The first Permian centipedes from Russia

ALEXANDER V. KHRAMOV, WILLIAM A. SHEAR, RANDY MERCURIO, and DMITRY KOPYLOV

While fossils of myriapods are well-known from the Devonian and Carboniferous, until recently sediments from the Permian have been largely devoid of the remains of this important group of terrestrial arthropods. Only one locality reported to yield fossils of a single species of millipede has been cited for the Permian, and that through a reevaluation of strata previously thought to be Triassic. We report fossils of two species of scolopendromorph centipedes (Chilopoda), *Permocrassacus novokshonovi* gen. et sp. nov., from the lower Permian of Tshekarda (the Urals, Russia) and *Permocryptops shelleyi* gen. et sp. nov., from the upper Permian of Isady (North European Russia). These are the first centipedes to be reported and the second and third myriapods to be formally named from the Permian Period. They are compared to previously described scolopendromorphs from the Carboniferous and Cretaceous. The new species possess enlarged ultimate legs, which probably were used as means of anchoring themselves to the substrate, or to aid in defense and prey capture.

Key words: Chilopoda, Scolopendromorpha, Permian, Russia, Tshekarda, Isady.

Alexander V. Khramov [a-hramov@yandex.ru] and Dmitry Kopylov [aeschna@yandex.ru], Borissiak Paleontological Institute of Russian Academy of Sciences, Profsoyuznaya str. 123, 117997 Moscow, Russia; Cherepovets State University, Lunacharskogo str 5, 162600 Cherepovets, Russia; William A. Shear [wshear@hsc.edu], Hampden-Sydney College, Hampden-Sydney, VA 23943, USA; Randy Mercurio [chilopods@yahoo.com], Eastern Research Group, Inc., Engineering and Science Division, 601 Keystone Park Drive, Suite 700, Morrisville, NC 27560, USA.

Introduction

In a recent review of the fossil record of the arthropod superclass Myriapoda, Shear and Edgecombe (2010) noted the rarity of Permian myriapod fossils: a single brief report of millipedes in a congress paper (Hannibal 2006) and early Permian records of the giant millipede *Arthropleura* (Kraus 2005) made up the sum total of our knowledge, until *Tomiulus angulatus* Dzik, 1981, a millipede previously thought to be from the Triassic, was moved to the Permian on geological grounds: fossil-bearing beds at Babii Kamen', from where *Tomiulus angulatus* comes, were shown to lie beneath the Permian–Triassic boundary (Aristov et al. 2013). This striking gap in the myriapod fossil record separates a rich Carboniferous fauna (almost entirely of millipedes) from a sparse, but more modernized, Mesozoic fauna. Only a few fossils of myriapods are known from the Triassic, Jurassic, and Cretaceous (Shear and Edgecombe 2010). With a few exceptions, the fossil myriapods from the Carboniferous represent extinct higher taxa, so it seems reasonable to suspect that the origins of at least some of the living orders and families of myriapods took place either at some time during the Permian, with most Carboniferous taxa going extinct in the Permo-Triassic crisis, or in the early Mesozoic. To decide between these hypotheses it is necessary to accumulate more data on Permian myriapods.

The centipede order Scolopendromorpha includes about 700 living species, grouped into 34 genera and five families. Among the order are some of the largest extant arthropods, some tropical species exceeding 30 cm in length, and much feared for their venomous bites. Smaller species, ranging down to 10 mm long, are relatively common inhabitants of soil and litter habitats in tropical, subtropical and temperate regions, where they play an important role as generalized or highly specialized predators (Edgecombe and Bonato 2011).

Extant scolopendromorphs lack mineralized cuticle and live in terrestrial habitats that are microbially active, including bacteria and fungi capable of digesting both chitin and the heavily cross-linked proteins that make up arthropod cuticle. The habitat and form of ancient scolopendromorphs is likely to have been similar to that of living ones, and this would largely account for the rarity of their fossils. Wilson (2003) reviewed the scanty Paleozoic fossil record of the Chilopoda, discounting most of the species described in the 19th and early 20th century.

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Aside from specimens in Cenozoic amber, practically everything we know of extinct members of Scolopendromorpha is based on only five examples, two from the Carboniferous, *Palenarthrus impressus* Scudder, 1890, and *Mazoscolopendra richardsoni* Mundel, 1979, both from Mazon Creek, USA, and three from the Cretaceous: *Craterocricus oberlii* Wilson, 2003, *Velocipede betimar* Martill and Barker, 1998, and a third, unnamed specimen (Menon et al. 2003), all from the Crato Formation of Brazil. *Permocrassacus novokshonovi* gen. et sp. nov., and *Permocryptops shelleyi* gen. et sp. nov., described below, are from the Permian of Russia and thus fall in the gap between the Carboniferous and Cretaceous species.

Institutional abbreviations.—PIN, Borissiak Paleontological Institute of Russian Academy of Sciences, Moscow, Russia; VSGM, Vernadsky State Geological Museum, Moscow, Russia.

Material and methods

The single known specimen of *Permocrassacus novokshonovi* gen. et sp. nov., was found in deposits of the Kungurian (lower Permian) Koshelevka Formation, which is exposed on the left bank of the Sylva river, 800 meters to the northwest of Tshekarda village (Perm region, the Middle Urals of Russia). The Tshekarda locality is famous for its rich fossil insect fauna, which comprises 25 orders and 99 families (Aristov and Rasnitsyn 2015). Besides fossil insects, whose number exceeds 8000 specimens, very few terrestrial arthropods have been found at Tshekarda. Among them are an undescribed trigonotarbid (Eskov and Selden 2005) and a harvestman (Opiliones: Laniatores) (Zhuzhgova et al. 2015: 102, fig. 34B). In addition to *Permocrassacus novokshonovi*, which was collected in 1946, one specimen of Diplopoda was found at the same site (Zhuzhgova et al. 2015), however, its current location is unknown (Danil S. Aristov, personal communication to AVK 2017). The fossil flora of the Tshekarda locality is abundant and contains almost all higher taxa of plants typical for the late Paleozoic, including lycopodiopsids, ferns and gymnosperms (Zhuzhgova et al. 2015).

The unique specimen of *Permocryptops shelleyi* gen. et sp. nov. was collected from the upper Permian of the Vologda Region (North European Russia) in 2011. It comes from the Isady (Mutovino) locality situated on the left bank of the Sukhona River opposite the village of Purtovino. An outcrop that yields fossils at Isady is a 200-meter-long lens constituted of clay and siltstone deposits. The lens is considered to be upper Severodvinian in age (Aristov et al. 2013). Numerous plant remains, ostracodes, insects, bivalves, fish, and tetrapods were found there. Insects, which were assigned to 25 orders and 69 families, are the most diverse and abundant group of Isady fossils (Aristov et al. 2013). Compared to 2500 insects collected there, other terrestrial arthropods are extremely rare: three fragmentary specimens of scorpions have been found at Isady (Fet et al. 2011), and the *Permocryptops shelleyi* specimen discussed herein.

The holotype of *Permocrassacus novokshonovi* (VSGM 1/viii/46 60 a, b) is housed at the Vernadsky State Geological Museum (Moscow, Russia), and the holotype of *Permocryptops shelleyi* (PIN 3840/3165) is at the Borissiak Paleontological Institute of Russian Academy of Sciences. The material was examined with a Leica M165C stereomicroscope. Drawings were made using Adobe Photoshop. Photographs were taken using a Leica M165C stereomicroscope with Leica DFC425 camera.

Systematic palaeontology

Class Chilopoda Latrielle, 1817
Order Scolopendromorpha Pocock, 1896
Family indet.
Genus *Permocrassacus* nov.

Etymology: In reference to the Permian period and to the encrassate ultimate legs of the species.

Type species: *Permocrassacus novokshonovi* sp. nov. (by monotypy); see below.

Diagnosis.—As for the type species by monotypy.

Permocrassacus novokshonovi sp. nov.

Fig. 1.

Etymology: After Russian paleoentomologist Viktor Novokshonov (1966–2003), who studied Permian insects and performed excavations at the Tshekarda fossil site.

Holotype: VSGM 1/viii/46 60 a, b, part and counterpart, partially preserved specimen, with a small portion of the head preserved.

Type locality: Tshekarda locality, Sylva river, Perm region, Russia.

Type horizon: Koshelevka Formation, Kungurian Stage, lower Permian.

Diagnosis.—A scolopendromorph centipede with 21 pedigerous segments and strongly modified ultimate legs much thicker than those in the other two well-described fossil species. The coxae of the ultimate legs lack pores.

Description.—The fossil preserves the entire length of the animal, including 21 pedigerous segments, some of which are partial, part of the head and the base of the right antenna. Length, 37–38 mm, greatest width about 3.1 mm at tergite 9. Head shield not preserved. Six basal segments of right antenna preserved, segments about as wide as long. Forcipules robust, claw curved. Anterior 7 pedigerous segments only partially preserved, along with probable coxae and prefemora of right legs 1–5; first leg significantly shorter and thinner than succeeding legs, legs 2–5 about four or five times thicker than leg 1. Tergites nearly uniform in size, with either straight or slightly concave, arcuate posterior margins and obvious paramedian sulci, which become less distinct posteriorly; tergite 21 with a vaguely indicated single median sulcus. Counterpart appears to preserve sterna 8–11, sterna roughly quadrate, without sulci. Legpair 20 similar in size to legpairs 1–5. Ultimate legs (legpair 21) greatly enlarged, five or six times thickness and estimated five to seven times as long as legpair 20 (more than 10 mm long),
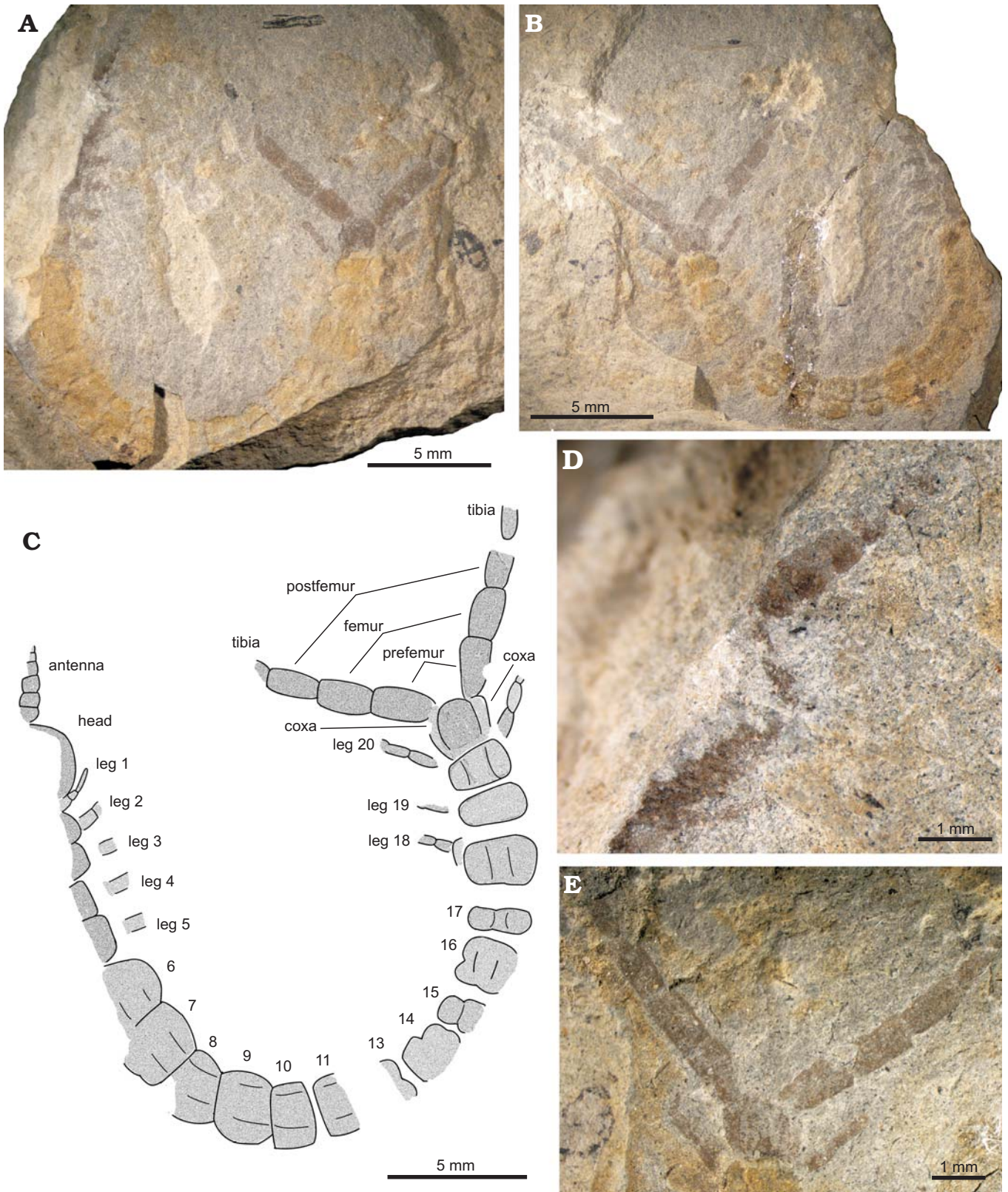
Fig. 1. Scolopendromorph chilopod *Permocrassacus novokshonovi* gen. et sp. nov., holotype VSGM 1/viii/46 60 a, b, Tshekarda locality, lower Permian of Russia. **A**, **B**. General view of part and counterpart, respectively. **C**. Drawing compiled from part and counterpart. **D**. Head, antenna, and 1st leg. **E**. Pairs of 20th and ultimate legs. Numbers indicate segments of trunk or legpairs.

without spines or processes, preserved podomeres subequal in length and thickness, about 3 times as long as thick.

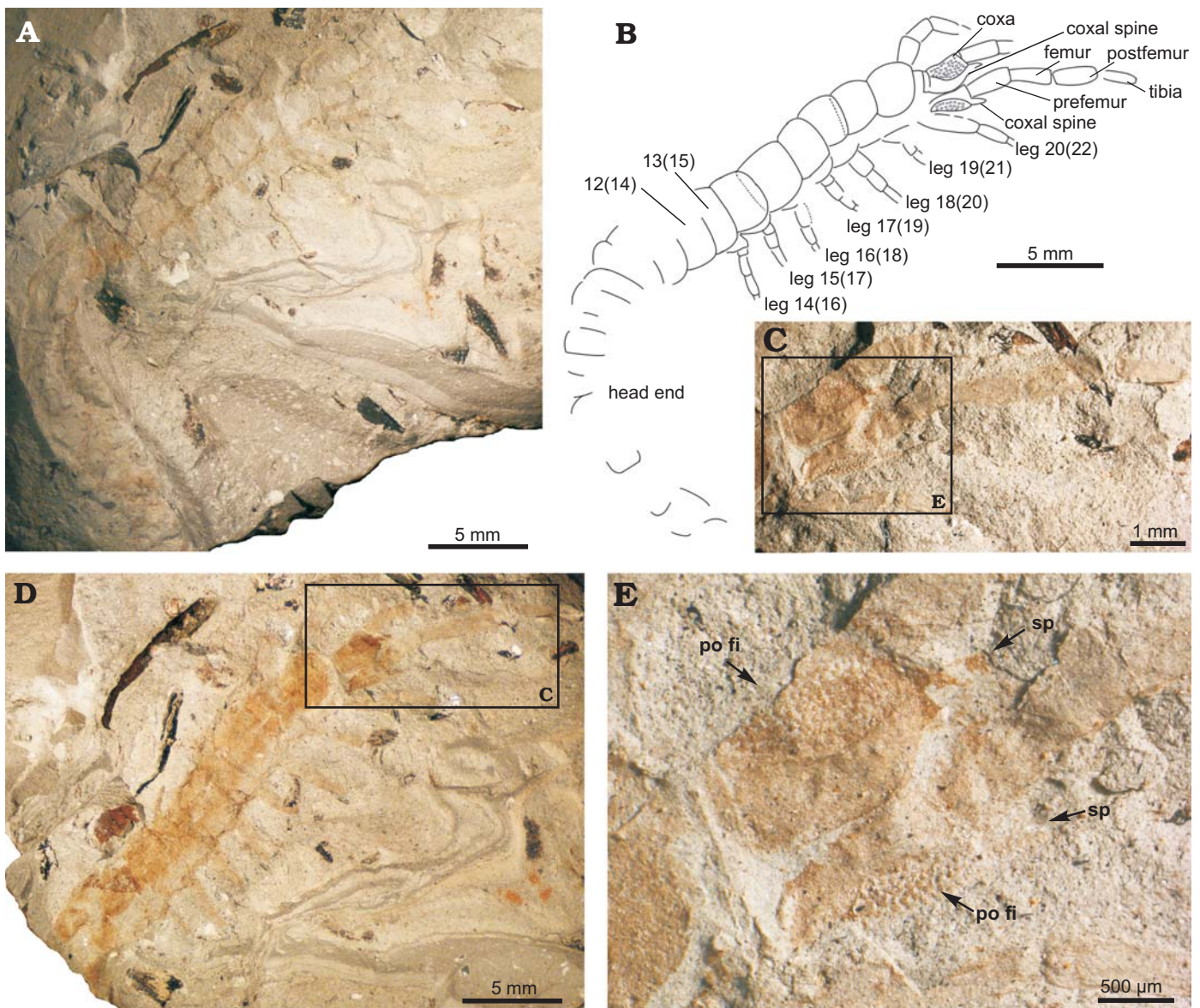*Stratigraphic and geographic range.*—Type locality and horizon only.

Fig. 2. Scolopendromorph chilopod *Permocryptops shelleyi* gen. et sp. nov., holotype, PIN 3840/3165, Isady locality, upper Permian of Russia. **A**, **D**. General view of part and counterpart (mirror-reversed), respectively. **B**. Drawing compiled from part and counterpart. **C**. Ultimate legs. **E**. Pore fields and ventrodistal spines on the ultimate coxae. Abbreviations: po fi; pore field, sp, coxal spine; numbers in parentheses are segment numbers assuming 23 segments are present.

Genus *Permocryptops* nov.

Etymology: In reference to the Permian period and resemblance of the fossil to extant members of the family Scolopocryptopidae.

Type species: *Permocryptops shelleyi* sp. nov. (by monotypy); see below.

Diagnosis.—As for the type species by monotypy.

Permocryptops shelleyi sp. nov.

Fig. 2.

Etymology: In honour of Rowland Shelley, formerly of the North Carolina State Museum of Natural History, who wrote a useful monograph on the scolopendomorph centipedes of North America.

Holotype: PIN 3840/3165, part and counterpart; distal part of the specimen well-preserved, proximal part badly damaged.

Type locality: Isady (Mutovino) locality, Sukhona River, Vologda Region, Russia.

Type horizon: Mutovino beds, Poldarsa Formation, Severodvinian Stage, upper Permian.

Diagnosis.—Distinct from previously known fossil scolopendromorph centipedes and from *Permocrassacus novokshonovi* gen. et sp. nov., described above, in having acute ventrodistal spines and pores on the coxae of the ultimate legs.

Description.—The fossil (part) preserves the 12 posteriormost segments and numerous legs, including the ultimate ones. The actual number of trunk segments cannot be counted, and based on extant species could be either 21 or 23. We assume for purposes of this description that the num-

ber is 21, but in Fig. 2B the numbers in parentheses indicate the segment designations if the actual number is 23. Some more anterior structures are preserved on the counterpart, but are too poorly preserved to describe. It appears that during preservation the animal was rolled over slightly to its left, exposing the intersegmental membrane particularly posteriorly on the right side. Length (from anterior margin of 10th tergite to posterior edge of 21st coxae), 17.7 mm, maximum width 2.7 mm. Posterior 12 pedigerous segments relatively well preserved, along with parts of legs 14–21 on the right side, and left leg 20. Tergites nearly uniform in size, with either straight or slightly convex, arcuate posterior margins, lacking paramedian sulci, which become less distinct posteriorly; tergite 21 missing, exposing the 21st coxae. Legpair 20 appears longer and stouter than the preceding pairs, but this may be due to the left leg 20 having been twisted slightly to give an anteriolateral view. Ultimate legs (legpair 21) elongate (11.2 mm long) but not much enlarged in thickness as compared to legpair 20, coxae with extensive ventrolateral pore fields and stout distal spine, preserved podomeres tapering from prefemur to tarsus, prefemur 3–4 times longer than thick.

Stratigraphic and geographic range.—Type locality and horizon only.

Discussion

Taxonomic placement of the new species.—Paramedian tergal sulci are characteristic of the extant families Scolopendridae Leach, 1814, Cryptopidae Kohlsrausch, 1881, and Plutoniumidae Bollman, 1893. Of these families, the ultimate legs of cryptopids are longer but often not much thicker than the preceding legs. Plutoniumids have the ultimate legs modified into stout forceps and have an elongated 21st tergite, while many scolopendrids, and particularly the genus *Scolopendra* Leach, 1814, have 21st legpairs that are strongly thickened and elongate, not forcep-like, and lack the elongate 21st tergite. The great thickness of the podomeres of those legs in our species, and the fact that the tibiae and tarsi are nearly as robust as the prefemora and femora may suggest an evolutionary transition between the enlarged ultimate legs of scolopendrids and the massive forceps of plutoniumids. But due to a lack of crucial characters, *Permocrassacus novokshonovi* cannot be placed in a described family, as is the case with the other Paleozoic scolopendromorphs. However, the very reduced first leg and the enormously enlarged ultimate legs support the placement of the fossil in a new genus, distinct from the other described Paleozoic and Mesozoic scolopendromorphs.

The absence of paramedian tergal sulci and the presence of distal spines on the ultimate coxae of *Permocryptops shelleyi* are suggestive of membership in the family Scolopocryptopidae Pocock, 1896. The relative slender form of the

elongate ultimate legs would also be consistent with such a placement. But due to a lack of crucial characters, *P. shelleyii* cannot be placed in a described family, as is the case with the other Paleozoic scolopendromorphs. However, the spines of the ultimate leg coxae support the placement of the fossil in a new genus, distinct from the other described Paleozoic and Mesozoic scolopendromorphs.

While the ultimate legs of our species are incomplete, comparisons with those discussed by Kenning et al. (2017) suggest that they were probably used much in the same way as the ultimate legs of *Scolopendra* species, mainly as a means of anchoring themselves to the substrate, or to aid in defense and prey capture. As for the pores in the ultimate leg coxae, it has been established that these pores are not secretory in modern scolopendrids, but are involved in the uptake of water (Rosenberg 1983).

Comparisons with previously described species.—*Mazoscolopendra richardsoni* Mundel, 1979 is known from four specimens collected at Mazon Creek. The trunk consists of 21 pedigerous segments, as in *Permocrassacus novokshonovi*, but the largest specimen of *M. richardsoni* is considerably larger, at about 53 mm long. The tergites all appear quite uniform and have straight posterior margins. The first legpair is smaller than those that follow, but not as reduced as seen in *P. novokshonovi*, and the ultimate legpair is significantly less robust. Although the ultimate legs of *P. novokshonovi* are incomplete, it is clear they would be longer than 13 mm, the measurement given by Mundel (1979) for *M. richardsoni*, and therefore much longer in comparison to the body length. Mundel (1979) described the ultimate coxae of *M. richardsoni* as "densely porous" but this character cannot be observed in the type specimen of *P. novokshonovi*. Scudder's (1890) description and illustration of the poorly preserved single specimen of *Palenarthrus impressus* Scudder, 1890 is not informative except that it seems likely the specimen is indeed a scolopendromorph centipede.

Cratoraricrus oberlii Wilson, 2003, from the Cretaceous Crato Formation of Brazil, is well-preserved, in dorsal view. The dorsal cranium is strongly displaced, so that Wilson (2003) was able to describe some of the mouthparts, but nothing about them is distinctive when compared to extant species. Like *Mazoscolopendra richardsoni*, the single specimen of *C. oberlii* has 21 trunk segments and is a little less than twice the length of *Permocrassacus novokshonovi*. The trunk of *C. oberlii* is more slender than in the other two Mesozoic scolopendromorphs, more suggestive of a living species of *Cryptops* rather than *Scolopendra*. However, the presence of divided tarsi and paramedian sulci on the tergites suggests Scolopendridae. The ultimate legs (incompletely preserved), while elongate (perhaps more than twice the length of preceding legs) are only a little thicker than legs 19 and 20, providing a significant difference from both *M. richardsoni* and *P. novokshonovi*. *Velocipede betimar* Martill and Barker, 1998, also from

the Crato Formation, is less well-preserved but shows few differences from *C. oberlii*. Martill and Barker (1998) show only 20 pairs of legs; the photograph of the specimen suggests that the first legs, possibly reduced, were not taken into account and the species had 21 pairs of legs. Individual tergites are hard to distinguish due to poor preservation, and, according to Martill and Barker (1998), poor preparation in the field. The ultimate legs are much as they appear in fossils of *C. oberlii*, and it is not unlikely that the two species from the same formation are congeneric, if not synonymous.

Menon et al. (2003) briefly described and illustrated another specimen from the Crato Formation that to this date has not received a detailed treatment or a name. However, it is unlikely that it is a specimen of *C. oberlii*, since the tarsi of the anterior legs are undivided. The specimen is preserved in right lateral aspect and shows a great deal of detail. Of particular interest in comparison with our species are the different proportions of the ultimate legs—more slender in *C. oberlii*, only a little thicker than the preceding legs though much longer—and the proportions of the antennal segments, which are about twice as long as wide. An additional detail of value in taxonomic placement is the preservation of a single spiracle. The spiracle is ovate to roundish in shape, as in the scolopendrid subfamily Otostigminae; in the Scolopendrinae the spiracle is triangulate and covered by a 3-valved flap.

Conclusions

The Permian centipedes described above represent significant extensions into a temporal gap in the fossil record of the Myriapoda. Our material links scolopendromorph fossils known from the Carboniferous and from the Cretaceous. While not as well preserved as the remains from those two periods, they are clearly members of two distinct groups of scolopendromorph centipedes. As with previously described fossils of scolopendromorphs, it is not possible to say exactly how these two groups, one possibly allied with the living Scolopendridae and the other with the living Scolopcrytopidae, relate exactly to either previously described fossils or extant taxa. Menon et al. (2003) and Wilson (2003) both emphasized the modern appearance of the specimens they studied and indeed it appears that the scolopendromorph body plan has changed little since the Carboniferous. Our Permian species, while distinct, do nothing to dispel that impression. This extreme evolutionary conservatism, however, is not unique among terrestrial arthropods, including other Myriapoda. As Shear and Edgecombe (2010) pointed out, many features of both millipedes and scutigeromorph centipedes have remained constant since the Late Silurian or Early Devonian. It would be no surprise to find scolopendromorph fossils earlier in the record than the Carboniferous examples (Mundel 1979) that now represent the earliest occurrence of the order. In

particular, Devonian remains consisting of fragmentary cuticle organically preserved, which are now being recovered from many sites using HF maceration techniques, should be carefully studied for clues to a myriapod, and possibly scolopendromorph, identity.

Acknowledgements

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