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Larval morphology of *Phaeochroops rattus* (Coleoptera Hybosoridae) and historical overview of known preimaginal stages of the family

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Abstract

Here we report the finding of the immature stages of *Phaeochroops rattus* Arrow 1909 in a dead fallen tree in Malaysia. A detailed and illustrated description of the last instar larval morphology is provided and their morphology is compared with larval morphology of other genera of the subfamily Hybosorinae. The trilobate labrum of *P. rattus* larvae is unique among the entire family, as well as the remarkable combination of spindle-form pretarsi and antennae with fused antennomeres III and IV but without the sensorium of antennomere III. The larvae fed on decaying wood, which is the second record of saproxylophagy in the entire family. A complete list of so far described immature stages of the entire family Hybosoridae is provided.

Key words: Scarabaeoidea, Hybosorinae, hybosorids, immature stages, key, larvae, Oriental Region, Malaysia.

Introduction

The Hybosoridae is a small cosmopolitan family of relatively heterogenous scarab beetles within the superfamily Scarabaeoidea (Scholtz and Grebennikov, 2016). The group is considered monophyletic and includes five subfamilies (Anaidinae, Ceratocanthinae, Hybosorinae, Liparochrinae, Pachyplectrinae) with 78 genera and 722 species and subspecies (Basílio, 2023; Schoolmeesters, 2023). Another 29 fossil species in 17 fossil genera were described (Schoolmeesters, 2023). While the status of subfamilies Anaidinae, Hybosorinae, Liparochrinae, Pachyplectrinae within Hybosoridae is not disputed, historically several authors considered the subfamily Ceratocanthinae to be a separate family especially based on larval morphology (Allsop, 1984; 1986; Ballerio, 1999a; 1999b; 2000a; 2000b; Scholtz and Grebennikov, 2016). Nevertheless, more recent papers based on morphological and/or molecular characters provide additional evidence for the classification of Ceratocanthinae at the subfamily level within Hybosoridae (Howden and Gill, 2000; Ocampo 2006a; 2006b; Ocampo and Ballerio, 2006; Ocampo and Hawks, 2006; Ballerio and Bezděk, 2016; Ballerio and Grebennikov, 2016; Grebennikov, 2019; Lu *et al.*, 2022; Basílio, 2023; Schoolmeesters, 2023).

Little is known about hybosorid biology. Adults and larvae usually exhibit a different food strategy (Grebennikov *et al.*, 2002). Adults feed on dung, carrion, fungi, and rotting wood (Ritcher, 1966; Davis, 2000; Ocampo, 2006a; 2006b; Scholtz and Grebennikov, 2016). Larvae have been collected in decomposing plant material, soil or in dead wood (Costa *et al.*, 1988; Scholtz and Grebennikov, 2016). However, many adults and larvae of primarily tropical subfamily Ceratocanthinae live directly in the nests of termites (Scholtz, 1990; Howden and Gill, 2000; Ballerio and Grebennikov, 2016). Scholtz (1990) mentioned also association with ants. Based on the morphology of their mouthparts, adults of Ceratocanthinae have been hypothesized to feed on fungi within the nest of their social host (Nel and Scholtz, 1990; Ballerio and Grebennikov, 2016, Matthews and Ballerio 2019). Howden (2001) mentioned the presence of a peculiar mandibular exoskeletal cavity in *Callosides genieri* Howden 2001(Anaidinae) calling it a 'mycangium' and hypothesised that the *Callosides* Howden 1971 members feed on fungi or fungal spores. However, Grebennikov and Leschen (2010) pointed out that fungal spores have not been observed in these cavities, and their mycangial function is thus inconclusive. In addition, such a structure was not observed in the closely related species *Callosides mafik* Kral et Hajek 2014 (Král and Hájek, 2014). There are several canopy dwelling species of Ceratocanthinae which are usually collected by canopy fogging, by beating of the leaves at forest edges or glades, or by netting (Ballerio, 2004; Ballerio and Wagner, 2005). Some species of Ceratocanthinae and Hybosorinae are attracted to light sources (Scholtz and Grebennikov, 2016). For example, numerous adults of *Hybosorus illigeri* Reiche 1853 were observed to prey in the vicinity of a light trap (Scholtz and Grebennikov, 2016; Shokhin, 2021). During a field trip of DK and DS to Somaliland in 2021 adults of *H. illigeri* were observed in the vicinity of a light trap while feeding on wounded or dead termites and flies (D. Král and D. Sommer, personal observation 2021). Observations on active predation are also supported by references in the literature, e.g., Rozas *et al.* (1991), Shokhin (2007; 2021). Kuijten (1981) reported that in Malaysia several specimens of *Phaeochroops rattus* Arrow 1909 have been attracted to pitfall traps baited with decaying fish. He assumed that the adults were attracted to carcasses and light sources. The author also tried to breed several living adults, which were active only at night and fed on meat and fish (Kuijten, 1981). Monteith (2009) reported that a pig which had been shot during the day was found early that evening to be covered by a vast, seething mass of beetles which proved to be *Phaechrous*, probably *Phaechrous emarginatus* Laporte 1840. For more information see also Matthews and Ballerio (2019).

Not surprisingly, immature stages of hybosorids are still poorly known. Until recently, the larvae of 21 species in 12 genera are known (table 2). In addition, there is also a reference to a larva from Dominican amber, which probably belongs to an unspecified representative of the family Hybosoridae (Poinar and Ballerio, 2017). This larva was illustrated also by Grimaldi and Engel (2005) but then not identified as an Hybosorid larva and is deposited in the personal collection of Ettore Morone (Turin, Italy). The majority of known preimaginal stages are from the subfamily Ceratocanthinae, while information on the immature stages of the subfamilies Liparochrinae and Pachyplectrinae is not available.

Following the discovery of three hybosorid larvae in the wood of a dead laying tree in Cameron Highlands (Perak, Malaysia) and their identification as larvae of *P. rattus* the aim of the current paper is i) to provide a detailed description of the immature stages of the species, ii) to summarize the knowledge of the hybosorid immature stages known up to date and finally, iii) to compare the larval morphology and ecology of *Phaechroops* Candeze 1876 larvae with those of other Hybosorinae genera. This is also the first time that a Hybosoridae larva is illustrated trough photographies.

Materials and methods

Larvae of *P. rattus* were found during a field trip of PŠ to Malaysia in 2010. Larvae were found in a dead lying trunk of an unidentified tree. Two larvae have been immediately killed and fixed in 96% alcohol and in Pampel's fluid (Švácha and Danilevsky, 1996), respectively. The remaining mature larva was reared to adult stage for identification. Adults were identified using the key in Kuijten, 1981. One year later (May 2011), at the same locality, numerous adults were found by PŠ, attracted to fish and shrimps baited pitfall traps.

The terminology for larval description follows Hayes (1929), Ritcher (1966) and Sousa *et al*. (2018). Antennomeres I-IV were labelled with the respective abbreviations (an I - an IV) in the description. To give the most accurate information on chaetotaxy, hair-like setae of the cranium and other structures were classified by their relative size into two groups: short or minute (5-40 µm or less) and medium or long (80-300 µm). Photographs were taken using a Canon EOS 70d DSLR camera equipped with a Canon EF-S 60mm f/2.8 macro usm lens and the Canon MP-E 65mm f/2.8 1-5× macro lens. Partially focused images of each specimen were combined using Zerene photo stacker software. Photographs of some details were taken on dried structures under a Keyence VHX-6000 digital microscope with VH-ZST lenses. All pictures were digitally enhanced using Adobe Photoshop 7.0 CE. Exact label data are cited for the material examined.

The specimens included in this study are deposited in the following institutional collections:

CUPC - Department of Zoology, Charles University, Prague, Czechia (Petr Šípek);

NMPC - National Museum, Prague, Czechia (Jiří Hájek).

Results

Phaeochroops rattus Arrow 1909

(figures 1-22)

Phaeochroops rattus Arrow 1909: 494 (diagnosis; type locality "Setinjak, Sumatra").

Phaeochroops rattus: Kuijten, 1981: 9, 55, figures 76-80.

Material of adults examined

Malaysia, Perak: 3 spec. (NMPC), Cameron Highlands, Batu (= Mile) 19 village env., 4°22.2'N 101°20.0'E, 590 m a.s.l., 8.-12.V.2009, baited pitfall trap - fish meat, J. Hájek lgt.; 1 spec. (CUPC) [reared from larva, see below], Batu (Mile) 19, road between Tapah and Tanah Rata, 4°22'12.800"N 101°19'58.944"E, ca. 600 m a.s.l., 12.III.2010, P. Šípek lgt.; 3 spec. (NMPC), Cameron Highlands, road 59 between Tapah and Tanah Rata (Batu 19), 4°22'12.1"N 101°20'01.2"E, 600-660 m a.s.l., 20.V.2011, fish and shrimps-baited trap, P. Šípek & D. Vondráček lgt.

Collecting events: several specimens were collected by light in rainforest, near the tree where the larvae had been collected (2010) or using baited pitfall traps (2009, 2011).

Geographic distribution: Indonesia (Bali, Java, Mentawei, Nias, Sumatra) and mainland Malaysia (Kuijten, 1981; Ocampo and Ballerio 2006; Schoolmeesters, 2023).

Immature stages of *P. rattus*

(figures 2-22)

Material of larvae examined

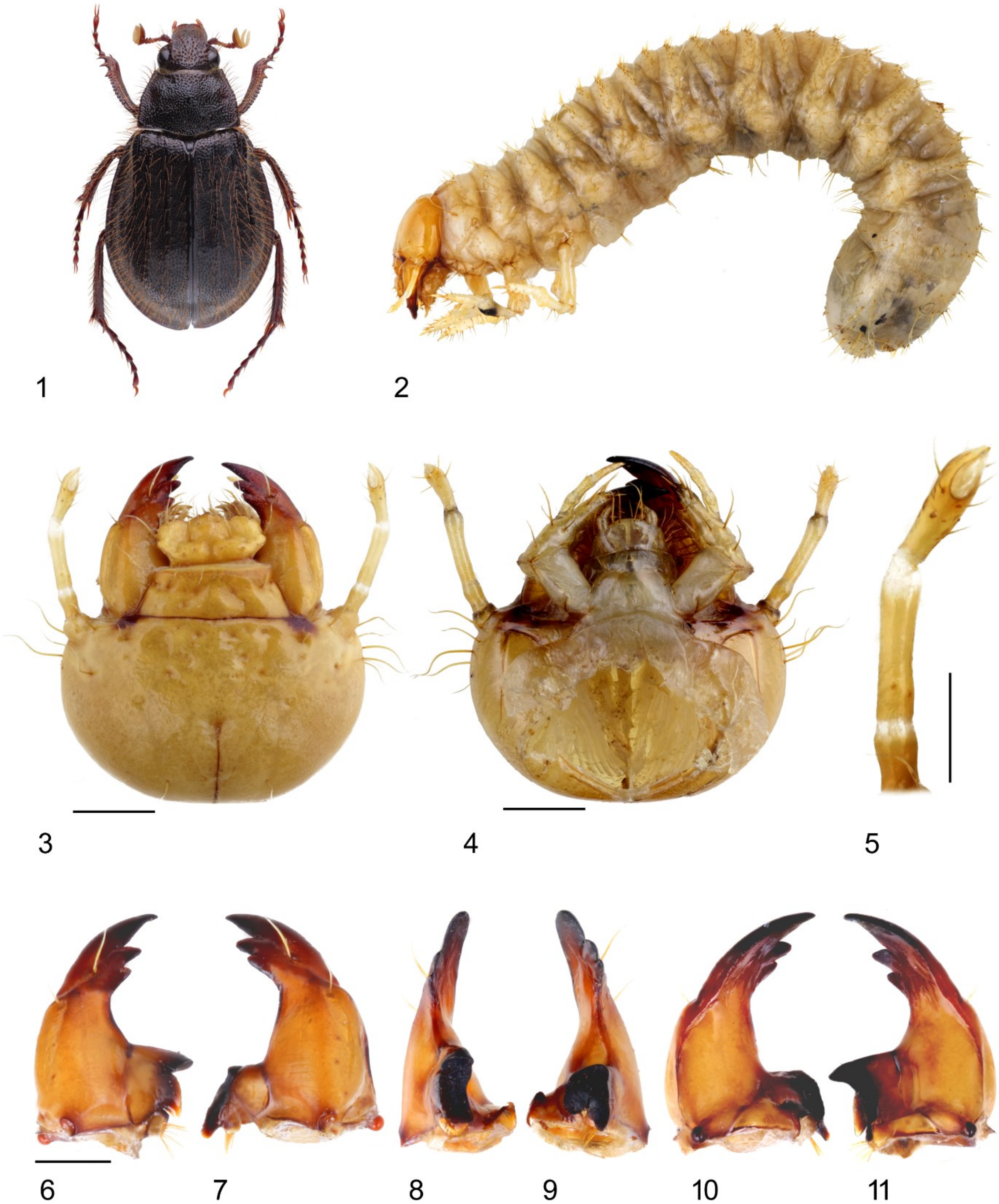
Three third instar larvae found in a dead fallen trunk of a tree, wood was grey and relatively solid, near a local settlement on Batu (Mile) 19, road between Tapah and Tanah Rata, Perak Sultanate, Malaysia, 4°22'12.800"N 101°19'58.944"E, ca. 600 m a.s.l., 12.III.2010, P. Šípek lgt. One larva was raised into adult beetle for identification, the remaining larvae were compared with the cast skin of the reared larva. Larval specimens are deposited in CUPC collection.

Description of third instar larva

(figures 2-22)

Scarabaeiform larva, total body length 24-26 mm, cranium pale brown to reddish-brown, body whitish. Abdomen with ten fully separate segments (figure 2).

Head capsule (figures 2-4): maximum width 3.6 mm. Surface of cranium smooth, faintly nodulate, coarse microsculpture absent. Cranium almost evenly coloured, yellow to pale brown with anterior parts of frons and clypeus only slightly; labrum darker than rest. Frontoclypeal suture and apices of mandibles dark brown. Cranial chaetotaxy summarized in table 1. Epicranial stem direct, dark brown, extending into middle of head. Frontal suture lyriform, very inconspicuous, toward its anterior rend almost indistinct. Anterior frontal setae considerable to reduced; one large and one or two minute exterior frontal setae present. Frontoclypeal suture distinct. Stemmata absent. Clypeus trapezoidal, narrowing apicad, almost evenly sclerotized.



Figures 1-11. *P. rattus*. (**1**) Adult male, dorsal view. Third-instar larva 2-11. (**2**) Habitus, lateral view; (**3**) head, dorsal view; (**4**) head, ventral view; (**5**) left antenna, dorsal view; 6-11 mandibles; (**6**) left, dorsal view; (**7**) right, dorsal view; (**8**) left, medial view; (**9**) right, medial view; (**10**) right, ventral view; (**11**) left, ventral view. Scale bars: 3-4 = 1 mm; 5-11 = 0.5 mm.

Antennae (figures 3-5): apparently 3-segmented (antennomeres III + IV fused) Relative length of antennomeres: II > III + IV > II. Antennomeres III + IV nearly as long as II; antennomere I more than twice as short as antennomere II. Antennomeres I and II without sensory spot and setae. Ultimate antennomere with one large apically joined membranous sensory spot on ventral and dorsal surface and nine setae. Apex of ultimate antennomere with slender pointed tip bearing minute circular sensillar field.

Labrum (figure 3): symmetrical, distal part narrowing toward clypeus, anterior margin trilobed in dorsal aspect. Anterior margin transverse, nearly perpendicular in frontal aspect, extending into blunt beak-like haptomeral

Table 1. Cranial chaetotaxy of the larva *Phaeochroops rattus* Arrow 1909.

Group of setae	Long and medium setae	Minute setae
Epicranium		
dorsoepicranial setae	1-2	0-2
posterior epicranial setae	-	0-32
anterior epicranial setae	1	2
exterior epicranial setae	2-5	-
Frons		
posterior frontal setae	1	2
exterior frontal setae	-	2
anterior frontal setae	-	3-4
setae on anterior frontal angle	1	-
Clypeus		
anterior clypeal setae	1	-
exterior clypeal setae	2	0-1
Labrum		
posterior labral setae	-	3-4
paramedial labral setae	1	-
exterior labral setae	1	-
setae on lateral labral lobe	4+2	-
setae on the median labral lobe	4+2	2

process laterad on the medial line. Lateral labral lobes with four long setae at dorsal margin and two shorter ventral setae. Median labral lobe with pair of setae posteriad to the dorsal margin, two prominent and two minute setae on dorsal margin and two ventral setae. Lateral margin with distinct tubercle posteriad to midline and prominent seta on each side. Posterior 1/3 of lateral labral margin strongly oblique. Clithra absent. Dorsal surface with a paramedian pair of long setae and four minute setae on each side of posterior surface. Chaetotaxy of labrum summarized in table 1.

Epipharynx (figures 14-15): anterior margin almost perpendicular, with strong and sclerotized, beak-like haptomeral process dextad to midline. Haptomeral process somewhat bend mediad. Lateral and anterior portion of epipharynx well sclerotised. Central and proximal parts of paria membranous. Pedium sclerotized with distinct oblique ridge extending to the haptomeral process. Tormae fused, narrow and asymmetric, right pternotorma long, narrow, left triangular. Dexiotorma with another posterior projection at its outer end. Haptolachus and mediposterior portion of pedium with distinctly sclerotized areas. The postero-median sclerite formed in low obtuse sclerotized tubercle with four pores (may be thus referred to as sense cone). Chaetotaxy of acroparia described above in the “labrum” section. Chaetoparia with a single row of 7-8 stout, flattened setae on right side and 11-14 on left side. Right half of haptolachus with row of 7-8 similar setae continuing the row from right chaetoparia. Postelateral margin of epipharynx with single external seta on each side.

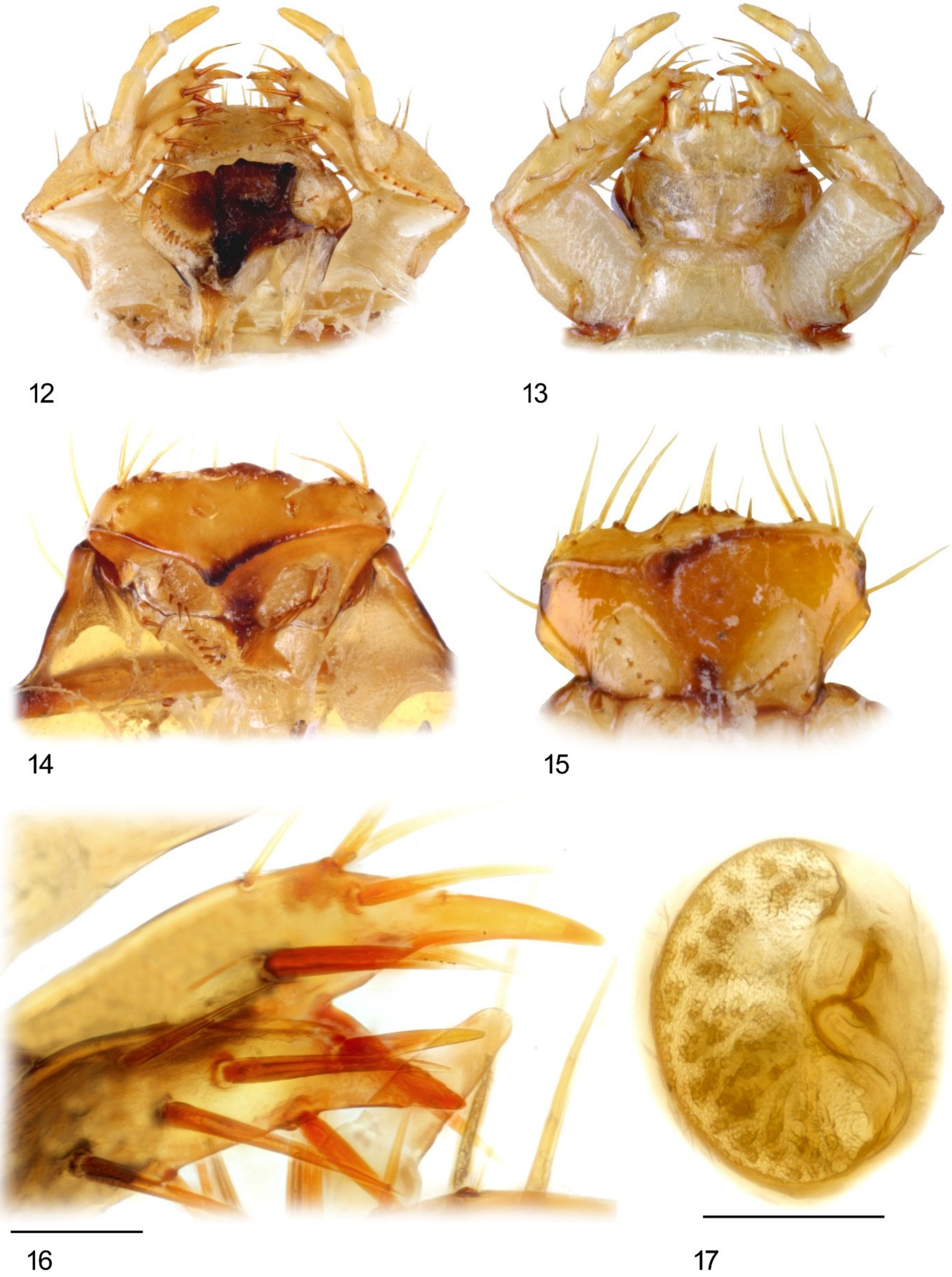
Mandibles (figures 3, 6-11): asymmetrical, scrobis without long setae, longitudinal furrow absent. Anterolateral portion of dorsal surface with two prominent setae. Dorsomolar, ventromolar and basolateral setae absent. External margin of ventral face forming sharp ridge in posterior third of mandible. Stridulatory area absent. Both mandibles with three, nearly symmetric scissorial teeth. Postartis bulbous. Molar lobes of both mandibles with sharp projections. Right mandible with well-developed acia. Posterior margin of left mandible bilobed (in medial aspect) with dorsal lobe about twice larger than ventral. Calyx of right mandible flattened with convex posterior margin. Right brustia with three, left with 10-12 setae.

Maxilla (figures 4, 12-13, 16): ventral surface of cardo with one seta. Ventromedial surface of stipes with three or four setae. Dorsal part of stipes without setae, but with row of 7-8 stridulatory teeth and one prominent seta. Galea and lacinia separated. Galea with single falcate uncus and 4-5 prominent setae, the innermost setae stout, the outer slenderer. Lacinia with one uncus; dorsally with 10-11 long setae; subapical setae more sturdy than basal ones. Galea with 3-4 setae ventrally. Palpifer with one seta. Maxillar palpus tetramerous, penultimate palpomera with two setae.

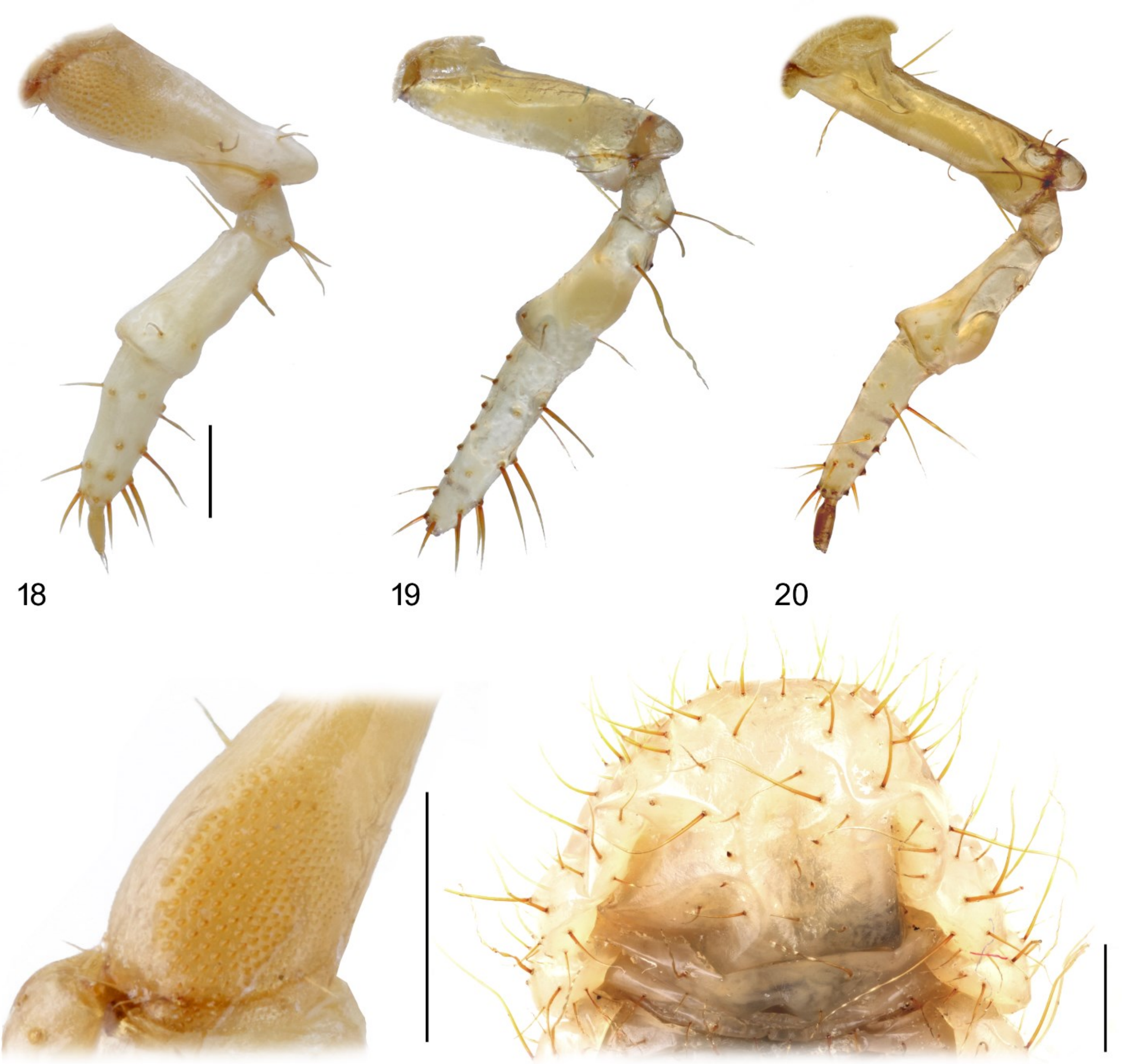
Hypopharyngeal sclerome (figure 13): asymmetrical, lateral lobes separated from central sclerome by distinct grooves. Central part heavily sclerotized, sub-rectangular with small anterior projection in right distal corner and large triangular posterior at left basal corner. Left anterior corner with another two small obtuse projections. Left lobe sclerotized, with S-shaped row of 16-19 long, flattened setae. Right lobe membranous with five setae.

Ligula (figure 12): dorsal surface proximally with transverse row of two setae on each side and paramedian pair of basiconical sensilla. Medial surface with 4-5 campaniform sensilla. Lateral margin fringed with 7-8 hair-like setae, gradually increasing in length apicad. Anterior margin between labial palpi with three pairs of setae on each side. Labial palpi bimerous.

Thorax (figure 2): prothorax with two, meso- and metathorax with three dorsal lobes. Each prothoracic sublobe with one or two rows of setae, anterior row shorter than posterior. Meso- and metathoracic sublobes I with one row of setae, meso- and metathoracic sublobes II and III



Figures 12-17. *P. rattus*, third-instar larva. (**12**) Maxillo-labial complex, dorsal view; (**13**) maxillo-labial complex, ventral view; (**14-15**) epipharynx; (**16**) tips of galea and lacinia, dorsal view; (**17**) right prothoracic spiracle, dorsal view. Scale bars: 12-15 = 0.5 mm; 16-17 = 100 µm.



Figures 18-22. *P. rattus*, third-instar larva. (**18**) Right prothoracic leg, posterior view; (**19**) right mesothoracic leg with stridulatory teeth, posterior view; (**20**) right metathoracic leg, posterior view; (**21**) stridulatory area on prothoracic leg, posterior view; (**22**) last abdominal segment, ventral view. Scale bars: 18-22 = 0.5 mm.

with one or two rows of setae, meso- and metathoracic sublobe III without setae. Mesothoracic spiracle (figure 17) bean-like, bulla oval, opened ventrally; spiracular slit stretched S-shaped; spiracle located in laterotergite, between pro- and mesothorax, thus appearing to be located on prothorax.

Legs: individual pairs (figure 2, 18-21) subequal; 5-segmented with claws. Prothoracic coxa on external side with large stridulatory area (figures 18, 21); stridulatory area composed of approximately 15 rows small peg-like projections and 2-5 setae. Trochanter with pair of setae. Femur with 4-6 setae. Tibiotarsus with approximately nine setae, mesocoxa with ventro-medial row of eight stridulatory teeths. Pretarsi spindle-shaped, with two slender apical setae. Metathoracic leg with eight stridulatory pegs on tibiotarsus and a single peg on femur.

Abdomen (figures 2, 22): with ten segments. Dorsal lobes of segments I-VII with three sublobes, segment VIII with two sublobes. Each sublobe bearing one to two (rarely three) row(s) of setae. Similarly, to thorax setae in anterior rows short, posterior row with longer setae. Last two segments (IX-X) dorsally with setae organized in two transverse rows. Abdominal spiracles quite similar to thoracic spiracles, but distinctly smaller.

Raster (figure 22): ventral surface with several minute or reduced setae. Tegilla sparsely covered with several long hair-like and short spine-like setae. Anal slit transverse fringed by three rows of hair-like setae.

Table 2. Historical overview of known preimaginal stages of Hybosoridae.

Taxon Reference, current status according to Schoolmeesters, 2023	Described as	Distribution pages (pp.) / plates (pls.) / figures (Figs.)	Egg	L1	L2	L3	Pupa	Number, way of identification of described material, and additional notes
Subfamily Anaidinae								
Anaides sp.		Neotropical						
Grebennikov *et al.*, 2004	*Anaides* sp.	p. 540				+ (?)		1 L3 (?), maybe *Anaides laticollis* Harold 1863 (only this species recorded from Mexico)
Anaides simplicicollis Bates 1887		Neotropical						
Grebennikov *et al.*, 2004	*Anaides simplicicollis* Bates 1887	p. 540, Figs. 5C-D, 6G-H, 9A-B, 10C				+ (?)		1 L3 (?), identification uncertain
Subfamily Ceratocanthinae								
Astaenomoechus sp. 1		?						
Ritcher, 1966	*Philarmostes* sp.	pp. 67-70, pl. 14, Figs. 162, 165				+ (?)		without specifying the instar of larva
Astaenomoechus sp. 2		Neotropical						
Grebennikov *et al.*, 2004	*Astaenomoechus* sp. 1	pp. 538-539, Figs. 7E-F			+	+		about 15 L2-3, 2 pupae* and 3 adults
Astaenomoechus sp. 3		Neotropical						
Grebennikov *et al.*, 2004	*Astaenomoechus* sp. 2	pp. 538-539, Fig. 10H				+		5 L3, 2 pupae* and 3 adults
Ceratocanthus aeneus (MacLeay 1819)		Nearctic						
Choate, 1987	*Ceratocanthus aeneus* (MacLeay 1819)	p. 302, Figs. 2–3				+	+	
Ceratocanthus relucens (Bates 1887)		Neotropical						
Morón and Arce, 2003	*Ceratocanthus relucens* (Bates 1887)	pp. 246-252, Figs. 1-20			+	+	+	8 L3 (but 125 together), 12 P
Grebennikov *et al.*, 2004	*Ceratocanthus relucens* (Bates 1887)	p. 537				+		2 L3
Cyphopisthes descarpentriesi Paulian 1977		Australian						
Grebennikov *et al.*, 2002	*Cyphopisthes descarpentriesi* Paulian 1977	pp. 368-371, Figs. 1-29				+	+	30 L3 and several pupae; collected together with adults, paratypes for the original description of the species
Grebennikov *et al.*, 2004	*Cyphopisthes descarpentriesi* Paulian 1977	pp. 536-537, Figs. 3, 4A-B, 5E-F				+		see Grebennikov *et al.*, 2002
Germarostes aphodioides (Illiger 1800)		Nearctic						
Ritcher, 1966	*Cloeotus aphodioides* (Illiger 1800)	pp. 67-70, pl. 14, Figs. 156-161, 163-164				+		6 L3 collected with 2 adults
Grebennikov *et al.*, 2004	*Germarostes aphodioides* (Illiger 1800)	p. 536, Figs. 8C, 8I, 10G			+	+	+	3 L2, 10 L3, 3 P
Germarostes globosus (Say 1835)		Nearctic, Neotropical						
Grebennikov *et al.*, 2004	*Germarostes globosus* (Say 1835)	p. 536, Figs. 8B				+		2 L3
Germarostes macleayi (Perty 1830)		Neotropical						
Ohaus, 1909	*Cloeotus globosus* Say 1835	pp. 23-25				+ ?	+	Grebennikov *et al.*, 2004 consider it likely to be *Germarostes macleayi* (Perty 1830)
Costa *et al.*, 1988	*Germarostes macleayi* (Perty 1830)	pp. 113-115, pl. 34, Figs. 1-16, pl. 149, Figs. 4-6				+	+	2 L3 and 1 pupa collected with 1 adult
Grebennikov *et al.*, 2004	*Germarostes macleayi* (Perty 1830)	p. 536						material not examined, description based on Costa *et al.*, 1988
Madrasostes kazumai Ochi, Johki et Nakata 1990		Palearctic						
Iwata *et al.*, 1992	*Madrasostes kazumai* Ochi, Johki et Nakata 1990	pp. 235 and 237, Fig. 2				+		1 L3; collected with adults
Madrasostes sculpturatum Paulian 1989		Oriental						
Grebennikov *et al.*, 2004	*Madrasostes sculpturatum* Paulian 1989	p. 538				+		2 L3; collected together pupae* and adult
? *Madrasostes variolosum* (Harold 1874)		Oriental						
Grebennikov *et al.*, 2004	*Madrasostes variolosum* (Harold 1874)	p. 538, Figs. 5H, 6L-M, 8F-G, 10E-F				+		3 L3; collected together with other species
Paulianostes acromialis (Pascoe 1860)		Oriental						
Grebennikov *et al.*, 2004	*Paulianostes acromialis* (Pascoe 1860)	p. 537, Figs. 5I, 6K, 10I				+		1 L3, 1 pupa grew to adult

(Continued)

(Table 2 continued)

Taxon Reference, current status according to Schoolmeesters, 2023	Described as	Distribution pages (pp.) / plates (pls.) / figures (Figs.)	Egg	L1	L2	L3	Pupa	Number, way of identification of described material, and additional notes
? *Pterorthochaetes insularis* Gestro 1899		Oriental, Palearctic						
Grebennikov *et al.*, 2004	*Pterorthochaetes insularis* Gestro 1899	p. 538, Figs. 5G, 6I-J, 8D-E, 10D				+		3 L3; larvae found in same locality where collected also adults
Subfamily Hybosorinae								
Chaetodus sp.		Neotropical						
Costa *et al.*, 1988	*Chaetodus* sp.	pp. 110-111, pl. 32, Figs. 1-17					+	pupa grew to adult
Cryptogenius fryi Arrow 1909		Neotropical						
Costa *et al.*, 1988	*Cryptogenius fryi* Arrow 1909	pp. 112-113, pl. 33, Figs. 1-19				+	+	1 L3, 1 larva grew to pupa, 1 pupa grew to adult
Hybosorus illigeri Reiche 1853		Oriental, Neotropical, Nearctic, Palearctic						
Medvedev, 1964	*Brenskea coronata* Reitter 1891	p. 140				+		1 L3
Nikolajev, 1987	*Hybosorus illigeri* Reiche 1853	p. 125				+		1 L3; same specimen as in Medvedev, 1964: 140
Grebennikov *et al.*, 2004	*Hybosorus illigeri* Reiche 1853	p. 539, Figs. 5A-B, 6C-F, 8A, 9A, 10B			+	+		8 L2, 5 L3
Hybosorus orientalis Westwood 1845		Oriental						
Fletcher, 1919	*Hybosorus orientalis* Westwood 1845	pp. 11-12, Fig. 7A-D				+		1 L3, grew to pupa
Ritcher, 1966	*Hybosorus orientalis* Westwood 1845	pp. 37-39, pl. 7, Figs. 77-83				+		3 L3, associated with one pupa* and reared adults
Patil and Veeresh, 1984	*Hybosorus orientalis* Westwood 1845	pp. 138-139, Figs. 1-5				+		4 L3
Phaeochrous emarginatus Laporte 1840		Australian, Oriental, Palearctic						
Gardner, 1935	*Phaeochrous emarginatus* Laporte 1840	pp. 9-10, pl. 1, Figs. 13-16				+		several L3, grew to adult
Ritcher, 1966	*Phaeochrous emarginatus* Laporte 1840	pp. 37-39, pl. 7, Figs. 84-88				+ (?)		without specifying the instar of larva
Grebennikov *et al.*, 2004	*Phaeochrous emarginatus* Laporte 1840	pp. 539-540, Figs. 6A-B, 7A-D, 8H, 9B-F, 10A				+		3 L3
Hybosoridae gen. sp. (fossil taxa)		Neotropical (Dominican amber)						
Poinar and Ballerio, 2017	Hybosoridae gen. sp.	pp. 125, 127, Fig. 4				+ (?)		probably Hybosoridae larva from Dominican amber; only mentioned, not described

* larva and/or pupa mentioned in the material only but not exactly described.

S e c o n d - i n s t a r   l a r v a

Unknown.

F i r s t - i n s t a r   l a r v a

Unknown.

P u p a

Unknown.

Differential diagnosis of third-instar larva

The studied larvae match with other larvae of the family Hybosoridae and share the combination of the following characters: body elongate, C-shaped, meso- and metathoracic segments as well as abdominal segments I-VII dorsally subdivided, in three folds. Stemmata absent. Frontal suture present, however very inconspicuous in some genera. Frontoclypeal suture present. Antennae 4-segmented (with two last segments completely fused in some genera and thus appearing 3-segmented); large sensory spot on apical antennomere present, covering about half of the surface of the antennomere. Galea and lacinia distinctly separated. Sound producing structures present on maxilla and on fore- and middle legs (absent in several Ceratocanthinae genera). Hind legs not reduced in length.

Larvae of *P. rattus* can be distinguished from all other known Hybosorinae larvae by the following combination of characters: labrum trilobed, ultimate antennomere (fused antennomeres III and IV) without the sensory field of antennomere III, mandibles with three scissorial teeth, pretarsus spindle-shaped, with two short setae and a minute tip. Mesotibial stridulatory area consisting of 7-8 stridulatory pegs.

Biological observations

Larvae of *P. rattus* have been collected on 12th March 2010 in a fallen trunk of a small unidentified tree (ca 30 cm in diameter). The wood was in initial stages of decay, only partially rotten, fairly wet, dark grey. The larvae have been found in a pocket of softer wood, presumably previously excavated by cockroaches or millipedes and fed presumably on the decaying wood.

The same locality was visited one year later in May

2011 by PŠ. Several imagoes were subsequently reared in captivity. In artificial breeding condition, the adults fed readily on carcasses of large insects, e.g., *Locusta migratoria* (L. 1758) or *Blaptica dubia* (Serville 1839). The adults were kept in a plastic vial with 8 cm layer of leaf litter and a large piece of soft decayed wood. The adults were observed to bore through the wood several times, however the reason for such a behaviour remains unclear, as no oviposition was observed.

Discussion

The current knowledge of immature stages (eggs, larvae, pupae) of the family Hybosoridae remains still far from complete. Out of the 78 extant hybosorid genera with 722 described species and subspecies, only immature stages of 12 genera and 21 species are known up to date, with the largest body of knowledge concentrated in the subfamily Ceratocanthinae. Including the herein reported larvae of *P. rattus*, immatures of only six Hybosorinae species from five genera are known up to date (see table 2, for details). A detailed morphological comparison of selected differential characters is given in table 3.

According to the key of larval Hybosoridae published by Grebennikov *et al*. (2004) the larvae of *P. rattus* will key to the point 2 and 2', so they are most similar to larvae of the genus *Hybosorus* W.S. Maclay 1819 and *Phaeochrous* Laporte 1840. From them they can be distinguished by the following characters: anterior margin of labrum with three lobes, mandibles with three scissorial teeth, lacinia with a single uncus at the apex and apical antennomere without the rudimental sensory field of antennomere III. All three genera share the unique arrangement of stridulatory area on mesothoracic legs (a row of 7-8 stridulatory pegs on tibiotarsus and one or two pegs on the distal end of femur), while other species of hybosorid larvae (including also representatives Anaidinae and Hybosorinae) have the stridulatory area on mesotibia composed of a field of fine microsculpture (pointed or transverse tubercles) or the stridulatory apparatus of pro- and mesothoracic legs is absent.

Table 3. Morphological and ecological comparison of known Hybosorinae larvae. Autapomorphies of *Phaeochroops* highlighted in bold. Asterisk "*" marks characters state given in Grebennikov *et al.*, 2004 which is incongruent with Ritcher, 1966.

	Hybosorus	*Phaeochrous*	*Cryptogenius*	*Chaetodus*	***Phaeochroops***
Anterior margin of labrum	with 2 lateral lobes and 3 medial truncate tubercles	with 3 medial truncate tubercles	anterior margin with 8 tubercles	with 8 tubercles	**with 3 equally sized lobes**
Frontal suture	present (absent*)	present (absent*)	present	present	present, faint
Tormae	fused	not fused, or connected only with narrow bar	connected only with narrow faintly sclerotised bar	fused	fused
Antonnomeres III and IV	fused with 10 setae, sensory field of AN III present	fused with 14 setae, sensory field of AN III present	separate, AN IV with 5 setae	separate, AN IV with 5 setae	fused with less than 10 setae, **sensory field of AN III absent**
Antennomere I	0 (2-3 setae, 5 pores*)	0 (2-3 setae, 5 pores*)	0	0	0
Number of setae of lacinia	more than 15	more than 15	less than 15	more than 15	less than 15
Dorsal transverse keel of mandible	present	present	present (?)	absent (?)	absent
Unci of lacinia	3	2	1	1	1
Number of mandibular scissorial teeth	2	2	2	2	**3**
Length of last maxillar palpomera	distinctly longer than penultimate	distinctly longer than penultimate	distinctly longer than penultimate	same as the penultimate	same as penultimate
Pretarsus (tarsal claw)	falcate with two apical setae	falcate with two apical setae	cylindrical with two long apical setae and minute pointed tip	conical, with two short setae	**spindle-shaped with two short setae and minute pointed tip**
Raster	with two caudally converging rows of pali	with two caudally converging rows of pali	palidia absent	two rows of pali	palidia absent
Larval habitat	forest soil	soil / roots of grasses	semi-decayed wood (fallen logs)	forest soil / roots	semi-decayed wood (fallen logs)

Grebennikov *et al*. (2004) failed to recover the monophyly of Hybosorinae based on the larval characters and state that this group is paraphyletic with the respect Ceratocantinae and Anaidinae. Also, our results corroborate such view, as we were not able to detect any larval morphological trait joining all Hybosorinae genera with known immature stages.

Costa *et al*. (1988) reported that Hybosorinae larvae are found in decaying fallen logs, but mention only a single specific case of immatures saproxylophagous Hybosorinae (genus *Cryptogenius* Westwood 1845). All other Hybosorinae genera as well as *Anaides* Westwood 1845 (subfamily Anaidinae) are reported to live in soil, feeding presumably on roots, while the representatives of Ceratocantinae are sometimes associated with termites. Thus, the herein reported association of *Phaeochroops* larvae with dead wood represents the second record of saproxylophagy for the entire family Hybosoridae.

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