

The first reliable fossil record of the tribe Centistini (Hymenoptera, Braconidae, Euphorinae): a new subgenus and species of braconid wasp in Danish amber

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Abstract

A new subgenus and species of the braconid parasitoid of the tribe Centistini s. l. (Euphorinae), *Centistoides* (*Palaeoides*) *magnioculus* Belokobylskij, **subgen. et sp. nov.**, from late Eocene Danish amber are described and illustrated from one female. This is the first time the tribe of euphorine parasitoids is reliably documented in the fossil record. A key to all genera and subgenera of this suprageneric taxonomic group is compiled. The discussion about position of the genus *Parasyrrhizus* Brues, composition of the tribe Centistini s. l., and the composition of the Danish amber hymenopteran fauna are provided.

Keywords

Asiacentistes, *Centistoides*, description, Eocene, ovipositor, subgenus, venation

Introduction

The extant members of the euphorine tribe Centistini include two genera with a mediocubital vein (M+CU1) of the fore wing that is distinctly desclerotised, namely *Allurus* Foerster, 1863 and *Centistes* Haliday, 1835 (with five subgenera: *Anartionyx*

van Achterberg, 1985, *Ancylocentrus* Foerster, 1863, *Centistes* s. str., *Chaetocentistes* Belokobylskij, 2000, and *Syrrhizus* Foerster, 1863). In addition, two morphologically very similar genera but with a distinctly sclerotised mediocubital vein (M+CU1) of the fore wing, *Asiacentistes* Belokobylskij, 1995 and *Centistoides* van Achterberg, 1992, were also attributed to this tribe (van Achterberg 1992; Belokobylskij 1995; Yu et al. 2016). However, a recent molecular phylogenetic study of Euphorinae genera obtained for *Asiacentistes* (Stigenberg et al. 2015) indicated its isolated phylogenetic position in the tribe as well as in the entire Euphorinae subfamily. Such a conclusion requires additional confirmation based on an analysis of more genes because the numerous morphological features clearly support belonging these genera to the Euphorinae.

The Centistini species are known as imagobionts (Shaw 2004), the endoparasitoids of the adults of beetles mainly from the families Chrysomelidae, Curculionidae (especially Scolytinae), Coccinellidae, Carabidae, etc. (Belokobylskij 1996; Yu et al. 2016). Members of this group of genera have a long, wide and strongly laterally compressed ovipositor mainly hidden inside of the metasoma, making Centistini species one of the most specialised and advanced forms of Euphorinae.

In this paper the first member (female) of the tribe Centistini sensu lato found in the fossil record is described and illustrated from a specimen in Danish amber.

Materials and methods

Priabonian Danish amber of late Eocene age (34–37 Mya) was reviewed by Heie (1967), Larsson (1978), Nadein et al. (2016) and references therein. Larsson (1978) supposed that the amber was redeposited to the Miocene lignites of Jutland from South Swedish Eocene forests.

The braconid specimens were examined with an Olympus SZ51 stereomicroscope. Photographs were obtained using a Leica Z16 APO stereomicroscope equipped with a Leica DFC 450 camera and processed with LAS Core.

The terminology employed for morphological features and sculpture, as well as body measurements, follow Belokobylskij and Maetô (2009). Wing venation nomenclature also follows Belokobylskij and Maetô (2009), with the terminology of van Achterberg (1993) shown in parentheses.

The material used for this study is deposited in the collection of the Natural History Museum of Denmark (NHMD). The holotype inclusion is located in a thin, nearly rectangular piece of amber measuring 8.0 × 6.5 mm.

Systematic part

Class Insecta Linnaeus, 1758

Order Hymenoptera Linnaeus, 1758

Family Braconidae Nees, 1811

Subfamily Euphorinae Foerster, 1863**Tribe Centistini Čapek, 1970****Key to the world genera and subgenera of the tribe Centistini sensu lato**

- 1 Mediocubital vein (M+CU1) of fore wing distinctly sclerotised and pigmented **2**
- Mediocubital vein (M+CU1) of fore wing unsclerotised and transparent **3**
- 2 Malar groove present, but sometimes incomplete. Apical segment of antenna without distal spine. Laterope of first metasomal tergite very shallow and small. Dorsal valve of ovipositor apically with wide and finely aciculate lobe. Ovipositor sheath thick and short (posterior view), very densely setose apically. Hind tibia with distinct small sparse spines at its external side.....
..... ***Asiacentistes* Belokobylskij, 1995**
- Malar groove and suture absent. Apical segment of antenna with distal spine. Laterope of first metasomal tergite rather deep. Dorsal valve of ovipositor apically without lobe. Ovipositor sheath thin and elongate (posterior view), glabrous or relatively sparsely setose apically. Hind tibia without spines at external sides ***Centistoides* van Achterberg, 1992**
- 3 Claw splitting apically. Hind coxa with distinct acuminate ventro-posterior projection. Metasomal sternites often medially with double teeth
..... ***Allurus* Foerster, 1863**
- Claw not splitting apically, simple. Hind coxa always without ventro-posterior projection. Metasomal sternites medially usually without teeth (*Centistes* Haliday, 1835)..... **4**
- 4 First abscissa of medial vein (1-SR+M) of fore wing absent; discoidal (discal) and second radiomedial (submarginal) cells fused. – Notauli always absent.....
..... ***Centistes* (subgenus *Syrrhizus* Foerster, 1863)**
- First abscissa of medial vein (1-SR+M) of fore wing present; discoidal (discal) and second radiomedial (submarginal) cells separated **5**
- 5 Fore coxa on posterior (inner) side in very dense and short brush-like setae. Ovipositor sheaths thick and widened distally (dorsal and lateral views). Apex of ovipositor narrow and sinuated. Hypopygium and two posterior sternites of metasoma in very dense and short setae
..... ***Centistes* (subgenus *Chaetocentistes* Belokobylskij, 2000)**
- Fore coxa on posterior (inner) side without brush-like setae. Ovipositor sheaths rather flat and usually parallel-sided or narrowed distally (dorsal and lateral views). Apex of ovipositor rather wide and straight. Hypopygium and two posterior sternites of metasoma with usual and rather sparse setae **6**
- 6 Mesoscutum completely without notauli ***Centistes* (subgenus *Centistes* s. str.)**
- Mesoscutum usually with rather distinct and complete notauli; however, sometimes notauli shallow and weakly visible; rarely notauli mainly absent anteriorly, but mesoscutum always with distinct medioposterior elongate or subround pit **7**

- 7 Inner claw of hind leg much larger than claw of fore leg (especially in female), hooked and larger than outer claw. Second abscissa of mediocubital vein (1-M) of hind wing shorter than basal vein (1 r-m). Ovipositor sheath widened submedially..... ***Centistes* (subgenus *Anartionyx* van Achterberg, 1985)**
- Inner claw of hind leg only slightly larger than claw of fore leg, subequal to its inner claw. Second abscissa of mediocubital vein (1-M) of hind wing subequal to basal vein (1 r-m). Ovipositor sheath often with subparallel-sided or evenly narrowed distally..... ***Centistes* (subgenus *Ancylocentrus* Foerster, 1863)**

Genus *Centistoides* van Achterberg, 1992

Type species. *Centistoides doesburgi* van Achterberg, 1992, by monotypy and original designation.

Notes. This small Madagascan-Neotropical genus includes two extant species, *Centistoides doesburgi* van Achterberg, 1992 from Suriname (van Achterberg 1992) and *C. ophthalmicus* (Granger, 1949) from Madagascar, a species that was only recently transferred to this genus from *Centistes* (Belokobylskij 2018).

The Eastern Palaearctic genus *Asiacentistes* Belokobylskij also has two extant species, *A. alekseevi* (Belokobylskij, 1992) and *A. sinicus* Chen & Belokobylskij, 2001 (Belokobylskij 1995; Chen et al. 2001), and is very similar to *Centistoides*. The differences between these taxa are given in the key above.

Documented here the first reliable fossil member of the tribe Centistini s. l. is found in Danish amber, and it possesses a distinctly sclerotised mediocubital vein (M+CU1) of the fore wing. On the basis of all visible characters of this amber inclusion (for example, malar suture absent, apical antennal segment with distinct distal spine, ovipositor apically without lobe, ovipositor sheath thin and elongate in posterior view, sparsely setose apically) it was placed in the genus *Centistoides*; however, this specimen has some features that necessitated a separate subgenus for it within *Centistoides*.

A short redescription of the genus *Centistoides* and descriptions of the new subgenus as well as the new fossil species are given below.

Diagnosis of the genus. Occipital carina absent dorsally, only developed on lateral and ventral parts of temple, joining hypostomal carina above base of mandible. Ocelli distinctly enlarged. Eye large. Malar suture absent, but sometimes present short malar groove. Mandible strongly twisted apically. Palpi short, maxillary palpus 3–5-segmented, labial palpus 1–2-segmented. Antenna weakly setiform, apical segment of antenna with distinct distal spine. Mesosoma short and high. Notauli completely absent. Prescutellar depression usually entirely smooth or weakly rugulose, without or only with medial carina. Prepectal carina complete. Mesopleuron mainly smooth; precoxal sulcus absent. Metapleural flange absent or very short. Propodeum without or with weak areolation, with incomplete or complete posterior areola. Radial (marginal) cell of fore wing distinctly shortened. Discoidal (discal) cell usually sessile; petiole (1-SR) absent. First abscissa of medial vein (1-SR+M) of fore wing present. Recurrent vein (m-cu) antefurcal.

Mediocubital vein (M+CU1) entirely sclerotized and pigmented. In hind wing, second abscissa of mediocubital vein (1-M) much shorter than first abscissa (M+CU) and shorter than basal vein (r-m). Hind coxa large and subround. Fore femur usually more robust than hind femur. Tarsal claws robust, distinctly curved apically, simple. First metasomal tergite wide and short, almost parallel-sided or weakly narrowed behind spiracles, smooth, without dorsope. Second metasomal tergite smooth; second suture usually absent. Ovipositor strongly compressed, strongly curved and without armament and ventral lobe apically. Ovipositor sheath short, wide, flattened, truncate apically.

***Palaeoides* Belokobylskij, subgen. nov.**

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Type species. *Centistoides* (*Palaeoides*) *magnioculus* sp. nov., by present designation.

Etymology. Named after “Palaeo” (Greek for “ancient”) and part of the generic name *Centistoides* from the tribe Centistini.

Description. Ocelli less distinctly enlarged (Fig. 1D, E). Palpi longer, maxillary palpus more than 3-segmented, perhaps with 5 segments; labial palpus at least 2-segmented (Fig. 1D). Prescutellar depression with five carinae (Fig. 1D). Precoxal sulcus present, but very shallow (Figs 1A, 2C). In fore wing, discoidal (discal) cell petiolate anteriorly, petiole (1-SR) medium length (Fig. 2A, B). Mediocubital vein (M+CU1) entirely distinctly sclerotised and pigmented (Fig. 2A, B). Fore femur not more robust than hind femur (Fig. 2C). Tarsal claws weakly curved apically (Figs 1A, 2A, C). Second metasomal suture present but fine (Fig. 1F). Ovipositor sheath weakly narrowed apically (Fig. 1F).

Diagnosis. The genus *Centistoides* (as well as *Asiacentistes*) characterised by the fore wing mediocubital vein (M+CU1) distinctly sclerotised and pigmented, when such a vein in most Centistini genera is clearly desclerotised and transparent (spectral). Both known *Centistoides* species, *C. doesburgi* van Achterberg, 1992 and *C. ophthalmicus* (Granger, 1949), together with the genus *Asiacentistes*, have a sessile or subsessile discoidal (discal) cell in the fore wing (van Achterberg 1992; Belokobylskij 1995, 2018), while in the new subgenus, *Palaeoides* subgen. nov., the discoidal (discal) cell of the fore wing is petiolate.

***Centistoides* (*Palaeoides*) *magnioculus* Belokobylskij, sp. nov.**

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Figs 1, 2

Type material. Holotype: female, NHMD # 115540, with labels “Braconidae A.K. Andersen 28-3 /1968” and “Euphorinae ? huge ovipositor”. Danish amber, late Eocene. Syninclusion: female of Chironomidae.

Description. Female. Body length 3.8 mm; fore wing length 3.6 mm.

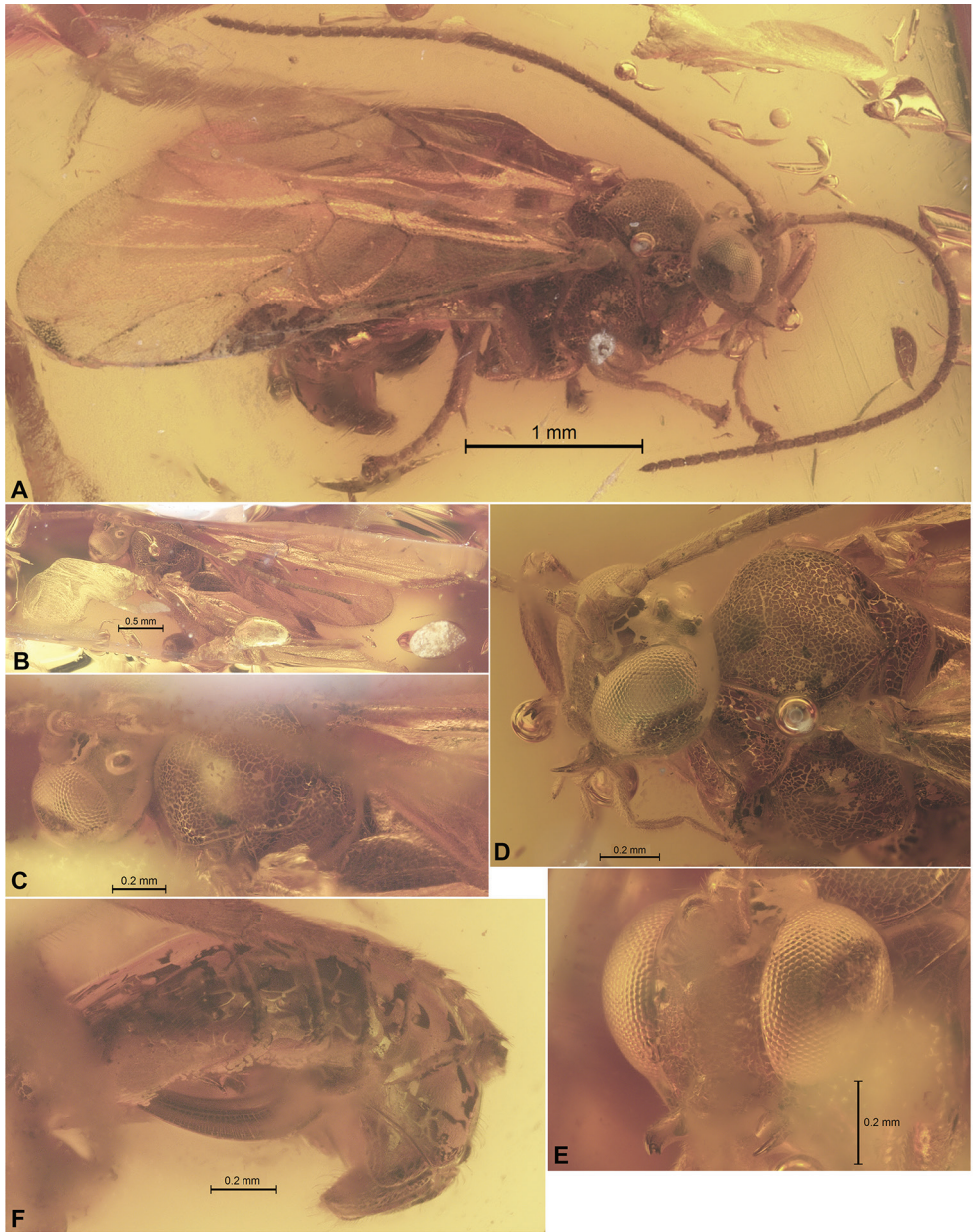


Figure 1. *Centistoides (Palaeoides) magniocolus* sp. nov. (female, holotype, Danish amber, NHMD # 115540) **A** habitus, right dorso-lateral view **B** habitus, dorsal view **C** head and mesosoma, dorsal view **D** head and anterior part of mesosoma, dorso-lateral view **E** head, fronto-lateral view **F** metasoma and ovipositor, lateral view.

Head: Head rather short; occiput distinctly concave. Eye large, glabrous, ~ 1.4 times as high as broad (sublateral view); transverse diameter of eye almost 2.0 times longer than temple (subdorsal view). Ocelli medium-sized, convex, situated almost in

equilateral triangle; POL approximately 0.8 times Od, 2.0 times OOL; Od ~ 2.2 times OOL. Face weakly convex, its width ~ 0.8 times mid-height. Clypeus distinctly convex, its width ~ 2.0 times mid-height, 0.8 times width of face. Malar space ~ 0.15 times height of eye, ~ 0.7 times basal width of mandible. Malar suture absent. Mandible distinctly twisted in apical half, with two apical teeth.

Antenna: Antenna long, almost filiform, 28-segmented, about as long as body. Scape 1.5 times longer than its maximum width, ~ 2.0 times longer than pedicel. First flagellar segment rather wide, 4.5 times longer than its maximum width, 1.2 times longer than second segment. Penultimate segment 1.5 times longer than its maximum width, 0.7 times as long as apical segment. Apical antennal segment with distinct distal spine.

Mesosoma: Mesosoma 1.2 times longer than its maximum height. Neck of prothorax short. Mesoscutum anteriorly distinctly convex and weakly protruding forward, without anterolateral corners. Notauli completely absent. Prescutellar depression (scutellar sulcus) rather short, densely crenulate. Scutellum short and weakly convex. Subalar depression shallow and narrow, smooth. Propodeum strongly curvedly narrowed posteriorly (lateral view).

Wings: Fore wing wide, 2.7 times longer than its maximum width. Pterostigma wide, 3.2 times longer than its width. Radial (marginal) cell distinctly shortened, 3.2 times longer than its maximum width. Metacarp (1-R1) 0.7 times as long as pterostigma. Radial vein (r) arising weakly behind middle of pterostigma. First (r) and second (3-RS+SR1) radial abscissae forming obtuse angle; first abscissa (r) 0.4 times as long as maximum width of pterostigma. Second radial abscissa (3-RS+SR1) evenly curved, almost 9.0 times longer than first abscissa (r), 2.7 times longer than first radiomedial vein (2-RS). Recurrent vein (m-cu) distinctly antefurcal, 2.0 times longer than second abscissa of medial vein (2-SR+M), 0.6 times as long as first radiomedial vein (2-RS), 0.45 times as long as basal vein (1-M). First abscissa of medial vein (1-SR+M) weakly sinuate. Discoidal (discal) cell 1.1 times longer than its maximum width. Nervulus (cu-a) 0.8 times as long as distance (1-CU1) between basal vein (1-M) and nervulus (cu-a). Parallel vein (CU1a) distinctly curved basally. Brachial (subdiscal) cell relatively short and rather wide. Hind wing ~ 4.5 times longer than its maximum width. Submedial (subbasal) cell long and wide; first abscissa of mediocubital vein (M+CU) ~ 4.0 times longer than second abscissa (1-M).

Legs: Fore femur wide, ~ 3.3 times longer than its maximum width. Fore tarsus shortened; tarsal segments mainly short. Hind coxa wide and short, massive, ~ 1.3 times longer than its maximum width. Hind femur ~ 4.0 times longer than its width. Hind tibia distinctly thickened. Hind tarsus shorter than hind tibia. Claw simple.

Metasoma: Metasoma curved down posteriorly, approximately as long as head and mesosoma combined. First metasomal tergite with distinct and complete dorsal carinae, approximately as long as propodeum. Second suture perhaps absent. Subposterior sternite with pair of short ventral teeth. Ovipositor wide, compressed and distinctly curved; dorsal valve of ovipositor apically without lobe. Ovipositor sheath rather thin (ventral view), short and wide, narrowed distally, with short apical tubercle (lateral view), covered by rather long and almost erect setae; sheath 2.2 times longer than its width, ~ 0.7 times as long as first tergite.

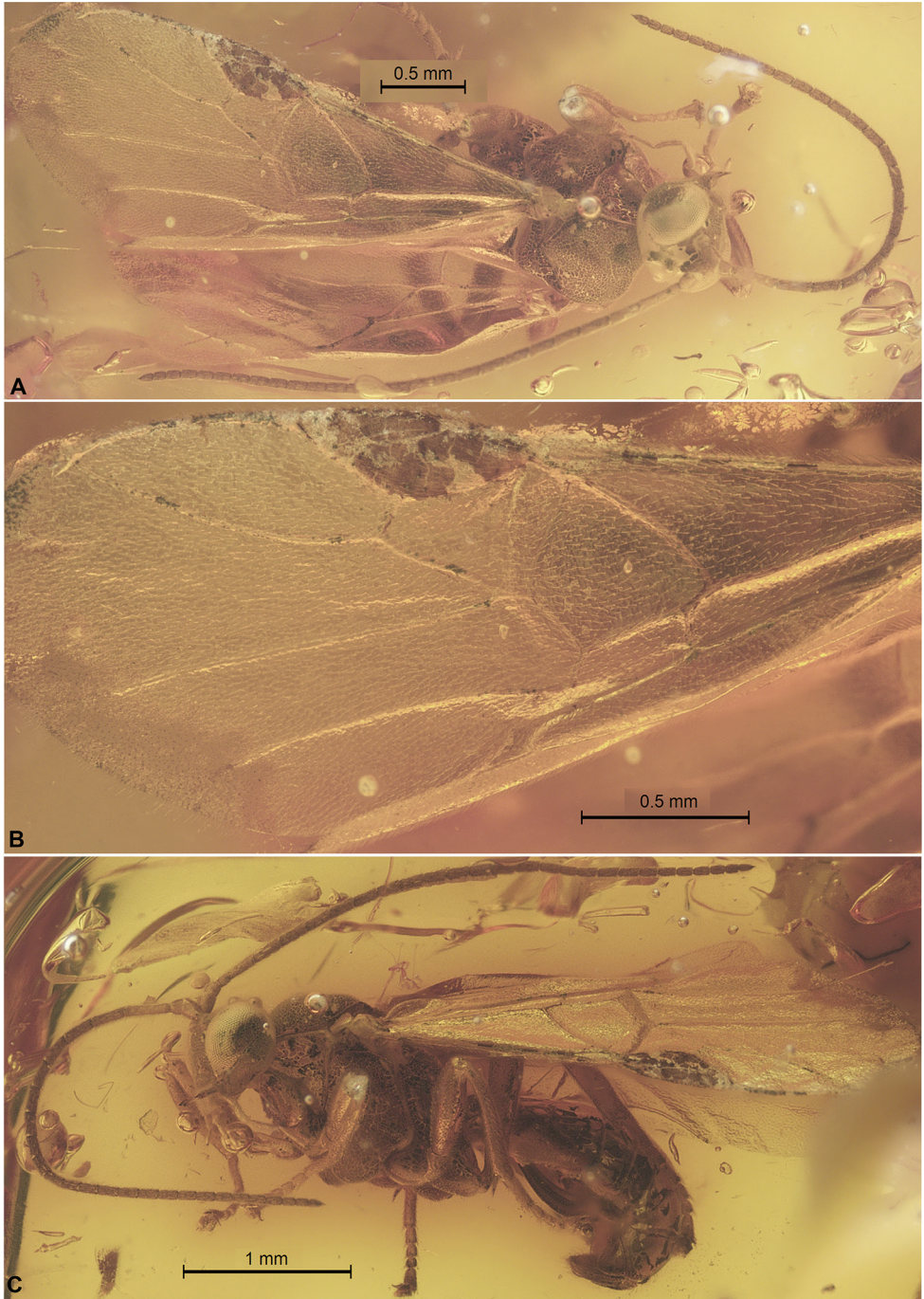


Figure 2. *Centistoides (Palaeoides) magniocolus* sp. nov. (female, holotype, Danish amber, NHMD # 115540) **A** wings, head and mesosoma, dorso-lateral view **B** fore wing **C** habitus, left sublateral view.

Sculpture: Body mainly smooth; sculpture of propodeum not visible, but perhaps with transverse carina.

Colour: Body dark brown to black. Palpi yellow. Antenna mainly black, brown basally. Legs mainly light reddish brown or reddish brown, hind tibia dark. Fore wing hyaline. Pterostigma entirely dark brown.

Male. Unknown.

Etymology. This species is named after Latin “magnus” (large) and “oculus” (eye), because the eyes of the new species are distinctly enlarged.

Comparative diagnosis. The new species differs from the type species of the genus *Centistoides*, *C. doesburgi* van Achterberg, 1992, primarily by subgeneric characters. The differences between all known species of *Centistoides* are shown in the key below.

Key to species of the genus *Centistoides*

- 1 Discoidal (discal) cell of fore wing petiolate anteriorly; first abscissa of medial vein (1-SR+M) arising from basal vein (1-M). Subposterior sternite of metasoma with pair of short ventral teeth. – Prescutellar depression with five transverse carinae. Tarsal claws weakly curved apically. Ovipositor sheath narrowed apically. Fore wing length 3.6 mm. Fossil..... *C. (Palaeoides) magniocus sp. nov.*
- Discoidal (discal) cell of fore wing sessile anteriorly; first abscissa of medial vein (1-SR+M) arising from parastigma. Subposterior sternite of metasoma without ventral teeth..... **2**
- 2 First medial abscissa (1-SR+M) of fore wing sinuate; second medial abscissa (2-SR+M) long, 0.6 times as long as recurrent vein. Discoidal (first discal) cell anteriorly narrowly sessile. First transverse anal vein (1a) present. Propodeum with distinct basomedian carina and with areola completely delineated by carinae. Prescutellar depression (scutellar sulcus) sculptured. Ovipositor sheath relatively thick, but flattened on narrow flanges dorsally and apically, rather densely setose apically. Fore wing length 4.7 mm. Afrotropics (Madagascar) *C. (s. str.) ophthalmicus (Granger, 1949)*
- First medial abscissa (1-SR+M) of fore wing straight; second medial abscissa (2-SR+M) short, ~ 0.3 times as long as recurrent vein. Discoidal (first discal) cell anteriorly broadly sessile. First transverse anal vein (1a) absent. Propodeum without basomedian carina, with areola incompletely delineated by carinae anteriorly. Prescutellar depression (scutellar sulcus) smooth. Ovipositor sheath entirely flatted, truncate and glabrous apically. Fore wing length 3.0 mm. Neotropics (Suriname) *C. (s. str.) doesburgi van Achterberg, 1992*

Discussion

The fossil genus and species presumably from the tribe Centistini, *Parasyrrhizus ludens* Brues, 1933, was described from Baltic amber based on two males in the subfamily

Leiophroninae (= Euphorinae) (Brues 1933). This genus was compared with euphorine genus *Syrrhizus* Foerster, 1863 (now the subgenus of *Centistes* Haliday, 1835) on the basis of the fore wing venation without first abscissa of medial vein (1-SR+M) and respectively fused first radiomedial (submarginal) and discoidal (discal) cells. However, already in the World Catalogue (Shenefelt 1970), *Parasyrrhizus* was transferred to the subfamily Calyptinae (= Brachistinae), though without explanation. Perhaps the reason for this transfer was based on the brachial (subdiscal) cell of the fore wing closed distally by the recurrent vein (CU1b) (according to the figure: Brues 1933: fig. 52), characters never recorded in Euphorinae members. It appears only the discovery of the female of this species with a visible ovipositor (both of its types, males, may have been lost after World War II) will finally resolve its suprageneric membership.

Thus, *Centistoides (Palaeoides) magniocolus* sp. nov. is the first reliable fossil record of Centistini sensu lato found as an inclusion in amber.

It should be noted that in a recent molecular phylogenetic analysis of the subfamily Euphorinae, it was shown that the genus *Asiacentistes* (which is very similar and probably closely related to *Centistoides*) does not belong to the Euphorinae s. str. (Stigenberg et al. 2015), and this genus may be the sister taxon to the clade Cenocoelinae+Euphorinae. On the other side, the members of the tribe Centistini are similar morphologically, especially on the basis of the wing venation, to the representatives of the tribe Brachistini (Brachistinae). However, the brachistine females never had such a peculiar ovipositor as presented in *Asiacentistes* and *Centistoides* together with all other members of the tribe Centistini s. str., namely wide, laterally compressed, curved and mainly hidden inside of the female metasoma. This type of ovipositor, which had been known only in euphorine imagobionts until now, allowed them to effectively penetrate the body of strongly sclerotised hosts through the intersegmental membrane between the sclerites of the abdomen. Such host stages are never used by brachistines, which are known as egg-larval endoparasitoids. Perhaps both of these genera, *Asiacentistes* and *Centistoides*, and the fossil subgenus described here, which differs from other Centistini s. str. by the distinctly sclerotized mediocubital vein (M+CU) of the fore wing, form a separate tribe. However, for confirmation of this suggestion, we would need additional molecular phylogenetic analysis of more genes.

The former braconid subfamily Betylobraconinae (currently Betylobraconini in Rogadinae), represented in the Eocene by the genus *Mesocentrus* Szépliget, 1900 (Butcher et al. 2014), and the ant tribe Leptomymecini (Dlussky et al. 2014), the two hitherto known suprageneric hymenopterans taxa with the oldest records from Danish amber, remain unrecorded from Baltic amber. For comparison, in the far better-studied non-ant hymenopteran fauna of Rovno amber, only two such taxa are known: parasitic wasps subfamily Eucoilinae (Figitidae) (they are very common now, so perhaps they have been overlooked in Baltic amber) as well as an extinct crabronid wasps tribe Protomicroidini (Perkovsky 2018). All six Danish Encyrtidae genera (Chalcidoidea) (Simutnik and Perkovsky 2017, 2018, 2023; Simutnik et al. 2023), three braconid genera (Butcher et al. 2014; Kittel 2018; this paper), three genera of ants and one of Bethyilidae (Perkovsky 2018) remain unknown from Baltic amber. Out of those, two encyrtid (Simutnik et al. 2021; Simutnik et al. 2023) and two ant genera

(Perkovsky 2016), together with the bethylid genus *Sierola* Cameron, 1881 (Ramos et al. 2014), are recorded from Rovno amber. At least Betylobraconini, Leptomyrmecini, *Centistoides*, *Sierola* and an ant genus *Pristomyrmex* Mayr, 1866 (Radchenko and Perkovsky 2021) can be classified as cryophobic taxa (Jenkins Shaw et al. 2023 and references therein). Thus, the discovery of a new subgenus described in the present paper confirms the theory that the fauna of Danish amber (as well as that of Rovno amber, see Kirichenko-Babko and Perkovsky 2023 and references therein) was likely noticeably more thermophilic than Baltic amber fauna (Perkovsky 2016, 2017).

Overall, 45% of Danish amber hymenopteran genera remain unknown from Baltic amber (authors' data) – one and a half times higher than the proportion of known Rovno amber hymenopteran genera not yet discovered in Baltic amber, and even higher than the proportion of non-ant Rovno amber hymenopteran genera unknown from Baltic amber (41%, Belokobylskij et al. 2023). Although the Danish amber hymenopteran fauna is in urgent need of revision, the high level of endemism suggests an independent geographic origin of this fauna.

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