A spider fossil from the Jurassic Talbragar Fossil Fish Bed of New South Wales

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The oldest fossil spider from Australia is described as *Talbragaraneus jurassicus* gen. et sp. nov., from the Jurassic Talbragar Fossil Fish Bed of central New South Wales. Though rather poorly preserved, the single juvenile or female specimen has an excavated, laterally compressed dorsal side to the fourth metatarsus, reminiscent of members of the extant family Uloboridae, to which the fossil is tentatively referred.

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THE Jurassic Talbragar Fossil Fish Bed, renowned for its eponymous vertebrate fossils (Woodward 1895), also yields many other animals and plants. Here, we report the first fossil spider from this locality. It is the oldest fossil spider from Australia; three other occurrences have been mentioned in the literature: one specimen from the Cretaceous Koonwarra Fossil Bed in Victoria (Jell & Duncan 1986), one from Pliocene copal in Victoria (Hickman 1957), and spiders are known, but not yet described, from Cenozoic Cape York amber, Queensland (Bickel 2009).

Fossil spiders in rock are rare (Selden & Penney 2010, Penney & Selden 2011), Jurassic specimens particularly so, and confined to Fossil-Lagerstätten. The first to be described was a single adult male specimen of an araneoid, *Juraraneus rasnitsyni* Eskov, 1984, from the Middle Jurassic Ichetuy Formation of Transbaikalia (redescribed by Selden 2012). Also in 1984, the first spider from the Middle Jurassic Jiulongshan Formation of China was described as *Mesarania hebeiensis* Hong, 1984, and placed in Araneoidea (more likely, it is one of the common but as yet undescribed cribellates from the Jiulongshan Formation, but the description and illustration are insufficient and the holotype specimen is lost). Eskov described a single specimen of a female archaeid, *Jurarchaea zherikhini* Eskov, 1987, from the Upper Jurassic Karabastau Formation of Kazakhstan. An undescribed single specimen from the Early Jurassic (Lower Toarcian) of Grimmen, Germany, was illustrated by Ansorge (2003). More recently, many more specimens have emerged from the Middle Jurassic Jiulongshan Formation of China (Selden *et al*. 2008, 2011, Selden & Huang 2010). The fossil described here is not well preserved but shows a distinctive curvature of the fourth metatarsus, which indicates it is possibly a member of the extant family Uloboridae.

Material and methods

Geological setting

Background. The Talbragar Fossil Fish Bed is situated north of Gulgong in central New South Wales. The Fish Bed occupies an area of approximately 4 ha on the gentle slopes of a hill paddock on private land and was thought to have been worked out until recently when, in 2006, Lynne Bean, a postgraduate student at the Australian National University (Canberra, Australia), organized an excavation at the site to collect fossil fish. The southern end of the deposit was found to be relatively rich in insect remains, and since then, numerous small-scale field excavations were carried out at the locality between 2006 and 2012 (Beattie & Avery 2012). Most of the Fish Bed site lies in a reserve administered by the National Parks and Wildlife Office at Mudgee, New South Wales.

Stratigraphy. The Fish Bed, correlated with part of the Purlawaugh Formation of the adjacent Surat Basin, appears to have formed as a lake infilling a depression in underlying Hawkesbury Sandstone, which is of Middle Triassic age. The first geological report of the Talbragar Fossil Fish Bed was by Woodward (1895) and included a locality map, geological map and sec-

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tions. A detailed investigation was subsequently carried out by Dulhunty & Eadie (1969), who revealed that the Fish Bed was highly eroded and faulted, probably representing only a small remnant of its original extent. Further investigations by Bean (2006) revealed that the Fish Bed has a largely tuffaceous composition, and more recent analysis of zircon crystals from the unit has provided an age of latest Oxfordian–Tithonian (Late Jurassic) age (Turner *et al*. 2009).

Fauna and flora. Diverse fossil fish have been described from the Talbragar site, including teleosts and rare chondrichthyans (Woodward 1895, Wade 1941, Bean 2006, Turner *et al*. 2009). The most commonly recovered fish species is the small leptolepid teleost *Cavenderichthys talbragarensis* (Beattie & Avery 2012). Until recently, only one insect had been described from the Talbragar Fossil Fish Bed, *Griphologus lowei* Etheridge & Olliff, 1890. Steven Avery, an amateur fossil collector, found several fossil insects at the northern end of the reserve during the 1990s (Beattie 2007), and subsequent exploration of the southern area between 2006 and 2011 yielded numerous additional insect specimens. The entomofauna is dominated by Hemiptera (>50%), followed by Coleoptera (<20%), then <5% each of Orthoptera, Diptera, Plecoptera, Mecoptera, Odonata (Beattie & Nel 2012), Neuroptera and Hymenoptera (Beattie & Avery 2012, table 2). Most recently, a specimen of Raphidioptera has also been identified (A. Ponomarenko, pers. com. 2012).

Terrestrial plants in the Talbragar Fossil Fish Bed include several families of conifers, a pentoxylalean gymnosperm, probable corystosperms, several true ferns, and other as yet unidentified plants (Walkom 1921, White 1981, McLoughlin 2007, Turner *et al*. 2009). Aquatic plants are represented by putative macroalgal remains. Lesser known and undescribed fossils include bivalves, an aquatic gastropod, fish coprolites and burrows (Beattie & Avery 2012).

Taphonomy and palaeoenvironment. The fossils are preserved in a tuffaceous siltstone with abundant opaline silica, and most of the matrix is stained rusty red by weathering, the original rock being grey in colour (Bean 2006). The depositional environment is interpreted to have involved a lahar that invaded a lake, which was subsequently covered by a blanket of ash (Beattie & Avery 2012). In this respect, the environment of deposition rather resembles that of the Eocene Florissant Fossil-Lagerstätte (Meyer 2003). Bean (2006) discussed the evidence of dorsal flexion of the smaller fish, and their open mouths, possibly caused by anoxia: mass mortality by seasonal temperature changes or, more likely in the volcanic context, due to ash fall. It is noteworthy that most other non-amber Lagerstätten bearing spider fossils are lacustrine, and many are tuffaceous, examples being Florissant (mentioned above) and the Jurassic beds at Daohugou, China (Ren *et al*. 2002). Fossil spiders occurring together with fish mass mortalities include those from the Cretaceous Koonwarra Fossil Bed of Victoria (Jell & Duncan 1986), the Crato Formation of Brazil (Selden *et al*. 2006), the Jinju Formation of Korea (Selden *et al*. 2012) and the Yixian Formation of China (Pan *et al*. 2012).

The spider fossil. The spider (Figs 1–3) was collected during a field trip in May 2009 by Steven Avery, at the southern end of the reserve. It is preserved in a block of rusty red tuffaceous siltstone, showing Liesegang rings produced by weathering, typical of the fish bed sediments. Parts of the fossil are replaced with a white mineral, which also occurs abundantly as spherules within the rock; this is presumably opaline silica (Bean 2006). The legs are fairly well preserved; at least femur to tarsus is known for all legs. The external moulds show coarse setation in low-angle light (Fig. 3A), which suggests thicker, plumose setae rather than simple, so-called serrate setae (Lehtinen 1967, figs 8–10). Internal moulds, by their nature, show no sculpture. The peculiar preservation reveals general setation on the legs yet, oddly, no macrosetae are visible; a similar condition to that prevailing in a Cretaceous spider from Korea (Selden *et al*. 2012). The pedipalp is preserved as a single podomere, possibly the tarsus; if this specimen were an adult male, then it would be expected to show the swollen tarsus, so the specimen is either a juvenile or an adult female. The carapace is represented by a plate, the edges of which are broken so that its outline can not be determined. There are no characteristic features preserved on the plate, which is rather contorted. The opisthosoma is poorly preserved; a sliver of opaline quartz could represent the flattened internal mould of the opisthosoma, in which case it would have been very wide (Figs 1–2).

Methods. The specimen was studied and photographed dry using Leica MZ series stereomicroscopes and photographed with Canon EOS 5D MkII and MkIII cameras mounted on the microscopes. Drawings were made using Adobe Illustrator from the photographs (and constant checking back to the specimen). Abbreviations: 1 2 3 4, leg numbers; car, carapace; fe, femur; mt, metatarsus; pa, patella; Pd, pedipalp; ta, tarsus; ti, tibia. All measurements are in mm.

Systematic palaeontology

Order ARANEAE Clerck, 1757
Suborder OPISTHOTHELAE Pocock, 1892
Infraorder ARANEOMORPHAE Smith, 1902
?Family ULOBORIDAE Thorell, 1869

Remarks. There is little evidence as to the familial identity of this fossil spider. However, there is one characteristic feature: the fourth metatarsus is laterally

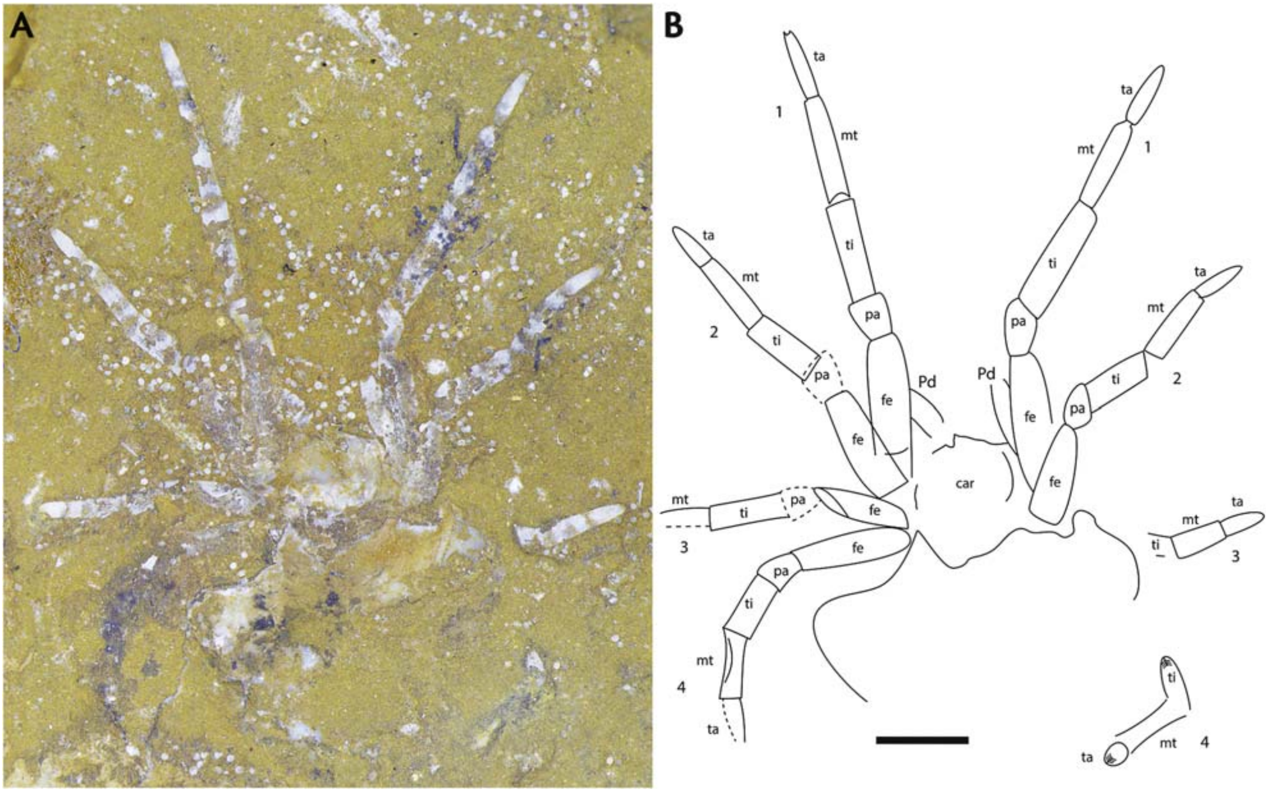

Fig. 1. Talbragaraneus jurassicus gen. et sp. nov., holotype F.136332, part. A, Photograph. B, explanatory drawing. Scale bar = 1 mm.

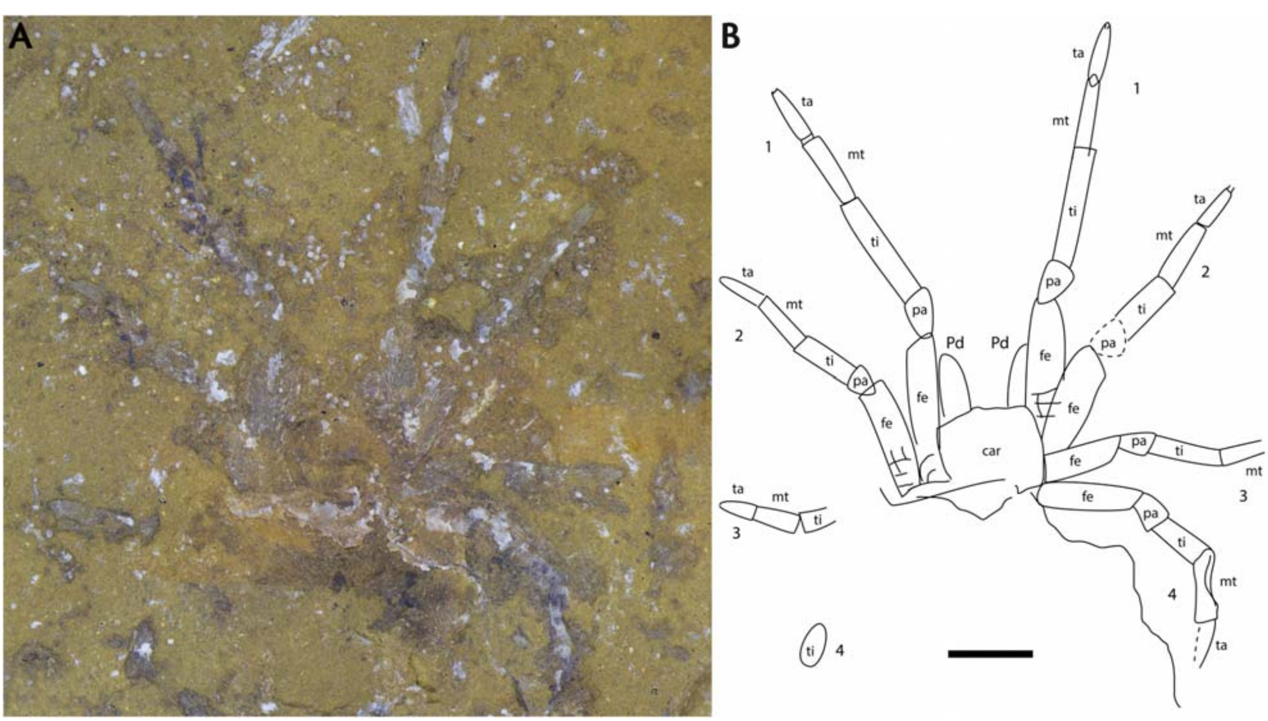

Fig. 2. Talbragaraneus jurassicus gen. et sp. nov., holotype F.136332, counterpart. A, Photograph. B, explanatory drawing. Scale bar = 1 mm.

compressed dorsally and bears an inwardly curved ridge, which presumably bore a calamistrum (Fig. 3B, C); this is a distinctive feature of members of the family Uloboridae (Opell 1979). Although not cited as a synapomorphy for the family, it does not, to our knowledge, occur in any other family. In the uloborid sister group, Deinopidae, the fourth metatarsus is laterally compressed dorsally, but the calamistrum is not inwardly curved (Peters 1992, fig. 8d; Coddington *et al*. 2012, fig. 5e). In addition, the setae are likely to

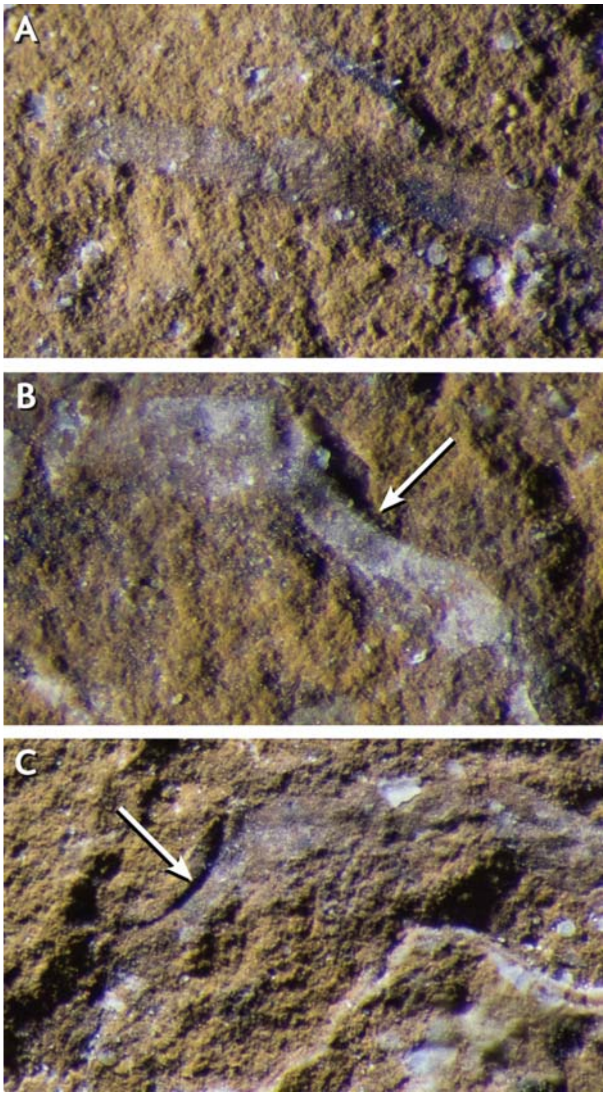

Fig. 3. Talbragaraneus jurassicus gen. et sp. nov., holotype F.136332, detailed morphology. A, Counterpart left leg 1 metatarsus and tarsus (distal to left), in low-angle light to illustrate coarse setation. B, Counterpart right leg 4 tibia and metatarsus, preserved as internal mould, showing laterally compressed dorsal side of metatarsus with inwardly curved ridge (arrowed) bearing calamistrum. C, Part left leg 4 tibia and metatarsus (i.e., same leg as in B), preserved as external mould, showing laterally compressed dorsal side of metatarsus with inwardly curved ridge (arrowed) bearing calamistrum.

be plumose, another character of this group of spiders. For this reason, the spider is tentatively assigned to the Uloboridae. The new genus is unusual among uloborids in that the calamistrum runs almost the full length of the metatarsus, rather than being confined to the proximal part, as in most extant uloborids (Opell 1979). Uloborids are known from the Cretaceous (Selden 1989, 1990, Selden & Penney 2003, Wunderlich 2008, 2011) and the Cenozoic (Dunlop *et al*. 2012), and very similar cribellate spiders (possibly uloborids) are the most abundant but as yet undescribed spiders in the Jurassic of Daohugou, Inner Mongolia, China (PAS pers. obs.).

Talbragaraneus gen. nov.

Type species. *Talbragaraneus jurassicus* sp. nov.

Etymology. Named after the type locality Talbragar, and araneus, the Latin word for spider.

Diagnosis. Spider with coarse (probably plumose) setae; calamistrum on distinct, inwardly curved ridge on fourth metatarsus, which is dorsally laterally compressed; calamistrum runs almost full length of the metatarsus.

Talbragaraneus jurassicus sp. nov. (Figs 1–3)

2012 Spider; Beattie & Avery, fig. 9D.

Etymology. Named after the Jurassic age of the fossil.

Holotype. F.136332, Australian Museum, Sydney.

Type stratum and locality. Talbragar Fossil Fish Bed, Late Jurassic (latest Oxfordian–Tithonian: 151 ± 4 mya); near Gulgong, New South Wales, Australia (32° 10.03′S 149°41.07′E).

Diagnosis. As for the genus.

Description. Female or juvenile. Carapace length >1.01, no distinguishing features. Pedipalp: visible podomere (ta?) length 0.77. Leg formula (longest to shortest): 1243. Podomere lengths: Leg 1 fe 1.45, pa 0.50, ti 1.27, mt 0.96, ta 0.73, total (fe–ta) 4.91; Leg 2 fe 1.20, pa 0.40, ti 0.74, mt 0.78, ta 0.56, total (fe–ta) 3.67; Leg 3 fe 0.98, pa 0.39, ti 0.82, mt 0.54, ta 0.45, total (fe–ta) 3.18; Leg 4 fe 1.20, pa 0.39, ti 0.64, mt 0.74, ta 0.53, total (fe–ta) 3.50. Podomeres covered in dense, coarse setation (therefore likely to be plumose rather than simple, serrate setae; Fig. 3A). Fourth metatarsus laterally compressed dorsally bearing an inwardly curved ridge along most of its length (Fig. 3B, C); this ridge is presumed to have carried a calamistrum. Calamistrum runs nearly full length of metatarsus. Opisthosomal features unknown.

Discussion

Uloborids are cribellate spiders; that is, they bear a cribellum (a plate bearing minute silk spigots, modified from a pair of spinnerets, which produces extremely fine silk) and a calamistrum (a comb of stiff, commonly curved, bristles on the dorsal side of the fourth metatarsus). The calamistrum is used to comb the fine silk exuded from the cribellum over core fibres produced from the posterior spinnerets. The resultant cribellate silk is woolly in appearance but dry; it entangles insects in much the same way as burrs become caught in sheep wool. Unlike all other cribellate spiders, most uloborids weave orb webs and the cribellate silk forms the capture spiral. Other, ecribellate, orb weavers make a capture spiral from sticky silk made from core fibres covered in glue droplets. Last century, a debate raged as to whether the orb web evolved more than once (in cribellates and ecribellates), or whether it appeared only once (in cribellates) and viscid silk evolved later within the orb weavers (see Shear 1986 for an excellent review). It is now apparent that the latter scenario is correct. Uloborids, together with deinopids, form the sister group to all other orb weavers within the Orbiculariae (e.g., Blackledge *et al*. 2009, Dimitrov *et al*. 2012). At some point, viscid silk production evolved, making the cribellate system redundant. Uloborids are rather unusual spiders in that they produce no venom; instead, they wrap their prey swiftly in silk to subdue it.

If *Talbragaraneus jurassicus* is, indeed, a uloborid, then it is the oldest one recorded to date. A Late Jurassic age for uloborids is not unexpected because, first, molecular phylogenetic studies indicate that orb weavers first appeared in the Triassic (Dimitrov *et al*. 2012), and second, likely, but as yet undescribed, uloborids are common in the Middle Jurassic beds at Daohugou, China (PAS pers. obs.). Orb webs are built to intercept prey flying through gaps in vegetation. The fauna and flora associated with *Talbragaraneus* indicate that there was abundant arborescent and herbaceous vegetation and insect prey at the lake margin at Talbragar, which is also a habitat commonly frequented by uloborids and other orb weavers today. One can imagine *Talbragaraneus* weaving its orb web in vegetation at the lake edge to capture the abundant insect prey there. However, much of this supposition relies on rather scant evidence as to the identity of the spider and it is to be hoped that further specimens will come to light during future excavations, which will provide more evidence of the Jurassic araneofauna of Talbragar.

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