



A New Genus and Species of Hetaeriinae (Coleoptera: Histeridae) from Southwestern North America

Authors: Kovarik, Peter W., and Tishechkin, Alexey K.

Source: The Coleopterists Bulletin, 58(3) : 317-327

Published By: The Coleopterists Society

URL: <https://doi.org/10.1649/617>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

**A NEW GENUS AND SPECIES OF HETAERIINAE (COLEOPTERA: HISTERIDAE)
FROM SOUTHWESTERN NORTH AMERICA**

PETER W. KOVARIK

Museum of Biological Diversity, The Ohio State University
1315 Kinnear Rd., Columbus, OH 43212, U.S.A.

AND

ALEXEY K. TISHECHKIN

Department of Entomology
LSU Agricultural Center, Baton Rouge, LA 70803-1710, U.S.A.

Abstract

A **new genus and species** of hetaeriine histerid is described. *Aritaerius pallidus* is known almost exclusively from specimens collected at UV light. It inhabits xeric areas in the U. S., in Arizona, and in Nuevo Leon and Tamaulipas, Mexico.

The Hetaeriinae is a Neotropical and Holarctic group of obligate myrmeco- and termitophilic histerid beetles. The North American hetaeriine fauna is fairly diverse including 14 genera and 48 species (Wenzel 1962; Mazur 1997; Kovarik and Caterino 2001). This paper focuses on an undescribed species discovered decades ago. Wenzel (1962) was the first to mention this species in print and assigned it to the genus *Chrysetaerius* Reichensperger. Until Wenzel's (1962) publication, all *Chrysetaerius* species were known only from northern Argentina and southern Brazil, so the occurrence of a new species in North America represented a considerable range extension for the genus. However, extremely broad ranges are characteristic of other myrmecophilic histerid genera and by itself this range extension is unremarkable. What is significant is that the supposed range extension placed the North American *Chrysetaerius* well beyond the northern limits of its ant host, *Eciton* Latreille. According to Helava *et al.* (1985), hetaeriine genera tend to exhibit a high degree of host specificity at the genus level. This discrepancy ultimately led to a comparison of the North American *Chrysetaerius* with the type species, *C. iheringi* Reichensperger. Once the male genitalia of the North American species was dissected and examined, it became clear that this species was not a *Chrysetaerius*, but rather a member of a new genus.

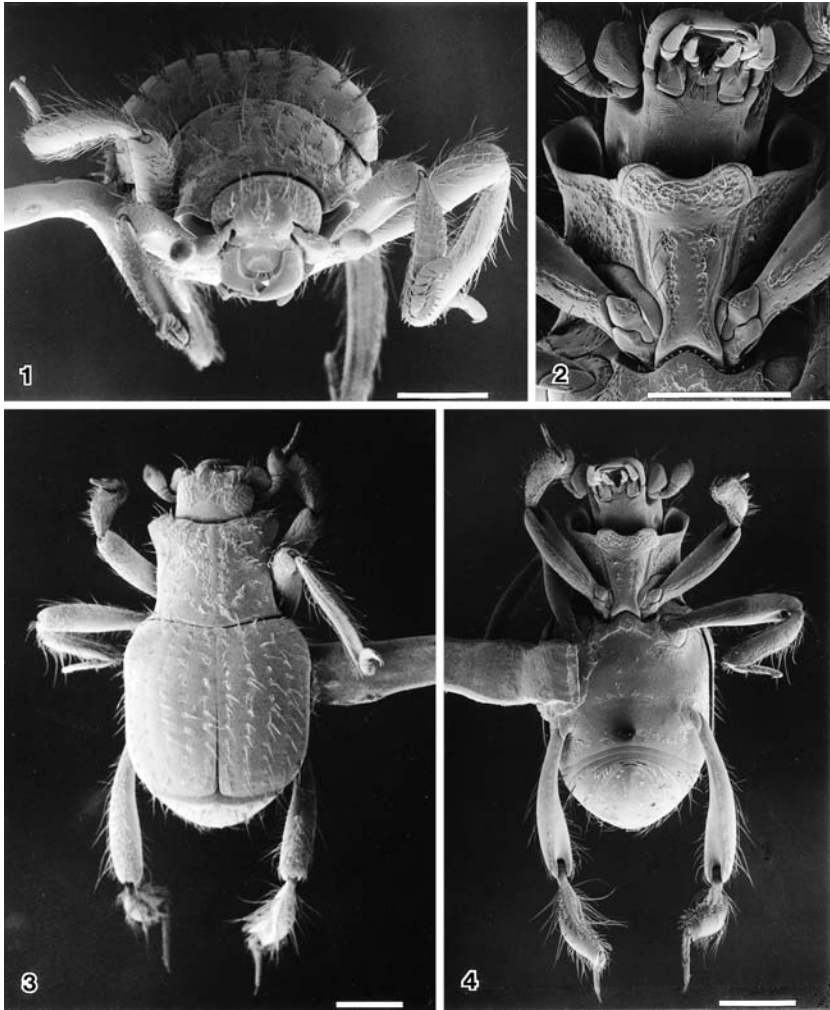
Materials and Methods

Structures intended for study via light microscopy, including male terminalia, mouthparts, and hind wings, were dissected, cleared in lactic acid, and slide mounted with Hoyers' medium. Depression slides were used for mounting male terminalia while standard slides were used for mounting mouthparts and hind wings. In order to prevent breakage and flattening of mouthparts, several shards of glass were used to suspend the cover slip above the subject to protect these structures. Hind wings were prepared for study by softening and expanding them in near-boiling soapy water. All slide-mounted material was studied and illustrated with a Wild M-20 compound microscope fitted with camera lucida. Specimens and structures intended for SEM were cleaned by sonication in Windex®, transferred to 100% ethanol, and subsequently air dried on filter paper. Dissected structures such as antennae, mandibles and the epipharynx were mounted on

aluminum stubs with double-stick tape. Whole specimens were glued to the bent, flattened end of a centimeter length of an # 000 insect pin. The mounted beetles were then secured in micro clips mounted on a large aluminum stub. Adjustments in specimen orientation were made via a surgical clamp. Specimens were gold/palladium sputter-coated and photographed using a J.E.O.L. Model JSM-820 S.E.M. operating at 20 kV.

Most morphological terminology for external features essentially follows Wenzel (1941, 1944). Terms used for surface sculpture were adopted from Harris (1979). Antennal club sensilla terminology follows Borden (1968). The epipharyngeal terminology essentially follows that of Kovarik and Caterino (2001) with a few minor additions. The two oblique rows of setae that demarcate the medial area are termed the *inner brushes* (IB). The fringe bordering the lateral areas is termed the *lateral fringe*. The group of short, stiff setae is generally borne on the medial area is termed the *medial brush*. Some terminology for the mandibles is also new. The upper mandibular surface is divisible into a *dorsolateral area* (DL), a *dorsomesal area* (DM). The surface of the dorsolateral area is commonly textured and setose. Long, robust setae located on the dorsolateral area appear to be contact chemoreceptors. The surface of the dorsomesal area is generally smooth. The prosthema (PR) is a setal fringe located along the inner margin of the mandibles. While gross morphological terminology of the maxilla is that of Crampton (1923) and Williams (1938), a detailed description of this structure in histrid beetles appears in Kovarik and Caterino (2001). Some new terms are applied to maxillary structures that were mentioned by Kovarik and Caterino (2001). The lateral cluster of sensilla digitiformia often borne on the terminal maxillary [and labial] palpomeres are termed the *palpal organ*. The large tooth-like structure partially imbedded in the distal anterior surface of the lacinia is a termed the *lacinial tooth*. Terminology for the gross morphology of the prementum follows that of Williams (1938) but the internal base or *substructure* of the prementum has apparently been overlooked and consequently terminology presented here is new. Each palpiger typically bears an inwardly curving projection extending its outer base termed a *basal extension* (BE). The basal substructure consists of a body that bears a pair of produced, elevated, and laterally flattened processes termed *alae* (AL). The alae are typically closed ventromesally by thin cuticle, termed the *cupule*. A pair of variable, dorsoventrally flattened projections termed *substructure legs* (SL) extend posteriorly from the substructure body. Hind wing venation follows that of Kukulová-Peck and Lawrence (1993). Aedeagal terminology follows Lawrence and Britton (1991). Terminology for the component structures of the male internal abdominal segments VIII and IX is that of Kovarik *et al.* (1999) and Kovarik and Caterino (2001). Some mention of how this terminology compares with that used by Helava *et al.* is warranted. Paired vela (VE), referred to as “disks” by Helava *et al.* (1985), are borne at the apex of the coxites in some hetaerines. The vela are inflatable membranes that apparently assist males in gaining purchase during copulation (Kovarik *et al.* 1999; Kovarik and Caterino 2001). The proper term for Helava *et al.* (1985) “sternite of 9th abdominal segment” is the spiculum gastrale. Helava *et al.* (1985) applied two different terms to what appear to be homologous structures: “internal guide” and “movable armature.” To reconcile this problem, we selected a more functionally neutral term “*ventral process*” (VP) as a replacement name.

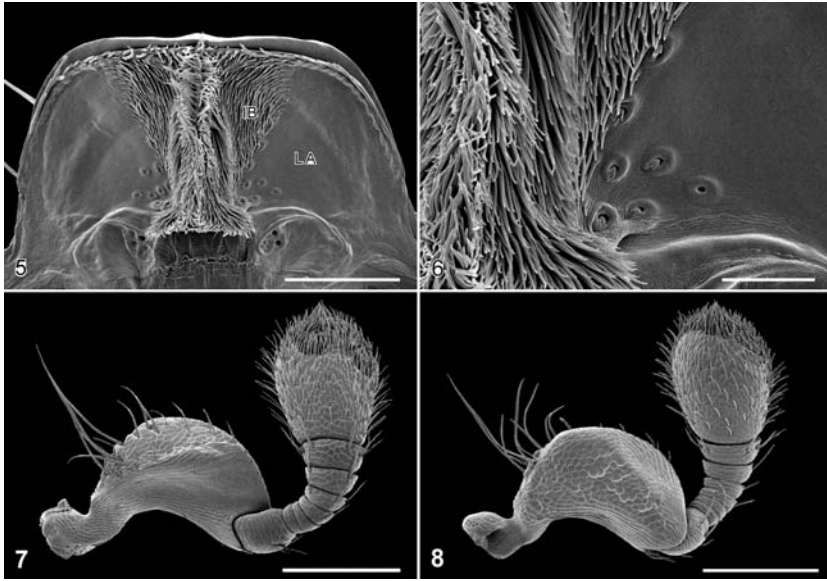
Length measurements were taken from the apex of pronotum to the elytral apices. Width measurements were taken between the humeral angles of the elytra. Information of different labels is divided by slashes. The following acronyms appear in the text below: FMNH—Field Museum of Natural History; UAIC—University of Arizona Insect Collection; AMNH—American Museum of Natural History; ATC—A.K.Tishechkin histrid collection; NDC—N. Dégallier histrid collection; PWKC—P. W. Kovarik histrid collection; SMC—S.Mazur histrid collection.



Figs. 1–4. *Aritaerius pallidus*. 1) Frontal habitus; 2) prosternum; 3) dorsal habitus; 4) ventral habitus. Line scales = 0.25 mm.

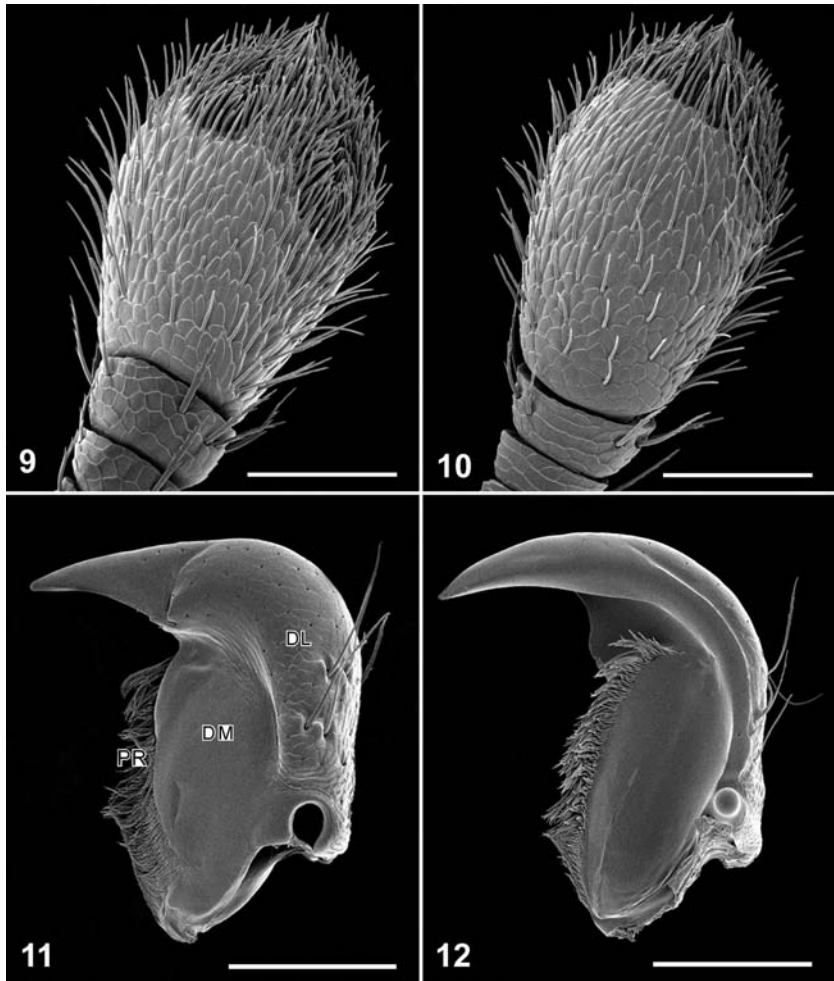
Aritaerius Kovarik and Tishechkin, new genus
(Figs. 1, 3, 5–28)

Description. Head: About as long as wide. Antenna (Figs. 7, 8): Slightly longer than width of head capsule. Scape: Petiolate basally, abruptly expanded distally with dorsal surface anteriorly imbricate and posteriorly substrigulate; ventral surface with uniform imbricate texture; minute to relatively long pectinate setae present mainly on anterior surface. Funicle: Antennomeres imbricately textured and with basal antennomere about as long as combined length of next 4 antennomeres and bearing several pectinate setae on posterior surface; subsequent antennomeres gradually expanding with 3 terminal antennomeres bearing distal whorl of short pectinate setae.



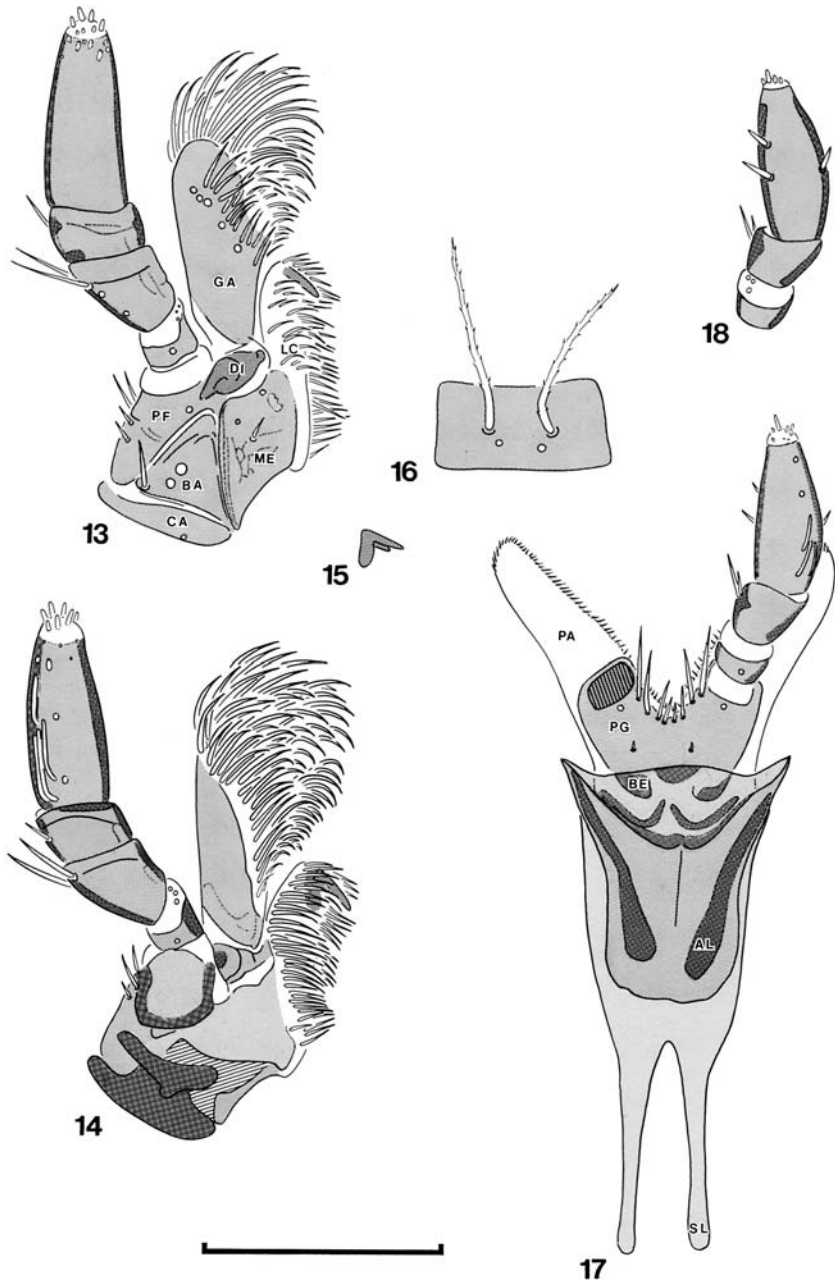
Figs. 5–8. *Aritaerius pallidus* epipharynx and antennae. **5)** Labrum epipharynx. Line scales = 0.45 mm.; **6)** labrum epipharynx, epipharyngeal sensillae detail. Line scales = 0.01 mm.; **7)** antenna, dorsal view; **8)** antenna, ventral view. Line scales = 0.1 mm.

Club (Figs. 9, 10): Oval, with imbricate surface somewhat sparsely covered with sensilla trichodea; terminal sensor plaque of sensilla basiconica present at antennal apex. Eyes (Figs. 1, 3): Large with large ommatidia. Epipharynx (Figs. 5, 6): Somewhat trapezoidal in outline; lateral area (LA) margin with inconspicuous fringe of long setae; lateral area broad, glabrous, and with mesal sensilla cluster; inner brush (IB) a mat of short dorsally oriented setae; medial area entirely covered with setae and bearing an elaborate comb-like structure at midline; medial brush setae short, robust, and thorn-like. Mandibles (Figs. 11, 12): Anterolateral area (AL) imbricate, basally constricted and apically expanded, and with numerous minute discal setae and several short to relatively long lateral contact chemoreceptors; anteromedial area (AM) largely glabrous with some imbricate texture at apex; prostheca setae short to medium length; posterior surface of mandible largely untextured. Maxilla (Figs. 13–15): Galea (GA): Elongate and nearly parallel-sided, only slightly expanded distally; dorsal surface sclerotized except for membranous areas along apical and mesal margins bearing brush of short to long hooked setae; ventral surface sclerotized and bearing comb of short setae and multiple pores near apex. Lacinea (LC): Anterior surface with several discal setae; lacinial tooth (Fig. 15) robust, with basal portion about as long as teeth; brush setae short and slender and covering most of dorsal lacineal surface. Mediostipes (ME): Slightly textured, about as long as wide, and with a short seta, 2 pores, and small internal cuticular cavity. Basistipes (BA): Untextured, and with medium-length slender, primary seta and 2 pores. Cardo (CA): Much wider than long and with single pore. Palpifer (PF): Slightly textured and with several short, slender setae near lateral margin and single ventral pore. Dististipes (DI): Small and well sclerotized. Palp: Proximal palpomere about half as long as wide; with ventral pore and lateral minute setal cluster; second palpomere about 1.5× as long as wide and bearing 2 medium-length distolateral setae and usually 2 lateral pores; third palpomere about as long as wide and with single distolateral seta; terminal palpomere about 3× as long as wide; with 2 or 3 lateral pores and several pores and sensilla near apex; palpal organ (Fig. 14) extending nearly to apex. Labium (Figs. 16–18): Mentum (Fig. 16): Rectangular in outline and with 2 long robust pectinate setae and 2 pores. Prementum (Fig. 17, 18): Paraglossae (PA): Lobes elongate, narrow and fringed with minute setae; glossal lobes

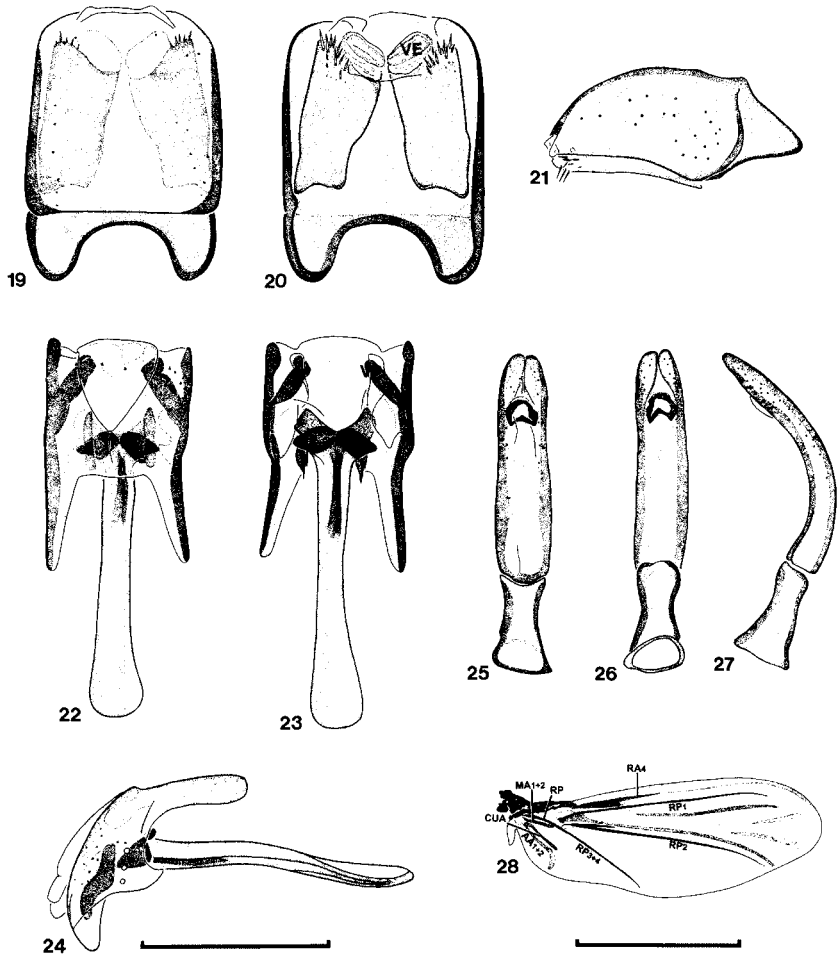


Figs. 9–12. *Aritaerius pallidus* antennae and mandibles. **9)** Antennal club, dorsal view; **10)** antennal club, ventral view. Line scales = 0.05 mm; **11)** right mandible, dorsal view; **12)** left mandible, ventral view. Line scale = 0.09 mm.

undifferentiated. Palp: Palpigers (PG) fused with 2 minute basal setae, several longer apical setae, and 2 pores on ventral surface; basal extension (BE) extremely short; proximal palpomere about half as long as wide; second palpomere about as long as wide and with 2 short distomesal setae; terminal palpomere nearly 3 times as long as wide, dorsal surface with 2 pores, ventral surface with 2 mesal and 1 lateral setae; palpal organ located in basal half of segment. Substructure: Pair of transversely pigmented sclerites subtending basal extensions of palpigers; cupule about as long as wide and overlying alae (AL); legs (SL) relatively short and parallel sided. Prothorax: Subcylindrical and laterally inwardly arcuate in dorsal view; apical angles expanded to receive antennae. Elytra: About as wide as long and wider than prothorax. Hind wings (Fig. 28): R4 and RP separate; RP relatively long; RA3+4 stigma more than 2× longer than wide; RA3 absent; RA4 and



Figs. 13–18. *Artaerius pallidus* maxilla and labium. **13)** Right maxilla, ventral view; **14)** right maxilla, dorsal view; **15)** maxillary tooth, dorsal view; **16)** mentum, ventral view; **17)** prementum, ventral view (left ligular fringe and right labial palp omitted for clarity); **18)** right labial palp, dorsal view. Line scale = 0.1 mm.



Figs. 19–28. *Aritaerius pallidus* ♂ terminalia and hind wing. 19) Eighth segment dorsal view; 20) ventral view; 21) lateral view; 22) ninth segment dorsal view; 23) ventral view; 24) lateral view; 25) aedeagus dorsal view; 26) ventral view; 27) lateral view. Line scale = 0.2 mm; 28) hind wing. Line scale = 1.5 mm.

RP1 dark and distinct with RP1 appearing vein-like; RP connected to but not fused with MA1+2; RP2 and RP3+4 complete, extending to wing margin as veins; Mp3+4 absent; CUA2+3+4 absent; CUA and AA1+2 represented by pigmented membranes and separated along their length; AP3+4 absent; jugal lobe reduced. Propygidium and pygidium: Convex and variably setose. Prosternum: Anteriorly and posteriorly emarginated. Legs: Very long, femora and tibiae sub-cylindrical. Male Terminalia (Figs. 19–21): Eighth segment (Figs. 19–21) with tergite obtusely emarginate proximally; coxites plate-like with apical velum. Ninth segment (Figs. 22–24) deeply emarginated proximally; ventral processes present; coxal carapace triangular and membranous, about as long as wide, and not extending much beyond apex of tergite; spiculum gastrale elongate and expanded distally. Aedeagus (Figs. 25–27) with parameres relatively long and strongly curved; phallobase short, tubular, and flaring distally.

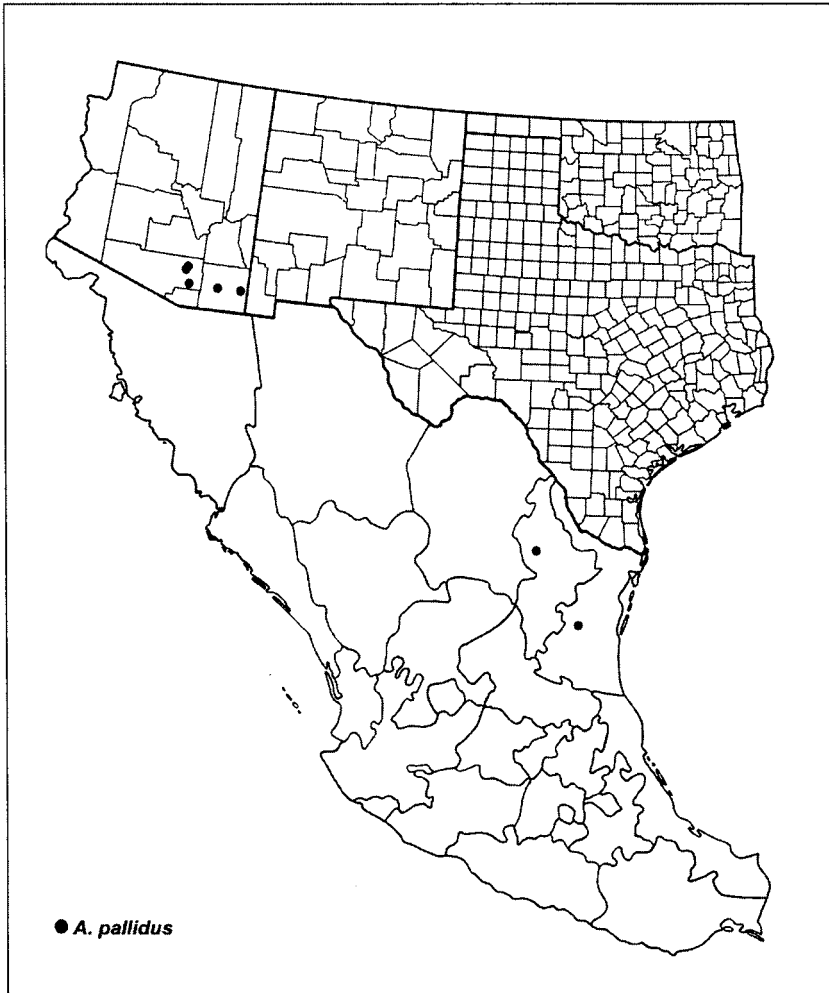


Fig. 29. Collection localities for *Aritaerius pallidus* in North America.

Aritaerius pallidus Kovarik and Tishechkin, new species
(Figs. 1–4, 19–27)

Description. Length: 1.34 mm, range 1.50–1.20; width 0.81 mm, range 0.7–0.9; (n = 17) Body outline (dorsal) (Fig. 3): Somewhat pear-shaped. Color: cuticle light to dark amber; setae golden. Head: Frons and vertex with areas of pustulate setose cuticle, one forming inverted “Y” on frons (Fig. 1) while another pair span area from antennal insertion to roughly middle of eye. Setae on head short to relatively long. Pronotum (Fig. 2): Disk with bilaterally symmetrical pattern of patches of pustulate setose cuticle; apical angles produced and broadly truncate. Elytra (Fig. 3): Broader than pronotal base; cuticle smooth except for regularly-spaced pustulate cuticular dots representing four dorsal, a sutural and subhumeral striae. A few additional spots of pustulate setose cuticle also present in humeral region. Propygidium: Structure approximately 1.5 as wide as long, mostly smooth, but with sparse and uniform covering of spots of pustulate setose cuticle. Pygidium: Similar

to propygidium but with fewer pustulate setal patches. Prosternum (Fig. 2): Anterior margin of prosternal lobe produced and medially emarginate, marginal stria of lobe complete, though shallow medially; lobe cuticle mostly setose and areolate-rugose in texture; carinal striae appear as twin rows of setose and areolate-rugose cuticle that may appear widely spaced, parallel, slightly convergent, or reduced; lateral prosternal stria convergent between procoxae, then diverging apically; lateral marginal prosternal stria cariniform and diverging near apex; hypomera cuticle areolate-rugose. Mesosternum (Figs. 2, 4): Acutely produced to fit prosternal emargination; meso-metasternal stria absent; cuticle anterior to marginal metasternal stria mostly setose and areolate-rugose in texture. Mesepimeron: Cuticle mostly untextured. Metasternum (Fig. 4): Cuticle smooth except for scattered patches and transverse row of patchy setose and areolate-rugose cuticle bordering the posterior margin of sternite. Metepisternum and metepimeron: Cuticle smooth but with smattering of pustulate setal patches. Abdominal sternites: First apparent sternite (Fig. 4) about 4× as wide as long with transverse band of setose and areolate-rugose cuticle starting at the coxal bases and extending medially to posterior margin of sternite; remaining sternites extremely short, each with lateral row of regularly-spaced setose and areolate-rugose cuticular patches. Legs: Procoxa with reticulate cuticle. Profemur roughly rectangular in outline; cuticle of anterior and posterior surfaces reticulate; anterior and posterior ventral margins fringed with setae; entire dorsal surface of femur setose; anterior and posterior surfaces sparsely setose subapically and becoming dense towards apex. Protibia about 4× as wide as long; anterior cuticle smooth along midline and areolate-rugose along margins; inner and outer margins setose both anteriorly and posteriorly; distal 1/3 of outer margin bearing 9–12 regularly-spaced stout amber spines increasing in length proximally. Tarsi always laterally compressed and about 0.5 the length of corresponding tibia; 1st–4th tarsomeres with a pair of long setae ventrally, tarsal claws slightly longer than 5th tarsomere. Mesofemur slightly bowed, proximally slender, distally expanded, and about 1.3× longer than profemur; vestiture rather long and dense dorsally and becoming sparse ventrally. Metafemur about 1.7× longer than profemur, more strongly curved than metafemur, but otherwise resembling the latter structure. Mesotibia about 1.4× as long as protibia and with 3 longitudinal setal rows on anterior surface; posterior surface densely setose. Metatibia nearly twice as long as protibia and with dorsal and ventral row of setae on anterior surface and dense covering of longer setae on posterior surface. Male Terminalia (Figs. 19–27): Eighth segment (Figs. 19–21) with tergite dorsum slightly longer than broad, somewhat truncate distally, with minute setae dorsolaterally and laterally; coxites somewhat rectangular, slightly longer than 0.5 tergite length, and bearing distal cluster of short and minute spines. Ninth segment (Figs. 22–24) about 2× as long as broad and with minute dorsolateral and lateral setae and lateral pores; ventral processes narrowly ovoid; coxal carapace triangular and membranous, about as long as wide, and not extending much beyond apex of tergite; pair of minute setae present on disc. Spiculum gastrale proximally lobed, with remainder somewhat flattened and slightly expanded distally. Aedeagus (Figs. 25–27) with parameres more than 2× as long as phallobase, parallel sided, and superficially bisected just distad to median lobe; minute pores present on dorsal, lateral and ventroapical surfaces.

Diagnosis. *Aritaerius pallidus* is the only long-legged and pilose hetaeriine without any modifications of the pronotal disc. The pronotum of this species is truly subcylindrical, lacking carinate margins and lateral pronotal striae. While species of *Chrysetaerius* and *Latronister* bear a superficial resemblance to *A. pallidus*, the pronotal margins of these taxa are carinate. *Aritaerius pallidus* further differs from *Chrysetaerius* in having a smooth metasternal disc without any microsculpture. The eyes of *A. pallidus* with their large ommatidia are quite different from those of other similarly looking long-legged hetaeriine species. The aedeagal phallobase of both *Latronister* and *Chrysetaerius* is longer than the parameres whereas the opposite holds true for *A. pallidus*.

Type Series. Holotype ♂: Deposited in the Field Museum of Natural History Collection labeled: Sabino Cn. W. sl. Sta Catalina Mts. Pima Co., ARIZ. 2500 ft VII–26–1948 sycamore-oak-mesquite, at light F. Werner W. Nutting. Paratypes (28) United States: **Arizona:** Pima Co., IBP site, Sta. Rita Rng. Res., UV trap VII–12/15–73 W. L. Nutting (2, PWKC); VII–16/19–73 (1, UAIC); VII–27/29–73 (1, ATC); VII–30/VIII–2–73 (2, ATC); VIII–6/9–73 (1, UAIC); VIII–10/13–73 (4, PWKC);

VIII-13/16-73 (3, ATC); VIII-27/30-73 (1, ATC); VIII-31/IX-2-1973 (1, UAIC); IX-27/30-1973 (1, UAIC); Sta. Rita Exp. Range 3-5 Aug. 1973 W. Nutting (2, FMNH; 1, NDC; 1, SMC); 31 Aug-3 Sep 1973 (1, ATC); Tucson 4 Aug 1968 K. Stephan leg (1, FMNH) Cochise Co. Portal, 22:VIII 1963 leg. M. Cazier, at black light (1, FMNH); Cochise Stghld. Dragoon Mts. VIII.13.1958, light trap C. W. O'Brien (1, UAIC). Douglas 7-14 July 1969 Vincent D. Roth collector (1, AMNH). Mexico: **Nuevo Leon:** Apodaco VII: 13: 1960 R. B. Selander "at light" (1, FMNH). **Tamaulipas:** Sta. Engracia at light 200 m. 20.II.1936 C. Plummer MF#53/0 FMNH Orlando Park Pselaphidae Clln. (1, SMC).

Etymology. The name represents a combination of the words "Arid" (this is a desert species) and "*Chrysetaerius*" (the genus to which *A. pallidus* was erroneously ascribed).

Biology/Ecology. Almost nothing is known about the biology of *A. pallidus* except that it is attracted to ultraviolet light, indicating that this species is occasionally active at night. The large ommatidia of the eyes are characteristic of nocturnal insects. The nocturnal habits of *A. pallidus* suggest that its ant host might also be nocturnally active. A possible candidate is the army ant *Neivamyrmex*. These army ants are mainly subterranean and most above-ground activities occurs from dusk to dawn, especially under hot desert conditions (Gottwald 1995). Dispersing *A. pallidus* would likely have a higher rate of success encountering a new host colony at night when *Neivamyrmex* are foraging.

Remarks. The collection localities of *A. pallidus* are shown in Figure 29.

Discussion

Aritaerius occupies a rather isolated position among the North American Hetaeriinae. Its affinities with other hetaeriine genera are not clear due to a paucity of information on the phylogenetic relationships within the subfamily (Helava *et al.* 1985). On the basis of male genitalic characters, *Aritaerius* appears to belong to Subgroup C 3 of Group C of Helava *et al.* (1985) that includes the genera *Hetaeriomorphus* Schmidt, *Pselaphister* Bruch, *Teratolister* Bruch, and *Ulkeus* Horn. *Aretareus* lacks two of the synapomorphic characters for this subgroup (Helava *et al.* 1985) including a setose patch on the prohypomera and the absence of vela on the 8th sternum of the male terminalia. With regard to the latter character, *Ulkeus*, as it is currently recognized (Helava *et al.* 1985; Mazur 1997), represents three distinct lineages (Tishechkin unpubl. data) some of which do have vela present on the 8th sternum. The body outline of *Aritaerius*, in combination with aspects of its external morphology such as the eyes, long legs, and prosternal structure, are reminiscent of *Pselaphister*. However, striking pronotal differences suggest a gap between these two genera. Unfortunately, male genitalia of *Pselaphister* are currently unavailable for study. Because the phylogenetic relationships of hetaeriines are so poorly known, a cladistic analysis of *Aritaerius* and its putative relatives was not attempted.

The single damaged specimen of *A. pallidus* from Mexico differs subtly from the Arizona specimens in both the profile of the prosternal keel and shape of the pronotum. Additional collecting in the deserts of northern Mexico will undoubtedly fill in distributional gaps for this species.

Acknowledgments

We wish to thank the following institutions and individuals for the loan of specimens for this study: Rupert L. Wenzel and Alfred F. Newton, Field Museum of Natural History, Carl Olson, University of Arizona, Tucson, Arizona, and Wade Sherbrooke of the Southwest Research Station, AMNH, Portal, Arizona. We also thank John Mitchell and Paul Skelley for help with Scanning Electron Microscopy. Thanks are due to Kim

Summers, Charles Triplehorn, and Kurt Pickett for manuscript review. The junior author acknowledges financial support from Louisiana State University Agricultural Center, Field Museum of Natural History (Visiting Research Fellowship), German Research Council (Grant 436 WER), and NSF (Grant DEB 9815394 to C. E. Carlton).

Literature Cited

- Borden, J. H. 1968.** Antennal morphology of *Ips confusus* (Coleoptera: Scolytidae). *Annals of the Entomological Society of America* 61:10–13.
- Crampton, G. C. 1923.** A phylogenetic comparison of the maxilla throughout the orders of insects. *Journal of the New York Entomological Society* 31:77–107.
- Gottwald, H. W. 1995.** *Army ants: the biology of social predators.* Cornell University Press, Ithaca, NY. 302 pp.
- Harris, R. A. 1979.** A glossary of surface sculpturing. *Occasional Papers in Entomology* 28:1–31.
- Helava, J. V. T., H. F. Howden, and A. J. Ritchie. 1985.** A review of the New World genera of the myrmecophilous and termitophilous subfamily Heteriinae (Coleoptera: Histeridae). *Sociobiology* 10:127–386.
- Kovarik, P. W., D. S. Verity, and J. C. Mitchell. 1999.** Two new Saprinine histerids from southwest North America. *Coleopterists Bulletin* 53:187–189.
- Kovarik, P. W., and M. Caterino. 2001.** Family 15. Histeridae Gyllenhal, 1808 [pp. 212–227]. *In: American Beetles. Volume 1. Archostemata, Myxophaga, Adepaga, Polyphaga: Staphyliniformia* (R. H. Arnett, Jr. and M. C. Thomas, editors). CRC Press, Boca Raton, London, New York and Washington, D.C.
- Kukalová-Peck, J., and J. F. Lawrence. 1993.** Evolution of the hind wing in Coleoptera. *Canadian Entomologist* 125:181–258.
- Lawrence, J. F., and E. B. Britton. 1991.** Coleoptera (beetles) [pp. 551–553]. *In: Volume II, The Insects of Australia: a textbook for students and research workers / The Division of Entomology, Commonwealth Scientific and Industrial Research Organization, 2nd ed.* Cornell University Press, Ithaca, New York. 1137 p.
- Mazur, S. 1997.** *A World catalogue of the Histeridae (Coleoptera).* Biologica Silesiae, Wroclaw, Poland. 373 pp.
- Reichardt, A. 1941.** Fam. Sphaeritidae et Histeridae (Part 1). *In Fauna SSSR, V, 3.* Moscow Leningrad. 419 pp.
- Wenzel, R. L. 1944.** On the classification of histerid beetles. *Field Museum of Natural History Zoology Series* 28:51–151.
- Wenzel, R. L. 1962.** Histeridae, the Hister Beetles [pp. 372–379]. *In: Beetles of the United States, fasc. 26* (R. H. Arnett, Jr.). The Catholic University of America Press, Washington, D.C.
- Williams, I. W. 1938.** The comparative morphology of the mouthparts of the order Coleoptera treated from the standpoint of phylogeny. *Journal of the New York Entomological Society* 46:245–288.

(Received 2 August 2002; accepted 28 January 2003. Publication date 18 October 2004. Publication funded in part by Coleopterists Society Foundation.)