Cretaceous Research 139 (2022) 105314

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

A unique record of the Late Cretaceous of East-Central Europe: The first fossil wasps (Hymenoptera: Bethylidae, Spathiopterygidae) from the ajkaite amber (Bakony Mts., western Hungary)

Márton Szabó [a, b, *, 1], Manuel Brazidec [c, 1], Vincent Perrichot [c], Imre Szenti [d], Ákos Kukovecz [d], Attila Ősi [a, b]

[a] Hungarian Natural History Museum, Department of Paleontology and Geology, Ludovika tér 2, Budapest 1083, Hungary
[b] ELTE Eötvös Loránd University, Institute of Geography and Earth Sciences, Department of Palaeontology, Pázmány Péter sétány 1/C, Budapest 1117, Hungary
[c] Univ Rennes, CNRS, Géosciences Rennes, UMR 6118, 35000 Rennes, France
[d] University of Szeged, Interdisciplinary Centre of Excellence, Department of Applied and Environmental Chemistry, Rerrich Béla tér 1, 6720 Szeged, Hungary

A R T I C L E I N F O

Article history:
Received 17 May 2022
Received in revised form
5 July 2022
Accepted in revised form 20 July 2022
Available online 4 August 2022

Keywords:
Santonian
Hungary
Ajkaite
Hymenoptera
Bethylidae
Spathiopterygidae

A B S T R A C T

The recently re-discovered, unique amber named ajkaite, coming from the Late Cretaceous (Santonian) Ajka Coal Formation is an unexpectedly rich source of arthropod inclusions. The present paper describes three new species of wasps from ajkaite, namely *Ajkanesia harmincipsziloni* Szabó & Brazidec gen. et sp. nov. (Bethylidae: Pristocerinae), *Amissidigitus belae* Szabó & Brazidec gen. et sp. nov. (Bethylidae: Scleroderminae) and *Spathiopteryx soosi* Szabó, Brazidec & Perrichot sp. nov. (Spathiopterygidae). Hymenopterans were already reported from the Miocene and Pliocene of Hungary as adpression fossils, but these have only remained identified at higher taxonomical rank. Therefore, the three new ajkaite taxa are the first formally described fossil hymenopteran species from Hungary. The three ajkaite wasps greatly improve our knowledge on the Cretaceous fossil record of their respective (sub)families, which is otherwise very poorly documented. The suggested paleoenvironmental preferences of the new hymenopteran taxa accord with the forested, swampy to lacustrine ecosystem, in which the Ajka Coal has been deposited. Further ajkaite hymenopterans are likely to be stored in Hungarian museum collections.

1. Introduction

Becoming an inclusion in amber is the most favourable way of fossilization for arthropods. Amber inclusions allow to observe much more anatomical features of the body than compression fossils (Poinar, 1992; Grimaldi and Engel, 2005). Therefore, inclusion-yielding amber deposits play an important role in understanding the evolution of many insect groups, since they provide an important glimpse into the fossil record of various taxa.

Late Cretaceous amber sites rich in bioinclusions are infrequent worldwide. In Europe, such deposits with arthropod inclusions are known only from France and Hungary (Schlüter, 1978; Perrichot et al., 2007, 2010; Choufani et al., 2013; Perrichot and Néraudeau, 2014: fig. A1; Néraudeau et al., 2017; Szabó et al., 2022a). Two Late Cretaceous sources of amber are known in Hungary, but only one source has yielded arthropod inclusions so far, the so-called ajkaite which is dug from the Santonian brown coal beds of Ajka (Bakony Mts., western Hungary). The fossiliferous potential of ajkaite has been known for a long time (Szabó, 1871; Hantken, 1878; Zechmesiter, 1926; Tasnádi Kubacska, 1957), yet only a handful of fossil arthropods have been formally described: the two biting midge species *Adelohelea hungarica* and *Leptoconops clava* (Borkent, 1997), the two-tailed spider *Hungarosilia verdesi* (Szabó et al., 2022a) and the click beetle *Ajkaelater merkli* (Szabó et al., 2022b).

Among the Santonian ambers known worldwide, only the Taimyr amber (Evans, 1973; Rasnitsyn, 1975) and the French amber

* Corresponding author. Hungarian Natural History Museum, Department of Paleontology and Geology, Ludovika tér 2, Budapest 1083, Hungary.
E-mail addresses: szaboomaarton@ttk.elte.hu, szabo.marton.pisces@gmail.com (M. Szabó), manuel.brazidec@gmail.com (M. Brazidec), vincent.perrichot@univ-rennes1.fr (V. Perrichot), szentiimre@gmail.com (I. Szenti), kakos@chem.u-szeged.hu (Á. Kukovecz), hungaros@gmail.com (A. Ősi).
[1] These authors contributed equally: Márton Szabó and Manuel Brazidec.

https://doi.org/10.1016/j.cretres.2022.105314
0195-6671/

from Provence (Perrichot et al., 2007) have yielded hymenopteran inclusions. This makes every new occurrence of Santonian amber hymenopterans of great importance in order to better assess the past diversity of various hymenopteran families.

The present study details exceptionally well-preserved hymenopteran inclusions recently discovered in ajkaite. The described specimens represent scientifically new taxa, and since Santonian Hymenoptera inclusions are extremely scarce, they provide useful informations to a better understanding of the evolution of Hymenoptera.

2. Geological background

The first outcrops of the Ajka brown coal (i.e. Ajka Coal Formation) were discovered in the Ajka-Csinger valley („Ajka-Csingervölgy" by its Hungarian name), approximately 4 km southeast from the city of Ajka (Bakony Mts., western Hungary) (Fig. 1A, B). Ajka-Csinger valley is now considered as part of the city of Ajka.

The Ajka Coal Formation occurs in the Bakony Mountains (Transdanubian Range), where it is concentrated in three different carbonate terrain sub-basins (Ajka, Magyarpolány-Devecser, and Gyepükaján) (see Császár and Góczán, 1988; Siegl-Farkas, 1988), sometimes reaching the thickness of more than 100 m. The formation is built up on Triassic, or more rarely Jurassic or Lower Cretaceous Limestones, and is overlain by either the marine Jákó Marl Formation, or discontinuously Eocene shallow marine Szőc Limestone Formation (Kozma, 1991; Haas et al., 1992) (Fig. 1C). The Ajka Coal Formation is composed by an alternation of coal or clayey coal beds, marls, sands and sandstone beds, as well as light grey to brownish carbonaceous to argillaceous pelitic rocks with interbedding molluscan lumachelles (Haas, 1983). The depositional area of the Ajka coal was characterized by swampy and lacustrine environments. This resulted in (among others) at least seven main coal-beds, with the oldest nr. 6 to the youngest nr. 0, with thicknesses of 80–360 cm (Kozma, 1991). Although ajkaite occurs in all coal-bearing layers of the formation, the largest quantities came from the so-called Coal bed 0, also called as 'amber bank' (borostyántelep or gyantástelep or nullás telep in Hungarian) during the coal mining activities in the late 1800's (Rozlozsnik, 1940).

Based on palynological and nannoplankton investigations, the formation was dated as Santonian in age (Siegl-Farkas and Wagreich, 1996; Bodrogi et al., 1998; Bodor and Baranyi, 2012; Ősi et al., 2016). The flora, and the invertebrate and vertebrate fauna of the formation have been described by numerous authors (for references see Szabó et al., 2022a).

3. Material and methods

Coal mining in the Ajka Subbasin has started in 1865 (Kozma, 1991), and it ceased in 2004. Mining has always been carried out on a subsurface basis. While the mines were in operation, amber specimens were collected by individual miners, geologists, and amateur collectors (especially from the very rich Coal bed 0), but unfortunately the number of specimens nowadays does not exceed

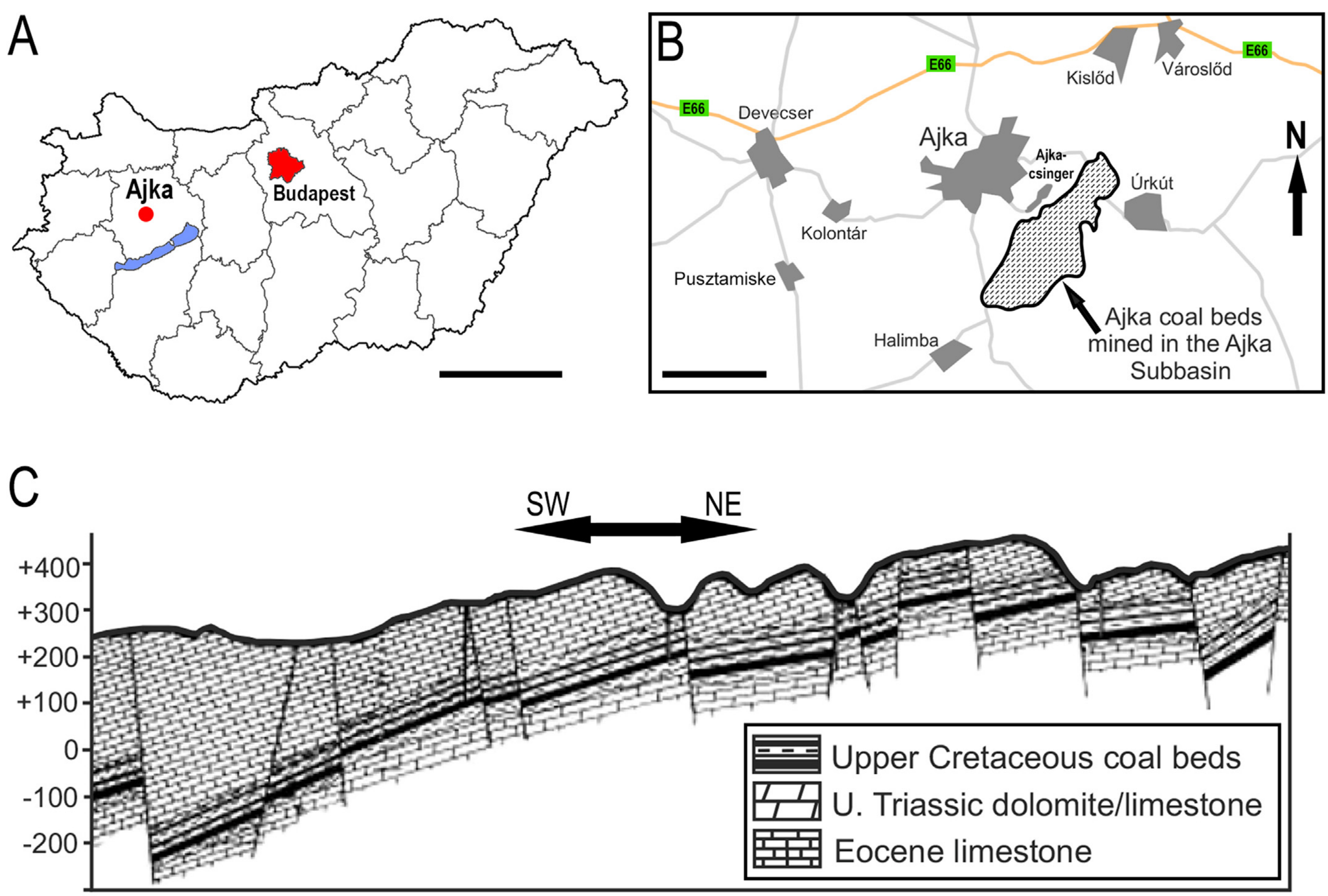

Fig. 1. A: Locality map of Ajka; B: Location of Ajka-Csinger valley and the Ajka Coal area in western Hungary; C: Simplified geological section of the Ajka Subbasin. Scale bars: A: 100 km; B: 3 km.

a few hundred. For this reason, ajkaite became extremely valuable for scientists and amateur collectors as well. The exact locality and stratigraphic origin of the ajkaite specimens within the Ajka Coal Formation investigated in the present study is unknown, all pieces have been donated by private collectors.

Two of the hereby described hymenopteran inclusions have been CT scanned at the University of Szeged, Hungary. The X-ray CT measurements were performed with a Skyscan 2211 (Skyscan, Bruker, Belgium). The resolutions (voxel sizes) used were 0.6 μm^3 (specimen NHMUS PAL 2022.3.1) and 1 μm^3 (specimen NHMUS PAL 2022.1.1). In both cases, a camera offset function was applied to double the width of the field of view. High-resolution images were obtained with a source voltage, current, and exposure time of 80 kV, 600 μA, and 200 ms, respectively. The CT data were reconstructed by using beam-hardening, post alignment, and ring artifact correction implemented in the NRecon (Skyscan, Bruker, Belgium) reconstruction software. For the 3D visualization, CT-Vox 3D Micro-CT Volume Rendering software (Skyscan, Bruker, Belgium) was utilized.

The amber pieces were subsequently embedded in epoxy resin (Araldite® 2020) for consolidation, and the resulting blocks were posteriorly polished using thin silicon carbide sanding papers on a grinder polisher (Buehler EcoMet 30) in order to facilitate observation of the specimens under light microscopes.

The examination and photomicrographs were conducted with a Leica DMC4500 camera attached to a Leica M205C stereomicroscope. All images are digitally stacked photomicrographic composites of several focal planes, which were obtained using Helicon Focus 6.7 software. Adobe Illustrator CC2019 and Adobe Photoshop Image.20 software were used to compose the figures.

Measurements of the specimens were taken using the free version of ImageJ 1.48v. The description of the characters follows the nomenclature of Lanes et al. (2020) for the Bethylidae, Santer et al. (2022) for the Spathiopterygidae, and the description of surface sculpturing follows Harris (1979) for both families. Main measurements and indices used are as follows: length of fore wing (LFW); length of head, measured from top of vertex to apex of clypeus (LH); width of head above eyes (WH); width of frons (WF); height/width of eye (HE); ocello-ocular line (OOL); width of ocellar triangle (WOT); diameter of anterior ocellus (DAO); vertex-ocular line (VOL). All ajkaite hymenopteran type specimens detailed in the present work have been housed in the paleontological collection of the Hungarian Natural History Museum (Magyar Természettudományi Múzeum, NHMUS; Budapest). This published work and its new nomenclatural acts are registered in ZooBank with the following LSID (reference): urn:lsid:zoobank.org:pub:023B8B4E-CAB8-4611-A80E-F808F798682E.

4. Systematic paleontology

Order Hymenoptera Linnaeus, 1758
Superfamily Chrysidoidea Latreille, 1802
Family Bethylidae Haliday, 1839
Subfamily Pristocerinae Mocsáry, 1881

Genus ***Ajkanesia*** Szabó & Brazidec, gen. nov.
urn:lsid:zoobank.org:act:742C53BD-F776-427F-BB21-D56DBA1664AE

Etymology. The name is a contraction of “Ajka” (referring to the city of Ajka, from where the type specimen originates) and *Apenesia*, name of a pristocerine genus with which the holotype shows some morphological similarities. Gender feminine.
Diagnosis. Male. Body flattened and slightly elongate (Figs. 2A, B, 3A, B). Head rounded, slightly longer than wide; eyes round, glabrous (Figs. 2A, C, 3C); clypeus with median lobe well-defined, projecting, acute triangular; mandibles thick, with four stout teeth (Figs. 2C, 3C); antennae as long as head + mesosoma combined; flagellomeres cylindrical, elongate; ocellar triangle large, distance between posterior ocelli equal to distance of posterior ocelli to vertex crest; vertex crest convex (Figs. 2A, 3C). Dorsal pronotal area short, posterior margin widely incurved; propleuron elongate; notauli straight, convergent; parapsidal signum present; mesoscuto-scutellar sulcus elongate and reniform; metapectal-propodeal complex carinate, metapostnotal-median carina long and straight, metapostnotal-propodeal suture shorter and slightly incurved; propodeal declivity smooth (Figs. 2B, 3C). Fore wing with C, Sc + R, M + Cu, A, Rs&M, cu-a, 2r-rs&Rs tubular; 2r-rs&Rs incurved toward wing margin without marked angle; R1 tubular on half length of second radial cell [2R1] (Figs. 2A, D). Metasoma fusiform, longer than mesosoma; tergites without modifications (Figs. 2A, 3A, B); hypopygium with outer surface flat, posterior margin slightly incurved.

Ajkanesia harmincipsziloni Szabó & Brazidec, sp. nov.
Figs 2, 3
urn:lsid:zoobank.org:act:5E0D365F-C261-4383-9F18-D556A53E507

Material. Holotype male, inventory number NHMUS PAL 2022.1.1.
Etymology. The specific name honours the alternative rock band 30Y. In Hungarian, the band's name is phonetically written as “harminc ipszilon”. The band got its name after the Szombathely (western Hungary) bus service nr 30Y. Three members of the band, namely Zoltán Beck, László Beck and Zoltán Sárközy spent part of their childhood in the city of Ajka, from where the holotype specimen originates. The specific epithet is to be treated as name in a genitive case.
Diagnosis. As for genus.
Type locality. Ajka-Csingervölgy [Ajka-Csinger valley], approximately 1 km SE of the city Ajka, Bakony Mountains, Hungary.
Horizon and age. Ajka Coal Formation, unknown shaft of the Ajka-Csingervölgy coal minery; Upper Cretaceous, Santonian, 86.3–83.6 Ma.
Description. Body rather flattened (length 2.80 mm). Head prognathous, rounded, slightly longer than wide; LH: 0.60 mm, WH: 0.45 mm; WF: 0.33 mm, HE: 0.18 mm; OOL: 0.21 mm; WOT: 0.11 mm; DAO: 0.06 mm; VOL: 0.11 mm; frons flat; compound eyes round, without pubescence, located anteriorly on head, closer to mandibular insertion than to vertex; clypeus with median lobe acute triangular, projecting forward, carina absent or poorly developed, lateral lobe short; mandibles thick, overlapping at apex, with four stout teeth, ventralmost longest; toruli widely separated by flat surface; antennae as long as head + mesosoma, uniformly pubescent, pubescence shorter than one third of flagellomere length; scape 1.4 times as long as pedicel (scape length 0.17 mm); pedicel elongate, longer than wide (length 0.12 mm), about as long as flagellomeres; 11 flagellomeres distinctly longer than wide, cylindrical, similar in length (length 0.11–0.13 mm); flagellomere 11 tapering at apex, longest; ocellar triangle large, distance between posterior ocelli equal to vertex-ocellus distance; vertex crest convex; occipital carina present.

Mesosoma with dorsum smooth, sparsely pubescent (mesosomal length 0.97 mm); dorsal pronotal area short, with posterior margin widely incurved, posterior corners slightly overlapped by anteromesoscutum; propleuron elongate, slightly visible dorsally; mesopleuron without transepisternal line; anteromesoscutum with notauli deeply impressed, straight and convergent posteriorly, posteriorly separated by length of mesoscuto-scutellar sulcus, parapsidal signum present; mesoscuto-scutellar suture with

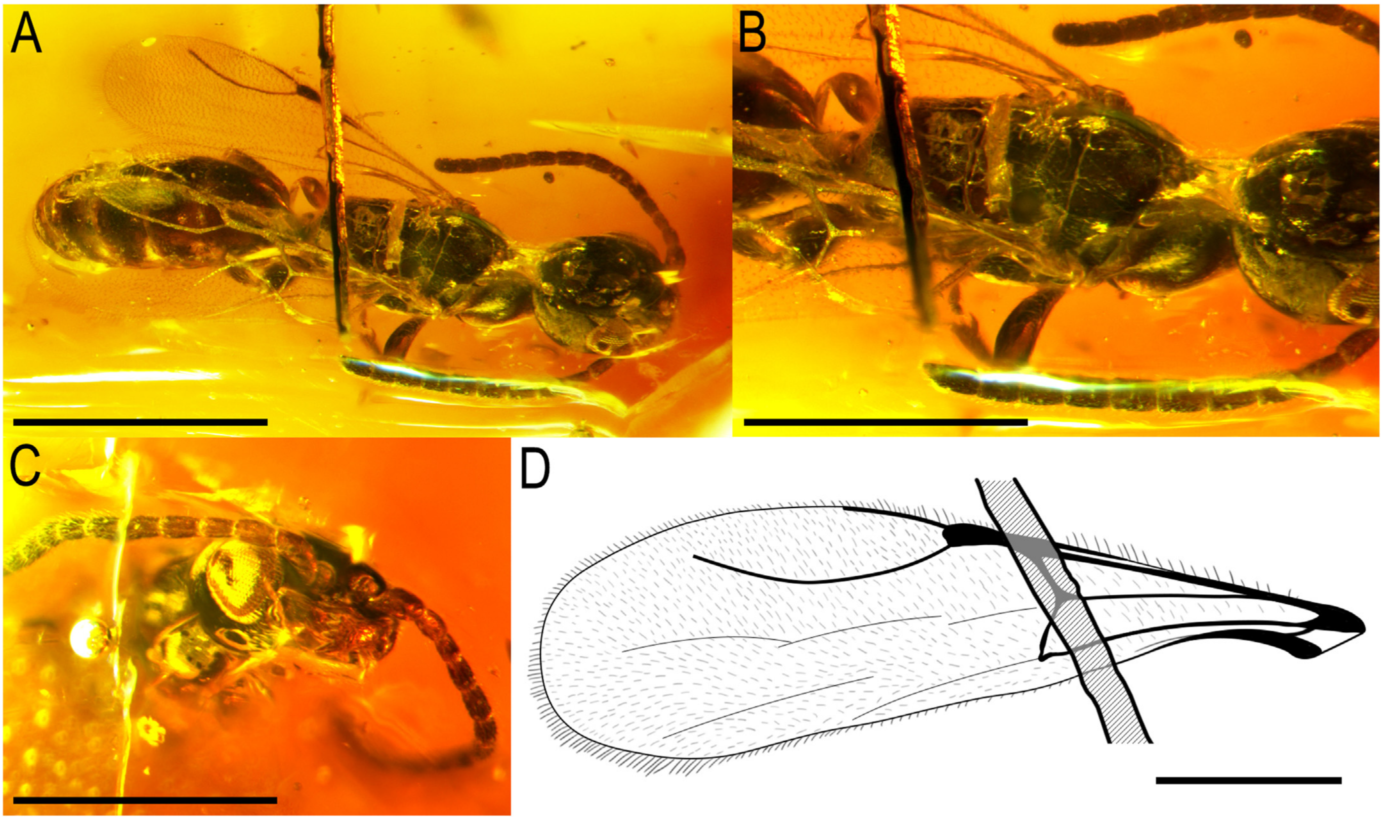

Fig. 2. *Ajkanesia harmincipsziloni* gen. et sp. nov. (holotype, NHMUS PAL 2022.1.1.); A: Habitus in dorsal view; B: Mesosoma in dorsal view; C: Head in frontal view; D: Line drawing of the fore wing venation (covered parts of the venation have been drawn after the opposite fore wing, see Fig. A). Scale bars: A: 750 μm; B, C: 500 μm; D: 250 μm.

Fig. 3. *Ajkanesia harmincipsziloni* gen. et sp. nov. (holotype, NHMUS PAL 2022.1.1.) as reconstructed by X-ray CT-scan; A: Habitus in dorsal view; B: Habitus in lateral view; C: Head (with antennae) and mesosoma in dorsal view. Scale bars: 0.5 mm.

conspicuous sulcus, elongate and reniform; mesoscutellum longer than anteromesoscutum, with posterior corners blunted; metanotum long, overlapping mesoscutellum posteriorly *sensu* Azevedo et al. (2018); metapectal-propodeal complex carinate dorsally, bordered laterally by marginal carina and posteriorly by transverse posterior carina, transverse posterior carina straight, no posterior spines or lateral projections of posterior corners; metapostnotal-median carina present, complete and straight; metapostnotal-propodeal suture present for half-length of metapectal-propodeal complex, very slightly incurved; propodeal declivity without carina. Fore wing extending beyond fourth metasomal terga (LFW: 1.60 mm), uniformly micropubescent and hyaline; tegula present; C, Sc + R, M + Cu, A, Rs&M, cu-a tubular; costal [C], radial [R] and first cubital [1Cu] cells closed; radial [R] and first cubital [1Cu] cells subequal in length: pterostigma slightly swollen, proximally narrower than distally; poststigmal abscissa of R1 tubular, half as long as second radial cell [2R1] cell; 2r-rs&Rs tubular, originating from distal half of pterostigma, without marked angles, incurved toward wing margin but not reaching it. Hind wing narrow, shorter than fore wing (length ca. 0.87 mm); no venation visible. Legs not especially pubescent, slender; metatrochanter without spines; tibial spurs formula 1–2–2.

Metasoma longer than mesosoma (length 1.23 mm), fusiform; six tergites visible, T3 and T4 longest but not dramatically (length of measurable tergites, T1: 0.15 mm, T2: 0.20 mm, T3: 0.24 mm, T4: 0.25 mm, T5: 0.20 mm), without modifications; hypopygium with outer surface flat, posterior margin slightly incurved.

Systematic remarks. Following the key to the subfamilies of Bethylidae of Azevedo et al. (2018), this specimen keys in the Pristocerinae for the following characters: specimen macropterous, fore wing with Rs + M absent, metanotum developed medially, overlapping mesoscutellum posteriorly. The taxonomic boundaries between pristocerine genera are mainly based on genitalic structures that cannot be observed on fossil specimens. Following the key to the genera of Pristocerinae of Azevedo et al. (2018), however, our specimen keys between *Apenesia* Westwood, 1874, *Foenobethylus* Kieffer, 1913, *Parascleroderma* Kieffer, 1904 and *Afgoiogfa* Argaman, 1988 for the body smaller than 15 mm, the hypopygium not divided in two lobes, with outer surface flat, the clypeus with median lobe clearly defined and the dorsal pronotal area short, with lateral margin much shorter than anterior one. Nevertheless, the new fossil differs from these genera by the following characters: from *Apenesia*, by the head longer than wide, flagellomeres elongate, thorax flattened, poststigmal abscissa of R1 present; from *Foenobethylus*, by the intersection of Sc + R and Rs&M close to pterostigma, poststigmal abscissa of R1 present, no spines on metatrochanter; from *Parascleroderma*, by the clypeus projecting, pronotum not elongate, intersection of Sc + R and Rs&M close to pterostigma, poststigmal abscissa of R1 present; from *Afgoiogfa*, by the intersection of Sc + R and Rs&M close to pterostigma, pterostigma not comma-like. We propose to create the new genus *Ajkanesia* gen. nov. for this specimen.

Subfamily Scleroderminae Kieffer, 1914

Genus ***Amissidigitus*** Szabó & Brazidec, gen. nov.
urn:lsid:zoobank.org:act:ABD45764-D591-4860-9C7F-A00600CDE371

Etymology. The name is a contraction of the Latin *amissus* (lost, gone) and digitus (toe). Gender masculine.
Diagnosis. Female. Body slightly depressed (Fig. 4A). Head subquadrate, longer than wide; eye glabrous, much closer to mandibles than to vertex, covering less than half of head; median clypeal lobe obtuse triangular, slightly projecting forward; mandibles with two teeth; antennae with 11 flagellomeres; ocellar triangle much posteriad on head, distance between posterior ocelli equal to distance of posterior ocelli to vertex crest; vertex crest angular; occipital carina present (Figs. 4A, B). Anteromesoscutum shorter than dorsal pronotal area, with notauli present; mesoscuto-scutellar sulcus wide, reniform; metapectal-propodeal complex with median postnotal carina and metapostnotal-propodeal carinae present (Fig. 4C). Fore wing with anterior board slightly incurved basally to prestigma; Sc + R, M + Cu, A, 1Rs&1M, cu-a tubular; pterostigma thin; 2r-rs&Rs tubular and arched toward wing margin, not reaching it; radial [R] and first cubital [1Cu] cells closed (Figs. 4A, D, E). Metasoma polished, longer than mesosoma; metasomal segments subequal in length (Fig. 4A).

Amissidigitus belae Szabó & Brazidec, sp. nov.
Fig. 4
urn:lsid:zoobank.org:act:FEEFA53C-1DF2-426B-8915-662661653DEF

Material. Holotype female, inventory number NHMUS PAL 2022.2.1.
Etymology. In honour of †Béla Szabó (1924–2007), paternal grandfather of the first author. Béla Szabó was a coal miner in Ajka, where he lost one of his toes in an accident while working in the underground coal shafts. The binomial name of the species can be translated as “Béla's lost toe”. The specific epithet is to be treated as name in a genitive case.
Diagnosis. As for genus.
Type locality. Ajka-Csingervölgy [Ajka-Csinger valley], approximately 1 km SE of the city Ajka, Bakony Mountains, Hungary.
Horizon and age. Ajka Coal Formation, unknown shaft of the Ajka-Csingervölgy coal minery; Upper Cretaceous, Santonian, 86.3–83.6 Ma.
Description. Body poorly flattened (length 1.97 mm). Head subquadrate, longer than wide; LH: 0.46 mm, WH: 0.40 mm; WF: 0.25 mm, HE: 0.16 mm; OOL: 0.18 mm; WOT: 0.11 mm; DAO: 0.02 mm; VOL: 0.11 mm; frons flat; compound eyes glabrous, elliptical, longer than high, located anteriorly on head, covering less than half of head length; clypeus with median lobe slightly projecting forward, obtuse triangular, median carina not extending on frons, lateral lobe poorly developed; mandibles slightly overlapping at apex, bearing two teeth, ventralmost longer, dorsalmost stouter; maxillary palpi with six palpomeres; toruli separated by their own diameter by shallow depression; antennae short, barely longer than head, with 13 antennomeres uniformly micro-pubescent, pubescence shorter than one third of flagellomere length; scape twice as long as pedicel (scape length 0.12 mm); pedicel longer than wide, longer than flagellomeres 1–10 that are barely longer than wide; flagellomere 11 longest (f1–f10 length 0.04 mm, f11 length 0.09 mm), tapering at apex; ocellar triangle large, much posteriad on head; vertex crest angular; occipital carina present.

Mesosoma with dorsum smooth (length 0.71 mm); dorsal pronotal area 1.18 times longer than anteromesoscutum (pronotal dorsal length 0.13 mm), slightly narrowing anteriorly, posterior pronotal margin incurved; propleuron not visible dorsally; prosternum small; anteromesoscutum short, notauli straight, converging posteriorly, posteriorly separated by half of width of mesoscuto-scutellar sulcus, parapsidal signum present; mesoscuto-scutellar sulcus wide, reniform; mesoscutellum as long as anteromesoscutum, with slightly outcurved posterior margin, almost touching metapectal-propodeal complex; mesopleuron without transepisternal line; metanotum hidden by mesocutellum; metapectal-propodeal complex carinate dorsally, bordered laterally by marginal carina and posteriorly by transverse posterior carina, transverse posterior carina straight, no posterior spines or lateral

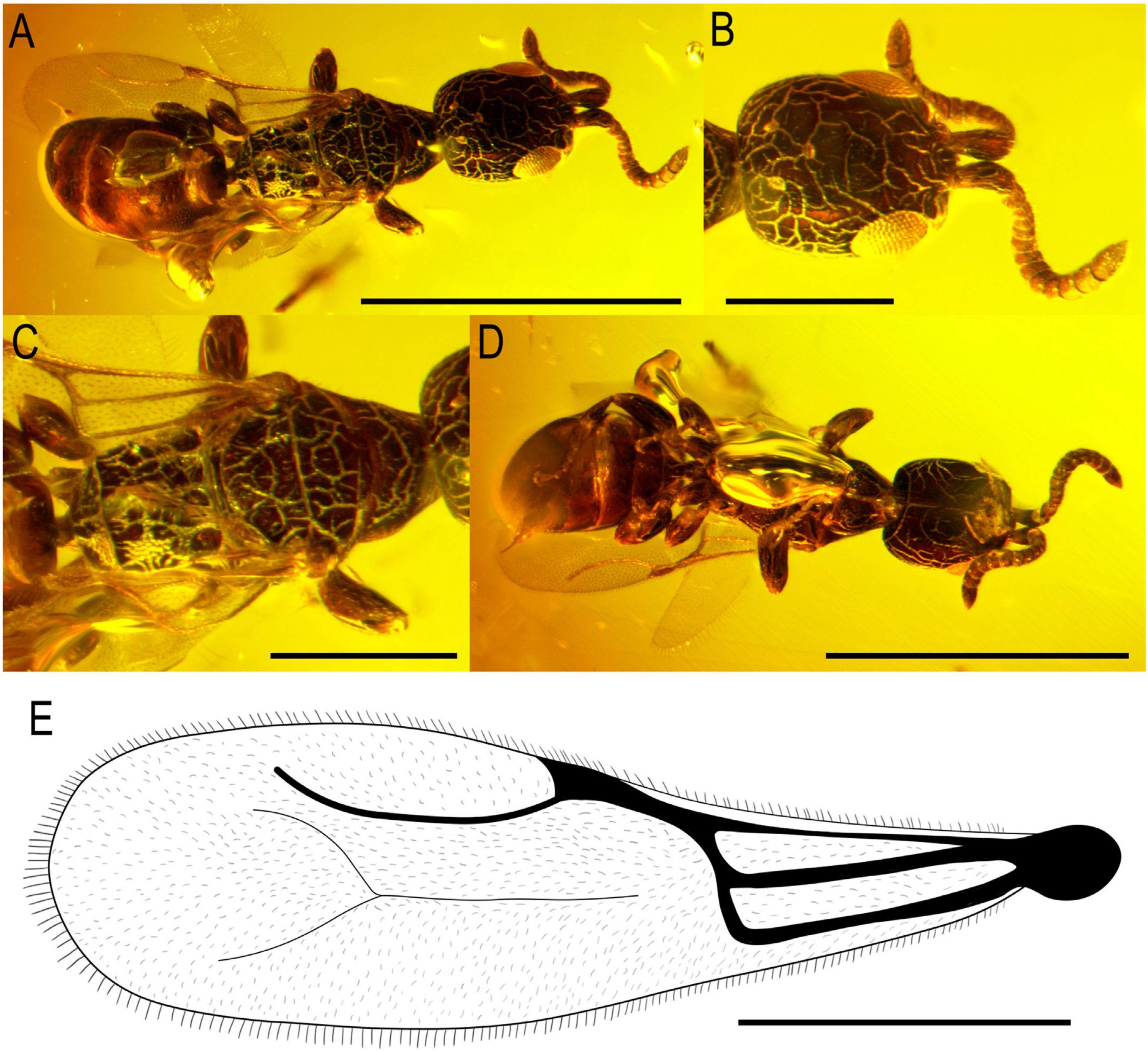

Fig. 4. *Amissidigitus belae* gen. et sp. nov. (holotype, NHMUS PAL 2022.2.1.); A: Habitus in dorsal view; B: Head in dorsal view; C: Mesosoma in dorsal view; d: Habitus in ventral view; e: Line drawing of fore wing. Scale bars: A, D: 750 μm; B, C, E: 250 μm.

projections of posterior corners; metapostnotal-median carina complete, straight; metapostnotal-propodeal suture present for two thirds of length of metapectal-propodeal complex, very slightly incurved; propodeal declivity without carina. Fore wing extending beyond fourth metasomal tergum (LFW: 1.17 mm), uniformly micropubescent and hyaline; tegula present; anterior board slightly incurved basally to prestigma; Sc + R, M + Cu, A, 1Rs&1M, cu-a tubular; radial [R] and first cubital [1Cu] cells closed, equal in length: pterostigma thin, elongate; poststigmal abscissa of R1 absent; 2r-rs&Rs tubular, originating from distal half of pterostigma, without marked angles, incurved toward wing margin but not reaching it. Hind wing narrow, shorter than fore wing (length ca. 0.68 mm); without venation. Legs sparsely pubescent; metafemur widest; tarsal claws slightly curved.

Metasoma polished, longer than mesosoma (length ca. 0.80 mm); petiole short; six visible segments of subequal length, with tergites not modified; sting exerted.

Systematic remarks. Following the key to the subfamilies of Bethylidae of Azevedo et al. (2018), this specimen keys in the Scleroderminae for the following characters: specimen macropterous, fore wing with Rs + M absent, metanotum not developed medially, metasomal segments regularly long, metapectal-propodeal complex without posterior spines, mesopleuron without transepisternal line, fore wing vein C absent. Following the key to the sclerodermine genera of Azevedo et al. (2018), it keys in *Nothepyris* Evans, 1973 for the antenna with 11 flagellomeres, the body not so depressed, the mandibles with less than five teeth, the fore wing vein C absent and vein A present, and the metasomal tergites 3 and 4 without tubercles; but it differs from *Nothepyris* by the head flattened, not globose, and the occipital carina present. Following the key to the fossil Scleroderminae of Colombo and Azevedo (2021), it keys in *Allobethylus bei* Colombo and Azevedo, 2021 for the antenna with 11 flagellomeres, the mandibles with less than five teeth, the head elongate and rectangular; but it differs from *Allobethylus bei* at least by the notauli present, and from all *Allobethylus* by the mandibles shorter, the head with the sides conspicuously outcurved rather than parallel, the occipital carina present, and the mesoscuto-scutellar suture fully sulcate. The genus *Paleoscleroderma* Falières and Nel, 2019 from lowermost Eocene French amber, not included in previous keys, differs from our specimen in having the mandibles with five teeth, the occipital carina absent, the metasomal tergite 2 longer than tergite 3. Therefore, we propose the new genus *Amissidigitus* gen. nov. to accommodate this morphotype.

Superfamily Diaprioidea Haliday, 1833
Family Spathiopterygidae Engel and Ortega-Blanco, 2013 (in Engel et al., 2013)

Genus *Spathiopteryx* Engel and Ortega-Blanco, 2013

Spathiopteryx soosi Szabó, Brazidec & Perrichot sp. nov.
Figs 5, 6
urn:lsid:zoobank.org:act:15625E01-DEC6-4F90-966C-F47F4B2ADE2E

Material. Holotype female, inventory number NHMUS PAL 2022.3.1.
Etymology. In honour of the geologist Dr. Miklós Soós, founder of the Hungarian Dinosaur Foundation and great supporter of the ajkaite amber research. The specific epithet is to be treated as name in a genitive case.
Diagnosis. Female. Eye occupying most of lateral surface of head, bulging, composed of about 20 ommatidia (Figs. 5A, D); back of head with coarse areolate-punctuate sculptures (Fig. 5A). Pronotum without visible striation, smooth (Fig. 5D). Fore wing paddle-like,

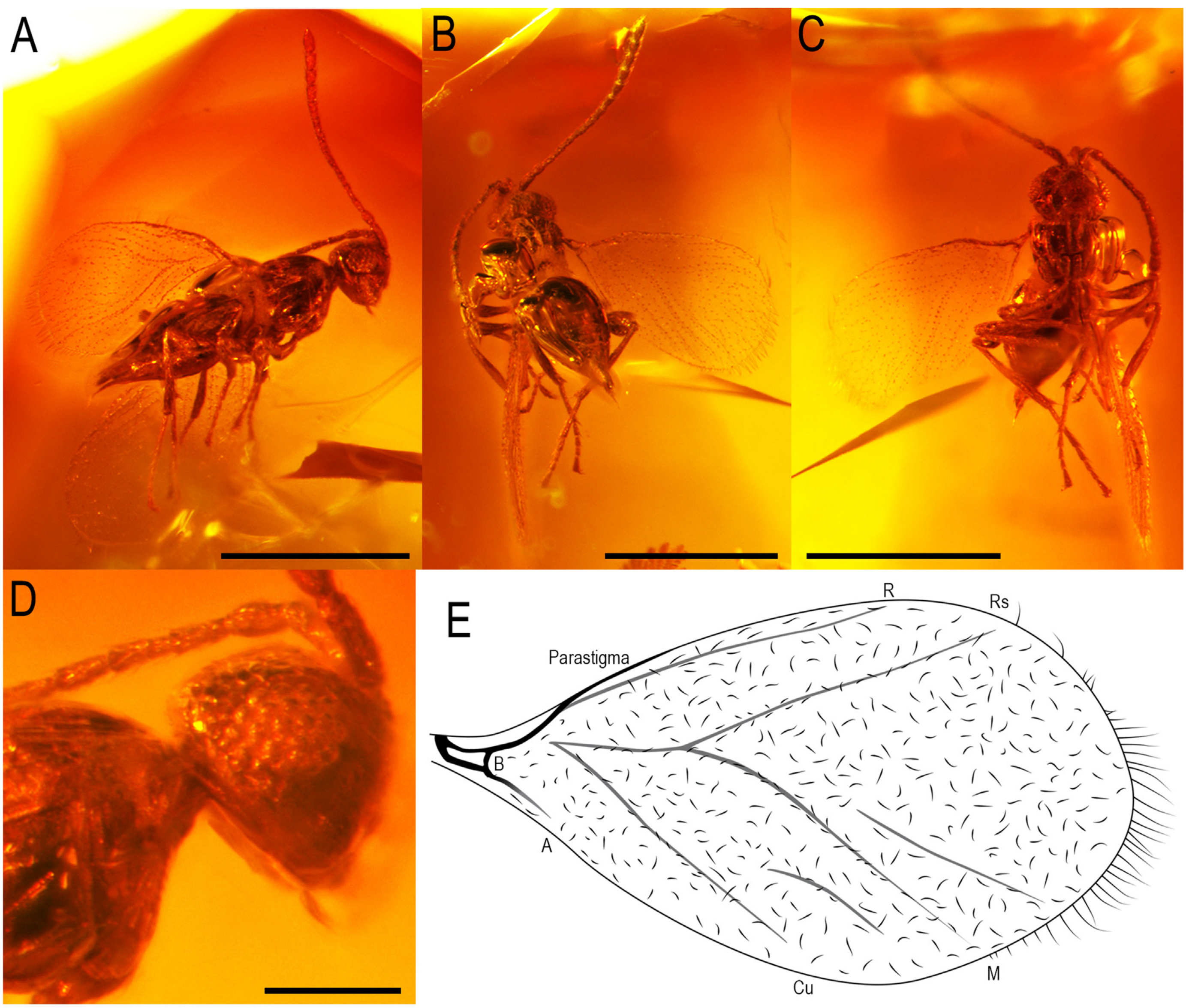

Fig. 5. *Spathiopteryx soosi* sp. nov. (holotype, NHMUS PAL 2022.3.1.); A: Habitus in lateral view; B: Habitus in oblique dorsal view; C: Habitus in oblique ventral view; D: Head in lateral view; E: Fore wing and interpretative line drawing. Scale bars: A–C: 500 μm; D: 100 μm.

longer than body; M + Cu and basal vein B sclerotized; Sc + R less sclerotized; parastigma sclerotized, thin, long, extending beyond anterior third of wing; petiole short (Figs. 5A, B, C, E); second metasomal tergite covering most of gaster (Fig. 5B).

Type locality. Ajka-Csingervölgy [Ajka-Csinger valley], approximately 1 km SE of the city Ajka, Bakony Mountains, Hungary.

Horizon and age. Ajka Coal Formation, unknown shaft of the Ajka-Csingervölgy coal minery; Upper Cretaceous, Santonian, 86.3–83.6 Ma.

Description. Body not pubescent (length 0.89 mm). Head hypognathous, globose (length 0.15 mm); compound eyes rounded (diameter 0.06 mm), bulging, with about 22 ommatidia ('berry-like'), glabrous; frons flat; antennae inserted on shelf of low elevation, at about midface level; antennae with homogeneous, short, nearly indistinct sensillae; scape 5.4 times as long as wide (length 0.08 mm), longer than pedicel and flagellomeres; pedicel bulbous, wider than flagellomeres 1–6, as long as flagellomere 1 (length 0.04 mm); 12 cylindrical flagellomeres, all longer than wide, not modified; flagellomere 1–4 thinnest, 5.5 times as long as wide; flagellomere 5–12, progressively but slightly widening; flagellomere 12 ovoid; back of head roughly punctate to areolate.

Mesosoma shorter than metasoma (length 0.24 mm); pronotum short and smooth, apparently not striated; mesopleuron smooth; mesoscutum hiding pronotum dorsally; notauli deep, straight, converging and meeting posteriorly. Fore wing paddle-like, extending much beyond apex of metasoma, longer than body (length ca. 1.25 mm), smooth, homogeneously micropubescent, i.e. without positive or negative gradient of setae towards apex; row of stiff setae present along apical margin; M + Cu and B sclerotized, Sc + R less sclerotized; Sc + R, M + Cu and B reduced to basal quarter of wing; parastigma sclerotized, thin, long, extending beyond anterior third of wing; short stub of Cu sclerotized; other veins Rs + M, Rs and M nebulous to spectral, setation outlining them. Hind wing hardly visible, just present as very short stub. Legs long and slender, bearing short pubescence; probasitarsomere much shorter than following protarsomeres combined; tibial spur formula 1–1–1; tarsal claws simple.

Metasoma smooth; petiole cylindrical, small, as long as wide (length 0.05 mm); gaster ovoid and fusiform at apex (length 0.45 mm); second metasomal tergite longest, twice as long as third metasomal tergite; following tergites much shorter; ovipositor partly exposed.

Systematic remarks. Among hymenopteran superfamilies, this specimen clearly belongs to the Diaprioidea for possessing a frontal shelf on which antennae are inserted (synapomorphy for Diaprioidea *sensu* Sharkey et al., 2012) and a long scape, oligomerous antennae, a specialized petiolar segment and the metasomal apex tightly closed (synapomorphies for Diaprioidea *sensu* Rasnitsyn and

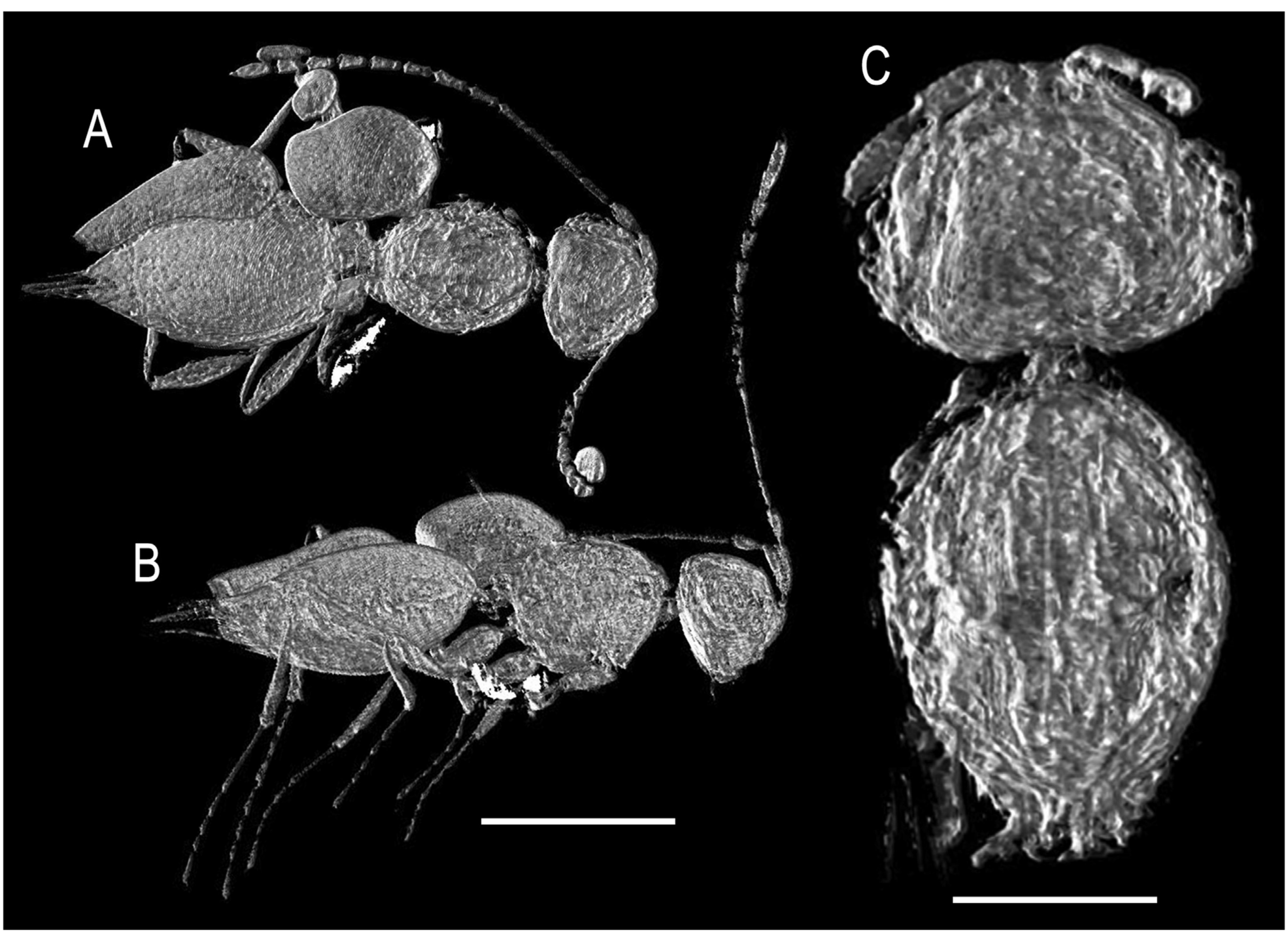

Fig. 6. *Spathiopteryx soosi* sp. nov. (holotype, NHMUS PAL 2022.3.1.) as reconstructed by X-ray CT-scan; A: Habitus in dorsal view; B: Habitus in lateral view; C: Head (without antennae) and mesosoma in lateral view. Scale bars: A, B: 250 μm; C: 100 μm.

Fig. 7. Artistic reconstruction of *Ajkanesia harmincipsziloni* gen. et sp. nov. (left), *Amissidigitus belae* gen. et sp. nov. (upper right) and *Spathiopteryx soosi* sp. nov. (lower right) in the Ajka coal area (western Hungary) during the Santonian, with a nodosaurid dinosaur in the background. Artwork by Márton Szabó.

Öhm-Kühnle, 2020). Regardless of the superfamily, our specimen can easily be identified as a Spathiopterygidae based on its unique shape and venation of the fore wing. Following the key to the genera and species of Spathiopterygidae of Santer et al. (2022), it keys in *Spathiopteryx* Engel and Ortega-Blanco, 2013 for the following characters: fore wing with a well-defined marginal fringe of setae, compound eyes bulging, with few ommatidia, parastigma thin, hind wing only present as a veinal stub, and notauli meeting posteriorly. It also displays diagnostic features of the genus, such as the flagellomeres 1–4 thinner than the following ones, the probasitarsomere much shorter than following protarsomeres combined, and the metasoma about as long as the remainder of body. It differs from *S. alavarommopsis* Engel and Ortega-Blanco, 2013, in having less ommatidia on the eyes, a coarser sculpture on head, and the pronotum without visible striation.

5. Discussion

Hymenopterans are known in the fossil record of Hungary, as they have been reported from Miocene and Pliocene localities in the form of compression fossils. According to Sziráki and Dulai (2002), Symphyta, Chrysididae, Formicidae and Vespoidea are unearthed from the Upper Miocene of Tállya. Katona et al. (2014) reported the remains of herbivorous sawflies (Symphyta) and eusocial wasps (Vespidae), as well as the parasitoid *Anastatus* sp. (Eupelmidae) from the Pliocene of Pula. Additionally, Formicidae has been documented from the Pliocene of Gérce by Krzemiński et al. (1997). But unlike the taxa previously cited, *Ajkanesia harmincipsziloni* gen. et sp. nov., *Amissidigitus belae* gen. et sp. nov. and *Spathiopteryx soosi* sp. nov. are the first formally described fossil hymenopterans from Hungary. The specimens assigned here to Bethylidae and Spathiopterygidae from the ajkaite amber represents the first Mesozoic hymenopterans from Hungary, and from the whole East-Central Europe. Given the fossiliferous potential of ajkaite, further Hymenoptera are likely to be housed in private and museum collections.

The Santonian hymenopteran record is rare, and is mostly known from the Taimyr amber. But this region of Siberia is actually composed of several deposits ranging from the Cenomanian to the Santonian. Formally Santonian-ascribed samples almost exclusively derive from Yantardakh but some Rotoitidae (Hymenoptera) have been mentioned from the neighbouring localities of Bulun, Romanikha and Ugolyak (Gumovsky et al., 2018). Additionally, Rasnitsyn (1980) indicates that two more amber sites (i.e. Sokolovskiy and Iaevskiy) could be correlated with Yantardakh. *Ajkanesia harmincipsziloni* gen. et sp. nov. and *Amissidigitus belae* gen. et sp. nov. both are the second known representative of their respective subfamily during the Santonian. For the Pristocerinae, Colombo and Azevedo (2021) described *Ekaterina volgatitan* Colombo and Azevedo, 2021 and for the Scleroderminae, Evans (1973) described *Celonophamia taimyria* Evans, 1973. Based on a female, *E. volgatitan* may be closely related to *Ajkanesia* gen. nov. but given the high sexual dimorphism within Pristocerinae, it is impossible to associate a male and a female unless rearing them together. Two other bethylid genera are known from Taimyr amber but they belong to extinct subfamilies. The presence of two specimens in Santonian ajkaite sheds more light on the evolution of the Bethylidae between the early Cenomanian (where Burmese amber is the most likely to reveal new taxa in the upcoming years) and the lower Eocene and further fill the Late Cretaceous gap for the Scleroderminae and Pristocerinae.

The Spathiopterygidae are known from most of the major Cretaceous amber deposits, having been described from Lebanese, Spanish, Burmese, and New Jersey amber (Santer et al., 2022, and references therein), additionally with undescribed, poorly preserved representatives in French Charentese amber (V.P., pers. obs.). They seemed to be relatively diverse during this period, at least in the Northern Hemisphere, but no record was known after the Turonian. The discovery of *Spathiopteryx soosi* sp. nov. extends the temporal range of the family by about 8 Ma as well as the temporal and geographical range of the genus *Spathiopteryx*, described originally from the Albian of Spain. It is unclear what drove the Spathiopterygidae to extinction but the addition of a specimen from Santonian shows that it occurred later than previously estimated.

Ajkaite was deposited in a forested, swampy and lacustrine ecosystem (Szabó et al., 2022b). This type of paleoenvironment matches that of Spanish amber ('brackish and freshwater swamps', Delclòs et al., 2007), New Jersey amber ('temperate coastal or deltaic swamps', Grimaldi et al., 2000) and more roughly Burmese amber ('coastal deltaic or estuarine deposit', Cruickshank and Ko, 2003), that have yielded Spathiopterygidae. The family appears to be particularly represented in swampy or flooded ecosystems. This might be related to the living habits of their hosts, that are supposed to be Diptera at immature stage, like most of Diapriidae (Santer et al., 2022) that are often associated with wet forests and marshes (Masner, 1993). It is also not surprising to record Bethylidae in such an environment. Bethylid wasps are known to exploit larvae in cryptic habitats like wood, stem or soil (Evans, 1964) which would correspond to the swamps and lakes where ajkaite was deposited. Furthermore, some Pristocerinae (*Pristepyris* Kieffer, 1905; *Pristocera* Klug, 1808) are known to parasitize larvae of Elateridae (Azevedo et al., 2018), the only family of Coleoptera described in Ajka amber for now (Szabó et al., 2022b).

The Santonian wasp specimens presented here provide an important contribution to a better understanding of the Cretaceous hymenopteran fauna of Europe. Members of the family Bethylidae, already known from western Europe, have been confirmed from the Late Cretaceous western Tethys archipelago and the occurrence of the family Spathiopterygidae has been extended by nearly 8 million years to an area from which they were previously not known at all. An artistic reconstruction of the ajkaite hymenopteran taxa detailed by the present study, depicted in the Ajka coal swamp, can be seen in Fig. 7.

6. Concluding remarks

The three wasps reported herein from the Upper Cretaceous ajkaite amber are the first formally described fossil hymenopteran species from Hungary. *Ajkanesia harmincipsziloni* Szabó & Brazidec gen. et sp. nov. and *Amissidigitus belae* Szabó & Brazidec gen. et sp. nov. are the second Santonian representatives of their respective subfamilies. *Spathiopteryx soosi* sp. nov. also attests of the occurrence of Spathiopterygidae later than previously assumed in the Cretaceous. Based on our findings, ajkaite is a promising source of Santonian hymenopterans.

Acknowledgements

The authors are grateful to Eduardo Koutsoukos, Alexandr Rasntisyn and an anonymous reviewer for their constructive comments. We thank the Eötvös Loránd University Paleontological Department and the Hungarian Natural History Museum for their support during preparation of the amber stone specimens and data analysis. The University of Szeged is acknowledged for the assistance in micro-CT scanning. The research was supported by the MTA-ELTE Lendület Dinosaur Research Group (Grant No. 95102), Hungarian National Research, Development and Innovation Office (NKFIH K 116665, K 131597, PD 130190, FK 130627 and TKP2021-NVA-19). This work is a part of M.B. Ph.D. project on 'The role of greenhouses on the diversification and evolution of the chrysidoid wasps'.

References

Azevedo, C.O., Alencar, I.D.C.C., Ramos, M.S., Barbosa, D.N., Colombo, W.D., Vargas, J.M., Lim, J., 2018. Global guide of the flat wasps (Hymenoptera, Bethylidae). Zootaxa 4489, 1–294. https://doi.org/10.11646/zootaxa.4489.1.1.

Bodor, E.R., Baranyi, V., 2012. Palynomorphs of the Normapolles group and related plant mesofossils from the Iharkút vertebrate site, Bakony Mountains (Hungary). Central European Geology 55 (3), 259–292.

Bodrogi, I., Fogarasi, A., Yazikova, E.A., Sztanó, O., Báldi-Beke, M., 1998. Upper Cretaceous of the Bakony Mts. (Hungary): sedimentology, biostratigraphy, correlation. Zentralblatt für Geologie und Paläontologie, Teil I 11/12, 1179–1194.

Borkent, A., 1997. Upper and Lower Cretaceous biting midges (Ceratopogonidae: Diptera) from Hungarian and Austrian amber and the Koonwarra Fossil Bed of Australia. Stuttgarter Beiträge zur Naturkunde Serie B 249, 1–10.

Choufani, J., Perrichot, V., Girard, V., Garrouste, R., Azar, D., Nel, A., 2013. Two new biting midges of the modern type from Santonian amber of France (Diptera: Ceratopogonidae). In: Azar, D., Engel, M.S., Jarzembowski, E., Krogmann, L., Nel, A., Santiago-Blay, J. (Eds.), Insect Evolution in an Amberiferous and Stone Alphabet, Proceedings of the 6th International Congress on Fossil Insects, Arthropods and Amber. Brill, Leiden, pp. 71–95.

Colombo, W.D., Azevedo, C.O., 2021. Synopsis of the fossil Scleroderminae (Hymenoptera, Bethylidae) with description of a new genus and four new species from Baltic amber. Historical Biology 33, 630–638. https://doi.org/10.1080/08912963.2019.1650275.

Cruickshank, R.D., Ko, K., 2003. Geology of an amber locality in the Hukawng Valley, Northern Myanmar. Journal of Asian Earth Sciences 21, 441–455. https://doi.org/10.1016/S1367-9120(02)00044-5.

Császár, G.H., Góczán, F., 1988. A Bakony felső-kréta kőszénkutatás és kőszén láp vizsgálat (Upper Cretaceous coal prospecting and peat bog studies in the Bakony Mts). In: Magyar Állami Földtani Intézet Évi Jelentése 1986-ról, pp. 155–178 (in Hungarian).

Delclòs, X., Arillo, A., Peñalver, E., Barrón, E., Soriano, C., López del Valle, R., Bernárdez, E., Corral, C., Ortuño, V.M., 2007. Fossiliferous amber deposits from the Cretaceous (Albian) of Spain. Comptes Rendus Palevol 6, 135–149. https://doi.org/10.1016/j.crpv.2006.09.003.

Engel, M.S., Ortega-Blanco, J., Soriano, C., Grimaldi, D.A., Delclòs, X., 2013. A new lineage of enigmatic diaprioid wasps in Cretaceous amber (Hymenoptera: Diaprioidea). American Museum Novitates 3771, 1–23. https://doi.org/10.1206/3771.2.

Evans, H.E., 1964. A synopsis of the American Bethylidae (Hymenoptera, Aculeata). Bulletin of the Museum of Comparative Zoology 132, 1–122.

Evans, H.E., 1973. Cretaceous aculeate wasps from Taimyr, Siberia (Hymenoptera). Psyche 80, 166–178.

Grimaldi, D., Engel, M., 2005. Evolution of the Insects. Cambridge University Press, p. 755.

Grimaldi, D.A., Shedrinsky, A., Wampler, T.P., 2000. A remarkable deposit of fossiliferous amber from the Upper Cretaceous (Turonian) of New Jersey. In: Grimaldi, D.A. (Ed.), Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey. Backhuys, Leiden, pp. 1–76.

Gumovsky, A., Perkovsky, E.E., Rasnitsyn, A.P., 2018. Laurasian ancestors and "Gondwanan" descendants of Rotoitidae (Hymenoptera: Chalcicoidea): what a review of Late Cretaceous *Baeomorpha* revealed. Cretaceous Research 84, 286–322. https://doi.org/10.1016/j.cretres.2017.10.027.

Haas, J., 1983. Senonian in the Transdanubian Central Range. Acta Geologica Hungarica 26, 21–40.

Haas, J., Jocha-Edelényi, E., Császár, G., 1992. Upper Cretaceous coal deposits in Hungary. In: McCabe, P., Parris, J.T. (Eds.), Controls on the Distribution and Quality of Cretaceous Coals, Geological Society of America, Special Paper, vol. 267, pp. 245–262.

Hantken, M., 1878. A magyar korona országainak széntelepei és szénbányászata. Bp., Légrády, p. 331.

Harris, R.A., 1979. A glossary of surface sculpturing. Occasional Papers in Entomology, State of California Department of Food and Agriculture 28, 1–31.

Katona, L.T., Kutasi, C., Papp, B., Tóth, S., 2014. Újabb szenzációs őslénytani leletek a pulai alginitbányából (New remarkable palaeontological finds at the alginite quarry in Pula). Annales Historico-Naturales Musei Nationalis Hungarici 106, 117–140 (in Hungarian).

Kozma, K., 1991. Az ajkai szénbányászat története (History of the Coal Mining at Ajka). Veszprémi Szénbányák Kiadó, Veszprém, p. 531 (in Hungarian).

Krzemiński, W., Krzemińska, E., Kubisz, D., Mazur, M., Pawlowski, J., 1997. Preliminary report on a Pliocene fauna from western Hungary. In: Hably, L. (Ed.), Early Pliocene Volcanic Environment, Flora and Fauna from Transdanubia, West Hungary, Studia Naturalia, vol. 10, pp. 177–192.

Lanes, G.O., Kawada, R., Azevedo, C.O., Brothers, D.J., 2020. Revisited morphology applied for systematics of flat wasps (Hymenoptera, Bethylidae). Zootaxa 4752, 1–127. https://doi.org/10.11646/zootaxa.4752.1.1.

Masner, L., 1993. Superfamily Proctotrupoidea. In: Goulet, H., Huber, J.T. (Eds.), Hymenoptera of the World: an Identification Guide to Families, 1894/E. Research Branch Agriculture Canada Publication, Ottawa, pp. 537–557.

Néraudeau, D., Perrichot, V., Batten, D., Boura, A., Girard, V., Jeanneau, L., Nohra, Y.A., Polette, F., Saint Martin, S., Saint Martin, J.P., Thomas, R., 2017. Upper Cretaceous amber from Vendée, north-western France: age dating and geological, chemical, and palaeontological characteristics. Cretaceous Research 70, 77–95. https://doi.org/10.1016/j.cretres.2016.10.001.

Ősi, A., Bodor, E.R., Makádi, L., Rabi, M., 2016. Vertebrate remains from the Upper Cretaceous (Santonian) Ajka Coal Formation, western Hungary. Cretaceous Research 57, 228–238. https://doi.org/10.1016/j.cretres.2015.04.014.

Perrichot, V., Néraudeau, D., 2014. Introduction to thematic volume "Fossil arthropods in Late Cretaceous Vendean amber (northwestern France)". Paleontological Contributions 10A, 1–4. https://doi.org/10.17161/PC.1808.15981.

Perrichot, V., Néraudeau, D., Nel, A., De Ploëg, G., 2007. A reassessment of the Cretaceous amber deposits from France and their palaeontological significance. African Invertebrates 48, 213–227.

Perrichot, V., Néraudeau, D., Tafforeau, P., 2010. Charentese amber. In: Penney, D. (Ed.), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, pp. 192–207.

Poinar, G.O., 1992. Life in Amber. Stanford University Press, p. 350.

Rasnitsyn, A.P., 1975. Hymenoptera Apocrita of Mesozoic. Trudy Paleontologiceskogo Instituta. Akademija Nauk SSSR 147, 1–134 (in Russian).

Rasnitsyn, A.P., 1980. Origin and Evolution of Hymenoptera. Trudy Paleontologiceskogo Instituta. Akademija Nauk SSSR 174, 1–192 (in Russian).

Rasnitsyn, A.P., Öhm-Kühnle, C., 2020. Taxonomic revision of the infraorder Proctotrupomorpha (Hymenoptera). Palaeoentomology 3, 223–234. https://doi.org/10.11646/palaeoentomology.3.3.2.

Rozlozsnik, P., 1940. A csingervölgyi bányászat múltja, jelene és jövője (Past, present and future of the coal mining in Csingervölgy). In: Magyar Királyi Állami Földtani Intézet Évi Jelentése az 1933-35 évekről, vol. 3, pp. 1231–1245 (in Hungarian).

Santer, M., Álvarez-Parra, S., Nel, A., Peñalver, E., Delclòs, X., 2022. New insights into the enigmatic Cretaceous family Spathiopterygidae (Hymenoptera: Diaprioidea). Cretaceous Research 133, 105128. https://doi.org/10.1016/j.cretres.2021.105128.

Schlüter, T., 1978. Zur Systematik und Palökologie harzkonservierter Arthropoda einer Taphozönose aus dem Cenomanium von NW-Frankreich. Berliner Geowissenschaftliche Abhandlungen (A) 9, 1–150.

Sharkey, M.J., Carpenter, J.M., Vilhelmsen, L., Heraty, J., Liljeblad, J., Dowling, A.P., Schulmeister, S., Murray, D., Deans, A.R., Ronquist, F., Krogmann, L., Wheeler, W.C., 2012. Phylogenetic relationships among superfamilies of Hymenoptera. Cladistics 28, 80–112. https://doi.org/10.1111/j.1096-0031.2011.00366.x.

Siegl-Farkas, Á., 1988. Az Ajkai Kőszén Formáció palynosztratigráfiája és fejlődéstörténete. In: Magyar Állami Földtani Intézet Évi Jelentése 1986-ról, pp. 179–209 (in Hungarian).

Siegl-Farkas, Á., Wagreich, M., 1996. Correlation of palyno- (spores, pollen, dinoflagellates) and calcareous nannofossil zones in the Late Cretaceous of the Northern Calcareous Alps (Austria) and the Transdanubian Central Range (Hungary). In: Advances in Austrian–Hungarian Joint Geological Research, Budapest, pp. 127–135.

Szabó, J., 1871. Az ajkai kőszéntelep a Bakonyban. (in Hungarian: The coal deposits of Ajka in the Bakony Mountains). Földtani Közlöny 1, 124–130.

Szabó, M., Hammel, J.U., Harms, D., Kotthoff, U., Bodor, E., Novák, J., Kovács, K., Ősi, A., 2022a. First record of the spider family Hersiliidae (Araneae) from the Mesozoic of Europe (Bakony Mts, Hungary). Cretaceous Research 131, 105097. https://doi.org/10.1016/j.cretres.2021.105097.

Szabó, M., Kundrata, R., Hoffmannova, J., Németh, T., Bodor, E., Szenti, I., Prosvirov, A.S., Kukovecz, Á., Ősi, A., 2022b. The first mainland European Mesozoic click-beetle (Coleoptera: Elateridae) revealed by X-ray micro-computed tomography scanning of an Upper Cretaceous amber from Hungary. Scientific Reports 12, 24. https://doi.org/10.1038/s41598-021-03573-512:24.

Sziráki, G., Dulai, A., 2002. Sarmatian (Late Miocene) arthropods from Tállya and neighbouring localities (Tokaj Mts, Hungary): A preliminary report. Annales Historico-Naturales Musei Nationalis Hungarici 94, 31–44.

Tasnádi Kubacska, A., 1957. Magyar ősgyanta (Hungarian Fossil Resin). Élet és Tudomány, 1957 (in Hungarian).

Zechmesiter, L., 1926. Adatok az ajkait, egy hazai fosszilis gyanta ismeretéhez (in Hungarian: Notes on ajkaite, a fossil resin from Hungary). Mathematikai és Természettudományi Értesítő 43, 332–341.