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First fossil Huttoniidae (Arthropoda: Chelicerata: Araneae) in late Cretaceous Canadian amber

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Abstract

The first fossils of the extant New Zealand spider family Huttoniidae are described from Cretaceous (Campanian) amber from Alberta and Manitoba, Canada. The specimens are juveniles and poorly preserved, but the following combination of characters permits identification as huttoniids: general habitus, carapace without a raised cephalic region or fovea, eight eyes in two rows of four, three-clawed tarsus (with tiny median claw), elongate patella, ventral preening comb on metatarsus 3, spines absent on legs 1 and 2 but present on legs 3 and 4, and spatulate setae on anterior metatarsi. The fossils cannot be assigned reliably to the single, extant, monotypic genus *Huttonia* O. Pickard-Cambridge, and no new taxa are erected. The fossils extend the known geological age of Huttoniidae back approximately 80 myr and, by inference, that of their putative sister taxon Spatiatoridae back approximately 35 myr, both to prior to the K/T extinction. The relative abundance of this family in the two Canadian amber deposits is similar, which suggests the deposits sampled are from similar habitats. The disjunct distribution of the fossil and extant members of this family supports the theory of ousted relicts over mobilistic biogeography for explaining the strictly austral distributions of the extant organisms.

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1. Introduction

Cretaceous Canadian amber has been known for more than a century, and fossil inclusions were first reported by Walker (1934). Spiders were listed as present in Canadian amber by McAlpine and Martin (1969) and Pike (1994, 1995), but the only works to formally describe spiders from this source are those of Penney (2004), who described a new genus of the enigmatic fossil family Lagonomegopidae from Cedar Lake, Manitoba, and Penney (2006) who described a new species of Oonopidae from Grassy Lake, Alberta. A research trip by DP to study Grassy Lake amber in the collections of the Royal Tyrrell Museum of Palaeontology (RTMP) in Drumheller, Alberta, Canada and a reassessment of Cedar Lake amber on loan to PAS from the Museum of Comparative Zoology

* Corresponding author. *E-mail address:* david.penney@manchester.ac.uk (D. Penney). (MCZ), Harvard, Massachusetts, USA identified specimens of the family Huttoniidae in both collections, which are reported here.

The spider family Huttoniidae Simon, 1893 (superfamily Palpimanoidea sensu Forster and Platnick, 1984) contains a single, described extant species, *Huttonia palpimanoides* O. Pickard-Cambridge, 1879, from New Zealand; although Forster and Forster (1999) mentioned about 20 undescribed species, all from New Zealand. This small spider resembles other palpimanoids in having distally spatulate setae prolaterally on metatarsi 1 and 2 but, in contrast to other palpimanoid families such as Palpimanidae and Stenochilidae, these do not form a thick scopula. From Archaeidae, huttoniids differ by not having a raised pars cephalica (Forster and Platnick, 1984), and from Lagonomegopidae, a strictly fossil family (see Penney, 2005), they are most easily separated by their eye arrangement.

The strictly fossil spider family Spatiatoridae Petrunkevitch, 1942 was erected for the following species preserved in Tertiary Baltic amber: *Adorator brevipes* Petrunkevitch, 1942,

A. samlandicus Petrunkevitch, 1942 and *Spatiator praeceps* Petrunkevitch, 1942. Petrunkevitch (1942) did not provide a differential diagnosis for the family, but gave a lengthy list of descriptive characters. He considered the family to share characters with Zodariidae, Lamponidae and Palpimanidae, but maintained it as a separate family in the Treatise on Invertebrate Paleontology (Petrunkevitch, 1955). Based solely on the figures of Petrunkevitch, Lehtinen (1967) supported the close relationship of Spatiatoridae with Zodariidae.

Wunderlich (1984) synonymized Spatiatoridae with Stenochilidae. Two years later he (Wunderlich, 1986) provided a revised diagnosis and placed the revalidated family in Palpimanoidea. He removed the genus Adorator Petrunkevitch, 1942 because it lacked spatulate leg setae and possessed a tibial apophysis on the male pedipalp, features that differ from other palpimanoids. Though he considered Adorator to have affiliations with the New Zealand family Huttoniidae, Wunderlich (2004) revised the genus and placed it in Zodariidae. Wunderlich (1986) also suggested that Idmonia Menge, 1854, also from Baltic amber, might be a senior synonym of Spatiator Petrunkevitch, 1942. However, because of the brevity of Menge's (1854) description and the fact that the type material of Idmonia was considered lost, this was merely a suggestion. Spatiatoridae was revised again by Wunderlich (2004, p. 767) who considered it monotypic, unrelated to Zodariidae, but retained his earlier opinion that it was most closely related to Huttoniidae and suggested that Spatiatoridae and Huttoniidae might be sister taxa. Spatiatoridae differs from Huttoniidae by having the cephalic region of the carapace distinctly raised, possessing a fovea, and lacking spines on legs 3 and 4, but the families are united by the presence of a preening comb on metatarsus 3 and prolateral, spatulate setae on the first pair of legs. They differ from the other sister pair in the classical Palpimanoidea (Stenochilidae-Palpimanidae) because their spatulate setae do not form dense scopulae (e.g., see the cladogram of Forster and Platnick, 1984, fig. 394). However, spatulate setae and a raised pars cephalica are features of other palpimanoids (e.g., archaeids) and the reduced spinnerets in Spatiatoridae (normal in Huttoniidae) are similar to those seen in Stenochilidae and Palpimanidae. There is considerable disagreement concerning the delimitation and phylogenetic relationships for extant families within the superfamily Palpimanoidea (see discussion in Penney, 2004) and because the majority of workers do not consider fossils, the correct placement of Spatiatoridae is unclear. The current Assembling the Tree of Life (AToL): Phylogeny of Spiders project (http:// research.amnh.org/atol/files/index.html) will include fossils in the cladistic analyses and should resolve this issue. However, until this project is complete, we tentatively accept Wunderlich's (2004) suggestion and consider Huttoniidae and Spatiatoridae as putative sister taxa.

2. Localities and stratigraphy of the Cretaceous Canadian amber deposits

The Canadian Grassy Lake amber originates from tailings of an abandoned coal strip-mine near the hamlet of Grassy Lake in south-eastern Alberta. The coal and amber were deposited in situ (Pike, 1995) near the top of the Foremost Formation, within the "Taber Coal Zone" (D.A. Eberth, pers. comm. 2005). The Foremost Formation is the lowest of three formations in the Judith River Group (sensu Eberth and Hamblin, 1993), which is equivalent to the Judith River Formation of Montana, USA (Eberth and Hamblin, 1993). Based on radiometric dating of bentonites from within and just above the Taber Coal Zone at Kennedy Coulee, Montana (Goodwin and Deino, 1989), the Grassy Lake amber locality is probably no younger than 78.2 Ma or middle Campanian in age. The Foremost Formation is interpreted as a paralic succession of interfingering marine and non-marine rocks (Ogunyomi and Hills, 1977; Hamblin and Abrahamson, 1996) consisting of a number of regressive cycles of barrier-island beach sands overlain by lagoonal and marsh deposits (Speelman and Hills, 1980; see also Ogunyomi and Hills, 1977).

The amber from Manitoba was first revealed to W.C. King of the Hudson Bay Company trading post by an aboriginal of the local Chemahawin Indian Reservation (McAlpine and Martin, 1969). The amber was initially studied by J.B. Tyrrell in 1890, whose field party subsequently traced its source back to the shore of Cedar Lake. However, there are no known amber-bearing sediments close to Cedar Lake, so it is possible that the amber originates more than 1000 miles farther to the west in Saskatchewan and Alberta and that it was transported to its present location by the easterly flowing Saskatchewan River (e.g., Poinar and Poinar, 1994). The amber dates from part of the Campanian age, 76.5–79.5 Ma (e.g., Poinar et al., 2000), i.e., shortly before the end-Cretaceous extinction event.

3. Material and methods

Seventy-one spiders in Grassy Lake (Alberta) amber in the RTMP and 36 specimens in Cedar Lake (Manitoba) amber from the MCZ were examined, and seven huttoniid specimens were identified (Table 1). Some specimens from both collections were prepared by PAS in Stuttgart by embedding them in synthetic resin prior to grinding and polishing. Six specimens of the strictly fossil spider family Spatiatoridae from the private collection of Jörg Wunderlich (Germany) were examined for comparative purposes. The fossils were studied under combined incident and transmitted light using a Wild M8 stereo-dissecting microscope and a Leica DMLM stereocompound microscope. Photographs were taken with a Nikon D1X digital camera attached to the microscopes. All measurements were made with an ocular graticule and are in millimetres. Abbreviations used in the text and figures are as follows: car, carapace; cm3, comb on metatarsus 3; ea, eye arrangement; ep, elongate patella; fe, femur; ls, leg spines; mt, metatarsus; pa, patella; ss, spatulate setae; ta, tarsus; ti, tibia.

4. Huttoniidae in Canadian amber

Superfamily: Palpimanoidea sensu Forster and Platnick, 1984 Family: Huttoniidae Simon, 1893 Table 1 Huttoniidae identified in Canadian amber collections from Cedar Lake, Manitoba (MCZ) and Grassy Lake, Alberta (RTMP)

Source	Specimen	Characters visible
Manitoba	¹ MCZ A 5022	cm3, ?ss
		(poor, partial specimen, Fig. 1B)
Manitoba	¹ MCZ A 5024	cm3, ep, ls, ss
		(poor specimen, Fig. 1A)
Alberta	² RTMP 79.16.15	car, cm3, ep, ls, ss
		(Fig. 1C,G)
Alberta	¹ RTMP 96.9.35	cm3, ep, ls, ss
		(Fig. 1D,H)
Alberta	¹ RTMP 96.9.234	car, cm3, ea, ep, ls, ss
		(Fig. 1E,F)
Alberta	³ RTMP 96.9.464	cm3 (very poor specimen in
		a tiny piece of amber)
Alberta	³ RTMP 96.9.1069	cm3, ss (very poor specimen in
		a tiny piece of amber)

¹ Mounted on a slide.

² Embedded in block of synthetic resin.

³ Loose amber.

Material. Amber specimens MCZ A 5022 and 5024 from Cedar Lake, Manitoba, Canada; RTMP 79.16.15, 96.9.35, 96.9.234, 96.9.464, and 96.9.1069 from Grassy Lake, Alberta.

Remarks. The presence of spatulate setae prolaterally on the anterior metatarsi places the specimens in Palpimanoidea; the lack of a full scopula formed of spatulate setae and lack of a raised cephalic region places them in Huttoniidae, rather than any other palpimanoid family (see Forster and Platnick, 1984). This assignment is confirmed by a combination of additional features of Huttoniidae: the general habitus and size (<2 mm), lack of a fovea, eight eyes in two rows of four, three-clawed tarsus (with tiny median claw), elongate patella, ventral preening comb on metatarsus 3, spines absent on legs 1 and 2 but present on legs 3 and 4.

Unnamed genus and species Fig. 1

Remarks. None of the specimens is preserved well enough to confirm that they belong in the single, extant genus *Huttonia*. Although the specimens are poorly preserved, it is not possible to distinguish any important morphological differences between them. Therefore, it is assumed that they all belong to the same species.

Description. All measurements were taken from RTMP 96.9.234. Juvenile spiders less than 2 mm in length. Carapace 0.6 long, distinctly longer than wide, without raised pars cephalica, lacking fovea and with several short, anteriorly directed setae along the midline; eight eyes in two rows of four. Sternum longer than broad, pointed posteriorly, with coxae 4 widely separated. Labium triangular, maxillae converging, fang and cheliceral structure not clear. Opisthosoma oval, 0.6 long; anterior spinnerets well developed, others unclear. Legs 1, 2 and 4 are distinctly longer than leg 3 and are equal

in length, although there is some difference in the relative segment lengths: legs 1 and 2 fe 0.4, pa 0.2, ti 0.2, mt 0.1, ta 0.2, total 1.1; leg 3 fe 0.3, pa 0.1, ti 0.1, mt 0.1, ta 0.1, total 0.7; leg 4 fe 0.4, pa 0.1, ti 0.2, mt 0.2, ta 0.2, total 1.1; tarsus 3-clawed, median claw minute; elongate patella; metatarsi 1 and 2 with prolateral patch of spatulate seta; ventral preening comb on metatarsus 3; spines absent on legs 1 and 2, but present on 3 and 4 as follows: leg 3 pa = one distal-dorsal, ti = one distal-prolateral; leg 4: mt = one pair distal-ventral.

5. Discussion

These specimens represent the first fossil record of the extant spider family Huttoniidae. They extend the known geological range of the family back by approximately 80 myr, from the single, described extant species, which occurs only in New Zealand. They extend the range of the family to before the K/T event at 65 Ma, thus providing additional evidence that this global catastrophe had little effect on spiders (Penney et al., 2003). In addition, if the strictly fossil family Spatiatoridae, known only from Tertiary Baltic amber, is the sister taxon of Huttoniidae, as suggested by Wunderlich (2004), then the presence of huttoniids in the Late Cretaceous predicts the presence of spatiatorids then too. The similarity of the percentages (of the total spider faunas) of huttoniids in the Cedar Lake (6%) and Grassy Lake (7%) spider faunas suggests that, despite their different geographical occurrences, it is likely that they were sampling similar habitats.

From a biogeographical viewpoint, the presence of Huttoniidae in Canadian amber may seem bizarre, because huttoniids have been recorded previously only from the Recent fauna of New Zealand and not from any other fossil fauna. Although fossils are less useful than Recent specimens for systematic studies because of their imperfect preservation, particularly evident in the specimens considered in this paper, they are of paramount importance in studies of historical biogeography. They can play a decisive part in the falsification of proposed hypotheses (e.g., Eskov, 1990). For example, the current Gondwanan distribution of many extant species supports the theory of mobilistic biogeography, i.e., that the fragmentation of Gondwana and the subsequent continental drift can explain their current distribution. However, palaeontological data in the form of Northern Hemisphere fossils of Gondwanan taxa contradict this hypothesis and a different explanation is required. The theory of ousted relicts (e.g., Eskov and Golovatch, 1986) proposes that austral disjunctions result from a formerly pancontinental distribution followed by the extinction of "intermediate links" from the northern continents. There is a considerable amount of palaeontological data, in the form of Northern Hemisphere fossil representatives of Recent austral taxa of numerous different animal groups, which tends to be the rule rather than the exception, in support of this theory. For example, Eskov (1987, table 2) provided 93 such examples and Eskov (1992, table 1) cited an additional 29 examples, many of which include extant austral taxa from New Zealand. The Northern Hemisphere fossils identified here as Huttonidae provide additional support for the

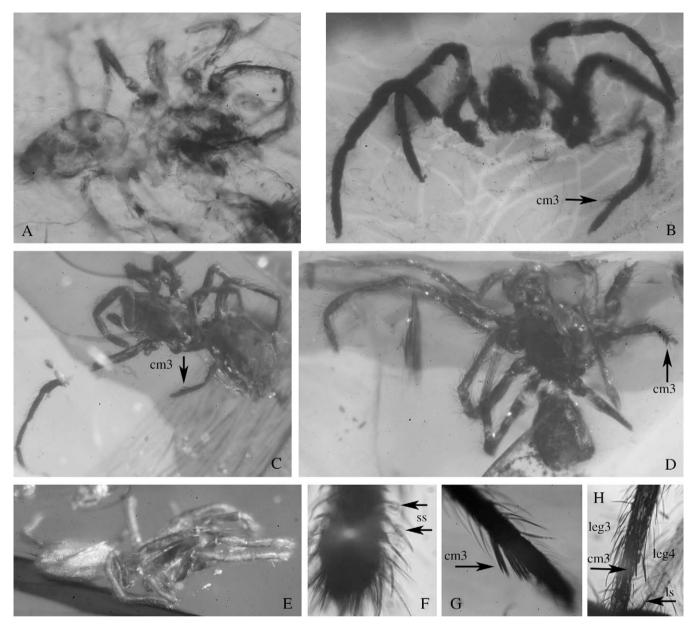


Fig. 1. Huttoniidae in Cretaceous (Campanian) Canadian amber. A, MCZ A 5024, whole specimen, dorsal view; \times 36. B, MCZ A 5022, whole specimen, posterior view; \times 50. C, RTMP 79.16.15, whole specimen, lateral view; \times 36. D, RTMP 96.9.35, whole specimen, ventral view; \times 50. E, RTMP 96.9.234, whole specimen, lateral view; \times 40. F, RTMP 96.9.234, showing spatulate setae; \times 400. G, RTMP 79.16.15, showing comb on metatarsus 3; \times 200. H, RTMP 96.9.35, showing comb on metatarsus 3 and ventral spines on leg 4; \times 75.

theory of ousted relicts over mobilistic biogeography to explain the currently observed distributions of extant austral taxa.

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