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Morphology of Termitophilous Larvae of *Orthogonius* and *Helluodes* and Position of the Tribes Orthogoniini and Helluodini in the Family Carabidae (Coleoptera)

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Abstract—Termitophilous larvae of the ground beetles *Orthogonius ?acutangulus* Chaud. and *Helluodes taprobanae* Westwood (Ceylon) are described. Larvae of *O. ?acutangulus* have a strongly differentiated secondary chaetome, lacking sensilla $PA_{1, 2, 3}$, while setae $ME_{13, 14}$ and $TE_{1, 10, 11}$ have specifically dilated bases. According to the general character set, Orthogoniini cannot be considered closely related to either Lebiitae or Masoreitae (Graphipterini). A number of significant larval characters, such as well-developed lacinia, biserial nasale, ligula with additional sensilla (LA_7), differentiated group of maxillary setae, pattern of the secondary leg chaetome, and structure of tarsus, suggest that Orthogoniini are remotely related to Pterostichitae and Harpalitae. Larvae of *H. taprobanae*, strongly differing from *Orthogonius* in habitus, have a number of convergently similar characters: weak pigmentation, reduced ocelli, etc. The unique characters of *Helluodes* are the specific morphology of ligula and the presence of a stout seta on 2nd maxillary palpomere. Larvae of Helluodini share no significant characters with the preimaginal stages of Anthiini and Helluonini. At the same time, *Helluodes* and Zuphiini have many significant larval characters in common: medially-directed angles of paraclypeus; elongate apical part of 4th antennal segment; 3rd antennal segment bearing a peculiarly flattened sensorium; small retinaculum; and absence of penicillus. Some of these characters are not found in other carabid larvae and thus can be considered synapomorphic, suggesting that Helluodini is a specialized group, derived from Zuphiini.

Two small Palaeotropical tribes Orthogoniini (about 100 species in 7 genera) and Helluodini (7 species in 3 genera) comprise forms more or less associated with termites (Wasmann, 1902; Fowler, 1912; Erwin, 1979; Kryzhanovskii, 1983). The taxonomic position of both groups remains obscure. Orthogoniini are usually placed in Lebiitae, without discussing their relationships in detail (Kryzhanovskii, 1983; Erwin, 1979). Arndt (1993), having examined the larvae of this tribe, suggested it to be closely related to Graphipterini. Helluodini is usually considered a group closely related to Anthiini; the preimaginal stages of these tribes have so far been unknown.

This communication describes larvae of *Orthogonius ?acutangulus* Chaud. and *Helluodes taprobanae* Westw., collected early in this century from termite nests in Ceylon and kept in collections of the Zoological Institute, Russian Academy of Sciences (St. Petersburg). In both cases, adults (and a pupa, for *Helluodes*) were collected together with the larvae, which allowed the species to be identified. Elements of the chaetome are named following the system of Bousquet and Goulet (1984), with subsequent modifications (Bousquet, 1985; Makarov, 1996).

Possible relationships of these specialized groups are discussed on the basis of the chaetotaxy investigation.

Orthogonius ?acutangulus Chaudoir, 1852

"Ceylon, Paradeniya 16.XI.1912, leg. O. John (from nest of *Termes obscuripes*, *Eutermes longicornia*)"—14 LIII.

Habitus. Massive physogastric larvae with short robust legs and head appendages (Figs. 1, *1*; 2, *5*). Thorax noticeably narrower than abdomen; urogomphi absent. Head hypergnathous. Body length 16.0–20.5 mm (M = 18.8, n = 12); major morphometric characters given in Table 1.

Coloration rather weak, with only mandibles and nasale area heavily pigmented, dark brown. Head capsule mostly pale brown, with noticeably weaker pigmentation at mediogular and frontal sutures. Antennae and mouthparts brownish yellow. Pronotum pale brown with darkened anterior margin and characteristic median stripe on pretergite. Meso- and (especially) metanotum and thoracic sternites with still weaker pigmentation. Distal leg segments brown, coxae

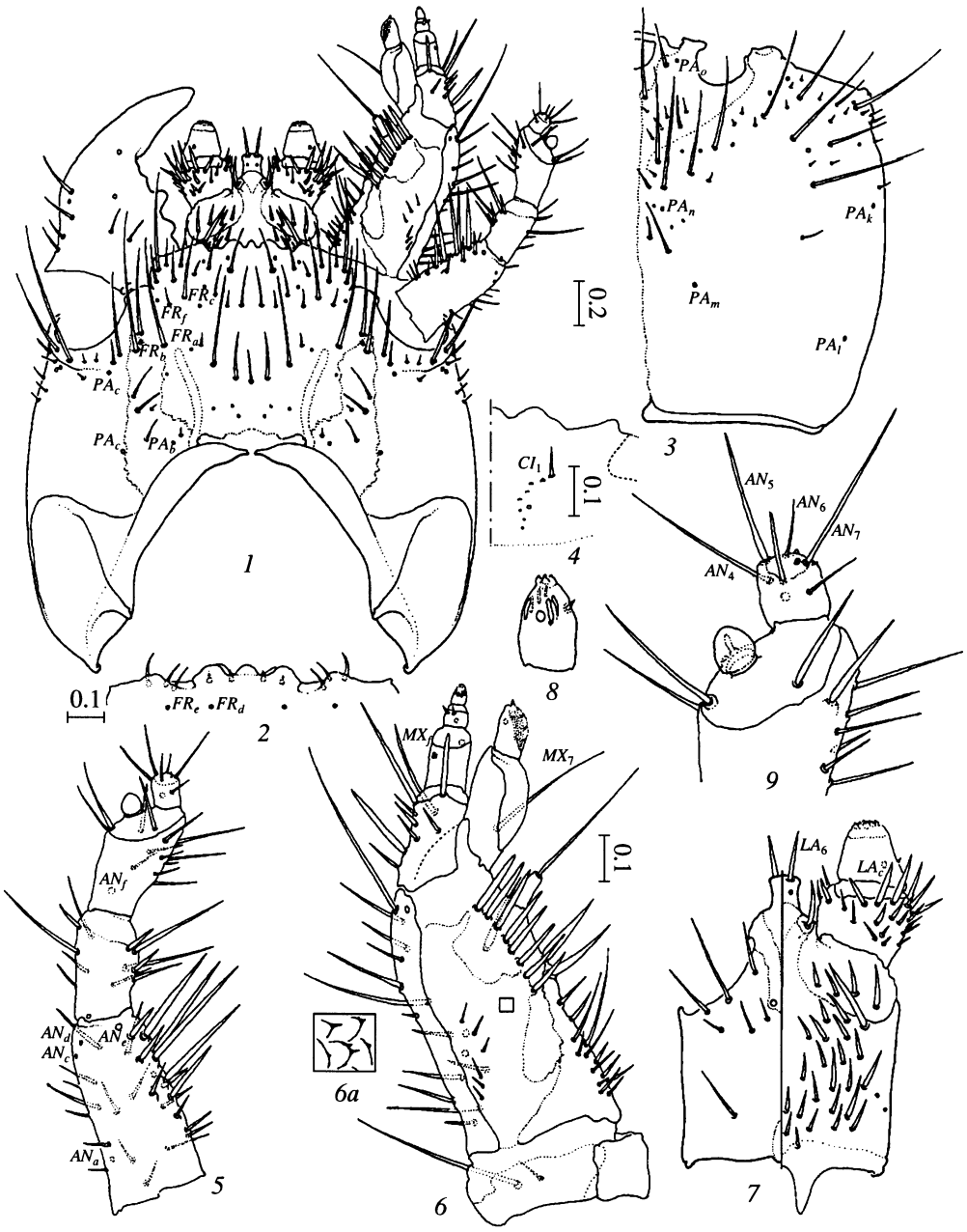

Fig. 1. Details of III instar larvae of *Orthogonius ?acutangulus*. (*1*) Dorsal view of head; (*2*) dorsal view of nasale; (*3*) ventral view of left parietal sclerite; (*4*) ventral view of dorsal cibarial membrane; (*5*) dorsal view of left antenna; (*6*) dorsal view of left maxilla [(*6a*), enlarged fragment of stipes sculpture]; (*7*) right half of labium in ventral (left) and dorsal (right) view; (*8*) 4th maxillary palpomere; (*9*) 3rd (apically) and 4th antennal segments. All scale bars marked in mm.

brownish yellow. Abdominal sclerites very pale, with hardly visible borders between them; sigillae unpigmented. Abdominal tergites I–VI somewhat more distinct due to groups of spines.

Microsculpture well-developed on most part of body surface. Sculpture of frontal and parietal sclerites squamulose, becoming tuberculate at sutures; smoothed ventrally. Mandibles also squamulose basally. Dorsal surface of maxilla spiculate (Fig. 1, *6a*); antennae and stipes ventrally with smooth isodiametric reticulate sculpture, becoming tuberculate on inner basal surface of 1st antennal segment. Mentum ventrally covered with denticles arranged in irregular rows. Thoracic tergites with irregular isodiametric reticula-

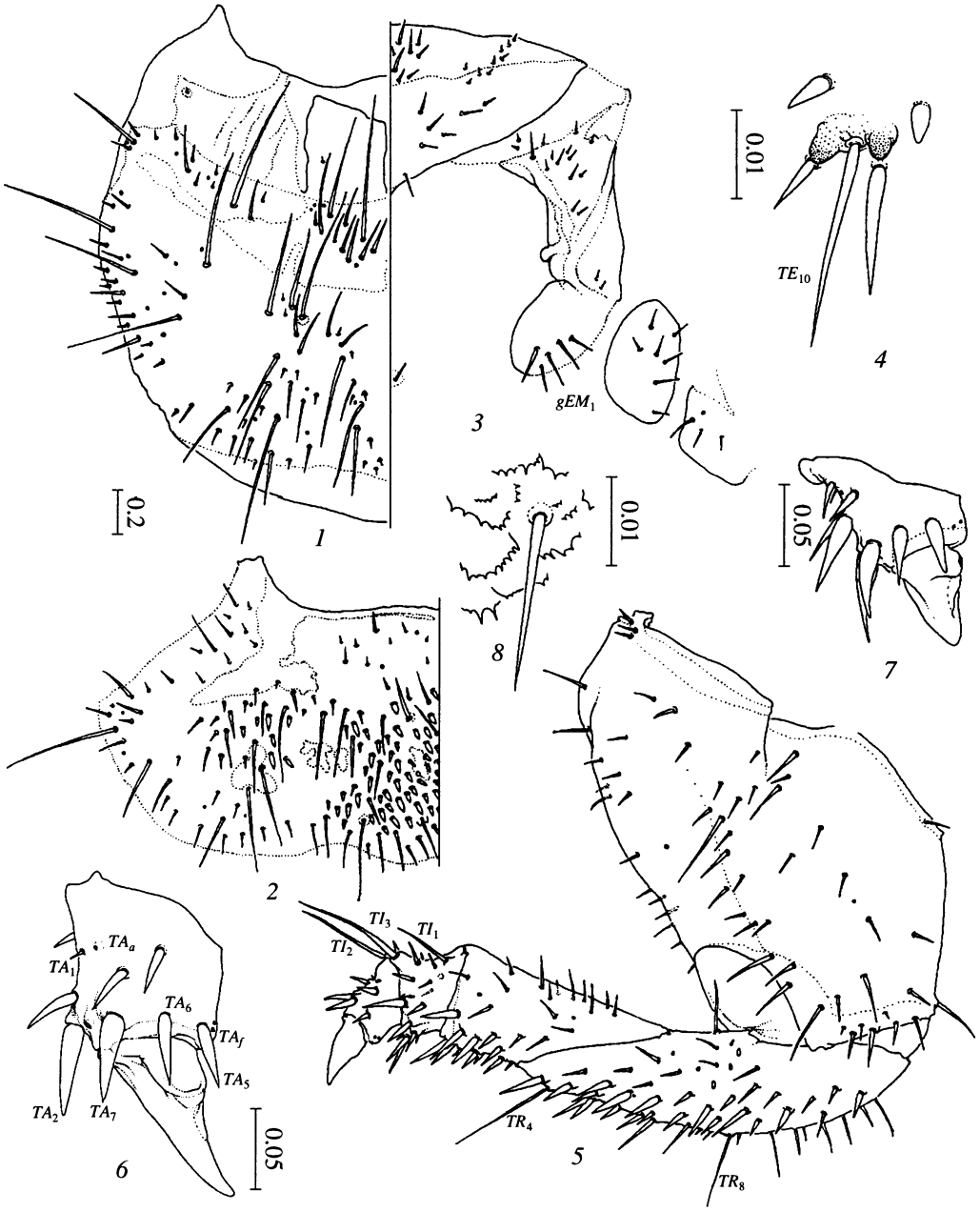

Fig. 2. Details of III instar larvae of *O. ?acutangulus*. (*1* and *2*) Left half of prothorax in dorsal (*1)* and ventral (*2*) view; (*3*) dorsal view of metathoracic tergite; (*4*) cuticular processes near seta TE_{10}; (*5*) frontal view of hind leg; (*6*) caudal view of middle tarsus; (*7*) caudal view of fore tarsus; (*8*) microsculpture of anterior surface of coxa.

tion, smoothed on disc. Coxae finely spiculate (Fig. 2, *8*) ; trochanter ventrally irregularly-reticulate; distal part of legs without microsculpture. All intersegmental membranes densely covered with microtrichia (Fig. 3, *7*). Sclerites of abdominal segments I–VI without microsculpture; those of segments VII–IX having pectinate rows of denticles.

Head (Fig. 1, *1, 3*) rounded, with frontal sclerite shortened due to strong hypergnathy: parietal sclerites 1.8–2.1 times as long as frontal one. Epicranial suture absent; occipital furrows developed only laterally; dorsal sutures of head blurred. Nasale (Fig. 1, *2*) tridentate, weakly protruding, biserial, with lateral denticles of ventral row slightly shifted inward. Paraclypeus with almost straight anterior margin and obtuse lateral angles. Ocelli absent. Head chaetome strongly modified: sensilla $PA_{1, 2, 3, a}$ absent; setae $PA_{4–8}$ shifted distally, forming a single group. Most of other generalized setae also forming groups of meso- and macro-

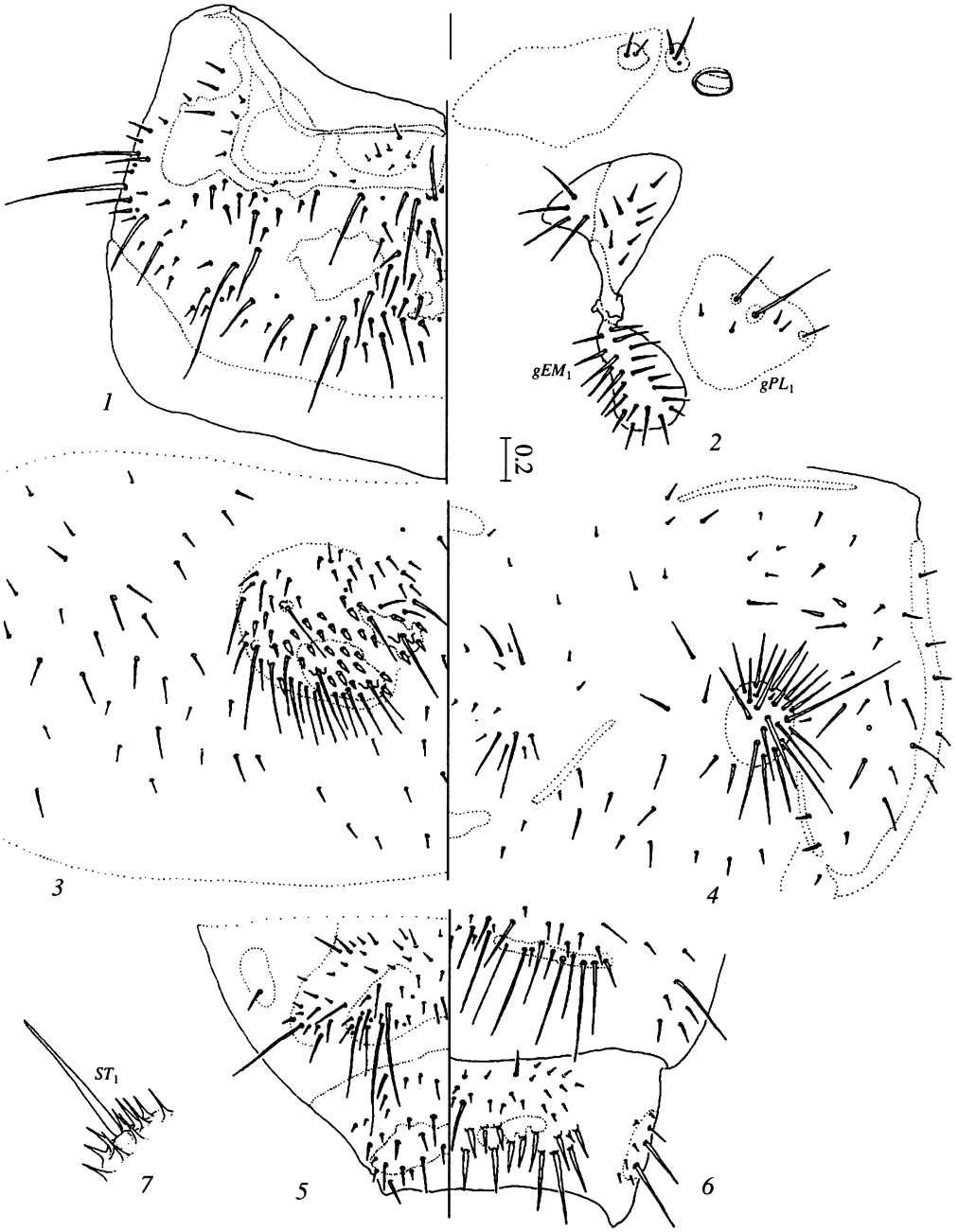

Fig. 3. Details of III instar larvae of *O. ?acutangulus*. (*1* and *2*) Left half of mesothorax in dorsal (*1*) and ventral (*2*) view; (*3* and *4*) left half of abdominal segment IV in dorsal (*3*) and ventral (*4*) view; (*5* and *6*) left half of abdominal segments IX and X in dorsal (*5*) and ventral (*6*) view; (*7*) sculpture of cuticle near seta ST_1.

chaetae; ventral head surface also bearing considerable number of microchaetae. Groups of setae FR_{4-4} and FR_{3-3} form distinct transverse rows. Seta FR_1 large, no shorter than FR_2. Setae FR_{10} and FR_{11} located between rows of denticles on nasale. Set of generalized placoid and campaniform sensilla weakly modified, lacking, besides PA_a, also FR_f and FR_g.

Mandibles massive, except for retinaculum, bearing 2 additional teeth. Group MN_1 consisting of 3–4 setae; 2–3 setae present dorsally on mandible base.

Antennae (Fig. 1, *5*) thick, 4-segmented, with strongly elongate 1st segment and noticeably shortened 4th segment. All segments bearing additional

setae, especially numerous on 1st and 2nd segments, inner setae being noticeably stouter and longer than outer ones. Sensory complex (Fig. 1, *9*) noticeably reduced: 3rd segment bearing 1 placoid and 1 rod-shaped sensilla, in addition to main sensorium; 4th segment bearing only 2 conical sensilla in addition to terminal seta AN_6.

Maxillae massive, noticeably larger than antennae and mandibles (Fig. 1, *1, 6*). Stipes lacking membranous part ventrally and with dorsal surface sclerotized only laterally. Lacinia long, subcylindrical; 1st palpomere enlarged and partly merged with 1st segment of galea. Galea only slightly shorter than palp, with weakly sclerotized inner surface, bearing (on 2nd segment) numerous fine pores and covered by thick layer of transparent secretion. Chaetome hypertrophied, with setae $MX_{2,\ 3,\ 10}$ present in groups of 6–10 and some setae thickened. Group *MX* differentiated, with 7–10 distal thickened setae forming dense dorsal row. Setae $MX_{4,\ 5}$ also strongly thickened, the latter often doubled. Apical palpomere, bearing in addition to common set of setae, bearing 3 pairs of digitiform sensilla (Fig. 1, *8*).

Labium (Fig. 1, *7*) wide, with short and thick palps. Ligula sclerotized, protruding beyond apex of 1st labial palpomere. Ligula bearing stout setae LA_6 apically and pair of large campaniform sensilla more basally. Groups LA_3 and LA_c consisting of 20–30 stout, mostly spiniform setae. Apical palpomere bearing no digitiform sensilla.

Cibarium (Fig. 1, *4*) bearing large seta CI_1 and group of 6–10 sensilla dorsally and compact group of haired processes ventrally (on the border with base of mentum). Sensilla of hypopharynx CI_a and CI_b located in its anterior 1/4.

Thorax. Pronotum (Fig. 2, *1*) discoid, not marginate except for generalized setae with numerous additional meso- and microchaetae; only $PR_{4,\ 5}$ single. Pleurites and ventrites of prothorax (Fig. 2, *3*) also having modified chaetome: group of spiniform setae present medially at anterior margin of prosternum. Meso- and metathorax (Figs. 2, *2*; 3, *1, 2*) also showing evident heteropolychaetosis; metathorax bearing numerous stout and short spinules in the area of setae $ME_{2–8–10–12}$. Group EM_1 comprising 22–28 thickened setae; group PL_1, 1–2 macro- and 4–6 microchaetae.

Legs short and massive (Fig. 2, *5*), with very short tibia and tarsus; femur longer than tibia and tarsus combined. Fore tarsi especially short (Fig. 2, *7*). On the contrary, trochanter very long, with ventral part nearly as long as femur, tibia, and tarsus combined. Claws merging with pretarsus to form claw-shaped structure, clearly (on fore legs) or indistinctly (on middle and hind legs) bifid (Fig. 2, *7, 6*); claw setae $UN_{1,\ 2}$ reduced. General chaetome of leg strongly reinforced by numerous additional setae. Coxa bearing meso- and macrochaetae, forming more or less clear groups $CO_{6–9}$, CO_7, and $CO_{12–13}$. Trochanter bearing ventrally single group of simple and spiniform mesochaetae, with macrochaetae $TR_{4,\ 8}$ standing out. Seta FE_2 on femur thin and shortened, while other generalized setae stout, spiniform; $FE_{4,\ 5}$ forming ventral group of 10–12 spines. Setae $TI_{2,\ 3}$ on tibia much longer than other setae and often longer than tibia, with strongly thickened articulations.

Abdomen weakly sclerotized, flattened ventrally and convex dorsally, with abundant additional setae. Borders between sclerites obsolete; setae present also on intersegmental membranes. Tergites of segments I–VI (Fig. 3, *3*) having paired groups consisting of 30–40 short and stout spinules and located in the area of setae $TE_{1–6–9–11}$; row of 10–16 macrochaetae present between $TE_{9–11}$. Small paired sclerotized protrusions present at bases of setae $TE_{1,\ 10,\ 11}$ and sometimes also $TE_{6,\ 9}$ (Fig. 2, *4*). Segments V and VI having no spinules but possess rows of macrochaetae. Segment IX having set of setae typical of heteropolychaetosis (Fig. 3, *5, 6*). Borders of epipleurites indistinct, setae forming no clear groups. Ventrites bearing poorly differentiated small groups ST_2, with other setae arranged quite uniformly. Hypopleurites noticeably sclerotized, strongly protruding, with compact group of robust macrochaetae (Fig. 3, *4*). Judging from the arrangement and length of setae, the hypopleurites function as sort of prolegs on which the abdomen rests. Last abdominal segment very short, with dorsal surface 2.5–3 times as long as ventral sclerotized surface. Urogomphi absent.

Helluodes taprobanae Westwood, 1847

"Ceylon, Paradeniya XI, XII.1912, leg. O. John (from nests of *Termes obscuripes*)"—6 LIII (ZIN 133–13).

Habitus. Typical campodeiform larvae with prognathous head, relatively long legs, and strongly elongated urogomphi. Body length 21.5–27.0 mm (M = 23.6, n = 4); morphometric characters given in Table 1.

Body pale, with strongest pigmentation of mandibles, part of frons before of dorsal condyles, and

Table 1. Major morphometric characters in larvae of *Orthogonius ?acutangulus* and *Helluodes taprobanae*

Character	*O. ?acutangulus*		*H. taprobanae*	
	n	*M* ± *SD*	*n*	*M* ± *SD*
Length of head	13	0.65 ± 0.021	6	2.03 ± 0.305
Width of head	13	1.57 ± 0.172	6	2.20 ± 0.201
Length of fore tarsus	20	0.15 ± 0.007	8	0.91 ± 0.012
Length of middle tarsus	20	0.17 ± 0.010	10	1.05 ± 0.019
Length of hind tarsus	20	0.21 ± 0.011	7	1.13 ± 0.023
Length of pronotum	14	1.67 ± 0.106	6	2.66 ± 0.577
Width of pronotum	14	2.46 ± 0.453	6	2.56 ± 0.378
Length of tergite IV	14	0.73 ± 0.133	6	1.41 ± 0.105
Width of tergite IV	14	1.91 ± 0.258	6	2.25 ± 0.140
Ratio of antennal segments (1 : 2 : 3 : 4)	20	5.4 : 2.6 : 3.3 : 1.0	7	3.7 : 2.1 : 1.7 : 1.1
Ratio of maxillary palpomeres (1 : 2 : 3 : 4)	20	4.0 : 2.5 : 1.0 : 1.5	2	1.1 : 1.3 : 1.1 : 1.0
Ratio of labial palpomeres (1 : 2)	20	1.6 : 1.0	5	1.0 : 1.1
Ratio of middle leg segments (coxa : trochanter : femur : tibia : tarsus)	20	6.3 : 1.1 : 4.0 : 1.4 : 1.0	10	3.8 : 1.0 : 2.4 : 1.5 : 2.1

small antero-lateral parts of parietal sclerites, approximately as far as the line drawn from base of antenna to ventral condyle of mandible. Mouthparts and antennae pale brown. Sclerites of body yellow with distinct yellowish brown sigillae; urogomphi and posterior angles of tergite IX brownish, clearly darker than tergites. Legs pale, yellowish brown, with tarsus, femur, and tibia darkened dorsally.

Microsculpture strongly reduced. Isodiametric reticulation distinct in anterior (pigmented) part of frons and traced also at ventral condyle of mandibles and on mentum. Dorsal membrane of maxilla with sparse blunt tubercles; that of mentum with dense sharp denticles. Legs, most part of tergite surface, and intersegmental membrane not sculptured; only tergite IX weakly and diffusely tuberculate. Sternites bearing sparse denticles forming obsolete rows; basal segments of urogomphi transverse-reticulate.

Head (Fig. 4, *1*, *3*) rounded, subrectilinear, noticeably flattened, without postocular and occipital furrows. Epicranial suture long, no shorter than 2nd antennal segment. Nasale tridentate, uniserial, with raised median tooth (Fig. 4, *2*). Paraclypeus at border with nasale forming clear tooth-like protrusions with finely serrate anterior margin (Fig. 4, *2a*). Ocellar tubercle absent, posterior row of ocelli reduced; anterior ocelli small and flat. Head chaetome modified, displaying moderate degree of heteropolychaetosis. Numerous microchaetae characteristically present in groups $FR_{4–6}$, $PA_{7–8}$, $PA_{9–10}$, $PA_{6–14–15}$, and PA_{17}. Generalized setae mostly rather short and thickened; setae FR_1 only slightly shorter than FR_2, while FR_7 hardly longer than FR_2. Setae $PA_{9, 13}$ rather long, no shorter than other temporal setae. Anterior margin of frons with peculiar chaetome: FR_8 form group of 4–5 macrochaetae, located laterally to tooth-like protrusion of paraclypeus, with FR_8 occurring as 2 small setae positioned medially to that protrusion, below the level of nasale. Sensillum FR_f reduced.

Mandibles having massive basal part and no additional teeth. Retinaculum rather small; penicillus absent. Outer margin of mandibles bearing group MN_1, consisting of 4–5 setae.

Antennae (Fig. 4, *4*, *5*) only slightly longer than mandibles, rather slender, with elongate basal segment and apex of 4th segment. 1st and 2nd segments having well-developed secondary chaetome; apical setae on 2nd segment noticeably longer and thicker than other ones. 3rd segment, besides large and flattened sensorium, bearing also 1 conical and 2 placoid sensilla. Seta AN_6 reduced, indistinguishable from apical sensilla (Fig. 4, *5*).

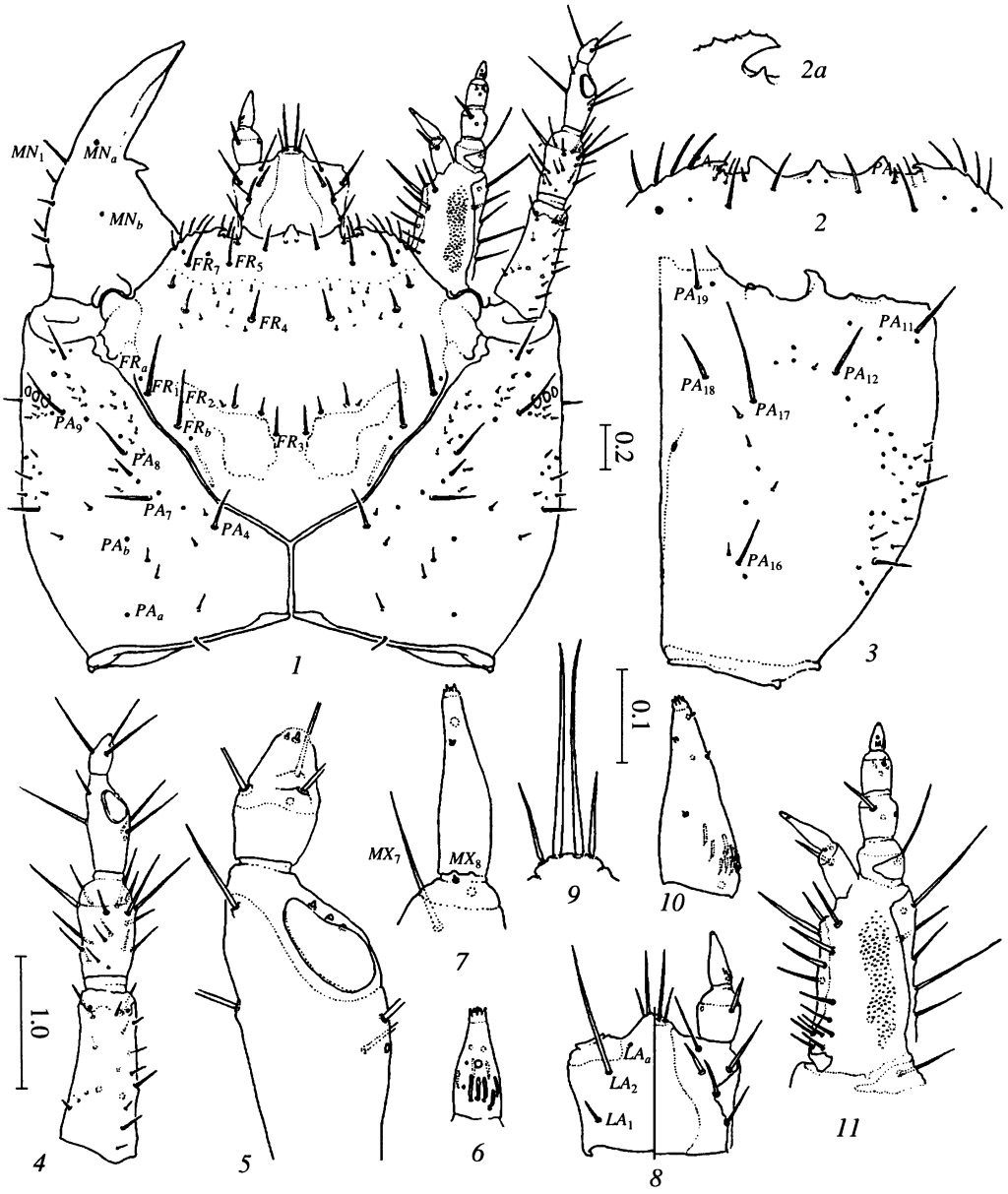

Fig. 4. Details of III instar larvae of *Helluodes taprobanae*. (*1*) Dorsal view of head; (*2*) dorsal view of nasale [(*2a*) enlarged fragment of left angle of paraclypeus]; (*3*) ventral view of left parietal sclerite; (*4*) dorsal view of right antenna; (*5*) 3rd (apically) and 4th antennal segments; (*6*) apical maxillary palpomere; (*7*) 2nd segment of galea; (*8*) right half of labium in ventral (left) and dorsal (right) view; (*9*) ligula; (*10*) apical labial palpomere; (*11*) dorsal view of right maxilla.

Maxillae typical of ground beetles (Fig. 4, *11*). Apical segment of galea (Fig. 4, *7*) rather long, with tapering apex extending as far as base of 3rd palpomere. Lacinia reduced. Groups *MX*, MX_2, and MX_3 relatively weakly developed; seta MX_8 small, no larger than MX_9. 2nd palpomere bearing large additional seta; apical palpomere having 7–9 digitiform sensilla (Fig. 4, *6*).

Labium (Fig. 4, *8*) wide, transverse, with strongly protruding conical ligula (Fig. 4, *9*), bearing 4 apical setae (?group LA_6). Mentum with no additional setae ventrally and 2–3 such setae dorsally, near LA_3. Palps relatively short, with large and stout secondary seta on 1st palpomere and latero-basal group of 10–12 digitiform sensilla on 2nd palpomere (Fig. 4, *10*).

Cibarium dorsally with large seta CI_1 and group of 6–8 sensilla (Fig. 6, *3*). Complex filtering apparatus of cibarium consisting of row of long haired processes positioned on the border with mentum. Band of scale-

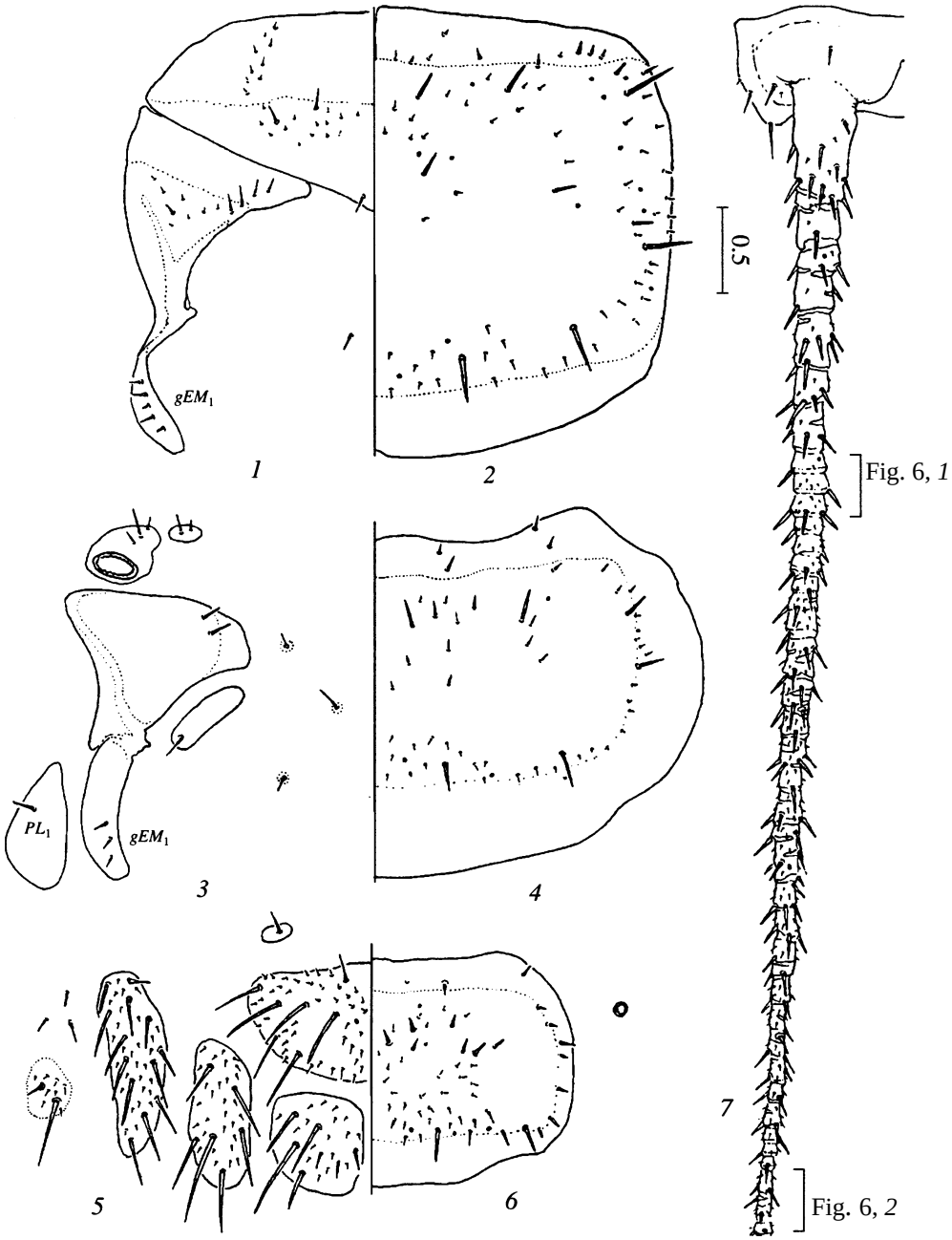

Fig. 5. Details of III instar larvae of *H. taprobanae*. (*1* and *2*) Right half of prothorax in ventral (*1*) and dorsal (*2*) view; (*3* and *4*) right half of mesothorax in ventral (*3*) and dorsal (*4*) view; (*5* and *6*) right half of abdominal segment IV in ventral (*5*) and dorsal (*6*) view; (*7*) dorsal view of left urogomphus.

like denticles, formed by merged denticles of microsculpture, lying basally to these processes and acts as sort of a grater. Another row of short haired processes present on border with hypopharynx. Sensilla of hypopharynx CI_a and CI_b located approximately in the middle.

Thorax rather wide, not narrower than abdominal segment I. Tergites well-sclerotized, not marginate laterally; anterior margin of meso- and metanotum with well-developed carina. Heteropolychaetosis moderate, with short and stout generalized setae surrounded by groups of microchaetae (Fig. 5, *2*, *4*). Sensilla $PR_{h,\ i,\ j}$ in posterior corners of pronotum reduced; the same pattern occurring in meso- and metanotum (Fig. 5, *4*). Prothoracic pro- and episternites having heterochaetous groups ES_1 and PS_2; epi-

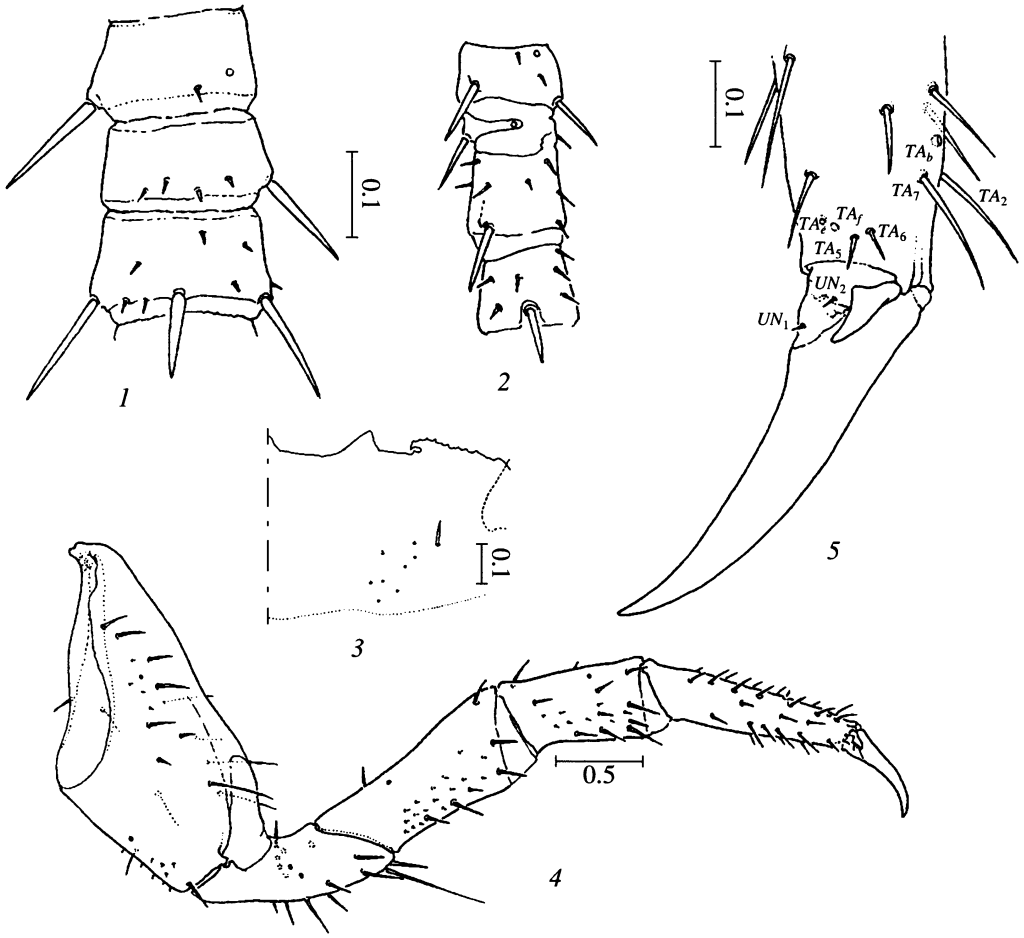

Fig. 6. Details of III instar larvae of *H. taprobanae*. (*1* and *2*) Enlarged basal (*1)* and apical (*2)* fragments of urogomphus; (*3*) ventral view of dorsal cibarial membrane; (*4*) caudal view of middle leg; (*5*) apex of middle tarsus.

merites bearing homochaetous groups EM_1 (Fig. 5, *1, 3*).

Legs (Fig. 6, *4*) rather long and slender, with tarsus longer than tibia and hardly shorter than femur. Claws distinctly uneven (Fig. 6, *5*): outer claw 4–5 times longer than inner one. Chaetome of coxa weakly modified (groups CO_{13} and $CO_{9–12}$ present); that of trochanter nearly unmodified. Femur and tibia heterochaetous, with microchaetae present mostly on ventrolateral surface. Dorso-apical setae FE_2 and TI_2 thin. Tarsus homopolychaetous, with secondary setae uniformly covering both dorsal and ventral surfaces. Setae $TA_{2, 7}$ and sensillum TA_b slightly shifted basally (Fig. 6, 5).

Abdomen cylindrical, with moderately sclerotized ventrites and tergites. Tergites (Fig. 5, *6*) not marginate, covered with numerous microchaetae and bearing short and stout generalized setae. Sensillum TE_b reduced. Ventrites (Fig. 5, *5*) with very elaborate chaetome; poststernites and pleurites uniformly covered with microchaetae and sparse macrochaetae.

Urogomphi long (Fig. 5, *7*), hardly shorter than abdomen, pseudosegmented, uniformly tapering, with high degree of heteropolychaetosis (Fig. 6, *1*, *2*). Generalized setae cannot be identified.

Myrmecophily and termitophily are rather uncommon phenomena in ground beetles, reported so far for representatives of only 7 tribes: Ozaenini, Paussini, Pseudomorphini, Orthogoniini, Helluodini, Metrini, and Graphipterini (Fowler, 1912; Moore, 1964, 1974; Erwin, 1979; Liebherr and Kavanaugh, 1985; Bousquet, 1986; Zetto Brandmayr *et al.*, 1993; Vigna Taglianti and Santarelli, 1995; Baehr, 1997). In a number of groups (Ozaenini, Paussini, Metrini, and probably some Pseudomorphini), the larvae are typical

symbionts, possessing specialized secretory organs and displaying a noticeable degree of morphological degeneration (Böving, 1907; Wasmann, 1918; Emden, 1936; Paulian, 1947; Bousquet, 1986; Arndt and Beutel, 1994; Baehr, 1997). In other tribes, including Orthogoniini and Helluodini, the larvae are in fact specialized predators (Fowler, 1912; Moore, 1964, 1974; Zetto Brandmayr *et al.*, 1993). The peculiar mode of hunting in ant and termite nests leads to formation of a specific type of a tunnel-dwelling ambuscader: a slow-moving form catching its prey in tunnels. In a number of species, the larvae live in vertical tunnels, resembling larval Cicindelinae in this respect, and have similar adaptations: heavily sclerotized, rounded head and pronotum; well-developed eyes and digitiform sensilla on labial palps; and cylindrical body with anchorage structures on abdominal segments VI–VII. These features are characteristic of *Graphipterus* (Graphipterini) and *Spallomorpha* (Pseudomorphini) (Moore, 1964; Zetto Brandmayr *et al.*, 1993). Other known larvae of Pseudomorphini (Moore, 1964, 1974; Baehr, 1997) and Orthogoniini (Gardner, 1936; Erwin, 1981), catching their prey in short horizontal tunnels, are characterized by physogastric abdomen; weakly sclerotized body, head with elongate parietal part, reduced eyes and a smaller number of digitiform sensilla, short legs adapted for digging, and elaborate chaetome and microsculpture of tegument. Larvae of some small species of *Pseudomorpha* appear to use ant cocoons as shelters.

The larvae of *Helluodes*, whose mode of life is quite obscure (Wasmann, 1918), strikingly differ in morphology from both types considered above.

Comparative analysis of adaptations in symphilous carabid larvae allows determining the primarily adaptive characters and outlining the probable phylogenetic relationships of the tribes Orthogoniini and Helluodini.

In addition to the previously described characters of habitus (Fowler, 1912; Gardner, 1936; Emden, 1942), the larvae of *O. ?acutangulus* are characterized by strongly differentiated secondary chaetome, including specific spiniform setae and microtrichia. The generalized chaetome is close to the typical carabid pattern, while the reduced sensilla $PA_{1,\ 2,\ 3,\ a}$ and weakly differentiated complex $PA_{4–8}$ are uncommon features. A number of discal setae of the tergites ($ME_{13,\ 14}$ and $TE_{1,\ 10,\ 11}$) have specifically thickened bases. The sets of sensilla on 3rd and 4th antennal segments, and especially on distal part of the legs, are strongly modified: the apical complex is reduced to $TA_{2,\ 3,\ 6,\ 7}$. The claws and pretarsus merge into a single claw-shaped structure.

Arndt (1993) considered Orthogoniini to be closely related to Graphipterini on the basis of such characters as the absence of some cephalic sutures and furrows and reduction of the penicillus and urogomphi. However, these features reflect the adaptive type of the tunnel-dwelling ambuscader; some of these characters are typical of all symphilous carabid larvae, being scattered among different tribes. At the same time, a number of larval characters of *Graphipterus* (set of sensilla on ligula and labial palps; structure of tarsi, and peculiar modifications of the chaetome) indicate a close relationship of this genus with Lebiitae s.l., clearly distinguishing it from Orthogoniini.

Judging from the general set of larval characters, the genus *Orthogonius* cannot be considered close to either Lebiitae or Masoreitae. In our opinion, a number of most significant features (well-developed lacinia; differentiated group *MX*; biserial nasale; additional sensilla on ligula; and the pattern of the secondary chaetome of legs) indicate a remote relationship with Pterostichitae and Harpalitae. The pattern of chaetome modification and the structure of sensilla in *Orthogonius* specifically suggest its relationship with Harpalitae; however, this problem remains unsolved in the present stage of investigation.

Larvae of *H. taprobanae*, strongly differing from those of *Orthogonius* in habitus (prognathous head with cervical constriction, elongate legs and other appendages, and long pseudosegmented urogomphi), have a number of convergently similar features: weak pigmentation, reduced ocelli, strongly reduced sensory complex of the 4th antennal segment, and considerably differentiated chaetome (except for the development of microtrichia). The unique features of this taxon are the ligula with 4 apical setae and a pair of sensilla, and the stout seta on the 2nd maxillary palpomere.

The preimaginal stages of *Helluodes* share no significant characters with the known larvae of *Anthia, Pachymorpha, Thermophilum* (Anthiini), and *Helluomorphodes* (Helluonini) (Emden, 1942; Bousquet, 1987). At the same time, they have many specific features in common with larvae of Zuphiini (known for one species only: Emden, 1942): unusual structure of the paraclypeus, elongate apical part of 4th antennal segment, 3rd antennal segment bearing a peculiar flattened sensorium, small retinaculum, absence of

penicillus, and structure of the urogomphi. Some of these characters are not found in other carabid larvae and may be treated as synapomorphic. In view of this, Helluodini should be considered a specialized group, derived from Zuphiini. As shown above, the nature of adaptation to living in termite nests remains obscure.

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