The oldest fossil pirate spider (Araneae: Mimetidae), in uppermost Eocene Indian amber, imaged using X-ray computed tomography

David Penney[1]
[1]Faculty of Life Sciences, The University of Manchester, Manchester, M13 9PT
email: david.penney@manchester.ac.uk

Andrew McNeil[2]
[2]School of Materials, The University of Manchester, Manchester, M1 7HS

David I. Green[3]
[3]Department of Geology, Amgueddfa Cymru–National Museum Wales, Cardiff, CF10 3NP

Robert Bradley[2]

Philip J. Withers[2]

Richard F. Preziosi[1]

Summary

A fossil pirate spider (Araneae, Mimetidae) is documented in amber from the Eocene Cambay Formation of India. It represents the first described spider from this deposit and the oldest fossil record of the family, extending its known geological range by approximately 3–8 million years from the previously oldest fossils in Eocene Baltic amber. It also represents the first Gondwanan geological locality for fossil mimetids. Despite the application of X-ray computed tomography to the study of this inclusion, the state of preservation of the juvenile spider did not permit identification beyond family level.

Introduction

Pirate spiders (family Mimetidae) are small to medium-sized (3–7 mm) entelegyne spiders, easily recognized by their modified spination of long spines interspersed by shorter spines on the tibiae and metatarsi of the first two pairs of legs, which in most species are long and slender (e.g. Jocqué & Dippenaar-Schoeman 2006, fig. 63). They are generally presumed to be free-living obligate araneophages (they eat other spiders) that prey particularly on web-building spiders such as Araneidae and Theridiidae, although the foraging behaviour of most species is unknown. They form a relatively small family with 156 extant species in 13 genera (Platnick 2012). The extant Indian pirate spiders are poorly known, with only two species in two genera (*Mimetus* Hentz, 1832 and *Melaenosia* Simon, 1906) recorded to date from the entire subcontinent, and these are known only from males (Keswani, Hadole & Rajoria 2012). An additional genus, *Phobetinus* Simon, 1895 is known from Sri Lanka (Brignoli 1972).

The spider fossil record is diverse (Selden & Penney 2010; Penney & Selden 2011; Dunlop, Penney & Jekel 2012; Penney, Dunlop & Marusik 2012) but mimetids are relatively uncommon (Harms & Dunlop 2009) and are known only from fossils preserved in Tertiary ambers, with the oldest records to date being in penecontemporaneous (44–49 Ma) Baltic and Rovno (Ukraine) ambers (Wunderlich 2012). Fossiliferous amber from India was first reported by Alimohammadian *et al*. (2005), with a more recent comprehensive synopsis by Rust *et al*. (2010), who listed the following spider families as present: Pholcidae, Mimetidae (based on the specimen described herein), Thomisidae, and Uloboridae. Based on examination of these undescribed fossils by DP, only the first two of these families can be confirmed at the present time. The amber was formed in a broad-leaved, tropical, everwet palaeoenvironment at the paleoequator and occurs in the Cambay Shale (early Ypresian, 50–52 Ma) of Gujarat, western India, where it is found in lignitic and muddy sediments concentrated by near-shore chenier systems. Its chemistry and the anatomy of associated fossil wood indicates a definitive source of Dipterocarpaceae (Rust *et al*. 2010). The amber is very partially polymerized and readily dissolves in organic solvents, thus allowing extraction of whole insects whose cuticle retains microscopic fidelity. Fourteen orders, more than 55 families, and 100 species of arthropod inclusions have been discovered so far (Rust *et al*. 2010), although few have been formally described. The investigation of its inclusions is still at a very early stage but has the potential to be informative from a palaeobiogeographic point of view because the amber was formed prior to the Indian–Asian collision, which occurred approximately 50 million years ago. However, at present, the fauna does not appear to be as distinctive as might have been expected (Rust *et al*. 2010). The present paper documents the first fossil spider from this deposit, which represents the oldest known, and first Gondwanan, fossil of the family Mimetidae.

Materials and Methods

The spider is preserved in a piece of yellowish Indian amber of the following dimensions: 9 × 5 × 4 mm, and is held in the collections of the American Museum of Natural History, New York (repository number Tad-52), but will eventually be deposited in the Birbal Sahni Institute for Palaeobotany, Lucknow. The body and legs have been slightly distorted through compression, and the amber contains air bubbles and other impurities which hinder a clear view from certain angles and prohibit accurate measurements. It originates from the Tadkeshwar lignite mine, Cambay Formation, Vastan, Gujarat. Prior to receipt by the authors the specimen had been prepared by embedding in synthetic resin following the technique of Nascimbene & Silverstein (2000).

The recent application of high-resolution computed tomography to amber spider inclusions has produced remarkable results (Dierick *et al*. 2007; Penney *et al*. 2007, 2011, 2012; McNeil *et al*. 2010; Dunlop *et al*. 2011, 2012), providing a non-destructive tool for the investigation of preserved specimens through three-dimensional digital dissection. However, in our experience, some amber inclusions produce much better results than others, and it is currently unclear why this is so. In this case the technique has been used to reveal characters that were difficult to visualize using traditional microscopy. Two scans were carried

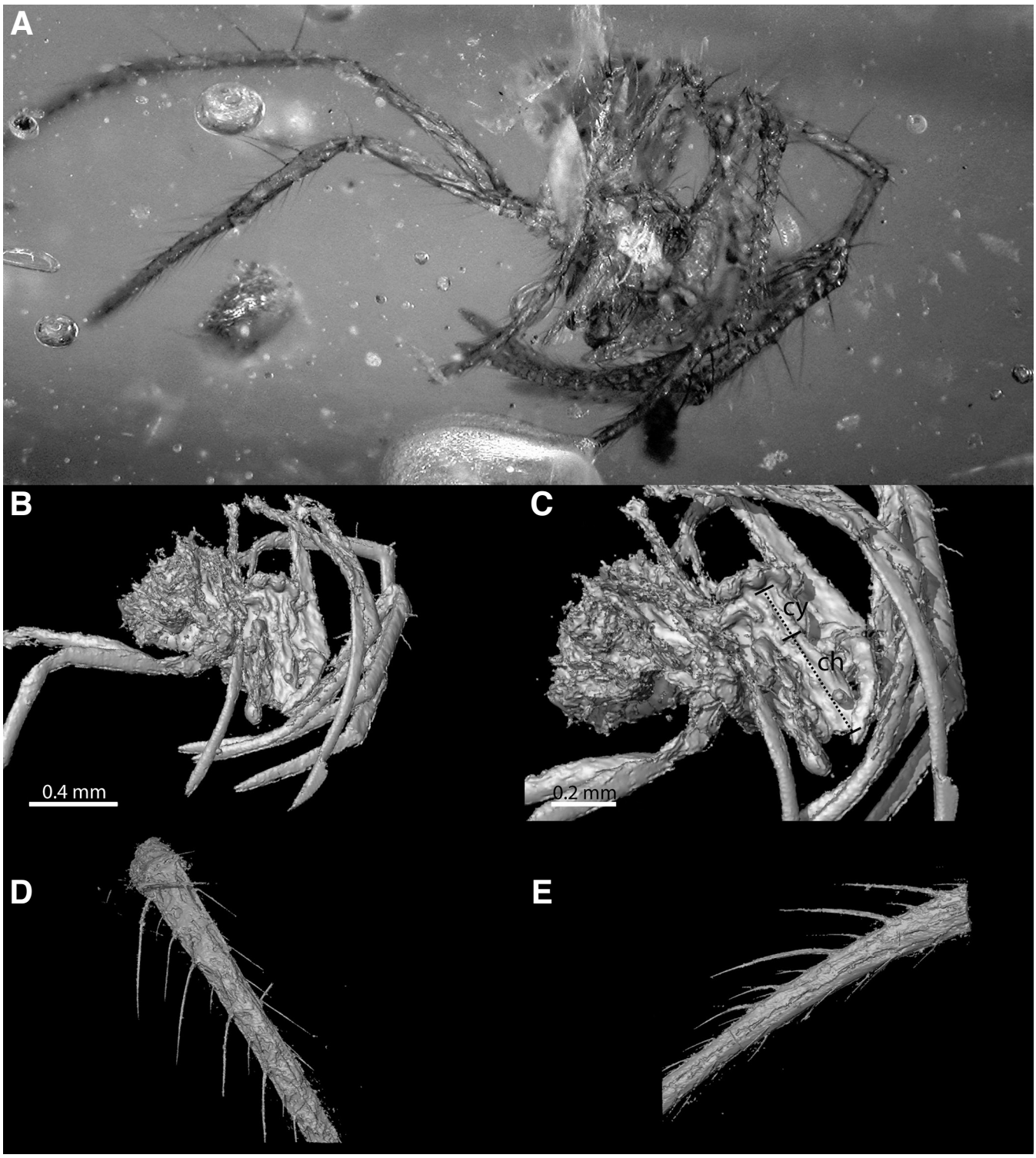

Fig. 1: Mimetidae in Eocene amber from the Cambay deposits of India. **A** microphotograph; **B–E** computed tomography reconstructions; **B–C** whole specimen; **D–E** right leg 1 metatarsus showing diagnostic spine pattern unique to the family Mimetidae; ch = chelicera, cy = clypeus.

out at the University of Manchester's Henry Moseley X-ray Imaging Facility using the Xradia MicroXCT system, which consists of a 10 W tungsten target microfocus X-ray source, a 2000 × 2000 pixel detector, and a 180° sample rotation stage. It has been shown that, in many cases, traditional attenuation-based X-ray CT is unable to accurately resolve fine anatomical features (McNeil *et al*. 2010), thus additional propagation-based phase contrast was generated by placing the detector an appropriate distance from the specimen. The low magnification scan (Fig. 1B–C) was acquired using the 4× optical magnification setting and comprises 2081 projections acquired at 40 kV, with a pixel size equivalent to 2.4 µm. The second region-of-interest scan of the legs (Fig. 1D–E) employed the 40× optics and was acquired at 100 kV with a pixel size of 0.57 µm, and a total of 1301 projections. Tomographic reconstruction was carried out using the TXMReconstructor software by Xradia, with each slice exported as a 16-bit TIFF image and imported into Avizo 6.3 for visualization. Segmentation was performed through simple thresholding of the phase fringes with the inherent

phase artefacts removed manually, along with surrounding air bubbles and other impurities. It is worth noting that prior embedding of the amber in synthetic resin did not affect the scan results, although the synthetic resin did discolour slightly, taking on a yellowish tinge.

The light photomicroscopy image was assembled from a stacked series of digital images recorded by a Nikon Coolpix 4500 camera mounted on a Leica M10 stereomicroscope with 0.63× and 1.6× planapochromatic objectives, following the combination technique described by Green (2005) and Betz & Green (2007). High-resolution images with low depth of field were recorded at appropriate intervals and combined to produce a single, high-resolution, high depth of field image using the pyramid stack function of the freeware program CombineZP. The final image was checked for artefacts to ensure faithful representation of the object under study.

Mimetidae Simon, 1881

Gen. & sp. indet. (Fig. 1)

Material. Juvenile specimen, AMNH Tad-52 (eventually to be deposited in the Birbal Sahni Institute for Palaeobotany, 53 University Road, Lucknow 226007, India). Indian amber, Cambay Shale of Gujarat State; Eocene (Ypresian).

Description. Body length approximately 1 mm. This is a poorly preserved specimen and little can be said of it other than it has the typical mimetid features. The prosoma is raised in the ocular region and appears to have eight eyes arranged typical for the family with the anterior medians largest. It has long chelicerae and a high clypeus with a ratio of 2:1 (Fig. 1C). The abdomen, although heavily denatured, does not show any evidence of having borne the humps characteristic of many mimetids; the spinnerets are short and unmodified. The legs are long and slender (Fig. 1A–C), with a formula of 1243, and possess the family-diagnostic spination pattern consisting of a single row of long prolateral spines interspersed with shorter spines on the metatarsi and tibiae of the first two pairs of legs (Fig. 1D–E). Each patella has a dorsal distal spine; the tibia of leg 3 has one proximal dorsal spine, whereas those of legs 1, 2 and 4 have a proximal and a distal spine.

Discussion

The leg spination pattern clearly places this fossil in the family Mimetidae. It represents the oldest known fossil of the family, extending its known geological range by approximately 3–8 million years, from the previously oldest known fossils in Eocene Baltic and Rovno ambers (Wunderlich 2004, 2012; Harms & Dunlop 2009). The taxonomy and systematics (in terms of interfamilial relationships) of this family are unclear. Most of the extant genera are in need of taxonomic revision. Brignoli (1979) suggested that once the genera of the Mimetidae had been revised, many of the described *Mimetus* and *Ero* C. L. Koch, 1836 species would have to be transferred to other genera, due to the morphology of their genitalia being significantly dissimilar from the type species, and concluded that *Mimetus* was a ". . . dump-heap of unrelated species" (Brignoli 1984, p. 201). These genera have not yet been revised.

Fossil pirate spiders were revised by Harms & Dunlop (2009), who recognized six species in two common and widespread extant genera: *Ero carboneana* Petrunkevitch, 1942, *E. longitarsus* (Wunderlich, 2004), *E. permunda* Petrunkevitch, 1942, all preserved in Eocene Baltic amber; *E. rovnoensis* (Wunderlich, 2004) from Eocene Ukranian (Rovno) amber; *Mimetus longipes* Wunderlich, 2004 from Baltic amber and *M. bituberculatus* Wunderlich, 1988 from Miocene Dominican amber (see additional comments in Penney 2008). Wunderlich (2012) disagreed with some of the taxonomic changes proposed by Harms & Dunlop (2009), removing *Mimetus brevipes* Wunderlich, 2004 from synonymy with *M. longipes*, treating *Ero aberrans* Petrunkevitch, 1958 as a valid species, and described three new species of *Ero* from Baltic amber. He provided a key to the eight fossil *Ero* species, considering his previously erected fossil genera (synonymized with *Ero* by Harms & Dunlop, 2009) as subgenera of *Ero*.

It can be expected that the fossil amber species will need to be reassigned to new genera following revision of the extant fauna, but the state of preservation and juvenile nature of the Indian specimen described here prohibits identification beyond the family level. Nonetheless, it is important as the oldest known fossil of the family and also as the first Gondwanan fossil record of pirate spiders.

Acknowledgements

Dmitri Logunov (Manchester Museum) is thanked for access to resources and we are grateful to Chris Martin for X-ray imaging support. David Grimaldi (American Museum of Natural History) is thanked for providing the amber. Danilo Harms and an anonymous reviewer are thanked for comments. DP acknowledges financial support from Siri Scientific Press. The financial support of EPSRC under grants EP/F028431 and EP/F007906 is acknowledged.

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