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Cave millipeds of the United States. VIII. New genera and species of polydesmidan millipeds from caves in the southwestern United States (Diplopoda, Polydesmida, Macrosternodesmidae)

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Abstract

Four new species of presumed troglobitic polydesmidan millipeds in two new genera are described from caves in the states of Arizona, Nevada and California. *Pratherodesmus***, n. gen.**, is comprised of the type species, *P. voylesi* **, n. sp.,** *P. ecclesia***, n. sp.,** and *P. despaini***, n. sp**. The genus is found in Arizona and California. *Nevadesmus ophimontis*, **n. gen., n. sp.**, is from White Pine Co., Nevada; the new genus also includes *N. hubbsi* (Chamberlin) 1943, **new combination**. All four species were collected in or near United States National Parks, Bureau of Land Management lands, and in a private preserve. All new taxa are authored by W. A. Shear only.

Key words:

Introduction

Cave habitats in the western United States are of exceptional interest, because even more than the caves of extensive karst regions of the eastern part of the country, they represent “islands” which preserve relictual fauna, dating back to the most recent glacial advance and retreat, or even older. While caves in the east are likely to be surrounded by forested habitats in which the litter and soil are amenable to the continued existence of source populations for troglobitic and troglophilic arthropods, western caves are most often located in desert or semi-desert regions, or at high altitudes. In the former case, the surrounding environments are inimical to soil-dwelling arthropods, and in the latter, conditions approximating those that obtained at lower altitudes during glacial maxima or the early stages of glacial retreat still exist.

Millipeds, animals generally adapted to cool, moist conditions, are rare in deserts (there are some exceptions) and above timberline (Golovatch 2009). During the so-called pluvial periods at glacial maxima in North America, however, grasslands, savannah, and even forest occurred where today desert and semidesert are seen. Conversely, during interglacials the climate may have been warmer and drier than at present, so that the severe climates at high altitudes would have been considerably ameliorated, probably with less winter snow and longer, warmer summers than exist today (Webb & Bartlein 1992). As these conditions changed with the advance or retreat of the continental ice sheets, caves in both climatic regimes could provide refuges for millipeds. During the dry, warm interglacials (such as our present time) millipeds that had colonized the wetter, cooler environments at low altitudes could find themselves isolated in caves now surrounded by dry grasslands, woodlands, or desert (Peck 1973, 1981, 1982). Conversely, as glaciers advanced, creating harsh climates at high altitudes, the generally milder conditions in caves could provide a haven for millipeds that

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had adapted to warmer temperatures and milder winters during an interglacial. In this model, both glacial retreat and advance could be responsible for the isolation in caves of millipeds and other soil-dwelling arthropods.

Despite this inherent interest, relatively little has been published on cave animals in the western part of the country (apart from Texas, which has a rich literature) compared to the east (summaries in Peck 1973, 1982; see Wynne *et al.* 2007, and references therein; Shear 2006, 2007, Shear & Shelley 2007, 2008). Western caves may be more difficult to access—situated in remote desert country or high in the mountains. Caves at high altitudes may be accessible to collectors only for relatively brief times of the year, due to snowfall and low temperatures. Many western caves are located on public lands—national parks or monuments, national forests or Bureau of Land Management (BLM) lands. It is important to document finds of animals in these caves for conservation purposes.

This paper describes two new genera and four new species of polydesmidan millipeds recently collected in caves in the states of Nevada, Arizona and California. Because the locations where three of these new taxa were collected are on U.S. public lands and a private preserve (Sequoia Kings Canyon National Park, Great Basin National Park, BLM -Arizona Strip Field Office lands, and Cathedral Cave Preserve), they are of significance for the conservation of their habitats. These animals likely retain a limited ability to disperse to other caves, microclimatic conditions of caves are critical to their survival, and their habitats are sensitive to disturbances from local and regional threats, so all four species are candidates for potential designation as species of concern.

Type specimens of the new species described below are deposited in the Field Museum of Natural History (FMNH), Chicago; paratype specimens of *Pratherodesmus voylesi* and *P. ecclesia* are curated at the Colorado Plateau Museum of Arthropod Biodiversity (CPMAB), Flagstaff, Arizona and additional paratypes of *Nevadesmus ophimontis* **n. sp.** are deposited in the collection of the Illinois Natural History Survey (INHS).

Taxonomy

Order Polydesmida Pocock, 1887

Suborder Polydesmidea Pocock, 1887

Infraorder Polydesmoides Pocock, 1887

Superfamily Trichopolydesmoidea Verhoeff, 1910

Family Macrosternodesmidae Brölemann, 1916

Shear and Shelley (2007, 2008) diagnosed and discussed the Family Macrosternodesmidae, but the line of demarcation between the macrosternodesmids and nearctodesmids remains rather unclear, particularly in light of the fact that the genera described below have smooth metaterga, rather than having them divided into subquadrate elevated areas, as in *Tidesmus* Chamberlin, 1943. Smooth metaterga, with few or no setae, are characteristic of nearctodesmids. The gonopods of at least two of the species of *Pratherodesmus*, new genus, have the process arising from the mediodistal side of the prefemur, called process B by Shear and Shelley (2007), reduced or absent, likewise the distal zone. The gonopods of macrosternodesmids and nearctodesmids are very similar, except that nearctodesmids have been maintained as having both process A and B, and macrosternodesmids only B, but in the present two genera, it would seem process A is indeed present, and as mentioned above, process B is absent in two species of *Pratherodesmus*. This blurring of the distinction between the families suggests to us that eventually they will need to be combined under Macrosternodesmidae, the older name, as more taxa are discovered and described.

A recent paper by Djursvoll (2008) on the Iberian polydesmid genus Schizomeritus Verhoeff, 1931, makes possible, through its clear SEM photographs and labeling, some reconciliation between the gonopod nomenclature originated by Shelley (1994) and used in previous papers on macrosternodesmids (Shear & Shelley 2007, 2008), and that adapted by Djursvoll *et al.* (2001 [2000]) and Golovatch and Wytwer (2007). It appears that our process B is the exomere of Djursvoll (**ex** in our figures), process A corresponds to the endomerite (**en** in our figures), and our distal zone is Djursvoll's tibiotarsus (**tt** in our figures). We previously have not used the term femorite, which Djursvoll (2008) uses for the part of the acropodite traversed by the seminal groove, but agree this term is a useful one, and apply it here. Our solenomere (**s** in our figures) and that of Djursvoll (2008) are the same. In the descriptions that follow we have decided to use the Djursvoll terminology, because it has the advantage of using terms that have already been in the literature for a considerable time, but now with clear definitions; application of this terminology allows for discussion of possible homologies between genera and families of the superfamilies Polydesmoidea and Trichopolydesmoidea. Earlier concerns expressed by Shear and Shelley (2007) now seem to us to be resolved.

Interestingly, the gonopod structure of species of *Schizomeritus* is very similar to that of the new genus *Pratherodesmus*, while the nonsexual characters are quite different. Species of *Pratherodesmus* have only small paranota, strongly produced posteriolaterally, and with regularly arranged rows of clavate setae on an otherwise featureless surface. Species of *Schizomeritus* are more typical of Polydesmidae, with large, squared, anteriorly elevated paranota not strongly produced posteriolaterally. The metazonite surfaces are deeply sculpted into bulging polygonal areas, and the setae are inconspicuous. On poriferous segments *Pratherodesmus* species have the ozopores nearly at the posterior corner and the edges of the paranota are not swollen, while in *Schizomeritus* the pores are more anterior and the edges strongly rebordered. Despite the similarity of the gonopods in general appearance, there are differences. The course of the seminal canal crosses over to the lateral side in *Schizomeritus* and ends in a vesicle and pulvillus. In *Pratherodesmus*, the canal stays mesal, does not end in a vesicle, and there is no pulvillus (although a dense group of cuticular fimbriae probably not homologous to a true pulvillus occurs). At this point it is not at all clear what the significance of these similarities and differences may be.

As previously remarked (Shelley and Shear 2007), the millipeds of the superfamilies Trichopolydesmoidea and Polydesmoidea need close re-examination. Several families in both superfamilies, including Polydesmidae, remain poorly diagnosed and have been used as "wastebaskets" for enigmatic genera and species. We believe that at least two undiagnosed polydesmoid families are to be found in the very diverse, but largely undocumented, North American fauna, and have on hand many new generic and species-level taxa, primarily from the Pacific northwest. In the course of describing these taxa it may be possible to begin to make some sense of the two superfamilies, but without much more knowledge of small tropical polydesmidans, the composition and fate of the Trichopolydesmoidea remains uncertain.

Presently four genera from southwestern North America, including the two new ones below, have been assigned to the family Macrosternodesmidae. They may be separated by the following key:

Key to macrosternodesmid genera in southwestern North America

1a. Adults 6 mm or less in length .... 2.
1b. Adults 8 mm or more in length .... 3.
2a. Paranota obselete or lacking; metazonites with scattered, thin, acute setae; male gonopod with solenomere longer than other gonopod processes .... *Sequoiadesmus* Shear & Shelley.
2b. Paranota more obvious, toothed; metazonites with three rows of clavate setae arising from low pustules; male gonopod with soleomere short .... *Nevadesmus*, **n. gen.**
3a. Metazonital setae arising from obvious pustules, 12–16 in anterior row, posteriorlateral corners of paranota not produced; male gonopod with exomere large, U-shaped; large, folded tibotarsus .... *Tidesmus* Chamberlin 1943.
3b. Metazonital setae not arising from pustules, no more than 8 in anterior row, posteriolateral corners of metazonites produced as acute processes beyond ozopore; gonopods with exomere small or absent, tibiotarsus small or lacking.. .... *Pratherodesmus*, **n. gen.**

***Pratherodesmus* Shear, new genus**

Type species: *Pratherodesmus voylesi* Shear, new species.

Etymology: Named for the late John W. Prather, former lead scientist and spatial ecologist for the ForestERA Project, and professor at Northern Arizona University, Flagstaff, Arizona.

Diagnosis: Small (<10.0 mm length) polydesmidan millipeds with 20 trunk segments, lacking pigment; metatergites smooth, with three transverse rows of short, acute or clavate setae, rows sometimes strongly recurved. Collum ovoid, narrower than head and first leg-bearing segment. Paranota low, margins toothed, posteriolateral angles sharply drawn out. Pygidium blunt, nearly hemispherical when viewed dorsally, sparsely setose, with usual four spinnerets (Shear 2008) arranged in a square and set in individual depressions; pygidial process blunt, decurved. Males with pregonopodal legs unmodified or encrassate. Gonopods with coxae globular, fixed, entirely filling gonostome, tightly appressed or fused in midline; prefemora sparsely setose, strongly transverse, articulating with coxae by process fitting into coxal notch. Exomere small or absent, endomerite large, bulky, dominating gonopod. Acropodite short, solenomere nearly sessile, opening of seminal canal widened, subtended by cuticular teeth and two processes, one proximal and one distal (distal process=tibiotarsus?).

Pratherodesmus differs from *Tidesmus* Chamberlin 1943 (Shear & Shelley 2007) in having a much smaller tibiotarsus of the male gonopod and in its smooth or nearly smooth metazonites. *Sequoiadesmus* Shear & Shelley 2008 occurs near the type locality of *P. despaini*, though at a much higher elevation and in a different cave group (see map in Shear & Shelley 2008); the gonopod of the single known species has an extremely long solenomere and lacks an exomere. *Sequoiadesmus krejcae* Shear & Shelley 2008 is also much smaller (5.8 mm long vs. 9.0 mm for *P. despaini*) and has densely scattered, acute metzonital setae rather than short, clavate ones ranged in rows.

Distribution: Known from caves in northwestern Arizona and the Sierra Nevada of California.

Notes: The genus presently consists of three species of small, white, presumably troglobitic, millipeds found only in caves in the states of Arizona and California. We surmise that the species are in effect cave-limited (troglobionts), because the habitats surrounding the caves are inimical to small millipeds (Fig. 38). The caves of the southwestern part of the United States have not been well-investigated for cave life, with the exception of limited studies of bats; and some investigations of caves where arthropods were opportunistically collected. Notable exceptions are cave-specific inventories of Carlsbad Caverns National Park, New Mexico (Barr and Reddell 1967) and Karchner Caverns, Arizona (Welbourn 1999). Broader surveys were published by Peck (1973, 1981, 1982). Given this, we expect more species of *Pratherodesmus* to be discovered in the future.

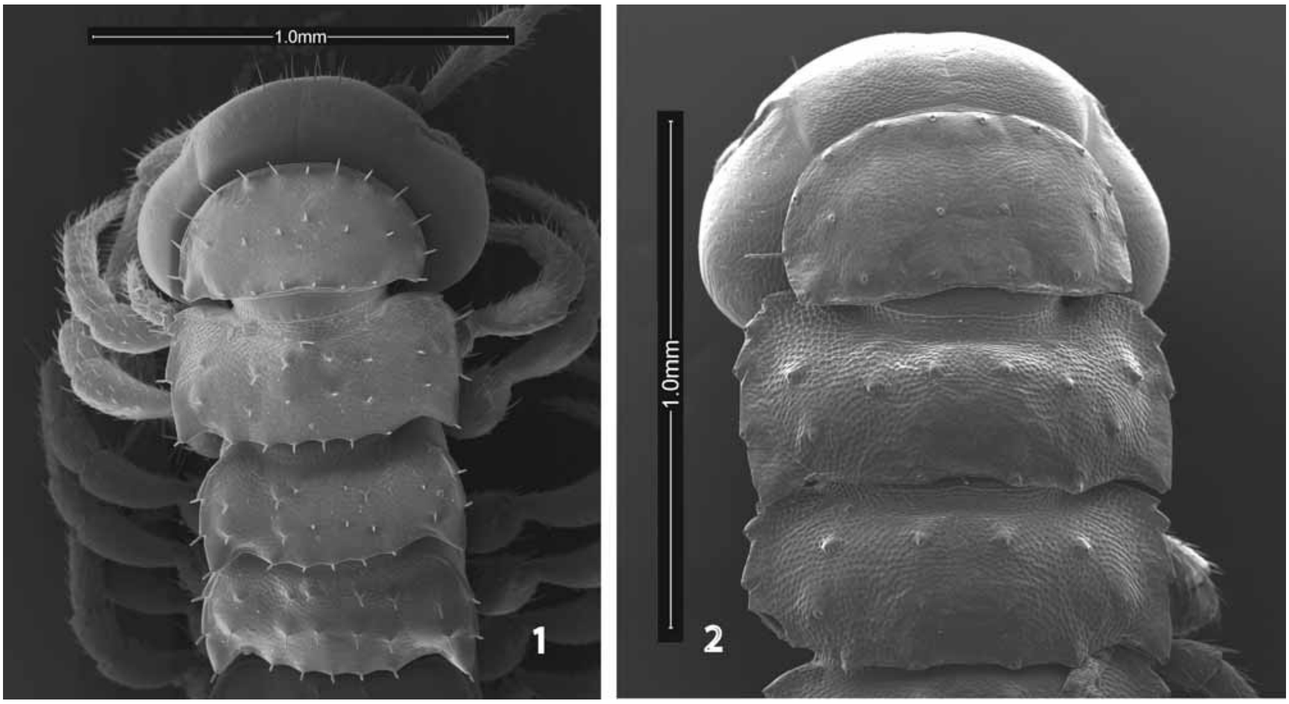
Key to Species

1a. First row of metazonital setae strongly recurved, lateralmost seta on each side widely separated from others in row; posterior marginal row with 5 or 6 setae (Fig. 5); endomerite of gonopod with two small apical lobes set with regularly distributed pustules (Figs.21–24); Tulare Co., California .... *P. despaini*, **n. sp.**

1b. First row of metazonital setae moderately recurved, lateralmost seta on each side not widely separated from others in row (Figs. 4, 6); posterior marginal row with 4 setae; endomerite of gonopod lacking terminal processes (Figs. 33, 34) .... 2.

2a. In anterior or posterior view, endomerite of gonopod narrow, slightly sinuous (Fig. 17); Yavapai Co., Arizona .... *P. ecclesia*, **n. sp.**

2b. In anterior or posterior view, endomerite of gonopod broad, in posterior view with distinct lateral notch (Figs. 11–13); Mohave Co., Arizona .... *P. voylesi*, **n. sp.**



FIGURES 1, 2. Heads, collums and first two segments of males, dorsal view. Fig. 1. *Pratherodesmus despaini*. Fig. 2. *P. voylesi*.

Pratherodesmus voylesi **Shear, new species**
Figs. 2, 6, 9, 11–14, 19, 33, 36.

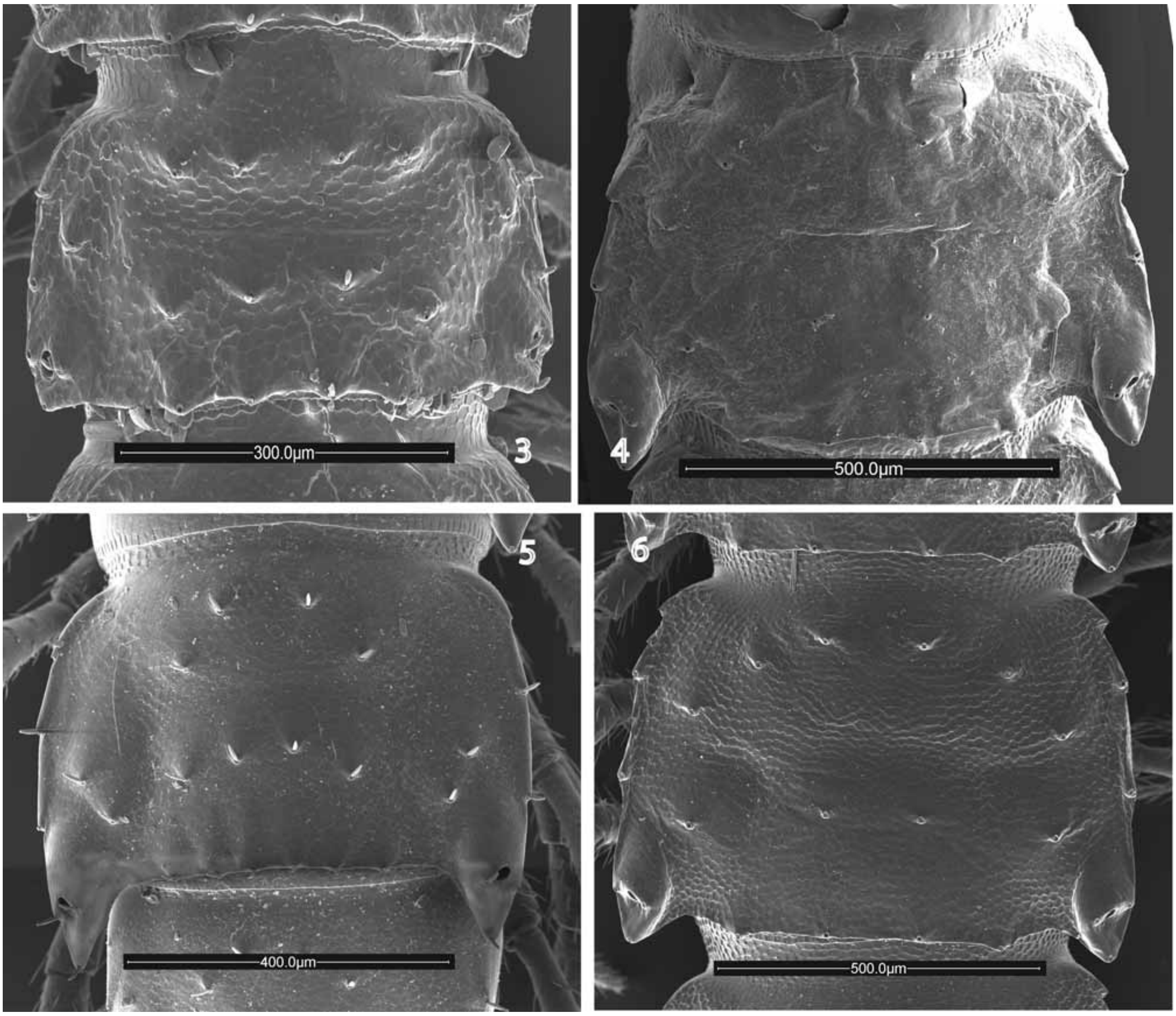
Types: Male holotype, five male and seven female paratypes from Millipede Cave, Mojave Co., Arizona, collected 16 February 2003 by K. Voyles, J. Jasper, M. Porter and K. Dittmar de la Cruz, deposited in FMNH. Four male and sixteen female paratypes from October Gyp Cave, collected 27 March 2004 by same collectors. All specimens deposited in FMNH and CPMAB.

Description: *Male*. Length, 7.5 mm, width 0.75 mm. Antennae long, extended backward reaching to posterior border of sixth segment. Head 20–25% wider than collum, anterior margin of collum (Fig. 2) nearly semicircular, with 10 marginal setae, posterior margin with six marginal setae, nearly straight; middle row with four setae. Typical midbody segment (segment 10; Fig. 6) with metazonite as broad as long, three prominent lateral marginal teeth, posteriolateral angles moderately extended beyond ozopores; marginal teeth each with seta; anterior setal row recurved, with six setae, posterior row nearly straight, with four setae, posterior marginal row with four setae; three setae arranged around ozopore. Posteriorly, setation of anterior row increases to eight. Pygidium (Fig. 9) nearly hemispherical in dorsal view, with about 10 setae visible dorsally, pygidial process short, with four spinnerets arranged in square, typical of polydesmideans. Legs long, slender.

Pregonopodal legs slender, unmodified. Gonopods (Figs.11–14, 33) with hemispherical coxae filling gonostome, tightly appressed, probably immovable, anteriorly excavate to receive telopodites. Prefemora strongly transverse, sparsely setose, distally narrowed to short stem connecting to acropodite. Exomere absent. Endomerite large, blunt, complex, with prominent lateral notch. Course of seminal canal along femorite straight. Solenomere with fine cuticular scales near seminal opening, subtended by short process; apical zone small, flattened, curved, ridged.

Female. Length, 8.2 mm, width, 0.9 mm. Nonsexual characters as in male, but segmental setae longer, more acute, body less slender. Cyphopods as single fused organ (Fig. 19), evidently permanently extruded, with two anterior pores.

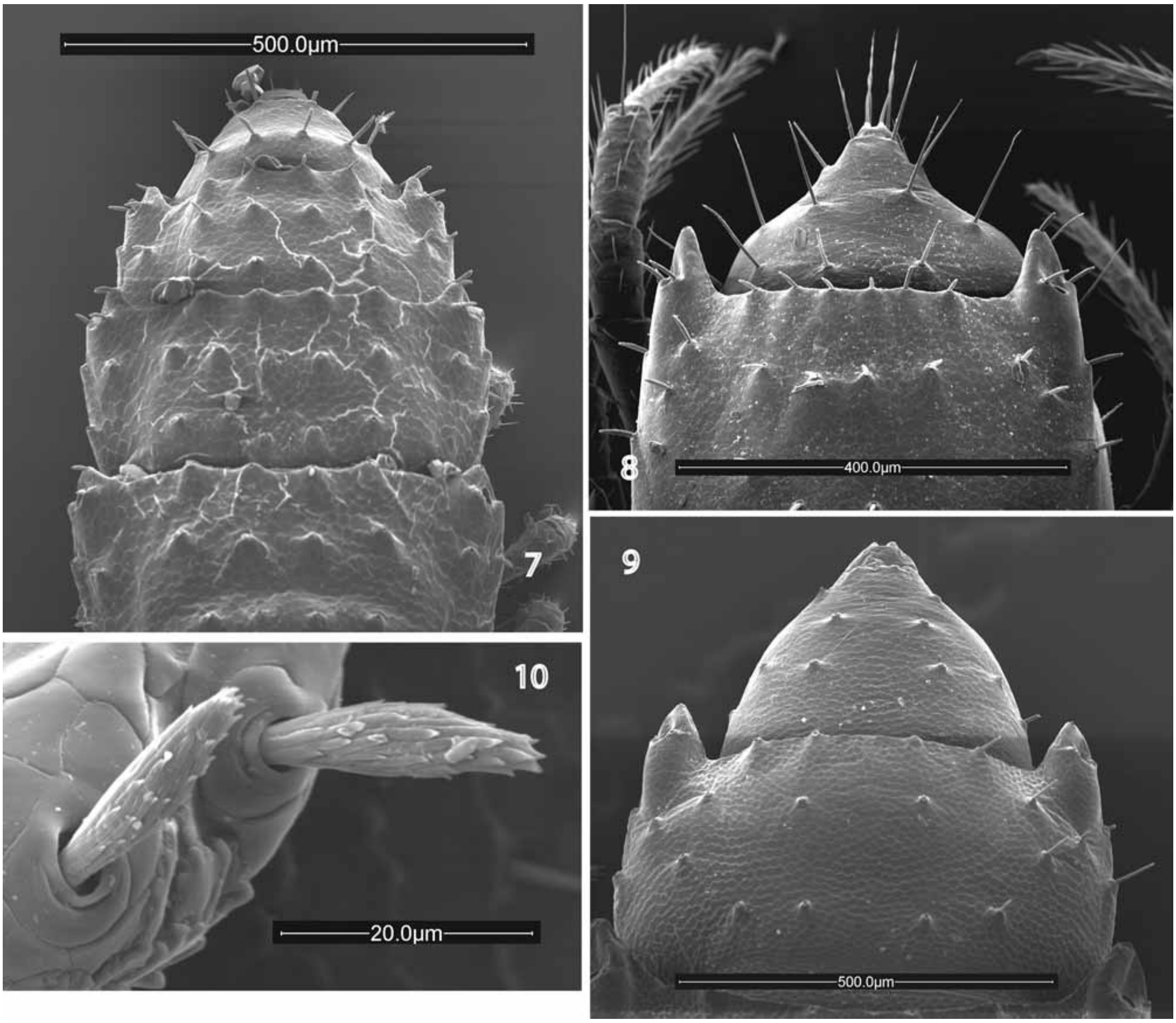
Distribution and habitat: Known only from the two caves named above, located in the northeastern corner of Mohave Co., Arizona, on BLM-Arizona Strip Field Office lands. The exact location of the caves is not given because of conservation concerns.



FIGURES 3–6. Segments 10, dorsal view. Fig. 3. *Nevadesmus ophimontis*. Fig. 2. *Pratherodesmus ecclesia*. Fig. 3. *P. despaini*. Fig. 6. *P. voylesi*.

Millipede Cave (elevation 1371 m [4497 ft.]) is a limestone and gypsum cave with 274 m (900 ft.) of mapped passage. This cave has a vertical entrance approximately 2 by 4m. Average passage height is < 2m. The cave floor is characterized by areas of medium to small breakdown, with unconsolidated silts and sands, stream gravels and exposed bedrock. A single trunk passage is characterized by medium-sized rooms; cave roof height varies from walkable to crawling passage. At the back of the cave, there are three large pools which create ~100% rH (relative humidity) at this depth, where the accessible cave ends in a sump. Floods periodically transport significant amounts of vegetation into this cave, including various types of weeds e.g., Russian thistle (*Salsola kali*), black brush (*Coleogyne ramosissima*), rabbit brush (*Chrysothamnus molestus*) and creosote (*Larrea tridentata*). Logs and branches have also been washed in; however, the source of this larger material is unknown. Detritus often covers portions of the cave floor and forms mounds towards the back of the cave. *P. voylesi* is commonly observed on this material; we suggest this animal is either feeding on detritus, or on fungus or bacteria growing on detritus. Individuals of *P. voylesi* occur from approximately 60 m

(200 ft.) within the cave to ~121 m (400 ft.) up to the sump. Unflooded passage does occur beyond the sump; however, it is unknown whether this species occurs in that part of the cave. Other arthropods detected in the cave include spiders (spp. not known) and pillbugs (*Porcellio laevis*, det. Stefano Taiti). Surface vegetation is inter-mountain basins mat saltbush shrubland (SWReGAP land cover type; Lowery *et al*. 2006).



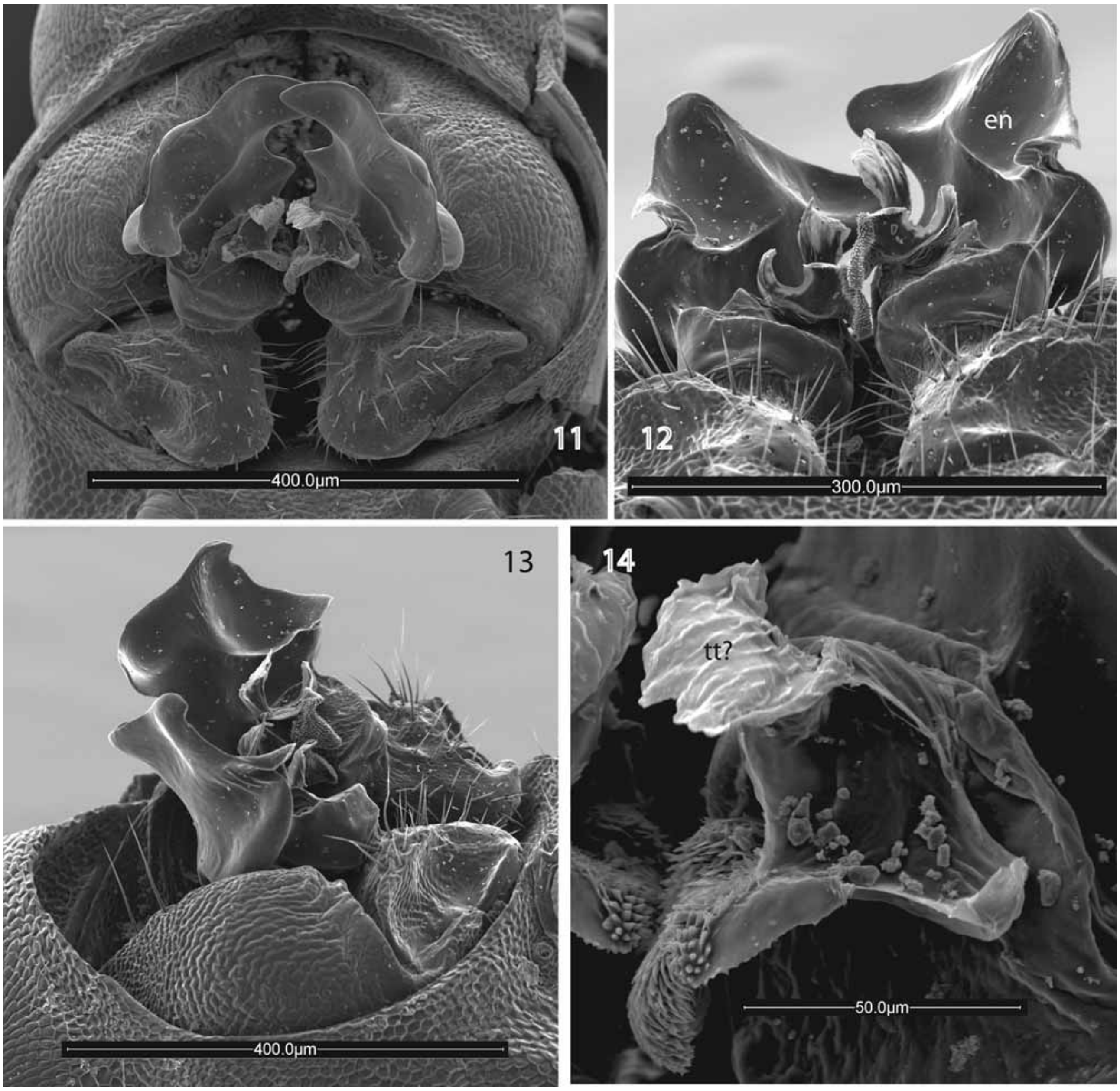
FIGURES 7–10. Figs. 7–9. Pygidia, dorsal view. Fig. 7. *Nevadesmus ophimontis*. Fig. 8. *Pratherodesmus despaini*. Fig. 9. *P. voylesi*. Fig. 10. Metazonital setae anterior to ozopore of segment 10, *Nevadesmus ophimontis*.

October Gyp Cave (elevation 1392 m [4566 ft.]) is a linear phreatic tube with two levels, and consists of 269 m (882 ft.) of passage. This cave has a vertical entrance ~ 2m in diameter. The upper extent is characterized by dry limestone passage, while the lower passageway is moist to wet gypsum. The lower passage contains 30m (100 ft.) of walkable passage tapering to a series of belly crawls to hands-and-knees crawls. The upper level is exposed hardpan with no millipeds, while the lower level is silt to silty clay; this is where the millipeds occur. This cave receives little to no flood detritus. Millipeds are observed from ~134 m (440 ft.) onward to the terminus of the cave. Other arthropods observed in the cave include crickets (*Ceuthophilus* sp.) and beetles (Family Tenebrionidae). Surface vegetation is inter-mountain basins mixed salt desert scrub (SWReGAP land cover type; Lowery *et al.* 2006).

There is one cave within two miles of Millipede and October Gyp caves that contains polydesmid millipeds. While unconfirmed, this likely represents an additional locality of this new species. In the course

of the survey that produced this species, about 300 individual caves were visited, and only the three mentioned here were found to support milliped populations. This does not prove the millipeds are absent from these caves, but they were not found during the time available for exploration.

Etymology: Named for Kyle Voyles, Arizona BLM Cave Coordinator, who organized and led the collecting effort that resulted in the type specimens.



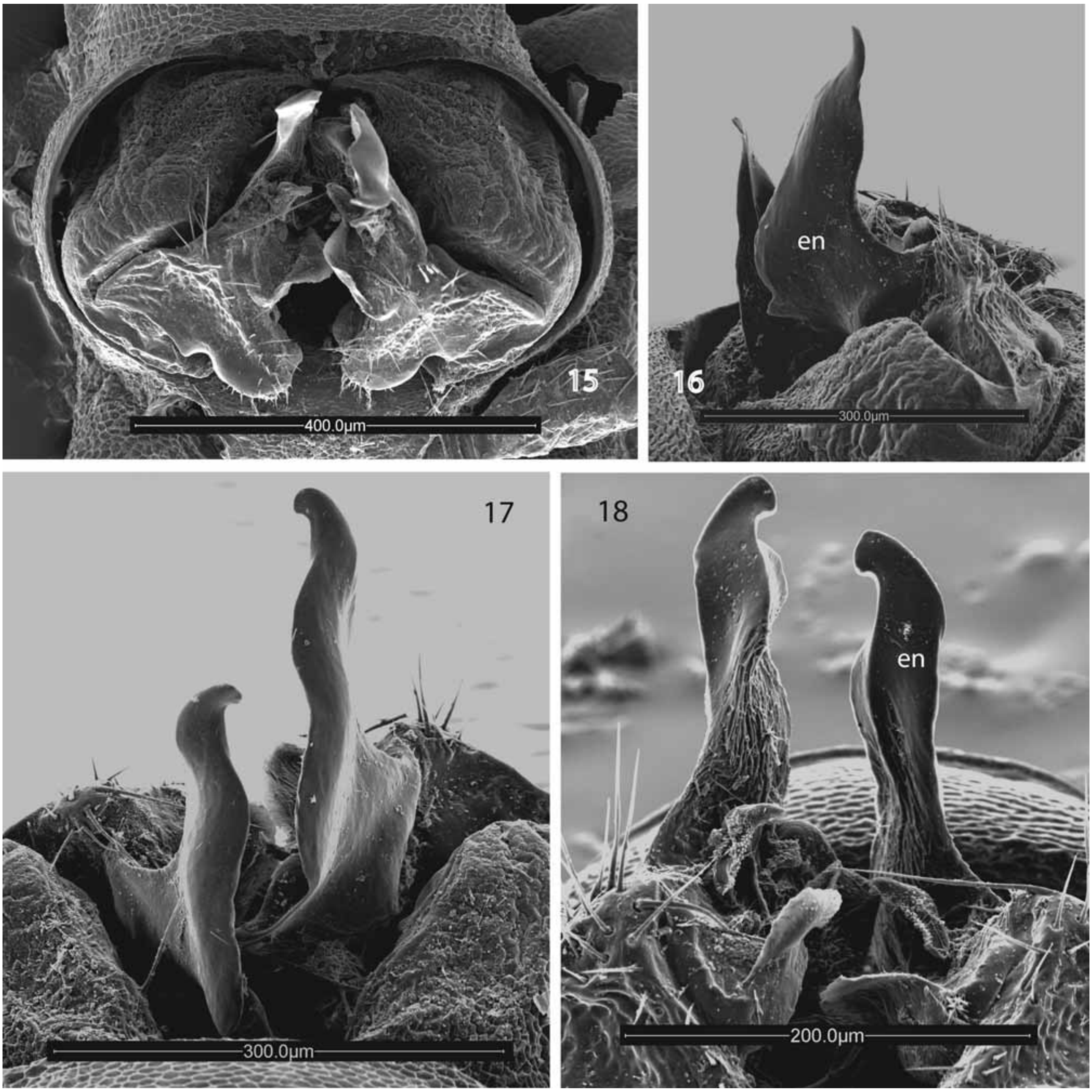
FIGURES 11–14. Gonopods of *Pratherodesmus voylesi*. Fig. 11. Gonopods in gonostome, ventral view. Fig. 12. Posterior view. Fig. 13. Lateral view. Fig. 14. Solenomere, distal zone, and subtending process, posterior view.

Pratherodesmus ecclesia **Shear, new species**
Figs. 4, 15–18, 34, 36.

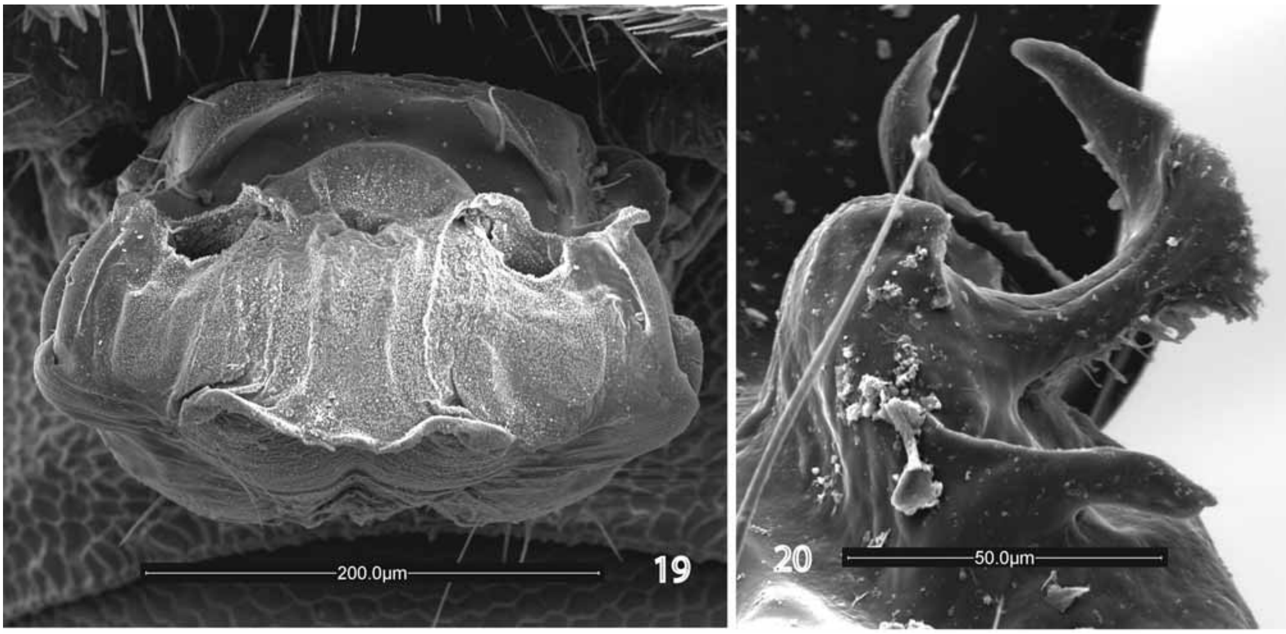
Types: Male holotype, two male, and four female paratypes from Cathedral Cave (part of Cathedral Cave Preserve), 10 miles south-southwest of Ash Fork, Yavapai Co., Arizona, collected 11 January 2007 by J. J. Wynne, deposited in FMNH; one male and one female paratype in CPMAB.

Description: *Male*. Length, 8.0 mm, width 0.75 mm. Nonsexual characters as described for *P. voylesi*, but metazonital setae are significantly longer and more acute (Fig 4). Pregonopodal legs slightly more crassate than postgonopodal legs. Gonopods (Figs. 15–18, 34, 35) large, gonostome walls bulging, prozonite of seventh segment notably swollen when seen dorsally. Gonocoxae hemispherical, filling gonostome, tightely appressed in midline, excavated to receive telopodites. Prefemora as in *P. voylesi*, but with lateral articulation less narrow, subtriangular; not obviously distally narrowed. Exomere absent, endomerite long, sinuous, appearing narrow in either anterior or posterior view, in lateral view, acute-triangular, with small basal tooth. Solenomere similar to *P. voylesi*, tibiotarsus reduced to absent, subtending process, large, lamellate.

Female. Length, 8.0 mm, width 0.83 mm. Nonsexual characters as male, cyphopods as described for *P. voylesi*.



FIGURES 15–18. Gonopods of *Pratherodesmus ecclesia*. Fig. 15. Gonopods in gonostome, ventral view. Fig. 16. Lateral view. Fig. 17. Anterior view. Fig. 18. Posterior view.



FIGS. 19, 20. Fig. 19. Cyphopods of *Pratherodesmus voylesi*, ventral view. Fig. 20. Solenomere, distal zone, and subtending process of gonopod of *P. despaini*, posterior view.

Distribution and habitat: Cathedral Cave (elevation 1621 m [5317 ft.]) is a limestone cave characterized by a large borehole passage, with two narrow side passageways. This cave has not been mapped. The vertical entrance is 1 x 3 m. During the winter months, Cathedral Cave is wet, with standing pools and high humidity, but prior to the summer monsoon it is quite dry. *P. ecclesia* is often observed in the deepest parts of this cave in association with tree branches, likely transported into the cave by human visitors (perhaps for use as torches); they also have been observed in association with candle wax. We suggest this animal is likely feeding directly on the wood or perhaps on the fungi and bacteria growing on the wood; there are often accumulations of dark brown milliped scat where these animals are observed. This species is commonly observed in association with two collembolans (*Sinella* sp., *Drepanura* sp.). Other arthropods occurring in this cave include two spider species (*Cicurina* sp., *Metellina curtisi*, det. Pierre Paquin), three beetles (*Bembidion rupicola*, det. Rolf Aalbu; *Nicrophorus* sp.; *Rhadine* n. sp. Thomas Barr), crickets (*Ceuthophilus utahensis*, det. Theodore Cohn) and ants (*Camponotus ocreatus*, det. Robert Johnson). Surface vegetation is Colorado Plateau pinyon-juniper woodland (SWReGAP land cover type; Lowery *et al.* 2006).

Etymology: The name *ecclesia* is a noun in apposition, Latin for "church."

***Pratherodesmus despaini* Shear, new species**
Figs. 1, 5, 8, 20–24, 32, 35, 36, 39

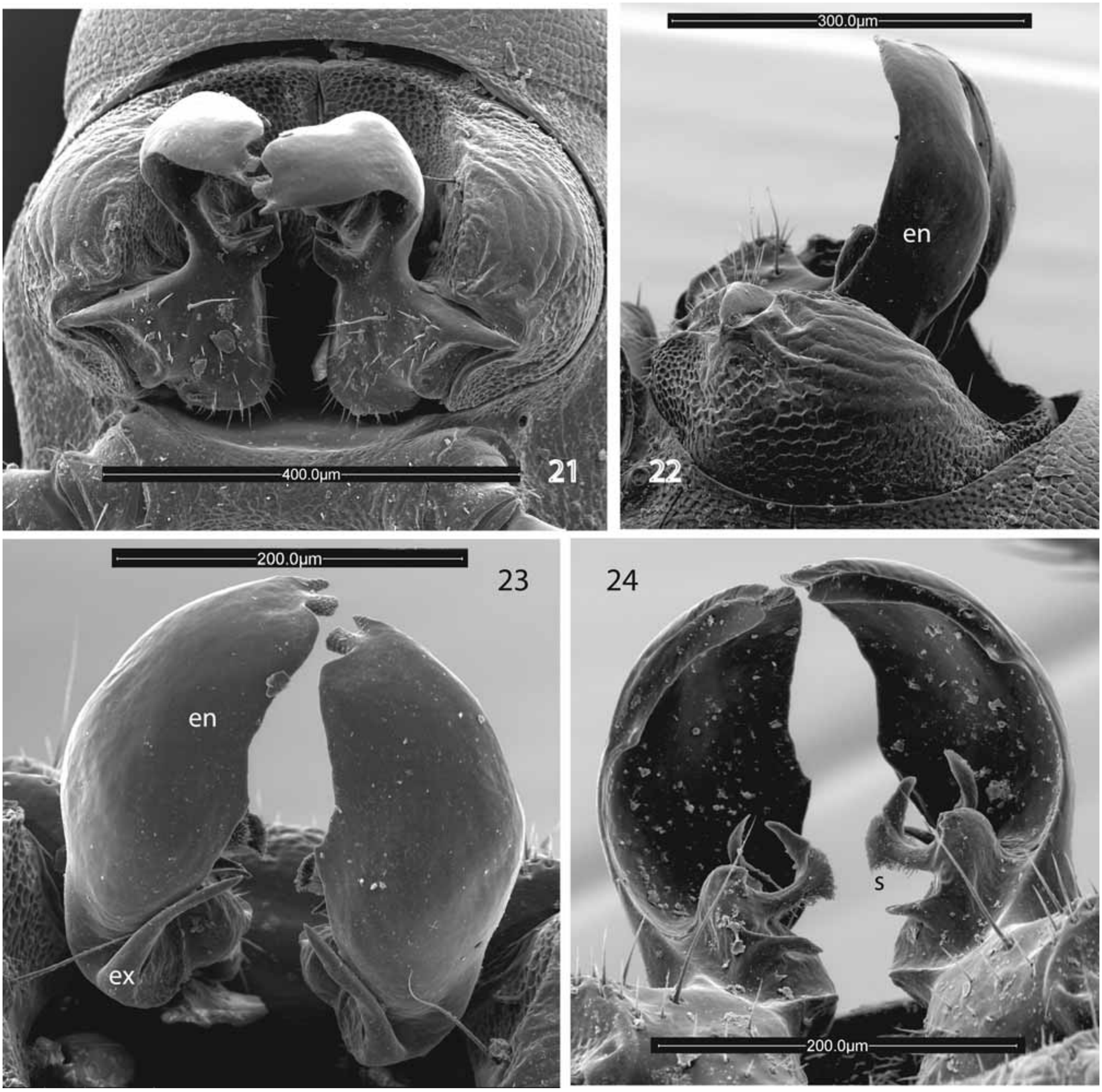
Types: Male holotype, two male and one female paratype from Kaweah Cave, Tulare Co., California, collected 28 April 2004 by J. Krejca, P. Sprouse, S. Fryer, D. Ubick, P. Paquin and W. Savary; one male and two female paratypes from the same locality, collected 10 August 2006 by J. Krejca and J. Despain, deposited in FMNH.

Description: *Male*. Length 9.0 mm, width 0.6 mm (Fig. 39). Head about 50% wider than collum (Fig. 1). Antennae long, extending back to posterior border of fifth segment. Collum with anterior margin arcuate, with 12 marginal setae, posterior margin straight to slightly sinuate, with eight setae, middle row with six setae; posteriolateral angles slightly produced (Fig. 1). Typical midbody segment (Fig. 5, segment 10) with three lateral marginal teeth, each subtended by a seta; anterior row of six setae very strongly procurved, lateralmost

seta of row widely separated, not appearing to be part of row; middle row of six setae slightly recurved; posterior marginal row with six setae. Posteriolateral metazonital corners strongly produced beyond ozopores, ozopores subtended by usual three setae. Pygidium as described for *P. voylesi*, but with 12 long setae (Fig. 8).

Pregonopodal legs markedly encrassate (Fig. 1). Gonopods (Figs. 20–24, 32, 35) with gonocoxae and gonostome as described for *P. voylesi*. Prefemora strongly transverse, articulating process narrow, pointed; prefemoral stem not marked. Exomere present, small, slightly curved, acute. Endomerite large, trullate, apically with two small lobes set with prominent, regular, small warts. Solenomere longer than in other species, with fewer cuticular scales; subtending process short, acute. tibiotarsus not flattened, as acute process similar in length to solenomere.

Female: Length, 9.0 mm, width 0.70 mm. Nonsexual characters similar to male. Cyphopods not observed, not extruded in available female specimens.



FIGURES 21–24. Gonopods of *Pratherodesmus despaini*. Fig. 21. Gonopods in gonostome, ventral view. Fig. 22. Lateral view. Fig. 23. Anterior view. Fig. 24. Posterior view.

Distribution and habitat: Known only from the type locality. Kaweah Cave is located close to the western boundary of Sequoia Kings Canyon National Park, and is unique among the caves in the park because it occurs at low elevation and has greater biodiversity than is found among the higher altitude caves (for locations of caves in the park, see the map in Shear & Shelley 2008). Four troglobitic species, including *P. despaini*, and two other endemic troglophiles are to be found there. The other troglobites are an unidentified trichoniscid isopod, a cambalid millipede, and a pseudoscorpion, probably a species of *Tuberochernes*. The endemic troglophiles include a harvestmen in the genus *Calicina* and a spider in the genus *Usofila*. These may all represent new unnamed species. The cave's accessible portion is a sinuous crawl less than 100 m long, ending in a large room where the animals were collected. One male was collected from a root, and the other specimens were associated with unidentified guano (probably rodent or bat) on the floor. The temperature was not measured on the day of collections, but during an earlier visit to the same room of the cave the temperature was recorded at 11 degrees Celsius. The surrounding vegetation is California lower montane blue oak-foothill pine woodland and savanna (SWReGAP land cover type; Lowery *et al.* 2006).

Etymology: Named for Joel Despain, Cave Management Specialist at Sequoia and Kings Canyon National Parks, who organized and performed much of the sampling that resulted in the discovery of many new cave species.

Notes: This species is more distant from the closely related *P. ecclesia* and *P. voylesi*. While the gonopods are built along the same basic plan, the presence of a small exomere in *P. despaini* suggests, in comparison with *Nevadesmus* and *Tidesmus*, that it would occupy a more basal phylogenetic position within *Pratherodesmus*.

Nevadesmus Shear, new genus

Type species: *Nevadesmus ophimontis* Shear, new species.

Etymology: Named for the state of Nevada, with the combining stem *–desmus*, traditionally used for the names of polydesmidan millipeds.

Diagnosis: Very small (<5.0 mm length) polydesmidan millipeds with 20 trunk segments, lacking pigment; metatergites (Fig. 3) with three transverse rows of short, brushlike or clavate setae (Fig. 10), rows straight, setae on low pustules. Collum ovoid, narrower than head and slightly narrower than first leg-bearing segment. Paranota low, margins not strongly toothed, posteriolateral angles right-angled to acute, but not produced into processes beyond ozopores (Figs. 3, 10). Pygidium blunt, nearly hemispherical when viewed dorsally, sparsely setose, with usual four spinnerets (Shear 2008) arranged in a square and set in individual depressions; pygidial process very short, continuing line of pygidium. Males with pregonopodal legs unmodified. Gonopods with coxae globular, fixed, entirely filling gonostome, tightly appressed or fused in midline; prefemora sparsely setose, strongly transverse, articulating with coxae by process fitting into coxal notch. Exomere long, sinuous, arising from distomesal margin of prefemur, endomerite large, distally with three sinuous processes, exceeding other parts of gonopod. Acropodite bulky, solenomere incurved, nearly sessile, opening of seminal canal widened, proximal subtending process widely separated from solenomere, thin, curved, acute; no obvious tibiotarsus.

Nevadesmus differs from all previously known southwestern macrosternodesmids in its small size. It may be distinguished from *Sequoiadesmus* by its much shorter solenomere.

Distribution: Known from caves in White Pine and Lincoln counties, Nevada.

Notes: This genus is closer in its gonopod to *Tidesmus* than to *Pratherodesmus*, particularly in the proportions of prefemoral processes. However, the gonopods most closely resemble those of the much larger *Harpogonopus* Loomis 1960, generally accepted as a nearctodesmid (Shelley 1993, 1994; Shelley & Shear 2006). Though having the general somatic appearance of a macrosternodesmid, the gonopods of species of this genus are quite nearctodesmid-like, with both endomerite and exomere well-developed, but without an obvious tibiotarsus.

It now seems likely, based on size, geographical proximity, and nonsexual characters that "Tidesmus" *hubbsi* Chamberlin 1943 (see Shear & Shelley 2007) is a member of this genus, and it is included here, though males still have not been collected. A female of *hubbsi* was illustrated by Shear & Shelley 2007, and the history and provenance of the species was discussed therein.

Nevadesmus ophimontis **Shear, new species**
Figs. 3, 7, 10, 25–31, 36, 37.

Types: Male holotype, male and two female paratypes from Model Cave, White Pine Co., Nevada, collected 23 May 2003 by S. J. Taylor, J. K. Krejca, K. Patel, M. Porter, K. Dittmar de la Cruz, deposited in FMNH. The following specimens (deposited at FMNH and INHS) are also paratypes: NEVADA: White Pine Co., same data as holotype, but collected 22 May 2006 by J. K. Krejca, M. E. Slay, G. Baker, 2 females; Snake Creek Cave, 29 May 2003, S. J. Taylor, J. K. Krejca, K. Patel, L. D. Seale, A. Hamilton, S. Johnson, 5 females; 21 May 2006, S. J. Taylor, J. Krejca, M. E. Slay, 3 males, juveniles; Lehman Caves, 26 May 2006, S. J. Taylor, J. K. Krejca, M. E. Slay, G. Baker, 3 males, 3 females; Little Muddy Cave, 23 May 2003. S. J. Taylor, J. K. Krejca, M. Porter, K. Dittmar de la Cruz, a juvenile male presumed this species; Wheeler's Deep Cave, 26 May 2003, S. J. Taylor, J. K. Krejca, M. Porter, K. Dittmar de la Cruz, 2 males, 2 females.

Description: *Male:* Length, 4.5 mm, width 0.45 mm (Fig. 37). Antennae short, clavate; head about 40% wider than collum. Collum with arcuate anterior margin bearing 12 short, clavate setae, posterior margin slightly procurved, with 6(5) marginal setae. Second segment slightly wider than collum. Typical midbody segment (segment 10; Fig. 3) with inconspicuous paranota, two paranotal teeth on each side (possible third tooth is directly opposite ozopore), posteriolateral corner right-angled to slightly obtuse, not drawn out beyond ozopore into sharp process. Metazonital setae on modest tubercles, short, clavate; anterior row of six, with lateralmost setae on each side posteriorly displaced; middle row of four setae, slightly procurved; marginal posterior row of four (six on some segments) setae; usual triad of setae subtends ozopore. Pygidium (Fig. 7) short, rounded, with eight setae, pygidial process very short, blunt, bearing usual four spinnerets.

Pregonopodal legs encrassate. Gonopods (Figs. 25–31) with hemispherical coxae tightly appressed in midline, excavated to receive retracted telopodites. Prefemora densely setose, strongly transverse, articulating process acute; exomere arising from anteriomesal margin of prefemur, long, thin, sinuous. Endomerite from distolateral edge of acropodite, basally broad, incurved, ending in three unequal processes, middle one longest. Subtending process of solenomere is set low and laterally on acropodite, seminal pore with relatively few cuticular teeth.

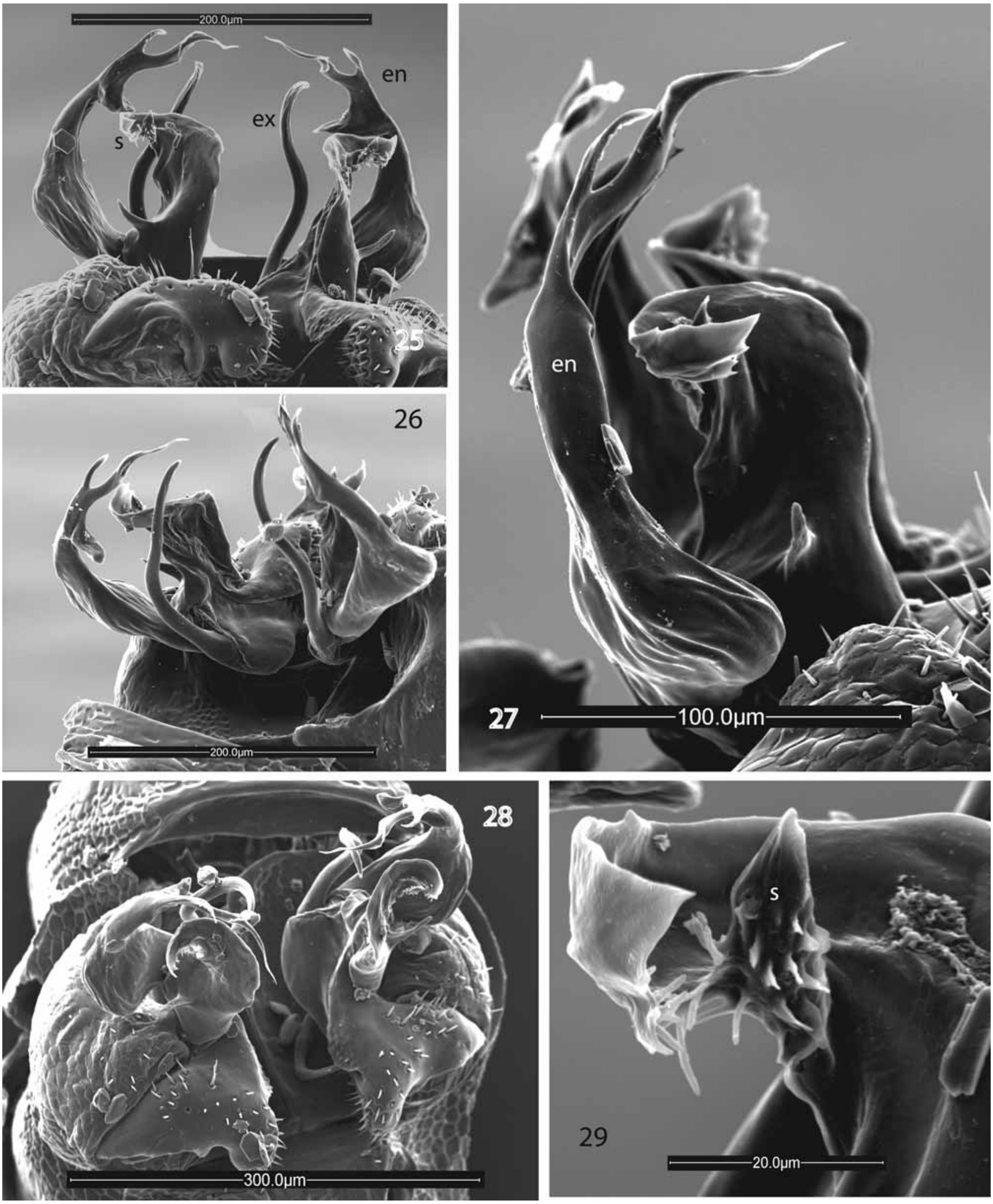
Female: Length, 4.8 mm, width 0.5 mm. Nonsexual characters as in male; cyphopods not studied.

Distribution and habitat: As shown by the map (Fig. 36), the caves occupied by *Nevadesmus ophimontis* are relatively closely clustered, and all are located in Great Basin National Park. Model Cave is a large cave (length 599.9 meters [1968.1 feet]) at an elevation of 2080 meters (6824 feet). The fauna of Model Cave is dominated numerically by Collembola, followed by mites, mayflies, and flies. Globular springtails (*Arrhopalites* spp.) including an undescribed species, were particularly abundant. In addition to *N. ophimontis*, three troglobitic or troglophilic species are present, including the sclerobunine harvestman *Cyptobunus ungulatus ungulatus* Briggs, the conotylid milliped *Idagona lehmanensis* Shear (see Shear 2006), and the pseudoscorpion *Microcreagris grandis* Muchmore. Surrounding vegetation (Fig. 38) for all the caves listed as supporting populations of *N. ophimontis* is Great Basin pinyon-juniper woodland (SWReGAP land cover type; Lowery *et al.* 2006).

Lehman Caves, at an elevation of 2096 meters (6877 feet), is the largest (length ~3352.8 meters [~11,000 feet]) cave in the Great Basin National Park. The fauna includes Collembola, Diptera, and mites, in addition to *M. grandis* and *N. ophimontis*. Notably absent from the Lehman Caves, in spite of intensive collecting, were *C. ungulatus ungulatus* and *Idagona lehmanensis*. Eight taxa of Collembola have been collected in this cave.

Little Muddy Cave is a large cave (length 309 meters [1010.5 feet]) at an elevation of 2045 meters (6709 feet). *Microcreagris grandis* occupies this cave; it is a possible predator on *N. ophimontis*.

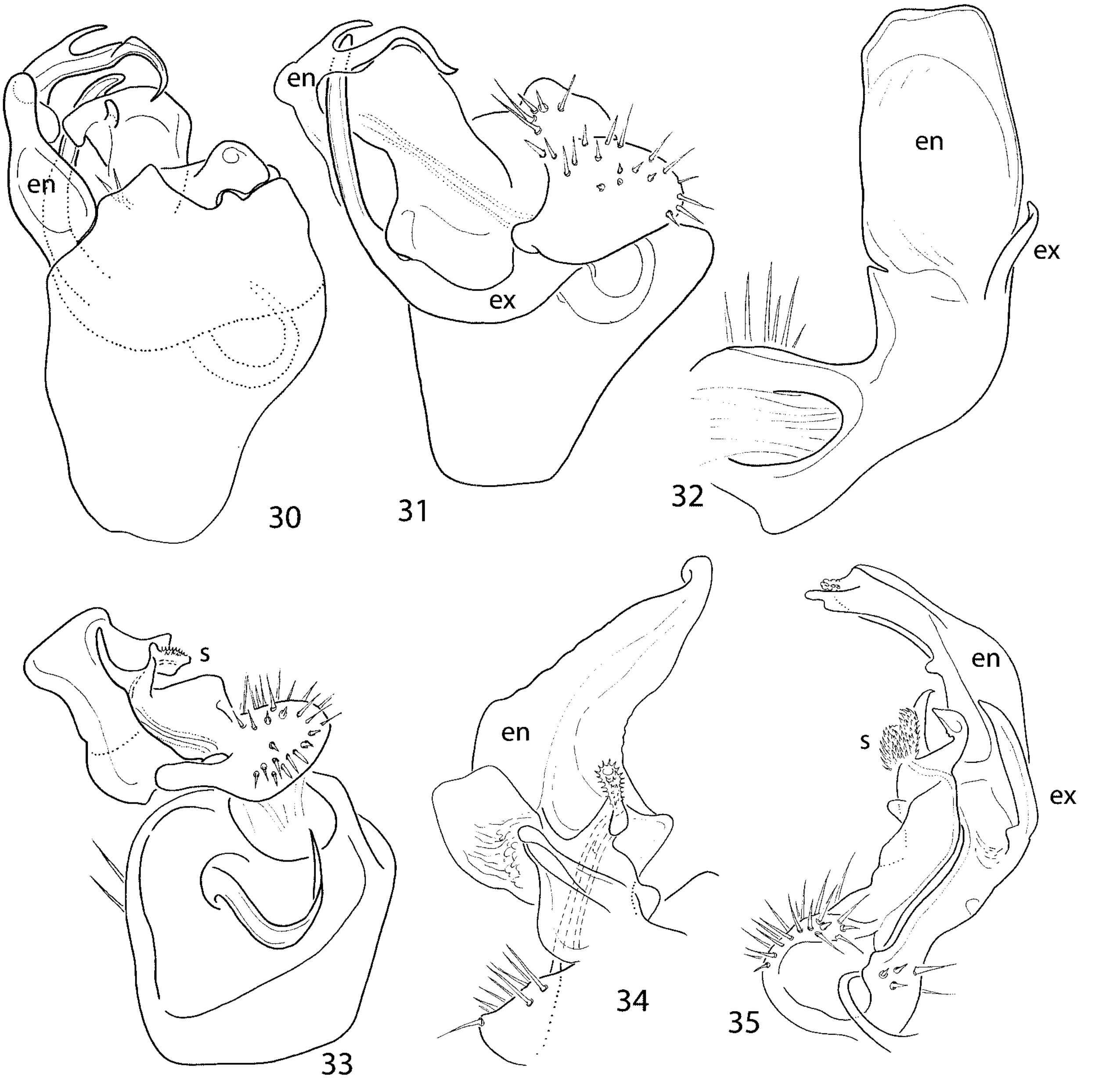
Snake Creek Cave is a large (length 51.3 meters [1682 feet]) cave at an elevation of 2030 meters (6660 feet), and located on a fairly barren, south facing slope (Fig. 38). Springtails and the psocopteran *Speleketor* sp. were dominant in collections.



FIGURES 25–29. Gonopods of *Nevadesmus ophimontis*. Fig. 25. Posterior view. Fig. 26. Anterioventral view. Fig. 27. Lateral view. Fig. 28. Gonopods in gonostome, ventral view. Fig. 29. Solenomere, posterior view.

Wheeler's Deep Cave is one of four interconnected caves making up the Baker Creek Cave System, Nevada's longest cave (length 1315 meters [4315 feet]). It is located at an elevation of 2147 meters (7044 feet) in a limestone outcrop adjacent to the riparian zone of Baker Creek. *Cyptobunus ungulatus ungulatus* and *N. ophimontis* are fairly common in the deeper, wetter parts of this cave, where a perennial stream is present.

Etymology: The species name refers to the Snake Mountain Range, and to Snake Valley, major geographical features associated with the collection localities.



FIGURES 30–35. Drawings of gonopods. Figs. 30, 31. *Nevadesmus ophimontis*. Fig. 30. Lateral view. Fig. 31. Mesal view. Fig. 32. *Pratherodesmus despaini*, posteriolateral view. Fig. 33. *P. voylesi*, mesal view. Figs. 34,35. *P. ecclesia*. Fig. 34. Posterior view. Fig. 35. *P. despaini*, mesal view.

Nevadesmus hubbsi (Chamberlin), new combination

Tidesmus hubbsi Chamberlin, 1943:36, fig. 4. Chamberlin & Hoffman, 1958:74 (list). Shear & Shelley, 2007:63, figs. 22–24.

Remarks: Shear & Shelley explained why *hubbsi* could not be congeneric with *Tidesmus episcopus* Chamberlin, 1943, the type species of *Tidesmus*. Repeated collecting efforts have failed to turn up male specimens, but the close resemblance between females of *N. hubbsi* and *N. ophimontis* makes it highly likely that they are congeneric. The type locality of this species is Cave Valley Cave, in northern Lincoln Co., Nevada (see Fig. 25 in Shear & Shelley 2007).

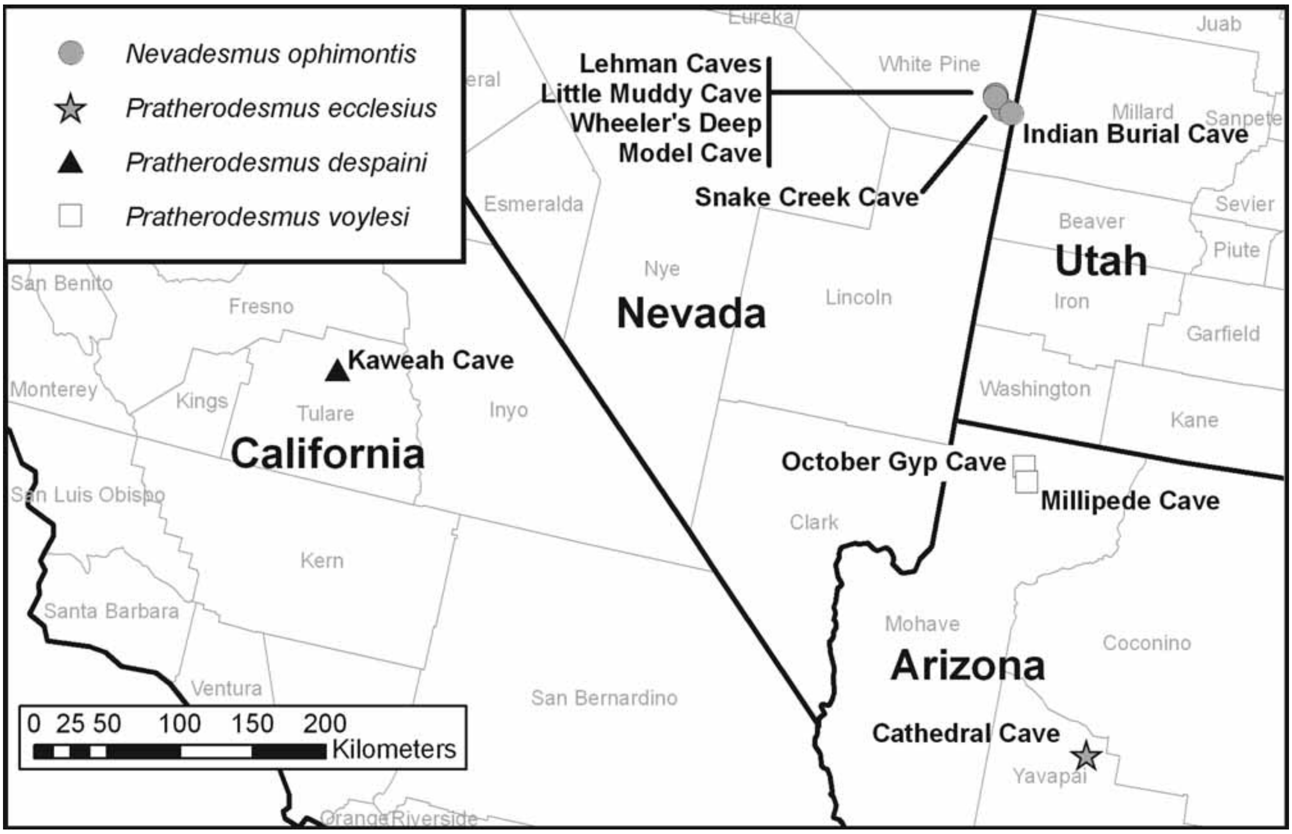
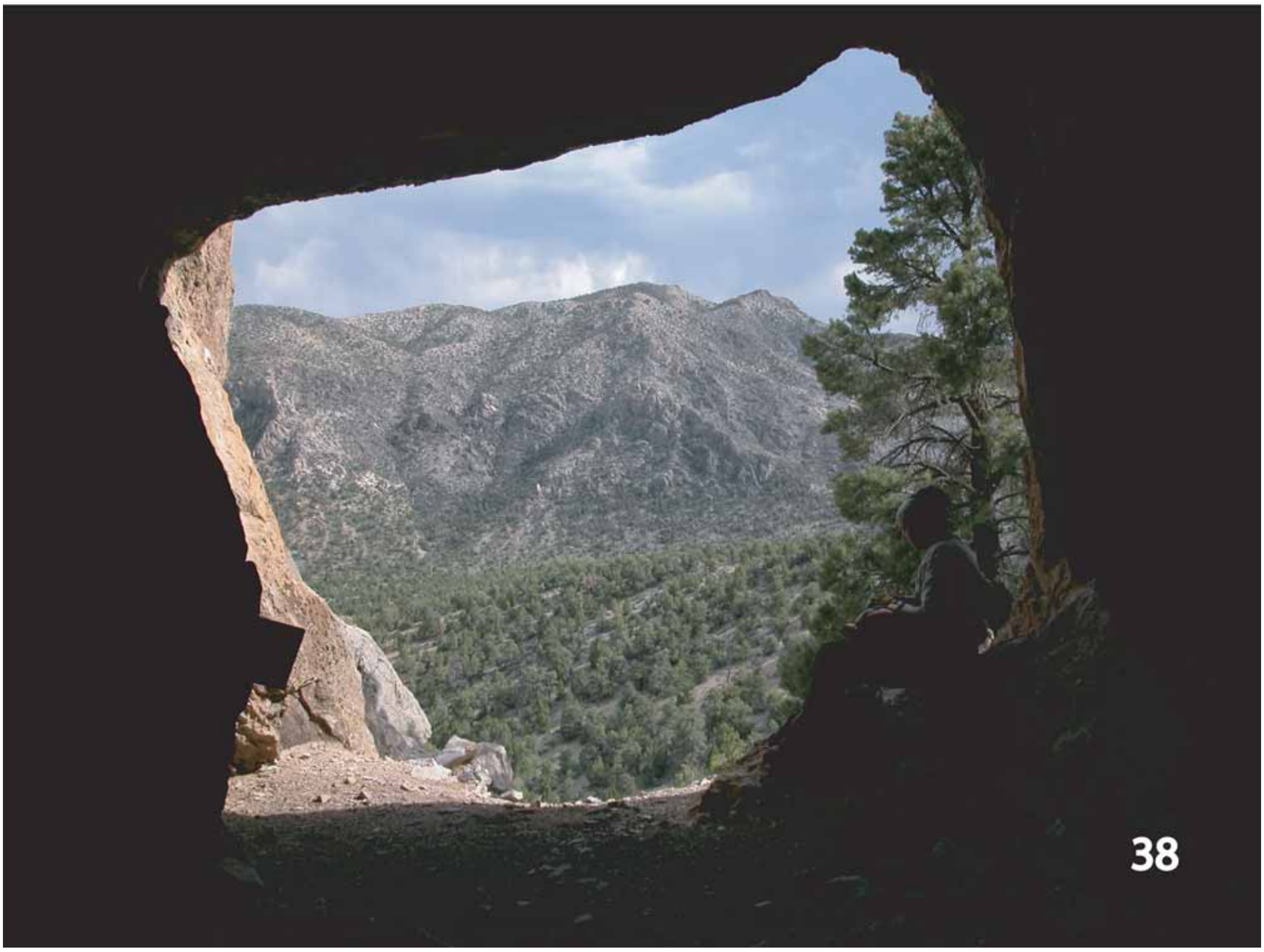


FIGURE 36. Map of parts of the states of Arizona, California, Nevada and Utah, showing localities for milliped collections (Map by S. Taylor).

Comments on the management status of these species

These four millipede species are sensitive to disturbance for multiple reasons. Local threats include inappropriate cave management strategies that could directly harm the species by trampling or habitat alteration (e.g. eutrophication, contamination). The species have extremely limited ranges in a handful of caves, and these caves may receive visitor impacts that are high relative to the total area of the cave. In the case of *P. voylesi*, some 300 caves in the vicinity were surveyed for arthropod populations, and only three of these, in a tightly circumscribed area, supported milliped populations. In addition, groundwater extraction could alter microclimate in some of the caves. Regional threats include global climate change, a factor that recent authors consider likely to become the greatest threat to biodiversity in most regions of the world (Thomas *et al.* 2004). For cave species, we typically lack complete distribution information, and do not have an understanding of their responses to rising surface temperatures (Wynne *et al.*, 2008a). Because their habitat is discontinuous, their ability to disperse may be dramatically affected by climate change. Sala *et al.* (2000) suggest climate change will have the greatest effect on biodiversity in biomes characteristic of extreme climates. Since caves are characterized as nutrient poor and aphotic, and often exhibit low climatic variability at depth, caves are indeed an extreme biome. Wynne *et al.* (2007, 2008b) have established that cave thermal behavior is influenced by surface temperatures. However, it is uncertain to what extent cave deep zones may be buffered from global climate change (Wynne *et al.* 2008a).



FIGURES 37, 38. Fig. 37. Living example of *Nevadesmus ophimontis*, photographed in Snake Creek Cave; length of animal is about 5 mm. Fig. 38. Great Basin pinyon-juniper woodland of the Snake Mountains seen from just inside the entrance to Snake Creek Cave (photos by J. Krejca).

Given the possible effects of mismanagement and potential groundwater withdrawls, and the uncertainties regarding the effects climate change on these species, we recommend establishing population monitoring protocols and regular habitat parameter measurements. Given the sensitive nature of the habitats in which

these four new millipede species occur, we recommend a conservative approach to protecting populations of species of *Nevadesmus* and *Pratherodesmus* species until more is known about their ecological requirements and distributions. Steps have already been taken in this direction, as BLM-Arizona Strip has closed Millipede and October Gyp Caves to visitation. Kaweah Cave and the Nevada caves with populations of *N. ophimontis* are on National Park Service lands and so receive some protection; further measures are under study.

FIGURE 39. Living example of *Pratherodesmus despaini*, photographed in Kaweah Cave (photo by J. Krejca).

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