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Authors: Hannibal, Joseph T., and May, William J.

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Permian millipedes from the Fort Sill fissures of southwestern Oklahoma, with comments on allied taxa and millipedes preserved in karstic environments

Joseph T. Hannibal[1] and William J. May[2]

[1]Cleveland Museum of Natural History, 1 Wade Oval Drive, Cleveland, Ohio 44106, USA <jhannibal@cmnh.org>
[2]Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, Norman, Oklahoma 73072, USA <paleogatherings@yahoo.com>

Abstract.—Permian millipedes are rare, especially so considering the relative abundance of millipedes in Carboniferous rocks. We report an early Permian millipede fauna containing three new genera and species of millipedes (*Oklahomasoma richardsspurense* new genus new species, *Karstiulus fortsillensis* new genus new species, and *Dolesea subtila* new genus new species) found in fossil-producing pockets of the Fort Sill fissures exposed in the Dolese Quarry near Richards Spur, southwest Oklahoma, USA. These are the first new genera of invertebrates to be described from this site, one of the most prolific fossil-vertebrate sites in the world. We also comment on taxa with morphological similarities and note previously described occurrences of Permian millipedes as well as occurrences of fossil myriapods (millipedes and centipedes) in karst deposits (caves and fissure fills) in Europe, Africa, Asia, North America, and the Caribbean. In contrast with the forms found at Richards Spur, most of these previous accounts of millipedes found in caves and fissure fills are of Pleistocene forms that are closely allied to modern taxa. The taxa from Richards Spur bear some similarities to Pennsylvanian forms. Karst (cave and fissure) faunas should be ranked with concretion faunas, cannel coals, and amber faunas as a major source of fossil myriapods.

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Introduction

The record of millipede body fossils extends from the lower Paleozoic into the Holocene. Fossil millipedes are particularly well known from Carboniferous strata, but two key reviews of fossil millipedes have noted Permian occurrences as being extremely rare (Shear et al., 2009, p. 9; Shear and Edgecombe, 2010, p. 186). Permian occurrences are rare, but a number of forms have been described to date. The record is complex, however. Some taxa that were described as being Permian, including those from the Gaskohle of the "Permformation" of Bohemia (Fritsch, 1901), are now known to be late Carboniferous. Thus, most of the specimens noted in Branson's *Bibliographic Index of Permian Invertebrates* (1948, p. 984–988) are Carboniferous. Some other supposed Permian millipedes have been determined not to be millipedes. Sterzel (1878) determined that the supposed millipede *Palaeojulus dyadicus* Geinitz, 1872, described from the 'Dyas' (Permian) of Saxony, was half of a fern leaf. And Hannibal et al. (2005) reidentified a supposed Permian millipede from New Mexico as an ichnofossil without any millipede affinities.

There are authentic Permian millipedes, however. These include *Arthropleura*, whose range extends into the Permian (Kraus, 2005; Schneider et al., 2010). Not all authors have agreed, however, on that taxon being a millipede. Several moderate-sized millipede species have been named from the lower Permian of central Europe. These include *Archiulus brassii* (Dohrn, 1868) from Lebach-Saar, *Xyloiulus permicus* (Beurlen, 1925) from Plauenschen Grund near Dresden, and *Pleurojulus steuri* Schneider and Werneburg, 1998 from Manebach, Thuringia.

Guthörl (1934) redescribed and illustrated *A. brassii* in his classic paper on the Permo-Carboniferous fossil arthropods from the Saar-Nahe-Pfalz region of Germany. This has resulted in other specimens from Central Europe being either assigned to, or compared with, this species. Three specimens from the lower Permian Rotliegend of the Palatinate have been identified as *Archiulus* cf. *A. brassii* (and one millipede specimen left indeterminate) by Heidtke (1983). Goretzki (1990) compared a millipede from the Permian Oberhöfer Schichten of the Rotliegendes (Permian) in Thuringia with *A. brassii*. More recently, Poschmann and Schindler (2004, p. 303, figs. 2G, 3H) have referred millipedes from the Permo-Carboniferous sites of Sitters and Grügelborn to '*Archiulus*' *brassii*. Their assignment was based on the presence of fine longitudinal grooves that are continuous across the prozonite and metazonite, and so they assigned this taxon to the Xyloiulidae Cook, 1895. The genus *Archiulus* Scudder in Dawson, 1868 (p. 496) is also in need of revision. Not all of the specimens referred to this genus are even millipedes (Hannibal, 2001).

Schneider and Werneburg (1998, p. 30) noted that *X. permicus* could belong to the Xyloiulidae or the

Nyraniidae Hoffman, 1969. Beurlen's (1925, p. 183) figures show *X. permicus* to have pleurotergites whose metazonites are marked with horizontal striae, and his figures show a very close similarity to the diagrammatic figures of *Xyloiulus* (*Xylobius*) made by Scudder (in Dawson, 1878, p. 56). On the basis of this comparison, *X. permicus* does belong to the genus *Xyloiulus* and the family Xyloiulidae.

Pleurojulus steuri is an elongate millipede with paranota, ozopores, and pleurotergites whose dorsal sides are marked with coarse longitudinal ornamentation. That species, however, does not belong in the genus *Pleurojulus* Fritsch, 1901 as what were interpreted as pleurites by Schneider and Werneburg (1998, figs. 11, 13, 14) are paranota (Wilson and Hannibal, 2005, p. 1106). It is closer to the Carboniferous *Hexecontasoma* Hannibal, 2000 in having both distinct paranota and longitudinal ornamentation on its dorsum.

Sharov (1962) referred the late Permian (formerly considered Triassic) form *Tomiulus angulatus* Martynov, 1936 from southwestern Siberia to the Archiulidae Scudder, 1873. Dzik (1981) referred this species to the Xyloiulida, but Hannibal and Shcherbakov (2019) have suggested a nematophoran affinity instead. They also noted that late Permian millipedes have recently been found in Russia.

There are also several occurrences of unnamed fossil millipedes known from the Permian of Central Europe, the United States, and Africa. These include millipedes from the Permian Tambach Formation of the Rotliegend of the Thuringian Forest of Germany (Martens et al., 1981, p. 82, pl. 3, figs. 5–7). Poschmann (2007), in a review that discussed various taxa of Permo-Carboniferous millipedes (and other fauna), noted a possible oniscomorph and xyloiulids from the Meisenheim Formation (lower Permian). Poschman et al. (2018) have also identified a specimen from the lower Permian Rotliegend strata of Pfeffelbach in the Saar-Nahe Basin of the Rhineland-Palatinate as a xyloiulid. Xyloiulid millipedes from the lower Permian of Texas have been briefly described by Baird (1958) and noted by Mamay (1966, p. E11), but neither author illustrated their material from their Texas sites. Fossils identified as millipede-like arthropods have been figured (Reisz and Laurin, 1991, fig. 1; Reisz and Scott, 2002, fig. 1) but not described from the late Permian *Cistecephalus* Assemblage Zone of South Africa (the locality was originally reported as Triassic). No centipedes have been described from the Permian, but there has been a mention by Wilson (2006, fig. 4) of a scolopendromorph centipede from the Permian.

It is clear that all of the previously described or noted Permian millipedes, with the possible exception of *Arthropleura,* are in need of restudy.

The purpose of this paper is to describe a millipede fauna, including three new genera of millipedes, found at the Dolese Quarry, a Permian fissure-fill locality near Richards Spur, Oklahoma, to compare these with other fossil millipedes and to bring to notice other occurrences of fossil myriapods (millipedes and centipedes) preserved in karst deposits. Specimens figured from this fauna are cited with Sam Noble Oklahoma Museum of Natural History numbers (OU). An additional Carboniferous specimen (*Hexecontasoma carinatum* Hannibal, 2000) illustrated is cited by its Field Museum of Natural History number (FMNH PE).

Geologic setting

The Richards Spur locality is at the Dolese Quarry, a limestone quarry located near the small town of Richards Spur, Comanche County, in southwest Oklahoma. The locality is north of Fort Sill Army Post, and so Olson (1967, p. 34) referred to this site as the "Richards Spur (Ft. Sill) site." It is located at 34°46′31.33″N and 98°24′22.00″W, which is about 5 miles (8 km) west of the center of the city of Elgin, Oklahoma. The Richards Spur locality has been documented in a number of publications, beginning with Gregory et al. (1956) and continuing to the present (e.g., Olson, 1967; May and Cifelli, 1998; Sullivan and Reisz, 1999; Burkhalter and May, 2002; Woodhead et al., 2010; deBraga et al., 2019). A fissure and cave complex has developed here on the north and south flanks of a small mountain in the Slick Hills in Ordovician bedrock belonging to the Arbuckle Formation. Millipedes described here were found at two localities, about 1 mile apart, at about the same elevation in the quarry.

The fillings of the cave systems at the location are highly mineralized. There are numerous stalactites and typical cave formations including stalagmites, flowstone, and a few cave popcorn and soda-straw structures. Large calcite crystals have been found measuring up to 30 cm (12 inches) long. The fissure and cave infill deposits are considered equivalent with the Arroyo Formation, lower Clear Fork Group, lower Permian (Woodhead et al., 2010). The formation belongs to the Cisuralian Series (MacDougall et al., 2017) in International Union of Geological Sciences (IUGS) stratigraphic terms. Tabor and Yapp (2005) and MacDougall et al. (2017) have described and illustrated aspects of the setting and nature of the fissure-fill material at Richards Spur. They determined that the fill material included sparry calcite, iron sulfides, and goethite. They, and previous studies cited by them, noted that the calcite mineralization occurred or was initialized in the Permian. Woodhead et al. (2010) dated a stalagmite from Richards Spur at 289 ± 0.68 Ma and analyzed speleothems from the caves/fissures as bearers of climatic information.

Varying concentrations of disarticulated and articulated skeletal remains are found within the soft clay and in some of the calcite-cemented rocks that have been deposited in the caves/fissures at Richards Spur. With more than 40 described species, Richards Spur is one of the richest known sources of early Permian, upland terrestrial tetrapod skeletal remains in the world. The site is unique in the early Permian because of the preservation of the vertebrate assemblages in undistorted condition. Most are disarticulate elements, however. Many bones have smaller calcite and pyrite crystals on and inside them. Many of the skulls that have been found are complete and cemented together with calcite. The primary tetrapod found at the site (May and Cifelli, 1998) is a reptile, *Captorhinus aguti* (Cope, 1882) that is believed to have been an insectivore and so was a potential predator of millipedes. An acleistorhinid parareptile from Richards Spur has been reported (Modesto et al., 2009) as having indeterminate arthropod cuticle preserved in its oral cavity. That material is composed of an antenna and an elongate, slightly curved "presumed cercal element." These fragments are relatively large, several millimeters in length. The illustrations of these fragments are not sufficiently detailed to allow assignment to a particular arthropod group (although the elongate element certainly does not belong to a millipede; the antenna is in need of a closer examination). Neither plants nor pollen have been recovered from this site.

Most of the fossils are found in the greenish clay within the caves/fissures. But there are also large pieces of calcite-cemented rock that contain hundreds of miscellaneous bones. The millipedes were recovered by wet-screening. Specimens are associated with calcite. Some specimens are infilled with calcite. Others are composed of a brown-colored material that overlays the calcite.

Materials and methods

Materials.—The fossil millipedes were found in the greenish-gray clay infill of the Permian cave/fissure system at the Dolese Richards Spur quarry. This clay also contains bones of fossil vertebrates. The millipedes were discovered during the recovery of the fossil bones by WJM.

Methods.—Collected clay was wet-screened through a 30-mesh screen. The screened residue was examined using a Bausch and Lomb BVB-73 dissecting microscope to recover the fossil vertebrate bones. Other than screen washing, no preparation was done on the recovered millipedes. All microphotographs except Figure 1.1 were taken with Scanning Electron Microscopes at the Sam Noble Oklahoma Museum of Natural History and the University of Akron Environmental Scanning Microscope Laboratory. Figure 1.1 was made using a camera through a light microscope. Photoshop was used to obtain optimal lighting levels and contrast, and burning and dodging was used to bring out details, of the photomicrographs.

Repositories and institutional abbreviations.—The fossil millipedes from the Fort Sill fissures described here are deposited in the Sam Noble Oklahoma Museum of Natural History (OU 12150 through OU 12154 and OU 44526). The holotype of *Hexecontasoma carinatum*, illustrated in this paper, is deposited in the Field Museum of Natural History (FMNH PE 23487).

Systematic paleontology

Class Diplopoda Blainville in Gervais, 1844
Subclass Chilognatha Latreille, 1802–1803
Infraclass Helminthomorpha Pocock, 1887
Superorder Juliformia Attems, 1926
Order Incertae sedis
Superfamily ?Xyloiuloidea Attems, 1926

Remarks.—The Xyloiuloidea, as used here (following Wilson, 2006), include cylindrical millipedes with ozopores and ornamentation consisting of horizontal striae or oblique ridges and grooves. Wilson (2006) also diagnosed members of this superfamily as having fused tergites, pleurites, and sternites (that is, having their body segments fused into complete rings). Because of incomplete preservation, complete fusion—or lack of complete fusion—of body segments of the new species from the Fort Sill fissures cannot be determined, and so assignment to the superfamily Xyloiuloidea is tentative. The nature of the ring structure of other forms that have been called xyloiulids is also debatable.

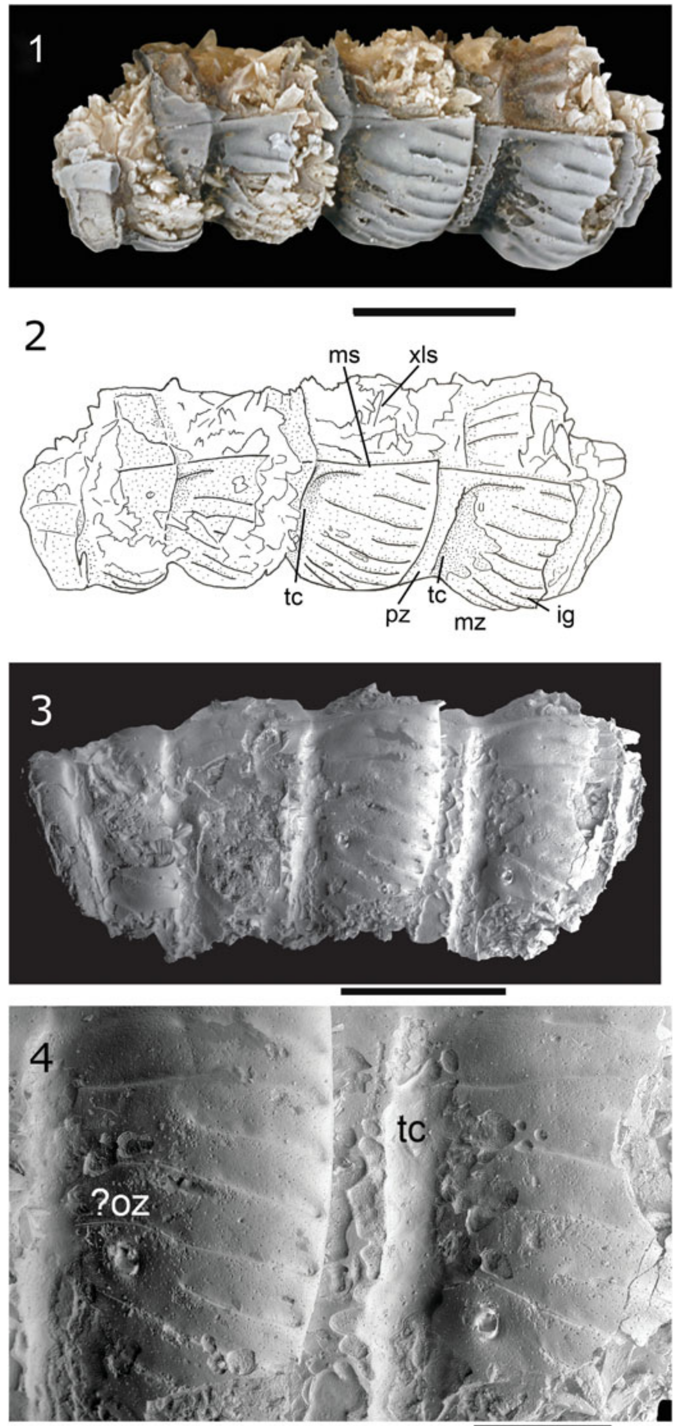

Figure 1. *Karstiulus fortsillensis* n. gen. n. sp., holotype (OU 12154), from the Fort Sill fissures. Scanning electron microscope (SEM) illustrations except where noted. (**1**) Dorsal view (light-microscope photograph); (**2**) interpretive drawing of (**1**) identifying features noted in text; (**3**) lateral view of left side; (**4**) detail of pleurotergites identifying possible ozopore and transverse constriction. ig = intercalary groove; ms = mid-dorsal suture; mz = metazonite; ?oz = possible ozopore; pz = prozonite; tc = transverse constriction; xls = crystals. (**1–3**) Scale bars = 1 mm; (**4**) scale bar = 500 µ.

The genus *Xyloiulus* Cook, 1895 is in great need of revision. The type species of *Xyloiulus*, the Carboniferous *Xylobius sigillariae* Dawson, 1860a, is poorly known but appears to have strongly expressed horizontal ridges on its metazonites. The genus includes species such as the late Carboniferous *Xyloiulus moniliformis* (Woodward, 1905), which was described backward and is cambaloid-like in some ways (Hannibal, 2000, p. 31). That species has a single transverse row of prominent longitudinal ridges on its metazonite.

Family incertae sedis
Genus *Karstiulus* new genus

Type species.—*Karstiulus fortsillensis* new genus new species, by original designation and monotypy.

Diagnosis.—As per species.

Occurrence.—Dolese Quarry, near Richards Spur, Comanche County, southwest Oklahoma, from the Fort Sill fissures. Collected on the north side of what was a small mountain (now quarried away). Cisuralian Series.

Etymology.—The name (masculine) is derived from the German word *Karst* (masculine), which is widely used for carbonate terrain, combined with a common millipede ending for julimorph millipedes.

Remarks.—This genus has deeper impressed and more varied striae than *Xyloiulus* Cook, 1895, *Nyranius* Hoffman, 1963, *Plagiacetus* Hoffman, 1963, *Blaniulus* Langiaux and Sotty, 1976, *Sigmastria* Wilson, 2006, and *Gaspestria* Wilson, 2006. It also differs from the enigmatic genus *Anthracojulus* Fritsch, 1901, which appears to have three pleurotergal sclerites (Hoffman, 1969, p. R588), and *Archiulus*, which may not have striae or may have subdued striae.

Karstiulus fortsillensis new genus new species
Figure 1

Holotype.—Holotype OU 12154, from the Fort Sill fissures, early Permian, Dolese Quarry, near Richards Spur, Oklahoma.

Diagnosis.—Very small millipede with shorter prozonite separated by transverse constriction from longer metazonite, which is also larger in diameter than the prozonite. Midline suture deep. Metazonites with widely spaced, deeply incised, oblique grooves and shorter intercalary grooves. Dorsalmost grooves converge dorsally but do not touch midline suture. Ozopores probably present.

Occurrence.—Dolese Quarry, near Richards Spur, Comanche County, southwest Oklahoma, from the Fort Sill fissures. Collected on the north side of what was a small mountain (now quarried away). Cisuralian Series.

Description.—Very small, cylindrical millipede. Preserved segments up to ~1.2 mm long. Prozonite shorter, poorly preserved, separated by transverse, dorsally shallowing constriction from longer metazonite. Midline suture distinct, deep. Metazonites inflated, marked by widely spaced, deeply incised, oblique grooves, the longer of which originate close to the anterior of the metazonite and terminate as a depression very close to the posterior of the metazonite. Shorter, intercalary grooves originate at about mid-metazonite. Dorsalmost grooves converge toward midline suture but do not connect at midline. Raised area between grooves generally convex dorsally. Probable rimmed (?)ozopores (Fig. 1.4) located close to anterior of metazonite. Groove posterior of (?) ozopore truncated, that is, an intercalary groove. Cuticle finely and irregularly punctate.

Etymology.—The trivial species name is an adjective denoting the Fort Sill fissures in which the specimen was found. The gender is masculine.

Material.—OU 12154, consisting of a somewhat laterally compressed specimen composed of cuticle over a crystallized internal filling. Specimen is composed of three better-preserved segments and two partial segments. The specimen is from a new fossil-producing pocket in the greenish-colored clay from the fissure-and-cave complex. This pocket has also produced five to six new genera of amphibians and reptiles that were unknown or had been represented only by isolated bones from the Richards Spur site.

Remarks.—Much of the cuticle of the specimen is broken away at the midline suture. The metazonites of this species may have flared outward posteriad (see position of fourth segment in Fig. 1.1, 1.2). This, along with the general form of the pleurotergites, the oblique ornamentation of the metazonites, and the placement of the ozopores, would have given this millipede an appearance that was generally similar to the modern julid *Unciger*, which is in the extant tribe Brachyiulini. On the basis of its general similarities with julimorphs, this species was probably elongate. Xyloiulidans are known as far back as the Lower Devonian (Wilson, 2006). The specimen is, in general form and in the probable presence of ozopores, similar to the specimens of xyloiulidans illustrated in classic papers (Scudder, 1873, 1878) as well as the xyloiulid specimen figured by Baird et al. (1985, fig. 5.3).

The ornamentation of the Richards Spur specimen, however, differs from that of those other specimens of xyloiulidans. The grooves of the Richards Spur specimen differ from those of the *Xyloiulus* as diagnosed by Hoffman (1963) in that the grooves of the Richards Spur specimen are not always continuous across a segment. In addition, at least some specimens referred to *Xyloiulus* (Hoffman, 1963, text-fig. 2) have longitudinal grooves that meet at the midline, in contrast to the grooves of the Richards Spur specimen, which do not meet at the midline.

The distinct midline suture of the new form also differentiates it from most other xyloiulidans, including *Gaspestria* Wilson, 2006. The new form differs from other genera including *Tomiulus angulatus* and *Sigmastria* Wilson, 2006 in both tergite form and ornamentation.

The supposed xyloiulidan that Baird (1958) briefly described from Texas is coeval in age and proximity to the Richards Spur specimen. That specimen is from the Arroyo Formation of the Clear Fork Group (lower Permian, Leonardian) at Coffee Creek, Baylor County, Texas. Baird (1958) referred this specimen to the genus *Xylobius* (now *Xyloiulus*). The specimen is in need of a more detailed redescription.

Superorder and Order incertae sedis

Remarks.—*Oklahomasoma* (Figs. 2, 3) shares a resemblance with a number of modern orders but most closely resembles the Carboniferous *Hexecontasoma carinatum* Hannibal, 2000 (Fig. 4) from Mazon Creek, Illinois, which Hannibal (2000) did not place in an order. He suggested, however, that *Hexecontasoma* may be a callipodidan. Wilson (2006, p. 643) placed *Hexecontasoma* as a basal nematophoran and agreed that it may be a callipodidan nematophoran. Shear and Edgecombe (2010, p. 186) subsequently noted that *Hexecontasoma* lacks the derived characters that define the callipodidans, but also agreed (p. 182) that it may be a nematophoran. More recently, Edgecombe (2015, p. 347) noted that *Hexecontasoma* could not be reliably placed in an order due to the lack of critical characters. This is even more true for *Oklahomasoma* as the ventral side of *O. fortsillensis* is poorly preserved.

Order incertae sedis
Family Oklahomasomatidae new family

Type genus.—*Oklahomasoma* new genus.

Diagnosis.—As for species.

Genus *Oklahomasoma* new genus

Type species.—*Oklahomasoma richardsspurense* new genus new species, by original designation and monotypy.

Diagnosis.—As for species.

Occurrence.—Dolese Quarry, near Richards Spur, Comanche County, southwest Oklahoma, from the Fort Sill fissures, a fissure on the south side of what was a small mountain (now quarried away). Cisuralian Series.

Etymology.—The name combines the name of the state in which the fossil was found and the Greek word for body (*soma*, neuter), a common ending for millipede genera.

Remarks.—The millipede is similar in a number of respects to *Hexecontasoma* from the upper Carboniferous of Mazon Creek, Illinois (Hannibal, 2001; Fig. 4) in that both genera have prominent subrectangular paranota and two rows of transverse longitudinal ornamentation on their metazonites. *Oklahomasoma* differs from *Hexecontasoma*, however, in having different dorsal ornamentation and a different number of notches on the lateral edges of its paranota. The new form, like *Hexecontasoma,* bears some resemblance to extant cambaloid millipedes (see discussion in Hannibal, 2000). The new form, however, has differently formed prozonites, strikingly different dorsal morphology, and differently shaped paranota from *Hexecontasoma* and extant cambaloids.

Oklahomasoma richardsspurense new genus new species
Figures 2, 3

Holotype.—OU 44526, composed of eight articulated anterior segments, the anteriormost of which is only partially preserved. From the Fort Sill fissures, early Permian, Dolese Quarry, near Richards Spur, Oklahoma.

Diagnosis.—Very small millipede with prominent mid-dorsal suture. Metazonite with pair of wide, subovoid, dorsal nodes located toward anterior. Metazonite below paranota with two transverse rows of irregularly bulbous, loaflike, longitudinal ornamentation. Paranota prominent, subrectangular, with a prominent notch located near anterior of lateral edge.

Occurrence.—Dolese Quarry, near Richards Spur, Comanche County, southwest Oklahoma, from the Fort Sill fissures, a fissure on the south side of what was a small mountain (now quarried away). Cisuralian Series. This specimen was found in a fissure that also produced the captorhinid reptile *Captorhinus magnus* Kissel, Dilkes, and Reisz, 2002.

Description.—Very small, cylindrical millipede. Length of holotype and sole specimen (composed of part of eight anterior segments) about 7.2 mm. Preserved segments ∼1 mm long. Mid-dorsal suture present. Prozonite relatively smooth to subtly striate, smaller in diameter than, and so transversely constricted compared with, metazonite. Metazonite with two anterior, laterally elongate, subovoid dorsal nodes that extend laterally from close to midline across most of metazonite. Indication of a less prominent lateral node located at intersection of posterolateral side of metazonite with the paranota. Paranota broad, elongate, subrectangular, with prominent notch located near anterior of lateral edge. Paranota horizontal or angled slightly upward from horizontal, subtriangular in transverse cross section. Ozopores not apparent. Metazonite below paranota with two transverse rows of longitudinal, bulbous, loaflike ridges. Sternites narrow. Coxal segments prominent (other leg segments not preserved).

Etymology.—The species epithet refers to the town nearest to the locality at which this taxon was found.

Remarks.—It is possible that the specimen was in a molting stage, accounting for the prominence of the mid-dorsal suture and separation along it. Both *Oklahomasoma richardsspurense* and *Hexecontasoma carinatum* (Fig. 4) bear some similarity to "*Pleurojulus*" *steuri* from the lower Permian of Germany (Schneider and Werneburg, 1998). "*Pleurojulus*" *steuri* differs from *O. richardsspurense* in having longitudinal ridges and ozopores on its dorsum. "*Pleurojulus*" *steuri* does resemble *H. carinatum* in having dorsal longitudinal ornamentation and paranota; "*P.*" *steuri* may belong to the Hexecontasomatidae. Additional millipedes with paranota have been described from the Carboniferous (see Wilson et al., 2005; Ross et al., 2018), but those have different paranotal configurations and been assigned to the Archipolypoda.

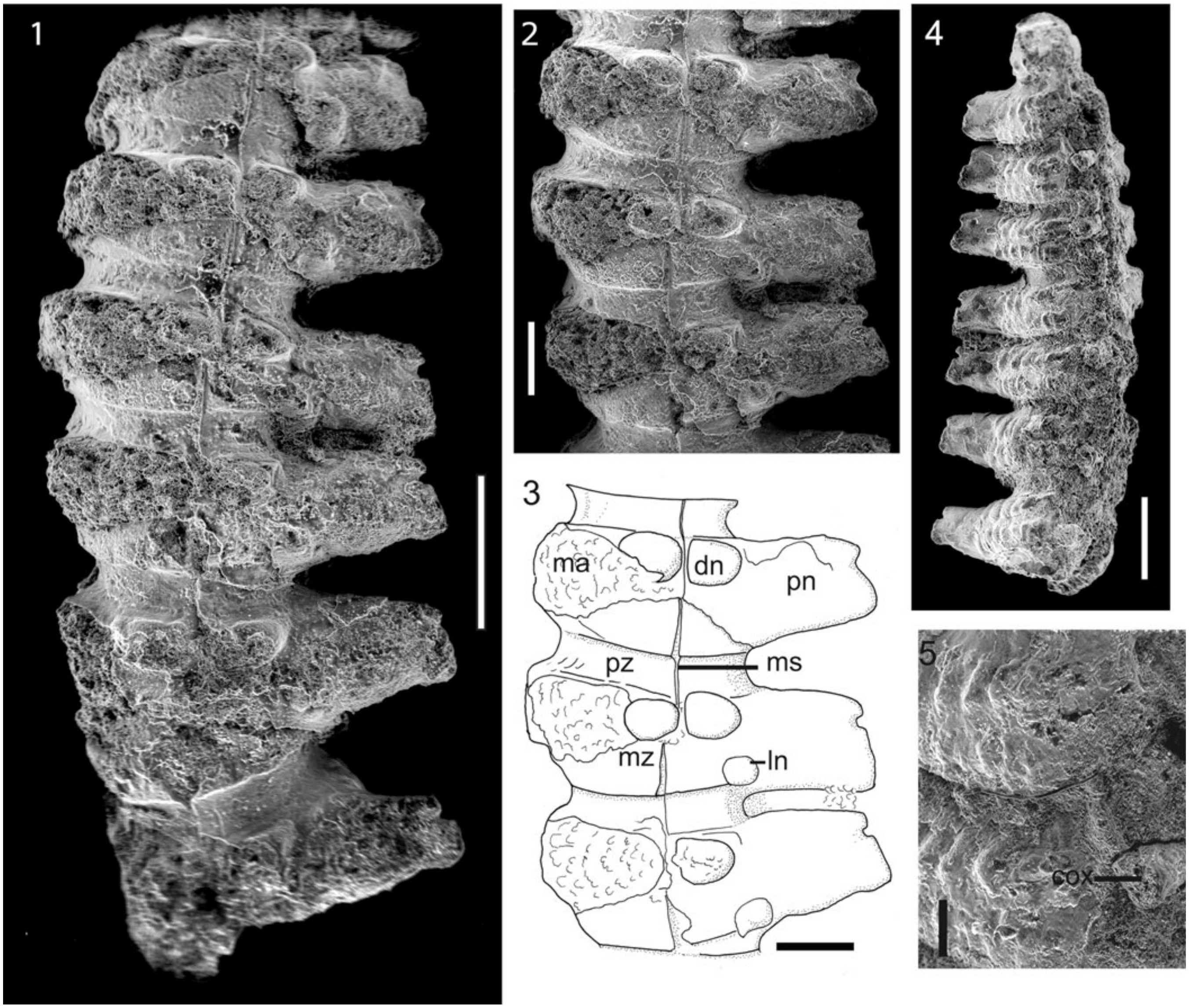

Figure 2. *Oklahomasoma richardsspurense* n. gen. n. sp., OU 44526, SEM microphotographs except for drawing. (**1**) Dorsal view; (**2**) close-up of dorsum; (**3**) interpretive drawing of (**2**) identifying features noted in text; (**4**) ventral view, slightly tilted to better see left side; (**5**) close-up of ventral side of two segments and one coxal segment. dn = dorsal node; cox = coxa; ln = lateral node; ma = mineralized area where cuticle is missing; ms = mid-dorsal suture; mz = metazonite; pn = paranota; pz = prozonite. (**1, 4**) Scale bars = 1 mm; (**2, 3**) scale bars = 500 μ; (**5**) scale bar = 200 μ.

Like a number of other millipedes found in more recent caves and fissures (see Remarks that follow), *O. richardsspurense* is preserved in three dimensions.

Superorder, order, and family incertae sedis
Genus *Dolesea* new genus

Type species.—*Dolesea subtila* new genus new species, by original designation and monotypy.

Diagnosis.—As per species.

Occurrence.—Dolese Quarry, near Richards Spur, Comanche County, southwest Oklahoma, from the Fort Sill fissures, a fissure on the north side of what was a small mountain (now quarried away). Cisuralian Series.

Etymology.—The name is derived from the Dolese Quarry in which the specimen was found. Its gender as used here is feminine.

Remarks.—The general form of the pleurotergites of this genus resembles that of the unornamented pleurojulid *Pleurojulus levis* Fritsch, 1901 (see Wilson and Hannibal, 2005). All *Pleurojulus* species, however, have distinctly separate pleurites. The relatively simple body structure of *Dolesea* also resembles that of the Triassic millipede genus *Hannibaliulus* Shear, Selden, and Gall, 2009, but *Hannibaliulus* has metazonites with prominent transverse depressions and a simpler termination of its pleurotergites.

Dolesea subtila new genus new species
Figures 5, 6

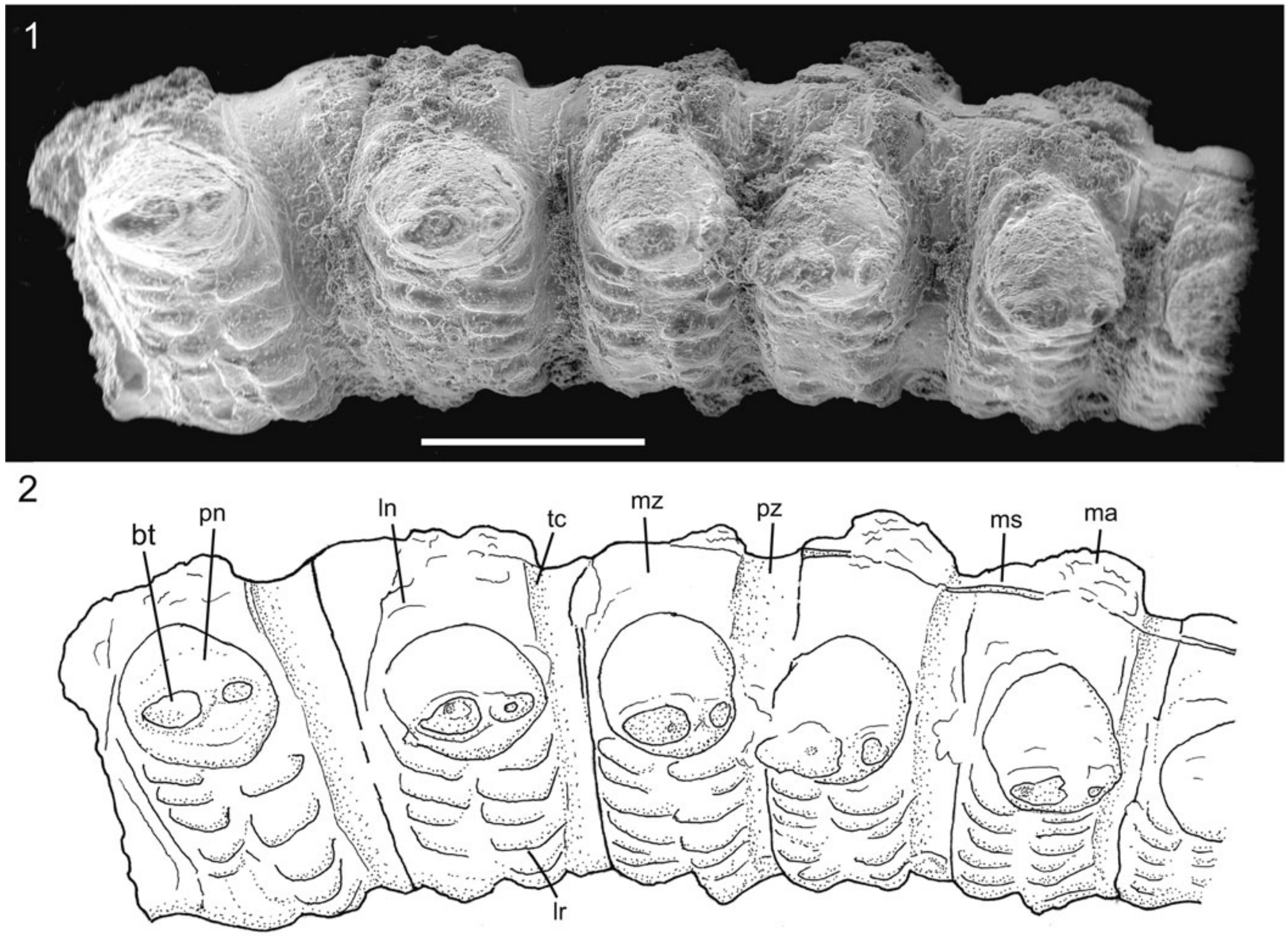

Figure 3. *Oklahomasoma richardspurense* n. gen. n. sp., OU 44526. (**1**) SEM micrograph of right side; anterior is to the right; (**2**) interpretive drawing identifying parts noted in text. bt = broken-off terminations of paranota; ln = lateral node; lr = longitudinal ridges (elevated loaf-like features); ma = mineralized area where cuticle is missing; ms = mid-dorsal suture; mz = metazonite; pn = paranota; pz = prozonite; tc = transverse constriction. Scale bar = 1 mm.

Holotype and paratype.—Holotype**,** OU 12152, mostly compressed, consisting of three segments. Another specimen (paratype, OU 12153) consisting of four more or less complete and one partial segment.

Diagnosis.—Cylindrical millipedes with shorter prozonites and longer metazonites. Midline suture present. Prozonites separated from metazonites by a ridge or ridge and narrow trough. Ozopores on most segments. Ornamentation subtle. Pleurotergites with ridges of various configurations near terminus.

Occurrence.—Dolese Quarry, near Richards Spur, Comanche County, southwest Oklahoma, from the Fort Sill fissures, a fissure on the north side of what was a small mountain (now quarried away). Cisuralian Series. These specimens were found in a fissure that also produced the captorhinid reptile *Captorhinus magnus*.

Description.—Cylindrical millipede. Prozonites short. Ornamentation of prozonite consisting of pronounced scalelike cytoscutes (cuticular platelets). Prozonites distinctly separated from metazonites by a transverse constriction, the anterior of which distinctly drops in elevation and the posterior of which may or may not be distinctly expressed. Ornamentation of metazonite similar to that of prozonite, but scalelike forms less well defined. Ozopores located closer to anterior than posterior of metazonite. Small cuticular pits (possible sites of setal attachment) scattered in metazonite. Pits also in irregular rows at anterior of metazonites. Midline suture distinct. Pleurotergites with anteriorly bifurcating ridge located near lateral edge. Lateral edge with up to five or more closely spaced ventral ridges giving corrugated appearance.

Etymology.—The trivial species name is from the Latin adjective *subtilis*, referring to its fine, delicate ornamentation.

Remarks.—Presence of a midline suture is inferred on the basis of the overlap of the anteriormost segment preserved, where the segment is broken longitudinally. This longitudinal break is more or less straight. The bifurcating ridge on the pleurotergites of this species is similar to that

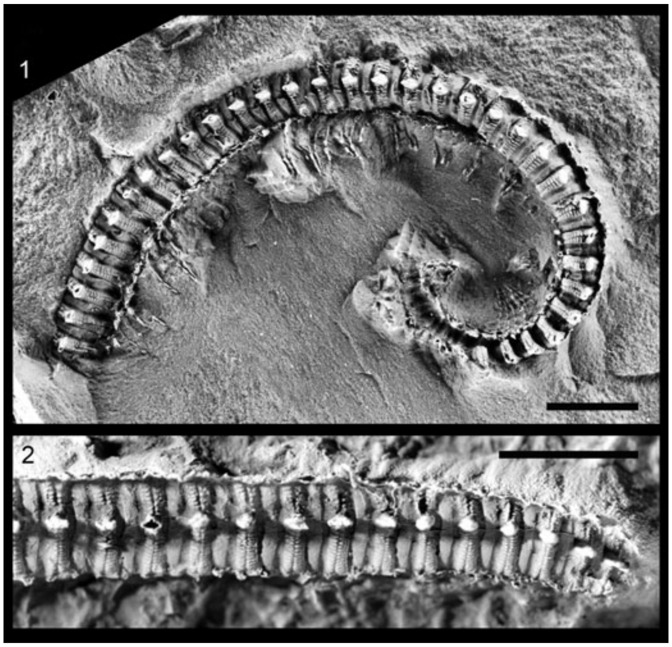

Figure 4. *Hexecontasoma carinatum* Hannibal, 2000, whitened latex molds of holotype, FMNH PE 23487, Carboniferous of Mazon Creek, Illinois. (**1**) View of midpoint and anterior of right side (from Hannibal, 2000); (**2**) posterior of left side. (**1**) Scale bar = 5 mm; (**2**) scale bar = 4 mm.

seen in illustrations of *Chordeuma sylvestre* Koch, 1847 (Blower, 1985, fig. 26A). Polygonal cuticular structures (cytoscutes) seen on this taxon are known for species in various millipede orders, including the Julida, Polydesmida, and the Spirostreptida (e.g., Eisenbeis and Wichard, 1987, pl. 63; Adis et al., 1997, figs. 4–6; Golovatch et al., 2009). The cytoscutes of *D. subtila* preserve very fine microstructure, consisting of randomly oriented fine (?)pits located ∼1 μ apart from each other.

This specimen bears an overall resemblance to *Xyloiulus platti* (Baldwin, 1911). *Xyloiulus platti*, however, is not a xyloiulid as it lacks longitudinal striae (see illustrations in Baldwin, 1911; see also Edgecombe, 2015, fig. 14.2A). Both taxa have short prozonites and longer metazonites and have pleurotergites that lack prominent striae and grooves. The lateral edge of the pleurotergite of *X. platti*, however, ends with a rim (rebordering of Shear et al., 2009) but lacks the anteriorly bifurcating ridge located near lateral edge of the pleurotergite of *D. subtila*.

The ventral ridges of *D. subtila* are partly preserved in an inwardly rolled position, with the ridges of the right and left sides converging (Fig. 6). This must have been due to the disarticulation or disintegration of the sternal area, allowing for the distal edges of the pleurotergite to deform and coil inward.

Superorder, order, family, genus, and species incertae sedis
Figure 7

Occurrence.—Dolese Quarry, near Richards Spur, Comanche County, southwest Oklahoma, from the Fort Sill fissures, a fissure on the south side of what was a small mountain (now quarried away). Cisuralian Series.

Descriptions.—Two elongate millipedes, OU 12150 (Fig. 7) and OU 12151, with relatively unornamented pleurotergites. These two specimens, one preserved in a coiled position and the other outstretched, are briefly described for completeness.

OU 12150 (Fig. 7) is a coiled specimen consisting of at least 20 midbody segments. Prozonite shorter than metazonite. Segments about 0.8–1 mm wide. Pleurotergites wide; with rim on dorsal, anterodorsal, and posterodorsal sides of pleurite; the left side has microgranular ornamentation, but the other side is coarsely pitted. Prozonite shorter than metazonite. Sternites separate, narrow. OU 12151 (not illustrated) is an outstretched specimen 0.6 mm wide, consisting of about seven segments. It is so highly weathered that pleurotergal details are obscured. It appears to have narrow subtriangular sternites.

Remarks.—These two additional specimens from the Fort Sill fissures are less well preserved than those we have assigned to new species. It was also difficult photographing key features of these specimens with the scanning electron microscopes available.

Discussion

Occurrence of fossil myriapods in karst.—The Richards Spur locality is the site of one of the oldest occurrences of fossil myriapods (millipedes and centipedes) in karst deposits, including limestone cave deposits and fissure fills. However, there are many additional occurrences in karstic deposits. It is clear from the number of examples in Table 1 that the occurrence of millipedes in karst is one of the most important modes of preservation of millipedes in the fossil record, especially when the relative scarcity of millipedes in the fossil record is considered. Most reports of such occurrences in karstic deposits have not cited other such occurrences in karst, so the relatively large number of karstic records of fossil millipedes has not been properly noted previously, and very little has been done comparing various occurrences with each other.

By contrast, occurrences of millipedes in amber and concretion faunas are widely known. A good number of diplopod taxa have been described from Carboniferous concretions from Europe (including Great Britain and France) and North America (the Mazon Creek deposits of Illinois, USA) and from Cretaceous, Cenozoic, and other amber faunas worldwide (notably amber from Myanmar [e.g., Stoev et al., 2019], the Baltic area [e.g., Haug et al., 2018], and the Dominican Republic). Other occurrences of fossil millipedes have been described from coal (e.g., the Gaskohle of the Czech Republic), siltstone, limestone, calcitic onyx, asphalt, and other types of rock.

The majority of the karstic sites are Pleistocene, reflecting the greater accessibility of cave entrances that have continued to be open since the Pleistocene. Some additional Pleistocene caves have been open for exploration only after accidental discovery during large-scale construction projects, the caves having been buried. These include Riverbluff Cave in Missouri, discovered while building a highway (Rovey et al., 2010). The Red Hills cave in Jamaica was probably exposed similarly (Donovan and Veltkamp, 1994). Geologically older sites are rarer,

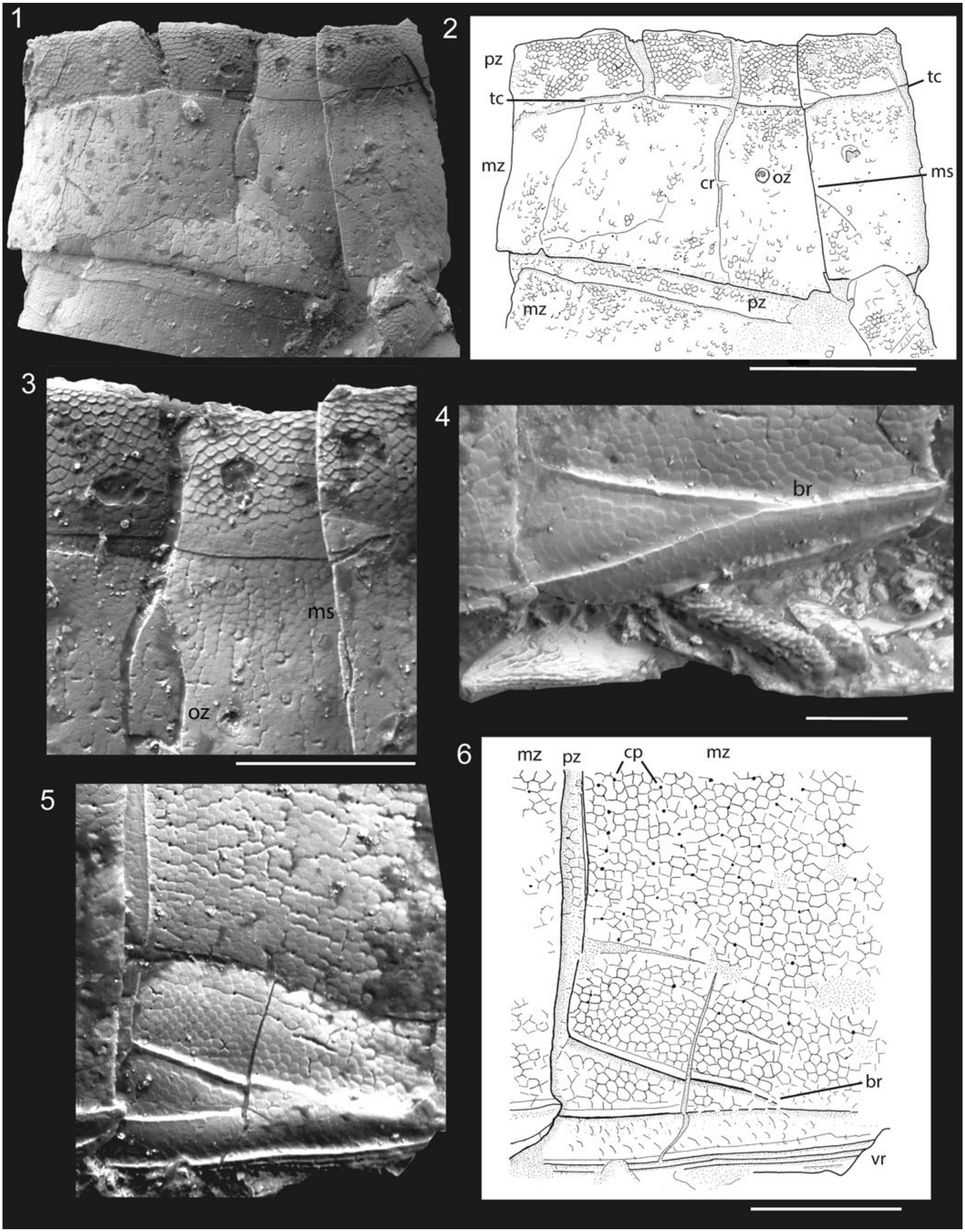

Figure 5. *Dolesea subtila* n. gen. n. sp. (**1, 2**) SEM microphotograph (**1**) and interpretive drawing (**2**) of anterior of holotype (OU 12152) mostly compressed, in dorsal view; specimen is tilted somewhat to the right; (**3**) detail of (**1**) showing cytoscutes in greater detail; (**4–6**) SEM microphotographs (**4, 5**) and interpretive drawing (**6**) of ventrolateral side of paratype (OU 12153). br = branching ridges; cp = cuticular pores; cr = crack; ms = mid-dorsal suture; mz = metazonite; oz = ozopore; pz = prozonite; tc = transverse constriction; vr = ventral ridges. (**2**) Scale bar = 500 µm; (**3**) scale bar = 200 µm; (**4, 6**) scale bars = approximately 100 µm.

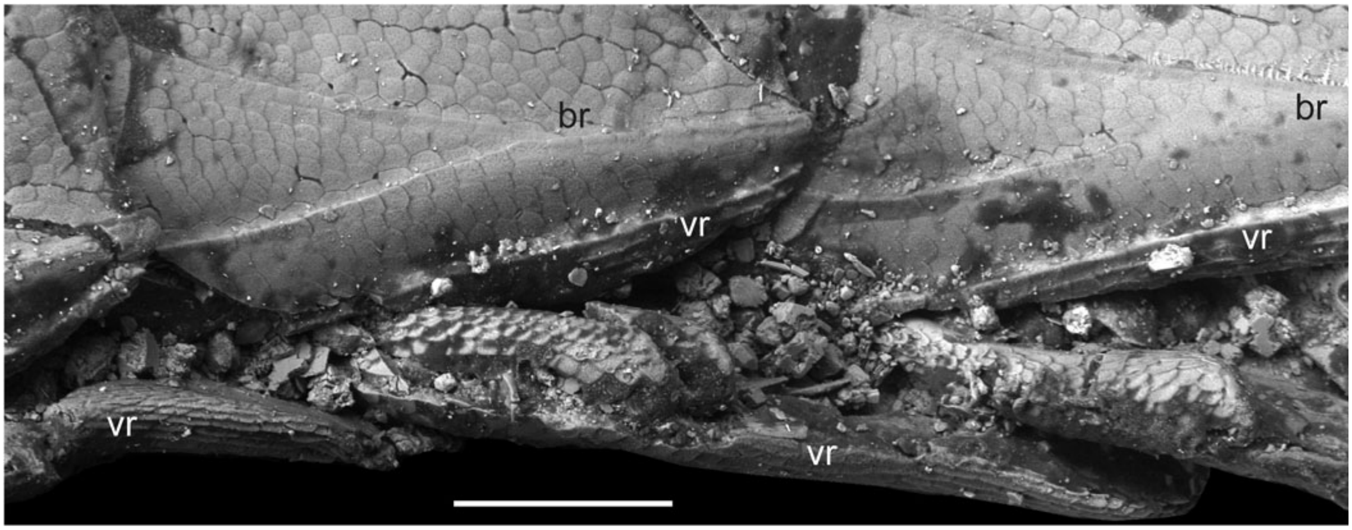

Figure 6. *Dolesea subtila* n. gen. n. sp., SEM microphotograph showing detail of inwardly rolled ventral edges of both sides of millipede. Upper set is that of the left side; lower set is that of right side. Scale bar = 100 µm. br = branching ridge; vr = ventral ridges.

doubtlessly due to their relative inaccessibility. The Fort Sill fissures, comprising filled-in karst that had been deeply buried, represent a deposit that would have never been found had the site not been quarried for carbonate rock. Likewise, a fossil chilopod is preserved in calcite at the Limeworks site of Makapanscat, South Africa (Kitching, 1980), where deposits containing fossils were first exposed by lime working.

Millipedes have relatively robust, calcium-impregnated exoskeletons. Various authors have independently commented on the preservation potential of millipedes in limestone crevices and caves. Náday (1917, p. 16) noted that thick but easily broken exoskeletons of myriapods are more easily preserved in cave fillings. Bachmayer (1953, p. 27), Bachmayer et al. (1976, p. 133, 138), and Mauriès (1979) briefly noted the calcification/encrustation with calcite of fossil millipedes preserved in karstic, calcium-rich environments. Bachmayer (1953, fig. 16) and Bachmayer et al. (1976, pl. 5) also illustrated calcite encrusted specimens in comparison with similar Recent taxa. Donovan and Veltkamp (1994) noted the preservation potential of millipedes in carbonate environments in their discussion of fossil millipedes found in a cave in Jamaica and convincingly postulated early diagenetic cementation of the material they studied. They also hypothesized that the millipedes at their Red Hills site were washed into the cave during tropical storms or hurricanes, drowned, and then coated with calcite, their calcareous skeleton acting as a depositional substrate in calcium-carbonate-rich water just before or during burial in sediment (Donovan and Veltkamp, 1994, fig. 7). They hypothesized that the set of conditions leading to such preservation was more likely to occur in the tropics. This may have been the case with the Richards Spur fauna as the site was in the tropics in the Permian. Tabor and Yapp (2005, p. 68) indicated that the Richards Spur area would have been warm and dry in the Permian, with some seasonality that could have included monsoons. Monsoonal conditions have been increasingly accepted for Richards Spur (deBraga et al., 2019), so it is possible that the Richards Spur site would have experienced the conditions envisioned by Donovan and Veltkamp (1994). However, this is not entirely consistent with Pleistocene occurrences (Table 1) in other parts of the world. Náday (1917), for example, noted that the Braşov, Transylvania, millipede fauna was deposited when the Braşov area was experiencing a Mediterranean (not tropical) climate, and specimens have been found in Austria (Bachmayer, 1953).

Macdougal et al. (2017, fig. 3) have published a set of scenarios for a vertebrate at the Fort Hill fissures locality that is also applicable to millipedes but different from the scenario envisioned by Donovan and Veltkamp (1994, fig. 7). Macdougal et al. (2017) included an animal dying and then disarticulating before being washed into a karst pit, an animal being washed into a pit after death but before disarticulation, and an animal falling in a pit and dying there.

To these scenarios can be added the possibility that millipedes found preserved in karst actually lived in the caves and fissures, or were occasional visitors to these sites, in which they are found. Millipedes are a common element of the modern cave fauna. Some caves have yielded both fossil and modern millipedes that might be conspecific. Mauriès (1979), for example, identified fossil millipede material in the genus *Typhloblaniulus* in the Grotte de la Carriére, in which the extant *Typhloblaniulus troglobius* (Latzel in Gadeau de Kerville and Latzel, 1886) was also found (see also discussions by Elliott et al., 2017).

In addition, various other animals may have transported them to these karstic environments. Mead and Van Devender (1981), for example, have reported millipedes in the feces of the extant ringtail *Bassariscus astutus* (Lichtenstein, 1830) at California's Vulture Cave. In fact, diplopods were the most common arthropods found in dung (it is also possible that the millipedes were feeding on the dung) and loose within the analyzed cave sediment at Vulture Cave.

Many extant millipedes are known to favor carbonate terrains, and such terrains are likely to have karst features. Extant millipedes may be found living both outside and inside caves and fissure openings. Numerous millipedes are troglobitic (Hopkin and Read, 1992, p. 181). Living millipedes and millipede

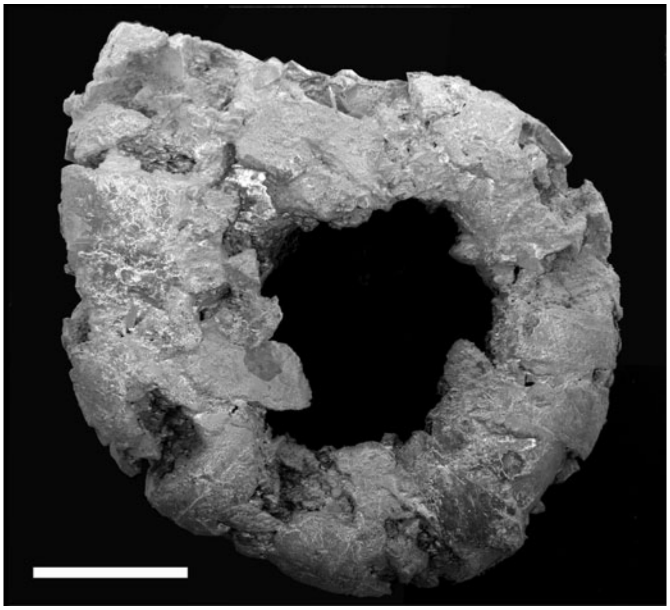

Figure 7. Left side of coiled helminthomorph millipede, OU 12150. Scale bar = 1 mm.

carcasses can also be carried into caves by streams and can be transported into fissures by sheet wash and floods. Millipedes can also be transported into caves by other animals.

Because of the variety of possibilities that could lead to a millipede being preserved as a fossil in a karst setting, any original habitat of the Richards Spur specimens cannot be determined, except that these millipedes were preserved in a carbonate terrain. A similar type of preservation of a Miocene millipede is known in lacustrine carbonates (Arp, 1995). In that case, like at Richards Spur, microstructures are preserved.

Preservation.—Some millipedes (e.g., Fig. 1) found at Richards Spur are preserved three dimensionally. This was facilitated by preservation in karstic environments that allowed for preservation before complete flattening. Such three-dimensionality is well known for specimens preserved within concretions, but it is also common in specimens preserved in karst (see illustrations in Náday, 1917; Bachmayer, 1953, 1965; Loksa, 1959; Bachmayer et al., 1976; Donovan and Veltkamp, 1994). Details preserved (Figs. 2–4), even when the specimens are not fully three-dimensionally preserved, can be extraordinary, including views of cytoscutes seen in some of the Richards Spur material (Figs. 2, 3). Various authors writing about fossil millipede faunas (Table 1) have commented on this mode of preservation. (Detailed, three-dimensional preservation is also found in some special nonkarst environments such as that described by Duncan et al., 1998.) In many cases of preservation in karst, however, the specimens are also relatively fragile. Specimens may also be coated in part with fine calcitic material that strengthens the fossil but, because it adheres to the fossil cuticle, also obscures features. Specimens may have easily recognizable calcite crystals (e.g., Fig. 1) adhering to their inside or outside.

Co-occurrence with vertebrates and gastropods.—The occurrence of millipedes at a site best known for vertebrates such as Richards Spur is unusual neither in general nor in the case of karstic localities. Co-occurrence of fossil millipedes and vertebrates has been known since the dawn of paleomyriapodological investigations, with the work of Dawson (1860a, p. 36–37), who described the Carboniferous millipede *Xyloiulus sigillariae* (Dawson, 1860a) as being found along with the tetrapod *Dendrepeton* (and land snails) within a single hollow tree stump found in a sequence of shales, siltstone, and coal at Joggins, Nova Scotia. Dawson (1860b, 1862) also elaborated on such co-occurrences, noting that segments of *Xyloiulus* were found in coprolites at Joggins. *Xyloiulus permicus* was found associated with the sphenacodon *Pantelosaurus* (Beurlen, 1925, p. 182).

Fossil myriapods found in cave and fissure sites (Table 1) are typically dominated by vertebrate remains (e.g., Donovan and Veltkamp, 1994). Several cave and fissure sites at which Cenozoic (mostly Pleistocene) fossil myriapods have been found are best known for vertebrates. These include the Austrian site of Hundsheim (Freudenberg, 1909; Bachmayer, 1953), the Greek site of Charkadio on Tilos Island (Bachmayer et al., 1976), and Braşov, Transylvania (Náday, 1917).

Interestingly, Reisz and Laurin (1991) hypothesized that a close co-occurrence of what are probably millipedes and procolophonid reptiles in a Permian (nonkarstic) fossil deposit in South Africa was due to the scavenging of reptiles by the millipede-like arthropods. This is a possibility as the probable millipedes are closely associated with the procolophonids, as seen in Reisz and Laurin (1991, fig. 1) and in Reisz and Scott (2002, fig. 1) (both figures of the same material). Abdala et al. (2006) have proposed an alternative scenario, postulating that a similar co-occurrence of tetrapods and millipedes in Lower Triassic rocks of South Africa was due to reptiles and millipedes sharing a burrow. When such previous accounts of finds of millipedes associated with reptiles are taken into account, it seems that the co-occurrences of millipedes and vertebrates may simply be due to the occurrence of both taxa in similar habitats.

Although gastropods have not been found in the Fort Sill fissures, the co-occurrence of millipedes and gastropods has been documented from other localities, karstic and nonkarstic, beginning with the well-known association of the Carboniferous *X. sigillariae* with land snails documented by Dawson (1860a, b). In a report of taxa found at Hundsheim, Freudenberg (1909, p. 199–200) specifically noted two groups of fossil invertebrates: gastropods and millipedes. Gastropods are a prominent part of the fossil-invertebrate fauna found at Braşov (Brassó) (Soós, 1916) and the Jamaican site of Red Hills (Donovan and Veltkamp, 1994), as are millipedes. This co-occurrence must be based on the relative abundances of snails and millipedes, the mineralogy of their shells and exoskeletons, and the high-calcium content of the material filling fissures and caves in karst terrain. No gastropods have been found to date at Richards Spur, however.

Millipedes are not the only arthropods found in karst. Moldovan et al. (2011), for example, reported oribatid mites, sparse cladocerids, and insects from a Pliocene–Pleistocene cave in Slovenia, and some deposits noted in Table 1, for example Makapansgat, contain a variety of insects and other animals, most famously hominids. Arthropods, other than the

Table 1. Examples of fossil myriapods found in karst deposits along with references describing these myriapods and/or the localities

Locality	Type of myriapod	Period, Epoch, or Age	Reference(s)
Austria: Hundsheim	Diplopoda: Polydesmida, Julida, Glomerida	Pleistocene	Freudenberg (1909); Bachmayer (1953); Strouhal (1959)
China: Choukoutien	Diplopoda: Julida	Pleistocene	Chia and Liu (1950)
France: Pyrenees	Diplopoda: Blaniulida, Polydesmida	Pleistocene	Mauriès, (1979)
Greece: Psychiko, Athens Metropolitan area	Diplopoda: Julida	Pleistocene	Bachmayer (1965)
Greece: Charkadio, Tilos Island	Diplopoda: Polydesmida, Julida	Pleistocene	Bachmayer et al. (1976)
Hungary: Ördöglyuk Cave, Solymár area	Diplopoda: Polydesmida	Middle Pleistocene	Loksa (1959); Fostowicz-Frelik and Gasparik (2006)
Jamaica: Red Hills	Diplopoda: Spirobolida	Late Pleistocene or Holocene	Donovan and Gordon (1989); Donovan and Veltkamp (1994)
Romania: Brașov (Brassó) and Magyarkő railway station on the Brassó-Zernesti line, Transylvania	Diplopoda: Polydesmida, Julida	Middle Pleistocene	Éhik (1913); Náday (1917)
South Africa: Limeworks quarry, Makapansgat,	Chilopoda: Scolopendromorpha	Pliocene	Kitching (1980); Latham et al. (2003)
United States: Bida Cave, Grand Canyon, Arizona	Diplopoda: indeterminate	late Quaternary	Elias et al. (1992)
United States: Crystal Caverns, Sierra Nevada Foothills, California	Diplopoda: Helminthomorpha, including (?) chordeumatids	Pleistocene (Rancholabrean)	University of California Museum of Paleontology records (Berkeley Fossil Insect PEN); Magoulick (2019)
United States: Richards Spur, Oklahoma, Dolese Quarry	Diplopoda: new genera and species	Cisuralian	This report
United States: Riverbluff Cave, Springfield, Missouri	Diplopoda: undescribed	Pleistocene	Rovey et al. (2010); personal observation (J.T.H.) 2010
United States: Samwell Cave, Shasta County, California	Diplopoda: Julida	Quaternary	Grinnell (1908); Elliott et al. (2017)
United States: Vulture Cave, Grand Canyon, Arizona	Diplopoda: indeterminate	Late Holocene (subfossil)	Mead and Van Devender (1981)

indeterminate elements noted under Geologic setting, and millipedes have yet to be identified at Richards Spur, however.

Comparison of early Permian and Carboniferous millipedes.— The three new genera described here, plus occurrences at other sites noted in the introduction, hint at the existence of a diverse millipede fauna of small millipedes in the Permian, although not as diverse as the fauna described from the Carboniferous. As the preceding individual comparisons indicate, the species of the Richards Spur fauna do bear some similarity to forms from the Carboniferous. The overall paleogeographical location of the major Carboniferous millipede-bearing sites of Mazon Creek and Nýřany was similar to that of the Richards Spur locality in the early Permian. The three sites were all located in the low latitudes that would have had considerable precipitation (Wilson and Hannibal, 2005, fig. 1; Woodhead et al., 2010, p. 456). On the basis of the vertebrate fauna, Richards Spur has been interpreted as more of an upland fauna (Woodhead et al., 2010), however, and this might have made a difference in habitats, with the Richards Spur locality being somewhat more xeric than most Pennsylvanian coal-forest faunas that include millipedes. To date, the Permian worldwide lacks any representative of the euphoberiidan archipolypods, the prominent spined millipedes of the Carboniferous Euroamerican coal belt (Hannibal, 1997).

Conclusions

The millipede fauna described here is important for a number of reasons: (1) it is composed of new Permian millipede taxa; (2) it includes morphologically diverse taxa; (3) details of the millipede exoskeletons are preserved, some in three dimensions; and (4) it is one of the oldest examples of a myriapod fauna preserved in karst. Karst faunas should be ranked with concretion faunas, cannel coals, and amber faunas as a major source of fossil myriapods. In very general form (that is, in being composed of juliform millipeds, forms that resemble nematophorans, and millipedes with prominent paranota), the millipedes from Richards Spur resemble those from Pleistocene cave faunas, but the taxa at Richards Spur appear to be more closely related to Carboniferous forms than to Pleistocene or extant taxa.

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