INTRODUCTION

Endomychidae is a relatively large and diverse family of Cucujoidea with approximately 1300 species in 120 genera (Lawrence 1991). The family, although represented throughout the world, is most diverse in the New World tropics, equatorial Africa, and southeast Asia. Within Endomychidae, the subfamily Anamorphinae is a relatively large, heterogeneous group of approximately 164 species in 35 genera. Most anamorphine species share the following characteristics: small size, relatively simple tarsi, and a coccinellid-like dorsal habitus.

All endomychid subfamilies except Danascelinae include at least one taxon with a larval description; however, many remain poorly documented in the literature. Pakaluk (1986) identified a number of characters that readily distinguish anamorphine larvae from concomillials, including the following: body with simple setae and no tergal plates; head lacking frontal sutures and stemmata; mandible lacking complete apex but having mola armed with distinct rows of denticles; maxillary mala falciform. Within Anamorphinae, larvae have been described or illustrated for only seven species representing four genera, most from the genus Bystus Guérin-Méneville (Table 1). The biology of anamorphine larvae is poorly known, but Pakaluk (1986) noted the presence of spores in the digestive tract of a species of Anagaricophilus Arrow. Leschen and Carlton (1993) speculated that members of the subfamily may be obligate spore feeders as adults and larvae. Burakowski and Ślipiński (2000) reported that anamorphine larvae are often collected on polypore fungi and noted the presence of anamorphines in decaying leaf litter and rotting wood. It seems probable that they are sporophagous in these habitats as well.

The Holarctic genus Symbiotes was erected by Redtenbacher (1849) for a distinct new endomychid species, S. latus. This beetle is often collected in association with ants (Hölldobler and Wilson 1990), and it is likely that the generic name was based on the assumption of obligate myrmecophily. Symbiotes species feed primarily on the spores of fungi (Walton 1912), and it is likely that S. latus also feeds on fungal spores inside ant nests. Currently, there are five valid species of Symbiotes (Strohecker 1953, 1986). Two species are endemic to the Palearctic region (S. armatus Reitter and S. latus Redtenbacher) and two are endemic to the Nearctic region (S. duryi Blatchley and S. impressus Dury). Symbiotes gibberosus (Lucas) is endemic to the Palearctic, but has now become widespread across the Nearctic region (Strohecker 1981), presumably due to human activity (Strohecker 1981).
MATERIALS AND METHODS

A single larva of *Symbiotes gibberosus* was identified by association with adult and dissected for illustration. The larva was preserved in glycerine, and all structures were illustrated using a camera lucida attached to an SZH 10 Olympus dissecting microscope. The disarticulated larva is deposited at the Museum and Institute of Zoology, Polish Academy of Sciences in Warszawa, Poland (MIZ).

DESCRIPTION OF MATURE LARVA

*Symbiotes gibberosus* (Lucas) (Figs 1–7)


**Description.** Length 3.15 mm; head width 0.62 mm; maximum width of thorax 1.10 mm; maximum width of abdomen 1.30 mm. Body elongate-oval, dorsoventrally flattened; widest across abdominal segment II, weakly tapering anteriorly and posteriorly; constricted between segments; urogomphi absent (Fig. 1). Dorsum and venter very lightly pigmented; mandible and apical half of tarsal claw dark brown. Vestiture simple, longer and denser on sides of body; ventral surfaces provided with sparse, simple setae; legs covered with sparse, long, pointed setae.

Table 1. Published descriptions or illustrations of larvae of Anamorphinae. D = Description (full or partial); DH = Dorsal Habitus; VH = Ventral Habitus; LH = Lateral Habitus; M = Mouthparts; A = Antenna; L = Leg (entire or partial).

<table>
<thead>
<tr>
<th>Species</th>
<th>Reference</th>
<th>Description/illustration(s) provided</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anagaricophilus sp.</td>
<td>Pakaluk 1986</td>
<td>X X X X X</td>
<td>314</td>
</tr>
<tr>
<td>Bystus decorator</td>
<td>Leschen and Carlton 1993</td>
<td>X X X X X</td>
<td>38, 40</td>
</tr>
<tr>
<td>Bystus pallidulus</td>
<td>Costa et al. 1988</td>
<td>X X X X X</td>
<td>201, pl. 96</td>
</tr>
<tr>
<td>Bystus ulkei</td>
<td>Boving and Craighead 1930</td>
<td>X X X X X</td>
<td>pl. 40</td>
</tr>
<tr>
<td>Bystus ulkei</td>
<td>Chu and Cutkomp 1992</td>
<td>X X X X X</td>
<td>224</td>
</tr>
<tr>
<td>Bystus sp.</td>
<td>Lawrence 1991</td>
<td>X X X X X</td>
<td>483</td>
</tr>
<tr>
<td>Idiophyes niponensis</td>
<td>Hayashi 1992</td>
<td>X X X X X</td>
<td>120</td>
</tr>
<tr>
<td>Mychothenus asiaticus</td>
<td>Sasaji 1978</td>
<td>X X X X X</td>
<td>7</td>
</tr>
<tr>
<td>Symbiotes gibberosus</td>
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Head hypognathous, strongly transverse, moderately flattened dorsoventrally; dorsally about 0.50 times as long as wide and 0.65 times as wide as prothorax (Fig. 4). Frontal arms absent. Stemmata absent. Hypostomal rods long and stout, divergent posteriorly. Fronto-clypeal suture absent. Labrum about as long as wide, sclerotized, free with anterior margin deeply emarginate, covered with numerous...
longer and shorter pointed setae. Antenna 3-segmented, short, stout (Fig. 3), surface weakly microgranulate; inserted posterolaterally in a membranous pocket near mandibular articulations. Antennomere I partially concealed, without setae, about 0.5 times as long as antennomere II and subequal to III; antennomere II covered with numerous short setae; antennomere III with long, terminal seta of the same length; sensorium weakly tapering towards apex, longer than antennomere III but shorter than antennomere III and its terminal seta together. Mandibles transverse, symmetrical, each with two dorsolateral setae and bearing a hyaline, protheca-like process anterior to mola; incisor lobe absent; mola well-developed with distinct rows of transverse, sclerotized ridges (Fig. 6). Maxillolabial complex retracted. Maxilla with cardo subtriangular; stipes elongate with 1 seta along outer edge; mala apically produced with 2 stout spurs and 3 flattened setose projections; maxillary palpi small, 3-segmented; palpomeres I and II transverse, equal in length; terminal palpomere about as long as 1 and 2 combined, weakly tapering, blunt at apex, and bearing a group of short, apical sensory processes (Fig. 5). Labium undivided; labial palpomere 2-segmented; palpomere I without setae, about 0.5 times shorter than terminal palpomere; terminal palpomere subcylindrical, blunt at apex with a group of apical sensillae (Fig. 2). Hypopharynx with sclerotized hypopharyngeal sclerome, bracon and parallel hypopharyngeal rods; submembranous anterior portion covered with 2 convergent anteriorly rows of short setae directed inwardly.

Thorax about 1/3 as long as total body length, widest across metathorax; meso- and metathorax equal in length and 2/3 as long as prothorax. Thoracic and abdominal terga without median ecdyssial lines (Fig. 1). Abdomen widest across segment II, gradually tapering apically; small pleural lobes present on abdominal segments I-VIII; segment IX 2/3 as wide as segment VIII, with posterior margin rounded and covered with long setae, urogomphi absent; segment X short, directed ventrad (Fig. 1). Spiracles small, annular, anterodorsal of pleural lobes. Leg with coxae widely separated basally, coxa with a few pointed setae, longer than trochanter and femur combined; trochanter elongate, with 2 mesal setae; femur cylindrical, about twice as long as wide, with 2 inner and 2 outer setae; tibiotarsus subequal in length to femur, weakly narrowing towards apex, bearing sparse, pointed setae; tarsungulus with a single, long, pointed seta.
sharp claw; claw with apical half strongly sclerotized, bearing single, short seta ventrally (Fig. 7).


**DISCUSSION**

Although it is difficult to generalize about anamorphine larval anatomy with so few taxa known, there are some interesting aspects of their morphological diversity that are noteworthy. Beutel et al. (2000) suggested that a triangular head and posteriorly-shifted antennae were larval synapomorphies supporting the family Endomychidae. He proposed that both were correlated with the hypognathous condition of many endomychid larvae; however, the degree to which the antennae are shifted appears to be variable in Anamorphinae. In *Bystus* spp. and *Mycothenus asiaticus*, the antennal bases are located near the posterior angles of the head. The antennae in *Symbiotes gibberosus* and *Idiophyes niponensis* (Gorham) are shifted less posteriorly than those of *Bystus* and *Mycothenus*. This feature may have some phylogenetic significance, but at present there are too few anamorphine larvae known to address this question.

Leschen and Carlton (1993) suggested that the transverse row of three setae along the base of the labrum (a feature found in *Bystus decorator*) was potentially important as an additional character for recognizing anamorphic larvae. Burakowski and Ślipiński (2000) and Tomaszewksa (2000) questioned the reliability and uniformity of this character for all larvae of Anamorphinae. Costa et al. (1988) showed four setae in this row in *B. pallidulus* (Gerstaecker).

A family-level phylogenetic study of the Endomychidae (Tomaszewksa 2005) found that the reduced or absent mandibular apex in larvae of Anamorphinae is derived only once within the family and readily separates anamorphic larvae from the larvae of the other endomychid subfamilies.

Within Anamorphinae, the genera for which larvae are known each have at least one unique feature or a combination of characters that readily distinguishes their larvae from each other. Sasaji (1978) described the larva of *Mycothenus asiaticus* as having the tibiotalus bearing elongate, paired, spatulate setae apically and antennomere III highly reduced and indistinct. The remaining anamorphines have simple setae on the tibiotalus and a distinct antennomere III that ranges in size from being half the length of the sensorium in some taxa, to being subequal to it in others. Hayashi (1992) illustrated the maxillary mala of *Idiophyes niponensis* as having capitate setae, a feature shared with the *Agaricophilus* larva illustrated and described by Pakaluk (1986). All other known anamorphines have only simple setae on the mala. The condition of antennomere III in *Idiophyes* (i.e., subequal in length to the sensorium) readily separates this genus from *Anagaricophilus*. Burakowski and Ślipiński (2000) recognized that antennomere II was unusually elongate (i.e., length 4 times width) in *Bystus* larvae. All other known anamorphic larvae have antennomere II no more than twice as long as wide.

The condition of the stemmata in the larvae of Anamorphinae is somewhat variable. Stemmata are absent in most anamorphic larvae, but stemmata may be present as a single pair in some *Bystus* spp. (e.g., *B. ulkei* and *B. pallidulus*). The condition of the lobes on the dorsum of the abdomen may also vary. The larvae of some *Bystus* spp. have prominent dorsal lobes on all abdominal segments (e.g., *B. decorator* and *B. pallidulus*), but *B. ulkei* larvae lack these lobes entirely. Similarly, *B. pallidulus* and the unidentified *Bystus* larva illustrated by Lawrence (1991) both have an additional pair of mesal genitalic lobes on abdominal segments VIII and IX. These lobes are absent in the larvae of *B. ulkei* and *B. decorator*. Most anamorphic larvae lack both types of these lobes, including *Symbiotes gibberosus*.

Interestingly, the mandibles of *Symbiotes gibberosus* lack an incisor lobe and bear a thin, membranous pre-molar hyaline process anteriorly, most likely a remnant of the prosthica. This feature was also described by Leschen and Carlton (1993) for *Bystus decorator*, but it does not occur in the other two known *Bystus* larvae or in the other three anamorphic genera with known larvae. It remains unclear what function, if any, this process may serve in their larvae or in the other three anamorphic subfamilies.

**Key to the known larvae of Anamorphinae**

1. Antennomere II short, 1–2 times as long as broad (Fig. 3) .................................................. 2

   – Antennomere II very long, 4 times as long as broad .................................................. 5

2. Antennomere III reduced, antenna appearing 2-segmented ........................................ Mycothenus asiaticus

   – Antennomere III distinct, antennae clearly 3-segmented (Fig. 3) .................................. 3

3. Mandible lacking premolar processes .................................................. 4

   – Mandible with premolar membranous processes (as in Fig. 6) .................................. Symbiotes gibberosus

4. Antennomere III short, less than half length of sensorium ................................. Anagaricophilus sp.

   – Antennomere III long, only slightly shorter than sensorium ................................ Idiophyes niponensis
ACKNOWLEDGEMENTS

We thank J. V. McHugh and S. A. Ślipiński for critically reviewing this manuscript. We further acknowledge J. Forrester, J. A. Giorgi and J. Robertson for reading and providing comments on an early draft of this manuscript. This work was partially supported by an NSF/PEET grant (DEB-0329115) to J. V. McHugh, M. F. Whiting, and K. B. Miller.

REFERENCES


Received: October 30, 2007
Accepted: November 22, 2007