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Taxonomy of the *Leiobunum calcar* species-group (Opiliones: Sclerosomatidae: Leiobuninae)

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Abstract. The *Leiobunum calcar* species-group is erected to accommodate four species of North American harvestmen, namely, *L. nigropalpi* (Wood 1868), *L. euserratipalpe* new species, *L. calcar* (Wood 1868) and *L. hoffmani* new species. The group is characterized by several sexually dimorphic characters, including an elongate penis lacking subterminal sacs, base of male palpal tibia projecting ventrally and denticulate, and unique female sterno-opercular mechanism that appears to act as a pregenital barricade. The four species are distinguished by penial and palpal features in the male and by details of the sterno-opercular mechanism in females. The history of confusion between *L. serratipalpe* Roewer 1910 and *L. calcar* is reviewed, and the new species *L. euserratipalpe* is proposed to accommodate the concept of *L. serratipalpe* developed by North American systematists as well as the synonymy of *L. serratipalpe* Roewer with *L. calcar*. All species are diagnosed, described and illustrated, and a key to species is provided.

Keywords: Harvestman, systematics, North America

The Opiliones fauna of the eastern and central parts of the United States and Canada is dominated by the ''daddy longlegs'' of the sclerosomatid subfamily Leiobuninae. With over 20 species, *Leiobunum* is the most species-rich genus in this region and also occurs in the Euro-Mediterranean Region and northeastern Asia as well as an area including Mesoamerica and the western USA and Canada. A recent phylogenetic analysis (Hedin et al. in press) has shown that each of these four regions is home to one or more *Leiobunum* clades that are more closely related to non-*Leiobunum* species in the same region than to the *Leiobunum* species from different regions. This insight demonstrates the need for significant taxonomic reorganization within *Leiobunum* and Sclerosomatidae generally, but it may also accelerate phylogenetic analysis and taxonomic revision within each regional clade. Specifically, intensive systematic analyses of regional taxa can now be undertaken with a low probability that closely related but geographically distant members will be overlooked. Indeed, the leiobunine fauna of North America is in particular need of taxonomic revision, and the current study was undertaken in part to capitalize upon these recent phylogenetic insights.

In an unpublished portion of his doctoral dissertation, McGhee (1970) delimited a small group of leiobunine harvestmen from eastern North America, the *Leiobunum calcar* species-group. The group encompassed two widely accepted species, *L. calcar* (Wood 1868) and *L. nigropalpi* (Wood 1868), as well as *L. serratipalpe* Roewer 1910 (subsequently synonymized with *L. calcar* by Cokendolpher 1981) and two undescribed species, *L. cumberlandense* and *L. hoffmani*. The *calcar* group was united by male characters, including a long penis lacking sacs or bulbs, palpal tibiae with an enlarged proximoventral surface with denticles, and, in most species, an apophysis or cluster of denticles on the subterminal retrolateral surface of the palpal femora. Here we assess McGhee's taxonomic proposals concerning the *L. calcar* group using a geographically diverse sample of specimens and a newly discovered suite of female characters, the sterno-opercular mechanism (Figs. 2, 3). The sternum (*arculi genitales*) is a sclerite that spans the ventral body surface between coxae III and is typically hidden by the anterior margin of the genital operculum. The sternum and operculum fit together to form an apparent barricade in females of *Leiobunum* species in which the penis lacks gift-bearing sacs. The taxonomic conclusions of our study concur with those of McGhee (1970) in recognizing the long-established species *L. calcar* and *L. nigropalpi* as well as the new species *L. hoffmani*. However, we consider *L. cumberlandense* to be a regional variant of *L. calcar*. In addition, we propose the name *L. euserratipalpe* for the species that American arachnologists called *L. serratipalpe* Roewer (Davis 1934; Bishop 1949; Edgar 1966; McGhee 1970) before the type specimen was shown to be a female *L. calcar* (Cokendolpher 1981).

METHODS

Morphology.—We examined all specimens in either isopropanol or ethanol, depending on the medium used by their home repositories. Dissections were performed using a needle and microscissors under a Leica MZ APO dissecting microscope with a 1× or 0.63× objective lens. Photos were obtained using PaxCam3 in Adobe Photoshop, and composite photos were created and edited in Helicon Focus software. We prepared illustrations in Adobe Illustrator from the composite photos and made measurements with a stage micrometer, ocular scale and drawing tube.

Specimen repositories.—We obtained specimens used in this study from the following museums and repositories: American Museum of Natural History, New York (AMNH); Academy of Natural Sciences of Philadelphia (ANSP); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); Mississippi Entomology Museum, Mississippi State University (MEM); North Carolina Museum of Natural Sciences, Raleigh (NCMNS); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH); U.S. National Park Service (NPS); University of Maryland, J.W. Shultz Collection, College Park (UMD); Virginia Museum of Natural History, Martinsville (VMNH).

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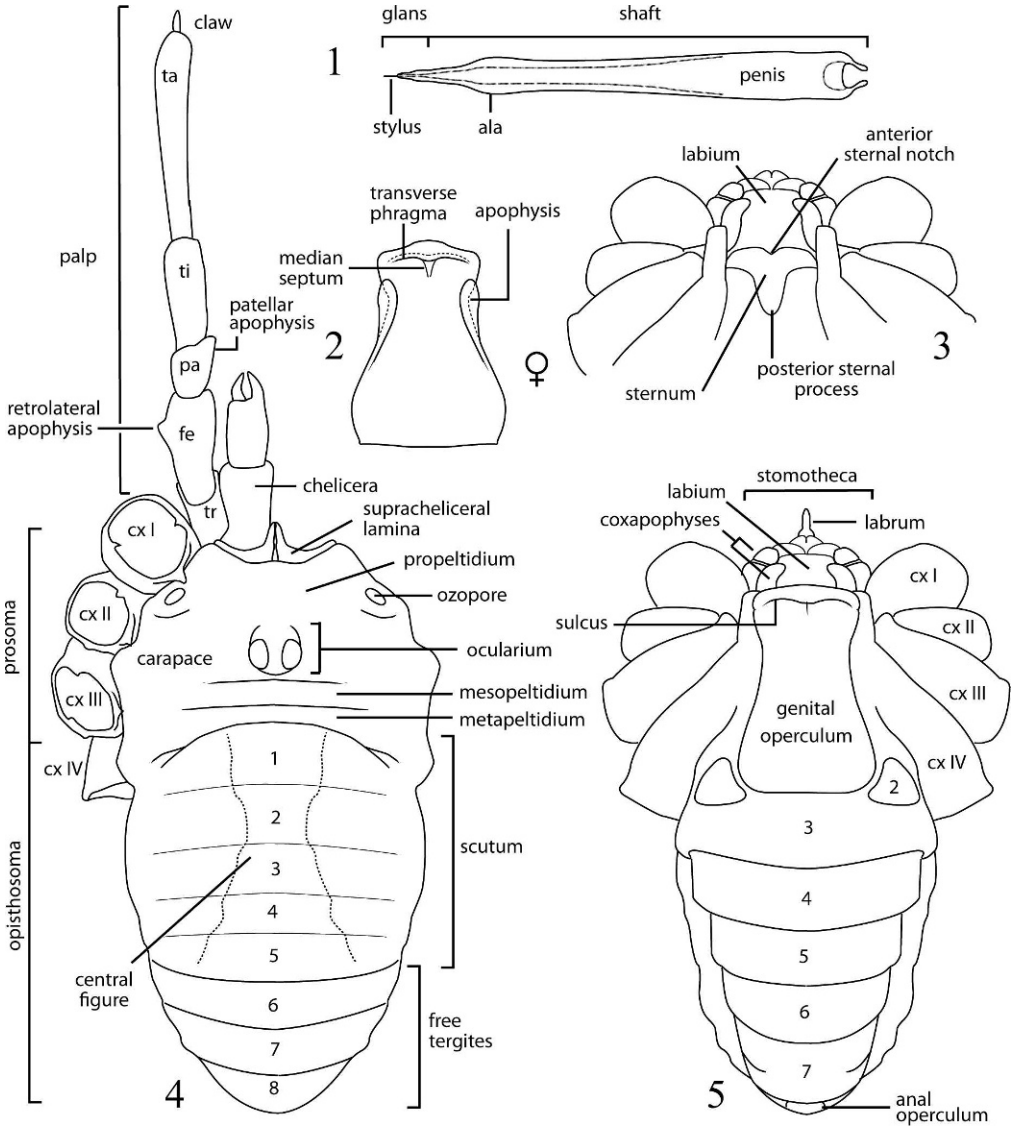


Figures 1–5.—Basic anatomy of the *Leiobunum calcar* species-group: 1. Penis, dorsal perspective; 2. Ventral view of female with genital operculum removed showing sternum (opisthosomal sternite 1); 3. Female genital operculum, detached, showing dorsal (inner) surface; 4. Dorsal view of male, with opisthosomal tergites numbered; 5. Ventral view of male, with opisthosomal sternites numbered. Abbreviations: cx, coxa; fe, femur; pa, patella; ta, tarsus; ti, tibia; tr, trochanter.

TAXONOMY

Family Sclerosomatidae Simon 1879
Subfamily Leiobuninae Banks 1893
Genus *Leiobunum* C.L. Koch 1839

Type species.—*Phalangium rotundum* Latreille 1798, by subsequent designation (Simon 1879:172)

Leiobunum calcar new species-group

Diagnosis.—Penis long (> 2/3 length of body), without subterminal sacs or bulbs but with variably developed lateral alae in some species, shaft dorsoventrally compressed over most of length, tapering gradually toward distal end (Fig. 1). Male palpal tibia with proximal ventral prominence with field of denticles, ventral surface concave in pro- or retrolateral view with coat of long, erect macrosetae, distal prolateral surface with row or field of denticles; prolateral tarsal denticles large, blunt-tipped, tightly packed, with row extending nearly full length of tarsus. Female genital operculum (Fig. 2) with deep transverse sulcus externally corresponding to internal transverse sclerotized phragma; phragma projecting dorsoposteriorly, forming a ventral space; ventral space divided by median septum; sternum (Fig. 3) typically with anterior median emargination and/or notch; posterior margin usually with median process projecting posteriorly into flexible cuticle of pregenital chamber.

Remarks.—The *calcar* species-group is monophyletic based on its unique reproductive morphology and unpublished results from molecular phylogenetic analysis (M. Burns, M. Hedin & J. Shultz, pers. comm.). The female genital operculum and sternum form an apparent pregenital barricade, with the anterior sternal margin projecting into the subphragmal space of the operculum and the median sternal notch engaging the median opercular septum. The sternal posterior process appears to act as a lever arm, with muscles extending to the base of the operculum rotating the

sternum and pressing it against the phragma. The barricade is frequently engaged in preserved specimens of *L. calcar* and *L. hoffmani* and may require unusual effort to open when dissecting the female genitalia. The presence of a female pregenital barricade suggests a role in excluding the penis during attempts at forced mating by males. Member species are limited to the central and eastern United States and adjacent southern Canada and its maritime provinces. We recognize four species: *L. nigropalpi* (Wood 1868), *L. calcar* (Wood 1868), *L. euserratipalpe* new species, and *L. hoffmani* new species.

KEY TO SPECIES OF THE *LEIOBUNUM CALCAR* SPECIES-GROUP

1. Male 2
   Female 5
2. Palpal femur with retrolateral denticles extending proximally, not limited to distal third (Fig. 10), retrolateral apophysis absent; penis narrowed at glans-shaft joint in dorsal perspective forming "neck" (Fig. 17) . . . . . *Leiobunum nigropalpi*
   Palpal femur with retrolateral denticles limited to distal third (Fig. 23, 37, 39, 51, 52), with retrolateral apophysis (Figs. 4, 37, 52, 54) or subterminal cluster of denticles (Fig. 23, 39); glans-shaft joint variable in dorsal perspective but without neck (Figs. 1, 31, 46, 61) 3
3. Penis shaft essentially straight, not curved in lateral perspective (Fig. 27), usually with a bilateral pair of small subterminal alae (Fig. 31); palpal femur with subterminal retrolateral cluster of sharp denticles, sometimes mounted on low mound; palpal femur gracile or slightly inflated distally, not strongly curved (Figs. 23, 24) . . . . . *Leiobunum euserratipalpe*
   Penis shaft strongly curved in lateral perspective (Figs. 42, 58), subterminal alae large to absent (e.g., Figs. 43, 46, 61); retrolateral apophysis present, varying from massive to small but rarely with a simple distal cluster of denticles; palpal femur inflated distally and usually strongly curved (Figs. 37–40, 52–55) 4
4. Penis bending dorsally in subterminal (alar) region in lateral perspective (Fig. 43), alae large to absent (Figs. 43, 46); penis length usually less than that of body (Fig. 43); widespread (Fig. 47) . . . . . *Leiobunum calcar*
   Penis shaft without subterminal dorsal bend or alae (Figs. 58, 61), penis length subequal to or longer than body (Fig. 58), northeastern North Carolina and southwestern Virginia (Fig. 47) . . . . . *Leiobunum hoffmani*
5. Sternum with short, weakly sclerotized posterior process distinct from the more sclerotized sternum (Fig. 15). . . *Leiobunum nigropalpi*
   Sternum without short, weakly sclerotized posterior process; process either absent (Fig. 29) or well sclerotized (Figs. 28, 44, 59) . . . 6
6. Posterior process of sternum absent (Fig. 29) to less than half width of sternum (Fig. 28) . . . . . *Leiobunum euserratipalpe*
   Posterior process of sternum present and long, more than half the width of the sternum (Figs. 44, 59) 7
7. Palpal femur with retrolateral denticles enlarged distally, with some mounted on variably developed, low, rounded retrolateral apophysis (Fig. 41); anterior sternal notch usually shallow (Fig. 44) (rarely absent) but deep in large-bodied, southern montane populations (see Fig. 59); widespread (Fig. 47) . . . . . *Leiobunum calcar*
   Palpal femur with retrolateral denticles, sometimes larger distally but without retrolateral apophysis (Fig. 56); anterior sternal notch deep, U- shaped, extending to midpoint of the sternum body (Fig. 59); northeastern North Carolina and southwestern Virginia (Fig. 47) . . . . . *Leiobunum hoffmani*

Leiobunum nigropalpi (Wood 1868)
(Figs. 6–17)

Phalangium nigropalpi Wood 1868:22–23, figs. 3a–d.

Liobunum nigropalpi (Wood): Weed 1887:935; Weed 1889a:87–88; Weed 1892:187–188, pl. 4, figs. 1, 2; Banks 1893:211; Banks 1901:675; Roewer 1910:213–214; Roewer 1923:896–897.

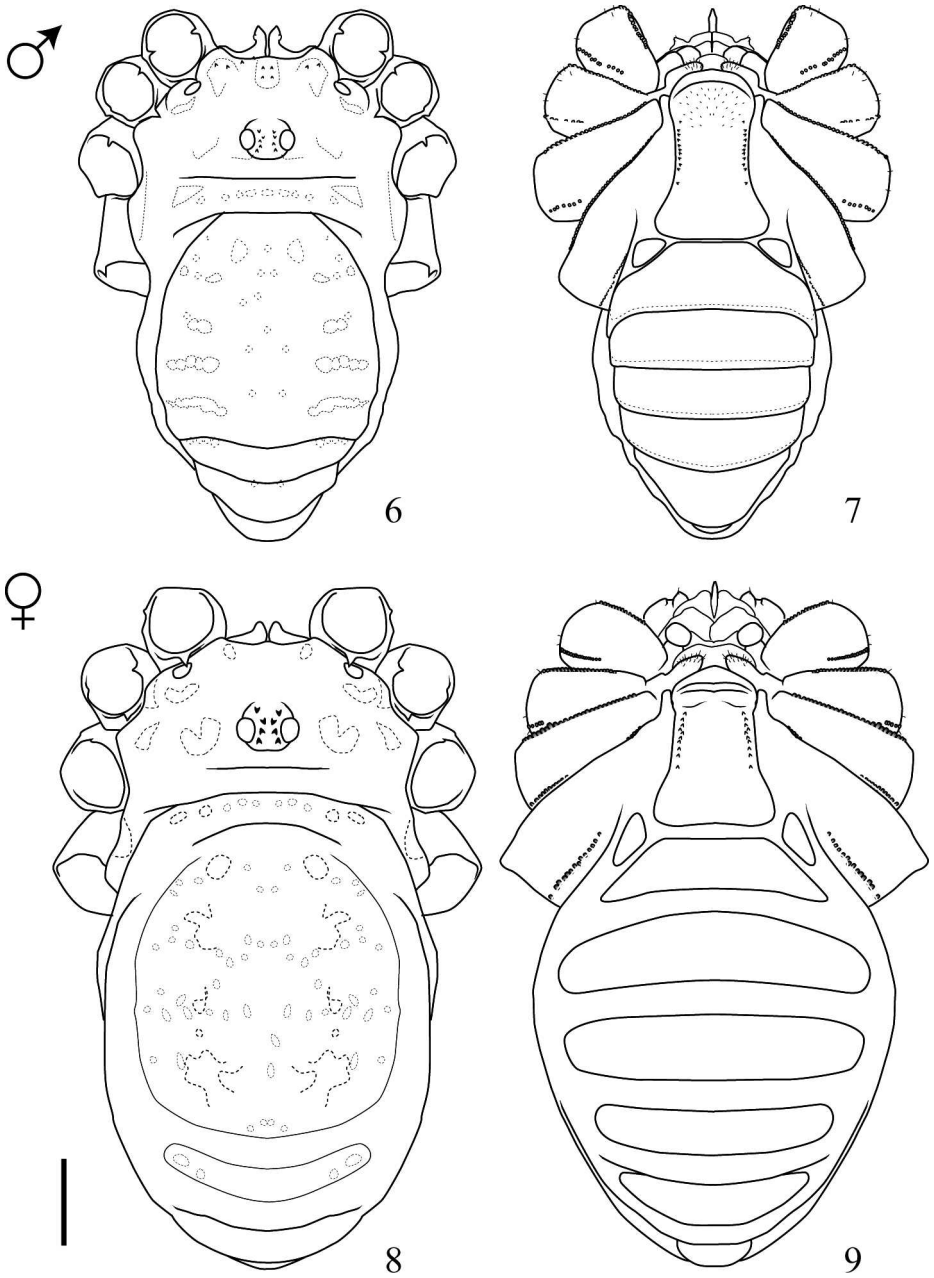
Liobunum nigripalpis (Wood): Weed 1890:918.

Leiobunum nigripalpi (Wood): Crosby & Bishop 1924:21; Walker 1928:163–164, pl. 2, fig. 14.

Leiobunum nigropalpi (Wood): Davis 1934:682–684, pl. 31, fig. 6; Bishop 1949:199–201, pl. 5, figs. 69–73; Edgar 1966:362; McGhee 1970:100, 106–113, figs. 21a, b, 24a, b, 26, 27 (unpublished dissertation).

Types examined.—*Phalangium nigropalpi*. Syntypes ♂ and ♀: USA: *Pennsylvania*: Huntingdon County (MCZ:14778).

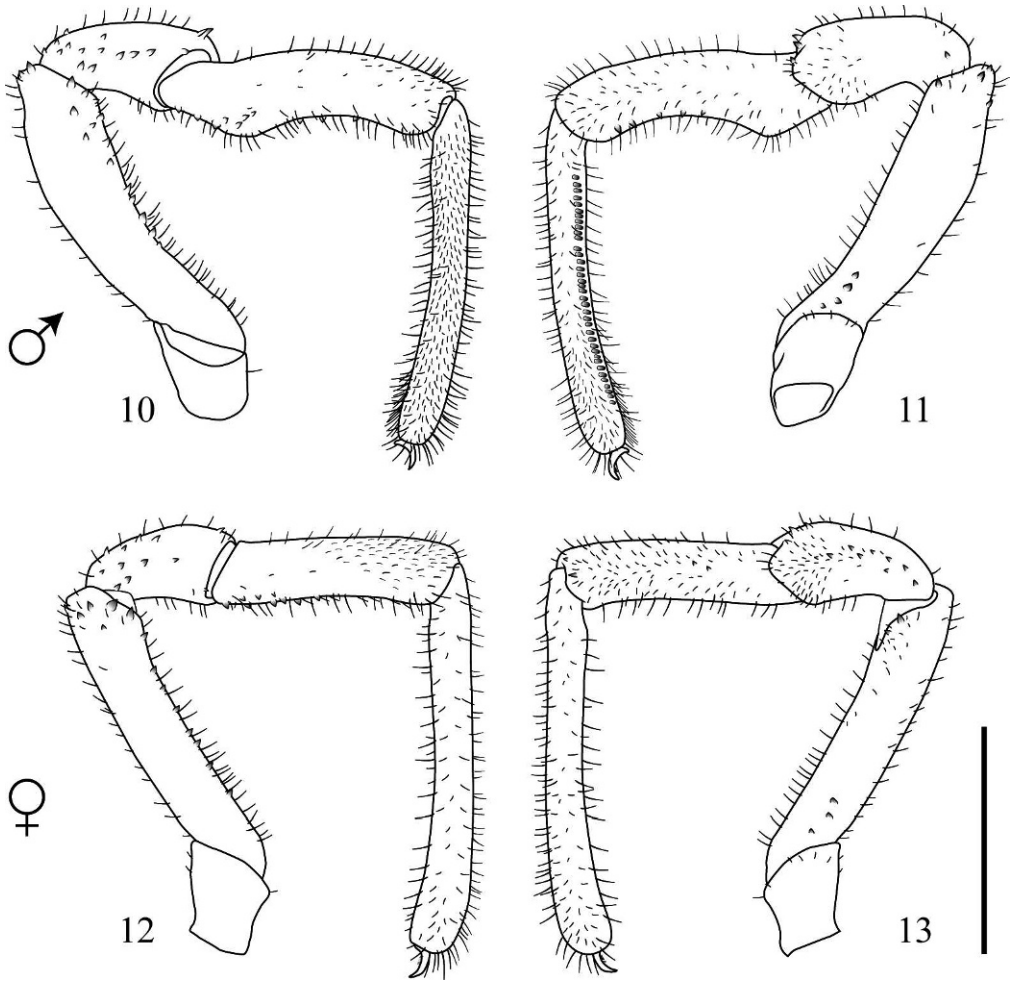
Other material examined.—USA: *Alabama*: Cleburne County: 2 ♂, Cheaha SP, vic. Campground #1 (046), 33.4864°N, 85.8125°W, 13 August 2005, M. Hedin et al. (UMD). *Connecticut*: Storrs County: 1 ♀, 41.8084°N, 72.2500°W, 28 July 1923, coll.? (AMNH). *Kentucky*: Bell County: 1 ♂, Pine Mt. State Park, "near lodge" 36.7357°N, 83.7375°W, 22 September 1963, Woods (AMNH). *Maryland*: Garrett County: 1 ♀, 3 km SE New Germany, Managed Oak Forest, 39.62°N, 79.105°W, elev. 779 m, 11–18 July 2005, M. Sarver; 2 ♀, 6 km NE Swanton, Managed Maple Forest, 39.489°N, 79.17°W, elev. 714 m, 21 June–6 July 2005, M. Sarver; 2 ♂, 4 ♀, 6 km NE Swanton, Managed Maple Forest, 39.489°N, 79.17°W, elev. 714 m, 22–29 August 2005, M. Sarver; 3 ♂, 4♀, 6 km NW Westernport, Old Growth Oak Forest, 39.509°N, 79.109°W, elev. 541 m, 3–10 August 2005, M. Sarver (UMD). *New York*: Cayuga County: 2 ♂, 2 ♀, N Fairhaven, 43.343°N, 76.6904°W, 31 July 1932, G. Hughes (AMNH). Ulster County: 1 ♂, 1 ♀, Cherrytown near Kerhonkson, 41.8251°N, 74.3293°W, 18 July 1976, Wygodzinsky (AMNH). *North Carolina*: Ashe County: 2 ♂, 1 ♀, 8.8 mi. [14.2 km] SSE Jefferson, 1183, 0.6 mi [1 km] N 1005, 36.29°N, 81.37°W, 21 July 1972, R.M. Shelley (NCMNS: 1217). Macon County: 3 ♂, 2 ♀, 5 mi [8.05 km] N of Highlands, 35.1269°N, 83.1924°W, August 1967, K. Kleinpeter (AMNH). Transylvania County: 1 ♀, 6.6 mi [10.6 km] WNW Brevard, Gov. Rd., 3.5 mi [5.6 km] W Fish Hatchery, 35.26°N, 82.85°W, 29 August 1973, R.M. Shelley (NCMNS: 1992). *Ohio*: Summit County: 2♂, 2 ♀, Bath Nature Preserve, 41.177°N, 81.642°W, 30 June 2005, J.W. Shultz (UMD). *Pennsylvania*: Bucks County: 1 ♀, Rushland, Wilkinson Rd., Coyne Farm, vernal marsh on wooded hilltop, 40.251°N, 75.038°W, 6–20 August 1998, H. O'Connor (ANSP). Huntington County: 1♂, 1♀, Huntington Mills, 41.1801°N, 76.2363°W, Woods (AMNH). Columbia



Figures 6–9.—Dorsal and ventral perspectives of *Leiobunum nigropalpi* (Wood 1868), male lectotype, female paralectotype. Scale bar = 1 mm.

County: 2 ♂, 2 ♀, Orangeville, 41.3392°N, 80.519°W, 13 August 1932, Hughes & Davis (AMNH). *South Carolina*: Oconee County: 2 ♂, Cherry Hill Rec. Area, Rt. 107, 34.9424°N, 83.0849°W, elev. 610 m, 11 August 1958, J.F. Hanson (AMNH). *Virginia*: Botetourt County: 2 ♀, Roaring Run, 37.6924°N, 79.8909°W, 4 July 1996, M. Donahue, B. Hogan (VMNH), 1 ♂, same locality, 30 July 1996, M. Donahue, B. Hogan (VMNH). Dickenson County: 1 ♂, 1 ♀, Breaks Interstate Park, ''DF site 2, off Nature Trail,'' 37.2864°N, 82.2964°W, 15–29 June 1991, VMNH survey (VMNH), 1M, same locality, 22 August–6 October 1991, VMNH Survey (VMNH). Floyd County: 1 ♂, Buffalo Mountain Natural Area Preserve, trailhead at parking lot, 37.4316°N, 78.6569°W, elev. 1067 m, 20 June 2004, R.L. Hoffman (VMNH). 1 ♂, Buffalo Mountain, ''ca 6 mi. [9.65 km] SE of Willis,'' 37.4316°N, 78.6569°W, elev. 1300 m, 25 August 1984, R.L. Hoffman (VMNH). Giles County: 4 ♂, Stony Creek Bog, off FS 10420, ca 2.3 km NW of Kire on Rt. 613, 37.4513°N, 80.5384°W, 9 August 2004, S.M. Roble (VMNH). Highland County: 1 ♂, Locust Spring Rec. Area, 8 mi [12.9 km] NW of Bluegrass, 38.5828°N, 79.6352°W, elev. 1158 m, 13 July 1974, Hoffman (VMNH). Russell County: 3 ♂, Mill Creek, ca 5.1 mi [8.2 km] E Carbo, 36.9432°N, 82.1386°W, late May 1998, J.C. Ludwig (VMNH). Wythe County: 1 ♂, 1 ♀, Sulphur Spring Picnic Area, ca 8 mi [12.9 km] west of Wytheville, 36.9692°N, 81.2222°W, 20 August 1967, Hoffman (VMNH).

Diagnosis.—Both sexes: Palpal femur, patella, and proximal tibia usually dark; distal tibia and tarsus light. Penis (Figs. 14,



Figures 10–13.—Palps of *Leiobunum nigropalpi* (Wood 1868), male lectotype, female paralectotype. Retrolateral perspectives on left, prolateral perspectives on right. Scale bar = 1 mm.

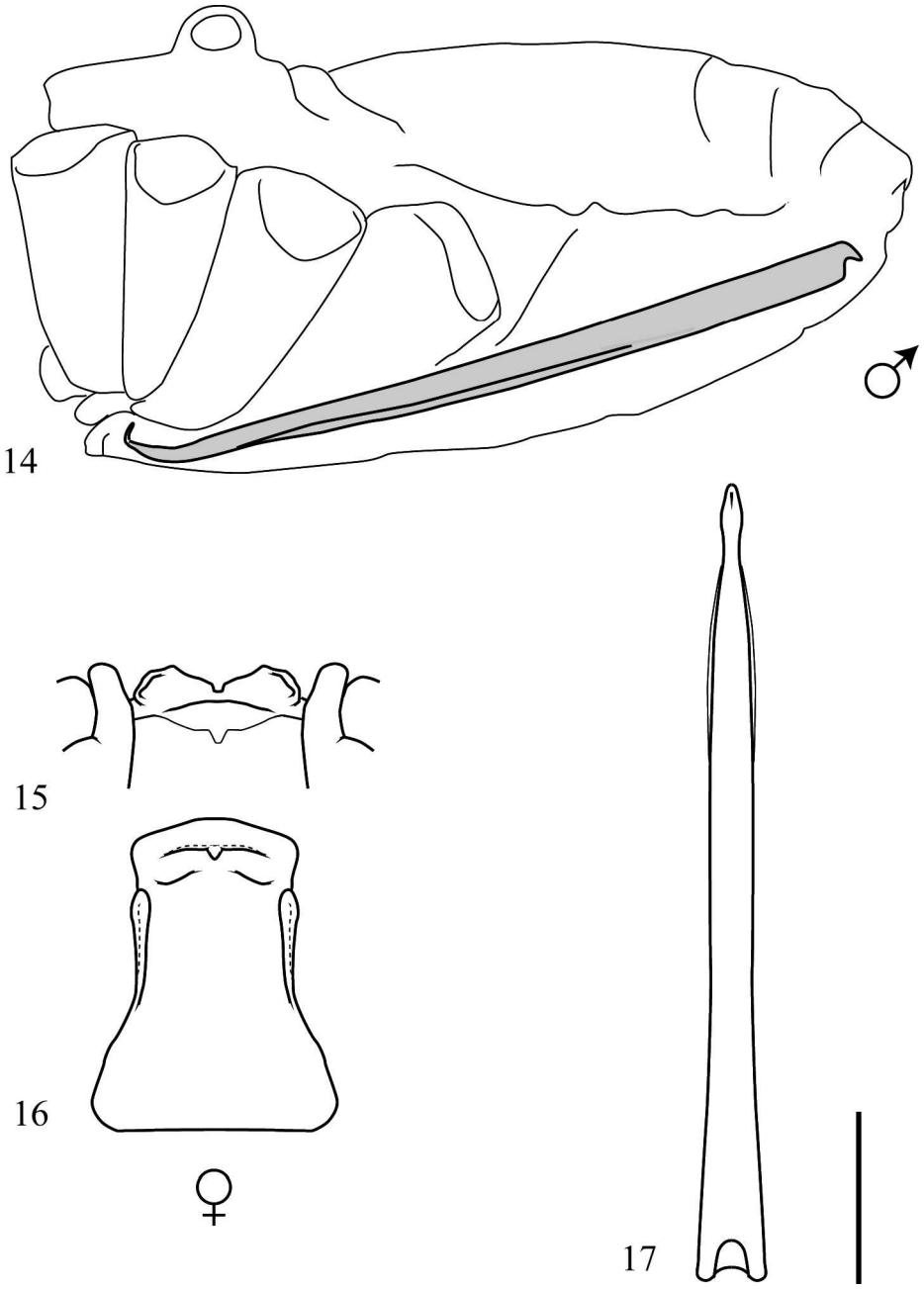
17): alae thin, translucent; shaft straight in lateral view, not widened or lobed proximally; glans-shaft union constricted transversely, glans broadened near base, tapering distally, terminating bluntly; glans held at slight dorsal angle to shaft; dorsal surface of glans with dorsal curvature. Male palp (Figs. 10, 11): femur without retrolateral apophysis; retrolateral denticles of femur distributed longitudinally, not restricted to distal field; tibia proximally with rounded-to-angular ventral prominence with field of short, stout denticles, especially proximally. Female sternum (Fig. 15): anterior margin with broad V-shaped median emargination with apex forming U-shaped notch; medial anterior margin reinforced by sclerotization; posterior margin with short, median process and weakly sclerotized cuticle.

Description of male lectotype.—Body length: 5.6 mm. *Dorsum* (Fig. 6): Carapace length, width: 1.8 mm, 2.8 mm. Cuticle dark golden brown and finely granulate, lighter and smooth along meso- and metapeltidium posterior margin; transverse row of white dots extending across metapeltidium. Anteromedian preocular prominence slightly darker than surrounding cuticle, with a few small denticles scattered medially and extending along anterior carapace margin. Anterior process of supracheliceral lamina with a few small denticles dorsally. Ozopore mound smooth. Ocularium dark brown to black and canaliculate, each carina with 5 sharp denticles. Opisthosoma: Cuticle dark golden brown, lacking a central figure. Scutum finely granulate, scutal tergites demarcated by short lateral rows of sigilla and sparsely scattered white dots. Free tergites and anal operculum smooth.

Venter (Fig. 7)*:* Sternum simple. Labrum smooth, curved dorsally. Posterior margin of genital operculum and margin of sternites well demarcated, with anterior sternite overlapping posterior sternite. Cuticle dark golden brown, smooth, with short erect setae scattered on anterior genital operculum. Anterior lateral portions of operculum protruding slightly; anterior margin rebordered, white; small pointed denticles arranged in a row along medial lateral margin.

Penis (Figs. 14, 17)*:* 4.2 mm long. Shaft straight, width constant throughout much of length but narrowing near junction with glans; glans curving slightly dorsad toward terminus. Alae, narrow, thin; ventral surface less sclerotized just posterior to glans; stylus missing but angled dorso-proximally in others.

Appendages: *Chelicerae*: Segments 1 and 2 pale yellow with a dorsal band of short, dark erect setae, becoming a dense prodistal patch near base of fixed finger.



Figures 14–17.—Genital structures of *Leiobunum nigropalpi* (Wood 1868): 14. Diagrammatic lateral perspective of male showing position of penis; 15. Ventral perspective of female sternum (genital operculum removed); 16. Dorsal (internal) perspective of female genital operculum; 17. Dorsal perspective of penis. All to same scale. Scale bar = 1 mm.

Palps (Figs. 10, 11)*:* Measurements in mm: femur 1.7; patella 0.8; tibia 1.1; tarsus 1.4. Palpal segments dark brown, tarsus lighter. Trochanter medium brown with a few erect setae; distoventral apophysis with 1 or 2 denticles and setae. Femur slender, curved with slight distodorsal expansion; retrolateral apophysis absent; long proventral row of small, distally pointing denticles interspersed with erect setae; dorsal surface with scattered erect setae and a few distal, submarginal denticles; a few denticles form a short proximal prolateral row. Patella slightly expanded distally, with a distal prolateral apophysis coated with erect setae, setae continuing proximally as a dorsal row; field of scattered denticles cover the proximal retrolateral surface; one large denticle points distally on distodorsal margin. Tibia slender and slightly curved, forming a ventral concavity; proximodorsal surface slightly inflated; proximal ventral surface expanded, creating a flat prominence slightly more pronounced anteriorly than posteriorly, with a field of pointed denticles; other denticles arranged in a distal proventral row; erect setae cover the tibia (longer setae ventrally); distodorsal surface with coat of short recumbent setae. Tarsus slender, slightly inflated distally; tarsal denticles arranged in a tight proventral row; short recumbent setae and

long erect setae covering surface, setae longer ventrally, denser distally. Tarsal claw with 6 teeth.

Legs: Measurements of femur, patella, tibia, metatarsus, tarsus in mm: I: 8.7, 1.7, 7.1, 10.5, 11.1; II: 15.3, 1.7, 14.3, 14.3, missing; III: 8.2, 1.8, 7.5, 9.8, 11.7; IV: 11.8, 2.1, 9.8, 14.4, missing. Coxae smooth, concolorous with sternites; long, erect setae proximally. Anterior row of flat, evenly-spaced denticles developed along length of each coxa, terminating in distoventral submarginal row of small denticles and setae; proximal denticle row distal on coxae I, II, III, along full length of coxae IV. Trochanters reddish brown, with scattered distally-pointing denticles laterally. Femur divided into basal piece and shaft by a circumferential groove; cuticle dark brown, lighter distally; shaft with irregular rows of distally pointing denticles associated with a distal setae, denticles, and setae not developed on ventral surface, denticles especially numerous on legs I and III; a few denticles along distal margin, larger dorsally, and in short lateral rows basally. Patellae reddish brown, wider distally; small distally-pointing denticles with accompanying setae scattered over surface, sometimes arranged in loose rows, reduced ventrally; sharp denticles larger on distal dorsal margin, smaller on ventral margin. Tibiae golden brown with a coat of fine recumbent setae, denser distally; scattered denticles with accompanying setae, some forming 4 or 5 rows, denser proximally and dorsally; proximal dorsal margin with rounded median process; distal margin with ventral row of pointed denticles terminating with lateral spines. Tibia II with reduced denticles, vestiture of microtrichia, 4 incomplete pseudoarticulations, and about 30 partial circumferential rings. Metatarsi golden brown with a coat of recumbent setae; Legs I and III with 3 pseudoarticulations, leg II with 9, leg IV with 5, each pseudoarticulation with a ventral pair of distally-pointing spines. Tarsi golden brown, distal-dorsal margin of each segment dark; longer segments each with ventral pair of spines; recumbent setae cover entire cuticle, setae denser, longer ventrally and distally.

Variation in male.—*Leiobunum nigropalpi* shows comparatively little variation. Most are yellowish ventrally and golden to orange-brown dorsally with medium to dark brown legs, but some are lighter in color, with a white ventral surface, pale yellow dorsal surface, or golden-brown legs. Tibial denticles of the palp and posterior coxal denticle rows may be reduced or absent. The proximo-ventral prominence of the palpal tibia usually flat, but occasionally with the distal portion projecting ventrad, forming a small spur.

Description of female paralectotype.—Body length: 7.3 mm. *Dorsum* (Fig. 8): Carapace length, width: 2.1 mm, 2.9 mm. Cuticle brown, coarsely granulate with a few pointed denticles on mound of ozopore; ocularium nearly black, strongly canaliculate, each carina with 5 curved denticles. Supracheliceral lamina smooth. Opisthosoma: Generally brown with a weak central figure indicated by irregular dark bordering with dark anterior blotches on tergite 1 and a dark medial region of tergite 4; cuticle coarsely granular anterior, smoother posterior. Tergites 1–5 (scutum) demarcated by bands of whitish dots; remaining tergites appear somewhat reduced and separated from scutum (possibly due to swelling during preservation); tergite 8 and anal operculum granulate, anal operculum with a few small denticles.

Venter (Fig. 9)*:* Labrum straight, smooth. Sternites finely granulate, dark golden brown, anterior half of each sternite with a lighter transverse band that terminates before lateral margins. Posterior margin of genital operculum and margins of sternites distinct. Genital operculum dark golden brown, lighter medially; dark denticles and setae form a longitudinal band, more numerous anteriorly; anterior body slightly bilobed with lobes protruding ventrad; margin thickly rebordered, white, protruding medially; a transverse sulcus with corresponding inner (dorsal) phragma developed between bilobed body and rebordering; phragma thicker and more prominent medially; small anterior-pointing apophyses developed on anterior lateral margins corresponding to the position of the sternum; sternum dark, nearly black medially around a broad v-shaped emargination; shoulders angled rather than square as in the other species in the group, median posterior process tiny, with tendons attached along posterior sternite margin.

Appendages: *Chelicerae*: Cuticle golden, basal article with short erect setae sparsely scattered on dorsal surface (denser distally), extending to distal dorsal and prolateral surfaces of second article; setae especially dense around the base of the fixed finger.

Palps (Figs. 12, 13)*:* Measurements in mm: femur 1.7; patella 0.6; tibia 0.9; tarsus 1.5. Cuticle golden to golden brown. Trochanter with a few scattered denticles and setae distoventrally. Femur expanded distally with 4 or 5 denticles in a proximal prolateral row; pointed denticles arranged in a retroventral row and extending along the distal-dorsal margin, long erect setae interspersed and forming a proventral row, a few scattered dorsally. Patella with distal prolateral apophysis densely covered in long erect setae; pointed denticles extend along distal dorsal margin and form prodorsal and retrodorsal bands, each interspersed with a row of long erect setae. Tibia ventral surface slightly curved, with a few distally pointing denticles in a loose proximal row; fine recumbent setae and long erect setae cover surface. Tarsus expanded distally; surface with a coat of fine recumbent setae, long erect setae in irregular rows; setae dense and longer distoventrally, especially around tarsal claw. Claw with six teeth.

Legs: Measurements of femur, patella, tibia, metatarsus, tarsus in mm: I: 7.7, 1.9, 6.0, 8.1, 10.2; II: 13.4, 1.7, missing, 12.3, 12.5; III: 7.3, 1.2, 5.9, 8.9, 10.2; IV: 11.0, 1.1, 8.4, 12.5, 14.9. Coxae dark golden brown, smooth, with sparse scattered setae. Large, flat denticles developed in a prolateral and retrolateral row on each coxa; tiny rounded denticles present submarginally; all prolateral rows and coxa IV retrolateral row extends full length of coxa (or nearly so); retrolateral rows of coxae I–III extend over half the length of the coxa; prolateral dorsal surface of coxa III and retrolateral dorsal surface of coxae I and II slightly protuberant; coxae I and II with a single dark tubercle. Trochanters smooth ventrally; dorsal surface with medial groove; distally-pointing denticles developed on lateral surfaces. Femur proximally reddish-brown, distally lighter; divided into basal piece and shaft by circumferential groove. Distally-pointing denticles scattered on basal piece and in 7–12 irregular rows down the shaft, most with accompanying distal erect setae; ventral surface smooth; two large denticles present on distal-dorsal margin. Patellae distal dorsal surface expanded, with 4 longitudinal rows of denticles, larger distally; distal ventral margin with a few distally-pointing denticles. Tibiae golden with vestiture of

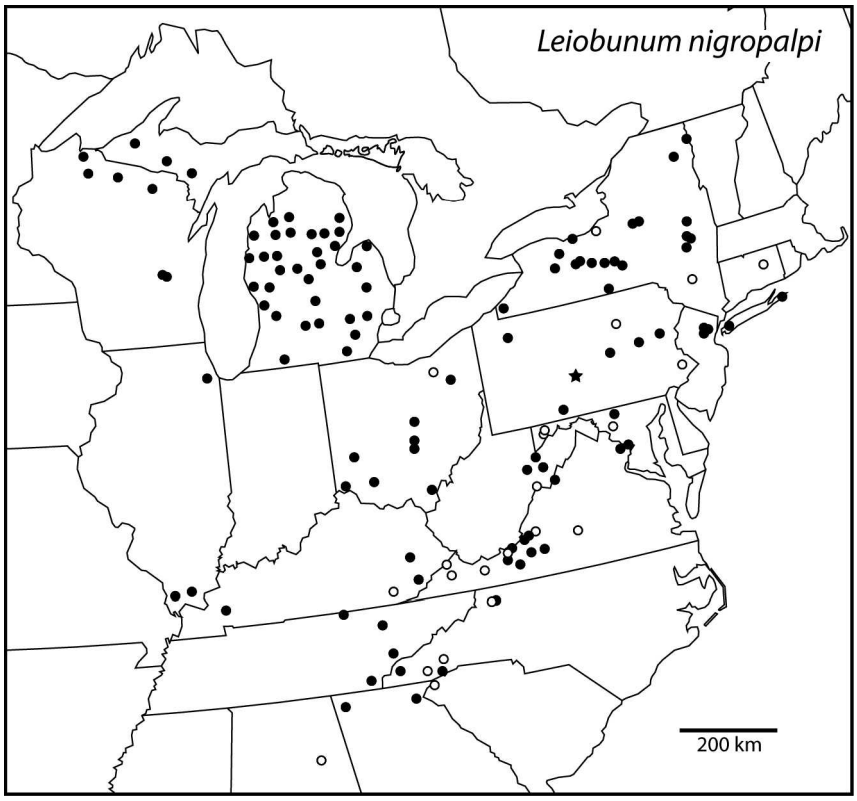


Figure 18.—Map of collection localities for *Leiobunum nigropalpi*. Open circles are localities of specimens observed in this study. Black circles are localities obtained from the literature (Bishop 1949; Davis 1934; Edgar 1971; Levi & Levi ; McGhee 1970; Weed 1892). A star indicates the type locality.

microtrichia and a coat of recumbent setae; proximal surface with 4 rows of denticles; dorsal margin with a few denticles and a small process. Left tibia II with 4 incomplete pseudoarticulations, right tibia II with 7, and both with numerous faint circumferential rings. Metatarsi golden with a coat of recumbent setae; a few scattered denticles proximal; erect setae form a few sparse rows; 5 pseudoarticulations on metatarsi I, III, and IV, 7 on II, each with ventral pair of spines and sometimes a dark dorsal spot. Telotarsi golden with a few rows of sparse erect setae and a coat of dark recumbent setae, denser distally and ventrally on each segment, especially distal segments; longer (proximal) segments with a pair of ventral submarginal spines. Tarsal claw smooth.

Ovipositor: Damaged, but two spermathecae visible between rings 4 and 5; otherwise typical: shaft dorsoventrally flattened; width constant to base of furca; anterior rings each with a transverse row of 2–10 erect setae (denser distally) on dorsal and ventral surfaces; furca lightly sclerotized, tapered anteriorly, and constricted at base; surface with many long setae; terminal sense organs anterior-lateral.

Variation in female.—As in males, there is little variation. The anterior genital operculum may be bilobed or straight, with or without anterior-lateral protuberance. The central figure, white spots, and sigilla color vary in intensity. Pro- and retrolateral rows of denticles may be reduced or absent on coxae II and III.

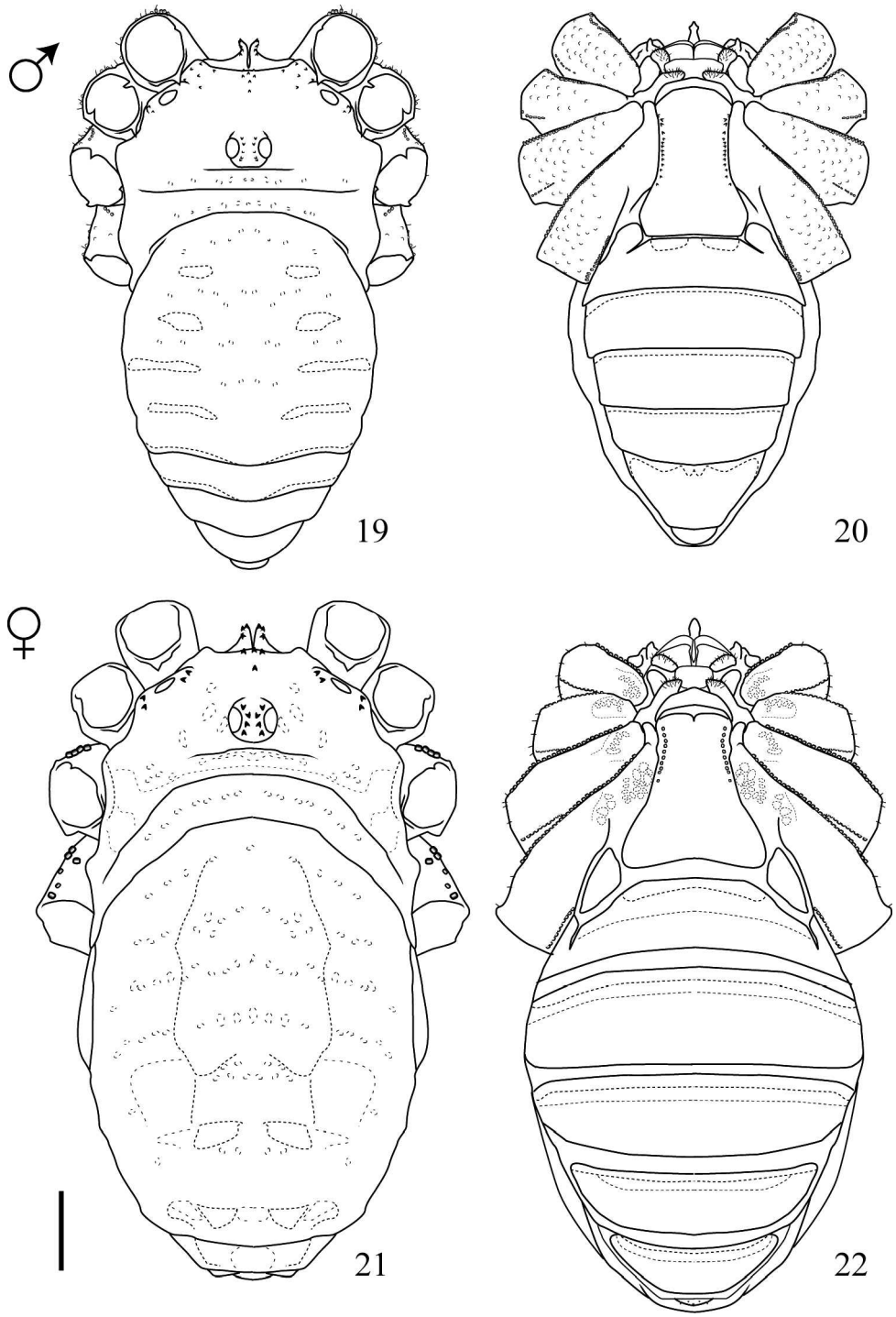
Range.—Forests of the eastern United States and, perhaps, southeastern Canada (Fig. 18).

Remarks.—*Leiobunum nigropalpi* is morphologically uniform throughout its range and many of its features are plesiomorphic relative to other members of the species-group based on outgroup comparision with closely related North American species (e.g., *L. politum* Weed 1890, *L. aldrichi* Weed 1893, *L. verrucosum* (Wood 1870), *L. ventricosum* (Wood 1870), *L. vittatum* species-group) (M. Burns, M. Hedin, J. Shultz., unpublished molecular phylogeny). Specifically, the male palps are generally gracile, with the retrolateral denticles of the femur occurring in a long longitudinal series, rather than being restricted to a distal region, and a retrolateral femoral apophysis is absent. Furthermore, the penis narrows at the glans-shaft junction, as in species with primitive sacculate penes, and the posterior process of the female sternum is only lightly sclerotized.

Leiobunum euserratipalpe new species
(Figs. 19–31)

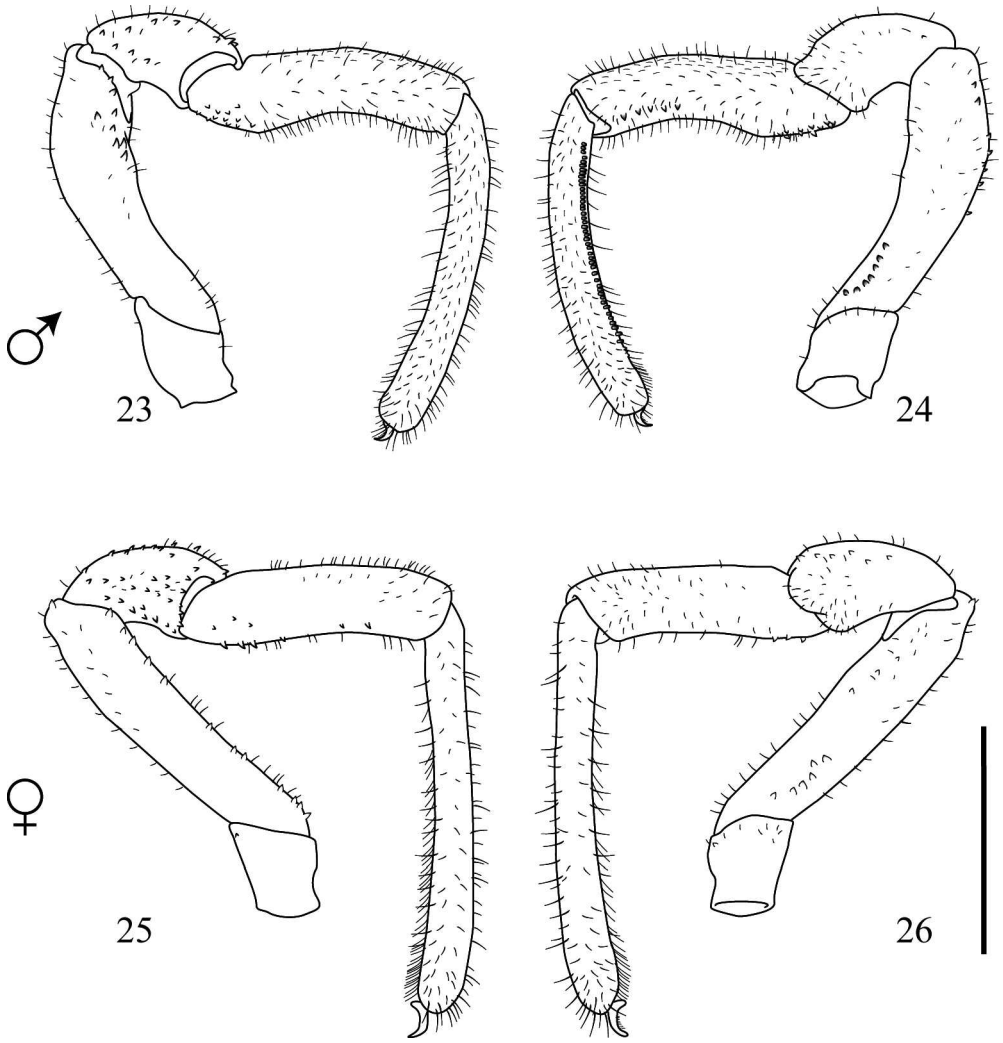
Leiobunum serratipalpe Roewer 1910: Davis 1934:689–690, pl. 31, figs. 3, 4, pl. 33, fig. 32; Bishop 1949:203–204, pl. 6, figs. 80–83; Edgar 1966:363, fig. 7; McGhee 1970:114–121, figs. 21c, d, 24c, 28, 29 (unpublished dissertation) (all misidentifications).

Types examined.—Holotype: USA: *Virginia*: Prince William County, Manassas National Battlefield Park, ~0.3 km S of Sudley Spring, 38.8168°N, 77.5164°W, 22 July 1999, A.C. Chazal (NMNH). Paratype: 1 ♀, collected with holotype (NMNH).



Figures 19–22.—Dorsal and ventral perspectives of *Leiobunum euserratipalpe* new species, male holotype, female paratype. Scale bar = 1 mm.

Other material examined.—USA: *Maryland*: Howard County: 3 ♂, 2 ♀, Middle Patuxent Environmental Area, 39.2056°N, 76.9081°W, 27 July 2007, R. Smith (UMD). Montgomery County: many ♂ and ♀, Upper Seneca Crest, 32.2575°N, 77.1735°W, Summer 2010, J.W. Shultz (UMD). *Michigan*: Livingston County: 2 ♂, George Reserve, 42.4667°N, 84.0000°W, 18 July 1936, I.J. Cantrall (AMNH). *Mississippi:* Lafayette County: 2 ♀, 1 mi [1.61 km] SW Abbeville, in deciduous woods on low vegetation, 34.489°N, 89.510°W, 10 July 2008, P. Miller (UMD), 1 ♂, same locality, 25 May 2008, P. Miller, G. Stratton (UMD). *North Carolina*: Graham County: 1 ♂, Joyce Kilmer Memorial Forest, 35.374°N, 83.975°W, 26 June 1977, W. Shear (VMNH). Jackson County: 1 ♂, 1 ♀, 7.3 mi [11.7 km] SSE Cashiers, 1177, 0.1 mi [0.16 km] N South Carolina state line, 35.019°N, 83.060°W, 28 August 1973, R.M. Shelley (NCMNS: 1944). Wake County: 1 ♀, Umstead Park, 35.859°N, 78.750°W, 12 September 1973, R.M. Shelley (NCMNS: 2023). Person County: 1 ♂, 8.4 mi

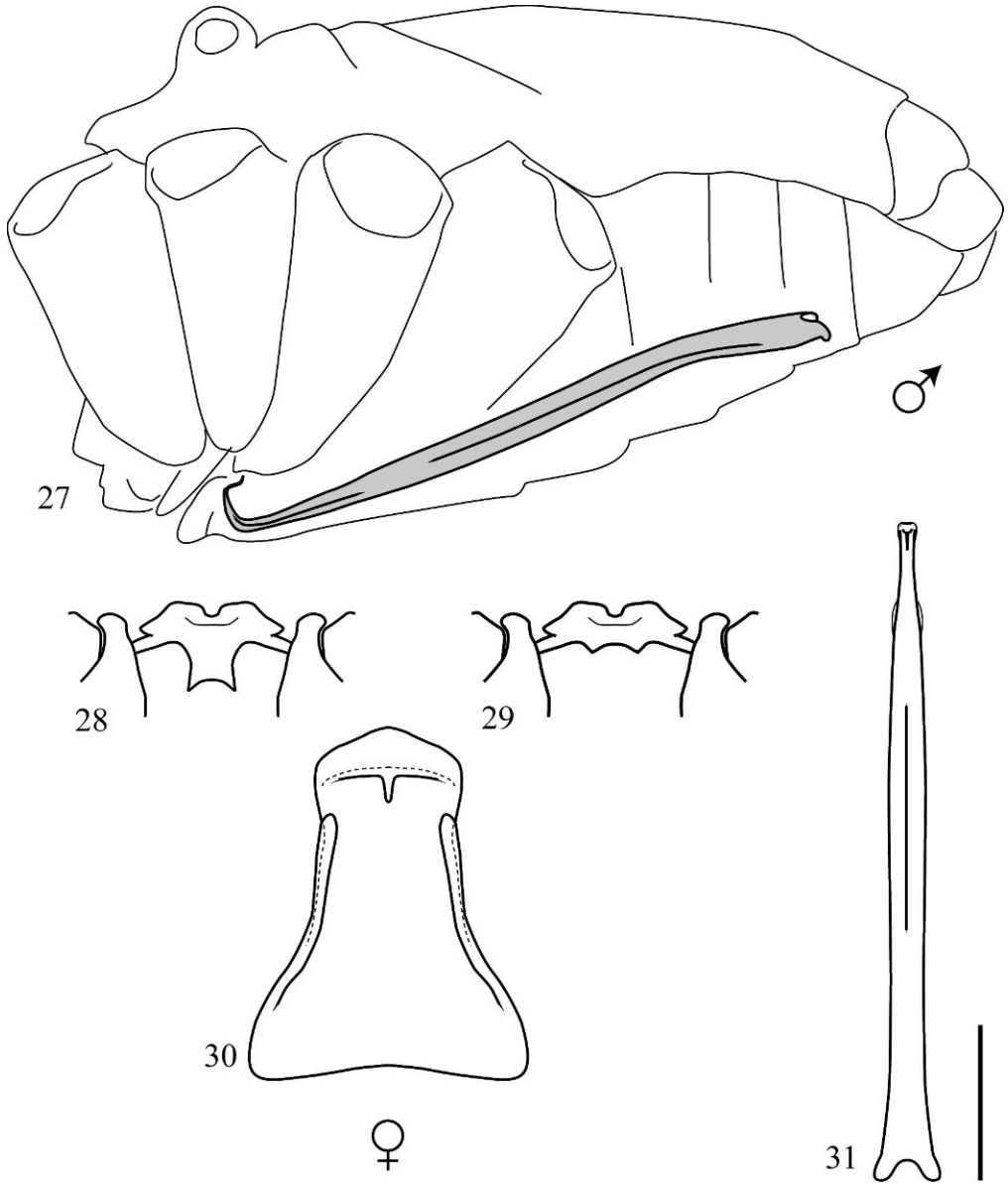


Figures 23–26.—Palps of *Leiobunum euserratipalpe* new species, male holotype, female paratype. Retrolateral perspectives on left, prolateral perspectives on right. Scale bar = 1 mm.

[13.5 km] NW Roxboro, 1392, 0.4 mi [0.64 km] E 1300, 36.45°N, 79.12°W, 18 July 1973, R.M. Shelley (NCMNS: 1824). *Ohio*: Hocking County: 2 ♂, Clear Creek Twp, 39.5406°N, 82.7356°W, 10 September 1931, T.H. Hubbell (AMNH). *Pennsylvania*: Bucks County: 2 ♂, 2 ♀, Rushland, Wilkinson Rd., Coyne Farm, vernal marsh on wooded hilltop, 40.250°N, 75.042°W, 6–20 August 1998, H. O'Connor (ANSP); many ♂ and ♀, same locality, 21 July–5 August 1998, H.O 'Connor (ANSP). Cumberland County: 1♀, Boiling Springs, 40.1498°N, 77.1283°W, 8 August 2010, J. Ryndock (MEM). *Virginia*: Clarke County: 5 ♂, Blandy Farm, ca 3 mi [4.8 km] south of Boyce, 39.0624°N, 78.0622°W, 1 August 1991, D.R. Smith (VMNH). Cumberland County: 2 ♂, "Hardwood site 1 (north)" 2 km SSW of Columbia, 37.732°N, 78.175°W, 1 August 1990, J.C. Mitchell (VMNH). Essex County: 4 ♂, 1 ♀, 1.5 km SE Dunnsville, "Malaise trap B1#1", 37.8473°N, 76.8015°W, 12 July 1991, D.R. Smith (VMNH). Fluvanna County: 6 ♂, 2 ♀, Kents Store, Bell drift fence site, 37.8779°N, 78.1286°W, 13 September 1995, M. Bell (VMNH). Henrico County: 1 ♂, Westhampton, west Richmond, 37.5741°N, 77.5146°W, June–July 1991, W. Mitchell (VMNH); 1 ♀, National Guard Facility, 2 mi [3.2 km] SE of Sandston on LaFrance Rd., 37.498°N, 77.292°W, 11 July–19 August 2001, K.L. Derge (VMNH). Henry County: 1 ♂, Broeski's Farm, ca 2 mi [3.2 km] E of Sandy Level in pitfall traps, 36.571°N, 79.681°W, 22 August–18 September 1987, RLH (VMNH); 1 ♂, 1 ♀, Vicinity of Martinsville, 36.692°N, 79.865°W, 4 August 1993, Career Club Excurs. (VMNH). Isle of Wight County: 2 ♂, Zuni Pine Barrens, 36.7803°N, 76.8914°W, 31 August [?], C.A. Pague (VMNH). Prince William County: 1 ♂, 1 ♀, Manassas NBP, 0.3 km S of Sudley Spring, 38.8168°N, 77.5164°W, 22 July 1999, A.C. Chazal (VMNH). York County: 3 ♂, 1 ♀, Cheatham Annex Naval Supply Base, "Cheatham Pond DF site", 37.2934°N, 76.619°W, 6 July 1989, DNH survey (VMNH).

Etymology.—The specific epithet means "true" *serratipalpe.* The name reinforces the distinctiveness of the species from the type of *L. serratipalpe* Roewer 1910, which Cokendolpher (1981) showed to be a female *L. calcar*, while acknowledging the later and more accurate concept of *L. serratipalpe* as developed by American workers (Davis 1934; Bishop 1949; Edgar 1966; McGhee 1970). See "Remarks" for details.

Diagnosis.—Penis (Figs. 27, 31): shaft essentially straight in lateral view, usually with a pair of small, subterminal alae;



Figures 27–31.—Genital structures of *Leiobunum euserratipalpe* new species: 27. Diagrammatic lateral perspective of male showing position of penis; 28, 29. Ventral perspective of typical variants of female sternum (genital operculum removed); 30. Dorsal (internal) perspective of typical female genital operculum; 31. Dorsal perspective of penis. All to same scale. Scale bar = 1 mm.

glans-shaft junction not demarcated dorsally, no constriction from dorsal or lateral view, glans tapering distally, with strong dorsal curvature. Male palps (Figs. 23, 24): generally gracile; femur inflated somewhat distally, with very low retrolateral apophysis or none, but with retrodistal field of large denticles; retrolateral armature limited to distal 1/3 of femur; tibia inflated ventroproximal forming a rounded-to-flat prominence with field of denticles. Female: sternum usually with small median anterior notch (sometimes absent) and with small (less than half sternum width) posterior median process (Figs. 28, 29), palpal femur lacking retrolateral apophysis (Fig. 25). Both sexes with a long prolateral row of denticles extending the full length, or nearly so, of each coxa.

Description of male holotype.—Body length: 6.3 mm. *Dorsum* (Fig. 19): Carapace length, width: 1.7 mm, 2.8 mm. Cuticle coarsely granulate, golden brown with dark sigilla lateral to ocularium. Supracheliceral lamina parallel with tips diverging, a few large denticles form a row down dorsal surface of each side. Median preocular prominence with 6 denticles in 2 transverse rows. Ozopore white, ringed in brown. Sharp denticles circling ozopore and scattered between mound and median prominence. Ocularium dark brown, lighter medially, weakly canaliculate; 7 denticles on left carina, 8 denticles on right carina. Mesopeltidium slightly elevated above surface of propeltidium; mesopeltidium and metapeltidium each with transverse row of white spots. Opisthosoma: Tapered posteriorly; cuticle golden brown, coarsely granulate, covered in tiny tubercles. Scutal tergites (tergites 1–5) distinguished by transverse, lateral rows of sigilla and bands of white dots; posterior margins of tergites 5 and 6 rebordered

medially, straight, brown; lateral margin of dorsum white, especially on posterior tergites. Anal operculum golden brown with small scattered denticles.

Venter (Fig. 20)*:* Labrum with slight dorsal curvature and a subterminal pair of small lateral tubercles. Sternites golden brown, darker anteriorly; cuticle finely granulate. Posterior margin of sternites 3–5 straight; sternite 7 trapezoidal. Two large sigilla extend from the posterolateral genital operculum to the anterior margin of sternite 3. Sternite 3 and lateral sternite 2 partially fused, genital operculum clearly demarcated. Operculum golden brown with lateral submarginal rows of pointed denticles and small scattered denticles and erect setae; anterior margin rebordered, white.

Appendages: *Chelicerae*: Golden brown with short darker bands on proximal prodorsal and retrodorsal surfaces of second article. Distodorsal surface of first article and dorsal and prolateral surfaces of second with scattered erect setae, denser on distal prolateral surface.

Palps (Figs. 23, 24)*:* Measurements in mm: femur 1.5; patella 0.7; tibia 1.2; tarsus 1.5. Primarily golden brown, dorsal femora surface with incomplete brown bands. Trochanter with 3 distal denticles and prolateral submarginal row of erect setae. Femur arched distally with a small distal retroventral process; large, dark, distally-pointing denticles clustered on the anterior surface of the process, a few scattered distally; distodorsal surface with 2–3 irregular rows of denticles; proximal prolateral surface with a row of 7 dark, blunt denticles on left femur, 9 on the right; setae scattered on dorsal, ventral, and distal prolateral surfaces. Patella with submarginal row of dark distally-pointing denticles and erect setae, interrupted ventrally; a few smaller denticles scattered on surface; distal prolateral margin protuberant with a coat of erect setae. Tibia slightly curved, forming a shallow ventral concavity; proximal ventral surface expanded, forming a square, flat region covered with small, dark proximally-pointing denticles (retrolateral denticles smaller and pointing distally); proximodorsal surface slightly inflated; distal proventral surface with longitudinal row of 5 evenly spaced, dark-tipped denticles; entire surface with a coat of long erect setae, fine recumbent setae present dorsally. Tarsus slightly arched and curving slightly prolaterally; surface coated with long erect and short recumbent setae; dark blunt denticles arranged in a tight row down the length of the proventral surface, with denticles at either end smaller and pointed; distal ventral tip with dense, fine erect setae. Tarsal claw with 5 distally pointing teeth increasing in length distally.

Legs: Measurements of femur, patella, tibia, metatarsus, tarsus in mm: I: 7.8, 1.6, 6.4, 8.4, 10.8; II: 13.5, 1.6, 12.7, 12.9, 28.3; III: 7.3, 1.6, 5.9, 8.9, 11.1; IV: 10.3, 1.9, 7.1, 8.6, 10.8. Coxae golden brown, slightly lighter, and mottled proximally; short erect setae and rounded denticles scattered over surface; large sharp denticles (some pointed, some flat-topped) arranged in a tight row down the anterior length of all coxae; coxa IV with complete posterior row, distal end of anterior row curving dorsally, adjacent to margin of coxa III, with smaller denticles scattered distally; coxae I, II, and III with a short, distal retrolateral row of denticles. Trochanters dark reddish-brown; small pointed denticles scattered over all but the ventral surface, increasing in size dorsally; small denticles arranged in a distal ventral submarginal row; denticles larger on trochanter I, smaller on trochanter IV. Femur basal piece defined by circumferential ring, concolorous with trochanters; row of small distally-pointing denticles circle the basal piece, larger dorsad; ventrally-pointing projection on proximal ventral margin; shaft golden brown with dark-tipped distally-pointing denticles arranged in loose longitudinal rows, prolateral and retrolateral denticles smaller and denser; femora I, III, and IV wider distally with a ventral submarginal row of denticles. Patellae golden with reddish-brown mottling; dorsal surface slightly arched distally; large sharp denticles arranged in a distal submarginal row, smaller denticles and setae arranged in a few longitudinal rows (reduced on patella II). Tibiae golden brown with dark flecks and blotches, leg II lighter; denticles with distally adjacent setae scattered over surface and forming a distoventral submarginal row; fine recumbent setae present; all denticles reduced on tibia II, but 5 rows of erect setae and 5–7 incomplete pseudoarticulations present. Metatarsi golden with a coat of fine recumbent setae and 5 rows of erect setae; 5 incomplete pseudoarticulations each with a ventral pair of spines on distal half of metatarsi I, III, and IV, 7 pseudoarticulations with reduced spines on metatarsus II. Tarsus with 5 rows of erect setae; ventral spines present only on proximal (longer) segments; fine erect setae on ventral surface, denser on the distal segments, longer setae clustered ventrally and dorsally around the tarsal claw. Tarsal claw curved, reddish, smooth.

Penis (Figs. 27, 31): 4.2 mm. Shaft without sacs or bulbs, but with a pair of small, subterminal alae; shaft straight with a slight ventral curve at base; shaft somewhat dorsoventrally flattened, rounder medially, tapers distally; no distinct joint present between the shaft and glans; glans narrow and curving dorsally at a 90° angle, slightly expanded laterally at curve; stylus projecting slightly posterior.

Variation in male.—Labrum may be straight or sharply curved dorsally. Size and number of denticles on the palpal tibia varies. Cuticle surface texture ranges from smooth to very coarse. Penis shaft usually straight, but infrequently curved dorsally; glans usually strongly curved, but may be less so, frequently due to preservation (distinguished by a wrinkled patch of cuticle on the ventral surface of the curve). Small alae absent or present, sometimes extending over curve of glans. Leg color ranges from golden to dark brown. Sternite 2 may or may not be distinct from genital operculum.

Description of female paratype.—Body length: 7.9 mm. *Dorsum* (Fig. 21): Carapace length, width: 2.1 mm, 3.4 mm. Cuticle covered with tiny scattered tubercles creating a coarsely granular texture; tubercles dark and more prominent on medial mesopeltidium and metapeltidium. Anteromedian prominence with three rows (1 median and 2 lateral) of 2–3 denticles. Ozopore mound with a few denticles scattered on each side. Ocularium weakly canaliculate with 5 pointed denticles and a few scattered erect setae on each carina; dark reddish-brown, darker around the eyes. Propeltidium golden brown, darker anterior to ocularium, with dark lateral sigilla and marginal border near leg III. Mesopeltidium and metapeltidium each with reddish-brown medial band, whitish posterior and lateral margins, gold anterior margins, and white lateral spots. Supracheliceral lamina golden brown with an irregular row of pointed denticles on dorsal and anterior surfaces of each parallel side. Opisthosoma: Abdomen oval and slightly tapered posterior; cuticle coarsely granular and

predominantly medium-reddish brown, darker laterally; tergites 1–6 form a scutum, with each tergite distinguished by color; faint central figure indicated by dark border; bordering breaks up at tergite 4, becoming two anterior dark blotches on tergites 5–7; transverse bands of white dots extend across tergites 1–3, limited to lateral regions of the posterior tergites; tergites 5–7 light in color lateral to the central figure, appearing as 2 large posterior white blotches from a distance. Anal operculum golden reddish-brown with a few tiny scattered erect setae.

Venter (Fig. 22)*:* Labrum straight with pair of small subterminal lateral tubercles. Sternites golden reddish-brown with a lighter anterior transverse band, darker anterior margin, and white posterior and lateral margins; surface smooth with short, scattered erect setae. Genital operculum golden brown with two posterolateral sigilla; cuticle smooth with a few scattered erect setae. Genital operculum and sternites well demarcated. Flat-topped denticles arranged in a lateral submarginal row (smaller posteriorly) on anterior half of the operculum. Anterior margin thickly rebordered and protruding anteriomedially, forming a thick white ''lip'' with posterior sulcus; a very short medial sulcus extends posteriorly from transverse sulcus. Inner (dorsal) surface (Fig. 30) with posterior-pointing ''shelf'' (phragma) and median septum, corresponding to the external sulci. Sternum (Fig. 28) straight and thick, with a small medial notch; posterior margin with rectangular median process about half the width of the sternum, muscles attached to the dorsal (inner) surface of the process.

Appendages: *Chelicerae*: Golden brown with scattered erect setae on dorsal surfaces of first and second article; second article with narrow prolateral distal band of erect setae becoming a dense cluster just proximal to fixed finger.

Palps (Figs. 25, 26)*:* Measurements in mm: femur 1.5; patella 0.7; tibia 1.2; tarsus 1.8. Palpal segments uniformly golden brown. Trochanter with 2 tiny submarginal distally-pointing retrodorsal and ventral denticles; setae form a distal prodorsal field and sparse, ventral submarginal row. Femur narrow, slightly wider distally; small distally pointing denticles arranged in a retroventral row terminating at a distal submarginal row, setae interspersed, denticles denser distally, setae denser proximally; weak proventral row diverging; proximal prolateral surface with a row of 7 denticles on left femur, 6 on right femur, and scattered erect setae; distal dorsal and prolateral margin each with one denticle, surfaces with erect setae arranged in a few irregular rows. Patella with a rounded distal prolateral apophysis; coat of short, erect setae covers process, distal ventral, and prolateral surfaces; prodorsal, retrodorsal, and retrolateral surfaces each with a wide longitudinal band of scattered distally-pointing denticles and setae; a distal submarginal row of denticles interrupted at process. Tibia with a coat of fine, dark recumbent setae on all but the ventral surface; erect setae scattered ventrally and forming loose rows dorsally; denticles scattered on the retrolateral surface and form a distal irregular pro- and retrolateral row; 2 denticles on distal prolateral margin. Tarsus with a coat of recumbent setae and 6–8 loose rows of erect setae (denser and finer distally, particularly around the tarsal claw). Tarsal claw reddish-brown, darker distally, with 7 teeth.

Legs: Measurements of femur, patella, tibia, metatarsus, tarsus in mm: I: 8.4, 1.7, 6.7, 8.3, 11.0; II: 15.5, 1.9, 14.0, 13.4, 29.7; III: 8.3, 1.6, 6.4, 8.9, 11.6; IV: 12.5, 2.0, 9.3, 13.9, 17.4. Coxae light reddish to golden brown, slightly lighter and mottled proximally; short erect setae and tiny rounded denticles sparsely scattered over surface and arranged in a ventral submarginal row; tight rows of flat-topped denticles extend nearly the full length of the prolateral and retrolateral surfaces, with prolateral denticles larger on coxae I, II, and III, and retrolateral denticles larger on coxa IV; coxa IV extends beyond the margin of coxa III, exposing the distal anterior-dorsal surface; a few small scattered denticles and 2 larger submarginal denticles present in the exposed region. Trochanters dark reddish-brown, pointed denticles scattered pro- and retrolaterally and arranged in a distal ventral submarginal row with a few interspersed erect setae; denticles larger on trochanter I, smaller on trochanter IV. Femora basal portion dark reddish-brown with a row of small denticles circling distally, interrupted ventrally; shaft golden brown and slightly expanded distally (except femur II); 6–7 loose rows of distally-pointing denticles and distally-adjacent seta on all but the ventral surface, dorsal denticles larger; two large submarginal distally-pointing denticles present dorsally and 3 smaller denticles pro- and retrolaterally; femur II denticles reduced. Patellae golden brown with darker dorsal mottling; small distally-pointing denticles in 4–6 loose longitudinal rows and in a distal submarginal row, dorsal denticles larger; denticles reduced on patella II. Tibiae golden brown with a coat of fine recumbent setae and 5 longitudinal rows of erect setae and small proximal denticles; distal margin dark with proventral and retroventral rows of small denticles, each terminating with a dark spine; tibia II mostly lacking denticles, but retaining ventrolateral spines; 5–6 incomplete pseudoarticulations on tibia II; vestiture of microtrichia present distally on all tibia. Metatarsi golden brown, distal margin reddish; cuticle with a coat of recumbent setae and 5–7 rows of short erect setae; 4–5 faint pseudoarticulations (11–12 on metatarsus II) indicated by a reddish dorsal mark, each with a pair of distally-pointing ventral spines (absent from some pseudoarticulations on metatarsus II). Tarsus golden brown, darker distally, proximal half of first segment and dorsal distal margins of all segments darker; a pair of spines present at the distal ventral margin of all but the most distal segments; recumbent setae cover entire surface, denser and longer ventrally and distally; short erect setae arranged in 5–7 rows down the length of the tarsus, longer erect setae clustered around tarsal claw. Tarsal claw reddish.

Ovipositor: Typical; two spermathecae visible in ring 6, shaft slightly expanded dorsoventrally around the spermathecae.

Variation in female.—The sternal notch is reduced in a few specimens we have seen, and the posterior sternal process is absent in specimens from eastern Pennsylvania, Maryland and northeastern Virginia. However, it is likely that the sternal process sclerotizes during the adult instar; in populations with sternal processes, it is variably expressed in early-season (June) individuals but is present and well sclerotized in specimens collected in August and September. Therefore, the collection date should be taken into consideration when identifying females that may belong to this species. Intensity of dorsal color, pattern, and central figure varies greatly, but posterior whitish blotches on the opisthosoma are usually visible. Leg

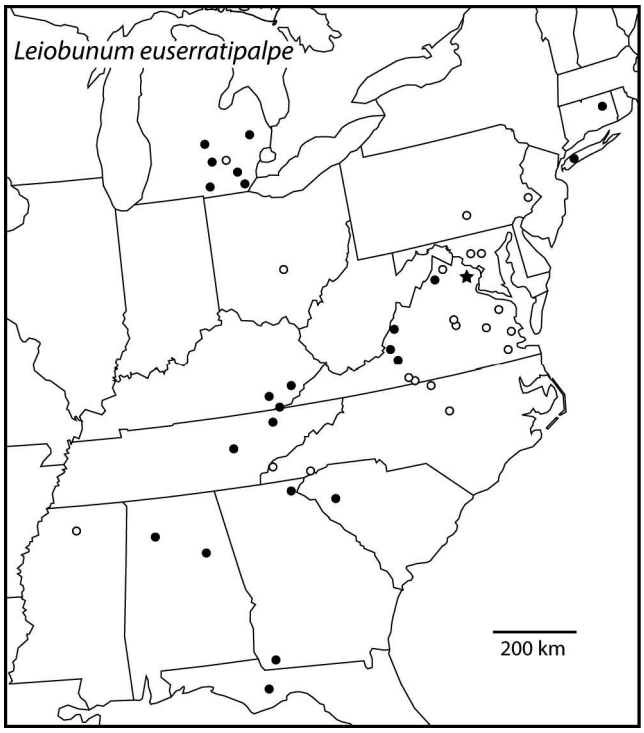


Figure 32.—Map of collection localites for *Leiobunum euserratipalpe* new species. Open circles are localities of specimens observed in this study. Black circles are localities obtained from the literature (Bishop 1949; Davis 1934; Edgar 1971; McGhee 1970). A star indicates the type locality.

color ranges from golden to dark brown. Denticles of the palpal tibia sometimes reduced.

Range.—This species is widely distributed east of the Mississippi River and is common in the Atlantic Coastal Plains and Piedmont of the eastern United States (Fig. 32).

Remarks.—Although it is technically a new species, *L. euserratipalpe* already has a complicated taxonomic history. *Leiobunum serratipalpe* Roewer 1910 was described from specimens collected in ''Long Lake'' and ''Cold River, North America.'' Cokendolpher (1981) examined the ''male'' cotype (the only specimen that appears to be available) and found it be an adult female *L. calcar,* an observation that we have confirmed. Without reference to the type material, Crosby & Bishop (1924) questioned the validity of *L. serratipalpe* and speculated that purported male specimens were actually subadult males of *L. calcar*. In addition, no confirmed adult female *L. serratipalpe* had been described (but see McGhee 1970), although it was assumed to closely resemble female *L. calcar*. Cokendolpher (1981) found several *L. serratipalpe*-like specimens within a large collection of *L. calcar* from Maine, USA, and concluded that *L. serratipalpe* was a junior synonym of *L. calcar*. This verdict was widely accepted, and *L. serratipalpe* was subsequently omitted from checklists and keys of North American harvestmen (e.g., Edgar 1990) and its records were lumped with those of *L. calcar* (e.g., Cokendolpher & Lee 1993).

However, one of the most common summer species in the Mid-Atlantic Coastal Plain and Piedmont of Pennsylvania, Maryland and Virginia (named here *L. euserratipalpe*) corresponds to the traditional descriptions of *L. serratipalpe* (e.g., Davis 1934; Bishop 1949; Edgar 1966; McGhee 1970). *Leiobunum calcar* is largely absent from this region but is common in the adjacent Appalachian Mountains. The two species are sometimes found together, but they are readily distinguished by size and reproductive structures. *Leiobunum euserratipalpe* also occurs in the southern portion of the United States (e.g., Mississippi), again where *L. calcar* is absent. Although it is clear that *L. euserratipalpe* is distinct from *L. calcar* in the regions cited above, it is premature to assume that all specimens that have been assigned to *L. serratipalpe* in the past are examples of *L. euserratipalpe*. It is possible, for example, that subadult males of *L. calcar* or individuals with reduced retrorolateral femoral apophyses on the palp have indeed been misidentified as this species. A more thorough examination of the harvestman fauna of the Appalachian Mountains and points north and west is needed to firmly establish the geographic range of *L. euserratipalpe*.

Leiobunum calcar (Wood 1868)
(Figs. 33–46)

Phalangium calcar Wood 1868:26–27, fig. 6.

Liobunum calcar (Wood): Weed 1887:935; Weed 1889a:90–91; Weed 1889b:102–103; Weed 1890:918; Weed 1893a:553–554; Weed 1893b:290–291; Banks 1893:211; Banks 1894:page?; Banks 1901:675; Roewer 1910:219; Roewer 1923:899, fig. 1054; Walker 1928:163, pl. 1, fig. 9.

Liobunum brunnea Walker 1928:167, pl. 2, fig. 12 (synonymized by Davis 1934:670).

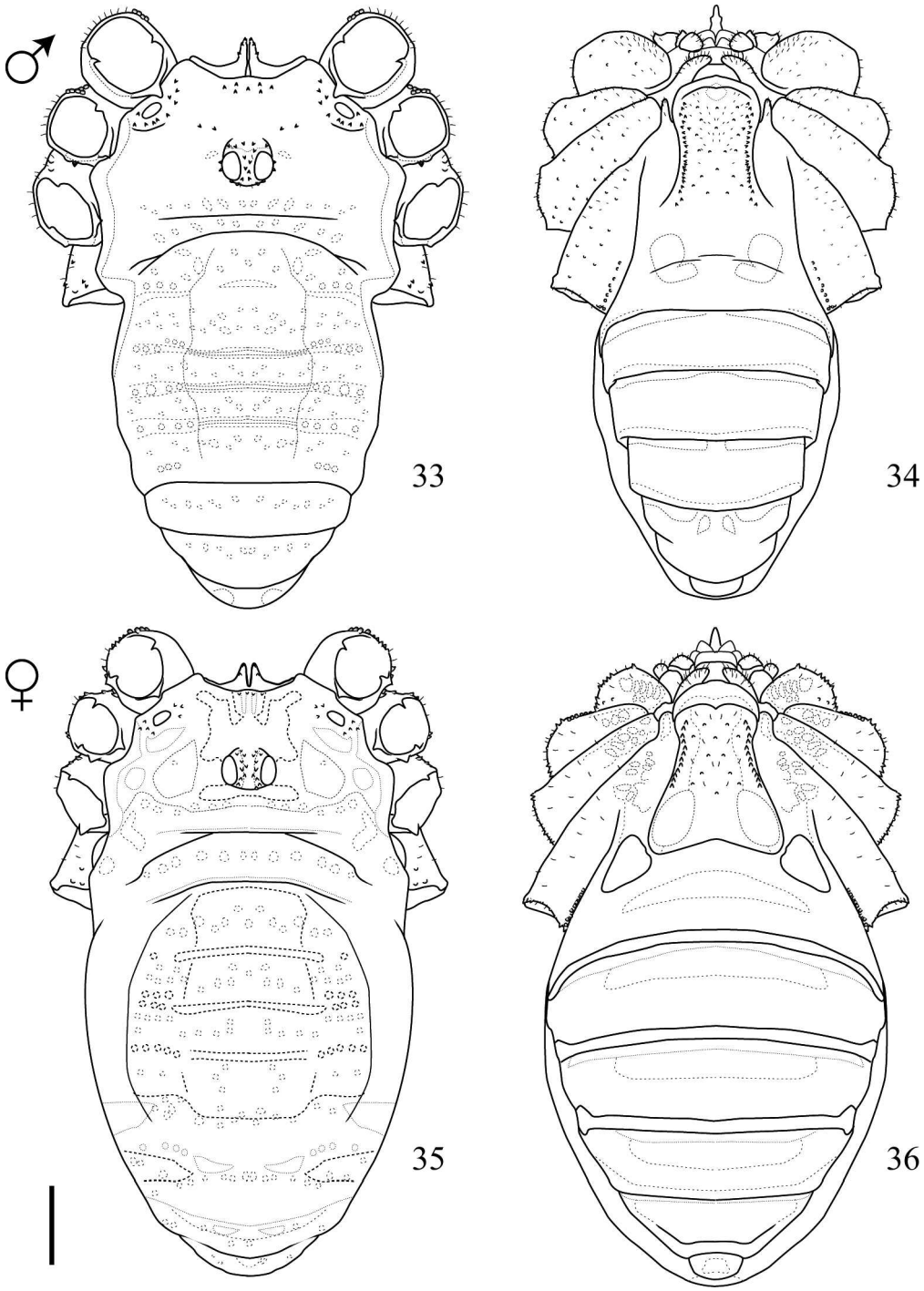
Leiobunum calcar (Wood): Crosby 1904:256; Davis 1934:670–672, pl. 32, figs. 16, 17, pl. 33, fig. 31; Bishop 1949:189–190, pl. 3, figs. 43–50; Edgar 1966:360, fig. 5; McGhee 1970:131–138, figs. 22a, 23b, 25a,b, 30, 31 [unpublished dissertation].

Leiobunum serratipalpe Roewer 1910:218; Roewer 1923:899, fig. 1054 (synonymized by Cokendolpher 1981:112–113).

''Leiobunum cumberlandense'' McGhee 1970:122–128, figs. 21e, 23c, 24e, f, 30, 31 [unpublished dissertation]. NEW SYNONYMY.

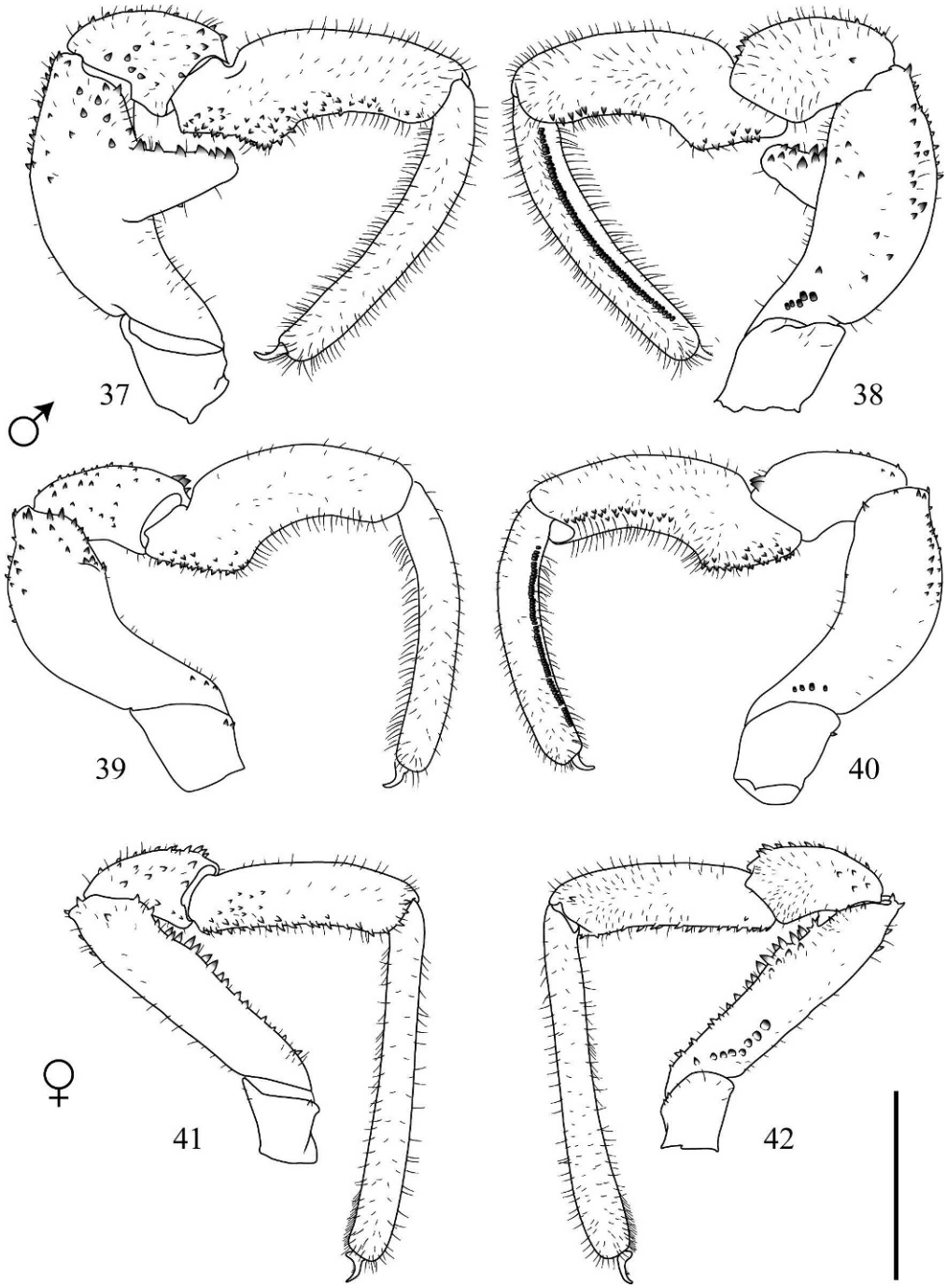
Type material.—*Phalangium calcar* Wood 1868. ♂ holotype, Type locality: ''mountains of South-western Virginia''. Not observed; presumed to be lost (Davis 1934:662).

Other material examined.—CANADA: *Ontario*: Manitoulin County: 1 ♂, Manitoulin Island, Square Bay, 45.75°N, 82.5°W, 26 July 1948, W. Ivie (AMNH). Parry Sound County: 1 ♂, Osawa Island, Georgian Bay, 9 mi [14.5 km] SSW of Pointe au Baril, on rock, 45.27.548°N, 80.25.808°W, 3 July 2007, P. Miller, G. Stratton, B. Suter (UMD). Simco County: 1 ♀, Orillia, 44.68°N, 79.31°W, 27 July 1938, C.H. Curran (AMNH); 1 ♂, South of Stirling, 44.15°N, 77.39°W, 16 July 1965, J. & W. Ivie (AMNH). USA: *Illinois*: McLean County: 1 ♀, Bloomington, 40.4842°N, 88.9937°W, [?] June [?], coll.? (INHS: 0007); 1 ♀, Lawnridge, 40.644°N, 89.605°W, 26 October 1959, Butler (MCZ: 36720). *Iowa*: Dickinson County: 2 ♂, Okoboji, sweeping grass, 43.3876°N, 95.138°W, 13 July 1916, coll.? (NMNH); 4 ♂, 7 ♀, same locality, [?] 1918, TCS (NMNH). *Kentucky*: Bell County: 1 ♀, Pine Mt. State Park, 36.7448°N, 83.7195°W, 27 August 1965, A. & L. Davis (AMNH: ''*L. cumberlandense*''), 2 ♂, same locality, 2 August 1963, A. & L. Davis (AMNH: ''*L. cumberlandense*''); 1 ♂, same locality, 23 August 1966, A. & N. Davis (AMNH: ''*L.



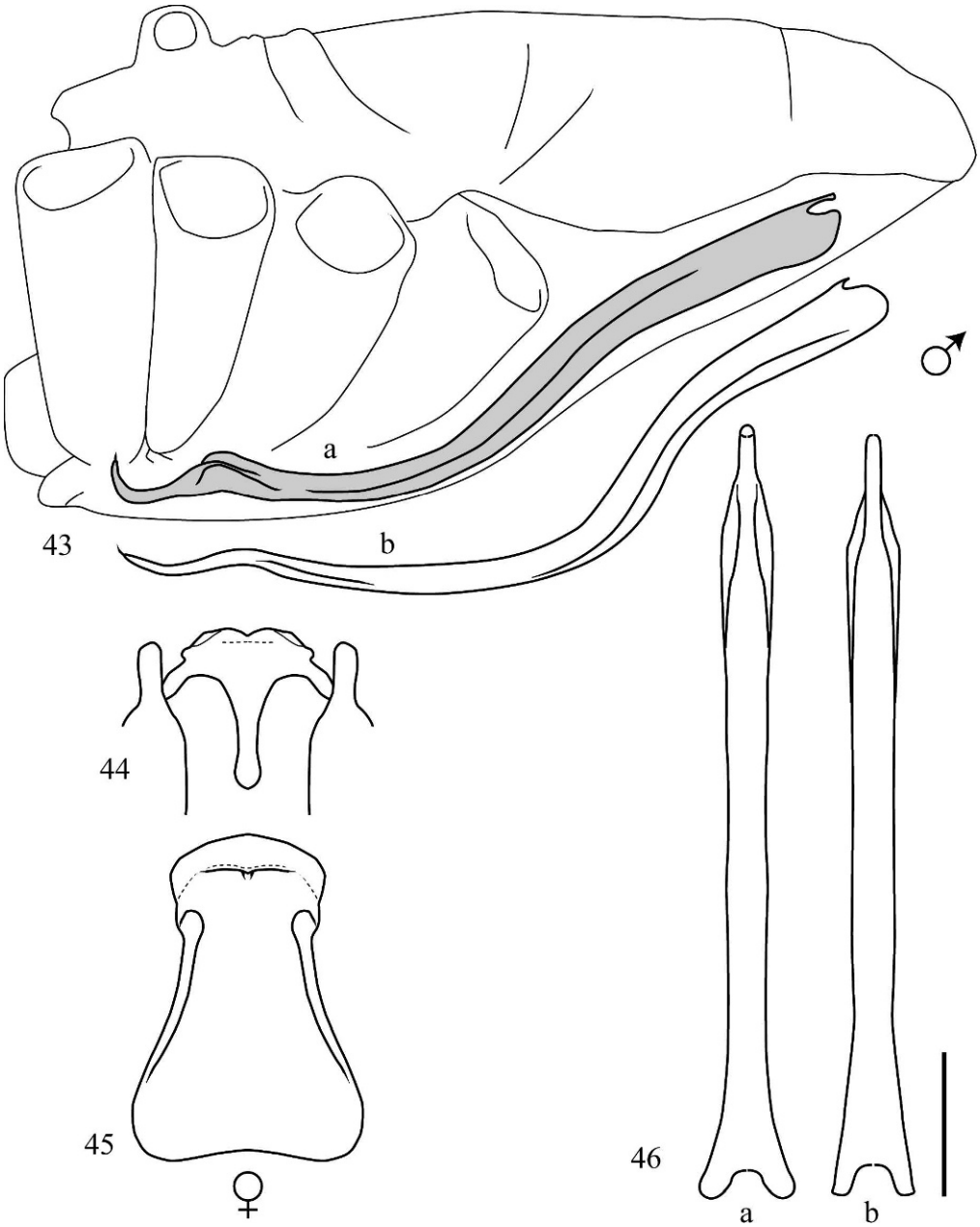
Figures 33–36.—Dorsal and ventral perspectives of *Leiobunum calcar* (Wood 1868), typical male and female from type region. Scale bar = 1 mm.

cumberlandense''). Knox County: 1 ♂, 1 ♀, Wooded hillside Trace Branch, near Heidrick, 36.8935°N, 83.8596°W, 17 June 1962, A. Davis (AMNH). Laurel County: 2 ♂, 1 ♀, Cumberland Natl. Forest [as of 1966, Daniel Boone National Forest], 36.8558°N, 84.3474°W, 22 August 1965, L. Davis (AMNH: ''*L. cumberlandense*''). *Maine*: Washington County: 3 ♂, 3 ♀, 8 km S. Milbridge, 44.4619°N, 67.8929°W, 22–27 July 1990, coll.? (AMNH). Penobscot County: 1 ♂, 1 ♀, Howland, 45.2387°N, 68.6636°W, 5 July 1987, coll.? (TTU-Z 58,786). *Maryland*: Garrett County: 2 ♂, 2 ♀, 3 km SE New Germany, ''Managed Oak Forest,'' (132, lot 003), 39.62°N, 79.105°N, elev. 779 m, 11–18 July 2005, M. Sarver (UMD). *Massachusetts*: Berkshire County: 13 ♂, 5 ♀ Lenox W. Mtn. Rd., Pleasant Valley Wildlife Sanctuary, 42.3513°N, 73.3378°W, [?] July 1976, J. Coddington (NMNH). *Michigan*: Charlevoix County: 1 ♂, no specific locality (county center used for coordinates), 45.318°N, 85.2584°W, T.H. Hubbell (AMNH). Cheboygen County: 2 ♂, 2 ♀, no specific locality (county center used for coordinates), 45.48°N, 84.50°W, 7 July 1983, coll.? (TTU Z-58,833); 1 ♂, Douglas Lake, Hook Point, 45.5674°N,



Figures 37–42.—Palps of *Leiobunum calcar* (Wood 1868): 37, 38. Typical male from type region, southwestern Virginia; 39, 40. Male "*cumberlandense*" variant; 41, 42. Typical female from type region. Retrolateral perspectives on left, prolateral perspectives on right. Scale bar = 1 mm.

84.6797°W, 3 July 1931, E.L. Miner (AMNH). St. Claire County: 3 ♀, New Baltimore, 42.6811°N, 82.7369°W, 5 July 1944, B. Malkin (AMNH). *Missouri*: Lincoln County: 2 ♂, 2 ♀, Cuivre River State Park, Hamilton Hollow Trail, elev. 550 ft [168 m], 39.03°N, 90.93°W, 21 June 1986, N.V. Horner (TTU Z-58,799). *New York*: Albany County: 5 ♂, Rensselaerville, 42.4794°N, 74.172°W, 15 July 1975, T. Eisner (AMNH). Chautaugua County: 2 ♀ , Chautaugua, 42.2098°N, 79.4667°W, July–August 1943, C. Widmer (AMNH). Herkimer County: 1 ♂, 1 ♀, Little Falls, 43.0434°N, 74.8596°W, 3 July 1918, coll.? (AMNH). Madison County: 1 ♀, Deruyter Lake, 42.8145°N, 75.8978°W, 3 July 1922, coll.? (AMNH). Oneida County: 1 ♂, Trenton Falls, 42.2715°N, 75.1602°W, 5 June 1931, coll.? (AMNH). Tioga County: 1 ♀, Spencer, 42.2124°N, 76.4963°W, 5 August 1923, coll.? (AMNH). Tompkins County: 4 ♂, 1 ♀, Ellis Hollow, 42.4273°N, 76.4108°W, 28 July 1932, N.W. Davis (AMNH); 1 ♂, Freeville, 42.514°N, 76.3466°W, 10 August 1924, Swank (AMNH). Ulster Co: 1 ♂, Cherrytown near Kerhonkson, 41.8251°N, 74.3293°W, 18 July 1976, Wygodzinsky (AMNH). *North Carolina*: Jackson County: 1 ♀, Whitewater Falls, Parking



Figures 43–46.—Genital structures of *Leiobunum calcar* (Wood 1868): 43. Diagrammatic lateral perspective of male showing position of penis; a. typical male, b. "*cumberlandense*" variant (southwestern Kentucky); 44. Ventral perspective of female sternum (genital operculum removed); 45. Dorsal (internal) perspective of female genital operculum; 46. Dorsal perspective of penis; a. typical male, b. "*cumberlandense*" variant (southwestern Kentucky). All to same scale. Scale bar = 1 mm.

Area, 35.071°N, 82.887°W, 28 August 1973, R.M. Shelley (NCMNS: 1937); 1 ♂, Brushy Fork of Greens Creek, 35.3249°N, 83.2822°W, 27 July 1971, F. Coyle (TTU Z-58,831); 1 ♂, Richland Balsam Mountain, elev. 6300–6400 ft [1920–1950 m], 35.3673°N, 82.9904°W, 4 August 1970, F. Coyle (TTU Z-58,783); 1 ♀, Dulany Bog at SR 1100 × 108 S of Cashiers, elev. 3020 ft [940 m], 35.0306°N, 83.0656°W, 21 July 1975, F. Coyle (TTU-Z 58,786). Cherokee County: 1 ♂, 11.2 mi [18 km] NW Murphy, along 1326, 35.222°N, 84.160°W, 27 July 1974, R.M. Shelley (NCMNS: 2437). Macon County: 1 ♂ 1 ♀, 5 mi [8 km] N of Highlands, 35.1269°N, 83.1924°W, August 1967, K. Kleinpeter (AMNH), 2 ♂, same locality, 9 July 1958, Hoffman (NMNH); 1 ♀, Highlands, "at Kleinpeter's place," 35.0365°N, 83.1921°W, 22 July 1967, Hoffman & Kleinpeter (VMNH), 2 ♂,1 ♀, Coweeta Hydrologic Station, 35.0596°N, 83.4205°W, 22 July 1977, L. Reynolds (NCMNS: A6823), 2 ♀, same locality, 22 September 1977, L. Reynolds (NCMNS: A6812, A6864), 1 ♀, same locality, 11 August 1978, L. Reynolds (NCMNS: A5258), 1 ♀, same locality, 6 September 1977, Lee Reynolds (NCMNS: A6818); 1 ♀, Glen Falls, 2 mi [3.2 km] SW Highlands, 3200 ft [975 m], 35.031°N, 83.238°W, 18 July 1988, K. Smith (NMNH); 1 ♂, Highlands Biological Station, elev. 3840 ft [1170 m], 35.054°N, 83.189°W, 18–28 July 1988, A.W. (NMNH); 1 ♂, Satulah Mtn., 1 mi [1.6 km] S of Highlands, 4500 ft [1372 m],

35.036N, 83.192W, 19 July 1988, W.A. Shear (VMNH). McDowell County: 1 ♂, Curtis Creek Campground, FR 482 N of Old Fort, 35.6889°N, 82.1976°W, elev. ~560 m, 20–21 August 2007, M. Hedin et al. (UMD). Swain County: 1 ♀, GSMNP, Clingman's Dome area, spruce-fir forest, 6500 ft [1981 m], 35.5627°N, 83.4985°W, 26 July 1988, AWS (NMNH). Transylvania County: 1 ♂, Davidson River Campground, off Hwy. 276, elev. ~650 m, 35.2813N, 82.7234W, 19–20 August 2007, M. Hedin (UMD); 1 ♂, 6.6 mi [10.6 km] WNW Brevard, Gov. Rd., 3.5 mi W Fish Hatchery, 35.26°N, 82.85°W, 29 August 1973, R.M. Shelley (NCMNS: 1992). Yancey County: 1 ♂, Mt. Mitchell, "camping area near top", 35.7601°N, 82.2709°W, 31 July 1972, R.L. Hoffman (VMNH). *Ohio*: Ottawa County: 1 ♂, Catawba Island, 41.583°N, 82.8346°W, date?, J.S. Hine (NMNH). *Pennsylvania*: Columbia County: 6 ♂, 1 ♀, Orangeville, 41.339°N, 80.519°W, 13 August 1932, Hughes & Davis (AMNH). Erie County: 1 ♀, no specific locality [counter center used for coordinates], 42.10°N, 80.10°W, 24 June 1987, C. Tugman (TTU-Z 58,708). *Tennessee*: Blount County: 3 ♂, Cades Cove, GSMNP, 35.4950°N, 84.0227°W, 12 September 1959, coll.? (AMNH). Cocke County: 1 ♂, Albright Grove, "ATBI Plot," 35.9359°N, 83.1220°W, 19 June–6 July 2001. M. McCord (NPS); 2 ♂, GSMNP, vic. Cosby ATBI residence house, 35.7779°N, 83.2135°W, elev. 518 m, 28 July–9 August 2000, M. Hedin, J. Cokendolpher (AMNH). Sevier County: 1 ♂, GSMNP, trail up Mt. Leconte, 35.6542°N, 83.4372°W, September 1959, PC Holt (NMNH); 1 ♂, 2 ♀, GRSM ATBI Plot: Goshen Prong, 35.6105°N, 83.5453°W, 27 August–17 September 2001, I.C. Stocks (NPS); 1 ♂ 2 ♀, Great Smoky Mtns., ATBI Plot: Indian Gap, 35.6108°N, 83.4436°W, 6 August–3 September 2001, R. Fox (NPS), 1♂, same locality, 35.6108°N, 83.4436°W, 3–26 September 2001, I.C. Stocks (NPS); 1 ♂, 1 ♀, Great Smoky Mtns., ATBI Plot: Twin Creeks, 35.685°N, 83.499°W, 10–30 September 2002, coll.? (NPS), 1 ♂, 1 ♀, same locality,5–18 July 2000, Parker, Stocks, Petersen (NPS), 1 ♀, same locality, 26 September–12 October 2000, Parker, Stocks, Petersen (NPS), 1 ♀, same locality, 15–23 May 2001, I. Stocks, M. Williams (AMNH). Pickett County: 3 ♂, 3 ♀, Pickett State Park, 36.558°N, 84.7916°W, 25 June 1967, C.R. McGhee (AMNH: "*L. cumberlandense*"). Roane County: 3 ♂, Kingston, 35.8809°N, 84.5085°W, 12 July 1933, W.J. Gertsch (AMNH). *Vermont*: 3 ♀, North Danville, 44.459°N, 72.094°W, 13 August 1967, A.M. Chickering (MCZ: 37203). 1 ♀, Lake Bomoseen, 43.645°N, 73.225°W, 10 July 1936, coll.? (MCZ: 37147). *Virginia*: Amherst County: 4 ♂, 1 ♀, Tarjacket Ridge, 37.4316°N, 78.6569°W, 9 July 1998, J. Schilling (VMNH); 3 ♂, 1 ♀, same locality, 4 August 1998, VMNH survey (VMNH). Augusta County: 1 ♂, GWNF, 5 mi [8 km] west of Stokesville Comp., "452-8A Trap 3," 38.3403°N, 79.2334°W, 8 July 1989, B. Flamm (VMNH); 1 ♂, GWNF, ca 5 mi [8 km] west of Stokesville Comp., "460-3 Trap 3," 38.3403°N, 79.2334°W, 1 September 1989, B. Flamm (VMNH). Bath County: 2 ♂, SE of Hot Springs, "crest of Warm Springs Mtn.," 38.0526°N, 79.7684°W, 19 August 1999, S.M. Roble (VMNH); 1 ♂, "headwaters of Smith Creek, across Middle Mtn. from Douthat State Park," 38.5713°N, 78.8298°W, 9 July 1988, R.L. Hoffman (VMNH); 2 ♂, Warm Springs Mtn, WFD, UV, 38.0526°N, 79.7684°W, 14 June 1999, J.C. Ludwig (VMNH). Botetourt County: 1 ♂, 3 ♀, Roaring Run, 37.6924°N, 79.8909°W, 21 August 1996, M. Donahue (VMNH). Clarke County: 1 ♂, 1 ♀, Blandy Farm, ca 3 mi [4.8 km] south of Boyce, 39.0624°N, 78.0622°W, 2 July 1991, D.R. Smith (VMNH); 5 ♀, same locality, 1 August 1991, D.R. Smith (VMNH). Dickenson County: 1 ♀, Breaks Interstate Park, "DF site 2, Nature Trail," 37.287°N, 82.296°W, 22 August–6 October 1991, VMNH survey (VMNH). Essex County: 3 ♂, 1 ♀, 1.5 km SE Dunnsville, "Malaise trap B1#1," 37.8473°N, 76.8015°W, 12 July 1991, D.R. Smith (VMNH). Floyd County: 1 ♂, Buffalo Mountain NAP, "north slope DF site," 36.796°N, 80.477°W, 15 July–29 August 2001, VMNH survey (VMNH); 3♂, 1 ♀, Buffalo Mountain NAP, "south slope DF," 37.4316°N, 78.6569°W, 9 August–6 September 2000, Joint Survey (VMNH). 1 ♀, Buffalo Mountain NAP, "UV trap at base of hump," 37.4316°N, 78.6569°W, elev. 1067 m, 3 June 2000, S.M. Roble (VMNH); 1 ♂, 1 ♀, Buffalo Mountain NAP, "trailhead at parking lot," 37.4316°N, 78.6569°W, 2 June 2004, R.L. Hoffman (VMNH); 2 ♀, Buffalo Mountain NAP, "upper foot trail to top," 37.4316°N, 78.6569°W, 29 July 2000, Joint Survey (VMNH); 4 ♂, Buffalo Mountain, ~1300 m, 6 mi [9.7 km] SE of Willis, 36.796°N, 80.477°W, 25 August 1984, R.L. Hoffman (VMNH). Giles County: 1 ♀, Mountain Lake, 37.3551°N, 80.5368°W, June–July 1947, H.H. Hobbs, Jr. and Zoology class (TTU); 1 ♂, Mountain Lake, 3800 ft [1158 m], 37.3551°N, 80.5368°W, [?] June 1959, Holt & Hoffman (NMNH). Henry County: 1 ♂, Breeski's Farm, "near Ridgeway," 36.9893°N, 79.4825°W, 22 August 1987, VMNH Exped (VMNH). Highland County: 1 ♂, Locust Springs, "Buck Run ponds," 38.5828°N, 79.6352°W, 5 August 1999, S.M. Roble (VMNH); 1 ♂, Locust Spring Recreation Area, 8 mi [13 km] NW of Bluegrass, 38.5828°N, 79.6352°W, elev. 1158 m, 13 July 1974, R.L. Hoffman (VMNH). Lee County: 1 ♂, Cumberland Gap National Historical Park, 36.623°N, 83.645°W, 13 June 1965, N. Davis (AMNH: "*L. cumberlandense*"). Montgomery County: 3 ♂, Blacksburg, 37.2296°N, 80.4139°W, 15 July 1956, Hoffman (NMNH). Nelson County: 2 ♂, The Priest, 4.5 mi [7.2 km] SE of Montebello, 37.8199°N, 79.0625°W, elev. 1189 m, 16–29 August 1991, VMNH survey (VMNH); 1 ♂, The Priest, "at drift fence site," 37.8199°N, 79.0625°W, elev. 1189 m, 20 September 1991, R.L. Hoffman (VMNH); 2 ♂, North Fork, Tye River, ~4 mi [~6.5 km] E of Montebello on Va. 687, PF, 37.8595°N, 79.0446°W, 6 September 1998, VMNH survey (VMNH). Russell County: 1 ♂, Cedar Creek Falls, ca 4 mi [6.4 km] NE of Lebanon, 36.9542°N, 82.0541°W, 2 July 1989, R.B. & R.L. Hoffman (VMNH). Wise County: 1 ♂, 0.8 mi [1.3 km] NW of Tacoma on VA Hwy.706, mixed woods, dry hillside, 36.9408°N, 82.5448°W, 19 July 1989, R.L. Hoffman (VMNH).

Diagnosis.—Penis (Figs. 43a, b, 46a, b): shaft with broad ventral bend in lateral view, followed by smaller dorsal bend subterminally in region of alae; alae varying from large and dorsally curved to essentially absent; glans curved dorsally. Male retrolateral apophysis present on palpal femur, varying from large (Fig. 37) to scarcely developed (Fig. 39) but always associated with a field of stout, pointed denticles. Female palpal femur usually with low retrolateral apophysis covered in enlarged spine-like denticles (Fig. 41). Posterior margin of female sternum with long median process (greater than half sternum width) projecting into soft cuticle of pregenital chamber, process essentially doubling length of sternum; anterior sternal margin usually with narrow median notch (Fig. 44), sometimes apparently absent.

Description of typical male from type region (Virginia: Buffalo Mountain NAP, "trailhead at parking lot," 37.4316°N,

78.6569°W, 20 June 2004, R.L. Hoffman (VMNH).—Body length: 6.5 mm. *Dorsum* (Fig. 33): Carapace length, width: 2.0 mm, 3.4 mm. Surface granulate and light brown to golden yellow-brown with medium brown bordering extending from the lateral margin of carapace to anterior opisthosoma margin. Anterior median prominence with 1 median denticle and a row of 2–3 lateral denticles on each side. Mesopeltidium and metapeltidium distinct medially, merging laterally; each with a single row of white dots; posterior margins light brown and rebordered. Ocularium reddish-brown with a dark circumocular band and acanaliculate, with a loose circle of 15 sharp, dark-tipped denticles and a few interspersed short erect setae around each eye; anterior denticles point posteriorly, posterior denticles point anteriorly, dorsal denticles larger and more numerous. Ozopore mound with sharp denticles scattered on all but the anterior-lateral surface, with a few extending to the ocularium. Supracheliceral lamina arching ventromedially with parallel parts divided by a deep cleft; sharp, distally-pointing dark-tipped denticles on dorsal and anterior surfaces. Opisthosoma: Tapers posteriorly; surface granular with a few tiny scattered setae laterally; predominantly light brown with a very faint central figure beginning around the ocularium and fading at tergite 6. Rows of sigilla demarcate tergites 1–6 lateral to central figure; tergites 1–7 with a complete medial transverse band of white spots and whitish anterior and posterior bordering; tergite 8 with two large lateral posterior sigilla. Anal operculum light brown with medial white blotch and a few scattered setae and small sharp denticles. *Venter* (Fig. 34): Labrum curved dorsally with a rough ventral surface. Sternites light yellow with white bordering on posterior margin and light brown on anterior margin; sparse erect setae scattered over surface. Sternite 3 overlaps sternite 4, sternite 4 overlaps sternite 5; sternites 7 and 8 fused medially but distinct laterally; posterior margin of sternites 3 and 4 slightly recurved, all other margins straight. Genital operculum yellowish and somewhat transparent posterior-medially; anterior margin strongly rebordered and whitish with a dark medial blotch; submarginal row of small, sharp, dark denticles lateral, smaller rounded denticles and setae scattered on medial surface. Genital operculum and sternites 2 and 3 fused; the posterior operculum margin demarcated by a shallow, incomplete recurved crease. Large sigilla on posterior lateral surface of operculum extend to anterior portion of sternite 3. Sternum simple, slightly narrower medially.

Appendages: *Chelicerae*: Light golden brown with slightly darker dorsal surface on proximal article, small dark retrodorsal blotches on distal article; setae scattered on dorsal surface of both articles, becoming denser distally and forming a distal prolateral row on distal article and a submarginal row on proximal article.

Palps (Figs. 37, 38)*:* Measurements in mm: femur 1.7; patella 0.8; tibia 1.5; tarsus 1.7. Trochanter light golden brown with distal prolateral row of erect setae. Femur brown, darker distally; narrow basally (but proximal dorsal surface slightly inflated), becoming strongly inflated and arched distodorsally, then narrowing slightly at distal end; ventral surface slightly curved. Sharp denticles and setae scattered on distal prolateral and dorsal surfaces and arranged in a dorsal retrolaterally curving row and a proximal prolateral row of 4 large denticles on the left femur, 6 on the right. Distal retroventral surface with a large (0.6 mm) conical ''spur'' or apophysis projecting ventrolaterally. A dense field of sharp denticles and interspersed setae extends from anterior apophysis surface to distal femoral margin. Patella dark brown; dorsal surface 3–4 times the length of the ventral surface; distal prolateral surface slightly protuberant; an irregular row of dark distally pointing denticles extends along the dorsal to retrolateral margin; smaller denticles scattered retrolaterally and in loose dorsal row; scattered erect setae cover all but the ventral surface. Tibia golden brown with darker dorsal and retrolateral blotches. Proximal dorsal surface slightly inflated; proximal ventral surface expanded, forming a large flat prominence densely covered with proximally-pointing, sharp, dark denticles. Ventral surface arched distal to prominence and covered with long erect setae. Dark denticles form a proventral band and loose distal retroventral row. All but the retrodorsal surface with a coat of dark, erect setae. Tarsus light golden brown and curving slightly ventrally and retrolaterally; tightly-packed proventral row of dark, flat-topped denticles extend nearly the full length of the tarsus; 6–7 rows of dark erect setae covering all but the ventral surface; short recumbent setae cover the surface, and fine erect setae form a scopula-like structure distoventrally. Tarsal claw golden brown with a dark tip with 6 teeth.

Legs: Measurements of femur, patella, tibia, metatarsus, tarsus in mm: I: 5.7, 1.6, 5.4, 6.1, 7.0; II: 11.0, 1.8, 10.7, 10.8, 22.4; III: 5.5, 1.5, 4.9, 7.1, 9.6; IV: 8.1, 1.8, 7.1, 11.8, 13.5. Coxae yellowish with condyles and proximal posterior margin dark; short erect setae and tiny blunt denticles scattered over surface and forming a ventral submarginal row. Coxae I and II with an anterior row of flat-topped denticles, coxa IV with a posterior row of flat-topped denticles. A few small denticles scattered on anterior surfaces of coxa III and IV, posterior of III, but not forming a distinct row. Coxa II with large dark-tipped denticle on posterior margin. Trochanters dark brown; small, distally pointing denticles scattered on dorsal, prolateral, and retrolateral surfaces and arranged in a distal submarginal circumferential row; dorsal surface with distal medial longitudinal groove. Femur base dark brown, wider proximally, with scattered distally-pointing denticles on pro- and retrolateral surfaces; distinguished from shaft by a circumferential groove; shaft light golden brown, dark brown distally (except femur II); distally-pointing dark-tipped denticles and accompanying distally adjacent seta arranged in 5–7 irregular longitudinal rows, more defined dorsally, absent ventrally (femur I denticles denser, rows less defined); distal ventral margin with a row of dark-tipped denticles, distal dorsal margin with 2 distally pointing denticles. Patellae with 4–6 loose longitudinal rows of tiny denticles and a distal submarginal row of larger denticles, cuticle dark brown. Tibiae golden brown, darker distally (except tibia II); tiny distally-pointing denticles arranged in 5–8 proximal longitudinal rows; each denticle accompanied by a distal erect seta, with setae continuing each row distally; tibia II with setae rows only and a few tiny denticles; distal margin with a ventral row of small denticles terminating in a single spine at either end (tibia II with spines only); surface with a coat of recumbent setae; vestiture of microtrichia present, especially distally. Tibia II with 5 incomplete pseudoarticulations. Metatarsi with 6–8 pseudoarticulations, each with a pair of distally pointing

ventral spines and a dark dorsal blotch; 5–6 rows of erect setae extend down the metatarsus and tarsus; metatarsi and tarsi golden brown with a coat of recumbent setae. Tarsi with fine, dense, erect setae on ventral surface, denser distally; longer (proximal) telotarsi with 2 distally pointing ventral spines on distal margin. Claw smooth.

Penis (Figs. 43a, 45a): 5.1 mm long. Dorsoventrally flattened (rounder basally), with a lateral ridge down most of the length of both sides of the shaft; base expanded laterally at attachment to stabilizing rods; shaft curved dorsally, thickly sclerotized distally. Alae thick and angled dorsally, with shaft bulging dorso-medially between alae; glans curving 90° dorsally and stylus projecting dorsally from tip.

Variation in male.—The species displays substantial variation in several characters. The central figure and dorsal rows of white spots and darker markings vary from apparent to faded, or may be absent. Trochanters and basal portions of the femora are generally dark, often contrasting with the femoral shaft but are concolorous. The legs and palps range from golden to dark brown. Denticle density varies on the carapace, particularly between the ozopore mound and median prominence, as well as on the coxa, although the presence or absence of rows shows little variation. The fusion between the genital operculum and sternites 2 and 3 may be partial or complete. The palps may occasionally be less robust, but not slender, and have a reduced but still-evident retrolateral apophysis (Figs. 39, 40). Penis curvature varies from shallow to pronounced, and alae may be horizontal (Figs. 43b, 46b) rather than angled dorsally, or reduced to a thickly sclerotized region near the base of the glans.

Description of typical female from type region: U.S.A.: Virginia: Floyd County: Buffalo Mountain NAP, "trailhead at parking lot," 37.4316°N, 78.6569°W, 20 June 2004, R.L. Hoffman (VMNH).—Body length: 7.5 mm. *Dorsum* (Fig. 35): Carapace length, width: 2.0 mm, 3.3 mm. Supracheliceral lamina similar to that of the male. Ozopore mound with a few scattered sharp denticles laterally. Ocularium acanaliculate but appearing canaliculate due to a dark medial band and lighter circumocular band; each carina with 10 sharp dark denticles; anterior denticles larger and point posterior, posterior denticles smaller and point anterior. Anteromedian preocular prominence light brown with two brown longitudinal stripes and a submarginal row of 4 small denticles. Cuticle between ocularium and median prominence dark brown with a dense field of tiny dark rounded tubercles, giving a coarsely granulate texture. Anterior margin of mesopeltidium slightly elevated above surface of propeltidium and fading laterally into the carapace surface; cuticle brown with white lateral blotches and medial anterior margin that breaks up to white dots laterally; posterior and lateral margin dark brown. Metapeltidium medium brown, white laterally, with posterior and lateral dark brown bordering and an anterior row of white dots. Opisthosoma: Rounded and gently tapering posterior. Tergites 1–5 marked by a slight ridge halfway between the medial and lateral lines of the dorsum, creating a distinct rounded medial region; cuticle coarsely granular with tiny rounded tubercles less dense but more distinct lateral (distal) to the ridge. Central figure defined by medium-dark bordering extending from tergite 1 to the anterior margin of tergite 5 and continuing as 2 dark anterior blotches on remaining tergites. Tergites 1–4 medium to dark brown, lighter laterally (distal to ridge), medial region with transverse rows of white dots along each tergite and short rows of small dark brown dots separating tergites between central figure and ridge. Remaining tergites light to golden brown, darker laterally, with medial white dots. Anal operculum medium brown with large white medial blotch and a few small submarginal denticles.

Venter (Fig. 36)*:* Sternites 3–6 smooth, light brown, anterior and posterior margins fading to white, with a brown anterior border; sternite 7 + 8 white with light brown posterior bordering and 4 medium brown dots in 2 rows; posterior and lateral margins rebordered. Genital operculum, and all sternites distinct. Operculum white medially and golden brown laterally with 2 large posterior sigilla; two smaller sigilla extend from proximal half of sternite 2 to anterior margin of sternite 3. Setae and small denticles scattered medially on operculum, sharp, dark-tipped denticles arranged in a lateral submarginal row; anterior denticles larger and denser. Anterior margin thickly rebordered and protruding, forming a whitish "lip" and a transverse sulcus with a corresponding transverse phragma on the inner (dorsal) surface; anterior body of operculum protuberant and slightly bilobed just posterior to transverse sulcus, forming a short medial sulcus and corresponding inner medial ridge in the posterior space formed by the phragma (Fig. 45). Sternum anterior margin notched medially and slightly angled ventrally; median posterior process as long as sternum width (Fig. 44). Labrum straight and expanded ventrally at base.

Appendages: *Chelicerae*: Light golden brown. Proximal article with medium brown dorsal surface and distal submarginal row of setae, second article with small dark retrodorsal blotches and setae scattered on dorsal surface and arranged in imperfect pro- and retrolateral rows (denser and less organized distally).

Palps (Figs. 41, 42)*:* Measurements in mm: femur 1.6; patella 0.7; tibia 1.2; tarsus 1.9. Trochanters golden brown with a distal retroventral row of setae and small median submarginal tubercle. Femur medium brown, darker dorsally; diameter slightly increases distally. A low, rounded process and a few large dark denticles located at the retrolateral position corresponding to the more prominent male apophysis. Parallel pro- and retroventral rows of denticles diverge distally, retroventral row terminating in short submarginal retrolateral row of smaller denticles; a few distally-pointing denticles scattered on distodorsal surface and arranged in a prolateral submarginal row; erect setae interspersed with denticles and forming a prolateral row; 8 large denticles form proximal prolateral row, with proximal half abruptly curving ventrally. Patella medium brown, dorsal surface twice the length of the ventral surface and wider distally; prolateral margin slightly protuberant. Erect setae cover all but the retroventral surface; distally pointing denticles form 2 dorsal rows and a loose retrolateral row, with a few small denticles scattered distal-retroventrally and proximal-prolaterally. Tibia golden brown, darker dorsally, with a coat of short recumbent setae and a single distal prolateral denticle; a ventral row of dark-tipped, distally-pointing denticles terminates in a distal retrolateral submarginal row; proximal denticles denser, smaller and more scattered, becoming a small retrolateral field; erect setae arranged in a retrolateral row and scattered

on dorsal, ventral, and distal prolateral surfaces. Tarsus golden brown with a narrow proventral dark stripe corresponding to the male denticle row; dense recumbent setae and 6–8 rows of dark erect setae extend the length of the tarsus (denser distally) with dense, fine, erect setae distoventrally; claw golden brown with 5–6 teeth.

Legs: Measurements of femur, patella, tibia, metatarsus, tarsus in mm: I: 6.3, 1.7, 5.2, 6.9, 9.6; II: 11.4, 1.7, 10.6, 11.4, 28.5; III: 6.0, 1.5, 5.2, 7.6, 10.2; IV: 8.5, 1.7, 7.7, 11.8, 14.2. Coxae golden brown with proximal golden brown blotches surrounded by white; surface smooth with scattered short erect setae and a ventral submarginal row of a few small denticles and interspersed setae (fewer denticles and more setae on coxae II and III). Coxae I, II, and III with anterior (prolateral) row of flat-topped denticles and tiny posterior (retrolateral) scattered denticles; coxa IV with posterior row of flat-topped denticles and small scattered denticles anterior; anterior coxa IV and posterior coxa II each with a dorsal submarginal denticle. Trochanters dark brown with denticles scattered on pro- and retrolateral surfaces (less dense on trochanter IV) and forming a distal circumferential submarginal row. Femur base defined by a circumferential groove and dark brown coloring, with distally-pointing denticles and erect setae scattered laterally and a few ventrally; shaft slightly expanded distally and golden brown with dark brown distal condyles, a submarginal row of distally-pointing sharp, dark denticles, and approximately 5 irregular rows of distally-pointing, dark-tipped denticles (densest on femur I) with accompanying distal erect seta (ventral surface bare). Patellae light brown with whitish mottling, especially on patella III; narrow white bordering on distal margin of patella I; small distally-pointing dark-tipped denticles with distally adjacent seta scattered over surface, some forming rows (reduced on patella II); a few larger denticles form a distal submarginal row. Tibiae golden brown with a coat of short recumbent setae; 5 proximal rows of distally-pointing dark-tipped denticles extending no more than half the length of the tibiae (reduced on tibia I); erect setae distally adjacent to each denticle continue in rows the full length of the tibia; distal ventral submarginal row of a few small, dark, distally pointing denticles terminate with a single spine at either end; vestiture of microtrichia present distally; tibia II lacking nearly all denticles, but with setae and spines as on other tibiae and 4 faint incomplete pseudoarticulations. Metatarsi golden brown with a coat of recumbent setae; 3–4 pseudoarticulations (8–9 on metatarsus II) each with a dark dorsal spot and a pair of dark, distally-pointing ventral spines; 5 rows of fine erect setae extend from metatarsus to proximal half of tarsus; longer (proximal) telotarsi with a distal pair of small ventral spines; surface with a dense coat of recumbent setae and a ventral scopula-like structure of fine, erect setae; tarsal claw smooth with a ventral tooth-like protuberance at base.

Ovipositor: Typical; two spermathecae visible between rings 6 and 7.

Variation in female.—The dorsal surface, palps, and legs vary from golden brown to dark brown, or even, rarely, predominantly white. The ventral surface ranges from white to dark golden brown, but is always lighter than the dorsal cuticle. Central figure may be more or less distinct and may begin on the carapace or tergite 1. Trochanters and femur base are often darker than the femur shaft, but can be concolorous. The number of denticles on the ocularium varies from a few to more than 20. Coxal denticle rows vary from dense, distinct rows to few and scattered. Sternum notch may be very shallow and the posterior sternal process ranges, although longer is more common. As in *L. euserratipalpe*, the posterior process completes its sclerotization during the adult stage and early-season (June) adults may appear to lack the process, although it may be present as a poorly sclerotized band. The small retrolateral femoral apophysis of the palp is sometimes greatly reduced, especially in smaller specimens.

Distribution.—*Leiobunum calcar* ranges from Saskatchewan (Holmberg 1998) to Newfoundland (Hackman 1956) in Canada. The northern limit is not known, but *L. calcar* appears to extend farther north than other North American *Leiobunum* species. This widespread distribution continues into the northern United States from the northern plains and Great Lakes Region to the New England States, with large regions remaining to be sampled (Fig. 47). The species appears to be increasingly restricted to the Appalachian Mountains in more southern states, which may reflect historical sampling effort or, if accurate, a propensity for cooler climates.

Remarks.—Male *L. calcar* are typically recognized by a prominent retrolateral femoral apophysis on the palp and a long, ventrally curved penis with large alae, and this is by far the most widespread association of characters in the species. However, there are many regional or even local variants that differ in the size of the retrolateral femoral apophysis and penial alae. McGhee (1970) proposed the species *L. cumberlandense* based on the association of reduced femoral apophysis and reduced alae in specimens from the Cumberland Region of Kentucky, Virginia, and Tennessee. However, specimens with well-developed femoral apophyses also occur in this region and are otherwise identical to *L. cumberlandense*. In addition, we have found several widely scattered populations with the *L. cumberlandense* syndrome (e.g., Manitaulin Island in Lake Huron and far-western Maryland). These and other variants may be monophyletic and reproductively isolated from other populations of *L. calcar*, but we cannot at present find compelling morphological evidence for this. In contrast, the subterminal dorsal bend in the penis and the presence of a long posterior sternal process in the female appear to be essentially universal features of the species.

Leiobunum hoffmani new species
(Figs. 48–61)

''Leiobunum hoffmani'': McGhee 1970:141–147, figs. 34, 35 [unpublished dissertation]

Type material examined.—Holotype male: USA: *Virginia*: Smythe County: Mt. Rogers NRA, 36.724°N, 81.4904°W, elev. 870 m, 10 August 2007, M. Hedin (NMNH). Paratype: 1 female: USA: *Virginia*: Grayson County: Whitetop Mountain, ''just off FS 89,'' 36.6387°N, 81.6059°W, elev. ~1524 m, 25 June–11 July 1998, VMNH Survey (NMNH).

Other material examined.—USA: *North Carolina*: Alleghany County: 2 ♂, 5 ♀, Doughton Park CG, ''on BRP, S of Sparta,'' 36.4290°N, 81.1539°W, elev. 1100 m, 11 August 2007, M. Hedin (UMD). Wilkes County: 8 ♂, 3 ♀, Doughton National Recreation Area, Blue Ridge Parkway, 36.4016°N, 81.1748°W, 30 July 1967, C.R. McGhee (AMNH). *Virginia*:

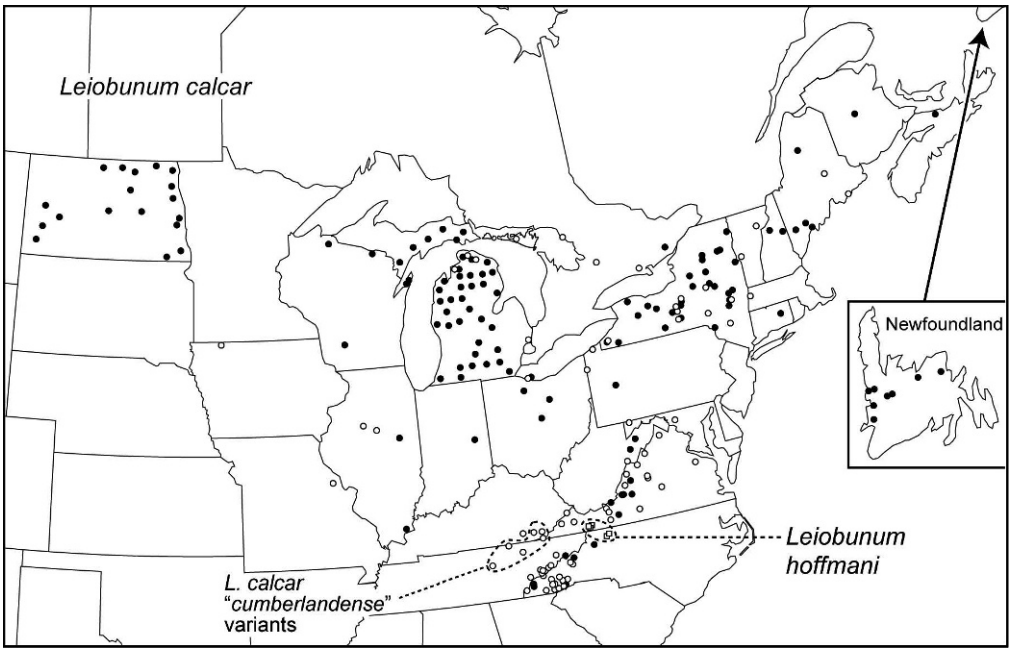


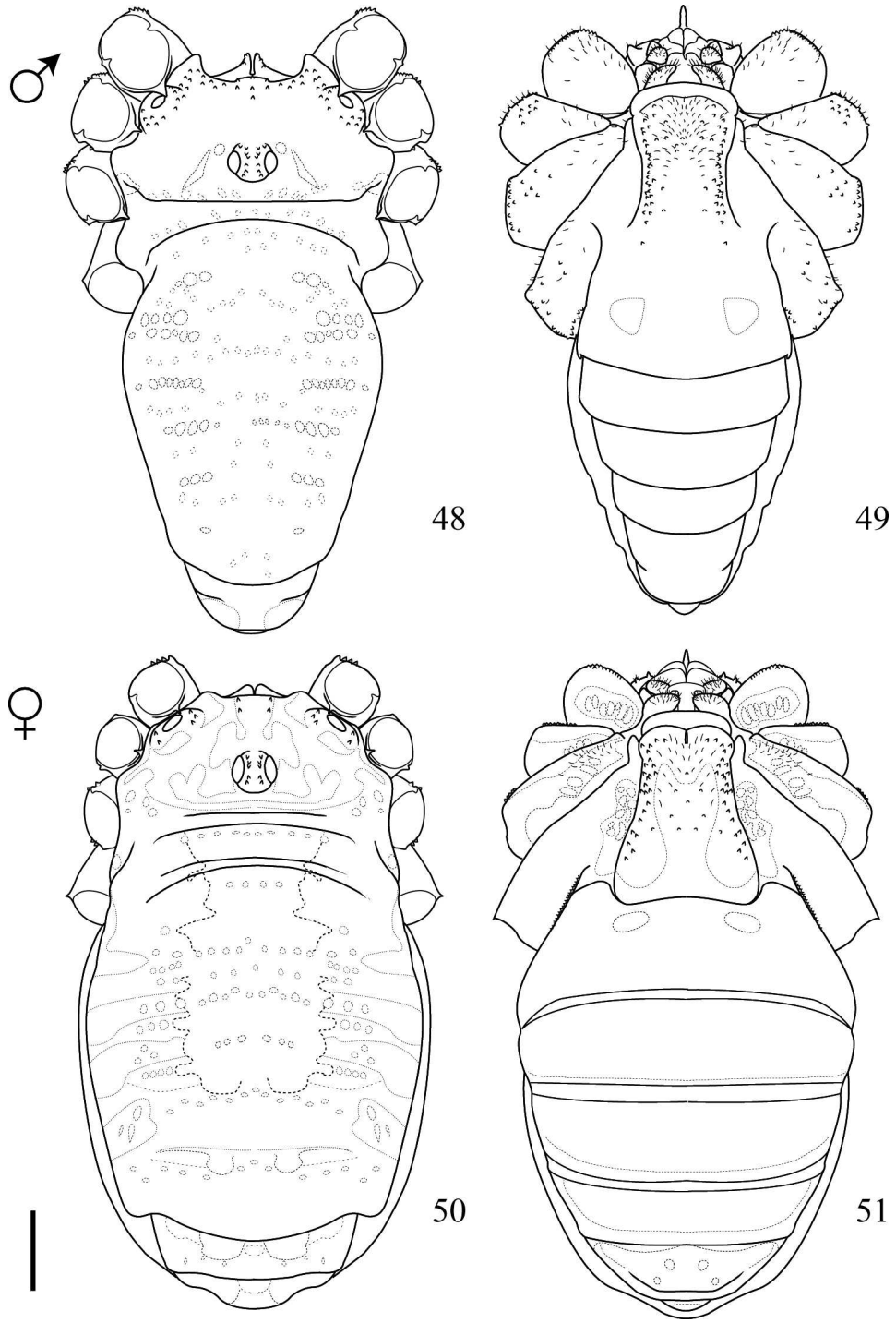
Figure 47.—Map of collection localites for *Leiobunum calcar* (Wood 1868) and *Leiobunum hoffmani* new species. Open circles are localities of *L. calcar* specimens observed in this study. Black circles are localities of *L. calcar* specimens obtained from the literature (Bishop 1949; Carter & Brown 1973; Davis 1934; Edgar 1971; Hackman 1956; Jennings et al. 1984; Katayama & Post 1974; Levi & Levi 1952; McGhee 1970; Weed 1889a). Open squares are localities of all known *L. hoffmani* specimens.

Grayson County: 12 ♂, 12 ♀, White Top Mountain, ''just off FS 89,'' 36.6387°N, 81.6059°W, elev. ~1524 m, 25 June–11 July 1998, Virginia Natural History Survey (VMNH); 1 ♂, White Top Mountain, ''beechwoods, off FS 89,'' 36.6387°N, 81.6059°W, elev. ~1524 m, 20 August 2001, Virginia Natural History Survey (VMNH), 6 ♂, same locality, 25 June–11 July 1993, Virginia Natural History Survey (VMNH); 3 ♂, 2 ♀ (penultimate), 1 ♂, 1 ♀ (antepenultimate), Grayson Highlands State Park, Haw Orchard Mountain, ''above water tank,'' 36.6270°N, 81.5048°W, 2–15 June 1991, Virginia Natural History Survey (VMNH), 13 ♂, 3 ♀, same locality, 36.6270°N, 81.5048°W, 30 August 1990, Virginia Natural History Survey (VMNH), 3 ♂, same locality, 8 July 1990, R.L. Hoffman (VMNH); 1 ♂, 3 ♀, Mount Rogers, ''horse trail to Helton Creek,'' elev. 1310–1370 m, 36.6599°N, 81.5451°W, 8 July 1990, R.L. Hoffman (VMNH); 10 ♂, 1 ♀, Highlands State Park, Haw Orchard Mountain, ''spruce woods near Visitor Cntr,'' 36.6270°N, 81.5048°W, 8 August 1990, Virginia Natural History Survey (VMNH). 3 ♂, 1 ♀, Grayson Highlands State Park, E of Visitor Center & Pinnacles Trail on Haw Orchard Mtn., elev. ~1500 m, spruce forest with rock outcrops, 36.6247°N, 81.5013°W, 11 August 2007, M. Hedin (UMD). Smythe County: 5 ♂, 2 ♀, Mt. Rogers NRA, Hurricane CG, W of Hwy. 16, 36.7240°N, 81.4904°W, elev. 870 m, 10 August 2007, M. Hedin (UMD).

Etymology.—The species is named in honor of Richard L. Hoffman for his contributions to invertebrate taxonomy.

Diagnosis.—Penis (Figs. 58, 61) elongate (> 7 mm, full length of body or more) gradually tapered distally, alae absent. Male palp massive with terminally inflated, incrassate femur and proximally inflated, incrassate tibia; femur with large retrolateral apophysis lined distally with denticles (Doughton Park Region, North Carolina) (Fig. 52) or low naked protuberance (Grayson Highlands, Virginia) (Fig. 54), no known intermediates. Female sternum large with long posterior process and deep anterior median notch extending to middle of sternum (Fig. 59), palpal femur lacking the femoral apophysis (Fig. 56) of most female *L. calcar* (Fig. 41).

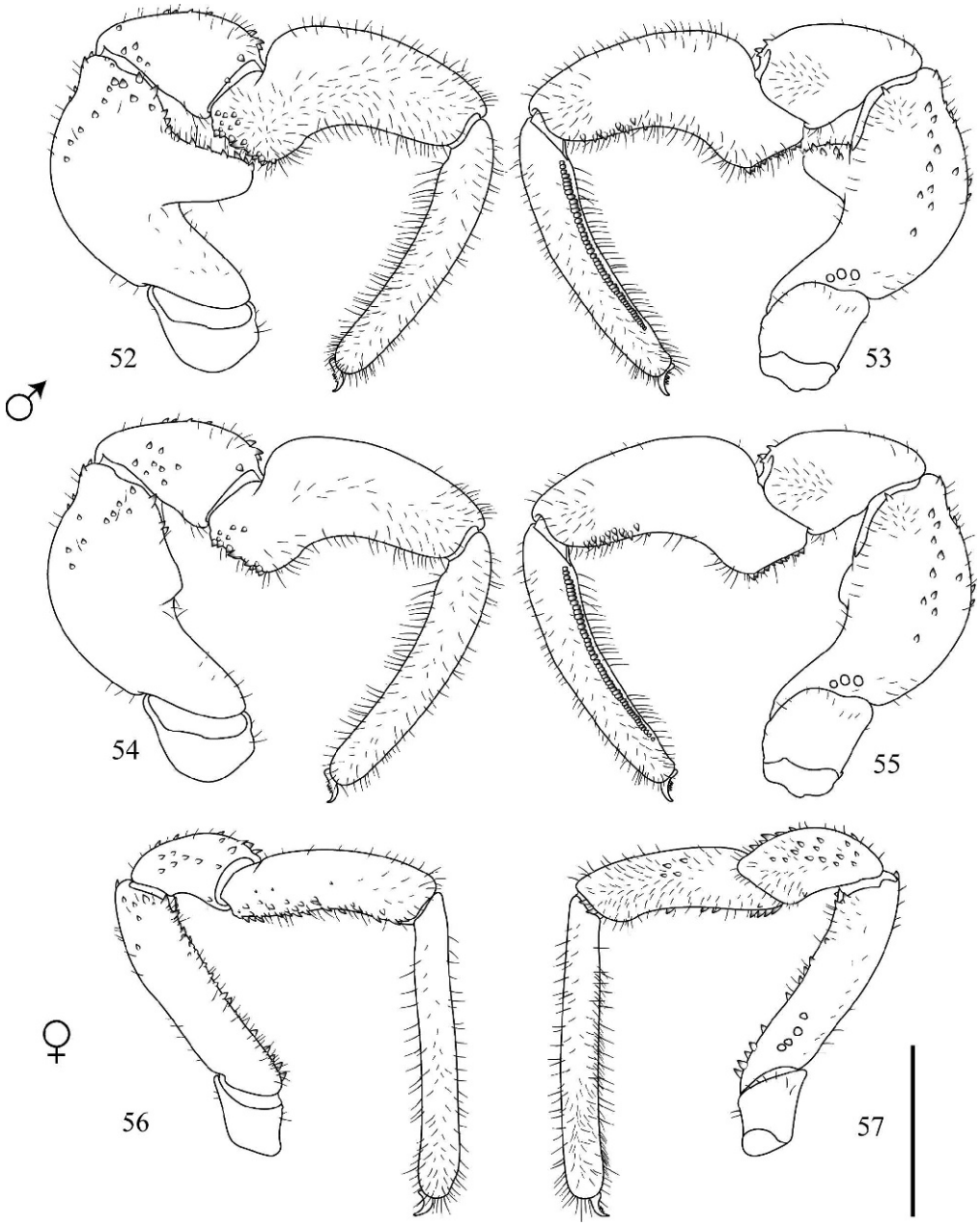
Description of male holotype.—Body length: 6.5 mm. *Dorsum* (Fig. 48): Carapace length, width: 1.8 mm, 3.5 mm. Supracheliceral lamina with a few small denticles on anterior and dorsal surfaces. Anterior median prominence with three loose longitudinal rows (one median, two lateral) of two or three small, sharp denticles; additional denticles scattered between prominence and ozopore, particularly along anterior carapace margin. Ozopore mound with sharp denticles at anterior and posterior ends, smooth with a few small setae laterally. Ocularium dark brown and weakly canaliculate; each carina with 10 sharp, curved denticles nearly circling the eye; anterior denticle pointing posterior, posterior denticles pointing anterior. Transverse postocular fold distinct medially, fading into general carapacal surface laterally; a transverse row of whitish dots extends across meso- and metapeltidium. Posterior margin recurved and rebordered. Cuticle otherwise orange-brown and granulate. Opisthosoma: Elongate, tapering posteriorly. In lateral view, dorsal surface bends gradually upward and then posteriorly. Granular cuticle predominantly light orange-brown and lacking a central figure. Scutal tergites (tergites 1–5) and free tergites 6 and 7 demarcated by lateral sigilla and a transverse band of white spots. A pair of large oval sigilla with dark bordering on tergite 8 indicate large penile retractor muscles. Anal operculum with median white blotch and a few small, sharp denticles. *Venter* (Fig. 49): Labrum curved dorsally with a pair of lateral subterminal tubercles. Genital operculum and sternites yellowish with a few darker markings, usually sigilla. Operculum and sternites



Figures 48–51.—Dorsal and ventral perspectives of *Leiobunum hoffmani* new species, male holotype, female paratype. Scale bar = 1 mm.

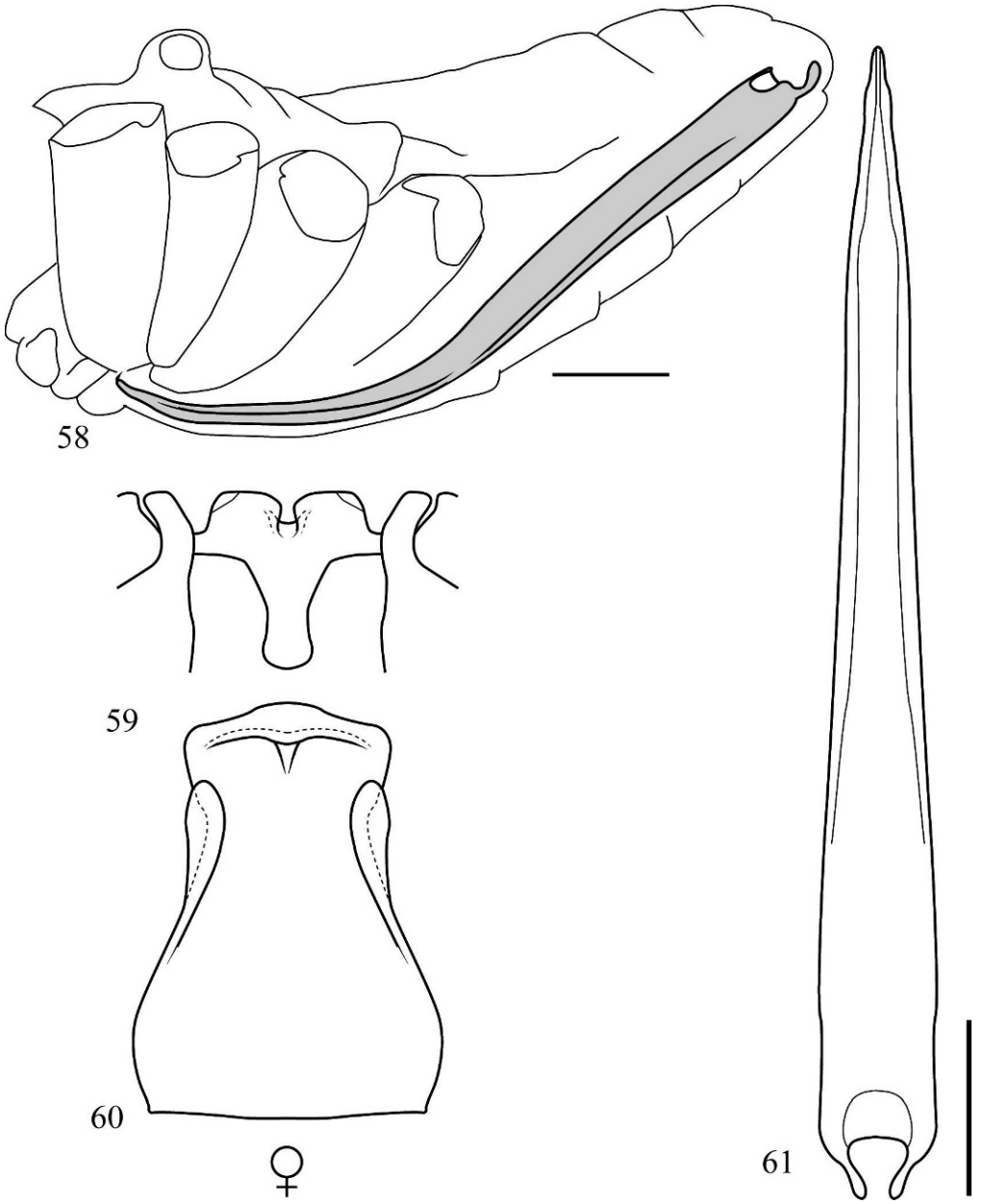
2 and 3 completely fused; demarcation between operculum and sternite 3 perceptible only as variation in color, with a short, shallow transverse fold indicating intersternal margins. Anterior margin of genital operculum strongly rebordered, with resulting ''lip'' protruding medially, folding over the penis tip; inner (dorsal) surface of ''lip'' with medial indentation. Pointed dark denticles form a lateral imperfect row; small rounded denticles and setae scattered on medial ventral surface. Supraopecular sternite simple. Sternites 3 − 7 + 8 smooth with a few short erect setae; each anterior sternite overlaps the posterior sternite; sternites 7 and 8 fused, but demarcated laterally by short transverse folds in the cuticle.

Appendages: *Chelicerae*: Dark brown, lighter on distal half of second article. Proximal segment with a few setae along distal margin. Second article with a band of short, dark, transverse stripes on proximal 3/4 of lateral and dorsal surfaces; dorsal surface with numerous erect setae, denser just proximal to fixed finger. Movable and fixed fingers dark; fixed longer.



Figures 52–57.—Right palps of *Leiobunum hoffmani* new species: 52, 53. Male holotype; 54, 55. Male variant from Grayson County, Virginia; 56, 57. Female paratype. Retrolateral perspective on left, prolateral perspective on right. Scale bar = 1 mm.

Palps (Fig. 52, 53)*:* Measurements in mm: femur 1.6; patella 0.6; tibia 1.2; tarsus 1.7. Cuticle dark brown, proximal surface of femur and distal tip of tarsus slightly lighter. Trochanteral tubercle with a few setae and denticles. Femur narrow basally, inflated and arched distally forming a ventral concavity; large conical apophysis (0.8 mm) projects from subterminal retrolateral surface; large, a field of sharp denticles extends over the anterior apophysis surface to the distoretrodorsal margin; two imperfect longitudinal rows of sharp denticles extend along the distodorsal surface and a few large denticles form a proximal prolateral row. Erect setae scattered on ventroproximal and apophysis anterior surfaces. Patella short, robust, with scattered erect setae in longitudinal retrodorsal and prodorsal bands; proximal retrolateral margin and distal dorsal margin each with a cluster of large denticles; distal prolateral surface slightly protuberant. Tibia robust; proximal ventral surface forming flat, anvil-like prominence covered in large, proximally pointing denticles and a few long, curved setae; tibia arches to form a large ventral concavity distal to prominence; proximodorsal surface inflated, coming into apposition with the distodorsal surface of patella; 9 recurved denticles form a proventral row. Widely spaced, long, erect setae cover all but proximodorsal surface, setae especially long in ventral concavity; distal margin of tibia with short, recumbent setae. Tarsus slightly inflated proximally; curved ventrally, with distal end slightly curved retrolaterally; flat-topped tarsal denticles in highly organized tightly packed row extend nearly full length of tarsus, denticles smaller distally;



Figures 58–61.—Genital structures of *Leiobunum hoffmani* new species: 58. Diagrammatic lateral perspective of male showing position of penis; 59. Ventral perspective of female sternum (genital operculum removed); 60. Dorsal (internal) perspective of female genital operculum; 61. Dorsal perspective of penis. Figs. 59–61 to same scale. Scale bars = 1 mm.

cuticle covered with long, erect setae loosely arranged in rows, and dense coat of short, recumbent setae. Tarsal claw with 4 or 5 teeth.

Legs: Measurements of femur, patella, tibia, metatarsus, tarsus in mm: I: 6.0, 1.6, 5.9, 6.6, 8.8; II: 12.1, 2.0, 12.3, 16.3, 23.0; III: 6.4, 1.5, 5.2, 8.1, 10.1; IV: 12.4, 1.9, 12.7, 12.3, 22.5. Row of flat, evenly-spaced denticles developed along distal anterior surface of coxae I and II and along distal posterior surface of coxa IV; coxa II with 1–2 denticles on posterior margin; coxa II–IV with scattered rounded denticles on distal ventral surface; all coxae golden with scattered erect setae and a ventral submarginal row of smaller denticles and setae. Trochanters golden-brown with small, distally pointing, dark, prolateral and retrolateral denticles and a distoventral row of submarginal denticles. Femora with basal piece defined by a circumferential groove; basal piece and immediately adjacent region of shaft concolorous with coxae or nearly so; shaft brown and increases in diameter distally; sharp, distally curved denticles, each typically accompanied by a distally adjacent erect seta, densely scattered on femur I and forming loose rows on femora II–IV; ventral surface smooth except for a distoventral submarginal row of denticles. Patellae dark brown with numerous small, sharp denticles, larger distodorsally, some accompanied by distal erect setae, often arranged in imperfect rows (much reduced on leg II). Tibiae slightly increased in diameter distally with numerous sharp, distally curved denticles (reduced on leg II, especially distally) and longitudinal rows of erect setae; vestiture of microtrichia

distally; tibia II with fine circumferential stripes (pseudoarticulations) and recumbent setae. Metatarsi with a coat of fine recumbent setae, denser dorsally, and 5–7 rows of short erect setae. Metatarsi I with 5–6 pseudoarticulations, II with 10, III with 5–6, IV with 8; each psuedoarticulation with a pair of ventral spines (reduced on metatarsi II). Tarsi with long, erect setae and recumbent setae, denser distally, especially on the ventral surface where it forms a scopula-like structure; a pair of long spines developed on distoventral margin of longer (proximal) tarsomeres. Claw curved, smooth with a single ventral, tooth-like protuberance at base.

Penis (Figs. 58, 61): 6.7 mm. Lanceolate, tapering gradually, and curving dorsally; dorsoventrally flattened at base, becoming somewhat rounder and more heavily sclerotized distally; slight lateral ridges extending the length of the shaft becoming somewhat more prominent distally. Glans flat dorsally and slightly curved; no distinct joint between glans and shaft, but ventral surface of shaft less sclerotized; stylus short compared to other species in the group and angled posteriorly. Penial fulturae nearly the length of the shaft and fused; weak medial sclerotization distally along fusion.

Variation in male.—Dorsal coloration varies greatly, with some displaying a more *calcar*-like coloring of predominantly light brown to orange with or without an apparent central figure, while others are highly patterned, with dark brown and white spotting on both the carapace and opisthosoma and a prominent central figure extending from ocularium to preanal tergite. The number and symmetry of carinal denticles varies and may encircle the eye or be present only dorsally. The most significant palpal variation is the greatly reduced male femoral apophysis observed in one Virginia population (Figs. 54, 55), present as only a raised protuberance, but with denticles developed along the anterior surface and distally to the femur margin, an arrangement similar to that of populations with large apophyses. Demarcation of the posterior margin of the genital operculum/sternite 2 and anterior margin of sternite 3 ranges from an incomplete transverse fold or groove to simply a variation in color. Sternites 7 and 8 may be completely fused or distinguished by a short transverse fold at the lateral margins. The tubercles of the supracheliceral lamina may be widely spaced or concentrated at the anteromedial end. Denticle rows on anterior coxa I and posterior coxa IV nearly the full length of the coxa; all other denticle rows extend half the length of each coxa or less, or may be completely absent.

Description of female paratype.—Body length: 7.6 mm. *Dorsum* (Fig. 50). Carapace length, width: 1.9 mm, 3.3 mm. Propeltidium with dark brown sigilla separated by white; lateral margin brown; surface finely granulate; anteromedian preocular prominence with 5 scattered denticles; ozopore mound with anterior and posterior denticles and a few anterior setae. Supracheliceral lamina smooth, projecting slightly, sides converging slightly. Ocularium weakly canaliculate, but appearing strongly canaliculate due to dark brown coloration with black circumocular ring; left carina with 5 sharp, curved denticles, right carina with 9 denticles. Mesopeltidium with dark brown transverse band bordered by anterior and narrow posterior white bands connected by a thin median bridge of white; bands indistinct laterally. Metapeltidium dark brown medially with a row of white spots (anterior portion of central figure), mottled brown and white laterally with a few large white spots. Opisthosoma: Distinct, dark, but transversely broken, longitudinally variable central figure most prominent on the scutum (tergites 1–5), darkest on tergites 1, 4 and 5, and represented by a pair of large dark anterior spots on remaining tergites. Scutal tergites transversely demarcated by white posterior bordering and dark brown, thin sigillary lines and small dots. Imperfect transverse rows of white dots extend across each tergite, restricted to central figure on anterior tergites. Cuticle lateral to central figure predominately whitish, darker on posterior tergites, often interrupted by brown transverse bands extending from central figure. Anal operculum with scattered, dark-tipped spines; white medially surrounded by brown margin.

Venter (Fig. 51)*:* Labrum straight with scattered minute tubercles; at midpoint, slightly expanded laterally. Tergites light brown, fading anteriorly, with whitish posterior and lateral bordering; dark longitudinal pleural band appearing continuous with dark, transverse sigillary lines between sternites. Sternite 7 + 8 lighter medially with four brown dots arranged in two rows. Sternites 2 and 3 fused; genital operculum and all other sternites distinct. Anterior genital operculum bilobed and rebordered, forming a broad white "lip" with a posterior transverse sulcus, inner (dorsal) surface with corresponding phragma and median septum (Fig. 60). Medial surface whitish with scattered setae (denser anteriorly) and weak denticles; brown laterally, becoming 2 large brown posterior spots; submarginal row of denticles (larger anteriorly) developed laterally. Lateral margins with prominent interior anterodorsally projecting apophyses that engage the posterodorsal surface of the sternum when operculum closed. Anterior sternal margin with large, rounded median notch (to sternum midpoint) between a pair of plate-like lobes; robust posterior median process with tendinous apodemes attached laterally comprises half the total operculum length.

Appendages: *Chelicerae*: Cuticle light brown. Basal article with a row of erect setae along dorsal surface curving laterally and terminating distally at a submarginal row of erect setae; a few scattered setae ventrally. Second article with scattered erect setae on dorsal and prolateral surface; prolateral setae denser distally.

Palps (Figs. 56, 57)*:* Measurements in mm: femur 1.4; patella 0.7; tibia 1.1; tarsus 1.7. Cuticle light brown, patella and distal ends of femur and tibia slightly darker. Trochanter with a distal prolateral row of erect setae extending from dorsal to ventral surface. Femur with proventral and retroventral rows of sharp spines, arising close together proximally and diverging distally toward the pro- and retrolateral condyles of the femur-patella joint; a few denticles scattered on subterminal dorsal surface and 4 or 5 denticles form a short imperfect proximal prolateral row; surface with scattered erect setae, especially numerous and elongate on ventral surface. Patella with setose process projecting distally from distal prolateral surface; scattered erect setae and small, distally curved sharp denticles cover all but the ventral surface; spines especially well developed near dorsal condyle of patella-tibia joint. Tibia with scattered erect setae and coat of fine recumbent setae; broad band of dark, distally projecting on ventro-proximal and ventro-retrolateral surfaces; a few well-developed spines on the distal prolateral surface. Tarsus with numerous long, erect setae, sometimes arranged in longitudinal rows, and a coat of fine recumbent setae that is especially dense on distoventral surface. Claw with 6 teeth.

Legs: Measurements of femur, patella, tibia, metatarsus, tarsus in mm: I: 6.1, 1.6, 5.1, 6.6, 6.4; II: 10.6, 1.6, 9.9, 10.5, 21.5; III: 6.2, 1.6, 4.7, 7.5, 7.9; IV: 9.0, 1.7, 7.0, 11.3, 12.6. Cuticle light brown, slightly darker on femur, patella and distally on tibia; light markings on trochanter. All coxae smooth with scattered, erect setae and a ventral submarginal row of small rounded denticles more developed anterior. Coxa I, II and III with distal anterior row of denticles and proximodorsal marginal projection; coxa IV with distal posterior row of denticles. Trochanters with small, sharp, distally pointing dark denticles scattered on prolateral and retrolateral surfaces and in a distoventral submarginal row; darker, medial groove dorsad.

Femora basal piece defined by a circumferential groove, 1–2 rows of denticles circling; femoral shaft with 5–8 imperfect rows of sharp, distally curved denticles; each denticle typically accompanied by a distally adjacent erect seta; ventral surface smooth; sharp denticles along distal margin. Patellae with small, distally curved, sharp denticles arranged in 2 rows of 6–7 dorsally, scattered proximally on ventral surface; sharp denticles on distal margin (reduced on patella II); erect setae scattered ventrad. Tibiae increase in diameter distally; surface with recumbent setae and longitudinal rows of erect setae; 5 proximal rows of distally curved denticles accompanied distally by erect setae (denticles reduced on tibia II); proximal denticles scattered ventrally; tibia II, III, IV with sharp denticles on distal margin; vestiture of microtrichia present, more dense distally; tibia II with fine, imperfect and incomplete circumferential light stripes. Metatarsus with 4–7 pairs of ventral spines; spine pairs 2–5 with increasing evidence of pseudoarticulation, but none complete; surface with scattered erect setae in loose rows and denser coat of short recumbent setae. Tarsus typical. Claws without teeth.

Ovipositor: Typical; two spermathecae present between segments 6 and 7.

Variation in female.—The median septum on the inner surface of the genital operculum ranges from short (but not absent) to very long, in some, extending nearly a third the length of the operculum and terminating with a long transverse ridge subequal in length to the anterior phragma. Fusion of sternites 2 and 3 may be incomplete. Dorsal coloration and patterning around the central figure varies, although the patterns are often more developed than on other species in the group. White bordering on the sternites may be more or less apparent. Legs, chelicerae, and palps often have similar coloration but range from light golden brown to dark brown. As with the male, the number and symmetry of carinal spines varies. The labrum surface may be smooth with a few scattered tubercles or rough from the presence of many tiny tubercles

Distribution.—The species appears to be limited to the Blue Ridge Mountains of northwestern North Carolina and southwestern Virginia (Fig. 47).

Remarks.—*Leiobunum hoffmani* shares several features with populations of *L. calcar* from the southern Appalachian Mountains, including males with very robust palps and elongate penes with reduced alae and females with very well-developed sterno-opercular mechanisms. However, *L. hoffmani* differs consistently from *L. calcar* in the simplification of the subterminal region of the penis (complete loss of alae and associated dorsal curvature) and the complete elimination of the retrolateral apophysis on the palpal femur of the female. The latter is particularly notable because there is a clear tendency for females in the montane *L. calcar* to have larger apophyses.

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