

REVISION OF THE HARVESTMAN GENUS *LEPTOBUNUS*
AND DISMANTLEMENT OF THE LEPTOBUNIDAE
(ARACHNIDA: OPILIONES: PALPATOIRES)

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Abstract.—The harvestman genus *Leptobunus* Banks is revised. *Leptobunus californicus* Banks and *Leptobunus borealis* Banks are redescribed, and *Leuronychus parvulus* Banks is transferred to *Leptobunus* and redescribed. Lectotypes for *L. borealis* and *L. parvulus* are designated. *Leptobunus aureus* n. sp. and *Leptobunus pallidus* n. sp. are described from California, U.S.A. and Bering Island, U.S.S.R., respectively. *Leptobunus atavus* Cockerell, *Leptobunus koreanus* Roewer, *Leptobunus mexicanus* Goodnight and Goodnight, and *Leptobunus spinulatus* Banks are all excluded from the genus *Leptobunus*. The North American Tertiary fossil species is maintained as *Amauropilio atavus* (Cockerell), whereas all Recent species excluded from *Leptobunus* are reported in the following new combinations: *Mitopus koreanus* (Roewer), *Paranelima mexicana* (Goodnight and Goodnight), and *Metopilio spinulatus* (Banks). In conjunction, the Mexican species *Diguetinus raptator* Roewer is removed from synonymy with "*Diguetinus*" *spinulatus* (Banks). All the species are illustrated, including the male and female genitalia, for which new anatomical terminology is presented. A dichotomous key to the species and many new distributional records from western North America and northeast Asia are provided.

The history of the family-group name Leptobunidae is discussed and the name is attributed to Banks (1901). The family is abandoned and morphological characters traditionally used for the classification of "Leptobunidae" are discussed. The type genus of the Leptobunidae, *Leptobunus* Banks, is transferred to the Phalangiidae, subfamily Phalangiinae. The genera *Cosmobunus* Simon, *Leuronychus* Banks, and *Homolophus* Banks are transferred to the Gagrellidae, subfamily Leiobuninae, and *Trachyrhinus* Weed is maintained in the Gagrellidae, subfamily Gagrellinae. The North American genus *Protolophus* Banks is tentatively placed in the Gagrellidae, subfamily Sclerosomatinae. The South American genus *Thrasychirus* Simon is retained in the Neopilionidae, subfamily Enantiobuninae. The North American genus *Globipes* Banks is maintained in an assemblage that is as yet unnamed. The New World members of the genera *Homolophus* and *Cosmobunus* are not congeneric with Old World members referred to those genera.

Attempts to establish phylogenetically meaningful classifications of the Phalangioidea have been hindered by the confusion regarding the Leptobunidae. Until the present, apparently no worker has studied examples of all genera assigned to this family. Nathan Banks described several Nearctic species and genera but apparently never studied any Old World members of the group. Carl-Friedrich Roewer examined and described examples of all the genera assigned to the Leptobunidae except for *Leptobunus* Banks, the type genus. Without knowing the true nature of *Leptobunus*, Roewer could not have arrived at a reasonable classification for the Leptobunidae. The lack of comparative material of *Leptobunus* spp. in European museums has also hindered the study of the family. Most classifications by European authors involving

the Leptobunidae have been based on the North African, southern European genus *Cosmobunus* Simon, which is not closely related to *Leptobunus*. To clear the confusion regarding this family, I examined examples of all nominal species ever referred to the Leptobunidae, and this is one of a series of papers dealing with those genera. In the present contribution *Leptobunus*, the type genus, is revised. Furthermore, the polyphyletic Leptobunidae is dismantled and placed in synonymy of the Phalangiidae.

MATERIALS AND METHODS

All anatomical measurements are in millimeters and were obtained using a binocular dissecting microscope equipped with an ocular micrometer (Cokendolpher, 1981a). Descriptions are based on all available specimens, but measurements were taken only on a maximum of 10 specimens per sex. Measurements are reported as ranges when more than one specimen was available. No measurements were taken of the relatively unsclerotized genital operculum. The chelicera, palpus, and penis were removed from the body and immersed in 100% glycerol for study, and then placed in microvials within the specimen vials. A tuft of cotton placed in the glycerol was used to support the structure when lateral views were desired. The female genitalia were first dehydrated with absolute ethyl alcohol and then examined in 100% clove oil. Ovipositors were soaked in absolute ethyl alcohol (to remove all traces of clove oil) prior to rehydration and placement in microvials. All illustrations were prepared with the aid of a camera lucida. The morphological terminology and description format essentially follows Cokendolpher (1981b).

The following terminology relating to the anatomy of the genitalia is being adopted.

Penis. In situ, the penis lies in a dorsoventral plane, thus the orientation of the truncus corresponds to that of the abdomen. As the penis truncus is attached to the gonads and related structures on the end opposite the glans, this attachment region becomes the basal or proximal portion of the truncus, and the basal portion of the glans is attached to the truncus. As the glans is not rigidly fixed to the truncus, it can be bent at any angle from 0° to about 160° to the plane of the truncus. This lack of rigidity results in the need to define the glans orientation surfaces. As the glans generally is at or near 135° to the truncus in preserved material, the glans surface that is more anterior (distal) is hereby considered the dorsal surface. The dorsal surface of the glans is generally straight, whereas the ventral surface is rounded. The paired primary setae are located laterad or laterally on the glans. The stylus, like the glans, is not rigidly attached (see Figs. 8, 9), but as no structures of taxonomic importance have been discovered on the stylus, the use of basal, or proximal, and distal (tip) will suffice.

Ovipositor. In situ, the ovipositor lies in a dorsoventral plane, and its orientation follows that of the abdomen. The distal end of the ovipositor consists of a three segmented furca. In the present descriptions, the furcal joints are numbered from the basal attachment, the distal joint being the 3rd. The setae bearing lobes on the 3rd furcal joint are the apical sensilla. The slit sensilla are located distally on the dorso- and ventromedial surfaces of the 2nd furcal joint. When specific sensilla numbers (#) are reported, they are given in the following formula: dorsal left # – dorsal right #/ventral left # – ventral right #. The 1st furcal joint lacks sensilla. The

ovipositor segments or rings are numbered from the distal end. The seminal receptacles are located within the 2nd and 5th ovipositor rings, with the basal portions generally located within the 2nd or 3rd ring, and the receptacles extend to about the 4th or 5th ring. Thus, the distal and proximal portions of the ovipositors and seminal receptacles are opposite. Each seminal receptacle consists of a large distal loop (=primary loop) and one to many basal loops or coils on the basilateral margin; the basal loops or coils are actually the extreme basilateral portion of the primary loop. The basimesal margin often has a small tube in which the termination is indistinct. This small tube is used as a marker for the region in which the basal loops should occur when the loops are less convoluted (see Figs. 31–33).

ACRONYMS FOR COLLECTIONS, LOCATIONS, AND CURATORS

AMNH	American Museum of Natural History, New York, N. I. Platnick
ARM	A. R. Moldenke, Corvallis
BMM	Thomas Burke Memorial Washington State Museum, Seattle, R. L. Crawford
BMNH	British Museum (Natural History), London, F. R. Wanless and P. D. Hillyard
CAS	California Academy of Sciences, San Francisco, D. H. Kavanaugh, W. J. Pulawski, and V. F. Lee
CNC	Canadian National Collections of Insects, Arachnids and Nematodes, Ottawa, C. D. Dondale and J. H. Redner
EP	Exline-Peck Collection, Warrensburg, W. B. Peck
JCC	J. C. Cokendolpher, Lubbock
LACM	Los Angeles County Museum of Natural History, Los Angeles, C. L. Hogue
MCZ	Museum of Comparative Zoology, Cambridge, H. W. Levi and J. M. Hunter
NHR	Naturhistoriska Riksmuseet, Stockholm, T. Kronstedt
NMB	Naturhistorisches Museum, Basel, E. Sutter
OSU	Oregon State University, Systematic Entomology Laboratory, B. B. Frost and G. M. Stonedahl
PDB	P. D. Bragg, Vancouver
RGH	R. G. Holmberg, Edmonton
ROM	Royal Ontario Museum, Toronto, D. Barr
SMF	Senckenberg Natur-Museum und Forschungsinstitut, Frankfurt, M. Grasshoff
UCB	University of California Berkeley, Essig Museum, Berkeley, C. E. Griswold
UCR	University of California Riverside Entomological Teaching and Research Collection, Riverside, S. E. Frommer
USNM	National Museum of Natural History (U.S. National Museum), Washington, R. E. Crabill, Jr.
ZIZM	Zoologisches Institut und Zoologisches Museum, Hamburg, G. Rack

SYSTEMATICS
PHALANGIIDAE SIMON
PHALANGIINAE SIMON

Leptobunus Banks

Liobunum: Banks, 1894a:160 (in part).

Leptobunus Banks, 1893:209 (in part), 1894a:163, 1894b:40 (misidentification), 1894c:146 (misidentification), 1898:182 (misidentification), 1899:350, 1900a:199, 1900b:484, 1901:674, 1904:362, 1911:420, 1923:238; Simon, 1902:45; Cockerell, 1907a:605 (in part), 1907b:620 (misidentification); Roewer, 1910:270, 1923:877, 1952:268, 1957:355 (misidentification); Kishida, 1930:55; Redikorzev, 1936:33; Comstock, 1940:71; Goodnight and Goodnight, 1942b:13 (in part); Staręga, 1965:5 (misidentification), 1978:209; Šilhavý, 1976:296 (misidentification); Cokendolpher, 1980:134, 1981b:309; Cokendolpher and Cokendolpher, 1982:1216.

Leptobrunus: Myers, 1921:19 (*lapsus calami*).

Leuronychus: Banks, 1901:675 (in part), 1911:420 (in part); Roewer, 1910:271 (in part), 1923:878 (in part), 1957:356 (in part); Comstock, 1940:73 (in part); Holmberg et al., 1981:19 (in part).

Liomitopus Schenkel, 1951:49; Forcart, 1961:53.

Type species. *Leptobunus californicus* Banks, by original designation.

Diagnosis and comparisons. *Leptobunus* is similar to *Mitopus* Thorell, *Tchapinius* Roewer, and *Liopilio* Schenkel. These four genera differ from other phalangiid genera by lacking large spines or tubercles on the preocular area and the ventral surfaces of the palpal femora, by having the supracheliceral lamellae short and smooth, palpi without apophyses (juveniles included), and generally by having a tooth on the basal segment of the chelicerae. *Leptobunus* and *Liopilio* differ from *Mitopus* and *Tchapinius* by having the palpal claws denticulate, penis glans convex beneath, glans primary setae very large and often bifurcate, and by lacking strong spines or tubercles anywhere on the body (except occasionally on appendages). *Leptobunus* differs from *Liopilio* by having the palpal tarsi of males globular proximally and devoid of denticles ventrally. The palpal femora and patellae of *Liopilio* are expanded distally and densely covered with setae medially. The paired primary setae of the penis glans are located near the stylus junction in *Liopilio*, whereas in *Leptobunus* they are centrally located. The stylus-glans junction membrane is dorsally expanded in *Liopilio*, ventrally expanded in *Leptobunus*. The 2nd furcal joint of the ovipositor of *Liopilio* has one or two slit sensilla per side, whereas *Leptobunus* has one to six (rarely one) sensilla per side.

Description. Medium to small sized phalangiids with soft smooth bodies (Figs. 1–5); dorsum and venter with only scattered setae; last abdominal sternite indented. Ocular tubercle low, canaliculate, round to slightly wider than long, with scattered setae. Chelicerae not enlarged, with tooth on ventral surface of basal joint; moveable finger with or without apophysis (Figs. 40–50). Supracheliceral lamellae short and smooth. Scent gland pores visible from above, elongate. Palpi (Figs. 36–39) covered only with setae, except for one or two tubercles on distodorsal surface of female femora; distomesal margins of femora and patellae not expanded (not even in juveniles); distal ends of femora with lyriform organs on dorsolateral margins, dorsomedial campaniform sensilla lacking; male tibiae and tarsi modified, proximal

portion of tibiae extended on mesal margin, proximal end of tarsi globular, expanded slightly on mesal margin, ventral rows of denticles lacking; claws with small pointed teeth at base. Legs relatively short; all articles round in cross-section. Penis truncus not grooved on distodorsal margin, glans round with large primary setae medially, stylus-glans junction membrane ventrally expanded (Figs. 6–21). Ovipositor often darkly pigmented with 19–35 rings plus 3 segmented furca; 1–6 slit sensilla per side on 2nd furca joint, seminal receptacles consisting of paired loops (Figs. 22–35).

INCLUDED SPECIES

Leptobunus consists of five species in two species groups. The *californicus* group contains *Leptobunus californicus* Banks, *Leptobunus borealis* Banks, and *Leptobunus pallidus*, new species. The *parvulus* group contains: *Leptobunus parvulus* (Banks), new combination, and *Leptobunus aureus*, new species.

Members of the *californicus* group can be easily recognized by the details of the genitalia and lack of a distinct apophysis on the moveable finger of the male chelicerae. The primary setae of the penis glans in members of the *californicus* group are often pointed or round and always much shorter in length than the stylus. *Californicus* group members have the primary loops of the seminal receptacles more than four times as long as wide. Members of the *parvulus* group often have tibiae IV with one or two pseudosegments. The male chelicerae in *parvulus* group members have a distinct apophysis on the moveable finger. The primary setae of the penis glans in members of the *parvulus* group are bilobed and equal to or slightly longer than the stylus. The primary loops of the seminal receptacles in members of the *parvulus* group are less than three times as long as wide.

EXCLUDED SPECIES

Amauropilio atavus (Cockerell)

Leptobunus atavus Cockerell, 1907a:605, fig. 2; 1907b:620.

Amauropilio atavus: Cokendolpher and Cokendolpher, 1982:1216–1217, fig. 1.

This species is known from one Tertiary fossil. The holotype female from the Florissant Formation, Teller Co., Colorado, U.S.A. (AMNH cat. no. FI-49 18834 Paleontology coll.) was not reexamined for the present study.

Mitopus koreanus (Roewer), **New Combination**

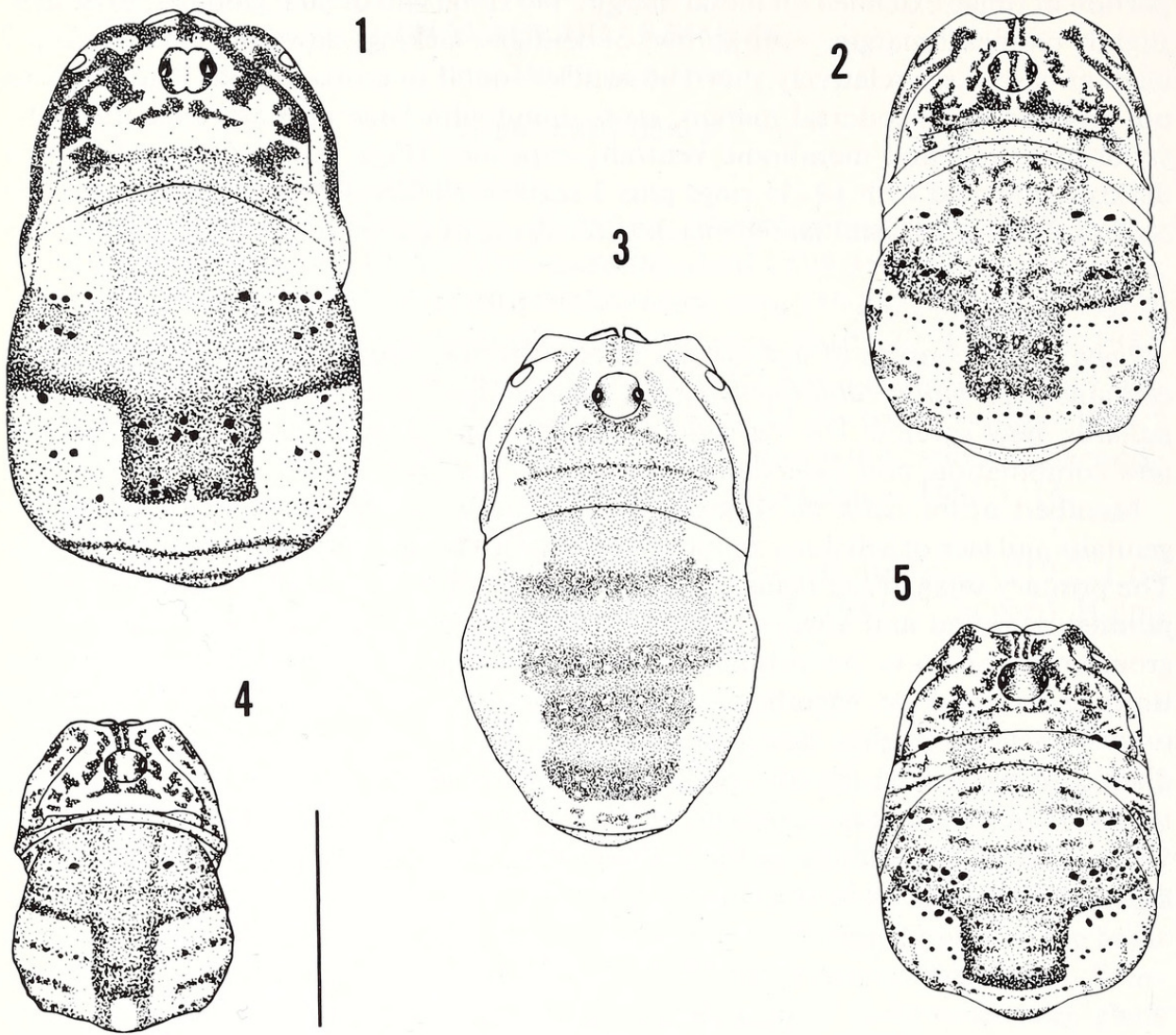
Leptobunus koreanus Roewer, 1957:355, pl. 26, fig. 23; Staręga, 1965:5; Šilhavý, 1976:296.

Female holotype from Korea (date, collector, and specific locality unknown), SMF cat. no. RII/3694/8, examined. This species conforms to *Mitopus* Thorell and is hereby transferred to that genus. A redescription is in preparation.

Paranelima mexicana (Goodnight and Goodnight), **New Combination**

Leptobunus mexicanus Goodnight and Goodnight, 1942b:13, fig. 31.

Female holotype from mountain meadow at Cerro Tancítaro, Michoacán, México,



Figs. 1–5. Dorsal views of *Leptobunus* spp. 1. *L. californicus* male. 2. *L. borealis* male. 3. *L. pallidus* female. 4. *L. aureus* male. 5. *L. parvulus* male. Scale line = 2.0 mm.

16 July 1941 (H. Hoogstraal), AMNH, examined. This species is related to other North American species of *Paranelima* di Caporiacco and Mexican species referred to *Nelima* Roewer. Until the mesoamerican species of these genera are revised, the affinities of *P. mexicana* will remain unresolved. Further material of both sexes of several species needs to be collected before such a revision can be realized.

Metopilio spinulatus (Banks), **New Combination**

Leptobunus spinulatus Banks, 1898:182; Pickard-Cambridge, 1905:585; Roewer, 1910:257.

Hadrobunus spinulatus: Roewer, 1923:920.

Diguetinus spinulatus: Goodnight and Goodnight, 1942b:11 (in part), 1945:13 (in part), 1947:45 (in part); Roewer, 1956:252 (misidentification).

Female holotype from Tepic, Nayarit, México (date and collector unknown), MCZ, examined. Comparisons of the holotype of *L. spinulatus* and paratypes of *Diguetinus*

raptator Roewer (2 males, 3 females, Guadalajara, Jalisco, México, SMF cat. no. RI/623) reveal they are not conspecific with one another as Goodnight and Goodnight (1942b) had indicated. *Leptobunus spinulatus* is properly a member of *Metopilio* Roewer. *Metopilio* and *Diguetinus* Roewer are quite similar, but are currently considered separate genera (Cokendolpher, 1984a).

KEY TO THE SPECIES OF THE GENUS *Leptobunus*

- 1a. Male chelicera with distinct apophysis on moveable finger (Figs. 46–50); stylus of penis equal to or shorter than primary setae of glans (Figs. 16, 18); primary loop of seminal receptacle short, less than three times as long as wide (Figs. 31–34) (*parvulus* group) 2
- 1b. Chelicera without apophysis on moveable finger (Figs. 40–45); stylus of penis much longer than primary setae of glans (Figs. 8, 12); primary loop of seminal receptacle long, more than four times as long as wide (Figs. 23, 29) (*californicus* group) 3
- 2a. Body color golden, legs speckled; primary setae of glans separated more than the length of the stylus (Fig. 16) *L. aureus*, new species
- 2b. Body color brown, gray or bronze, legs banded; primary setae of glans closely spaced (Fig. 18) *L. parvulus* (Banks)
- 3a. Tibiae II with 1–4 pseudosegments; male palpal tibiae expanded on ventral and mesal surfaces (Figs. 57–60); dorsum of abdomen with a well defined pattern (Figs. 1, 2) ... 4
- 3b. Tibiae II without pseudosegments; male palpal tibiae not expanded or enlarged (Figs. 51, 52); dorsum with faint pattern at most (Fig. 3) *L. pallidus*, new species
- 4a. Male palpal tibiae and tarsi noticeably expanded on mesal margins (Figs. 59, 60); dorsum of penis glans slightly depressed (Figs. 8, 9); basal loops of seminal receptacles consisting of three coils or loops (Figs. 23, 24) *L. californicus* Banks
- 4b. Male palpal tibiae and tarsi only slightly expanded (Figs. 57, 58); dorsum of penis glans straight (Fig. 12); basal loops of seminal receptacles consisting of two coils or loops (Figs. 26, 27) *L. borealis* Banks

Distribution. Aleutian and Bering Sea Islands, southern Alaska, and south along coastal states to central California and western Nevada in western North America.

Leptobunus californicus Banks

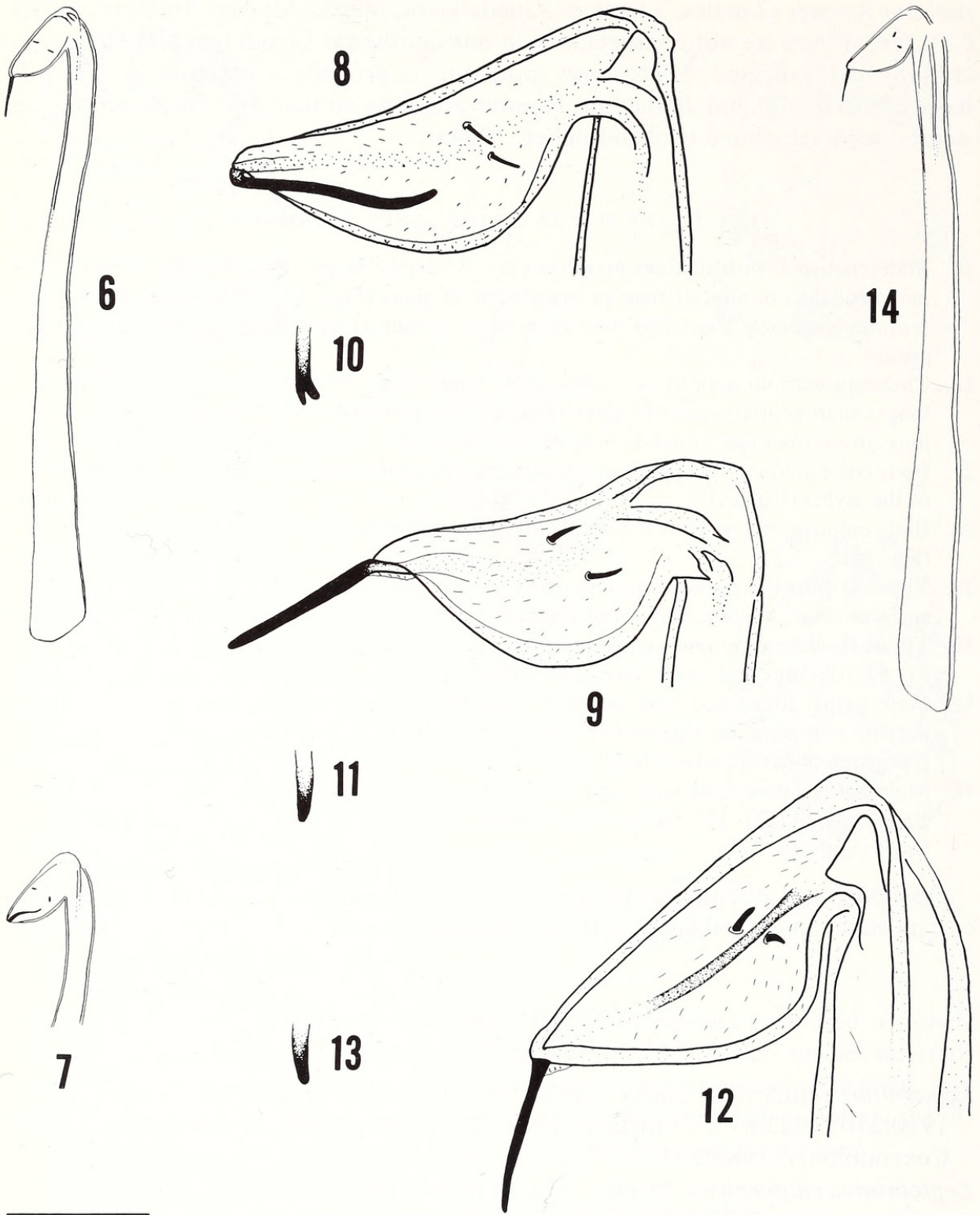
Figs. 1, 6–10, 22–24, 36–41, 59, 60, 63

Leptobunus californicus Banks, 1893:210, 1901:674, 1904:362, 1911:420; Roewer, 1910:270, 1923:877; Comstock, 1940:72; Goodnight and Goodnight, 1942b:14; Cokendolpher, 1980:134.

Leptobrunus californicus: Myers, 1921:19 (*lapsus calami*).

Liomitopus laevis Schenkel, 1951:49, fig. 47; Forcart, 1961:53.

Types. Female holotype of *Leptobunus californicus* in Nathan Banks Coll., MCZ, examined. Banks (1893) stated that the specimen was collected by Davidson in southern California and later (1904) stated that Davidson collected the specimen but restricted the locality to Los Angeles. As no further material of this species has been collected in southern California, and because the type vial is simply labeled "Cal.," I believe the type locality was erroneously designated and restricted. As *Liomitopus laevis* is the only synonym, I choose its type locality as that of *L. californicus*. Male



Figs. 6-14. Male genitalia of *Leptobunus* spp. 6-11. *L. californicus*. 6. Lateral view penis. 7-9. Distal ends of penes, lateral views. 10, 11. Glans setae. 12-14. *L. borealis*. 12. Distal end of penis, lateral view. 13. Glans seta. 14. Lateral view penis. Scale line = 0.50 mm for Figs. 6, 7, 14; 0.12 mm for Figs. 8, 9, 12; 0.03 mm for Figs. 10, 11, 13.

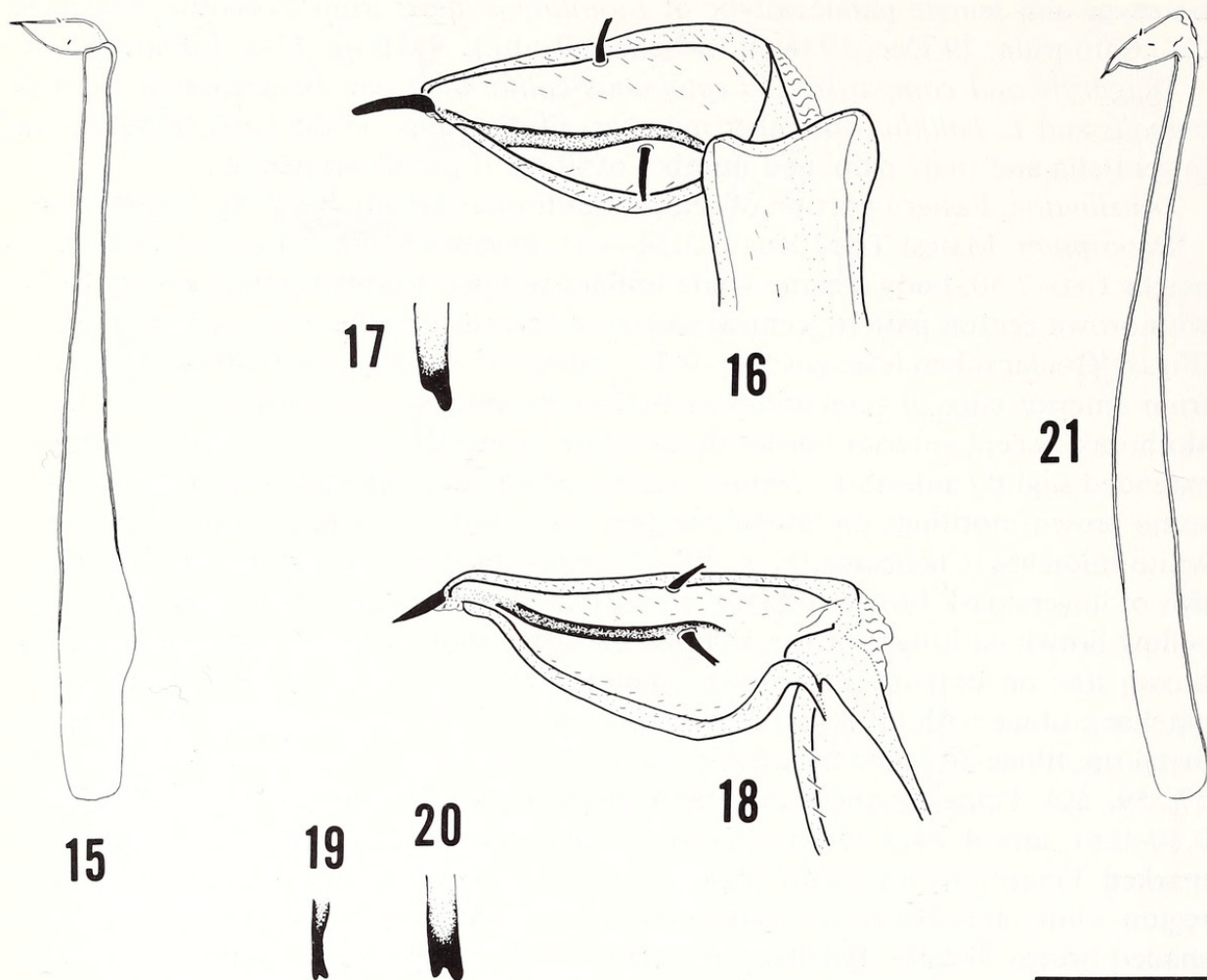
lectotype and female paralectotype of *Liomitopus laevis* from Yosemite, Mariposa Co., California, 29 Dec. 1938 (H. Schenkel-Rudin), NMB no. 81-a, examined.

Diagnosis and comparisons. *Leptobunus californicus* can be separated from *L. borealis* and *L. pallidus*, the other members of its group, on the basis of differences in genitalia and male palpi and number of tibiae II pseudosegments.

Distribution. Eastern portion of central California and adjoining Nevada (Fig. 63).

Description. Males: Total length 3.34–5.41, greatest width 2.75–3.82, maximum height 1.80–2.50; body creamy white to light yellowish-brown (rarely silvery white) with brown central pattern; central pattern with considerable spotting and splotches (Fig. 1). Ocular tubercle length 0.43–0.51, width 0.46–0.55, height 0.20–0.24, distance from anterior edge of cephalothorax 0.32–0.40; concolorous with dorsum of cephalothorax, except anterior border shaded dark brown; black ring encircling eyes, ring extended slightly anteriorly. Venter creamy white, always lighter than dorsum; with some brown mottlings on lateral margins posteriorly; anal operculum brown with white splotches. Chelicerae (Figs. 40, 41) yellow brown with no marking, teeth and tips of fingers dark brown to black; moveable fingers lacking apophyses. Palpi light yellow brown with light brown shading on distal ends of femora; faint longitudinal brown line on dorsum and brown splotches (often lacking on lateral surfaces of patellae); tibiae with (at most) a dark spot on dorsoproximal tip; tarsi darkened on distal tip; tibiae and tarsi noticeably enlarged ventrally and ventromesally (Figs. 36, 37, 59, 60). Palpal segment lengths: femora 0.96–1.22, patellae 0.48–0.65, tibiae 0.70–0.81, tarsi 1.24–1.35. Legs yellowish-brown to creamy light brown. Coxae unmarked. Femora with extreme basal end, dorsal and lateral distal tips, and subdistal region white; area between subdistal and distal white regions dark brown; basal $\frac{3}{4}$ shaded brown distally. Patellae subdistally shaded dark brown, extreme distal end white, basal end yellowish-brown. Tibiae I, III, IV with subbasal and subdistal dark brown bands; II with subdistal dark brown band and brown shading on proximal sides of pseudosegment junctions. Tarsi shaded brown at pseudosegment junctions. Metatarsi I with single pseudosegment; tibiae II with 2–3 (commonly 3) pseudosegments; tibiae IV lacking pseudosegments. Femora I–IV lengths (respectively): 3.77–4.06, 7.90–8.20, 4.30–4.46, 5.64–6.20; tibiae I–IV lengths (respectively): 3.27–3.52, 6.03–6.41, 3.40–3.50, 4.09–4.70. Penis (Figs. 6–11) with glans slightly concave dorsally; glans primary setae simple or bifurcate, spaced approximately one setal length apart or slightly more, setae much shorter than stylus length.

Females: Total length 5.31–7.31, greatest width 3.50–4.53, maximum height 2.00–4.18; generally larger and more robust than males, with more distinct and darker color patterns, except basal bands on leg femora and basal bands on tibiae II absent or greatly reduced. Leg coxae often with mottlings, lacking distal band; palpal tibiae rarely with brown line (faint when present). Ocular tubercle length 0.38–0.50, width 0.45–0.60, height 0.18–0.26, distance from anterior edge of cephalothorax 0.30–0.42. Palpal segment lengths: femora 0.90–1.02, patellae 0.51–0.65, tibiae 0.69–0.84, tarsi 1.21–1.50. Metatarsi I with 0–2 (rarely 0) and tibiae II with 2–4 (averaging 3) pseudosegments, tibiae IV lacking pseudosegments. Femora I–IV lengths (respectively): 2.72–4.19, 6.60–8.50, 3.00–4.53, 4.53–6.67; tibiae I–IV lengths (respectively): 2.45–3.48, 4.65–6.80, 2.49–4.51, 3.19–4.42. Ovipositor (Fig. 22) with considerable variation in ring segment counts: the five examined with 19, 23, 30, 32, and 35 rings



Figs. 15–21. Male genitalia of *Leptobunus* spp. 15–17. *L. aureus*. 15. Lateral view of penis. 16. Distal end of penis, lateral view. 17. Glans seta. 18–21. *L. parvulus*. 18. Distal end of penis, lateral view. 19, 20. Glans setae. 21. Lateral view penis. Scale line = 0.50 mm for Figs. 15, 21; 0.12 mm for Figs. 16, 18; 0.03 mm for Figs. 17, 19, 20.

each; furca 3 segmented (one female from Norden, California, with 4 segmented furca; distal two joints normal, first joint split in two on both sides). Slit sensilla generally 2–2 (range 1–2 to 4–4) per side on furca segment II. Seminal receptacles with long, often convoluted, primary loops and three basal loops (Figs. 23, 24).

Immatures: As adult females, except leg femora II and IV lacking proximal brown bands; palpi often white to light yellowish-brown, generally without markings.

Natural history. Adults are known from late June to late September, and a single collection on 29 December. The majority of collections are from August. Juveniles (later instars) are known from late June to late September. Several of the females collected during August are filled with eggs. A dozen eggs from two different individuals average 0.54 mm in size (range 0.40–0.68 mm). Specimens have been collected at altitudes from 1,850 to 3,350 m, almost all from 2,350–2,450 and 2,900–3,100 m. In general, the more northern localities are at lower elevations. The few collections that were labeled as to habitat indicated that adults and immatures were beneath rocks, from crevices in large granite rocks, and were on snow at night (during

June). This species appears to be restricted to the Sierra District (Schick, 1965) of the Sierra Nevadan Biotic Province.

Specimens examined. U.S.A. CALIFORNIA: *Placer Co.*, Norden, 5 Aug. 1951 (J. F. Gustafson), 3 females (AMNH); *Tuolumne Co.*, Sonora Pass, 26 Aug. 1965 (V. Lee), 2 immatures (CAS), Sonora Pass Summit, 26 Aug. 1965 (V. Lee), 1 female (CAS), 4.8 km W Sonora Pass, 14–16 Aug. 1966 (R. R. Snelling), 1 immature (LACM), Tioga Pass, Yosemite Park, 8–10–1931 (W. Ivie), 3 females (AMNH); *Madera Co.*, Lake Ediza, 2 Aug. 1951 (P. Raven), 1 female (CAS); *Inyo Co.*, South Lake, Bishop Creek, 17 Aug. 1941 (W. M. Pearce), 3 females (AMNH), Mirror Lake, 14 Aug. 1953 (W. McDonald), 1 female (AMNH); *Mono Co.*, E slope White Mountain, 27 June 1979 (D. H. Kavanaugh), 1 female, 3 immatures (CAS), E shore Silver Lake, 8 Aug. 1957 (R. Casebeer), 1 female (LACM), Sawmill Campground, 6.5 km N of Tioga Pass, 30 July 1980 (C. Griswold), 1 immature (UCB), Big Bend Campground, 8 km W Lee Vining, 21 Sept. 1961 (W. Ivie and W. J. Gertsch), 1 female (AMNH); *Wildyrie*, Mammoth Lakes, 18 Aug. 1941 (W. M. Pearce), 2 males, 2 females (UCR); *Mariposa Co.*, Yosemite, 29 Dec. 1938 (H. Schenkel-Rudin), lectotype male, paralectotype female (NMB), Yosemite Creek Camp, Yosemite Park, 18 Sept. 1941 (W. Ivie), 1 immature (AMNH); *Nevada Co.*, Sagehen Creek, 12.9 km N Truckee, 21 July 1966 (G. B. Wiggins), 1 female (ROM); *Alpine Co.*, Silver Creek, 14.5 km SW Markleeville, 26 July 1980 (T. C. Meikle and C. Griswold), 1 male, 2 females (UCB); *Fresno Co.*, Inyo National Forest, John Muir Wilderness, Cascade Valley, 7 Aug. 1972 (V. F. Lee), 1 male, 1 female (CAS); *Fresno Co.*, Graveyard Meadows, 12 Aug. 1959 (B. Firstman), 13 males, 3 females, 4 immatures (AMNH), Graveyard Lakes, 13 Aug. 1959 (B. Firstman), 1 male, 1 female, 2 immatures (AMNH), Anne Lake, 15 Aug. 1959 (B. Firstman), 1 female (AMNH), Olive Lake, 16 Aug. 1959 (B. Firstman), 3 females, 2 immatures (AMNH), locality uncertain—"Southern California," pre-1893 collection (Davidson), holotype female (MCZ). NEVADA: *Washoe Co.*, Mt. Rose, 2.4 km W Pass Summit, 27 Aug. 1969 (H. B. Leech), 3 males, 2 females (CAS).

Leptobunus borealis Banks

Figs. 2, 12–14, 25–27, 42, 43, 57, 58, 61

Leptobunus borealis Banks, 1899:350, pl. a, fig. 7, 1900b:484, 1901:674, 1911:420, 1923:238; Roewer, 1910:271, 1923:877, fig. 1,039; Redikorzev, 1936:33; Comstock, 1940:72; Staręga, 1978:209; Strand, 1906:473.

Types. Banks (1899) based his description on "several specimens" collected on Bering Island and Copper Island. In the description he attributes measurements to a male and female, but from his description of the palpi and his illustration there is no doubt he examined only females and immatures. Only a female and three immatures of the original type series are still available. This series collected on Bering Island, July–Aug. 1897, by Barrett-Hamilton is clearly labeled in Banks' handwriting "*Leptobunus borealis* Bks Type." The vial also contains a label "Type No. 4060 U.S.N.M." which corresponds to the data given by Banks. As no single specimen was designated as the holotype, I hereby designate the adult female as the lectotype and three immatures as paralectotypes.

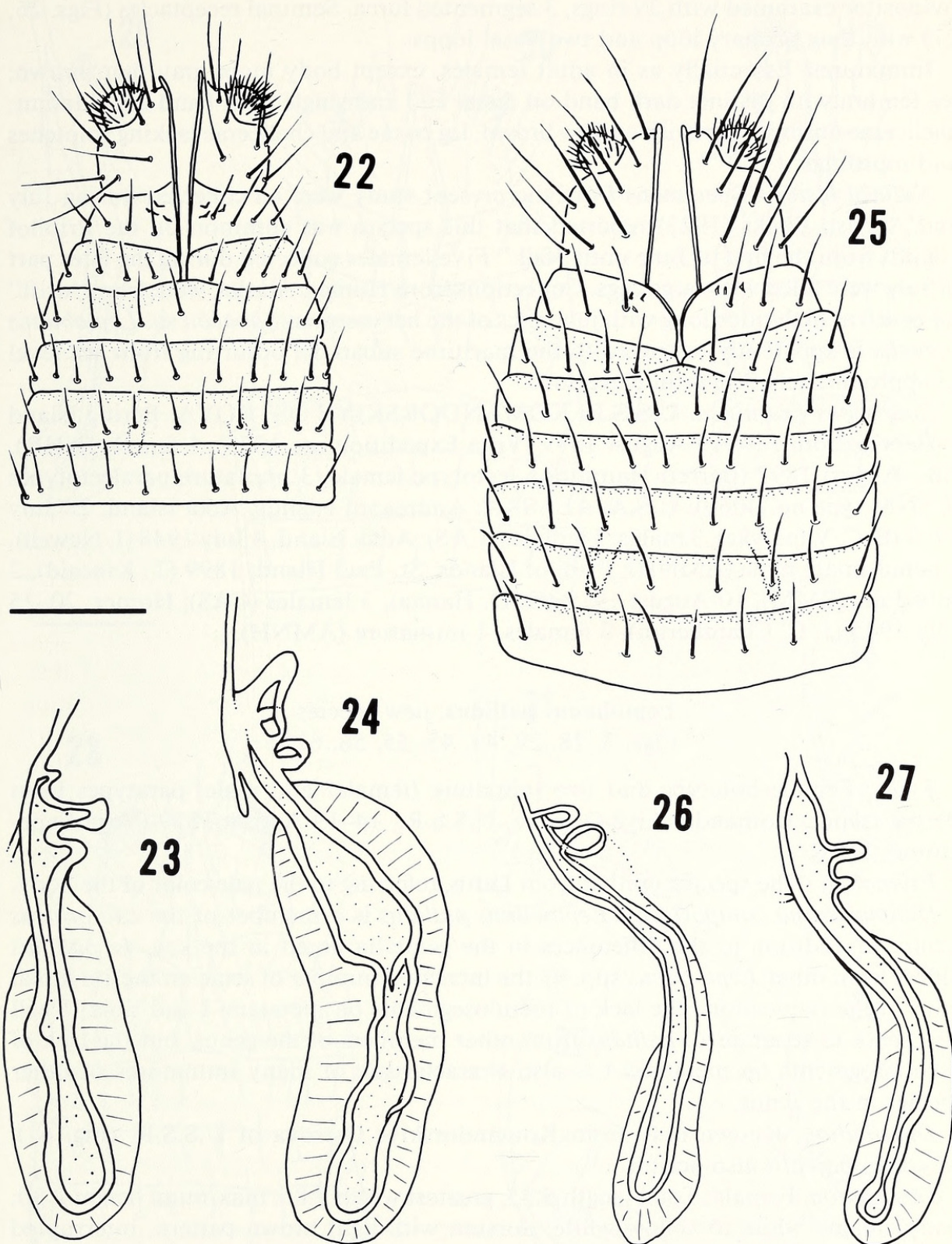
Diagnosis and comparisons. In addition to differences in the genitalia and male

palpi noted in the key, *L. borealis* can be distinguished from *L. californicus* by its shorter legs.

Distribution. Komandorskiye Ostrova of U.S.S.R., Aleutian Islands, Pribilof Islands and southern Alaska of U.S.A. (Fig. 61).

Description. Males: Total length 3.56–4.12, greatest width 2.89–3.50, maximum height 2.07–2.27; dorsum white to creamy white with extensive dark brown markings, those on cephalothorax appearing velvety; abdomen with pattern of cross with many white spots and splotches, area surrounding cross mottled with brown splotches and rows of brown dots (Fig. 2). Ocular tubercle length 0.35–0.40, width 0.37–0.42, height 0.18–0.19, distance from anterior edge of cephalothorax 0.30–0.31; brown with dark ring encircling eyes, paler half ring on areas dorsal to dark eye ring. Venter white to light tan, with two dark brown spots at base and posterior to base of genital operculum; row of brown spots on anterior areas of sternite junctions (less distinct on the most posterior sternites) and lateral margins of all sternites shaded brown (lighter in color than spots). Leg coxae yellowish-brown, mottled with brown, distally shaded to indistinct brown band. Chelicerae (Figs. 42, 43) with basal segment creamy yellowish-white; distal segment light yellow brown; both segments with light brown mottlings on lateral surfaces; teeth and tips of fingers black; moveable fingers lacking apophyses, rarely with slight “bump” (Fig. 43). Palpi yellow brown with darker brown markings on distodorsal surfaces of femora, lateral and mesal surfaces of patellae and tibiae, and semidistinct line down patellae and proximal $\frac{2}{3}$ to $\frac{3}{4}$ of tibiae dorsally; basal portion of tarsi enlarged (Figs. 57, 58). Palpal segment lengths: femora 0.90–0.94, patellae 0.56, tibiae 0.68–0.73, tarsi 1.18–1.23. Legs yellowish-brown to tan; femora with distal dark brown leg bands, extreme distal ends white dorsally on lateral regions, often with indistinct subdistal white band; patellae mottled with brown except for thin light line dorsally; all tibiae with brown bands (often indistinct) distally, I, III, IV with a second brown band on proximal $\frac{1}{3}$, extreme proximal end tan to yellowish-white; dorsa of tibiae I, III, IV (rarely II) with faint light brown lines; tarsi and metatarsi pseudosegment junctions shaded brown; metatarsi I and tibiae II both with single pseudosegments, tibiae IV lacking pseudosegments. Femora I–IV lengths (respectively): 2.63–2.67, 4.62–5.18, 2.94–3.10, 4.25–4.57; tibiae I–IV lengths (respectively): 2.30–2.42, 3.92–4.16, 2.42–2.48, 3.15–3.25. Penis with glans dorsum straight to slightly convex (Figs. 12–14); primary setae of glans simple, approximately one setal length apart; setae much shorter than stylus.

Females: Total length 5.27–6.02, greatest width 3.20–4.28, maximum height 2.60–3.27; similar to males except ocular tubercle lighter in color, creamy white; leg femora and tibiae have more brown splotches; leg coxae and trochanters of some females with considerable amount of brown splotches and mottlings. Ocular tubercle length 0.40–0.46, width 0.40–0.41, height 0.19–0.23, distance from anterior edge of cephalothorax 0.28–0.41. Palpal segment lengths: femora 0.82–1.00, patellae 0.51–0.60, tibiae 0.59–0.75, tarsi 1.11–1.28. Metatarsi I with single pseudosegment (one specimen had 2), tibiae II with one pseudosegment (rarely 2 or 3), tibiae IV lacking pseudosegments. Femora I–IV lengths (respectively): 1.92–2.48, 3.80–4.46, 2.30–2.80, 3.21–4.11; tibiae I–IV lengths (respectively): 1.90–2.33, 3.19–4.00, 1.98–2.54, 2.58–3.08. Ovipositor (Fig. 25) with considerable variation in furca II slit sensilla counts; range 2–6 per side, counts of 3–3/6–4 and 5–4/5–4 not uncommon; the single



Figs. 22–27. Female genitalia of *Leptobunus* spp. 22–24. *L. californicus*. 22. Distal end ovipositor. 23, 24. Seminal receptacles. 25–27. *L. borealis*. 25. Distal end of ovipositor. 26, 27. Seminal receptacles. Scale line = 0.22 mm for Figs. 22, 25; 0.05 mm for Figs. 23, 24, 26, 27.

ovipositor examined with 29 rings, 3 segmented furca. Seminal receptacles (Figs. 26, 27) with long primary loop and two basal loops.

Immatures: Essentially as in adult females, except body more gray than brown; leg femora with distinct dark band on distal end and single dark band at midpoint; chelicerae uniformly grayish-yellow brown; leg coxae and chelicerae lacking splotches and mottlings.

Natural history. Specimens from the present study were all collected during July and August. Banks (1923) reported that this species was common on the Pribilof Islands from the first of June until "fall." Five females collected during the later part of July were filled with large eggs. Collections from Homer, Alaska, were from "drift" on beach at high tide along with juveniles of the harvestman *Sabacon* sp. *Leptobunus borealis* is apparently restricted to the maritime subarctic, occurring from sea level to approximately 300 m in elevation.

Specimens examined. U.S.S.R. KOMANDORSKIYE OSTROVA: Bering Island (=Behrings oñ), 14–19 August 1879 (Vega Expedition no. 1079), 1 female (NHR), July–August 1897 (Barrett-Hamilton), lectotype female, 3 immature paralectotypes (USNM type no. 4060). U.S.A. ALASKA: Andreanof Islands, Atka Island, 28 July 1907 (E. C. VanDyke), 3 males, 5 females (CAS); Adak Island, 4 July 1948 (I. Newell), 1 penultimate male (AMNH); Pribilof Islands, St. Paul Island, 1899 (T. Kincaid), 2 subadults (BMM), 10 August 1919 (G. D. Hanna), 3 females (CAS); Homer, 20–25 July 1945 (J. C. Chamberlin), 3 females, 1 immature (AMNH).

***Leptobunus pallidus*, new species**

Figs. 3, 28, 29, 44, 45, 55, 56, 61

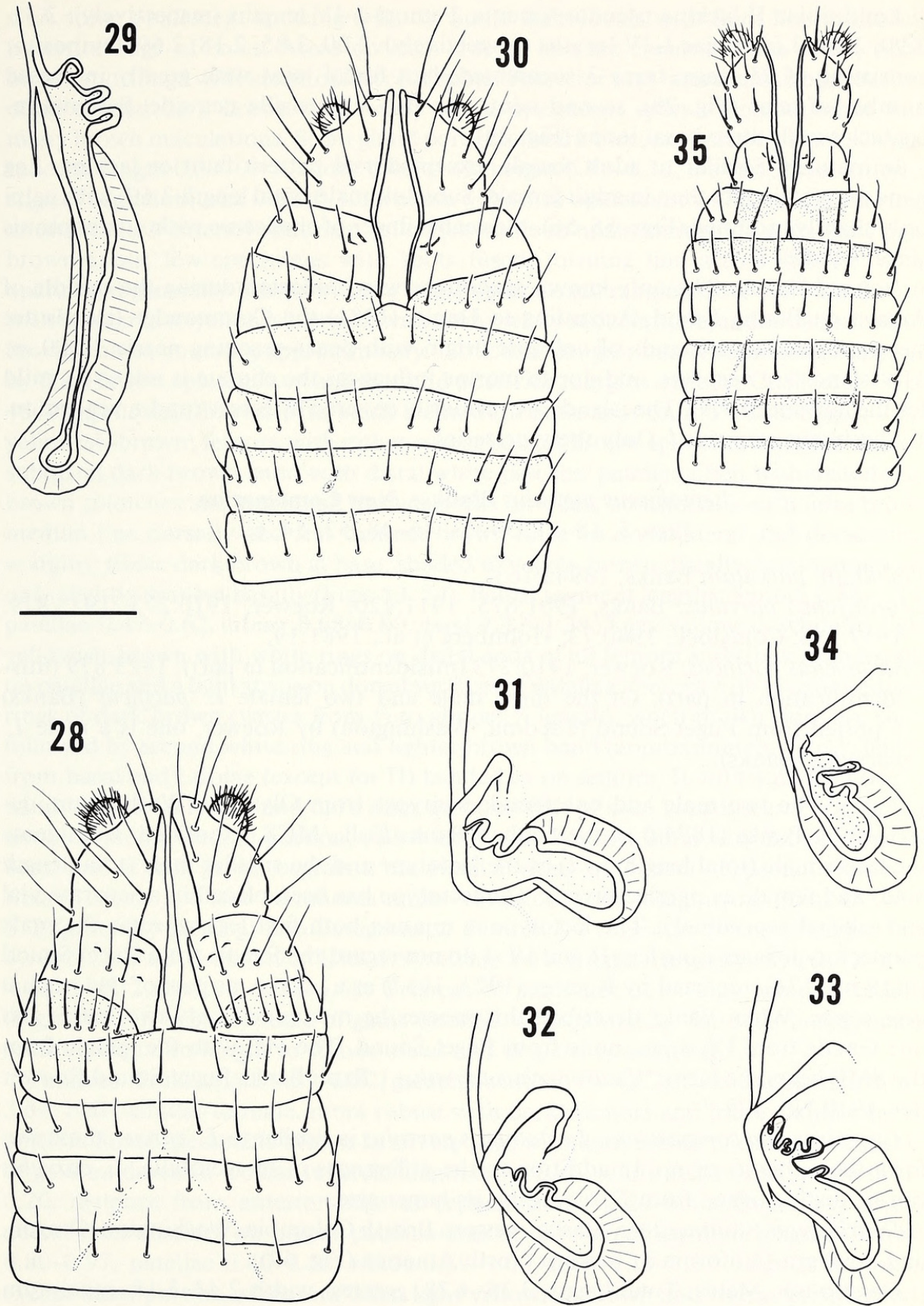
Types. Female holotype and two immature (female? and male) paratypes from Bering Island, Komandorskiye Ostrova, U.S.S.R., 14–19 August 1879 (Vega Expedition), NHR.

Etymology. The specific epithet from Latin, referring to the pale color of the body.

Diagnosis and comparisons. *Leptobunus pallidus* is a member of the *californicus* group. In addition to the differences in the genitalia noted in the key, *L. pallidus* differs from other *Leptobunus* spp. by the increased number of setae on the 1st furcal joint of the ovipositor. The lack of pseudosegments on metatarsi I and tibia II will also serve to separate *L. pallidus* from other members of the genus, but the lack of pseudosegments on metatarsi I is also characteristic of many immatures of other species in the genus.

Distribution. Known only from Komandorskiye Ostrova of U.S.S.R. (Fig. 61), where *L. borealis* also occurs.

Description. Female: Total length 5.35, greatest width 2.86, maximum height 2.90; body creamy white to yellow white; dorsum with light brown pattern, interrupted with scattered white spots (Fig. 3). Ocular tubercle length 0.40, width 0.45, height 0.15, distance from anterior edge of cephalothorax 1.27; white with light brown rings around eyes. Coxae, genital operculum, and abdominal sternites creamy white. Chelicerae light yellow brown with dark brown teeth. Palpi whitish-yellow to light yellow brown, without markings. Palpal segment lengths: femur 0.80, patella 0.51, tibia 0.69, tarsus 1.26. Legs whitish-yellow to light yellow brown with faint bands of brown on distal ends of femora, dorsum of patellae, and subdistal portions of tibiae; metatar-



Figs. 28–35. Female genitalia of *Leptobunus* spp. 28, 29. *L. pallidus*. 28. Distal end of ovipositor. 29. Seminal receptacle. 30–33. *L. parvulus*. 30. Distal end of ovipositor. 31–33. Seminal receptacles. 34, 35. *L. aureus*. 34. Distal end of ovipositor. 35. Seminal receptacle. Scale line = 0.22 mm for Figs. 28, 30, 35; 0.05 mm for Figs. 29, 31–34.

si I and tibiae II lacking pseudosegments. Femora I–IV lengths (respectively): 2.31, 3.90, 2.51, 3.69; tibiae I–IV lengths (respectively): 2.00, 3.85, 2.18, 2.69. Ovipositor consisting of 25 rings; furca 3 segmented, first furcal joint with greatly increased number of setae (Fig. 28), second joint with 3–5 slit sensilla per side. Seminal receptacles with three basal loops (Fig. 29).

Immatures: Similar to adult female, except dorsal pattern faint or lacking. Leg bands more distinct than in adult female. Subadult male (total length 3.60) with palpi only slightly modified (Figs. 55, 56). Moveable finger of chelicerae without apophysis (Figs. 44, 45).

Natural history. The only known specimens were collected during the middle of August on Bering Island. According to Danks (1981) the Commander Islands are steep mountainous islands of volcanic origin with peaks reaching nearly 1,000 m. The islands are very wet, and due to marine influences the climate is relatively mild for the latitude (55°N). The islands are primarily covered by forest-tundra vegetation.

Specimens examined. Only the type series.

Leptobunus parvulus (Banks), **New Combination**

Figs. 5, 18–21, 30–33, 46–48, 53, 54, 62

Liobunum parvulum Banks, 1894a:163.

Leuronychus parvulus: Banks, 1901:675, 1911:420; Roewer, 1910:273, 1923:879, 1957:356; Comstock, 1940:73; Holmberg et al., 1981:19.

Leuronychus pacificus: Roewer, 1910:273 (misidentification in part), 1923:879 (misidentification in part). Of the three male and two female *L. pacificus* (Banks) reported from Puget Sound (Tacoma, Washington) by Roewer, one is a male *L. parvulus* (Banks).

Types. The two male and one female syntypes from Olympia, Washington, described by Banks (1894a) in the Nathan Banks Coll., MCZ, examined. I designate the larger male (total length 3.72) as the lectotype and the smaller male (total length 3.45) and female as paralectotypes. The lectotype has been placed in a separate vial and labeled accordingly. The lectotype is missing both first legs whereas the male paralectotype is missing legs II and IV. I do not regard the female from Puget Sound (SMF no. 174), reported by Roewer (1923, 1957) as a cotype, as part of the original type series. When Banks described this species he mentioned only two males and one female from Olympia, none from Puget Sound. The vial with the female from the SMF bears the label: "*Leuronychus parvulus* 1 Expl. Banks Puget Sound Roewer det. 1910 No. 174."

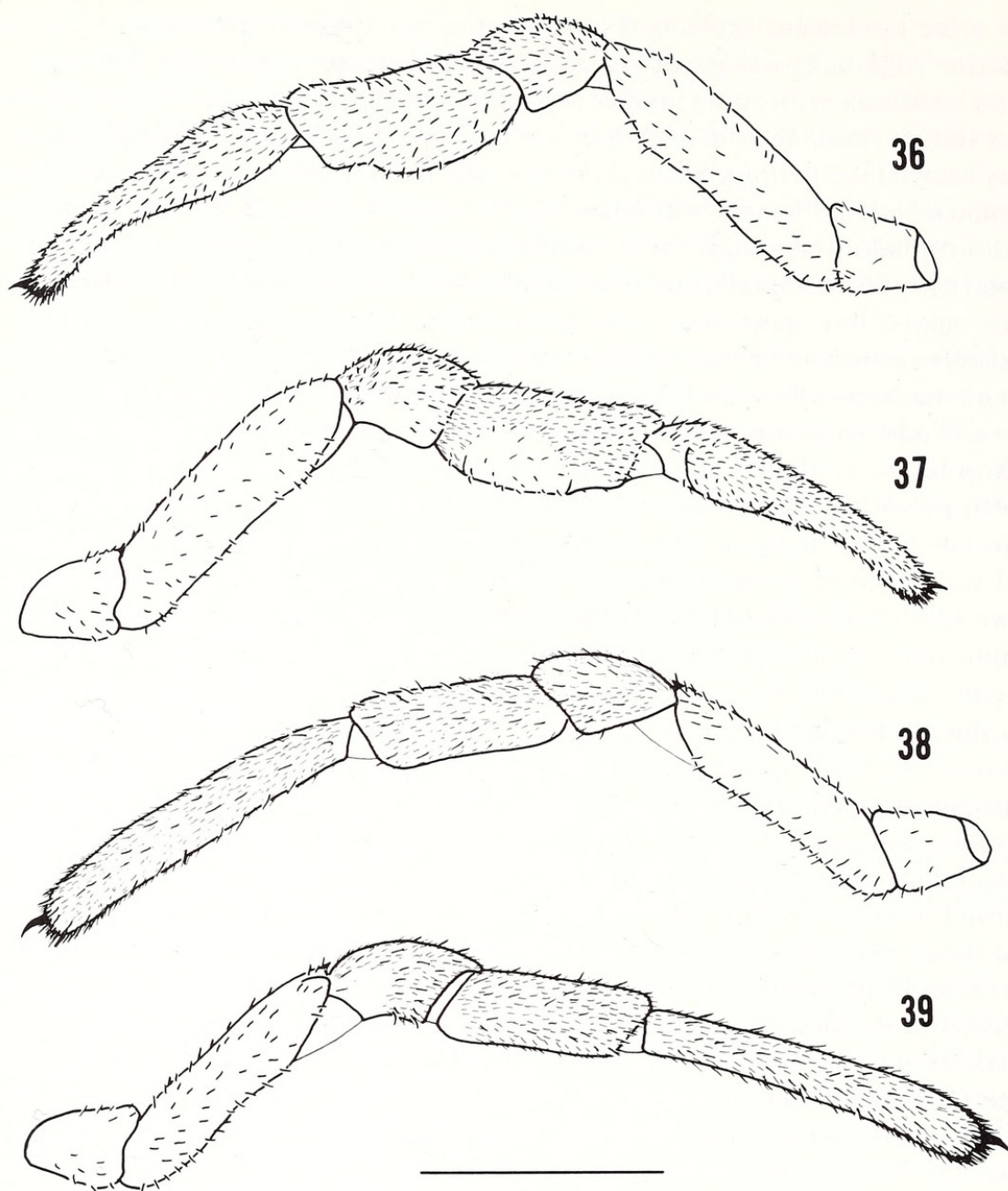
Diagnosis and comparisons. *Leptobunus parvulus* is similar to *L. aureus*; these two form the *parvulus* group. In addition to the differences in the genitalia, *L. parvulus* can be distinguished from *L. aureus* by its larger size.

Distribution. Southeastern Alaska, western British Columbia, Washington, Oregon, and northern California in western North America (Fig. 62).

Description. Males: Total length 3.35–4.78, greatest width 2.43–3.18, maximum height 1.85–2.60; body generally whitish-yellow, but ranges from golden tan to opalescent white; often with many tiny white specks and larger white splotches. Abdomen with faint cross pattern of brown spots and splotches; pattern most distinct posteriorly

with some opalescent spotting (Fig. 5). Some individuals with faint line indicating posterior edge of cross. Areas on each side of line are essentially the same, small brown mottlings with some opalescent spots. Posterior and lateral areas of abdomen often shaded dark brown with many white opalescent spots. Cephalothorax with many brown maculations. Scent gland pore often dark blue, encircled by black. Ocular tubercle length 0.37–0.41, width 0.40–0.43, height 0.13–0.22, distance from anterior edge of cephalothorax 0.22–0.32; whitish-yellow to opalescent white with black rings around eyes. Venter of abdomen yellowish-white to opalescent white with some light brown spots; few specimens with spots fused, forming line across sternite. Anal operculum generally brown without white spot. Coxae ranging from yellowish-white with no marks to yellowish-brown with many white reticulations, and broad subdistal brown bands, covering approximately $\frac{1}{3}$ of coxae length; bands sometimes replaced by faint brown splotches on anterior and posterior margins distally. Chelicerae (Figs. 46–48) yellowish-brown with black teeth, noticeable spur on moveable finger. Palpi yellowish-brown; femora with either two subdistal brown splotches on sides or with subdistal dark brown band with distal white patches; patellae often with distodorsal brown splotches and two small brown specks on sides, occasionally with faint brown median line dorsally and less distinct brown lines on dorsolateral and dorsomesal margins; tibiae dark brown at base, shaded to yellow brown distally; tarsi unmarked, only slightly swollen basally (Figs. 53, 54). Palpal segment lengths: femora 0.88–1.16, patellae 0.47–0.62, tibiae 0.68–0.80, tarsi 1.13–1.39. Legs yellowish-white to light yellowish-brown with white rings on distal ends of all femora and tibiae, subdistally on patellae and a light stripe on dorsal surfaces of patellae; femora with broad subdistal rings of dark brown (varies from $\frac{1}{3}$ to almost $\frac{3}{4}$ length), when brown rings are short followed by second white ring and lighter brown band (approximately $\frac{1}{3}$ to $\frac{1}{2}$ length from basal end); tibiae (except for II) banded as on femora, II with subdistal brown band $\frac{1}{4}$ to $\frac{1}{5}$ its length and dark rings on basal half of each pseudosegment; patellae dark brown on median portion, yellowish-brown basally. Tarsi with brown rings on basal half of each pseudosegment; metatarsi I with 1 or 2 (rarely 2) pseudosegments, tibiae II with 2–6 (see comments under variation) pseudosegments, tibiae IV with 0–2 (generally lacking) pseudosegments. Femora I–IV lengths (respectively): 3.02–4.93, 5.78–9.88, 3.00–5.90, 4.36–8.30; tibiae I–IV lengths (respectively): 2.33–4.62, 4.63–6.80, 2.63–5.00, 3.18–6.62. Truncus of penis not noticeably enlarged basally (Figs. 18–21); primary setae of glans bilobed, approximately one setal length apart, setae subequal in length to stylus; distal end of glans constricted.

Females: Total length 4.59–6.82, greatest width 2.79–4.62, maximum height 2.50–3.84; body similar to male, more robust with darker colors and more distinct dorsal pattern. Some specimens bronze to silvery gold with dark brown patterns, and specks of gold on dorsum. Ocular tubercle length 0.40–0.46, width 0.39–0.50, height 0.11–0.20, distance from anterior edge of cephalothorax 0.24–0.40. Generally, brown dorsal lines distinct on palpal patellae and tibiae. Palpal segment lengths: femora 0.80–0.97, patellae 0.40–0.58, tibiae 0.59–1.00, tarsi 1.19–1.37. Legs as on males except basal portion of femora often light yellowish-brown and characteristic bands of males mottled with brown splotches; tarsi and metatarsi speckled with brown, often lacking bands. Metatarsi I with 1–3 (rarely lacking) pseudosegments, tibiae II with 3–7 (see comments under variation), tibiae IV without pseudosegments (rarely



Figs. 36–39. *Leptobunus californicus* palpi. 36. Male, lateral view. 37. Male, mesal view. 38. Female, lateral view. 39. Female, mesal view. Scale line = 1.0 mm.

one present). Femora I–IV lengths (respectively): 2.81–3.94, 6.18–9.40, 3.18–4.24, 4.89–6.80; tibiae I–IV lengths (respectively): 2.52–3.55, 5.20–6.42, 2.60–4.06, 3.68–4.64. Ovipositor with 24–30 darkly pigmented rings ($N = 3$); furca 3 segmented, 2nd joint with 1–4 (averaging 2, $N = 14$) slit sensilla per side (Fig. 30). Seminal receptacles (Figs. 31–33) with very short primary loop; basal loops very irregular (see comments under variation).

Immatures: Similar to adult females, except with body ranging from opalescent white with few marks to pale yellowish-white with dark brown patterns. The distinctive abdominal cross pattern is present on juveniles as small as 1.0 mm total length.

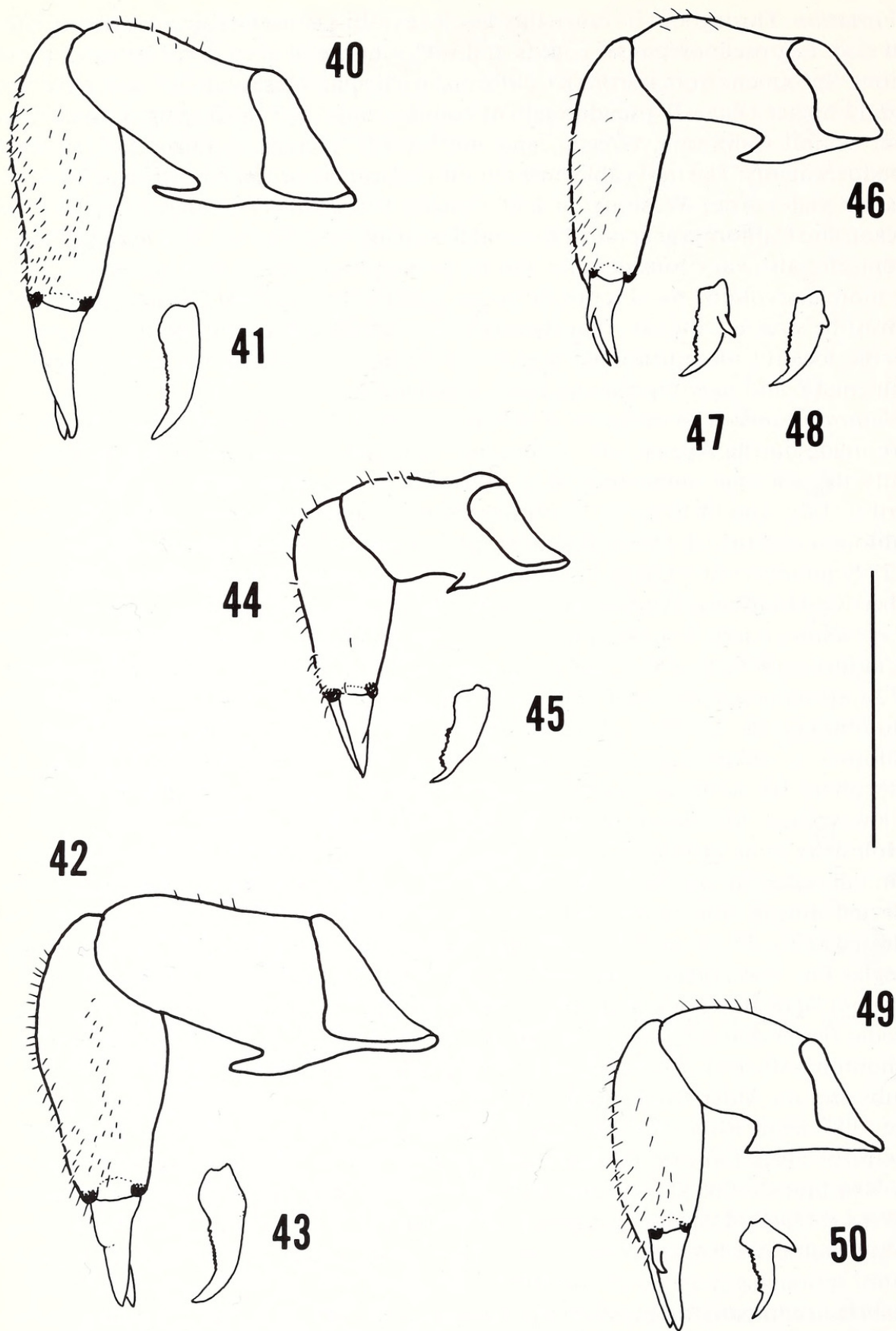
Variation. Throughout its range this species exhibits considerable variation in color and size. Leg pseudosegment counts and male chelicerae also differ between populations. Specimens from northern California, particularly Siskiyou Co., generally have slightly higher tibiae II pseudosegment counts: range 3–7, averaging 5. Specimens from central California, Oregon, and northwards average 3, range 2–5, tibiae II pseudosegments. The moveable finger of the chelicera is equipped with a large apophysis on males from Washington and Canada (Figs. 46–47), whereas males from Oregon and California generally have smaller apophyses (Fig. 48). The female seminal receptacles also vary considerably, but no geographical trends were noted except for the more convoluted basal loops on some females from central California (Fig. 33). It must be stressed, though, that these are only trends and cannot be relied upon for specific locality identifications. Specimens from Siskiyou County are particularly problematic and may represent a relict population.

Natural history. The majority of the collections of juveniles (all stages) and adults were made during August and September. Latitude does not seem to affect significantly the seasonal abundance of *L. parvulus*. A few collections are known from April to July, and October to December. Some females collected during September (California and British Columbia) were filled with eggs. A female collected and caged on 28 September (by PDB at Vancouver) laid 21 eggs (letter dated 8 June 1982 from Robert G. Holmberg, Athabasca University, Edmonton, Alberta).

Leptobunus parvulus appears to be restricted to the Sierra Nevadan Biotic Province of California (Schick, 1965) and the Vancouverian Province of Van Dyke (see Leech, 1972). Specimens have been collected from sea level (Alaska, Oregon, and British Columbia) to ca. 2,700 m elevation (central California). Throughout the range in California *L. parvulus* occurs under 2,700 m, Oregon under about 1,800 m, and under about 100 m further north. These are only general trends, though, as exceptions are known (i.e., Mt. Blunt, Alaska at 760–1,020 m).

Holmberg et al. (1981) reported that this species has been taken from the tops of 29 m tall cedar, fir, and hemlock trees. Those specimens were all juveniles and were collected during June, July, and August in British Columbia. The juveniles were collected at 20, 23, 26, and 29 m heights in Western Red Cedar (*Thuja plicata* Donn), Douglas Fir (*Pseudotsuga menziesii* (Mirb.) Franco), and Western Hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and additional juveniles were also obtained at 17 m height in cedar (letter dated 8 June 1982 from Robert G. Holmberg, Athabasca University, Edmonton, Alberta). This species is commonly encountered on low branches and shrubs and on Alder trunks in forests of southern British Columbia (letter dated 8 June 1982 from Robert G. Holmberg, Athabasca University, Edmonton, Alberta). Specimen labels indicate that adults and immatures were also collected from the leaves or branches of *Abies grandis* (Dougl.) Lindl., *Picea* sp., *Pinus contorta* Dougl., *Quercus garryana* Dougl., *Gaultheria shallon* Pursh, and *Vaccinium occidentale* Gray. Two immatures were also collected from the fern *Polystichum*, and one of these had mature sporangia attached to two different leg tarsi.

Labels accompanying museum specimens indicate this species is active at night and is attracted by UV light. Specimens from Haines, Alaska, were found under “drift” on beach, whereas specimens in the Trinity Alps, California, were at snowfield edges.



Figs. 40-50. *Leptobunus* spp. male chelicerae. 40, 42, 44, 46, 49. Mesal views. 41, 43, 45, 47, 48, 50. Anterior views of moveable fingers. 40, 41. *L. californicus*. 42, 43. *L. borealis*. 44, 45. *L. pallidus*, subadult. 46-48. *L. parvulus*. 49, 50. *L. aureus*. Scale line = 1.0 mm.

Specimens examined. U.S.A. ALASKA: Glacier Bay Natl. Mon., Lituya Bay, Mt. Blunt, 8–9 Aug. 1979 (D. H. Kavanaugh), 1 immature (CAS); Haines, 20–24 Aug. 1945 (J. C. Chamberlin), 8 males, 3 females, 34 immatures (AMNH). WASHINGTON: *Thurston Co.*, Olympia, pre-1894 collection (T. Kincaid), lectotype male, male and female paralectotypes (MCZ), Tacoma, Puget Sound, 9 Sept. 1906 (Kpt. R. Paessler), 1 male (ZIZM); *Jefferson Co.*, Port Ludlow, Puget Sound, 12 Oct. 1907 (Kpt. R. Paessler), 1 female (ZIZM), Puget Sound, pre-1910 collection (Kpt. R. Paessler?), 1 female (SMF); *Grays Harbor Co.*, Moclips, 25 Aug. 1981 (A. Moldenke), 1 immature (JCC). OREGON: *Polk Co.*, 12.8 km W Grande Ronde, 27 Nov. 1940 (W. Ivie), 1 female (AMNH); *Hood River Co.*, Mt. Hood, Still Creek, Still Creek Forest Camp, 28–29 Sept. 1966 (Wiggins, Yamamoto, Odum), 11 males, 4 females (ROM); *Benton Co.*, Parker Creek, Mary's Peak, 24 Sept. 1966 (Wiggins, Yamamoto, Odum), 5 males, 6 females, 1 immature (ROM), McDonald Experimental Forest, 13 Sept. 198?, 29 July 1981, 1 Sept. 1981, 16 Oct. 1981, 25 June 1982, 15 Sept. 1982, 24 Nov. 1982 (B. Fichter and A. Moldenke), 14 males, 9 females, 17 immatures (JCC), Lewisberg Saddle, 30 May 1981, 29 July 1981, 27 Aug. 1981, 16 Oct. 1981, 1 Nov. 1981, 25 June 1982 (B. Fichter and A. Moldenke), 13 males, 3 females, 61 immatures (ARM), Ballards Bay State Park, 24 Nov. 1981 (B. Fichter and A. Moldenke), 5 males, 3 females (JCC), Corvallis Chip Ross Park, 25 June 1982, 16 Aug. 1982 (A. Moldenke and B. Fichter), 4 immatures (ARM), Mary's Peak summit, 2 Oct. 1981 (B. Fichter and A. Moldenke), 1 female (ARM), Mary's Peak subsummit, 2 Sept. 1981, 2 Nov. 1981, 6 Aug. 1982, 2 Sept. 1982 (B. Fichter and A. Moldenke), 3 males, 8 females, 20 immatures (ARM); *Jefferson Co.*, head Metolius River, Riverside Forest Camp, 19–23 Sept. 1966 (Wiggins, Yamamoto, Odum), 4 males, 1 female (ROM), Spring Creek, 19–20 April 1952 (V. Roth), 1 female (CAS); *Lane Co.*, Honeyman State Park, 20 June 1966 (T. Briggs and V. Lee), 1 immature (CAS); Fairview Peak summit, 28 May 1981 (A. Moldenke), 17 immatures (ARM), Mutton Meadow, SE of Rigdon, 14 July 1981 (A. Moldenke), 2 immatures (ARM), Rujada Campground, 26 May 1981 (A. Moldenke), 1 immature (ARM), Neptune State Beach, 5 Aug. 1982, 10 Oct. 1982, 24 Nov. 1982 (B. Fichter and A. Moldenke), 2 males, 2 females, 9 immatures (JCC), Willamette National Forest, Sacandaga Campground, 15 July 1981, 21 Aug. 1982 (B. Fichter and A. Moldenke), 5 immatures (ARM), West Lake, 23 June 1982, 10 Oct. 1982 (B. Fichter and A. Moldenke), 7 males, 8 females, 12 immatures (ARM), Washburn State Park, 24 Oct. 1981, 24 June 1982, 5 Aug. 1982, 10 Oct. 1982 (B. Fichter and A. Moldenke), 6 females, 19 immatures (JCC), Andrews Experimental Forest, 11 July 1981, 2 Aug. 1981, 3–5 Sept. 1981, 13 Oct. 1981, 10–12 July 1982, 12–18 Aug. 1982 (B. Fichter and A. Moldenke), 11 males, 18 females, 62 immatures (JCC); *Deschutes Co.*, South Sister, 31 Aug. 1941 (B. Malkin), 1 female (AMNH), 32 km S of Sisters, 11 Sept. 1948 (Roth), 1 female (AMNH), Sisters Mtns., Green Lake, 28–30 Aug. 1952 (V. Roth), 1 male (CAS), Crescent Lake, 22 Aug. 1982 (A. Moldenke), 1 male (JCC); *Jackson Co.*, 32 km NE of Ashland, 1 Sept. 1959 (W. J. Gertsch and V. Roth), 1 immature (AMNH); *Klamath Co.*, Odell Lake, 30 Aug. 1981 (B. Fichter and A. Moldenke), 6 immatures (JCC); *Tillamook Co.*, Cascade Head, 5 Aug. 1982 (B. Fichter and A. Moldenke), 2 immatures (JCC); *Linn Co.*, Rooster R. Rock, 24 Oct. 1981 (B. Fichter), 1 female (JCC); *Coos Co.*, Brandon, 24 Nov. 1981 (B. Fichter and A. Moldenke), 1 male (JCC); *Lincoln Co.*, Gleneden Beach, 13 Sept. 1981, 24 June 1982, 5 Aug. 1982 (B. Fichter

and A. Moldenke), 6 males, 5 females, 25 immatures (JCC), Cascade Head, N of Lincoln City, 18 June 1981, 13 Sept. 1982 (B. Fichter and A. Moldenke), 1 male, 2 females, 6 immatures (ARM); *Marion Co.*, Silver Creek Falls, July 1941 (J. C. Chamberlin), 1 immature (AMNH), Ochoco National Forest, Summit Campground, 11 June 1982 (B. Fichter and A. Moldenke), 1 immature (JCC). CALIFORNIA: *Del Norte Co.*, Middle Fork Smith River, 4 Sept. 1963 (J. and W. Ivie), 1 immature (AMNH); *Siskiyou Co.*, Trinity Alps, Caribou Basin (south rim), at snowfield edges, 12 Aug. 1980 (D. H. Kavanaugh), 1 immature (CAS), Panther Meadows, Mt. Shasta Ski Bowl, 2 Sept. 1959 (V. Roth and W. J. Gertsch), 5 males, 5 females (AMNH), Tule Lake, 14.4 km SW Tulelake, 15 Sept. 1965 (J. and W. Ivie), 6 immatures (AMNH), Paynes Creek, 8 km by road SE of Medicine Lake, 22 Aug. 1966 (H. B. Leech), 3 males, 1 female, 1 immature (CAS); *Plumas Co.*, S side Lake Almanor, 5 Sept. 1959 (V. Roth and W. J. Gertsch), 3 females, 2 immatures (AMNH); *Butte Co.*, Little Butte Creek, Toadtown, 4 April 1977 (C. L. Hogue), 1 female (LACM); *Sierra Co.*, 3.2 km N Calpine, 6 Sept. 1959 (W. J. Gertsch and V. Roth), 1 male, 1 female, 2 immatures (AMNH); *Placer Co.*, Squaw Valley, 20 Sept. 1961 (W. Ivie and W. J. Gertsch), 2 females (AMNH); *Eldorado Co.*, Fallen Leaf Lake, 9 Sept. 1959 (W. J. Gertsch and V. Roth), 1 male, 1 female (AMNH); *Tuolumne Co.*, Pinecrest, 10 Sept. 1959 (W. J. Gertsch and V. Roth), 1 male, 2 females (AMNH), Tamarak Flat, Yosemite Natl. Park, 11 Sept. 1959 (W. J. Gertsch and V. Roth), 1 male (AMNH); *Mariposa Co.*, 1.6 km S Fish Camp, 23 Sept. 1961 (W. Ivie and W. J. Gertsch), 1 female (AMNH). CANADA. BRITISH COLUMBIA: Queen Charlotte Islands, Masset, 1891-7-2-16-26 (J. H. Keen), 4 females (BMNH), W of Dawson Inlet, 29 Aug. 1961 (J3=), 1 immature (CNC), Alleford Bay (=Alliford Bay), 26 Aug. 1961 (collector unknown), 1 female (CNC), Vancouver Island, Coombs, spring 1979 (D. Salter), 1 male (JCC), Golden Ears Prov. Park, 2 Sept. 1973 (C. Holmberg), 1 female (RGH), Alouette Lake, 24 Aug. 1973 (R. G. Holmberg), 1 immature (RGH), Burnaby Mountain, Simon Fraser University, 16 Oct. 1971 (R. G. Holmberg), 1 male (JCC), 1 Oct. 1973 (R. G. Holmberg), 1 female (RGH), Point Gray, Vancouver, 18-28 May 1973 (J. R. Vockeroth), 1 immature (CNC), Vancouver, 25 Sept. 1965 (P. D. Bragg), 1 female (PDB), 14 Sept. 1968 (P. D. Bragg), 1 male (PDB), 28 Sept. 1968 (P. D. Bragg), 1 male (PDB), 28 Oct. 1968 (P. D. Bragg), 3 males (PDB), 23 Nov. 1968 (P. D. Bragg), 1 male (PDB).

***Leptobunus aureus*, new species**

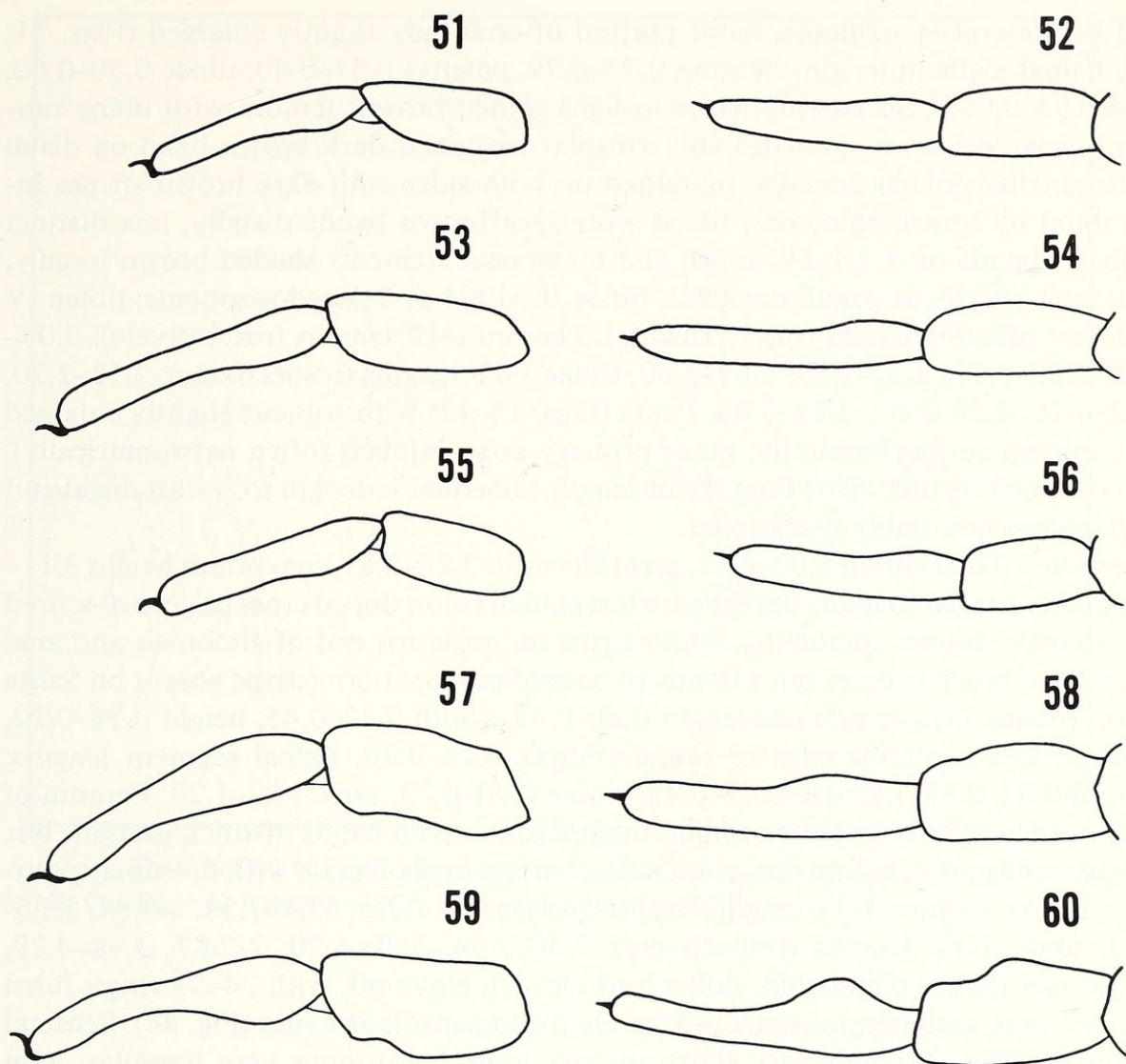
Figs. 4, 15-17, 34, 35, 49, 52, 63

Types. Male holotype from Inverness, 60 m elev., Marin Co., California, 11-13 Jan. 1964 (P. H. Arnaud, Jr.), CAS; seven paratypes (listed under specimens examined).

Etymology. The specific epithet from Latin, referring to the golden color of the body.

Diagnosis and comparisons. *Leptobunus aureus* is one of two species in the *parvulus* group. In addition to differences in the genitalia, *L. aureus* can be distinguished from other *Leptobunus* spp. by its small size and golden color.

Distribution. Known only from Santa Cruz, Marin, and Mendocino Counties in California (Fig. 63).



Figs. 51–60. Tibiae and tarsi of male *Leptobunus* spp. palpi (semi-diagrammatic). 51, 53, 55, 57, 59. Lateral views. 52, 54, 56, 58, 60. Dorsal views. 51, 52. *L. aureus*. 53, 54. *L. parvulus*. 55, 56. *L. pallidus*, subadult. 57, 58. *L. borealis*. 59, 60. *L. californicus*.

Description. Males: Total length 2.90–3.15, greatest width 2.00–2.30, maximum height 1.56–1.77; dorsum light golden brown with dark brown velvety reticulations on cephalothorax, faint cross pattern on abdomen which is invaded by many golden brown and white spots, and last 4 to 5 distal tergites and anal operculum with creamy white stripe (Fig. 4). Ocular tubercle length 0.34–0.35, width 0.37–0.39, height 0.15–0.17, distance from anterior edge of cephalothorax 0.23–0.25; white with dark brown to black rings around eyes, rings thicker anteriorly and appearing elliptical. Coxae, genital operculum, and abdominal sternites creamy white to light yellow brown with numerous white blotches. Chelicerae silvery white to yellow brown, lateral surface of basal segment and proximal half of distal segment mottled with brown; basal portions of fingers yellow brown, tips of fingers and teeth dark brown to black; moveable finger with conspicuous spur (Figs. 49, 50), concolorous with finger. Palpi creamy white to light yellow brown; dark brown mottlings on femora dorsally; dark brown stripes on dorsum and basolateral half of patellae, proximal half of dorsum

and basolateral $\frac{1}{2}$ of tibiae; basal portion of tarsi only slightly enlarged (Figs. 51, 52). Palpal segment lengths: femora 0.73–0.79, patellae 0.37–0.40, tibiae 0.50–0.60, tarsi 0.94–0.98. Legs creamy white to light golden brown; femora with many randomly spaced brown splotches and irregular margined dark brown band on distal ends; patellae golden dorsally, margined on both sides with dark brown stripes interrupted by brown splotches; tibiae with dark brown bands distally, less distinct subbasal bands on I, III, IV; tarsal and metatarsal elements shaded brown basally; metatarsi I with one pseudosegment; tibiae II with 4 or 5 pseudosegments; tibiae IV with one pseudosegment (rarely lacking). Femora I–IV lengths (respectively): 3.00–3.25, 6.25–6.71, 3.30–3.50, 4.89–5.00; tibiae I–IV lengths (respectively): 2.58–2.70, 5.63–5.70, 2.56–2.67, 3.81–3.86. Penis (Figs. 15–17) with truncus slightly enlarged on subbasal surface ventrally; glans primary setae bilobed (often asymmetrically), spaced much further apart than stylus length, subequal in length to stylus; distal end of glans not noticeably constricted.

Females: Total length 5.00–6.81, greatest width 3.26–3.61, maximum height 3.11–3.21; body similar to male, darker with less golden color; dorsal cross pattern obscured by extensive brown splotching, white stripe on posterior end of abdomen and anal operculum much thinner but extends to base of cross pattern (stripe absent on Santa Cruz female). Ocular tubercle length 0.40–0.42, width 0.42–0.45, height 0.18–0.22, distance from anterior edge of cephalothorax 0.28–0.30. Palpal segment lengths: femora 0.81–0.83, patellae 0.42–0.48, tibiae 0.70–0.73, tarsi 1.17–1.20. Femora of legs with fewer brown splotches than male; distal brown bands distinct, margins less irregular. Leg pseudosegments as in males, except single female with $6\frac{1}{4}$ tibiae pseudosegments. Femora I–IV lengths (respectively): 3.15–3.75, 6.64–7.34, ?–3.74, 5.12–5.74; tibiae I–IV lengths (respectively): 2.80–2.94, 5.80–6.20, ?–2.87, 3.98–4.29. Ovipositor darkly pigmented, difficult to clear in clove oil, with 24–29 rings; furca 3 segmented, second joint with 1–3 (rarely 3) slit sensilla per side (Fig. 34). Seminal receptacle (Fig. 35) with very short primary loop; basal loops very irregular, loop constricting in size basally; basimesal tube undetected (lacking ?).

Immatures: Similar to adult female, except abdominal cross pattern distinct. One specimen with 1 and 3 pseudosegments in metatarsi I, all others have single pseudosegment; tibiae II with 3 pseudosegments; tibiae IV occasionally with 1 pseudosegment.

Natural history. Juveniles are known from late June and August, whereas adults are known from September to November. The majority of specimens were collected at 60 m elevation, but others are from 150 and 460 m. This species appears to be restricted to lowland forests of the lower Humboldtian and Santa Cruzian biotic districts of the Pacific Maritime Province (Schick, 1965). A female from Santa Cruz was captured by beating the branches of redwoods.

Specimens examined. Male holotype and female paratypes. U.S.A. CALIFORNIA: *Mendocino Co.*, Mendocino, 20 June 1955 (J. R. Helfer), penultimate female (UCB); *Marin Co.*, Inverness, 19 Oct. 1946 (E. S. Ross), 2 males (CAS), 11–31 Jan. 1964 (P. H. Arnaud, Jr.), 1 male (CAS), Lagunitas, 15 Sept. 1946 (E. S. Ross), 1 female (CAS), North Toll Bridge, Bolinas Ridge, 3.2 km NW Bolinas, 13 Aug. 1965 (V. Lee and T. Briggs), 2 immatures (CAS); *Santa Cruz Co.*, University of California, Santa Cruz Campus, 26 Nov. 1981 (A. Moldenke), 1 female (JCC).

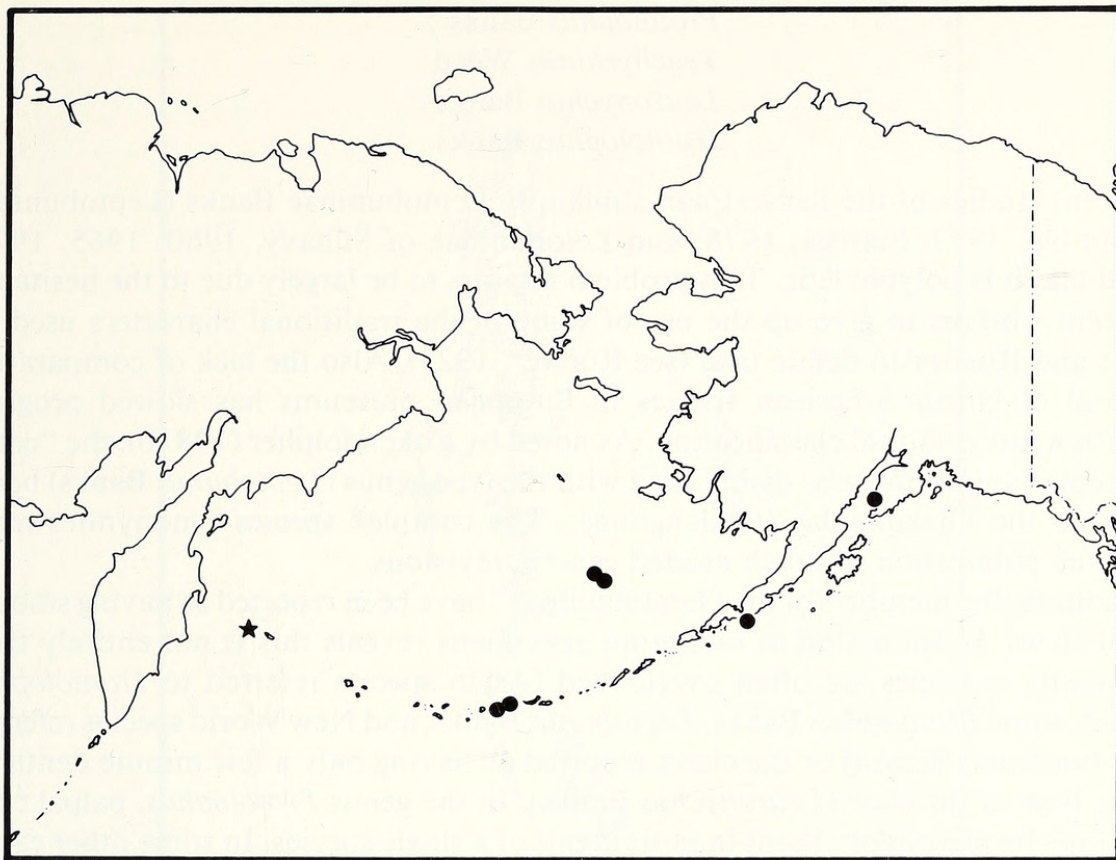


Fig. 61. Distribution of *Leptobunus* spp. in Mainland Alaska, and Aleutian and Bering Sea Islands. Circles = *L. borealis*, star = *L. borealis* and *L. pallidus*.

SYSTEMATIC RELATIONS AND HIGHER CATEGORIES

There has been confusion regarding the date of publication of the family-group name Leptobunidae in the past. Banks described *Leptobunus* in 1893 and placed it in the tribe Liobunini Banks. Roewer (1910, 1923) cited Banks (1894a) as the author of Leptobunini, and stated that it appeared on page 165. Šilhavý (1960) claimed Banks described it in 1893, and Rambla (1967) listed "Banks 1894." Nowhere in Banks (1893, 1894a) does the name Leptobunini appear; furthermore the latter article ends on page 164. Likewise, Banks (1894b, 1894c, 1898, 1899, 1900a, 1900b) did not mention the Leptobunini. The first reference to the tribe Leptobunini is Banks (1901). In that paper, Banks did not discuss the name, simply listing it in the key to the Phalangiidae. Nonetheless, Banks (1901) is to be credited with the establishment of the family-group name Leptobunini (Stoll, 1961, art. 16). Roewer (1910) was the first to diagnose and describe the "Leptobunini" as a subfamily. The following classification, proposed by Roewer (1910, 1923), has been essentially followed up to the present:

Family Phalangiidae Simon
 Subfamily Leptobuninae Banks
Leptobunus Banks
Cosmobunus Simon

Protolophus Banks

Trachyrhinus Weed

Leuronychus Banks

Homolophus Banks

Recent studies of the harvestman subfamily Leptobuninae Banks (Leptobunidae of Rambla, 1977; Staręga, 1978; and Leiobunidae of Šilhavý, 1960, 1965, 1976) reveal that it is polyphyletic. This problem appears to be largely due to the hesitancy of recent workers to give up the use of some of the traditional characters used by Banks and Roewer to define taxa (see Roewer, 1923). Also the lack of comparative material of North American species in European museums has slowed progress towards a more natural classification. As noted by Cokendolpher (1981b), the "catch all" Leptobuninae must be dismantled with the type genus (*Leptobunus* Banks) being placed in the Phalangiidae (Phalangiinae). The complex species synonymies must await the publication of much needed generic revisions.

Traditionally, members of the "Leptobuninae" have been reported as having smooth palpal claws. Examination of numerous specimens reveals this is not entirely true. Apparently denticles are often overlooked (Asian species referred to *Homolophus* Thorell, some *Protolophus* Banks, *Leptobunus* Banks, and New World species referred to *Cosmobunus* Simon) or the claws reported as having only a few minute denticles on the base of the claw (*Leuronychus* Banks). In the genus *Protolophus*, palpal claw teeth may be present or absent in individuals of a single species. In some other cases, the immatures have well developed palpal claw teeth which presumably wear down or break off with age (see Suzuki, 1973). Additionally, two genera (*Trachyrhinus* Weed and *Cosmobunus*) have bare palpal claws but agree in all other details with members of the Gagrellidae (Leiobuninae and Gagrellinae), which characteristically have denticulate claws. "Atypical" palpal claws are also known in other subfamilies. Lawrence (1962) remarked on some of the problems with the African genus *Cheops* Soerenson. The North American genus *Liopilio* Schenkel (see Cokendolpher, 1981b) and the South American genus *Thrasychirus* Simon also have atypical palpal claws. The "Dentizacheinae" (=Phalangiinae) of Šilhavý (1960) likewise suggest the use of alternate characters as pointed out by Staręga (1973). Therefore, the presence or absence of denticles on the ventral surface of the palpal claw is of limited taxonomic use.

Traditionally, the lack of a cheliceral hook was used to characterize the subfamily Phalangiinae, but this character appears to be plesiomorphic. Martens (1978) maintained two species in the genus *Paroligolophus* Lohmander: *P. agrestis* (Meade) with a cheliceral hook, and *P. meadii* (Pickard-Cambridge) without it. Cokendolpher (1981b) pointed out the similarity of *Leptobunus* to *Liopilio*, but noted that *Leptobunus* always has a cheliceral hook, whereas in *Liopilio* the hook varies in size due to age and sex of the specimen, and may be entirely lacking. Thus, the presence or absence of a hook or tooth ventrally on the first joint of the chelicera is of restricted value.

The angle of insertion of the endites of coxa II is often difficult to ascertain. All genera referred to the Leptobuninae are reported as having the endites straight, parallel to the lip of the genital operculum. In reality, several of these genera have the endites slanted anteriorly as in the Phalangiinae. As the angle of insertion of the

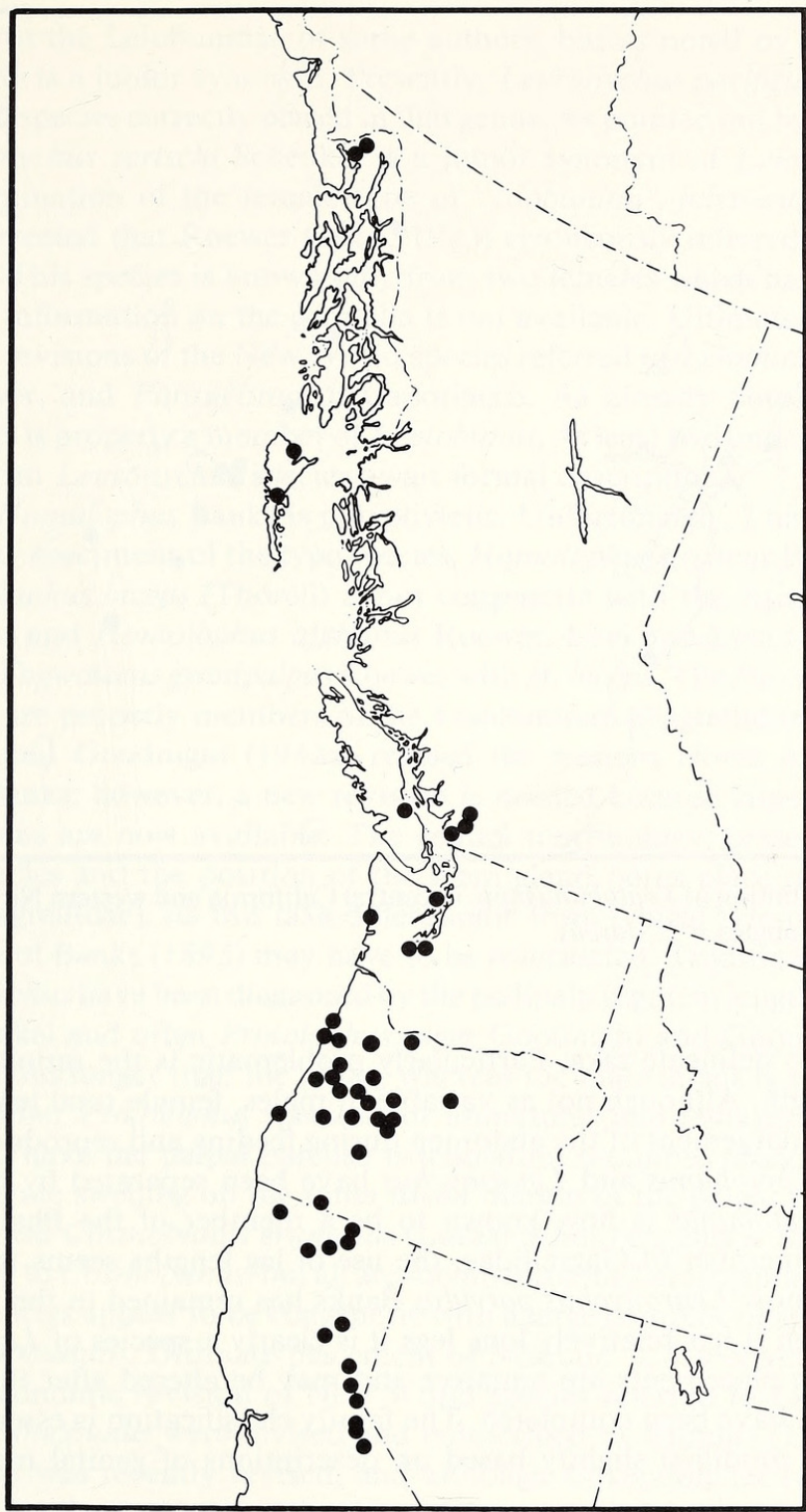


Fig. 62. Distribution of *Leptobunus parvulus* in western North America (Alaska to California).

endites is altered, to some extent, by the method of preservation and the age and sex of the animal, it should be used with great caution.

Comparative lengths of the legs has been used to distinguish genera in the Phalangioidea. Although often useful in verifying identifications, it should not be used as the

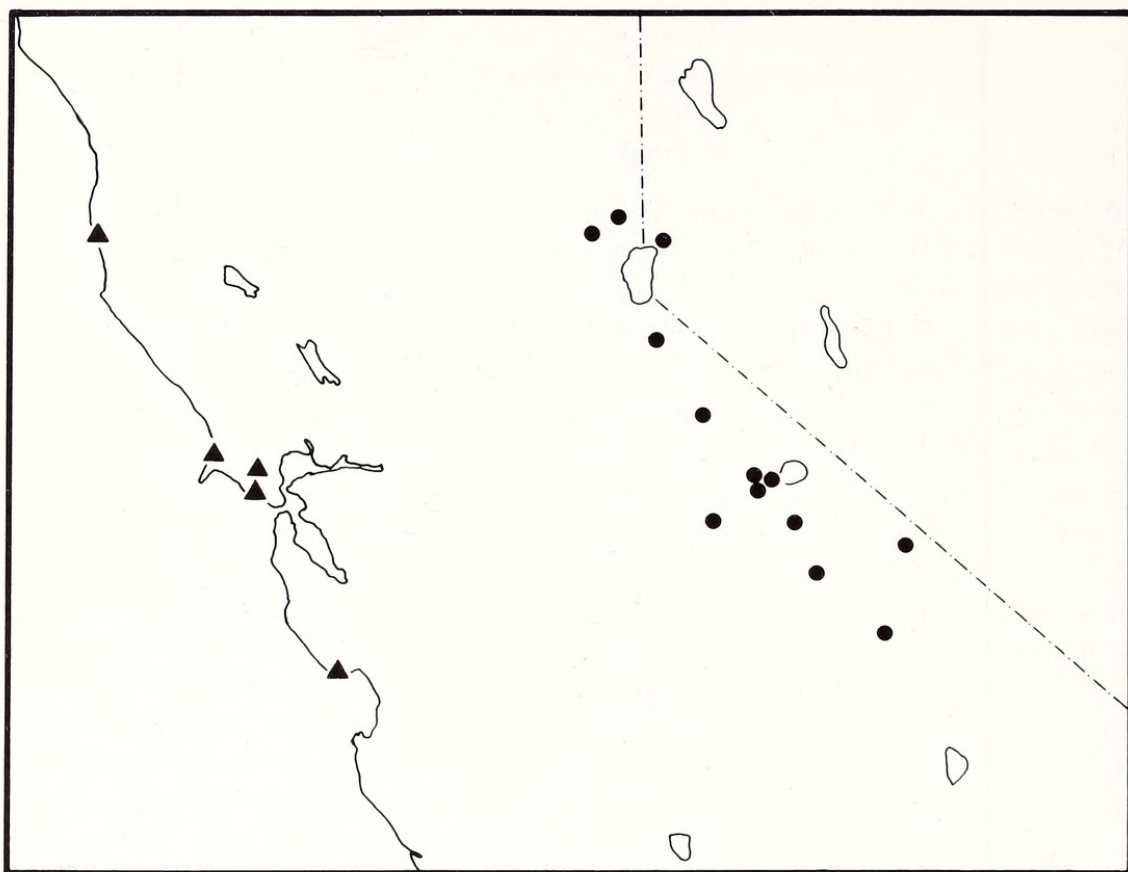


Fig. 63. Distribution of *Leptobunus* spp. in central California and western Nevada. Circles = *L. californicus*, triangles = *L. aureus*.

sole character to delineate taxa. Particularly problematic is the ratio of leg lengths to the body length. Although not as variable in males, female total length is greatly influenced by enlargement of the abdomen during feeding and reproductive periods. Traditionally, *Leptobunus* and *Leuronychus* have been separated by the lengths of the legs. As *Leptobunus* is now known to be a member of the Phalangidae and *Leuronychus* a member of Gagrellidae, the use of leg lengths seems trivial. Unfortunately, up to now *Leuronychus parvulus* Banks has remained in the wrong genus, and, even though it has relatively long legs it is clearly a species of *Leptobunus*.

The following placements are tentative and may be altered after thorough taxonomic revisions have been completed. The family classification is essentially that of Šilhavý (1960), modified slightly based on descriptions of genital morphology by Martens (1978).

As already noted the genus *Leptobunus* is a member of the Phalanginae (Phalangidae). Members of the genus, as well as others incorrectly placed in the genus, are discussed earlier in this paper in the context of a generic revision.

Cokendolpher (1981b) reported that the monotypic East Asian genus *Tchapinius* Roewer is most similar to *Mitopus* Thorell. A revision of *Mitopus* currently underway will further document this affinity. Both genera are members of the Phalanginae (Phalangidae).

Leuronychus Banks is a member of the Leiobuninae (Gagrellidae). The Gagrellidae

is equivalent to the Leiobunidae of some authors, but as noted by Staręga (1972), the latter name is a junior synonym. Presently, *Leuronychus pacificus* (Banks) is the only described species correctly placed in that genus. As pointed out by Cokendolpher (1980) *Leuronychus gertschi* Schenkel is a junior synonym of *Leiobunum exilipes* (Wood). Examination of the female type of "*Liobunum*" *fulviventris* O. Pickard-Cambridge revealed that Roewer (1910, 1923) erroneously referred this species to *Leuronychus*. This species is known only from two females which have been pinned and dried, so information on the genitalia is not available. Ultimate placement will have to await revisions of the New World species referred to *Leiobunum* C. L. Koch, *Nelima* Roewer, and *Paranelima* di Caporiacco. As already noted, *Leuronychus parvulus* Banks is properly a member of *Leptobunus*. At least two undescribed western North American *Leuronychus* species await formal description.

The genus *Homolophus* Banks is polyphyletic. Unfortunately, I have been unable to examine any specimens of the type species, *Homolophus arcticus* Banks. The New World *Homolophus biceps* (Thorell) is not congeneric with the Asian *Homolophus iranensis* Roewer and *Homolophus afghanus* Roewer. Levi and Levi (1955) correctly synonymized *Togwoteeus granipalpus* Roewer with *H. biceps*. The *Homolophus* species known to me are properly members of the Leiobuninae (Gagrellidae).

Goodnight and Goodnight (1942a) revised the western North American genus *Protolophus* Banks; however, a new revision is needed because large series of additional specimens are now available. The genital morphology, presence of low abdominal tubercles and the position of the scent gland pores place it in the Sclerosomatinae (Gagrellidae). As this taxa differs some from typical Sclerosomatinae, the Protolophinae of Banks (1893) may have to be resurrected. Traditionally, the members of *Protolophus* have been diagnosed by the pedipalp segment lengths. *Protolophus longipes* Schenkel and often *Protolophus niger* Goodnight and Goodnight have the male palpal tarsus longer than the tibiae, whereas the male tarsus is shorter than the tibiae on all other *Protolophus* species. All immatures and females of *Protolophus* spp. examined have the palpal patellae extended on the inner margin, as well as a slight to moderate swelling on the inner distal margin of the palpal tibiae.

The Old World *Cosmobunus granarius* (Lucas) is not congeneric with New World species referred to *Cosmobunus*, but all are members of the Leiobuninae (Gagrellidae). New World species appear to be congeneric with a large complex of species presently referred to *Leiobunum*. Ultimate placement of Nearctic "*Cosmobunus*" must await a thorough taxonomic revision of New World species referred to *Leiobunum*. The Old World *Cosmobunus* were revised and redescribed by Rambla (1970).

Trachyrhinus was recently revised, and although Cokendolpher (1981a) did not state to which family *Trachyrhinus* belongs, the presence of pseudoarticular nodules of femora II was noted. *Trachyrhinus* was subsequently transferred to the Gagrellinae (Gagrellidae) by Cokendolpher (1984a).

Staręga (1978) suggested that the North American genus *Globipes* Banks may be a member of the Leptobuninae. *Globipes* is properly a member of an assemblage of phalangoid genera which is as yet unnamed (Cokendolpher 1984b; Cokendolpher and Cokendolpher 1984).

The South American genus *Thrasychirus* Simon was referred to the Leptobuninae by Canals (1935). However, Šilhavý (1970) noted Ringuelet's (1959) synonymy of

Enantiobunus Mello-Leitão with *Thrasychirus*, and transferred *Thrasychirus* to the Enantiobuninae (Neopilionidae).

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