

Arachnids from the Carboniferous of Russia and Ukraine, and the Permian of Kazakhstan

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Received: 23 May 2013 / Accepted: 1 August 2013 / Published online: 18 August 2013
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Abstract New finds of Late Palaeozoic arachnids, based on three well-preserved carapaces from the Carboniferous of Russia and Ukraine and one complete, albeit poorly preserved, specimen from the Permian of Kazakhstan, are described. The spider genus *Arthrolycosa* is reported from the Late Carboniferous (Late Pennsylvanian: Kasimovian–Gzhelian) of Chunya in the Tunguska Basin of Siberia; it is the first find of a spider outside the Carboniferous tropics. Another fossil assigned to the same genus comes from the Late Carboniferous (Early Pennsylvanian: Bashkirian) of Kamensk–Shakhtinsky in the Donets Basin of Russia; it is probably the oldest fossil spider known. A thelyphonid (whip scorpion) carapace is described from the Late Carboniferous (Late Pennsylvanian: Kasimovian) of the adjacent Lugansk Province of the Donets Basin of Ukraine.

Keywords Arachnida · Araneae · Carboniferous · Permian · Thelyphonida · Uropygi

Schlüsselwörter Arachnida · Araneae · Karbon · Perm · Thelyphonida · Uropygi

Kurzfassung Neue Funde fossiler Spinnentiere werden basierend auf drei gut erhaltenen Carapaxen aus dem Karbon Russlands und der Ukraine und einer schlecht erhaltenen, kompletten Spinne aus dem Perm Kazakhstans beschrieben. Die Spinnengattung *Arthrolycosa* wird im Oberkarbon (Kasimovium–Gzhelium, spätes Pennsylvanium) von Chunya im Tunguska-Becken Sibiriens nachgewiesen. Ein weiteres Fossil, das derselben Gattung zugewiesen wird, stammt aus dem Oberkarbon (frühes Pennsylvanium: Bashkirium) von Kamensk–Shakhtinsky im Donez-Becken von Russland. Es handelt sich wahrscheinlich um die älteste bekannte Spinne. Der Carapax eines Geißelskorpions wird aus dem Oberkarbon (Kasimovium, spätes Pennsylvanium) von dem benachbarten Gebiet Lugansk des Donez-Beckens der Ukraine beschrieben.

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Introduction

Arachnids have been known as fossils from the Upper Carboniferous Coal Measures of Europe and North America for many years (Corda 1835; Buckland 1837; Meek and Worthen 1865). Economic exploitation of coal resources during the late 19th and early 20th centuries, together with the popularity of fossil hunting on the associated spoil heaps, contributed greatly to these discoveries. They offer important insights into early arachnid evolution and have resulted in significant monographs, particularly those by Frič (1904), Pocock (1911) and Petrunkevitch (1913, 1949) which described the faunas in some detail. Less well known are finds from Russia and Ukraine,

despite the fact that both of these countries also host rich coal deposits. While there has been considerable work on the late Palaeozoic insect faunas (Rohdendorf et al. 1961; Shcherbakov 2008), there are only three published records of arachnids from this region. Eskov (1999) reported trigonotarbid from the Kasimovian–Gzhelian of the Kuznetsk and Tunguska basins, one of them (from the Chunya locality, see below) was tentatively assigned to the genus *Eophrynus*. Eskov and Selden (2005) described two arachnids from well-known fossil insect localities in Permian strata of the Ural Mountains of Russia. *Permarachne novokshonovi* Eskov and Selden 2005 was originally described as a mesothele spider (Araneae), but was later shown to belong to an extinct order of spider-like arachnids named Uraraneida (Selden et al. 2008). Eskov and Selden (2005) also reported an isolated spider carapace, assigned to the fossil genus *Arthrolycosa* Harger 1874 which had previously been known only from North America. Fet et al. (2011) described several scorpion fragments from the Late Permian and basal Triassic of European Russia, one Permian leg fragment resembling that of the Carboniferous genus *Eobuthus* (Eobuthidae).

In this paper, we describe three new arachnid carapaces from Carboniferous strata of the Tunguska Basin of Siberia, and from the Kamensk–Shakhtinsky and the Lugansk Province in the Donets Basin of western Russia and Ukraine, respectively. A complete, though poorly preserved, spider specimen from the Permian of Kurty, Almaty Province, Kazakhstan, is described as Araneae *incertae sedis*. Two of the carapaces can be assigned to Araneae, and one to Thelyphonida; although the possibility that late Palaeozoic carapaces resembling mesothele spiders actually belonged to uraraneids cannot be ruled out. The only true spiders yet described from Palaeozoic rocks belong to the primitive suborder Mesothelae; putative opisthotheles reported from the Palaeozoic either belong to other arachnid orders or are too poorly preserved to be identified as such (Penney and Selden 2006). The extension of the fossil record of spiders to the Carboniferous of Russia, including the cool temperate climatic zone of that period (the Tunguska carapace), is of interest, while the whip scorpion carapace is remarkable for its modern morphology.

Materials and methods

The specimens reported here are held in the Borissiak Paleontological Institute, Russian Academy of Sciences (PIN). Other institutional abbreviations are: YPM, Yale Peabody Museum; UMMP, University of Michigan Museum of Paleontology; MfN, Museum für Naturkunde Berlin; PAS, personal collection of Paul A. Selden. All fossil mesothelae have been studied by Paul Selden; those

particularly relevant to this study include *Arthrolycosa antiqua* Harger 1874 (YPM 000161 (holotype), YPM 000162, YPM 000163), and *A. danielsi* Petrunkevitch 1913 (UMMP 7219). The fossils were also compared with extant material of mesothele (and other) spiders and to whip scorpions in collections, including *Ryuthela nishihirai* Haupt 1983, Japan (MfN ZMB 48325); *Heptathela kimurai* (Kishida 1920), Japan (MfN ZMB 48319; PAS); cf. *Liphistius thaleban* Schwendinger 1990, Thailand (MfN ZMB 48313); *L. lannaianus* Schwendinger 1990, Thailand (PAS); and *L. niphanae* Ono 1988, Thailand (PAS).

The specimens were studied and drawn using a Leica MX12.5 stereomicroscope, photographed dry using a Leica M165C stereomicroscope and Leica DFC425 camera, and imaged without coating with backscattered electron (BSE) detectors of a Tescan Vega XMU scanning electron microscope. All measurements are in millimetres.

Geological setting and taphonomy

The Donets Basin of Ukraine and Russia contains one of the most complete and well-studied successions of paralic Carboniferous sediments. Arachnids are found there in two sites. The first is Kamensk–Shakhtinsky (5 km SSE of railway station), Rostov Province, Russia (herein called Kamensk). A spider carapace and a trigonotarbid were collected by a PIN field party in 2011, in siltstone laterally replacing coal seam i_3 beneath limestone I_4^1 , together with conchostracans, eurypterids, insects, and diverse plants. Dmitry V. Vasilenko (PIN) collected the spider carapace described herein. The site was discovered by Dmitry V. Shaposhnikov. The fossil bed is assigned to the upper part of the Belaya Kalitva Formation (Krasnodonsky Horizon), terminal Bashkirian (Melekessian), Lower Pennsylvanian in age, and dated slightly older than 315 Ma. This interval was correlated with the Westphalian B (Duckmantian) of western Europe (Davydov et al. 2012) but, according to newer isotopic ages, the top of Duckmantian is located above the top of Bashkirian (Pointon et al. 2012). So the spider from Kamensk is probably slightly older than *Eoecteniza* from the Middle Duckmantian of Coseley, UK, and therefore the oldest spider currently known.

The second site in the Donets Basin is Kartanash sandstone quarry on the left bank of Lomovatka River, 0.8 km SSE Kalinovo, Lugansk Province, Ukraine (herein called Lomovatka). A thelyphonid carapace was found by Daniil S. Aristov (PIN) during a PIN field trip in 2012, in alluvial siltstone between limestones N_5^1 and O_1 , together with conchostracans, eurypterids, insects, and Early Stephanian plants (the Westphalian flora is replaced by a Stephanian flora at approximately limestone N_4 in this section). The site was discovered by palaeobotanist

Alexander K. Shchegolev, and a palaeodictyopteran from there was described by Sharov and Sinitshenkova (1977). The bed is assigned to the upper part of the Isaevskaya Formation (Kartanashsky Horizon), which is middle Kasimovian (early Khamovnikian), Upper Pennsylvanian, in age, and dated to ca. 306 Ma (Schmitz and Davydov 2012). This interval is correlated with the Stephanian A of western Europe (Davydov et al. 2012).

Another spider was found in the Tunguska Basin, at the left bank of Chunya River (right tributary of Podkamennaya Tunguska) 12 km downstream of Eroba (Yuraba) River mouth, Central Siberia, Russia (herein called Chunya). The spider carapace and a trigonotarbid tentatively identified as *Eophrynus* sp. (Eskov 1999), along with diverse insects and plants, were collected by PIN field parties headed by Alexander G. Sharov in 1970–1971 in mudstone of the upper part of the Kata Formation, which is correlated with the Upper Pennsylvanian (Kasimovian–Gzhelian; Betekhtina et al. 1988). The site was discovered by palaeobotanist E. S. Rasskazova who described the flora of Kata Formation. The Chunya spider carapace is preserved in a pale grey to buff, weakly laminated mudstone.

The three arachnid carapaces mentioned above were collected during special searches for fossil insects which, in these and many other localities, are represented chiefly by isolated wings and body fragments, and only rarely by more or less complete body fossils. Before burial, these remains were concentrated in places of fine sediment deposition after being transported by flowing water for some distance, so that sclerotized wings are sometimes found complete, and the more delicate, membranous wings are usually fragmented. The isolated carapaces described here, being the most durable parts of the arachnids, and which are almost completely removed from the rest of the body during ecdysis, are most likely moults.

A complete but poorly preserved fossil spider was found at the Kurty locality, 8 km NW of Zhal-Pak-Tas granite quarry, Almaty Province, southern Kazakhstan. Along with plants and several hundred specimens of the seymouriamorph tetrapod *Utegenia shpinari*, it was collected by a PIN field party headed by Nikolay N. Kalandadze in 1975, in the Kugaly Formation, which is Late Pennsylvanian or Early Permian in age. Now, this formation is divided into two, and the age considered to be Late Bashkirian to Gzhelian, on the basis of lithological data (Seitmuratova 2011). However, the plant fossils collected at Kurty were identified as Permian by the late S.V. Meyen (unpublished data). All other seymouriamorphs are Permian in age, including the Middle Permian *Urumqia liudaowanensis* from Xinjiang, China, which was synonymized under *Utegenia shpinari* by Ivakhnenko (1987). Therefore, the Permian age of Kurty seems more probable. The fossiliferous beds (bituminous shale

impregnated with chalcedony) alternating with sandstones are considered to be deposits of seasonally drying floodplain pools (Kuznetsov and Ivakhnenko 1981). This region was in a tropical climatic zone in the Late Carboniferous (Raymond and Scotese 2009). The Kurty specimen is preserved as an external mould in a buff-coloured, finely laminated siltstone which is oxidized to yellowish and contains much darker (pyrolusite?) mineralization around the edges of the piece. The mould is very irregular, possibly resulting from dissolution of minerals replacing the spider; the distal parts of the legs are not visible, giving it the appearance of a very short-legged animal.

Morphological interpretation

Three of the specimens described here are arachnid carapaces, one of which (PIN 3115/294) shows an attached sclerite which is the dorsal sclerite of the pedicel (first opisthosomal tergite). One carapace (PIN 1866/100), with its distinctive, subheptagonal outline and eyes in three clusters, is clearly that of a thelyphonid (whip scorpion). The other two belong to either spiders (Araneae) or the extinct order of spider-like Uraraneida, whose carapace is poorly known (Selden et al. 1991, 2008). The fourth specimen (PIN 3630/1) is a tiny but poorly preserved spider.

Carapaces PIN 3115/294 and 5431/9 are very similar to those of modern mesothele spiders—a suborder containing a single extant family: Liphistiidae Thorell 1869 (Platnick 2013). In overall shape, the carapaces of modern liphistiids vary somewhat from rather broad at front and back, with only slightly bowed lateral margins (e.g., *Ryuthela*, Fig. 1a), to those with greater constriction of the cephalic region anteriorly, which gives a more piriform shape (e.g., *Heptathela kimurai yanbaruensis* Haupt 1983, Fig. 44H in Haupt 2003). The posterior margin is recurved to a small extent. In all cases, the cephalic region is quite well defined by posterolateral sulci and distinctly raised, with the eye tubercle situated at the anterior. The foveae of *Liphistius* and *Heptathela* consist of a deep, somewhat diamond-shaped pit with a transverse and a deeper longitudinal groove (Platnick and Sedgwick 1984; Schwendinger 2009; pers. obs.); in the moult of *Ryuthela* (Fig. 1a) the fovea consists of a pair of pits within a shallow transverse depression. The fovea of mesotheles is thus symmetrical and without a preferred direction, unlike the generally strongly recurved or procurved foveae of mygalomorphs (Raven 1985) or the longitudinal slits found in many araneomorph spiders (Jocqué and Dippenaar-Schoeman 2007). The fovea is the external expression of a large apodeme which anchors the musculature of the sucking stomach to the carapace. Radiating from the fovea are

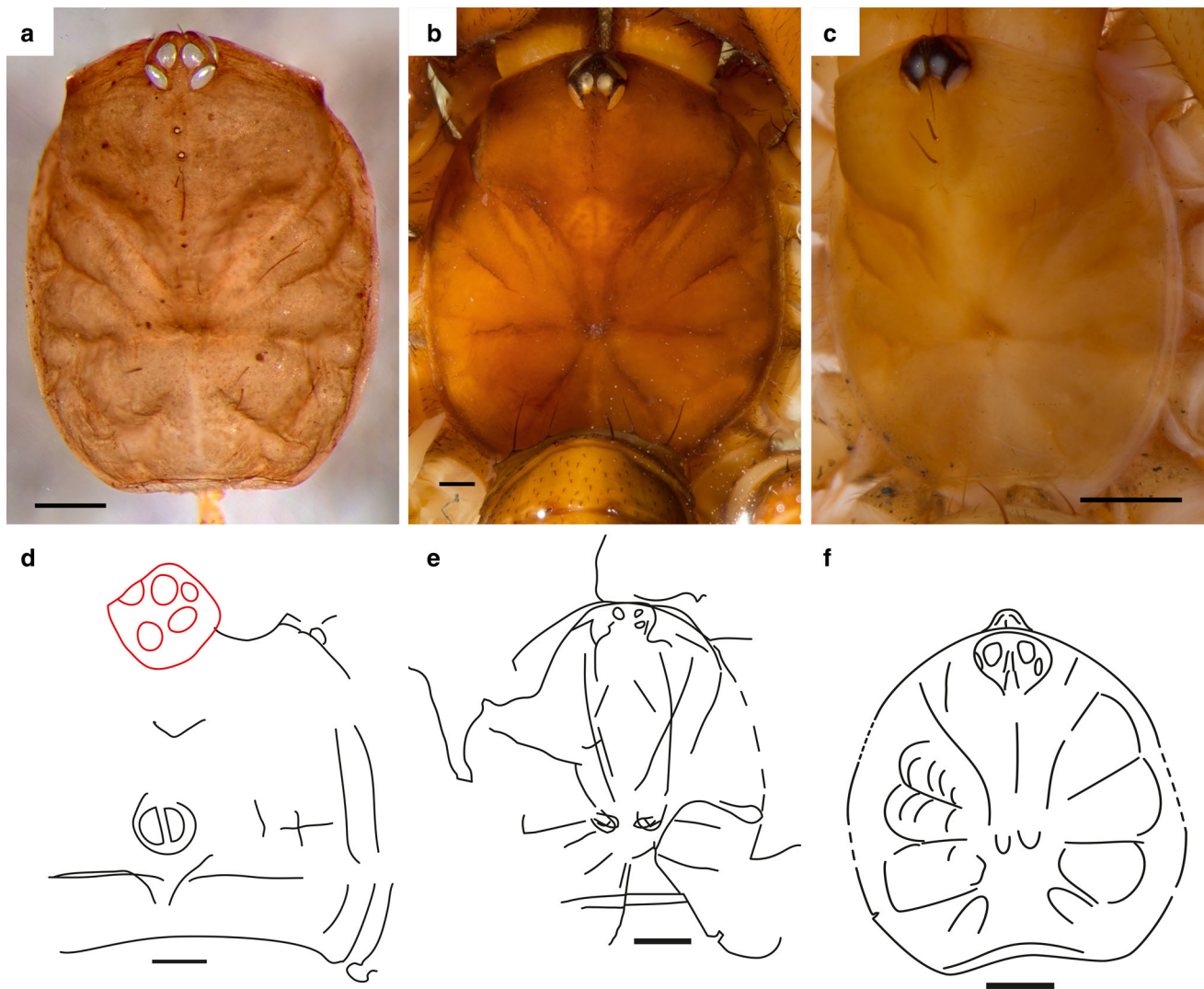


Fig. 1 Carapaces of Recent (**a–c**) and Palaeozoic (**d–f**) mesotheles. **a** *Ryuthela nishihirai*. **b** *Liphistius niphanae*. **c** *Heptathela kimurai*. **d** *Arthrolycosa antiqua* holotype YPM 000161; eye cluster

superimposed from counterpart. **e** *A. antiqua* YPM 000162; part and counterpart superimposed. **f** *A. danielsi* UMMP 7219. Photographs: **a** dry; **b**, **c** under 70 % ethanol. Scale bars equal 1 mm

clear, shallow sulci, the anterior pair bordering the cephalic region, while the other three radiate to the intercoxal regions (thus, four pairs in all). Prominent macrosetae (bristles) occur in a longitudinal line from in front of the eye tubercle (the clypeus), through the tubercle, and behind it part way to the fovea (Fig. 1). The lateral borders of the carapace show narrow margins; these widen posterolaterally, where there may be some setae. In modern mesotheles, the posterior median (PME), posterior lateral (PLE) and anterior lateral (ALE) eyes are subequal in size, while the anterior medians (AME) are tiny. The PME and the tiny AME are located on the dorsal side of the eye tubercle, the PLE are on the dorsoposterolateral side of the tubercle, but the ALE are located on the anterolateral side, where they look forwards and a little sideways, so they are barely noticeable in dorsal view (Fig. 1).

The carapace is poorly preserved in the only unequivocal fossil mesothele so far described: *Palaeothele* (Selden 1996a, b), but is much better known in some of the Palaeozoic fossils which have been attributed to Mesothelae. These belong to the following genera: *Arthrolycosa* Harger 1874, *Arthromygale* Petrunkevitch 1923, *Eocteniza* Pocock 1911, *Geralycosa* Kušta 1888, *Protocteniza* Petrunkevitch 1949, and *Protolycosa* Roemer 1866. Study of all specimens of Palaeozoic Araneae for another work (in prep.) has indicated that at least *Arthrolycosa* is a genuine mesothele, and that *Protolycosa*, also, most likely belongs to this genus (in which case the latter name has nomenclatural priority). Within this genus, there is some degree of variation in carapace shape, from somewhat equant, with rather parallel lateral margins, and a distinct eye tubercle (e.g., the holotype of *Arthrolycosa antiqua* Harger 1874, YPM

IP.000161, Fig. 1d; *A. sp.*, Figs. 9–12 in Eskov and Selden 2005), through more suboval in shape with a distinct eye tubercle (*A. danielsi* Petrunkevitch 1913, UMMP 7219; Fig. 1f), to suboval with an eye cluster not distinctly set on a tubercle (*A. antiqua* YPM IP.000162; Fig. 1e). Two of these (*A. antiqua* holotype, *A. sp.*) have a distinctly deep fovea with paired depressions within, while the other two (*A. antiqua* IP.000162, *A. danielsi*) show paired depressions not set within such a distinct fovea. *Protolycosa cebbennensis* Laurentiaux-Vieira and Laurentiaux 1963 and undescribed specimens from Writhlington, Somerset, UK (pers. obs.) have carapaces with deep foveae and paired depressions within; that of *Protolycosa* is suboval in outline while the Writhlington specimens are more equant in shape. In all cases, the carapace posterior margin is slightly recurved. Work in progress will decide on any taxonomic changes relating to these morphological variations; here, we discuss how the Chunya and Kamensk carapaces compare with modern mesotheles and arthrolycosids.

The outlines of both of the fossil spider carapaces described here are closer to the elongate, suboval or piri-form shape, with curved lateral margins. The eyes of both are in discrete clusters, but not on such well defined tubercles as in the holotype of *Arthrolycosa* and modern mesotheles. The PME and PLE are easily distinguishable in the fossils, but the AME (being very small) and the ALE (facing forwards) are not so discernible (Figs. 2, 3). The fovea of the Chunya specimen is the typical deep form with paired depressions, while that of the Kamensk specimen 5431/9 is transverse, and more similar to *A. antiqua* YPM IP.000162. The radiating grooves and thin lateral and broader posterolateral margins of our Russian carapaces are very similar to those seen not only in modern mesotheles but also in all arthrolycosids. Moreover, the Chunya carapace shows setal follicles along the posterolateral margins and in the midline behind the eye cluster, just as in modern mesotheles.

Palaeothele is a true mesothele, as evidenced by the original descriptions (Selden 1996a, b) and later work showing that it did not possess the anal flagellum of uraneids (Selden et al. 2008). *Arthrolycosa antiqua* YPM IP.000162, at least, is also a true mesothele because of its spinneret configuration (unpublished pers. obs. by PAS). It is not yet known what the carapaces of Uraraneida looked like, so we cannot be certain the carapaces described here and, indeed, those of some other arthrolycosids, are mesotheles, but their close morphological similarity to modern mesotheles suggests that this is the most likely scenario.

The small specimen PIN 3630/1 consists of an external mould of the body preserving dorsal features, the proximal parts of eight legs, and fragments of the pedipalps. The carapace is very poorly preserved; distal parts of the legs (tarsi and most of the metatarsi) are concealed by rock

matrix; strong ridges and/or rows of macrosetae (spines) on the dorsal side of some podomeres are preserved as grooves. Podomere boundaries can be determined only approximately. Judging from the habitus, the specimen is most likely a spider, although synapomorphies are lacking. It does not look like any other arachnid order.

Systematic palaeontology

Order Araneae Clerck 1757

Araneae incertae sedis

Material: PIN 3630/1 (negative impression only). From Kurty, Almaty Province, Kazakhstan; Permian, Upper Kugaly Formation.

Description

Small spider (body *c.* 5.0 long) with elongate abdomen and short, stout legs (Fig. 4). Carapace broadly oval, *c.* 2.0 long, 1.6 wide (judging by position of leg bases). Abdomen 3.0 long, 1.4 wide, narrowly triangular, widest anteriorly, tapering to posterior. Legs robust, apparently well sclerotized, provided with strong ridges and possible spines. Leg length and width increase from anterior to posterior (leg formula probably 1234); preserved lengths: leg 1, 2.2; leg 2, 2.4; leg 3, 2.8; leg 4, 3.4; widths: leg 1, 0.4; leg 4, 0.5. Femur about as long as tibia and longer than patella (fe:pa:ti = *c.*1:0.7:1). In dorsal aspect, legs widest at patella and distal femur, femora tapered to base, tibiae (and preserved parts of metatarsi) tapered to apex. Strong, closely parallel ridges (preserved as grooves) along dorsal side of femur (at least five), patella and proximal tibia (at least four); at least three more spaced rows of spines or stout setae along dorsal side of distal tibia and probably proximal metatarsus.

Remarks The apparently short, powerful legs, with well developed armature, are broadly similar to those of Liphistiidae and indicate fossorial habits. However, the abdomen shape immediately distinguishes the fossil from known Mesothelae.

Suborder Mesothelae Pocock 1892

Family Arthrolycosidae Frič 1904

Remarks Petrunkevitch (1913) referred all Carboniferous spiders to Arthrolycosidae. He erected Arthromygalidae Petrunkevitch 1923 to accommodate those Carboniferous mesotheles which appeared to lack eyes, while in Arthrolycosidae eyes are present in a compact group (Petrunkevitch 1923). Modern mesotheles have an eye tubercle, so the family is poorly defined on just this character, and the

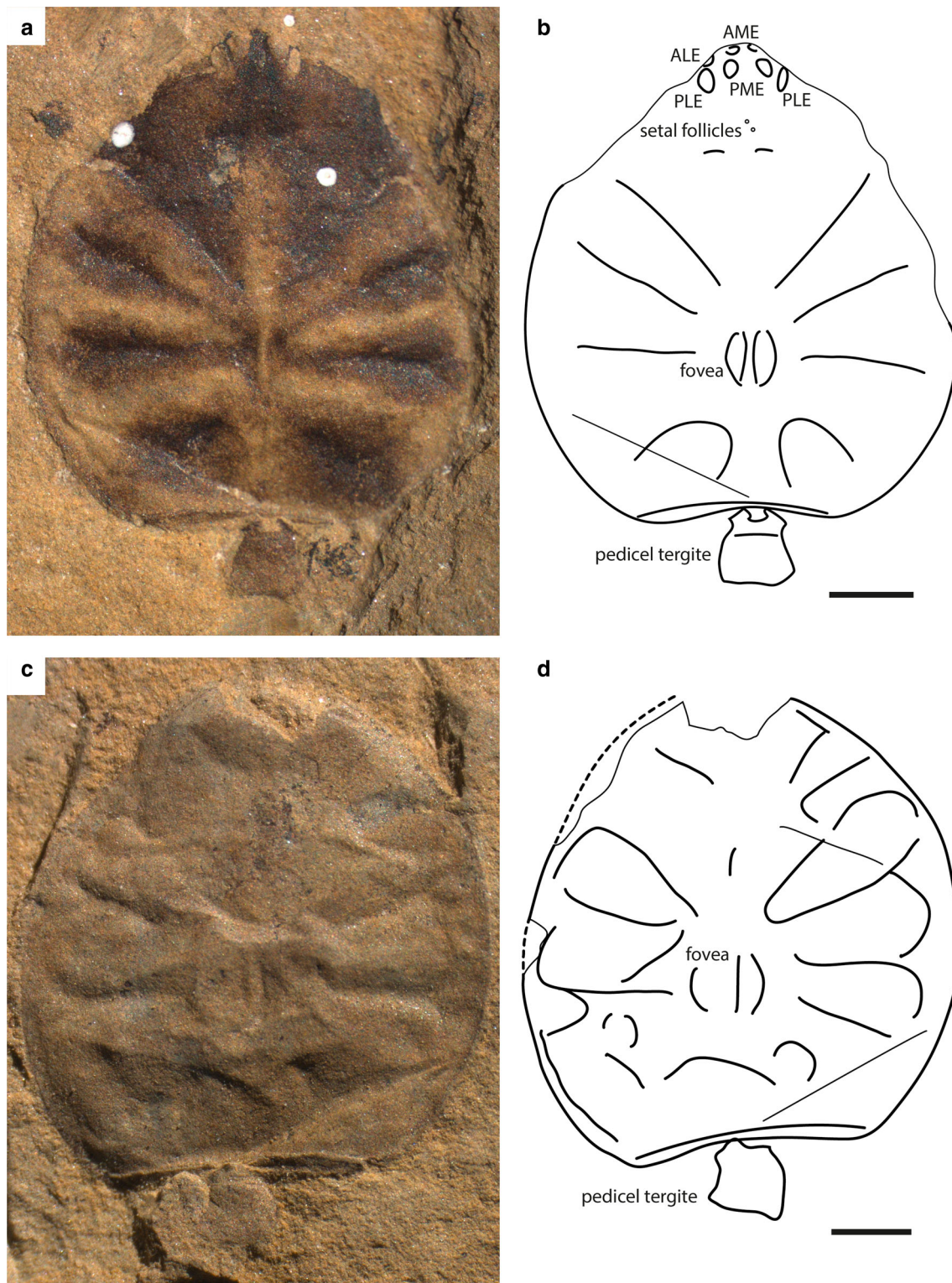


Fig. 2 *Arthrolycosa* sp. A, specimen PIN 3115/294, from the Upper Carboniferous of Chunya, Tunguska Basin, Russia. **a** Photograph of negative impression. **b** Camera lucida drawing of negative impression, showing eyes, pedicel tergite, and fovea. **c** Photograph of positive impression. **d** Camera lucida drawing of positive impression.

ALE anterior lateral eyes, *AME* anterior median eyes, *PLE* posterior lateral eyes, *PME* posterior median eyes. *Scale bars* equal 1 mm. *Finer lines* indicate outline of fossil (not outline of carapace in life); *dashed lines* indicate presumed carapace outline

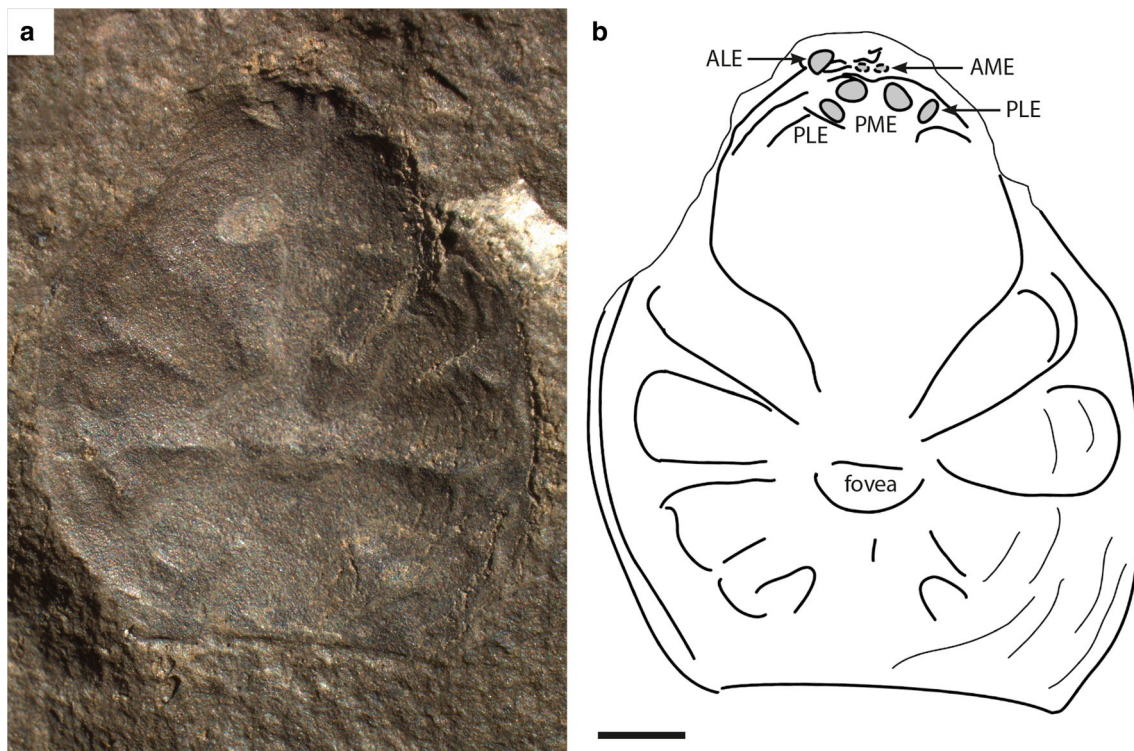


Fig. 3 *Arthrolycosa* sp. B, specimen PIN 5431/9, from the Upper Carboniferous (Upper Bashkirian) of Kamensk–Shakhtinsky, Donetsk Basin, Russia. **a** Photograph of specimen. **b** Camera lucida drawing of

specimen, showing eyes and fovea. *ALE* anterior lateral eyes, *AME* anterior median eyes, *PLE* posterior lateral eyes, *PME* posterior median eyes. Scale bar equals 1 mm

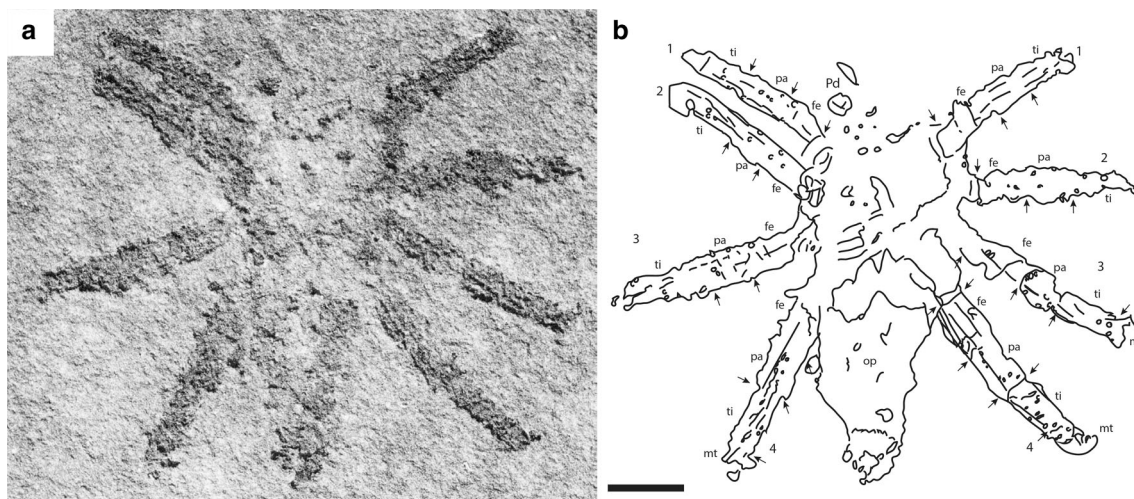


Fig. 4 *Araneae incertae sedis*, specimen PIN 3630/1, from the Permian of Kurty, Almaty Province, Kazakhstan. **a** Photograph, dry in low-angle light. **b** Camera lucida drawing. Scale bar equals 1 mm. 1,

2, 3, 4 leg numbers, *fe* femur, *op* opisthosoma, *Pd* pedipalp, arrows mark probable leg joints

apparent lack of eyes in Arthromygalidae is almost certainly a result of preservational artefacts. In the *Treatise on Invertebrate Paleontology*, Petrunkevitch (1956) included in Arthrolycosidae: *Arthrolycosa antiqua* and *A. danielsi* from Mazon Creek, USA, and *Eocteniza silvicola* Pocock

1911 from Coseley, UK. Eskov and Selden (2005) referred an isolated carapace from the Middle Permian Belebeyev Formation of Russia to *Arthrolycosa*.

Genus *Arthrolycosa* Harger 1874

Arthrolycosa sp. A

Material: PIN 3115/294 (positive impression: Fig. 2c, d; negative impression: Fig. 2a, b). From Chunya, Tunguska Basin, Russia. Upper Carboniferous, upper part of Kata Formation.

Description

Carapace, length 6.0, maximum width 5.6, and pedicel tergite (Fig. 2). Carapace suboval in outline, with slight projection of anterior cephalic region. Strong surface relief but no ornament (e.g., tubercles). Eye region slightly raised and offset with shallow groove posteriorly along midline, bearing four subequal, suboval eye lenses (PME and PLE) preserved together as two slightly separated pairs, and left ALE and pair of small AME discernible anteriorly. Remainder of carapace dominated by four pairs of grooves radiating from foveal region and bifurcating near carapace margin, the anterior pair delimiting the slightly raised cephalic region. Fovea situated 2/3 of carapace length behind anterior margin, consists of elliptical depression bearing median ridge and lateral paired depressions within. Carapace lateral margins smoothly curved, posterior margin slightly recurved, margins unbordered anteriorly, with narrow border appearing posterolaterally, widest laterally on posterior margin. Pedicel tergite approximately subtrapezoidal, widening slightly posteriorwards, with anterolateral projections, ca. 0.7 across, immediately behind carapace.

Remarks Among the described specimens of *Arthrolycosa*, the Chunya specimen most closely resembles *A. danielsi* in their shared possession of a suboval carapace and a deep fovea with paired depressions. *A. danielsi*, however, has a distinct eye tubercle, which is not so marked in our *A. sp. A*. In this respect, the Chunya specimen resembles *A. sp. B* from Kamensk.

This fossil is of special biogeographic interest because it is the first find of a spider outside the Carboniferous tropics (at palaeolatitude c. 45°), in the cool temperate climate of the Tunguska Basin (Raymond and Scotese 2009). Other Carboniferous spiders are found at low palaeolatitudes of Euramerica.

Arthrolycosa sp. B

Material PIN 5431/9 (positive impression only). From Kamensk–Shakhtinsky, Donetsk Basin, Russia. Upper Carboniferous (early Pennsylvanian), upper part of Belaya Kalitva Formation.

Description

Carapace, length 6.8, maximum width 6.1 (Fig. 3). Outline oval, but distinctly projecting cephalic region anteriorly.

Cephalic region bears four subequal, suboval eye lenses (PLE and PME), with traces of small, paired AME and one PLE. Remainder of carapace with four pairs of wide grooves defining series of lobes radiating from fovea, situated 2/3 of carapace length behind anterior margin; fovea a transverse depression with procurved posterior margin. Carapace margins smoothly rounded, narrowly bordered, posterior margin slightly procurved, posterolateral angles distinct. Pale with faint pigmentation in grooves.

Remarks According to the current stratigraphic correlation (Davydov et al. 2010; Pointon et al. 2012), this fossil is approximately 315 Ma old, i.e., much older than the spiders from Mazon Creek (Westphalian D, =Asturian, =Upper Moscovian), probably slightly older than *Eocteniza* from the Westphalian B, or Duckmantian (=Upper Bashkirian) of the Middle Coal Measures. *Eocteniza* is rather problematic as a spider; its carapace is quite unlike the typical mesotheles discussed herein, so the Kamensk specimen may represent the earliest spider known.

Thelyphonida Latreille 1804

Thelyphonida sp.

Material: PIN 1866/100 (negative impression only). From Lomovodka, Donetsk Basin, Ukraine. Upper Carboniferous (Upper Pennsylvanian), upper part of Isaevskaya Formation.

Description

Carapace length 8.8, maximum width 6.7, width of posterior margin 5.5. Outline distinctly subheptagonal, posterior margin straight, slightly raised dorsal surface, narrow border present around entire carapace, widened at sides of posterior margin. Surface ornamented with irregular transverse wrinkles. Thin marginal rim expands along posterior margin, where sparse row of setal follicles occur along inside edge of marginal rim (Fig. 5). Pair of median eyes at anterior end, set in shallow depressions and separated by short ridge. Lateral eye tubercles only slightly raised (individual lenses equivocal), but each connected to median eye region by a raised keel (best seen on right side). Carapace with distinct pattern of sulci: central longitudinal depression on midline (fovea) deepest, merging posteriorly into shallower groove along midline; three pairs of transverse sulci: one stronger behind lateral eyes; second weaker slightly behind level of fovea, extending laterally and bifurcating slightly less than halfway to lateral margins into an anterior branch which runs towards lateral margin at about 50°, and a posterior branch which runs at low angle from transverse towards lateral margin, posterior-most sulcus runs towards posterolateral corner of carapace.

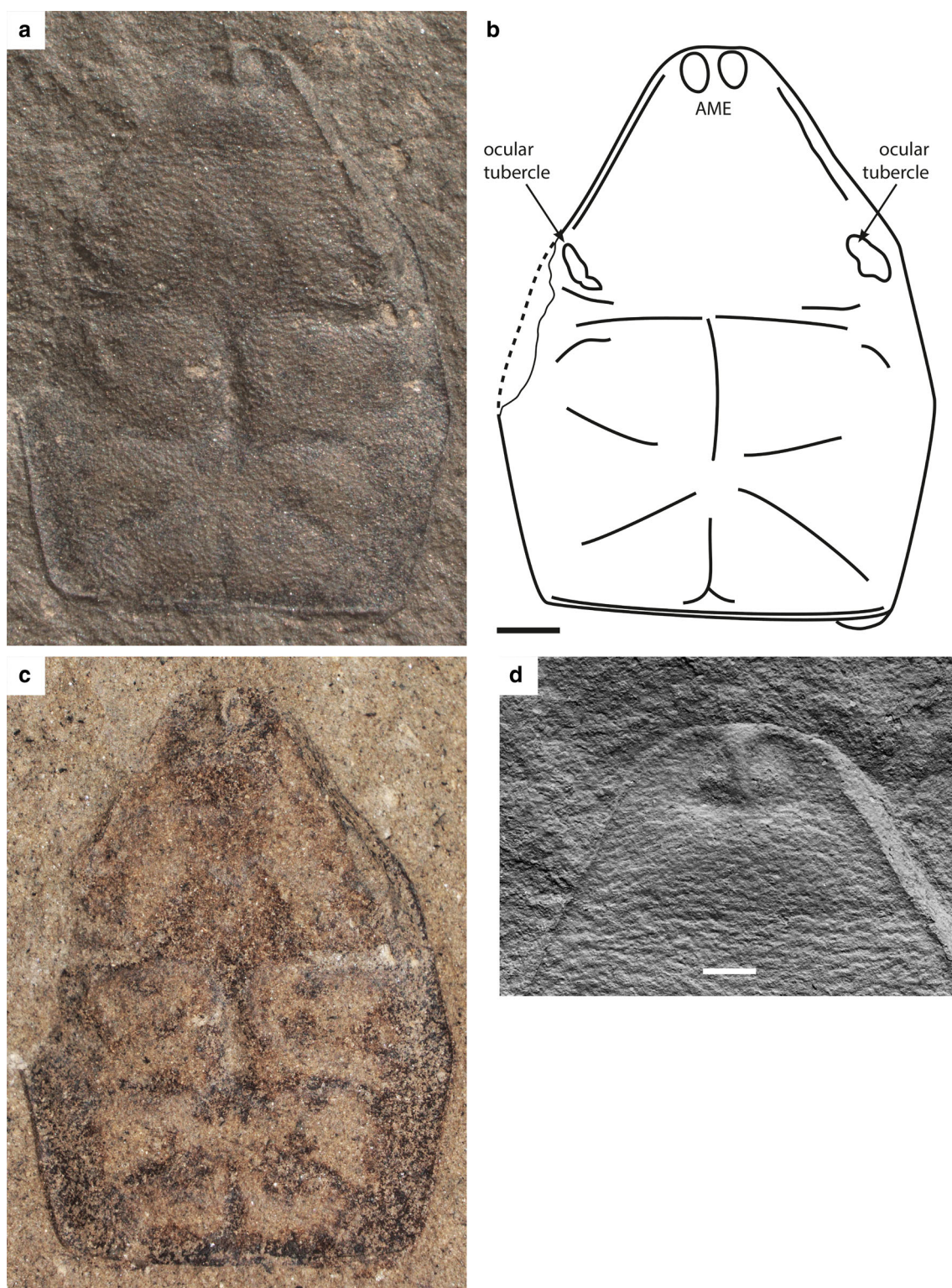


Fig. 5 Thelyphonid specimen PIN 1866/100 from Upper Carboniferous (Lower Kasimovian) of Lomovatka, Lugansk Province, Donets Basin, Ukraine. **a** Photograph of specimen (*dry*). **b** Camera lucida drawing of specimen, showing anterior median eyes (AME) and

ocular tubercles. **c** Photograph of specimen (under 70 % ethanol). **d** SEM photograph of eye region. Scale bars equal 1 mm (**a–c**), 0.5 mm (**d**)

Dark pigmented at periphery, along midline, and in grooves, with small spots around fovea.

Remarks This fossil can convincingly be assigned to Thelyphonida (equivalent to Uropygi in some systematic schemes) based on the characteristic shape of the carapace, which is subheptagonal and distinctly longer than wide (Fig. 5). No other arachnid group, living or extinct, has a carapace of this form. The Coal Measures whip scorpions were revised most recently by Tetlie and Dunlop (2008). These authors recognized six species in four genera, treating all of them as plesion taxa outside of the Cretaceous—Recent crown-group family Thelyphonidae which was defined on fully subchelate pedipalps. In detail, the Coal Measures fossils discovered so far all lack apophyses on the patella and tibia of their pedipalps which contribute to the subchelate nature of these appendages in living species.

In this context, it is interesting to note that the Donets Basin carapace preserves an extremely modern pattern of sulci. The previously described Coal Measures whip scorpions (Kušta 1884; Scudder 1884; Frič 1904; Pocock 1911; Petrunkevitch 1913; Dunlop and Horrocks 1996) did not clearly reveal sulci on the carapace which match so precisely the arrangement seen in living species (cf. Millot 1949, fig. 287). We should caution that taphonomy could play a role here, and that sulci may be less apparent in compressed and/or poorly preserved material. The new fossil does, however, differ from modern species in that the carapace is clearly wider in the middle. In this sense it is close to the previously described Carboniferous genus *Geralinura* Scudder 1884. By contrast, modern whip scorpions tend to have slightly more elongate carapaces with more parallel sides.

Based on the pattern of sulci, it is tempting to assign the Donets Basin fossil to the extant family Thelyphonidae; in which case it would be the oldest example of the crown group, extending the range of the family from the Early Cretaceous back to the Late Carboniferous. However, in the absence of the diagnostic pedipalp apophysis character (which currently defines the family) we are reluctant to make a formal assignment, and simply record the presence and morphology of this significant material. Similarly, given the differences to the Coal Measures whip scorpions described thus far, the new fossil might also belong to a new (perhaps quite derived) species. Yet given its incompleteness as an isolated carapace, we feel it would be premature to formally name it at this stage.

Acknowledgments We thank Yulia V. Mosseichik (Geological Institute, Moscow), Dmitry V. Shaposhnikov (Kamensk–Shakhtinsky), and Alexander K. Shchegolev (Institute of Geological Sciences, Kiev) for providing information on fossil localities; Nikolay I. Udovichenko (University of Lugansk) for assistance in field work; and

Roman A. Rakitov (PIN) for taking SEM micrographs. PAS is grateful to Peter J. Schwendinger (Natural History Museum, Geneva) and Hirotsugu Ono (National Museum of Nature and Science, Japan) for supplying specimens of modern mesothelae for comparative morphology. The visit by PAS to Berlin was funded by the Alexander von Humboldt Foundation. The work was supported by RFBR grants 10-04-01713 and 13-04-01839 to DES and KYE.

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