

ABSTRACT

Title of Document:

**TAXONOMY OF THE *LEIOBUNUM*
NIGROPALPI SPECIES GROUP
(OPILIONES: SCLEROSOMATIDAE:
LEIOBUNINAE)**

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Eastern North America is a center of diversity for leiobunine harvestmen (daddy longlegs), but many species are poorly delimited or undescribed. My research attempts to bring taxonomic order to one newly circumscribed assemblage, here named the *Leiobunum nigropalpi* species group. It includes two named species, *L. nigropalpi* (Wood 1868) and *L. calcar* (Wood 1868), and several undescribed or problematic species. This research clarifies the taxonomy and morphological diversity of this group and delimits four morphospecies. Information is derived from traditional characters (e.g., male palps, penis, coxal denticles, ocularium) and newly discovered structures, such as those associated with the pregenital chamber in females. The results indicate that the *nigropalpi* species group contains four well-delimited morphospecies (namely, *L. nigropalpi*, *L. hoffmani* new species, *L. euserratipalpe* new species and *L. calcar*), although the latter two each encompasses substantial variation and may be paraphyletic.

TAXONOMY OF THE *LEIOBUNUM NIGROPALPI* SPECIES GROUP
(OPILIONES: SCLEROSOMATIDAE)

By

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Chapter 1: Introduction

Sclerosomatid harvestmen (Opiliones: Sclerosomatidae), or daddy longlegs, are common and highly visible inhabitants of many terrestrial ecosystems worldwide, particularly in the Northern Hemisphere, where they are especially diverse. Their behavior, life history, and morphology have inspired numerous common names and an extensive folklore (Pinto da Rocha et al., 2007), but widespread casual curiosity about these arthropods has rarely translated into professional taxonomic interest. Even in well-studied regions like eastern North America, taxonomic keys are inadequate and outdated (e.g. Edgar 1990), with the identification of females being especially unreliable; misidentification is rampant in museum collections and on the internet; no phylogenetic hypotheses have been proposed; geographic ranges of even common species are uncertain; and distinctive new species are discovered by each new worker, one of whom appears (and then rapidly disappears) every few decades. Consequently, the basic taxonomy of the sclerosomatid fauna is in disarray even within eastern North America.

In an unpublished dissertation, McGhee (1970) delimited a small clade of sclerosomatid harvestmen from eastern North America, the *Leiobunum nigropalpi* species group (but referred to as the *Leiobunum calcar* group). The group contains two widely accepted species, *L. calcar* (Wood 1868) and *L. nigropalpi* (Wood 1868), a problematic species, *L. serratipalpe* Roewer 1910, which has since been synonymized with *L. calcar* (Cokendolpher 1981), and two informally described species “*L. cumberlandense*” and “*L. hoffmani*” (McGhee 1970) united by male characters: a long penis lacking sacs or bulbs, palpal tibiae with an enlarged

proximoventral surface with stout spines, and, in most species, an apophysis or cluster of spines on the retrolateral surface of the palpal femora. The implicit hypothesis that the group is monophyletic is consistent with phylogenetic interpretations of genitalic anatomy and unpublished analyses of molecular sequence data (M. Hedin & J. Shultz, in prep.).

Here I provide a morphology-based revision of the *L. nigropalpi* species group, incorporating both traditional male characters and newly-recognized female characters. This revision includes a review of known biology, detailed descriptions and diagnoses of the long-established species *L. calcar* and *L. nigropalpi* and of two proposed species *L. euserratipalpe* and *L. hoffmani*, and standardized line drawings highlighting significant characters.

Chapter 2: Material And Methods

Morphology

All specimens were examined in either isopropanol or ethanol, depending on medium used by their home repositories. Dissections were performed using a needle and micro scissors under a Leica MZ APO dissecting microscope with a 1x or 0.63x objective lens. Photos were taken using PaxCam3 in Adobe Photoshop, and composite photos were created and edited in Helicon Focus software. Illustrations were prepared in Adobe Illustrator from the composite photos. Measurements were made with a stage micrometer, ocular scale, and drawing tube.

Specimen Repositories

Specimens used in this study were obtained from the following museums and repositories: AMNH: American Museum of Natural History (New York, NY), McGhee: Personal Collection of Charles McGhee (Tennessee); NMNH: National Museum of Natural History (Smithsonian Institution) (Washington, D.C.); UMD: University of Maryland (J.W. Shultz Collection) (College Park, MD); VMNH: Virginia Museum of Natural History (Martinsville, VA)

Phylogenetic Analysis

Each proposed morphospecies within the *L. nigropalpi* species group (i.e., *L. nigropalpi*, *L. euserratipalpe*, *L. cumberlandense*, *L. calcar* and *L. hoffmani*) was represented in the phylogenetic analysis by specimens obtained from multiple locations. The analysis included only locations from which both males and females

were sampled. The outgroups included *L. ventricosum*, *L. aldrichi*, *L. vittatum*, *L. uxorium* and *L. politum*, the latter four of which are consistently recovered as a close relative of the *L. nigropalpi* species group by molecular data (M. Burns, M. Hedin & J. Shultz, personal communication). A survey of external and genitalic morphology (Table 1) yielded a 35-taxon-by-60-character matrix (Tables 2, 3) that was analyzed using parsimony in the program Tree Analysis Using New Technology (T.N.T.) (Goloboff et al., 2003).

The matrix was analyzed using the traditional search algorithm (TBR branch swapping, 1000 replicates). The strict consensus of all minimal-length trees was taken as the best estimate of the phylogeny given the data. Due to high levels of homoplasy in several characters, I also performed a traditional search using implied weighting (Goloboff, 1993), a method that gives greater weight to characters of low homoplasy during the analysis, rather than after the analysis as in successive weighting. Nonparametric bootstrap percentages (Felsenstein, 1985) were determined for both weighted and unweighted data based on 1000 replicates.

Table 1. Characters coded for phylogenetic analysis.

Male

1. Carapace texture: 0, smooth; 1, granular; 2, coarsely granular
2. Carina denticles: 0, absent; 1, present
3. Tergite texture: 0, granular; 1, coarsely granular
4. Sternite texture: 0, smooth; 1, granular
5. Genital operculum and sternite 3 fusion: 0, complete (Fig. 48); 1, partial (Fig. 34); 2, unfused (Figs. 8, 20)
6. Sternites 2 and 3 fusion: 0, complete (Fig. 34, 48); 1, partial (Fig. 20); 2, unfused (Fig. 8)
7. Palp color: 0, light; 1, dark
8. Palpal retrolateral femoral apophysis: 0, absent (Fig. 11); 1, present (Figs. 37, 39, 51, 53)
9. Palpal retrolateral femoral apophysis, shape: 0, small/raised; 1, conical (see 8)
10. Palpal retrolateral femoral denticles: 0, absent; 1, scattered; 2, row; 3, anterior cluster
11. Palpal retrolateral femoral denticles, size: 0, small; 1, large; -, inapplicable (see 10)
12. Palpal femur size: 0, slender (Figs. 11, 12); 1, robust (Figs. 37, 38)
Slender palpal segments are those that have a roughly constant diameter, similar to the tarsus; robust segments appear inflated or swollen.
13. Palpal femur strongly curved: 0, absent; 1, present
14. Palpal prolateral femoral denticle row, distribution: 0, proximal only; 1, full length
15. Palpal patella process: 0, absent; 1, present
16. Palpal tibia size: 0, slender; 1, robust
17. Palpal tibia ventral curvature: 0, straight; 1, curved; 2, strongly curved
18. Palpal tibia ventral process: 0, absent; 1, present (Figs. 23, 24, 51, 52)
19. Palpal tibia ventral process, shape: 0, flat (Figs. 37, 38); 1, angled (Figs. 11, 12) (see 18)
20. Palpal tibia ventral denticles: 0, absent; 1, present
21. Palpal tibia ventral denticles, distribution: 0, proximal only; 1, entire surface; -, inapplicable (see 20).
22. Palpal tibia ventral denticles, arrangement: 0, scattered; 1, row; -, inapplicable (see 20)
23. Palpal tibia denticle size: 0, small; 1, large; -, inapplicable (see 20)
24. Palpal tibia prolateral denticle row: 0, absent; 1, present
25. Coxa I anterior denticle row: 0, anterior 2/3 of coxa or less; 1, >2/3 coxa length
26. Coxa I posterior denticle row: 0, absent; 1, present
27. Coxa II anterior denticle row: 0, anterior 3/4 of coxa or less; 1, >3/4 coxa length
28. Coxa II posterior denticle row: 0, absent; 1, anterior 3/4 of coxa or less; 2, >3/4 coxa length
29. Coxa III anterior denticle row: 0, absent; 1, anterior 3/4 of coxa or less; 2, >3/4 coxa length
30. Coxa III posterior denticle row: 0, absent; 1, anterior 3/4 of coxa or less; 2, >3/4 coxa length

31. Coxa IV anterior denticle row: 0, absent; 1, anterior 3/4 of coxa or less; 2, >3/4 coxa length
32. Coxa IV posterior denticle row: 0, anterior 3/4 of coxa or less; 1, >3/4 coxa length
33. Coxa IV posterior denticle size: 0, small; 1, large; -, inapplicable (see 32)
34. Penis sacs or bulbs: 0, absent; 1, present
35. Penis shaft: 0, straight; 1, slight dorsal curve; 2, strong dorsal curve
36. Penis shaft cross-section: 0, round; 1, flat
37. Penis shaft diameter: 0, equivalent to glans; 1, wider than glans
38. Glans: 0, angled < 90° dorsal; 1, angled ~90° dorsal
39. Alae: 0, absent (Figs. 60); 1, present (Fig. 32, 46)
40. Alae, size: 0, tiny (Fig. 32); 1, large (Fig. 46); -, inapplicable (see 39)
41. Alae location: 0, shaft only; 1, over glans; -, inapplicable (see 39)

Female

42. Genital operculum anterior rebordering (Fig. 6): 0, narrow; 1, wide
At its widest point, the rebordering may be either narrower than or as wide as the free (anterior) portion of the operculum body.
43. Genital operculum anterior body: 0, straight (Fig. 10); 1, bilobed (Fig. 22)
The anterior portion of the operculum just posterior to the transverse sulcus may or may not be bilobed.
44. Genital operculum protuberance (Fig. 10): 0, absent; 1, present
The anterior/free portion of the operculum is sometimes protuberant, resulting in two rounded expansions posterior to transverse sulcus.
45. Genital operculum median septum (Fig. 4): 0, absent; 1, present
46. Genital operculum and sternite 3 fusion: 0, partial; 1, unfused (Figs. 10, 22, 36, 50)
47. Sternites 2 and 3: 0, separate (Figs. 10, 22, 36); 1, fused (Fig. 50)
48. Sternum anterior notch (Fig. 3): 0, absent; 1, present
49. Sternum anterior notch, size: 0, shallow (Fig. 44); 1, deep (Fig. 58); -, inapplicable (see 48)
Shallow notches extend no further than the anterior body of the sternum; deep notches extend to the middle of the sternum body or more.
50. Sternum posterior process (Fig. 3): 0, absent; 1, present
51. Sternum posterior process, length: 0, short (Figs. 16, 28, 29); 1, long (Figs. 44, 58); -, inapplicable (see 50)
A short process no more than doubles the total length of the sternum; a long process doubles the total length or more.
52. Palpal retrolateral femoral denticles, arrangement: 0, absent; 1 scattered; 2, row; 3, anterior cluster
53. Palpal retrolateral femoral denticles, size: 0, small; 1, large; -, inapplicable (see 52)
54. Palpal femoral retrolateral process (Fig. 41, 42): 0, absent; 1, present
55. Palpal patella process (Fig. 5): 0, absent; 1, present.
56. Palpal patella process, size: 0, small; 1, large; -, inapplicable (see 55)

“Small” and “large” processes are differentiated by whether the process extends to the posterior tibia margin (or less) or past the tibia margin, respectively.

57. Palpal tibia ventral curvature: 0, straight; 1, slight curve; 2, strong curve
58. Palpal tibia ventral denticles, distribution: 0, absent; 1, proximal only; 2, entire surface
59. Coxa III anterior denticle row: 0, absent; 1, anterior 3/4 of coxa or less; 2, >3/4 coxa length
60. Coxa III anterior denticles, size: 0, small; 1, large; -, inapplicable (see 59)

Table 2. Taxon-by-character matrix for outgroups, *L. nigropalpi*, *L. euserratipalpe*, *L. cumberlandense* (syn. *L. calcar*), *L. calcar* and *L. hoffmani*. Abbreviations: ?, unknown; -, inapplicable; A = [01], B=[02], C=[03], D=[12], E=[23]

Taxa	Characters
	111111111122222222223333333333444444444455555555556
	123456789012345678901234567890123456789012345678901234567890
Outgroups	
<i>L. aldrichi</i> (Maryland)	11002200-200001000-0---A11112A211101100--1000100-0-210100021
<i>L. politum</i> (Maryland)	11002100-0-0000000-0---?1000D0100101100--1000100-A-A-01000D0
<i>L. ventricosum</i> (Virginia)	10002200-2000100A0-10000111B21211101100--0000100-0-200100221
<i>L. ventricosum</i> (Pennsylvania)	10012200-200010000-11100111121211101100--0000100-0-2000-1220
<i>L. uxorium</i> (Virginia)	11002100-100000000-1010111122211000010--1000100-0-0-00-0020
<i>L. vittatum</i> (Virginia)	11002200-210100000-11111111121211000000--1000100-0-2A0A-0221
<i>L. nigropalpi</i>	
Maryland: Garrett Co.	11002D1A-2000010D1A10001AAA12A2A1001101001A111A1010200110121
New York: Ulster Co.	21112210-200011011010001010122211001100--1010101010200111120
North Carolina: Macon Co.	11002210-200001011110001111121211001100--11111010A-200111121
Pennsylvania: Columbia Co.	11012210-B00001011110001A1A1212A10A1101001A111A10A-20011A121
Virginia: Botetourt Co.	11002210-20000102111000111121211001101001A111010102A01A0121
Virginia: Dickenson Co.	11002210-200001021110001111121211001101001111101010200111121
Virginia: Wythe Co.	11002210-2000010111100010101212110?1101001111101010200111121
<i>L. euserratipalpe</i>	
Michigan: Livingston Co.	110022011300001021010001101021211001111011000100-102000-1220
Virginia: Clarke Co.	D1A12A0113100010D10100011111212110011110A11111010111110D210
Virginia: Fluvanna Co.	D11ADD011300001011010001111A212110011A10A1111101010200101121
Virginia: Prince William Co.	111121011310001011010001101121211001111001011101010210111221
Virginia: York Co.	110021011300001011010001111121211001111001011100-10210101221
<i>L. cumberlandense</i> (syn. <i>L. calcar</i>)	
Tennessee: Pickett Co.	1100000103101000210100010101212110?1101101011101A11210111221
Kentucky: Laurel Co.	110010010301A0112101A0011111211A10?1101001111111011211102221
<i>L. calcar</i>	
Kentucky: Knox Co.	211011011311101111010001111121201021111101111011011211111221
Maine: Washington Co.	11001111131110112101100100001000002111110101111011211101210
Maryland: Garrett Co.	1100A01103A1101021011001000010001021110--1A111110111A0111210
New York: eastern counties	1100AAA113A100A12101100100001000101111100111110101131011120-
New York: Tompkins Co.	110010111311101121011001000010001011110--1101111011E10102210
North Carolina: Swain Co.	A1000011131110102101A0010000A00010?11A1101111111011311112210
Tennessee: Sevier Co.	110010A113A110102101A0010000100AA0?1111101AA11A10112111A12D0
Virginia: Botetourt Co.	A1001A11131110112101100?A01A1A0A10?11A11010A1110-11E1111A211
Virginia: Floyd Co.	21100011131100112101101?0100100010?1111101A1110101A21A11DDA
Virginia: Nelson Co.	211101111311A0112101A00?A000100010?111110101111101111111210
Virginia: western counties	D1AA10111311A0012101100?1000A00010111110101111101121111120-
<i>L. hoffmani</i>	
North Carolina: Alleghany Co.	1100A01113111011210100A10000000010?1100--111111111D11111210
North Carolina: Wilkes Co.	D1A00011131110A1210100010000000-011100--110111111111111210
Virginia: Grayson Co.	1100A01103A110A1210100010000000A021100--1111111112101112A-
Virginia: Smythe Co.	1100D011131110112101000100000001011100--11A1011111111112A-

Chapter 3: Results

Section 1: Taxonomy

Sclerosomatidae Simon 1879:

Leiobuninae Banks 1893:208

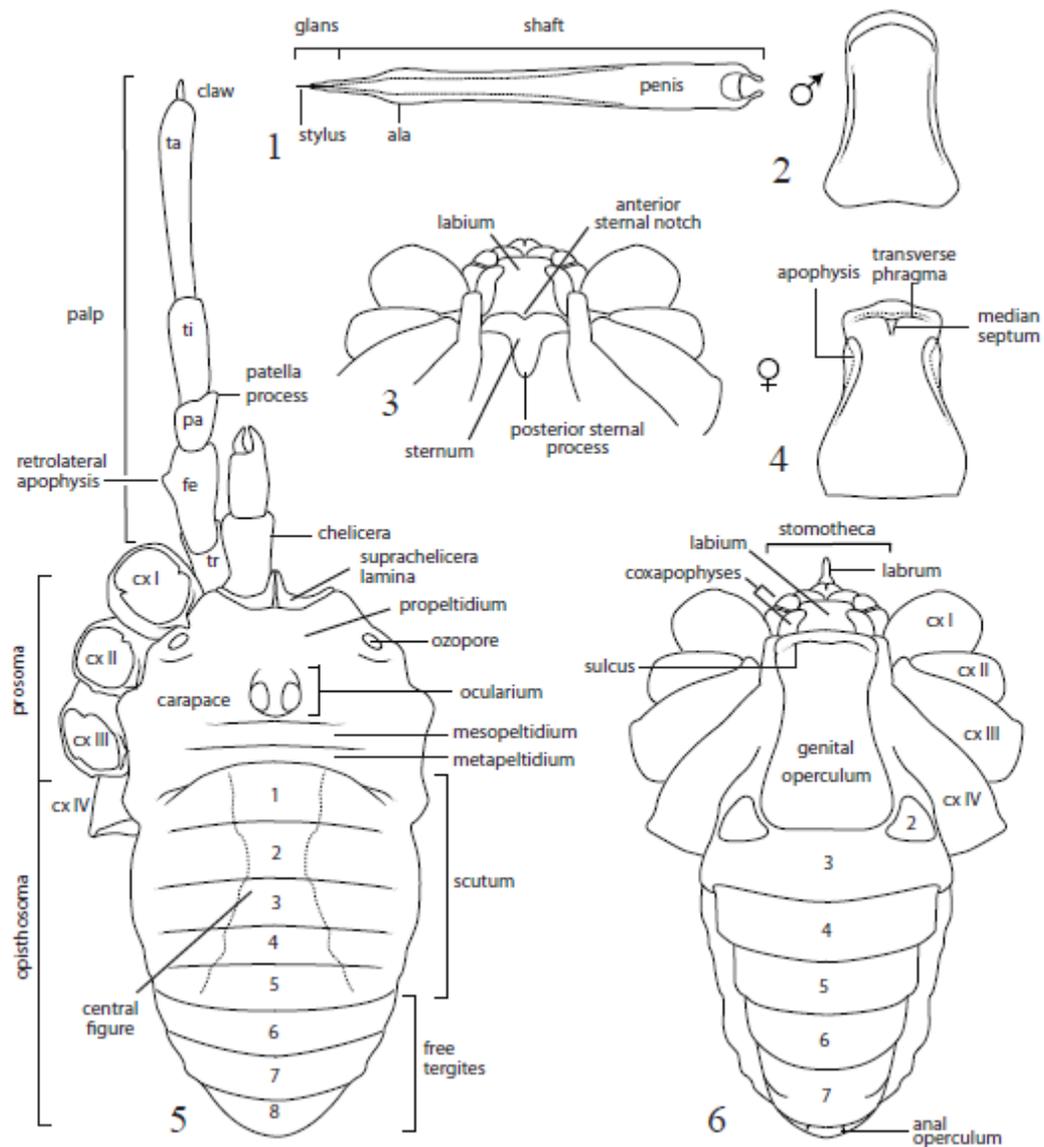
Leiobunum C.L.Koch 1839:35

Leiobunum nigropalpi Species Group new taxon

Type species: *Phalangium nigropalpi* Wood 1868, by subsequent designation.

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 palp: femur with retrolateral denticles in a longitudinal row or distal field; 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: In contrast to the male's simple operculum (Fig. 2), female genital operculum (Fig. 4) with deep transverse sulcus externally corresponding to internal transverse sclerotized phragma; phragma projecting posteriorly, forming a ventral space; ventral space divided by median septum; lateral margins with small anterior-pointing apophyses that engage the sternum; sternum (Fig. 3) typically with anterior median emargination and/or notch; posterior margin with median process projecting posteriorly into flexible cuticle of pregenital chamber.

Remarks. The *nigropalpi* group is monophyletic based on its unique reproductive morphology and unpublished results from molecular phylogenetic analysis (M. Burns, M. Hedin & J. Shultz, personal communication). 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 (where present) engaging the median opercular septum. The sternal posterior process acts 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 requires 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. There are four known species: *L. nigropalpi* (Wood), *L. calcar* (Wood), *L. euserratipalpe* new species, and *L. hoffmani* new species.



Figures 1-6. Basic anatomy of the *Leioibunum nigropalpi* species group. 1. Penis, dorsal perspective. 2. Male genital operculum, detached, showing dorsal (inner) surface. 3. Ventral view of female with genital operculum removed to show sternum (opisthosomal sternite 1). 4. Female genital operculum, detached, showing dorsal (inner) surface. 5. Dorsal view of male, with opisthosomal tergites numbered. 6. Ventral view of male, with opisthosomal sternites numbered. Abbreviations: cx, coxa; fe, femur; pa, patella; ta, tarsus; ti, tibia; tr, trochanter.

Leiobunum nigropalpi (Wood, 1868)

(Figs. 7-18)

Phalangium nigropalpi Wood, 1868:22-23, figs. 3a-3d (Type Locality: Hamilton County, Pennsylvania, U.S.A., male and female syntypes MCZ 14778 – examined)

Liobunum nigropalpi Weed, 1887:935; Weed, 1889:87-88; 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 Weed, 1890:918.

Leiobunum nigripalpi Crosby & Bishop, 1924:21; Walker, 1928:163-164, pl. 2, fig. 14.

Leiobunum nigropalpi 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 [unpubl. dissertation].

Diagnosis. Penis (Figs. 15, 18): Penis: alae thin and translucent; 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 slight dorsal curvature. Male palp (Figs. 11, 12): 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; femur, patella and proximal tibia usually darkly

colored. Female sternum (Fig. 16): anterior margin with broad V-shaped median emargination; posterior margin with short, narrow, flexible median process.

Remarks. *L. nigropalpi* is morphologically similar throughout its range and many of its features are plesiomorphic relative to other members of the species group. The male palps are 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. The glans of the penis is not strongly curved, and is thus similar to most other *Leiobunum* species. In contrast to other members of its species group, the glans-shaft articulation is distinctly constricted, rather than a tapering continuously from the shaft with a smooth, dorsal curvature. The female sternal posterior process is present but is only lightly sclerotized.

Description of male lectotype. Body length: 5.6 mm. *Dorsum* (Fig. 7): 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. 8): 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. 15, 18): 4.2 mm long. Shaft straight, width constant throughout much of length but narrowing near junction with glans; glans curving slightly dorsad. 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.

Palps (Figs. 11, 12): 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 protuberance 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 coxa 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. *L. nigropalpi* displays 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. Palpal tibia ventral prominence usually flat, but occasionally with distal portion projecting ventrad, forming a small spur. Anterior protrusions on genital operculum may be present or absent.

Description of female paralectotype. Body length: 7.3 mm. *Dorsum* (Fig. 9): 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. 10): 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. 13, 14): 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 prodorsal process 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 coxae; 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 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 spermotheca 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.

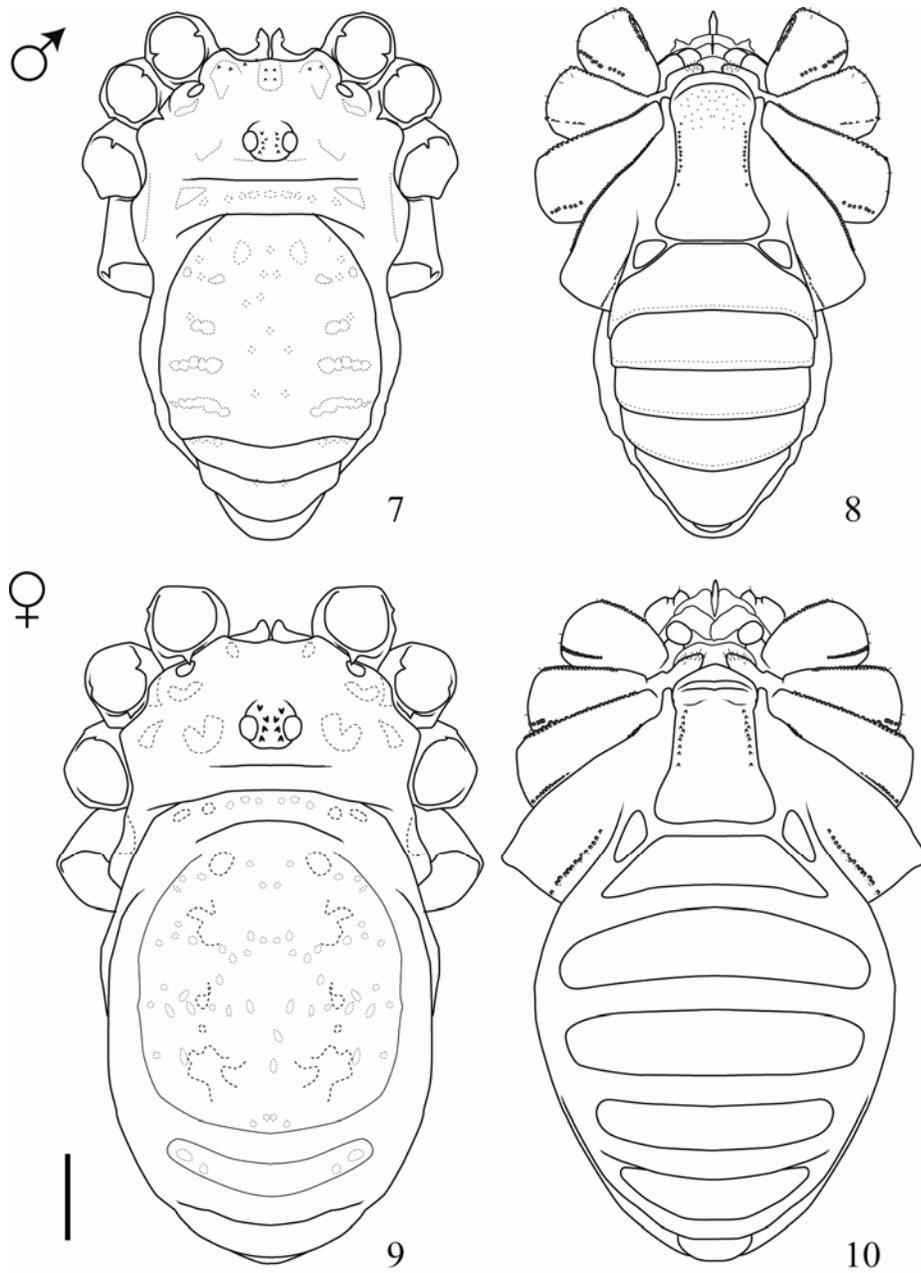
Variation in female. As in males, there is comparatively little variation. The anterior genital operculum may be bilobed or straight, with or without anterior-lateral protuberance. The central figure, white spots, and sigilla color vary in intensity. Rarely, the anterior margin of the sternum lacks a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

Range. Forests of eastern United States and southeastern Canada.

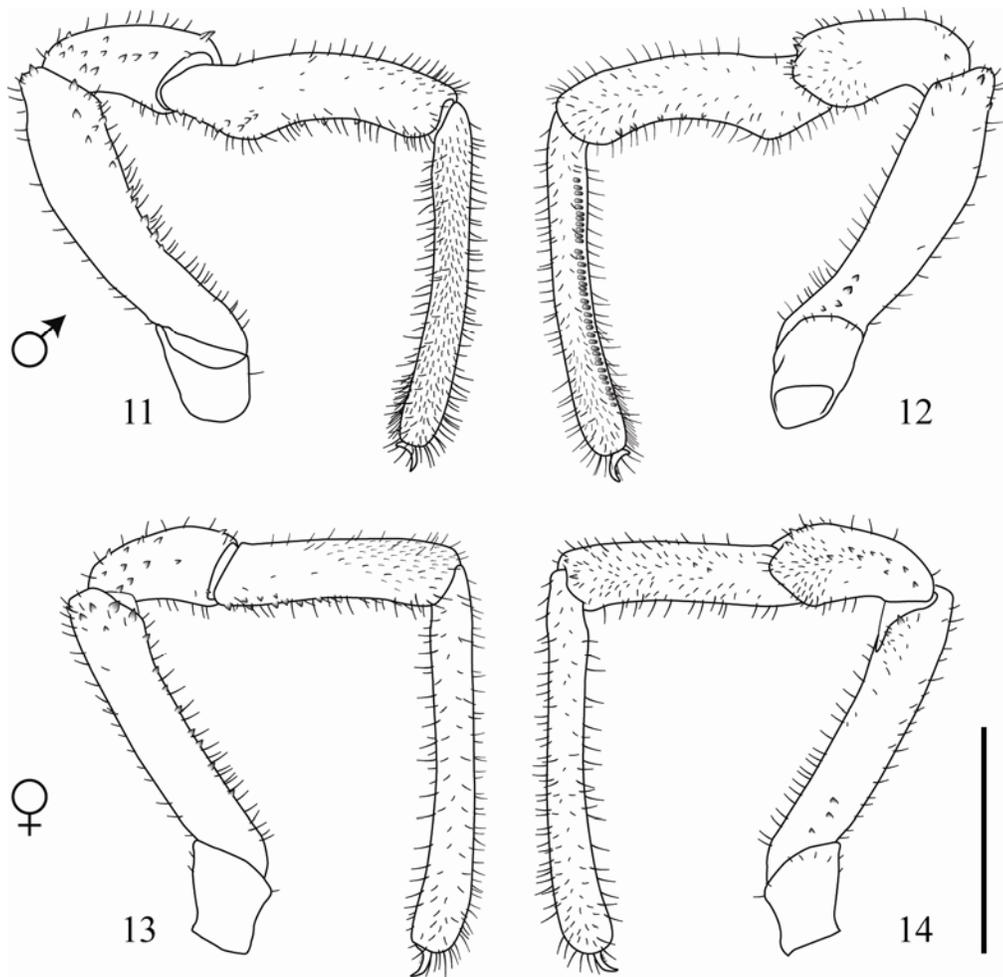
Material examined. U.S.A.: *Alabama*: Cleburne Co.: 2M, Cheaha SP, “vic. Campground #1 (046)”, 33.4864° N, 85.8125° W, 13 August 2005, M. Hedin et al.

(UMD). *Connecticut*: Storrs Co: 1F, 41.8084° N, 72.2500° W, 28 July 1923, no collector (AMNH). *Kentucky*: Bell Co.: 1M, Pine Mt. State Park, “near lodge” 36.7357° N, 83.7375° W, 22 September 1963, Woods (AMNH). *Maryland*: Garrett Co.: 1F, 3 km SE New Germany, "Managed Oak Forest", 39.62° N, 79.105° W, ele. 779 m, 11-18 July 2005, M. Sarver; 2F, 6 km NE Swanton, "Managed Maple Forest", 39.489° N, 79.17° W, ele. 714 m, 21 June – 6 July 2005, M. Sarver; 2M 4F, 6 km NE Swanton, "Managed Maple Forest", 39.489° N, 79.17° W, ele. 714 m, 22-29 August 2005, M. Sarver; 3M 4F, 6 km NW Westernport, "Old Growth Oak Forest", 39.509° N, 79.109° W, ele. 541 m, 3-10 August 2005, M. Sarver (UMD). *New York*: Cayuga Co.: 2M N Fairhaven, 43.343° N, 76.6904° W, 31 July 1932, G. Hughes (AMNH). Ulster Co.: 1M 1F, “Cherrytown nr Kerhonkson”, 41.825093° N, 74.329318° W, 18 July 1976, Wygodzinsky (AMNH). *North Carolina*: Macon Co.: 3M 2F, 5 mi N of Highlands, 35.1269° N, 83.1924° W, August 1967, K. Kleinpeter (AMNH). *Pennsylvania*: Huntington Co.: 1M 1F, 41.1801° N, 76.2363° W, Woods (AMNH); Columbia Co.: 2M 2F, Orangeville, 41.3392° N, 80.519° W, 13 August 1932, Hughes, Davis (AMNH). *South Carolina*: Oconee Co.: 2M, Cherry Hill Rec. Area, Rt. 107, 34.9424° N, 83.0849° W, ele. 610 m, 11 August 1958, J.F. Hanson (AMNH). *Virginia*: Botetourt Co.: 2F, Roaring Run, 37.6924° N, 79.8909° W, 4 July 1996, M. Donahue, B. Hogan (VMNH); 1M, Roaring Run, 37.6924° N, 79.8909° W, 30 July 1996, M. Donahue, B. Hogan (VMNH). Dickenson Co.: 1M 1F, Breaks Interstate Park, “DF site 2, off Nature Trail”, 37.2864° N, 82.2964° W, 15-29 June 1991, VMNH survey (VMNH). Floyd Co.: 1M, Buffalo Mountain Natural Area Preserve, “trailhead at parking lot”, 37.4316° N, 78.6569° W, ele. 1067 m, 20 June 2004, R.L.

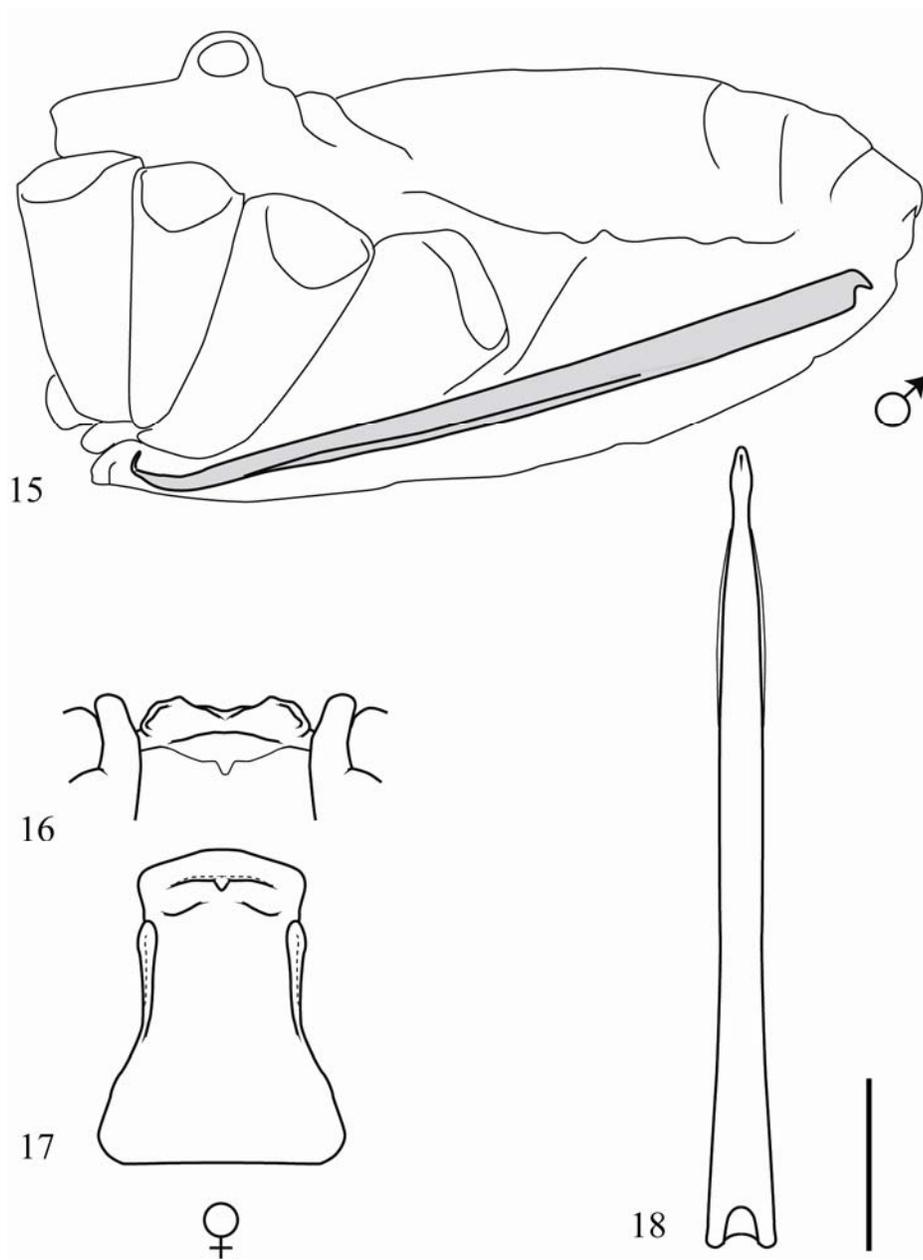
Hoffman (VMNH). 1M, Buffalo Mountain, "ca 6 mi SE of Willis", 37.4316° N, 78.6569° W, ele. 1300 m, 25 August 1984, R.L. Hoffman (VMNH). Giles Co.: 4M, Stony Creek bog, "off FS 10420, ca 2.3 km NW of Kire on Rt. 613", 37.4513° N, 80.5384° W, 9 August 2004, S.M. Roble (VMNH). Highland Co.: 1F, Locust Spring Rec area, "8 mi NW of Bluegrass", 38.5828° N, 79.6352° W, ele. 1158 m, 13 July 1974, Hoffman (VMNH). Russel Co.: 3M, Mill Creek, "ca. 5.1 mi E Carbo, UV", 36.9432° N, 82.1386° W, late May 1998, J.C. Ludwig (VMNH). Wythe Co.: 1M 1F, Sulphur Spg. Picnic Area, "ca 8 mi. west of Wytheville", 36.9692° N, 81.2222° W, 20 August 1967, Hoffman (VMNH).



Figures 7-10. Dorsal and ventral perspectives of *Leibobunum nigropalpi* (Wood 1868), male lectotype, female paralectotype. Scale bar = 1 mm.



Figures 11-14. Palps of *Leibunum nigropalpi* (Wood 1868), male lectotype, female paralectotype. Retrolateral perspectives on left, prolateral perspectives on right. Scale bar = 1 mm.



Figures 15-18. Genital structures of *Leibunum nigropalpi* (Wood 1868). 15. Diagrammatic lateral perspective of male showing position of penis. 16. Ventral perspective of female sternum (genital operculum removed). 17. Dorsal (internal) perspective of female genital operculum. 18. Dorsal perspective of penis. All to same scale. Scale bar = 1 mm.

***Leiobunum euserratipalpe* new species**

(Figs. 19-32)

Leiobunum serratipalpe 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.

Diagnosis. Penis (Figs. 27, 32): shaft essentially straight in lateral view, usually with a pair of small, subterminal alae; 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, without prominent retrolateral apophysis 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 (<1/2 sternum length) posterior median process (Figs. 28, 29), palpal femur lacking femoral apophysis often present in female *L. calcar* (Fig. 25). Both sexes with a long prolateral row of denticles extending the full length, or nearly so, of each coxae.

Etymology. The name means “true *serratipalpe*.” This term acknowledges the formal synonymy of *L. serratipalpe* Roewer 1910 with *L. calcar* (Wood 1868), while also recognizing the distinctiveness of the new species and its historical connection to the traditional concept of *L. serratipalpe sensu* Davis (1934), Bishop, (1949), Edgar (1966) and McGhee (1970).

Type locality. U.S.A.: *Virginia*: Prince William County, Manassas National Battlefield Park, ~0.3 km south of Sudley Spring. 38.8168 N, 77.5164 W. Deposited

in the National Museum of Natural History (Smithsonian Institution), Washington, D.C.

Remarks. While it is technically a new species, *L. euserratipalpe* already has a complicated taxonomic history. *Leiobunum serratipalpe* Roewer 1910 was described from specimens collected in New York State 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. Even without reference to the type material, however, several workers had questioned the validity of *L. serratipalpe* and speculated that purported male specimens were actually subadult males of *L. calcar* (e.g. Crosby & Bishop, 1924). 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*. In light of this history, when Cokendolpher (1981) found several *L. serratipalpe*-like specimens within a large collection of *L. calcar* from Maine, U.S.A., he concluded that *L. serratipalpe* was actually 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, we have found that one of the dominant 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). *L. calcar* is largely absent from this region but is common in the adjacent Appalachian Mountains. The

two species are sometimes found together in the mountains, but they are readily distinguished by size, reproductive structures, and habitat preference, with *L. calcar* being found on the ground and *L. euserratipalpe* on low vegetation. *L. 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* have indeed been misidentified as a separate species. A more thorough examination of the harvestman fauna of the Appalachian Mountains and points north and west will be needed to firmly establish the geographic range of *L. euserratipalpe*.

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. Suprachelicera 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; femur 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, 32): 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. Suprachelicera 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 length of the sternite, muscles attached to the dorsal (inner) surface of the process.

Appendages: *Chelicera*: 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 process; 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

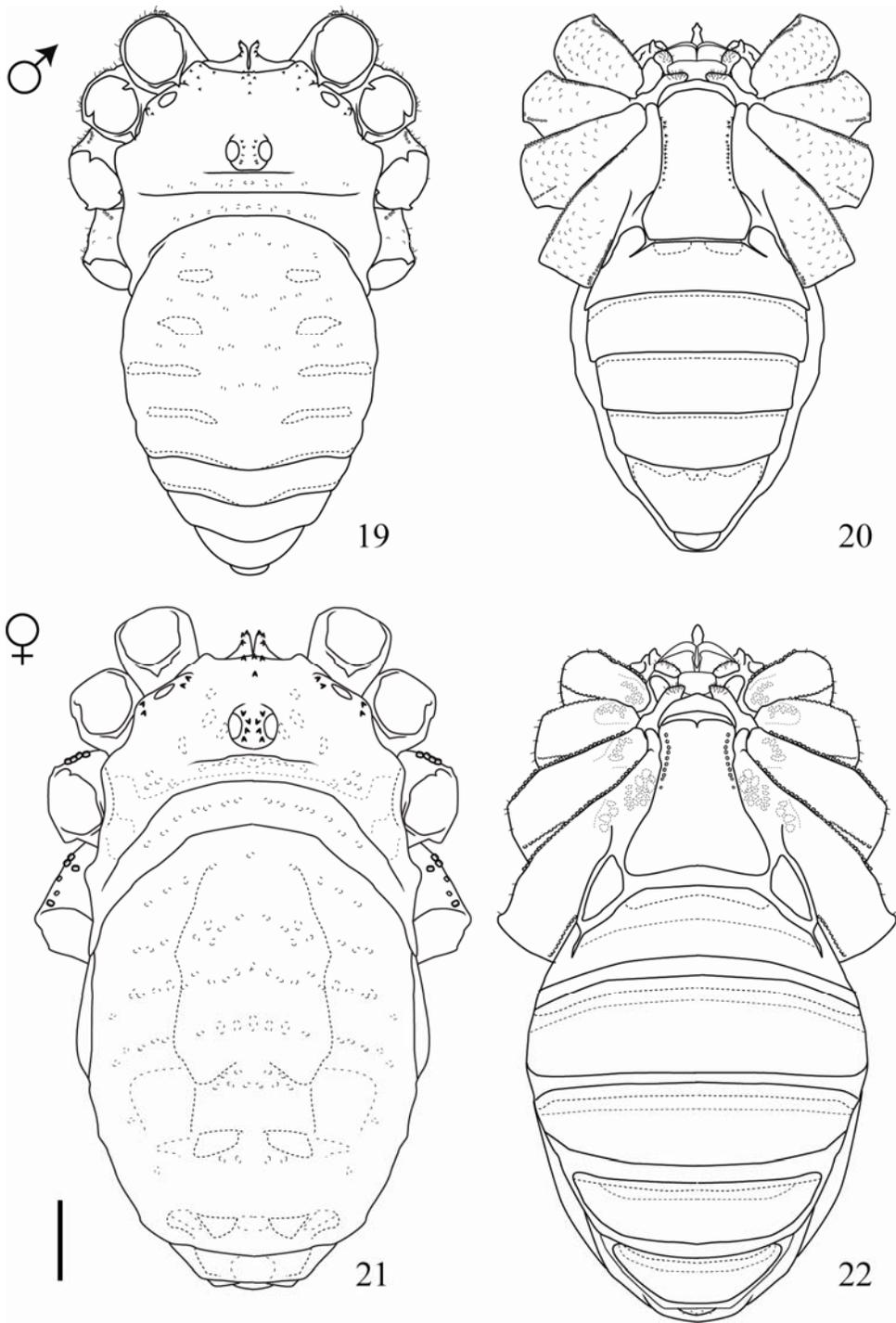
setae cover entire surface, denser and longer ventrally and distally; short erect setae arranged in 5-7 rows down the length of the tarsus, longer erect setae clustered around tarsal claw. Tarsal claw reddish.

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

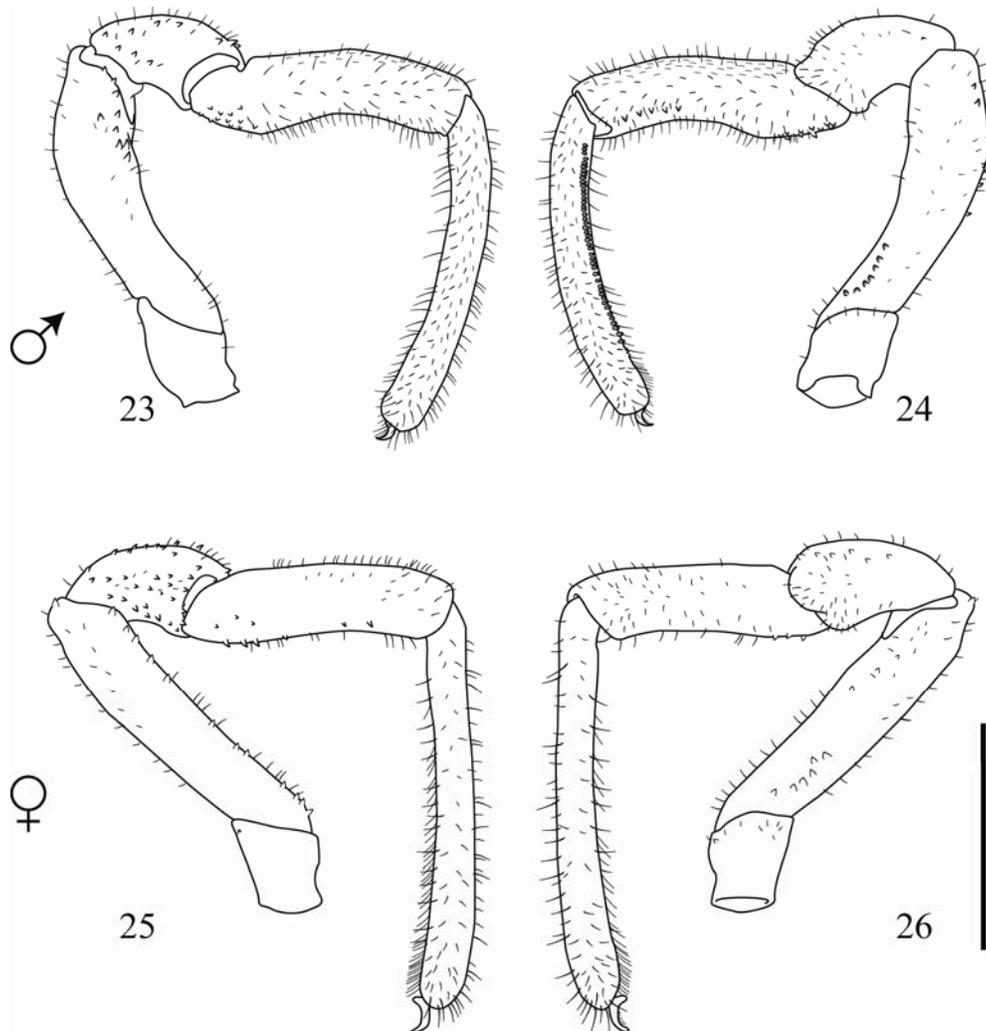
Variation in female. Frequently, the sternal posterior process is greatly reduced and the anterior notch is reduced or absent (fig. 29). The genital operculum median septum and corresponding sulcus may also be reduced or absent (fig. 31). Intensity of dorsal color, pattern, and central figure varies greatly, but posterior whitish blotches on opisthosoma are usually visible. Leg color ranges from golden to dark brown. Palpal tibia denticles sometimes reduced.

Material examined. U.S.A.: *Kentucky*: Bell Co.: 1M, Pine Mt. State Park, 36.7479° N, 83.7119° W, 29 September 1963, N.M. Davis (AMNH). *Michigan*: Livingston Co.: 1M 1F, George Reserve, 42.4667° N, 84.0000° W, 18 July 1936, I.J. Cantrall (AMNH). *Ohio*: Hocking Co.: 1M, Clear Creek Twp, 40.9475° N, 82.3628° W, 10 September 1931, T.H. Hubbell (AMNH). *Virginia*: Clarke Co.: 2M 1F, Blandy Farm, "ca 3 mi south of Boyce" 39.0624° N, 78.0622° W, 1 August 1991, D.R. Smith (VMNH). Dickenson Co.: 4M 2F, Breaks Interstate Park, "DF site 2 Nature Trail" 37.2868° N, 82.2964° W, 22 August – 6 October 1991, VMNH survey (VMNH). Fluvanna Co.: 6M 2F, Kents Store, "Bell drift fence site" 37.8779° N, 78.1286° W, 1995, M. Bell (VMNH). Henrico Co.: 1M, Westhampton, west Richmond, 37.5741° N, 77.5146° W, June – July 1991, W. Mitchell (VMNH). Isle of Wight Co.: 2M, Zuni Pine Barrens, "river bluff site", 36.7803° N, 76.8914° W, 31 August [year ?], C.A.

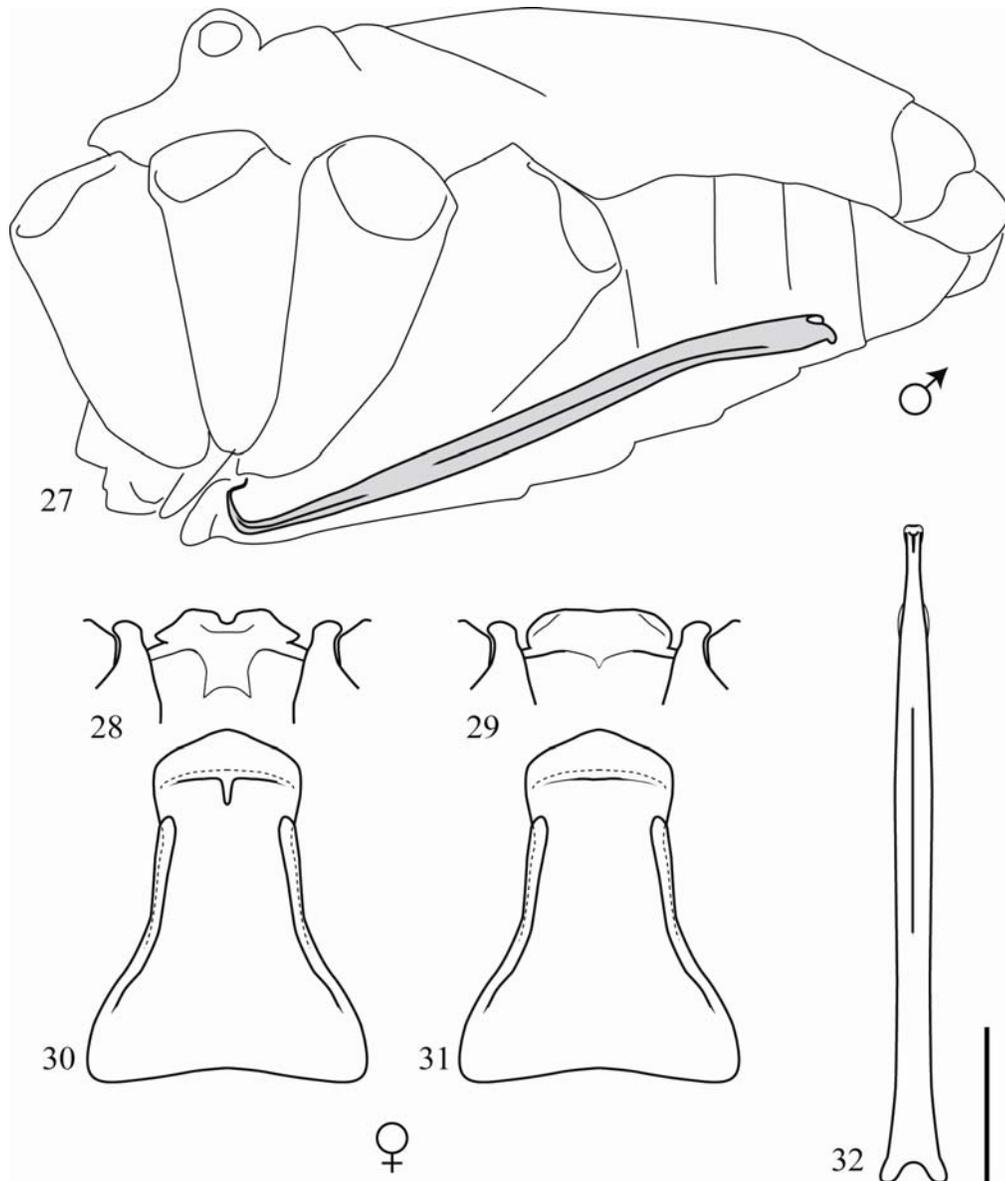
Pague (VMNH). Lee Co.: 1M 1F, The Cedars, ~10 km WSW of Jonesville, 36.6627° N, 83.2016° W, 9-11 August 1995, S.M. Roble & C.S. Hobson (VMNH). Prince William Co.: 1M 1F, Manassas NBP, "0.3 km S. of Sudley Spring", 38.8168° N, 77.5164° W, 22 July 1999, A.C. Chazal (VMNH). Russel Co.: 1M, Cedar Creek Falls, "ca. 4 mi. NE of Lebanon", 36.9542° N, 82.0541° W, 2 July 1989, R.B. & R.L. Hoffman (VMNH). Wise Co.: 1M, "0.8 mi. NW of Tacoma on VA Hy. 706 mixed woods, dry hillside", 36.9408° N, 82.5448° W, 19 July 1989, R.L. Hoffman (VMNH). York Co.: 4M 1F, Cheatham Annex Naval Supply Base, "Cheatham Pond DF site", 37.2934° N, 76.619° W, 6 July 1989, DNH survey (VMNH).



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



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



Figures 27-32. Genital structures of *Leioibunum euserratipalpe* new species. 27. Diagrammatic lateral perspective of male showing position of penis. 28, 29. Ventral perspective of female sterna (genital opercula removed); paratype on left, common variation on right. 30, 31. Dorsal (internal) perspective of female genital opercula; paratype on left, common variation on right. 32. Dorsal perspective of penis. All to same scale. Scale bar = 1 mm.

Leiobunum calcar (Wood, 1868)

(Figs. 33-46)

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

Leiobunum calcar Walker, 1928:163, pl. 1, fig. 9; Davis, 1934:670-672, pl. 32, figs 16, 17, pl. 33, fig. 31; Bishop, 1949: Edgar, 1966:360, fig. 5.

Leiobunum brunnea Walker 1928:167, pl. 2, fig. 12.

Leiobunum serratipalpe Roewer, 1910:218; Roewer, 1923:899, fig. 1054. Male cotype is a misidentified female *L. calcar* (Cokendolpher, 1981; original obs.).

Diagnosis. Penis (Figs. 43a, b, 46a, b): curved dorsally, usually with prominent dorsally-curved alae flanking a medial dorsal expansion at the base of the glans; glans curved dorsally. Male with retrolateral apophysis on palpal femur (Fig. 37), female usually with corresponding denticle-covered protuberance (Fig. 42). Posterior margin of female sternum with pronounced median process, anterior margin frequently with median notch (Fig. 44).

Remarks. Although traditional identification of *L. calcar* has focused primarily on the male's prominent femoral apophysis and curved, alate penis, variation is common in these characters, particularly in the size of the apophysis, which Cokendolpher (1981) noted when synonymizing *L. serratipalpe* with *L. calcar*. The hypothesized species *L. cumberlandense* also displays reduced apophyses (Fig. 39), but has a curved penis with variably-developed alae (Figs. 43b), as in *L. calcar*, suggesting it is a variant of *L. calcar* (a similar reduced-apophyses variant is known in *L. hoffmani* n. sp.), and is not here established as its own species. However, because of the relatively high level of variation compared to other members of the *L.*

nigropalpi group, the boundaries of the *L. calcar* morphospecies may yet be revised in the future with a more complete sampling of the species' large range.

Description of male neotype. Locality: U.S.A.: *Virginia*, Floyd County, Buffalo Mountain NAP, "trailhead at parking lot", 37.4316° N, 78.6569° W, 2 June 2004. Deposited in the Virginia Museum of Natural History, Martinsville, Virginia.

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. Suprachelicera 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: *Chelicera*: 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,b, 46a,b): 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 a large amount of variation in a number of characters. The central figure and dorsal rows of white spots and darker markings vary from apparent to faded, or may be absent completely. Trochanters and basal portion of femur are generally dark, often contrasting with the femur shaft, but some are concolorous with the femur shaft, which, along with the palps, ranges 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, with a reduced but still-present conical spur. Penis curvature varies from shallow to strong, 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 female paratype. Locality: U.S.A.: *Virginia*: Floyd County, Buffalo Mountain NAP, “upper foot trail to top”, 37.4316°N, 78.6569°W, 29 July 2000. Deposited in the Virginia Museum of Natural History, Martinsville, Virginia.

Body length: 7.5 mm. *Dorsum* (Fig. 35): Carapace length, width: 2.0 mm, 3.3 mm. Suprachelicera 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 denticals.

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 twice the length of the sternite body (Fig. 44). Labrum straight and expanded ventrally at base.

Appendages: *Chelicera*: 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, while 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 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 ocularium denticles 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 or absent, or reach the anterior sternum body, and posterior process ranges from half the length of the sternum to as much as twice the length, although longer is more common. The small palpal apophysis is occasionally absent.

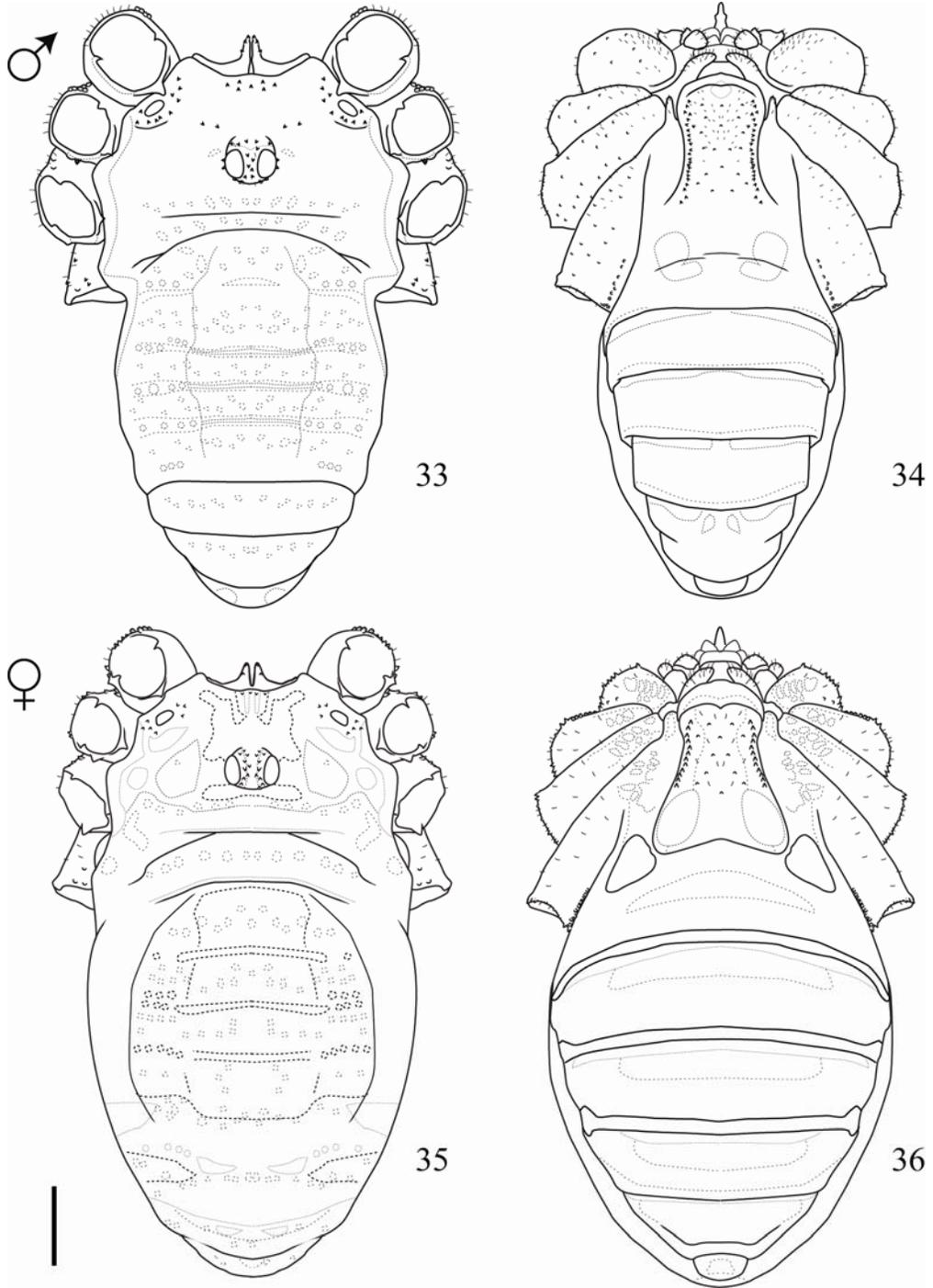
Distribution. The species is known from southern Canada from southern Manitoba east into the Maritime Provinces. This widespread distribution continues into the northern United States from the northern Midwest and Great Lakes Region to the New England States. It is increasingly restricted to the Appalachian Mountains in more southern states.

Material examined: CANADA: Ontario: 1F, Orillia, 44.6° N, 79.416667° W, 27 July 1938, CH Curran (AMNH). U.S.A.: *Kentucky*: Knox Co.: 1M 1F, Wooded hillside Trace Branch, near Heidrick, 36.8935° N, 83.8596° W, 17 June 1962, A. Davis (AMNH). Laurel Co.: 2M 1F, Cumberland Natl. Forest [as of 1966, Daniel Boone National Forest], 36.8558° N, 84.3474° W, 22 August 1965, L. Davis, “*L. cumberlandense*” variant (AMNH). *Maine*: Washington Co.: 3M 3F, 8 km S. Milbridge, 44.4619° N, 67.8929° W, 22-27 July 1990, collector ? (AMNH). *Maryland*: Garrett Co.: 2M 2F, 3 km SE New Germany, "Managed Oak Forest", (132, lot 003), 39.62° N, 79.105° N, ele. 779 m, 11-18 July 2005, M. Sarver (UMD). *Michigan*: Charlevoix Co.: 1M, 45.318° N, 85.2584° W, T.H. Hubbell (AMNH). *New York*: Albany Co.: 5M, Rensselaerville, 42.4794° N, 74.172° W, 15 July 1975, T. Eisner (AMNH). Madison Co.: 1F, Deruyter Lake, 42.8145° N, 75.8978° W, 3 July 1922, (AMNH). Ulster Co: 1M, “Cherrytown nr Kerhonkson”, 41.8251° N, 74.3293° W, 18 July 1976, Wygodzinsky. *North Carolina*: Macon Co.: 1M 1F, 5 mi N of Highlands, 35.1269° N, 83.1924° W, August 1967, K. Kleinpeter (AMNH). 1F, Highlands, “at Kleinpeter's place”, 35.0365° N, 83.1921° W, 22 July 1967, Hoffman & Kleinpeter (VMNH). Yancey Co.: 1M, Mt. Mitchell, “camping area near top”, 35.7601° N, 82.2709° W, 31 July 1972, R.L. Hoffman (VMNH). *Pennsylvania*:

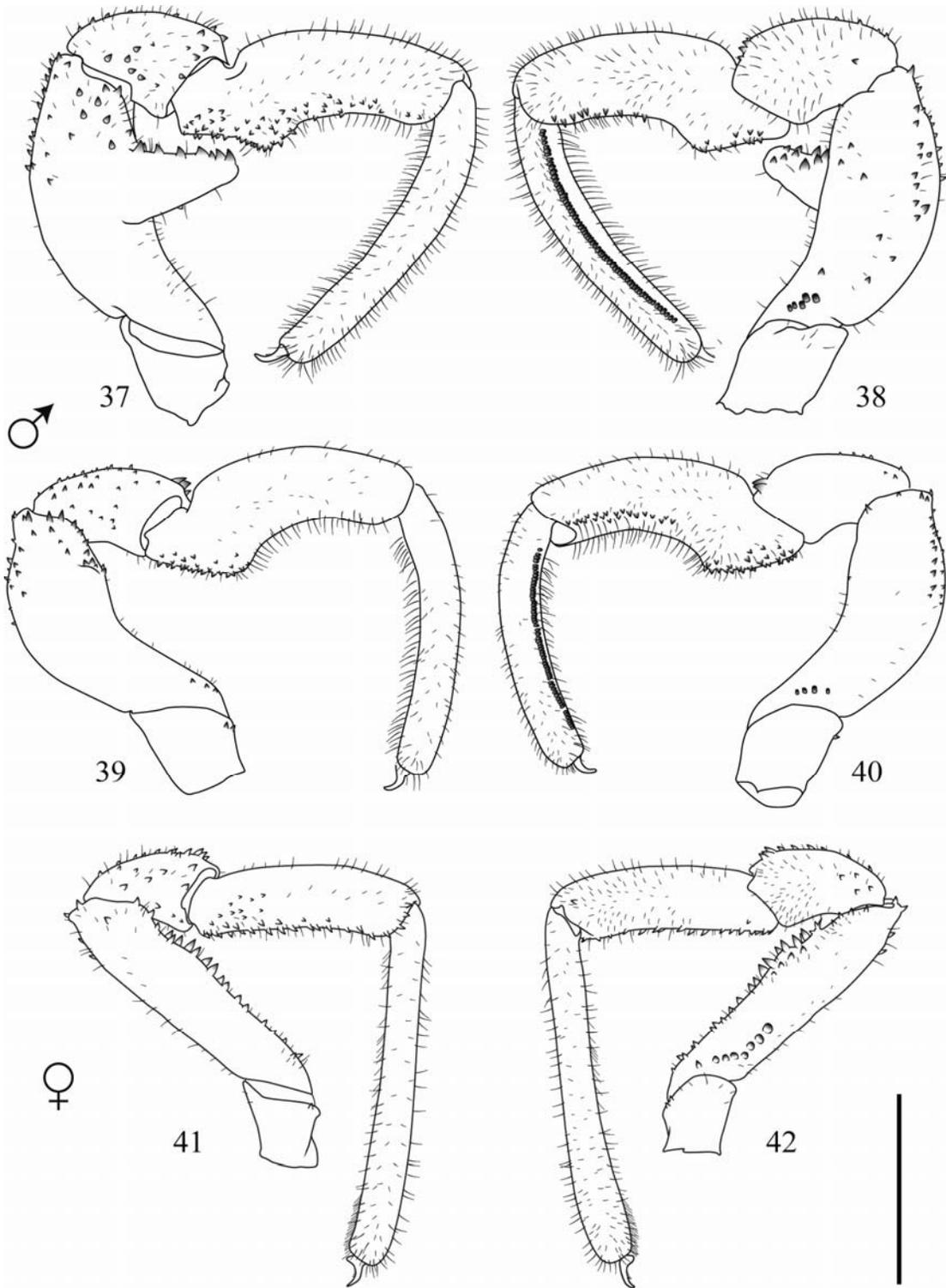
Columbia Co.: 1M, Orangeville, 41.3392° N, 80.519° W, 13 August 1932, Hughes, Davis (AMNH). *Tennessee*: Cocke Co.: 1M, Albright Grove, “ATBI Plot”, 35.7333° N, 83.2806° W, 19 June – 6 July 2001. M. McCord. 2M, GSMNP, vic. Cosby ATBI residence house, 35.7779° N, 83.2135° W, ele 518 m, 28 July – 9 August 2000, M. Hedin, J. Cokendolpher (AMNH). Sevier Co.: 1F, GRSM ATBI Plot: Goshen Prong, 35.6105° N, 83.5453° W, 27 August – 17 September 2001, I.C. Stocks. 1M 2F, GRSM ATBI Plot: Goshen Prong, 35.6105° N, 83.5453° W, 27 August – 17 September 2001, I.C. Stocks. 1M 2F, GRSM ATBI Plot: Indian Gap, 35.6108° N, 83.4436° W, 6 August – 3 September 2001, R. Fox. 1M, GRSM ATBI Plot: Indian Gap, 35.6108° N, 83.4436° W, 3-26 September 2001, I.C. Stocks. 1M 1F, GRSM ATBI Plot: Twin Creeks, 35.685° N, 83.499° W, 10-30 September 2002, no collector. 1M 1F, GRSM ATBI Plot: Twin Creeks, 35.685° N, 83.499° W, 5-18 July 2000, Parker, Stocks, Petersen. 1F, GRSM ATBI Plot: Twin Creeks, 35.685° N, 83.499° W, 26 September – 12 October 2000, Parker, Stocks, Petersen. 1F, GRSM ATBI Plot: Twin Creeks, 35.685° N, 83.499° W, 15-23 May 2001, I. Stocks, M. Williams (AMNH). Roane Co.: 3M 2F, 35.8809° N, 84.5085° W, 12 July 1933, W.J. Gertsch (AMNH). Pickett Co.: 3M 3F, Pickett State Park, 36.558° N, 84.7916° W, 25 June 1967, C.R. McGhee, “*L. cumberlandense*” variant (McGhee). *Virginia*, Amherst Co.: 4M 1F, Tarjacket Ridge, “DF site off FS 1167”, 37.4316° N, 78.6569° W, 9 July 1998, J. Schilling (VMNH). 3M. 1F, Tarjacket Ridge, 37.4316° N, 78.6569° W, 4 August 1998, VMNH survey, (VMNH). Augusta Co.: 1M, GWNF, 5 miles west of Stokesville Comp., “452-8A Trap 3”, 38.3403° N, 79.2334° W, 8 July 1989, B. Flamm (VMNH). 1M, GWNF, ca 5 miles west of Stokesville Comp., “460-3 Trap 3”,

38.3403° N, 79.2334° W, 1 September 1989, B. Flamm (VMNH). Bath Co.: 2M, S and E of Hot Springs, “crest of Warm Springs Mtn.”, 38.0526° N, 79.7684° W, 19 August 1999, S.M. Roble (VMNH). 1M, “headwaters of Smith Creek, across Middle Mtn. from Douthat State Park”, 38.5713° N, 78.8298° W, 9 July 1988, R.L. Hoffman (VMNH). 2M, Warm Springs Mtn, WFD, UV, 38.0526° N, 79.7684° W, 14 June 1999, J.C. Ludwig (VMNH). Botetourt Co.: 1M 3F, Roaring Run, 37.6924° N, 79.8909° W, 21 August 1996, M. Donahue (VMNH). Clarke Co.: 1M 1F, Blandy Farm, “ca 3 mi south of Boyce”, 39.0624° N, 78.0622° W, 2 July 1991, D.R. Smith (VMNH). Essex Co.: 3M 2F, 1.5 km SE Dunnsville, “Malaise trap B1#1”, 37.8473° N, 76.8015° W, 12 July 1991, D.R. Smith (VMNH). Floyd Co.: 1M, Buffalo Mountain NAP, “north slope DF site”, 36.796° N, 80.477° W, 15 July – 29 August 2001, VMNH survey (VMNH). 3M 2F, Buffalo Mountain NAP, “south slope DF”, 37.4316° N, 78.6569° W, 9 August – 6 September 2000, Joint Survey (VMNH). 1F, Buffalo Mountain NAP, “UV trap at base of hump”, 37.4316° N, 78.6569° W, ele. 1067 m, 3 June 2000, S.M. Roble (VMNH). 1M 1F, Buffalo Mountain NAP, “trailhead at parking lot”, 37.4316° N, 78.6569° W, 2 June 2004, R.L. Hoffman (VMNH). 1F, Buffalo Mountain NAP, “upper foot trail to top”, 37.4316° N, 78.6569° W, 29 July 2000, Joint Survey (VMNH). Giles Co.: 1F, Mountain Lake, 37.3551° N, 80.5368° W, June - July 1947, HH Hobbs, Jr. and Zoology class (TTU). Henry Co.: 1M, Breeski's Farm, “near Ridgeway”, 36.9893° N, 79.4825° W, 22 August 1987, VMNH Exped (VMNH). Highland Co.: 1M, Locust Springs, “Buck Run ponds”, 38.5828° N, 79.6352° W, 5 August 1999, S.M. Roble (VMNH). 1M, Locust Spring Rec area, 8 mi NW of Bluegrass, 38.5828° N, 79.6352° W, ele. 1158 m, 13 July

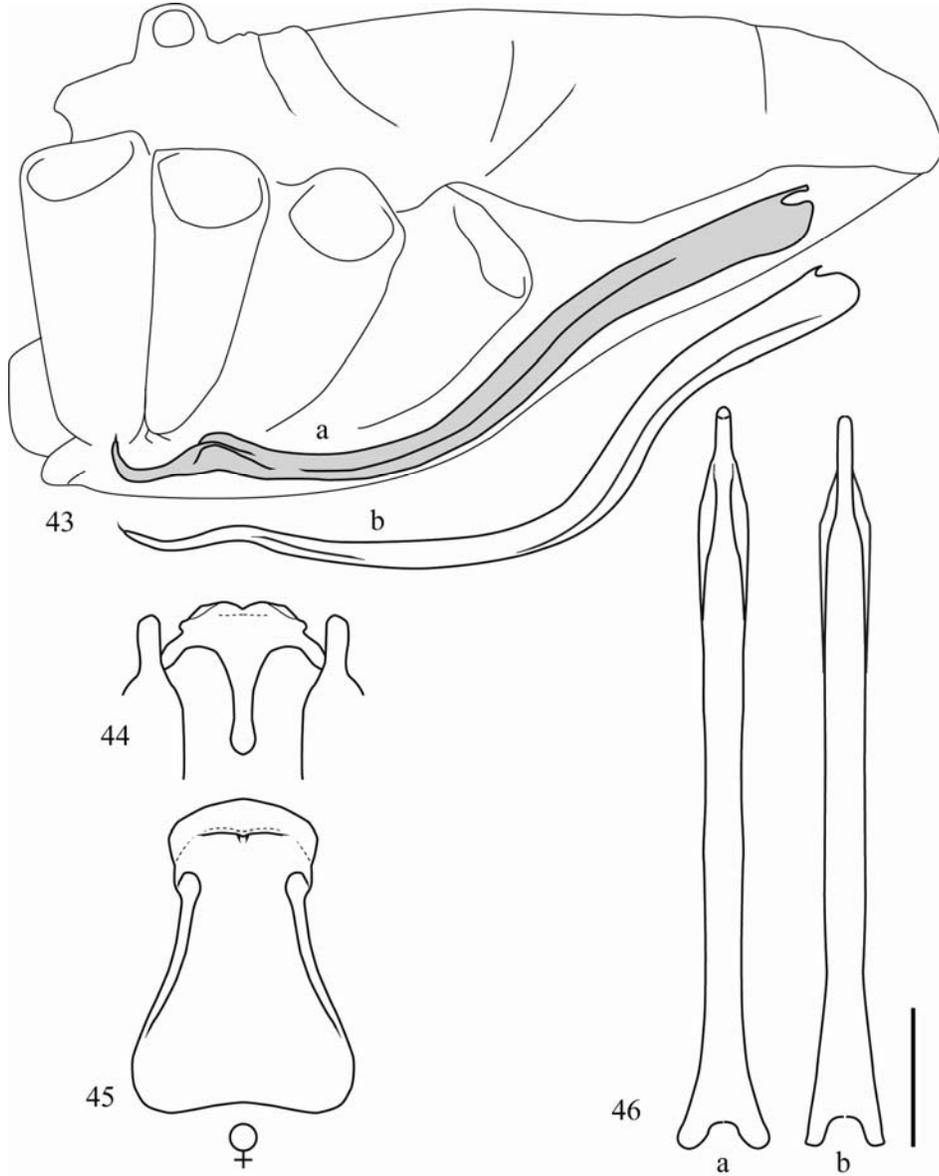
1974, R.L. Hoffman (VMNH). Nelson Co.: 1F 1M, The Priest, 4.5 mi SE of Montebello, 37.8199° N, 79.0625° W, ele. 1189 m, 16-29 August 1991, VMNH survey (VMNH). 1M, The Priest, “at drift fence site”, 37.8199° N, 79.0625° W, ele. 1189 m, 20 September 1991, R.L. Hoffman (VMNH). 2M, North Fk Tye River, ~4 mi E of Montebello on Va. 687, PF, 37.8595° N, 79.0446° W, 6 September 1998, VMNH survey (VMNH).



Figures 33-36. Dorsal and ventral perspectives of *Leibunum calcar* (Wood 1868), male neotype, female allotype. Scale bar = 1 mm.



Figures 37-42. Palps of *Leobunum calcar* (Wood 1868). 37, 38. Male neotype. 39, 40. Male “cumberlandense” variant. 41, 42. Female allotype. Retrolateral perspectives on left, prolateral perspectives on right. Scale bar = 1 mm.



Figures 43-46. Genital structures of *Leioibunum calcar* (Wood 1868). 43. Diagrammatic lateral perspective of male showing position of penis; a. male neotype, b. “cumberlandense” variant. 44. Ventral perspective of female sternum (genital operculum removed). 45. Dorsal (internal) perspective of female genital operculum. 46. Dorsal perspective of penis; a. male neotype, b. “cumberlandense” variant. All to same scale. Scale bar = 1 mm.

***Leiobunum hoffmani* new species**

(Figs. 47-60)

Diagnosis. Penis (Fig. 57, 60): elongate (full length of body or more), gradually tapered, and lanceolate, lacking sacs, bulbs or alae. Male palps massive, comprising terminally inflated, incrassate femora and proximally inflated, incrassate tibiae; femur with retrolateral apophysis of *L. calcar* (Fig. 51). Female supraopercular sternite large with long posterior process and deep anterior median notch (to middle of sternum) (Fig. 58), palpal femur lacking femoral apophysis of female *L. calcar* (Fig. 55).

Etymology. The name is retained from the unpublished dissertation of McGhee (1970).

Remarks. Superficially, *L. hoffmani* males are readily distinguished from other members of the *L. nigropalpi* group by their dorsally-angled opisthosoma (Fig. 57) and large, robust palps with conical femoral apophyses. The angle of the opisthosoma provides space to house the unusually long, curved penis (usually slightly longer than the animal's body length). Even when fully retracted, it is not uncommon for the penis tip to still extend just beyond the opening of the genital chamber, with the anterior margin of the genital operculum folded over it.

However, although sharing this and all other features of *L. hoffmani* from other locations, one population from Grayson County., Virginia lacks the large palpal apophyses on all males examined. Instead, a reduced and somewhat flattened process is present, with denticles still clustered on its anterior surface, as on the large apophysis. This variation has not been observed in any other *L. hoffmani* population,

and is considered here to be a regional variant. Sampling of more populations will better determine the species range and any further variation.

Description of male holotype. Locality: U.S.A.: *Virginia*: Smythe County, Mt. Rogers NRA, 36.72402° N, 81.49041° W, 870 m. Deposited in National Museum of Natural History, Smithsonian Institution (Washington, D.C.).

Body length: 6.5 mm. *Dorsum* (Fig. 47): 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 carapacial 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. 48): 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 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. Supraopercular 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. *Palps* (Fig. 51, 52): 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; 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 pseudoarticulation 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 (Fig. 60): 6.7 mm. Lancolate, 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, 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 on the large apophysis. 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. Locality: U.S.A.: *Virginia*, Grayson Co.: Whitetop Mountain, “just off FS 89”, 36.6387° N, -81.6059° W, ele. ~1524 m, 25 June – 11 July 1998. Deposited in the National Museum of Natural History.

Body length: 7.6 mm. *Dorsum* (Fig. 49). 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. 50): Labrum straight with scattered minute tubercles; at midpoint, slightly expanded laterally. Termites 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. 59). 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* (Fig. 55, 56): 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 forming 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 coxa 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.

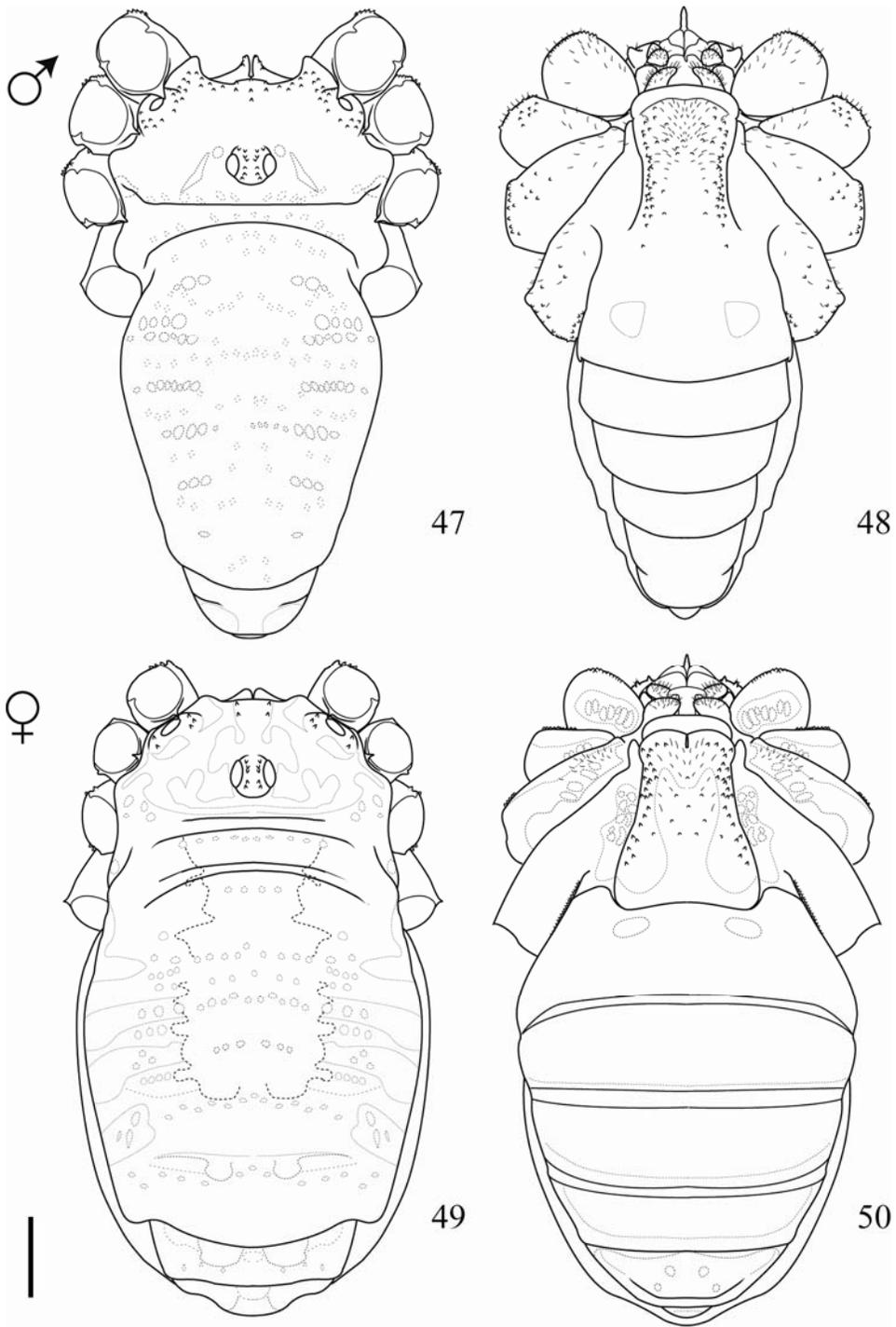
Ovipositor: Typical; two spermathecae present between segments 6 and 7.

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

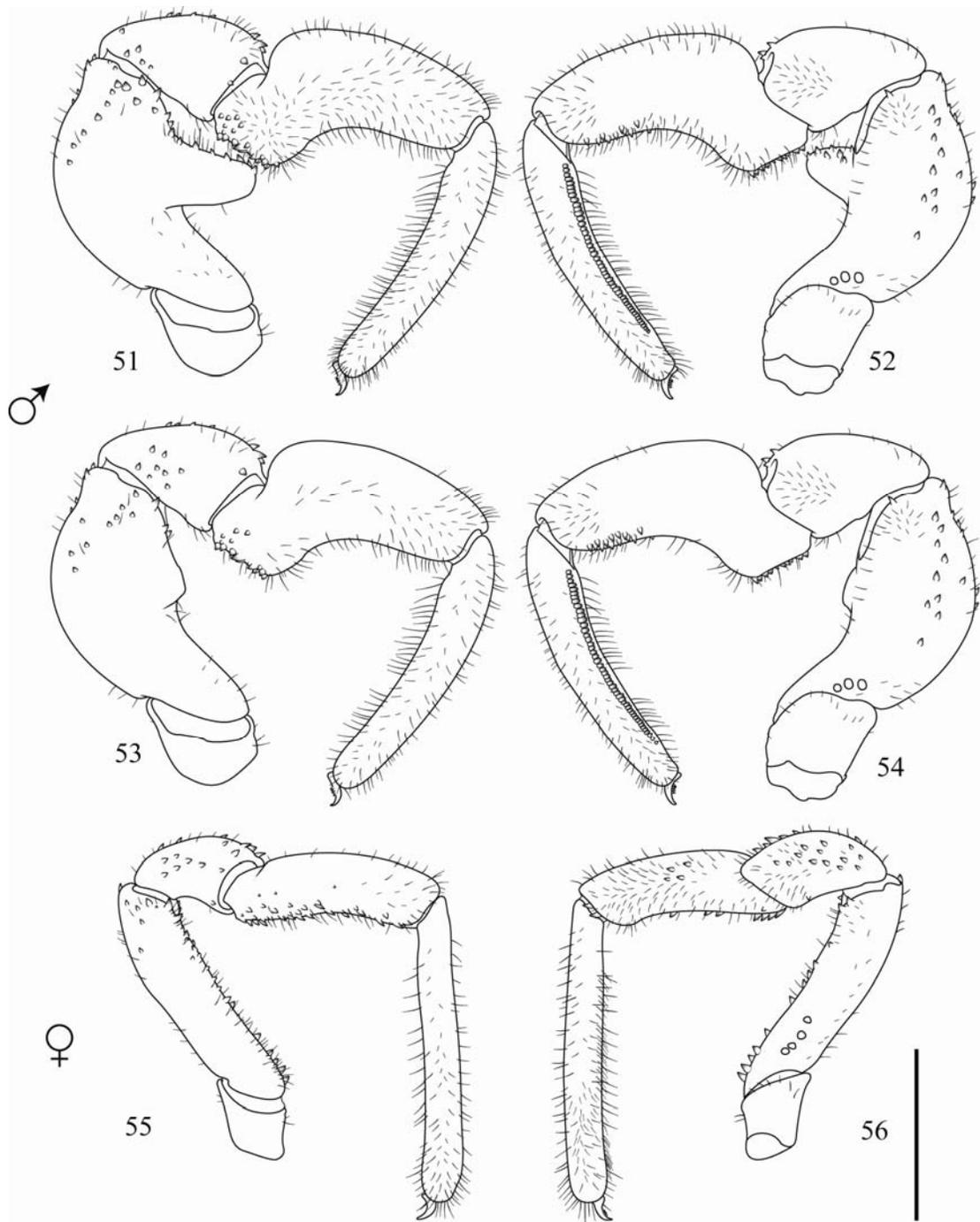
Distribution. Limited to the Blue Ridge Mountains of northwest North Carolina and southwest Virginia.

Material examined. U.S.A: *North Carolina*: Alleghany Co.: 2M 5F, Doughton Park CG, “on BRP, S of Sparta,” 36.4290° N, 81.1539° W, ele. 1100 m, 11 August 2007, M. Hedin (UMD). Wilkes Co.: 8M 3F, Doughton National Recreation Area, “Blue Ridge Parkway,” 36.4016° N, 81.1748° W, 30 July 1967, C.R. McGhee (AMNH). *Virginia*: Grayson Co.: 12M 12F, White Top Mountain, “just off FS 89”, 36.6387° N, 81.6059° W, ele. ~1524 m, 25 June – 11 July 1998, Virginia Natural History Survey (VMNH); 1M, White Top Mountain, “beechwoods” “off FS 89”, 36.6387° N, 81.6059° W, ele. ~1524 m, 20 August 2001, Virginia Natural History Survey (VMNH); 6M, White Top Mountain, “beechwoods” “off FS 89”, 36.6387° N, 81.6059° W, ele. ~1524 m, 25 June – 11 July 1993, Virginia Natural History Survey (VMNH); 3M 2F (penultimate), 1M 1F (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); 13M 3F, Grayson Highlands State Park, Haw Orchard Mountain, “above water tank”, 36.6270° N, 81.5048° W, 30 August 1990, Virginia Natural History Survey (VMNH); 3M, Grayson Highlands State Park, Haw Orchard Knob, 36.6270° N, 81.5048° W, 8 July 1990, R.L. Hoffman (VMNH); 1M 3F, Mount Rogers, “horse trail to Helton Creek”, 36.6599° N, 81.5451° W, ele. 1310 – 1370 m, 8 July 1990, R.L. Hoffman (VMNH); 10M 1F, Highlands State Park, Haw Orchard Mountain, “spruce woods nr Visitor Cntr”, 36.6270° N, -81.5048° W, 8 August 1990, Virginia Natural History Survey (VMNH).

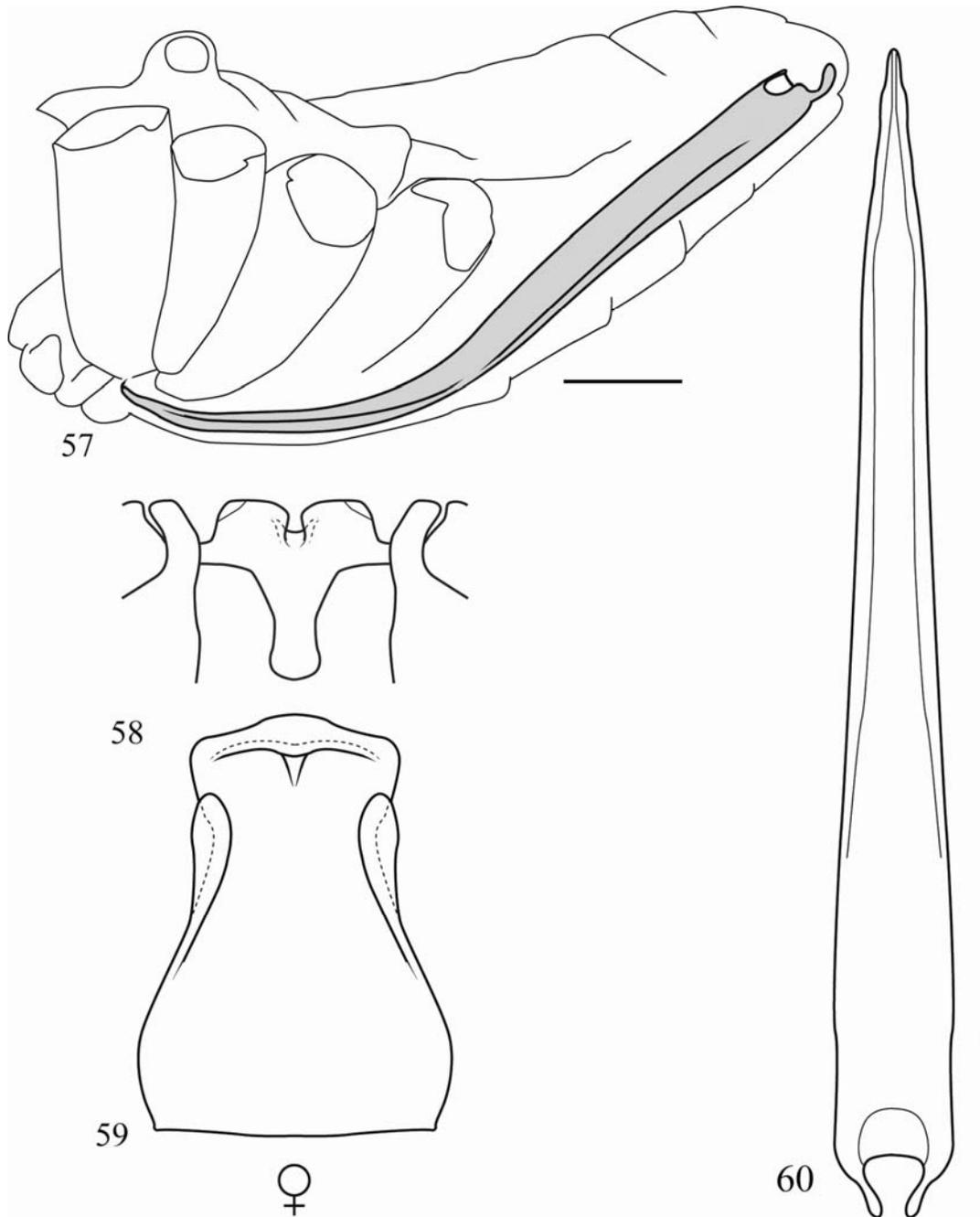
Smythe Co.: 5M 2F, Mt. Rogers NRA, Hurricane CG, "w of hwy 16", 36.7240° N,
81.49041° W, ele. 870 m, 10 August 2007, M. Hedin (UMD).



Figures 47-50. Dorsal and ventral perspectives of *Leïobunum hoffmani* new species, male holotype, female paratype. Scale bar = 1 mm.



Figures 51-56. Right palps of *Leobunum hoffmani* new species. 51, 52. Male holotype. 53, 54. Male variant from Grayson, Virginia. 55, 56. Female paratype. Retrolateral perspective on left, prolateral perspective on right. Scale bar = 1 mm.



Figures 57-60. Genital structures of *Leio bunum hoffmani* new species. 57. Diagrammatic lateral perspective of male showing position of penis. 58. Ventral perspective of female sternum (genital operculum removed). 59. Dorsal (internal) perspective of female genital operculum. 60. Dorsal perspective of penis. Figs. 58-60 to same scale. Scale bars = 1 mm.

Key to Species

- 1'. Male 2
- 1''. Female. 5
- 2'(1'). Palpal femur without retrolateral apophysis (Fig. 11), retrolateral row of denticles extending along length of femur (Fig. 11); penis narrowed at glans-shaft joint in dorsal perspective forming “neck” (Fig. 18)
Leiobunum nigropalpi (Wood 1868)
- 2''. Palpal femur with retrolateral apophysis (Figs. 5, 37, 51) or distal cluster of denticles (Fig. 23, 39, 53), retrolateral denticles limited to distal portion of femur (Figs. 23, 39, 51); glans-shaft joint variable in dorsal perspective but without a distinct neck (Figs. 1, 32, 46, 60) 3
- 3'(2''). Palpal femur not greatly inflated or strongly curved and with distal retrolateral cluster of denticles, sometimes mounted on small apophysis (Fig. 23); penis glans held at distinct angle with respect to shaft in lateral perspective; shaft not strongly curved in lateral perspective (Fig. 27), usually with small subterminal alae in dorsal perspective (Fig. 32)
Leiobunum euserratipalpe new species
- 3''. Palpal femur inflated and strongly curved, with or without large retrolateral apophysis, but never with a simple distal cluster of denticles (Figs. 37, 39, 51, 53); penis shaft strongly curved in lateral perspective (Figs. 43, 57), with large subterminal alae (Figs. 43, 46) or none (Fig. 60) 4

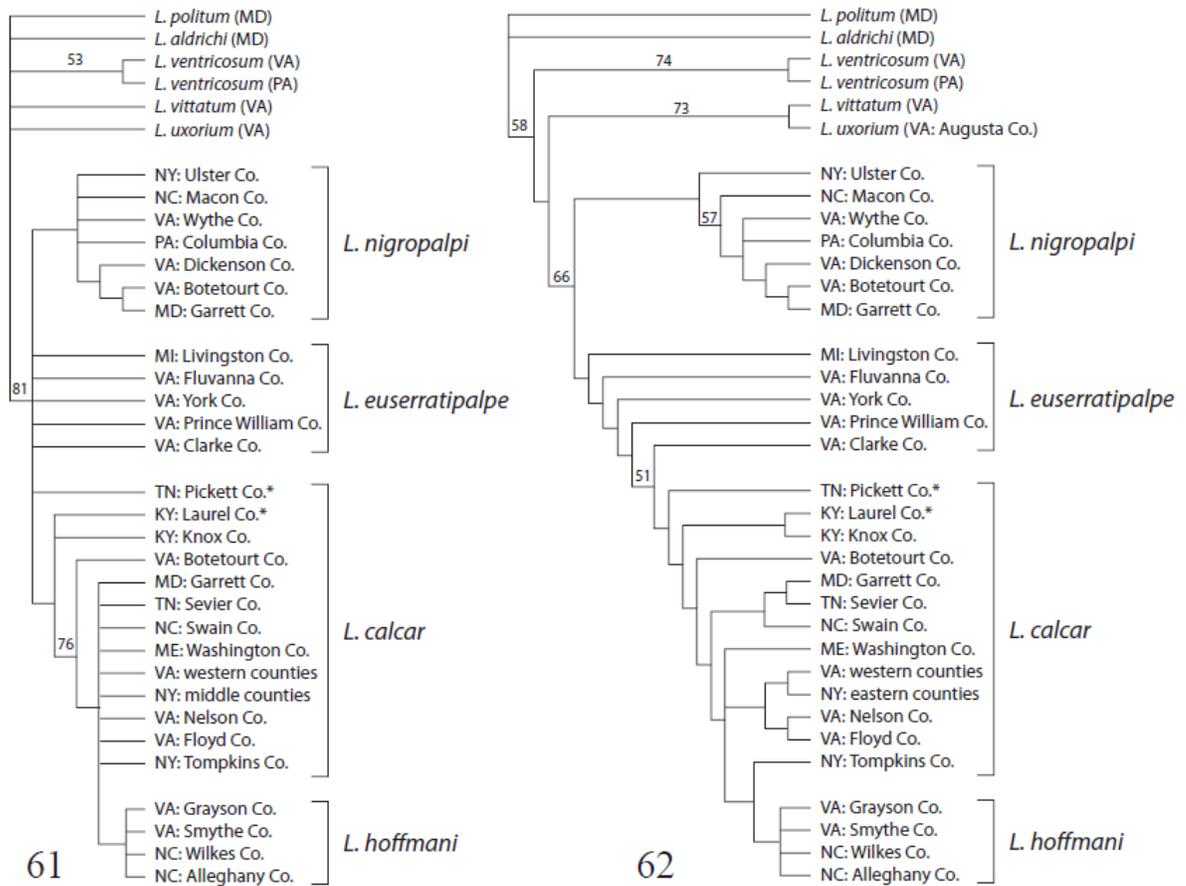
- 4'(3''). Penis shaft with large subterminal alae, penis with a slight dorsal curve between alae (Fig. 43) or slight curve only (Fig. 47)
. *Leiobunum calcar* (Wood 1868)
- 4''). Penis shaft without subterminal alae and corresponding curve (Figs. 60)
. *Leiobunum hoffmani* new species
- 5'(1'') Sternum with short, narrow, membranous posterior process distinct from the more sclerotized sternum body; anterior sternal notch a broad "V" (Fig. 16)
. *Leiobunum nigropalpi* (Wood 1868)
- 5'' Anterior notch narrow (Figs. 28, 44, 58) or absent (Figs. 29); posterior process long (Figs. 44, 58) or short (Figs. 28, 29), but not distinct from the sternum body 6
- 6'(5'') Palpal femur with small retrolateral denticles (Fig. 25) or none; sternal posterior process short to very short (Figs. 28, 29)
. *Leiobunum euserratipalpe* new species
- 6'' Sternal posterior process long, at least doubling the length of the sternum (Figs. 44, 58); palpal femur with row of retrolateral denticles (Figs. 39, 55). 7
- 7'(6'') Palpal femur with retrolateral denticles, larger distally; small, rounded retrolateral apophysis often present (Fig. 39); anterior notch of sternum shallow or absent (Fig. 44) *Leiobunum calcar* (Wood 1868)
- 7'' Anterior sternal notch U- shaped and deep, extending to the midpoint of the sternum (Fig. 58); palpal femoral retrolateral denticles sometimes larger

distally, but never on a retrolateral apophysis (Fig. 55); genital operculum
median septum often long (Fig. 45) . *Leiobunum hoffmani* new species

Section 2: Phylogenetic Analysis

The *L. nigropalpi* species group was recovered as monophyletic in analyses using unweighted data (Fig. 61) and implied weighting (Fig. 62), although bootstrap support was modest each case. *L. nigropalpi* was consistently recovered as the monophyletic sister to the remaining members of the species group, but bootstrap support for this conclusion was consistently low (< 50%). The morphospecies *L. euserratipalpe* and *L. calcar* were reconstructed as sequential, paraphyletic clusters, although *L. hoffmani* was consistently recovered as a monophyletic element emerging from the paraphyletic *L. calcar*. The species "*L. cumberlandense*" proposed by McGhee (1970) was not recovered as a monophyletic group, and clustered with the *L. calcar* specimens obtained from the same geographic region.

Several morphological characters showed little homoplasy, and their distribution could be readily mapped on the phylogeny. The *nigropalpi* species group is united by a proximal tibial process of the male palp, posterior process of the female sternum, and lanceolate penis, although the latter also occurs in *L. uxorium* and *L. vittatum*. *L. nigropalpi* is united by darkly colored palps, and the remaining members of the species group share the retrolateral femoral apophysis and distally clustered denticles of the male palp. *L. calcar* and *L. hoffmani* are united by a prominent posterior process of the female sternum. *L. hoffmani* is distinguished by reduced denticles on the male's anterior coxa III and the female's deep anterior sternal notch.



Figures 61-62. Strict-consensus trees. 61. Results from traditional parsimony analysis (unweighted characters, TBR branch swapping, 1000 replicates, 80 trees, 189 steps). 62. Results from traditional parsimony analysis (implied weights, K=1; TBR branch swapping, 1000 replicates, 3 trees, best score = 29.26). Bootstrap values >50% shown above branches; based on 1000 replicates. All analyses conducted in TNT (Goloboff et al., 2003). Names followed by an asterisk indicate specimens proposed as "*L. cumberlandense*" by McGhee (1970).

Chapter 4: Discussion

Although *L. cumberlandense* was originally proposed as a new species (McGhee 1970), eastern Kentucky *L. cumberlandense* clusters with eastern Kentucky *L. calcar*, supporting the conclusion that *L. cumberlandense* is not a distinct species. Its distinguishing male characters, a reduced palpal femoral apophysis and flat alae, are present in other *L. calcar*, while females do not appear to have any characteristic features that distinguish them from *L. calcar* females. The weak support and paraphyly of *L. calcar*, including the *L. cumberlandense* variant, does not suggest any obvious divisions to the *L. calcar* species.

The paraphyletic *L. euserratipalpe* and *L. calcar* form a gradient from the more basal *L. euserratipalpe* to the more derived *L. calcar*, reflecting the species group's evolutionary trend toward larger a larger penis and palps, more elaborate female pregenital barricade, and reduced coxal denticles. The presence of distinguishing female characters is significant, both as a means for identifying the different morphospecies and as indicators of the type of selective pressures the species are under. The traditional male characters appear to function coercively: robust, muscular palps with the femoral retrolateral apophysis and tibial ventral process acting as clamps allows the male to better grip the female during mating, a larger, more muscled penis potentially capable of prying open the female's genital operculum, and a loss of the enticement-strategy of nuptial-gift-carrying sacs found on the penis of many other harvestmen. These coercive features are indicative of conflict-based or sexually antagonistic coevolution, where males are under selective pressure from female resistance to copulation, and females are likewise under

selective pressure from male coercion, resulting in their pregenital barricades that appear capable of excluding the penis and reduced coxal denticles, potentially reducing friction from the male palp and loosening the male's grip.

Historically, however, females of the *L. nigropalpi* group have been only superficially described, if at all, or those of different species assumed to look alike (eg. Davis 1934), resulting not only in the frequent misidentifications of females in collections, but, often, a noticeable lack of female specimens at all. However, in light of sexually antagonistic coevolution, in which female characters can be under as much selective pressure as male characters and may be what is driving the evolution of those male characters, their inclusion in the delimiting of morphospecies should be considered valuable in further work with the *L. nigropalpi* species group.

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