Spider origins: a palaeontological perspective

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Abstract

Spiders (Araneae) can be placed within a series of nested clades within Arachnida. Arachnopulmonata encompasses all arachnids with book lungs. Pantetrapulmonata encompasses arachnids with four pairs of lungs in their ground pattern. Tetrapulmonata potentially encompasses pantetrapulmonate arachnids which have reduced the number of lateral eye lenses and endites on the coxae of the first pair of walking legs. Seriko-diastida encompasses arachnids with opisthosomal silk glands. Several spider-like fossils, some of which were previously interpreted as spiders, may belong either here or in the wider tetra-pulmonate group. Araneida encompasses arachnids with spinnerets and a male palpal organ, and fossils reveal that the common ancestor of spiders would have retained a flagelliform telson. Araneae can thus be defined as spiders which have lost the telson, something which appears to have occurred multiple times among arachnids. The oldest fossil example of each of these clades is documented, and compared to molecular estimates of origination dates where available, to yield a broad temporal and phylogenetic framework for spider origins.

Keywords: Arachnida • Araneae • Araneida • fossil • phylogeny

Introduction

Spiders (Arachnida: Araneae) are a diverse, widespread and highly successful group of predatory arthropods with more than 50,000 living species described so far (World Spider Catalog 2022). They also have a substantial fossil record, with almost 1400 currently recognised species (Dunlop, Penney & Jekel 2020). Most of the known fossil spiders are preserved in amber and date from the Cretaceous onwards (Figs. 1–3), but records going back as far as the late Carboniferous are known (e.g. Selden 2021). Overviews of the spider fossil record can be found in Selden & Penney (2010), Penney & Selden (2011), and Magalhaes *et al.* (2020).

In recent years, several discoveries and/or reinterpretations of fossil material have yielded new perspectives on spider origins. Selden, Shear & Sutton (2008) demonstrated that the oldest putative spider, which comes from the Devonian of the USA, actually belongs to an extinct order (also known from the Permian) which they named Uraraneida. These animals resembled spiders, possessed spigots for producing silk, but lacked spinnerets. Uraraneids also retained a flagelliform telson at the posterior of the opisthosoma, similar to the tail of whip scorpions (Thelyphonida). Garwood *et al.* (2016) described a spider-like fossil from the late Carboniferous of France (Fig. 4) which appeared to bridge the gap between uraraneids and spiders in that it had an opisthosoma still lacking spinnerets, but also without a telson. This transitional sequence was challenged by the remarkable discovery of spiders in mid-Cretaceous

Burmese amber bearing both spinnerets and a tail (Wang *et al.* 2018; Huang *et al.* 2018; Wunderlich 2022). These fossils (Figs. 1–2) are evidently too young to be ancestral to any modern groups, but may be late survivors of a lineage which is sister group to all other spiders (e.g. Wunderlich 2019).

Most recently, Selden (2021) revised the Palaeozoic fossils and showed that, while several are, indeed, *bone fide* spiders, and referable to the extant suborder Mesothelae, others lack demonstrable spinnerets (Fig. 5), and appear to be further examples of Palaeozoic spider-like arachnids, albeit without a tail. In the present paper, I review these developments and summarize them in a phylogenetic and temporal framework (Fig. 6) for the evolutionary pathway which may have led to modern spiders.

Material and methods

Fossil taxa and molecular date estimates were reviewed from the primary literature as elucidated below. Fossils of amber spiders for Figs. 1–3 were examined and photographed (immersed in water) with a Leica Z16 APO A stereomicroscope running the software package Leica Application Suite, generating stacks of images. These images were combined using Helicon Focus 6 and corrected for brightness and contrast using Adobe Photoshop. The reconstruction in Fig. 5 was derived from the original images in Pocock (1911) and Selden (2021), with missing parts based on comparisons to modern arachnids, especially mesothele spiders.

Arachnopulmonata

Recent phylogenetic work (reviewed by Giribet 2018) increasingly supported the hypothesis that all arachnids with book lungs belong in a clade together. Sharma *et al.* (2014) proposed the name Arachnopulmonata for this group, which includes scorpions (Scorpiones) alongside those arachnids with two pairs of lungs, at least in their ground pattern. Howard *et al.* (2020) and Ontano *et al.* (2021) proposed that pseudoscorpions may belong here too, as the sister-group of the scorpions, together forming a clade which the latter authors named Panscorpiones. In this scenario, the lungs in the ancestors of pseudoscorpions must have been transformed into (or replaced by) tracheae. The oldest currently accepted arachnid, which at the same time would be the oldest member of Arachnopulmonata (Fig. 6), is the scorpion *Dolichophonus loudonensis* (Laurie, 1899) from the Pentland Hills of Scotland. It constrains both lineages to the mid-Silurian (Telychian, *c.* 433–438 Ma). A marginally older Silurian fossil from the USA which was described as a scorpion is a misidentification (Anderson *et al.* 2021; Braddy & Dunlop 2021).

Dated molecular phylogenies offer an alternative approach for investigating the origins of clades. Molecular estimates almost invariably predate the fossil record and, in turn, rely to some extent on fossils for calibration. Arach-

Figs. 1–3: Fossil spiders in mid-Cretaceous Burmese amber from Myanmar; note in both the posterior position of the spinnerets. **1** previously unpublished specimen of the remarkable tailed spider *Chimerarachne yingae* Wang, Dunlop, Selden, Garwood, Shear, Müller & Lei, 2018, from the private collection of Patrick Müller; **2** detail of the same showing the male pedipalp (arrowed), note the slight constriction in the terminal (tarsal?) article, the membranous connection between the two branches of the cymbium and the narrow putative embolus lying between them; **3** holotype of *Intermesothele pulcher* Wunderlich, 2019 belonging to the mesothele family Eomesothelidae, from the private collection of Jörg Wunderlich. Scale bars = 1 mm. Photos courtesy of Christian Bartel (Berlin).

nids in general have been predicted to have originated near the Cambrian-Ordovician boundary (*c*. 485 Ma) (e.g. Lozano-Fernandez *et al*. 2020) with the putative Arachnopulmonata group appearing, according to these authors, a little later at *c*. 473 Ma. Other studies have suggested similar, or slightly older, dates for arachnid origins. For example, Howard *et al*. (2020: supplementary table 4) offered median dates of between 485–510 Ma for Arachnida and 473–476 Ma for Arachnopulmonata; the variation being influenced by the precise methods used and whether hard or soft boundaries were used for calibrations. In brief, a hard minimum boundary uses fossils to indicate when a given lineage appeared. *Dolichophonus loudonensis* proves that scorpions must have evolved by at least the mid-Silurian. More controversial is the use of fossils as hard maximum boundaries. Using *D. loudonensis* as a maximum boundary would imply that scorpions are also no older than the mid-Silurian. An obvious weakness here that there may be earlier members of a group which have yet to be discovered. The concept of soft boundaries addresses this by allowing an ever-diminishing chance of finding older representatives. In the same example, a soft bound *D. loudonensis* implies that scorpions might have existed in the early Silurian or even, albeit less likely, in the Ordovician. For further details of these approaches see Ho & Phillips (2009) and references therein.

Pantetrapulmonata

Exceptionally preserved members of the extinct arachnid order Trigonotarbida from the early Devonian Rhynie Chert of Scotland occasionally preserve two pairs of book lungs, which are anatomically indistinguishable from the lungs of spiders (Kamenz *et al*. 2008). Trigonotarbids share other characters with spiders, uraraneids, whip spiders (Amblypygi), whip scorpions (Thelyphonida), and schizomids (Schizomida), such as chelicerae shaped like a clasp-knife, as opposed to a chelate claw, and usually a degree of narrowing between the prosoma and opisthosoma. All these arachnids form the putative clade Pantetrapulmonata *sensu* Shultz (2007). The oldest pantetrapulmonate is the trigonotarbid *Palaeotarbus jerami* (Dunlop, 1996) from the Welsh Borderland of England (Jeram, Selden & Edwards 1990). It remains one of the oldest known terrestrial arthropods and constrains pantetrapulmonate origins (Fig. 6) to the late Silurian (Pridoli, *c*. 419 Ma).

Tetrapulmonata

The clade for which Shultz's (1990) name Tetrapulmonata has now become commonplace is one of the few stable groups within arachnid phylogeny (Giribet 2018). The hypothesis that spiders, whip spiders, and whip scorpions share a common ancestor goes back to the 19th century (e.g. Pocock 1893). Despite this, there is an unresolved issue as to which characters (if any) define Tetrapulmonata with respect to Pantetrapulmonata. In other words, what

resolves the extinct trigonotarbids outside the tetrapulmonate group? One possibility relates to the lateral eyes. At least the Rhynie Chert trigonotarbids had semi-compound lateral eyes with *c*. 15 individual lenses (Miether & Dunlop 2016). All tetrapulmonates have a basic ground pattern of three lateral eye lenses, together with two barely visible minor lenses in whip scorpions. Reduction of the lateral eyes to five lenses or fewer could define Tetrapulmonata (Fig. 6), although a caveat here is that several fossils assigned to Trigonotarbida by Shear *et al*. (1987) show three large lenses with a variable number of minor lenses.

Another possible character is the presence of endites on the limb coxae, which may be plesiomorphic for chelicerates, and are clearly expressed as the dentate gnathobases in horseshoe crabs (Xiphosura) and in the extinct eurypterids (Eurypterida). The Rhynie Chert trigonotarbids, and at least one Carboniferous species, also retain endite-like structures on the coxae of the first pair of legs (Haug 2020: figs. 7–8). Loss of endites on the leg 1 coxae could thus be another synapomorphy of Tetrapulmonata, but see comments in Howard *et al*. (2020) about the extent to which these arachnid endites may be considered homologous with gnathobases. The oldest unequivocal tetrapulmonate is the uraraneid *Attercopus fimbriunguis* (Shear, Selden & Rolfe, 1987) from Gilboa in the USA, which constrains this clade to the mid-Devonian (Givetian, *c*. 390 Ma) (Shear *et al*. 1987). Molecular dating specifically aimed at the origins of Tetrapulmonata is currently lacking, but Howard *et al*. (2020: fig. 2) implied an Early Devonian date of *c*. 410 Ma, which would be broadly consistent with the fossil record. Tetrapulmonates can be divided into two groups: Schizotarsata and Serikodiastida.

Schizotarsata

Schizotarsata *sensu* Shultz (2007), see also Garwood & Dunlop (2014), includes the monotypic Carboniferous order Haptopoda as well as the traditional clade Pedipalpi comprising whip spiders, whip scorpions, and schizomids. Schizotarsata is principally defined by the tarsi of legs II–IV being subdivided into three tarsomeres. The first pair of legs is also slightly (Haptopoda), or noticeably (Pedipalpi) elongate. The principal synapomorphy of Pedipalpi is the subraptorial to subchelate pedipalps which give the group its name. It should be noted that some older hypotheses placed whip spiders as the sister group of spiders, e.g. the Labellata concept of Petrunkevitch (1949), although this was not the most parsimonious result in most of the recent phylogenetic studies (reviewed by Giribet 2018: fig. 2). There is a fragmentary mid-Devonian fossil with trichobothria in a position only seen today in whip spiders (Selden, Shear & Bonamo 1991), but the oldest unequivocal member of Schizotarsata is the whip scorpion *Parageralinura naufraga* (Brauckmann & Koch, 1983) from the Upper Carboniferous (Namurian, *c*. 318 Ma) of Hagen-Vorhalle in Germany. Clouse *et al*. (2017) suggested that Thelyphonida diverged from Schizomida in the late Carboniferous (*c*. 329±10 Ma),
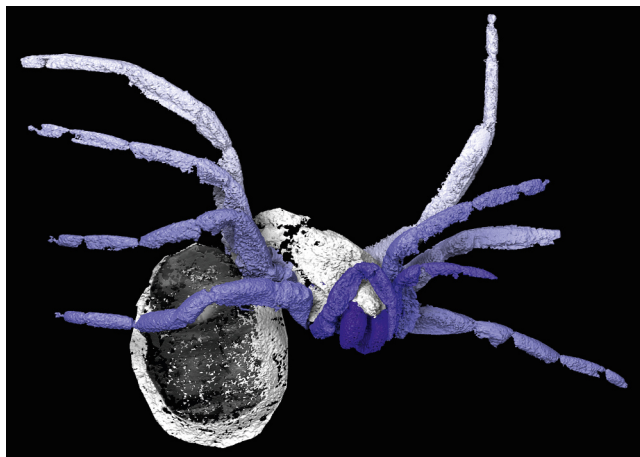
Fig. 4: Computed tomographic reconstruction of *Idmonarachne brasieri* Garwood, Dunlop, Selden, Spencer, Atwood, Vo & Drakopoulos, 2016, from the late Carboniferous of Montceau-les-Mines, France. The reconstruction was created by scanning the void in the matrix where the animal was originally preserved, and turning this negative space into a positive 3D image. Despite the superficially spider-like appearance, spinnerets could not be identified. There is also no evidence for a telson. Image courtesy of Russell Garwood (Manchester, UK).

which marginally predates the fossil record. Howard *et al*. (2020) estimated origins for the whole Pedipalpi group of either 361 (hard bound) or 436 Ma (soft bound). The hard bound date seems intuitively more likely, and is preferred here (Fig. 6), as the soft bound one would place the clade's origins deep into the Silurian.

Serikodiastida

Selden, Shear & Sutton (2008) suggested that spiders and uraraneids (see below) could be distinguished from the pedipalp orders by the possession of: 1) a naked cheliceral fang, and 2) opisthosomal silk glands opening via spigots. An explicit (Uraraneida + Araneae) clade was recovered in a cladistic analysis of fossil arthropods by Legg, Sutton & Edgecombe (2013). The same result was obtained by Garwood & Dunlop (2014), who introduced the clade name Serikodiastida, derived from the Greek word for silk worker. Shultz (1987) reviewed hypotheses for the origins of silk use, favouring a reproductive role either for protecting eggs and/or transferring sperm; see also below. Serikodiastida includes both described uraraneid species as well as the spiders and, as discussed below, it may include several other spider-like fossils. As for Tetrapulmonata, the uraraneid *Attercopus fimbriunguis* from Gilboa constrains this clade to the mid-Devonian (Givetian, *c*. 390 Ma) (Fig. 6).

Uraraneida

Attercopus fimbriunguis was initially described as a trigonotarbid (Shear *et al*. 1987), before being reinterpreted as the oldest spider (Shear *et al*. 1989; Selden, Shear & Bonamo 1991), based on the presence of a spinneret. The fossil material from Gilboa consists of macerated pieces of cuticle. These are often fragmentary, which can make it challenging to reconstruct the overall appearance of the arthropods in life. Selden, Shear & Sutton (2008) subsequently recognised that the putative spinneret was a folded piece of opisthosomal cuticle bearing spigots and that the original animal thus lacked spinnerets, but also retained a flagelliform telson similar to that of whip scorpions. Combining this with a more complete fossil, albeit with less detail preserved, from the Permian of Russia, Selden, Shear & Sutton (2008) proposed a new arachnid order, Uraraneida, for these tailed, spider-like animals which ranged from at least the mid-Devonian (*c*. 390 Ma) to the mid-Permian (*c*. 280 Ma).

Other spider-like arachnids

Some fossils are hard to place within this phylogenetic framework. *Xenarachne wilwerathensis* Dunlop & Poschmann, 1997, from the early Devonian of Germany, has a narrowing between the prosoma and opisthosoma suggestive of a tetrapulmonate arachnid, but its ventral anatomy and limb series is too incomplete to allow meaningful comparison with any of the established orders. Indeed, Selden, Shear & Bonamo (1991) suggested that there may have been extinct arachnids in the Palaeozoic with unique combinations of characters. *Idmonarachne brasieri* Garwood, Dunlop, Selden, Spencer, Atwood, Vo & Drakopoulos, 2016, from the late Carboniferous of Montceau-les-Mines in France, is a particularly interesting example of this in that it has an ostensibly spider-like appearance (Fig. 4), but differs from spiders in retaining sternites on the ventral opisthosoma. By contrast, mesothele spiders still have sclerites covering each pair of book-lungs, but other sternites are lacking. Furthermore, despite the application of highly sensitive synchrotron computed tomography Garwood *et al*. (2016) found no evidence for spinnerets in *I. brasieri*, even through the sternites which should have borne them could be resolved. There was also no evidence for a telson.

Spiders have been described from the late Carboniferous Coal Measures of Europe and North America since the mid-19th century. Revision of these fossils by Selden (2021) confirmed that several are indeed unequivocal spiders belonging to extinct families of the Mesothelae. All these fossils have a dorsally segmented opisthosoma. However, at least three other species differ from *bone fide* spiders in having ventral sternites, a small postabdomen of ring-like segments (but no telson), and no evidence of spinnerets. The fossils in question are *Rakovnicia antiqua* Kušta, 1884 from Rakovník in the Czech Republic, and *Eocteniza silvicola* Pocock, 1911 (Fig. 5) and *Protocteniza britannica* Petrunkevitch, 1949 from the British Middle Coal Measures of the West Midlands. While it is conceivable that these animals had spinnerets which did not survive the fossilisation process, this seems unlikely because the ventral sternites are quite well preserved when present and there are no holes or
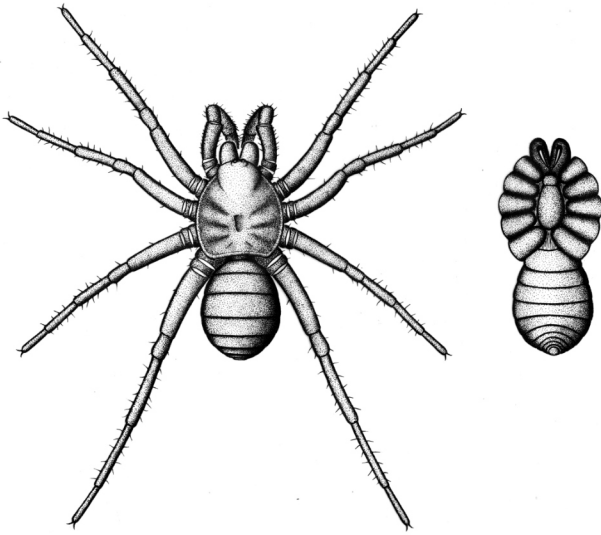
Fig. 5: Sketch reconstruction of the possible appearance in life of *Eocteniza silvicola* Pocock, 1911 from the late Carboniferous British Middle Coal Measures of Coseley, Staffordshire, based on drawings of the fossils by Pocock (1911) and photographs in Selden (2021). Although resembling a spider, the ventral opisthosoma still has a full complement of sternites and spinnerets appear to be lacking. There is also no evidence for a telson.

impressions in the matrix which might represent remnants of appendage-like structures.

The next question is whether these fossils represent a clade or a grade, and where do they belong in relation to the other tetrapulmonate arachnids? Their overall habitus suggests that they are probably closer to spiders than to the Schizotarsata/Pedipalpi orders, but the fact that they lack a telson, which is present in both uraraneids and in at least one lineage of spiders (see below), complicates the resolution of their affinities. A simple progression from Uraraneida (telson, no spinnerets) to *Idmonarachne*, etc. (no telson, no spinnerets) to Araneae (no telson, spinnerets) is no longer tenable. Outgroup comparison with horseshoe crabs and eurypterids suggest that the earliest arachnids probably had a telson of some description, but there were likely to have been multiple convergent losses across the arachnid phylogenetic tree. It may be worth noting that arachnids with a more elongate opisthosoma (Palpigradi, Thelyphonida, Schizomida, Scorpiones) usually retain a telson, while those with shorter and more rounded opisthosomas tend to lose this structure. Depending on the phylogeny chosen, we can document at least six or seven (convergent?) losses of the telson across arachnids as a whole. Perhaps these spider-like arachnids also lost their telson independent of its reduction in modern spiders? Unfortunately, the Carboniferous spider-like fossils known so far are not preserved well enough to test whether they had 1) spigots for producing silk, which would support their explicit placement in Serikodiastida, or 2) a modified male palpal organ for sperm transfer.

Araneida

In a discussion paper on the recently described *Chimerarachne yingae* from Burmese amber, Wunderlich (2019) posed the fundamental question: what is a spider?

For him, spiders should be defined by the presence of spinnerets and a modified male palpal organ; both of which are seen in in *C. yingae* (see below). I concur with this approach, which means both uraraneids and the spider-like fossils without spinnerets are excluded from being true spiders. A caveat here is that the condition of the mature male palp is not yet known from uraraneids, or any of the other spider-like fossils, and discovery of a palpal organ in one or more of these outgroups would force us to reconsider where the boundary to being a spider should be drawn. Wunderlich (2019) thus recognised Araneida as an order, divided into two suborders: Chimerarachnida (the extinct tailed spiders) and Araneae (spiders in their traditional sense which have lost the telson). This classification was also adopted by Selden (2021), but does go against more traditional approaches (e.g. Platnick & Gertsch 1976) of recognising Araneae as the order with two suborders: Mesothelae and Opisthothelae. Semantics aside, the novel appearance of spinnerets as one of the defining characters of spiders does pose a conundrum. When a tarantula walks slowly its spinnerets often move up and down in time with its steps (pers. obs.). Spinnerets thus appear to be modified opisthosmal limbs, but articulated appendages on the 4th and 5th opisthosomal segments are not seen in immediate outgroups of spiders. Selden, Shear & Sutton (2008) recognised this, and suggested that genes for limb production may have been reactivated in spiders allowing the development of spinnerets to bear the silk spigots. The advantage of spinnerets is fairly obvious, in that they offer more control over how and where the silk is deployed.

The oldest unequivocal spider is an *Arthrolycosa* sp. from Russia (Selden *et al*. 2014), which is incomplete, but preserves a typical mesothele eye arrangement. It constrains the group to the late Carboniferous (Bashkirian, *c*. 315 Ma). This means there is currently a gap of about 75 million years between the oldest known spider and the youngest age (*c*. 390 Ma) when spiders should have diverged from the uraraneids (Fig. 6). Again, molecular estimates for when spiders originated are illuminating here, although it should be cautioned that different authors offer different ranges and, in at least one case (Garrison *et al*. 2016), the youngest part of their estimate (287–398 Ma) is falsified by the 315 Ma fossils noted above. Other authors offered dates/ranges of 334–397 Ma (Fernández *et al*. 2018), 397–398 Ma (Opatova *et al*. 2019), and 315–352 Ma (Lozano-Fernandez *et al*. 2020; Howard *et al*. 2020). These dates thus correspond quite well with the *c*. 315–390 Ma gap in the fossil record, and suggest that spiders probably existed in the early Carboniferous and may have originated as far back as the early Devonian.

Chimerarachnida

The Burmese amber fossil *C. yingae* has important bearings on our understanding of spider origins. In the original description, Wang *et al*. (2018) favoured placing it as the sister group of all other spiders, while Huang *et al*. (2018), who described some further specimens in a companion paper, recovered the species closer to uraraneids. As noted
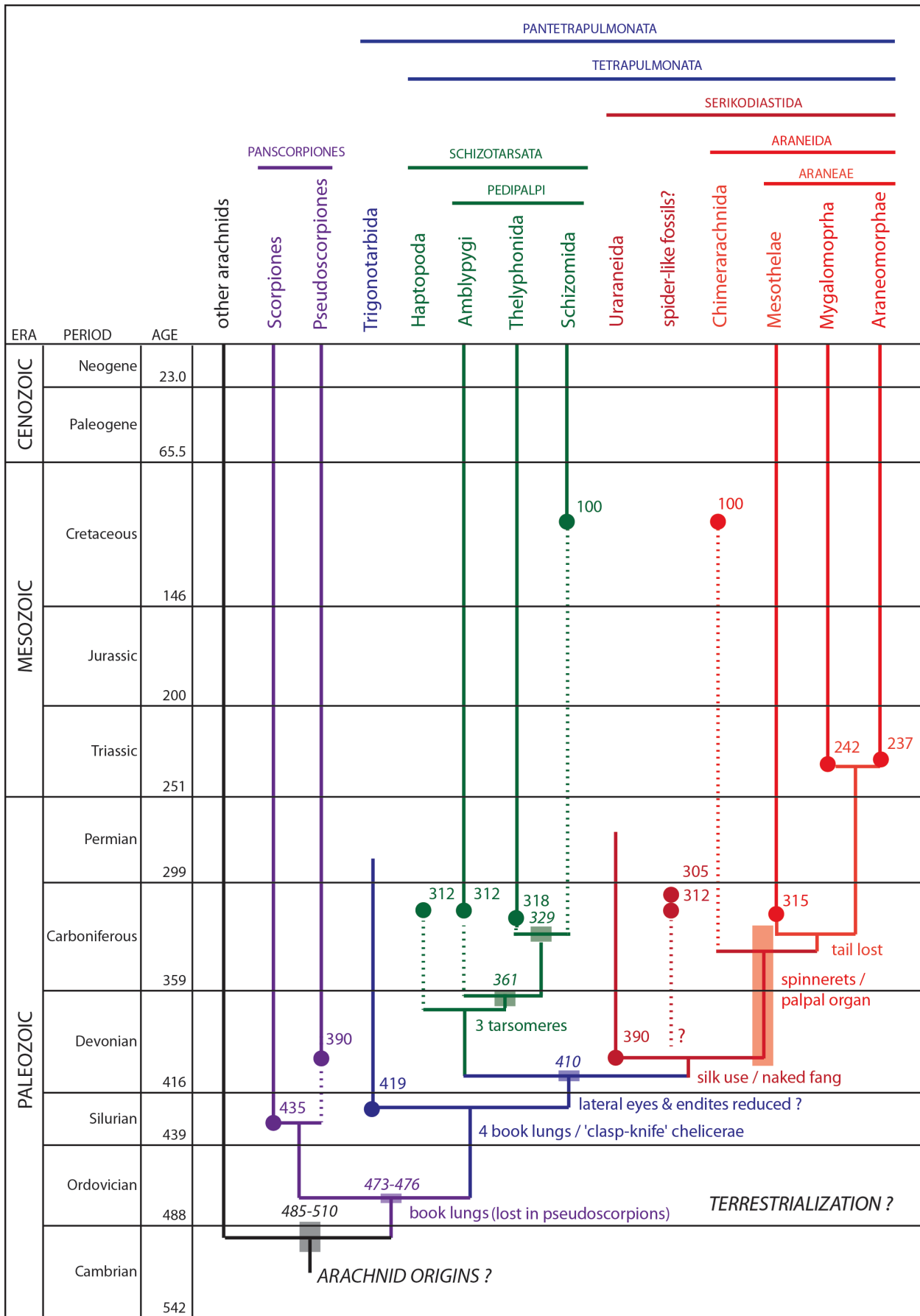
Fig. 6: Possible evolutionary tree of the spiders and their relatives based on the recent literature, with major clades colour coded for clarity. Circles with dates indicate the oldest known unequivocal fossil of a lineage; squares with italicized dates indicate approximate dates of cladogenesis based on published molecular clock estimates, and dotted lines show gaps in the fossil record from which a given lineage would be predicted based on their sister group; see text for details. Significant morphological apomorphies are highlighted. Arachnids may have originated as early as the late Cambrian, and perhaps made the transition onto land during the Ordovician. The exact position of the spider-like fossils such as *Idmonarachne* and *Eocteniza* has not been satisfactorily resolved.

above, the presence of both spinnerets and a putative male palpal organ are strong arguments for treating this animal as a spider, albeit a highly unusual one. Wunderlich (2019) subsequently proposed the family name Chimerarchnidae and the higher taxon Chimerarachnida (as a suborder of spiders) to accommodate this species. Note that a second genus and species from Burmese amber, *Parachimerarachne longiflagellum* Wunderlich, 2022, was recently added and differentiated primarily on the length of the telson and details of its telson segmentation.

As well as retaining an externally segmented dorsal opisthosoma like mesothele spiders, the most striking feature of *C. yingae* and *P. longiflagellum* is the tail. Retention of a flagelliform telson is presumably a plesiomorphic character, as it is seen in outgroups like uraraneids, whip scorpions and (in a reduced form) schizomids. A telson of this nature may well have been present in the common ancestor of (Pan)tetrapulmonates, and we can now argue that it belongs to the ground pattern of spiders too. It is also interesting to note that *C. yingae* bears a small postabdomen of four ring-like segments, similar to the ring-like postabdominal segments seen in some of the spider-like fossils (see above).

The spinnerets of *P. longiflagellum* are not well preserved, but those of *C. yingae* are important for two reasons. First, they appear to be positioned towards the rear of the opisthosoma rather than directly in the middle, as in extant mesothele spiders (Platnick & Gertsch 1976). In the classic interpretation, spider spinnerets originated in a more central position and later migrated backwards. In support of this is the hypothesis (*sensu* Shultz 1987; see also above) that the first function of silk was egg wrapping and thus the spinnerets originally emerged near the genital opening. In this scenario, the subsequent shift to a more terminal position may have been advantageous for other modes of silk use requiring more precise placement of strands such as web building, tunnel lining and/or draglines.

An apparently more posterior position for the spinnerets is seen not only in *C. yingae*, but in at least some of the Cretaceous mesotheles (Fig. 3) where they are clearly visible at the rear of the animal even in dorsal view. Wunderlich (2019, table 1) summarized the diversity of spinneret positions across modern and amber mesotheles, which range from being terminal on the opisthosoma (Eomesothelidae, Fig. 3), to being in the posterior half (Parvothelidae, Cretaceothelidae) to being near the middle of the ventral opisthosoma (Burmathelidae) or middle to posterior (the extant family Liphistiidae). So is the spinneret position of modern mesotheles derived, as implied by Wunderlich? Huber & Haug (2021, fig. 2) seem to show a slight anterior shift of the spinnerets in extant mesotheles during ontogeny, although these authors still maintained (e.g. their fig. 6) that the ground pattern for mesotheles is spinnerets located in the middle of the opisthosoma. Further fossils may contribute to resolving this debate. It would be especially interesting to know which opisthosomal segments bore the openings of the silk glands in *Attercopus*, i.e. were they in a homologous position to the spider spinnerets on the posterior margins of the fourth and fifth sternites? Since the material largely consists of cuticle fragments (see above), this is currently difficult to resolve.

Second, the spinnerets of *C. yingae* consist of prominent and annulated anterior and posterior lateral spinnerets (ALS, PLS). However, posterior median spinnerets (PMS) are absent and, where we would expect anterior median spinnerets (AMS) to occur, there are only small mounds albeit bearing what look like additional spigots. This pattern differs from the predicted model for a hypothetical spider ancestor (e.g. Marples 1967), which was expected to show a full complement of all four pairs of spinnerets. What remains unclear is the extent to which *C. yingae* reflects the spider ground pattern on this character. In other words are these spinnerets in the process of development, or was this a lineage in which the median spinnerets were in the process of being reduced? Living spiders also show considerable diversity in their spinneret configurations, as summarized by Murphy & Roberts (2015).

The palpal organ is another interesting character. Although modern mesotheles are the sister group of all other spiders, their male palpal organ is actually quite complex; see e.g. the excellent photographs in Xu *et al*. (2015). In *C. yingae*, the palpal organ appears to be comparatively simple. In the original descriptions, the pedipalp tarsus (or cymbium) was interpreted as a long structure ending in two blunt apophyses and a fairly simple-looking embolus emerging between these two projections. In this scenario, the embolus would be more like the often fairly simple, pyriform organ of mygalomorph spiders or the fused bulb and embolus in some of the probably basal araneomorph spiders like members of the Filistatidae; see e.g. figures in Brescovit *et al*. (2016) or Zamani & Marusik (2020).

Subsequent data, including Wunderlich's (2022) account of the palpal organ in *P. longiflagellum*, offers alternative perspectives. He suggested that, in both species, the pedipalp may include a metatarsus, with the cymbium composed of a prolateral and reterolateral branch with a bulbus/embolus between them. Inferring a metatarsus in the pedipalp is controversial. No modern spiders have a palpal metatarsus, not do any of their closest relatives among the Pantetrapulmonata. As Wunderlich noted, only palpigrades as potential outgroups have a pedipalp metatarsus. A new specimen of *C. yingae* is also figured here (Fig. 2) for comparison. Whether the tarsus is fully divided is difficult to say, but there is at least a narrowing before the emergence of the embolus/bulbus. The new material also implies that the two branches of the cymbium are actually connected on one side by a membranous element, effectively forming something like a half cylinder, with the bulbus/embolus as a narrow (i.e. non-bulbous) projection of similar thickness along its length lying within this gutter-like structure. Wunderlich's (2022: fig. 3) drawing also seems to reflect this interpretation. Further amber specimens, perhaps amenable to tomographic studies, could reveal the exact three-dimensional structure of the male palpal organ in the tailed spiders. This might allow us to determine to what extant their morphology reflects the putative ground pattern condition for spiders: intuitively a simple, tube-like structure for carrying sperm which was inserted into the female genital opening?

It should be stressed that at mid-Cretaceous (*c*. 100 Ma), *C. yingae* is far too young to be directly ancestral to any other spiders. If it is the sister group of the remaining spiders, it must belong to a lineage which diverged from them more than 215 million years earlier (Fig. 6); based on the (*c*. 315 Ma) record of mesotheles. *C. yingae* is thus best envisaged as a late survivor of a much earlier radiation of spiders into tailed and tailless lineages. This does introduce the possibility that *C. yingae* is, to some extent, a derived member of the tailed spider lineage, and that some of its characters may no longer reflect the original spider ground pattern, as per the remarks on the spinnerets above.

Araneae

The final group is thus what most people would traditionally regard as spiders, namely Araneae, treated here as a subdivision of Araneida (see above). Their defining trait is loss of the telson, albeit probably convergent with several other arachnid lineages. Cheliceral venom glands are also typical for almost all modern spiders, but their presence is difficult to test in fossils as one would need to see the opening of the venom gland at the tip of the cheliceral fang. As above, the oldest spider belonging to a group without a tail is the Russian fossil assigned to *Arthrolycosa* sp., which constrains crown-group spiders to the late Carboniferous (Bashkirian, *c*. 315 Ma). More complete spiders are known from several slightly younger localities (reviewed in Selden 2021). A key observation from the fossil record is the fact that during the Carboniferous period, spiders were one group among several coexisting, and probably closely related lineages, namely uraraneids and spider-like fossils such as *I. brasieri* and *E. silvicola* (Figs. 4–5). Uraraneids lived alongside spiders until at least the Permian, while the fossil record also suggests that the tailed (Chimerarachnida) and tail-less spiders (Araneae) coexisted in at least some parts of the world for more than 200 million years until at least the mid-Cretaceous.

Spiders today are diverse and successful. Both mygalomorph (Selden & Gall 1992) and araneomorph spiders (Selden *et al*. 1999) had appeared by the Triassic (Fig. 6). Increasing numbers of modern families appeared in the Jurassic, including groups which probably built aerial capture webs, possibly in response to radiations of insects pollinating the newly evolving flowering plants (angiosperms). Penney, Wheater & Selden (2003) suggested that most families of spiders known from the Mesozoic survived the end-Cretaceous (K–T) mass extinction event relatively unscathed. Subsequently, a substantial change in the spider fauna at the end of the Cretaceous has been proposed (Magalhaes *et al*. 2020), with several families becoming extinct. Some of these, such as Lagonomegopidae, are certainly quite different from any living spiders and are unequivocally restricted to the Cretaceous (see e.g. Guo *et al*. 2020, and references therein). However, several other putative Cretaceous families (for an overview see Wunderlich 2020), may turn out to be stem-group members of extant groups and their validity as distinct, extinct taxa has not been tested through cladistic analysis.

At the same time, many of today's most diverse and common families (gnaphosids, clubionids, thomisids, etc.) first appeared after the Cretaceous. A case in point are the jumping spiders (Salticidae). Although this is the most species-rich family today, jumping spiders are first recorded from Eocene (*c*. 35–47 Ma) Baltic amber (e.g. Wunderlich 2004) and have not been found in, for example, the slightly older (*c*. 53 Ma) Oise amber of France (Penney 2007) which does contain other dionychan families. For details and possible explanations of why some families evolved so late see, e.g. Magalhaes *et al*. (2020) or Wunderlich (2020), and references therein.

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