

The identity of *Hadrobunus grandis*: reassignment of *Leiobunum aurugineum* to *H. grandis* and *H. nonsacculatus* new species (Opiliones: Sclerosomatidae: Leiobuninae)

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Abstract. Even though *Hadrobunus grandis* (Say 1821) is the type species of *Hadrobunus*, its identity has been uncertain since its original description. The type specimens were collected in coastal Georgia and/or northeastern Florida during the winter of 1817–1818, not from the mid-Atlantic Region (e.g., Virginia, Maryland) as assumed by some authors. This error has resulted in persistent confusion with *H. maculosus* (Wood 1868), the dominant *Hadrobunus* species in the mid-Atlantic region. The type specimens of *H. grandis* were lost or destroyed, but all surviving evidence suggests that the species known as *Leiobunum aurugineum* Crosby & Bishop 1924 is a synonym of *H. grandis*. Examination of available museum specimens revealed two species. Populations east of the Apalachicola River correspond to the historical description of *L. aurugineum* in having sacculate penes, and are thus identical to *H. grandis*; those west of the river lack penial sacs and are placed in the new species *H. nonsacculatus*.

Keywords: Harvestmen, taxonomy, North America

The recent discovery of new species of the endemic North American genus *Hadrobunus* Banks 1900 (Shultz 2010) highlights the need to resolve a long-standing uncertainty about the identity of the type species *Hadrobunus grandis* (Say 1821). Thomas Say based his description of *Phalangium grandis* on specimens collected during an expedition by the Academy of Natural Sciences of Philadelphia to northeastern Florida and the coastal islands of Georgia (Fig. 1) that lasted from December 1817 to April 1818 (Bennett 2002). The type specimens were not illustrated and were soon lost or destroyed (LeConte 1859; Weiss & Zeigler 1931). Therefore, Say's (1821:67–68) terse description is critical to identifying *H. grandis* and is reprinted here, with the current author's clarifications in brackets.

P. grandis. Body oval, covered with short spines; ocular tubercle spinous; feet rather short. Inhabits the Southern States... *Body* oblong-oval, scabrous [hard and rough, scab-like], with approximated [closely spaced], robust, short, acute spinules; rufo-ferugineous [sic] [reddish brown; color of iron rust], two impressed transverse lines before the middle [demarcations of meso- and metapeltidia]; *ocular tubercle* prominent, slightly contracted at base, crowned with numerous, robust, acute spinules; *clypeus* hardly elevated; *feet* rather short; *pectus* [coxae] with numerous, minute, acute granules; *venter* with but few. Length, female nearly seven-twentieths of an inch [~ 9 mm]. Much the largest I have seen.

The locality, cuticular armature, color and body size correspond uniquely to *Leiobunum aurugineum* Crosby & Bishop 1924. Consequently, I propose *L. aurugineum* as a junior synonym of *Hadrobunus grandis*. Significantly, results from recent molecule-based phylogenetic analysis (Hedin et al. 2012; Burns et al. 2012) show that *L. aurugineum* is more closely related to *Hadrobunus maculosus* and *Leiobunum formosum* (soon to be transferred to *Hadrobunus*: J.W. Shultz unpublished data) than to other *Leiobunum* species.

Summary of the *H. grandis* problem.—Say often used the vague term “the Southern States” in describing the distribution of specimens collected during his 1817–1818 expedition, and many subsequent researchers appear to have been unaware of the original collection locality of *Phalangium*

grandis. Given Say's association with Philadelphia, the range of the species was widely thought to include such comparatively northern locales as Maryland and Virginia. Thus, when Wood (1868) described *Phalangium maculosum* (now *Hadrobunus maculosus*) from Pennsylvania and West Virginia without having seen *P. grandis* or making any association between the two species, the stage was set for more than a century of confusion.

For example, during a brief but active period (1887–1893), Weed published several treatments on the harvestman fauna of the northern midwestern states (summarized by Cokendolpher & Zeiders 2004) and his opinions on the taxonomy of *Phalangium grandis* and *P. maculosum* changed frequently, leading to the transfer of these and many other harvestman species to “*Liobunum*.” Based on my own unpublished work, there appear to be four typical *Hadrobunus* species in the region: three are currently undescribed and one, *H. maculosus*, had been introduced to Illinois by 1883 (i.e., Livingston County: 1 ♂, Dwight, 41.0930°N, 88.4273°W, 8 August 1883, coll.?, Illinois Natural History Survey, Specimen Number 0006). Given the inadequate species descriptions of Say and Wood and persistent taxonomic emphasis on coloration as a diagnostic feature, it is understandable that Weed and others found it difficult to stabilize the concepts of *Phalangium maculosum* and *P. grandis*.

Banks (1900) erected the genus *Hadrobunus* to accommodate *Phalangium grandis* and *P. maculosum* and then added to the confusion by stating that *H. grandis* occurs in the “E. States” and *H. maculosus* occurs in the “S. States” (Banks 1901:677; repeated in Comstock 1912, 1968). This apparently led Crosby & Bishop (1924:21) to identify a *Hadrobunus* specimen from Richmond, Virginia as “*H. grande*” and specimens from southern Georgia as “*H. maculosum*.” However, the specimen from Virginia was almost certainly *H. maculosus*, and the specimens from Georgia were most likely not *H. maculosus*, because this species reaches its southern limit in central North Carolina (J.W. Shultz unpublished observation). In her survey of Ohio harvestmen, Walker (1928) appeared to surrender to this confusion in stating that both species occur in “all counties,” although it appears that neither does.

Bishop (1949) offered his own geographic criterion for distinguishing between the two species, which has been used by most subsequent researchers (e.g., Cokendolpher & Lee 1993). He considered *H. maculosus* to be a northern species that reaches its southern limit in Kentucky, Ohio, and West Virginia and *H. grandis* to be a southern species that occurs in the “southeast and ... [is] particularly abundant in the Atlantic coastal states” (Bishop 1949:214). These distributions correspond roughly to that of an undescribed species that dominates the Great Lakes Region (J.W. Shultz unpublished observation) and *H. maculosus*, respectively. Bishop’s geographic demarcation implies that he had established morphological criteria to distinguish between two *Hadrobunus* species, even if they do not correspond to *H. maculosus* and *H. grandis*. But this does not appear to be the case. Following the strategy of most previous researchers, Bishop emphasized coloration in distinguishing among harvestman species.

Hadrobunus maculosus differs from *H. grandis* in being generally lighter in color, in lacking conspicuous, sharp-pointed denticles on the dorsal surface of the body, in having the legs with a banded appearance rather than mottled or blotched, and in having more prominent rows of light spots on the dorsal surface of the abdomen (Bishop 1949: 216).

These criteria are problematic. In Maryland, for example, coloration in adult *H. maculosus* changes during late summer and autumn, with high contrast patterns in early summer (light-brown background, transverse rows of prominent spots, distinct banding on legs) and with progressive darkening of background and loss of contrast throughout the season (J.W. Shultz original observation). Thus early-season specimens correspond to Bishop’s description of *H. maculosus* and late-season specimens correspond to his description of *H. grandis*. Furthermore, I have seen several of the specimens Bishop used in his 1949 treatment of *Hadrobunus*. Those “*H. maculosus*” from eastern New York (Albany Co.) are *H. maculosus*, those from central New York (Tompkins County) include both *H. maculosus* and the undescribed Great Lakes species, and those from Quicksand, Kentucky (which I have not seen) were almost certainly a second undescribed species that ranges from the northern Great Smoky Mountains north through the western Appalachians to the Ohio River (J.W. Shultz unpublished observation).

I conclude that past error and confusion has been so profound that, except for its initial description and those of its junior synonym *Leiobunum aurugineum*, all previous criteria aimed at diagnosing *Hadrobunus grandis* should be rejected. *Hadrobunus grandis*, which has heavy dorsal armature and a short sacculate penis (Fig. 2), occurs in the extreme southeastern United States (South Carolina, Georgia, Florida) (Fig. 1). Its distribution does not overlap or abut that of the poorly armed and nonsacculate (Fig. 8) *H. maculosus*, which is distributed along the eastern seaboard of the United States from central North Carolina to New Hampshire and has a westward limit that roughly corresponds to the Eastern and St. Lawrence Continental Divides (J.W. Shultz unpublished observations). The distribution of *H. maculosus* abuts or overlaps those of at least four undescribed *Hadrobunus* species, a situation that served to perpetuate confusion in distinguishing between *H. grandis* and *H. maculosus*.

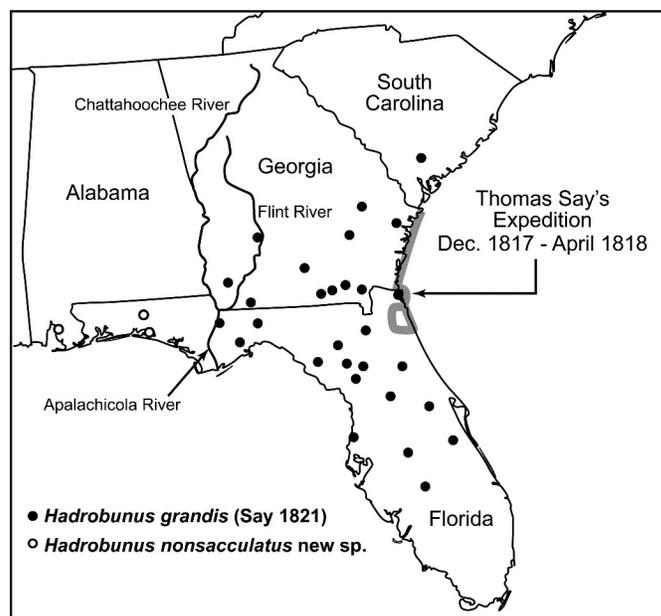


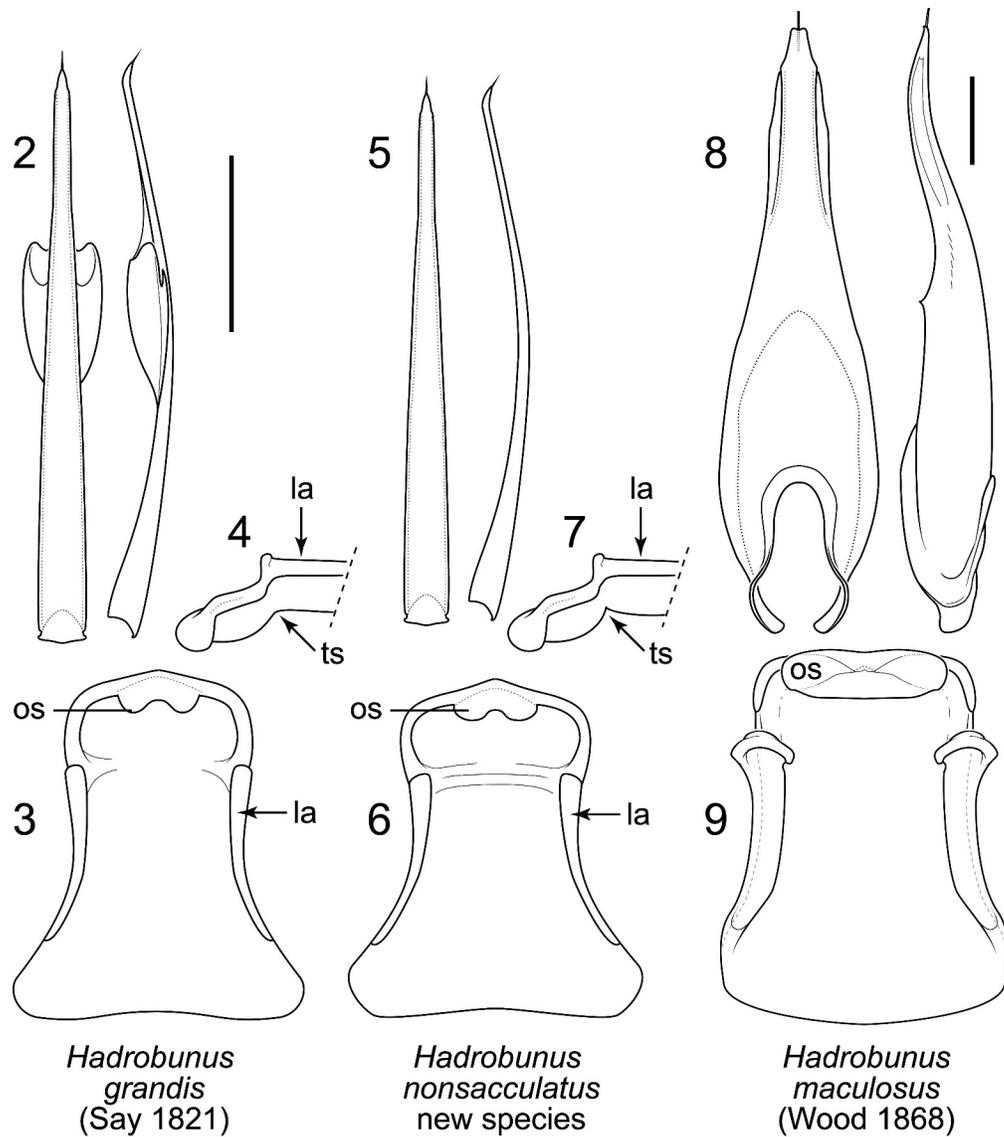
Figure 1.—Map of the southeastern United States showing collection localities of specimens used in the current study and the approximate route taken by Thomas Say during the 1817–1818 expedition by the Academy of Natural Sciences of Philadelphia.

A new species.—In attempting to establish the geographic range and morphological variation of *Hadrobunus grandis*, I found significant differences between populations separated by the Apalachicola River and its major western tributary, the Chattahoochee River (Fig. 1). Specifically, all male specimens obtained east of these rivers had sacculate penes (Fig. 2), and all male specimens west of the rivers lacked sacs (Fig. 5). Inspection of females suggested that the populations west of the Apalachicola River have a deep transverse sulcus spanning the genital operculum (Figs. 6, 7), while those east of the rivers have a shallow sulcus (Figs. 3, 4). Thus, the species historically known as *Leiobunum aurugineum* represents two species, *Hadrobunus grandis* east of the Apalachicola River and *H. nonsacculatus* west of that river. The river appears to be a major phylogeographic barrier in the southeastern United States (Soltis et al. 2006).

METHODS

I conducted all observations using a Leica MZ APO dissecting microscope (16× ocular, 0.63× objective, 8–80× zoom). Drawings were made with a drawing tube and then digitized and traced in Adobe Illustrator. Photographs were obtained with a PaxCam 3 digital camera mounted on a Wild Heerbrugg Makrozoom 1:5 with 6.3–32× objective. Images obtained at different focal planes were combined using Helicon Focus software (HeliconSoft, Kharkov, Ukraine).

Specimen repositories and abbreviations.—Specimens examined for this study were obtained from the following institutions: American Museum of Natural History, New York (AMNH); Field Museum of Natural History, Chicago (FMNH); Florida State Collection of Arthropods, Gainesville (FSCA); Illinois Natural History Survey, Champaign (INHS); Museum of Comparative Zoology, Harvard University (MCZ); Mississippi Entomological Museum, University of



Figures 2–9.—Genital structures of *Hadrobunus grandis*, *H. nonsacculatus* and *H. maculosus*. 2–4. *H. grandis*; 2. Penis in dorsal (on left) and lateral (on right) perspectives; 3. Dorsal view of inner surface of female genital operculum; 4. Lateral view of anterior portion of female genital operculum (semi-diagrammatic) showing shallow transverse sulcus (*ts*); 5–7. *H. nonsacculatus*; 5. Penis in dorsal (on left) and lateral (on right) perspectives; 6. Dorsal view of inner surface of female genital operculum showing transverse phragma connecting the anterior margins of levator muscle apodemes (*la*); 7. Lateral view of anterior portion of female genital operculum (semi-diagrammatic) showing deep transverse sulcus (*ts*). 8, 9. *H. maculosus*; 8. Penis in dorsal (on left) and lateral (on right) perspectives; 9. Dorsal view of inner surface of female genital operculum. Figs. 2–7 are depicted at the same scale. Scale bars = 1 mm.

Mississippi (MEM); National Museum of Natural History, Washington, D.C. (NMNH); Texas Memorial Museum, University of Texas, Austin (TMM); Museum of Texas Tech University, Lubbock (TTU); University of Maryland, College Park, author's collection (UMD).

TAXONOMY

Family Sclerosomatidae Simon 1879
Subfamily Leiobuninae Banks 1893
Hadrobunus Banks 1900

Hadrobunus Banks 1900:199.

Type species.—*Phalangium grandis* Say 1821, by original designation (Banks 1900). Banks erected *Hadrobunus* to

accommodate *P. grandis* and *P. maculosum* Wood 1868, but he misidentified *P. maculosum* as *P. grandis*. I advocate retaining *Phalangium grandis*, as diagnosed here, as the type species for *Hadrobunus*. As detailed above, early descriptions of the two species were too superficial to allow them to be reliably distinguished, so retaining *P. grandis* as the type species introduces no complications and stabilizes the literature.

Diagnosis.—Anterior margin of female genital operculum with median sclerotized lobe or sclerite (Figs. 3, 6, 9). Coxa II with conical spike with accessory lateral point located near retrolateral articulation with trochanter (i.e., retrolateral coxal spur II) (Fig. 12). Scutum of both sexes with variably expressed sharp, posteriorly-curved (retorse) tubercles. Ventral surface of palpal tibia with sexually dimorphic armature:

male with field of small, blunt-tipped tubercles, female with sharp, conical, distally slanted denticles. Prolateral rows of denticles present on all pedal coxae; retrolateral rows of denticles present on all pedal coxae except leg III. Legs of female (and usually male) relatively short: length of femur I subequal to body length or shorter. Pedal femora of both sexes without pseudoarticulations or nodules, tibiae without pseudoarticulations. Surfaces of pedal coxae tuberculate. Ocularium domelike, not constricted at base, not canaliculate, each carina usually with a row of 5 to 8 denticles.

Hadrobunus grandis (Say 1821)

Figs. 2–4

Phalangium grandis Say 1821:67; Say 1859:14 [“Southern States” = coastal Georgia and northeastern Florida].

Phalangium grande Say: Wood 1868:34; Underwood 1885:168.

Phalangium (?) *grande* Say: Weed 1889a:105.

Liobunum grande (Say): Weed 1892a:192–193 [Illinois, Ohio: misidentifications; Virginia, District of Columbia: misidentifications, *H. maculosus*]; Banks 1911:456 [North Carolina: Swannanoa Valley, misidentification, *H. fusiformis*?].

Liobunum similis Weed 1890:918 [Ohio: misidentification]; Cokendolpher & Zeiders 2004:9.

Liobunum grande variant *similis*: Weed 1892a:193, plate 9, Figs. 1–2g [Ohio: misidentification]; Roewer 1910:255.

Astrobunus (?) *grande* (Say): Weed 1890:917.

Leptobunus grande (Say): Banks 1893:209–210.

Hadrobunus grande (Say): Banks 1900:199; Banks 1901:677; Banks 1904:256 [misidentification of *H. maculosus*].

Hadrobunus grandis (Say): Roewer 1910:254–255 [USA: Illinois, Ohio, Virginia: misidentifications]; Roewer 1923:919 [British Columbia: locality incorrect; see also Cokendolpher & Lee 1993; Bragg & Holmberg 2009]; Walker 1928:168, fig. 24 [Ohio: misidentification]; Crosby, Wolf & Bishop 1928:1076 [New York: misidentification of *H. maculosus*]; Muma 1944:24 [Maryland: misidentification of *H. maculosus*]; Edgar 1966:353, 359, Edgar 1990:568 [description incorrect].

Leibunum aurugineum Crosby & Bishop 1924:13–14, pl. 2, fig. 8; Davis 1934:664–666, fig. 2; Edgar 1990:574,578 [East of Apalachicola and Chattahoochee Rivers]. NEW SYNONYMY.

Type material examined.—*Leibunum aurugineum* Crosby & Bishop 1924. Holotype male, USA: Georgia: Charleton County: Okefenokee Swamp, Billy’s Island, 30.8052°N, 82.3404°W, [?] June 1912, coll.? (AMNH).

Other material examined.—USA: Florida: Alachua County: 1 ♂, Gainesville, Live Oak Hammock, 26.6516°N, 82.3248°W, 22 July 1942, coll.? (INHS: 00075); many ♂ and ♀, same locality, 4 September 1929, N.W. Davis (AMNH), 1 ♀; same locality, 27 June 1969, D.L. Brown (TTU Z-58,743); 1 ♀, Newberry, 29.6463°N, 82.6065°W, 19 April 1930, T.H. Hubbell (AMNH); Bradford County: 1 ♂, 1 ♀, near Starke, 29.9441°N, 82.1098°W, November–December 1943, H.S. Dybas (FMNH). Columbia County: 2 ♂, Santa Fe River, 29.8478°N, 82.6913°W, 29 October 1929, T.H. Hubbell (AMNH). Dixie County: many ♂ and ♀, no specific locality [county center used for coordinates], 29.6516°N, 83.1649°W, date?, coll.? (AMNH). Glades County: 1 ♀, Fishheating Creek, ~15 mi [~24 km] NW Moore Haven, 5 mi [8 km] E Palmdale, in rotten log, 27.1731°N, 81.4632°W, 28 August 1963, K.J.

Stone (FSCA). Hernando County: 1 ♂, 9 ♀, Withlacoochee State Forest, McKethan Lake State Park, mesic to dry woodland, 27.6648°N, 81.5157°W, 17–19 September 1982, G.B. Edwards (FSCA); 1 ♂, 2 ♀, Weeki Wachee, off Hwy 50, Boy Scout Reservation, sand hill S power line, 28.5155°N, 82.5729°W, 18 September 1987, D. Corey (TTU Z-58,827). Lake County: 3 ♀, no specific locality [county center used for coordinates], 28.7028°N, 81.7787°W, 17 May 1982, W.W. Smith (FSCA). Leon County: 2 ♀, 5 mi [8 km] N Tallahassee, under pine log, 30.5498°N, 84.2823°W, 14 June 1982, W.H. Cross (MEM). Levy County: 1 ♂, Williston, 29.3875°N, 82.4468°W, 30 May 1981, L. O’Berry (FSCA). Liberty County: 1 ♂, Torreya State Park, 30.33°N, 84.47°W, 18 December 1967, W. Ivie (AMNH). Marion County: 5 ♂, 5 ♀, Belleview, under log, 29.0552°N, 82.0623°W, 20 May 1960, H.A. Denmark (FSCA). Nassau County: 1 ♀, Fort Clinch State Park, edge of oak forest in old dunes, 30.6997°N, 81.4444°W, 14 September 1958, T.J. Walker (FSCA). Orange County: 1 ♂, Orlando, University of Central Florida Campus, 28.5378°N, 81.3775°W, [?]1983, D.T. Corey (NMNH). Putnam County: Ordway Preserve, night, 27.6648°N, 81.5157°W; 1 ♀, 25 October 1983, G.B. Edwards, M.K. Stowe (FSCA); 1 ♂, 1 ♀, same locality, 30 August 1984, G.B. Edwards, M.K. Stowe (FSCA). Wakulla County: 1 ♀, St. Mark’s National Wildlife Refuge, 1 mi [1.61 km] SW Panacea, 30.0518°N, 84.4068°W, 21 June 1979, C.R. Smith (FSCA).

Georgia: Bacon County: 1 ♀, no specific locality [county center used for coordinates], 31.5412°N, 82.4319°W, 2 October 1929, T.H. Hubbell (AMNH). Berrien County: 1 ♀, Nashville, 31.2074°N, 83.2502°W, 10 June 1955, H.S. Dybas (FMNH). Bulloch County: 1 ♀, 6 mi [9.65 km] S Statesboro, sphagnum bog, 32.3277°N, 81.7781°W, 12–13 October 1984, G.B. Edwards, L.S. Vincent (FSCA). Charlton County: 2 ♂, Mixon’s Hammock, Okefenokee Swamp, 30.8183°N, 82.3918°W, 16 June 1912, coll.? (AMNH); many ♂ and ♀, no specific locality [county center used for coordinates], 30.7917°N, 82.0843°W, 29 September 1929, T.H. Hubbell (AMNH). Deatur County: 2 ♀, Eldorado, 31.0441°N, 84.6519°W, 12 September 1929, T.H. Hubbell (AMNH); many ♂ and ♀, Faceville, 30.7532°N, 84.6399°W, 12 September 1929, T.H. Hubbell (AMNH). Lanier County: 1 ♂, 1 ♀, Stockton, 30.9376°N, 83.0072°W, 1 November 1929, N.W. Davis (AMNH). Liberty County: 3 ♂, 3 ♀, Midway, 31.8050°N, 81.4307°W, 3 October 1930, T.H. Hubbell (AMNH). Lowndes County: 1 ♂, Valdosta, 30.8327°N, 83.2784°W, 26 October 1929, N.W. Davis (AMNH). Sumter County: many ♂ and ♀, Maddox, 31.9969°N, 84.24225°W, 1 October 1929, T.H. Hubbell (AMNH).

South Carolina: Colleton County: 4 ♂, 1 ♀, no specific locality [county center used for coordinates], 33.0399°N, 80.8823°W, 26 September 1930, T.H. Hubbell (AMNH).

Diagnosis.—*Adult males and females:* Scutum distinctly convex (more so in female); mesopeltidium, metapeltidium, scutum and free tergites densely armed with robust retrorse tubercles; dorsal cuticle well sclerotized, thick and hard. Body rusty brown to yellow-orange; lighter ventrally. *Male:* Penis (Fig. 2) with pair of large, thin-walled sacs occupying about 25% penis length; sacs positioned usually far from glans-shaft joint, specifically, anterior margin of sac separated from joint by 20–25% penis length. *Female:* Genital operculum flexed ventrally (Fig. 4) with transverse bend at anterior margin of

apodemes of levator muscles (Fig. 3), but not forming deep transverse cleft as in female *H. nonsacculatus* (Figs. 6, 7). Otherwise uniquely similar to female *H. nonsacculatus*: ventral surface somewhat inflated anterior to transverse flexure (Figs. 4, 7); opercular sclerite (Figs. 3, 6) occupying median half of anterior lip, with prominent median notch.

Description.—For descriptions see *Leiobunum aurugineum* in Crosby & Bishop (1924) and Davis (1934).

Distribution.—Extreme southeastern United States, including Florida, southern and eastern Georgia, southeastern South Carolina; western limit appears to correspond to Apalachicola and Chattahoochee Rivers (Fig. 1).

Hadrobunus nonsacculatus new species

Figs. 5–7

Leiobunum aurugineum Crosby & Bishop 1924:13–14, pl. 2, fig. 8; Davis 1934:664–666, Fig. 2; Edgar 1990:574, 578 [in part, specimens from Coastal Alabama and coastal Florida west of Apalachicola River].

Type material.—Holotype male, USA: *Florida*: Okaloosa County: Fred Gannon Rocky Bayou State Park, 30.4965°N, 86.4292°W, [?] June 1983, L. Robbins (TTU-Z 58,740). Paratype: ♀, same data as holotype (TTU-Z 58,742).

Other material examined.—*Alabama*: Baldwin County: 2 ♂, Daphne, on beach, 30.6061°N, 87.9126°W, 19 July 1931, Dietrich (AMNH).

Florida: Okaloosa County: 1 ♂, near Delaco, 30.7448°N, 86.5954°W, 11–12 August 1935, T.H. Hubbell (MCZ 37083); 2 ♂, 1 ♀, Fred Gannon Rocky Bayou State Park, 30.4965°N, 86.4292°W, [?] June 1983, L. Robbins (TTU-Z 58,738; 58,741; 58,742).

Diagnosis.—Essentially identical to *Hadrobunus grandis* except for the following: *Male*: Penis without sacs (Fig. 5). *Female*: Transverse anterior sulcus of genital operculum a deep cleft (Fig. 7: *ts*), expressed internally as a low, transverse phragma appearing to connect the anterior ends of the apodemes of the levator muscles (Fig. 6).

Description of male holotype.—Measurements in mm. Male holotype: body length 6.14. Palp: femur 1.56, patella 0.72, tibia 1.05, tarsus 1.57. Leg I: femur 4.87, patella 1.23, tibia 3.93, basitarsus 4.50, telotarsus 6.63. Leg II: femur 7.75, patella 1.51, tibia 6.28, basitarsus 6.37, telotarsus 14.68. Leg III: femur 5.20, patella 1.43, tibia 3.40, basitarsus 3.31, telotarsus 6.54. Leg IV: femur 7.41, patella 1.54, tibia 4.97, basitarsus 6.03, telotarsus 8.39. Penis: 3.98.

Dorsum (Fig. 10): Carapace unarmed near ocularium but with scattered conical-to-retrorse denticles on submarginal surfaces. Median preocular margin slightly elevated with three imperfect rows of sharp conical denticles (one median, two lateral) extending about half way to ocularium. Ozophore slightly elevated. Ocularium well armed with six conical denticles surrounding each lens, an additional four denticles on anterior surface and single lateral denticle on right side behind lens; a few scattered erect setae. Supracheliceral lamina well developed; thin laterally but with bilateral pair of prominent, closely spaced anterior processes; each process bearing small denticles, concentrated terminally. Meso- and metapeltidia with dense covering of robust tubercles, most terminating in dark spinules; metapeltidial tubercles retrorse. Scutum convex, heavily sclerotized, with dense coat of robust,

retrorse tubercles, most tubercles with posteriorly projecting dark spinule. Scutum with five tergites. Three free tergites armed like scutum, but tubercles decreasing in size and density posteriorly. Anal operculum with a few small, simple tubercles. Dorsum without setae.

Venter. Genital operculum with rebordered anterior margin, anterior median portion protruding slightly; operculum armed with submarginal rows of well-developed flat-topped to weakly tricuspid denticles; surface with small scattered tubercles and erect macrosetae. Sternites with low tubercles medially, tubercles more pronounced laterally; pleurosternites present. Labrum with bilateral pair of distal tubercles.

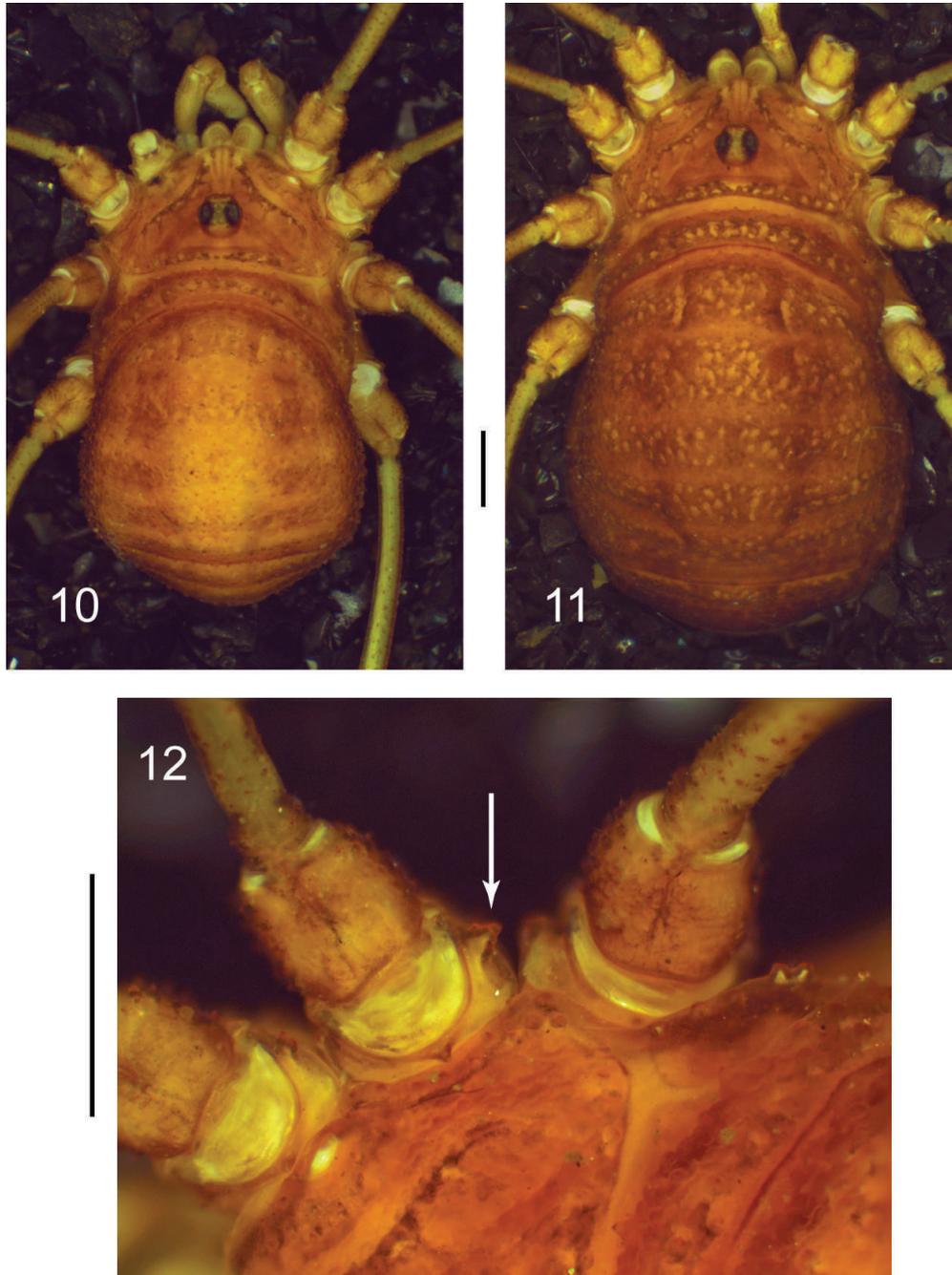
Appendages. Chelicera: Unremarkable. Basal article with proximoventral triangular apophysis and imperfect proventral row of macrosetae; second article with dorsal field of erect macrosetae, prolateral surface with field of sort macrosetae increasing in density toward base of fixed cheliceral digit, small tubercle present at base of fixed finger.

Palps: Femur with long retrolateral row and distodorsal-to-retrolateral field of thorn-like denticles and erect macrosetae; prolateral surface largely unarmed except for long row of blunt denticles and erect macrosetae; prodistal margin with two large, thornlike denticles. Patella armed with scattered thorn-like denticles and erect macrosetae, but retrodistal surface largely unarmed; prodistal apophysis undeveloped, but indicated by tuft of macrosetae. Tibia with field of scattered peg-like denticles proximoventrally; three denticles on retroventral distal margin, proventral distal margin unarmed; two small denticles on proximodorsal surface; erect macrosetae scattered on all surfaces although substantially reduced on prolateral surface; fine distally recumbent setae on prolateral surface. Tarsus with dense coat of fine, distally recumbent microsetae and erect macrosetae; proventral surface with long row of dark peg-like denticles; retroventral surface with short proximal row of small, sharp denticles. Claw with a short proximal row of three teeth ventrally.

Legs: Coxae with numerous low tubercles, each coxa with long prolateral row of prominent, flat-topped to weakly tricuspid denticles; all but coxa III with similar retrolateral row of denticles. Coxa II with retrolateral spur (Fig. 12) in form of sharp conical denticle with accessory lateral cusp, similar but smaller retrolateral spur on coxa I. Prolateral surface of coxa III opposite retrolateral spur II protuberant (Fig. 12). Trochanters with small thorn-like denticles on pro- and retrolateral surfaces. Distal leg articles unremarkable.

Penis. Dorsoventrally flattened, tapering gradually toward tip, glans-shaft joint indicated by slight constriction; no sacs or alae (Fig. 5).

Coloration. Body a general orange-brown (Fig. 10). Ocularium with light median stripe. Surface of carapace lightly mottled by darker and lighter sigillary markings. A bilateral pair of dark lines punctuated by light spots begins anteriorly on either side of preocular region and passes posterolaterally, terminating laterally; a similar color pattern on meso- and metapeltidia. Scutum with segmentation reflected in alternating transverse bands of slightly darker tergal regions and slightly lighter intertergal regions; median mark subobsolete, limited largely to slight median darkening on scutal tergite 1. Venter lighter than dorsum but anterior and posterior sternal



Figures 10–12.—*Hadrobunus nonsacculatus*. 10. Male, dorsal perspective. 11. Female, dorsal perspective. 12. Male, dorsal perspective highlighting retrolateral spur of coxa II as indicated by arrow. Figs. 10 and 11 are depicted at the same scale. Scale bars = 1 mm.

margins slightly darkened. Pedal coxae and trochanters essentially concolorous with venter or slightly darker, but legs becoming lighter distally; tarsi yellow-brown. Coloration of palps similar to that of legs. Chelicerae light yellow-brown, except for darker sigillary markings.

Description of female paratype.—Measurements in mm: body length: 7.48. Palp: femur 1.26, patella 0.61, tibia 0.92, tarsus 1.64. Leg I: femur 4.76, patella 1.07, tibia 3.50, basitarsus 5.79, telotarsus 6.21. Leg II: femur 7.66, patella 1.27, tibia 5.84, basitarsus 6.14, telotarsus 11.03. Leg III: femur 4.65, patella 1.39, tibia 3.42, basitarsus 4.58, telotarsus

5.84. Leg IV: femur 7.28, patella 1.65, tibia 4.68, basitarsus 7.62, telotarsus 7.77.

As in the male, except of the following: *Venter*: Genital operculum with wide anterior lip, median portion protruding anteriorly; anterior portion flexing ventrally in lateral perspective at distinct transverse sulcus (Fig. 7), sulcus expressed internally as transverse phragma (Fig. 6); portion of operculum anterior to sulcus slightly inflated (Fig. 7); inner margin of anterior lip with pronounced sclerite projecting posteriorly, posterior margin of sclerite with broad median notch (Fig. 6). Labrum smooth, simple. *Appendages*: Chelicera: With fewer

setae than male. Palp: Femur less well-armed on the distodorsal and retrolateral surfaces, but retroventral row of denticles well developed; blunt prolateral denticles arranged in long proventral row, not prolateral row of the male. Patella with prodistal apophysis slightly developed. Tibia armed with sharp, distally slanted denticles on ventral and prolateral surfaces; no peg-like denticles. Tarsus unarmed, without pro- and retroventral rows of denticles. *Coloration*: Meso- and metapeltidium with more pronounced pattern of light dots against dark background (Fig. 11). Scutal and free tergites with numerous light dots and elongated markings, scutal tergites separated by lighter transverse bands; median dorsal figure expressed by darkened outline in scutal terga (and light lateral outline anteriorly).

Distribution.—Coastal Florida west of Apalachicola River and southern Alabama; western and northern limits unknown. *Hadrobunus grandis* and *H. nonsacculatus* appear to be separated by the Apalachicola River (Fig. 1).

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