SYSTEMATICS OF DERMESTIDAE (INSECTA: COLEOPTERA) BASED ON THE LARVAL STAGE

by

TATIANA KISELYOVA

(Under the Direction of Joseph V. McHugh)

ABSTRACT

The results of an extensive investigation of larval morphology of Dermestidae (skin, larder, and carpet beetles) are presented and illustrated with over 150 original illustrations. The gastric caeca in *Dermestes* L., the structure of mandible base in Thylodriini Beal and Trinodini Beal, and the number of Malpighian tubules and abdominal nervous ganglia in various species of Dermestidae are reported for the first time. The first descriptions of the larvae of *Cryptorhopalum triste* LeConte, *Anthrenocerus stigmacrophilus* Armstrong, and *Myrmeanthrenus frontalis* Armstrong are presented. A parsimony analysis based on larval morphological data indicates the monophyly of Dermestidae exclusive of *Orphilus* Erichson. The phylogenetic position of *Orphilus* remains ambiguous. A provisional classification of Dermestidae based on larval data is proposed. The character evolution, the fossil record, and the distribution of extant Dermestidae are discussed in light of phylogeny.

INDEX WORDS: Coleoptera, Dermestidae, Phylogeny, Cladistics, Larvae, Morphology, Beetles

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CHAPTER 1

INTRODUCTION

This study was undertaken to investigate the larval morphology of the beetle family Dermestidae (skin, larder, and carpet beetles), especially the aspects that have not been studied previously. The generated data served two purposes: firstly, to contribute to the knowledge of coleopteran larval anatomy, and secondly, to be used in a cladistic parsimony analysis. The latter was conducted for the purpose of testing the monophyly of Dermestidae using modern phylogenetic methodology and as a means of developing a phylogenetic hypothesis for this family. This work is the first experiment of utilizing the data exclusively from immature stages (69 larval and 5 pupal characters) in a phylogenetic study of this beetle family. The resulting cladogram serves as a framework for discussion of some issues in systematics, classification, biology, distribution, and fossil record of Dermestidae. The larvae of many species of Dermestidae have not been previously described, and little is known about their biology. This work provides the first descriptions of immature stages for a North American dermestid *Cryptorhopalum triste* LeConte and for two unusual myrmecophilous species from Australia: *Anthrenocerus stigmacrophilus* Armstrong and *Myrmeanthrenus frontalis* Armstrong. Novel morphological data on larvae and pupae are recorded for Dermestidae and for representative species of Eucinetidae, Nosodendridae, Derodontidae, Anobiidae, and Bostrichidae. Morphological features are illustrated with numerous line drawings, halftone illustrations, scanning electron micrographs, and color photographs.

CHAPTER 2

DESCRIPTION OF THE LARVAL AND PUPAL STAGES OF *CRYPTORHOPALUM TRISTE* LECONTE (COELOPTERA: DERMESTIDAE), WITH NOTES ON BIOLOGY AND REARING[1]

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[1] Kiselyova, T. 2002. *The Coleopterists Bulletin*. 56(1):41–49. Reprinted here with permission of editor.

ABSTRACT

The first descriptions of the larval and pupal stages of *Cryptorhopalum triste* LeConte (Coleoptera: Dermestidae) are presented. A diagnosis is provided for the larval form of *Cryptorhopalum* Guérin-Méneville. The first instance of rearing this species in captivity is documented. Corn Salad, *Valerianella radiata* (L.) (Valerianaceae), Cat's-ear, *Hypochoeris radicata* L. (Asteraceae), *Senecio* sp. (Asteraceae), and Queen Anne's lace, *Anthriscus sylvestris* (L.) (Apiaceae), are new adult floral hosts. Adults widely occur in disturbed habitats in Northern Georgia in April through October.

INTRODUCTION

The genus *Cryptorhopalum* Guérin-Méneville is represented in the Nearctic region by 22 species (Beal 1985, 1995). Beal (1985) revised the Nearctic species of *Cryptorhopalum* and supplied geographic and floral host information. In other respects, the genus remains poorly studied.

The knowledge of immature stages is particularly limited. Taxonomic descriptions of the larvae exist for only two species: the Neotropical *C. dubium* Sharp (Rees 1943) and the Nearctic *C. poorei* Beal (Beal 1975). Larval morphological characters that distinguish *Cryptorhopalum* from related genera were discussed by Beal (1975, 1979, and 1985), but no formal diagnosis of the larval stage has been provided for the genus. The pupal stage has not been described.

Observations of larval biology have been documented for two species. Beal (1975) reported the occurrence of *C. poorei* larvae under the loose bark of standing dead ponderosa pines, *Pinus ponderosa* Douglas, in close proximity to spider webs. Mason and Ticehurst (1984) described predation of *C. ruficorne* LeConte larvae on gypsy moth eggs.

The subject of the present paper, *Cryptorhopalum triste* LeConte, occupies a disjunct distribution with one population east of the Rocky Mountains and another along the Pacific Coast (Beal 1985). Floral records were summarized by Beal (1979). The species is common in Georgia, and an opportunity was taken to collect a series of adults and rear them in laboratory. The elusive immatures were observed for the first time and successfully reared to adulthood. The resulting descriptions of larva and pupa, along with notes on biology, are presented here in an effort to encourage further research on the systematics and biology of this little-studied genus of Dermestidae.

MATERIALS AND METHODS

Beetles were collected on April 25–26, 1998, in Oconee National Forest, Greene Co., GA, on inflorescences of Corn Salad, *Valerianella radiata* (L.) Dufr. (Valerianaceae), and on May 16, 1998, in Athens, Clarke Co., GA, on Cat's-ear, *Hypochoeris radicata* L. (Asteraceae). They were subsequently reared in the laboratory. Last instar larvae (>50 specimens) and pupae (10 specimens) were killed in hot water and preserved in 75% ethanol. For observation of external morphology, specimens were cleared in warm 10% solution of KOH and mounted on slides in glycerin, glycerin jelly, or CMC 10 permanent media. Drawings were made using a *camera lucida* mounted on a dissecting or compound stereomicroscope.

RESULTS

Diagnosis of the larval stage of *Cryptorhopalum* Guérin-Méneville

Hastisetal tufts inserted on each side of intersegmental membrane behind the abdominal tergum 7 only. Spicisetae inserted near the midline of nota and terga short, no longer than 1/8 the width of a tergum. Short spicisetae present on acrotergites. Sensorium of the antennal segment 2 broad and occupying more than half the length of the segment. Middle setal series of labro-epipharyngeal margin with slender setae only, outer setae subequal in length to inner setae. Epipharynx with 6 sensory papillae in compact, sharply defined, circular group, a median pair of sensory cups, and a proximal transverse series of sensory cups. Pretarsal setae subequal in length.

Cryptorhopalum triste LeConte

Descriptions

Mature larva (Fig. 2.1). Length 3.8–4.6 mm. Integument of head, nota, and terga fuscous, sterna hyaline, coxae with diffuse fuscous pigmentation anteriorly, femora and tibiae yellowish. Setae golden-brown, some spicisetae on the terga dark brown. Hastisetae with shape of head as illustrated (Figs 2.2, 2.3); shaft of longest hastiseta about 1.8 times as long as pronotum. Longest terminal spiciseta about 8.2 times as long as pronotum. Frons without median tubercle. Antennal segment 2 ventrally with a filiform sensillum sunken in a cuticular cup (Fig. 2.4). Labro-epipharyngeal margin with 6 setae in the outer series. Epipharynx with 9–12 sensory cups in the proximal transverse series, epipharyngeal rods as illustrated (Fig. 2.6). Mandible with a short, asperate prostheca; mesal surface at the apex excavated and delimited by the rounded cutting edges dorsally and ventrally (Fig. 2.5). Apex of galea with strong recurved setae ventrally and slender setae dorsally (Figs 2.7, 2.8). Ligula bilobed, with strong setae apically; hypopharynx with a deep median furrow and numerous scale-like asperities (Fig. 2.9). Hypopharyngeal sclerome hyaline. Setal patterns of abdominal tergum 1 as illustrated (Fig. 2.10); no spicisetae inserted on the posterior margins of nota and abdominal terga 1–6. Antecostal suture present on tergum 7, variable on tergum 8. Tergum 9 with a small circular depression medially (Fig. 2.11). Ratio of length of mesosternal femur to width of pronotum 1: 3.1. Ratio of length of tibia to length of femur 1: 1.1. Anterior pretarsal seta on each leg 0.3 as long as pretarsus; posterior pretarsal seta 4/5 as long as anterior pretarsal seta.

Pupa (Fig. 2.12): Length 3.5–3.9 mm. Integument creamy-white, with long, erect, honey-colored spicisetae distributed in patches on the head and dorsum, uniformly on wing pads. Gin traps and urogomphi absent. Pupa remains within the last larval exuvium (Fig. 2.13), in which it is anchored by 2 clusters of long fine setae inserted on each side of the abdominal tergum 8. The setae from opposite sides cross over and adhere to the inner surface of segment 9 of the larval exuvium, on each side of the rectum.

Biology

Adults were observed in April and May in disturbed habitats, such as roadsides and forest clearings. In spring, *V. radiata*, *H. radicata*, and *Senecio* sp. (Asteraceae) were the only noted hosts, despite the proximity of other flowering plants, such as Blackberry (*Rubus* sp., Rosaceae). In June, beetles were common on Queen Anne's lace, *Anthriscus sylvestris* (L.) (Apiaceae). On October 3, 1999, a single adult specimen was collected by J. Overmyer in Ben Burton Park, Athens, GA, where he observed numerous adults on Goldenrod, *Solidago* sp., (Asteraceae) (pers. comm.).

Efforts were made to find the larvae at the sites of spring collection later in the season. Possible habitats, such as under loose bark of standing trees and near spider webs, were searched extensively, but with no success. However, cast skins of early instar larvae identified as *Cryptorhopalum* sp. were found on November 25, 1998, in Whitehall

Forest, Clarke Co., GA, under loose bark of a standing oak charred by a forest fire. It is probable that larvae of *C. triste* are to be found in a similar habitat.

Rearing

Adults collected in April and May were kept in a clear plastic container at room temperature, with exposure to natural light. Dead insects and pieces of rotten wood with bark were provided. Inflorescences of *H. radicata* and *Spiraea* sp. (Rosaceae) were regularly placed in the container and, when flowers were not available, sugar water (one part sugar to four parts water) was provided as food source. Beetles were active during the day, with most of the feeding, flight, and mating observed whenever the container was exposed to direct sunlight.

On June 1, 1998, first instar larvae were observed. They fed on dry insects and readily drank sugar water, congregating around it in large numbers. Most adults died by the end of June. Pupae were observed in the beginning of July, and first teneral adults, on July 16. They remained quiescent within the last larval exuvia until August 25. In winter, they were transferred to a rearing chamber with constant temperature of 70ºF and photoperiod of 12 hours. They fed only rarely. Flight and mating were not observed. Most died in late spring. At that time, several small larvae were observed, but they died before reaching maturity. It is likely that unnatural photoperiod and temperature interfered with the normal life cycle.

DISCUSSION

The relative length of the legs may be added to the list of characters suggested by Beal (1975) for species identification of *Cryptorhopalum* larvae. The absence of spicisetae on posterior margins of terga distinguishes *C. triste* from *C. poorei* (see Beal 1975: Fig. 2, A). The taxonomic significance of this character is doubtful, however, since both states were observed on the specimens of *Thaumaglossa libochoras* Beal and *Orphinus fulvipes* (Guérin-Méneville), two species of genera that are hypothesized to be closely related to *Cryptorhopalum* (Beal 1979).

The structure of sensilla on the ventral side of the second antennal segment may be a generic character for *Cryptorhopalum*.

The hypopharynx with strong setae at the apex, deep median fold, and scale-like asperities plus the circular depression on the abdominal tergum 9 were observed by the author on eight other species representing six genera of Anthrenini (*Megatoma* Herbst, *Trogoderma* Dejean, *Orphinus* Motschulsky, *Thaumaglossa* Redtenbacher, *Labrocerus* Sharp, and *Anthrenus* Schaeffer). Together with the presence of hastisetae, these characters may support the monophyletic status of Anthrenini. The distribution and state of these characters in other dermestid genera are currently being investigated by the author for incorporation into a phylogenetic study.

Except for *Solidago* sp., the floral hosts reported here are new for *C. triste*. This is not surprising, however, since this species has been previously collected on a wide variety of hosts from 16 plant families (Beal 1979).

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The author is grateful to R. S. Beal, Jr., for confirmation of identity of adult specimens of *C. triste*, for his critical reading of the manuscript, and for his unwavering encouragement and generous gifts of specimens for this and forthcoming studies. Special thanks go to Joseph V. McHugh for his guidance and support. The quality of this manuscript was dramatically improved owing to the criticism provided by Erica W. Chiao, Joseph V. McHugh, and Erich H. Tilgner. The author would like to thank Dr. Ray Noblet and the Department of Entomology at the University of Georgia for supporting this work. Thanks go to Jay Overmyer for supplying a specimen of *C. triste* and for biological information relating to it.

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FIGURE CAPTIONS

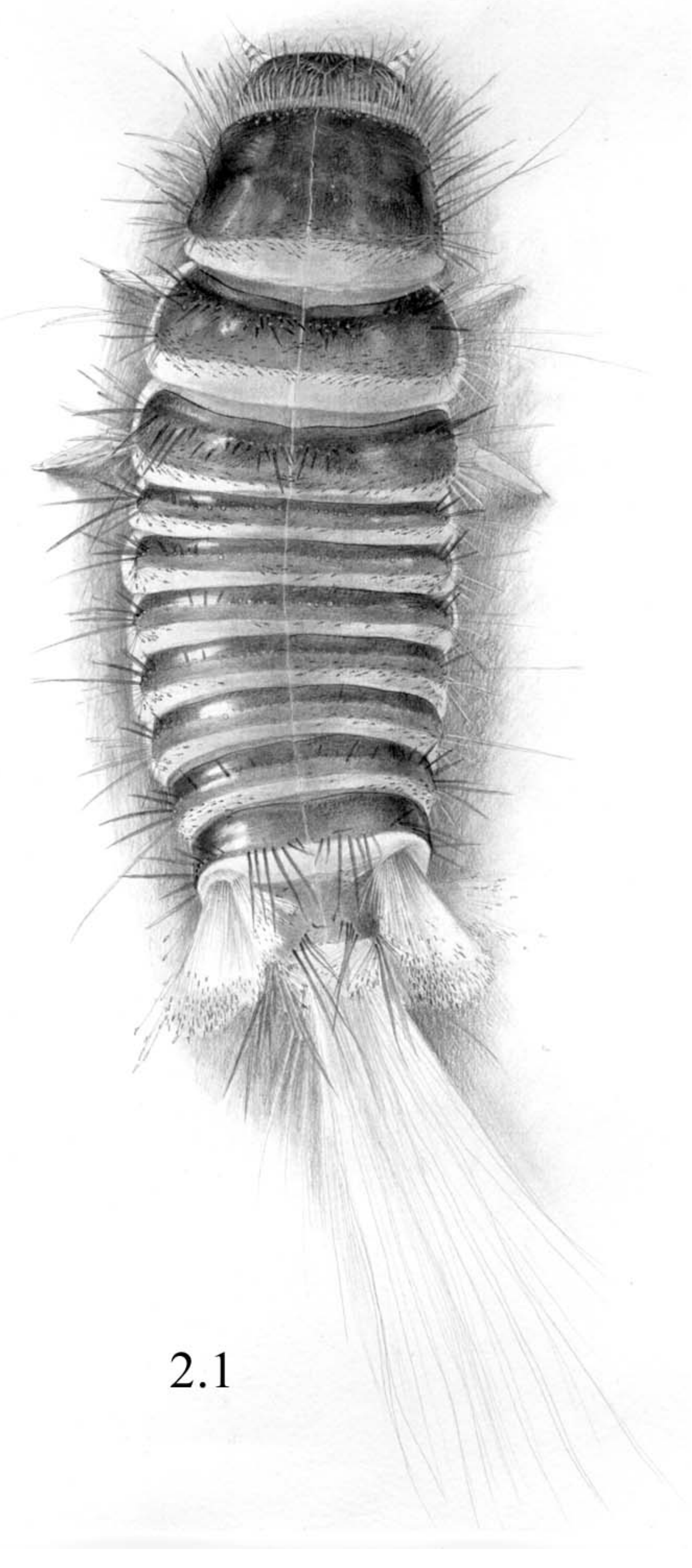
Figure 2.1. Mature larva, dorsal habitus.

Figures 2.2–2.8. 2.2, head of hastiseta from abdominal tergum 1; 2.3, same, from membrane behind abdominal tergum 7; 2.4, antenna, ventral view; 2.5, mandible, left, dorsal view; 2.6, epipharynx; 2.7, maxilla, left, dorsal view; 2.8, right, ventral view. Scale line 0.1 mm.

Figures 2.9–2.11. 2.9, hypopharynx, fronto-lateral view; 2.10, abdominal tergum 1, left side, partially denuded; 2.11, abdominal tergum 9, denuded. Scale line 0.1 mm.

Figure 2.12. Pupa, lateral habitus.

Figure 2.13. Pupa within the last larval exuvium, dorsal view.



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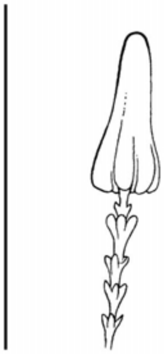
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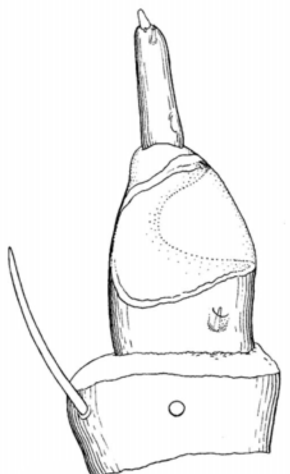
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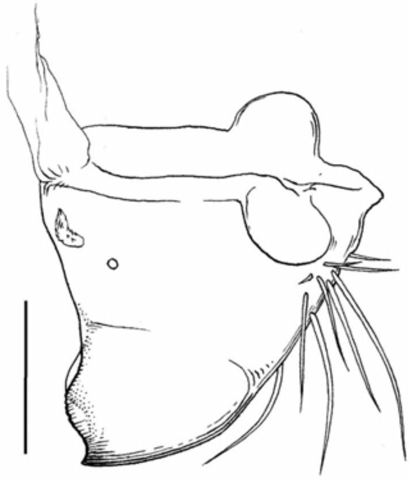
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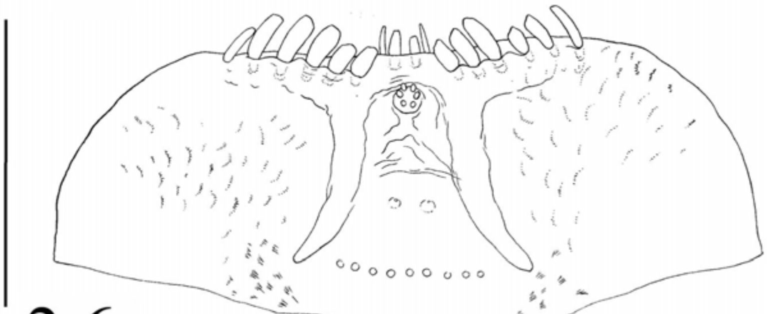
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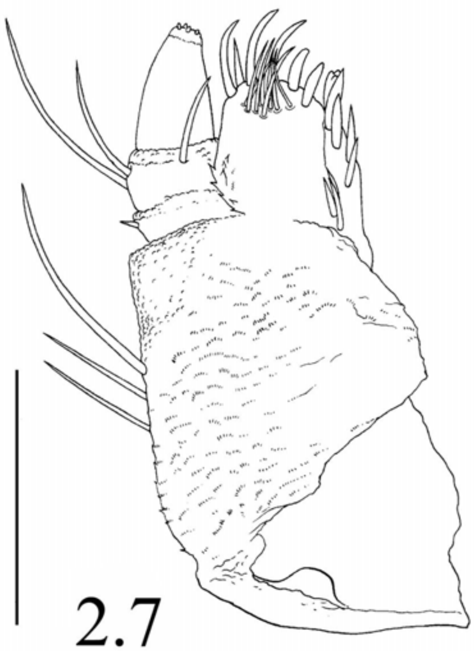
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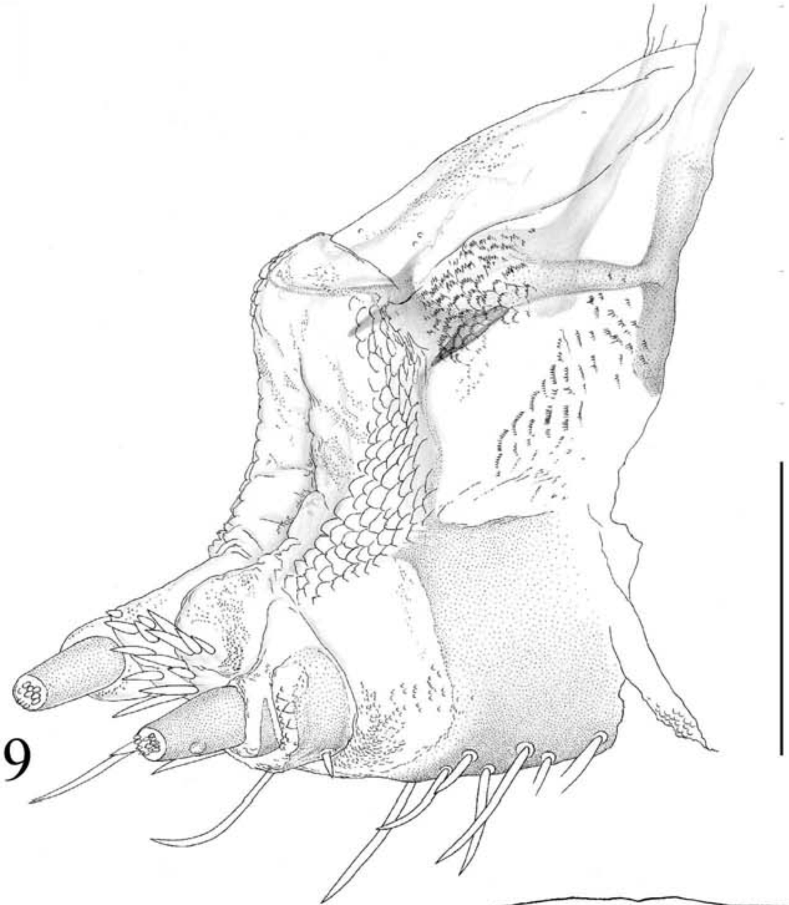

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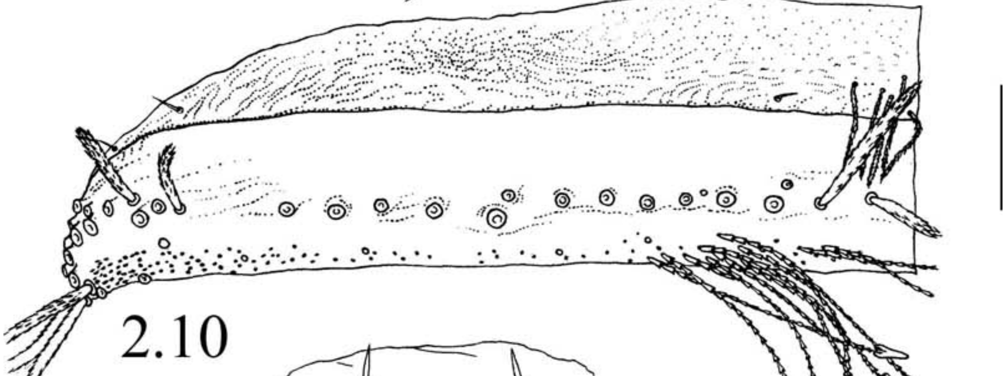

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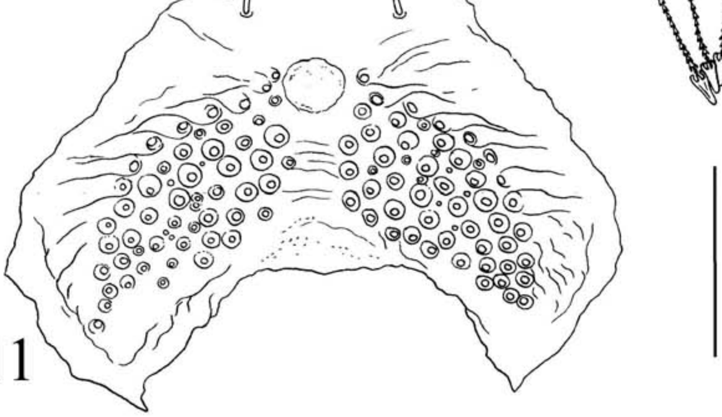

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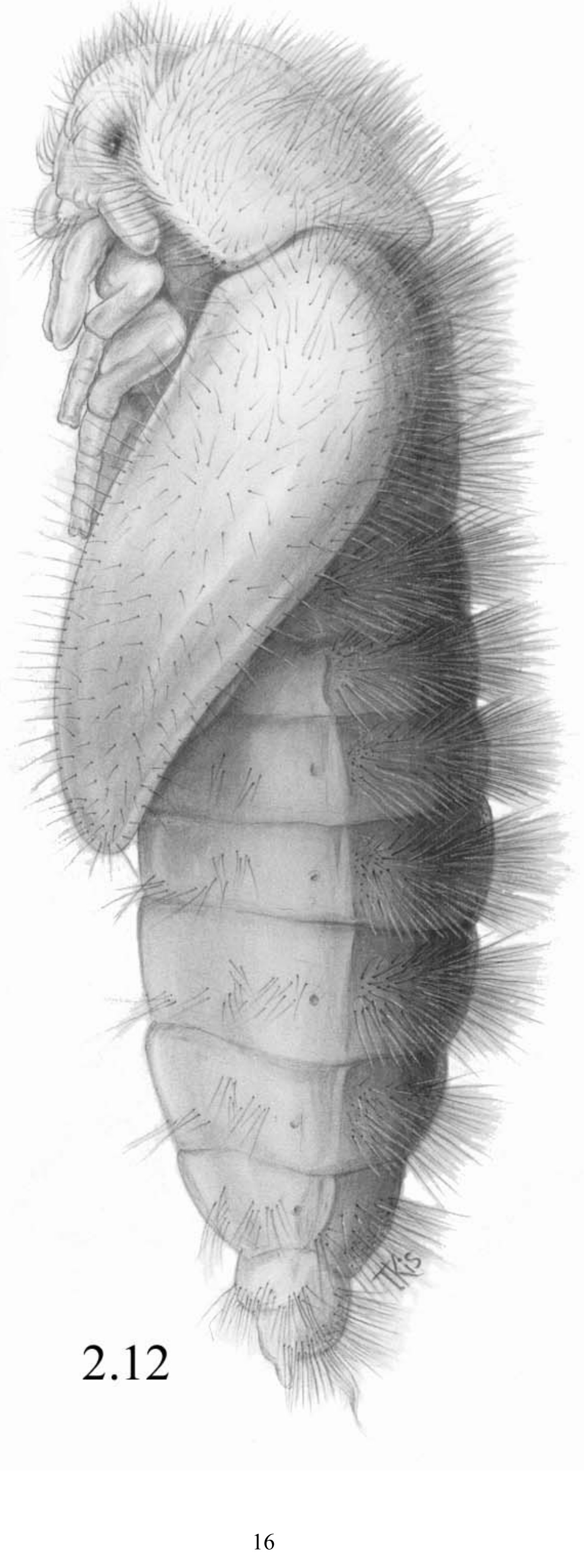

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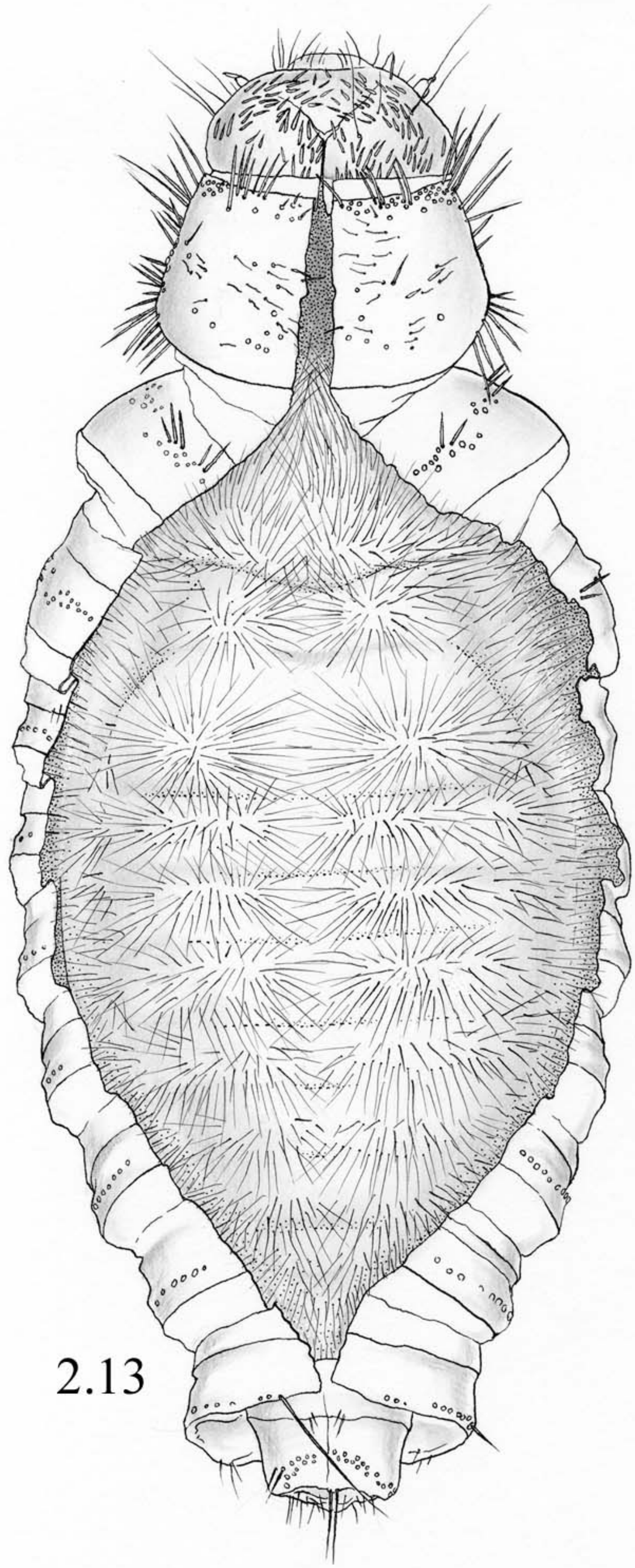

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CHAPTER 3

DESCRIPTION OF THE LARVAL STAGE OF *MYRMEANTHRENUS FRONTALIS* ARMSTRONG AND *ANTHRENOCERUS STIGMACROPHILUS* ARMSTRONG (COLEOPTERA: DERMESTIDAE), WITH A DISCUSSION OF THEIR PHYLOGENETIC RELATIONSHIPS[2]

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[2] Kiselyova, T. 2003. Submitted to *The Coleopterists Bulletin*, 3.12.2003

ABSTRACT

The first descriptions of the larval stage of *Myrmeanthrenus frontalis* Armstrong and *Anthrenocerus stigmacrophilus* Armstrong (Coleoptera: Dermestidae) are presented. The larva of *Anthrenocerus australis* (Hope) is illustrated and briefly characterized. In light of a morphology-based phylogenetic study, *A*. *stigmacrophilus* is more closely related to *M*. *frontalis* than it is to *A*. *australis*.

INTRODUCTION

The genus *Myrmeanthrenus* with a single species, *M. frontalis* Armstrong, was created by Armstrong (1945) for a remarkable dermestid beetle from Victoria, Australia, with an unusually modified head. The description was based on two specimens that were collected “in ants’ nests under stones”. Armstrong thought the new genus to be most closely related to *Anthrenocerus* Arrow. No other information about this interesting species is available, and immature stages have not been previously described.

Anthrenocerus stigmacrophilus Armstrong is another Australian myrmecophile found in New South Wales. Armstrong described this species in 1949, providing a brief discussion and a sketch of the larva. He noted that the larval specimens were submitted to B. E. Rees for description. Unfortunately, the description apparently was never published.

To fill in this gap, the descriptions of the larval form of both species are provided below. Incidentally, the remarkable similarities between the two species raise the question about their relationship and the validity of their current taxonomic placement. This question was addressed by including them in a phylogenetic analysis of Dermestidae (Kiselyova and McHugh 2003, in prep.).

MATERIALS AND METHODS

Three ethanol-preserved specimens of *M. frontalis* identified by association with adults were kindly sent to the author by A. A. Calder of CSIRO, Australia. The particular instar of the larvae is not known, but it is unlikely that they are full-grown. Label data:

"3 mls. E of Queanbeyan, NSW, under stone with *Stigmacris* [sic] *foreli* ants/ 7 aug. 1966 K. W. Taylor".

Armstrong's specimens of larval *A. stigmacrophilus* were borrowed by the author from the National Museum of Natural History. As noted by Armstrong (1949), the collection of adults and larvae was made in N.S.W., “in nests of a small ant (*Stigmacros foreli* Viehm.)”. Thirteen larvae of different instars are preserved in ethanol. Label data: "Australia/J. W. T. Armstrong/ through B. E. Rees/ letter 19-V-1948" and "Bogan R, N.S.W., Australia/ 13-VI-1948/ fr. nest *Stigmacros foreli*/ J. Armstrong coll."

For observation of external morphology, 2 specimens of *M. frontalis* and 1 exuvium of *A. stigmacrophilus* were cleared in warm 10% solution of KOH, and parts were mounted on slides in CMC–10 (Masters Company, Inc., Bensenville, IL) permanent medium. Drawings were made using a camera lucida mounted on a dissecting (Leica WILD M10) or compound (LEITZ DM RB) stereomicroscope. The largest specimens in the series were used for measurements.

RESULTS

Myrmeanthrenus frontalis Armstrong

Larva (Fig. 3.1). Length 3.9–4.4 mm. Body strongly convex dorsally and flattened ventrally. Integument of head, terga, and legs weakly sclerotized, yellowish; sterna hyaline. Head and body dorsally covered with short, pale, club-shaped setae (fiscisetae *sensu* Beal 1960) (Fig. 3.2). Stemmata absent. Nota and terga laterally fringed with longer spicisetae and some simple setae, posteriorly sparsely fringed with fiscisetae. Normal hastisetae absent, but short hastisetae with blunt apices are present on the terga (Fig. 3.3). Venter sparsely covered with pale, fine spicisetae.

Antennal segment 2 about 3 times longer than segment 3; sensorium subapical, with a narrow, elongate base and conical apex (Fig. 3.4). Labro-epipharyngeal margin with 8 setae in the outer series. Epipharynx with 9–12 sensory cups in the proximal transverse series; distal sensory papilla in 2 groups: the proximal group of 2 and the distal of 4; epipharyngeal rods slender (Fig. 3.5). Mandible (Fig. 3.6) with a short, asperate prostheca; mesal surface at the apex excavated and delimited by the rounded cutting edges dorsally and ventrally. Apex of galea with strong recurved setae ventrally and slender setae dorsally (Figs 3.7, 3.8). The apical seta in the dorsomesal series on lacinia recurved, as thick as the lacinial spur (Fig. 3.8). Ligula bilobed, with 3 pairs of strong setae apically; hypopharynx with a deep median furrow and numerous scale-like asperities. Hypopharyngeal sclerome hyaline.

Setal patterns of abdominal tergum 1 as illustrated (Fig. 3.9). Antecostal suture present on abdominal terga 1 through 8. Acrotergites without setae[*], their integument sculptured with scale-like pattern. Segment 9 small, partially withdrawn into segment 8, with a crescent-shaped tergum and membranous sternum. Tergum 9 is densely set with short spicisetae, except for a small median depression (Fig. 3.10). Pretarsal setae of equal length.

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[*] This might be an artifact of clearing, since small circles similar to setal sockets are visible on one specimen.

Anthrenocerus stigmacrophilus Armstrong

Larva (Fig. 3.11). Length 3.8–4.6 mm. Body strongly convex dorsally and flattened ventrally. Integument of head, nota, terga, and legs yellowish-brown; sterna hyaline. Head and body dorsally covered with short, brown fiscisetae (Fig. 3.12). Head with 6 stemmata on each gena; frons prominently bulging (Fig. 3.11). Pronotum strongly convex. Nota and terga laterally fringed with longer spicisetae and some simple setae, posteriorly densely fringed with fiscisetae. Normal hastisetae absent, but short hastisetae with blunt apices are present on the terga (Fig. 3.13). Venter covered with pale spicisetae.

Antennal segment 2 about 3 times longer than segment 3; sensorium subapical, with a narrow, elongate base and conical apex (Fig. 3.14). Labro-epipharyngeal margin with 10 setae in the outer series. Epipharynx with 12 sensory cups in the proximal transverse series; distal sensory papilla in 2 groups: the proximal group of 2 and the distal of 4; epipharyngeal rods slender (Fig. 3.15). Mandible with a short, asperate prostheca; mesal surface at the apex excavated and delimited by the rounded cutting edges dorsally and ventrally. Apex of galea with strong recurved setae ventrally and slender setae dorsally (Figs 3.16, 3.17). The apical seta in the dorsomesal series on lacinia recurved, as thick as the lacinial spur (Fig. 3.17). Ligula bilobed, with 3 pairs of strong setae apically; hypopharynx with a deep median furrow and numerous scale-like asperities. Hypopharyngeal sclerome hyaline.

Setal patterns of abdominal tergum 1 as illustrated (Fig. 3.18). Antecostal suture present on abdominal terga 1 through 8. Acrotergites with fine spicisetae, their integument sculptured with scale-like pattern. Segment 9 small, partially withdrawn into segment 8, with a crescent-shaped tergum and membranous sternum. Tergum 9 is densely set with short spicisetae, except for a small median depression. Pretarsal setae of equal length (Fig. 3.19).

DISCUSSION

As admitted by Armstrong (1949), the larvae of *A. stigmacrophilus* bear no resemblance to those of *A. australis* (Hope), the only other *Anthrenocerus* with a described larva (Figs 20–24). On the other hand, only slight differences in the shape of pronotum and frons, details of vestiture, and the presence of stemmata differentiate this species from *M. frontalis*.

In a cladistic study performed by the author (Kiselyova and McHugh 2003, in prep.), *M. frontalis* and *A. stigmacrophilus* are sister taxa and form a clade that, in turn, is the sister group to *A. australis*. The three species share one synapomorphy: a recurved apical seta in the dorsomesal row on lacinia (Figs 3.8, 3.17, 3.22).

The *M. frontalis* – *A. stigmacrophilus* clade is supported by two synapomorphies: the presence of short blunt fiscisetae in place of normal spicisetae, and the unusually short (shorter than segment 8) setae that form lateral setal patches on tergum 9. Normally, in Anthrenini, these setae reach the length of several segments and form the typical caudal brush, like in *A. australis*.

In light of this phylogeny, the genus *Anthrenocerus* is paraphyletic. To rectify this, either *M. frontalis* should be assigned to *Anthrenocerus*, or, conversely, *A. stigmacrophilus* should be moved to *Myrmeanthrenus*. The latter seems more justified, considering derived larval morphology and myrmecophily of the two species. The taxonomic changes would be premature at this point, however. More taxonomic and biological information needs to be accumulated on these and other Australian Dermestidae, particularly *Anthrenocerus* and *Trogoderma*, which seem to be in need of major revision. For example, *T. boganense* Armstrong and *T. carteri* Armstrong "unquestionably belong to another genus" (Beal 1960), and their larvae, described by Beal (1960), possess synapomorphies of the (*Trogoderma ballfinchae* (*A. australis* (*A. stigmacrophilus* + *M. frontalis*))) clade (see Kiselyova and McHugh 2003, in prep.). They have long second antennal segment with elongated sensorium (see Figs 3.4, 3.14, and 3.22) and distal papilla on epipharynx in two groups (see Figs 3.5, 3.15, and 3.23). Interestingly, they have fiscisetae in place of normal spicisetae, like *M. frontalis* – *A. stigmacrophilus*.

The unusual morphology of *M. frontalis* and *A. stigmacrophilus* larvae is probably shaped by their commensalism with ants. The shortened vestiture and the lack of caudal brush of hairs probably facilitate the larva's movement within the nest's galleries. Absence of long hairs might also point to a lack of need for defense, which, in turn, might indicate that the larvae have some means of appeasing their hosts, a characteristic trait in myrmecophiles. Notably, the hastisetae, which are primary means of defense in Anthrenini larvae, are short, blunt, and have a thick, spiciseta-like stalk. The setae of this kind would not be able to break off easily and lock onto each other, which seemingly would make them rather dysfunctional as defense.

According to Armstrong (1949), larvae and pupae of *A. stigmacrophilus* can be found in the galleries of their host's nests all year round. The same is probably true for

M. frontalis. Interestingly, both were collected in nests of ants of the same species, *S. foreli*.

ACKNOWLEDGEMENTS

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FIGURE CAPTIONS

Figure 3.1. *Myrmeanthrenus frontalis*. Lateral habitus. Scale line 1mm.

Figures 3.2–3.8. *Myrmeanthrenus frontalis*. Figs 3.2, 3.3 scale line 0.05mm; figs 3.4–3.8 scale line 0.1mm. 3.2, fiscisetae from pronotum; 3.3, hastisetae from pronotum and abdominal tergum 1; 3.4, left antenna, ventral, segments 2 and 3; 3.5, epipharynx; 3.6, left mandible, dorsal; 3.7, apex of maxilla, ventral; 3.8, apex of maxilla, dorsal.

Figures 3.9–3.10. *Myrmeanthrenus frontalis.* 3.9, abdominal tergum 1, right half, lateral setae abbreviated, scale line 0.5mm; 3.10, abdominal segment 9, denuded, scale line 0.1mm.

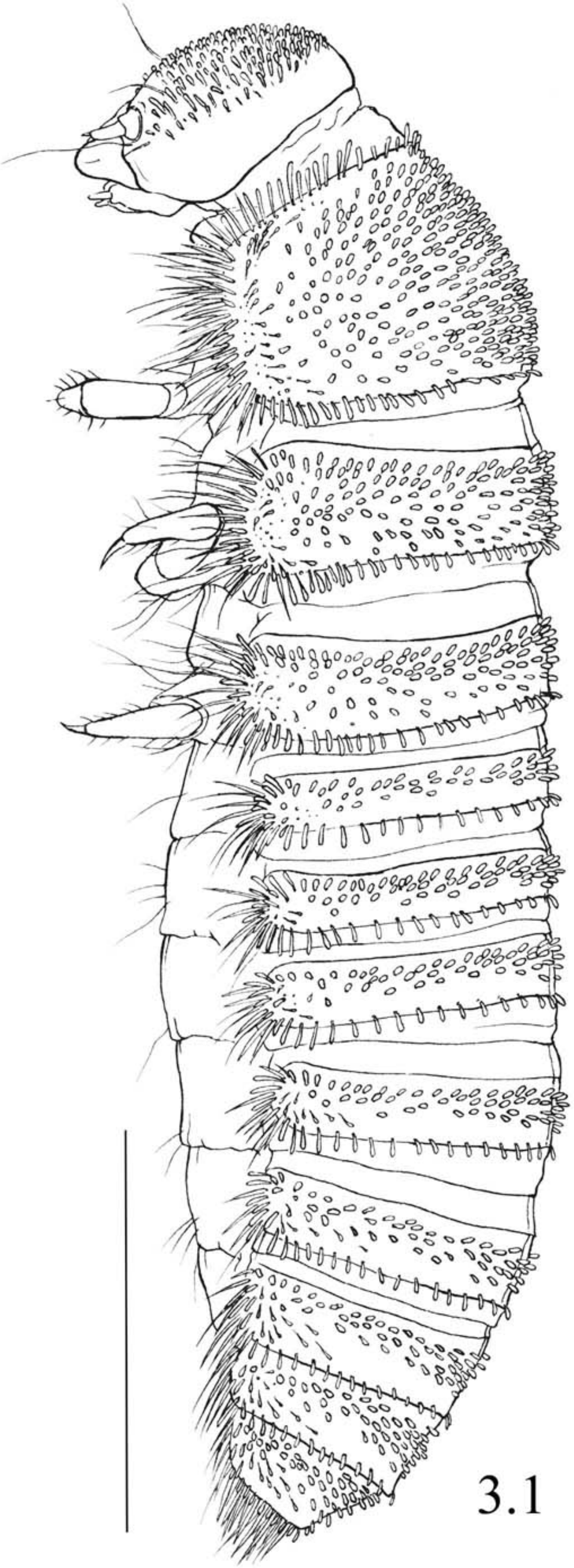
Figure 3.11. *Anthrenocerus stigmacrophilus*. Lateral habitus. Scale line 0.5mm.

Figures 3.12–3.17. *Anthrenocerus stigmacrophilus*. Figs 3.12, 3.13 scale line 0.05mm, figs 3.14–3.17 scale line 0.1mm. 3.12, fisciseta from abdominal tergum 8; 3.13, hastiseta from abdominal tergum 8; 3.14, Left antenna, fronto-ventral, segments 2 and 3; 3.15, epipharynx; 3.16, maxilla, ventral; 3.17, apex of maxilla, dorsal.

Figures 3.18–3.19. *Anthrenocerus stigmacrophilus*. Scale line 0.1mm. 3.18, abdominal tergum 1, right half; 3.19, tibia and tarsungulus of prothoracic leg, posterior view.

Figure 3.20. *Anthrenocerus australis*. Lateral habitus, caudal brush abbreviated. Scale line 0.5mm.

Figures 3.21–3.24. *Anthrenocerus australis*. Scale line 0.1mm. 3.21, maxilla, dorsal; 3.22, right antenna, ventral; 3.23, epipharynx; 3.24, abdominal tergum 1, right half, long setae abbreviated.



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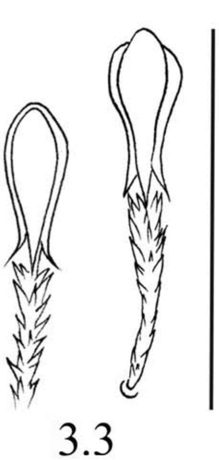

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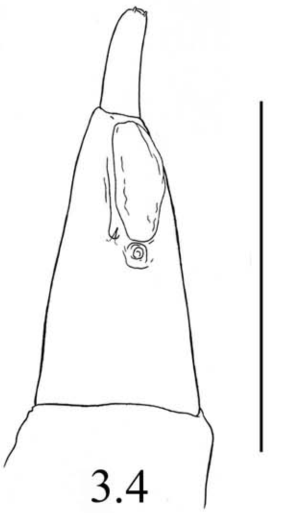

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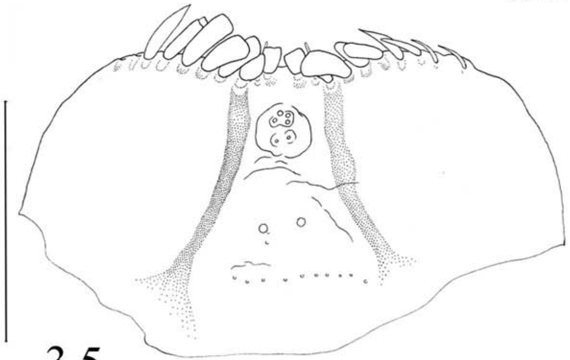

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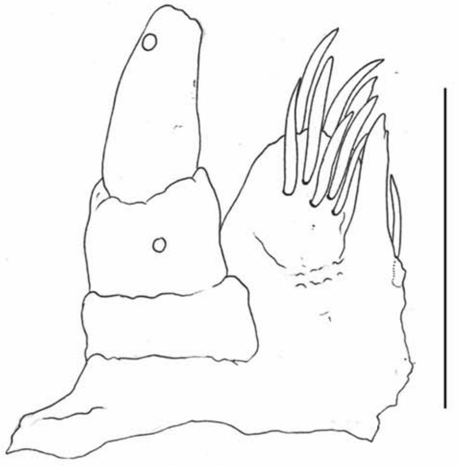

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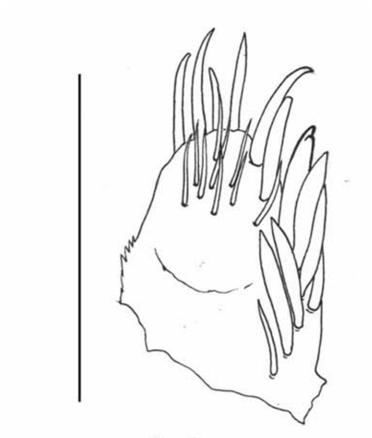

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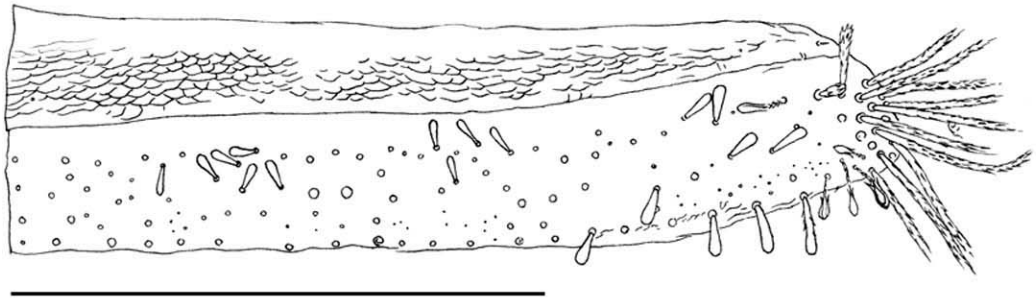

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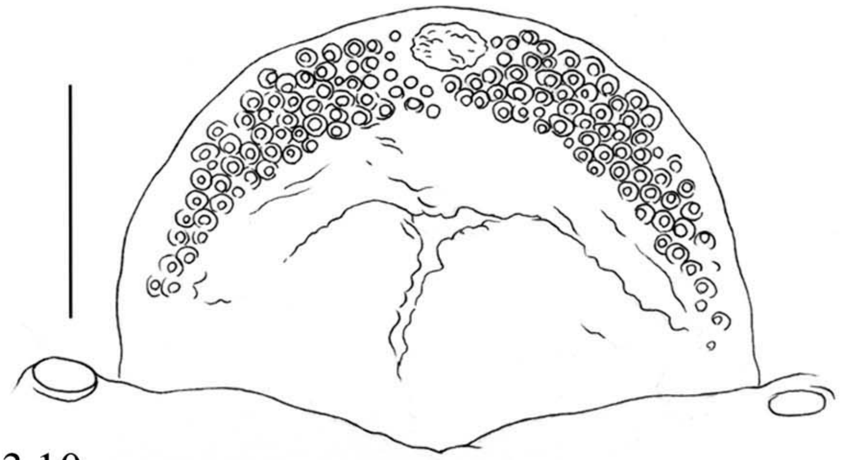

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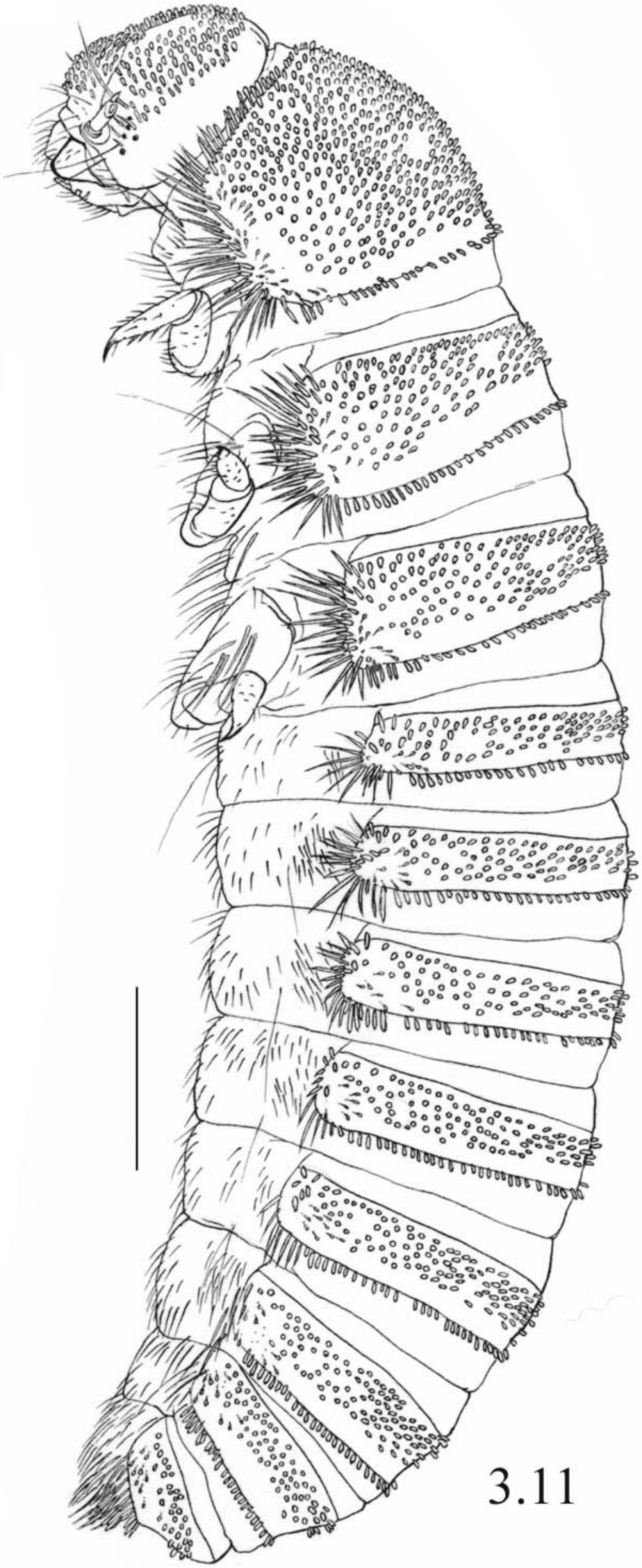

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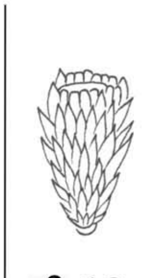

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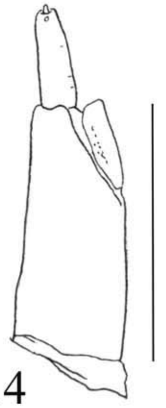

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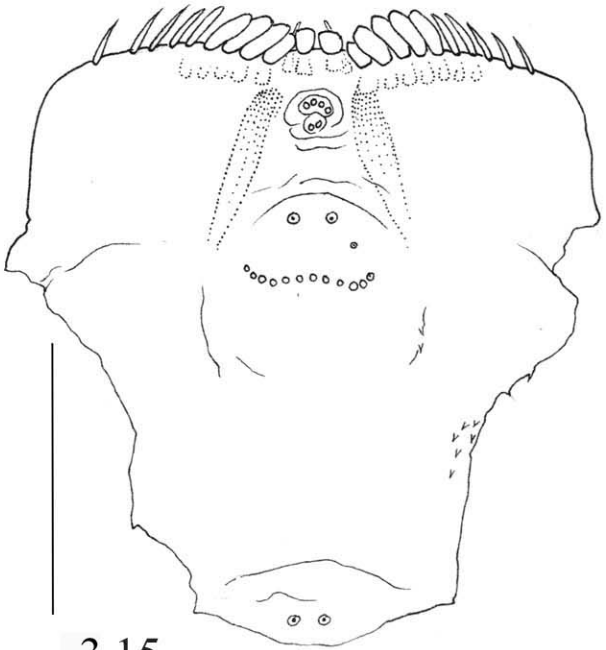

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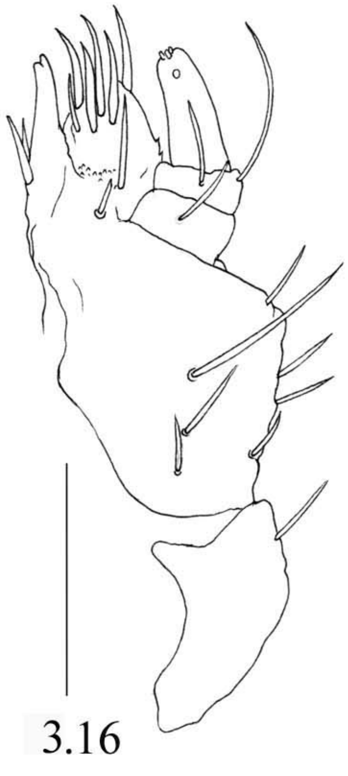

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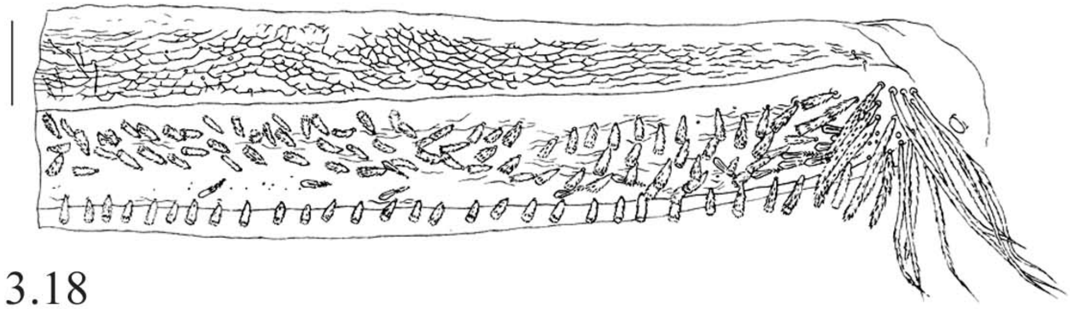

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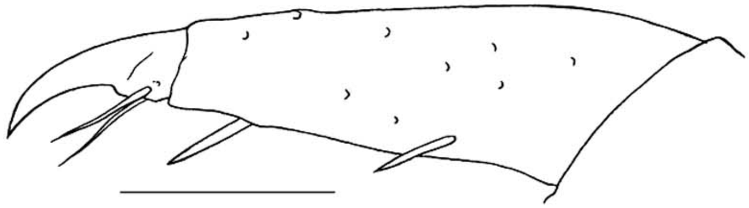

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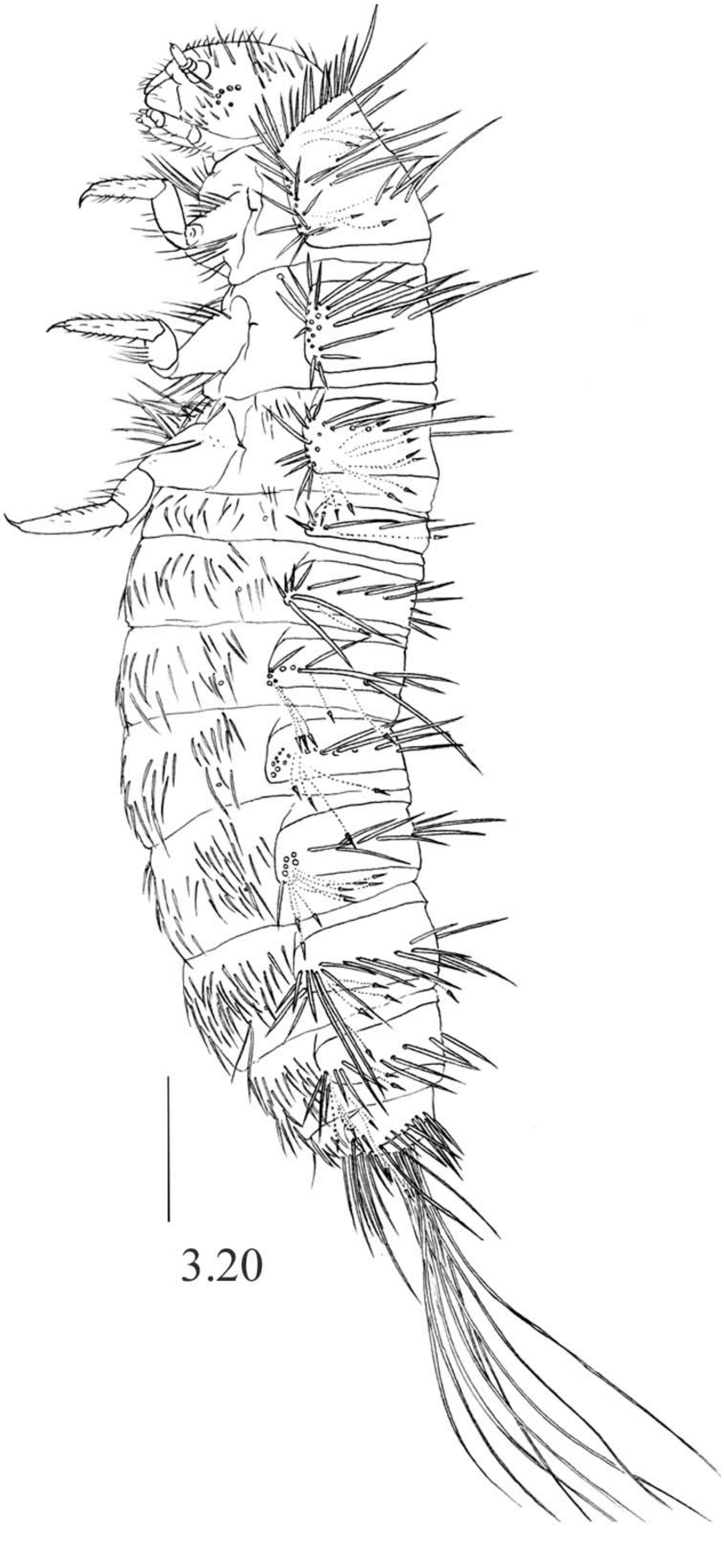

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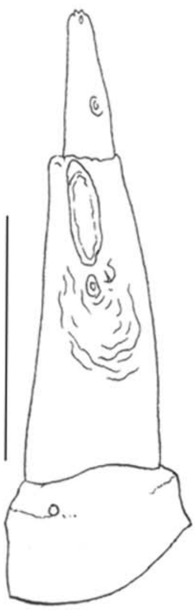
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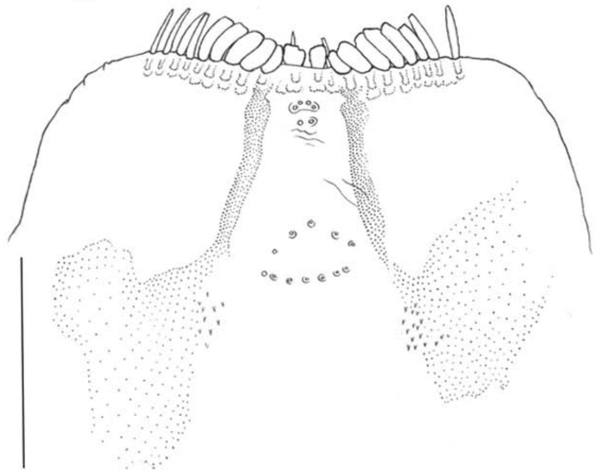
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CHAPTER 4

A PHYLOGENETIC STUDY OF DERMESTIDAE (COLEORTERA) BASED ON LARVAL MORPHOLOGY[3]

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[3] Kiselyova, T. and J. V. McHugh. 2003. To be submitted to *Annales Zoologici.*

ABSTRACT

The results of a phylogenetic parsimony analysis of Dermestidae (Coleoptera) based on morphology of immature stages are presented, along with the implications for classification. Dermestidae exclusive of *Orphilus* Erichson are a monophyletic group. The phylogenetic status of *Orphilus* is discussed. Morphological characters of larvae and pupae are illustrated and discussed in the context of phylogeny. First records are presented of gastric caeca in *Dermestes* L., of the structure of mandible base in Thylodriini Beal and Trinodini Beal, and of the number of Malpighian tubules and abdominal nervous ganglia in some species of Dermestidae, Bostrichidae, Anobiidae, Nosodendridae, and Derodontidae. The fossil record and the distribution of extant Dermestidae are discussed in light of phylogeny.

INTRODUCTION

The beetle family Dermestidae (skin, larder, and carpet beetles) comprises over 880 species in 46 genera distributed all over the world (Beal 1991, Mroczkowski 1968). Most Dermestidae are xerophilic scavengers of animal materials in the larval stage and nectar and pollen feeders or aphages as adults. Within this niche, however, there is a range of ecological variation, from free-living *Dermestes*, that feed on animal carcasses, to generalist scavenger inquilines of spider, insect, bird and rodent nests, to specialized myrmecophiles in Thorictini (see Cammaerts and Cammaerts 1994). Although feeding on vegetable matter is not typical for the family, a number of species, especially of the genera *Trogoderma* and *Anthrenus*, are capable of completing their entire developmental cycle in stored grain and cereal (Hinton 1945). Tolerance to very low humidity enables many dermestids to infest various stored foods and raw materials, such as dried fish, meat, hides, etc. Dermestids are well known pests of stored products and museum collections.

Several taxonomic schemes have been proposed for the family (see Table 1). The classification by Beal (1959) will be used in this paper as it is the simplest and the least controversial. Ivie (1985) removed *Orphilus* from Dermestidae and postulated it to be a sister taxon to *Nosodendron*, an hypothesis rejected by Beutel (1996).

Dermestidae are generally regarded as “a well-defined, monophyletic group” (Lawrence and Newton 1982). This status is accepted by default, since it has not been tested by a cladistic analysis. In the cladogram presented by Beutel (1996), Dermestidae are resolved as monophyletic, but the problematic Thorictini were not included in the analysis. Zhantiev's (2000) phylogenetic analysis includes all recognized and supposed dermestid taxa. Characters in his analysis are polarized *a priori* based on general evolutionary tendencies and morpho-functional analysis. Outgroups mentioned are representatives of Archostemata, Polyphaga, and especially Bostrichoidea, but they are not shown in the resulting tree and their character states are not documented. The monophyly of the family remains, in effect, untested by modern cladistic methodology.

Crowson (1955, 1967) placed Dermestidae, together with Derodontidae, Nosodendridae, Thorictidae, and Sarothriidae (= Jacobsoniidae) in superfamily Dermestoidea. Dermestoidea and Bostrychoidea (Anobiidae, Ptinidae, Bostrychidae and Lyctidae) form the series Bostrychiformia (Crowson 1981). According to Lawrence and Britton (1991), Dermestidae belong to Bostrichoidea[*] (with Bostrichidae, Anobiidae, Nosodendridae and Endecatomidae). Bostrichoidea is regarded as a member of the Cucujiform lineage (Lawrence and Newton 1982). Beutel (1996), in a cladistic analysis, showed a sister group relationship between Dermestidae and the clade composed of Bostrichidae, Anobiidae, and Ptinidae, which suggests that Bostrichoidea should be redefined to exclude Nosodendridae. He also showed that placement of Bostrichoidea, thus defined, in Cucujiformia is supported by at least one synapomorphy, cryptonephridic Malpighian tubules.

The fossil record of Dermestidae is sparse (see Mroczkowski 1968, Beal 1972). The earliest fossils tentatively assigned to Dermestidae are elytra from the Triassic deposits of Queensland described by Dunstan (1923). There are no fossils known between the Triassic and Oligocene, and those from the Oligo– and Miocene belong to modern genera (see Table 2 and Figs 4.1–4.3). There is an argument, however, that Burmese amber

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[*] See Ivie (1985) for the summary of the spelling of "Bostrichoidea".

dates back to the Cretaceous (Ross and York 2000, Zherikhin and Ross 2000). Furthermore, biogeographic data suggest traces of a Pangean distribution (Beal and Zhantiev 2001), possibly dating the origin of the family as far back as the Permian. For example, a new species of *Egidyella*, formerly considered a monospecific genus endemic to the deserts of Central Asia, was recently discovered in the sand dunes of California (Beal and Zhantiev 2001). Considering *Egidyella*'s limited capacity for dispersal, these authors hypothesized that its ancestral species had a widespread Pangean distribution.

Mroczkowski (1968) thoroughly reviewed the biogeography of dermestid genera of the world and characterized the "centers of distribution" of major groups. He pointed out, however, that in order to draw any conclusions on the place of origin of Dermestidae, biogeographical and morphological data must be combined with paleontological information, and the latter is frustratingly sparse. Furthermore, the original distribution patterns of many synanthropic and pest species are distorted by their following the routes of human trade and migration. On the other hand, it is reasonable to assume that our knowledge of many species' distributions is incomplete, since they are restricted to remote and cryptic habitats and rarely collected, as is the case with *Egidyella*.

The biology of synanthropic dermestids has been investigated in considerable detail. Yet, it can be said that most species remain understudied. For example, adults of *Orphilus ater* and *Cryptorhopalum triste* are common on flowers in the Southeastern U.S., but hardly anything is known about the rest of their life cycles.

Larvae have been an important focus of research of Dermestidae, largely because of their importance as pests. Most damage to stored products is inflicted by the feeding activities of the larvae or, in case of *Dermestes*, by their burrowing into hard substrates for pupation. Knowledge of larval morphology proved useful for taxonomy and identification. Several excellent taxonomic keys have been developed for the larval stage (see Hinton 1945, Rees 1943, Beal 1959, Zhantiev 1976, Peacock 1993). Zhantiev (1976) presented a detailed summary of larval external anatomy. A concise morphological description is given by Beal (1991). Das (1938) described the musculature of the mouthparts of *Dermestes vulpinus* F., and Dorsey (1943), that of *Dermestes caninus* Germ. Pradhan (1948) provided a treatment of the head capsule and mouthparts of *Anthrenus fasciatus* Herbst.

Larval data have not been utilized extensively for a phylogenetic analysis, although Zhantiev (2000) used a number of larval characters, along with those of adults and pupae, in his combined analysis of dermestid genera. Deriving phylogeny from the larval data is an intriguing idea. Being structurally and biologically different from adults, subjected to different ecological pressures, larvae of Holometabola provide an essentially independent source of data for phylogenetic research. Recently, careful morphological investigations of larvae have been utilized in a number of cladistic analyses of Holometabola (see Beutel 1996, McHugh 1995, Schultz and Meier 1995), proving that this type of data contains valuable phylogenetic information.

This study was undertaken to investigate the larval morphology of Dermestidae, especially the aspects that have not been studied previously. The generated data served two purposes: firstly, to contribute to the knowledge of coleopteran larval anatomy, and secondly, to be used in a cladistic parsimony analysis. The latter was conducted for the purpose of testing the monophyly of Dermestidae and as a means of developing a phylogenetic hypothesis for this family. The resulting cladogram serves as a framework for discussion of some issues in systematics, biology and distribution of Dermestidae.

MATERIALS AND METHODS

Methods

Last instar larvae were used whenever possible. If the instar was unknown, the largest specimens from a series were chosen. The larval exoskeleton, including internal structures, such as the tentorium and apophyses, was examined, along with some aspects of the digestive and nervous systems. The musculature was observed where necessary, for example, to determine the number of maxillary palpomeres. In cases when larval exuvia were the only material available, only the exoskeletal characters were scored, with the exception of apodemes and apophyses, which are not retained on exuvium. Fresh material was dissected in Ringer's solution; preserved specimens, in 75% ethanol. For observation with a dissecting microscope (Leica WILD M10), specimens were placed in Syracuse dishes with the bottom lined with a thin layer of cotton obtained by carefully unraveling cotton balls. By catching onto hairs on the specimen, cotton prevented it from floating out of position, which was particularly important for drawing. This simple method was found superior to the traditional use of glass beads. With the latter method, the specimen has to be pressed into the substrate, and even then, a slightest vibration causes it to change position. Additionally, beads become firmly lodged between the hairs of the specimen and are difficult to remove without damaging the vestiture. For further study with a compound light stereomicroscope (LEITZ DM RB), specimens were cleared in a 10% solution of potassium hydroxide, dissected, and mounted on slides in glycerin jelly or CMC–10 mounting medium

(Masters Company, Inc., Bensenville, IL). For observations with a LEO 982 scanning electron microscope, additional specimens were critical point dried or chemically fixed using DMSH. When available, at least two specimens of each species were examined. Pen and ink illustrations of phylogenetically important characters, along with necessary habitus drawings, were made by the senior author using a *camera lucida*. Microphotographs were taken using a Sony DKC 5000 digital camera mounted on a Leica WILD M10 microscope. All multistate characters were coded as unordered. The data matrix was created in WinClada ver. 0.9.99m 24 (BETA). Parsimony analysis of the data was conducted using the parsimony ratchet as implemented by WinClada (Nixon, 1999) using Nona (Goloboff, 1997) ver. 2.0.

Taxa

The species for the analysis were selected to best reflect the diversity of Dermestidae. An effort was made to include species from more than one genus of each tribe, especially for polythetic taxa. All the tribes recognized by Beal (1959) are represented in the analysis. It should be noted, however, that *Megatoma giffardi* (Blaisdell) might not be a typical representative of the genus (Beal, *pers. comm.*). Pupal characters for *Orphilus* were scored based on literature (Zhantiev 2001a). Outgroup taxa were selected from Nosodendridae, Derodontidae, Bostrichidae, and Anobiidae, since close relationships of Dermestidae with each of these groups have been proposed (see Crowson 1955, 1959, 1981; Beutel 1996). The list of species used is provided below, along with author names and collection data:

Dermestidae

Orphilus subnitidus LeConte, 2 larvae, label data: "Calif., Trinity Co./ 4 mi W Forest Glen/Apr 23, 1976 4105 JFL *Antrodia sepium* on *Arbutus menziesii* branch.

Thorictodes heydeni Reitter, 2 larvae on slides, loan from NMNH, label data: "Beaumont, Tex, 3-10-1940/ August/ I. Balzer/ thr. R. T. Cotton".

Dermestes ater Degeer, numerous larvae and pupae from laboratory culture.

Dermestes marmoratus Say, 1 larva, loan from NMNH. Label data: "Camp Ucatilla, W.T. June 26, '82".

Dermestes caninus Germar, numerous larvae and pupae from laboratory culture. Origin: USA, Louisiana, nr. Baton Rouge, ex. dead dog.

Also examined, but not included in the analysis were: *Dermestes maculatus* Degeer, numerous larvae and pupae from laboratory culture, and *Dermestes carnivorus* Fabricius, 1 larva, loan from NMNH, label data: "Texas, Comal Co./ Brehmmer Cave/ nr. New Braunfels/ 25 June 1972/ Davis and Bush".

Attagenus elongatulus Casey, 6 larvae and 2 pupae, loan from University of Wisconsin, label data: "Lab reared/ U.W. — Madison/ Normal strain/ 9-IV-1976", "Lab reared/ U.W. — Madison/ Black form/ 9-IV-1976".

Attagenus rufipennis LeConte, numerous larvae and pupae from laboratory culture. Origin: 2 mi E of Wilhoit, Yavapai Co., AZ, ex. bird nest box, R. S. Beal, Jr.

Also examined but not included in the analysis were: *Attagenus fasciatus* (Thunberg), 4 larvae on slides in balsam, label data: "Lahaina, Maui, Haw./ 3-III-75, reared 1977, R. S. Beal"; *Attagenus unicolor* (Brahm), 3 larvae, loan from NMNH, label data: "Wayne St. Univ. Detroit Mich./ B laboratory culture 9-2-65/W. J. Arnold coll."; *Attagenus* *brunneus* Falderman, 1 larva, loan from University of Wisconsin, label data: "lab culture/ Russel laboratories/ U.W. Madison/ W. Burkholder/Dec. 1998".

Novelsis horni (Jayne), numerous larvae and pupae from laboratory culture. Origin: AZ, Yavapai Co., ex. dense mass of spider webbing beneath bridge at Skull Valley. 14.XII.1998. R. S. Beal, Jr.

Novelsis varicolor (Jayne), 1 larval and 1 pupal exuvium, label data: "Sonoita AZ, 31/XII/1990, R. S. Beal, Jr.".

Aethriostoma undulata Motschulsky, 3 larvae on slides, label data: "last larval instar cast, Kahili Valley, 1.5 mi No. Jct. H'w'ys 50 & 53, Kauai, Haw., R. S. Beal, Reared Aug. 71", "Batu Caves, Kuala Lumpur, Malaya, May'59, H. E. McClure" (2 slides).

Thylodrias contractus Motschulsky, numerous larvae and pupae from laboratory culture. Origin: rodent food, Athens, GA.

Trinodes sp., 1 larva and 1 pupa, loan from NMNH, label data, larva: "Dermestidae/ Keelung, Taiwan/ San Diego, S. Diego Co., Cal/ Burlap covering on reed fencing/ coll. A. D. Atnip/ XII-1-64 6424-33/ *Trinodes* sp. det. JMK 1965"; pupa: "*Trinodes* sp. (B. E. R.)/ L.191/ Dried mushrooms/ Japan Honolulu 23,037/ March 18, 1941 42-3303/ Exuvia on slide".

Apsectus araneorum Beal, numerous larvae and pupae from laboratory culture. Origin: AZ, Yavapai Co., Walnut Creek Ranch, ex. spider webs in horse barn, 2.VI.2000, Coll. R. S. Beal, Jr., E. Tilgner and T. Kiselyova, reared 22.XI.2000.

Apsectus hispidus (Melsheimer), 1 larval and 1 pupal exuvium, label data: "USA, GA, Athens Clarke Co., S. Milledge Ave., ex. mud dauber nest on porch of building, Dec.1998, T. Kiselyova".

Megatoma giffardi (Blaisdell), 3 larval and 1 pupal exuvia from same specimen, label data: "Sparks lake, OR/ collected 13-VIII-93/ R. S. Beal, Jr.".

Reesa vespulae (Milliron), numerous larvae and pupae from laboratory culture. Origin: student insect collection, UGA, Athens, GA, December 1999.

Trogoderma variabile Ballion., 2 larvae and 1 pupa loaned by University of Wisconsin, label data: "lab culture/ Russel laboratories/ U.W. Madison, Dec. 1998 W. Burkholder"; 1 larva on slide, label data: "mature larva/ head diss/ FLA: Gainesville/ 3-ii-78/ M. W. Lucas/ Balsam/ RSB-91" (from R. S. Beal, Jr.).

Trogoderma grassmani Beal, 2 larvae, 1 pupa, loan from University of Wisconsin, label data: "Lab culture/ Russel laboratories/ U.W. — Madison/ W. Burkholder/ Dec. 1998".

Trogoderma simplex Jayne, 2 larvae, 1 pupa, loan from University of Wisconsin, label data: "Lab culture/ Russel laboratories/ U.W. — Madison/ W. Burkholder/ Dec. 1998".

Trogoderma ballfinchae Beal, 4 larval exuvia, donated by R. S. Beal, Jr., label data: "Sonoita, AZ, 31/XII/1990/R. S. Beal, Jr.".

Also examined: *Trogoderma megatomoides* Reitter, 2 larvae on slides, label data: "mature larva/ Ex. Hinton Coll./ Bred PICL Slough/ 1942 BM 1977-566/ Balsam RSB'84"; *Trogoderma inclusum* LeConte, 1 larva, loan from University of Wisconsin, label data: "24 July 1962/ Madison Wis./ Insect Coll./ *Trogoderma inclusum* LeConte/ Det. R. S. Beal' 69"; *Phradonoma tricolor* (Arrow), 2 larvae, loan from NMNH, label data: "9L, 2SK-Alive-on +in 829 Bales of licorice Root in Hold 2LH Nor M/V Concordia/ Tadj 2/21/68/Phil. 51, 389 (det. Cary J. Hansel)".

Neoanthrenus ocellifer Blackburn, disarticulated exuvia, loan from CSIRO, label data: "Bogan R. N.S.W./ J. Armstrong/ det. A. A. Calder 1999".

Anthrenocerus australis (Hope), 2 larvae, label data: "From culture, Pest infestation/ Lab, Slough, Bucks, England/ Communicated by R. W. Howe".

Anthrenocerus stigmacrophilus Armstrong, 6 larvae, loan from NMNH, label data: "Australia/ J. W. T. Armstrong/ through B. E. Rees/ letter 19-V-1948" and "Bogan R, N.S.W., Australia/ 13-VI-1948/ fr. nest *Stigmacros foreli*/ J. Armstrong coll.".

Myrmeanthrenus frontalis Armstrong, 3 larvae, loan from CSIRO, label data: "3 mls. E of Queanbeyan/ NSW under stone with *Stigmacris* ants/ 7 aug 1966 K. W. Taylor;

Labrocerus sp., 4 larvae on slides, label data: "slide b Coll. H-12/Puu Honolulu/ Hawaii, HAW./ 13-I-71 RS Beal/ under Koa bark/ Reared/ '71/ Hoyer's / Mature larval cast"; “Coll. H-12/ Puu Honolulu/ Hawaii, HAW./ 13-I-71. R. Beal/ under Koa bark/ Hoyer’s/ ‘71/ Mature larval cast”; “c-2 Coll. H-12/ Puu Honolulu/ Hawaii, HAW./ 13-I-71. R. S. Beal/ under Koa bark/ Reared/ Balsam/ ‘72/ body of mature larval skin cast”; “a2 Coll. H-12/ Puu Honolulu/ Hawaii, HAW./ 13-I-71. R. S. Beal/ under Koa bark/ Reared/ Balsam/ ‘72/ body of mature larval skin cast”.

Cryptorhopalum triste LeConte, numerous larvae and pupae from culture. Origin: GA, Greene Co., Oconee National Forest, April 25–26, 1998, ex. inflorescences of *Valerianella radiata* (L.), and GA, Athens, Clarke Co., May 16, 1998, ex. *Hypochoeris radicata* L., T. Kiselyova and E. Tilgner.

Thaumaglossa libochoras Beal, 5 larval and pupal exuvia, loan from NMNH, label data: "Huachuca Mts. Ariz. V-29-93 R. S. Beal".

Thaumaglossa rufocapillata Redtenbacher, 3 larval and pupal exuvia, 1 larva, loan from NMNH, label data: "(adults in coll. det. H. S. B.)/ reared ex. ootheca of Mantid/ found on grass stem at Chabua, Assam/ Oct.-Nov. 1943/W. I. Jellison".

Orphinus fulvipes (Guérin-Méneville), 2 larvae, loan from NMNH, label data: "Tampico, Mexico 12/I/66".

Anthrenus verbasci (L.), numerous larvae and pupae from laboratory culture. Origin: GA, Greene Co., Oconee National forest, Scull Shoals, ex. spider webs and mud dauber nests on remnants of brick wall, 18.IX.1999, reared 8.2.2000, T. Kiselyova.

Anthrenus lepidus LeConte, 6 larval and pupal exuvia, donated by R. S. Beal, Jr., label data: "USA, AZ, Granite Reef Dam/ ex. Swallow nest/ 1/1/76 emerged 3/3/76/R. S. Beal" and “23 mi. So. Flagstaff/ 13-viii-83. RSB/ Reared 16-iii-84”.

Anthrenus scrophulariae (L.), 5 larval and pupal exuvia, reared, label data: "Russia, 80 km SW of Moscow, ex. dry insects in house, 20.VI.1998, T. Kiselyova".

Anthrenus flavipes LeConte, 2 larval and pupal exuvia, loan from NMNH, label data: "Saudi Arabia/July 22, 1970/in leather/Boston, 1659/70 25746".

Eucinetidae

Eucinetus morio, 2 larvae, label data: "GA, Clarke Co., Athens, Memorial Pk., J. V. McHugh/7-VI-98 ex. *Diachea leucopodia*".

Derodontidae

Derodontus esotericus, numerous larvae, laboratory reared, source: GA, Clarke Co., Athens, Memorial Pk., ex. orange polypore, 16.XI.1999, reared 21.II.2000, coll. J. V. McHugh,.

Nosodendridae

Nosodendron unicolor Say, 3 larvae, GA, Clarke Co., Athens, Memorial Pk., ex. sap on white oak trunk, 8.XI.99 and 19.III.01, coll. T. Kiselyova and E. Tilgner.

Bostrichidae

Endecatomus rugosus, 2 larvae, 1 pupa, loaned by R. Leschen, label data: "USA AR Logan Co./ Lee lake of Hwy 23E/ Mt. Magazine/ on Forest Rd./ II May 1986/ in shelf polypore/ R. Leschen".

Heterobostrichus brunneus (Murray), 2 larvae, loan from NMNH, label data: "Wood crates + mahogany veneer/ Gold Coast South Africa/ adults det. by R. H. Arnett/ OLC 20.VI.'50/ 50-6954/ New Orleans 31175".

Scobicia chevrieri Villa, 2 larvae, loan from NMNH, label data: "French Morocco/ 13-V-1946/ unknown wood used/ as stay on bale of cork/ 46.6841/NY #96504".

Anobiidae

Lasioderma serricorne (F.), numerous larvae and pupae from culture, donated by B. Forschler, GA, Clarke Co., Athens, University of Georgia.

Caenocara sp., 2 larvae, 2 pupae, label data: "USA, GA, Clarke Co., Athens, 3.IX.2001, Nr. Memorial Pk., ex. puffballs, coll. J. V. McHugh.

Character selection

One of the main criteria for character selection was that there were discrete character states occurring among the taxa. It is possible, however, that this character state discontinuity is an artifact of the set of taxa selected for this particular study, i.e., if more taxa were included, the "gaps" between character states would be filled. Although pupae were not available for all taxa, pupal characters were included in the analysis. Adding characters with some missing data increases the phylogenetic accuracy of a given data set (Poe and Wiens 2000). The same justification was used for including internal characters, that could not be scored for all of the taxa. Morphological terminology used is that of Snodgrass (1935) and Lawrence (1991).

Characters

0. Body**:** fusiform (0) (Figs 4.4–4.9), scarabaeiform (1). Body is more or less fusiform in Eucinetidae, Nosodendridae, Derodontidae (Fig. 4.4), and Dermestidae (Fig. 4.5). Larvae of *Endecatomus*, Anobiidae, and Bostrichidae have a soft, C-shaped body. There are many variations of the basic spindle-like body shape within Dermestidae, e.g., body is cylindrical in *Orphilus*, strongly tapered caudally in Attagenini, short and "hunchbacked" in Trinodini (Fig. 4.7), and rather "roly-poly like" in *Thylodrias* (Fig. 4.6). These variations, however, are the sum effect of many morphological features, making it difficult to translate them into discrete, independent characters.

On the other hand, these variations, for the most part, are autapomorphies for taxa that are well defined on the basis of other features, and as such do not contribute to discovery of cladistic relationships between them.

1. Sclerotized tergal plates**:** absent (0) (Fig. 4.4), present (1) (Figs 4.5–4.9).
2. Head: protracted (0) (Figs 4.10–4.14, 4.18), retracted (1) (Fig. 4.15).
3. Head: prognathous (0) (Figs 5.10, 5.11, 5.15, 5.18), hypognathous (1) (Figs 5.11–14).
4. Frontal tubercles: absent (0), 2 (1) (Fig. 4.50), 1 (2) (Fig. 4.24). Paired tubercles on the frons are found in some *Dermestes* species. A single medial tubercle is characteristic of many *Orphinus*, *Thaumaglossa*, and *Labrocerus*. Since both types of tubercles arise in the same area of the frons and look structurally identical, they are hypothesized to be homologous.
5. Position of stemmata: all on genae (0) (Figs 4.10, 4.11, 4.13, 4.14, 4.16–4.18, 4.22), 1 in close proximity to epistomal ridge (1) (Fig. 4.23, 4.25). Normally, stemmata are situated on each gena in a loose group. In *Lasioderma*, *Caenocara*, and *Endecatomus*, however, one stemma occupies an unusual position, appearing to be "squeezed" very close to the edge of epistoma. This arrangement, however, is found in a number of unrelated taxa and seems to be independently derived, possibly as an adaptation to burrowing into hard substrates, such as wood and fungi.
6. Gula: absent or short and synsclerotic with postmentum (0) (Figs 4.26–4.28), present and separate from postmentum (1) (Figs 4.29–4.31). A short gular region appears in *Dermestes* as a mere extension of postmentum proximal to posterior tentorial pits. This condition differs from the absence of the gula only by the amount of sclerotization, which is hard to judge on small and overall lightly sclerotized species.

The criterion for the presence of the gula, therefore, is its complete separation from postmentum by a sulcus.

7. Epicranial stem: absent (0) (Figs 4.17, 4.18), present (1) (Figs 4.19–4.23).
8. Median endocarina: absent (0) (Figs 4.26, 4.32), moderately developed, sclerotized (1), developed into a hyaline septum (2) (Fig. 4.33).
9. Postoccipital ridge: narrow (0) (Figs 4.26, 4.30, 4.32, 4.35), moderately developed or wide (1) (Figs 4.33, 4.34).
10. Tentorial bridge: present (0) (Figs 4.33–4.37), absent (1) (Fig. 4.32).
11. Dorsal tentorial arms: of uniform thickness (0) (Figs 4.35, 4.36), thick basally and thread-like distally (1) (Figs 4.33, 4.34, 4.37).
12. Antennae: oriented anterolaterally (0) (Figs 4.16–4.19, 4.21), oriented anteriorly (1) (Figs 4.12, 4.15, 4.20, 4.33). The normal orientation of antennae is anterolateral, i.e., perpendicular to the surface of the head capsule at the point of antennal articulation. The anterior orientation of antennae is seen in *Orphilus*, *Endecatomus*, and Bostrichidae.
13. Sensorium base: round in cross section (0) (Figs 4.38, 4.39, 4.41), elongate-oval in cross section (1) (Fig. 4.40).
14. Sensorium position: apical (0) (Figs 4.38, 4.39), ventral (1) (Figs 4.40, 4.41).
15. End of frontal arm: well separated from antennal socket (0) (Figs 4.16, 4.17), touching or almost touching antennal socket (1) (Figs 4.18, 4.20–4.22). Frontal arms of epistomal sulcus end anteriorly in the antennal socket in Dermestidae. In *Thylodrias*, *Trinodes*, and *Apsectus*, however, there is a slight deviation from this state: the frontal arm curves posteriad near antennal socket never reaching it (see Fig.

4.22). The present sampling of taxa is too broad to recognize this condition as a separate state, but it is a possible synapomorphy of these genera.

16. Mandibular mola: present (0) (Figs 4.42, 4.43, 4.51), absent (1) (Figs 4.44–4.49). The mola is understood to be a mesal tuberculate sclerotized projection at the very base of the mandible. It is present in *Eucinetus*, *Derodontus*, and *Nosodendron*.
17. Pseudomola: absent (0) (Figs 4.42, 4.43, 4.45, 4.47–4.49, 4.51), present (1) (Figs 4.44, 4.46). The term is used for a non-tuberculate sclerotized projection located mesally, a short distance from the base of the mandible. Following Lawrence (1991), the pseudomola is not considered to be homologous with a true mola.
18. Hyaline lobe at the ventral base of the mandible: absent (0) (4.42–4.48, 4.51), present (1) (Fig. 4.49). This structure is present in *Thylodrias* and *Apsectus*.
19. Penicillus: absent (0) (Figs 4.42–4.46, 4.48, 4.49, 4.51, 4.53), present (1) (Fig. 4.47, 4.52). A penicillus is understood to be a brush of setae located mesally near the base of the mandible, basal of the prostheca.
20. Prostheca: falciform (0) (Figs 4.42, 4.43, 4.45, 4.47, 4.48, 4.52, 4.53), bubble-like (1) (Figs 4.44, 4.46), absent (2) (Fig. 4.49). The base of the prostheca in Dermestidae is not sclerotized and is easily located on slide preparations as a "hole" in the sclerotization of the mandible. In all Dermestidae observed, as well as in *Endecatomus*, and, seemingly, in Bostrichidae and Anobiidae, there is a single placoid sensillum located dorsally of the prosthecal base (Figs 4.44–4.49, pls). Since the large membranous "bubble" found on the mandible of *Orphilus* and *Endecatomus* has the same location as the prostheca in other species, it is considered to be homologous with the prostheca.

21. Surface structure of prostheca: smooth (0) (Figs 4.43–4.46, 4.53), asperate (1) (Figs 4.42, 4.47, 4.48, 4.52).
22. Number of apical teeth on mandible: 1 (0) (Fig. 4.42), 2 (1) (Figs 4.43, 4.45, 4.46), 3 (2) (Fig. 4.44), 0 (i. e., cusp) (3) (Figs 4.47–4.49). Cusp-like mandibles often appear to have 3 teeth: apical, dorsal, and ventral. They are flange-like and together form the edge of the mesal concavity of the mandible. They are not considered homologous with true teeth, since they are positionally and structurally dissimilar to them. Apparently, the degree of their development depends on the wear of the mandible.
23. Ventral accessory process of mandible: present (0) (Fig. 4.51), absent (1).
24. Sclerotization of mandible: continuous (0) (Figs 4.42–4.46), apical part abruptly and heavily sclerotized (1) (Figs 4.47–4.49). Apical half of the mandible is heavily sclerotized and sharply delineated from the basal half in Attagenini, Anthrenini, Trinodini, and Thylodriini.
25. Spatulate setae on labral margin: absent (0) (Figs 4.54, 4.56, 4.57), present (1) (Figs 4.55, 4.58–4.65).
26. Mesal pair of setae on labroepipharyngeal margin: simple (0) (Figs 4.56, 4.57, 4.59), spatulate (1) (Figs 4.58, 4.60–4.65). Two or more pairs of setae are located on labroepipharyngeal margin between the epipharyngeal rods. Here, they are referred to as the mesal, the second, and the third pair respectively. Homologies were not extended to *Eucinetus*, *Derodontus*, and *Nosodendron*, since they lack the epipharyngeal rods.

27. Second pair of labroepipharyngeal setae: slender (0) (Figs 4.60, 4.61, 4.65), spatulate (1) (Figs 4.58, 4.64), stout (2) (Figs 4.56, 4.57, 4.59), very stout, spur-like (3) (Fig. 4.63).
28. Third pair of labroepipharyngeal setae: absent (0) (Figs 4.59–4.65), simple (1) (Figs 4.56, 4.57), spatulate (2) (Fig. 4.58).
29. Additional pairs of labroepipharyngeal setae in mesal series: absent (0) (Figs 4.59–4.65), spatulate (1) (Fig. 4.58), stout (2) (Figs 4.56, 4.57).
30. Epipharyngeal rods: divergent (0) (Figs 4.58–4.65), parallel (1) (Figs 4.56, 4.57).
31. Lateral setae on epipharynx: absent (0) (Figs 4.54, 4.55, 4.57–4.65), slender to thick (1), spur-like (2) (Fig. 4.56).
32. Basal transverse row of placoid sensilla on epipharynx: absent (0) (Fig. 4.56), present (1) (Figs 4.54, 4.55, 4.57–4.65).
33. Two subproximal sensilla on epipharynx: absent (0) (Figs 4.54–4.60, 4.64), present (1) (Figs 4.61–4.63).
34. Medial transverse row of 6 basiconic sensilla on epipharynx: absent (0) (Figs 4.54, 4.56–4.58, 4.61–4.65), present (1) (Figs 4.59, 4.60).
35. Distal group of 2 sensilla on epipharynx: absent (0) (Figs 4.54–4.65), present (1).
36. Distal group of 6 sensilla on epipharynx: absent (0) (Figs 4.54–4.60), enclosed by a circular furrow (1) (Fig. 4.63), divided into a group of 2 and another of 4 (2) (Figs 4.61, 4.62), grouped but not encircled by a furrow (3) (Fig. 4.65).
37. A pair of triangular sclerites on epipharynx between rods and tormae: absent (0), present (1). In Anthrenini, epipharyngeal rods and tormae are connected by broad,

flat, triangular areas of sclerotization that seem to provide support for the base of epipharynx.

38. Maxillary articulating areas: well-developed (0), narrow (1).
39. Maxillary palpomeres: 4 (0) (Figs 4.69–4.74, 4.98, 4.99), 3 (1) (Figs 4.75–4.79). In several cases it was possible to check the true number of palpomeres based on the muscle attachment. In most taxa, this character was scored based on the apparent number of palp articles.
40. Number of lacinial teeth: 4 (0) (Fig. 4.67), 3 (1) (Fig. 4.68), 2 (2) (Figs 4.71–4.78, 4.98–4.100), 1 (3) (Fig. 4.70), 0 (4).
41. Sclerotization of lacinia: continuous with stipes (0), separate from stipes (1).
42. Sclerotization of lacinial teeth: moderate (0), heavy (1).
43. Shape of lacinial teeth: curved at the tip (0) (Figs 4.68, 4.74, 4.100), straight at the tip (1) (Figs 4.67, 4.70–4.73, 4.75–4.78).
44. Mesal row of setae on lacinia: slender setae only (0) (Fig. 4.67), 2 thick setae apically (1) (Fig. 4.74), 1 thick seta basally (2) (Figs 4.75–4.79), absent (3) (Figs 4.68–4.73, 4.99).
45. Setae in the dorsomesal row on lacinia: absent (0) (Figs 4.67, 4.71, 4.74), many, thick (1) (Figs 4.68–4.70), 3 thick (2), 4 to 7 thick to slender (3) (Figs 4.75, 4.78, 4.79).
46. Shape of apical setae in the dorsomesal row: straight (0) (Figs 4.75, 4.78), curved inward (1) (Fig. 4.79).
47. Microsculpture on ligula: microtrichia (0) (Figs 4.80–4.82, 4.86–4.88, 4.89, 4.91, 4.92, 4.101), none (Figs 4.85, 4.86, 4.90, 4.94–4.97) (1).

48. Setae on ligula: absent (0) (Figs 4.81, 4.82, 4.87–4.89, 4.91–4.93, 4.87), slender (1) (Figs 4.80, 4.85, 4.86, 4.90), slender and 1 pair of spur-like setae (2), all setae spur-like (3) (Figs 4.94–4.97).
49. Proximal median element of hypopharynx: present, joining the suspensoria (0) (Figs 4.80–4.84, 4.86, 4.87), absent (1) (Figs 4.88–4.97), present and separate from suspensoria (2) (Fig. 4.85).
50. Anterior branch of suspensoria: short (0) (Figs 4.80–4.84, 4.87), elongated (1) (4.85, 4.86, 4.88, 4.90–4.93, 4.94–4.97).
51. Bridge sclerite: fused medially (0) (Figs 4.80–4.84, 4.86–4.93), appearing jointed medially (1) (Figs 4.95, 4.96), not connected medially (2). The distinctive "bridge sclerite" is the central part of the distal element of hypopharyngeal sclerome. There is always a bulge on the hypopharynx over this sclerite. The sclerite is shaped like a simple curved bar in *Dermestes*, and is narrowed medially in Attagenini, *Thylodrias*, and *Apsectus*. In Anthrenini it resembles a butterfly in its general shape; it is hyaline medially, which makes it appear jointed. In Anobiidae the bridge sclerite is interrupted medially. The condition in Bostrichidae is probably similar to the state 0, however, since the hypopharyngeal sclerome in these taxa is very lightly sclerotized, the condition was difficult to determine, therefore it was coded with question marks.
52. Anterior arms of bridge sclerite: prominent (0) (Figs 4.80–4.84, 4.86–4.88), short, prong-like (1) (Figs 4.90–4.92), absent (2) (Figs 4.85, 4.89, 4.96).
53. Distal lateral sclerites: absent (0) (Figs 4.80–4.88, 4.94–4.97), separate and short (1) (Fig. 4.89), elongate, with hyaline connection to the bridge (2) (Fig. 4.90), elongate, fused to bridge (3) (Figs 4.91–4.93).

54. Lateral hypopharyngeal microsculpture: microtrichia (0) (Figs 4.80–4.82, 4.86–4.89), scale-like asperities (1) (Figs 4.90–4.97), none (2) (Fig. 4.85).
55. Median fold of hypopharynx: absent (0) (Figs 4.80–4.82, 4.85–4.89, 4.101), present (1) (Figs 4.90–4.92, 4.94–4.97). Median fold of hypopharynx is especially well developed in Anthrenini, where the membrane of the fold is thickened and appears somewhat rigid.
56. Antecostal ridge: smooth (0) (Fig. 4.105), denticulate (1) (Fig. 4.106), scalloped (2) (Fig. 4.102), corrugated (3), absent (4) (Fig. 4.119).
57. Abdominal segment 8: without lateral pits (0) (Fig. 4.108), with a pair of lateral pits (1). The unusual lateral pits on the abdominal segment 8 in Trinodini are probably modified spiracles, based on their location in the pleural membrane.
58. Abdominal segment 10: present, well-developed (0) (Figs 4.5, 4.120, 4.147), reduced (1) (Fig. 4.107), vestigial or absent (2) (Figs 4.102–4.104, 4.108, 4.109).
59. Abdominal segment 9: penultimate, not modified (0) (Figs 4.5, 4.120), subterminal or terminal, reduced in size (1) (Figs 4.107–4.109), terminal, enlarged (2) (Fig. 4.102, 4.132, 4.133), absent (3).
60. Urogomphi: present (0) (Figs 4.5, 4.120), absent (1) (Figs 4.103, 4.104, 4.107–4.109).
61. Setae in lateral patches on tergum 9: long, 1/2 body length or longer (0) (Figs 4.9, 4.103), short, up to 2 terminal abdominal segments in length (1) (Fig. 4.104).
62. Tergum 9: entire (0), with rounded rough spot medially (1) (Fig. 4.107), with rounded depression medially (2) (Fig. 4.109), reduced to 2 lens-shaped sclerites (3).
63. Spicisetae: absent (0), present in typical or modified form (1) (Figs 4.105, 4.106, 4.110).

64. Hastisetae on terga: absent (0), present (1) (Figs 4.103, 4.105, 4.106, 4.111–4.114).

65. Posterior portions of abdominal terga membranous: absent (0), present on terga 5–7 (1), present on tergum 7 (2) (Fig. 4.115), present on terga 7 and 8 (3).

66. Fiscisetae (Fig. 4.114): absent (0), as long as corresponding body segment (1), shorter than 1/4 length of corresponding body segment (2).

67. Ribbed setae: absent (0), present (1).

68. Strong setae on terga: absent (0) (Figs 4.102, 4.104, 4.119), present (1) (Figs 4.103, 4.105, 4.106). These are thick, erect or semierect setae arranged, often in a definite pattern, on the terga of most Dermestidae.

69. Urogomphi in pupa: present (0) (Fig. 4.139, 4.140), absent (1) (Fig. 4.127).

70. Gin-traps in pupa (Figs 4.121, 4.123): absent (0), 6 pairs (1), fewer than 6 pairs (2) (Fig. 4.126).

71. Last larval exuvium: cast (0) (Figs 4.124, 4.125), retained (1) (Figs 4.122, 4.126, 4.127). In Dermestini and Attagenini, larval exuvium is shed in a stocking-like fashion and may stay loosely draped over the pupal abdomen (see Fig. 4.125). It is not attached, however, and slips off easily if the pupa is disturbed. In Trinodini, Thylodriini, and Anthrenini, the larval exuvium splits along the middle of dorsum, but is not shed by the pupa, which stays within this protective shell attached to it by two hair tufts on the 8th abdominal segment (termed here "anchor setae"). These setae cling to the inside of the shed larval exuvium and, once it has dried, the setae become firmly "glued" to it, making it difficult to remove the pupa from the exuvium.

72. Pupal dorsal vestiture: short bristles (0) (Fig. 4.121), long setae (1) (Figs 4.123, 4.124, 4.127), absent (2).

73. Anchor setae on pupal segment 8: absent (0) (Figs 4.139, 4.140), dorsal, cross over (1), dorsal, do not cross over (2), lateral, do not cross over (3). Crossing over of the anchor setae may be an artifact of the pupa turning over inside the larval exuvium. However, where series of pupae were examined, the patterns were consistent within species.
74. Gastric caeca: absent (0) (Figs 4.128, 4.129, 4.137), present (1) (Figs 4.130, 4.131, 4.134, 4.135).
75. Gut: loop of hindgut not appressed to membrane near anus (0) (Figs 4.132, 4.133, 4.135, 4.137), loop of hindgut appressed to membrane near anus (1) (Fig. 4.130).
76. Malpighian tubules: free (0), attached to hindgut in a single bundle (1) (Figs 4.131, 4.132, 4.135, 4.137).
77. Anal papillae: present (0) (Fig. 4.120, 4.147), absent (1) (Figs 4.107–4.109).
78. Longitudinal anal pads: absent (0), present (1).

RESULTS AND DISCUSSION

Phylogenetic analysis

A NONA Ratchet search of the data matrix (Table 3) performed via WinClada resulted in 9 most parsimonious trees, 197 steps in length, with CI = 61 and RI = 87. The strict consensus of these trees (206 steps, CI = 58, RI = 86) is shown in Fig. 4.152. Unambiguous optimization setting was used to assess character transformation. The successive weighting procedure in NONA yielded a single tree identical to one of the most parsimonious trees (Fig. 4.153). The Bremer support values are shown in Fig. 4.154.

Monophyly of Bostrichoidea. The monophyly of (*Orphilus*) + (Dermestidae) + (Endecatomidae (Bostrichidae + Anobiidae)) is strongly supported by 9 uncontroverted synapomorphies (Bremer index = 5). Although superfamilial relationships are not a focus of this study, this result is consistent with Beutel's (1996) hypothesis that Nosodendridae are not a part of Bostrichoidea. Interestingly, *Endecatomus* is the sister clade to Bostrichidae + Anobiidae, rather than to two species of Bostrichidae. Moving *Endecatomus* to the base of the Bostrichidae clade increases the number of steps by 2 and decreases both CI and RI by 1 by creating an unsupported clade. If this result were confirmed by a more comprehensive phylogenetic analysis, Bostrichidae would need to be redefined to exclude *Endecatomus*.

Monophyly of Dermestidae. The monophyly of Dermestidae exclusive of *Orphilus* (Bremer index = 3) is supported by three uncontroverted synapomorphies (presence of a transverse row of 6 basiconic sensilla on epipharynx (34), presence of spicisetae (63), and presence of strong setae on terga (68)) and a homoplastic synapomorphy (absence of the proximal median element of hypopharyngeal sclerome (49)). The hypopharyngeal sclerome is similarly reduced in Anobiidae.

Position of *Orphilus*. The position of *Orphilus* in the (*Orphilus*) + (Dermestidae) + (*Endecatomus* (Bostrichidae + Anobiidae)) clade is unresolved in the strict consensus tree. The placement of *Orphilus* in Nosodendridae by Ivie (2002) is not confirmed by the present analysis.

In six of the nine most parsimonious trees, *Orphilus* is the sister taxon to the (*Endecatomus* + (Bostrichidae + Anobiidae)) clade. This relationship is supported by two uncontroverted synapomorphies: the anterior orientation of antenna (12) and the bubble-like prostheca (20). The same type of prostheca is found in some Bostrichidae (Costa et al. 1988, Lawrence 1991), that also possess the pseudomola. A denser sampling of Bostrichidae would probably provide a better resolution in this part of the cladogram. Interestingly, *Orphilus* and *Endecatomus* share many other similarities. The overall shape of the mandible, which could not be coded as discrete characters, is almost identical in the two species (see Figs 4.44, 4.46). The structure of hypopharyngeal sclerome, the microsculpture of hypopharynx (see Figs 4.86, 4.87) and epipharynx (see Figs 4.57, 4.58), the shape of labrum, and the soft, downy vestiture of the head (see Figs 4.12, 4.25, 4.102, 4.142) bear strong resemblance. In light of this study, these similarities should be treated as either retained plesiomorphies or convergences that are probably due to similar wood boring habits. However, if further evidence suggests a closer link between the two taxa, this would hardly be surprising.

In three of the most parsimonious trees and in the successive weighting tree, *Orphilus* is the sister clade to the rest of Dermestidae. An unambiguous synapomorphy linking the two groups is the presence of spatulate setae on labroepipharyngeal margin (25). Arrangement and number of these setae are consistent with the basal position of *Orphilus* in the Dermestidae clade: they are numerous and rather homogenous, except for becoming gradually wider towards the middle of the labrum (see Fig. 4.58). The spatulate setae in the mesal series (between the epipharyngeal rods) are numerous and similar in shape, whereas in the rest of Dermestidae their number does not exceed 3 pairs, and each pair has a distinctive shape. Two homoplastic synapomorphies supporting *Orphilus* + Dermestidae clade are: frontal arm of the epicranial suture ending in the antennal socket or very close to it (15), and abdominal segment 10 vestigial or absent

(58). The former character is shared by all Dermestidae, except for *Thorictodes*, which lacks a distinct frontal arm due to weak sclerotization of the entire head capsule (see Fig. 4.19). The maxilla of *Orphilus* is distinctly Dermestid-like, although this impression results from overall proportions and shape, rather than from discrete characters. Interestingly, it is quite similar to the maxilla of *Thorictodes* (see Figs 4.71–4.73).

The fact that *Orphilus* shares synapomorphies with both Dermestidae and the *Endecatomus* + (Bostrichidae + Anobiidae) clade may indicate its possible sister group relationship to the entire Bostrichoidea, i. e., ((Dermestidae) + (*Endecatomus* + (Bostrichidae + Anobiidae)). This hypothetical relationship, however, was not recovered by the present analysis.

<u>Position of *Thorictodes*</u>. *Thorictodes* is the sister group to the remainder of Dermestidae. The presence of spicisetae in *Thorictodes* may not be obvious. However, the short, truncated setae on the terga are denticulate and corrugated, rather than smooth, and are, therefore, treated as homologous to the true spicisetae (see Fig. 4.110). Interestingly, they appear to be positionally and structurally similar to the short spicisetae of *Dermestes depressus* Gebl., a species that inhabits bumblebee nests (Zhantiev 2001b). Notably, the weak sclerotization and reduced vestiture of this species is unlike that of other *Dermestes*, but is similar to the condition in *Thorictodes*.

The arrangement of strong setae was not coded for the character matrix, because of the difficulty of drawing homologies between the taxa (see below). However, when this character is traced on the cladogram, it can be seen that in the basal dermestid taxa these setae are arranged on each abdominal tergum in eight oblique rows, which may become eight groups or eight single setae, if their number is reduced. Anderson (1949) used this similarity between *Dermestes* and *Thorictodes* to partly justify the placement of the latter in Dermestidae. In the Attagenini clade the strong setae are reduced in number and appear similar to the rest of the scale-like setae covering the body. This may be an adaptation to moving through sand and other loose substrates, since the body of Attagenini shows a definite tendency towards streamlining. In the (*Thylodrias* + (*Trinodes* + *Apsectus*)) clade, whose members are inquilines of rodents or spiders, no traces of 8-group arrangement can be seen. Similarly, in Anthrenini strong setae are lost in myrmecophilous *A. stigmacrophilus* and *M. frontalis*. This may indicate that an 8–group arrangement is unfavorable for specialized inquilines. On the other hand, at least traces of the basic arrangement are retained in other, less specialized Anthrenini, particularly in many *Trogoderma*.

The present placement of *Thorictodes* differs from that presented in Zhantiev's (2000) cladogram, where Thorictini form a clade with Dermestini based on two synapomorphies of adults: absence of the median ocellus and shortened prosternal posterior process not separating front coxae. Forcing *Thorictodes* into this position on any of the most parsimonious trees or on the strict consensus tree results in up to four additional steps in tree length. More data are needed to evaluate the position of *Thorictodes*.

<u>Position of *Dermestes*</u>. *Dermestes* is the sister taxon to the remainder of Dermestidae (Bremer index = 3). This relationship is supported by two uncontroverted synapomorphies: sclerotization of lacinia separate from stipes (41) and antecostal ridge smooth (56). Homoplastic synapomorphies are: sclerotized tergal plates present (1),

surface of prostheca asperate (21), setae of the second pair on labroepipharyngeal margin slender (27), and the lacinial teeth curved at the apex (43).

The monophyly of *Dermestes* (Bremer index = 3) is supported by two uncontroverted synapomorphies (3 thick setae present in the dorsomesal row on lacinia (45), and the distal lateral sclerites of the hypopharynx short and separate from the bridge sclerite (53)) and two homoplastic synapomorphies (gastric caeca present (74), and the anal papillae present (77)). Within Dermestidae, the presence of gastric caeca are unique to *Dermestes*.

Attagenini. The Attagenini clade is the sister group to the rest of Dermestidae. This relationship is supported by six uncontroverted and two homoplastic synapomorphies (Bremer index = 4): gula present and separate from postmentum (6); apical part of the mandible heavily sclerotized and separated from the basal part by a shallow, often indistinct, surface groove (24); mesal row of setae on lacinia consists of 2 setae located apically (44); hypopharynx bears a median fold (55); abdominal segment 9 is terminal or subterminal and reduced in size (59); and pupa covered in long setae dorsally (72). Homoplastic synapomorphies supporting this relationship are: hypopharynx with scale-like asperities laterally (54) (also present in *Caenocara* and *Scobicia*); urogomphi absent (60) (also in the Bostrichoidea clade).

The monophyly of Attagenini (Bremer index = 3) is supported by the presence of 2 distal sensilla on epipharynx (35), slender setae and 2 spur-like setae on ligula (48), and ribbed setae on the body (67). The elongated condition of distal lateral sclerites of hypopharynx and their hyaline connection with the bridge sclerite (53) is a homoplastic synapomorphy, since a similar condition is found in *Caenocara*.

The *Thylodrias* clade. The (*Thylodrias* + (*Trinodes* + *Apsectus*)) clade is the sister group to the rest of Dermestidae (i. e., Anthrenini) (Bremer index = 1). The relationship is supported by the reduction of the tentorial bridge (10) and by the retention of the last larval exuvium by the pupa (71).

Possession by *Trinodes* of uniquely shaped setae, recognizable as modified hastisetae (see Fig. 4.111), is additional, albeit indirect, evidence of relationship with Anthrenini. This type of setae was first reported by Beal (1959a).

Thylodrias is a sister group to *Trinodes* + *Apsectus*. This non-traditional placement is strongly supported by distinctive synapomorphies (Bremer index = 3). The presence of a hyaline lobe (18) of unknown function at the ventral base of the mandible is unique among Dermestidae. The lobe projects into the head capsule and may serve for muscle attachment. Elongate distal lateral sclerites of the hypopharynx fused to the bridge sclerite (53) are also unique, although this condition is similar to that in Attagenini. Under fast optimization, the presence of dorsal, non-crossing anchor setae on pupal segment 8 (73) is also a synapomorphy of this clade. An apparent reduction of postoccipital ridge (9) to a narrow strip may be related to the "hunchbacked" habitus and reduced mobility of the head (postoccipital ridge is also narrow in *Eucinetus*, *Derodontus*, and *Nosodendron*). The prostheca was not observed and was coded as absent (20), but the possibility remains that this is an artifact of clearing with KOH. Spatulate setae in the second pair of the mesal series on labroepipharyngeal margin (27) are also found in *Orphilus*.

Biologically, this group may be characterized by close association with the host's habitat. Cosmopolitan in its present distribution, *T. contractus* is believed to be a native of Central Asia (Zhantiev 1976) where it has been collected in rodent burrows. The recent discovery of the larvae in the hair of rodents gave rise to a hypothesis of their phoretic behavior (Zhantiev 2000). *Trinodes* and *Apsectus* are closely associated with spider nests, and *Apsectus* larvae consume spider webbing, rather than dry insects caught in it (Beal, 1959b and pers. obs., TK).

Monophyly of Anthrenini. The monophyly of Anthrenini is supported by five uncontroverted synapomorphies (Bremer index = 5): a pair of triangular sclerites connecting the tormae and epipharyngeal rods (37); 1 thick seta in the mesal row located near the base of lacinia (44); all setae on ligula spur-like (48); bridge sclerite that appears to be jointed medially (51); and the abdominal tergum 9 with a small rounded depression medially (62). There are six homoplastic synapomorphies: the presence of 2 subproximal sensilla on epipharynx (33); medial row of 6 basiconic sensilla on epipharynx lacking (34); the number of maxillary palpomeres reduced to 3 (39); lacinial teeth straight at the apex (43); the dorsomesal row of setae on lacinia consisting of 4 to 7 setae of varying thickness (45); and the presence of hastisetae on terga (64).

The monophyly of *Anthrenus* is supported by the lack of sclerotization of posterior portions of terga 5–7. *Anthrenus verbasci* is the sister taxon to the rest of the included species, that share the reduction of the lacinial spur to a lightly sclerotized spine, and of abdominal tergum 9 to two small, lens-shaped sclerites.

The crown clade. The monophyly of the crown clade is weakly supported and some of its resolution is probably spurious (Bremer index = 1), except for the *A. stigmacrophilus–M. frontalis* clade and the (*Cryptorhopalum* + (*Labrocerus* + (*Orphinus* + *Thaumaglossa*))) clade. Most of these species look, even in detail, like "generalized", *Trogoderma*-like Anthrenini, and where they do differ, the distribution of character states among species forms a mosaic, rather than a hierarchical pattern. This lack of character congruence, which resulted in poor resolution, is likely due to high rates or recency of speciation not accompanied by specialization, which would cause morphological divergence. Other sources of data (e. g., adults, DNA, etc.) should be examined to provide resolution in this portion of the cladogram.

The *Cryptorhopalum* clade. *Cryptorhopalum*, *Labrocerus*, *Orphinus*, and *Thaumaglossa* form a clade supported by a homoplastic synapomorphy: mesal pair of setae on labroepipharyngeal margin simple (26) (Bremer index = 1). *Orphinus* and *Thaumaglossa* have membranous posterior portions of terga 7 and 8 (65), whereas in *Cryptorhopalum* only tergum 7 is so modified (see Fig. 4.115). Ecologically, these species seem to occupy a position between general scavengers and inquilines. The larvae are found in sheltered or closely fitting spaces: under bark, in tree holes, in mantid oothecae (*Orphinus* and *Thaumaglossa*). In the latter case, the association with the host is obvious, in other genera it has not been specifically observed, but the larvae of *Cryptorhopalum* are likely to be found in proximity of spider webs under bark (Beal 1975). With its distinctive morphology (see Figs 4.2, 4.3, 4.9), this clade may deserve recognition at the level of a tribe.

Paraphyly of *Anthrenocerus*. *Anthrenocerus* is paraphyletic with respect to *Myrmeanthrenus* (see Kiselyova 2003). In the highly unusual myrmecophiles *A. stigmacrophilus* and *M. frontalis*, the terga are covered in short fiscisetae in place of spicisetae (66), the caudal tuft consists of short setae (61), and the strong setae on terga are absent (68). Other than the curved apical setae in the dorsomesal row on lacinia (an uncontroverted synapomorphy, 46), these two species bear little resemblance to their sister taxon, *A. australis* (see Figs 4.103, 4.104).

Polyphyletic *Trogoderma*. *Trogoderma* is polyphyletic, appearing scattered through the crown group. Whether this indicates inadequacy of larval data for this level of analysis, or reflects the current state of taxonomy for this genus, can only be tested by a more comprehensive analysis including more species and types of data. The present study failed to discover any larval synapomorphies for this genus as a whole. Mouthparts, which provided many informative characters for this study, are very uniform in Anthrenini, leaving only the structure of the distal group of epipharyngeal sensilla and the mesal setal series on labroepipharyngeal margin subject to variation. Neither of these potentially promising characters provided resolution for *Trogoderma* as a clade. Notably, the structure of the distal group of epipharyngeal sensilla (6 sensilla enclosed by a circular furrow vs. divided into 2 groups of 2 and 4) may have intraspecific variation in *Trogoderma* (Beal 1960). Taxonomic characters that have been successfully used to separate the species (see Beal 1960) appear to have no phylogenetic significance in the context of this study. The relative length of antennal segments was originally scored for the character matrix, but was subsequently discarded for two reasons: the difficulty to partition the states for the character due to continuous variation, and the widely homoplastic condition of this character within the present broad sampling of taxa. Elongated antennae are found in *Eucinetus*, Attagenini, *Anthrenus*, and some other species of Anthrenini, including *T. boganense* Armstrong, *T. carteri* Armstrong, *T. primum* (Jayne) (see Beal 1960, Fig. 2), and *T. ballfinchae*. These *Trogoderma* species also have the sensorium of antenna in the ventral position, the state also found in *N.*

ocellifer, *M. giffardi*, and the *Anthrenocerus* clade. Denticulate antecostal ridge occurs in *T. ballfinchae*, *T. simplex*, *T. carteri*, *T. boganense*, and *A. australis*. Fiscisetae are found in *T. carteri*, *T. boganense*, *A. stigmacrophilus*, and *M. frontalis*. Distal epipharyngeal sensilla separated into 2 groups (36) place *T. ballfinchae* with the *Anthrenocerus clade*. The same state is found in *T. boganense*, *T. carteri*, and *T. primum*. *Trogoderma ballfinchae*, *T. boganense*, *T. carteri*, *T. primum,* and the *Anthrenocerus* clade seem to have a similar arrangement of the setae in the mesal series on the labroepipharyngeal margin: the second pair is slightly displaced onto the dorsal (labral) surface. This character, noted and discussed by Beal (1960) was not scored for the present matrix. This collection of similarities suggests that these characters may provide a phylogenetic signal in a different context, such as an analysis limited to Dermestidae with a denser sampling of Anthrenini and with inclusion of different types of data.

Character evolution

Fate of individual characters

Gula (6). The absence of the gula appears to be a plesiomorphic state for the present sampling of taxa. With the posterior tentorial pits located just anteriad of the postoccipital ridge, the tentorial bridge serves to support the head capsule ventrally, and the cervical membrane attaches directly to the postmentum. This condition is found in *E. morio*, *D. esotericus*, *N. unicolor*, *E. rugosus*, Bostrichidae and Anobiidae. In cases where the head capsule is more elongated ventrally, with some distance between the posterior tentorial pits and the occipital foramen, a short gular region is usually found. It appears to be an extension of the postmentum and may be sclerotized (*Dermestes*) or hyaline (some *Attagenus*, *Anthrenus verbasci*). The gula is separated from postmentum by a sulcus in the species with a more pronounced ventral elongation of the head capsule.

Median endocarina (8). A moderately developed, sclerotized median endocarina (like in *Dermestes*) is probably a plesiomorphic state for Dermestidae. A median endocarina developed into a hyaline septum seems to be linked with wood- or fungus-boring habits in *Endecatomus*, Bostrichidae, Anobiidae, and *Orphilus*. Interestingly, another group with the endocarina developed into a hyaline septum is Attagenini, which are primarily substrate dwellers (see Zhantiev 2000). This might be a further evidence of independent evolution of this feature as an adaptation to moving through solid substrates.

Tentorial bridge (10). The presence of a tentorial bridge is a plesiomorphic state in Dermestidae. Its reduction in Anthrenini and the (*Thylodrias* + (*Trinodes* + *Apsectus*)) clade seems to be associated with the ventral elongation of the head capsule and the development of gula. In these taxa, the tentorial bridge may have become fused with the gula, but a much more careful investigation is needed to determine if this is the case. It appears that the gula takes over the function of reinforcing the head capsule ventrally.

Antennae (12). Anteriorly oriented antennae are seemingly associated with wood- and fungus-boring habits. It is conceivable that this state evolved independently in *Orphilus* and the (*Endecatomus* + (Bostrichidae + Anobiidae)) clade.

Posterior portions of abdominal terga membranous (65). Progressive desclerotization of posterior portions of some abdominal terga is a tendency that can be traced in Anthrenini. In *Trogoderma* and *Reesa* the hastisetae are concentrated on the lateral portions of the posterior abdominal terga, behind the row of stout spicisetae (similar to condition in Fig. 4.106). Comparing terga 7 and 8 between several genera, it is evident that in *N. ocellifer* and *M. giffardi* this concentration is even more pronounced (see Figs 4.116–4.118). In *Cryptophopalum* (tergum 7), *Orphinus* and *Thaumaglossa* (terga 7 and 8), the cuticle of the area bearing hastisetae is desclerotized and membrane-like, yet clearly belongs to the tergum with which it shares the posterior margin. In *Anthrenus*, the desclerotized portion of the posterior tergal margin is obliterated on terga 5–7, and the posterior margin of remaining tergite is characteristically sinuate in front of the hastisetal patch, which now seems to be located on intersegmental membrane. This arrangement enables the larva to spread the hastisetal tufts when it is disturbed (see Fig. 8), probably ensuring a more efficient defense against predation.

Urogomphi in pupa (69). The presence of urogomphi in pupa is probably an ancestral character. Their absence in *Orphilus* may be explained by its pupation in tunnels that the larva makes in rotting wood (Zhantiev 2001a). Their presence in *Dermestes* and in some Attagenini may be a retained plesiomorphic trait. The rest of Dermestidae lack urogomphi and pupate within the last larval exuvium.

Gin-traps (70). Gin-traps are present in their most developed form in *Dermestes*. Higher up the tree, there is a tendency towards reduction in the number and sclerotization of these structures (compare Figs 4.125 and 4.126), up to their complete absence. Gin-traps are considered to serve the function of protecting the soft-bodied pupa from predators. *Dermestes* larvae, however, burrow into wood and other hard substrates to pupate, making themselves inaccessible to most predators. It was observed in laboratory that gin-traps may be used to crush mites that enter the intersegmental region of the pupa (pers. obs., TK). In nature, the larvae of most *Dermestes* species live in and under the carcasses of vertebrate animals in a butyric stage of decomposition, which must be relatively moist to satisfy their need for water. One such carcass (pers. obs., TK) that sustained a large number of adult and larval *D. caninus*, also served as habitat for mites, as well as earwigs, and beetles of the families Staphylinidae, Histeridae, and Scarabaeidae. The larvae collected from natural habitats often have mites attached to intersegmental membranes. Zhantiev (1976) reported that in cases of severe infestation mites may cause death of the larvae. The mites probably stay attached when the larva makes its pupation tunnel and, as the last exuvium is shed, seek a new host. If this scenario is correct, the gin-traps may provide a partial protection to the pupa.

Interestingly, the pupae of Trinodini, Thylodriini, and Anthrenini, in which the gin-traps are poorly developed or lacking, retain their larval exuvium to which they remain firmly attached by the means of anchor setae. The part of dorsum that remains exposed is covered in long, soft or stiff hairs (see Figs 4.123, 4.126, 4.127). In Anthrenini, the larval hastisetae provide additional protection. These species pupate where they have been feeding, without burrowing or hiding in any way.

Characters not included in the matrix

Many of the observed features were not included in the final data matrix for various reasons: some exhibited continuous variation, some were autapomorphies of particular genera or species, some were too complex to be translated into discrete character states; many visceral structures were not preserved in the majority of taxa.

Body and general habitus. *Eucinetus*, *Derodontus*, and *Dermestes* have an unspecialized, fusiform body, rounded in cross section, with ten abdominal segments (see Figs 4.4, 4.5). There is a pair of non-articulated urogomphi on segment 9 (except for

Eucinetus) (see Figs 4.5, 4.120); the 10th segment is modified into a pygopod with eversible anal papillae (see Figs 4.120, 4.147). The larva of *Nosodendron* deviates from this generalized body form by being strongly dorsoventrally flattened and having the apex of the abdomen modified as an adaptation to living in the flowing tree sap. The integument is weakly sclerotized in *Eucinetus* and *Derodontus* larvae that lack definitive tergal plates. The larvae of *Nosodendron* are strongly sclerotized dorsally. In both *Nosodendron* and *Derodontus,* the integument is granulose, with the granules forming distinctive patterns on head and terga (Figs 4.17, 4.18). The larvae of Dermestidae have, as a rule, well sclerotized tergites. Two known exceptions are the minute *Thorictodes heydeni* and the unusual *Dermestes depressus* Geb. found exclusively in the nests of bumble bees (Zhantiev 2000, 2001b). The general habitus of *T. heydeni* is similar to that of *Dermestes*, except that abdominal segment 10 is reduced. The body of Attagenini is shaped like an elongate teardrop, with the greatest width across the thorax, and tapered caudally. Anthrenini have a compact body, slightly compressed dorsoventrally, with the greatest width across the middle of the body (Figs 4.8, 4.9). *Apsectus* and *Trinodes* have a somewhat "hunchbacked" appearance due to the convexity of posterior terga and the reduction of the corresponding sterna (Figs 4.7, 4.149, 4.151). The body of *Thylodrias contractus* is flattened ventrally and capable of rolling into a ball when the larva is disturbed (Figs 4.6, 4.141). The most atypical is the habitus of *Orphilus*, whose body is cylindrical and well sclerotized both dorsally and ventrally (Figs 4.102, 4.142). This is most likely an adaptation to wood boring habits of the larva (see Zhantiev 2001a). The larvae of *Endecatomus*, *Heterobostrichus*, *Scobicia*, *Caenocara*, and *Lasioderma* have scarabaeiform body, a common adaptation in wood- and fungus-boring Coleoptera larvae.

Arrangement of stemmata. Six stemmata arranged in two vertical rows on the genae are found in *Derodontus esotericus* and *Dermestes* (Figs 4.11, 4.13). The same arrangement is found in *Eucinetus morio* and *Nosodendron unicolor*, but here the number of stemmata is reduced to five (Fig. 4.10). This arrangement is apparently plesiomorphic in relation to other taxa treated in this study. A distinctive pattern is characteristic of Anthrenini exclusive of *Anthrenus*. They have five stemmata arranged in an anterior semicircle and one stemma posteriorly. In *Anthrenus*, six stemmata are arranged in two horizontal rows: a dorsal row of four and a ventral row of two. In the (*Thylodrias* + (*Trinodes* + *Apsectus*)) clade the arrangement is similar to that in *Anthrenus*, but the number of stemmata is reduced to five in *Apsectus* and to four in *Thylodrias* and *Trinodes*, and stemmata in the dorsal row are larger than those in the ventral row (see Fig. 4.22). In *Endecatomus rugosus*, *Lasioderma serricorne*, and *Caenocara* sp., one stemma is situated directly on the epistoma (Figs 4.23, 4.25). This arrangement, however, is found in a number of unrelated taxa and seems to be independently derived, possibly as an adaptation to burrowing into hard substrates, such as wood and fungi.

Labium. Snodgrass (1935) stated that in the larvae of Coleoptera the prementum is often composed of two plates: proximal and distal, and the proximal plate is commonly confused with the mentum. This seems to be the case with Dermestidae, where the labium has three sclerotized plates, traditionally referred to as prementum, mentum, and submentum. In *Dermestes*, however, the insertion of the median bundle of muscles (*rst* of Snodgrass) on the middle plate indicates that it belongs to prementum (Fig. 4.143), since the postmentum (mentum + submentum) is defined as an area lying proximal to the insertions of all labial muscles (Snodgrass 1935). In spite of this evidence, traditional terminology still prevails in the taxonomic literature on Dermestidae.

Invagination of episternum in meso- and metathorax. Invaginations of the episternum forming an apodeme are found in the meso- and metathorax of *Nosodendron* (Fig. 4.144) and many Dermestidae, where they are particularly well developed. They may be present together with pleural apophyses, but more often seem to replace them functionally, whereas pleural apophyses become reduced (Fig. 4.145) or atrophied (Fig. 4.146).

Gut. The gut is straight in *Eucinetus*, *Derodontus*, and *Nosodendron*, and looped in the rest of the taxa. In Dermestidae, the midgut is straight or nearly straight (see Figs 4.132, 4.133, 4.135, 4.137), while in Bostrichidae and Anobiidae it has a strong S-curve anterior to the origin of Malpighian tubules (see Figs 4.128–4.131). In *Endecatomus* the condition is somewhat intermediate.

Abdominal ganglia. *Heterobostrichus*, *Dermestes*, *Attagenus*, and *Orphilus* have eight ganglia in the abdomen; in *Thylodrias* and *Reesa*, only seven were found, whereas *Caenocara* has nine abdominal ganglia.

Number of Malpighian tubules. Six Malpighian tubules were counted in *Dermestes*, *Attagenus*, *A. verbasci*, and the outgroup taxa (except *Lasioderma* and *Scobicia*). Only four Malpighian tubules were found in *O. subnitidus*, *T. contractus*, *R. vespulae*, *T. grassmani*, *T. variabile*, and *T. simplex*. Due to the large proportion of missing data, this character was not included in the analysis, and its significance is not known.

Pretarsal setae. Pretarsal setae are paired in all taxa studied, except for *Eucinetus*.

Behavior. The larvae of *Eucinetus*, *Derodontus*, and *Nosodendron* are slow moving. *Nosodendron* are particularly sluggish, which probably helps them blend with the moist, sap-saturated bark they live on. The integument of *Nosodendron* larvae is usually covered with small particles of fermented sap and bark, which makes them even less conspicuous. Interestingly, a similar cloaking behavior was reported by Zhantiev (2001a) for *Orphilus niger* Rossi that feeds on fungi in rotting wood. *Dermestes* larvae are fast and erratic movers. In response to disturbance or bright light they might "freeze" for a moment, but then escape rapidly. The larvae of *Derodontus* and the early instar larvae of *Dermestes* were observed by the author using the pygopod in regular locomotion (see Fig. 4.148). Older *Dermestes* larvae used the pygopod while crawling about artificial, smooth surfaces, such as glass, with the anal papillae serving as a suction cup. The larvae of Attagenini are very agile in loose substrates. Their catalepsy reaction is more pronounced than in *Dermestes*: in response to the touch or bright light, they often "play dead" for several minutes. If touched repeatedly, they thrash around spastically before attempting to escape. In lab colonies, *Attagenus rufipennis* larvae "froze" when disturbed, while *Novelsis horni* wiggled, thrashed, and waved the end of abdomen. Larvae of *Cryptorhopalum* and *Anthrenus* react to disturbance by "freezing" and spreading the tufts of hastisetae inserted in the membranous portions of posterior terga. Unlike most dermestids, the larvae of *Apsectus* and *T. contractus* are sluggish (see Figs 4.150, 4.151). They roll themselves into a ball when disturbed (see Figs 4.6, 4.149), but eventually move away from negative stimuli, especially bright light.

Taxonomy

Based on the present analysis, five major clades (six if *Orphilus* belongs in Dermestidae) may be recognized at the rank of subfamilies: Thorictinae, Dermestinae, Attageninae, Thylodriinae, and Anthreninae (Fig. 4.154). Within the Thylodriinae, *Thylodrias* and the *Trinodes* + *Apsectus* clade may each be given the status of a tribe. This, however, is not formally proposed at this time, but should be addressed following a more comprehensive study based on all available data.

Origin, age, and distribution

Dermestidae seem to have a Gondwanan or even Pangean distribution, which would imply Mesozoic, if not Permian origin of the group. In all taxa, however, except *Dermestes*, adults feed on pollen and nectar of angiosperms (unless they are secondarily aphagous), seemingly giving preference to close inflorescences of small flowers, such as Asteraceae and some Rosaceae. Even the basal-most dermestid, *Orphilus*, feeds on flowers as adult. Although the angiosperms had probably first appeared in the Triassic, they did not become common until the late Cretaceous. Late Cretaceous, therefore, is a more conservative estimate of the origin of Dermestidae.

Although the earliest fossils assigned to Dermestidae are known from the Triassic, they are not Dermestidae in the modern sense, and their placement is but a best fitting hypothesis. The first unquestionable dermestid fossils from the Tertiary amber deposits are as recent as Oligo- and Miocene, 30 – 20 Mya. They belong to modern genera, showing the results of evolution that must have occurred between the late Cretaceous and the Oligocene. During that time, Gondwana had broken up, Laurasia had drifted farther apart, and North America joined Asia through the Bering land bridge. The late Eocene and Oligocene were marked by global cooling and drying, conditions favorable to the xerophilic dermestids.

If this was the background for the evolution of Dermestidae, their worldwide distribution may be understood, albeit in the most general sense, without evoking Pangea. It is conceivable that the family originated on the continent of Laurasia. The relict distribution pattern of extant *Orphilus*, as well as the existence of the Mediterranean and the Central-Asiatic distribution centers defined by Mroczkowski (1968) may attest to this hypothesis. The distribution of Dermestini and, possibly, Attagenini seems to follow an archaic pattern: they mostly occupy the Northern Hemisphere and are absent from the Australian and the Neotropical regions (only four *Dermestes* species are known from the Neotropics). Their spread into Africa probably occurred after it collided with Asia in the Miocene.

Interestingly, *Dermestes larvalis* may be the only fossil species from a recent genus dating as far back as the Cretaceous. It is possible that the Cretaceous *Dermestes* feasted on dinosaur carcasses.

In contrast to the "northern" distribution of Dermestini and Attagenini, *Trogoderma* and the (*Cryptorhopalum* + (*Labrocerus* + (*Orphinus* + *Thaumaglossa*))) clade have a "southern", or Gondwanan distribution. It is curiously similar, especially in the case of *Trogoderma*, to that of marsupial mammals, whose dispersal from North America to South America and Australia took place 65 – 30 Mya. There are specific similarities between several Australian and North American species assigned to *Trogoderma* (see Beal, 1960), which might indicate an even closer link. The migration routes might have been similar to those of mammals, while the small size and flight ability probably aided the beetles in dispersal.

Finally, the puzzling distribution of *Egidyella* may be either a relic of a wider Laurasian distribution similar to that of *Attagenus*, or a remnant of a range established through the Bering land bridge, which might have been similar to that of *Megatoma* (see Mroczkowski, 1968, Map 12).

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TABLES

Table 1. Classification schemes (order of the taxa matched to facilitate comparison).

Table 2. Fossil Dermestidae.

Table 3. Character matrix.

FIGURE ABBREVIATIONS

aa – anterior arm of bridge sclerite

ab – anterior branch of suspensoria

an – anus

ar – antecostal ridge

ata – anterior tentorial arm

avp – accessory ventral process

bg – bridge sclerite of hypopharynx

br – basal row of epipharyngeal sensilla

cm – cervical membrane

dls – distal lateral sclerites of hypopharynx

dmr – dorsomesal row of setae on lacinia

dst – distal epipharyngeal sensilla

dta – dorsal tentorial arm

cx – coxa

ei – invagination of episternum

er – epipharyngeal rods

ft – frontal tubercle

g – gula

gc – gastric caeca

hst – hastisetae

m – mola

me – median endocarina

mf – median fold of hypopharynx

mmt – membrane enclosing Malpighian tubules

mp – mesal pair of setae on labroepipharyngeal margin

mr – medial row of epipharyngeal sensilla

msr – mesal row of setae on lacinia

mt – Malpighian tubules

p2 – second pair of setae on labroepipharyngeal margin

pla – pleural apophysis

pls – placoid sensillum

pm – pseudomola

pme – proximal median element of hypopharyngeal sclerome

pnc – penicillus

por – postoccipital ridge

prm – prementum

prst – prostheca

ptm – postmentum

rd – rounded depression of abdominal tergum 9

rs – rounded area of abdominal tergum 9

rst – median retractor muscle

s – sensorium

sbp – subproximal epipharyngeal sensilla

sps – spicisetae

ss – suspensorial sclerites

st – sternum

T – thoracic tergum

tb – tentorial bridge

uro – urogomphi

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Figures 4.143–4.147. 4.143, *Dermestes ater*, labial musculature; 4.144–4.146, thorax, internal view, muscles removed; 4.144, *Nosodendron unicolor*, stipples indicate membrane; 4.145, *Novelsis horni*; 4.146, *Anthrenus verbasci*; 4.147, *Dermestes ater*, pygopod, ventrolateral.

Figures 4.148–4.151. Live larvae. 4.148, *Derodontus esotericus*; 4.149, *Apsectus araneorum*, contracted in response to bright light; 4.150, *Thylodrias contractus* on dead katydid; 4.151, *Apsectus araneorum* on spider webbing.

Figure 4.152. Strict consensus tree. Green circles indicate homoplasy.

Figure 4.153. Successive weighting tree.

Figure 4.154. Bremer support values.

Figure 4.155. Subfamilies of Dermestidae based on present analysis.

TABLE 1. Classification schemes (order of the taxa matched to facilitate comparison)

Rees 1943	Hinton 1945	Beal 1959	Mrocskowski 1968	Zhantiev 1976	Zhantiev 2000
			s/f Marioutinae		
			s/f Egidyellinae		
s/f Dermestinae	s/f Dermestinae	tr. Dermestini	s/f Dermestinae	s/f Dermestinae tr. Dermestini tr. Marioutini tr. Thaumaphrastini	s/f Dermestinae tr. Dermestini tr. Marioutini tr. Thorictini
s/f Attageninae	s/f Attageninae	tr. Attagenini	s/f Attageninae		
s/f Trinodinae	s/f Trinodinae	tr. Trinodini	s/f Trinodinae		
s/f Thylodriinae	s/f Thylodriinae	tr. Thylodriini	s/f Thylodriadinae		
			s/f Megatominae	s/f Megatominae tr. Attagenini tr. Trinodini tr. Thylodriadini	s/f Anthreninae tr. Attagenini tr. Trinodini tr. Anthrenini tr. Thylodriini
s/f Anthreninae tr. Megatomini tr. Anthrenini tr. Ctesiini	s/f Anthreninae tr. Megatomini tr. Anthrenini tr. Ctesiini	tr. Anthrenini	s/f Anthreninae		
	s/f Orphilinae	tr. Orphilini	s/f Orphilinae	s/f Orphilinae	s/f Orphilinae
		tr. Thorictini	s/f Thaumaphrastinae		

TABLE 2. Fossil Dermestidae

Species	Location	Period
Dermestes larvalis Cockerell (1917)	Burma	Tertiary (m.b. Cretaceous)
Dermestes pauper Heer (1847)	Yugoslavia	Tertiary
Dermestes tertiarius Wickham (1912)	Florissant, Colorado	Tertiary, Miocene
Attagenus sopitus Scudder (1900)	Florissant, Colorado	Tertiary, Miocene
Cryptorhopalum electron Beal (1972)	Mexico	Tertiary
Cryptorhoplaum (?) sp. (larva)	Dominican Republic	Tertiary, Oligo- Miocene (?)
Orphilus dubius Wickham (1912)	Florissant, Colorado	Tertiary, Miocene
†*Reeveana intermedia* Dunstan (1923)	Queensland	Triassic
†*Reeveana major* Dunstan (1923)	Queensland	Triassic
†*Reeveana minor* Dunstan (1923)	Queensland	Triassic
†*Tryoniopsis granulata* Dunstan (1923)	Queensland	Triassic
†*Tryoniopsis punctata* Dunstan (1923)	Queensland	Triassic

TABLE 3. Character matrix

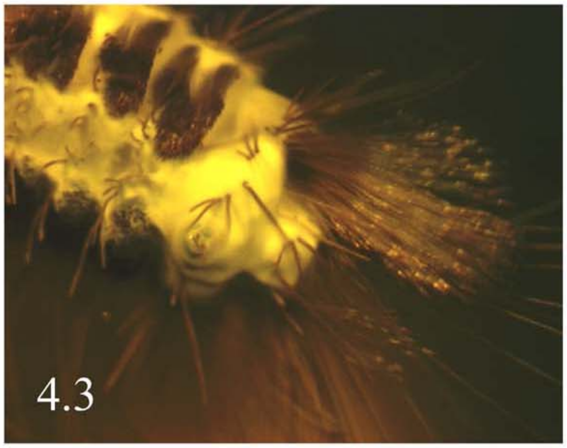
Species/Character	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Eucinetus morio	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	-
Derodontus esotericus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	-
Nosodendron unicolor	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	-
Dermestes marmoratus	0	1	0	1	1	0	0	1	1	1	0	1	0	0	0	1	1	0	0	1	0	1	2	1	0	1	1
Dermestes caninus	0	1	0	1	1	0	0	1	1	1	0	1	0	0	0	1	1	0	0	1	0	1	2	1	0	1	1
Dermestes ater	0	1	0	1	0	0	0	1	1	1	0	1	0	0	0	1	1	0	0	1	0	1	2	1	0	1	1
Attagenus rufipennis	0	1	0	1	0	0	1	1	2	1	0	1	0	0	0	1	1	0	0	1	0	1	3	1	1	1	1
Attagenus elongatulus	0	1	0	1	0	-	1	1	2	1	0	1	0	0	0	1	1	0	0	1	0	1	3	1	1	1	1
Novelsis horni	0	1	0	1	0	0	1	1	2	1	0	1	0	0	0	1	1	0	0	1	0	1	3	1	1	1	1
Novelsis varicolor	0	1	0	1	0	?	1	1	2	1	0	1	0	0	0	1	1	0	0	1	0	1	3	1	1	1	1
Aethriostoma undulata	0	1	0	1	0	0	1	1	2	1	0	1	0	0	0	1	1	0	0	1	0	1	3	1	1	1	1
Orphilus subnitidus	0	1	0	1	0	-	0	1	2	1	0	1	1	0	0	1	1	1	0	0	1	0	1	1	0	1	1
Thylodrias contractus	0	1	0	1	0	0	1	1	0	0	1	1	0	0	0	1	1	0	1	0	2	-	3	1	1	1	1
Apsectus araneorum	0	1	0	1	0	0	1	1	0	0	1	1	0	0	0	1	1	0	1	0	2	-	3	1	1	1	1
Apsectus hispidus	0	1	0	1	0	0	1	1	0	0	1	1	0	0	0	1	1	0	1	0	2	-	3	1	1	1	1
Megatoma giffardi	0	1	0	1	0	0	1	1	0	1	0	1	0	1	1	1	1	0	0	0	0	1	3	1	1	1	1
Trogoderma variabile	0	1	0	1	0	0	1	1	0	1	1	1	0	0	0	1	1	0	0	0	0	1	3	1	1	1	1
Trogoderma grassmani	0	1	0	1	0	0	1	1	0	1	1	1	0	0	0	1	1	0	0	0	0	1	3	1	1	1	1
Trogoderma simplex	0	1	0	1	0	0	1	1	0	1	1	1	0	0	0	1	1	0	0	0	0	1	3	1	1	1	1
Reesa vespulae	0	1	0	1	0	0	1	1	0	1	1	1	0	0	0	1	1	0	0	0	0	1	3	1	1	1	1
Labrocerus sp.	0	1	0	1	2	0	1	1	0	1	1	1	0	0	0	1	1	0	0	0	0	1	3	1	1	1	1
Neoanthrenus ocellifer	0	1	0	1	0	0	1	1	0	1	1	1	0	0	1	1	1	0	0	0	0	1	3	1	1	1	1
Anthrenocerus stigmacrophilus	0	1	0	1	0	0	1	1	0	1	1	1	0	1	1	1	1	0	0	0	0	1	3	1	1	1	0
Anthrenocerus australis	0	1	0	1	0	0	1	1	0	1	1	1	0	1	1	1	1	0	0	0	0	1	3	1	1	1	1
Myrmeanthrenus frontalis	0	1	0	1	0	-	1	1	0	1	1	1	0	1	1	1	1	0	0	0	0	1	3	1	1	1	1
Cryptorhopalum triste	0	1	0	1	0	0	1	1	0	1	1	1	0	0	1	1	1	0	0	0	0	1	3	1	1	1	0
Thaumaglossa libochoras	0	1	0	1	2	0	1	1	0	1	1	1	0	0	0	1	1	0	0	0	0	1	3	1	1	1	0
Thaumaglossa rufocapillata	0	1	0	1	2	0	1	1	0	1	1	1	0	0	0	1	1	0	0	0	0	1	3	1	1	1	0
Orphinus fulvipes	0	1	0	1	2	0	1	1	0	1	1	1	0	0	0	1	1	0	0	0	0	1	3	1	1	1	1
Anthrenus lepidus	0	1	0	1	0	0	1	1	0	1	1	1	0	0	0	1	1	0	0	0	0	1	3	1	1	1	1
Anthrenus verbasci	0	1	0	1	0	0	1	1	0	1	0	1	0	0	0	1	1	0	0	0	0	1	3	1	1	1	1
Anthrenus scrophulariae	0	1	0	1	0	0	1	1	0	1	1	1	0	0	0	1	1	0	0	0	0	1	3	1	1	1	1
Anthrenus flavipes	0	1	0	1	0	0	1	1	0	1	1	1	0	0	0	1	1	0	0	0	0	1	3	1	1	1	1
Endecatomus rugosus	1	0	0	1	0	1	0	1	2	1	0	1	1	0	0	-	1	1	0	0	1	0	2	1	0	0	0
Heterobostrichus brunneus	1	0	1	0	0	-	0	1	2	1	0	1	1	0	0	-	1	0	0	0	0	?	3	1	0	0	0
Scobicia chevrieri	1	0	1	0	0	-	0	1	2	1	0	1	1	0	0	-	1	0	0	-	2	?	3	1	0	0	0
Lasioderma serricorne	1	0	0	1	0	1	0	1	2	1	0	1	1	0	0	0	1	0	0	1	2	-	1	1	0	0	0
Caenocara sp.	1	0	0	1	0	1	0	1	2	1	0	1	0	0	0	0	1	0	0	0	2	-	1	1	0	0	0
Trinodes sp.	0	1	0	1	0	0	1	1	0	0	1	1	0	0	0	1	1	0	?	0	2	-	3	1	1	1	1
Thorictodes heydeni	0	0	0	1	0	-	0	1	1	1	0	1	0	0	0	-	1	0	0	0	0	0	1	1	0	1	0
Trogoderma ballfinchae	0	1	0	1	0	0	1	1	0	1	1	1	0	1	1	1	1	0	0	0	0	1	3	1	1	1	1

Species/Character	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
Eucinetus morio	-	-	-	-	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	-	0	1	0	?	0	0
Derodontus esotericus	-	-	-	-	0	1	0	0	0	0	0	0	0	1	0	0	0	3	1	0	0	0	0	0	0	0
Nosodendron unicolor	-	-	-	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	-	0	0	0	0	0	0
Dermestes marmoratus	0	0	0	0	0	1	0	1	0	0	0	1	0	2	1	1	0	3	2	0	0	0	1	0	0	2
Dermestes caninus	0	0	0	0	0	1	0	1	0	0	0	1	0	2	1	1	0	3	2	0	0	0	1	0	0	2
Dermestes ater	0	0	0	0	0	1	0	1	1	0	0	1	0	2	1	1	0	3	2	0	0	0	1	0	0	2
Attagenus rufipennis	0	0	0	0	0	1	0	1	1	0	0	1	0	2	1	1	0	1	0	-	1	2	1	1	0	1
Attagenus elongatulus	0	0	0	0	0	1	0	1	1	0	0	1	0	2	1	1	0	1	0	-	1	1	1	1	0	1
Novelsis horni	0	0	0	0	0	1	0	1	1	0	0	1	0	2	1	1	0	1	0	-	1	2	1	1	0	1
Novelsis varicolor	0	0	0	0	0	1	1	1	1	0	0	1	0	2	1	1	0	1	0	-	1	2	1	1	0	1
Aethriostoma undulata	0	0	0	0	0	1	0	1	1	0	0	1	0	2	1	1	0	3	0	-	?	2	1	1	0	1
Orphilus subnitidus	1	2	1	0	0	1	0	0	0	0	0	1	0	2	0	1	1	3	0	-	1	1	0	0	0	0
Thylodrias contractus	1	0	0	0	0	1	0	1	0	0	0	1	0	2	1	1	0	1	0	-	0	0	1	1	0	1
Apsectus araneorum	1	0	0	0	0	1	0	0	0	0	0	1	0	2	1	1	0	1	0	-	0	0	1	1	0	1
Apsectus hispidus	1	0	0	0	0	1	0	0	0	0	0	1	0	2	1	1	0	1	0	-	0	0	1	1	0	1
Megatoma giffardi	2	0	0	0	0	1	1	0	0	3	1	1	1	2	1	1	1	2	3	0	1	3	1	1	1	2
Trogoderma variabile	3	0	0	0	0	1	1	0	0	1	1	1	1	2	1	1	1	2	3	0	1	3	1	1	1	2
Trogoderma grassmani	2	0	0	0	0	1	1	0	0	1	1	1	1	2	1	1	1	2	3	0	1	3	1	1	1	2
Trogoderma simplex	3	0	0	0	0	1	1	0	0	1	1	1	1	2	1	1	1	2	3	0	1	3	1	1	1	2
Reesa vespulae	2	0	0	0	0	1	1	0	0	1	1	1	1	2	1	1	1	2	3	0	1	3	1	1	1	2
Labrocerus sp.	2	0	0	0	0	1	1	0	0	2	1	1	1	2	1	1	1	2	3	0	1	3	1	1	1	2
Neoanthrenus ocellifer	2	0	0	0	0	1	1	0	0	1	1	1	1	2	1	1	1	2	3	0	1	3	1	1	1	2
Anthrenocerus stigmacrophilus	0	0	0	0	0	1	1	0	0	2	1	1	1	2	1	1	1	2	3	1	1	3	1	1	1	2
Anthrenocerus australis	0	0	0	0	0	1	1	0	0	2	1	1	1	2	1	1	1	2	3	1	1	3	1	1	1	2
Myrmeanthrenus frontalis	0	0	0	0	0	1	1	0	0	2	1	1	1	2	1	1	1	2	3	1	1	3	1	1	1	2
Cryptorhopalum triste	2	0	0	0	0	1	1	0	0	1	1	1	1	2	1	1	1	2	3	0	1	3	1	1	1	2
Thaumaglossa libochoras	2	0	0	0	0	1	1	0	0	1	1	1	1	2	1	1	1	2	3	0	1	3	1	1	1	2
Thaumaglossa rufocapillata	2	0	0	0	0	1	1	0	0	1	1	1	1	2	1	1	1	2	3	0	1	3	1	1	1	2
Orphinus fulvipes	2	0	0	0	0	1	1	0	0	1	1	1	1	2	1	1	1	2	3	0	1	3	1	1	1	2
Anthrenus lepidus	0	0	0	0	0	1	1	0	0	3	1	1	1	3	1	0	1	2	3	0	1	3	1	1	1	2
Anthrenus verbasci	0	0	0	0	0	1	1	0	0	3	1	1	1	2	1	1	1	2	3	0	1	3	1	1	1	2
Anthrenus scrophulariae	0	0	0	0	0	1	1	0	0	3	1	1	1	3	1	0	1	2	3	0	1	3	1	1	1	2
Anthrenus flavipes	0	0	0	0	0	1	1	0	0	3	1	1	1	3	1	0	1	2	3	0	1	3	1	1	1	2
Endecatomus rugosus	2	1	2	1	0	1	0	0	0	0	0	1	0	3	0	1	1	3	1	0	1	1	0	1	0	0
Heterobostrichus brunneus	2	1	2	1	1	0	0	0	0	0	0	1	1	3	0	1	1	3	0	-	1	1	2	1	?	2
Scobicia chevrieri	2	1	2	1	1	0	0	0	0	0	0	1	1	3	0	1	1	3	0	-	1	1	2	1	?	2
Lasioderma serricorne	2	1	2	1	2	0	0	0	0	0	0	1	1	4	0	-	-	3	3	0	1	1	1	1	2	2
Caenocara sp.	3	1	0	-	2	0	0	0	0	0	?	1	1	4	0	-	-	3	0	-	1	1	1	1	2	2
Trinodes sp.	?	0	0	0	0	1	?	1	0	0	0	1	0	2	1	1	0	?	?	?	?	?	?	?	0	1
Thorictodes heydeni	2	0	0	0	0	1	0	1	0	0	0	1	0	2	0	1	1	3	0	-	0	0	1	1	0	0
Trogoderma ballfinchae	2	0	0	0	0	1	1	0	0	2	1	1	1	2	1	1	1	2	3	0	1	3	1	1	1	2

Species/Character	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
Eucinetus morio	0	0	0	4	0	0	0	1	-	0	0	0	0	0	0	0	?	?	?	?	?	0	?	0	0	0
Derodontus esotericus	0	0	0	4	0	0	0	0	-	0	0	0	0	0	0	0	?	?	?	?	?	0	0	0	0	0
Nosodendron unicolor	0	0	0	4	0	2	3	-	-	-	0	0	0	0	0	0	?	?	?	?	?	0	-	0	1	0
Dermestes marmoratus	1	0	0	0	0	0	0	0	-	0	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0
Dermestes caninus	1	0	0	0	0	0	0	0	-	0	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0
Dermestes ater	1	0	0	0	0	0	0	0	-	0	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0
Attagenus rufipennis	2	1	1	0	0	1	1	1	0	0	1	0	0	0	1	1	0	1	0	1	0	0	0	1	1	0
Attagenus elongatulus	2	1	1	0	0	1	1	1	0	0	1	0	0	0	1	1	0	1	0	1	0	0	0	1	1	0
Novelsis horni	2	1	1	0	0	1	1	1	0	1	1	0	0	0	1	1	0	2	0	1	0	0	0	1	1	0
Novelsis varicolor	2	1	1	0	0	1	1	1	0	1	1	0	0	0	1	1	1	2	0	1	0	0	0	1	1	0
Aethriostoma undulata	2	1	1	0	0	1	1	1	0	0	1	0	0	0	1	1	?	?	0	?	0	0	0	1	1	0
Orphilus subnitidus	0	0	0	2	0	2	2	0	-	0	0	0	0	0	0	0	1	0	0	?	?	?	0	1	1	0
Thylodrias contractus	3	1	1	0	0	2	1	1	-	0	1	0	0	1	0	1	1	0	1	1	3	0	0	1	1	0
Apsectus araneorum	3	1	1	0	1	2	1	1	-	0	1	0	0	0	0	1	1	0	1	1	3	0	0	1	1	0
Apsectus hispidus	3	1	1	0	1	2	1	1	-	0	1	0	0	0	0	1	1	0	1	1	3	0	0	1	1	0
Megatoma giffardi	0	1	1	0	0	2	1	1	0	2	1	1	0	0	0	1	1	2	1	1	2	0	0	1	1	0
Trogoderma variabile	0	1	1	0	0	2	1	1	0	2	1	1	0	0	0	1	1	2	1	1	2	0	0	1	1	0
Trogoderma grassmani	0	1	1	0	0	2	1	1	0	2	1	1	0	0	0	1	1	0	1	1	2	0	0	1	1	0
Trogoderma simplex	0	1	1	1	0	2	1	1	0	2	1	1	0	0	0	1	1	2	1	1	2	0	0	1	1	0
Reesa vespulae	0	1	1	0	0	2	1	1	0	2	1	1	0	0	0	1	1	0	1	1	1	0	0	1	1	0
Labrocerus sp.	0	1	1	0	0	2	1	1	0	2	1	1	0	0	0	1	1	-	1	?	?	0	0	1	1	0
Neoanthrenus ocellifer	0	1	1	0	0	2	1	1	0	2	1	1	0	0	0	1	?	?	1	?	?	0	0	1	1	0
Anthrenocerus stigmacrophilus	0	1	1	0	0	2	1	1	1	2	1	1	0	2	0	0	?	?	1	?	?	0	0	1	1	0
Anthrenocerus australis	0	1	1	1	0	2	1	1	0	2	1	1	0	0	0	1	1	?	1	?	?	0	0	1	1	0
Myrmeanthrenus frontalis	0	1	1	0	0	2	1	1	1	2	1	1	0	2	0	0	?	?	?	?	?	0	0	1	1	0
Cryptorhopalum triste	0	1	1	0	0	2	1	1	0	2	1	1	2	0	0	1	1	0	1	1	2	0	0	1	1	0
Thaumaglossa libochoras	0	1	1	3	0	2	1	1	0	2	1	1	3	0	0	1	1	0	1	1	2	0	0	1	1	0
Thaumaglossa rufocapillata	0	1	1	3	0	2	1	1	0	2	1	1	3	0	0	1	1	0	1	1	2	0	0	1	1	0
Orphinus fulvipes	0	1	1	0	0	2	1	1	0	2	1	1	3	0	0	1	1	0	1	?	?	0	0	1	1	0
Anthrenus lepidus	0	1	1	0	0	2	1	1	0	3	1	1	1	0	0	1	1	0	1	1	1	0	0	1	1	0
Anthrenus verbasci	0	1	1	0	0	2	1	1	0	2	1	1	1	0	0	1	1	0	1	1	1	0	0	1	1	0
Anthrenus scrophulariae	0	1	1	0	0	2	1	1	0	3	1	1	1	0	0	1	1	0	1	1	1	0	0	1	1	0
Anthrenus flavipes	0	1	1	0	0	2	1	1	0	3	1	1	1	0	0	1	1	0	1	1	1	0	0	1	1	0
Endecatomus rugosus	0	0	0	4	0	0	0	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Heterobostrichus brunneus	0	0	0	4	0	0	0	1	-	0	0	0	0	0	0	0	?	0	?	?	-	0	1	1	1	1
Scobicia chevrieri	0	2	0	4	0	1	0	1	-	0	0	0	0	0	0	0	-	0	-	-	-	-	1	1	1	1
Lasioderma serricorne	0	0	0	4	0	0	0	1	-	0	0	0	0	0	0	0	1	0	0	2	0	1	1	1	1	1
Caenocara sp.	2	1	0	4	0	1	0	1	-	0	0	0	0	0	0	0	1	0	0	2	0	1	1	1	1	1
Trinodes sp.	3	?	?	0	1	2	1	1	-	0	1	1	0	0	0	1	1	0	1	1	3	0	0	1	1	0
Thorictodes heydeni	0	0	0	4	0	2	0	0	-	0	1	0	0	0	0	1	?	?	?	?	?	?	0	1	?	0
Trogoderma ballfinchae	0	1	1	1	0	2	1	1	0	2	1	1	0	0	0	1	1	?	1	?	?	0	0	1	1	0

4.1

4.2



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4.4


4.5


4.6


4.7


4.8


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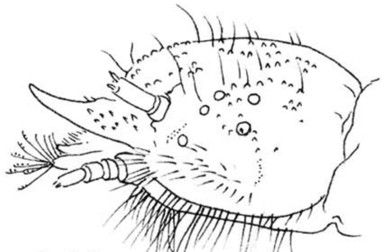

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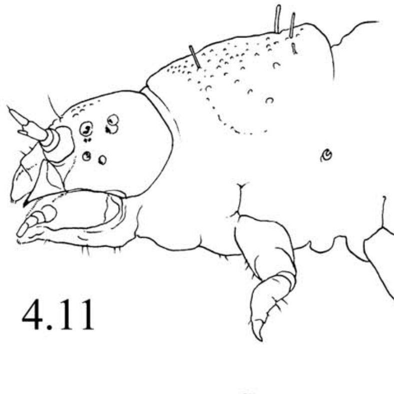

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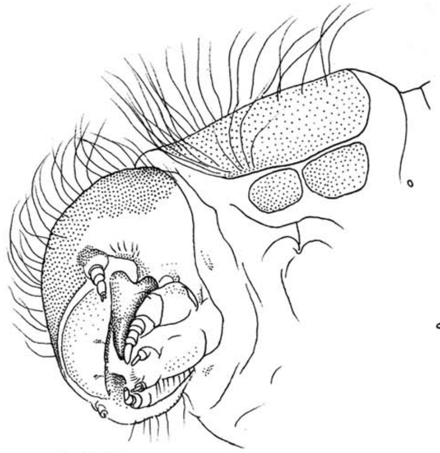

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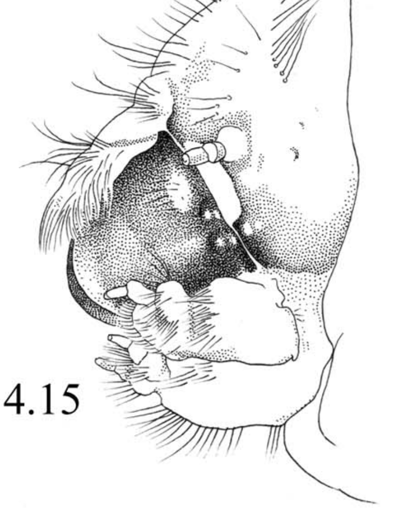

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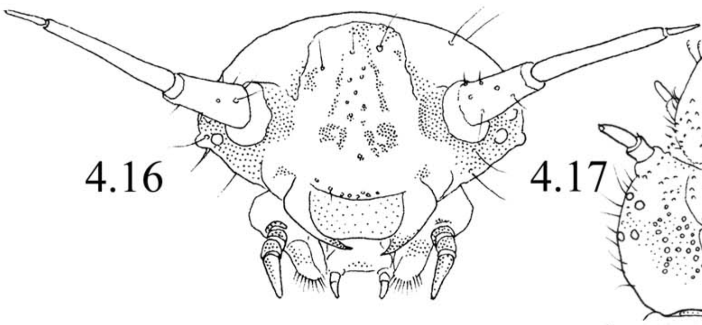
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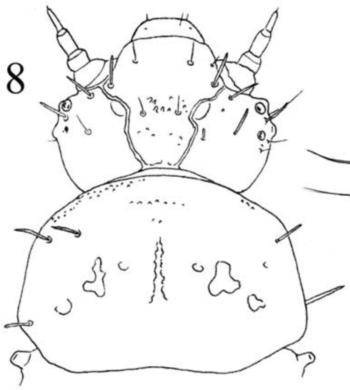
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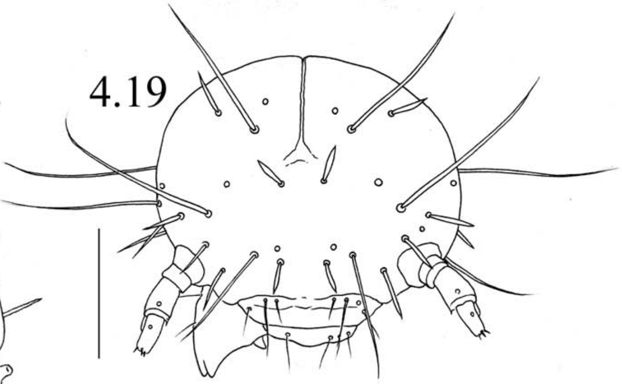
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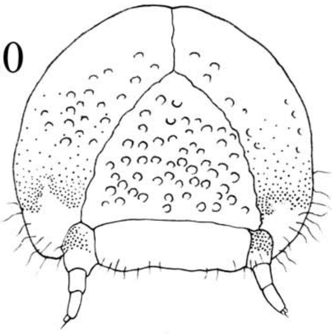
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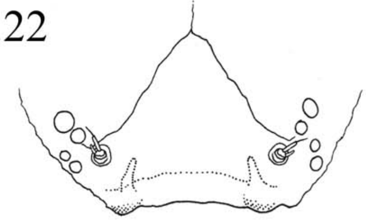
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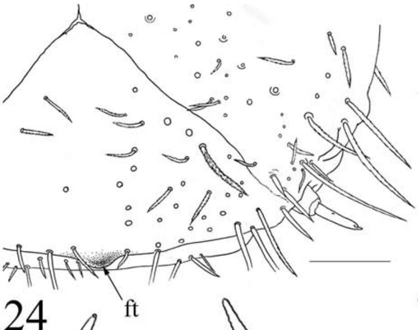

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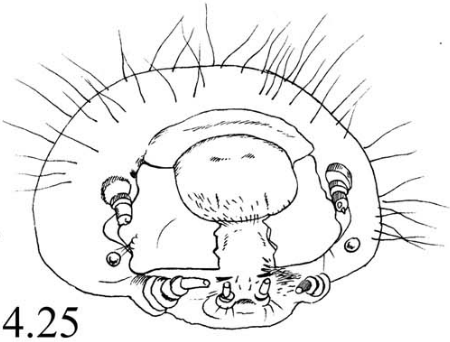

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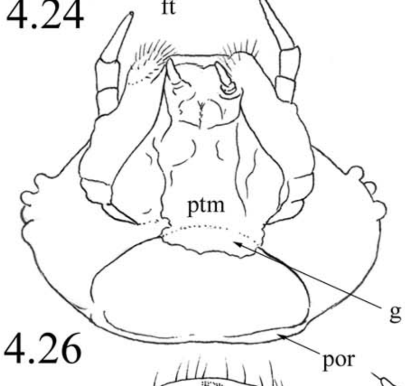

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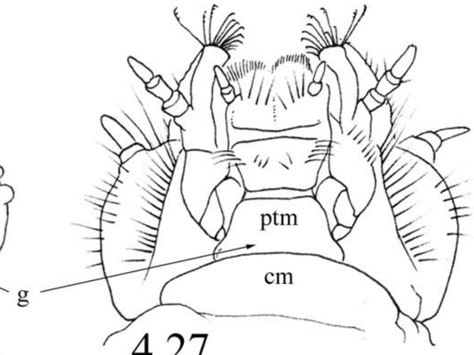

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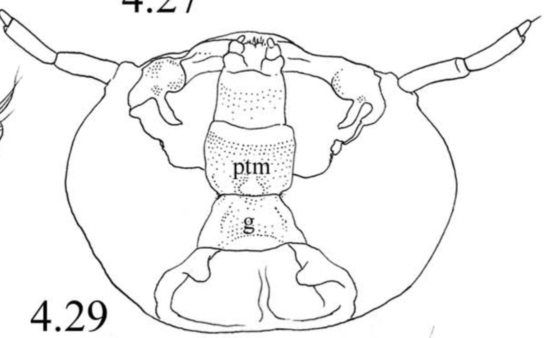

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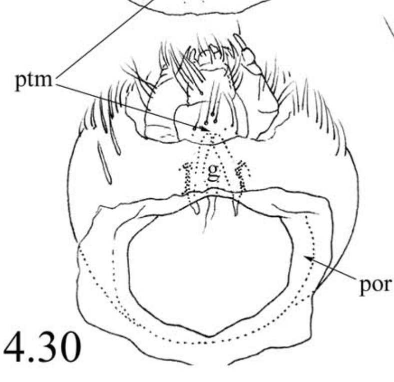

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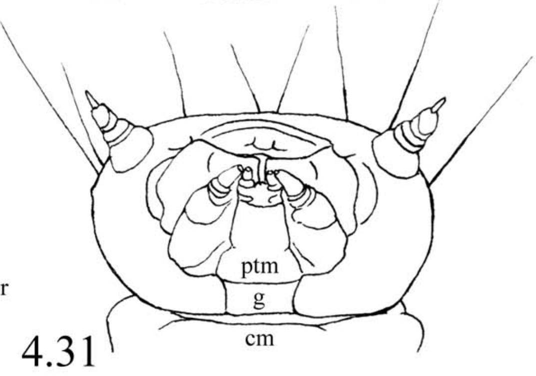

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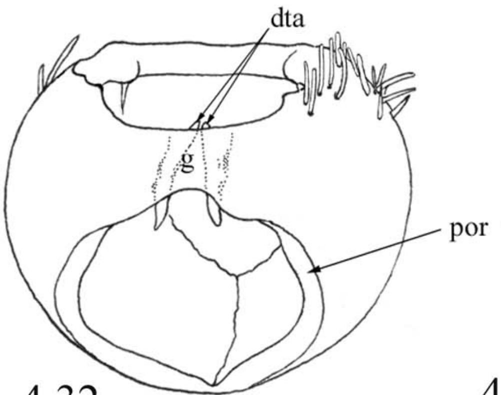

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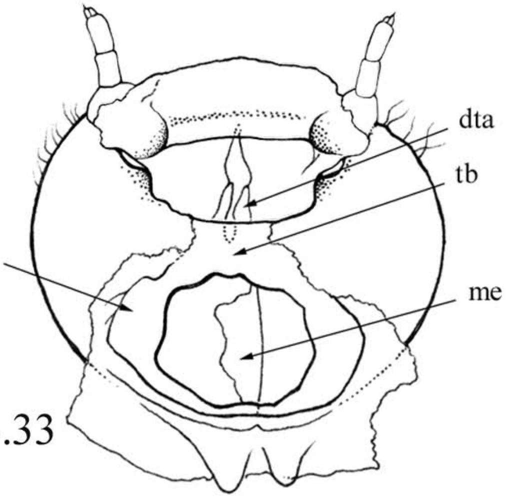

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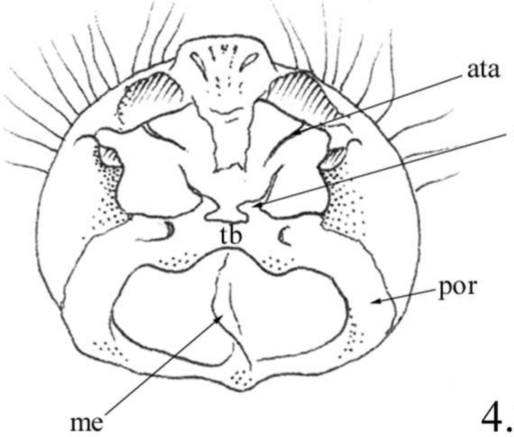

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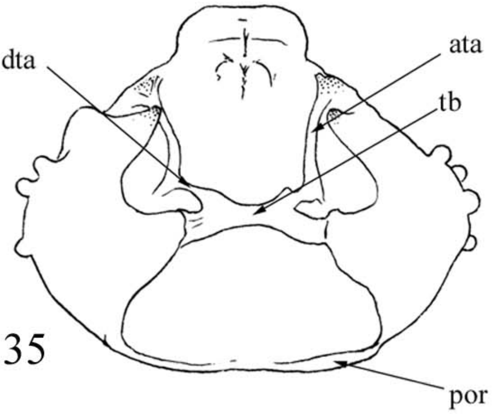

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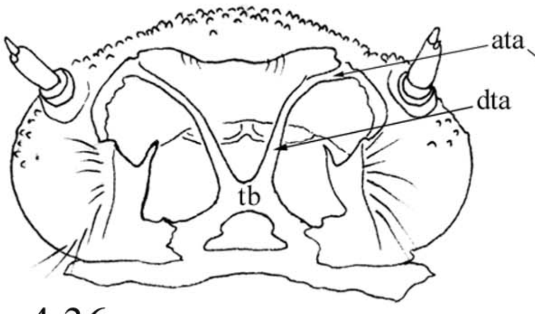

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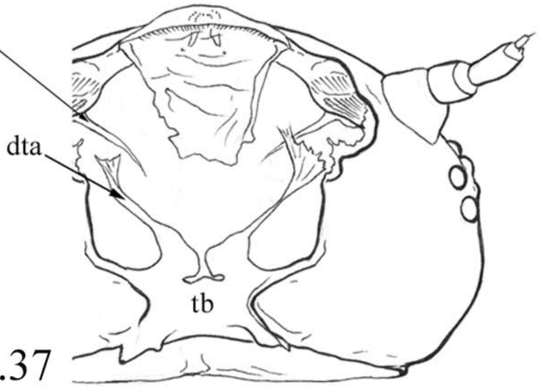

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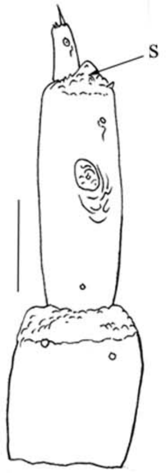

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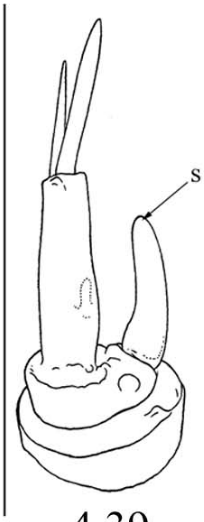

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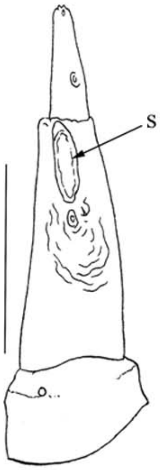

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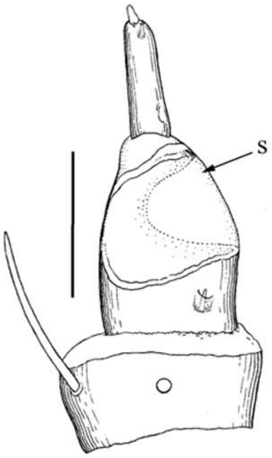

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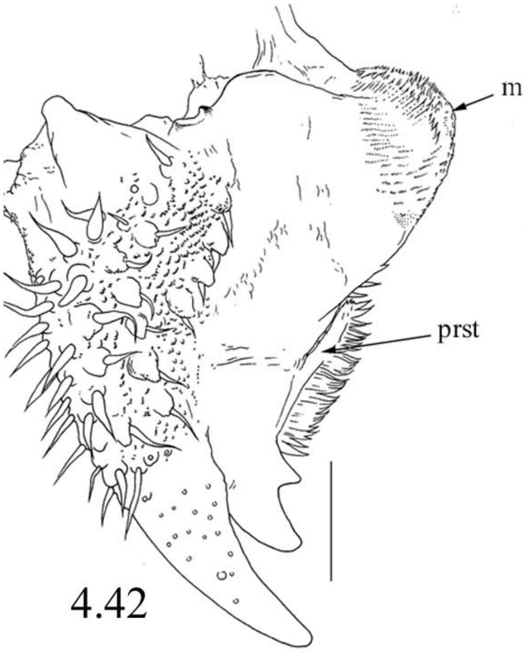

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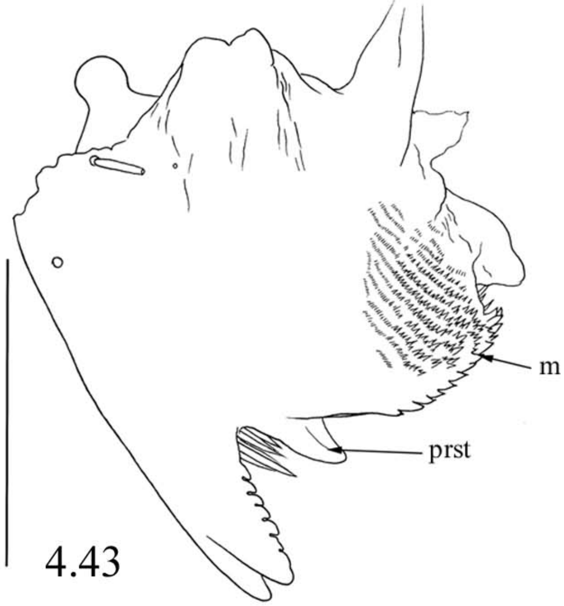

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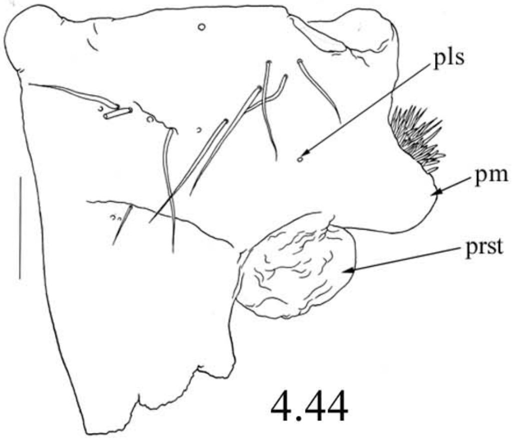

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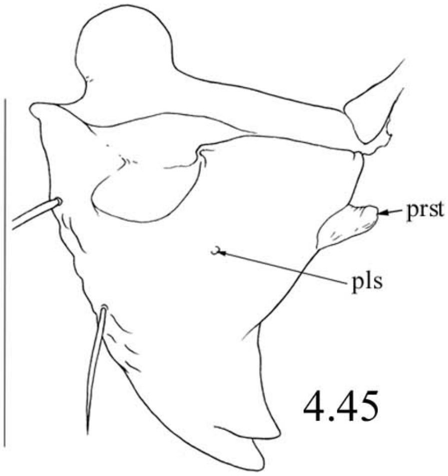

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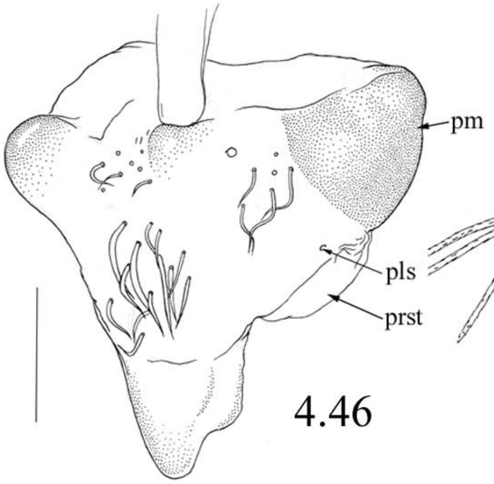

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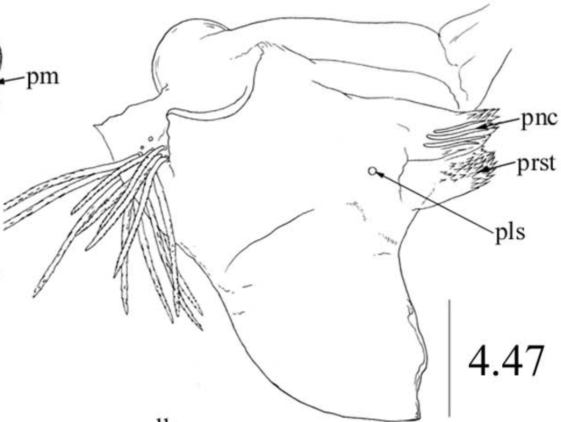

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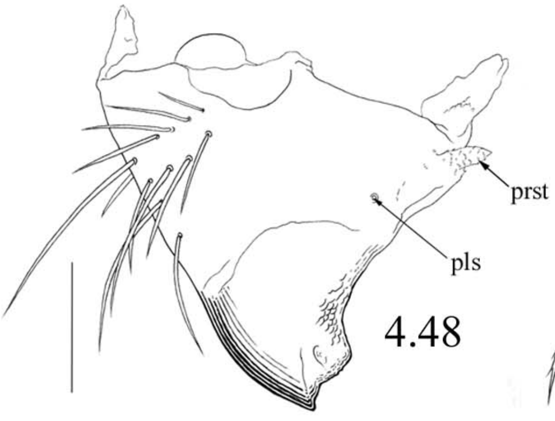

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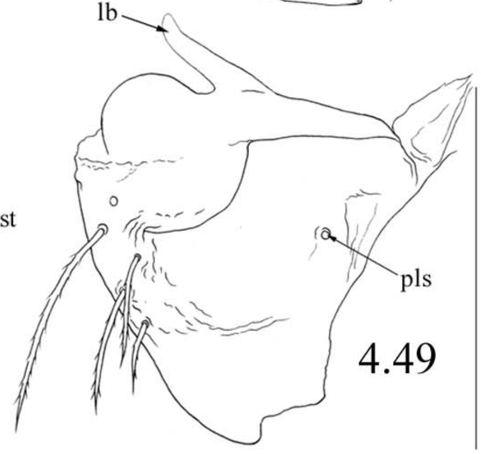

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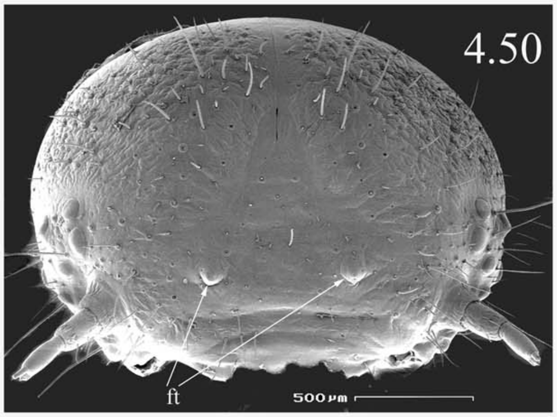
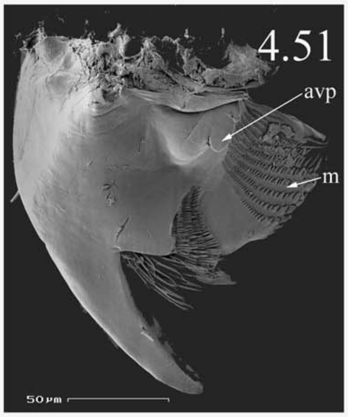
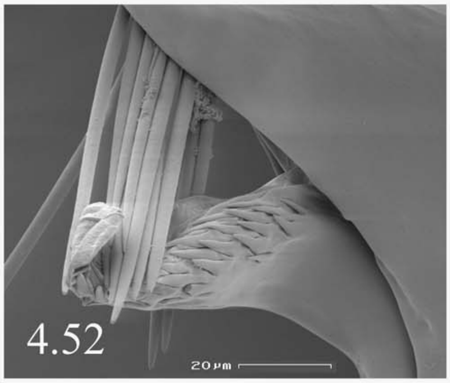

4.50
ft
500 µm


4.51
avp
m
50 µm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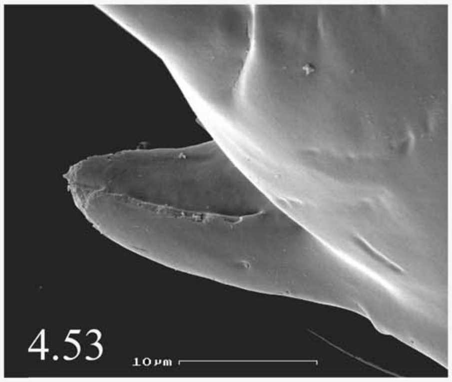
20 µm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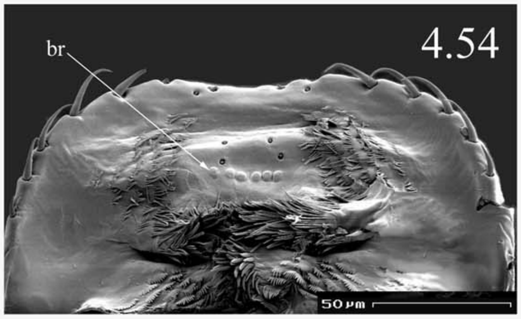
10 µm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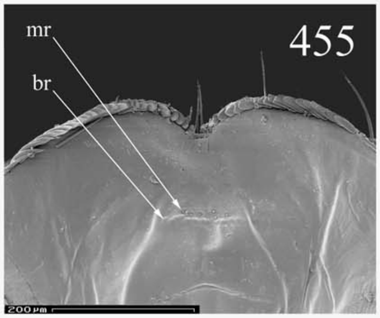
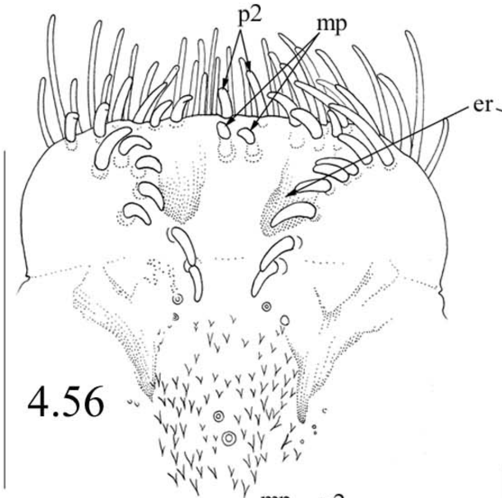
50 µm


455
mr
br
200 µm



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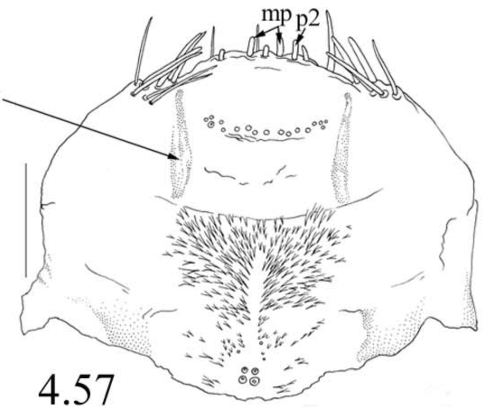

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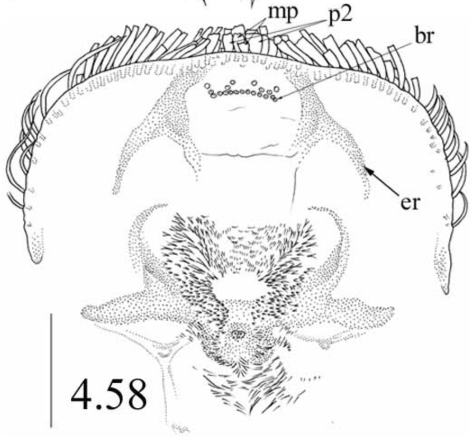

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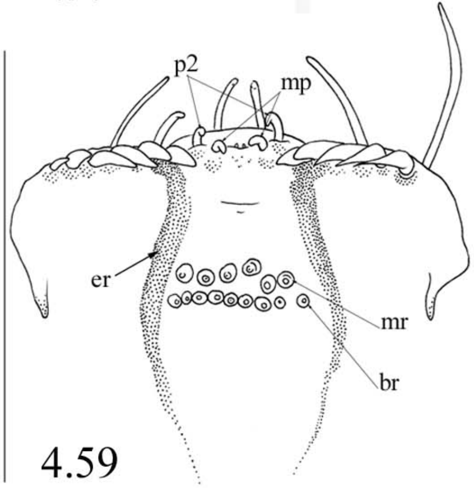

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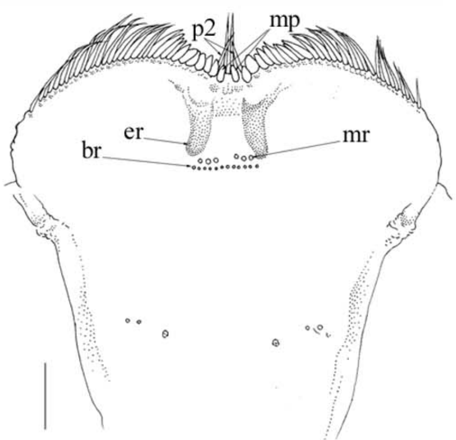

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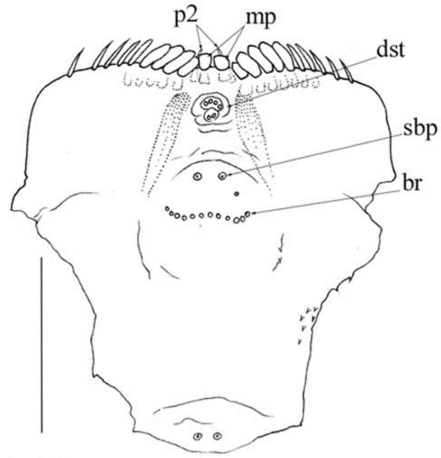

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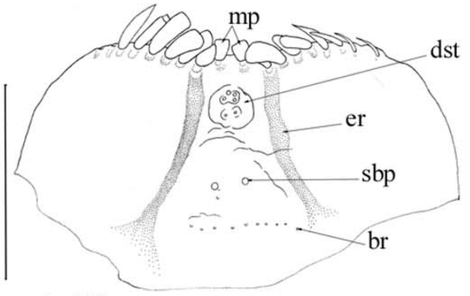

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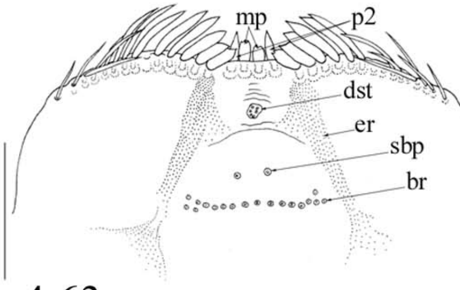

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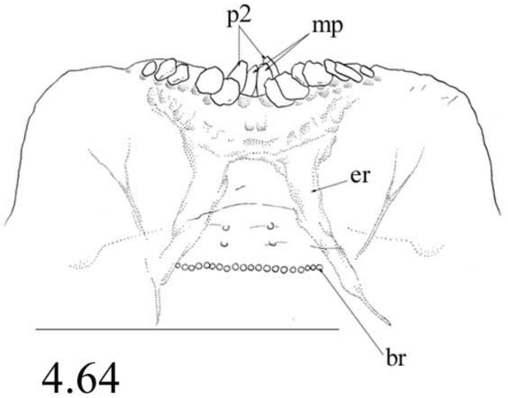

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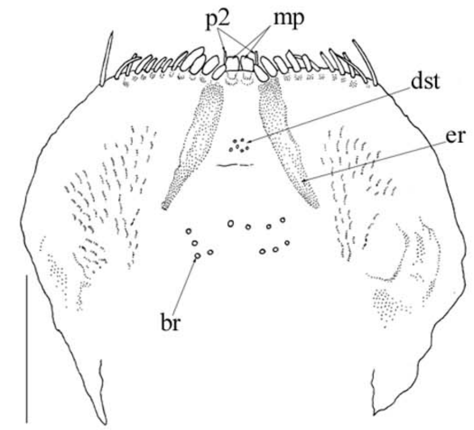

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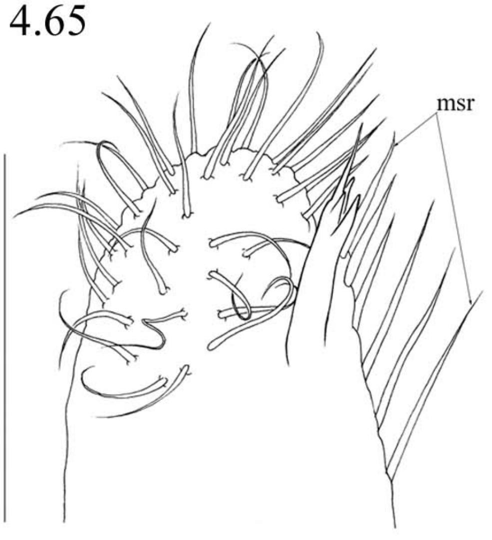

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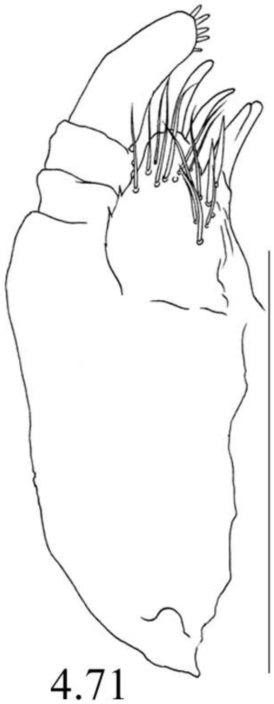

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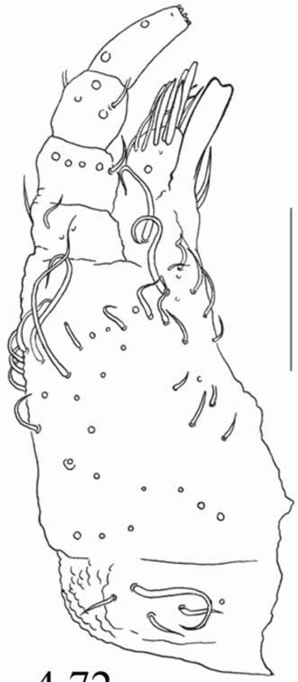

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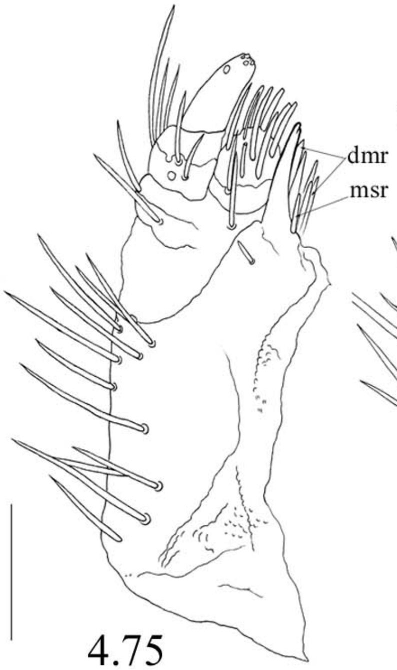

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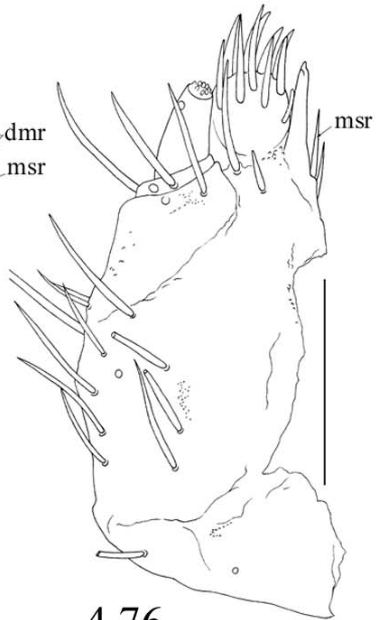

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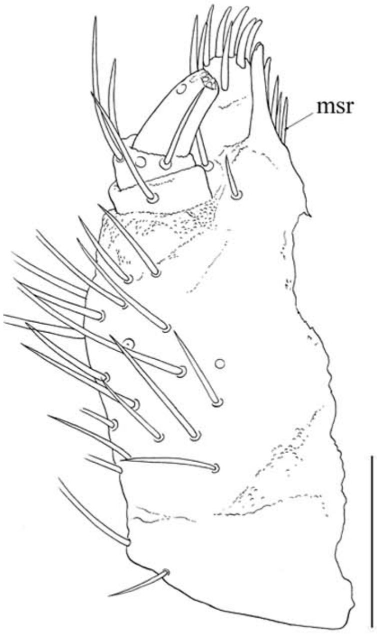

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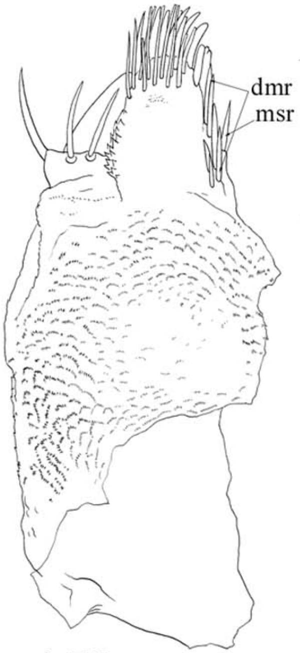

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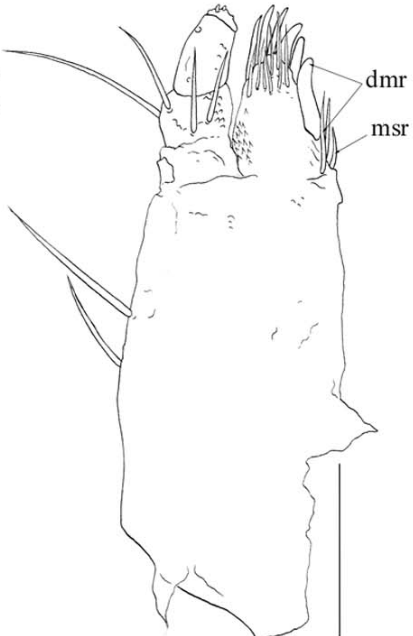

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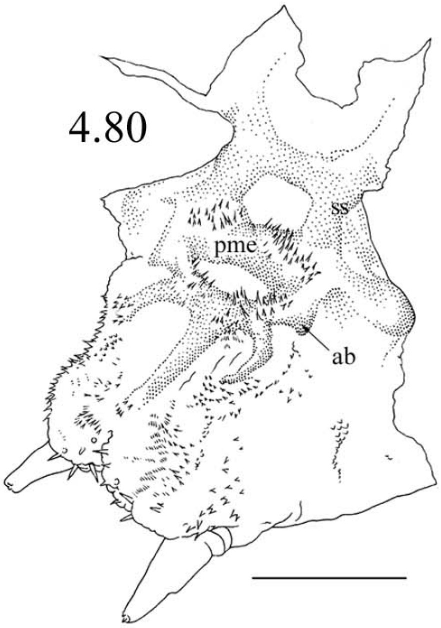

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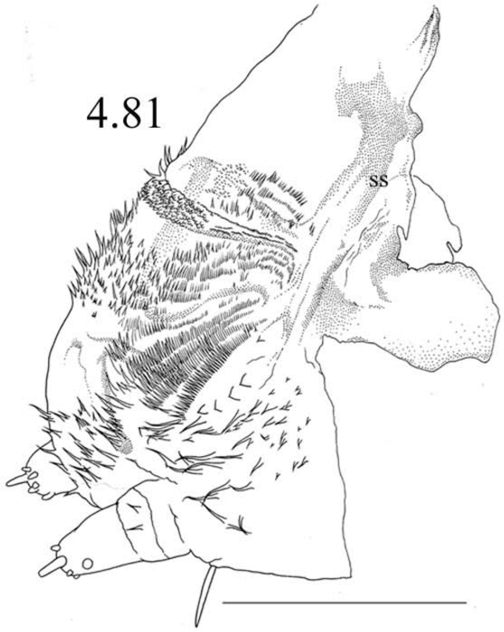

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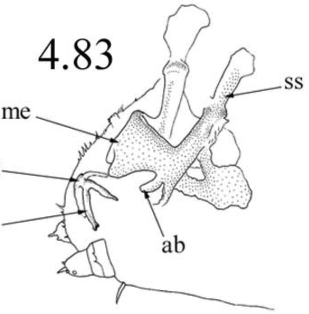

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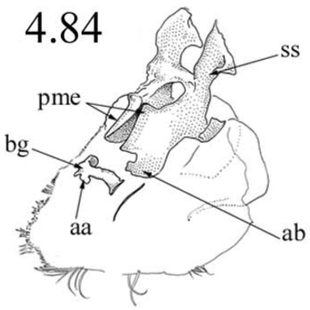

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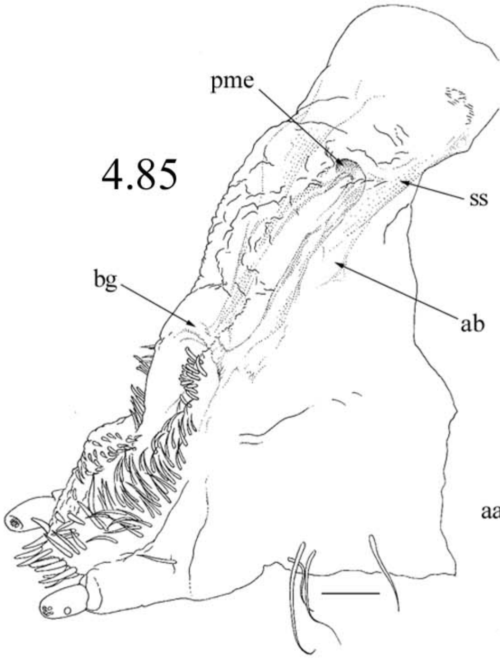

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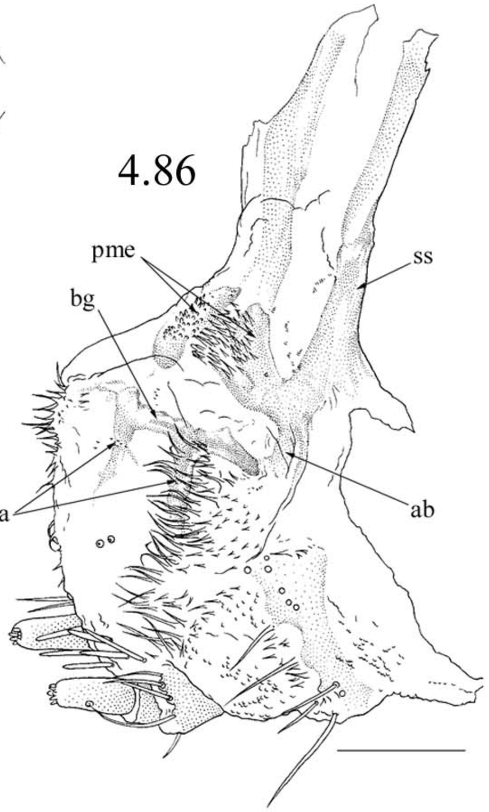

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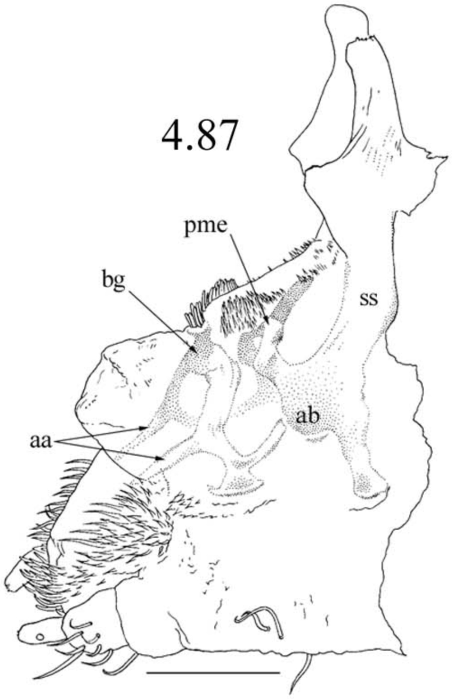

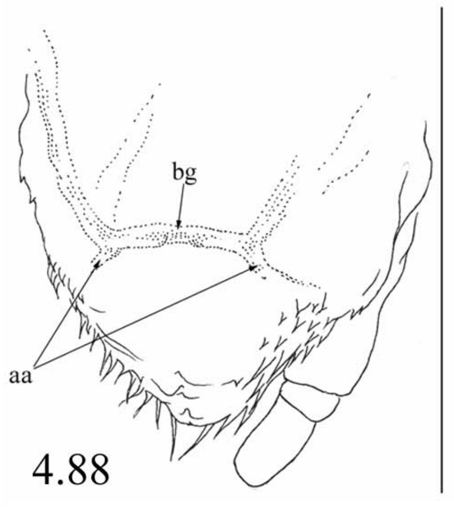

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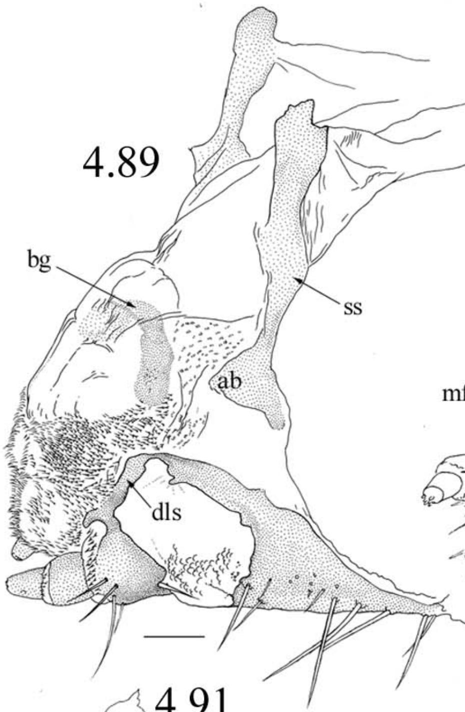

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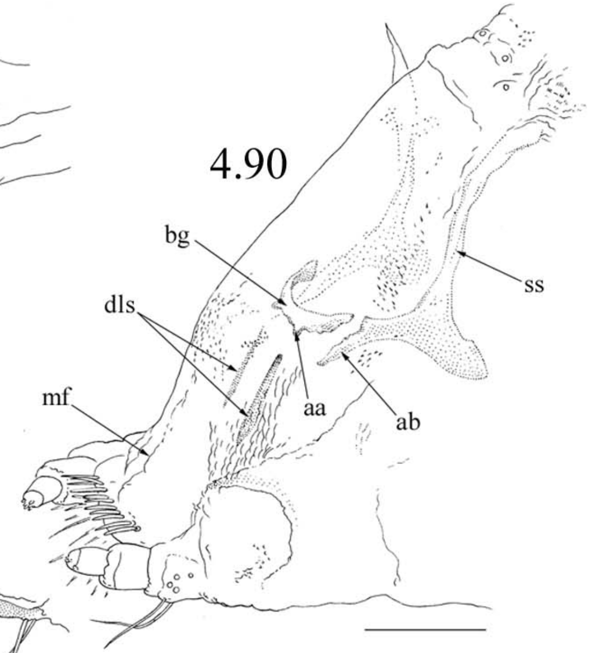

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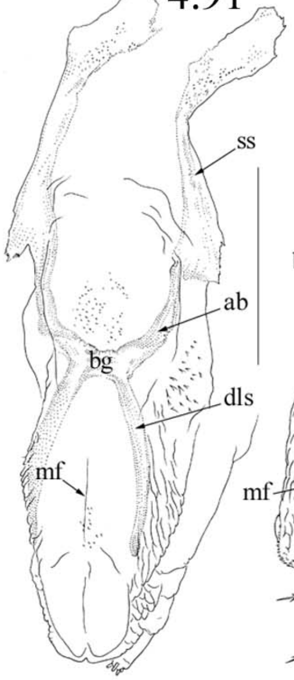

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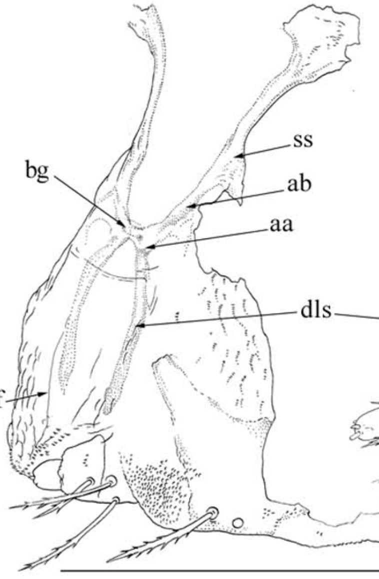

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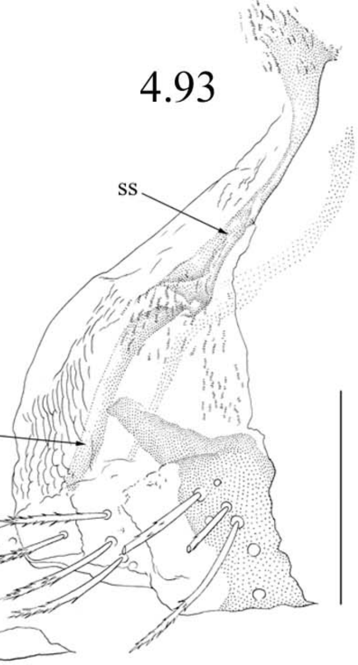

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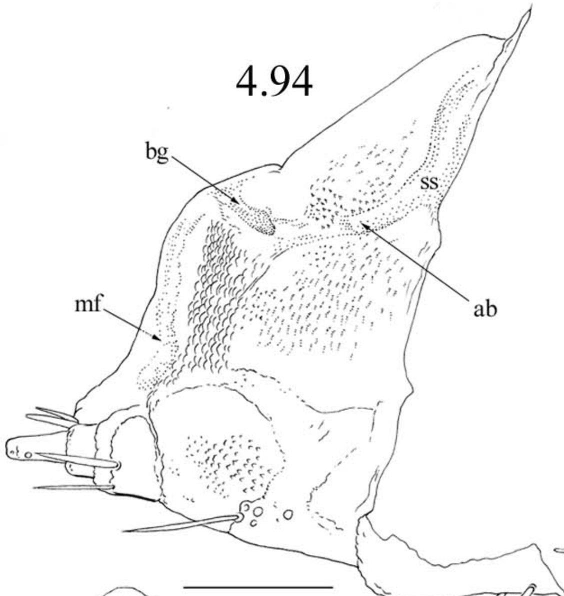

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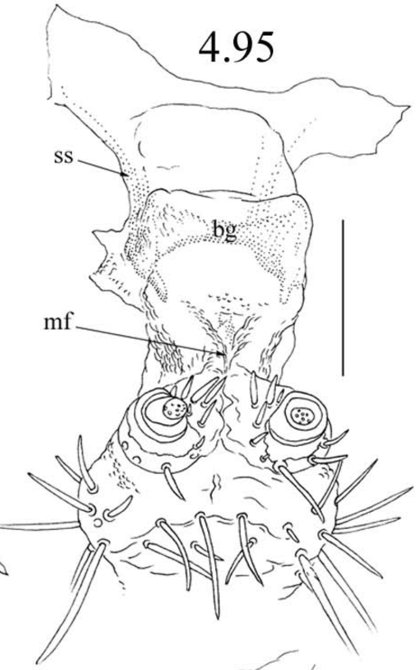

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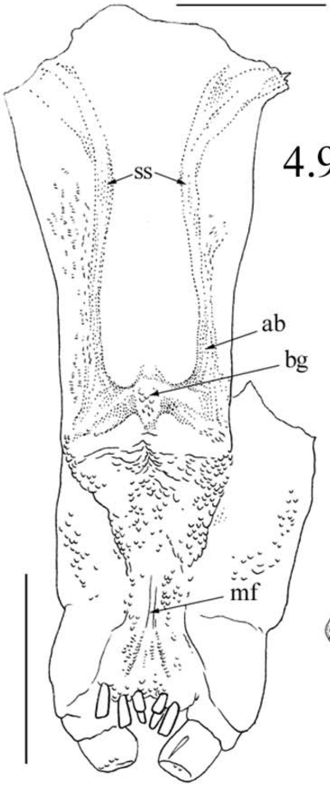

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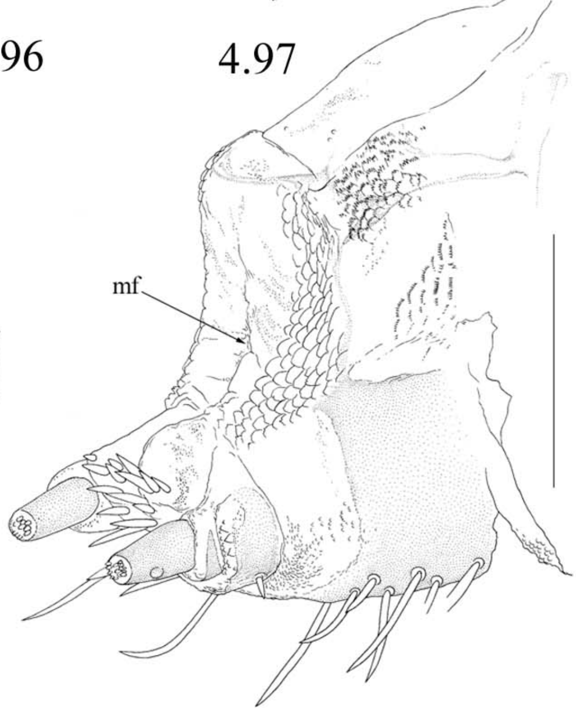

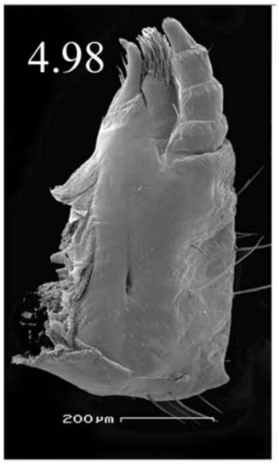
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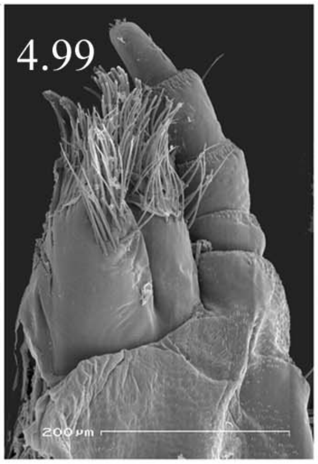
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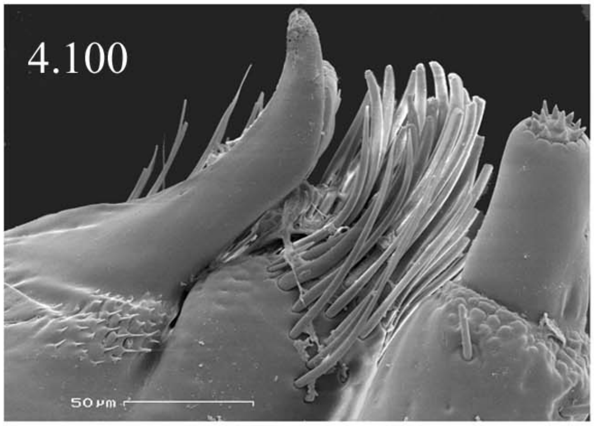
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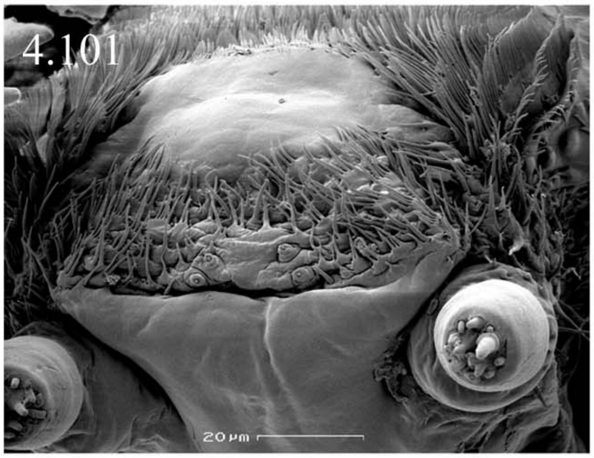
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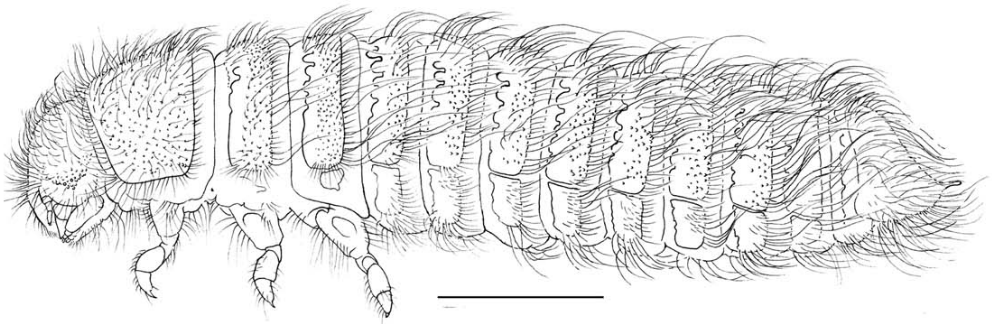

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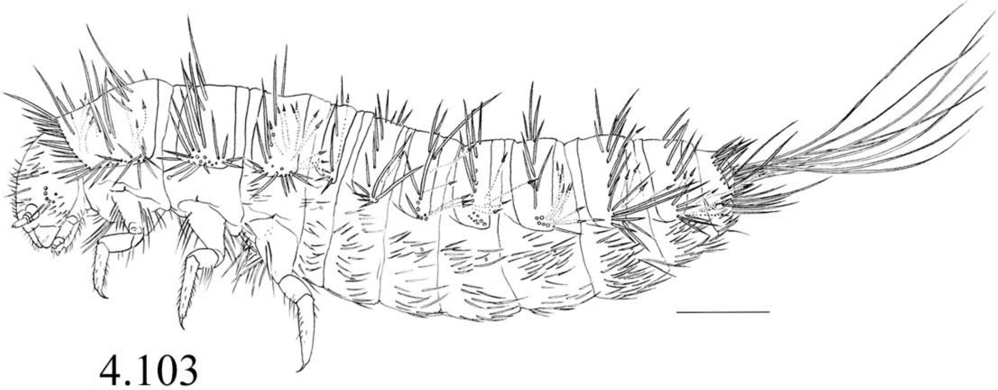

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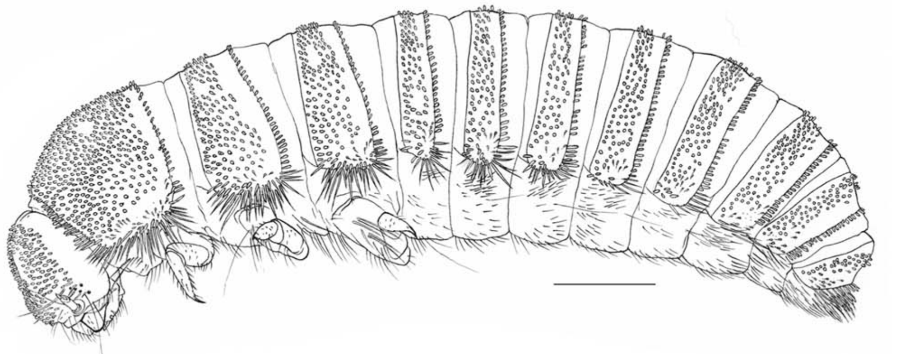

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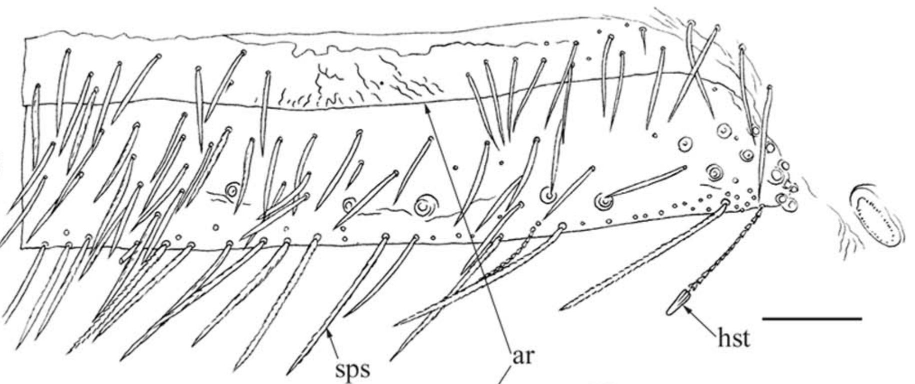

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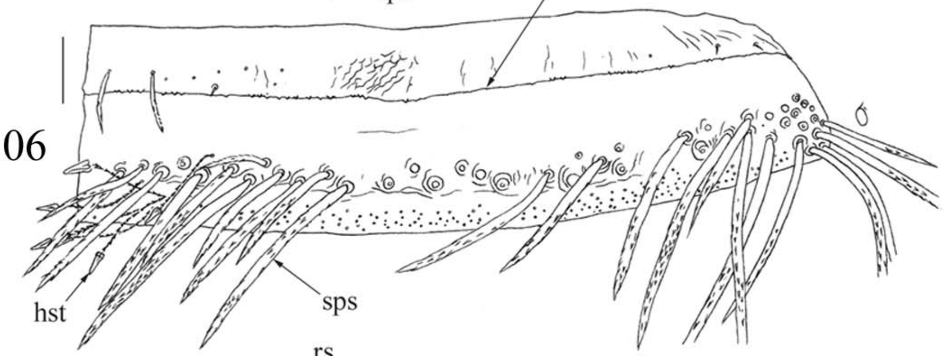

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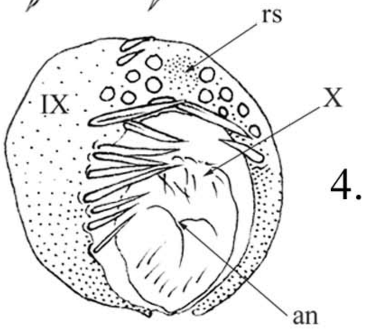

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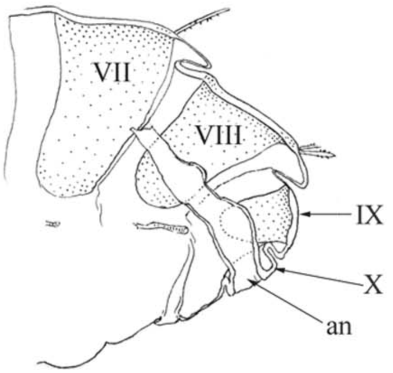

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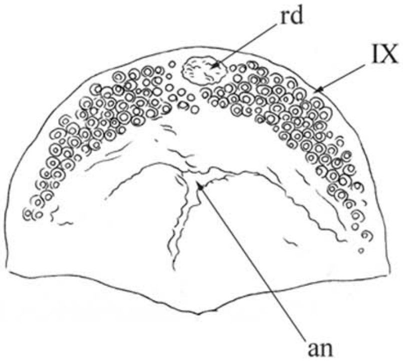

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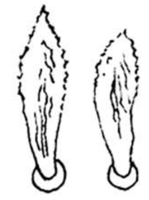

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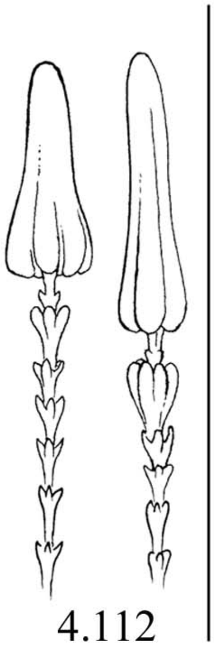

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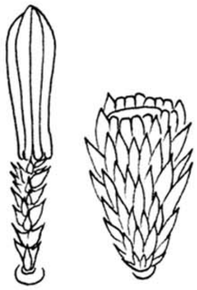

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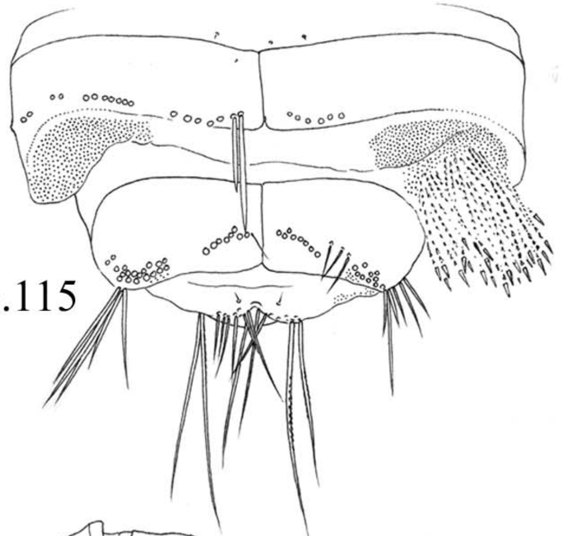

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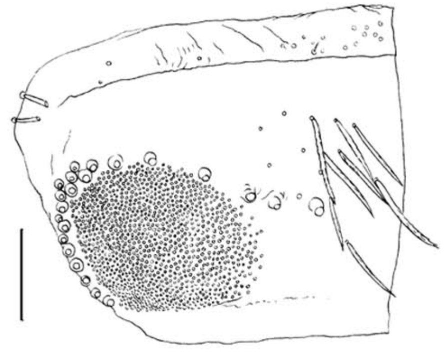

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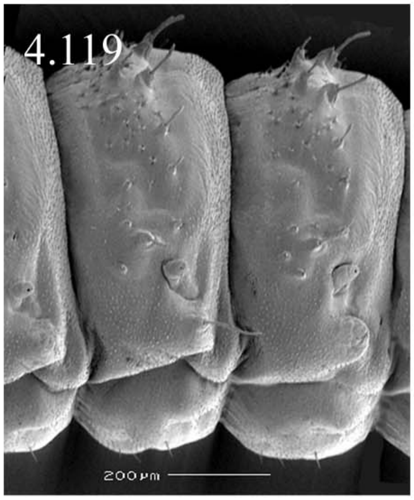

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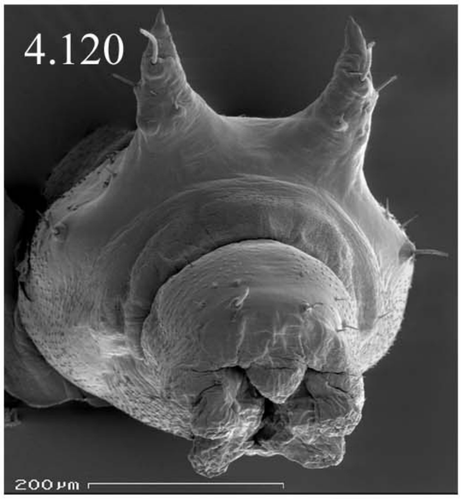

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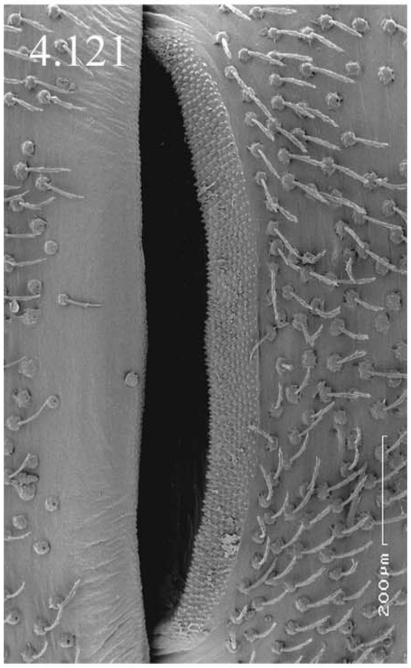

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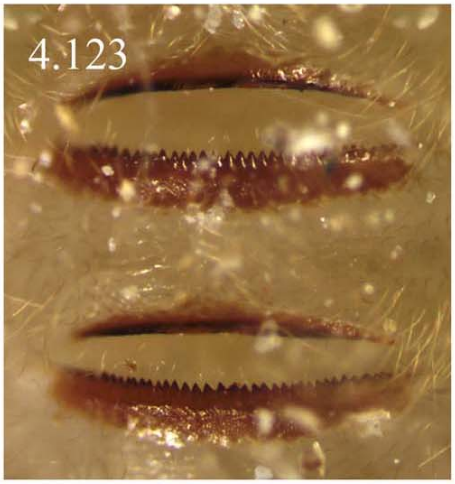
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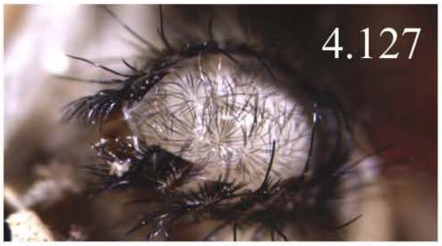
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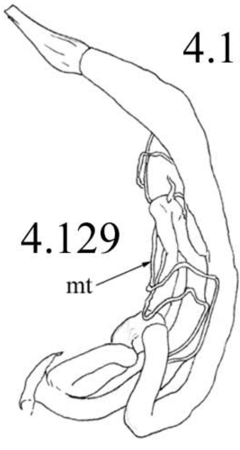

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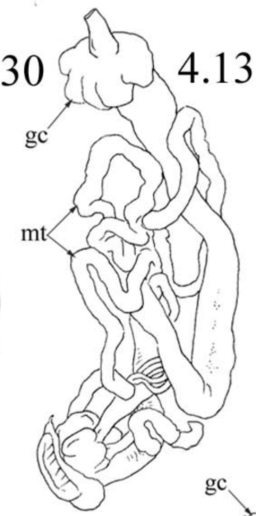

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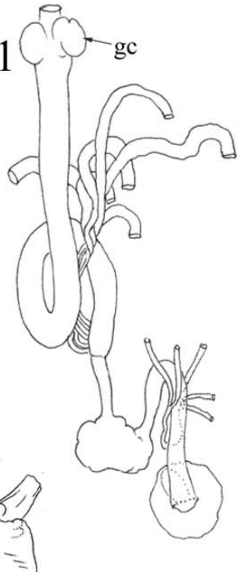

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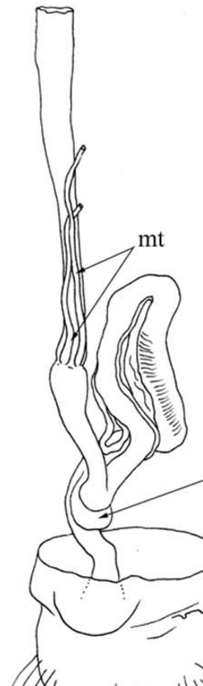

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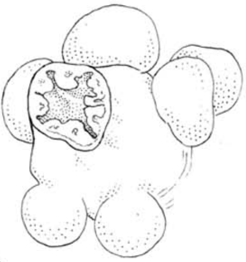

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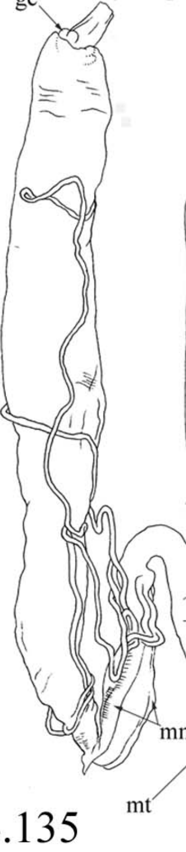

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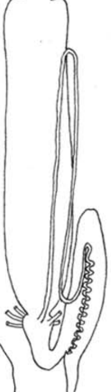

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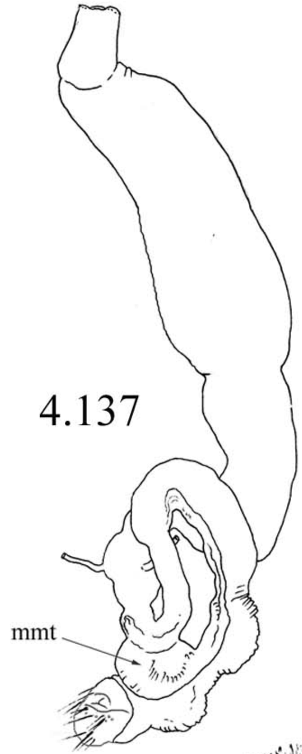

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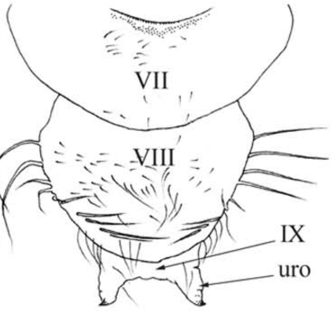

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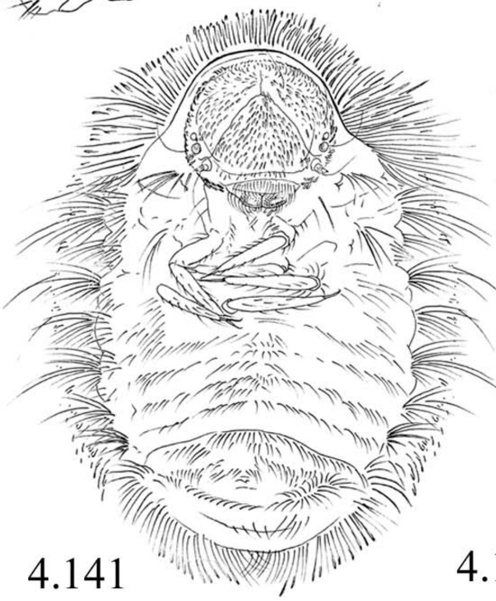

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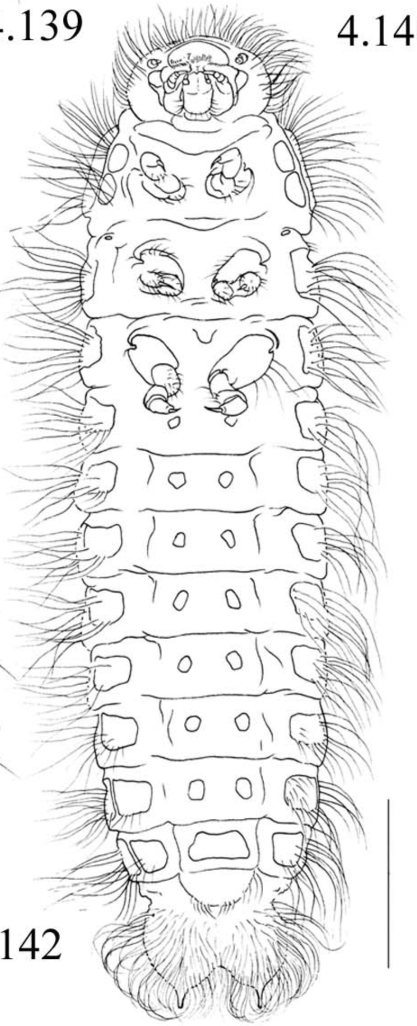

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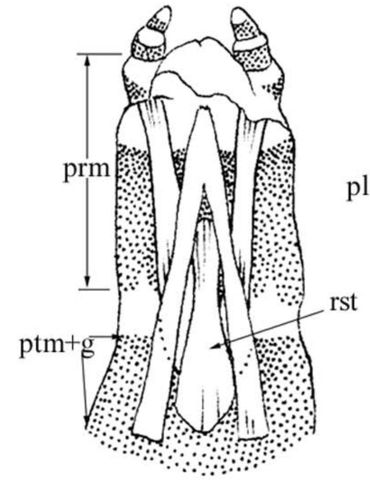

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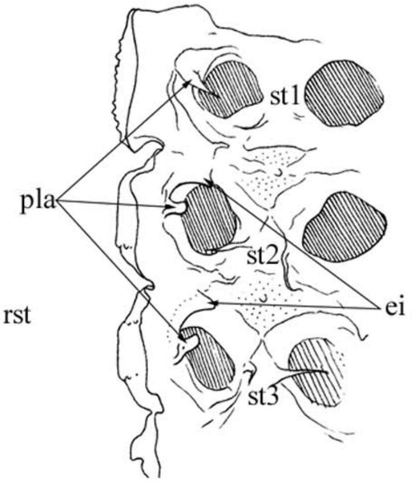

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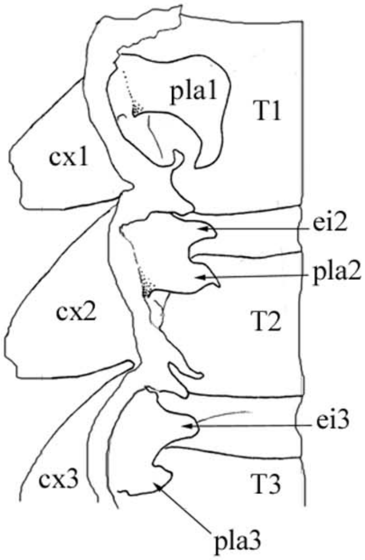

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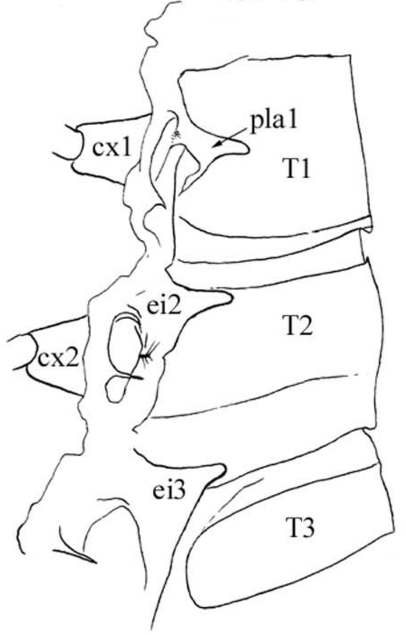

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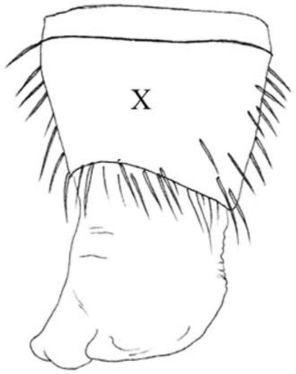

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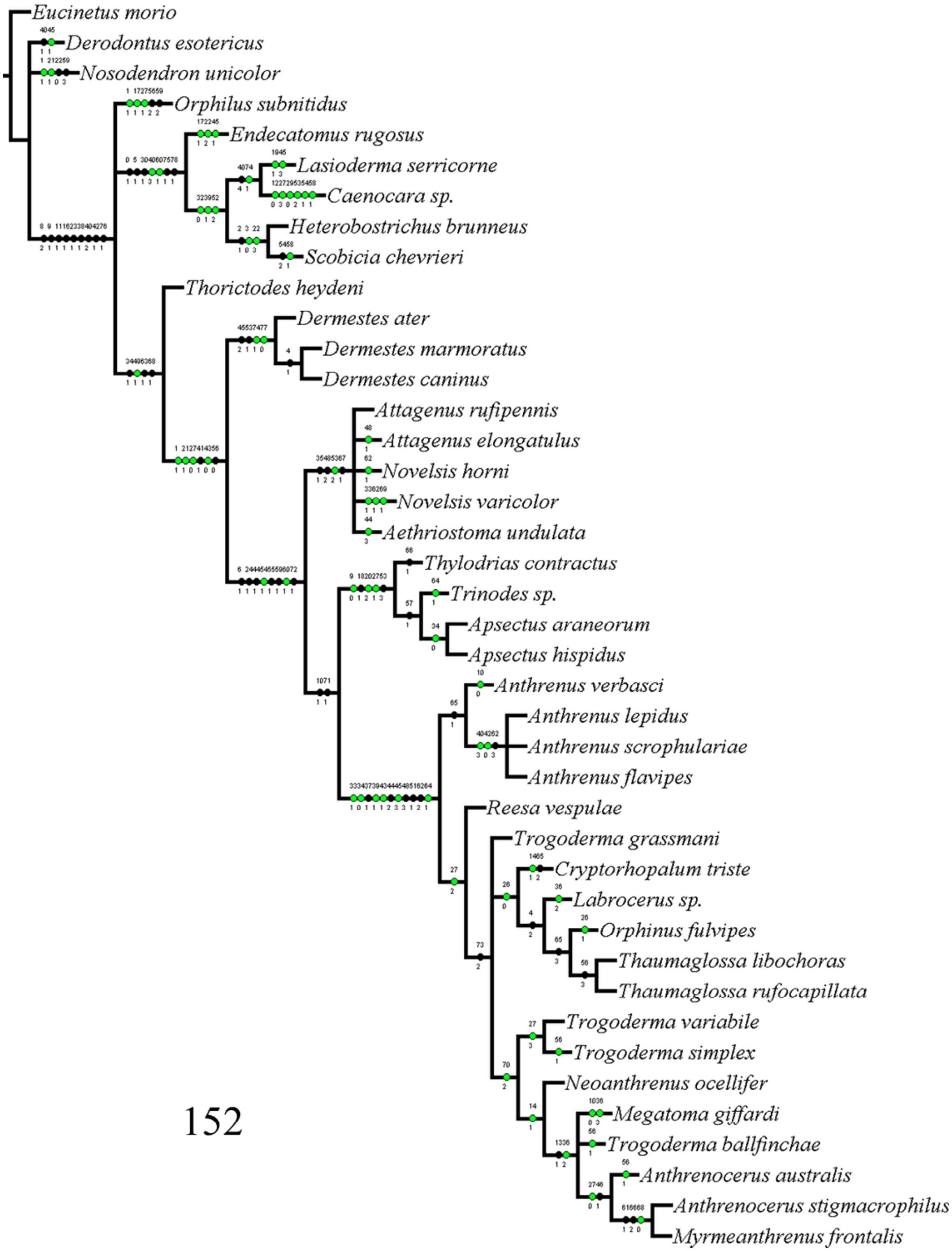
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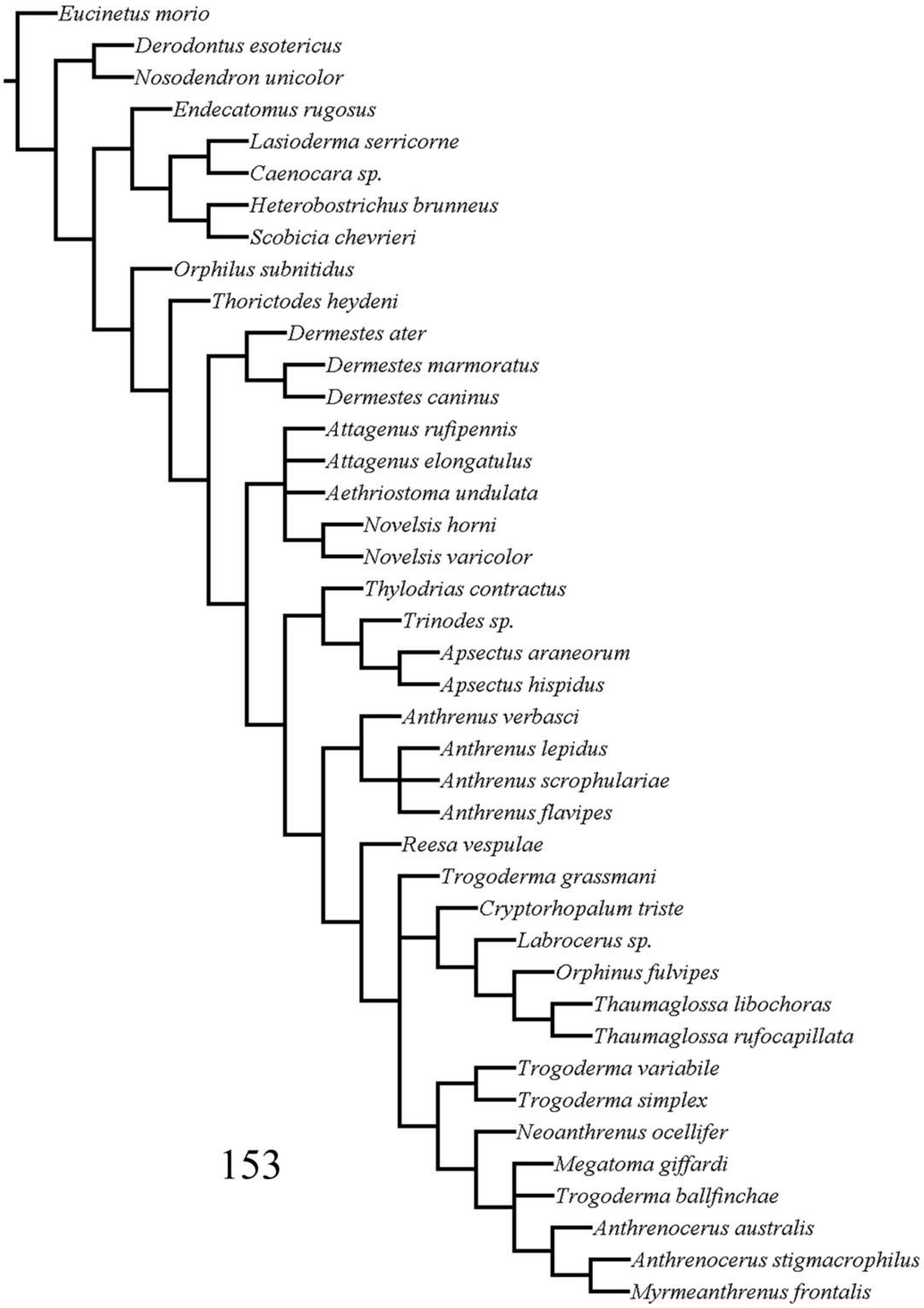
Derodontus esotericus
Nosodendron unicolor
Orphilus subnitidus
Endecatomus rugosus
Lasioderma serricorne
Caenocara sp.
Heterobostrichus brunneus
Scobicia chevrieri
Thorictodes heydeni
Dermestes ater
Dermestes marmoratus
Dermestes caninus
Attagenus rufipennis
Attagenus elongatulus
Novelsis horni
Novelsis varicolor
Aethriostoma undulata
Thylodrias contractus
Trinodes sp.
Apsectus araneorum
Apsectus hispidus
Anthrenus verbasci
Anthrenus lepidus
Anthrenus scrophulariae
Anthrenus flavipes
Reesa vespulae
Trogoderma grassmani
Cryptorhopalum triste
Labrocerus sp.
Orphinus fulvipes
Thaumaglossa libochoras
Thaumaglossa rufocapillata
Trogoderma variabile
Trogoderma simplex
Neoanthrenus ocellifer
Megatoma giffardi
Trogoderma ballfinchae
Anthrenocerus australis
Anthrenocerus stigmacrophilus
Myrmeanthrenus frontalis
152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Derodontus esotericus
Nosodendron unicolor
Endecatomus rugosus
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Heterobostrichus brunneus
Scobicia chevrieri
Orphilus subnitidus
Thorictodes heydeni
Dermestes ater
Dermestes marmoratus
Dermestes caninus
Attagenus rufipennis
Attagenus elongatulus
Aethriostoma undulata
Novelsis horni
Novelsis varicolor
Thylodrias contractus
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Apsectus araneorum
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Orphinus fulvipes
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Thaumaglossa rufocapillata
Trogoderma variabile
Trogoderma simplex
Neoanthrenus ocellifer
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Trogoderma ballfinchae
Anthrenocerus australis
Anthrenocerus stigmacrophilus
Myrmeanthrenus frontalis
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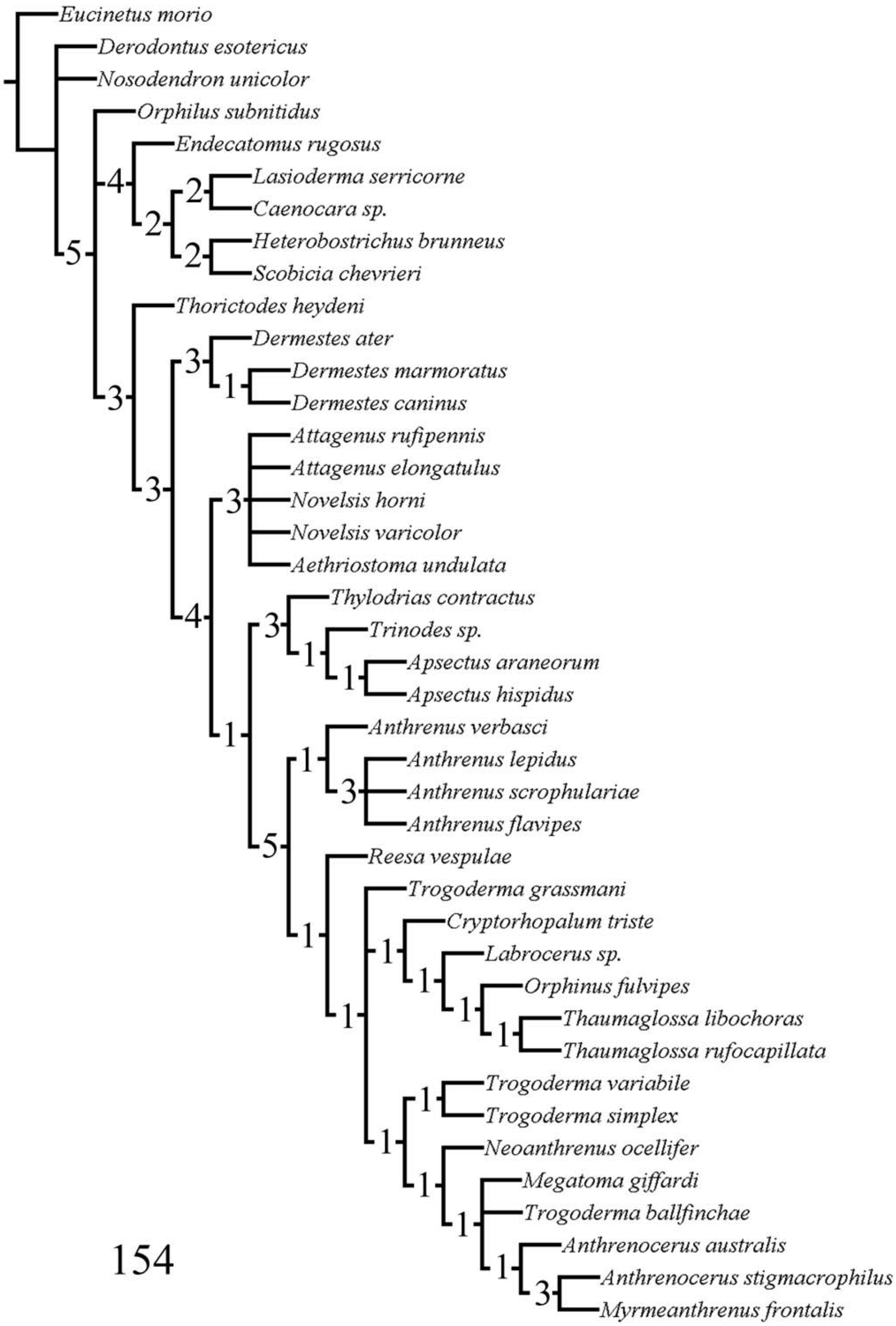
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Derodontus esotericus
Nosodendron unicolor
Orphilus subnitidus
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Endecatomus rugosus
2
Lasioderma serricorne
Caenocara sp.
2
5
2
Heterobostrichus brunneus
Scobicia chevrieri
Thorictodes heydeni
Dermestes ater
3
1
Dermestes marmoratus
Dermestes caninus
3
Attagenus rufipennis
Attagenus elongatulus
3
3
Novelsis horni
Novelsis varicolor
Aethriostoma undulata
Thylodrias contractus
4
3
Trinodes sp.
1
1
Apsectus araneorum
Apsectus hispidus
1
Anthrenus verbasci
1
Anthrenus lepidus
3
Anthrenus scrophulariae
Anthrenus flavipes
5
Reesa vespulae
Trogoderma grassmani
1
Cryptorhopalum triste
1
Labrocerus sp.
1
Orphinus fulvipes
1
1
Thaumaglossa libochoras
1
Thaumaglossa rufocapillata
Trogoderma variabile
1
Trogoderma simplex
1
Neoanthrenus ocellifer
1
Megatoma giffardi
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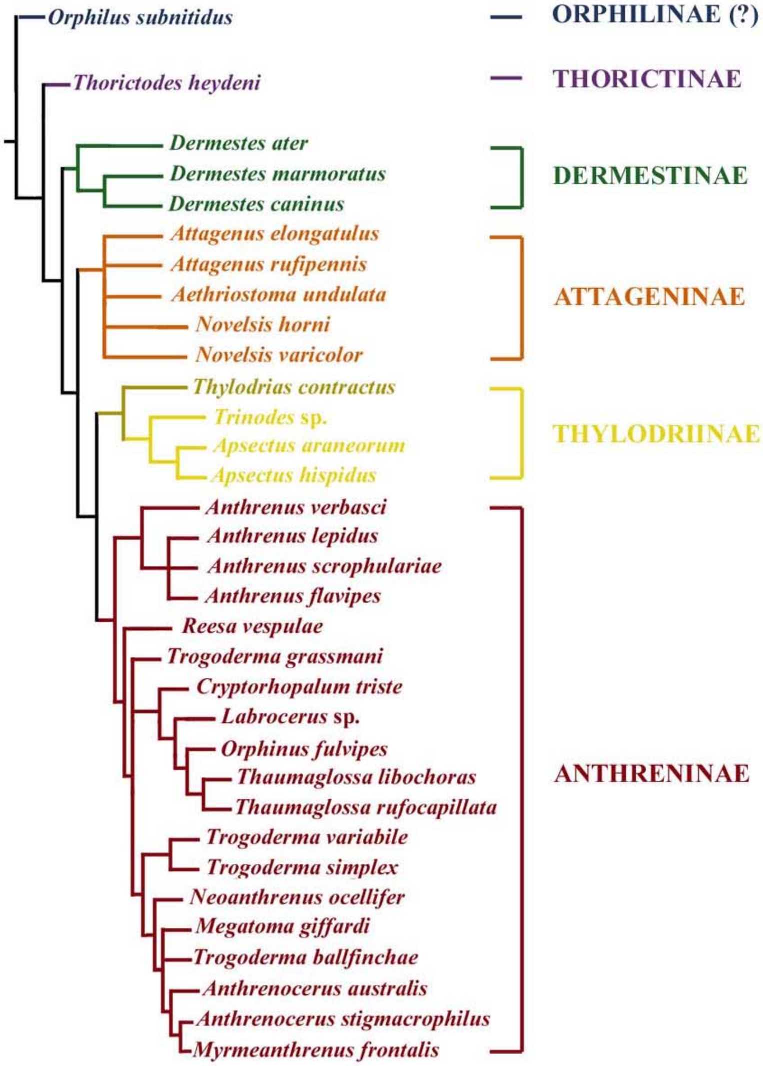
1
3
Anthrenocerus stigmacrophilus
Myrmeanthrenus frontalis

154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ORPHILINAE (?)
Thorictodes heydeni
THORICTINAE
Dermestes ater
Dermestes marmoratus
Dermestes caninus
DERMESTINAE
Attagenus elongatulus
Attagenus rufipennis
Aethriostoma undulata
Novelsis horni
Novelsis varicolor
ATTAGENINAE
Thylodrias contractus
Trinodes sp.
Apsectus araneorum
Apsectus hispidus
THYLODRIINAE
Anthrenus verbasci
Anthrenus lepidus
Anthrenus scrophulariae
Anthrenus flavipes
Reesa vespulae
Trogoderma grassmani
Cryptorhopalum triste
Labrocerus sp.
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Trogoderma simplex
Neoanthrenus ocellifer
Megatoma giffardi
Trogoderma ballfinchae
Anthrenocerus australis
Anthrenocerus stigmacrophilus
Myrmeanthrenus frontalis
ANTHRENINAE

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CHAPTER 5

CONCLUSIONS

According to the results of a phylogenetic parsimony analysis based on morphology of immature stages, Dermestidae (Coleoptera) exclusive of *Orphilus* Erichson form a monophyletic group. More data from different sources, such as adult morphology and DNA, are needed to determine the phylogenetic status of *Orphilus*. Five subfamilies of Dermestidae can be recognized based on the present analysis. Morphological characters of larvae and pupae are illustrated and discussed in the context of phylogeny. First records are presented of gastric caeca in *Dermestes* L., of the structure of mandible base in Thylodriini Beal and Trinodini Beal, of the number of Malpighian tubules and abdominal nervous ganglia in some species of Dermestidae, Bostrichidae, Anobiidae, Nosodendridae, and Derodontidae, and of other characters. The fossil record and the distribution of extant Dermestidae are discussed in light of phylogeny.

The first descriptions of the larval and pupal stages of *Cryptorhopalum triste* LeConte are presented. A diagnosis is provided for the larval form of *Cryptorhopalum* Guérin-Méneville. The first instance of rearing this species in captivity is documented, along with new adult floral hosts.

The first descriptions of the larval stage of *Myrmeanthrenus frontalis* Armstrong and *Anthrenocerus stigmacrophilus* Armstrong (Coleoptera: Dermestidae) are presented.

The larva of *Anthrenocerus australis* (Hope) is illustrated and briefly characterized. In light of a morphology-based phylogenetic study, *A. stigmacrophilus* is more closely related to *M. frontalis* than it is to *A. australis*.