#### Systematics

# First Description of Immature Stages of Tribe Mayetiini: The Larva and Pupa of *Mayetia pearsei* (Staphylinidae: Pselaphinae: Mayetiini)

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ABSTRACT Approximately 9,100 species belonging to the staphylinid beetle subfamily Pselaphinae have been described based on adults, but the larvae of only 19 species and 15 genera have been described in sufficient detail for systematic study, and the pupa of only a single species has been described. Larvae of the euplectine tribe Mayetiini (152 species, all in the genus Mayetia) have not been described previously. The larva and pupa of Mayetia pearsei Schuster et al. are described herein based on two larvae, a cast exuvium, and five pupae from soil wash samples containing numerous adults of the species. Larvae are distinguished from other described larvae of pselaphines based on the following combination of characters: eversible frontal vesicle simple, sac-like, with fine, dense terminal papillae; stemmata absent; epicranial stem absent; antenna two segmented, segment two bearing unbranched, elongate, sinuate sensorium; mesothoracic spiracle with large, fusiform peritreme; abdominal spiracles absent; A9 with V-shaped, apical emargination between short, fixed urogomphi. Pupae are similar to those of the European pselaphine *Plectophloeus fischeri* (Aubé) in having elongate prothoracic setate processes and spinose tubercles covering the antennae. The pupal description may represent the smallest coleopteran pupa described to date. Larvae and pupae of M. pearsei were found during July and August, whereas adults were found July-October in loamy sand in the floodplain of the Meramec River, Crawford County, MO.

KEY WORDS Staphylinidae, Pselaphinae, Euplectitae, short-winged mold beetles, rove beetles

The subfamily Pselaphinae (Coleoptera: Staphylinidae) is one of the most diverse groups of staphylinoid beetles, with  $\approx 9,100$  described species and 1,220 genera (Newton and Chandler 1989, Thayer 2005). Despite this diversity, larvae of a mere 19 species and 15 genera have been described and significant gaps exist in the representation of these larvae across higher pselaphine taxa (Carlton and Leschen 2008). Pupae are almost completely unknown, with that stage described for only a single species, *Plectophloeus fischeri* (Aubé), in sufficient detail to allow comparative study (Besuchet 1952). Besuchet (1956) also provided a few notes on the pupa of *Euplectus karsteni* Reichenbach but did not describe it.

The tribe Mayetiini includes only the genus *Mayetia*, with 130 Palearctic, 19 Nearctic, two Neotropical, and one Afrotropical species (Carlton and Robison 1996, Löbl and Besuchet 2004). Six species are known from the eastern United States, with the remainder of North American species known from Pacific Coastal regions. *Mayetia pearsei* Schuster et al. is apparently the most widespread eastern species, known from throughout the southeastern United States as far north as Indiana (Carlton and Robison 1996). In appropriate

habitats the species can be taken in large numbers using soil flotation and Berlese extractions of soil shaken from the roots of low vegetation, especially sedges (Cyperaceae) in bottomland woodlands. Using soil washing techniques, the second author was able to collect larvae and pupae that were reliably associated with adults of *M. pearsei*, and the morphology of those stages is the subject of this study, including notes on habitat and seasonality of the species. A second species, *Mayetia domestica* Schuster et al., also was collected during fieldwork in Missouri, and distributional and seasonal data for that species also are provided.

## Materials and Methods

Larval specimens were obtained by soil washing/flotation to separate heavy mineral soil from the beetles and other organic material. For most samples, the floated material was then processed in Berlese funnels. Although large numbers of adults were found by this method, only one larval specimen was recovered by Berlese extraction. Three samples of the floated organic material were processed with a modified heptane separation method described by Kethley (1991) rather than by Berlese extraction. Kethley's method was modified by using gasoline rather than pure heptane for the separation, and by using naphtha to clean the oily gasoline residue from the specimens. This gasoline separation method yielded a second larval

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specimen, five pupal specimens, and a larval exuvium attached to one of the pupae. Larvae, including the cast exuvium, were mounted on microscope slides in Hoyer's medium.

Some pupae were initially mounted with adults in euparal but were removed because of collapse from osmotic shock. After floating specimens off the original slides into 100% ethanol (EtOH), they were transferred through a concentration gradient of alcohol: water (100% EtOH, 95% EtOH, 50% EtOH) for  $\approx$ 1 h per stage and then to pure water. They were then placed into weak ( $\approx$ 5%), cold KOH solution until the original shapes of the pupal integuments were restored (≈30 min). After returning to 100% water, pupae were stained with chlorozol black, with addition of a few drops of weak KOH to destain to desired level. Pupae were then transferred through increasing concentrations of EtOH to 100% EtOH. A 1:1 mixture of EtOH and glycerine was added and mixed into the dish containing the pupae. The amount added was approximate equal to the original volume. The dish was allowed to air dry under a dust cover overnight. The specimens were then temporarily slide mounted in glycerine for study. Another pupal specimen was slide-mounted without staining in Hoyer's medium.

Most adults were lightly cleared in 10% KOH, transferred to 95% EtOH then 100% EtOH, and mounted on microscope slides in euparal. Some adults were studied in temporary cavity-slide mounts in lactic acid medium and then stored in 80% EtOH. Identifications were based on the key to females of eastern *Mayetia* species in Carlton and Robison (1996).

Material on which these descriptions were based was limited to two larvae and five pupae, one with a cast exuvium attached apically. The exuvium was too deformed to contribute to a detailed description but had sufficient integrity to confirm its association with the intact larvae and, in turn, confirm their association with the pupae. One of the two larvae was in excellent condition, mounted ventral side up, without distortion. The second larva was dorsal side up, but twisted laterally. It was suitable for checking individual characters in different orientations. The pupae initially mounted in euparal with the adults were in good condition, despite being unmounted and subsequently subjected to extensive handling and osmotic changes. One pupa was oriented ventral side up, and a second in lateral view during compound microscope study.

The species identification of immature stages is based on the association and dominance of *Mayetia pearsei* adults in the samples that yielded larvae and pupae. However, two specimens of *M. domestica* (among 102 *M. pearsei*) also were recovered from these samples, so the possibility that the larvae and/or pupae represent this species cannot be completely discounted.

Illustrations were prepared using a camera lucida mounted on a BMAX 50 compound microscope (Olympus, Tokyo, Japan). Figures were optimized for bilateral symmetry and assembled into plates using Adobe Photoshop (Adobe Systems, Mountain View, CA).

Specimens are deposited in the Louisiana State Arthropod Museum (LSAM) and in Larry Watrous' private collection (LEWC).

Larval Material Examined (n=3). USA, MO, Crawford Co., 5.3 miles SE Bourbon, 38.1173° N, 91.1519° W, 1-VII-2007, bottomland soil, #908, L. E. Watrous (one larva, LSAM); USA, MO, Crawford Co., 5.3 miles SE Bourbon, 38.1173° N, 91.1519° W, 8-VIII-2007, bottomland soil, #944, L. E. Watrous (1 larva, 1 exuvium, LSAM).

Pupal Material Examined (*n* = 5). USA, MO, Crawford Co., 5.3 miles SE Bourbon, 38.1173° N, 91.1519° W, 8.VIII.2007, bottomland soil, #944, L. E. Watrous (3 pupae, 1 with attached larval exuvium, LSAM); same locality, 16-VII-2008, bottomland soil, #1059, L. E. Watrous (2 pupae, LEWC).

Mayetia pearsei Adults Examined (n = 102). USA, MO, Crawford Co., 5.3 miles SE Bourbon, 38.1173° N, 91.1519° W, 1-VII-2007, bottomland soil, #908, L. E. Watrous (11  $\Omega$ , LSAM); same locality, 3-VII-2007, bottomland soil, #910, L. E. Watrous (1  $\mathcal{Q}$ , LSAM); same locality, 8.VIII.2007, bottomland soil, #944, L. E. Watrous (33  $\mathcal{Q}$ , LSAM); same locality, 27-VII-2007, bottomland soil, #935, L. E. Watrous (6 ♀, LSAM); USA, MO, Crawford Co., 6 miles SE Leasburg, 38.0299° N, 91.2141° W, 30-VI-2007, bottomland soil, #906, L. E. Watrous  $(2 \ \mathcal{Q}, LSAM)$ ; same locality, 3-VII-2007, bottomland soil, #911, L. E. Watrous (2 ♀, LSAM); USA, MO, Jefferson Co., 3.4 miles SE Pacific, 38.4564° N, 90.6895° W, 20-VI-2007, bottomland soil, #897, L. E. Watrous (1 ♀, LSAM); USA, MO, Jefferson Co., 1.8 miles SE Pacific, 38.4751° N, 90.7116° W, 19-VI-2007, sedge roots, #893, L. E. Watrous (2 ♀, LSAM); same locality, 31-V-2007, bottomland soil, #873, L. E. Watrous (2  $\Omega$ , LSAM); same locality, 16-VII-2008, bottomland soil, #1059, L. E. Watrous (31  $\Omega$ , LEWC): same locality, 31-VII-2008, bottomland soil, #1060 (11 LEWC).

Mayetia domestica Adults Examined (n = 40). USA, MO, Crawford Co., 5.3 miles SE Bourbon, 38.1173° N, 91.1519° W, 8-VIII-2007, bottomland soil, #944, L. E. Watrous (2 &, LSAM); USA, MO, Crawford Co., 6 miles SE Leasburg, 38.0299° N, 91.2141° W, 30-VI-2007, bottomland soil, #906, L. E. Watrous (2 &, LSAM); USA, MO, Lincoln Co., Cuivre River State Park, 39.0211° N, 90.91019097° W, 14-X-2007, prairie soil, #989, L. E. Watrous (1 Q, LSAM); same locality, 39.0199° N, 90.9101° W, 29.X.2007, prairie soil, #1016, L. E. Watrous (4 \, LSAM); USA, MO, Taney Co., Ozark Underground Lab, Resurrection Glade, 36.5810° N, 92.8643° W, 18-X-2007, glade soil, #990, L. E. Watrous (5  $\delta$ , 8  $\Omega$ , LSAM); same locality, 36.5818° N, 92.8643° W, 9-X-2007, glade soil, #997, L. E. Watrous (1  $\Omega$ , LSAM); same locality, 36.5789° N, 92.8641° W, 19-X-2007, soil under fungi, #998, L. E. Watrous  $(2 \, \mathring{\circ}, 1 \, \mathring{\circ}, LSAM)$ ; same locality,  $36.5585^{\circ} \, N$ , 92.8134° W, 21-X-2007, soil at base of slope, #1007, L. E. Watrous  $(2 \ \delta, 1 \ Q, LSAM)$ ; USA, MO. Washington Co., 15 miles. W. Potosi, 37.9282° N, 91.0627° W,

9-VII-2007, woodland soil, #917, L. E. Watrous (5 &, 6  $\mathbb{Q}$  , LSAM).

Mature Larva of *M. pearsei*. *Diagnosis*. Form elongate parallel, size minute, total length 1.0 mm. Setae of head and body simple, aciculate. Eversible frontal vesicle simple, sac-like, with fine, dense terminal papillae barely visible at 1,000×. Stemmata absent. Epicranial stem absent. Apparent antennal segment two bearing unbranched, elongate, sinuate sensorium. Mala triangular, extending beyond maxillary palpus. Mesothoracic spiracle with large, fusiform peritreme. Abdominal spiracles absent. A9 with V-shaped, apical emargination between short, fixed urogomphi.

Description. General (Fig. 1). Length 1.00 mm, greatest width (across mesothorax) 0.15 mm, head capsule width 0.11 mm (n=1). Mouthparts, antennae, and urogomphi lightly sclerotized, otherwise pale and apparently unsclerotized. Body surfaces smooth. Setae simple, straight, relatively short except elongate on A9.

Head (Fig. 2). Oval. Epicranial stem absent, frontal arms V-shaped, weakly convergent from frons then strongly convergent to midline. Stemmata absent. Dorsum of head bearing four pairs of lateral and two pairs of paramedial setae, and three pairs of frontal setae. Eversible frontal process broad, saccular, rounded apically, bearing minute papillae around apical surface (visible under oil at 1,000×). Antenna (Fig. 3) apparently two-segmented; segment I 0.06 mm long, 0.05 wide, glabrous, weakly annulate; segment II 0.04 mm long, 0.04 mm wide; bearing one basolateral seta and seven setae across dorsal, ventral, and distal aspects; large sensorium borne basolaterally, strongly curved medially, then weakly anteriorly, surpassing antennal apex; presumed segment III not differentiated from II, antennal apex bearing a long terminal seta. Anterior margin of labrum (Fig. 5) with two lateral pairs and one medial pair of minute tubercles. Mandibles (Fig. 4) nearly symmetrical, simple, sickleshaped, each with a lateral scrobe seta in basal onethird; dorsal and ventral cutting edges not differentiated, bearing low weak crenulations only. Articulation of maxilla (Fig. 6) with head capsule membranous, gula short, sutures widely separated. Maxillary cardines triangular, bearing a pair of setae; stipes broadly elongate, bearing one pair of ventral setae, one pair of anterolateral setae, and several distal setae that are continuous with malar setae; mala triangular, with at least 12 setae along mesial margin and an elongate seta at apex; maxillary palpi three-segmented, segment I short, segment II ovate, twice length of I, segment III conical, subequal in length to II, bearing a short sensory appendix. Mentum and postmentum not differentiated, bearing two pairs of ventral setae and two pairs of marginal setae; labial palpi minute, 1-segmented, widely separated.

Thorax. Prothoracic tergal plates paired, quadrate, each bearing six anterior marginal setae, two lateral marginal setae, and three posterior marginal setae, two submedian discal setae and one lateral discal seta; mesonotal plates paired, each bearing two rows of three discal setae each, and three lateral setae; meso-

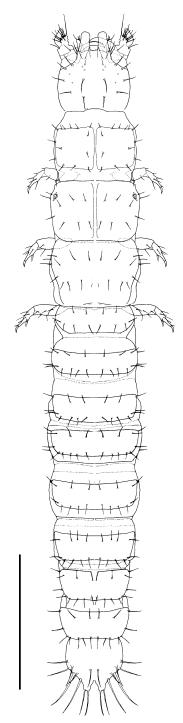
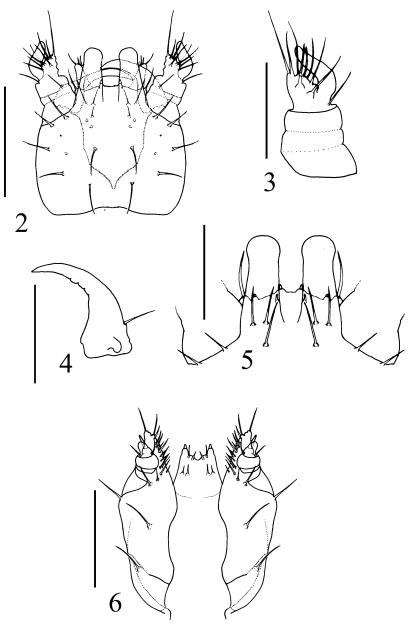


Fig. 1. M. pearsei mature larva, dorsal habitus (scale bar = 0.20 mm).

thoracic spiracles (Fig. 10) large (0.02 long by 0.01 mm wide) visible in both dorsal and ventral orientations, borne in ventrolateral pleural region between pro and mesothorax, annular with large fusiform peritreme; metanotal plate undivided, with three pairs of discal

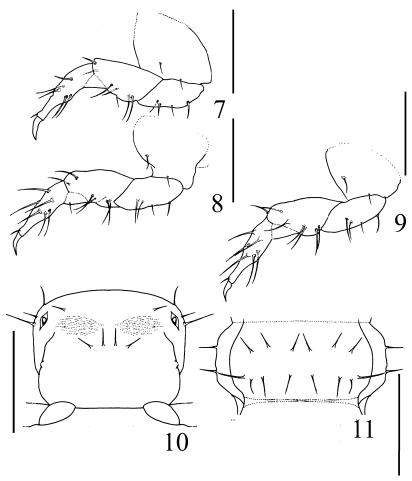


Figs. 2–6. M. pearsei. (2) Head. (3) Antenna. (4) Right mandible. (5) Eversible vesicles of frontal area. (6) Ventral mouthparts (scale bars = 0.10 mm [Fig. 2] and 0.05 mm [Figs. 3–6]).

setae in two rows and four pairs of lateral setae. Thoracic pleura and sterna (Fig. 10) nonsclerotized, each bearing an anterolateral pair of setae and a median transverse row of four setae. Legs (Figs. 7–9) similar to each other, lacking tubercles and other modifications; coxae short conical, each bearing one sublateral seta and one distal seta at junction with trochanter; trochanters  $1.9\times$  longer than wide, bearing three anterior setae and two posterior setae; femora  $1.7\times$  longer than wide, each with three anterior and two posterior ventral setae, and two setae near dorsal apex; tibiae  $5.0\times$  longer than greatest width, narrowing in

apical one third, each bearing three anterior setae and two posterior setae, and a single pretarsal seta; pretarsal claw simple sickle-shaped.

Abdomen. Tergal plates narrow transverse, A1–A8 (Fig. 11) with six setae across anterior margin, eight setae along posterior margin, and two pairs of lateral dorsal setae, A9 more heavily sclerotized, especially adjacent to urogomphi, bearing two pairs of discal setae and three pairs of lateral setae, plus a pair of elongate setae at base of urogomphus. Urogomphi short, rigid, blunt, each ramus with a pair of elongate apical setae. Abdominal ventrites 1–8 each with an



Figs. 7–11. *M. pearsei*. (7) Prothoracic leg. (8) Mesothoracic leg. (9) Metathoracic leg. (10) Mesothoracic ventrite. (11) Abdominal ventrite 2 (scale bars = 0.05 mm [Figs. 7–9] and 0.10 mm [Figs. 10–11]).

anterior row of six setae and a posterior row of ten setae, the latter with six normal sized setae and four smaller (one half length of normal) setae, plus two pairs of lateral ventral setae. A10 short triangular, ventrally oriented. Abdominal spiracles absent.

**Pupa of M. pearsei.** Description. Pharate pupa with larval exuvium attached to abdomen of one specimen in original sample. Length 0.90 mm, greatest width (across elytra) 0.19 mm, width of pronotum 0.16 mm (n = 1). Pupa exarate, head strongly deflexed against prosternum. Nine abdominal segments visible dorsally, seven ventrites, counting fleshy appendagebearing terminal segment (A9). Pupal integument pale yellow, adult integument clearly visible within pupa. Sacs enclosing appendages undifferentiated (i.e., lacking clearly defined segmental boundaries) and lacking surface detail, except antennae, which are covered by large, broad spinose tubercles. Head not clearly differentiated and lacking setae. Pronotum bearing two pairs of anterior, two pairs of sublateral, one pair of discal setae, and one pair of posterior marginal setae. Pronotum bearing a pair of submedian elongate setate processes expanding at bases and continuous with pupal integument (i.e., lacking typical setal bases). Meso- and metathorax dorsally with two pairs of anteriolateral setae and two pairs of discal setae. Setae absent from thoracic ventrites. Each leg with a single long seta at femoral-tibial angle. Each elytral pad with three setae. Metathoracic wing pads visible posterior to elytral pads, but lacking traces of adult flight wings. Dorsal A1-A2 short  $(0.6 \times \text{length of})$ A3), with two pairs of closely spaced submedian setae and a pair of sublateral setae; A3 with two lateral setae and four discal setae arranged in a transverse row, A4-A7 with a pair of submedian setae, a pair of dorsolateral setae, and two pairs of posterior setae, A8 with a pair of submedian and two pairs of dorsolateral setae. Ventrite 1 with a single pair of lateral setae, ventrites 2-4 with a pair of posterior submedian setae and two pairs of postlateral setae, ventrite 5 with two pairs of lateral setae and a pair of postlateral setae, ventrite 6 with a pair of postlateral setae. A9 fleshy and bearing two long filaments that are minutely, sparsely serrate under 1,000× magnification. Functional spiracles visible on A1-A2 only.

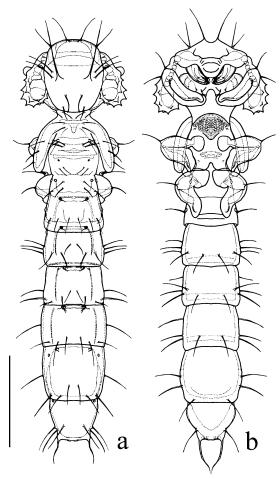


Fig. 12. M. pearsei pharate pupa. (a) Dorsal habitus. (b) Ventral habitus (scale bar = 0.20 mm).

# Discussion

The tribe Mayetiini is currently placed in the supertribe Euplectitae, one of six supertribes in the sub-

family (Newton et al. 2001), but in older classifications it was included within the Faronini (=supertribe Faronitae in current classification) (Jeannel and Coiffait 1955), apparently based on the elongate, typically staphylinid-like body form of adults, which is reminiscent of other faronines. The presence of an eversible vesicle on the head of larvae of M. pearsei corroborates the exclusion from Faronitae (Newton 1991). Based on the few available descriptions of other euplectine larvae, M. pearsei larvae are typically euplectine, but with a suite of character losses that are probably associated with minute body size. The elongate, parallel body form, simple sac-like eversible vesicle of the head, simple unbranched antennal sensorium, and the presence of short, fixed urogomphi are all typical of described euplectine larvae (Besuchet 1952, De Marzo 1987, Newton 1991, Kaupp 1997). By contrast, the larva of M. pearsei lacks stemmata and possesses only a single pair of large mesothoracic spiracles, with the typical complement on A1-A8 completely absent. These losses may be associated with extreme small size as noted by Grebennikov and Beutel (2002) working with larvae of the featherwing beetle species *Ptinella tenella* (Erichson) (Ptiliidae), which are approximately the same size as the larvae considered here.

To our knowledge, the pupa of M. pearsei is the smallest Coleoptera pupa described to date. Many pupae of Ptiliidae are undoubtedly smaller, but only the pupae of Acrotrichis spp., with relatively large species, have been described in that family (Hinton 1941, DeConinck and Coessens 1981). The pupa of M. pearsei is similar in several ways to the pupa of P. fischeri described and illustrated by Besuchet (1952). The broad tubercles of the antennae, elongate setaelike processes of the pronotum, and the paired fleshy processes of A9 seem identical in the two species insofar as can be determined from Besuchet's illustration and brief description. These three points of similarity can serve as a beginning of comparative study of pselaphine pupae if and when those stages become known for additional species. The pupa of M.



Fig. 13. M. pearsei habitat, Crawford County, MO, USA. (a) General view of understory vegetation. (b) Herbaceous plants and soil surface.

*pearsei* is obviously smaller (0.9 versus 1.3 mm), much more elongate, and lacks stemmata.

The immature stages of M. pearsei were collected in a floodplain area of the Meramec River, Crawford County, MO (Fig. 13). The site was  $\approx$ 50 m from the river edge and 300 m from the nearest hillside and rock outcrops. The soil itself was loamy sand, with no rocks for as deep as was sampled ( $\approx$ 75 cm). The largest trees in the habitat were American sycamore (*Platanus oc*cidentalis L.), oaks (Quercus spp.), and black walnut (Juglans nigra L.), with under-story trees of box elder (Acer negundo L.), and common paw paw [Asimina triloba (L.) Dunall. Ground cover was mostly wood nettle [Laportea canadensis (L.) Wedd.], with a few grasses and other scattered plants; leaf litter was thin to absent. The grasses in the habitat were small, with very little grass sod, and the soil lacked a concentrated root mat of any type. The site also lacked poorly drained areas with associated sedges. Perhaps because of the thin plant cover and root mat, the M. pearsei were evenly dispersed in the soil, and not concentrated around grass sod or other plant roots.

During early spring 2008, the Meramec River flooded to near record levels, and the *M. pearsei* collecting site was covered by 4–5 m of water for a period of time. All the sampling disturbance from the previous season was washed away or filled, and 2–3 cm of new sand was deposited on top. Despite the flooding, the soil beetle population seemed unaffected. During July of the flood year, *M. pearsei* was found in the same places and in about the same population density as observed in 2007.

M. domestica was also relatively common in soil wash samples from numerous localities in Missouri. Most of the records are from the Ozark Region of southern Missouri; however, specimens from Cuivre River State Park in east central Missouri represent the northern and eastern distribution limits for the species, and are the first records of M. domestica from a glaciated region. The vast majority of specimens were collected from relatively xeric upland forest and glade habitats, though a few were taken in bottomlands, where they apparently are syntopic with M. pearsei. The sex ratio for *M. domestica* was about even (18  $\delta$ :22 ♀), indicating sexually reproducing populations. All M. pearsei collected were females, suggesting parthenogenesis, as reported previously by Carlton and Robison (1996).

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### References Cited

- Besuchet, C. 1952. Larves et nymphes de *Plectophloeus* (Col. Pselaphidae). Bull. Soc. Entomol. Suisse 25: 251–256
- Besuchet, C. 1956. Larves et nymphes de Psélaphides (*Coléoptères*). Rev. Suisse Zool. 63: 697–705.
- Carlton, C. E., and R.A.B. Leschen. 2008. Description of the larva of *Pselaphophus atriventris* (Westwood) (Staphylinidae: Pselaphinae: Pselaphini) with notes on its life history and a list of described pselaphine immature stages. Ann. Entomol. Soc. Am. 101: 13–19.
- Carlton, C. E., and H. W. Robison. 1996. Notes on Mayetia pearsei Schuster, Marsh and Park, with a revised key to eastern Mayetia species (Staphylinidae: Pselaphinae). Coleopt. Bull. 50: 244–250.
- DeConinck, D., and R. Coessens. 1981. Life cycle and reproductive pattern of Acrotrichis intermedia (Coleoptera: Ptiliidae) in experimental conditions. J. Nat. Hist. 15: 1047–1055.
- De Marzo, L. 1987. Morfologia delle larva matura in alcuni Pselafidi (Coleoptera). Entomologica (Bari) 22: 97–135.
- Grebennikov, V. V., and R. G. Beutel. 2002. Morphology of the minute larva of *Ptenella tenella*, with special reference to effects of miniaturisation and the systematic position of Ptiliidae (Coleoptera: Staphylinoidea). Arthropod Struct. Dev. 31: 157–172.
- Hinton, H. E. 1941. The immature stages of Acrotrichis fascicularis (Herbst) (Col., Ptiliidae). Entomol. Mon. Mag. 77: 245–250.
- Jeannel, R., and H. Coiffait. 1955. Les Mayetia M. et R. sont des Pselaphides. Rev. Fr. Entomol. 22: 5–8.
- Kaupp, A. 1997. Beitrag zur Larvalmorphologie der Palpenkäfer (Coleoptera: Pselaphidae). Entomol. Blätter. 93: 57–68
- Kethley, J. 1991. A procedure for extraction of microarthropods from bulk soil samples with emphasis on inactive stages. Agric. Ecosyst. Environ. 34: 193–200.
- Löbl, I., and C. Besuchet. 2004. Subfamily Pselaphinae Latreille, 1802, pp. 272–329. In I. Löbl and A. Smetana [eds.], Catalogue of Palearctic Coleoptera, vol. 2. Apollo Books, Stenstrup, Denmark.
- Newton, A. F., Jr. 1991. Pselaphidae (Staphylinoidea), pp. 353–355. In F. W. Stehr [ed.], Immature insects, vol. 2. Kendall/Hunt Publishing Co., Dubuque, IA.
- Newton, A. F., Jr., M. K. Thayer, J. S. Ashe, and D. S. Chandler. 2001. 22. Staphylinidae Latreille, 1802, pp. 271–418.
  In R. H. Arnett, Jr., and M. C. Thomas [eds.], American beetles, vol. 1. CRC, New York.
- Newton, A. F., Jr., and D. S. Chandler. 1989. World catalog of the genera of Pselaphidae (Coleoptera). Fieldiana Zool. NS 53: iv + 93 pp.
- Thayer, M. K. 2005. 11.7. Staphylinidae Latreille, 1802, pp. 296–344. In R. G. Beutel & R.A.B. Leschen [eds.], Coleoptera, beetles volume 1: morphology and systematics. Handbuch der Zoologie Band IV Arthropoda: Insecta. W. de Gruyter, Berlin, Germany.

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