

Debris cloaking in Endomychidae: a new species from Peru (Coleoptera)

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Adults and immature stages of the mychothenine endomychid *Bystus decorator* sp. nov. from Peru are described. All life stages occur together on rotting logs and feed on fungal spores. Larval debris cloaking and morphological adaptations associated with it are discussed in detail. Some larval setae are apically clubbed and barbed along the shafts to facilitate particle adhesion. Pronation of the thoracic lateral lobes bring the setae into contact with the substrate to gather particles of debris. The anatomy and functional morphology of the thoracic musculature is considered in the context of cloaking behaviour. Variations in debris cloaking behaviours among mychothenine endomychids are discussed and compared to other debris-cloaking insects.

KEY WORDS: —Coleoptera – Endomychidae – behaviour – *Bystus* – debris cloaking – morphology – mycophagy – taxonomy.

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INTRODUCTION

Larvae of some insects, including species of Reduviidae (Hemiptera), Chrysopidae (Neuroptera), Derodontidae (Coleoptera) and synchlorine Geometridae (Lepidoptera) (Butler, 1923; Killington, 1936; Brown & Clark,

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1962; Eisner *et al.*, 1978; Ferguson, 1985) cloak themselves with debris and other material gathered from their habitat. These behaviours enable the insects to avoid predation by camouflage. In this paper we describe *Bystus decorator*, **sp. nov.**, including immature stages, and discuss the form and function of debris cloaking in the larva and the life history of the species.

Members of *Bystus* are included in the endomychid subfamily Mychotheninae, recently defined by Sasaji (1978a). The subfamily is distributed worldwide and currently contains 13 genera (Sasaji, 1978a; Pakaluk, 1986). *Bystus* contains mainly Neotropical (25 spp.) and African (3 spp.) species. Strohecker (1953) apparently doubted the occurrence of *Bystus* in Africa, since there is a question mark after his comment on distribution.

Based upon comparisons of our material with published descriptions, and comparisons made by the senior author and colleagues with specimens in the Natural History Museum, London, Museum d'Histoire Naturelle, Paris, and the Florida State Collection of Arthropods, Gainesville, the species discussed in this paper appears to represent a new species and is described herein.

Among mychothenines, larval stages for *Mychothenus* (Sasaji, 1978a), *Anagoricophilus* (Pakaluk, 1986) and *Bystus* (Böving & Craighead, 1931; Costa, Vanin, & Casari-Chen, 1988, listed as *Rhymbus* which was synonymized by Strohecker, 1953; Lawrence, 1991) have been described or illustrated. Differences among these taxa, variation within *Bystus*, and lack of information on remaining immature stages prompted us to describe the immature stages in this paper.

The life history and behaviours of Endomychidae are poorly known, but most species are mycophagous, feeding upon spores and hyphae of a variety of fungal taxa (Arrow, 1925; Lawrence, 1991). Currently, the only known exception is the predator *Saula japonica* Gorham (Sasaji, 1978b). Also *Amphix* species may consume lichens and algae along with fungal food (Erwin & Erwin 1976; Leschen, personal observation). Lawrence (1991) reviewed in a general way the trophic behaviour of endomychids. Pakaluk (1986) mentioned that the larval gut of the mychothenine *Anagoricophilus* contained spores of an undetermined imperfect fungus. *Bystus* species also appear to be spore feeders.

Despite extraordinary diversity within the Endomychidae, life histories are known for only a few mycophagous species: *Lycoperdina ferruginea* LeConte (Eumorphinae; Pakaluk, 1984), *Endomychus biguttatus* Say (Endomychinae; Leschen & Carlton, 1988) and a Panamanian *Amphix* (Eumorphinae; Erwin & Erwin, 1976). Erwin & Erwin included information about the relationship between *Amphix* and its ectoparasitoid *Eurycoleus macularis* Chevrolat (Carabidae; Lebiini). The species *Mycetina perpulchra* (Newman) and *Aphorista vittata* (F.) associated with Coniophoraceae are noted in Hoebeke, Wheeler, & Gilbertson (1987).

METHOD

Specimens of *B. decorator* were collected in Peru during the dry season in a lowland rainforest reserve from 1 July to 19 July 1989. Larvae and adults were collected from host fungi and placed into cardboard rearing containers or petri dishes for observation. A dissecting microscope was used for observing behaviour. Laboratory observations were made during the day and night. Field observations were made daily.

Material was fixed in Trump's solution (Karnovsky, 1965) and later transferred to 70% alcohol. For serial sectioning, larvae were embedded either in Epon plastic or paraffin.

For sectioning in plastic, larvae were removed from alcohol and placed into a standard fix (2.5% Glutaraldehyde in 0.1 m Sodium Cacodylate at pH 7.4) for 24 hrs, followed by a 1:1 mixture of distilled water and 0.2 m Cacodylate buffer, washed twice in distilled water for 5 min each, then passed through a dehydration series to 100% alcohol. Specimens were infiltrated through a graded Epon:alcohol series to two changes of 100% Epon. After 24 hrs, specimens were transferred to Epon moulds and oven cooked at 67°C for 24 hrs. Serial sections were cut on a Sorvall MT2B microtome and mounted on microscope slides in Permount.

Paraffin sections were prepared by dehydrating through an ethanol-tetrahydrofuran series (Salhouse, 1958), then infiltrating and embedding at 56–58°C. Serial sections were cut in transverse, sagittal, and frontal planes at 10 µm. Sections were stained according to the procedure outlined by Schmitz (1967) and mounted on microscope slides in Permount.

Gross morphology of larvae was examined using whole mounts, scanning electron microscopy, and dissection. For whole mounts, larvae were decapitated and cleared either in Nesbitt's solution (Borror *et al.*, 1989), cold 10% KOH, or a combination of both. The first preparation enabled us to observe muscular and nervous tissue, and the combination of the two was useful for transmitted light observation of the chitin exoskeleton.

For scanning electron microscopy (SEM), larval specimens were sonicated for 10 seconds in alcohol, then dehydrated in acetone. The specimens were gold coated in a Hammer 2 sputter coater. A Philips 500 SEM was used for the examination.

Dissections were performed with the specimens immersed in glycerin-alcohol (1:1) by incising the cuticle along the dorsal midline using iridectomy scissors. The alimentary canal was severed and removed, and the fat body tissue was teased away from the thoracic musculature.

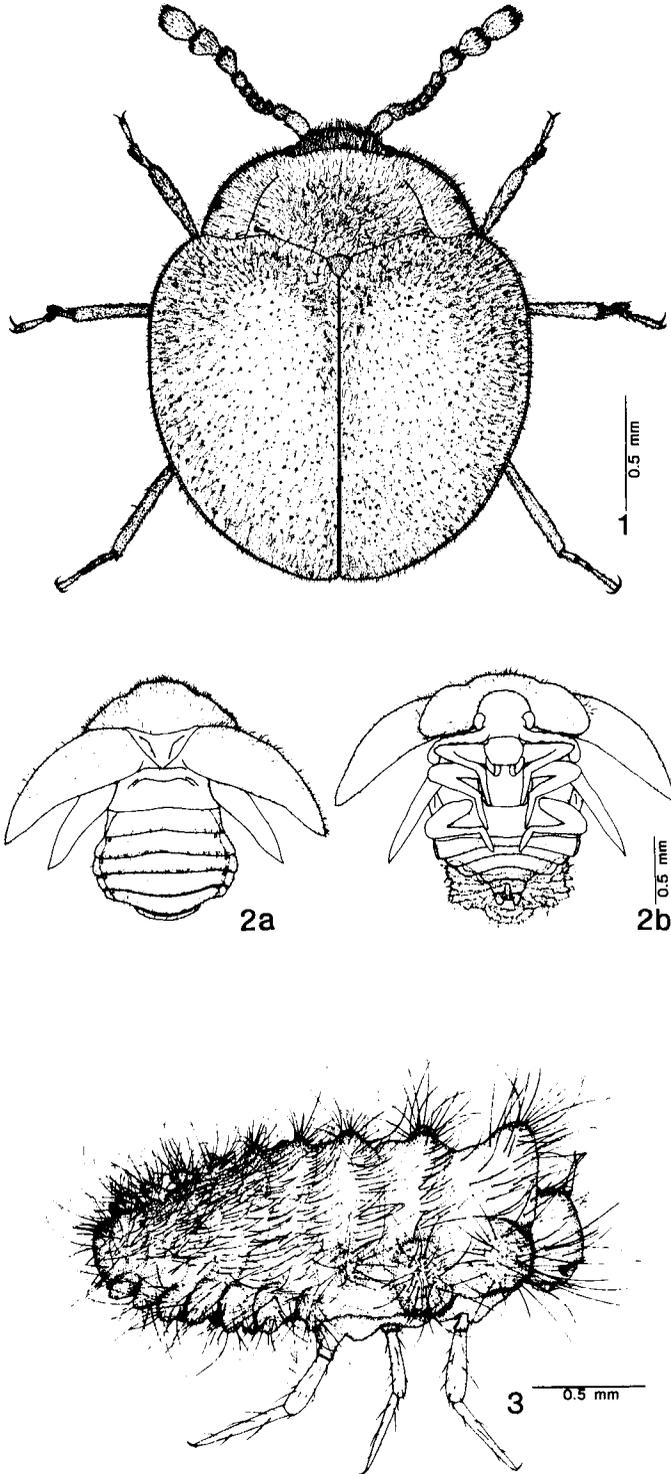
Measurements in the text are in millimeters.

Specimens are deposited in the following collections: R. Leschen Collection, Snow Entomological Museum Collection (Lawrence, Kansas, USA), University of Arkansas Arthropod Museum (Fayetteville, Arkansas, USA), Florida State Collection of Arthropods (Gainesville, Florida, USA), The National Museum of Natural History (Washington, D.C., USA), Museo de Historia Natural, Universidad de San Marcos (Lima, Peru), The Natural History Museum (London, UK), and the Museum d'Histoire Naturelle (Genève, Switzerland).

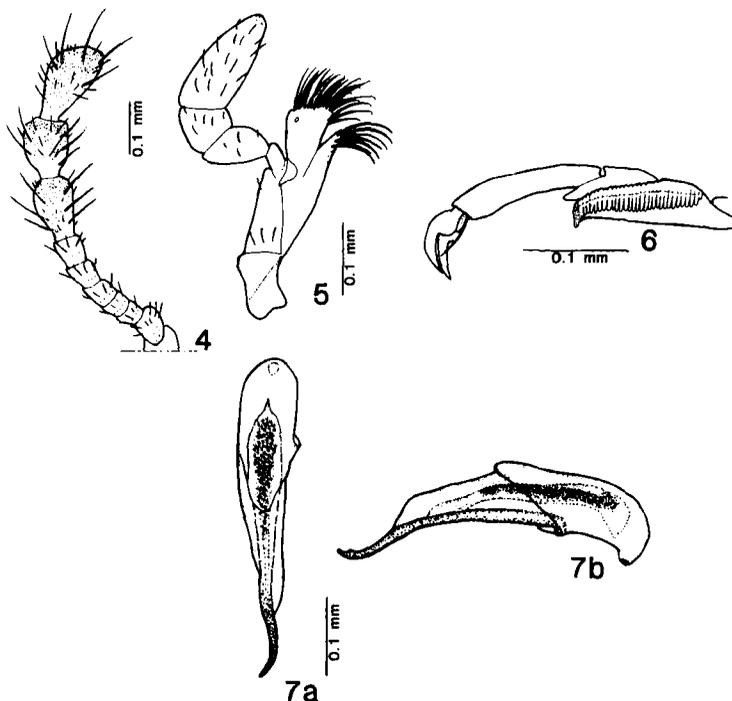
***Bystus decorator* sp. nov.**

(Figs 1–15)

Adult. With the characteristics of *Bystus* (Strohecker, 1953). Dimensions (x = means of type specimens): length (anterior of pronotum to apex of elytra) 1.65–2.45 (x = 1.98); width at base of pronotum 1.00–1.50 (x = 1.25); width of elytra 1.45–2.15 (x = 1.71). Dorsal surfaces light to dark brown in colour; lateral areas of pronotum lighter than disc in some specimens; elytral disc with a distinct light brown macula, humeral region light brown, contacting macula in some



Figs 1-3. *B. decorator* sp. nov. Fig. 1. Adult, dorsal view. Fig. 2. Pupa, dorsal (2a) and ventral (2b), attached last larval exuvium indicated on 2b by light stippling. Fig. 3. Late instar larva, dorso-lateral view.

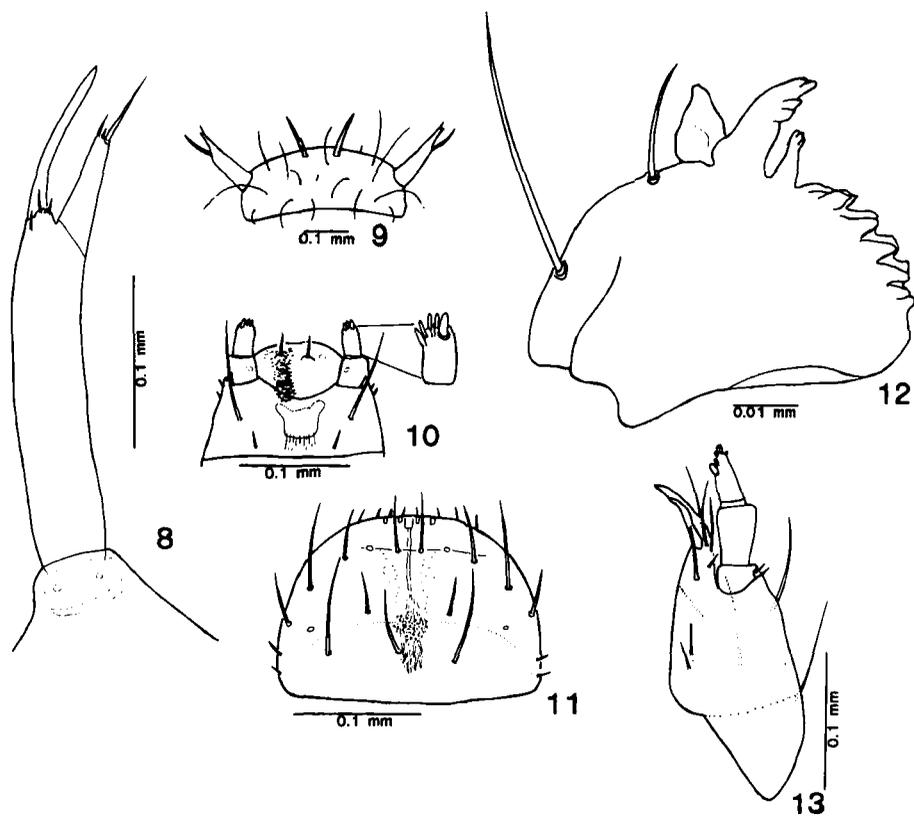


Figs 4–7. *B. decorator* sp. nov., adult. Fig. 4. Antenna. Fig. 5. Maxilla. Fig. 6. Male front tarsus. Fig. 7. Aedeagus, dorsal (7a) and lateral (7b) views.

specimens, lateral area of elytron light or dark brown; mouthparts, legs and epipleura light brown to yellow; antennomeres 1,2, and 5–10 dark brown, remaining segments light brown or yellow; venter often infuscate. Dorsal vestiture of long, erect setae, setae on head shorter than those on pronotum and elytra; ventral vestiture of decumbent setae. Head and pronotum with poorly defined microsculpture; disc of pronotum sparsely punctate; punctures separated by $4\times$ puncture width. Antebasal pronotal fovea well-developed. Elytron densely punctate; punctures $3\times$ larger than those on pronotal disc; punctures separated by $1/2$ puncture diameter. Antenna (Fig. 4) with antennomere 10 asymmetrical, slightly longer than 9. Maxilla with palpomere 3 normal in shape, not slightly expanded apically (Fig. 5). Male first leg tarsomere 1 bearing pectinate comb (Fig. 6); fifth visible sternite with posterior semicircular notch; aedeagus as shown (Fig. 7a,b).

Egg. Approximately 0.55 long, 0.31 wide; white, oval without microsculpture.

Larva (Figs 8–15). Dimensions (L=length, HW=head width, PW=prothoracic width, n=number examined, x=mean, and r=range): first instar ($n=4$): (L) $x=0.87$, $r=0.75$ – 1.0 ; (HW) $x=0.30$, $r=0.30$ – 0.31 ; (PW) $x=0.52$, $r=0.4$ – 0.7 . Second instar ($n=8$): (L) $x=1.05$, $r=0.70$ – 1.5 ; (HW) $x=0.41$, $r=0.40$ – 0.44 ; (PW) $x=0.77$, $r=0.60$ – 1.0 . Third instar ($n=19$): (L) $x=1.36$, $r=0.8$ – 1.7 ; (HW) $x=0.5$, $r=0.5$ – 0.56 ; (PW) $x=0.91$, $r=0.8$ – 1.0 . Fourth instar ($n=24$): (L) $x=2.0$, $r=1.35$ – 2.41 ; (HW) $x=0.67$, $r=0.60$ – 0.75 ; (PW) $x=1.29$, $r=1.0$ – 1.45 . Form dorsoventrally flattened. Body white throughout. Vestiture consisting of simple and modified barbed and hooked setae.



Figs 8–13. *B. decorator* sp. nov., larva. Fig. 8. Antenna. Fig. 9. First instar head capsule showing vertexal egg bursters. Fig. 10. Labium and detail of second palpomere and hypopharynx. Fig. 11. Epipharynx. Fig. 12. Mandible. Fig. 13. Maxilla.

Head hypognathous. Stemmata absent. Ecdysial lines absent. Antenna (Fig. 8) inserted posterodorsally in a membranous socket; article I (within socket) unisetose; article II 5 times longer than article I, asetose, bearing elongate sensory appendage; article III slightly shorter than sensory appendage, bearing 2 solenidia. First instar with two divergent and strongly sclerotized spinose egg bursters on vertex of head (Fig. 9). Labrum distinct (Fig. 10), posterior setal row composed of three setae. Anterior labral margin with four subcuticular glands. Epipharynx (Fig. 11) with anterior gutter connected to region of microtrichia by a small channel, microtrichial region followed by a basal region of spines. Mandibles (Fig. 12) virtually symmetrical; each with two lateral setae and a single dorsal pore, variously developed hyaline process anterior to 'molar region', molar region composed of an elongate incisor-like lobe, followed basally by middle prosthema-like process, three rows of five teeth, and laterally placed mandibular articulations. Maxilla (Fig. 13) with small membranous juxtacardo, triangular cardo, and elongate stipes. Mala composed of one large apical spur, one subapical spine, and three subapical setae. Maxillary palpus 3-segmented, article 1 with small basal seta, sensory area composed of one large and several small papillae. Hypopharynx (Fig. 10) composed of anterior region of microtrichia and small tubercles, sclerome composed of pits and small tubercles

at anterior edge. Labium (Fig. 10) with square submentum and transverse mentum. Labial palpus 2-segmented; article I unisetose; article II with campaniform sensilla. Venter of head with well-developed ridge extending posteriorly from the posterior mandibular articulation to beyond posterior antennal insertion.

Thoracic and abdominal terga without median ecdysal lines. Prothorax and mesothorax with well developed lateral lobes, these lobes 1/6 wider than those of the metathorax. Abdominal segments I-III subequal in width to metathorax, remaining abdominal segments gradually decreasing in width toward apex; pleural lobes present on abdominal segments I-VII. Ninth abdominal segment about 2/3 width of segment VIII, urogomphi absent, four dorsal setae present. Tenth abdominal segment (pygopod) short, trilobate. Spiracles annular and asetose; prothoracic spiracle located posteroventrally to prothoracic side lobe; abdominal spiracles dorsal to pleural lobes. Legs long, multisetose, similar, tarsungular setae simple.

Pupa. (Fig. 2a,b). Length $x=2.17$, $r=1.8-2.4$, white, exarate. Vestiture of simple setae. Head deflexed ventrad, not visible in dorsal view. Dorsal setae fine, erect, evenly distributed, longer on lateral margins of pronotum and elytra than on discs, shortest on abdominal tergites. Exuvia attached to abdomen by paired apical papillae. Spiracles located at anterolateral angles of abdominal terga 2-5.

Type material. HOLOTYPE adult male: PERU; Departamento Madre de Dios, Provincia Tambopata, Reserva Cuzco Amazónico, 15 km NE Puerto Maldonado, 12° 33'S, 69° 03'W, 200 m, ex red imperfect fungus, 10 July 1989, J. Ashe, R. Leschen (deposited in the Snow Entomological Museum). PARATYPES: same data as holotype, but 1 July (30 adults, 4 larvae); 4 July (33 adults, 6 larvae); 13 July (20 adults, 12 larvae); 19 July (11 adults, 9 larvae); 19 July (laboratory material originally collected 10 and 15 July): 95 adults, 37 larvae, 7 pupae, 2 eggs.

Comments. Specimens of *B. decorator* were compared to the types of 15 (of 18) described species of New World *Bystus*, and were compared to descriptions of the three remaining neotropical species. *Bystus decorator* can be distinguished from all species based upon the following combination of characters: colour light brown with central elytral macula, strong elytral punctation, decumbent setae present on disc and anterior region of metasternum, antennomere 10 slightly larger than 9, maxillary palpomere normal (not slightly securiform), antebasal pronotal fovea well developed, and the male fifth visible abdominal sternite apically notched. Most of the larger species of *Bystus* (greater than 2.5 mm) are red in colour and all we have examined lack the antebasal pronotal fovea. Some of the smaller species (the size of *B. decorator*) are black (e.g. *B. hirtulus* (Kirsch, 1876) or red brown (e.g. *B. bruchi* (Weise, 1905) and *B. drakei* (Weise, 1903), and lack the elytral and antennal colour patterns.

Eggs of *Bystus* are similar to those of *E. biguttatus* (Leschen & Carlton, 1988). The pupa differs from other described endomychid pupae (Bates, 1862; Costa, Vanin & Casari-Chen, 1988; Leschen & Carlton, 1988; Kemner, 1924; Pakaluk, 1984; Smith, 1886) by the absence of pedunculate setae or well-developed processes on the terminal abdominal segment.

Bystus larvae differ from those of *Mychothenus* and *Anagaricophilus* by the following characters: antennae (Fig. 8) with elongate sensory appendage (see Pakaluk, 1986); spines of mala (Fig. 13) not on a process; mandible (Fig. 12)

with laterally placed articulations; mola composed of a few rows of teeth; two mandibular setae; prothorax and mesothorax with well-developed lobes.

Pakaluk (1986) lists characters that separate mychothenine larvae from those of the remaining endomychids. One character that may be important for uniting mychothenines is the posterior row of three setae on the labrum (Fig. 11). This is an unusual feature, since setae are usually symmetrical between body halves. This character occurs in *Bystus*, *Anagaricophilus*, and undetermined Mexican mychothenines. Costa *et al.* (1988) show four setae in this row, possibly in error.

Other interesting features are the first instar larval egg bursters on the vertex of the head (Fig. 9). In first instar *E. biguttatus* the egg bursters are small spines at the edge of the pronotum. Within the cerylonid series, egg bursters are only known in Coccinellidae where they occur as paired processes on the pronotum (Van Emden, 1949).

Bystus decorator larvae can be distinguished from other described *Bystus* by the presence of 'premolar' hyaline processes, spines, and absence of stemmata. Presence of modified setae could have been overlooked by Costa *et al.* (1988). Lawrence (1991) and Costa *et al.* (1988) show in their illustrations of *Bystus* spp. genitalic lobes on the last two abdominal segments. These lobes are absent from our specimens.

The mandibles (Fig. 12) of *B. decorator* larvae are variable. The hyaline processes that are present are often asymmetrical, and all look contorted and twisted, suggesting that they are a thin membrane. The function of these processes is unknown. The 'molar' teeth are also variable, with the first and second sets separated by a space from the remaining sets. The homologies of these sets of teeth are difficult to ascertain, but it appears that at least the molar region is retained in all mychothenines. Differentiation of the prostheca and incisor lobes, if they are present, is not possible.

MORPHOLOGY

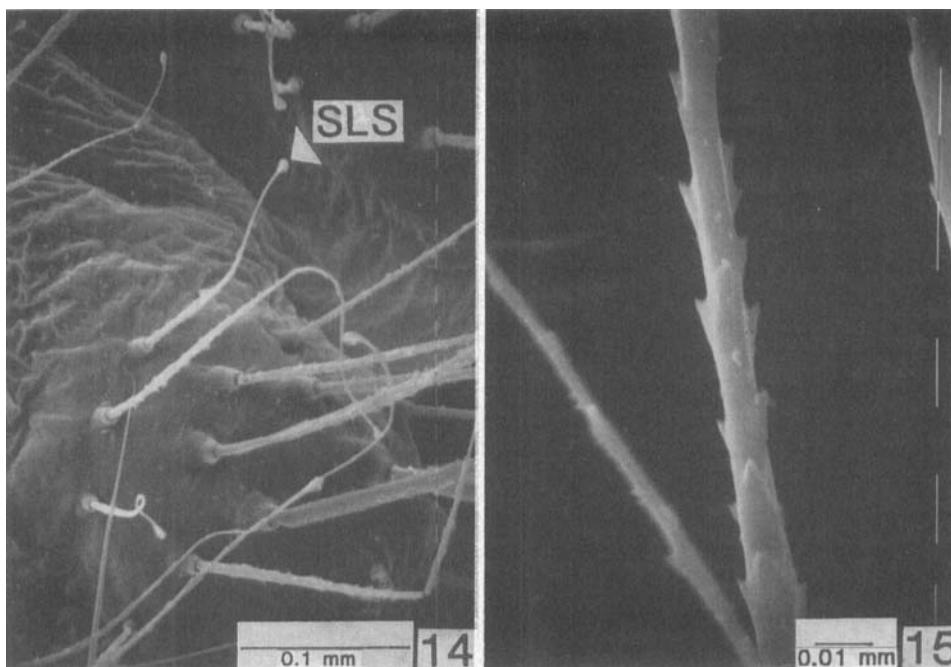
Description of Setae

This section describes the vestiture of larval *Bystus* that assists in debris cloaking. Although the integument is covered with asperities, it is highly improbable that debris comes into contact with anything other than the setae.

There are three morphological types of setae that make up the vestiture of *B. decorator* larvae. Simple setae occur on the head, the legs and the venter. There are two types of modified setae. All modified setae are barbed along the setal shaft (Fig. 15), and these are found predominantly on the dorsal part of the larva. Type I setae (Fig. 14) are whip-like and terminate to a flared spoon-like structure (SLS), and appear clubbed or recurved. Type I setae are located at the head vertex and over all dorsal surfaces. The SLS is composed of a flared end bearing a gutter that runs a shorter distance along the shaft and terminates into a reservoir at the inferior surface of the spoon.

Type II setae are similar to Type I setae except they are not whip-like and lack the SLS. Type II setae are located at the head vertex, the anterior and posterior prothoracic and mesothoracic lobes, at the posterior abdominal pleural lobes, and at the ventral lateral aspects of the abdominal segments.

Modified setae are distributed mainly at the dorsal areas of the body and occur in a variety of sizes. The longest of these setae are restricted to the margins



Figs 14-15. *B. decorator* sp. nov., larval setae. Fig. 14. Type I setae on prothoracic lobe. Fig. 15. Detail of barbed setal shaft. SLS, spoon-like structure.

of the thorax and the abdomen. Shorter modified setae are located on the vertex of the head (only one row) and the discs of the thoracic and abdominal terga.

Comments. The short modified setae may function in securing debris to the dorsum, and the long modified setae may function during grasping and arranging debris during cloaking. The barbs of the setae seem to play a role in securing the debris in place by providing an irregular surface for greater friction. Barbed setae also occur in some debris cloaking chrysopid and reduviid larvae (Tauber, 1975; personal observation).

The function of the SLS is enigmatic. The only glands we observed were subcuticular glands located at the base of the setae. These glands appeared to be typical setal secreting glands, although glands at the base of some chrysopid larval setae have also been attributed to some debris adherence function (Lurie, 1898, cited in Killington, 1936). Lurie (1898) also observed that the setae of chrysopid larvae are hollow. We cannot determine if the modified setae are hollow, and they appear similar to setae in many other Coleoptera larvae.

Eisner *et al.* (1978) reported observations on a chrysopid larva that cloaks itself with wax collected from woolly alder aphids (*Paraprociophilus tessellatus* (Fitch), Homoptera). The setae of this species of *Chrysopa* are hooked (as well as other chrysopid larvae [Killington, 1936; Tauber, 1975]), and are considered by these researchers to function in the retention of the wax shield. Thus the clubbed setae of chrysopids and *B. decorator* may function similarly. Killington (1936) noted that the body form of chrysopid larvae is broad and flattened, which he believed to be an adaptation to debris cloaking. The body form of *Bystus* larvae is similarly shaped to the extent that, in both groups, only the prothorax and mesothorax have elongate lobes.

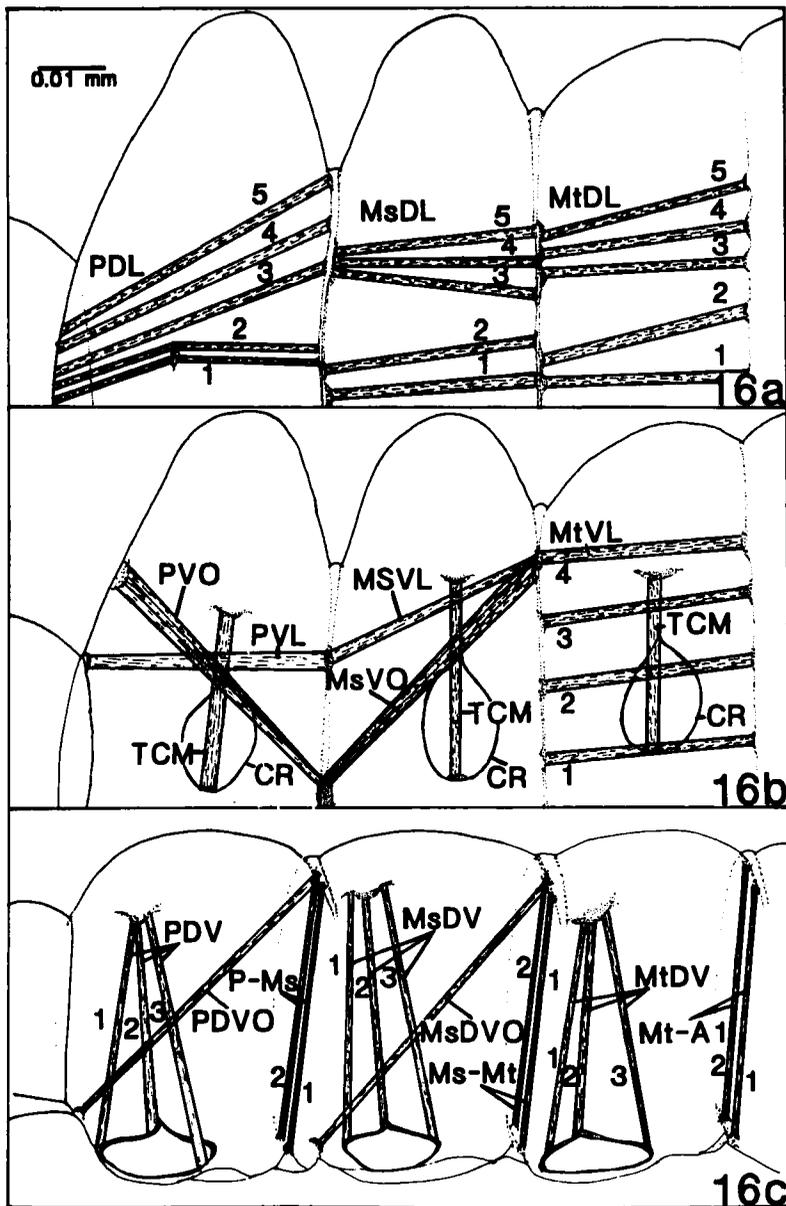


Fig. 16. *B. decorator* sp. nov., larval thoracic musculature. 16a, dorsal muscles, dorsal view. 16b, ventral muscles, dorsal view. 16c, dorsoventral muscles, slightly oblique lateral view. Cr, coxal ring; Ms-Mt, meso-metathoracic dorso-ventral muscles; MsDL, mesothoracic dorsal longitudinal muscles; MsDV, mesothoracic dorsoventral muscles; MSDVO, mesothoracic dorsoventral oblique muscle; MsVL, mesothoracic ventral longitudinal muscle; MsVO, mesothoracic ventral oblique muscles; MT-A1, metathoracic-first abdominal dorsoventral muscle; MtDL, metathoracic dorsal longitudinal muscles; MtDV, metathoracic dorsoventral muscles; MTVL, metathoracic ventral longitudinal muscles; PDV, prothoracic dorsoventral muscles; P-Ms, pro-mesothoracic dorsoventral muscles; PDVO, prothoracic dorsoventral oblique muscle; PVL, prothoracic ventral longitudinal muscle; PVO, prothoracic ventral oblique muscle; TCM, transverse coxal muscles.

Thoracic musculature

The musculature of the thoracic body cavity of *B. decorator* larvae (Fig. 16a,b,c) was studied to gain a better understanding of the movements involved in the debris cloaking behaviour. The thoracic musculature consists of dorsal longitudinal, ventral longitudinal and dorsoventral muscle groups, and several major oblique and transverse muscles. Terms describing individual muscles are based on their location and orientation within the body, not their presumed function. Numerals refer to the position of the muscles in series, from median to lateral in transverse series of longitudinal muscles, and anterior to posterior in longitudinal series of dorsoventral muscles. All muscles described are paired. Descriptions of muscle function are based on the presumed movements at the points of attachment and the potential effects of hydrostatic pressure, limb anchoring and muscle interaction.

Dorsal musculature (Fig. 16a). A series of five longitudinal muscles occurs in each thoracic segment; they are designated pro-, meso- and metathoracic dorsal longitudinal muscles 1–5 (PDL 1–5; MsDL 1–5; MtDL 1–5). PDL 1–5 insert along the dorsal margin of the occipital foramen of the head capsule and diverge to origins along the anterodorsal aspect of the promesothoracic intersegmental apodeme. MsDL 1–2 and MsDL 3–5 have a pair of common insertions on the posterodorsal aspect of the pro-mesothoracic intersegmental apodeme and diverge to separate origins along the anterodorsal aspect of the meso-metathoracic intersegmental apodeme. Arrangement of the MtDL is similar to that of the MsDL.

Ventral musculature (Fig. 16b). The ventral pro-mesothoracic musculature is dominated by a cross-shaped arrangement of muscle fibres (in dorsal view) that originate from a common intercoxal apodeme at the pro-mesothoracic midline. One pair, the prothoracic ventral oblique muscles (PVO) diverge anteriorly to insertions at cuticular apodemes on the ventrolateral aspects of the prothoracic lobes. The other pair, the mesothoracic ventral oblique muscles (MsVO), diverge posteriorly to insertions on the posterolateral aspects of the mesothoracic lobes. Each bundle in this cross-shaped configuration consists of three to four partially fused muscle fibres. The prothoracic ventral longitudinal muscle (PVL) inserts on the ventrolateral aspect of the occipital foramen and extends to the pro-mesothoracic intersegmental apodeme, where it is continuous with the mesothoracic ventral longitudinal muscle (MsVL), which in turn extends to the meso-metathoracic intersegmental apodeme. The metathoracic longitudinal muscles are arranged as a series of four delicate muscles (MtVL 1–4) sub-equally spaced from the midline. A transverse coxal muscle (TCM) originates from a cuticular apodeme on the ventrolateral aspect of each thoracic lobe and inserts on the mesial margin of the coxal ring (CR).

Dorsoventral musculature (Fig. 16c). The major dorsoventral muscles of each segment are arranged as a tripod, diverging from a common origin at a cuticular apodeme on the anterodorsal aspect of the thoracic lobes, to insertions on the anterior, lateral and posterior margins of the coxal ring (PDV 1–3; MsDV 1–3; MtDV 1–3). A dorsoventral oblique muscle occurs in the pro- and mesothorax (PDVO, MsDVO), extending from an anteroventral intersegmental apodeme to a dorsolateral cuticular apodeme. Each intersegmental region contains two dorsoventral muscles in transverse series (P-Ms 1–2; Ms-Mt 1–2; Mt-Al 1–2).

Comments. The muscles of the pro- and mesothorax are slightly larger and their arrangement is more complex than those of the metathorax, features that are probably related to the greater mobility requirements of the anterior end of the body, including head movement, turning and debris cloaking. The latter action is accomplished primarily by bringing the pro- and mesothoracic lobes into contact with the substrate, a process referred to here as pronation.

Contraction of the longitudinal muscles shortens the longitudinal axis of the body. Contraction of these muscles on one side of the body, accompanied by relaxation of the other side, results in turning as a consequence of the displacement of hemolymph to the relaxed side and shortening of the contracted side. Contraction of the prothoracic dorsal longitudinal muscles elevates the head capsule or assists in turning it. Contraction of either dorsal or ventral longitudinal muscle groups results in arching. The cross-shaped arrangement of pro- and mesothoracic ventral oblique muscles and adjacent longitudinal muscles plays a role in pronation by pulling the head capsule to an opisthognathous position beneath the prothorax. Sequential contraction of the longitudinal muscles of each body segment contributes to peristaltic-like body movements.

Coordinated movements of the dorsoventral muscles 1-3 and the transverse ventral muscles that insert on the coxal ring extend and rotate the coxa if the legs are free of the substrate. Contraction of the dorsoventral muscles compresses the dorsoventral axis of the segment if the legs are firmly anchored to the substrate. The anterodorsal origin of these muscles results in anterior movement of the lobe during contraction, an action that plays a role in pronation. The transverse coxal muscle pulls the coxa mesially, and may serve to lock the leg in position during anchoring. It may also contribute to thoracic lobe pronation by further contracting the ventral area of the thorax and expanding the dorsal area.

This analysis of muscle function suggests that pronation of the pro- and mesothoracic lobes involves the following: (1) contraction of ventral oblique, transverse coxal and ventral longitudinal muscles and relaxation of dorsal longitudinal muscles; (2) anchoring of legs to substrate; and (3) contraction of pro- and mesothoracic dorsoventral muscle groups.

Although the abdominal musculature was not examined in detail, it appeared to be dominated by rather massive intersegmental dorsal and ventral longitudinal muscles, in addition to a small number of delicate dorsoventral muscles. Aside from a gradual reduction in size, the arrangement of abdominal muscles did not appear to vary among segments.

The only study of cucujoid larval musculature available for comparison is that of Böving & Rosen (1962) for the nitidulid *Lobiopa insularis* (Castelnau), a much larger and more sclerotized beetle (full grown length about 15 mm). One important correction to their published manuscript should be noted: figures 4 and 8 are reversed, since figure 4 clearly illustrates the ventral musculature and figure 8 the dorsal.

The most obvious difference between the thoracic musculature of *B. decorator* and *L. insularis* is the greater complexity of the musculature in the latter. Since consolidation and reduction is a trend commonly associated with comparatively smaller organisms, this is not surprising. A further contributing factor may be that some of the smaller muscles of *B. decorator* were overlooked during our dissections and serial section analysis. Muscles that originate in the ventral

intersegmental regions of *L. insularis* attach to heavily sclerotized furcasterna or radiate from the spinasterna. By contrast, the similar muscles of *B. decorator* attach directly to the body wall, which is non-sclerotized and only slightly thickened between the segments. Only the mesothorax possesses an obvious spinasternal apodeme that serves as the origin for a radiating arrangement of muscles. Böving and Rozen (1962) depict a complex system of coxal rotators originating on the pleural region and furcasternum of each segment and inserting at various points around the coxal ring. These coxal rotators were not found in *B. decorator*. They may have been overlooked, or, if they are indeed absent, coxal movements may be accomplished by coordinated contraction of the dorsoventral and transverse coxal muscles that insert around the coxal ring.

BIOLOGY

Life history

The rainforest at the type locality is strongly affected by flooding of the Madre de Dios River during the rainy season. Despite these floods there is a well-developed canopy and understory. Additional information about this locality is found in Duellman & Koechlin (1991). Adults of *Bystus* spp. are usually collected in association with fungal growth on the surfaces of rotting wood, or on the sporocarps of Basidiomycetes. In Peru, all life stages of *B. decorator* were observed feeding on an undetermined fungus encrusting the surface of rotting logs. This fungus consists of a mat of white mycelium that produces dense layers of brick-red spores that appear as red blotches from a distance of several metres. The brick red fungus serves as a host for two additional *Bystus* spp. (one from Costa Rica, another from Peru). Adults of the North American species *Clemmus minor* Crotch also fed upon this fungus in the laboratory.

Based upon existing collections, New World mychothenines are usually taken in low numbers from fungi, sift samples and rotting wood. On several occasions, series of *Clemmus minor* have been collected from spore fields on decaying trees or fallen rotten logs, but such concentrations are unusual. Likewise the large population of *B. decorator* in Peru may have been an unusual occurrence.

Gut contents of most individuals (adults and larvae) of mychothenines are filled with spores (Pakaluk, 1986; Leschen, personal observation), indicating that members of the subfamily may be obligate spore feeders. The adult mandibles of *Bystus*, *Clemmus* and other genera appear typical for spore feeders and are composed of a bifid apical incisor lobe, a brushy prosthema and a well-developed molar region (see Lawrence, 1991). Based upon published illustrations and available material, larval mychothenines often have the incisor lobe reduced or completely absent (e.g. *Mychothenus*, Sasaji, 1978a; *Anagaricophilus*, Pakaluk, 1986). The lack of a well-developed incisor lobe may indicate a strong functional association to sporophagy in some beetle groups (Lawrence, 1991; Leschen, 1992).

Adults and larvae of *B. decorator* sp. were discovered grazing upon the red fungus on 1 July 1989. The fungus was growing on a fallen log with the bark largely rotted off. The log was broken in four places, and the total length of the log was about 22.5 m. Beetle larvae were concentrated near broken edges of the log in two locations. The red fungus was the most common sporulating fungus growing on the log. An undetermined basidiomycete (Exidiales) was also present

on the log. The fallen log was located in a region of dense foliage, and the forest received about 2% direct sunlight at mid-day. The log was inspected daily from 1 July to 19 July.

Mating was observed repeatedly from 4 to 19 July. Mating position was typical for Coleoptera in that the male grasped the dorsum of the female. The pectinate comb of the male (Fig. 6) was not observed to be used in any special way.

A first instar larva collected on July 11 was found with an egg attached to its setae on the left pronotal margin.

Based upon measurements of head capsule width and assuming Dyar's Rule, there are four larval instars (described below). Since individual larvae were not separated during observation, durations of instars are unknown. Larvae of all instars were covered with debris (e.g. frass, wood fragments and unidentified debris), a habit that is discussed in more detail below. Adults and larvae exhibited no pattern of diel activity.

Seven pupae were recovered between 15 July and 19 July. Pupae were attached to the substrate, with anus flat against substrate. The last larval exuvium remained attached at the anus. The pupae rotated when disturbed, pivoting on the pygopod.

Comments. In contrast to *Endomychus biguttatus*, the egg of *B. decorator* is not concealed by adults at oviposition (Leschen & Carlton, 1988). Since an egg was found attached to a larva, it appears that females lay eggs singly on the surface of the feeding substrate. This habit is similar to that of the corylophid *Sericoderus lateralis* (Gyllenhal) (Hinton, 1944).

Pupal attachment to the substrate by the prepupal exuvium is similar to the habits of *Amphix* (Bates, 1862; Erwin & Erwin, 1976), many coccinellid larvae of the subfamilies Coccinellinae and Sticholodotinae (Hodek, 1973) and some Corylophidae (Hinton, 1944; Leschen, personal observation).

Presence of four larval instars is consistent with Leschen & Carlton's (1988) observations of *E. biguttatus* and four is the number of instars for most larval Coccinellidae (Hodek, 1973) and the cerylonid *Murmidius ovalis* (Beck) (Halstead, 1968). However, other members of the Cucujoidea are known to have three larval instars (Phalacridae, Steiner & Singh, 1987; Cryptophagidae, Hinton & Stephen, 1941; Erotylidae *et al.*, 1991; Corylophidae, Heeger, 1844 cited in Hinton, 1944; and Latridiidae, Hinton, 1945). Hinton (1945) states that there are 'probably three molts' in *Carpophilus hemipterus* (Linnaeus) and *C. dimidiatus* (Fabricius). Based upon the occurrence of three instars within the more primitive Cucujoidea, four larval instars may be a synapomorphy for the cerylonid series.

Debris cloaking behaviour

Larvae were observed to pick up debris in the following manner: after approaching a particle, the larva flexed the head to an opisthognathous position against the procoxae. This was followed by a pronation of the anterior pronotal lobes downward and forward, bringing them into contact with the substrate. Debris adhered to setae on the pronotal lobes. When the head and pronotum returned to their normal positions, the debris was positioned above the head on the pronotum. This debris was then shifted posteriorly and adjusted by peristaltic-like motions of the thorax and abdomen to the desired location on the body.

Mychothenine larvae of two unknown species were observed in Mexico. They also collected debris but behaved somewhat differently. In one, debris was collected only by passive contact of particles and setae, without the special manoeuvres observed in *B. decorator*. The other larva tested debris particles, possibly for assessing size. This behaviour involved lifting the debris particle with the mouthparts and manipulating it with the front legs. Inappropriate particles were abandoned. However, if the particle was appropriate, the larva lowered its head and the debris adhered to the modified setae on the head (different from *B. decorator*). The debris was transferred to the anterior portion of the pronotal disc when the head was raised. Thoracic and abdominal movements were minimal. The setae of both of these larvae lack barbs on the setal shafts.

Behaviours for chrysopid larvae reported by Killington (1936) and Eisner *et al.* (1978) included peristaltic movements for positioning debris and debris testing by the mouthparts and forelegs. Both behaviours are exhibited by cloaking mychothenines, but there exists considerable variation in behaviours among mychothenine species.

Eisner *et al.* (1978) showed that in *Chrysopa slossonae*, wax collected from woolly alder aphids was used as protection from predatory ants. When the wax material was removed from the larva, wax replenishing and feeding were given equal priority. By contrast, *B. decorator* larvae eventually stopped collecting debris after it had been removed several times.

Debris cloaking has evolved several times within Chrysopidae (Tauber, 1975), possibly in Sisyridae (Killington, 1936), in Lepidoptera (Ferguson, 1985), in Reduviidae (Butler, 1923) and in Mychotheninae. Debris cloaking and other mimicry behaviours are thought to have evolved as a defence against predators for prey, or as a disguise against detection by prey for predators. Experimental data presented by Eisner *et al.* (1978) for *Chrysopa slossonae* support this argument.

We cannot attribute debris cloaking as an evolved behaviour for predator defence in *B. decorator* until more is known about mychothenine behaviour and the potential predators in its microhabitat. A feature that may be shared by all debris cloaking taxa is that they are active on open substrates, independent of their trophic status (predator or prey).

The Mexican mychothenine larvae noted above possess smooth-shafted, whip-like setae with modified tips, lacking the characteristic setal barbs that occur in *B. decorator*, such that the overall vestiture is composed mainly of simple setae. Other described mychothenine larvae also lack barbed setae. It is conceivable that debris cloaking evolved first, followed by morphological elaboration, or we may have overestimated the functional significance of barbed setae. We will be better able to understand the evolution of mychothenine debris cloaking when more taxa have been studied and the behaviours involved can be evaluated in a phylogenetic context.

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