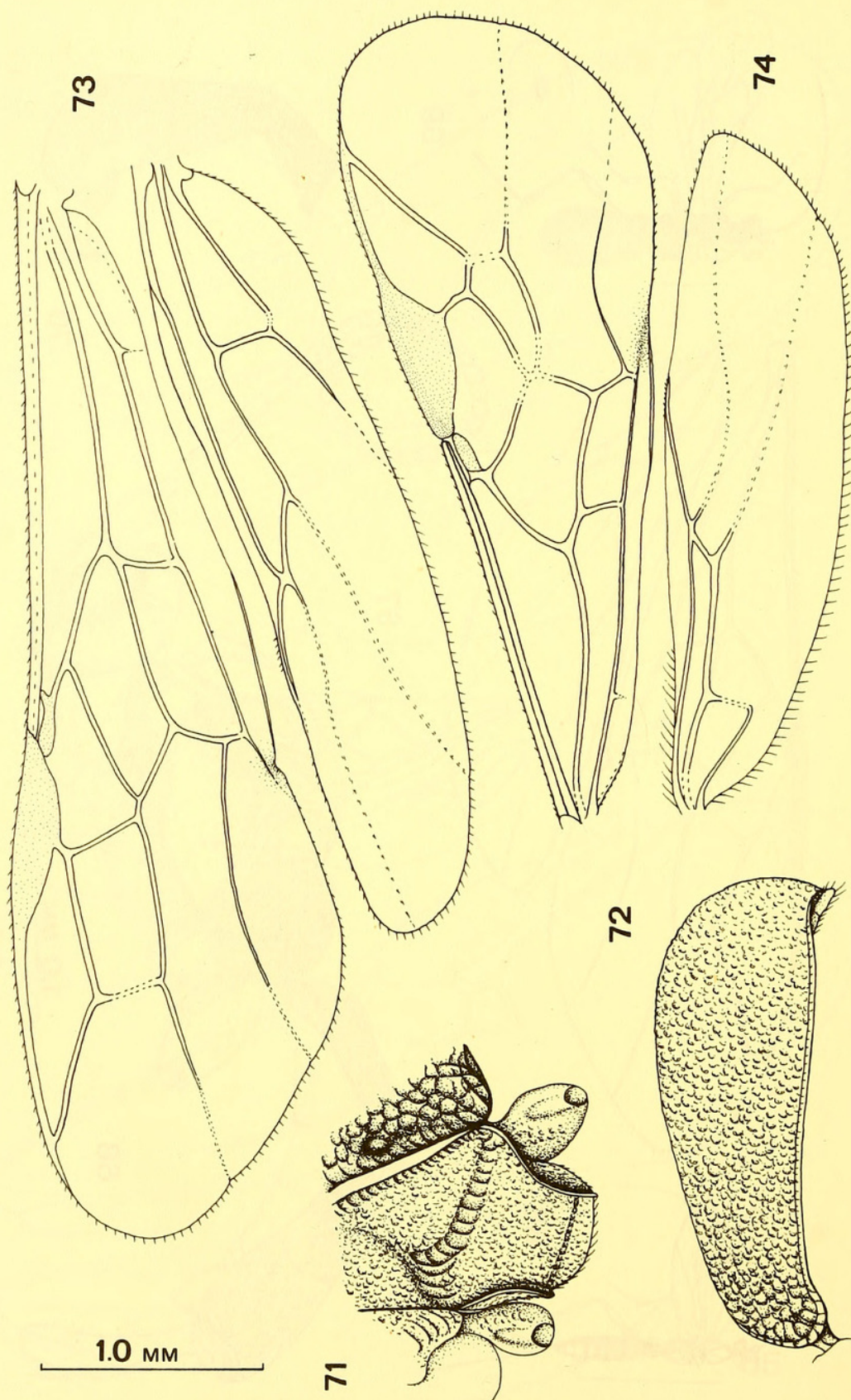
Fig. 71, 72, 74, *Ascogaster instabilis* Wesmael, ♀, Netherlands, Asperen. 71, mesosoma, ventro-lateral aspect; 72, metasoma, lateral aspect; 74, wings. Fig. 73, *Sigalphus irrorator* (Fabricius), ♀, Netherlands, Naaldwijk; wings. Fig. 71, 72, 74: scale-line; Fig. 73: 0.5 times scale-line
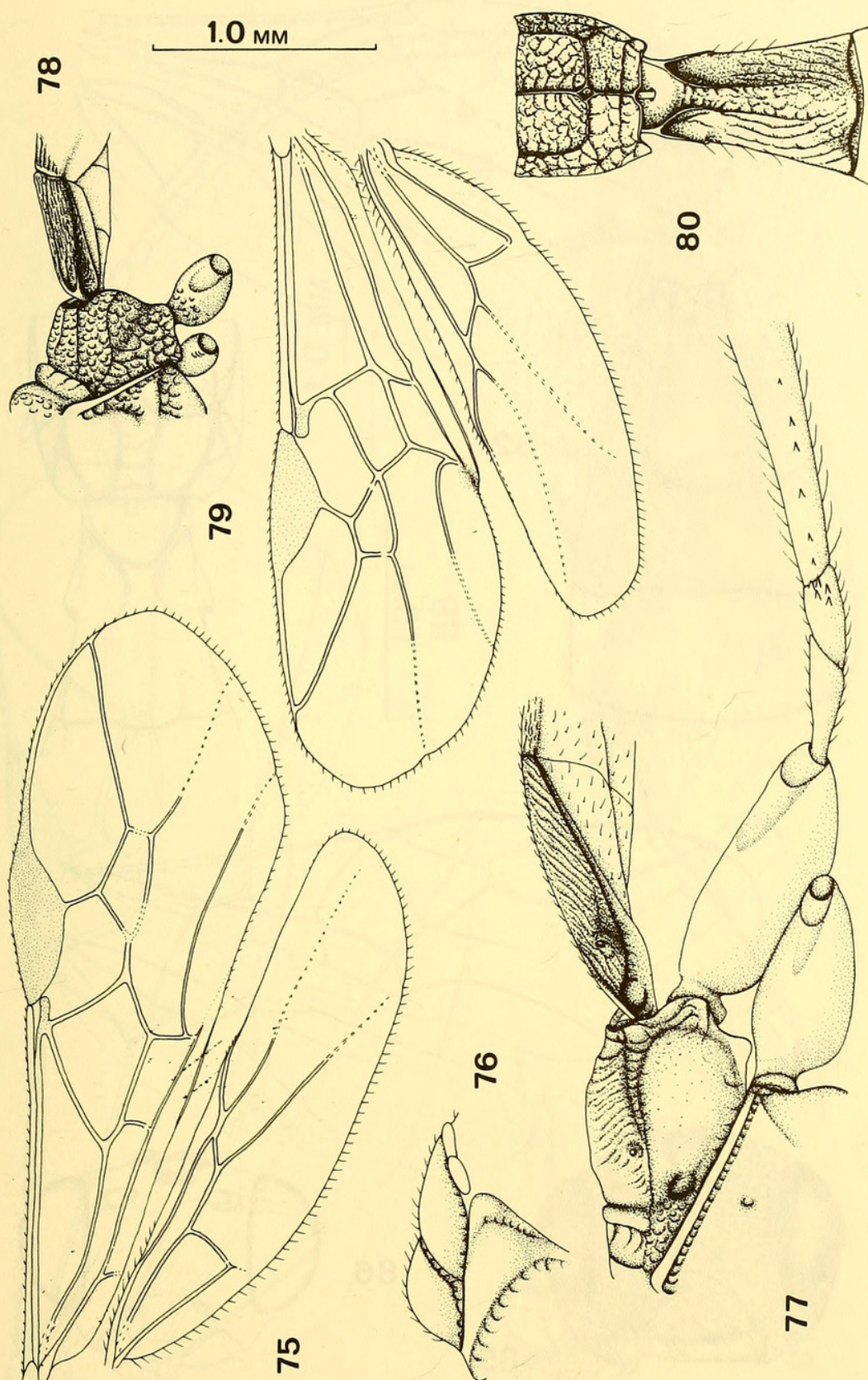
Fig. 75—77, *Macrocentrus thoracicus* (Nees), ♀, Netherlands, Meijendel. 75, wings; 76, mesoscutum, lateral aspect; 77, propodeum and first metasomal segment, lateral aspect. Fig. 78, 79, *Cenocoelius analis* (Nees), ♀, Netherlands, Wijster. 78, propodeum and first metasomal segment, lateral aspect; 79, wings. Fig. 80, *Blacus* (*Ganychorus*) *striatus* Van Achterberg, ♀, holotype; propodeum and first metasomal tergite, dorsal aspect. Fig. 75: 0.5 times scale-line; Fig. 76-79: scale-line; Fig. 80: 2.5 times scale-line
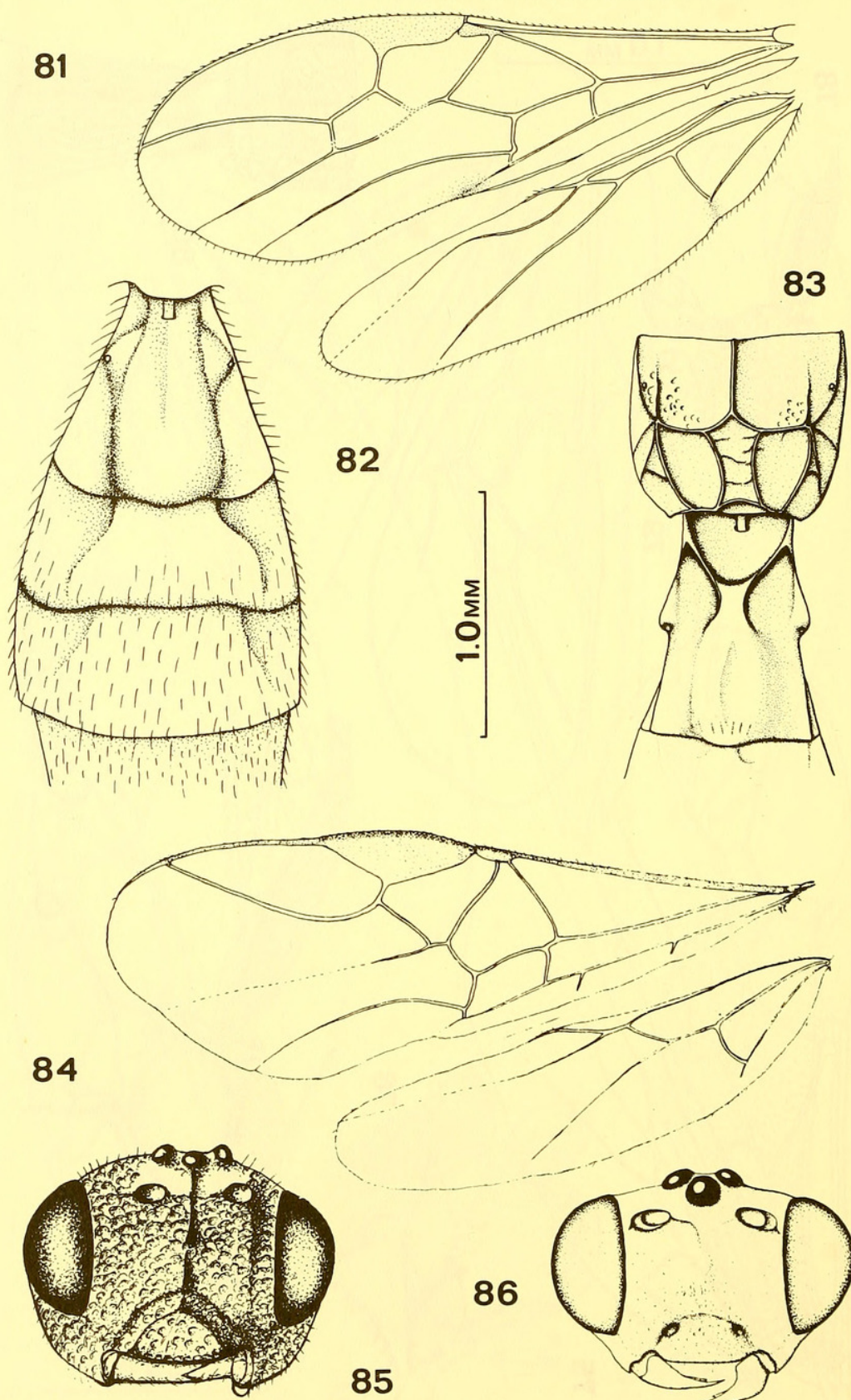
Fig. 81, 86, *Austrozele brevicaudis* (Szépligeti), ♀, lectotype. 81, wings; 86, head, frontal aspect. Fig. 82, *Proterops nigripennis* Wesmael, ♀, Netherlands, Kralo; basal half of metasoma, dorsal aspect. Fig. 83, *Elachistocentrum similis* (Szépligeti), ♀, lectotype; propodeum and first metasomal tergite, dorsal aspect. Fig. 84, *Eubazus* (*Brachistes*) *lapponicus* (Thomson), ♀, lectotype; wings. Fig. 85, *Ichneutes* spec., ♀, Netherlands, Waarder; head, frontal aspect. Fig. 81: 0.4 times scale-line; Fig. 82: scale-line; Fig. 83: 1.8 times scale-line; Fig. 84: 0.7 times scale-line; Fig. 85: 1.2 times scale-line; Fig. 86: 0.8 times scale-line
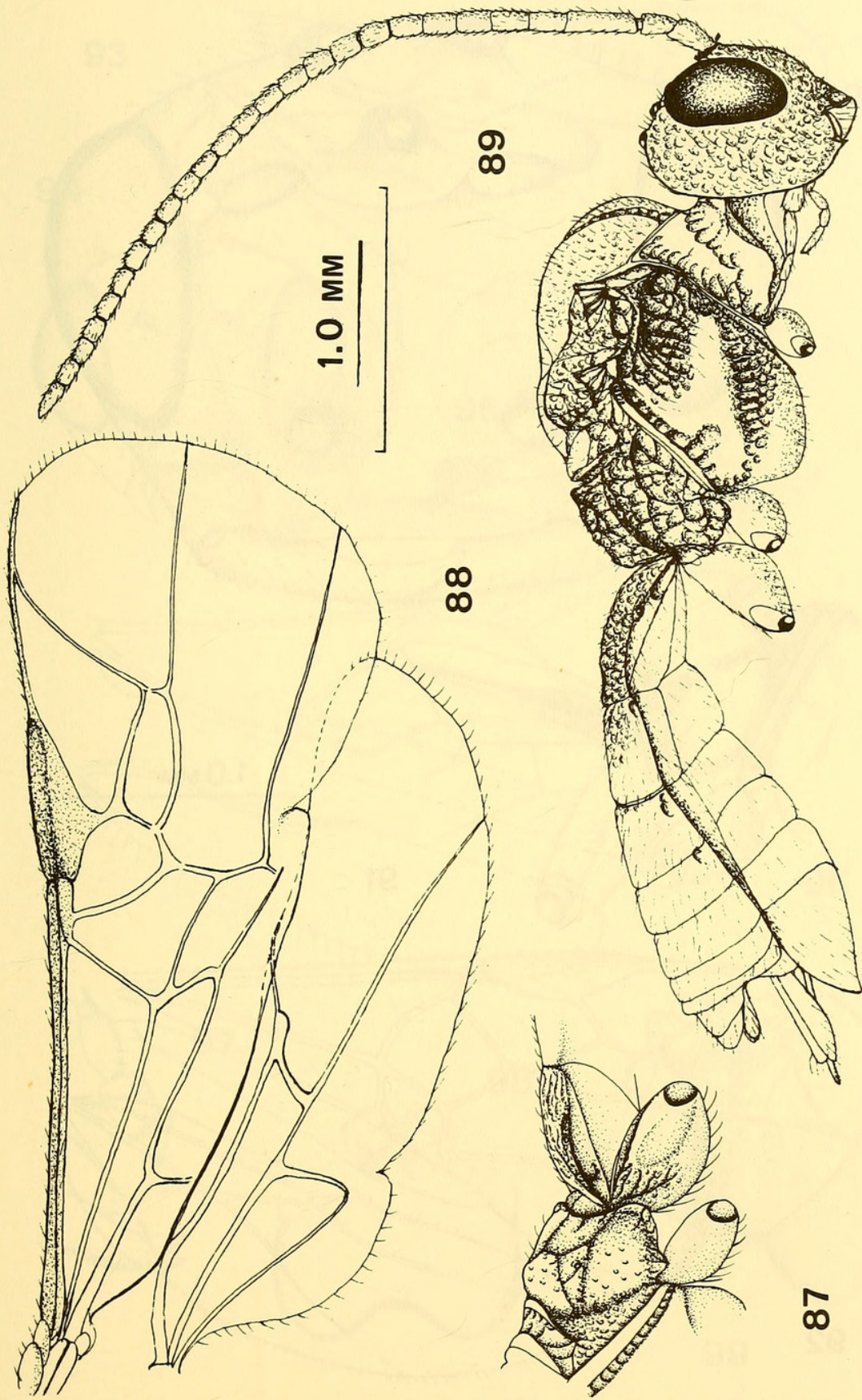
Fig. 87, *Eubazus* (*Foersteria*) *tibialis* (Haliday), ♂, Netherlands, Wijster; propodeum and first meta-somal segment, lateral aspect. Fig. 88, 89, *Ichneutes* spec., ♀, Netherlands, Waarder. 88, wings; 89, habitus, lateral aspect. Fig. 87-89: scale-line
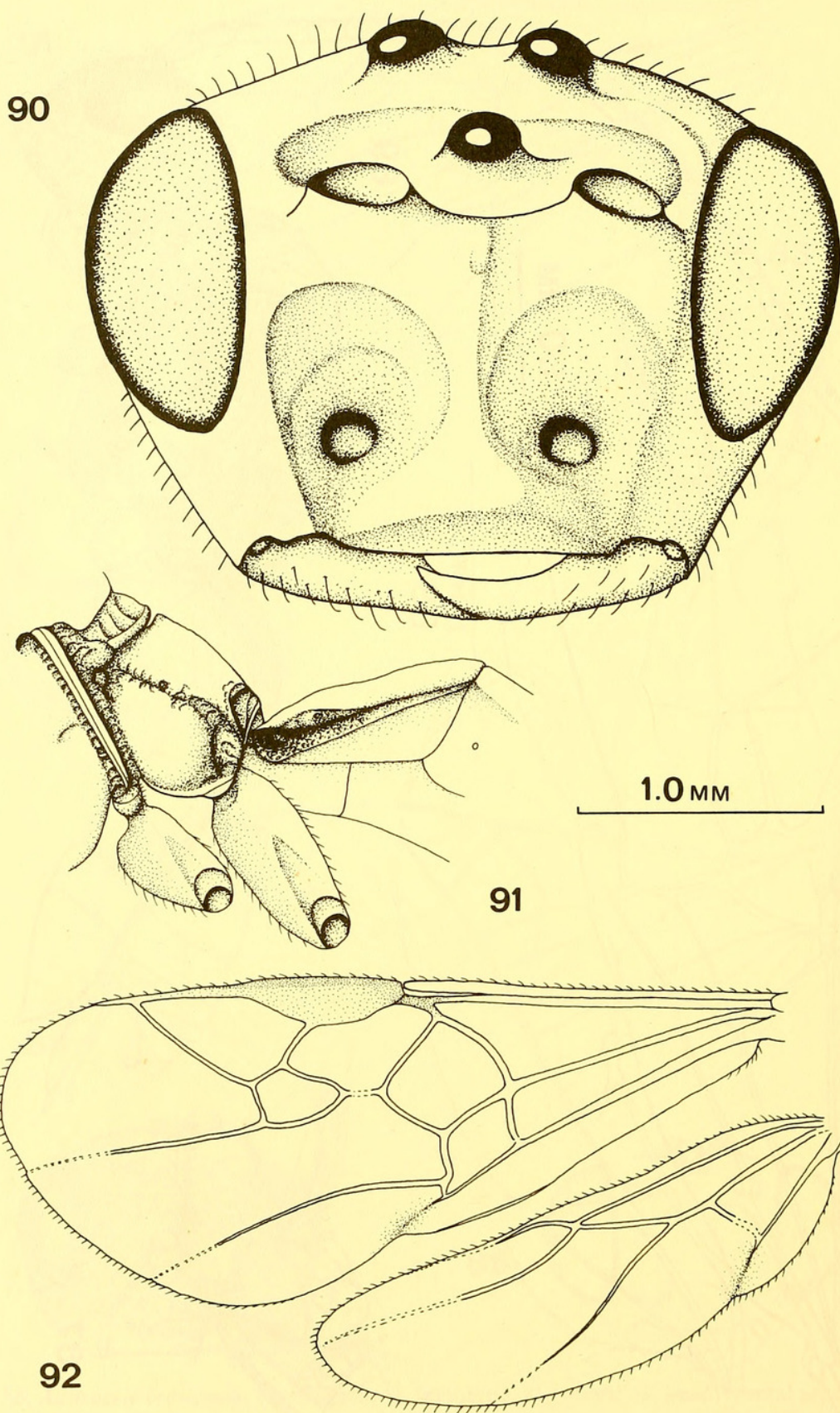
Fig. 90, 92, *Proterops nigripennis* Wesmael, ♂, Netherlands, Kralo. 90, head, frontal aspect; 92, wings. Fig. 91, *Charmon extensor* (Linnaeus), ♀, Netherlands, Naardermeer; propodeum and first metasomal segment, lateral aspect. Fig. 90: 2.5 times scale-line; Fig. 91: scale-line; Fig. 92: 0.6 times scale-line

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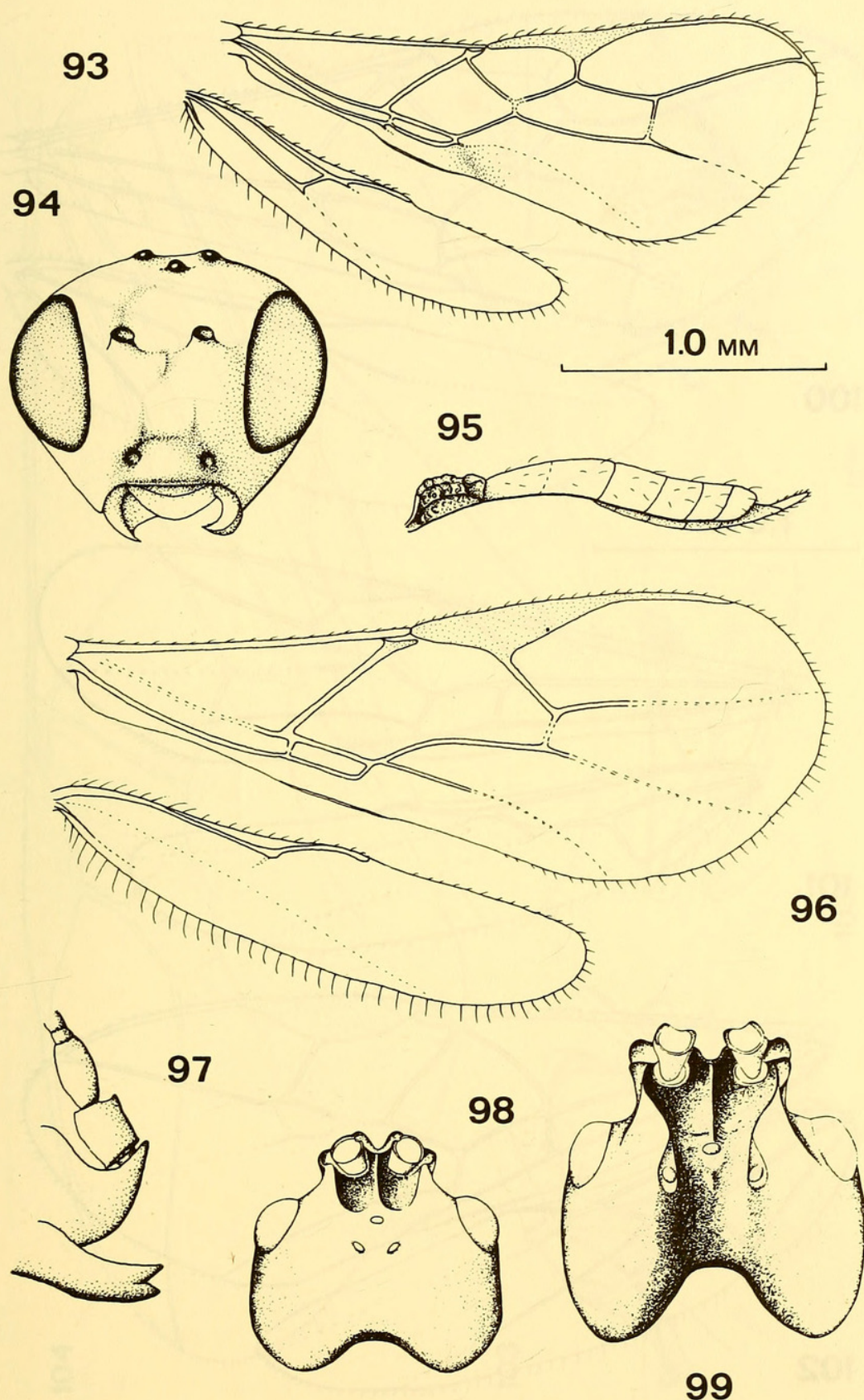
Fig. 93—95, *Ephedrus plagiator* (Nees), ♀, Netherlands, Maastricht. 93, wings; 94, head, frontal aspect; 95, metasoma, lateral aspect. Fig. 96, *Aphidius ervi* Haliday, ♀, Netherlands, Asperen; wings. Fig. 97, *Cosmophorus cembrae* Ruschka, after Hedqvist, 1955; anterior part of head, lateral aspect. Fig. 98, *Cosmophorus klugi* Ratzeburg, after Watanabe, 1968; head, dorsal aspect. Fig. 99, *Cosmophorus regius* Niezabitowski, id. Fig. 93, 95, 96: scale-line; Fig. 94: 2.5 times scale-line
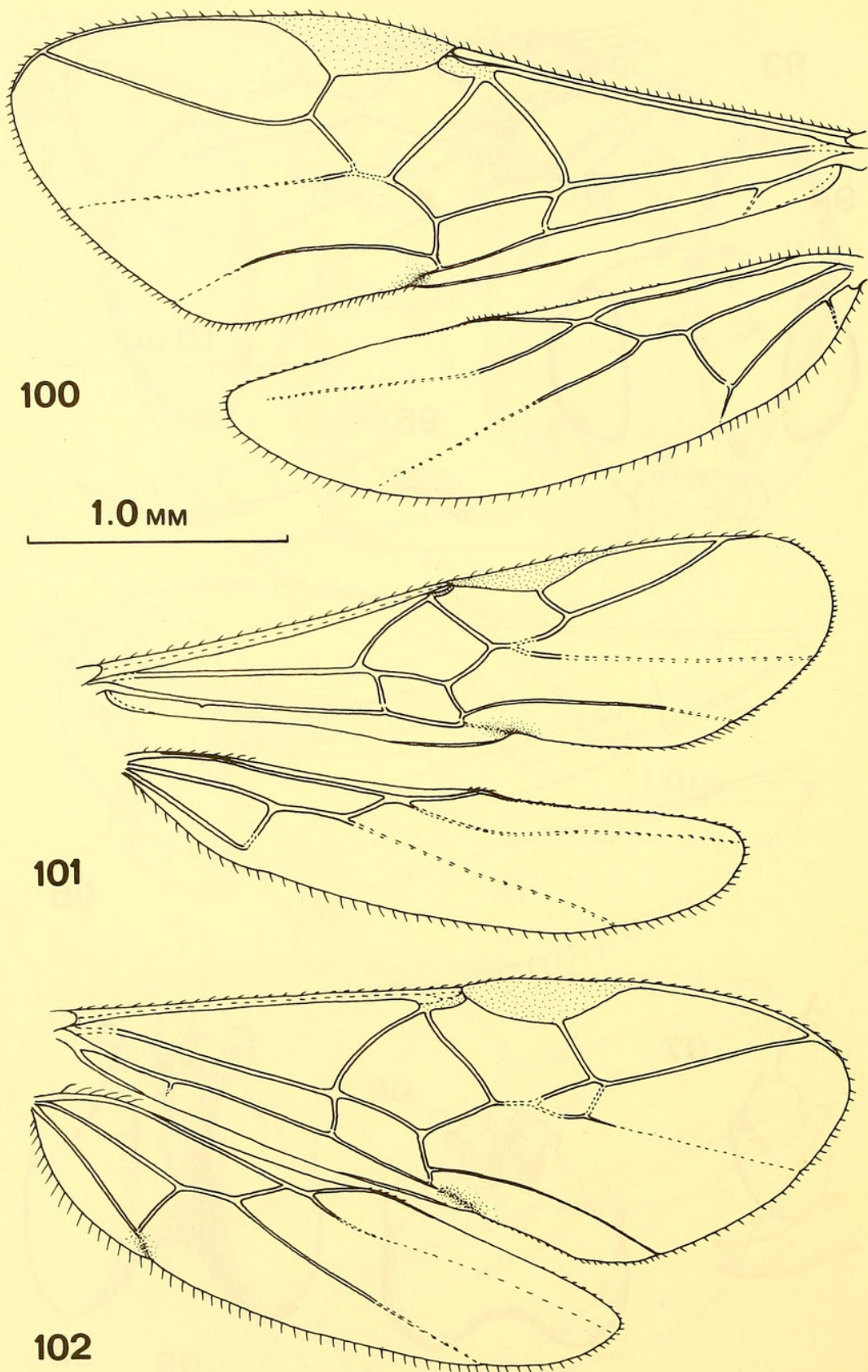
Fig. 100, *Charmon extensor* (Linnaeus), ♀, Netherlands, Naardermeer; wings. Fig. 101, *Orgilus laevigator* (Nees), ♀, Netherlands, Waarder; wings. Fig. 102, *Microtypus wesmaeli* Ratzeburg, ♀, Netherlands, Crailo: wings. Fig. 100, 102: 0.6 times scale-line; Fig. 101: scale-line
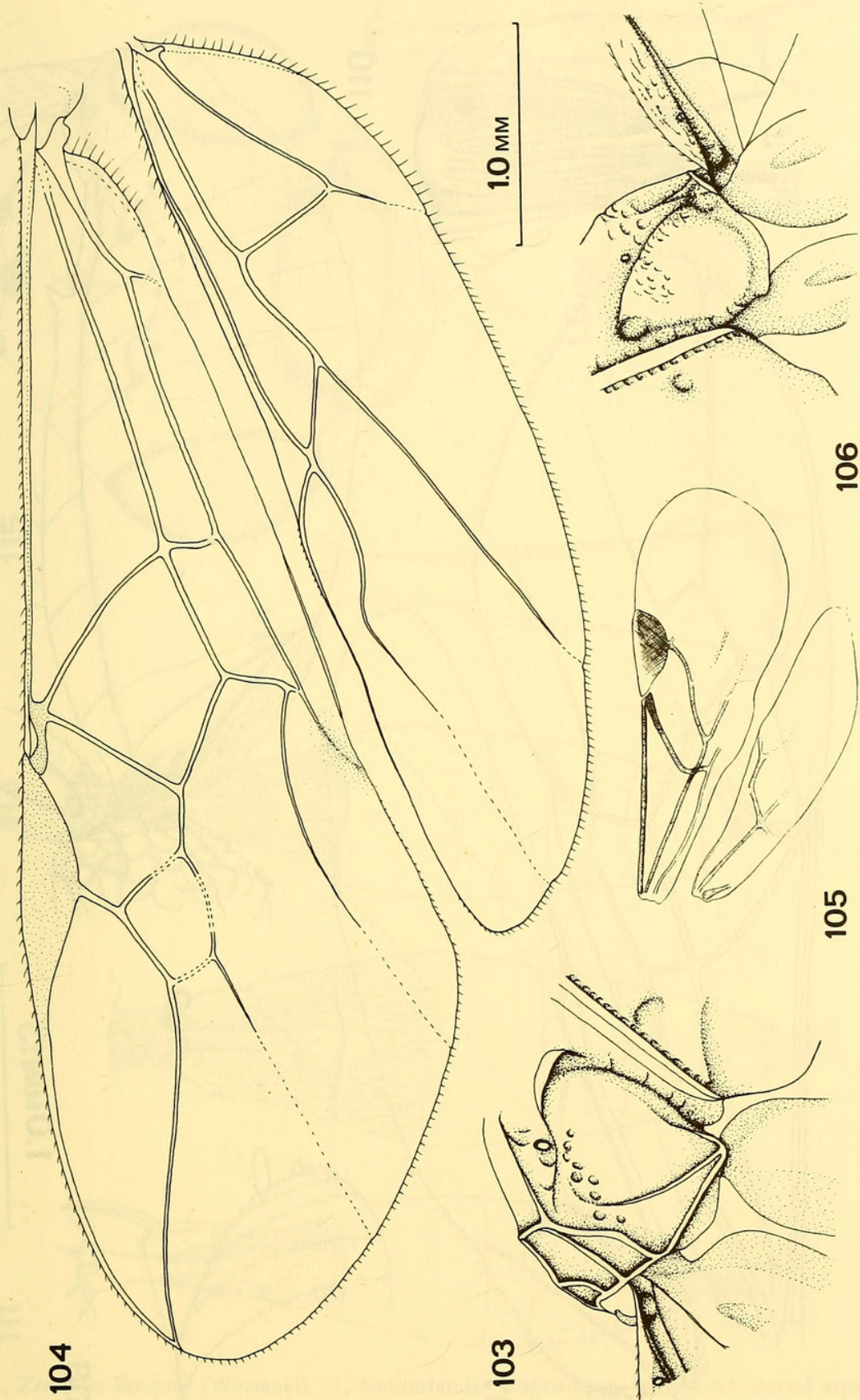
Fig. 103, 104, *Zele infumator* Lyle, ♀, Netherlands, Crailo. 103, Propodeum, lateral aspect; 104, wings.
Fig. 105, *Cosmophorus regius* Niezabitowski, after Watanabe, 1968; wings. Fig. 106, *Microtypus wesmaeli*
Ratzeburg, ♀, Netherlands, Crailo; propodeum, lateral aspect. Fig. 103, 104: 0.6 times scale-line;
Fig. 106: scale-line
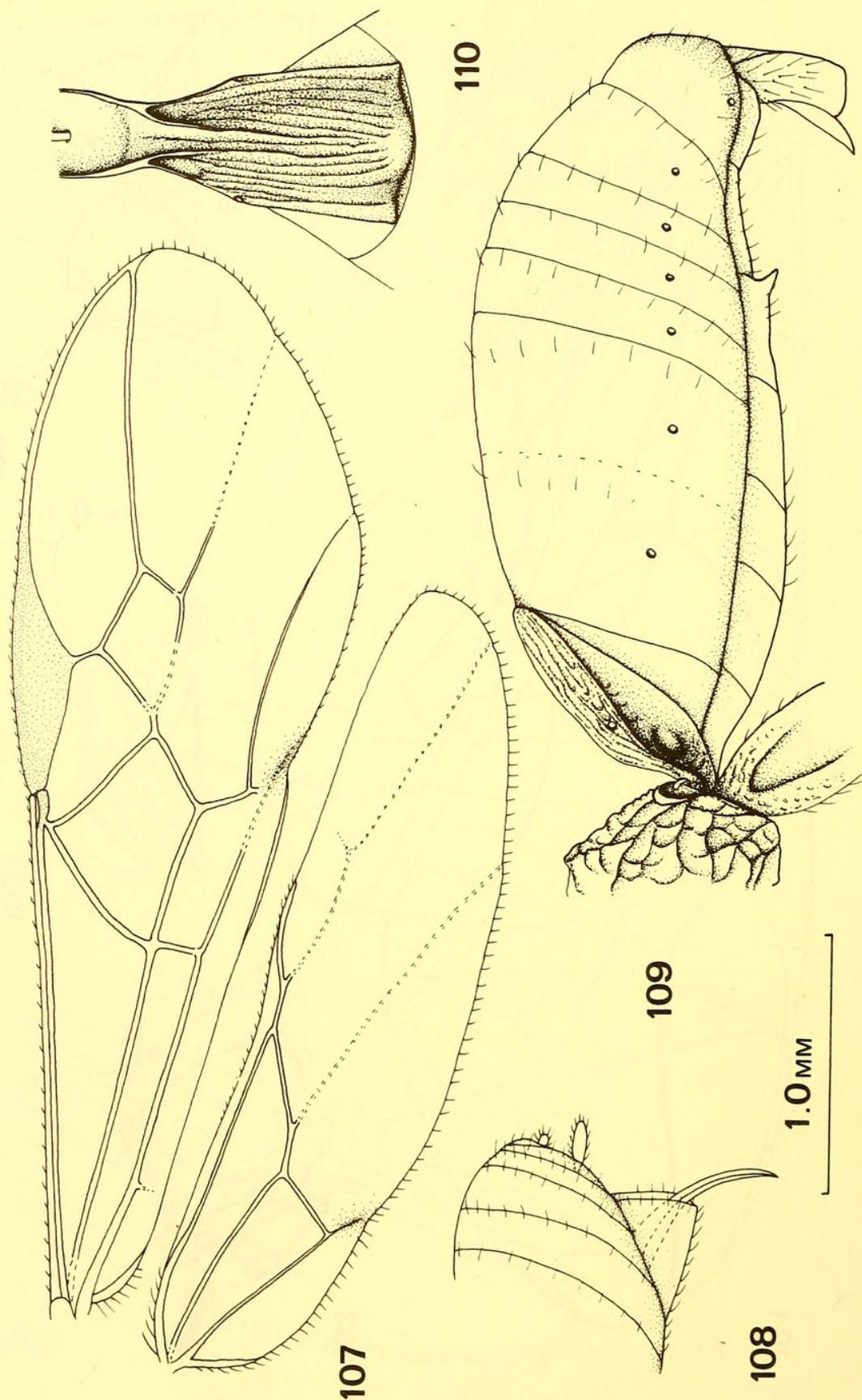
Fig. 107, *Zemiotes deceptor* (Wesmael), ♀, Netherlands, Wageningen; wings. Fig. 108, *Leiophron* (*Leiophron*) *apicalis* Haliday, ♀, Netherlands, Wijster; apex of metasoma, lateral aspect. Fig. 109, *Ancylocentrus ater* (Nees), ♀, Netherlands, Waarder; metasoma, lateral aspect. Fig. 110, *Streblocera macroscapa* (Ruthe), ♀, Netherlands, Waarder; first metasomal tergite, dorsal aspect. Fig. 107: 0.6 times scale-line; Fig. 108-110: 2.5 times scale-line
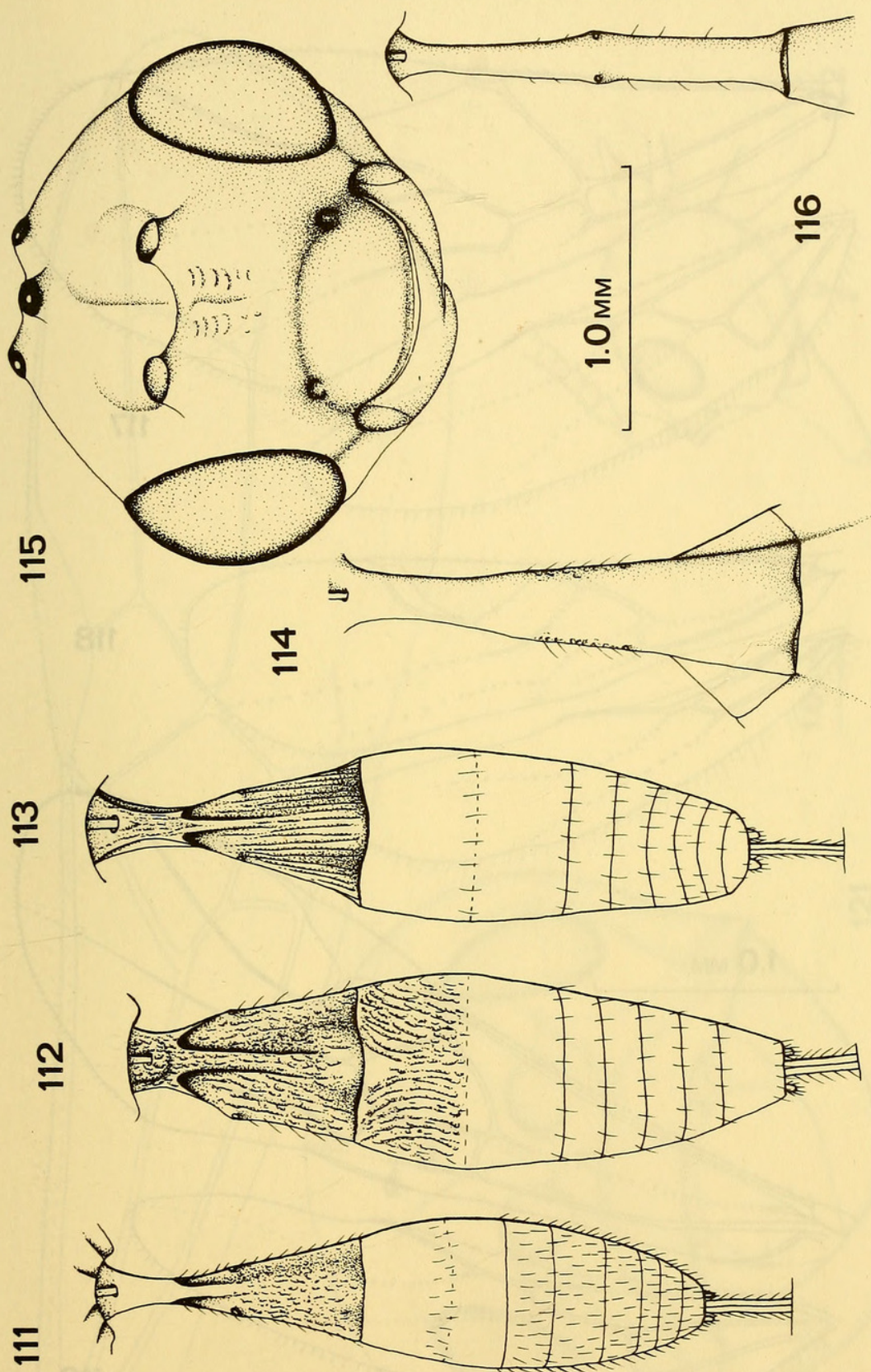
Fig. 111, *Zemiotes deceptor* (Wesmael), ♀, Netherlands, Wageningen; metasoma, dorsal aspect. Fig. 112, *Meteorus* cf. *sulcatus* Szépligeti, ♀, Netherlands, Wijster; metasoma, dorsal aspect. Fig. 113, *Meteorus ictericus* (Nees), ♀, Netherlands, Waarder; metasoma, dorsal aspect. Fig. 114, *Syntretus* cf. *conterminus* (Nees), ♀, Netherlands, Waarder; first metasomal tergite, dorsal aspect. Fig. 115, *Perilitus* (*Microctonus*) cf. *deceptor* Wesmael, ♀, Netherlands, Putten (G.); head, frontal aspect. Fig. 116 *Chrysopophthorus* spec., ♀, Costa Rica, Turrialba; first metasomal tergite, dorsal aspect. Fig. 111: 0.6 times scale-line; Fig. 112, 113, 116: scale-line; Fig. 114, 115: 2.5 times scale-line
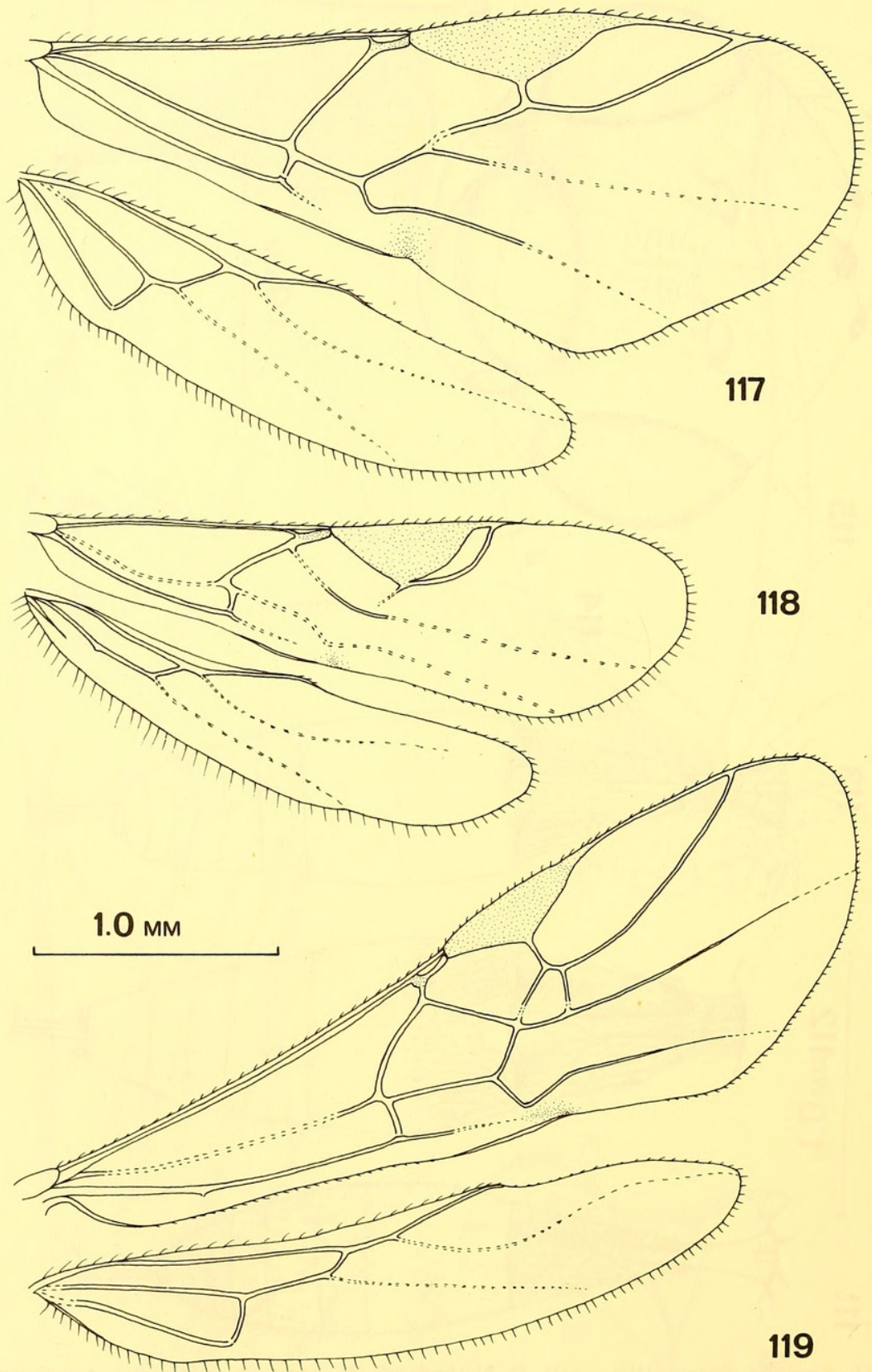
Fig.117, *Perilitus* (*Microctonus*) cf. *deceptor* Wesmael, ♀, Netherlands, Putten (G.); wings. Fig. 118, *Leiophron* (*Leiophron*) *apicalis* Haliday, ♀, Netherlands, Oostvoorne; wings. Fig. 119, *Chrysopophthorus* spec., ♀, Costa Rica, Turrialba; wings. Fig. 117, 118: 1.2 times scale-line; Fig. 119: scale-line
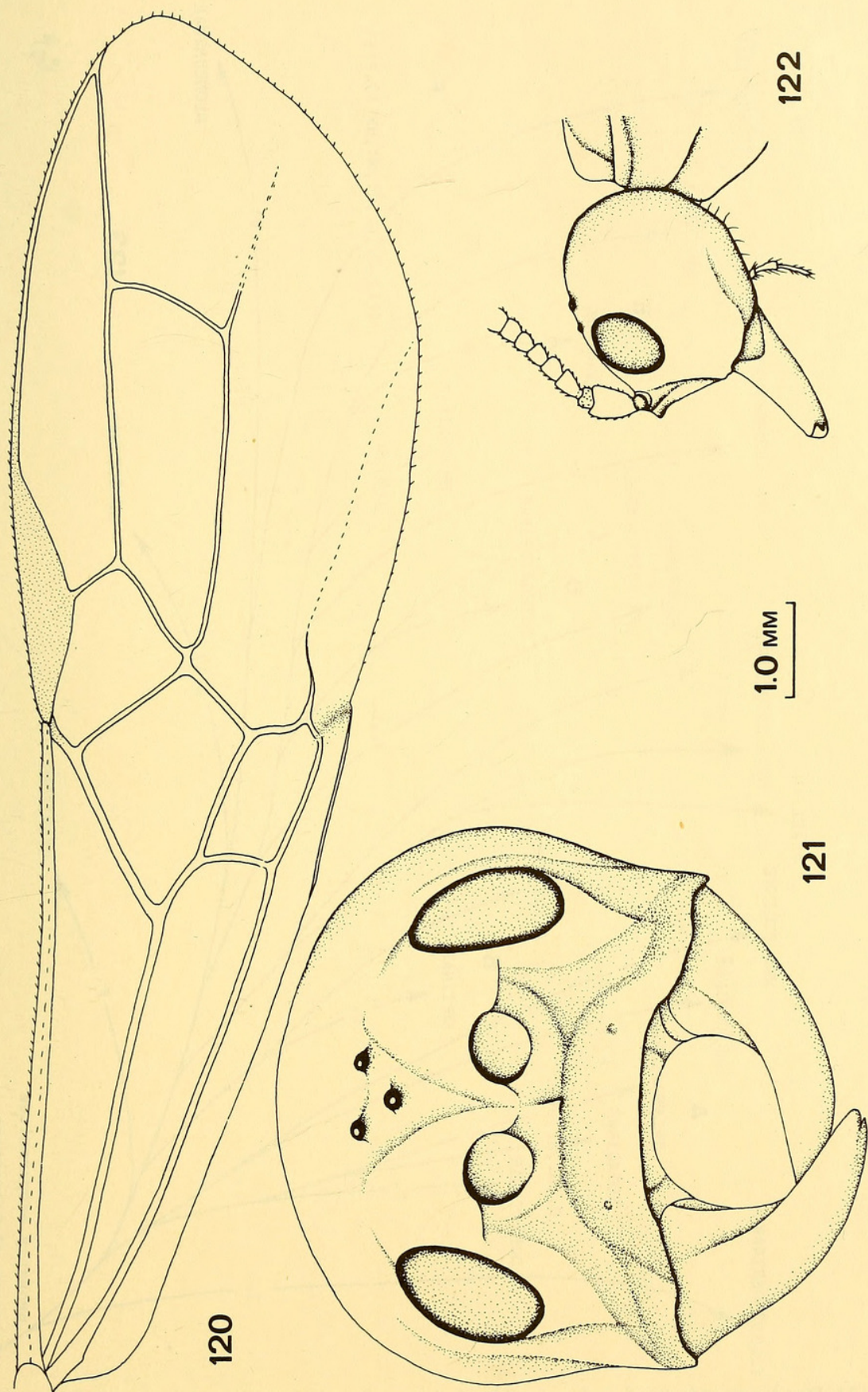
Fig. 120—122, *Pseudodicrogenium monstrosum* Fahringer. 120, fore wing, paralectotype; 121, head, frontal aspect, lectotype; 122, head, lateral aspect, lectotype. Fig. 120, 122: scale-line; Fig. 121: 2.0 times scale-line
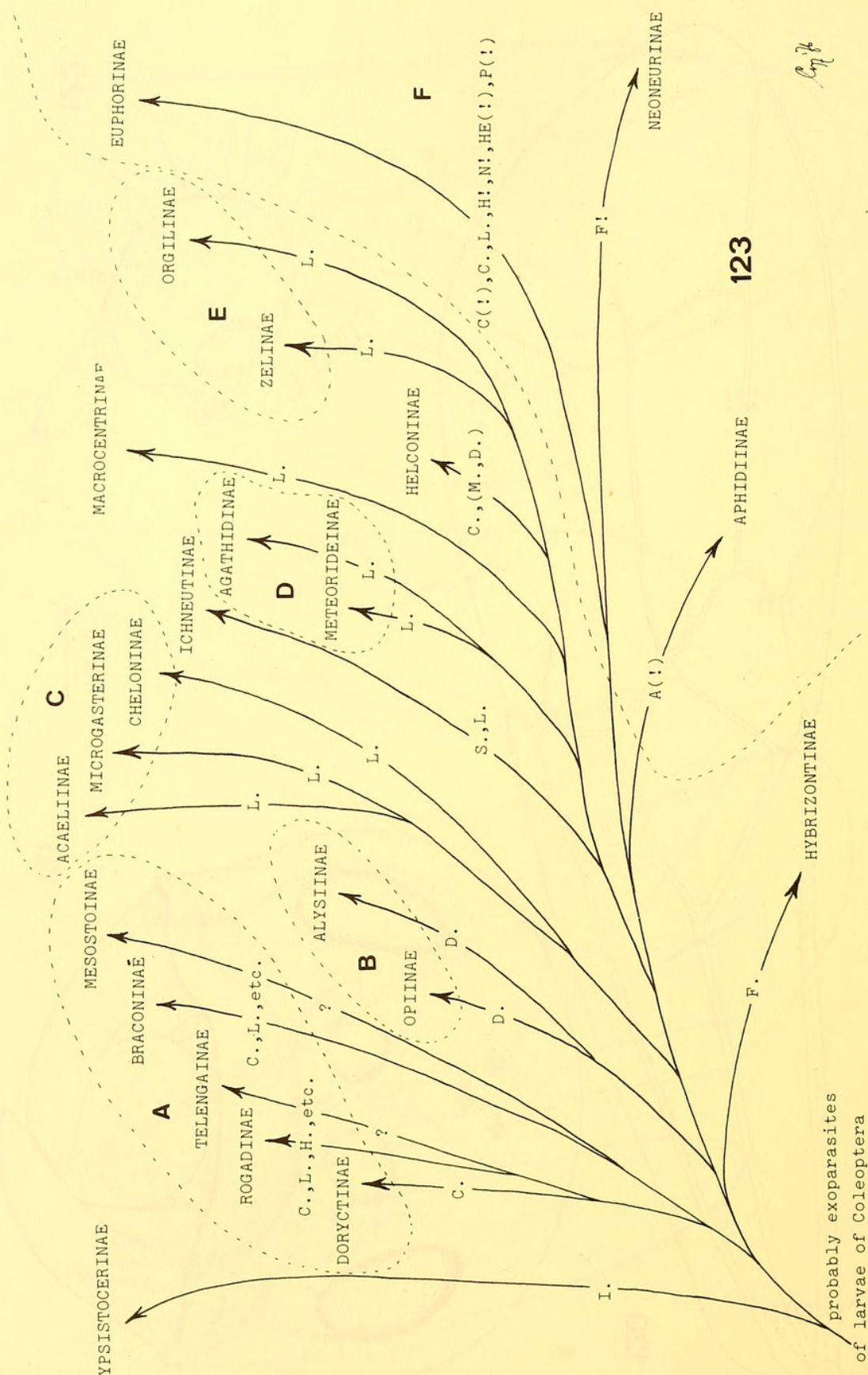
Fig. 123. Dendrogram indicating the possible phylogenetic relationship and the hosts of the subfamilies belonging to the Braconidae. A(!) = parasites of nymphs and adults of aphids; C = parasites of larvae of Coleoptera; C! = parasites of adult Coleoptera; D = parasites of larvae of Diptera; F = parasites of ant-larvae; F! = parasites of adult ants; H = parasites of larvae of Hymenoptera; H! = parasites of adult Hymenoptera; HE(!) = parasites of nymphs and adults of Heteroptera; I = associated with termites; L = parasites of larvae of Lepidoptera; M = parasites of larvae of Mecoptera; N! = parasites of adult Neuroptera; P(!) = parasites of nymphs and adults of Psocoptera; S = parasites of larvae of Symphyta; ? = host unknown