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A camel spider from Cretaceous Burmese amber

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ABSTRACT

The first camel spider (Arachnida, Solifugae) from the Upper Cretaceous (lowermost Cenomanian, ca. 99 Ma) Burmese amber from Myanmar is described as *Cushingia ellenbergeri* gen. et sp. nov. It represents one of only a handful of fossils belonging to this arachnid order, but its precise systematic affinities are difficult to resolve. It shares characters with Karschiidae, the subfamily Gylippinae among the Gylippidae and the subfamily Dinorhaxinae containing a single, monotypic genus *Dinorhax* Simon, 1879 in the family Melanoblossiidae; the latter genus occurring in South-East Asia today. Its general habitus is closest to *Dinorhax*, but differences between the fossil and this modern genus remain. On balance, the uncertain nature of some features precludes unequivocal referral to any one of the families above. We prefer to place this new genus as Solifugae *incertae sedis* and further discuss the wider biogeographical implications of this find. Our new fossil is also significant for coming from a presumed forest habitat, whereas most camel spiders today are associated with arid environments.

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1. Introduction

Camel spiders (Solifugae) are a fascinating, but poorly-known order of arachnids. For an overview of their biology see Punzo (1998). Usually extremely hairy, camel spiders possess chelicerae which are very large in relation to the rest of the body. Some species can reach a few centimetres in length and are capable of capturing small vertebrates, in addition to their normal invertebrate prey. Unique features of the group include the presence of malleoli, small club-shaped sensory organs on the coxa and trochanters 1 and 2 of the fourth pair of legs, and a suctorial organ at the tip of the pedipalps used for climbing and prey capture. The common name camel spider hints at the fact that these animals are predominantly found in arid environments; indeed they can be found in all desert regions of the world, with the curious exception of Australia. They are also sometimes known as wind scorpions. This relates to their great speed – facilitated by an extensive tracheal system – and thus ability to 'run like the wind'. Prendini (2011) reported 1113 living species of camel spider distributed across 141 genera and twelve

families (see also Muma, 1976 and Harvey, 2003). However, much of their systematics draws on an older, and problematic, scheme developed by Roewer (1932–34). A modern phylogeny for the group is lacking. However, the last few years have witnessed renewed interest in camel spiders, including aspects of their anatomy (Cushing et al., 2005; Klann et al., 2008; Klann and Alberti, 2010), behavioural ecology (Peretti and Willemart, 2007; Hrušková-Martišová et al., 2007, 2008, 2010; Willermart et al., 2011) and genomics (Masta et al., 2008).

Camel spiders are extremely rare as fossils. The enigmatic *Schneidarachne saganii* Dunlop and Rössler, 2003 from the lower Carboniferous (ca. 340 Ma) Coal Measures of Kamienna Góra in Poland expresses some solifuge-like features. The oldest unequivocal camel spider is *Protosolpuga carbonaria* Petrunkevitch, 1913 from the upper Carboniferous (ca. 306 Ma) Coal Measures of Mazon Creek, USA. According to the revision of Selden and Shear (1996), it is barely recognisable as such and impossible to place in relation to the living families. The next youngest record is *Cratosolpuga wunderlichi* Selden in Selden and Shear, 1996 from the Lower Cretaceous (ca. 115 Ma) Crato Formation of Brazil. This find is of particular interest in being assigned to the extant family Ceromidae: a group restricted today to sub-Saharan Africa. The Brazilian fossils suggest that ceromids were once more widely distributed across Gondwana, becoming extinct in South America, presumably after the

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continents rifted apart. Further examples of *C. wunderlichi* were described by Dunlop and Martill (2004). There are two records from Eocene (ca. 44–49 Ma) Baltic amber. *Palaeoblossia groehni* Dunlop, Wunderlich and Poinar, 2004 was tentatively placed in the family Daesiidae. A further, slightly larger, Baltic amber fossil was described by Dunlop and Klann (2009), but lacked sufficient characters for a confident family referral. Finally, *Happlodontus proterus* Poinar and Santiago-Blay, 1989 was described from Miocene (ca. 16 Ma) Dominican Republic amber. This species was assigned to the family Ammotrechidae, which makes biogeographical sense as a group which is widespread throughout the Americas today.

Here, we describe the first fossil camel spider from the ca. 99 Ma Burmese amber from Myanmar (Fig. 1). This discovery (Figs. 2–6) is particularly significant for being only the second Mesozoic (Upper Cretaceous) record of Solifugae, slightly younger than the Brazilian Crato Formation material. Burmese amber is also of much interest as one of the few fossil localities which samples late Mesozoic



Fig. 1. Map of Myanmar showing the position of the Hukawng Valley, the locality from which most of the Burmese amber originates. Copyright: Uwe Dedering, Wikimedia Commons, under free GNU/CC licence.

terrestrial arthropods from South-East Asia. A camel spider is a remarkable addition to the fauna (see Discussion) given the overall rarity of this group in the fossil record and the fact that living species tend to be associated with arid habitats today. In this context we should also stress that while the central Asian desert regions boast a rich camel spider fauna, only a handful of modern species (see below) have been recorded from the more tropical habitats spanning South to South-East Asia.

2. Materials and methods

The holotype and only known specimen originated from the private collection of Sieghard Ellenberger (Kassel, Germany). It has been acquired by – and deposited in – the Staatliches Museum für Naturkunde Stuttgart (SMNS) under the repository number Bu-161. The holotype is preserved in a flat, teardrop-shaped piece of clear yellow amber with approximate dimensions of $36 \times 19 \times 5$ mm. The specimen is thus most easily visible in dorsal and ventral view (Figs. 2–3). It was drawn on a Leica stereomicroscope with a camera lucida attachment and photographed using 90 mm Tamron macro lens on a Canon 650 for the overviews, and for details a Leica Macroscope 420 generating ca. 60 image stacks subsequently combined using the Helicon Focus software. The amber inclusion was compared to extant camel spider material in the collections of the American Museum of Natural History, New York, the Denver Museum of Nature and Science, Colorado, the Museum für Naturkunde Berlin, and the Royal Museum for Central Africa, Tervuren; supplemented by the literature (e.g. Roewer, 1932-34; Harvey, 2003). Leg segment interpretation follows Roewer (1934). Cheliceral length is measured in lateral view from tip to base of chelicera; width is measured in dorsal view across the widest part of the chelicera. All measurements are in millimetres.

We are also aware of at least three other fossil camel spiders in Burmese amber, one of which could potentially be the female of our newly described species. Another of these specimens was recently figured by Wunderlich (2015b, photo 188) as "Solifugae indet.", but cannot be meaningfully compared in detail to our material based on the published habitus photograph. The fossil has apparently since been sold to a collector in China (J. Wunderlich, pers. comm. 2015). Indeed, all these other known fossils reside in private collections and/or dealerships and were not available for study during the preparation of this manuscript.

2.1. Burmese amber

Fossil-bearing Burmese amber has mostly been collected from northern Myanmar, and in particular the Hukawng Valley (Fig. 1). For an overview of the amber deposit and its geological setting see, e.g., Zherikhin and Ross (2000), Grimaldi et al. (2002) and Ross et al. (2010). U–Pb zircon dating (Shi et al., 2012) recently constrained this amber to a maximum age of 98.79 \pm 0.62 Ma, which is equivalent to the Late Cretaceous (earliest Cenomanian). The original habitat of the amber forest has been assumed to be a tropical Araucaria forest (Grimaldi et al., 2002) and given the fact that modern camel spiders tend to be found under arid conditions, it would be interesting to know whether there are any other faunal or floral elements consistent with a xerothermic environment. We are not aware of any such evidence from the published literature.

3. Systematic palaeontology

Order Solifugae Sundevall, 1833 Solifugae *incertae sedis*



Fig. 2. Cushingia ellenbergeri gen. et sp. nov., the first camel spider (Arachnida: Solifugae) from Cretaceous Burmese amber. SMNS Bu-161. A. Dorsal view. B. Ventral view. Scale bar equals 2 mm.

Remarks. Our new fossil is most likely to be an adult male. The shape of the genital sternites (second opisthosomal sternites), typical of that of adult males, provides the strongest, but not the only support for the fossil specimen to be an adult male. Elongate setae are situated mesally towards the distal end of the fixed (dorsal) finger (Fig. 4A); in females and juveniles of extant camel spiders setae situated in a similar position on the chelicera are usually not differentiated and are more uniform in length. The movable (ventral) cheliceral finger is narrow - a feature rarely found in females, and not known in juveniles, of extant taxa. Finally, the long legs relative to body size tend to be more typical of male than female camel spiders. Therefore, although we cannot exclude the possibility that it is an immature, we strongly suggest it is an adult male.

Determining the fossil's precise affinities is more challenging. Harvey (2003) offered a modified family key, largely based on Muma (1976). The apparently undivided tarsi of legs II–IV (Fig. 6) provisionally key the fossil specimen out to the Rhagodidae, which is broadly distributed across North Africa, the Middle East, Asia, and the Indian subcontinent. However, males belonging to a number of families/genera can express this condition. Undivided tarsi do enable us to completely exclude the families Ammotrechidae, Ceromidae, Eremobatidae, Galeodidae, Mummuciidae and Solpugidae. Undivided tarsi also occur in Hexisopodidae, but members of this psammophilous family are stocky, robust arachnids with short legs, quite unlike the new amber specimen.

The fossil's habitus and limb morphology is more consistent with Daesiidae, Gylippidae, Karschiidae, Rhagodidae and the unusual genus *Dinorhax* Simon, 1879 belonging to the monotypic subfamily Dinorhaxinae from the family Melanoblossiidae. Some members of the subfamily Melanoblossiinae, which is restricted to southern Africa, also have undivided tarsi (see Discussion). From this list of taxa, Daesiidae seems to be the least likely. No modern members of this family show such a strongly tapering opisthosoma (Figs. 2–3) and, if male, a membranous flagellum on the fixed finger of the chelicera. Furthermore, the tarsus of the fourth pair of legs appears to lack pseudosegments (Fig. 6D); a common feature amongst those modern daesiid camel spiders which have a single segmented leg IV tarsus. Melanoblossiinae are unlikely since a broad transition from the prosoma to the opisthosoma is characteristic of extant melanoblosiine species, quite unlike the distinct narrowing posterior to the propeltidium in the amber specimen (Figs. 2–3). Affinities with Rhagodidae are also problematic. Members of this family typically have a more cylindrical opisthosoma and more robust chelicerae, albeit with less teeth. In detail, rhagodids have a pronounced proximal tooth on each cheliceral finger which are not seen in the fossil (Fig. 5A). The distinct (male) rhagodid flagellum is also absent in the amber specimen.

The subfamily Gylippinae of the family Gylippidae includes the genera *Gylippus* Simon, 1879 and *Acanthogylippus* Birula, 1913 restricted to the Middle East and Central Asia. Similar to gylippines, the amber fossil has a flat dorsal surface of the fixed finger of the chelicera. Arguing against this assignment is, however, the general shape of the chelicerae and rostrum, and the presence of dentition towards the distal end of the cheliceral fixed finger (Fig. 5A). Teeth tend to be vestigial or absent here in extant gylippines. Furthermore, and contrary to extant gylippines, the chelicerae and pedipalps in the fossil lack robust spiniform setae, and the tarsus of the pedipalps is not broad and distinctly separated from the metatarsus (Figs. 2–3).

Extant members of the family Karschiidae have a Palaearctic distribution from North Africa, through the Middle East, and into Central Asia and western China. Putative karschiid features in the fossil include a row of long, possibly plumose, setae on the fixed finger of the chelicera (Fig. 4A), the shape of the rostrum, the presence of more cheliceral teeth (as compared to gylippines; see



Fig. 3. Camera lucida drawings of the specimen shown in Fig. 1 A. Dorsal view. B. Ventral view. Abbreviations: ch, chelicera; pp, pedipalp; legs numbered from I–IV. Scale bar equals 2 mm.

above) and the presence of one distal spiniform seta on the tibia and three spiniform setae on the metatarsi of legs II and III (Fig. 6B–C). Arguing against Karschiidae are (again) the fossil's tapering opisthosoma and the absence of spiniform setae on the pedipalp, and the apparent absence of a distinct, karschiid-type filiform flagellum on the chelicerae. A further character of importance for camel spider systematics is the position of the anus, which can be terminal or subterminal. In the amber fossil the anus appears to be subterminal (Figs. 4B and 5B), forming a slit restricted to the ventral surface of the last opisthosomal segment. A subterminal position argues against its inclusion in Daesiidae, Karschiidae and the subfamilies Lipophaginae and Melanoblossiinae of the families Gylippidae and Melanoblossiidae respectively. The subterminal position would be more consistent with Rhagodidae, Gylippinae or *Dinorhax* (see below).

Dinorhax is an unusual genus which is found today in Indonesia and Vietnam and is thus geographically close to Myanmar as the source of the amber. There is a single species, *D. rostrumpsittaci* (Simon, 1877) which is the only representative of a subfamily Dinorhaxinae in the family Melanoblossidae. Similarities between the amber fossil and *Dinorhax* include the distally tapering opisthosoma with a subterminal anus (Figs. 2–3, 4B, 5B), the absence of spiniform setae on the pedipalp (see also above), and the presence of one tibial and three metatarsal spiniform setae on legs II and III (Fig. 6B–C); the latter character having been previously used to diagnose the modern genus (e.g. Kraepelin, 1901; Roewer,



Fig. 4. Morphological details. A. Chelicerae in dorsal view showing possible flagellar complex (arrowed). B. Terminal segments of the opisthosoma in ventral view showing subterminal (i.e. ventral) anus (arrowed). C. Distal end of the pedipalp showing spoon-shaped flap (arrowed) probably representing the everted suctorial organ. Scale bars equal 0.5 mm.

1933). However, we should note that the tibial/metatarsal spiniform setae in *Dinorhax* are much shorter and thicker (Roewer, 1933: fig. 248) than those in the fossil. A further possible point of similarity is the apparent presence of one or two thickened, but simple setiform structures of approximately equal size emerging close to the tip of the fixed finger (Fig. 5A). In *Dinorhax* the male flagellum is unique under camel spiders in that it is a ventrally directed filiform structure. One or two spiniform setae are situated directly dorsal to and ventral to the flagellum in *Dinorhax* (Simon, 1879: fig. 16; Kraepelin, 1901: fig. 12; Roewer, 1932: fig. 142). However, the precise nature of the putative flagellum in the amber fossil remains equivocal. Also arguing against affinities with *Dinorhax* are the shape of the rostrum and the presence of (weak) claws on tarsus I (Fig. 6A). Claws here are apparently absent in the modern genus.

In conclusion, the general habitus of the Burmese amber fossil appears to be closest to *Dinorhax rostrumpsittaci*. Affinities with this South-East Asian genus would also make biogeographical sense, but should not overrule arguments based on morphology. Noticeable differences to *Dinorhax* remain, e.g., claws on leg I, while the slender chelicerae are unlike the more robust 'parrot beak'-like morphology alluded to in the species name of the modern animal. At ca. 14 mm long, the fossil is also less than half the size of *Dinorhax*, although it should be noted that such a large intraspecific difference in size is not uncommon in camel spiders. Taken together, we feel these differences justify a new (extinct) genus as diagnosed below. It is tempting to formally refer our new genus to Dinorhaxinae, but uncertainties in some key characters (e.g. flagellum shape) remain, while other preserved features are consistent with either Gylippinae or Karschiidae. As noted above, a modern cladistic analysis into which we could score our new fossil is lacking and we cannot exclude the possibility that this Mesozoic form possessed a mosaic of characters inconsistent with the living family groups. Perhaps it belongs to a stem-lineage, rather than the crown-group? Given this uncertainty we refer our camel spider to Solifugae *incerate sedis*.

Genus Cushingia gen. nov.

Type-species. Cushingia ellenbergeri sp. nov., designated herein. *Etymology.* In honour of Paula Cushing (Denver Museum of Nature and Science Colorado) in recognition of her important contributions towards camel spider biology and systematics.

Diagnosis. Gracile camel spider with all leg tarsi undivided; leg I with weak claws, legs II and III with one slender distal tibial and three slender metatarsal spiniform setae. Chelicerae with a row of elongated mesal setae; fixed finger dorsally flat and with narrow ridge along outer margin, but with acute ventral bend towards distal end. Opisthosoma strongly tapering; anus subterminal.



Fig. 5. *Camera lucida* drawings of the features shown in **Fig. 3** A. Chelicerae in dorsal view slightly tilted to the left to better reveal dentition and the putative flagellar complex; note the thickened setae towards the distal end of the fixed finger, which may represent the aforementioned putative flagellar complex, and the narrowing of the fixed finger with a depression and ridge morphology immediately beyond to this structure. Some setae omitted for clarity. B. Terminal segments of the opisthosoma in ventral view; note again the subterminal position of the slit-like anus. Setae partly omitted for clarity. C. Distal end of the pedipalp showing spoon-shaped flap. Abbreviations: an, anus; ff, fixed finger; fg, putative flagellum; fl, flap; mf, movable finger; ro, rostrum?; ta, tasus; ti, tibia. Scale bar equals 0.5 mm.

Cushingia ellenbergeri gen. et sp. nov. Figs. 2–6.

Etymology. In honour of the holotype's original owner, Sieghard (Ziggi) Ellenberger, who kindly made this important specimen available for study.

Holotype. SMNS Bu-161.

Type-locality. Burmese amber, Hukawng Valley, Myanmar. Upper Cretaceous (lowermost Cenomanian).

Diagnosis. As for the genus.

Description. Complete specimen (Figs. 2–3) visible in both dorsal and ventral view; slightly obscured by some imperfections in the matrix, particularly on the right side and around the prosoma–opisthosoma junction. Total body length, 13.7 (including chelicerae) or 9.3 (excluding chelicerae). Propeltidium inversely trapezoid, lobed anterolaterally; total length 2.3, anterior width 3.4, posterior width 2.0. Small median eyes appear to be present on midline at anterior margin of propeltidium. Sclerites behind

propeltidium not well-defined, but probable mesopeltidium preserved as transverse band; length 0.3.

Chelicerae large, length 4.4. Basal part robust and bulbous, maximum width 1.6, distal part drawn out into slender fixed and movable fingers (Figs. 4A and 5A). Chelicerae highly setose, especially on mesal side. Brushes of elongate mesal setae present, especially medially on the fixed finger. Fixed finger dentate with at least six teeth; the larger ones towards the proximal end. Dorsal surface of fixed finger flattened; terminally with acute ventral bend directing the slightly splayed tip of the fixed finger downwards. Two thickened setae – possibly representing the (male) flagellar complex - originate mesally towards the distal end of the fixed finger and hang downwards, surrounded by further mesal setae adjacent to these structures. Fixed finger becomes noticeably narrower beyond insertion points of putative flagellar complex; the narrowness expressed as an elongate, mesal depression flanked by a thin outer lateral ridge. Movable finger narrow, simple, perhaps with two or three weakly expressed proximal teeth.



Fig. 6. Details of the distal ends of the legs. A. Leg I. B. Leg II. C. Leg III. D. Leg IV. Note the presence of an undivided tarsus on all legs, a vestigial claw on tarsus I and the presence of one tibial and three metatarsal spiniform setae on legs II and III (all numbered). Abbreviations: ac, accessory claws; cl, claws; mt, metatarsus; ta, tasus; ti, tibia. Scale bar equals 0.5 mm.

Pedipalps robust, length 9.4. Lengths of individual articles: femur, 2.1; patella, 3.6; tibia, 2.7; tarsus, 1.0. Pedipalps highly setose, particularly towards distal end where tarsus bears dense brush of setae. Patella and tibia can bear some very long setae (lengths up to 4.0), but lack strong proventral spiniform setae. Tip of pedipalp preserves spoon-shaped flap (Figs. 4C and 5C); assumed here to represent a partly everted suctorial organ. Legs generally slender and setose. Leg I particularly gracile; length 6.9. Lengths of individual articles: femur, 0.4, patella, 1.0; tibia, 2.6; metatarsus, 1.7, tarsus, 1.2; tarsus ends in weak claws (equivocal on right leg I). Leg II length 5.4. Lengths of individual articles: femur 1.2, patella 1.2, tibia 1.6, metatarsus 0.9, tarsus 0.5. Claws of legs II–IV well developed; all strongly curved, with additional accessory claws at their tips (Fig. 6). Tibia II with one distal spiniform seta; metatarsus II with three prominent angled spiniform setae, increasing in length from proximal to distal (Fig. 6B). Leg III length at least 3.1. Lengths of individual articles: tibia 1.4, metatarsus 1.2, tarsus 0.5. Tibia III with one large distal spiniform seta; metatarsus with three prominent more or less sub-equal spiniform setae (Fig. 6C). Leg IV length ca. 7. Lengths of individual articles patella 2.2, tibia uncertain, metatarsus 1.9, tarsus 0.7. Malleoli cannot be seen on basal articles of leg IV and must be regarded as equivocal.

Opisthosoma sac-like, relatively slender and distinctly tapering posteriorly; curved slightly to the left (Figs. 2–3). At least seven segments visible, all with straight posterior margins, segments becoming successively shorter posteriorly. Presence/absence of postgenital ctenidia (i.e. thickened setae) on ventral opisthosoma equivocal. Anus subterminal, restricted to ventral surface of last segment (Figs. 5B and 6B). Opisthosoma generally highly setose; posteriormost segments in particular bearing numerous long setae (lengths up to 6.0).

4. Discussion

Arachnids have been known from Burmese amber since the early part of the 20th century. For a full species list see Dunlop et al. (2015). In detail, Cockerell (1917a,b, 1920) described two pseudoscorpions from the families Garypinidae and Neobisiidae and an acariform mite belonging to Chyletidae. After a long hiatus further study of Burmese amber arachnids began in the 21st century, essentially following on from the rediscovery and overview of the deposit published by Grimaldi et al. (2002). Most arachnid species described so far are spiders (Penney, 2003, 2004, 2005; Wunderlich, 2008, 2012a, 2015a; Poinar and Buckley, 2012), but Burmese amber is also now yielding significant records of less frequently encountered arachnid groups. For parasitiform mites these include an opilioacarid (Dunlop and Bernardi, 2014) and two hard ticks (Poinar and Brown, 2003; Poinar and Buckley, 2008). For acariform mites the heterostigmatan family Resinacaridae was added by Khaustov and Poinar (2010). Many new family records of acariform mites are currently in preparation (E. Sidorchuk, pers. comm.). There are two scorpions, one assignable to an uncertain position in Buthoidea (Lourenço, 2002), the other to Chaerilidae (Santiago-Blay et al., 2004). Harvestmen are represented by a largeeyed dyspnoid (Giribet and Dunlop, 2005) and a cypophthalmid originally described in Sironidae (Poinar, 2008), but probably better placed in Stylocellidae.

A remarkable discovery was the presence of Burmese amber ricinuleids (Wunderlich, 2012b, 2015b), a very rare arachnid group restricted today to West Africa and the Americas. These Burmese fossil ricinuleids retain eyes, and one of them has a highly unusual morphology which led Wunderlich (2015b) to propose a new suborder. Other recent additions are whip spiders (Amblypygi) described by Engel and Grimaldi (2014) and placed as the sistergroup of the derived Neoamblypygi clade. Wunderlich (2015b) added two more whip spider species and also the first record of a whip scorpion (Thelyphonida). It seems that the Burmese amber arachnids may have been quite different to the modern fauna. Note Wunderlich's (2008, 2012a, 2015a) proposal of numerous novel spider families, Giribet and Dunlop's (2005) harvestman of uncertain familial affinities and Engel and Grimaldi (2014), who left the familial position of their new Burmese amber whip spider genus open. The camel spider Cushingia ellenbergeri is a new addition to the fauna and may also differ notably from its living relatives.

As noted above, camel spiders are generally associated with arid environments today, although Harvey (2003) commented on the fact that Dinorhax (see above) apparently lives in rainforests, or on their margins. We should also recall the presence of fossil camel spiders in Baltic amber, again thought to be a (warm) forest environment. Furthermore, the oldest camel spider comes from the Carboniferous Coal Measures which are generally interpreted as tropical, even swampy, in nature. Our new species from Burmese amber is also likely to have been a forest-dweller. It is thus interesting to speculate whether forests were the original home of camel spiders and whether specialisation for drier habitats came later? Cushingia ellenbergeri also suggests that there have been camel spiders in South-East Asian forests for nearly a hundred million years. Given the uncertainties about the fossil's affinities, it is less clear whether there has been an unbroken (dinorhaxine?) lineage here since the Cretaceous, or whether different families have occupied this rainforest niche at different stages of geological time.

If the affinities of Cushingia do lie close to Dinorhax, then it is worth reiterating that the family to which this genus belongs (Melanoblossidae) expresses a curious and highly disjunct distribution, being found in southern Africa and South-East Asia (Harvey, 2003). This clearly raises a question about its monophyly. If melanoblossids are a natural group then this distribution pattern either implies a deep divergence time – perhaps even going back to the supercontinent of Pangea – or a remarkable migration history. The presence of our ca. 99 Ma fossil in Myanmar is particularly interesting in this context. If it is related to *Dinorhax*, it would falsify the hypothesis that melanoblossids rafted from Africa to Asia on the Indian tectonic plate. India is currently thought to have collided with Asia about 53 million years ago (e.g., Zahirovic et al., 2014), by which time a putative Dinorhax-like animal was already long present in South-East Asia. Alternatively, the region encompassing modern Myanmar originated on the so-called Sibumasu terrain which is thought to have rafted off northern Australia somewhat earlier, perhaps around the ca. 145 million year Jurassic-Cretaceous boundary (Metcalfe, 2011; Zahirovic et al., 2014). This terrain could potentially have brought Gondwanan taxa with it into Asia. With respect to camel spiders in general, a difficulty with this hypothesis is the complete absence of Solifugae in modern Australia. If camel spiders did come into South-East Asia via the Sibumasu terrain they should have been in Australia too, at least during the Mesozoic. In this scenario, any Australian species must subsequently have become extinct. Alternatively, did camel spiders enter South-East Asia via a more northern route such as through Central Asia? Investigating these biogeographical hypotheses for camel spiders further requires a robust phylogenetic framework, and in particular a test of the monophyly of the twelve modern families.

Finally, fossil taxa are becoming increasingly important as a means to help calibrate molecular-based trees of arachnid phylogeny. Using the mitochondrial genome, Masta et al. (2008) suggested that the two families they investigated, Eremobatidae and Ammotrechidae - both of which are found in the Americas diverged in the Triassic about 240 million years ago. There are, unfortunately, hardly any arachnid fossils from this time period which could constrain and/or calibrate this result. Our new Cretaceous fossil is somewhat younger, and again we reiterate that we do not have a modern phylogenetic tree. In other words, we do not yet have a reliable cladogram onto which we can project the known fossil record of the camel spiders and resolve minimum ages for cladogenesis. Pseudoscorpions (e.g. Shultz, 2007) or acariform mites (e.g. Pepato et al., 2010) have been proposed as the sistergroup of camel spiders. Both of these putative sister-taxa have a fossil record extending back to the Devonian: ca. 390 and 411 Ma respectively. On current data, we can delimit total-group Solifugae to (at least) 306 Ma, Ceromidae to 115 Ma, Daesiidae to 44–49 Ma, and Ammotrechidae to 16 Ma. The other nine families lack a fossil record, but if further Burmese amber specimens enable us to place *Cushingia* unequivocally into Dinorhaxinae, Gylippinae or Karschiidae then we would also have an important 99 Ma calibration point for one of these suprageneric taxa too.

5. Concluding remarks

Fossil camel spiders are extremely rare and *Cushingia ellenbergeri* gen. et sp. nov. is the first example to be formally described from the Cretaceous Burmese amber of South-East Asia. Its familial affinities cannot be unequivocally resolved, but it appears to have most characters in common with the living genus *Dinorhax*. This is itself a rarity, being the only living species found in South-East Asia and one of the few camel spiders not associated with an exclusively arid environment.

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