



The milliped genus *Tidesmus* Chamberlin, 1943 (Polydesmida: Macroster- nodesmidae)

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Abstract

The family Macrosternodesmidae is redefined and recorded from western North America. Four small-bodied species in Arizona and California, USA, and Baja California Norté, Mexico, are assigned to *Tidesmus* Chamberlin 1943; *Phreatodesmus* and *Oodedesmus*, both authored by Loomis, 1960, are placed in synonymy. *Phreatodesmus torreyanus* Loomis, 1960 and *O. variabilis* Loomis, 1960, are transferred into *Tidesmus* as valid species; *P. cooki* Loomis, 1960, is a synonym of *T. episcopus* Chamberlin, 1943, the type species, and *P. dentatus* Loomis, 1960, is a synonym of *P. torreyanus*. *Brachydesmus hastingsus* Chamberlin, 1941, also is referable to *Tidesmus*; a topotypical male is needed to establish its identity in the absence of authentic type specimens. *Tidesmus hubbsi* Chamberlin, 1943, based on unidentifiable females, is geographically segregated and incompatible with the otherwise coherent generic distribution. A topotypical male is also necessary to determine its identity; for now, we remove *hubbsi* from *Tidesmus* and leave it unassigned.

Key words: Macrosternodesmidae, Nearctodesmidae, *Tidesmus*, *Oodedesmus*, *Phreatodesmus*, California, Arizona, Baja California Norté

Introduction

Because they lack the functional desiccation barrier of an external waxy cuticle, millipeds primarily inhabit moist environments. Diversity diminishes as habitats become drier, but a few milliped species thrive in deserts. The southwestern United States (US) and northwestern Mexico harbor a surprising diversity of diplopods in, primarily, three families—Spirostreptidae (Spirostreptida), Atopetholidae (Spirobolida), and Schizopetalidae (Callipodida)—all of which have received initial alpha-taxonomic treatments (Hoffman & Orcutt 1960, Causey 1975, Shelley 1996a). Herein and in planned future contributions, we address a fourth component of the North American desert milliped fauna, the minute representatives of the order Polydesmida that have been labeled "micro-nearctodesmids" (Shelley 1994, Shelley & Shear 2006) and formally placed in the families Polydesmidae (Chamberlin 1943, Chamberlin & Hoffman 1958), Vanhoeffeniidae (Loomis 1960), Fuhrmannodesmidae (Hoffman 1999; Golovatch 1994), and "Trichopolydesmoidea of uncertain family position" (Hoffman 1980). They are active primarily in cooler seasons of the year in summit forests on inselberg mountains or in close proximity to springs and other water sources.

Tidesmus Chamberlin 1943 was proposed in the Polydesmidae (Polydesmida) to accommodate two new species in the western US that Shear (1969) thought were not congeneric and possibly not even confamilial: *T. episcopus*, the type species, represented by males and females from Los Angeles, and *T. hubbsi*, based solely on females from an unnamed cave in Cave Valley, Lincoln Co., Nevada. Both were cited in Chamberlin and

Hoffman's (1958) checklist but escaped notice, along with the genus, in Hoffman's (1999) compendium. In placing *Tidesmus* under "Trichopolydesmoidea of uncertain family position," Hoffman (1980) indicated that he did not consider it a polydesmoid, but he could not decide among the three New World trichopolydesmoid taxa (sensu Shelley (2003a), which are difficult to distinguish: Macrosternodesmidae, Nearctodesmidae, and Fuhrmannodesmidae (= Vanhoeffeniidae). Of these taxa, only Nearctodesmidae has been revised (Shelley 1994) and rediagnosed (Shelley & Shear 2006); Fuhrmannodesmidae, a "dumping ground" for small Neotropical trichopolydesmoids, is not known north of Mexico and is irrelevant to our considerations even though Golovatch (1994) thought three southwestern US genera—*Harpogonopus*, *Oodedesmus*, and *Phreatodesmus*, all by Loomis (1960)—belong here. *Harpogonopus*, often misspelled as "*Harpagonopus*," really belongs to the Nearctodesmidae (Shelley 1994), and our research shows that *Oodedesmus* and *Phreatodesmus* are representatives of the Macrosternodesmidae and, moreover, synonyms of *Tidesmus*. We therefore confirm the first author's suggestion of nearly 40 years ago (Shear 1969) that *Tidesmus* may be a senior synonym of *Phreatodesmus*.

In the past 14 years, the second author (Shelley 1993, 1996b, c, 1997, 2003b) has reviewed poorly described representatives of the Polydesmidae from the western US and proposed two additional genera. Subsequent research has revealed that the Macrosternodesmidae, represented by *Chaetaspis* Bollman, 1887, east of the Central Plains (Hoffman 1999, Lewis 2002), also occurs west of the Continental Divide. Hoffman (1975, 1980, 1982) and Simonsen (1990) redefined Macrosternodesmidae, and we refine these concepts before addressing *Tidesmus* and its components. Hoffman (1982) submerged Nearctodesmidae under Macrosternodesmidae, and Simonsen (1990) considered Nearctodesminae as a subfamily under the latter. Shelley (1994) returned Nearctodesminae to familial status, action that was supported by Hoffman (1999); more recently, he (Shelley 2003a) again recognized it as a family, citing the paucity of material and the absence of consideration of gonopodal features by Simonsen (1990) as the basis for discounting this author's decision. We cannot now resolve the "Macrosternodesmidae-Nearctodesmidae" controversy and defer the matter to future studies.

As noted by Shelley & Shear (2006), the composition of the Polydesmidea in western North America has been greatly underestimated because of sporadic sampling and inattention to small, soil and litter-dwelling forms that are active primarily in winter; the same holds for trichopolydesmoids. Consequently, this contribution is based on just 20 samples, only 12 with adult males, and gonopods are missing from the lone males in three samples. Fortunately, authentic male type specimens, which conclusively support the new synonymies and assignments to the Macrosternodesmidae, are available for all but two species, *T. hubbsi* and *Brachydesmus hastingsus*. In the ensuing species accounts, we present a full description for *T. variabilis*, n. comb., whose specimens are in the best condition for illustrations, and abbreviated accounts for the other species. Repository acronyms are FMNH, Field Museum of Natural History, Chicago, Illinois; FSCA, Florida State Collection of Arthropods, Gainesville; NCSM, North Carolina State Museum of Natural Sciences, Raleigh; USNM, United States National Museum, Smithsonian Institution, Washington, DC; and VMNH, Virginia Museum of Natural History, Martinsville.

Taxonomy

Order Polydesmida Pocock, 1887

Suborder Polydesmidea Pocock, 1887

Infraorder Polydesmoides Pocock, 1887

Superfamily Trichopolydesmoidea Verhoeff 1910

Family Macrosternodesmidae Brölemann 1916

Macrosternodesmini Brölemann, 1916:585.

Macrosternodesmidae: Hoffman, 1980:177; 1982:722; 1999:457. Kevan, 1983:2969. Blower, 1985:209. Shelley, 1988:1650; 2000:190; 2002a:1870. Simonsen, 1990:64, 81–82. Lewis, 2002:103. Kime, 2004:39.

Diagnosis: (adapted from those of Hoffman (1982) and Simonsen (1990)). Generally colorless to reddish-brown, small to moderate-size Trichopolydesmoidea (6–12 mm long but occasionally ca. 30 mm long) with 20 segments including epiproct; collum narrower than head, not overlapping epicranium; segments 3–4 generally smaller than 2 and 5; metaterga with transverse sulci and three or four rows of variably rounded to subconical pustules giving rise to clavate setae; paranota small but distinct; limbi smooth to irregularly scalloped and ragged, one termination occasionally elongated and spiniform; tarsi ca. twice as long as next longest podomeres, male prefemora swollen and convex dorsally; sphaerotrichomes present on at least ambulatory tibiae and tarsi. Gonopodal aperture large, broadly ovoid, completely filling metazonite, not extending onto prozonite but sometimes spreading caudad between 9th legs. Gonocoxae large, completely filling respective halves of aperture, excavated medially to accommodate telopodites; prefemora horizontal or angling ventromedially, giving rise to acropodite and additional projection homologous to process B of Nearctodesmidae (terminology of Shelley (1994)); acropodite part distal to origin of solenomere (distal zone) variably configured, sometimes folded, flattened, and not recognizable as such; solenomere long and narrow, arising subterminally, without hairpad and ampulla, prostatic groove opening terminally.

Components. *Chaetaspis* Bollman, 1887; *Ophiodesmus* Cook, 1896; *Macrosternodesmus* Brölemann, 1908; *Tidesmus* Chamberlin, 1943. Additional genera, currently assigned to Polydesmidae, Trichopolydesmidae, or other families, may also belong here.

Caucasodesmus inexpectatus, Golovatch 1984, from North Ossetia, Russia, was originally placed in the Macrosternodesmidae but from published figures obviously does not belong here as the family is now understood. The prefemora are globose, not transverse; process B is missing; and there is no solenomere branch. Indeed, according to Golovatch (1984), there is no prostatic groove and no solenite (= cannula), conditions almost unique in the Polydesmoidea and Trichopolydesmoidea. On the other hand, the gonopod plan of the long-established genus *Archipolydesmus* Attems, 1898 (Spain and North Africa; see Abrous-Kherbouche and Mauriès 1996), appears close to those of a series of undescribed macrosternodesmid genera from Arizona, USA, though largely by tradition, *Archipolydesmus* is formally included in the Polydesmidae. Furthermore, Mauriès (1980) re-established the family Mastigonodesmidae Attems, 1914, for *Mastigonodesmus* Silvestri, 1898, an action that seems justified because the genus cannot be considered a polydesmid in the classical sense as it lacks the torted prostatic groove (= seminal canal) and characteristic cuticular fimbriae surrounding the distal opening of the latter, which we consider defining characters of the Polydesmidae. Lack of process B seems to eliminate *Mastigonodesmus* from the Macrosternodesmidae.

Distribution. Holarctic. Indigenous to northern coastal Croatia; western Europe (southern Sweden, Denmark to the Pyrenees of France); eastern US east of the Central Plains (central Oklahoma to central North Carolina, southern Illinois and southcentral Indiana to northern Arkansas & Alabama and northcentral Mississippi); southwestern US (Arizona, California, ?New Mexico); northwestern Mexico (Baja California Norte, ?Sonora) (Jeekel 1953; Enghoff 1973, 1974; Shelley 1978, 2000; Hoffman 1980, 1982, 1999; Blower 1985; Simonsen 1990; Geoffroy 1996; Lewis 2002; Kime 2004); introduced to Newfoundland, Canada (Palmén 1952; Kevan 1983; Blower 1985; Shelley 1988, 2002a; Hoffman 1999). Simonsen (1990:88, Map 3) depicts the distribution in Europe and part of that in the eastern US.

Remarks. Clearly much remains to be learned about relationships within the superfamilies Polydesmoidea and Trichopolydesmoidea, especially with continued discoveries of new taxa in western North America and elsewhere. Major familial realignments seem likely in the near future.

The Macrosternodesmidae has received little attention since it was established by Brölemann (1916) as a tribe in the subfamily Devilleinae, family Leptodesmidae; 64 years later, Hoffman (1980) elevated it to family status. Subsequent anatomical characterizations (Hoffman 1982, Simonsen 1990) must be modified to accommodate *Tidesmus*, in which the gonopodal prefemora are not entirely transverse as they are in *Chaetaspis* and representatives of the Nearctodesmidae in northwestern North America. Macrosternodesmidae may be distinguished from Nearctodesmidae in that it possesses telopodal process B but lacks branch A (terminology of Shelley (1994)) and from the Polydesmidae by the presence of process B and by the essentially direct course of the prostatic groove, which lacks loops and opens apically on a solenomere instead of in a pore surrounded by cuticular fimbriae on the telopodal stem. Our illustrations show that process B arises from the body of the gonopod at the anteromesial base of the prefemur. Characters are lacking to distinguish Macrosternodesmidae from the other New World trichopolydesmoidean family, Fuhrmannodesmidae, whose limits are unknown. It has become a wastebasket taxon for small tropical trichopolydesmoideans, but no US genera are presently assigned to this family.

Golovatch (1991) attempted to resolve polydesmoidean families based on positional homologies of gonopodal branches. However, his scheme is unworkable for the North American fauna because his gonopod terminology differs from those in other studies; unfortunately, old terminology, with established (although possibly incorrect) meanings, was employed. Djursvoll *et al.* (2000) subsequently changed the meaning of several terms whereas others seem to have been abandoned.

A stable terminology for polydesmoidean gonopods is desirable. The quest began in the 19th century with the contribution of Attems (1894), continued in the 20th century (*e.g.* Hoffman 1974, Golovatch 1991), and still continues in the 21st century (Djursvoll *et al.* 2000). None of the systems has gained much acceptance, and the most recent one (Djursvoll *et al.* 2000) was almost immediately abandoned by one of its proposers (Golovatch 2006). By studying gonopod development, a few authors attempted to homologize parts of the gonopod with ambulatory podomeres; the most recent (Petit 1976) concluded that no articles distal to the prefemur were represented. Such studies are made difficult by the "metamorphic" transformation of the lump-like primordia to gonopods in the final molt. At present, however, establishing homologies with podomeres, while desirable, is of secondary importance. What is needed is consensus on a set of names, or even alphabetical symbols, for structures in comparable positions on the gonopods of related species (this tactic has worked for similarly complex structures like the palpi of male spiders). Most terminologies mix names (*i.e.* tibiotarsus), which suggest homologies, and letters. An acceptable terminology must be based on careful studies of as wide a spectrum of genera as possible (Djursvoll *et al.* 2000 arbitrarily excluded the North American genera *Pseudopolydesmus* Attems, 1898, and *Scytonotus* C.L. Koch, 1847) using both compound light microscopy and SEM. It will be an herculean task.

Our gonopod terminology follows Shelley (1994). All structures distal to the coxa are referred to as the **telopodite**, which is based on the clearly observable homology of this part of the gonopod with the postcoxal (telopodal) elements of walking legs. Petit (1976) showed that the setose basal part of the gonopod telopodite derives from the ambulatory **prefemur**, and we so designate it here. The prostatic groove originates in a fossa on the medial side of the prefemur into which an articulated and movable coxal projection, the **solenite** (= **cannula**), inserts. **Process B** arises from the anterodistal margin of the prefemur and is U-shaped or strongly curved in *Tidesmus*, with the outer branch of the "U" being shorter. The telopodite distal to the indistinct boundary of the prefemur is the **acropodite**, and in light of Petit's work, we believe the terms "femorite" and "tibiotarsus" should be abandoned. Macrosternodesmid acropodites bear a number of processes, the most easily recognizable being the **solenomere**, a tubular projection with the prostatic groove opening apically. The base of the solenomere may be thickened and bear one or more subsidiary processes in *Tidesmus*. The **distal zone**, which has been labeled "tibiotarsus," "endomerite," and "exomerite," is the part of the acropodite distal to the solenomere; in *Tidesmus*, it is a blocky structure that often is folded.

Tidesmus Chamberlin, 1943

Tidesmus Chamberlin, 1943:35. Chamberlin and Hoffman, 1958: 74. Loomis, 1960:68. Buckett, 1964:12. Shear, 1969:134. Jeekel, 1971:356. Hoffman, 1980:179. Shelley, 2002b:107.

Oodedesmus Loomis, 1960:60. Hoffman, 1980:179; 1999:469. Shelley *et al.*, 2000:116. **NEW SYNONYMY.**

Phreatodesmus Loomis, 1960:62. Buckett, 1964:12. Hoffman, 1980:179; 1999:470. Shelley *et al.*, 2000:122. Shelley, 2002b:107. **NEW SYNONYMY.**

Type species: Of *Tidesmus*, *T. episcopus* Chamberlin, 1943, by original designation; of *Oodedesmus*, *O. variabilis* Loomis, 1960, by original designation; of *Phreatodesmus*, *P. torreyanus* Loomis, 1960, by original designation.

Diagnosis: Pallid to light yellowish Macrosternodesmidae, lengths ca. 6.0–12.0 mm, widths ca. 0.8–2.5 mm. Gonopods with femoral setae, process B (see Shelley 1994) broad, curving strongly mediad, with or without basal subbranch; acropodite short and "blocky," distal zone clearly present or folded, flattened, and apparently absent, with distal, dentate shelf and transparent lamina bent caudad, mediad, or laterad; solenomere arising centrally from acropodal mass, extending generally ventrad.

Distribution. Coastal southern California, USA, and adjacent Baja California Norté, Mexico, to central and southeastern Arizona; potentially present in southwestern New Mexico, USA, and northern Sonora, Mexico. Potential presence in the former is indicated by occurrence 50 mi (80 km) to the west in Cochise County (Co.), Arizona; that in Sonora is implied by occurrence 35 & 50 mi (56 & 80 km) to the north in Cochise and Pima cos., Arizona.

Etymology. In addition to his biological work, R. V. Chamberlin studied native North American languages and compiled dictionaries of several of them. *Tida* means "small" in the Gosiute language and was combined with the traditional "...*desmus*" suffix to form the generic name (Chamberlin 1943).

Remarks. Aside from a 1976 collection of *T. variabilis*, all of the material we saw was collected in the early 1920s. After more than 85 years, these specimens are in poor condition; they may have been preserved for years in vials stoppered with cork or rubber, resulting in stained, brittle, and decalcified cuticles, and accumulated deposits that cannot be safely removed. Because of decalcification, which we did not anticipate from the appearances of the specimens, they tended to collapse during preparation for SEM examination. In the future, old, suspect specimens should be dehydrated in methanol, hexamethyldisilazane (Nation 1983) or xylene before drying, or be subjected to critical point drying. However, we are confident that the heavily sclerotized gonopods were not distorted, based on comparisons of the SEM micrographs with drawings made before SEM preparation.

Because of the better condition of the specimens, we base our detailed description of somatic features of *T. variabilis*, which in all respects is as representative of the genus as the generotype *T. episcopus*.

The only habitat information, either on vial labels or in published accounts, is the statement, "under stones," for the types of *T. episcopus*. Little is therefore known about preferred environments, although one can plausibly suggest very close to water. The collection dates show a decided seasonality and a marked preference for cool-weather seasons of the year. As shown in the ensuing table, 15 (75%) of the samples were collected from November through March, in winter, late autumn, and early spring, whereas only 2 were taken in April and 3 in summer. Future collecting efforts should coincide with this seasonality pattern.

Seasonality of western macrosternodesmids; number of samples collected per month.

Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
6	4	1	2	-	1	1	1	-	-	4	-

Tidesmus hubbsi, the second species originally assigned to the genus, was based on a single female; Chamberlin's accounts (1943) provide no differences except size (at 9 mm *T. episcopus* is about twice as long as the 5 mm *T. hubbsi*), and it is also geographically disjunct. We cannot address the species or present a meaningful diagnosis, and therefore remove *hubbsi* from *Tidesmus* and leave it unassigned.

Tidesmus episcopus Chamberlin, 1943

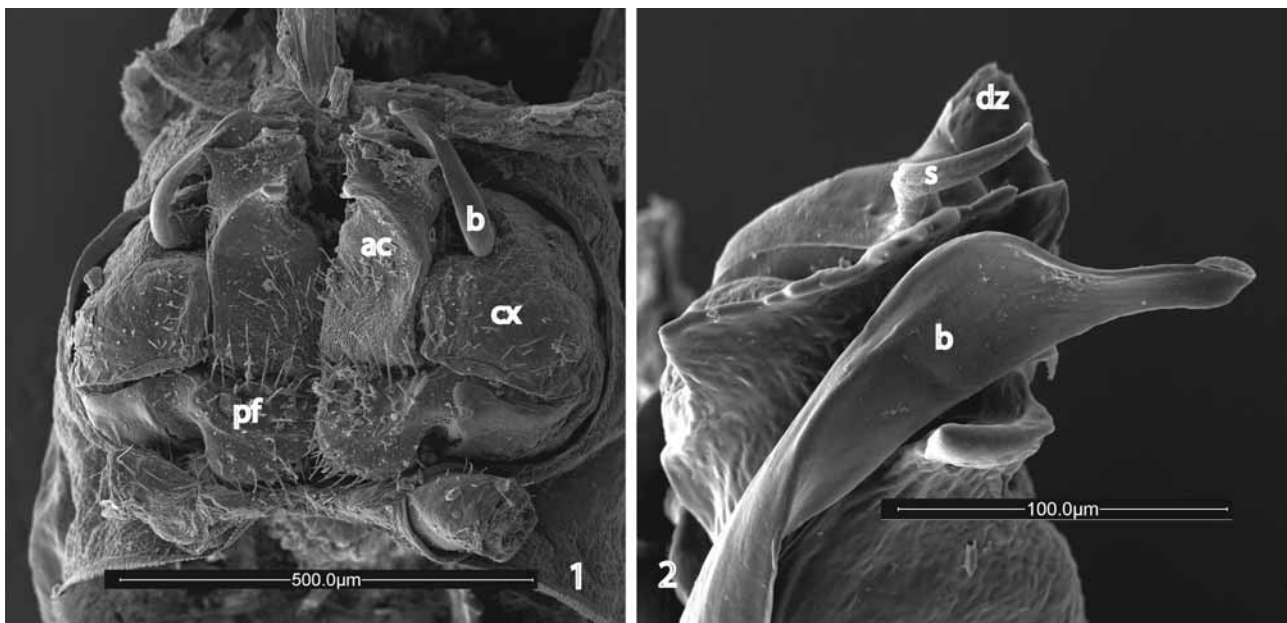
Figs. 1–4

Tidesmus episcopus Chamberlin, 1943:35, figs. 1–3; 1952:558. Chamberlin and Hoffman, 1958:74. Buckett, 1964:12. Shelley, 2002b:107.

Phreatodesmus cooki Loomis, 1960:64, fig. 12. Buckett, 1964:12. Hoffman, 1999:470. Shelley, 2002b:107. **NEW SYNONYMY.**

Type specimens: Of *T. episcopus*, male lectotype and male and female paralectotypes (FMNH) collected by G. Grant, 2 January 1939, on Bishop's Road, Reservoir Hill, Los Angeles, Los Angeles Co., California. Today, Bishop's Road is a one or two block street bordering Elysian Park between the Pasadena Freeway and North Broadway St., near Dodger Stadium. The vial containing the types and only known specimens is labeled "male holotype, female allotype," but it contains fragments of at least three males and two females, with one male segregated in a microvial. Chamberlin (1943) did not designate a holotype nor did he designate a lectotype in his subsequent report of this sample (Chamberlin 1952), so the specimens are thus syntypes. His handwriting is on the label, so we designate the male in the microvial, the least damaged specimen, as the lectotype; the others thus become paralectotypes. Parts of one male paralectotype were mounted for examination by scanning electron microscopy. Of *P. cooki*, male holotype & 11 juv. paratypes (USNM) collected by O.F. Cook, 15 February 1929, along Clear Creek, Tehachapi Pass, Kern Co., California.

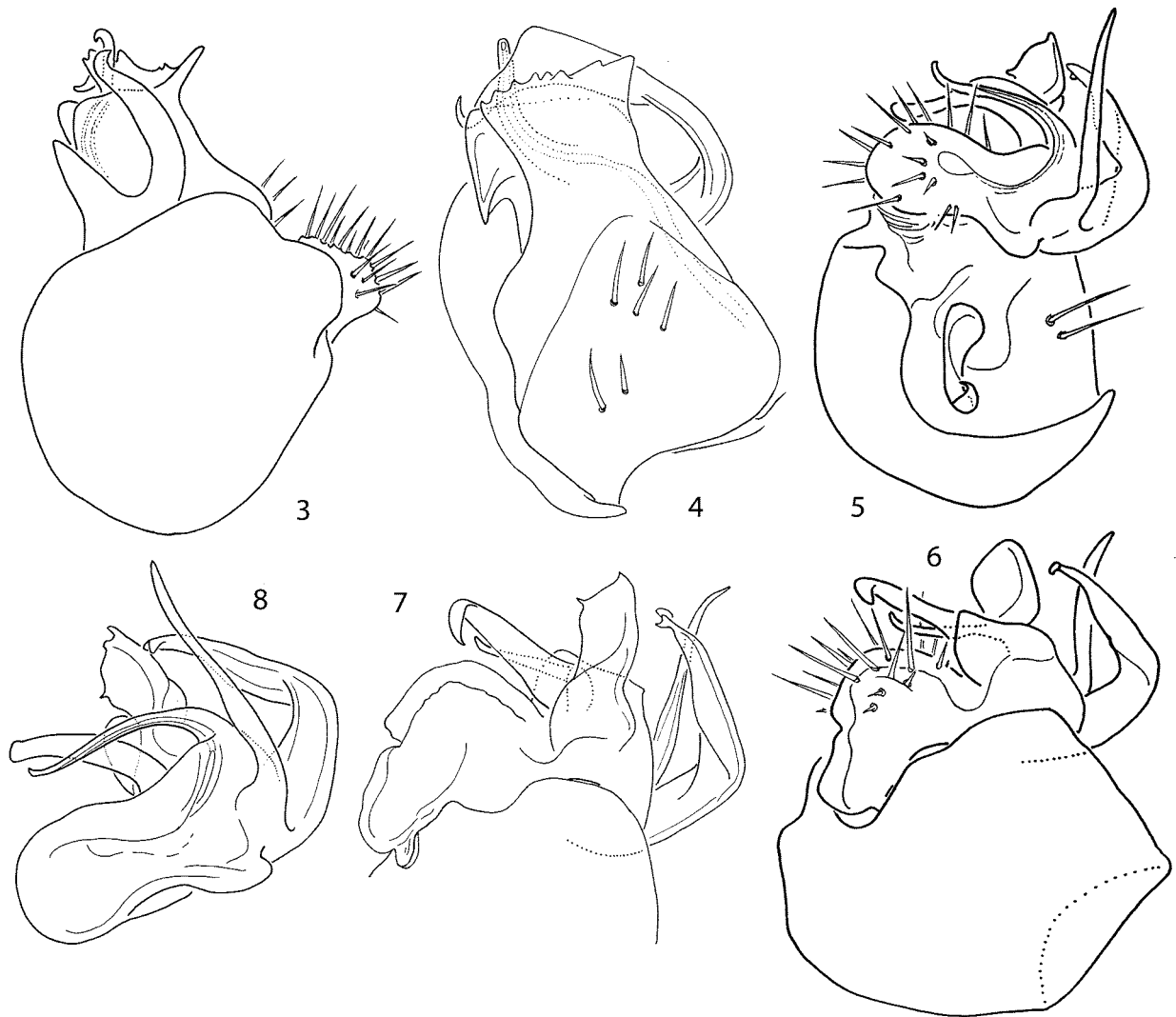
Diagnosis. Process B a simple, curved projection overhanging ventrolateral margin of acropodite, without basal branch or other substructures; acropodite without true distal zone, margin irregularly folded with short spiniform projection and elevated, transverse lamella.



FIGS. 1, 2. *Tidesmus episcopus* gonopods. 1, *in situ*, ventral view. 2, terminal structures, mesial view.

Description. Length ca. 9–9.5 mm, maximum width ca. 0.85 mm; somatic features agreeing with those of *T. variabilis* (detailed description in succeeding account). Gonopodal aperture (Fig. 1) large, broadly ovoid, completely filling 7th metazonite, not extending anteriorly onto prozonum or caudad between 9th legs, sides slightly elevated. Gonopods *in situ* (Fig. 1) completely filling respective halves of aperture, prefemora contiguous in midline. Gonopod structure as follows (Figs. 1–4): Coxa (*cx*, Fig. 1) large, globose, tapering into blunt, anterolateral projection; telopodites comparatively small, arising caudomedial from coxae. Prefemur (*pf*, Fig. 1) rounded basally at insertion of cannula, angling anteroventrad distad, not horizontal, process B (*b*, Figs. 1,2) arising distad on anterolateral margin, with broad, subtriangular basal lobe (best seen in Fig. 3), projection extending laterad basally then curving broadly ventromedial, overhanging and terminating near level of distolateral acropodal margin, apically uncinata; acropodite (*ac*, Fig. 1) short, "blocky," and irregularly folded with a few short, spiniform projections, longest arising anterodistad at base of distal zone (*dz*, Fig. 2); latter a minute, inconspicuous, sublinear lamella oriented transversely across ventral acropodal surface, margin irregularly notched; solenomere (*s*, Fig. 2) moderately long, extending caudad then curving medial over distal zone and ventral acropodal surface, apically uncinata.

Females with somatic features subsimilar to those of males but without swellings on ambulatory prefemora (see description of *T. variabilis*).



FIGURES 3–8. Gonopods of *Tidesmus* species. 3–4, *T. episcopius*. 3, right gonopod, lateral view. 4, right gonopod telopodite, mesial view. 5–8, *T. variabilis*. 5, left gonopod, mesial view. 6, the same, lateral view. 7, left gonopod telopodite, lateral view. 8, the same, mesial view.

Habitat. According to the vial label, the types of *T. episcopus* were found "under stones."

Distribution. A small area extending from the Tehachapi Mountains southward through the western San Gabriels to the foothills of northern metropolitan Los Angeles (Fig. 25); *T. episcopus* should be expected in Griffith Park and the Hollywood Hills. The two Kern Co. sites are close together and lie roughly 80 mi (128 km) north-northwest of the type locality. In addition to the types, the following locality is available: CALIFORNIA: Kern Co., Woodford (near Tehachapi), m, 8 January 1929, O. F. Cook (VMNH).

Etymology. The specific name refers to the type locality, Bishop's Road (Chamberlin 1943).

Remarks. Chamberlin (1952) merely repeated the type locality and the number of specimens in the sample.

The VMNH male from Kern Co. was in a jar of *P. cooki* labeled "PARATYPE" and there is a label in the vial stating such. The individual was available to Loomis (1960), but he did not designate it as a paratype in the published description and thus it does not hold this status (Article 72.4.6 of the Code).

***Tidesmus variabilis* (Loomis, 1960), new combination**

Figs. 5–8, 13–21

Oodedesmus variabilis Loomis, 1960:60, figs. 6–7. Hoffman, 1999:469–470.

Type specimens. male holotype and 1 male & 2 female paratypes (USNM) collected by H. F. Loomis, 21 January 1923, along Fish Creek (a tributary of the Salt River), ca. 5 mi (8 km) NE Tortilla Flat, Maricopa Co., Arizona.

Diagnosis. Process B overhanging lateral margin of acropodite, with flange distal to midlength but without distal tooth, basal lobe long and narrow, extending ventrad beyond outermost point of process; acropodite with true distal zone prolonged beyond origin of solenomere and expanding into anterior and caudal branches.

Description. Length 11.4–12.0 mm, width 1.6–2.5 mm. All regions of head densely pilose with short, parallel-sided setae; antennae reaching back to around caudal margin of 2nd metatergite, comprising seven densely pilose articles, relative lengths of antennomeres 2>3>6>5>4>7>1, 1 subglobose, 2–5 clavate, 6 subovoid and swollen, 7 truncate with 4 terminal sensory cones, no other sensory structures evident. Collum (Fig. 13) short, not overlapping epicranium, surface granular, giving rise to clavate setae in five poorly defined rows. Prozonites smooth on pregonopodal segments, lightly costulate in midbody region, becoming granular to smooth caudad, occasionally giving rise to clavate setae (Figs. 18, 19). 2nd–7th metatergites (Fig. 13) generally smooth, with three faintly delineated rows of clavate setae arising from low, rounded to lightly conical pustules, 4th–7th metaterga (Figs. 13, 15) also with shallow, moderately distinct, transverse grooves between 1st and 2nd rows of pustules; 8th–18th metaterga (Fig. 16) with grooves sharper & more distinct, and four rows of setae arising from pustules; 19th metatergite (Fig. 18) shorter and with faint groove. Limbi (Fig. 19) deeply serrate with one part as elongated bristle. Paranota short but distinct, margins generally smooth on pregonopodal segments, with three short teeth on segments 8–17; ozopores opening in short caudolateral swellings on segments 5, 7, 9–10, 12, 13, and 15–19. Epiproct (Fig. 17) bluntly subtriangular, overhanging but not extending beyond level of paraprocts, surface generally smooth, with four poorly defined rows of pustules giving rise to clavate setae and 4 long, thin, additional setae arising terminally & subterminally; paraprocts granular, with at most only a few scattered setae; hypoproct short & rounded, with a pair of long, thin, parallel-sided, apical setae.

Pregonopodal sterna (Fig. 14) with at most only faint elevations between leg pairs, otherwise without modifications; postgonopodal sterna with only low elevations between legs. 1st legs short, crassate; legs 2–7 (Fig. 14) longer and slightly less crassate, dorsal surfaces of prefemora swollen & rounded; postgonopodal legs continuing through segment 18, prefemoral swellings becoming progressively shorter and more lobe-like

caudally; all legs moderately hirsute, distal articles more so; tarsal claws short & gently curved, apically acuminate.

Gonopodal aperture (Fig. 14) extending caudad between 9th legs, caudal margin elevated and flared. Gonopod structure as follows (Figs. 4–8, 20–21): Coxa as in *T. episcopus*. Prefemur (*pf*, Fig. 20) angling generally ventrad, subhorizontal basally in some males, process B (*b1* and *b2*, Figs. 20, 21) extending laterad basally then bending ventromedial and overhanging ventrolateral margin of acropodite, bent sharply dorsad apically and with moderate-size flange on lateral margin distal to bend, basal lobe (*b2*, Figs. 20–21) long and narrow, expanding slightly at midlength then tapering distad, extending ventrad to level of or even beyond outermost point of process, crossing opposite member *in situ*; distal margin of acropodite prolonged into two branches thereby constituting true distal zone, extending ventrad beyond origin of solenomere (*s*, Figs. 20, 21), anterior branch (*sp*, Figs. 20, 21) variably narrow to blade-like, curving broadly anteriorly and recurved apically, possibly partly enveloping main branch of process B, caudal branch variably subspatulate, expanding and curving distomedial and partly enclosing main branch of process B, margin lightly irregular; solenomere relatively long and lightly bisinuate, extending ventrad.

Variation. Variation in *T. variabilis* involves the relative lengths of all branches other than the solenomere and the breadths of the acropodal projections that constitute the distal zone. The males from between Miami and Superior, Pinal/Gila cos., agree closely with the holotype except for the breadths and angles of the branches of the distal zone. In that from Prescott, Yavapai Co., the anterior branch is narrower than those in the types or the males from Pinal/Gila cos., so as to appear as yet another separate projection apart from the caudal branch.

Habitat. Unknown.

Distribution. Central Arizona; occurring in the Prescott, Coconino, and Tonto National Forests from central Yavapai to northern Pinal/Gila cos., a distance of roughly 125 mi (200 km) in a northwestern-southeastern direction. The samples from Pinal/Gila cos. are only ca. 20 mi (32 km) south of the type locality, and because of its proximity to the male from Prescott, ca. 40 mi (64 km) to the west-southwest, we include the juvenile sample from Rimrock under *T. variabilis*. In addition to the types, the following samples were examined:

ARIZONA: *Maricopa Co.*, along Fish Cr. ca. 5 mi (8 km) NE Tortilla Flat, m, February 1924, H. F. Loomis (VMNH). *Pinal/Gila cos.*, along US hwy. 60 between Miami and Superior, m, ca. 9 ff, juvs., 1 March 1925, H. F. & E. M. Loomis (VMNH) and 2 mm, ca. 9 ff, juvs., 25 July 1976, A. K. Johnson (NCSM). *Yavapai Co.*, Prescott, m, ca. 16 ff, juvs., 9 August 1930, H. F. Loomis (VMNH); and Rimrock, V Bar V Ranch, juvs., 8 April 1976, K. Silivari (NCSM).

Remarks. The gonopod of *T. variabilis* is highly complex with five separate branches and flanges extending subventrad; when paired with its counterpart *in situ*, 10 projections emanate from the anterior position on segment 7, some of which cross each other. Consequently, it is difficult to comprehend the gonopodal structure *in situ* or even to determine which projections arise from which gonopod. Despite this complexity, the gonopod is just an extreme manifestation of the basic generic pattern exemplified by *T. episcopus*. Though not helpful in determining the acropodal configuration, this pattern of several branches and lamellae extending ventrad is another justification for assigning *B. hastingsus* to *Tidesmus* (see subsequent account), as the two incomprehensible illustrations accompanying the original description (Chamberlin 1941:39, figs. 48–49) show several projections arising from a large, subglobose coxa, in a pattern that conceivably could apply to *variabilis*.

The samples from the VMNH were in a jar labeled "PARATYPES" but were not so designated by Loomis (1960) in the original description and hence do not hold this status (Article 72.4.6 of the Code).

***Tidesmus torreyanus* (Loomis, 1960), new combination**

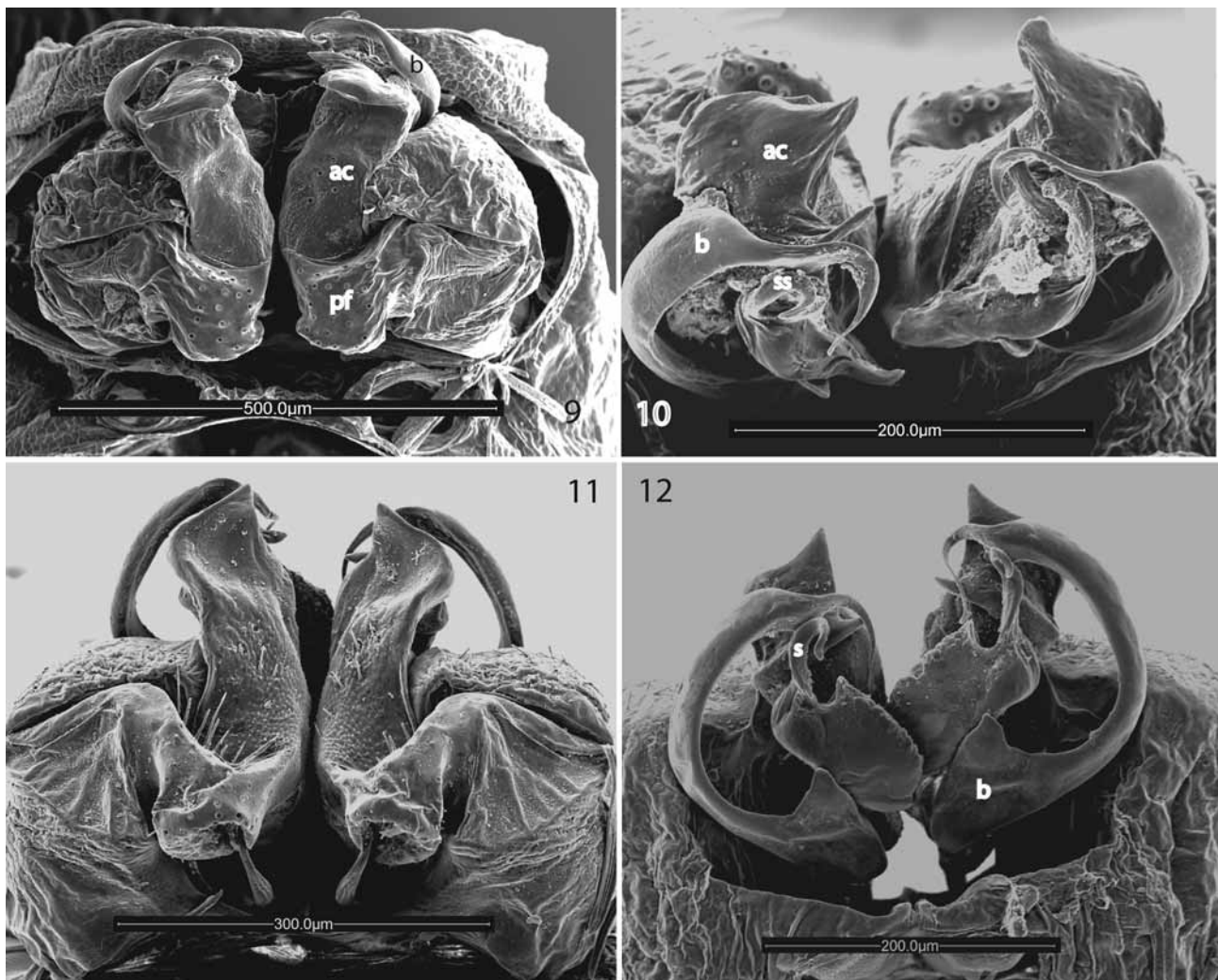
Figs. 9–12.

Phreatodesmus torreyanus Loomis 1960:63, figs. 8–11. Buckett, 1964:12. Hoffman, 1999:470. Shelley, 2002b:107.

Phreatodesmus dentatus Loomis 1960:64, fig. 13. Buckett, 1964:12. Hoffman, 1999:470. Shelley, 2002b:107. **New Synonymy.**

Type specimens. Of *P. torreyanus*, male holotype and ca. 13 female & juvenile paratypes (USNM) and 1 male paratype (VMNH) collected by O. F. Cook, 29 November 1925, in a garden at Torrey Pines State Beach and Reserve, ca. 4.5 mi (7.2 km) N La Jolla, San Diego Co., California. Of *P. dentatus*, male holotype and 1 female and ca. 9 juvenile female paratypes (USNM) collected by O. F. Cook, 14 February 1929, 7 mi. W Cajon on Big Pine Road in Cajon Pass, Angeles National Forest, San Bernardino Co., California.

Diagnosis. Process B overhanging essentially entire ventral surface of acropodite, terminating over medial margin, apically falcate or sigmoid with tip directed toward or away from acropodal stem, with flange distal to midlength and more distal tooth on inner margin, basal subbranch short and subtriangular; acropodite without true distal zone, margin bent variably caudad.



FIGURES 9–12. *Tidesmus torreyanus* gonopods in situ. 9, ventral view. 10, anteroventral view. 11, posterior view. 12, anterior view.

Description. Agreeing closely with *T. variabilis* in somatic features with following exceptions: Setae on collum arranged in three well defined rows. Prozonites glabrous, entirely without setae. Transverse metatergal grooves faint, evident on 7th–16th metaterga.

Gonopods *in situ* (Fig. 9) not completely filling respective halves of aperture, prefemora not contiguous in midline. Gonopod structure as follows (Figs. 9–12): Coxa as described for *T. episcopus*. Prefemur (*pf*, Fig. 9) subhorizontal, process B (*b*, Figs. 10, 12) extending laterad basally then curving broadly ventromedial and overhanging entire ventral surface of acropodite (*ac*, Figs. 9, 10), apically falcate or sigmoid, terminating over medial acropodal margin, with short basal subbranch, flange on caudal surface distal to midlength, and blunt tooth on inner margin distal to flange; distal margin of acropodite bent abruptly caudomedial forming "shoulder" on caudal margin, with medially directed spine on anterior edge, and shorter, acuminate projections in between; solenomere (*s*, Fig. 12) relatively short, apically uncinata.

Variation. The few available males with gonopods from Pacific coastal localities agree closely with those of the holotype. The holotype of *P. dentatus*, however, differs in that the basal subbranch of process B is larger and the apical curvature of process B is sigmoid with the tip directed dorsad, away from acropodal stem. The male from Arizona differs from all the California males in that process B does not extend as far over the ventral surface of the acropodite, and the apical curvature is less sigmoid; the overall length of process B is somewhat intermediate between those of *T. episcopus* and *T. torreyanus*.

Habitat. Unknown.

Distribution. Southern California, USA, and northern Baja California Norte, Mexico, extending from Cajon Pass in the San Bernardino Mountains to the Pacific Coast north of San Diego and southward essentially as far as Ensenada; also with an allopatric population in southeastern Arizona, some 475 mi (760 km) to the east-southeast. The California and Mexico localities cover a distance of ca. 170 mi (272 km), and the known range along the Pacific Coast extends for 75 mi (120 km); the sample from Cajon Pass is some 95 mi (152 km) north-northeast of the northernmost coastal site. As the Dragoon Mountains in Arizona are only around 50 mi (80 km) west of New Mexico, *T. torreyanus* can be reasonably expected in the Peloncillo Mountains of Hidalgo Co. in that state. In addition to the types, the following samples are available:

USA: CALIFORNIA: *San Diego Co.*, Torrey Pines State Reserve, ca. 4.5 mi (7.2 km) N La Jolla, m, 2 ff, 1 November 1925, Hardy (VMNH).

ARIZONA: *Cochise Co.*, Dragoon Mountains (Coronado National Forest) near Dragoon, m, date unknown, H. F. Loomis (FSCA).

MEXICO: BAJA CALIFORNIA NORTE: "Wharf Gulley 20 mi down" (= ? coastal site ca. 20 mi (32 km) S of US Border), m (gonopods lost), 4 January 1925, O. F. Cook (VMNH); and 14.5 mi (23.2 km) N Ensenada (= ca. 33.5 mi [53.6 km] S of US border), m, 7 January 1925, O. F. Cook (VMNH).

Remarks. The name *dentatus* was assigned to the variant from Cajon pass, which may represent a separate subspecies; however, documentation of this status by intermediate or intergrade specimens is not presently possible, so we combine the names. From a geographical standpoint, both samples from Riverside Co., California, listed under "*Tidesmus* spp." in the concluding account likely refer to *T. torreyanus* and that from Temescal Canyon is from a somewhat intermediate location and might constitute an intermediate form, but the gonopods are missing. As tiny as these millipedes are and as difficult as they are to find, we may never have solid documentation of subspecific or specific statuses. One could even legitimately argue for a single California species with *torreyanus* and *dentatus* being subspecies of *episcopus*, but we believe that association of *torreyanus* and *dentatus* in a separate species is defensible by the flanges, distal teeth, and basal branches on processes B, which are absent from *episcopus*.

While its gonopods differ as described above under "Variation," we nonetheless assign the Arizona male to *T. torreyanus*, the named species that it most closely resembles. This action seems preferable to naming and describing a dubious new species, the only other option.

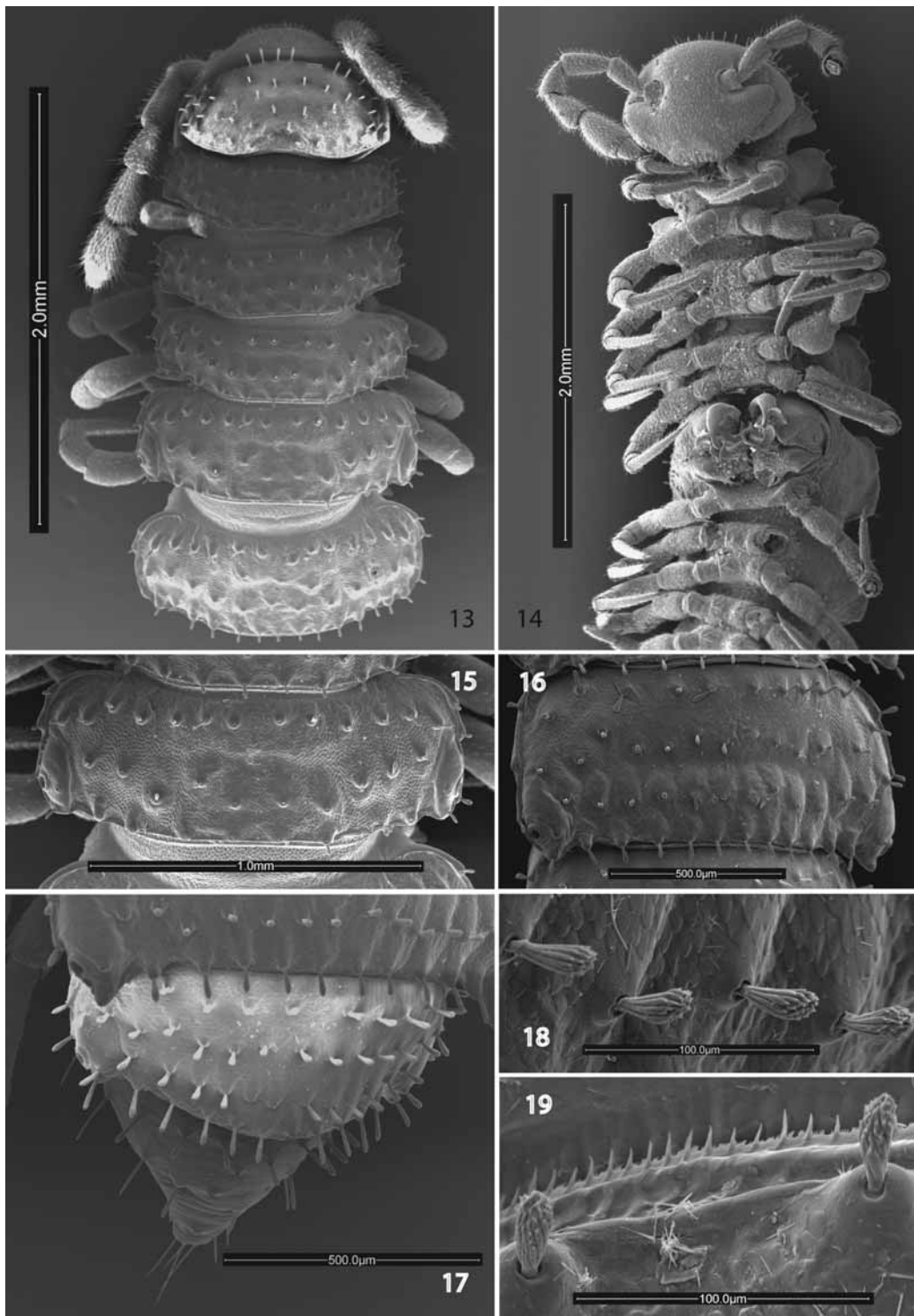
The VMNH samples from Mexico were in a jar labeled "PARATYPES" but were not so designated by Loomis (1960) in the original description and hence do not hold this status (Article 72.4.6 of the Code).

***Tidesmus hastingsus* (Chamberlin, 1941), new combination**

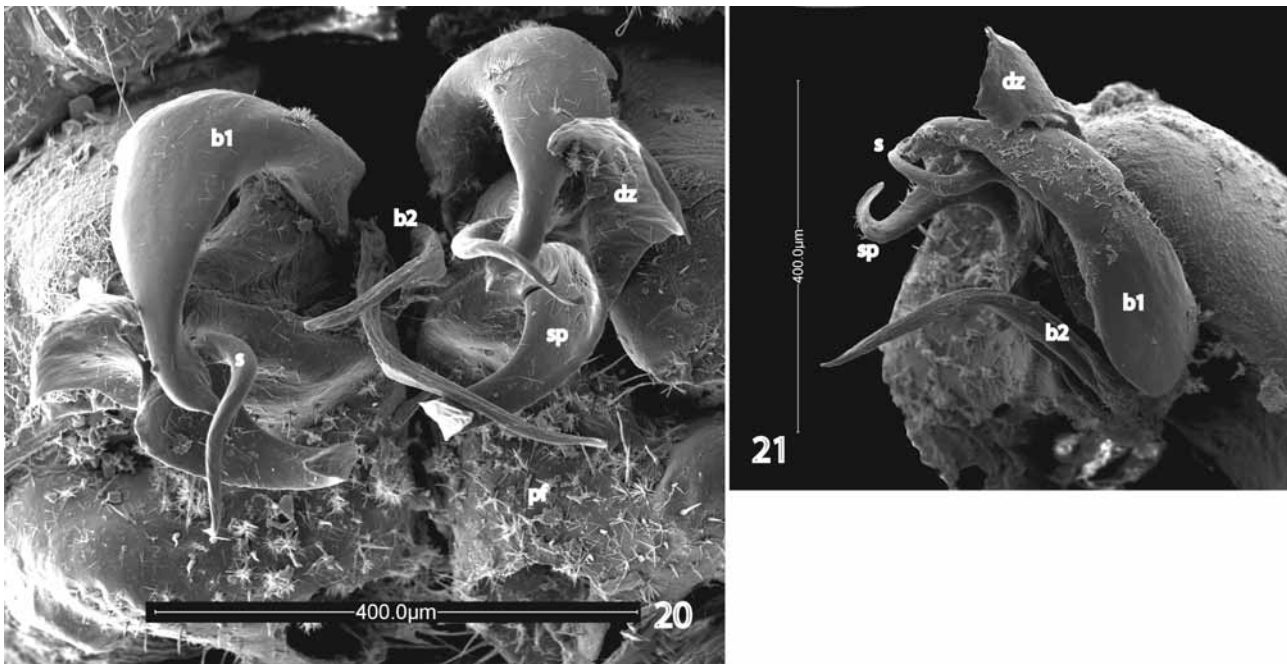
Brachydesmus hastingsus Chamberlin, 1941:27, figs. 48–49. Chamberlin & Hoffman, 1958:64.

Phreatodesmus hastingsus, Loomis, 1960:65. Buckett, 1964:12. Shelley, 1997:66–67; 2002b:107. Hoffman, 1999:470.

Type specimen. The male holotype was collected by J. M. Linsdale, 20 February 1941, on the Hastings Reservation, Monterey Co., California. A vial labeled "Holotype" exists at the USNM, but the specimens inside bear no resemblance to the original description and illustration as discussed below. The holotype of *B. hastingsus* is therefore lost, and a definitive assessment of the species and its true generic assignment await collection of a topotypical male.



FIGURES 13–19. *Tidesmus variabilis*. 13, anterior end of female, dorsal view. 14, anterior end of male, ventral view. 15, segment 5 of female, dorsal view. 16, segment 13 of female, dorsal view. 17, posterior end of female, subdorsal view. 18, segmental setae, dorsal view. 19, limbus, dorsal view.



FIGURES 20–21. Gonopods of *Tidesmus variabilis*. 20, *in situ*, ventral view. 21, right telopodite, mesial view.

Remarks. Because of the difficult-to-interpret drawings of Chamberlin (1941) this species has been enigmatic for years. Having just examined extensive material of his new genera *Phreatodesmus* and *Oodedesmus*, Loomis (1960) gained insight into Chamberlin's drawings and opined that *hastingsus* belonged in *Phreatodesmus*; however, he did not look at specimens. In an attempt to resolve the matter, Shelley (1997) examined the purported type material and found that it consisted of parts of individuals from at least two different polydesmids, one being an undescribed species and genus then known only from northern Idaho. He postulated that a previous worker had mixed these specimens with the actual type material, thus permanently confusing the situation.

We here add additional information based on a re-examination of these "types." The vial (USNM) contains no locality label and no original type-designation label in Chamberlin's style (with underlining in indelible red ink) at the time the species was described. Instead, only a newly inked, hand-written label reading "Brachydesmus hastingsi Chamberlin [male] Holotype" is in the vial that obviously was added rather recently, and whoever did so misspelled the species' name. The vial contains three microvials, two of which contain even smaller microvials; their contents are as follows:

"Microvial 1" contains crushed and very fragmented segments of a small polydesmidan with acute parantotal corners and laterally serrate metazonites. The smaller, inner vial contains a single gonopod of a species of *Speodesmus*, probably *S. bicornourus* Causey, 1959 (Polydesmidae).

"Microvial 2" contains a male polydesmidan that lacks the head and first five segments. One gonopod is *in situ*, the other is in a smaller, inner microvial. The gonopods are from an undescribed species and genus that occurs in Latah Co., Idaho, more than 740 mi (1,180 km) to the northeast. It is highly unlikely that this species also occurs in Monterey Co., California.

"Microvial 3" contains the caudal ends of two specimens of this same undescribed genus and species, as indicated by the unique epiroct that expands into a distinct, distal knob.

Thus the "type" vial of *Brachydesmus hastingsus* contains nothing that can even tentatively be associated with this species as described and illustrated by Chamberlin (1941). The last person to examine this material prior to Shelley was Charles Withrow, then a graduate student at Ohio State University, whose unpublished doctoral research was a revision of *Pseudopolydesmus* Attems, 1898 (Polydesmida: Polydesmidae) in eastern North America. In his unpublished thesis, Withrow also illustrated *S. bicornourus* and described the Idaho species as "*Idahodesmus dentatus*," generic and specific names that are invalid because they were never published in accordance with the Code (Shelley 1996c). Thus all the components presently in the vial were studied at or about the same time by Withrow, and it seems likely that he is the source of the confusion that may

have involved the destruction or misplacement of the true types of *B. hastingsus*. No wonder Shelley (1997) stated "...Chamberlin's gonopod illustrations are among the worst in all his publications, and it is impossible to gain an impression of their structure from these drawings." None of the gonopods in the vial are even remotely like those Chamberlin illustrated! However, having carefully studied *Tidesmus* gonopods, we now see what Loomis (1960) may have detected in Chamberlin's rather cartoonish drawings, the deeply divided, U-shaped process B, the long, sinuate solenomere, the flattened, lobe-like distal zone, and even the transverse prefemur. We therefore agree with Loomis (1960) that *hastingsus* is referable to *Tidesmus* (= *Phreatodesmus*). Assuming this to be correct, none of the somatic fragments in the vial seem part of the original specimen, as they lack the setiferous nodules and clavate setae typical of the genus. A male topotype is therefore imperative to determine if *hastingsus* is a distinct species of *Tidesmus* or a senior or junior synonym of a congener.

"*Tidesmus*" *hubbsi* Chamberlin, 1943

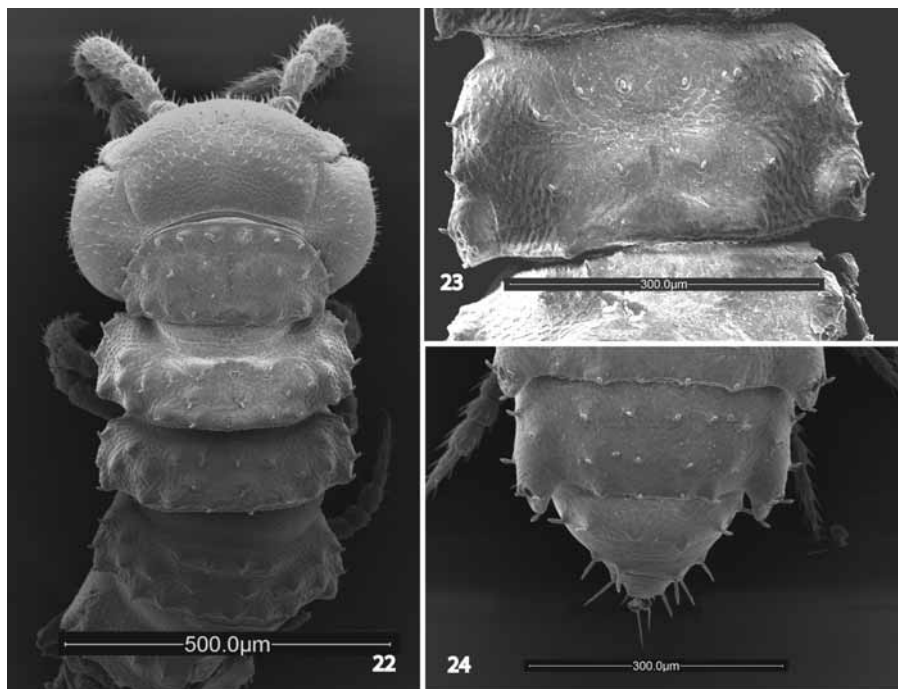
Figs. 22–24.

Tidesmus hubbsi Chamberlin, 1943:36, fig. 4. Chamberlin and Hoffman, 1958:74.

Type specimens: Presently lost. "Several females" were collected by C. L. and E. L. Hubbs, 25 June 1942, from an unnamed cave in Cave Valley, northern Lincoln Co., Nevada.

Remarks. The types, the only specimens mentioned by Chamberlin (1943), were retained in his personal collection that was transferred to the National Museum of Natural History, Smithsonian Institution, Washington, DC, in 1972, five years after his death. However, the specimens are not in the USNM type collection, and *T. hubbsi* is not on the institution's list of myriapod types; they appear to have been lost sometime after 1943. A search for them in the general collection was unsuccessful.

According to Chamberlin (1943), the types of *T. hubbsi* were 5 mm long and 0.43 mm wide, which is substantially smaller than those of *T. episcopus*. As Loomis (1960) correctly surmised, it is unlikely that the species are congeneric with this substantial size difference and the geographical and ecological lacunae between them. Gretchen Baker of the US National Park Service has visited Cave Valley Cave on two occasions in the past two years (2006, 2007) to try to collect males of this species, but only a few females were found; one is illustrated in Figs. 22–24. We defer designating one of these females as the neotype for a male that will resolve the true identity of the species.



FIGURES 22–24. "*Tidesmus*" *hubbsi*. 22. Anterior end, dorsal view. 23. Midbody segment, dorsal view. 24. Epiproct, dorsal view.

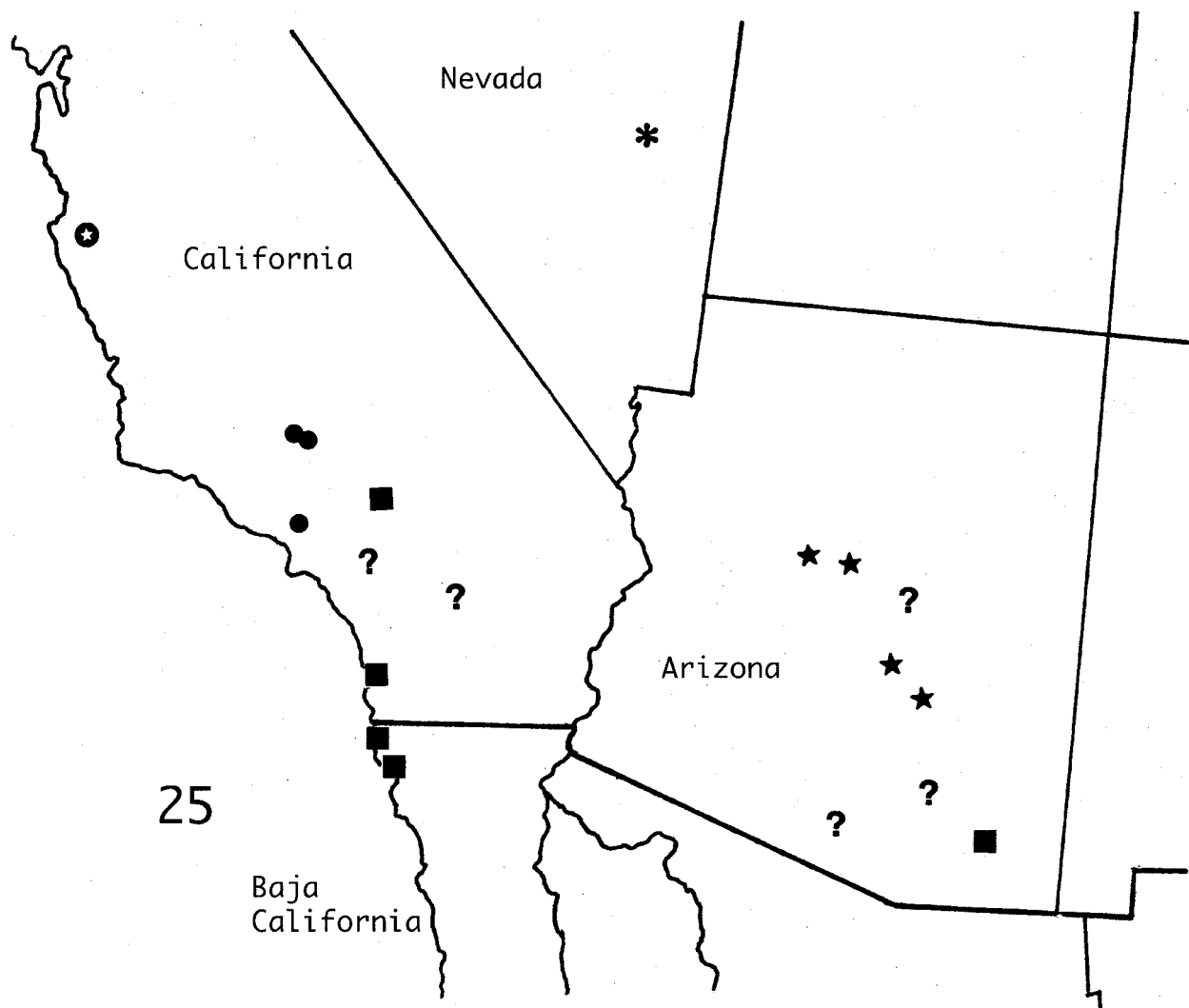


FIGURE 25. Southwestern United States and northwestern Mexico, showing localities of *Tidesmus* spp. Dots, *T. episcopus*; Stars, *T. variabilis*; Squares, *T. torreyanus*; Star in dot, *T. hastingsus*; Asterisk, "*T. hubbsi*"; Question marks, samples tentatively assigned to *Tidesmus*.

Chamberlin (1943) provided no reason for including *hubbsi* in *Tidesmus*, and since only females were available, it could not have been based on gonopodal features. We surmise that it was the shared presence of clavate dorsal setae, which are exhibited by many small polydesmidans. The type locality of *hubbsi* is far removed from the closest authentic site of *Tidesmus*, that of *T. variabilis* in Prescott, Yavapai Co., Arizona, around 320 mi (512 km) to the south-southeast, and congeneric status is unlikely. Other minute-bodied macrosternodesmids, belonging to undiagnosed genera, occur in caves in Great Basin National Park, White Pine Co., Nevada, only some 50 mi (80 km) to the northeast, as well as in the Arizona Strip, the region between the Grand Canyon and the northern border of the state, and *hubbsi* is more likely to be congeneric with these more proximate forms. Consequently, we remove *hubbsi* from *Tidesmus* and leave it unassigned.

?Tidesmus spp.

In addition to the previous species, all based on samples with identifiable adult males, unidentifiable samples without males exist from within the generic distribution that plausibly are referable to *Tidesmus*. Specific

identities cannot be determined at present, so we cite them below for future reference. The VMNH samples from Arizona were in a jar of "*Oodedesmus*" *variabilis* labeled "PARATYPES," but they were not so designated by Loomis (1960) in the original description and hence do not hold this status (Article 72.4.6 of the Code).

CALIFORNIA: *Riverside Co.*, off Temescal Canyon Rd. S of Corona, m (gonopods lost), 1 November 1925, "Hardy" (VMNH); and 5 mi (8 km) S Palm Desert, along Deep Cr. in Deep Canyon Preserve, f, 18 January 1985, C. R. Nelson, R. W. Baumann (NCSM).

ARIZONA: *Gila Co.*, Barber Pole Cave ca. 10 mi (16 km) NE Payson, Tonto National Forest, f (18 segs.), 19 June 1965, D. R. Davis, G. T. Lane (FSCA). *Pima Co.*, ca. 20–30 mi (32–48 km) NE Tucson, Santa Catalina Mts., juv., April 1921, H. F. Loomis (VMNH); and ca. 40 mi (64 km) SW Tucson, Baboquivari Mts., m (gonopods lost), 21 November 1923, H. F. Loomis (VMNH).

Remarks. The California specimens could plausibly be either *T. episcopus* or *T. torreyanus*; the site south of Palm Desert is roughly equidistant (75 mi [120 km]) from the type localities of both *T. torreyanus* and *T. dentatus*, lying northeast of the former and southeast of the latter. The female from Barber Pole Cave, Arizona, has only 18 segments and may not be applicable to *Tidesmus*, in which all authentic females have 20 segments; an undescribed genus whose species possess 18 segments has been found in at least one Utah cave.

Acknowledgments

We thank P. Sierwald (FMNH), for loan of the lectotype and paralectotypes of *T. episcopus*; and J. Coddington (USNM), for loan of the holotypes of *P. cooki*, *torreyanus*, *dentatus*, and *O. variabilis*, and the type vial of *B. hastingsus*. G. B. Edwards and R. L. Hoffman loaned material from the FSCA and VMNH, respectively. We are especially grateful to Gretchen Baker for her assiduous attempts to collect males of the Cave Valley Cave species, "*Tidesmus*" *hubbsi*. Thanks to Jason Bond (East Carolina University) for the use of the scanning electron microscope, and to Paul Marek and Matt Walker for technical assistance. This research was supported in part by NSF PEET grant DEB 05-2917 to W. A. Shear, P. Sierwald and J. Bond, and by a grant from the Professional Development Committee of Hampden-Sydney College.

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