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First record of the spider family Hersiliidae (Araneae) from the Mesozoic of Europe (Bakony Mts, Hungary)

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A B S T R A C T

An adult male Hersiliidae spider is described from amber that originates from the Upper Cretaceous (Santonian) Ajka Coal Formation (Ajka-Csingervölgy, Hungary), the so-called ajkaite. The spider has elongate posterior spinnerets and a short third pair of legs III, both characteristics of the family, but differs from all known Mesozoic (discovered in burmite) and fossil and Recent European representatives of Hersiliidae so that a new genus and species name is proposed for *Hungarosilia verdesi* gen. et sp. nov. The new taxon is distinguishable by the following unique combination of characters: pro- and opisthosoma nearly circular in dorsal view; posterior spinnerets with a distal article more than three times longer than the basal article; pedipalpal tibia and patella short and stout but pedipalpal femur as long as the cymbium, cymbium egg-shaped and without cymbial apophysis; bulbus of circular shape in ventral view and slightly flattened is lateral view. The fossil represents the first record of Hersiliidae from the Mesozoic of Europe and establishes the second record of this family in the Mesozoic Era. The estimated paleoclimate and paleoflora of the Ajka coal sub-basin correspond well with habitat preferences of Recent relatives that are often arborical and found in association with tree bark. Overall, our findings highlight the importance of a neglected amber type, the ajkaite, for documenting and studying the European arthropod fauna during the Mesozoic.

1. Introduction

Arthropod fossils preserved in amber offer exciting possibilities to study morphology but also aspects of behaviour and ecology because the preservation is three-dimensional, often complete, and at a fine-scale that is unusual for other preservation modes, e.g., compressions fossils. Sporadic occurrences of amber are reported from numerous localities in Hungary that represent various ages (see Csillag and Földvári, 2005; Papp, 2002), but systematically collectable Mesozoic amber with a potential for arthropod-inclusions is only known from two localities: Iharkút (Csehbánya Formation) and Ajka (Ajka Coal Formation). Both ambers are estimated to be of Late Cretaceous (Santonian, 86.3–83.6 Mya) age. Our study focuses on the amber material collected from the Ajka Coal Formation, as despite the large sample size and almost identical geochemical composition (Kovács et al., 2015), arthropod inclusions are yet unknown from Iharkút amber (Hajdu, 2015; Ősi, 2012). The study of Santonian amber of the Ajka area (denominated as *ajkaite*) has a long tradition in Hungary and numerous experts have investigated amber from these deposits. A few

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hundred pieces have been collected by either scientists or amateur collectors in the last 160 years but, unfortunately, no one made comprehensive, layer-by-layer excavations or collections to increase the number of valuable inclusions. This may be the reason that very few arthropod fossils are still known from this type of amber although it preserves, amongst others, spiders and other arachnids.

The family Hersiliidae is an ecribellate entelegyne spider family that presently includes 183 species belonging to 16 genera (see the online database of the World Spider Catalog, Version 22.5). This family has quite a rich fossil record with roughly 20 species known mostly from fossil resins, i.e. the Cretaceous amber of Myanmar, Baltic amber in Europe from the Eocene, Dominican and Chiapas ambers of Miocene age, and even copal in Madagascar (see Table 1). Also termed "two-tailed spiders" or "tree trunk spiders", these animals reside on or under the bark of trees where they hunt for prey at night. These spiders use their characteristic, elongate posterior lateral spinnerets for prey capture, usually insects, and rotate around the prey at great speed while holding the spinnerets over the victim so that it is fixed to the substrate with strong silk threads (Dippenaar-Schoeman, 2014; Eberhard, 1967; Murphy and Murphy, 2000; Rheims and Brescovit, 2004a; Yağmur et al., 2008).

The aim of the present study is to describe a male Hersiliidae individual discovered in ajkaite and place it in a systematic framework. We also evaluate the fossil within the climate and paleobotanical framework that has been proposed for the Ajka Coal paleoenvironment during the Santonian.

2. Previous work on ajkaite

The presence of amber in the brown coal deposits of Ajka (Ajka Coal Formation, see below) has been known since the 19th century when coal mining in the area of Ajka had begun. Scientific evaluation of the Ajka amber started only in the 1920's (Kozma, 1991). The earliest report about the fossil resins of the Ajka Coal was established by Miksa Hantken (data from 1866, in Szabó, 1871) who mentioned „*amber-like resin*" from the Upper Cretaceous brown coal deposits. Later, this fossil resin was mentioned as ajkite (Anonymous, 1878) and the term ajkaite (*ajkait* in Hungarian) was first used by Zechmesiter (1926). For physical and chemical characteristics of ajkaite see Csillag and Földvári (2005), Hlasiwetz (1871), Kovács et al. (2015), Papp (2002, and references therein), Rozlozsnik (1940) and Zechmesiter (1926). The composition is clearly different from the much younger Eocene succinites (Baltic-, Bitterfeld- and Rovno ambers) or rentinite and the most probable origin is copal (Góczán, 1961).

Although amber inclusions are rather poorly documented from Hungary, the arthropod inclusions preserved in ajkaite did attract the interest of some researchers. The earliest report about these inclusions belongs to Tasnádi Kubacska (1957) who mentioned "(…) *mites, spiders, mosquitos, flies, tropical and subtropical species*". Koch (1985) wrote the following notes: "*Insect inclusions are rather common in the amber pieces coming from here* (Ajka)". The first detailed paleoentomological report belongs to Borkent (1997) who described two new ceratopogonid species, *Leptoconops clava* and *Adelohelea magyarica*, from ajkaite. Czirják (2012), Czirják and Hajdu (2011), Főzy and Szente (2012), Hajdu and Czirják (2012) and Ősi (2012) briefly mentioned Arachnida, Coleoptera, Hymenoptera and Diptera inclusions. In her unpublished MSc thesis, Hajdu (2015) described the ajkaite fauna of flies (Diptera) in detail.

3. Locality, geological background and age

The first outcrops of the Ajka Coal Formation were discovered in the 1860's in the Ajka-Csinger Valley (or Ajkacsinger), roughly four kilometres southeast from the city Ajka (Bakony Mountains, western Hungary) (see Hantken, 1878; Szabó, 1871; see also Fig. 1A, B of the present study). Most if not all the available ajkaite specimens come from underground mines or spoil-banks along the Csinger Valley.

The Ajka Coal Formation occurs in the Bakony Mountains (Transdanubian Range) and is sometimes over 100 m thick. It is concentrated in three different carbonate terrain sub-basins (Ajka, Magyarpolány-Devecser, and Gyepükaján) (see Császár and Góczán, 1988; Siegl-Farkas, 1988). With Upper Triassic or, more rarely, Jurassic or Lower Cretaceous limestones forming a geological basement, the Ajka Coal Formation is built up 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 interbedded molluscan lumachelles (Haas, 1983). The depositional area was characterized by swampy and lacustrine environments resulting in among others at least seven main coal-beds (with the oldest coal bed 6. to the youngest coal bed 0.) with thicknesses ranging from 80 to 360 cm (Kozma, 1991).

Based on palynological and nannoplankton investigations, the age of the formation is Santonian (Bodor and Baranyi, 2012; Bodrogi et al., 1998; Ősi et al., 2016; Siegl-Farkas and Wagreich, 1996). The Ajka Coal Formation is overlain by either the marine Jákó Marl Formation (Haas et al., 1992), or discontinuously Eocene shallow-marine limestones of the Szőc Limestone Formation (Fig. 1C).

In fact, ajkaite occurs in varying amounts across all coal-bearing layers of the formation. However, the largest quantities come from the strata of the so-called Coal bed 0, also called 'amber bank' (*borostyántelep* or *gyantástelep* or *nullás telep* in Hungarian) in the late 1800's (Rozlozsnik, 1940).

Besides amber fossils, a diverse flora and fauna of the Ajka Coal Formation have been described by numerous authors. The fossil flora of the formation has been described in detail by Greguss (1949), Kedves et al. (2000, 2001, 2002), Kedves and Alvarez Ramis (2002), Rákosi (1991), Rákosi and Barbacka (2000), Siegl-Farkas (1988) and Tasnádi Kubacska (1957). Kedves and Párdutz (2002) reported the presence of three different types of morphologically intact bacteria preserved in ajkaite. The Ajka Coal Formation is famous for its extremely rich mollusc fauna, which was documented in several papers (Bandel and Riedel, 1994; Czabalay, 1988; Oppenheim, 1892; Tausch, 1886). Ostracods were investigated by Monostori (1988). Vertebrates are represented by fishes, turtles, mosasauroids, crocodyliforms, and dinosaurs (Ősi et al., 2016).

4. Material and methods

Since coal mining in the area of Ajka ceased in 2004, ajkaite is collectable only at the coal refuses nearby the city (e.g. at the so-called Jókai coal refuse), usually as tiny splinters, or opaque, oxidated drops. For this reason, ajkaite is highly valued both by scientists and private collectors. Several hundreds of ajkaite pieces, housed in official and private collections, were inventoried first and then checked for arthropod remains. The present specimen results from this inventory and is deposited in the collection of the Department of Palaeontology and Geology of the Hungarian Natural History Museum (NHMUS, Budapest).

Károly Kozma (1936–2014) donated a large piece of ajkaite to the Paleontological Department of the Eötvös University (Budapest), supervised by Attila Ősi. The specimen came from an unknown shaft of the Ajka-Csingervölgy coal mine and it was, arguably, the largest piece of ajkaite ever known to science (Fig. 2A). Since it was almost completely opaque and too dark for examination under a light microscope, the piece was scanned by using the NIKON Metrology Model XT H225 ST X-Ray tomograph of the University of Pannonia (Veszprém, Hungary). During the scanning

Table 1
Fossil record of family Hersiliidae.

Fossil Hersiliidae of the World				
Horizon		Taxon	Locality	References
Mesozoic	Cenomanian (Cretaceous)	*Burmesiola cretacea*	Myanmar	Wunderlich, 2011a
		Burmesiola daviesi		Wunderlich, 2015
		?Burmesiola kachinensis		Wunderlich and Müller, 2020
		Spinasilia dissoluta		Wunderlich, 2015
		Hersiliidae indet.		Wunderlich, 2015
	Santonian (Cretaceous)	***Hungarosilia verdesi* gen. et sp. nov.**	**Hungary**	**Present study**
Cenozoic	Ypresian (Eocene)	*Hersiliola* sp.	U.S.A.	Selden and Wang, 2014
	Lutetian (Eocene)	*Gerdia myura*	Baltic region	Menge, 1869
		Gerdiopsis infringens		Wunderlich, 2004
		Gerdiorum inflexum		Wunderlich, 2004, 2011b
		Hersilia longipes		Giebel, 1856
		Hersilia miranda		Koch and Berendt, 1854
		Hersiliidae indet. 1-3		Wunderlich, 2004
	upper Oligocene	*Hersilia aquisextana*	France	Gourret, 1887
	upper Oligocene to lower Miocene	*Fictotama extincta*	Mexico	Petrunkevitch, 1963; Penney, 2006
		Perturbator corniger		Petrunkevitch, 1971; Penney, 2006
		Prototama antiqua		Petrunkevitch, 1971; Penney, 2006
		Prototama succinea		Petrunkevitch, 1971; Penney, 2006
	upper lower Miocene to lower middle Miocene	*Fictotama maculosa*	Dominican Republic	Wunderlich, 2011c
		Prototama maior		Wunderlich, 1988; Penney, 2006
		Prototama media		Wunderlich, 1988; Penney, 2006
		Prototama minor		Wunderlich, 1987; Penney, 2006
		Prototama sp.		Wunderlich, 1988
		Tama sp.		Schawaller, 1981
	Quaternary (Pleistocene–Holocene)	*Gorgorops jadis*	Madagascar	Wunderlich, 2011d
		Hersilia madagascarensis		Wunderlich, 2004
		Hersiliana brevipes		Wunderlich, 2004
		Hersiliidae indet.		Wunderlich, 2015

procedure, multiple arthropod inclusions were discovered inside the piece, including a relatively large-sized spider that we describe here (Fig. 2B, C).

For the best available resolution of modelling, the ajkaite specimen was carefully broken into pieces around the spider. To achieve the highest resolution possible, the piece containing the spider was examined further at the Deutsches Elektronen Synchrotron (Hamburg, Germany) where it was studied using synchrotron radiation based micro-computed tomography (SRμCT). Imaging was performed at the Imaging Beamline P05 (IBL) (Greving et al., 2014; Haibel et al., 2010; Wilde et al., 2016) operated by the Helmholtz-Zentrum Hereon at the storage ring PETRA III (Deutsches Elektronen Synchrotron – DESY, Hamburg, Germany). Imaging was done at a photon energy of 32.6 keV and a sample to detector distance of 80 mm. Projections were recorded using a custom-developed 20 MP CMOS camera system (Lytaev et al., 2014) with an effective pixel size of 1.28 μm. For each tomographic scan 2401 projections at equal intervals between 0 and π have been recorded. Tomographic reconstruction has been done by applying a transport of intensity phase retrieval approach and using the filtered back projection algorithm (FBP) implemented in a custom reconstruction pipeline (Moosmann et al., 2014) using Matlab (Math-Works) and the Astra Toolbox (van Aarle et al., 2015, 2016; Palenstijn et al., 2011). For the processing, raw projections were binned for further processing two times, resulting in an effective pixel size of the reconstructed volume of 2.56 μm.

5. Systematic paleontology

Order Araneae Clerck, 1757
Infraorder Araneomorphae Smith, 1902

Family Hersiliidae Thorell, 1870
Type genus: *Hersilia* Audouin, 1826

Remarks. Based on the elongate, tapering posterior lateral spinnerets and the short third pair of legs, the specimen described below clearly represents the family Hersiliidae (Mirshamsi et al., 2013; Wunderlich, 2004, 2015; Wunderlich and Müller, 2020) although some other diagnostic characters remain equivocal. Based on the listed characteristics below, the Ajka-Csingervölgy specimen cannot be referred to any known Hersiliidae genus from the Mesozoic, nor to any fossil or extant European representative of the family. A new genus is therefore proposed to accommodate the fossil.

Genus ***Hungarosilia*** gen. nov.
urn:lsid:zoobank.org:act: A59579E8-0D0D-4E5C-9711-63419C044573

Etymology. After Hungary; combined with the term „*silia*", part of the family name Hersiliidae.
Type species. Hungarosilia verdesi gen. et sp. nov. (by monotypy).
Type horizon, age and locality. Ajka Coal Formation (Santonian, Upper Cretaceous), unknown shaft of the Ajka-Csingervölgy coal mine; Ajka-Csingervölgy (Hungary).
Diagnosis. The diagnosis is given for ♂, the ♀ is unknown. Details of clypeus, eyes, chelicerae, dorsal surface of prosoma and opisthosoma are unknown. Pro- and opisthosoma nearly as long as wide. Legs I, II and IV incomplete; metatarsus of legs III undivided and lacking long trichobothria; tarsi of legs III short without any sign of long trichobothria. Posterior lateral spinnerets elongate and roughly as long as the opisthosoma, their apical segment is more than three times longer than the basal article; anterior spinnerets separated by a triangular colulus. Pedipalpal tibia and patella short and stout but pedipalpal femur long (as long as the cymbium); cymbium egg-shaped, without cymbial apophysis; questionable apical cymbial bristles present; bulbus of circular shape in ventral view and slightly flattened is lateral view.
Remarks. Due to the incompleteness of the only known specimen, the key given by Wunderlich (2004: 815) to fossil and extant hersiliid

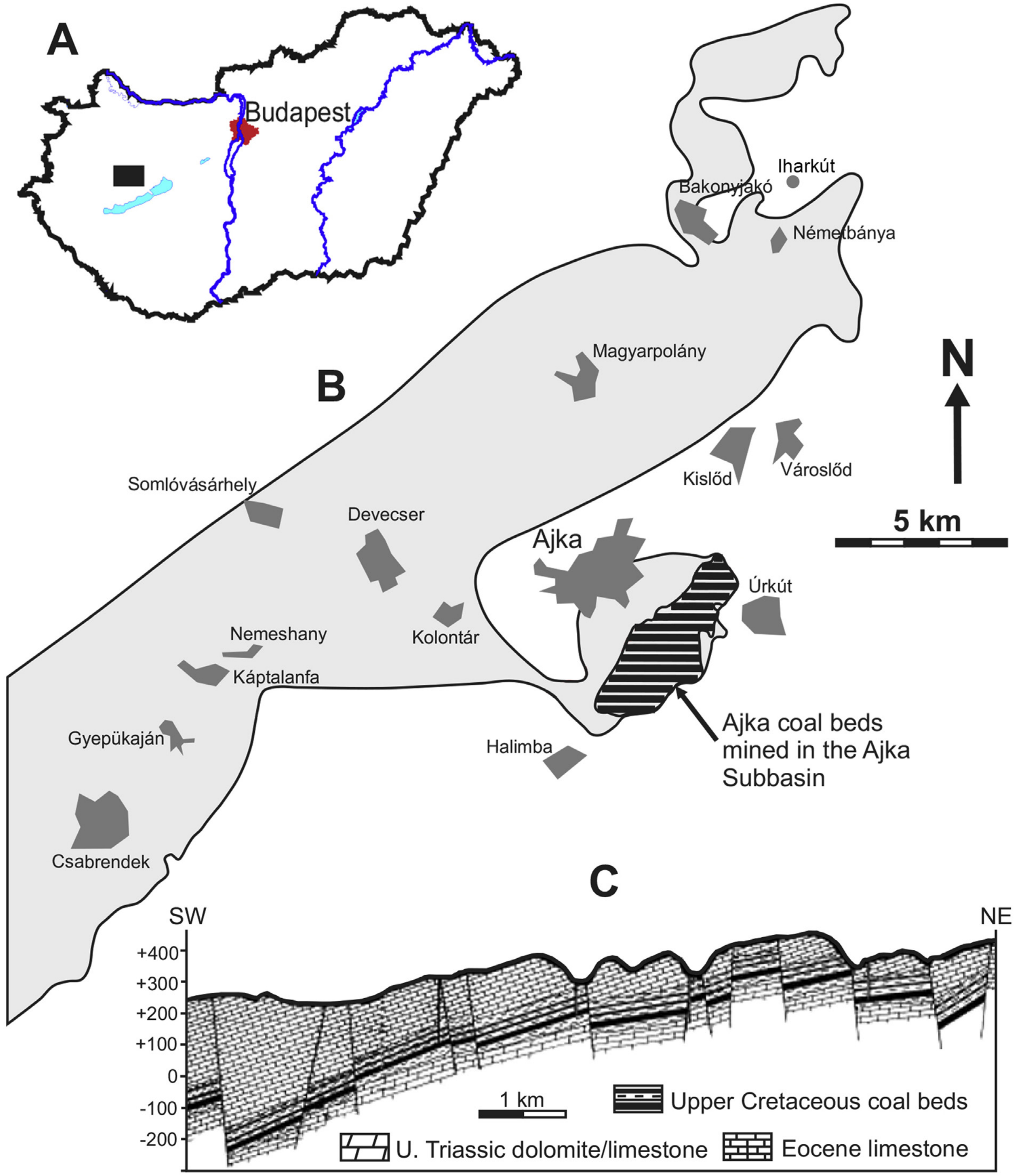

Fig. 1. A: Location of Ajka-Csingervölgy and the Ajka Coal area in western Hungary. B: distributional map of the Ajka Coal Formation (light grey) (modified after Császár and Góczán, 1988). C: Simplified geological section of the Ajka Subbasin (modified after Kozma, 1991).

genera cannot be used here. However, the new genus differs from both the extinct and extant genera in a number of characters.

Up to the present study only two Mesozoic genera of the family have been described, namely *Burmesiola* and *Spinasilia* (Wunderlich, 2011a, 2015; Wunderlich and Müller, 2020), both from the Burmese amber of the Cenomanian (ca. 99 Ma) of Myanmar. *Burmesiola* has 5 long trichobothria on metatarsi III, and posterior spinnerets at least 2/3 as long as the opisthosoma, with the apical article at best slightly longer than the basal article (Wunderlich, 2011a: 551, fig. 9 and photo 53a,b; 2015: 303–304; photo 142; Wunderlich and Müller, 2020, photo 27). By contrast, preserved metatarsi III of *Hungarosilia* gen. nov. possess no signs of long trichobothria. The posterior spinnerets are as long as the opisthosoma and the apical article is much (more than three times) longer than the basal one. *Hungarosilia* gen. nov. differs from *Spinasilia* in having posterior spinnerets about as long as the opisthosoma (posterior spinnerets of *Spinasilia* are longer than the opisthosoma), in the more egg-shaped cymbium, and in the lack of a cymbial apophysis (present in *Spinasilia*, see in Wunderlich, 2015).

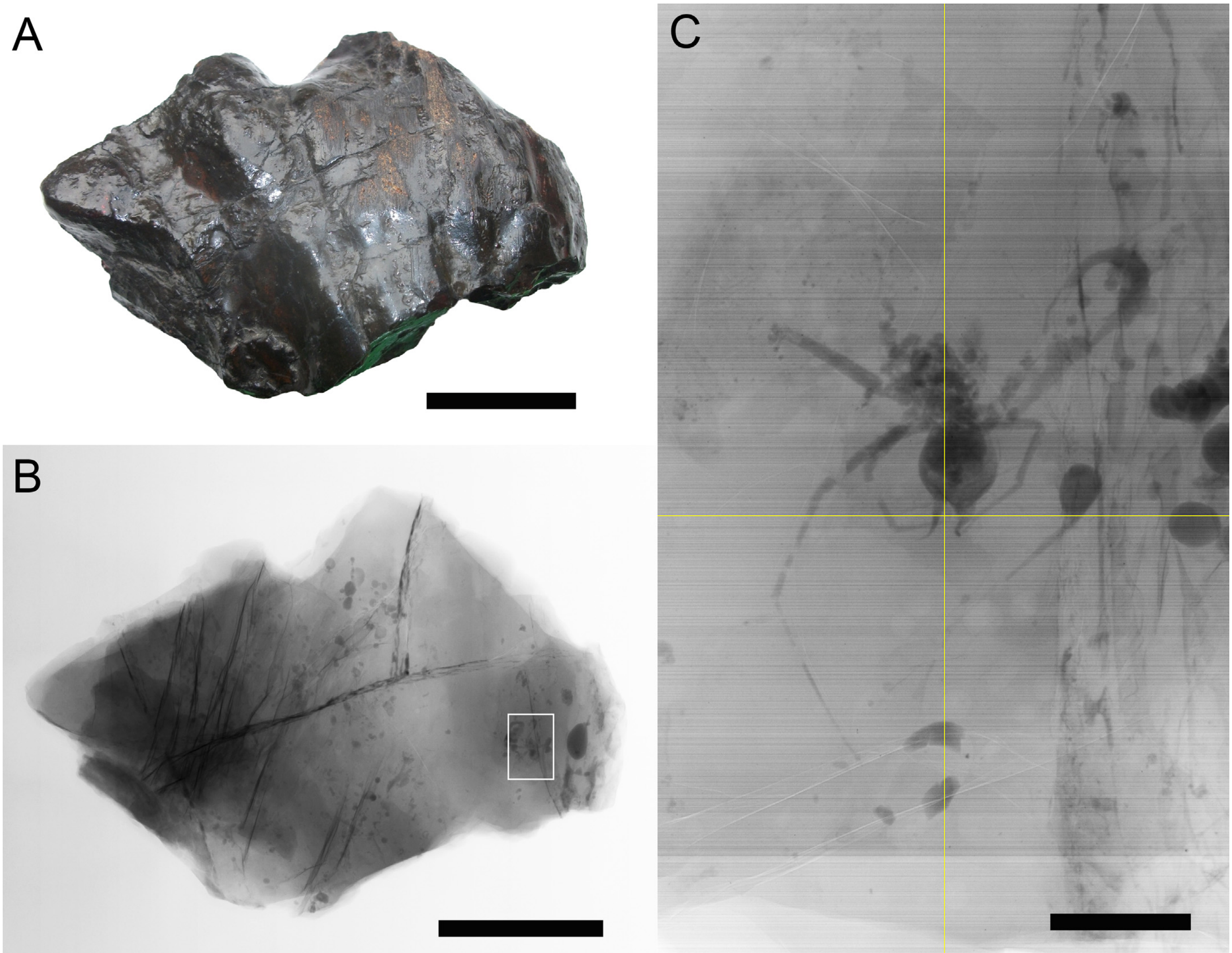

Fig. 2. A: The possibly largest ever known piece of ajkaite. B, C: CT scan picture of the same specimen, showing the spider inclusions inside (area indicated by a white rectangle in figure B is enlarged in figure C). Pictures of B and C were taken at the University of Pannonia (Veszprém, Hungary). Scale bars: A, B: 3 cm; C: 2 mm.

Gerdia, a hersiliid genus described from the Eocene Baltic amber, differs from *Hungarosilia* gen. nov. in having an ovally elongate pro- and opisthosoma (Menge, 1869; Wunderlich, 2004). *Gerdiopsis*, another Eocene genus also described from the Baltic amber, possesses pedipalpi with long tibiae (see Wunderlich, 2004, fig. 7). Conversely, in *Hungarosilia* gen. nov. the pedipalpal tibia is short and stout. Unlike in *Hungarosilia* gen. nov., the pedipalp of the Baltic amber genus *Gerdiorum* also has long tibia (see Wunderlich, 2004, fig. 7a).

Hungarosilia gen. nov. also differs from extant Hersiliidae genera. According to Foord and Dippenaar-Schoeman (2006), *Hersilia* has armed chelicerae with teeth on the pro- and retromargin. Unfortunately, chelicerae of *Hungarosilia* gen. nov. are not visible in detail. An important difference between *Hungarosilia* gen. nov. and *Hersilia* is that the opisthosoma of *Hersilia* is oval to elongated (Chen, 2007; Pravalikha et al., 2014), sometimes wider in its posterior half (see *Hersilia jajat* in Rheims and Brescovit, 2004b), while in *Hungarosilia* gen. nov. it is circular. Compared to *Hungarosilia* gen. nov., the extant genera *Bastanius*, *Delshevia*, *Duninia*, *Hersiliola*, *Ovtsharenkoia* have short posterior lateral spinnerets and a pedipalpal cymbium with a long tip (Marusik and Fet, 2009; Mirshamsi et al., 2015). Genera *Iviraiva*, *Neotama*, *Prima*, *Tamopsis*, *Tama* and *Ypypuera* possess pedipalpal characteristics (i.e. proportion of pedipalpal cymbium, tibia, patella and femur; shape of cymbium) very different from hose of *Hungarosilia* gen. nov.. (see Rheims and Brescovit, 2004a; Foord and Dippenaar-Schoeman, 2005b; Foord, 2008b). The genus *Tama* also has an opisthosomal shape that is wider in its posterior half and a markedly flattened bulbus (Foord and Dippenaar-Schoeman, 2005a, table 1) while in *Hungarosilia* gen. nov. the opisthosoma is almost circular in dorsal view and the bulbus is flattened only slightly. The pedipalpal cymbium of *Neotama* is digiform but that of *Hungarosilia* gen. nov. is egg-shaped (Foord and Dippenaar-Schoeman, 2005b). The opisthosoma of *Murricia* is often subtriangular to subquadrate (Javed and Tampal, 2010), in contrast to *Hungarosilia* gen. nov. which has an almost circular opisthosoma. *Tyrotama* has short posterior lateral spinnerets (Foord and Dippenaar-Schoeman, 2005a) and differs from *Hungarosilia* gen. nov., that has posterior lateral spinnerets nearly as long as the opisthosoma. *Yabisi* has a somewhat deltoid opisthosoma wider in its posterior half (see figures of Rheims and Brescovit, 2004a) while opisthosoma of *Hungarosilia* gen. nov. is circular in dorsal view. The genus *Promurricia* includes a single species, *P. depressa* (Baehr and Baehr, 1993), which is based on a female specimen. It shows a wide opisthosoma which is rather

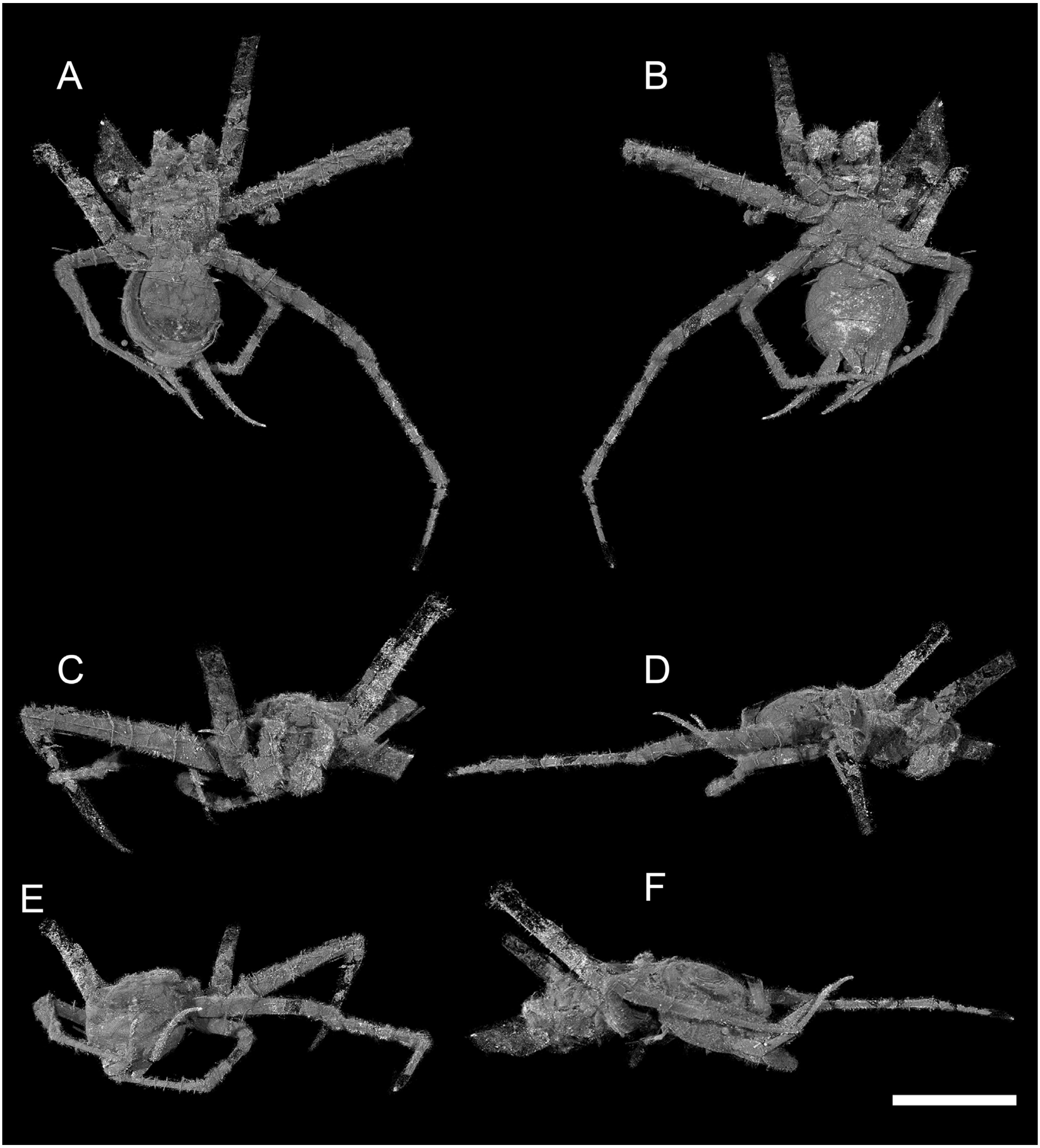

Fig. 3. *Hungarosilia verdesi* gen. et sp. nov., holotype (NHMUS PAL 2021.30.1.), body habitus. A: dorsal view; B: ventral view; C: anterior view; D: right lateral view; E: posterior view; F: left lateral view. Scale bar: 2 mm.

triangular but *Hungarosilia* gen. nov., which has a nearly circular opisthosoma.

Hersiliola and *Tama* are the only extant representatives of the family in Europe (Nentwig et al., 2021; Wunderlich, 2011e). Note here that the genus *Tama* might be present in the Baltic amber arachnofauna (see the short posterior lateral spinnerets of the figured Hersiliidae indet. in Wunderlich, 2004, photos 90, 91).

Hungarosilia verdesi gen. et sp. nov.
(Figs 3-5)
urn:lsid:zoobank.org:act: 2ABE0ED0-FD7E-4E51-ACBB-7EA7875EC9FE

Etymology.: In honour of †Gábor Verdes (1937–2010), grandfather of the first author who worked in Ajka for decades as a coal miner.

Type specimen. NHMUS PAL 2021.30.1., adult ♂ (only known specimen).
Type horizon, age and locality. Ajka Coal Formation (Santonian, Upper Cretaceous), unkown shaft of the Ajka-Csingervölgy coal minery; Ajka-Csingervölgy (Hungary).
Diagnosis. See the diagnosis of the genus.
Description. Habitus and legs: Prosoma nearly as wide as long (ca. 1.6 × 1.5 mm), with a closely circular outline in dorsal view, dorsal side is damaged; no characters of the clypeus and eyes are observable; order of legs cannot be given (as all I, II and IV legs are incomplete), however, based on their preserved parts, legs III seem to be the shortest; based on the preserved portions, the legs I, II and IV long and slender (although femur I is incomplete, it is still longer than the anteroposterior length of the prosoma); legs III with unarticulate metatarsi and short tarsi; opisthosoma about as long as wide (ca. 1.7 × 1.8 mm), nearly circular in ventral and dorsal view.
Spinnerets. posterior spinnerets elongate and about as long as the opisthosoma (ca. 1.8 mm, resulting in a body length/posterior spinneret ratio of 1:1; see Fig. 4A), with feathery hairs medially (Fig. 4, psh), their distal article (ca. 1.4 mm; Fig. 4, daps) tapering and much longer than the basal article (ca. 0.4 mm; Fig. 4, baps); anterior spinnerets (Fig. 4, as) much smaller than posteriors, separated by a distinct, triangular colulus (Fig. 4, co).
Copulatory organs. Both pedipalpi are preserved, however, several microfractures run across the amber and it hard to identify fine structures (e.g., hairs). Tibia (ca. 0.3 mm long; Fig. 5, t) and patella (ca. 0.25 mm long; Fig. 5, p) stout, femur (ca. 0.7 mm long; Fig. 5, f) elongate; cymbium (Fig. 5, c) with egg-shaped dorsal outline, as long as the pedipalpal femur; bulbus with circular shape in ventral view (Fig. 5E, J); questionable remains of apical cymbial bristles are present; no signs of a cymbial apophysis are visible.
Remarks: We compared *Hungarosilia verdesi* gen. et sp. nov. to chronologically (Late Cretaceous) or geographically close (European) hersiliid taxa. Except for *Hungarosilia verdesi* gen. et sp. nov., four Mesozoic hersiliid species, representing two genera are known, all from Burmese amber: *Burmesiola cretacea*, *B. daviesi*, ?*B. kachinensis* and *Spinasilia dissoluta* (Wunderlich, 2011a, 2015; Wunderlich and Müller, 2020). For a figurative summary of their comparison to *Hungarosilia verdesi* gen. et sp. nov. see Fig. 6. Unlike *Hungarosilia verdesi* gen. et sp. nov., the type specimen of *Burmesiola cretacea* has posterior spinnerets with the distal article slightly (~1.1–1.2x) longer than the basal, while the posterior spinnerets of *B. daviesi* have articles of about the same length (Wunderlich, 2011a, fig. 9; 2015). *Hungarosilia verdesi* gen. et sp. nov. has posterior spinnerets with a distal article more than three times longer than the basal article. The posterior spinnerets of *B. cretacea* are shorter while those of *B. daviesi* are longer than the opisthosoma (Wunderlich, 2011a, 2015). Conversely, the posterior spinnerets of *Hungarosilia verdesi* gen. et sp. nov. are as long as the opisthosoma. The pedipalpal tibiae of ?*Burmesiola kachinensis* (a species tentatively referred into genus *Burmesiola*) are elongate and longer than the cymbium. The prosoma of this species is longer than wide, and the posterior spinnerets are slightly longer than the opisthosoma (Wunderlich and Müller, 2020). By contrast, *Hungarosilia verdesi* gen et sp. nov. has stout pedipalpal tibiae that are shorter than the cymbium, the prosoma is nearly as long as wide, and the posterior spinnerets are as long as the opisthosoma. The type specimen of *Spinasilia dissoluta* is hard to observe in detail due to decomposition and the darkness of the embedding amber matrix (see Wunderlich, 2015). Cymbia of *S. dissoluta* are short and circular (Wunderlich, 2015) while those of *Hungarosilia verdesi* gen. et sp. nov. are egg-shaped. Cymbia of *S. dissoluta* bear a large cymbial apophysis while those of *Hungarosilia verdesi* gen. et sp. nov. lack this character. A further important difference is that posterior spinnerets of *S. dissoluta* are ~1.3x longer than the opisthosoma while the posterior spinnerets and opisthosoma of *Hungarosilia verdesi* gen. et sp. nov. are more or less of the same length.
Five hersiliid species have been described from the Eocene Baltic amber so far: *Gerdia myura*, *Gerdiopsis infringens*, *Gerdiorum inflexum*, *Hersilia longipes* and *Hersilia miranda* (Giebel, 1856; Koch and Berendt, 1854; Menge, 1869; Wunderlich, 2004, 2011b). The prosoma of *Gerdia myura* is elongate to oval (Wunderlich, 2004), unlike that of *Hungarosilia verdesi* gen. et sp. nov., which is almost as wide as long. The pedipalpal tibia of *Gerdiopsis infringens* and *Gerdiorum inflexum* is elongate, longer than wide (as long as the cymbium, see Wunderlich, 2004, fig. 7, 7a) while that of *Hungarosilia verdesi* gen. et sp. nov. is short and stout (less than half of the length of the cymbium). The description of *Hersilia longipes* (see Giebel, 1856) is fairly incomplete and lacks illustrations, therefore a detailed comparison of *Hungarosilia verdesi* gen. et sp. nov. with this Baltic amber species is not possible. The description of *Hersilia miranda* does not include important characteristics of the male copulatory organs, but according to Koch and Berendt (1854) the opisthosoma of *Hersilia miranda* is egg-shaped whereas that of *Hungarosilia verdesi* gen. et sp. nov. is circular. Note that the only available illustration of *Hersilia miranda* (Koch and Berendt, 1854, pl. 17, fig. 147) is controversial because legs III are not the shortest (which questions the figured specimen's assignment to Hersiliidae). A revision of the validity of *Hersilia longipes* and *Hersilia miranda* would be helpful but the current location of the holotype specimen is unknown. We also note that Koch and Berendt (1854) did not produce accurate drawings of the appearance of their fossils but rather produced somewhat idealised pictures of their appearance.
Hersilia aquisextana has been published from the Oligocene of Aix-en-Provence (France) (Gourret, 1887). The validity of *Hersilia aquisextana* requires a detailed revision because the specimen is poorly illustrated and its relation to Hersiliidae remains dubious (see Gourret, 1887, pl. 21, fig. 14; note the lack of elongate posterior spinnerets and the relative length of legs III). Yet, if *Hersilia aquisextana* is tentatively accepted as member of family Hersiliidae and it differs from *Hungarosilia verdesi* gen. et sp. nov. in having an ovally elongate opisthosoma.
Hersiliola and *Tama* are represented in the Recent European arachnofauna by *Hersiliola simoni*, *Hersiliola macullulata* and *Tama edwardsi* (see Nentwig et al., 2021). These species differ from *Hungarosilia verdesi* gen et sp. nov. in the following characters: *Hersiliola simoni* has an elongate (somewhat deltoid shaped) opisthosoma (Foord and Dippenaar-Schoeman, 2005a, fig. 3e) while that of *Hungarosilia verdesi* gen et sp. nov. is circular. The pedipalpi of *Hersiliola simoni* possess more tapering cymbia and a more flattened bulbus (see Foord and Dippenaar-Schoeman, 2005a, fig. 3a, b; Marusik and Fet, 2009, figs. 4.2, 5.2, 6.2–3; Rheims and Brescovit, 2004a, figs 39, 40), compared to *Hungarosilia verdesi* gen et sp. nov.. The same is true of the male copulatory organs of *Hersiliola macullulata* (Marusik and Fet, 2009, figs 4.1, 5.1, 6.1). The pedipalp of *Tama edwardsi* has tibiae that are as long as the cymbia, unlike *Hungarosilia verdesi* gen et sp. nov., that has a stout pedipalpal tibia much shorter than the pedipalpal cymbium.

6. Discussion

Up to the present study, fossil spiders from Hungary were known only from the Pula Alginite Formation (Pula, Bakony

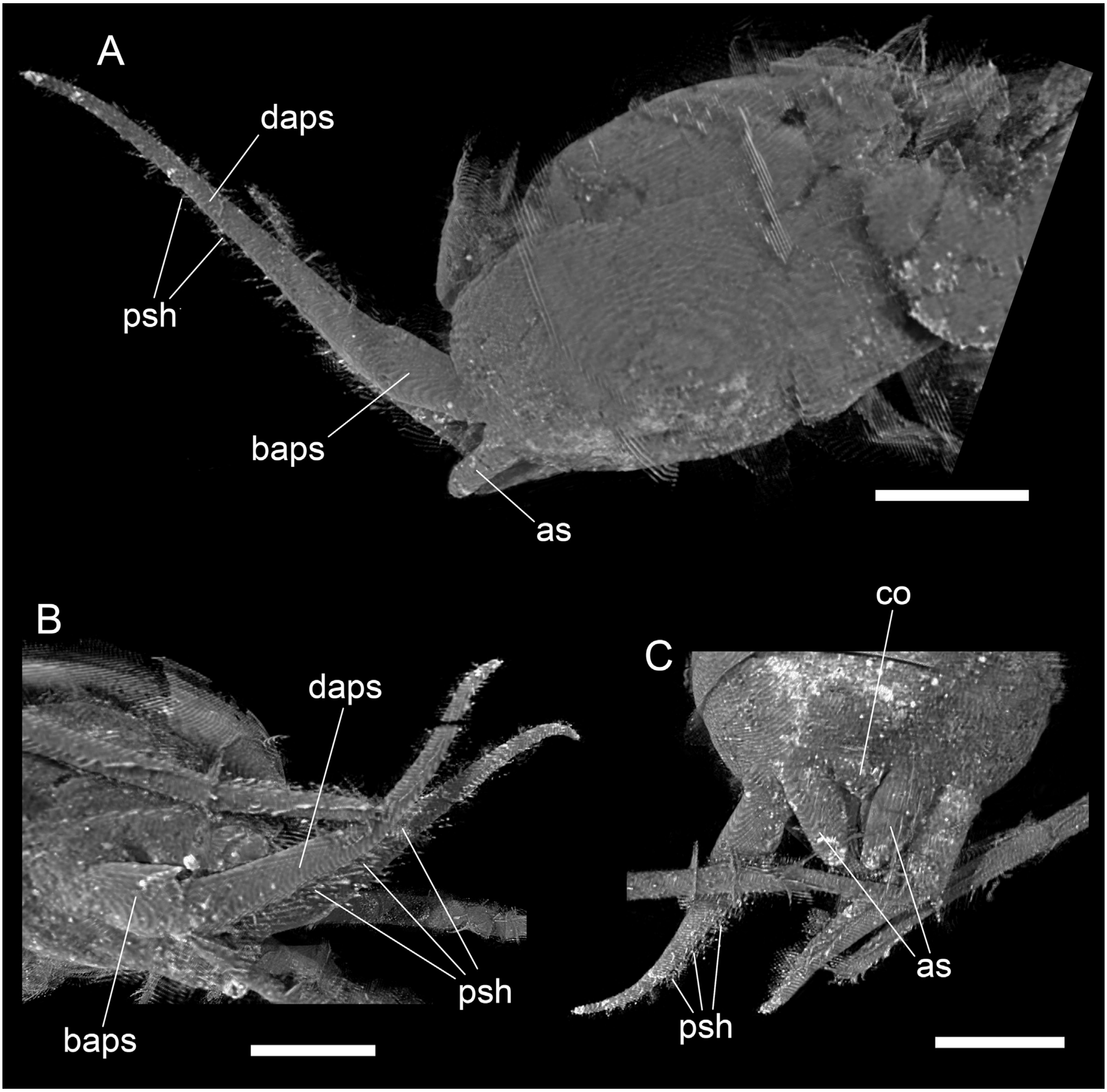

Fig. 4. *Hungarosilia verdesi* gen. et sp. nov. (holotype); opisthosoma with spinnerets. A: right lateral view, with slight saggital cross-cut on the lateral edge of the opisthosoma; B: oblique posterior view; C: ventral view. Abbreviations: as: anterior spinnerets; baps: basal article of the posterior spinneret; co: colulus; daps: dorsal article of the posterior spinneret; psh: medial feathery hairs of the posterior spinneret. Scale bars: 500 µm.

Mountains, Hungary) of Pliocene age and a single fossil crab spider (*Xysticus* sp.) had been reported from this deposit (Katona et al., 2014, fig. 14).

Upper Cretaceous amber-bearing deposits are rather rare in Europe but some localities in France, Germany and Hungary are known (see Adl et al., 2011; Girard, 2009; Néraudeau et al., 2003, 2020; Perrichot, 2014; Perrichot et al., 2007a, b; Schlüter, 1978; Schmidt et al., 2001; Valentin et al., 2020; present study). Although some of these localities preserve rich assemblages of arthropods, only a few spiders or spider-related inclusions have been identified to date (Néraudeau et al., 2009; Penney, 2014; Saint Martin et al., 2014). The occurrence of Hersiliidae in the Santonian ajkaite establishes the oldest known record for this family in Europe, but also the second record of this family from the Mesozoic because all other fossils from this period are from Burmese amber in Myanmar (Table 1). Nowadays, only two hersiliid genera, namely *Hersiliola* and *Tama*, occur in Europe (Nentwig et al., 2021) and both are ground-dwelling members of the family found under stones where they build irregular webs plastered with small pebbles (Foord and Dippenaar-Schoeman, 2005a; Lawrence, 1964; Smithers, 1945).

The presence of Hersiliidae in the ajkaite arachnofauna corresponds well with the estimated paleoclimate and vegetation of the

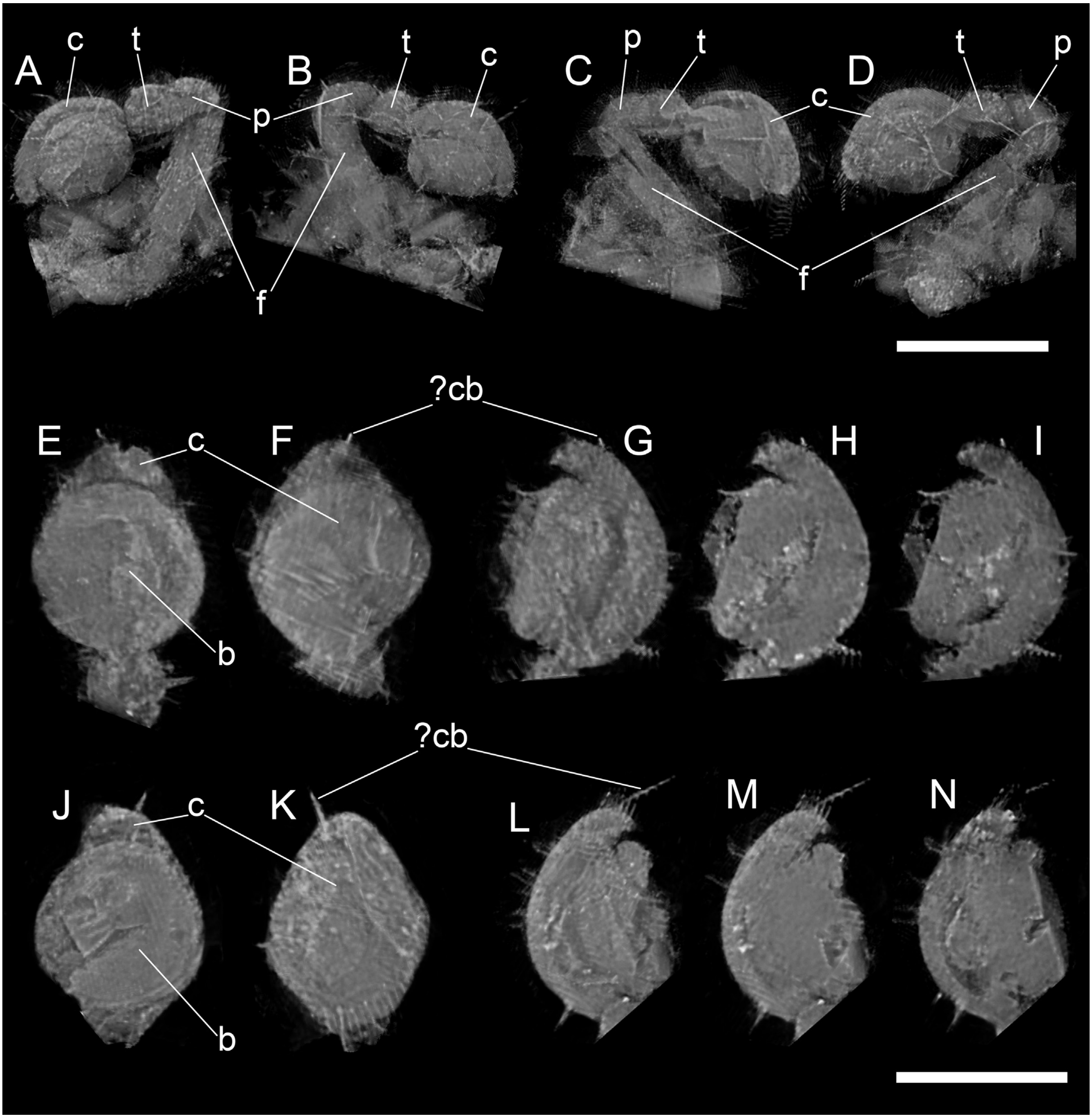

Fig. 5. *Hungarosilia verdesi* gen. et sp. nov. (holotype); palpal morphology. A: left pedipalp in lateral view; B: in medial view. C: right pedipalp in lateral view; D: in medial view. E: left palpal tarsus (showing the cymbium and the bulbus) in ventral view; F: left cymbium in dorsal view; G–I: saggital cross-section (in lateromedial order) of the left palpal tarsus. J: right palpal tarsus (showing the cymbium and the bulbus) in ventral view; K: right cymbium in dorsal view; L–N: saggital cross-sections (in lateromedial order) of the right palpal tarsus. Abbreviations: c: cymbium; ?cb: possible cymbial bristles; b: bulbus; f: palpal femur; p: palpal patella; t: palpal tibia. Scale bars: A–D: 750 μm; E–N: 500 μm.

Ajka Coal paleoenvironment. Extant members of the family are medium-sized, often cryptic spiders that occur in warm climates and have the highest diversity in the tropics or subtropics. Based on drill core samples (Siegl-Farkas, 1988), the climate for the Ajka Coal Formation has been estimated to be tropical monsoon climate with high precipitation (2000–2500 mm per year). The later palynological and paleocarpological studies suggest Normapolles-related forests with fern-dominated underwood, but gymnosperm pollen and branches can be also found in the fossil record (Bodor and Baranyi, 2012). The climate might have been tropical or subtropical according to the ecological needs of the nearest living relatives of the fossil plant forms (Bodor et al., 2012). Seasonality of the precipitation can be presumed based on the tree rings of fossil woods (L. Rákosi pers. comm.).

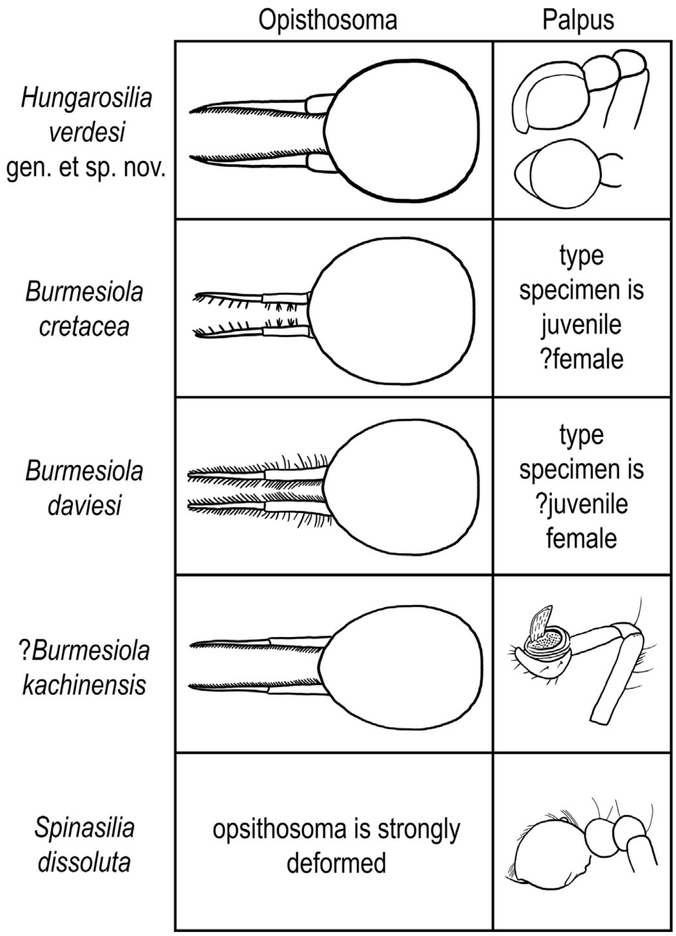

Fig. 6. Schematic drawings of characteristics of Mesozoic Hersiliidae (depictions of *Burmesiola* spp. and *Spinasilia dissoluta* are re-drawn after the text figures and photographs in Wunderlich, 2011a, 2015; Wunderlich and Müller, 2020).

Life history traits and habitat choice of extant hersiliid spider species vary greatly between genera and some are arboreal hunters, living on the bark of tree trunks, whilst others are ground-dwelling spiders that prefer rock or boulders as shelters. The new species resembles the typical morphology of extant arboreal hersiliids (e.g., enlarged posterior spinnerets, elongate first, second and fourth pairs of legs, short third pair of legs). An arboreal lifestyle similar to many present-day hersiliid spiders is therefore probable (see in Foord, 2008a; Rheims and Brescovit, 2004a; also in Wunderlich, 2015:306 in fossil species *S. dissoluta*).

The swamp where the Ajka Coal was formed was arboreous and dominated by large angiospermes with possible affinity to Fagales (Normapolles-related; compare Friis et al., 2006). However, Platanacae-related leaf fragments have also been found in the drill cores from the Ajka Coal Formation and Magnoliaceae-related *Padragkutia* and *Operculispermum* seeds were found in several layers of Ajka Coal Formation (Rákosi unpublished reports; Bodor et al., 2013). Rákosi also reported Araucariaceae trunks from the formation and recent relatives of this gymnosperm group have large trunks (reaching a height of 5–80 m) with deeply seamed bark (Stockey and Rothwell, 2020) which could have been a potential habitat for this species. This variety in the floral assemblage indicates a complex ecosystem in which *Hungarosilia verdesi* gen. et sp. nov. may have found suitable habitat.

7. Conclusion

The present study provides the first data on the Santonian arachnofauna of the western Tethyan archipelago. The discovery of *Hungarosilia verdesi* gen. et sp. nov. improves our knowledge on the Mesozoic diversity of family Hersiliidae. The suggested arboreal life style of our new hersiliid genus matches with the climate and paleoflora of the Ajka Coal paleoenvironment. There are further specimens of spiders from the Santonian ajkaite available for study, some of which are better preserved and will most likely reveal a greater diversity of spiders from the Mesozoic of Europe. The occurrence of further arboreal arachnids in ajkaite is expected.

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