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First record of spiders from the Permian period (Araneae: Mesothelae)

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Summary

Fossil spiders are rare; none is known from strata between late Carboniferous and late Triassic in age, including the whole of the Permian period, and extending across the Permo-Triassic mass-extinction event. A fossil spider of Permian (*c.* 275 Ma) age from the Ural Mountains, Russia: *Permarachne novokshonovi* gen. & sp. n., is described. *Permarachne* is a mesothele but differs from other members of the suborder in having elongate, pseudosegmented spinnerets, and is placed in Permarachnidae fam. n. These morphological features indicate that it was probably a funnel-web weaver, a new mode of life for Mesothelae, and provide evidence for a greater diversity of mesotheles in late Palaeozoic times than today. In addition, a spider carapace recovered from a nearby locality in younger strata, is referred to *Arthrolycosa* Harger, 1874.

Introduction

The arachnid fossil record can be compared to the life of a soldier: long periods of boredom interspersed with brief moments of chaos (with acknowledgement to Ager, 1981). The peaks of relative abundance occur in Fossil-Lagerstätten (localities with extraordinary preservation) and both these and single occurrences can dramatically affect our knowledge of the evolution of the group. By far the longest interval without spider fossils within the record of Arachnida lies between late Carboniferous and late Triassic times, a gap of some 70 Ma, which includes the whole of the Permian period and extends across the Earth's greatest mass extinction event (Permo-Triassic: 251 Ma BP). Therefore, the find of a fossil spider from beds of Permian (Cisuralian: *c.* 275 Ma) age from the type Permian area of the Ural Mountains, Russia (Fig. 1) fills a significant gap. The fossil shows clear evidence of belonging to the Mesothelae. Members of this suborder show the most plesiomorphic character states among living spiders (e.g. a segmented abdomen), and all verifiable Palaeozoic spiders are either mesotheles or show still more plesiomorphic states. The Permian specimen

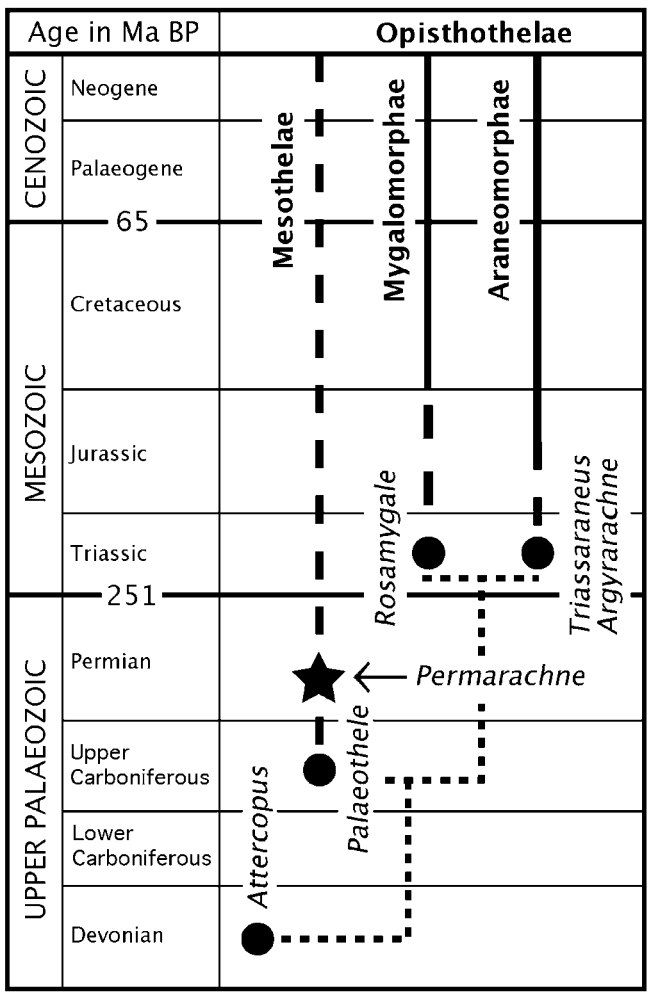

Fig. 1: Phylogenetic tree of spider infraorders. Black circles denote earliest representatives; solid lines show reasonably complete record, dashed lines no record. Star marks stratigraphic position of *Permarachne* gen. n.

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described here differs from all other mesotheles, living or extinct, in having elongate, pseudosegmented spinnerets. These indicate that it was probably a weaver of funnel webs, a new mode of life for Mesothelae, and provide evidence for a greater diversity of Mesothelae in late Palaeozoic times than today.

Material and methods

The main specimen described here (PIN 4909/12) came from the Koshelevka Formation of the Kungurian Stage, Cisuralian Series (latest Early Permian) (International Union of Geological Sciences, 2002). There are several outcrops of the Koshelevka Formation in the Sylva River basin, the most intensively studied of which is the Chekarda locality from where, in addition to abundant plants and fish, more than 8000 insect specimens, from 24 orders, 65 families, 120 genera and 165 species, have been recovered (Ponomaryova *et al*., 1998). Fewer than two dozen fossil insects have been described from the Krutaya Katushka locality (Martynov, 1930), of which several species are also present at the Chekarda locality. Hitherto, no arachnid fossils have been recorded from any of these localities, but recently a poorly preserved trigonotarbid (PIN 1700/357) has come to light from the Chekarda locality, which will be described elsewhere. In addition, a fossil spider carapace (PIN 1366/490), from the Kityak locality (left bank of the Kityak River opposite the village of Bol'shoi Kityak, Vyatka River basin, Malmyzha district, Kirov region), younger than the first specimen: Belebeevo Formation, upper Kazanian (=Capitanian), Upper Permian (Aristov, 2004), is described here.

Both spider specimens are preserved as fragments of organic material in grey-brown mudstone, and both part and counterpart are present, though the counterparts of both specimens show few morphological details and the systematic descriptions refer to the part only. The part of PIN 4909/12 appears to be a dorsal view, with the carapace displaced so that ventral structures are apparent in the prosoma. The disposition of the chelicerae, apparently collapsed one on top of the other and both directed laterally, suggests that this specimen is a moult rather than a dead carcass because a dead animal would exhibit more robustness whereas the process of moulting commonly causes displacement, particularly of anterior appendages.

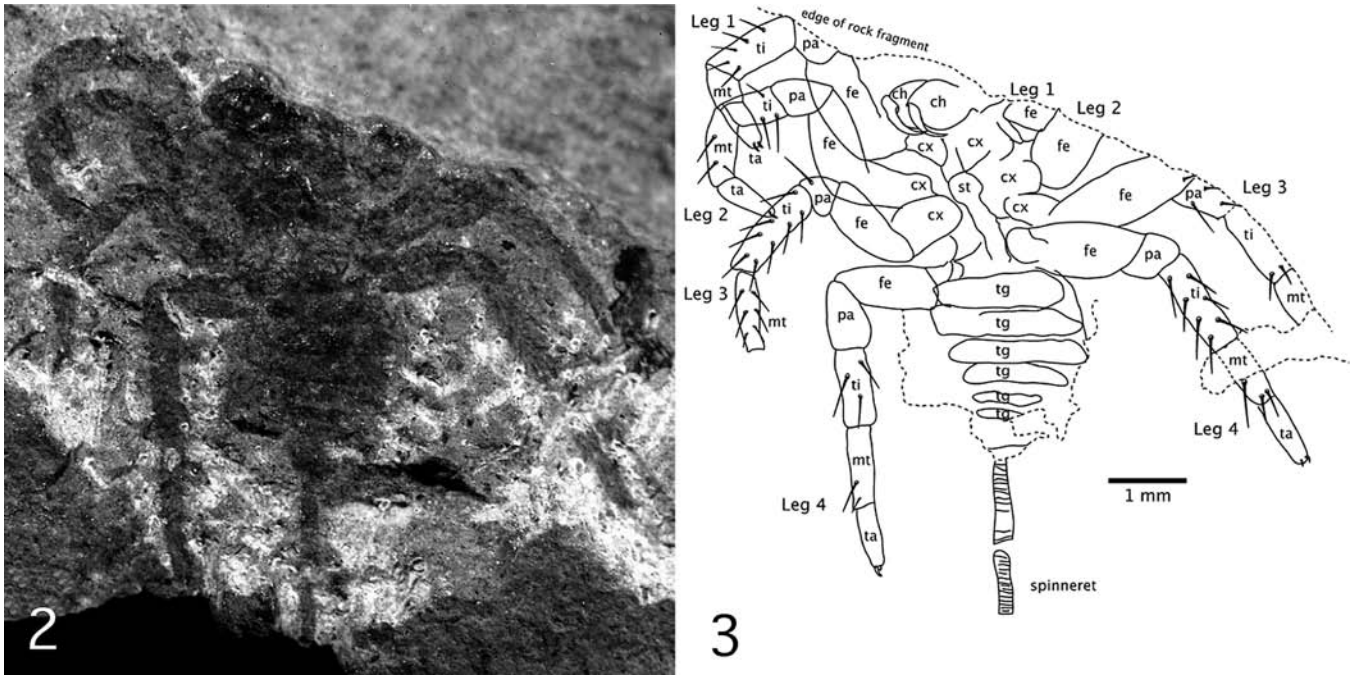
The fossils were studied using a Wild M7S stereomicroscope, drawn using a camera lucida attachment, and photographed with a Nikon D1X digital camera attached to the microscope. Photographs were taken with the specimens under ethanol to enhance contrast. Drawings were prepared for publication with Adobe Illustrator CS, and digital photographs manipulated with Adobe Photoshop CS, on a Macintosh PowerBook G4 computer operating under Mac OS X. All measurements are in mm. Abbreviations: ch=chelicera, cx=coxa, fe=femur, L=left, mt=metatarsus, pa=patella, R=right, st=sternum, ta=tarsus, ti=tibia, tg=tergite.

Order Araneae Clerck, 1757

Suborder Mesothelae Pocock, 1892

Family Permarachnidae fam. n.

Diagnosis: Permarachnidae can be clearly distinguished from all other mesothele families, Recent and fossil, by the presence of an elongated, cylindrical, multisegmented, distal article of one of the spinnerets.



Figs. 2–3: *Permarachne novokshonovi* gen. & sp. n., PIN 4909/12, part, general view. **2** Photograph; **3** Camera lucida drawing. Note: macrosetae are drawn as they appear in the rock, but on most podomeres they originate on the inferior surface, and are seen through from the superior side.

Composition: Only *Permarachne* gen. n., from the Permian of Russia.

Genus *Permarachne* gen. n.

Type species: *Permarachne novokshonovi* sp. n.

Etymology: The name *Permarachne* is derived from the Permian period and the Greek word for spider: *arachne*.

Diagnosis: As for the family.

Included species: Only the type.

Permarachne novokshonovi sp. n. (Figs. 2–8)

Etymology: After the late Dr Viktor Novokshonov, a palaeoentomologist who made a huge contribution in the study of Permian insects from the Chekarda locality.

Material: Holotype and only specimen (a moult?), PIN 4909/12, part and counterpart, deposited in the Palaeontological Institute of the Russian Academy of Sciences, Moscow (PIN), from the Krutaya Katushka outcrop, left bank of the Barda River, upstream of Matveyevka, Russia: Koshelevka Formation, Kungurian Stage, Cisuralian Series (Permian).

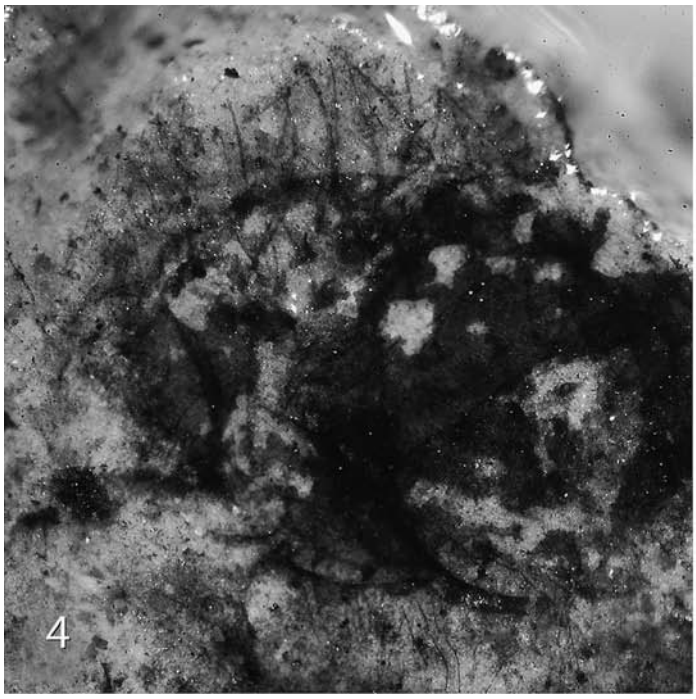
Description: Body length (excluding spinneret) 5.0. Carapace unknown. Chelicera subcircular in lateral view, narrowed at base, naked fang possibly as long as paturon; chelicera length ≥ 0.7. Line of ≥ 6 small, acute teeth on cheliceral promargin (evidence: left cheliceral fang overlies the tooth line). Pedipalp not preserved (except for long setae anterior to right chelicera which may represent dense setation of pedipalp coxa). Leg formula 4321, legs not dissimilar in length, short relative to body, stout, clothed in fine setae. At least tibia and metatarsus of all legs with macrosetae arranged in parallel rows of ≥ 4 pairs on presumed inferior surface of tibia and metatarsus (NB: post-patellar podomeres of legs 3 and left leg 4 appear to be rotated). Relative lengths of podomeres (all legs): femur>tibia> metatarsus>tarsus>patella. Tarsus with curved paired claws. Approximate lengths of major podomeres: Leg I: fe 1.5, pa 0.7, ti 1.1, mt 0.5, ta 0.7 (total 4.5); II: fe 1.4, pa 0.7, ti 0.7, mt 0.9, ta 0.8 (total 4.5); III: fe 1.5, pa 0.7, ti 1.3, mt 1.0 (total >4.5); IV: fe 1.4, pa 0.7, ti 1.1, mt 1.0, ta 1.0 (total 5.2). Visible coxae short; sternum narrow. Opisthosoma with at least 6 tergites, becoming smaller posteriorly (lengths range from 0.5–0.1), anterior and posterior borders straight and parallel, lateral edge rounded. Second preserved tergite 2.0 wide, narrowing to 0.7 (6th preserved tergite). At least one spinneret (preserved length 2.0, width 0.2) with extremely long, cylindrical, distal article showing pseudosegmentation (sclerotised rings with setal rows) and possible ventral spigots.

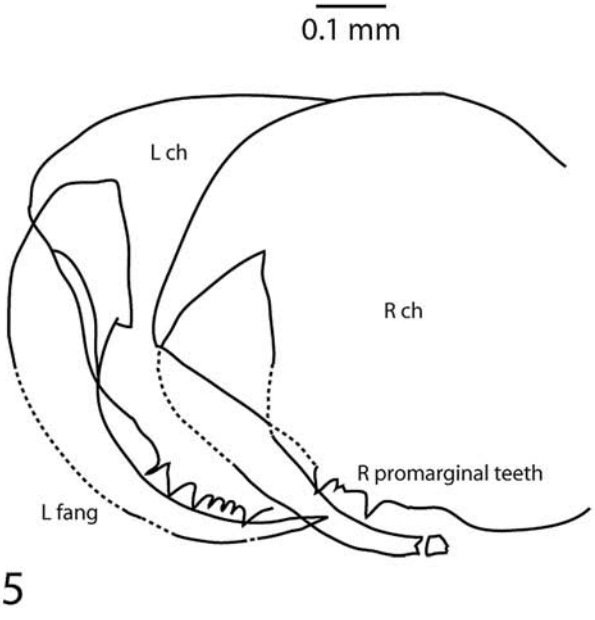
Family Arthrolycosidae Frič, 1904

Arthrolycosa Harger, 1874 (Figs. 9–12)

Material: Single carapace, PIN 1366/490, part and counterpart, deposited in the Palaeontological Institute of the Russian Academy of Sciences, Moscow (PIN), from the Kityak locality, left bank of the Kityak River opposite the village of Bol'shoi Kityak, Vyatka River basin, Malmyzha district, Kirov region, Russia; Belebeevo Formation, upper Kazanian, Upper Permian.

Description: Subcircular carapace about as wide (6.7) as long (6.6), with subcircular, enclosed, pit-like fovea (0.9 diameter) situated about $\frac{2}{3}$ of carapace length from its anterior border. Fovea bears left and right reniform cavities (apodemes). Grooves radiate from fovea to border, situated at about 90°, 65° and 35° from longitudinal axis. Subcircular (1.0 × 1.2) ocular





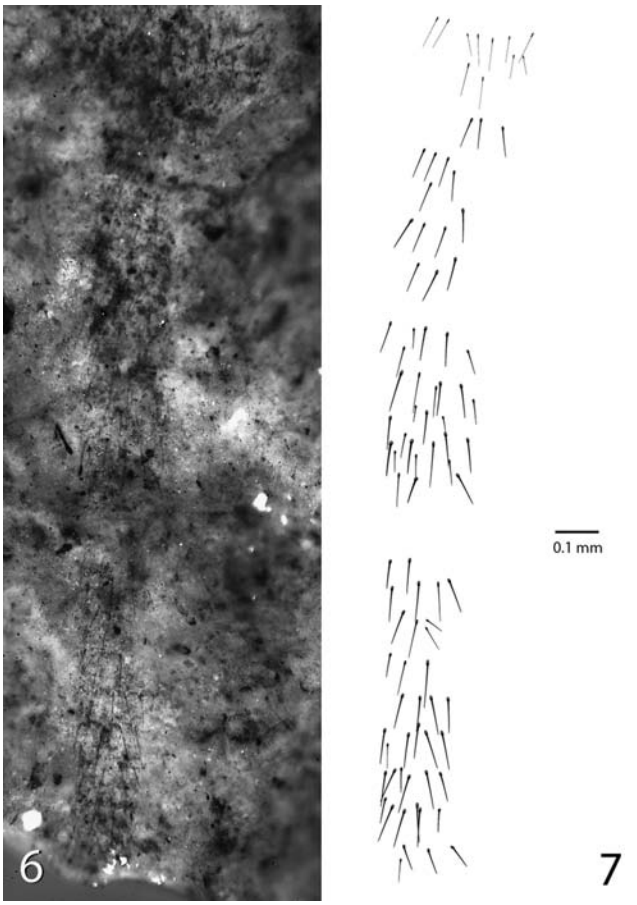
Figs. 4–5: *Permarachne novokshonovi* gen. & sp. n., PIN 4909/12, part, chelicerae. **4** Photograph; **5** Camera lucida drawing.

tubercle bearing eight eyes (*c*. 0.2 diameter) sits atop low median anterior cephalic lobe which projects *c*. 0.5 forward of rest of anterior border and is separated from lateral areas by grooves. Some indication of lateral and posterior perimeter ledges. Large posterior embayment behind fovea leads to slightly procurved median posterior border. In front of fovea a pair of cardiac ridges extend at about 15° from longitudinal axis.

Discussion

Permarachne

The initial impression of the fossil is that it has an elongate tail, i.e. could be referred to one of the arachnid orders with a caudal flagellum, namely Uropygi or Palpigradi, but this is illusory. The tail of *Permarachne* is pseudosegmented whereas those of uropygids and palpigrades consist of true, articulated segments which are distinctly longer than wide (Hansen & Sörensen, 1897; Moro & Bali, 1986). Moreover, modern palpigrades are minute, poorly sclerotised arachnids with three-segmented (not clasp-knife-type) chelicerae, no sternum, and their leg segmentation includes divided tarsi. Uropygids have walking leg I modified into a sensory appendage, small chelicerae, huge raptorial pedipalps, and divided tarsi. It is possible that *Permarachne* belongs in a separate, undescribed, arachnid order



Figs. 6–7: *Permarachne novokshonovi* gen. & sp. n., PIN 4909/12, part, (anterior lateral?) spinneret. **6** Photograph; **7** Camera lucida drawing. Note the whorls of setae.

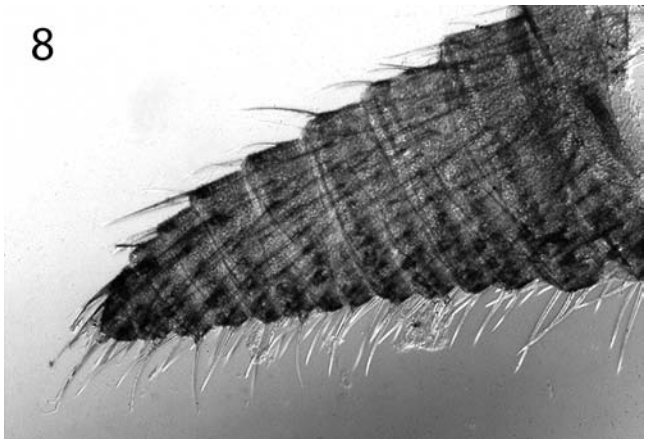


Fig. 8: Distal article of anterior lateral spinneret of a Recent *Liphistius* sp.

but, as the following discussion concludes, it can be accommodated in Araneae: Mesothelae.

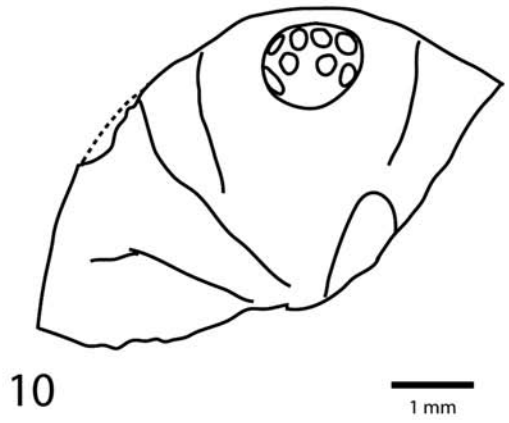
The specimen is a spider because of its possession of at least one synapomorphy of Araneae: a naked cheliceral fang (Selden *et al*., 1991), and a combination of characters unique to spiders: clasp-knife chelicera, typical aranean leg segmentation (short patella, undivided tarsus), appendages with dense setation and macrosetae. The spider is a mesothele because it shows at least one synapomorphy of Mesothelae: a narrow sternum (Raven, 1985), as well as the plesiomorphic condition of opisthosomal tergites (seen only in mesotheles today) and other, plesiomorphic, conditions of Araneae such as: legs being short and of similar lengths, and orthognath chelicera. The disposition of the chelicerae, with their sagittal planes and fangs parallel (Figs. 4–5) suggests that they were crushed together with little separation; labidognath chelicerae would most likely show opposing fangs. The regular rows of macrosetae on the inferior surface of the tibia and metatarsus are features of the modern mesothele genus *Liphistius*, as is the shape of the chelicera: narrowed at the base and with a dorsal hump.

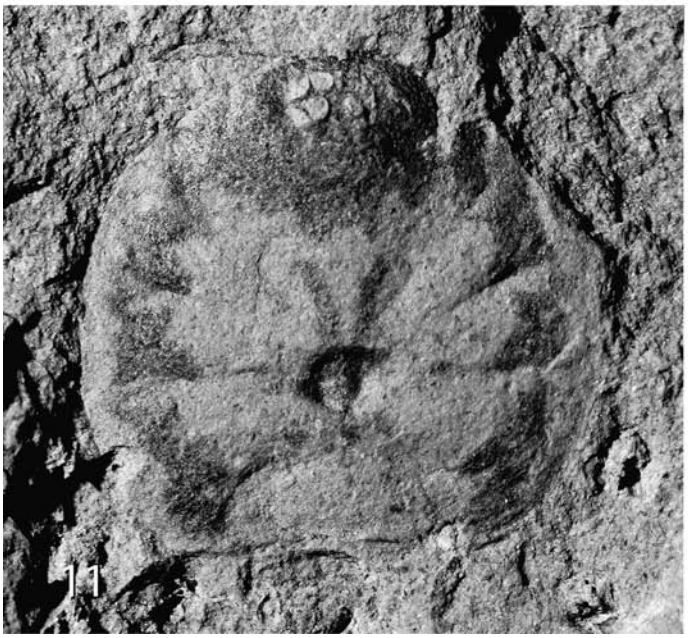
The most unusual feature of *Permarachne* is the elongate opisthosomal appendage. An interesting flagellar structure was found alongside the Devonian spider *Attercopus*, described by Selden *et al.* (1991). This consists of a row of up to 12 true segments, each about one and a half times longer than broad, and with a conspicuous row of setae arising from the distal edge of each segment. This structure was placed in Arachnida *incertae sedis* on the grounds that it bore tiny cuticular structures resembling arachnid slit sensilla (these are also abundant on the uropygid flagellum), but it could not be linked to any other identifiable body fragments. The opisthosomal structure of *Permarachne* is clearly of a different type from this or the uropygid flagellum; the segments are very short and terminate in more sclerotised cuticle and setal rows rather than true articulations, i.e. they are pseudosegments. In addition, there are a number of circular structures resembling setal follicles, but larger, occurring mainly on the left side of the structure (ventral in life), which could be interpreted as spigots. We therefore consider this structure to be a

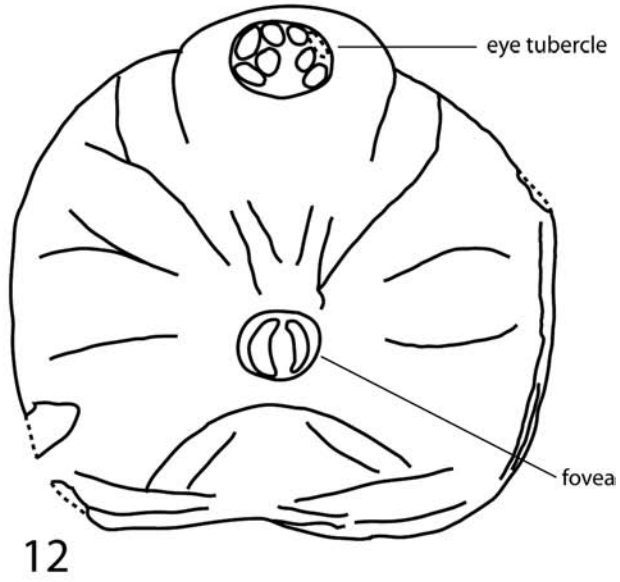
greatly elongated distal article of a spinneret. Direct comparison may be made with pseudosegmentation and spigot arrangement of the distal article of the anterior lateral spinneret of *Liphistius* (Fig. 8), so we suggest that the structure in *Permarachne* also belonged to the anterior lateral pair.

Modern mesotheles have relatively short spinnerets compared with *Permarachne*, and they are used primarily to line a burrow with silk and lay out radiating signal lines for prey detection. Long spinnerets occur in a number of spider groups today, e.g. Dipluridae and Hexathelidae in Mygalomorphae, Hersiliidae and Agelenidae in Araneomorphae. The spinnerets of these groups are not pseudosegmented but consist of a number of elongate articles. Elongate spinnerets are usually associated with funnel webs: large sheets of dense, fine silk emanating from a retreat, which capture prey which lands, jumps or walks across the sheet and is entangled long enough for the spider to run out and capture it. Hersiliids are an exception in that they run rapidly on tree trunks and use their long posterior lateral spinnerets to swathe prey in fine silk. This is a unique form of wrap-attack, clearly derived from web-building ancestors (Dippenaar-Schoeman & Jocqué, 1997). *Permarachne* can be compared most closely to the funnel-web weavers because it is likely to have been a slow-moving spider (short legs) and in general appearance more closely resembles the mygalomorph funnel-web weavers. However, the method by which *Permarachne* has achieved elongation of the spinneret is different from that of the diplurids and hexathelids. A simple extension of the pseudosegmentation seen in the anterior lateral spinneret of *Liphistius* would result in the elongate spinneret seen in *Permarachne*, whilst in the mygalomorphs each article is elongated.

A number of putative Carboniferous Mesothelae are known; most of these were attributed to the suborder on the basis of plesiomorphies (e.g. opisthosomal tergites), though one unequivocal Carboniferous mesothele has been described (Selden, 1996a, b). None shows the unusual elongated spinnerets seen in *Permarachne*, although it is possible that they were present in some specimens but not preserved in the fossils. Either the funnel-web lifestyle did not occur in Mesothelae at that







Figs. 9–12: *Arthrolycosa* Harger, 1874, sp., PIN 1366/490, carapace. **9** Photograph of counterpart; **10** Camera lucida drawing of counterpart; **11** Photograph of part; **12** Camera lucida drawing of part.

time or has yet to be found in the palaeontological record. One can envisage the development of a sheet web in mesotheles from the *Liphistius* type, which consists of a burrow and radiating signal lines, by laying down a mesh of fine silk over the area occupied by the signal lines, thus producing a capture area. Later, the burrow could be transferred above ground to form a tubular retreat (Coyle, 1986). We cannot be sure whether *Permarachne* lived in a burrow with a sheet or in an aerial funnel web. By the Permian period insects were flying and jumping, so such a web would have been able to exploit this type of insect prey. No mesothele today makes such a web, so *Permarachne* implies a greater diversity of Mesothelae in the late Palaeozoic than today. The funnel-web niche was later occupied by hexathelid and diplurid mygalomorphs, and many araneomorphs.

Arthrolycosa

The isolated carapace cannot be referred to *Permarachne* because of its size. The length of the carapace of *Permarachne* would have been in the order of 2.7 but the *Arthrolycosa* carapace is some 6.6 in length. It is possible that *Permarachne* is a juvenile, in which case the carapace could belong to that genus. The carapace is of a common mesothele type, similar to that of other Palaeozoic spiders. A monograph on Palaeozoic spiders is in preparation by PAS, in which the taxonomy of the numerous genera used for Palaeozoic mesotheles will be clarified; but for the moment, the isolated carapace can be referred to the genus *Arthrolycosa* Harger, 1874. This genus shows the cephalic lobe, eye tubercle, radiating grooves and posterior embayment on a subcircular carapace.

Acknowledgement

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