**Cretaceous arachnid *Chimerarachne yingi* gen. et sp. nov. illuminates spider origins**

Bo Wang1,2, Jason A. Dunlop3, Paul A. Selden4,5, Russell J. Garwood5,6, William A. Shear7, Patrick Müller8 and Xiaojie Lei1,9

1 State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China.

2 Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Science, Beijing 100101, China.

3 Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University Berlin, D-10115 Berlin, Germany.

4 Department of Geology, University of Kansas, Lawrence, KS 66045, USA.

5 Earth Sciences Department, Natural History Museum, London SW7 5BD, UK.

6 School of Earth and Environmental Sciences, University of Manchester, Manchester M13 9PL, UK.

7 Department of Biology, Hampden-Sydney College, Hampden-Sydney, VA 23943, USA.

8 Friedhofstraße 9, 66894 Käshofen, Germany.

9 University of Sciences and Technology of China, Hefei 230026, China.

**Spiders (Araneae) are a hugely successful lineage, with a long history. Details of their origins remain obscure, with little knowledge of their stem group, and few insights into the sequence of character acquisition during spider evolution. Here, we describe *Chimerarachne yingi* gen. et sp. nov., a remarkable arachnid from the mid-Cretaceous (approximately 100 million years ago) Burmese amber of Myanmar which documents a key transition stage in spider evolution. Like uraraneids, the two fossils available retain a segmented opisthosoma bearing a whip-like telson, but also preserve two traditional synapomorphies for Araneae: a male pedipalp modified for sperm transfer and well-defined spinnerets, resembling those of modern mesothele spiders. This unique character combination resolves *C. yingi* within a clade including both Araneae and Uraraneida, however, its exact position relative to these orders is sensitive to different parameters of our phylogenetic analysis. Our new fossil most likely represents the earliest branch of the Araneae, and implies that there was a lineage of tailed spiders which presumably originated in the Palaeozoic and survived at least into the Cretaceous of South-East Asia.**

Spiders (Araneae) are a diverse and successful arthropod clade, for which 47,001 living and 1,342 extinct species have been described1. The oldest fossils currently assigned to this group date from the Late Carboniferous (approximately 305 million years ago (Ma))2,3, while an earlier report of a Devonian (around 380 Ma) spider4,5 was later reinterpreted as belonging to an extinct arachnid order named Uraraneida6. Uraraneids are also known from the Permian (approximately 275 Ma) and resemble spiders, but possess a long, flagellate telson. Another key difference is that uraraneids have spigots for producing silk4, but lacked the spinnerets which facilitate a more precise deposition of the threads7,8.Phylogenetic analysis5,9 often recovers spiders as the sister-group to a clade comprising whip spiders (Amblypygi), whip scorpions (Thelyphonida) and schizomids (Schizomida). Spiders and their relatives are known as the Pantetrapulmonata and are characterized by a ground pattern of two pairs of book-lungs. Whip scorpions and schizomids express a flagelliform telson, a character also seen in the non-tetrapulmonate order Palpigradi, a group which has been postulated as retaining several plesiomorphic character states among arachnids10. Key autapomorphies of spiders – which presumably underlie their high modern species diversity – are silk glands opening via spigots on spinnerets, chelicerae with venom glands, and male pedipalps modified for sperm transfer. Male spiders possess additional epiandrous silk spigots anterior to their genital opening. Spiders are conventionally divided into two suborders7. Mesothelae retain opisthosomal tergites, and the spinnerets are in the middle of the ventral opisthosoma. Opisthothelae (= Mygalomorphae + Araneomorphae) lack most external evidence of opisthosomal segmentation, and the spinnerets emerge towards the posterior of the body. Recently, a handful of Palaeozoic fossils have been placed close to spider origins through preserving at least some of their diagnostic features. Uraraneida (Devonian–Permian) retained the presumably plesiomorphic flagelliform telson and possessed spigots, but no spinnerets6. Subsequent analyses11,12 formally recovered (Uraraneida + Araneae) as a clade named Serikodiastida. Another spider-like fossil is *Idmonarachne brasieri* (Carboniferous)13 which lacked both spinnerets and a telson. It was postulated as being more closely related to Araneae than the uraraneids, but also had divided opisthosomal tergites like members of the extinct arachnid order Trigonotarbida.

**Results**

**Systematic Palaeontology.**

Arachnida Lamarck, 180114

Pantetrapulmonata Shultz, 20079

***Chimerarachne yingi*** gen. et sp. nov.

**Etymology.** Genus: Χίμαιρα (chimera: a she-goat), in Greek mythology, a hybrid creature composed of the parts of more than one animal, and ἀράχνη (arachne: a spider), a weaver in Greek mythology; specific epithet, yingi, patronymic, honouring the collector, Yanling Ying.

**Holotype.** NIGP 166870 (Fig. 1 and Supplementary Fig. 1). Deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

**Paratype.** NIGP166871 (Fig. 2). Deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

**Horizon and locality.** Mid-Cretaceous (approximately 100 Ma); Burmese amber, from the Hukawng Valley, Kachin State, Myanmar.

**Diagnosis.** Arachnid with a segmented opisthosoma bearing two large, and one residual, pairs of spinnerets; opisthosoma terminating in a short pygidium bearing a long, annulated flagellum; pedipalp diverging distally into two bluntly rounded apophyses.

**Description of the holotype.** Adult male. Body length (inc. pygidium, exc. flagellum) 2.42. Cuticular ornament of fine scales. Carapace widest posteriorly, narrowing to acute anterior border, L 1.12, W 0.84 (L/W ratio 1.28). Pair of median eyes close to anterior margin, apparently also with two adjacent lateral eye tubercles; number of lenses here equivocal.

Chelicerae of orthognath spider-type, L 0.30, fang short, stout, gently curved lacking setae. Chelicerae angled downwards at c. 45° and thus largely concealed in dorsal view. Pedipalps: fe L 0.50, pa L 0.12, ti L 0.36, ta L 0.40 (total L fe–ta 1.41). Pedipalp tibia with prolateral triangular flange, tarsus slightly inflated at about ⅓ of its length, distally bearing two blunt apophyses of equal length (0.23) and sausage-like shape (Figs. 3e,f and 4a). Legs pediform, leg formula IV II/I III, legs I and II subequal in length (2.42, 2.43, resp.). Legs bear gently curved bristles arising from small tubercles on all fe–ta, especially at distal end of mt. Paired tarsal claws borne on onychium, claws gently curved, slender, hooked tip; small, gently curved median claw; both paired and median claws with 4 ventral spines increasing in length in distal half; also arising from onychium a spatulate lobe (pulvillus) as long as paired claw (L c. 0.05) (Figs. 3i,j and 4b,c). Trichobothrium present on all metatarsi at 0.6 position. Cluster of at least 5 trichobothria at distal end of at least tarsus II. Podomere lengths (ta exc. claw): Leg I fe 0.74, pa 0.28, ti 0.60, mt 0.45, ta 0.36 (total fe–ta 2.42; mt/ta ratio 0.79); Leg II fe 0.78, pa 0.29, ti 0.54, mt 0.42, ta 0.40 (total fe–ta 2.43; mt/ta ratio 0.95); Leg III fe 0.59, pa 0.28, ti 0.54, mt 0.45, ta 0.40 (total fe–ta 2.26; mt/ta ratio 0.89); Leg IV fe 0.85, pa 0.34, ti 0.78, mt 0.62, ta 0.46 (total fe–ta 3.05; mt/ta ratio 0.75). Mean mt/ta ratio 0.84.

Prosoma and opisthosoma connected by narrow pedicel (L 0.15, W 0.13). Opisthosoma suboval, L (inc. pygidium, exc. flagellum) 1.22, W 0.90 (L/W ratio 1.36). Dorsal surface of opisthosoma bears 7 visible tergites (segments VIII–XIV), anterior and posterior borders straight, rounded lateral borders. Opisthosomal tergite measurements: 1 L 0.18, W 0.53; 2 L 0.20, W 0.68; 3 L 0.23, W 0.78, 4 L 0.20, W 0.74; 5 L 0.16, W 0.64; 6 L 0.04, W 0.46; 7 L 0.02, W 0.40. Posterior end of opisthosoma forms four-segmented pygidium, total L 0.43; segment measurements: 1 L 0.06, W 0.25; 2 L 0.06, W 0.21; 3 L 0.09, W 0.20; 4 L 0.21, W 0.15. Opisthosoma terminates in flagellum, L 2.86, consisting of approximately 30 alternating short and long segments; long segments bear median bulge bearing ring of bristles (Fig. 1a).

Ventral opisthosoma bears 7 sternites (segments VIII–XIV, including opercula 1 & 2) preceding pygidium, measuring 1 L 0.35, W 0.62; 2 L 0.30, W 0.74; 3 L 0.16, W 0.72; 4 L 0.15; 5 0.07; 6 L 0.06; 7 L 0.06. Median posterior edge of first operculum bears oval structure, W 0.24, covered by row of c. 10 bristles (Fig. 1c). Median posterior border of sternite 3 bears two pairs of spigots (i.e. equivalent to anterior median spinnerets: AMS). Median posterior border of sternite 4 bears V-shaped, collulus-like structure (Fig. 3h). Anterior lateral spinnerets (ALS), L 0.65, emerge from beneath posterior edge of sternite 3, consisting of eight annular segments and cone-shaped terminal segment. Posterior lateral spinnerets (PLS), L 0.70, emerge from beneath posterior edge of sternite 4, consisting of ten annular segments and cone-shaped terminal segment.

**Description of the paratype.** Adult male. Body length (inc. pygidium, exc. flagellum) 2.80. Cuticular ornament of fine scales. Carapace widest posteriorly (Fig. 4i), parallel-sided in posterior two-thirds, narrowing to acute anterior anteriorly, L 1.26, W 0.74 (L/W ratio 1.72). Subtriangular (apex rearward) ocular tubercle close to anterior margin, eyes not clearly discernible.

Chelicera L 0.27. Pedipalps: fe L 0.39, ta L 0.42. Pedipalp tarsus distally bearing two blunt apophyses of subequal length, with median ?embolus of similar length between (Figs. 3f and 4j). Legs pediform, leg formula IV II I III. Legs bear gently curved bristles arising from small tubercles on all fe–ta, especially at distal end of mt. Paired tarsal claws borne on onychium, claws gently curved, slender, hooked tip; small, gently curved median claw; both paired and median claws with 4 ventral spines increasing in length in distal half; also arising from onychium a spatulate lobe (pulvillus) as long as paired claw (L c. 0.05). Trichobothrium present on all metatarsi at 0.6 position. Podomere lengths (ta exc. claw): Leg I fe 0.61, pa 0.34, ti 0.58, mt 0.45, ta 0.44 (total fe–ta 2.45; mt/ta ratio 0.98); Leg II fe 0.80, pa 0.29, ti 0.69, mt 0.57, ta 0.48 (total fe–ta 2.84; mt/ta ratio 0.84); Leg III fe 0.57, pa 0.29, ti 0.55, mt 0.46, ta 0.43 (total fe–ta 2.30; mt/ta ratio 0.93); Leg IV fe 0.64, pa 0.40, ti 0.83, mt 0.66, ta 0.48 (total fe–ta 3.02; mt/ta ratio 0.73). Mean mt/ta ratio 0.87.

Opisthosoma suboval, L (inc. pygidium, exc. flagellum) 1.43, W 0.72 (L/W ratio 1.97). Posterior end of opisthosoma forms four-segmented pygidium, total L 0.34. Opisthosoma terminates in flagellum, L 3.56, of approximately 50 segments preceding spindle-shaped terminal region consisting of 7 segments, terminal spine-like (Fig. 3k); highly setose throughout length. Ventral opisthosoma bears opercula 1 & 2 (segments VIII & IX). Median posterior border of sternite 3 bears two pairs of spigots (i.e. equivalent to AMS). Anterior lateral spinnerets (ALS), L 0.35, emerge from beneath posterior edge of sternite 3, consisting of annular segments and cone-shaped terminal segment. Posterior lateral spinnerets (PLS), L 0.42, emerge from beneath posterior edge of sternite 4, consisting of annular segments and cone-shaped terminal segment (Fig. 3g).

**Remarks.** Differences between the holotype and paratype can largely be attributed to taphonomy. Both are adult males, and are presumed to belong to the same species. The paratype is more shrivelled (as commonly seen in Burmese amber preservation). However, there is a distinct difference in the flagella of these two specimens: that of the holotype is shorter, lacks the terminal spindle-shaped thickening, has fewer segments (c. 30, cf. c. 60 in the paratype), and the segments are alternately short and long. We explain these differences by assuming that the flagellar segments were telescopic to some extent, so that the smaller segments can be hidden inside the distal end of the larger segments. Furthermore, the holotype must have lost the distal half of its flagellum; this would explain the missing terminal thickening and the fewer segments seen in this specimen. It is possible that *Chimerarachne* could lose its tail when threatened, as lizards do.

**Discussion**

*Chimerarachne yingi* gen. et sp. nov. from mid-Cretaceous Burmese amber is a key fossil for understanding spider origins. It essentially resembles a spider with a tail (Supplementary Fig. 2). The 2.4–2.8 mm body is divided into a prosoma and opisthosoma connected by a narrow waist, or pedicel. The carapace is undivided and appears to show both median and lateral eye tubercles (Figs. 1b and 3c). The chelicerae are spider-like, and of the clasp-knife type (Fig. 3d). They lie in an orthognathous position, but point down at an angle of about 45°. The fang appears to be naked. The pedipalps are pediform, but end in a bifurcate tarsus (Figs. 3e,f and 4a) which we interpret as a cymbium covering a bulb and embolus. The legs are pediform, bearing several large macrosetae and trichobothria, and end in toothed claws set on a projecting onychium, as well as a toothed median claw and empodium (Figs. 3i,j and 4c,d). The opisthosoma is segmented and terminates in a short, four-segmented postabdomen bearing a flagellum (Figs. 3k and 4h) which is slightly longer than the body. Ventrally the third opisthosomal segment bears a pair of prominent multi-articled spinnerets (Figs. 3g,h and 4g), which we interpret as equivalent to the anterior lateral spinnerets (ALS) of spiders, plus a pair of less developed spigot-bearing mounds in a median position which may be equivalent to the anterior median spinnerets (AMS). The fourth segment again has prominent spinnerets, equivalent to the posterior lateral spinnerets (PLS), but no corresponding median structures.

Retention of the telson is presumably plesiomorphic, thus a remarkable aspect of this discovery is that animals with such a body plan were still present in the terminal Mesozoic. *Chimerarachne yingi* lived alongside Cretaceous spiders belonging to a number of modern families15,16. A corollary of this is that the new fossils are not ancestral to living spiders which, as noted above, were present by the Carboniferous2. Rather, *Chimerarachne yingi* presumably represents a survivor from an earlier (Palaeozoic?) radiation of Pantetrapulmonata (Figs. 5 and 6).

The amber inclusions are also of considerable interest because they reveal key information about character acquisition on the spider stem, and the likely ground pattern morphology of Araneae. The eyes in the fossil appear not to be on a single tubercle (Figs. 1b and 3c), as in mesothele spiders for example, consisting instead of a pair of median eyes and two lateral tubercles with an undetermined number of lenses. This condition is seen in whip spiders, whip scorpions and some spiders such as the mygalomorph superfamily Atypoidea and the araneomorph family Hypochilidae17, both of which resolve as early branches in their respective parts of the spider tree of life18.

The chelicerae of *Chimerarachne yingi* are essentially spider-like with a naked (hairless) fang (Fig. 3d), but the preservation does not reveal whether the fang had an opening for a venom gland. A key feature in the new fossils is the modification of the pedipalp into what we interpret here as a palpal organ with the tarsus forming a cymbium (Fig. 3e,f) plus the development of a bulb, presumably for transferring sperm. The deeply bifurcate nature of the tarsus/cymbium (Fig. 4a) in the new fossil is unique and potentially diagnostic for the genus (see above). However, we should note that in some mygalomorph spiders the tarsus is short and consists of two similar rounded lobes19. We note that the pedipalp of *C. yingi* is more like that of a mygalomorph spider than that of a mesothele8. This may have bearing on the question whether the pyriform palpal bulb of mygalomorph spiders is closer to the plesiomorphic condition than the structurally more complex palp of mesotheles; Kraus20 for example inferred that the simpler bulbs of mygalomorphs contained secondarily fused elements. The present material is not preserved well enough to resolve this question, but future finds may prove informative here.

Perhaps the most interesting aspect of the new fossils is the position and configuration of the spinnerets (Figs. 3h and 4f,g). It has been suggested that the initial function of spider silk was not web-building, but egg-wrapping21. Mesothelae, as the sister group of all other spiders retaining plesiomorphic characters like segmentation, could support this scenario in having their spinnerets in the middle of the ventral opisthosoma8, close to the genital opening. Spinnerets transposed posteriorly is a traditional synapomorphy of Opisthothelae. *Chimerarachne yingi*, as a potential outgroup to all living spiders, challenges this scenario by preserving spinnerets in a more posterior (opisthothele) position. Another widespread assumption is that spiders originally had four pairs of spinnerets22: the anterior median and laterals and posterior median and laterals. In *C. yingi* both the anterior and posterior lateral spinnerets are well-developed and composed of multiple short articles (pseudosegments). They are similar to the spinnerets of modern mesotheles, but differ in having two or three large basal articles, and in emerging from sclerotized ventral plates (Fig. 3h). In mesotheles there are only one or two large basal articles and no ventral sclerites associated with the spinnerets. Where we would expect anterior median spinnerets there are only a pair of spigot-bearing mounds in the new fossil (Fig. 3h), while the posterior median spinnerets appear to be entirely absent.

Selden *et al*.6 discussed a paradox in that spider spinnerets are modified opisthosomal appendages, probably representing the original telopod23. Outgroup comparison24 implies that retaining these limbs should be plesiomorphic, but spider relatives like uraraneids lack opisthosomal appendages. Selden *et al*. postulated that there may be a genetic mechanism in spiders which reactivated the development of (lost) appendages, allowing the evolution of movable spinnerets which facilitate a more precise manipulation of silk strands. *C. yingi* preserves only part of the predicted ground pattern for spiders, leaving the question open whether the median spinnerets in the amber fossils are in the process of formation or reduction. Loss of the ventral sclerites associated with the spinnerets on opisthosomal segments 3 and 4 clearly differentiates all modern spiders from the new fossils and the retention of these sclerites in *Chimerarachne* may support the hypothesis that it reflects a plesiomorphic ventral anatomy.

So is *Chimerarachne yingi* a spider? Phylogenetic reconstruction consistently recovers it in a clade with Uraraneida, Araneae and *Idmonarachne*, but different analysis techniques yield different internal topologies. Under parsimony with equal weights the strict consensus tree resolves the new species as sister-group to the uraraneids, implied weights places it as sister-group of all extant spiders, and the alternative Bayesian majority rule consensus recovers Uraraneida, Araneae, *Idmonarachne* and *Chimerarachne* in a polytomy (see Supplementary Information for full results and discussion). This instability is likely to result from several key characters, such as the arrangement of the eyes and any modification of the male pedipalp, that are unknown in both uraraneids and *Idmonarache*. This problem is particularly acute in the latter, where the morphology preserved is enigmatic13. To test the impact of this fossil we excluded *Idmonarachne* from the analysis and recovered a uraraneid / spider / *Chimerarachne* polytomy under equal weights parsimony and *Chimerarachne* as an ingroup spider (specifically sister-group to mesotheles) under implied weights. Our preferred tree (Fig. 5) is based on the Bayesian results (without *Idmonarachne*), which yield a phylogeny of the form (Uraraneida (*Chimarachne* (Mesothelae + Opisthothelae))) with strong support. We suggest the collapse of this region of the tree when *Idmonarachne* is included probably reflects genuine uncertainty when all the terminal taxa are included, to which the Bayesian methodology may be more sensitive25.

**Conclusions**

Irrespective of its exact relationships, we conclude that *Chimerarachne* reveals a grade of organization when spiders, or one of their closest relatives, had developed a male palpal organ and at least part of the modern spinning apparatus, but retained the ancestral character of a whip-like telson. We reiterate that must have been a continuum of character reduction and character acquisition on the lineage towards the modern spiders, and we leave open the question whether Araneae *sensu stricto* should be defined by loss of the telson, or by the appearance of the spinnerets and/or male palpal organ.

**METHODS**

**Material studied.** The two specimens (NIGP166870 and NIGP166871) are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. Both inclusions were obtained from an amber mine located near Noije Bum Village, Tanaing Town. The U-Pb dating of zircons from the volcanoclastic matrix of the amber gave a maximum age of 98.8 ± 0.6 million years26. However, multiple lines of evidence, including the high degree of roundness of the amber and the presence of bivalve borings on the surface, suggest that the amber was most likely reworked before deposition in the volcanoclastic matrix, which implies that the age of the amber should be older than that of the matrix27,28.

**Observations.** To reduce the deformation caused by differential refractivity, we sandwiched the amber specimens between two coverslips and filled the space with glycerol. Photographs were taken using a Zeiss Stereo Discovery V16 microscope system at the State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. In most instances, incident and transmitted light were used simultaneously. All images are digitally stacked photomicrographic composites of approximately 40 individual focal planes that were obtained using the software Helicon Focus 6 (http://www.heliconsoft.com) for better illustration of the 3D structures. Photomicrographs with a green background were taken using a CLSM Zeiss LSM710 with × 20 and × 10 objectives and a laser at 488 nm at the State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

To three dimensionally reconstruct the fossil (Supplementary Video), we scanned the specimen NIGP166871 at micro-CT lab of NIGPAS, using a 3D X-ray microscope (3D-XRM), Zeiss Xradia 520 versa. Unlike conventional micro-CT which relies on maximum geometric magnification and flat panel detector to achieve high resolution, 3D-XRM uses CCD-based objectives to achieve higher spatial resolution. Depending on the size of the fossil specimen, a CCD-based 4X objective was used, providing isotropic voxel sizes of 3.7 μm with the help of geometric magnification. During the scan, the acceleration voltage for the X-ray source was 40 kV, and a thin filter (LE1) was used to avoid beam hardening artefacts. To improve signal- to-noise ratio, 2500 projections of 3s exposure over 360° were collected. Volume data processing was performed using software Vgstudio Max (version 3.0, Volume Graphics, Heidelberg, Germany).

Drawings and measurements were made from the photographs using Autodesk Graphic (www.graphic.com) on an Apple MacBook Pro computer. Due to the three-dimensional nature of amber-preserved specimens, appendage measurements are difficult to obtain because podomeres may lie at an angle to the viewer, so lengths of appendages must be considered as approximate. All measurements are in mm. Abbreviations: I II III IV leg numbers, ALS anterior lateral spinneret, car carapace, ch chelicera, cx coxa, fe femur, lb labium, mt metatarsus, op operculum, p pedicel, pa patella, Pd pedipalp, PLS posterior lateral spinneret, pig pygidium, st sternum, t trichobothrium, ta tarsus, ti tibia, tr trochanter.

**Phylogenetic treatment**. The new taxon was scored into an existing data matrix12 modified to test the position of the Carboniferous fossil *Idmonarachne*13 and the phylogeny of fossil whip spiders29. Full methods, results, and discussion are provided in the Supplementary Information. In brief, four characters have been added to the matrix to test the placement of *Chimerarachne*. Trees were recovered using both parsimony (equal and implied weights) and Bayesian approaches, and interrogated through the exclusion of differing taxa and characters to explore their impact.

**Data availability**. Taxonomic data have been deposited in ZooBank (http://zoobank.org/) under the following LSIDs: urn:lsid:zoobank.org:pub:58DF4E2B-E284-486D-BD4E-FF2A2DBD8201 (article); urn:lsid:zoobank.org:act:8D6B77E2-C02F-48CD-BDB6-3590076F4E71 (genus); and urn:lsid:zoobank.org:act:9C0C78E5-6E05-4E92-BA34-456907C443E2 (species). The matrix is provided in both tnt and MrBayes formats (see Supplementary Data). Higher resolution versions of the figures can be obtained upon request from the corresponding author.

**References**

* 1. *World Spider Catalog*. Natural History Museum Bern, online at http://wsc.nmbe.ch, version 18.5, accessed on 16.11.2017.
  2. Selden. P. A. Fossil mesothele spiders. *Nature* **379**, 498-499 (1996).
  3. Selden, P. A., Shcherbakov, D. E., Dunlop, J. A. & Eskov, K. Y. Arachnids from the Carboniferous of Russia and Ukraine, and the Permian of Kazakhstan. *Paläont. Z.* **88**, 297–307 (2014).
  4. Shear, W. A., Palmer, J. M., Coddington, J. A. & Bonamo, P. M. A Devonian spinneret: Early evidence of spiders and silk use. *Science* **246**, 479–481 (1989).
  5. Selden, P. A., Shear, W. A. & Bonamo, P. M. A spider and other arachnids from the Devonian of New York, and reinterpretations of Devonian Araneae. *Palaeontology* **34**, 241–281 (1991).
  6. Selden, P. A., Shear, W. A. & Sutton, M. D. Fossil evidence for the origin of spider spinnerets, and a proposed arachnid order. *Proc. Natl. Acad. Sci. USA* **105**, 20781–20785 (2008).
  7. Platnick, N. I. & Gertsch, W. J. The suborders of spiders: a cladistics analysis. *Am. Mus. Novit*. **2607**, 1–15 (1976).
  8. Haupt, J. The Mesothelae – a monograph of an exceptional group of spiders (Araneae: Mesothelae). *Zoologica* **154**, 1–102 (2003).
  9. Shultz, J. W. A phylogenetic analysis of the arachnid orders based on morphological characters. *Zool. J. Linn. Soc*. **150**, 221–265 (2007).
  10. Savory, T. On the arachnid order Palpigradi. *J. Arachnol*. **2**, 43-45 (1974).
  11. Legg, D. A., Sutton, M. D. & Edgecombe, G. D. Arthropod fossil data increase congruence of morphological and molecular phylogenies. *Nat. Comm.* **4**, Article 2485 (2013).
  12. Garwood R. J. & Dunlop, J. A. Three-dimensional reconstruction and the phylogeny of extinct chelicerate orders. *PeerJ* **2**, e641 (2014).
  13. Garwood, R. J. *et al*. Almost a spider: a 305-million-year-old fossil arachnid and spider origins. *Proc. R. Soc. B* **283**, 20160125 (2016).
  14. Lamarck, J. B. *Système des Animaux sans Vertebres*. (Deterville, Paris, 1801).
  15. Wunderlich, J. New and rare fossil spiders (Araneae) in mid Cretaceous amber from Myanmar (Burma), including the description of new extinct families of the suborders Mesothelae and Opisthothelae as well as notes on the taxonomy, the evolution and the biogeography of the Mesothelae. *Beitr. Araneol.* **10**, 72–279 (2017).
  16. Selden, P. A. & Ren, D. A review of Burmese amber arachnids. *J. Arachnol*. **45**, 324–343 (2017).
  17. Miether, S. T. & Dunlop, J. A. Lateral eye evolution in the arachnids. *Arachnology* **17**, 103–119 (2016).
  18. Wheeler, W. C., *et al.* The spider tree of life: phylogeny of Araneae based on target-gene analyses from an extensive taxon sampling. *Cladistics* **33**, 574–616 (2017).
  19. Raven, R. J. The spider infraorder Mygalomorphae (Araneae): cladistics and systematics. *Bull. Am. Mus. Nat Hist*. **182**, 1–180 (1985).
  20. Kraus, O. *Liphistius* and the evolution of spider genitalia. *Symp. Zool. Soc. Lond.* **42**, 235–254 (1978).
  21. Shultz, J. W. The origin of the spinning apparatus in spiders. *Biol. Rev.* **62**, 89–113 (1987).
  22. Marples, B. J. The spinnerets and epiandrous glands of spiders. *J. Linn. Soc. Zool.* **46**, 209–222 (1967).
  23. Sharma, P. P. Chelicerates and the conquest of land: a view of arachnid origins through an evo-devo spyglass. *Int. Comp. Biol.* **57**, 510–522 (2017).
  24. Dunlop, J. A. & Lamsdell, J. C. Segmentation and tagmosis in Chelicerata. *Arth. Struct. Develop.* **46**, 395–418 (2017).
  25. O'Reilly, J. E. *et al.* Bayesian methods outperform parsimony but at the expense of precision in the estimation of phylogeny from discrete morphological data. *Biol. Lett.* **12**, 20160081 (2016).
  26. Shi, G. H. *et al*. Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretac. Res.* **37**, 155–163 (2012).
  27. Ross, A., Mellish, C., York, P. & Crighton, B. in *Biodiversity of Fossils in Amber from the Major World Deposit*s (ed. Penney, D.) 208–235 (Siri Scientific Press, Manchester, 2010).
  28. Wang, B. *et al*. Debris-carrying camouflage among diverse lineages of Cretaceous insects. *Sci. Adv.* **2**, e1501918 (2016).
  29. Garwood, R. J., Dunlop, J. A., Knecht, B. J. & Hegna, T. A.. The phylogeny of fossil whip spiders. *BMC Evol. Biol.* **17**, 105 (2017).

**Acknowledgements**

We are grateful to M. Engel and J. Wunderlich for helpful initial comments, Y. Huang and Y. Ying for kindly providing specimens, Z. Yin and S. Wu for the micro-CT reconstruction, J. Keating for advice on Bayesian inference of phylogeny, three anonymous reviewers for their comments, and D. Yang for the reconstruction. This research was supported by the National Natural Science Foundation of China (41572010, 41622201, 41688103), the Chinese Academy of Sciences (XDPB05), and Youth Innovation Promotion Association of CAS (No. 2011224).

**Author Contributions**

B.W. designed the project; B.W., J.A.D., P.A.S., R.J.G. and W.A.S. all contributed to observation and interpretation of the fossils and drafted the manuscript. B.W. and X.L. produced the photographs, P.A.S. produced the line drawings, measurements and description, R.J.G. ran the phylogenetic analysis and P.M. collected data.

**Additional information**

**Supplementary Information** is available for this paper.

**Reprints and permissions information** is available at www.nature.com/reprints.

**Correspondence and requests for materials** should be addressed to B.W.

**Competing interests**

The authors declare no competing financial interests.

**Fig. 1 | *Chimerarachne yingi*.** **a**, **c,** Holotype NIGP166870, entire specimen in dorsal and ventral view. **b**, **d,** Interpretative drawings of the same. I II III IV, leg numbers; ALS, anterior lateral spinneret; car, carapace; ch, chelicera; cx, coxa; fe, femur; lb, labium; mt, metatarsus; op, operculum; p, pedicel; pa, patella; Pd, pedipalp; PLS, posterior lateral spinneret; pyg, pygidium; st, sternum; t, trichobothrium; ta, tarsus; ti, tibia; tr, trochanter. Scale bars, 1 mm.

**Fig. 2 | *Chimerarachne yingi*. a**, **c,** Paratype NIGP166871, entire specimen in dorsal and ventral view. **b, d,** Interpretative drawings of the same. I II III IV, leg numbers; ALS, anterior lateral spinneret; car, carapace; ch, chelicera; cx, coxa; fe, femur; lb, labium; mt, metatarsus; op, operculum; p, pedicel; pa, patella; Pd, pedipalp; PLS, posterior lateral spinneret; pyg, pygidium; st, sternum; t, trichobothrium; ta, tarsus; ti, tibia; tr, trochanter. Scale bars, 1 mm.

**Fig. 3 | Morphological details and reconstruction**. **a, b,** Reconstruction in dorsal and ventral view. **c,** Eyes in NIGP166870. **d,** Chelicerae in NIGP166870. **e,** Ventral palps in NIGP166870. **f,** Ventral palps in NIGP166871. **g,** Spinnerets in NIGP166871. **h,** Abdomen in NIGP166870, CLSM image. **i, j,** Leg II claw in NIGP166870. **k,** Flagellum in NIGP166871. ap, apophysis; ALS, anterior lateral spinneret; ch, chelicera; em, embolus; ey, eye; mc, median claw; op, operculum; pc, paired claws; PLS, posterior lateral spinneret; pu, pulvillus; sp, spigots; ta, tarsus. Scale bars, 1 mm (**a, b**), 0.2 mm (**e–h, k**), 0.1 mm (**c, d**), and 0.05 mm (**i, j**).

**Fig. 4 | *Chimerarachne yingi*. a–h,** NIGP166870. **a,** Cymbium, CLSM image. **b,** Leg II tarsus and claw. Note at least 5 trichobothria at distal end of tarsus II. **c,** Right leg IV claw. **d,** Left leg IV claw. **e,** Dorsal pedicel. **f,** Dorsal abdomen. **g,** Ventral Abdomen. **h,** Flagellum. **i, j,** NIGP166871. **i,** Dorsal prosoma. **j,** Dorsal palps. Scale bars, 0.2 mm (**f, g, i, j**), 0.1 mm (**a, d, e, h**), and 0.05 mm (**b, c**).

**Fig. 5 | Phylogenetic relationships**. Consensus cladogram (bayesian majority rule consensus with support values) showing the position of *C. yingi* within the Pantetrapulmonata branch of the arachnids, which encompasses the spiders and their closest relatives (See Supplementary Fig. 3 for the full annotated tree). Both *Attercopus* and *Permarachne* are incomplete and scoring them individually collapses the tree, thus we combined characters from the two genera into one terminal. Full methods, results, discussion, and sources for line drawings are provided in the Supplementary Information.

**Fig. 6 | Evolutionary history of spiders and spider-related arachnids.** Thick lines indicate the known extent of the fossil record. Branches representing modern spiders are yellow. The branch of *Chimerarachne* is red. See Supplementary Information for details of the phylogenetic analysis.