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THE HARVESTMAN FAMILY PHALANGODIDAE 4. A REVIEW OF THE GENUS *BANKSULA* (OPILIONES, LANIATORES)

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ABSTRACT. Two new species of *Banksula* are described. *Banksula incredula* enlarges the concept of the genus and is assigned to a new species group which is the likely sister group to the other *Banksula*. The species is unique in numerous morphological features, being the largest species in the genus, the first non-cavernicolous species, and occurring in the Coast Ranges of California, rather than in the Sierra Nevada foothills. The second new species, *B. tutankhamen*, is a typical member of the *californica* group but with more pronounced troglomorphy. Clinal variation is documented for *B. grahami* Briggs 1974, with *B. elliotti* Briggs & Ubick 1981, now placed as its junior synonym, representing the northern and most troglomorphic populations.

Keywords: *Banksula*, Phalangodidae, Opiliones, cavernicoles, California

The phalangodid genus *Banksula* Roewer 1949 was established for *Scotolemon californica* Banks 1900, a troglobitic species from Alabaster Cave in the Sierra Nevada, California. Eight additional species were subsequently added by Briggs (1974) and Briggs & Ubick (1981). Although some of these have large apparently functional eyes, all are restricted to the caves of the central Sierra Nevada foothills. Given the narrow distribution and habitat preference for the genus, it came as quite a surprise to discover an epigean species, and especially one from the Coast Ranges of California. This species, which we are describing here as *Banksula incredula* new species, also extends the generic limits on morphological grounds, being the largest species in the genus and having a leg hypertrophy which, in some individuals at least, exceeds that of most troglobitic *Banksula*. Despite these and other unique features, which are discussed below, the species is clearly a member of the genus *Banksula* given that its palpal femur bears a dorsal row of setose tubercles (Figs. 2, 3). Although similar tubercles occur in some species of *Sitalcina* (Figs. 4, 5), these do not bear setae and thus are not homologous to those in *Banksula*. Also, and even more fundamentally, the penis of *B. incredula* is typical of *Banksula*, having a bifurcate ventral plate with ventrally situated prongs and a relatively simple glans consisting of a stylus and a pair of parastylar lobes (Figs. 18–22).

METHODS

Specimen preparation and observation follows the format described in earlier papers (Briggs & Ubick 1981; Ubick & Briggs 1989). All measurements not labeled otherwise are in millimeters. ‘Fig.’ and ‘Figs.’ refer to this paper, ‘fig’ and ‘figs’ to previously published works.

All specimens are deposited at the California Academy of Sciences, San Francisco, California, apart from the type series of *Banksula californica* (Banks), which is at the Museum of Comparative Zoology, Cambridge, Massachusetts.

The following abbreviations are utilized: AS = apical spine of VPP; AT = apical tooth of ovipositor; EMH = eyemound height; EML = eyemound length; GO = genital operculum; GOW = genital operculum width; PSL = parastylar lobes; SL = scute length; SW = scute width; TBL = total body length; TC = tarsal count; VP = ventral plate; VPP = ventral plate prong; VPW = VPP width.

TAXONOMY

Genus *Banksula* Roewer

Banksula Roewer 1949: 33; Briggs 1974: 1; Briggs & Ubick 1981: 315.

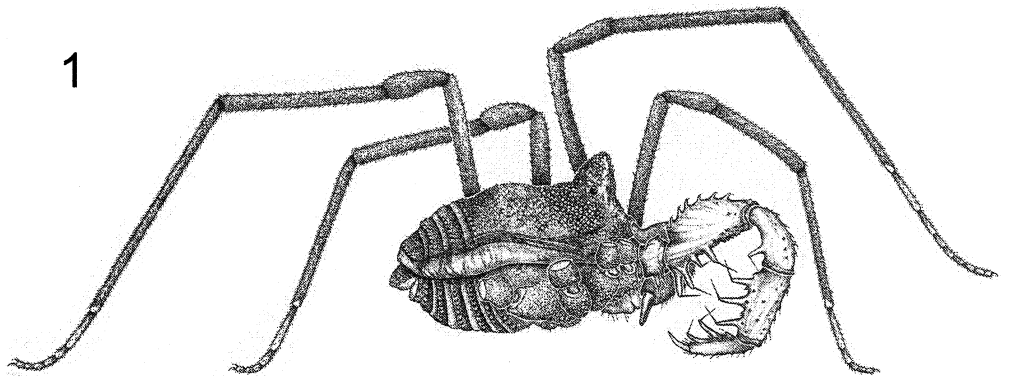


Figure 1.—*Banksula incredula*, lateral view (drawing by Jenny Speckels).

Type species.—*Scotolemon californica* Banks 1900.

Diagnosis.—Species of *Banksula* are unique among the Nearctic Phalangodidae in having a row of setiferous dorsal tubercles on the palpal femur (Figs 2, 3) and a penis with a bifurcate ventral plate with ventrally positioned prongs (Figs. 18, 19).

Description.—Color of body yellowish to orange; appendages white to yellowish white. Body length 1.5–3.0 mm. Body covered with tubercles. Scute with eyemound low and rounded to high and conical; cornea and retina present or absent. Anterior margin of scute with 0 to a few pairs of small anterior tubercles; ozopores lateral. Palpal megaspines: femur with one to two mesodistal and three to four ectobasal; patella with two mesal and one ectal; tibia with three mesal and three ectal; tarsus with two mesal and two ectal. Palp with dorsal row of setiferous tubercles on femur and smaller tubercles dorsally on other segments, laterally on femur, and between megaspines; basal megaspine of femur with mesal and ectal tubercles in most species, mesal tubercle absent in most females. Tarsal count 4–6–5–6, in most species, and 4 or 5–7 to 9–5–5 or 6 in *B. incredula*. Ovipositor surface wrinkled; smooth or covered with microspines; apical teeth present or absent; with 6 pairs of apical and 1 pair of subapical setae; setae slightly curved, apically pointed. Penis with folding glans; stylus short, narrow or wide, with lateral carinae present or absent, surrounded by 1 pair of parastylar lobes; ventral plate bifurcate, with 1 pair of apical spines, 7–12 pairs of long setae and up to 12 pairs of short setae.

The *incredula* species group

Diagnosis.—The single species representing this group differs from other *Banksula* in several characters: it is large, has a higher tarsal count, occupies an epigean habitat, has large eyes and a high eyemound, and has additional palpal megaspines, with 4 ectobasal and 2 mesoapical on the femur As regards the genitalia, males have a ventral plate with large apical spines and long setae and females an ovipositor with smooth cuticle and a pair of apical teeth.

Distribution.—Known only from a single locality in San Mateo County, California.

Banksula incredula new species
Figs. 1–3, 6, 9–22

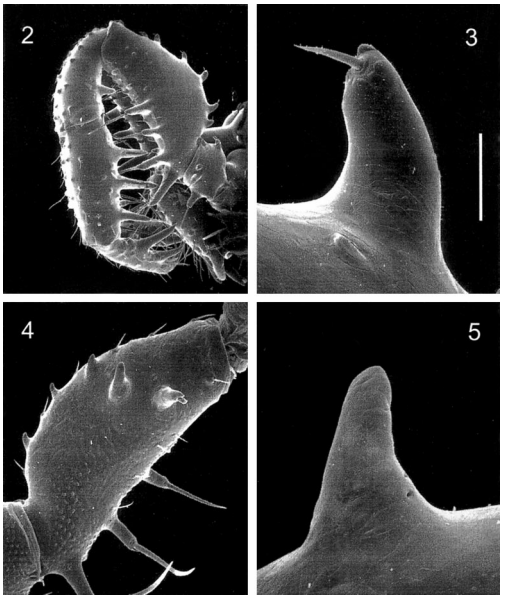
Type.—Male holotype from within a sandstone talus on San Bruno Mountain, San Mateo County, California (10 May 1991; D Ubick) deposited in CAS.

Etymology.—The species name refers to the unexpected morphology, habitat, and distribution of the species, and is considered feminine in gender

Diagnosis.—Same as for species group.

Description.—Total body length, 2.56–3.00. Scute length, 1.79–2.18. Leg II length, 8.81–10.51. Leg II/Scute length, 4.64–5.64. Tarsal count, 4 to 5–7 to 9–5–5 to 6. (N = 8)

Color orange, appendages pale orange, tarsi white. Body uniformly coarsely tuberculate. Scute margin without apparent anterior tubercles. Eyemound a prominent cone, as high as long. Cornea and retina large and conspicuous. Genital operculum relatively small: GOW/SW = 0.2. Palpal megaspines: femur



Figures 2–5.—Phalangodid palpi. 2, *Banksula incredula*, lateral view of male left palp; 3, same, close-up showing dorsal femoral tubercle; 4, *Sitalcina chalona* Briggs, lateral view of male left palpal femur; 5, same, close-up showing dorsal tubercle. Scale bar: 2 = 610 μm; 3 = 38 μm; 4 = 150 μm; 5 = 30 μm.

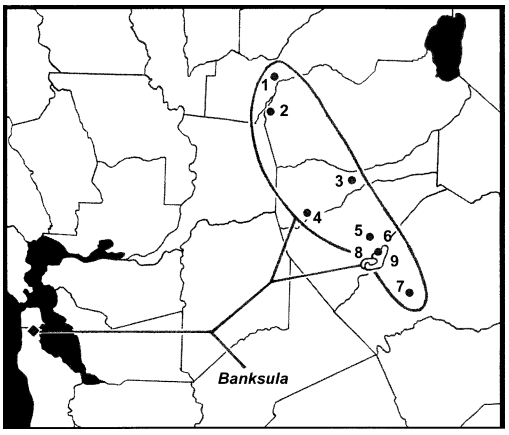
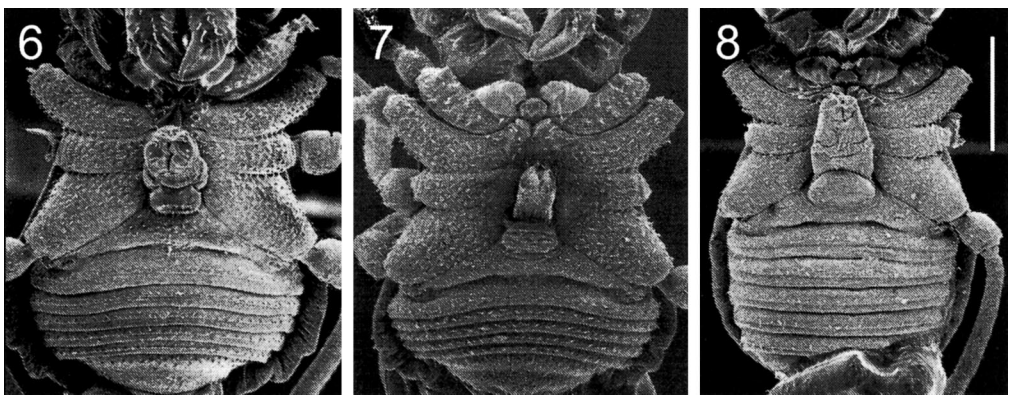


Figure 9.—Map of central California showing distribution and area cladogram of *Banksula*. Symbols: diamond = *B. incredula*; dots = *B. californica* group (1, *B. galilei*; 2, *B. californica*; 3, *B. grubbsi*; 4, *B. rudolphi*; 5, *B. tutankhamen*; 6, *B. martinorum*; 7, *B. tuolumne*); oblong region = *B. melones* group (8, *B. melones*; 9, *B. grahami*).

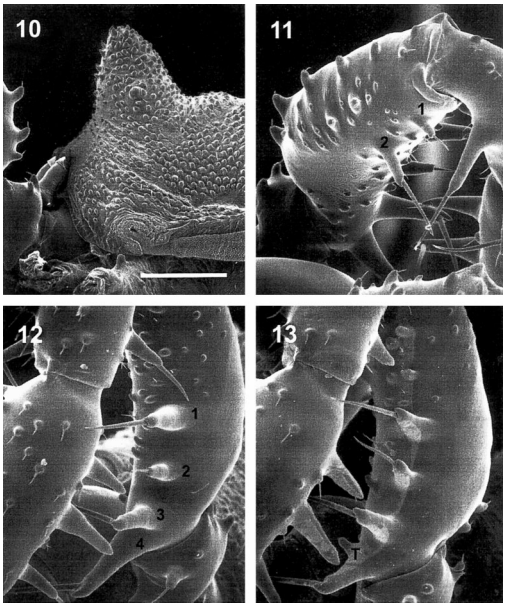
with 4 ventrobasal and 2 mesodistal; patella with 1 ectal and 2 mesal; tibia with 3 ectal and 3 mesal; tarsus with 2 ectal and 2 mesal. Palpal femur with 5–7 setiferous tubercles dorsally.

Male (holotype): Total body length, 2.59. Scute length, 2.18; width, 2.01. Eyemound length, 0.49; width, 0.64; height, 0.49. Operculum width, 0.32. Leg II length, 10.12. Leg II/scute length, 4.64. Tarsal count, 5–8 and 9—5–6. Proximal megaspine of palpal femur with mesal tubercle at base; lacking ectal tubercle.

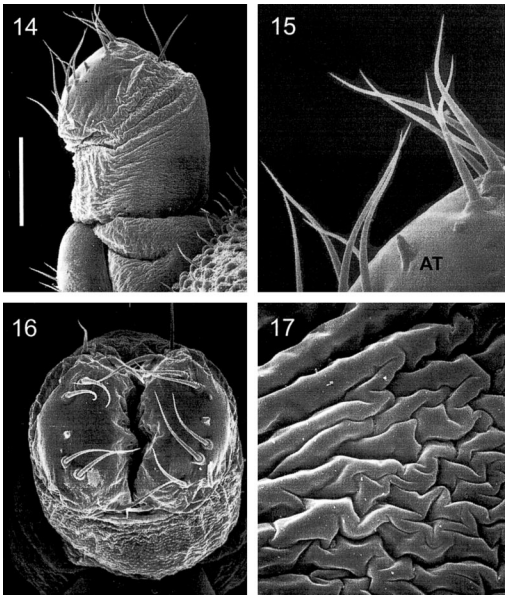
Penis (Figs. 18–22): VPP subparallel, separated by width of one prong; with large slightly curved AS; with 10 long setae in apical half and 12 short setae basally on each prong; long setae clearly longer than to twice the length of AS; short setae about half the length of AS. Glans with apical stylar region consisting of triangular pointed stylus and a pair of ribbon-like apically rounded PSL.



Figures 6–8.—Venters of female *Banksula* representing the three species groups. 6, *B. incredula*; 7, *B. galilei* (*californica* group); 8, *B. melones*. Scale bar: 6 = 750 μm; 7 = 430 μm; 8 = 600 μm.



Figures 10–13.—*Banksula incredula*. 10, anterior half of female scute showing eyemound; 11, female left palpus showing two mesoapical megaspines (1, 2); 12, female left palpus showing four ectobasal megaspines (1, 2, 3, 4); 13, male left palpus showing mesal tubercle (M) on ventral megaspine. Scale bar: 10 = 430 μm; 11–13 = 300 μm.



Figures 14–17.—*Banksula incredula*, ovipositor. 14, lateral view; 15, close-up showing apical tooth (AT); 16, apical view; 17, close-up of lateral surface showing absence of misrospines. Scale bar: 14 = 200 μm; 15 = 60 μm; 16 = 150 μm; 17 = 20 μm.

Female (paratype): Total body length, 2.92. Scute length, 1.87; width, 1.95. Eyemound length, 0.36; width, 0.51; height, 0.41. Leg II length, 8.81. Leg II/scute length, 4.71. Tarsal count, 4–7 and 8–5–5 and 6.

Ovipositor (Figs. 6, 14–17): cuticle smooth, wrinkled laterally; apex with 12 apical setae arranged in 4 triads, 1 pair of subapical dorsal setae, and 1 pair of apical teeth.

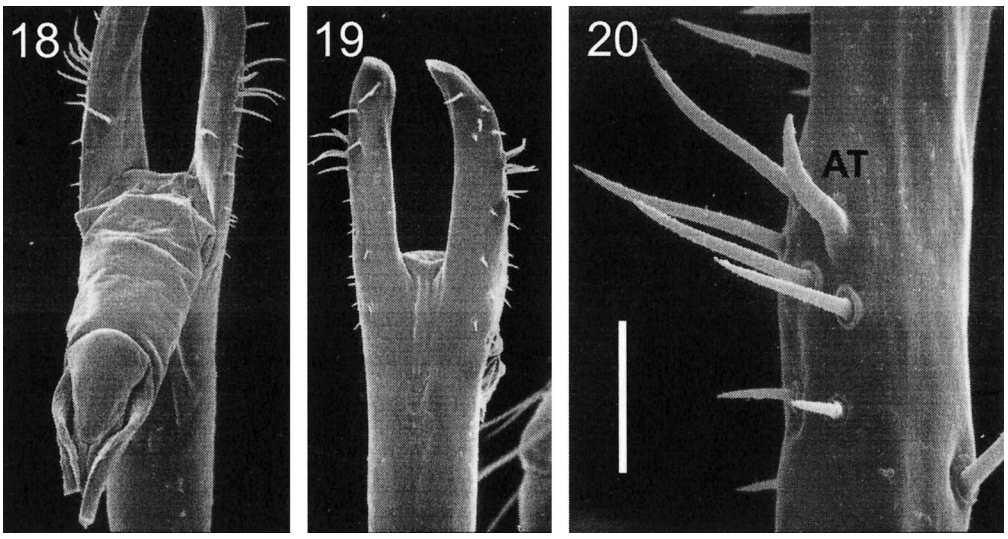
Sexual dimorphism.—The patellar ectal megaspine is slightly shorter in males, being about 1/2 the length (as opposed to about 2/3, in females) of the tibial ectobasal megaspine. Females lack both mesal and ectal tubercles at the proximal megaspine of the palpal femur.

Juveniles.—Two juvenile specimens were collected with the adults, and several others were observed. The later instar is white with slight yellowish pigmentation on the posterior half of the abdomen; integument smooth; chelicerae lacking ectobasal knob; retina and cornea present; palpal megaspines as in adult; and tarsi III and IV with two claws and large aroleum. Measurements: TBL, 1.72; SL, 1.38; SW, 1.28; EML 0.23; EMH 0.21; GOW / SW, 0.16; Leg II, 7.31; Leg II/SL, 5.30; TC, 2–2–3–3.

The other instar is similar in appearance but smaller. Measurements: TBL, 1.31; SL, 1.10; SW, 1.28; Leg II, 7.97; Leg II/SL, 7.25; TC, 2–2–3–3.

Remarks.—This species is known only from a single trailside talus slope of Franciscan sandstone with a dense chaparral canopy on the north slope of San Bruno Mountain ridge. The talus is not a natural exposure but was artificially excavated during the installation of a gas pipeline several decades ago. Collecting at similar talus areas along other sections of this pipeline at San Bruno Mountain, as well as other localities along the central Coast Ranges, has not yielded additional *Banksula*. Specimens were found in the talus cavities along with other phalangodid harvestmen (*Sitalcina californica* (Banks) and *Microcina* sp.) and troglophilic spiders (*Nesticus silvestrii* Fage, *Archoleptoneta schusteri* Gertsch, and *Blabomma* sp.).

Material examined.—All from the type locality: 1 ♀(10 May 1991, D. Ubick); 3 ♂, 3 ♀, 2 juveniles (11 May 1991, T. Briggs, D.

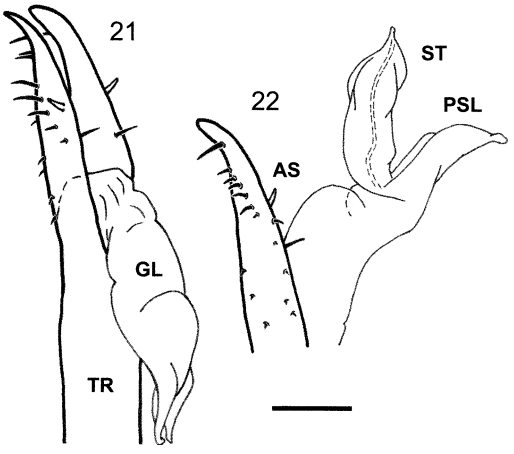


Figures 18–20.—*Banksula incredula*, penis. 18, dorsal view; 19, ventral view; 20, dorsal view of left ventral plate prong showing apical spine (AS). Scale bar: 18, 19 = 150 μm; 20 = 30 μm.

Ubick); 1 ♀(18 Jan. 1992, T. Briggs, W. Rauscher, D. Ubick); 1 ♂, 1 ♀ (26 Jan. 1992, T. Briggs, W. Savary, D. Ubick).

The *californica* species group

Diagnosis.—Members of this group are distinguished from *B. incredula* in being smaller, having a relatively lower and uniform TC of 4—6—5—6, and a palpal femur with only 3 ventrobasal and 1 mesoapical megaspines. They differ from the *melones* group in having a smaller GO, with a GO/SW ratio of 0.2 as opposed to 0.3, and in having sexually dimorphic palpi, with males having enlarged femora and reduced ectal megaspines on the tibia and patella (Fig. 44, 45).



Figures 21–22.—*Banksula incredula*, lateral view of penis. 21, unexpanded glans (GL) and truncus (TR); 22, expanded glans showing stylus (ST), parastylar lobes (PSL), and apical spine (AS). Scale bar = 100 μm.

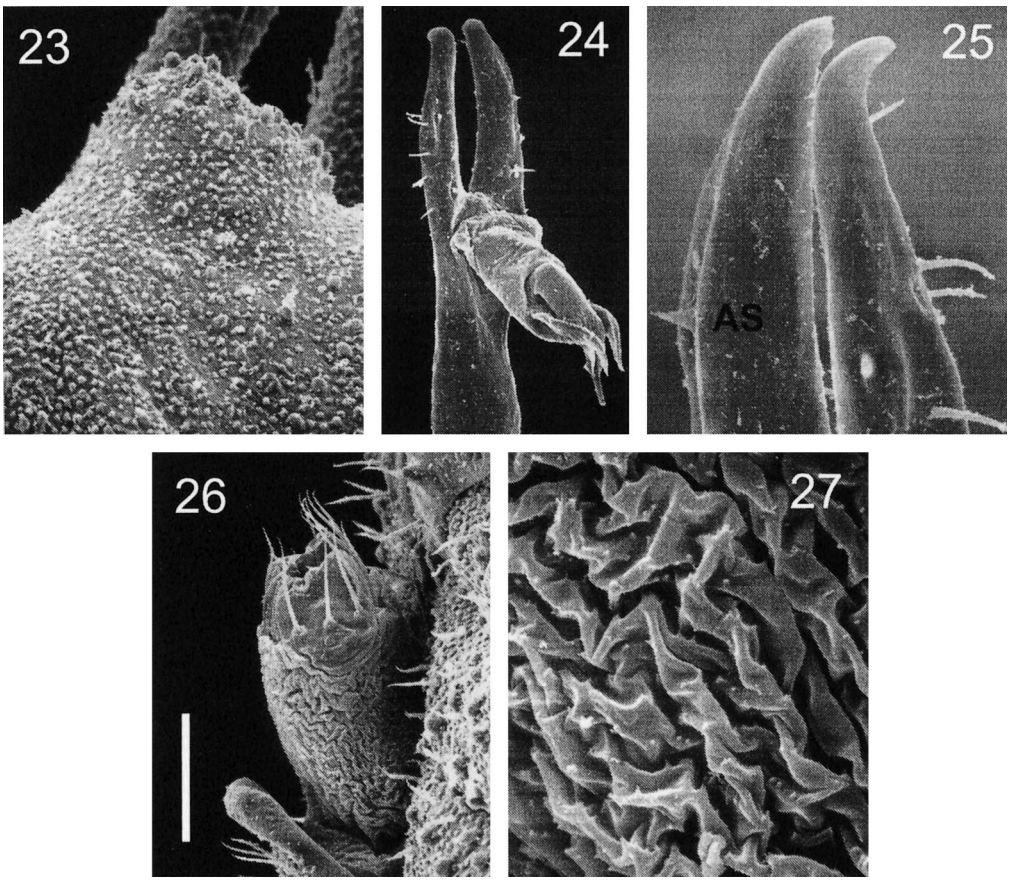
Included species.—*Banksula californica* (Banks 1900), *Banksula galilei* Briggs 1974, *Banksula grubbsi* Briggs & Ubick 1981, *Banksula martinorum* Briggs & Ubick 1981, *Banksula rudolphi* Briggs & Ubick 1981, *Banksula tuolumne* Briggs 1974 and *Banksula tutankhamen* new species.

Variation.—The species of the *californica* group are morphologically very similar, including in details of the genitalia, and were we to use the same criteria of distinctness as for other phalangodids (i.e., *Calicina* and most *Texella*) the number of species here could be reduced to just one. However, given that the species are strongly disjunct, being found in isolated caves, and because of the presence of distinct, if minor, differences in their somatic and genitalic features, we are here recognizing them all as valid.

Distribution.—Known from caves in the Sierran Motherlode Region from Placer to Tuolumne Counties, California.

Banksula galilei Briggs
Figs. 7, 9, 23–27

Banksula galilei Briggs 1974: 6; Briggs & Ubick 1981: 316.



Figures 23–27.—*Banksula galilei*. 23, eyemound of female showing absence of cornea (anterior to left); 24, dorsolateral view of penis; 25, close-up of ventral plate prong showing small apical spine (AS); 26, lateral view of ovipositor; 27, close-up of lateral surface of ovipositor showing microspines. Scale bar: 23, 24, 26 = 100 μm; 25 = 25 μm; 27 = 15 μm.

Diagnosis.—This species differs from others in the *californica* species group by its obliquely truncate eyemound, dark retina, and a short AS.

Additional description.—Eyemound H/L 0.50, eye with dark retina and small cornea. Proximal megaspine of palpal femur with adjacent ectal tubercle.

Male: Proximal megaspine of palpal femur with mesal tubercle at base; palpal patellar ectal and tibial ectobasal megaspines 1/2 length or less than the corresponding spines in females. Penis: AS relatively short (AS/VPP width about 0.2); VPP with 7–9 long setae; VPP distal separation less than prong width.

Female: Proximal megaspine of palpal femur lacking mesal tubercle at base.

Material examined.—All nine known specimens.

Distribution.—Known only from the Lime Rock Caves, near Auburn, Placer County, California.

Banksula californica (Banks)
Fig. 9

Scotolemon californica Banks 1900:200.
Banksula californica (Banks): Roewer 1949:33; Briggs 1974:4; Briggs & Ubick 1981:315.

Diagnosis.—This species differs from others in the *californica* species group in having a low rounded eyemound, eye lacking retina, and female palp with a somewhat reduced ectal tubercle at the base of the proximal megaspine.

Additional description.—Eyemound H/L 0.55, eyes without retina and with small, degenerate cornea. Palpal femur with 5–7 dorsal setiferous tubercles; proximal megaspine with adjacent ectal tubercle.

Male: Proximal megaspine of palpal femur with curved ectal and robust mesal tubercle; palpal patellar ectal and tibial ectobasal megaspines 1/2 length or less than the corresponding spines in females. Penis with VPP distal separation about equal to prong width.

Female: Proximal megaspine of palpal femur lacking mesal tubercle at base; ectal tubercle reduced, not curved at apex. Ovipositors not expanded in the fragile specimens available.

Material examined.—El Dorado County, Alabaster Cave (Marx, MCZ), ♀lectotype, 3 ♂, 1 ♀ paralectotypes.

Distribution.—Known only from Alabaster Cave.

Remarks.—Alabaster Cave has been partially destroyed by mining and as the remaining portions have been sealed off with concrete, it is not possible to determine whether the species still survives.

Banksula grubbsi Briggs & Ubick
Fig. 9

Banksula grubbsi Briggs & Ubick 1981: 319.

Diagnosis.—This species differs from others in the *californica* species group by its obliquely truncate eyemound lacking retina and a low rounded ectal tubercle at the base of the proximal megaspine of the palpal femur.

Additional description.—Eyemound H/L 0.60, eye without retina and with degenerate cornea.

Male: Proximal megaspine of palpal femur with mesal tubercle and low, rounded ectal tubercle at base; palpal patellar ectal and tibial ectobasal megaspines reduced. Penis with VPP distal separation about equal to prong width.

Female: Unknown.

Material examined.—The male holotype.

Distribution.—Known only from Black Chasm Cave, near Volcano, Amador County, California.

Banksula rudolphi Briggs & Ubick
Figs. 9, 28–32

Banksula rudolphi Briggs & Ubick 1981: 316.

Diagnosis.—This species differs from others in the *californica* species group by its relatively tuberculate subconical eyemound, absence of retina, and presence of an ectal tubercle at the proximal megaspine of the palpal femur in both sexes.

Additional description.—Eyemound H/L 0.62, eye lacking retina and with degenerate cornea. Proximal megaspine of palpal femur with adjacent ectal tubercle.

Male: Proximal megaspine of palpal femur with mesal tubercle at base; palpal patellar ectal and tibial ectobasal megaspines 1/2 length or less than the corresponding spines in females. Penis: AS relatively short (AS/VPP width about 0.4); VPP with 9 long setae; VPP distal separation about equal to or wider than prong width.

Female: Proximal megaspine of palpal femur lacking mesal tubercle at base.

Material examined.—The 36 known specimens.

Distribution.—Known only from Chrome Cave, near Pardee Reservoir, Amador County, California.

Banksula tutankhamen new species
Figs. 9, 33–40

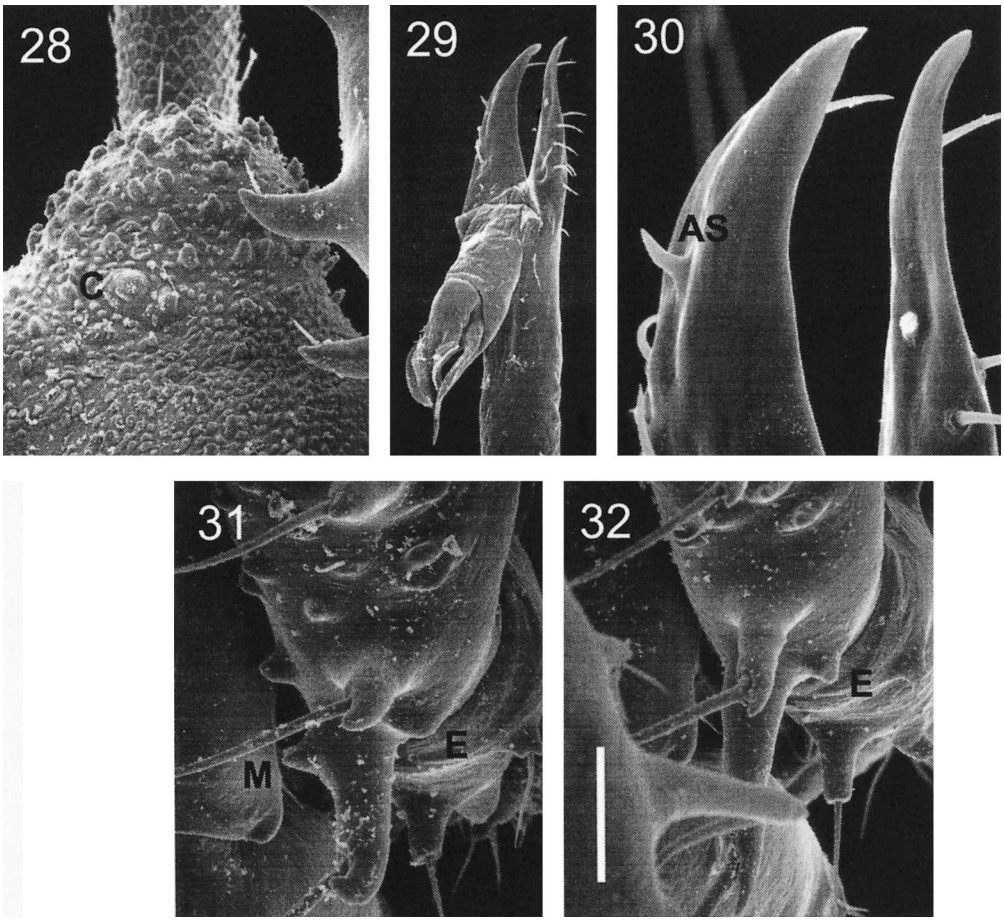
Type.—Male holotype from King Tut Cave, near Cave City and O'Neil Creek, Calaveras County, California (24 Aug. 1991; T. Briggs, D. Cowan, G. Malliet, W. Rauscher, D. Ubick), deposited in CAS.

Etymology.—The species name refers to the type locality.

Diagnosis.—This species differs from all other *Banksula* by its longer legs (having the highest Leg II/Scute length ratio in the genus) and in the tuberculation at the basal megaspine of the palpal femora, where the male has an enlarged or double mesal tubercle and both sexes lack an ectal one.

Description.—Total body length, 1.45–1.54. Scute length, 1.00–1.14. Leg II length, 6.45–6.77. Leg II/Scute length, 5.94–6.45. Tarsal count, 4—6—5—6. (N = 3)

Color yellow to pale yellow. Scute with segmentation delineated by small tubercles, lateral anterior margins with numerous tubercles; eyemound and area behind tuberculate. Eyemound subconical with retina and cornea degenerate. Genital operculum small; GOW/SW, 0.2. Palpal megaspines: femur with 3 ventrobasal and 1 mesodistal; patella with 1 ectal and 2 mesal; tibia with 3 ectal and 3



Figures 28–32.—*Banksula rudolphi*. 28, eyemound of male showing small cornea (C)(anterior to right); 29, dorsolateral view of penis; 30, close-up of ventral plate prong showing medium-sized apical spine (AS); 31, ventrobasal portion of male palpal femur showing mesal (M) and ectal (E) tubercles at basal megaspine; 32, ventrobasal portion of female palpal femur showing ectal (E) tubercle at basal megaspine. Scale bar: 28, 29, 31, 32 = 100 μm; 30 = 25 μm.

mesal; tarsus with 2 ectal and 2 mesal. Palpal femur with 7 setiferous tubercles dorsally, apical pair transversely to subtransversely arranged. Proximal megaspine of palpal femur lacking ectal tubercle (except on one palp of a single male).

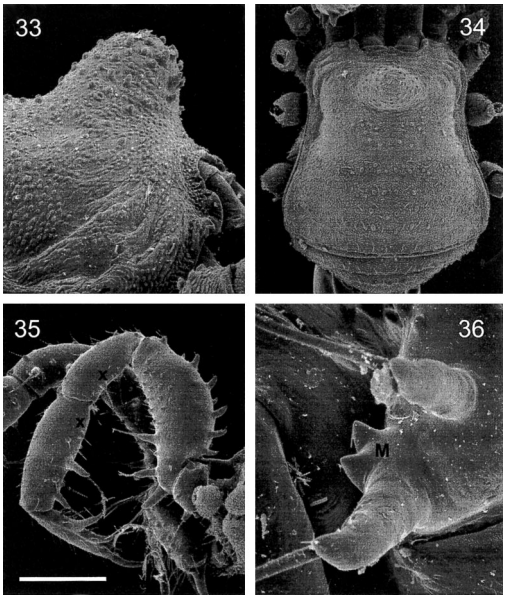
Male (holotype): Total body length, 1.45. Scute length, 1.09; width, 1.18. Eyemound length, 0.23; width, 0.41; heigth, 0.18. Leg II length, 6.68. Leg II/Scute length, 6.13. Proximal megaspine of palpal femur with enlarged or double tubercle mesally.

Penis (Figs. 37–40): VPP curved inward, with maximum separation greater than prong width; AS distally curved, as long as longest VPP setae; with 10 long setae on each prong. Glans with apical stylar region consisting of triangular pointed stylus and a pair of curved, apically pointed PSL.

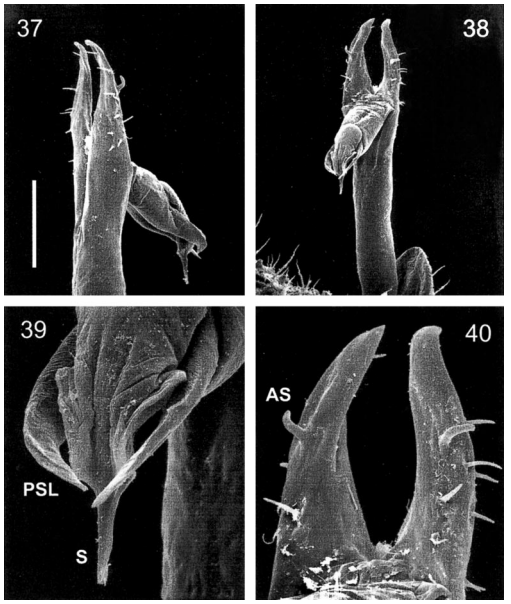
Female (paratype): Total body length, 1.54. Scute length, 1.00; width, 0.91. Eyemound length, 1.54. Scute length, 1.00; width, 0.91. Eyemound length, 0.27; width, 0.32; heigth, 0.18. Leg II length, 6.45. Leg II/Scute length, 6.45.

Ovipositor not expanded due to the fragile condition of the single known female specimen.

Sexual dimorphism.—Male with enlarged or double mesal tubercle at base of proximal megaspine of palpal femur; tubercles absent in female. The palpal patellar ectal and tibial



Figures 33–36.—*Banksula tutankhamen*, male. 33, anterior of scute, lateral view, with eyemound showing absence of cornea; 34, dorsal view of body; 35, lateral view of left palp showing reduced ectal megaspines on patella and tibia (X); 36, ventrobasal view of left palpal femur showing absence of ectal end presence of double mesal tubercle (M) at ventral megaspine. Scale bar: 33 = 150 μm; 34, 35 = 430 μm; 36 = 75 μm.



Figures 37–40.—*Banksula tutankhamen*, penis. 37, lateral view; 38, dorsal view; 39, close-up of glans showing stylus (S) and parastylar lobes (PSL); 40, dorsal view of ventral plate prongs showing curved apical spines (AS). Scale bar: 37 = 100 μm; 38 = 150 μm; 39 = 30 μm; 40 = 43 μm.

ectobasal megaspines are shorter in males, being at most 1/2 the length of those in females.

Juveniles.—The single juvenile collected with the adults is an early instar with depigmented and smooth integument; chelicerae lacking ectobasal knob; with gray retina and small cornea present; palpal megaspines as in adult except that tibia has 1 ectal and 2 mesal megaspines, and base of femur without mesal or ectal tubercle; tarsi III and IV with 2 claws and small aroleum; TC, 1–1–2–2.

Remarks.—Collected from the steep inner chamber of the dark zone of King Tut Cave in the Calaveras Limestone.

Material examined.—All from the type locality: 2♂, 1 ♀, 1 juvenile (same data as holotype), CAS.

Distribution.—Known only from King Tut Cave, Calaveras County, California.

Banksula martinorum Briggs & Ubick
Figs. 9, 41–45

Banksula martinorum Briggs & Ubick 1981:318.

Diagnosis.—This species differs from others in the *californica* group by the presence of a thick blunt AS on the penis and the absence of an ectal tubercle at the proximal megaspine of the palpal femur in females.

Additional description.—Eyemound H/L 0.68; eye with degenerate retina and cornea.

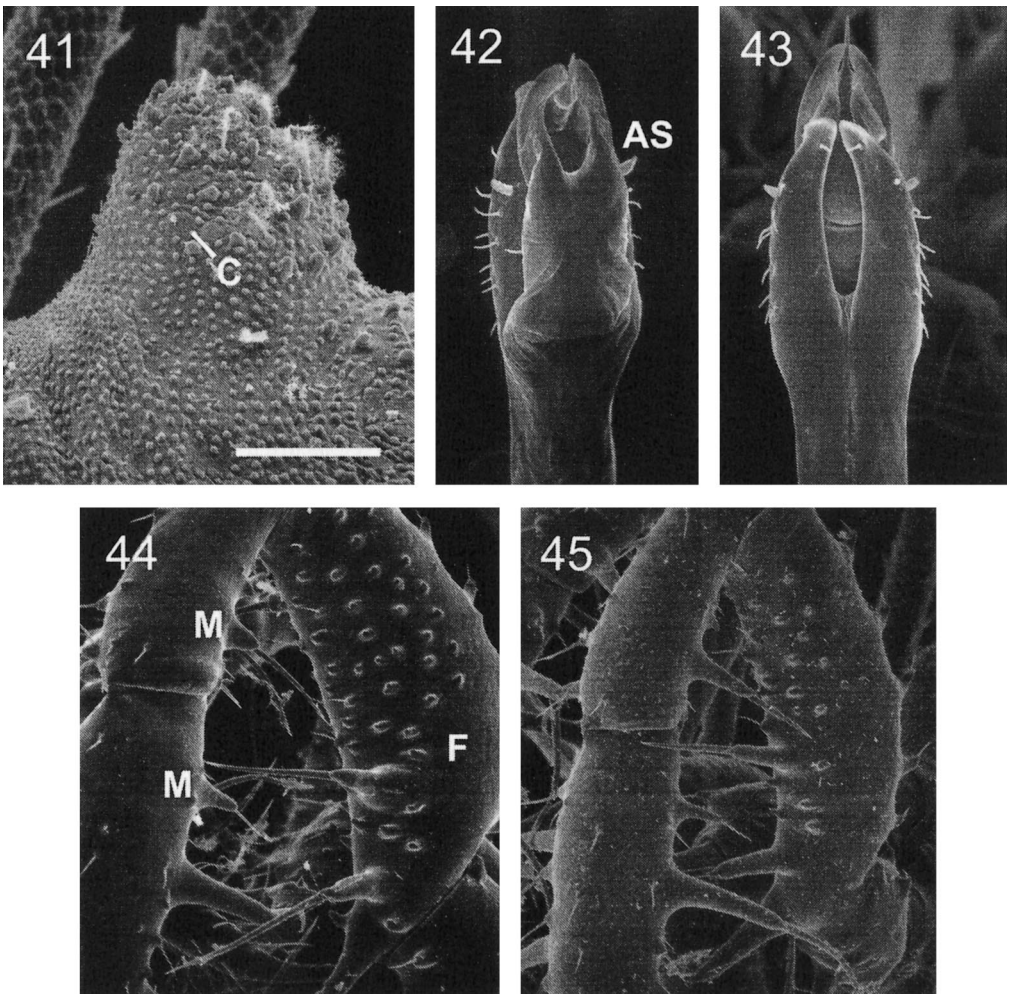
Male: Proximal megaspine of palpal femur with mesal and ectal tubercles at base; palpal patellar ectal megaspine 1/2 length or less than the corresponding spine in females. Penis: AS truncate; AS/VPW ratio 0.5; VPP with 11 long setae. Distal separation of VPP less than prong width.

Female: Proximal megaspine of palpal femur lacking tubercles at base.

Material examined.—All 15 known specimens.

New record.—Calaveras County: Heater Cave, 8 km N Columbia, 6 ♂, 2 ♀, 2 juveniles (15 Oct. 1994, T. Briggs, W. C. Rauscher, D. Ubick).

Distribution.—Known only from Heater Cave, 8 km N Columbia, Calaveras County, California.



Figures 41–45.—*Banksula martinorum*. 41, eyemound of female showing degenerate cornea (C), anterior to left; 42, dorsal view of penis showing thick apical spine (AS); 43, ventral view of penis; 44, left male palp, ectal view, showing enlarged femur (F) and reduced ectal megaspines (M) on patella and tibia; 45, left female palp, ectal view, showing unmodified femur and ectal megaspines on patella and tibia. Scale bar: 41–43 = 100 μm; 44, 45 = 250 μm.

Banksula tuolumne Briggs
Figs. 9, 46–49

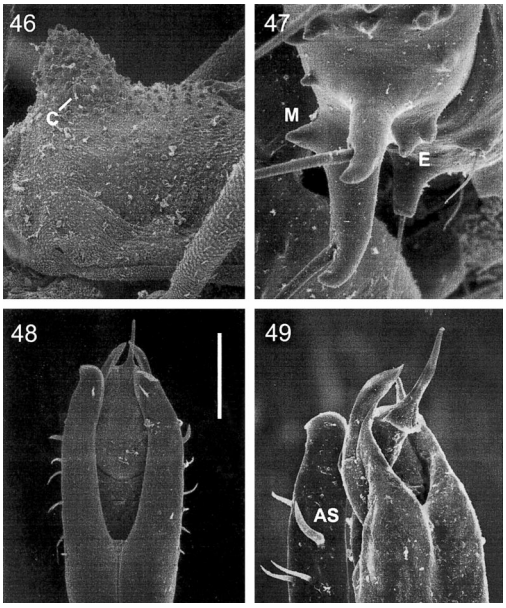
Banksula tuolumne Briggs 1974: 5; Briggs & Ubick 1981: 316.

Diagnosis.—This species differs from others in the *californica* group by the presence of a rounded double ectal tubercle at the base of the proximal megaspine on the palpal femur in males and the reduced proximal ectal megaspine of the palpal tibia in females.

Additional description.—Eyemound H/L 0.69; eye with degenerate retina and cornea. Proximal ectal megaspine on palpal tibia less than 1/2 length of distal ectal one.

Male: Proximal megaspine of palpal femur with robust mesal and rounded double ectal tubercles at base; palpal patellar ectobasal megaspine 1/2 length or less than the corresponding spines in females. Penis: AS/VPW ratio 0.7; VPP with 7–9 long setae. Distal separation of VPP equal to or wider than prong width.

Female: Palpal tibia with reduced ectal proximal megaspine; proximal megaspine of



Figures 46–49.—*Banksula tuolumne*, male. 46, anterior of scute with eyemound showing cornea (C); 47, ventrobasal portion of palpal femur showing mesal tubercle (M) and double ectal tubercle (E) at ventrobasal megaspine; 48, ventral view of penis; 49, dorsolateral view of penis showing curved apical spine (AS). Scale bar: 46 = 250 μm; 47 = 100 μm; 48 = 75 μm; 49 = 43 μm.

femur with acute ectal tubercle and lacking mesal tubercle at base.

Material examined.—All 18 known specimens.

New record.—Tuolumne County: Tuolumne Crystal Cave, 8 mi SE Tuolumne, 2♂, 4 ♀, 1 juvenile (16 Jun. 1979, D. Cowan, J. Espinal).

Distribution.—Known only from Tuolumne Crystal Cave, near Tuolumne, Tuolumne County, California.

The *melones* species group

Diagnosis.—Members of this species group are distinguished from *B. incredula* in having a relatively lower TC of 4—6—5–6 and a palpal femur with only 3 ventrobasal and 1 mesoapical megaspines. They differ from members of the *californica* group in having a larger GO, with a GO/S width ratio of 0.3 as opposed to 0.2 (Fig. 8), and in lacking sexually dimorphic palpi.

Included species.—*B. grahami* and *B. melones*.

Remarks.—These two species, in contrast to those of the *californica* group, have distinctive genitalia, and are the only species in the genus with a broadly parapatric distribution. Also unique in the *melones* group, until just a couple of decades ago, was the presence of sympatry in *Banksula* species. *Banksula melones* and *B. grahami* both occurred in Mclean's Cave until it was flooded by the damming of the Stanislaus River. Prior to the flooding, individuals of both species, along with about 30 other cavernicole species, were transplanted to a nearby limestone mine (Transplant Mine) in 1975 and again in 1978 (Elliott 1978). About 90 individuals of *B. melones* and over 200 of *B. grahami* were transplanted. When we visited the Transplant Mine in 1986 it appeared that one species had become extinct as we encountered only a thriving population (50 individuals) of the larger species, *B. melones* (Briggs 1987). And more recently, in 1996, even that species seems to be on the decline as we observed only six individuals.

Distribution.—Known only from caves and mines in the Sierran Motherlode Region along the Stanislaus River in Calaveras to Tuolumne Counties, California.

Banksula melones Briggs
Figs. 8, 9, 50–57

Banksula melones Briggs 1974: 8; Briggs, 1987: 12; Briggs & Ubick 1981: 320; Elliott 1978: 6.

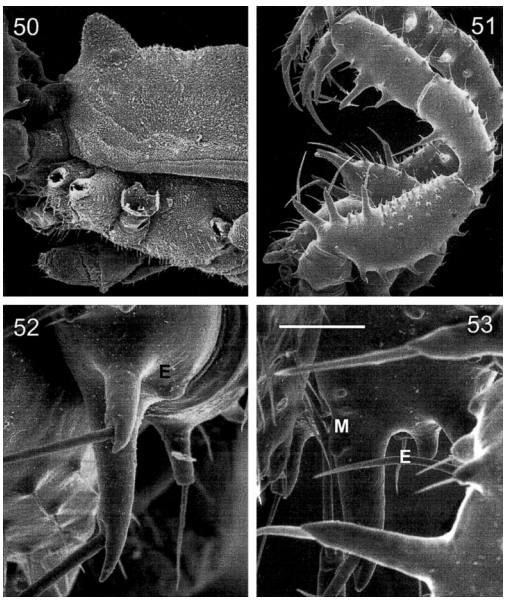
Diagnosis.—This species differs from *B. grahami* in having a larger body size, well developed eyes, and pointed PSL on the glans penis.

Additional description.—Male: Proximal megaspine of palpal femur with mesal and large ectal tubercles basally. Penis: VPP broad with narrow separation, less than 0.5 prong width; AS straight, pointed, and of moderate length, about 0.5 prong width; with 9 setae, slightly shorter than AS, on each prong. Glans with broad rounded stylus and curved pointed PSL.

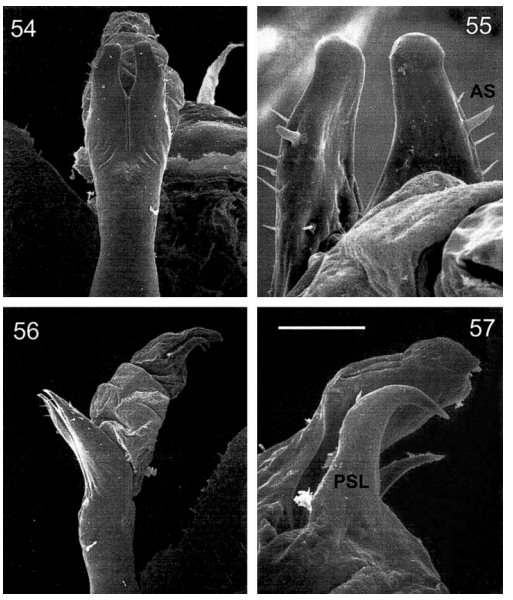
Female: Proximal megaspine of palpal femur with rounded ectal tubercle, lacking mesal tubercle. Ovipositor with sparsely microspined cuticle; without AT at apex.

Material examined.—All 145 known specimens.

New records.—Tuolumne County: McLean's Cave, 4.5 km N Columbia, 3 ♂, 2 ♀



Figures 50–53.—*Banksula melones*, female from McLeans Cave (50–52), male from Lost Piton Cave (53). 50, anterior half of body; 51, lateral view of palpi; 52, ventrobasal part of left palpal femur showing ectal tubercle (E) of ventrobasal megaspine; 53, ventrobasal part of left palpal femur showing ectal (E) and mesal (M) tubercles of ventrobasal megaspine. Scale bar: 50, 51 = 430 μm; 52, 53 = 100 μm.



Figures 54–57.—*Banksula melones*, male from Lost Piton Cave. 54, ventral view of penis; 55, dorsal view of ventral plate showing stout apical spines (AS); 56, lateral view of penis showing expanded glans; 57, close-up of glans tip showing wide stylus and hook-like parastylar lobes (PSL). Scale bar: 54, 56 = 200 μm; 55 = 60 μm; 57 = 43 μm.

(5 Mar. 1981, G. Hunter, D. Kavanaugh, D. Ubick); Transplant Mine, 3 km N Columbia, 9 ♂, 5 ♀ (11 Jun. 1982, T. Briggs); 1 ♀ (6 Dec. 1986, T. Briggs, V. Lee, D. Ubick).

Distribution.—Known from caves, and one population transplanted to a mine (Briggs 1987; Elliott 1978), along the Stanislaus River in Calaveras and Tuolumne Counties, California.

Banksula grahami Briggs
Figs. 9, 58–66

Banksula grahami Briggs 1974: 7; Briggs 1987: 12; Briggs & Ubick 1981: 320; Elliott 1978: 6.
Banksula elliotti Briggs & Ubick 1981: 319. **New synonymy.**

Diagnosis.—This species differs from *B. melones* in having a smaller body size, at least somewhat reduced eyes, and rounded PSL on the glans penis.

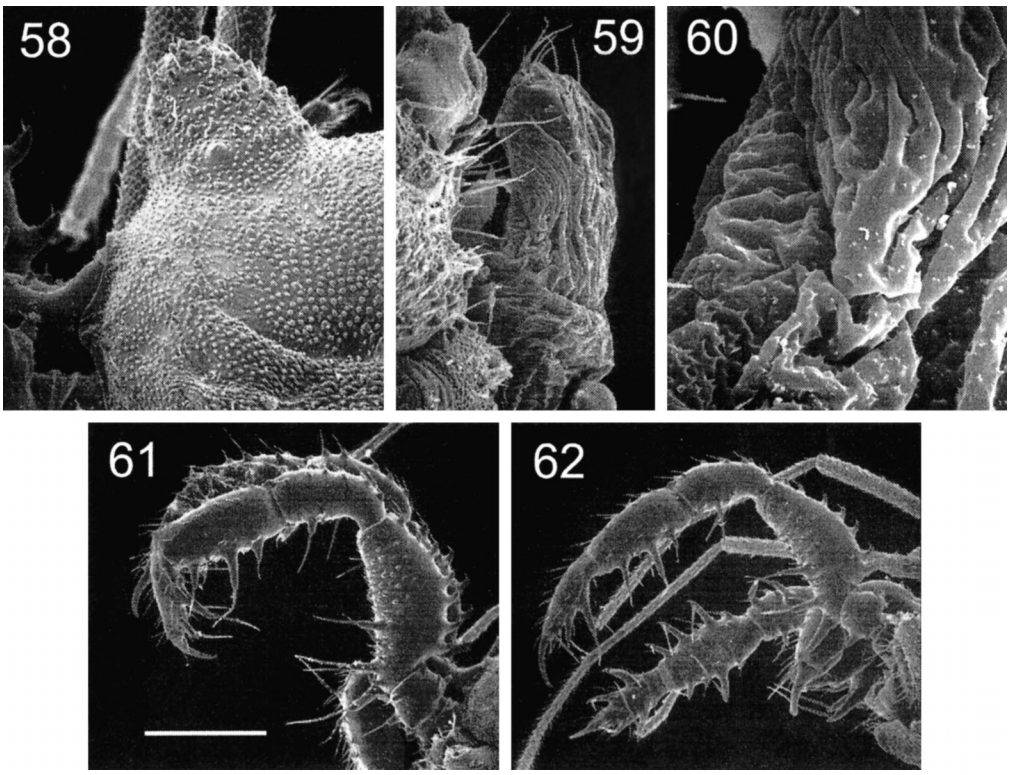
Additional description.—Eye with cornea and retina small to vestigial to absent. Proximal megaspine of palpal femur with curved ectal tubercle basally.

Male: Palpal femur with mesal tubercle at base of proximal megaspine. Penis: VPP broad with narrow separation, from less than 0.5 to 0.2 prong width; AS straight and very short, about 0.2 prong width; with about 9 setae, subequal to AS length. Glans with broad rounded stylus and curved apically rounded PSL.

Female: Ovipositor with densely microspined cuticle; without AT at apex.

Variation: About 20% of the females have a small mesal tubercle at the basal megaspine on one or both palpi.

Remarks.—The diagnostic character for recognizing *B. elliotti*, the absence of eyes, does not stand up to close scrutiny. Although the majority of specimens from the northeastern most locality (Pinnacle Point Cave) show no trace of eyes, those at *elliotti*'s southern end (Rabbit Hole, Grapevine Gulch, and Digger Pine Caves) show degenerate although clearly vestigial eyes, similar to the condition in some *grahami* populations (Banksula Cave). There appears to be a clinal variation taking place with the general trend of increas-



Figures 58–62.—*Banksula grahami*, male from Crystal Palace Cave (58, 61), female from Banksula Cave (59, 60, 61). 58, lateral view of anterior half of scute; 59, lateral view of ovipositor; 60, close-up of ovipositor showing microspines; 61, 62, lateral view of palpi. Scale bar: 58 = 180 μm; 59 = 150 μm; 60 = 30 μm; 61 = 430 μm; 62 = 530 μm.

ing troglomorphy from the SW part of the *grahami* distribution (Moaning to Carlow's Cave) to the NE sector (Pinnacle Point Cave). Similar clinal variation has been recorded for *Texella*, especially *T. reddelli* and *T. reyesi* (Ubick & Briggs 1992).

Material examined.—All 152 known specimens.

New record.—Tuolumne County: McLean's Cave, 4.5 km N Columbia, 3 ♂, 2 ♀ (5 Mar. 1981, G. Hunter, D. Kavanaugh, D. Ubick).

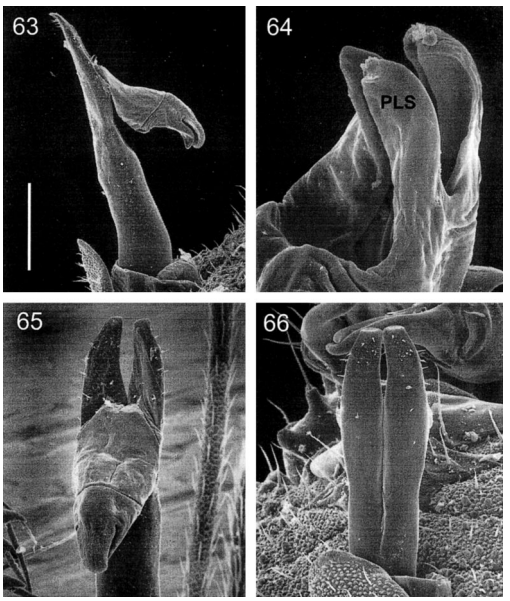
Distribution.—Known from caves and mines along the Stanislaus River in Calaveras and Tuolumne Counties, California.

PHYLOGENY

The relationship of *B. incredula* to other *Banksula* was examined using outgroup comparison. *Calicina mariposa* (Briggs) and *Sitalcina californica* (Banks) were used as examples of taxa with unmodified (entire) ventral plates. For the genera with bifurcate ventral plates, the ''bifurcate complex'', we used *Texella bifurcata* (Briggs) and a *Crosbyella* species, the latter to represent the eastern Nearctic genera. We found 18 characters useful in inferring relationships within *Banksula* and to other Phalangodidae. These are presented in tabular form in Table 1 and elaborated below.

Character 1. Glans type. Of the two types of glans construction in Phalangodidae, the folding glans is found in the vast majority of species. This is believed to be the derived condition based on its greater complexity and is a synapomorphy for all Nearctic genera except *Calicina* (Ubick & Briggs 1989).

Character 2. Ventral plate type. An unmodified, or entire, ventral plate is found in most western Nearctic and all Palearctic phalangodids. The ventrally incised, or bifurcate, condition is considered derived and a synapomorphy for *Banksula*, *Texella*, and all eastern



Figures 63–66.—*Banksula grahami*, male from Crystal Palace Cave. 63, lateral view of penis; 64, ventroapical view of glans showing rounded parastylar lobes (PSL); 65, dorsal view of penis; 66, ventral view of penis. Scale bar: 63 = 200 μm; 64 = 43 μm; 65, 66 = 150 μm.

Nearctic phalangodids (Ubick & Briggs 1992).

Character 3. Ventral plate position. In *Banksula* the ventral plate prongs are ventrally positioned, as they are in the unmodified (entire) ventral plate. The lateral placement of the VPP is thus as an apparent synapomorphy for *Texella* and the eastern genera (Ubick & Briggs 1992).

Character 4. Ventral plate with apical spine. An inarticulate apical spine is present on the ventral plate prongs of all *Banksula* and *Texella* species but has not yet been discovered, even in vestigial form, in the eastern taxa. This character contradicts the grouping by the previous one by appearing to be a synapomorphy for *Banksula* and *Texella* (Ubick & Briggs 1992).

Character 5. Palpal femur with setiferous dorsal tubercles. These tubercles are not known from other phalangodids apart from *Banksula* (Figs. 2, 3), although similar but asetose tubercles may occur in some species of *Sitalcina* (Figs. 4, 5).

Character 6. Ovipositor with apical teeth. A pair of apical teeth occurs on the ovipositor of *B. incredula* (Fig. 15) and most *Texella* species, including *T. bifurcata* (Ubick & Briggs 1992: fig. 19). The presence of these teeth in *B. incredula* is interpreted as a plesiomorphic retention and their absence a synapomorphy for the remaining *Banksula*.

Character 7. Ventral plate setal length. In *T. bifurcata* and most other species of *Texella* the setae on the ventral plate are long, at least as long as the width of a ventral plate prong (Ubick & Briggs 1992: fig. 15). In *B. incredula*, the setae are about equal to the VPP width (Fig. 20), in the *B. californica* group, the setae are about one-half VPP width (Fig. 24), and in the *B. melones* group they are about one-third or less (Fig. 55). Reduction in size of ventral plate setae in *Banksula* appears to be derived.

Character 8. Meso-apical megaspines of palpal femur. *B. incredula* has 2 meso-apical megaspines on the palpal femur (Fig. 11), whereas other *Banksula* have only one. The former appears to be the generalized condition, perhaps another synapomorphy for the bifurcate complex of genera, and is found in most species of *Texella* and the eastern genera. The loss of one meso-apical megaspine is thus synapomorphic for the remaining *Banksula* species.

The above three characters are plesiomorphic retentions in *B. incredula*. In addition to these we have identified six characters that appear to be autapomorphies for *B. incredula*, further attesting to its uniqueness and arguing for its placement in a separate species group:

Character 9. Ovipositor cuticle texture. *B. incredula* females have a smooth ovipositor surface (Fig. 17), in contrast to the spiny cuticle of other *Banksula* (Fig. 27, 60), *Texella* (Ubick & Briggs 1992: fig. 21), *Sitalcina* (Ubick & Briggs 1989: fig. 1d), and *Calicina* (Ubick & Briggs 1989: fig. 5).

Character 10. Ventral megaspines on palpal femur. The presence of four ventrobasal megaspines on the palpal femur in *B. incredula* (Fig. 12, 13), is unique in the Nearctic phalangodids that have only three (as in *T. bifurcata* in Ubick & Briggs 1992: fig. 21).

Character 11. Eyemound height. *B. incredula* has a high pointed eyemound (Fig. 10). Measured as a ratio of height/length, the eyemound in *B. incredula* (1.0) is greater than in other *Banksula* (0.6–0.8), *T. bifurcata* (0.7),

Table 1.—Character matrix for *Banksula* species groups and selected Nearctic phalangodid genera. Bold character states are derived. (See text for explanation.)

	Calicina mariposa	*Sitalcina californica*	*Banksula incredula*	*Banksula californica*	*Banksula melones*	*Texella bifurcata*	*Crosbyella* sp.
1.—glans type	telescoping	folding	folding	folding	folding	folding	folding
2.—ventral plate	entire	entire	bifurcate	bifurcate	bifurcate	bifurcate	bifurcate
3.—vp position	ventral	ventral	ventral	ventral	ventral	lateral	lateral
4.—vp w/as	no	no	yes	yes	yes	yes	no
5.—p fm w tubs	no	no	yes	yes	yes	no	no
6.—ovip w at	no	no	yes	no	no	yes	no
7.—vp setal length	short	short/long	long	short	very short	long	short
8.—mes mgsp p fm	1–	2–	2–	1–	1–	2–	2–
9.—ovip cuticle	spiny	spiny	smooth	spiny	spiny	spiny	?
10.—vent mgsp p fm	3–	3–	4–	3–	3–	3–	3–
11.—eyemound h/1	<1	1–	1–	<1	<1	<1	<1
12.—leg II/scute	2.4–	2.6–	4.6–5.6	4.2–5.2(–6.4)	3.6–4.7	2.6–3.3	3.4–
13.—tarsal count	3–5–5–5	3–5–5–5	>4–6–5–6	4–6–5–6	4–6–5–6	<3–5–5–5	4–6–5–6
14.—body length	<1.5	1.5–2.5	>2.5	1.5–2.5	1.5–2.5	1.5–2.5	>2.5
15.—m p fm	normal	normal	normal	enlarged	normal	normal	normal
16.—ect mgsp m p	normal	normal	normal	reduced	normal	normal	normal
17.—go/scute w	0.2–	0.2–	0.2–	0.2–	0.3–	0.2–	0.2–
18.—stylus width	thin	thin	thin	thin	fat	thin	thin

and most other nearctic phalangodids (except *Sitalcina californica*, but not other *Sitalcina*).

Character 12. Leg II/scute length. The relative leg length (measured as Leg II length/Scute length) of *B. incredula* (4.6–5.6) is greater than that of *C. mariposa* (2.4), *S. californica* (2.6), *T. bifurcata* (2.6–3.3), and *Crosbyella* (3.4). It is also greater than or as large as most species of *Banksula* (3.6–5.2), except that of *B. tutankhamen* (6.0–6.4).

Character 13. Tarsal count. The tarsal count in *B. incredula* varies from 4–7–5–6 to 5–9–5–6 and is greater than in other *Banksula* species, where it is a constant 4–6–5–6. It is also higher than in *Calicina mariposa* (3–5–5–5), *Sitalcina* (3–5–5–5), *Crosbyella* (4–6–5–6), and the basal species of *Texella* (3–5–4–5).

Character 14. Body length. The body length of *B. incredula* (2.6–3.0 mm) is significantly larger than that of other *Banksula* (1.5–2.2), *C. mariposa* (1.4–1.5), *S. californica* (1.4–1.9), *T. kokoweef* (1.7–1.8) and *T. bifurcata* (1.5–2.1), but is subequal to that of *Crosbyella* species.

The above three characters seem to be linked. Certainly in troglobitic opilionids both leg hypertrophy and increased tarsal counts are strongly correlated. Hypertrophy of legs and other appendages is a common occurrence in cavernicole animals. In our studies of phalangodids, we have examined numerous instances of this phenomenon in *Calicina* (Ubick & Briggs 1989), *Texella* (Ubick & Briggs 1992), and *Sitalcina* (Briggs 1968). In all instances, we found that the appendages of cavernicole species (or populations) are relatively longer than those of their epigean counterparts and in troglobitic forms, longer than those of their troglophilic relatives. In *B. incredula* we now have an interesting example of a leg hypertrophy that is not a consequence of troglomorphy and which, therefore, requires a different explanation. Even were we to allow that the species' talus habitat is sufficiently cave-like, the harvestman is nonetheless endowed with well-developed eyes and dark pigmentation. A more plausible scenario, however, is that this is an example of allometric growth and that the increased appendage length and tarsal count is a consequence of greater body size.

Character 15. Male palpal femur. In the *Banksula californica* species group, but not in other *Banksula*, the male palpal femur is enlarged, being thicker than the female's.

Character 16. Ectal megaspines on male palp. Also unique to the *B. californica* group is a sexual dimorphism in which males have reduced mesal megaspines on the palpal patella and tibia (Fig. 44, 45).

Character 17. Genital operculum size. The *B. melones* group is most readily defined on the basis of its enlarged genitalia. Measured in terms of the relative size of the genital operculum, the GO/S width is about 0.3 in the *melones* group (Fig. 8), but only 0.2 in the *incredula* (Fig. 6) and *californica* groups (Fig. 7).

Character 18. Stylus width. In most phalangodids the stylus is slender, except for the *B. melones* group where it is very broad (Figs. 57, 64).

Our interpretation of these characters place the *melones* and *californica* groups as sisters and derived relative to the *incredula* group. The position of *Banksula* within the bifurcate complex is not yet resolved due to character discordance but, because of its relatively simple glans and ventrally positioned VPP, the genus is most probably basal within the complex.

The relationships of the species groups are presented as an area cladogram (Fig. 9). *Banksula* is endemic to California with the most derived groups restricted to the Sierra Nevada and the basal *incredula* group currently known from a single coastal locality. Upon examining the distributions, an immediate difference between the two Sierran groups becomes apparent. The seven species of the *californica* group are spread across a wide area of territory and each species is known from a single isolated cave. By contrast, the two species of the *melones* group, which exhibit a parapatric boundary, are known from a total of over 30 caves, all clustered in a small area.

As mentioned earlier, species in the *californica* group show little variation of the male reproductive structures. Although there are differences in the VPP placement and armature among these species, their glans morphology is remarkably uniform (compare Figs. 24, 29, 38, 43). In the *melones* group, however, the two species are readily recognized by the form of the glans (Figs. 57, 64). Why this difference? This may well be an example, on one hand, of morphological con-

stancy in consequence of isolation and, on the other, of genitalic divergence in consequence of close proximity. We have encountered a similar trend in *Texella*, with the genitalic homogeneity of the isolated troglobitic species of the *mulaiki* group (Ubick & Briggs 1992, figs. 85–108) compared to the genitalic exuberance of the largely epigean *spinoperca* group (figs. 168–200).

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