

## The Harvestman Family Phalangodidae. 6. Revision of the *Sitalcina* Complex (Opiliones: Laniatores)

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The *Sitalcina* complex, currently encompassing species placed in *Sitalcina* Banks and *Microcina* Briggs and Ubick, is revised and shown to be much more diverse than previously envisioned. Both *Sitalcina* and *Microcina* are now restricted to include only those species most closely related to their types, *Sitalcina californica* (Banks) and *Microcina tiburona* (Briggs and Hom), respectively. For the remaining species currently in *Sitalcina*, three new genera are proposed: *Enigmina* (for *S. granita* Briggs), *Megacina* (for *S. cockerelli* Goodnight and Goodnight and *S. madera* Briggs), and *Tularina* (for *S. scopula* Briggs). A fourth new genus, *Microcinella*, is proposed for *Microcina homi* Briggs and Ubick. The following species are newly described: *Enigmina warrenorum*, *Megacina mayacma*, *Megacina schusteri*, *Microcina potrero*, *Microcina sanbruno*, *Microcina stanford*, *Microcina tamalpais*, *Microcinella coensis*, *Sitalcina catalina*, *S. peacheyi*, *S. rothi*, *S. seca*, *Tularina plumosa*, and *T. tularensis*. The subspecies, *S. flava chalonga* Briggs, is elevated to species status.

We examined over three dozen characters, of which 29 were found to be informative and analyzed in a parsimony analysis (PAUP\*). The *Sitalcina* complex is not supported by any apparent synapomorphies. Its most divergent member, *Microcinella*, has the most plesiomorphic genitalia, which suggests it is basalmost in the folding-glans clade. The relationships among the remaining genera are not fully resolved. The clades, (*Microcina* (*Sitalcina* + *Enigmina*)) and (*Megacina* + bifurcate clade), seem well supported as they were recovered in virtually all searches. The placement of *Tularina* is less clear, but its relationship with *Megacina* is suggested by some genitalic characters.

Biogeographically, the *Sitalcina* complex is primarily Californian, with extensions into Oregon and Arizona. A vicariance model suggests some probable barriers, although considerable dispersal is necessary to account for the several cases of sympatry.

Ecologically, the species represent two body types, which correlate with habitat: 1) large, eyed species found in forests (*Sitalcina*, *Megacina*, *Enigmina*); and 2) small, blind species from grasslands (*Microcinella*, *Microcina*, *Tularina*). Interestingly, although the habitus of grassland species is most likely derived (paedomorphy), the three genera are phylogenetically relatively basal.

KEYWORDS: Opiliones, Laniatores, Phalangodidae, *Sitalcina*, California, taxonomy, biogeography

The Nearctic harvestmen of the family Phalangodidae are remarkable in many ways. These small laniatorids (Fig. 1), easily recognized by their yellowish to orange coloration (Figs. 2–3) and slow movements, occur in cryptozoic habitats and were previously only rarely collected. Recent

studies are showing that these organisms are both abundant and diverse. In fact, the family turns out to be amazingly speciose, being by far the largest opilionid family in the Nearctic. With this study, the number of phalangodids is increased to 108, representing some 40% of all Nearctic opilionid species. Evolutionarily, the hotspot of diversity is the Californian region, which now includes 66 species, some 60% of Nearctic phalangodids.

Phalangodids are also morphologically very diverse, showing much variation in both somatic and genitalic characters. Somatically, the species differ in the degree and arrangement of cuticular ornamentation and the form of the secondary sexual structures. Many species show adaptations to cave and interstitial life through varying degrees of depigmentation, appendage elongation, and eye reduction.

However, it is the genitalic characters that are most variable, especially the bewildering array of structures on the male penis.

Our studies of the male genitalic characters suggest a division of the family into three groups. The first, represented by *Calicina* Ubick and Briggs, has a glans that telescopes out of the truncus during expansion (Fig. 4c–e). As this mode of expansion is interpreted as plesiomorphic in the family (Ubick and Briggs, 1989), the genus is placed as sister to all remaining Nearctic phalangodids, those with a folded glans that unfolds during expansion (Figs. 8a–e). This “folding glans clade” further divides into two groups. Of these, the “bifurcate clade” includes those species with a deeply divided ventral plate (Figs. 5d–e), currently placed in *Banksula* Roewer, *Texella* Goodnight and Goodnight, and *Phalangodes* Tellkamp et al. (Ubick 2007). (This latter group, henceforth referred to in this study as *Phalangodes* et al., also includes the following closely related genera of the eastern Nearctic: *Bishopella* Roewer, *Crosbyella* Roewer, *Tolus* Goodnight & Goodnight, *Undulus* Goodnight & Goodnight, and *Wespus* Goodnight & Goodnight). All of the remaining species, those with entire (unmodified) ventral plates and presently contained in *Sitalcina* and *Microcina*, are referred to as the “*Sitalcina* complex”. In this study we revise this complex and, in so doing, also complete our preliminary survey of the Californian phalangodid fauna.

The genus *Sitalcina* was defined by Banks (1911) to include only his previously described species, *Sitalces californica* Banks (1893) (Fig. 1). Two additional species, *S. cockerelli* and *S. lobata*, were later added to the genus by Goodnight and Goodnight (1942). Our knowledge of the genus was greatly expanded in the 1960s, when intense collecting and study increased the

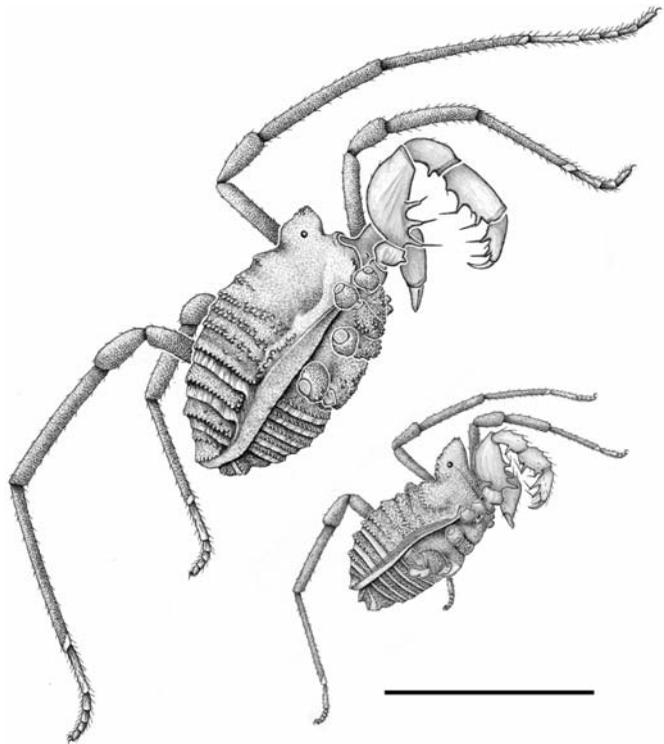


FIGURE 1. *Megacina cockerelli* (Goodnight and Goodnight), upper left, and *Sitalcina californica* (Banks), lower right, the two commonest sitalcinoid species, males in lateral view. Scale bar = 2mm. (Illustrated by J. Speckels)

species number ten fold (Briggs and Hom 1966, 1967; Briggs 1968). Since that time, additional collecting has produced a steady stream of new species, which still continues to flow. With the help of improved imaging, especially through scanning electron microscopy, a more detailed study of the morphology became possible and revealed a number of surprises, especially the unexpectedly high variation in male genitalic structures. The genus *Sitalcina* turned out to include species with two radically different forms of the male genitalia. In the first, the glans telescopes out of the truncus during expansion, in the second it unfolds. As the type species, *S. californica*, has a folding glans, those species with a telescoping glans were moved to a new genus, *Calicina* (Ubick and Briggs, 1989). However, the remaining species in *Sitalcina* were also somatically diverse. Whereas most species have the dorsal cuticle composed of discrete tubercles (Figs. 15a–c), in some the tubercles are connected by ridges giving a honeycombed, or areolate, sculpturing (Figs. 7a–b). On the basis of this apparent synapomorphy, these latter species were moved to another new genus, *Microcina* (Briggs and Ubick, 1989).

As the *Sitalcina* complex was not defined by synapomorphies, one important challenge for the study was to find one. However, our search for characters failed to turn up even a single shared derived character for the complex. Furthermore, our character analysis indicates that not even *Microcina* and *Sitalcina* as currently maintained are monophyletic. In fact, newly discovered synapomorphies from both somatic and genitalic characters now suggest the presence of four additional genera.

The first is *Microcinella*, whose single described species, *M. homi*, was previously included in *Microcina* (Briggs and Ubick, 1989). In that study, we defined *Microcina* on the basis of a single synapomorphy, the areolate cuticular ornamentation. However, examination of a wider sample of sitalcinoids now indicates that areolate cuticle is much more widespread than previously noted (Figs. 38, 45, 47, 49), being found in additional species which, on both genitalic and other somatic features, are clearly unrelated to *Microcina*. Although areolate cuticle may turn out to be phylogenetically relevant at higher levels, it no longer supports the monophyly of *Microcina*. Thus, the differences observed between the two included species groups become more significant. In the *tiburona* group (= *Microcina* in the present interpretation), the male genitalia have a dorsal lobe (Figs. 8, 10a–c), the female ovipositor trifurcate apical setae (Figs. 11g), and the male a unique sexual dimorphism, an enlarged eyemound (Figs. 9a–d), all of which are absent in the *homi* group (= *Microcinella*) (Figs. 6–7). However, it is the male genitalia of *Microcinella homi* that are fundamentally different, not just from *Microcina*, but from all remaining phalangodids. Here, the glans both unfolds and telescopes during expansion (Figs. 6a–b), a condition that to our knowledge is unique in the family and whose interesting evolutionary ramifications are discussed in the Phylogeny section. The validity of *Microcinella* is further supported by the discovery of a second species, here described as *M. coensis*.

The genus *Sitalcina* as presently maintained is even more polymorphic than *Microcina*, with species differing in numerous genitalic and somatic characters. It is here restricted to include only those species closely related to the type species, *Sitalcina californica*. These species share synapomorphies in the male genitalia (glans with large flap-like dorsal lobe, Figs. 13–14a–f), female genitalia (ovipositor with microspines in imbricate arrangement, Fig. 16i), and the form of the secondary sexual structures (male with TrIV spur, Figs. 15g–h). Excluded from *Sitalcina* are four currently described species (along with five new ones) that lack these synapomorphies and are here assigned to three new genera.

The first of these is represented by *Sitalcina scopula*, the only remaining blind member of *Sitalcina*, as the others were previously transferred to *Calicina*, *Microcina*, and (now) *Microcinella*. This species lacks a TrIV spur (although it does have a ventral tubercle, Fig. 42f), has fused PSL

on the glans (Figs. 37j–k, 43a–d), and lacks ovipositor microspines (Figs. 43e–g). This species, along with two new ones (*T. tularensis* and *T. plumosa*), is here assigned to the new genus, *Tularina*.

Two additional species, *Sitalcina cockerelli* and *S. madera*, differ from *Sitalcina*, and all other known phalangodids, in having a glans that folds asymmetrically, with the dorsal and ventral surfaces occupying lateral positions in the folded glans (Figs. 44c–d, 46a–c, 53a–e). This unique and unusually complex mechanism is clearly a strong synapomorphy for the new genus, *Megacina*, which also includes two new species, *M. schusteri* and *M. mayacma*. These species also differ from *Sitalcina* in other characters. The female has a glabrous ovipositor, lacking microspines (Figs. 46g–i, 48f–i, 50g–i, 54a–c) and the male TrIV lacks a spur, but may have tubercles (Figs. 52f–g, i). In three species (the *madera* group) leg IV has an unusual modification: a somewhat swollen Tr and a Fm with a basoventral process (Figs. 45e–f, 47e–g, 49d–e).

Finally, *Sitalcina granita* does not share any convincing synapomorphies with the above genera. It resembles *Megacina* and (most) *Tularina* in lacking ovipositor microspines (Figs. 34h, 36j), but *Sitalcina* in having a glans with full complement of lobes (Figs. 14g–h, 34a–d, 36a–f) and TrIV with short processes resembling spurs (Figs. 33e–f, 35e–g). The species is unique in the complex in having a short, stout stylus (Figs. 14g–h, 34a–c, 36a–d) and is here placed in a new genus, *Enigmina*, which also includes the new species, *E. warrenorum*.

## METHODS

The format of this study follows that of Ubick and Briggs (1989). Standard observations and measurements were through a dissecting microscope (Leica MZA 12.5), using magnifications up to 100x. Closer examination was with a compound microscope (Nikon YS2-H) and some specimens were also imaged with auto montage (using Syncroscopy software). Where possible, few to several specimens per species were also examined through scanning electron microscopy (Hitachi S-520), indicated as “(SEM)” in the species accounts. As the distributions of the taxa are presented all in one place (Figs. 56 and 57), this reference is not repeated in the Taxonomy section. All measurements, unless otherwise stated, are in mm.

Abbreviations: **1.** Somatic morphology: AT = anterior tubercles of scute, GO = genital operculum, EM = eyemound, Fm = femur, FmIV = femur of leg IV, LII/SL = leg II/ scute length, TC = tarsal count, TrIV = trochanter of leg IV. **2.** Penis morphology: DL = dorsal lobe of glans, PSL = parastylar lobe(s) of glans, S = stylus, SB = stylar base, VP = ventral plate of penis, VS = ventral setae of ventral plate, AS = apical spine of ventral plate. (Note that the ventral and dorsal aspects of the glans refer to that of a fully expanded penis. These positions thus appear reversed in a folded glans; i. e., the ventral surface assumes a dorsal position.) **3.** Ovipositor morphology: OV = ovipositor, OVM = ovipositor microspines, OVS = ovipositor apical setae.

The majority of the 1800 specimens examined are deposited at the California Academy of Sciences (CAS). Other material is from the American Museum of Natural History (AMNH), Museum of Comparative Zoology (MCZ), and Universities of California at Berkeley (UCB), Davis (UCD), and Riverside (UCR), along with the personal collections of James Cokendolpher (CJC), William Shear (CWS), and D. Ubick (CDU).

## TAXONOMY

**Phalangodidae Simon, 1879****Key to the Genera of Nearctic Phalangodidae****Males**

1. Penis with VP bifurcate (Figs. 5d–e) ..... 2  
 Penis with VP entire (Fig. 4d) ..... 4
2. VP prongs in ventral position (Fig. 5e); palpal Fm with dorsal tubercles (Fig. 5b) ..... *Banksula* Roewer  
 VP prongs in lateral position (figs. 4.35f–g: Ubick 2007); palpal Fm lacking dorsal tubercles ..... 3
3. VP prongs thin; glans large (fig. 4.35f: Ubick, 2007) ..... *Texella* Goodnight and Goodnight  
 VP prongs swollen; glans small (fig. 4.35g: Ubick, 2007) ..... *Phalangodes* Tellkampff, et al.
4. Glans expands only by telescoping out of truncus (Figs. 4c–e) ... *Calicina* Ubick and Briggs  
 Glans unfolds from truncus ..... 5
5. S telescopes out of glans; DL absent (Fig. 6) ..... *Microcinella*, gen. nov.  
 S does not telescope out of glans; DL usually present ..... 6
6. Glans folding complex, asymmetrical (Fig. 44) ..... *Megacina*, gen. nov.  
 Glans folding simple, symmetrical ..... 7
7. Eyes present (Fig. 15a) ..... 8  
 Eyes absent (Figs. 9a–d) ..... 9
8. TrIV with ventral process (spur) longer than 1/2 Tr width (Figs. 15g–h) ..... *Sitalcina* Banks  
 TrIV with ventral process shorter than 1/3 Tr width (Fig. 35e) ..... *Enigmina*, gen. nov.
9. Glans with DL broad; PSL separate (Fig. 8) ..... *Microcina* Briggs and Ubick  
 Glans with DL absent or, when present, pointed; PSL fused (Fig. 37) ..... *Tularina*, gen. nov.

**Females (excluding *Phalangodes* et al.)**

1. OV with one pair of apical teeth (Fig. 5i) ..... 2  
 OV lacking apical teeth (Fig. 4f) ..... 3
2. OVM absent (Fig. 5j); palpal Fm with dorsal tubercles (Fig. 5b) .. *Banksula* Roewer (in part)  
 OVM present (figs. 18–21: Ubick and Briggs, 1992); palpal Fm lacking dorsal tubercles ..... *Texella* Goodnight and Goodnight
3. Eyes present (Fig. 15a) ..... 4  
 Eyes absent (Figs. 9a–d) ..... 8
4. OVM present (Fig. 4g) ..... 5  
 OVM absent (Fig. 36j) ..... 6
5. OVM in random arrangement (Fig. 4g) ..... *Calicina* Ubick and Briggs (in part)  
 OVM in imbricate arrangement (Fig. 16f) ..... *Sitalcina* Banks (in part)
6. Palpal Fm with row of dorsal tubercles (Fig. 17a) ..... *Sitalcina* Banks (in part)  
 Palpal Fm lacking row of dorsal tubercles ..... 7

7. EM at anterior scute margin (Figs. 35a–b) . . . . . *Enigmina*, gen. nov.  
EM posteriad of anterior scute margin (Figs. 45b–c, 47a, 49a–b, 51) . . . . . *Megacina*, gen. nov.
8. OVM in transverse rows (Figs. 39j, 41i), or absent (Fig. 43g) . . . . . *Tularina*, gen. nov.  
OVM in random arrangement (Fig. 4g) . . . . . 9
9. Scute cuticle tuberculate (Fig. 4b) . . . . . 10  
Scute cuticle areolate (Figs. 7a–b) . . . . . 11
10. Palpal Fm with dorsal tubercles (Fig. 5b) . . . . . *Banksula* Roewer (in part)  
Palpal Fm lacking dorsal tubercles (Fig. 4a) . . . . . *Calicina* Ubick and Briggs (in part)
11. OVS with pointed tips (Figs. 7c–d) . . . . . *Microcinella*, gen. nov.  
OVS with trifurcate tips (Fig. 11g) . . . . . *Microcina* Briggs and Ubick

### Genus *Microcinella* Ubick and Briggs, gen. nov.

TYPE SPECIES: *Microcina homi* Briggs and Ubick, 1989.

**DIAGNOSIS.**— *Microcinella* differs from all known phalangodids in having a penis where the glans both unfolds and telescopes during expansion (Figs. 6a–b). Females are unique in having an ovipositor with randomly distributed microspines and apical setae hooked and with pointed tips (Figs. 7c–d). A possible synapomorphy for the genus is the form of parastylar lobes, which are rounded and with a papillate surface (Fig. 7g–h).

**ETYMOLOGY.**— The genus name is a diminutive of *Microcina* and is considered feminine in gender.

**DESCRIPTION.**— Body length 0.85–0.97. Dorsum with areolate sculpturing, scute with 1 pair of small AT, additional tubercles lacking except for few along posterior tergal margins. EM broad and low, lacking eyes. Cheliceral base with abrupt dorsodistal swelling, somewhat larger in female. Palpal trochanter with tuberculate dorsal swelling. Palpal megaspines: femur 3 ventrobasal, 1 mesodistal; patella 1 mesal; tibia and tarsus each 2 ectal, 2 mesal. TC, 3-4-4-4

*Male:* Penis with VP entire, bearing 5 pairs of short and 1 pair of long setae; glans unfolds during expansion, with one pair of rounded papillate PSL, without DL, S sinuous and attenuate, with subapical tubule, telescopes out of glans at base of PSL.

*Female:* Ovipositor cuticle with randomly distributed microspines, with 7 pairs apical setae, hooked and with pointed tips.

*Sexual dimorphism:* None observed.

**INCLUDED SPECIES.**— *M. homi* (Briggs and Ubick), *M. coensis* sp. nov.

**DISTRIBUTION.**— Known only from the south of San Francisco Bay, California: Santa Clara, Stanislaus, and Monterey counties.

### *Microcinella homi* (Briggs and Ubick, 1989), comb. nov

Figs. 2a, 3a, 6a–b, 7.

*Sitalcina minor* [part] Briggs and Hom, 1966:263.

*Microcina homi* Briggs and Ubick, 1989:210. Kury, 2003:219.

**DIAGNOSIS.**— See *M. coensis*.

**NEW RECORD.**— CALIFORNIA: **Santa Clara Co.:** San Jose: Communication Hill, SW of County Fair-ground, under serpentine rock in grassland, 24 February 1993 (R. White, CAS), 1 male, 1 female.

**DISTRIBUTION.**— Known only from Santa Clara County, California.

***Microcinella coensis* Ubick and Briggs, sp. nov.**

Figs. 6d–f.

**TYPE MATERIAL.**— Male holotype from under basalt rock in oak chaparral at 8.9 mi N of Bell Station, Henry Coe State Park, Santa Clara County, California, collected on 31 March 1989 by T. Briggs, K. Hom, W. Rauscher, and D. Ubick, deposited at CAS.

**ETYMOLOGY.**— The species name refers to the type locality.

**DIAGNOSIS.**— The male of this species differs from that of *M. homi* in having a more strongly curved stylus with a more complex tip.

**DESCRIPTION.**— Body length 0.89–0.97, LII/SL 2.48–2.76 (N = 2). Color pale orange yellow, abdomen lighter with many white globules visible through integument, appendages yellowish. Body with tubercles arranged in areolate pattern, except at eye mound and venter, posterior tergal margins with tubercles; scute with one pair of AT. EM low, lacking retina and cornea. Palpal megaspines: trochanter 0; femur 3 ventrobasal, 1 mesodistal; patella 1 mesal, 0 ectal; tibia and tarsus 2 mesal, 2 ectal. TC, 3-4-4-4.

*Male*, holotype (paratype): Body length 0.97 (0.89). Scute length 0.65 (0.64), width 0.64 (0.61). EM length 0.14 (0.14), width 0.15 (0.15), height 0.08 (0.08). Genital operculum length 0.12 (0.13), width 0.15 (0.15). Leg II length 1.62 (1.78), LII/SL 2.48 (2.76). TrIV lacking spur or tubercles. GO rounded hexagonal. Penis VP apically rounded, with 1 pair of long and 5 pairs of short setae, AS absent; glans both folds and telescopes, with 1 pair of rounded papillate PSL; S sinuous, with apical tube long, curved ventrally to form loop.

*Female*, unknown.

*Juvenile* (probably this species): Color of body yellowish white, appendages white. Body smooth, lacking tubercles, dorsally with uniform areolate network. Abdomen without apparent segments, but with transverse rows of long setae. Body length 1.00. Scute length not discerned, width 0.55. EM length 0.10, width 0.14. Palpal megaspines as in adult. TC not clearly visible, appears as 2-2-2-2.

**NATURAL HISTORY.**— Specimens have been collected from beneath serpentine and basalt rocks in oak and oak-pine chaparral.

**MATERIAL EXAMINED.**— CALIFORNIA: **Santa Clara Co.:** Henry Coe State Park, 8.9 mi N of Bell Station, under basalt rock in oak chaparral, 31 March 1989 (T. Briggs, K. Hom, W. Rauscher, D. Ubick, CAS), male holotype; Henry Coe State Park, halfway between Manzanita Point Group Camp and Madrone Soda Spring, under rock, 11 March 1989 (T. Briggs, K. Hom, A. Jung, D. Ubick, CAS), 1 juvenile, probably this species. **Stanislaus Co.:** Henry Coe State Park, 15.0 mi N of Bell Station, under serpentine rock in digger pine-oak chaparral, 31 March 1989 (T. Briggs, K. Hom, W. Rauscher, D. Ubick, CAS), 1 male paratype.

**DISTRIBUTION.**— Known only from Henry Coe State Park, Santa Clara and Stanislaus counties, California.

***Microcinella* species**

**NOTE.**— A female collected in Monterey County is clearly a *Microcinella*, given its small size, areolate cuticular ornamentation, and an ovipositor with hooked, pointed apical setae. Because of the disjunction from other *Microcinella*, the specimen most probably represents a new species. Although a description of the species is not possible until the discovery and study of male specimens, this record is mentioned here to document the dramatic range extension of the genus.

**MATERIAL EXAMINED.**— CALIFORNIA: **Monterey Co.:** SE corner of Ft. Ord, oak forest, under sandstone, 5 January 1997 (T. Briggs, D. Ubick, CAS), 1 female.

***Microcina* Briggs and Ubick, 1989**TYPE SPECIES: *Sitalcina tiburona* Briggs and Hom, 1966*Microcina* Briggs and Ubick, 1989:208. Kury, 2003:219.

**DIAGNOSIS.**— These small and blind harvestmen are somatically similar to those in *Microcinella* and *Tularina*, but the genus differs from all sitalcinoid genera by the form of the male genitalia (glans with a small dorsal lobe and a pair of small triangular parastylar lobes, Fig. 8), female genitalia (ovipositor setae with trifurcate tips, Fig. 11g), and a unique sexual dimorphism (the male with an enlarged eyemound, Figs. 9a–d).

**DESCRIPTION.**— Body length 0.82–1.20. Dorsum with areolate sculpturing, scute with 1 pair of small AT, usually lacking additional larger tubercles. EM broad and low, enlarged in male, lacking eyes. Cheliceral base with abrupt dorsodistal swelling somewhat larger in female. Palpal trochanter with tuberculate dorsal swelling. Palpal megaspines: femur 3 ventrobasal, 1 mesodistal; patella 1 mesal; tibia and tarsus each 2 ectal, 2 mesal. TC, 3-4-4-4

*Male:* Penis with VP entire, bearing 3–4 pairs of short and 1 pair of longer setae; glans only unfolds during expansion, with small DL, PSL separate, triangular in shape, surfaced with oblique rows of fringes; S sinuous, lacking subapical tubule.

*Female:* Ovipositor cuticle with randomly distributed microspines, with 7 pairs of apical setae, strongly sinuous and with trifurcate tips.

*Sexual dimorphism:* Male eyemound enlarged.

**INCLUDED SPECIES.**— This genus includes those species previously placed in the *tiburona* group of *Microcina* (Briggs and Ubick, 1989) and the new species described here: *M. potrero*, *M. sanbruno*, *M. stanford*, and *M. tamalpais*.

**DISTRIBUTION.**— Known from the San Francisco Bay Region, from Marin County south to Santa Clara County, California.

***Microcina tiburona* (Briggs and Hom, 1966)**

Figures 2b, 3b.

*Sitalcina tiburona* Briggs and Hom, 1966:265. Briggs, 1968:27.*Microcina tiburona*, Briggs and Ubick, 1989:212. Kury, 2003:219.

**DIAGNOSIS.**— This species is slightly larger than other *Microcina*, from which the male differs by the combination of stylus moderately curved and parastylar lobes rounded and with a coarse fringe.

**NEW RECORD.**— CALIFORNIA: **Marin Co.:** South Tiburon Ridge: Marinero Estates, W122°27'6", N37°53'5", under serpentine rock in oak chaparral, 18 April 1993 (D. Ubick, CDU), 3 males, 2 females.

**DISTRIBUTION.**— Known only from the Tiburon Peninsula.

***Microcina tamalpais* Ubick and Briggs, sp. nov.**

Figures 8a–e, 12.

**TYPE MATERIAL.**— Male holotype from beneath basalt rock in grassland-woodland ecotone, Bald Hill, between Worn Springs Fire Rd. and W Upper Rd., Ross, Marin County, California, collected on 17 February 1991, by T. Briggs, P. and L. Hoch, deposited at CAS.

**ETYMOLOGY.**— The species name is a noun in apposition taken from the type locality on Mount Tamalpais.

**DIAGNOSIS.**— Males of this species differ from other *Microcina* in having short triangular parastylar lobes, similar to but shorter than those in *M. edgewoodensis*.

**DESCRIPTION.**— Body length 0.90–0.95, LII/SL 2.57–2.74 (N = 3). Color light orange, abdomen yellowish with white masses (gut diverticula) visible through integument; appendages yellowish. Body with areolate sculpturing throughout, lacking tubercles on scute and tergal margins; scute with 1 pair of AT. EM low and rounded, eyes absent, lacking retina and cornea. Palpal megaspines: trochanter 0; femur 3 ventrobasal, 1 mesodistal; patella 1 mesal (with apical seta), 0 ectal; tibia and tarsus each with 2 mesal, 2 ectal. TC, 3-4-4-4.

*Male*, holotype (2 paratypes): Body length 0.95 (0.90–0.92). Scute length 0.62 (0.62–0.65), width 0.57 (0.57–0.59). EM length 0.14 (0.15), width 0.16 (0.14–0.16), height 0.10 (0.10). GO length 0.13 (0.11–0.12), width 0.14 (0.13–0.15). Leg II length 1.70 (1.63–1.67), LII/SL 2.74 (2.57–2.63). TrIV spur absent. GO rounded, pentagonal. Penis VP entire, with 1 pair long and 4 pairs short lateral setae, AS absent; glans with short DL, with PSL short and triangular; S sinuous, projecting more than half its length beyond PSL.

*Female*, unknown.

**NATURAL HISTORY.**— Specimens have been collected under basalt rock in a grassland-woodland ecotone.

**MATERIAL EXAMINED.**— CALIFORNIA: **Marin Co.:** Ross, Bald Hill, between Worn Springs Fire Rd. and W Upper Rd., grassland-woodland ecotone, under basalt rock, 17 February 1991 (T. Briggs, P. and L. Hoch, CAS), male holotype, 2 male paratypes (SEM).

**DISTRIBUTION.**— Known only from the type locality.

***Microcina potrero* Ubick and Briggs, sp. nov.**

Figures 8f–i.

**TYPE MATERIAL.**— Male holotype from beneath serpentine rocks in *Eucalyptus* grassland, on Potrero Hill (Lot E of Potrero Avenue between 20<sup>th</sup> and 21<sup>st</sup> streets and Highway 101), San Francisco, California, collected on 26 December 1990, by T. S. Briggs, deposited at CAS.

**ETYMOLOGY.**— The species name is a noun in apposition taken from the type locality.

**DIAGNOSIS.**— Males of this species differ from other *Microcina* in having long parastylar lobes, resembling those in *M. leei* and *M. lumi*, but apically more slender.

**DESCRIPTION.**— Body length 0.97–1.06, LII/SL 2.43–2.54 (N = 4). Color pale orange, abdomen yellowish with white bodies (gut diverticula) visible through integument; appendages yellowish-white. Body with areolate sculpturing throughout, lacking tubercles on scute and tergal margins; scute with 1 pair of AT. EM low and rounded, eyes absent, lacking retina and cornea. Palpal megaspines: trochanter 0; femur 3 ventrobasal, 1 mesodistal; patella 1 mesal, 1 ectal; tibia and tarsus each with 2 mesal, 2 ectal. TC, 3-4-4-4.

*Male*, holotype (paratype): Body length 0.97 (0.99). Scute length 0.69 (0.70), width 0.69 (0.69). EM length 0.18 (0.18), width 0.20 (0.20), height 0.10 (0.10). GO length 0.12 (0.12), width 0.13 (0.14). Leg II length 1.69 (1.71), LII/SL 2.44 (2.43). TrIV spur absent. GO rounded, subpentagonal. Penis VP entire, with 1 pair of long and 4 pairs short lateral setae, AS absent; glans with DL, PSL broadly pointed, weakly rugose; S short, sinuous.

*Female*, allotype (paratype): Body length 1.00 (1.06). Scute length 0.72 (0.73), width 0.76 (0.77). EM length 0.15 (0.17), width 0.18 (0.20), height 0.10 (0.10). GO length 0.11 (0.12), width 0.15 (0.16). Leg II length 1.84 (1.80), leg II/ scute length 2.54 (2.44). Genital operculum rounded, subpentagonal. Ovipositor surface sparsely set with microspines, apical teeth absent, with 7 pairs of apical setae, curved, trifurcate.

**Sexual dimorphism.**— The male has a larger eyemound.

**NATURAL HISTORY.**— Specimens have been collected from beneath serpentine rocks in *Euca-*

*lyptus* grassland. Current status of this species is uncertain due to destruction of the only known locality from construction at the San Francisco General Hospital.

**MATERIAL EXAMINED.**— CALIFORNIA: **San Francisco Co.:** San Francisco, Potrero Hill (Lot E of Potrero Avenue between 20th and 21st streets near Highway 101), beneath serpentine rocks in *Eucalyptus* grassland, 26 December 1990, by (T. Briggs, CAS), male holotype, female allotype, 1 male and 1 female paratypes.

**DISTRIBUTION.**— Known only from the type locality.

***Microcina sanbruno* Ubick and Briggs, sp. nov.**

Figures 9–10.

**TYPE MATERIAL.**— Male holotype from beneath serpentine rock in grassland, Serbian Ravine, San Bruno Mountain, San Mateo County, collected on 1 March 1992 by D. Ubick and T. Briggs, deposited at CAS.

**ETYMOLOGY.**— The species name is a noun in apposition taken from the type locality.

**DIAGNOSIS.**— Males of this species resemble those of *Microcina tiburona*, but differ in having a straighter stylus and narrower parastylar lobes.

**DESCRIPTION.**— Body length 0.92–1.09, LII/SL 1.94–2.82 (N = 8). Color pale orange, abdomen yellowish, with white bodies (gut diverticula) visible through integument; appendages yellowish-white. Body with areolate sculpturing throughout, with some larger tubercles along tergal margins; scute with 1 pair of AT. EM low and rounded, eyes absent, lacking retina and cornea. Palpal megaspines: trochanter 0; femur 3 ventrobasal, 1 mesodistal; patella 1 mesal, 1 ectal; tibia and tarsus each with 2 mesal, 2 ectal. TC, 3-4-4-4.

*Male*, holotype (3 paratypes): Body length 1.09 (0.92–1.08). Scute length 0.78 (0.62–0.77), width 0.70 (0.58–0.67). EM length 0.22 (0.17–0.22), width 0.27 (0.20–0.25), height 0.10 (0.10–0.12). GO length 0.11 (0.11–0.12), width 0.13 (0.13–0.14). Leg II length 1.91 (1.64–1.87), LII/SL 2.45 (2.39–2.71). TrIV spur absent. GO subpentagonal. Penis VP entire, with 1 pair of long and 4 pairs short lateral setae, AS absent; glans with small DL, PSL broadly pointed; S long, weakly sinuous.

*Female*, allotype (3 paratypes): Body length 1.09 (0.95–0.98). Scute length 0.90 (0.62–0.72), width 0.72 (0.65–0.72). EM length 0.15 (0.14–0.15), width 0.19 (0.18–0.19), height 0.09 (0.10). GO length 0.11 (0.10–0.12), width 0.13 (0.13–0.14). Leg II length 1.75 (1.69–1.80), LII/SL 1.94 (2.35–2.82). GO rounded. Ovipositor surface sparsely set with microspines, apical teeth absent, with 7 pairs of apical setae, strongly curved, trifurcate.

**Sexual dimorphism.**— The male has a slightly larger eyemound.

**NATURAL HISTORY.**— Specimens have been collected from beneath serpentine and sandstone rocks in grassland and chaparral.

**MATERIAL EXAMINED.**— CALIFORNIA: **San Mateo Co.:** San Bruno Mountain, Buckeye Canyon, Indian Mound, under sandstone, 22 June 1991 (T. Briggs, CAS), 1 male, 1 female; Serbian Ravine, grassland, under serpentine, 1 March 1992, D. Ubick, T. Briggs, male holotype, female allotype, 1 male (SEM); Trail just N of ridge at first set of powerlines E of towers, ca 1000' el, chaparral, under sandstone, 11 May 1991 (D. Ubick, T. Briggs, CAS), 1 female (SEM); 18 Jan 1992 (D. Ubick, T. Briggs, W. Rauscher, CAS), 1 female; 26 Jan 1992 (D. Ubick, T. Briggs, W. Savary, CAS), 1 male. All specimens paratypes, unless indicated otherwise.

**DISTRIBUTION.**— Known only from San Bruno Mountain, San Mateo County.

***Microcina stanford* Ubick and Briggs, sp. nov.**

Fig. 11.

**TYPE MATERIAL.**— Male holotype from beneath basalt rock in oak grassland, at Stanford Antenna

Farm, east slope, E of Alpine Rd and Hwy 280, Santa Clara County, on 9 January 1998, by T.S. Briggs, deposited at CAS.

**ETYMOLOGY.**— The species name is a noun in apposition taken from the type locality.

**DIAGNOSIS.**— The male of this species has a very short stylus and most closely resembles that of *Microcina lumi*, but differs in having narrower PSL.

**DESCRIPTION.**— Body length 0.94–1.14, LII/SL 1.72–2.75 (N = 5). Color pale orange, abdomen yellowish-white. Appendages yellowish-white. Body with areolate sculpturing throughout, lacking tubercles on scute and tergal margins, scute with 1 pair of AT. EM low and rounded, eyes absent, lacking retina and cornea. GO rounded, pentagonal. Palpal megaspines: trochanter 0; femur 3 ventrobasal, 1 mesodistal; patella 1 mesal, 1 ectal; tibia and tarsus each with 2 mesal, 2 ectal. TC, 3-4-4-4.

*Male*, holotype (paratype): Body length 1.14 (0.94). Scute length 1.06 (0.73), width 0.76 (0.68). EM length 0.24 (0.21), width 0.24 (0.25), height 0.14 (0.12). GO length 0.12 (0.12), width 0.14 (0.14). Leg II length 1.82 (2.01), LII/SL 1.72 (2.75). TrIV spur absent. Penis VP entire, with 1 pair of long and 5 pairs short lateral setae, AS absent; glans with DL, PSL broadly pointed, weakly fringed; S short, sinuous.

*Female*, allotype (2 paratypes): Body length 1.00 (0.94–1.08). Scute length 0.70 (0.70–0.74), width 0.66 (0.66–0.75). EM length 0.16 (0.12–0.15), width 0.18 (0.20), height 0.10 (0.14). GO length 0.12 (0.10–0.13), width 0.14 (0.12–0.15). Leg II length 1.86 (1.66–1.87), LII/SL 2.66 (2.37–2.53). Ovipositor surface sparsely set with microspines, apical teeth absent, with 6 pairs of apical setae, curved, trifurcate, few setae with polyfurcate tips.

*Sexual dimorphism.*— The male eyemound is slightly larger.

**NATURAL HISTORY.**— Specimens have been collected from beneath basalt rocks in oak grassland.

**MATERIAL EXAMINED.**— CALIFORNIA: **Santa Clara Co.**: Stanford Antenna Farm, east slope, E of Alpine Rd and Hwy 280, oak grassland, under basalt rock, 9 January 1998 (T. Briggs, CAS), holotype male, allotype female, 7 male paratypes (SEM), 5 female paratypes (SEM).

**DISTRIBUTION.**— Known only from the type locality.

### *Microcina* species

**NOTE.**— A male specimen from northern Marin County possibly represents a new species, although additional specimens are necessary to confirm this. It is mentioned here to document the northern range extension of the genus.

**MATERIAL EXAMINED.**— CALIFORNIA: **Marin Co.**: Novato, Rush Creek Preserve, volcanic hill, 8 March 2001 (T. Briggs, CAS), 1 male.

### *Sitalcina* Banks, 1911

TYPE SPECIES: *Sitalces californica* Banks, 1893.

*Sitalces* (part) Banks, 1893:151.

*Metapachylus* Banks, 1909:230.

*Sitalcina* Banks, 1911:415. Goodnight and Goodnight, 1942:8. Briggs and Hom, 1966:262. Briggs, 1967:89; 1968:8. Rambla, 1969:397. Briggs and Ubick, 1989:207. Ubick and Briggs, 1989:96. Edgar, 1990:548. Kury, 2003:220.

*Paramitraceras* (part) Roewer, 1912:155.

*Pachylicus* (part) Roewer, 1923:118.

**DIAGNOSIS.**— *Sitalcina* differs from other phalangodids by the combination of penis having an

entire ventral plate, a folding glans (Fig. 16a), trough-like dorsal lobes (Fig. 16c) (but divided in *S. seca*), two (separate) parastylar lobes (Fig. 13), and an ovipositor with microspines in imbricate arrangement (Fig. 16i). Males differ from all Nearctic phalangodids with entire ventral plates in having a large ventral process (spur) ectally on trochanter IV (Figs. 15g–h).

**DESCRIPTION.**— Body length 1.25–2.50. Body finely rugose with variable number of larger tubercles scattered throughout, especially on tergite margins; scute with few to several AT. EM rounded to conical, eyes present. Cheliceral base with sloping dorsodistal swelling. Palpal megaspines: trochanter 1–2 small, femur 3 ventrobasal, 1 mesodistal; patella 1 mesal, 2 ectal; tibia and tarsus each 2 ectal, 2 mesal. TC, 3-5-5-5.

*Male:* Penis with VP entire, bearing several pairs of setae, AS lacking (except in *S. californica*); glans unfolds during expansion, with trough-like DL (divided in *S. seca*), with one pair of PSL; S variable in shape, lacking subapical tubule.

*Female:* Ovipositor cuticle with microspines in imbricate arrangement, apex lacking tooth, with 8 pairs of setae, hooked or sinuous, with simple or polyfurcate tips.

*Sexual dimorphism:* Male TrIV with ectoventral spur.

**INCLUDED SPECIES.**— To the previously described species, *S. borregoensis* Briggs, *S. californica* (Banks), *S. chalonga* Briggs, *S. flava* Briggs, *S. lobata* Goodnight and Goodnight, and *S. sura* Briggs, the following new species are here added: *S. catalina*, *S. peacheyi*, *S. rothi*, and *S. seca*.

**DISTRIBUTION.**— California and Arizona.

### Key to the Species Groups of *Sitalcina*

1. Palpal Fm lacking dorsal tubercles (Figs. 15e–f); EM strongly conical, weakly tuberculate (Fig. 15a); male TrIV normal, ventroectally with 1 straight knobby spur (Figs. 15g–h); VP with AS (Fig. 16f); PSL unilobed (Figs. 16d–e); OV setae hooked, with pointed tips (Figs. 16g–h) ..... *S. californica* group  
Palpal Fm with dorsal tubercles; EM weakly conical to rounded, with variable tuberculation; male TrIV normal to elongate, ventroectal spur usually curved, if straight then not knobby; VP lacking AS; PSL bi- or tri- lobed; OV setae variable ..... 2
2. Palpal Fm dorsal tubercles asetose (Figs. 21b–c); EM weakly tuberculate, subconical to rounded (Fig. 21a); male TrIV normal, with 1 (ectal) spur, curved to straight with rounded tip (Figs. 19e, 21d); PSL bilobed (Fig. 13); OV setae curved, with brush tips (Figs. 20f, j) ..... *S. sura* group  
Palpal Fm dorsal tubercles setose (Figs. 31c–e); EM strongly tuberculate, rounded (Fig. 31a–b); male TrIV enlarged, with 2 spurs, ectal pointed and forming loop (Figs. 31f–g); PSL trilobed (Figs. 32e–f); OV setae hooked, with pointed tips (Figs. 32g–h). . . . *S. lobata* group

Characters for the *Sitalcina* species groups are given below, with the likely synapomorphies shown in bold. Apomorphies are identified on the basis of states that are apparently unique in the family (#1, 2, 3, 4, 5) or genus (6, 8, 9, 12), and by comparison with probable outgroups, *Microcinella* and *Microcina* (10, 11). Some of these characters are further discussed in the Phylogeny section.

	<i>californica</i> group	<i>sura</i> group	<i>lobata</i> group
1. Pfm dorsomesal tubercle row	absent	<b>present</b>	absent
2. Pfm dorsal setose tubercles	absent	absent	<b>present</b>
3. TrIV length	normal	normal	<b>elongate</b>
4. TrIV ectal spur	straight	<b>curved</b> -straight	<b>looped</b>
5. TrIV ectal spur tip	rounded	rounded	<b>pointed</b>
6. TrIV mesal spur	absent	absent	<b>present</b>
7. EM shape	strongly conical	subconic-round	rounded
8. EM tuberculation	weak	weak	<b>strong</b>
9. VP AS	<b>present</b>	absent	absent
10. PSL form	unilobed	<b>bilobed</b>	<b>trilobed</b>
11. OVS shape	hooked	<b>curved</b>	hooked
12. OVS tip	pointed	<b>brush</b>	pointed

### *Sitalcina californica* Group

**DIAGNOSIS.**— The single species representing this group, *Sitalcina californica*, is easily recognized by its distinctive eyemound: large, conical, and anteriorly projecting (Fig. 15a–c). Unlike other *Sitalcina*, the palpal femur lacks dorsal tubercles (Fig. 15e–f), and the male differs in having a penis with a pair of apical spines on the ventral plate (Fig. 16b, f) and a TrIV spur that is relatively straight and bears an ectal knob (Fig. 15g–h).

**INCLUDED SPECIES.**— Only *S. californica* (Banks).

**DISTRIBUTION.**— Central Coast Ranges of California.

#### *Sitalcina californica* (Banks, 1893)

Figures 1, 2d, 3d, 14a–c, 15–16.

*Sitalces californica* Banks, 1893:151; 1901:672; 1904:363; 1911:415.

*Sitalcina californica*, Banks, 1911:415.

*Sitalcina californicus*, Goodnight and Goodnight, 1942:8. Briggs and Hom, 1966: 263. Briggs, 1967:89; 1968:10. Edgar, 1990:548.

*Paramitraceras californicus*, Roewer, 1912:155.

*Pachylicus californicus*, Roewer, 1923:118.

*Sitalcina californica*, Ubick and Briggs, 1989:89. Kury, 2003:220.

**TYPE MATERIAL.**— Female holotype from Southern California (“So. Calif.”), Nathan Banks Coll., at MCZ (#14679), examined. Although the holotype is a female, it is unusual in having well developed TrIV spurs, uniquely so of the specimens examined. Although extraction of the genitalia was not attempted, due to the brittleness of the type, examination through the genital opening reveals an ovipositor with its characteristic crossed setae. The TrIV spurs are shorter and more slender than in males. Similarly “masculinized” females (2 specimens) were observed in another phalangodid, *Texella reyesi* Ubick & Briggs (1992:211).

**DIAGNOSIS.**— Same as for species group.

**DESCRIPTION.**— Body length 1.40–1.96, LII/SL 2.65–3.10 (N = 10). Color orange to orange-brown, appendages lighter orange, tarsi whitish. Body dorsum finely rugose, with larger tubercles along median line to eyemound, in transverse rows on scute, and along tergal margins; scute with 3–6 pairs of AT. EM large, conical, anteriorly directed, with some larger tubercles, especially at apex; eyes present. GO rounded, subrectangular. Palpal femur with dorsal row of 3–5 setae. Palpal megaspines: trochanter 0; femur 3 ventrobasal, 1 mesodistal; patella 2 mesal, 1 ectal; tibia 2 mesal (with 3rd represented by distal setose tubercle), 2 ectal; tarsus 2 mesal, 2 ectal. TC, 3-5-5-5.

*Male* (N = 6): Body length 1.40–1.90. Scute length 1.04–1.30, width 1.10–1.34. EM length

0.26–0.41, width 0.26–0.40, height 0.23–0.40. GO length 0.15–0.22, width 0.18–0.20. Leg II length 3.22–3.72, LII/SL 2.77–3.10. TrIV spur a straight rounded process with ectal knob, length from 0.5–1.0 trochanter diameters. Penis VP subtriangular, entire with rounded apical projection, with 8–10 pairs of lateral setae, short AS present; glans with trough-like DL, roughly square in shape, PSL trough-like, apically rounded and with small ventrodistal ornamentation; S short, straight, pointed and with laterobasal sculpturing.

*Female* holotype (additional specimens, N = 4): Body length 1.80 (1.40–1.96). Scute length 1.14 (1.10–1.20), width 1.30 (1.26–1.34). EM length 0.37 (0.26–0.34), width 0.32 (0.30–0.32), height 0.30 (0.26–0.38). GO length 0.15 (0.16–0.18), width 0.20 (0.20–0.22). Leg II (missing in holotype) length ? (3.18–3.44), LII/SL ? (2.65–3.00). TrIV lacking ventral tubercle. Ovipositor of two segments, basal finely wrinkled, distal with microspines in imbricate pattern; with 7–8 pairs of setae, apically hooked, pointed.

*Sexual dimorphism.*— The male has a TrIV spur which is usually absent in females, except the aberrant holotype.

*Variation.*— Individuals vary in the degree of tuberculation. Larger males have more robust and strongly bent TrIV spurs. Males also show slight differences in the ornamentation of the PSL. The TrIV spur on the female holotype appears to be unique in the sample studied.

**NATURAL HISTORY.**— Most specimens have been collected in forest biomes, including both coniferous and broadleaf evergreen forests, from beneath rocks, in decomposing wood, and in leaf litter. These harvestmen can be quite common, especially in redwood forests. Individuals of both sexes, as well as juveniles, have been collected throughout the year.

Several individuals were kept in the lab and maintained on a diet of collembola and/or mites for several weeks. (J. Cokendolpher, pers. comm.)

**MATERIAL EXAMINED.**— CALIFORNIA: **Mendocino Co.:** 2.0 mi N Albion along Hwy 1, pine-tanoak forest, under logs and crumbly sandstone, 20 July 1990 (D. Ubick, CDU), 3 males, 3 females, 1 juvenile; Big River, ca 2 mi W James Creek on Hwy 20, under redwood logs, 19 July 1990 (D. Ubick, CDU), 2 males, 3 females, 2 juveniles; redwood duff, 5 May 1991 (D. Ubick, CDU), 3 males, 4 females; Cameron Road, 0.1 mi NW Philo Greenwood Road, redwood duff, 3 May 1991 (D. Ubick, CDU), 5 males, 5 females; Camp Dunlap, redwood forest, 25 July 1993 (J. Boutin, CDU), 3 males, 1 female, 1 juvenile; 2 August 2006 (D. Ubick, CAS), 9 males, 2 females; Caspar, 7 March 1954 (J. Helfer, AMNH), 7 males, 3 females [collected with *Calicina sequoia*]; Dimmick State Recreation Area, under redwood log, 7 December 1968 (V. Lee, CAS), 1 male; Faulkner County Park, redwood duff, 3 May 1991 (D. Ubick, CDU), 3 males, 1 female; Highway 128, ca. 5 km E Hwy 1, N39°10.2', W123°42', redwood forest, 3 August 2006 (D. Ubick, CDU), 1 male, 1 female; Jackson State Forest, 0.5 mi W Camp Dunlap, el 400', redwood duff, 16 September 1990 (D. Ubick, CDU), 1 male; 0.5 mi W Dunlap Pass along Big River, under redwood logs, 19 July 1990 (D. Ubick, CDU), 1 female; 20 July 1990 (D. Ubick, CDU), 1 male, 3 females, 1 juvenile; 15 mi W Willits on Hwy 20, N39°20.84', W123°30.87', sifting redwood duff, 27 May 2005 (D. Ubick, CDU), 1 male, 1 female, 1 juvenile; James Creek at Hwy 20, 19 April 1971 (A. Jung, CAS), 1 male, 2 females; Little River, 7 June 1955 (J. Helfer, UCB), 1 male; 11 June 1955 (J. Helfer, UCB), 1 male; 3 August 1957 (G. Marsh, J. Helfer, UCB), 2 males, 4 females; 1.5 mi S-SE Little River, 3 July 1966 (T. Briggs, V. Lee, K. Hom, CAS), 4 females, 2 juveniles; MacKerricher State Park, berlese ex *Alnus* litter, 7 November 1976 (J. Doyen, UCB), 3 males, 1 female; Mendocino, 25 July 1954 (J. Helfer, AMNH), 4 males, 10 females [collected with *Calicina sequoia* and *Metanonychus* sp.]; 10 October 1954 (J. Helfer, AMNH), 4 males, 2 females; 4 July 1955 (J. Helfer, UCB), 2 males; 3 March 1957 (J. Helfer, AMNH), 2 females; in redwood duff, 4 May 1963 (no collector, CAS), 1 male; N of Mendocino, humus nr swamp, 6 July 1957 (J. Helfer, R. Schuster, UCB), 3 males, 1 female; Mendocino Woodlands, S end nr Big River, el 80', redwood duff, 16 September 1990 (D. Ubick, CDU), 6 males, 6 females; under redwood logs, 17 September 1990 (D. Ubick, CDU), 1 juvenile; Montgomery Woods State Reserve, old growth redwood forest, under logs, 21 July 1990 (D. Ubick, CDU), 1 female, 1 juvenile; same collection, but in redwood duff, 1 male, 1 female; Mushroom Corners, berlese ex Douglas fir litter, 10 November 1974 (T. Ham-

mer, CAS), 1 female; Ryan Creek, 8 November 1951 (J. MacSwain, UCB), 1 male; no date (no collector, UCB), 1 male, 1 female; nr E entrance Standley State Park, 4 July 1966 (T. Briggs, V. Lee, K. Hom, CAS), 5 males, 2 females, 1 juvenile; Tranquility, 1.5 mi S Caspar, riparian litter, 17 September 1990 (D. Ubick, CDU), 2 males, 1 female; 18 September 1990 (D. Ubick, CDU), 2 males, 2 females; same collection but from tanoak-bishop pine litter, 2 males, 2 females; same collection but from mossy leaf mold in pine forest, 6 males, 1 female; same collection but from bishop pine duff, 8 males, 5 females; redwood duff, 3 May 1991 (D. Ubick, CDU), 2 males, 3 females; under pine-tanoak logs, 4 May 1991 (D. Ubick, CDU), 2 females; same collection but from pine litter, 6 males, 5 females; same collection but under rocks in pine forest, 1 female; berlese of redwood-tanoak litter, 5 May 1991 (D. Ubick, CDU), 2 females, 1 juvenile; Van Damme State Park, Fern Canyon, under redwood logs, 21 July 1990 (D. Ubick, CDU), 4 males, 1 juvenile; 4 mi N Yorkville, under redwood log, 2 March 1968 (T. Briggs, CAS), 1 male, 3 females; [no locality], 23 July 1955 (J. Helfer, AMNH), 2 females. **Sonoma Co.:** Annapolis, 23 February 1955 (J. Helfer, AMNH), 1 male; 1.5 mi E junction Anapolis and Skaggs Springs roads, 18 April 1971 (A. Jung, CAS), 1 male, 1 female; nr Armstrong Redwoods State Park, under rocks and logs, 12 February 1966 (T. Briggs, CAS), 1 male, 1 female; 1 mi N Camp Meeker, redwood forest, under serpentine, 12 Mar 1967 (T. Briggs, CAS), 4 females; 2.1 mi NW Camp Meeker, el 90m, 14 January 1983 (T. Briggs, V. Lee, D. Ubick, CAS), 4 males, 2 females, 4 juveniles; 0.2 mi N Camp Meeker, 12 December 1985 (V. Lee, L. Zinn, CAS), 1 male; 3.5 mi W El Verano, Canyon Drive at Deer Park Drive, 11 February 1983 (T. Briggs, V. Lee, D. Ubick, CAS), 18 males (SEM), 29 females, 20 juveniles; broadleaf forest, under volcanic rocks, 6 February 1988 (T. Briggs, V. Lee, D. Ubick, CAS), 1 male, 3 females; near El Verano, junction of Spring and Prospect roads at Diamond Estates Recreation Area, 18 January 1988 (T. Briggs, CAS), 4 males, 3 females, 1 juvenile; 3.5 mi W El Verano, grassland, under volcanic rocks, 6 February 1988 (D. Ubick, T. Briggs, CDU), 1 female, 5 juveniles; 4.1 mi SE Ft. Ross Historical State Park, 3 July 1966 (T. Briggs, V. Lee, A. Jung, K. Hom, CAS), 8 males, 7 females, 1 juvenile; Franz Creek, just E of Chalk Hill Road, redwood forest, under logs, 12 April 1990 (D. Ubick, T. Briggs, W. Rauscher, B. Lym, CAS), 1 male; Glen Ellen, 15 February 1954 (V. Roth, R. Schuster, AMNH), 1 male, 1 female; 8 mi N Guerneville, 18 August 1959 (V. Roth, W. Gertsch, AMNH), 1 male; Harrison Grade Road nr Green Valley Road, redwood forest, under logs, 12 April 1990 (D. Ubick, T. Briggs, W. Rauscher, B. Lym, CAS), 3 females; Healdsburg, 11 January 1981 (T. Briggs, CAS), 2 males; 1.5 mi E Healdsburg on Bailache Avenue, broadleaf evergreen forest, under volcanic rocks, 27 December 1980 (D. Ubick, CDU), 1 male; oak leaf litter, 29 March 1981 (D. Ubick, CDU), 1 female; 15 June 1981 (D. Ubick, CDU), 2 males, 1 female, 1 juvenile; 21 December 1981 (D. Ubick, CDU), 1 female; 13 January 1991 (D. Ubick, W. Savary, K. Dabney, CDU), 3 males, 9 females; same as previous but from berlese of moss, 1 male; Jenner, redwood forest, under serpentine, 12 March 1967 (K. Hom, T. Briggs, CAS), 4 males, 2 females; nr Lytton, 1.6 mi W Soda Rock Lane from Alexander Valley Road, 25 February 1968 (T. Briggs, CAS), 3 females; W of Mark West Reservoir, douglas fir litter, 22 January 1958 (F. Raney, R. Schuster, UCB), 2 females, (AMNH), 2 males, 2 females; Mark West Springs, 31 December 1953 (G. Marsh, V. Roth, R. Schuster, AMNH), 1 male, 2 females; SE of Monte Rio, Bohemian Highway, 0.3 mi N of Main St., 9 January 2007, N38°27', W122°59', oak-douglas fir forest, under metamorphic rocks (D. Ubick, T. Briggs, CDU), 1 male, 2 females; 2 mi due SW Occidental, 7 January 1967 (T. Briggs, A. Lee, CAS), 5 males, 1 juvenile; 0.15 mi E Occidental, N of Graton Road, redwood forest, under schist, 12 April 1990 (D. Ubick, T. Briggs, W. Rauscher, B. Lym, CAS), 3 males, 6 females, 4 juveniles; 4 mi NE Penngrove, 26 November 1965 (J. Bucket, UCD), 2 males, 4 females; Plantation, 23 February 1955 (J. Helfer, AMNH), 1 female; 0.3 mi W Plantation, sifting redwood litter, 12 February 1966 (T. Briggs, K. Hom, D. Owyang, CAS), 5 males, 2 females; same collection but from under rocks and logs (T. Briggs, K. Hom, A. Jung, CAS), 4 males, 3 females; Salt Point State Park, Wildcat Creek, el 400', redwood duff, 22 September 1990 (D. Ubick, CDU), 10 males, 9 females; 8 mi N Santa Rosa, nr bridge on Chalk Hill Road, 5.8 mi NE junction Pleasant and Chalk Hill avenues, 21 May 1966 (T. Briggs, V. Lee, K. Hom, CAS), 3 males, 5 females, 1 juvenile; Seaview, 23 February 1955 (J. Helfer, AMNH), 1 male; Sebastopol, leaf mould (R. Darby, AMNH), 2 females; Sonoma Mountain, end of Sonoma Mountain Road, 18 January 1988 (T. Briggs, CAS), 1 female; 1 mi E Stewart's Point, redwood forest, under rocks, 12 February 1966 (K. Hom, A. Jung, CAS), 1 male, 2 females; 7.4 mi SE Stewart's Point, 3 July 1966 (T. Briggs, V. Lee, CAS), 1 female; 8.9 mi SE Stewart's Point, 3 July 1966 (T. Briggs, V. Lee, CAS), 1 female; 13.4 mi SE Stewart's Point, 3 July 1966 (V. Lee, CAS), 1 male, 1 female; 1 mi S Trenton, 15 May 1957 (R. Schuster, UCB), 2 females. **Napa**

Co.: Mount St. Helena, 31 December 1953 (G. Marsh, R. Schuster, V. Roth, AMNH), 1 female; 7 mi W Oakville, oak-redwood duff, 13 December 1957 (L. Smith, R. Schuster, AMNH), 3 males, 1 female; 15 February 1954 (V. Roth, R. Schuster, AMNH), 3 males. **Marin Co.:** 1.8 mi SW Alpine Dam, under rock, 27 January 1966 (K. Hom, T. Briggs, CAS), 1 female; 3 mi NE Alpine Dam, Alpine Lake, under rocks, 27 January 1966 (A. Jung, K. Hom, P. Chin, CAS), 2 males, 4 females; Bolinas, 24 March 1960 (R. Schuster, AMNH), 2 females; Bolinas Ridge, N of Toll Station, under rocks, 5 December 1965 (V. Lee, CAS), 1 female; 13 August 1965 (V. Lee, T. Briggs, CAS), 3 females; 1 January 1966 (T. Briggs, CAS), 1 female; nr Bootjack Camp, along Bootjack Trail, undersurface of redwood log, 27 January 1973 (T. Briggs, R. Lem, CAS), 1 male, 2 females; Inverness, 8 November 1953 (G. Marsh, R. Schuster, AMNH), 1 male; 1 mi S Inverness, berlese bishop pine duff, 12 March 1966 (C. O'Brien, UCB), 1 female; 25 December 1966 (C. O'Brien, UCB), 1 male, 1 female; berlese douglas fir duff, 25 December 1960 (C. O'Brien, UCB), 2 males; 30 January 1959 (D. Linsdale, UCB), 2 males, 8 females, 2 juveniles; 1 mi SE Inverness, douglas fir duff, 8 January 1961 (C. O'Brien, UCB), 1 female; 1 mi W Inverness, 1 March 1960 (Grigarick, Smith, R. Schuster, AMNH), 1 male; 2 air mi W Inverness, berlese of *Alnus rubra* litter, 1 May 1976 (J. Doyen, UCB), 4 males, 3 females; Lake Lagunitas, 19 July 1966 (T. Briggs, CAS), 1 male, 1 female; under rocks, 5 February 1966 (K. Hom, CAS), 2 males; Lily Lake, E of Alpine Lake, berlese of redwood litter, 23 November 1966 (V. Lee, CAS), 1 male, 3 females; Mill Valley, forest duff, 27 May 1952 (H. Leech, CAS), 1 male, 1 female; sifting forest floor, 30 May 1952 (H. Leech, CAS), 14 males, 20 females; 28 May 1952 (H. Leech, CAS), 4 males, 3 females, 4 juveniles; 3 June 1952 (H. Leech, CAS), 1 male, 5 females, 1 juvenile; sifting old *Neotoma* nest, 14 June 1952 (H. Leech, CAS), 2 males, 1 female; 9 July 1952 (H. Leech, CAS), 5 females; sifting debris under trees, June 1952 (H. Leech, CAS), 11 males, 39 females, 6 juveniles; 2 September 1953 (G. Marsh, R. Schuster, AMNH), 10 males, 18 females, 1 juvenile; Mount Tamalpais State Park, 0.7 mi due N Muir Woods N. M. on Old Railroad Grade, redwood forest, under rocks, 31 May 1968 (V. Lee, CAS), 1 male, 3 females; Muir Woods, 5 September 1927 (no collector, AMNH), 1 male; nr Muir Woods, 21 August 1965 (T. Briggs, V. Lee, CAS), 4 females; Fern Creek, undersurface of redwood log, 27 January 1973 (T. Briggs, R. Lem, CAS), 1 male; 0.3 mi N Muir Woods, redwood litter, 21 August 1965 (T. Briggs, K. Hom, V. Lee, D. Owyang, CAS), 1 male, 1 female; 1 mi SE Nicasio, under redwood log, 10 February 1968 (K. Hom, G. Leung, CAS), 1 male, 1 female; Novato, saddle SW Burdell Mountain, el 550', oak forest, under serpentine, 2 January 1986 (T. Briggs, D. Ubick, CAS), 1 female; Paradise Valley, 2 mi NW Bolinas, redwood litter, 22 March 1966 (C. O'Brien, UCB), 4 males, 4 females, 1 juvenile; Phoenix Lake, 14 May 1966 (V. Lee, CAS), 2 males, 4 females, 5 juveniles; Point Reyes, 14 February 1980 (R. Kimsey, R. Schuster, UCD), 1 male, 2 females; Point Reyes, 0.5 mi E entrance to park, thick riparian, under rock, 24 February 1979 (D. Ubick, CAS), 1 female; Point Reyes, Mt. Whittenburg, 12 November 1972 (T. Briggs, CAS), 4 females; Point Reyes, Redwood Grove, nr Dogtown, 10 July 1982 (T. Briggs, CAS), 1 male; 6 mi E Point Reyes Station, 1 March 1960 (Grigarick, Smith, R. Schuster, AMNH), 1 female; Ross, Bald Hill, 1 March 1991 (D. Ubick, T. Briggs, CAS), 2 males, 1 female, 4 juveniles; 1.8 mi E Stinson Beach on Panoramic Hwy, 3 July 1966 (T. Briggs, A. Jung, K. Hom, CAS), 1 female, 1 juvenile; San Geronimo, W122.42°, N37.59°, 27 September 1963 (J. W. Ivie, AMNH), 2 females; Taylor State Park, 24 October 1953 (V. Roth, AMNH), 1 male, 1 female; berlese redwood duff, 19 December 1966 (C. O'Brien, UCB), 2 males, 2 females, 2 juveniles; 12 June 1993 (D. Ubick, CDU), 5 males, 8 females, 5 juveniles; 1 mi S Taylor State Park, redwood duff, 17 January 1959 (C. O'Brien, UCB), 1 male. **San Mateo Co.:** 7 mi S Crystal Springs Dam, redwood grove, under sandstone, 19 February 1966 (T. Briggs, V. Lee, CAS), 1 male, 2 females; 6 mi SE Half Moon Bay, 1 June 1957 (R. Schuster, UCB), 10 males, 9 females; 21 July 1957 (R. Schuster, UCB), 4 males, 5 females; Kings Mountain, 1 September 1958 (R. Schuster, UCB), 1 male; 8 February 1959 (R. Schuster, UCB), 1 male, 3 females; 16 October 1994 (D. Ubick, CAS), 1 male; 1.0 mi N La Honda, along La Honda Creek, redwood-douglas fir duff, 16 May 1991 (D. Ubick, CDU), 3 males, 1 female; Linda Mar, coastal scrub, ex fern litter, 17-18 February 1967 (T. Briggs, V. Lee, CAS), 4 males, 8 females; Pilarcito Lake, berlese of *Adenostoma* and *Arctostaphylos*, 17 February 1964 (C. O'Brien, UCB), 3 males; berlese, 27 February 1966 (C. O'Brien, UCB), 2 males, 3 females, 1 juvenile; San Bruno Mountain, 19 December 1970 (T. Briggs, CAS), 2 males, 3 females; Crystal Cave Canyon, dense *Ceanothus* forest, under rock, 20 July 1982 (D. Ubick, CDU), 1 male; Owl Canyon, 20 March 1994 (D. Ubick, T. Briggs, W. Rauscher, CAS), 1 female, 1 juvenile; trail at power line, ca 1000' el, dense chaparral, under sandstone, 10-11 May 1991 (D. Ubick, T. Briggs, CDU), 4 males, 1 female,

3 juveniles; Serbian Ravine, 1 March 1992 (D. Ubick, T. Briggs, CAS), 2 juveniles; San Pedro Valley County Park, riparian canyon, under sandstone, 18 May 1991 (D. Ubick, CDU), 1 male, 1 juvenile; Skyline Boulevard, 1 mi NW Kings Mountain, redwood duff, 29 June 1990 (D. Ubick, CDU), 4 males, 3 females. **Santa Cruz Co.:** Big Basin, 23 December 1953 (V. Roth, AMNH), 4 males, 3 females; Cave Gulch, under rock, 17 November 1966 (T. Briggs, CAS), 1 male, 2 females; 18 June 1984 (T. Briggs, D. Ubick, CAS), 4 males (SEM), 3 females; Bat Cave, under rocks, 11 June 1966 (T. Briggs, V. Lee, CAS), 1 male, 2 females; 21 April 1979 (D. Rudolph, S. Winterath, E. vanIngen, D. Cowan, CAS), 1 male; near Dolloff Cave, 19 March 1966 (T. Briggs, K. Hom, CAS), 2 males; 0.25 mi S Dolloff Cave, 19 March 1966 (T. Briggs, K. Hom, CAS), 1 male, 3 females; Empire Cave, under rock in cave, 24 June 1990 (D. Ubick, CDU), 1 male; Empire Grade Rd., 18 February 1991 (D. Ubick, CJC), 1 male, 2 females, 1 juvenile; IXL Cave, 21 April 1979 (D. Rudolph, D. Cowan, E. van Ingen, S. Winterath, CAS), 2 males, 1 female, 1 juvenile; Stearns Cave, 21 April 1979 (D. Rudolph, D. Cowan, S. Winterath, E. van Ingen, CAS), 2 males, 1 juvenile; Stump Cave, 17 November 1966 (T. Briggs, CAS), 1 male, 1 female; 21 April 1979 (D. Rudolph, B. Martin, E. van Ingen, S. Winterath, D. Cowan, CAS), 2 males, 1 juvenile; 27 July 2001 (D. Ubick, CDU), 2 males; 22 January 2005 (D. Ubick, CDU), 1 female; Soquel, Grover Glade, redwood forest, 3 May 1980 (S. Muzzio, CDU), 1 female. **Alameda Co.:** Berkeley, 17 November 1947 (J. MacSwain, UCB), 1 male, 1 juvenile; 17 December 1947 (J. MacSwain, CJC), 3 males, 3 females; 9 May 1948 (J. MacSwain, UCB), 1 male, 4 females, 2 juveniles; Chabot Road, 0.6 mi E MacArthur Boulevard, 4 December 1966 (V. Lee, CAS), 1 male, 1 female; 1.5 mi NE Crow Canyon Road, 22 January 1984 (T. Briggs, D. Ubick, CAS), 1 female, 4 juveniles; Niles, canyon off Niles Canyon, 1 January 1964 (V. Roth, AMNH), 1 female; Oakland, 14 June 1953 (R. Schuster, AMNH), 2 females; Oakland, Mountain Boulevard at Park, 17 October 1953 (V. Roth, R. Schuster, AMNH), 1 male; Redwood Regional Park, in redwood litter, 13 February 1976 (J. Doyen, UCB), 2 females; Redwood Road at Grizzley Peak Boulevard, 4 May 1985 (T. Briggs, T. Ohsumi, CAS), 2 females; Ward Canyon at Campus Drive, near Hayward State University, 10 May 1999 (T. Briggs, CAS), 1 male, 1 female, 2 juveniles; Woolsey Canyon, Berkeley, end of LeConte Street, under bark dead bay tree, 27 October 1946 (J. MacSwain, CJC), 1 male; 21 December 1983 (T. Briggs, V. Lee, D. Ubick, CAS), 1 male, 2 females, 7 juveniles; S side Woolsey Canyon, 17 February 1960 (A. Gray, AMNH), 1 male. **Contra Costa Co.:** 2 mi W Moraga, Canyon at Pinehurst Road, redwood litter, 19 August 1965 (T. Briggs, V. Lee, CAS), 1 male, 4 females; Moraga Redwoods, at end of Pinehurst Road, 26 May 1985 (T. Briggs, T. Ohsumi, CAS), 5 males, 2 females, 3 juveniles; nr Richmond, Wildcat Creek at Hill Road, 30 January 1984 (T. Briggs, CAS), 2 males, 4 juveniles. **San Benito Co.:** 3 mi NW San Juan Bautista, oak woodland, under rocks, 28 February 1967 (V. Lee, CAS), 1 male, 1 female; **San Luis Obispo Co.:** 3 mi SW Atascadero, oak forest, under rocks, 25 March 1967 (T. Briggs, V. Lee, CAS), 1 male, 4 females; San Luis Obispo, 4 January 1953 (no collector, AMNH), 1 male; 1.1 mi W San Luis Obispo on Perfumo Road, oak forest, under rocks, 26 February 1967 (V. Lee, CAS), 1 female; 1 mi W Los Osos Valley Road on Perfumo Canyon Road, el. 60 m, live oak forest, berlese leaf litter, 14 February 1987 (T. Briggs, V. Lee, CAS), 5 males, 16 females, 5 juveniles.

**DISTRIBUTION.**— This widespread species ranges from Mendocino County south to San Luis Obispo.

### *Sitalcina sura* Group

**DIAGNOSIS.**— This species group differs from other *Sitalcina* in having the palpal femur armed with asetose tubercles: one mesally and a short row dorsally (Figs. 21b–c). The male has a penis with the ventral plate lacking an apical spine (Fig. 13) and trochanter IV with a single, typically curved, ectal process (Figs. 19e, 21d, 26b–g); the female ovipositor has microspines in imbricate arrangement (Fig. 24f), except in some *S. seca* and *S. sura* (Figs. 18f, 20g), and curved setae with polyfurcate tips (Figs. 20f, j).

**INCLUDED SPECIES.**— *S. borregoensis* Briggs, *S. chalonga* Briggs, *S. flava* Briggs, and *S. sura* Briggs, and the new species: *S. catalina*, *S. peacheyi*, *S. rothi*, and *S. seca*.

**DISTRIBUTION.**— Central to southern Coast Ranges, California, and southeastern Arizona.

***Sitalcina sura* Briggs, 1968**

Figures 2e, 3e, 13a–b, 17–18.

*Sitalcina sura* Briggs, 1968:17. Kury, 2003:220.

**TYPE MATERIAL.**— Female holotype collected from beneath rocks in redwood forest at Big Sur, Monterey County, California, on 20 March 1966, by T. Briggs and K. Hom, deposited at CAS, examined.

**DIAGNOSIS.**— This species differs from others in the group by its distinctive male genitalia, with large apically ornate parastylar lobes and extremely short setae on the ventral plate. The female ovipositor cuticle is only weakly imbricate to glabrous. Somatically, *S. sura* most closely resembles *S. seca*, from which it may be distinguished by its larger size and much larger genitalia: *S. sura* has a scute length of 1.30–1.54 (1.10–1.32 in *S. seca*) and a GO width of 0.32–0.39 (0.22–0.26 in *S. seca*).

**DESCRIPTION.**— Body length 2.00–2.50, LII/SL 2.90–3.60 (N = 13). Color orange-brown, appendages lighter. Body finely rugose, with scattered larger tubercles on tergite margins, along scute posterior, and on eyemound, particularly along anterior face; scute with 3–5 pairs of AT. EM subconical, eyes present. GO rounded, subtriangular. Palpal femur with median dorsobasal row of 3–5 small asetose tubercles and 1 mesal tubercle. Palpal megaspines: trochanter 1, small; femur 3 ventrobasal (and 2 tubercles), 1 mesodistal (and 1 tubercle); patella 2 mesal, 1 ectal; tibia 3 mesal, 2 ectal; tarsus 2 mesal, 2 ectal. TC, 3-5-5-5.

*Male*, allotype (additional specimens, N = 5): Body length 2.14 (2.14–2.50). Scute length 1.30 (1.40–1.54), width 1.50 (1.50–1.70). EM length 0.30 (0.30), width 0.33 (0.30–0.35), height 0.27 (0.22–0.25). GO length 0.28 (0.28–0.32), width 0.33 (0.32–0.37). Leg II length 4.28 (4.38–5.14), LII/SL 3.30 (3.10–3.60). TrIV spur present, short, stout, curved. Penis VP apically truncate, apical surface with 14–16 short setae, AS absent; glans large, with long rectangular DL, PSL broadly spatulate, ridged mesally, ornate apically; S not visible, presumed to be short.

*Female*, holotype (additional specimens, N = 6): Body length 2.20 (2.00–2.20). Scute length 1.44 (1.30–1.46), width 1.60 (1.54–1.74). EM length 0.33 (0.27–0.30), width 0.36 (0.30–0.33), height 0.30 (0.22–0.25). GO length 0.31 (0.29–0.34), width 0.36 (0.35–0.39). Leg II length 4.14 (4.10–4.66), LII/SL 2.90 (3.15–3.30). Ovipositor surface with microspines weak to absent, apex lacking teeth, with 6 pairs of curved apical setae, 1 pair ventral subapical, setal tips polyfurcate.

**Sexual dimorphism.**—The male has a TrIV spur.

**Variation.**—Ovipositor microspines are reduced in this species, being absent in some individuals.

**NATURAL HISTORY.**— This species occurs in redwood forests and adjacent woodlands, where it is common in leaf litter, as well as in decaying wood and beneath rocks. It has been collected from December to August, and is probably active year-round.

**MATERIAL EXAMINED.**— CALIFORNIA: **Monterey Co.:** Big Sur (Type Locality), redwood forest, under rocks, 20 March 1966 (T. Briggs, K. Hom, CAS), 1 male allotype, 1 female holotype; Big Sur, nr Pfeiffer Falls, redwood forest, under log, 2 July 1967 (T. Briggs, T. Lee, L. Lee, G. Leung, CAS), 1 male; nr Big Sur State Park, 20 March 1966 (T. Briggs, K. Hom, CAS), 2 males, 4 females, 3 juveniles; 7 mi S Big Sur, 22 December 1953 (V. Roth, UCB), 2 males; Bixby Canyon, maple duff, 23 February 1959 (E. Lindquist, UCB), 3 males, 3 females, 1 juvenile; Bixby Canyon Road, 3.5 mi E Hwy 1, redwood forest, under log, 9 July 1967 (T. Briggs, CAS), 1 male; False Point Sur, under Monterey pine logs, 20 March 1966 (T. Briggs, K. Hom, CAS), 3 females; Ghost Cave, SE side of Pico Blanco, el 550 m, 22 August 1982 (T. Briggs, V. Lee, CAS), 2 females; Pfeiffer Big Sur State Park, redwood duff, 8 June 1972 (E. Fisher, UCR), 4 females; Ventana Camp, 13 April 1976 (T. Briggs, K. Hom, CAS), 5 males (SEM), 4 females (SEM).

**DISTRIBUTION.**— Known only from coastal Monterey County, California.

***Sitalcina seca* Ubick and Briggs, sp. nov.**

Figures 13c–d, 19–20.

**TYPE MATERIAL.**— Male holotype and female allotype collected from beneath granite rocks at talus slope SW of Lakes at Arroyo Seco Campground, Monterey County, California, on 6 May 1995, by D. Ubick and W. Savary, deposited at CAS.

**ETYMOLOGY.**— The name refers to the type locality, Arroyo Seco.

**DIAGNOSIS.**— This species differs from others in the group by its distinctive male genitalia, the divided dorsal lobe and large spatulate parastylar lobes. The female ovipositor cuticle lacks microspines or is only weakly imbricate. Somatically, *S. seca* most closely resembles *S. sura*, from which it may be distinguished by its smaller size and much smaller genitalia (see diagnosis of *S. sura*).

**DESCRIPTION.**— Body length 1.66–2.20, LII/SL 3.25–4.33 (N = 8). Color orange-brown, appendages lighter. Body covering of fine tubercles, larger tubercles along tergal margins and on anterior slope of scute and eyemound; scute with 3 to 4 pairs of AT. EM subconical, eyes present. GO rounded, subtriangular. Palpal femur with median dorsobasal row of 4 long tubercles and 1 mesal tubercle. Palpal megaspines: trochanter 1, small; femur 3 ventrobasal, 2 mesodistal; patella 2 mesal, 1 ectal; tibia 2 mesal (and 1 distal seta), 2 ectal; tarsus 2 mesal, 2 ectal. TC, 3-5-5-5.

*Male*, holotype (other specimens, N = 3): Body length 2.00 (1.90–2.20). Scute length 1.26 (1.12–1.32), width 1.34 (1.28–1.40). EM length 0.28 (0.26–0.30), width 0.30 (0.26–0.30), height 0.26 (0.22–0.25). GO length 0.22 (0.22–0.25), width 0.26 (0.22–0.25). Leg II length 5.19 (4.10–5.14), LII/SL 4.12 (3.40–4.05). TrIV spur present, short stout and strongly curved. Penis VP entire with rounded apical extension, with about 17 pairs of medium length setae, AS absent; glans with divided DL, PSL large, spatulate; S not fully interpreted, but appears to be a slender prong.

*Female* allotype (other specimens, N = 3): Body length 1.74 (1.66–2.10). Scute length 1.26 (1.10–1.20), width 1.36 (1.28–1.50). EM length 0.26 (0.24–0.33), width 0.28 (0.24–0.32), height 0.24 (0.22–0.25). GO length 0.22 (0.20–0.25), width 0.24 (0.23–0.25). Leg II length 5.46 (3.90–4.78), LII/SL 4.33 (3.25–4.27). Ovipositor surface finely wrinkled, microspines absent or small and in imbricate arrangement, apical teeth absent, with 7 pairs curved apical setae with polyfurcate tips.

**Sexual dimorphism.**— The male has a TrIV spur.

**Variation.**— Ovipositor microspines are small to absent.

**NATURAL HISTORY.**— This species is known from dense forests. In mixed broadleaf evergreen forest (Arroyo Seco), it has been collected only beneath rocks in March and May. In the more mesic redwood forests (other localities), it was also found beneath decaying logs and in forest litter, and has been collected from February to June.

**MATERIAL EXAMINED.**— CALIFORNIA: **Monterey Co.:** Arroyo Seco Campground, under rocks, 22 March 1986 (T. Briggs, A. Jung, K. Hom, CAS), 1 juvenile; under granite in oak leaf litter, 13–15 May 1994 (D. Ubick, J. Boutin, CDU), 2 females; talus slope SW of Lakes, oak w maple, under granite, 6 May 1995 (D. Ubick, W. Savary, CAS, CDU), 8 males (including holotype, SEM), 13 females (including allotype, SEM); Kirk Creek at Nacimiento Road, el ca 1000', redwood forest, under rocks and in duff, 31 May 1991 (D. Ubick, CDU), 3 males, 4 females, 1 juvenile; Landels Hill Big Creek Reserve, 23 May 1987 (T. Briggs, W. Rauscher, A. Hui, CAS), 3 males, 6 females (SEM), 2 juveniles; Limekiln Creek, redwood forest, under limestone, 30–31 May 1991 (D. Ubick, CDU), 6 males, 10 females, 4 juveniles; redwood-bay litter, 31 May 1991 (D. Ubick, CDU), 4 males, 1 female; Limekiln Redwoods, nr Lucia, 3 February 1973 (T. Briggs, CAS), 5 females; N Fork Mill Creek at Nacimiento Road, el 1500–1600', redwood-tanoak duff, 1 June 1991 (D. Ubick, CDU), 2 males, 4 females; redwood forest, under rocks, 1 June 1991 (D. Ubick, CDU), 5 males, 7 females, 2 juveniles; maple litter, 1 June 1991 (D. Ubick, CDU), 1 male, 1 female. All specimens paratypes, unless indicated otherwise.

**DISTRIBUTION.**— Known only from Monterey County, California.

***Sitalcina chalona* Briggs, 1968, status nov.**

Figures 13e–f, 21–22.

*Sitalcina flava chalona* Briggs, 1968:15. Ubick and Briggs, 2002:437. Kury, 2003:220.

**TYPE MATERIAL.**— Male holotype and female allotype collected from under rhyolite in dense chaparral at N-facing slope of Bear Gulch Canyon, Pinnacles National Monument, San Benito County, California, on 26 November 1966, by T. Briggs, deposited at CAS, examined.

**DIAGNOSIS.**— This species differs from others in the group by its distinctive male genitalia: the short trough-like parastylar lobes and bifurcate stylus. The female ovipositor cuticle is only weakly imbricate, unlike most *Sitalcina*, but similar to *S. seca* and *S. sura*.

**NOTE ON STATUS.**— *S. chalona* is here regarded as a full species as it differs from *S. flava* in both somatic and genitalic characters. In *S. chalona*, the eyemound is longer and more conical than in *S. flava* and the parastylar lobes of the male genitalia are apically entire, lacking the sickle-shaped lobe of *S. flava*.

**DESCRIPTION.**— Body length 1.64–1.90, LII/SL 3.06–3.87 (N =6). Color orange, appendages lighter. Body finely rugose, with larger tubercles along tergal margins, on scute posterior, and on eyemound; scute with 3 to 5 pairs of AT. EM conical, eyes present. GO apically rounded. Palpal femur with median dorsobasal row of 3 tubercles and 1 large mesal tubercle. Palpal megaspines: trochanter 2 small; femur 3 ventrobasal, 1 mesodistal (and 1 setose tubercle); patella 2 mesal, 1 ectal; tibia 2 mesal (and 1 setose tubercle), 2 ectal; tarsus 2 mesal, 2 ectal. TC, 3-5-5-5.

*Male* holotype (additional specimens, N =2): Body length 1.64 (1.70–1.78). Scute length 1.08 (1.14–1.18), width 1.18 (1.24–1.28). EM length 0.26 (0.28), width 0.30 (0.30), height 0.24 (0.26–0.28). GO length 0.22 (0.24), width 0.22 (0.22). Leg II length 4.18 (3.92–4.28), LII/SL 3.87 (3.44–3.63). TrIV spur present, short stout and curved. Penis VP entire with about 18 pairs of lateral setae, AS absent; glans with rectangular DL, PSL short and broad; S straight and tubular with subapical prong.

*Female* allotype (additional specimens, N =2): Body length 1.90 (1.76–1.82). Scute length 1.28 (1.10–1.15), width 1.30 (1.16–1.20). EM length 0.26 (0.24–0.26), width 0.30 (0.25–0.26), height 0.24 (0.22–0.24). GO length 0.20 (0.22–0.24), width 0.24 (0.24–0.25). Leg II length 3.92 (3.78–4.04), LII/SL 3.06 (3.44–3.51). Ovipositor surface with microspines in imbricate pattern, apical teeth absent, with 7 pairs of apical setae, curved, polyfurcate.

**Sexual dimorphism.**— The male has a TrIV spur.

**NATURAL HISTORY.**— Specimens have been collected from beneath volcanic rocks in broadleaf evergreen and chaparral forests, from November to May.

**MATERIAL EXAMINED.**— CALIFORNIA: **San Benito Co.:** Pinnacles National Monument, N facing slope of Bear Gulch Canyon, dense chaparral, under rhyolite, 26 November 1966 (T. Briggs, CAS), 2 male (including holotype), 3 females (including allotype); Bear Gulch Trail at Chalona Creek, under talus in oak-buckeye litter, 3 May 1992 (T. Briggs, D. Ubick, W. Rauscher, CAS), 8 males (SEM), 3 females (SEM), 2 juveniles; 0.5 mi E Chalona Campground, chaparral, under volcanic rocks, 20 March 1967 (J. Tom, CAS), 1 male, 1 female; Old Pinnacles Campground, moist chaparral slope, under rocks, 19 March 1967 (J. Tom, CAS), 3 males, 4 females.

**DISTRIBUTION.**— Known only from Pinnacles National Monument, San Benito County, California.

### *Sitalcina* species

**NOTE.**— The following material clearly represents a new species, but as the available specimens were badly damaged, a description was not possible. However, the record is nonetheless noteworthy as it bridges the northern and southern elements of the *sura* group.

**MATERIAL EXAMINED.**— CALIFORNIA: **Santa Barbara Co.:** Montecito, E Mountain Drive, 0.9 OD mi from San Ysidro Road junction, undersurface of rock in closed canopy oak forest, 23 June 2003 (D. Palmer, J. Starrett, CAS), 1 male, 2 females; 4 June 2005 (J. Starrett, CAS), 1 male.

### *Sitalcina flava* Briggs, 1968

Figures 13g–i, 23–24.

*Sitalcina flava flava* Briggs, 1968:15. Kury, 2003:220.

**TYPE MATERIAL.**— Male holotype and female allotype from under sandstone rocks in dense live oak forest at 1 mile S of Topanga Beach, Los Angeles County, California, collected on 24 March 1967, by T. Briggs and K. Hom, deposited at CAS, examined.

**DIAGNOSIS.**— This species differs from others in the group by its distinctive male genitalia, with the parastylar lobes apically divided and with the ventral branch sickle-shaped. The female ovipositor cuticle is strongly imbricate.

**DESCRIPTION.**— Body length 1.42–1.70, LII/SL 2.88–3.28 (N = 4). Color orange, appendages lighter. Body finely rugose, with larger tubercles along tergal margins and eyemound; scute with 2–3 pairs of AT. EM low, rounded, eyes present. GO rounded, triangular. Palpal femur with median dorsobasal row of 4 tubercles and 1 mesal tubercle. Palpal megaspines: trochanter 2 tubercles; femur 3 ventrobasal (and 1 tubercle), 1 mesodistal (and 1 tubercle); patella 2 mesal, 1 ectal (small); tibia 2 mesal (and 1 tubercle), 2 ectal (and 1 tubercle); tarsus 2 mesal, 2 ectal. TC, 3-5-5-5.

*Male*, holotype (paratype): Body length 1.70 (1.60). Scute length 1.08 (1.02), width 1.12 (1.06). EM length 0.28 (0.24), width 0.28 (0.26), height 0.18 (0.16). GO length 0.18 (0.16), width 0.18 (0.16). Leg II length 3.54 (2.94), LII/SL 3.28 (2.88). TrIV spur present, short stout and curved. Penis VP entire with about 11 pairs of lateral setae, AS absent; glans with DL distolaterally produced, PSL long, with sickle-shaped ventroapical lobe; S short and straight, enclosed by PSL.

*Female*, allotype (paratype): Body length 1.56 (1.42). Scute length 1.02 (1.02), width 1.10 (1.08). EM length 0.24 (0.22), width 0.24 (0.22), height 0.16 (0.14). GO length 0.16 (0.16), width 0.18 (0.18). Leg II (missing in allotype) length ? (2.98), LII/SL ? (2.92). Ovipositor surface with distinctly imbricate microspines, apical teeth absent, setae 6 pairs apical, 1 pair ventral subapical, curved, polyfurcate.

*Sexual dimorphism.*— The male has a TrIV spur.

*Variation.*— A female paratype is missing a retina.

**NATURAL HISTORY.**— Specimens have been collected from beneath sandstone rocks in dense oak and oak-sycamore forests, from December to April.

**MATERIAL EXAMINED.**— CALIFORNIA: **Los Angeles Co.:** Santa Monica Mountains, Sepulveda Canyon, 1 July 1958 (V. Roth, AMNH), 1 male; Topanga Canyon, 1 mi S Topanga, dense live oak forest, under sandstone, 24 March 1967 (T. Briggs, K. Hom, CAS), male holotype, female allotype, and 1 male and 2 female paratypes; 3.3 mi N Topanga Beach, dense live oak forest, under sandstone, 7 April 1966 (T. Briggs, K. Hom, V. Lee, CAS), 6 males (1 SEM), 2 females (1 SEM); 4.7 mi N Topanga, in oak-sycamore litter, 27 December 1966 (T. Briggs, CAS), 1 female.

**DISTRIBUTION.**— Known only from the Santa Monica Mountains, Los Angeles County, California.

***Sitalcina borregoensis* Briggs, 1968**

Fig. 25.

*Sitalcina borregoensis* Briggs, 1968:30. Kury, 2003:220.

**TYPE MATERIAL.**— Female holotype from Mountain Palm Spring, Anza-Borrego State Park, collected on 5 April 1967, by T. Briggs, deposited at CAS, examined.

**DIAGNOSIS.**— This species, known only from the female, differs from others in the group by the extremely low eyemound. The ovipositor cuticle appears to be only moderately imbricate.

**DESCRIPTION.**— Body length 1.26–1.40, LII/SL 2.96–3.20 (N = 2). Color orange-brown, appendages lighter. Body finely rugose, few larger tubercles along tergal margins, 1 pair anteriorly on eyemound; scute with 3 pairs of AT. EM low, flattened, eyes present. Palpal femur with median dorsobasal row of 4 tubercles and 1 small mesal tubercle. Palpal megaspines: trochanter 1 ventral, small; femur 3 ventrobasal, 1 mesodistal; patella 2 mesal, 1 ectal; tibia 2 mesal, 2 ectal; tarsus 2 mesal, 2 ectal. TC, 3-5-5-5.

*Male*, unknown.

*Female* holotype (paratype): Body length 1.26 (1.40). Scute length 0.90 (0.90), width 0.92 (0.88). EM length 0.18 (0.20), width 0.20 (0.22), height 0.14 (0.16). GO length 0.16 (0.16), width 0.18 (0.18). Leg II length 2.66 (2.88), LII/SL 2.96 (3.20). GO subtriangular. Ovipositor surface with microspines arranged in moderately imbricate pattern, apical teeth absent, 7 pairs apical setae, curved, polyfurcate.

**NATURAL HISTORY.**— Specimens were collected from beneath granite boulders in a palm canyon oasis.

**MATERIAL EXAMINED.**— CALIFORNIA: **San Diego Co.**: Anza-Borrego State Park, Mountain Palm Spring, 5 April 1967 (T. Briggs, CAS), 3 females (including holotype).

**DISTRIBUTION.**— Known only from the type locality.

### Arizona species

The following three species seem to be most closely related, based on similarity in the male genitalia. The penis of *S. rothi* (Figs. 13j, 26a–c) could only be examined through a compound microscope and has the general form to the other two, although it was not possible to see much detail. The penes in both *S. peacheyi* (Figs. 13k–m, 26f–g, 29–30) and *S. catalina* (Figs. 26d–e, 27–28) are similar in having a glans with bilobed and interlocking PSL lobes, a ventrobasal structure probably representing the stylar base, and a short, straight S that lies on the dorsal surface between the PSL and DL. These two species do differ in some details: the ventral lobe of the PSL is distinctly toothed in *S. peacheyi* (Figs. 30c–f), but not in *S. catalina* (Figs. 28c–d); and the DL is medially notched in *S. catalina* (Fig. 28d), but not in *S. peacheyi* (Fig. 30f). The three species also differ in somatic characters, with differences in the eyemound size and tuberculation and in the form of the male TrIV, which are detailed in the species' diagnoses.

***Sitalcina peacheyi* Ubick and Briggs, sp. nov.**

Figures 13k–m, 26f–g, 29–30.

**TYPE MATERIAL.**— Male holotype from beneath rocks in Cave of the Bells, Gardner Canyon, Santa Rita Mountains, Santa Cruz County, Arizona, collected on 28 June 1988 by D. Ubick, T. Briggs, B. Peachey, W. Savary, and W. Rauscher, deposited at CAS.

**ETYMOLOGY.**— This species is named after Bill Peachey, whose knowledge of Arizona caves and hospitality made our visit to the type locality possible.

**DIAGNOSIS.**— This species is most readily distinguished from others in Arizona by somatic characters: eyemound medium-sized with few pointed tubercles (Figs. 29a–b), and male TrIV spur broadly rounded and recumbent (Figs. 26f–g).

**DESCRIPTION.**— Body length 1.36–1.90, LII/SL 2.90–4.30 (N = 9). Color pale yellow to orange, appendages lighter. Body finely rugose, with few larger tubercles along tergal margins and at eyemound; scute with 3–4 pairs of AT. EM rounded, eyes present. GO rounded, subtriangular. Palpal femur with median dorsobasal row of 3–4 tubercles and 1 moderately sized mesal tubercle. Palpal megaspinules: trochanter 2, small; femur 3 ventrobasal, 2 mesodistal; patella 2 mesal, 1 ectal; tibia 2 mesal, 2 ectal; tarsus 2 mesal, 2 ectal. TC, 3-5-5-5.

*Male*, holotype (paratypes, N = 4): Body length 1.90 (1.36–1.65). Scute length 1.15 (1.03–1.16), width 1.10 (1.00–1.66). EM length 0.30 (0.23–0.30), width 0.30 (0.22–0.32), height 0.20 (0.17–0.24). GO length 0.16 (0.14–0.18), width 0.18 (0.16–0.18). Leg II length 4.24 (3.14–4.45), LII/SL 3.70 (3.00–4.30). TrIV spur present, short, broad, curved. Penis VP entire, apically rounded, with 10 pairs of setae, AS absent; glans with DL quadrate, PSL apically bilobed with interlocking dorsal branch and ventral lobe with apical serrations; S straight, tubular.

*Female* allotype (paratypes, N = 3): Body length 1.53 (1.44–1.64). Scute length 1.02 (1.02–1.08), width 1.10 (1.04–1.10). EM length 0.25 (0.22–0.26), width 0.25 (0.22–0.24), height 0.15 (0.15–0.24). GO length 0.18 (0.15–0.16), width 0.21 (0.18–0.20). Leg II length 3.27 (2.95–4.02), LII/SL 3.20 (2.90–3.70). Ovipositor surface strongly imbricate with microspines, apical teeth absent, with 7 pairs of curved apical setae, polyfurcate.

*Sexual dimorphism.*— The male has a TrIV spur.

*Variation.*— Individuals from caves are paler in color and have relatively longer legs: LII/SL (caves) = 3.10–4.30 (3 males) and 3.20–3.70 (2 females); LII/SL (epigeal) = 3.00–3.10 (2 males) and 2.90–3.04 (2 females). The size of the TrIV spur varies, being largest in specimens from the Baboquivari Mountains.

**NATURAL HISTORY.**— Most specimens have been collected from caves, others are from beneath rocks and in leaf litter.

**MATERIAL EXAMINED.**— ARIZONA: **Pima Co.:** Baboquivari Mountains, Brown Canyon, 19 July 1959 (V. Roth, AMNH), 3 males, 2 females; Colossal Cave County Park, Arkenstone Cave, ex register room under rocks, 11 August 1990 (B. Pape, CAS), 2 males; Colossal Cave Mountain Park, Bearpaw Cave, 23 September 1994 (B. Pape, CAS), 1 female; Madera Canyon, Madera Picnic Grounds, under rocks in duff, 30 April 1972 (W. Icenogle, CAS), 2 males, 6 females; Madera Canyon, Santa Rita Mountains, 27 July 1949 (W. Gertsch, CJC), 1 male. **Santa Cruz Co.:** Santa Rita Mountains, Cave Creek Canyon, N31°42'55.8", W110°45'46.1", oak-juniper-pine forest, under rocks, 2 August 1996 (D. Ubick, P. Craig, CDU), 2 males, 1 female, 1 juvenile; Santa Rita Mountains, Gardner Canyon, Cave of the Bells, el 5300', 24 June 1988 (D. Ubick, T. Briggs, B. Peachey, W. Rauscher, W. Savary, CDU, CAS), 5 males (including holotype), 6 females (including allotype, SEM), 2 juveniles; same as above but Hilton's Hole Cave, 5 males (SEM), 5 females; same as above but Onyx Cave, 1 male, 5 females; Hidden Cave, 6 mi WNW Sonoita, 21 March 1992 (B. Pape, CAS), 1 male, 2 females. All specimens paratypes, unless indicated otherwise.

**DISTRIBUTION.**— Known from Santa Cruz and southern Pima counties, Arizona.

### *Sitalcina catalina* Ubick and Briggs, sp. nov.

Figures 26d–e, 27–28.

**TYPE MATERIAL.**— Male holotype and female allotype from beneath fallen bark at 30 mi NE Tucson, Santa Catalina Mountains, el 8000', Pima County, Arizona, on 17 August 1968, by T. Briggs, K. Hom, A. Jung, D. Owyang, and J. Tom, deposited at CAS.

**ETYMOLOGY.**— The species name refers to the known distribution, Santa Catalina Mountains.

**DIAGNOSIS.**— This species is most readily distinguished from others in Arizona by somatic characters: eyemound large, with several pointed tubercles (Figs. 27a–b), and male TrIV spur short, narrow and projecting (Figs. 26d–e).

**DESCRIPTION.**— Body length 1.25–1.72; LII/SL 3.11–4.51 (N = 7). Color yellowish-orange, appendages lighter. Body finely rugose, with few larger tubercles along tergal margins and several at eyemound; scute with 2–3 pairs of AT. EM rounded, eyes present. GO apically rounded. Palpal femur with median dorsobasal row of 3–4 tubercles and 1 moderately sized mesal tubercle. Palpal megaspines: trochanter none; femur 3 ventrobasal, 2 mesodistal (distalmost small); patella 2 mesal, 1 ectal; tibia 2 mesal, 2 ectal; tarsus 2 mesal, 2 ectal. TC, 3-5-5-5.

*Male*, holotype (paratypes, N = 3): Body length 1.70 (1.25–1.61). Scute length 1.15 (1.04–1.15), width 1.16 (1.03–1.20). EM length 0.25 (0.23–0.25), width 0.26 (0.25–0.28), height 0.18 (0.13–0.17). GO length 0.14 (0.14–0.16), width 0.18 (0.17–0.19). Leg II length 3.58 (3.54–5.00), LII/SL 3.11 (3.40–4.35). TrIV spur present, slender, projecting from Tr. Penis VP entire, apically rounded, with 8 pairs of setae, AS absent; glans with quadrate DL, apically notched, PSL apically bilobed with interlocking dorsal branch, ventral lobe lacking apical serrations; S straight, tubular.

*Female* allotype (paratypes, N = 2): Body length 1.72 (1.50–1.53). Scute length 1.20 (1.00–1.15), width 1.15 (1.10). EM length 0.22 (0.22–0.23), width 0.26 (0.24–0.26), height 0.15 (0.15–0.16). GO length 0.18 (0.15–0.16), width 0.25 (0.22). Leg II length 3.92 (3.62–4.51), LII/SL 3.27 (3.15–4.51). Ovipositor surface strongly imbricate with microspines, apical teeth absent, with 7 pairs of curved apical setae, polyfurcate.

*Sexual dimorphism.*— The male has a TrIV spur.

*Variation.*— Individuals from caves have slightly longer legs: LII/SL (caves) = 4.25–4.35 (2 males) and 4.51 (female); LII/SL (epigean) = 3.11–3.40 (2 males) and 3.15–3.27 (2 females). The cavernicolous males have a TrIV spur both broader and longer than in surface populations.

**NATURAL HISTORY.**— Two of the three collections are from caves. The epigean sample is from beneath accumulated layers of fallen coniferous bark.

**MATERIAL EXAMINED.**— ARIZONA: **Pima Co.:** Santa Catalina Mountains, Water Cave, January 1969 (K. Stephen, CWS), 2 males; 30 mi NE Tucson, el 8000', under bark, 17 August 1968 (T. Briggs, K. Hom, D. Owyang, J. Tom, CAS), 6 males (including holotype, SEM), 11 females (including allotype, SEM), 1 juvenile. **Pinal Co.:** Santa Catalina Mountains, Nugget Cave, 21 August 1993 (R. Pape, CAS), 2 males, 1 female, 1 juvenile. All specimens paratypes, unless indicated otherwise.

**DISTRIBUTION.**— Known from the Santa Catalina Mountains in Pinal and northern Pima counties, Arizona.

***Sitalcina rothi* Ubick and Briggs, sp. nov.**

Figures 13j, 26a–c.

**TYPE MATERIAL.**— Male holotype from Yarnell, Yavapai County, Arizona, collected by V. Roth on 3 September 1961, deposited in AMNH.

**ETYMOLOGY.**— This species is named in honor of the late Vince Roth, collector of this and many other interesting phalangodids.

**DIAGNOSIS.**— This species differs from other *Sitalcina* by its very low eyemound that lacks pointed tubercles (Fig. 26a) and the form of the male TrIV spur: long, straight and projecting (Figs. 26b–c).

**DESCRIPTION.**— Body length 1.50–1.56, LII/SL 2.98–3.08 (N = 2). Color yellowish-orange, appendages yellow. Body finely rugose, with few larger tubercles, mostly along tergal margins;

scute with 2–3 pairs of AT. EM low, flattened, eyes present. Palpal femur with median dorsobasal row of 3 small tubercles and 1 small mesal tubercle. Palpal megaspines: trochanter none; femur 3 ventrobasal, 1 mesodistal; patella 2 mesal, 1 ectal; tibia and tarsus 2 mesal, 2 ectal. TC, 3-5-5-5.

*Male* (holotype): Body length 1.50. Scute length 0.98, width 1.00. EM length 0.24, width 0.24, height 0.10. GO length 0.14, width 0.18. Leg II length 3.02, LII/SL 3.08. TrIV spur present, short, straight. GO oval, longer than wide. Penis with VP entire, bearing about 6 pairs of setae, AS absent; glans with quadrate DL, PSL trough-like; S not visible.

*Female* (allotype): Body length 1.56. Scute length 0.94, width 1.04. EM length 0.23, width 0.24, height 0.10. GO length 0.12, width 0.18. Leg II length 2.80, LII/SL 2.98. GO oval. Ovipositor not expanded.

*Sexual dimorphism*.— The male has a TrIV spur.

**NATURAL HISTORY**.— Unknown.

**MATERIAL EXAMINED**.— ARIZONA: **Yavapai Co.**: Yarnell, 3 September 1961 (V. Roth, AMNH), male holotype, female allotype.

**DISTRIBUTION**.— Known only from the type locality.

### *Sitalcina lobata* Group

**DIAGNOSIS**.— The single species representing this group differs from other sitalcinoids in having a dorsal row of setose tubercles on the palpal femur (Figs. 31c–e), unlike those in the *sura* group which are asetose (Figs. 21b–c), but superficially resembling those in *Banksula*, of the bifurcate clade (Figs. 5b–c). The male is unique in phalangodids in having the trochanter IV elongated and bearing two spurs, one strongly curved (Figs. 31f–g). The male genitalia have the unique combination of threadlike stylus, trilobed parastylar lobes, and long ventral plate setae (Figs. 32a–f). The female resembles that of *S. californica* in having pointed ovipositor setae (Figs. 32g–h), rather than polyfurcate as in the *sura* group (Figs. 20f, j).

**INCLUDED SPECIES**.— Only *S. lobata* Goodnight and Goodnight.

**DISTRIBUTION**.— Southern California.

### *Sitalcina lobata* Goodnight and Goodnight, 1942

Figures 2f, 3f, 14d–f, 31–32.

*Sitalcina lobatus* Goodnight and Goodnight, 1942:9. Briggs and Hom, 1966:263. Briggs, 1968:12.

*Sitalcina lobata*, Kury, 2003:220.

**TYPE MATERIAL**.—Female holotype from Oceanside, California, collected on 11 July 1931, [collector unknown], deposited at AMNH, examined.

**DIAGNOSIS**.— Same as for species group.

**DESCRIPTION**.— Body length 1.38–2.02, LII/SL 2.73–3.80 (N = 13). Color brownish-orange, appendages paler. Body coarsely rugose, with numerous larger tubercles along tergal margins, in transverse rows across scute, and on and surrounding eyemound. Scute with 3–5 pairs of AT. EM rounded, eyes present. Palpal femur with median dorsobasal row of 5–6 small tubercles, each bearing a seta, lacking mesal tubercle. Palpal megaspines: trochanter 0 (but with 2 setose tubercles); femur 3 ventrobasal (and large tubercle), 1 mesodistal (and 1 apical seta); patella 2 mesal, 1 ectal; tibia 2 mesal (and 1 apical seta), 2 ectal (and 1 basal seta); tarsus 2 mesal, 2 ectal. TC, 3-5-5-5.

*Male* (N = 6): Body length 1.50–1.84. Scute length 1.02–1.28, width 1.24–1.44. EM length 0.24–0.28, width 0.25–0.27, height 0.15–0.20. GO length 0.17–0.21, width 0.23–0.25. Leg II length 3.10–4.26, LII/SL 2.96–3.44. TrIV greatly elongated, with 2 distoventral spurs, ectal large, tapering, strongly curved. GO rounded, trapezoidal. Penis VP entire with rounded extension pro-

jecting beyond setae, with 12 pairs of long setae, AS absent; glans with DL quadrate, PSL broad, apically trilobed; S long, slender, curved.

*Female* holotype (additional specimens, N = 6): Body length 1.78 (1.38–2.02). Scute length 1.14 (1.04–1.26), width 1.30 (1.12–1.50). EM length 0.25 (0.20–0.27), width 0.24 (0.20–0.27), height 0.17 (0.13–0.19). GO length 0.15 (0.14–0.18), width 0.18 (0.18–0.21). Leg II length 3.12 (3.02–4.24), LII/SL 2.73 (2.73–3.80). GO rounded hemispherical. Ovipositor surface with microspines in imbricate arrangement, apical teeth absent, with 6 pairs apical setae, hooked, pointed.

*Sexual dimorphism.*— The male has a greatly elongated TrIV with 2 distoventral spurs and a larger GO than in the female.

*Variation.*— The male TrIV varies greatly in size, equaling femur length in some specimens, to about half that size in others. Of the 18 specimens measured, most have the TrL/FmL from 0.6 to 1.0, but in the single specimen from Whitewater Canyon, it is distinctly shorter (TrL/FmL = 0.4). Although this specimen seems to be conspecific in other features, additional material from this locality would be necessary to confirm its placement. In most specimens the ectal TrIV spur is usually evenly curved, but is angular in some.

*Juveniles.*— A penultimate male (from San Timoteo) has an elongate TrIV, which falls into the range of variation of adults. The ectal spur is a stout projection, rather than the tapering loop found in adults.

**NATURAL HISTORY.**— Most specimens have been collected in oak forests, with records also from chaparral, pine, and sycamore, from beneath rocks and in leaf litter. Specimens are also from woodrat (*Neotoma*) nests and tarantula (*Aphonopelma*) burrows. Most collections are from December to May, with one female in July. A large series collected in August is from tarantula burrows.

**MATERIAL EXAMINED.**— CALIFORNIA: **Los Angeles Co.:** 7 mi N Claremont on road to Mount Baldy, under logs and rocks in deep canyon, 31 December 1966 (T. Briggs, K. Hom, A. Jung, CAS), 2 males, 4 females. **Orange Co.:** NE Laguna Beach, San Joaquin Hills on ridge E of Emerald Canyon, N33.57091°, W117.78193°, el. 489m, live pitfall in chaparral, 22 May 2003 (D. Hogan, CAS), 1 female; 3 mi W San Juan, Cleveland National Forest, sycamore litter, 2 March 1958 (I. Newell, AMNH), 1 female. **Riverside Co.:** 3 mi W Beaumont, oak litter, 3 November 1957 (I. Newell, AMNH), 1 male, 1 female; same but 15 February 1959, 1 female; Box Springs Grade, nr Riverside, under stones on desert hillside, 26 November–1 December 1925 (J. Chamberlin, AMNH), 3 males, 4 females; Hurkey Creek Campground, San Bernardino National Forest, under rocks and in pine litter, 3 April 1966 (T. Briggs, K. Hom, CAS), 3 males, 2 females; 1 mi W Lake Elsinore, Slater Canyon, under wood, 21 December 1966 (T. Briggs, CAS), 1 male; 2 mi NW Perris, chaparral, under granite, 24 March 1967 (V. Lee, CAS), 2 males (SEM); 2.5 mi N Sage, 10 November 1957 (I. Newell, AMNH), 1 female; 9.5 mi N San Jacinto on Hwy 79, under rocks, 3 April 1966 (V. Lee, K. Hom, CAS), 1 male, 2 females; San Timoteo Canyon, ex *Neotoma* nest, 24 April 1952 (R. Ryckman et al, AMNH), 1 penultimate male; 18 May 1952, 1 female; Whitewater Canyon, *Neotoma* nest, 27 December 1979 (no collector, UCR), 1 male; Winchester, under rock, 19 January 1971 (J. Rowland, CAS), 1 male, 1 female; 1 mi NW Winchester, in tarantula burrow, 19 August 1967 (W. Icenogle, CAS), 2 males, 2 females; 20 August 1967, 2 males (SEM), 18 females, (SEM). **San Bernardino Co.:** San Bernardino Mtns., Hwy 18, 2 mi E junction Hwy 138, N34°13'23", W117°16'07", el. 4411 ft, oak duff, 14 December 2002 (R. Vetter, CAS), 1 male. **San Diego Co.:** Oceanside, 11 July 1931 (no collector, AMNH), 1 female (holotype); 5.9 mi N Lakeside, under rocks in oak leaves, 28 December 1966 (T. Briggs, K. Hom, CAS), 2 males, 4 females (SEM); Mt. Palomar, below Henshaw Dam, 25 July 1931 (W. Ivie, AMNH), 1 female; 7 mi E Rincon Spring, oak forest, under granite, 28 March 1970 (T. Briggs, CAS), 2 females.

**DISTRIBUTION.**— Los Angeles to San Diego counties, California.

### Genus *Enigmina* Ubick and Briggs, gen. nov.

TYPE SPECIES: *Sitalcina granita* Briggs, 1968

**DIAGNOSIS.**— This genus differs from all other sitalcinoids by the combination of the following characters: eyes present (Fig. 33b), palpal femur lacking dorsal and mesal tubercles (Fig. 35d), ovipositor lacking microspines (Fig. 34h), male with 2 short ventral spurs on trochanter IV (Fig. 33e) and penis with stout stylus, large dorsal lobe, and separate parastylar lobes (Figs. 14g–h).

**DESCRIPTION** — Body length 1.56–2.20. Dorsum finely rugose, with rows of larger tubercles along posterior tergal margins; scute with 1 pair of small AT. EM rounded, conical or cylindrical, with eyes. Cheliceral base with abrupt dorsodistal swelling. Palpal megaspines: femur 3 ventrobasal, 1–2 mesodistal; patella 1 ectal, 2 mesal; tibia 2–3 ectal, 2–3 mesal; tarsus 2 ectal, 2 mesal. TC, 3-5-5-5

*Male*: Penis with VP entire, bearing 8 pairs of setae; glans only unfolds during expansion, with large DL, posteriorly rounded, apically flattened, with PSL not fused, broadly rounded; S short, stout.

*Female*: Ovipositor cuticle lacking microspines, lacking apical teeth, with 8 pairs apical setae.

*Sexual dimorphism*: The TrIV has a pair of short spurs in males and a single small tubercle in females.

**INCLUDED SPECIES.**— *E. granita* (Briggs), *E. warrenorum* sp. nov.

**DISTRIBUTION.**— Southern Sierra Nevada, California.

#### *Enigmina granita* (Briggs, 1968)

Figs. 2g, 3g, 33–34.

*Sitalcina granita* Briggs, 1968:14. Kury, 2003:220.

**TYPE MATERIAL.**— The male holotype, female allotype, and 10 paratypes (4 males, 6 females), collected under granite in an oak grassland, 7 mi E Fountain Springs, Tulare County, California, on 14 March 1967, by T. Briggs, V. Lee, A. Jung, and K. Hom, deposited at CAS, examined.

**DIAGNOSIS.**— This species differs from *E. warrenorum* in having an eyemound that is both smaller and lacking apical tubercles, a more coarsely tuberculate scute, only 2 pairs of megaspines on the palpal tibia, shorter and subequal processes on the male trochanter IV (mesal prong larger in *E. warrenorum*), and an ovipositor with apical setae curved and (at least in some specimens) polyfurcate (hooked and pointed in *E. warrenorum*). Only minor differences were noted in the male genitalia: parastylar lobe surface less densely toothed in *E. granita*.

**DESCRIPTION.**— Body length 1.56–2.18, LII/SL 2.84–3.46 (N = 14). Color yellowish-orange, appendages lighter. Body finely rugose, with larger tubercles along tergal margins; scute with 1 pair of AT. EM conical, lacking sharp tubercles, eyes present. GO apically rounded. Palpal femur with dorsal row of a few setae, lacking mesal or dorsal tubercles. Palpal megaspines: trochanter 1 short; femur 3 ventrobasal, 1 mesodistal (and apical seta); patella 2 mesal (apical small), 1 ectal; tibia 2 mesal (with basal seta), 2 ectal (with basal tubercle); tarsus 2 mesal, 2 ectal. TC, 3-5-5-5.

*Male*, holotype (additional specimens, N = 6): Body length 1.84 (1.56–2.18). Scute length 1.26 (1.00–1.46), width 1.20 (0.98–1.44). EM length 0.30 (0.24–0.44), width 0.32 (0.26–0.42), height 0.28 (0.20–0.36). GO length 0.22 (0.16–0.20), width 0.14 (0.14–0.18). Leg II length 3.80 (3.40–4.16), LII/SL 3.17 (2.85–3.42). TrIV with 2 spurs, short, subequal. Penis VP entire, with 8 pairs of lateral setae (of which 2 pairs are along the lateral VP margin), AS absent; glans with DL posteriorly rounded, apically flattened, PSL broadly rounded; S short, stout.

*Female*, allotype (additional specimens, N = 6): Body length 1.72 (1.68–1.96). Scute length

1.18 (1.00–1.22), width 1.14 (1.14–1.34). EM length 0.26 (0.26), width 0.26 (0.28–0.30), height 0.24 (0.18–0.30). GO length 0.16 (0.15–0.17), width 0.18 (0.18–0.20). Leg II length 3.40 (3.30–3.82), LII/SL 2.88 (2.84–3.46). TrIV with tiny ventroapical tubercle. Ovipositor surface finely wrinkled, lacking microspines, apical teeth absent, with 7 pairs of apical setae, curved, with polyfurcate tips.

*Sexual dimorphism.*— The male has 2 short TrIV spurs.

*Variation.*— Individuals vary in body size, even at a single locality; both small and large individuals of both sexes were collected on a single visit to Bonsall Hill. Larger males have a slightly larger and more apically projecting EM. Although leg length varies directly to body size in the specimens measured, LII/SL appears to vary inversely to body size, especially in males. The two smallest males (SL = 1.0) have the highest LII/SL ( $\geq 4.0$ ), and the two largest (SL  $\geq 1.4$ ) have the lowest LII/SL ( $\leq 3.0$ ). This difference in relative leg length is unexpected and needs closer examination.

**NATURAL HISTORY.**— Specimens were collected beneath granite boulders in oak forests.

**MATERIAL EXAMINED.**— CALIFORNIA: **Tulare Co.:** Hungry Hollow, 5.8 mi SE Avenue 264 on Avenue 120, oak woodland, under granite, 28 March 1991 (D. Ubick, T. Briggs, W. Rauscher, CAS), 1 female; Rd 296, 0.3 mi N Deer Creek Rd, N35°5.9'46.0", W118°54'38.4", oak grassland, under granite, 18 January 2004 (D. Ubick, T. Briggs, CAS), 6 males, 3 females; N slope Bonsall Hill, 1 mi W Mtn. Rd. 160 on Mtn. Rd. 137, under granite in oak-buckeye gully, 28 March 1991 (D. Ubick, T. Briggs, W. Rauscher, CAS, CDU), 6 males, 3 females, 1 juvenile; 6.3 mi E Fountain Springs, oak grassland, under granite, 19 March 1967 (T. Briggs, K. Hom, A. Jung, P. Lum, CAS), 7 males, 7 females, 2 juveniles; 7 mi E Fountain Springs, oak grassland, under granite, 14 March 1967 (T. Briggs, V. Lee, A. Jung, and K. Hom, CAS), 5 males (including holotype), 7 females (including allotype). **Kern Co.:** 1.4 mi E Granite Station, under granite, 22 January 1967 (K. Hom, CAS), 1 male.

**DISTRIBUTION.**— Known from Tulare and Kern counties, California.

### *Enigmia warrenorum* Ubick and Briggs, sp. nov.

Figs. 14g–h, 35–36.

**TYPE MATERIAL.**— The female holotype and male allotype were collected under logs and in duff in a mixed coniferous forest, el 5200', 2.25 mi W Johnsondale, Tulare County, California, on 2 July 1988, by D. Ubick, T. Briggs, W. Rauscher, and W. Savary, deposited at CAS.

**ETYMOLOGY.**— This species is named in honor of Warren C. Rauscher and Warren E. Savary, not only for their help in collecting the type series, but for their continuing assistance in many areas.

**DIAGNOSIS.**— See *E. granita* (Briggs).

**DESCRIPTION.**— Body length 1.80–2.20 (N = 4), LII/SL 3.87–3.91 (N = 3). Color yellowish-orange, appendages lighter. Body finely rugose, with few larger tubercles along tergal margins and dorsally on eyemound; scute with 1 pair of AT. EM high, cylindrical, with sharp tubercles, eyes present. Palpal femur with dorsal row of a few setae, lacking mesal tubercle. Palpal megaspines: trochanter 1 short; femur 3 ventrobasal, 1 mesodistal (and apical seta); patella 2 mesal, 1 ectal; tibia 3 mesal, 3 ectal; tarsus 2 mesal, 2 ectal. TC, 3-5-5-5.

*Male* allotype (SEM): Body length 2.20 (1.84). Scute length 1.40 (1.44), width 1.20 (1.22). EM length 0.22 (0.22), width 0.32 (0.32), height 0.25 (0.25). GO length 0.22 (0.22), width 0.19 (0.19). Leg II missing. TrIV with 2 short spurs. GO apically rounded. Penis VP entire, with 8 pairs of lateral setae (of which 2 pairs are along the lateral VP margin), AS absent; glans with DL posteriorly rounded, apically flattened, PSL broadly rounded; S short, stout.

*Female* holotype (2 paratypes): Body length 1.80 (1.90–1.96). Scute length 1.26 (1.24–1.40), width 1.30 (1.30–1.44). EM length 0.25 (0.25–0.28), width 0.30 (0.30–0.32), height 0.22

(0.21–0.24). GO length 0.18 (0.17–0.18), width 0.22 (0.22). Leg II length 4.82 (4.80–5.48), LII/SL 3.38 (3.87–3.91). TrIV with small ventroapical tubercle. Genital operculum hemispherical, apically rounded. Ovipositor surface finely wrinkled, lacking microspines, apical teeth absent, with 7 pairs of hooked, pointed apical setae.

*Juvenile*: Body length 1.20, scute length 0.91, leg II length 4.04, LII/SL 4.44. Color white. Palpal megaspines as in adult. TC, 1-1-2-2. TrIV with 2 small ventral tubercles, mesal larger (indicating that the specimen is a male).

*Sexual dimorphism*.— The male has a pair of short ventral spurs on the TrIV (a single small tubercle in the female), a slightly higher EM, and a relatively longer GO.

**NATURAL HISTORY**.— Specimens have been collected under logs and in duff in a coniferous forest.

**MATERIAL EXAMINED**.— CALIFORNIA: **Tulare Co.**: 2.25 mi W Johnsondale, el 5200', mixed coniferous forest, under logs and in duff, 2 July 1988 (D. Ubick, T. Briggs, W. Rauscher, W. Savary, CAS), female holotype, male allotype (SEM), 1 male paratype, 3 female paratypes (SEM), 1 juvenile.

**DISTRIBUTION**.— Known only from the type locality.

### **Genus *Tularina* Ubick and Briggs, gen. nov.**

TYPE SPECIES: *Tularina tularensis* Ubick and Briggs, sp. nov.

**DIAGNOSIS**.— This genus differs from all other sitalcinoids, except *Microcinella* and *Microcina*, in lacking eyes and having a low eyemound (Figs. 38a–e). Males differ from these two genera in having modified parastylar lobes which are elongated and fused (Fig. 37); females in having ovipositor microspines arranged in linear series (Fig. 39j) or absent (Fig. 43g) (rather than being randomly distributed).

**ETYMOLOGY**.— The genus name is a contraction of Tulare County, the known distribution of the genus, and *Sitalcina* and is considered feminine in gender.

**DESCRIPTION**.— Body length 0.91–1.70. Dorsal sculpturing of fine tubercles, in random or areolate arrangement; scute lacking AT. EM broad and low, lacking eyes. Cheliceral base with abrupt dorsodistal swelling. Palpal trochanter with tuberculate dorsal swelling. Palpal megaspines: femur 3 ventrobasal, 1 mesodistal; patella 1 mesal; tibia and tarsus each 2 ectal, 2 mesal. TC, 3-5-4-4 and 3-5-5-5.

*Male*: Penis VP entire, mesoapically elongated, bearing 8 to about 30 pairs of short to extremely long setae, lacking AS; glans only unfolds during expansion, DL absent or present, PSL elongate and fused, sometimes with apical notch; S straight to slightly curved, with or without subapical tubule.

*Female*: Ovipositor cuticle with small microspines arranged in transverse series, or smooth (*T. scopula*), with 7 pairs apical setae, apically hooked, with tips entire (*T. tularensis*) or bifurcate.

*Sexual dimorphism*: None observed in *T. plumosa* and *T. tularensis*. The male of *T. scopula* has a ventral tubercle on TrIV, absent in females.

**INCLUDED SPECIES**.— *T. plumosa* sp. nov., *T. scopula* (Briggs), *T. tularensis* sp. nov.

**DISTRIBUTION**.— Known only from the southern Sierran foothills, Tulare County, California.

### ***Tularina tularensis* Ubick and Briggs, sp. nov.**

Figs. 2c, 3c, 37a–d, 38–39.

**TYPE MATERIAL**.— Male holotype from beneath serpentine boulders in grassland on the W slope of Rocky Hill, just E of Exeter on Hwy. 130, Tulare County, California, collected on 26 January 1991 by D. Ubick and M. Moody, deposited at CAS.

**ETYMOLOGY**.— The specific name refers to the type locality.

**DIAGNOSIS.**— This species differs from others in the genus by its areolate abdominal dorsum, the relatively short setae on the male ventral plate, and the pointed apical setae on the female ovipositor.

**DESCRIPTION.**— Body length 0.91–1.14, LII/SL 2.95–3.22 (N = 4). Color yellowish-orange, appendages paler. Body covering of fine tubercles, in areolate arrangement on opisthosoma; scute lacking AT. EM low and quadrate, eyes absent (lacking both retina and cornea). GO rounded. Palpal megaspines: trochanter 0; femur 3 ventrobasal, 1 mesodistal; patella 1 mesal, 1 ectal; tibia 2 mesal, 2 ectal; tarsus 2 mesal, 2 ectal. TC, 3-5-4-4.

*Male*, holotype (paratype): Body length 0.91 (0.92). Scute length 0.68 (0.69), width 0.65 (0.70). EM length 0.18 (0.19), width 0.19 (0.19), height 0.12 (0.12). GO length 0.10 (0.10), width 0.14 (0.14). Leg II length 2.10 (2.22), LII/SL 3.09 (3.22). TrIV spur absent. Penis VP entire with rounded apical extension, with 7–8 pairs of setae (2 pairs along lateral margin of VP), AS absent; glans divided distally into dorsal and ventral lobes, narrow, pointed, subequal in size; S short, straight, enclosed by lobes.

*Female*, allotype (paratype): Body length 1.06 (1.14). Scute length 0.74 (0.74), width 0.79 (0.76). EM length 0.19 (0.18), width 0.18 (0.18), height 0.12 (0.12). GO length 0.12 (0.12), width 0.16 (0.14). Leg II length 2.18 (2.26), LII/SL 2.95 (3.05). Ovipositor surface with short microspines, arranged in short transverse series, apical teeth absent, 6 pairs of setae (arranged in 4 triads) and 1 dorsal subapical pair; apical setae strongly hooked, tips pointed.

*Sexual dimorphism.*— None observed.

**NATURAL HISTORY.**— All specimens have been collected beneath serpentine boulders in grassland biomes, in January and March.

**MATERIAL EXAMINED.**— CALIFORNIA: **Tulare Co.:** W slope of Rocky Hill, just E of Exeter on Hwy 130, grassland, under serpentine, 26 January 1991 (D. Ubick, M. Moody, CAS, CDU), male holotype, female allotype and 1 male; 28 March 1991 (D. Ubick, T. S. Briggs, W. Rauscher, CAS, CDU), 1 male, 1 female; 17 January 2004 (D. Ubick, T. Briggs, CAS, CDU), 6 males (SEM), 4 females (SEM); N access to Rocky Hill, 17 January 2004 (D. Ubick, T. Briggs, CAS, CDU), 1 male, 2 females. All specimens paratypes, unless indicated otherwise.

**DISTRIBUTION.**— Known only from the type locality.

### ***Tularina plumosa* Ubick and Briggs, sp. nov.**

Figs. 37e–h, 40–41.

**TYPE MATERIAL.**— Male holotype collected from beneath granite rock in grassland, on Bacon Hill, Tulare County, California, on 24 March 1991 by D. Ubick, T. Briggs, and W. Rauscher, deposited at CAS.

**ETYMOLOGY.**— The specific name refers to the long ventral plate setae of the male.

**DIAGNOSIS.**— This species differs from all sitalcinoids, except *T. scopula*, by the combination of eyes absent, tarsal count 3-5-5-5, and cuticular ornamentation not in areolate arrangement. From *T. scopula* it is distinguished by its smaller size and genitalic differences. Males of this species most closely resemble *S. tularensis* in having strongly fused parastylar lobes, but differ in having long ventral plate setae.

**DESCRIPTION.**— Body length 0.98–1.20, LII/SL 3.17–3.37 (N = 6). Color pale orange, appendages lighter. EM low, eyes absent (lacking both retina and cornea). Body finely rugose, not in areolate pattern; scute lacking AT. GO quadrate, apically truncate, wider than long. Palpal megaspines: trochanter 0; femur 3 ventrobasal, 1 mesoapical; patella 2 mesal, 1 ectal; tibia and tarsus each with 2 mesal, 2 ectal. TC, 3-5-5-5.

*Male*, holotype (paratypes, N = 2): Body length 1.07 (0.98–1.20). Scute length 0.72 (0.65–0.73), width 0.69 (0.69–0.78). EM length 0.18 (0.16–0.18), width 0.20 (0.18–0.20), height

0.12 (0.11–0.12). GO length 0.13 (0.13), width 0.17 (0.17–0.19). Leg II length 2.35 (2.35–2.46), LII/SL 3.27 (3.27–3.62). TrIV lacking process. Penis VP subquadrate, with 10–12 pairs of setae, distal longest, 3 pairs on lateral margin of which 2 pairs appear to have dorsal origin (Fig. 41e), AS absent; glans apically divided into two short lobes, dorsal broad and rounded (PSL) and ventral narrow and pointed (S).

*Female*, allotype (2 paratypes): Body length 1.08 (1.05–1.10). Scute length 0.76 (0.72–0.76), width 0.76 (0.76–0.81). EM length 0.165 (0.165–0.18), width 0.19 (0.18–0.20), height 0.12 (0.10–0.12). GO length 0.12 (0.12–0.14), width 0.17 (0.17–0.18). Leg II length 2.41 (2.38–2.43), LII/SL 3.17 (3.17–3.31). Ovipositor similar to that in *T. tularensis*, but with tips bifurcate.

*Sexual dimorphism*.— None observed.

**NATURAL HISTORY**.— Specimens have been collected in grasslands from beneath rocks, serpentine (Twin Buttes) and granite (Bacon Hill), in March.

**MATERIAL EXAMINED**.— CALIFORNIA: **Tulare Co.**: Bacon Hill, grassland, under granite, 24 March 1991 (D. Ubick, T. Briggs, W. Rauscher, CAS, CDU), male holotype, female allotype, 1 male (SEM), 1 female (SEM); Twin Buttes, grassland, under serpentine, 28 March 1991 (D. Ubick, T. Briggs, W. Rauscher, CAS, CDU), 1 male, 1 female. All specimens paratypes, unless indicated otherwise.

**DISTRIBUTION**.— Known only from the two localities in Tulare County, California.

***Tularina scopula* (Briggs, 1968), comb. nov.**

Figs. 37i–k, 42–43.

*Sitalcina scopula* Briggs, 1968:28. Kury, 2003:220.

**TYPE MATERIAL**.— Male holotype from beneath granite boulder in moist grassland pasture, 2.8 miles NW Fountain Springs, Tulare County, California, collected on 19 March 1967 by T. Briggs, K. Hom, and A. Jung, deposited at CAS, examined.

**DIAGNOSIS**.— This species differs from all sitalcinoids, except *T. plumosa*, by the combination of eyes absent, tarsal count 3-5-5-5, and cuticular ornamentation not in areolate arrangement. From *T. plumosa*, it is distinguished by its larger size and genitalic differences. The male differs from all other phalangodids by the ornate ventral plate, mesoapically produced and fringed with very long setae. The female is the only known blind sitalcinoid lacking ovipositor microspines.

**DESCRIPTION**.— Body length 1.48–1.70, LII/SL 3.38–3.82 (N = 5). Color yellowish-orange to yellowish-brown, appendages paler. Body finely rugose, not in areolate arrangement, tergites lacking marginal tubercles; scute lacking AT. EM low and flattened, eyes absent (both retina and cornea). GO quadrate-oval, wider than long. Palpal megaspines: trochanter 0; femur 3 ventrobasal, 1 mesoapical; patella 2 mesal (distal small), 1 ectal; tibia and tarsus with 2 mesal, 2 ectal. TC, 3-5-5-5.

*Male*, holotype: Body length 1.48. Scute length 1.05, width 1.07. EM length 0.23, width 0.28, height 0.15. GO length 0.19, width 0.29. Leg II length 4.01, LII/SL 3.82. TrIV with ventral tubercle. Penis VP entire with spatulate mesoapical elongation, with about 12 pairs of long apical setae and about 6 pairs of short basal setae, AS absent; glans with short pointed DL, PSL fused along dorsal margin; S ventral, curved, claw-like, with slender subapical tubule.

*Female*, allotype (additional specimens, N = 3): Body length 1.56 (1.56–1.70). Scute length 1.18 (1.15–1.18), width 1.17 (1.10–1.19). EM length 0.23 (0.225–0.24), width 0.25 (0.25–0.27), height 0.15 (0.15). GO length 0.20 (0.175–0.20), width 0.30 (0.29–0.31). Leg II length 4.32 (3.99–4.32), LII/SL 3.66 (3.38–3.66). TrIV lacking ventral tubercle. Ovipositor surface with longitudinal folds, lacking microspines, apical teeth absent, with 7 pairs of apical setae, curved, bifurcate.

*Sexual dimorphism.*— The male has a ventral tubercle on the TrIV, lacking in female.

**NATURAL HISTORY.**— Specimens, all from beneath granite boulders in a grassland, have been collected in January and March.

**MATERIAL EXAMINED.**— CALIFORNIA: **Tulare Co.:** 11 mi SE Porterville, under granite in level marshland, 22 January 1967 (A. Jung, CAS), 1 female paratype; 2.8 mi NW Fountain Springs, moist grassland, under granite, 19 March 1967 (T. Briggs, K. Hom, A. Jung, CAS), male holotype, female allotype, 4 female paratypes; same locality, 26 January 1991 (D. Ubick, M. Moody, CDU), 1 male (SEM); ca 3 mi N Fountain Springs, N35°55'52", W118°56'17.1", grassland, under granite, 18 January 2004 (D. Ubick, CDU), 2 females (SEM).

**DISTRIBUTION.**— Known only from the type locality. The different mileages refer to a single patch of granite outcrop, approximately 50 meters in diameter.

### **Genus *Megacina* Ubick and Briggs, gen. nov.**

TYPE SPECIES: *Sitalcina cockerelli* Goodnight and Goodnight, 1942.

**DIAGNOSIS.**— The male genitalia of *Megacina* are unique among the known phalangodids in having a glans which folds asymmetrically onto the truncus (Fig. 44). Males also differ from other sitalcinoids in having a ventral plate with a dense vestiture of short setae and, except for *Sitalcina lobata*, a threadlike stylus (Fig. 44). The female ovipositor lacks microspines, as in *Tularina scopula* and *Enigmina granita*.

**ETYMOLOGY.**— The genus name is a contraction of *Mega* (Gr., large) and *Sitalcina* and is considered feminine in gender.

**DESCRIPTION.**— Body length 1.20–2.50. Dorsal sculpturing tuberculate or areolate; scute with 1–2 (–8) pairs of small AT. EM angular to rounded, eyes present. Cheliceral base with moderate to abrupt dorsodistal swelling. TC, 3-5-5-5.

*Male:* Penis with VP entire, bearing 15–25 pairs of short to medium length setae; glans with asymmetrical folding, DL absent or pointed and sac-like, PSL bilobed, fused or free; S long and slender.

*Female:* Ovipositor cuticle lacking microspines, with 7 pairs apical setae, straight to slightly curved and with pointed tips.

Sexual dimorphism: Male with enlarged or more tuberculate TrIV, with enlarged palpi and modified megaspines (*M. cockerelli*), with modified genital operculum (*M. madera*).

**INCLUDED SPECIES.**— Contains the previously described *M. cockerelli* (Goodnight and Goodnight) and *M. madera* (Briggs), and the new species, *M. mayacma* and *M. schusteri*.

**DISTRIBUTION.**— Known from the Sierran foothills and the north central Coast Ranges, California, and extending into SW Oregon.

#### **Key to the Subgroups of *Megacina***

1. Cuticle areolate, at least in part (Figs. 45b–c, 47a, 49a–b); cheliceral boss absent (Figs. 45b–c); TrIV with ventrodiscal swelling, lacking tubercles (Fig. 45e); FmIV with ventrobasal process (Fig. 45e) . . . . . *M. madera* group  
Cuticle tuberculate (Fig. 51); cheliceral boss present (Figs. 51b–d); TrIV with tubercles, lacking ventrodiscal swelling (Figs. 52f–j); FmIV lacking ventrobasal process  
. . . . . *M. cockerelli* group

#### ***Megacina madera* group**

**DIAGNOSIS.**— Members of this species group differ from other sitalcinoids in having a ven-

trobasal process on femur IV, which is present in both sexes. The scute cuticle is areolate, unlike that in the *cockerelli* group. The male penis (Figs. 44c–i) lacks a dorsal lobe and has the parastylar lobes bilobed and fused dorsally (see discussion of homology in Phylogeny). The female ovipositor lacks microspines and has curved, pointed apical setae (Fig. 48f–i).

**INCLUDED SPECIES.**— *M. madera* (Briggs), *M. mayacma* sp. nov., *M. schusteri* sp. nov.

**DISTRIBUTION.**— Sierran foothills and north central Coast Ranges, California.

***Megacina madera* (Briggs, 1968), comb. nov.**

Figures 44g–i, 45–46.

*Sitalcina madera* Briggs, 1968:17. Kury, 2003:220.

**TYPE MATERIAL.**— Male holotype from beneath granite boulders in yellow pine and oak forest 5 mi S of Coursegold, Madera County, California, collected on 16 April 1967 by T. Briggs, deposited at CAS, examined.

**DIAGNOSIS.**— This species differs from other *Megacina* by the form of the male glans, which has the dorsal part of the parastylar lobe rounded and bilobed, the ventral spatulate, and a straight stylus.

**DESCRIPTION.**— Body length 1.42–1.84, LII/SL 3.25–3.58 (N = 5). Color yellowish-orange, appendages lighter. Body covering of fine tubercles, in areolate arrangement on posterior dorsum, with larger tubercles along tergal margins and on scute, transversely in posterior half and in dorsal line through eyemound; scute with 2–3 pairs of small AT. EM rounded, eyes present. Palpal femur with dorsal row of a few setae, lacking mesal tubercle. Palpal megaspines: trochanter 0; femur 3 ventrobasal, 1 mesodistal (and apical seta); patella 2 mesal (1 short), 1 ectal; tibia 2 mesal (and setose tubercle), 3 ectal; tarsus 2 mesal, 2 ectal. Leg IV with Tr unmodified and Fm with short ventrobasal process in both sexes. TC, 3-5-5-5.

*Male*, holotype (paratype): Body length 1.84 (1.48). Scute length 1.26 (0.88), width 1.26 (1.12). EM length 0.28 (0.22), width 0.32 (0.24), height 0.22 (0.20). GO length 0.16 (0.16), width 0.16 (0.18). Leg II length 4.10 (2.96), LII/SL 3.25 (3.36). GO apically excavated. Penis VP entire with rounded apex, lacking extension, AS absent, distal third with 16 to 20 pairs of short setae, including 1 dorsoapical pair; glans with PSL bilobed, ventral ribbon-like, apically spatulate, dorsal rounded, basally fused; S basally wide, apically attenuated, slightly curved, extending beyond PSL by less than PSL length.

*Female*, allotype (2 paratypes): Body length 1.66 (1.42–1.66). Scute length 1.10 (1.04–1.10), width 1.18 (1.00–1.18). EM length 0.26 (0.22–0.26), width 0.28 (0.26–0.28), height 0.20 (0.18–0.22). GO length 0.18 (0.14–0.18), width 0.18 (0.18–0.20). Leg II length 3.54 (3.54–3.58), LII/SL 3.22 (3.22–3.44). GO apically rounded. Ovipositor surface finely wrinkled, lacking microspines; apical teeth absent, apex with 6 pairs setae, curved, pointed.

**Sexual dimorphism.**— The male has the GO apically excavated (rounded in the female), the cuticle less distinctly areolate, and FmIV process longer than in female.

**NATURAL HISTORY.**— Specimens have been collected beneath serpentine and granite boulders in yellow pine and oak forest, from January to June.

**MATERIAL EXAMINED.**— CALIFORNIA: **Madera Co.:** 5 mi S of Coursegold, yellow pine and oak, under granite, 16 April 1967 (T. Briggs, CAS), male holotype, female allotype, 1 male (SEM) and 2 female paratypes (SEM); 4 mi SW Coursegold, under board, 16 January 1995 (W. Tyson, CDFA), 1 male. **Mariposa Co.:** 0.7 mi N of Bagby, under serpentine, 12 June 1966 (T. Briggs, CAS), 1 female (SEM).

**DISTRIBUTION.**— Known from Madera and Mariposa Counties, California.

***Megacina schusteri* Ubick and Briggs, sp. nov.**

Figures 44c–d, 47–48.

**TYPE MATERIAL.**— Male holotype collected from beneath meta-volcanic rock in dense oak-pine forest just E of Miocene Circle (0.2 mi SE of Pentz Road and ca. 14 mi N of Oroville), N39°40' 18.5", W121°34' 3.2", Butte County, California, on 3 May 2005 by D. Ubick and T. Briggs, deposited at CAS.

**ETYMOLOGY.**— The name honors the late Robert Schuster, a collector of this and many other rare phalangodid species.

**DIAGNOSIS.**— The male of this species differs from others in the group by the form of the parastylar lobe: dorsal part narrow, curved, and apically produced; ventral serrated (Figs. 48a–e).

**DESCRIPTION.**— Body length 1.36–1.60, LII/SL 2.93–4.26 (N = 7). Color orange, appendages lighter. Body covering of fine tubercles in areolate arrangement, with larger tubercles on eyemound, in transverse rows on scute, and along tergal margins; scute with 1–2 pairs of small AT. EM low, rounded, eyes present. Chelicera lacking laterobasal projection (boss), basal segment with abrupt dorsodistal swelling. Palpal femur with dorsal row of 5 setae, lacking mesal tubercle. Palpal megaspines: trochanter 0; femur 3 ventrobasal, 1 mesodistal (and 1 distal seta); patella 2 mesal (distal small), 1 ectal; tibia 2 mesal, 2 ectal (and 1 basal seta); tarsus 2 mesal, 2 ectal. TrIV lacking spur, but femur with short ventrobasal process. TC, 3-5-5-5.

*Male*, holotype (paratypes, N = 4): Body length 1.45 (1.36–1.60). Scute length 0.95 (0.91–1.05), width 0.90 (0.92–1.12). EM length 0.20 (0.17–0.25), width 0.23 (0.22–0.30), height 0.15 (0.13–0.24). GO length 0.15 (0.15–0.22), width 0.16 (0.16–0.20). Leg II length 3.52 (3.08–3.56), LII/SL 3.71 (2.93–3.87). GO subrectangular, apically truncate. Penis VP entire with rounded apical extension, bearing 15 pairs of lateral and 1 pair of dorsodistal setae, AS absent; glans with PSL venter serrate, dorsum fused, elongate, bent; S long, slender, curved.

*Female*, allotype (paratype): Body length 1.50 (1.45). Scute length 0.90 (0.90), width 0.99 (1.00). EM length 0.17 (0.19), width 0.23 (0.23), height 0.15 (0.15). GO length 0.16 (0.17), width 0.19 (0.18). Leg II length 3.58 (3.38), LII/SL 3.98 (4.26). GO subtriangular, apically rounded. Ovipositor surface lacking apparent microspines, apical teeth absent, apex with 6 pairs setae, curved, apically pointed.

*Juvenile* (N = 2, larger instar in parentheses): Body length 0.64 (0.90). Scute length 0.46 (0.62), width 0.36 (0.55). EM length 0.08 (0.12), width 0.10 (0.16), height 0.03 (0.10). GO not visible. Leg II length 1.76 (2.83), LII/SL 3.83 (4.56). *Earlier instar*: Color white with yellowish diverticula visible through abdominal cuticle. Body finely rugose, lacking larger tubercles. Dorsum of abdomen and legs with erect thick setae (not in later instar or adults). EM low, rounded, eyes present. Palpal megaspines: trochanter 0; femur 1 ventrobasal, 0 mesodistal; patella 1 mesal, 0 ectal; tibia 1 mesal, 1 ectal; tarsus 2 mesal, 1 ectal. Legs with conspicuous macrosetae (not evident in adults). Front tarsi with single claw, hind tarsi with arolium, claws not visible at 100x. TC appears to be 1-1-2-2. *Later instar*: Color and rugosity as in earlier instar. EM higher, rounded, eyes present. Chelicera basal segment with conspicuous dorsodistal swelling. Palpal megaspines: trochanter 0; femur 3 ventrobasal (distal small), 1 mesodistal; patella 1 mesal, 1 ectal; tibia 2 mesal, 2 ectal; tarsus 2 mesal, 2 ectal. Front tarsi with single claw, hind tarsi with arolium, claws not visible at 100x. TC appears to be 2-2-3-3.

**Sexual dimorphism.**— The male has more strongly modified leg IV: a larger ventrobasal process on the femur and a ventral swelling on the trochanter. Females have slightly longer legs than males.

**Variation.**— The males from Dry Creek Road are both larger and have relatively shorter legs than those from Miocene Circle.

**NATURAL HISTORY.**— The type locality is a gully in a dense forest of primarily live oaks with some digger pine and large manzanita. Specimens were found on the undersides of large (boulder-sized) meta-volcanic rocks, under mesic conditions. No specimens were found beneath smaller rocks and decaying logs. Most of the specimens, 4 adults and 1 juvenile, were collected beneath one large rock, two of the adults being in close proximity. Collembola and campodeiform diplura, typical indicators and probable prey of these phalangodids, were common.

**MATERIAL EXAMINED.**— CALIFORNIA: **Butte Co.:** Dry Creek Road, 14 mi N Oroville, 2 March 1956 (R. Schuster, UCB), 2 male paratypes. E of Miocene Circle, 0.2 mi SE of Pentz Road (ca. 14 mi N Oroville), N39°40' 18.5", W121°34' 3.2", under meta-volcanic rocks in dense oak-pine forest, 3 May 2005 (D. Ubick, T. Briggs, CAS), male holotype, female allotype, 2 male paratypes (SEM), 1 female paratype (SEM), 2 juveniles.

**DISTRIBUTION.**— The species is known only from the above two localities. The "Dry Creek Road" referred to by Schuster could not be located on topographic maps of the region. It is likely that the locality is actually along Messilla Valley Road, which is the only road paralleling Dry Creek. This area is about 1 kilometer due west from the type locality.

***Megacina mayacma* Ubick and Briggs, sp. nov.**

Figures 2h, 3h, 44e-f, 49-50.

**TYPE MATERIAL.**— Male holotype and female allotype collected under serpentine rocks along Socrates Mine Road, 10.8 mi W Hwy 29, Mayacma Mountain, Sonoma County, California, on 2 March 1968 by T. Briggs, deposited in CAS.

**ETYMOLOGY.**— The species name refers to the type locality, Mayacma Mountain.

**DIAGNOSIS.**— This species differs from other *Megacina* by the form of the male parastylar lobes, which are attenuated ventrally and serrate and fused dorsally (Figs. 50a-f).

**DESCRIPTION.**— Body length 1.18-1.76, LII/SL 2.96-3.50 (N = 6). Color yellowish-orange, appendages lighter. Body covering of fine tubercles, in areolate arrangement, with larger tubercles along tergal margins and on scute, transversely in posterior half and with few in dorsal line through eyemound; scute with 2-3 pairs of small AT. EM low, eyes present. Cheliceral basal segment with strong dorsodistal swelling. Palpal femur with dorsal row of a few setae, lacking mesal tubercle. Palpal megaspines: trochanter 1, small; femur 3 ventrobasal, 1 mesodistal (and 1 distal seta); patella 2 mesal (apical small), 1 ectal; tibia 2 mesal (and 1 apical seta), 2 ectal (and 1 basal seta); tarsus 2 mesal, 2 ectal; Leg IV lacking trochanteral process, but with short ventral process at base of femur. TC, 3-5-5-5.

*Male*, holotype (paratype): Body length 1.76 (1.28). Scute length 1.04 (0.92), width 1.18 (0.96). EM length 0.22 (0.20), width 0.30 (0.24), height 0.16 (0.18). GO length 0.16 (0.16), width 0.20 (0.18). Leg II length 3.64 (2.96), LII/SL 3.50 (3.22). TrIV spur absent. GO rounded, subhexagonal. Penis VP entire with rounded apical extension, lacking AS, distal half with about 20 pairs of short setae, absent from median region; glans with PSL ventral lobe slender, attenuated, dorsal serrate, fused; S long, slender, curved, extending beyond PSL by more than length of PSL.

*Female*, allotype (3 paratypes): Body length 1.46 (1.18-1.40). Scute length 1.04 (0.84-0.96), width 1.12 (0.86-1.00). EM length 0.22 (0.20-0.22), width 0.24 (0.20-0.22), height 0.16 (0.16). GO length 0.18 (0.14-0.18), width 0.20 (0.20). Leg II length 3.42 (2.66-3.10), LII/SL 3.29 (2.96-3.26). GO rounded, hemispherical. Ovipositor bent when fully expanded, surface finely wrinkled, lacking microspines, apical teeth absent, with 6 pairs of setae, curved, pointed.

**Sexual dimorphism.**— The areolate cuticle is more strongly defined in the female and the ventro-femoral process and trochanter on leg IV is slightly larger in the male.

**NATURAL HISTORY.**— Most specimens have been collected beneath serpentine boulders in oak

forests. Other specimens are from a mixed forest, a cypress grove, and from beneath pine logs. Collections are from January through March. This species has been collected sympatrically with *Megacina cockerelli* in Sonoma County (Healdsburg).

**MATERIAL EXAMINED.**— CALIFORNIA: **Lake Co.:** 1.5 mi W of Adobe Creek Reservoir on Highland Spring Road, under serpentine in cypress grove, 3 March 1968 (T. Briggs, CAS), 3 males (1 SEM), 8 females (1 SEM). **Mendocino Co.:** Hopland, Feliz Creek Road, under serpentine in oak woodland, 21 January 1991 (D. Ubick, CDU), 2 males (SEM), 2 females; 3 mi S of Hopland on Country Road # 111, under serpentine, 3 March 1968 (T. Briggs, CAS), 5 males, 6 females; 3.5 mi S of Hopland on road to Hwy 128, under serpentine in oak woodland, 10 February 1985 (T. Briggs, CAS), 1 female. **Sonoma Co.:** 1.5 mi NE Healdsburg, 11 January 1981 (T. Briggs, CAS), 1 male; 7 March 1982 (D. Ubick, CDU), 1 male; Mayacma Mountain, Socrates Mine Road, 10.8 mi W Hwy 29, under serpentine, 2 March 1968 (T. Briggs, CAS), holotype male, allotype female, 2 additional females; 9.8 mi W of Hwy 29, under pine logs, 2 March 1968 (T. Briggs, CAS), 4 males, 9 females; Pine Flat Road, 2.0 mi NE Highway 128, N38°41', W122°47', recently burned digger pine-chaparral, under serpentine rocks, 9 January 2007 (D. Ubick, T. Briggs, CDU), 4 males, 3 females; 5.7 mi NE Red Winery Rd. on Pine Flat Rd., mixed forest, under serpentine, 3 January 1993 (D. Ubick, T. Briggs, W. Rauscher, CAS), 3 males, 5 females. All specimens are paratypes, unless indicated otherwise.

**DISTRIBUTION.**— Known from the north central Coast Ranges, California.

### *Megacina cockerelli* group

**DIAGNOSIS.**— *Megacina cockerelli*, the only representative of this group, is the largest of the sitalcinoids and the only one with a cheliceral boss (Figs. 51a-d). Males differ from those in the *madera* group in having a dorsal lobe which is pointed (flap-like in *Microcina* and *Sitalcina*) and the parastylar lobes separate, not fused dorsally (Fig. 53). The species has a sexually dimorphic palp (tibia enlarged in male and with additional megaspines, patella with enlarged and displaced ectal megaspine, Fig. 52) and TrIV (more heavily tuberculate in male, Fig. 52). The female has the unique combination of the ovipositor typically bent, the cuticle glabrous and wrinkled, and the apical setae short and straight (Fig. 54).

**INCLUDED SPECIES.**— Only *M. cockerelli* (Goodnight and Goodnight).

**DISTRIBUTION.**— North to central coast of California.

### *Megacina cockerelli* (Goodnight and Goodnight, 1942), comb. nov.

Figures 1, 2i, 3i, 51-54.

*Sitalcina cockerelli* Goodnight and Goodnight, 1942:9. Briggs and Hom, 1966:263. Briggs 1968:18. Briggs and Ubick, 1989:214. Edgar, 1990:539. Kury, 2003:220.

**TYPE MATERIAL.**— “Female” holotype from Myers Auto Camp, Redwood Highway, California, collected by T.D.A. Cockerell, deposited at AMNH, examined. Note—The holotype is actually a male with a fully extruded penis.

**DIAGNOSIS.**— Same as for species group.

**DESCRIPTION.**— Body length 2.08-3.02, LII/SL 2.85-4.37 (N = 11). Color yellowish-orange, appendages lighter. Body finely rugose with larger tubercles on eyemound dorsum, and in transverse rows on scute posterior and along tergal margins; scute with 1-8 pairs of small AT. EM angular, eyes present. GO rounded subtriangular. Cheliceral basal segment with lateral swelling (boss). Palpal femur with dorsal row of few setae, lacking mesal tubercle. Palpal megaspines: trochanter 1, small; femur 3 ventrobasal, 2 mesodistal (distalmost small); patella 2 mesal, 1 ectal; tibia 2 mesal, 2 ectal; tarsus 2 mesal, 2 ectal. TC, 3-5-5-5.

*Male*, holotype (additional specimens, N = 5): Body length 2.72 (2.16-3.02). Scute length 1.96

(1.78-2.22), width 1.82 (1.70-2.04). EM length 0.45 (0.40-0.58), width 0.50 (0.48-0.64), height 0.35 (0.35-0.46). GO length 0.26 (0.26-0.32), width 0.26 (0.26-0.30). Leg II length 5.58 (5.58-7.94), LII/SL 2.85 (2.85-4.17). TrIV spur absent, but with few to several ventral tubercles. Palpal tibia with several spinose tubercles between the megaspines; patella with basal megaspines enlarged and contiguous. Penis VP entire with slight apical extension, with 13-16 pairs lateral, 1 pair dorsoapical setae, AS absent; glans folds asymmetrically, with dorsal and ventral surfaces in lateral position when folded, DL conical when expanded, PSL bilobed, with complex ornamentation; S long, slender, apically notched, basally swollen.

*Female* (N = 5): Body length 2.08-2.68. Scute length 1.50-2.00, width 1.44-1.92. EM length 0.30-0.46, width 0.34-0.52, height 0.24-0.40. GO length 0.24-0.30, width 0.28-0.30. Leg II length 5.60-7.10, LII/SL 2.92-4.73. Palpal tibia lacking tubercles associated with the megaspines; patella with basal megaspines separated. TrIV with small ventral tubercle, sometimes absent. Ovipositor surface finely wrinkled, lacking microspines, apical teeth absent, with 7 pairs of short, straight apical setae.

*Variation*— Members of this species show much somatic variation. Some specimens (from Marin County) have missing retinæ, and individuals also vary in body size and relative appendage length. However, the most important differences are those between the northern and southern populations. In general, specimens from the north (to Mendocino County) are more strongly tuberculate, having increased AT and more TrIV tubercles, especially in males (Figs. 52f, g). These males also have additional mesoapical setiferous tubercles on the palpal femur (Fig. 52b) and palpal patellae with somewhat longer mesobasal megaspines. There are also differences in the male genitalia, principally in the proportions of the glans lobes (Figs. 44a-b). Closer study is needed to determine whether this variation represents additional species.

*Sexual dimorphism*.— Male TrIV with few to several tubercles, female typically with a single small one. Male palpal tibia enlarged, with several spinose tubercles associated with megaspines (Fig. 52c); absent in female. Male palpal patella with megaspines enlarged, contiguous (Fig. 52c), and more basal than in female (Fig. 52d).

**NATURAL HISTORY**.— Most specimens have been collected in dense forests, especially redwood, fewer records are from oak grassland and chaparral. The species occurs in a wide variety of habitats, having been collected from beneath rocks, under and within decomposing logs and fallen bark, and in various types of leaf litter. Individuals of both sexes have been collected in about equal abundance and throughout the year, although most commonly from January through June. This species is fully sympatric with the phalangodids *Calicina sequoia* (Briggs) and *Sitalcina californica* (Banks), largely parapatric with *Megacina mayacma* sp. nov., and largely pseudosympatric with *Microcina* species, which are typically found in grasslands.

**MATERIAL EXAMINED**.— OREGON: **Coos Co.**: Camp Myrtlewood, nr Bridge, 28-31 July 1954 (V. Roth, CAS), 2 males; Charleston, 28 August 1947 (I. Newell, JCC), 1 male; Charleston, woods behind Marine Biological Institute, berlese of spruce, cedar, alder duff, 30 April 1967 (E. Benedict, WAS), 1 male, 1 female; 33.9 mi S Charleston, 2 September 1970 (T. Briggs, CAS), 1 male, 1 female. **Curry Co.**: Boardman State Park, 18 June 1966 (T. Briggs, V. Lee, K. Hom, A. Jung, CAS), 5 males (SEM), 6 females (SEM), 1 juvenile; 2 mi N Brookings, 31 September 1959 (V. Roth, AMNH), 2 males, 2 females; 7 mi N, 3 mi W Brookings, T40S/R14W/S4, 12 February 1972 (E. Benedict, CWS), 1 female; 7 mi E Brookings, Myrtle Grove, Chetco River, 29 May 1952 (V. Roth, CAS), 2 males; Geisel Mon. State Park, 1.5 mi SSE Nesils Beach, berlese of sitka spruce litter from under sword fern, no date (no collector, CAS), 1 female; Gold Beach, Douglas fir duff, 21 June 1955 (J. Capizzi, CAS), 1 female; 4.5 mi S Gold Beach, 19 June 1966 (T. Briggs, V. Lee, A. Jung, K. Hom, CAS), 8 males, 4 female, 4 juveniles; virgin spruce fern forest, under spruce bark on ground, 29 January 1967 (K. Hom, V. Lee, T. Briggs, CAS), 2 males, 5 females, 1 juvenile; 2 September 1970 (R. Lem, W. Lum, CAS), 1 male, 1 female; old growth forest, 1 August 2000 (T. Briggs, CAS), 2 males, 1 female; 8 mi

E Gold Beach on Rogue River, 28 May 1952 (V. Roth, CAS), 1 male, 1 juvenile; 3 mi E Pistol River on Pistol River Road, 18 June 1966 (V. Lee, K. Hom, CAS), 2 males, 6 females; 1 mi N Sixes, 30 September 1959 (V. Roth, AMNH), 1 male, 1 female.

CALIFORNIA: **Del Norte Co.:** nr. Crescent City, Smith River, redwood duff, 9 November 1956 (J. Schuh, JCC), 1 female; 2.1 mi NE Crescent City on Hwy 101, 25 June 1966 (K. Hom, CAS), 1 male, 1 female; 6 mi NE Crescent City, 25 June 1978 (J. Schuh, L., N. Herman, AMNH), 1 female; nr. N entrance Del Norte Coast Redwoods State Park, 18 June 1966 (V. Lee, CAS), 1 male, 1 female; 1.6 mi N Del Norte Coast Redwoods State Park, 25 June 1966 (A. Jung, K. Hom, T. Briggs, V. Lee, CAS), 2 males, 2 females, 1 juvenile; Ft. Dick, berlese of redwood litter, 2 December 1966 (C. O'Brien, CAS), 1 male (SEM), 2 females, 1 juvenile; 0.3 mi SE E entrance of Jedediah Smith Redwoods State Park, 25 June 1966 (A. Jung, K. Hom, CAS), 4 males, 1 female; Smith River Cutoff, redwood forest, 13 October 1954 (V. Roth, CAS), 1 male, 1 female. **Humboldt Co.:** Arcata Redwood Tree Farm, nr. Prairie Creek State Park, 18 June 1966 (V. Lee, CAS), 1 female; Benbow, nr. Richardson Grove, 19 July 1962 (V. Roth, AMNH), 1 female; Carlotta, 15 September 1961 (W. Ivie, W. Gertsch, AMNH), 1 male, 2 females; 1 mi S Dyerville, 19 September 1953 (E. Gilbert, R. Schuster, AMNH), 1 male; 0.5 mi S Founder's Tree, Dyerville, 18 August 1947 (Remington, AMNH), 1 male, 1 female; Freshwater, 13 August 1953 (C. Marsh, R. Schuster, AMNH), 1 female; 2.9 mi S Garberville, under log, 13 March 1966 (K. Hom, CAS), 1 female; Humboldt Redwoods State Park, Founder's Grove, redwood duff, 28 October 1990 (D. Ubick, W. Rauscher, CDU), 3 males, 5 females, 5 juveniles (3 instars); Myers Auto Camp, Redwood Hwy, no date (T. Cockerell, AMNH), 1 female (holotype); nr. Orick, 18 June 1966 (V. Lee, K. Hom, CAS), 2 males, 1 female, 2 juveniles; 1 mi N Pepperwood, redwood forest, under redwood logs, 25 January 1967 (T. Briggs, V. Lee, CAS), 5 males, 1 female; Trinidad, 16 July 1968 (W. Ivie, AMNH), 1 female; Underwood Park, nr. Garberville, 13 March 1966 (T. Briggs, K. Hom, CAS), 2 males, 2 females. **Mendocino Co.:** Cummings, under rocks, 12 March 1966 (K. Hom, CAS), 2 females; 6 air mi E Cummings, oak forest, under serpentine, 19 October 1989 (D. Ubick, W. Rauscher, CDU), 1 male, 1 female; Mill Creek County Park, oak-bay forest, under rocks, 5 May 1991 (D. Ubick, CDU), 3 females; Noyo River, 14.5 air mi E Ft. Bragg, W123°32', N39°25.5', under log in redwood forest, 25-26 May 1996 (D. Ubick, CAS), 1 female; 2.3 mi S Piercy, under rocks and logs in redwood forest, 13 March 1966 (K. Hom, T. Briggs, CAS), 21 males, 10 females, 5 juveniles; 18 June 1966 (V. Lee, K. Hom, CAS), 5 females; 4.2 mi S Piercy, 17 February 1967 (V. Roth, AMNH), 1 female, 1 juvenile; Rockport, 17 February 1967 (V. Roth, AMNH), 1 female; 3.0 mi S Rockport, el 300', under redwood logs, 19 September 1990 (D. Ubick, CDU), 1 juvenile; Spyrock Road, 9.2 mi NE Hwy 101, el 2100', oak-madrone litter, 21 September 1990 (D. Ubick), 1 male, 1 juvenile; 1 mi N Squaw Rock on Hwy 101, 13 March 1966 (T. Briggs, K. Hom, CAS), 3 females; nr E entrance Standley State Park, 4 July 1966 (K. Hom, CAS), 2 males, 1 female; 5 mi S Usal Creek, 17 April 1976 (T. Briggs, CAS), 1 male, 1 female; 2.0 mi S Usal Campground, el 1000', under redwood logs, 19 September 1990 (D. Ubick, CDU), 2 females, 3 juveniles; 1 mi NE Usal Road along Hwy 1, el 200', redwood duff, 20 September 1990 (D. Ubick, CDU), 1 male, 2 juveniles; 9.8 mi SW Hwy 101, along Hwy 1, el 1000', redwood duff, 20 September 1990 (D. Ubick, CDU), 1 female, 1 juvenile. **Sonoma Co.:** Bohemian Hwy., 2.4 mi SE Monte Rio, N38°26'37", W 122°59'19", oak-chaparral, under serpentine, 20 December 2001 (T. Briggs, G. Giribet, D., S. Ubick, CAS), 1 male, 1 female; nr El Verano, junction of Spring and Prospect Roads at Diamond Estates Recreation Area, 18 January 1988 (T. Briggs, CAS), 1 female; 3.5 mi W El Verano, broadleaf evergreen forest, under volcanic rocks, 6 February 1988 (T. Briggs, D. Ubick, V. Lee, CAS), 3 males, 3 females, 4 juveniles; Franz Creek, just E Chalk Hill Road, redwood forest, under logs, 12 April 1990 (D. Ubick, T. Briggs, W. Rauscher, B. Lym, CAS), 2 females; 5 mi due E Geyserville, 25 February 1968 (T. Briggs, CAS), 1 male; 1.5 mi NE Healdsburg, mixed broadleaf forest, under volcanic rocks, 11 January 1981 (T. Briggs, CAS), 2 females; 27 December 1980 (D. Ubick, CAS), 1 male; 13 January 1991 (D. Ubick, W. Savary, K. Dabney, CDU), 1 male, 2 females; 2.3 km E Healdsburg on Bailache Ave., 90 m el, 21 December 1981 (T. Briggs, D. Ubick, V. Lee, CAS), 1 female; NE of Healdsburg, W Soda Rock Lane at Alexander Valley Road, 23 March 1968 (T. Briggs, CAS), 1 female; 17 April 1976 (T. Briggs, CAS), 1 female; W Soda Rock Lane, 0.8 mi SE Alexander Valley Road, N38°39', W122°49', madrone-oak forest, under log, 9 January 2007 (D. Ubick, T. Briggs, CDU), 1 male; Jenner, 12 February 1969 (T. Briggs, CAS), 1 male, 1 female; Mark West Springs, 13 April 1981 (T. Briggs, CAS), 1 male; nr Lytton, 0.3 mi W West Soda Rock Lane on Alexander Valley Road, 25 February 1968 (T. Briggs, CAS), 2 females; Pepperwood Ranch Natural Preserve, 10 mi N Santa Rosa,

under volcanic rocks, mixed woodland, 8 May 1993 (D. Ubick, CAS), 3 males, 1 female; Santa Rosa, redwood grove on bridge on Chalk Hill Road, 5.8 mi NE junction Pleasant and Chalk Hill Ave., 21 May 1966 (K. Hom, CAS), 1 female; 1 mi S Trenton, 15 May 1957 (R. Schuster, UCB), 1 male. **Napa Co.:** Clay Cave, nr St. Helena, N38.5435°, W122.4666°, 230m, 8 June 1980 (T. Briggs, CAS), 1 female; 26 Feb 2005, (D. Kavanaugh, CAS), 1 female; Helena, 2.5 mi W Hwy 29 on Spring St., el ca 450', mixed evergreen forest, under volcanic rocks and Douglas fir logs, 10 December 2004 (T. Briggs, H. Tu, CAS), 2 males, 2 females; Diamond Mtn Rd (=Kortum Cyn Rd), 1 mi SW Hwy 29, mixed evergreen, under volcanic rocks and Douglas fir logs, 11 December 2004 (T. Briggs, H. Tu, CAS), 2 males, 1 female; Spring Mtn Rd, 2.5 mi W Hwy 29, mixed evergreen, under volcanic rocks, 11 December 2004 (T. Briggs, H. Tu, CAS), 4 males, 1 female; nr Hennessy Dam, digger pine forest, under serpentine, 12 March 1967 (T. Briggs, CAS), 1 male, 1 female; 10 mi S Monticello, 12 May 1957 (L. Smith, R. Schuster, UCB), 1 male, 2 females; E of Napa, Skyline Wilderness Park, Camp Coombs, mixed broadleaf forest, under volcanic rock and in decomposing log, 22 January 1999 (T. Briggs, W. Rauscher, D. Ubick, CAS), 2 males, 3 females, 1 juvenile; E of Napa; Skyline Wilderness Park, Lake Marie Road, oak forest, under volcanic rock, 22 January 1999 (D. Ubick, CAS), 1 female; 4.3 mi NW Napa on Redwood Road, 21 May 1966 (T. Briggs, K. Hom, CAS), 1 male, 2 females; 1 mi W Oakville, 22 February 1968 (T. Briggs, CAS), 1 male. **Marin Co.:** W side Black Point Ridge, nr Novato, oak forest, under volcanic rocks, 12 Jan 1985 (D. Ubick, T. Briggs, CAS), 1 male; 0.75 mi E Bon Tempe Lake Dam, redwood grove, under logs, 3 April 1966 (T. Briggs, K. Hom, CAS), 2 males, 2 females; along Bootjack Trail, nr Bootjack, beneath redwood log, 27 January 1973 (T. Briggs, R. Lem, CAS), 1 male; Burdell Mountain, SE slope, Buck property, 16 March 1990 (D. Ubick, T. Briggs, CDU), 2 males (1 SEM), 3 females (1 SEM); oak grassland ecotone, under serpentine, 8 March 1991 (D. Ubick, CDU), 2 females; saddle W of Burdell Mountain, 2 Jan 1986 (D. Ubick, T. Briggs, CAS), 3 males, 4 females; Fairfax, 24 November 1947 (J. MacSwain, UCB), 1 female; Lake Lagunitas, 19 July 1966 (T. Briggs, CAS), 1 male, 1 female; Novato, Bahia Memorial Park, under rock in laurel grove, 8 February 2001 (T. Briggs, CAS), 1 female; Novato, Rush Creek Preserve, under volcanic rock, 8 March 2001 (T. Briggs, CAS), 1 male, 1 female; Ring Mountain, 27 December 1981 (T. Briggs, CAS), 1 male; serpentine grassland, 19 March 1994 (D. Ubick, CAS), 1 male; Ring Mountain, N37°54.65', W122°29.24', under serpentine boulder in grassland about 10m from oak forest, 3 March 2007 (D. Ubick, CDU), 2 males; Ross, Bald Hill, broadleaf evergreen-grassland ecotone, under basalt, 17 February 1991 (T. Briggs, P. and L. Hoch, CAS), 1 female; 1 March 1991 (D. Ubick, T. Briggs, CAS), 1 female; N side of Burdell Mtn, World College West, W side of campus, 1 mi W Hwy 101 on San Antonio Road, el 60 m, 11 January 1986 (T. Briggs, D. Ubick, V. Lee, CAS), 5 males, 15 females, 2 juveniles. **Contra Costa Co.:** Berkeley Hills, Berkeley, 16 February 1945 (Linsley, Smith, MLG), 1 male, 1 female; Redwood Peak, Oakland Hills, 5 March 1954 (H. Leech, CAS), 1 male; Tilden Park, Berkeley, 4 February 1961 (P.R. Craig, J.K. Anderson, CAS), 1 female; West Pittsburg, 21 March 1957 (J. Powell, UCB), 2 males, 1 female; Wildcat Canyon Regional Park, under bay trees, 19 March 1980 (J. Connors, CAS), 5 males; Wildcat Canyon and Hill Road, nr Richmond, bay grove, under rocks, 30 January 1984 (T. Briggs, CAS), 4 males. **Alameda Co.:** Dwight Way Hill, Berkeley, 2 feet down in ground, 12 April 1947 (J. MacSwain, CJC), 1 male.

**DISTRIBUTION.**— Known from the San Francisco Bay Region, California, north to southwest Oregon.

## PHYLOGENY

**HOMOLOGY.**— The homology of most phalangodid characters studied is self-evident, being based on obvious similarities in form and placement. However, in the three situations discussed below, the homologies are unclear and so subject to interpretation.

1.— The *Tularina* glans. Two of the three known species have a very simple glans. The simplest is in *T. plumosa*, which has only two terminal lobes visible: a narrow ventral and broad dorsal (Figs. 37e-h). *T. tularensis* is similar, but has a stylus visible between the lobes, which are subequal in size (Figs. 37a-d). One interpretation of this is that the dorsal lobe of *Tularina* (DLt) is homologous to the dorsal lobe of other sitalcinoids (DLs) and, by extension, that the ventral lobe (VLt) is homologous to that of the PSL. Arguing against this, is the fact that the DLt is longer and

more apical in position than the DLs and that the VLt is a single structure, in contrast to the separate lobes of the PSL. Additionally, a different interpretation is suggested by comparison to the glans of the third species of *Tularina*, *T. scopula*. Here the glans is more complex in having two sets of lobes along the dorsal surface, a short pointed basal lobe (DL1) and a long one that is apically bifurcate (DL2). Its ventral lobe is curved and pointed and has a slender tubule originating on its dorsal surface (Figs. 37i-k). The homology of this glans to that of other sitalcinoids now seems straight forward. Both the position and length of DL1 resemble DLs. The DL2 is spatulate in shape and at least apically separate and so resembles PSL. This leaves the ventral lobe and its dorsal tubule as the stylus, as similar “tubulated” styli occur in other phalangodids (*Microcinella* and some *Calicina* species).

Comparing all three species suggests the following conclusions:

- a) that the ventral lobes of *T. plumosa* and *T. tularensis* are homologous to the stylus of *T. scopula*. This is supported by their similarities in position and form, being both tapering and ventrally curving. This further suggests that the “stylus” visible in *T. tularensis* is the homologue to the styler tubule in *T. scopula*. Thus, VLt = stylus.
- b) that the DLt in *T. plumosa* and *T. tularensis* are homologous to the DL2 in *T. scopula*, or DLt = DL2 = PSL.
- c) that only *T. scopula* has a possible homologue of the DLs.

Thus, the glans in *Tularina* is best interpreted as having fused PSL and lacking a DL, except possibly in *T. scopula*.

2.— The *Megacina* glans. The glans in *M. cockerelli* does not pose a problem, as it has both a pair of PSL and a DL (Figs. 44a-b), although the latter is pointed, unlike the broad flap in *Sitalcina* (Figs. 13, 14a-c). However, in the *M. madera* group, the glans is much different, having only a single multipronged lobe, fused along the dorsal surface (Figs. 44c-i). Although the dorsal part of this lobe may be interpreted as a DL, it is considerably distad from the standard DL position and seems to be too rigid for a DL, which is typically membraneous and inflatable. It is more likely that this lobe represents PSL, which are dorsally fused and bilobed, and that the DL is absent.

3.— The *Enigmina* male TrIV structures. In *Enigmina*, the male TrIV has a pair of short ventral processes, one each on the mesal and ectal margins (Figs. 33d-e, 35e-f). As this combination does not exist in other sitalcinoids, it is clearly an autapomorphy for the genus. Less clear is the homology of these structures. Being small, they may be regarded as tubercles, such as the ones in male *Tularina scopula* (Fig. 42f) and *Megacina cockerelli* (Figs. 52f-g, i). But, unlike tubercles, they are somewhat larger and setiferous, as are the spurs in *Sitalcina* (Figs. 15g-h, 17f, 31g-f). Additionally, both the prongs and spurs are inserted laterally on the trochanter, whereas tubercles are typically medial (but widespread in some *Megacina cockerelli*). Thus, it is likely that the structures in *Enigmina* are probable homologues to the spurs in *Sitalcina*. Of the two prongs found in *Enigmina*, the ectal is represented in all *Sitalcina* by the much larger process (spur), but a mesal prong only occurs in *S. lobata* (Figs. 31f-g). That both *Enigmina* and *S. lobata* have similar mesal prongs seems to suggest a relationship between the two. The two taxa, however, are morphologically very different, with no other apparent synapomorphies we could detect, and *S. lobata* seems to be well nested in *Sitalcina* on the basis of both male and female genitalic characters (see diagnoses of the taxa). Our interpretation here is that the ectal processes are a synapomorphy for *Enigmina* and *Sitalcina*, and that the mesal ones are independently derived in *Enigmina* and *S. lobata*.

**CHARACTER POLARITIES.**— Our interpretation of the polarities of character states is discussed below and summarized in tabular form in Fig. 55. For the outgroup we used *Calicina mariposa*, which appears to be the most plesiomorphic member of the genus (Ubick & Briggs, 1989).

## Penis

### *Glans expansion.*

1.— Telescoping v folding. A telescoping glans (T) occurs in *Calicina* (Figs. 4c-e) and a folding glans (F) in all other Nearctic taxa (e.g., Figs. 14a-c), with two exceptions. In *Phalangodes et al.*, the glans is reduced in size and has a different expansion, an accordion-like folding which is yet to be fully described (see fig. 4.35g of Ubick, 2007). As these harvestmen are clearly derived in both somatic and other genitalic features, being highly nested in the bifurcate clade, their glans expansion is best interpreted as secondarily derived. The situation in *Microcinella* (Figs. 6a-b), on the other hand, where the glans both telescopes *and* folds (TF), is clearly of primary significance. Earlier (Ubick and Briggs, 1989), we had argued that the folded glans is a derived condition (T→F), but the presence of a composite (TF) glans increases the number of possible transformations, of which we see a total of five:

a) if TF = plesiomorphic, then TF→T *and* TF→F. Here, T and F are independently derived, which leads to an unresolved trichotomy: (T) TF (F). Although this transformation is plausible, given that the mechanism of TF is more complex than in other phalangodids (being a composite of T and F) suggests that it is not plesiomorphic, but derived.

b) if TF = apomorphic with F plesiomorphic, then F→TF. Here TF is derived from an F ancestor by gaining T, resulting in T (TF + F). This possibility is not regarded as likely since it requires the independently derivation of T, and the resulting clade, TF + F, is not supported by known synapomorphies. Additionally, the structural complexity of the F glans suggests that it is derived (elaborated below).

c) if TF = apomorphic with T plesiomorphic, then T→TF. Here TF derives from a T clade by gaining F, resulting in (T + TF) F. This is also seen as unlikely because of independent derivation of F, and the clade, T + TF, is not supported by known synapomorphies.

d) if TF = transitional state with F plesiomorphic, then F→TF→T, resulting in F (TF + T). The strongest argument that F is not plesiomorphic is that this glans type is morphologically more complex. In addition to the obvious complexity of the bifurcate clade (the deeply incised ventral plate), both *Sitalcina* and *Megacina* have complex glandes. Even the simplest F glans (in *Microcina*) is more complex than the TF of *Microcinella* in having an additional lobe (DL, Fig. 8). Finally, the apparent simplicity of the glans in some *Tularina* has been argued above to be secondarily derived (based on apparent fusion of structures).

e) if TF = transitional state with T plesiomorphic, then T→TF→F. Here, F is derived once, resulting in T (TF + F). However, the presence of telescoping in TF, using outgroup comparison, is a plesiomorphic retention, giving T (TF (F)), or *Calicina* (*Microcinella* (other phalangodids)). For now, we provisionally accept this interpretation and regard *Calicina* and *Microcinella* as progressive outgroups to the remaining Nearctic Phalangodidae.

2.— Symmetrical v asymmetrical folding. Glans folding is symmetrical in most members of the folding glans clade (State 0). However, in *Megacina* (Figs. 44, 46, 48, 50, 53) the glans folds asymmetrically onto the truncus (State 1), with the morphologically dorsal and ventral surfaces positioned laterally in the folded glans. As this type of folding is not known in other phalangodids, it is a strong synapomorphy for the genus.

### *Ventral plate.*

3.— Entire v bifurcate. In most phalangodids, the VP is entire (State 0), or with a short apical notch in some species of the European *Scotolemon* Lucas, 1860 and *Ausobskya* Martens, 1972. A deeply cleft VP (Figs. 5d-e) is thus derived (State 1) and a strong synapomorphy for the bifurcate clade (*Banksula*, *Texella*, and *Phalangodes et al.*, see Ubick and Briggs, 1992, 2002).

4.— Ventral v lateral. The VP is in a ventral position in *Calicina* (Figs. 4c-e) and all sitalcinoids (State 0). Within the bifurcate clade, the VP prongs are also ventral in *Banksula* (Figs. 5d-e) but lateral in the other members (see figs. 4.35f-g of Ubick 2007), where it is a synapomorphy (State 1).

5.— Apical spine. An AS is absent in *Calicina* and most sitalcinoids (State 0), so its presence

is considered derived (State 1). It is found in *Banksula* (Fig. 5f) and *Texella* and suggests another synapomorphy for the bifurcate clade, although it appears to be absent in *Phalangodes et al.* The AS is also present in *Sitalcina californica* (Figs. 16b, f), where it is probably independently derived as that species is morphologically distinct from the bifurcate clade.

6.— Dorsal setae. Dorsal setae are absent in most taxa (State 0), so that their presence in *Megacina* (Figs. 44, 46d, 48b, 53d) and the bifurcate clade (Fig. 5d) is clearly derived (State 1). A complication arises in *Tularina plumosa*, where the distal two pairs of lateral setae are dorsally displaced (Fig. 41e). Without further study, it is not clear if this condition represents a transition state or an autapomorphy for the species, and is scored as unresolved.

7.— Setal number. As fewest setae (5-6 pairs) occur in *Microcinella* (Fig. 6) and *Microcina* (Fig. 8), and only slightly more (< 9 pairs) in *Calicina* (Fig. 4d), an increased number is regarded as derived. Scoring is: < 9 pairs = State 0; 9-15 pairs = State 1; > 15 pairs = State 2.

8.— Setal length. Very short setae are found in *Microcinella* (Fig. 6) and *Microcina* (Fig. 8) and moderately longer ones in most sitalcinoids (State 0). Very long setae (State 1) are derived, and interpreted as an autapomorphy for *Sitalcina lobata* and a synapomorphy for *Tularina plumosa* and *T. scopula*.

#### **Dorsal lobe (DL).**

9.— Presence. This typically flap-like structure is present on the dorsal surface of the glans, basad of the S. As it is absent (State 0) in *Calicina* (Figs. 4c-e) and *Microcinella* (Fig. 6), its presence is regarded as derived (State 1). However, given our interpretation of homology (above), the DL is also apparently absent in *Tularina tularensis* (Figs. 37a-d), *T. plumosa* (Figs. 37e-h), and the *madera* group of *Megacina* (Figs. 44c-i), the relatively basal elements of the two genera. This suggests that the DL in *Tularina scopula* (Figs. 37j-k) and *Megacina cockerelli* (Figs. 44a-b) are independently derived. The fact that this DL in these species is a more pointed structure than found in other sitalcinoids, may support this interpretation.

10.— Size. As the DL in *Microcina* is a small flap (Fig. 8), the larger state in others is derived (State 1).

#### **Parastylar lobes (PSL).**

11.— Fusion. PSL are separate structures in all sitalcinoids except in *Tularina* (Figs. 37e-h) and the *madera* group of *Megacina* (Figs. 44c-i), where they are dorsally fused and considered derived (State 1). The separate lobes in *M. cockerelli* are interpreted as a character reversal.

12.— Complexity. In most taxa (*Calicina*, *Microcinella*, *Microcina*, and *Enigmina*), the PSL are simple rounded or pointed lobes (Figs. 4c-e, 5d-g, 6, 8, 14a-c, g-h). Ornate, multilobed PSL (State 1) are regarded as derived. In the *Sitalcina sura* (Fig. 13) and *lobata* (Figs. 14d-f) groups, they are bilobed and trilobed, respectively. Complex PSL are also present in *Megacina* (Fig. 44), but are structurally different from those in *Sitalcina* and probably represent independent origin. They are fused and bilobed in the *M. madera* group and interlocking and with papillate edges in the *M. cockerelli* group.

#### **Stylus.**

13.— Origin. The stylus typically originates at the ventral surface of the glans (Figs. 4c, 5g, 6, 8, 14g-h, 37, 44; State 0); the dorsal position in most *Sitalcina* (except *S. chalonga*) is considered derived (Figs. 13, 14a-f; State 1).

14.— Thickness. Most S are of moderate thickness (State 0), so the long slender S (State 1) of *Megacina* (Figs. 44a-b) and some *Sitalcina* (Figs. 13k, 14e), and the very short stout S (State 2) of *Enigmina* (Figs. 14g-h), are each considered derived.

### Ovipositor

15.— Apical teeth. Apical teeth do not occur in basal *Calicina* (Fig. 4f), nor in the sitalcinoids (e.g., Fig. 16g-h), so their presence is derived (State 1). They are found in two species groups of *Calicina* (figs. 5e-h of Ubick and Briggs, 1989) and at least in *Banksula* (Figs. 5i) and *Texella* (figs. 18-19, 73, 154, 195 of Ubick and Briggs, 1992) of the bifurcate clade, suggesting independent derivation in the two groups.

#### Microspines.

16.— Presence. Microspines are found in most phalangodids, including the presumed basal elements; their absence (Fig. 54) is considered derived (State 1).

17.— Arrangement. Microspines are randomly distributed in *Microcina* (Fig. 10g), *Microcinella* (Fig. 7d), and the two basal groups of *Calicina* (Fig. 4g). The more orderly arrangements are derived: imbricate (State 1) in *Sitalcina* (Fig. 16i) and in transverse clusters (State 2) in *Tularina tularensis* and *T. plumosa* (Figs. 39j, 41i).

#### Apical setae.

18.— Shape. As weakly curved apical setae occur in *Calicina* (Fig. 4f), they are considered plesiomorphic (State 0). Strongly curved (hooked) setae in *Microcinella* (Fig. 7d), *Microcina* (Fig. 11e), two *Sitalcina* groups (Figs. 16g, 32g), and *Tularina tularensis* (Fig. 39h) are derived (State 1), as are straight setae in *Megacina cockerelli* (Fig. 54b) and some members of the bifurcate clade (State 2). Weakly curved setae in the remaining (more highly nested) sitalcinoids is more likely a synapomorphy (character reversal) rather than a plesiomorphic retention.

19.— Form of tip. Simple pointed setae are found in *Calicina* (Fig. 4f) and *Microcinella* (Fig. 7d), so additional points may be regarded as derived. Three derived states have been found: bifid (State 1) in *Tularina plumosa* (Fig. 41h) and *T. scopula* (Fig. 43h); trifurcate (State 2) in *Microcina* (Fig. 11g); and polyfurcate (State 3) in the *Sitalcina sura* group (Fig. 20j). The relationship between the derived states is ambiguous.

### Somatic structures

20.— Eye loss. Most phalangodids have eyes, including the basal groups of *Calicina*, so their loss is clearly derived (State 1). Among the sitalcinoids, eyes are absent in *Microcinella* (Fig. 7b), *Microcina* (Fig. 9b), and *Tularina* (Fig. 40b).

21.— Anterior tubercle number. A high AT number (Fig. 4b) occurs in the basal elements of *Calicina* (Ubick and Briggs, 1989) and *Texella* (Ubick and Briggs, 1992) and is interpreted as plesiomorphic. A reduced AT number would then be derived, and may be regarded as a synapomorphy for the sitalcinoids. In most instances, a strongly reduced AT number correlates with small body size, as in all pedomorphic species, and seems to be an adaptive character. Exceptions to this trend is the AT reduction in some larger species (of *Enigmina*, *Megacina*, and *Banksula*). The scoring is: >6 pairs = State 0; 3-6 pairs = State 1; 2 pairs = State 2; 1 pair = State 3; none = State 4.

22.— Cuticle texture. In most phalangodids, including *Calicina* (Fig. 4b), the tubercles on the scute are randomly arranged (State 0) so that the more complex, areolate, arrangement is considered derived (State 1). This condition occurs in *Microcinella* (Figs. 7a-b), *Microcina* (Fig. 9a-d), *Tularina tularensis* (Figs. 38a-c), and the *Megacina madera* group (Figs. 45a-c, 47a-b, 49a-b). Given its presence in relatively basal sitalcinoid groups, it may well be a synapomorphy for the entire complex, with independent losses (character reversals to random state) occurring in *Sitalcina-Enigmina*, *Tularina plumosa* and *T. scopula*, and *Megacina cockerelli*.

#### Chelicerae.

23.— Boss. A pointed lateral process (boss), observed only in *Megacina cockerelli* (Figs. 51a-d) and *Banksula* (Fig. 5a), is considered derived (State 1).

**Palpal femur.**

24.— Setose dorsal tubercles. In most phalangodids the palpal femur bears a dorsomedian row of setae (State 0). In *Sitalcina lobata* (Figs. 31c-e) and *Banksula* (Figs. 5b-c), these setae are situated on tubercles and considered derived. The form of the tubercles differs in the two taxa, being low and rounded in *S. lobata* (State 1) and long and pointed in *Banksula* (State 2), and suggests independent origin.

25.— Asetose dorsal tubercles. Asetose tubercles, which are located between (and thus not homologous to) the standard dorsal setae, are known only from the *Sitalcina sura* group (e.g., Fig. 21b), and are clearly derived (State 1).

26.— Mesal tubercle. This is found only in the *Sitalcina sura* group (e.g., Fig. 21b) and represents a continuation of the dorsal asetose tubercle row (State 1).

**Legs.**

27.— Male trochanter IV (TrIV). In *Calicina*, *Microcinella*, and *Microcina* the TrIV is unmodified (e.g., Fig. 9e), so the presence of any structures is derived. Ventral tubercles (State 1) are found in *Tularina scopula* (Fig. 42f), *Megacina cockerelli* (Fig. 52f-j), *Banksula*, and *Texella bifurcata* (fig. 11 of Ubick and Briggs, 1992). Larger ventral processes (spurs, State 2) occur in other *Texella*, *Sitalcina* (Figs. 15g, 17f, 31g), and *Enigmina* (Figs. 35e-f). The shortest spurs are in *Enigmina*, medium-sized in *Sitalcina*, and largest in *Texella*.

28.— Femur IV. In the *Megacina madera* group, a ventrobasal projection on Fm IV (Figs. 45e-f, 47e-g, 49d-e) occurs in both sexes, although typically larger in males. As this modification is not found in other Nearctic phalangodids, it is clearly derived (State 1).

29.— Tarsal count. The tarsal count is 3-5-5-5 in *Calicina mariposa* and the majority of phalangodids, so both a tarsomere decrease (State 1) and increase (State 2) are derived. This modification is adaptive, with a TC reduction in paedomorphs and an increase in troglomorphs.

**ANALYSIS.**— We used MacClade (versions 2.1 and 4.08) for studying character transformations and branching patterns and PAUP\* (versions 3.0 and 4.0b10) for finding the shortest trees. All trees discussed are also presented as branching diagrams in Fig. 56.

A heuristic search was run using the entire matrix (27 taxa, 29 characters), with characters unordered and unweighted, but was aborter after an hour, having already produces over 700 shortest trees of 77 steps.

For the second run, redundant taxa were removed from the matrix. The *Sitalcina sura* group was represented only by *S. sura* and *S. peacheyi*, *Enigmina* by *E. warrenorum*, and the *Megacina madera* group by *M. madera* and *M. schusteri*. A heuristic search of this reduced matrix produced three shortest trees of 74 steps (CI=0.57). The three trees are very similar and differ only in the branching within the clade composed of *Microcinella* (MI), *Microcina* (Mc), and *Tularina* (T). This clade groups with the one composed of *Sitalcina* (S) plus *Enigmina* (E), and the two together with *Megacina* (Mg) plus the bifurcate clade (BC), as:

[Tree 1] C (((MI+Mc+T) (S+E)) (Mg+BC)).

Two of the clades suggested by this tree appear reasonable, as they are each supported by genitalic and secondary sexual characters: Mg+BC by VP with dorsal setae (character 6) and S+E by large DL (10) and male TrIV spurs (27). However, the third clade, MI+Mc+T, seems to be supported only by adaptive characters [the reduction in tarsal count (29), eyes (20), and AT number (21)], and so appears to be less well justified (see also section below on Paedomorphy).

For the third run, we omitted these characters from the matrix and obtained 16 shortest trees of 61 steps (CI=0.57), which represent two basic topologies:

[Tree 2] C (MI+Mc+Ttp+(S (E (Ts (Mg+BC))))).

[Tree 3] C ((MI+Mc+Ttp+(S+E)) (Ts (Mg+BC))).

With the omission of the adaptive characters, MI+Mc+T no longer form clade, but remain unresolved and basal, either to all other sitalcinoids plus BC (tree 2) or in a clade with S+E (tree 3). Interestingly, in all trees, *T. scopula* (Ts) groups with Mg+BC, and not with other *Tularina* (Ttp). Although *T. scopula* does differ markedly from other *Tularina*, as detailed above in the Homology section, it is clearly congeneric on the basis of synapomorphies of both male and female genitalia, as the fused PSL (11) and the bifid OV setae (19), the latter shared with *T. plumosa*. Another problem with these trees is the position of *Microcinella* which, given its fundamentally different mode of glans expansion (character 1), is most likely the basal member of the “folding glans clade”, as argued above. Accepting these constraints, with *Microcinella* basal and *Tularina* monophyletic, results in a tree that is only one step longer, 62 steps (CI=0.56):

[Tree 4] C (MI ((Mc (S+E)) (T) (Mg+BC))).

In this tree, the placement of T is ambiguous, as grouping with either (Mc(S+E)) or (Mg+BC) does not change the tree length. This study has failed to turn up any potential synapomorphies between T and (Mc(S+E)). However, one important genitalic character state, fused PSL (11), is found only in *Tularina* and the *Megacina madera* group and suggests a relationship between the two genera. Further support for this grouping is the presence of dorsolateral VP setae in *T. plumosa* which, as we have argued above, may represent the precursor state for the VP dorsal setae (6) found in *Megacina* and the bifurcate clade. Thus, the shortest tree that represents our basic assumptions is the following:

[Tree 5] C (MI ((Mc (S+E)) (T) (Mg+BC))).

## BIOGEOGRAPHY

In previous studies of phalangodid biogeography, we examined the distributions of *Calicina*, *Banksula*, and *Texella* (Ubick and Briggs 1989, 1992, 2002) and described intricate groupings of largely allopatric species. Not surprisingly, similar patterns are found in the *Sitalcina* complex, which is primarily Californian, with extensions into SW Oregon and SE Arizona (Fig. 57). The species are fully allopatric within genera, with the single exception of sympatry between *Megacina cockerelli* and *M. mayacma*, species representing different species groups. The genera are also mostly allopatric, except in the central coast region (Fig. 58). Here *Sitalcina* is sympatric with *Megacina* in the north, with *Microcina* in the south, and with both in the central portion (Marin and Alameda counties). *Microcina* is also sympatric with *Microcinella* in Santa Clara County.

**VICARIANCE.**— The largely allopatric distributions in the *Sitalcina* complex suggest vicariance as the obvious mechanism. The barriers necessary to account for the current distributions would have been, most parsimoniously, between the ranges of the extant taxa, with the sequence of these barriers suggested by the cladogram (Fig. 56: T5). The first barrier would have been at the periphery of the distribution of *Microcinella*, separating it from the non-telescoping clade (which also includes the bifurcate clade). The second set of barriers, separating the clades (Mc (S+E)) from (T (Mg+BC)), would have required a coastal, Sierran, and Mojavian component. The Coast Range portion is now obscured by sympatry, but the Sierran portion is clear, being the boundary between E and T, and the Mojavian portion would have been at the eastern boundary of *S. lobata*, separating it from *Texella deserticola* (see Ubick and Briggs, 1992). A third set of barriers would have separated Mc from S+E and T from M+BC). Again, only the Sierran boundary is clear, being the disjunction between T and M. Finally, the fourth set of barriers would have been between S and E, currently a disjunction, and between M and BC. The bifurcate clade is almost entirely allopatric

with *Megacina* (see Ubick and Briggs, 1992, 2002). *Texella bifurcata* occurs in NW California, largely E of *Megacina cockerelli* and N of the *M. madera* group. The coastal range of *Banksula* is S of *Megacina cockerelli* and its Sierran range currently in the disjunction between *Megacina madera* and *M. schusteri*. Subsequent sets of barriers would have been necessary to separate the species groups (of *Sitalcina* and *Megacina*) and, ultimately, the species themselves.

**DISPERSAL.**— Although vicariance can explain most of sitalcinoid distribution, some dispersal is also necessary to account for the cases of sympatry. These are, at present, restricted to the greater San Francisco Bay area, which also happens to be the best sampled region. No doubt more sympatry can be expected with additional sampling.

The location of the vicariance barrier is obscured because of sympatry. However, if the direction of the dispersal and the dispersers could be identified, then a more precise location of the barriers would be possible. As relictual species persist through time, it seems parsimonious to assume that they also persist in space. With this assumption, the relatively basal groups would have priority for the territory (i.e., their current range coinciding more closely with the ancestral) and the more derived groups would then represent a dispersal into the range of the relict. Applying this reasoning to the above sympatries, it follows that: 1) *Microcina jungi* dispersed into the range of *Microcinella*, 2) *Sitalcina californica* into that of *Microcina*, and 3) *Megacina cockerelli* into that of *Microcina* (in Marin County). Less clear is the sympatry between *M. cockerelli* and *S. californica*, as both are clearly derived elements. However, given that the former is the most derived branch of the *Tularina-Megacina* clade and the latter the least derived of *Sitalcina-Enigmina*, suggests that of the two, *S. californica* is relatively more plesiomorphic and that *M. cockerelli* is the disperser. Finally, in the sympatry between *M. cockerelli* and *M. mayacma*, the former (being more derived) would then have dispersed into the range of *M. mayacma*.

Although this is the minimum dispersal necessary to account for the known sitalcinoid distributions, clearly much more is necessary to take into account the remaining phalangodids in California. The bifurcate clade intrudes into the sitalcinoid range most sharply with *Banksula incredula*, the presumed basal member of the clade, where it is sympatric with both *Sitalcina* and *Microcina*. The remaining bifurcate members, *Texella* and other *Banksula* are closely parapatric with the sitalcinoids, with known instances of sympatry only in the extreme northwest (between *Texella bifurcata* and *Megacina cockerelli*) and south (between *Texella deserticola* and *Sitalcina lobata*). Adding the distribution of *Calicina* into the analysis (Ubick and Briggs 1989) dramatically increases the amount of dispersal needed to account for all Californian Phalangodidae.

**PAEDOMORPHY.**— Species of sitalcinoids (Figs. 57, 59) occur in either grassland or forest habitats, and very rarely in both. At the generic level they divide evenly, with *Microcinella*, *Microcina*, and *Tularina* known almost exclusively from grasslands, and *Sitalcina*, *Enigmina*, and *Megacina* from forests. The grassland species occur in two disjunct regions, the San Francisco Bay area and central Tulare County, and occupy a much smaller total distribution than do the forest dwellers.

As has been previously observed (Briggs, 1968), grassland species differ from forest dwellers morphologically, being small, blind, and having reduced structures. The mechanism of paedomorphy was proposed to account for this situation, specifically progenesis: the reduction in body size and structure resulting from a shortened life cycle (Ubick and Briggs, 1989). These are obvious adaptations to the grassland environment, which is relatively xeric and provides a shorter growing season. Blindness suggests a prolonged subterranean existence, such as found in cave species (Briggs and Ubick 1989; Ubick and Briggs 1989).

As paedomorphy is a derived condition, these characters might be viewed as synapomorphies for the grassland sitalcinoids. However, our interpretation of genitalic characters places these gen-

era relatively basal, with *Microcinella* the most plesiomorphic member of the folding glans clade, *Microcina* basal to *Sitalcina* and *Enigmina*, and *Tularina* basal to *Megacina* and the bifurcate clade. Alternately, the theoretical possibility that paedomorphy is derived for the sitalcinoids and then lost in the forest taxa, also does not seem likely as these adaptations would seem to operate within relatively short time frames and not persist through phylogenetic time. Indeed, in *Calicina*, paedomorphic taxa appear to have been independently derived in several lineages (Ubick and Briggs 1989), as are troglomorphic taxa in *Texella* (Ubick and Briggs 1992). The plausible conclusion, then, is that paedomorphy evolved independently in the three sitalcinoid genera, in relatively recent time, and that all sitalcinoids were originally non-paedomorphic forest dwellers.

As to a possible origin of paedomorphy, the simplest hypothesis may be that it arose in response to an environmental shift towards more xeric conditions; in other words, the grasslands and paedomorphics evolved synchronically. In sitalcinoids, *Tularina* may represent this mode, given that the species currently reside in grasslands that are typically well isolated from forests. By contrast, most *Microcina* and *Microcinella* occur in grasslands that have adjacent forests, with some species even occupying grassland-forest ecotones. Here, an alternate hypothesis is possible, that these species migrated from the forest and onto pre-existing grassland, there to become paedomorphic. This possibility is further suggested by the presence of forest-dwelling sitalcinoids in close proximity to *Microcina*, *Sitalcina californica* occurring throughout its range and *Megacina cockerelli* in the north. As the forest species are clearly more successful than the grassland ones, being larger organisms, more widely distributed, and (based on our collection records) far more abundant, it is certainly plausible that they negatively impacted *Microcina*, perhaps even displacing it to a less favorable habitat.

#### FUTURE STUDY

Although this study greatly increases our knowledge of sitalcinoid harvestmen, much work still remains for a full description of the fauna. Due to time constraints, it has not been possible adequately to analyze some of the material on hand. The morphological variation in *Megacina cockerelli*, and to a lesser extent in *Sitalcina californica*, needs to be more carefully examined for the presence of additional species. Also, the male genitalia of some *Sitalcina* need to be more fully described, especially the form of the often hidden stylus. However, some existing gaps will only be filled through study of additional specimens, such as the status of the currently recognized species in Arizona, the unknown male of *S. borregoensis*, and the known but currently undescribed species of *Microcina* and *Sitalcina*. But the most interesting and potentially surprising information is likely to come from the discovery of new species and populations. These are most probable in the larger disjunctions between the known distributions, and especially in the disjunctions between genera (*Tularina* and *Megacina*, *Sitalcina* and *Enigmina*). Their discovery would not only increase the net knowledge based on these organisms but, more importantly, test the relationships proposed.

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Thanks go to the many collectors who gathered these rarely encountered organisms: Lisa J. Boutin, Gonzalo Giribet, Kevin Hom, Wendell R. Icenogle, Albert K. S. Jung, David H. Kavanaugh, Joel Ledford, Vincent F. Lee, Robert Lem, Robert Pape, Pierre Paquin, Bill Peachey, Warren C. Rauscher, Vincent D. Roth, Warren E. Savary, and Robert Schuster. Also appreciation is extended to the curators who kindly loaned material for this study: Norman I. Platnick, Lorenzo Prendini, and Randy Mercurio (AMNH), Gonzalo Giribet and Laura Leibensperger (MCZ), Cheryl

Barr (UCB), Lynn Kimsey and Steve Hayden (UCD), Richard Vetter (UCR), William Shear (CWS), and James C. Cokendolpher (CJC). Special appreciation goes to Wendell Icenogle and Robert Pape for their donation of important specimens. Appreciation is extended to Charles E. Griswold and the Entomology Department at CAS for generous use of facilities, Tony Walecka, Larry Arndt, Favio Penny, and others in Computer Services for solving many computer puzzles and especially their magical powers in restoring the dead (computers). Hilbert Tu very generously donated a copy of Adobe Illustrator to help produce the maps. Suzanne Ubick graciously edited various versions of this manuscript and provided assistance and companionship throughout. Charles Griswold and William Shear critically reviewed earlier versions of the manuscript and provided many helpful comments.

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**Illustrations**

**Figures 2–58**

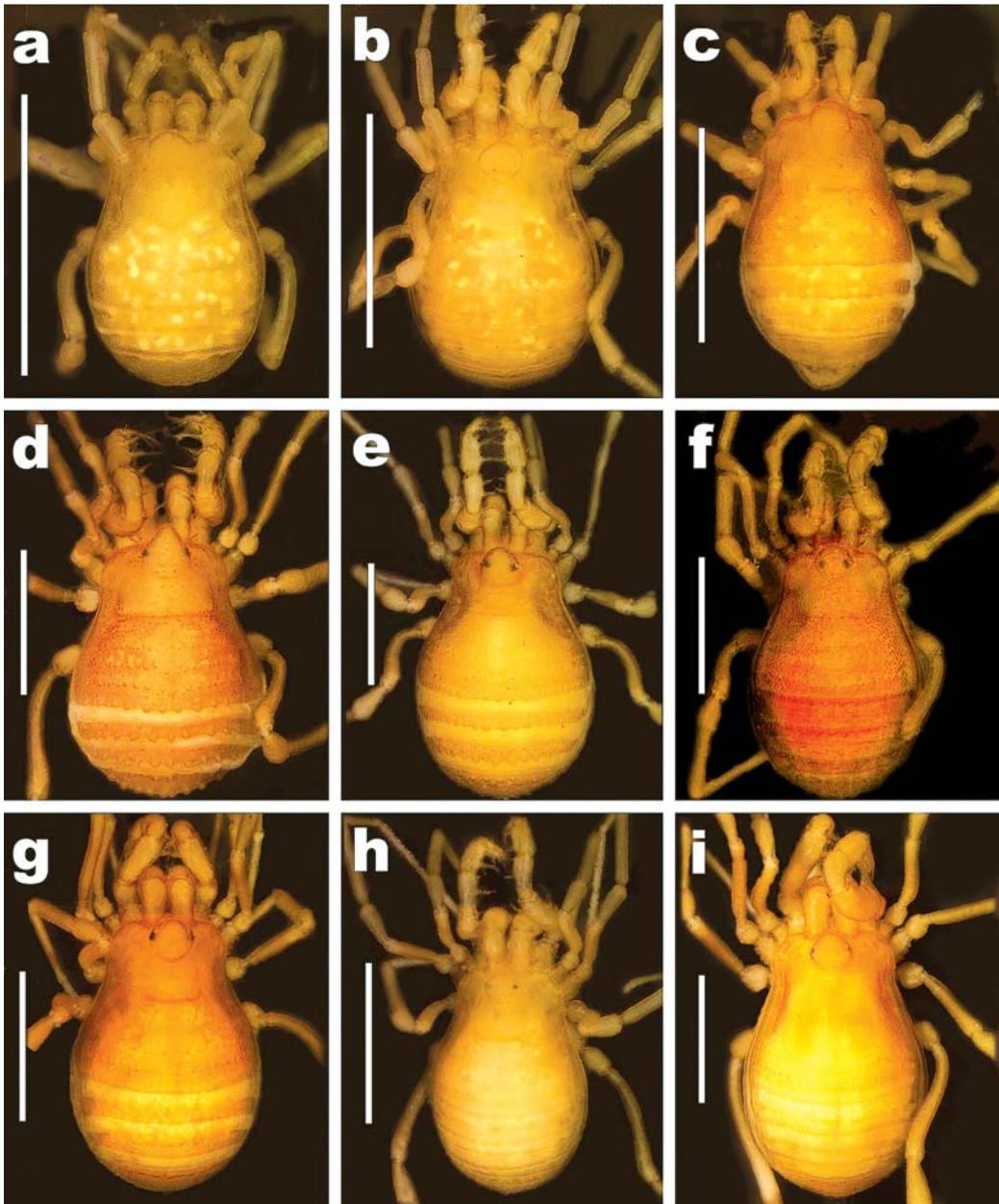


FIGURE 2. *Sitalcina* complex, females, dorsal view: a. *Microcinella homi* (Briggs and Ubick). b. *Microcina tiburona* (Briggs and Hom). c. *Tularina tularensis* sp. nov. d. *Sitalcina californica* (Banks). e. *S. sura* Briggs. f. *S. lobata* Goodnight and Goodnight. g. *Enigmina granita* (Briggs). h. *Megacina mayacma* sp. nov. i. *Megacina cockerelli* (Goodnight and Goodnight). Scale bar = 1mm.

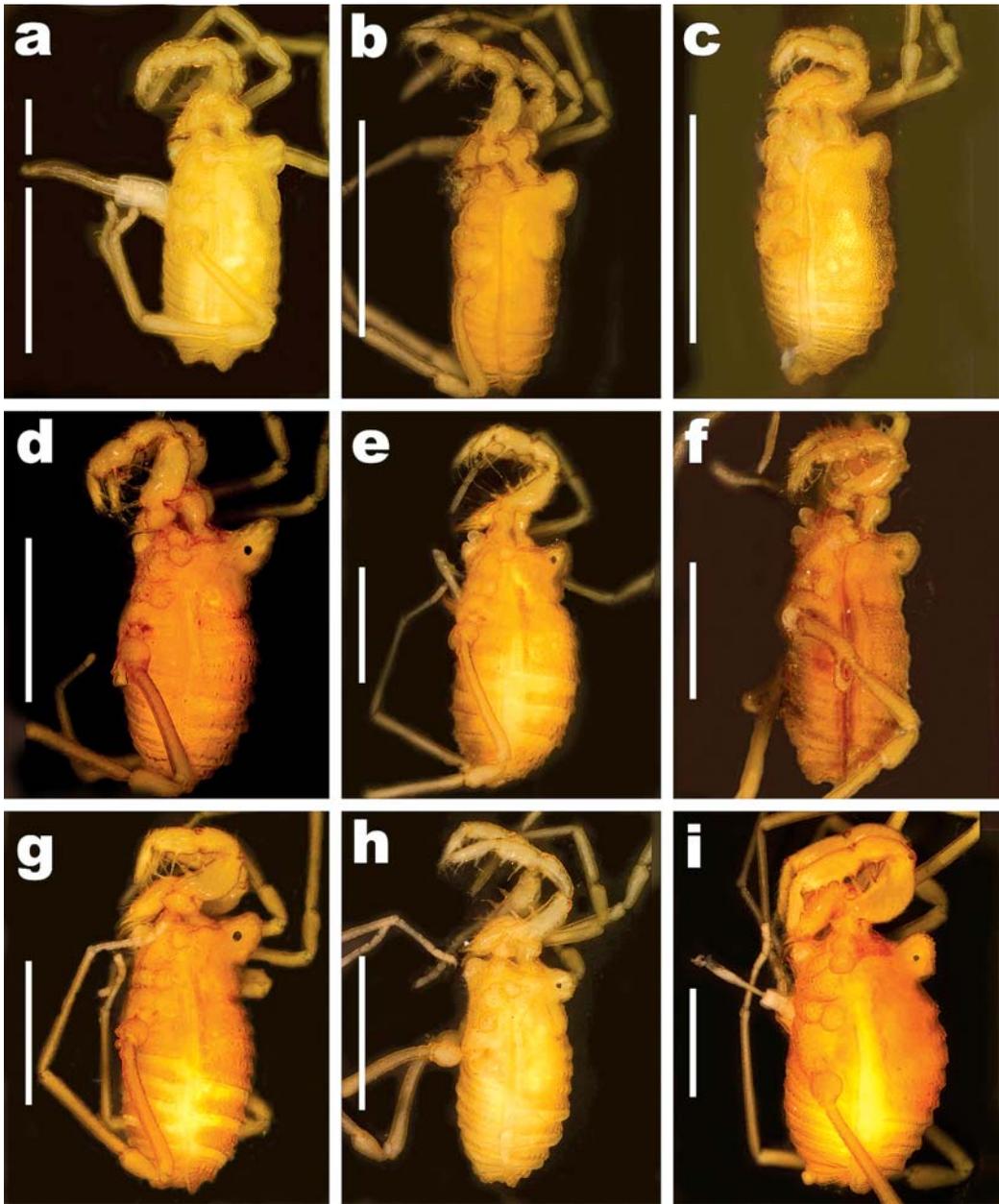


FIGURE 3. *Sitalcina* complex, males, lateral view: a. *Microcinella homi* (Briggs and Ubick). b. *Microcina tiburona* (Briggs and Hom). c. *Tularina tularensis* sp. nov. d. *Sitalcina californica* (Banks). e. *S. sura* Briggs. f. *S. lobata* Goodnight and Goodnight. g. *Enigmina granita* (Briggs). h. *Megacina mayacma* sp. nov. i. *Megacina cockerelli* (Goodnight and Goodnight). Scale bar = 1mm.

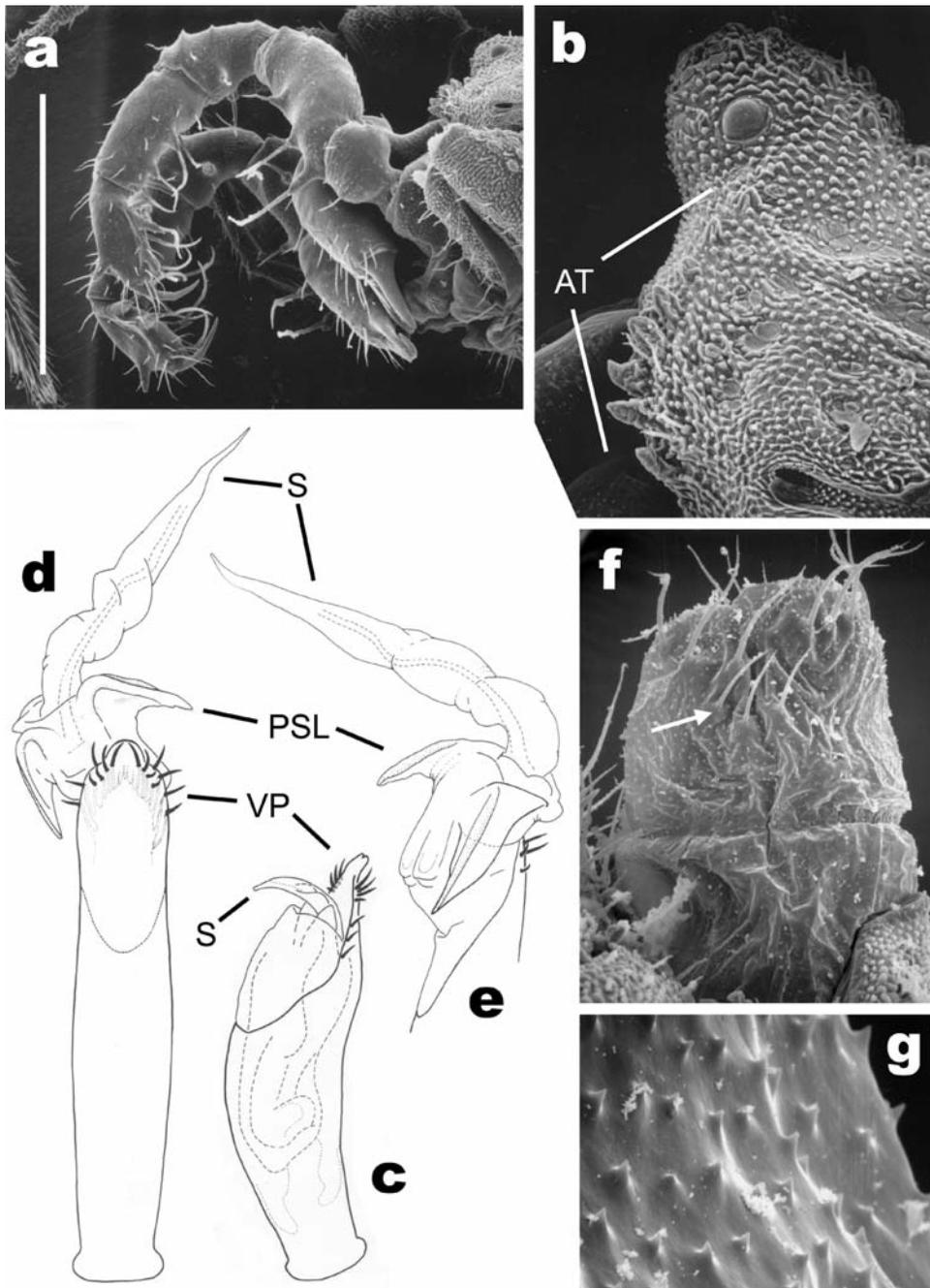


FIGURE 4. *Calicina* Ubick and Briggs, morphology. *C. mariposa* (Briggs) (a–b, d–g), *C. yosemitensis* (Briggs) (c). **a–e. Male.** a. Palpi, lateroventral view. b. Cephalon, lateral view, showing row of anterior tubercles (AT). c–e. Penis, unexpanded glans in dexterolateral view (c), and expanded glans in ventral (d) and dexterolateral (e) views. **f–g. Female,** ovipositor in dexterolateral view (f) showing subapical setae (arrow) and lateral surface with microspines (g). AT = anterior tubercles, PSL = parastylar lobes, S = stylus, VP = ventral plate. Scale bar = 475 $\mu$ m (a), 435 $\mu$ m (d, e), 350 $\mu$ m (c), 200 $\mu$ m (b), 195 $\mu$ m (f), 20 $\mu$ m (g).

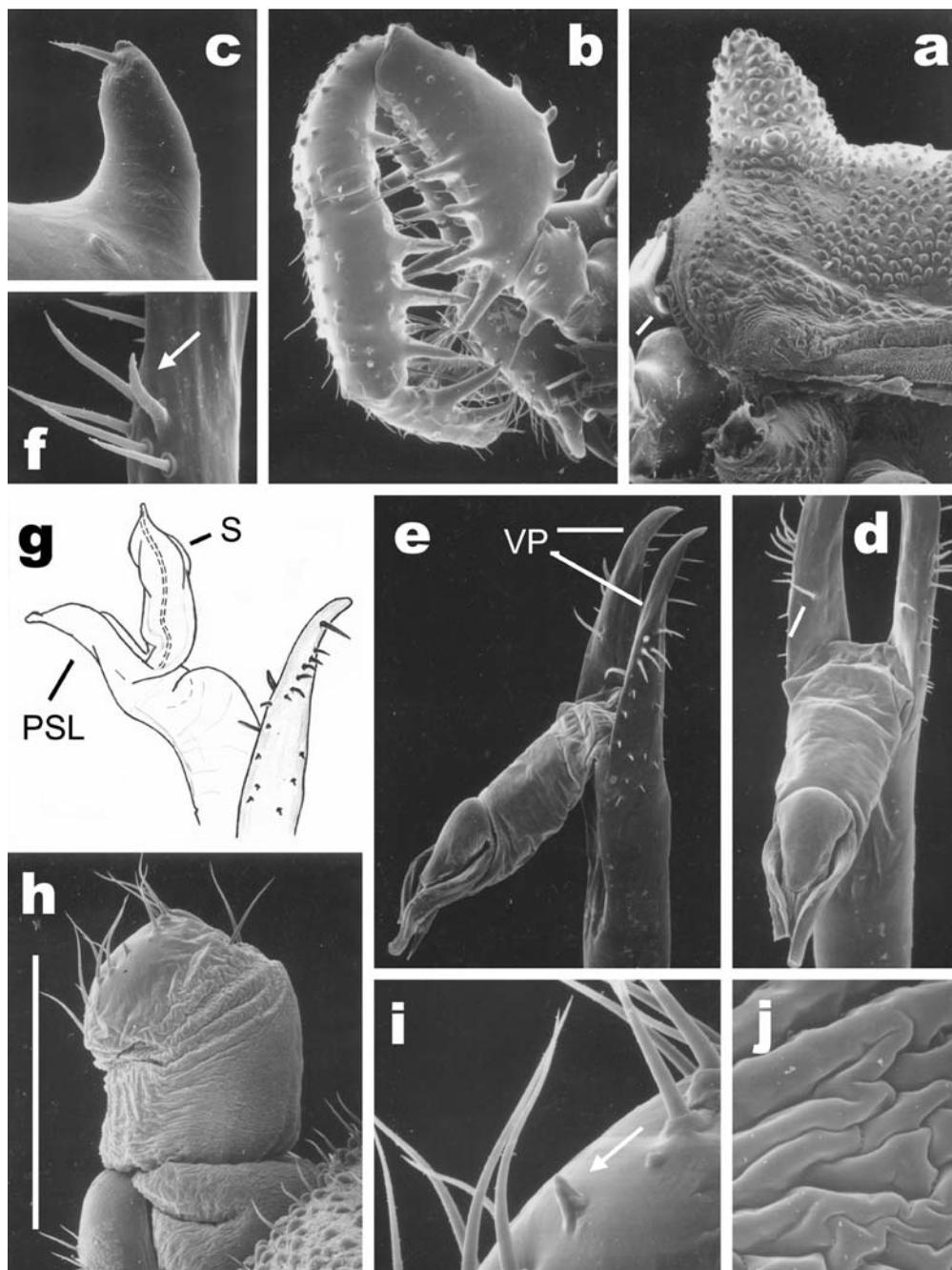


FIGURE 5. *Banksula incredula* Ubick and Briggs, morphology: **a-g. Male.** a. Cephalon, lateral view, with line showing cheliceral boss. b-c. Palpi, lateral view, showing setose dorsal femoral tubercle (c). d-g. Penis, with partially expanded glans in dorsal (d, f) and dexterolateral (e) views, showing AS (arrow) and dorsal seta (line), and fully expanded glans in dexterolateral view (g). **h-j. Female,** ovipositor, sinistrolateral view (h), with close-up showing apical tooth (i, arrow) and lateral surface lacking microspines (j). PSL = parastylar lobe, S = stylus, VP = ventral plate. Scale bar = 1.1mm (b), 880 $\mu$ m (a), 445 $\mu$ m (h), 310 $\mu$ m (g), 200 $\mu$ m (d-e), 120 $\mu$ m (i), 117 $\mu$ m (c), 86 $\mu$ m (f), 33 $\mu$ m (j).

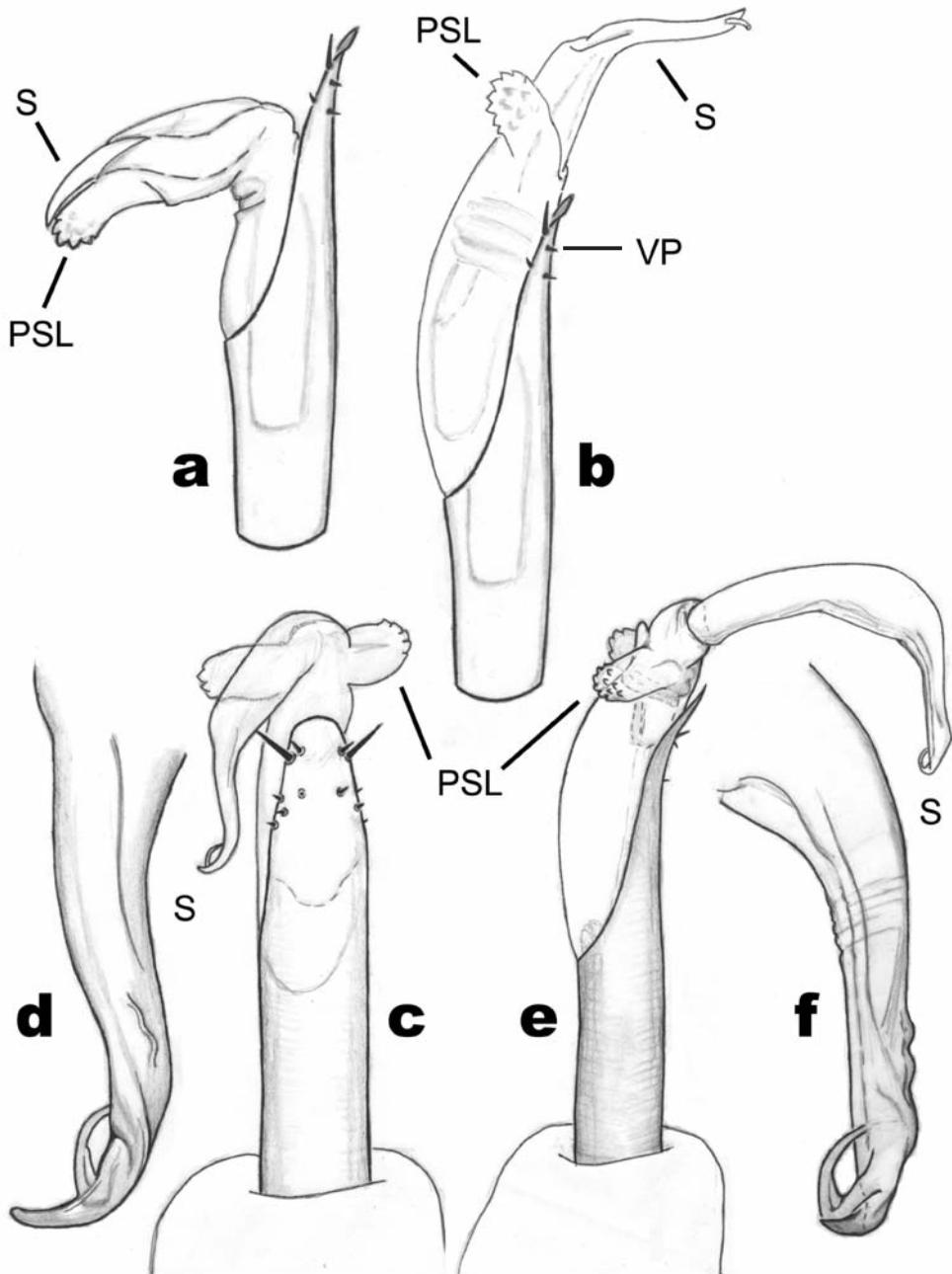


FIGURE 6. *Microcinella* gen. nov., male genitalia. a-b. *M. homi* (Briggs and Ubick) penis, dexterolateral view, with glans partially (a) and fully (b) expanded. c-f. *M. coensis* sp. nov. penis, fully expanded, in ventral (c-d) and dexterolateral (e-f) views. PSL = parastylar lobe, S = stylus, VP = ventral plate.

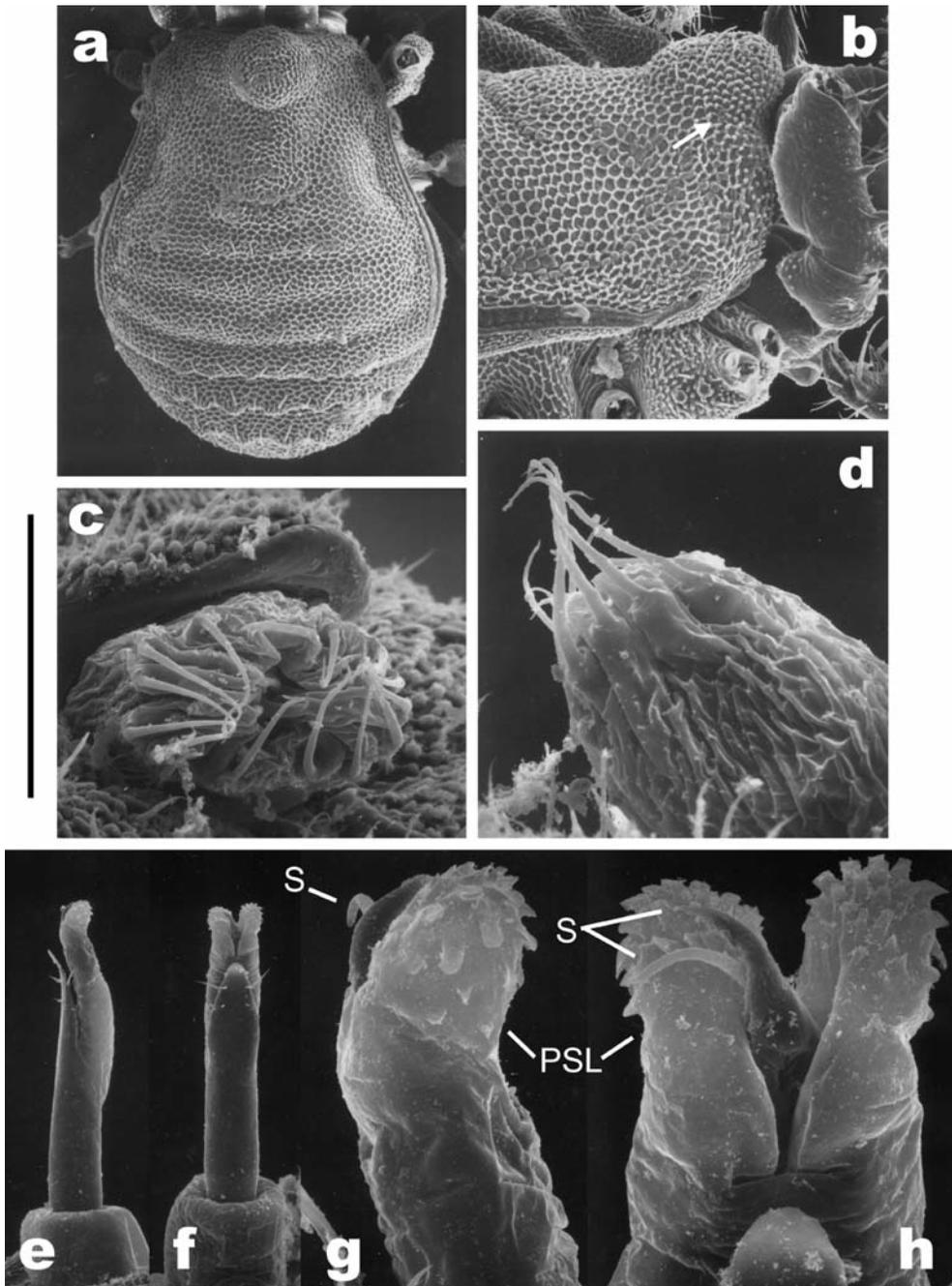


FIGURE 7. *Microcinella homi* (Briggs and Ubick), morphology. a–b, e–h. Male. c–d. Female. a–b. Body, dorsal (a) and lateral (b) views, with arrow showing corneal vestige. c–d. Ovipositor, apical (c) and dexterolateral (d) views. e–h. Penis with partially expanded glans (unfolded but not telescoped) in sinsitrolateral (e) and ventral (f) views with close-up of glans (g–h). PSL = parastylar lobe, S = stylus. Scale bar = 480 $\mu$ m (a), 475 $\mu$ m (g–h), 290 $\mu$ m (e–f), 286 $\mu$ m (b), 82 $\mu$ m (c), 57 $\mu$ m (d).

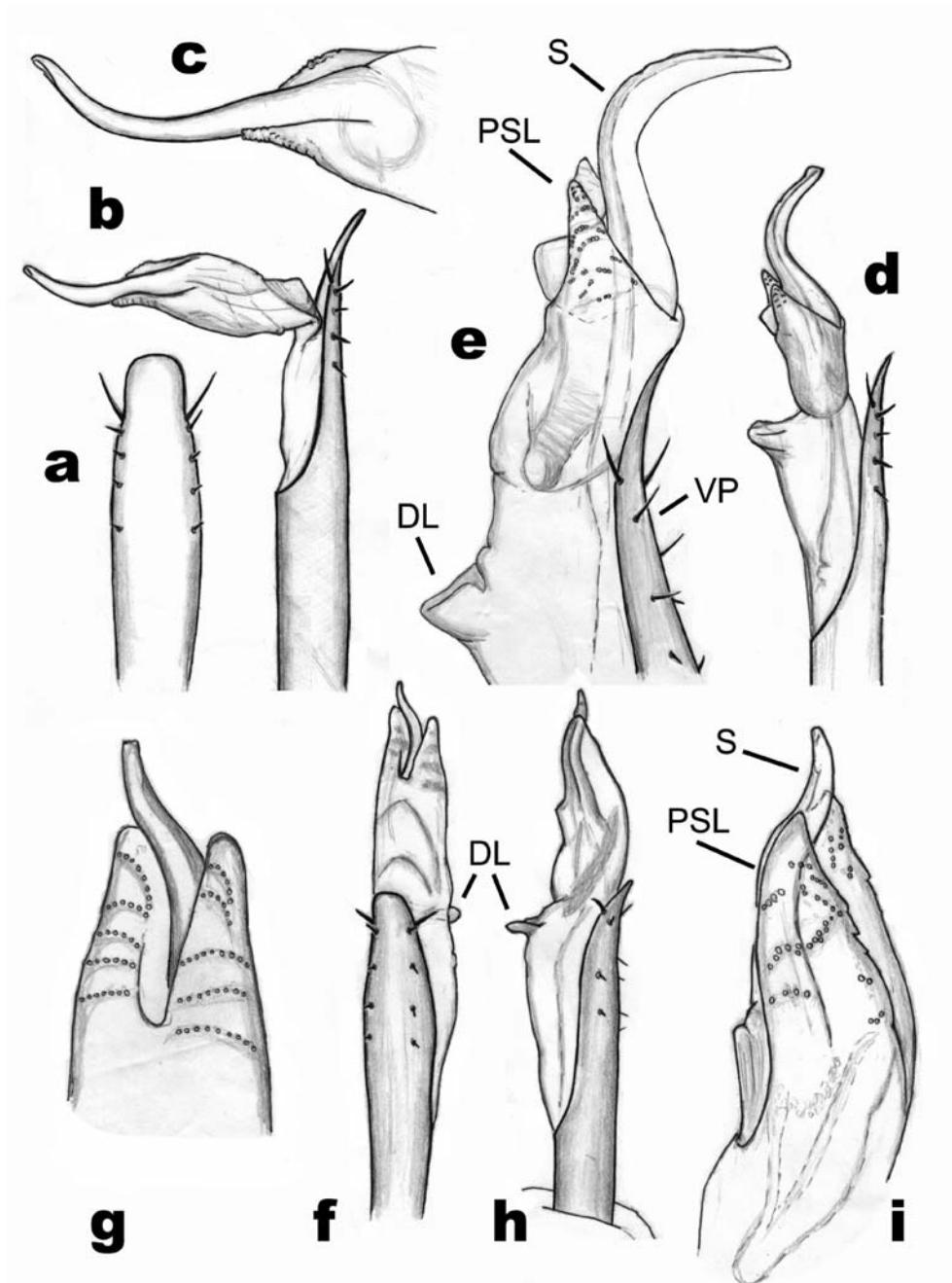


FIGURE 8. *Microcina* Briggs and Ubick, male genitalia. a-e. *M. tamalpais* sp. nov. penis, in ventral (a) and dexterolateral (b-e) views, showing glans partially (b-c) and fully (d-e) expanded, with close-ups (c, e). f-i. *M. potrero* sp. nov. penis, fully expanded, in sub-ventral (f-g) and dexterolateral (h-i) views, with close-ups of glans (g, i). DL = dorsal lobe, PSL = parastylar lobe, S = stylus, VP = ventral plate.

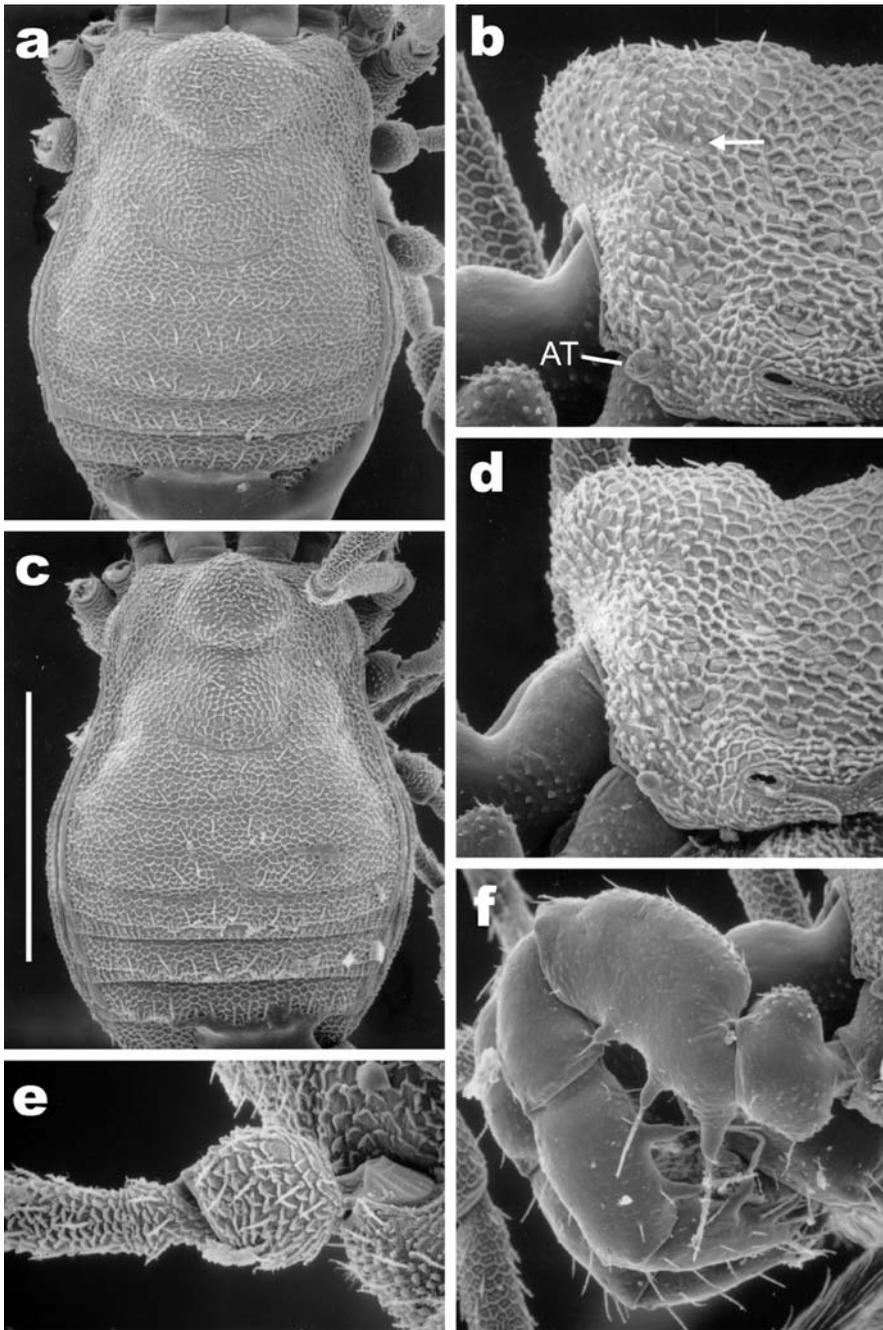


FIGURE 9. *Microcina sanbruno* sp. nov., somatic morphology. a–b, e–f. Male. c–d. Female. a, c. Body, dorsal view. b, d. Cephalon, lateral view, with arrow showing corneal vestige. e. Trochanter IV, lateral view. f. Palpi, lateral view. AT = anterior tubercle. Scale bar = 435 $\mu$ m (a, c), 250 $\mu$ m (f), 175 $\mu$ m (b, d), 167 $\mu$ m (e).

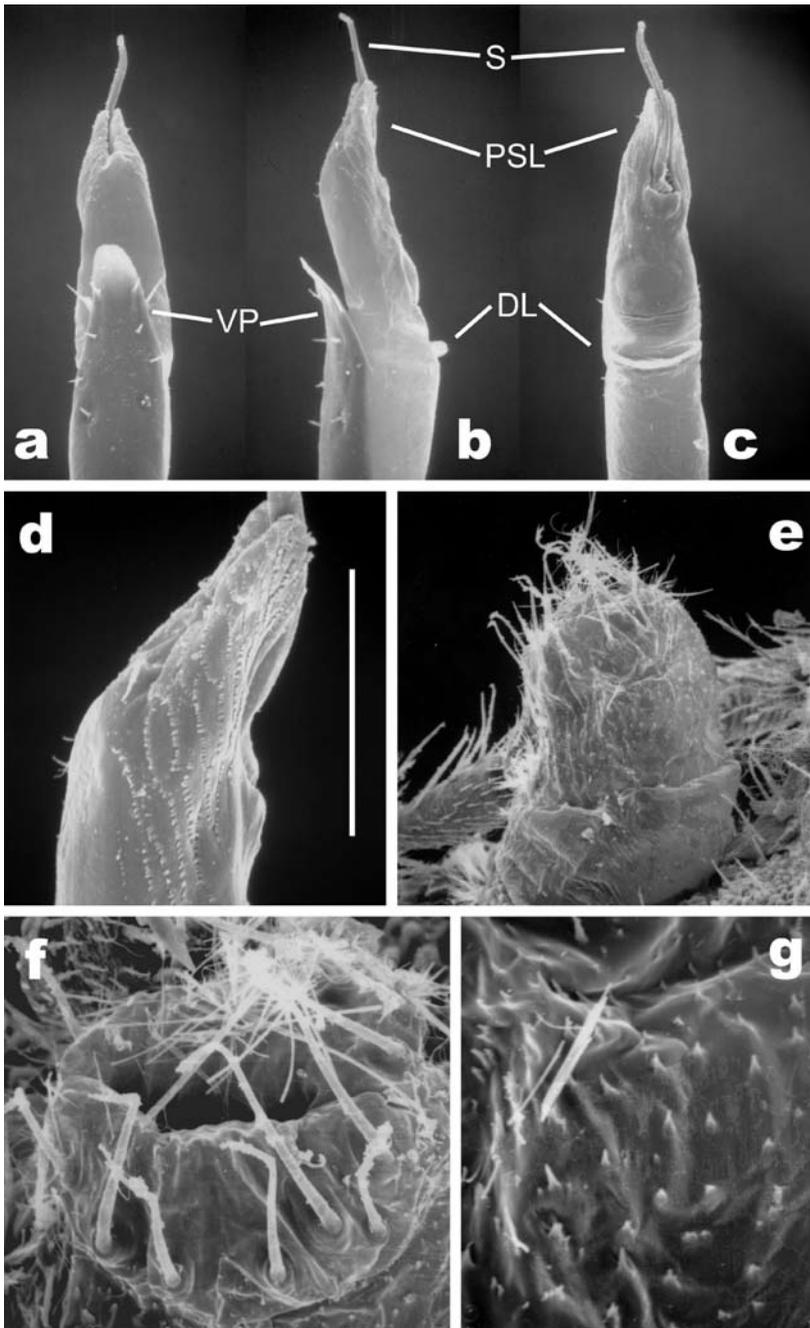


FIGURE 10. *Microcina sanbruno* sp. nov., genitalic morphology. a–d. Male, penis fully expanded in ventral (a), sin-sitrolateral (b, d), and dorsal (c) views, with close-up of glans (d). e–g. Female, ovipositor in sin-sitrolateral (e) and apical (f) views, with lateral surface showing microspines (g). DL = dorsal lobe, PSL = parastylar lobe, S = stylus, VP = ventral plate. Scale bar = 545 $\mu$ m (f), 455 $\mu$ m (d), 130 $\mu$ m (a–c, e), 26 $\mu$ m (g).

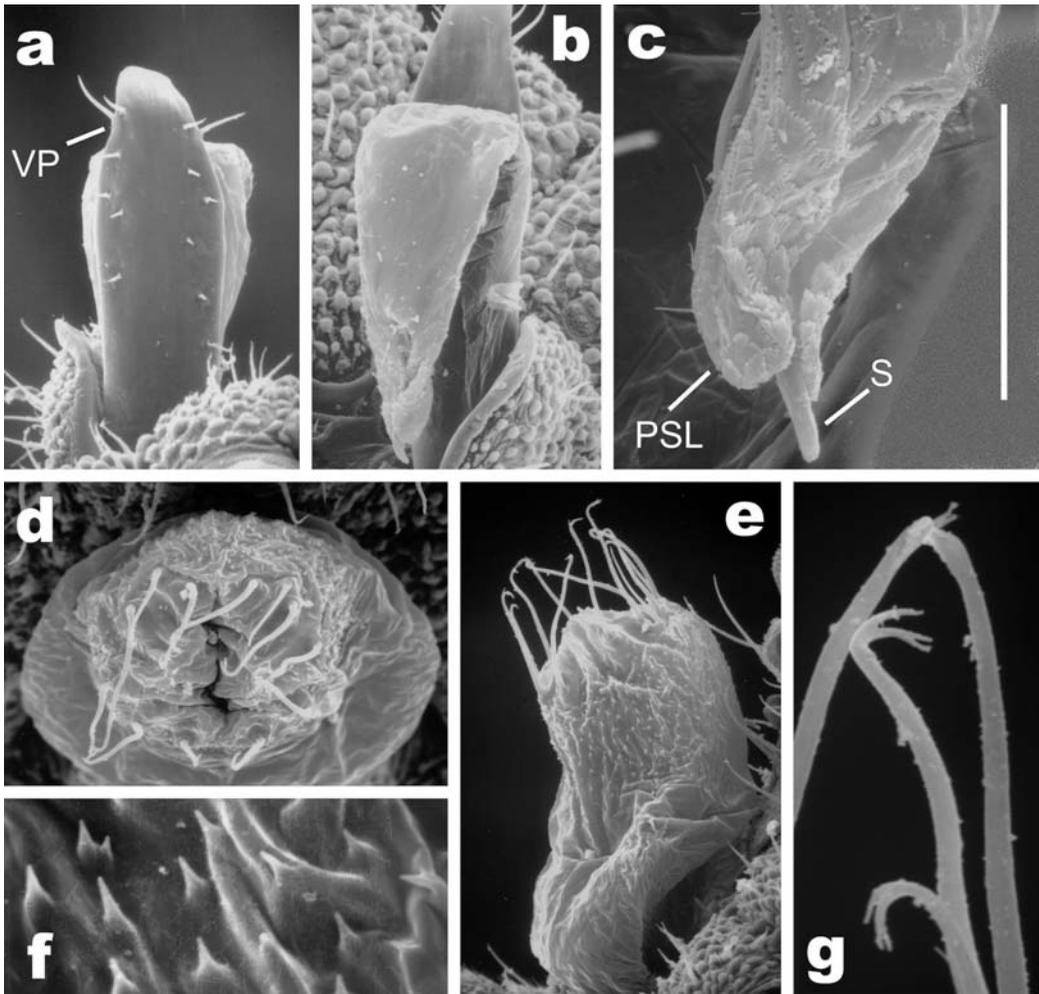


FIGURE 11. *Microcina stanford* sp. nov., genitalic morphology. a–c. Male, penis unexpanded in ventral (a) and subdorsal (b) views, with glans apex in dexterolateral view (c). d–g. Female, ovipositor in apical (d) and sinistrolateral (e–g) views, with close-up of lateral surface showing microspines (f) and of apical setae (g). PSL = parastylar lobe, S = stylus, VP = ventral plate. Scale bar = 143 $\mu$ m (e), 115 $\mu$ m (a–b, d), 38 $\mu$ m (c), 30 $\mu$ m (g), 19 $\mu$ m (f).

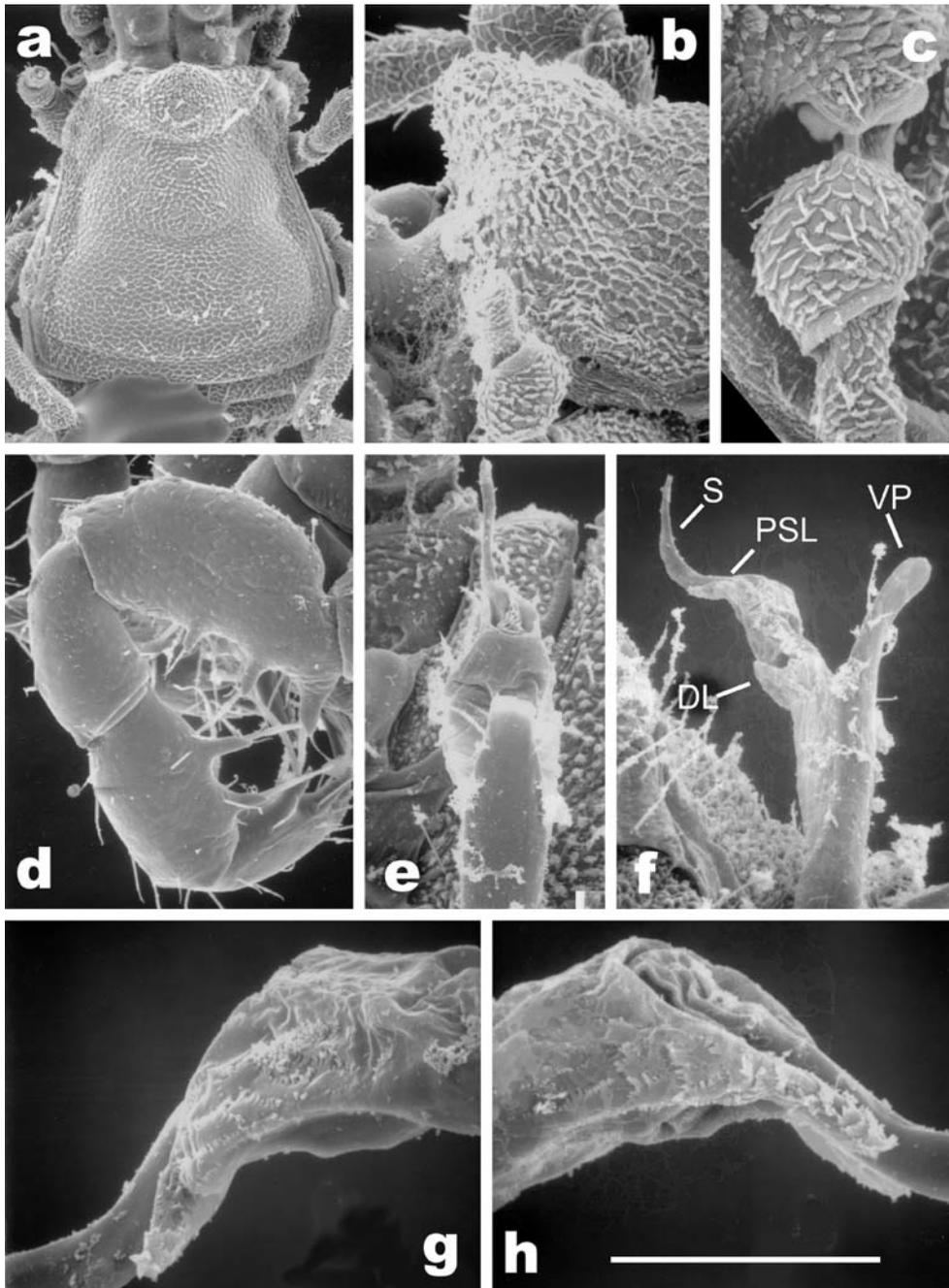


FIGURE 12. *Microcina tamalpais* sp. nov., male. a–d. Somatic morphology. a–b. Body dorsal (a) and cephalon lateral (b) views. c. Right trochanter IV, lateral view. d. Left palp, lateral view. e–h. Genital morphology. e–h. Penis, fully expanded in ventral (e) and dexterolateral (f) views, with glans apex in dexterolateral (g) and sinistrolateral (h) views. DL = dorsal lobe, PSL = parastylar lobe, S = stylus, VP = ventral plate. Scale bar = 475 $\mu$ m (a), 200 $\mu$ m (d), 190 $\mu$ m (b), 150 $\mu$ m (e–f), 30 $\mu$ m (g), 116 $\mu$ m (c), 38 $\mu$ m (g–h).

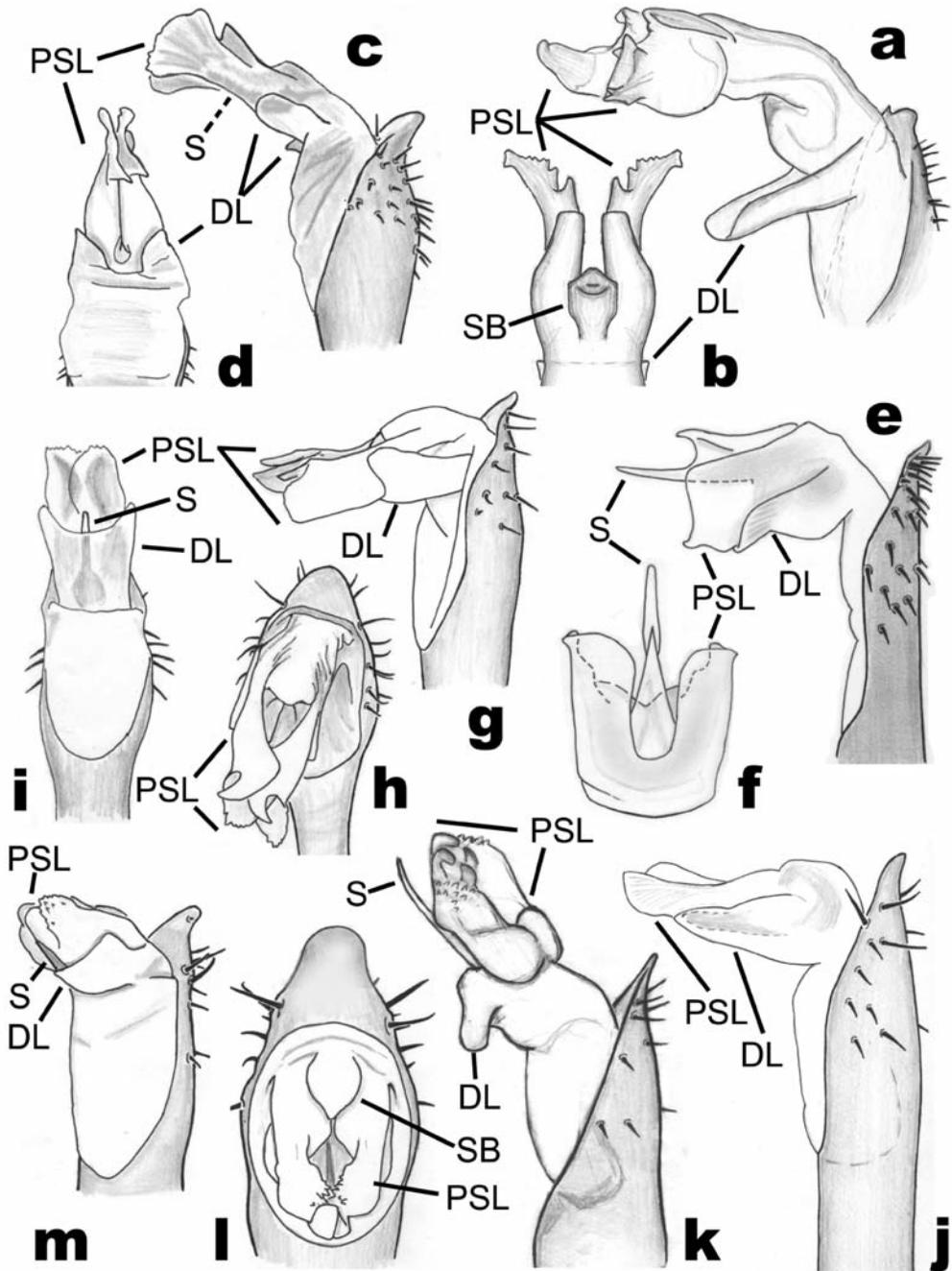


FIGURE 13. *Sitalcina sura* group, male genitalia. a-b. *S. sura* Briggs, fully expanded penis in dexterolateral view (a) and glans in ventral view (b). c-d. *S. seca* sp. nov., fully expanded penis in dexterolateral (c) and dorsal (d) views. e-f. *S. chalona* Briggs, partially expanded penis in dexterolateral view (e) and glans in ventral view (f). g-i. *S. flava* Briggs, partially expanded penis in dexterolateral (g) and subdorsal (h) views and fully expanded penis in dorsal view (i). j. *S. rothi* sp. nov., partially expanded penis in dexterolateral view. k-m. *S. peacheyi* sp. nov., penis, unexpanded in dorsal view (l), partially expanded in dorsolateral view (m), and fully expanded in dexterolateral view (k). DL = dorsal lobe, PSL = parastylar lobe, S = stylus, SB = styler base, VP = ventral plate.

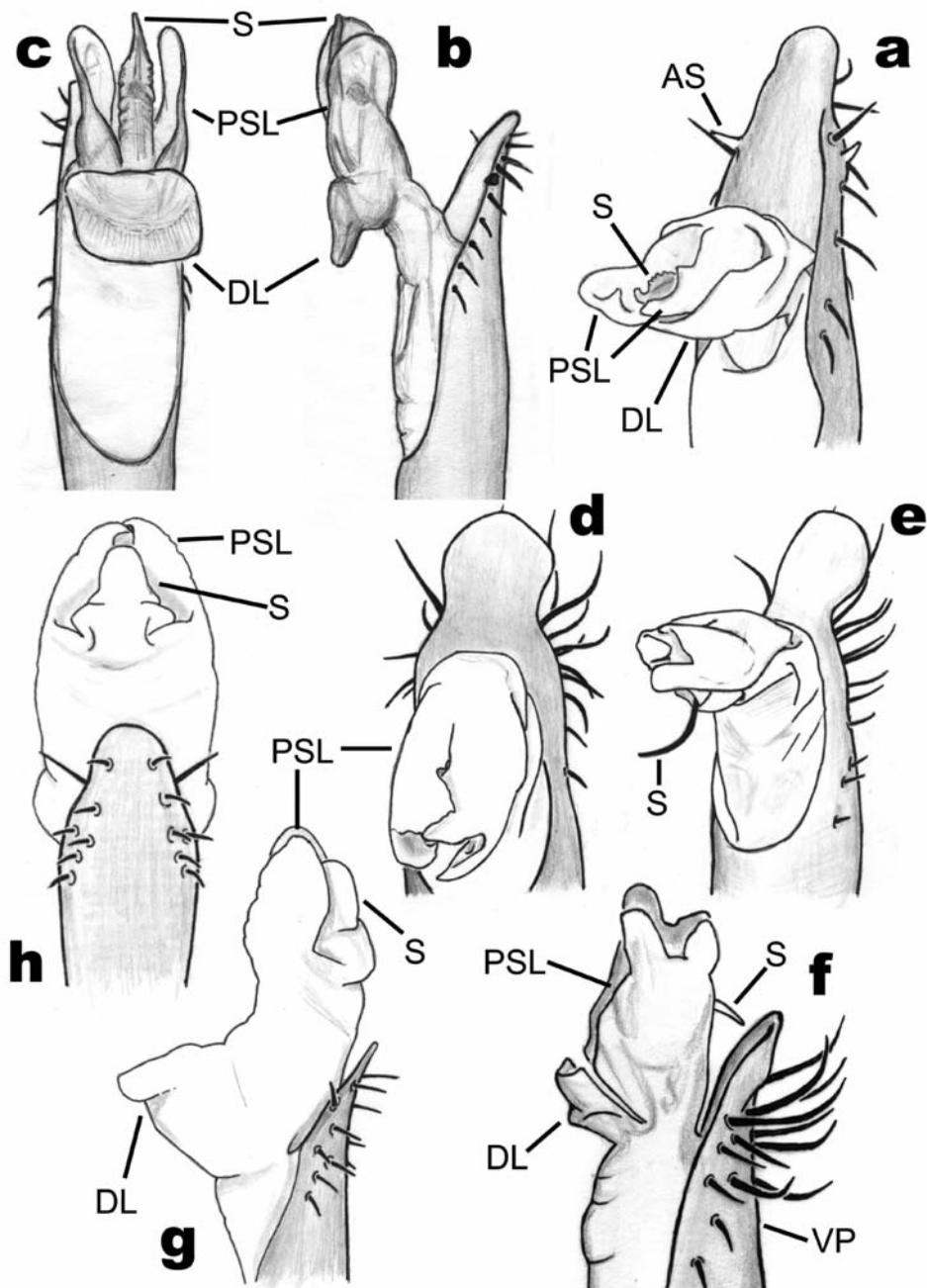


FIGURE 14. *Sitalcina californica* and *lobata* groups and *Enigmina* gen. nov., male genitalia. a–c. *S. californica* (Banks), penis with partially expanded glans in dorsolateral view (a) and with fully expanded glans in dexterolateral (b) and dorsal (c) views. d–f. *S. lobata* Goodnight and Goodnight, penis with glans folded in dorsal view (d), partially expanded in dorsolateral view (e), and fully expanded in dexterolateral view (f). g–h. *E. warrenorum* sp. nov., penis fully expanded in dexterolateral (g) and ventral (h) views. AS = apical spine, DL = dorsal lobe, PSL = parastylar lobe, S = stylus, VP = ventral plate.

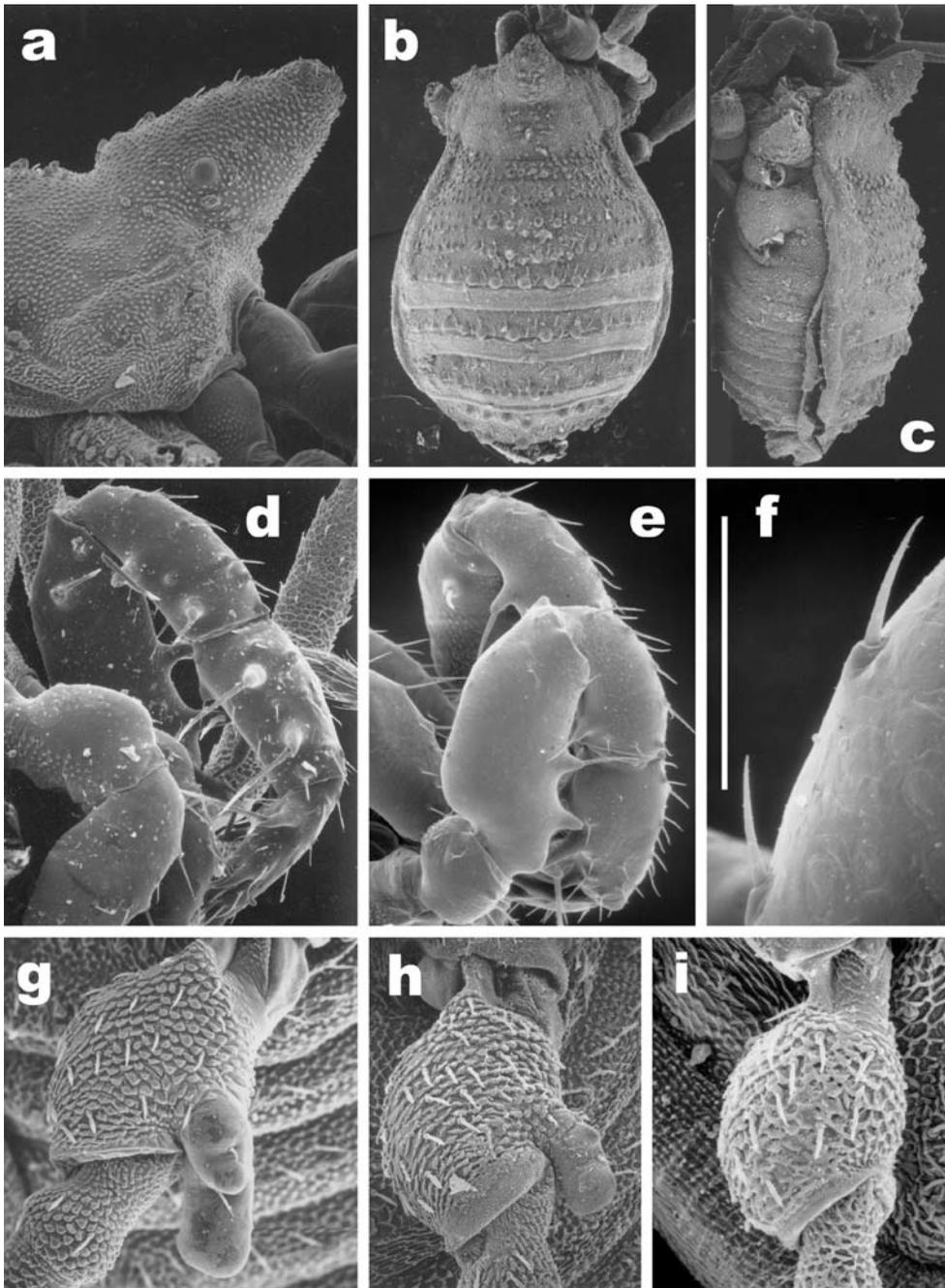


FIGURE 15. *Sitalcina californica* (Banks), somatic morphology. a, d–h. Male. b–c, i. Female. a–c. Body. a. Cephalon of male, lateral view. b–c. Body of female, dorsal and lateral views. d–f. Palpi of male, mesal (d) and ectal (e) views and femur dorsum showing setae (f). g–i. Trochanter IV of male (g–h) and female (i), ectal views. Scale bar = 1mm (b–c), 475 $\mu$ m (a), 380 $\mu$ m (d–e), 286 $\mu$ m (g–h), 200 $\mu$ m (i), 60 $\mu$ m (f).

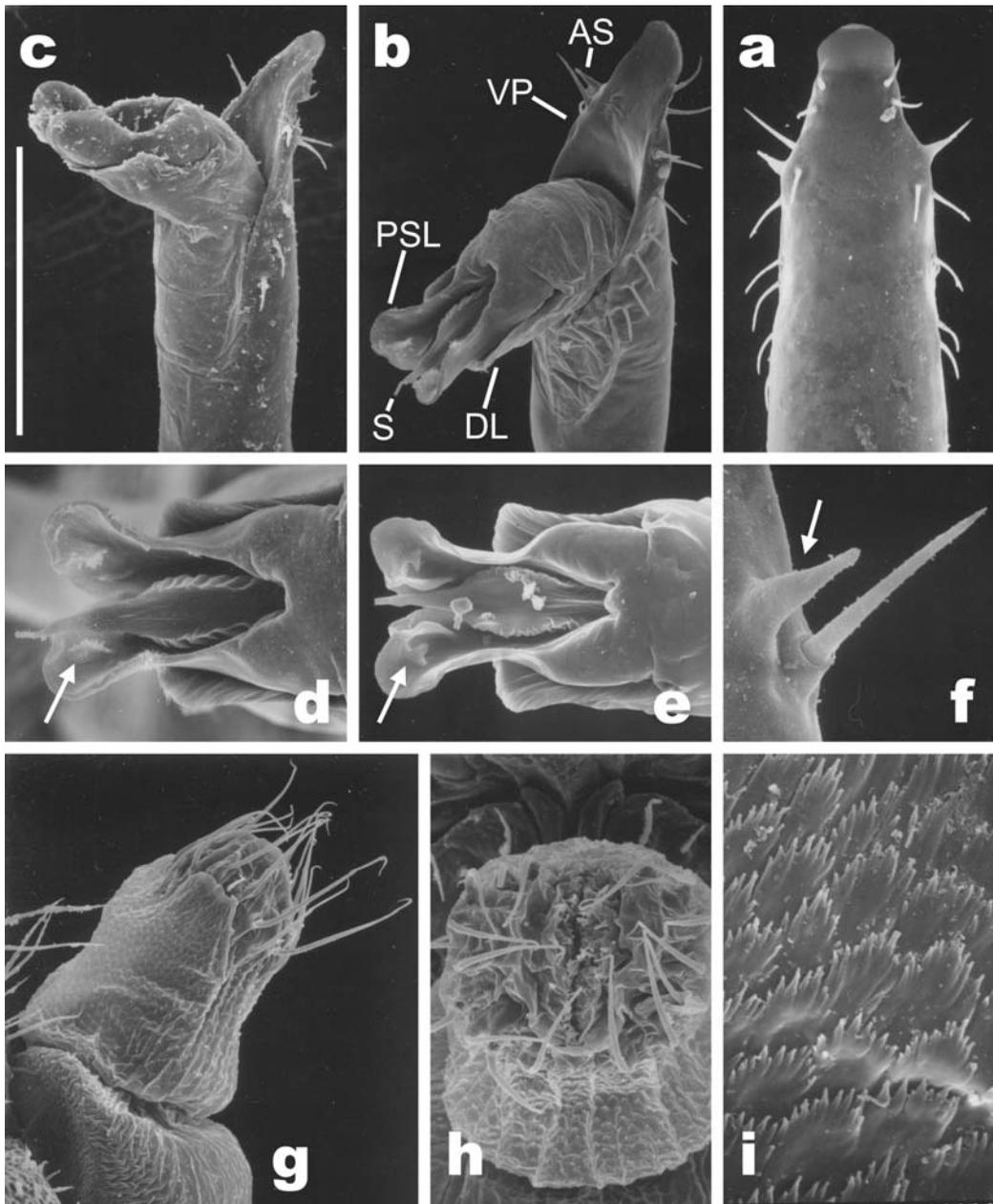


FIGURE 16. *Sitalcina californica* (Banks), genitalic morphology. a–f. Male, penis in ventral (a) and dexterolateral (b–c) views with glans partially (b) and more fully expanded (c), and glans, ventral view, of specimens from Cave Gulch (d) and El Verano (e), showing variation in PSL apicoventral ornamentation (arrows), and (f) lateroapical margin of VP showing apical spine (arrow). g–i. Female, ovipositor in dexterolateral (g) and apical (h) views, and lateral surface showing microspines (i). AS = apical spine, DL = dorsal lobe, PSL = parastylar lobe, S = stylus, VP = ventral plate. Scale bar = 190 $\mu$ m (g), 143 $\mu$ m (b–c), 126 $\mu$ m (h), 114 $\mu$ m (a), 82 $\mu$ m (d–e), 30 $\mu$ m (f), 19 $\mu$ m (i).

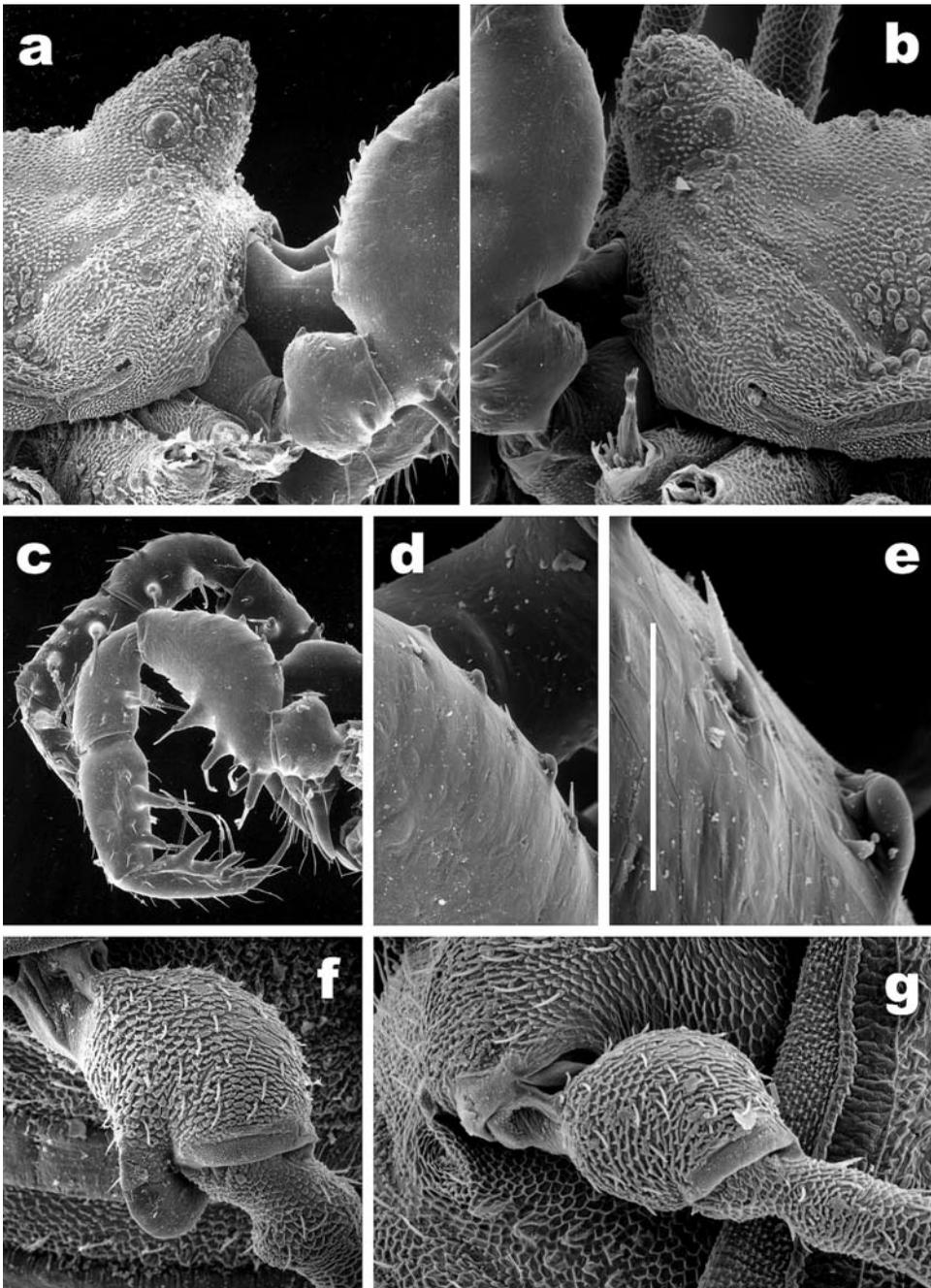


FIGURE 17. *Sitalcina sura* Briggs, somatic morphology. a, c, f. Male. b, d–e, g. Female. a–b. Cephalon, lateral view. c–e. Palpi, lateral view (c), with dorsolateral view of femur dorsum (d–e), showing dorsal setae and asetose tubercles. f–g. Trochanter IV, ectal view. Scale bar = 825 $\mu$ m (c), 490 $\mu$ m (a), 385 $\mu$ m (b), 320 $\mu$ m (f), 250 $\mu$ m (g), 130 $\mu$ m (d), 39 $\mu$ m (e).

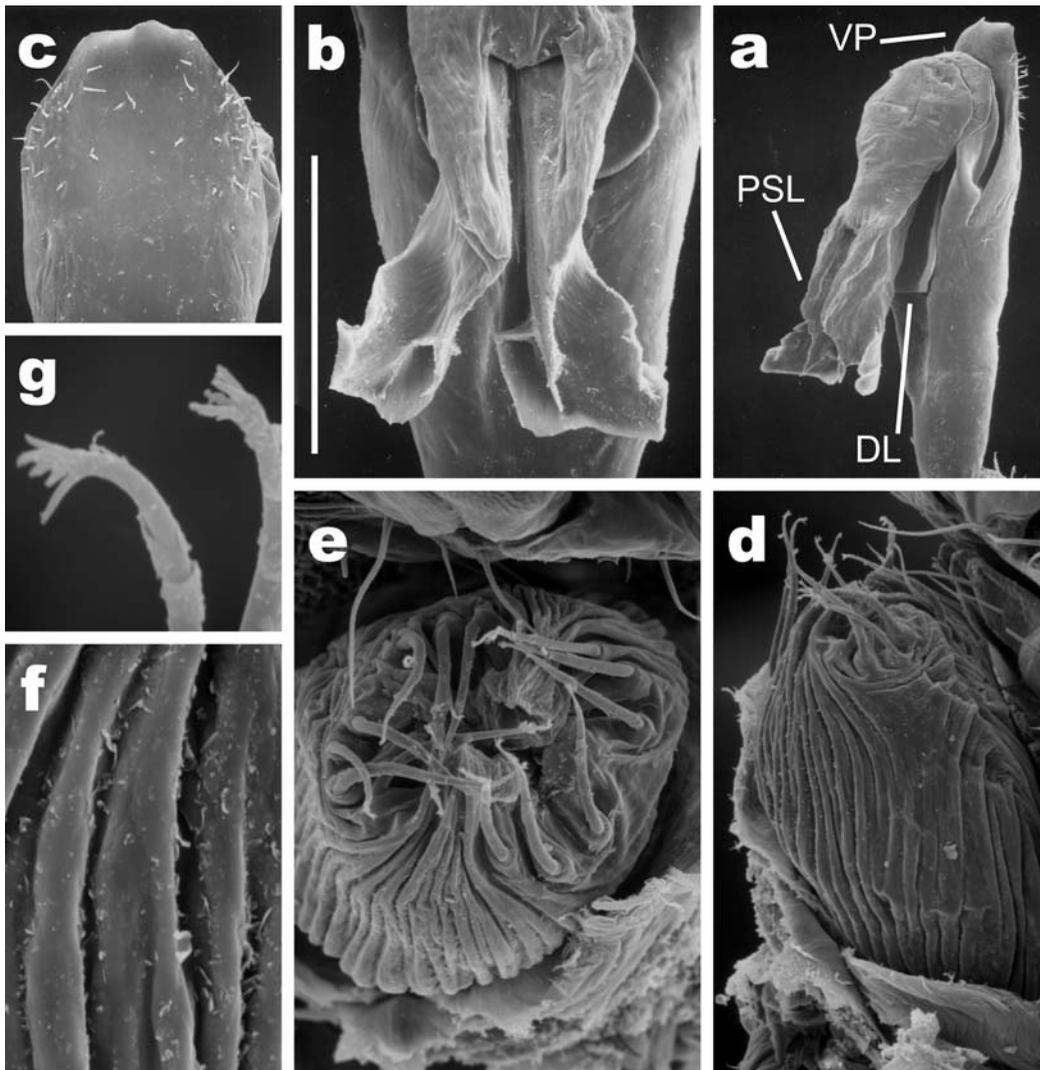


FIGURE 18. *Sitalcina sura* Briggs, genitalic morphology. a–c. Male, penis with unexpanded glans in (dextero)laterodorsal (a), dorsal (b), and ventral (c) views. d–g. Female, ovipositor, sinistrolateral (d) and apical (e) views, showing lateral surface lacking microspines (f) and setal tips (g). DL = dorsal lobe, PSL = parastylar lobe, VP = ventral plate. Scale bar = 460 $\mu$ m (a), 310 $\mu$ m (c), 230 $\mu$ m (d), 190 $\mu$ m (b), 98 $\mu$ m (e), 38 $\mu$ m (f), 21 $\mu$ m (g).

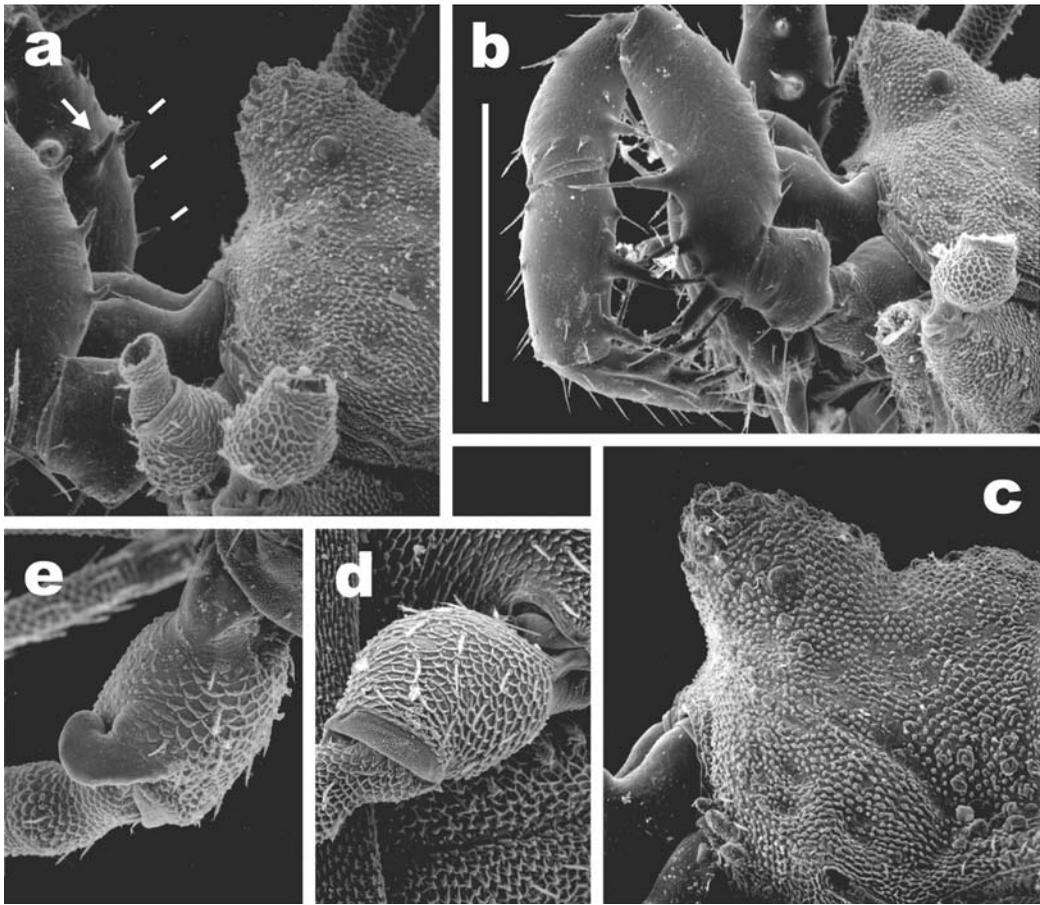


FIGURE 19. *Sitalcina seca* sp. nov., somatic morphology. a, e. Male. b–d. Female. a–c. Cephalon and palpi, lateral view, with palpal femur showing asetose dorsal tubercles (lines) and mesal tubercle (arrow). c. cephalon of female from Big Creek. d–e. Trochanter IV in lateral (d) and ventral (e) views. (All specimens from Arroyo Seco, except 'c' from Big Creek.) Scale bar = 550 $\mu$ m (b), 400 $\mu$ m (c), 380 $\mu$ m (a), 290 $\mu$ m (d–e).

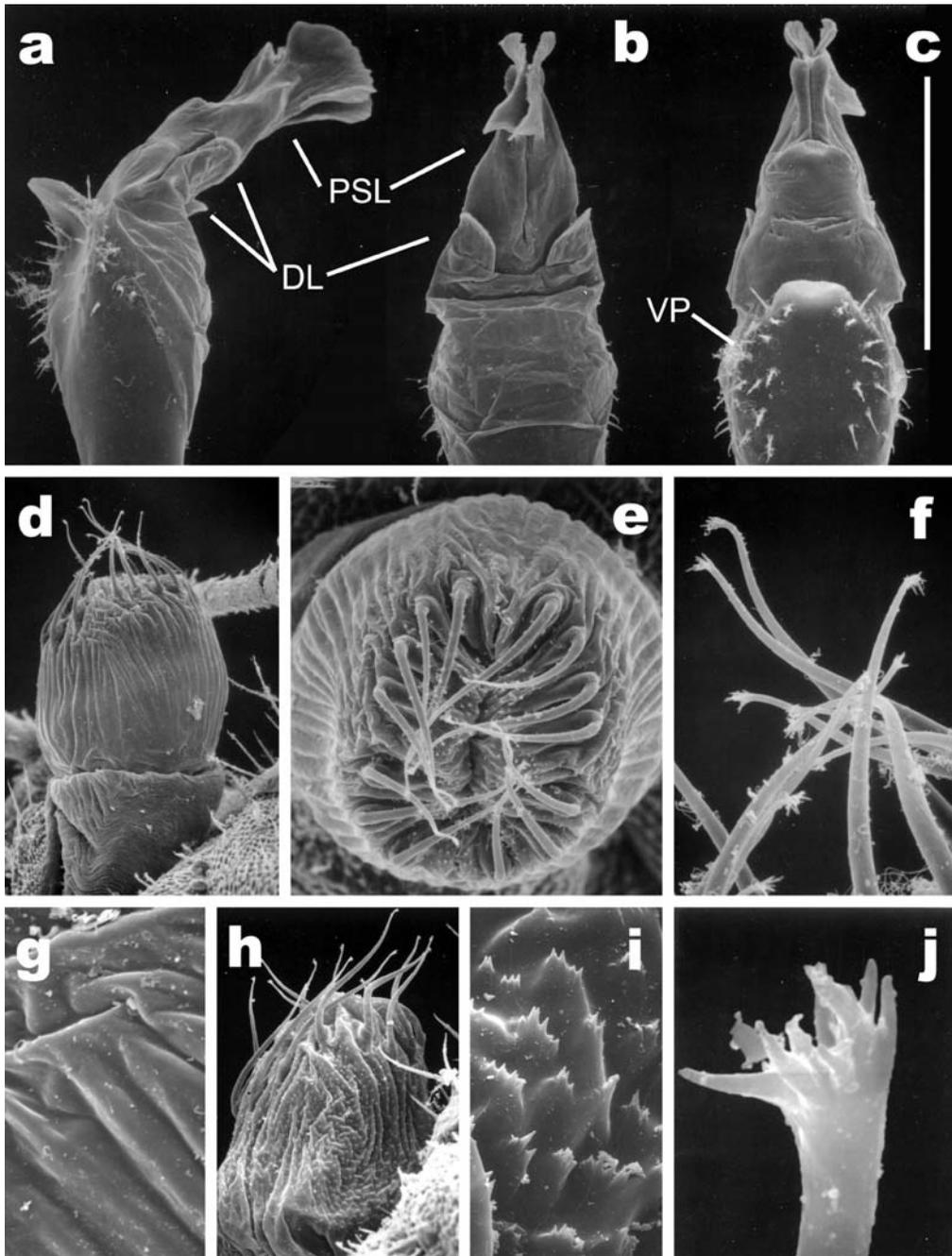


FIGURE 20. *Sitalcina seca* sp. nov., genitalic morphology. a–c. Male, penis with expanded glans in sinistrolateral (a), dorsal (b), and ventral (c) views. d–g. Female from Arroyo Seco, ovipositor in sinistrolateral (d) and apical (e) views, with close-up of apical setae (f) and lateral surface lacking microspines (g). h–j. Female from Big Creek, ovipositor in sinistrolateral view (h), with close-up of lateral surface showing microspines (i) and apical setae (j). DL = dorsal lobe, PSL = parastylar lobe, VP = ventral plate. Scale bar = 300 $\mu$ m (d), 190 $\mu$ m (a–c), 235 $\mu$ m (h), 143 $\mu$ m (e), 56 $\mu$ m (f), 38 $\mu$ m (g), 27 $\mu$ m (i), 5 $\mu$ m (j).

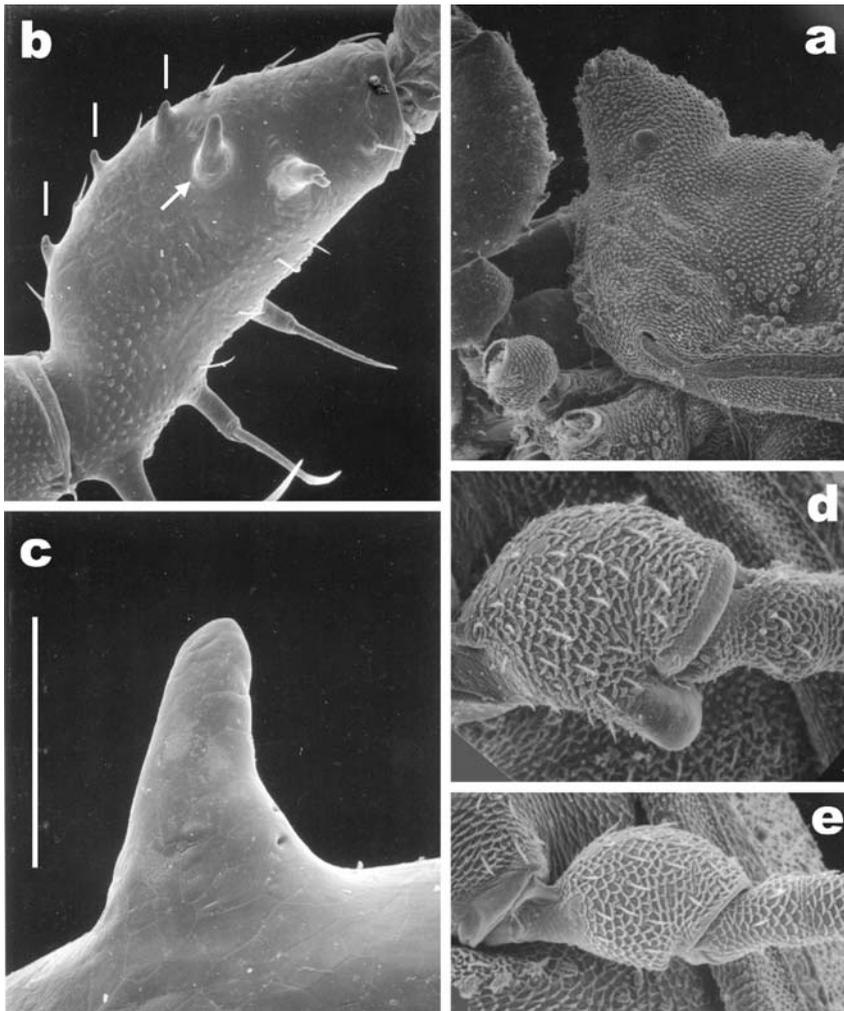


FIGURE 21. *Sitalcina chalonga* Briggs, somatic morphology. a–d. Male. e. Female. a. Cephalon, lateral view. b. Palpal femur, mesal view showing dorsal (lines) and mesal (arrow) asetose tubercles. c. Dorsal asetose tubercle. d–e. Trochanter IV, ectal view. Scale bar = 480 $\mu$ m (a), 275 $\mu$ m (e), 230 $\mu$ m (b, d), 48 $\mu$ m (c).

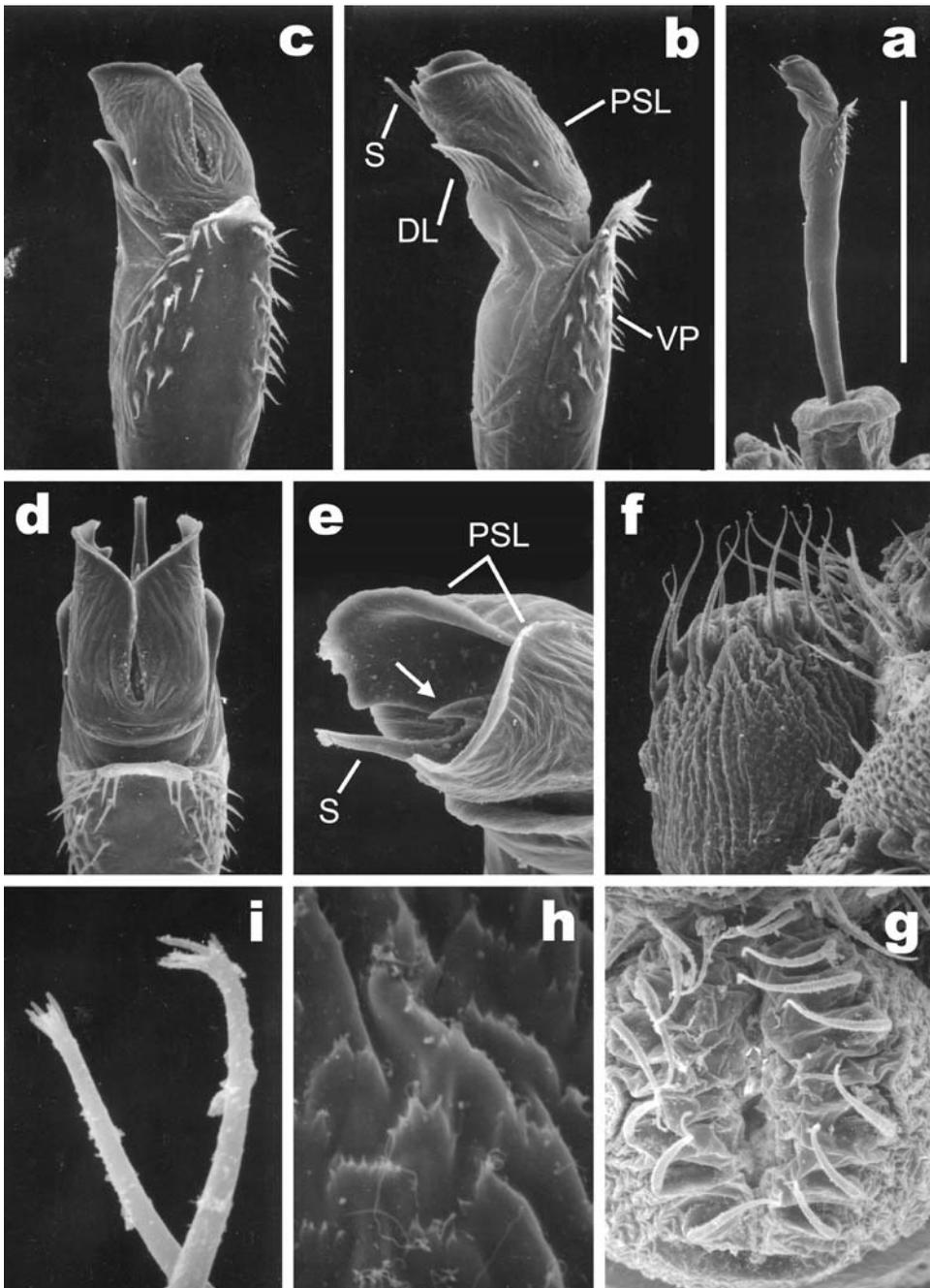


FIGURE 22. *Sitalcina chalona* Briggs, genital morphology. a–e. Male, penis with expanded glans in sinistrolateral view (a) and glans in lateral (b), lateroventral (c), ventral (d), and lateroapical (e) views, with arrow showing ventral prong of stylus. f–i. Female, ovipositor, sinistrolateral (f) and apical (g) views, with lateral surface showing microspines (h), and apical setae (i). DL = dorsal lobe, PSL = parastylar lobe, S = stylus, VP = ventral plate. Scale bar = 570 $\mu$ m (a), 190 $\mu$ m (b–d, f), 145 $\mu$ m (g), 100 $\mu$ m (e), 19 $\mu$ m (h–i).

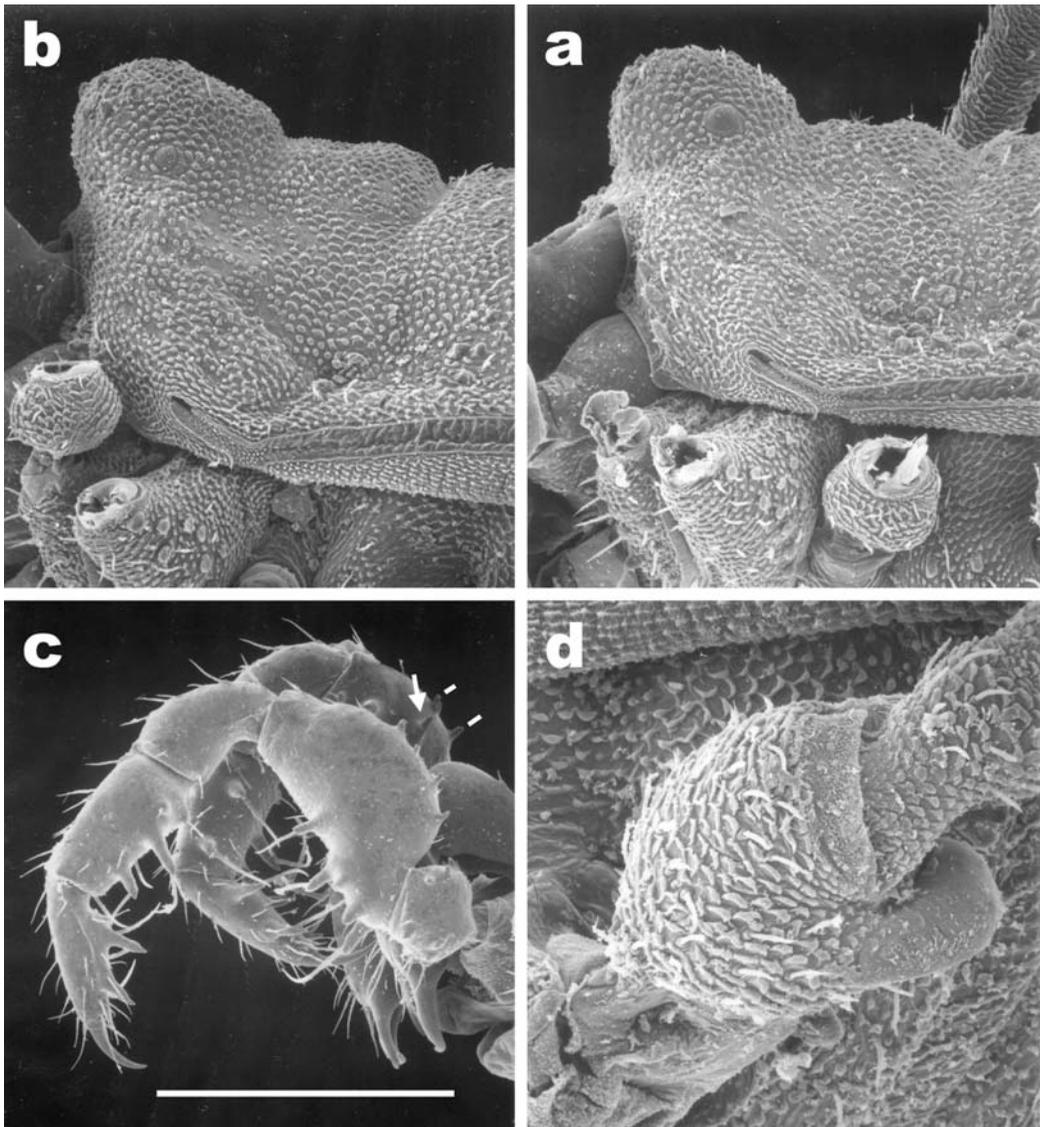


FIGURE 23. *Stalcina flava* Briggs, somatic morphology. a. Female. b–d. Male. a–b. Cephalon, lateral view. c. Palpi, lateral view showing dorsal (lines) and mesal (arrow) asetose tubercles. c. Trochanter IV, ectal view. Scale bar = 490 $\mu$ m (c), 330 $\mu$ m (a–b), 165 $\mu$ m (d).

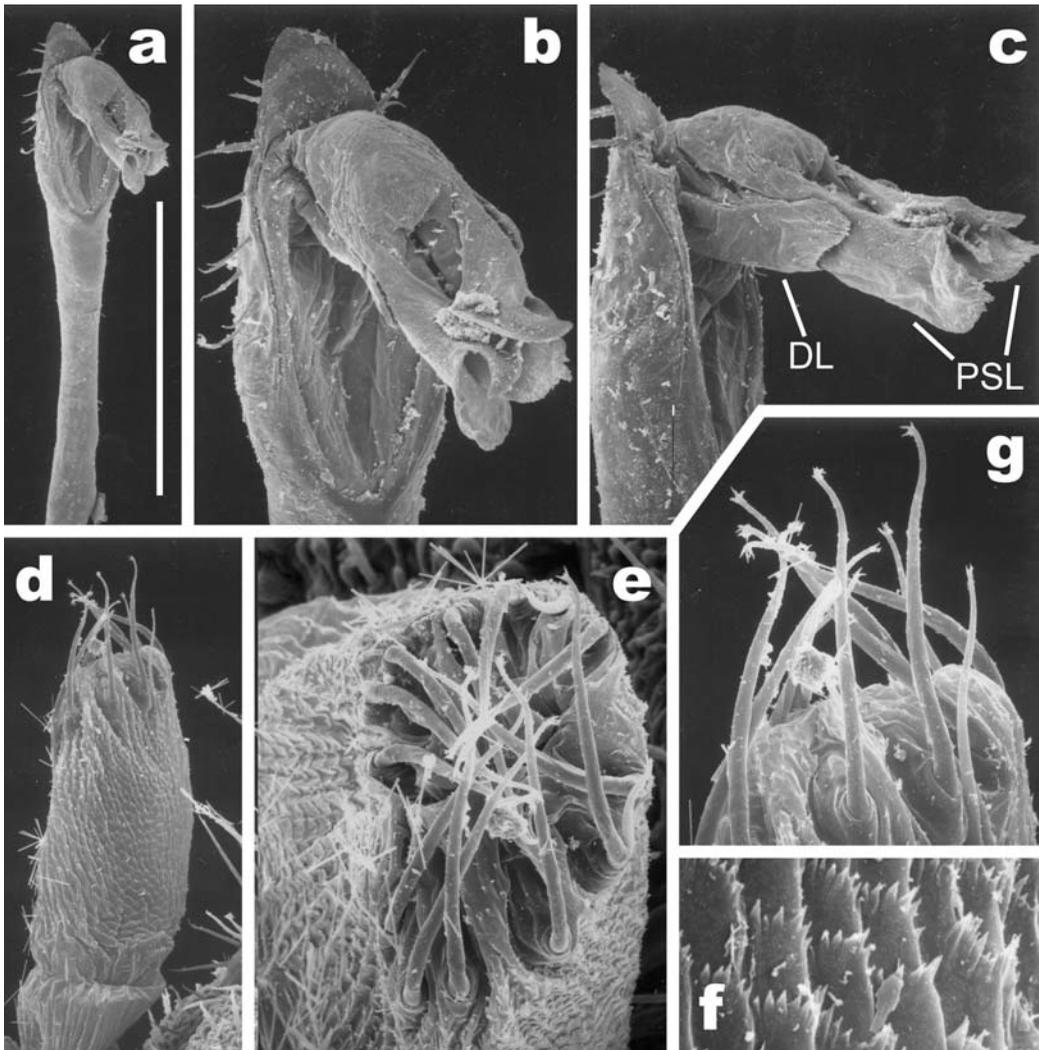


FIGURE 24. *Sitalcina flava* Briggs, genitalic morphology. a-c. Male, penis with partially expanded glans in (sinistro)dorsolateral view (a) and glans in dorsolateral (b) and sinistrolateral (c) views. d-g. Female, ovipositor, sinistrolateral (d) and apical (e) views, with lateral surface showing microspines (f), and apex showing setae (g). DL = dorsal lobe, PSL = parastylar lobe. Scale bar = 285 $\mu$ m (a), 190 $\mu$ m (d), 115 $\mu$ m (b-c), 82 $\mu$ m (e), 70 $\mu$ m (g), 19 $\mu$ m (f).

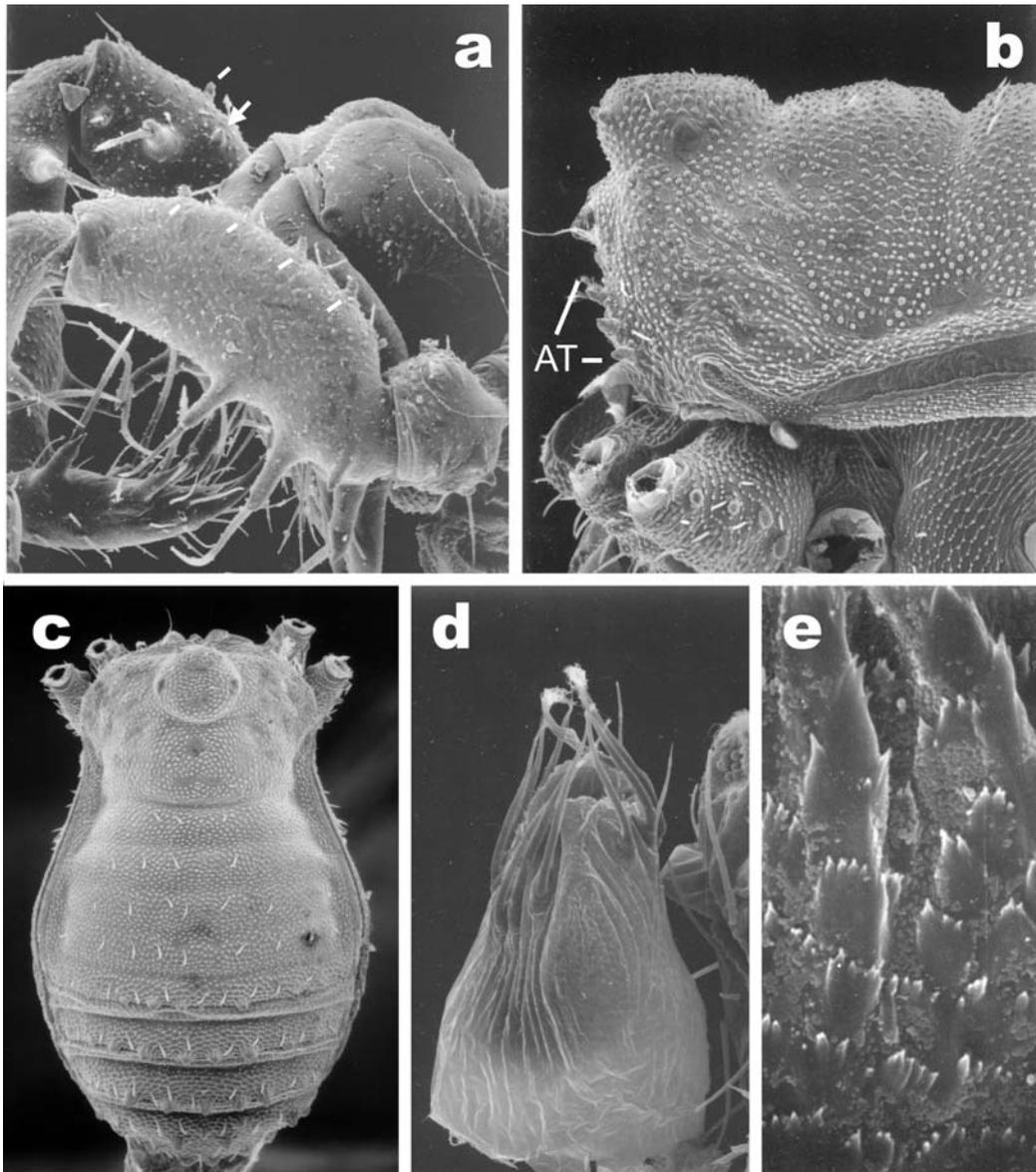


FIGURE 25. *Sitalcina borregoensis* Briggs, female, morphology. a. Palpi and chelicerae, lateral view showing dorsal (lines) and mesal (arrow) aetose tubercles. b. Cephalon, lateral view. c. Body, dorsal view. d. Ovipositor, lateral view. e. Ovipositor surface showing microspines. AT = anterior tubercles. Scale bar = 610 $\mu$ m (c), 260 $\mu$ m (b), 250 $\mu$ m (a), 130 $\mu$ m (d), 13 $\mu$ m (e).

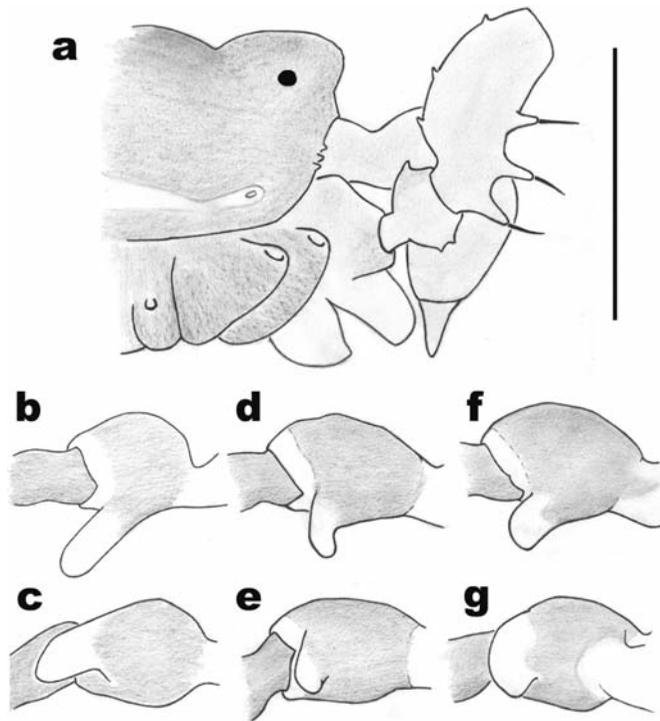


FIGURE 26. *Sitalcina* spp., Arizona clade, somatic morphology. a–c. *S. rothi* sp. nov. d–e. *S. catalina* sp. nov. f–g. *S. peacheyi* sp. nov. a. Cephalic region, lateral view of female. b–g. Male TrIV in ectal (b, d, f) and ventral (c, e, g) views; shading indicates regions of rugosity. Scale bar = 500 $\mu$ m (a), 350 $\mu$ m (b–g).

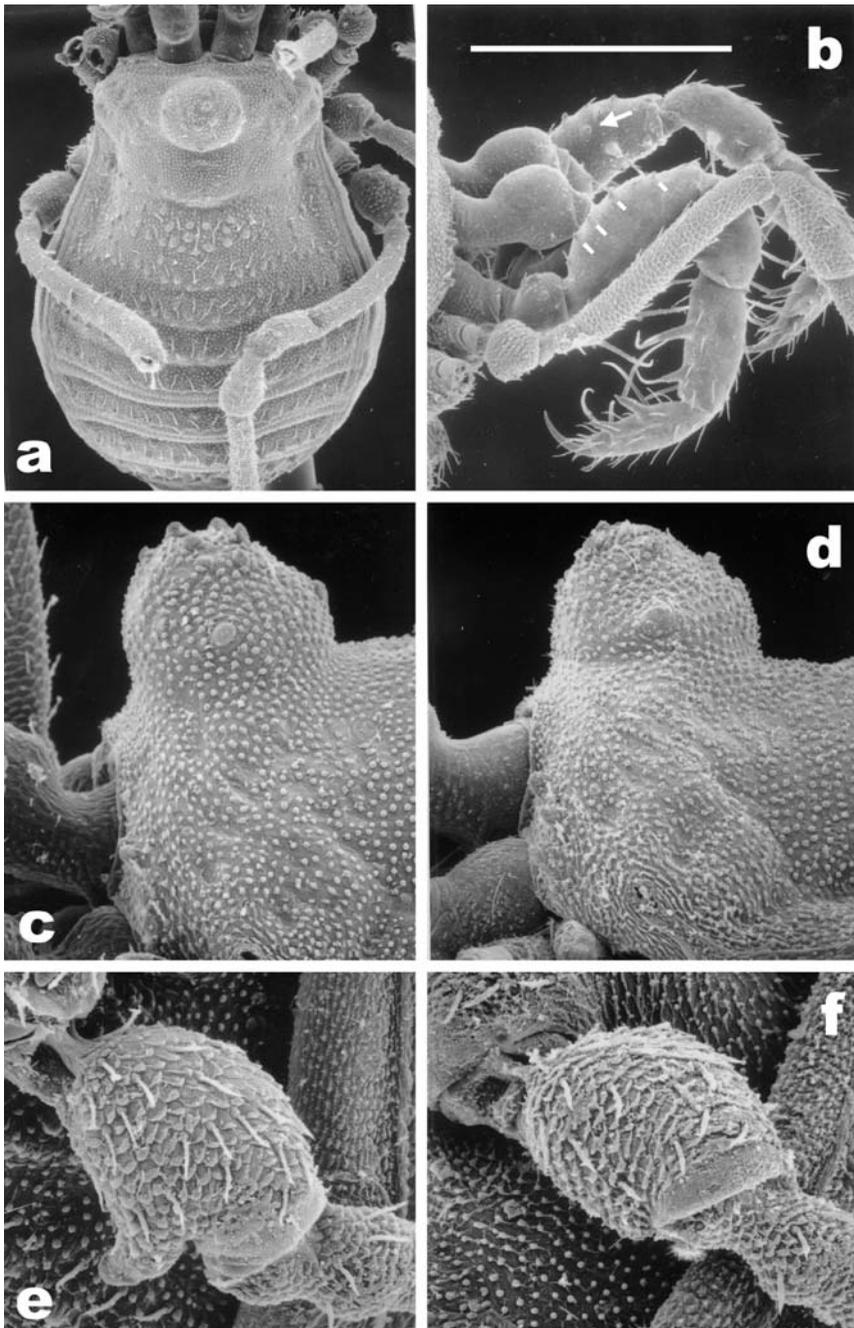


FIGURE 27. *Sitalcina catalina* sp. nov., somatic morphology. a, c, e. Male. b, d, f. Female. a. Body, dorsal view. b. Palpi and chelicerae, lateral view showing dorsal (lines) and mesal (arrow) asetose tubercles. c–d. Cephalon, lateral view. e–f. Trochanter IV, ectal view. Scale bar = 750 $\mu$ m (a), 530 $\mu$ m (b), 180 $\mu$ m (e–f), 175 $\mu$ m (c–d).

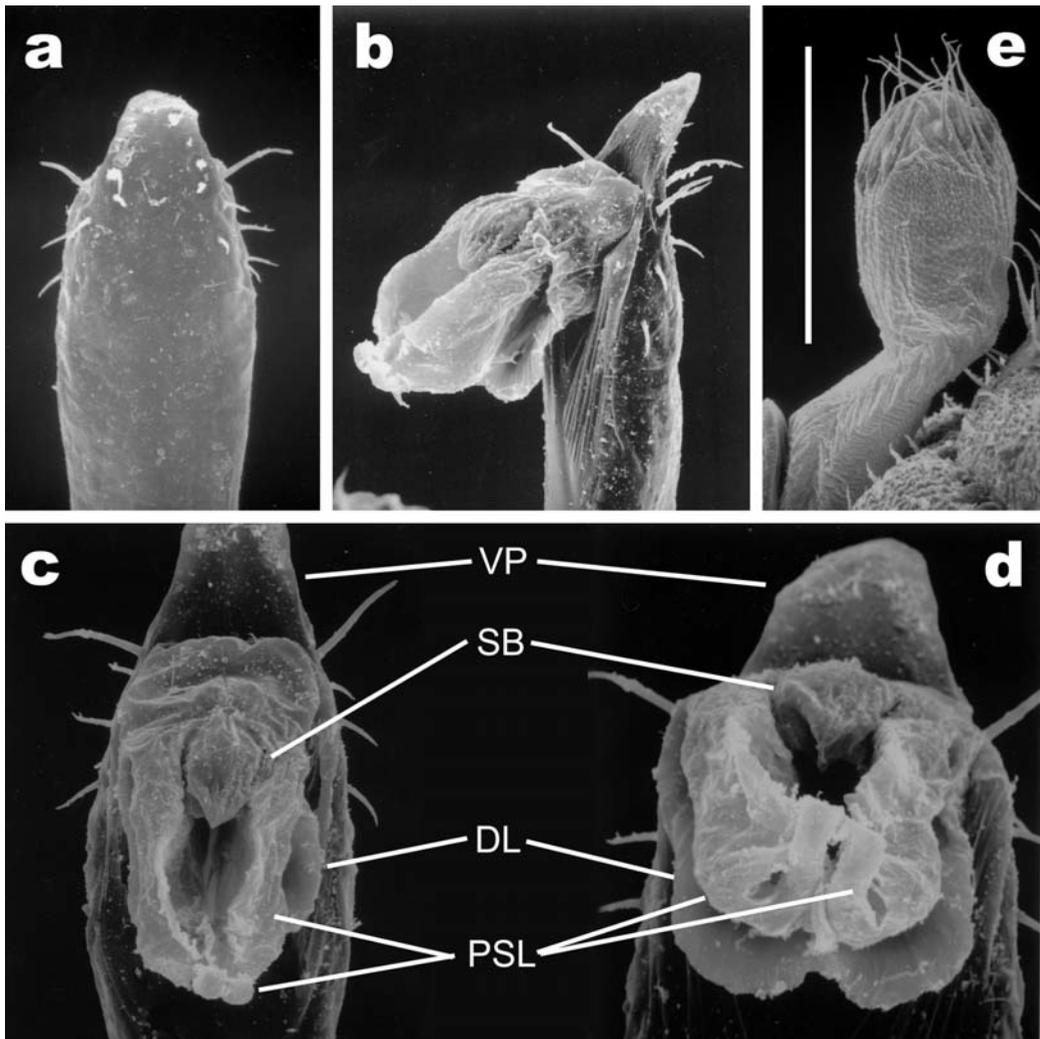


FIGURE 28. *Sitalcina catalina* sp. nov., genitalic morphology. a–d. Male, penis with partially expanded glans in ventral (a), dexterolateral (b), and dorsal (c) views, and tilted dorsal showing apical view of glans (d). e. Female, ovipositor, lateral view. DL = dorsal lobe, PSL = parastylar lobe, SB = stylar base, VP = ventral plate. Scale bar = 230 $\mu$ m (e), 115 $\mu$ m (a–b), 82 $\mu$ m (c), 57 $\mu$ m (d).

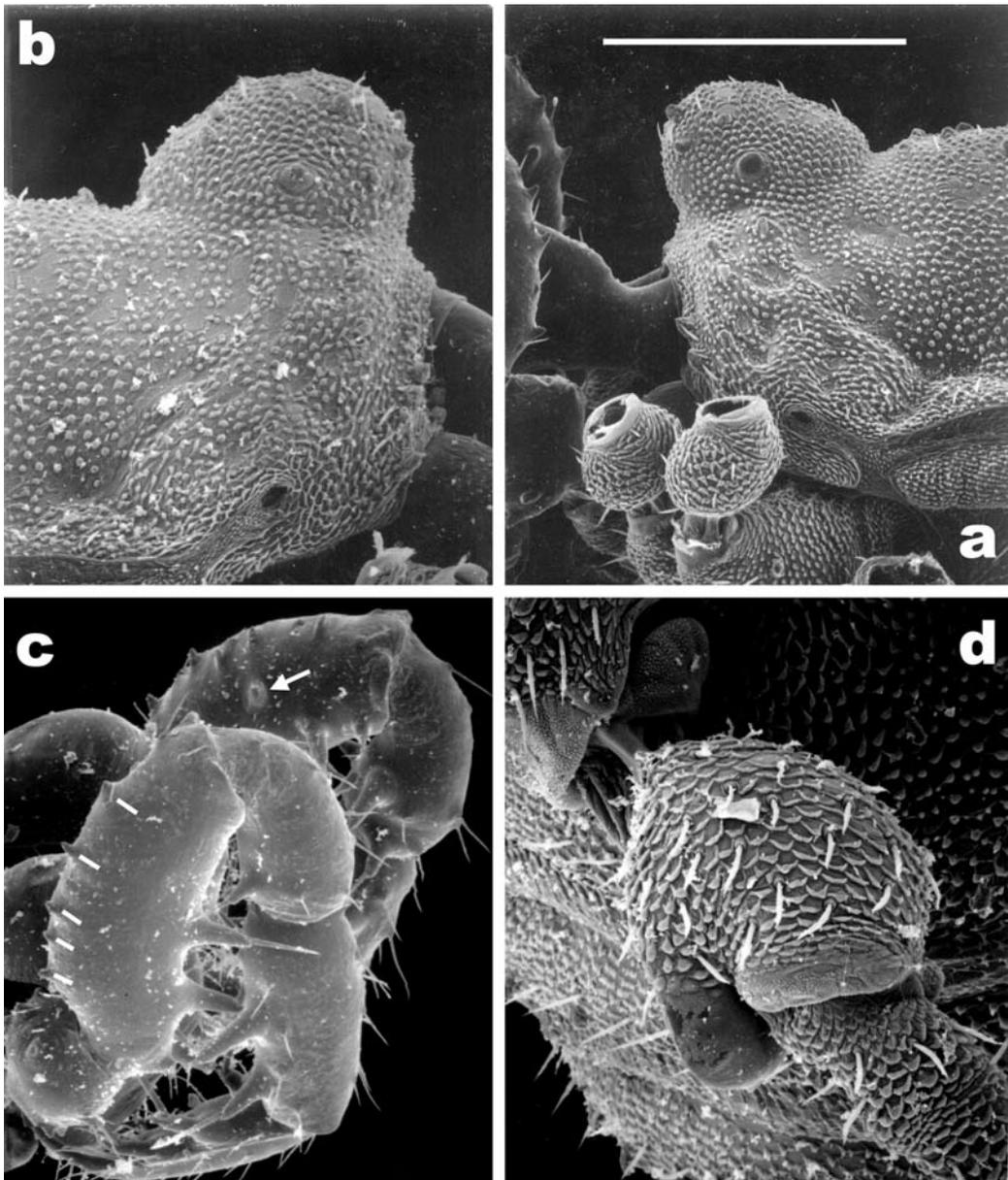


FIGURE 29. *Stalcina peacheyi* sp. nov., somatic morphology. a. Female. b–d. Male. a–b. Cephalon, lateral view. c. Palpi, lateral view showing dorsal (lines) and mesal (arrow) setose tubercles. d. Trochanter, ectal view. Scale bar = 330 $\mu$ m (a, c), 250 $\mu$ m (b), 165 $\mu$ m (d).

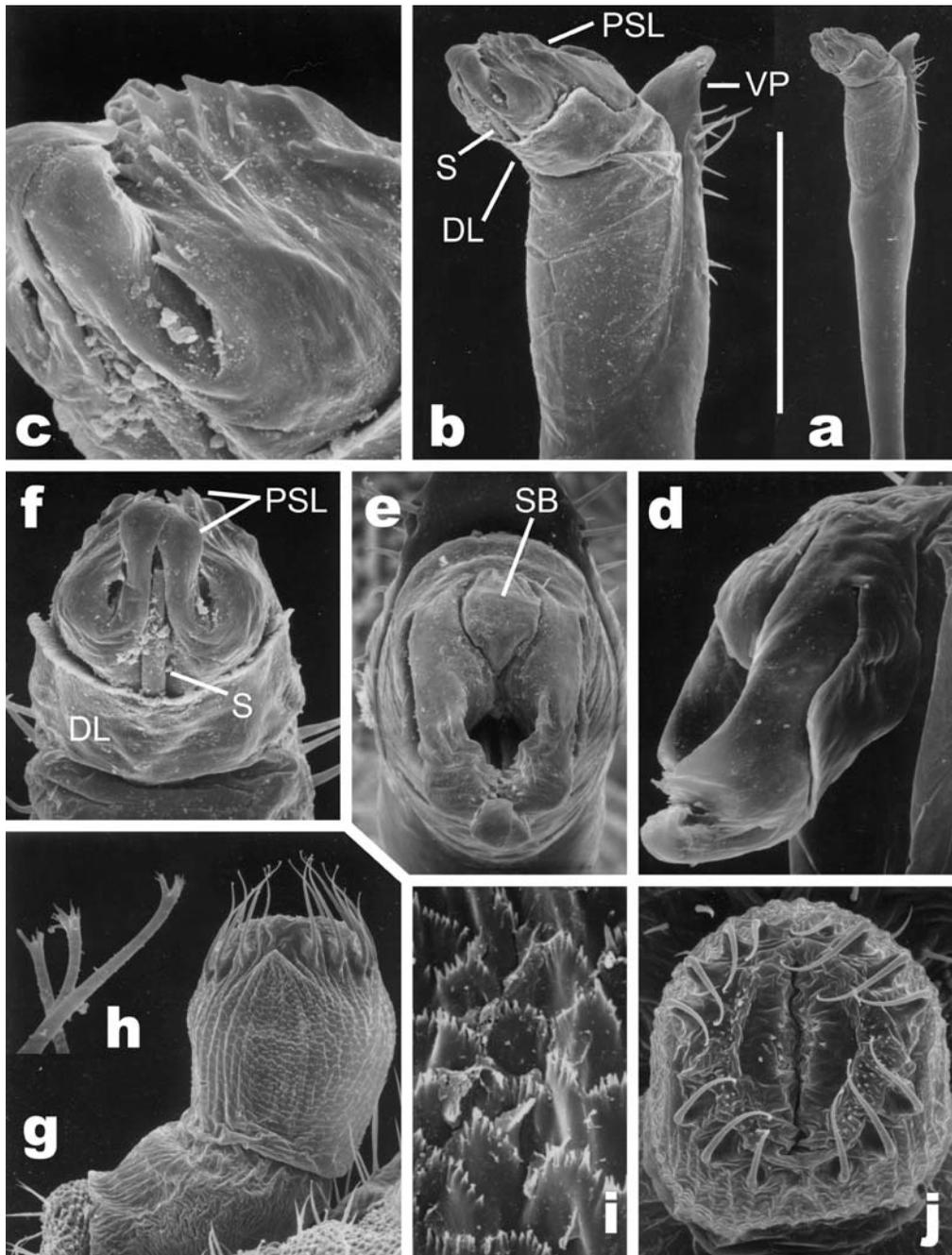


FIGURE 30. *Sitalcina peacheyi* sp. nov., genitalic morphology. a–f. Male, penis. a–c, f. Partially expanded glans, in dexterolateral views (a–c) and in dorsal view showing ventroapical aspect of glans (f). d–e. Folded glans in dorsolateral (d) and ventroapical (e) views. g–j. Female, ovipositor, lateral (g) and apical (j) views with apical setae (h) and lateral surface showing microspines (i). DL = dorsal lobe, PSL = parastylar lobe, S = stylus, SB = stylus base, VP = ventral plate. Scale bar = 270µm (a), 230µm (g), 150µm (j), 115µm (b), 90µm (e), 67µm (d), 63µm (f), 30µm (c), 20µm (i).

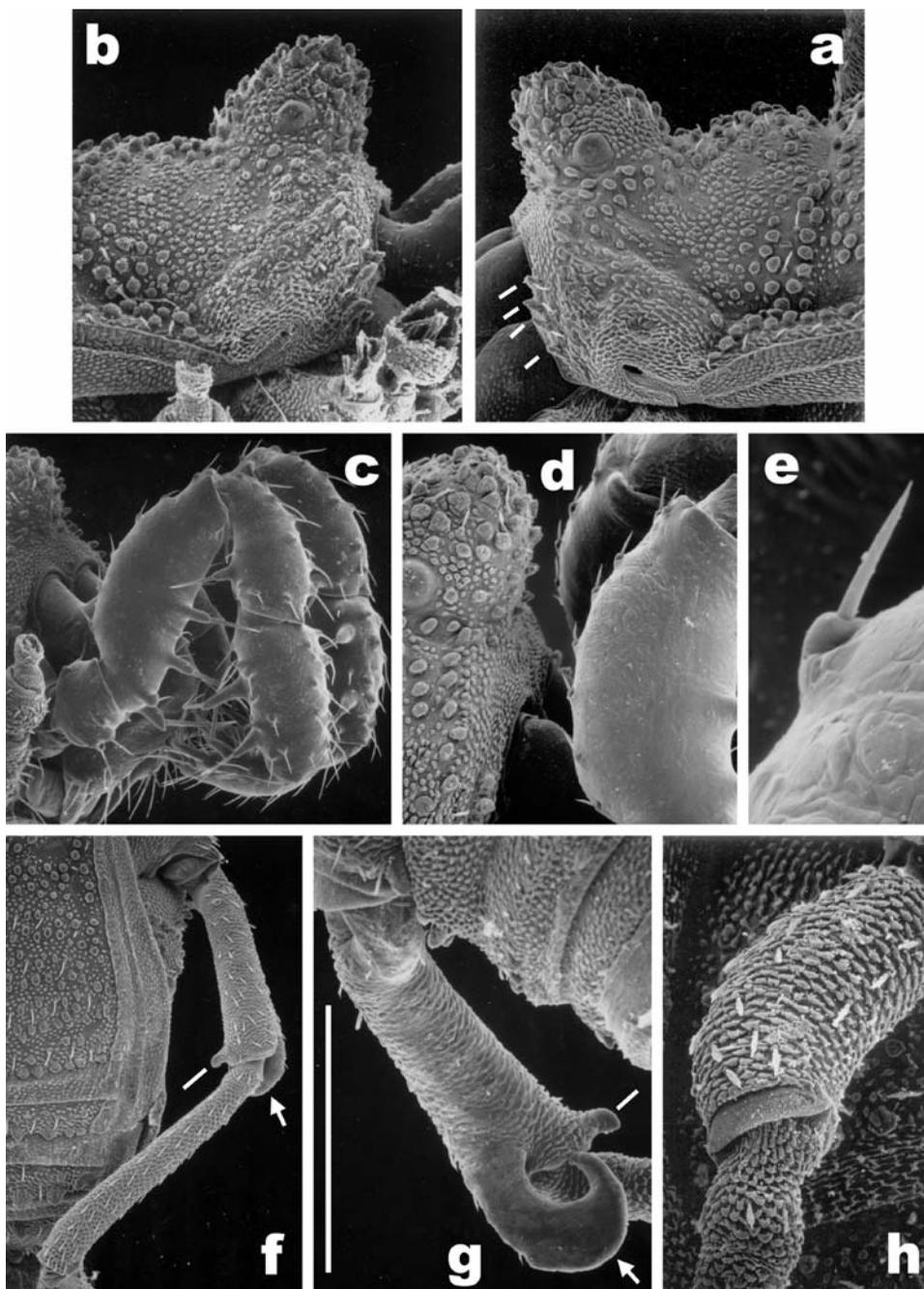


FIGURE 31. *Sitalcina lobata* Goodnight and Goodnight, somatic morphology. a, h. Female. b–g. Male. a–b. Cephalon, lateral view, showing prominent AT (lines). c–e. Palpi, lateral view, with detail of femur (d) and setose tubercle (e). f–h. Trochanter IV, of male in dorsal (f) and ventral (g) views, showing mesal (line) and ectal (arrow) distal processes (spurs), and female in ectal view (h). Scale bar = 570 $\mu$ m (f), 475 $\mu$ m (c), 380 $\mu$ m (a–b), 330 $\mu$ m (d), 285 $\mu$ m (g), 210 $\mu$ m (h), 55 $\mu$ m (e).

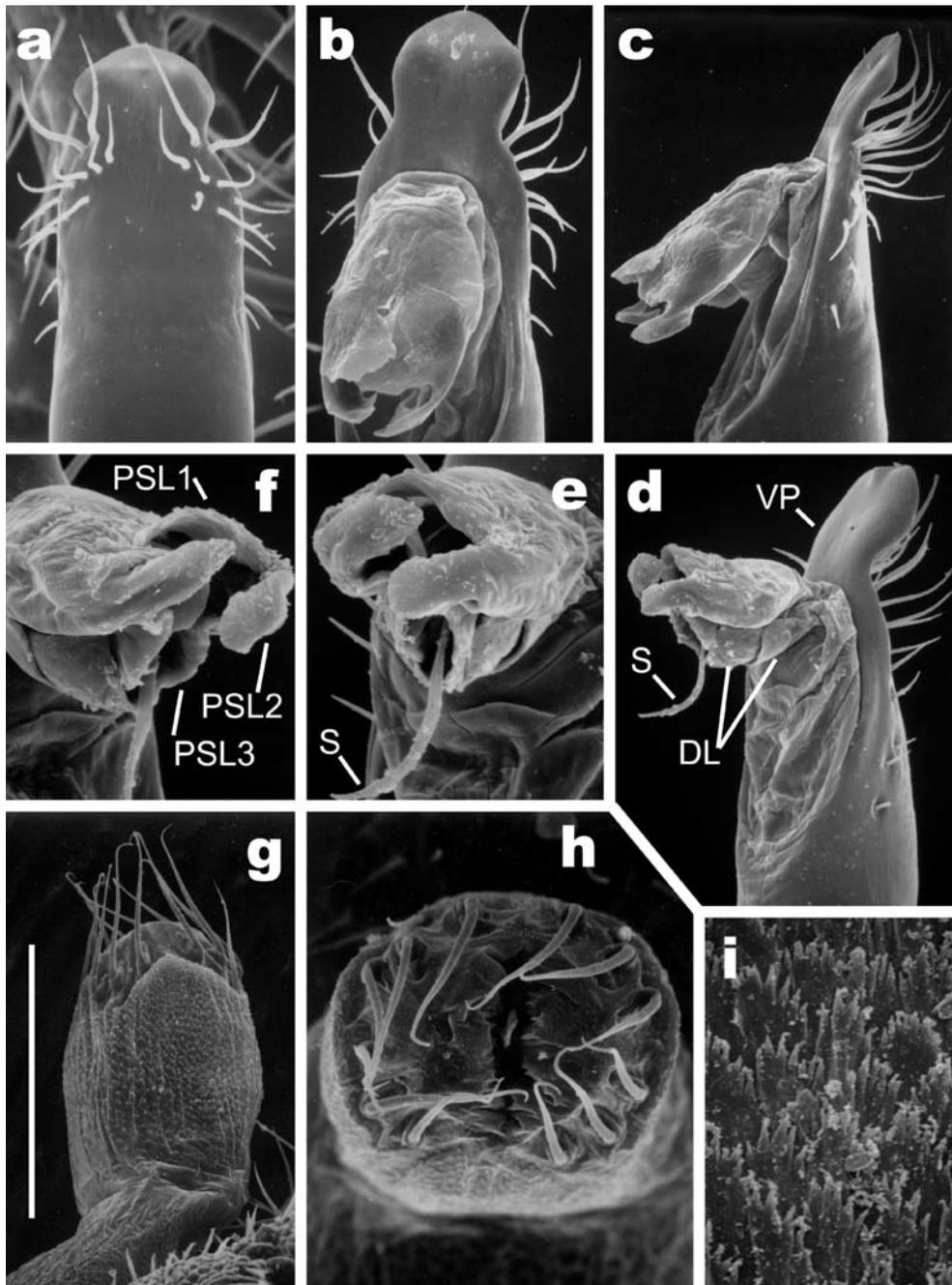


FIGURE 32. *Sitalcina lobata* Goodnight and Goodnight, genitalic morphology. a–f. Male. a–c. Penis with partially expanded glans in ventral (a), dorsal (b), and dexterolateral (c) views. d–f. Penis more fully expanded, dorsolateral view (d), with glans in apical (e) and sinistrolateral (f) views. g–i. Female, ovipositor in sinistrolateral (g) and apical (h) views, with lateral surface showing microspine arrangement (i). DL = dorsal lobe, PSL1 = ventral branch of parastylar lobe, PSL2 = lateral branch, PSL3 = dorsal branch, S = stylus, VP = ventral plate. Scale bar = 190 $\mu$ m (g), 120 $\mu$ m (a–d), 115 $\mu$ m (h), 75 $\mu$ m (e–f), 19 $\mu$ m (i).

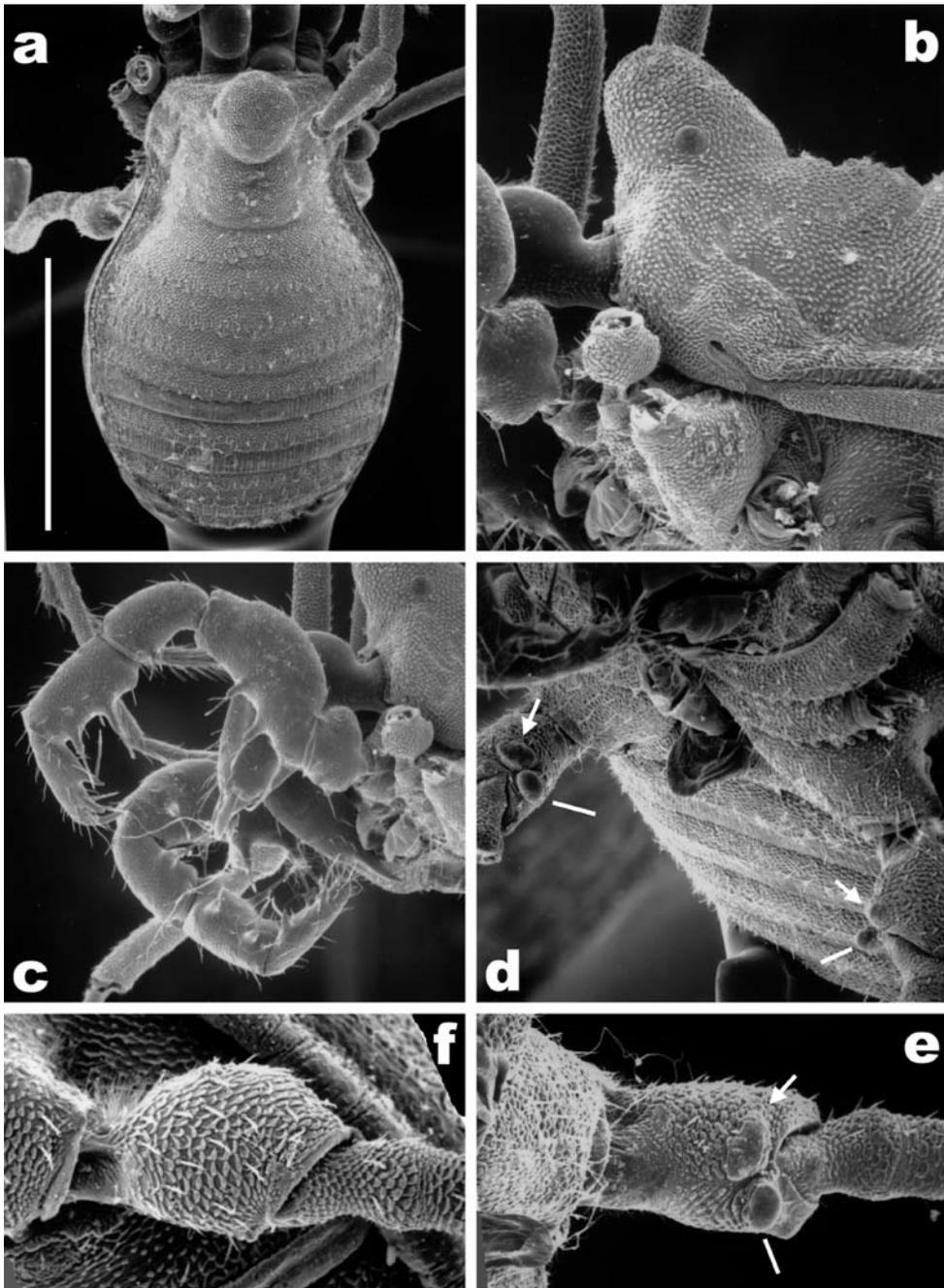


FIGURE 33. *Enigmima granita* (Briggs), somatic morphology. a–e. Male. f. Female. a. Body, dorsal view. b. Cephalon, lateral view. c. Palpi, lateral view. d. Venter showing trochanters with ectal (arrow) and mesal (line) processes. e. Male trochanter IV, ventral view. f. Female trochanter IV ectal view. Scale bar = 1mm (a), 720 $\mu$ m (c–d), 500 $\mu$ m (b), 330 $\mu$ m (e), 260 $\mu$ m (f).

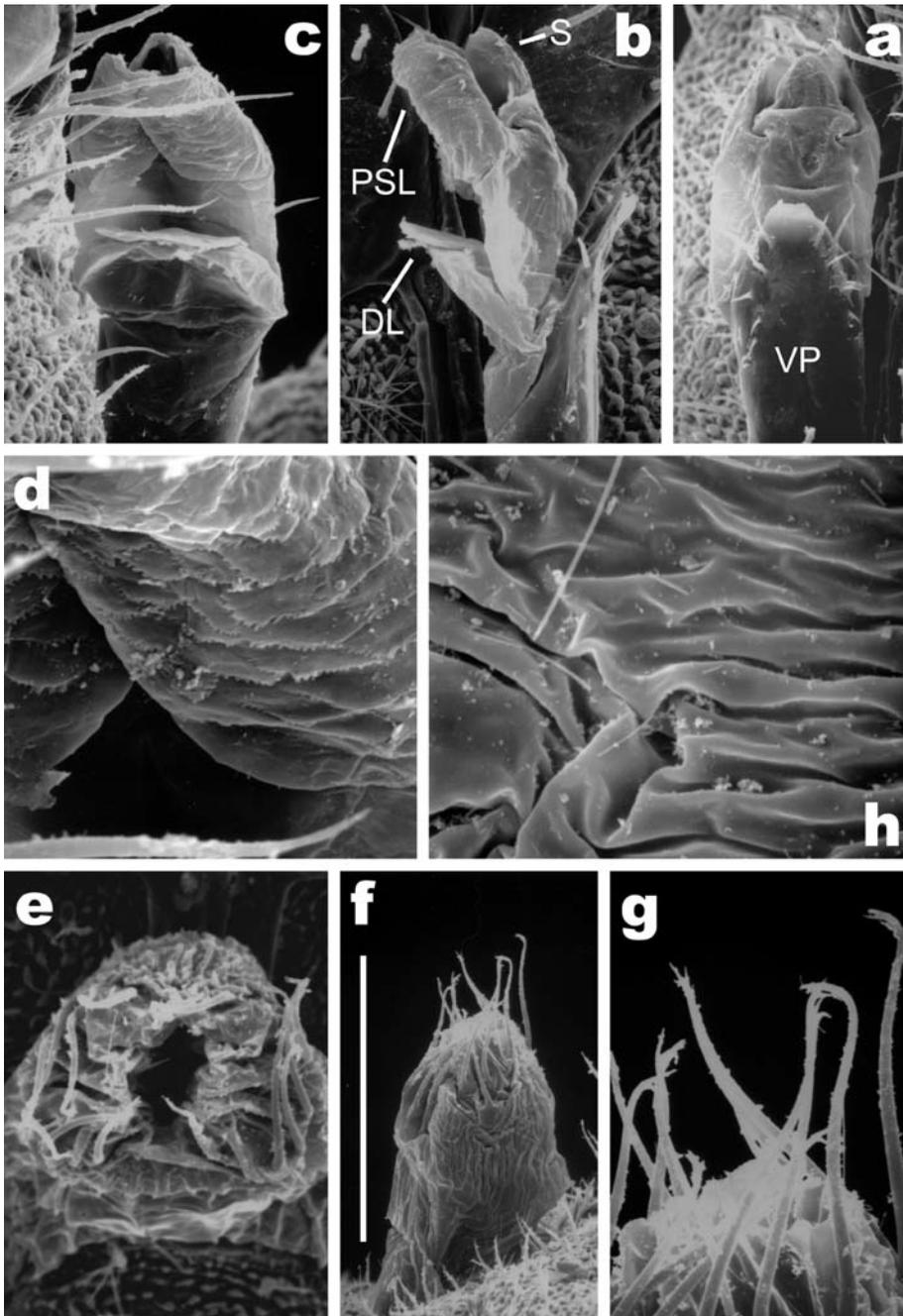


FIGURE 34. *Enigmima granita* (Briggs), genitalic morphology. a–d. Male, penis fully expanded in ventral (a), dextrolateral (b), and dorsal (c) views, with dorsal aspect of PSL (d). e–h. Female, ovipositor in apical (e) and sinistrolateral (f) views showing polyfurcate apical setae (g) and lateral surface of ovipositor (distal end to left) lacking microspines (h). DL = dorsal lobe, PSL = parastylar lobe, S = stylus, VP = ventral plate. Scale bar = 180 $\mu$ m (f), 135 $\mu$ m (a), 115 $\mu$ m (b), 110 $\mu$ m (c, e), 55 $\mu$ m (g), 27 $\mu$ m (d, h).

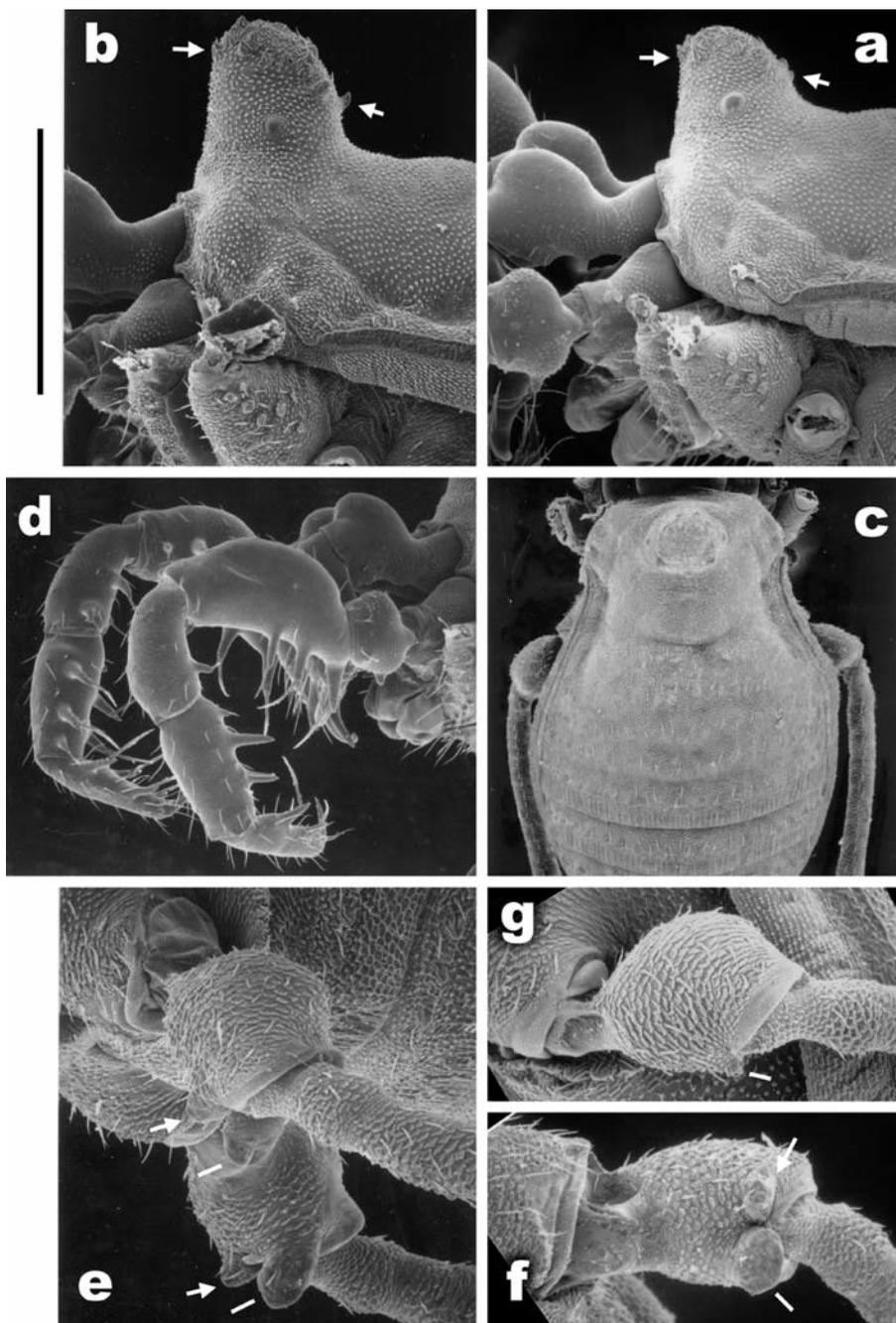


FIGURE 35. *Enigmina warrenorum* sp. nov., somatic morphology. a, g. Female. b–f. Male. a–b. Cephalon, lateral view showing crown of pointed tubercles (arrows). c. Body, dorsal view. d. Palpi, lateral view. e–f. Male trochanter IV in lateral (e) and ventral (f) views, showing ectal (arrow) and mesal (line) processes. g. Female trochanter IV, ectal view, showing small tubercle (line). Scale bar = 1.1mm (c), 820 $\mu$ m (d), 560 $\mu$ m (a), 520 $\mu$ m (b), 360 $\mu$ m (e–f), 300 $\mu$ m (g).

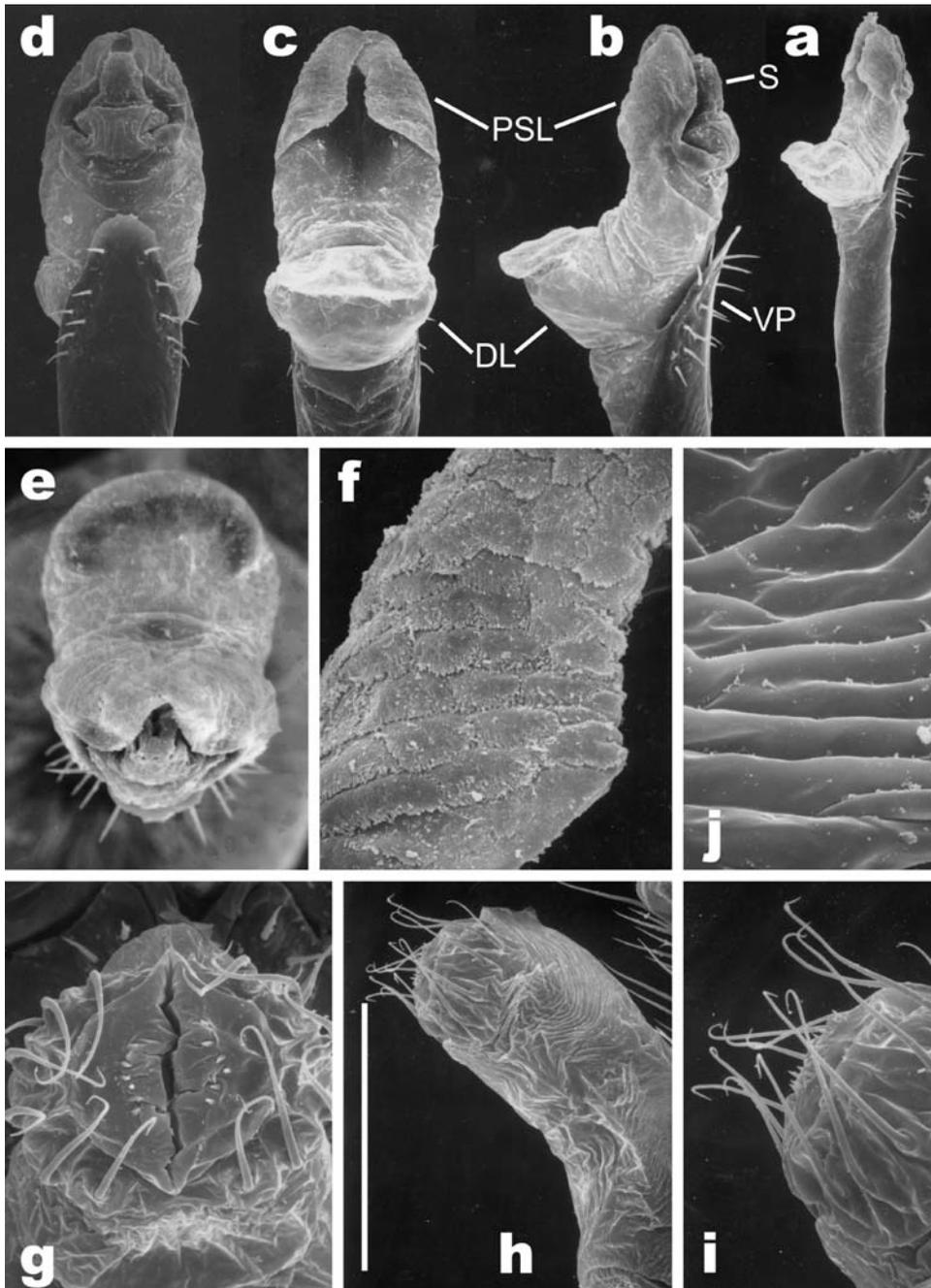


FIGURE 36. *Enigmima warrenorum* sp. nov., genitalic morphology. a–f. Male, penis fully expanded in dexterolateral (a–b), dorsal (c), ventral (d), and apical (e) views, with dorsal aspect of PSL (f). g–j. Female, ovipositor, in apical (g) and sinistrolateral (h) views, showing pointed apical setae (i) and lateral surface lacking microspines (j). DL = dorsal lobe, PSL = parastylar lobe, S = stylus, VP = ventral plate. Scale bar = 300 $\mu$ m (a), 285 $\mu$ m (h), 170 $\mu$ m (b–d), 145 $\mu$ m (g, i), 110 $\mu$ m (e), 28 $\mu$ m (f, j).

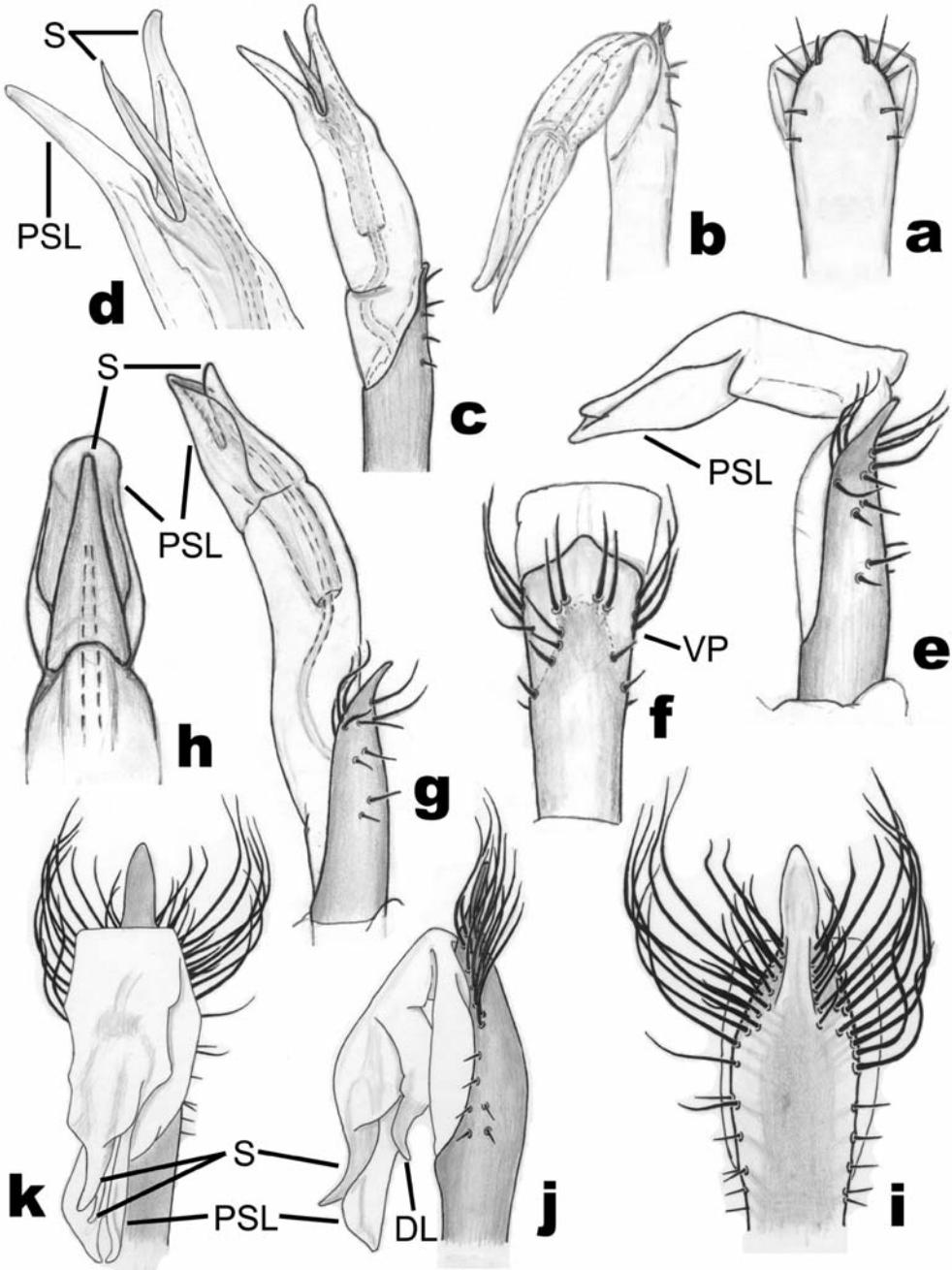


FIGURE 37. *Tularina* gen. nov., male genitalia. a-d. *T. tularensis* sp. nov., penis, unexpanded in ventral (a) and dexterolateral (b) views, and expanded in dexterolateral view (c-d). e-h. *T. plumosa* sp. nov., penis, partially expanded in dexterolateral (e) and ventral (f) views, and fully expanded in dexterolateral (g) and ventral views (h). i-k. *T. scopula* (Briggs), penis unexpanded in ventral (i), dexterolateral (j), and dorsal (k) views. DL = dorsal lobe, PSL = parastylar lobe, S = stylus, VP = ventral plate.

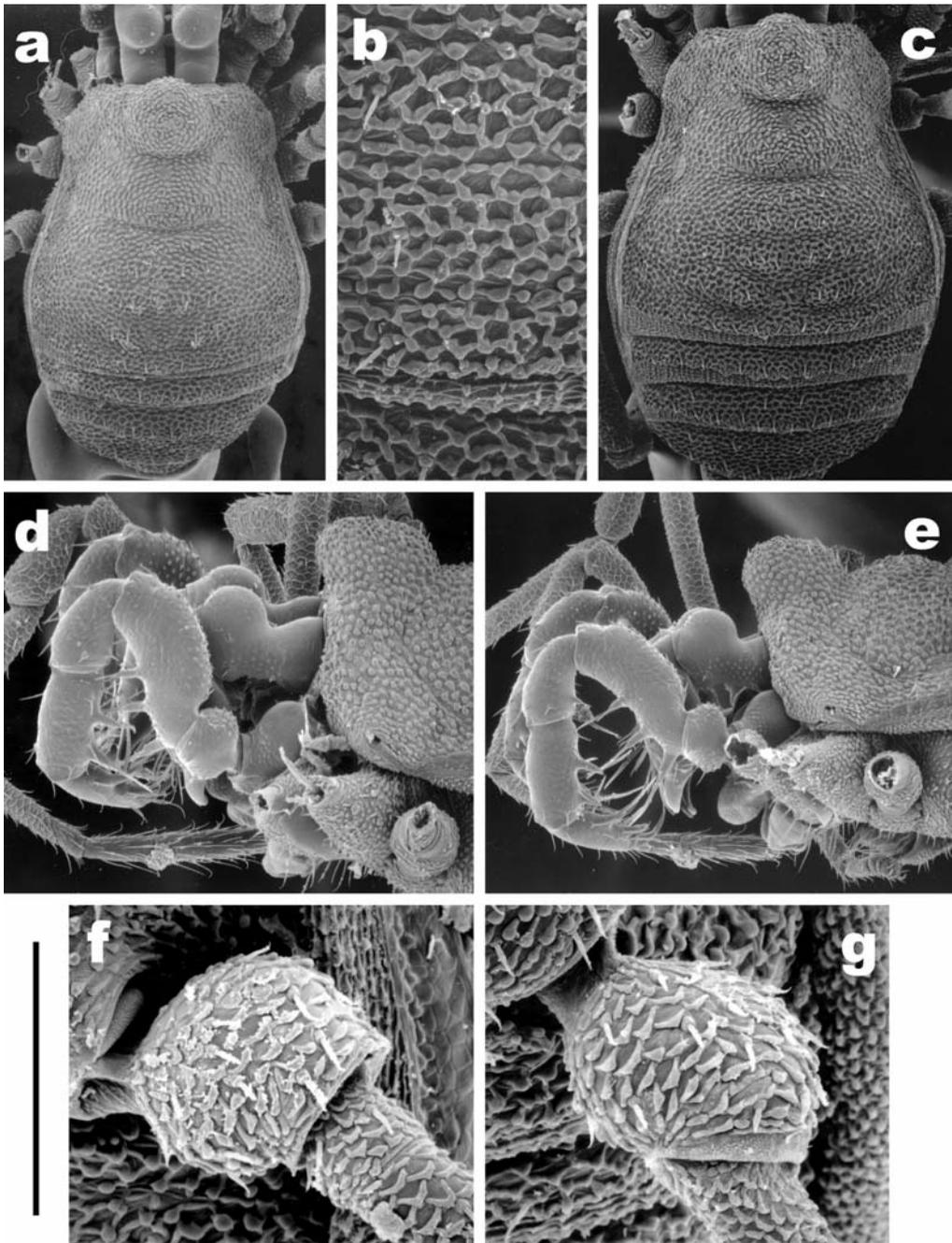


FIGURE 38. *Tularina tularensis* sp. nov., somatic morphology. a–b, d, f. Male. c, e, g. Female. a–c. Body, dorsal view, with central region showing areolate cuticle (b). d–e. Cephalon and palpi, lateral view. f–g. Trochanter IV, ectal view. Scale bar = 600 $\mu$ m (a, c), 475 $\mu$ m (e), 380 $\mu$ m (d), 135 $\mu$ m (b), 115 $\mu$ m (f–g).

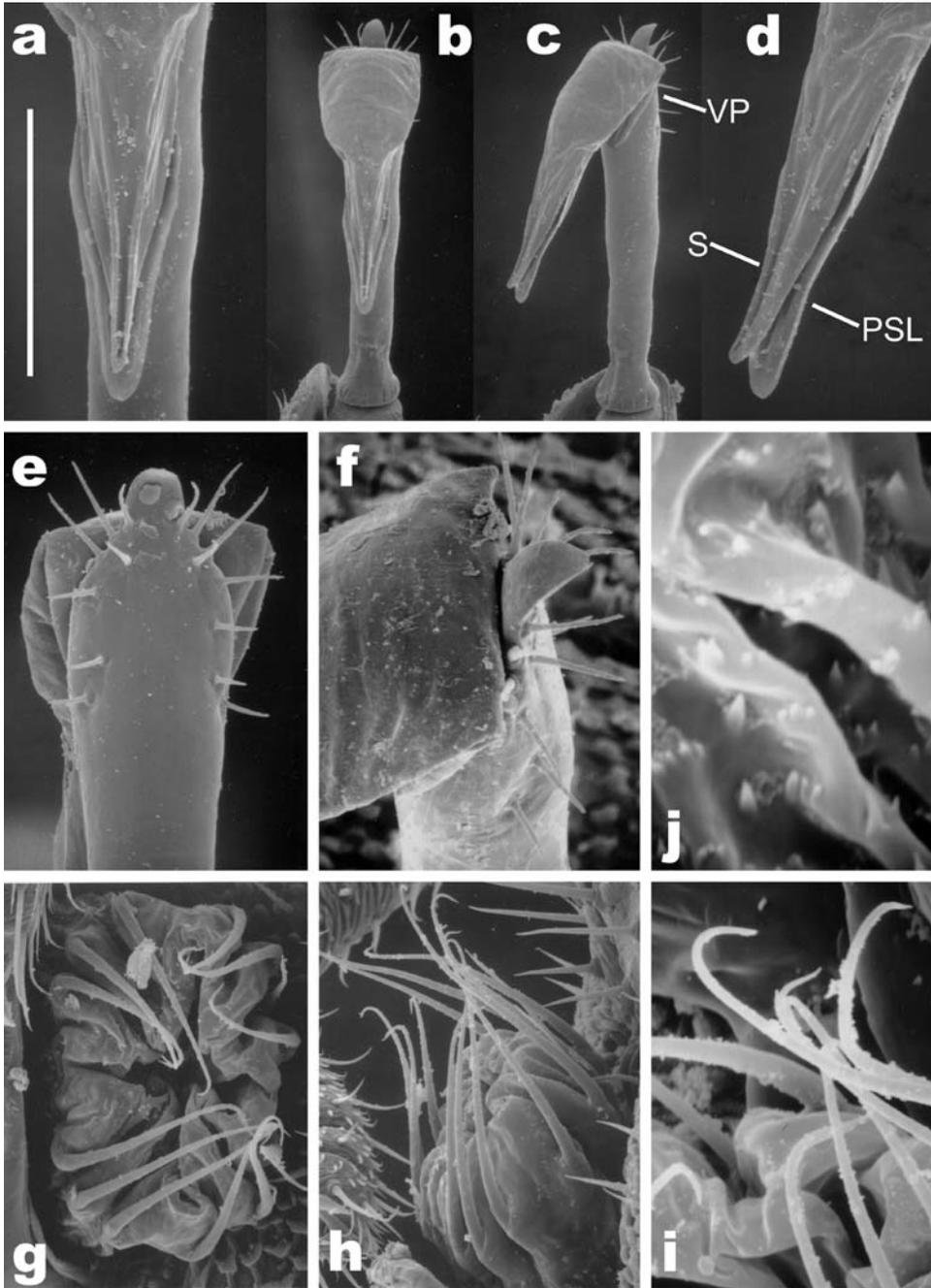


FIGURE 39. *Tularina tularensis* sp. nov., genitalic morphology. a–f. Male, penis partially expanded, in dorsal (a–b), dorsolateral (c–d), ventral (e), and apical (f) views. g–j. Female, ovipositor in apical (g) and sinistrolateral (h) views, showing hooked pointed apical setae (i) and lateral surface of ovipositor with microspines (j). PSL = parastylar lobe, S = stylus, VP = ventral plate. Scale bar = 190 $\mu$ m (b–c), 86 $\mu$ m (h), 78 $\mu$ m (a, d–e, g), 55 $\mu$ m (f), 28 $\mu$ m (i), 11 $\mu$ m (j).

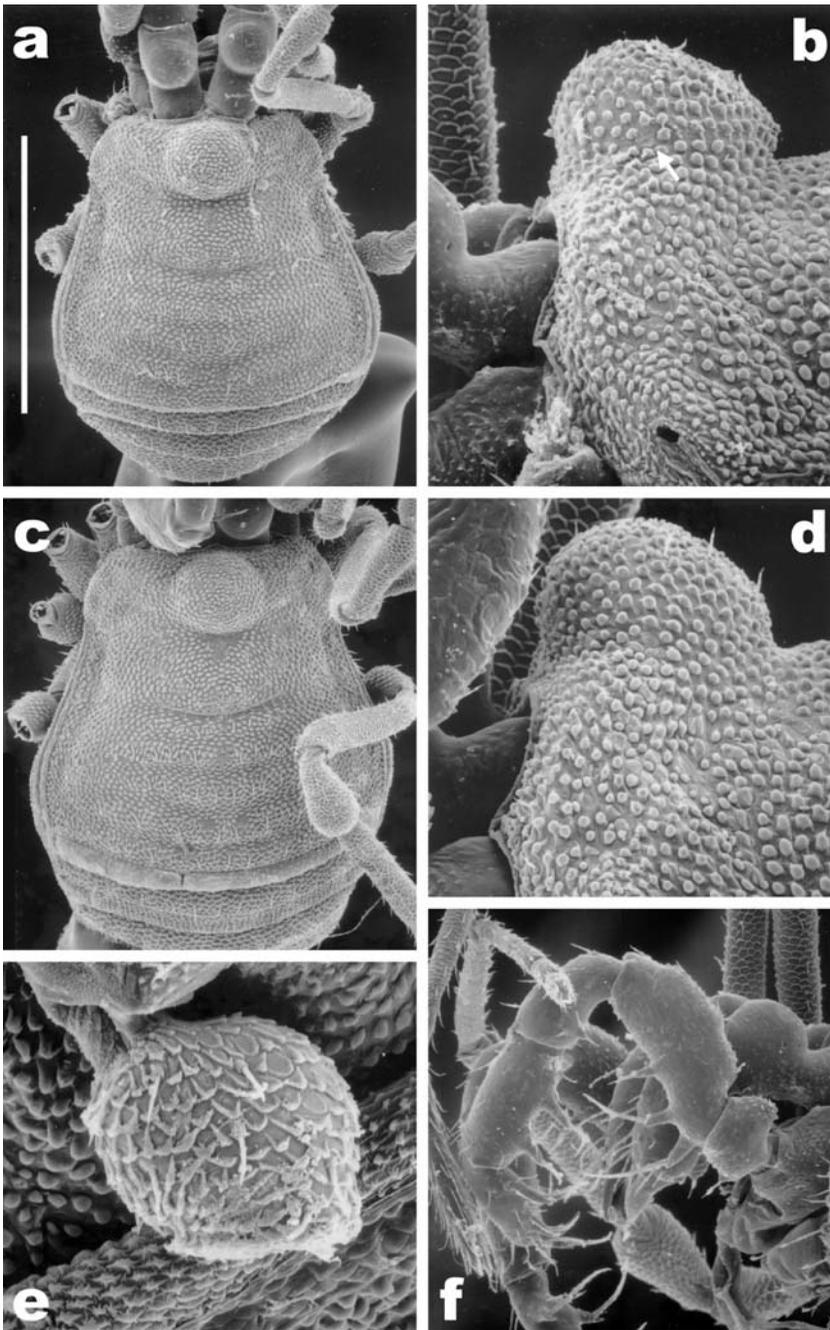


FIGURE 40. *Tularina plumosa* sp. nov., somatic morphology. a–b, e–f. Male. c–d. Female. a, c. Body, dorsal view. b–d. Cephalon, lateral view, showing degenerate eye (arrow). e. Male trochanter IV, ectal view. f. Chelicerae and palpi, lateral view. Scale bar = 570 $\mu$ m (a), 550 $\mu$ m (c), 360 $\mu$ m (f), 180 $\mu$ m (b, d), 110 $\mu$ m (e).

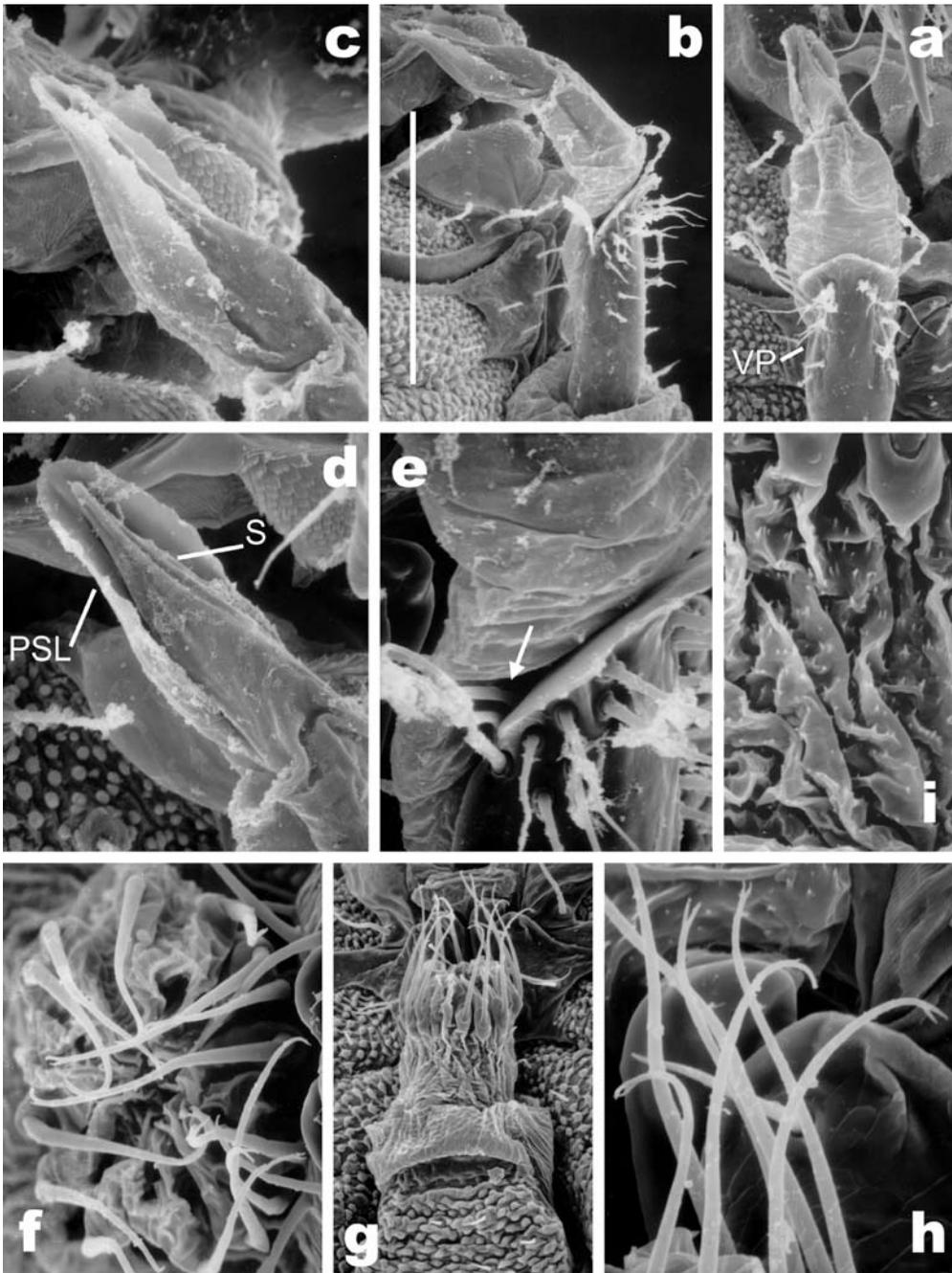


FIGURE 41. *Tularina plumosa* sp. nov., genitalic morphology. a–e. Male, penis, fully expanded, in ventral (a) and dexterolateral (b, e) views, with glans in lateral (c) and ventrolateral (d) views, and VP (e) showing dorsal setae (arrow). f–i. Female, ovipositor, in apical (f) and ventral (g) views, showing bifid apical setae (h) and lateral surface of ovipositor with microspines (i). PSL = parastylar lobe, S = stylus, VP = ventral plate. Scale bar = 190 $\mu$ m (a–b, g), 82 $\mu$ m (c–d), 60 $\mu$ m (e–f), 40 $\mu$ m (h–i).

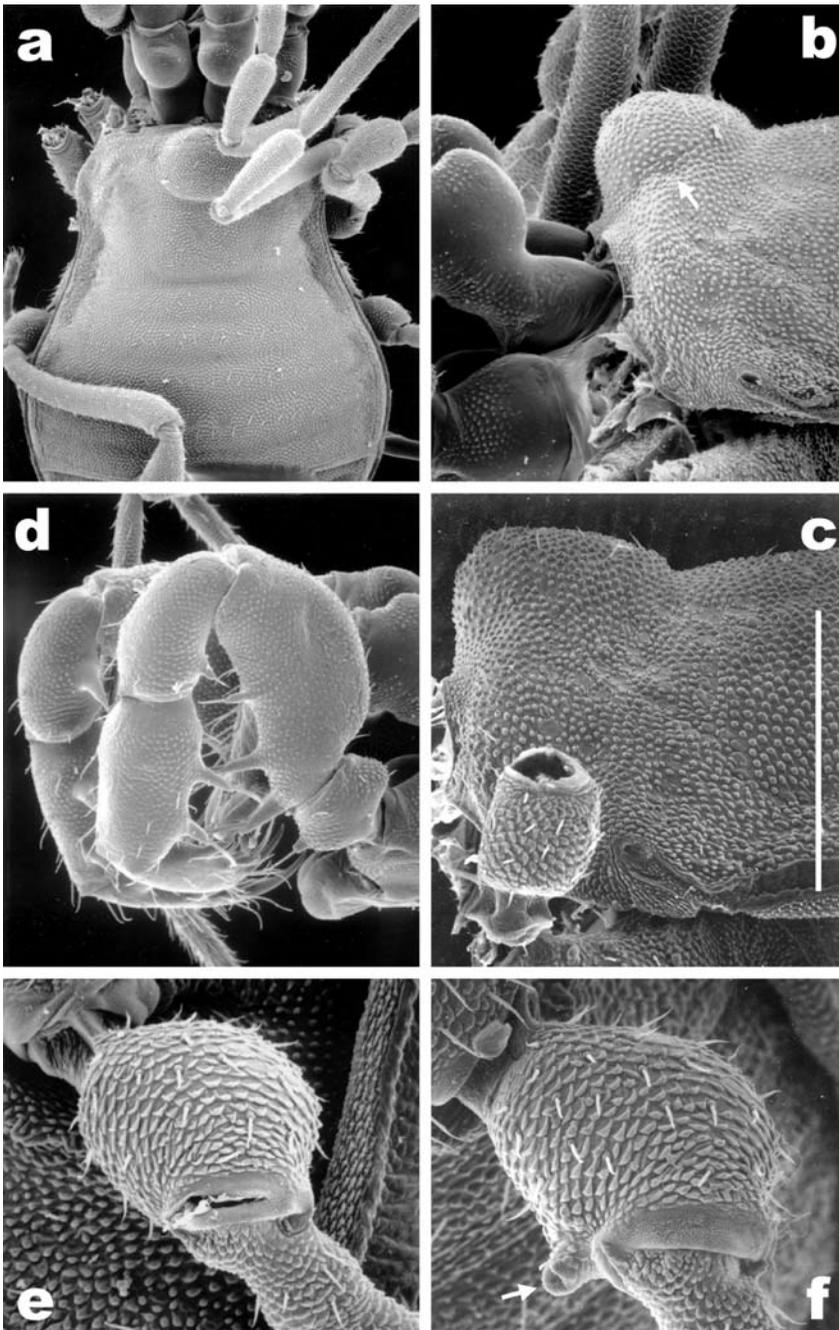


FIGURE 42. *Tularina scopula* (Briggs), somatic morphology. a–b, d–e. Female. c, f. Male. a. Body, dorsal view. b–c. Cephalon, lateral view, with arrow showing degenerate eye. d. Palpi, lateral view. e–f. Trochanter IV, ectal view, with arrow indicating tubercle in male. Scale bar = 780 $\mu$ m (a), 475 $\mu$ m (d), 380 $\mu$ m (b), 285 $\mu$ m (c), 190 $\mu$ m (e–f).

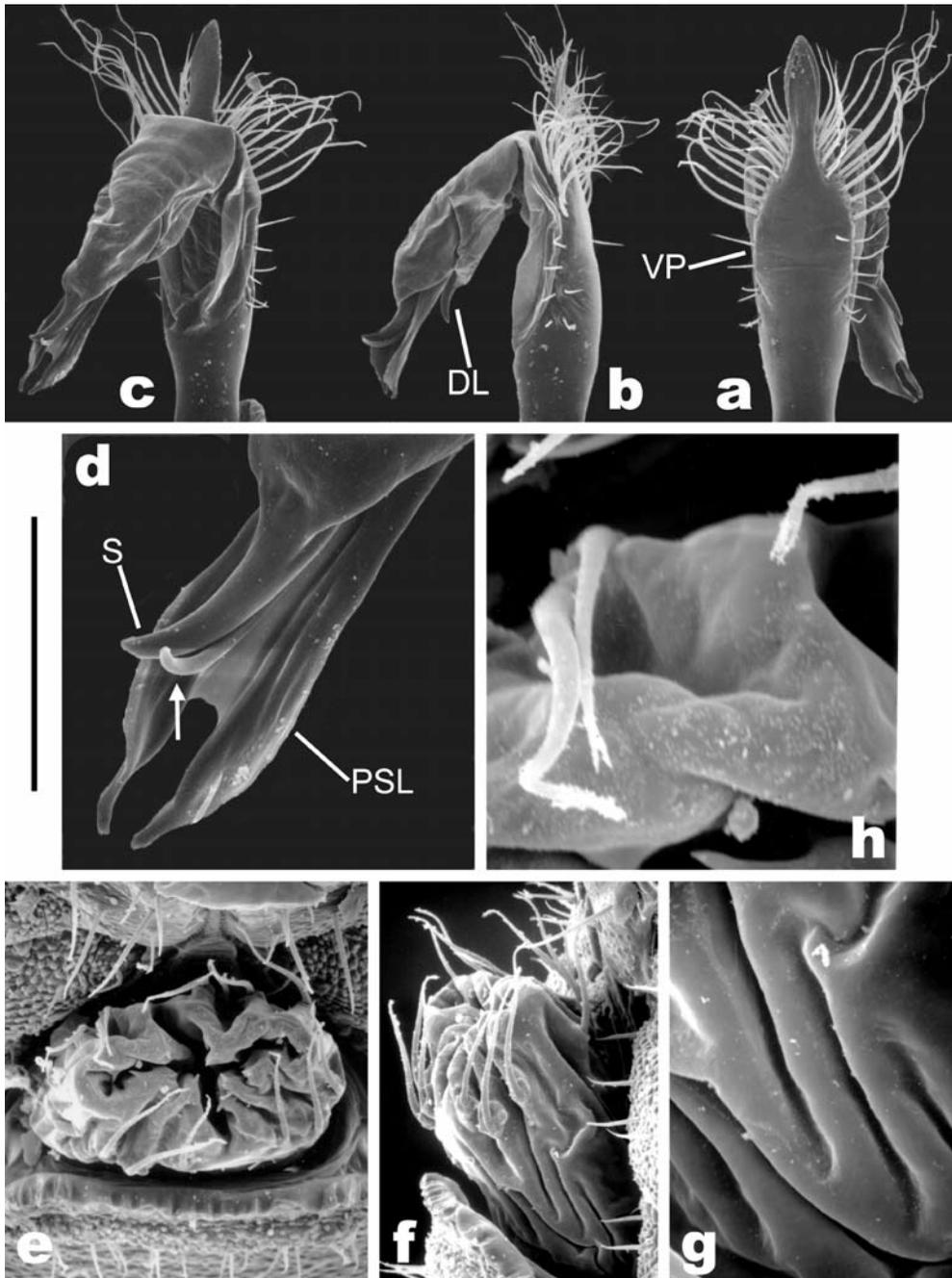


FIGURE 43. *Tularina scopula* (Briggs), genitalic morphology. a–d. Male, penis partially expanded in ventral (a), dexterolateral (b), and subdorsal (c) views, with ventroapical part of glans (d), showing stylus with tubule (arrow). e–h. Female, ovipositor in apical (e) and sinistrolateral (f) views, showing lateral surface of ovipositor lacking microspines (g), and bifid apical setae (h). DL = dorsal lobe, PSL = parastylar lobe, S = stylus, VP = ventral plate. Scale bar = 300 $\mu$ m (a–c), 180 $\mu$ m (e–f), 82 $\mu$ m (d), 57 $\mu$ m (g), 38 $\mu$ m (h).

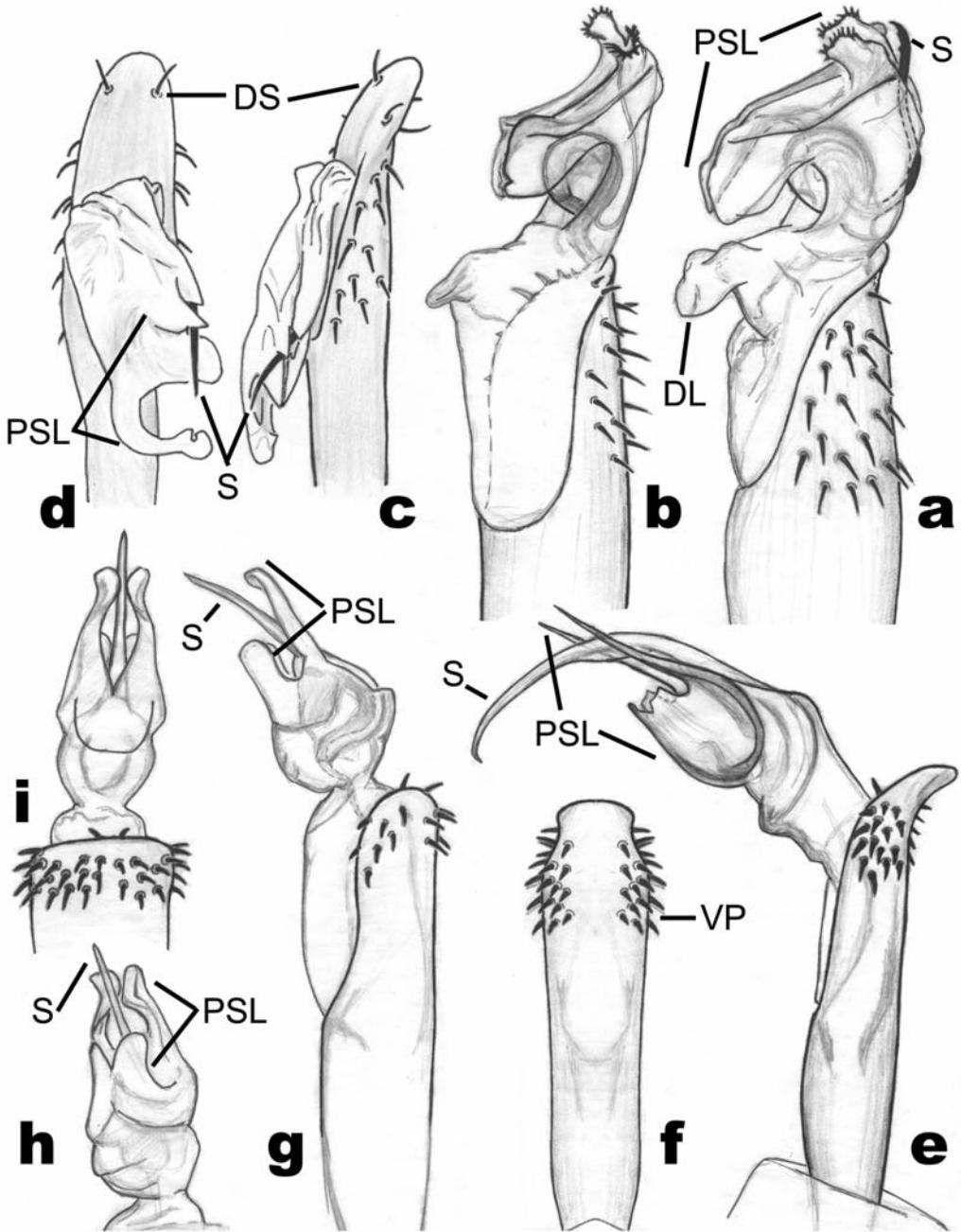


FIGURE 44. *Megacina* gen. nov., male genitalia. a–b. *M. cockerelli* (Goodnight and Goodnight), penis fully expanded in dexterolateral view with specimen from Crescent City (a) and Soda Rock Lane (b). c–d. *M. schusteri* sp. nov., penis unexpanded in dexterolateral (c) and dorsal (d) views. e–f. *M. mayacma* sp. nov., penis fully expanded in dexterolateral view (e) and truncus in ventral view (f). g–i. *M. madera* (Briggs), penis fully expanded in dexterolateral (g), dorsal (h), and ventral (i) views. DL = dorsal lobe, DS = dorsal seta, PSL = parastylar lobe, S = stylus, VP = ventral plate.

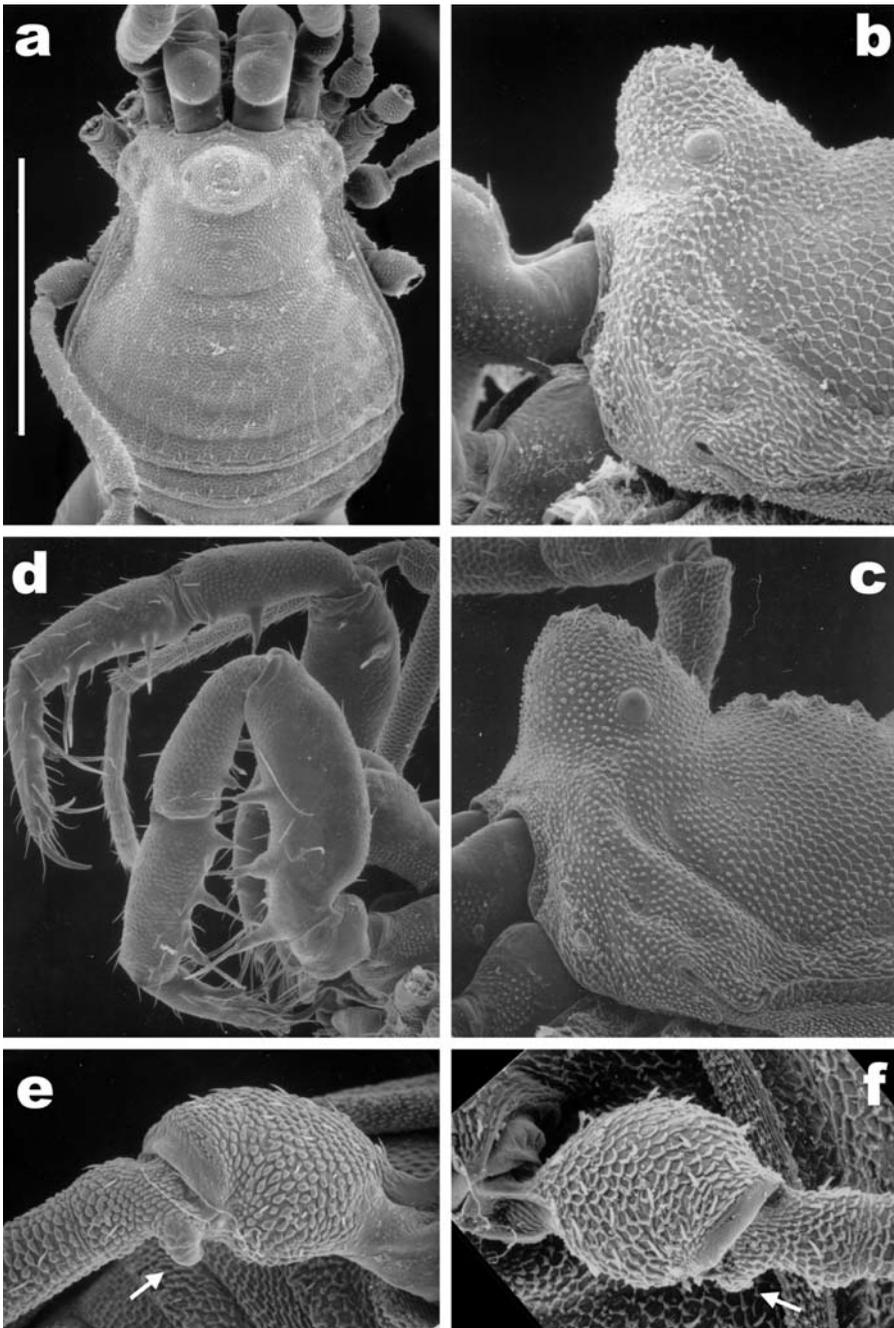


FIGURE 45. *Megacina madera* (Briggs), somatic morphology. a–b, f. Female. c–e. Male. a. Body, dorsal view. b–c. Cephalon, lateral view, showing areolate cuticle. d. Palpi, lateral view. e–f. Trochanter IV, ectal view, showing femoral processes (arrows). Scale bar = 720 $\mu$ m (a), 500 $\mu$ m (d), 330 $\mu$ m (c), 250 $\mu$ m (b, e), 190 $\mu$ m (f).

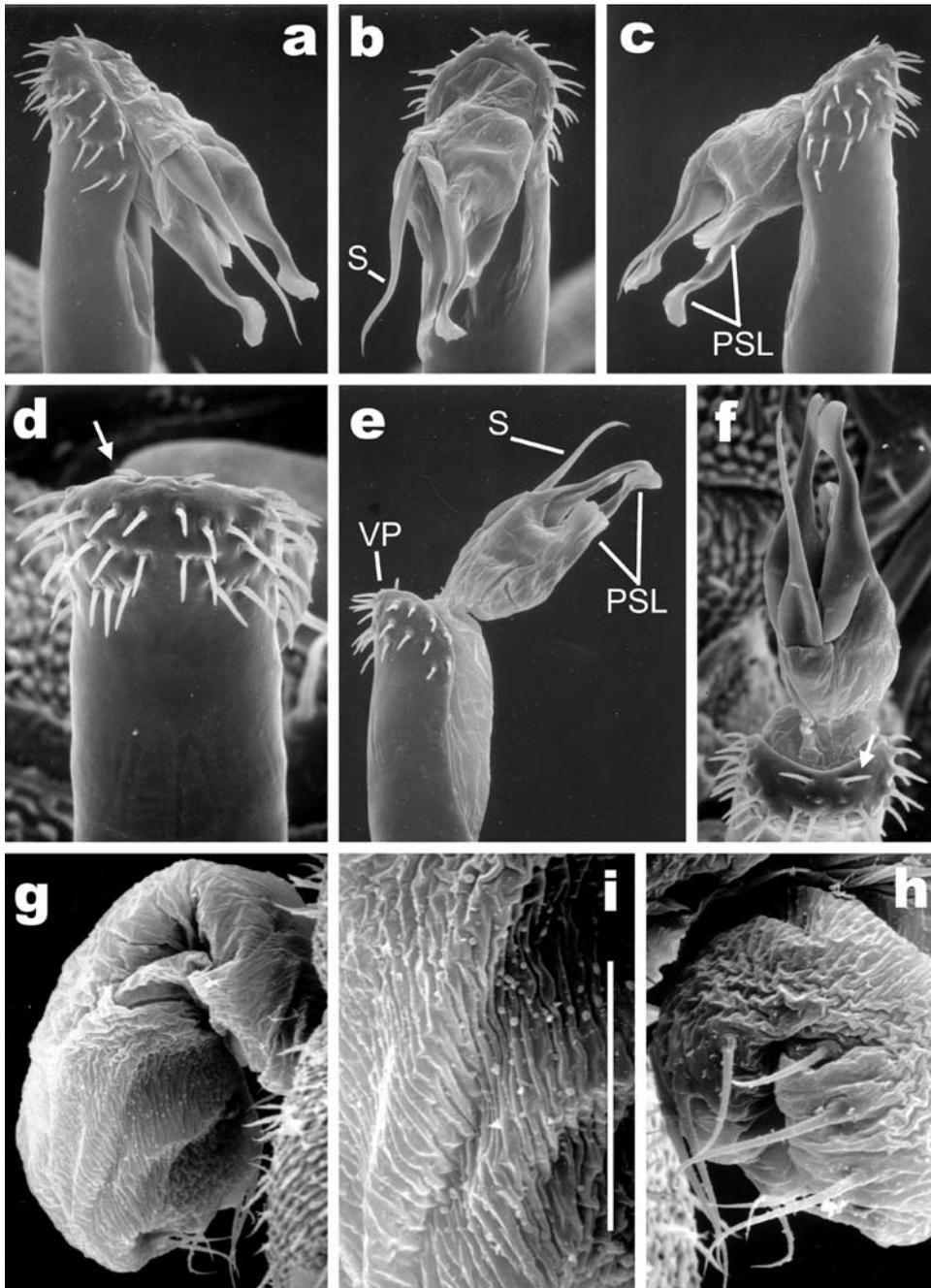


FIGURE 46. *Megacina madera* (Briggs), genitalic morphology. a–f. Male, penis. a–c. Partially expanded, in sinistrolateral (a), dorsal (b), and dexterolateral (c) views. d–f. Fully expanded, in ventral (d), sinistrolateral (e), and apical (f) views, with arrows showing dorsal setae. g–i. Female, ovipositor, poorly expanded, in sinistrolateral (g) and dexterolateral (h) views, and lateral surface lacking microspines (i). PSL = parastylar lobe, S = stylus, VP = ventral plate. Scale bar = 140 $\mu$ m (g), 135 $\mu$ m (a–c, e), 115 $\mu$ m (f), 84 $\mu$ m (d), 82 $\mu$ m (h), 57 $\mu$ m (i).

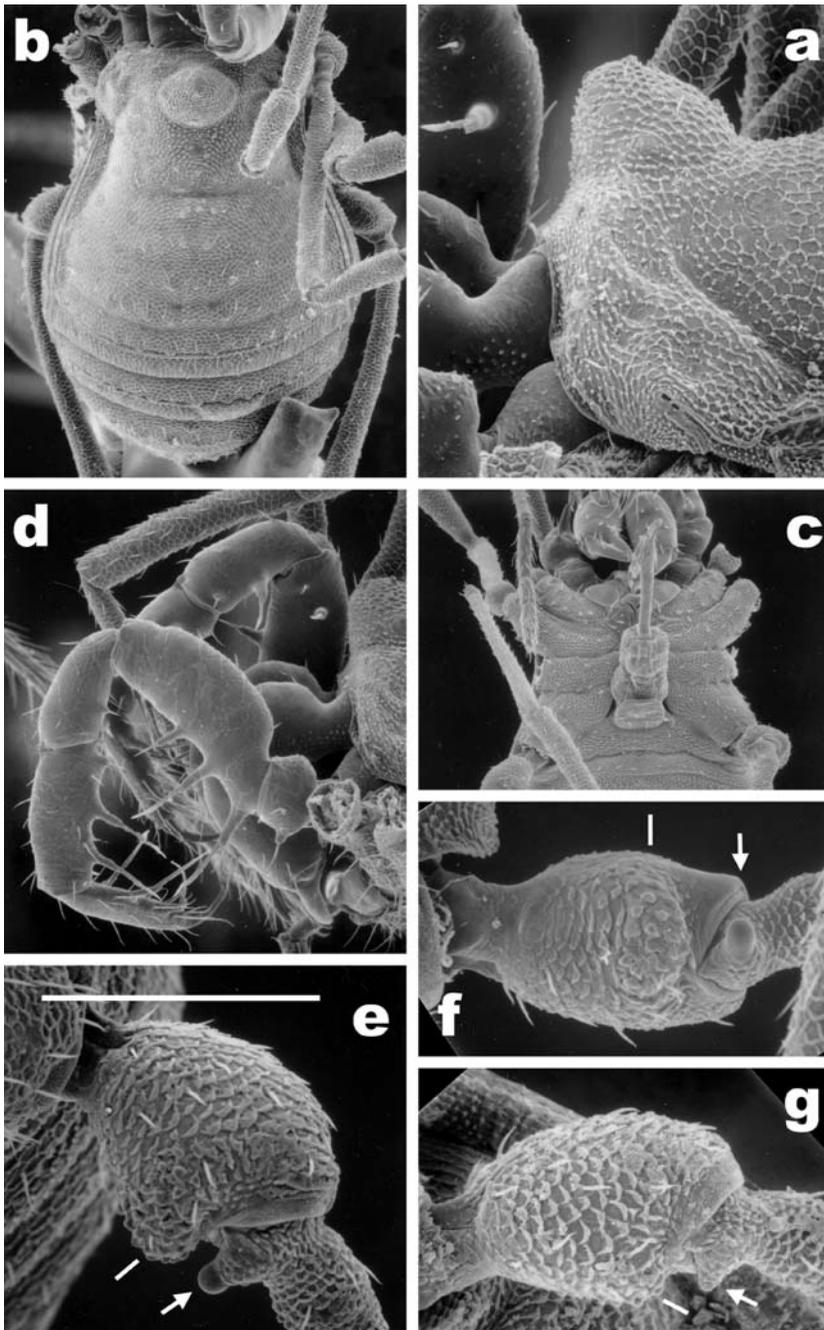


FIGURE 47. *Megacina schusteri* sp. nov., somatic morphology. a–b, g. Female. c–f. Male. a. Cephalon, lateral view, showing areolate cuticle. b–c. Body, dorsal (b) and ventral (c) views. d. Palpi, lateral view. e–g. Trochanter IV, in ectal (e, g) and ventral (f) views showing femoral process (arrow) and trochanteral swelling (line). Scale bar = 780 $\mu$ m (b–c), 450 $\mu$ m (d), 270 $\mu$ m (a), 180 $\mu$ m (e–g).

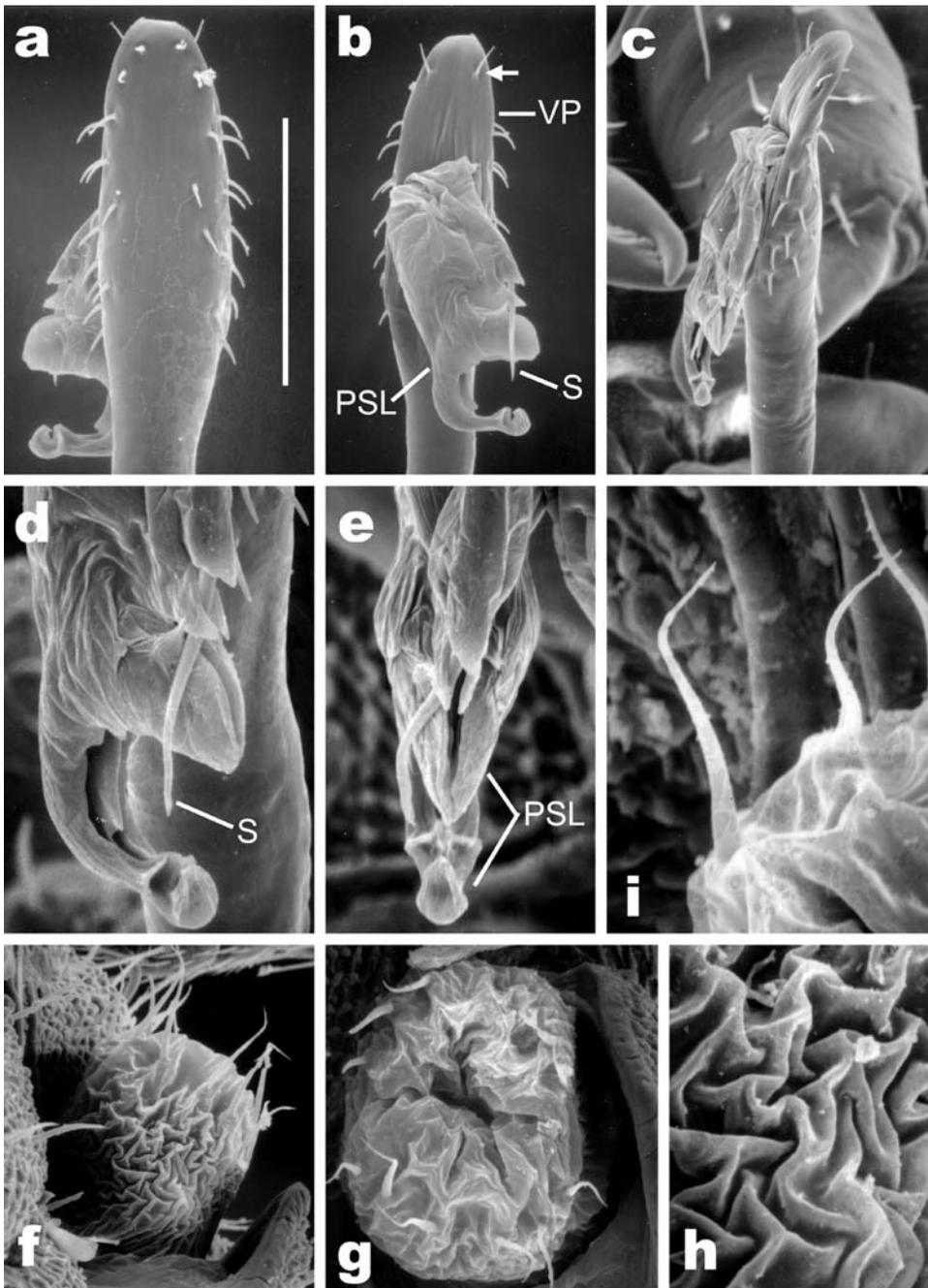


FIGURE 48. *Megacina schusteri* sp. nov., genitalic morphology. a–e. Male, penis unexpanded in ventral (a), dorsal (b), and dexterolateral (c) views, and distal half of glans in lateral (d) and ventral (e) views, with arrow showing dorsal seta. f–i. Female, ovipositor, in dexterolateral (f) and apical (g) views, with lateral surface lacking microspines (h), and close-up of apical setae (i). PSL = parastylar lobe, S = stylus, VP = ventral plate. Scale bar = 150 $\mu$ m (b–c), 145 $\mu$ m (f), 115 $\mu$ m (a, g), 57 $\mu$ m (d), 45 $\mu$ m (e), 38 $\mu$ m (h–i).

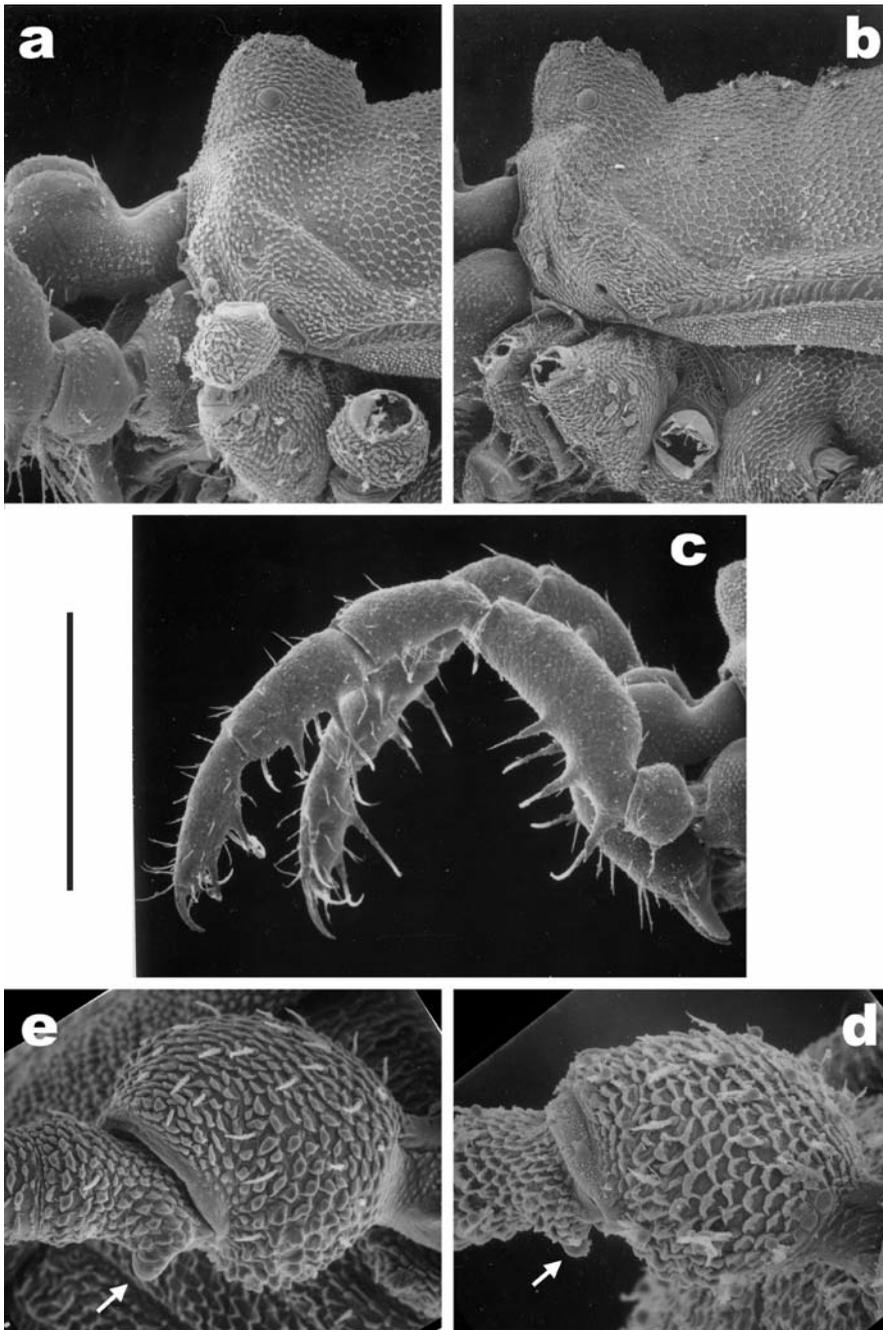


FIGURE 49. *Megacina mayacma* sp. nov., somatic morphology. a, e. Male. b–d. Female. a–b. Cephalon, lateral view showing areolate cuticle. c. Palpi, lateral view. d–e. Trochanter IV, in ectal view showing femoral process (arrows). Scale bar = 430 $\mu$ m (c), 350 $\mu$ m (a–b), 160 $\mu$ m (d–e).

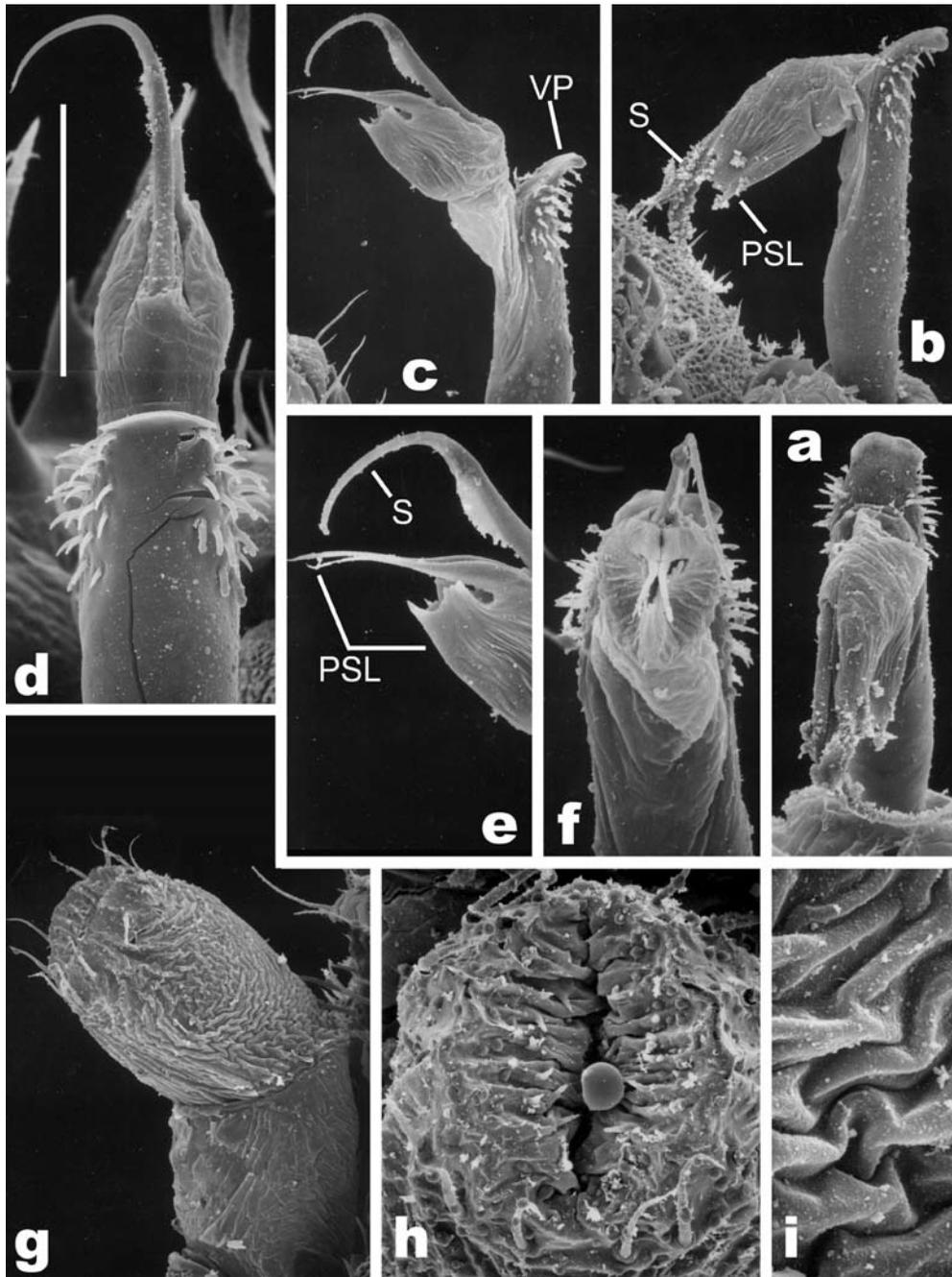


FIGURE 50. *Megacina mayacma* sp. nov., genital morphology. a–f. Male, penis. a–b. Partially expanded, in dorsal (a) and dexterolateral (b) views. c–f. Fully expanded, in dexterolateral (c, e), ventral (d), and dorsal (f) views. g–i. Female, ovipositor in sinistrolateral (g) and apical (h) views, with lateral surface lacking microspines (i). PSL = parastylar lobe, S = stylus, VP = ventral plate. Scale bar = 200 $\mu$ m (c), 190 $\mu$ m (a–b, g), 123 $\mu$ m (d), 115 $\mu$ m (e–f), 82 $\mu$ m (h), 19 $\mu$ m (i).

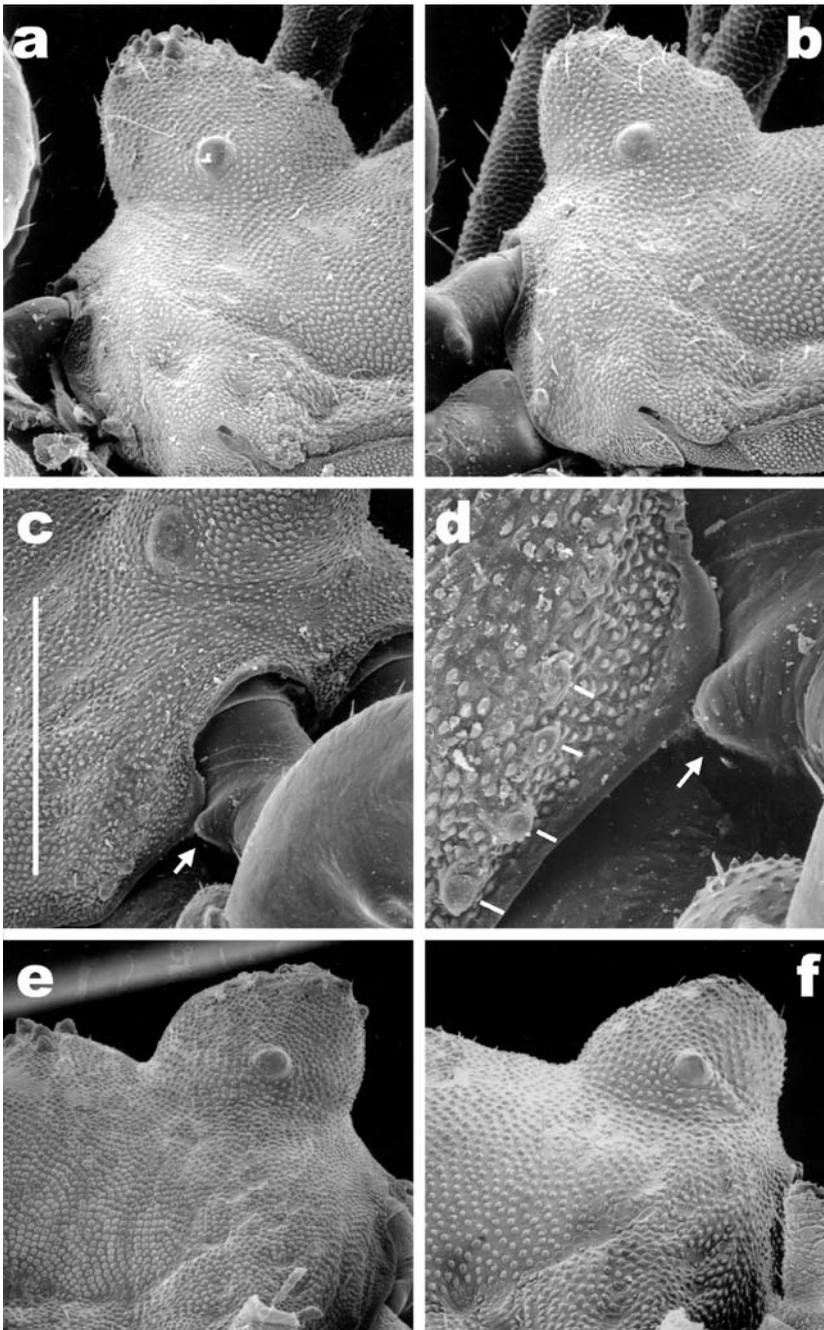


FIGURE 51. *Megacina cockerelli* (Goodnight and Goodnight), somatic morphology, cephalic region. a, c–e. Male. b, f. Female. a–b, e–f. Cephalon, lateral view. c–d. Cephalon, anteriolateral view, showing cheliceral boss (arrow) and AT (lines). N population: Boardman (a–b), Ft. Dick (c–d). S population: Burdell (e–f). Scale bar = 550 $\mu$ m (a, e), 450 $\mu$ m (b), 380 $\mu$ m (f), 360 $\mu$ m (c), 135 $\mu$ m (d).

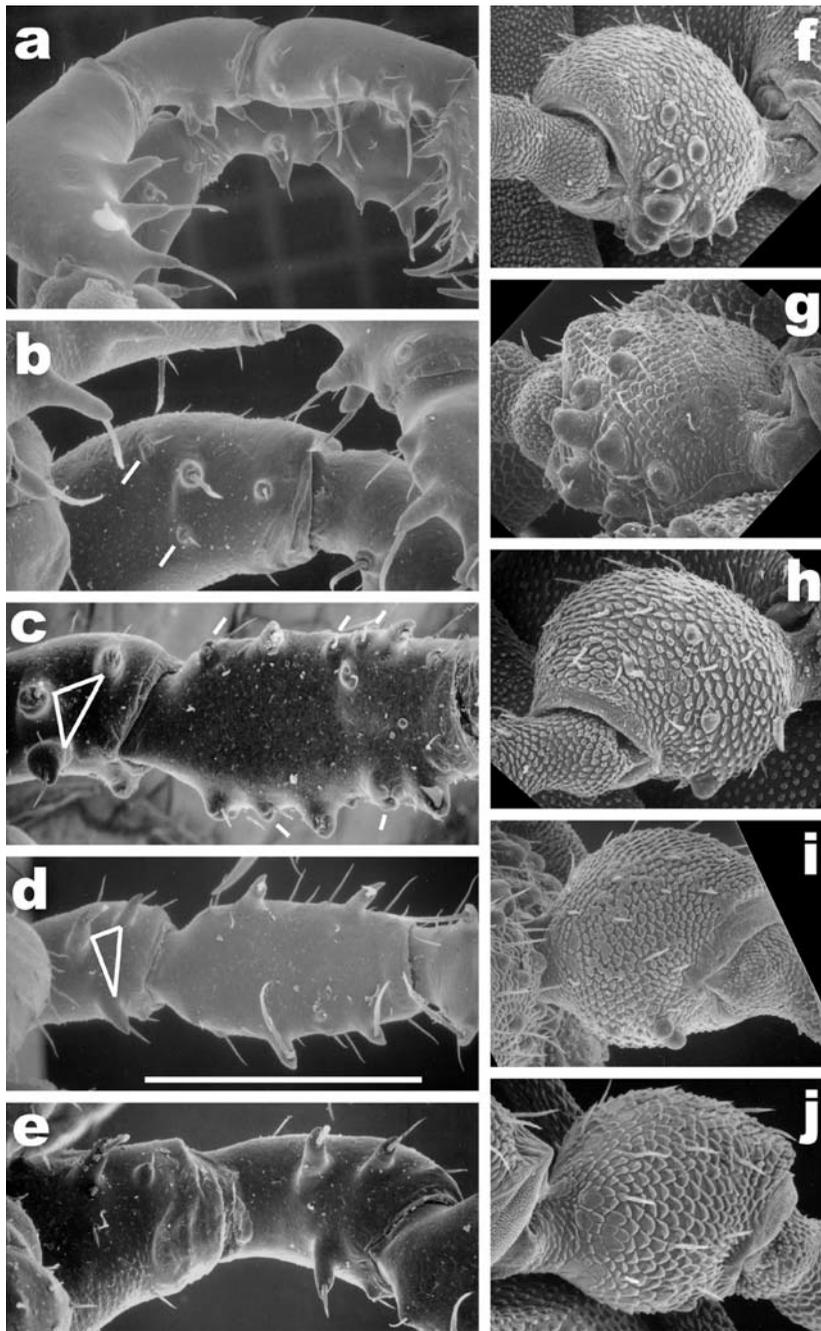


FIGURE 52. *Megacina cockerelli* (Goodnight and Goodnight), somatic morphology, appendages. a–c, f–g, i. Male. d–e, h, j. Female. a–e. Palpi. a. Palpi, lateroventral view. b. Palpal femur, mesoventral view showing additional tubercles (lines). c–d. Palpal tibia and patella, ventral view, with triangle showing arrangement of patellar megaspines in male (c) and female (d), and lines showing the additional tibial tubercles in male (c). e. Palpal patella and femur, ventral view. f–j. Trochanter IV in ventral (g) and lateral views (f, h–j). N population: Ft. Dick (b), Boardman (c–h). S population: Burdell (a, i–j). Scale bar = 780 $\mu$ m (a), 550 $\mu$ m (c–d), 460 $\mu$ m (f), 450 $\mu$ m (e), 375 $\mu$ m (g, i), 360 $\mu$ m (b), 315 $\mu$ m (h), 130 $\mu$ m (j).

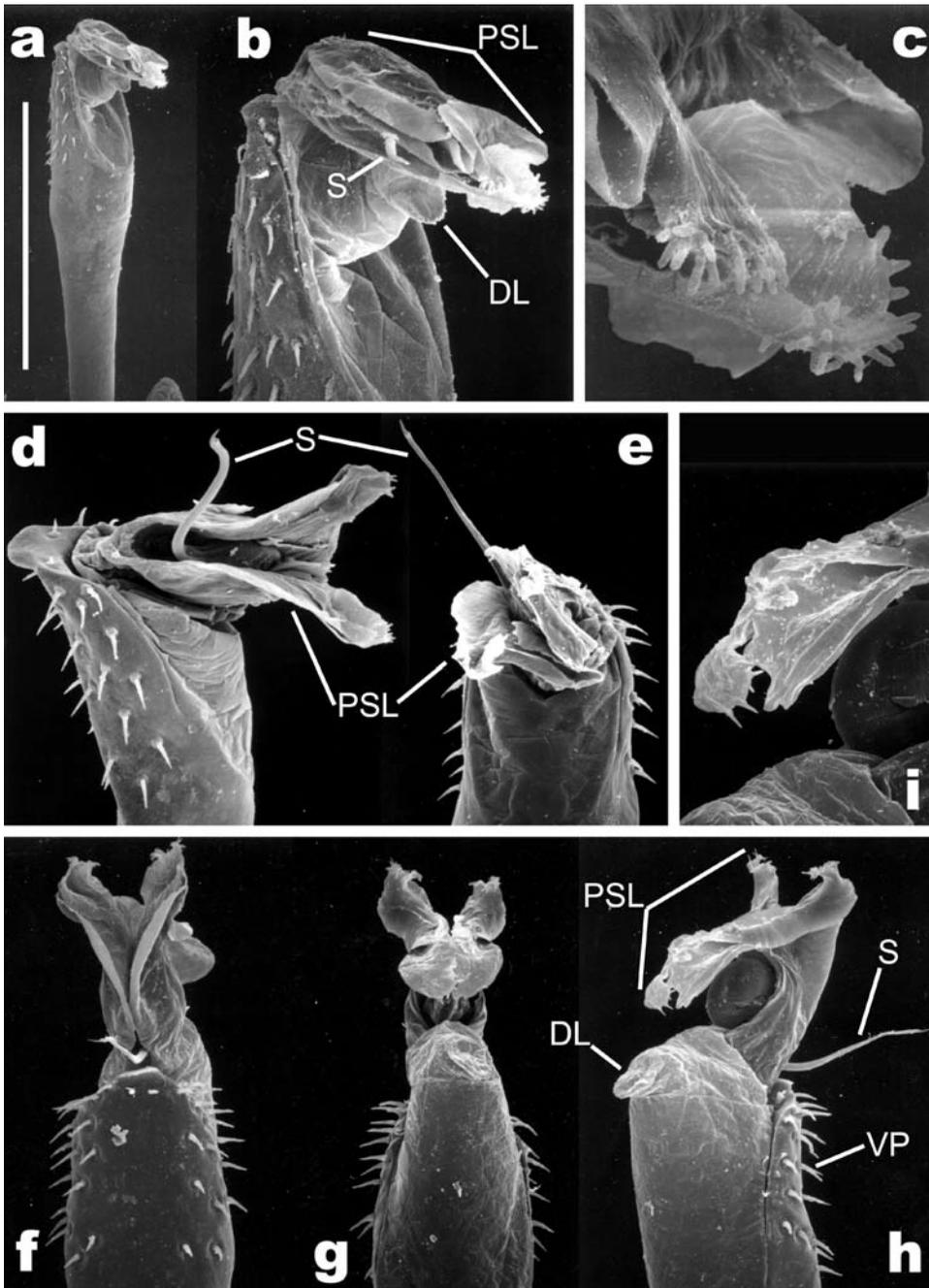


FIGURE 53. *Megacina cockerelli* (Goodnight and Goodnight), male genitalia. a-c. Penis with largely folded glans, dorso(sinistro)lateral view. d-e. Penis with partially expanded glans, in sinistrolateral (d) and dorsal (e) views. f-i. Penis with fully expanded glans in ventral (f), dorsal (g), and dexterolateral (h-i) views. N population: Ft. Dick (d-e), Boardman (a-c). S population: Soda Rock Lane (f-i). DL = dorsal lobe, PSL = parastylar lobe, S = stylus, VP = ventral plate. Scale bar = 380 $\mu$ m (a), 165 $\mu$ m (e-h), 145 $\mu$ m (d), 75 $\mu$ m (i), 38 $\mu$ m (c).

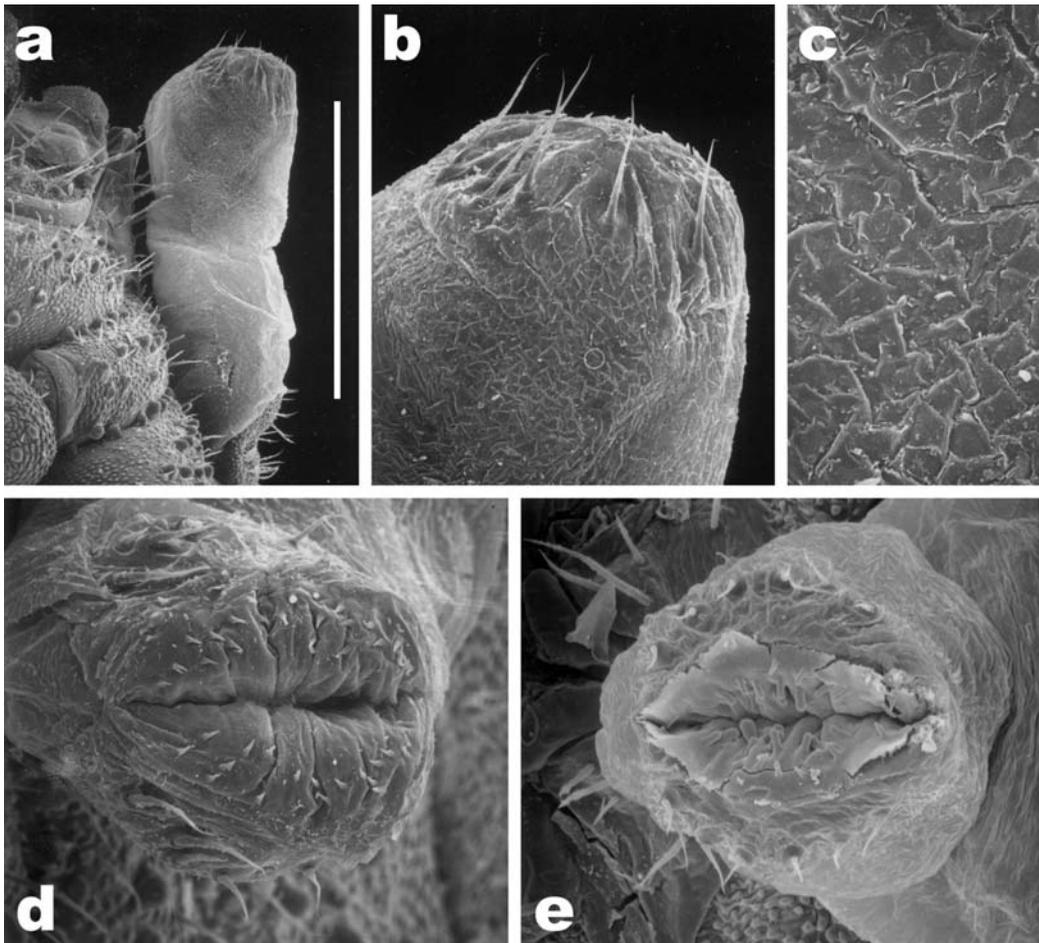


FIGURE 54. *Megacina cockerelli* (Goodnight and Goodnight), female genitalia. a–c. Ovipositor, dexterolateral view with apex showing setae (b) and lateral surface (c) showing absence of microspines. d–e. Ovipositor, apical view, clean (d) and with some sort of apical secretion (e). N population: Boardman (a–d). S population: Burdell (e). Scale bar = 570 $\mu$ m (a), 190 $\mu$ m (b, d–e), 60 $\mu$ m (c).

	Callitina maritima	Microcnella spp	Microcna spp	Stalaina californica	Stalaina sura	Stalaina seca	Stalaina chalona	Stalaina flava	Stalaina borreogensis	Stalaina peacheyi	Stalaina catalina	Stalaina rothi	Stalaina lobata	Enigmina granita	Enigmina warrenorum	Tularina plumosa	Tularina scopula	Megacina madera	Megacina schusteri	Megacina mayama	Megacina cockerelli	Banksia incredula	Texella bifurcata	Texella kokowef	Texella mutakki	Phalangodes et al
C	MI	Mc	S+E											Tularina		Megacina		Mg+BC		Bifurcate Clade						
			Mc (S+E)											Enig.		Tularina		Megacina		Mg+BC		T (Mg+BC)				
			non-telescoping-glans clade											non-telescoping-glans clade		folding-glans clade										
1	0	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	?	
2	x	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	
3	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	
4	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	
5	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	
6	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	?	0	1	?	?	1	1	1	1	
7	0	0	0	1	1	1	2	1	?	1	1	1	1	1	0	0	1	2	2	2	2	2	1	2	2	
8	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	
9	0	0	1	1	1	1	1	1	?	1	1	1	1	1	1	0	0	0	1	0	0	1	0	0	0	
10	x	0	1	1	1	1	1	1	?	1	1	1	1	1	1	x	x	1	x	x	x	x	x	x	x	
11	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	
12	0	0	0	0	1	1	1	1	?	1	1	1	1	1	0	0	0	1	1	1	1	0	0	0	0	
13	0	0	0	1	?	?	0	1	?	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	
14	0	0	0	0	?	?	0	1	?	1	1	?	1	2	2	?	?	0	1	1	1	0	0	0	0	
15	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	0	
16	0	0	0	0	0/1	0	0	0	0	?	?	?	?	1	1	0	0	1	1	1	1	1	0	0	0	
17	0	0	0	1	x/1	1	1	1	1	1	1	?	1	x	x	2	x	x	x	x	x	x	0	0	x	
18	0	1	1	1	0	0	0	0	0	0	0	?	1	0	1	1	0	0	0	0	0	2	0	2	2	
19	0	1	2	0	3	3	3	3	3	3	3	?	0	3?	0	0	1	1	0	0	0	0	0	0	0	
20	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	
21	0	3	3	1	1	1	1	1	1	1	1	1	1	3	3	4	4	2	3	2	0-3	4	0	0	4	
22	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	
23	0	0	0	0	0	0	0	0	?	0	0	?	0	0	0	?	?	?	?	?	?	1	1	0	0	
24	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	
25	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	
26	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	
27	0	0	0	2	2	2	2	2	2	2	2	2	2	2	2	0	0	1	0	0	1	1	1	2	2	
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	
29	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	1	0	

FIGURE 55. Character matrix and analysis of Nearctic Phalangodidae. X-axis. Y-axis. Taxa. Y-axis. Characters: male genitalia (# 1–14), female genitalia (# 15–19), somatic (#20–29). Matrix. 0 plesiomorphic, 1–4 derived states, ? not known, x not applicable.

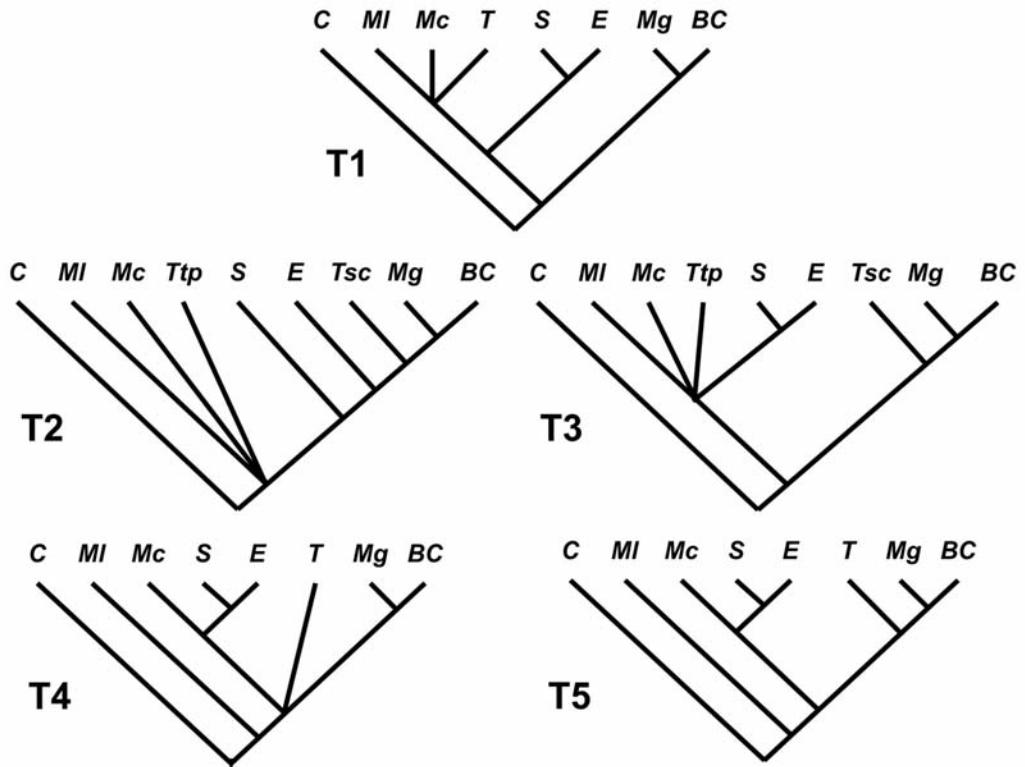


FIGURE 56. Cladograms of the Nearctic Phalangodidae, showing the five trees (T1-T5) discussed in the text. Abbreviations: BC = bifurcate clade, C = *Calicina* Ubick and Briggs, E = *Enigmina* gen. nov., Mc = *Microcina* Briggs and Ubick, Mg = *Megacina* gen. nov., MI = *Microcinella* gen. nov., S = *Sitalcina* Banks, T = *Tularina* gen. nov., Tsc = *Tularina scopula* (Briggs), Ttp = *Tularina plumosa* sp. nov. and *T. tularensis* sp. nov.



FIGURE 57. Maps of California and adjacent regions showing the distribution of species in the *Sitalcina* complex: **a:** (San Francisco Bay area) *Microcinella* gen. nov. (squares) and *Microcina* Briggs and Ubick (dots). *Microcina*: 1, *M. tamalpais* sp. nov.; 2, *M. tiburona* (Briggs and Hom); 3, *M. leei* Briggs and Ubick; 4, *M. lumi* Briggs and Ubick; 5, *M. potrero* sp. nov.; 6, *M. sanbruno* sp. nov.; 7, *M. edgewoodensis* Briggs and Ubick; 8, *M. stanford* sp. nov.; 9, *M. jungi* Briggs and Ubick. *Microcinella*: 10, *M. homi* (Briggs and Ubick); 11, *M. coensis* sp. nov. **b:** (Central California) *Tularina* gen. nov. and *Megacina* gen. nov. Area encircled by dashed line at bottom represents *Enigmina* gen. nov. (see also fig. c:). **c:** (California and Arizona) *Sitalcina* Banks and *Enigmina* gen. nov. Undescribed new species are indicated by an asterisk.



FIGURE 58. Map of California, Arizona and adjacent regions showing the distribution of genera and species groups of the *Sitalcina* complex. *Mi-la* = *Microcinella* gen. nov., *Mi-na* = *Microcina* Briggs and Ubick.

## APPENDIX 1

*Sitalcina* complex: Classification and natural history

<i>Taxa</i> (bold = new)	<i>habitat</i>	<i>biome</i>
<b><i>Microcinella</i></b> gen. nov.		
<i>coensis</i> sp. nov.	serpentine	oak-chaparral
<i>homi</i> (Briggs and Ubick, 1989)	serpentine, sandstone	grassland
sp. (Monterey Co.)	sandstone	oak
<i>Microcina</i> Briggs and Ubick, 1989		
<i>edgewoodensis</i> Briggs and Ubick, 1989	serpentine	grassland
<i>jungi</i> Briggs and Ubick, 1989	serpentine	grassland
<i>leei</i> Briggs and Ubick, 1989	sandstone	oak-grassland
<i>lumi</i> Briggs and Ubick, 1989	serpentine	grassland
<i>potrero</i> sp. nov.	serpentine	<i>Eucalyptus</i> grassland
<i>sanbruno</i> sp. nov.	serpentine, sandstone	grassland, chaparral
<i>stanford</i> sp. nov.	basalt	grassland
<i>tamalpais</i> sp. nov.	basalt	forest-grassland ecotone
<i>tiburona</i> (Briggs and Hom, 1966)	serpentine	grassland
sp. (Marin Co.)	volcanic, sandstone	oak
<i>Sitalcina</i>		
<i>californica</i> group		
<i>californica</i> (Banks, 1893)	rocks, logs, duff, caves	oak, redwood, mixed forests
<i>sura</i> group		
<i>borregoensis</i> Briggs, 1968	granite	palm canyon
<i>chalonga</i> Briggs, 1968	various rocks	broadleaf evergreen, chaparral
<i>flava</i> Briggs, 1968	sandstone	oak, oak-sycamore
<i>catalina</i> sp. nov.	caves, rocks, logs, duff	oak, +
<i>peacheyi</i> sp. nov.	caves, rocks, logs, duff	oak, +
<i>rothi</i> sp. nov.	?	?
<i>seca</i> sp. nov.	granite, logs, duff	broadleaf evergreen, redwood
<i>sura</i> Briggs, 1968	various rocks, logs, duff	redwood
sp. (Santa Barbara Co.)	rock	oak
<i>lobata</i> group		
<i>lobata</i> Goodnight and Goodnight, 1942	rocks, duff, <i>Neotoma</i> nests, tarantula burrows	oak, chaparral, pine, sycamore
<b><i>Enigmina</i></b> gen. nov.		
<i>granita</i> (Briggs, 1968)	granite	oak, oak-grassland
<i>warrenorum</i> sp. nov.	logs, duff	coniferous
<b><i>Tularina</i></b> gen. nov.		
<i>plumosa</i> sp. nov.	serpentine, granite	grassland
<i>scopula</i> (Briggs, 1968)	granite	grassland
<i>tularensis</i> sp. nov.	serpentine	grassland
<b><i>Megacina</i></b> gen. nov.		
<i>madera</i> group		
<i>madera</i> (Briggs, 1968)	serpentine, granite, wood	oak-yellow pine
<i>mayacma</i> sp. nov.	serpentine, logs	oak, pine
<i>schusteri</i> sp. nov.	meta-volcanic	oak-digger pine
<i>cockerelli</i> group		
<i>cockerelli</i> (Goodnight and Goodnight, 1942)	rocks, logs, duff	dense forests, oak-grassland, chaparral