DESCRIPTION OF THE EGG AND FIRST-INSTAR LARVA OF *SCOTOBIUS PILULARIUS* GERMAR, 1823 (COLEOPTERA: TENEBRIONIDAE: SCOTOBIINI), AND ANALYSIS OF LARVAL PRIMARY CHAETOTAXY

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Abstract.— Larval morphology of the New World tenebrionid genus *Scotobius* Germar is studied based on a description of the first instar of *S. pilularius* Germar, with emphasis on chaetotaxic analysis of the cephalic capsule, head appendages, legs, and thoracic and abdominal segments. This represents the first description of a larva of *Scotobius*, and the first detailed treatment of the larval primary chaetotaxy pattern of a tenebrionid. A short description and photographs of the eggs are also provided, which are deposited individually and agglutinate small substrate particles. As remarkable characteristics of the studied larvae, the sclerome is a simple oval structure, the tergum IX is acuminate posteriorly, the segment X is extremely small and almost completely concealed by the sternum IX, and prothoracic legs are somewhat more robust than the meso- and metathoracic pairs, which is generally the case in soil-dwelling larvae. Some discussion is provided on a long-standing controversy regarding homology and terminology of the last leg segments in coleopteran larvae.

Key words.— Tenebrioninae, *Scotobius pilularius*, Neotropical region, larval description, chaetotaxy.

INTRODUCTION

The tribe Scotobiini, which belongs to the subfamily Tenebrioninae, comprises ~113 species and subspecies and is endemic to South America, occurring mainly in arid environments of Ecuador, the Galapagos Islands, Peru, Bolivia, Chile, and Argentina (Matthews *et al*. 2010). Several species also inhabit mesic environments in Eastern Argentina, Uruguay, and Southeastern Brazil (Kulzer 1955). The tribe presently includes six genera (Silvestro *et al*. 2015), of which *Scotobius* Germar is the most speciose including 67 species and subspecies. *Scotobius pilularius* Germar, 1823, the type species, is widely distributed in southern South America, including Uruguay, Southeastern Brazil (state of Rio Grande do Sul), and most of the Argentinean territory (Kulzer 1955; Carrara *et al*. 2016 this volume). It has recently been subject of several studies describing, for example, the effect of climate and human influence on its distribution patterns, and others focused on forensic, taxonomic and paleoentomological aspects (Aballay *et al*. 2016, Carrara *et al*. 2016, Ramirez *et al*. 2016, Silvestro and Flores 2016).

Larvae of this species, however, are unknown, and larval morphology of members of Scotobiini is in general very poorly known. Only the mature larva of one

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species (*Emmallodera multipunctata curvidens* Kulzer, 1955) has thus far been described (Cekalovic and Quezada 1973). Some photographs of the larvae of three species of *Scotobius* (*S. asperatus* Erichson, 1834, *S. gayi* Solier, 1838 and an unidentified species) were also provided as part of a generalized morphological characterization which does not include formal descriptions (Vidal and Guerrero 2007). In all cases, first instars were not included and therefore primary chaetotaxy (i.e., socketed setae and pores present in the first instar) was not described. Regarding the eggs, only those of *S. gayi* are known, based on photographs and lacking description (Vidal and Guerrero 2007).

In this contribution we present a description of the egg and first-instar larva of *S. pilularius*, which represents the first detailed treatment of the morphology and chaetotaxy of the young larva of a tenebrionid. Given that larval morphology within the family is scarcely known, comparisons in the context of previous descriptions are difficult. However, as it was demonstrated for other beetle families (e.g., Alarie and Michat 2014), chaetotaxy offers useful characters for separation of taxa at all taxonomic levels. This emphasizes the potential of this character set both for phylogenetic and diagnostic purposes, and encouraged us to provide, for the first time, a detailed chaetotaxic analysis that may establish a framework useful for comparisons when more larvae are described.

Materials and methods

Between January and March 2014, 20 adults of *S. pilularius* were collected in Costa Chica town, eastern Buenos Aires province, Argentina (36°30'18''S, 56°42'35''W). Due to the difficulty of conclusively determining the sex of the specimens without dissection, all of them were brought alive to the laboratory and placed in a single breeding plastic container (22 cm long, 22 cm wide and 30 cm in depth) filled with cleaned substrate from the collecting site up to a depth of 10 cm. Temperature and humidity conditions were those of the environment. Adults of *S. pilularius* are generalists, therefore they were fed with fruits (apple, banana), vegetables (lettuce, tomato) and mashed dog food. On approximately four-day intervals, the breeding container was checked for eggs. Once the eggs were identified, they were placed individually and checked every day until the larvae hatched. First instars thus obtained were fixed and stored in 96% ethanol.

Sixteen first-instar larvae were used for the description. They were cleared in lactic acid for ~10 days, dissected and mounted on glass slides with polyvinyl-lacto-glycerol. Observation at magnifications up to 1000× and drawings were made using an Olympus CX41 compound microscope equipped with a camera lucida. Drawings were scanned and digitally inked using a Genius PenSketch tablet. Voucher specimens are deposited in the collection of the senior author (Laboratory of Entomology, Buenos Aires University, Argentina).

Ten eggs were used for the description. They were observed with the same microscope and magnifications as for larvae. Photographs were taken with a Panasonic Lumix digital camera adapted to a Leica MZ6 stereomicroscope.

The terminology for larval structures used in this paper follows Matthews *et al.* (2010). In the chaetotaxic analysis, setae and pores present on the cephalic capsule, head appendages, legs, and thoracic and abdominal segments were carefully identified, described, and illustrated. However, they were not labeled because a system of nomenclature for primary sensilla of the family Tenebrionidae has not been developed so far.

Results

Description of the egg and first-instar larva of *Scotobius pilularius* Germar

Egg, description (Figs. 1–3). Total length = 1.60–1.75 mm, maximum width = 0.89–0.92 mm (n = 7); oblong oval, colour uniformly pale white (Figs. 1, 2); chorion lightly sclerotized, surface smooth, lacking any peculiar structures visible at 1000× magnification; covered with a substance that agglutinates substrate particles, like grains of sand (Figs. 1–3); deposited individually on the substrate (Fig. 1).

First-instar larva, description (Figs. 4–24).

Colour. Uniformly white to yellowish.

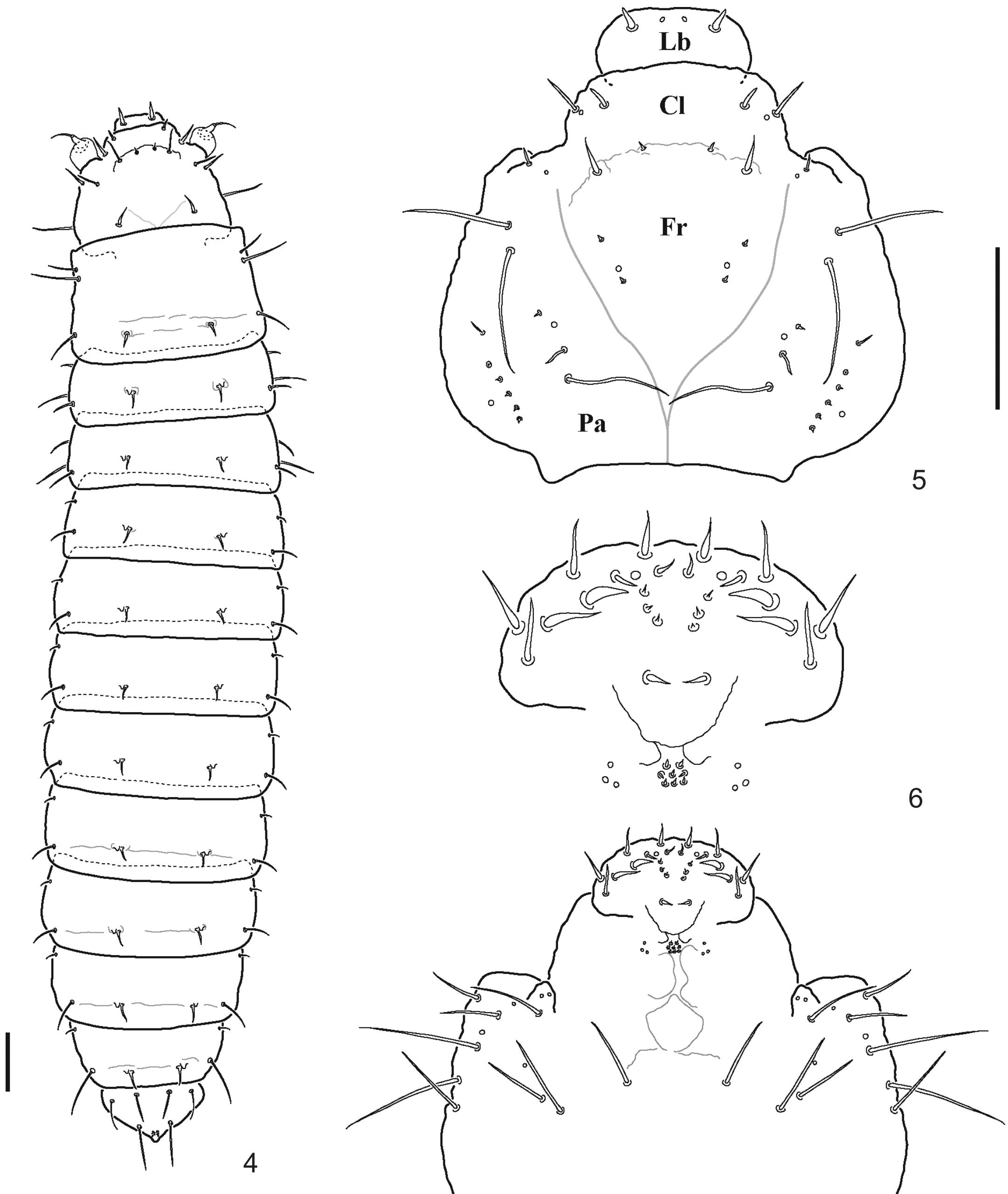
Body (Fig. 4). Elongate, parallel sided, circular in cross-section; surface smooth, lightly sclerotized. Total length = 2.06–2.79 mm (mean = 2.36 mm, n = 10).

Head. Prognathous. *Cephalic capsule* (Figs. 5–7). Globous, subcircular to subquadrate in dorsal view, widest at about posterior third (maximum head width = 0.50–0.62 mm, mean = 0,56 mm, n = 15), strongly narrowed posteriorly up to short neck constriction, progressively narrowed anteriorly up to abrupt constriction at antennal insertions; frontal sutures almost straight, V-shaped, slightly or not visible anteriorly, epicranial suture short, covered by anterior margin of pronotum; clypeus transverse, convex, lower than frons, anterior margin bent down; labrum free, transverse, lower than clypeus, subovate to subrectangular in dorsal view, dorsal surface slightly convex, ventral (epipharyngeal) surface prominent; stemmata absent. *Antenna* (Figs. 8, 9). Antennifer broad, well developed; antenna short, three segmented; antennomere 1 broad,

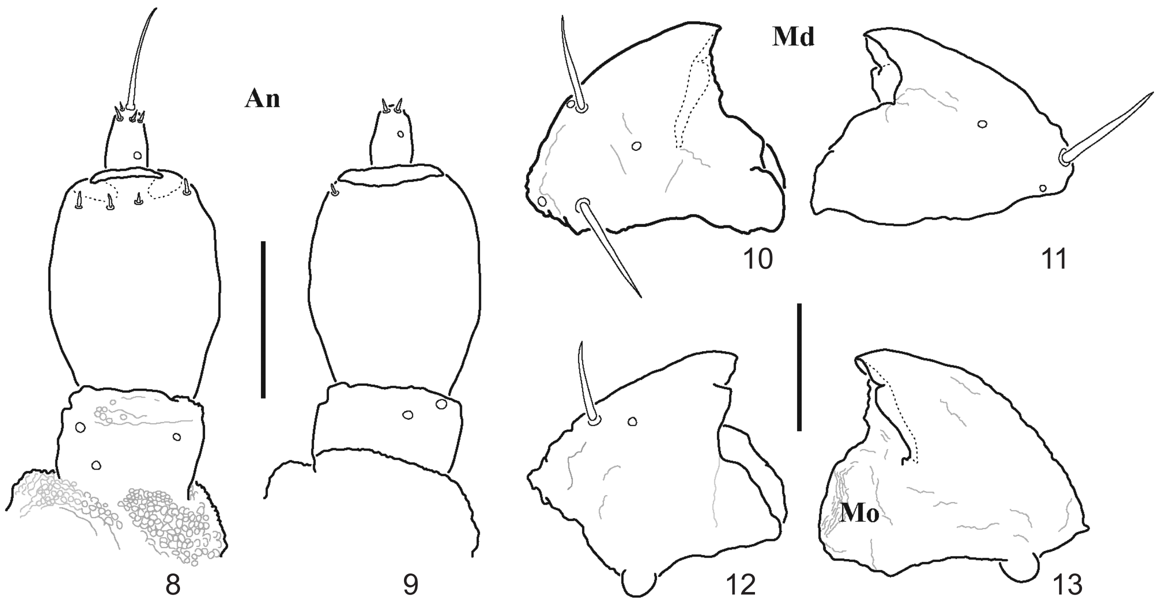
Figures 1–3. *Scotobius pilularius*, eggs. (1) eggs in the substrate of the breeding container; (2) detail of two eggs of fig. 1; (3) general view of isolated eggs with agglutinated substrate particles. Scale bars = 1.0 mm.

approximately twice as wide as long; antennomere 2 approximately 2–3 times longer than antennomere 1, broad, somewhat globous, widest at mid length, bearing an apical sensorium crescent-shaped and a dorsoapical elongate sclerite at base of antennomere 3; antennomere 3 slightly shorter than antennomere 1, much narrower than antennomeres 1 and 2. *Mandible* (Figs. 10–13). Broad, robust, subtriangular; asymmetrical: right mandible slightly smaller, more globous, with mesal margin less excavated, and with somewhat more developed mola than left mandible. *Maxilla* (Figs. 14, 15). Cardo well developed; juxtacardo subovate, evident ventrally between cardo and mentum; stipes robust, well developed, bearing strongly developed, fingerlike mala on inner margin; apex of mala reaching base of third palpomere; palpifer short, well delineated from stipes; palpus short, robust, composed of three palpomeres progressively narrowed to apex, palpomeres 1 and 2 shortest, subequal, palpomere 3 longest, bearing an elongate sensorium (Fig. 14). *Labium* (Figs. 14, 15). Mentum well developed, subtrapezoidal, broader than long; prementum subrectangular, broader than long, anterior margin projected forward into short dorsal ligula; palpus short, robust, shorter than maxillary palpus, composed of two palpomeres progressively narrowed to apex, palpomere 2 longer than palpomere 1. *Hypopharynx* (Fig. 14). Sclerome transverse, suboval.

Thorax (Figs. 4, 20). Strongly convex; pronotum well developed, subquadrate in dorsal view, about as long as meso- and metanota combined; meso- and metanotum subequal, transverse, slightly wider than pronotum, bearing one small blunt tubercle contiguous outer to the base of central robust seta; spiracles present on



Figures 4–7. *Scotobius pilularius*, first-instar larva. (4) habitus, dorsal view (not all sensilla represented); (5) cephalic capsule, dorsal view; (6) detail of epipharynx, ventral view; (7) cephalic capsule, ventral view. Cl – clypeus; Fr – frons; Lb – labrum; Pa – parietal. Scale bars = 0.2 mm.

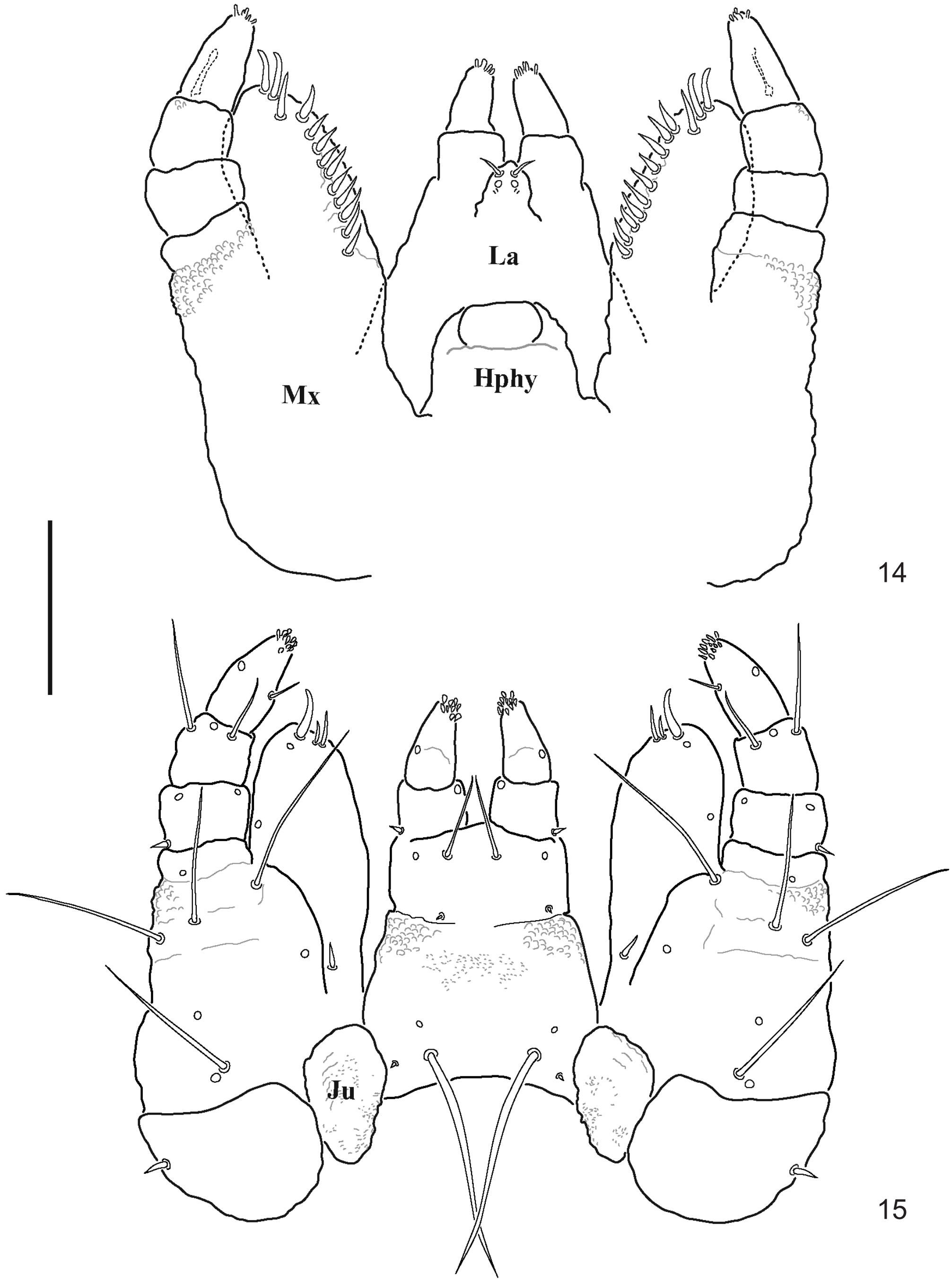


Figures 8–13. *Scotobius pilularius*, first-instar larva. (8) right antenna, dorsal view; (9) left antenna, ventral view; (10) left mandible, dorsal view; (11) right mandible, dorsal view; (12) right mandible, ventral view; (13) left mandible, ventral view. An – antenna; Md – mandible; Mo – Mola. Scale bars = 0.1 mm.

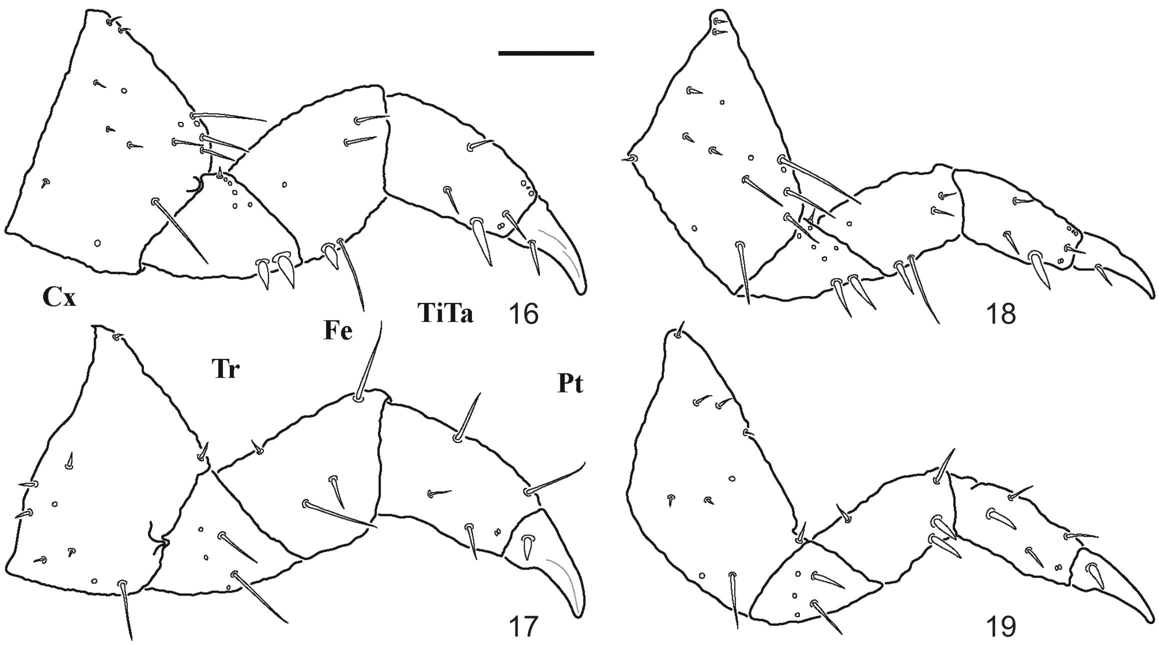
mesothorax. *Legs* (Figs. 16–19). Short; prothoracic leg more robust than meso- and metathoracic legs, with coxa broader than long; meso- and metathoracic legs subequal, with coxa longer than broad; all three legs with trochanter subtriangular, femur and tibiotarsus subcylindrical, and well developed, strongly sclerotized pretarsus.

Abdomen (Figs. 4, 21–24). Ten-segmented. Segments I–VII subequal, broader than long, segment VIII somewhat narrower, segment IX narrowest, subconical, sharp apically, somewhat directed dorsally in lateral view, segment X inconspicuous, only visible ventrally below tergite IX (Fig. 22), bearing two papillae; segments I–VIII bearing dorsally one small blunt tubercle contiguous outer to the base of central robust seta. Spiracles present on lateral margins of segments I–VIII.

Chaetotaxy (Figs. 5–24). *Cephalic capsule*. Frons with four setae (two on anterior margin, two near frontal suture) and one pore on lateral margin on each side (Fig. 5); clypeus with two setae and one pore on lateral margin on each side (Fig. 5); labrum with one seta near lateral margin and one pore on anteromedial region on each side (Fig. 5); epipharynx with 16 setae (eight near anterior margin, three minute forming a row posterior to them, one near posterior margin, four minute between tormae) and four pores (one near anterior margin, three contiguous to torma) on each side (Fig. 6); dorsal surface of each parietal with 12 setae (one near antennal base, two on anterior third, three forming a row near frontal suture, six forming a row near lateral margin) and three pores (one near antennal base, one at mid length near frontal suture, one on posterior fourth near lateral margin) (Fig. 5); ventral surface of each parietal with nine setae (six near lateral margin, three on central portion) and five pores (four near anterolateral angle, one on central portion) (Fig. 7); *Antenna* (Figs. 8, 9). Antennomere 1 with five pores (three on dorsal surface, two on ventral surface); antennomere 2 with five distal setae (four on dorsal surface, one on ventral surface); antennomere 3 with seven apical setae and two pores (one dorsal on basal third, one ventromedial). *Mandible* (Figs.10–13). With two setae and three pores near external margin. *Maxilla* (Figs. 14, 15). Cardo with one external seta; stipes with four setae and three pores on ventral surface; mala with 17 setae (one basoventral, 13 forming a row on dorsointernal margin, three ventroapical) and two pores (one at mid length on ventroexternal margin, one ventroapical); palpifer with one pore on ventral surface; palpomere 1 with one basoexternal seta and two pores on ventral surface; palpomere 2 with two setae and one pore on ventrodistal margin; palpomere 3 with one internal seta and one external pore on ventral surface, and several minute setae at apex. *Labium* (Figs. 14, 15). Mentum with two setae and one pore on basoventral surface on each side; prementum with two ventral setae (one near anterior margin, one near posterior margin) and one ventral pore near anterolateral angle on each side; ligula with one seta and one



Figures 14–15. *Scotobius pilularius*, first-instar larva. (14) maxillae, labium and hypopharynx, dorsal view; (15) maxillae and labium, ventral view; Hphy – hypopharynx; Ju – Juxtacardo; La – labium; Mx – maxilla. Scale bar = 0.1 mm.

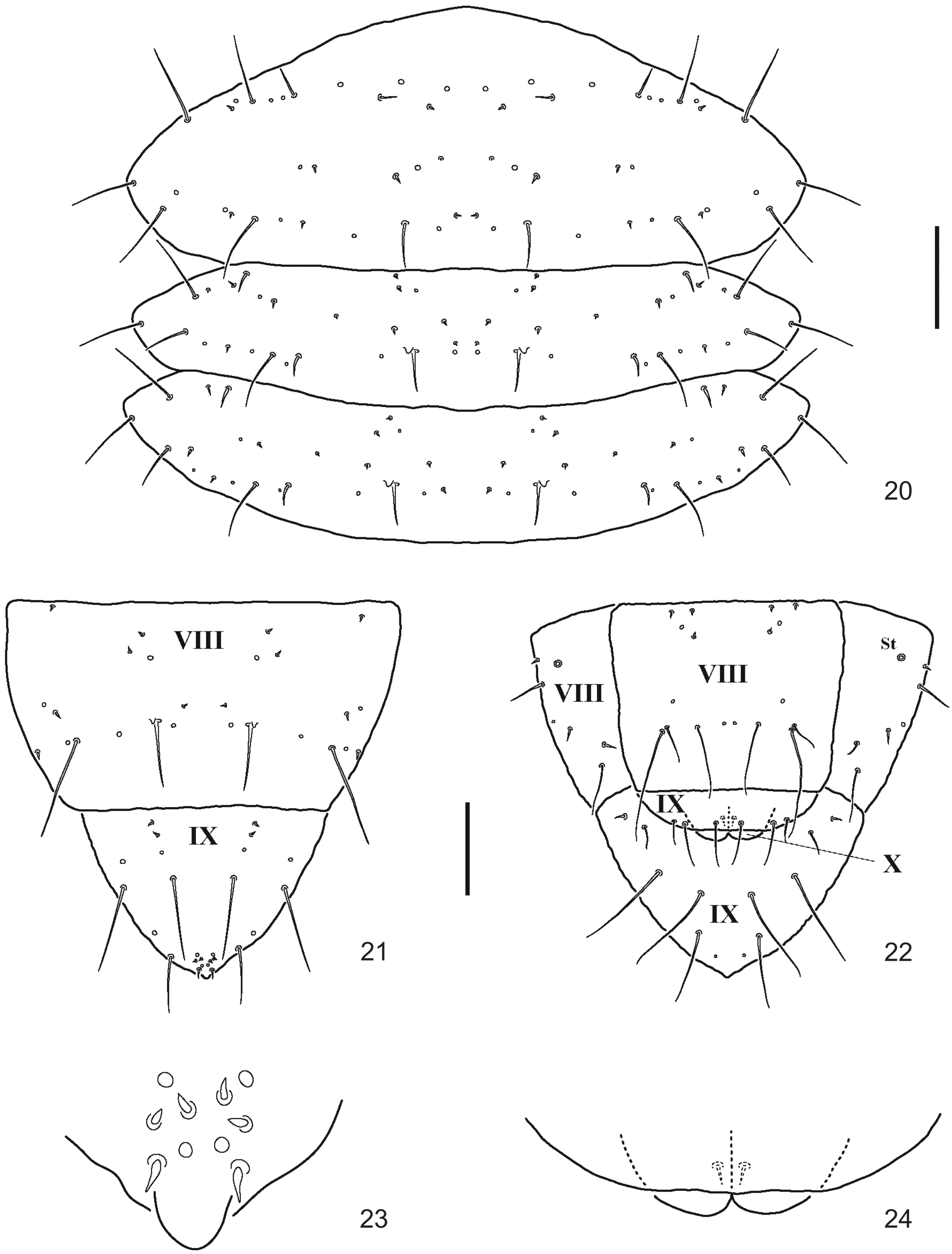


Figures 16–19. *Scotobius pilularius*, first-instar larva. (16) left prothoracic leg, anterior view; (17) right prothoracic leg, posterior view; (18) left metathoracic leg, anterior view; (19) right metathoracic leg, posterior view; Co – coxa; Fe – femur; Pt – pretarsus; TiTa – tibiotarsus; Tr – trochanter. Scale bar = 0.1 mm.

pore on dorsal surface on each side; palpomere 1 with one basoventral seta on external margin and one ventrodistal pore on internal margin; palpomere 2 with one ventroexternal pore at mid length and several minute setae at apex. *Thorax* (Fig. 20). Pronotum with 16 setae (six on anterior margin, seven on posterior margin, three on central portion) and 13 pores (six on anterior margin, five on posterior margin, two on central portion) on each side; meso- and metanotum with 17 setae and seven pores on each side. *Legs* (Figs. 16–19). Anterior surface of coxa with 11 setae (six on proximal half, five on distal half) and four pores (one on proximal half, three on distal half); posterior surface of coxa with eight setae (six on proximal half, two on distal half) and two pores (one on proximal half, one on distal half); trochanter with five setae (one on dorsal margin, two on anteroventral surface, two on posterior surface) and eight pores (five on anterodorsal surface, two on posterior surface, one on ventral margin); femur with eight setae, (two on anterodistal portion, two on anteroventral margin, two on dorsal margin, two on posteroventral surface) and one anteroproximal pore; tibiotarsus with nine setae (two on anterodorsal margin, one of them minute, two on anteroventral margin, one on anterodistal portion, two on posterodorsal margin, two on posterior surface) and six pores (four on anterodistal margin, two on posterodistal margin); pretarsus with one basal seta on ventral margin and one basal seta on posterior surface. *Abdomen* (Figs. 21–24). Tergites I–IX with 13 setae (eight on dorsal view, five on ventral view) and six pores (five on dorsal view, one on ventral view) on each side; sternites I–VIII with six setae (three on anterior half, three on posterior half) and three pores (one on anterior half, two on posterior half) on each side; sternite IX with three setae on posterior margin on each side (Fig. 22); sternite X with one seta on each side (Fig. 24).

Some considerations about homology and terminology of leg segments in coleopteran larvae

It is well known that larval legs in the coleopteran suborders Archostemata and Adephaga are composed of six articles (Coxa, trochanter, femur, tibia, tarsus, pretarsus), whereas in the suborders Myxophaga and Polyphaga (exception made for those groups with reduced legs) are composed of five articles (Matthews *et al.* 2010). There is also a general agreement about homology of the three basal leg articles (i.e., coxa, trochanter and femur). However, homology of the last two or three articles has been subject of much debate (see for example discussions in Crowson (1981) and Lawrence (1991)). Many authors, following Bøving and Craighead (1931), considered that the polyphagan leg is composed of coxa, trochanter, femur, tibia, and an apical article representing the fusion of the tarsus and ungulus (i.e., the tarsungulus). Another widely accepted



Figures 20–24. *Scotobius pilularius*, first-instar larva. (20) thoracic tergites, dorsal view; (21) abdominal segments VIII and IX, dorsal view; (22) abdominal segments VIII, IX and X, ventral view; (23) detail of apex of segment IX, dorsal view; (24) detail of segment X, ventral view. VIII–X – abdominal segments VIII–X; St – stigma. Scale bars = 0.1 mm.

Table 1. Number of primary setae and (pores) on the last leg articles of first-instar larvae in some beetle families. Labeling of each leg article as in the original publication.

Suborder	Family	Tibia	Tarsus	Tibiotarsus	Tarsungulus	Pretarsus	Source
Adephaga	Carabidae	7 (1)	7 (6)			2	Bousquet and Goulet (1984)
	Dytiscidae	7 (1)	7 (6)			2	Nilsson (1988); Alarie and Michat (2014)
	Gyrinidae	7 (1)	7 (6)			2	Archangelsky and Michat (2007); Michat *et al*. (2010); Michat and Gustafson (2016)
Polyphaga	Histeridae	16 (2)			2		Kovarik and Passoa (1993)
	Hydraenidae	8–9 (1–2)			2		Delgado and Soler (1995, 1996, 1997a,b,c)
	Hydrophilidae			9–20 (1–6)		2	Byttebier and Torres (2009); Torres (2009); Torres *et al*. (2011); Rodríguez *et al.* 2015); Archangelsky *et al*. (2016)
	Tenebrionidae			9 (6)		2	This paper

view was proposed by Bøving and Henriksen (1938) and Crowson (1955), who suggested that the leg of polyphagan larvae is composed of coxa, trochanter, femur, a fourth article representing the fusion of the tibia and tarsus (i.e., the tibiotarsus), and an apical pretarsus (which includes the ungulus or claw). Both interpretations coexist in the literature on beetle larvae, even within the same paper.

Larval primary chaetotaxy within Coleoptera is not well known, with some exceptions in the Archostemata (Grebennikov 2004), Adephaga (e.g., Bousquet and Goulet 1984, Nilsson 1988, Alarie and Michat 2014 and references therein), and Polyphaga (e.g., Kovarik and Passoa 1993, Grebennikov and Beutel 2002, Delgado and Archangelsky 2005 and references therein, Fikacek *et al* 2008, Torres 2009, Torres *et al*. 2011), and papers describing primary leg chaetotaxy in detail are scarce. This character source, however, offers a chance to investigate homology of the terminal leg articles within Coleoptera, considering that primary chaetotaxy is likely a conservative expression of the phenotype. In Table 1 we compare the primary chaetotaxy pattern of the terminal leg articles in some beetle families, taking into consideration the evidence available in the literature and that presented herein. According to Table 1 and evidence in Crowson (1981), the ultimate leg article of most beetle larvae bears only two setae. This element, together with the characteristic shape of the structure, may be taken as evidence to homologize the ultimate leg article throughout Coleoptera. From a chaetotaxic point of view, this hypothesis contradicts the existence of a tarsungulus, as homology of the ultimate article of Polyphaga with tarsus + pretarsus of Adephaga would imply the lost of all the sensilla observed on the adephagan tarsus. In our opinion, the hypothesis homologizing the penultimate leg article of larval Polyphaga (and probably also Myxophaga) with the tibia + tarsus of Adephaga and Archostemata (i.e., hypothesis of a tibiotarsus) is more plausible.

Discussion

As mentioned above, the eggs of *S. pilularius* are deposited individually on the substrate, and are covered with a substance that agglutinates small substrate particles, in this case composed of grains of sand from the place where the adults were collected. To agglutinate substrate particles to the eggs is an adaptation commonly observed in Tenebrionidae, presumably to avoid mechanical damage, dehydration, or predation (Vidal and Guerrero 2007).

The morphological characters exhibited by the larvae described here are generally consistent with those mentioned in the general description of a Tenebrioninae larva (Matthews *et al*. 2010). However, as descriptions within the family are based on later instars, comparison with characters of the first instar should be taken with care as the shape of several structures may vary considerably throughout the ontogenetic development. The sclerome is a simple oval structure in the first instar, whereas often it is anteriorly tridentate in later instars (Matthews *et al*. 2010). The tergum IX is acuminate posteriorly in the first instar of

S. pilularius. In later instars of other *Scotobius* species it is either acuminate or more or less rounded (Vidal and Guerrero 2007). Abdominal segment X, on the other hand, is extremely small and almost completely concealed by the sternum IX in the first instar of *S. pilularius*, whereas it is somewhat more produced in the later instars (Vidal and Guerrero 2007). Finally, the prothoracic legs are somewhat more robust than the meso- and metathoracic pairs, which is generally the case in soil-dwelling larvae, in which they are generally enlarged and more heavily armed (Matthews *et al*. 2010).

Comparisons among species considering different instars may be particularly problematic when chaetotaxic characters are considered, as it is well known that larvae add a variable number of secondary sensilla with successive moults. The description provided in this paper represents the first detailed treatment of the primary chaetotaxy of a tenebrionid larva. Comparisons of this chaetotaxy pattern, however, are not possible until first instars of other taxa within the family will be described.

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References

Aballay, F. H., Flores, G. E., Silvestro, V. A., Zanetti, N. I. and N. D. Centeno. 2016. An illustrated key to, and diagnoses of the species of Tenebrionidae (Coleoptera) associated with decaying carcasses in Argentina. Annales Zoologici, 66(4): 703–726.

Alarie, Y. and M. C. Michat. 2014. Bridging ecology and systematics: 25 years of study of larval morphology of world Dytiscidae (Coleoptera), pp. 17–47. *In*: Yee, D. A. (ed.). Ecology, systematics, and the natural history of predaceous diving beetles (Coleoptera: Dytiscidae). Springer, New York.

Archangelsky, M. and M. C. Michat. 2007. Morphology and chaetotaxy of the larval stages of *Andogyrus seriatopunctatus* Régimbart (Coleoptera: Adephaga: Gyrinidae). Zootaxa, 1645: 19–33.

Archangelsky, M., G. Rodríguez and P. L. M. Torres. 2016. Primary chaetotaxy and larval morphometry of *Phaenonotum exstriatum* and *Dactylosternum cacti* (Coleoptera: Hydrophilidae). Acta Entomologica Musei Nationalis Pragae, 56(1).

Bousquet, Y. and H. Goulet. 1984. Notation of primary setae and pores on larvae of Carabidae (Coleoptera: Adephaga). Canadian Journal of Zoology, 62: 573–588.

Bøving, A. G. and F. C. Craighead. 1931. An illustrated synopsis of the principal larval forms of the order Coleoptera. Entomologica Americana (N.S.), 11: 1–351.

Bøving, A. G. and K. L. Henriksen. 1938. The developmental stages of the Danish Hydrophilidae (Ins., Coleoptera.). Videnskabelige meddelelser fra Dansk Naturhistorisk Forening, 102: 27–162.

Byttebier, B. and P. L. M. Torres. 2009. Description of the preimaginal stages of *Enochrus* (*Hugoscottia*) *variegatus* (Steinheil, 1869) and *E.* (*Methydrus*) *vulgaris* (Steinheil, 1869) (Coleoptera: Hydrophilidae), with emphasis on larval morphometry and chaetotaxy. Zootaxa, 2139: 1–22.

Carrara, R., Silvestro, V. A., Cheli, G. H., Fernández Campón, F. and G. E. Flores. 2016. Disentangling the effect of climate and human influence on distribution patterns of the darkling beetle *Scotobius pilularius* Germar, 1823 (Coleoptera: Tenebrionidae). Annales Zoologici, 66(4): 693–701.

Cekalovic, T. and A. Quezada. 1973. Descripción de la larva, pupa y distribución geográfica de *Emmallodera multipunctata curvidens* Kulzer, 1955 (Coleoptera: Tenebrionidae). Anales del Instituto de la Patagonia, 4(1–3): 417–422.

Crowson, R. A. 1955. The Natural Classification of the Families of Coleoptera. Nathaniel Lloyd, London, 187 pp.

Crowson, R. A. 1981. The Biology of the Coleoptera. Academic Press, London, 802 pp.

Delgado, J. A. and M. Archangelsky. 2005. Description of the larval stages of *Gymnochthebius jensenhaarupi* and phylogenetic analysis of the relationships with other species of the subfamily Ochthebiinae (Coleoptera: Hydraenidae). European Journal of Entomology, 102: 231–240.

Delgado, J. A. and A. G. Soler. 1995. Descripción de la larva de *Ochthebius* (*Cobalius*) *subinteger* Mulsant and Rey, 1861 (Coleoptera, Hydraenidae). Graellsia, 51: 121–128.

Delgado, J. A. and A. G. Soler. 1996. Morphology and chaetotaxy of the first-instar larva of *Hydraena* (*Phothydraena*) *hernandoi* Fresneda & Lagar (Coleoptera: Hydraenidae). Koleopterologische Rundschau, 66: 147–154.

Delgado, J. A. and A. G. Soler. 1997a. Morphology and chaetotaxy of larval Hydraenidae (Coleoptera) I: genus *Limnebius* Leach, 1815 based on a description of *Limnebius cordobanus* d'Orchymont. Aquatic Insects, 19(1): 37–49.

Delgado, J. A. and A. G. Soler. 1997b. Morphology and chaetotaxy of larval Hydraenidae (Coleoptera) II: the subgenus *Ochthebius* s. str. Leach. Bulletin de l'Institut royal des Sciences Naturelles de Belgique, 67: 45–55.

Delgado, J. A. and A. G. Soler. 1997c. Morphology and chaetotaxy of larval Hydraenidae (Coleoptera) III. The genus *Calobius* Wollaston, 1854. Aquatic Insects, 19(3): 165–175.

Fikácek, M., Archangelsky, M. and P. L. M. Torres. 2008. Primary chaetotaxy of the larval head capsule and head appendages of the Hydrophilidae (Coleoptera) based on larva of *Hydrobius fuscipes* (Linnaeus, 1758). Zootaxa, 1874: 16–34.

Grebennikov, V. V. 2004. Review of larval morphology of beetles of the suborder Archostemata (Insecta: Coleoptera), including first-instar chaetotaxy. European Journal of Entomology, 101: 273–292.

Grebennikov, V. V. and R. G. Beutel. 2002. Morphology of the minute larva of *Ptinella tenella*, with special reference to effects of miniaturisation and the systematic position of Ptiliidae (Coleoptera: Staphylinoidea). Arthropod Structure and Development, 31: 157–172.

Kovarik, P. W. and S. Passoa. 1993. Chaetotaxy of larval Histeridae (Coleoptera: Hydrophiloidea) based on a description of *Onthophilus nodatus* LeConte. Annals of the Entomological Society of America, 86(5): 560–576.

Kulzer, H. 1955. Monographie der Scotobiini (Zehnter Beitrag zur Kenntnis der Tenebrioniden). Entomologische Arbeiten aus dem Museum Georg Frey, 6: 383–478.

Lawrence, J. F. 1991. Order Coleoptera, pp. 144–658. *In:* Stehr, F. W. (ed.). Immature Insects. Vol. 2, Kendall/Hunt Publishing Company, Iowa.

Matthews, E. G., Lawrence, J. F., Bouchard, P., Steiner, W. E. and S. A. Ślipiński. 2010. Tenebrionidae Latreille, 1802, pp. 574–659. *In*: Leschen, R. A. B., Beutel, R. G. and Lawrence, J. F. (eds.). Handbook of Zoology. Coleoptera, Beetles. Vol. 2. Morphology and systematics (Elateroidea, Bostrichiformia partim). De Gruyter, Berlin, New York.

Michat, M. C., Archangelsky, M. and L. A. Fernández. 2010. Larval description and chaetotaxic analysis of *Gyrinus monrosi* Mouchamps, 1957 (Coleoptera: Gyrinidae). Koleopterologische Rundschau, 80: 1–14.

Michat, M. C. and G. T. Gustafson. 2016. Larval morphology and chaetotaxy of *Macrogyrus oblongus* (Bois-duval, 1835) (Coleoptera: Gyrinidae). Aquatic Insects. (In press).

Nilsson, A. N. 1988. A review of primary setae and pores on legs of larval Dytiscidae (Coleoptera). Canadian Journal of Zoology, 66: 2283–2294.

Ramirez L. C., Carrara, R., Silvestro, V. A. and G. E. Flores. 2016. First fossil assemblage of darkling beetles (Coleoptera: Tenebrionidae) from Buenos Aires, Argentina: evidence of dry climate during the late pleistocene in the humid pampas. Annales Zoologici, 66(4): 643–652.

Rodríguez, G., Archangelsky, M. and P. L. M. Torres. 2015. Description of immatures of *Berosus decolor* Knisch, 1924 (Coleoptera: Hydrophilidae: Berosini), with emphasis on chaetotaxy and morphometry. Zootaxa, 3981(4): 577–591.

Silvestro, V. A., Giraldo-Mendoza, A. E. and G. E. Flores. 2015. *Pumiliofossorum* gen. nov, a new genus and two new species of Scotobiini (Coleoptera: Tenebrionidae) from Peru, with a revised key to the genera of Scotobiini. Zootaxa, 3986(4): 461–471.

Silvestro, V. A. and G. E. Flores. 2016. Notes on types of some species described by Billberg and Germar belonging to the South American genera *Scotobius* Germar, 1823 and *Nyctelia* Berthold, 1827 (Coleoptera: Tenebrionidae), with new synonymies and taxonomic implications. Annales Zoologici, 66(4): 653–663.

Torres, P. L. M. 2009. Sistemática y bionomía de Hydrophilina argentinos (Coleoptera: Hydrophilidae). Doctoral thesis, University of Buenos Aires, 331 pp.

Torres, P. L. M., Michat, M. C. and M. Archangelsky. 2011. The immature stages of *Tropisternus* (*Pleurhomus*) *sahlbergi* (Sharp) (Coleoptera: Hydrophilidae), with considerations on the primary chaetotaxy of *Tropisternus* Solier. Zootaxa, 2777: 25–40.

Vidal, P. and M. Guerrero. 2007. Los tenebriónidos de Chile. Ediciones Universidad Católica de Chile. Santiago, Chile, 478 pp.

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