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Morphology and Ontogeny of Postembryonic Larval *Agathidium* and *Anisotoma* (Coleoptera: Leiodidae)

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ABSTRACT

The morphology and ontogeny of the three postembryonic larval instars are described for three North American species of the staphylinoid genus *Agathidium*: *A. pulchrum* LeConte, *A. aristerium* Wheeler, and *A. oniscoides* Palisot de Beauvois; and for one species of *Anisotoma*: *A. basalis* (LeConte). Because most characters were found to transform between larval instars I and II (II and III being similar for most characters), three semaphoronts were distinguished: semaphoront A (= instar I only), semaphoront B (= instars II and III), and semaphoront C (= instars I, II, and III). Two species, *Agathidium pulchrum* and *Anisotoma basalis,* feed on mature Myxomycetes, while the other two, *Agathidium oniscoides* and *aristerium,* are known to feed on plasmodia of host slime molds. Possible functional correlates of these habits are discussed, and a preliminary key is given to these North American species.

INTRODUCTION

This is a companion paper to a study (Wheeler, 1990) comparing the efficacy of Nelson's restatement of the biogenetic law and the outgroup comparison criterion for the polarization of character states (cf. Nelson, 1978; Watrous and Wheeler, 1981). The goals here are to describe the morphology and ontogeny of the postembryonic larval instars of three North American species of *Agathidium* and one of *Anisotoma* and to present a tentative diagnostic key to these American representatives of the tribe.

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TABLE 1
Larval Descriptions of Agathidiini
Modified from summary by Angelini and De Marzo, 1984

GENUS	SPECIES	REFERENCE	GEOGRAPHIC REGION
Anisotoma	basalis (LeConte)	current paper	Nearctic
	castanea (Herbst)	Perris, 1855	Palearctic
	glabra Kugel	Schiodte, 1861	Palearctic
		Boving & Craighead, 1931	
	humeralis F.	Erichson, 1847	Palearctic
		Henriksen, 1922	
		Paulian, 1941	
		Saalas, 1917	
Agathidium	?badium Erichson	Henriksen, 1922	Palearctic
	mandibulare Sturm	Fowler, 1889	Palearctic
		Kuhnt, 1909, 1913	
		Vaternahm, 1919	
	?nigripenne (F.)	Saalas, 1917	Palearctic
		Henriksen, 1922	
	sphaerulum Reitt. (=rotundatum Gyll.)	Henriksen, 1922	Palearctic
	seminulum (L.)	Perris, 1851	Palearctic
		Schaum, 1853	
		Chapuis & Candeze, 1853	
		Lacordaire, 1854	
		Fowler, 1889	
		Saalas, 1917	
		Vaternahm, 1919	
		Henriksen, 1922	
	varians Beck	Angelini & De Marzo, 1984	Palearctic
	pulchrum LeConte	current paper	Nearctic
	oniscoides Palisot	current paper	Nearctic
	aristerium Wheeler	current paper	Nearctic
Sphaeroliodes	rufescens Portevin	Morimoto & Hayashi, 1984	Palearctic

Staphylinoid beetles of the tribe Agathidiini (Leiodidae: Leiodinae) are primarily associated with true slime molds, Myxomycetes or Mycetozoa (Martin and Alexopoulos, 1969; Olive, 1975). All of the genera occurring in North and Central America have recently been or are currently being revised, including *Anisotoma* (Wheeler, 1979), *Stetholiodes* (Wheeler, 1981c; Angelini, 1985), *Cainosternum* (Wheeler, 1986), and *Agathidium* (Wheeler, in prep.). Adult agathidiines vary considerably in body form, coloration, size, convexity and contractility, and male secondary sexual characters of the mandible, metasternum, and tarsi. But few agathidiine larvae have been described in detail. And in spite of many common and widespread species in the New World, all existing descriptions are of Palearctic species (Angelini and De Marzo, 1984 and table 1).

This lack of published information is unfortunate for several reasons. Difficulties in making identifications of larvae interfere with collection of additional larval specimens and new host records. Like other staphylinoids, agathidiines have a variety of characters ranging from chaetotaxy to mouthpart structure (e.g., Ashe, 1986; Ashe and Wheeler, 1988; Dybas, 1976; Paulian, 1941). Attributes of these character-rich larvae remain unavailable for either cladistic analysis or formal classification. Ontogenetic transformation series in postembryonic larval agathidiines remain unstudied but may contribute to our understanding of the relationship between ontogeny and phylogeny in general and of the phylogeny of agathidiines in particular.

ACKNOWLEDGMENTS

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ONTOGENY

given an ontogenetic character transformation, from a character observed to be more general to a character observed to be less general, the more general character is primitive and the less general advanced (Nelson, 1978: 327).

Staphylinoid larvae are excellent animals in which to study ontogeny. Holometabolous insect larvae are sometimes said to be poor choices for ontogenetic studies because of the drastic molting changes between instars, unusual in animal development in general. But the conceptual problems are identical: how do changes occur during the development of the individual, and do character systems show any kind of orderliness that might correspond with phylogeny? If holometaboly forced such studies to artificially view ontogeny in discrete (but wholly arbitrary) units, then it might indeed be a poor and unrepresentative system in which to examine ontogeny. But, in fact, it is the distribution of character states among semaphoronts (periods in the development of individuals of the species, or in the life-cycle) that determines the units compared (Hennig, 1966; Wheeler, 1990). The postembryonic larval agathidiine passes through three instars, undergoing potentially significant morphological transformations at two ontogenetic times (fig. 3: OT^1, OT^2) corresponding with molts. In my study, almost without exception, character transformations occurred between instars I and II (fig. 4). Even though the molting between II and III is not necessarily any less physiologically complex, the characters analyzed simply did not identify this period as an informative one. Molts did not arbitrarily demarcate the units studied, but the "unfolding" set of characters did. For my study only three semaphoronts were required to explain all of the characters: semaphoront A corresponding to instar I (fig. 5: sA); semaphoront B corresponding to instars II + III (fig. 6: sB); and semaphoront C, representing all three instars combined or simply characters of "larva" (fig. 7: sC). Further, because the study of characters, semaphoronts, and ontogenetic sequences are conceptually similar in gradual embryonic and comparatively saltatory postembryonic holometabolous insects, the Holometabola simply have the added advantage of markers of ontogenetic time scales that cannot be missed, the molts. Given the difficulties of recognizing temporal "sameness" in developmental sequences, at least outside the framework of absolute time measured in hours or days, it could be argued that punctuated developmental programs, like those of arthropods, are better places in which to perfect our techniques for the general study of ontogeny and that our methods can then be applied to other, more gradualistic, systems.

For other taxa, and for other characters in these taxa, it might prove necessary to recognize other semaphoronts (say instars II and III individually). The important observation here is the reciprocal relationship between semaphoront and character. Semaphoronts are, as Hennig (1966) put it, the "character-bearers," and are in fact recognized by the appearance of attributes. Characters are analyzable only when the appropriate semaphoront is compared for each. It might also be noted that the semaphoront in this regard

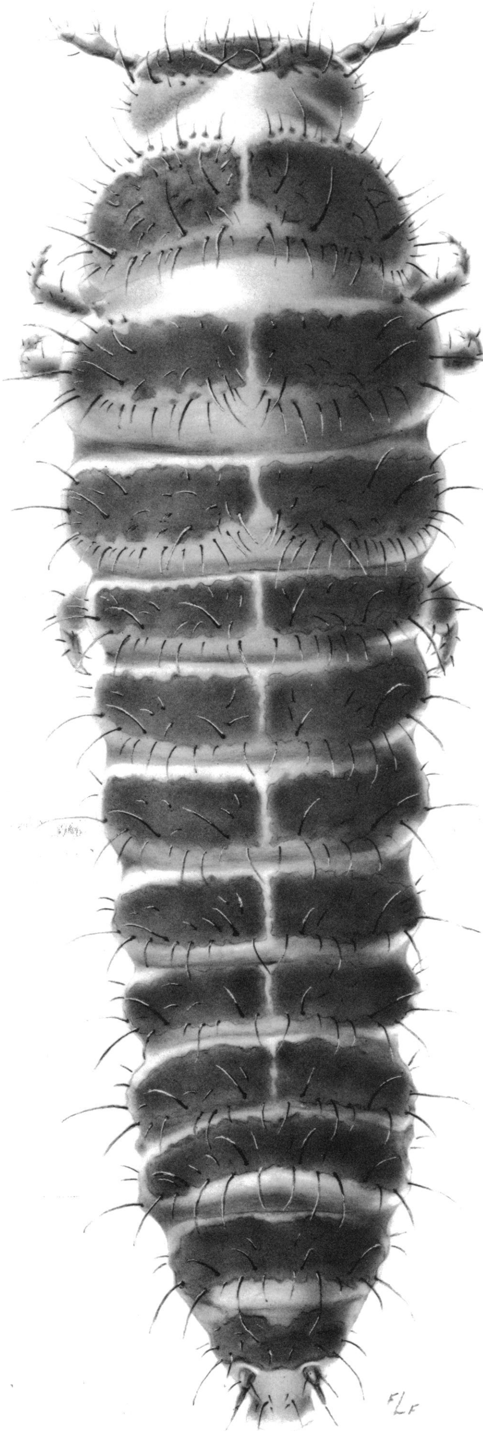


Fig. 1. *Agathidium aristerium* Wheeler, larval habitus, dorsal, Trumansburg, New York.

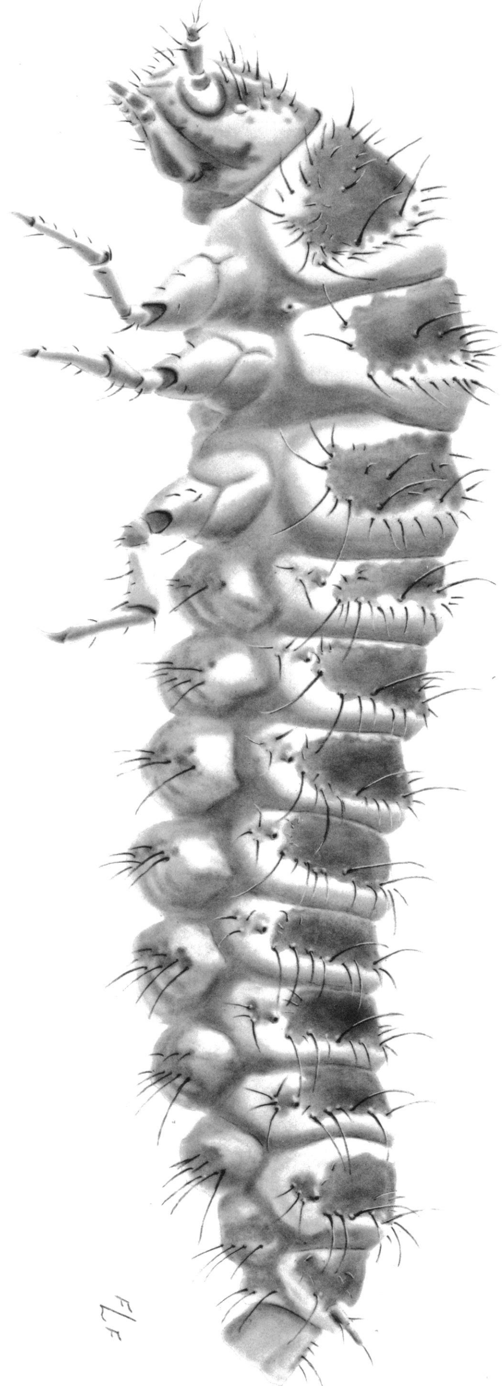
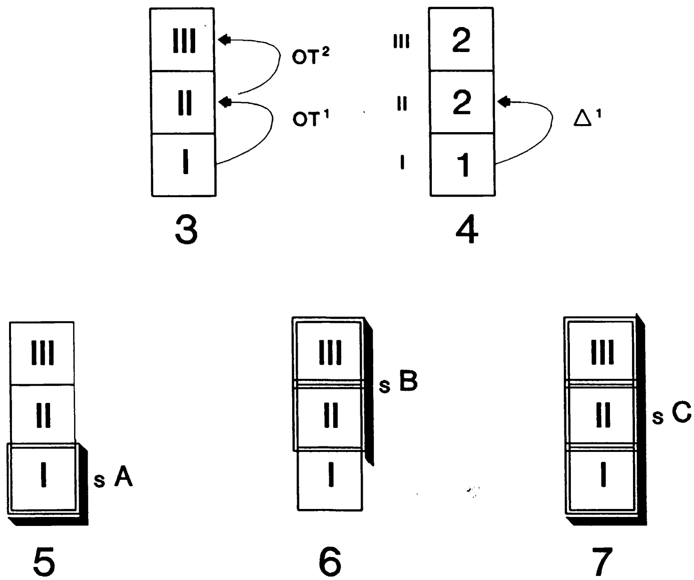


Fig. 2. *Agathidium aristerium* Wheeler, larval habitus, lateral, Trumansburg, New York.



Figs. 3–7. Diagrams depicting relationships among instars and semaphoronts with regard to ontogeny. Larvae have three instars (I, II, and III), the character states of which are continuations or modifications of neonatal conditions such that transformations occur in ontogenetic time frames 1 or 2 (fig. 3). In fact, all characters studied here transform between instars I and II (fig. 4), such that three semaphoronts are necessary and sufficient: semaphoront A (fig. 5), semaphoront B (fig. 6), and semaphoront C (fig. 7). See text for discussion.

varies depending on the character studied. For most chaetotaxic characters, semaphoronts at individual instar levels are appropriate and necessary. For a study of the origin of a pupal stage within the neopterous insects, a broader semaphoront would be necessary, including at least all postovarian and preimaginal stages. And comparisons of modifications of life cycles themselves may necessitate looking at the whole life cycle as one semaphoront (O'Grady, 1985). This does not impede the simultaneous use of other semaphorontic levels for other characters, such as postembryonic larvae for comparison of urogomphi.

Character polarity refers to hypotheses designating which of two character states is apomorphic and plesiomorphic, relative to the other. As recently as a decade ago, there were authors contending that many credible criteria existed for estimating polarity (e.g., Crisci and Stuessy, 1980; but see Wheeler, 1981b). More recently, a consensus has emerged that the number of criteria is three: outgroup comparison, fossil precedence, and ontogenetic sequence, each ultimately explainable in terms of parsimony (Farris, 1982, 1983). The role of fossils in polarity assessment has been called into question by Elredge and Cracraft (1980), Patterson (1981), and others. These authors have suggested that fossils be viewed and analyzed just like neontological specimens and that they offer no fundamentally unique insights into character analysis. Gauthier et al. (1988) have questioned this harsh assessment. Fossils do provide views of extinct taxa and character states and some measure of minimum absolute age, but their analysis remains conceptually a special application of the outgroup comparison criterion (e.g., Nixon and Crepet, 1989). Outgroup comparisons have long been employed, but, like cladistics as a whole, with a mixed degree of rigor. Maslin (1952), Hennig (1966), and Ross (1974, "ex groups") more or less clearly recognized the procedure, which was formalized as a criterion by Watrous and Wheeler (1981). More recent discussions about outgroup comparison include a paper by Maddison et al. (1984) stressing global parsimony.

Ontogeny has remained somehow more enigmatic, held out with great promise seldom realized. In the preface to *Ontogeny and Phylogeny,* Stephen Jay Gould (1977) quipped:

> I tell a colleague that I am writing a book about parallels between ontogeny and phylogeny. He takes me aside, makes sure that no one is looking, checks for bugging devices, and admits in markedly lowered voice: "You know, just between you, me, and that wall, I think that there really is something to it afterall." (pp. 1–2)

But what is that something? If, as is widely supposed, it has been shown by von Baer that ontogenies do not recapitulate adult phylogenies but ancestral ontogenies, how might ontogeny be applied to the problem of evolving characters? The answer was given by Gareth Nelson (1978; see quotation above), who suggested a simple, explicit, and rigorous criterion by which the ontogenetic sequence can be analyzed in order to arrive at polarized character states. Kluge (1985) referred to this restatement of the biogenetic law as "Nelson's Law," but I will term it simply "Nelson's Rule." Nelson's Rule has met with acceptance and criticism in the systematics community and many papers have been published as a direct consequence of it. Some, but by no means all, of them are Kluge (1985), Kluge and Strauss (1985), de Queiroz (1985), Nelson (1985), Kraus (1988), and a book edited by Humphries (1988).

Based on my comparative study of postembryonic larval agathidiine data and a review of the recent literature, I decided to compare the efficacy of the two principal competing criteria for polarizing data: outgroup comparison (as formulated by Watrous and Wheeler, 1981) and Nelson's Rule (sensu Nelson, 1978). The details of that analysis are discussed at length elsewhere (Wheeler, 1990), and the evidence for it presented herein.

CHARACTER ANALYSIS

The terms character and character state have been used in many ways in recent literature and a brief explanation of my view on their definitions is in order. I follow Platnick (1979) in regarding characters as original attributes or novelties and all their subsequent modifications. This can be expressed simply as follows: $C^x = \Sigma\, cs^{0-n}$, where C^x stands for character x, cs^0 for an original constantly distributed attribute, and c^{1-n} for subsequent modifications $1 - n$ of the original character state, cs^0. In evolutionary terms, we are theoretically estimating the *character-state transformation* from a plesiomorphic to a relatively apomorphic condition. Because each transformation is a unique event, all characters can ultimately be seen in terms of bistate characters progressing from the unmodified ancestral state to the modified descendant state (Nelson and Platnick, 1981). In practice, there is sometimes utility in speaking of multistate characters, but these are in the final analysis simply unresolved situations. It is possible to estimate character state adjacencies, i.e., the relative position of each state in a transformation series (Nixon and Wheeler, MS) prior to explicit hypotheses about polarity. As Platnick (1979) has explained, every character state is a modification of some preexisting one; and characters are related to one another as a series of nested sets. States summed within a single character are, therefore, assumed to be related to one another in a singular and at least potentially (in the case of multistate characters) specifiable order.

A set of 60 characters that looked potentially cladistically informative were compiled from this comparative study (table 2) and analyzed by both Nelson's Rule and the outgroup comparison rule (Wheeler, 1990). Of these, a total of 25 synapomorphies were hypothesized by the two criteria combined. Twenty-three were resolved by Nelson's Rule and 14 by the Outgroup Rule, of which some were the same. In all, 52 out of 60 characters studied involved setae of various regions of the body including the head, thorax, abdomen, urogomphus, and legs.

PHYLOGENY

The cladogram in figure 8 shows one of four equally parsimonious hypotheses of the relationships among the larvae described below, based on polarities arrived at by Nelson's Rule and analyzed using J. S. Farris's (1988) microcomputer program Hennig 86 (Wheeler, 1990). Numbers on the cladogram were arbitrarily assigned for use in the computer program ClaDos (Nixon, 1988) and correspond to characters in table 2 (as indicated in table 3). This and alternative cladograms are presented with additional discussion elsewhere (Wheeler, 1990).

Agathidium pulchrum and *A. aristerium* are hypothesized to be sister species, supported by six characters, one of which is a reversal. This relationship was supported in all analyses done, but one based on the outgroup criterion of Watrous and Wheeler (1981) produced an equally parsimonious cladogram in which *A. aristerium* and *A. oniscoides* are sister species.

Support for *Agathidium oniscoides* as the sister species of *pulchrum* + *aristerium* involved a large number of characters which, in some analyses, primarily involved features subsequently reversed.

These relationships are tentative and will be tested as additional larval characters and adult characters are analyzed in future studies. Conclusions here are based on larvae of three *Agathidium* species out of a world fauna of several hundred species; and adult character systems have not yet been analyzed formally for any portion of the genus.

MORPHOLOGY

Characters presented in the formal descriptions involve external morphological structures and measures. Morphometrics, including a key to the acronyms used in the text, are summarized in figure 9. The largest number of characters are those that can be collectively called chaetotaxic, loosely defined to include both setae and sensilla.

The chaetotaxic system used here resembles, but is not a faithful application of, the one proposed by Ashe and Watrous (1984). I found the longitudinal orientation of setae into imaginary rows more easily adapted to descriptions of agathidiine larvae than Paulian's (1941) transversely oriented system. Homology statements across larvae of the Staphylinoidea are difficult because of a paucity of described taxa, although, for a limited number of setae and sensilla, such hypotheses seem reasonable (e.g., the bands of campaniform sensilla of the trochanter; the "digitiform organ" solenidium of antennomere II; and posterior setae of the nota). My intent in this paper has only been to describe the morphology and ontogeny of the four species studied. I wished to facilitate my own comparisons among them, but made no particular attempt to assure such comparisons with other taxa. My comparison of Nelson's Rule and the outgroup comparison rule necessitated comparisons among the larvae included in the analyses. It did not require absolute homologies to be drawn to staphylinoids or coleopterans more generally.

As in the Ashe-Watrous system, my labels proceed in general from anterior to posterior in rows, and from mesad to laterad in order of rows. Simple designations of position, again following Ashe and Watrous's recommendations, were used to name rows, such as D for dorsal, L for lateral, and so forth. Setae were numbered within rows from anterior to posterior beginning with 1, and rows lettered from midline laterad beginning with *a*. Morphological area codes are uppercase letters; rows lowercase letters; and setal numbers given as Arabic numerals. On the head, for example, rows of setae begin near the midline with row D (dorsal), and include rows Da, Db, Dc, Dd, and De. Variable numbers of setae are included within each row, Da1, Da2, Da3, etc. The head also bears a number of small posterior setae, generally four but sometimes five in number. When structures, like the antenna or urogomphus, are subdivided into segments, roman numerals are used to signify the segment, beginning with the basal one and proceeding to the distal end, while numbers of setae or other structures are presented in Arabic numerals, with the exception of acronyms applied to figure 9.

Characters are organized by body region, and within region by instar, in my formal descriptions. Actually or potentially useful cladistic characters, totaling 60 (table 2), were extracted and discussed in a separate paper (Wheeler, 1990).

At various places in this paper I will refer to the species studied by acronyms. BAS for *Anisotoma basalis,* PUL for *Agathidium pulchrum,* ARI for *Agathidium aristerium,* and ONI for *Agathidium oniscoides.* When single

TABLE 2

Characters Used in Cladistic Studies by Wheeler (1990)

Figure references to illustrations in this paper. B = *Anisotoma basalis*; P = *Agathidium pulchrum*; O = *Agathidium oniscoides*; A = *Agathidium aristerium*. Plus means present; minus absent; first symbol for semaphoront A, second for B. Discussion of position of each character relative to other structures given in descriptions in text. Meristic characters given as number in semaphoront A followed by number in semaphoront B, separated by a period (.)

no.	character state	figures	distribution B	P	O	A
	CRANIAL CHARACTERS	10-20				
1	Seta Da1 present	10-17	--	++	++	++
2	Seta Da* present	18-20	-+	--	--	--
3	Seta Da*a present	12,14,15,17	-+	--	++	-+
4	Seta Db1	10-14,18-20	++	++	--	++
5	Seta Db*	12,14,19,20	-+	--	--	-+
6	Seta Db**	12,14	--	--	--	-+
7	Seta Dc1	10-17,19,20	-+	++	++	++
8	Seta Dc2	10-12,14,15-17 19,20	-+	++	++	-+
9	Seta Dc**	11,12,14	--	-+	--	-+
10	Seta Dc*	11,12,14,15,17	--	-+	-+	-+
11	Posterior seta P5	18-20	++	--	--	--
12	Seta Dd1	11,12,14,15-17	--	-+	++	-+
13	Dd2a	11,12-14,19,20	-+	-+	--	++
14	Seta Df1	10-11,15-20	++	++	++	--
15	Stemmata #	10-20	2.2	2.2	2.2	1.1
16	Lateral seta L2	12,14,15-17	--	--	++	-+
17	Lateral seta L*a	11,12,14,15,17	--	-+	-+	-+
18	Lateral seta L*b	11,12,14,15	--	-+	-+	-+
19	Lateral seta L*c	11	--	-+	--	--
	ANTENNAL CHARACTERS	10-20,23,42				
20	Solenidia of ant.II		2.3	1.2	1.2	1.2
21	Digitiform organ divided	10	--	++	--	--
	PRONOTAL CHARACTERS	56-64				
22	Mesal Da seta	57, 59	--	-+	--	-+
23	Posterior Db setae, no. (and, rarely)	56-64	1.5 1.7	0.5	1.3	1.5
24	Seta Db*	59,61,63-64	-+	--	-+	-+
25	Posterior Dc setae	56-64	1.3	3.12	1.3	3.12
26	Dc setae anterior to Dc1	56-64	0.1	0.0	0.1	0.3
27	Dd setae posterior to Dd1	56-64	0.2	0.5	0.2	0.1
28	Lateral setae post. L1	56-64	0.1	0.2	0.2	0.2
29	Lateral seta ant. L1	56-64	1.1	0.3	1.5	0.6
30	Medial posterior seta (PM)	57,59,64	-+	-+	--	-+
31	Posteriors between P1/P2	58-59,62-64	0.1	0.1	0.1	0.2
32	Posteriors between P2/P3	56-64	0.3	0.2	0.2	0.6

TABLE 2—(*Continued)*

no.	character state	figures	distribution B	P	O	A
	PRONOTAL CHARACTERS (Cont'd)					
33	Posteriors between P3/P4	59,64	0.1	0.1	0.1	0.3
34	Setae between D1's	59,61,64	0.0	0.1	0.1	0.3
	UROGOMPHAL AND NINTH ABDOMINAL SEGMENT CHARACTERS (Figs. 98-105)					
35	Setae anterior to P4,P5	99,103	0.0	0.1	0.1	0.3
36	Setae between V1/V2 posts. presence of 2nd seta	103,105	--	--	-+	-+
37	Setae ventral and mesad to posterolaterals	98-105	0.1	0.2	0.2	0.2
38	Anterior mid-dorsals	98-105	0.1	0.1	1.4	0.2
39	Urogomphal setae	98-105	7.7	4.6	4.5	3.3
	ANAL VESICLE CHARACTERS					
40	Ventral setae	98-105	4.11	4.11	4.11	3.11
41	Dorsal setae	98-105	2.3	2.3	2.3	2.7
	LEG CHARACTERS	74-87				
42	Lateral setae of femur	74-87	0.2	0.3	0.1	0.3
43	Posterior laterals	74-87	0.3	0.0	0.1	0.4
44	Anteroventral setae	75	1.1	1.1	0.1	1.1
45	Trochantal seta	85	-+	--	--	-+
	MICROSCULPTURAL CHARACTER					
46	0=absent or sparse;1=dense; 2=very dense	11 (right)	222	122	000	002
	ABDOMINAL CHARACTERS	88-97				
47	P3 seta of segment I	89,96,97	++	--	--	++
48	Median seta between P1's	89,91	--	-+	--	-+
49	Postprimary P setae, between P4/P5; 2nd seta	89,91,93	--	-+	-+	-+
50	Setae anterior to P row	88-97	2.12	5.7	7.15	8.16
	MANDIBULAR AND MAXILLARY CHARACTERS					
51	Prostheca sclerotization -=sclerotized;+=membranous	22	--	--	++	--
52	Frimbriate galea loss: -=present;+=loss	25,43	--	--	++	++
	METANOTAL CHARACTERS	65-73				
53	Third posterior seta	70-73	++	--	-+	--
54	Lateral seta L1	71-73	++	--	++	++
55	Second lateral seta, L2	71-73	++	--	++	++
56	Number large discal setae	65-73	2.2	0.3	2.2	2.2
57	Median setal pair	68,70	--	--	-+	-+
58	Small setae between P1/P4	65-73	2.7	1.2	3.8	3.8
	HYPOPHARYNGEAL SCLEROMIC CHARACTERS (Figs. 48-55)					
59	Posterior bridge +=complete;-=incomplete	48-50,54,55	++	++	--	+-
60	Anterior arms, fused and heavily sclerotized (+)	cf. 52,53	++	++	-+	++

TABLE 3
Conversion of Character Numbers from Figure 8 Cladogram to Table 2
See Wheeler, 1990, for details

Fig. 8:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Tab. 2:	3	5	9	10	12	13	16	17	18	22	24	26	30	34	36	44	45	46	48	53	57	59	

letters are used in the text, they will refer to semaphoronts *not* species (and specifically to semaphoronts A [instar I], B [II + III], and C [I + II + III]).

Noteworthy change between instars involves simple growth (e.g., increase of total body length) and changes in proportions and ratios of linear measures. Color was not reliably studied in either long-term alcohol preserved or slide-mounted specimens and is therefore not reported in the descriptions. Larvae were, in general, grayish in color.

Some interesting trends in microsculpturing exist. The surface of the dorsal integument of some semaphoronts was covered by dense, minute asperities, sometimes arranged into more or less distinct transverse rows. These were present and dense in all instars of *Anisotoma basalis,* but varied within *Agathidium.* They were sparse in semaphoront A of PUL, and dense in B. They were absent or very sparse in instars I and II of ARI, but dense in instar III (an unusual pattern in its deviation from the usual similarity of instars II and III in comparison to I). And they were uniformly sparse to absent in ONI.

Measures and abbreviations explained in figure 9 include A1 (antennomere I length), A2 (antennomere II length), A3 (antennomere III length), AS (antennal sensillum, i.e., "digitiform" solenidium, length), A1L (abdominal segment I length), A1W (abdominal

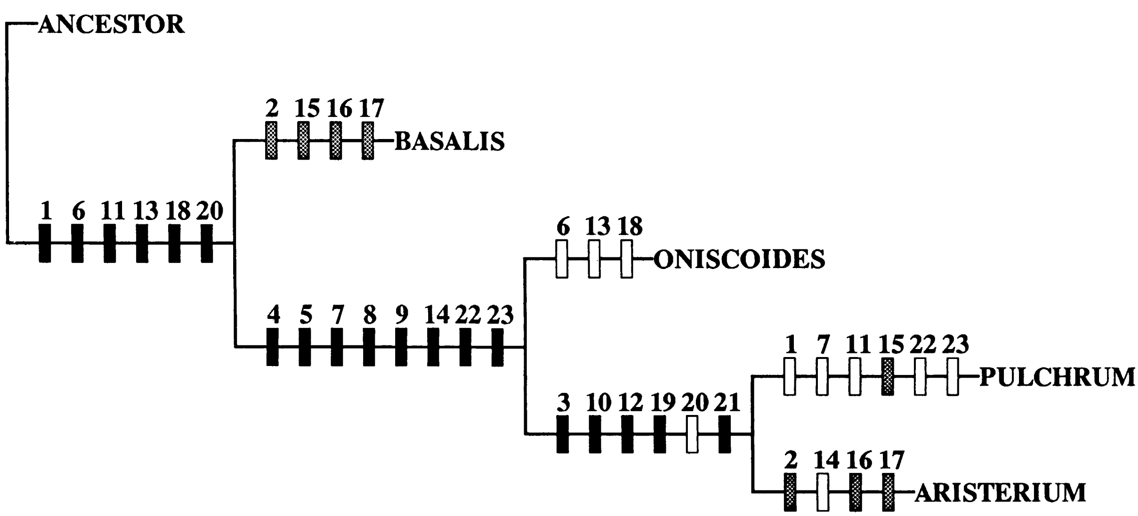


Fig. 8. Cladogram depicting hypothesized relationships among taxa described in text, based on polarities arrived at by Nelson's (biogenetic) Rule. One of four equally parsimonious cladograms with consistency index equal to 0.62. Black bars = synapomorphs; white bars = reversals; gray bars = parallelisms. Character numbers correspond to characters in table 2 as explained in table 3. After Wheeler (1990).

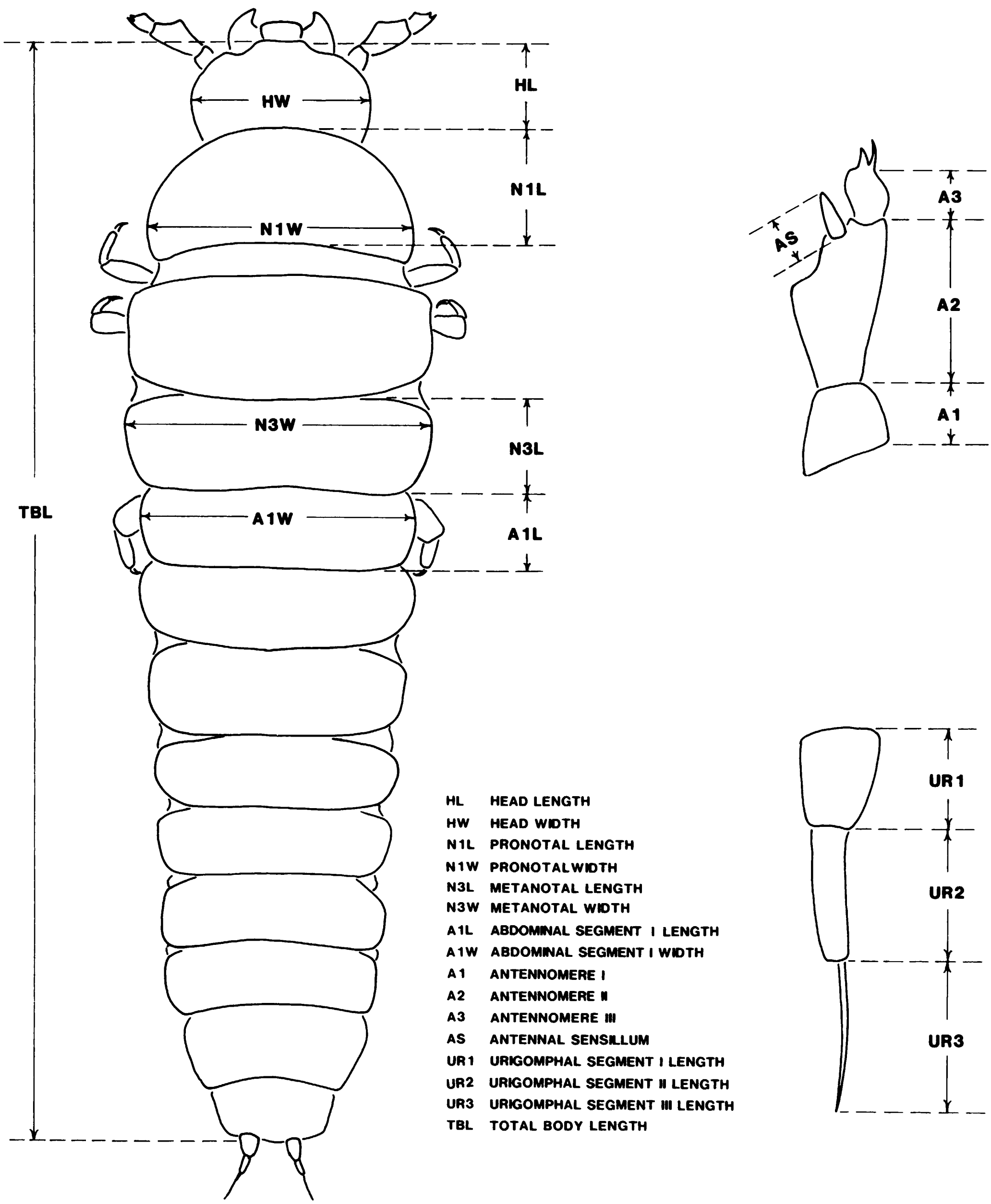
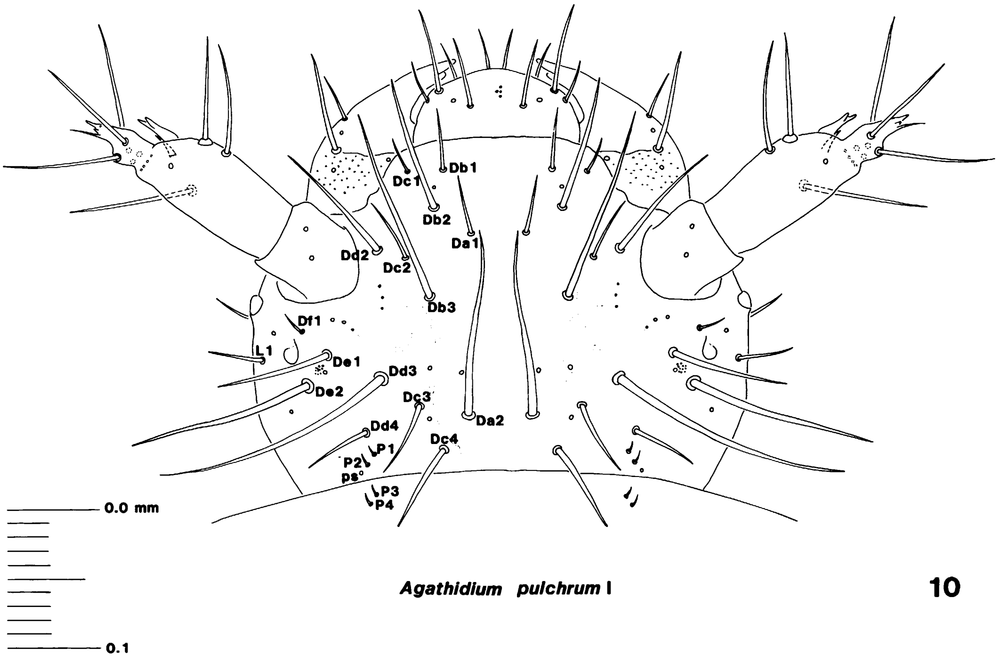
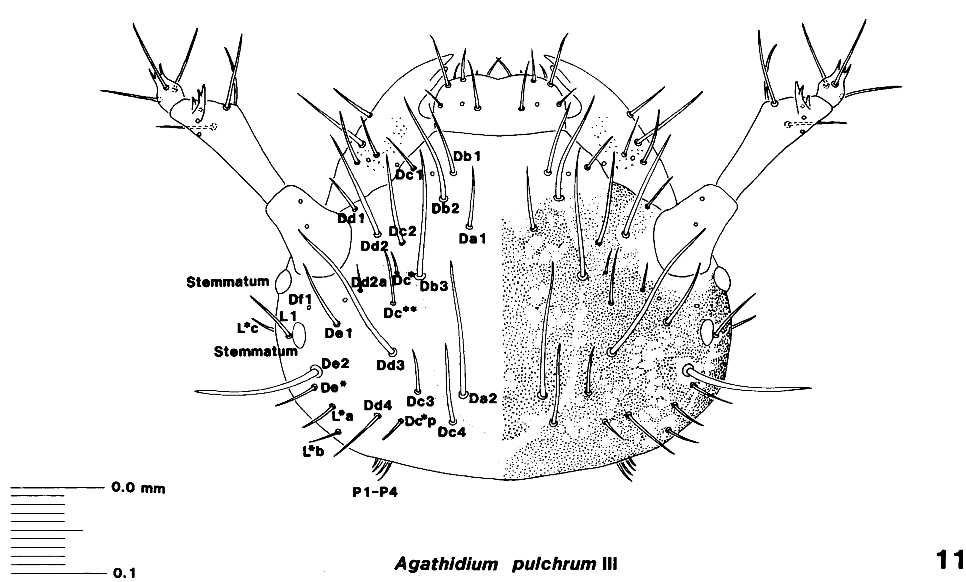


Fig. 9. Generalized *Agathidium* larva showing measures used in descriptions and their acronyms.

segment I width), HL (head length, from base of labrum), HW (head width, at middle), N1L (pronotal length, at middle), N1W (pronotal width, the widest point in species studied), N3L (length metanotum at midline), N3W (width metanotum near anterior end, the widest point in taxa seen), TBL (total body length, extended), UR1 (length urogomphus segment I), UR2 (length urogomphus segment II), and UR3 (length urogomphus apical stylus).

An "antennal formula" is used to describe





Figs. 10, 11. Cranium of *Agathidium pulchrum,* dorsal. **10.** Instar I. **11.** Instar III.

relative lengths in the following sequence: antennomere I: antennomere II: antennomere III: digitiform organ (of antennomere II). A similar urogomphus formula is used where lengths are reported for segment I, II, and apical stylus, respectively.

The shape of the cranium, including a width/length ratio, is given, along with information on the average absolute width of the cranium. Details of chaetotaxic differences are given in the descriptions and table 2. It is worth noting that the dominant trend was one of *addition*. Setae were added at the molt between instars I and II and retained in similar number and position in instar III. This is a trend echoed throughout all the chaetotaxic data. Primary setae are those of constant number and placement present in the neonatal larva. Secondary setae are of variable size, placement, and presence, generally added in later instars, but of comparatively little taxonomic value beyond a description of the degree of "hairiness" of a larva (agathidiines being not hairy). Setae that are constant in number and placement, but added in instars after the first, are termed subprimary.

The mouthparts of *Agathidium oniscoides*, which is known to feed on plasmodia (Newton, 1984; Wheeler, 1984a, 1984b), are unusual among agathidiines. The molar lobe of the mandible is greatly reduced and traces of asperities on it lost (fig. 22). And the fimbriate galea typical of primitive staphylinoids (Dybas, 1976) is absent (fig. 25). The plesiomorphic condition is evident in *Anisotoma basalis* and *Agathidium pulchrum* (cf. figs. 28–31 and 36–39) where the galea is fimbriate and the mola is well developed and bears dense asperities putatively associated with spore crushing (Lawrence, 1977, 1989). Both of these species have been associated with mature sporocarps. *Agathidium aristerium* has also been bred from a slime mold plasmodium (Wheeler, 1987), but has a well-developed mola bearing dense asperities (fig. 46). The galea, however, is narrow and only slightly fimbriate (fig. 43).

MATERIALS, METHODS, AND FORMAT

In general, larvae were collected or reared and stored in ethanol before study. This is true of specimens I personally collected and generally of those borrowed for examination. For this study, the following larvae were studied (number of larvae slide mounted given parenthetically): (200+) *Anisotoma basalis* from Ithaca (Tompkins Co.), New York, collected 4 June 1983 from sporocarp of *Lycogala flavofuscum* by E. Richard Hoebeke and myself (see Wheeler and Hoebeke, 1990); *Agathidium pulchrum* (8) from Still Creek Campground (Clackamas Co.), Oregon, 3700 ft elevation, collected 10 July 1975 by M. Thayer and A. Newton (J. F. Lawrence lot number 4037) and (6) from Mt. Rainier National Park (Pierce Co.), Washington, 1.7 mi north of junction of West Side Road and Washington Rte. 76 at 2400 ft elevation, 19 July 1975, collected by M. Thayer and A. Newton (JFL 4044); *Agathidium oniscoides* from (5) Wahkeena Nature Preserve (Hocking Co.), Ohio, collected from gray plasmodium (*Stemonitis* sp.?) on log on 27 June 1980 by me (QDW Lot number 8051) and (20) Concord Field Station of the Museum of Comparative Zoology (Middlesex Co.), Mass., collected from fine debris under dead bark of *Quercus* with yellow plasmodium, 18 July 1980 by A. Newton and M. Thayer. Larvae of *Agathidium oniscoides* and *A. aristerium* were field collected and reared in my lab; larvae of *Anisotoma basalis* were collected on the Cornell campus by E. Richard Hoebeke; and larvae of *Agathidium pulchrum* were supplied to me by Dr. Alfred F. Newton, Jr. (formerly of Harvard University's Museum of Comparative Zoology and now of the Field Museum of Natural History) and Dr. Stephen Stevenson (Fairmont State College, Fairmont, W. Va.). Additional specimens of *oniscoides* were lent by Dr. Newton. Slide-mounted voucher specimens are deposited in the American Museum of Natural History and the Cornell University insect collection.

In all, I have examined approximately 250 specimens of which 200 were *Anisotoma basalis*, 11 *Agathidium aristerium*, 26 *Agathidium oniscoides*, and 14 *Agathidium pulchrum*. In almost all cases, detailed comparisons were made of slide-mounted larvae. These were removed from 70 percent ethanol, cleared in Nesbitt's solution, and mounted in Hoyer's medium. They were examined at magnifications up to ×1000, and routinely at ×400, using a Leitz Dialux-22 compound microscope equipped with differential interference contrast illumination. Additional specimens were seen in fluid, but were inappropriate for most comparative purposes.

Figures are grouped according to body region. Because this is a comparative morphology and ontogeny study, and because the comparative data are referred to extensively in a companion theoretical paper, it was desirable to locate illustrations of each structure near one another. Thus all the cranium drawings immediately follow one another, and so forth. This poses a slight inconvenience for reading through one description and looking at the appropriate figures, but the comparative advantages far outweigh this problem.

There are several sources of potential error in this study that deserve mention. I do not know the extent to which any of these factors have, in fact, introduced errors, but as incongruities are found between these and other data, the following are places one can begin to look for an explanation of homoplasy within the larval character states. Slide-mounted larvae are never perfectly oriented and both rotation and compression distortions are introduced to some degree. Infraspecific variation could not adequately be assessed for all taxa, given the material available for this study. This is true particularly with regard to possible geographically correlated variation, for all taxa, and in general for the three species of *Agathidium. Anisotoma basalis,* on the other hand, was represented by about 200 slide mounts. More variability was observed in this species, but the kind of variability seen involved small-size setae that were more sporadic in their distribution, coming and going from one specimen examined to the next and sometimes even from one side to the other of the same specimen. I feel that this variation represents a difference between this species and the others studied that is not due to the fact that more individuals were examined.

KEY TO NORTH AMERICAN AGATHIDIINI LARVAE

There have been few attempts at either keys or diagnoses to distinguish larvae of the closely related genera *Agathidium* and *Anisotoma.* The few descriptions given here do not support Hatch's (1927) attempt to use a single posterior transverse row of setae in *Anisotoma* to separate it from *Agathidium,* suggested to have a more or less well-defined second row. Angelini and De Marzo (1984) suggested that the ratio of the length of the second urogomphal segment to the first might separate the genera. Values greater than 1.0 were suggested for *Anisotoma* and less than 1.0 for *Agathidium.* This is not supported by the species studied here.

I have larval material for a number of additional North American species of both *Anisotoma* and *Agathidium,* including many lent by Dr. A. F. Newton, Jr. As more of this material is studied and described, no doubt the following preliminary key will be improved upon.

1. Posterior transverse setal row of abdominal tergum I with seta P3 present (fig. 95); lesser solenidia of antennomere II, located near base of digitiform organ, number 2 in instar I and 3 in late instars (cf. figs. 18, 20) .... *Anisotoma*
– Abdominal tergum I with posterior seta P3 of posterior transverse row small (fig. 91) or absent (fig. 93); antennomere II with 2 solenidia basal to digitiform organ in late instar larvae (1 in first instar larvae, rarely absent) .... *Agathidium* 2
2. Mola of mandible with well-developed rows of teeth (fig. 29); digitiform organ of antennomere II entire or bifurcate; dorsal surface of body with or without dense asperities; total length less than 6 mm 3
– Mola of mandible without rows of teeth (fig. 22); digitiform organ (solenidium) of antennomere II entire (fig. 23); dorsal surface of body without asperities (fig. 61); third instar larvae large, up to 6.3 mm distended .... *oniscoides* Beauvois
3. Digitiform organ (solanidium) of antennomere II bifurcate (fig. 11); dorsal surface more or less covered with dense asperities (fig. 57); head with 2 stemmata on either side (fig. 11) .... *pulchrum* LeConte
– Digitiform organ (solanidium) of antennomere II undivided, simple, thumblike; dorsal surface of body with sparse (late instars: fig. 59) or no (neonatal larvae: fig. 58) asperities; head with single stemmatum on either side (fig. 14) .... *aristerium* Wheeler

MORPHOLOGY AND ONTOGENY OF POSTEMBRYONIC LARVAE OF SEVERAL *AGATHIDIUM* AND *ANISOTOMA*

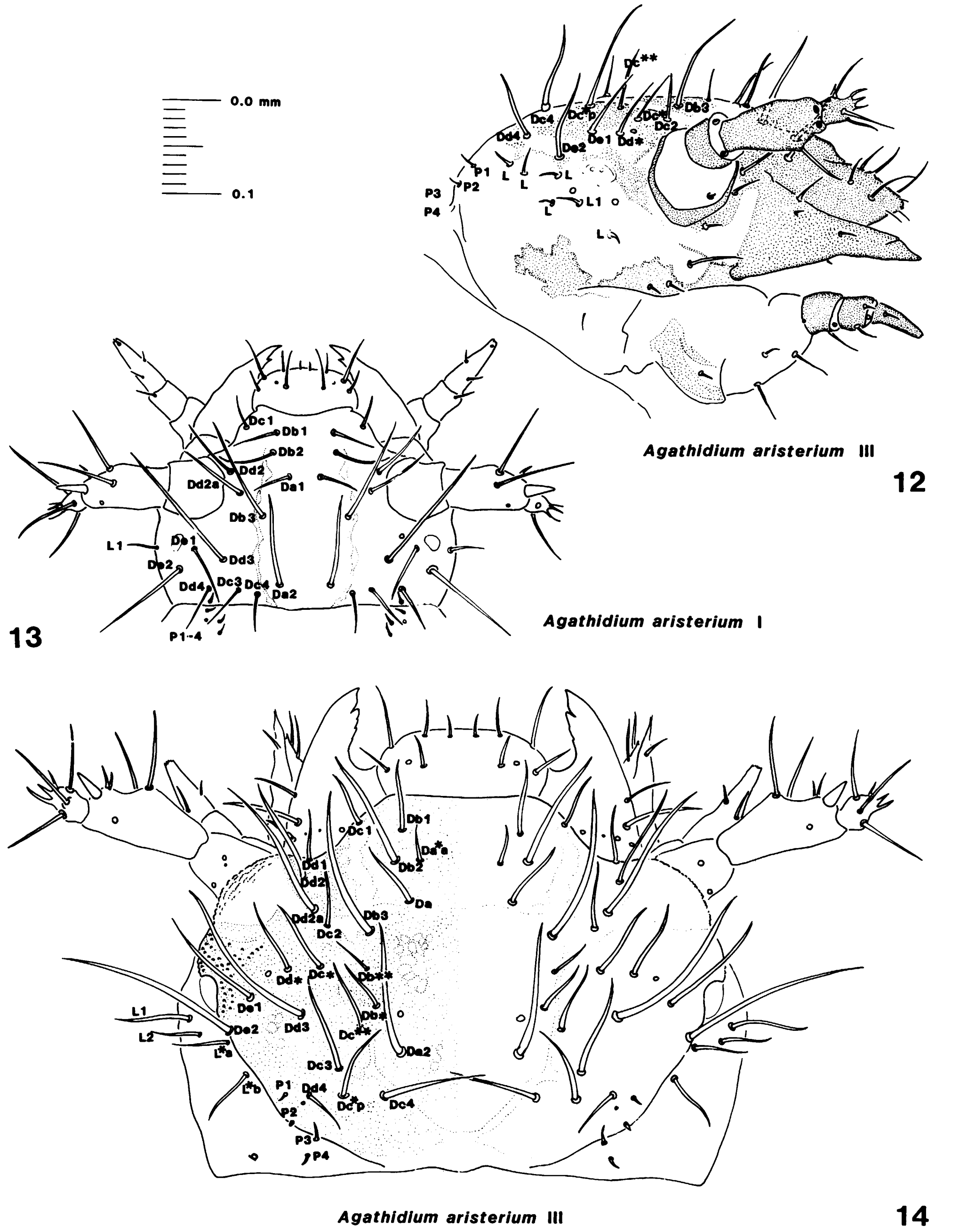
AGATHIDIUM PULCHRUM LECONTE

(Figures 10, 11, 34–41, 48, 49, 56, 57, 65, 66, 74, 75, 88, 89, 98, 99)

Agathidium pulchrum LeConte, 1853: 286.

DIAGNOSIS

Large larvae, from about 2 mm in first instar to 4 mm in final instar; principal soleni-



Figs. 12–14. Cranium of *Agathidium aristerium*. **12.** Instar III, lateral. **13.** Instar I, dorsal. **14.** Instar III, dorsal.

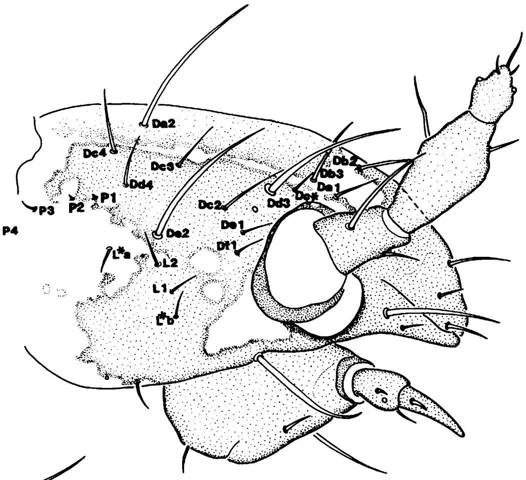
dium of antennomere II ("digitiform organ" of authors) bifurcate; 2 stemmata on each side of head; and dorsal surface of body more or less densely covered in minute asperities (late instars), often arranged in distinctly transverse rows.

Description

Body: Instar I. – Body shape similar to that of *oniscoides.* Length about 2.1 mm.

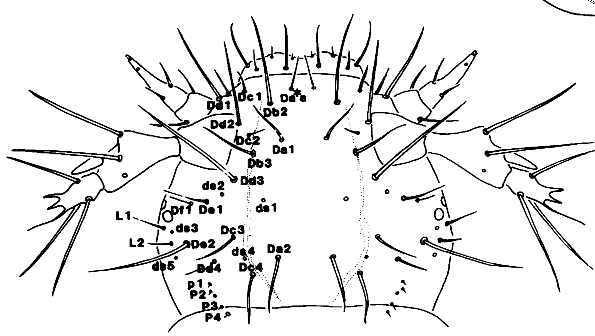
Instar II. – Length about 3.0 mm.

Instar III. – Length about 4.0 mm.



Agathidium oniscoides III

15

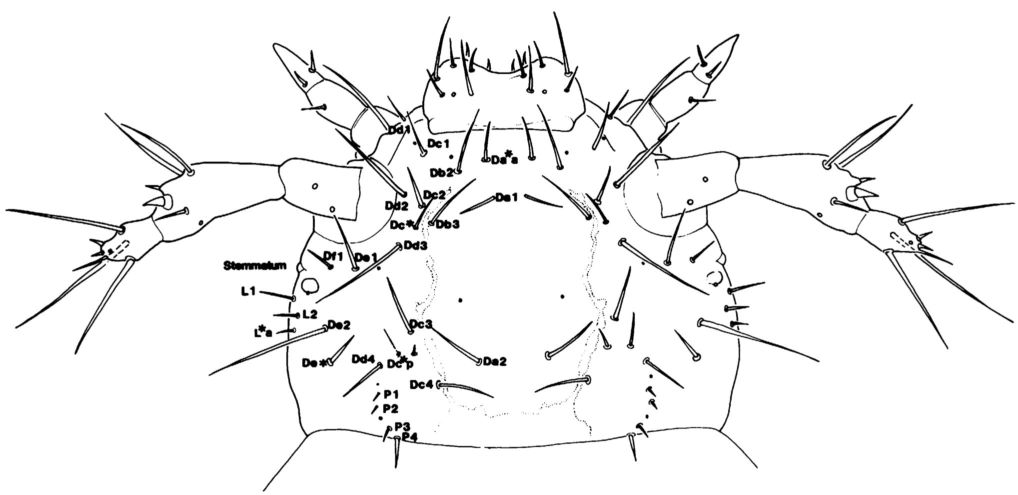


Agathidium oniscoides I

16

0.0 mm

0.1

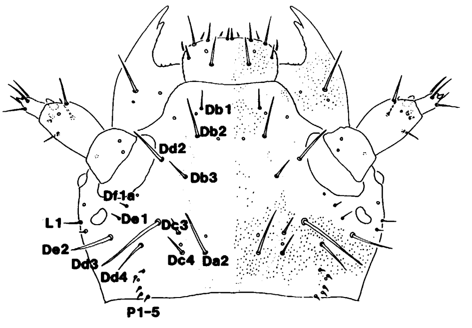


Agathidium oniscoides III

17

Figs. 15–17. Cranium of *Agathidium oniscoides*. **15.** Instar III, lateral. **16.** Instar I, dorsal. **17.** Instar III, dorsal.

Head (figs. 10, 11): Instar I. – Cranium wider than long; HW/HL = 1.35; average head width about 0.35 mm. Chaetotaxy as follows and in figure 10: row Da with 2 setae (Da1, Da2); row Db with 3 setae (Db1–Db3); row Dc with 4 setae (Dc1–Dc4); row Dd with 3 setae (Dd2–Dd4); row De with 2 setae (De1–De2); 1 lateral seta (L1); posterior row with 4 setae (P1–P4). Campaniform sensilla include 1 anteriorly near Db2, 1 postero-medially on frons anterior to Da2, 1 laterad to frontal sensillum on or near suture, 1 pos-



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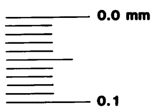
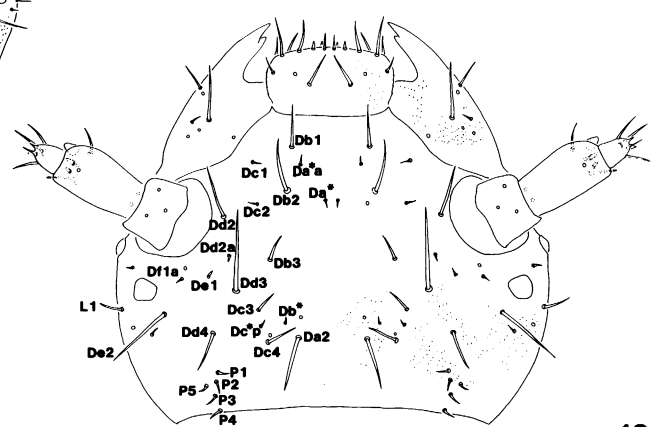
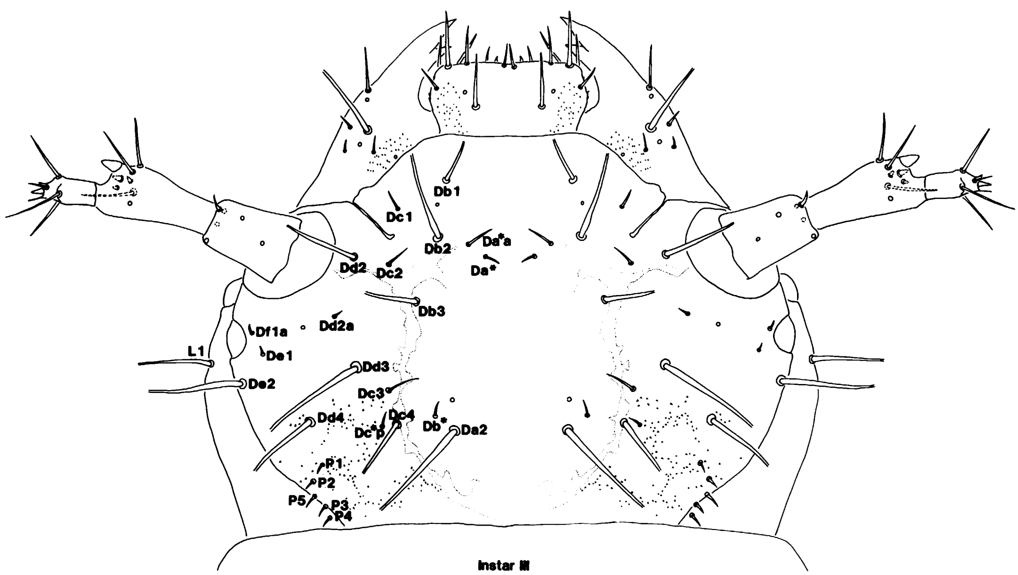
Instar I





Instar II

19



Instar III

Anisotoma basalis

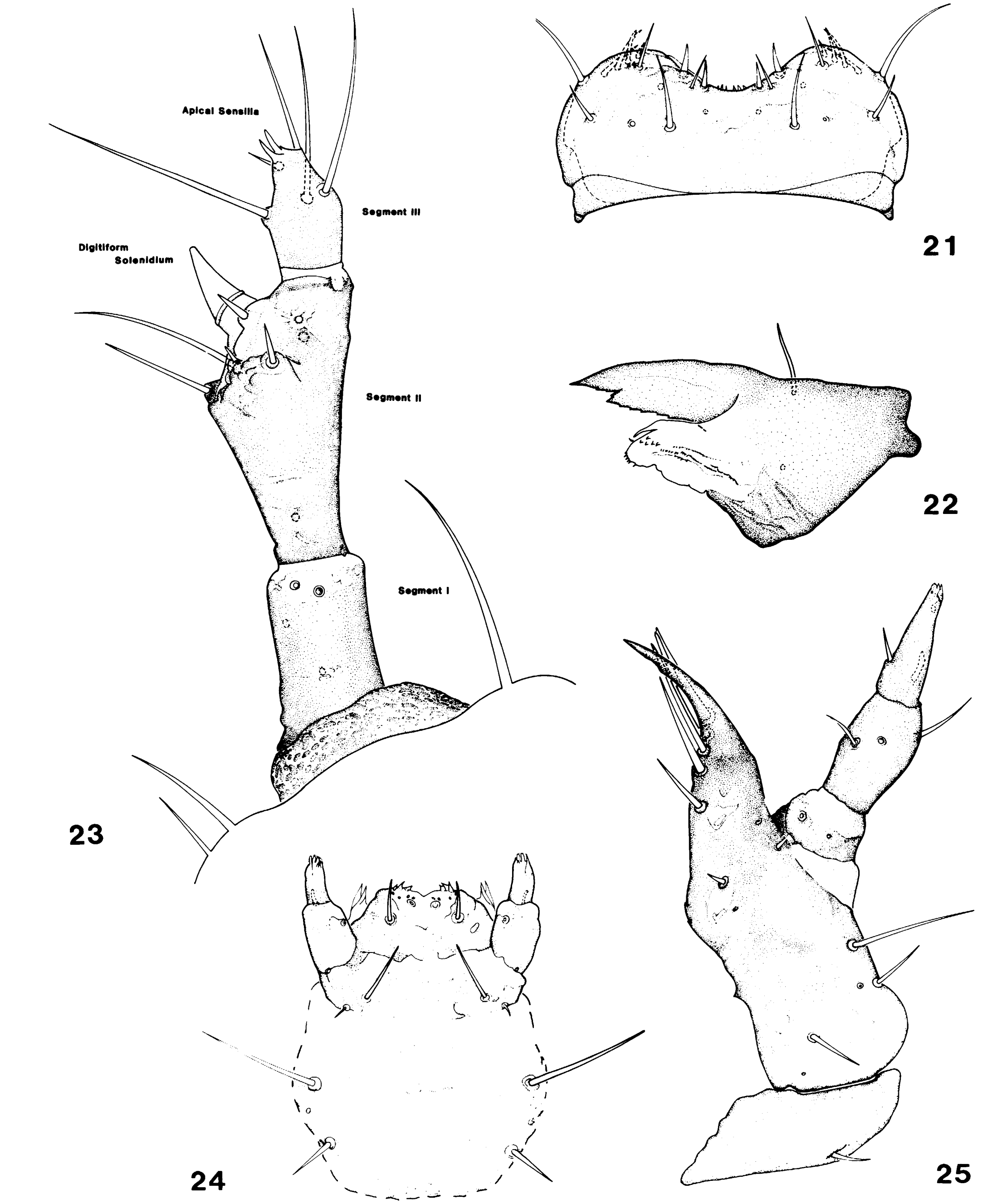
20

Figs. 18–20. Cranium of *Anisotoma basalis*, dorsal. **18.** Instar I. **19.** Instar II. **20.** Instar III.

terior to Dc3, 2 laterally, 1 between P2/P3, and 1 surrounded by asperities posterior to De1; integument otherwise smooth. With two stemmata.

Instar II. – Similar to instar III. HW/HL = 1.28; average cranial width 0.45 mm.

Instar III. – HW/HL = 1.26; average cranial width 0.53 mm. Chaetotaxy as in instar I, except as follows and in figure 11: row Dc with 2 additional setae between Dc2/Dc3; row Dd with Dd1 present (absent in instar I) and an additional seta between Dd2/Dd3; row

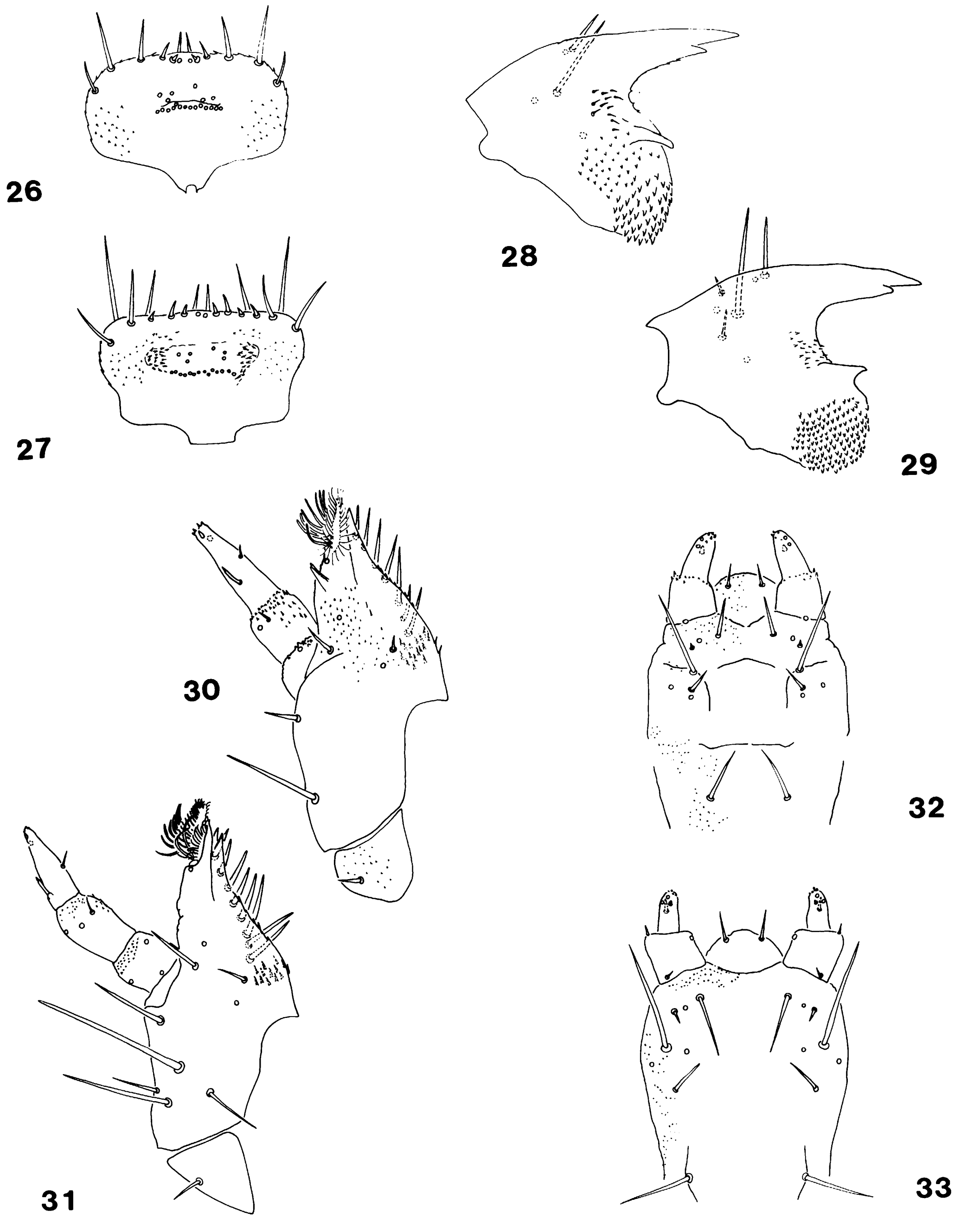


Figs. 21–25. *Agathidium oniscoides*. **21.** Labrum, dorsal. **22.** Mandible. **23.** Antenna. **24.** Labium, ventral. **25.** Maxilla.

De with additional seta posterior to De2; row L with 2 setae posterior to L1 and De row. Integument with dense asperities.

Antenna (figs. 10, 11): Instar I. – As in instar III, except as noted here. Antennal formula = 1:4:1.3:1. Antennomere II length/digitiform organ length = 3.7; II/III = 2.8. Single solenidium in membranous area at base of digitiform organ.

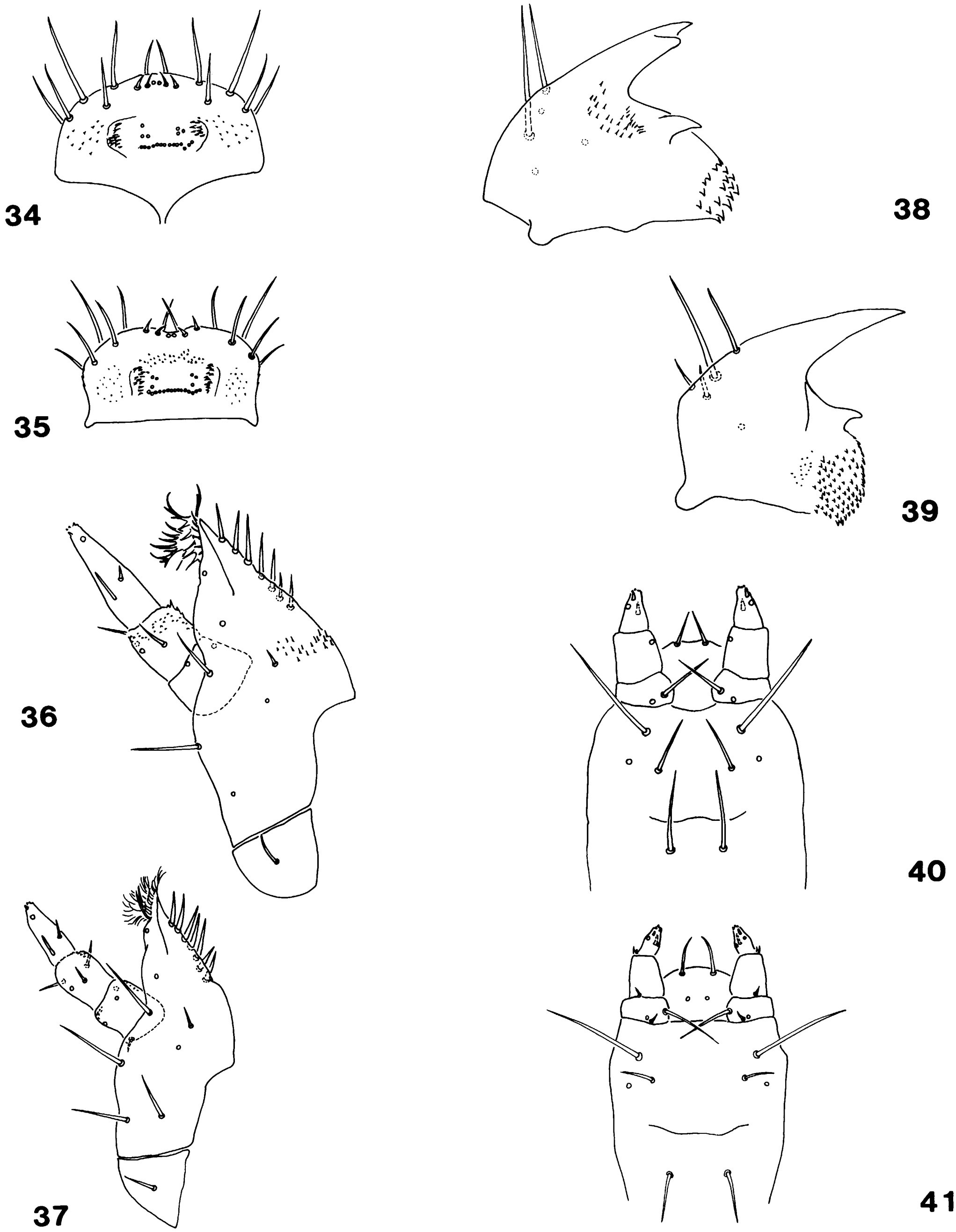
Instar II. – As in instar III, except formula



Figs. 26–33. *Anisotoma basalis,* mouthparts. **26.** Labrum, instar I, ventral. **27.** Labrum, instar III, ventral. **28.** Mandible, instar I. **29.** Mandible, instar III. **30.** Maxilla, instar I. **31.** Maxilla, instar III. **32.** Labium, instar I, ventral. **33.** Labium, instar III, ventral.

1:3.25:1:0.75; length II/digitiform organ = 4.1; II/III = 3.0.

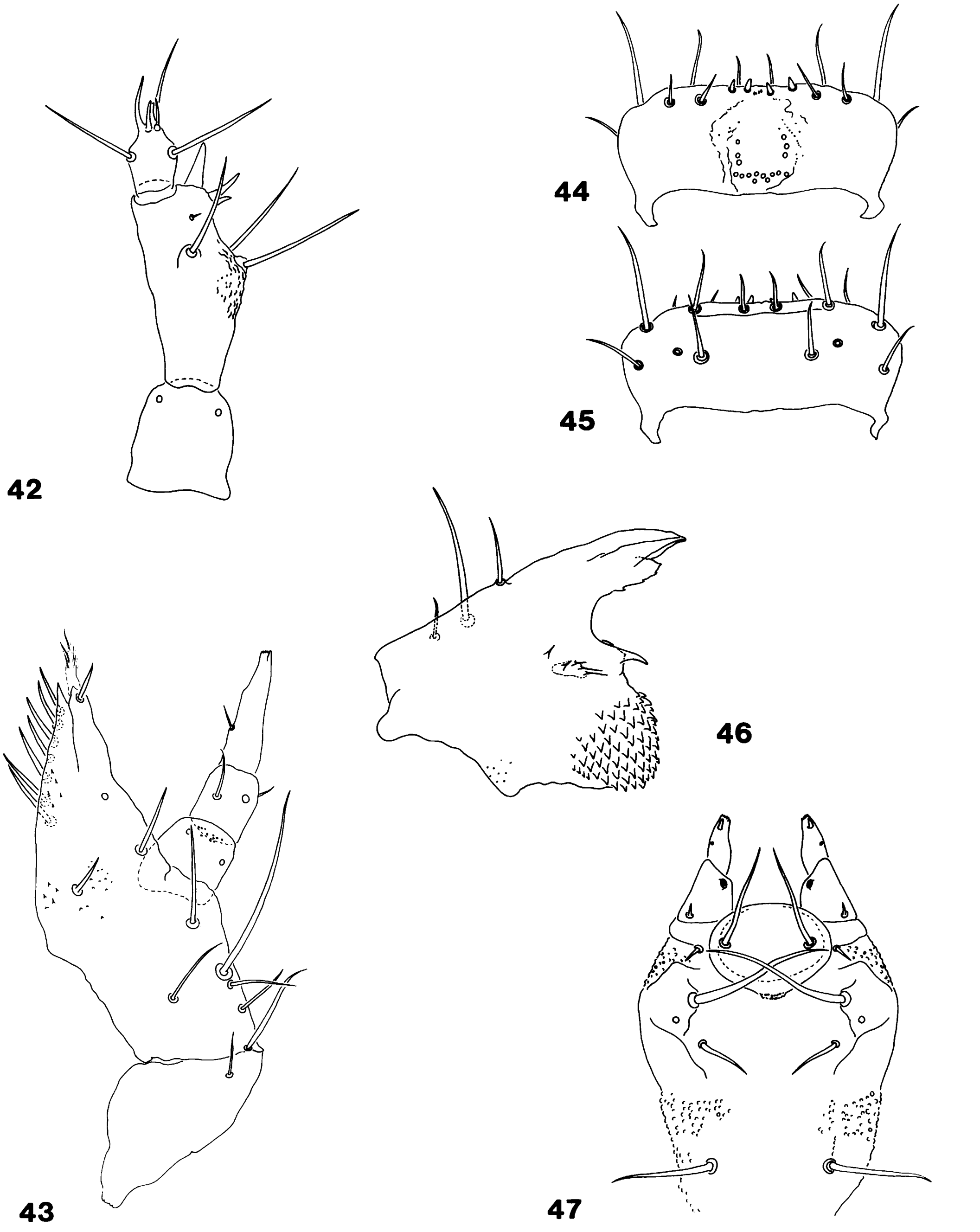
Instar III. – Antennal formula 1.7:4.8:1.4:1. Length II/digitiform organ = 4.8; II/III = 3.6. Two solenidia in membranous area at base of digitiform organ. Antennomere I asetose, with 2 dorsal campaniform sensilla; II with 3 long subapical setae; III small, with 3



Figs. 34–41. *Agathidium pulchrum,* mouthparts. **34.** Labrum, instar I, ventral. **35.** Labrum, instar III, ventral. **36.** Maxilla, instar I. **37.** Maxilla, instar III. **38.** Mandible, instar I. **39.** Mandible, instar III. **40.** Labium, instar I, ventral. **41.** Labium, instar III, ventral.

long subapical setae, several accicuate terminal processes; digitiform organ bifurcate, set in membranous area near apex of antennomere II.

Mouthparts (figs. 34–41): Instar I. – As in instar III, except as noted. Labrum (fig. 34) not apically emarginate. Maxilla similar to instar III (fig. 36). Mandibular mola (fig. 38)

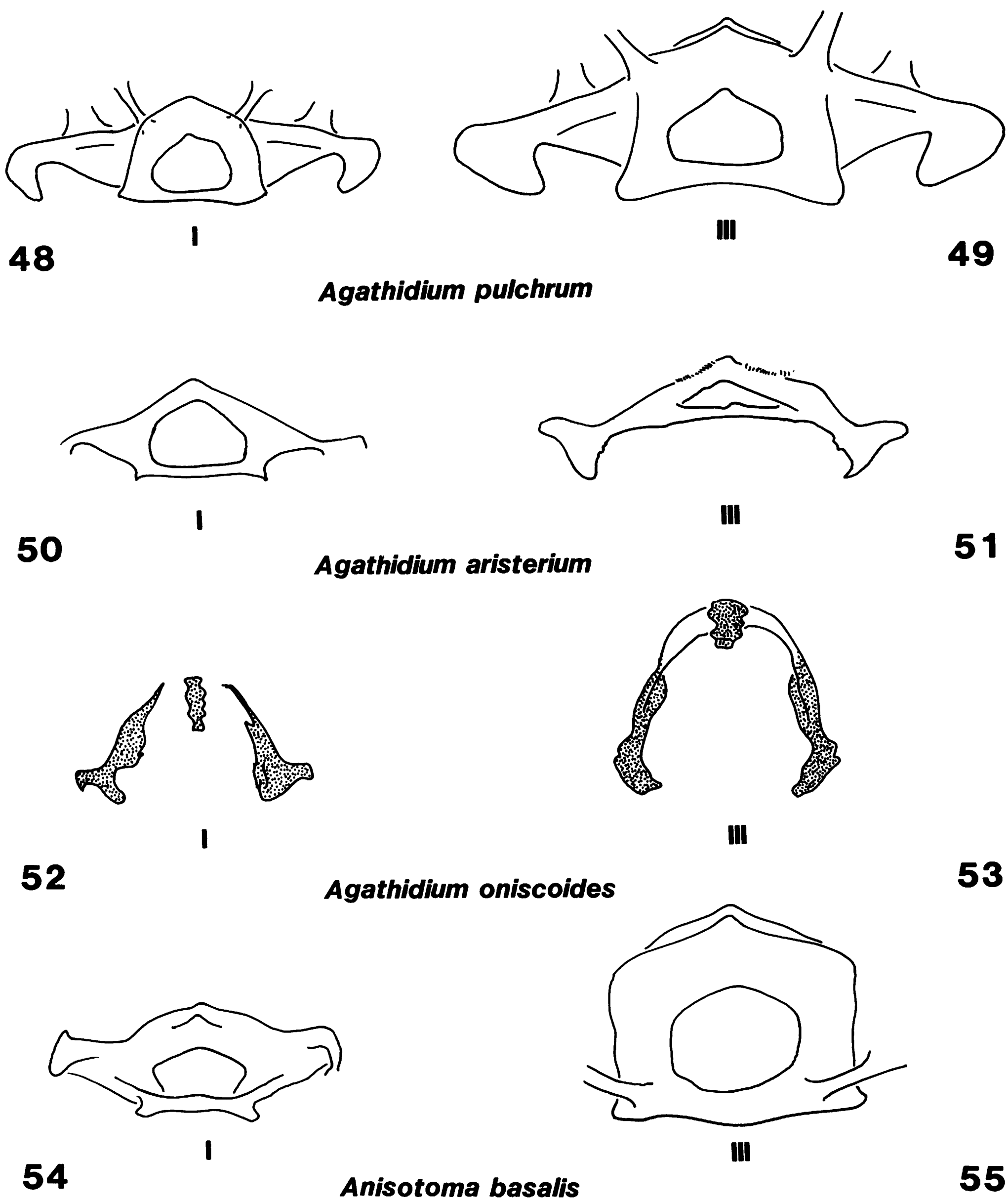


Figs. 42–47. *Agathidium aristerium.* **42.** Antenna, instar III. **43.** Maxilla, instar III. **44.** Labrum, instar III, dorsal. **45.** Labrum, instar III, ventral. **46.** Mandible, instar III. **47.** Labium, instar III, ventral.

with about 20 teeth visible. Labial palpomere II lacking basolateral sensilla, ventromesal sensillum.

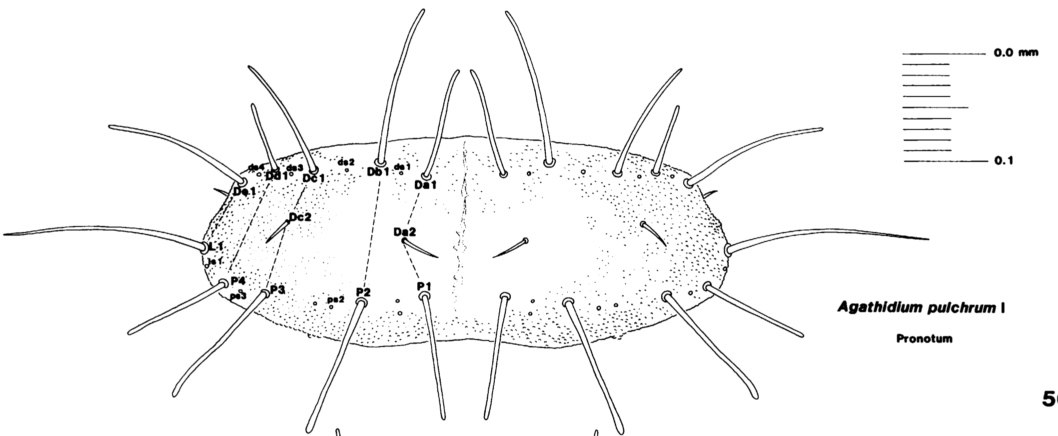
Instar II. – As in instar III.

Instar III. – Labrum transverse (fig. 35), apically emarginate, with 2 pair setae on anterior margin, single pair near middle, single lateral pair, campaniform sensilla between middle and lateral seta on each side. Epipharyngeal area, including adoral surface la-



Figs. 48–55. Hypopharyngeal bridge. **48, 49.** *Agathidium pulchrum.* 48, instar I; 49, instar III. **50, 51.** *Agathidium aristerium.* 50, instar I; 51, instar III. **52, 53.** *Agathidium oniscoides.* 52, instar I; 53, instar III. **54, 55.** *Anisotoma basalis.* 54, instar I; 55, instar III.

brum, with large pair anterolateral setae, 2 pair small anteromedial setae, pair anteromedial campaniform sensilla, posterior transverse row of about 15 campaniform sensilla, 3 pair campaniform sensilla anterolaterally positioned relative to transverse row, paired patch of microtrichiae laterad of transverse row. Mandible simple (fig. 39); apically bidentate; prostheca short; mola distinct, with about 70 visible teeth. Maxilla with apically accicuate lacinia, 7 mesal spines, narrow fimbriate galea; otherwise generally similar to *oniscoides,* differing only in slight chaetotaxic detail (fig. 37). Labial palpiger with long ven-



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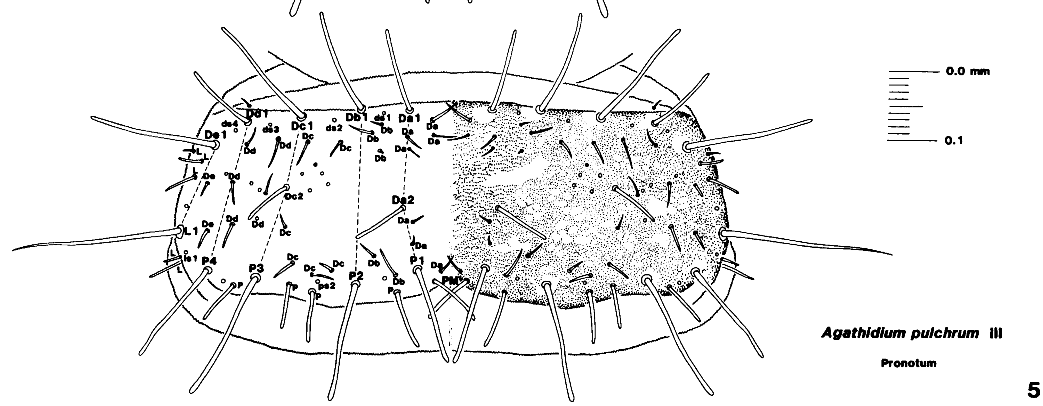


57

Figs. 56–57. *Agathidium pulchrum* pronotum, dorsal. **56.** Instar I. **57.** Instar III.

tromesal seta, 1 ventrobasal campaniform sensillum; palpomere I with apicomesal campaniform sensillum (not visible in figure), basal ventral seta; II with dorsal recumbent sensillum, ventral subapical sensillum, ventrolateral campaniform sensillum, ventromesal peglike sensillum, 2 basolateral minute sensilla, several minute apical sensilla. Hypopharyngeal sclerome transverse, with complete anterior and posterior bridge (fig. 49).

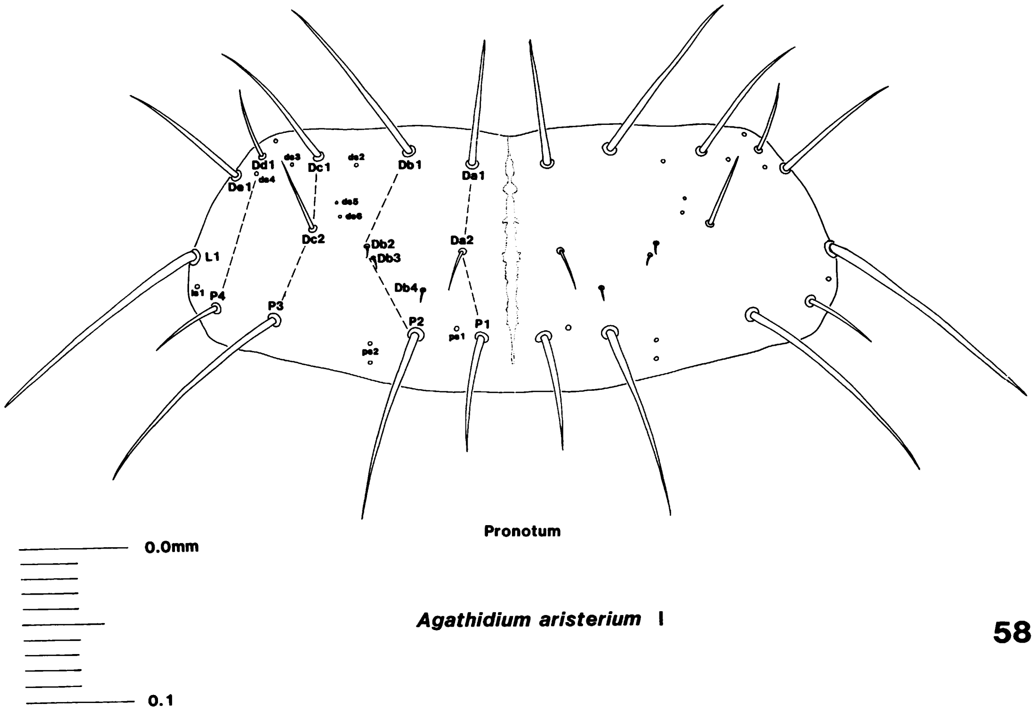
Leg (figs. 74, 75): Instar I. – Chaetotaxy and structure as follows and in figure 74: Coxa large, with about 10 dorsal setae. Trochanter subquadrate: anterior surface with 6 setae, including ventral seta, 5 campaniform sensilla; posterior surface with 3 setae, 2 campaniform sensilla. Femur with 2 posterodorsal setae, 2 posterior setae (P1, P2), 1 anterolateral, 2 anteroventral setae (Av1, Av2). Tibia with 2 anterodorsal setae (Ad1, Ad2), 1 dorsal seta (D1), 1 anterior seta (A1), 1 anteroventral seta (av1), 2 posterodorsal setae (Pd1, Pd2), 1 posterior seta (P1), 1 posteroventral seta (Pv1). Tarsungulus with pair setae (Av1, Pv1).

Instar II. – Similar to instar III.

Instar III. – Similar to instar I, except as follows and in figure 75. Femur with 2 additional anterolateral setae (Al2, Al3).

Pronotum (figs. 56, 57): Instar I. – Transverse; PL/PW = 0.39. Chaetotaxy as follows and in figure 56: 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); single lateral seta (L1); posterior transverse row with 4 setae (P1–P4). Campaniform sensilla include anterior transverse row with 1 each between Da1/Db1, Db1/Dc1, Dc1/Dd1, Dd1/De1; 1 posterior to L1; 2 between P1/P2, 2 between P2/P3, 1 between P3/P4. Integument with sparse asperities, absent at middle.

Instar II. – Same as instar III, except PL/PW = 0.37.



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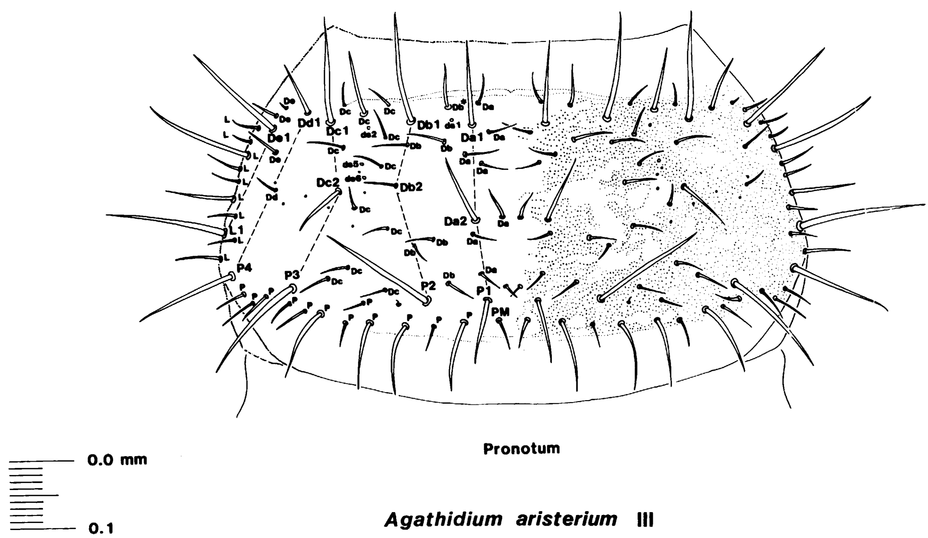

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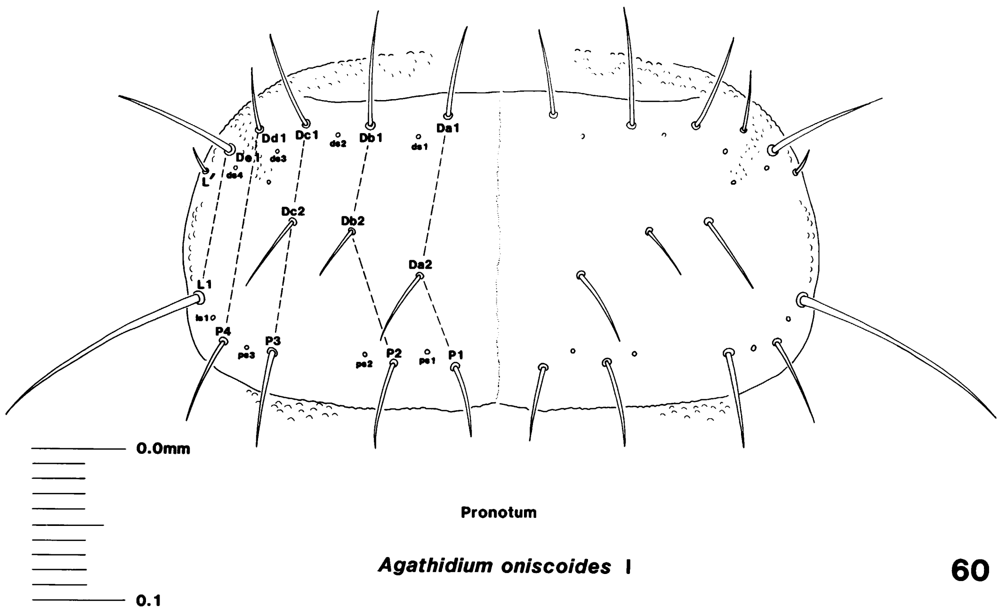
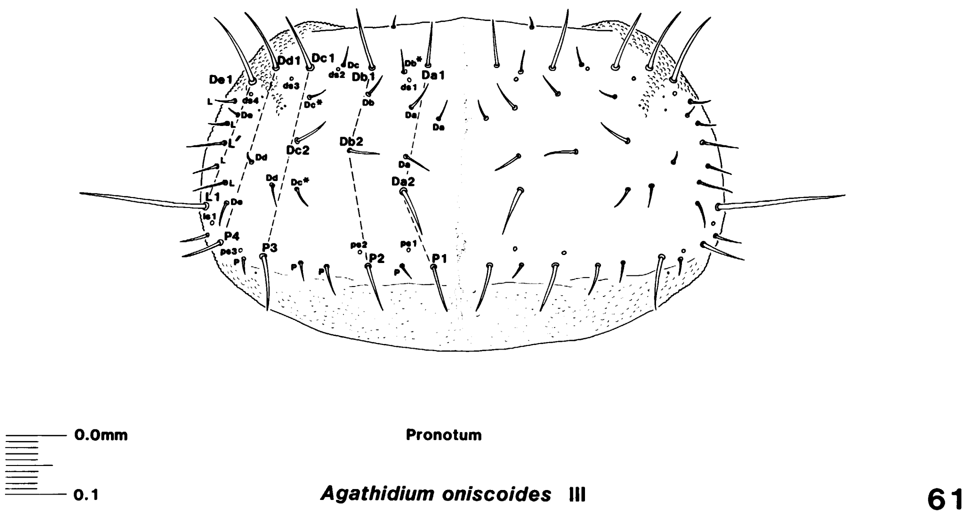
Figs. 58–59. *Agathidium aristerium* pronotum, dorsal. **58.** Instar I. **59.** Instar III.

Instar III. – PL/PW = 0.52. Similar to instar I, except as follows and in figure 57: row Da with 7 additional setae; row Db with 5 additional setae; row Dc with 6 additional setae; row Dd with 5 additional setae; row De with 2 additional setae; lateral row with 5 additional setae; posterior row with 5 additional setae, including 1 pair at midline, 1 between P1/P2, 2 between P2/P3, 1 between P3/P4. Campaniform sensilla include an anterolateral patch of about 6 near seta Dc2 and dark "spot" anterolateral to Dc2. Integument





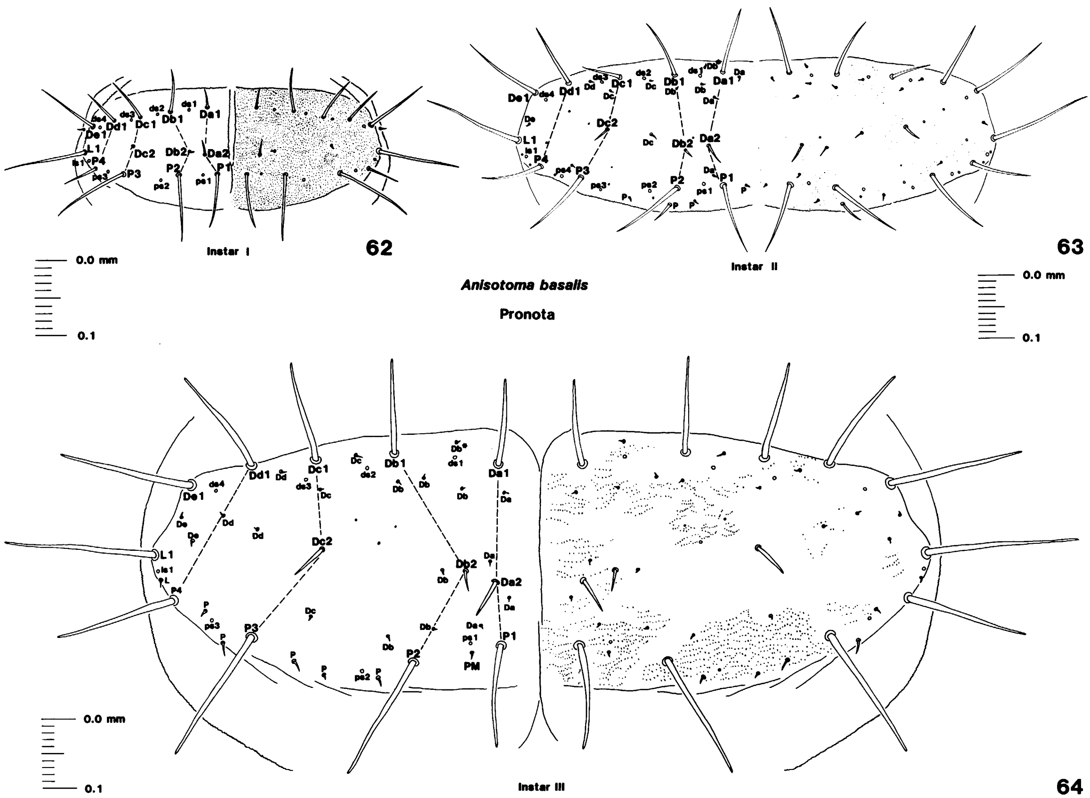
Figs. 60–61. *Agathidium oniscoides* pronotum, dorsal. **60.** Instar I. **61.** Instar III.

with dense asperities, denser at posterior margin, forming more or less distinct parallel rows anteromedially.

Metanotum (figs. 65, 66): Instar I. – N3L/N3W = 0.25. Chaetotaxy as follows and in figure 65: row Da with 2 minute (Da1, Da2), 1 larger (Da3) setae; row Db with 2 setae (Db1, Db2); row Dc with 1 seta (Dc1); row Dd with 1 seta (Dd1); lateral row with 2 setae (L1, L2); posterior transverse row with 4 setae (P1–P4). Campaniform sensilla include 2 posterior to Da2, 1 anterior to Dd1, 1 posterior to L1 (ls1), 1 each between P1/P2, P2/P4, P4/P5. Integument similar to pronotum in instar I.

Instar II. – Similar, except in proportion, to instar III.

Instar III. – N3L/N3W = 0.23. Similar to



Figs. 62–64. *Anisotoma basalis* pronotum, dorsal. **62.** Instar I. **63.** Instar II. **64.** Instar III.

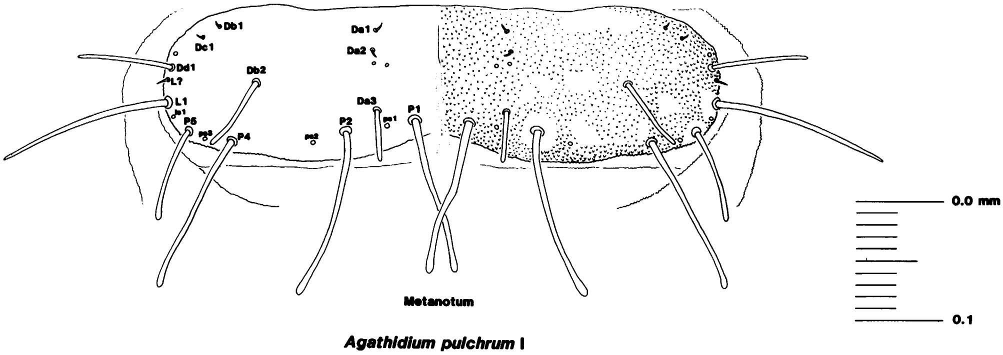
instar I, except for addition of following setae (fig. 66): row Da, 3 additional setae including pair at middle; row Db, 3 additional setae; row Dc, 2 additional setae; posterior row, 8 additional setae including 1 pair at middle between P1s, 2 between P1/P2, 3 between P2/P4, 1 between P4/P5, 1 between P5/L1. Integument similar to that of pronotum in instar III. Transverse band of campaniform sensilla added, as on pronotum. Dark spot anterolateral to Da2.

Abdominal Segment I (figs. 88, 89): Instar I. – A1L/A1W = 0.19. Tergum with chaetotaxy as follows and in figure 88: row Da with single seta; rows Db, Dc absent; row Dd with single seta; row De with 2 setae; single lateral seta; posterior row with 5 setae (P1, P2, P4, P5, P6); posterior setae more or less blunt, subspatulate. Campaniform sensilla include 2 near Da1, 2 near L1, 1 between P1/P2, 2 between P4/P5. Integument with sparse asperities.

Instar II. – Similar to instar III, except in proportions.

Instar III. – A1L/A1W = 0.15. Tergum with following *additional* setae (fig. 89): row Db with additional seta near P2/P4; row De with additional seta near P5/P6, posterior row with 1 additional setal pair at middle, 2 additional setae between P4/P5. With at least an additional campaniform sensillum near seta De2. Dark "spot" similar to that seen in third instar pronota and metanota present. Integument with dense asperities, mesally more or less arranged into parallel rows.

Abdominal Tergum IX (figs. 98, 99): Instar I. – Transverse; 3 pair dorsolateral setae (Dl1–Dl3). Urogomphus long; formula = 1.2: 2.8:1; URI/URII = 0.39; URII/URS = 2.9. Urogomphus segment I short with 4 dorsal



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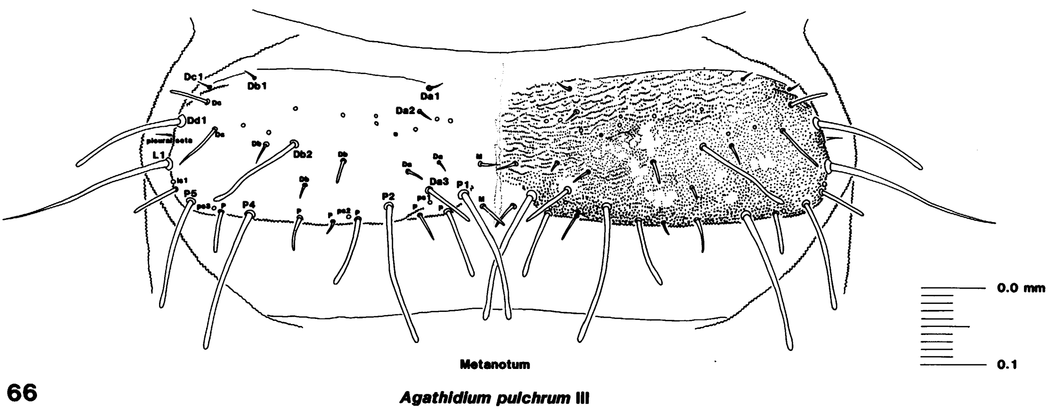


66

Figs. 65, 66. *Agathidium pulchrum* metanotum, dorsal. **65.** Instar I. **66.** Instar III.

setae, about 5 dorsal campaniform sensilla, 1 ventral campaniform sensillum. Urogomphus segment II long, with apical stylus only. Integument with very sparse asperities on segment I, few in basal half of segment II only.

Instar II. – Similar to instar III, except as follows: urogomphus formula = 2:3.8:1; URI/URII = 0.53; URII/URS = 3.9.

Instar III. – More transverse in form, with 1 additional basal seta, 1 additional seta laterally between Dl1/Dl2, 1 additional seta mesad to Dl3. Urogomphus formula = 2.2:3.7:1; URI/URII = 0.58; URII/URS = 3.6. Urogomphus segment I with 1 ventral seta, denser cover of asperities. Urogomphus segment II wrinkled in basal portion, without asperities or nearly so.

Abdominal Sternum IX and Anal Membrane (figs. 98, 99): Instar I. – Abdominal sternum IX with 1 ventral seta (V1), 5 ventral posterior setae (Vp1–Vp5). Anal membrane with 4 ventral pairs setae (V1–V4), 2 pair ventral campaniform sensilla (vs1–vs2).

Instar II. – Similar to instar III.

Instar III. – Abdominal sternum IX with 2 additional ventral setae anterior and near to Vp4/Vp5. Anal membrane with 7 additional pairs ventral setae, 2 additional medial pairs dorsal setae.

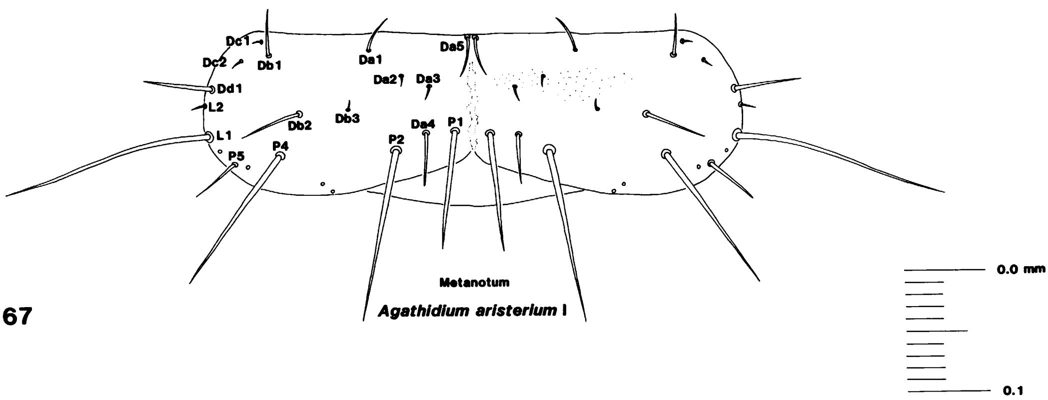
AGATHIDIUM ARISTERIUM WHEELER

(Figures 1, 2, 12–14, 42–47, 50, 51, 58, 59, 67, 68,76–80, 90, 91, 101, 103)

Agathidium aristerium Wheeler, 1987: 399.

DIAGNOSIS

Larvae 1.3 (instar I)–4.7 mm (instar III) in length; mandibular mola with dense asperities arranged in transverse rows; digitiform organ of antennomere II undivided; dorsal



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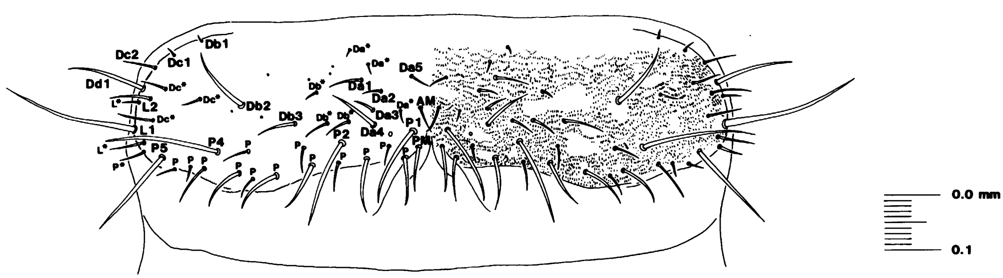


68

Figs. 67, 68. *Agathidium aristerium* metanotum, dorsal. **67.** Instar I. **68.** Instar III.

surface of body with no or at most sparse asperities; head with single stemmatum on each side.

Description

Body (figs. 1, 2): Instar I. – Elongate, cylindrical, narrowed posteriorly, widest at metanotum. Terga with well-defined sclerites; pleural and ventral surfaces with small indistinct sclerites. Average length about 1.3 mm.

Instar II. – Length about 2.8 mm.

Instar III. – Length about 4.7 mm.

Head (figs. 12–14): Instar I. – Cranium broad, width/length = 1.3; average absolute width about 0.32 mm. Chaetotaxy as follows, and as in figure 13: row Da with 2 setae (Dal, Da2); row Db with 3 setae (Db1–Db3); row Dc with 3 setae (Dcl, Dc3, Dc4); row Dd with 4 setae (Dd2, Dd2a, Dd3, Dd4); row De with 2 setae (Del, De2); single lateral (L1); 4 posteriors (P1–P4; not visible in figure). Dorsal campaniform sensilla include 1 pair anterior to Da2, 1 laterad to stemmatum, 1 posterior to De2, 1 mesad to Dd2b.

Instar II. – Head width about 0.42 mm; HW/HL = 1.3. Chaetotaxy as in instar III.

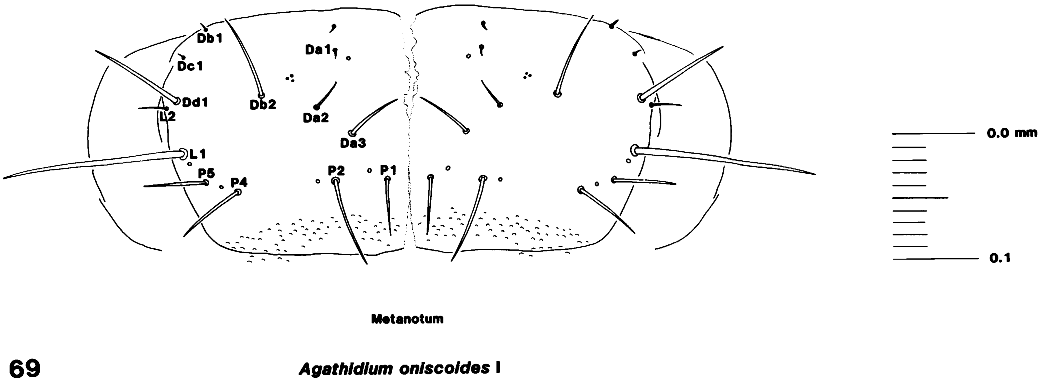
Instar III. – Head width about 0.62 mm; HW/HL = 1.6. Chaetotaxy differs from that of instar I as follows, and as in figures 12, 14: Row Da with 3 setae (Da*, Da, Da2); row Db with 2 additional setae (Db**); row Dc with 3 additional setae (Dc***); row L with 3 additional setae (L***).

Antenna (figs. 12–14, 42): Instar I. – Antennal formula = 1.3:3.3:1.3:1; antennomere II/digitiform organ = 2.4; as in instar III, except single solenidium ventral to digitiform organ (compared to 2 in later instars).

Instar II. – Antennal formula = 1.7:3.3:1.3:1; as in instar III.

Instar III. – Antennal formula = 1.5:3.25:1:1; see description for instar I.

Mouthparts (figs. 43–47): Instar I. – As in instar III, except as noted. Epipharynx with posterior transverse field of campaniform sensilla absent. Mola of mandible with fewer



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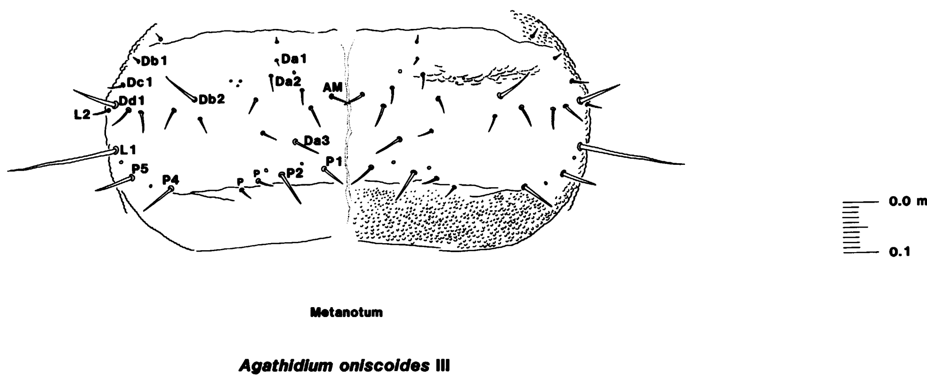


70

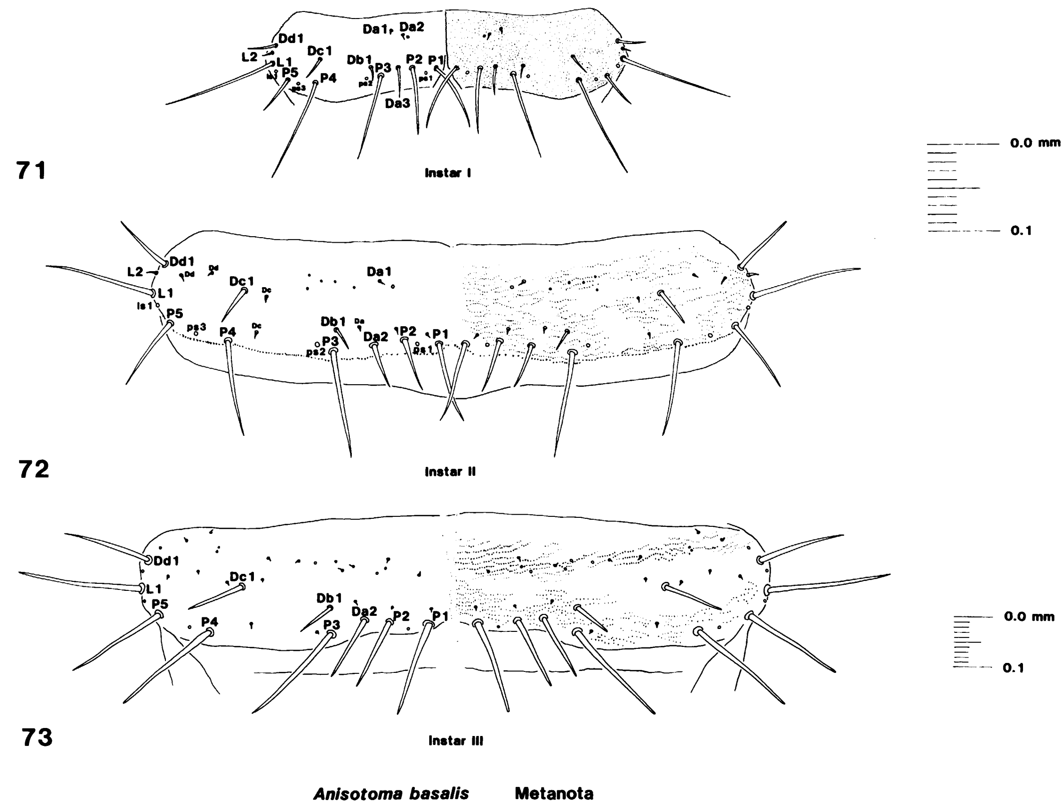
Figs. 69, 70. *Agathidium oniscoides* metanotum, dorsal. **69.** Instar I. **70.** Instar III.

teeth, about 30 visible ventrally. Hypopharyngeal sclerome with complete anterior and posterior bridges, narrower in form.

Instar II. – As in instar III.

Instar III. – Labrum transverse, not emarginate at middle; dorsal surface with 1 pair median setae, 1 pair campaniform sensilla laterad to median setae, 1 lateral pair setae, 3 apical pair setae, lateral pair much larger; adoral surface with 2 median pair short stout peglike setae, 2 pair longer setae laterad at anterior margin, about 6 campaniform sensilla at middle, posterior transverse field of about ten campaniform sensilla, with about 6 sensilla in two patches anterior to transverse row (figs. 44, 45). Mandible (fig. 46) short, stout; apex with large dens, smaller serrate secondary dens; prostheca short, pointed; mola with 50–60 teeth visible ventrally. Maxilla (fig. 43) with cardo simple, with single seta; stipes with about 7 setae, 1 campaniform sensillum basal to galea; galea narrow, fimbriate and membranous at apex, and with single seta subapically; lacinia narrow, terminating in point, with 7 large lateral setae; palpus 2-segmented; palpifer with 2 ventral campaniform sensilla; I with 1 ventral campaniform sensillum, 1 ventral seta, 1 dorsal seta; III elongate, narrowed apically, with mesal seta near base, dorsal recumbent sensillum, apical sensilla. Labial mentum with 2 pair setae, single pair campaniform sensilla (fig. 47); ligula ovate, with single pair setae; palpus 2-segmented: I short, with basal seta and apical campaniform sensillum, II small, narrower, with lateral campaniform sensillum, subapical recumbent sensillum, apical setae. Hypopharyngeal sclerome transverse, with complete anterior and posterior bridge, median foramen triangular, sometimes slightly ill-defined at middle anteriorly.

Leg (figs. 76–80): Instar I. – Coxa large, irregularly shaped, with about 9 anterior, 1 posterior setae. Trochanter subtriangular;



Figs. 71–73. *Anisotoma basalis* metanotum, dorsal. **71.** Instar I. **72.** Instar II. **73.** Instar III.

anterior face with 2 anteroventral (Av), 2 anterolateral (Al) setae in addition to ventral seta (V1), and transverse row of 3 sensilla; posterior face with single ventral (Pv1) and lateral (Pl1) setae. Femur short, broad; anterior face with campaniform sensillum near base, ventral seta (V1), 2 anteroventral setae (Av1–2), single anterolateral seta (Al1), single apical anterodorsal seta (Ad); posterior face with 2 lateral setae (Pl1–2), single posterodorsal seta (Pd1). Tibia elongate, slightly sinuate; anterior face with 2 dorsal setae (D1–2), single anterodorsal near apex (Ad1), 2 anterolateral setae (Al1–2), single anteroventral seta (Av1). Tarsungulus long, narrow, with single anterior and posterior seta.

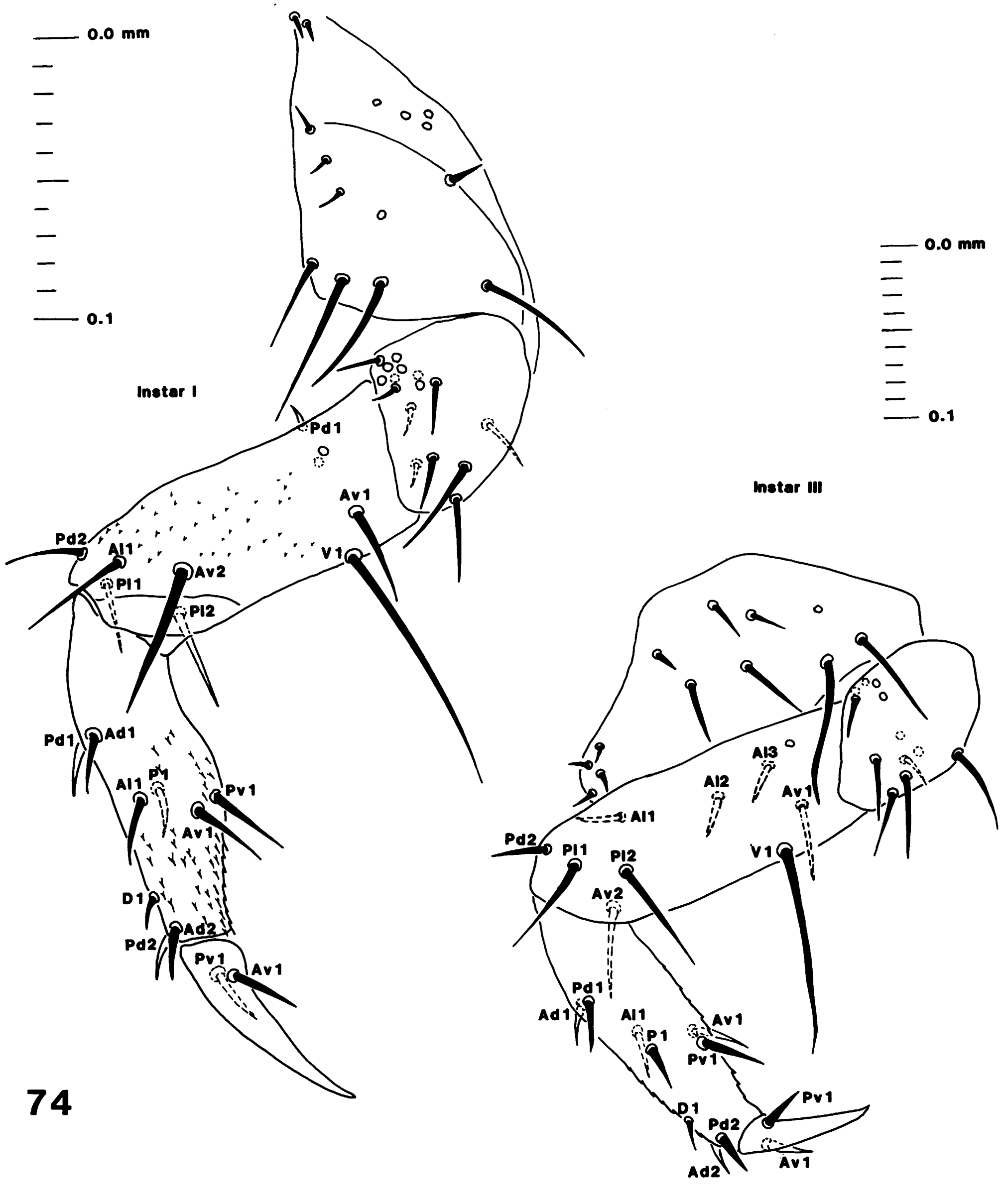
Instar II. – As in instar III.

Instar III. – Chaetotaxy as in instar I, except with following *additional* setae. Trochanter with apical posterolateral (Pl*), second posteroventral (Pv2). Femur with four additional posterolateral setae (Pl3–Pl6); anterodorsal near middle of length, 3 additional anterolateral setae (Al2–Al4).

Pronotum (figs. 58, 59): Instar I. – Transverse, narrower anteriorly than posteriorly; N1L/N1W = 0.44. Chaetotaxy as follows, and in figure 58: Row Da with 2 setae (Da1, Da2); row Db with 4 setae (Db1–Db4); row Dc with 2 setae (Dc1, Dc2); single seta each in rows Dd, De, L; posterior transverse row with 4 setae (P1–P4); campaniform sensilla distributed as follows, 1 between setae P1/P2, 1 between Db1/Dc1, 2 posteromesad to Dc1, 2 posterolaterad of P2, 1 between Dc1/Dd1, 1 anterior to Dd1, 1 posterior to Dd1, 1 laterad of P4.

Instar II. – Same as instar III, except P1L/P1W = 0.43.

Instar III. – Including unpigmented anterior and posterior areas, only slightly wider than long: P1L/P1W = 0.62; L/W of sclerotized area only = 0.36. Chaetotaxy as in figure 59, including following setae in *addi-*



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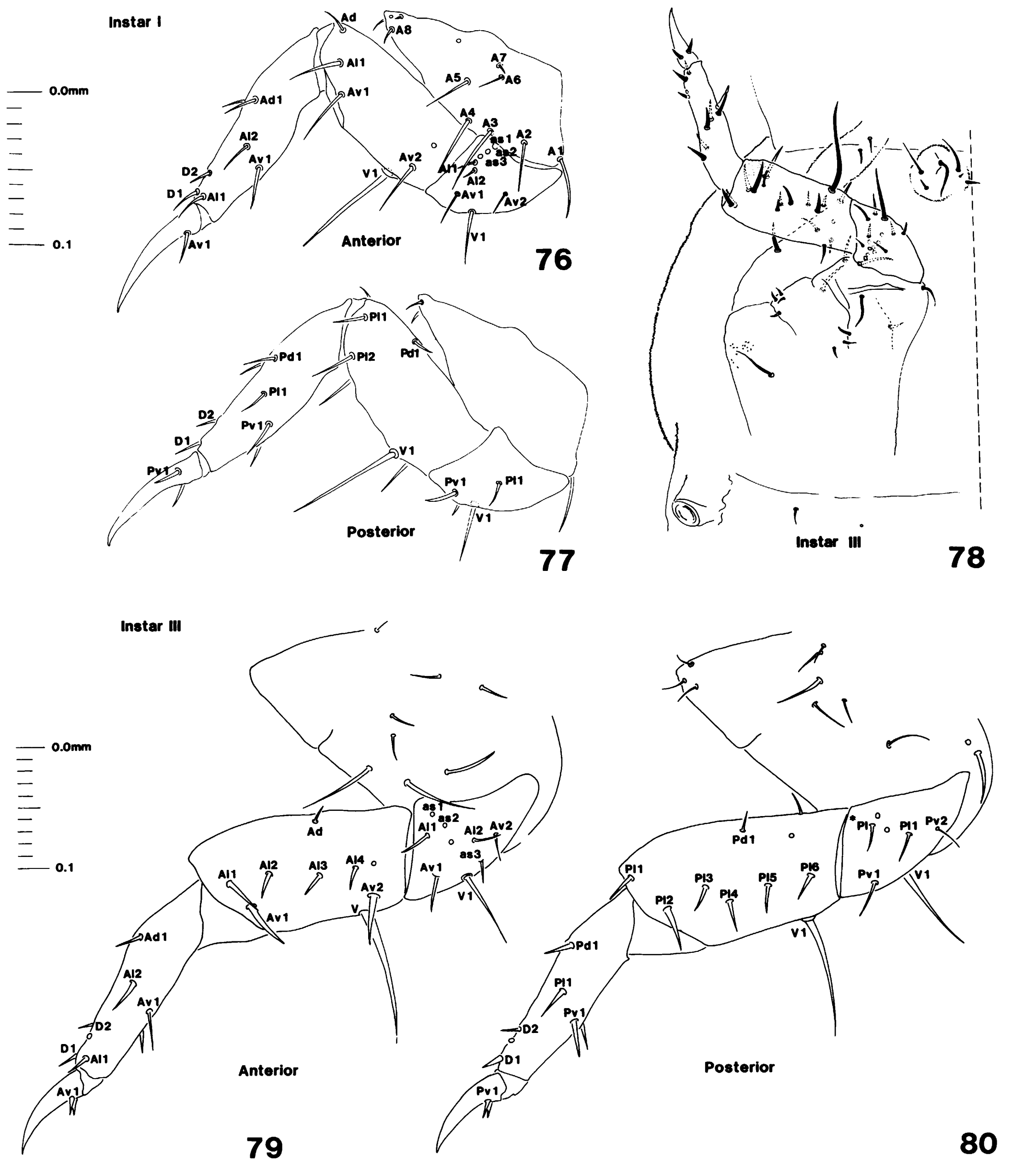
75

Agathidium pulchrum

Proleg

Figs. 74, 75. *Agathidium pulchrum* leg. **74.** Instar I, anterior. **75.** Instar III, posterior.

tion to those of instar I: Row Da with 7 added setae, 1 anterior to Da1, 3 between Da1/Da2, 1 laterad of Da2, 2 between Da2/P1; row Db with 6 added setae, 1 anterior to Db1, 2 between Db1/Db2, 4 between Db2/P2; row Dc with 11 added setae, 3 anterior to Dc1, 3 between Dc1/Dc2, 5 posterior to Dc2 and anterior to P3; row Dd with 1 added seta; row De with 3 added setae, 2 anterior to De1; row L with 9 added setae including 1 large



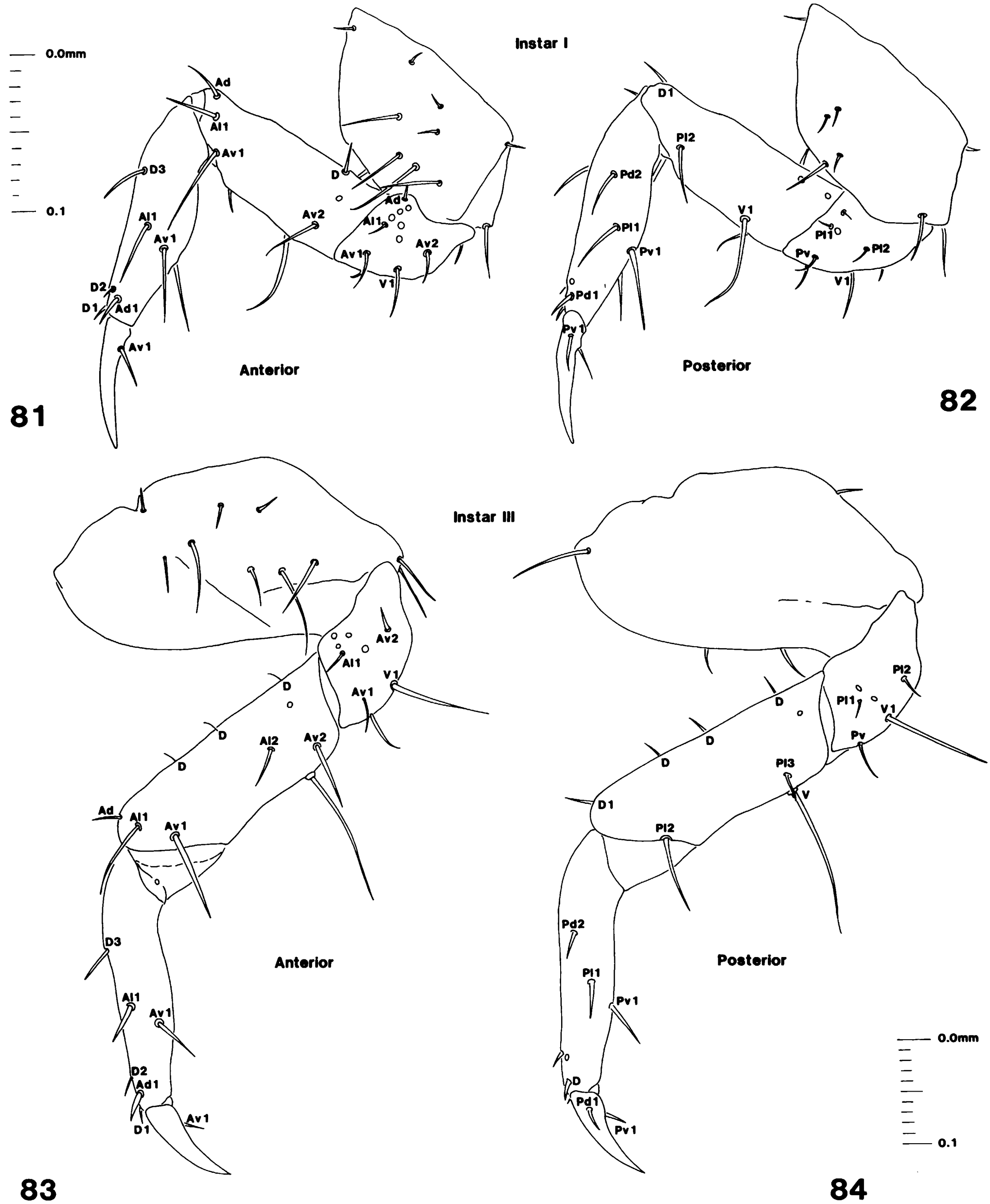
Agathidium aristerium

Proleg

Figs. 76–80. *Agathidium aristerium* leg. **76.** Instar I, anterior. **77.** Instar I, posterior. **78.** Prothorax, ventral, instar III. **79.** Instar III, anterior. **80.** Instar III, posterior.

seta anterior to L1, single small seta posterior to L1; transverse row P with 12 added setae, 1 pair between P1s, 2 between P1/P2, 7 between P2/P3, 3 between P3/P4.

Metanotum (figs. 67, 68): Instar I.—N3L/N3W = 0.4. Chaetotaxy as follows and in figure 67: Row Da with 5 setae (Da1–Da5); row Db with 3 setae (Db1–Db3); row Dc with 2 setae; row Dd with single seta; row L with 2 setae; transverse posterior row with 4 setae



Agathidium oniscoides

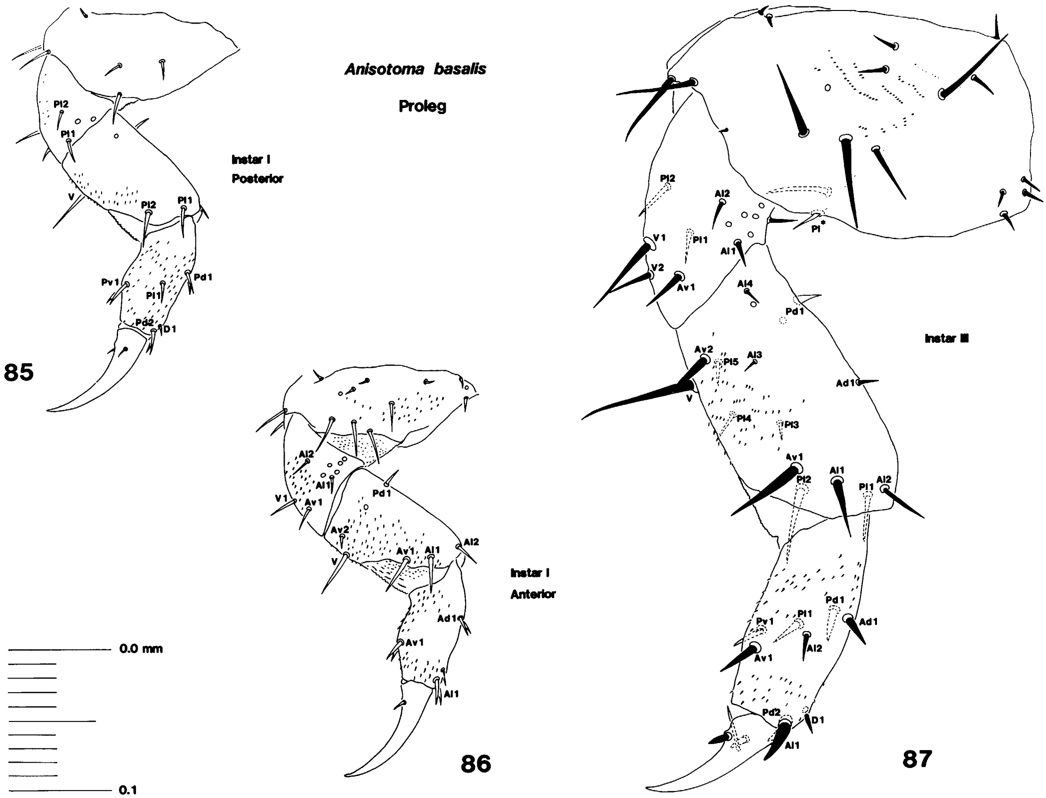
Proleg

Figs. 81–84. *Agathidium oniscoides* leg. **81.** Instar I, anterior. **82.** Instar I, posterior. **83.** Instar III, anterior. **84.** Instar III, posterior.

(P1–P4). Campaniform sensilla include 2 between P2/P4, 1 between P4/P5, 1 between P5/L1.

Instar II. – Similar to instar III.

Instar III. – Shape, excluding broad posterior membrane, very transverse; N3L/N3W = 0.24. Chaetotaxy includes following setae *in addition to* those of instar I (fig. 68): row



Figs. 85–87. *Anisotoma basalis* leg. **85.** Instar I, posterior. **86.** Instar I, anterior. **87.** Instar III, anterior.

Da with 4 added setae; row Db with 3 added setae; row Dc with 3 added setae; row L with 2 added setae; transverse row P with 15 added setae.

Abdominal Segment I (figs. 90, 91): Instar I. – A1L/A1W = 0.27. Tergum and chaetotaxy as follows and as in figure 90: 8 dorsal setae (Db1–Db4, Dd1, De1–De3), 5 posterior setae (P1–P3, P5, P6), 1 lateral seta (L1). Campaniform sensilla include one between Db1/Dd1 anteriorly, 1 between P4/P5 posteriorly, and 1 between P6/L1 posterolaterally.

Instar II. – Similar to instar III.

Instar III. – Short and wide, A1L/A1W = 0.17, excluding posterior membrane. Chaetotaxy includes following setae *in addition to* those present in instar I (fig. 91): row Da with 3 added setae in addition to 2 added pair of "median setae" (M); row Dc with 1 seta added; row Dd with 1 seta added; row De with 1 minute seta added anteriorly; 2 additional lateral setae; posterior row with 3 additional setae, 1 between P1/P2 and 2 between P4/P5.

Abdominal Tergum IX (figs. 101, 103): Instar I. – Transverse, subquadrate: 2 small (Dl1, Dl2) and 1 large (Dl3) dorsolateral setae; with irregular transverse basal patches of "pores" and campaniform sensilla; posterior half with sparse asperities. Urogomphus short; formula = 1:1.25:1.5. Length URI/URII = 0.7; length URII/URS = 0.8. Urogomphus segment I with 3 setae and 3 campaniform sensilla dorsally. Urogomphus segment II with terminal stylus only.

Instar II. – Similar to instar III. Urogomphus formula = 1:2.13:1.5.

Instar III. – Similar to instar I, except as noted. With 5 additional dorsal pairs of setae: 1 posteromedially, 2 anteromedially but farther from midline, 2 posterolaterally mesad to seta Dl3. Dorsal surface covered with moderately dense asperities, more or less arranged in transverse rows. Urogomphus with second segment smaller proportional to first;

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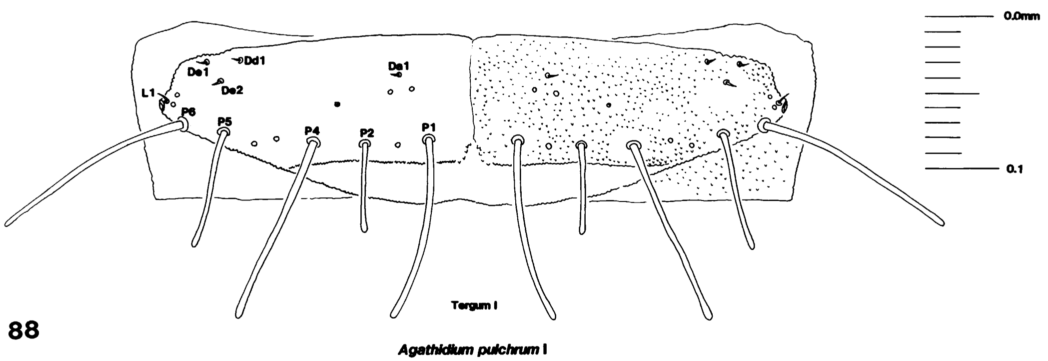

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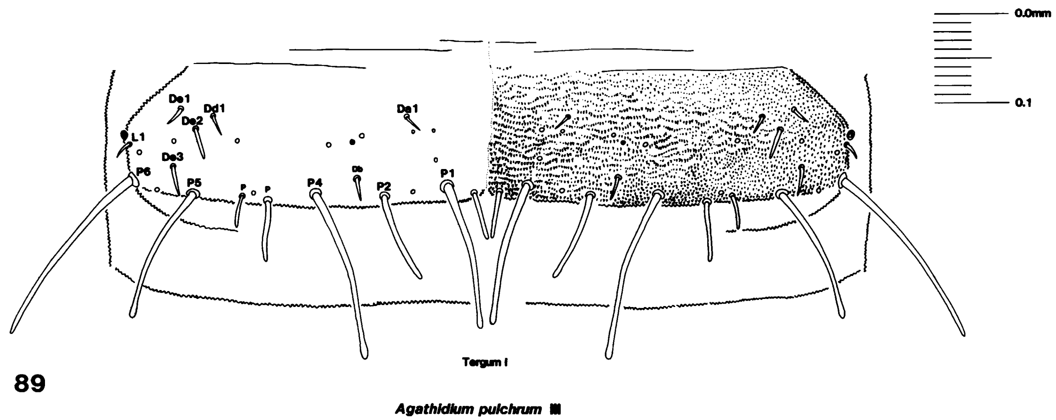


Figs. 88, 89. *Agathidium pulchrum,* abdominal tergum I, dorsal. **88.** Instar I. **89.** Instar III.

formula = 1:1.4:1.2. Length URI/URII = 0.7. Length URII/URS = 1.1.

Abdominal Sternum IX and Anal Membrane (figs. 101, 103): Instar I. – Sternum IX with single setal pair near middle (V1), posterior row of 5 setae (Vp1–Vp5). Anal membrane with 2 large dorsal setal pairs (D1, D2), 2 lateral setae (L1, L2); 3 ventral setae (V1–V3); campaniform sensilla between V1/V2 (vs1), V2/L2 (vs2).

Instar II. – Similar to instar III.

Instar III. – Sternum IX with 2 added setae basal to V1, 1 seta added between V1/Vp1, 1 seta added between Vp3/Vp4, 2 lateral setae added (L1, L2). Anal membrane with 2 setae added laterad D2, 2 setae added posterior to D1 dorsally; 2 setae added anterior to V1, 4 setae added posterior to V3. [Note: setae L1, L2 of instar I not present in similar position in instar III; 2 setae laterad D2 could correspond to same setae with a relative positional change. These setae were counted as one character and the possible loss of lateral setae not counted (Wheeler, 1990).]

AGATHIDIUM ONISCOIDES PALISOT DE BEAUVOIS

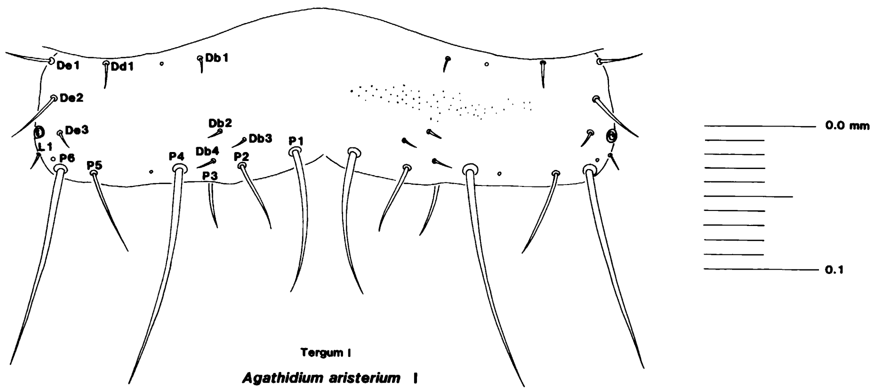
(Figures 15–17, 21–25, 52, 53, 60, 61, 69, 70, 81–84, 92, 93, 104, 105)

Agathidium oniscoides Palisot de Beauvois, 1805: 160.

DIAGNOSIS

Larvae 2 (first instar) to 6.3 (final instar) mm in length; mandible with mola somewhat reduced and without dense transverse rows of asperities; digitiform organ of antennomere II undivided; dorsal surface of body without asperities; head with 2 stemmata on either side; first instar larvae with inordinately prolonged second segment of urogomphus, relative to first (fig. 104).

Body: Instar I. – Elongate, cylindrical, narrowed posteriorly, widest at metanotum. Terga with well-developed sclerites; pleural region membranous; sternal region with weakly sclerotized plates. Length about 2.0 mm.



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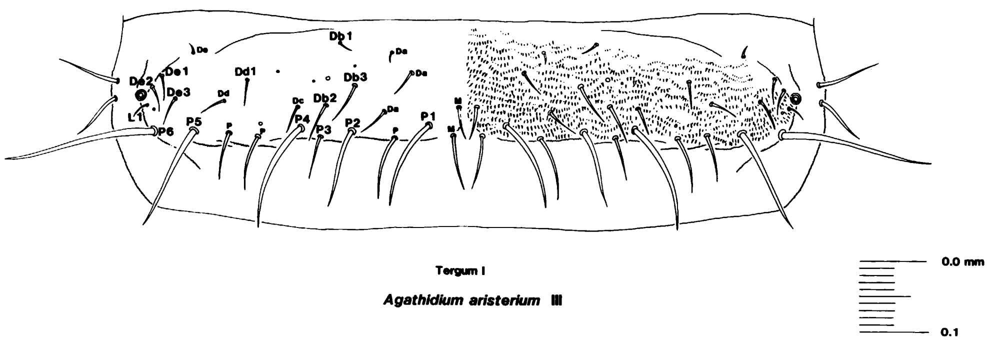

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Figs. 90, 91. *Agathidium aristerium,* abdominal tergum I, dorsal. **90.** Instar I. **91.** Instar III.

Instar II. – Length about 4.1 mm.

Instar III. – Length about 6.3 mm.

Head (figs. 15–17): Instar I. – Cranium wider than long; HW/HL = 1.3; average head width 0.30 mm. Chaetotaxy as follows, and in figure 16: row Da with three setae (Da1–Da2, Da*a); Db with 2 setae (Db2–Db3); Dc with 4 setae (Dc1–Dc4); and Dd with 4 setae (Dd1–Dd4); 2 lateral setae (L1–L2); and 4 minute posterior setae (P1–P4). Campaniform sensilla include 1 between Dc3/Dc4, 1 mesad to De1, and 1 between P2 and P3. With two stemmata.

Instar II. – Head width about 0.48 mm; HW/HL = 1.4. Chaetotaxy as in instar III.

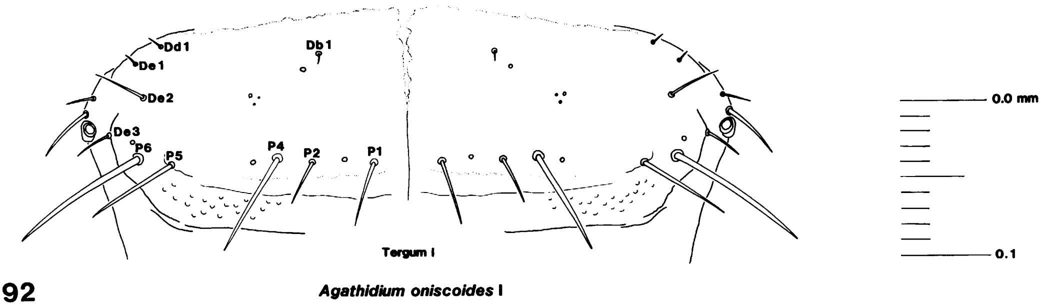
Instar III. – Head width about 0.56 mm; HW/HL = 1.5. Chaetotaxy as in instar I, except as follows: row Dc with additional seta between Dc2 and Dc3; row De with 1 additional seta posterior to De2; lateral row with 1 additional seta posterior to seta L2.

Antenna (figs. 15, 16, 23): Instar I. – As in instar III, except as noted here. Antennal formula = 1:3:1.6:1.6. Antennomere II length/digitiform organ length = 1.8. Antennomere II length/III length = 1.8. Minute sensillum ventral to digitiform organ absent.

Instar II. – As in instar III.

Instar III. – Formula = 2.6:4.7:2:1. Antennomere II length/digitiform organ length = 1.7. Antennomere II length/III length = 2.5. Antennomere I with 3 dorsal and 2 ventral campaniform sensilla. Antennomere II with 3 large setae: 1 dorsal, 1 ventral, 1 mesad; small subapical dorsal seta; subapical ventral campaniform sensillum; digitiform organ large, peglike; 1 narrow, small sensillum ventral to digitiform organ; 1 and sometimes 2 minute sensilla basal to small one. Antennomere III with 2 ventral, 1 dorsal setae; large pointed apical sensillum, 3 smaller apical sensilla.

Mouthparts (figs. 21, 22, 24, 25): Instar I. – As in instar III, except as noted. Labrum:



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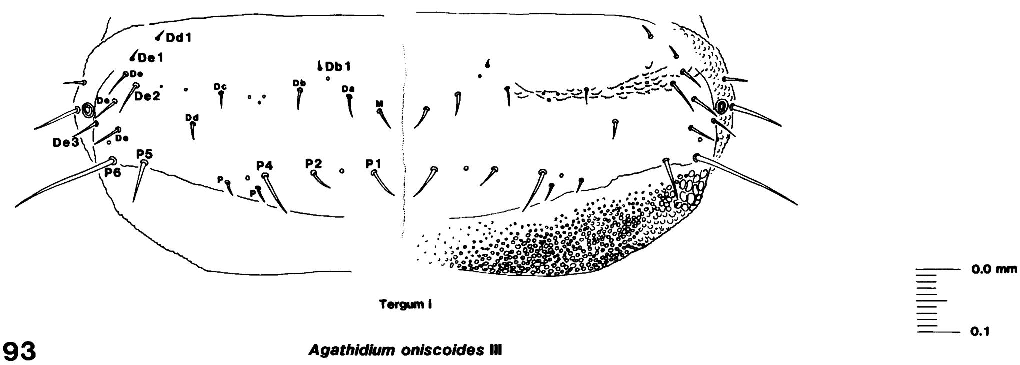

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Figs. 92, 93. *Agathidium oniscoides,* abdominal tergum I, dorsal. **92.** Instar I. **93.** Instar III.

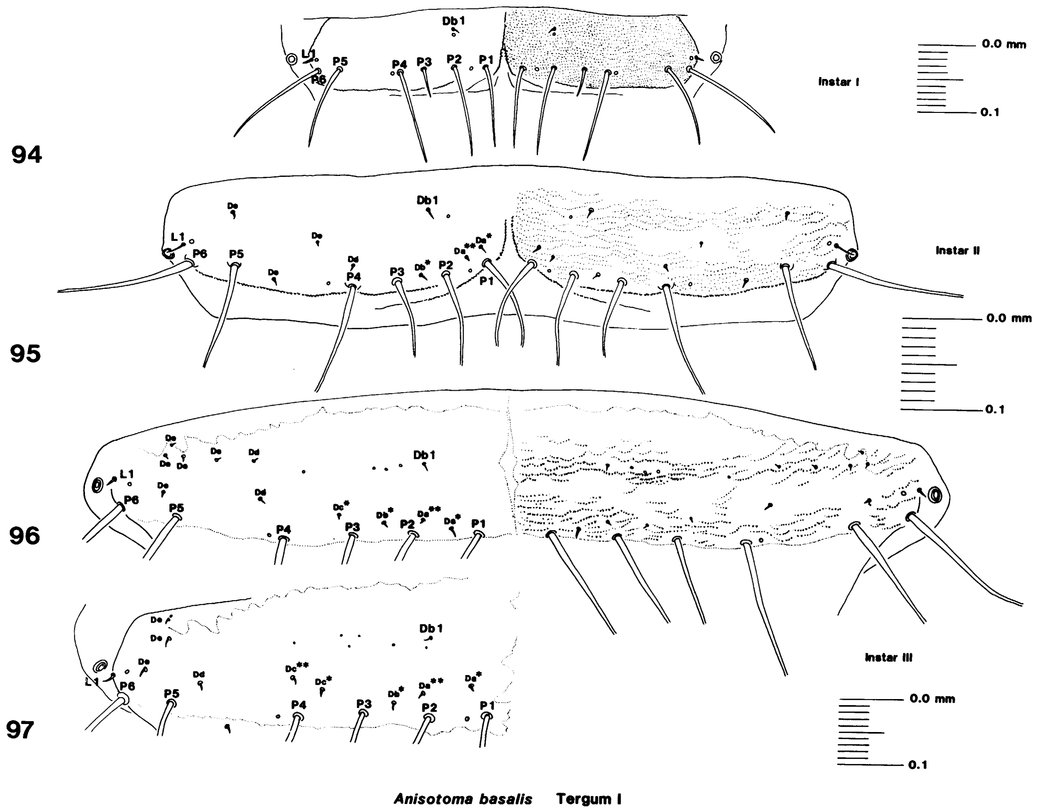
seta D3 absent. Hypopharyngeal sclerome with anterolateral areas very weakly sclerotized to invisible.

Instar II. – As in instar III.

Instar III. – Labrum transverse, deeply emarginate at apex. Dorsal surface with 6 pair dorsal setae (D1–D6) and 1 campaniform sensillum behind setae D1–D2. Epipharynx with 2 pair apicomedial short stout setae, minute setae at middle, 3 pair apicolateral spatulate setae, 1 pair anteromesal sensilla, transverse posterior field of 12 sensilla. Mandible short, simple; apex bidentate; prostheca large, membranous; mola not developed, without teeth. Maxillary cardo simple with single seta; stipes with 5 setae, 1 apicomedial campaniform sensillum; mala undivided, apex long accicuate, 5 mesal setae, 1 campaniform sensillum near apical seta of mesal "comb"; palpus 2-segmented: I with 1 seta, 1 campaniform sensillum ventrally, 1 seta dorsally; II with dorsal recumbent sensillum, subapical campaniform sensillum, 1 seta on mesal margin, apical sensilla; palpifer with pair campaniform sensilla near apex. Labial mentum with 2 setae, 1 campaniform sensillum; palpus 2-segmented: I with apicodorsal campaniform sensillum mesad, minute basolateral (dorsal) minute seta; II with dorsal recumbent sensillum, subapical lateral lobe, apical sensillum; ligula with 1 pair setae, 1 pair campaniform sensilla near apex. Hypopharyngeal sclerome "quadrate" in proportions, with posterior bridge absent, and anterior bridge weakly sclerotized anterolaterally.

Leg (figs. 81–84): Instar I. – Coxa large, irregularly shaped, with about 10 anterior, 5 posterior setae. Trochanter subquadrate: anterior face with 5 setae and 5 campaniform sensilla; posterior face with 3 setae and 2 campaniform sensilla. Femur anterior face with 5 setae, 1 campaniform sensillum; posterior face with 3 setae, 1 campaniform sensillum. Tibial anterior face with 5 setae; posterior with 4 setae. Tarsungulus with single pair setae.

Instar II. – Same as instar III.



Figs. 94–97. *Anisotoma basalis,* abdominal tergum I, dorsal. **94.** Instar I. **95.** Instar II. **96.** Instar III. **97.** Instar III, another specimen showing variation.

Instar III. – Femur with 3 additional minute dorsal setae.

Pronotum (figs. 60, 61): Instar I. – Transverse; PL/PW = 0.58. Chaetotaxy as follows, and in figure 60: Row Da with 2 setae (Da1–Da2); row Db with 2 setae (Db1–Db2); row Dc with 2 setae (Dc1–Dc2); lateral row with 2 setae (L1–L2); posterior transverse row with 4 setae (P1–P4). Campaniform sensilla include 1 between setae Da1–Db1 (dc1); 1 between setae Db1–Dc1 (dc2); 1 between setae P1–P2 (pc1); 1 between setae P2–P3 (pc2); 1 between setae P3–P4 (pc3).

Instar II. – Same as instar III, except PL/PW = 0.46.

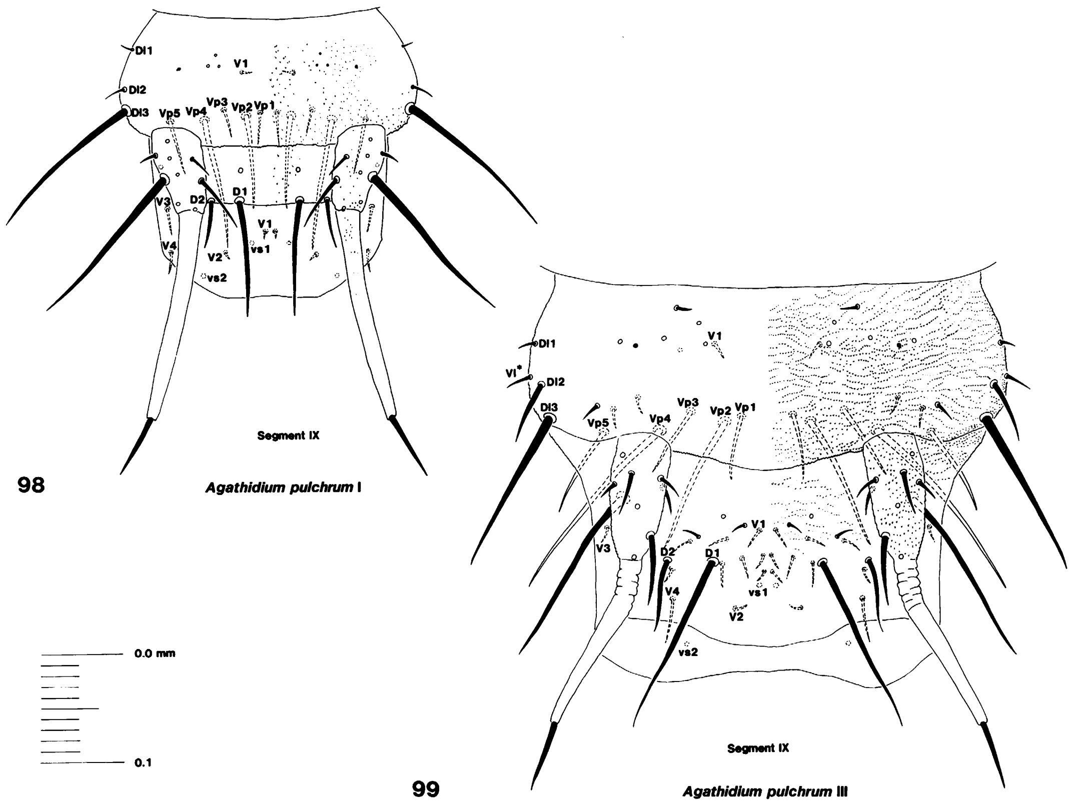
Instar III. – PL/PW = 0.43. Chaetotaxy differs from instar I by addition of following setae (fig. 61): row Da with 4 setae along or mesad to imaginary line drawn between seta Da1 and Da2; row Db with 2 setae mesad to line between seta Db1 and Db2; row Dc with 2 setae posterior to seta Dc2; additional 2 setae in row Dd; additional 3 setae in row De; 5 lateral setae, 2 between seta L′ and L1, 2 anterior to seta L′; 4 setae in posterior transverse row, 1 between seta P1 and P2, 2 between P2 and P3, 1 between P3 and P4.

Metanotum (figs. 69, 70): Instar I. – N3L/N3W = 0.4. Chaetotaxy as follows and in figure 69: 7 dorsal setae (Da1-3, Dbl-2, Dc1, Dd1); 1 minute, 1 large lateral seta (L1–L2); 4 posterior setae (P1–P5). Campaniform sensilla include 1 posterior to seta Da1 (dc), 1 between setae P1/P2 (pc1), 1 between P2/P4 (pc2), 1 between P5/L1 (1c). Sensillum and bumps anteromesad to Db2.

Instar II. – Similar to instar III.

Instar III. – N3L/N3W = 0.31. Similar to instar I, except for following additional setae: 3 Da (including "Au"); 3 Db; 3 Dc, 1 posterior and slightly mesad Db2; 1 Dd (fig. 70).

Abdominal Segment I (figs. 92, 93): Instar I. – A1L/A1W = 0.29. Tergum with chaetotaxy as follows and as in figure 92: 5



Figs. 98, 99. *Agathidium pulchrum,* abdominal tergum IX, urogomphi, and anal membrane. **98.** Instar I. **99.** Instar III.

dorsal setae (Db1, Dd1, De1–De3), 5 posterior setae (P1–P2, P4, P5, P6), 2 lateral setae anterior to spiracle. Campaniform sensilla include 1 posterolateral to Db1, 1 near middle of notal disc (copositioned with 2 bumps), 1 between P1/P2, 1 between P4/P5, 1 between P6/De3.

Instar II. – Similar to instar III.

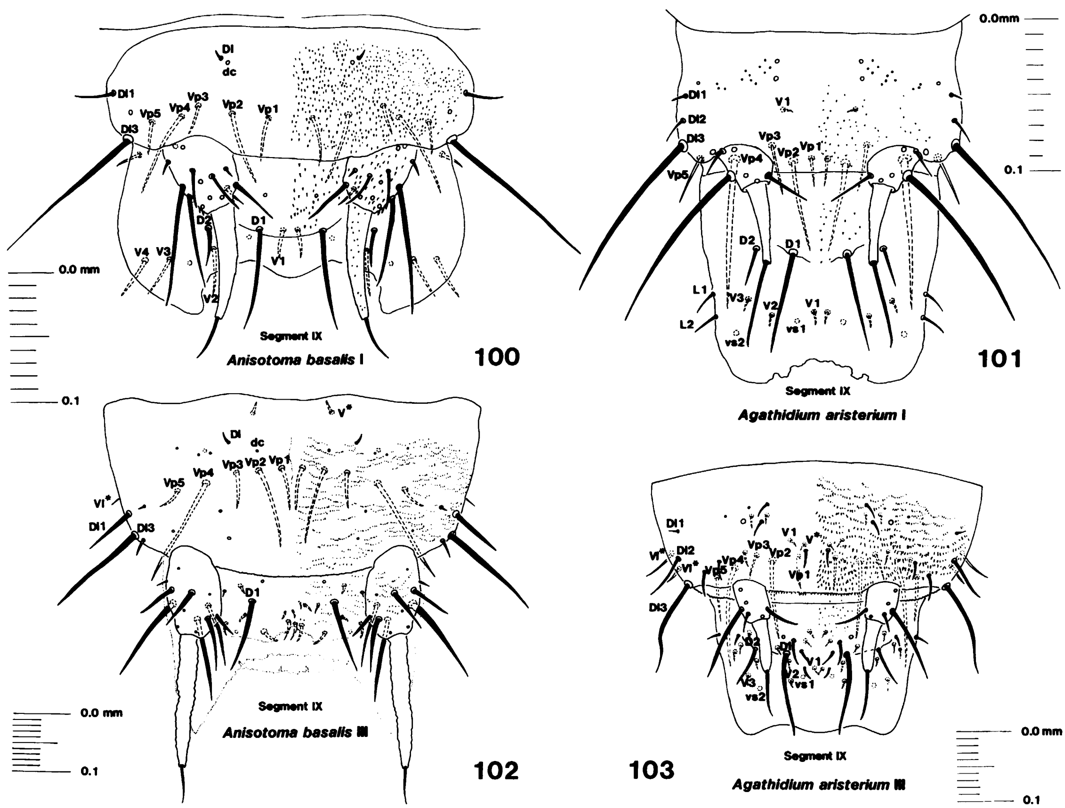
Instar III. – Proportions of tergum similar to instar I, A1L/A1W = 0.31. Additions to setae include following (see fig. 93): 1 Da and one median to it (M), 1 Db posterolaterad of Db1, 1 Dc, 1 Dd anteromesad De2, 3 De in row between De2/De3, 2 posterior posterolaterad of P4. Two additional campaniform sensilla mesad De2.

Abdominal Tergum IX (figs. 104, 105): Instar I. – Transverse, subquadrate: 1 pair small dorsal setae (D1), 1 pair dorsal campaniform sensilla (dc), "asperite organ" composed of 2 sensilla with surrounding wrinkles and asperities, large posterolateral seta (L1). Urogomphus long, narrow; formula = 1:2.7:2. Length URI/URII = 0.38; length URII/URS = 1.3. Urogomphus segment I with 1 dorsal seta, 4 dorsal campaniform sensilla; 2 small, 1 large ventral setae. Urogomphus segment II with large apical seta only.

Instar II. – Similar to instar III. Urogomphus formula = 1:2:1.3.

Instar III. – Similar to instar I, except as noted. Transverse: 9 pair dorsal setae (D1–D9), 6 pair campaniform sensilla (dc1–dc6). Urogomphus with second segment smaller proportionately compared to first; formula = 1.2:1.5:1. Length URI/URII = 0.77; length URII/URS = 1.9. Urogomphus segment I with 3 dorsal setae.

Abdominal Sternum IX and Anal Membrane (figs. 104, 105): Instar I. – Abdominal sternum IX with 2 lateral setae and 5 ventral setae arranged in posterior transverse row (P1–P5). Anal membrane with dorsal (D) and ventral (V) setae as follows: 1 large (D1), 1



Figs. 100–103. Abdominal tergum IX, urogomphi, and anal membrane, dorsal. **100.** *Anisotoma basalis,* instar I. **101.** *Agathidium aristerium,* instar I. **102.** *Anisotoma basalis,* instar III. **103.** *Agathidium aristerium,* instar III.

moderate (D2) size anteromedial setae; 1 pair campaniform sensilla (dc1) anteromesad to seta D1; 1 lateral (V1), 3 posterior (V2–V4) setae; 2 posterior campaniform sensilla ventrally (vc1–vc2).

Instar II. – Similar to instar III.

Instar III. – Abdominal sternum IX as in instar I, except with 9 ventral setae (additional setae V6–V9). Anal membrane with 10 ventral pairs setae; 7 pairs dorsal setae (fig. 105).

ANISOTOMA BASALIS (LECONTE)

(Figures 18–20, 26–33, 54, 55, 62–64, 71, 73, 85–87, 94–97, 100, 102)

Leiodes basalis LeConte, 1853: 285.
Leiodes dichroa LeConte, 1853: 285.
Liodes basalis LeConte; Horn, 1880: 299.
Anisotoma basalis (Leconte); Brown, 1937: 200.
Anistoma basalis (LeConte); Wheeler, 1979: 292.

DIAGNOSIS

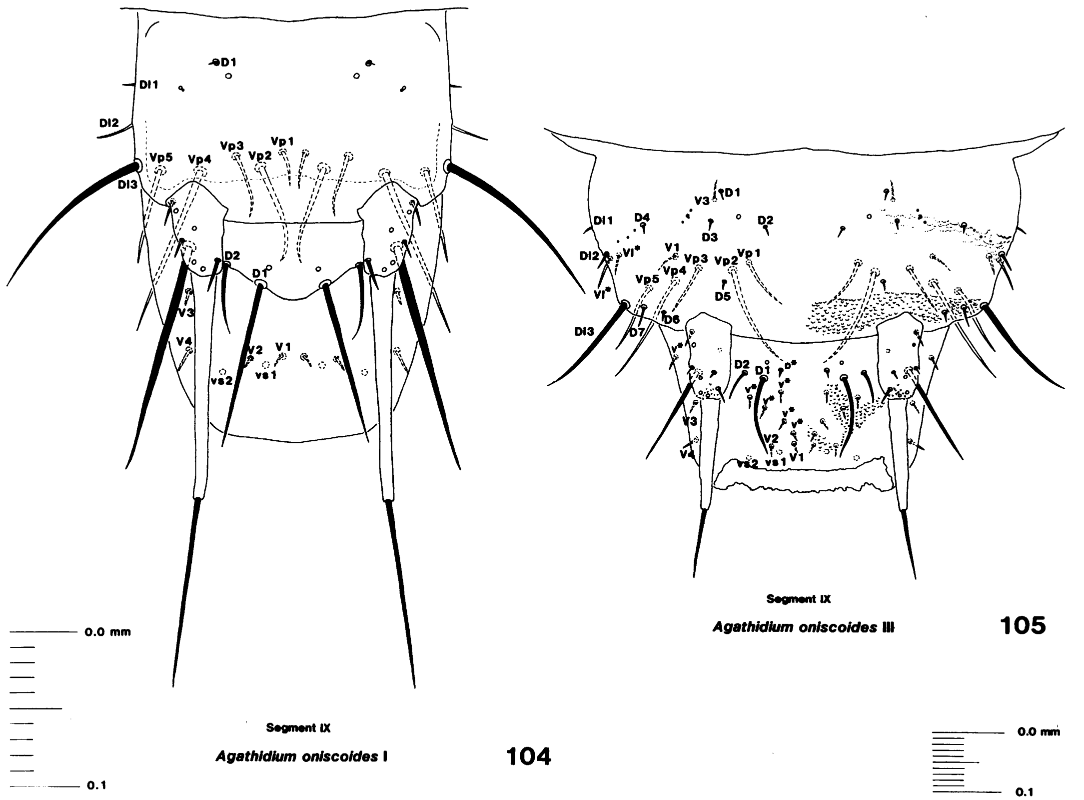
Posterior transverse setal row of terga with seta P4 present; secondary solenidia located near base of digitiform organ of antennomere II number 2 in instar I and 3 in later instars; mola of mandible with rows of asperities; digitiform organ undivided; dorsal surface with sparse to moderately dense rows of asperities; head with 2 stemmata on either side.

DESCRIPTION

Body: Instar I. – Elongate, cylindrical, narrowed posteriorly, widest at metanotum. Terga with well-developed sclerites. Average total body length about 2.1 mm. Metanotal width 0.4 mm.

Instar II. – Similar to instar III; total body length about 3.9 mm.

Instar III. – Total body length about 6.1 mm.



Figs. 104, 105. *Agathidium oniscoides,* abdominal tergum IX, urogomphi, and anal membrane, dorsal. **104.** Instar I. **105.** Instar III.

Head (figs. 18–20): Instar I. – Cranium wider than long; HW/HL = 1.5; average head width 0.36 mm. Chaetotaxy as follows and in figure 18: row Da with single seta (Da2); row Db with 3 setae (Db1–Db3); row Dc with 2 setae (Dc3, Dc4); row Dd with 3 setae (Dd2–Dd4); rows De, Df with 3 setae (De1, Df1a, De2); lateral row with single large seta (L1); 5 posterior setae (P1–P5). Campaniform sensilla include 2 pair in anterior portion of frons, 1 pair in posterior area of frons, 1 pair above bases of mandibles, 1 between Dc3/Dc4, 1 anterior to L1. Integument along midline and especially posteriorly with moderately dense minute asperities. Stemmata 2, lateral.

Instar II. – HW/HL = 1.48; cranium width about 0.49 mm. Chaetotaxy similar to that of instar III, and as in figure 19.

Instar III. – HW/HL = 1.4; cranium width about 0.65 mm. Chaetotaxy as in figure 20; with following setae *in addition to* those present in instar I: row Da with seta Da* added, and 1 added seta (Da**); row Db with 1 seta added posterior to Db3; row Dc with Dc1 and Dc2 added, and 1 seta added near Dc4; row Dd with 1 seta added between Dd2/Dd3 (seta Dd1 *absent in all instars*). Asperities very sparse, restricted to parts of labrum and mandibles and to posterolateral patches on dorsum of cranium.

Antenna (figs. 18–20): Instar I. – As in instar III, except as noted. Antennal formula = 1.5:3:1:1. Length antennomere II/digitiform solenidium length = 3.7. Length antennomere II/III = 2.7. Two solenidia near digitiform solenidium. Antennomere I with 2 dorsal campaniform sensilla, 1 ventral campaniform sensillum.

Instar II. – As in instar III, except antennal formula = 3:5.5:2.5:1; length antennomere

II/digitiform solenidium = 5.2; length II/III = 2.4.

Instar III. – Antennal formula = 3:4.7:2.7:1. Length antennomere II/digitiform solenidium = 4.4. Length antennomere II/III = 1.87. Three solenidia in membranous area at base of digitiform solenidium. Antennomere I with apical dorsal seta, 3 dorsal campaniform sensilla, 2 ventral apical campaniform sensilla. Antennomere II with 2 setae basal and near digitiform solenidium, 1 dorsal campaniform sensillum, 1 ventral seta. Antennomere III small, with 4 subapical seta, 1 subapical pointed process, 1 subapical peglike sensillum.

Mouthparts (figs. 26–33): Instar I. – As in instar III, except as noted.

Instar II. – As in instar III.

Instar III. – Labrum subquadrate, without apical emargination. Epipharynx with median transverse row of about 14 campaniform sensilla, preceded by about 6 more anteriorly placed, irregularly distributed ones; lateral fields of microtrichiae. Mandible apically bidentate; prostheca short, pointed; mola distinct, with about 90 visible teeth. Maxilla with lanceolate lacinia, 7–8 mesal spines, narrow galea, with large fimbriate apex. Labial palpus segment I ventrally with small basal seta, small apicolateral seta, and subapical mesal campaniform sensillum; II with dorsal peglike sensillum; 2 subapical ventral campaniform sensilla; apical sensilla. Ligula membranous, lobate, with 2 subapical setae. Hypopharyngeal sclerome subquadrate, with complete anterior and posterior bridges.

Leg (figs. 85–87): Instar I. – Coxa large, with about 3 posterior and 11 anterior setae. Trochanter triangular, with 2 posterior setae, 2 posterior campaniform sensilla; anterior face with 1 anteroventral seta, 2 anterolateral setae (Al1–Al2); with single ventral seta (V1). Femur short, broad, with ventral seta (V1); 2 posterolateral setae (Pl1, Pl2), 1 posterodorsal seta (Pd1); 2 anteroventral setae (Av1, Av2), 2 anterolateral setae (Al1, Al2). Tibia short, broad, with 1 anteroventral seta (Av1), 1 anterodorsal seta (Ad1), 1 anterolateral seta (Al1); 2 posterodorsal seta (Pd1, Pd2), 1 posterolateral seta (Pl1), 1 posteroventral seta (Pv1); 1 subapical dorsal seta (D1). Tarsungulus long, pointed, with single pair setae.

Instar II. – Similar to instar III.

Instar III. – Similar to instar I, except as follows and in figure 87: Coxa with about 15 anterior setae (total); trochanter with 1 added ventral seta (V2); femur with 2 added anterolateral setae (Al3, Al4), 1 added anterodorsal seta (Ad1), 4 added posterolateral setae (Pl2–Pl5); tibia with 1 added anterolateral seta (Al2).

Pronotum (figs. 62–64): Instar I. – Transverse; N1L/N1W = 0.31. Chaetotaxy as follows and in figure 62: Row Da with 2 setae (Da1, Da2); row Db with 2 setae (Db1, Db2); row Dc with 2 setae (Dc1, Dc2); row Dd with 1 seta (Dd1); row De with 1 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 Db1/Dc1 (ds2), 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). Dorsal surface with dense minute asperities.

Instar II. – Similar to instar III (see fig. 63); N1L/N1W = 0.33.

Instar III. – N1L/N1W = 0.28. Chaetotaxy as in instar I, except *additional setae* as follows and in figure 64: row Da with 2 added setae between Da1/Da2, 1 added seta between Da2/P1; row Db with 7 additional setae; row Dc with 3 added setae; row Dd with 3 added setae; row De with 2 added setae; row L with 1 added seta; row P with 6 added setae. Dorsal asperities sparse, scattered, sometimes arranged in transverse rows.

Metanotum (figs. 71–73): Instar I. – N3L/N3W = 0.21. Chaetotaxy as follows, and in figure 71: Row Da with 2 setae (Da1, Da2); row Db with 1 seta; row Dc with 1 seta; row Dd with 1 seta; row L with 2 setae; posterior transverse row with 5 setae (P1–P5). Campaniform sensilla include 1 between P1/P2 (ps1), 1 between P3/P4 (ps2), 1 between P4/P5 (ps3), 1 posterior to L1 (ls1), 1 near Da2.

Instar II. – Similar to instar III (fig. 72), except L2 and Da1 present, and fewer minute secondary setae added; N3L/N3W = 0.16.

Instar III. – N3L/N3W = 0.18. Chaetotaxy as in instar I, except as follows (fig. 73): Row Da with 1 or 2 setae (seta Da1 often absent or greatly reduced); lateral row with seta L2 absent; and numerous minute secondary setae *added* anterior to other setae.

Abdominal Segment I (figs. 94–97): Instar I. – A1L/A1W = 0.47. Tergum with chaetotaxy as follows and in figure 94: 1 minute dorsal seta (Db1); single lateral seta (L1) near spiracle; six posterior setae (P1–P6), P3 smaller than others of posterior row.

Instar II. – Similar to instar III.

Instar III. – A1L/A1W = 0.60. Chaetotaxy differs from instar I by addition of following setae (figs. 96, 97): row Da with 2 additional small setae (Da*, Da**); row Db with 1 additional small seta (Db*); row Dc with 2, 1, or no additional small setae (cf. figs. 95–97); row Dd with 1–2 additional small setae; row De with 3–5 additional small setae.

Abdominal Tergum IX (figs. 100, 102): Instar I. – Transverse, with 1 pair small dorsal setae (D1) positioned near a dorsal campaniform sensillum (dc); with 2 dorsolateral setae, anterior one smaller than one near posterolateral angle (Dl1, Dl3). Urogomphus comparatively short; formula = 1:2.75:1. Length URI/URII = 0.37; length URII/URS = 2.8. Urogomphus segment I with about 6 setae and 6 campaniform sensilla; with 2 ventral setae. Urogomphus segment II with large apical seta only. Both segments with sparse asperities, present to apex of segment II though less dense.

Instar II. – Similar to instar III.

Instar III. – Similar to instar I, except as noted. Tergum with 2 additional small lateral setae. Urogomphus formula: 2.1:3.1:1. Length urogomphus segment I/II = 0.7; II/URS = 3.1. Basal urogomphal segment with few asperities, more or less arranged into transverse rows (fig. 102); apical segment with very sparse or no asperities.

Abdominal Sternum IX and Anal Membrane (figs. 100, 102): Instar I. – Abdominal sternum IX with transverse row of 5 posterior setae (fig. 100). Anal membrane with dorsal (D) and ventral (V) setae as follows: 1 pair large median (D1) and smaller pair laterad dorsals (D2); with median ventral pair (V1), and 3 laterad ventral pair (V2–4). Some specimens have what appears to be an additional basolateral seta. One pair dorsal campaniform sensilla anterior to setae D1; ventral campaniform sensilla between V1/V2 and between V2/V3.

Instar II. – Similar to instar III.

Instar III. – Abdominal sternum IX as in instar I, except as follows: basal, median pair of ventral setae (V*). Anal membrane as in instar I, except as follows: with 11 ventral setae, and 3 dorsal setae.

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