A redescription of *Jurararaneus rasnitsyni* Eskov, 1984 (Araneae: Jurararaneidae), from the Jurassic of Russia

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Summary

The holotype and only known specimen of *Jurararaneus rasnitsyni* Eskov, 1984, the first spider to be described from Jurassic strata, is redescribed and re-illustrated using modern photographic techniques. *Jurararaneus* is shown to be a cribellate araneoid, and thus forms part of the cribellate stem-group orbweavers which pre-dated the ecribellate araneoids found today.

Introduction

Jurassic spiders are very rare, and are important because the early Mesozoic was a time when many modern spider families are thought to have originated and diversified (e.g. Dimitrov *et al*. 2012). No amber deposits with fossil spider inclusions are known from strata older than the early Cretaceous (Selden & Penney 2010), so earlier records are from rock-matrix preservation. The first spider to be described from rocks of Jurassic age was *Jurararaneus rasnitsyni* Eskov, 1984, which consists of a single specimen from the Upper Jurassic Ichetuy Formation of Transbaikalia (Eskov 1984) (Fig. 1). Eskov placed the spider into a monotypic family, Jurararaneidae Eskov, 1984, within the superfamily Araneoidea Latreille, 1806, on account of it showing a unique mosaic of characters also found in other araneoid families.

Few other Jurassic spiders have been described to date. 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 (1987) 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; Selden & Huang 2010; Selden *et al*. 2011).

Studies of Jurassic spiders from China (e.g. Selden *et al*. 2011), have indicated that most orbicularians from that period were cribellate, so it was decided to re-examine *Jurararaneus* for this and other possible plesiomorphic features. Lo and behold, *Jurararaneus* does, indeed, possess a calamistrum (Figs. 1–3). This paper presents a new description of the specimen, with new illustrations, and a brief discussion on the loss of the cribellate condition in Mesozoic araneoid spiders.

Material and Methods

Jurararaneus rasnitsyni Eskov, 1984 comes from the Ichetuy Formation of the Tugnuy river valley near Novospasskoye village, Transbaikalia, Siberia, of Upper Jurassic (Oxfordian) age (Metelkin *et al*. 2007). The Ichetuy Formation is a thick volcanic sequence interbedded with mudstones containing rich, well-preserved remains of conchostracans and insects. The fossiliferous beds of the Ichetuy Formation were probably deposited in lakes in a mountain region (Eskov 1984). The holotype and only known specimen consists of part and counterpart (the latter poorly preserved) and is preserved as fragments of organic material in a mudstone matrix. The specimen is partly buried within the mudstone matrix and needles have been used to remove the matrix where this covers important parts of the specimen (circular pits in Fig. 1). However, in some places, thin mudstone still covers parts of the specimen, which can be seen through the translucent matrix, e.g. next to the calamistrum in the leg 4 metatarsus (Figs. 3A; 4A), or matrix has been broken away, e.g. parts of the left palp cymbium (Figs. 5–6). The Ichetuy Formation is highly fossiliferous with insects (Rasnitsyn & Zherikhin 2002) but, to date, no other spiders have been found in these strata.

The specimen was studied, drawn, and photographed using Leica MZ12.5 and MZ16 stereomicroscopes and Canon 5D MkII and MkIII cameras, both dry in low-angle light, and under 70% ethanol and/or in polarized light to enhance contrast of the organic material within the mudstone matrix. Final illustrations were prepared using Adobe Photoshop CS6 Extended, Illustrator CS6, and InDesign CS6. All measurements are in millimetres and were made from the photographs using Photoshop. Leg formula is from longest shortest; leg lengths are given as femur–tarsus only. Abbreviations: a t, anal tubercle; ca, calamistrum; car, carapace; ch, chelicera; cr, cribellum; cy, cymbium; cx, coxa; fe, femur; L, length; m, maxilla; mt, metatarsus; op, opisthosoma; pa, patella; Pd, pedipalp; st, sternum; ta, tarsus; ti, tibia; W, width.

Results

The basic description and measurements given by Eskov (1984) are largely corroborated, but differences in detailed interpretation of structures and previously overlooked morphology result in rather different phylogenetic conclusions. As mentioned above, it was the discovery of a calamistrum that led to this redescription. The calamistrum was probably overlooked because, where it is best seen on the left side, a piece of matrix covers the leg and abuts against the calamistrum, partly concealing it (Figs. 3A; 4A). Moreover, the calamistrum bristles are rather short, and the whole structure could easily have been mistaken for aligned macrosetae. Also, the fossil presents a ventral view, so the calamistrum (on the dorsal side) is seen through the cuticle and setae of the ventral side of the metatarsus. On the right side, the calamistrum is faint, and partly destroyed by needle marks, but is nevertheless visible.

On the palp, Eskov (1984) saw details which are present in the fossil, but his interpretations differ from those

Fig. 1: *Jurararaneus rasnitsyni* Eskov, 1984. General view of part (PIN 3000/3000), from the Upper Jurassic (Oxfordian) Ichetuy Formation of Transbaikalia. See Fig. 2 for explanation.

presented here. On the left palp (Fig. 5) the matrix bearing part of the palp has been broken away, thus apparently separating it onto two sclerites, which were interpreted as such by Eskov (1984). The more proximal piece was interpreted as attached to a dark object slightly separated from the fossil in the nearby matrix, and thus as a complex paracymbium. In this analysis, the separate dark object appears to resemble other dark objects within the matrix and, because there is no trace of a paracymbium on the right palp, the dark object is considered not to be part of the fossil. The more distal piece is here interpreted at the tibia folded over. In fossils such as this, the darkness of the cuticle reflects its thickness, and so folded cuticle (i.e. double thickness) appears twice as dark as a single layer of cuticle. The thin, straight, styliform conductor of Eskov (1984) is here interpreted as the joint between the femur and patella. The most obvious part of both palps, as defined by many short setae, is the cymbium. That on the right is suboval, but the left one appears less distinct; nevertheless, numerous setae indicate its presence. Beneath the left cymbium, several structures can be seen (Figs. 5–6), but their identifications are not clear. Eskov (1984) identified these other parts of the palp as a complex median apophysis. While shapes can be seen, Eskov's interpretations cannot be verified. Nevertheless, his conclusion that the palp is complex, and thus belonging to the araneoids, a derived araneomorph clade, is logical.

Additional morphological structures not recognized by Eskov (1984) are the cluster of trichobothria in the basal part of the tibia; these are faint, and represented only by bothria, but seen at least on tibiae 3 and 4 (Fig. 4B). No

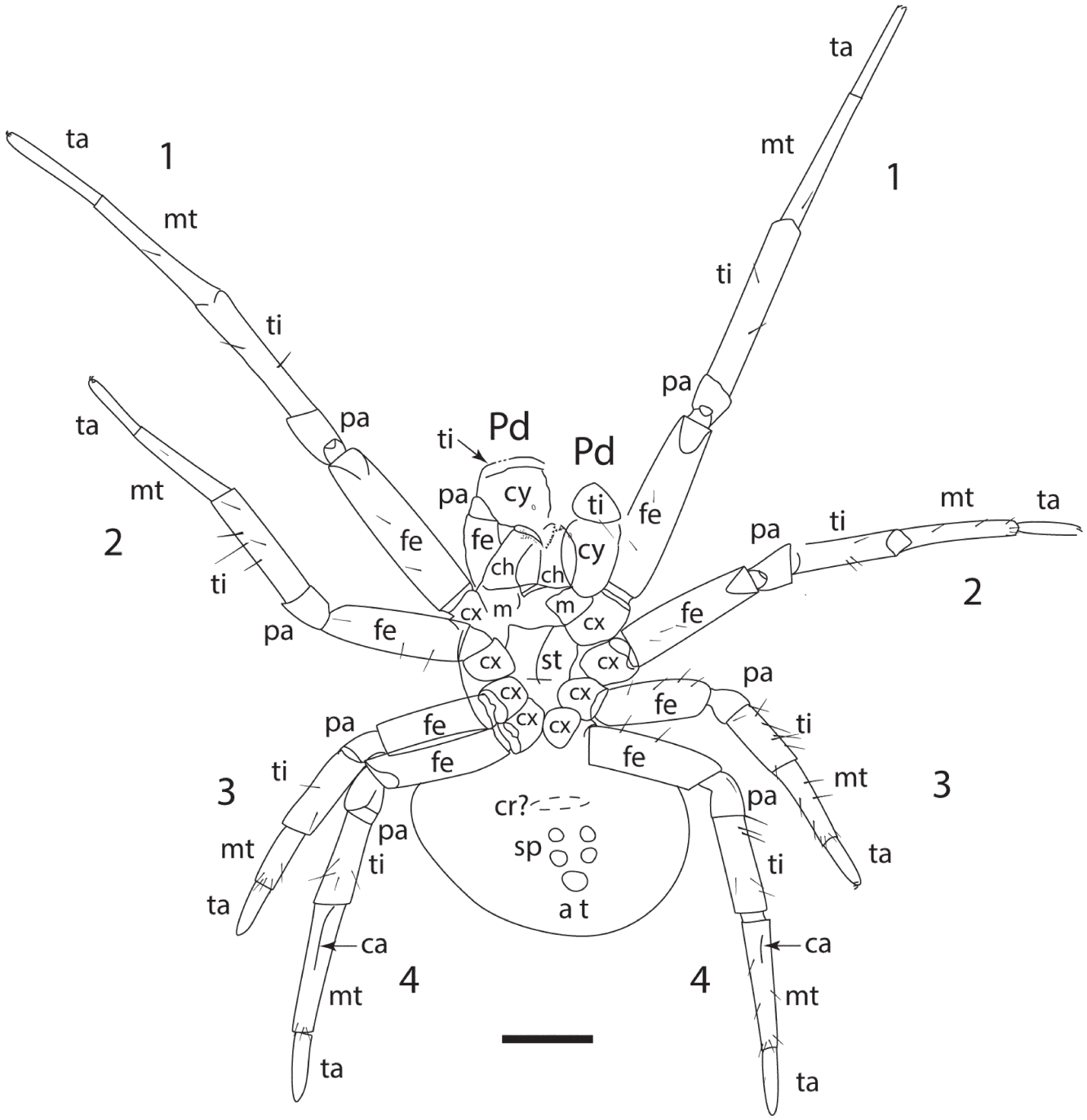

Fig. 2: *Juraraneus rasnitsyni* Eskov, 1984. Explanatory drawing of Fig. 1. Scale bar = 1 mm.

femoral trichobothria can be seen. There are three claws and accessory claws on the tarsi.

Araneoidea Latreille, 1806

Juraraneidae Eskov, 1984

Emended diagnosis: Cribellate araneoid spiders resembling Araneidae; of normal proportions of araneids; opisthosoma wider than long; sternum subtriangular, straight anterior border; labium wider than long; chelicera stout, not porrect; male palp short, complex; leg formula 1243; trichobothria on at least ti3&4; calamistrum composed of single row of short, curved bristles in proximal half of mt4.

***Juraraneus* Eskov, 1984**

Diagnosis: As for the family.

***Juraraneus rasnitsyni* Eskov, 1984** (Figs. 1–6)

Type material: Holotype ♂, only known specimen, PIN 3000/3000 (part and counterpart) in the Paleontological Institute of the Russian Academy of Sciences, Moscow, from the Upper Jurassic (Oxfordian) Ichetuy Formation of the Tugnuy river valley near Novospasskoye village, Transbaikalia, Siberia.

Description: Cuticular structures: serrate setae, no plumose or feathery setae; generally thin, rather sparse

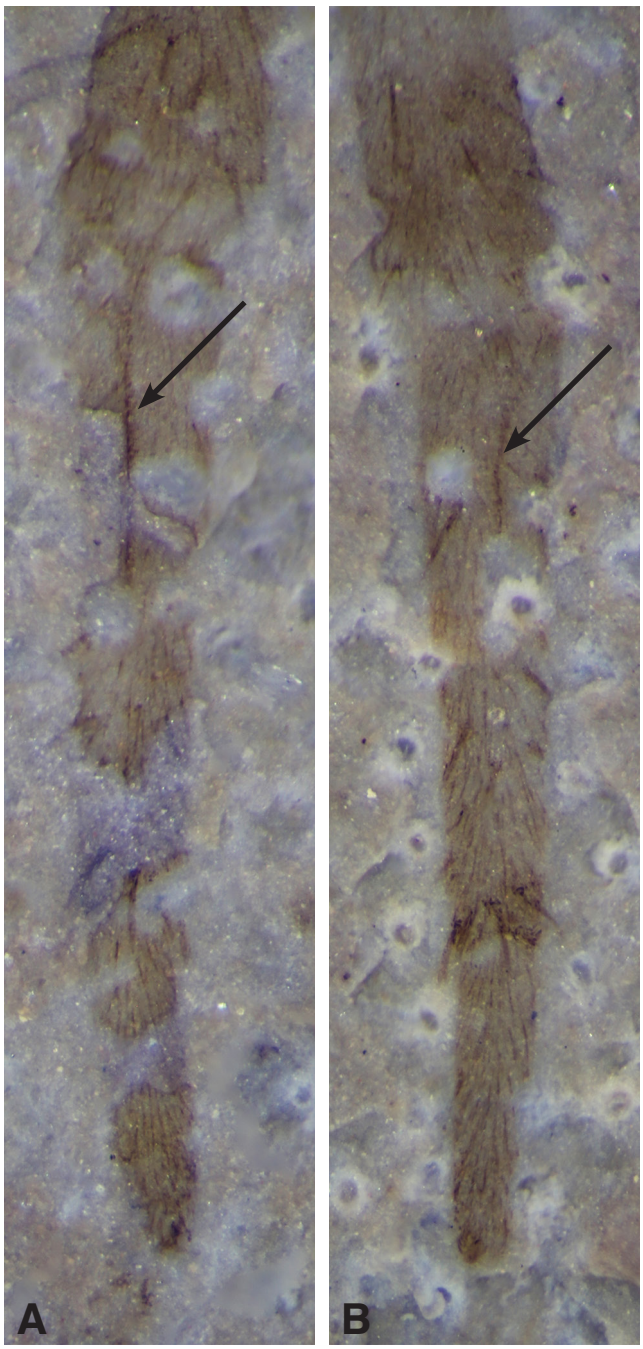

Fig. 3: *Jurararaneus rasnitsyni* Eskov, 1984. **A** left leg 4 mt & ta, showing calamistrum (arrow) in proximal half of mt; **B** right leg 4 mt & ta, showing calamistrum (arrow) in proximal half of mt.

macrosetae on all post-trochanteral podomeres except tarsi, stronger and more numerous on tibiae and at distal edge of metatarsi (Figs. 1, 3, 4C). Cluster of trichobothria in basal half of at least tibiae 3 & 4 (Fig. 4B).

Carapace not well visible, but appears to be suboval, longer than wide. Sternum subtriangular, gently scalloped lateral margins, anterior margin straight; labium outline not clear but would be wider than long. Chelicerae short and stout, subconical, curved fang, many triangular denticles along cheliceral furrow. Pedipalp (Figs. 4–5) short, complex. Legs not especially long/slender nor short/stout; tarsi with 3 claws and accessory claws. Calamistrum composed of very short, curved bristles, in proximal half of mt4, mostly straight, curving gently proximally (Figs. 3A,B; 4A). Opisthosoma wider than long, with subterminal anal tubercle, spinnerets and ?cribellum (Fig. 1).

Measurements: car L ~2.04, W ~1.80; st L 0.99, W 0.75; ch L 0.73, W 0.63, L/W ratio 1.16, fang L 0.40; Pd fe ≥0.79, ti 0.50, cy 0.93; leg formula 1243; leg 1 fe 2.02, pa 0.60, ti 1.81, mt 1.63, ta 1.20, total 7.26; leg 2 fe 1.53, pa 0.48, ti 1.30, mt 1.30, ta 0.75, total 5.36; leg 3 fe 1.23, pa 0.40, ti 0.90, mt 0.85, ta 0.62, total 4.00; leg 4 fe 1.40, pa 0.49, ti 1.10, mt 1.46, ta 0.75, total 5.20; op L ~2.43, W 3.10, L/W ratio 0.78.

Discussion

Phylogenetic placement. Eskov placed *Jurararaneus* into a monotypic family, Jurararaneidae, in Araneoidea because he considered it to show a unique mosaic of characters, mostly palpal, also found in other araneoid families. Ignoring the palpal morphology of the fossils, here considered to be unverifiable, other features would also place the spider into Araneoidea. Most araneoid synapomorphies relate to the silk glands, spinning apparatus, and web behaviours (e.g. Griswold *et al*. 1998; Kuntner *et al.* 2008), all of which are difficult or impossible to see in Jurassic fossils. However, a number of features of *Jurararaneus* are suggestive of the superfamily. First, the fossil lacks distinctive synapomorphies of most other families; most identification keys to spider family work by dismissing distinctive characters

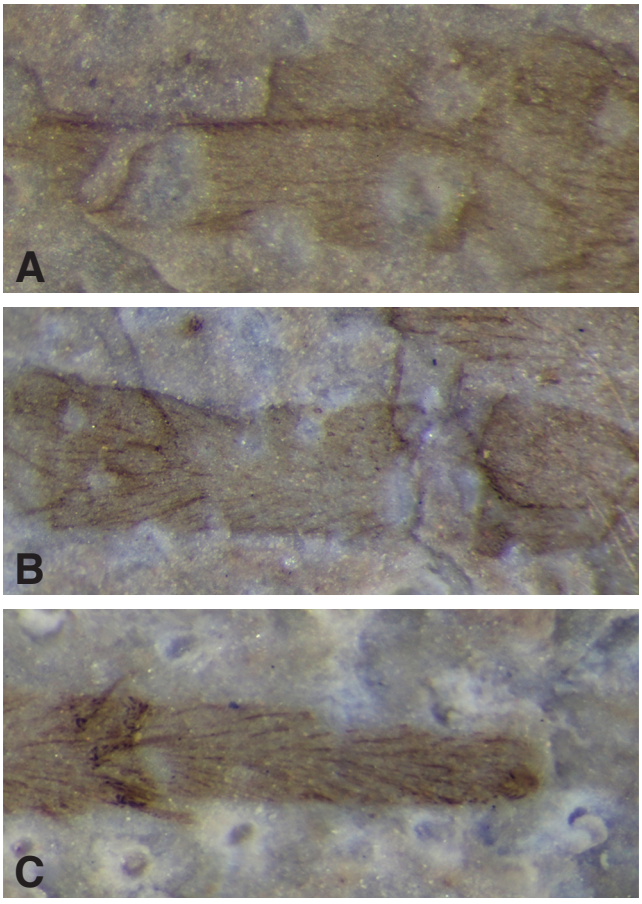

Fig. 4: *Jurararaneus rasnitsyni* Eskov, 1984. **A** left leg 4 mt calamistrum, detail of bristles, distal to left; **B** left leg 4 ti showing trichobothrial bases in proximal half, distal to left; **C** right leg 4 distal mt + ta showing macrosetae, distal to right.

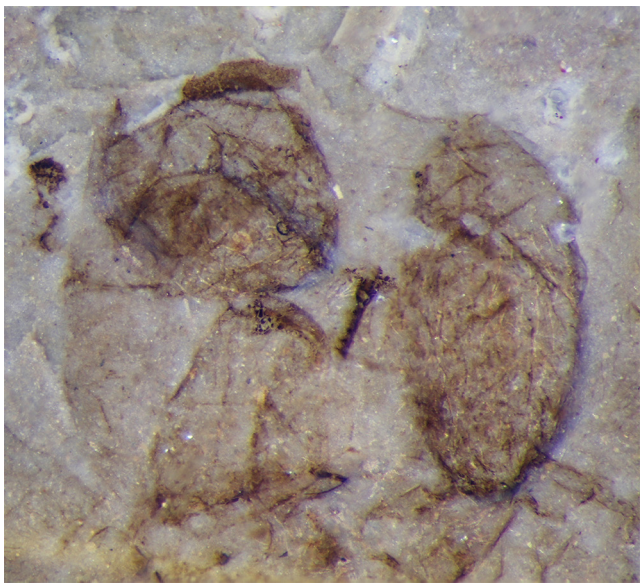

Fig. 5: *Jurararaneus rasnitsyni* Eskov, 1984. Chelicerae and pedipalps; for interpretation see Fig. 6.

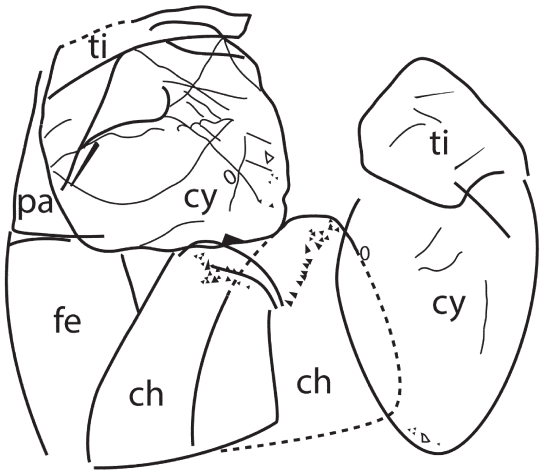

Fig. 6: *Jurararaneus rasnitsyni* Eskov, 1984. Camera lucida drawing of chelicerae and pedipalps; interpretation of Fig. 5.

first, and the araneoids are thus normally the last group to key out. Second, no feature of *Jurararaneus* (apart from the cribellum and calamistrum, discussed below) cannot be found in araneoids. Third, features commonly found in araneoids and *Jurararaneus* include the three-clawed tarsus with accessory claws; tibial trichobothria; a complex palp; undistinguished size, shape and leg length; opisthosoma wider than long (common in male araneids, for example); and sparse, slender macrosetae on all post-trochanteral podomeres except the tarsus. *Jurararaneus* is not a deinopoid because it lacks the distinctive plumose and feathery hairs and the femoral trichobothria of this superfamily. Uloborids (or close relatives of them) occur commonly in volcanic lacustrine rocks of Jurassic age in China and Kazakhstan (unpublished observations) and are distinctively different from *Jurararaneus*.

Wunderlich (1986) concluded that, from its habitus, the proportions of the legs, and the numerous and rather thick spines of the legs, he could not rule out the inclusion of *Jurararaneus* in Araneidae. (Note that I consider the macrosetae not to be particularly thick). Wunderlich also considered that the details of the palp are not sufficiently preserved, and that the supposed paracymbium could be an artifact. However, he did not synonymize the families. Araneidae is not an easy family to define, and unambiguous synapomorphies mentioned by Griswold *et al*. (1998) included: a mesal cymbium, radix in the embolic division of the male palp, tapetum of the posterior median eyes displaced towards the sagittal plane, and a sustentaculum on tarsus IV. These features cannot be confirmed in the fossil. I consider it best to retain the genus within its monotypic family pending the discovery of any more fossils which would provide additional evidence for placement in another araneoid family. However, its diagnosis, based on on symplesiomorphies, means that the family could be directly ancestral to the Araneidae, and so is shown as such in Fig. 7.

The cribellate problem. The discovery of a calamistrum on a supposed araneoid spider was clearly something of a surprise. Araneoids are informally recognized as the ecribellate orb-weavers but, as Coddington (2005, p. 23) has noted: "… the cribellum is primitive for Araneomorphae … araneoids or their ancestors must therefore have lost it …". Now, since *Jurararaneus rasnitsyni* is known to be cribellate, it seems that the ecribellate condition is characteristic of later araneoids. In Fig. 7, recent phylogenies of the Orbiculariae by Blackledge *et al*. (2009) and Dimitrov *et al*. (2012) are superimposed on the fossil record of orbweavers. In both cases, the cribellum and calamistrum must have been lost numerous times within the orbicularians: in the Nicodamidae and more than once in the araneoids.

Mode of life. Few features of this fossil spider can provide evidence as to its mode of life. Whilst it is clearly an orbicularian, this group of spiders includes sheet- and tangle-web weavers, and other weaving behaviours, in addition to makers of orb webs, so we cannot be certain that *Jurararaneus* constructed an orb. Many cribellate orbicularians (most Uloboridae) weave orb webs, but not all (Deinopidae, Nicodamidae); however, its position on the phylogenetic tree (Fig. 7) suggests that it likely built an orb web. Also of interest is that it appears to have a functional calamistrum yet is an adult male. Males of many cribellate species lose their cribellum and calamistrum, or they become vestigial, on reaching adulthood, when they no longer need to build webs but wander in search of a mate. The retention of an apparently functional calamistrum in *Jurararaneus* suggests either that the adult male of this spider continued to weave a capture web, or that the apparatus was retained into adulthood even though a web was no longer constructed: most likely a primitive character state. Whether the calamistrum was, indeed, functional, however, cannot be determined without evidence of functioning cribellum spigots.

Conclusions

In this restudy of the adult male Jurassic araneoid *Jurararaneus rasnitsyni* Eskov, 1984, the only specimen known of the monotypic family Jurararaneidae Eskov, 1984, it has

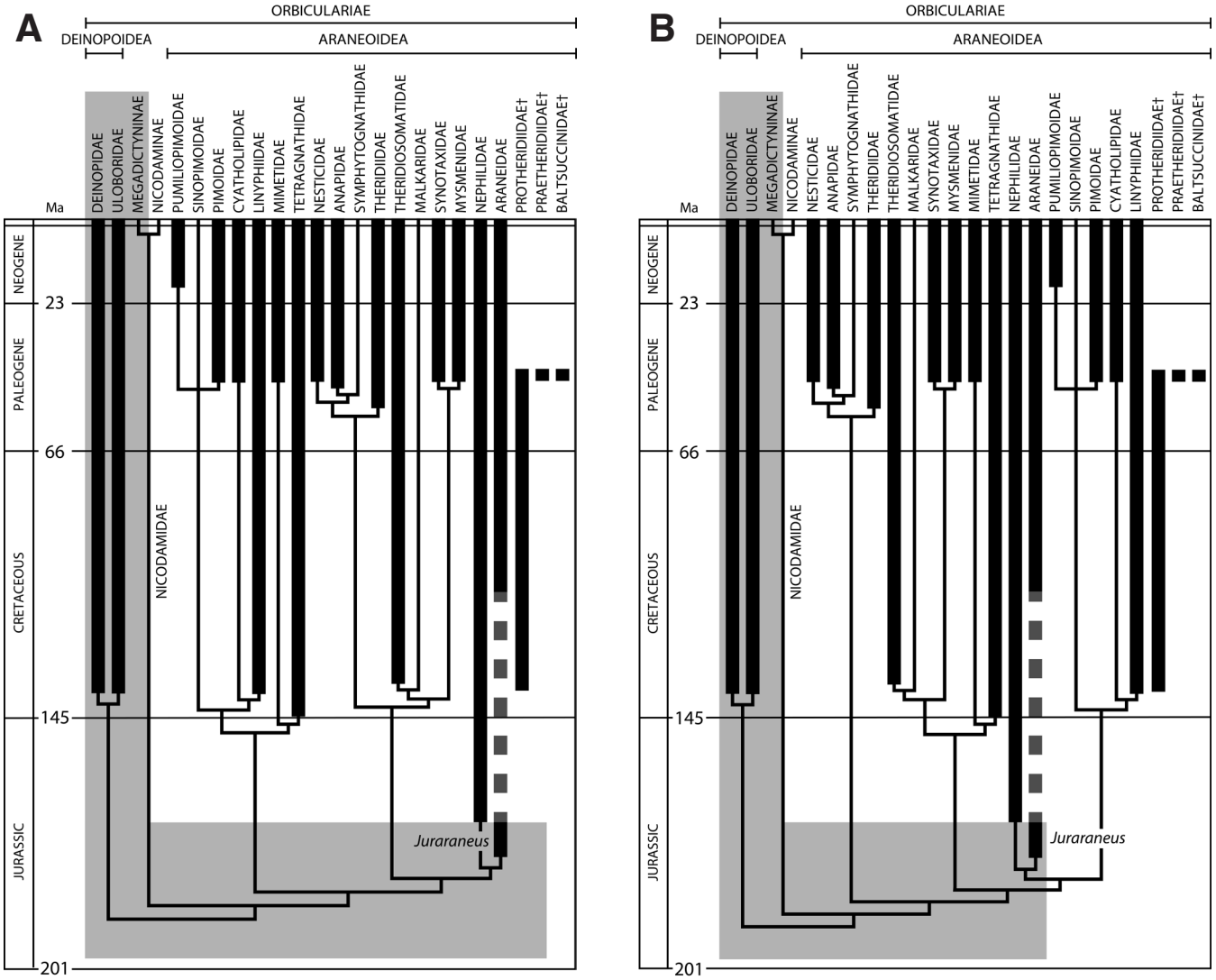

Fig. 7: Phylogenetic trees of Orbiculariae and the fossil record of orbweavers (e.g. Penney, Dunlop & Marusik 2012). **A** based on the phylogeny of Blackledge *et al*. (2009); **B** based on the phylogeny of Dimitrov *et al*. (2012). The extinct families of Wunderlich (e.g. 2012) are included at the right. Solid bars represent known fossil records; dashed grey bar represents range extension of Araneidae based on the possibility that *Jurararaneus* is an araneid. Grey area encloses cribellate taxa. Dates in million years (Ma) before present, after International Commission on Stratigraphy (2012).

been shown that it possesses a calamistrum, and is thus a cribellate araneoid. The pedipalp structures are not well preserved, but appear to be complex, as in araneoids. Jurararaneidae cannot be defined on apomorphies and thus could be ancestral to Araneidae, or possibly *Jurararaneus* is an araneid. According to recent phylogenies of Orbiculariae (Fig. 7), and since *Jurararaneus* is now known to be cribellate, the ecribellate condition could have evolved more than once in the Orbiculariae and, indeed, within Araneoidea.

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