



Minute larvae of Leptotyphlinae (Coleoptera: Staphylinidae): description of three genera with discussion on the monophyly and phylogenetic position of the subfamily as inferred from larval morphology

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Abstract

External morphology of larvae belonging to three unidentified genera of the rove-beetle subfamily Leptotyphlinae (Coleoptera: Staphylinidae) collected in Mexico, Chile and Australia, respectively, is described and illustrated. Larvae of Leptotyphlinae can be distinguished from all other Staphylinoidae larvae by the combination of their small size (maximum documented head width 0.128 mm), along with complete absence of eyes, lyriform frontal ecdysial lines, long coronal suture extending for about 40% of head length, short antennae not longer than 1/3 of head length, non-serrate mandibles with a single pre-apical tooth, tibiotarsi swollen in middle with two ventral spines, and indistinctly articulated short urogomphi not longer than twice their basal width. At least some of these characters are likely to support monophyly of the subfamily. Leptotyphlinae are hypothesized to belong to the Staphylinine Group of subfamilies sharing with at least some of them the following larval characters: labrum fully fused with clypeus; posterior tentorial arms extremely thin, thread-like and more than 20 times longer than wide; posterior tentorial pits short, rounded to elongate; cardo lacking transverse sclerotized ridge. The sister-group relationships of Leptotyphlinae to a clade of Pseudopsinae+Paederinae+Staphylininae is hypothesized with the following larval characters in support: lyriform frontal arms; each maxilla articulated laterally to head capsule by a condyle; maxillary mala parallel-sided (=finger-shaped) and articulated to stipes. A larval identification key to all three presently described genera is given.

Key words: rove beetles, Staphylinidae, Leptotyphlinae, Neotyphlini, larvae

Introduction

Adult members of the rove-beetle subfamily Leptotyphlinae are elongate cryptic depigmented dwellers of deep soil (Fig. 1), and are rarely encountered in nature or collections. These blind and flightless beetles are small with body lengths between 0.8 and 2.1 mm (Pace 1996). Their small size and cryptic habits contribute to our lack of knowledge about this group. Members of Leptotyphlinae are rather uniform in shape and appearance. Five hundred and twenty five species of Leptotyphlinae are described and attributed to five tribes and 44 genera, among which 17 genera are monotypic, 19 others include between two and five species, six have between 10 and 29 species, while two large genera, *Entomoculia* Croissandeau, 1891 and *Leptotyphlus* Fauvel, 1874 account for almost 65% of species diversity with 122 and 203 species, respectively (Newton & Thayer 2005, updated). Judging by the existence of a number of known undescribed Leptotyphlinae species already in collections, and frequent new discoveries, it is plausible that the number of described taxa is far from final.

World distribution of Leptotyphlinae is peculiar. About 90% of species are known from the West Palearctic Region, which has also the most studied fauna (Herman 2001). Leptotyphlinae are also known from South and North America (faunas of California and Chile are particularly rich), with one genus recorded as far north as Alaska (Smetana 1986). Four genera of the subfamily are known from central and southern Africa, and one genus from New Guinea (Naomi 1996). Two undescribed genera are recorded from Australia (Newton 1989), and at least one more new genus is known from New Zealand. No Leptotyphlinae are known from the Palearctic Region east of Slovakia, Turkey, Lebanon and Israel, or from the Oriental Region, New Caledonia, or any distant oceanic islands (Newton & Thayer 2005).

Prior to the present work, larvae of Leptotyphlinae were only reported in the literature three times. Coiffait (1959, p. 266) briefly mentioned finding distinctive larvae with short thick urogomphi in association with leptotyphline adults on multiple occasions. Newton (1990) included Leptotyphlinae at the subfamily level in an identification key to North American Staphylinidae larvae (based in part on the larvae described in the present study). Later Pace (1996) described larvae collected in association with the adults of, and therefore attributed to, *Allotyphlus pacei* Coiffait, a west-Palearctic species. This description mentions the pre-apical mandibular tooth (Pace 1996, Fig. 38a) and elongate antennal sensorium (Pace 1996, Fig. 38b). These two characters are diagnostic for Leptotyphlinae larvae (see Diagnosis below) supporting Pace's identification.

The subfamily Leptotyphlinae is likely monophyletic based on a number of adult morphological characters such as complete blindness and absence of flight wings among them, although this hypothesis has never been explicitly demonstrated or seriously questioned. The sister-group of Leptotyphlinae is not known, although it is was hypothesised to be nested within the Staphylinine Group of subfamilies (Lawrence & Newton 1982).

In the present work we describe larval morphology of three presumably distantly related Leptotyphlinae species collected together with adults in widely separated localities in Mexico, Chile, and Australia. In all three cases, the associated and presumably conspecific adult beetles would fall within the current concept of the tribe Neotyphlini (e.g., Pace 1996), the most geographically and generically diverse tribe, but could not be placed with certainty in known genera, so we refer to these taxa by informal names. We believe, however, that these remarkable larvae warrant immediate detailed morphological description, partly because these data will allow testing monophyly of the subfamily using the new larval characters. More importantly, detailed data on Leptotyphlinae larval morphology will facilitate ongoing analysis of phylogenetic relationships within the Staphylinine Group. This presumably monophyletic assemblage was hypothesized to include the staphylinid subfamilies Oxyporinae, Megalopsidiinae, Leptotyphlinae, Steninae, Euaesthetinae, Pseudopsinae, Paederinae and Staphylininae, with possible inclusion of the families Scydmaenidae and Silphidae (Lawrence & Newton 1982; Leschen & Newton 2003). With the exception of Leptotyphlinae, larvae of all these taxa are adequately described, which further necessitates our present task to produce detailed morphological descriptions of Leptotyphlinae larvae.

Material and methods

All larvae analyzed in the present work were discovered by Al Newton while sorting Berlese samples of leaf-litter and soil-dwelling arthropods. Identification of these larvae as Leptotyphlinae was made based on the following combination of factors: 1) judging by their morphology, the larvae obviously belong to Staphylinidae and are small enough to be those of Leptotyphlinae; 2) Leptotyphlinae larvae are expected to be deep soil dwellers and, likely, to be blind, which is not common among other Staphylinidae subgroups with smaller-than-the average adult beetles, like Aleocharinae, Pselaphinae or Scydmaenidae; 3) adults of undescribed Leptotyphlinae species were found in the same samples with the larvae; 4) the larvae attributed to Leptotyphlinae resemble each other, thus indicating that they represent a natural group of organisms. Furthermore, these

larvae agree morphologically with Pace's (1996) description of a Mediterranean larva of this subfamily. All these considerations led us to conclude that these are true Leptotyphlinae larvae.

These minute Leptotyphlinae larvae were treated in warm 10% water solution of KOH (for 10 minutes), rinsed with water, and mounted on microscope slides in Hoyer's medium (Figs. 2, 3) or Euparal. Images (Figs. 1–11) were taken from microscope slides using compound microscope with attached digital camera. Morphological drawings (Figs. 12–31) were prepared from microscope slides using compound microscope with attached camera lucida. A habitus photograph of an adult Leptotyphlinae beetle (Fig. 1) is provided with the purpose to illustrate just any member of the subfamily in the adult stage; it was meant mainly for those readers who are unfamiliar with the rove-beetles well enough to have a mental picture of these rarely collected and minute animals. Five larvae representing three Leptotyphlinae taxa were studied on microscope slides and illustrated by line drawings. In some cases minute morphological structures, like pore-like sensillae, were not clearly seen and, therefore, not illustrated; thus an absence of some structures on illustrations may indicate our inability to detect them on the available material, rather than their true absence. To facilitate comparison, larvae representing all subfamilies of the Staphylinine Group (see Introduction) were studied (except Solieriinae, recently added to this group, for which larvae are unknown). All material examined is preserved at the Field Museum of Natural History, Chicago, USA.

Larvae of Leptotyphlinae

Diagnosis. Larvae of Leptotyphlinae can be separated from those of most Staphylinoida by their small size (body length 1–2 mm in the oldest instar). From the larvae of other small staphylinoids (Ptiliidae, Leiodidae, Hydraenidae, Scydmaenidae, Aleocharinae, Pselaphinae and some others) larvae of Leptotyphlinae can be distinguished using the following combination of characters: stemmata absent (Figs. 8, 9, 12, 13, 18, 23); head prognathous, with long coronal suture (about 40% of head length), lyriform dorsal ecdysial lines (Figs. 8, 12, 18, 23) and parallel ventral ecdysial lines along the ventral mid-line of the head (Fig. 13); antennae shorter than one third of the head length (Figs. 12, 18), with elongate sensorium (Fig. 20); maxilla with articulated mala bearing elongate process at apex (Fig. 22); mandibles non-serrate, with single large mesal pre-apical tooth (Figs. 12, 13, 18, 19, 23); tibiotarsi swollen at middle with two large ventral spines (Figs. 14, 28); separate abdominal laterotergites absent and apparently fused with terga thus completely encircling spiracles (Figs. 15, 17); and urogomphi indistinctly articulated to tergite IX, short and stout (Figs. 15–17, 29, 30). Larvae of some Euaesthetinae with reduced number of stemmata might resemble those of Leptotyphlinae; but the mandibles of known euaesthetine larvae lack a pre-apical tooth.

Description. Habitus. Larvae small, normally about 1mm in body length. Frayed setae absent; trichobothria absent; each side of epicrania and all thoracic and abdominal terga with one large pore-like opening dorsally.

Head. Stemmata absent; coronal suture about half length of head capsule; constricted neck region absent; occipital foramen wide, about 0.7–0.8X as wide as maximum head width; dorsal ecdysial lines lyriform; nuchal carina apparently absent; ventral wall of head capsule on each side of the prementum without anteriorly directed large sclerotized tooth; posterior tentorial pits short, 2–3X as long as wide; posterior tentorial arms thread-like and more than 20X longer than wide; tentorial bridge originates from posterior tentorial arms, narrow; attachment of anterior tentorial arms to dorsum of head capsule rounded, not transverse; ventral ecdysial lines present, linear, extending from base of head to near posterior tentorial pits; oblique hypostomal ridge on ventral surface of head capsule near maxillary foramina long, about twice as long as length of cardo; labrum fused to clypeus forming nasale; lateral sclerites on each side of labrum near fusion to clypeus absent; anterior edge of nasale serrate or not, if serrate, then without median tooth; tormae absent.

Antennae. Basal antennomere at its middle not constricted or interrupted by membrane; antennae 3-segmented; antennae shorter than 1/3 of length of head capsule; main sensory appendage on antenna elongate and narrow, parallel-sided along much of length, located antero-mesally on penultimate antennomere, longer than the width of penultimate antennomere; ultimate antennomere of regular shape or slightly shortened, length to width ratio 1–2.5; membrane connecting basal antennomere with head capsule absent or short, not longer than membrane between antennomere 2 and 3; first (basal) antennomere without setae; second (penultimate) and third (ultimate) antennomeres each with three long setae in apical half.

Mandibles. Mola absent; each mandible without mesal serration, with preapical tooth directed dorso-mesad; mandibles not asymmetrical, almost straight or slightly curved, apices directed anteriorly and partly mesad.

Maxillae articulated with ventral wall of head through condyle, membranous maxillary articulation highly reduced; cardo as wide as base of stipes, or 1.2X wider, without transverse ridge; stipes not narrowed apicad, lateral edges without obvious constriction; maxillary palpomere 2 straight; maxillary palpomere 3 not flexible, about 4 times as long as wide; galea and lacinia completely fused forming finger-shaped subparallel mala articulated to stipes; mala subequal in length to apical width of stipes, attached to mesal surface of stipes, protruding mesally; first (basal) maxillary palpomere (immediately apicad of maxillary palpifer) without setae; second (penultimate) maxillary palpomere with two setae; third (apical) maxillary palpomere entire, without setae and with one digitiform sensillum; submentum and mentum free, not incorporated in the ventral head wall; mentum with triangular or subquadrate sclerite bearing two pairs of setae; maxillary foramina open anteriorly and mesally; ligula present, not sclerotized or digitiform, as wide as, or narrower than basal labial palpomere, at apex straight, pointed or rounded, not bilobed; about as long as width of basal labial palpomere; labial palpomere 2 rigid and about 5X as long as its basal width; ligula without long membranous and microsetose anterior projection; apical labial palpomere and ventral sclerite of prementum entire, not subdivided by membrane.



FIGURE 1. Leptyphlinae, habitus image of an adult beetle (*Eutyphlops* sp., Chile), dorsal..

Thorax. Pro-, meso- and metatergum without anterior and posterior carinae; cervicosternum transverse, anterior to proepisterna; longest seta on trochanter not more than 1.5X as long as width of trochanter; leg's longest seta located on trochanter; tibiotarsus stout, not styliform; tibiotarsus at middle wider than at distal or proximal end; setae at apex of tibiotarsus short, as long as, or shorter than, claw width at base.

Abdomen. Terga and sterna longitudinally not divided by membrane; abdominal segment IX without elongate and latero-posteriorly directed tube-like process on each side; openings of abdominal (and thoracic) spiracles not or slightly elevated above body surface; laterotergites absent and apparently fused with terga, completely encircling spiracles; urogomphi present, each with apical seta about as long as urogomphus; urogomphi one-segmented, about as long as tergum IX, indistinctly articulated to abdominal segment IX but probably immobile.

Australian genus

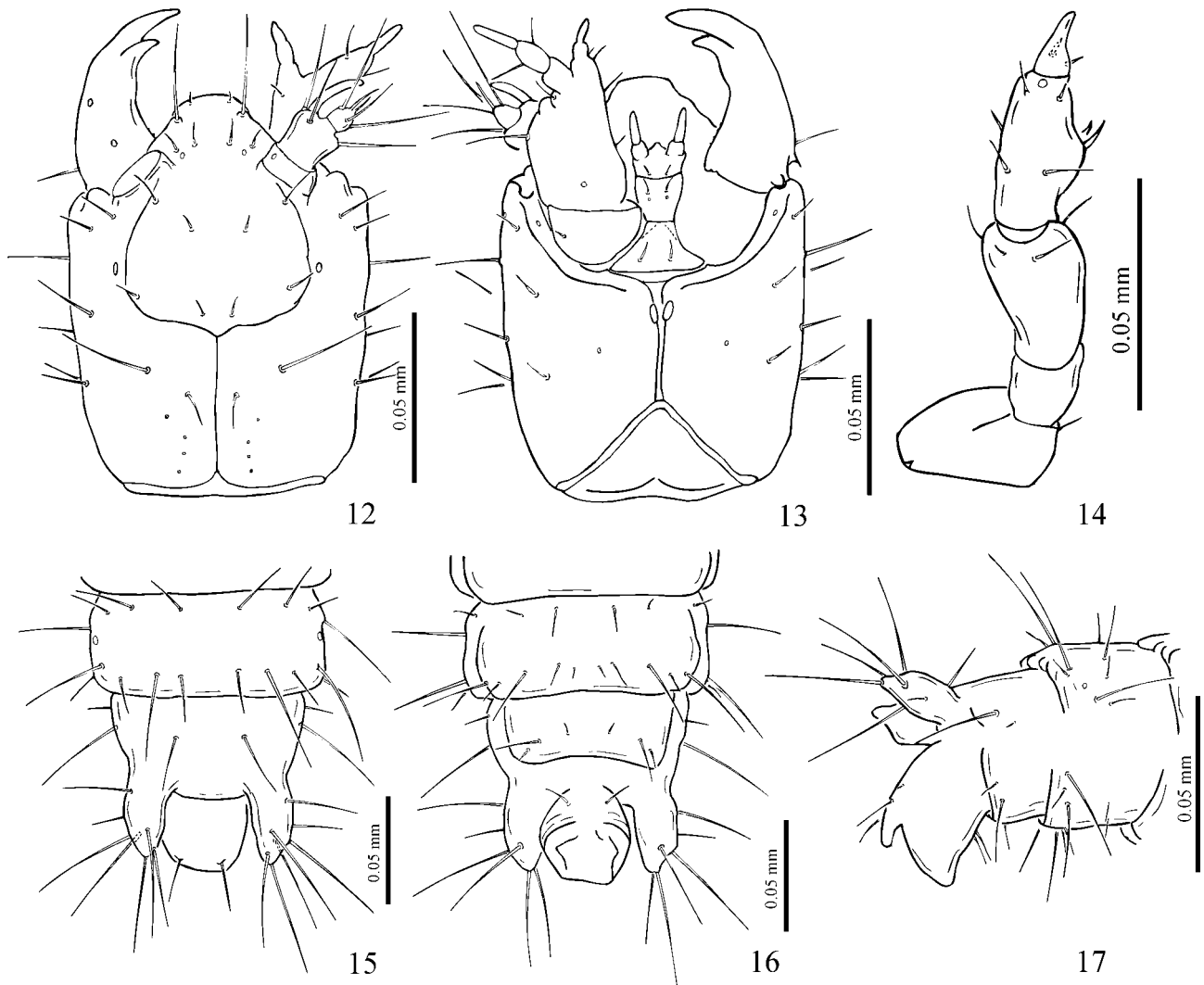
(Figs. 2–17)

Material. AUSTRALIA: Western Australia: 5 larvae (description is based on two apparently older instar larvae) and 3 adults, Walpole National Park, Giant Red Tingle Area, 6 km NE Coalbine beach, Berl. #130B, sand and fungus under litter Reg Tingle, 13.XII.1976, J. Kethley leg. FM(HD)#76-496.

Larval diagnosis. Head width 0.087–0.095 mm (n=2); nasale evenly convex, not serrate; baso-median and baso-lateral setae on each side of frontale separated by distance 2–3X longer than that between two baso-median setae; baso-lateral setae on frontale located basad of the level of large epicranial pores; antennal sensory appendage weakly curved, slightly shorter than antennomeres 2 and 3 combined; mandibular seta and basal mandibular pore located basad of distal mandibular pore (Fig. 12); mala with apical projection about as wide as mala itself; urogomphi about twice as long as their width at base.



FIGURES 2–11. Leptotyphlinae, larval morphology of the undescribed genus from Australia. 2—habitus, ventral view (head inserted; ventral view); 3—habitus, lateral view (head inserted, dorsal view); 4—anterior part of head showing right antenna with elongate and slightly curved sensorium, dorsal view; 5—base of stipes, cardo, labial palpi, prementum, mentum, free triangular submentum, and oblique hypostomal ridge, ventral view; 6—abdominal segments VIII, IX (bearing 1-segmented urogomphi indistinctly attached to tergum) and X, lateral view; 7—abdominal segments VI–X, dorsal view; 8—head, dorsal view; 9—head, ventral view; 10—right maxilla, ventral view; 11—thorax and abdominal segments I–IV, lateral view. Scale bar 0.05 mm.



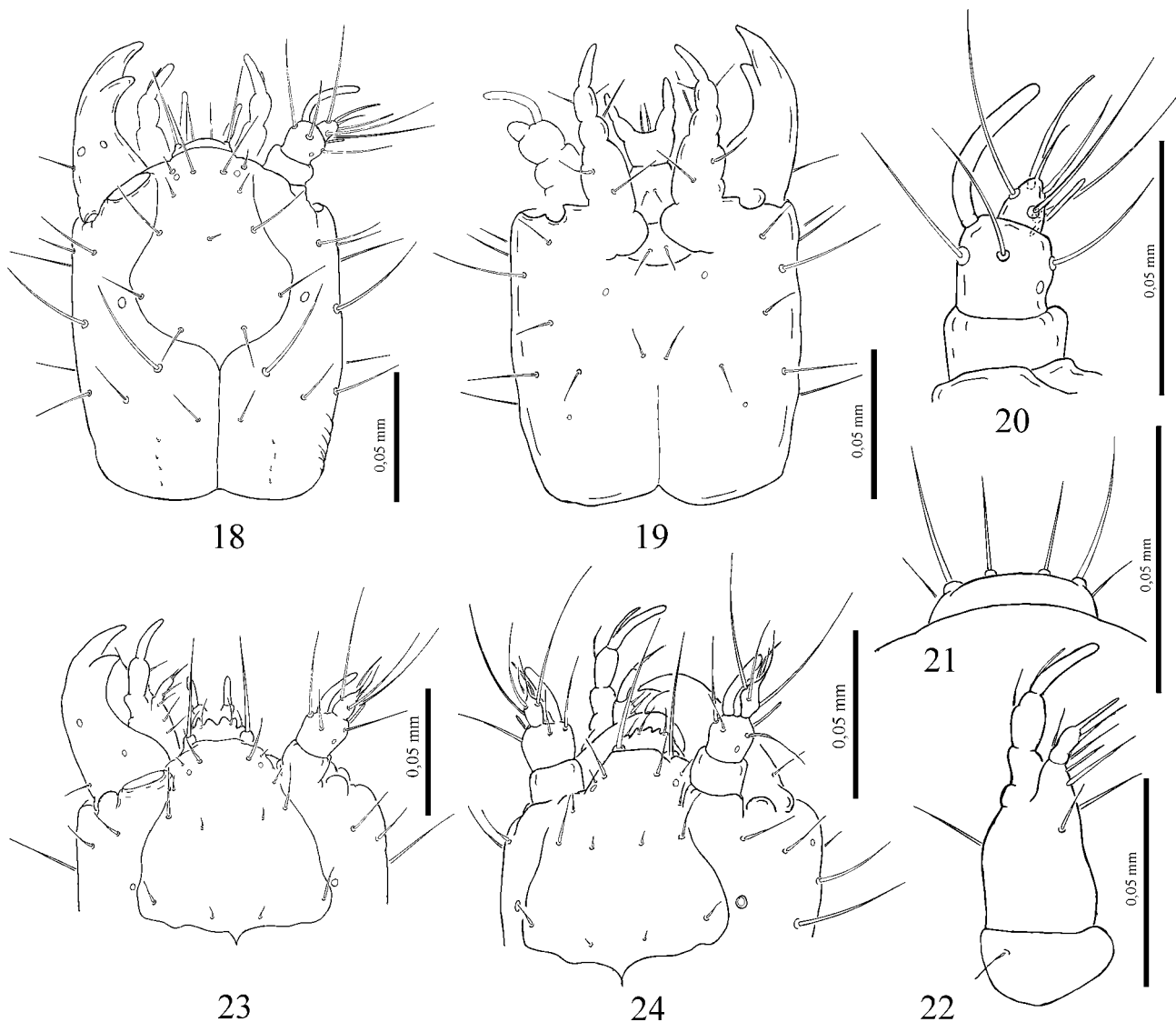
FIGURES 12–17. Leptotyphlinae, larval morphology of the undescribed genus from Australia. 12, 13—head (left mandible, right antenna and maxilla omitted), dorsal (12) and ventral (13); 14—right foreleg; 15, 16, 17—abdominal segments VIII, IX (with urogomphi) and X, dorsal (15), ventral (16) and lateral (17).

Mexican genus

(Figs. 18–22, 25–31)

Material. MEXICO: Hidalgo: 5 larvae (description is based on one apparently older instar larva) and 31 adults, 2.5–3.5 mi N Tlanchinol, 5100–5200', 10–11.VII.1973, cloud forest, berl., leaf & log litter, A. Newton leg. FMHD#73-1002.

Larval diagnosis. Head width 0.128 mm (n=1); nasale not serrate; frontale with baso-median and baso-lateral setae on each side separated by distance equal to that between two baso-median setae, baso-lateral setae located on about same level with epicranial pores; antennal sensory appendage curved, longer than antennomeres 2 and 3 combined; mandibular seta and basal mandibular pore located at about same level as distal mandibular pore (Fig. 18); mala with apical projection seta-like in appearance and at least half as wide as mala itself; urogomphi about as long as their width at base.



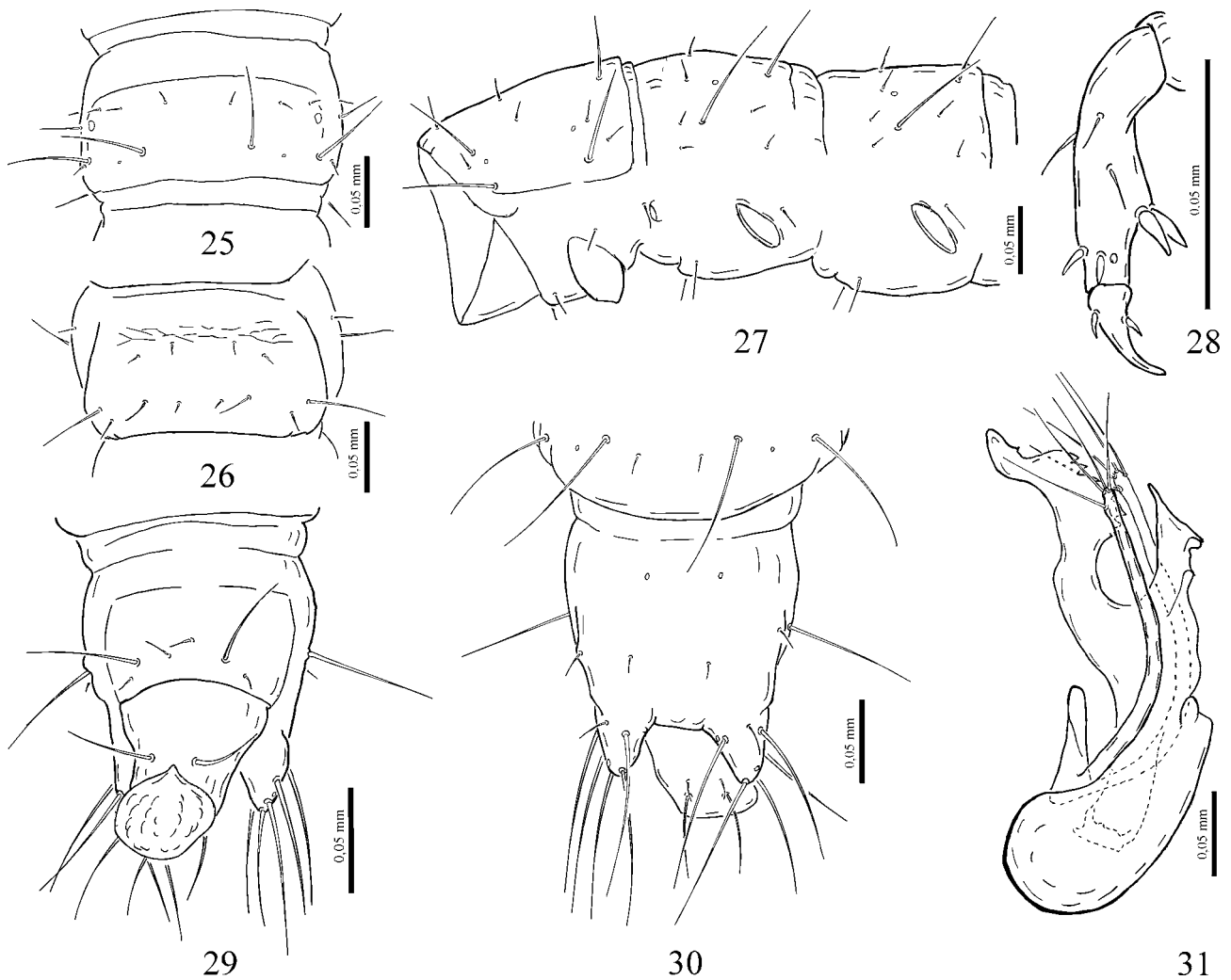
FIGURES 18–24. Leptotyphlinae, larval morphology of the undescribed genus from Mexico (18–22) and undescribed genus from Chile (23, 24). 18, 19, 23, 24—head, dorsal (18, 23, 24) and ventral (19) (left antenna and right mandible omitted); 20—right antenna, dorsal; 21—nasale, dorsal; 22—left maxilla, dorsal.

Chilean genus

(Figs. 23, 24)

Material. CHILE: Concepción: 5 larvae (description is based on two apparently older instar larvae) and 4 adults (one adult tentatively identified as *Eutyphlops* sp.), 8.4 km W La Florida, 170 m, 2.I.1983, subtropical xerophytic forest, berl. forest leaf & log litter, A. Newton & M. Thayer leg.

Larval diagnosis: Head width 0.106–0.118 mm (n=2). Nasale serrate; baso-median and baso-lateral setae on each side of frontale separated by distance about 1.5X longer than that between two baso-median setae; baso-lateral setae on frontale located basad of the level of large epicranial pores; antennal sensory appendage weakly curved, shorter than antennomeres 2 and 3 combined; mandibular seta and basal mandibular pore located basad of distal mandibular pore; mala with apical projection seta-like in appearance and at least half as wide as mala itself; urogomphi about twice as long as their width at base.



FIGURES 25–31. Leptotyphlinae, larval (25–30) and adult (31) morphology of the undescribed genus from Mexico. 25, 26—abdominal segment VI, dorsal (25) and ventral (26); 27—pro-, meso-, and metathorax, left lateral (legs omitted); 28—left fore tibiotarsus and claw, posterior; 29, 30—abdominal segments IX (with indistinctly articulated short urogomphi) and X, ventral (29) and dorsal (30); 31—aedeagus.

Key to the genera of Leptotyphlinae based on larvae

1. Antennal sensory appendage curved, longer than antennomeres 2 and 3 combined (Fig. 20); urogomphi about as long as their width at base (Fig. 30); mandibular seta and basal mandibular pore located at about same level with distal mandibular pore (Fig. 18); baso-lateral setae on frontale located on about same level with large epicranial pores (Fig. 18) Mexican genus
- 1'. Antennal sensory appendage almost straight, shorter than antennomeres 2 and 3 combined (Figs. 12, 23); urogomphi about twice as long as their width at base (Fig. 15); mandibular seta and basal mandibular pore located basad of distal mandibular pore (Figs. 12, 23); baso-lateral setae on frontale located basad of large epicranial pores (Figs. 12, 23) 2
2. Nasale serrate (Fig. 23); mala with apical projection seta-like in appearance, about half as wide as mala ..
.....Chilean genus
- 2'. Nasale not serrate (Fig. 12); mala with apical projection about as wide as mala itself..... Australian genus

Phylogenetic affinities of Leptotyphlinae inferred from larval morphology

This discussion is preliminary due to the lack of phylogenetic analysis of the Staphylinine Group of rove-beetle subfamilies, which is, however, in progress, and in the discussion to follow we partly rely on our preliminary results (Grebennikov & Newton 2007).

Presently described larval morphology supports the monophyly of the subfamily Leptotyphlinae. This assumption is based on the presence of the following character states, which are absent, or rarely encountered, among known Staphylinidae larvae: 1) stemmata are completely absent; 2) antennae are very short, only about 1/3 of length of head capsule; 3) mandibles have a single pre-apical tooth; 4) mandibles are almost straight and slightly curved with apices directed anteriorly; 5) all tibiotarsi are swollen at middle with two large ventral spines; 6) urogomphi are short and broad and only indistinctly articulated to tergum IX.

It is likely that the subfamily Leptotyphlinae is indeed a member of the Staphylinine Group of subfamilies (Lawrence & Newton 1982; Thayer 2005). Some of the character states of Leptotyphlinae supporting this placement are: 1) labrum fully fused with clypeus; 2) posterior tentorial arms thread-like and more than 20 times as long as wide; 3) posterior tentorial pits short, rounded to elongate; 4) cardo lacking transverse sclerotized ridge. These character states are also found in larvae of Steninae, Euaesthetinae, Pseudopsinae, Paederinae, Staphylininae, and in larvae of the family Scydmaenidae. The latter group is currently kept as an independent family, however it has been repeatedly suggested that Staphylinidae are paraphyletic with respect to Scydmaenidae (Lawrence & Newton 1982; Caterino *et al.* 2005; Beutel & Leschen 2005) and the latter group might well be a sub-unit of the Staphylinine Group of rove-beetle subfamilies (Lawrence & Newton 1982).

The sister-group relationships of the subfamily Leptotyphlinae based on larval characters remain unclear. Internal phylogeny of the Staphylinine Group is not yet fully resolved, although it is plausible to suggest that Megalopsidiinae are not most closely related to a clade of Steninae+Euaesthetinae (Leschen & Newton 2003) and that Pseudopsinae, Paederinae and Staphylininae form a clade (Grebennikov 2005). The present study of the larval morphology of Leptotyphlinae suggests that this subfamily might be a sister group to Pseudopsinae+Paederinae+Staphylininae, with the following morphological characters in support: 1) frontal arms lyri-form; 2) each maxilla articulated to head capsule by condyle and 3) maxillary mala parallel-sided (=finger-shaped) and articulated to stipes. However, phylogenetic analysis (now in progress by the authors for the Staphylinine Group using adult and larval characters) will be needed to obtain a well-supported conclusion.

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