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MORPHOLOGY AND PHYLOGENY OF THE LARVAL STAGES OF THE TRIBE AGATHIDIINI (COLEOPTERA: LEIODIDAE: LEIODINAE)

ALEKSANDRA KILIAN

Zoological Institute, University of Wrocław, Sienkiewicza 21, 50-335 Wrocław, Poland

Abstract.— The larval morphology of 7 species belonging to 3 genera of the tribe Agathidiini is given. Third larval instar of *Agathidium discoideum* Erichson and *Liodopria serricornis* (Gyllenhal), the first larval instar of *Ag. varians varians* Beck and *Anisotoma orbicularis* (Herbst) are described for the first time, third larval instar of *Ag. varians varians* and *Ag. mandibulare* Sturm are redescribed in detail, and third larval instar of two species without exact identification (*Ag. pisanum* or *Ag. badium* and *Ag. bescidicum* or *Ag. plagiatum* or *Ag. confusum*) are also included. Based on comparative morphology of all known larvae of Agathidiini, cladistic analysis was made and phylogenetic relationships within this tribe of family Leiodidae was hypothesised. Sixty two characters were polarized using outgroup comparison and ontogenetic criterion. No apomorphies distinguish genera *Anisotoma* from *Agathidium*, thus synonimization of them is suggested. Position of *Liodopria serricornis* in the tribe Agathidiini is doubtful because of lack of synapomorphic characters.

Key words.— entomology, taxonomy, morphology, phylogeny, larva, Coleoptera, Leiodidae, Agathidiini, *Anisotoma* sp., *Agathidium* spp., *Liodopria* sp.

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INTRODUCTION

The tribe Agathidiini (Leiodidae: Leiodinae; sensu Newton and Thayer, 1992) contains 9 genera and about 600 species in the world (Angelini, 1995). Among them larvae of only 6 species of the genus *Anisotoma* Panzer, 9 species of the genus *Agathidium* Panzer and 1 species of *Sphaeroliodes* Panzer (Morimoto and Hayashi, 1984) are known.

The list of papers containing descriptions of larval stages of these beetles was given by Angelini and De Marzo (1984) and modified by Wheeler (1990a) but a part of them (old descriptions of some European species: *Anisotoma castanea castanea* (Herbst), *Anisotoma glabra* (Fabricius), *Anisotoma humeralis* (Fabricius), *Agathidium badium* Erichson, *Agathidium mandibulare* Sturm, *Agathidium nigripenne* (Fabricius), *Agathidium rotundatum* (Gyllenhal), *Agathidium seminulum* (Linnaeus)) have only historical value and are not useful for identification of specimens and phylogenetic study.

The first modern descriptions were given by Wheeler (1990a) for all larval instars of New World *Anisotoma basalis* (LeConte), *Agathidium pulchrum* LeConte, *Agathidium aristerium* Wheeler, *Agathidium oniscoides* Palisot de Beauvois. The chaetotaxic system proposed by Wheeler and based on longitudinal arrangements of setae is a modification of such a system for Staphylinidae (Aleocharinae) by Ashe and Watrous (1984). A general rule is addition of setae during ontogeny. The last larval instar has the most complete setal pattern and the terminology is based on its chaetotaxy.

Next detailed descriptions of the larvae of all European *Anisotoma*: *An. humeralis* (Ratajczak, 1995), *An. orbicularis* (Herbst) (Ratajczak, 1996), *An. castanea castanea* (Ratajczak, 1996), *An. glabra* (Růžička, 1996), *An. axillaris* Gyllenhal (Růžička, 1996) follow this system of chaetotaxy.

Poor knowledge of larvae of the tribe Agathidiini has several reasons: general lack of studies on immatures at lower taxonomic levels because of small interest in larvae till the last decades; insufficient information in standard catalogs and the Zoological Record, especially concerning descriptions of new taxa of larvae without nomenclatural significance (Newton, 1990); all problems arising from biology and ecology of these beetles.

The tribe Agathidiini is regarded as primarily and primitively connected with Myxomycetes (slime molds), feeding and breeding either on mature sporocarps (primitively) or plasmodial stage of the host. Most *Anisotoma*, *Amphicyllis* Erichson and primitive *Agathidium* are associated with fruiting bodies of Myxomycetes (Blackwell, 1984; Lawrence, 1989; Lawrence and Newton, 1980; Newton, 1984; Newton and Stephenson, 1990; Wheeler, 1979a, 1990a; Wheeler and Hoebeke, 1990), although there are records of *Anisotoma* from plasmodia (Russel, 1979; Wheeler, 1980). The most diverse genus, among insects associated with slime molds, is *Agathidium*. The subgenera of this genus seem to (cited by Newton and Stephenson, 1990): "differ in their choice of slime mold stage for larval development, with correlated strong differences in larval mouthpart morphology" (Newton, 1984; Wheeler, 1984a). Species of *Agathidium* (*Cyphoceble*) Thomson and *Ag.* (*Neoceble*) Gozis live on fruiting bodies whereas members of *Ag.* (*Agathidium*) develop on plasmodia (Newton, 1984; Wheeler, 1984a; 1984b; 1987). No such strong correlation was observed in *Ag. aristerium*, which has galea slightly fimbriate and mola with asperities, in spite of beeing bred from plasmodium (Wheeler, 1990a). *Anisotoma plasmodiophaga* Wheeler, which feed and breed on plasmodia has well developed mola with asperities in both larvae and adults (Wheeler, 1980).

Collecting species feeding on mature Myxomycetes is the most fruitful during slime mold propagation (early spring to late autumn). Time of frutification of Myxomycetes is short and needs special conditions (Martin and Alexopoulus, 1969). Also larval development is rapid, taking, according to Newton, 2 days in some *Anisotoma* species (1991). Label data of Dr. B. Burakowski's rearing of *An. castanea*, *An. humeralis*, and other species described in this paper confirmed that metamorphosis runs fast. More difficult is finding and identifying of plasmodial stage, because are translucent and small. Many slime molds are distributed before frutification inside fallen trunks, floor litter, debris. For all these reasons it is not easy to find and rear agathidiines, especially their larvae.

In this paper, I give descriptions of larval morphology of 7 species belonging to 3 genera: *Agathidium*, *Anisotoma* and *Liodopria* Reitter: the third larval instar of *Agathidium* (*C.*) *discoideum* Erichson, the first and third instar of *Agathidium* (*N.*) *varians varians* Beck and *Ag.* (*N.*) *mandibulare*, the first instar of *An. orbicularis*, the third instar of *Liodopria serricornis* (Gyllenhal) and the third instar of two species collected in the Bieszczady Mountains, which are presumed to be *Agathidium* (*Ag.*) *pisanum* Brisout (or *Ag.* (*Ag.*) *badium*) and *Agathidium* (*N.*) *bescidicum* Reitter or *Agathidium* (*N.*) *plagiatum* (Gyllenhal) or *Agathidium* (*N.*) *confusum* Brisout.

Adults of these species were collected together with larvae. Based on differences in morphology of mouthparts among subgenera *Neoceble*, *Cyphoceble* and *Agathidium*, I suggest that the specimen without mola of mandible and fringed galea is either *Ag.* (*Ag.*) *badium* or *Ag.* (*Ag.*) *pisanum* and the second specimen with well developed mola and fimbriate galea belongs to one of the 3 species of *Neoceble* found along with the larvae.

In this paper I present the first description of larvae of *Ag. discoideum* and *L. serricornis*. *Ag. varians varians* was described very well by Angelini and De Marzo (1984), but there was a need to compare details of terga, mouthparts and prolegs. The first information about larva of *Ag. mandibulare* was given by Schiödte (1861–1862) with figures of labrum, antennae, maxilla, galeal fringe and total habitus (the last in: 1864). Fowler (1889) cited Schiödte, also Kuhnt (1909, 1913) and Vaternahm (1919) repeated figure of total habitus, of much worse quality than Schiödte's original drawing, with little information. Saalas (1917) and Henriksen (1922) mentioned larvae of *Ag. badium* but without certainty of correct determination.

Distribution of the tribe Agathidiini is hypothesized to be primarily Holarctic but nowadays the number of species of Oriental *Agathidium*, *Liodopria*, *Stetholiodes* exceeds that of both Nearctic and Palaearctic members of these genera. Also Mexico – Guatemala species of *Anisotoma* are more numerous than Palaearctic ones (Wheeler, 1979a). Moreover, *Pseudoagathidium*, *Afroagathidium* and a few subgenera of *Agathidium* are restricted to Ethiopian, Oriental and Australian (New Guinea) regions (Angelini, 1995). Agathidiini are also widespread in Neotropical region (Peck, Gnaspini and Newton, in press).

Ag. (*N.*) *varians varians* and *Ag.* (*N.*) *mandibulare* are widespread in whole Europe. *Ag.* (*C.*) *discoideum* was recorded from Europe, Mongolia, Oriental Siberia. *Ag.* (*N.*) *plagiatum* is a mountain species known from Europe, Caucasus, Turkey, Iran. *Ag.* (*N.*) *confusum* is distributed in Europe, Caucasus, Siberia, Mongolia, Japan, *Ag.* (*N.*) *bescidicum* is a mountain and submountain species of Central and Southern Europe, *Ag.* (*Ag.*) *pisanum* is widespread in Europe, Turkey, Azerbaijan, *Ag.* (*Ag.*) *badium* has localities in Europe, Turkey, Caucasus, Iran. *L. serri-*

cornis is rare in Central Europe (Burakowski et al.,1978; Wanat, 1990), one of the 2 Palaearctic species of the small (only 7 species in the world) genus (Angelini, 1995).

Phylogenetic relationships within the tribe Agathidiini are far from solved, especially those based on larval characters. The only papers concerning this subject are revision of adult *Anisotoma* (Wheeler, 1979a) and, the most important for this study, "Ontogeny and character phylogeny" with cladistic analysis of 4 species (Wheeler, 1990b). Based on Wheeler's phylogenetic studies of larval Agathidiini, my own study and all known larval Agathidiini, cladistic analysis was made. Two criteria were applied for polarizing characters: outgroup comparison and ontogenetic (Nelson's Rule).

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Materials and methods

Most of the specimens were loaned from collection of the Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw. They were collected (*Ag. varians*, no 2732; *An. humeralis*, no 1783a) or reared (*Ag. discoideum*; *Ag. mandibulare*, *Ag. varians*, no 3622; *An. castanea*; *An humeralis*, no 6654) and stored in 75 percent ethanol by Dr. Bolesław Burakowski. The specimen of *Liodopria serricornis* was collected by Dr. Marek Wanat. The specimens of larvae named here as BI and BII were collected by Prof. Lech Borowiec.

Label data

Anisotoma orbicularis

Instar I: Puszcza Białowieska [Białowieża Forest]: National Park, forest sector 192, 2 VII 1968, imagines, 8 VII 1986, larvae, 1 ex., no 4528, leg. B. Burakowski. Beskid Zachodni [W Beskidy Mts]: Wisła Głębce, 10 VII 1965, imagines, 14 VII 1965, larvae, 2 exx., no 3622, leg. B. Burakowski.

Agathidium (Cyphoceble) discoideum

Instar III: Puszcza Białowieska [Białowieża Forest]: National Park, forest sector 370, 25 IX 1974, imagines, 9 X 1974, larvae, 2 exx., no 5869, leg. B. Burakowski. Góry Świętokrzyskie [Świętokrzyskie Mts]: mt Łysica, 28 X 1968, imagines, 5 XI 1968, larvae, 2 exx., no 4718, leg. B. Burakowski. Roztocze: Res. Obrocz, distr. Zamość, 3 X 1974, imagines, 19 X 1974, larvae, 20 exx., no 5880, leg. B. Burakowski.

Agathidium (Neoceble) mandibulare

Instar I: Puszcza Białowieska [Białowieża Forest]: National Park, forest sector 399, 29 IX 1968, imagines, 28 XI 1968, larvae, 3 exx., no 4696, leg. B. Burakowski.

Instar III: Puszcza Białowieska [Białowieża Forest]: National Park, forest sector 399, 29 IX 1968, imagines, 28 XI 1968, larvae, 2 exx., no 4696, leg. B. Burakowski; National Park, forest sector 369, 29 VI 1961, imagines, 4 VII 1961, larvae, 1 ex., no 2167, leg. B. Burakowski. Bieszczady [Bieszczady Mts]: ad. Pełuki, distr. Sanok, 7 VI 1970, imagines, 16 VI 1970, larvae, 5 exx., no 5136, leg. B. Burakowski.

Agathidium (Neoceble) varians

Instar I: Beskid Zachodni [W Beskidy Mts]: Wisła Głębce, 8 IX 1963, larvae found, 11 exx., no 2732, leg. B. Burakowski.

Instar III: Beskid Zachodni [W Beskidy Mts]: Wisła Głębce, 8 IX 1963, larvae found, 4 exx., no 2732, leg. B. Burakowski; Wisla Głębce, 10 VII 1965, imagines, 16 VII 1965, larvae, 4 exx., no 3622, leg. B. Burakowski.

BI ***(Agathidium (s. str) pisanum*** or ***Ag. (s. str) badium*** and BII ***(Ag. (Neoceble) bescidicum*** or ***Ag. (N) plagiatum or Ag. (N) confusum)***

Instar III: Bieszczady [Bieszczady Mts]: Połonina Wetlińska, south slope of "Hnatowe Berdo", 1000 m , 20 VII 1994, larvae found, Myxomycetes-infested log (*Acryria denudata*, det. W. Stojanowska), leg. L. Borowiec.

Liodopria serricornis

Instar III: Roztocze: "Bukowa Góra" Res., 29 VI 1990, 1 ex. with numerous adults and pupa (1 ex.), on Myxomycetes: *Cribraria argillacea* Pers. (det. W. Stojanowska) on fallen trunk of *Abies alba*, leg. M. Wanat.

Specimens used for scanning electron micrographs

Anisotoma castanea

Instar III: Bieszczady [Bieszczady Mts]: Chryszczata, distr. Lesko, 19 VII 1969, imagines, 22 VII 1969, ova, 28 VII 1969, larvae, 5 exx, no 4905, leg. B. Burakowski.

Anisotoma humeralis

Instar III: Nizina Mazowiecka [Mazowiecka Lowland]: Warszawa-Bielany, 7 V 1960, larvae found, 2 exx., no 1783a, leg. B. Burakowski; Grodzisk Mazowiecki-Piaskowa, 27 VIII 1987, imagines, 3 IX 1987, larvae, 2 exx., no 6654, leg. B. Burakowski.

Agathidium (Neoceble) varians

Instar III: Beskid Zachodni [W Beskidy Mts]: Wisła Głębce, 8 IX 1963, larvae found, 2 exx., no 2732, leg. B. Burakowski.

Agathidium (Cyphoceble) discoideum

Instar III: Puszcza Białowieska [Białowieża Forest]: National Park, forest sector 370, 25 IX 1974, imagines, 9 X 1974, larvae, 2 exx., no 5869, leg. B. Burakowski.

Preparation

All detailed comparisons were made of slide-mounted larvae, mainly in glycerine-gelatin. The specimens were removed from 75 percent ethanol, boiled in 10 percent KOH solution, cleared in distilled water and mounted in glycerine-gelatin. Head, mouthparts and legs were prepared in glycerine.

Habitus drawings were made from the stereomicroscope "Citoval 2". The larvae of instar I and all details were examined at magnifications up to 840, using the Phase Contrast "Jeneval" microscope with a drawing attachment. The scanning electron micrographs were made with the "Tesla" S.E.M. in the Museum and Insitute of Zoology PAS in Warsaw.

I examined 3 specimens of *An. orbicularis*, 26 specimens of *Ag. discoideum*, 11 specimens of *Ag. mandibulare*, 21 specimens of *Ag. varians varians*, 1 specimen of uncertain *Ag. pisanum* or *Ag. badium*, 1 specimen of uncertain *Ag. confusum* or *Ag. plagiatum* or *Ag. bescidicum*, 1 specimen of *L. serricornis*.

Format

The drawings and micrographs of described species, four tables (distribution of characters used in cladistic analyses, Outgroup and Nelson pairwise comparisons of character matrix, summary of cladograms data), appendix to distribution and polarity of characters and cladograms are located at the end of this paper.

The figures, scanning photos are grouped into species. It is a little inconvenient for comparative studies but gives a general view of morphology of species.

Morphology

Characters used in descriptions of larvae in this study include external morphological structures and measurements. Chaetotaxy system, morphometrics, abbreviations and designations of chaetae positions follow Wheeler (1990a). Additional measurements are given by Ratajczak (1996). Acronyms of species in the text of appendix and in the tables for *Anisotoma basalis* – BAS, *Agathidium pulchrum* – PUL, *Agathidium aristerium* - ARI, *Agathidium oniscoides* – ONI follow Wheeler (1990a), for the remaining species they are the following: *Anisotoma axillaris* – AXI, *Anisotoma glabra* - GLA, *Anisotoma humeralis* – HUM, *Anisotoma orbicularis* – ORBI, *Anisotoma castanea castanea* - CAS, *Agathidium* (*Cyphoceble*) *discoideum* – DIS, *Agathidium* (*Neoceble*) *varians varians* – VAR, *Agathidium* (*Neoceble*) *mandibulare* – MAN, *Agathidium* (*s.str*) *pisanum*/*Ag.* (*s.str*) *badium* – BI, *Agathidium* (*Neoceble*) *confusum*/*Ag.* (*Neoceble*) *plagiatum*/*Ag.* (*Neoceble*) *bescidicum* – BII, *Liodopria serricornis* – L.

Most characters pertain to chaetotaxy, which concerns such structures as setae, spines, sensilla. As observed by Wheeler (1990a), agathidiine larvae have a variety of characters: besides chaetotaxy they involve mouthpart structures, microsculpture etc. Some characters of mouthparts, e.g. presence of lobes on ligula called paraglossae (Böving and Craighead, 1931), lobes on epipharynx (absent in *Ag. varians*), number of mesal spines and group of small spines on maxilla, number of pairs of setae on labrum, are included into diagnoses.

The structure of mandible is also interesting: there is a group of small spines (or styli) arising on the ventral surface in a more or less membraneous area. Such a "mandible sensillum" was described in *Scotocrypus meliponae* Girard (Wheeler, 1985). It is absent in species with reduced mola, like *Agathidium oniscoides* (Wheeler, 1990a) and in the specimen representing *Ag. confusum* or *Ag. plagiatum* or *Ag. bescidicum*.

The integument of the dorsal side of the head, thorax and abdomen is noteworthy. Newton (1991) noticed that larval surfaces are "smooth to microspinose" and "sclerotic patches of thoracic terga and abdominal sterna are without patches or rows of asperities". I accept definition of asperities from Glossary in "Immature Insects" (Stehr ed., 1991): "small, tooth-like, spine-like, or peg-like structures, frequently in rows or patches (microspines, microtrichiae, spinules, spinulae)". According to this definition and Wheeler (1985, 1990a), Růžička (1996), Ratajczak (1995, 1996), the tribes Agathidiini and Scotocryptini have rows, patches or honeycomb-like asperities (polygoneal meshworks, Crowson, 1981). Because of the difference between microsculpture of the head and the rest of body they are treated as two particular characters. Another character useful for identifying larvae is dividing of IX abdominal tergum.

Liodopria serricornis is probably the most interesting species, described in this work, because of its different form of urogomphi, which are fixed and seem to be joined with VIII abdominal segment. Newton (1991) mentioned some Hydnobiini and Leiodini having 1-segmented or fixed urogomphi. Perris (1855) described *Agathidium seminulum* with 1-segmented urogomphi. Lawrence (1991) considered many different possible modifications of abdominal segments VIII, IX and X. The most similar structure is found in a silvanid Cucujoidae (Fig. 166, p. 209, Lawrence, 1991; Crowson, 1981, Fig. 106, p.121): reduction of IX abdominal segment to plate bridge (to which urogomphi are articulated). On the other hand, the way in which urogomphi are joined with IX abdominal segment is similar to that in *Coprophilus striatulus* (Crowson, 1981, Fig. 105, p.120 after Verhoeff, 1919). What more, in *Liodopria serricornis*, IX segment is concealed by abdominal segment VIII. Another feature of *L. serricornis* is the presence of tormae: "a pair of backward – projecting sclerotised rods" of labrum (Crowson, 1981, Fig. 114).

The difference between *An. humeralis* and *An. axillaris* is very subtle and visible only in the presence of Dd2 of pronotum, seta Db1 and number of setae in posterior transverse row of abdominal terga I–VIII (Růžička, 1996). This example shows the need of detailed descriptions.

Longitudinal arrangement of setae proposed by Wheeler (1990a) is a novelty for Staphylinoidea, whereas Paulian (1941), Ashe and Watrous (1984) found a transverse arrangement of setae. Morphological studies on further species of Agathidiini, described in this work, lead to a conclusion that transverse rows of setae better suit description of these larvae (e.g. arrangement of setae on segments, mesonota and IX abdominal sternum of *An. castanea*).

It should be said about the suggested (Wheeler, 1990a; Angelini and De Marzo, 1984) generic features that the examination of larvae of other species does not confirm their validity.

The length ratio of the 2nd and 1st segment of urogomphi which is thought to be lower than 1 in *Agathidium*, but higher in *Anisotoma* (Angelini and De Marzo, 1984), turned out to be lower than 1 only in *Ag. varians varians*. Seta P3 of abdominal segment I (according to Wheeler, 1990a) is absent or small in *Agathidium* and present in *Anisotoma*. Unfortunately, it is absent in larvae of *An. glabra* (Rika, 1996), *An. orbicularis* and *An. castanea castanea* (Ratajczak, 1995, 1996).

Also the number of solenidia at the base of large digitiform solenidium of antennomere II is not the same for all known species of *Agathidium* (1 in the first instar, 2 in the second and third) and *Anisotoma* (2→3) (Wheeler, 1990a), (see Table 1).

Thus, as far as we know, the presence of seta P3 does not distinguish the genus *Anisotoma* from *Agathidium*; the same is true of the number of solenidia and length URII/URI.

It is very difficult to propose other generic features which suggests a need of further detailed studies on other species of the tribe and search for new characters to ensure that the genera *Agathidium* and *Anisotoma* are really distinct.

Descriptions of larvae

Species described by me recently (Ratajczak, 1995, 1996) are included only in these cases if diagnoses and seta characteristics have been changed.

Anisotoma humeralis (Fabricius, 1792)

Diagnosis. Two stemmata. Three solenidia at base of digitiform solenidium. Digitiform solenidium large, undivided. Mola of mandible with rows of sclerotized, dense asperities. Maxilla: galea fimbriate, lacinia with a group of small spines and 7 mesal spines. Dorsal integument with dense asperities arranged into transverse rows, especially in anterior part of segment, sparse in mid part and changed in posterior part of integument into granulation. Head with sparse asperities, setae Da*a, De1 present and Dd1 absent. Antennae comparatively short. Labrum without emargination, with a pair of medial setae. Setae of thorax and abdomen long and stout. Pronotum without Dd2. Abdominal segments I–VIII with seta Db1 large, shifted to posterior transverse row (between P3/P4), seta P3 present. Abdominal tergum IX divided, with asperities. Urogomphi: comparatively short, segment I with 9 setae and sparse asperities.

Description. Head (Fig. 4; Ratajczak, 1995). Row Da with small seta Da*a now called Da1.

Mouthparts. Maxilla. Maxillary formula = 1 : 1.14 : 1.26; length maxillary segment I/II = 0.9; length maxillary segment II/III = 0.9. Labium (Figs 10–11; Ratajczak, 1995). Dorsal side of labium with 2 (no 3) of subapical setae, 2 pairs of medial setae and 2 (no 1) of campaniform sensilla; labial palp: LBI/LBII = 1.15.

Leg. Femur (Figs. 22–23; Ratajczak, 1995). 4–5 posterolateral setae (Pl1–Pl5, Pl4* additional).

Thorax. Mesonotum (Fig. 25; Ratajczak, 1995). Change of interpretation of setae of transverse row: P1→P4, P4→P5, P5→P6. Metanotum (Fig. 26; Ratajczak, 1995). Change of interpretation of setae of transverse row: row Da with 2 setae (Da1, Da2; Da3→P3 shifted to posterior transverse row); posterior transverse row with 6 setae (P1, P2, P3, P3→P4, P4→P5, P5→P6); campaniform sensilla include: 1 between P1/P2 (ps1), between P4/P5 (ps2), 1 between P5/P6 (ps3), 1 between P6/L1 (ls1), 1 near Da1 and Da2 (ds1).

Anisotoma castanea (Herbst, 1792)

Diagnosis. Two stemmata. Three solenidia. Digitiform solenidium large, undivided. Mola with toothed-like asperities. Maxilla: galea fimbriate, lacinia with 8 mesal spines and a group of small spines. Dorsal integument of abdomen and thorax with asperities in anterior part of sclerites. Head with Dd1, De1, Dd*a, 1 pair of campaniform sensilla and numerous additional setae. Asperities: lacking. Antennae, urogomphi and setae of thorax and abdomen comparatively long, slender. Labrum without emargination, with 2–3 pairs of medial setae. Pronotum without Dd2 and asperities. Abdominal terga I–VIII with 5 large setae of posterior transverse row, lack of setae P3 and Db1. Abdominal tergum IX undivided, with asperities. Abdominal sternum with additional transverse row of setae (Vp1*–Vp5*). Urogomphi with asperities on segment I and II, segment I with 11 setae.

Description. Head (Figs 4–6; Ratajczak, 1996). Chaetotaxy: row Da with Da*a→Da1, seta between Db1/Db2→Da*a; posterior setae also variable in number, generally 4.

Mouthparts. Maxilla. Maxillary formula = 1 : 1.15 : 1.2; length maxillary segment I/II = 0.9; length maxillary segment II/III = 0.9. Labium. Labial palp: LBI/LBII = 1.7.

Thorax. Mesonotum (Figs 35, 38–40; Ratajczak, 1996). Posterior transverse row with 3 setae (P1→P4, P4→P5, P5→P6). Metanotum (Figs 36, 41–42; Ratajczak, 1996). Posterior travsverse row with 4 setae (P1, P2→P4, P4→P5, P5→P6).

Abdomen. Abdominal Segment I (Figs 37, 44–47; Ratajczak, 1996). Posterior transverse row with 5 setae (P1, P2, P3→P4, P4→P, P5, P6).

Anisotoma orbicularis (Herbst, 1792)

Diagnosis. Two stemmata. Three solenidia at base of digitiform organ of antennomere II. Digitiform solenidium large, undivided. Mola of mandible with rows of sclerotized tooth-like asperities. Maxilla: galea fimbriate, lacinia with 6–8 mesal spines and a group of small spines. Dorsal integument of thorax and abdomen with asperities arranged into honeycomb-like figures. Tergum of pronotum, mesonotum, metanotum and abdominal tergum X (in instar III) more sclerotized partly (posterior transverse row of meso- and metanotum beside sclerits). Setae of whole body generally long. Dorsal side of head with asperities on whole dorsal side arranged into honeycomb-like figures in instar III and without in instar I; Da1, Dd1, Dd1*, De1 and 1 pair of campaniform sensilla present; lack of Da*a. Labrum without emargination, with 1 pair of medial setae. Pronotum without seta Dd2. Abdominal terga I–VIII with 5 large setae in posterior transverse row, setae Db1 and P3 absent. Abdominal tergum IX undivided. Urogomphus segment I with 8 setae in instar III and 6 in instar I. Tibia with campaniform sensilla near D1 and Pd2.

Description. Body. *Instar I*: cylindrical, narrowed posteriorly, widest at metanotum. Total body length: 2.53 mm. Average metanotal width: 0.6 mm.

Head (Figs 1–2). *Instar I*: cranium wider than long; HW/HL = 1.23; head width: 0.43 mm. Chaetotaxy as follows: row Da with Da1, Da2; row Db with 3 setae (Db1–Db3); row Dc with 5 setae (Dc1–Dc4, Dc*); row Dd with 6 setae (Dd1–Dd4, Dd1*, Dd2a); row De with De1 and De2; lateral row with c. 1–2 setae; 4 posterior setae; campaniform sensilla include 3–4 pairs; ventral side of head with c. 4 ventrolateral setae. Stemmata 2, laterally and lateroventrally. Asperities absent. *Instar III*: changes: row Dd with 7 setae (Dd1, Dd1*, Dd2–Dd4, Dd2a, Dd*); seta Df1 present. Antenna (Fig. 6). *Instar I*: antennal formula = 2.8 : 5.7 : 1.7 : 1; length antennomere II/ digitiform solenidium length = 5.7; length antennomere II/III = 3.3; antennomere II with one large, undivided, thumb-like digitiform solenidium on internal, lateral edge; 2 small solenidia at base of digitiform solenidium; probably 3 setae; antennomere III: the smallest one with 3 subapical setae, 1 apical pointed process, 2 apical peg-like sensilla, 1 subapical, ventral, small seta.

Mouthparts. Labrum. *Instar I*: subquadrate, without apical emargination, rounded marginally; labrum width = 0.15 mm; length = 0.1 mm. Mandible (Fig. 14). *Instar I*: Apically bidentate with slightly serrate incisor edge; prostheca pointed, sclerotized with group of spines at base of it; mola distinct with c. 65 sclerotized teeth on ventral side. At dorsal surface 1 sensillum and 2 dorsolateral setae; mandible width = 0.16 mm; length = 0.2 mm. Maxilla (Figs 4–5). *Instar I*: lanceolate lacinia with 7 mesal spines, a group of small spines below and 1 campaniform sensillum; galea with fimbriate, bibranched apex, 2 setae between branches; maxillary palp as in figures 4, 5; maxillary formula = 1 : 0.9 : 1.5; length maxillary segment I/II = 1.1; length maxillary segment II/III = 0.6. *Instar III*: maxillary formula = 1 : 0.98 : 1.18; length maxillary segment I/II = 0.9; length maxillary segment II/III = 0.8. Labium (Figs 15–17). *Instar I*: labial palp: LBI/LBII = 1.05; ligula with a pair of apical setae, dorsally with a pair of serrate lobes and a pair of subapical setae; ventral side of labium with 2 pairs of setae and 1 pair of campaniform sensilla; hyphopharyngeal sclerome subquadrate (Fig. 17), with complete anterior and posterior bridges. *Instar III*: labial palp: LBI/LBII = 1.1.

Leg (Fig. 3). Coxa. *Instar I*: small, with 8 anterior setae and 2 posterior setae. Trochanter. *Instar I*: triangular; anterior side with 1 anteroventral seta (Av1), 1 anterolateral setae (Al1), 1 anterodorsal seta (Ad1), 1 ventral seta (V1). Femur. *Instar I*: short, broad, with single ventral seta (V), 2 anteroventral setae (Av1, Av2), 2 anterolateral setae (Al1, Al2), 2 posterolateral setae (Pl1, Pl2), 1 anterodorsal campaniform sensillum (ads). Tibia. *Instar I*: longer than femur, with 1 anteroventral seta (Av1), 1 anterodorsal seta (Ad1), 2 anterolateral setae (Al1, Al2), 1 subapical dorsal seta (D1) and 2 campaniform sensilla near, 2 posterodorsal setae (Pd1, Pd2), 1 posterolateral seta (Pl1), 1 posteroventral seta (Pv1). Tarsungulus. *Instar I*: long, sharp pointed, with a single pair of setae (Pv1, Av1).

Thorax. Pronotum (Fig. 7). *Instar I*: transverse; N1L/N1W = 0.42; chaetotaxy as follows: row Da with 2 setae (Da1, Da2); row Db with 2 setae (Db1, Db2); row Dc with setae Dc1, 1 asymmetric seta above and asymmetric Dc2; row Dd with single seta (Dd1); row De with single seta

(De1); 1 asymmetric seta between Db1 and Dc1; row L with 3 setae; posterior transverse row with 4 setae (P1, P2, P3, P4) and setae between P1/P2 (1), between P2/P3 (3); campaniform sensilla include: 1 between P1/P2 (ps1), 1 between P4/L1 (ls1); dorsal surface with asperities arranged into honeycomb-like figures. *Instar III*: changes: posterior transverse row with setae P1, P1→P2, P2→P, P3, P4. Mesonotum (Fig. 8). *Instar I*: transverse; chaetotaxy as follows: row Da with Da1, Da2; row Db sometimes present asymetric seta Db2; row Dc with 1 seta (Dc1); row Dd with 1 seta (Dd1); lateral row with 2–3 setae; posterior row with P1, P2, P4, P5, P6 and small setae: 1–2 setae between P1/P4 and 2–3 between P4/P5; campaniform sensilla include: ds1, ps1, ps3; dorsal surface with asperities arranged into honeycomb-like figures. *Instar III*: posterior row with D1→P1, D2→P2, D3→P4 (the longest), P1→P, P3→P, P4→P5, P5→P6 and 1–2 setae between P1/P4, c. 8 setae between P4/P5. Metanotum (Fig. 9). *Instar I*: transverse; N3L/N3W = 0.32; row Da with Da1, Da2; row Db absent; row Dc with 1 seta (Dc1); row Dd with 1 seta (Dd1); lateral row 2–3 setae; posterior row with: P1, P2, P4, P5, P6 and small setae between P4/P5; campaniform sensilla include: ds1, ps1, ps2, ps3; dorsal surface with asperities arranged into honeycomb-like figures. *Instar III*: posterior row with: D1→P1, D2→P2, D3→P4, P1→P, P2→P, P3→P, P4→P5, P5→P6.

Abdomen. Abdominal Segment I (Fig. 10). *Instar I*: Transverse; A1l/A1W = 0.32; Row Da with 1 seta (Da1); posterior transverse row with: P1, P2, P4, P5, P6, between P4/P5 1 or 2 setae; small setae above posterior row (3–4); campaniform sensilla include: ps1, ps2; dorsal surface with asperities arranged into honeycomb-like figures. *Instar III*: posterior transverse row with: P1, P2, P3P4, P5, P6, between P4/P5 1 or 2 setae. Abdominal Tergum IX (Fig. 11). *Instar I*: with 2 pairs of campaniform sensilla; 3 dorsolateral setae (Dl1, Dl2, Dl3); a pair of small setae in posterior part of segment; tergum undivided with asperities arranged into transverse rows. *Instar III*: Dl1 present. Urogomphus (Fig. 13). *Instar I*: formula URI:URII:URIII = 1.96 : 4.3 : 1; length URI/URII = 0.54; length URII/URIII = 4.3; urogomphus segment I with 6 setae and 1 dorsal campaniform sensillum; urogomphus segment II with 1 apical stylus; sparse asperities arranged into transverse rows on both sides of segment I and minute asperities on apical part of segment II. Abdominal Sternum IX and Anal Membrane (Fig. 12). *Instar I*: abdominal sternum with 1 posterior, transverse row of 5 setae (Vp1–Vp5) and asperities; anal membrane on ventral side with 2 pairs of campaniform sensilla; 15–20 small setae; dorsal side with 1 pair of campaniform sensilla and 3 pairs of setae.

Agathidium (*Cyphoceble*) *discoideum* Erichson, 1845

***Diagnosis*.** Two stemmata. Three solenidia at base of digitiform organ. One of them spine-like. Digitiform solenidium large, undivided. Mola of mandible covered with toothed-like asperities. Maxilla: galea fimbriate, lacinia with 6–8 mesal spines and a group of small spines. Dorsal integument of thorax and abdomen with asperities. Dense asperities on whole head, lack of Dd1. Labrum without emargination, with 1 pair of medial setae. Setae of thorax and abdomen short. Pronotum with Dd2 absent. Abdominal terga I–VIII with 5 large setae (P3 and Db1 absent). Abdominal tergum undivided, covered with asperities arranged into transverse rows. Urogomphi: comparatively short, segment I with 9 setae, segment II with minute processes at base of apical stylus.

***Description*.** Body (Figs 18–20). Cylindrical, narrowed posteriorly, widest at metanotum. Total body length: 3.8–5.2 mm (average: 4.6 mm). Average metanotal width: 1.1 mm.

Head (Figs 21–25, 222). Cranium wider than long; HW/HL = 1.4; average head width: 0.63 mm; chaetotaxy as follows: row Da with Da*a and Da2; row Db with 3 setae (Db1, Db2, Db3); row Dc with 4 setae (Dc1–Dc4, Dc*); row Dd with 4 setae (Dd2–Dd4, Dd*); row De with 3 setae (De1, De2, De*); row Df with Df1; c. 3 lateral setae; c. 4–5 ventral setae; small setae varying in their positions and number between Dc3/Dd4; 3 campaniform sensilla; 4 posterior setae; dense asperities (Fig. 222); 2 stemmata, laterally and lateroventrally. Antenna (Figs 27, 28, 32, 33): Antennal formula = 4 : 6.1 : 1.95 : 1; length antennomere II/digitiform solenidium length = 6.1; length antennomere II/III = 3.2; antennomere I with 2 dorsal and 2 ventral campaniform sensilla; antennomere II with 1 large, undivided digitiform solenidium and 3 solenidia at base of it (one of them often spine-like), 1 dorsal seta, 1 dorsal campaniform sensilla; antennomere III with 3 subapical seta, 2 peg-like sensilla, 1 pointed process and 1 subapical setiform sensilla.

Mouthparts. Labrum (Figs 29–31): rounded marginally; without emargination; epipharynx with median, transverse row c.11 campaniform sensilla preceded by 3 pairs of campaniform sensilla, all of them surrounded by pair of lobes fringed with microtrichiae; sparse asperities posterolaterally to them; margin of labrum with 7 pairs of setae and 2 pairs of campaniform sensilla (variations of margin: see Figs 30–31); dorsal side of labrum with 2 pairs of setae (1 in the mid, 1 lateromarginally) and 1 pair of campaniform sensilla. Mandible (Figs 34–35): apically bidentate, incisor edge smooth or slightly serrate, prostheca pointed, sclerotized, with a few small spines, mola with c. 70 visible, sclerotized teeth, 1 lateral seta, 3 dorsal setae, 2 dorsal campaniform sensilla, apical part of mandible as in Fig. 34; sparse asperities dorsally. Maxilla (Figs 36–38, 226–227): length maxillary segment I/II = 1.1; length maxillary segment II/III = 0.8; maxillary formula: 1 : 0.98 : 1.18; lanceolate lacinia with 6–8 large mesal spines, a group of small spines below, 2 campaniform sensilla, 2 setae; galea (Figs 226–227) with fimbriate apex, bibranched, 2 setae and campaniform sensillum between branches, stipes with 2 setae. Labium (Figs 39–41, 224–225): labial palp: LBI/LBII = 1.2; ligula with 1 pair of apical setae; dorsal side (Fig. 225) with a pair of serrate lobes and 3 pairs of pores in the mid part; hyphopharyngeal sclerome as in Fig. 39, with complete anterior and posterior bridges; asperities on ventral side presence; ventral side of labium with 2 pairs of subapical setae and 1 pair of campaniform sensilla; labial palp: segment I with ventral peg-like sensillum (digitiform peg or organ); segment II with minute apical spines, 3 campaniform sensilla and 1 minute seta; palpifer with 2 setae.

Leg (Fig. 26). Coxa: slender, elongate; 7 anterior setae: 5 anterolateral (Al1–Al5), 1 anterodorsal (Ad1), 1 anteroventral (Av1); 6 posterior setae: 3 posterolateral (Pl1–Pl3), 2 posterodorsal (Pd2, Pd3), 1 posteroventral (Pv1), 1 anterior campaniform sensillum; 2 basal setae. Trochanter: triangular; 4 anterior setae: 2 anterolateral (Al1, Al2), 1 anterodorsal (Ad1), 1 anteroventral (Av1); 4 posterior setae: 2 posterolateral setae (Pl1, Pl2), 2 ventral (V1, V2); 5 anterior campaniform sensilla, 2 posterior ones. Femur: long, broad; 8 anterior setae: 5 anterolateral (Al1–Al5), 2 anteroventral (Av1, Av2), 2 dorsal (D1, D2); 7 posterior setae: 4 posterolateral (Pl1–Pl4), 2 posterodorsal (Pd1, Pd2), 1 ventral (V); campaniform sensilla include: 1 anterior, 1 posterior; asperities on ventral margin. Tibia: shorter than femur; 4 anterior setae: 2 anterolateral (Al1, Al2), 1 anteroventral (Av1), 1 anterodorsal (Ad1), 1 dorsal (D1); 4 posterior setae: 2 posterodorsal (Pd1, Pd2), 1 posterolateral (Pl1), 1 posteroventral (Pv1). Tarsungulus: long, pointed with 2 setae (Pv1, Av1).

Thorax. Pronotum (Fig. 42). Transverse; N1L/N1W = 0.99; chaetotaxy as follows: row Da with Da1, Da2; row Db with Db1; row Dc with 2 setae Dc1, Dc2; row Dd with single seta Dd1; row De with single seta De1; lateral row with L1, 5 setae anterior to L1, 1 seta posterior to L1; campaniform sensilla include: ds1 between Da1/Db1, ds2 between Db1/Dc1, ds3 between Dc1/ Dd1, ds4 between Dd1/De1, ls1 between P4/L1, ps1 between P1/P2, ps2 between P2/P3, ps3 between P3/P4; c. 20–30 small setae between and below Da1/Db1/Dc1/Dd1/De1; 4–8 small posterior setae (between P1–P4); asperities present. Mesonotum (Fig. 43). Transverse; chaetotaxy as follows: row Da with 1 seta Da1; row Db absent; row Dc with 1 seta Dc1; row Dd with 1 seta Dd1; lateral row with L1 and c. 4 small setae; posterior transverse row with 5 setae (P1, P2, P4, P5, P6); campaniform sensilla include: ds1, ps1, ps2, ps3, ls1; c. 5–6 small posterior setae and 10–12 anterior to posterior row; asperities arranged into transverse rows. Metanotum (Fig. 44). Transverse; N3L/N3W = 0.37; chaetotaxy as follows: row Da with 2 setae (Da1,Da2); row Db absent; row Dc with 1 seta Dc1; row Dd with 1 seta Dd1; lateral row with L1 and c. 3 small setae; posterior transverse row with 5 setae (P1, P2, P4, P5, P6); campaniform sensilla include: ds1, ps1, ps2, ps3, ls1; c. 6 small posterior setae and c. 13 anterior additional setae; asperities arranged into transverse rows.

Abdomen. Abdominal Segment I (Figs 45, 223): A1L/A1W = 0.33; chaetotaxy as follows: row Da with 1 seta Da1; row Db absent; row Dc absent; row Dd absent; lateral row with c. 2 small setae; posterior transverse row with 5 setae (P1, P2, P4, P5, P6); campaniform sensilla include: ds1, ps1, ls1; c. 5–8 additional setae anterior to P1–P6; c. 2–3 small setae between P1–P6; asperities arranged into transverse rows (Fig. 223). Abdominal Tergum IX (Fig. 48): 3 dorsolateral setae (Dl2 and Dl3 shifted to lateral side); c. 5 small setae and 1 campaniform sensillum; tergum undivided, completely covered with aspeirties arranged into transverse rows. Urogomphus (Figs 50–51): formula URI:URII:URIII = 3.2 : 4 : 1; length URI/URII = 0.8; length URII/URIII = 4; urogomphus segment I with 9 setae (4 ventral, 3 dorsal, 2 dorsolateral); 4 dorsal campaniform sensilla and 1 ventral: urogomphus segment II with 1 apical stylus and 3 small processes around base of it; asperities on segment I arranged into tranverse rows on dorsal side, sparse on apical part of segment II. Abdominal Sternum IX and Anal Membrane (Figs 46, 47, 49): with posterior transverse row of 5 pairs of setae (Vp1–Vp5), 2 pairs of small anterior setae (V1, V2) and asperities arranged into transverse rows; anal membrane: dorsal side with 2 pairs of setae (D1, D2), 2–3 pairs of small setae, 1–2 pairs of campaniform sensilla and often with asperities in the mid part; ventral side with 5–6 pairs of small setae, 3–4 pairs of campaniform sensilla.

Agathidium (Neoceble) varians varians Beck, 1817

Diagnosis. Two stemmata. Two solenidia at base of digitiform organ of anntenomere II in instar I and three in instar III. Digitiform solenidium large, undivided. Mandible with toothed prostheca, additional subdistal teeth ventrally and dorsally ("cresta subdistale denticolata", see Angelini and De Marzo,1984). Maxilla: apex of galea setose with a few sensilla and setae, see Fig. 233, 7 mesal spines, without a group of small spines at base of lacinia. Dorsal integument of thorax and abdomen in instar I covered with distinct granules, in instar III also with distinct granulation (especially lateral surface) and dense asperities (asperities arranged into honeycomb-like shape). Head: dense asperities arranged into honeycomb-like figures in instar III, in instar I sparse or absent. Ligula (of labium) without lobes (paraglosse) but with numerous microtrichiae. Labrum incised, without lobes, with 2 pairs of medial setae. Setae of thorax and abdomen short. Adult hipertrichia. Pronotum without Dd2. Abdominal terga I–VIII with 5 large setae in posterior transverse row, setae P3 and Db1 absent. Abdominal tergum IX undivided, in instar III covered with asperities. Urogomphi: segment I with 7 setae, in instar III with asperities, a small spine at base of apical stylus.

Description. Body: cylindrical, narrowed posteriorly, widest at metanotum. In instar I antennae and urogomphi comparatively long. Total body length: *Instar I* (Figs 55–57): 1.6–1.9 mm; *Instar III* (Figs 52–54): 3.9–4.8 mm (average *Instar I* : 1.8 mm; *Instar III*: 4.4 mm). Average metanotal width: *Instar I*: 0.47 mm; *Instar III*: 1.2 m.

Head. *Instar I* (Figs 61, 63, 69): cranium wider than long; HW/HL = 1.34; average head width = 0.37 mm. Chaetotaxy as follows: row Da with Da1 and Da2; row Db with 3 setae (Db1, Db2, Db3); row Dc with 3 setae (Dc2–Dc4); row Dd with 3 setae (Dd2–Dd4); row De with 2 setae (De1, De2); lateral row with 1 seta; 4 posterior setae; campaniform sensilla include 1–2 pairs; ventral side of head with 4 setae. Stemmata 2, laterally and lateroventrally; asperities sparse or absent. *Instar III* (Figs 60, 62, 228, 229): HW/HL = 1.34; average head width = 0.62 mm. Additional setae: c. 60 additional seta, varying in their number and position (also asymetrically), some of them are determined: Da*, Da*a, Db*, Db**, Dc*, Dc**, Dd1, Dd1*, Dd2a, Dd*; lateral row with 2–3 setae; ventral side of head with 5–6 setae; asperities dense, arranged into honeycomb-like figures (Figs 97, 229). Antenna. *Instar I* (Figs 64–65): antennal formula = 2.2 : 4.9 : 1.6 : 1; length antennomere II/ digitiform solenidium length = 4.9; length antennomere II/III = 3; antennomere I with 2 dorsal campaniform sensilla; antennomere II with one large, undivided, thumb-like digitiform solenidium on internal, lateral edge; 2 small solenidia at base of digitiform solenidium (one of them is slightly sharp-pointed); 1 dorsal seta, 1 ventral, 1 lateral near digitiform solenidium, 1 dorsal campaniform sensillum; antennomere III: the smallest one with 3 subapical setae, 1 apical pointed process, 2 apical peg-like sensilla, 1 subapical ventral setiform sensillum. *Instar III* (Figs 66–67, 232): antennal formula = 3.3 : 6.5 : 1.8 : 1; length antennomere II/ digitiform solenidium length = 6.5; length antennomere II/III = 3.6; antennomere I same as in instar I; antennomere II with the 3rd solenidium at base of digitiform solenidium; antennomere III (Fig. 232): same as in instar I.

Mouthparts. Labrum. *Instar I* (Figs 72–73): subquadrate, with apical emargination, rounded marginally; epipharynx with median, transverse row of c. 4 very small campaniform sensilla, preceeded by c. 4 ones above and surrounded with microtrichiae (lack of lobes); setae on the margin of labrum: 1 pair of lateral, 3 pairs of apical, 2 pairs of campaniform sensilla; dorsal surface of labrum with a pair of large setae in the mid part, 1 pair of smaller; labrum width = 0.16 mm; length = 0,06 mm. *Instar III* (Figs 76–77): epipharynx with median, transverse row of 8 campaniform sensilla, 2 campaniform sensilla anterolaterally and 2 minute setae slightly above; 5 pairs of setae on ventral margin, 3 pairs of additional setae on dorsal side of margin and 1 pair of campaniform sensilla in the mid part; labrum width = 0.24 mm; length = 0.91 mm. Mandible. *Instar I* (Fig. 68): apically dentate with toothed internal (incisor) and external edge; prostheca pointed, sclerotized with teeth; mola distinct with c. 50 sclerotized teeth on ventral side; dorsal surface with 2 setae; mandible width = 0.12; mandible length = 0.08 mm. *Instar III* (Figs 74–75, 230–231): dorsal side with 2 additional campaniform sensilla, subdistal toothed crest, pecten/ and asperities; c. 70 sclerotized teeth; mandible width = 0.19 mm; mandible length = 0.14 mm. Maxilla. *Instar I* (Fig. 70): lanceolate lacinia with 6 mesal setae, lack of group of spines at base of lacinia; apex of galea setose; stipes with 2 setae, 2 campaniform sensilla; maxillary palp as in figure 70; maxillary formula = 1 : 0.9 : 2.3; length maxillary segment I/II = 1.15; length maxillary segment II/III = 0.4. *Instar III* (Fig. 78, 233): similar, except as follows: lacinia with 7 large mesal spines and 1 small, 1 campaniform sensillum basal to galea; stipes with 3 additional setae; maxillary formula = 1 : 1.2 : 1.8; length maxillary segment I/II = 0.8; length maxillary segment II/III = 0.7. Labium. *Instar I*: lack complete data, ligula (Fig. 81) with numerous microtrichiae, without lobes (paraglosse); hyphopharyngeal sclerome (Fig. 71) subquadrate, with complete anterior and posterior bridges. LbI/LbII = 1.3. *Instar III* (Figs 79–80): labial palp: segment I with small subapical peglike sensilla (digitiform organ – Crowson, 1981); 1 campaniform sensillum and apical sensilla; segment II with 1 subapical campaniform sensillum; ligula: with microtrichiae, 2 apical setae, 2 pairs of campaniform sensilla in the mid part; ventral side of labium with 3 pair of large setae, 1 pair of small setae and 1 pair of campaniform sensilla (this arrangement varies, also asymetric: lack of 1–2 setae or c.s); hyphopharyngeal sclerome subquadrate, with complete anterior and posterior bridges. LbI/LbII = 1.3.

Leg (Figs 58–59). Coxa. *Instar I*: large; 9 anterior setae, 3 posterior setae, 4 basal setae, 1 anterior campaniform sensilla. *Instar III*: similar, except as follows: 2 additional posterior setae, 1 posterior campaniform sensilla, 4 basal setae, asperities. Trochanter. *Instar I*: triangular; 2 anterolateral setae (Al1, Al2), 1 anteroventral seta, 2 ventral setae (V1, V2); 4 anterior and 2 posterior campaniform sensilla. *Instar III*: similar to instar I, except as follows: 5 anterior campaniform sensilla, 1 anterodorsal seta (Ad1), 2 posterolateral setae (Pl1, Pl2). Femur. *Instar I*: 2 anteroventral setae (Av1, Av2),1 anterolateral (Al1), 2 dorsal setae (D1, D2), 1 ventral seta (V), 1 posterolateral seta (Pl1), 1 posterodorsal seta (Pd1); 1 anterior campaniform sensillum (ads). *Instar III*: similar to instar I, except as follows: additional posterodorsal seta (Pd2), anterolateral setae (Al2, Al3, Al4), posterolateral setae (Pl2, Pl3, Pl4); asperities. Tibia. *Instar I*: as long as femur; 1 anterodorsal seta (Ad1), 1 dorsal seta (D1), 2 anterolateral setae (Al1, Al2), 2 posterolateral setae (Pl1, Pl2), 1 posteroventral seta (Pv1). *Instar III*: shorter than femur; additional posterodorsal seta Pd1 and asperities. Tarsungulus: *Instar I*: Long, pointed, with 2 setae. *Instar III*: same as in instar I, comparatively shorter.

Thorax. Pronotum. *Instar I* (Fig. 83): transverse; N1L/N1W = 0.46; chaetotaxy as follows: row Da with 2 setae (Da1, Da2); row Db with 2 setae (Db1, Db2); row Dc with 2 setae (Dc1, Dc2); row Dd with single seta (Dd1); row De with single seta (De1); row L with 1 seta (L1); posterior transverse row with 4 setae (P1–P4); campaniform sensilla include: 1 between Db1/Dc1 (ds2), 1 between P1/P2 (ps1), 1 between P2/P3 (ps2), 1 between P3/P4 (ps3), 1 below Dc1; dorsal surface with granulation. *Instar III* (Fig. 82): N1L/N1W = 0.5; lack of ds2, ps2, ps3; additional campaniform sensilla anteromedially; c. 40 small setae between, sligthly below and slightly above Da1/Db1/Dc1/Dd1/De1; c. 7–9 setae above and between setae of posterior transverse row; dorsal surface with asperities arranged into honeycomb-like figures. Mesonotum. *Instar I* (Fig. 85): transverse; chaetotaxy as follows: row Da with single seta Da1; row Db with 1 seta Db1; row Dc with 1 seta Dc1; row Dd with single seta Dd1; row De absent; row L with 1 seta (L1); posterior transverse row with 5 setae (P1, P2, P4, P5, P6); campaniform sensilla include: 2–3 near Da1, 1 between P1/P2 (ps1), 2 between P4/P5 (ps2, ps3); 1 assymetric seta between P4/P5; dorsal surface with granulation. *Instar III* (Fig. 84): numerous additional different size setae between posterior transverse row and above; campaniform sensilla: ps2 probably absent; numerous anterior sensilla beside sclerit. Metanotum. *Instar I* (Fig. 87): transverse; N3L/N3W = 0.39; chaetotaxy as follows: row Da with 2 setae (Da1, Da2); row Db with 1 seta Db1; row Dc with 1 seta Dc1; row Dd with single seta Dd1; row De absent; row L with 1 seta (L1) and 1 small seta anterior to L1; posterior transverse row with 5 setae (P1, P2, P4, P5, P6); 2 small setae above Dd1; campaniform sensilla include: ds1 near Da1, 1 between P1/P2(ps1), 1 between P4/P5 (ps2), 1 between P5/P6 (ps3), 1 between P6/L1 (ls1), 1 near Da2 (ds2); dorsal surface with granulation. *Instar III* (Fig. 86): N3L/N3W = 0.37; posterior transverse row with 4 setae (P2, P4, P5, P6); c. 20 additional small setae between posterior transverse row, above and laterally; campaniform sensilla include: ds1 near Da1, ps1 absent, ps2 assymetric; numerous anterior sensilla beside sclerit; dorsal surface with asperities arranged into honeycomb-like figures.

Abdomen. Abdominal Segment I. *Instar I* (Fig. 89): transverse; A1l/A1W = 0.3; chaetotaxy as follows: row Da with 1 seta Da1; row Db absent; row Dc absent; row Dd absent; row De absent; row L with 1 seta (L1); posterior transverse row with 5 setae (P1, P2, P4, P5, P6); campaniform sensilla include: ds1 near Da1, 1 between P1/P2 (ps1), 1 between P4/P5 (ps2), 1 between P6/L1 (ls1), 1 above P4 (ds2); dorsal surface with granulation. *Instar III* (Fig. 88): A1l/A1W = 0.28; posterior transverse row with additional setae: 1 between P1/P2, 1 between P2/P4, 2 between P4/P5, 0–1 between P5/P6; 5–6 setae above posterior row of setae; Da1, ds1 probably absent; numerous anterior sensilla beside sclerites; asperities arranged into honeycomb-like figures. Abdominal Tergum IX. *Instar I* (Fig. 91): with 1 pair of small, dorsal setae (D1); 2 pairs of campaniform sensilla; 3 dorsolateral setae (Dl1, Dl2, Dl3); asperities sparse in posterior part of tergum; tergum undivided. *Instar III* (Figs 90, 234): similar, except as follows: 1 additional pair of campaniform sensilla; 5–6 setae in posterolateral part of segment; asperities dense, arranged into honeycomb-like figures. Urogomphus. *Instar I* (Fig. 93): comparatively very long, segment I shorter than segment II; formula URI:URII:URIII = 1.2 : 1.98 : 1; length URI/URII = 0.63; length URII/URIII = 1.98; urogomphus segment I with c. 7 setae (3 ventral, 4 dorsal); 3 dorsal and 3 ventral campaniform sensilla; urogomphus segment II with 1 apical stylus; asperities on both sides of segment I. *Instar III* (Figs 92, 235): segment I longer than segment II; formula URI:URII:URIII = 4.2 : 3.45 : 1; length URI/URII = 1.2; length URII/URIII = 3.45; urogomphus segment I with c. 7 setae (3 ventral, 4 dorsal); 4–5 dorsal and 0–1 ventral campaniform sensilla; urogomphus segment II with 1 apical stylus and asperities at base (see Fig. 235) of it; asperities on both sides of segment I and till a half of segment II.

Abdominal Sternum IX and Anal Membrane. *Instar I* (Fig. 95): abdominal sternum IX with posterior, transverse row of 5 setae (Vp1–Vp5) and probably a pair of small setae V1 anteriorly; anal membrane on ventral side with 2 pairs of campaniform sensilla and 4 pairs of small setae; dorsal side with 1 pair of campaniform sensilla and 2 pairs of setae. *Instar III* (Figs 94, 96, 98, 99): similar, except as follows: abdominal sternum IX with 1–2 smaller setae above Vp4/Vp5 (Vp6, Vp6*) and asperities arranged into transverse rows; anal membrane on ventral side with c. 15–20 assymetric small setae and asperities; dorsal side with 4 additional pairs of setae and asperities.

Agathidium (Neoceble) mandibulare Sturm, 1807

Diagnosis. Two stemmata. Three solenidia at base of digitiform organ of anntenomere II (2 are setiform). Digitiform solenidium large, undivided. Mola of mandible with toothed-like asperities. Maxilla with bibranched fimbriate galea, rows of spines at base of lacinia and 7 mesal large setae. Dorsal integument of thorax and abdomen with asperities (honeycomb-like shaped) in instar III, wihout in instar I. Dorsal side of head with Da1, Dd1, Dd2a and small additional setae; lack of Da*a; 3–4 pairs of campaniform sensilla; asperities on whole dorsal side, dense in instar III, sparse in instar I. Antennomere II in instar III with asperities. Labrum without emargination, with a pair of medial setae. Setae of thorax and abdomen terga medium. Pronotum (Dd2 absent), mesonotum, metanotum with Db1 seta present. Abdominal terga I–VIII with 5 large posterior setae, setae P3, Db1 absent. Abdominal tergum IX with asperities, divided in instar III. Urogomphus: segment I with 7 setae, spinules at base of apical stylus.

Description. Body. *Instar I*: cylindrical, narrowed posteriorly, widest at metanotum. Total body length: 2.61 mm Average metanotal width: 0.67 mm. *Instar III* (Figs 100–102): total body length: 4.15–4.7 mm (average: 4.4 mm). Average metanotal width: 1 mm.

Head. *Instar I* (Fig. 105): as in instar III except as noted. Asperities less dense. HW/HL = 1.34; HW = 0.43 mm; minute seta above and laterad to Db2; lack of Dc**. *Instar III* (Figs 103, 104, 106, 107): Cranium wider than long; HW/HL = 1.3; average head width: 0.57 mm. Chaetotaxy as follows: row Da with Da1 and Da2; row Db with 3 setae (Db1, Db2, Db3); row Dc with 6 setae (Dc1–Dc4, Dc*, Dc**); row Dd with 6 setae (Dd1–Dd4, Dd2a, Dd*); row De with 2 setae (De1, De2); row Df with Df1; lateral row with c. 5 setae; 4 posterior setae; campaniform sensilla include 4–5 pairs; ventral side of head with 3–4 ventrolateral setae. Stemmata 2, laterally and lateroventrally. Asperities dense, on whole dorsal side (see Figs 58, 59). Antenna. *Instar I* (Fig. 109): same as instar I, except as noted: asperities on antennomere II absent; different shape of solenidia at base "digitiform organ"; antennal formula = 3 : 7.2 : 2.2 : 1, length antennomere II/ digitiform solenidium length = 7.2; length antennomere II/III = 3.25. *Instar III* (Fig. 108): antennal formula = 2.05 : 4.15 : 1.3 : 1; length antennomere II/ digitiform solenidium length = 4.15; length antennomere II/III = 3.1; antennomere I with 2 ventral campaniform sensilla and 2 dorsal; antennomere II with one large, undivided, thumb-like digitiform solenidium on internal, lateral edge, 3 small solenidia at base of digitiform solenidium (2 of them setiform), 2 dorsal setae, 1 ventrolateral, 1 ventral campaniform sensillum; dorsal and ventral asperities arranged into transverse, short rows; antennomere III: the smallest one with 3 subapical setae, 1 apical pointed process, 2 apical peg-like sensilla, 1 subapical, dorsal, setiform sensillum.

Mouthparts. Labrum. *Instar I* (Figs 123–124): similar except in proportion to instar III. Labrum width = 0.15 mm; length = 0.11 mm. *Instar III* (Figs 120–121): subquadrate, without apical emargination, rounded marginally; labrum width = 0.13 mm; length = 14 mm; epipharynx with median, transverse row of c. 14 campaniform sensilla, preceeded by c. 6 ones above; lobes fringed with microtrichiae; laterally to them sparse asperities; dorsal surface of labrum with a pair of large setae in the mid part and 3 pairs dorsolateral, 1 pair of campaniform sensilla medially; 6 pairs of setae on the ventral side of margin of labrum and a pair of tubercles; dorsal side with asperities. Mandible. *Instar I* (Fig. 111): same as instar III except as follows. Only 3 dorsal setae. Mandible width = 0.16 mm; length = 0.21 mm. *Instar III* (Fig. 110): apically bidentate with saw-toothed incisor edge; prostheca short pointed, sclerotized with a group of minute ventral spines at base of it in unsclerotized area (similar to "mandibular sensillum"of *Scotocryptus*; Wheeler, 1985); mola distinct with c. 70 sclerotized teeth on ventral side; dorsal side with 3 campaniform sensilla and 4 dorsolateral setae; mandible width = 0.19 mm; length = 0.25 mm. Asperities on dorsal side. Maxilla. *Instar I* (Fig. 113): similar except as follows. Lacinia with 7 mesal spines, 3 campaniform sensilla: the 1st c.s and a lot of spines basal to galea. the 2nd c.s apically to "comb", the 3rd below rows of spines; maxillary palpus III with peg-like sensillum and subapical sensillum but lack of campaniform sensillum; maxillary palpus II with asperities, 2 setae and 1 campaniform sensillum; maxillary palpus III with asperities and 2 campaniform sensilla (lack of small seta); maxillary formula = 1 : 0.95 : 1.7; length maxillary segment I/II = 1.1; length maxillary segment II/III = 0.55. *Instar III* (Fig. 112): lanceolate lacinia with 7 mesal spines, a group of small spines below and 2 campaniform sensilla (1 near apical seta of mesal "comb", 2nd in a half of "comb"); stipes with 4 setae, galea with fimbriate, bibranched apex, 2 setae between branches; maxillary formula = 1 : 1.3 : 2; length maxillary segment I/II = 0.8; length maxillary segment II/III = 0.65. Labium. *Instar I* (Figs 117–119): similar to instar III, except number of campaniform sensilla on ligula (4 or less, also assymetrically), number of ventral setae and campaniform sensilla (1 assymetrical); labial palp: LBI/LBII = 0.7. *Instar III* (Figs 114–116): labial palp: LBI/LBII = 0.7; segment I with small subapical peg-like sensilla (digitiform organ – Crowson, 1981) and a group of sensilla; segment II with 1 subapical campaniform sensillum, 1 small seta nr the base and a few spinules on external apical edge; labial palpiger with 2 setae (large and small), 1 campaniform sensillum and asperities; ligula: a pair of serrate lobes, a pair of apical setae, 6 pairs of campaniform sensilla in the mid part; ventral side of labium with 2 pairs of setae, 1 pair of campaniform sensilla and asperities; hyphopharyngeal sclerome subquadrate, with complete anterior and posterior bridges.

Leg (Figs 122, 125). Coxa. *Instar I.*: with 5 anterior setae, 2 basal setae; 4 posterior setae. *Instar III*: large, 1 additional anterior seta, 1 additional basal seta, 3 additional posterior setae. Trochanter. *Instar I*: triangular; anterior side with 1 anteroventral seta (Av1), 2 anterolateral setae (Al1, Al2), 2 campaniform sensilla; 2 ventral setae (V1, V2); posterior side with 2 posterolateral setae (Pl1, Pl2), 5 posterior campaniform sensilla. *Instar III*: 1 anterodorsal seta (Ad1). Femur. *Instar I*: with single ventral seta (V), 2 anteroventral setae (Av1, Av2), 2 anterolateral setae (Al1, Al2), 1 posterodorsal seta Pd1. *Instar III*: 2 additional anteroventral setae (Al3, Al4); 4 posterolateral setae (Pl1–Pl4), 2 posterodorsal (Pd2, D1); 1 posterodorsal campaniform sensillum (pds), 1 anterodorsal campaniform sensillum (ads). Tibia. *Instar I*: as long as femur, with 1 anteroventral seta (Av1), 1 anterodorsal (Ad1), 2 anterolateral setae (Al1, Al2), 1 posteroventral seta (Pv1). *Instar III*: similar with additional: 1 subapical dorsal seta (D1), 1 posterodorsal seta (Pd1), 1 posterolateral seta (Pl1). Tarsungulus. *Instar I*: long, pointed, with single pair of setae (Pv1, Av1). *Instar III*: same as instar I.

Thorax. Pronotum. *Instar I* (Fig. 132): similar to instar III except as follows. Lack of ds1, ds3, ls1; anterior median setae present; lack of asperities; N1L/N1W= 0.5; less number of small setae. *Instar III* (Figs 126–128, 137): transverse; N1L/N1W= 0.54; chaetotaxy as follows: row Da with 2 setae (Da1, Da2); row Db with 2 setae (Db1, Db2); row Dc with 2 setae (Dc1, Dc2); row Dd with single seta (Dd1); row De with single seta (De1); row L with c. 6 setae; posterior transverse row with 4 setae (P1, P2, P3, P4), between P1/P2 0–2 setae (assymetrically), between P2/P3 3 setae, between P3/P4 1 seta; sometimes pairs of median setae, sometimes median assymetrical setae; campaniform sensilla include: 2 between Da1/Db1, 2 between Db1/Dc1, 1 between Dc1/Dd1 (ds3), 1 between Dd1/De1 (ds4), 1 between P1/P2 (ps1), 1 between P2/P3 (ps2), 1 between P3/P4 (ps3), 1 between P4/L1 (ls1); c. 8–14 small setae between and below Da1/Db1/Dc1/Dd1; setae Da2/Db2/Dc arranged into transverse row; dorsal surface with dense asperities arranged into honeycomb-like figures. Mesonotum. *Instar I* (Fig. 133): similar. Lack of Da2, Db1, ls1, ps1, ps2, ps3; 2 lateral setae (L1, 1 posterior to L1) present; less number of small setae; lack of asperities. *Instar III* (Fig. 129): transverse; chaetotaxy as follows: row Da with Da1, Da2; row Db with 1 seta Db1; row Dc with 1 seta (Dc1); row Dd with 1 seta (Dd1); lateral row: 3 setae; posterior row with P1, P2, P4, P5, P6 and 0–1 setae between P1/P2, 0–1 b. P2/P4, 1–2 b. P4/P5, 0–1 b. P5/P6; a pair of median setae sometimes; campaniform sensilla include: ds1, ps2, ps3, ls1 (sometimes absent).

Metanotum. *Instar I* (Fig. 134): lack of ps3, ls1, Da2, Db1; lack of asperities; less number of small setae; N3L/N3W = 0.34. *Instar III* (Fig. 130): transverse; N3L/N3W = 0.38: row Da with Da1, Da2; row Db with Db1; row Dc with 1 seta (Dc1); row Dd with 1 seta (Dd1); lateral row: L1 and 3 small setae; posterior row with: P1, P2, P4, P5, P6; small additional setae: between P1/P2 0–1, b. P2/P4 0–2, b. P4/P5 2–3, b. P5/P6 1, 8–12 anteriors to posterior transverse row; campaniform sensilla include: ds1, ps1, ps2, ps3, ls1.

Abdomen. Abdominal Segment I. *Instar I* (Fig. 135): lack of asperities; less number of small setae; A1l/A1W = 0.26. *Instar III* (Fig. 131): transverse; A1l/A1W = 0.32; row Da with 1 seta (Da1); posterior transverse row with: P1, P2, P4, P5, P6; small additional setae: c. 7 above posterior transverse row of setae; 1–2 lateral setae; campaniform sensilla include: ds1, ps1, ps2, ls1; asperities dense. Abdominal Tergum IX. *Instar I* (Fig. 136): only 1 pair of small setae (D1). *Instar III* (Figs 138–139): With 4–5 pairs of small setae; a few pairs of campaniform sensilla; 3 dorsolateral setae (Dl1, Dl2, Dl3); tergum divided with asperities arranged into transverse rows. Urogomphus. *Instar I* (Fig. 143): asperities smaller, lack on segment II. Formula URI:URII:URIII = 2.7 : 4.6 : 1; length URI/URII = 0.6; length URII/URIII = 4.6. *Instar III* (Fig. 141): formula URI:URII:URIII = 2.4 : 3.7 : 1; length URI/URII = 0.65; length URII/URIII = 3.7; urogomphus segment I with 7 setae and 1 ventral campaniform sensilla; urogomphus segment II with 1 apical stylus and spinules at base of it; asperities arranged into transverse rows on both sides of segment I and II. Abdominal Sternum IX and Anal Membrane. *Instar I* (Fig. 140): same as instar III, lack of asperities on sternum. *Instar III* (Fig. 142): with 1 posterior, transverse row of 5 setae (Vp1–Vp5), seta Vp6 above Vp4/Vp5, 1 anterior seta V1; anal membrane on ventral side with 1 pair of campaniform sensilla; 8 small setae assymetrically; dorsal side with 2 pairs of campaniform sensilla and 2 pairs of small setae and 2 pairs of bigger setae (D1, D2). Asperities on abdominal sternum and dorsal side of anal membrane arranged into transverse rows.

BI - ***Agathidium* (*s. str*) *pisanum*** Brisout, 1872 or ***Agathidium* (*s. str*) *badium*** Erichson, 1845

Diagnosis. Two stemmata. Three solenidia at base of digitiform organ of anntenomere II. Two of them setiform. Digitiform solenidium large, undivided. Mandible with mola not developed and with large membraneous setose prostheca. Maxilla: mala undivided narrow and accicuate at apex, without fimbriate galea, lack of rows of minute spines at base, 8 mesal large spines. Dorsal integument of pronotum partially granulated without asperities. Tergum of mesonotum, metanotum and abdominal segments with sparse asperities anteriorly. Dorsal side of head with very sparse, only posterior asperities, seta Da1, Dd1 and 5 pairs of campaniform sensilla present; lack of small, additional setae, Db2a and Dd2a. Antennae comparatively short. Labrum incised, with 2 pairs of medial setae. Setae of whole body generally medium, the longest on a head. Pronotum without Dd2. Abdominal terga I–VIII with 4 large setae in posterior row (P2, P3 absent). A numerous additional setae on dorsal surface of all thorax and abdomen segments and nearly as big as subprimary setae so differentation of Db1, Db2, Da2 is difficult. Abdominal tergum IX divided in a half with asperities. Urogomphus: segment I with 8 setae, segment II without asperities. Tibia with 2 campaniform sensilla near D1, Pd2.

Description. Body (Fig. 144): cylindrical, elongate. Total body length: 4.2 mm. Total body the same width as metanotal width: 0.5 mm.

Head (Figs 149–150): cranium wider than long; HW/HL = 1.37; head width: 0.41 mm. Chaetotaxy as follows: row Da with Da1 and Da2; row Db with 3 setae (Db1 assymetrically, Db2, Db3); row Dc with 5 setae (Dc1–Dc4, Dc*); row Dd with 3 setae (Dd1, Dd3, Dd4); row De with 2 setae (De1, De2); row Df with seta Df1; 2 lateral setae; 4 posterior setae; campaniform sensilla include 4 pairs; ventral side of head with 3 ventrolateral setae. Stemmata 2, laterally and lateroventrally. Asperities in posterior part of head, sparse. Antenna (Figs 146, 151): antennal formula = 1.5 : 3.9 : 2 : 1; length antennomere II/ digitiform solenidium length = 3.9; length antennomere II/III = 1.96; antennomere I with 2 dorsal campaniform sensilla and 1 ventroapical; antennomere II with one large, undivided, thumb-like digitiform solenidium on internal, lateral edge; 3 small solenidia at base of digitiform solenidium, 2 of them setiform; 1 dorsal seta, 1 ventral, 1 lateral near digitiform solenidium, 1 dorsal campaniform sensillum; antennomere III: 3 subapical setae, 1 apical pointed process, 2 apical peg-like sensilla, 1 subapical, dorsal setiform sensillum.

Mouthparts. Labrum (Fig. 149): incised, subquadrate, without apical emargination, rounded marginally; labrum width = 0.16 mm; dorsal surface of labrum with 2 pairs of setae in the mid part, 1 pair of campaniform sensilla; 3 setae on the margin of labrum: 1 pair of lateral ones, 2 pairs of apical ones and a pair of tubercles. Mandible (Fig. 145): apically bidentate; incisor edge slightly serrate; mola reduced without teeth; prostheca large, membraneous, setose; 3 lateral setae; mandible width = 0.1 mm; length = 0.16 mm. Maxilla (Fig. 148): mala undivided, apex accicuate, spinose, 8 mesal spines, without transverse group of spines; 3 setae and 1 campaniform sensillum on stipes; cardo without setae; maxillary palp as in figure 148; maxillary formula = 1: 1.46 : 1.85; length maxillary segment I/II = 0.7; length maxillary segment II/III = 0.8. Labium. Labial palp: LBI/LBII = 1.8. Lack of more data.

Leg (Fig. 153). Coxa: large, with 4 anterior setae, 1 campaniform sensillum (s1); 6 posterior setae; 4 small basal setae. Trochanter: triangular; anterior side with 1 anteroventral seta (Av1), 1 anterodorsal seta (Ad1); 2 ventral setae (V1, V2); posterior side with 1 posterolateral setae (Pl1) and 1 campaniform sensillum. Femur: as long as tibia, with single ventral seta (V), 6 anterolateral setae (Al1, Al3, Al4, Al5, Al6, Al7), 6 posterolateral setae (Pl1– Pl5, Pl8), 1 anterodorsal campaniform sensillum.Tibia: as long as femur, with 1 anteroventral seta (Av1), 2 anterodorsal (Ad1, Ad2), 2 anterolateral setae (Al1, Al2), 1 subapical dorsal seta (D1) and 2 campaniform sensilla near D1, 2 posterodorsal setae (Pd1, Pd2), 1 posterolateral seta (Pl1). Tarsungulus: long, pointed, with single pair of setae (Pv1, Av1).

Thorax. Pronotum (Fig. 152). Transverse; N1L/N1W = 0.68; chaetotaxy as follows: row Da with 2 setae (Da1, Da2); row Db with 2 setae (Db1, Db2); row Dc with 1 seta (Dc1); row Dd with single seta (Dd1); row De with single seta (De1); row L with 1 large seta L1 and 6 small setae (L); posterior transverse row with 4 setae (P1, P2, P3, P4), between P1/P2 1 seta, between P2/P3 1 or 2 setae, between P3/P4 2 setae; 2 pairs of median setae; campaniform sensilla include: 1 between Da1/Db1 (ds1), 1 between Db1/Dc1 (ds2), 1 between Dc1/Dd1 (ds3), 2 near De1, 1 between P1/P2 (ps1), 1 between P2/P (ps2), 1 between P3/P4 (ps3), 1 between P4/L1 (ls1); c. 14 setae between and below Da1/Db1/Dc1/Dd1; dorsal surface without asperities only with granulation laterally. Mesonotum (Fig. 155). Transverse; chaetotaxy as follows: row Da with Da1, Da2; row Dc with 1 seta (Dc1); row Dd with 1 seta (Dd1); lateral row: L1, 1 anterior to L1,1 posterior to L1; posterior row with P1, P2, P4, P5, P6 and 8–10 setae between P1/P6; campaniform sensilla include: ds1, ps1, ps3, ls1. Sparse asperities and numerous setae (c. 17) in anterior-mid part. Metanotum (Fig. 156). Transverse; N3L/N3W = 0.66; row Da with Da1, Da2; row Db absent; row Dc with 1 seta (Dc1); row Dd with 1 seta (Dd1); lateral row: L1, 1 posterior to L1, 1 anterior to L1; posterior row with: P1, P2, P4, P5, P6; campaniform sensilla include: ds1, ps1, ps2, ps3, ls1.

Abdomen. Abdominal Segment I (Fig. 157). Transverse; A1l/A1W = 0.48; row Da with 1 seta (Da1); posterior transverse row with: P1, P4, P5, P6; between P1/P5 2 setae; 1 lateral seta L1; campaniform sensilla include: ds1, ps1, ps2, ls1. Abdominal Tergum IX (Fig. 158). With large number of setae (c. 14) anteromedially and 3 dorsolateral setae (Dl1, Dl2, Dl3); 5 pairs of campaniform sensilla anteromedially and 1 pair posteriorly; tergum divided in a half with asperities arranged into transverse rows. Urogomphus (Fig. 159). Formula URI:URII:URIII = 1.3 : 1.65 : 1; length URI/URII = 0.8; length URII/URIII = 6.5; urogomphus segment I with c. 8 setae (3 ventral, 2 dorsal, 3 dorsolateral) and 4 dorsal campaniform sensilla; urogomphus segment II with 1 apical stylus; asperities on both sides of segment I. Abdominal Sternum IX and Anal Membrane (Figs 158, 160). With 1 posterior, transverse row of 5 setae (Vp1–Vp5), 1 seta above Vp4/Vp5 and a pair of anterior setae; anal membrane on ventral side with 1 pair of campaniform sensilla and c. 12 small setae; dorsal side with 2 transverse rows; row I with a pair of small setae, row II with 4 pairs of setae.

BII - ***Agathidium (Neoceble) bescidicum*** Reitter, 1884 or ***Agathidium (Neoceble) plagiatum*** (Gyllenhal, 1810) or ***Agathidium (Neoceble) confusum*** Brisout, 1863

Diagnosis. Two stemmata. Two solenidia at base of digitiform organ of anntenomere II. Digitiform solenidium large, undivided. Mola of mandible with toothed-like asperities. Maxilla with row of spines on lacinia; galea bibranched, fimbriate, 6 mesal large spines. Dorsal integument of thorax and abdomen with dense asperities. Dorsal side of head with Da1, Dd1, Dd2 and 3–4 pairs of campaniform sensilla; lack of Da*a; asperities on whole dorsal side; small, additional setae: Dd1* and between Dd3/Dd4/Dc3. Labrum with 1 pair of median setae. Setae of whole body generally short, the longest on a head. Pronotum without Dd2. Abdominal tergum I–VIII with 5 posterior setae (lack of Db1, P3). Abdominal tergum IX undivided with dense asperities arranged into transverse rows and with setae Dl1, Dl2 absent. Urogomphal segment I with 3 setae. Urogomphal segment II comparatively long, without asperities. Lack of large setae on dorsal side of anal membrane.

Description. Body (Fig. 161): cylindrical, narrowed posteriorly, widest at metanotum. Total body length: 4.1 mm. Metanotal width: 0.41 mm.

Head (Figs 162–164): cranium wider than long; HW/HL = 1.5; head width: 0.54 mm. Chaetotaxy as follows: row Da with Da1 and Da2; row Db with 3 setae (Db1, Db2, Db3); row Dc with 6 setae (Dc1–Dc4, Dc*, Dc*p); row Dd with 5 setae (Dd1–Dd4, Dd1*); row De with 2 setae (De1, De2); lateral row with c. 5 setae; 4 posterior setae; small additional setae between Dd3/Dd4/Dc3; campaniform sensilla include 4 pairs; ventral side of head with 4 ventrolateral setae. Stemmata 2, laterally and lateroventrally. Dense asperities on whole dorsal side. Antenna (Figs 172–173): antennal formula = 3.3 : 9 : 6 :1; length antennomere II/ digitiform solenidium length = 9; length antennomere II/III = 1.5; antennomere I with 2 dorsal campaniform sensilla and 2 ventral apical ones; antennomere II with one large, undivided, thumb-like digitiform solenidium on internal, lateral edge; 2 small solenidia at base of digitiform solenidium; 3 setae near digitiform solenidium; antennomere III: 3 subapical setae, 1 apical pointed process, 2 apical peg-like sensilla, 1 subapical, dorsal, setiform sensillum.

Mouthparts. Labrum (Figs 169–170): subquadrate, without apical emargination, rounded marginally; labrum width = 0.17 mm; length = 0.14 mm; epipharynx with median, transverse row of c. 12 campaniform sensilla, preceeded by c. 6 ones above; lobes with microtrichiae; laterally to them sparse asperities; dorsal surface of labrum with a pair of large setae in the mid part, 1 pair of campaniform sensilla medially; 9 setae on the margin of labrum: 2 pairs of lateral ones (dorsal, ventral), 6 pairs of apical ones, 2 pairs of sensilla.

Mandible (Figs 165–166): apically bidentate with smooth incisor edge; prostheca pointed, sclerotized; mola distinct with c. 70 sclerotized teeth on ventral side. At dorsal surface 1 campaniform sensillum in the mid, 3–4 dorsolateral setae, sparse asperities. Mandible width = 0.19 mm; length = 0.25 mm. Maxilla (Fig. 167): lanceolate lacinia with 6 mesal spines and a group of small spines below; galea with fimbriate, bibranched apex; maxillary palp as in figure 167 (incomplete, lack data); length maxillary segment I/II = 0.9.

Labium (Figs 168, 171): labial palp: LBI/LBII = 1.7; segment I with small subapical peg-like sensilla (digitiform organ – Crowson, 1981) and a group of sensilla; segment II with 1 subapical campaniform sensillum, palpiger with a few spines apically; ligula: a pair of serrate lobes dorsally, a pair of apical setae, a pair of campaniform sensilla in the mid part of dorsal side; ventral side of labium with 2 pairs of large setae and 1 pair of campaniform sensilla; 3 pairs of setae apically; hyphopharyngeal sclerome subquadrate, with complete anterior and posterior bridges.

Leg (Fig. 182). Coxa: large, with 7 anterior setae, 2 anterolateral setae, 4 basal seta, 1 anteroventral seta; 3 posterior setae: 1 posteroventral (Pv1), 2 posterolateral. Trochanter: triangular; anterior side with 2 anteroventral seta, posterior side with 2 posterolateral setae, 5 posterior campaniform sensilla. Femur: with single ventral seta (V), 2 anteroventral setae (Av1, Av2), 4 anterolateral setae (Al1–Al4), 3 posterolateral setae (Pl2–Pl4), 2 posterodorsal setae (Pd1, D1), 1 posterodorsal campaniform sensillum (pds). Tibia: shorter than femur, with 1 anteroventral seta (Av1), 1 anterodorsal (Ad1), 2 anterolateral setae (Al1, Al2), 1 subapical dorsal seta (D1) and campaniform sensillum near, 2 posterodorsal setae (Pd1, Pd2), 1 posterolateral seta (Pl1), 1 posteroventral seta (Pv1). Tarsungulus: long, pointed, with single pair of setae (Pv1, Pv2).

Thorax. Pronotum (Fig. 174). Transverse; N1L/N1W = 0.69; chaetotaxy as follows: row Da with 2 setae (Da1, Da2); row Db with 1 seta (Db1); row Dc with 2 setae (Dc1, Dc2); row Dd with single seta (Dd1); row De with single seta (De1); row L with 1 large seta L1 and 2 anterior to, 1 posterior to L1; posterior transverse row with 4 setae (P1–P4), between P1/P4 6–7 setae; campaniform sensilla include: 1 between Da1/Db1 (ds1), 1 between Db1/Dc1 (ds2), 1 between Dc1/Dd1 (ds3), 1 between Dd1/De1 (ds4), 1 between P3/P4 (ps3), 1 between P4/L1 (ls1), setae between P1/P2 and P2/P3 assymetrically; c. 14 small setae between and sligthly below Da1/Db1/Dc1/Dd1/De1; dorsal surface with asperities. Mesonotum (Fig. 175). Transverse; chaetotaxy as follows: row Da with Da1; row Db absent; row Dc with 1 seta (Dc1); row Dd with 1 seta (Dd1); lateral row: L1 and 1 between P6/L1; posterior row with P1, P2, P4, P5, P6; 2–3 setae between P1/P2; 3–4 setae between P4/P5; a pair of median posterior setae; campaniform sensilla include: ds1, ps1, ps2 (assymetrically), ps3. Metanotum (Fig. 176). Transverse; N3L/N3W = 0.93; row Da with Da1, Da2; row Db absent; row Dc with 1 seta (Dc1); row Dd with 1 seta (Dd1); lateral row: L1 and 1 seta between P6/L1; posterior row with: P1, P2, P4, P5, P6; c. 7 additional small setae; 1 seta between P1/P2; 1 seta between P2/P4; 2 setae between P4/P5; a pair of median posterior setae; campaniform sensilla include: ds1, ps1, ps2 (assymetrically), ps3 (assymetrically).

Abdomen. Abdominal Segment I (Fig. 177). Transverse; A1l/A1W = 0.43; row Da with 1 seta (Da1); row Dc with 1 seta Dc1; a pair of median posterior setae; 5–6 additional small setae; posterior transverse row with: P1, P2, P4, P5, P6; between P4/P5 2 setae; 1 campaniform sensillum ps1. Abdominal Tergum IX (Fig. 179). With 1 dorsal setae (D1); 2 campaniform sensilla; 1 dorsolateral seta (Dl3); 2–4 setae in posterior part of segment; tergum undivided with dense asperities arranged into transverse rows. Urogomphus (Fig. 180). Formula URI:URII:URIII = 1.8 : 4.4 : 1; length URI/URII = 0.41; length URII/URIII = 4.4; urogomphus segment I with 3 setae and 1 dorsal campaniform sensillum; urogomphus segment II with 1 apical stylus; asperities on both sides of segment I. Abdominal Sternum IX and Anal Membrane (Figs 179, 181). With 1 posterior, transverse row of 5 setae (Vp1–Vp5), 1 seta Vp6 above Vp4/Vp5 and 1 seta V1 anteriorly; anal membrane on ventral side with 4 pairs of campaniform sensilla; 14 small setae; dorsal side without transverse rows of setae, only single setae arranged irregularly.

Liodopria serricornis (Gyllenhal, 1813)

Diagnosis. Two stemmata. Two solenidia at base of digitiform organ of anntenomere II. Digitiform solenidium large, undivided. Mandible with sclerotized toothed mola. Maxilla with fimbriate galea, lacinia with 6 large mesal setae and small spines. Dorsal integument of thorax and abdomen with very sparse asperities in anterior part of sclerome. Head with sparse asperities in lateral part, small number of setae and 2 pairs of campaniform sensilla. Antennae comparatively long. Labrum without apical emargination, with tormae present and 1 pair of medial setae. Setae of thorax and abdomen long, stout. Pronotum with a group of setae-spines on lateral surface, seta Dd2 absent. Abdominal posterior transverse row with 5 setae, setae Db1 and P3 absent. Abdominal segment VI, VII, VIII without sclerites. Abdominal segment IX reduced to plate bridge and concealed by VIII abdominal segment. Non segmented, unsclerotized urogomphi with 2 small setae and minute asperities. Tibia with campaniform sensillum near Al1.

Description. Body (Figs 183, 184, 186): cylindrical, narrowed posteriorly.

Head (Figs 189, 194). Chaetotaxy as follows: row Da with Da2; row Db with 2 setae (Db2, Db3); row Dc with 3 setae (Dc1, Dc2, Dc4); row Dd with 3 setae (Dd2–Dd4); row De with single seta (De2); lateral row with 1 seta; 4 posterior setae; campaniform sensilla include 2 pairs; ventral side of head with c.3 setae. Asperities sparse, laterally. Stemmata 2, laterally and lateroventrally. Antenna (Fig. 188): length antennomere II/ digitiform solenidium length = 7.44; antennomere I with 2 dorsal campaniform sensilla and 3 ventral; antennomere II with one large, undivided, thumb-like digitiform solenidium on internal, lateral edge; 2 solenidia at base of digitiform solenidium (one of them is sharp-pointed); 1 dorsal seta, 1 ventral, 1 lateral near digitiform solenidium, 1 ventral campaniform sensillum; antennomere III: the smallest one.

Mouthparts. Labrum (Figs 192–193): subquadrate, without apical emargination, rounded marginally; with tormae, epipharynx with median, transverse row of c.9 campaniform sensilla, 2 pairs of apical setae, lobes with microtrichiae and asperities around them; dorsal surface of labrum with a pair of setae in the mid part and 1 pair of campaniform sensilla, 4 pairs of setae on the margin of labrum; labrum width = 0.2 mm; labrum length = 0.11 mm. Mandible (Figs 190–191): Apically bidentate with slightly serrate internal edge; prostheca pointed, sclerotized; mola distinct with c. 90 sclerotized teeth on ventral side. At dorsal surface 1 campaniform sensillum and 2 lateral setae; mandible width = 0.17 mm; mandible length = 0.18 mm. Maxilla (Figs 195–196): Lanceolate lacinia with 6 large mesal setae, group of small spines below, 1–2 setae and campaniform sensillum; galea with fimbriate, bibranched apex, 2 setae between branches; cardo with 1 seta; stipes with 2 setae; maxillary palp as in fig. 196; maxillary formula = 1: 0.6 : 0.3; length maxillary segment I/II = 1.6; length maxillary segment II/III = 1.9. Labium (Figs 197–199): labial palp: segment I with 2 campaniform sensilla and 1 digitiform peg, segment II with campaniform sensillum; ligula: a pair of apical setae, 2 pairs of campaniform sensilla, serrate lobes; dorsal side of labium with 3 pair of setae and 1 pair of campaniform sensilla (this arrangement varies, also assymetric); hyphopharyngeal sclerome subquadrate, with complete anterior and posterior bridges; LbI/LbII = 1.2.

Leg (Fig. 187). Coxa: large; 6 anterior setae; 5 posterior setae; 4 basal setae; 1 anterior campaniform sensillum. Trochanter: triangular; 1 anterodorsal seta Ad1; 1 posterolateral seta Pl1; 2 ventral setae (V1, V2); 2 anterior and 6 posterior campaniform sensilla. Femur: short, broad; 3 anterolateral setae (Al1–Al3); 2 anteroventral setae (Av1, Av2); 1 ventral seta (V); 2 posterodorsal setae (Pd1, Pd2); 4 posterolateral (Pl1–Pl4); 1 anterior and 1 posterior campaniform sensillum; sparse asperities anteroventrally. Tibia: slender, long; 2 anterolateral setae (Al1, Al2); 1 anteroventral seta (Av1); 1 anterodorsal seta (Ad1); 1 posterodorsal seta (Pd1); 1 posterolateral seta (Pl1); 1 posteroventral seta Pv1; 1 dorsal seta D1; 1 campaniform sensillum next to Al1; sparse asperities anteroventrally. Tarsungulus: long, pointed, with a pair of setae.

Thorax. Pronotum (Fig. 200). Transverse; N1L/N1W = 0.4; chaetotaxy as follows: row Da with 2 setae (Da1, Da2); row Db with 1 seta (Db1); row Dc with 2 setae (Dc1, Dc2); row Dd with single seta (Dd1); row De with single seta (De1); row L with 1 seta (L1); posterior transverse row with 4 setae (P1–P4); campaniform sensilla include: 1 between Da1/Db1 (ds1), 1 between Dd1/De1 (ds2), 1 between P1/P2 (ps1), minute seta b. Da1/Db1; dorsal surface with a group of asperities in anterior part (b. Dc1/ Dd1/Dc2). Mesonotum (Fig. 201). Transverse; chaetotaxy as follows: row Da absent; row Db absent; row Dc with single seta Dc1; row Dd with single seta Dd1; 2 lateral setae (L1, 1 anterior to L1); posterior transverse row with 5 setae (P1, P2, P4, P5, P6); 1 small seta between P5/P6; campaniform sensilla include: ps1 between P1/P2, ls1 between P6/L1; asperities absent. Metanotum (Fig. 202). Transverse; chaetotaxy as follows: row Da absent; row Db absent; row Dc with single seta Dc1; row Dd with single seta Dd1; 2 lateral setae (L1, anterior to L1); 5 posterior setae (P1, P2, P4, P5, P6); 1 campaniform sensillum ps1; asperities sparse, anteromedially.

Abdomen. Abdominal Segment I (Fig. 203). Transverse; A1l/A1W = 0.2; chaetotaxy as follows: 5 posterior setae; 2–4 assymetrical campaniform sensilla; sparse asperities arranged into transverse rows. Abdominal Tergum IX (Fig. 185). Reduced, without setae, campaniform sensilla, asperities. Urogomphus (Fig. 185). Non segmented, articulated at the base, hook-like, 2 small setae, sparse asperities. Abdominal Sternum IX and Anal Membrane (Fig. 185). Reduced; both abdominal sternum and anal membrane without setae, campaniform sensilla and asperities.

Character analysis

Sixty two characters were selected as potentially bearing cladistic information (Table 1). They were polarized using outgroup comparison (Watrous and Wheeler, 1981) and ontogenetic criterion (Nelson, 1978). Fourteen species of 2 genera (*Anisotoma: basalis, humeralis, axillaris, glabra, castanea, orbicularis, Agathidium: aristerium, oniscoides, pulchrum, varians, mandibulare, discoideum*, 2 uncertain species of *Agathidium*) and 1 member of a third genus as an outgroup (*Liodopria serricornis*) were included in the analysis.

Liodopria serricornis is the only species of Leiodidae most probably feeding on Myxomycetes (like other species studied in this paper), which does not belong to neither genus *Agathidium* nor *Anisotoma* and which larva is described. Other well-described larvae of Leiodidae: *Scotocryptus meliponae* (Wheeler, 1985) and *Creagrophorus spinaculeus* Wheeler (Wheeler, 1979b) are specialized in different habitat. *S. meliponae* is inhabitant of nests of stingless bees whereas *C. spinaculeus* eats fruiting bodies of puffballs. They both have larval features differ from "typical pattern of characters" for "Leptinid Association" (Wheeler, 1979b) and it seems to be questionable to choose them as an outgroup.

The terminology of characters and character states follows Wheeler (1990a, b). The selection of characters was also based on Wheeler's set of characters (1990a) although some of them were removed and some were added. The rejected characters include: lateral setae L*a, L*b, L*c of head (17, 18, 19 in table 2, Wheeler, 1990a), because of difficulties with homology of setae of other species; presence of the second seta between V1/V2 of IX abdominal segment (36), setae ventral and mesad to posterolaterals (37), posterior median seta (54), number of large discal setae of metanotum (56) and all characters of leg (42–45), since these characters are unclear to me. The following features were added: characters of mandible as: serrate margin (incisor area) (54); presence of mola (55); hipertrichia of third larval instar (23); number of setae of urogomphal segment I (43); characters of head: microsculpture (47), incised clypeus (24), presence of seta L1 (21), Dd1* (15), Db2a (16), small setae in front of Db2 (17), between Dd4/Dc3/Dc4 (18), between Dc4's and Da2's (19) and number of lateral setae (22).

Most features pertain to setae. The terminology of setae according to their time of appearance during ontogeny (primary, subprimary, secondary) was given by Wheeler (1990b). Based on this, setae varying within a semaphoront of a species are not considered in the analysis of polarity. However, there are a few characters (posterior Db setae and posterior Dc setae of pronotum, dorsal setae of anal vesicle) which were included in the analysis by Wheeler, but they could not be polarized when more numerous species were analysed. They are included in the tables and in the discussion to provide evidence of the difficulties. Other features which could be polarized with neither criterion are included in the tables for the same reason (lateral setae of head; presence of setae Dc1, Dc2, L1 of head; number of urogomphal setae; number of ventral setae of anal vesicle; setae anterior to P row of abdomen).

There are some characters (31, 32, 33, 34, 36, 37, 38, 41, 47, 59 in tab.1) whose polarity seems to be problematic; in such cases the absence of setae was regarded as plesiomorphic and the presence of setae independently of their number – as apomorphic.

The terminology of semaphoronts is also used after Wheeler (1990a). Although II larval instar was absent in my study, I use acronyms sA for instar I, sB for instar III and sC for both instar I and III. I analysed only I and III larval instars and sometimes only III. The rest of instars were unavailable to me. Since transformations took place between instars I and II in the previously examined larvae of *Agathidium* and *Anisotoma* (Wheeler, 1990a) and were not observed between II and III, I hope that using the term semaphoront B for instar III only in discussion of polarity is acceptable. Discussion of character distribution and polarity is given at the end of this paper.

Forty five characters were polarized with outgroup comparison, 34 – with ontogenetic criterion, 32 – with both these criteria, and only these characters were used to construct the cladograms, 31 – polarized with both criteria with the same polarity. There is only one character with opposed polarity decision resulting from the two criteria (58 – presence of lateral seta L2 of metanotum). Autapomorphies were excluded from the analysis.

Kinds of error

Some possibilities of mistakes were explained above. Some other errors are also possible. When using ontogenetic criterion, the lack of data about character state of instar I may cause wrong interpretation of polarity (see type D, E, F); when applying outgroup comparison errors may arise from insufficient knowledge of morphology and ontogeny of *Liodopria serricornis*. In this species, terga as well as cranium are strongly sclerotized. The body is comparatively short and wide. In addition, the only available specimen has an irregular arrangement of terga and during clearing in water with KOH was desintegrated. All this suggests that it could be a prepupal stage of this larva or a teratogenic form. The first and second larval instars are unknown. For this reason the morphological data are incomplete.

Moreover, a simple overlooking of setae or other morphological characters may cause an error.

Wheeler (1990b) distinguished six kinds of errors, which cause some character polarities to be unresolved. All these types of errors are listed below, with characters where each respective error is possible:

Type A: "differences existing between taxa only occured within instar I (semaphoront A)". Characters 7, 8, 62.

Type B: "no differences exist between taxa within the taxonomic ingroup". Characters 7, 8, 40, 62.

Type C: "multistate characters exist for which the most plesiomorphic state could be established, but from which more than one apomorphy and no synapomorphy was determinable". Characters 30 and a few with high level of variability (28, 34, 43).

Type D:"neither ingroup state is present in the outgroup". Characters 21, 43, 44, 45, 51.

Type E: "no transformation occur between instars but only across taxa". Characters 1, 4, 11, 17, 20, 24, 26, 48, 52, 53, 54, 55, 56, 57.

Type F: "transformation exist between instars of every taxon". Characters 28, 30, 36, 37, 44, 51.

PHYLOGENY

Character matrices are presented in tables 2 and 3. Cladograms were constructed using microcomputer programs Henning86 and CLADOS 88. The resulting cladograms are presented in figs I–XV. Gray bars denote parallelisms, white bars – reversals and black bars – synapomorphies.

Cladistic results

Several groups of cladograms, based on somewhat different character sets, were obtained. Cladogram in Fig. I was based on characters whose polarization with both criteria (outgroup and ontogenetic) was compatible. Figure II represents cladogram based on characters polarized with ontogenetic criterion, with exclusion of characters which could not be polarized according to either method. Cladogram in Figure III was based on characters polarized according to outgroup comparison, with exclusion of characters that could not be polarized with ontogenetic criterion. A large group (Figs IV–IX) includes cladograms based on characters polarized according to ontogenetic criterion only. Another such group (Figs X–XV) comprises cladograms based on characters polarized solely with outgroup comparison.

Cladograms statistics are summarised in Table 4.

Consistency indices are the same for all cladograms and amount to 39, except for one (Fig. II – 38). All the cladograms include many homoplasies (parallelisms and reversals). In view of their high number, attempts at character weighting do not seem reasonable. There are only 10 non-homoplastic synapomorphies, the same in all the obtained cladograms: seta Da1 of head; seta Dc* of head; lateral setae anterior to L1 of pronotum; posterior setae between P3/P4 of pronotum; seta V1 of IX abdominal segment; anterior mid-dorsals setae of IX abdominal segment; microsculpture of head; small seta between P1–P5 of metanotum; sclerotization of prostheca; presence of mola.

Cladogram in Fig. I is the shortest (L = 79) and has the highest retention index (RI = 61) and rescaled consistency index (RC = 0.24). Because of this and considering difficulties with polarization of some characters mentioned under "character analysis" this cladogram is selected as the best hypothesis of phylogenetic relationships, at least at the present state of knowledge.

Phylogenetic relationships

The criterion of recognition of a monophyletic group is at least 1 synapomorphy (disregarding its later reversals). Only 10 characters turned out to be non-homoplastic. As a result some clusters of species are supported only by homoplasis; in such cases no monophyletic groups and their sister lineages can be distinguished.

The most inclusive monophyletic cluster of species (including all species in Fig. I) is supported by 4 non-homoplastic synapomorphies, three of which (15, 16, 20) later undergo reversal. The next most inclusive cluster (*An. humeralis*, *An. castanea*, *Ag. oniscoides*, *Ag. pisanum/ badium*, *Ag. discoideum*, *An. orbicularis*, *Ag. bescidicum/ plagiatum/ confusum*, *Ag. mandibulare*, *Ag. pulchrum*, *Ag. aristerium*, *An. glabra*, *Ag. varians*) is supported by synapomorphy 29, which later undergoes reversal. Characters 5, 6 and 28 characterized the cluster including *An. castanea*, *Ag. oniscoides*, *Ag. pisanum/ badium*, *Ag. discoideum*, *An. orbicularis*, *Ag. bescidicum/ plagiatum/ confusum*, *Ag. mandibulare*, *Ag. pulchrum*, *Ag. aristerium*, *An. glabra*, *Ag. varians*. One of them (6) later reverts to its ancestral condition. The cluster comprising *Ag. discoideum*, *An. orbicularis*, *Ag. bescidicum/ plagiatum/ confusum*, *Ag. mandibulare*, *Ag. pulchrum*, *Ag. aristerium*, *An. glabra*, *Ag. varians* is supported by apomorphy 25 which does not undergo reversal. Synapomorphy 4 is shared by *Ag. mandibulare*, *Ag. pulchrum*, *Ag. aristerium*, *An. glabra*, *Ag. varians* and later undergoes reversal.

Thus, there are five unequivocally monophyletic clusters of species, each supported by one or more non-homoplastic synapomorphies. The remaining groupings are supported exclusively by homoplastic apomorphies: *An. basalis* + *An. axillaris* by 0, 7, 14; *Ag. discoidum* + *An. orbicularis* + *Ag. bescidicum/ plagiatum/ confusum* by 23, 29, *An. orbicularis* + *Ag. bescidicum/ plagiatum/ confusum* by 9, 27; *Ag. pulchrum* + *Ag. aristerium* + *An. glabra* + *Ag. varians* by 11, 22, 27; *Ag. aristerium* + *An. glabra* + *Ag. varians* by 1, 2, 3, 8 and *An. glabra* + *Ag. varians* by 0, 9, 11, 12.

Wheeler (1979a) proposed informal species groups for adult *Anisotoma*. He formed them for what he regarded as monophyletic lineages. In his view *An. humeralis*, *axillaris*, *basalis* belong to the same informal species group, *An. castanea* – to geminata, *An. orbicularis* – to blanchardi, *An. glabra* – to glabra group. In his phylogenetical hypothesis *An. basalis* and *An. axillaris* are sister species of *An. humeralis*. Such relationships resemble these resulting from the cladistics analysis of the larvae (Fig. I).

It is noterworthy that adult beetles of *An. axillaris* and *An. basalis* are very similar whereas the larval morphological similarity is low between *An. axillaris* and *An. humeralis*.

In all the cladograms obtained *An. glabra* and *Ag. varians* are sister species.

Phylogenetic relationships of larval *Ag. pulchrum*, *Ag. oniscoides* and *Ag. aristerium* in this study is, of course, difficult to establish because of the number of homoplasies.

There is no strict division into the genera *Agathidium* and *Anisotoma*, some species of these two genera are closer to each other than those of the same genus. I suggest that the genera *Agathidium* and *Anisotoma* should be synonimized.

Conclusions

1) The transverse arrangement of setae seems to be more suitable than longitudinal to describe European larvae of the tribe Agathidiini.

2) Generic features proposed by different authors (i.e. number of solenidia of antennomere II; length ratio of urogomphal segment I/II, presence of seta P3) do not distinguish the genus *Agathidium* from *Anisotoma*.

There is no strict division into the genera *Anisotoma* and *Agathidium* based on these cladograms. Some species of these two genera are closer to each other than those of the same genus.

Based on the morphological and cladistic studies I suggest a synonymization of the genera *Agathidium* and *Anisotoma*.

3) The larva of *Liodopria serricornis* displays some characters (non-segmented urogomphi, structure of IX abdominal segment, presence of tormae of labrum), which significantly differ it from other members of Agathidiini.

It has, after excluding autapomorphies, only plesiomorphic characters so its position in the tribe Agathidiini is doubtful.

4) Because of the lack of data to reevaluate homoplasies, the shortest cladogram with the highest retention index and rescaled consistency index was chosen from the competing cladograms. It is based on characters whose polarization with both criteria (ontogenetic and outgroup) was compatible (Fig. I).

5) There are 5 unequivocally monophyletic clusters of species, each supported by one or more non-homoplastic synapomorphies, the remaining 6 clusters being supported by homoplastic apomorphies.

6) Errors: 6 "kind of errors" (Wheeler, 1990b), took place in the analysis and caused some character polarity to be unresolved; overlooking some morphological characters; small knowledge of the outgroup taxon; lack of data of some larval instars.

7) All characters, which appear to be homoplastic, should be examined in further studies.

8) There is a need to test character states present in outgroup taxa.

SUMMARY OF CHARACTERS, DISTRIBUTIONS AND POLARITIES

Acronyms of species used in summary, tables and cladograms

ARI – *Agathidium aristerium*
AXI – *Anisotoma axillaris*
BAS – *Anisotoma basalis*
BI – *Agathidium* (s. str) *pisanum* or *Ag.* (s. str) *badium*
BII – *Agathidium* (*Neoceble*) *bescidicum* or *Ag.* (*N.*) *confusum* or *Ag.* (*N.*) *plagiatum*
CAS – *Anisotoma castanea castanea*
DIS – *Agathidium* (*Cyphoceble*) *discoideum*
GLA – *Anisotoma glabra*
HUM – *Anisotoma humeralis*
MAN – *Agathidium* (*Neoceble*) *mandibulare*
L – *Liodopria serricornis*
ONI – *Agathidium oniscoides*
ORBI – *Anisotoma orbicularis*
PUL – *Agathidium pulchrum*
VAR – *Agathidium* (*Neoceble*) *varians varians*

Head characters

1. Seta Da1 present. A primary seta. Distribution: present in sC of PUL, ONI, ARI, ORBI, VAR, MAN; present in sB of GLA, HUM, CAS, DIS, BI, BII. It is absent in sC of BAS and in sB of AXI, L. *Nelson*: unresolved, because characters do not transform within any of the taxa. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of PUL, ONI, ARI, GLA, HUM, CAS, ORBI, DIS, VAR, MAN, BI, BII.

2. Seta Da* present. A subprimary seta. Distribution: absent in sA and present in sB of BAS, VAR; absent in sC of PUL, ONI, ARI, ORBI, MAN; absent in sB of HUM, CAS, DIS, BI, BII, L; present in sB of AXI and GLA. *Nelson*: absence is plesiomorphic, presence is synapomorphy of BAS, AXI, GLA, VAR. *Outgroup*: Absence is plesiomorphic, presence is synapomorphy of BAS, AXI, GLA, VAR.

3. Seta Da*a present. A subprimary seta. Distribution: absent in sC of PUL, ORBI, MAN; absent in sB of BI, BII, L; absent in sA and present in sB of BAS, VAR, ARI; present in sC of ONI; present in sB of AXI, GLA, HUM, CAS, DIS. *Nelson*: absence is plesiomorphic, presence is synapomorphy of BAS, ARI, AXI, GLA, HUM, CAS, DIS, VAR and ONI. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of BAS, ARI, AXI, GLA, HUM, CAS, DIS, VAR, ONI.

4. Seta Db1 present. A primary seta. Distribution: absent in sC of ONI; present in sC of BAS, PUL, ARI, ORBI, VAR, MAN; present in sB of AXI, GLA, HUM, CAS, DIS, BI, BII; absent in sB of L. *Nelson*: unresolved, because characters do not transform within any of the taxa. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of BAS, PUL, ARI, AXI, GLA, HUM, CAS, ORBI, DIS, VAR, MAN, BI, BII.

5. Seta Db* present. A subprimary seta. Distribution: absent in sA and present in sB of BAS, ARI, VAR; present in sB of AXI, GLA, HUM, CAS; absent in sC of PUL, ONI, ORBI, MAN; absent in sB of DIS, BI, BII, L. *Nelson*: absence is plesiomorphic, presence is synapomorphy of BAS, ARI, AXI, GLA, HUM, CAS, VAR. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of BAS, ARI, AXI, GLA, HUM, CAS, VAR.

6. Seta Db** present. A subprimary seta. Distribution: present in sB of ARI, AXI, GLA, CAS, VAR but absent in sA of ARI, VAR; absent in sC of BAS, PUL, ONI, ORBI, MAN; absent in sB of HUM, DIS, BI, BII, L. *Nelson*: absence is plesiomorphic, presence is synapomorphy of ARI, AXI, GLA, CAS, VAR. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of ARI, AXI, GLA, CAS, VAR.

7. Seta Dc1 present. A primary seta. Distribution: present in sC of PUL, ONI, ARI, ORBI, MAN; present in sB of BAS, AXI, GLA, HUM, CAS, DIS, VAR, BI, BII, L but absent in sA of BAS, VAR. *Nelson*: unresolved, because state occurs later in ontogenetic sequence. *Outgroup*: unresolved, because the same state shared by all sB taxa.

8. Seta Dc2 present. A primary seta. Distribution: present in sC of PUL, ONI, ORBI, VAR, MAN; present in sB but absent in sA of BAS, ARI; present in sB of AXI, GLA, HUM, CAS, DIS, BI, BII, L. *Nelson*: unresolved, because state occurs later in ontogenetic sequence. *Outgroup*: unresolved, because the same state shared by all sB taxa.

9. Seta Dc** present. A subprimary seta. Distribution: present in sB and absent in sA of PUL, ARI, VAR, MAN; absent in sC of BAS, ONI, ORBI; absent in sB of AXI, GLA (I changed name of seta Dc** for Db2a according to rest of taxa where seta Dc** is placed lower), HUM, CAS, DIS, BI, BII, L. *Nelson*: absence is plesiomorphic, presence is synapomorphy of PUL, ARI, VAR, MAN. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of PUL, ARI, VAR, MAN.

10. Seta Dc* present. A subprimary seta. Distribution: present in sC of ORBI, MAN; present in sB and absent in sA of PUL, ONI, ARI, VAR; present in sB of GLA, CAS, DIS, BI, BII; absent in sC of BAS; absent in sB of AXI, HUM, L. *Nelson*: absence is plesiomorphic, presence is synapomorphic for PUL, ONI, ARI, GLA, ORBI, CAS, DIS, VAR, MAN, BI, BII. *Outgroup*: absence is plesiomorphic, presence is synapomorphic for PUL, ONI, ARI, GLA, ORBI, CAS, DIS, VAR, MAN, BI, BII.

11. Posterior seta P5 present. A primary seta. Distribution: present in sC of BAS; absent in sC of PUL, ONI, ARI, ORBI, VAR, MAN; absent in sB of AXI, HUM, CAS, DIS, BI, BII, L; present sometimes in sB of GLA. *Nelson*: unresolved, characters do not transform within any of the taxa. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of BAS and GLA.

12. Seta Dd1 present. A primary seta. Distribution: present in sC of ONI, ORBI, MAN; absent in sA and present in sB of PUL, ARI, VAR,; absent in sC of BAS; present in sB of GLA, CAS, BI, BII; absent in sB of AXI, HUM, DIS, L. *Nelson*: absence is plesiomorphic, presence is synapomorphy of PUL, ONI, ARI, GLA, ORBI, CAS, VAR, MAN, BI, BII. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of PUL, ONI, ARI, GLA, ORBI, CAS, VAR, MAN, BI, BII.

13. Seta Dd2a present. A primary seta. Distribution: present in sC of ARI, ORBI, MAN; present in sB of BAS, PUL, AXI (assymetrically), GLA, VAR but absent in sA of BAS, PUL, VAR; absent in sC of ONI; absent in sB of HUM, CAS, DIS, BI, BII, L. *Nelson*: absence is plesiomorphic, presence is synapomorphy of BAS, PUL, ARI, AXI, GLA, ORBI, VAR, MAN. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of BAS, PUL, ARI, AXI, GLA, ORBI, VAR, MAN.

14. Seta Df1 present. A primary seta. Distribution: present in sC of BAS, PUL, ONI, VAR, MAN; absent in sC of ARI; absent in sA and present in sB of ORBI; absent in sB of AXI, GLA, HUM, CAS, BII, L; present in sB of DIS, BI. *Nelson*: absence is plesiomorphic, presence is synapomorphic for BAS, PUL, ONI, ORBI, DIS, VAR, MAN, BI. *Outgroup*: absence is plesiomorphic, presence is synapomorphic for BAS, PUL, ONI, ORBI, DIS, VAR, MAN, BI.

15. Seta Dd1* present. Its spresence in sC of ORBI suggests it is primary. Distribution: absent in sC of BAS, PUL, ONI, ARI, MAN; absent in sB of AXI, HUM, CAS, DIS, BI, L; present in sB of GLA, BII; absent in sA but present in sB of VAR; present in sC of ORBI. *Nelson*: absence is plesiomorphic, presence is synapomorphy of GLA, ORBI, VAR, BII. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of GLA, ORBI, VAR, BII.

16. Seta Db2a present. A subprimary seta. Distribution: absent in sC of BAS, PUL, ONI, ARI, VAR, MAN; absent in sA but present in sB of ORBI; present in sB of GLA,; absent in sB of AXI, HUM, CAS, DIS, BI, BII, L. *Nelson*: absence is plesiomorphic, presence is synapomorphy of ORBI and GLA. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of ORBI and GLA.

17. Small setae in front of Db2. Their presence in sC of ONI suggests they are primary. Distribution: absent in sC of BAS, PUL, ARI, ORBI, VAR, MAN; absent in sB oif BI, L; present in sC of ONI; present in sB of AXI, GLA, HUM, CAS, DIS, BII (assymetrically, one specimen). *Nelson*: unresolved, characters do not transform within the taxa. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of ONI, AXI, GLA, HUM, CAS, DIS, BII.

18. Small setae between Dd4, Dc4, Dc3. A primary setae. Distribution: absent in sC of BAS, PUL, ARI; absent in sA but present in sB of ONI, VAR; absent in sB of AXI, BI, L; present in sB of GLA, HUM, CAS, DIS, BII; present in sC of ORBI, MAN. *Nelson*: absence is plesiomorphic, presence is synapomorphy of ONI, GLA, HUM, ORBI, CAS, DIS, VAR, MAN, BII. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of ONI, GLA, HUM, ORBI, CAS, DIS, VAR, MAN, BII.

19. Small setae between Dc4's and Da2's. A subprimary setae. Distribution: absent in sC of BAS, PUL, ONI, ARI, ORBI, MAN; absent in sB of AXI, HUM, DIS, BI, BII, L; present in sB of GLA, CAS; present in sB but absent in sA of VAR. *Nelson*: absence is plesiomorphic, presence is synapomorphy of GLA, CAS, VAR. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of GLA, CAS, VAR.

20. Stemmata. A single stemmata is present in sC of ARI, 2 stemmata are present in sC of BAS, PUL, ONI, ORBI, VAR, MAN and in sB of AXI, GLA, HUM, CAS, DIS, BI, BII, L. *Nelson*: unresolved, no transformations within species. *Outgroup*: presence of second stemmata is plesiomorphic, 1 stemmata is autapomorphy of ARI.

21. Seta L1 present. A primary seta. Distribution: present in all taxa in sC beyond L. *Nelson*: unresolved, because no transformatons within species. *Outgroup*: unresolved, because the same state exist in all ingroup taxa.

22. Lateral setae, no. I give only total number (without diversification of L*a, L*b, L*c), because of difficulties with homologize these lateral setae. There is also possibility of oversight. In cases I am not sure, I give question mark. Distribution: in BAS 1?→1?; 1?→4? in PUL and ARI; 2?→4? in ONI; 2→5 in VAR; 4→4 in ORBI; 4→5 in MAN; 1 in sB of L; BI; 3 in sB of AXI, HUM ?, DIS; 5 in sB of BII; 6 in GLA; 7 in CAS. *Nelson*: unresolved, because of high level of variability. *Outgroup*: unresolved, because of high level of variability.

23. Adult hipertrichia. Distribution: present in VAR; absent in rest of species.

Nelson: unresolved, because it is character of mature larvae. *Outgroup*: absence is plesiomorphic, presence is autapomorphy of VAR.

24. Clypeus incised. Distribution: incised in sC of VAR, sB of BI (probably); straight in rest of the taxa. *Nelson*: unresolved, no transformations between instars, only across taxa. *Outgroup*: straight is plesiomorphic, incised is synapomorphic for VAR, BI.

Antennal characters

25. Solenidia of antennomere II. Distribution: one to several solenidia are present. 1 solenidium in sA of PUL, ONI, ARI and second added in sB; 2 solenidia in sA of BAS, VAR and third added in sB; 3 solenidia in sA and sB of ORBI, MAN; 3 solenidia in sB of AXI, GLA, HUM, CAS, DIS, BI; 2 solenidia in sB of BII, L. *Nelson*: unresolved, because of high level of variability. *Outgroup*: unresolved? If 2 solenidia in sB are plesiomorphic, 3 seems to be synapomorphy of BAS, AXI, GLA, HUM, ORBI, CAS, DIS, VAR, MAN, BI.

26. Digitiform organ divided. Distribution: present in sC of PUL; absent in rest of taxa. *Nelson*: unresolved, characters do not transform within any of the taxa.

Outgroup: absence is plesiomorphic, presence is autapomorphy of PUL.

Pronotal characters

27. Mesal Da seta. A subprimary seta. Distribution: absent in sC of BAS, ONI, ORBI; absent in sB of AXI, GLA, HUM, DIS, BI, BII, L; absent in sA but present in sB of PUL, ARI, VAR; present in sB of CAS; present in sA but absent in sB of MAN. *Nelson*: unresolved, because character sometimes appear later in ontogenetic sequence and sometimes is present primary and disappear in sB. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of VAR, CAS, ARI, PUL, autapomorphy of MAN.

28. Posterior Db setae, no. Distribution: in PUL 0→5; in ARI 3→8 (according to Figures 58, 59 in Wheeler's paper); in ONI 1→3; in ORBI 1→4; in BAS 1→5; in VAR 1→8; in MAN 2→4; 1 in sB of L; 3 in sB of BII; 5 in sB of HUM and DIS; 6 in sB of CAS, BII; 8 in sB of AXI, 21 in sB of GLA. *Nelson*: unresolved, because of high level of variability. *Outgroup*: unresolved, because of high level of variability.

29. Seta Db* present. A subprimary seta. Distribution: absent in sA but present in sB of BAS, ONI, ARI, ORBI, VAR, MAN; absent in sC of PUL; absent in sB of AXI, HUM, L; present in sB of GLA, CAS, DIS, BI (assymetrically), BII. *Nelson*: absence is plesiomorphic, presence is synapomorphy of BAS, ONI, ARI, GLA, ORBI, CAS, DIS, VAR, MAN, BI, BII. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of BAS, ONI, ARI, GLA, ORBI, CAS, DIS, VAR, MAN, BI, BII.

30. Posterior Dc setae, no. Distribution: in ONI 1→3; in ORBI 1→5; in BAS 1→6 (no. in sB changed, see Fig. 64); in PUL 1→7 (changed, see Figs 56, 57); in ARI 1→9; in VAR 1→14; in MAN 2→4; 1 in sB of L; 2 in BI; 4 in HUM; 6 in AXI; 7 in BII; 8 in CAS; 9 in DIS; 20 in GLA. *Nelson*: unresolved, because of high level of variability. *Outgroup*: unresolved, because of high level of variability.

31. Dc setae anterior to Dc1, no. Distribution: in PUL 0→0; in BAS, ONI 0→1; in ORBI, VAR 0→2; in ARI 0→3; in MAN 1→1; 0 in sB of HUM, L; 1 in AXI, GLA, CAS, DIS, BI, BII. *Nelson*: 0 is plesiomorphic, 1,2,3 is synapomorphy of BAS, ONI, ARI, AXI, GLA, ORBI, CAS, DIS, VAR, MAN, BI, BII. *Outgroup*: 0 is plesiomorphic, 1,2,3 is synapomorphy of BAS, ONI, ARI, AXI, GLA, ORBI, CAS, DIS, VAR, MAN, BI, BII.

32. Dd setae posterior to Dd1, no. Distribution: 0→1 in ARI; 0→2 in BAS, ONI; 0→3 in VAR; 0→5 in PUL, ORBI; 1→1 in MAN; 0 in sB of BII, L; 1 in HUM; 2 in BI; 3 in AXI; 4 in DIS; 6 in CAS; 21 in GLA. *Nelson*: 0 is plesiomorphic but character do not transform in any taxa so it is unresolved. *Outgroup*: 0 is plesiomorphic, more than 0 is synapomorphy of BAS, PUL, ONI, ARI, AXI, GLA, HUM, ORBI, CAS, DIS, VAR, MAN, BI.

33. Lateral setae posterior to L1, no. Distribution: 0→0 in VAR; 0→1 in BAS, ONI (according to Fig. 61); 0→2 in PUL, ARI; 1→1 in MAN; 1→2 in ORBI; 0 in sB of L; 1 in AXI, HUM, DIS, BI, BII; 3 in GLA, CAS. *Nelson*: 0 is plesiomorphic, more than 0 is apomorphy of BAS, PUL, ONI, ARI, AXI, GLA, HUM, ORBI, CAS, DIS, MAN, BI, BII. *Outgroup*: 0 is plesiomorphic, more than 0 is apomorphy of BAS, PUL, ONI, ARI, AXI, GLA, HUM, ORBI, CAS, DIS, MAN, BI, BII.

34. Lateral setae anterior to L1, no. Distribution: 0→0 in BAS (according to Figs. 62–64); 0→3 in PUL (according to Fig. 56); 0→4 in VAR; 0→7 in ARI; 1→2 in ORBI; 1→5 in ONI; 4→4 in MAN; 0 in sB of L; 1 in AXI; 2 in HUM, BII; 4 in GLA; 5 in CAS, DIS, BI. *Nelson*: 0 is plesiomorphic, more than 0 is apomorphy of PUL, ONI, ARI, AXI, GLA, HUM, ORBI, CAS, DIS, VAR, MAN, BI, BII. *Outgroup*: 0 is plesiomorphic, more than 0 is apomorphy of PUL, ONI, ARI, AXI, GLA, HUM, ORBI, CAS, DIS, VAR, MAN, BI, BII.

35. Medial posterior seta (PM). A subprimary seta. Distribution: absent in sC of ONI, ORBI, VAR, MAN; absent in sB of AXI, GLA, HUM, DIS, BI, L; absent in sA and present in sB of BAS (very small, present only in II instar, lack in third larval instar), PUL, ARI; present in sB of CAS, BII. *Nelson*: absence is plesiomorphic, presence is synapomorphy of BAS (?), PUL, ARI, CAS, BII. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of BAS (?), PUL, ARI, CAS, BII.

36. Posterior setae between P1/P2, no. Distribution: 0→1 in BAS (see Fig. 64), PUL, ONI; 0→2 in ARI, VAR; 1→2 in ORBI, MAN (0–2 in instar III of MAN); 0 in sB of AXI, L; 1 in HUM, BI, BII; 2 in GLA, DIS; 3 in CAS. *Nelson*: 0 is plesiomorphic, more than 0 is apomorphy of BAS, PUL, ONI, ARI, GLA, HUM, ORBI, CAS, DIS, VAR, MAN, BI, BII. *Outgroup*: 0 is plesiomorphic, more than 0 is apomorphy of BAS, PUL, ONI, ARI, GLA, HUM, ORBI, CAS, DIS, VAR, MAN, BI, BII.

37. Posterior setae between P2/P3, no. Distribution: 0→2 in PUL, ONI; 0→3 in BAS; 0→4 in VAR; 0→7 in ARI (see Fig. 59); 2→3 in MAN; 3→7 in ORBI; 0 in sB of BI, L; 1 in AXI, DIS; 2 in HUM; 3 in BII; 4 in GLA; 5 in CAS. *Nelson*: 0 is plesiomorphic, more than 0 is apomorphy of BAS, PUL, ONI, ARI, AXI, GLA, HUM, ORBI, CAS, DIS, VAR, MAN, BII. *Outgroup*: 0 is plesiomorphic, more than 0 is apomorphy of BAS, PUL, ONI, ARI, AXI, GLA, HUM, ORBI, CAS, DIS, VAR, MAN, BII.

38. Posterior setae between P3/P4, no. Distribution: 0→1 in PUL, ONI, ORBI; 0→2 in BAS (see Fig. 64), VAR; 0→3 in ARI; 1→1 in MAN; 0 in sB of L; 1 in GLA, DIS, BII; 2 in AXI, HUM, CAS, BI. *Nelson*: 0 is plesiomorphic, more than 0 is apomorphy of BAS, PUL, ONI, ARI, AXI, GLA, HUM, ORBI, CAS, DIS, VAR, MAN, BI, BII. *Outgroup*: 0 is plesiomorphic, more than 0 is apomorphy of BAS, PUL, ONI, ARI, AXI, GLA, HUM, ORBI, CAS, DIS, VAR, MAN, BI, BII.

39. Setae between Da1's, no. A subprimary setae. Distribution: 0→0 in BAS, ONI (see Fig. 61), MAN; 0→1 in PUL, ORBI, VAR, ARI; 0 in sB of AXI, HUM, CAS, DIS, BI, BII, L; 1 in GLA. *Nelson*: absence is plesiomorphic, presence is synapomorphy of PUL, ARI, GLA, ORBI, VAR. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of PUL, ARI, GLA, ORBI, VAR.

Urogomphal and 9th abdominal segment characters

40. Seta V1 present. A primary seta. Distribution: present in sC of PUL, ARI, ORBI, VAR, MAN; in sB of HUM, CAS, DIS, BI, BII; absent in sA but present in sB of BAS and ONI; lack of homolog seta in L; lack data about AXI and GLA. *Nelson*: absence is plesiomorphic for L, presence is synapomorphy of BAS, PUL, ONI, ARI, HUM, ORBI, CAS, DIS, VAR, MAN, BI, BII. *Outgroup*: unresolved, the same state of characters in all ingroup taxa.

41. Setae anterior to Vp4/Vp5, no. Distribution: 0→0 in BAS, ORBI; 0→1 in ONI, ARI (see Fig. 103 in Wheeler, 1990), VAR; 0→2 in PUL; 1→1 in MAN; 0 in sB of DIS, L; 1 in HUM, BI, BII; 1–2 in CAS; lack data about AXI, GLA. *Nelson*: 0 is plesiomorphic, more than 0 is apomorphy of PUL, ONI, ARI, HUM, CAS, VAR, MAN, BI, BII. *Outgroup*: 0 is plesiomorphic, more than 0 is apomorphy of PUL, ONI, ARI, HUM, CAS, VAR, MAN, BI, BII.

42. Anterior mid-dorsal setae, no. Distribution: 0→1 in PUL; 0→2 in ARI, ORBI; 1→1 in BAS (see Fig. 100 in Wheeler, 1990a), VAR, MAN; 1→4 in ONI; 0 in sB of L; 1 in DIS, BII; 2 in HUM, CAS; 6 in BI; 8 in AXI; 11 in GLA. *Nelson*: 0 is plesiomorphic, more than 0 is apomorphy of BAS, PUL, ONI, ARI, AXI, GLA, HUM, ORBI, CAS, DIS, VAR, MAN, BI, BII. *Outgroup*: 0 is plesiomorphic, more than 0 is apomorphy of BAS, PUL, ONI, ARI, AXI, GLA, HUM, ORBI, CAS, DIS, VAR, MAN, BI, BII.

43. Urogomphal setae, no. Distribution: 3→3 in ARI; 4→5 in ONI; 4→6 in PUL; 6→8 in ORBI; 7→7 in BAS, VAR, MAN; 0 in L; 3 in BII; 7 in AXI; 8 in BI; 9 in HUM, DIS; 11 in CAS; 14 in GLA. *Nelson*: unresolved, because of high level of variability. *Outgroup*: unresolved, there is no possibility to compare because of lack of segmented urogomphi within outgroup.

Anal vesicle characters

44. Ventral setae, no. Distribution: 3→11 in ARI; 4→11 in BAS, PUL, ONI, VAR; 7→11 in ORBI; 9→8 in MAN; 6 in sB of DIS, BI; 8 in BII; 11 in AXI, HUM; 18 in CAS; 21 in GLA; 0 in L. *Nelson*: unresolved, transformations occur in all taxa. *Outgroup*: unresolved, because ancestral state 0 doesn't occur within ingroup.

45. Dorsal setae, no. Distribution: 2→3 in BAS, ONI; 2→4 in PUL (see Fig. 99 in Wheeler, 1990), MAN; 2→6 in VAR; 2→7 in ARI; 3→6 in ORBI; 0 in sB of L; 2 in AXI, BII; 4 in HUM; 5 in DIS; 6 in GLA, BI; 7 in CAS. *Nelson*: unresolved, transformations occur in all species. *Outgroup*: unresolved, because ancestral state 0 doesn't occur within ingroup.

Microsculptural characters

46. Microsculpture of pronotum. Because of differences between density of asperities on head and pronotum, I take microsculpture of pronotum as another character. Distribution: 0→0 (instar I→ instar III) in ONI; 0→2 in ARI, MAN; 1→2 in PUL, VAR; 2→2 in BAS, ORBI; 0 in third instar of L, AXI, CAS, BI; 1 in DIS; 2 in GLA, HUM, BII. *Nelson*: 0 is plesiomorphic, 1,2 apomorphic for BAS, PUL, ARI, GLA, HUM, ORBI, DIS, VAR, MAN, BII. *Outgroup*: 0 in third instar L, AXI, CAS, BI, ONI is plesiomorphic, dense or very dense asperities are apomorphy of BAS, PUL, ARI, GLA, HUM, ORBI, DIS, VAR, MAN, BII.

47. Microsculpture of head. Because of lack data about II larval instar, I take instars I and III. Distribution: 0→0 in BAS, ONI; 0→1 in ARI (see Fig. 14 in Wheeler, 1990); 0→2 in PUL, VAR; 1→2 in MAN; 2→2 in ORBI; 0 in third instar of L, AXI, HUM, CAS, BI; 2 in GLA, DIS, BII. *Nelson*: 0 is plesiomorphic, 1,2 is apomorphy of PUL, ARI, GLA, ORBI, DIS, VAR, MAN, BII. *Outgroup*: 0 in third instar of BAS, L, AXI, HUM, CAS, BI is plesiomorphic, 1, 2 is apomorphy of PUL, ARI, GLA, ORBI, DIS, VAR, MAN, BII.

Abdominal characters

48. P3 seta of segment I. A primary seta. Distribution: present in sC of BAS, ARI; present in sB of AXI, HUM; absent in sC of PUL, ONI, ORBI, VAR, MAN; in sB of GLA, CAS, DIS, BI, BII, L. *Nelson*: unresolved, state of characters do not transform in any of the taxa. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of BAS, ARI, AXI, HUM.

49. Median setae between P1's. A subprimary setae. Distribution: absent in sC of BAS, ONI, ORBI; absent in sA and present in sB of PUL, ARI, VAR, MAN; absent in sB of HUM, DIS, BI, L; present in sB of AXI (there are very minute), GLA, CAS, BII. *Nelson*: absence is plesiomorphic, presence is synapomorphy of PUL, ARI, AXI, GLA, CAS, VAR, MAN, BII. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of PUL, ARI, AXI, GLA, CAS, VAR, MAN, BII.

50. Postprimary P setae between P4/P5 (presence of 2nd seta). Distribution: absent in sC of BAS, MAN; absent in sA but present in sB of PUL, ONI, ARI, ORBI, VAR; absent in sB of AXI, HUM, CAS, DIS, BI, L; present in sB of GLA and BII. *Nelson*: absence is plesiomorphic, presence is synapomorphy of PUL, ONI, ARI, GLA, ORBI, VAR, BII. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of PUL, ONI, ARI, GLA, ORBI, VAR, BII.

51. Setae anterior to P row, no. Distribution: 2→6 in VAR; 2→13 in BAS (see Fig. 96 in Wheeler 1990); 5→7 in MAN, PUL; 6→10 in ORBI; 7→15 in ONI; 9→17 in ARI (see Figs. 90–91 in Wheeler 1990); 0 in third instar L; 7 in BII; 12 in HUM; 13 in DIS; 16 in CAS; 17 in AXI; 19 in BI; 29 in GLA. *Nelson*: unresolved, transformations occur in all species. *Outgroup*: unresolved, because ancestral state 0 doesn't occur within ingroup.

Mandibular and maxillary characters

52. Prostheca sclerotization. Distribution: membraneous in sC of ONI and sB of BI; sclerotized in rest of species. *Nelson*: unresolved, state of characters do not transform in any of the taxa. *Outgroup*: sclerotized is plesiomorphic, membraneous is apomorphic for ONI and BI.

53. Fimbriate galea loss. Distribution: loss in sC of ONI, ARI, VAR and sB of BI; present in rest of the taxa. *Nelson*: unresolved, state of characters do not transform in any of the taxa. *Outgroup*: absence of fimbriate galea is synapomorphy of ONI, ARI, VAR, BI; presence is plesiomorphic .

54. Presence of serrate margin. Distribution: present in sC of VAR; absent in rest of species. *Nelson*: unresolved, state of characters do not transform in any of the taxa. *Outgroup*: presence is autapomorphy of VAR.

55. Presence of mola. Distribution: present in sC of BAS, PUL, ARI, ORBI, VAR, MAN; present in sB of AXI, GLA, HUM, CAS, DIS, BII, L; absent in sC of ONI; in sB of BI. *Nelson*: unresolved, state of characters do not transform in any of the taxa. *Outgroup*: presence is plesiomorphic, absence is synapomorphy of ONI, BI.

56. Labrum incised. Margin of labrum is incised or straight. Distribution: incised in sC of BAS, PUL, ARI, ORBI, MAN; in sB of AXI, GLA, HUM, CAS, DIS, BII, L; straight in sC of ONI, VAR; straight in sB of BI. *Nelson*: unresolved, because state of characters do not transform in any of the taxa. *Outgroup*: straight is plesiomorphic, incised is synapomorphy of ONI, VAR, BI.

Metanotal characters

57. Presence of seta P3. A primary seta. Distribution: present in sC of BAS, in sB of AXI, HUM; absent in sC of PUL, ONI, ARI, ORBI, VAR, MAN; in sB of GLA, CAS, DIS, BI, BII, L. *Nelson*: unresolved, state of characters do not transform within any of the taxa. *Outgroup*: absence is plesiomorphic, presence is synapomorphy of BAS, AXI, HUM.

58. Lateral seta L2 present. A primary seta. Distribution: present in sC of ONI, ARI, ORBI, VAR, PUL (I treat this small pleural seta as L2), BAS (there is present in instar I and II but lost in III one); present in sB of AXI, GLA, CAS, DIS, BI, L (assymetrically); absent in sA and present in sB of MAN; absent in sB of HUM, BII. *Nelson*: absence is plesiomorphic, presence is synapomorphy of BAS, PUL, ONI, ARI, AXI, GLA, ORBI, CAS, DIS, VAR, MAN, BI, L. *Outgroup*: presence is plesiomorphic, absence is synapomorphy of BII, HUM; MAN – autapomorphy.

59. Small setae between P1-P5, no. A subprimary setae. Distribution: 0→0 in BAS; 0→2 in ONI; 0→5 in VAR, MAN; 0→6 in PUL; 0→13 in ARI; 2→3 in ORBI; 0 in sB of AXI, HUM, L; 2 in BI; 4 in BII, CAS; 6 in DIS; 12 in GLA. *Nelson*: 0 is plesiomorphic, more than 0 is apomorphy of PUL, ONI, ARI, GLA, ORBI, CAS, DIS, VAR, MAN, BI, BII. *Outgroup*: 0 is plesiomorphic, more than 0 is apomorphy of PUL, ONI, ARI, GLA, ORBI, CAS, DIS, VAR, MAN, BI, BII.

60. Median setal pair (AM). A subprimary setae. Distribution: absent in sC of BAS, ORBI; absent in sA but present in sB of PUL (according to figure 66 in Wheeler's paper), ONI, ARI, VAR, MAN; absent in sB of AXI, GLA, DIS, BII, L; present in sB of HUM, CAS, BI. *Nelson*: absence is plesiomorphic, presence is apomorphy of PUL, ONI, ARI, HUM, CAS, VAR, MAN, BI. *Outgroup*: absence is plesiomorphic, presence is apomorphy of PUL, ONI, ARI, HUM, CAS, VAR, MAN, BI.

Hyphopharyngeal scleromic characters

61. Posterior bridge complete. Distribution: complete in sC of BAS, PUL, ORBI, VAR, MAN; complete in sA but incomplete in sB of ARI; complete in sB of AXI, GLA, HUM, CAS, DIS, BII, L (lack of data about BI); incomplete in sC of ONI . *Nelson*: complete is plesiomorphic, incomplete is synapomorphy of ONI, ARI. *Outgroup*: complete is plesiomorphic, incomplete (absence or lack) is synapomorphy of ONI and ARI.

62. Anterior arms, fused and heavily sclerotized. Distribution: fused and heavily sclerotized in sC of BAS, PUL, ARI, ORBI, VAR, MAN; in sB of AXI, GLA, HUM, CAS, DIS, BII, L; fused in sB but separate in sA of ONI; lack of data about BI. *Nelson*: fused and heavily sclerotized is plesiomorphic, separate in sA of ONI is neotenic autapomorphy. *Outgroup*: unresolved, because there is no variation in sB of all taxa.

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No	Characters	*Bas*	Pul	Oni	Ari	*Axi*	*Gla*	*Hum*	*Orbi*	*Cas*	Dis	Var	Man	BI	BII	L
	CRANIAL CHARACTERS															
1	seta Da1 present	- -	+ +	+ +	+ +	-	+	+	+ +	+	+	+ +	+ +	+	+	-
2	seta Da* present	- +	- -	- -	- -	+	+	-	- -	-	-	- +	- -	-	-	-
3	seta Da*a present	- +	- -	+ +	- +	+	+	+	- -	+	+	- +	- -	-	-	-
4	seta Db1 present	+ +	+ +	- -	+ +	+	+	+	+ +	+	+	+ +	+ +	+	+	-
5	seta Db* present	- +	- -	- -	- +	+	+	+	- -	+	-	- +	- -	-	-	-
6	seta Db** present	- -	- -	- -	- +	+	+	-	- -	+	-	- +	- -	-	-	-
7	seta Dc1 present	- +	+ +	+ +	+ +	+	+	+	+ +	+	+	- +	+ +	+	+	+
8	seta Dc2 present	- +	+ +	+ +	- +	+	+	+	+ +	+	+	+ +	+ +	+	+	+
9	seta Dc** present	- -	- +	- -	- +	-	-	-	- -	-	-	- +	- +	-	-	-
10	seta Dc* present	- -	- +	- +	- +	-	+	-	+ +	+	+	- +	+ +	+	+	-
11	posterior seta P5	+ +	- -	- -	- -	-	+?	-	- -	-	-	- -	- -	-	-	-
12	seta Dd1 present	- -	- +	+ +	- +	-	+	-	+ +	+	-	- +	+ +	+	+	-
13	seta Dd2a present	- +	- +	- -	+ +	+?	+	-	+ +	-	-	- +	+ +	-	-	-
14	seta Df1 present	+ +	+ +	+ +	- -	-	-	-	- +	-	+	+ +	+ +	+	-	-
15	seta Dd1* present	- -	- -	- -	- -	-	+	-	+ +	-	-	- +	- -	-	+	-
16	seta Db2a present	- -	- -	- -	- -	-	+	-	- +	-	-	- -	- -	-	-	-
17	small setae in front of Db2	- -	- -	+ +	- -	+	+	+	- -	+	+	- -	- -	-	+?	-
18	small setae b. Dd4,Dc3,Dc4	- -	- -	- +	- -	-	+	+	+ +	+	+	- +	+ +	-	+	-
19	small setae b. Dc4's and Da2's	- -	- -	- -	- -	-	+	-	- -	+	-	- +	- -	-	-	-
20	stemmata	2. 2	2. 2	2. 2	1. 1	.2	.2	.2	2. 2	.2	.2	2. 2	2. 2	.2	.2	.2
21	seta L1 present	+ +	+ +	+ +	+ +	+	+	+	+ +	+	+	+ +	+ +	+	+	-
22	lateral setae no.	1? 1?	1? 4?	2? 4?	1? 4?	.3	.6	.3?	4. 4	.7	.3	2. 5	4. 5	.2	.5	.1
23	adult hipertrichia	-	-	-	-	-	-?	-	-	-	-	+	-?	-	-	-
24	clypeus incised	- -	- -	- -	- -	-	-	-	- -	-	-	+ +	- -	+ ?	-	-
	ANTENNAL CHARACTERS															
25	solenidia of ant. II	2. 3	1. 2	1. 2	1. 2	.3	.3	.3	3. 3	. 3	.3	2. 3	3. 3	.3	.2	.2
26	digitiform organ divided	- -	+ +	- -	- -	-	-	-	- -	-	-	- -	- -	-	-	-
	PRONOTAL CHARACTERS															
27	mesal Da seta	- -	- +	- -	- +	-	-	-	- -	+	-	- +	+ -	-	-	-
28	posterior Db setae, no.	1. 5	0. 5	1. 3	3z. 8z	.8	.21	.5	1. 4	.6	.5	1. 8	2. 4	.6	.3	.1
29	seta Db* present	- +	- -	- +	- +	-	+	-	- +	+	+	- +	- +	+?	+	-
30	posterior Dc setae, no.	1. 6z	1z. 7z	1. 3	1z. 9z	.6	.20	.4	1. 5	.8	.9	1. 14	2. 4	.2	.7	.1
31	Dc setae anterior to Dc1, no	0. 1	0. 0	0. 1	0. 3	.1	.1	.0	0. 2	.1	.1	0. 2	1. 1	.1	.1	.0
32	Dd setae posterior to Dd1.	0. 2	0. 5	0. 2	0. 1	.3	.21	.1	0. 5	.6	.4	0. 3	1. 1	.2	.0	.0
33	lateral setae post. L1	0. 1	0. 2	0. 1z	0. 2	.1	.3	.1	1. 2	.1-3	.1	0. 0	1. 1	.1	.1	.0
34	lateral seta ant. L1	0z. 0z	0z. 3	1. 5	0. 7	.1	.4	.2	1. 2	.5	.5	0. 4	4. 4	.5	.2	.0
35	medial posterior seta (PM)	- + ?	- +	- -	- +	-	-	-	- -	+	-	- -	- -	-	+	-
36	posteriors between P1/P2	0. 1z	0. 1	0. 1	0. 2	.0	.2	.1	1. 2	.3	.2	0. 2	1. 0-2	.1	.1	.0
37	posteriors between P2/P3	0. 3	0. 2	0. 2	0. 7z	.1	.4	.2	3. 7	.5	.1	0. 4	2. 3	.0	.3	.0
38	posteriors between P3/P4	0. 2z	0. 1	0. 1	0. 3	.2	.1	.2	0. 1	.2	.1	0. 2	1. 1	.2	.1	.0
39	setae between Da1's	0. 0	0. 1	0. 0z	0. 1	.0	.1	.0	0 .1	.0	.0	0. 1	0. 0	.0	.0	.0

No	Characters	*Bas*	Pul	Oni	Ari	*Axi*	*Gla*	*Hum*	*Orbi*	*Cas*	Dis	Var	Man	BI	BII	L
	UROGOMPHAL AND IX ABDOMINAL SEGMENT CHARACTERS															
40	seta V1 present	- +	+ +	- +	+ +	?	?	+	+ +	+	+	+ +	+ +	+	+	-
41	setae anterior Vp4/Vp5, no.	0. 0	0. 2	0. 1	0. 1?	?	?	.1	0. 0	1-2	.0	0. 1	1. 1	.1	.1	.0
42	Anterior mid-dorsals, no.	1z. 1	0. 1	1. 4	0. 2	.8	.11	.2	0. 2	.2	.1	1. 1	1. 1	.6	.1	.0
43	urogomphal setae, no.	7. 7	4. 6	4. 5	3. 3	.7	.14	.9	6. 8	.11	.9	7. 7	7. 7	.8	.3	-
	ANAL VESICLE CHARACTERS															
44	ventral setae	4. 11	4. 11	4. 11	3. 11	.11	.21	.11	7. 11	.18	.6	4. 11	9. 8	.6	.8	.0
45	dorsal setae	2. 3	2. 4z	2. 3	2. 7	.2	.6	.4	3. 6	.7	.5	2. 6	2. 4	.6	.2	.0
	MICROSCULPTURAL CHARACTERS 0=absent or sparse, 1=dense, 2= very dense															
46	pronotum	2. 2	1. 2	0. 0	0. 2	.0	.2	.2	2. 2	.0	.1	1. 2	0. 2	.0	.2	.0
47	head	0. 0	0. 2	0. 0	0. 1?	.0	.2	.0	2. 2	.0	.2	0. 2	1. 2	.0	.2	.0
	ABDOMINAL CHARACTERS															
48	P3 seta of segment I	+ +	- -	- -	+ +	+	-	+	- -	-	-	- -	- -	-	-	-
49	median seta between P1's	- -	- +	- -	- +	+?	+	-	- -	+	-	- +	- +	-	+	-
50	postprimary P setae between P4/P5; 2nd seta	- -	- +	- +	- +	-	+	-	- +	-	-	- +	- -	-	+	-
51	setae anterior to P row	2. 13z	5. 7	7. 15	9z. 17z	.17	.29	.12	6. 10	.16	.13	2. 6	5. 7	.19	.7	.0
	MANDIBULAR AND MAXILLARY CHARACTERS															
52	prostheca sclerotization - =scler, +=membraneous	- -	- -	+ +	- -	-	-	-	- -	-	-	- -	- -	+	-	-
53	fimbriate galea loss (+)	- -	- -	+ +	+ +	-	-	-	- -	-	-	+ +	- -	+	-	-
54	serrate margin (+)	- -	- -	- -	- -	-	-	-	- -	-	-	+ +	- -	-	-	-
55	mola present (+)	+ +	+ +	- -	+ +	+	+	+	+ +	+	+	+ +	+ +	-	+	+
56	labrum incised (-)	+ +	+ +	- -	+ +	+	+	+	+ +	+	+	- -	+ +	-	+	+
	METANOTAL CHARACTERS															
57	Third posterior seta:P3	+ +	- -	- -	- -	+	-	+	- -	-	-	- -	- -	-	-	-
58	lateral seta L2	+ +	+ +	+ +	+ +	+	+	-	+ +	+	+	+ +	- +	+	-	+?
59	small setae b. P1-P5	0. 0	0. 6	0. 2	0. 13	.0	.12	.0	2. 3	.4	.6	0. 5	0. 5	.2	.4	.0
60	median setal pair (AM)	- -	- +z	- +	- +	-	-	+	- -	+	-	- +	- +	+	-	-
	HYPOPHARYNGEAL SCLEROMIC CHARACTERS															
61	posterior bridge +=complete; - = incomplete	+ +	+ +	- -	+ -	+	+	+	+ +	+	+	+ +	+ +	?	+	+
62	anterior arms, fused and heavily sclerotized	+ +	+ +	- +	+ +	+	+	+	+ +	+	+	+ +	+ +	?	+	+

Table 1. Distribution of characters used in cladistic studies. (+ means present; first symbol for instar I, second for instar III, question marks are explained in Summary of characters, distributions and polarities, p. 142 z means changed value of character in relation to Wheeler's (1990a), acronyms of species see page 142, members of Anisotoma in italics).

text[1]	both[2]	same[3]	No[4]	Nelson	*Bas*	Pul	Oni	Ari	*Axi*	*Gla*	*Hum*	*Orbi*	Cas	Dis	Var	Man	BI	BII	L
				CRANIAL CHARACTERS															
2	0	0	0	seta Da* present	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0
3	1	1	1	seta Da*a present	1	0	1	1	1	1	1	0	1	1	1	0	0	0	0
5	2	2	2	seta Db* present	1	0	0	1	1	1	1	0	1	0	1	0	0	0	0
6	3	3	3	seta Db** present	0	0	0	1	1	1	0	0	1	0	1	0	0	0	0
9	4	4	4	seta Dc** present	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0
10	5	5	5	seta Dc* present	0	1	1	1	0	1	0	1	1	1	1	1	1	1	0
12	6	6	6	seta Dd1 present	0	1	1	1	0	1	0	1	1	0	1	1	1	1	0
13	7	7	7	seta Dd2a present	1	1	0	1	1	1	0	1	0	0	1	1	0	0	0
14	8	8	8	seta Df1 present	1	1	1	0	0	0	0	1	0	1	1	1	1	0	0
15	9	9	9	seta Dd1* present	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0
16	10	10	10	seta Db2a present	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
18	11	11	11	small setae b. Dd4,Dc3,Dc4	0	0	1	0	0	1	1	1	1	1	1	1	0	1	0
19	12	12	12	small setae b. Dc4's and Da2's	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0
				PRONOTAL CHARACTERS															
29	13	13	13	seta Db* present	1	0	1	1	0	1	0	1	1	1	1	1	1	1	0
31	14	14	14	Dc setae anterior to Dc1, no.	1	0	1	1	1	1	0	1	1	1	1	1	1	1	0
32	15	15	15	Dd setae posterior to Dd1, no.	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
33	16	16	16	lateral setae post. L1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0
34	17	17	17	lateral setae ant. L1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0
35	18	18	18	medial posterior seta (PM)	1	1	0	1	0	0	0	0	1	0	0	0	0	1	0
36	19	19	19	posteriors between P1/P2	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0
37	20	20	20	posteriors between P2/P3	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0
38	21	21	21	posteriors between P3/P4	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
39	22	22	22	setae between Da1's	0	1	0	1	0	1	0	1	0	0	1	0	0	0	0
				UROGOMPHAL AND IX ABDOMINAL SEGMENT CHARACTERS															
40	-	-	23	seta V1 present	1	1	1	1	-	-	1	1	1	1	1	1	1	1	0
41	23	23	24	setae anterior Vp4/Vp5, no.	0	1	1	1	-	-	1	0	1	0	1	1	1	1	0
42	-	-	25	anterior mid-dorsals	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
				MICROSCULPTURAL CHARACTERS 0=absent or sparse, 1=dense, 2= very dense															
46	24	24	26	pronotum	1	1	0	1	0	1	1	1	0	1	1	1	0	1	0
47	25	25	27	head	0	1	0	1	0	1	0	1	0	1	1	1	0	1	0
				ABDOMINAL CHARACTERS															
49	26	26	28	median setae b. P1's	0	1	0	1	1	1	0	0	1	0	1	1	0	1	0
50	27	27	29	postprimary P setae b. P4/P5; 2nd seta	0	1	1	1	0	1	0	1	0	0	1	0	0	1	0
				METANOTAL CHARACTERS															
58	28	-	30	lateral seta L2 present	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1
59	29	28	31	small setae b. P1-P5, no.	0	1	1	1	0	1	0	1	1	1	1	1	1	1	0
60	30	29	32	median setal pair (AM)	0	1	1	1	0	0	1	0	1	0	1	1	1	0	0
				HYPOPHARYNGEAL SCLEROMIC CHARACTERS															
61	31	30	33	posterior bridge +=complete; - = incomplete	0	0	1	1	0	0	0	0	0	0	0	0	-	0	0

Table 2. Nelson pairwise comparison character matrix (autapomorphies excluded).

[1] - numbers used in table 1 (distribution of characters). [2] - numbers that refer to characters resolved also by Outgroup comparison, whether same polarity or not.

[3] - numbers of characters resolved by both methods with the same polarity conclusions. [4] - numbers of characters used in Nelson comparison, acronyms of species see page 142, members of Anisotoma in italics.

text[1]	both[2]	same[3]	No[4]	Outgroup	*Bas*	Pul	Oni	Ari	*Axi*	*Gla*	*Hum*	*Orbi*	*Cas*	Dis	Var	Man	BI	BII	L
				CRANIAL CHARACTERS															
1	-	-	0	seta Da1 present	0	1	1	1	0	1	1	1	1	1	1	1	1	1	0
2	0	0	1	seta Da* present	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0
3	1	1	2	seta Da*a present	1	0	1	1	1	1	1	0	1	1	1	0	0	0	0
4	-	-	3	seta Db1 present	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0
5	2	2	4	seta Db* present	1	0	0	1	1	1	1	0	1	0	1	0	0	0	0
6	3	3	5	seta Db** present	0	0	0	1	1	1	0	0	1	0	1	0	0	0	0
9	4	4	6	seta Dc** present	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0
10	5	5	7	seta Dc* present	0	1	1	1	0	1	0	1	1	1	1	1	1	1	0
11	-	-	8	posterior seta P5	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
12	6	6	9	seta Dd1 present	0	1	1	1	0	1	0	1	1	0	1	1	1	1	0
13	7	7	10	seta Dd2a present	1	1	0	1	1	1	0	1	0	0	1	1	0	0	0
14	8	8	11	seta Df1 present	1	1	1	0	0	0	0	1	0	1	1	1	1	0	0
15	9	9	12	seta Dd1* present	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0
16	10	10	13	seta Db2a present	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
17	-	-	14	small setae in front of Db2	0	0	1	0	1	1	1	0	1	1	0	0	0	1	0
18	11	11	15	small setae b. Dd4,Dc3,Dc4	0	0	1	0	0	1	1	1	1	1	1	1	0	1	0
19	12	12	16	small setae b. Dc4's and Da2's	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0
24	-	-	17	clypeus incised	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
				ANTENNAL CHARACTERS															
25	-	-	18	solenidia of ant.II	1	0	0	0	1	1	1	1	1	1	1	1	1	0	0
				PRONOTAL CHARACTERS															
27	-	-	19	mesal Da seta	0	1	0	1	0	0	0	0	1	0	1	1	0	0	0
29	13	13	20	seta Db* present	1	0	1	1	0	1	0	1	1	1	1	1	1	1	0
31	14	14	21	Dc setae anterior to Dc1, no	1	0	1	1	1	1	0	1	1	1	1	1	1	1	0
32	15	15	22	Dd setae posterior to Dd1, no.	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
33	16	16	23	lateral setae post. L1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0
34	17	17	24	lateral seta ant. L1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0
35	18	18	25	medial posterior seta (PM)	1	1	0	1	0	0	0	0	1	0	0	0	0	1	0
36	19	19	26	posteriors between P1/P2	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0
37	20	20	27	posteriors between P2/P3	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0
38	21	21	28	posteriors between P3/P4	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
39	22	22	29	setae between Da1's	0	1	0	1	0	1	0	1	0	0	1	0	0	0	0
				UROGOMPHAL and IX ABDOMINAL SEGMENT CHARACTERS															
41	23	23	30	setae anterior Vp4/Vp5, no.	0	1	1	1	0	0	1	0	1	0	1	1	1	1	0
				MICROSCULPTURAL CHARACTERS 0=absent or sparse, 1=dense, 2= very dense															
46	24	24	31	pronotum	1	1	0	1	0	1	1	1	0	1	1	1	0	1	0
47	25	25	32	head	0	1	0	1	0	1	0	1	0	1	1	1	0	1	0
				ABDOMINAL CHARACTERS															
48	-	-	33	P3 seta of segment I	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0
49	26	26	34	median setae b. P1's	0	1	0	1	1	1	0	0	1	0	1	1	0	1	0
50	27	27	35	postprimary P setae b. P4/P5; 2nd seta	0	1	1	1	0	1	0	1	0	0	1	0	0	1	0

text[1]	both[2]	same[3]	No[4]	Outgroup	*Bas*	Pul	Oni	Ari	*Axi*	*Gla*	*Hum*	*Orbi*	*Cas*	Disc	Var	Man	BI	BII	L
				MANDIBULAR and MAXILLARY CHARACTERS															
52	-	-	36	prostheca sclerotization	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
53	-	-	37	fimbriate galea loss	0	0	1	1	0	0	0	0	0	0	1	0	1	0	0
55	-	-	38	presence of mola	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
56	-	-	39	labrum incised	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0
				METANOTAL CHARACTERS															
57	-	-	40	presence of seta P3	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0
58	28	-	41	lateral seta L2 present	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
59	29	28	42	small setae b. P1-P5, no.	0	1	1	1	0	1	0	1	1	1	1	1	1	1	0
60	30	29	43	median setal pair (AM)	0	1	1	1	0	0	1	0	1	0	1	1	1	0	0
				HYPOPHARYNGEAL SCLEROMIC CHARACTERS															
61	31	30	44	posterior bridge: + = complete; -= incomplete	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0

Table 3. Outgroup comparison of character matrix (autapomorphies excluded). Numbers in the first, second and third columns refer to character numbers in table 2. [4] – number of characters used in outgroup comparison, acronyms of species see page 142, members of Anisotoma in italics.

Analysis	Nelson/Outgroup same[1]	Nelson both[2]	Outgroup both[3]	Nelson[4]						Outgroup[5]					
Figures	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV
Length	79	83	82	86	86	86	87	87	87	114 all					
Consistency index	0.39	0.38	0.39	0.39 all						0.39 all					
Retention index	0.61	0.59	0.60	0.59	0.59	0.59	0.58	0.58	0.58	0.56 all					
Rescaled consistency index	0.24	0.22	0.23	0.23 all						0.22 all					
No. of trees	1	1	1	6						6					

Table 4. Summary of cladograms analysis made using microcomputer programs Henning 86 and CLADOS

[1] - cladograms based on characters, whose polarization with both criteria (outgroup and ontogenetic) was compatible.
[2] - cladograms based on characters polarized with Nelson criterion, with exclusion of characters, which could not be polarized according to either methods.
[3] - cladograms based on characters polarized according to outgroup comparison, with exclusion of characters that could not be polarized with ontogenetic criterion.
[4] - cladograms based on characters polarized according to ontogenetic criterion only.
[5] - cladograms based on characters polarized according to outgroup comparison only.

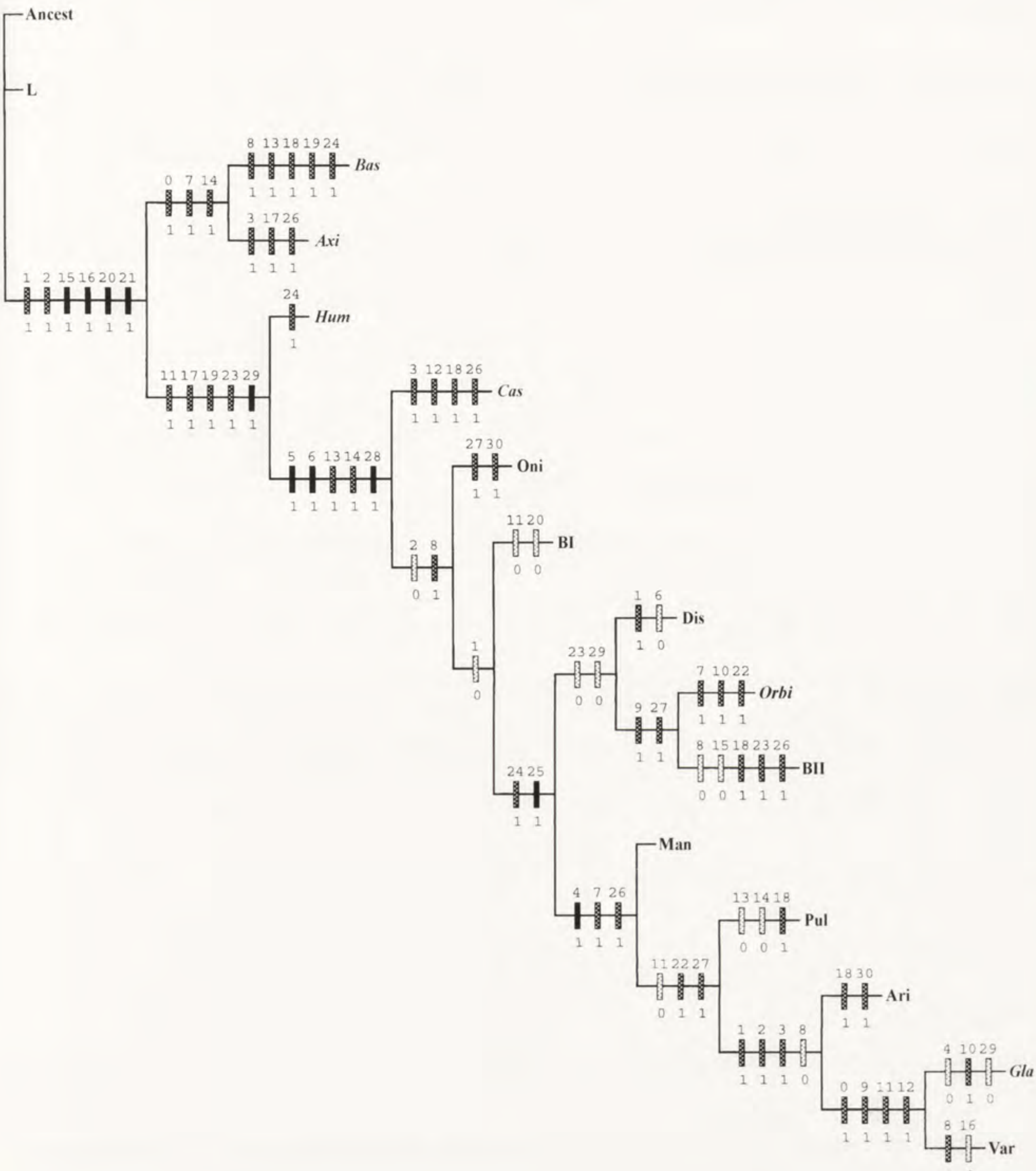


Figure I. Cladogram based on characters resolved with the same polarity by both methods (acronyms of species used in cladograms see page 142, members of *Anisotoma* in italics).

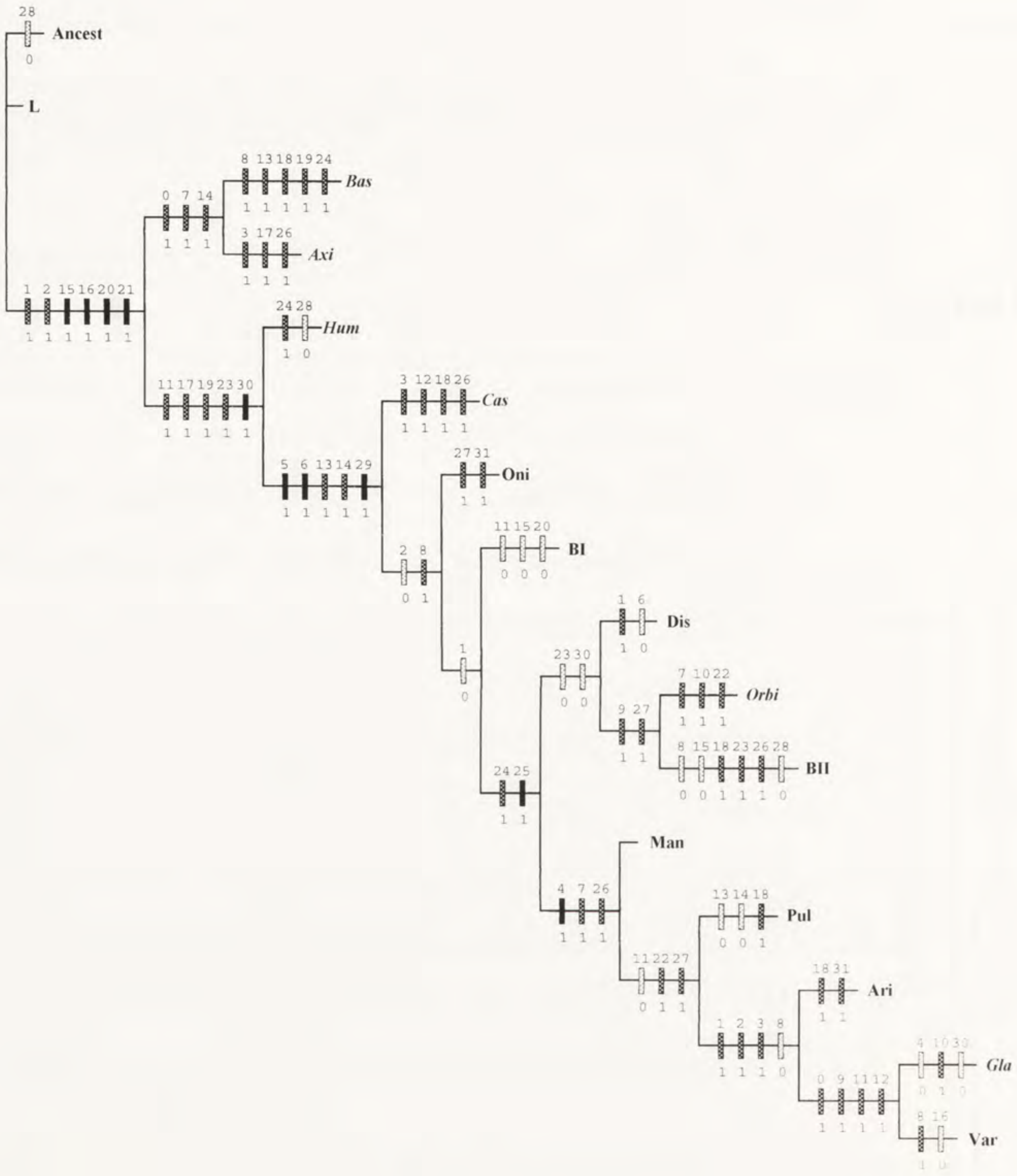


Figure II. Cladogram based on Nelson's Rule analysis of characters resolved by both methods.

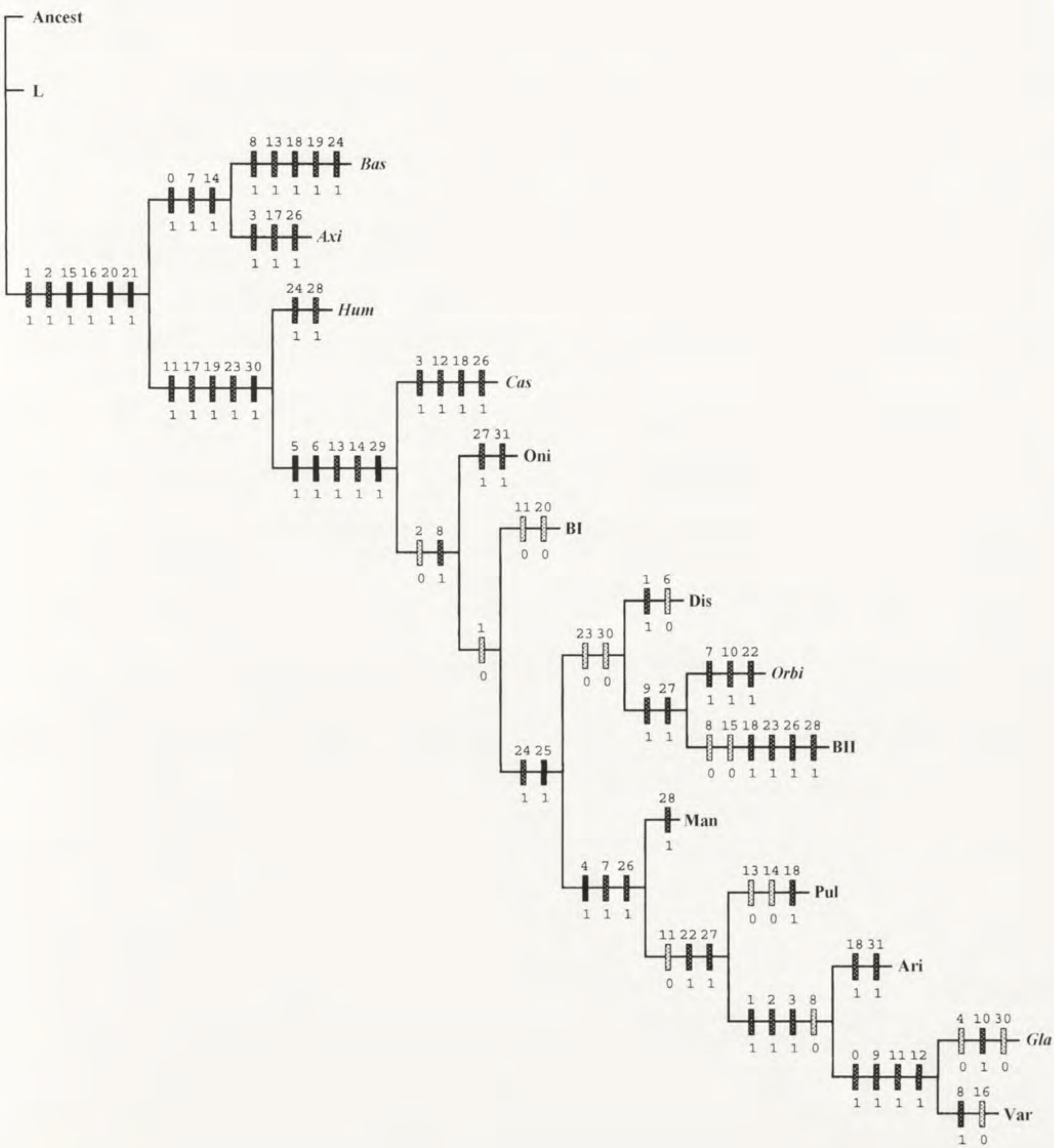


Figure III. Cladogram based on Outgroup Comparison Rule analysis of characters resolved by both methods.

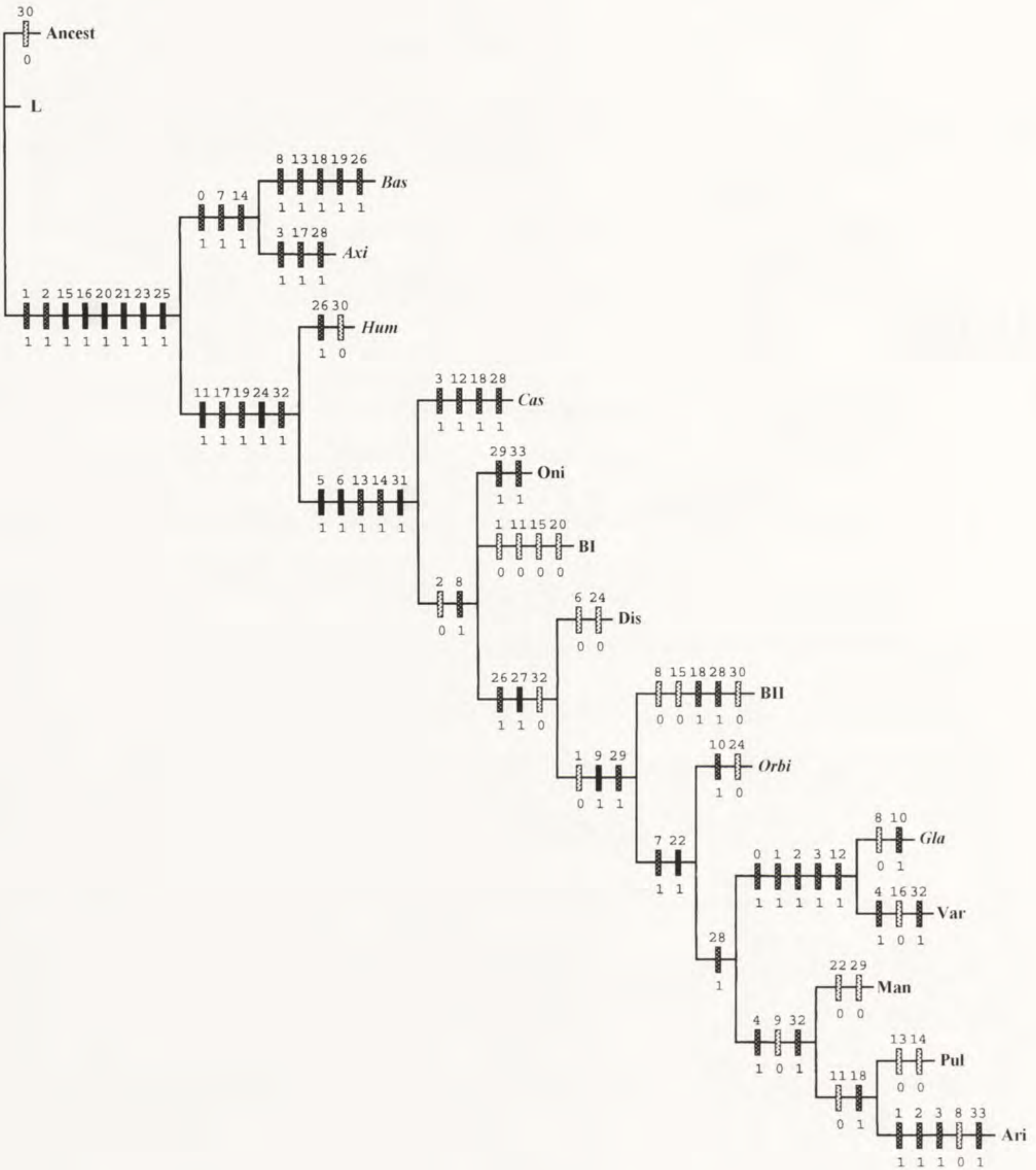


Figure IV. Cladogram based on Nelson's Rule data alone.

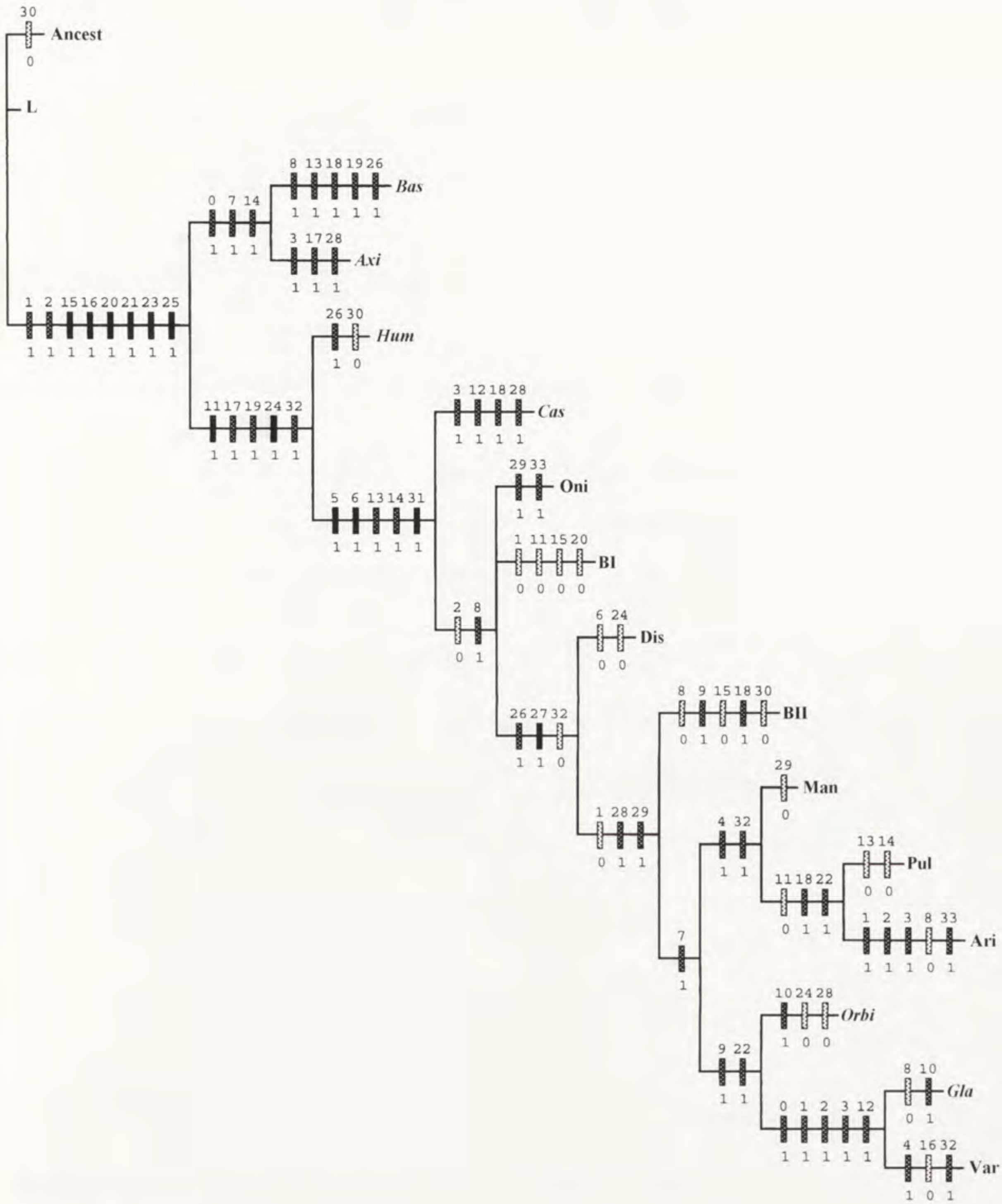


Figure V. Cladogram based on Nelson's Rule data alone.

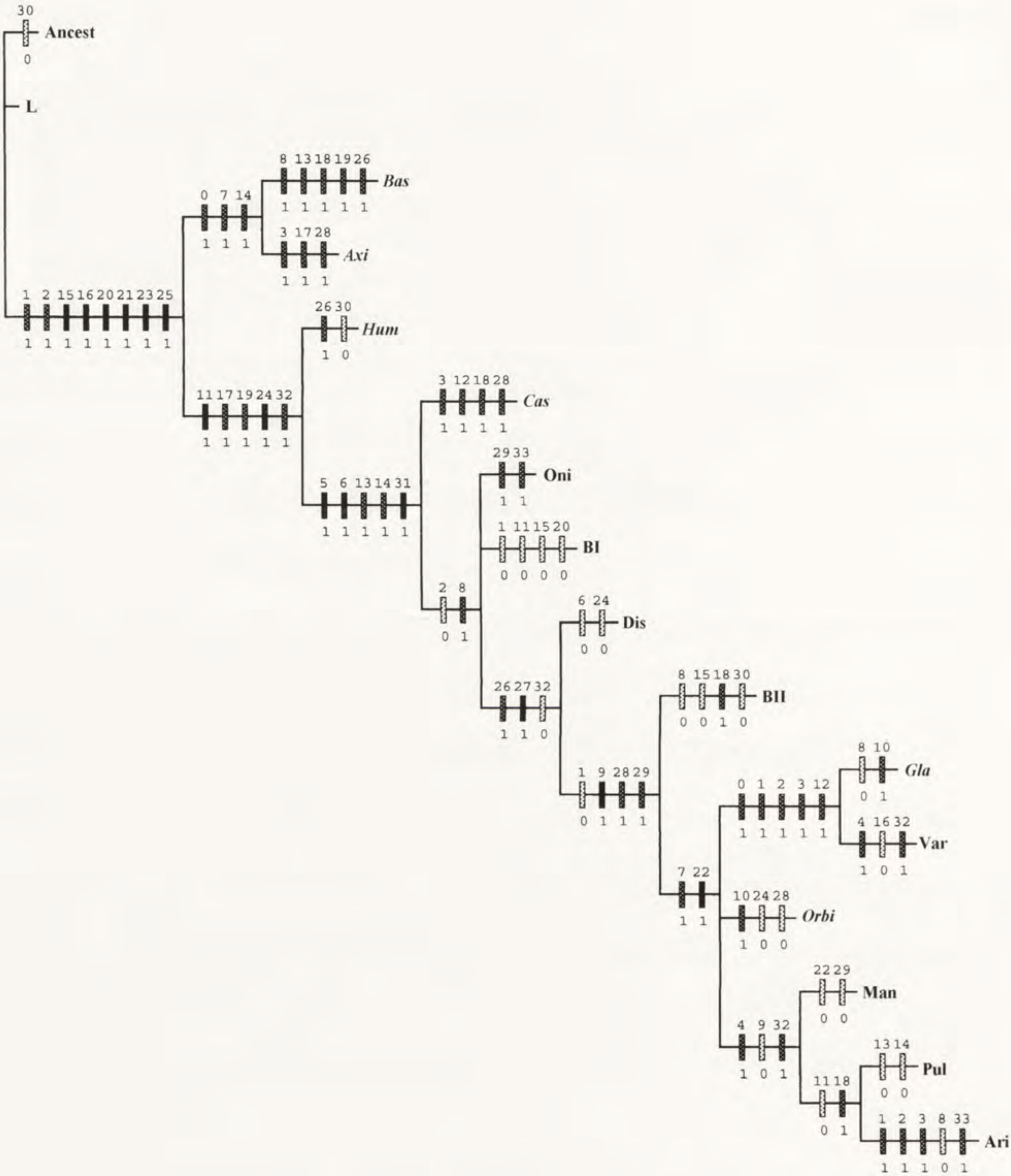


Figure VI. Cladogram based on Nelson's Rule data alone.

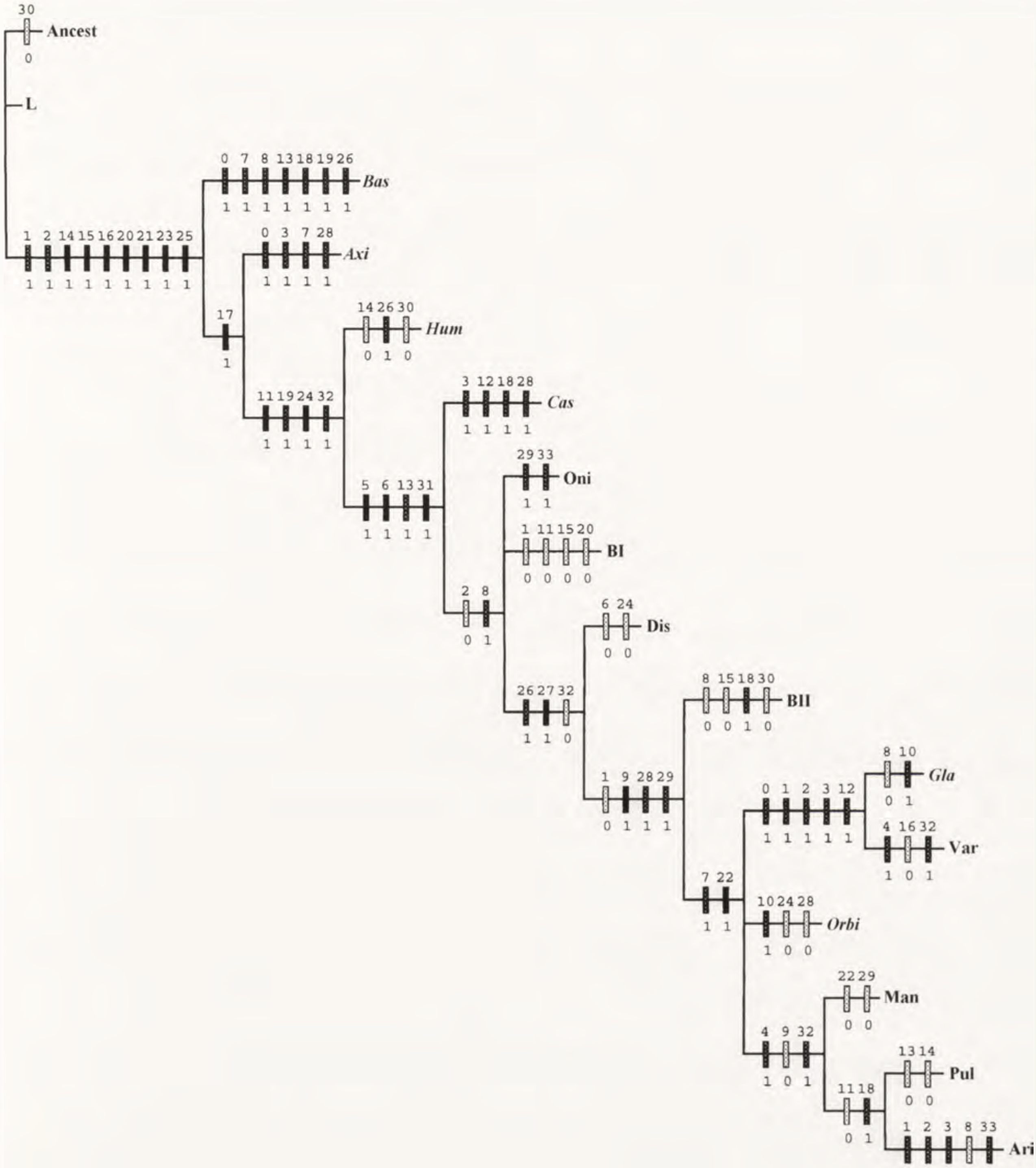


Figure VII. Cladogram based on Nelson's Rule data alone.

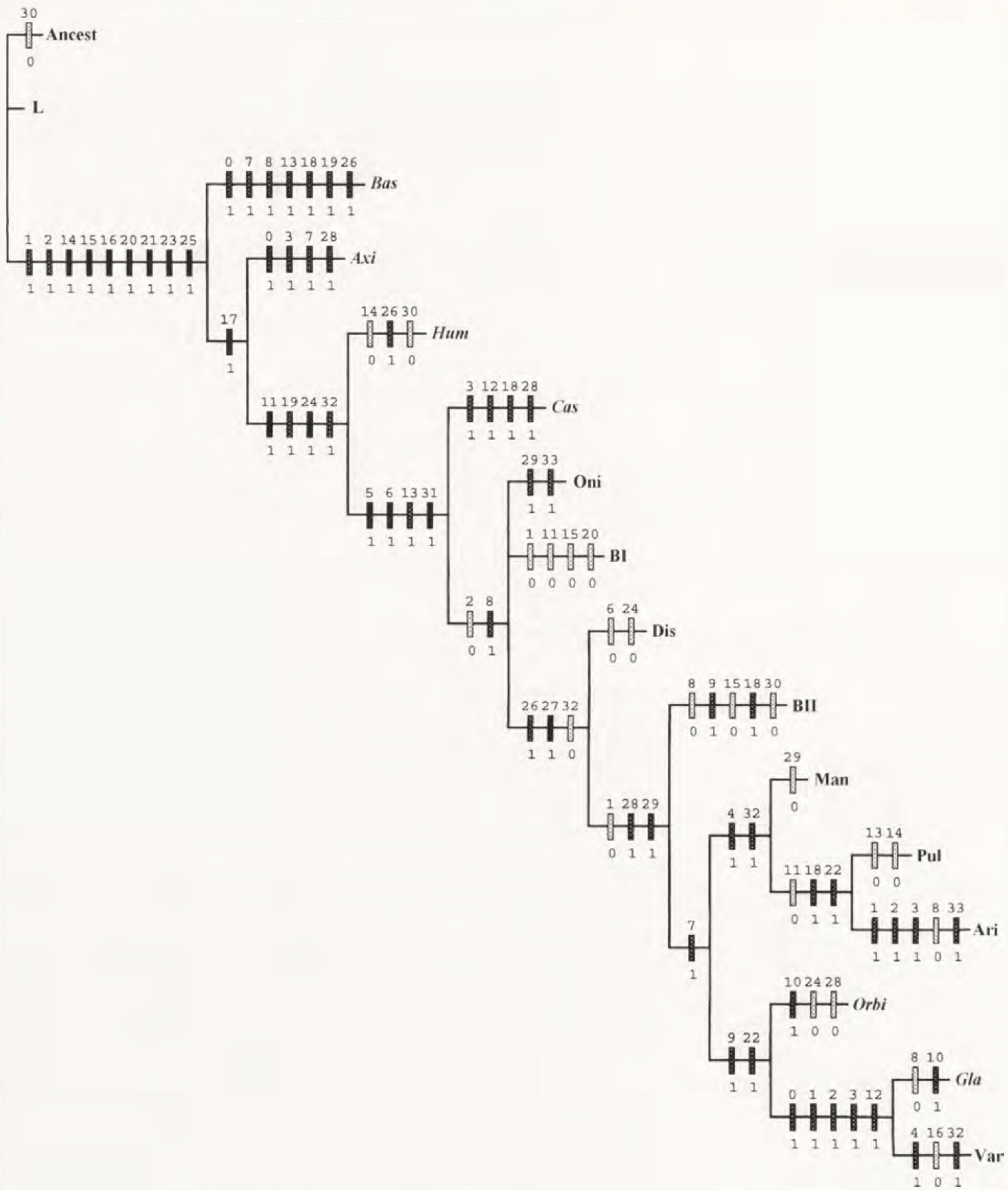


Figure VIII. Cladogram based on Nelson's Rule data alone.

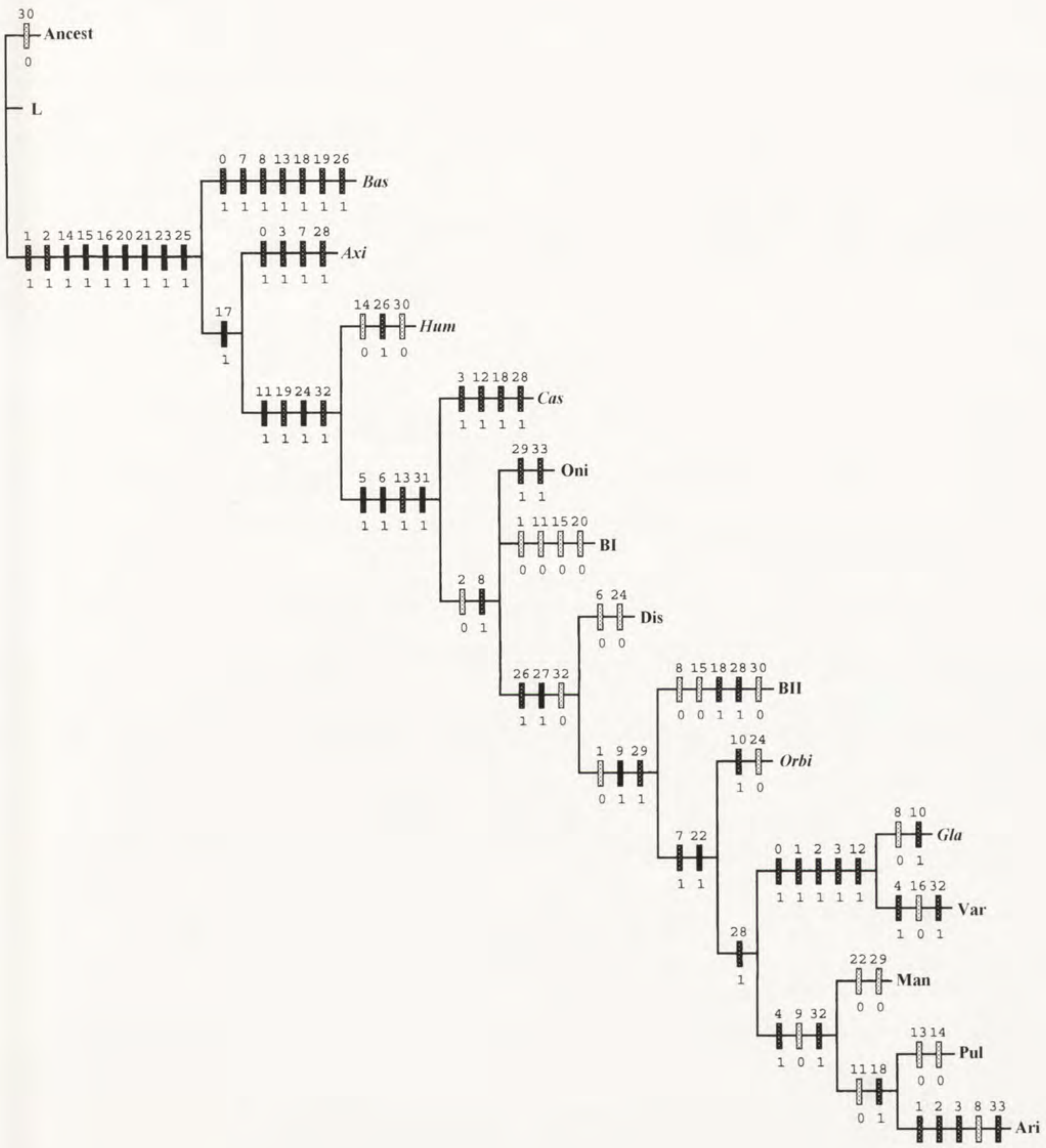


Figure IX. Cladogram based on Nelson's Rule data alone.

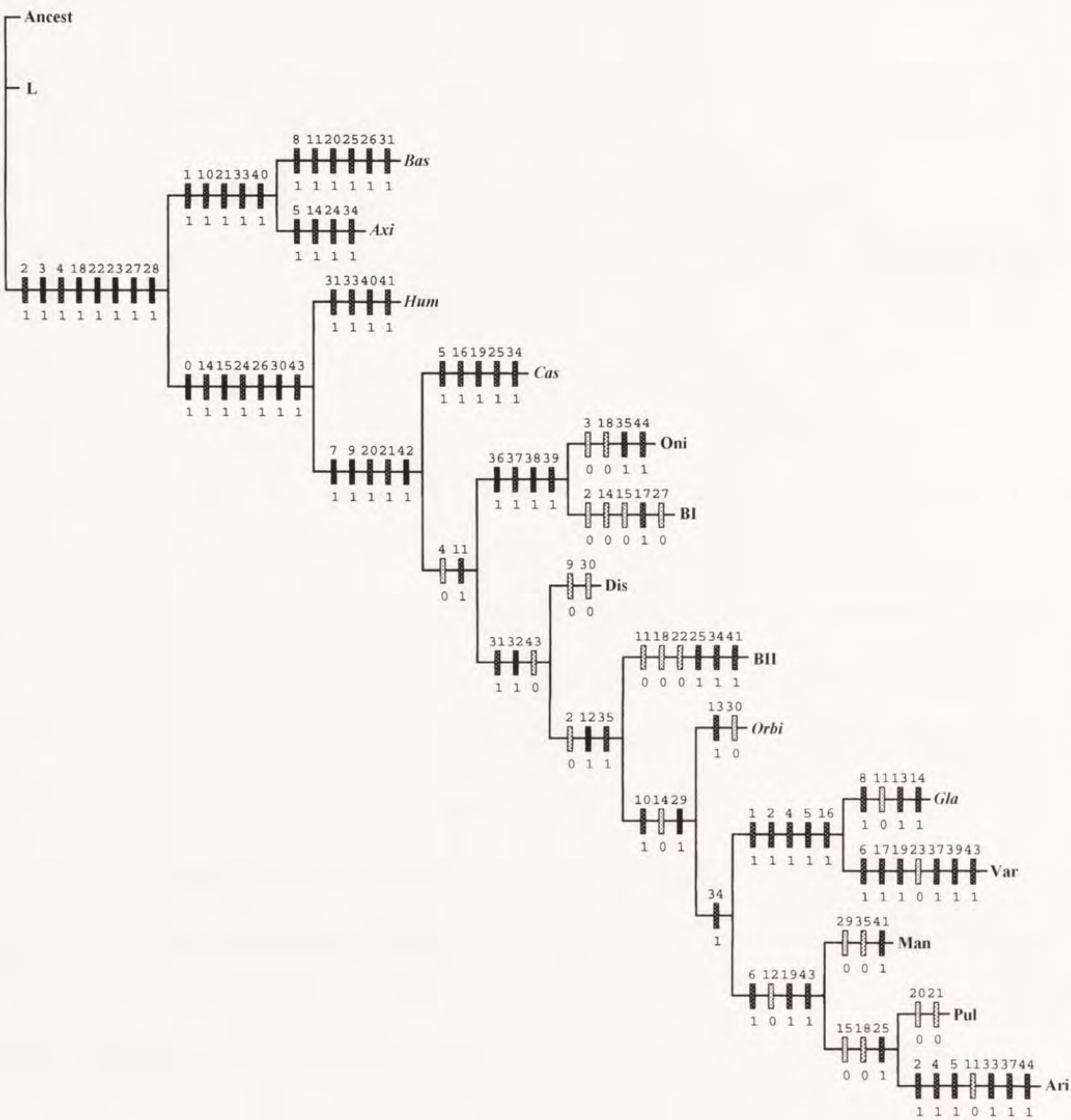


Figure X. Cladogram based on Outgroup Comparison Rule data alone.

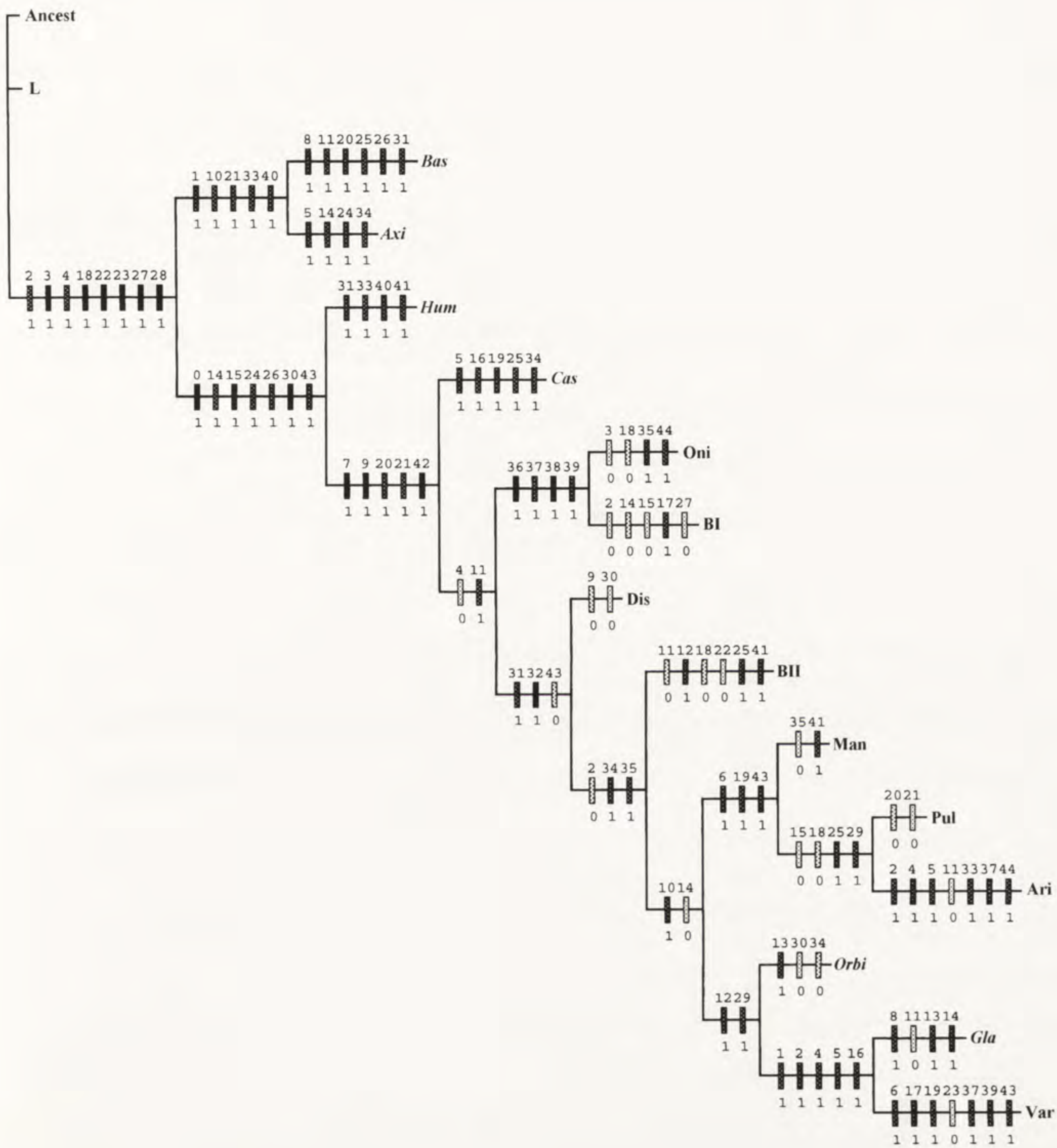


Figure XI. Cladogram based on Outgroup Comparison Rule data alone.

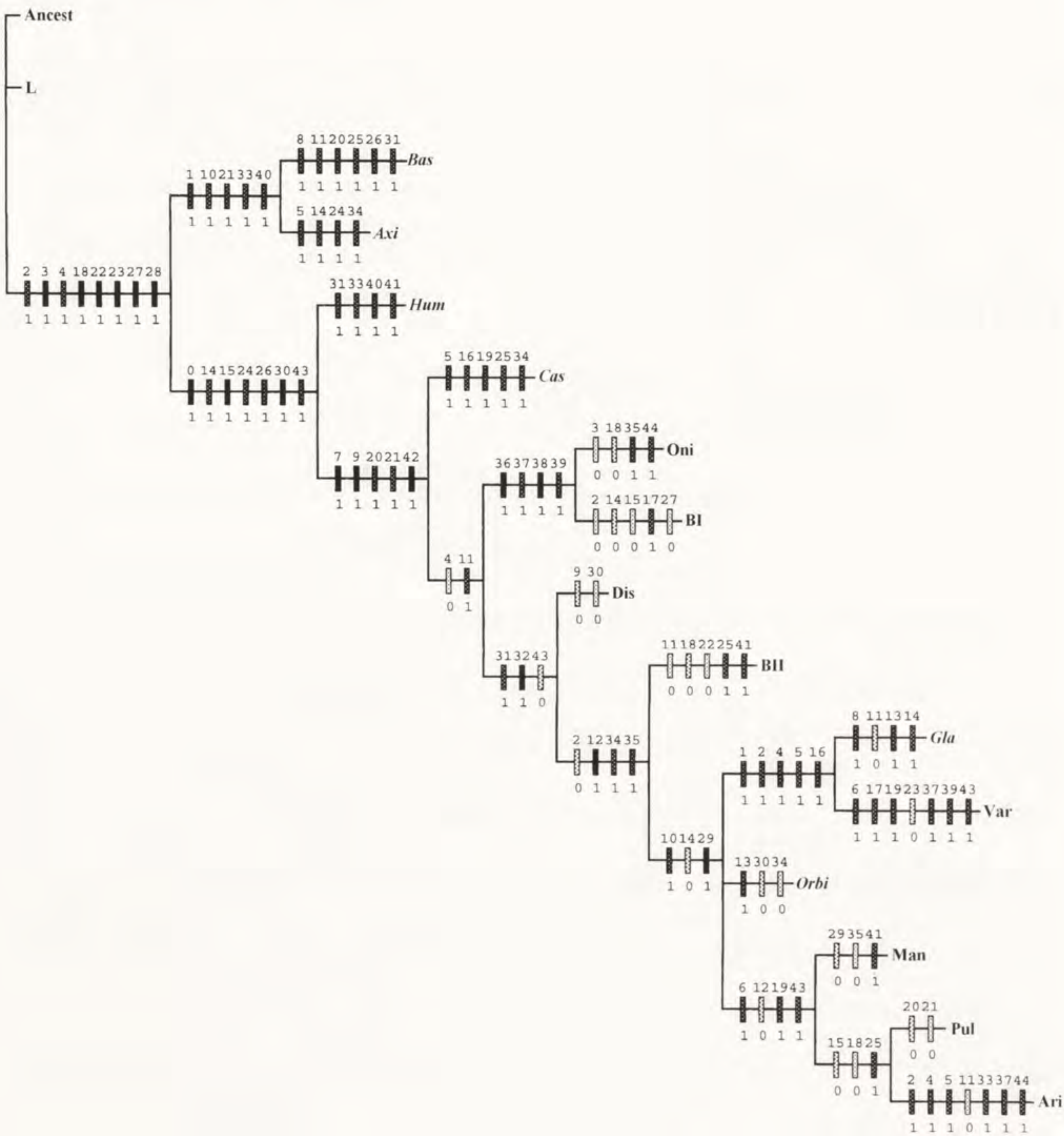


Figure XII. Cladogram based on Outgroup Comparison Rule data alone.

Figure XIII. Cladogram based on Outgroup Comparison Rule data alone.

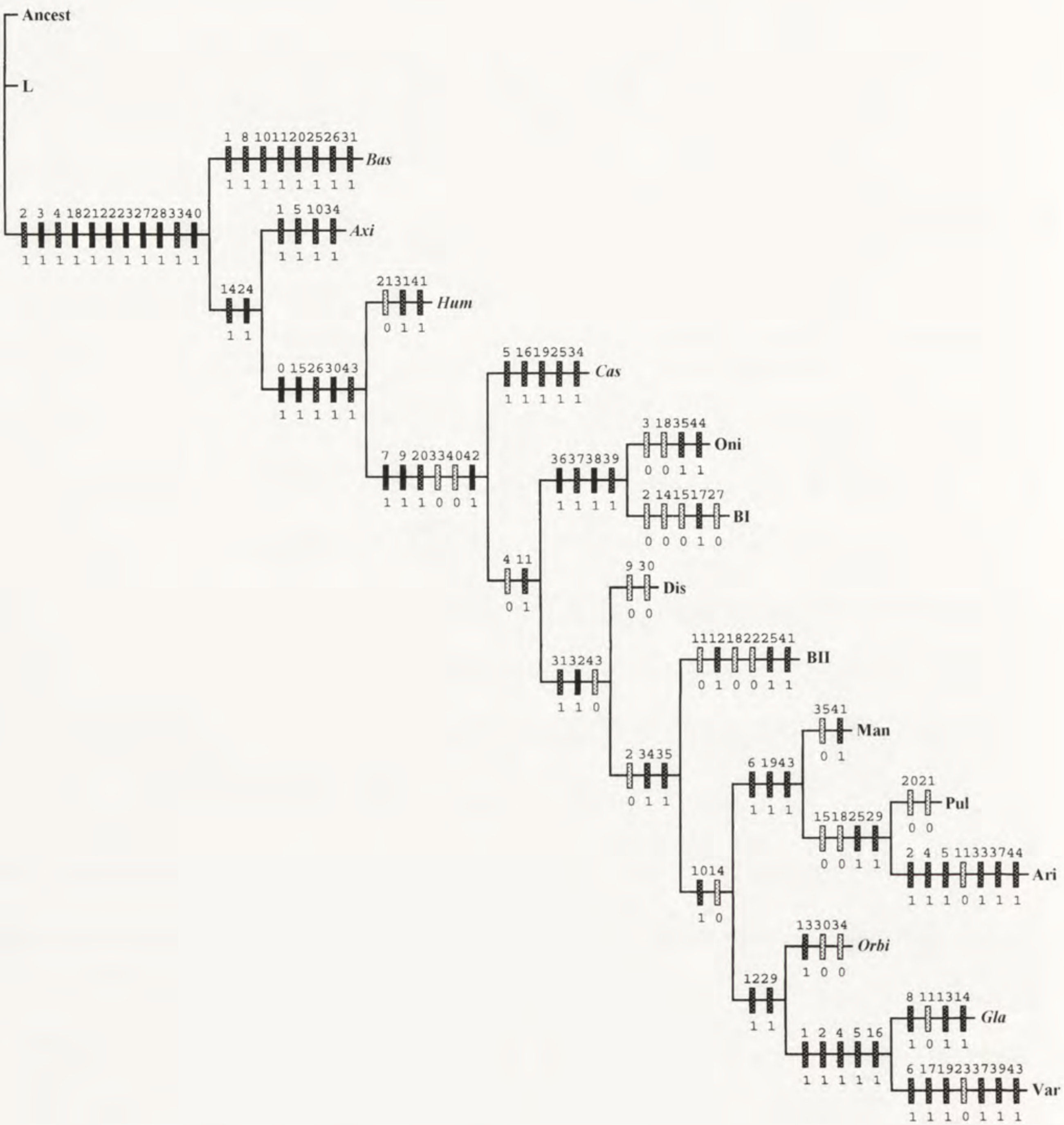


Figure XIV. Cladogram based on Outgroup Comparison Rule data alone.

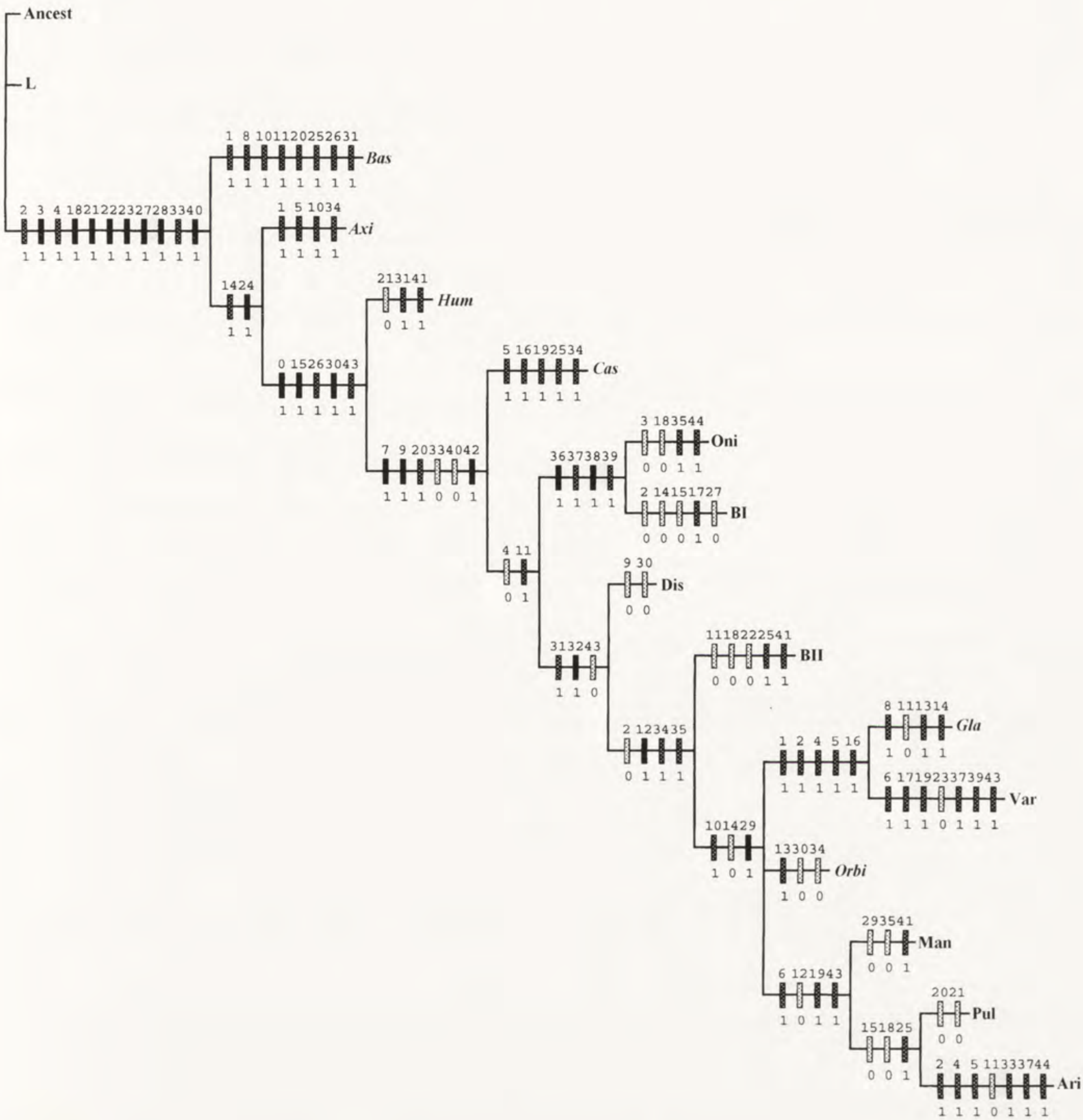
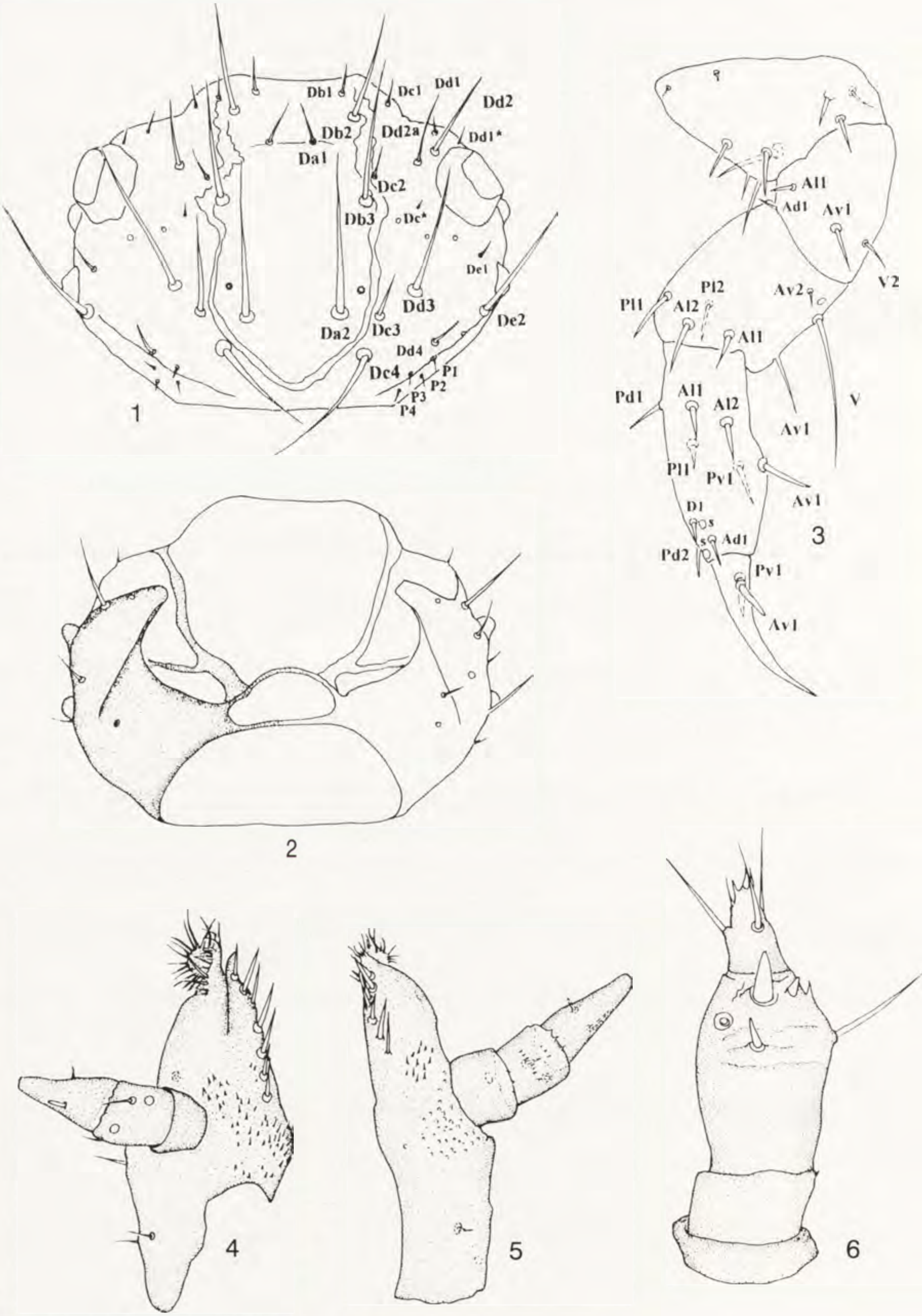
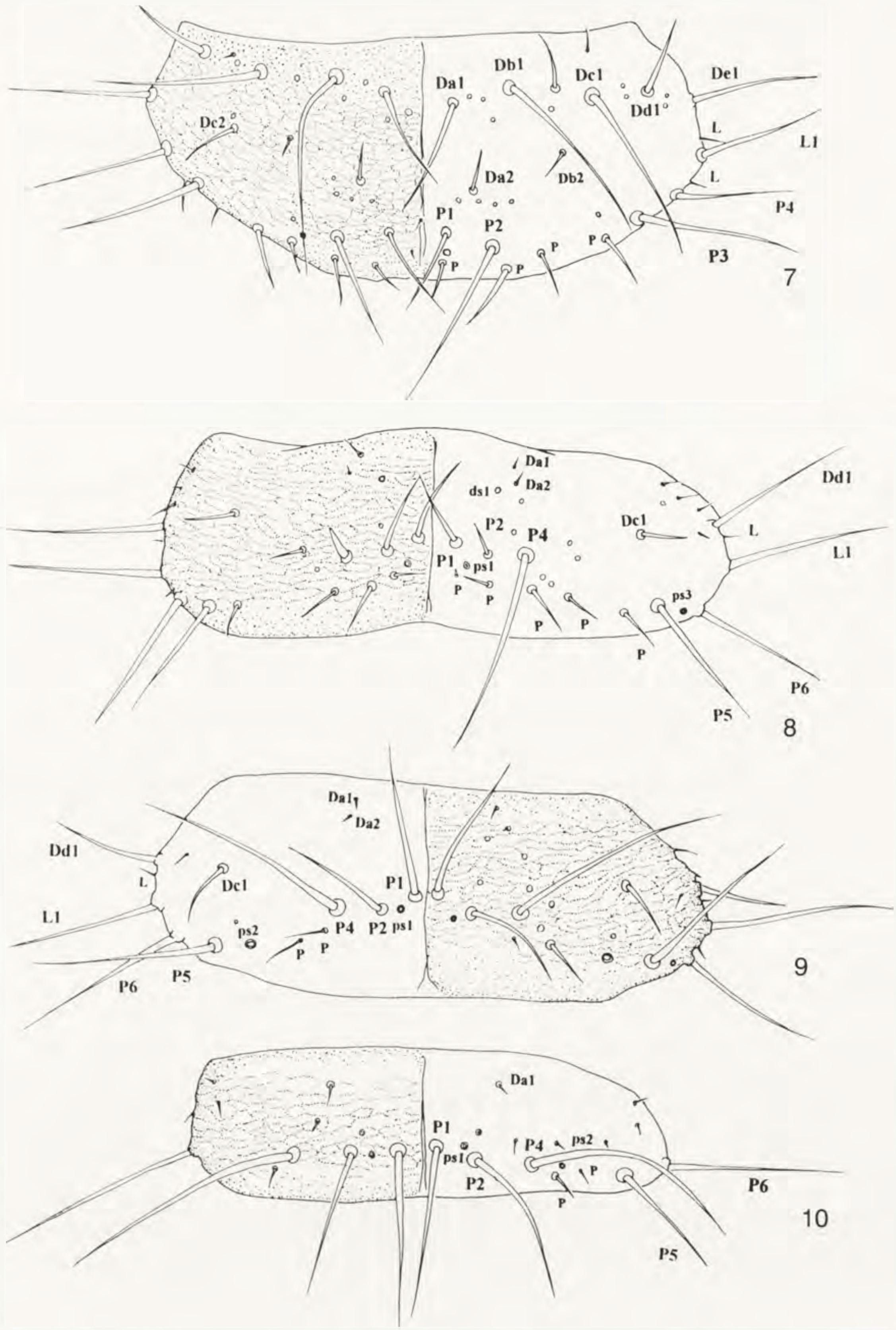


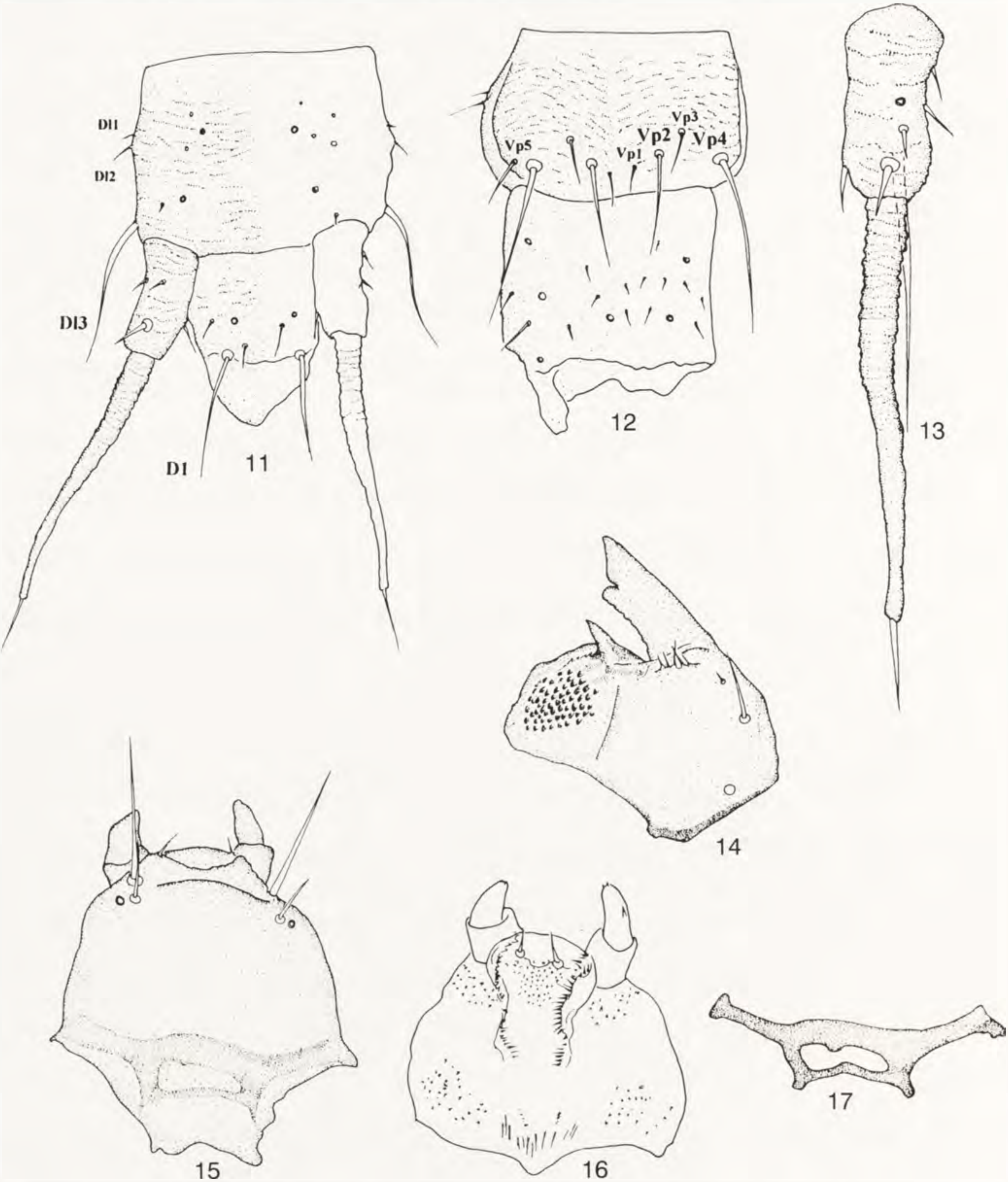
Figure XV. Cladogram based on Outgroup Comparison Rule data alone.



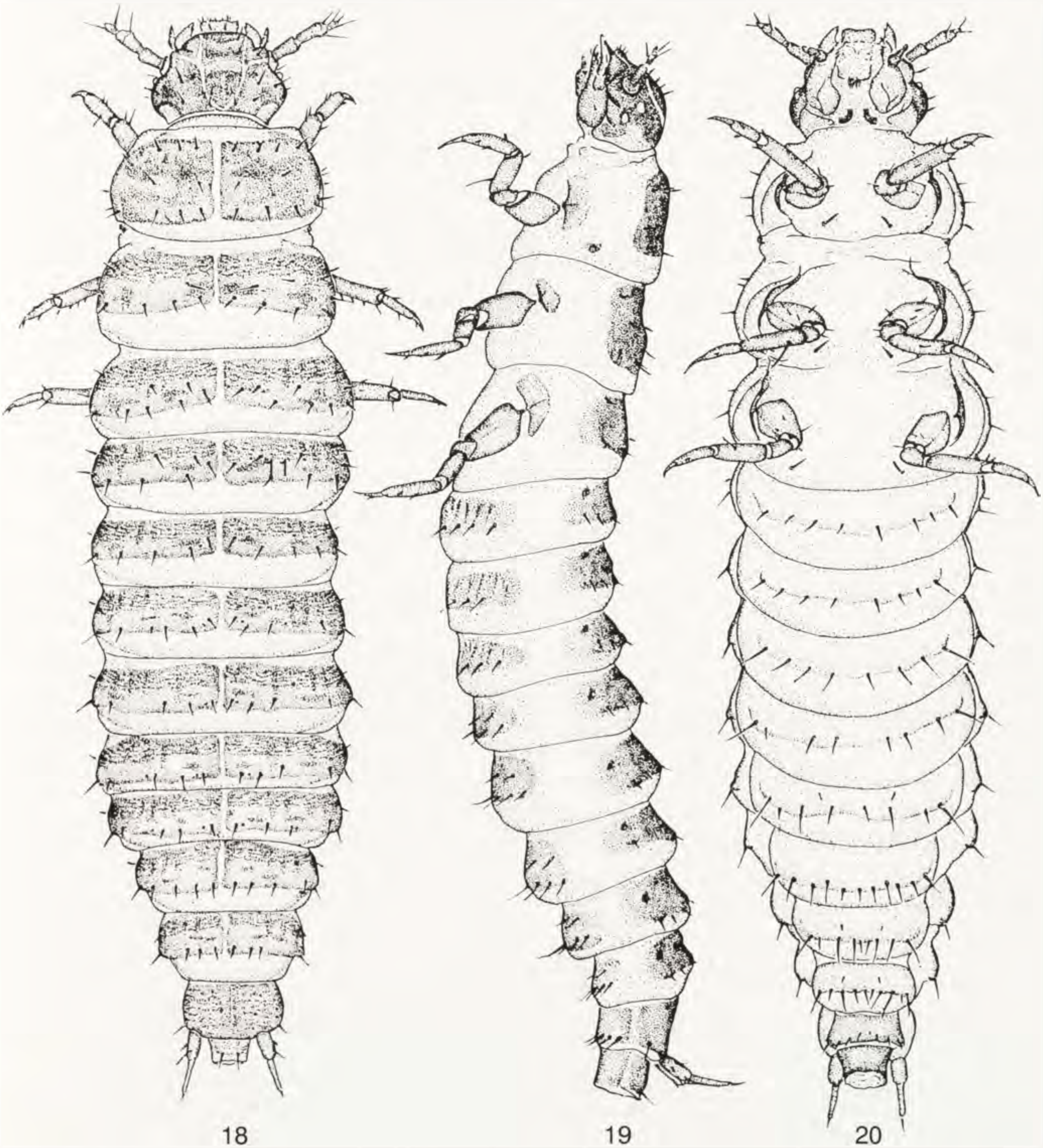
Figures 1–6. *Anisotoma orbicularis*, instar I. (1) dorsal and (2) ventral view of head, (3) proleg, (4–5) maxilla, (6) antenna.



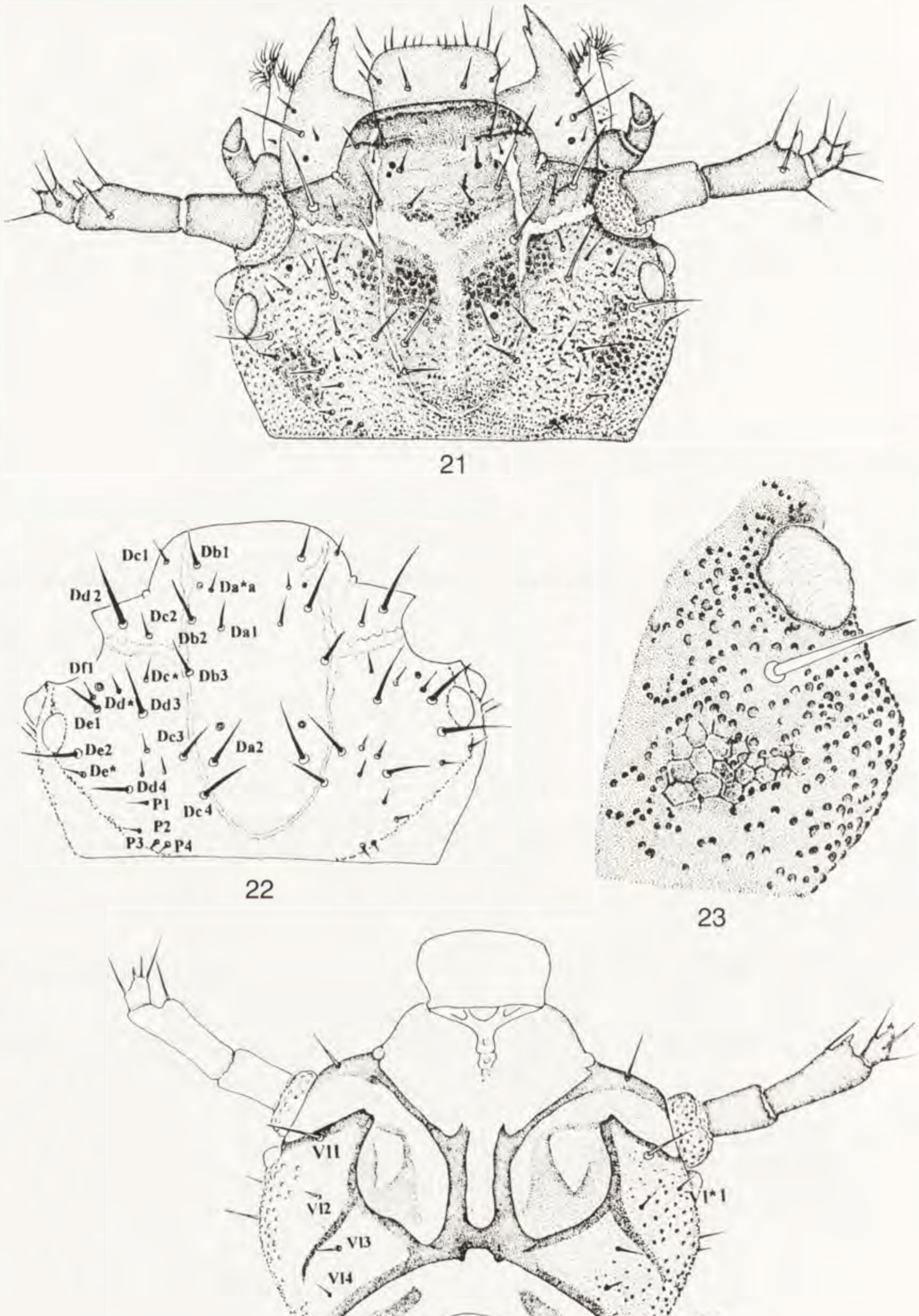
Figures 7–10. *Anisotoma orbicularis*, instar I. (7) pronotum, (8) mesonotum, (9) metanotum, (10) abdominal segment I.



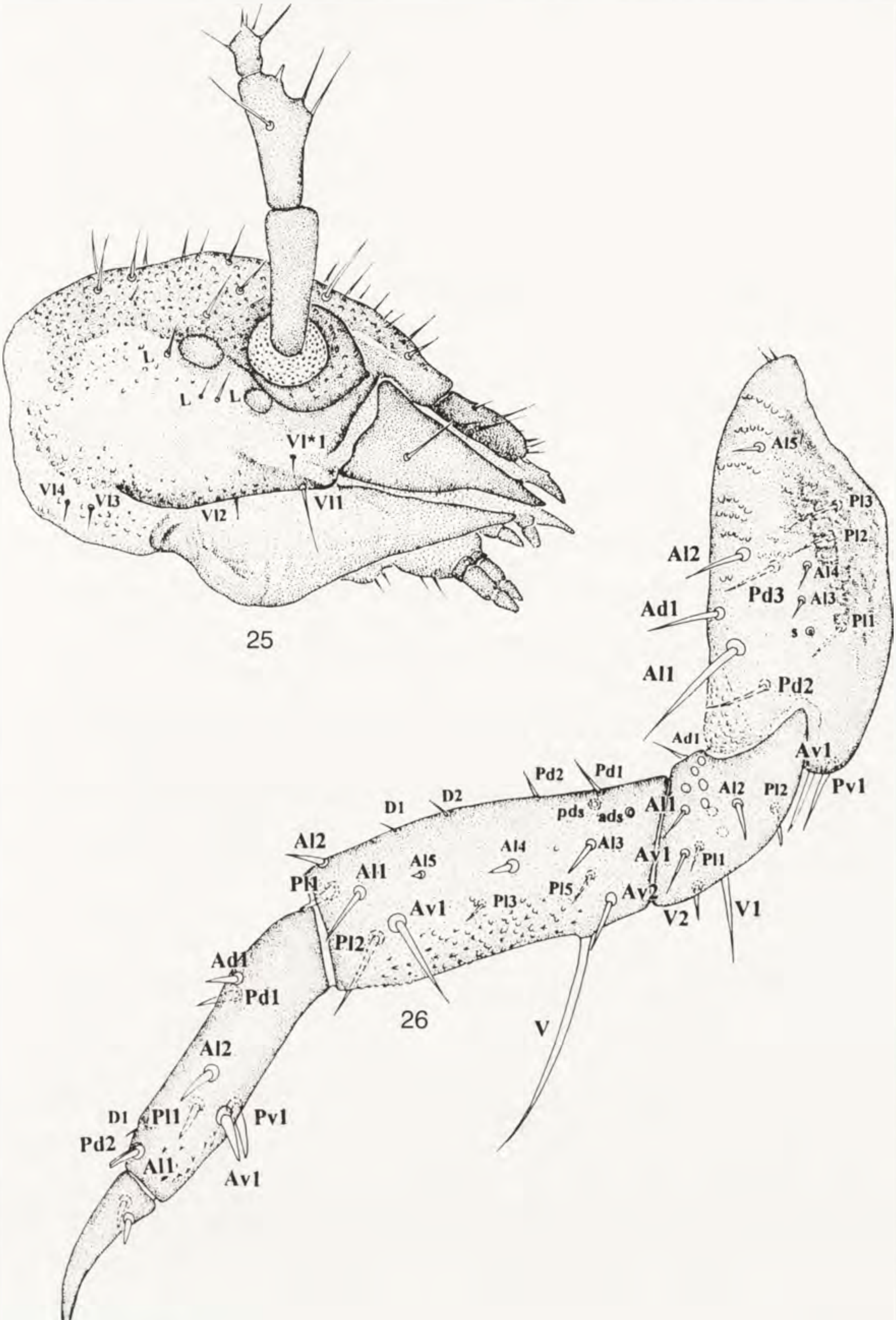
Figures 11–17. *Anisotoma orbicularis*, instar I. (11) abdominal tergum IX, (12) abdominal sternum IX and anal membrane, (13) urogomphus, (14) mandible, (15) ventral and (16) dorsal view of labium, (17) hyphopharyngeal sclerome.



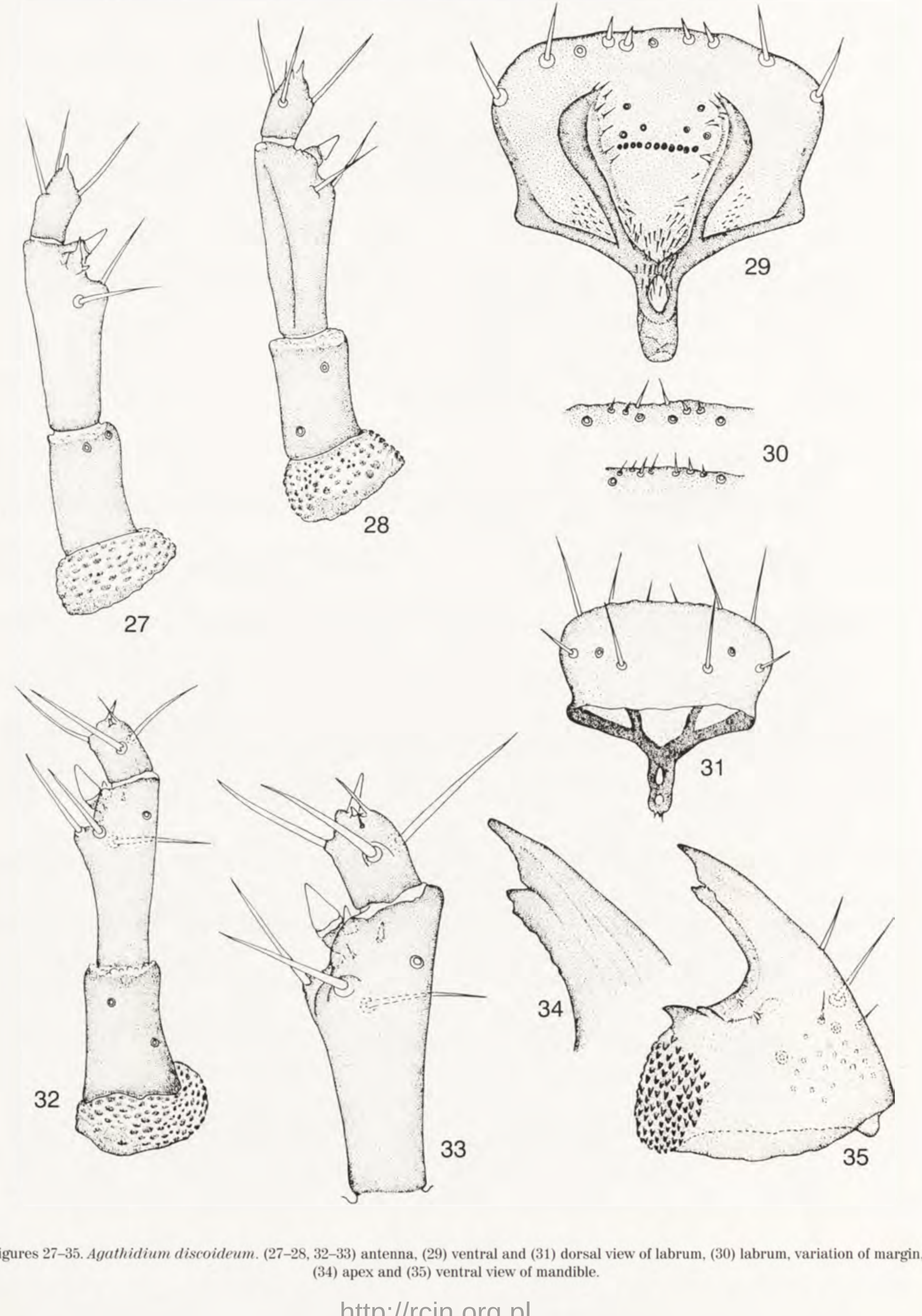
Figures 18–20. *Agathidium discoideum*. (18) dorsal, (19) lateral and (20) ventral view of larval habitus.



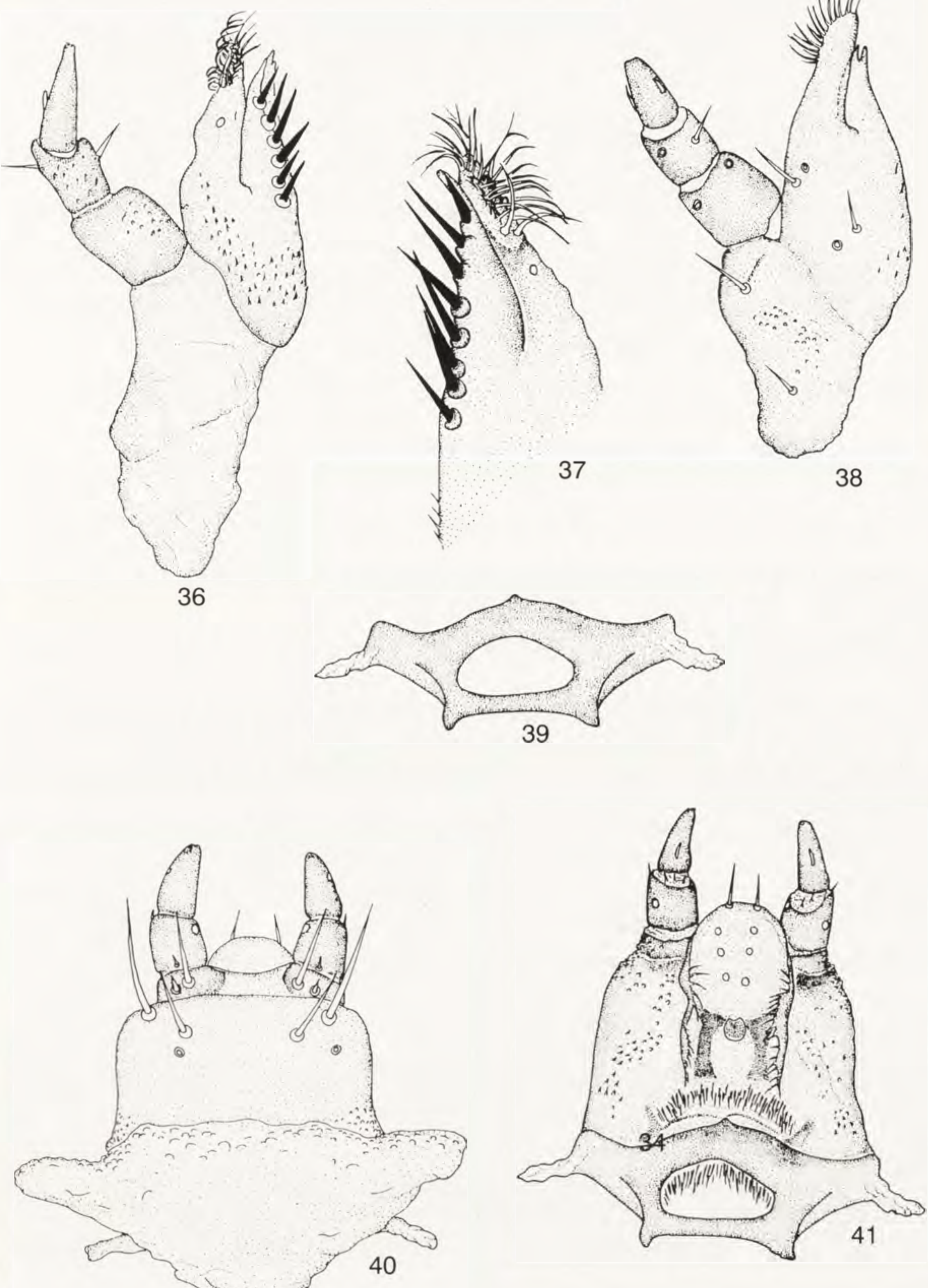
Figures 21–24. *Agathidium discoideum*. (21–23) dorsal and (24) ventral view of head.



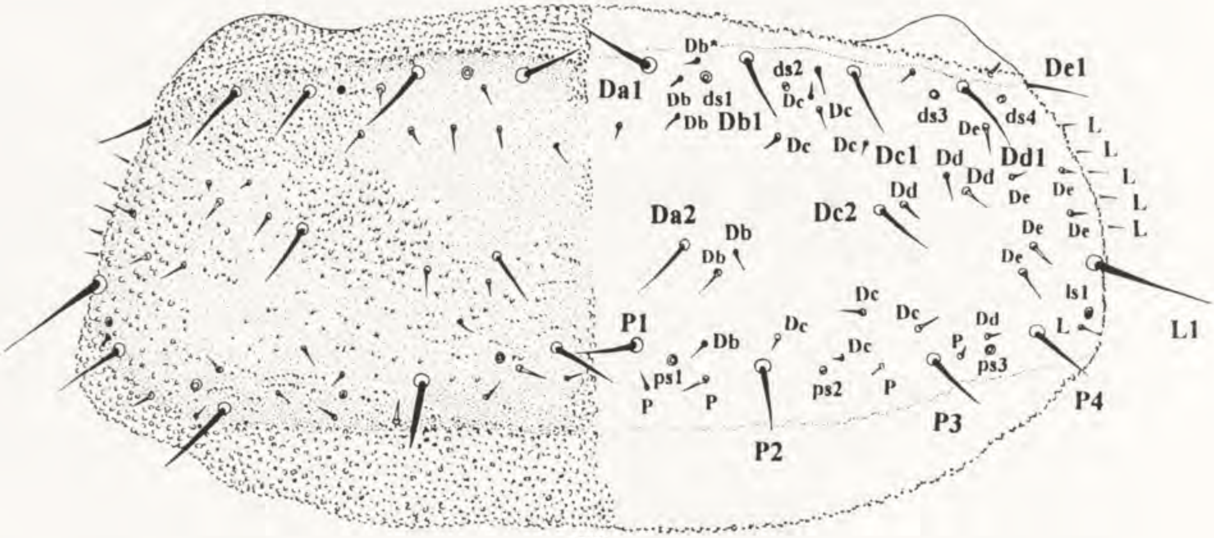
Figures 25–26. *Agathidium discoideum*. (25) lateral view of head, (26) proleg.



Figures 27–35. *Agathidium discoideum*. (27–28, 32–33) antenna, (29) ventral and (31) dorsal view of labrum, (30) labrum, variation of margin, (34) apex and (35) ventral view of mandible.



Figures 36–41. *Agathidium discoideum*. (36–38) maxilla, (39) hyphopharyngeal sclerome, (40) ventral and (41) dorsal view of labrum.



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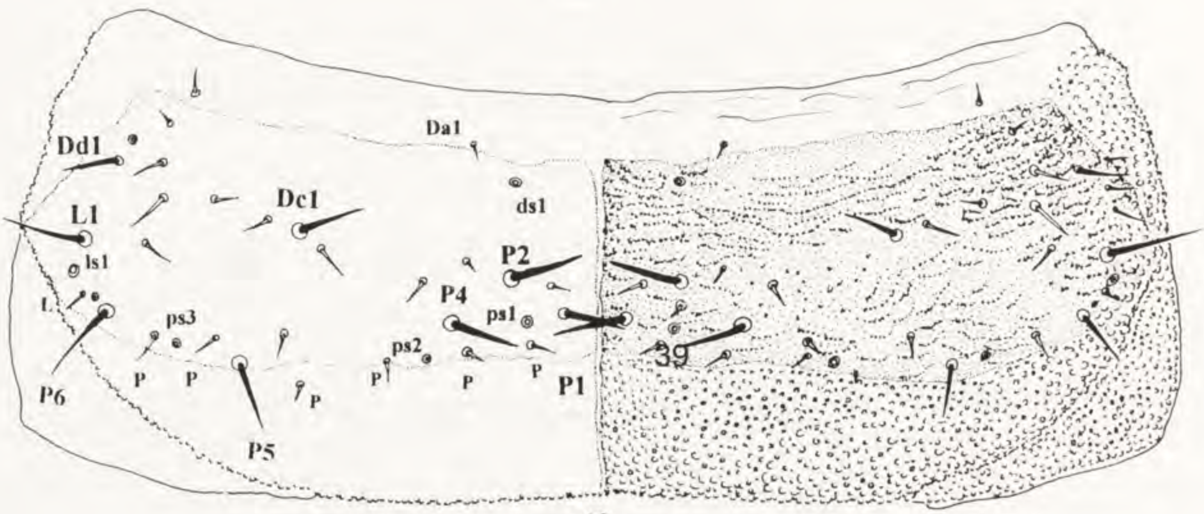

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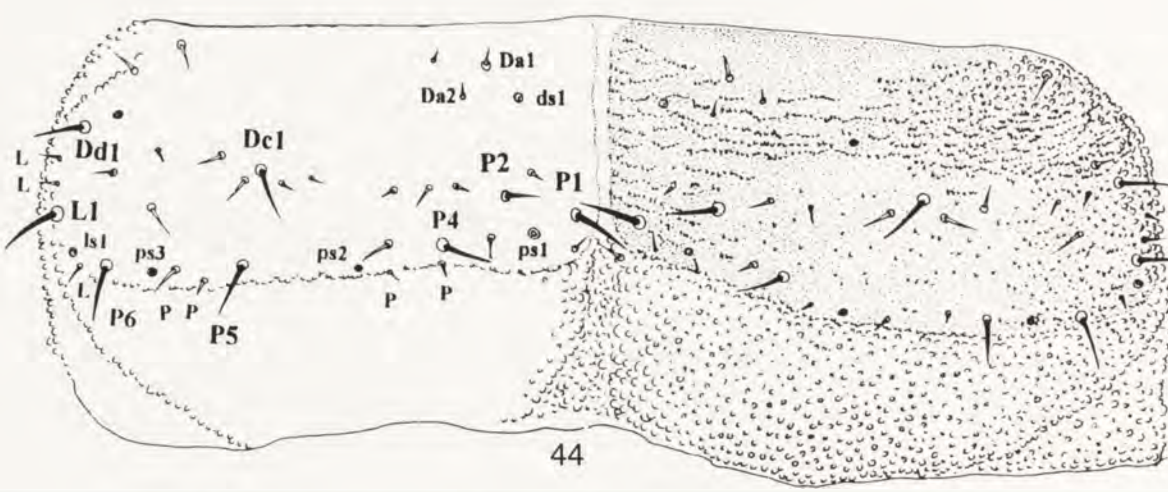

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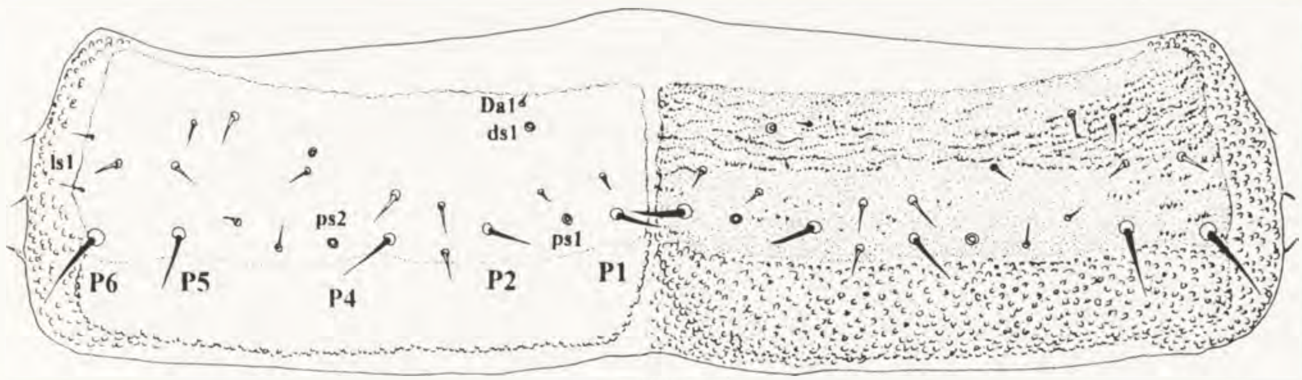
Figures 42–44. *Agathidium discoideum*. (42) pronotum, (43) mesonotum, (44) metanotum.



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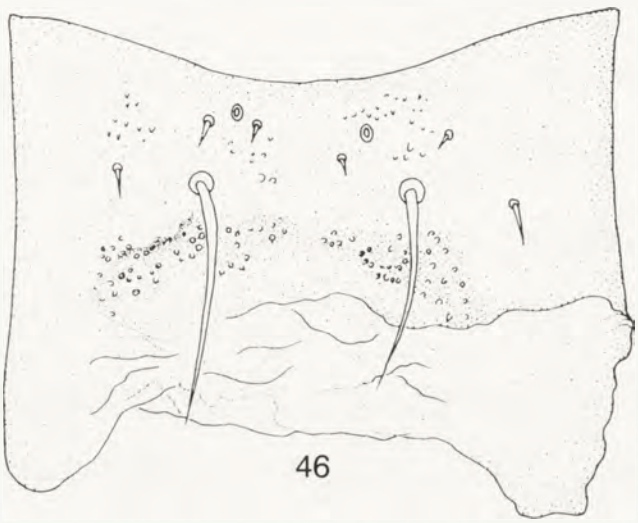

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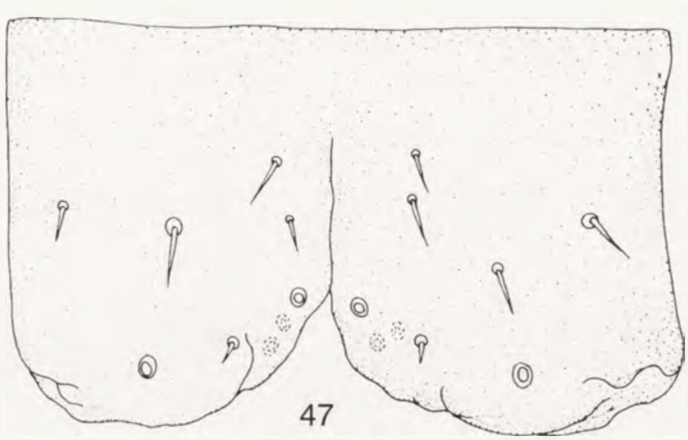

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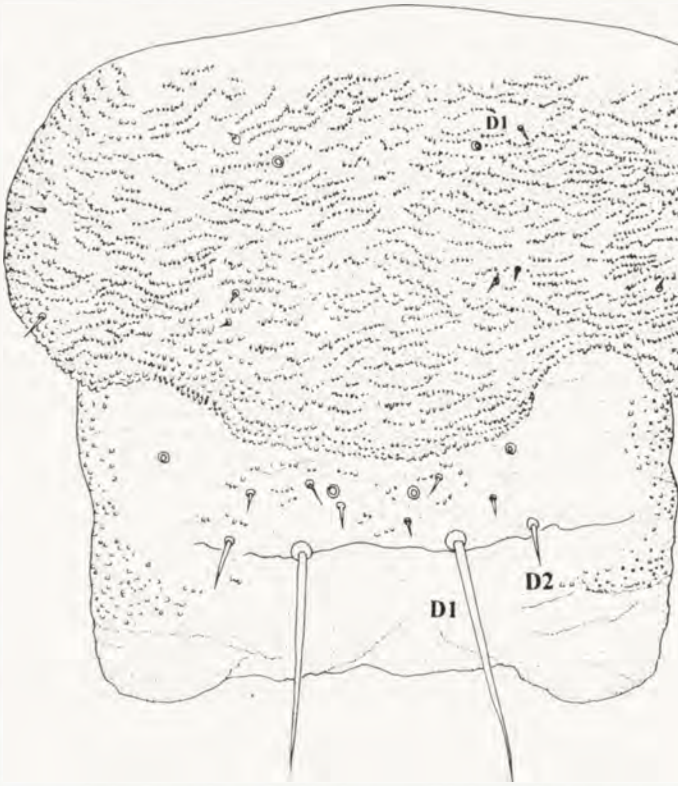
Figures 45–47. *Agathidium discoideum*. (45) abdominal segment I, (46) dorsal and (47) ventral view of anal membrane.



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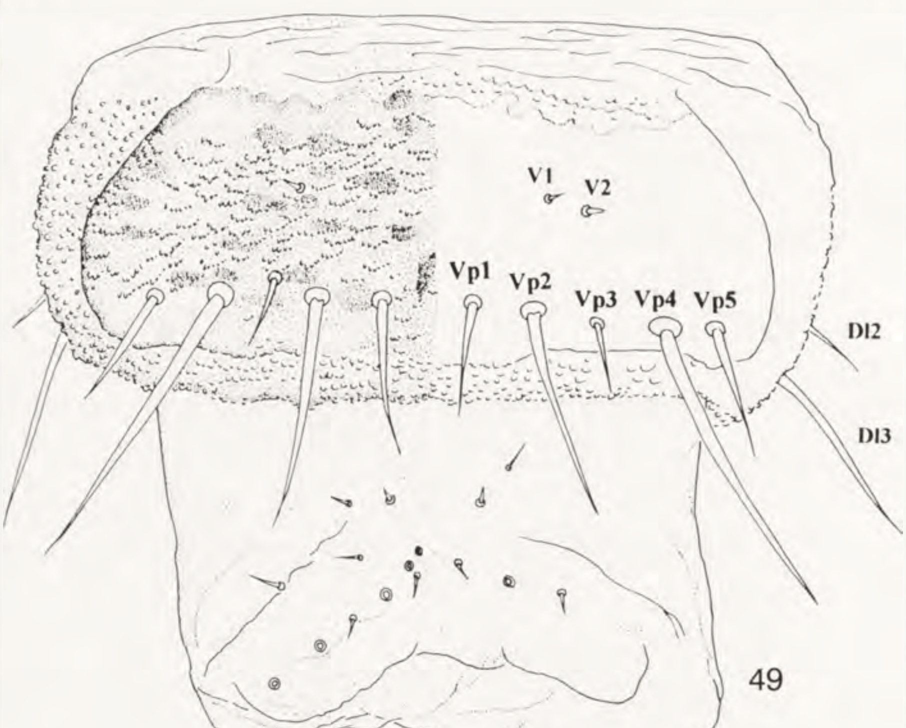

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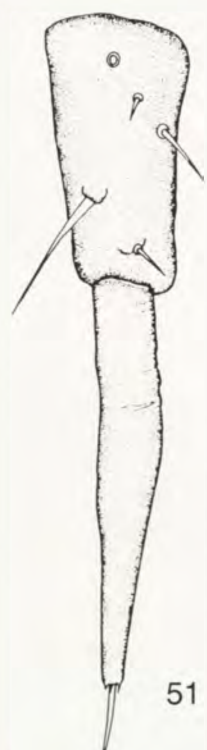

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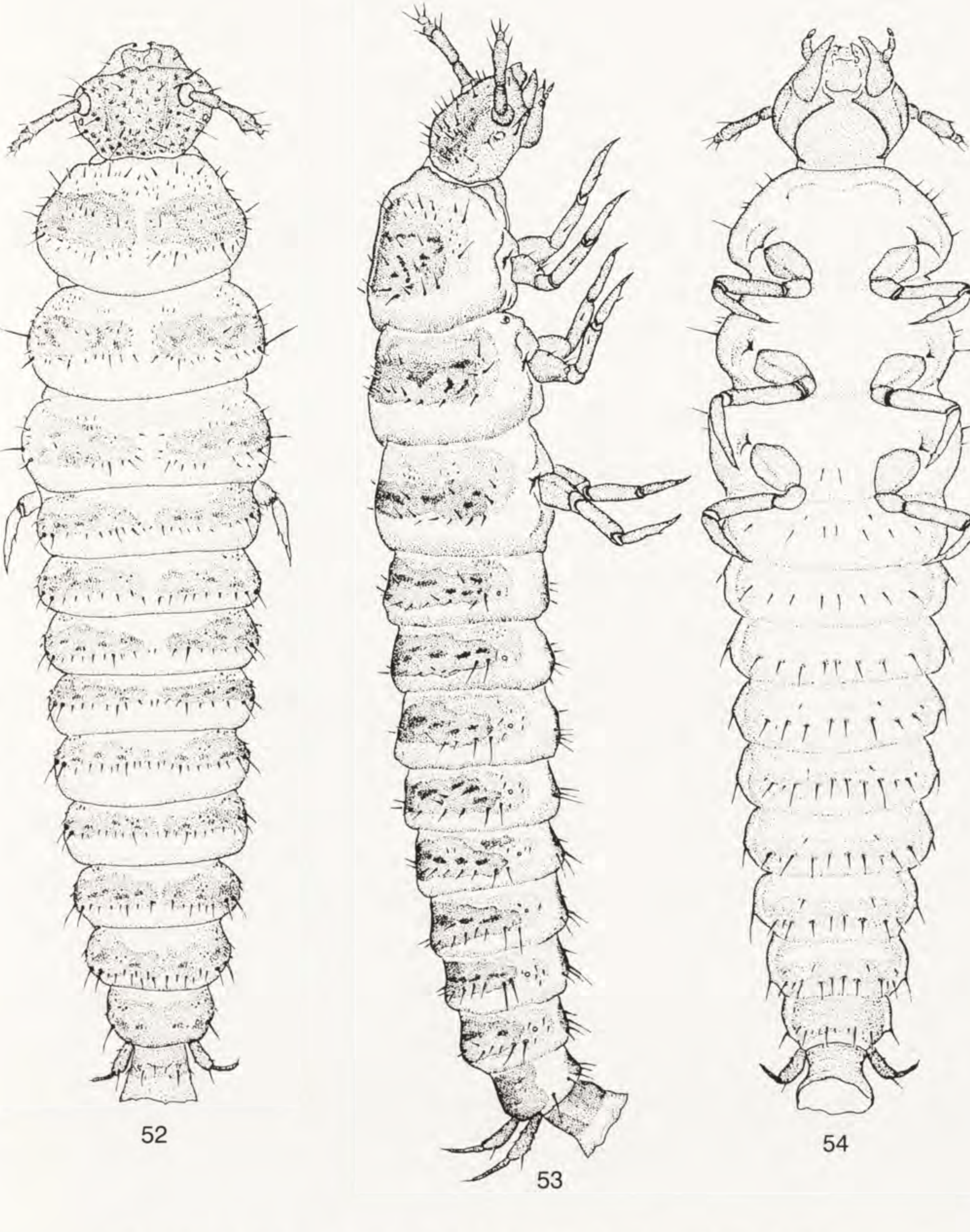
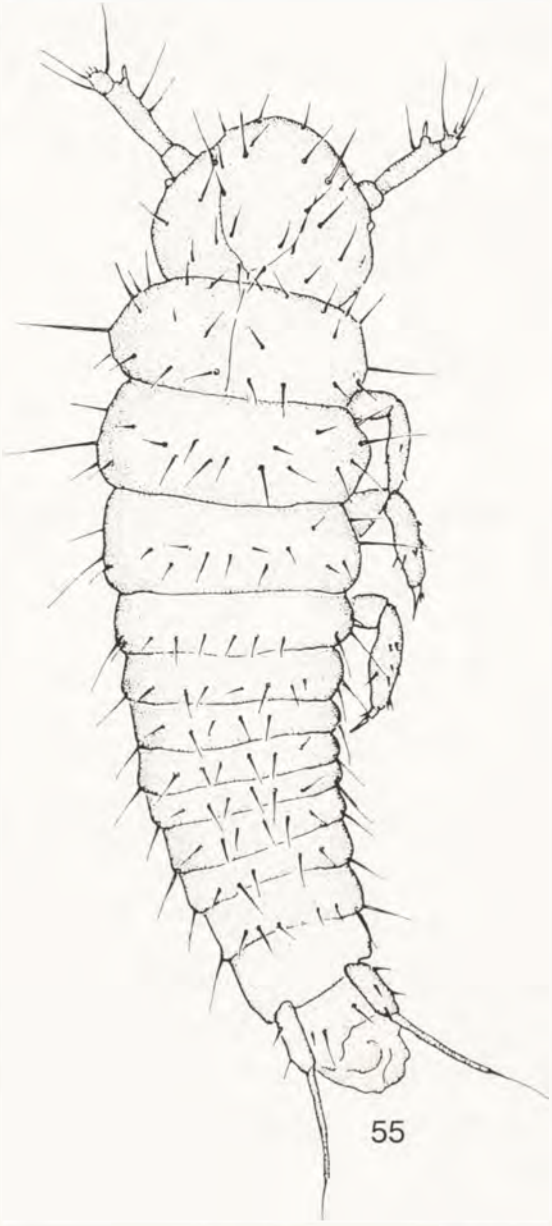
Figures 48–51. *Agathidium discoideum.* (48) abdominal tergum IX, (49) abdominal sternum IX, (50–51) urogomphus.



52 53 54

Figures 52–54. *Agathidium varians*, instar III. (52) dorsal, (53) lateral and (54) ventral view of larval habitus.



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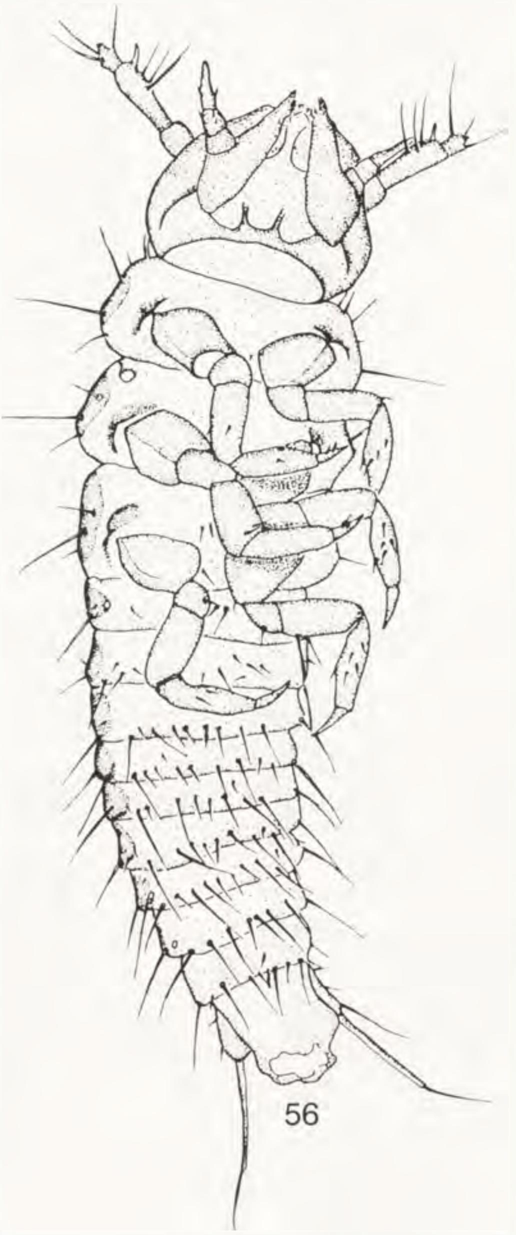

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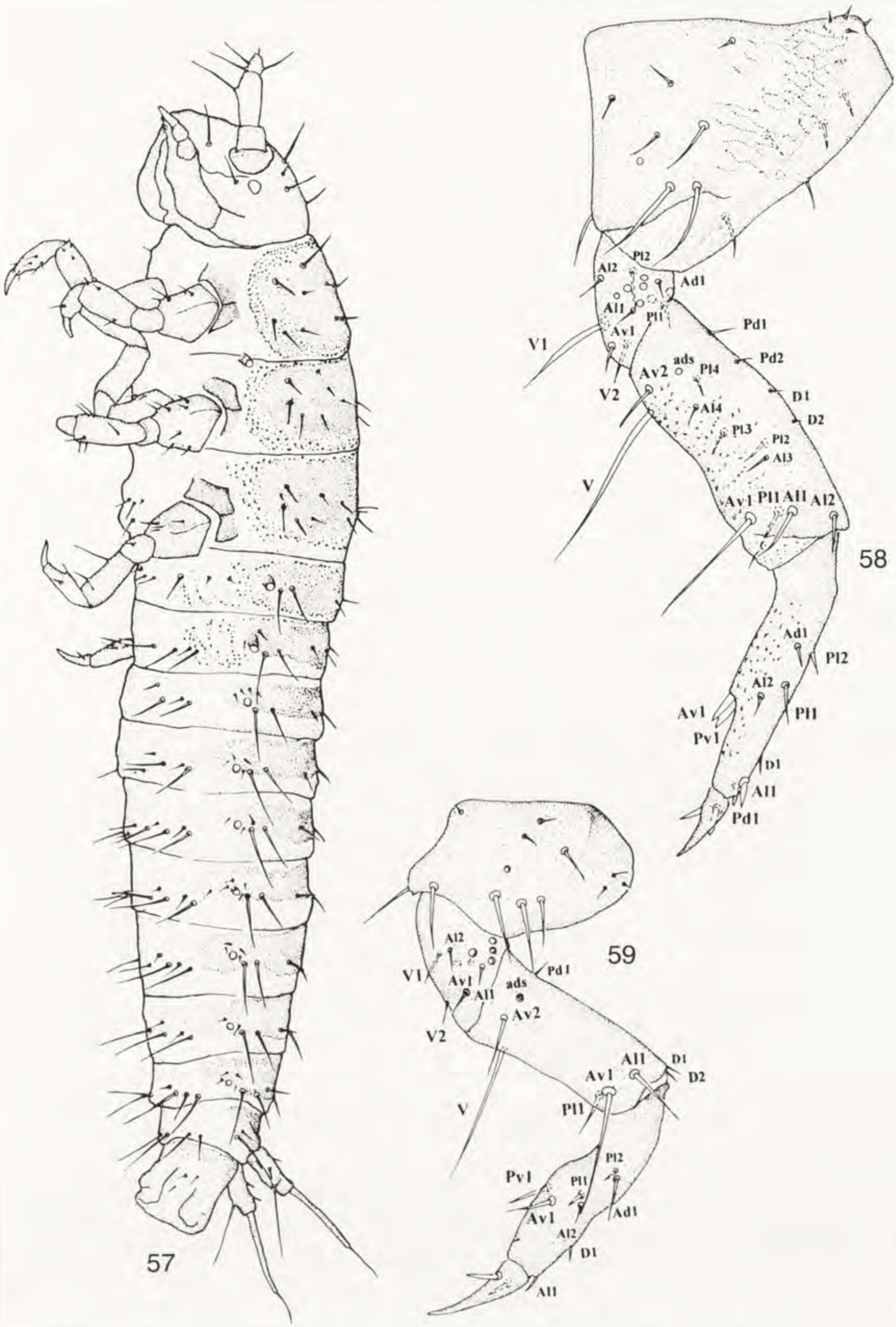
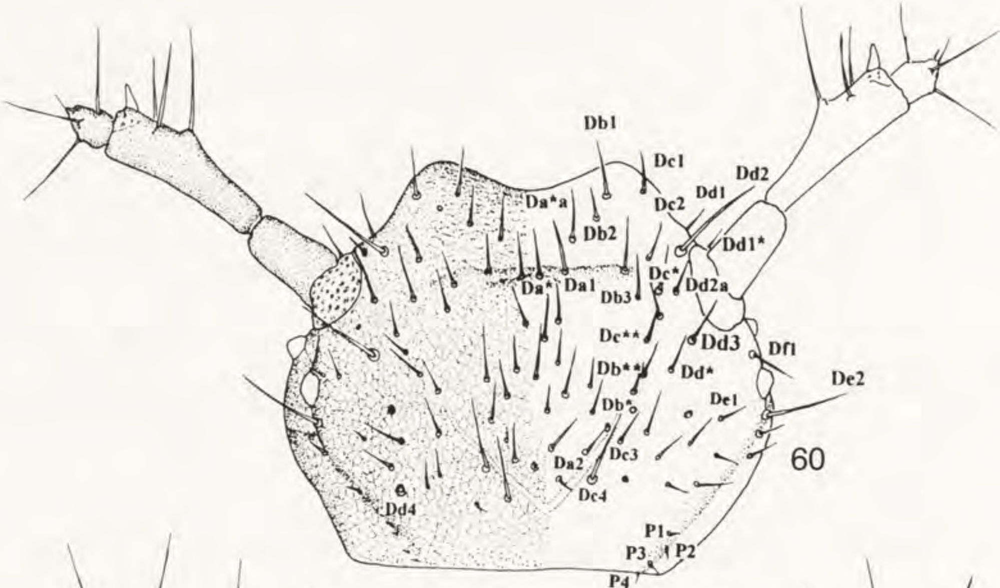
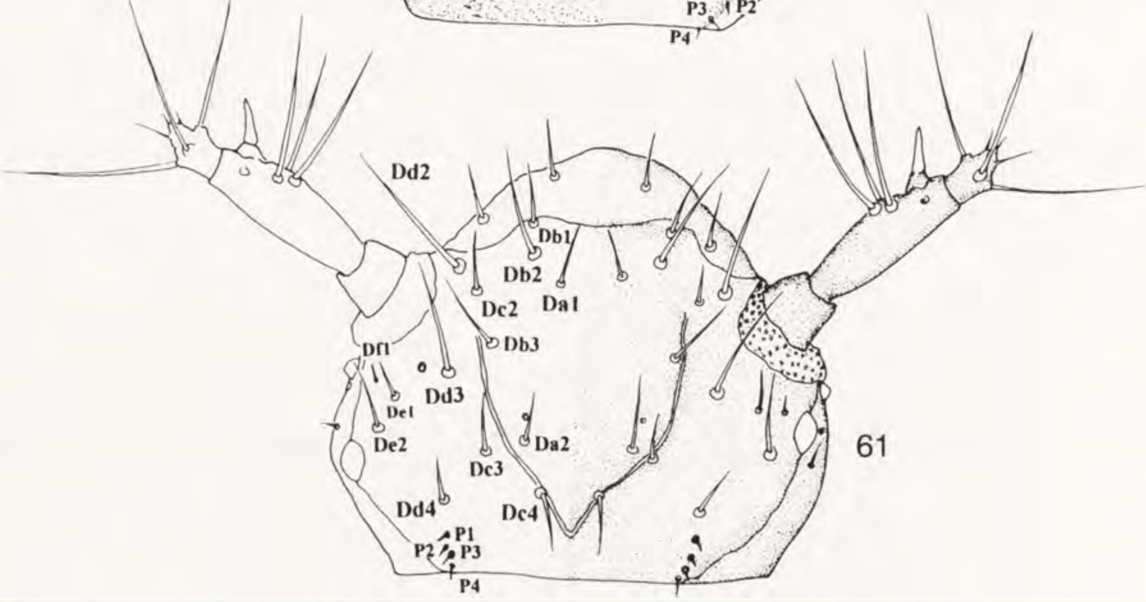
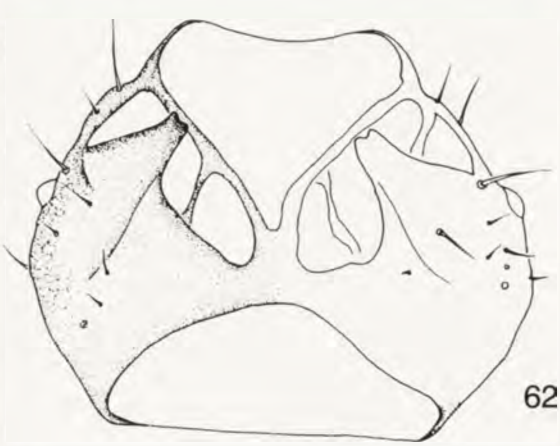
Figures 55–56. *Agathidium varians*, instar I. (55) dorsal and (56) ventral view of larval habitus.

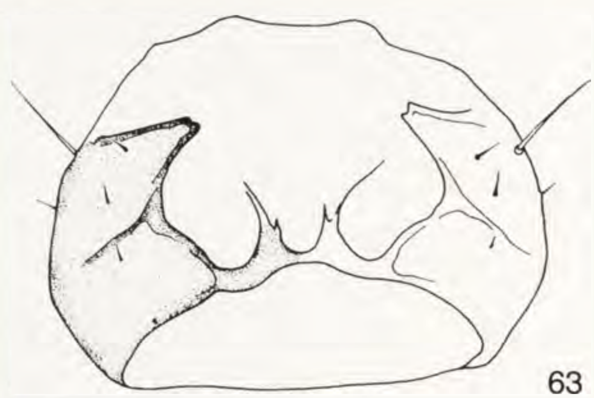


Figures 57–59. *Agathidium varians*. (57) lateral view of larval habitus, instar I, (58) proleg, instar III, (59) proleg, instar I.

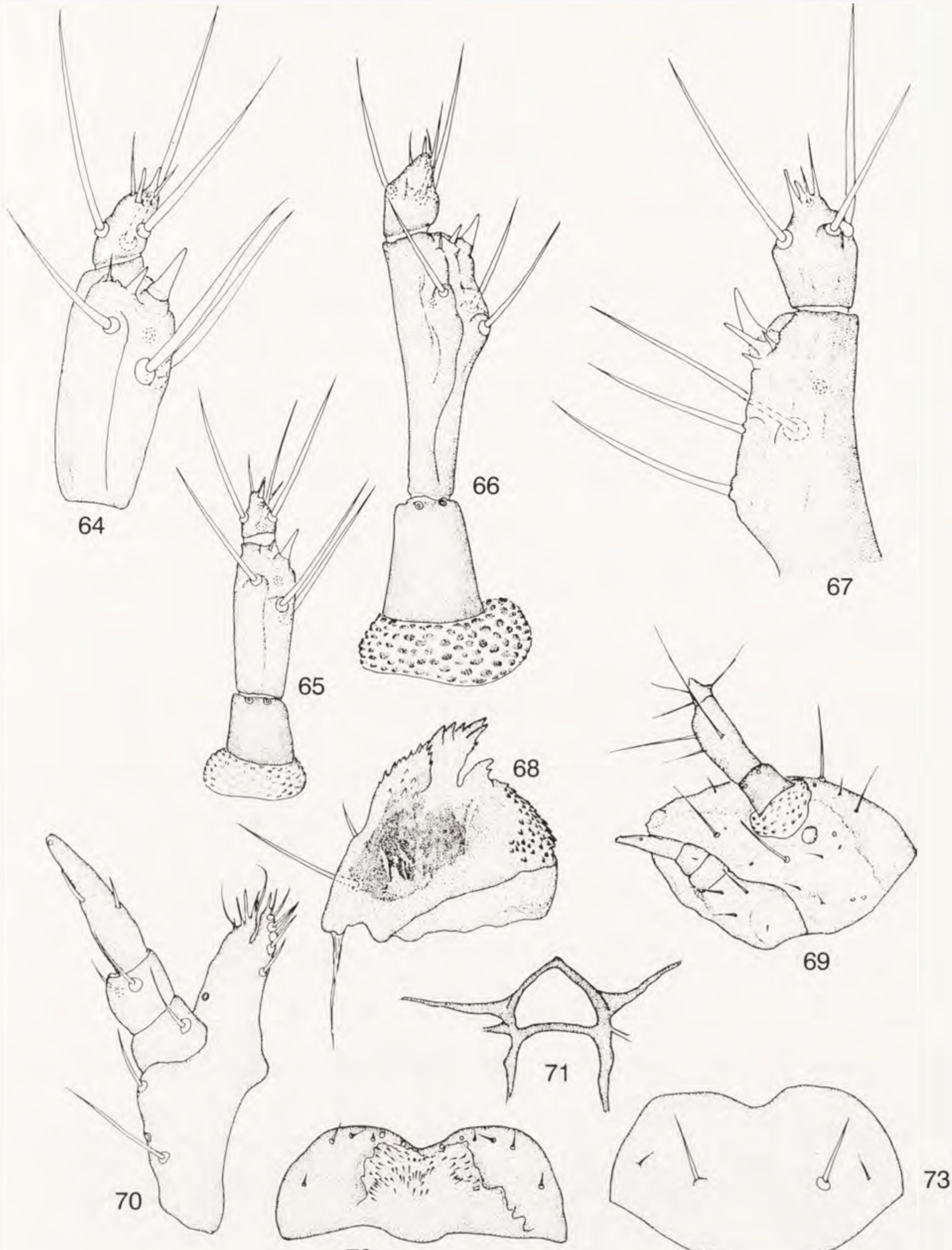




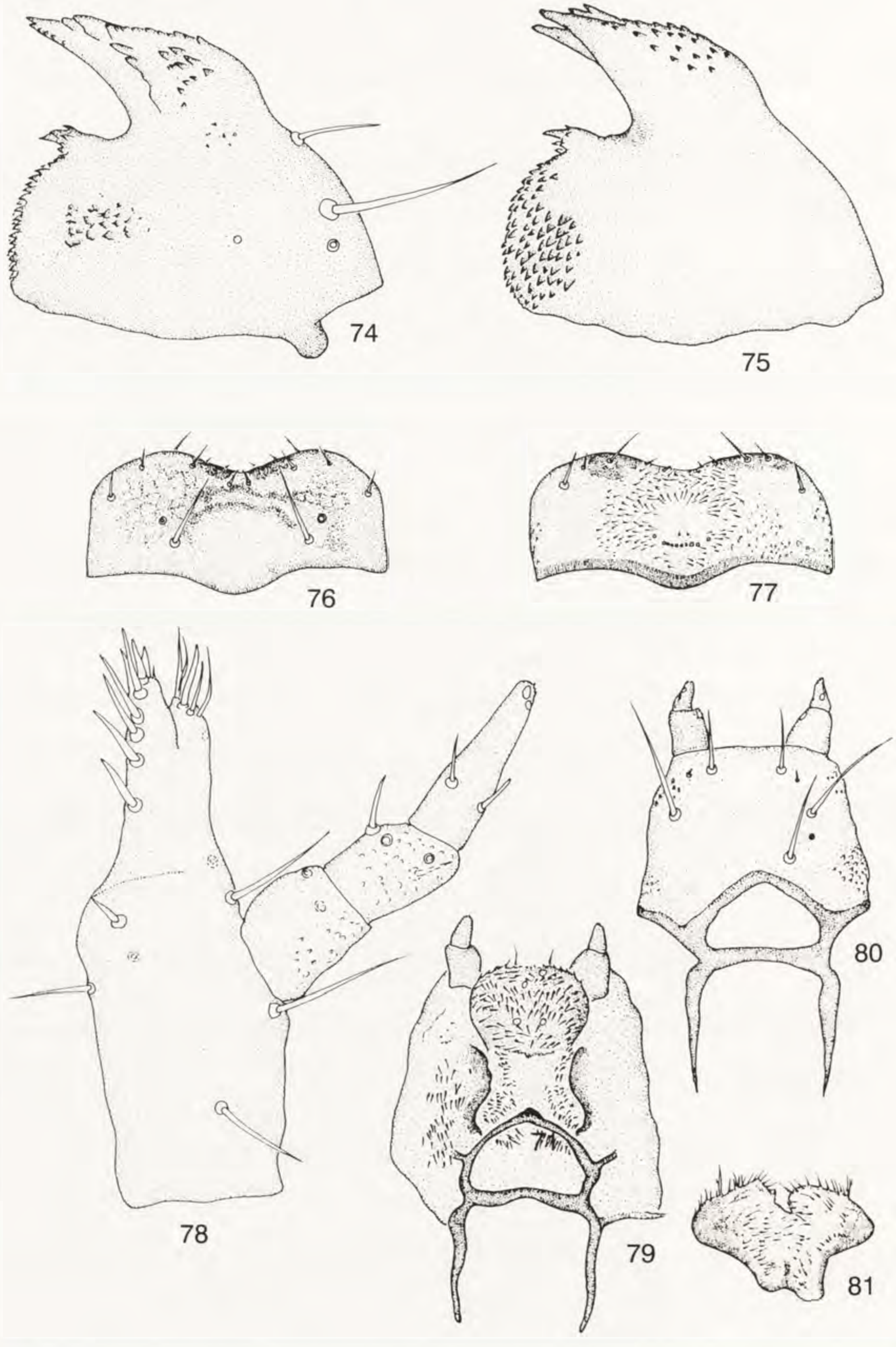




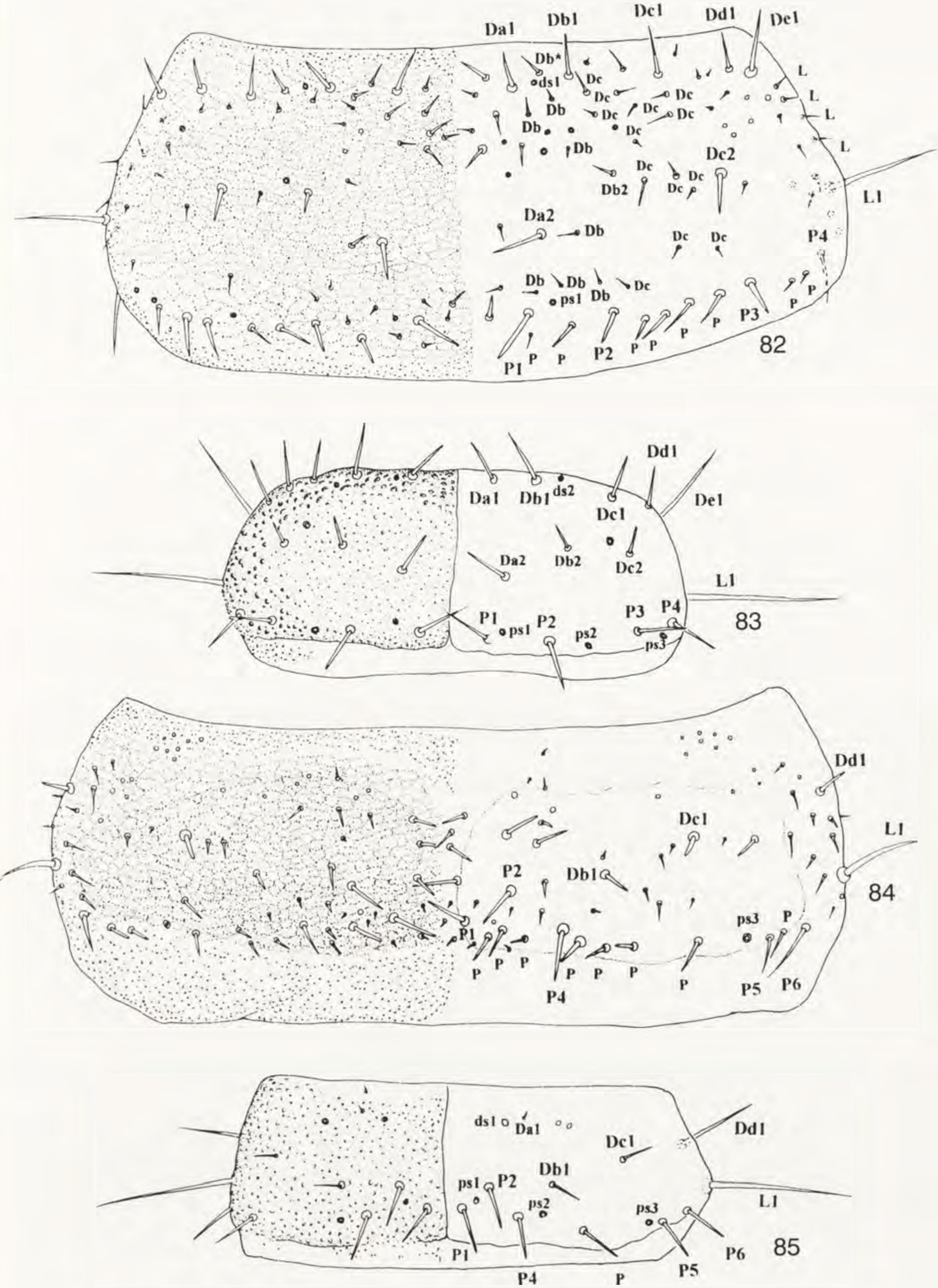
Figures 60–63. *Agathidium varians.* (60) dorsal and (62) ventral view of head, instar III, (61) dorsal and (63) ventral view of head, instar I.



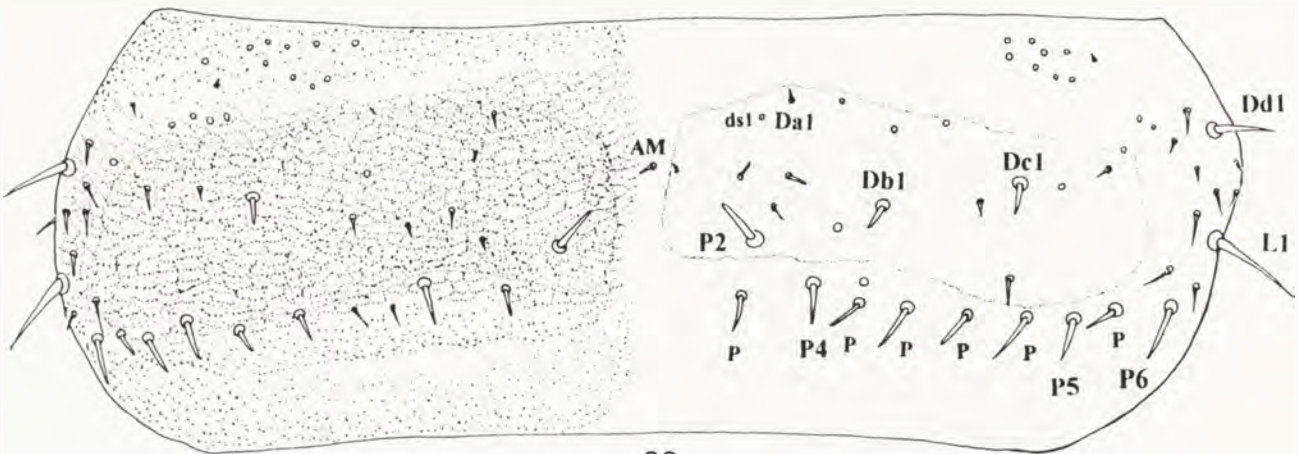
Figures 64–73. *Agathidium varians*. Antenna, (64–65) instar I and (66–67) instar III; (68) mandible, instar I, (69)lateral view of head, instar I, (70) maxilla, instar I, (71) hyphopharyngeal sclerome, instar I, (72) ventral and (73) dorsal view of labrum, instar I.



Figures 74–81. *Agathidium varians.* (74) dorsal and (75) ventral view of mandible, instar III, (76) dorsal and (77) ventral view of labrum, instar III; (78) maxilla, instar III; (79) dorsal and (80) ventral view of labium, instar III, (81) labium, dorsal view of ligula, instar I.



Figures 82–85. *Agathidium varians*. Pronotum, (82) instar III and (83) instar I; mesonotum, (84) instar III and (85) instar I.



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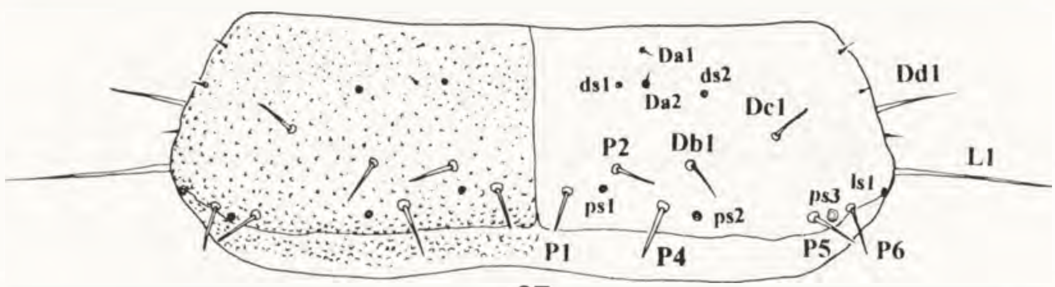

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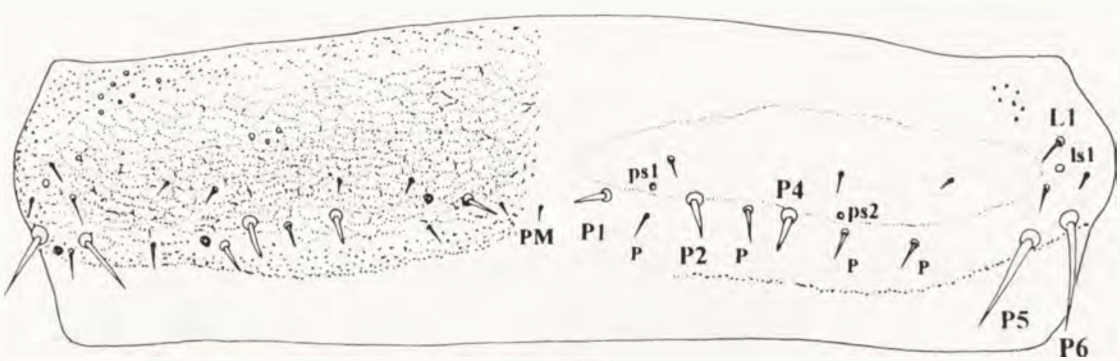

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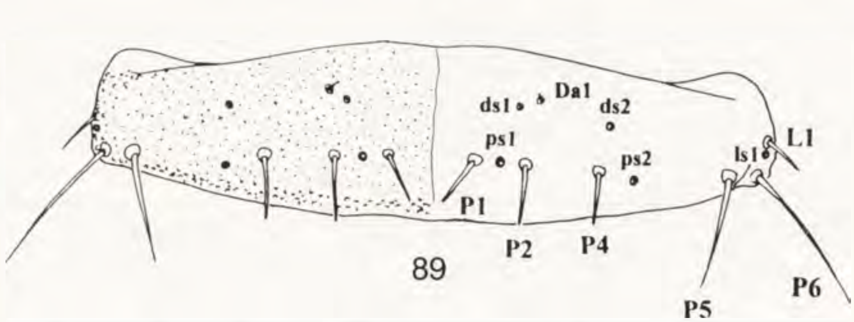

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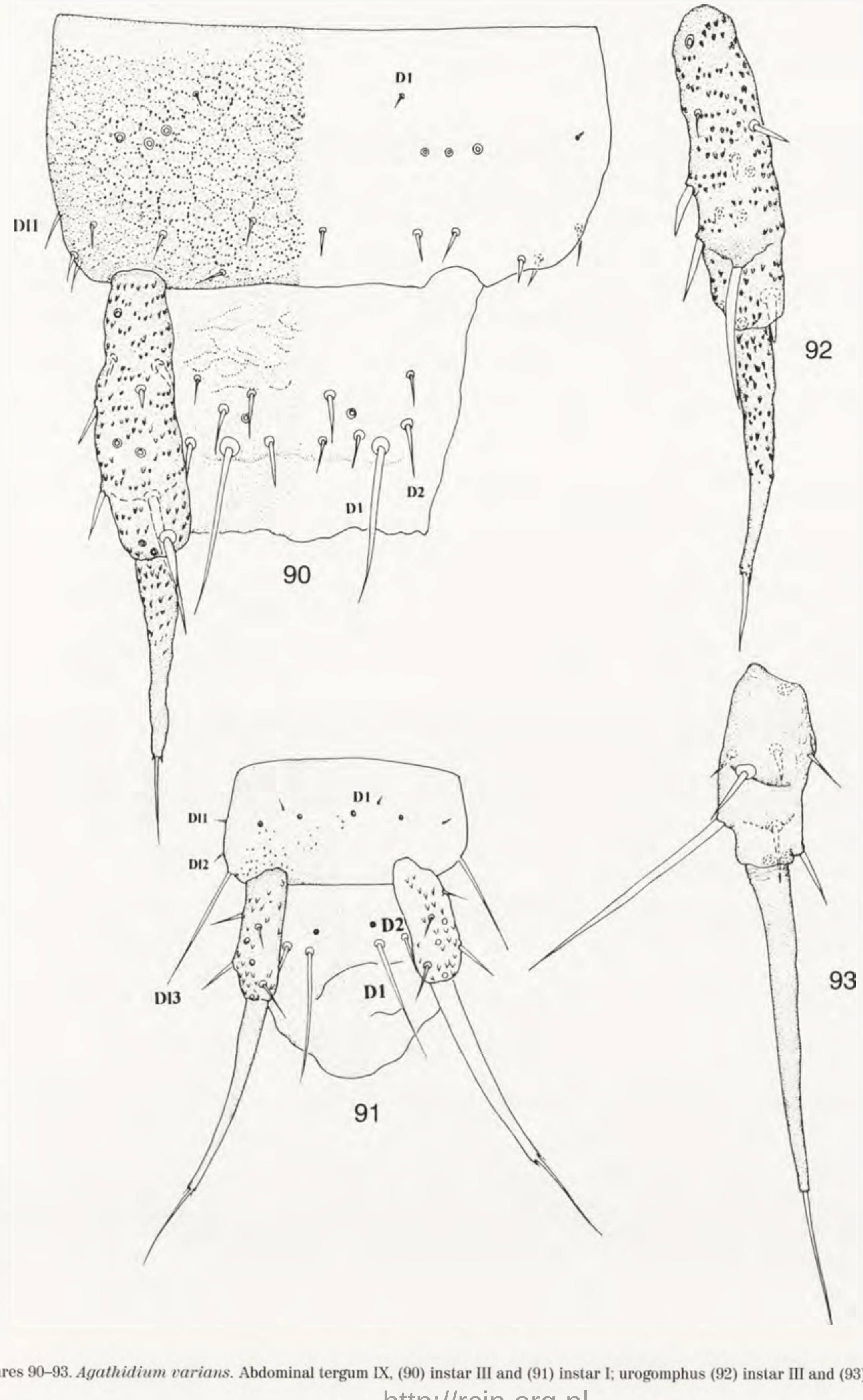
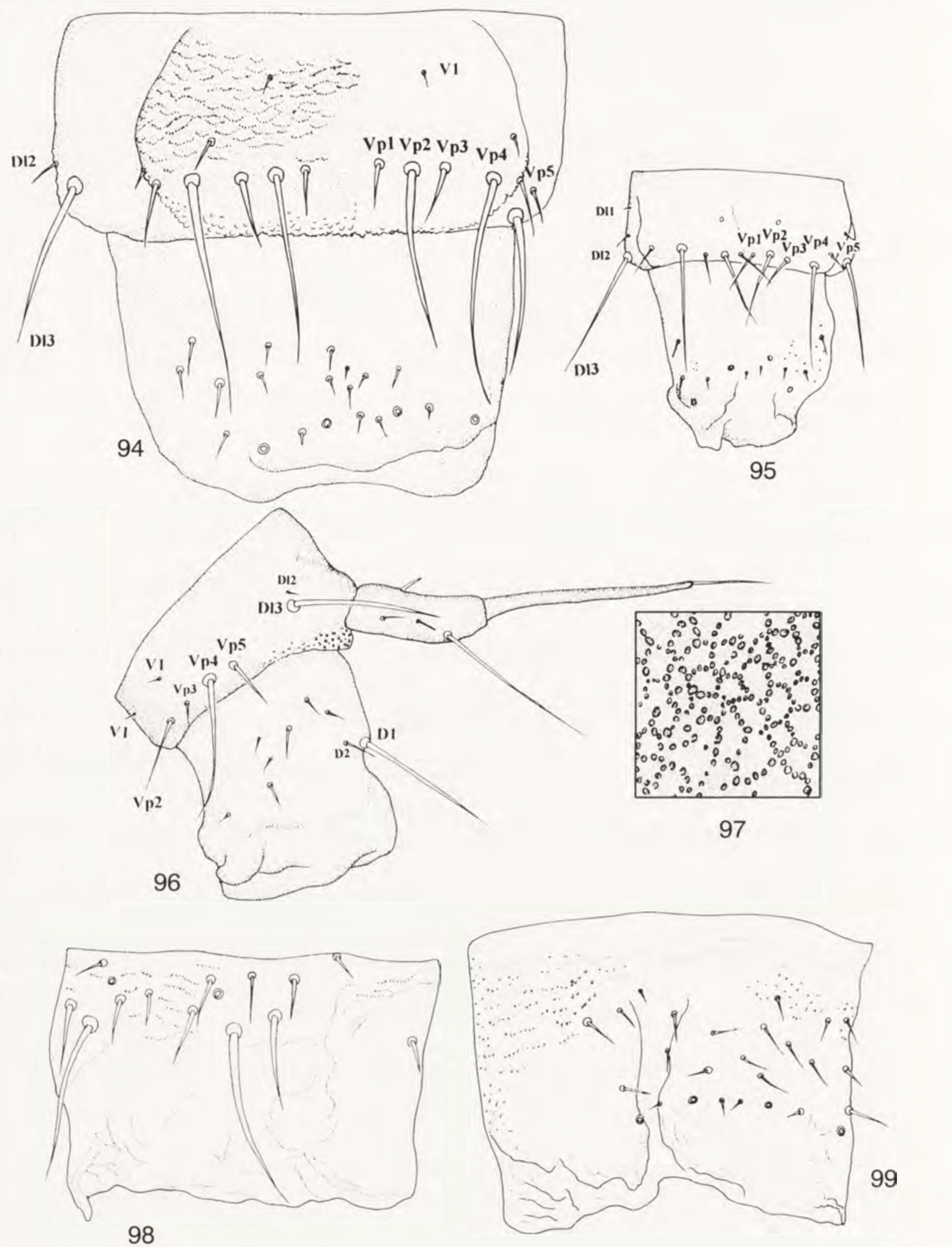
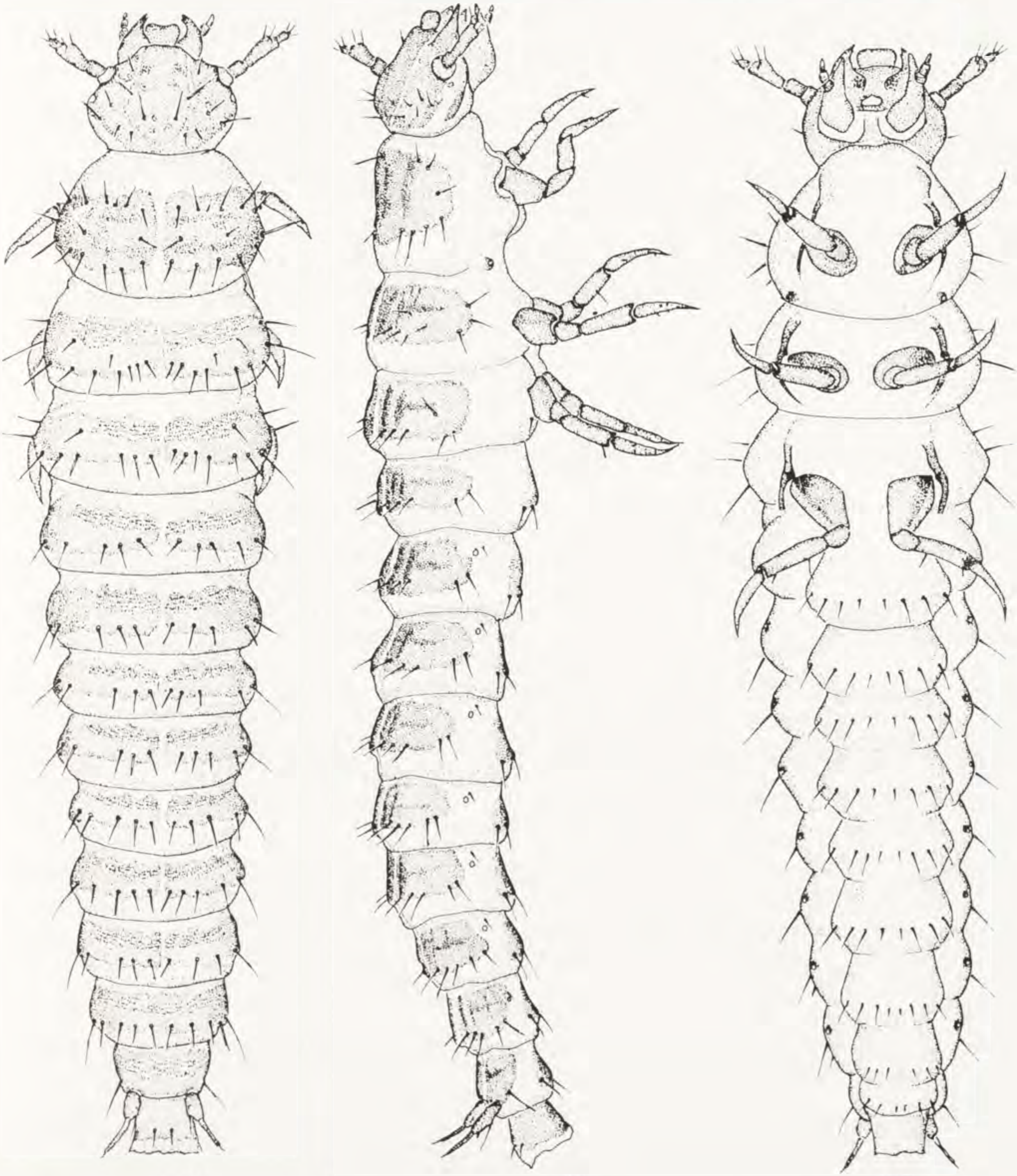
Figures 86–89. *Agathidium varians*. Metanotum, (86) instar III and (87) instar I; abdominal segment I, (88) instar III and (89) instar I.



Figures 90–93. *Agathidium varians.* Abdominal tergum IX, (90) instar III and (91) instar I; urogomphus (92) instar III and (93) instar I.



Figures 94–99. *Agathidium varians*. Abdominal sternum IX, (94, 96) instar III and (95) instar I; (97) asperities on head, instar III, (98) dorsal and (99) ventral view of anal membrane.



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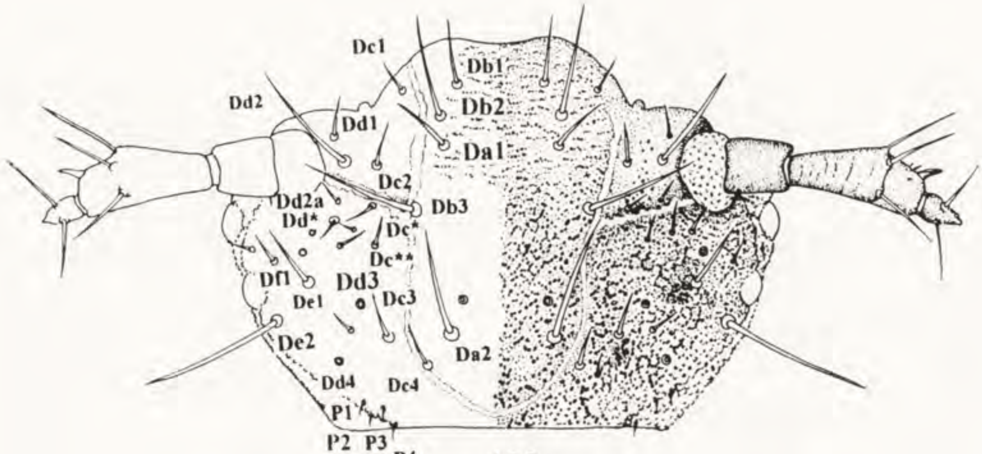
Figures 100–102. *Agathidium mandibulare*. (100) dorsal, (101) lateral and (102) ventral view of larval habitus.



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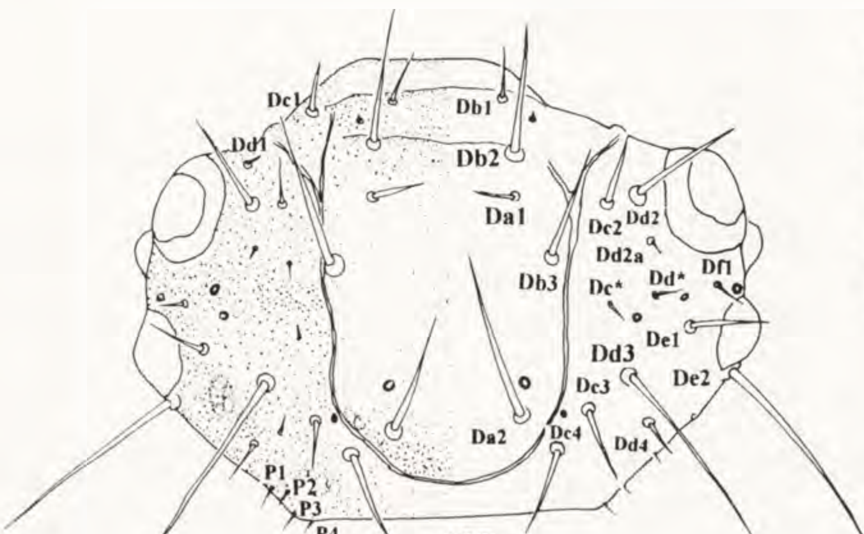

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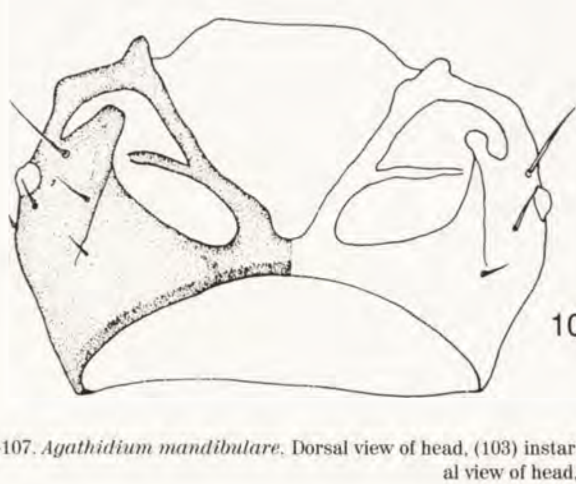
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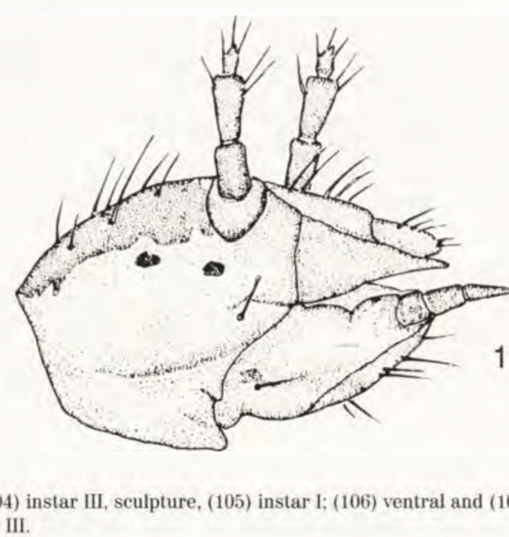
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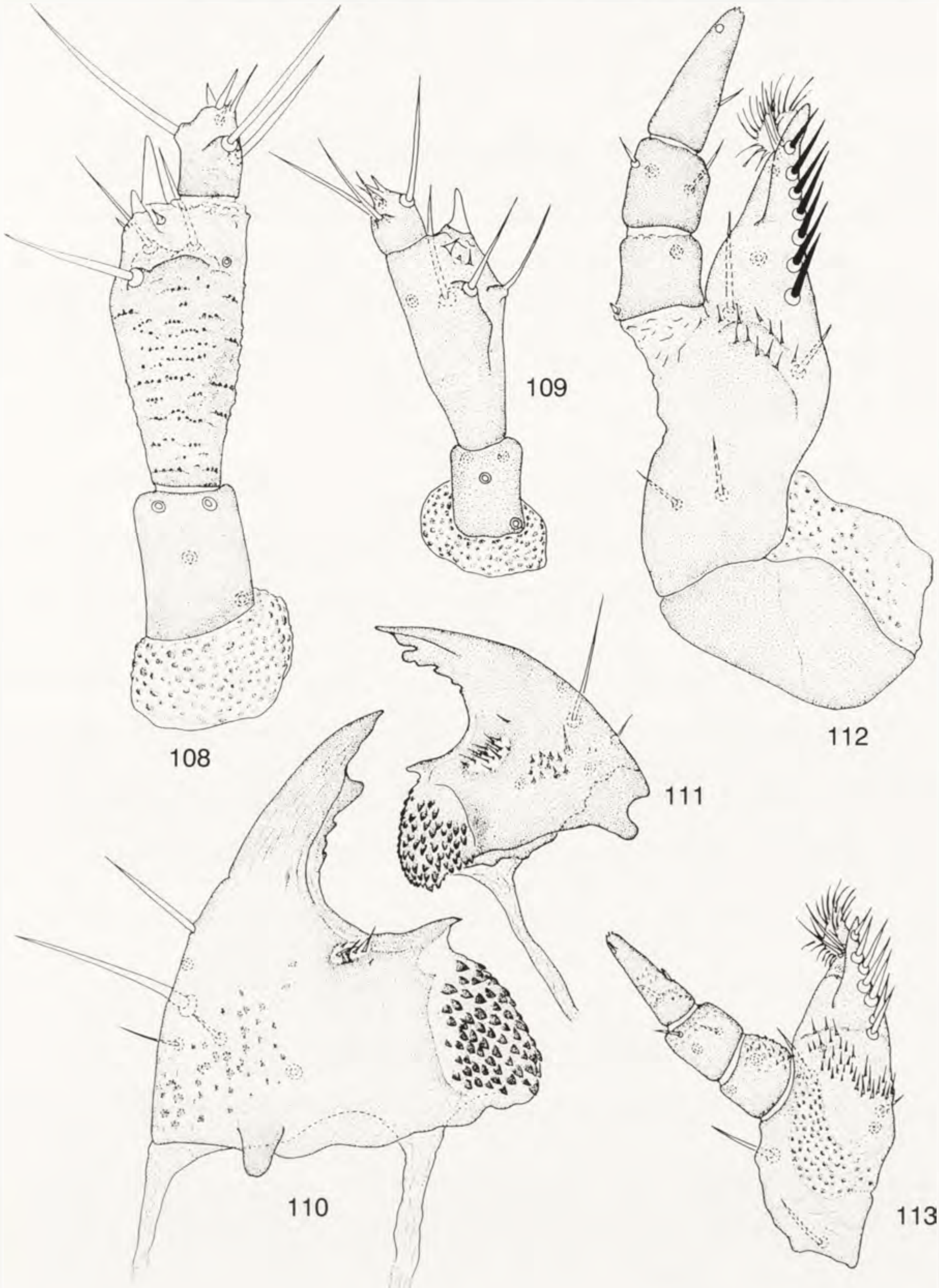
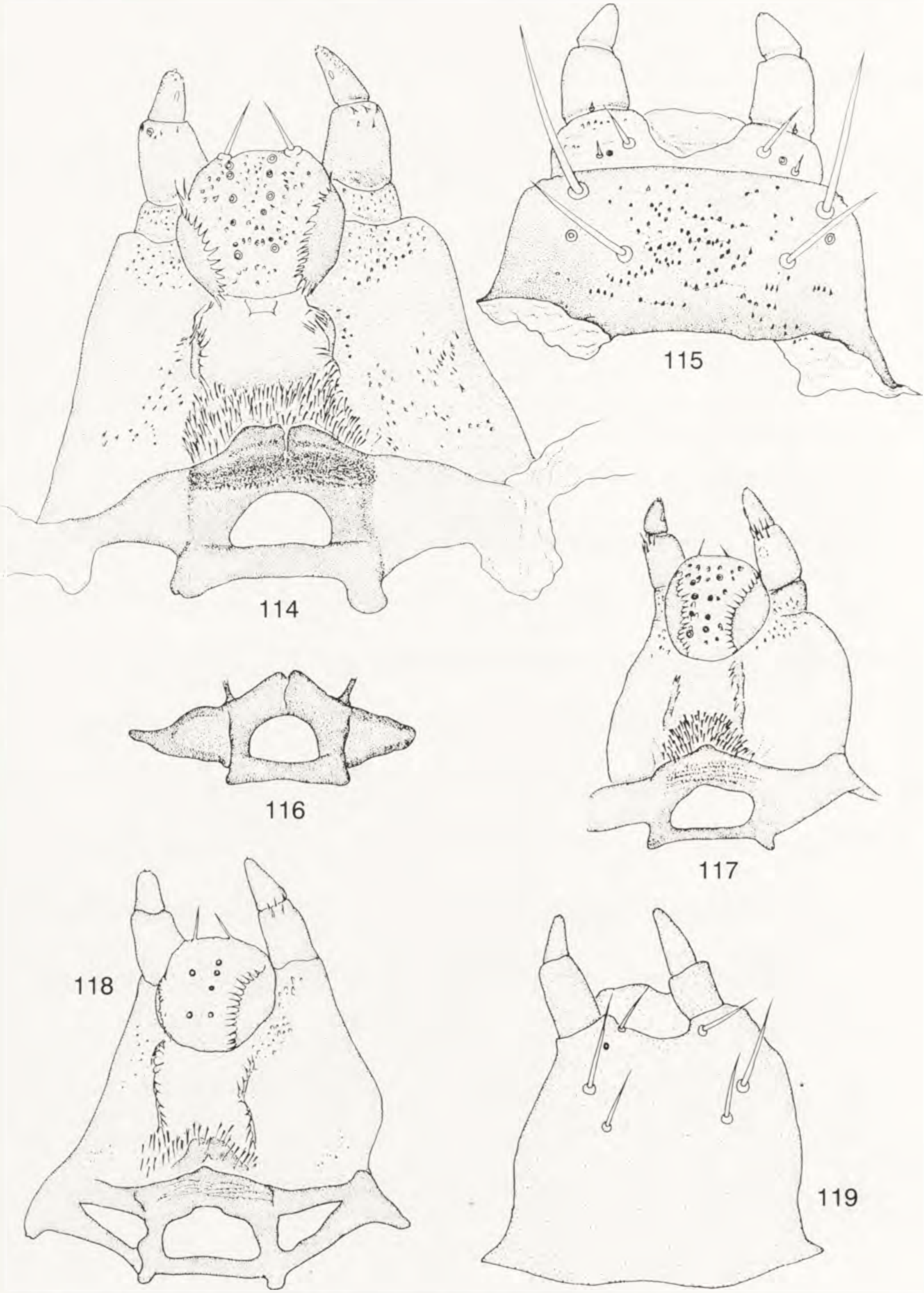
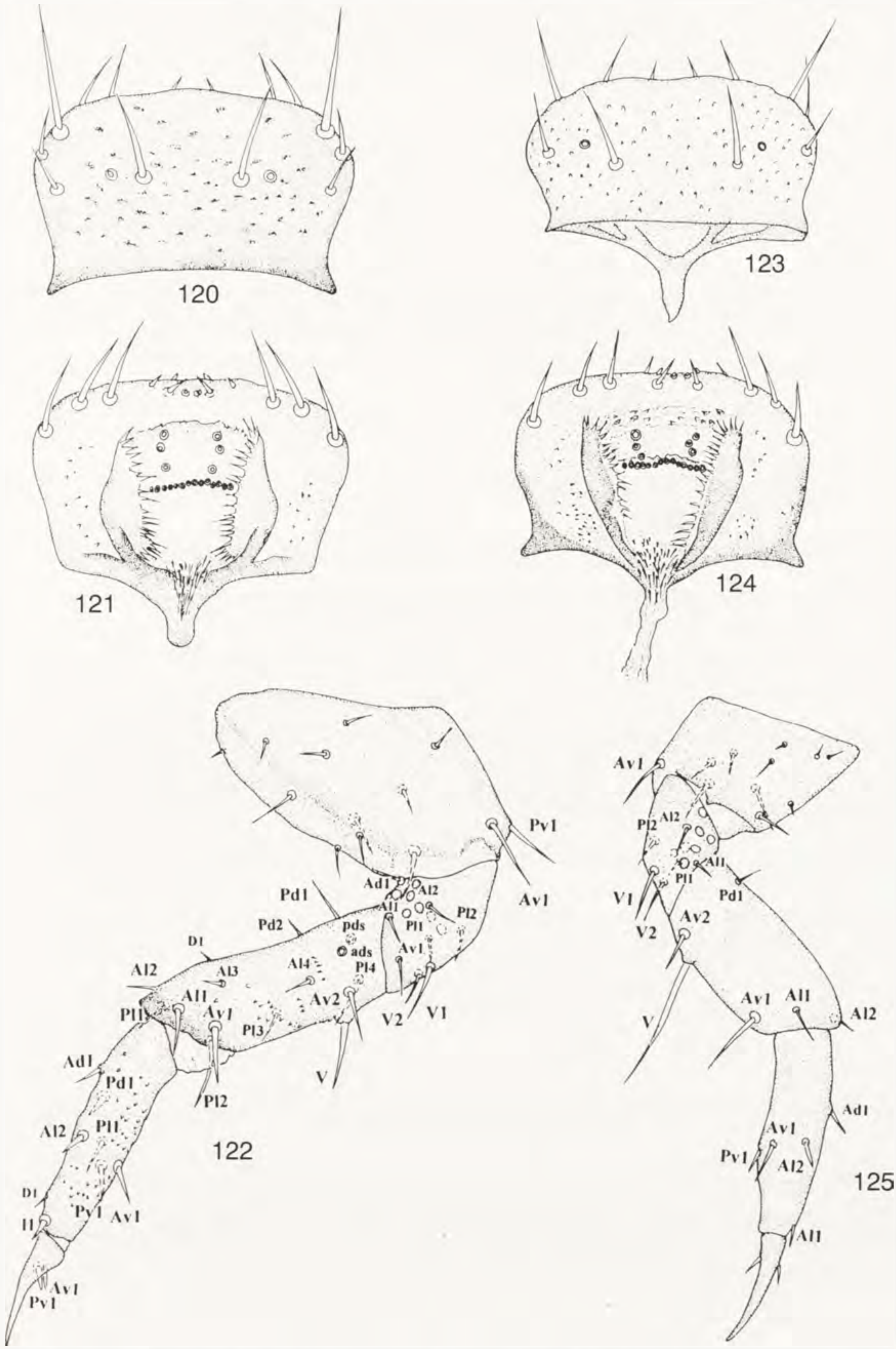
Figures 103–107. *Agathidium mandibulare*. Dorsal view of head, (103) instar III, (104) instar III, sculpture, (105) instar I; (106) ventral and (107) lateral view of head, instar III.



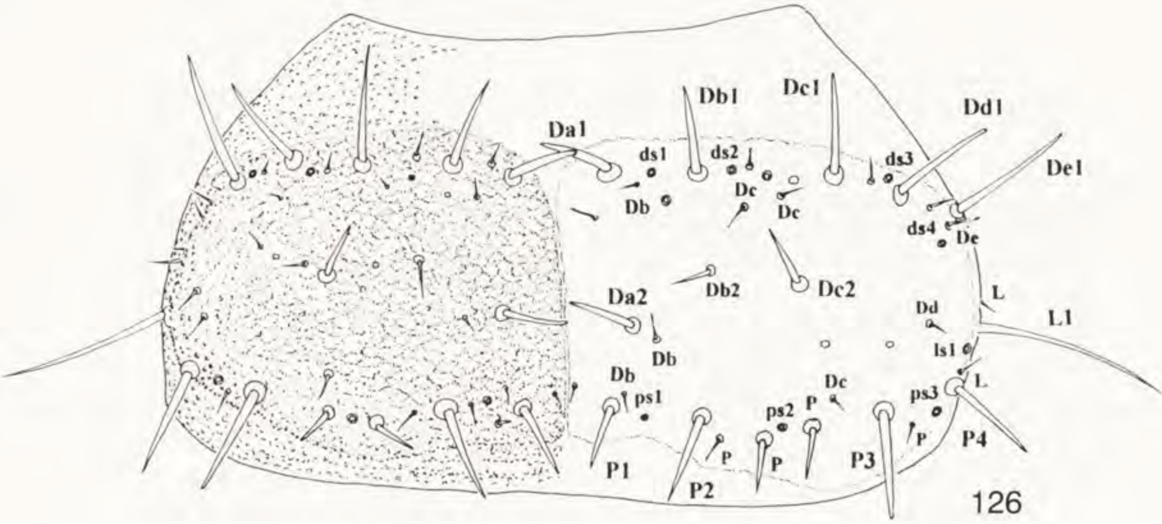
Figures 108–113. *Agathidium mandibulare*. Antenna, (108) instar III and (109) instar I; mandible, (110) instar III and (111) instar I; maxilla, (112) instar III and (113) instar I.



Figures 114–119. *Agathidium mandibulare*. Labium. (114) dorsal and (115) ventral view of labium, instar III, (117–118) dorsal and (119) ventral view of labium, instar I, (116) hyphopharyngeal sclerome, instar III.



Figures 120–125. *Agathidium mandibulare*. Labrum, (120–121) instar III and (123–124) instar I; proleg, (122) instar III and (125) instar I.



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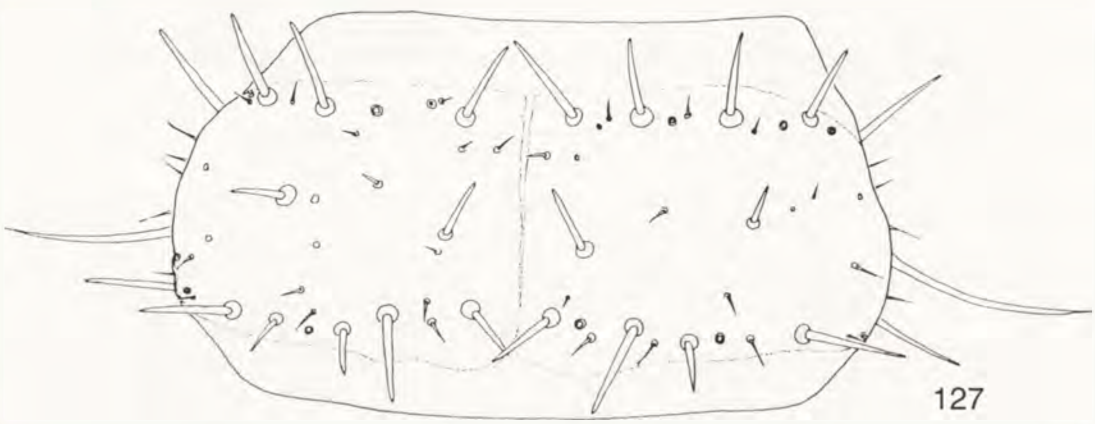
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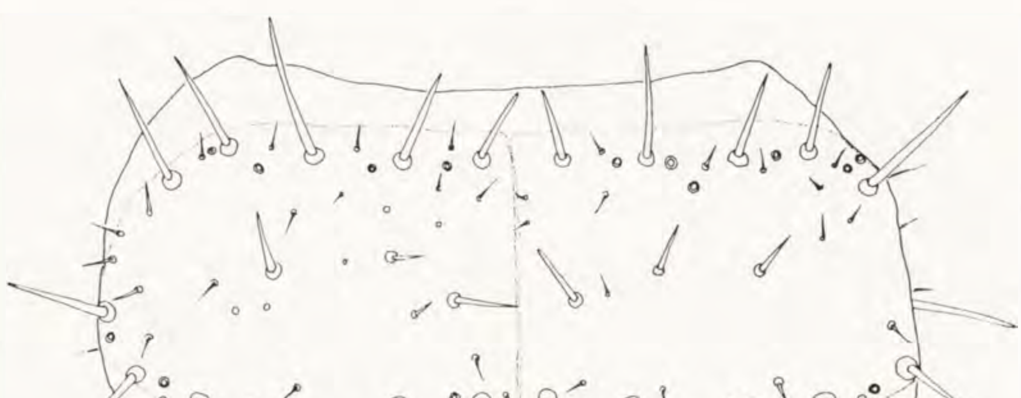
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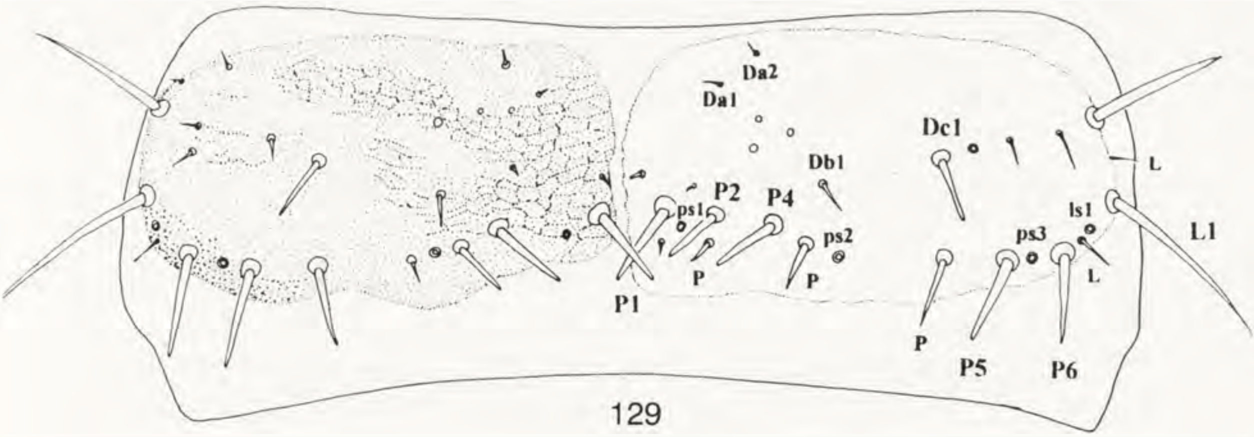
Figures 126–128. *Agathidium mandibulare*. Pronotum.



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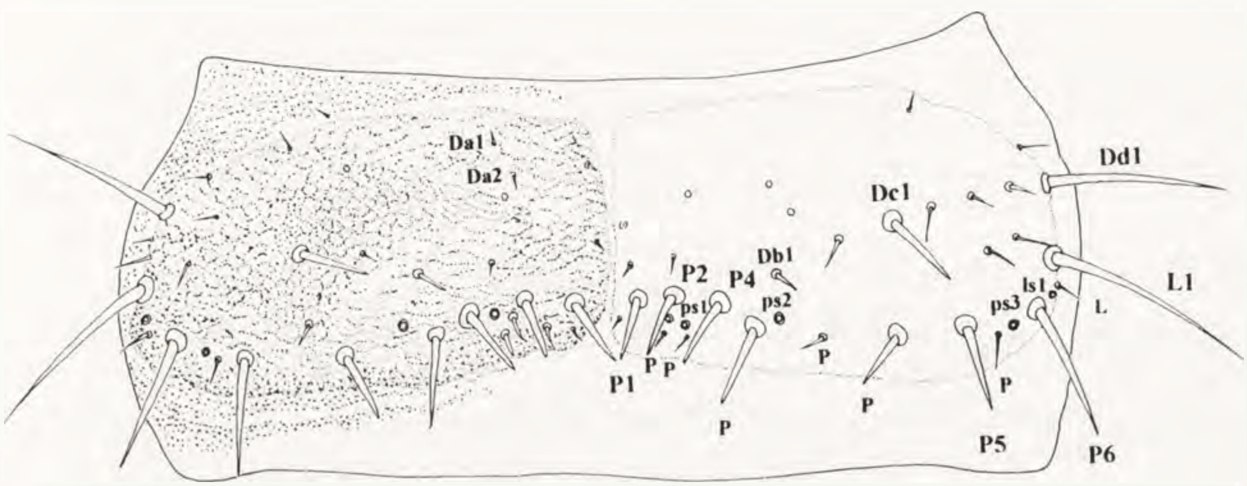

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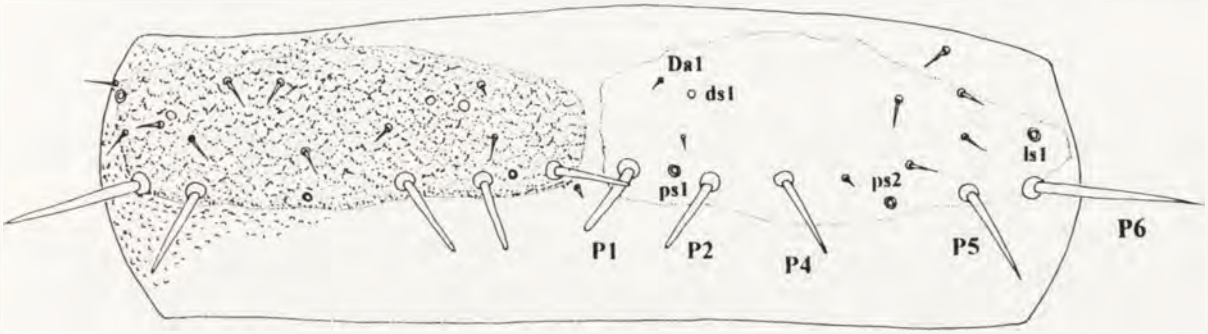

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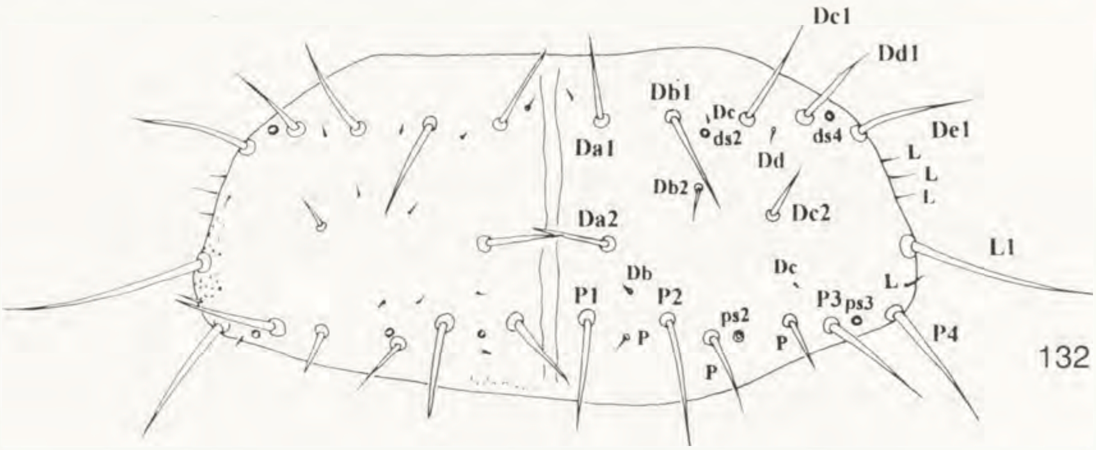
Figures 129–131. *Agathidium mandibulare*. (129) mesonotum, (130) metanotum, (131) abdominal segment I.



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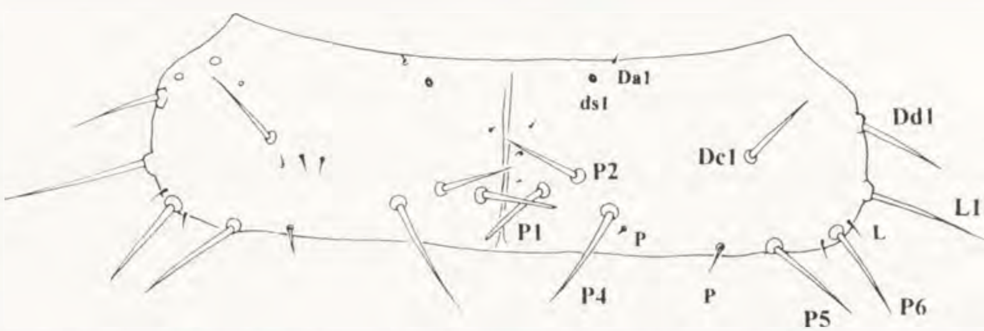

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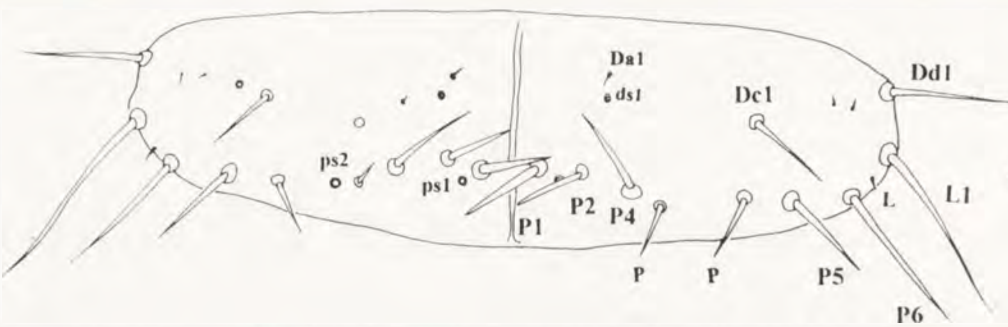

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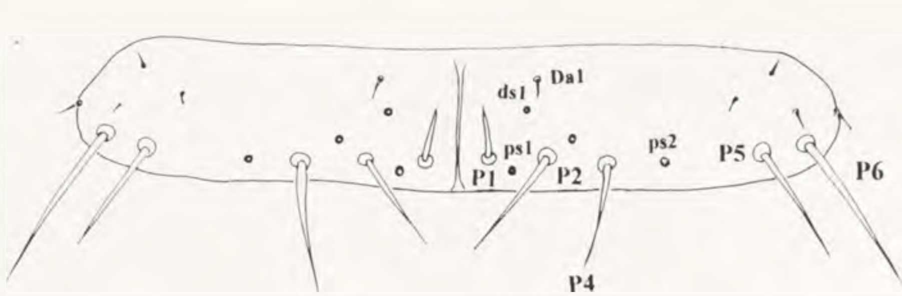

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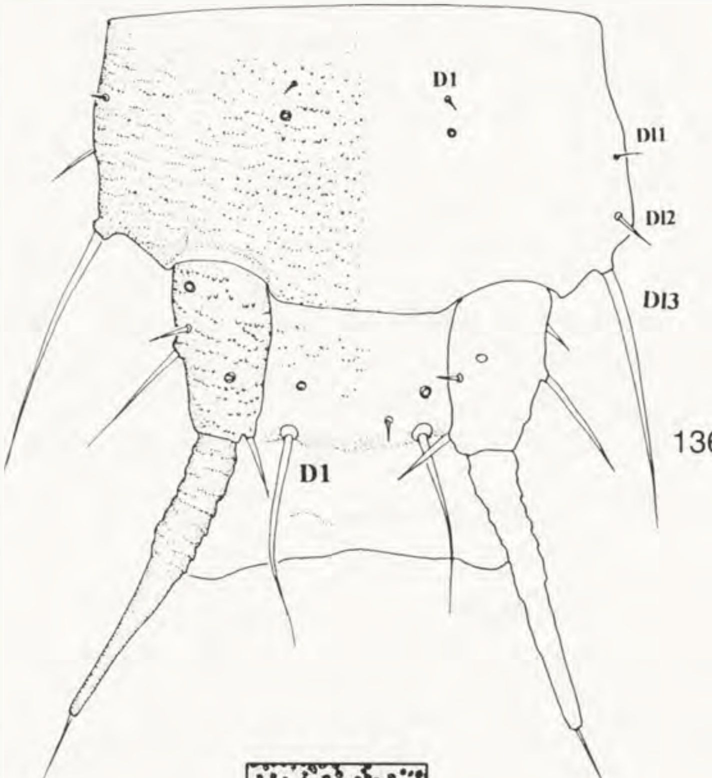
Figures 132–135. *Agathidium mandibulare*, instar I. (132) pronotum, (133) mesonotum, (134) metanotum, (135) abdominal segment I.



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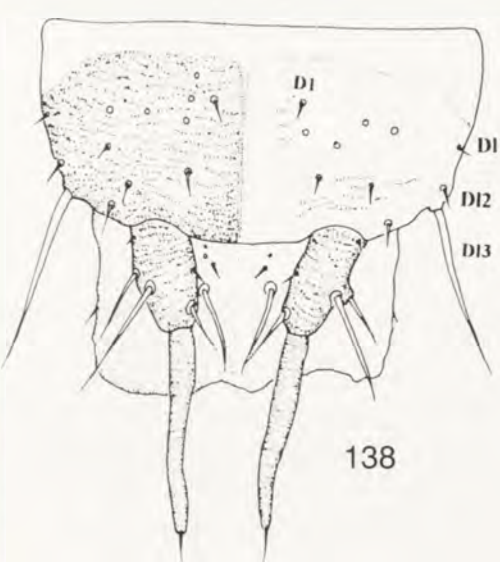

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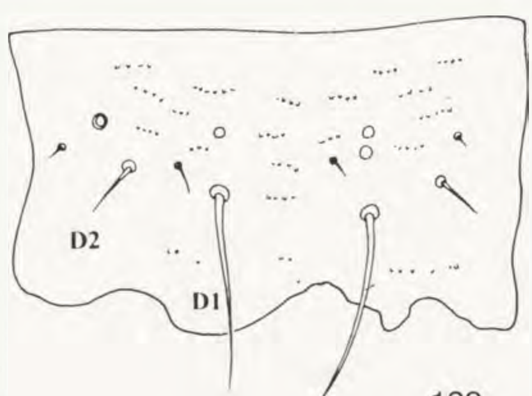

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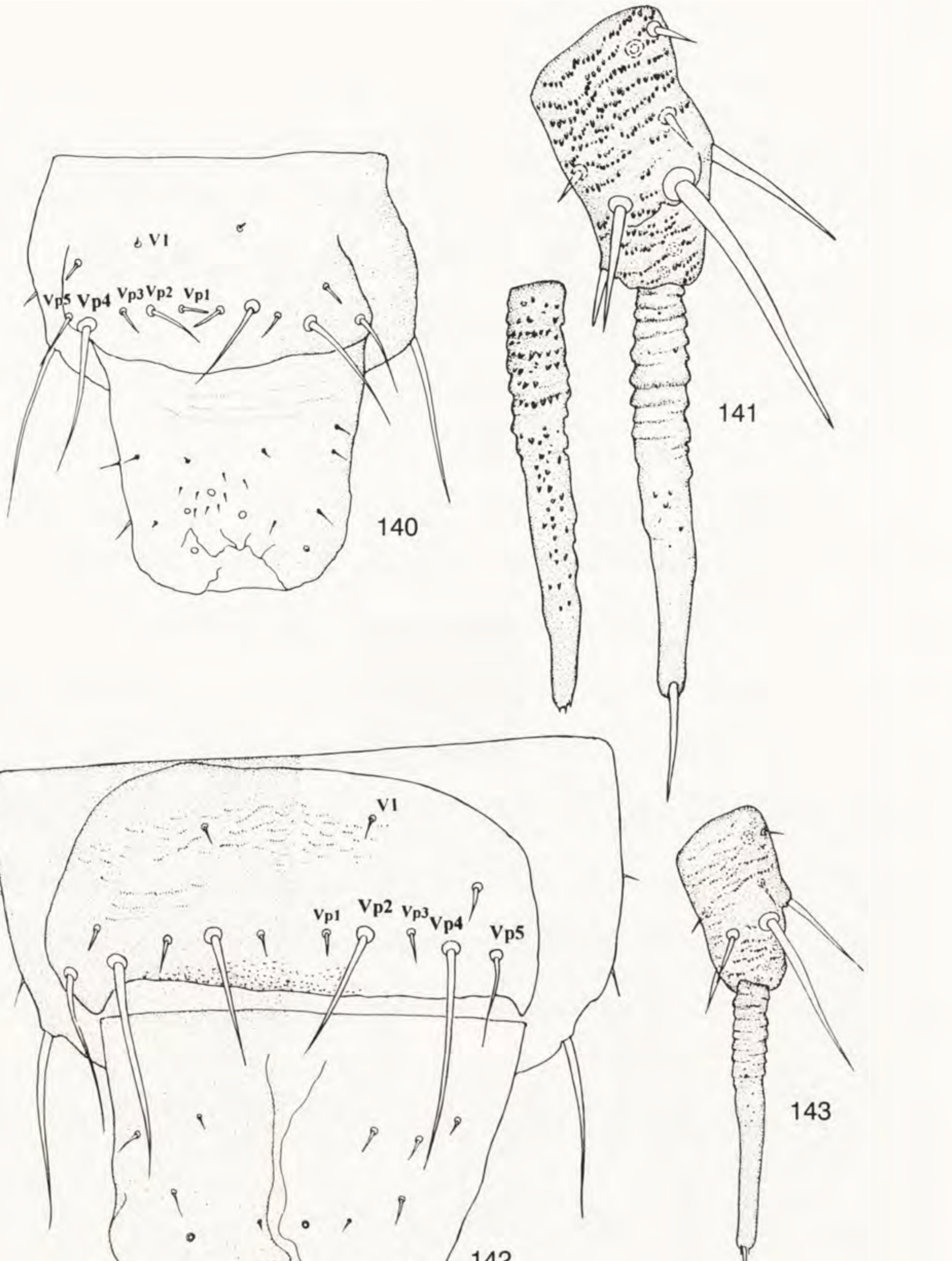
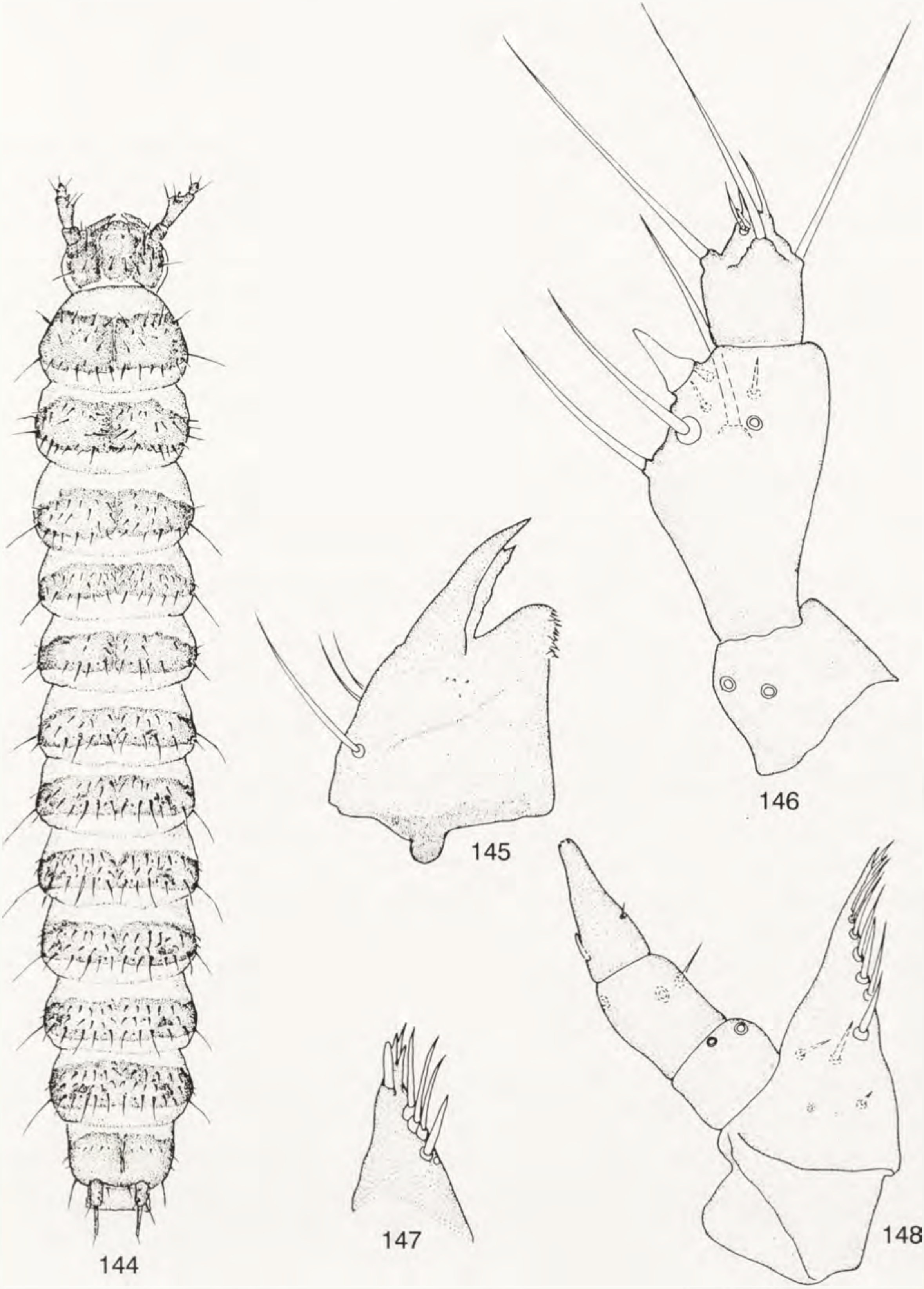
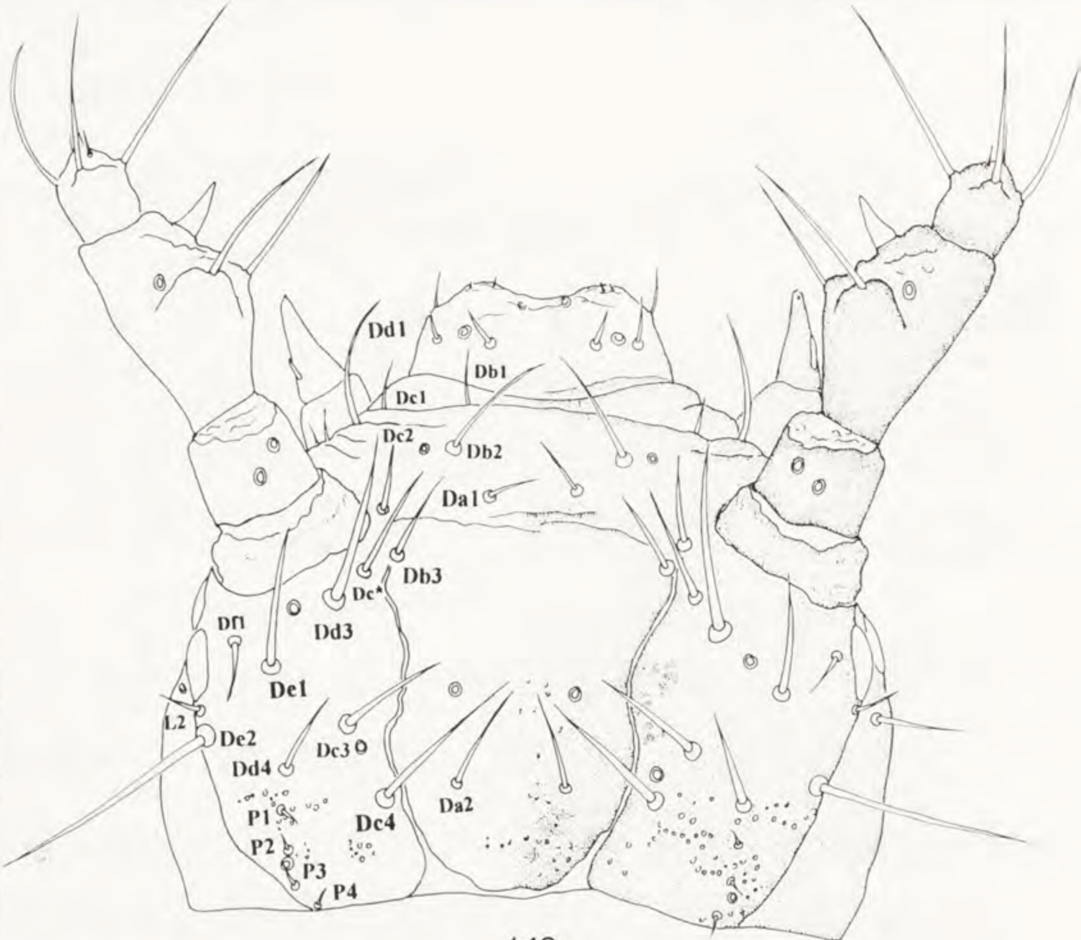
Figures 136–139. *Agathidium mandibulare*. (136) abdominal tergum IX, instar I; (137) microsculpture of pronotum, instar III; (138) abdominal tergum IX, instar III; (139) anal membrane, dorsal, instar III.



Figures 140–143. *Agathidium mandibulare*. (140) abdominal sternum IX and anal membrane, instar I; (141) urogomphus, instar III; (142) abdominal sternum IX and anal membrane, instar III; (143) urogomphus, instar I.



Figures 144–148. Bl. (144) larval habitus, (145) mandible, (146) antenna, (147–148) maxilla.



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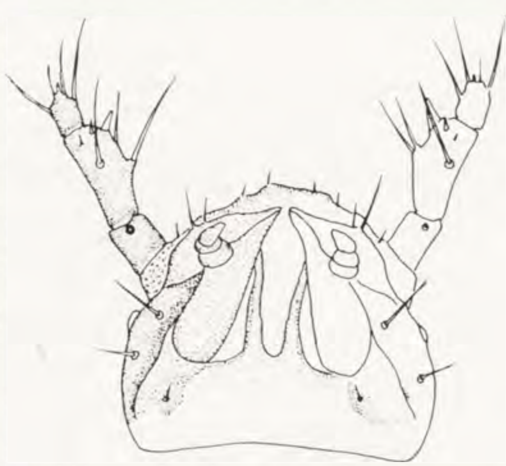

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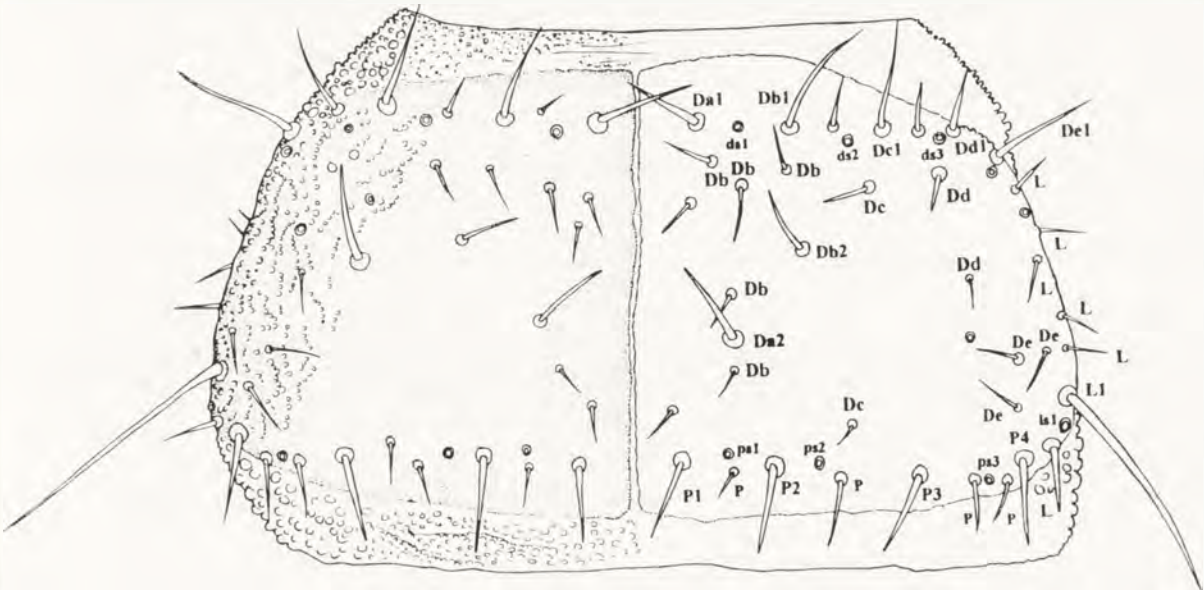
Figures 149–151. Bl. (149) dorsal and (150) ventral ventral view of head, (151) antenna.



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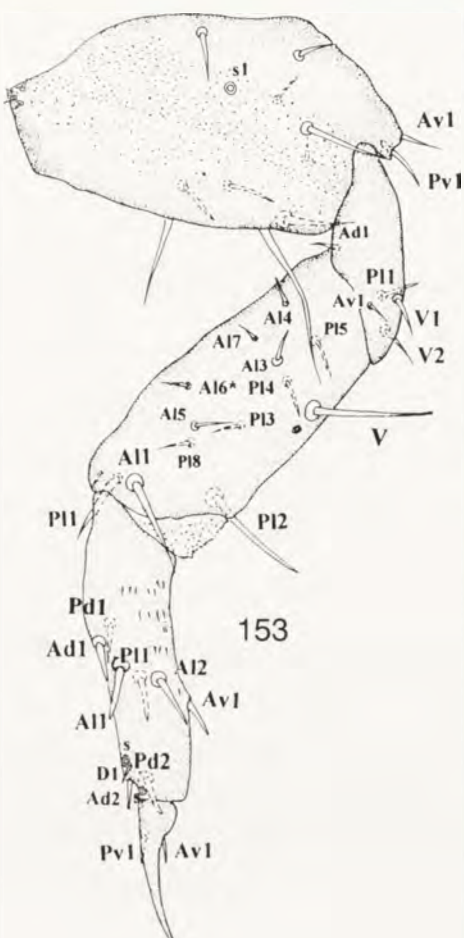

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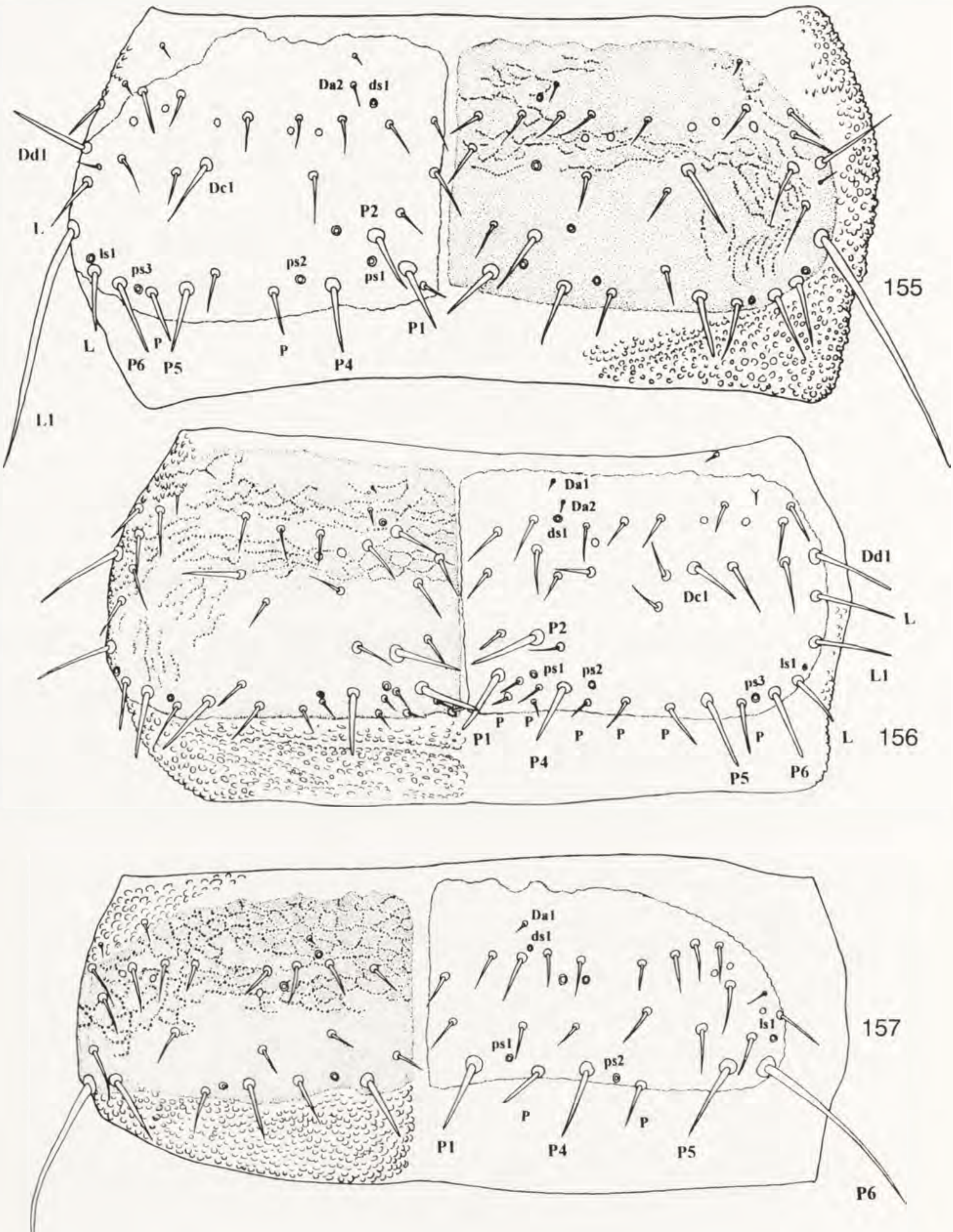
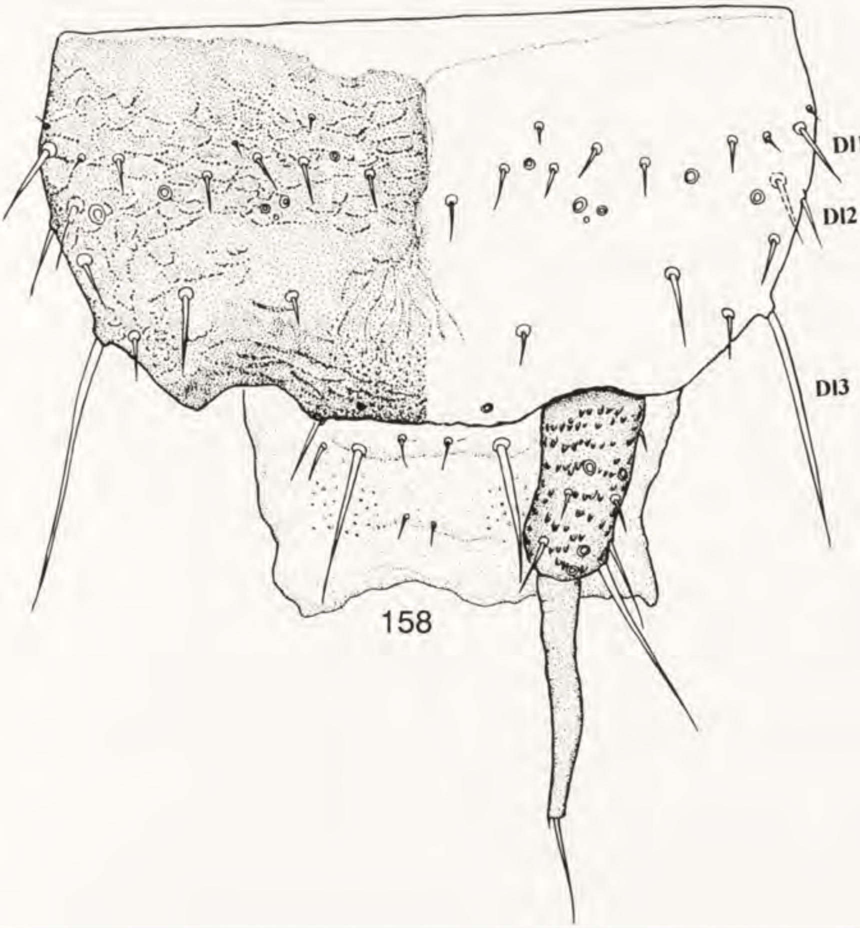
Figures 152–154. Bl. (152) pronotum, (153) proleg, (154) coxa and trochanter.



Figures 155–157. Bl. (155) mesontum, (156) metanotum, (157) abdominal segment I.



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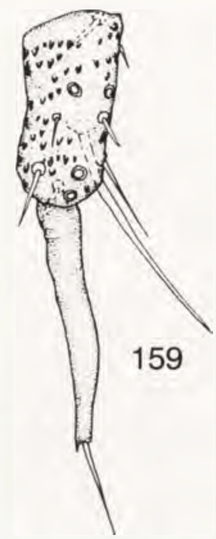

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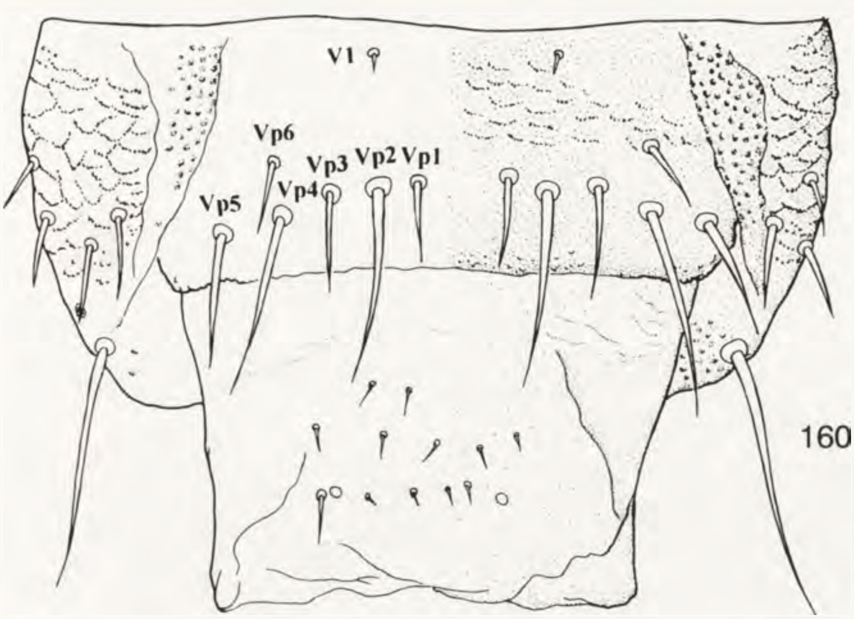

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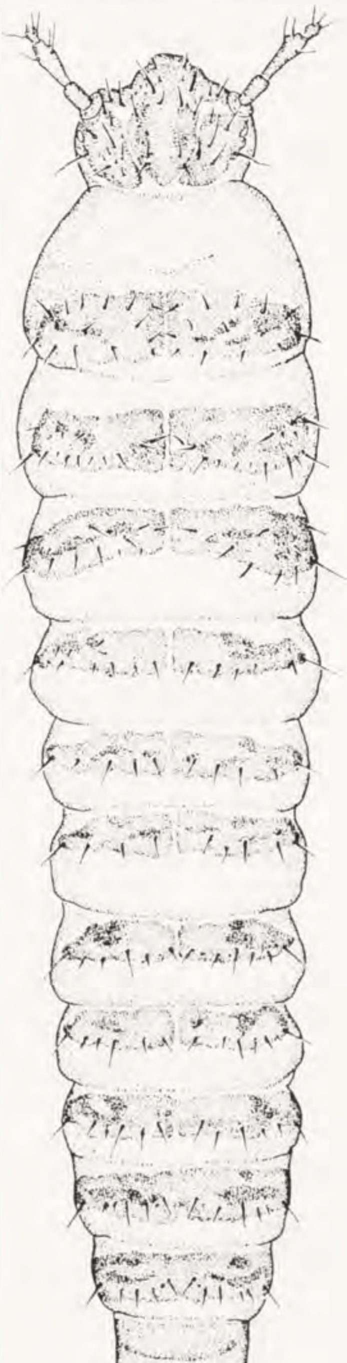
Figures 158–160. Bl. (158) abdominal tergum IX and anal membrane; (159) abdominal sternum IX and anal membrane; (160) urogomphus.



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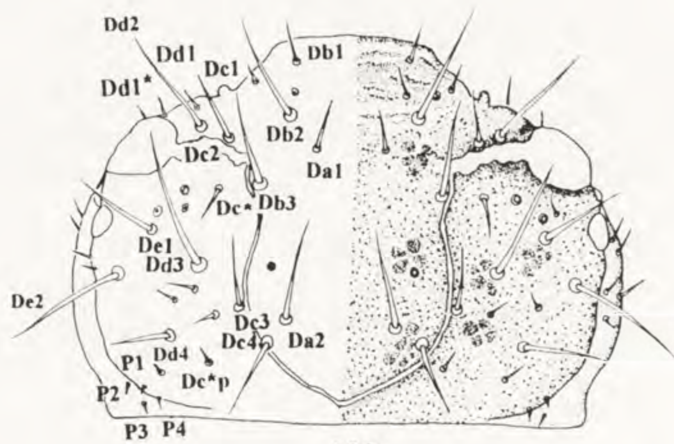

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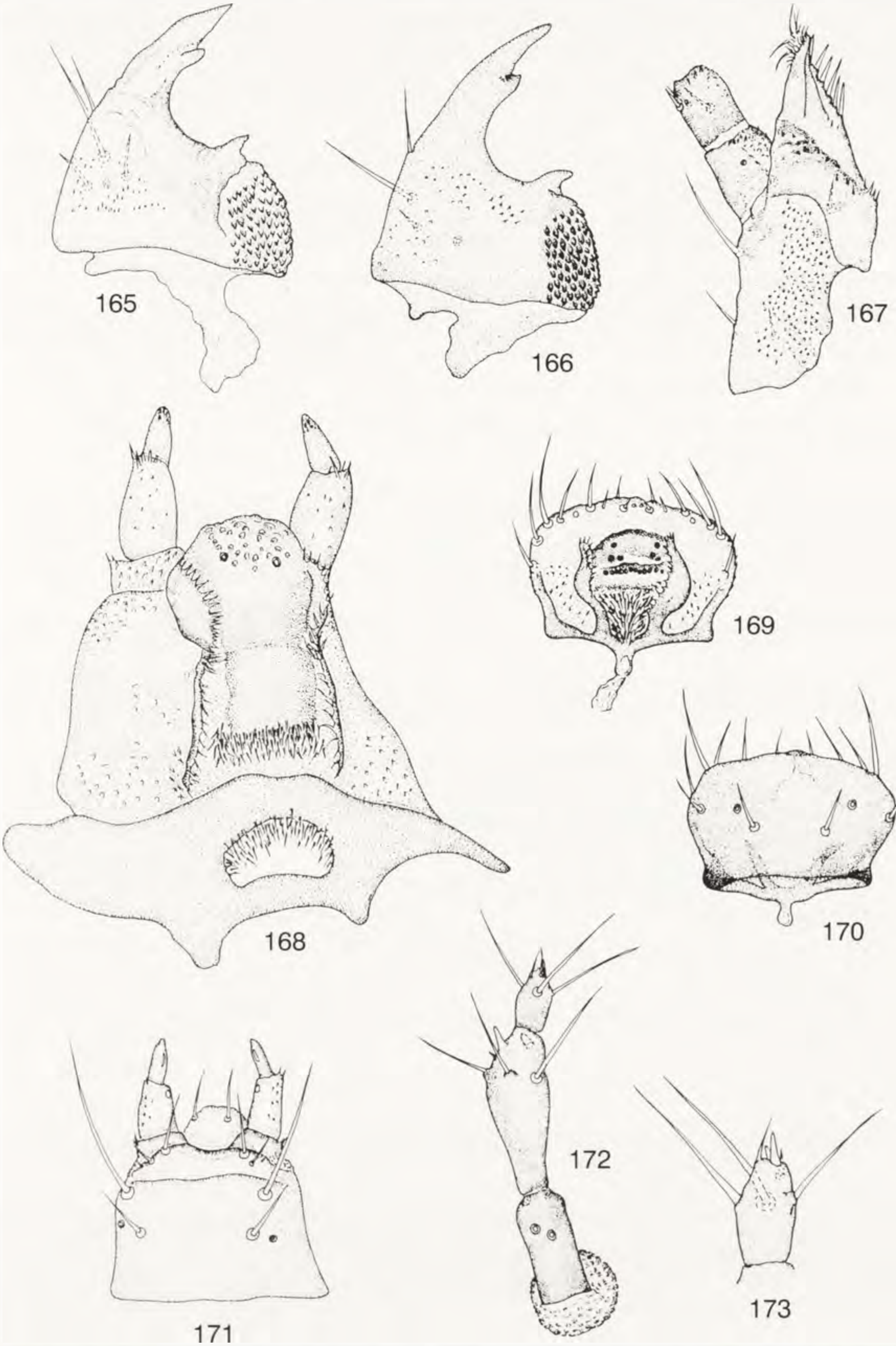
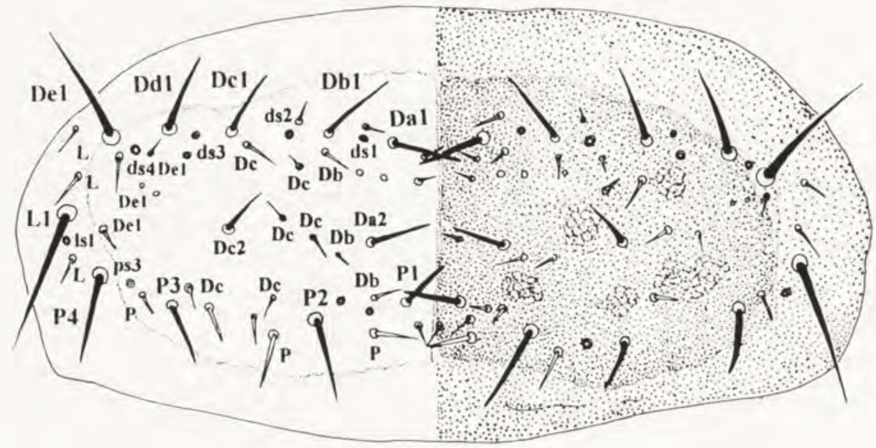
Figures 161–164. BII. (161) larval habitus, (162) dorsal, (163) microsculpture and (164) ventral view of head.



Figures 165–173. BII. (165–166) mandible, (167) maxilla, (168) dorsal and (171) ventral view of labium, (169) ventral and (170) dorsal view of labrum, (172–173) antenna.



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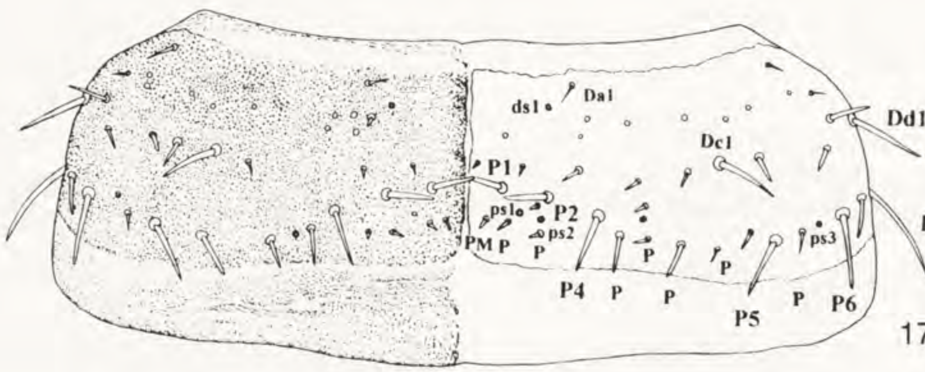

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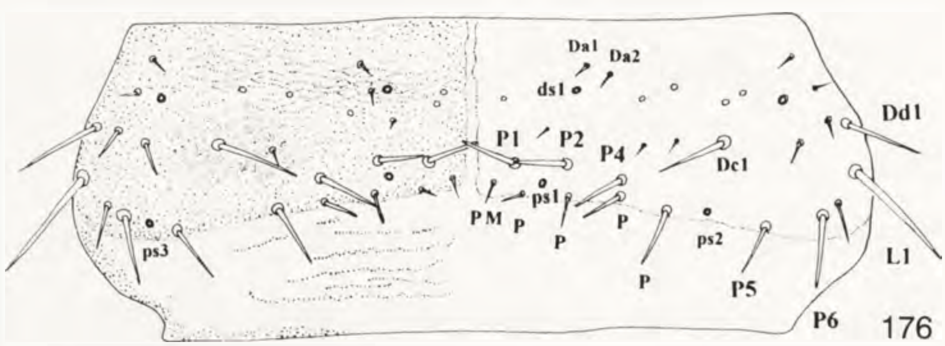

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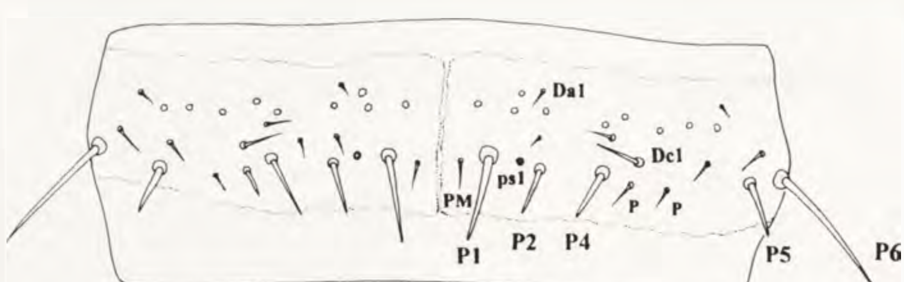

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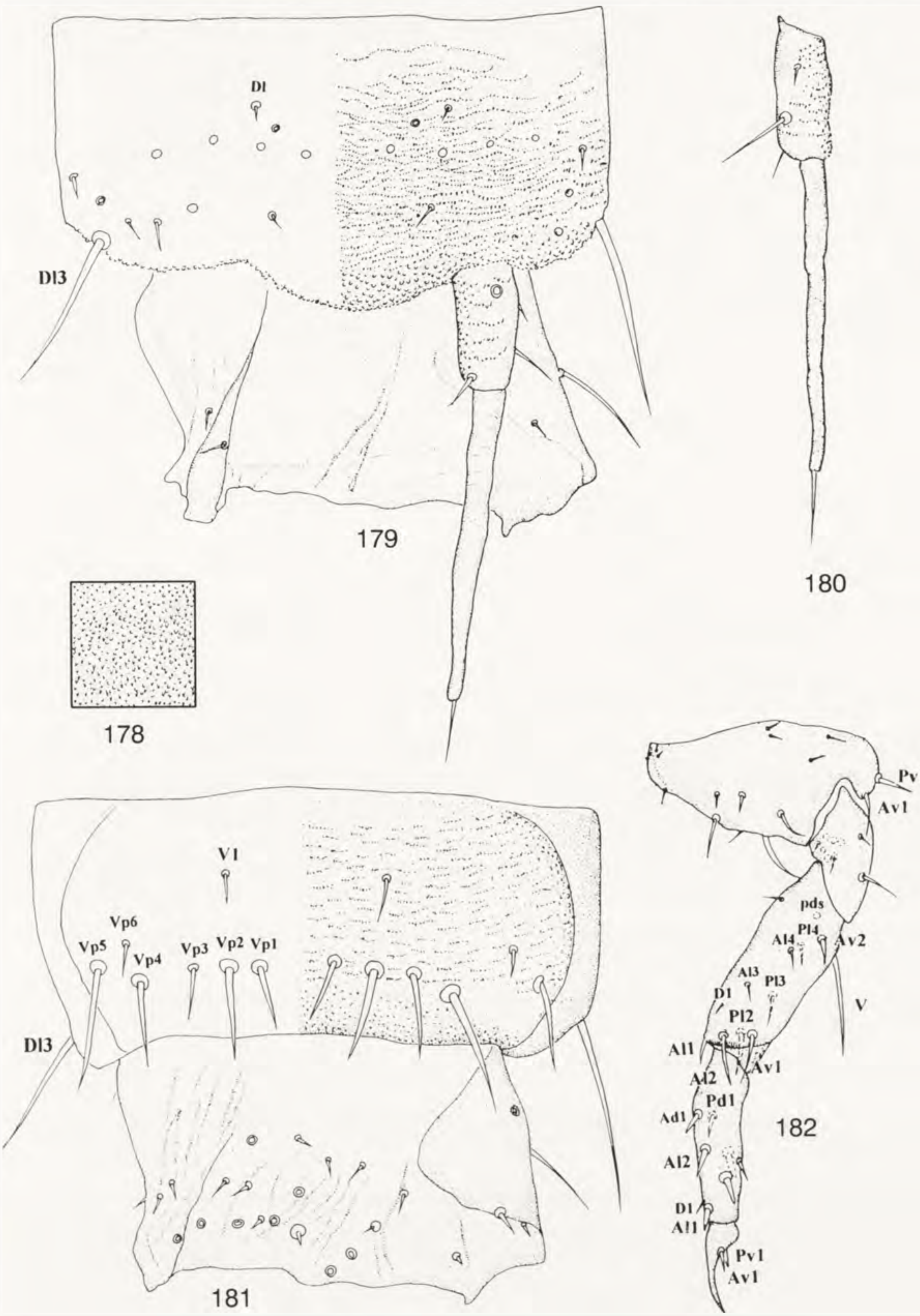
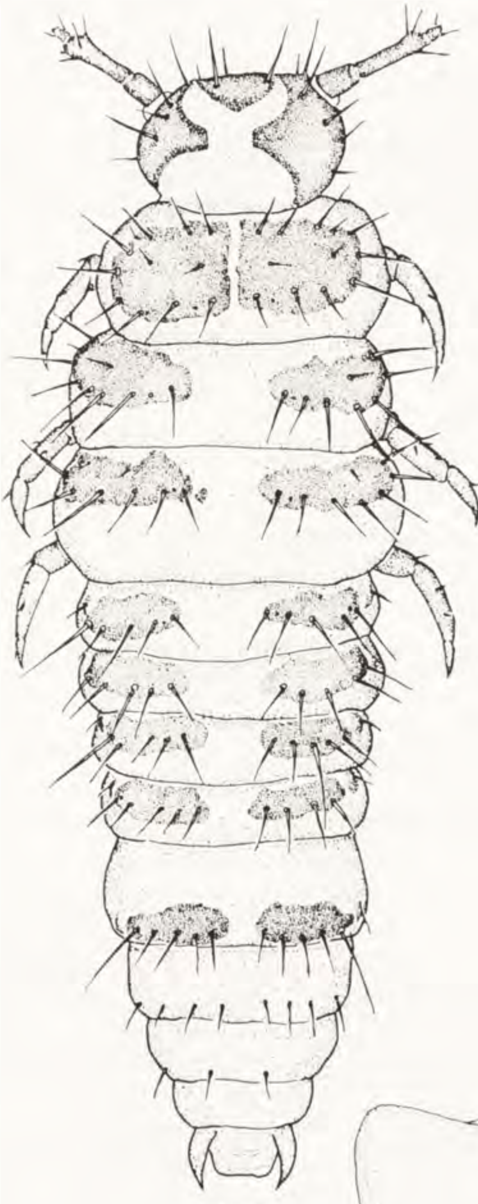
Figures 174–177. BII. (174) pronotum, (175) mesonotum, (176) metanotum, (177) abdominal segment I.



Figures 178–182. BII. (178) microsculpture of pronotum; (179) abdominal tergum IX and anal membrane; (180) urogomphus; (181) abdominal sternum IX and anal membrane; (182) proleg.



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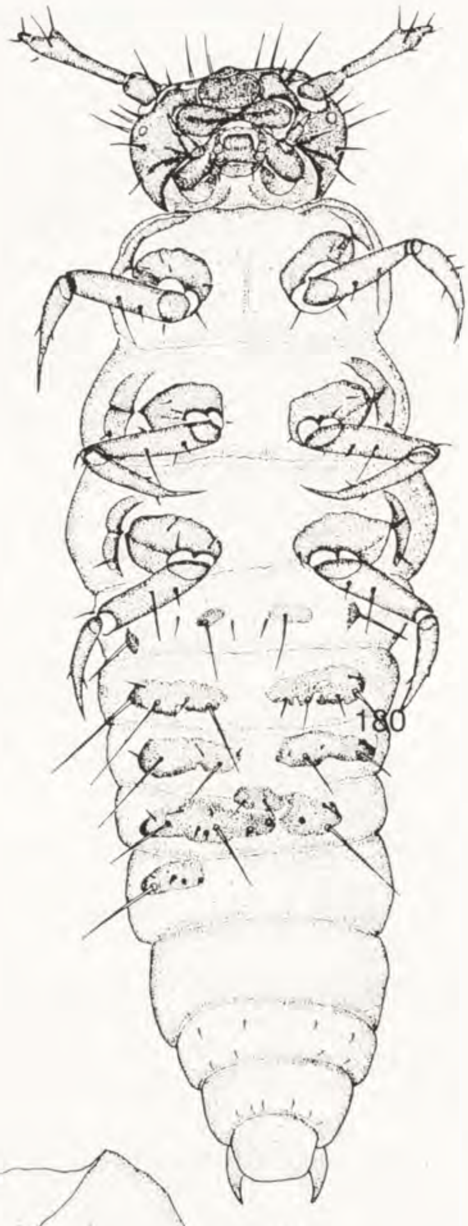

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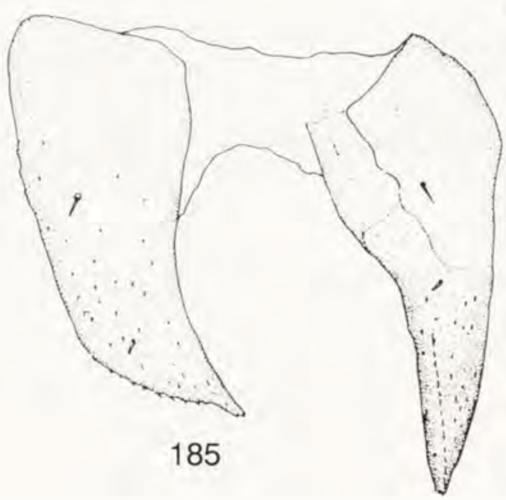

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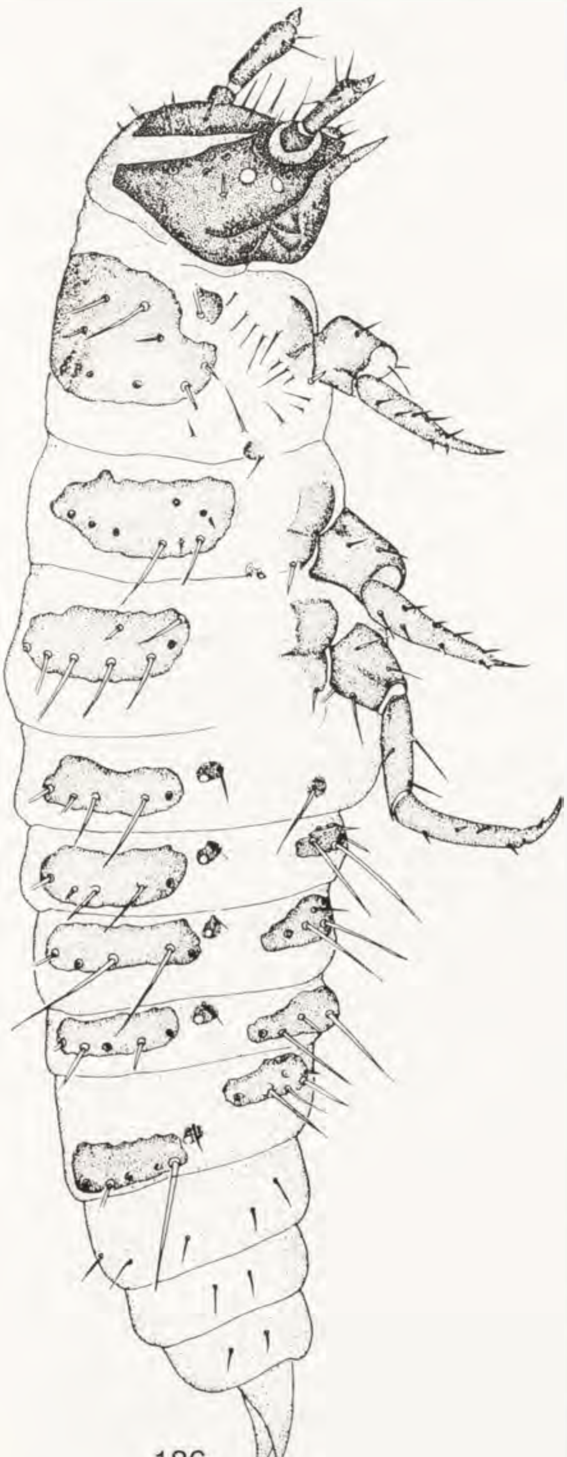
Figures 183–185. *Liodopria serricornis*. (183) dorsal and (184) ventral view of larval habitus, (185) urogomphi.



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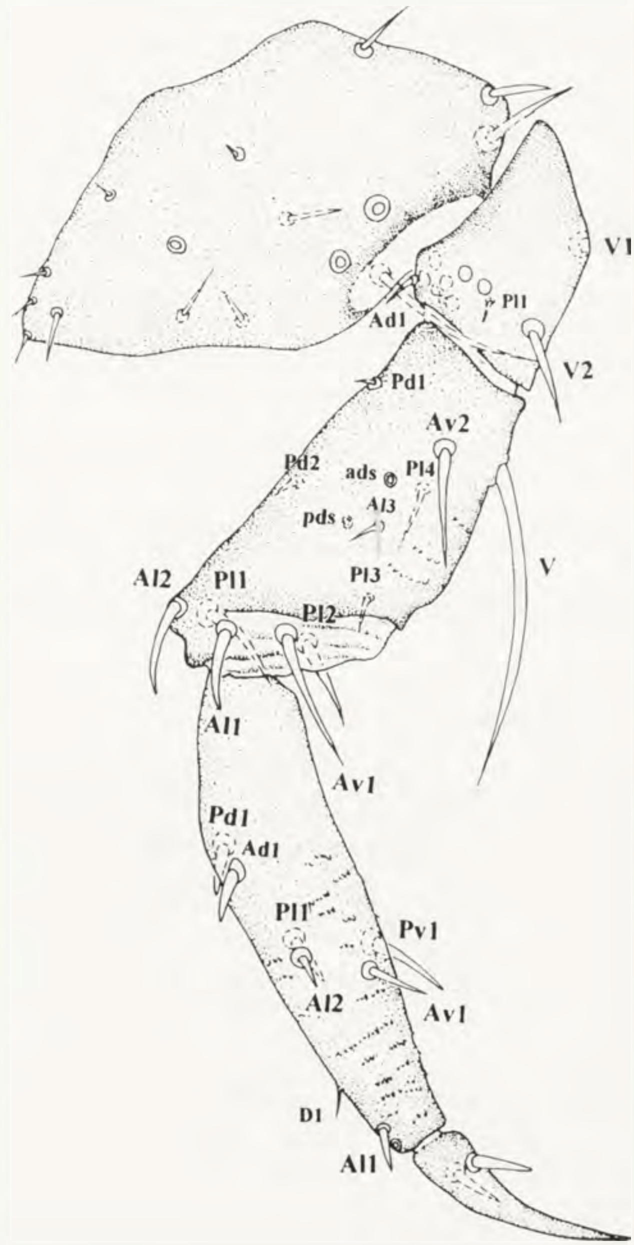

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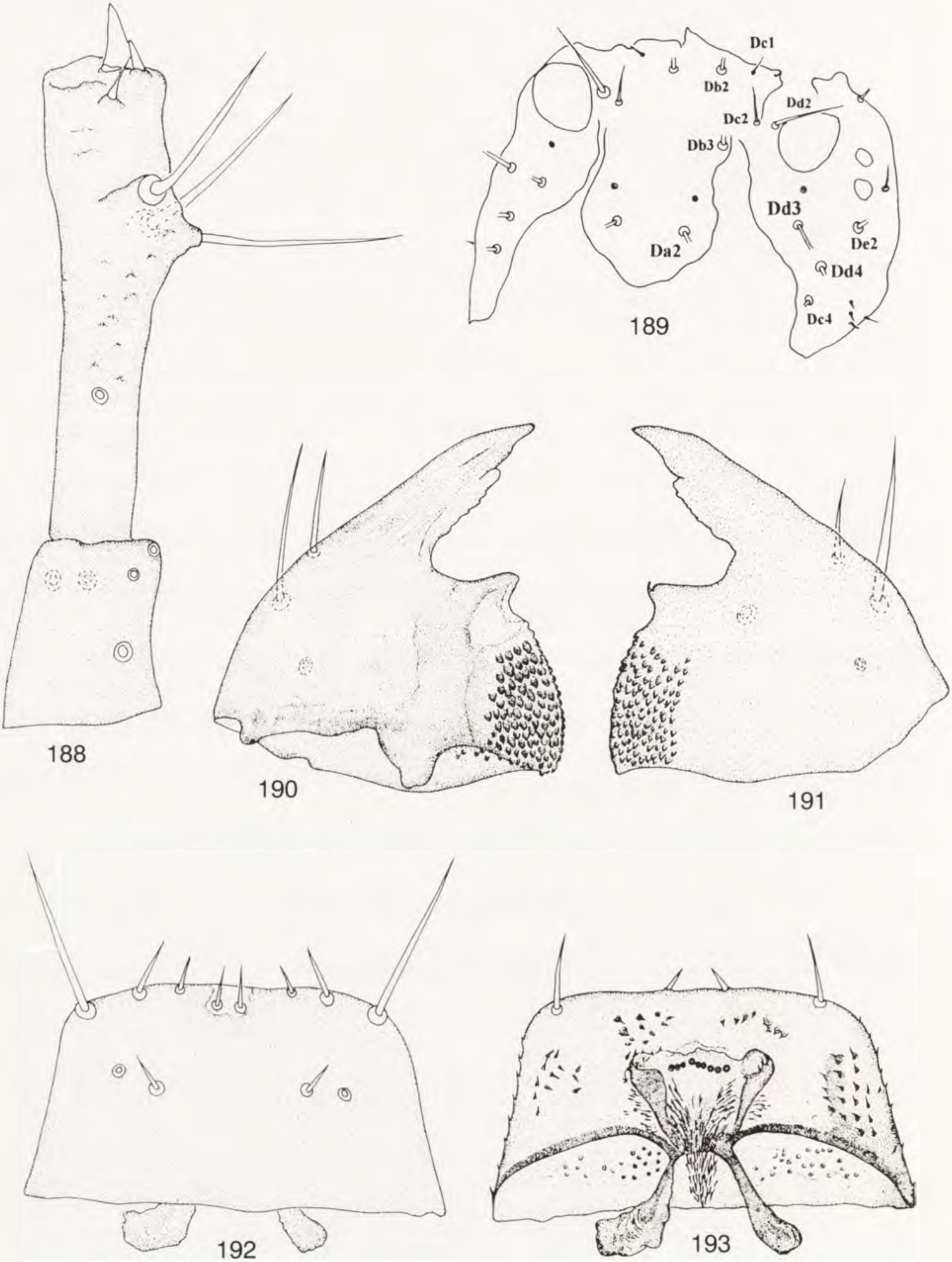
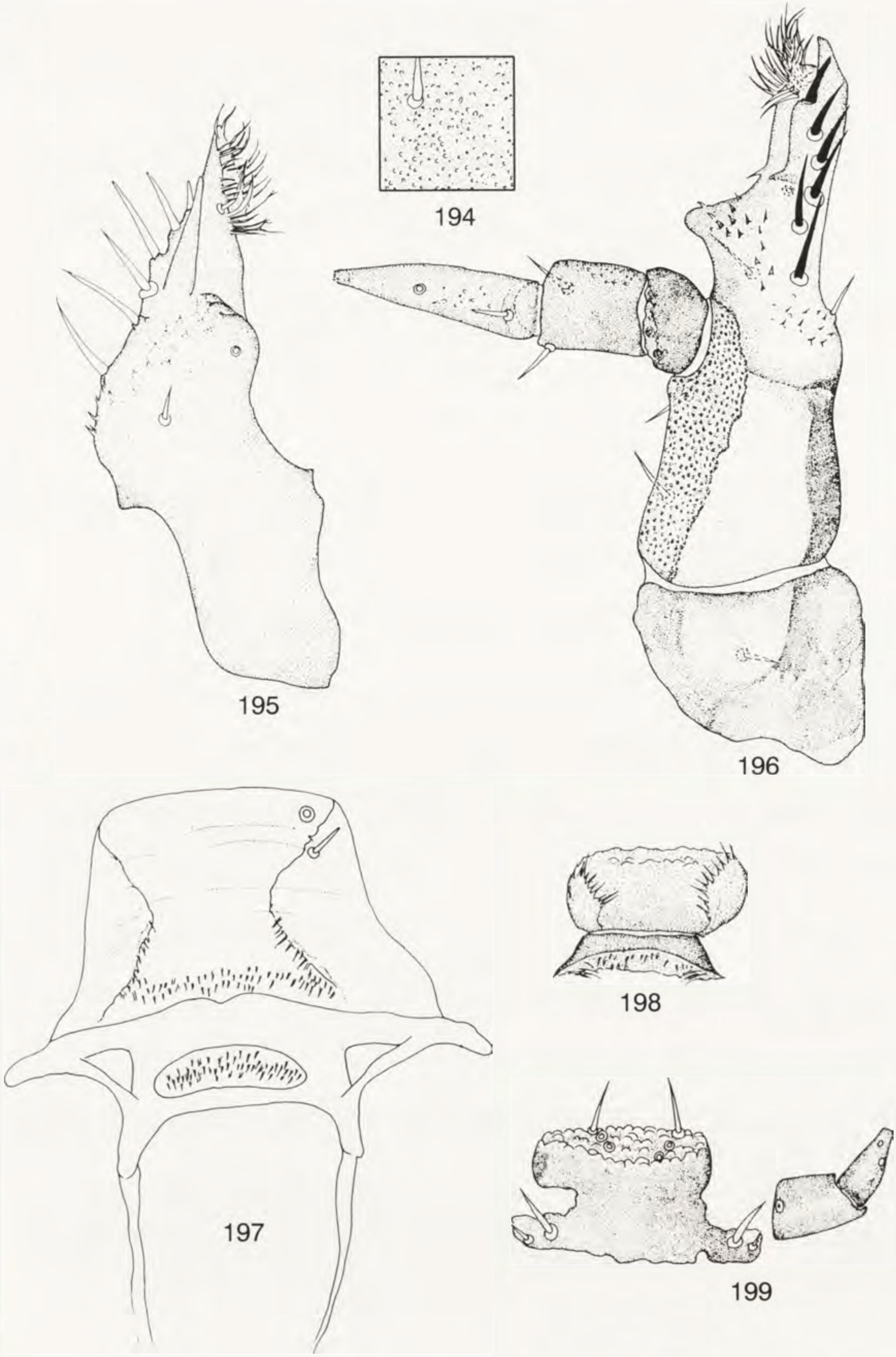
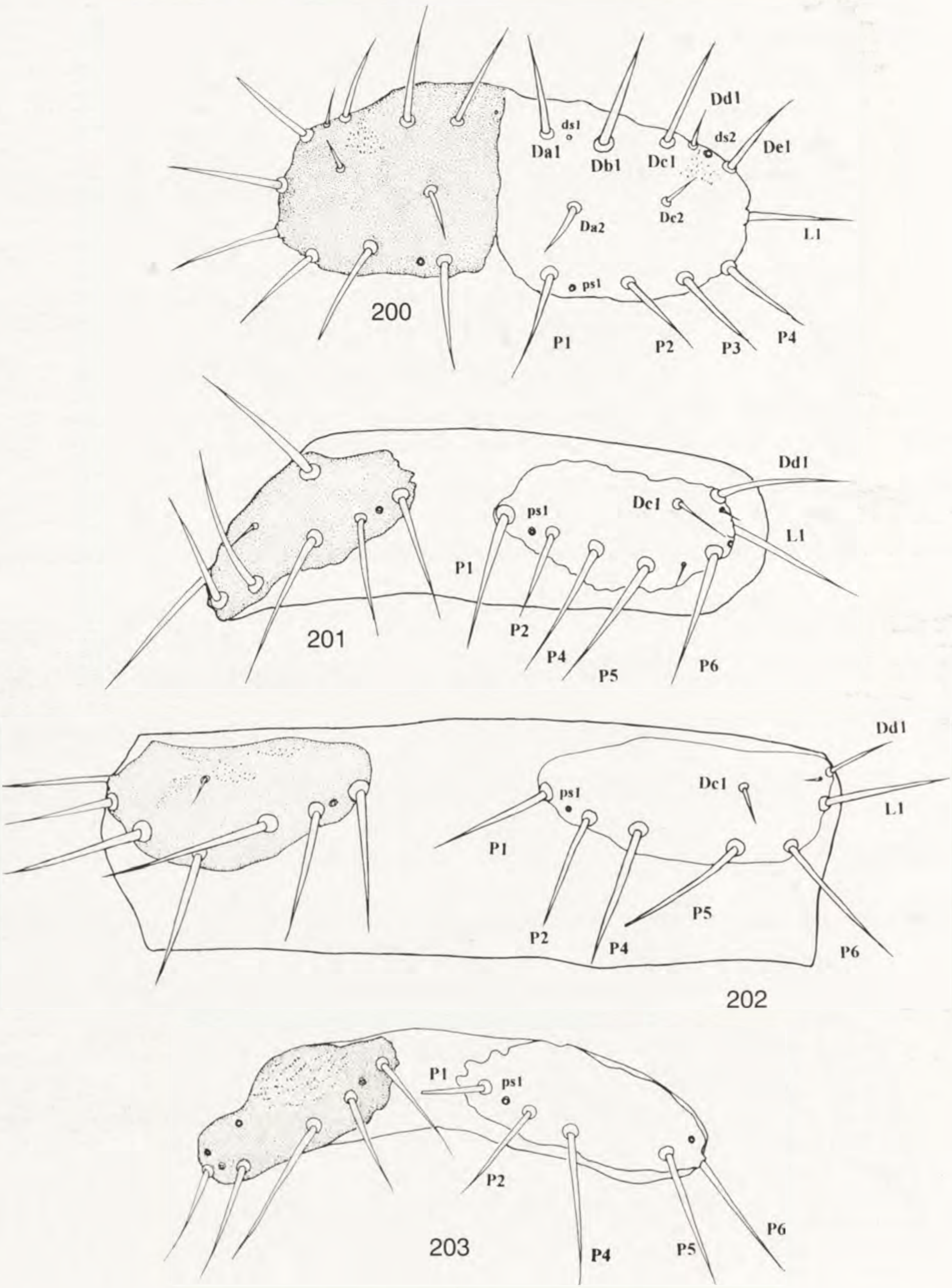
Figures 186–187. *Liodopria serricornis.* (186) lateral view of larval habitus, (187) proleg.



Figures 188–193. *Liodopria serricornis.* (188) antenna, (189) head, (190–191) mandible, (192) dorsal and (193) ventral view of labrum.



Figures 194–199. *Liodopria serricornis*. (194) microsculpture of head, (195–196) maxilla, (197) labrum and (198–199) ligula.



Figures 200–203. *Liodopria serricornis.* (200) pronotum, (201) mesonotum, (202) metanotum, (203) abdominal segment I.

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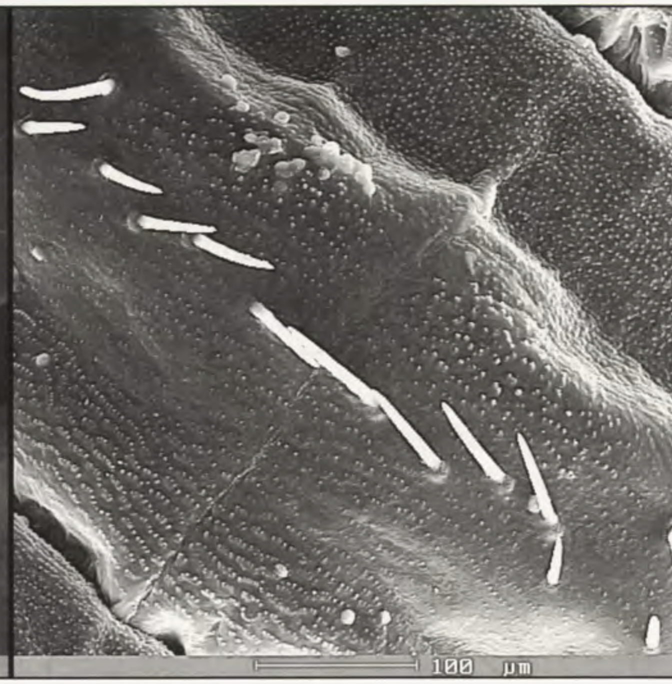

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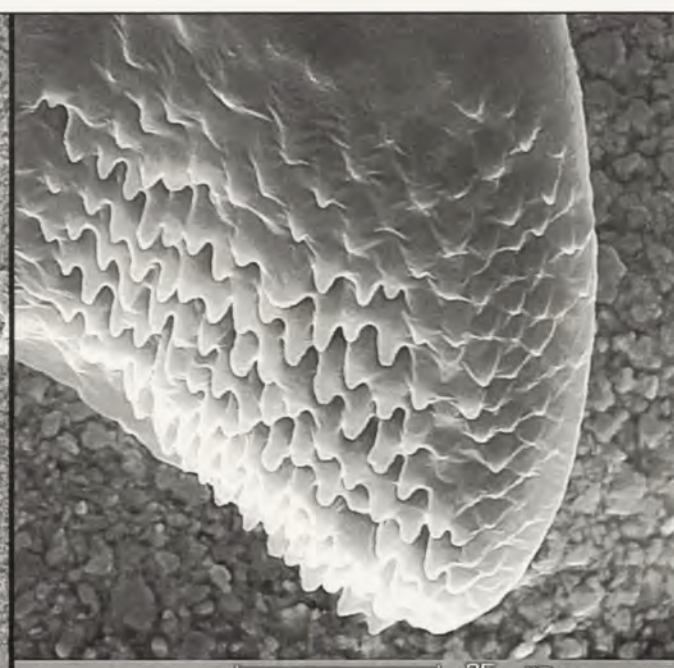

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Figures 204–207. *Anisotoma humeralis*. (204) cranium, (205) microsculpture of mesonotum, (206) mandible, (207) mandible, mola.

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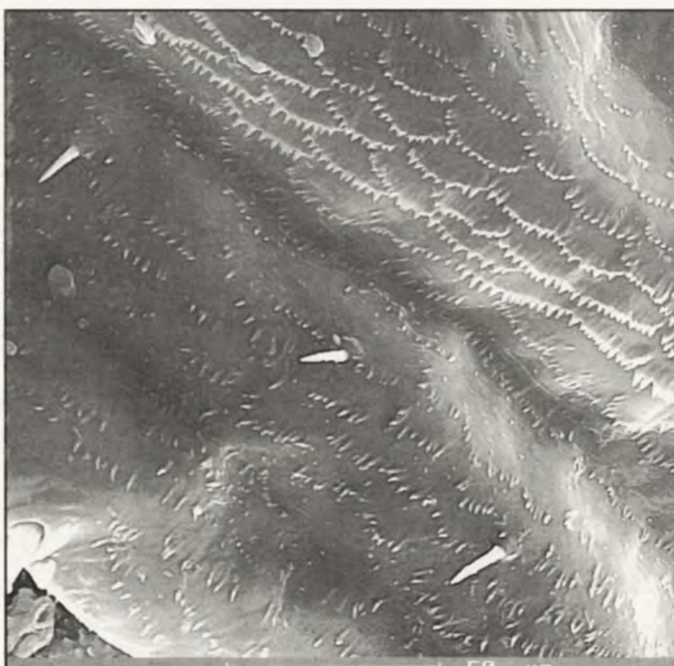

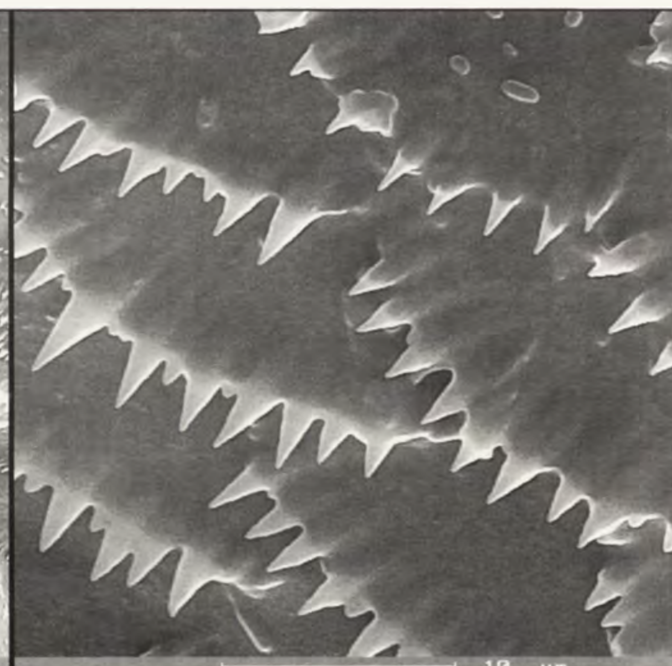

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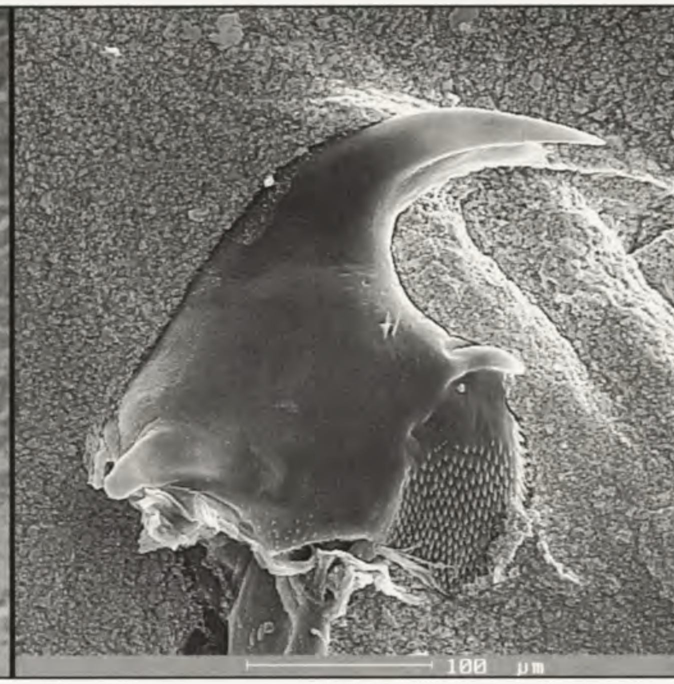
Figures 208–211. *Anisotoma castanea.* (208) lateral view and (209) microsculpture of cranium, (210–211) abdominal segment, microsculpture.



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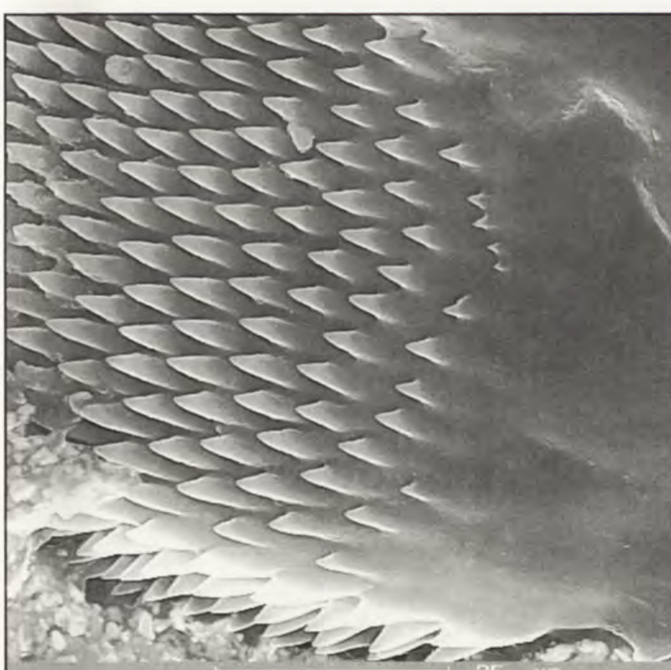

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Figures 212–215. *Anisotoma castanea*. (212) head with mouthparts, (213) mandible, (214) mandible, mola, (215) maxilla.

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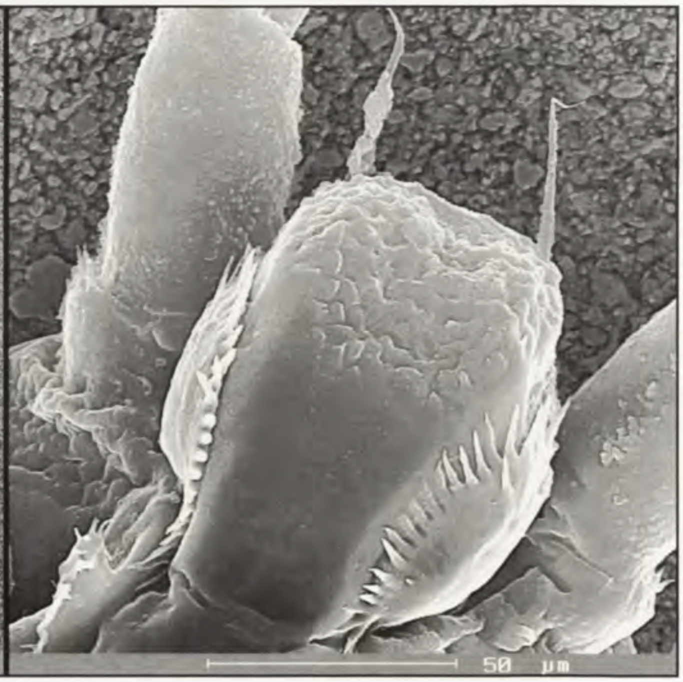

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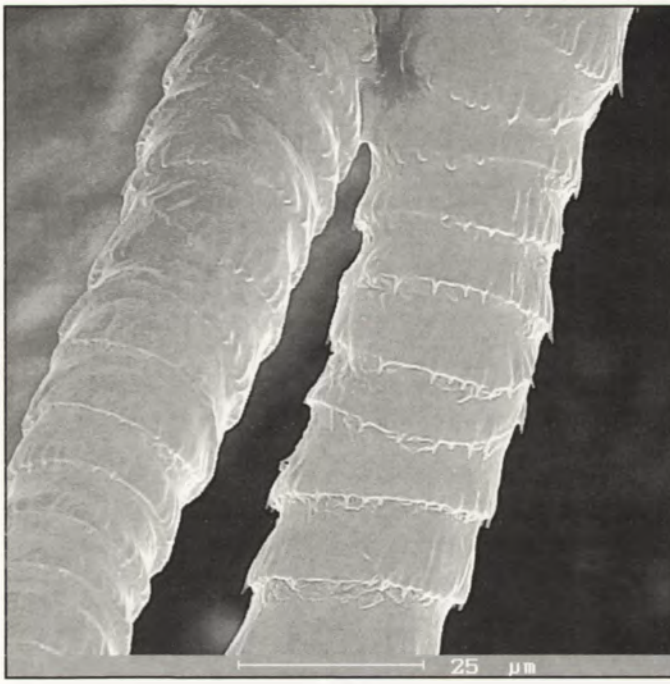
Figures 216–219. *Anisotoma castanea*. (216) maxillary palp, (217) galeal fringe, (218) labium, dorsal side and (219) ligula.



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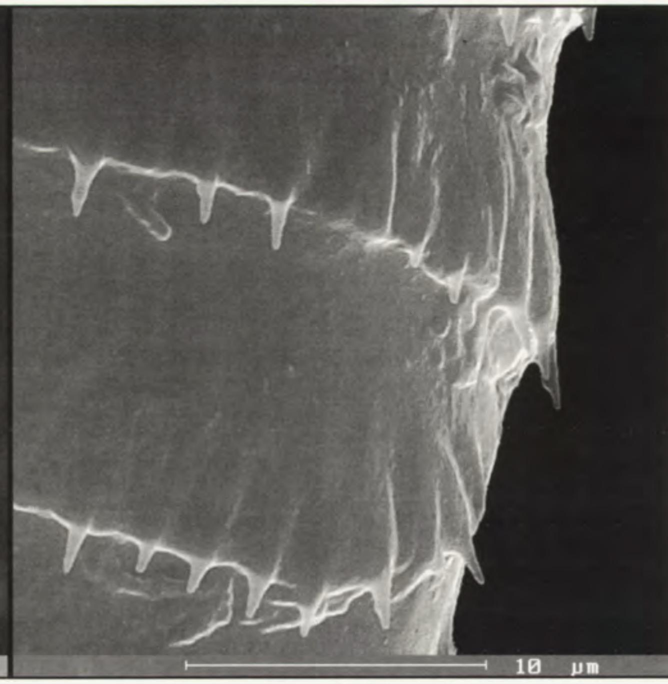

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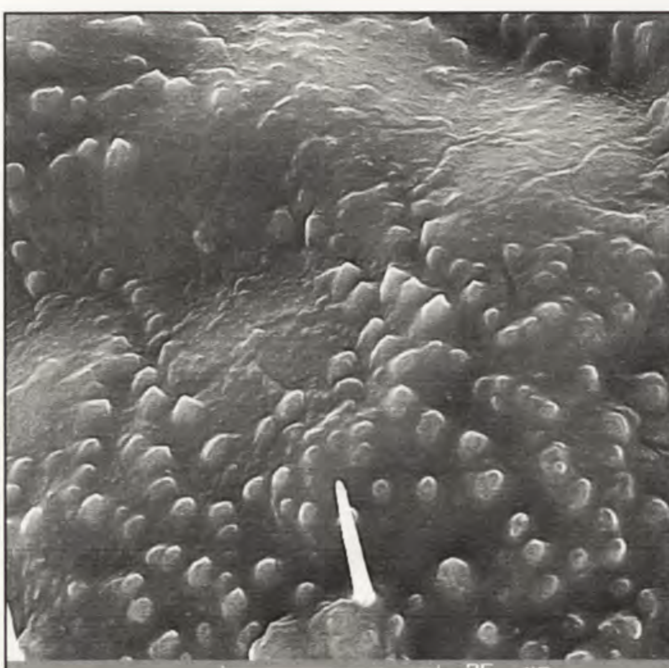

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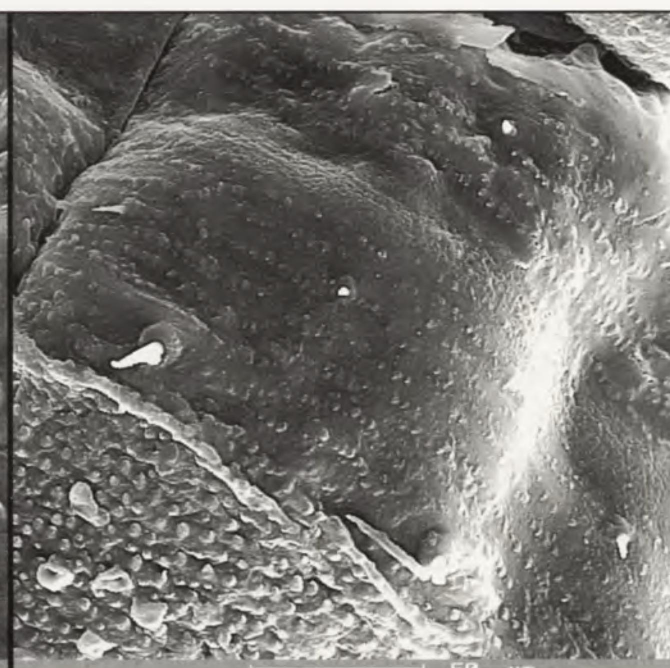

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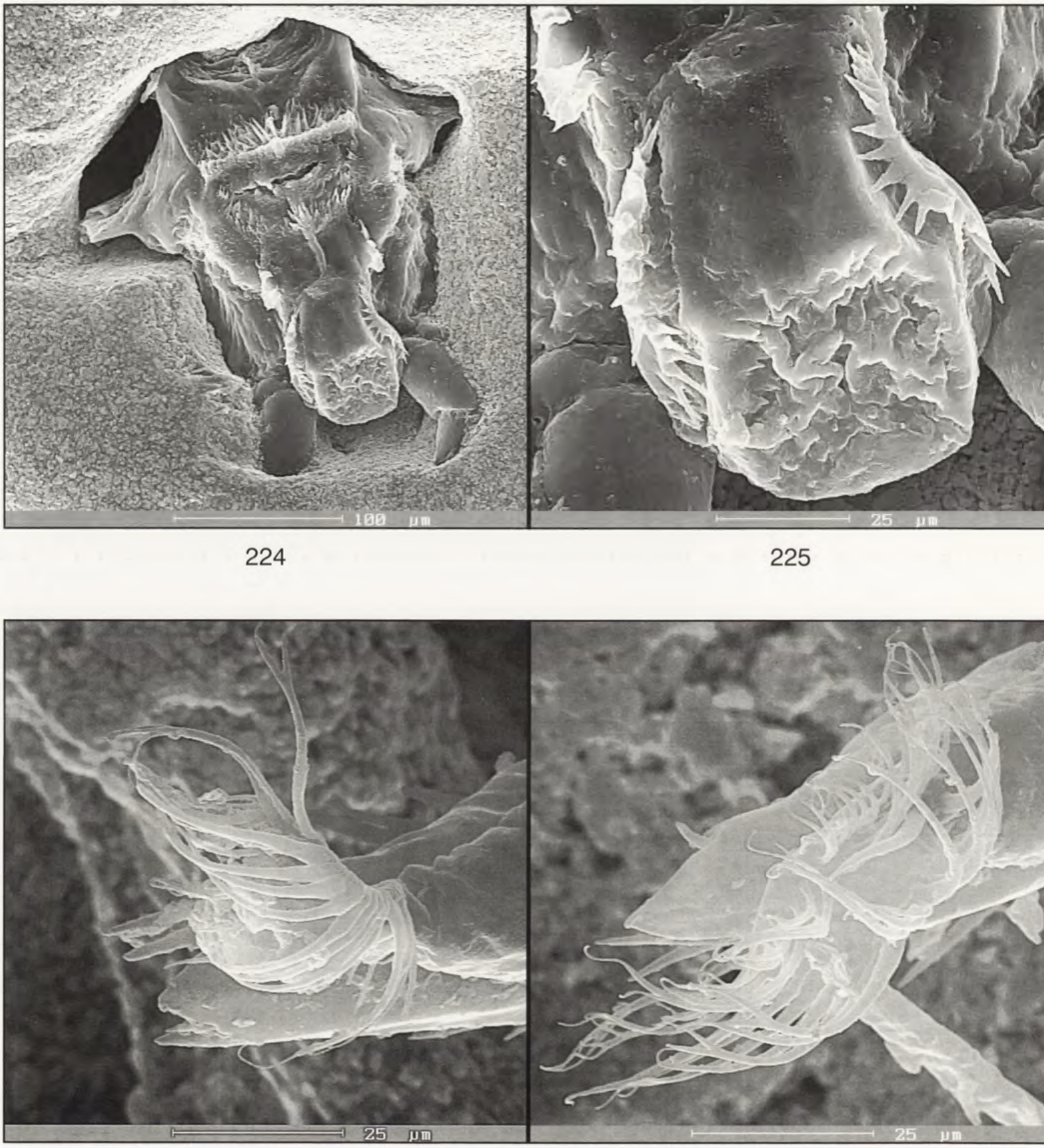
Figures 220–223. 220–221. *Anisotoma castanea*, 222–223. *Agathidium discoideum*. (220–221) urogomphus, asperities of segment II, (222) microsculpture of cranium, (223) abdominal segment, microsculpture.



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Figures 224–227. *Agathidium discoideum*. (224) labium, (225) labium, ligula, (226–227) galeal fringe.

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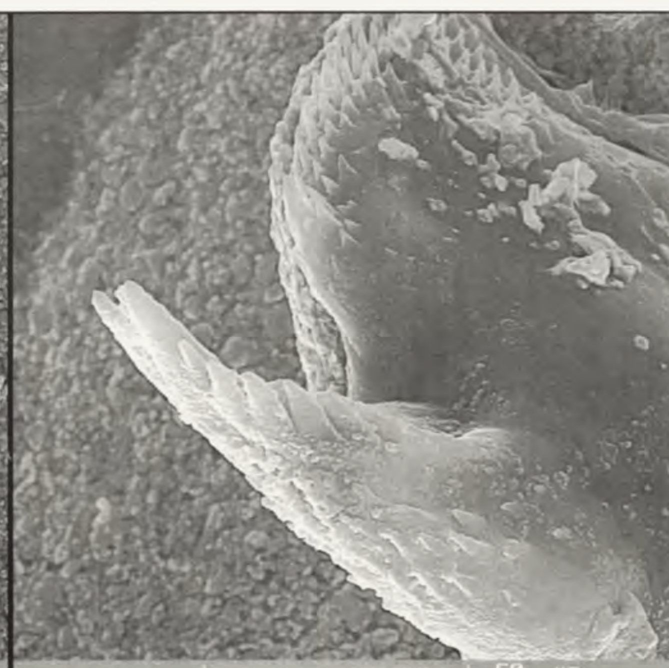

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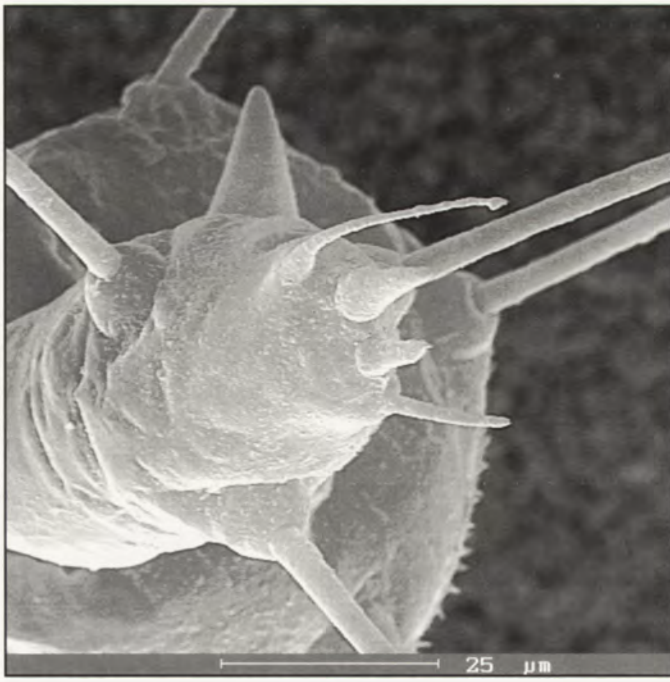
Figures 228–231. *Agathidium varians*. (228) cranium and thorax, (229) microsculpture of cranium, (230–231) mandible.



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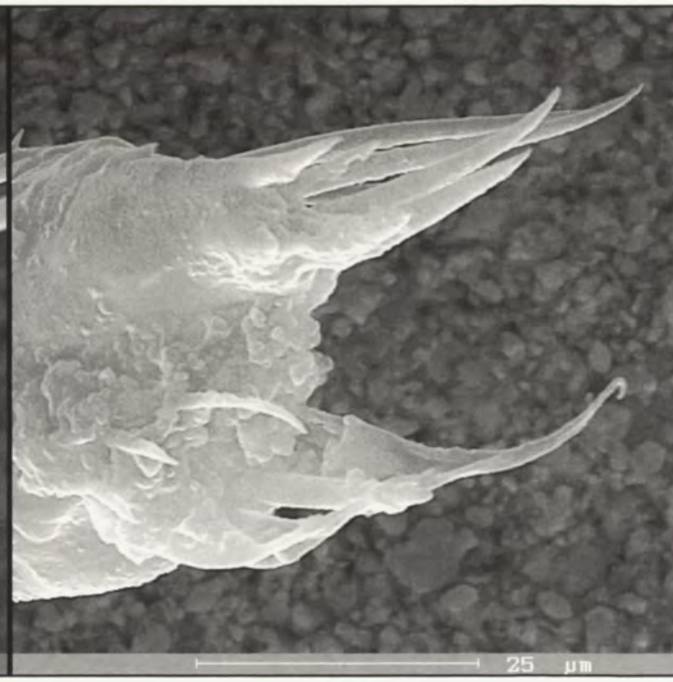

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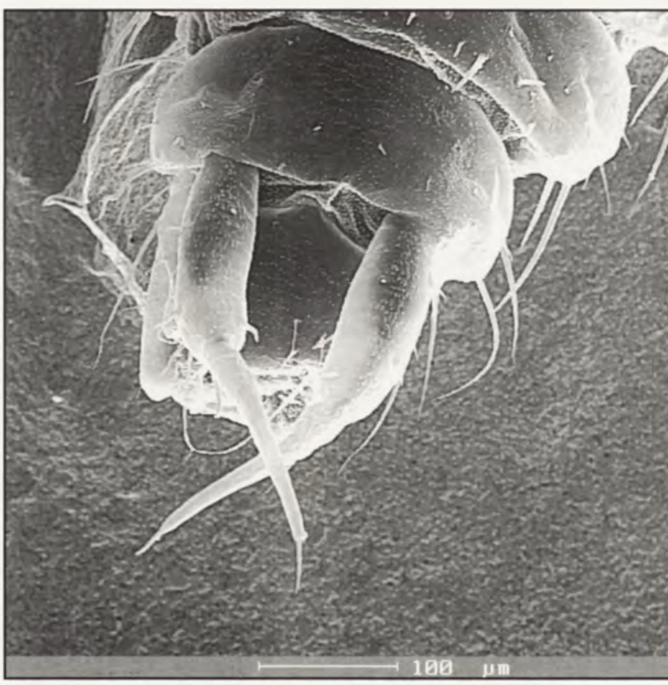

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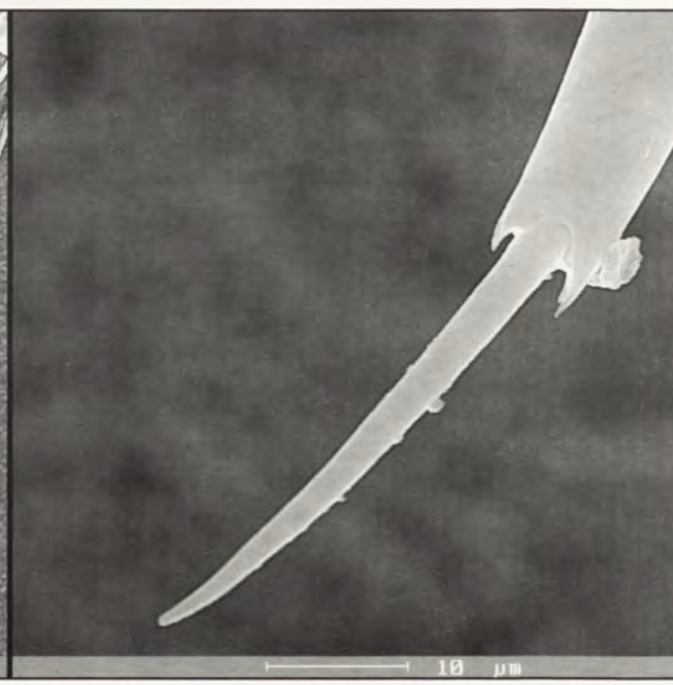

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Figures 232–235. *Agathidium varians*. (232) antennomere III, apex with sensilla; (233) galea, apex; (234) abdominal tergum and urogomphi; (235) urogomphus, apical stylus.