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### Research article

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## New species of belytine and diapriine wasps (Hymenoptera: Diapriidae) from Eocene Baltic amber

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**Abstract.** The fossil diversity of Diapriidae in Baltic amber, dated Upper Eocene, has been poorly investigated. However, some studies suggest that this family was already diversified at this time. This is supported by our present study of the Baltic amber collection of the Natural History Museum of Denmark, from which we describe and figure ten new species belonging to the subfamilies Belytinae: *Belyta knudhoejgaardi* sp. nov., *Cinetus breviscapus* sp. nov., *Cinetus elongatus* sp. nov., *Pantoclis globosa* sp. nov., *Pantolyta augustinusii* sp. nov., *Pantolyta chemyrevae* sp. nov., *Pantolyta similis* sp. nov.; and Diapriinae: *Basalys villumi* sp. nov., *Doliopria baltica* sp. nov. and *Spilomicrus succinalis* sp. nov. The diversity of extant genera observed leads us to propose an origin in the early Cenozoic for these taxa. The fossil record of the Diapriidae in Baltic amber is also summarized.

**Keywords.** Belytinae, Diapriinae, fossil record, Bartonian–Priabonian, Cenozoic.

Brazidec M. & Vilhelmsen L. 2022. New species of belytine and diapriine wasps (Hymenoptera: Diapriidae) from Eocene Baltic amber. *European Journal of Taxonomy* 813: 57–86. <https://doi.org/10.5852/ejt.2022.813.1733>

### Introduction

The Diapriidae Haliday, 1833 are a diverse family of small parasitoid wasps, comprising more than 2000 extant species (Johnson *et al.* 2021), which corresponds to less than half of the estimated diversity (~ 4500 spp.; Johnson 1992). They occur in all ecozones except the Antarctic but are more abundant in the southern hemisphere and are generally associated with wet forests and marshes, where they live near water or in the soil (Perrichot & Nel 2008). The biology of most species of diapriid wasps is unknown; those from which information is available are mainly pupal endoparasitoids on flies but also on beetles or ants (Loiácono 1987; Masner 1993).

Among Proctotrupoidea Latreille, 1802, the Diapriidae as a family are not defined by any remarkable apomorphies but rather by a unique combination of characters that does not occur in other related

families: antennae inserted on a shelf, scape elongate, males with antennomeres 3 and/or 4 modified, fore wing without clearly defined pterostigma and at most with three closed cells, hind wing with at most one closed cell, tubular petiole (Masner 1993). The phylogenetic relationships of the family are not clear, principally because of the apparent paraphyly of proctotrupoids (Sharkey 2007; Klopstein *et al.* 2013; Peters *et al.* 2017). Morphological analyses suggest a sister-group relationship of the Diaprioidea Haliday, 1833 complex sensu Sharkey *et al.* (2012) (i.e., Diapriidae + Monomachidae + Maamingidae + †Spathiopterygidae) and Cynipoidea Latreille, 1802 (Rasnitsyn 1988; Sharkey & Roy 2002; Vilhelmsen *et al.* 2010a) whereas molecular analyses place Chalcidoidea + Platygastroidea as sister to Diaprioidea (Castro & Downton 2006; Heraty *et al.* 2011; Klopstein *et al.* 2013; Peters *et al.* 2017). The concave/convex vein M(+Cu) on the hind wing and the basal male flagellomere modified to accommodate the gland secretion releaser are two putative synapomorphies to distinguish Cynipoidea and Diaprioidea from other proctotrupoids (Rasnitsyn 1988, 2002). The synapomorphies “long scape, oligomeric antenna, presence of specialized petiolar segment and metasomal apex tightly closed at rest” have been proposed for the Diaprioidea sensu Rasnitsyn & Öhm-Kühnle (2020). Four subfamilies were recognized within Diapriidae s. lat.: Ambositrinae Masner, 1961, Belytinae Förster, 1856, Diapriinae Haliday, 1833 and Ismarinae Thomson, 1858. The last one has been raised to family-level by Sharkey *et al.* (2012) and included within the Diaprioidea alongside with the Spathiopterygidae Engel & Ortega-Blanco, 2013 (Rasnitsyn & Öhm-Kühnle 2020).

Compared with the extant fauna, studies on fossil Diapriidae are sparse. Perrichot & Nel (2008: appendix 1) summarized the fossil record of the family, showing great contrasts between each of the subfamilies. To date, Ambositrinae are only known from two Cenozoic deposits (Masner 1969; Antropov *et al.* 2014). On the contrary, more than thirty Belytinae have been documented in various deposits from Quaternary African copal to Albian French amber, making it the most frequently encountered subfamily. Though Belytinae is hypothesized to be sister to the rest of the family (Masner 1993), it does not include the oldest known fossil diapriid, which is the Ismarinae *Cretapria tsudakai* Fujiyama, 1994 from Aptian Choshi amber (ca 121 Ma; Fujiyama 1994). Another undetermined ismarine is known from Cenomanian French amber (Schlüter 1978). Finally, Diapriinae are almost exclusively known from Cenozoic deposits but one is mentioned from Cenomanian Taimyr amber (Zherikhin & Sukatsheva 1973). Since Perrichot & Nel (2008), very few studies have focused on fossil diapriids: Lak & Nel (2009), Engel *et al.* (2013), van de Kamp *et al.* (2018), Jouault & Nel (2020), Jouault *et al.* (2020) and Brazidec *et al.* (2021) described new taxa from Cenomanian French amber (ca 100 Ma), Albian Spanish amber (ca 110 Ma), Paleogene phosphorites of the Quercy Region in France, Late Eocene Baltic amber and mid-Cretaceous Burmese amber (ca 100 Ma), respectively, while Antropov *et al.* (2014) revised the family from the Eocene of Isle of Wight. In total, around sixty fossils of diapriids have been documented but many specimens are only identified to the genus, subfamily or even family level.

Baltic amber is renowned for being one of the largest amber deposits, at least from the Cenozoic, with Cretaceous Burmese amber rivalling it, and probably the best studied (Poinar 1992; Grimaldi 1996; Weistchat & Wichard 2002). Many studies have been published since Sendel (1742): Penney & Jepson (2014) estimated that more than 3000 species have been described from Baltic amber. Some taxa such as ants (Cheney *et al.* 2019; Perkovsky 2016) or bees (Engel 2001) have been treated extensively, others are little studied, e.g., many of the parasitoid wasp families. The Diapriidae is one of those: only eight species have been documented, all belonging to Belytinae (Table 1). Maneval (1938) was the first to describe fossil diapriids from Baltic amber, followed by Szabó & Oehlke (1986). Buhl (1999, 2002) described three new species and reported one extant species. Finally, Jouault & Nel (2020) described the latest species. However, these are just a small fraction of the known diapriid diversity in Baltic amber: Buhl (1999, 2002) highlighted the presence of several extant belytine genera (i.e., *Aclista* Förster, 1856, *Belyta* Jurine, 1807, *Miota* Förster, 1856, *Pantoclis* Förster, 1856 and *Zygota* Förster, 1856) and

**Table 1.** Fossil record of the Diapriidae Haliday, 1833 in Baltic amber (<sup>1</sup> *Pantolyta similis* sp. nov. was originally identified as *P. macrocera* (Thomson, 1858)).

Taxa	Reference (number of specimens)
<b>Subfamily Ambositrinae Masner, 1961</b>	
Genus <i>Ambositra</i> Masner, 1961	
<i>Ambositra</i> sp.	Masner 1969 (80+)
<b>Subfamily Belytinae Förster, 1856</b>	
Genus <i>Aclista</i> Förster, 1856	
<i>Aclista</i> sp.	Buhl 2002 (~1–10)
Genus <i>Belyta</i> Jurine, 1807	
<i>Belyta</i> sp.	Buhl 2002 (~1–10)
<i>Belyta knudhoejgaardi</i> sp. nov.	This study (2)
Genus <i>Cinetus</i> Jurine, 1807	
<i>Cinetus balticus</i> Szabó & Oehlke, 1986	Szabó & Oehlke 1986 (1)
<i>Cinetus breviscapus</i> sp. nov.	This study (1)
<i>Cinetus elongatus</i> sp. nov.	This study (1)
<i>Cinetus inclusus</i> Maneval, 1938	Maneval 1938 (1)
Genus <i>Miota</i> Förster, 1856	
<i>Miota</i> sp.	Buhl 2002 (~1–10)
Genus <i>Pantoclis</i> Förster, 1856	
<i>Pantoclis</i> sp.	Buhl 2002 (~1–10)
<i>Pantoclis globosa</i> sp. nov.	This study (2)
Genus <i>Pantolyta</i> Förster, 1856	
<i>Pantolyta antiqua</i> Buhl, 1999	Buhl 1999 (1)
<i>Pantolyta augustinusii</i> sp. nov.	This study (5)
<i>Pantolyta chemyrevae</i> sp. nov.	This study (1)
<i>Pantolyta janzeni</i> (Buhl, 2002)	Buhl 2002 (1)
<i>Pantolyta perrichoti</i> (Jouault & Nel, 2020)	Jouault & Nel 2020 (1)
<i>Pantolyta similis</i> sp. nov. <sup>1</sup>	This study (1)
<i>Pantolyta somnulenta</i> Maneval, 1938	Maneval 1938 (1)
Genus <i>Synacra</i> Förster, 1856	
<i>Synacra microptera</i> Buhl, 2002	Buhl 2002 (1)
Genus <i>Zygota</i> Förster, 1856	
<i>Zygota</i> sp.	Buhl 2002 (~1–10)
<b>Subfamily Diapriinae Haliday, 1833</b>	
Diapriinae indet.	Buhl 1999, 2002 (46)
Genus <i>Basalys</i> Westwood, 1833	
<i>Basalys villumi</i> sp. nov.	This study (2)
Genus <i>Doliopria</i> Kieffer, 1910	
<i>Doliopria baltica</i> sp. nov.	This study (1)
Genus <i>Spilomicrus</i> Westwood, 1832	
<i>Spilomicrus succinalis</i> sp. nov.	This study (3)

numerous undetermined Diapriinae. Masner (1969) reported numerous undetermined Ambositrinae. Consequently, a closer survey of the existing material is likely to reveal new species.

Here, we study the collection of Diapriidae in Baltic amber pieces of the Natural History Museum of Denmark in order to describe and illustrate ten new species belonging to the Belytinae and Diapriinae. We also summarize the fossil record of Diapriidae in Baltic amber (Table 1).

## **Material and methods**

### **Amber deposit**

The collection of Diapriidae included in Baltic amber pieces from the Natural History Museum of Denmark, 19 inclusions in particular, have been studied. The amber-bearing layer is the Blue Earth Formation which occurs throughout northern Europe just under the sea-level around the Baltic shore (Weistchat & Wichard 2010: fig. 1). Palynological data indicate an Upper Eocene age, late Bartonian to Priabonian (ca 34–38 Ma; Aleksandrova & Zaprozhets 2008). An older Lutetian age ( $44.1 \pm 1.1$  Ma; Ritzkowski 1997) has been proposed for this formation but this was probably an overestimate (Clauer *et al.* 2005). Small amounts of amber occasionally occur in older lower layers (Weistchat & Wichard 2010) as well as in Oligocene sediments; these may be redeposited Eocene material (Standke 2008). In this paper, we assume a Priabonian age for Baltic amber (Seyfullah *et al.* 2018).

### **Preparation, morphological examination and repository**

Amber pieces were polished to facilitate the observation of the specimens using a grinder polisher (Buehler EcoMet 30), a very thin silicon carbide sanding paper (grit size = 7000) and a diamond disk. The specimens were examined and photographed with a Canon EOS 250D attached to a Leica M80 stereo microscope, under incident and transmitted light. All images are digitally stacked photomicrographic composites of several focal planes, which were obtained using HeliconFocus ver. 6.7. Adobe Illustrator CC2019 and Photoshop CC2019 software were used to compose the figures and ImageJ ver. 1.53 for measurements (following the method of Yoder 2004). The description of the characters follows the nomenclature of Masner & García (2002). All the specimens are housed in the amber collection of the Natural History Museum of Denmark (NHMD), University of Copenhagen, Denmark.

### **Abbreviations used in text and figures**

asp	=	anterior scutellar pit
BL	=	body length (from toruli to tip of gaster)
ED	=	eye diameter
F	=	flagellomere
fe	=	flagellomere emargination
FwL	=	fore wing length (from tegula to tip of wing)
GH	=	gaster height (middle height)
GL	=	gaster length (from anterior margin of T2 to tip of gaster)
HeL	=	head length (from toruli to occiput)
HwL	=	hind wing length (from tegula to tip of wing)
mlr	=	mesopleural longitudinal ridge
mpk	=	median propodeal keel
MsL	=	mesosoma length (from anterior margin of pronotum to posterior margin of propodeum)
mtr	=	metapleural ridge
OL	=	ovipositor length
P	=	pedicel
PtL	=	petiole length
PtW	=	petiole width (middle width)

S = metasomal sternite  
Sc = scape  
T = metasomal tergite  
t = toruli  
te = tergite excision

## Results

### *Systematic palaeontology*

Class Insecta Linnaeus, 1758  
Order Hymenoptera Linnaeus, 1758  
Suborder Apocrita Latreille, 1810  
Superfamily Diaproidea Haliday, 1833  
Family Diapriidae Haliday, 1833  
Subfamily Belytinae Förster, 1856  
Genus *Belyta* Jurine, 1807

*Belyta knudhoejgaardi* sp. nov.

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Figs 1A, 2A–D, Table 1

### Diagnosis

Head nasiform; antennal shelf strongly projecting forward; scape as long as head; F1 longest; following flagellomere shorter but gradually lengthening (Fig. 2A); mesopleuron with one prominent longitudinal ridge (Fig. 2B); median propodeal keel simple (Fig. 2C); radial cell open, Rs fading before reaching fore margin; marginal vein hardly longer than r-rs (Fig. 1A); petiole 1.7 times as long as wide; gaster fusiform (Fig. 2B–C).

### Etymology

We dedicate this species to the Knud Højgaard Foundation, who generously contributed to funding for purchasing the amber pieces studied. The specific epithet is to be treated as a noun in genitive case.

### Type material

Holotype NHMD-608408, a complete female; paratype NHMD-608400, a slightly damaged female.

### Locality and horizon

Baltic amber is considered to be of Bartonian–Priabonian age, ca 34–38 Ma.

### Description

#### Female

BODY. BL = 4.8–5.3 mm. Body slightly pubescent, smooth and shiny. Head nasiform (HeL = 0.77–0.89 mm), with sparse short hairs posteriorly; eye almond-shaped, glabrous; antennal shelf strongly prominent; antenna 15-segmented, with short heterogeneous setae; scape as long as head; pedicel thinner; F1 one and a half times as long as pedicel or other flagellomeres; F2–F13 gradually lengthening; F13 tapering at apex and slightly shorter than F1 (antennomere length of holotype, in mm: Sc-0.72; P-0.19; F1-0.29; F2-0.11; F3-0.12; F4-0.11; F5-0.12; F6-0.10; F7-0.11; F8-0.13; F9-0.13; F10-0.14; F11-0.15; F12-0.15; F13-0.28); mandibles simple.

**MESOSOMA.** Almost as long as metasoma, flattened (MsL = 1.62–1.90 mm); pronotum with epomia extending from front coxa to posterodorsal pronotal corners; posterior margin of pronotum curved; mesoscutum with several hairs; notauli complete and deeply impressed; scutellum without posterior scutellar pits; mesopleuron with prominent longitudinal keel; propodeum with plicae, median propodeal keel simple. Fore wing hyaline, micro-pubescent, extending beyond metasoma (FwL = 2.74–3.78 mm); C, Sc+R, M+Cu, basal vein, marginal vein and r-rs pigmented; marginal vein shorter than its distance from basal vein; postmarginal vein barely longer than r-rs, pigmented on half length of radial cell; Rs nebulous proximally and pigmented distally from r-rs, projecting distally to postmarginal vein but fading before reaching wing margin; radial cell open. Hind wing hyaline, reduced and narrow (HwL = ?–2.39 mm). Legs slender, with hind femur and coxa enlarged, covered with scattered setae; tibial spur formula 1-2-2; tarsal claws simple.

**METASOMA.** Petiole glabrous, longitudinally striated and with transverse keels, 1.7 times longer (PtL = 0.50 mm) than wide (PtW = 0.30 mm); gaster fusiform, depressed (GL = 1.90–1.95 mm, GH = 0.48–0.58 mm); S2 and T2 longest, covering two-thirds of gaster, T2 striated at junction with petiole; four ring-like segments distinguishable beyond large tergite, hypopygium bearing several long setae; ovipositor not exerted.

#### Male

Unknown.

#### Comments

Using Nixon's (1957) key, *Belyta knudhoejgaardii* sp. nov. keys out to *Belyta* because of the following characters: macropterous, notauli present, mandibles of ordinary form, scutellum without a row of foveae along posterior margin, marginal vein shorter than its distance from basal vein, pronotum elongate, without a hollow on each side (= pronotal pits), epomia present, median keel of propodeum simple, petiole more than one and a half time as long as wide. The flattened body is generally accepted to diagnose *Belyta* spp. (Macek 1996) and is present in *Belyta knudhoejgaardii*, strengthening the placement of the species in *Belyta*.

Following the key to European species of *Belyta* of Macek (1996), *Belyta knudhoejgaardii* sp. nov. keys out between *B. subclausa* Kieffer, 1916 and *B. validicornis* Thomson, 1858. It differs from the first by having a marked epomia and from the second by having the median propodeal keel simple (Macek 1996). The diagnostic character for *Belyta knudhoejgaardii* is the curiously marked longitudinal keel on the mesopleuron, which is absent in other species of *Belyta*. From the Eocene of Florissant is known *B. mortuella* Brues, 1910 (attributed to *Belyta* s. lat.), which differs from *B. knudhoejgaardii* by being shorter and having a less flattened body (Brues 1910).

Genus *Cinetus* Jurine, 1807

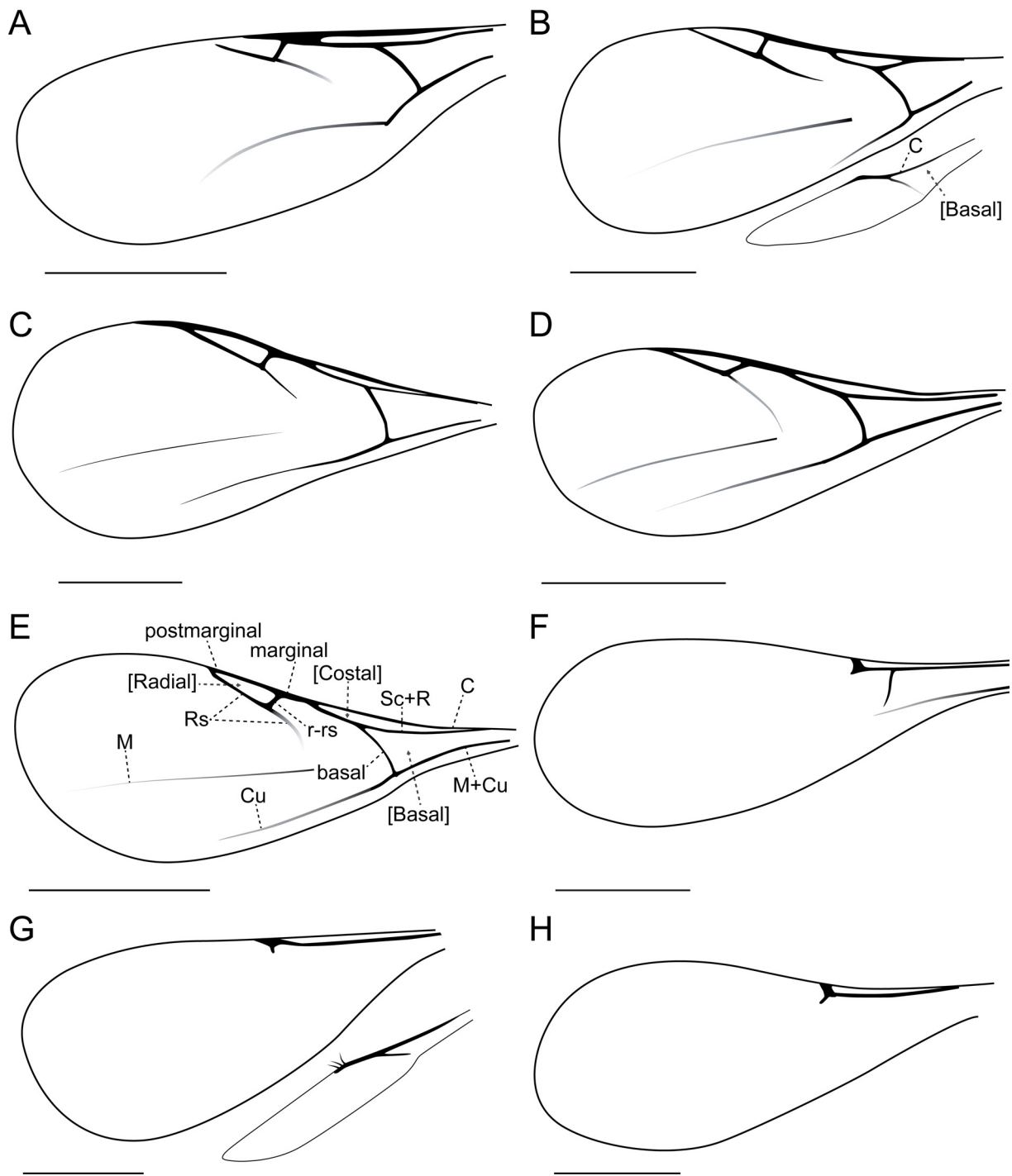
*Cinetus breviscapus* sp. nov.

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Figs 1B, 2E–F, Table 1

#### Diagnosis

Head with sparse long hairs; antenna with uniform pilosity; scape less than five times as long as wide; pedicel rounded, as long as wide; flagellomeres cylindrical, elongate, longer than wide; F1 1.2 times as long as scape, deeply emarginated (Fig. 2F); anterior scutellar pits bean-shaped; propodeum with strong plicae; median propodeal keel simple; marginal vein longer than its distance from basal vein and as long as radial cell; postmarginal vein present on half radial cell; Rs directed toward base of wing; hind wing



**Fig. 1.** Wing venation of the species described here. **A.** *Belyta knudhoejgaardi* sp. nov. **B.** *Cinetus breviscapus* sp. nov. **C.** *Cinetus elongatus* sp. nov. **D.** *Pantoclis globosa* sp. nov. **E.** *Pantolyta augustinusii* sp. nov. **F.** *Basalys villumi* sp. nov. **G.** *Doliopria baltica* sp. nov. **H.** *Spilomicrus succinalis* sp. nov. Scale bars: A–E = 1 mm; F, H = 0.5 mm; G = 0.25 mm.

with basal cell open (Fig. 1B); hind tibia and tarsomeres with long recumbent hairs; petiole 2.8 times as long as high, with longitudinal ribs; gaster globose; T2 covering two thirds of gaster; S2 longer than T2 (Fig. 2E).

### Etymology

The specific epithet is to be treated as an adjective and is composed of ‘*brevi-*’, meaning ‘short’, and ‘*-scapus*’, a reference to the small size of the scape.

### Type material

Holotype NHMD-300622, a complete male.

### Locality and horizon

Baltic amber is considered to be of Bartonian–Priabonian age, ca 34–38 Ma.

### Description

#### Male

**BODY.** BL = 3.61 mm. Head with sparse long hairs (HeL = 0.47 mm); eye oval, glabrous; antennae inserted on transverse shelf; 14 antennomeres with uniform pilosity; scape elongate, less than five times as long as wide; pedicel rounded, as long as wide; flagellomeres elongate, cylindrical; F1 1.2 times as long as scape, with a deep emargination covering almost half of segment; F2–F6 slightly shorter, of subequal length; F6–F12 decreasing in size but still much more longer than wide; F12 tapering at apex (antennomeres length, in mm, when possible: Sc-0.32; P-0.06; F1-0.39; F2-0.34; F3-0.32); mandibles of ordinary form, not forming a beak.

**MESOSOMA.** Shorter than metasoma (MsL = 1.21 mm); pronotum without epomia, only visible in lateral view; mesoscutum smooth; notauli deep, diverging at posterior terminations toward a point outside scutellum; anterior scutellar pit bean-shaped; scutellum without posterior scutellar pits; mesopleuron with epicnemial pit, epicnemial bridge and subalar bridge present; propodeum with prominent plicae; median propodeal keel simple. Fore wing hyaline, uniformly micropubescent (FwL = 3.58 mm); venation complete with C, Sc+R, basal vein, M+Cu, marginal vein, r-rs and Rs pigmented; marginal vein very long, longer than its distance from basal vein and as long as radial cell; postmarginal vein fading after middle of radial cell; Rs proximally directed toward base of wing; M inconspicuous towards apex; Cu short and nebulous; radial cell closed. Hind wing narrow, with C pigmented and basal cell opened (HwL = 2.23 mm). Legs slender, covered with setae; tibial spur formula 1-2-2; hind tibia and tarsomeres with long recumbent hairs.

**METASOMA.** Petiole elongate, almost three times as long as its middle height (PtL = 0.56 mm; PtW = 0.19 mm), with longitudinal ribs; gaster globose, oval, smooth (GL = 1.37 mm; GH = 0.71 mm); six segments identifiable; T2 longest, covering two thirds of gaster; other tergites reduced, decreasing in length until they become indistinguishable; S2 longest, longer than T2; following sternites very short; pygidium and hypopygium at least as long as previous segments; genitalia internalized.

#### Female

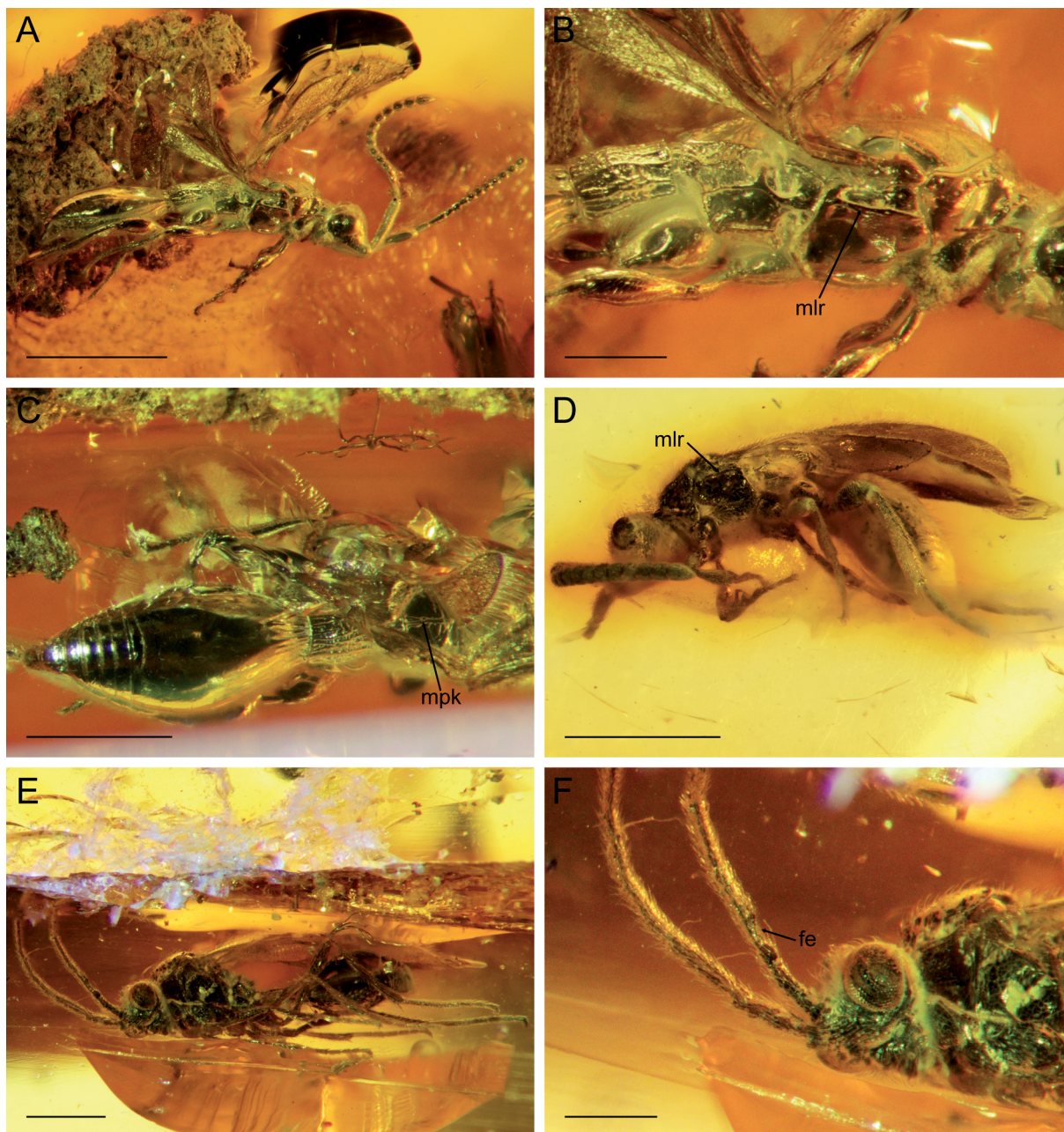
Unknown.

### Comments

Using Nixon’s (1957) key, *Cinetus breviscapus* sp. nov. keys out to *Cinetus* Jurine, 1807 because of the following characters: mandibles of ordinary form, scutellum without a row of foveae posteriorly, marginal vein very long, notauli slightly divergent posteriorly. Following Nixon’s (1957) key to male



species of *Cinetus*, *Cinetus breviscapus* keys out near *C. aletes* Nixon, 1957 because of its scape that is shorter than F1 but differs in having the first flagellomere less distinctly longer than the scape (ratio scape length/F1 length: 1.2 vs 1.43; Nixon 1957), the petiole longer (three times as long as wide vs “about two and a half times as long as wide”) and being bigger (body length ca 3.6 mm vs ca 2.2 mm).



**Fig. 2.** A–D. *Belyta knudhoejgaardi* sp. nov. A–C. Holotype (NHMD-608408). A. habitus in lateral view. B. Mesosoma and petiole in lateral view. C. Petiole and gaster in dorsal view. D. Paratype NHMD-608400, habitus in lateral view. E–F. *Cinetus breviscapus* sp. nov., holotype (NHMD-300622). E. Habitus in lateral view. F. Head in lateral view. Abbreviations: fe = flagellomere emargination; mlr = mesopleural longitudinal ridge; mpk = median propodeal keel. Scale bars: A = 2 mm; B, F = 0.5 mm; C–E = 1 mm.

In Baltic amber, *Cinetus breviscapus* sp. nov. is considered as separate from *Cinetus inclusus* Maneval, 1938 and *Cinetus balticus* Szabó & Oehlke, 1986 because it clearly does not fit with their descriptions. The petiole of *C. balticus* is longer than that of *C. breviscapus* (ratio length/middle height: 4 vs 2.8) and the fore wing venation is different (*C. breviscapus* has a longer marginal vein, a longer radial cell, the postmarginal vein does not extend beyond the radial cell and Rs is conspicuous for almost all its length). *Cinetus inclusus* has a shorter petiole (ratio length/middle height: 1.5) and the scape as long as pedicel, F1 and half of F2 combined, unlike *C. breviscapus* whose scape is shorter than flagellomere 1.

***Cinetus elongatus* sp. nov.**

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Figs 1C, 3A–C, Table 1

**Diagnosis**

Scape longer than head length, F1 longest flagellomere, deeply emarginated on anterior half, wider at apex of emargination (male; Fig. 3A–B); metapleural carina extending from hind coxa and forked anteriorly (Fig. 3C); marginal vein slightly shorter than its distance from basal vein, radial cell elongate, longer than marginal vein, postmarginal vein 1.5 times as long as radial cell (Fig. 1C); petiole 5.3 times as long as wide, with a few long setae (Fig. 3C).

**Etymology**

The species name derives from the general elongate aspect of the species. The specific epithet is to be treated as an adjective.

**Type material**

Holotype NHMD-608402, a complete male but partially hidden by a milky coat.

**Locality and horizon**

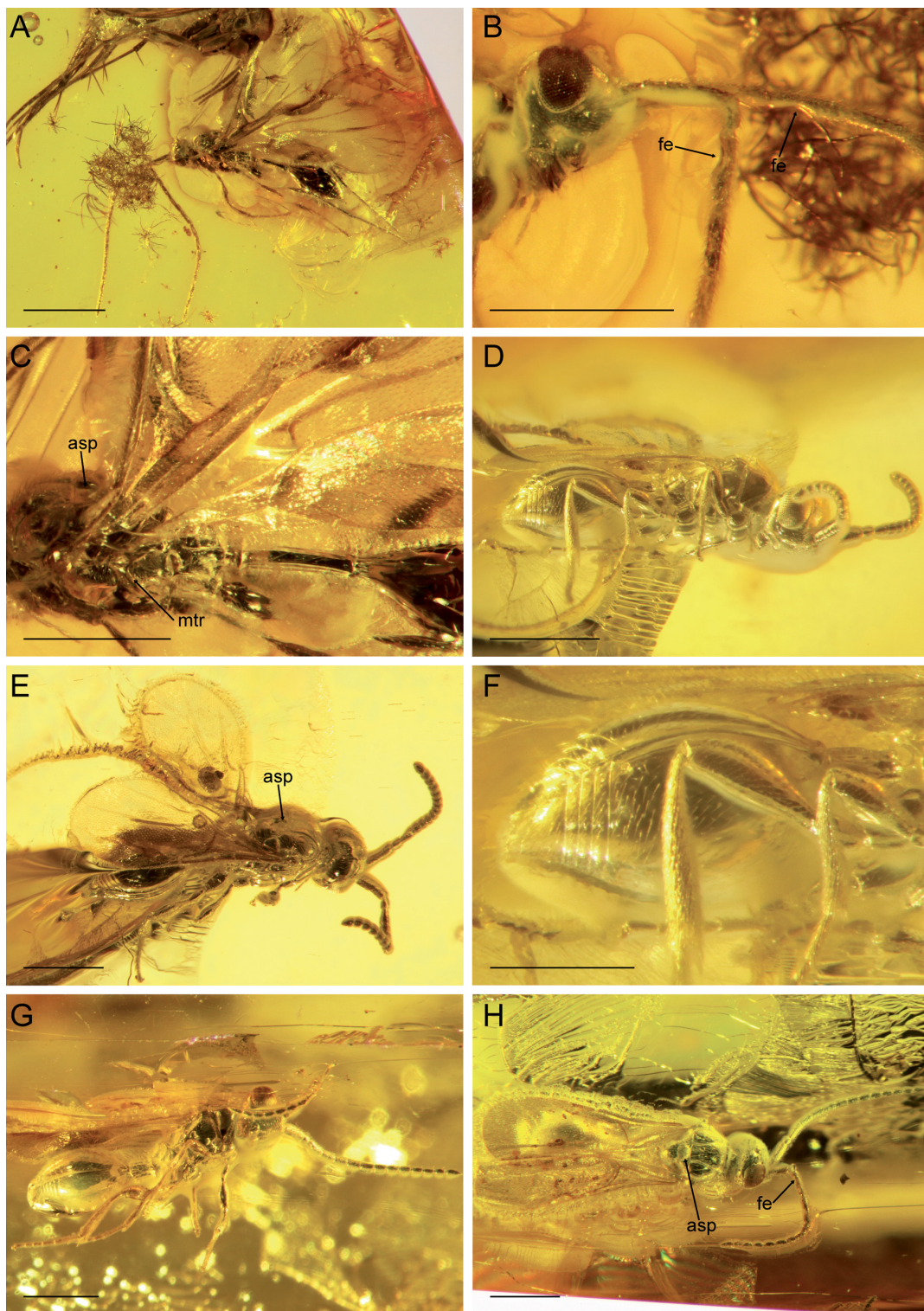
Baltic amber is considered to be of Bartonian–Priabonian age, ca 34–38 Ma.

**Description**

**Male**

**BODY.** 4.46 mm. Head higher than long, homogeneously pubescent (HeL = 0.54 mm); eye oval; antenna inserted on distinct shelf; toruli broadly separated; antenna with numerous short hairs; scape longer than head length; pedicel more than two times as short as shortest flagellomere, almost as wide as long; flagellomeres cylindrical, elongate, much longer than wide; F1 longest, with deep emargination basally, wider at apex of emargination; F2–F11 shorter, slightly decreasing in length; F12 longer than F7–F11, conical (antennomeres length of holotype, in mm: Sc-0.61; P-0.12; F1-0.41; F2-0.38; F3-0.36; F4-0.34; F5-0.35; F6-0.33; F7-0.31; F8-0.32; F9-0.29; F10-0.29; F11-0.26; F12-0.33); mandibles of ordinary form, bidentate, slightly crossing at tip.

**MESOSOMA.** Pubescent, with short setae (MsL = 1.52 mm); pronotum reduced in length, epomia present; mesoscutum large, convex, notauli complete, convergent anteriorly, slightly diverging posteriorly but terminating in anterior scutellar pit; anterior scutellar pit deep, large, suboval with posterior margin convex; metapleural carina distinct, forked anteriorly; propodeum with plicae, median propodeal keel simple. Fore wing extending beyond metasoma, homogeneously micro-pubescent (FwL = 3.89 mm); C, Sc+R, basal vein, M+Cu, M, Cu, marginal vein, postmarginal vein, r-rs and Rs fully pigmented; marginal vein slightly shorter than its distance from basal vein; r-rs well developed; Rs closing radial cell in straight line; radial cell elongate, longer than marginal vein; postmarginal vein 1.5 times as long as radial cell. Hind wing shorter and narrower than fore wing; C pigmented; basal cell opened; three



**Fig. 3.** A–C. *Cinetus elongatus* sp. nov., holotype (NHMD-608402). **A.** Habitus in lateral view. **B.** Head in lateral view. **C.** Mesosoma and petiole in lateral view. **D–H.** *Pantoclis globosa* sp. nov. **D–F.** Holotype (NHMD-608414). **D.** Habitus in lateral view. **E.** Habitus in dorsal view. **F.** Gaster in lateral view. **G–H.** Paratype (NHMD-608394). **G.** Habitus in lateral view. **H.** Habitus in dorsal view. Abbreviations: asp = anterior scutellar pit; fe = flagellomere emargination; mtr = metapleural ridge. Scale bars: A = 2 mm; B–E, G–H = 1 mm; F = 0.5 mm.

hamuli present. Legs slender, bearing numerous un-organized setae; tibial spur formula 1-2-2; tarsal claws simple.

METASOMA. Petiole 5.3 times as long as wide (PtL = 0.79 mm; PtW = 0.15 mm), longitudinally ribbed, with sparse very long setae; gaster ellipsoidal (GL = 1.61 mm; GH = 0.68 mm), pointed at apex, with sparse setae on first segments, more numerous at apex; T2 and S2 longest; four ring-like segments posterior to large tergite, genitalia externalized.

#### Female

Unknown.

#### Comments

Using Nixon's (1957) key, *Cinetus elongatus* sp. nov. keys out near *Leptorhaptus* Förster, 1865 sensu Nixon (1957) because of the following characters: fourth antennal segment not modified, mandibles of ordinary form, scutellum without a row of foveae along posterior margin, marginal vein hardly shorter than the radial cell, petiole much longer than wide, notauli subparallel, terminates in scutellar hollow. *Leptorhaptus* is currently regarded as a synonym of *Cinetus* (Masner 1964). *Cinetus elongatus* displays all the diagnostic characters of *Cinetus* provided by Quadros & Brandão (2017), especially the large anterior scutellar pit, the posterior extremity of notauli directed toward a point within the anterior scutellar pit, the marginal vein shorter than radial cell and slightly shorter than its distance to basal vein.

Among the Baltic amber species, it differs from other *Cinetus* species as follow: *C. balticus* has the scape as long as F1 (longer in *Cinetus elongatus* sp. nov.), the petiole shorter (ratio length/middle height: 4 vs 5.3) and the marginal vein longer than its distance from basal vein; *Cinetus breviscapus* sp. nov. has the scape shorter than F1, the petiole shorter (ratio length/middle height: 2.8), the marginal vein longer than its distance from basal vein and the postmarginal vein shorter than radial cell; *C. inclusus* has a shorter petiole (ratio length/middle height: 1.5) and a smaller body (1.9 mm).

Genus *Pantoclis* Förster, 1856

#### *Pantoclis globosa* sp. nov.

urn:lsid:zoobank.org:act:4BF21BF6-7925-4F2A-8A84-5D8C49BBD8D7

Figs 1D, 3D–H, Table 1

#### Diagnosis

Eye glabrous; female antenna with: scape 5.5 times as long as wide, pedicel shorter than F1, F1 longest, F2–F13 as long as wide (Fig. 3D–E); male antenna with: scape 5.5 times as long as wide, pedicel rounded, F1 longest, emarginate on anterior third, F2–F12 subequal in length (Fig. 3G–H); mesosoma sparsely pubescent, shorter than metasoma; pronotum not elongate with epomia extending from pronotal shoulders to front coxa; notauli on mesoscutum complete and convergent posteriorly; propodeum with plicae; marginal vein shorter than radial cell and as long as three quarters of its distance to basal vein; radial cell closed; Rs inconspicuous proximally to r-rs (Fig. 1D); petiole as long as wide; gaster globous (Fig. 3F–G).

#### Etymology

The species name refers to the globular gaster of the species. The epithet is to be treated as an adjective.

#### Type material

Holotype NHMD-608414, a complete female but partially hidden by a milky coat; paratype NHMD-608394, a complete male.

**Locality and horizon**

Baltic amber is considered to be of Bartonian–Priabonian age, ca 34–38 Ma.

**Description****Female**

**BODY.** BL = 2.83 mm. Head oval, subtriangular in frontal view (HeL = 0.48 mm), bearing several short hairs, stouter on frons; eye oval, glabrous; antenna inserted on frontal shelf, at level with lower margin of eyes; toruli well separated; antenna bearing numerous short sensilla; scape shorter than head length, 5.5 times as long as wide; pedicel shorter than F1, longer than wide; 13 flagellomeres; F1 longest, two times as long as wide; F2–F13 as long as wide; F13 tapering at apex (antennomeres length of female holotype, in mm: Sc-0.44; P-0.14; F1-0.16; F2-0.10; F3-0.10; F4-0.09; F5-0.09; F6-0.09; F7-0.09; F8-0.08; F9-0.09; F10-0.09; F11- 0.09; F12-0.09; F13-0.10); mandibles of ordinary form; occipital carina foveate.

**MESOSOMA.** Smooth and shiny, shorter than metasoma (MsL = 0.97 mm), sparsely pubescent; pronotum not elongate with distinct and uninterrupted epomia; mesoscutum distinctly convex, notauli complete and convergent; anterior scutellar pit suboval, slightly narrower than apical distance between notauli; scutellum without posterior scutellar pit; propodeum with two prominent plicae; median propodeal keel simple. Fore wing hyaline, homogeneously micropubescent, extending beyond metasoma (FwL = 2.71 mm); C, Sc+R, M+Cu, basal vein, marginal vein, postmarginal vein and r-rs pigmented; Cu nebulous; marginal vein length around three quarters of its distance from basal vein; marginal vein shorter than radial cell; radial cell closed by Rs; Rs pigmented distally to r-rs, inconspicuous proximally. Legs slender, with short hairs; tibial spur formula 1-2-2; tarsal claws simple.

**METASOMA.** Petiole twice as long as wide (PtL = 0.27 mm; PtW = 0.12 mm), longitudinally striated, bearing long hairs dorsally; gaster globular, slightly longer than high (GL = 1.05 mm; GH = 0.67 mm), with sparse pubescence; S2 and T2 longest; four ring-like segments discernible beyond large tergite.

**Male**

BL = 3.50 mm; similar to female but antennae sexually dimorphic: scape shorter than head length (HeL = 0.53 mm), 5.5 times as long as wide, pedicel rounded, as long as wide, 12 flagellomeres elongate, cylindrical, longer than wide, F1 longest, with marked emargination on anterior third of segment, F2–F12 subequal in length, F12 tapering at apex (antennomeres length of male paratype, in mm: Sc-0.38 mm; P-0.11; F1-0.25; F2-0.19; F3-0.19; F4-0.19; F5-0.18; F6-0.17; F7-0.16; F8-0.16; F9-0.16; F10-0.16; F11- 0.15; F12; 0.21).

Remaining measurements: HeL = 0.53 mm; MsL = 1.24 mm; FwL = 2.84 mm; PtL = 0.32 mm; PtW = 0.15 mm; GL = 1.41 mm; GH = 0.82 mm.

**Comments**

Using Nixon's (1957) key, *Pantoclis globosa* sp. nov. keys out to *Pantoclis* because of the following characters: antennae inserted on a frontal prominence, mandibles not forming a beak or sickle-shaped, notauli present, scutellum without foveae along posterior margin, marginal vein nearly as long as its distance from basal vein and presence of ring-like segments beyond the large tergite, marginal vein shorter than radial cell, epomia distinct, median propodeal keel simple, petiole at most one and a third times as long as its apical width. *Pantoclis globosa* also fits in *Pantoclis* according to the diagnosis of Hou *et al.* (2016). It differs from most extant representatives of *Pantoclis* by having the marginal vein much longer than the r-rs (Nixon 1957; Sharma 1980; Buhl 1998). *Pantoclis longiscapa* Chambers, 1974 has a similar fore wing configuration but differs by having F1 very long and F2 distinctly longer than the following flagellomeres (Chambers 1974). *Pantoclis deperdita* Brues, 1906, from the Eocene

of Florissant has a shorter radial cell and marginal vein (Brues 1906) and is therefore considered as a different species from *P. globosa*.

Genus *Pantolyta* Förster, 1856

*Pantolyta augustinusii* sp. nov.

urn:lsid:zoobank.org:act:DD4A2A42-E41A-4731-B91D-AD9EFC205E50

Figs 1E, 4, Table 1

### Diagnosis

Eye not pubescent; toruli protruding; antenna distinctly pubescent; F1 with indistinct emargination; F1 half of scape length (Fig. 4A–B); mesoscutum bearing long hairs; median propodeal keel simple; fore wing radial cell closed; postmarginal vein extending little beyond radial cell; Rs nebulous proximally to r-rs, marginal vein 0.7 times as long as its distance from basal vein; r-rs distinct (Fig. 1E); petiole 2.4 times as long as wide (Fig. 4D).

### Etymology

We dedicate this species to the Augustinus Foundation, who generously contributed to the funding for purchasing the amber pieces studied. The specific epithet is to be treated as a noun in genitive case.

### Type material

Holotype NHMD-300829, a complete male; paratypes NHMD-608391, a complete male; NHMD-608406, a complete male but partially hidden by a milky coat; NHMD-608412, a complete male; NHMD-608404, a complete male.

### Locality and horizon

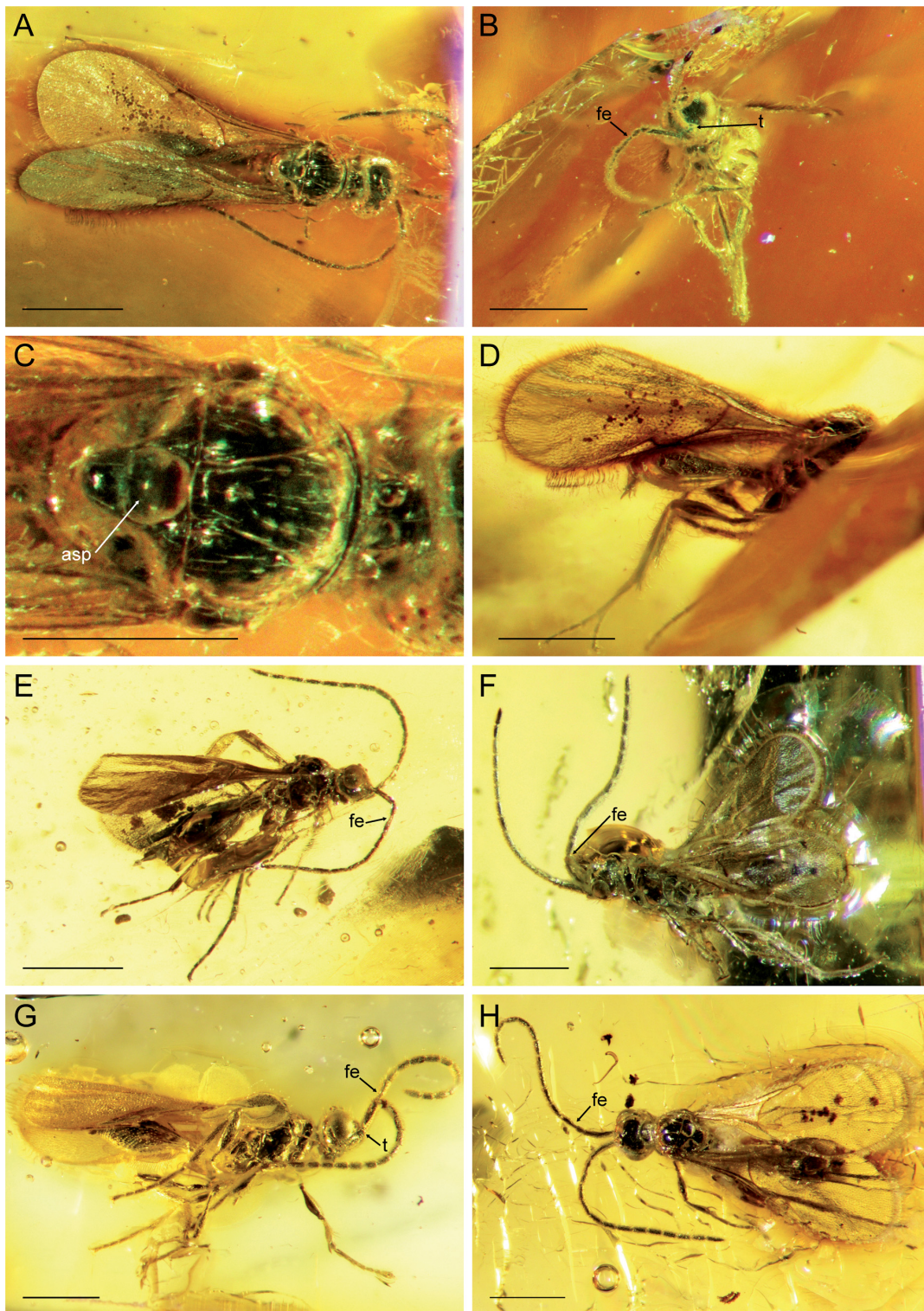
Baltic amber is considered to be of Bartonian–Priabonian age, ca 34–38 Ma.

### Description

#### Male

**BODY.** BL = 2.51–3.47 mm. Head subtriangular in frontal view (HeL = 0.39–0.48 mm); eye large, not pubescent; several hairs on frons; antennae inserted on distinct but not prominent shelf; toruli well developed, as long as one sixth of scape length from base to apex, separated by distinct cleft; antennae bearing numerous short setae; scape almost six times as long as wide; pedicel slightly longer than wide; flagellomeres elongate, cylindrical; F1 half of scape length, with an indistinct emargination basally; F2–F11 subequal in length; F12 longer and tapering at apex (antennomeres length of holotype, in mm: Sc-0.38; P-0.08; F1-0.21; F2-0.19; F3-0.19; F4-0.19; F5-0.19; F6-0.20; F7-0.19; F8-0.20; F9-0.21; F10-0.21; F11-0.21; F12-0.23); mandibles short, not forming a beak.

**MESOSOMA.** Shorter than metasoma (MsL = 0.90–1.29 mm); pronotum visible in dorsal view; epomia present as a simple keel; pronotal shoulders rounded; mesoscutum smooth, bearing long hairs; notauli deeply impressed, anteriorly converging towards scutellum, posteriorly parallel just before transscutal sulcus; anterior scutellar pit large, deep; scutellum without posterior scutellar pits; mesopleuron bare, mesopleural pit present; propodeum with median keel simple. Fore wing hyaline, extending far beyond metasoma (FwL = 2.60–3.54 mm), covered with micropubescence; C, Sc+R, M+Cu, basal vein and Cu pigmented; basal and costal cells closed; marginal vein slightly widened, about two thirds as long as its distance from basal vein and twice as long as r-rs; postmarginal vein pigmented, extending slightly beyond radial cell; radial cell closed; Rs tubular distally to r-rs, nebulous proximally; M inconspicuous towards apex. Legs slender, hind femur slightly thicker; tibial spur formula 1-2-2; tarsal claws simple.



**Fig. 4.** *Pantolyta augustinusii* sp. nov. **A–D.** Holotype (NHMD-300829). **A.** Habitus in dorsal view. **B.** Head in frontal view. **C.** Detail of the anterior mesosoma in dorsal view. **D.** Gaster and petiole in lateral view. **E.** Paratype (NHMD-608391), habitus in lateral view. **F.** Paratype (NHMD-608406), habitus in lateral view. **G.** Paratype (NHMD-608412), habitus in lateral view. **H.** Paratype (NHMD-608404), habitus in dorsal view. Abbreviations: asp = anterior scutellar pit; fe = flagellomere emargination; t = toruli. Scale bars: A–B, D–H = 1 mm; C = 0.5 mm.

**METASOMA.** Petiole cylindrical, 2.4 times as long as its middle width (PtL = 0.27–0.37 mm; PtW = 0.11–0.15 mm), with longitudinal ribs, long hairs laterally and ventrally; gaster fusiform (GL = 0.90–1.33 mm; GH = 0.42–0.58 mm), smooth; T2 longest, narrowing toward petiole; other segments much shorter.

#### **Female**

Unknown.

#### **Comments**

Using Nixon's (1957) key to the genera of Belytinae, *Pantolyta augustinusii* sp. nov. keys out near *Acropiesta* Förster, 1856 because of the following characters: notauli present, second flagellomere not modified; scutellum without foveae; mandibles not forming a beak; marginal vein shorter than both radial cell and its distance from basal vein; pronotum with reduced epomia; large tergite markedly tapering towards petiole. *Pantolyta augustinusii* especially share with *Acropiesta* the antennal shelf prominent with toruli separated by a furrow, the 14-segmented antennae with F1 modified, the pronotal shoulders rounded, the notauli complete, the anterior scutellar pit large and quadrate, the propodeum with median keel simple, the fore wing venation with C, Sc+R, M+Cu, Rs, basal and marginal vein tubular, the petiole cylindrical (Macek 1998). However, due to their close similarities, *Acropiesta* has recently been synonymized under *Pantolyta* by Chemyreva & Kolyada (2021). Four other *Pantolyta* species are present in Baltic amber, two having been described under *Acropiesta* and not duly transferred by Chemyreva & Kolyada (2021): *Pantolyta antiqua* Buhl, 1999, *Pantolyta janzeni* (Buhl, 2002) comb. nov., *Pantolyta perrichoti* (Jouault & Nel, 2020) comb. nov. and *Pantolyta somnulentata* Maneval, 1938. *Pantolyta antiqua* has the marginal vein as long as its distance from basal vein whereas it is distinctly shorter in *Pantolyta augustinusii* (Buhl 1999); *P. janzeni* has a distinct emargination of F1 in the male antenna, the marginal vein is shorter and the postmarginal vein is longer than in *Pantolyta augustinusii* (Buhl 2002); *P. perrichoti* has the median propodeal keel bifid (Jouault & Nel 2020) and *P. somnulentata* has the radial cell shorter than the marginal vein (Maneval 1938).

#### *Pantolyta chemyrevae* sp. nov.

urn:lsid:zoobank.org:act:626E3F04-AB34-45C2-AA5A-82AD0A85CC8E

Fig. 5A–C, Table 1

#### **Diagnosis**

Eye round, extending at most a fourth of head length; scape as long as pedicel and first three flagellomeres combined; F1 two times as long as wide, narrower than pedicel; F2–F13 gradually widening towards apex (Fig. 5A–B); epomia present; anterior scutellar pit suboval, wider than shortest distance between notauli; plicae projecting posteriorly; fore wing not reaching middle of propodeum (brachypterous morph; Fig. 5A–B); petiole slightly longer than wide (Fig. 5C); gaster fusiform, elongate and tapering at apex; T2 striated dorsally at junction with petiole; ovipositor long, subequal in length to gaster (Fig. 5A).

#### **Etymology**

The species is dedicated to Vasilisa Chemyreva, Russian entomologist, in acknowledgment of her numerous publications on Diapriidae from the Palearctic region. The specific epithet is to be treated as a noun in the genitive case.

#### **Type material**

Holotype NHMD-608448, a complete female partially hidden by a milky coat.

#### **Locality and horizon**

Baltic amber is considered to be of Bartonian–Priabonian age, ca 34–38 Ma.



## Description

### Female

**BODY.** BL = 2.43 mm. Head smooth, bare (HeL = 0.37 mm); eye round, small, less than a third of head length (ED = 0.11 mm); antenna bearing numerous short setae; toruli separated by shallow cleft; scape as long as pedicel and first three flagellomeres combined, at least as long as head; pedicel three times as long as wide; 13 flagellomeres; F1 two times as long as wide, narrower than pedicel; following flagellomeres gradually widening towards apex; F13 largest and longest of all (antennomeres length of holotype, in mm: Sc-0.46; P-0.16; F1-0.12; F2-0.08; F3-0.08; F4-0.08; F5-0.09; F6-0.08; F7-0.08; F8-0.08; F9-0.08; F10-0.10; F11- 0.10; F12; 0.11; F13-0.19); mandibles simple, just crossing at tip; labial palpi three-segmented, first long, second narrowing at apex and third wider.

**MESOSOMA.** Shorter than metasoma (MsL = 0.75 mm); pronotum not elongate, epomia present; notauli deep and complete, convergent posteriorly; anterior scutellar pit suboval, wider than shortest distance between notauli; mesopleuron bare, with epicnemial pit and carina present; propodeum with plicae projecting posteriorly, forming teeth, median propodeal keel simple. Fore wing reduced, not reaching middle of propodeum (FwL = 0.32 mm). Hind wing shorter (HwL = 0.17 mm). Legs slender with few unorganized erect setae; tibial spur formula 1-2-2; tarsal claws simple.

**METASOMA.** Petiole cylindrical, slightly longer than wide (PtL = 0.20 mm; PtW = 0.18 mm), with distinct longitudinal sculpture, and short hairs dorsally; gaster subcylindrical, elongate and tapering at apex (GL = 1.11; GH = ca 0.40 mm); T2 and S2 longest; T2 slightly striated dorsally at junction with petiole; T6 and T7 not clearly separated and forming long triangle; ovipositor exerted, slightly shorter than gaster (OL = 0.89 mm).

### Male

Unknown.

## Comments

Using Nixon's (1957) key, *Pantolyta chemyreae* sp. nov. keys out to *Pantolyta* Förster, 1856 because of the following characters: brachypterous, toruli rims without a distinct cleft, antennae 15-segmented, epomia on pronotum defined at pronotal collar, notauli present on mesoscutum, lower side of gaster slightly down curved. With the keys to species of *Pantolyta* provided in Chemyreva & Kolyada (2019) and Nixon (1957), *P. chemyreae* keys out near *P. stylata* Kieffer, 1908 (= *P. vernalis* sensu Nixon 1957) but has the antennal shelf less prominent and a longer scape (Chemyreva & Kolyada 2019).

Among the Baltic amber species, it differs from other *Pantolyta* species as follow: *P. antiqua* is macropterous and has F1 more than two times as long as pedicel; *Pantolyta augustinusii* has the toruli separated by a distinct cleft, the mesoscutum bearing long hairs and the plicae not projecting posteriorly; *P. janzeni* and *P. perrichoti* has a longer petiole, more than two times as long as wide; *P. somnulenta* is very similar to *P. chemyreae* sp. nov. but is macropterous, has anterior scutellar pit narrower than *P. chemyreae* and the plicae less produced posteriorly.

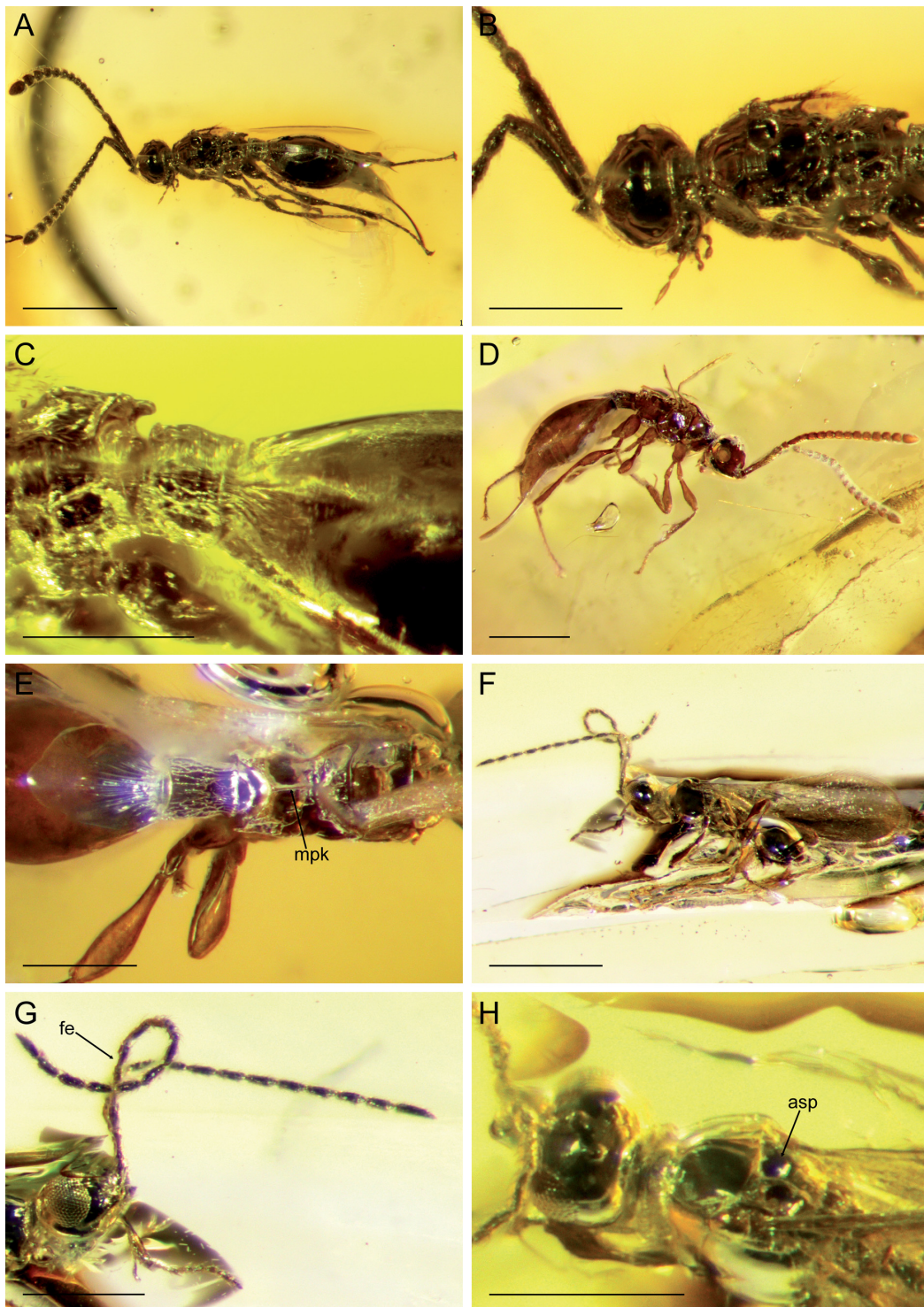
### *Pantolyta similis* sp. nov.

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Fig. 5D–E, Table 1

## Diagnosis

Head as high as long; eye small but functional; antennal shelf projecting forward and upward; antenna with homogeneous short setae; pedicel conical, with base narrower; F1 second longest; F2–F13 gradually widening; F13 longest and widest (Fig. 5D); epomia absent; median propodeal keel simple (Fig. 5E);



**Fig. 5.** A–C. *Pantolyta chemyrevae* sp. nov., holotype (NHMD-608448). A. Habitus in dorsolateral view. B. Head and mesosoma in dorsal view. C. Petiole in lateral view. D–E. *Pantolyta similis* sp. nov., holotype (NHMD-608468). D. Habitus in lateral view. E. Mesosoma, petiole and anterior gaster in dorsal view. F–H. *Basalys villumi* sp. nov., holotype (NHMD-608360). F. Habitus in lateral view. G. Head in lateral view. H. Head and mesosoma in dorsal view. Abbreviations: asp = anterior scutellar pit; fe = flagellomere emargination; mpk = median propodeal keel. Scale bars: A, D, F = 1 mm; B, E, G–H = 0.5 mm; C = 0.25 mm.

fore wing not extending beyond petiole (brachypterous morph); petiole 1.3 times as long as wide; gaster fusiform, elongate; T2 and S2 covering anterior half of gaster; T2 with numerous fine and long striations medially at junction with petiole (Fig. 5D).

### Etymology

The specific epithet refers to its similarity with the extant species *Pantolyta macrocera* (Thomson, 1858) and is to be treated as an adjective.

### Type material

Holotype NHMD-608468, a complete female.

### Locality and horizon

Baltic amber is considered to be of Bartonian–Priabonian age, ca 34–38 Ma.

### Description

#### Female

**BODY.** BL = 3.52 mm. Head glabrous, smooth, as high as long (HeL = 0.50 mm); eye round, small, less than a third of head length (ED = 0.18 mm); frontal prominence elongate; toruli facing upwards; antenna slightly but homogeneously pubescent; scape longer than head length; pedicel conical, thinner at base; F1 second longest; F2–F12 of subequal length, gradually widening; F12 as long as wide; F13 widest and longest, conical (antennomeres length, in mm: Sc-0.58 mm; P-0.11; F1-0.17; F2-0.10; F3-0.10; F4-0.11; F5-0.11; F6-0.11; F7-0.12; F8-0.11; F9-0.11; F10-0.11; F11-0.11; F12-0.12; F13-0.21); mandibles of ordinary form.

**MESOSOMA.** Shorter than metasoma (MsL = 1.10 mm); pronotum not elongate, with straight posterior margin, epomia absent; mesoscutum convex, with notauli deep and complete; anterior scutellar pit large, rounded; scutellum sub-quadrangle, without posterior scutellar pits; propodeum dorsally with prominent plicae, median keel simple. Fore wing very reduced, hardly reaching posterior margin of petiole (FwL = 1.04 mm). Hind wing reduced, shorter than fore wing (HwL = 0.52 mm). Legs slender, with only hind coxa widened; erect setae along hind tibia and tarsomere; tibial spur formula 1-2-2; tarsal claws simple.

**METASOMA.** Petiole 1.3 times as long as wide (PtL = 0.28 mm; PtW = 0.22 mm), longitudinally ribbed; gaster fusiform and elongate (GL = 1.64 mm; GH = 0.59 mm); S2 and T2 longest, covering anterior half of gaster; T2 striated medially at junction with petiole; three ring-like segments visible posteriorly to large tergite; apical sternites fused into long, smooth triangle; ovipositor exerted, shorter than gaster (OL = 0.74 mm).

#### Male

Unknown

### Comments

The specimen was originally identified as the extant species *Pantolyta macrocera* (Thomson, 1858) by Buhl (2002) because of the brachypterous morph. However, we can observe some differences on the petiole and gaster. *Pantolyta similis* sp. nov. displays numerous fine longitudinal ribs dorsally on the petiole whereas there are fewer ribs in *P. macrocera*. Additionally, *P. macrocera* has shorter and stronger medial striations on T2 than *Pantolyta similis* (Chemyreva & Kolyada 2021: fig. 11g).

Among the Baltic amber species, it differs from other *Pantolyta* species as follows: *P. antiqua* and *P. somnulenta* are macropterous and have a shorter petiole; *Pantolyta augustinusii* sp. nov. has the epomia present, whereas it is absent in *Pantolyta similis* sp. nov.; *Pantolyta chemyrevae* sp. nov. has the epomia present, the anterior scutellar pit more quadrate, the petiole more elongate and the striations on T2 shorter; *P. janzeni* and *P. perrichoti* has a longer petiole, more than two times as long as wide.

Subfamily Diapriinae Haliday, 1833

Genus *Basalys* Westwood, 1833

*Basalys villumi* sp. nov.

urn:lsid:zoobank.org:act:4204B17E-4659-432C-9266-1C723B434E35

Figs 1F, 5F–H, 6A, Table 1

### Diagnosis

Body smooth; scape seven times as long as wide; pedicel conical; flagellomeres cylindrical and longer than wide; F1 longest; F2–F11 similar in length; F2 conspicuously emarginate (Fig. 5D–E); scutellum subquadrate without posterior scutellar pits (Fig. 5F); fore wing bordered with small hairs, r-rs short but distinct, M+Cu nebulous (Fig. 1F); hind wing narrow, two thirds of fore wing length, with long hairs along posterior margin; petiole three times as long as wide (Figs 5D, 6A).

### Etymology

We dedicate this species to Villum Fonden, who generously contributed to funding for purchasing the amber pieces studied. The specific epithet is to be treated as a noun in the genitive case.

### Type material

Holotype NHMD-608360, a complete male; paratype NHMD-608369, a complete male.

### Locality and horizon

Baltic amber is considered to be of Bartonian–Priabonian age, ca 34–38 Ma.

### Description

#### Male

**BODY.** BL = 1.82 mm. Body highly glabrous. Head globular, as long as high (HeL = 0.33 mm), with sparse short hairs; eye round; toruli situated at middle of eye height; antenna 14-segmented; scape seven times as long as wide; pedicel conical; flagellomeres cylindrical, elongate, distinctly longer than wide, with short hairs; F1 longest, F2–F11 subequal in length; F2 emarginate on anterior third; F12 as long as F1; tapering at apex (antennomeres length of holotype, in mm: Sc-0.22 mm; P-0.09; F1-0.15; F2-0.09; F3-0.11; F4-0.10; F5-0.11; F6-0.10; F7-0.12; F8-0.10; F9-0.11; F10-0.12; F11-0.11; F12-0.14); mandibles weakly crossing at tip, not sickle or beak-shaped; occipital flange foveate, rather concave.

**MESOSOMA.** Shorter than metasoma (MsL = 0.63 mm); pronotum not elongate, anterior part setose, epomia absent; mesoscutum slightly convex, smooth, notauli absent; anterior scutellar pit present, round; scutellum subquadrate, without posterior scutellar pits. Fore wing extending beyond metasoma (FwL = 1.78 mm), bordered with small hairs; Sc+R distinctly separated from anterior margin; marginal vein thickened along wing margin, longer than wide; r-rs short; basal vein curved, perpendicular to Sc+R, almost reaching M+Cu; M+Cu nebulous. Hind wing narrow, two thirds of fore wing length; bordered with long setae along posterior margin. Legs slender, covered with scattered setae; femur clavate; tibia weakly broadened apically; tibial spur formula 1-2-2; tarsal claws simple.

**METASOMA.** Petiole cylindrical, narrow, three times as long as wide (PtL = 0.21 mm; PtW = 0.07 mm), longitudinally striated; gaster ellipsoidal (GL = 0.61 mm; GH = 0.30 mm), glabrous; T2 and S2 longest, covering two thirds of gaster, anterior margin T2 straight; segments 3 and 4 ring-like, segment 5 longer than 3 and 4 combined.

#### **Female**

Unknown.

#### **Comments**

Using Nixon's (1980) and Masner & García's (2002) keys, *Basalys villumi* sp. nov. keys out to *Basalys* Westwood, 1833 because of the following characters: antenna with 14 segments, notauli absent, scutellum with anterior scutellar pit, wings fully developed, Sc+R separated from fore margin of wing, fore wing with distinct basal vein, basal margin of large tergite straight. The description of the species is also consistent with the diagnosis of Hou & Xu (2016).

*Basalys villumi* sp. nov. differs from extant *Basalys* by having F1 longer than F2 (Nixon 1980; Hou & Xu 2016).

Genus *Doliopria* Kieffer, 1910

*Doliopria baltica* sp. nov.

urn:lsid:zoobank.org:act:36E9B60D-6971-454F-AD9F-DD69D430C16B

Figs 1G, 6B–D, Table 1

#### **Diagnosis**

Head globular, with sparse long hairs on vertex; apical segment of maxillary palpi bearing one long seta (Fig. 6C); antenna 11-segmented; scape as long as pedicel + F1–F5 combined, scape with apical rim slightly notched; pedicel cylindrical, elongate; F1 narrower; F2–F6 widening; F7–F9 forming distinct club; F7–F8 two times as wide as long; F9 as wide as long (Fig. 6B); anterior scutellar pit suboval, not divided; scutellum subquadrate; propodeum punctuate and carinate (Fig. 6D); hind wing bordered with long setae along posterior margin and distal part of fore margin; petiole cylindrical, slightly longer than wide; gaster ellipsoidal; tergite 2 with anterior margin excised (Fig. 6D).

#### **Etymology**

The species name refers to the origin of the amber piece containing the specimen. The specific epithet is to be treated as an adjective.

#### **Type material**

Holotype NHMD-608374, a complete female partially hidden by a milky coat.

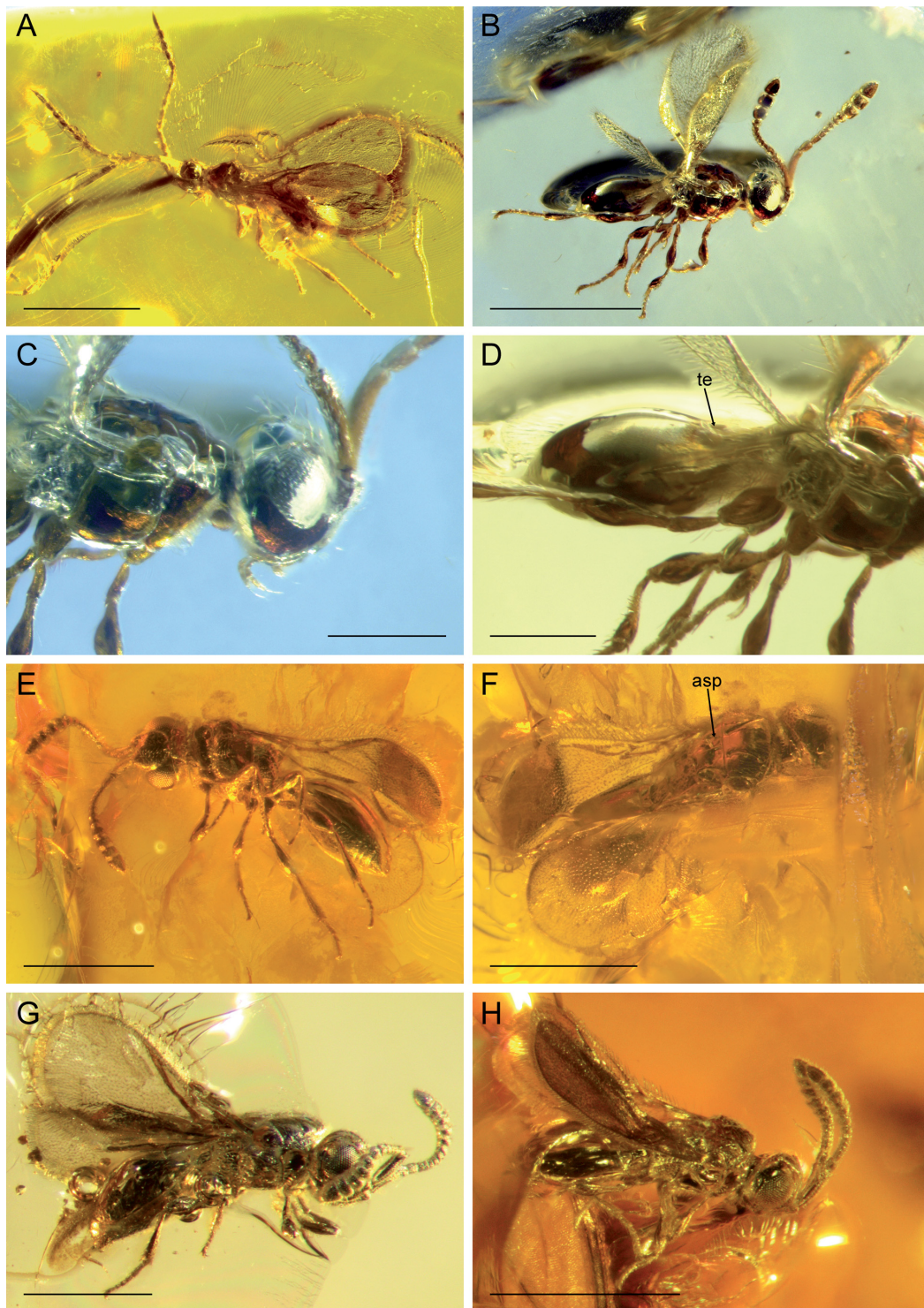
#### **Locality and horizon**

Baltic amber is considered to be of Bartonian–Priabonian age, ca 34–38 Ma.

#### **Description**

##### **Female**

**BODY.** BL = 1.20 mm. Body smooth and shiny, sparsely pubescent, hairs very long. Head globular, slightly higher than long with hairs posteriorly (HeL = 0.23 mm); eye oval, glabrous; maxillary palpi 5-segmented with one long seta on apical segment; antenna 11-segmented inserted on transverse shelf of low elevation; toruli separated by shallow cleft; scape as long as pedicel + F1–F5 combined, as long as



**Fig. 6.** A. *Basalys villumi* sp. nov., paratype (NHMD-608369), habitus in lateral view. B–D. *Doliopria baltica* sp. nov., holotype (NHMD-608374). B. Habitus in lateral view. C. Head in lateral view. D. Mesosoma and metasoma in lateral view. E–H. *Spilomicrus succinalis* sp. nov. E–F. Holotype (NHMD-607131). E. Habitus in ventrolateral view. F. Head and mesosoma in dorsal view. G. Paratype (NHMD-608344), habitus in lateral view. H. Paratype (NHMD-608354), habitus in lateral view. Abbreviations: asp = anterior scutellar pit; te = tergite excision. Scale bars: A, E–H = 1 mm; B = 0.5 mm; C–D = 0.25 mm.

head, with apical circumference slightly notched; pedicel as wide as scape, cylindrical; F1 narrower than pedicel and longer than wide; F2–F5 slightly shortening and widening; F6 two times as wide as long; F7–F9 wider than long, longer than previous flagellomeres, forming clava; F9 ovoid (antennomeres length of holotype, in mm: Sc-0.19; P-0.05; F1-0.03; F2-0.02; F3-0.02; F4-0.03; F5-0.03; F6-0.03; F7-0.07; F8-0.07; F9-0.10); mandibles short, only crossing at tips.

**MESOSOMA.** Slightly shorter than metasoma (MsL = 0.43 mm); pronotum with lateral posterior margin straight; mesoscutum large and slightly convex, without notauli or any other sulci; anterior scutellar pit deep, not divided, suboval; scutellum subquadrate; propodeum minutely punctate in anterior part and carinate. Fore wing extending beyond metasoma (FwL = 0.77 mm), micropubescent and bordered with short setae; only Sc+R present, slightly separate from anterior margin of wing, distally ending in slight thickening of marginal vein. Hind wing length two thirds of length of fore wing (HwL = 0.55 mm), micropubescent; with long setae along posterior margin and distal part of costal margin; three hamuli present; basal cell open. Legs slender, with only hind coxa and femur stouter; tibial spur formula 1-2-2; tarsal claws simple.

**METASOMA.** Petiole cylindrical, narrow, longer than wide (PtL = 0.10 mm; PtW = 0.06 mm), longitudinally striated, bearing several long hairs; gaster ellipsoidal (GL = 0.44 mm; GH = 0.21 mm), not sharply pointed at apex, smooth and glabrous; T2 and S2 longest; T2 covering at least two thirds of gaster, its anterior margin medially excised for distance subequal to petiole length; ovipositor slightly exerted.

#### Male

Unknown.

#### Comments

In Masner & García's (2002) keys to the genera of Diapriinae, *Doliopria baltica* sp. nov. keys out to *Doliopria* Kieffer, 1910 because of the following characters: frons unarmed, antenna 11-segmented, notauli absent, wings fully developed, Sc+R separate from anterior margin of wing, basal vein absent. The description of the specimen is consistent with the original diagnosis of the genus by Kieffer (1910) and the revised diagnosis of Masner & García (2002). *Doliopria baltica* differs from extant representatives of this genus as follow: *D. americana* Fouts, 1926 has a two-segmented club (Fouts 1926); *D. brachyptera* Ogloblin, 1960 has F9 more lengthened and is brachypterous; *D. foersteri* Ogloblin, 1960 has short hairs on eyes, flagellomeres longer than wide and lacks the anterior scutellar pit; *D. equatoriana* Ogloblin, 1960 has F2–F5 longer than wide (Ogloblin 1960); *D. collegii* Ferrière, 1929 has F9 longer (Loiácono *et al.* 2013); *D. flavipes* Kieffer, 1910 has F5–6 as long as wide and the petiole shorter (Kieffer 1910); *D. myrmecobia* Kieffer, 1921 has a two-segmented club and the apical flagellomere sharply pointed at the apex (Loiácono *et al.* 2013).

Genus *Spilomicrus* Westwood, 1832

#### *Spilomicrus succinalis* sp. nov.

urn:lsid:zoobank.org:act:C6DACEAE-5CBB-4BC5-A414-FC2458978B3D

Figs 1H, 6E–H, Table 1

#### Diagnosis

Head higher than long, minutely punctate on vertex; scape with distinct punctuations; pedicel pear-shaped, narrower at base; F1–F5 as long as wide; F6–F11 forming non-abrupt clava; F11 conical, longer than F10 (Fig. 6E, G–H); occipital flange foveate (Fig. 6F); pronotum laterally with small foveae along posterior margin (Fig. 6E); mesoscutum flat and smooth, with long hairs; notauli convergent, interrupting before posterior margin of mesoscutum; anterior scutellar pit bifoveate; posterior scutellar

pits present (Fig. 6F); propodeum carinate; Sc+R pigmented, marginal vein wider than long, r-rs as long as marginal vein (Fig. 1H); first fore tarsomere bearing row of setae along inner margin; first hind tarsomere not longer than following two combined; petiole 1.5 times as long as wide; T2 with anterior margin wrinkled (Fig. 6F); two ring-like segments visible after T2.

### **Etymology**

The species name derives from ‘Succinite’, a name given to Baltic amber due to its chemical composition. The specific epithet is to be treated as an adjective.

### **Type material**

Holotype NHMD-607131, a complete female; paratype NHMD-608344, a complete female; paratype NHMD-608354, a complete female.

### **Locality and horizon**

Baltic amber is considered to be of Bartonian–Priabonian age, ca 34–38 Ma.

### **Description**

#### **Female**

**BODY.** BL = 1.96–2.65 mm. Head higher than long (HeL = 0.29–0.50 mm), with several hairs dorsally; head minutely punctate on vertex; eye oval, higher than long; antennae inserted on shelf at level with lower half of eye; toruli distinct and slightly protruding; scape with distinct punctuations, 4.2 times as long as wide; pedicel pear-shaped, narrower at base; F1–F5 compact, as long as wide; following flagellomeres widening to form non-abrupt club; F11 wider and longer than F10, conical (antennomeres length of holotype, in mm: Sc-0.25; P-0.09; F1-0.05; F2-0.04; F3-0.04; F4-0.04; F5-0.05; F6-0.06; F7-0.06; F8-0.06; F9-0.08; F10-0.08; F11-0.10); mandibles simple, not forming beak; occipital flange foveate.

**MESOSOMA.** Shorter than metasoma (MsL = 0.67–0.83 mm); pronotum not elongate, not visible in dorsal view, laterally with small foveae on posterior margin; mesoscutum wide, flat and smooth, with several long hairs; notauli present, deep, convergent posteriorly but not reaching posterior margin of mesoscutum; anterior scutellar pit bifoveate; scutellum with posterior scutellar pits present; propodeum carinate, with prominent median keel. Fore wing extending beyond gaster (FwL = 1.27–1.81 mm), hyaline and covered with micropubescence, rounded, bordered with long setae shortening toward wing apex; Sc+R pigmented and distinctly separated from wing margin; marginal vein thickening at apex of Sc+R and almost two times as wide as long; r-rs pigmented and elongate, almost as long as marginal vein. Hind wing half as long as fore wing; only C pigmented. Legs slender, with numerous long setae; first fore tarsomere bearing row of erect setae on inner margin; fore tibial spur long, curved; tibial spur formula 1-2-2; first hind tarsomere not longer than following two combined.

**METASOMA.** Petiole longer than wide (PtL = 0.14–0.21 mm; PtW = 0.10–0.13 mm), covered with longitudinal carinae, glabrous; gaster beyond petiole broadly oval and narrowed at apex (GL = 0.87–1.11 mm; GH = 0.23–0.43 mm), smooth and with few setae; T2 longest, covering two thirds of gaster, with anterior margin slightly wrinkled, overlapping petiole; S2 longest, as long as T2; segments 3 and 4 ring-like; segment 5 longer than 3 and 4 combined and sharply pointed at apex; ovipositor projecting as short stub.

#### **Male**

Unknown.



## Comments

Using Nixon's (1980) and Masner & García's (2002) keys to the genera of Diapriinae, *Spilomicrus succinalis* sp. nov. clearly keys out to *Spilomicrus* because of the following characters: antenna with 13 segments, flagellum thickened towards apex, frons unarmed, ocellar triangle in the ocular zone, notauli present, scutellum with an anterior bifoveate pit, wings fully developed, fore wing with pigmented Sc+R, marginal vein not more than one and a half times as long as wide, anterior margin of syntergite straight, without a furrow or a cleft at base.

Following the key to the British species of Nixon (1980) and to Eastern Palaearctic species of Chemyreva (2018), *S. succinalis* sp. nov. keys out near *S. comatus* Chemyreva, 2015. It differs from this species by having F11 longer than F10, the petiole less than two times as long as wide and lacking the long hairs on the postgena (Chemyreva 2015).

## Discussion

It has been known for 20 years that Baltic amber held a remarkable diversity of fossil Diapriidae (Buhl 1999, 2002) but only seven species have been described prior to this study (Table 1). By describing ten new species, the fossil record of the family in this deposit is more than doubled. While specimens belonging to the extant belytine genera *Cinetus* and *Pantolyta* were already studied, *Belyta knudhoejgaardi* sp. nov. and *Pantoclis globosa* sp. nov. represent the earliest temporal occurrence for these genera. This is also the case for the extant diapriine genera because none of them have previously been recorded as early as the Late Eocene: *Basalys villumi* sp. nov., *Doliopria baltica* sp. nov. and *Spilomicrus succinalis* sp. nov. The other species *Cinetus breviscapus* sp. nov., *Cinetus elongatus* sp. nov., *Pantolyta augustinusii* sp. nov., *Pantolyta chemyrevae* sp. nov. and *Pantolyta similis* sp. nov. extend the records for their genera.

However, genera such as *Pantolyta* and *Spilomicrus* are represented by numerous specimens of several species that are yet to be described from Baltic amber. Today, these genera are very diverse and widely distributed in the world and it seems that a similar diversity exists in Baltic amber. This means that the current world fauna of Diapriidae had already radiated by the Late Eocene and that earlier representatives of extant taxa can potentially be found in the Paleocene. Thus, it could be interesting to explore older hymenopteran assemblages to elucidate the first phases of the Cenozoic radiation of Diapriidae. The Lutetian Kishenehn formation (USA) and the Ypresian deposits of the Okanagan Highlands (USA–Canada), respectively dated around 46 Ma and 50 Ma, already provided exquisitely preserved Diapriidae, but they have not been studied taxonomically yet (Greenwalt & Labandeira 2013; Archibald *et al.* 2018). Additionally, there is at least five major deposits, older than Baltic amber, that are likely to yield modern Diapriidae in the Early Paleogene: Oise amber (France), Fushun amber (China) or Cambay amber (India) dated Ypresian around 50–55 Ma, the Fur Formation (Denmark) dated from the Paleocene–Eocene boundary, and the Menat fossil site (France) dated from the middle Paleocene.

Finally, for the twelve genera documented in Baltic amber (Table 1), we see that only two of them show a geographic regression since the Bartonian–Priabonian: *Ambositra* Masner, 1961 (Ambositrinae) and *Doliopria* (Diapriinae). Masner (1969) estimated that he was able to observe more than eighty specimens belonging to *Ambositra* of which one species is very common. This genus is currently recorded in Congo, South Africa and Madagascar (Masner 1969). Today's *Doliopria* are restricted to the New World, with most species in the Neotropic region (Masner & García 2002). Other genera are cosmopolitan (*Aclista*, *Belyta*, *Cinetus*, *Miota*: Quadros & Brandão 2017; *Pantoclis*: Hou *et al.* 2016; *Basalys*: Masner & García 2002; *Spilomicrus*: Chemyreva 2018) or distributed in the Holarctic (*Pantolyta*: Chemyreva & Kolyada 2019, 2021; *Zygota*: Macek 1997). The distribution of *Ambositra* or *Doliopria* is probably relictual, probably being correlated with the general cooling of the climate in the last 50 Ma. This pattern with fossil taxa occurring in Baltic amber and the extant fauna in different biogeographic regions is not

unique among Hymenoptera with examples in other families, as the Formicidae Latreille, 1809 (e.g., *Carebara* Westwood, 1840, *Gesomyrmex* Mayr, 1868, *Tetraoponera* Smith, 1852: Perkovsky 2016) or the Megalyridae Schletterer, 1890 (Vilhelmsen *et al.* 2010b). However, the major proportion of the Diapriidae fauna from Baltic amber lacks tropical affinity, meaning that the current distribution of this family cannot be exclusively explained by climate.

## Acknowledgments

We are sincerely grateful to Dr Vincent Perrichot for giving us access to the laboratory and facilities of the University of Rennes. We warmly thank the Augustinus Foundation (Grant 17-3904), the Knud Højgaard Foundation (Grant 17-11-2728) and the Villum Fonden (Grant 00021155) which, through their generous contributions, enabled the acquisition of the Karin Nordmann Ernst amber collection to which the specimens studied here originally belonged. We also thank two anonymous reviewers for their useful comments on this manuscript.

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*Manuscript received: 6 June 2021*

*Manuscript accepted: 19 January 2022*

*Published on: 13 April 2022*

*Section editor: Christian de Muizon*

*Desk editor: Pepe Fernández*

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