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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)

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Journal Pre-proof

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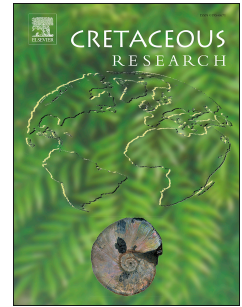
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Author contributions

Conceptualization M Szabó, M Brazidec; **Data Curation** M Szabó, M Brazidec; **Formal Analysis** L Kocsis; **Funding Acquisition** A Ósi; **Investigation** M Szabó, M Brazidec, V Perrichot; **Software** Á Kukovecz, I Szent; **Writing – Original Draft Preparation** M Szabó, M Brazidec, V Perrichot; **Writing – Review and Editing** M Szabó, M Brazidec, V Perrichot, Á Kukovecz, I Szent, A Ósi

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

4
5 Márton Szabó^{1,2*}, Manuel Brazidec³, Vincent Perrichot³, Imre Szenti⁴, Ákos Kukovecz⁴,
6 Attila Ósi^{1,2}

7
8 ¹Hungarian Natural History Museum, Department of Paleontology and Geology, Ludovika tér
9 2, Budapest 1083, Hungary; e-mail: szaboomarton@ttk.elte.hu,
10 szabo.marton.pisces@gmail.com

11 ²ELTE Eötvös Loránd University, Institute of Geography and Earth Sciences, Department of
12 Palaeontology, Pázmány Péter sétány 1/C, Budapest 1117, Hungary; e-mail:
13 hungaros@gmail.com

14 ³Univ Rennes, CNRS, Géosciences Rennes, UMR 6118, 35000 Rennes, France; e-mail:
15 manuel.brazidec@gmail.com, vincent.perrichot@univ-rennes1.fr

16 ⁴University of Szeged, Interdisciplinary Centre of Excellence, Department of Applied and
17 Environmental Chemistry, Rerrich Béla tér 1., 6720, Szeged, Hungary; szentiiimre@gmail.com,
18 kakos@chem.u-szeged.hu

19
20 *corresponding author

21 These authors contributed equally: Márton Szabó and Manuel Brazidec

22
23 Key words: Santonian, Hungary, ajkaite, Hymenoptera, Bethylidae, Spathiopterygidae

24 25 Highlights

- 26 - *Ajkanesia harmincipsziloni* gen. et sp. nov., *Amissidigitus belai* gen. et sp. nov.
27 (Bethylidae) and *Spathiopteryx soosi* sp. nov. (Spathiopterygidae) are the first formally
28 described fossil hymenopterans from Hungary, and the first Mesozoic hymenopterans from
29 East-Central Europe
- 30 - The species *Ajkanesia harmincipsziloni* gen. et sp. nov. and *Amissidigitus belai* gen. et sp.
31 nov. both represent the second data of their subfamily from the Santonian
- 32 - The Spathiopterygidae became extinct later in the Cretaceous than previously assumed

35 Abstract

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

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69 1. Introduction

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

75 Late Cretaceous amber sites rich in bioinclusions are infrequent worldwide. In Europe,
76 such deposits with arthropod inclusions are known only from France and Hungary (Schlüter,
77 1978; Perrichot et al., 2007, 2010; Choufani et al., 2013; Perrichot and Néraudeau, 2014: fig.
78 A1; Néraudeau et al., 2017; Szabó et al., 2022a). Two Late Cretaceous sources of amber are
79 known in Hungary, but only one source has yielded arthropod inclusions so far, the so-called
80 ajkaite which is dug from the Santonian brown coal beds of Ajka (Bakony Mts., western
81 Hungary). The fossiliferous potential of ajkaite has been known for a long time (Szabó, 1871;
82 Hantken, 1878; Zechmeister, 1926, Tasnádi Kubacska, 1957), yet only a handful of fossil
83 arthropods have been formally described: the two biting midge species *Adelohelea hungarica*
84 and *Leptoconops clava* (Borkent, 1997), the two-tailed spider *Hungarosilia verdesi* (Szabó et
85 al., 2022a) and the click beetle *Ajkaelater merkli* (Szabó et al., 2022b).

86 Among the Santonian ambers known worldwide, only the Taimyr amber (Evans, 1973;
87 Rasnitsyn, 1975) and the French amber from Provence (Perrichot et al., 2007) have yielded
88 hymenopteran inclusions. This makes every new occurrence of Santonian amber
89 hymenopterans of great importance in order to better assess the past diversity of various
90 hymenopteran families.

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

95

96 2. Geological background

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

101 The Ajka Coal Formation occurs in the Bakony Mountains (Transdanubian Range),
102 where it is concentrated in three different carbonate terrain sub-basins (Ajka, Magyarpolány-

103 Devecser, and Gyepükaján) (see Császár and Góczán, 1988; Siegl-Farkas, 1988), sometimes
104 reaching the thickness of more than 100 m. The formation is built up on Triassic, or more rarely
105 Jurassic or Lower Cretaceous Limestones, and is overlain by either the marine Jákó Marl
106 Formation, or discontinuously Eocene shallowmarine Szóc Limestone Formation (Haas et al.,
107 1992; Kozma, 1991) (Fig. 1C). The Ajka Coal Formation is composed by an alternation of coal
108 or clayey coal beds, marls, sands and sandstone beds, as well as light grey to brownish
109 carbonaceous to argillaceous pelitic rocks with interbedding molluscan lumachelles (Haas,
110 1983). The depositional area of the Ajka coal was characterized by swampy and lacustrine
111 environments. This resulted in (among others) at least seven main coal-beds, with the oldest nr.
112 6 to the youngest nr. 0, with thicknesses of 80 to 360 cm (Kozma, 1991). Although ajkaite
113 occurs in all coal-bearing layers of the formation, the largest quantities came from the so-called
114 Coal bed 0, also called as 'amber bank' (borostyántelep or gyantástelep or nullás telep in
115 Hungarian) during the coal mining activities in the late 1800's (Rozlozsnik, 1940).

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

120

121 3. Material and Methods

122 Coal mining in the Ajka Subbasin has started in 1865 (Kozma, 1991), and it ceased in
123 2004. Mining has always been carried out on a subsurface basis. While the mines were in
124 operation, amber specimens were collected by individual miners, geologists, and amateur
125 collectors (especially from the very rich Coal bed 0), but unfortunately the number of specimens
126 nowadays does not exceed a few hundred. For this reason, ajkaite became extremely valuable
127 for scientists and amateur collectors as well. The exact locality and stratigraphic origin of the
128 ajkaite specimens within the Ajka Coal Formation investigated in the present study is unknown,
129 all pieces have been donated by private collectors.

130 Two of the hereby described hymenopteran inclusions have been CT scanned at the
131 University of Szeged, Hungary. The X-ray CT measurements were performed with a Skyscan
132 2211 (Skyscan, Bruker, Belgium). The resolutions (voxel sizes) used were $0.6 \mu\text{m}^3$ (specimen
133 NHMUS PAL 2022.3.1) and $1 \mu\text{m}^3$ (specimen NHMUS PAL 2022.1.1). In both cases, a camera
134 offset function was applied to double the width of the field of view. High-resolution images
135 were obtained with a source voltage, current, and exposure time of 80 kV, 600 μA , and 200 ms,
136 respectively. The CT data were reconstructed by using beam-hardening, post alignment, and

137 ring artifact correction implemented in the NRecon (Skyscan, Bruker, Belgium) reconstruction
138 software. For the 3D visualization, CT-Vox 3D Micro-CT Volume Rendering software
139 (Skyscan, Bruker, Belgium) was utilized.

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

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

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

161

162 4. Systematic Paleontology

163 **Order** Hymenoptera Linnaeus, 1758

164 **Superfamily** Chrysidoidea Latreille, 1802

165 **Family** Bethyliidae Haliday, 1839

166 **Subfamily** Pristocerinae Mocsáry, 1881

167 **Genus** *Ajkanesia* Szabó & Brazidec gen. nov.

168 urn:lsid:zoobank.org:act:742C53BD-F776-427F-BB21-D56DBA1664AE

169 **Etymology.** The name is a contraction of “Ajka” (referring to the city of Ajka, from where the
 170 type specimen originates) and *Apenesia*, name of a pristocerine genus with which the holotype
 171 shows some morphological similarities. Gender feminine.

172 **Diagnosis.** Male. Body flattened and slightly elongate (Figs. 2A, B, 3A, B). Head rounded,
 173 slightly longer than wide; eyes round, glabrous (Figs. 2A, C, 3C); clypeus with median lobe
 174 well-defined, projecting, acute triangular; mandibles thick, with four stout teeth (Figs. 2C, 3C);
 175 antennae as long as head + mesosoma combined; flagellomeres cylindrical, elongate; ocellar
 176 triangle large, distance between posterior ocelli equal to distance of posterior ocelli to vertex
 177 crest; vertex crest convex (Figs. 2A, 3C). Dorsal pronotal area short, posterior margin widely
 178 incurved; propleuron elongate; notauli straight, convergent; parapsidal signum present;
 179 mesoscuto-scutellar sulcus elongate and reniform; metapectal-propodeal complex carinate,
 180 metapostnotal-median carina long and straight, metapostnotal-propodeal suture shorter and
 181 slightly incurved; propodeal declivity smooth (Figs. 2B, 3C). Fore wing with C, Sc+R, M+Cu,
 182 A, Rs&M, cu-a, 2r-rs&Rs tubular; 2r-rs&Rs incurved toward wing margin without marked
 183 angle; R1 tubular on half length of second radial cell [2R1] (Figs. 2A, D). Metasoma fusiform,
 184 longer than mesosoma; tergites without modifications (Figs. 2A, 3A, B); hypopygium with
 185 outer surface flat, posterior margin slightly incurved.

186

187 *Ajkanesia harmincipsziloni* Szabó & Brazidec sp. nov.

188 Figs 2, 3

189

190 urn:lsid:zoobank.org:act:5E0D365F-C261-4383-9F18-D556A53E507

191 **Material.** Holotype male, inventory number NHMUS PAL 2022.1.1.

192 **Etymology.** The specific name honours the alternative rock band 30Y. In Hungarian, the band’s
 193 name is phonetically written as “harminc ipszilon”. The band got its name after the
 194 Szombathely (western Hungary) bus service nr 30Y. Three members of the band, namely Zoltán
 195 Beck, László Beck and Zoltán Sárközy spent part of their childhood in the city of Ajka, from
 196 where the holotype specimen originates. The specific epithet is to be treated as name in a
 197 genitive case.

198 **Diagnosis.** As for genus.

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

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

203 **Description.** Body rather flattened (length 2.80 mm). Head prognathous, rounded, slightly
204 longer than wide; LH: 0.60 mm, WH: 0.45 mm; WF: 0.33 mm, HE: 0.18 mm; OOL: 0.21 mm;
205 WOT: 0.11 mm; DAO: 0.06 mm; VOL: 0.11 mm; frons flat; compound eyes round, without
206 pubescence, located anteriorly on head, closer to mandibular insertion than to vertex; clypeus
207 with median lobe acute triangular, projecting forward, carina absent or poorly developed, lateral
208 lobe short; mandibles thick, overlapping at apex, with four stout teeth, ventralmost longest;
209 toruli widely separated by flat surface; antennae as long as head + mesosoma, uniformly
210 pubescent, pubescence shorter than one third of flagellomere length; scape 1.4 times as long as
211 pedicel (scape length 0.17 mm); pedicel elongate, longer than wide (length 0.12 mm), about as
212 long as flagellomeres; 11 flagellomeres distinctly longer than wide, cylindrical, similar in length
213 (length 0.11–0.13 mm); flagellomere 11 tapering at apex, longest; ocellar triangle large,
214 distance between posterior ocelli equal to vertex-ocellus distance; vertex crest convex; occipital
215 carina present.

216 Mesosoma with dorsum smooth, sparsely pubescent (mesosomal length 0.97 mm);
217 dorsal pronotal area short, with posterior margin widely incurved, posterior corners slightly
218 overlapped by anteromesoscutum; propleuron elongate, slightly visible dorsally; mesopleuron
219 without transepisternal line; anteromesoscutum with notauli deeply impressed, straight and
220 convergent posteriorly, posteriorly separated by length of mesoscuto-scutellar sulcus,
221 parapsidal signum present; mesoscuto-scutellar suture with conspicuous sulcus, elongate and
222 reniform; mesoscutellum longer than anteromesoscutum, with posterior corners blunted;
223 metanotum long, overlapping mesoscutellum posteriorly *sensu* Azevedo et al. (2018);
224 metapectal-propodeal complex carinate dorsally, bordered laterally by marginal carina and
225 posteriorly by transverse posterior carina, transverse posterior carina straight, no posterior
226 spines or lateral projections of posterior corners; metapostnotal-median carina present,
227 complete and straight; metapostnotal-propodeal suture present for half-length of metapectal-
228 propodeal complex, very slightly incurved; propodeal declivity without carina. Fore wing
229 extending beyond fourth metasomal terga (LFW: 1.60 mm), uniformly micropubescent and
230 hyaline; tegula present; C, Sc+R, M+Cu, A, Rs&M, cu-a tubular; costal [C], radial [R] and first
231 cubital [1Cu] cells closed; radial [R] and first cubital [1Cu] cells subequal in length: pterostigma
232 slightly swollen, proximally narrower than distally; poststigmatal abscissa of R1 tubular, half as
233 long as second radial cell [2R1] cell; 2r-rs&Rs tubular, originating from distal half of
234 pterostigma, without marked angles, incurved toward wing margin but not reaching it. Hind
235 wing narrow, shorter than fore wing (length ca. 0.87 mm); no venation visible. Legs not
236 especially pubescent, slender; metatrochanter without spines; tibial spurs formula 1–2–2.

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

241 **Systematic remarks.** Following the key to the subfamilies of Bethyridae of Azevedo et al.
242 (2018), this specimen keys in the Pristocerinae for the following characters: specimen
243 macropterous, fore wing with Rs+M absent, metanotum developed medially, overlapping
244 mesoscutellum posteriorly. The taxonomic boundaries between pristocerine genera are mainly
245 based on genitalic structures that cannot be observed on fossil specimens. Following the key to
246 the genera of Pristocerinae of Azevedo et al. (2018), however, our specimen keys between
247 *Apenesia* Westwood, 1874, *Foenobethylus* Kieffer, 1913, *Parascleroderma* Kieffer, 1904 and
248 *Afgoiogfa* Argaman, 1988 for the body smaller than 15 mm, the hypopygium not divided in two
249 lobes, with outer surface flat, the clypeus with median lobe clearly defined and the dorsal
250 pronotal area short, with lateral margin much shorter than anterior one. Nevertheless, the new
251 fossil differs from these genera by the following characters: from *Apenesia*, by the head longer
252 than wide, flagellomeres elongate, thorax flattened, poststigmal abscissa of R1 present; from
253 *Foenobethylus*, by the intersection of Sc+R and Rs&M close to pterostigma, poststigmal
254 abscissa of R1 present, no spines on metatrochanter; from *Parascleroderma*, by the clypeus
255 projecting, pronotum not elongate, intersection of Sc+R and Rs&M close to pterostigma,
256 poststigmal abscissa of R1 present; from *Afgoiogfa*, by the intersection of Sc+R and Rs&M
257 close to pterostigma, pterostigma not comma-like. We propose to create the new genus
258 *Ajkanesia* gen. nov. for this specimen.

259

260 **Subfamily** Scleroderminae Kieffer, 1914

261 **Genus** *Amissidigitus* Szabó & Brazidec gen. nov.

262 urn:lsid:zoobank.org:act:ABD45764-D591-4860-9C7F-A00600CDE371

263 **Etymology.** The name is a contraction of the Latin *amissus* (lost, gone) and *digitus* (toe).
264 Gender masculine.

265 **Diagnosis.** Female. Body slightly depressed (Fig. 4A). Head subquadrate, longer than wide;
266 eye glabrous, much closer to mandibles than to vertex, covering less than half of head; median
267 clypeal lobe obtuse triangular, slightly projecting forward; mandibles with two teeth; antennae
268 with 11 flagellomeres; ocellar triangle much posteriad on head, distance between posterior
269 ocelli equal to distance of posterior ocelli to vertex crest; vertex crest angular; occipital carina
270 present (Figs. 4A, B). Anteromesoscutum shorter than dorsal pronotal area, with notauli

271 present; mesoscuto-scutellar sulcus wide, reniform; metapectal-propodeal complex with
 272 median postnotal carina and metapostnotal-propodeal carinae present (Fig. 4C). Fore wing with
 273 anterior board slightly incurved basally to prestigma; Sc+R, M+Cu, A, 1Rs&1M, cu-a tubular;
 274 pterostigma thin; 2r-rs&Rs tubular and arched toward wing margin, not reaching it; radial [R]
 275 and first cubital [1Cu] cells closed (Figs. 4A, D, E). Metasoma polished, longer than mesosoma;
 276 metasomal segments subequal in length (Fig. 4A).

277

278 *Amissidigitus belai* Szabó & Brazidec sp. nov.

279 Fig. 4

280

281 urn:lsid:zoobank.org:act:FEEFA53C-1DF2-426B-8915-662661653DEF

282 **Material.** Holotype female, inventory number NHMUS PAL 2022.2.1.

283 **Etymology.** In honour of †Béla Szabó (1924-2007), paternal grandfather of the first author.
 284 Béla Szabó was a coal miner in Ajka, where he lost one of his toes in an accident while working
 285 in the underground coal shafts. The binomial name of the species can be translated as “Béla’s
 286 lost toe”. The specific epithet is to be treated as name in a genitive case.

287 **Diagnosis.** As for genus.

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

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

292 **Description.** Body poorly flattened (length 1.97 mm). Head subquadrate, longer than wide;
 293 LH: 0.46 mm, WH: 0.40 mm; WF: 0.25 mm, HE: 0.16 mm; OOL: 0.18 mm; WOT: 0.11 mm;
 294 DAO: 0.02 mm; VOL: 0.11 mm; frons flat; compound eyes glabrous, elliptical, longer than
 295 high, located anteriorly on head, covering less than half of head length; clypeus with median
 296 lobe slightly projecting forward, obtuse triangular, median carina not extending on frons, lateral
 297 lobe poorly developed; mandibles slightly overlapping at apex, bearing two teeth, ventralmost
 298 longer, dorsalmost stouter; maxillary palpi with six palpomeres; toruli separated by their own
 299 diameter by shallow depression; antennae short, barely longer than head, with 13 antennomeres
 300 uniformly micro-pubescent, pubescence shorter than one third of flagellomere length; scape
 301 twice as long as pedicel (scape length 0.12 mm); pedicel longer than wide, longer than
 302 flagellomeres 1–10 that are barely longer than wide; flagellomere 11 longest (f1–f10 length
 303 0.04 mm, f11 length 0.09 mm), tapering at apex; ocellar triangle large, much posteriad on head;
 304 vertex crest angular; occipital carina present.

305 Mesosoma with dorsum smooth (length 0.71 mm); dorsal pronotal area 1.18 times
306 longer than anteromesoscutum (pronotal dorsal length 0.13 mm), slightly narrowing anteriorly,
307 posterior pronotal margin incurved; propleuron not visible dorsally; prosternum small;
308 anteromesoscutum short, notauli straight, converging posteriorly, posteriorly separated by half
309 of width of mesoscuto-scutellar sulcus, parapsidal signum present; mesoscuto-scutellar sulcus
310 wide, reniform; mesoscutellum as long as anteromesoscutum, with slightly outcurved posterior
311 margin, almost touching metapectal-propodeal complex; mesopleuron without transepisternal
312 line; metanotum hidden by mesocutellum; metapectal-propodeal complex carinate dorsally,
313 bordered laterally by marginal carina and posteriorly by transverse posterior carina, transverse
314 posterior carina straight, no posterior spines or lateral projections of posterior corners;
315 metapostnotal-median carina complete, straight; metapostnotal-propodeal suture present for
316 two thirds of length of metapectal-propodeal complex, very slightly incurved; propodeal
317 declivity without carina. Fore wing extending beyond fourth metasomal tergum (LFW: 1.17
318 mm), uniformly micropubescent and hyaline; tegula present; anterior board slightly incurved
319 basally to prestigma; Sc+R, M+Cu, A, 1Rs&1M, cu-a tubular; radial [R] and first cubital [1Cu]
320 cells closed, equal in length: pterostigma thin, elongate; poststigmatal abscissa of R1 absent; 2r-
321 rs&Rs tubular, originating from distal half of pterostigma, without marked angles, incurved
322 toward wing margin but not reaching it. Hind wing narrow, shorter than fore wing (length ca.
323 0.68 mm); without venation. Legs sparsely pubescent; metafemur widest; tarsal claws slightly
324 curved.

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

327 **Systematic remarks.** Following the key to the subfamilies of Bethyridae of Azevedo et al.
328 (2018), this specimen keys in the Scleroderminae for the following characters: specimen
329 macropterous, fore wing with Rs+M absent, metanotum not developed medially, metasomal
330 segments regularly long, metapectal-propodeal complex without posterior spines, mesopleuron
331 without transepisternal line, fore wing vein C absent. Following the key to the sclerodermine
332 genera of Azevedo et al. (2018), it keys in *Nothepyris* Evans, 1973 for the antenna with 11
333 flagellomeres, the body not so depressed, the mandibles with less than five teeth, the fore wing
334 vein C absent and vein A present, and the metasomal tergites 3 and 4 without tubercles; but it
335 differs from *Nothepyris* by the head flattened, not globose, and the occipital carina present.
336 Following the key to the fossil Scleroderminae of Colombo and Azevedo (2021), it keys in
337 *Allobethylus bei* Colombo and Azevedo, 2021 for the antenna with 11 flagellomeres, the
338 mandibles with less than five teeth, the head elongate and rectangular; but it differs from

339 *Allobethylus bei* at least by the notauli present, and from all *Allobethylus* by the mandibles
 340 shorter, the head with the sides conspicuously outcurved rather than parallel, the occipital carina
 341 present, and the mesoscuto-scutellar suture fully sulcate. The genus *Paleoscleroderma* Falières
 342 and Nel, 2019 from lowermost Eocene French amber, not included in previous keys, differs
 343 from our specimen in having the mandibles with five teeth, the occipital carina absent, the
 344 metasomal tergite 2 longer than tergite 3. Therefore, we propose the new genus *Amissidigitus*
 345 gen. nov. to accommodate this morphotype.

346

347 **Superfamily** Diaprioidea Haliday, 1833

348 **Family** Spathiopterygidae Engel and Ortega-Blanco, 2013 (in Engel et al., 2013)

349 **Genus** *Spathiopteryx* Engel and Ortega-Blanco, 2013

350 *Spathiopteryx soosi* Szabó, Brazidec & Perrichot sp. nov.

351 Figs 5, 6

352

353 urn:lsid:zoobank.org:act:15625E01-DEC6-4F90-966C-F47F4B2ADE2E

354 **Material.** Holotype female, inventory number NHMUS PAL 2022.3.1.

355 **Etymology.** In honour of the geologist Dr. Miklós Soós, founder of the Hungarian Dinosaur
 356 Foundation and great supporter of the Ajkaite amber research. The specific epithet is to be
 357 treated as name in a genitive case.

358 **Diagnosis.** Female. Eye occupying most of lateral surface of head, bulging, composed of about
 359 20 ommatidia (Figs. 5A, D); back of head with coarse areolate-punctuate sculptures (Fig. 5A).
 360 Pronotum without visible striation, smooth (Fig. 5D). Fore wing paddle-like, longer than body;
 361 M+Cu and basal vein B sclerotized; Sc+R less sclerotized; parastigma sclerotized, thin, long,
 362 extending beyond anterior third of wing; petiole short (Figs. 5A, B, C, E); second metasomal
 363 tergite covering most of gaster (Fig. 5B).

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

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

368 **Description.** Body not pubescent (length 0.89 mm). Head hypognathous, globose (length 0.15
 369 mm); compound eyes rounded (diameter 0.06 mm), bulging, with about 22 ommatidia ('berry-
 370 like'), glabrous; frons flat; antennae inserted on shelf of low elevation, at about midface level;
 371 antennae with homogeneous, short, nearly indistinct sensillae; scape 5.4 times as long as wide
 372 (length 0.08 mm), longer than pedicel and flagellomeres; pedicel bulbous, wider than

373 flagellomeres 1–6, as long as flagellomere 1 (length 0.04 mm); 12 cylindrical flagellomeres, all
374 longer than wide, not modified; flagellomere 1–4 thinnest, 5.5 times as long as wide;
375 flagellomere 5–12, progressively but slightly widening; flagellomere 12 ovoid; back of head
376 roughly punctate to areolate.

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

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

391
392 **Systematic remarks.** Among hymenopteran superfamilies, this specimen clearly belongs to
393 the Diaprioidea for possessing a frontal shelf on which antennae are inserted (synapomorphy
394 for Diaprioidea *sensu* Sharkey et al., 2012) and a long scape, oligomeric antennae, a
395 specialized petiolar segment and the metasomal apex tightly closed (synapomorphies for
396 Diaprioidea *sensu* Rasnitsyn and Öhm-Kühnle, 2020). Regardless of the superfamily, our
397 specimen can easily be identified as a Spathiopterygidae based on its unique shape and venation
398 of the fore wing. Following the key to the genera and species of Spathiopterygidae of Santer et
399 al. (2022), it keys in *Spathiopteryx* Engel and Ortega-Blanco, 2013 for the following characters:
400 fore wing with a well-defined marginal fringe of setae, compound eyes bulging, with few
401 ommatidia, parastigma thin, hind wing only present as a veinal stub, and notauli meeting
402 posteriorly. It also displays diagnostic features of the genus, such as the flagellomeres 1–4
403 thinner than the following ones, the probasitarsomere much shorter than following
404 protarsomeres combined, and the metasoma about as long as the remainder of body. It differs
405 from *S. alavarommopsis* Engel and Ortega-Blanco, 2013, in having less ommatidia on the eyes,
406 a coarser sculpture on head, and the pronotum without visible striation.

407

408 5. Discussion

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

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

440 The Spathiopterygidae are known from most of the major Cretaceous amber deposits,
441 having been described from Lebanese, Spanish, Burmese, and New Jersey amber (Santer et al.,
442 2022, and references therein), additionally with undescribed, poorly preserved representatives
443 in French Charentese amber (V.P., pers. obs.). They seemed to be relatively diverse during this
444 period, at least in the Northern Hemisphere, but no record was known after the Turonian. The
445 discovery of *Spathiopteryx soosi* sp. nov. extends the temporal range of the family by about 8
446 Ma as well as the temporal and geographical range of the genus *Spathiopteryx*, described
447 originally from the Albian of Spain. It is unclear what drove the Spathiopterygidae to extinction
448 but the addition of a specimen from Santonian shows that it occurred later than previously
449 estimated.

450 Ajkaite was deposited in a forested, swampy and lacustrine ecosystem (Szabó et al.,
451 2022b). This type of paleoenvironment matches that of Spanish amber ('brackish and
452 freshwater swamps', Delclòs et al., 2007), New Jersey amber ('temperate coastal or deltaic
453 swamps', Grimaldi et al., 2000) and more roughly Burmese amber ('coastal deltaic or estuarine
454 deposit', Cruickshank and Ko, 2003), that have yielded Spathiopterygidae. The family appears
455 to be particularly represented in swampy or flooded ecosystems. This might be related to the
456 living habits of their hosts, that are supposed to be Diptera at immature stage, like most of
457 Diapriidae (Santer et al., 2022) that are often associated with wet forests and marshes (Masner,
458 1993). It is also not surprising to record Bethylidae in such an environment. Bethylid wasps are
459 known to exploit larvae in cryptic habitats like wood, stem or soil (Evans, 1964) which would
460 correspond to the swamps and lakes where ajkaite was deposited. Furthermore, some
461 *Pristocerinae* (*Pristepyrus* Kieffer, 1905, *Pristocera* Klug, 1808) are known to parasitize larvae
462 of Elateridae (Azevedo et al., 2018), the only family of Coleoptera described in Ajka amber for
463 now (Szabó et al., 2022b).

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

471

472 6. Concluding remarks

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

479

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490

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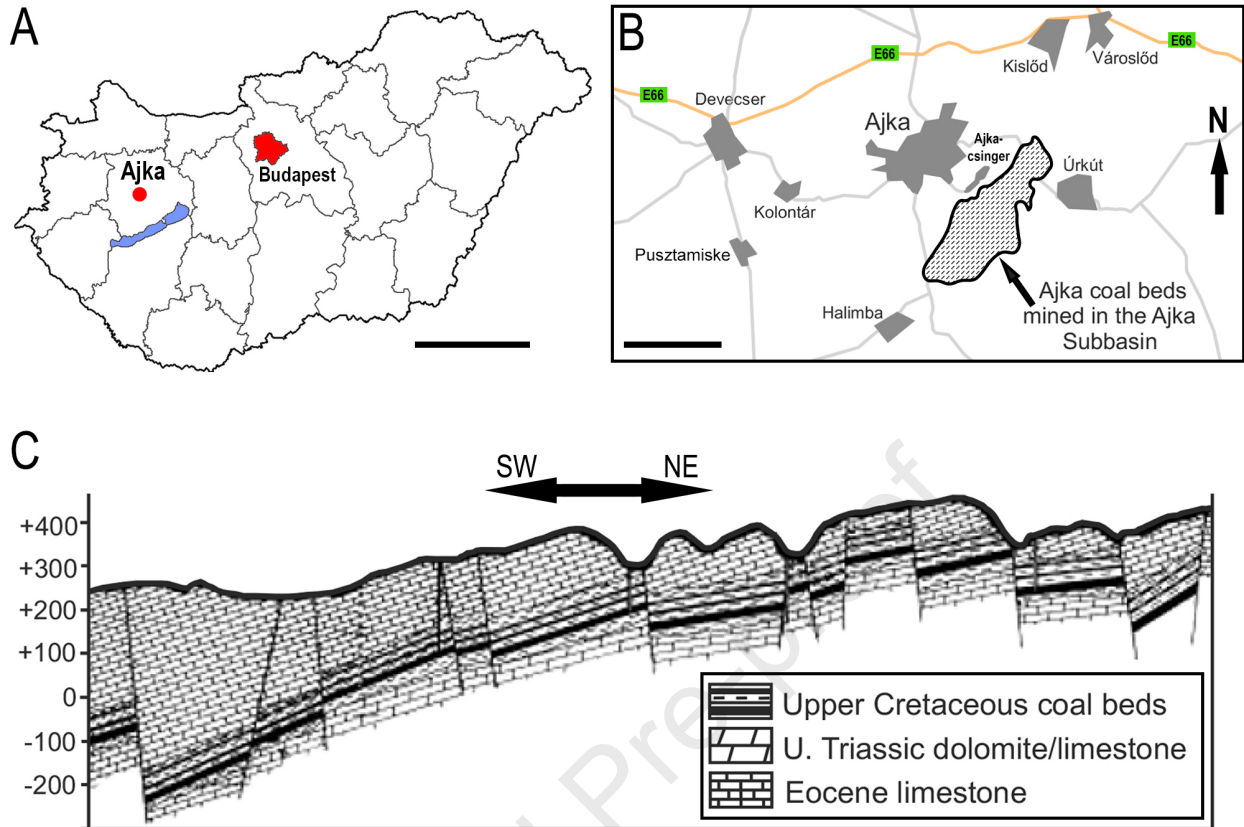
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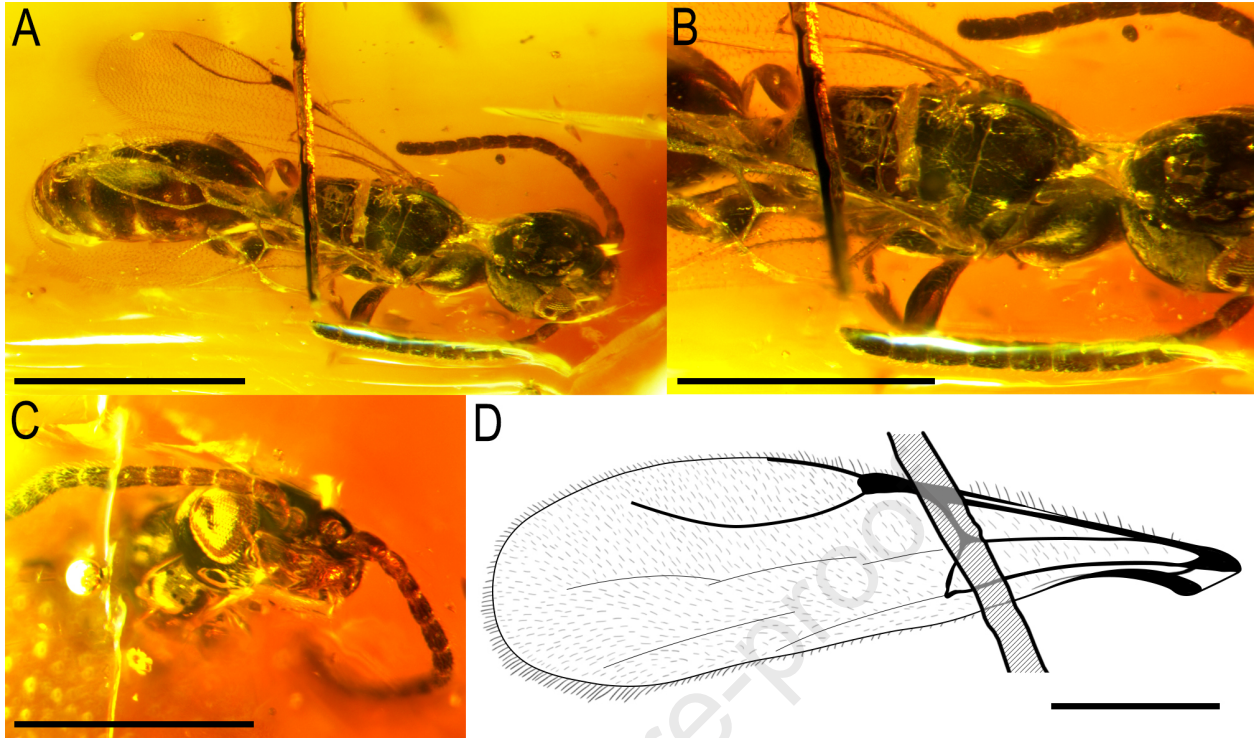
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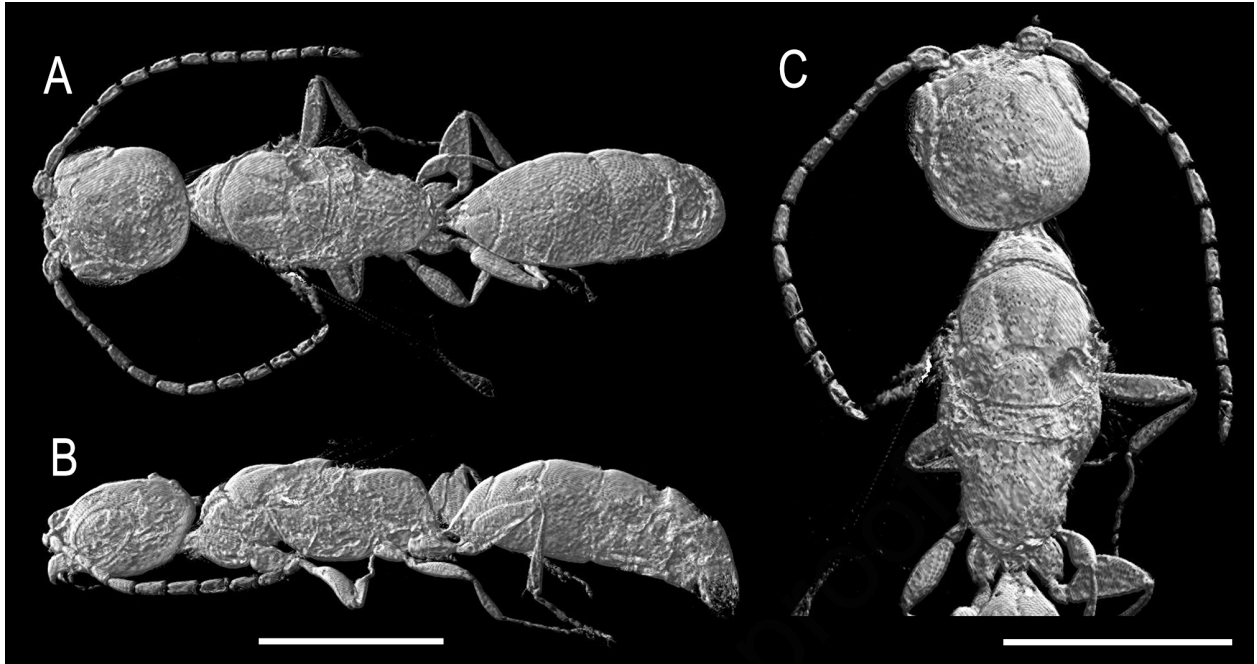
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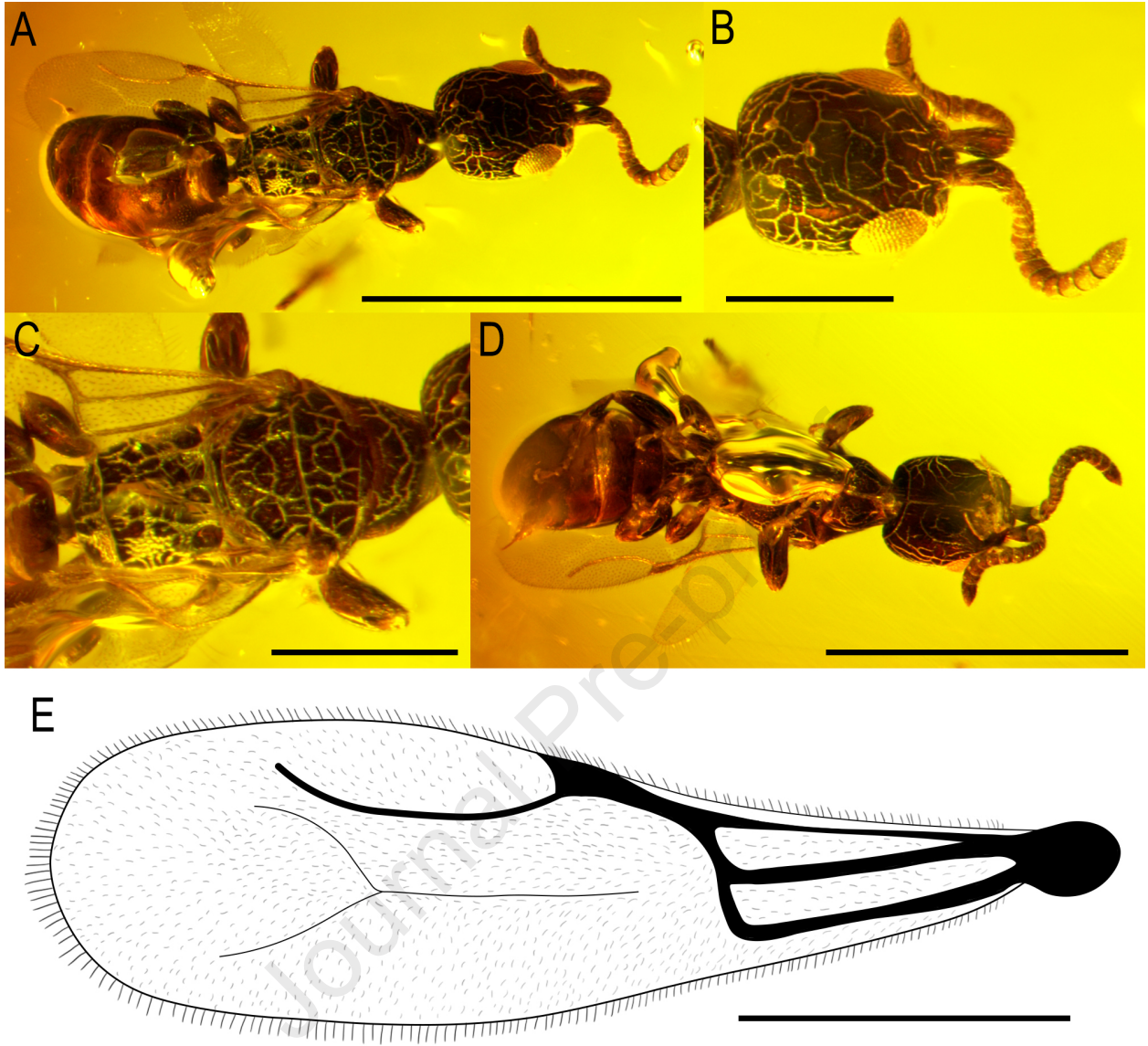
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- 626
- 627 Figure captions
- 628 Figure 1. A: Locality map of Ajka; B: Location of Ajka-Csinger valley and the Ajka Coal area
629 in western Hungary; C: Simplified geological section of the Ajka Subbasin. Scale bars:
630 A: 100 km; B: 3 km.
- 631 Figure 2. *Ajkanesia harmincipsziloni* gen. et sp. nov. (holotype, NHMUS PAL 2022.1.1.); A:
632 Habitus in dorsal view; B: Mesosoma in dorsal view; C: Head in frontal view; D: Line
633 drawing of the fore wing venation (covered parts of the venation have been drawn after
634 the opposite fore wing, see Fig 2A). Scale bars: A: 750 µm; B, C: 500 µm; D: 250 µm.
- 635 Figure 3. *Ajkanesia harmincipsziloni* gen. et sp. nov. (holotype, NHMUS PAL 2022.1.1.) as
636 reconstructed by X-ray CT-scan; A: Habitus in dorsal view; B: Habitus in lateral view;
637 C: Head (with antennae) and mesosoma in dorsal view. Scale bars: 0.5 mm.

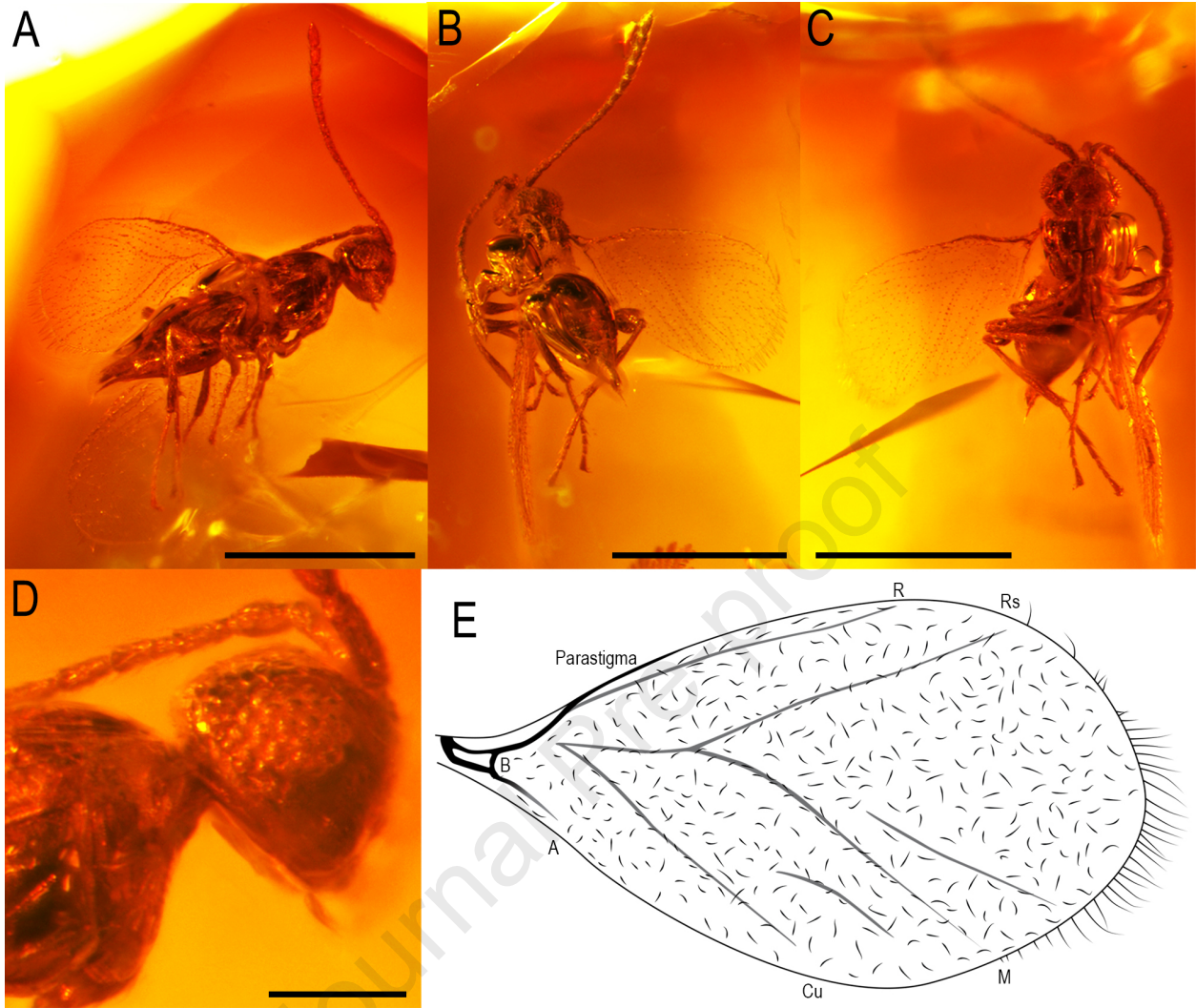
- 638 Figure 4. *Amissidigitus belai* gen. et sp. nov. (holotype, NHMUS PAL 2022.2.1.); A: Habitus
639 in dorsal view; B: Head in dorsal view; C: Mesosoma in dorsal view; d: Habitus in ventral
640 view; e: Line drawing of fore wing. Scale bars: A, D: 750 μm ; B, C, E: 250 μm
- 641 Figure 5. *Spathiopteryx soosi* sp. nov. (holotype, NHMUS PAL 2022.3.1.); A: Habitus in lateral
642 view; B: Habitus in oblique dorsal view; C: Habitus in oblique ventral view; D: Head in
643 lateral view; E: Fore wing and interpretative line drawing. Scale bars: A–C: 500 μm ; D:
644 100 μm
- 645 Figure 6. *Spathiopteryx soosi* sp. nov. (holotype, NHMUS PAL 2022.3.1.) as reconstructed by
646 X-ray CT-scan; A: Habitus in dorsal view; B: Habitus in lateral view; C: Head (without
647 antennae) and mesosoma in lateral view. Scale bars: A, B: 250 μm ; C: 100 μm
- 648 Figure 7. Artistic reconstruction of *Ajkanesia harmincipsiloni* gen. et sp. nov. (left),
649 *Amissidigitus belai* gen. et sp. nov. (upper right) and *Spathiopteryx soosi* sp. nov. (lower
650 right) in the Ajka coal area (western Hungary) during the Santonian, with a nodosaurid
651 dinosaur in the background. Artwork by Márton Szabó.

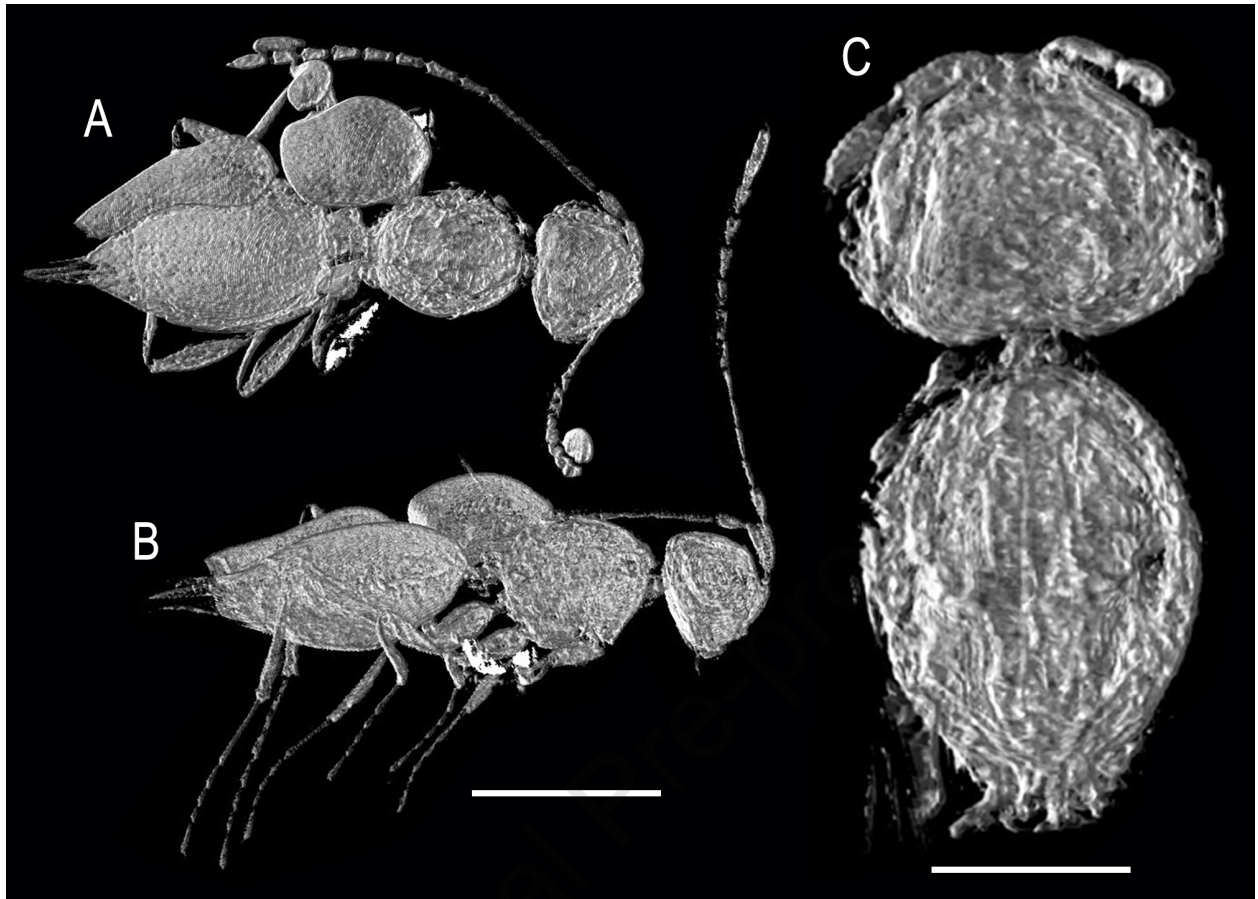














Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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