

A new genus of eurypterid (Chelicerata, Eurypterida) from the Upper Devonian salt deposits of Belarus

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Abstract.—We describe a new stylonurid eurypterid from the evaporitic potassium-salt deposits of the Upper Devonian (Famennian) Soligorsk Formation in the Pripyat Trough of Belarus. All specimens are assigned to *Soligorskopterus tchepeliensis* new genus new species, which represents the first formally described eurypterid species from Belarus. The occurrence of well-preserved eurypterids in these unusual evaporite deposits is most likely due to transport from freshwater stream habitats into a hypersaline setting following death. *Soligorskopterus tchepeliensis* n. gen. n. sp. appears to be intermediate between the traditionally considered parastylonurids and stylonurids and thus extends our understanding of stylonurid evolution in the mid-Paleozoic. *Soligorskopterus* n. gen. extends the occurrence of Famennian eurypterids into eastern Laurussia and the Stylonuridae into the Upper Devonian, and this taxon could be part of a global eurypterid habitat shift that took place in the Late Devonian.

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Introduction

Eurypterids (Arthropoda, Chelicerata) are extinct aquatic chelicerates that achieved widespread geographic distribution between their origination in the Middle Ordovician and extinction at the end of the Permian (Tetlie, 2007; Lamsdell et al., 2015). Within the order are significant differences in the extent to which some taxa were dispersed, and this could be a reflection of relative swimming abilities, morphospace occupation, and the eurypterid marine–freshwater environmental transition that took place in the mid-Paleozoic (Lamsdell and Braddy, 2010; Lamsdell and Selden, 2017). For example, in the transitional Silurian–Devonian, walking-legged stylonurines were confined to the paleocontinents that make up Laurussia (Tetlie, 2007); most stylonurids known from this time occur in the USA and Scotland (eastern Laurentia), with only a few known from mainland Europe. A few Silurian–Devonian-age swimming eurypterine taxa are known from eastern Europe, the Baltics, Ukraine, and Russia (Plotnick, 1983, 1999; Tetlie, 2007, and references therein), but stylonurines in this region are rare, having only been found (but not named) in Belarus (Plax et al., 2009; Obukhovskaya et al., 2010; Plax and Barbikov, 2012, 2013).

Over the last 40 years, several stylonurine specimens have been obtained during mining excavations in the Belarusian Starobin potassium-salt evaporite basin, all from within the Osovet Beds of the Upper Devonian Soligorsk Formation (Plax

et al., 2009; Fig. 1). These specimens are exceptionally preserved as carbonized, nearly fully articulated bodies (to 34 cm in length) and isolated appendages. Aside from eurypterids, the only other organismal remains known from these beds are rare terrestrial plants and local miospores. Although the occurrence and general morphology of the eurypterids in these potassium-salt deposits has been documented previously (Plax et al., 2009; Obukhovskaya et al., 2010; Plax and Barbikov, 2012, 2013), they have not yet been described within a detailed morphological or systematic context.

In this paper, we present a comprehensive morphological description of these stylonurine eurypterids and describe their systematic and phylogenetic affiliation. All specimens are assigned to *Soligorskopterus tchepeliensis* new genus new species, the first eurypterid taxon formally described from Belarus. We consider the paleoecology and unusual preservation of *S. tchepeliensis* n. gen. n. sp. in this evaporitic lithofacies, and the paleogeography of stylonurids in the Late Devonian. The exceptional preservation of eurypterid material from this region provides a unique perspective on global eurypterid distributions at a critical time in their history.

Geological setting and stratigraphy

All specimens described herein were found in the Upper Devonian Soligorsk Formation (middle Famennian; Streshin regional stage; Osovet Beds) in the northwestern edge of the Pripyat

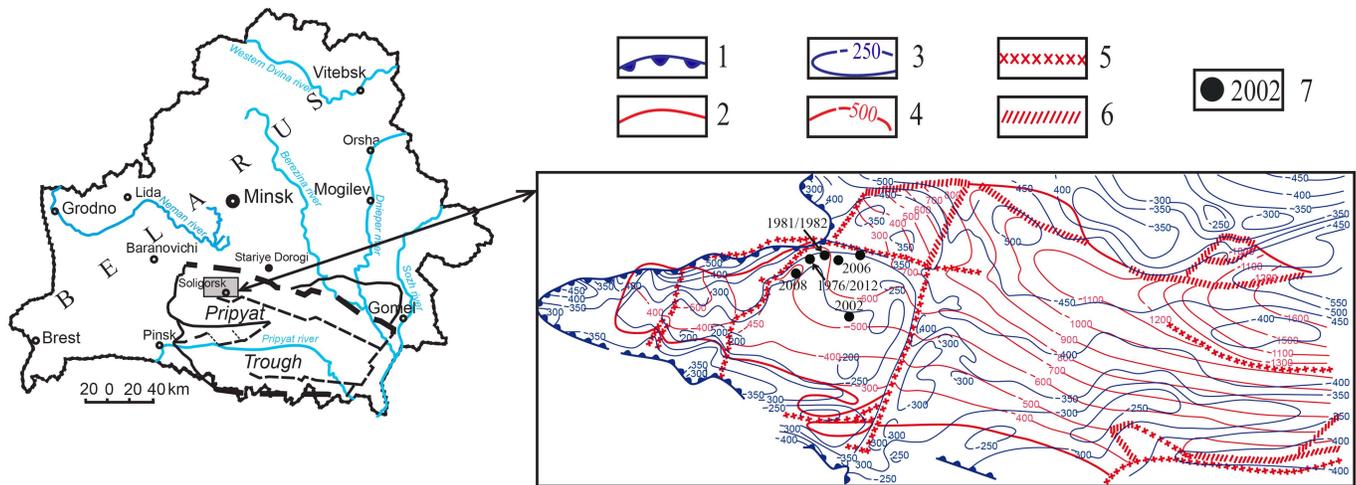


Figure 1. Map of Belarus and the area of study, and structural geology map of the Upper Devonian (middle–upper Famennian) evaporite deposits bounding the Soligorsk Formation. 1 = distribution boundary of the halite deposits; 2 = distribution boundary of the potassium salt (sylvinite) beds; 3 = isohypses of the roof of halite deposits; 4 = isohypses of the bottom of sylvinite deposits; 5 = known rifts in salt deposits; 6 = potential rifts in salt deposits; 7 = sites of eurypterid discoveries (*Soligorskopterus tchepeliensis* n. gen. n. sp.) with years of discovery: 1976/2012, specimen lost/BKM 1052 (holotype); 1981/1982, BSUM P-276/P-170; 2002, specimen lost; 2006 (2 dots), BKM 942; 2008, BKM 943. See Table 1 for the exact latitude/longitudes of individual eurypterid occurrences. Modified from Plax et al. (2009).

Basin in the Pripyat Trough (or Rift) of Belarus (Kruchek et al., 2001; Obukhovskaya et al., 2010) (Fig. 2). The Pripyat Basin was formed during tectonic rifting that began before the middle Frasnian (ca. 369 Ma) and extended to the Famennian (367–364 Ma) (Garetsky et al., 2001). As tectonic activity decreased in the Late Devonian, the area and water depth of the sedimentation basin was concomitantly reduced. An arid climate and repeated oceanic influxes into the continental margin at this time resulted in thick evaporite deposits, primarily composed of halite (NaCl) or potassium salt minerals (carnallite: $\text{KMgCl}_3 \cdot 6\text{H}_2\text{O}$), that were later altered by subsurface brines to sylvite (KCl) or a mixture of halite and sylvite known as sylvinite (Konishchev et al., 2001). These thick evaporite units are interbedded with thinner layers of carbonates, clays, and marls, as well as significant amounts of plant remains and miospores. The siliciclastic deposits and plant remains suggest that the evaporative and restricted environment in the basin was occasionally interrupted by periods of humidity and freshwater input from temporary creeks or small rivers in the basin that carried terrigenous sediments (Vysotsky et al., 1988; Plax et al., 2009).

The subsurface Soligorsk Formation in the Storobin region is one of several evaporitic units formed during an oceanic influx and comprises five thick halite and sylvinite deposits, numbered I–V. Multiple specimens of a single eurypterid species, *Soligorskopterus tchepeliensis* n. gen. n. sp., were found during mining activity in the upper Soligorsk Formation, at 630–700 m depth, at several localities within an approximately three kilometer wide region (Table 1). *Soligorskopterus tchepeliensis* n. gen. n. sp. occurs as isolated, dark grey-black carbonized remains within thin, light gray to greenish halopelite (halite-bearing clay) beds interbedded within layers of potassium-salt minerals (carnallite, sylvite). The halopelite interbeds vary in thickness from a few millimeters to 10–15 cm and occur within thicker, multiyear, rhythmic halite and sylvinite beds (Garetsky et al., 1984; Vysotsky et al., 1988). In at least one collected specimen (BKM 1052; Fig. 3), a very thin halopelite bed containing a eurypterid lies directly adjacent to a thicker sylvite layer.

Eurypterid specimens are oriented parallel to the bedding plane, and specimen completeness ranges from almost fully articulated exoskeletons to isolated tagma. The generally excellent preservation of the eurypterids was previously taken as evidence that they were not transported far prior to burial and thus represent an autochthonous assemblage (Plax et al., 2009). Rare, carbonized, and unidentified terrestrial plant remains and miospores (*Discernisporites* Neves, 1958, *Retispora* Staplin, 1960) have been found with the eurypterids at some localities in the formation and are the only other organic material to occur in this unit.

Materials and methods

Specimens were photographed using a Canon 600 D camera with a 24–105 mm objective lens. Interpretive drawings were prepared in CorelDRAW X3 (Corel Corporation, USA).

Eurypterid terminology largely follows Tollerton (1989) for morphology of the carapace, metastoma, lateral eyes, prosomal appendages, genital appendage, opisthosomal differentiation, telson, and patterns of ornamentation. The terminology of the ventral plate morphologies follows Tetlie et al. (2008). Terminology for prosomal structures and cuticular sculpture, and the labeling of the appendages, follows Selden (1981) with additions from Lamsdell et al. (2015). Minor modifications to the terminology used in these papers follows Lamsdell (2011).

Repositories and institutional abbreviations.—Types, figured, and other specimens examined in this study are deposited in the following institutions in Belarus: BKM, Trudovoy Slavy Museum, Soligorsk; BSUM, Geological Museum of Belarusian State University, Minsk.

Systematic paleontology

Arthropoda Von Siebold in Von Siebold and Stannius, 1848
Chelicerata Heymons, 1901

DEVONIAN										System	International Chronostratigraphic Chart
Upper										Series	
Famennian										Stage	
middle					upper					Substage	
362.0										Age, Ma	
<i>Cyrtospirifer lebedianicus</i> - <i>Productella schemardensis</i>		<i>Volgospirifer volgensis</i> - <i>Cyrtospirifer bolschinskiensis</i>			<i>Sinotectirostrum otrada</i> - <i>Cyrtospirifer kapsedensis</i>			<i>Sinotectirostrum potschtovica</i> - <i>Centrorhynchus robustus</i>		Brachiopods (Rzhonsnikskaya, 2000)	Biostratigraphic zones
<i>Cornispora varicornata</i>				<i>Grandispora famenensis</i> - <i>Diducites versabilis</i>			<i>Retispora lepidophyta typica</i>		Miospores (Arkhangelskaya, 1985; Avkhimovich et al., 1993)		
Lebedjan		Oressa			Streshin			Starobin		Regional Stage	Regional Stratigraphic Units
Borichev	Zalesie	Naidov	Shatilki	Osovets	Ljuban	lower Starobin	upper Starobin	Beds			
<i>Zonomonoletes vulgaris</i> - <i>Cornispora bicornata</i>		<i>Cristatisporites lupinovitshi</i>			<i>Raistrickia macroreticulata</i> - <i>Discernisporites golubinicus</i>		<i>Grandispora distinctus</i> - <i>Spelaeotriletes papulosus</i>	<i>Retispora lepidophyta</i> - <i>Grandispora facilis</i>	<i>Retispora lepidophyta</i> - <i>Apiculiretusispora verrucosa</i>	Miospore local zones	Regional Biostratigraphic Units
Kopatsevichi Formation											Local stratigraphic units Pripyat Trough
lower subformation; marls, limestones, dolomites, oncolites; brachiopods; 11 m		middle subformation; fine-grained sandstones; 17 m				upper subformation; dolomite; brachiopods; 41 m					
Slutsk Formation Dolomites, dolomitic limestones, anhydrites, with rare interbeds of sandstones and clays; brachiopods, ostracods, and miospores; 9–84 m		Shestovichi Formation Halite with interbeds of sulfate-carbonates and clay; miospores; 5.5–50 m			Soligorsk Formation lower subformation; halite with interbeds of clays, marls, sulfate-carbonate rocks and potassium salts; miospores; 100–550 m		Ljuban Formation Clays, marls, sandstones, gypsums; miospores; 80–180 m	Starobin Formation Clays, dolomites, kerogeniferous marls, stromatolites, miospores; 90–300 m			

Figure 2. Stratigraphy and biostratigraphic zonation of the Upper Devonian (middle–upper Famennian) Pripyat Trough of Belarus. Formation thicknesses are indicated in meters. See Table 1 for the subsurface depths at which individual specimens of *Soligorskopterus tchepeliensis* n. gen. n. sp. were discovered in the Soligorsk Formation. Adapted from Obukhovskaya et al. (2010).

Table 1. Stratigraphic and locality information for all specimens of *Soligorskopterus tchepeliensis* n. gen. n. sp. examined in this study.

Specimen	Year	Depth (m)	Latitude (°N)	Longitude (°E)	Lithologic and Stratigraphic Notes
BSUM P-276/P-170	1981/1982	690	52.88	27.51	Halopelite interbedded within a thick bed of halite separating sylvinite beds III and IV
BKM 942	2006	740	52.89	27.57	Halopelite interbed located at the bottom of package 3 of sylvinite bed IV
BKM 943	2008	630	52.85	27.42	Halopelite interbedded within layers of sylvinite, which are interbedded within a thick bed of halite separating sylvinite beds III and IV
BKM 1052 (holotype)	2012	670	52.87	27.64	Halopelite interbed of sylvinite bed III
Lost	1976	640	52.87	27.45	Halopelite interbedded within a thick bed of halite separating sylvinite beds III and IV
Lost	2002	700	52.84	27.57	Halopelite interbed, at the bottom of sylvinite bed V

Eurypterida Burmeister, 1843

Stylonurina Diener, 1924

Stylonuroidea Diener, 1924

Stylonuridae Diener, 1924

Soligorskopterus new genus

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Type species.—*Soligorskopterus tchepeliensis* n. gen. n. sp., by monotypy.

Diagnosis.—Stylonurid of medium size, 12–34 cm in length. Prosoma is horseshoe-shaped with a relatively narrow marginal rim. Compound lateral eyes are crescentic, located in the anterior half of the prosoma. Opisthosoma is wide, the metasoma bearing slight epimera, and tapering into a styliform telson. Prosomal appendages are robust, gradually increasing in length anteriorly to posteriorly. Prosomal appendages II–IV are spiniferous *Ctenopterus*-type; prosomal appendages V and VI are nonspiniferous *Parastylonurus*-type. The metastoma is petaloid in shape, markedly narrower than long with an angular anterior notch and a flattened posterior margin. Type A genital appendage is long, reaching beyond the fifth opisthosomal segment, and is composed of at least two segments with a median ridge. Type B genital appendage is short and narrow. The pretelson is elongated and bears a pair of ridges ventrally comprised of large overlapping scales. Cuticular ornament is in the form of small, contiguous or separate, semilunate, linguoid-shaped and acicular scales, which in some places transform into ridges and crests.

Etymology.—The genus name is derived from the words Soligorsk (the town in Belarus closest to where the specimens were found) and *pterus*, meaning wing.

Remarks.—*Soligorskopterus* n. gen. is differentiated from all other stylonurid taxa in possessing a prosomal shield and opisthosoma morphologically similar to *Parastylonurus* Kjellesvig-Waering, 1966, but prosomal appendages reminiscent of *Pagea* Waterston, 1962 and *Laurieipterus* Kjellesvig-Waering, 1966.

Soligorskopterus tchepeliensis new species

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Figures 3–6; Table 1

Type specimens.—Holotype, BKM 1052, Upper Devonian (middle Famennian), upper Soligorsk Formation, Pripyat Basin in the Pripyat Trough of Belarus. Paratypes, BKM 942, 943; BSUM P-276/P-170.

Diagnosis.—As for the genus.

Occurrence.—Upper Devonian (middle Famennian, Streshin regional stage), upper Soligorsk Formation (Osovet beds), near Soligorsk, Belarus.

Description.—The holotype (BKM 1052; Fig. 3) is the largest specimen of *Soligorskopterus tchepeliensis* n. gen. n. sp. recovered, with a length of 34 cm, and represents a mostly complete individual preserved in ventral aspect. The prosoma (71 mm in length; 80 mm in width; length/width ratio 0.89) is horseshoe-shaped with a comparatively narrow (3 mm) marginal rim. The lateral eyes are crescentic, located in the anterior half of the prosoma. The prosomal ventral plates are of *Eurypterus*-type, bearing a single median suture. Transverse sutures are evident on the ventral plates, expanding forward anteriorly. The prosomal appendages are incomplete, with appendages III–VI evident on the left and appendages IV–VI evident on the right. On appendage III, only the third and fourth podomeres are fragmentarily preserved, largely in the form of an imprint. The appendages of limb pair IV are also preserved fragmentarily, being known from the second, third, fourth, and fifth podomeres. Podomeres four and five bear multiple rows of fixed spines. The cuticular ornament of these podomeres consists of weakly expressed small scales. Appendages V and VI are better preserved than the previous appendage pairs. Appendage V is known from the coxa to the seventh podomere and is nonspiniferous. Appendage VI, also known from the coxa to the seventh podomere, also lacks spines. The fourth podomere of appendage VI is the longest, with subsequent podomeres reducing in length consecutively. Both appendages exhibit cuticular ornamentation of a row of small, closely situated semilunate scales along the anterior third of each podomere. The lateral margins of the podomeres are also ornamented with a series of thickened scales. The metastoma is petaloid in shape with an angular anterior notch and a flattened posterior margin.

The opisthosoma is generally broad but does not exceed the maximum width of the prosomal carapace. The opisthosoma consists of 12 segments, divided between the six-segmented mesosoma anteriorly and the six-segmented metasoma posteriorly.

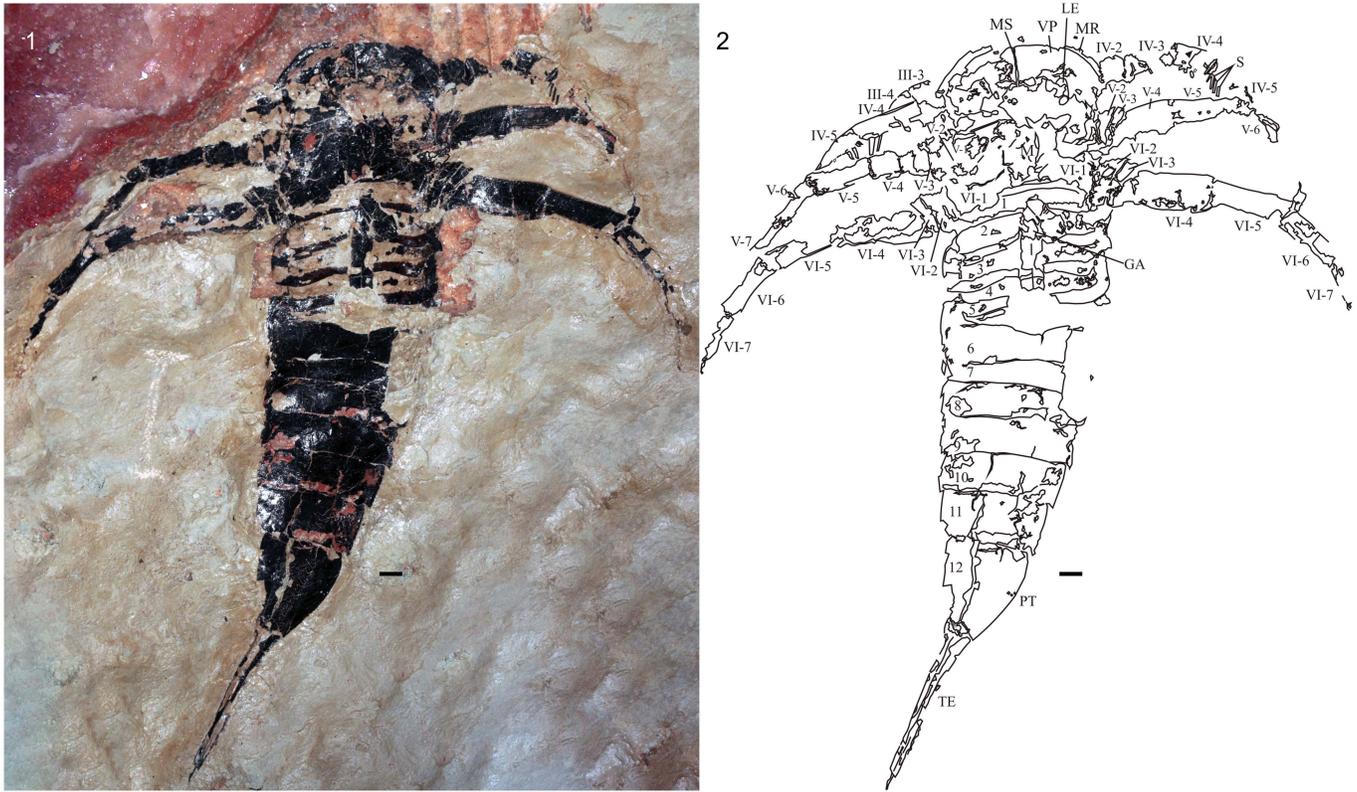


Figure 3. *Soligorskopterus tchepeliensis* n. gen. n. sp., holotype, BKM 1052, specimen preserving the ventral surface: (1) specimen photograph (note the pink-red sylvinite directly adjacent to and under the specimen); (2) interpretive drawing. GA, genital appendage; LE, lateral eyes; M, metastoma; MR, marginal rim; MS, median suture; PT, pretelson; S, spines; TE, telson; VP, ventral plate; 1–12, sternites. Prosomal appendages are labeled with Roman numerals (I–VI), and individual podomeres are labeled with Arabic numerals (1–9), ordered proximally to distally. Scale bar = 10 mm.

The mesosoma is of generally constant width, with the metasoma narrowing from the seventh opisthosomal segment onward. Because the specimen is preserved in ventral aspect, the dorsal tergites of the mesosoma are not seen; however, the ventral structures of the genital appendage and opisthosomal opercula are evident. The genital operculum comprises a clear median and posterior opercular plate, with evidence of a narrow anterior opercular plate provided through imprints within the sediment. The median opercular plate is 9 mm long, with a posterior width of 70 mm, whereas the posterior opercular plate has a length of 12 mm and a posterior width of 76 mm. A large Type A genital appendage is present (8 mm wide, at least 38 mm long), extending to at least the fourth opisthosomal segment. A deltoid plate is apparent to the right of the insertion of the genital appendage into the median opercular plate. The genital appendage itself has a carina running along its length and is composed of at least two segments, with the division occurring slightly posterior to the posterior margin of the third opisthosomal segment. The first postgenital operculum (corresponding to the third opisthosomal segment) is 13 mm in length with a posterior width of 75 mm. The operculum of the fourth segment has a length of 13 mm with a posterior width of 74 mm, that of the fifth segment has a length of 14 mm and a posterior width of 74 mm, and that of the sixth segment has a length of 15 mm and a posterior width of 71 mm.

The metasoma is represented by the sternites, which are fused laterally to the tergites to form ankylosed segments. The seventh segment has a length of 11 mm and a posterior width of

69 mm; the eighth segment has a length of 15 mm and a posterior width of 68 mm; the ninth segment has a length of 16 mm and a posterior width of 61 mm; the tenth segment has a length of 17 mm and a posterior width of 54 mm; the eleventh segment has a length of 21 mm and a posterior width of 45 mm. The pretelson is elongated, having a length of 40 mm and a posterior width of 20 mm, resulting in a length/width ratio of 2.0. The posterolateral margins of each metasomal segment are produced into short epimera. The epimera of the pretelson are reduced to appear almost absent. The cuticular sculpture of the metasomal sternites consists of small, closely situated semilunate scales. These scales exponentially increase in size (from 0.4–0.5 mm to 5 mm) on sternites 10–12, with some becoming acicular and forming a pair of crests running in parallel flanking the center of the sternites.

The telson is styliform and 73 mm in length. Where the cuticle has worn away impressions of the sediment reveal the presence of a moderate dorsal keel. The ventral surface of the telson is shown to bear a continuation of the enlarged scale ridge that runs down the center of the telson, with the scales progressively decreasing in size toward its tip.

The first paratype (BKM 943; Fig. 4) is an almost intact specimen in ventral view preserving the opisthosoma and portions of the prosomal appendages and metastoma. The total length of the specimen is 25 cm. The prosoma is fragmentary, preserving some evidence of a narrow marginal rim and the ventral plate and its transverse suture. The prosomal appendages are incomplete, with

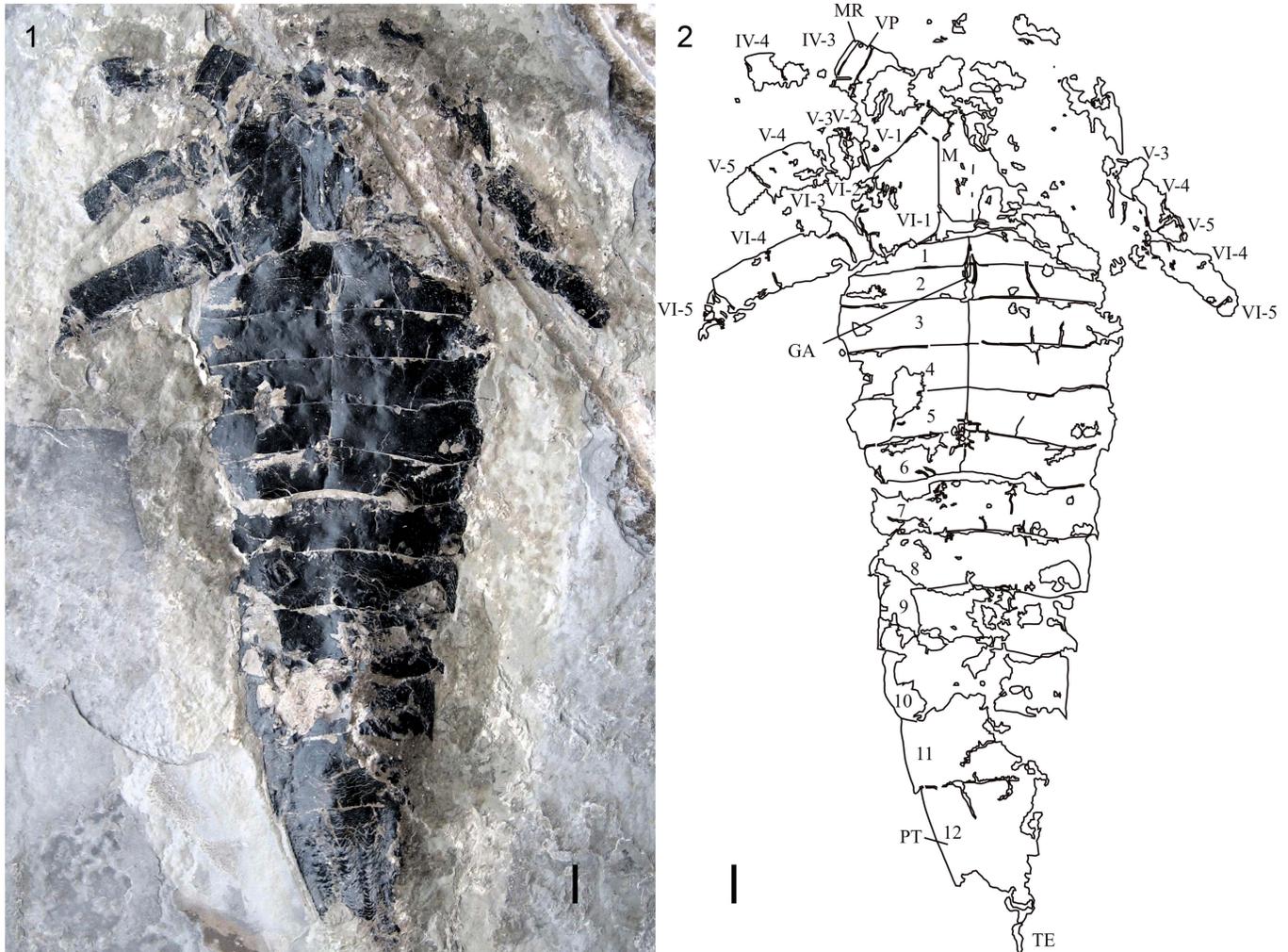


Figure 4. *Soligorskopterus tchepeliensis* n. gen. n. sp., paratype BKM 943; specimen preserving the ventral surface: (1) specimen photograph; (2) interpretive drawing. Abbreviations as in Figure 3. Scale bar = 10 mm.

only the proximal podomeres of appendages IV–VI preserved. Only the third and fourth podomeres of appendage IV are preserved, but they are fragmentary and do not preserve the armature. Appendages V and VI are both known from the coxa to the fifth podomere. Both appendages show the characteristic lateral border of thickened scales. The metastoma is petaloid, with an anterior notch and a truncated, flattened posterior. The lateral margins of the metastoma are remarkably straight, resulting in an almost rectangular appearance. A slight median ridge runs down the center of the metastoma. Small semilunate scales are present on the metastoma and the coxae.

The opisthosoma is relatively broad and tapers regularly throughout the metasoma. The mesosoma is generally well preserved. It is somewhat wider than the metasoma. The genital operculum is clearly composed of an anterior opercular plate, a median opercular plate (corresponding to the first opisthosomal segment), and a posterior opercular plate (corresponding to the second opisthosomal segment). The median opercular plate is 8 mm in length and 73 mm in width at the base, whereas the posterior opercular plate is 9 mm in length and 75 mm in width at the base. A clear suture is present

between them. Both opercular plates have an ornament of small semilunate scales, whereas the posterior opercular plate also has acicular scales. A type B genital appendage is present, oval and elongated in shape, with a length of 13 mm and a width of 3 mm. The terminal part of the genital appendage is missing, and so it is impossible to ascertain how many segments it comprises. There are no deltoid plates evident alongside the insertion of the genital appendage, despite the region being well preserved.

The remaining opercula are generally uniform in morphology. The operculum of the third segment is 10 mm in length with a posterior width of 77 mm; that of the fourth segment is 11 mm in length with a posterior width of 77 mm; the fifth segment is 12 mm in length with a posterior width of 71 mm; and the sixth operculum is 12 mm in length and 64 mm in width at the base. The cuticular sculpture of the opercula comprises small semilunate and acicular scales. A median furrow is present on all the postgenital opercula, shallowing out just before the posterior margin of the sixth operculum. The opercula of segments 4–6 appear medially fused, however those of the third opisthosomal segment exhibit a median



Figure 5. *Soligorskopterus tchepeliensis* n. gen. n. sp., paratype BSUM P-276/P-170; prosoma with appendage pair VI viewed from the ventral surface. Scale bar = 10 mm.

notch where they join, which indicates they might have been separate or only partially fused.

The metasoma is preserved in slightly rougher condition than the mesosoma. The metasomal segments narrow regularly posteriorly: the seventh segment is 14 mm in length, 62 mm in width across its posterior; the eighth segment is 14 mm in length, 58 mm in width; the ninth segment is 15 mm in length, 55 mm in width; the tenth segment is 16 mm in length, 50 mm in width; the eleventh segment is 18 mm in length, 40 mm in width; and the pretelson is 32 mm in length, 18 mm in width. The cuticular ornament of the metasomal sternites comprises small semilunate and acicular scales, which enlarge and form paired ridges on segments 10–12. Small epimera are present at the posterolateral margins of the metasomal segments. The telson is poorly preserved and present as only a few small fragments of cuticle posterior to the pretelson.

The second paratype (BSUM P-276/P-170; Fig. 5) is represented by a fragmentary prosoma comprising the outline of the prosonal carapace with the prosonal appendage coxa, metastoma, and a complete paired appendage VI. The prosoma is horseshoe-shaped with a length of 75 mm and a width of 83 mm, resulting in a length/width ratio of 0.90. The narrow 2–3 mm wide marginal rim extends around the anterior and lateral edge of the carapace and tapers to its posterior. The metastoma is petaloid in shape, narrow, with relatively straight sides and a shallow anterior notch. The cuticle at its posterior is absent but imprints in the sediment suggest it had a truncated, flattened posterior margin. Paired appendage VI is preserved in its entirety, revealing a narrow coxa with no anteriorly expanded

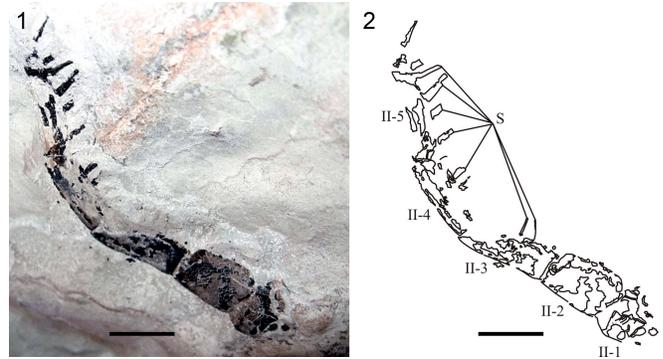


Figure 6. *Soligorskopterus tchepeliensis* n. gen. n. sp., paratype BKM 942; prosomal appendage II: (1) specimen photograph; (2) interpretive drawing. Abbreviations as in Figure 3. Scale bar = 10 mm.

ear. The appendages are long and nonspiniferous, with the fourth podomere being the longest and all subsequent podomeres shortening consecutively. No modified podomere 7a is present. Distal podomeres are not expanded into a swimming paddle. The anterodistal margin of podomere VI-8 is drawn out into a long projection, extending for three-fifths the length of podomere VI-9. The ornamentation on the appendages comprises small semilunate scales, with a thickened border of scales along the lateral podomere margins. Dense scale ornament is also visible on the coxa.

The final paratype (BKM 942; Fig. 6) is a partially exfoliated but fairly complete prosomal appendage II. The appendage tapers in width from 10 mm proximally to 3 mm distally; its total length is 75 mm and it is comprised of six podomeres, including the coxa. The coxa and second podomere are devoid of armature, whereas podomeres II-3–II-5 bear numerous short (5–8 mm) and thin (0.9–1.1 mm) spines, at least five per podomere. These spines bear slight striations running along their length. The surface of the first two podomeres of the appendage has sculpture in the form of dense semilunate and acicular scales.

Etymology.—The species name is derived from the village of Tchepeli, near where one of the eurypterid specimens was found.

Remarks.—The new eurypterid (Fig. 7) exhibits a number of characteristics that place it firmly within the stylonurines. The most obvious of these is the retention of prosomal appendage VI as a walking limb lacking a modified podomere 7a, however the assignment is also supported by the lack of an expanded ear on coxa VI, the transverse suture on the prosonal ventral plates, and the possession of a visible anterior opercular plate (Lamsdell et al., 2010b). Within the Stylonurina, *Soligorskopterus* n. gen. exhibits closest affinities to the Stylo-nuroidea, lacking as it does the spiniferous appendage V characteristic of Kokomopteroidea (Tetlie, 2008; Lamsdell et al., 2010b) and the cleft posterior metastoma and sweep-feeding modifications seen in Mycteropoidea (Lamsdell et al., 2009; Lamsdell, 2013). The multiple spines per podomere on appendages II–IV also preclude the new species from assignment to Rhenopteroidea (Lamsdell et al., 2010a). Multiple spines per podomere are, however, known from some members

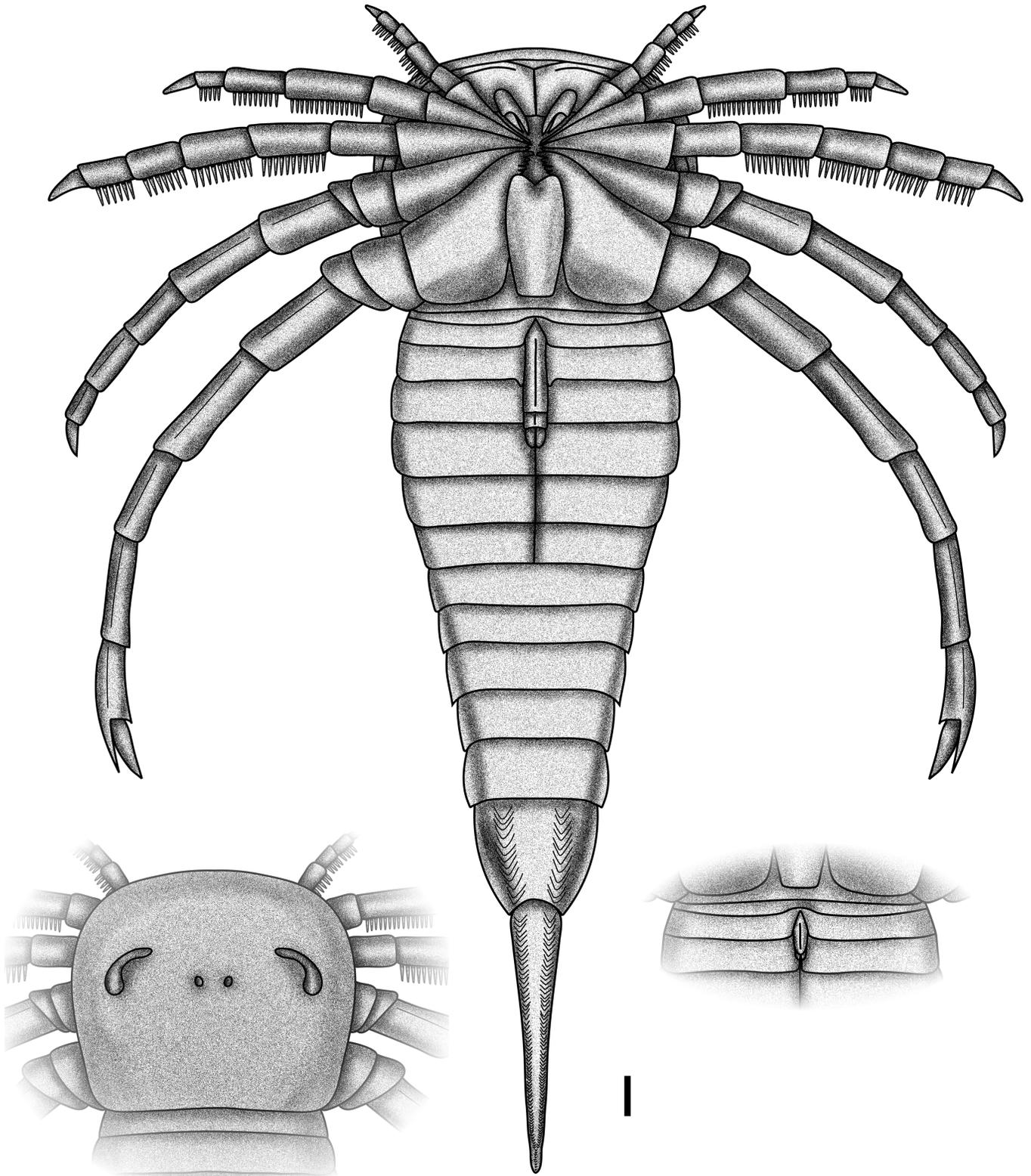


Figure 7. Reconstruction of *Soligorskopterus tchepeliensis* n. gen. n. sp. Complete ventral reconstruction showing type A genital appendage, flanked by dorsal view of the prosoma and ventral view of the type B genital appendage. Scale bar = 10 mm.

of the Stylonuroidea. An assignment to Stylonuroidea is further supported by the flattened posterior of the metastoma in *Soligorskopterus* n. gen.

Within Stylonuroidea, *Soligorskopterus* n. gen. bears closest similarity to *Parastylonurus* (Waterston, 1979), sharing a number of characteristics that are apparently plesiomorphic for

the clade. The prosomal carapace in *Parastylonurus* and *Soligorskopterus* n. gen. has a more rounded outline, being horseshoe-shaped rather than quadrate as in species of *Pagea* (Waterston, 1962), *Stylonurus* Page, 1856 (Woodward, 1872), and *Stylonurella* Kjellesvig-Waering, 1966 (Waterston, 1979), spatulate as in *Laurieipterus* (Waterston, 1962), or triangular as in *Ctenopterus* Clarke and Ruedemann, 1912. The prosomal ventral plates are of the *Eurypterus*-type as in *Parastylonurus* and *Stylonurella* rather than possessing an epistoma as in *Laurieipterus*. The metastoma is generally narrow and straight-sided as in *Parastylonurus* and *Pagea*, quite unlike the broad metastoma of *Laurieipterus*. As in *Pagea* and *Parastylonurus*, *Soligorskopterus* n. gen. has a slight median ridge on the metastoma; however, the anterior notch is more reminiscent of *Parastylonurus* rather than the flattened anterior margin present in *Pagea*.

Soligorskopterus n. gen. differs from *Parastylonurus* primarily in the armature of prosomal appendages II–IV, which bear multiple spines per podomere and are of the *Ctenopterus*-type. This appendage morphology is shared with *Laurieipterus*, *Pagea*, and *Ctenopterus*, the appendages of *Parastylonurus* and *Stylonurella* only having a single pair of fully-developed spines per podomere. The spines of *Soligorskopterus* n. gen. are all equal in length along each podomere and so more closely resemble the armature of *Laurieipterus* and *Ctenopterus* than that of *Pagea*. The spines bear longitudinal striations, as do those of *Laurieipterus* and *Stylonurella*. The structure of prosomal appendages V and VI in *Soligorskopterus* n. gen. closely resemble those of *Parastylonurus*, with a row of enlarged scales present on the anterior third of each podomere and with each podomere possessing a margin of thickened overlapping scales. This type of appendage ornament is shared with *Stylonurus*, *Laurieipterus*, and *Stylonurella*. However, *Parastylonurus* and *Soligorskopterus* n. gen. are distinct in having the anterodistal margin of podomere VI–8 developed into a long spur. *Soligorskopterus* n. gen. differs from *Parastylonurus* in lacking the crenulate distal podomere margins.

The available material of the genital appendages in *Soligorskopterus* n. gen. reveals them to be almost identical to those in *Parastylonurus*, with the type A appendage being large, composed of at least two segments, and possessing a median ridge running along its length. The type B appendage is short, narrow, and also has a median ridge. The only other genital appendage known from Stylonuroidea is the type B genital appendage of *Stylonurella*, which agrees in overall morphology with those of *Parastylonurus* and *Soligorskopterus* n. gen. The postgenital opercula of both *Soligorskopterus* n. gen. and *Parastylonurus* also have small median keels running along their lengths. The overall shape of the opisthosoma is broad as in *Parastylonurus* and *Stylonurus*, although never expanding beyond the width of the prosomal carapace. The metasomal segments of *Soligorskopterus* n. gen. are extended into epimera, although they are short projections as in *Pagea* and not elongated like those of *Parastylonurus*. The epimera do, however, exhibit the same terraced ornamentation as observed in *Parastylonurus*. An elongate pretelson is common between *Soligorskopterus* n. gen., *Parastylonurus*, and *Pagea*, with *Ctenopterus* and *Stylonurus* having the regular, short pretelson morph. The general cuticular ornamentation, consisting of a

mixture of semilunate and acicular scales, is also consistent between *Soligorskopterus* n. gen. and *Parastylonurus*. The scale ridges on the pretelson of *Soligorskopterus* n. gen. are not known from any other stylonuroid eurypterid and appear to be an autapomorphy for the genus; however, they could be an indication of trilobation as seen in *Pagea*.

Soligorskopterus n. gen. appears to be an intermediate between the traditionally considered parastylonurid (*Parastylonurus* and *Stylonurella*) and stylonurid (*Stylonurus*, *Pagea*, *Ctenopterus*, and *Laurieipterus*) groups. Parastylonurids are paraphyletic, with *Stylonurella* resolving closer to the stylonurids and *Parastylonurus* forming the sister taxon to all other stylonuroids (Lamsdell et al., 2010a, 2010b). *Soligorskopterus* n. gen. likely resolves intermediately between *Stylonurella* and the *Stylonurus/Pagea* + *Laurieipterus/Ctenopterus* clade due to the armature of appendages II–IV comprising multiple spines per podomere (as in the Stylonuridae) and the morphology of appendage VI and the horseshoe-shaped carapace (which are parastylonurid in form).

Paleoecology of *Soligorskopterus* n. gen

The evaporitic nature of the eurypterid-bearing halopelite and the close proximity of the eurypterid-bearing beds to thick evaporite layers suggests deposition in a hypersaline environment. Moreover, potassium salts (e.g., carnallite, sylvite) are some of the last evaporite minerals to precipitate out of solution in marine settings (Warren, 1997), and therefore the occurrence of one specimen (BKM 1052; Fig. 3) on a thin lamina of halopelite that is immediately adjacent to a sylvite layer would suggest deposition in or near a supersaline seawater brine. Yet despite the occurrence of *Soligorskopterus tchepeliensis* n. gen. n. sp. in this extreme environment, it is unlikely that this setting is representative of its preferred life habitat. Eurypterids, including stylonurids, in the Late Devonian were almost entirely constrained to freshwater habitats (Lamsdell and Braddy, 2010). In addition, a previous study of eurypterids preserved in evaporitic settings has demonstrated that the onset of hypersaline conditions (and any subsequent formation of associated intra-sedimentary evaporites) occurred after burial of the eurypterid specimens, and thus are not reflective of life habitat (Vrazo et al., 2016).

Eurypterids have been suggested to congregate in sheltered regions to molt (Braddy, 2001; Vrazo and Braddy, 2011), and it is possible that the specimens of *Soligorskopterus* n. gen. are shed exuvia of individuals molting within a nearshore lagoon or tidal flat prior to the onset of hypersaline conditions. However, the majority of specimens are well articulated and do not exhibit any of the characteristic patterns of disarticulation or contortion characteristic of exuvia (Tetlie et al., 2008; McCoy and Brandt, 2009), and thus it seems more likely that the specimens are allochthonous carcasses transported into the environment of preservation following death. The co-occurrence of terrestrial plant material with the eurypterids indicates some terrestrial influence on the paleoenvironment and it is probable that the carcasses of *Soligorskopterus* n. gen. were transported into the Soligorsk environment via freshwater streams. Additionally, the general lack of disarticulation suggests that the individuals were only recently dead when transport occurred. Modern horseshoe

crab mortalities have been shown to float intact for up to two days after death before settling on the sediment surface (Babcock et al., 2000), facilitating the transport potential of recent carcasses (see also Allison, 1986). Alternatively, living *Soligorskopterus* n. gen. might have been swept into the hypersaline lagoon during storm events before expiring in the toxic environment—a similar scenario to that suggested for occurrences of the horseshoe crab *Mesolimulus* Størmer, 1952 in the Upper Jurassic Solnhofen Limestone in Germany (Lomax and Racay, 2012). However, a large influx of meteoric water would likely have lowered the salinity of the lagoon at the same time that the eurypterids were swept in, and hence it seems more likely that the specimens were transported into the lagoon soon after death. Once in this setting, burial of the arthropod carcasses in fine-grained clays, and the onset of hypersaline conditions in the water column or subsurface, would have been inimical to growth of decay bacteria and conducive to long-term preservation (Seki and Taga, 1963; McMahon et al., 2016). The occurrence of *Soligorskopterus* n. gen. in what appear to be semiregular intervals in the Soligorsk Formation could also reflect a broader sequence stratigraphic control on preservation (see Vrazo et al., 2017), and it is clear that further sedimentological and stratigraphic work is needed to fully understand the environmental factors that facilitated eurypterid preservation in this evaporitic lithofacies.

There is no direct evidence for the diet of *Soligorskopterus* n. gen.; however, analysis of the visual system of *Rhenopterus diensti* Størmer, 1936, a stylonurine eurypterid from the Early Devonian of Germany, indicates that at least some stylonurines had a visual acuity comparable to that of modern horseshoe crabs (Poschmann et al., 2016). It is unlikely that *Soligorskopterus* n. gen. would have been an active predator like certain swimming eurypterids (Anderson et al., 2014; McCoy et al., 2015). *Soligorskopterus* n. gen. most likely had a diet like that of modern horseshoe crabs, consisting of small invertebrates (ostracods, gastropods, bivalves, polychaetes, etc.; Botton and Haskin, 1984). The morphology of appendages II–IV, with their rows of multiple spines per podomere, indicates that *Soligorskopterus* n. gen. was a dragnet-style sweep-feeder (Lamsdell et al., 2010b) and would have raked the spines of these appendages through the sediment to entangle and excavate partially buried prey.

Eurypterid paleogeography and patterns of extinction

Stylonuroidea was until now known with confidence from the lower Silurian (Llandovery) to the Lower Devonian (Pragian), with *Ctenopterus* (?) *beechei* (Hall, 1884), a species of questionable taxonomy, potentially extending the range of the group into the Famennian (Lamsdell and Braddy, 2010). *Soligorskopterus tchepeliensis* n. gen. n. sp. is the first confirmed occurrence of Stylonuroidea in the Famennian and as such extends the age range of the clade some 50 million years.

The extension of Stylonuroidea into the Famennian means that four clades (Mycteropoidea, Kokomopteroidea, Stylonuroidea, and Adelophthalmoidea) persisted beyond the major drop in eurypterid diversity in the Early Devonian and into the Late Devonian biotic crisis (Lamsdell and Selden, 2017). However, each of these clades are represented by only a few species (in the case of adelophthalmoids and mycteropods) or a

single species (for kokomopterooids and stylonurooids), and the discovery of *Soligorskopterus* n. gen. does not suggest that Late Devonian eurypterid diversity was significantly higher than previously suggested. It is noteworthy that three of these clades are members of Stylonurina, which are consistently lower in diversity than the swimming Eurypterina and tend to have a more cryptic fossil record (Lamsdell et al., 2010b). The fact that the majority of Late Devonian eurypterids are stylonurines—including the new species described here—supports existing hypotheses regarding the global collapse of eurypterid diversity during the Devonian (Lamsdell and Selden, 2017). The nektonic and nektobenthic Eurypterina were particularly hard hit by the biotic crisis, dwindling exponentially in diversity from the latest Silurian through to the Middle Devonian. The survivors were relegated to the margins of eurypterid niche space and invaded continental freshwater ecosystems (Lamsdell and Braddy, 2010; Lamsdell and Selden, 2017), although the exact timing of this transition is still uncertain (Vrazo et al., 2017).

The morphological disparity of eurypterids has also been demonstrated to decrease over the course of the Devonian, with an associated reduction of morphospace occupation (Lamsdell and Selden, 2017). The discovery of *Soligorskopterus* n. gen. does not alter these patterns in disparity and morphospace occupation. Stylonuroid morphospace almost wholly overlaps with the kokomopterooid and mycteropoid morphospace, and as such does not expand the occupied morphospace of Famennian eurypterids. *Soligorskopterus* n. gen. does, however, expand the geographic occurrence of eurypterids during the Famennian. Previous records of Famennian eurypterids are known from western and central Laurussia and largely comprise stylonurines from the continental United States (Hall, 1884; Ehlers, 1935; Tetlie, 2008), with a single stylonurine known from southwestern England (Lamsdell et al., 2009) and another from Belgium (Fraipoint, 1889). The eurypterine genus *Adelophthalmus* Jordan in Jordan and von Meyer, 1854 is also known from the Famennian of the USA (Hall and Clarke, 1888) and Belgium (Fraipoint, 1889). *Soligorskopterus* n. gen. therefore extends the occurrence of Famennian eurypterids into eastern Laurussia. Despite Famennian eurypterids only being known from Laurussia, however, it is likely that they had a global distribution. In the Frasnian, eurypterids are known from both Laurussia (Ruedemann, 1921) and Gondwana (Tetlie et al., 2004), and the same is true for the Tourmasian (Waterston, 1985; Tetlie and Poschmann, 2008).

Whatever the cause of the eurypterid shift from marine to freshwater habitats during the Devonian, it seems likely to have been the result of widespread, global pressure rather than an inherited trait through the chance survival of a few eurypterid groups within a single biogeographic region. As supported by phylogenetic information (Lamsdell and Selden, 2017), the concerted, independent habitat shift among eurypterids during this time period represents a case of macroevolutionary convergence driven by a selective trend (Lamsdell et al., 2017; Congreve et al., 2018). Such data are integral to expanding our understanding of biotic responses to environmental processes in the Late Devonian; further studies into other contemporaneous clades will undoubtedly refine our understanding of the events underpinning the biotic crisis that characterizes the end of the period (Stigall, 2010, 2012).

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