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Cave millipedes of the United States. XVII. A new troglobiotic Nevadesmus Shear, 2009 from an Arizona cave (Diplopoda, Polydesmida, Macrosternodesmidae) with observations on associated fauna and ecology

WILLIAM A. SHEAR^{1,*}, ROBERT B. PAPE² & PAUL E. MAREK³

¹Professor Emeritus, Department of Biology, Hampden-Sydney College, Hampden-Sydney VA 23943 USA, current address: 1950 Price Drive, Farmville VA 23901 USA.

■ wshear@hsc.edu; • https://orcid.org/0000-0002-5887-7003

²Department of Entomology, University of Arizona, Tucson AZ 85719 USA.

spinelessbiol@aol.com; https://orcid.org/0000-0001-9726-0674

³Department of Entomology, Virginia Tech, Blacksburg VA 24061 USA.

marek@vt.edu; https://orcid.org/0000-0002-7048-2514

*Corresponding author

Abstract

A third species of the macrosternodesmid millipede genus *Nevadesmus* Shear, 2009 is described from a cave in Tonto National Forest, Pinal Co., southern Arizona, USA. This new species, *Nevadesmus superstitiona* Shear, Pape & Marek, **sp. nov.** occurs significantly distant from the localities of the two other species, which occur in Nevada. The epigean and hypogean settings of the cave site and remarks on its natural history are provided. Thirty-two animal taxa are present in the cave, including the new millipede. Four other endemic troglobiotic species are present: a scorpion (*Pseudouroctonus* sp.: Vaejovidae), a terrestrial isopod (*Brackenridgia* sp.: Trichoniscidae), a silverfish (*Speleonycta* sp.: Nicoletiidae) and a thread-legged bug (*Gardena* cf. *elkinsi*: Reduviidae). A resident population of the tailless whip scorpion (*Paraphrynus tokdod*: Amblypygi: Phrynidae) is the first record of this family in an Arizona Cave. Tonto National Forest Cave #34 is the second most species diverse cave currently known in Arizona.

Key words: new species, troglobiont, Pinal County, cave fauna, Cave #34, Tonto National Forest

Introduction

The polydesmidan millipede genus *Nevadesmus* was described by Shear (Shear *et al.* 2009) from caves in White Pine Co., Nevada, USA, and includes the genotype, *Nevadesmus ophimontis* Shear, 2009, and *N. hubbsi* (Chamberlin, 1943). Both of these species show troglobiotic adaptations. Our new species, *N. superstitiona* **sp. nov.,** occurs significantly distant from the localities of the two established species in Nevada. Nevertheless the gonopods and somatic characters clearly indicate that this is a species of *Nevadesmus*.

Millipedes occurring in Arizona caves are poorly known, with only three described species documented prior to the current study: *Colactis utorum* Chamberlin, 1925 (Tynommatidae), *Pratherodesmus ecclesia* Shear, 2009, and *Pratherodesmus voylesi* Shear, 2009 (Macrosternodesmidae) (Shelley 1996; Shear *et al.* 2009; Pape 2016; Shear & Reddell 2017a, 2017b). This seemingly depauperate species richness is unlikely due to a minimal presence of these animals in caves in the state but rather to a lack of search effort. We describe this new species from a cave in the Sonoran Desert in Arizona. With few exceptions the ecology of Arizona caves has received little study, with most of our knowledge resulting from brief inventories of individual caves. Exceptions are longer-term studies at Kartchner Caverns and Arkenstone Cave in southern Arizona, and Bat Cave in Grand Canyon National Park (Welbourn 1999; Muchmore & Pape 1999; Pape 2014, 2016, 2024; Pape & OConnor 2014). We include a preliminary faunal list for the cave supporting the new millipede species. As is typical the majority of species occurring in the cave are arthropods. The epigean and hypogean settings and brief remarks on the biology and ecology of the cave are provided.

Methods

Sampling was accomplished by hand using forceps or a small camelhair brush dipped in ethanol (EtOH). Specimens required for DNA analyses were preserved in 95% EtOH, and others were preserved in 75% EtOH. Field sampling of invertebrates was limited to the minimum number of specimens needed for species identification, description and as vouchers. No pit or other passive trapping devices were used, and therefore preclude bycatch impacts, predation of trapped animals, and potential for spills of toxic fixatives. Ecological notes on the epigean environmental setting and the hypogean cave setting were recorded and are provided for the cave. Cave temperature and humidity were obtained using a Bacharach Instruments sling psychrometer model P/N 0012-7011.

Morphological studies were done using an Olympus SZH stereomicroscope and an Olympus BX50 compound microscope equipped with Nomarski optics. For scanning electron microscopy (SEM), specimens were first cleaned in an ultrasonic cleaner, then mounted on 12.7 mm diameter aluminum stubs using double-sided adhesive carbon discs and allowed to air-dry. These were sputter coated with a 40-nm thick layer of gold and palladium using a Cressington 208HR sputter coater and a Cressington MTM20 thickness controller. SEM micrographs were taken with a FEI Quanta 600 FEG environmental scanning electron microscope. Micrographs were edited and refined using GIMP, and plates were composed in InkScape. An Olympus TG6 F2.0 12.0 megapixel digital camera was used for photographing live animals in the field.

All millipede specimens discussed below are deposited in the Virginia Museum of Natural History, Martinsville, Virginia (VMNH), unless otherwise noted. The remaining arthropod taxa are deposited in the University of Arizona Insect Collection (UAIC) Tucson, Arizona.

The following ecological classifications, modified from Sket (2008), are used in this paper. A troglobiont is an obligate cave animal that cannot live outside of the cave environment. A eutroglophile is a facultative cave animal (population) that is capable of completing its life cycle within caves but may also do so outside caves and in other, similar habitats. A subtroglophile is an animal that has a proclivity for regularly using caves to meet one or more of its ecological needs, such as food, water, shelter and/or reproduction, but must return to the epigean surface environment to meet some required need(s) of its life cycle. A trogloxene is an animal that opportunistically uses cave resources present within its territory. The term incidental (rather than "accidental") is reserved for animals that are attracted to caves, usually due to detection of humidity or odors associated with potential resources, or that randomly enter caves. Animals listed as incidental occurrences, by definition, derive no ecological benefit from their presence in these habitats.

Elliott's biodiversity index (B₁) was calculated for Tonto National Forest Cave #34 [here after TNF Cave #34] (Elliott *et al.* 2017).

Project permission was granted by the Tonto National Forest (2720 permission letter dated March 16, 2023; extended and expanded March 5, 2024; and extended March 24, 2025).

Abbreviations

AMSL Above mean sea level

SEM Scanning electron microscopy

TNF Tonto National Forest

UAIC University of Arizona Insect Collection

USGS United States Geological Survey
VMNH Virginia Museum of Natural History
WRCC Western Region Climate Center

cx gonopod coxa en endomere ex exomere

pf prefemur of gonopod

s solenomere

Taxonomy

Order Polydesmida Pocock, 1887

Family Macrosternodesmidae Brölemann, 1916

The family Macrosternodesmidae was based by Brölemann on the genus and species Macrosternodesmus palicola Brölemann, 1916, a species that occurs in western Europe mostly as a synanthrope in gardens and disturbed habitats. Shear & Reddell (2017b), in the most recent comprehensive examination of the family, suspected that M. palicola may not be a European native, but an immigrant from North America. The gonopods of M. palicola are indeed so similar to those of the North American genus Chaetaspis Bollman, 1887 that Macrosternodesmus could be a junior synonym of Chaetaspis, but not of one of the described species of that genus (unpublished SEM study by WAS and PEM). See Lewis (2002) for a review of the genus Chaetaspis. The two species of the European genus Ophiodesmus Cook, 1896 have also been assigned to Macrosternodesmidae, but have quite different gonopods and may not belong there. One of the Ophiodesmus species has been found in Newfoundland, Canada, having been transported there from Europe by humans, and indicating a propensity for these small millipedes to be spread about with some ease (Palmén 1952). Aside from these three species, all remaining macrosternodesmids are endemic to North America. Shear & Reddell (2017b) grouped the American genera into two subfamilies, (1) Macrosternodesminae, including the two European genera and the North American genera Chaetaspis; Speorthus Chamberlin, 1952; Speodesmus Loomis, 1939; Tidesmus Chamberlin, 1943; Sequoiadesmus Shear & Shelley, 2008; Pratherodesmus Shear, 2009; Packardesmus Shear & Shelley, 2019; and Nevadesmus Shear, 2009; and (2) Nearctodesminae Chamberlin & Hoffman, 1950, with the genera Nearctodesmus Silvestri, 1910; Kepolydesmus Chamberlin, 1910; Bistolodesmus Shelley, 1994; Ergodesmus Chamberlin, 1949 and Leonardesmus Shelley & Shear, 2006. Shear & Reddell (2017b) were unsure of the position of the genus Harpogonopus Loomis, 1960 but a recent SEM study of this genus by WAS and PEM, to be published elsewhere, indicates a close relationship with *Tidesmus* and placement in the Macrosternodesminae. Additional research is necessary to further clarify the internal classification of the family.

Genus Nevadesmus Shear, 2019

Two species from Nevada, *N. ophimontis* (the type species) and *N. hubbsi* (Chamberlin, 1943), have been assigned to *Nevadesmus. Nevadesmus hubbsi* is known only from females (Shear & Shelley 2007; Shear *et al.* 2009), and the type locality is near that of *N. ophimontis*, so when males are finally collected, the latter may become a junior synonym of the former. Gonopod structure suggests that *Nevadesmus* is close to *Tidemus*, surface-dwelling species of which are found in the same region of Arizona as the troglobiotic *Nevadesmus superstitiona*, **sp. nov.** (Shear & Shelley 2007).

Nevadesmus superstitiona Shear, Pape & Marek, sp. nov.

Figs. 1-8

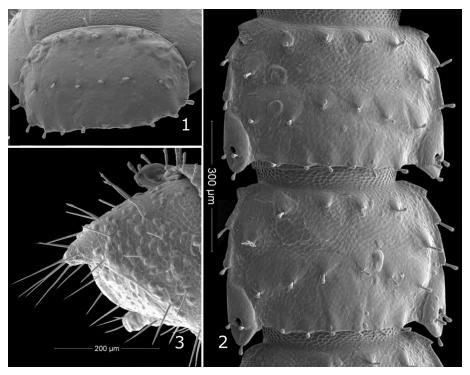
Types. Male holotype (VMNH) and numerous male and female paratypes from Cave #34, Tonto National Forest, Pinal Co., Arizona, collected 28 January and 16 June 2024 by R. B. Pape and C. Poole and 16 June 2024 by R. B. Pape, C. Poole and Sarah Jorgenson. The holotype and paratypes are deposited in VMNH, and additional paratypes are deposited in UAIC.

Etymology. The species epithet, a noun in apposition, refers to the Superstition Mountains, where the cave is located in the southern foothills of the range.

Diagnosis. Distinct from *Nevadesmus ophimontis*, the only other species of the genus for which males are known, in details of the gonopods. In *N. superstitiona*, the solenomere branch bears a long, curved, acute, distal process (**s**, Fig. 6) that is absent in *N. ophimontis*. In *N. ophimontis* the endomere is distally divided into three branches, while *N. superstitiona* the endomere is unbranched except for a small tooth near the tip (**en**, Figs 4, 5).

Description. *Male paratype.* Length, 4.5 mm, width 0.42 mm. Head sparsely setose. Collum (Fig. 1) ovoid, with three rows of clavate setae; the anterior marginal row with 10 setae, the median row with 8, and the posterior

marginal row with 8 setae. Typical midbody poriferous rings (Fig. 2) with very narrow paranota; paranota appearing much as a simple low ridge. Metazonites with three rows of clavate setae originating from low pustules. Clavate setae (Fig. 7) obscurely grooved, with tiny apical and subapical teeth. Anterior row of six setae set slightly back from metazonital margin; lateralmost seta on paranota. A single isolated seta posteriolateral to the row may represent a displaced member of the anterior row, in which case the row actually includes eight setae. Median row slightly curved posteriad, of six setae. Posterior marginal row of six setae. Ozopores opening from prominent calluses, subtended by three clavate setae. Telson (Fig. 3) with long, acute setae. Epiproct short, rounded, with the usual four spinnerets. Paraprocts with three marginal setae. Pregonopodal legpairs markedly crassate.



FIGURES 1–3. *Nevadesmus superstitiona*, **sp. nov. 1**, Collum, dorsal view; **2**. Midbody poriferous rings, dorsal view. **3**. Telson, lateral view.

Gonopods (Figs 4–7) set tightly in socket, coxae closely appressed. Coxae (**cx**, Fig. 4) hemispherical, with groove receiving gonopod telopodites in folded position. Prefemora (**pf**, figs. 4, 5) transverse, lobed, articulating with coxae *via* a long lateral process fitting into a coxal socket. Exomere (**ex**, Figs. 4–6) curved, two-branched, anterior branch broad, blunt, posterior branch gracile, curved, acute. Endomere (**en**, Figs. 4–6) the longest branch, basally broad, curved laterad at nearly a right angle, with small, bifid, subapical tooth. Solenomere (**s**, Fig. 6) roughened with tiny cuticular teeth, bearing long, curved, acute, distal branch that seems to partially lie in a groove in the endomere.

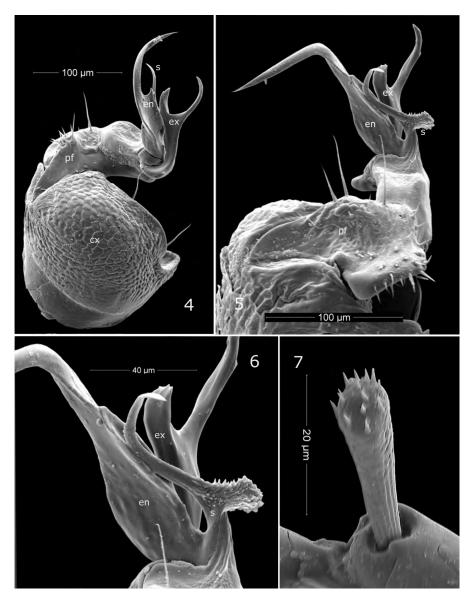
Female paratype. As the male in nonsexual characters, 5.0 mm long, 0.5 mm wide (Fig. 8). **Distribution.** Known only from the type locality.

Natural History Remarks about Tonto National Forest Cave #34, Pinal County, Arizona

Setting

The cave is located south of Superior, Arizona and north of the Gila River (Fig. 9) on lands managed by the Tonto National Forest, United States Department of Agriculture. The cave is a complex consisting of several karst features contained within a single small hill, and is situated in steeply dipping (35-55°) Mississippian Age (359–323 mya) Escabrosa Limestone. The complex is developed within a subsidiary fault of the Central Branch of the Concentrator Fault (Richard & Spencer 1998). There are approximately 1,500 meters of humanly traversable passage in the

complex, which are accessible through separate surface connections, and not all of which are connected by human-negotiable passage. The cave temperature is 21° C, and relative humidity varies from 72 to 98% in different areas of the cave.



FIGURES 4–7. *Nevadesmus superstitiona*, **sp. nov. 4**. Right gonopod, lateral view. **5**. Right gonopod, ventral view. **6**. Distal elements of right gonopod, ventral view. **7**. Segmental seta. **Abbreviations**: **cx**, gonopod coxa; **en**, endomere; **ex**, exomere, **pf**, prefemur; **s**, solenomere.

The elevation at the site is approximately 1028 m AMSL. Annual precipitation recorded at the Superior, Arizona meteorological station (028348; 1920-2006) is 46 centimeters (WRCC 2025). The cave occurs near the northern and eastern limits of the Sonoran Desert biome. The habitat at the site is ecotonal between Arizona Upland Subdivision Sonoran Desert and Semidesert Grassland (Turner 1982; Brown & Makings 2014). The saguaro cactus (*Carnegiea gigantea*) is a defining element and keystone species in the Sonoran Desert (Drezner 2014; USGS 2023), but is only sparsely present in the study area. The 180,000 acre Telegraph Fire in 2021, fueled in large part by non-native, invasive red brome grass (*Bromus rubens*), heavily impacted local vegetation. Few saguaros survived this event, and whether they will persist in the area is considered doubtful. Livestock grazing is currently active in the area, and trampling of small saguaros likely inhibits plant recruitment. The presence of fire tolerant non-native invasive grasses has permanently altered the historic plant community and fire regime in the area.

Currently, dominant plant species are mostly forbs and grasses. Common species include flatspine bur ragweed (Ambrosia acanthacarpa), desert marigold (Baileya multiradiata), brittlebush (Encelia farinosa), little

deserttrumpet (Eriogonum trichopes), desert globemallow Sphaeralcia ambigua), Texas sleepydaisy (Xanthisma texanum), purple threeawn (Aristida purpurea) and red brome. Significant woody and succulent species are catclaw acacia (Senegalia greggii), blue paloverde (Parkinsonia florida), crucifixion thorn (Canotia holacantha), velvet mesquite (Neltuma velutina), Arizona rosewood (Vauquelinia californica), skunkbush sumac (Rhus trilobata), ocotillo (Fouquieria splendens), red barberry (Mahonia haematocarpa), banana yucca (Yucca baccata), cactus apple (Opuntia engelmannii), and saguaro.



FIGURES 8–13. 8. *Nevadesmus superstitiona*, **sp. nov.**, female. **9**. Map showing approximate location of TNF Cave #34. **10**. *Brackenridgia* sp. **11**. *Pseudouroctonus* sp. **12**. *Gardena* cf. *elkinsi*. Fig. **13**. *Paraphrynus tokdod*.

Cave ecology

While all elements of the cave complex are not connected through passages that are navigable by humans, arthropod movement between these areas is considered likely. Thus, the invertebrate biota is suspected to be ecologically connected, and concentrated in areas of suitable habitat within the complex. Studies are ongoing, but to date we have documented 32 animal taxa, predominantly arthropods, integrated into the cave's ecology (Table 1). There is no evidence of current or historic use of the cave by bats. The configuration of the entrance to the main portion of the cave is shaped such that use by bats is likely precluded. Important nutrient input is provided by guano deposited by the resident cave cricket (*Ceuthophilus pinalensis* Hubbell, 1936) population, and scats of the white-throated wood rat (*Neotoma albigula* Hartley, 1894). Other nutrient input is mostly limited to organic materials falling into entrances and meteoric water-borne nutrients transported through the overlying soil horizon and fractured bedrock.

TABLE 1. Animal taxa recorded from Tonto National Forest Cave #34, Pinal County, Arizona.

Order	Family	Species	Association
Rodentia	Muridae	Undet.*	Unknown
	Muridae	Neotoma albigula	Trogloxene
Anura	Bufonidae	Anaxyrus punctatus	Trogloxene
Urodela	Ambystomatidae	Ambystoma tigrinum	Trogloxene
Scorpiones	Vaejovidae	Pseudouroctonus sp.	Troglobiont
Amblypygi	Phrynidae	Paraphrynus tokdod	Subtroglophile
Araneae	Pholcidae	Psilochorus sp.	Eutroglophile
	Nesticidae	Eidmannella pallida	Eutroglophile
	Undet. (Agelenidae?)	Undet.	Trogloxene?
	Cybaeidae?	Undet.	Subtroglophile?
	Liocranidae	Neoanagraphis chamberlini	Trogloxene
Pseudoscorpiones	Chernetidae	Allochernes sp.?	Eutroglophile
Isopoda	Trichoniscidae	Brackenridgia sp.	Troglobiont
	Trichoniscidae	Trichoniscus sp.?	Eutroglophile?
Polydesmida	Macrosternodesmidae	Nevadesmus superstitiona sp. nov.	Troglobiont
Callipodida	Tynommatidae	Colactis sp.	Eutroglophile
Lithobiomorpha	Lithobiidae	Undet.	Subtroglophile
Collembola	Entomobryidae?	Undet.	Eutroglophile
Microcoryphia	Machilidae	Undet.	Subtroglophile
Zygentoma	Nicoletiidae	Speleonycta sp.	Troglobiont
Orthoptera	Rhaphidophoridae	Ceuthophilus pinalensis	Subtroglophile
Blattodea	Corydiidae	Arenivaga sp.	Subtroglophile
Hemiptera	Reduviidae	Gardena cf. elkinsi	Troglobiont
	Pyrrhocoridae	Dysdercus mimulus	Incidental
	Rhopalidae	Liorhyssus hyalinus	Incidental
Coleoptera	Staphylinidae	Undet. #1	Trogloxene?
	Staphylinidae	Undet. #2	Subtroglophile
	Staphylinidae?	Undet. #3 (larva)	Unknown
	Histeridae	Haeterius sp.	Subtroglophile
	Dermestidae	Anthrenus sp.? (larva)	Trogloxene
	Anobiidae	Niptus ventriculus	Subtroglophile
	Tenebrionidae	Eleodes c. carbonaria	Trogloxene
	Tenebrionidae?	Undet. (larva)	Unknown
Hymenoptera	Braconidae	Undet.	Unknown
	Formicidae	Neivamyrmex nigrescens	Subtroglophile
	Formicidae	Nylanderia terricola	Subtroglophile
Diptera	Mycetophilidae	Subf. Keroplatinae? (larva)	Subtroglophile
	Sphaeroceridae	Spelobia sp.?	Subtroglophile?
	Tachinidae?	Calyptrate muscoid pupa	Potential parasite**

^{*}Mouse skeleton embedded in calcite flowstone on floor breakdown.

 $^{{\}tt **Potential\ internal\ parasite\ of\ } {\it Ceuthophilus\ pinalensis}.$

The top invertebrate predator in the cave is the tailless whip scorpion *Paraphrynus tokdod*, Cazzaniga & Prendini, 2024 (Amblypygi: Phrynidae; (Fig. 13). Amblypygids are primarily a tropical group, and were previously recorded from caves in the United States only from the Edwards Plateau in central Texas. This is the first cave record of an amblypygid in Arizona. The population is considered subtroglophilous. The other large predator is an undescribed scorpion (Vaejovidae: *Pseudouroctonus* sp.; Fig. 11). Five of the arthropod taxa found in the cave are considered endemic troglobiotic species, including *N. superstitiona* (Fig. 8), the *Pseudouroctonus* sp. scorpion (Fig. 11), a terrestrial isopod (Trichoniscidae: *Brackenridgia* sp.?; Fig. 10), a nicoletiid silverfish (Nicoletiidae: *Speleonycta* sp.), and an undescribed thread-legged bug (Reduviidae: *Gardena* cf. *elkinsi*); Fig. 12.

The diverse and exceptional fauna found in the cave make it the second most diverse cave currently known in Arizona after Kartchner Caverns in Kartchner Caverns State Park, near Benson, Arizona. Elliott's biodiversity score (B₁) for TNF Cave #34 is 608. The B₁ score for Kartchner Caverns is 4408 (Pape, unpublished data).

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Literature cited

Bollman, C.H. (1887) Description of fourteen new species of North American myriapods. *Proceedings of the United States National Museum*, 10, 617–627.

https://doi.org/10.5479/si.00963801.10-670.617

Brölemann, H.W. (1916) Essai de classification des Polydesmiens (myriapodes). *Annales de Société Entomologique de France*, 84, 523–608.

https://doi.org/10.1080/21686351.1915.12279415

Brown, D.E. & Makings, E. (2014) Semidesert grassland. *In*: Siegwarth, M.D. (Ed.), A guide to North American grasslands. *Desert Plants*, 29 (2), 71–82.

http://www.journals4free.com/link.jsp?l=43971469

Cazzaniga, N. & Prendini, L. (2024) Integrative systematics reveals cryptic diversity in *Paraphrynus* whip spiders (Amblypygi: Phrynidae) from southwestern North America. *Diversity*, 16 (11), 669. https://doi.org/10.3390/d16110669

Chamberlin, R.V. & Hoffman, R.L. (1958) Checklist of the millipeds of North America. *Bulletin of the United States National Museum*, 212, 1–236.

https://doi.org/10.5479/si.03629236.212

Chamberlin, R.V. (1910) Diplopoda from the western states. *Annals of the Entomological Society of America*, 3, 233–262. [https://www.biodiversitylibrary.org/page/10181143] https://doi.org/10.1093/aesa/3.4.233

Chamberlin, R.V. (1925) Notes on some centipeds and millipeds from Utah. *Pan-Pacific Entomologist*, 2, 55–63. [https://www.biodiversitylibrary.org/page/53385474]

Chamberlin, R.V. (1943) On nine North American polydesmoid millipeds. *Proceedings of the Biological Society of Washington*, 56, 35–40. [https://www.biodiversitylibrary.org/page/34564498]

Chamberlin, R.V. (1949) Some millipeds of the families Polydesmidae and Xystodesmidae. *Journal of the Washington Academy of Sciences*, 39, 94–102. [https://www.biodiversitylibrary.org/page/39703388]

Chamberlin, R.V. (1952) Three cave-dwelling Millipeds. *Entomological News*, 63, 10–12. [https://www.biodiversitylibrary.org/page/2561658]

Cook, O.F. (1895) Introductory note on the families of Diplopoda. *In*: Cook, O.F. & Collins, G.N. (Eds.), The Craspedosomatidae of North America. *Annals of New York Academy of Science*, 9, pp. 1–7. https://doi.org/10.1111/j.1749-6632.1896.tb55430.x

Drezner, T.D. (2014) The keystone saguaro (*Carnegiea gigantea*, Cactaceae): a review of its ecology, associations, reproduction, limits, and demographics. *Plant Ecology*, 215, 581–595. https://doi.org/10.1007/s11258-014-0326-y

- Elliott, W.R., Reddell, J.R., Rudolph, D.C., Graening, G.O., Briggs, T.S., Ubick, D., Aalbu, R.L., Krejca, J. & Taylor, S.J. (2017) The cave fauna of California. *Proceedings of the California Academy of Sciences*, Series 4, 64 (1), 1–311. [https://research.fs.usda.gov/treesearch/54815]
- Hartley, F. (1894) Description of a new species of wood-rat from Arizona. *Proceedings of the California Academy of Sciences*, Series 2, 4, 157. [https://www.biodiversitylibrary.org/item/54481#page/167/mode/1up]
- Hubbell, T.H. (1936) A monographic revision of the genus *Ceuthophilus* (Orthoptera, Gryllacrididae, Rhaphidophorinae). *University of Florida Publication. Biological Science Series*, 2 (1), 1–551. https://doi.org/10.1093/aesa/29.3.448
- Lewis, J.J. (2002) *Chaetaspis aleyorum*, a new species of milliped from Tumbling Creek Cave, Missouri, with a synopsis of the cavernicolous species of *Chaetaspis* (Diplopoda: Polydesmida). *Myriapodologica*, 7 (11), 101–111. [https://www.vmnh.net/content/vmnh/uploads/PDFs/research and collections/myriapodologica/myriapodologica v7 11.pdf]
- Loomis, H.F. (1939) The millipeds collected in Appalachian caves by Mr. Kenneth Dearolf. *Bulletin of the Museum of Comparative Zoology*, 86 (4), 165–193. [https://www.biodiversitylibrary.org/page/2775915]
- Loomis, H.F. (1960) Millipeds of the order Polydesmida from the western states and Baja California. *Journal of the Kansas Entomological Society*, 33, 57–68. [https://www.jstor.org/stable/25083168]
- Muchmore, W.B. & Pape, R.B. (1999) Description of an eyeless, cavernicolous Albiorix (Pseudoscorpionida: Ideoroncidae) in Arizona, with observations on its biology and ecology. *Southwestern Naturalist*, 44 (2), 138–147. [https://www.jstor.org/stable/30055419?seq=1]
- Palmén, E. (1952) Survey of the Diplopoda of Newfoundland. Annales Zoolocici Societatis *Zoologicae Botanicae Fennicae* 'Vanamo', 15 (1), 1–31.
- Pape, R.B. (2014) Biology and ecology of Bat Cave, Grand Canyon National Park, Arizona. *Journal of Cave and Karst Studies*, 76 (1), 1–13.
 - https://doi.org/10.4311/2012LSC0266
- Pape, R.B. (2016) The importance of ants in cave ecology, with new records and behavioral observations of ants in Arizona caves. *International Journal of Speleology*, 45 (3), 185–205. https://doi.org/10.5038/1827-806X.45.3.1936
- Pape, R.B. (2024) Biology and ecology of a deep cave nesting spider wasp, *Ageniella evansi* Townes, (Hymenoptera: Pompilidae), in Arizona. *Journal of Natural History*, 58 (29–32), 963–1054. https://doi.org/10.1080/00222933.2024.2374542
- Pape, R.B. & OConnor, B.M. (2014) Diversity and ecology of the macro-invertebrate fauna (Nematoda and Arthropoda) of Kartchner Caverns, Cochise County, Arizona, United States of America. *CheckList Journal*, 10 (4), 761–794. https://doi.org/10.15560/10.4.761
- Pocock, R.I. (1887) On the classification of the Diplopoda. *Annals and Magazine of Natural History*, 5 20, 283–295. https://doi.org/10.1080/00222938709460057
- Richard, S.M. & Spencer, J.E. (1998) Compilation geologic map of the Ray-Superior Area, central Arizona Geological Survey open file report, OFR-98-13, 3 map sheets, map scale 1:24,000, 1–47. Available from: http://hdl.handle.net/10150/630771 (accessed 27 July 2025)
- Shear, W.A. & Reddell, J.M. (2017a) The milliped genus *Tidesmus* Chamberlin, 1943, (Polydesmida: Macrosternodesmidae). *Zootaxa*, 1656 (1), 51–68.
 - https://doi.org/10.11646/zootaxa.1656.1.2
- Shear, W.A. & Reddell, J.M. (2017b) Cave millipedes of the United States. XIV. Revalidation of the genus Speorthus Chamberlin, 1952 (Diplopoda, Polydesmida, Macrosternodesmidae), with a description of a new species from Texas and remarks on the families Polydesmidae and Macrosternodesmidae in North America. *Insecta Mundi*, 1034. [https://digitalcommons.unl.edu/cgi/viewcontent.cgi?article=2034&context=insectamundi]
- Shear, W.A. & Shelley, R.M. (2007) The millipede genus *Tidesmus* Chamberlin, 1943 (Polydesmida: Macrosternodesmidae). *Zootaxa*, 1656 (1), 51–68.
 - https://doi.org/10.11646/zootaxa.1656.1.2
- Shear, W.A., Taylor, S.J., Wynne, J.D. & Krejca, J.K. (2009) Cave millipeds of the United States. VIII. New genera and species of polydesmidan millipeds from caves in the southwestern United States (Diplopoda, Polydesmida, Macrosternodesmidae). *Zootaxa*, 2151 (1), 47–65.
 - https://doi.org/10.11646/zootaxa.2151.1.2
- Shelley, R.M.; Shear, W.A. (2006) *Leonardesmus injucundus*, n. gen., n. sp., an aromatic, small-bodied milliped from Washington State, U. S. A., and a revised account of the family Nearctodesmidae (Polydesmida). *Zootaxa*, 1176 (1), 1–16. https://doi.org/10.11646/zootaxa.1176.1.1
- Shelley, R.M. (1994) The milliped family Nearctodesmidae in northwestern North America, with accounts of *Sakophallus* and *S. simplex* Chamberlin (Polydesmida). *Canadian Journal of Zoology*, 72 (3), 470–495. [https://cdnsciencepub.com/doi/pdf/10.1139/z94-066]
 - https://doi.org/10.1139/z94-066
- Shelley, R.M. (1996) The millipede order Callipodida in western North America (Schizopetalidae: Tynommatinae), and a summary of the New World fauna. *Entomologica Scandinavica*, 27, 25–64. https://doi.org/10.1163/187631296X00197

- Silvestri, F. (1910) Descrizioni preliminari di novi generi di Diplopodi. *Zoologischer Anzeiger*, 35, 357–364. [https://biodiversitylibrary.org/page/9741798]
- Sket, B. (2008) Can we agree on an ecological classification of subterranean animals? *Journal of Natural History*, 42 (21/22), 1549–1563.
 - https://doi.org/10.1080/00222930801995762
- Turner, R.M. (1982) Sonoran Desertscrub. *In*: Brown, D.E. (Ed.), Biotic communities of the American Southwest United States and Mexico. *Desert Plants*, 4 (1–4), pp. 181–221. [http://www.journals4free.com/link.jsp?l=43971469]
- United States Geological Survey [USGS]—Southwest Biological Science Center (2023) Winkler, D.E. The iconic giant saguaro cactus in the Sonoran Desert. Available from: https://www.usgs.gov/centers/southwest-biological-science-center/science/iconic-giant-saguaro-cactus-sonoran-desert (accessed 21 October 2025)
- Welbourn, W.C. (1999) Invertebrate Cave Fauna of Kartchner Caverns, Kartchner Caverns, Arizona. *Journal of Cave and Karst Studies*, 61 (2), 93–101. [https://scholar.google.com/scholar?hl=en&as_sdt=0%2C3&as_vis=1&q=Welbourn%2C+W.+C. +1999.+Invertebrate+Cave+Fauna+of+Kartchner+Caverns%2C+Kartchner+Caverns%2C+Arizona.+Journal+of+Cave+a nd+Karst+Studies+61+%282%29%3A+93–101.+&btnG=]
- Western Region Climate Center [WRCC] (2025) Arizona Cooperative Network; WRCC Superior Station 028348. Available from: https://wrcc.dri.edu/ (accessed 27 July 2025)