

Origin of spiders and their spinning organs illuminated by mid-Cretaceous amber fossils

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Understanding the genealogical relationships among the arachnid orders is an onerous task, but fossils have aided in anchoring some branches of the arachnid tree of life. The discovery of Palaeozoic fossils with characters found in both extant spiders and other arachnids provided evidence for a series of extinctions of what was thought to be a grade, Uraraneida, that led to modern spiders. Here, we report two extraordinarily well-preserved Mesozoic members of Uraraneida with a segmented abdomen, multi-articulate spinnerets with well-defined spigots, modified male palps, spider-like chelicerae and a uropygid-like telson. The new fossils, belonging to the species *Chimerarachne yingi*, were analysed phylogenetically in a large data matrix of extant and extinct arachnids under a diverse regime of analytical conditions, most of which resulted in placing Uraraneida as the sister clade of Araneae (spiders). The phylogenetic placement of this arachnid fossil extends the presence of spinnerets and modified palps more basally in the arachnid tree than was previously thought. Ecologically, the new fossil extends the record of Uraraneida 170 million years towards the present, thus showing that uraraneids and spiders co-existed for a large fraction of their evolutionary history.

Spiders (Arachnida, Araneae) constitute a megadiverse clade of terrestrial predators¹, nearly ubiquitous, with the first fossils dating back to the Carboniferous², and an origin—based on molecular estimates—in the Devonian/Permian³ (the time when putative stem-Araneae or stem-Tetrapulmonata first appeared in the fossil record^{4–8}). Salient characters preserved in some of these non-spider Palaeozoic arachnids^{2,4–7,9,10} include one or more of the following features: a segmented opisthosoma similar to that found in modern Mesothelae spiders; silk spigots (without differentiated spinnerets); and a flagellum similar to that of extant Uropygi (whip scorpions) and Palpigradi (micro whip scorpions). The co-occurrence of silk spigots and the flagellum are thus an exclusively Palaeozoic combination of characters that served to recognize a new group of arachnids named Uraraneida⁶, although this is sometimes considered a grade. Uraraneida and its relatives are thus known from a handful of Palaeozoic fossils from the Devonian–Permian, in the genera *Attercopus* and *Permarachne*. This order of arachnids has long been thought to have missed the Palaeozoic/Mesozoic transition and uraraneids have been interpreted as a transitional form between spiders and their flagellate tetrapulmonate counterparts (that is, Uropygi). However, our understanding of the anatomy of these fossils was rather limiting, restricted to a few Devonian cuticular fragments of *Attercopus fimbriunguis*^{1–3} from Gilboa, New York, complemented by additional fragments from Middle Devonian strata from Schoharie County of a supposed conspecific⁶, or a single compression fossil of *Permarachne novokshonovi*, from the Permian of the Ural Mountains, Russia⁹.

A third fossil, *Idmonarachne brasieri*, from the late Carboniferous of Montceau-les-Mines, France, was recently described⁷ as a spider-like arachnid with spider chelicerae, a pedicel separating the prosoma and opisthosoma, and a segmented opisthosoma lacking spinnerets

or a flagellum. While Uraraneida was not tested for its monophyly (the two uraraneid fossils were combined into a single composite terminal), phylogenetic analyses based on an extensive morphological data matrix for living and extinct arachnids^{11,12} have suggested a sister group relationship of Araneae + *Idmonarachne*^{7,13}, with uraraneids branching earlier, giving the impression that Uraraneida and *Idmonarachne* are some sort of stem-group Araneae that became extinct around the time that spiders started diversifying.

Here, we present two Burmese Cretaceous amber specimens of Uraraneida closing a fossil record gap of 170 million years. The new fossils (named *Chimerarachne yingi* based on additional specimens in a companion paper¹⁴), which are extraordinarily well preserved, exhibit all the characters described for Uraraneida and other stem-group spiders, such as the segmented abdomen with spigots and a long flagellum, while also bearing characters previously only known from Araneae, such as a modified male palp (presumably to function as a sperm transfer organ) and typical spider spinnerets with spigots. We place the new fossils in a phylogenetic context with the previously described uraraneids and with *Idmonarachne* to evaluate the relationships among these Palaeozoic, Mesozoic and extant arachnids.

Results

Systematic palaeontology.

Arthropoda
Chelicerata
Arachnida
Serikodiastida
Uraraneida

Chimerarachne yingi Wang et al., 2018 (Figs. 1–3 and Supplementary Figs. 1–11)

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Fig. 1 | Light micrographs of *C. yingi* (NIGP167161). **a**, General habitus. **b**, General view of pedipalps. **c**, Detail of chelicerae (arrow points at cuticular striae). **d**, Detail of palpal tarsi. **e**, Detail of leg III (arrow points to metatarsal trichobothrium). **f**, Detail of the posterior lateral spinneret with the spigots. The red arrows indicate segments. **g**, Ventral view showing the clear, broad sternum. **h**, Detail of the spinnerets, pygidium and proximal portion of the flagellum. Scale bars: 1 mm in **a**; 0.2 mm in **b–f**; 0.5 mm in **g** and **h**.

Material examined. NIGP167161, male (Figs. 1 and 2, and Supplementary Figs. 1–8 and 10), co-occurs with several other syninclusions: two spiders, two millipedes (an adult and a nymph), seven mite nymphs, one beetle (Staphylinidae: Scydmaeninae), one orthopteran nymph, one nymph of ensign scale insect (Ortheziidae), one collembolan and many plant trichomes. NIGP167162, male (Supplementary Fig. 9), co-occurs with a collembolan. Both amber pieces are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing.

Horizon and locality. The specimens are from mid-Cretaceous (late Albian or earliest Cenomanian) amber from Hukawng Valley, Kachin State, northern Myanmar^{15,16}.

Chimerarachne yingi can be distinguished from other arachnids by the unique combination of an externally segmented opisthosoma ventrally bearing two pairs of lateral, long multi-articulated spinnerets with spigots, two pairs of small non-articulated median spinnerets, a long flagellum and a modified male pedipalpal tarsus. Earlier uraraneids also have a flagellum, but the other two known fossils (*Attercopus* and *Permarachne*) lack spinnerets and modified palps. While spinnerets and modified palps are present in Araneae, spiders lack a flagellum. While extant Mesothelae have a segmented abdomen, this is only evident dorsally, in the reduced tergites, while *Chimerarachne* has complete segmentation in all opisthosomal segments.

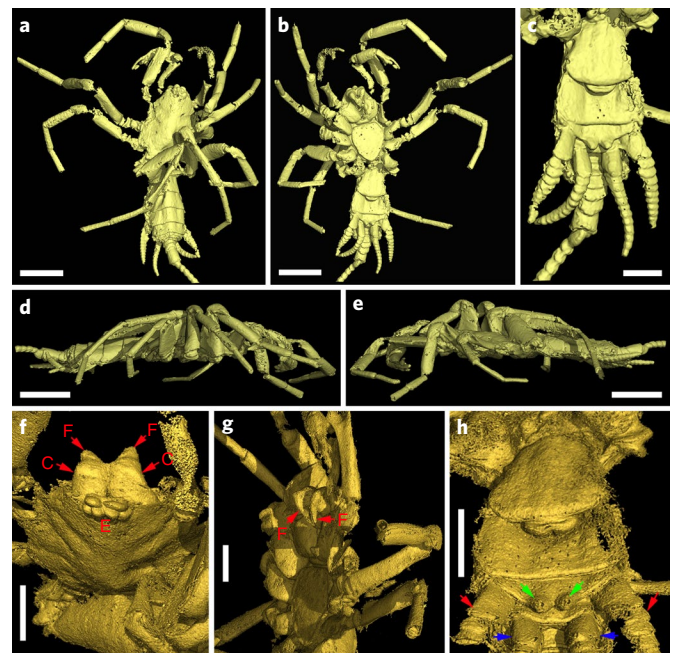


Fig. 2 | Micro computed tomography reconstructions of *C. yingi* (NIGP167161). **a**, General habitus in dorsal view. **b**, General habitus in ventral view. **c**, Detail of opisthosoma in ventral view. **d**, Right lateral view. **e**, Left lateral view. **f**, Frontal view illustrating the eyes (E) and chelicerae (C and F). **g**, Ventrolateral view showing the cheliceral fangs (F) and sternum. **h**, Detail of the proximal region of the spinnerets (anterior median, green arrows; anterior lateral, red arrows; posterior lateral, blue arrows). Scale bars: 0.5 mm in **a**, **b**, **d** and **e**; 0.2 mm in **c**, **f**, **g** and **h**.

Phylogenetic analyses. As suggested previously¹⁷, we coded individual species as terminals instead of a composite terminal called ‘Uraraneida’ that combined information from multiple species in the original data matrix of ref. ¹³, which in turn evolved from previous matrices^{7,11,18} (see Supplementary Information for the list of characters and codings). However, with the aim of having a critical amount of information, we merged data from the Devonian cuticular fossils^{4–6,10} into a single terminal, *A. fimbriunguis*, despite it coming from different strata. Our data matrix therefore includes our codings of the two previously known Palaeozoic uraraneid species, as well as our Cretaceous fossils. The resulting data matrix is publicly available in MorphoBank (project P2792).

Initial analyses coding *A. fimbriunguis* and our interpretation of *P. novokshonovi* resulted in a clade with *C. yingi*, thus supporting the monophyly of Uraraneida, although with low nodal support. We coded some characters more conservatively than ref. ¹³—especially with reference to the presence of a sternum in *Permarachne* and *I. brasieri*, which we coded as ‘unknown’—and tested our dataset, coding the presence of a cheliceral venom gland as either ‘present’ or ‘unknown’ in *Attercopus* (see a discussion of character codings in Supplementary Information). Whether a venom gland was coded as ‘present’ or ‘missing data’ in *Attercopus* made no difference in our results and thus we proceeded with the matrix with the gland venom coded as present, as assumed in previous work.

Results under parsimony, using both equal weights and implied weighting, all coincided in the monophyly of Uraraneida (except for implied weights, concavity value (k)=2, where it was unresolved; Fig. 4d). The equal weights analysis did not resolve the position of *Idmonarachne* and Uraraneida with respect to Araneae (Fig. 4b), but all other analyses (Bayesian, implied weights under all k values except 2) supported *Idmonarachne* as a sister group to Serikodiastida¹⁹ (amber clade in Fig. 4), and Uraraneida

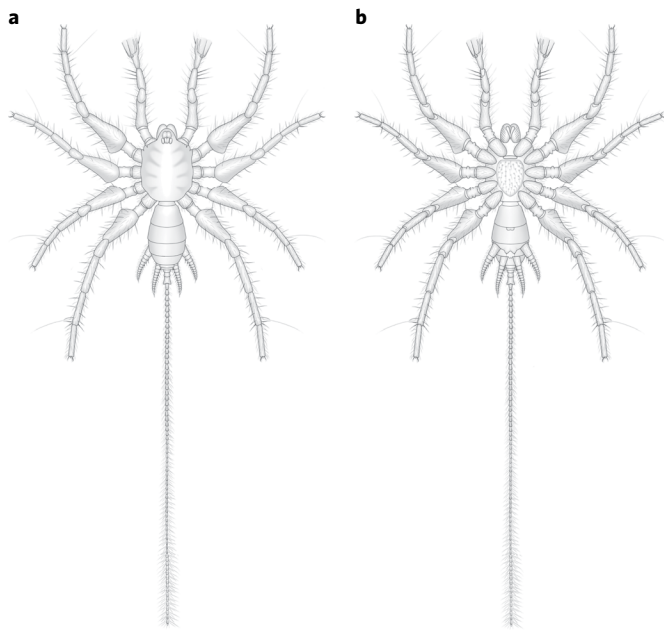


Fig. 3 | Morphological reconstruction of male *C. yingi*. a, Dorsal. b, Ventral.

(collapsed in the Bayesian tree) as a sister group to a monophyletic Araneae, with Mesothelae as a sister group to Opisthothelae (Mygalomorphae + Araneomorphae) (Fig. 4a,c). Serikodiastida is also found under $k=2$ when only the more complete uraraneid—our Cretaceous specimen—is included in the analyses. Likewise, all analyses (except for implied weights, $k=2$) support Tetrapulmonata. The Bayesian analysis produced a similar tree, supporting *Idmonarachne* as a sister group to Serikodiastida, with monophyletic Araneae (including the clades Mygalomorphae and Araneomorphae, as a sister group to Mesothelae) but collapsed Uraraneida (Fig. 4e).

Discussion

It is well known that extant mesothele spiders retain traces of external abdominal segmentation (clearly visible as plate-like tergites) and have multi-segmented spinnerets²⁰, but opisthosomal segmentation is only visible dorsally, while in *Chimerarachne* segmentation occurs throughout the opisthosoma (Fig. 2a,d and Supplementary Figs. 1e, 3b, 9a,e and 10a), including ventrally and laterally. The spinnerets and spigots of extant mesothele spiders and our fossil species nonetheless are remarkably similar, both having two long pairs of lateral, multi-articulated, distally tapering-off spinnerets and two pairs of median spinnerets that are very small in comparison and not articulated. Like in mesotheles, *Chimerarachne* has mesoventrally placed spigots—at least one per spinneret article in the section of the posterior lateral spinnerets where this character is discernible. The morphology of these spigots (Figs. 1, 2 and 4f; see also Supplementary Figs. 7 and 9) is similar to that of the extant mesothele genus *Liphistius*, with a high spigot base and a long shaft (Fig. 1h and Supplementary Fig. 6a). It is therefore not surprising that most analyses placed Uraraneida as a sister group to Araneae, while *Idmonarachne*, which was originally proposed to be closer to spiders than uraraneids⁷, is the sister group of Serikodiastida. The monophyly of Serikodiastida is supported by nearly all analyses and weighting schemes. While the transformation series between having a flagellum and the anal tubercle of spiders was not evident in the literature and previous arachnid data matrices, examination of the anal tubercle of *Liphistius* clearly suggests an intermediate character state, with a putative pygidium homologue formed of

two ring-like segments (Fig. 4g,h) (similar to that of Ricinulei)—a character state also found in some araneomorph spiders.

Aside from the phylogenetic importance of the new fossil, there are major ecological and evolutionary implications that derive from finding a uraraneid in the mid-Cretaceous, since the youngest uraraneids (or stem-group uraraneids or serikodiastids) were known from the Permian, and these lack key features like spinnerets. Our fossils therefore help to corroborate multiple characters that had been tentatively assigned to uraraneids based on partial reconstructions of *Attercopus* and *Permarachne*, such as the presence of a flagellum, which was originally interpreted as an elongate middle spinneret in *Permarachne*⁸. The well-preserved spider-like sternum (Figs. 1g and 2b,g) or the presence of spigots in the spinnerets (Fig. 1f), together with the highly modified male palp—possibly for sperm transfer (Fig. 1b,d), as in modern spiders—cast little doubt about the close relationship of *Chimerarachne* (and probably the Palaeozoic uraraneids, at least *Permarachne*) with the members of the order Araneae. However, details of the chelicerae remain difficult to observe and the homologies of the palp remain difficult to interpret.

The Cretaceous Burmese amber has yielded fossil representatives belonging to all extant arachnid orders^{15,21–28}, although fossil schizomids are not formally named. A total of 244 described arachnid species are known to date²⁹, most of which are spiders. The co-existence of extant groups with this small extinct arachnid order in the Cretaceous of Myanmar is unique, as no other ecosystem is known to host such diversity of arachnids, probably illustrating the maturity and complexity of the region in the Cretaceous, even though some lineages found in Burmese amber are now entirely missing from that part of the world (most notably, Ricinulei, which is now restricted to west Africa and the Neotropical region³⁰). Perhaps most importantly, the co-existence of uraraneids with spiders at least until the Cretaceous shows that uraraneids were not direct ancestors or stem-group spiders, but an independent lineage that continued evolving in parallel with spiders since the Carboniferous (when the spider *Palaeothele montceauensis* was already present^{31,32}) for at least 200 million years.

Methods

Light imaging. The amber pieces were polished with sand paper of different grain sizes and diatomite mud, and observed and photographed using a Zeiss Discovery V20 stereomicroscope and a Zeiss Axio Imager 2 light microscope with a digital camera attached. Photomicrographs with a green background were taken using fluorescence as a light source attached to the Zeiss Axio Imager 2 light microscope (Supplementary Figs. 3a–f, 4d, 5b, 8e and 9e–g). Focus stacking software (Helicon Focus 3.10; <http://www.heliconsoft.com/>) was used to increase the depth of field. Measurements are expressed in mm.

X-ray microscopic tomography. The specimen NIGP167161 was scanned at the micro computed tomography laboratory of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, using a Zeiss Xradia 520 Versa. As a three-dimensional X-ray microscope, Zeiss Xradia 520 Versa provides non-destructive tomographic imaging of fossils with high resolution. Depending on the size of the amber specimen, a charge-coupled-device-based 4× objective was employed, providing an isotropic voxel size of 2.4 μm with the help of geometric magnification. As the absorb contrast of the fossil is extremely low, we applied the propagation phase contrast mode to detect the fossil. To obtain good contrast, the running voltage for the X-ray source was set to 40 kV. During the scan, 3,201 projections over 360° were obtained. The exposure time for each projection was 30 s. Volume data processing was performed using the software VGStudio Max (version 3.0; Volume Graphics; <https://www.volumegraphics.com/>).

Phylogenetic analyses. We used three search strategies in the computer programme TNT version 1.5 (ref. 33): equal weights, implied weights³⁴ and the more recently implemented implied weights where characters with missing entries are down-weighted faster, as characters with missing data have relatively smaller chances of being homoplastic³⁵. For the implied weights analyses, we tested a set of concavity (k) values of 1, 2, 3, 4, 5, 10 and 100, as we found a switch of topologies between $k=2$ and $k=3$. Likewise, we explored two data matrices with alternative codings for the presence of a venom gland in *Attercopus*. Nodal support was calculated using symmetric resampling in TNT, as it takes into account distortion by weights and costs.

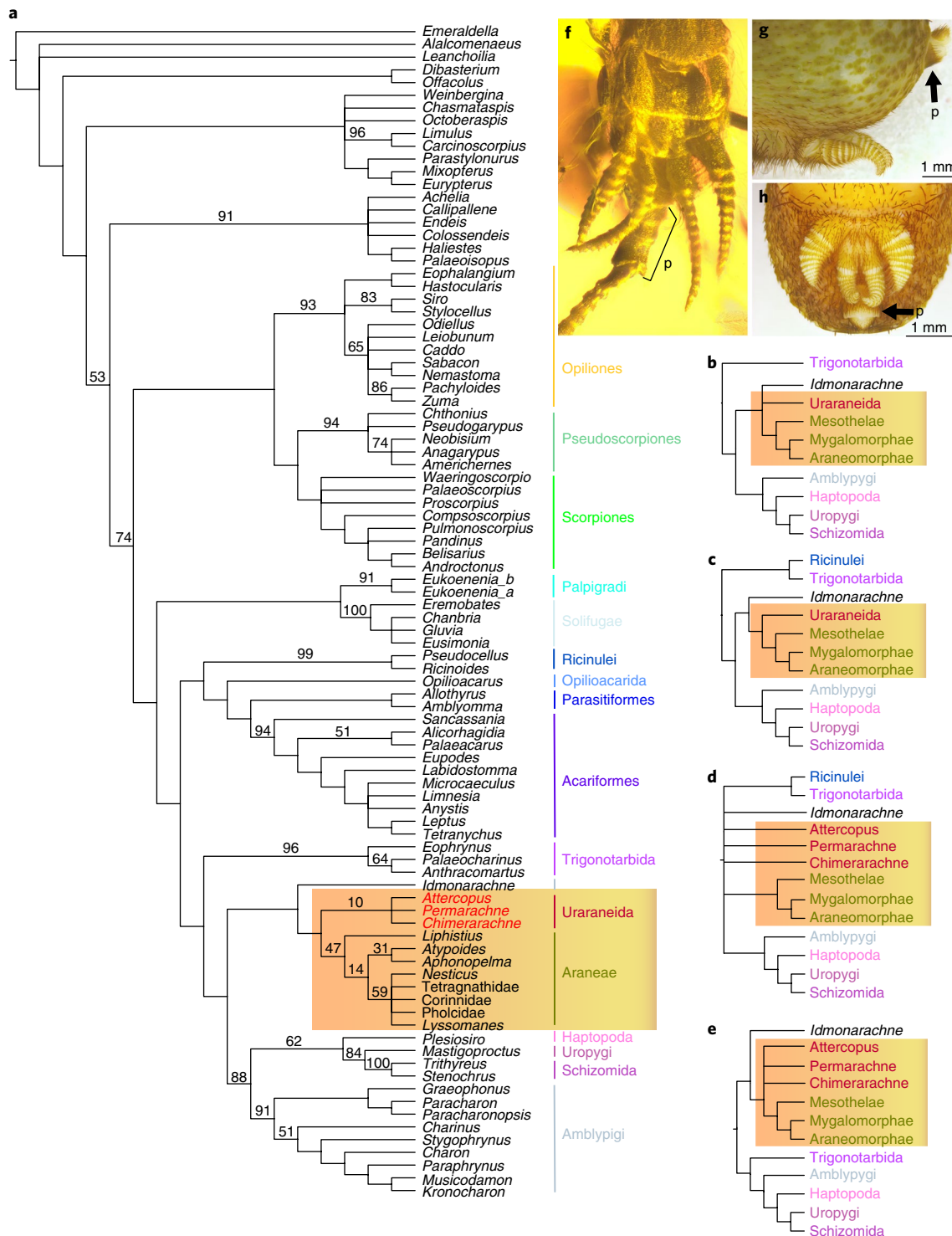


Fig. 4 | Phylogenetic results of the parsimony and Bayesian analyses of the morphological dataset. a, Strict consensus of 18 trees ($k=3$, 41,2441 weighted steps; similar topology obtained under $k=4, 5, 10$ or 100) based on the implied weights analysis of our dataset with the arachnid orders highlighted. *Chimerarachne* is in bold and Serikodiastida is framed in an amber-coloured box. Support values over 50% are provided for the general tree at $k=3$, and all values for Serikodiastida are plotted. **b–d**, Alternative topologies obtained under different concavity values (**b**, unweighted; **c**, $k=1$; **d**, $k=2$). **e**, Topology obtained under Bayesian analysis. **f**, Detail of the posterior end (ventral view) of *C. yingi*, showing the spinnerets, pygidium (p) and telson. **g,h**, Details of the caudal abdominal region of a *Liphistius* species (GH2776, male from northern Thailand) showing the spinnerets and the pygidium-like (p) anal tubercle in lateral (**g**) and ventral (**h**) views.

A Bayesian analysis was conducted in MrBayes³⁶ using the discrete Markov k model of ref. ³⁷, with four chains of 15 million generations each, sampled every 10,000 generations. MrBayes excluded the six invariant characters from the analysis as incompatible with the model. The consensus tree was estimated after

a burn-in of 25% of the sampled trees. Convergence of the independent runs was confirmed with Tracer version 1.6.0 (<http://tree.bio.ed.ac.uk/software/tracer/>). The analysis produced 4,504 post-burn-in trees that were combined in a majority-rule consensus tree.

Life Sciences Reporting Summary. Further information on experimental design is available in the Life Sciences Reporting Summary.

Data availability. The specimens studied (NIGP167161 and NIGP167162) are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. The morphological data matrix has been deposited in MorphoBank (project P2792).

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Author contributions

D.H., G.G., G.H., C.C., Y.S., Z.Y. and F.X. participated in the morphological studies. D.H. coordinated the study. G.G. and G.H. conducted the phylogenetic analyses. G.G., D.H. and G.H. prepared the manuscript.

Competing interests

The authors declare no competing financial interests.

Additional information

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