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Snakefly diversity in Early Cretaceous amber from Spain (Neuropterida, Raphidioptera)

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Abstract

The Albian amber from Spain presently harbors the greatest number and diversity of amber adult fossil snakeflies (Raphidioptera). Within Baissopteridae, *Baissoptera*? *cretaceoelectra* **sp. n.**, from the Peñacerrada I outcrop (Moraza, Burgos), is the first amber inclusion belonging to the family and described from western Eurasia, thus substantially expanding the paleogeographical range of the family formerly known from the Cretaceous of Brazil and eastern Asia. Within the family Mesoraphidiidae, *Necroraphidia arcuata* **gen. et sp. n.** and *Amarantoraphidia ventolina* **gen. et sp. n.** are described from the El Soplao outcrop (Rábago, Cantabria), whereas *Styporaphidia*? *hispanica* **sp. n.** and *Alavaraphidia imperterrita* **gen. et sp. n.** are described from Peñacerrada I. In addition, three morphospecies are recognized from fragmentary remains. The following combinations are restored: *Yanoraphidia* gaoi Ren, 1995, **stat. rest.**, *Mesoraphidia durlstonensis* Jepson, Coram and Jarzembowski, 2009, **stat. rest.**, and *Mesoraphidia heteroneura* Ren, 1997, **stat. rest.** The singularity of this rich paleodiversity could be due to the paleogeographic isolation of the Iberian territory and also the prevalence of wildfires during the Cretaceous.

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Keywords
Holometabola, taxonomy, paleontology, paleogeography, Mesozoic, Albian

Introduction

Raphidioptera (snakeflies) are regarded as one of the most primitive lineages of holometabolous insects, their fossil record dating back to the Early Jurassic (Grimaldi and Engel 2005). There is consensus that Raphidioptera forms a distinct clade together with Megaloptera and Neuroptera, the superorder Neuropterida. However, there is controversy whether Raphidioptera is sister to Megaloptera or to [Megaloptera + Neuroptera] (see Haring et al. 2011). Nowadays, the active, predatory larvae of snakeflies are long-lived, with a high number of instars and distinctive hibernating periods, living under the bark of trees and shrubs or in soil detritus; moreover, their pupation needs a period of cold to break diapause, and the pupae are exarate and active, a plesiotypic condition within Holometabola (Aspöck 2002). Adults are arboreal and also predatory, but short-lived (ibid.), exhibiting a prognathous head, a long pronotum, and a long ovipositor in females, features that give them a snake-like appeareance. The extant diversity of the order is relictual, as the Mesozoic diversity of Raphidioptera, as suggested by morphological disparity more-so-than total numbers, was greater than that observed today (e.g., Martynov 1925; Martynova 1961; Ponomarenko 1988, 1993; Oswald 1990; Ren 1997; Engel 2002; Engel et al. 2006; Perrichot and Engel 2007; Jepson and Jarzembowski 2008; Jepson et al. 2009, 2011). Moreover, while the group was once distributed throughout the world and in diverse habitats, today their range is contracted into the cold temperate regions of the Northern Hemisphere. The fossil record of Raphidioptera is comprised principally of compressions ranging from the Early Jurassic through the Miocene (Engel 2002). Snakefly inclusions in amber are far more uncommon (e.g., Carpenter 1956; Engel 1995; Aspöck and Aspöck 2004), particularly those in Cretaceous resins (Grimaldi 2000; Engel 2002; Perrichot and Engel 2007; Engel and Grimaldi 2008; Pérez-de la Fuente et al. 2010; Bechly and Wolf-Schwenninger 2011).

Raphidioptera currently comprises six families, i.e., four extinct families, Mesoraphidiidae Martynov, 1925 (Late Jurassic – Late Cretaceous), Baissopteridae Martynova, 1961 (Late Jurassic – Early Cretaceous), Priscaenigmatidae Engel, 2002 (Early Jurassic; classified into its own suborder and considered the most primitive raphidiopterans), and Metaraphidiidae Bechly and Wolf-Schwenninger, 2011 (Early Jurassic); and two extant families that date back to the Eocene, Raphidiidae Latreille, 1810 and Inocelliidae Navás, 1913 (Grimaldi and Engel 2005), with ca. 210 and ca. 30 extant species respectively (Haring et al. 2011). The extinct family Baissopteridae currently comprises about 20 species distributed in five genera (Table 1). The family is considered to represent a plesiomorphic condition within Raphidioptera owing to the dense crossvenation of its representatives (Engel 2002), and it could be paraphyletic (Willmann 1994; Bechly and Wolf-Schwenninger 2011). To date, baissopterids have been exclusively recorded from Cretaceous localities, hitherto restricted to Brazil

Table 1. Currently recognized genera classified within the extinct families Baissopteridae and Mesoraphidiidae.

Family Baissopteridae Martynova, 1961
Genus *Austroraphidia* Willmann, 1994
Genus *Baissoptera* Martynova, 1961
Genus *Cretoraphidia* Ponomarenko, 1993
Genus *Cretoraphidiopsis* Engel, 2002
Genus *Lugala* Willmann, 1994
Family Mesoraphidiidae Martynov, 1925
Genus *Alavaraphidia* Pérez-de la Fuente, Peñalver, Delclòs & Engel, gen. n.
Genus *Alloraphidia* Carpenter, 1967
Genus *Amarantoraphidia* Pérez-de la Fuente, Peñalver, Delclòs & Engel, gen. n.
Genus *Archeraphidia* Ponomarenko, 1988
Genus *Baisoraphidia* Ponomarenko, 1993
Genus *Cantabroraphidia* Pérez-de la Fuente, Nel, Peñalver & Delclòs, 2010
§ Genus *Cretinocellia* Ponomarenko, 1988
Genus *Grimaldiraphidia* Bechly and Wolf-Schwenninger, 2011
Genus *Huaxiaraphidia* Hong, 1992
Genus *Iberoraphidia* Jepson, Ansorge & Jarzembowski, 2011
Genus *Jilinoraphidia* Hong and Chang, 1989
Genus *Kezuoraphidia* Willmann, 1994
Genus *Lebanoraphidia* Bechly & Wolf-Schwenninger, 2011
Genus *Mesoraphidia* Martynov, 1925
Genus *Nanoraphidia* Engel, 2002
Genus *Necroraphidia* Pérez-de la Fuente, Peñalver, Delclòs & Engel, gen. n.
Genus *Ororaphidia* Engel & Ren, 2008
Genus *Pararaphidia* Willmann, 1994
Genus *Proraphidia* Martynova, 1947
Genus *Siboptera* Ponomarenko, 1993
Genus *Sinoraphidia* Hong, 1982
Genus *Styporaphidia* Engel & Ren, 2008
Genus *Xuraphidia* Hong, 1992
Genus *Yanoraphidia* Ren, 1995

§ Recently transferred from Baissopteridae by Bechly and Wolf-Schwenninger (2011).

and eastern Eurasia (China, Mongolia, and Russia) (Fig. 1). The extinct family Mesoraphidiidae currently comprises about 60 species classified in 24 genera (Table 1). For an up-to-date view of the family, there is a catalog provided by Engel (2002), supplemented by Engel and Ren (2008), Jepson and Jarzembowski (2008), Jepson et al. (2009, 2011), Pérez-de la Fuente et al. (2010), and Bechly and Wolf-Schwenninger (2011). Hitherto, less than 10% of this diversity is described from amber inclusions and thus from specimens potentially more informative (Table 2). Mesoraphidiidae has been recorded from several Jurassic and Cretaceous localities primarily of the Northern Hemisphere (see Pérez-de la Fuente et al. 2010: fig. 1, supplemented by the species described from new localities by Jepson et al. 2011, Bechly and Wolf-Schwenninger 2011, and the present contribution).

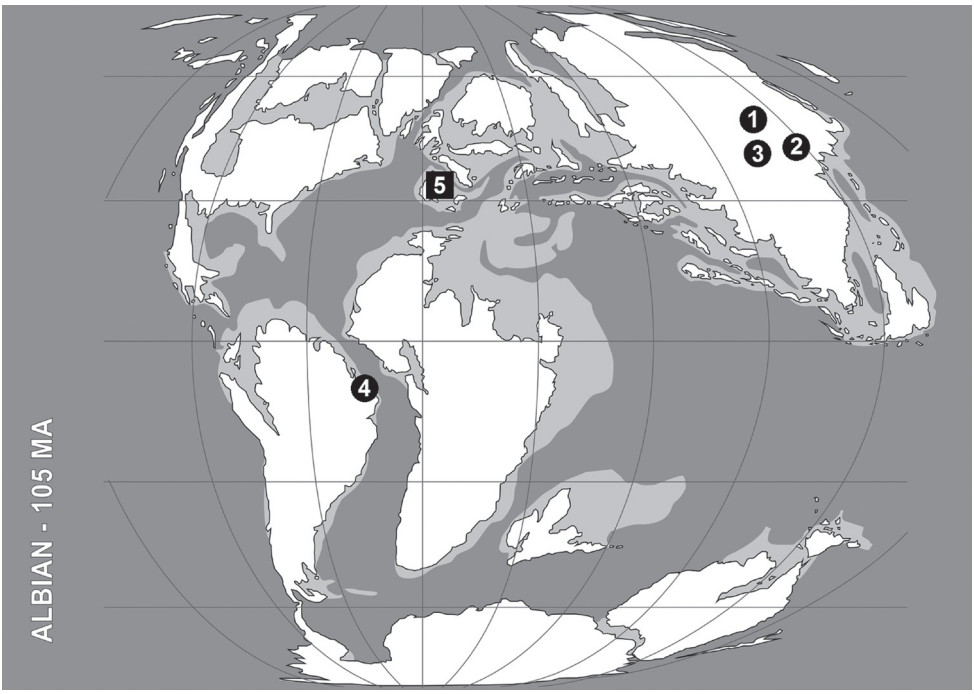

Figure 1. Distribution of the Early Cretaceous snakeflies currently classified within the Baissopteridae. The paleogeographic map (redrawn from Blakey 2008) corresponds to middle Albian (ca. 105 Ma). Data summarized in Engel (2002) and complemented with Jepson et al. (2011) and this paper. Circles correspond to compression localities, whereas the square represents the single amber locality in which baissopterids have been described up to date. Localities appear in chronological order after the ages summarized in Grimaldi and Engel (2005), although the age of the localities from Eastern Asia are considered generically as Early Cretaceous. Note that *Cretinocellia cellulosa* Ponomarenko, 1988 was transferred to Mesoraphidiidae s.s. by Bechly and Wolf-Schwenninger (2011) **1** Baissa, Buryat Republic, Russia (Neocomian, Valanginian). *Baissoptera cellulosa* Ponomarenko, 1993, *B. elongata* Ponomarenko, 1993, *B. kolosnitsynae* Martynova, 1961, *B. martinsoni* Martynova, 1961, *B. minima* Ponomarenko, 1993, and *B. sibirica* Ponomarenko, 1993; *Cretoraphidia certa* Ponomarenko, 1993, *C. macrocella* Ponomarenko, 1993, *C. magna* Ponomarenko, 1993, and *C. reticulata* Ponomarenko, 1993 **2** Liaoning, China (Neocomian: Hauterivian?). *Baissoptera euneura* Ren, 1997, *B. grandis* Ren in Ren et al., 1995, and *B. liaoningensis* Ren, 1994. **3** Bon-Tsagan, Mongolia (Barremian). *Cretoraphidiopsis bontsaganensis* (Ponomarenko, 1988); *Lugala longissima* (Ponomarenko, 1988) **4** Ceará, Brazil (Aptian). *Austroraphidia brasiliensis* (Nel, Séméria, and Martins-Neto, 1990); *Baissoptera brasiliensis* Oswald, 1990, *B. pulchra* (Martins-Neto & Nel, 1992), and *B. lisae* Jepson, Ansorge and Jarzembowski, 2011 **5** Peñacerrada I (=Moraza) amber, Burgos, Spain (Albian). *Baissoptera*? *cretaceoelectra* sp. n.

The recent discovery of a significant paleodiversity of snakeflies in Spanish amber stimulated the present work. Herein we describe this diversity and place it in the context of other Mesozoic snakeflies, highlighting some factors that could explain the uniqueness of this record when compared to other Cretaceous ambers.

Table 2. Cretaceous amber snakeflies (Neuropterida: Raphidioptera).

Age, taxa	Amber locality (country)
Neocomian (Barremian–Aptian)	
Lebanoraphidia nana Bechly and Wolf-Schwenninger, 2011	Jezzine (Lebanon)
Mesoraphidiid larva (in Perrichot and Engel 2007)	Jezzine (Lebanon)
Albian	
Baissoptera? *cretaceoelectra* sp. n.	Peñacerrada I (Spain)
Alavaraphidia imperterrita gen. et sp. n.	Peñacerrada I (Spain)
Styporaphidia? *hispanica* sp. n.	Peñacerrada I (Spain)
Mesoraphidiid gen. et sp. indet. 1 (MCNA 9218)	Peñacerrada I (Spain)
Mesoraphidiid gen. et sp. indet. 3 (MCNA 9316)	Peñacerrada I (Spain)
Cantabroraphidia marcanoi Pérez-de la Fuente et al., 2010	El Soplao (Spain)
Amarantoraphidia ventolina gen. et sp. n.	El Soplao (Spain)
Necroraphidia arcuata gen. et sp. n.	El Soplao (Spain)
Mesoraphidiid gen. et sp. indet. 2 (CES 376)	El Soplao (Spain)
Nanoraphidia electroburmica Engel, 2002	Hukwang (Myanmar)
Mesoraphidiid larva 1 (in Engel 2002)	Hukwang (Myanmar)
Mesoraphidiid larva 2 (in Perrichot and Engel 2007)	Hukwang (Myanmar)
Mesoraphidiid larva 3 (in Perrichot and Engel 2007)	Hukwang (Myanmar)
Late Albian	
Mesoraphidiid larva (in Perrichot and Engel 2007)	Archingeay-Les Nouillers (France)
Turonian	
Grimaldiraphidia luzzii (Grimaldi, 2000)	New Jersey (USA)
Mesoraphidiid larva (in Grimaldi 2000)	New Jersey (USA)
Campanian	
Mesoraphidiid larva (in Engel and Grimaldi 2008)	Grassy Lake (Canada)

Material and methods

Samples designated by the institutional abbreviation CES are housed in the laboratory of the El Soplao Cave, Celis, Cantabria (Spain) encompassing the Institutional Collection from the El Soplao outcrop; whereas those designated as MCNA are housed in the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain. The higher classification followed herein is modified from that of Engel (2002), Perrichot and Engel (2007), and Bechly and Wolf-Schwenninger (2011). We prefer not to recognize subfamilies within Mesoraphidiidae as it is unclear what the monophyletic lineages of this complex truly comprise. Morphological terminology generally follows that of Aspöck et al. (1991). Vein and cell nomenclature is after Engel (2011): the term "radial" is used for cells bounded between R and Rs, "discal" is used for the cell bounded between Rs and MA, "medial" is used for cells bounded between MA and MP, and "discoidal" is reserved for cells bounded anteriorly by MP and posteriorly by MP or CuA (Fig. 9). Also, the number of Rs branches is considered as those that reach the wing margin. Genitalia nomenclature follows that of Aspöck and Aspöck (2008), i.e., the numbers 9, 10 or 11 accompanying abdominal/genitalic structures indicate to which abdominal

segment they allegedly belong; the parameres are considered to be the fused gonocoxites, gonapophyses and gonostyli from the 10th abdominal segment; and the term trichobothria refers to the bristles located in the center of a depressed ring in the cuticle of tergite 10 (+11?) in Neuropterida.

Drawings were prepared with a camera lucida attached to an Olympus BX51 microscope. Photomicrographs were prepared using a Nikon D1x digital camera attached to an Infinity K-2 long-distance microscopic lens. Images were merged using Combine ZP and Helicon Focus 4.2.1 (HeliconSoft Ltd.) softwares. All measurements are in millimeters and were taken using an ocular graticule.

Abbreviations. Veins: A, anal; C, costa; CuA, cubital anterior; CuP, cubital posterior; MA, medial anterior; MP, medial posterior; ptc, pterostigmal crossvein; R, radial; Rs, radial sector; Sc, subcosta. Wing fields (in italics): *dcal*, discal cell; *doi*, discoidal cell; *m*, medial cell; *pt*, pterostigma; *r*, radial cell; *sr*, subradial cell.

Geological setting

The Peñacerrada I (in Moraza, Burgos. 42°40'22"N, 2°42'57"W) and El Soplao (in Rábago, Cantabria. 43°18'20"N, 4°26'50"W) amber-bearing deposits are included within the Basque-Cantabrian Basin (BCB) in the north of the Iberian Peninsula. To the south, the BCB constitutes a thrust sheet on the Cenozoic Duero and Ebro basins, while to the north it extends offshore to the Gulf of Biscay. BCB's oriental limit is in the Pyrenees, and its occidental limit is in the Asturian Paleozoic Massif. The evolution of the BCB during the Late Jurassic-Early Cretaceous was contextualized into a stretching rift setting related with the opening of both the North Atlantic Ocean and the Biscayan Gulf. This regional extension produced a complex distribution of sub-basins and depositional areas, with different sedimentation features between them.

The amber localities are Albian in age, about 110 Mya (Peñalver and Delclòs 2010), and are always associated with coal layers. The amber is included within the Escucha Formation (Peñacerrada I, in the oriental part of the BCB) (Martínez-Torres et al. 2003; Delclòs et al. 2007) and within Las Peñosas Formation (El Soplao, in the occidental part of the BCB) (Najarro et al. 2009, 2010). In Peñacerrada I, the amber is embedded into a siliciclastic unit with organic-rich silts, clays, and coal levels. These levels were deposited in non-marine environments, into interdistributary bays within a deltaic plain, and sometimes were related with channel infillings which drained the surrounding forests. The discontinuous presence of dinoflagellate cysts (Núñez-Betelu 1998) and orbitolinids (Martínez-Torres et al. 2003) suggests a periodical seawater influence. In El Soplao, the amber also occurs in organic-rich silt-claystones which were deposited into interdistributary and coastal bays, or marshes. This deposit is characterized by the presence of some decimetric levels of cuticle-plant remains indicating strong continental influence. They are interbedded with other levels containing brackish or marine gastropods, bivalves, bryozoans, and serpulids (Najarro et al. 2010), some of them fixed on the surfaces of the amber

pieces, and this circumstance suggests a more marine-influenced environment than in the Peñacerrada I outcrop. The Albian amber occurrences in the BCB are coinciding with transitions from maximum regional regressions to deltaic progradations (Martínez-Torres et al. 2003; Najarro et al. 2009).

Paleoecological setting

From Peñacerrada I two different vegetational assemblages were distinguished in palynological analyses (Barrón et al. 2001; Diéguez et al. 2010). One assemblage developed on the alluvial plains and was composed of a mixed conifer forest (chiefly Araucariaceae and Taxodiaceae–Cupressaceae, but also with some Pinaceae, Podocarpaceae and Ginkgoaceae) with an understory characterized by lycopsids and Schizaeaceae. The other assemblage was composed of xeromorphic vegetation that grew on coastal environments, containing Cheirolepidiaceae, Cycadophyta, Gnetophyta, and some arboreal ferns adapted to dry conditions, such as Matoniaceae and Cyatheaceae/Dicksoniaceae/Dipteridaceae. In El Soplao, the area was covered by a mixed forest that grew close to the seaside and was composed by Cheirolepidiaceae, Cupressaceae, and Miroviaceae, with an understory containing pteridophytes, cycads, ginkgoales, and/or bennettitales; swamp and pond areas were occupied by cryptogams and early angiosperms (Najarro et al. 2009, 2010).

Different tree groups have been interpreted as the resin producers. For the oriental area of the BCB (Peñacerrada I), araucariaceans close to the Recent genus *Agathis* were suggested as original producers of the resin (Alonso et al. 2000; Chaler and Grimalt 2005), while in the occidental area (El Soplao), the conifer genus *Frenelopsis*, of the extinct family Cheirolepidiaceae, plus another unidentified plant, were indicated (Menor-Salván et al. 2010; Najarro et al. 2010). The presence in both outcrops of abundant charcoal in the amber-bearing sediments and charcoalified plant fibers embedded into the amber indicates the occurrence of wildfires in the paleoenvironment (Najarro et al. 2010).

Systematic paleontology

Order Raphidioptera Navás, 1916
Suborder Raphidiomorpha Engel, 2002
Family Baissopteridae Martynova, 1961
Genus *Baissoptera* Martynova, 1961

***Baissoptera*? *cretaceoelectra* Pérez-de la Fuente, Peñalver, Delclòs & Engel, sp. n.**
urn:lsid:zoobank.org:act:94EB4ADD-CCC8-46CB-98AF-F2EC4D47BDDC
Figs 2, 3

Holotype. MCNA 12068.4, from Peñacerrada I amber; fore- and hind wing distal fragments. Three associated hymenopterans are preserved as syninclusions.

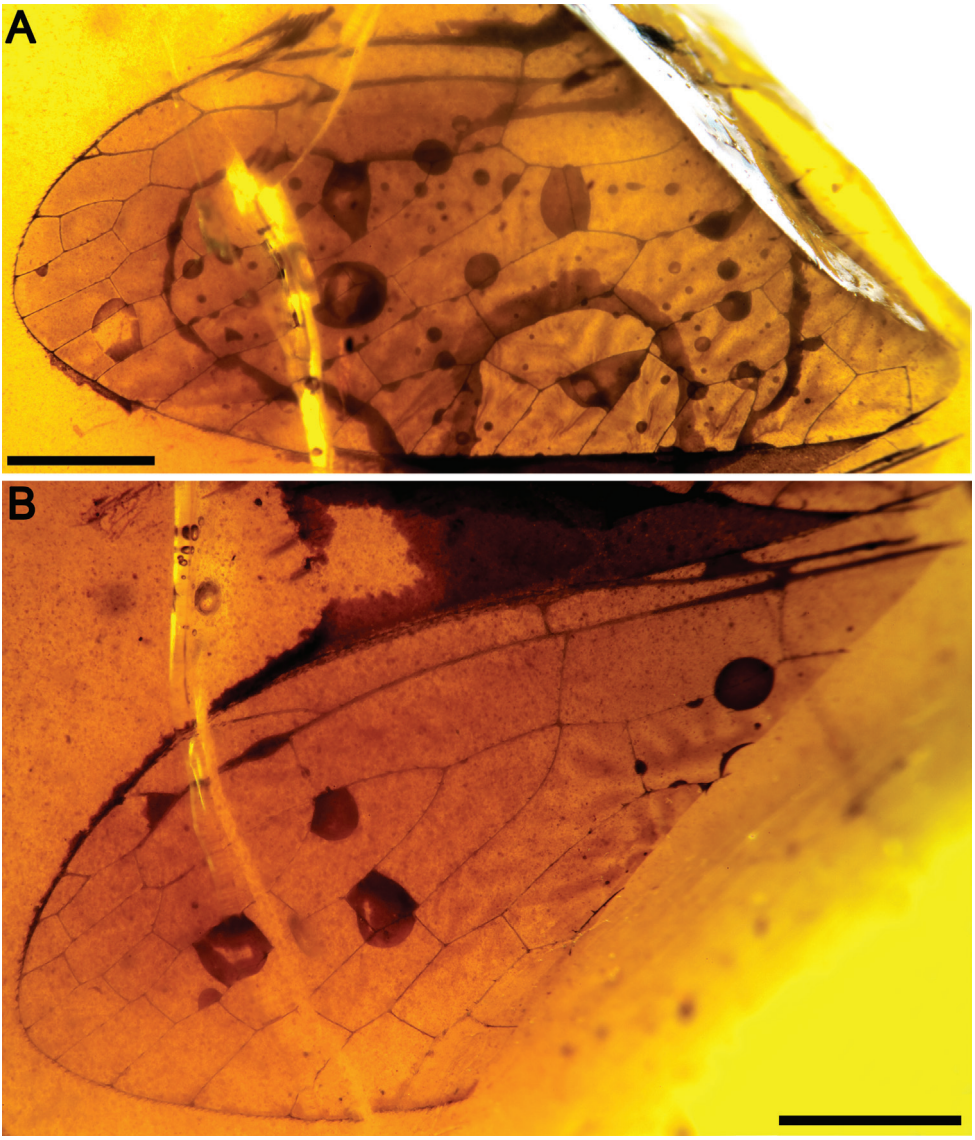

Figure 2. *Baissoptera*? *cretaceoelectra* sp. n., holotype MCNA 12068.4. **A** forewing **B** hind wing. Scale bars = 1 mm.

Diagnosis. Fore- and hind wing with a relatively long pterostigma with a strongly oblique and slightly sinusoid pterostigmal crossvein placed beyond pterostigmal midlength; fore- and hind wing with one closed radial cell distal to pterostigma; forewing Rs with six branches; forewing with at least eight closed subradial cells.

Description. Sex unknown. Veins with some strong, very short setae preserved, membrane hyaline. *Forewing.* Length of preserved fragment 6.4, maximum width 2.8; wing apex relatively rounded; pterostigma relatively long (2.4 long, length ca. eight

times basal pterostigmal width), slightly widening distally, not conspicuously infumate as preserved; pterostigma with a strongly oblique and slightly sinusoid pterostigmal crossvein placed beyond pterostigmal midlength, basally closed by a crossvein; pterostigma longer than any radial cell; R with two branches beyond pterostigma; at least three radial cells present, one closed radial cell partly distal to pterostigma; Rs with six branches and at least eight closed subradial cells; MA at least with two branches; gradate series very regular, almost following a staircase-like pattern. *Hind wing.* Length of preserved fragment 5.9, maximum width as preserved 2.7; wing apex more pointed than in forewing; costal field distinctly narrower than in forewing; one c-sc crossvein preserved; pterostigma relatively long (2.5 long, length ca. 10 times basal pterostigmal width), slightly widening distally, not conspicuously infumate as preserved, starting 0.5 (twice pterostigmal basal width) beyond termination of Sc; pterostigma with a strongly oblique and slightly sinusoid pterostigmal crossvein placed beyond pterostigmal midlength, basally closed by a crossvein; pterostigma longer than any radial cell; R with two branches beyond pterostigma; at least five radial cells present, one small closed radial cell distal to pterostigma; Rs with five branches and at least seven closed subradial cells; MA at least with two branches; gradate series very regular, almost following a staircase-like pattern.

Etymology. The specific epithet is a combination of the Greek words *cretaceus* (taken from the period name, although specifically meaning "chalky") and *elektron*, meaning "amber".

Comments. Within the current taxonomic framework, the numerous crossveins of MCNA 12068.4 are indicative of placement in the Baissopteridae. Unfortunately, neither base of the wing is preserved, thus important characters such as the maximum width of the costal field, the pattern of distribution of c-sc crossveins (= costal crossveins), the separation between M and CuA in the forewing, and the shape of the basal piece of MA, are unknown. Also, the infumation of the pterostigma is not evident in the holotype, but it is uncertain if this could have been caused by taphonomical processes and is, therefore, not used as a diagnostic character although if the absence of infumation is true of the species in life, then it would represent a remarkable difference from all other described baissopterids. Fortunately, the pterostigma can be delimited thanks to the relative parallelness of C and R (R tends to conspicuously change its slope beyond the pterostigma in the other baissopterids) and also the greater thickness of both veins.

The specimen is tentatively classified within the genus *Baissoptera* as it has the pterostigmal crossvein most similar to the diversity found within this genus. Today just two of the 12 species currently classified within the genus *Baissoptera*, i.e., *B. brasiliensis* Oswald, 1990 and *B. lisae* Jepson, Ansorge & Jarzembowski, 2011, lack a pterostigmal crossvein in both fore- and hind wings (Oswald 1990: p. 156, figs 3, 4; Jepson et al. 2011: p. 393, text-figs 6A, B). Some genera can even show an additional, straight pterostigmal crossvein in a more basal position at least in the hind wing, i.e., *B. kolosnitsynae* Martynova, 1961 and *B. pulchra* (Martins-Neto and Nel, 1992) (Martynova 1961: p. 81, fig. 7; Martins-Neto and Nel 1992: p. 428, figs 2, 3). Regarding the other taxa currently classified within the Baissopteridae, the genera *Lugala* and *Cretoraphidia* lack a pterostigmal crossvein, at

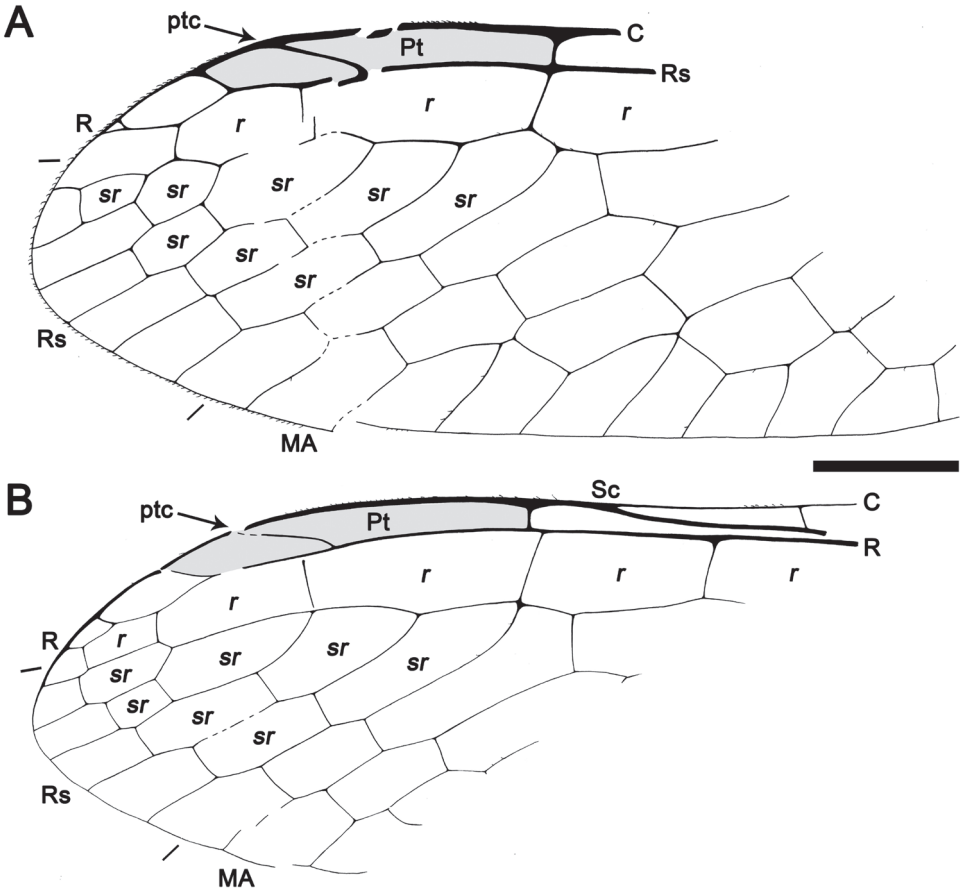

Figure 3. Drawings of *Baissoptera*? *cretaceoelectra* sp. n., holotype MCNA 12068.4. **A**, forewing **B** hind wing. Scale bar = 1 mm (both wings at the same scale).

least in the hind wing (Ponomarenko 1988: p. 75, fig. 4; 1993: p. 70, figs 7, 9, 10); whereas the genera *Cretoraphidiopsis* and *Austroraphidia*, although showing a pterostigmal crossvein situated beyond pterostigmal midlength, have it not as strongly oblique as in *B.*? *cretaceoelectra* sp. n., both showing irregular gradate series in both wings and a much lesser number of Rs branches in the forewing (three in *Austroraphidia*, four in *Cretoraphidiopsis*). *Cretinocellia cellulosa* Ponomarenko, 1988 has been recently transferred from the Baissopteridae to the Mesoraphidiidae by Bechly and Wolf-Schwenninger (2011) based on its lack of pterostigmal crossvein(s) and a Sc ending about midwing length. Although these two characters are also present in *Cretoraphidia certa* Ponomarenko, 1993 and *C. magna* Ponomarenko, 1993 (Ponomarenko 1993: p. 70, figs 7, 10), in both, the crossvenation is relatively higher than in *C. cellulosa* and should therefore remain in Baissopteridae for the moment. Consequently, Bechly and Wolf-Schwenninger (2011) also noted that the genus *Cretinocellia* might occupy a basalmost position within Mesoraphidiidae according to its relatively high crossvenation compared to the other mesoraphidiids. On the other

hand, we still consider *Arariperaphidia rochai* Martins-Neto and Vulcano, 1989 as incertae sedis rather than as a baissopterid (*contra* Bechly and Wolf-Schwenninger 2011), owing to its lack of preserved characters indicating a more conclusive assignment. The shape and location of the pterostigmal crossvein is quite diagnostic for *B.*? *cretaceoelectra*. Only *Baissoptera minima* Ponomarenko, 1993 shows such a strongly oblique pterostigmal crossvein within the family, even slightly sinusoid as in the new species, in a relatively elongate pterostigma (length ca. eight times basal pterostigmal width) (Ponomarenko 1993: p. 64, fig. 2). However, the pterostigmal crossvein is located before pterostigmal midlength and Rs is poorly branched in *B. minima*. *Baissoptera*? *cretaceoelectra* has Rs in the forewing with more branches currently described within the genus. The remaining *Baissoptera* species always show a lesser number of branches of Rs in the forewing, i.e., five (*B. brasiliensis*, *B. grandis* Ren in Ren et al., 1995, *B. liaoningensis* Ren, 1994, *B. lisae*, and *B. sibirica* Ponomarenko, 1993), four (*B. elongata* Ponomarenko, 1993, *B. euneura* Ren, 1997, *B. kolosnitsynae*, and *B. martinsoni* Martynova, 1961), or three Rs branches (*B. pulchra* and *B. minima*) (Martynova 1961; Oswald 1990; Martins-Neto and Nel 1992; Ponomarenko 1993; Ren 1994, 1997; Ren et al. 1995; Jepson et al. 2011). Although *B. cellulosa* Ponomarenko, 1993 (based on a forewing lacking the apex) could also possess six branches of Rs and does have a sinuate pterostigmal crossvein presumably beyond pterostigmal midlength (Ponomarenko 1993: p. 65, fig. 3), it differs from *B.*? *cretaceoelectra* in that the pterostigmal crossvein is just slightly oblique and the more abundant crossvenation. The only other described baissopterid with such an elevated number of branches of Rs is *Cretoraphidia certa*, but it lacks a pterostigmal crossvein as has been discussed, and in addition Sc ends in a more basal position. Furthermore, the pterostigmal length of the new species is elongate when compared to the other lengths shown by the other species within the genus *Baissoptera*. Only *B. grandis* has a longer pterostigma, its length about 11 times its basal pterostigmal width (Ren et al. 1995: p. 175, fig. 2). The shortest pterostigmata within the genus are found in *B. martinsoni* and *B. elongata*, their lengths ca. four and six times their basal pterostigmal widths, respectively (Martynova 1961: p. 80, fig. 6; Ponomarenko 1993: p. 67, fig. 5). Naturally, our placement of this species in *Baissoptera* is a conservative position based on the lack of complete material. More completely-preserved specimens, in which the wing base characters noted above could be assessed, may force a reconsideration of the generic assignment.

Family Mesoraphidiidae Martynov, 1925

Necroraphidia Pérez-de la Fuente, Peñalver, Delclòs & Engel, gen. n.

urn:lsid:zoobank.org:act:BF4F7D74-232F-4F2E-8754-E3940CD9D8B0
http://species-id.net/wiki/Necroraphidia

Type species. *Necroraphidia arcuata* sp. n.

Diagnosis. Small size; costal field very broad; pterostigma with a single, subdistal, strongly oblique, slightly sinuose to arcuate crossvein; pterostigma with a

diffuse base; forewing with Rs and MA each forked twice; forewing with second radial cell proximally broad.

Etymology. The new genus-group name is a combination of the Greek word *nekros*, meaning, "dead", and *Raphidia*, common generic stem for snakeflies. The name is feminine.

Comments. *Necroraphidia* gen. n. is most similar to *Ororaphidia* and *Styporaphidia* from the Late Jurassic of Inner Mongolia, China (Engel and Ren 2008). These three genera show the very diagnostic character of a diffuse base to the pterostigma, lacking a crossvein as the proximal boundary of this wing region (figs 4D–E). Also, they share the presence of, at least, one pterostigmal crossvein subdistally, three discoidal cells posterior to MP in the forewing (forming a triangle), and a larger size if compared with other minute mesoraphidiids. *Caloraphidia glossophylla* Ren, 1997 (combination restored by Bechly and Wolf-Schwenninger 2011) shares these three characters, but it lacks the diffuse pterostigmal base according to Ren (1997: p. 184, fig. 11). Hence, to consider this species as closely related (i.e., as an ororaphidiine in their system) as suggested by Bechly and Wolf-Schwenninger (2011) seems dubious. *Necroraphidia* can be separated from *Styporaphidia* by the presence of a single pterostigmal crossvein (two in *Styporaphidia*) and the three branches of both Rs and MA (two branches in *Styporaphidia*), while it can be distinguished most readily from *Ororaphidia* by the strongly oblique and arcuate shape of the pterostigmal crossvein (less oblique and straight in *Ororaphidia*), the proximally broader second radial cell (narrowly triangular proximad in *Ororaphidia*), the smaller second discoidal cell, and also by the smaller size (forewing length 11.4 in *Ororaphidia*) (Engel and Ren 2008).

Necroraphidia arcuata Pérez-de la Fuente, Peñalver, Delclòs & Engel, sp. n.

urn:lsid:zoobank.org:act:A0CA422D-FD60-4753-B8DE-7C5A4E75BDAE
http://species-id.net/wiki/Necroraphidia_arcuata
Figs 4, 5

Holotype. CES 391.1, from El Soplao amber; incomplete specimen, almost complete left fore- and hind wings (lacking their basalmost part), distal half of right hind wing and apex of right forewing, partial abdomen, and two leg fragments. Dense fungal hyphae infestate the abdomen and wings. The specimen is preserved together with the following syninclusions: two coleopterans, two hymenopterans (one of them, CES 391.2, belonging to the Megalyridae; Pérez-de la Fuente et al. 2012), one immature aphid, a cluster of trichomes, a few charcoalified plant fibers (Fig. 7A), a few timber debris, as well as other indeterminate organic remains.

Diagnosis. As for the genus (*vide supra*).

Description. Sex unknown. Legs patterned as follows (at least in the preserved fragments): femur with three dark areas, tibia with proximal area darkened and a dark area beyond midlength. Wing veins brown; veins with strong, very short setae, especially abundant on C; membrane hyaline. *Forewing.* Length of preserved frag-

Figure 4. *Necroraphidia arcuata* gen. et sp. n., holotype CES 391.1. **A** ventral habitus, note some charcoalified plant fibers nearby the specimen (arrow) **B** right forewing pterostigmal crossvein **C** right hind wing pterostigmal crossvein **D** right forewing pterostigmal diffuse base **E** right hind wing pterostigmal diffuse base. Scale bars: **A** = 2 mm; **B, C, D, E** = 0.5 mm.

ment 6.9 (estimated total wing length > 9), maximum width 2.7; costal field very broad (costal field about two times wider than pterostigmal base at widest preserved point; Sc terminating into C around two-thirds of estimated wing length; three c-sc

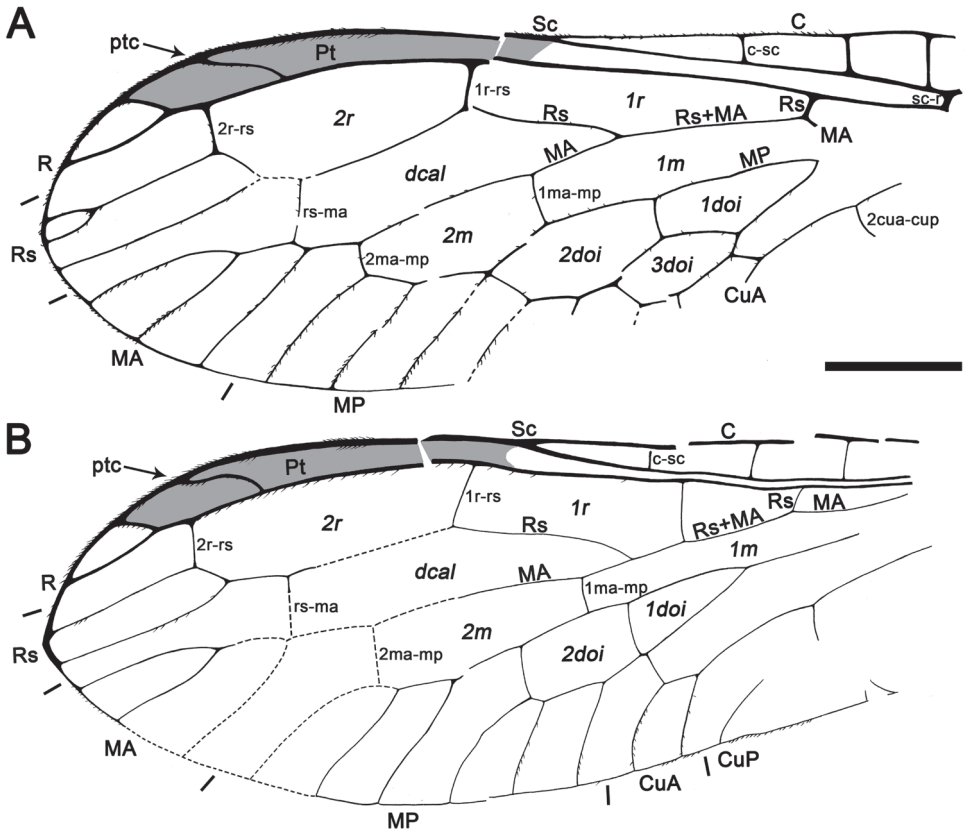

Figure 5. Drawings of *Necroraphidia arcuata* gen. et sp. n., holotype CES 391.1. **A** right forewing **B** right hind wing with reconstructed part taken from the left hind wing (dashed line). Only the distalmost c-sc crossvein has been tagged for both wings. Scale bar = 1 mm (both wings at the same scale).

crossveins preserved; single, proximal sc-r crossvein; pterostigma elongate (3.2 long, longer than either radial cell), widening distally (maximum width almost twice basal width), and faintly infumate, starting at termination of Sc; pterostigma with a single, subdistal, strongly oblique, slightly sinuose crossvein; pterostigma with a diffuse base (i.e., lacking a crossvein as proximal boundary of this wing region); Rs with three branches, distalmost fork very short; two large radial cells present; first radial cell about 1.3 times longer than second radial cell; second radial cell proximally broad; MA arising slightly distad midpoint of first radial cell, with three branches; three discoidal cells posterior to MP; 1cua-cup crossvein not preserved; anal veins not preserved; jugal lobe not visible. *Hind wing.* Length of preserved fragment 6.6 (estimated total wing length 8–9), maximum width 2.7; costal field distinctly narrower than in forewing; four c-sc crossveins preserved; pterostigma elongate (2.9 long, longer than either radial cell), widening distally (maximum width almost twice basal width), and faintly infumate, starting at termination of Sc; pterostigma with a single, subdistal, strongly oblique, arcuate crossvein; pterostigma with a diffuse base;

Rs with two branches; two radial cells present; MA with three branches; two discoidal cells posterior to MP, the first one trianguloid, not much smaller than second one; 1ma-mp crossvein not especially close to fork between Rs and MA; anal area not preserved. *Abdomen*. Length 3.8. Genitalia degraded, with dorsal part missing, and badly seen due to presence of dense fungal hyphae.

Etymology. The specific epithet is the Latin term *arcuatus*, meaning "bent", and refers to the arcuate form of the pterostigmal crossvein.

Genus *Styporaphidia* Engel & Ren, 2008

Styporaphidia? *hispanica* Pérez-de la Fuente, Peñalver, Delclòs & Engel, sp. n.

urn:lsid:zoobank.org:act:0AAD19B5-EF08-4B10-B704-DBF6D56A0D6F
Fig. 6

Holotype. MCNA 9343, from Peñacerrada I amber; hind wing fragment and abdominal apex, including the genitalia.

Diagnosis. The new species is similar to *Styporaphidia magia* Engel and Ren, 2008 from the Late Jurassic of Inner Mongolia, China, in the presence of two pterostigmal crossveins. *Styporaphidia*? *hispanica* sp. n. differs in that the distance between 1ptc and 2ptc is three times the distance between 2ptc and the end of the pterostigma (two times in *S. magia*), the forking of Rs at the apicalmost r-rs crossvein (rather than prior to it in *S. magia*), and R meeting the apicalmost r-rs crossvein beyond the pterostigma (within in *S. magia*).

Description. Male. *Hind wing.* Length as preserved 3.5, maximum width as preserved 2.5; wing apex relatively rounded; C especially thick when compared to other veins; pterostigma almost with constant width along its entire length, infumate; pterostigma with two crossveins, distalmost crossvein oblique and slightly arcuate, proximal crossvein apparently straight, distance between 1ptc and 2ptc three times distance between 2ptc and end of pterostigma; Rs with two branches, forking at r-rs crossvein; R meeting apicalmost r-rs crossvein beyond pterostigma; rs-ma crossvein meeting MA after its distalmost fork; MA with two branches. *Abdomen.* Gonocoxites 9 with a few long setae; gonostyli 9 segment rather short, rounded (not acute), slightly upcurved; tergite 10 (+11?) with distal setae; paired, contiguous, acute genital structures located dorsad to gonostyli 9, interpreted as distalmost part of parameres (Fig. 6A).

Etymology. The specific epithet refers to the occurrence of this species in ancient Spain (*Hispania* in Latin).

Comments. Although the base of the pterostigma is not preserved and it is accordingly impossible to ascertain if it was diffuse (i.e., lacking a crossvein), this species is tentatively placed in the genus *Styporaphidia* owing to the presence of two pterostigmal crossveins. The presence of two pterostigmal crossveins is a rare feature among the Raphidioptera and otherwise known in a few other raphidiopterans, i.e, namely the baissopterids *B. kolosnitsynae* and *B. pulchra* (Martynova 1961: p. 81, fig. 7; Martins-

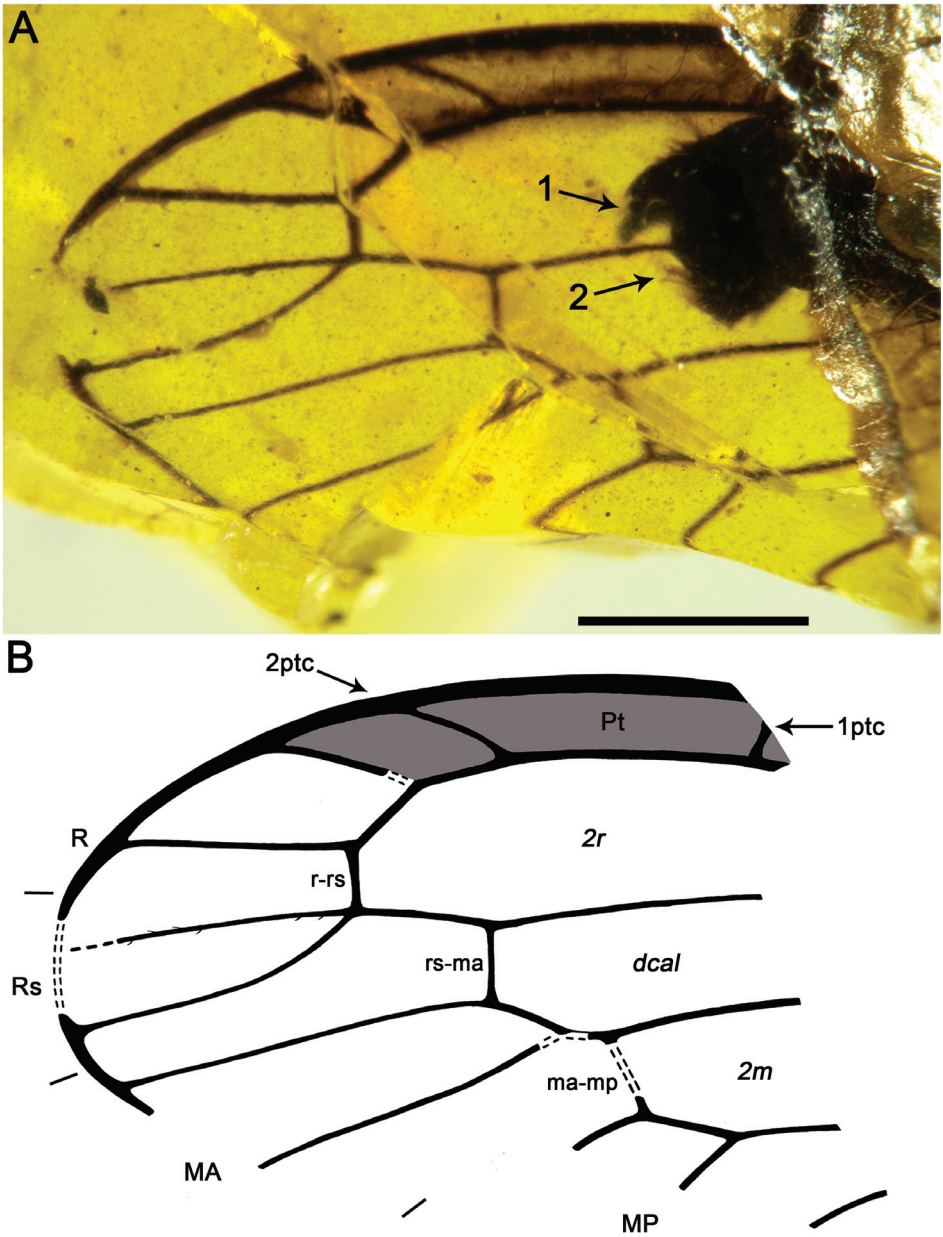

Figure 6. *Styporaphidia*? *hispanica* sp. n., holotype MCNA 9343. **A** hind wing apical fragment and genitalia; arrow 1 points to gonostyli 9, whereas arrow 2 points to the paired genital sclerites interpreted as the distalmost part of the parameres **B** drawing of preserved hind wing apical fragment. Scale bar = 1 mm.

Neto and Nel 1992: p. 428, figs 2, 3), but the present fossil is clearly not a baissopterid. The fragment is considered as corresponding to a hind wing due to the more distal disposition of both crossveins as occurs in *S. magia* (the distance between them being

greater than the distance between 2ptc and the end of the pterostigma), and by the relative position of the abdomen. The veins C and R appear to be especially thickened close to the wing apex as occurs also in *S. magia* (Engel and Ren 2008: fig. 2), though this effect could be enhanced by the darkening of the margins of the pterostigma. Although the species is represented by a wing fragment and the genitalia, it is distinctive enough that it should be easy to associate with more complete material that may become available in the future.

Amarantoraphidia Pérez-de la Fuente, Peñalver, Delclòs & Engel, gen. n.

urn:lsid:zoobank.org:act:EA2F19D0-E3C8-43A7-BA92-BFC73C2FA208
http://species-id.net/wiki/Amarantoraphidia

Type species. *Amarantoraphidia ventolina* sp. n.

Diagnosis. Minute size. Head ovoid, with the portion posterior to the compound eyes longer than the eye diameter and tapering caudad; three large ocelli present, situated between anterior half of compound eyes; antennae with a low number of flagellomeres (i.e., ≤ 26). Pronotum slightly longer than head, with a constant height along its entire length. Mesotibiae especially swollen; process at midlength of the metatibiae absent. Forewing with costal field moderately broad; pterostigma elongate, without crossveins; Sc terminating into C slightly distad wing midlength; six c-sc crossveins present; two discoidal cells posterior to MP; apicalmost branch of CuA simple; 1cua-cup crossvein located at the M-CuA separation.

Etymology. The new genus-group name is a combination of the Greek term *amarantos*, meaning "that never fades, ageless", and *Raphidia*, common generic stem for snakeflies. The name is feminine.

Comments. *Amarantoraphidia* gen. n. is first compared with the other described minute mesoraphidiid genera, which have a forewing length around 6 or less. They include amber inclusions but also some compression fossils. Apart from the minute size, in all of these taxa the pterostigma is very elongate, without crossveins, and basally closed by a crossvein. Regarding those as amber inclusions, *Amarantoraphidia* is readily distinct from the other two currently described Spanish mesoraphidiid genera, *Cantabroraphidia* and *Alavaraphidia* gen. n., as well as *Lebanoraphidia*, by its ovoid head shape (subquadrate in *Cantabroraphidia*, and rhomboidal in the other two genera) and by its lesser number of antennal flagellomeres (26 flagellomeres in *Cantabroraphidia*, 38 flagellomeres or more in *Lebanoraphidia*, and 44 in *Alavaraphidia*). The two genera *Nanoraphidia* (type species *N. electroburmica* Engel, 2002, Burmese amber, latest Albian in age) and *Grimaldiraphidia* (type species *G. luzzi* (Grimaldi, 2000), New Jersey amber, Turonian in age) share with *Amarantoraphidia* the ovoid head shape. However, in both of these genera the ocelli are placed between the posterior half of the compound eyes, not between the anterior part as in *Amarantoraphidia*. Additionally, whereas *Amarantoraphidia* has two discoidal cells posterior to MP in the forewing, *Grimaldiraphidia* has three and *Nanoraphidia* just a single

cell. Also, in *Nanoraphidia* the M-CuA separation is located near midpoint of the first and second cua-cup crossveins (Engel 2002; Jepson et al. 2011), not at the 1cua-cup crossvein as in *Amarantoraphidia*.

In addition to the aforementioned taxa, five mesoraphidiids with minute size have been hitherto described from compression fossils: *Grimaldiraphidia parvula* (Martynov, 1925), from Karatau (South Kazakhstan), Late Jurassic in age; *G. mitchelli* (Jepson, Coram and Jarzembowski, 2009), *G. purbeckensis* Jepson, Coram and Jarzembowski, 2009, and *Mesoraphidia websteri* Jepson, Coram and Jarzembowski, 2009, the three species from the Purbeck Limestone Group, Dorset (UK), Berriasian in age; and *Nanoraphidia lithographica* Jepson, Ansorge and Jarzembowski, 2011 (tentatively assigned to this genus), from El Montsec (Spain), Early Barremian in age. *Grimaldiraphidia parvula* (described from a complete specimen but its wings unresolved dorsoproximally) has more proximal positions of the fork of Rs and the 2r-rs and rs-ma crossveins than *Amarantoraphidia* (Martynov 1925: p. 242, figs 7–9). *Grimaldiraphidia mitchelli* (described from a wing, most likely a forewing, with not preserved base and pterostigma), although possessing two discoidal cells posterior to MP as in the forewing of *Amarantoraphidia*, has a venation somewhat different, with the second radial cell relatively wide compared to its length, and more proximal positions of the fork of Rs and the 2r-rs and rs-ma crossveins (Jepson et al. 2009). *Grimaldiraphidia purbeckensis* possesses three discoidal cells posterior to MP in the forewing, the M-CuA separation is located near midpoint of the first and second cua-cup crossveins, and has more proximal positions of the fork of Rs and the 2r-rs and rs-ma crossveins (ibid.). *Mesoraphidia websteri* (based on a hind wing) has the Sc ending beyond the first radial cell, relatively shorter second radial and discal cells, and a single discoidal cell (two discoidal cells posterior to MP in *Amarantoraphidia*) (ibid.). Lastly, *N. lithographica* shows only one discoidal cell posterior to MP in the forewing as in the type species for the genus, *N. electroburmica* (Jepson et al. 2011).

Amarantoraphidia ventolina **Pérez-de la Fuente, Peñalver, Delclòs & Engel, sp. n.**

urn:lsid:zoobank.org:act:79F0A7A3-789D-4B3F-8E34-A021073A86AD
http://species-id.net/wiki/Amarantoraphidia_ventolina
Figs 7–9

Holotype. CES 364.1, from El Soplao amber; almost complete female, just lacking the distalmost portion of both forewings beyond the end of the pterostigma and the distal third of the right hind wing. The first left leg is disarticulated. The specimen is preserved together with the following syninclusions: one evaniid (a new *Cretevania* species; CES 364.2, Pérez-de la Fuente et al. 2012, in prep.) and three other indeterminate hymenopterans, four dipterans (one chimeromyiid among them), one thysanopteran, a few charcoalified plant fibers, and a few timber debris, as well as other indeterminate organic remains.

Diagnosis. As for the genus (*vide supra*).

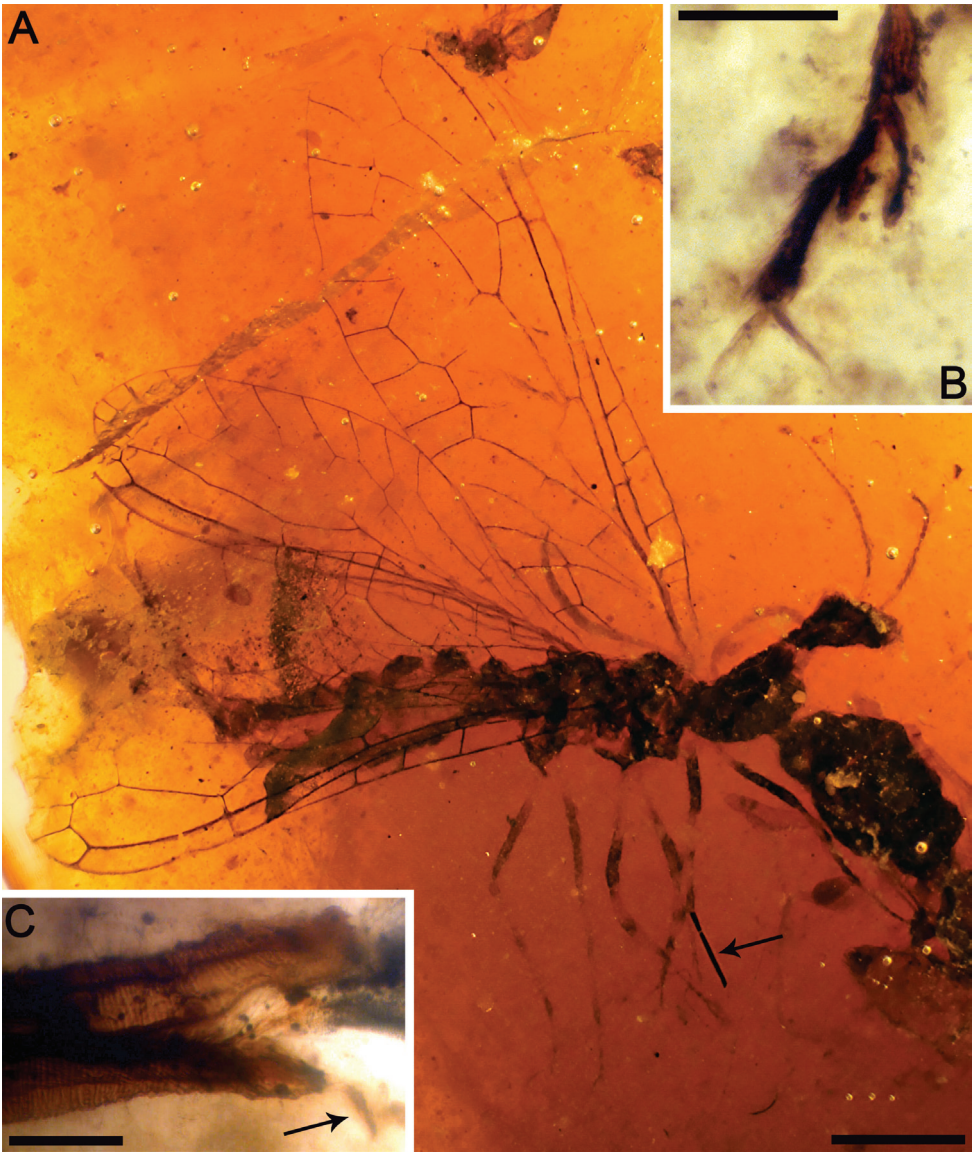

Figure 7. *Amarantoraphidia ventolina* gen. et sp. n., holotype CES 364.1. **A** lateral habitus, note a charcoalified plant fiber nearby the specimen (arrow) **B** left metatarsi showing bilobed third tarsomere **C** distal portion of ovipositor, note its dense annulation; arrow points to a gonostylus. Scale bars: **A** = 1 mm; **B, C** = 0.1 mm.

Description. Female. Integument dark brown; legs patterned as follows: femora darkened from just before their midlength to their end; three dark areas on tibiae, proximally, medially and distally; tarsomere 1 not darkened, distal tarsomeres darkened. *Head.* Ovoid, about 0.7–0.8 long, with portion posterior to compound eyes longer than eye diameter and tapering caudad; three large ocelli present, situated between an-

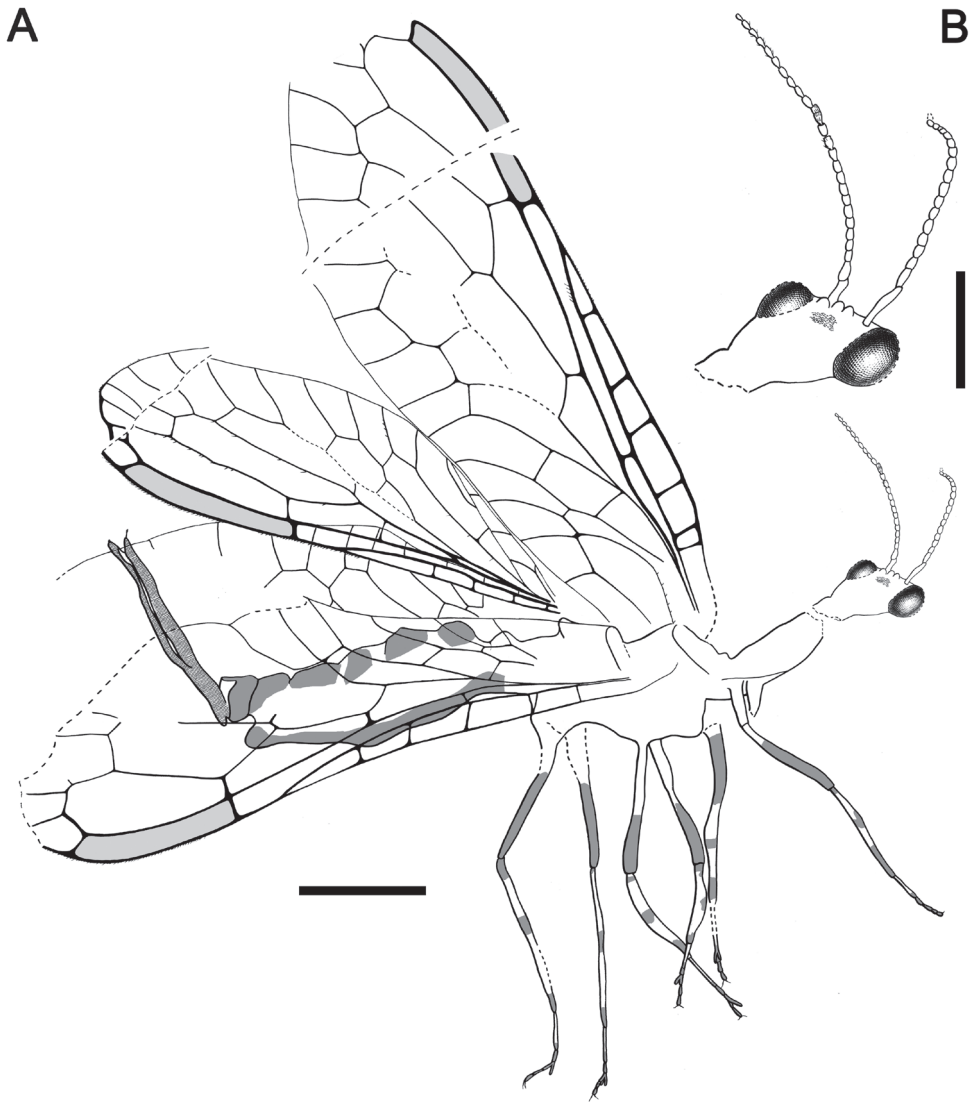

Figure 8. Drawings of *Amarantoraphidia ventolina* gen. et sp. n., holotype CES 364.1. **A** lateral habitus **B** head, magnified. Scale bars: **A** = 1 mm; **B** = 0.5 mm.

terior half of compound eyes; mandibles with teeth not visible; palps short; compound eyes large and exopthalmic, separated by distance slightly greater than compound eye length; antennae inserted around anterior tangent of compound eyes (exact insertion not visible); scape and pedicel gracile, both measuring about length of four flagellomeres and being subequal in thickness to them; 24 flagellomeres present, slightly longer than wide, with sparse, minute setae; coronal ecdysial cleavage line not evident; posterior border of head with a distinct collar-like lip. *Thorax.* Prothorax about 1.1 long, meso- plus metathorax 1.4 long; pronotum slightly longer than head, with a constant

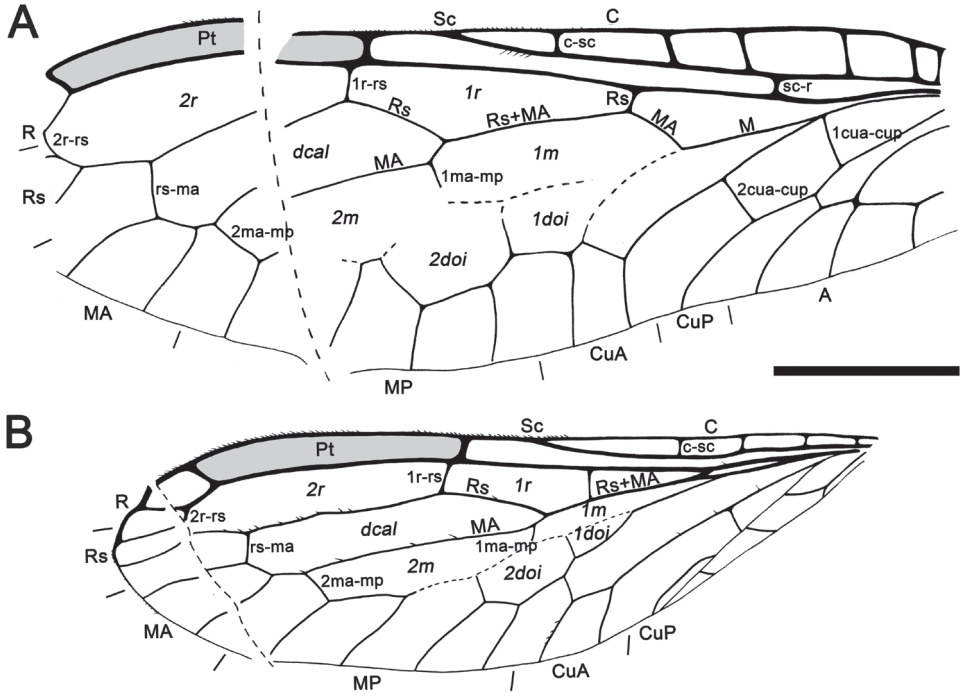

Figure 9. Drawings of *Amarantoraphidia ventolina* gen. et sp. n., holotype CES 364.1. **A** left forewing **B** left hind wing, depicted with its preservational folding, i.e., the basal part of MA is superimposed by the basal part of MP and the anal field is folded upwards. Only the distalmost c-sc crossvein has been tagged for both wings. Scale bar = 1 mm (both wings at the same scale).

height along its entire length (i.e., without a distinct change of slope in lateral view); a few spines visible on prothorax, dorsoanterior mesothorax apparently with a few small spines; all tibiae with apical spines; mesotibiae especially swollen; metatibiae significantly more elongate and thinner than the other tibiae; process at midlength of metatibiae absent; five tarsomeres, third with bilobed extensions lacking digitiform processes (Fig. 7B); pretarsal claws simple, with a basal enlargement; arolium large. Wing veins brown, meeting wing margins without bifurcating; veins with strong, very short setae, especially abundant on C; membrane hyaline. *Forewing.* Length about 5.6 (tip not preserved), maximum width 1.9; costal field moderately broad (at widest point costal field about 1.4 wider than pterostigma); six c-sc crossveins present, two basalmost c-sc crossveins particularly close to each other; Sc terminating into C slightly distad wing midlength; single, proximal sc-r crossvein; pterostigma elongate (1.5 long), slightly longer than either radial cell; pterostigma with constant width along its entire length, faintly infumate, starting 0.4 (about three times pterostigmal width) beyond termination of Sc; pterostigma without crossveins, basally closed by a crossvein; Rs with two branches; two large radial cells present; first radial cell nearly as long as second radial cell, with MA arising slightly distad its midpoint; MA with two branches; two dis-

coidal cells posterior to MP; apicalmost branch of CuA unforked; 1cua-cup crossvein located at M-CuA separation; 2A arcuate; jugal lobe not visible. *Hind wing.* Length about 4.1, maximum width 1.3; costal field distinctly narrower than in forewing; four c-sc crossveins present; sc-r crossvein absent; pterostigma elongate (1.5 long), slightly longer than second radial cell; pterostigma with about a constant width along its entire length, faintly infumate, starting 0.3 (slightly more than two times pterostigmal width) beyond termination of Sc; pterostigma without crossveins, basally closed by a crossvein; Rs with two branches; two radials cells present; MA with two branches; two discoidal cells posterior to MP, first one smaller and trianguloid; 1ma-mp crossvein close to fork between Rs and MA; anal area folded. *Abdomen.* Length 2.4; ovipositor robust, 1.7 long as preserved, 0.1 thick (about 15 times as long as wide); ovipositor showing dense annulations (Fig. 7C); ovipositor with faint, stiff, short sensory setae along its entire length; ovipositor gonostyli most likely club-shaped.

Etymology. In the Cantabrian mythology, the "ventolines" are tenacious and always cheerful fairy-like air beings that dwell in the depths of the sky and, when summoned, help defenseless fishermen by placidly steering their boats to the shore while embracing them with their warm green wings. The term has been singularized and feminized for combination.

Comments. In extant snakeflies, the dense annulations of the ovipositor (cf. Fig. 7C) provide the flexibility necessary for introduction into irregular cavities, similar to a flexible metallic hose (Mickoleit 1973). It has been noted how mesoraphidiids would have had a shorter and thicker ovipositor than Recent Raphidioptera (Bechly and Wolf-Schwenninger 2011). The shape of the ovipositor in this specimen and also in *Alavaraphidia* gen. n. supports such a conclusion.

Alavaraphidia Pérez-de la Fuente, Peñalver, Delclòs & Engel, gen. n.

urn:lsid:zoobank.org:act:070A3E8E-1F78-4663-A909-1872E5EEA80E
http://species-id.net/wiki/Alavaraphidia

Type species. *Alavaraphidia imperterrita* sp. n.

Diagnosis. Minute size. Head rhomboidal, with clypeus especially elongate and the portion posterior to the compound eyes shorter than the eye diameter and strongly tapering caudad; three large ocelli present, situated near the posterior tangent of compound eyes; antennae extremely elongate, with a high number of flagellomeres (i.e., ≥ 38). Pronotum shorter than head, with a constant height along its entire length. All tibiae especially swollen medio-apically; process at midlength of the metatibia indistinct. Bilobed extensions of third tarsomeres with distal digitiform processes.

Etymology. The new genus-group name is a combination of Álava, from Álava amber (the name of the group for Peñacerrada I and Peñacerrada II amber localities), and *Raphidia*, common generic stem for snakeflies. The name is feminine.

Comments. Although most of the wings are not preserved, the other features of *Alavaraphidia* gen. n. are distinctive enough to justify the creation of a distinct taxon.

The minute size of *Alavaraphidia* mainly limits its comparison to other minute taxa mainly described from amber inclusions (refer to comments for *Amarantoraphidia* gen. n.). Although a few other taxa based on wings from compressions are minute in size it is not possible to compare them with the new genus and species due to the absence of most of its wings. The genus *Lebanoraphidia* shares with *Alavaraphidia* the rhomboidal shape of the head with the compound eye length greater than that of the head posterior to the eyes (Bechly and Wolf-Schwenninger 2011); the head shape is ovoid in the genera *Grimaldiraphidia*, *Nanoraphidia*, and *Amarantoraphidia*, and subquadrangular in the genus *Cantabroraphidia*. Moreover, the genus *Lebanoraphidia* differs from *Alavaraphidia* in the lesser number of flagellomeres (note how the number of flagellomeres depicted for *L. nana* Bechly and Wolf-Schwenninger, 2011, type and only species of the genus, seems to not match the description and photographs), the shorter clypeus, the shorter portion posterior to the compound eyes, the longer relative length of the pronotum, and the assumed absence of distal digitiform processes on the third tarsomere's bilobed extensions. The high number of flagellomeres of *Alavaraphidia* (44) is most similar to that of *Lebanoraphidia*, itself with around 38 flagellomeres (Bechly and Wolf-Schwenninger 2011). Otherwise, 20 flagellomeres are present in the genus *Nanoraphidia* (Engel 2002), 23 in *Grimaldiraphidia* (Grimaldi 2000), 24 in *Amarantoraphidia*, and 26 in *Cantabroraphidia* (Pérez-de la Fuente et al. 2010). The distal digitiform processes from the third tarsomere's bilobed extensions (fig. 10C) have not been reported from any other taxon and thus it is considered a unique character. Regarding the leg patterning, the medial dark patch found on the tibia in *Cantabroraphidia* (ibid.) and *Amarantoraphidia* is absent in *Alavaraphidia*. However, this character is not considered relevant at the generic level and hence has been discarded from the present diagnosis.

***Alavaraphidia imperterrita* Pérez-de la Fuente, Peñalver, Delclòs & Engel, sp. n.**
urn:lsid:zoobank.org:act:E1406721-46BE-4F26-869E-EC6C5AE6CD01
http://species-id.net/wiki/Alavaraphidia_imperterrita
Figs 10, 11

Holotype. MCNA 13608, from Peñacerrada I amber; partial specimen showing head and ventral parts of thorax and abdomen, including the ovipositor. Only the basalmost part of the wings is preserved.

Diagnosis. As for the genus (*vide supra*).

Description. Female. Body length excluding ovipositor 5.7. Integument dark brown; legs patterned as follows: femora darkened from just before their midlength to their end; two dark regions on tibiae, proximally and distally (medial dark region absent); tarsomere 1 not darkened, distal tarsomeres darkened. *Head.* Rhomboidal, about 1.2 long, with portion posterior to compound eyes shorter than eye diameter (about 0.7 times) and strongly tapering caudad; three large ocelli present, situated near posterior tangent of compound eyes; mandible with teeth not visible; palps short; clypeus especially elongate; compound eyes separated by about compound eye length;

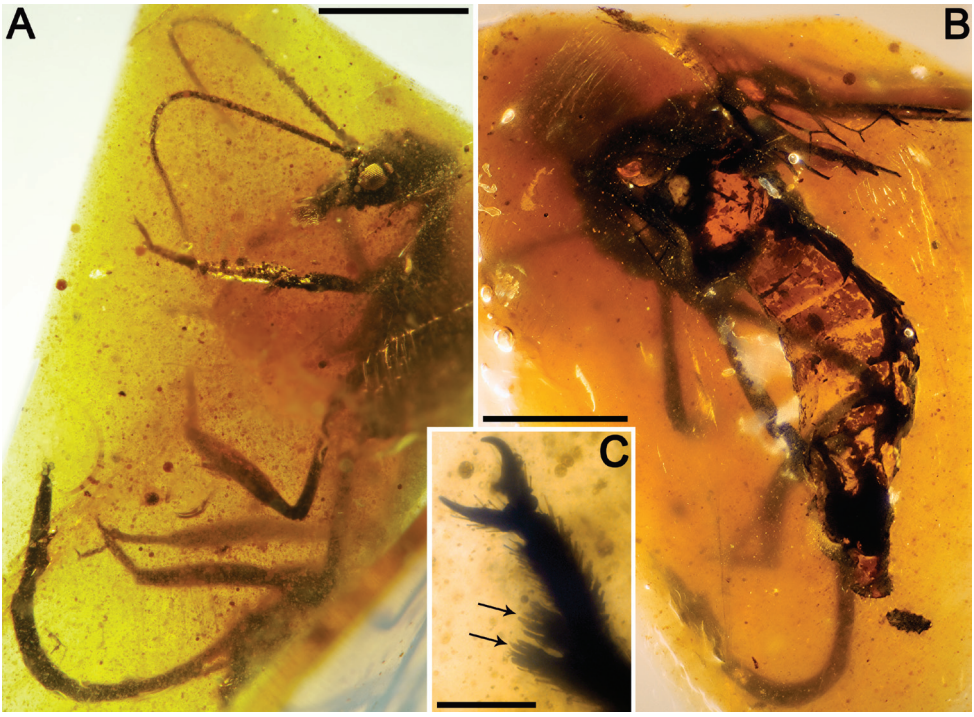

Figure 10. *Alavaraphidia imperterrita* gen. et sp. n., holotype MCNA 13608. **A** lateral habitus **B** dorsal habitus **C** left distal foretarsus, showing bilobed third tarsomere with digitiform processes (arrows). Scale bars: **A, B** = 1 mm; **C** = 0.1 mm.

three large ocelli present, situated near posterior tangent of compound eyes; antennae inserted posterior to clypealfrons sulcus, basad anterior tangent of compound eyes; antennae extremely elongate, with 44 flagellomeres; flagellomeres elongate, about 1.5 times longer than wide; scape and pedicel thicker than flagellomeres, scape measuring about two flagellomeres, pedicel measuring slightly more than a flagellomere; coronal ecdysial cleavage line not evident; posterior border of head not visible. *Thorax.* Prothorax about 0.8 long; meso- and metathorax about 1.1 long; pronotum shorter than head, with a constant height along its length (i.e., without a distinct change of slope in lateral view); thoracic dorsal spines not visible, if present; all tibiae especially swollen medio-apically, with apical spines, spines also visible on metatarsomeres; process at midlength of metatibia indistinct; five tarsomeres, third with bilobed extensions having six to eight distal digitiform processes (Fig. 10C), different in shape than regular leg setae (not tapering apically); pretarsal claws simple, with a basal enlargement; arolium large. Preserved wing veins brown, with strong, very short setae; preserved membrane hyaline. *Forewing.* Costal field not especially broad. Three c-sc crossveins preserved. *Hind wing*. Costal field distinctly narrower than in forewing. Three c-sc crossveins preserved. *Abdomen.* Length 2.7; ovipositor robust but rather elongate, about 2.7 long as preserved, 0.2 thick (about 15 times as long as wide); ovipositor with dense an-

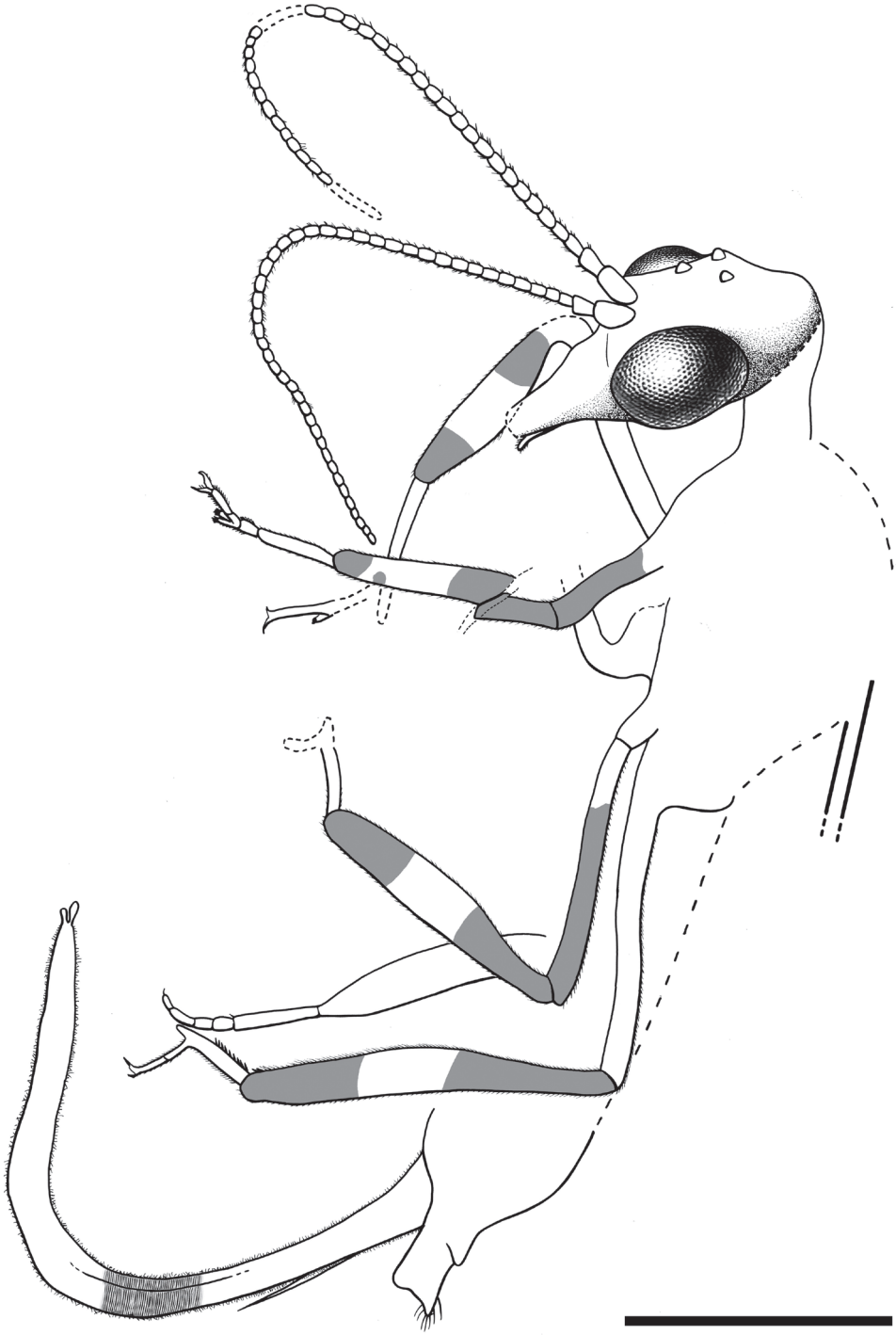

Figure 11. Drawing of *Alavaraphidia imperterrita* gen. et sp. n., holotype MCNA 13608. Lateral habitus. The annulations of the ovipositor have been depicted partially. Scale bar = 1 mm.

nulations; ovipositor with conspicuous faint, stiff, small sensory setae along its entire length; ovipositor gonostyli club-shaped; tergite 10 (+11?) with a distalmost stripe of stiff trichobothria (some probably from tergite 9).

Etymology. The specific epithet is the Latin term *imperterritus*, meaning "fearless", and symbolizes the unalterable condition of an organism entrapped in amber.

Genus *Cantabroraphidia* Pérez-de la Fuente, Nel, Peñalver & Delclòs, 2010

http://species-id.net/wiki/Cantabroraphidia
Fig. 12

Cantabroraphidia Pérez-de la Fuente, Nel, Peñalver, and Delclòs, 2010: 109. Type species: *Cantabroraphidia marcanoi* Pérez-de la Fuente, Nel, Peñalver, and Delclòs, 2010, by original designation.

Comments. According to the original diagnosis, this monospecific genus was characterized by the following combination of characters: minute size (forewing length 5.5). Head more or less quadrangular; with portion posterior to the compound eyes slightly shorter than the eye diameter and not tapering caudad; three large ocelli present, situated between anterior half of the compound eyes; posterior border of head with a distinct collar-like lip. Pronotum subequal in length to head length, with anterior half narrowed dorsoventrally relative to posterior half (i.e., with slight downward curve in lateral view). Process present at midlength of the metatibiae in a posterior position. Forewing with costal field relatively broad (at widest point costal field as broad as pterostigma); pterostigma elongate, without crossveins; Sc terminating into C in distal two-thirds of wing length; four c-sc crossveins; two discoidal cells posterior to MP; 1cua-cup crossvein strongly basad M-CuA separation; posterior branch of MP forked. Refer to Pérez-de la Fuente et al. (2010) for a complete description of the type and only known species from El Soplao amber, based on an adult of unknown sex.

Genus and species indet. 1

Figs 13A, 14A

Material. MCNA 9218, from Peñacerrada I amber; wing apex plus two minute wing fragments lacking formal descriptive significance. The sample consists of part and counterpart after the amber piece broke following the plane of the inclusion.

Descriptive notes. Sex unknown. *Hind wing(?).* Length of preserved fragment 2.4, maximum width of preserved fragment 2.4; wing apex rounded; pterostigma slightly increasing in width distally, infumate; pterostigma with an almost straight subdistal crossvein; all apical branches relatively short; Rs with three branches, distalmost fork

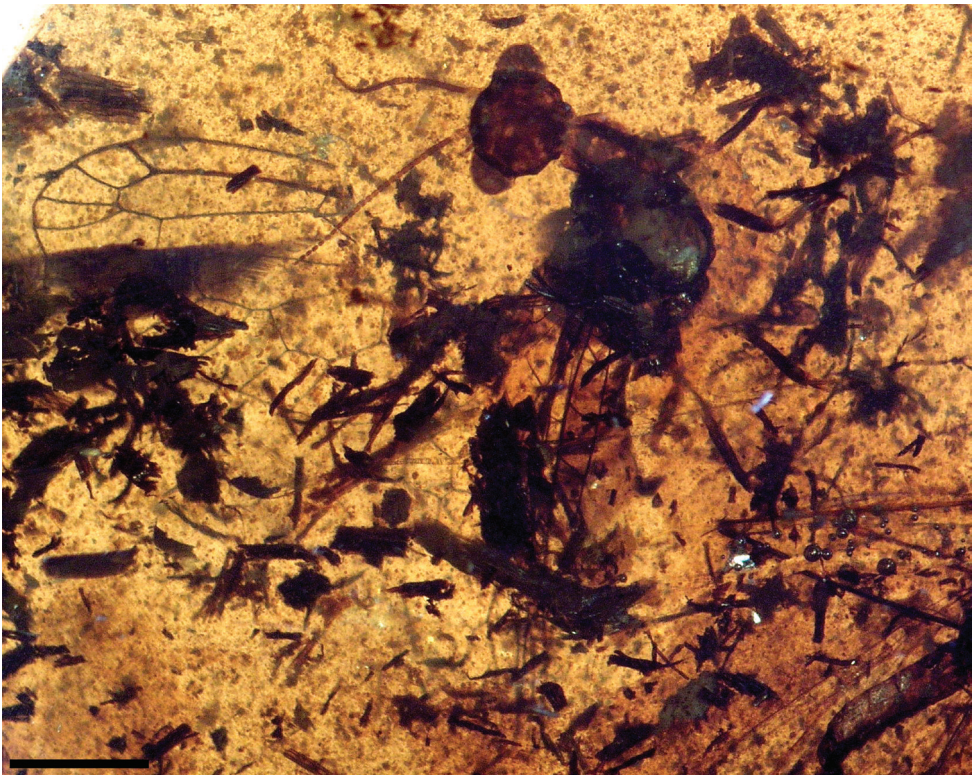

Figure 12. *Cantabroraphidia marcanoi* Pérez-de la Fuente et al., 2010. Laterodorsal habitus. Sex unknown. Note the abundant presence of timber debris in the amber piece, surrounding the specimen. Scale bar = 1 mm.

very short; apicalmost r-rs crossvein (2r-rs?) meeting R distal to the pterostigma; rs-ma crossvein situated at distalmost fork of MA; MA with two branches.

Comments. The present material is distinct from other Spanish amber snakeflies but does not preserve enough detail to permit formal designation as a taxonomic entity. The presence of a pterostigmal crossvein immediately discounts *Cantabroraphidia* and *Amarantoraphidia* gen. n. MCNA 9218 highly resembles the hind wing of *Styporaphidia* in the shape and location of the distalmost pterostigmal crossvein. In fact, its venation is very similar to *S.*? *hispanica* sp. n., though in the present material Rs is forked very close to the wing margin and the shape of its distalmost radial cell (most likely the second one) is somewhat different. Furthermore, the less pointed wing apex, shorter apical branches, and apical shapes of the radial, discal, and presumed second medial cells immediately distinguish MCNA 9218 from *Necroraphidia* gen. n. and genus and species indet. 2 (*vide infra*), and the almost straight pterostigmal crossvein and positions of the apicalmost r-rs (2r-rs?), rs-ma, and apicalmost ma-mp (2ma-mp?) crossveins further differentiate MCNA 9218 from *Necroraphidia*.

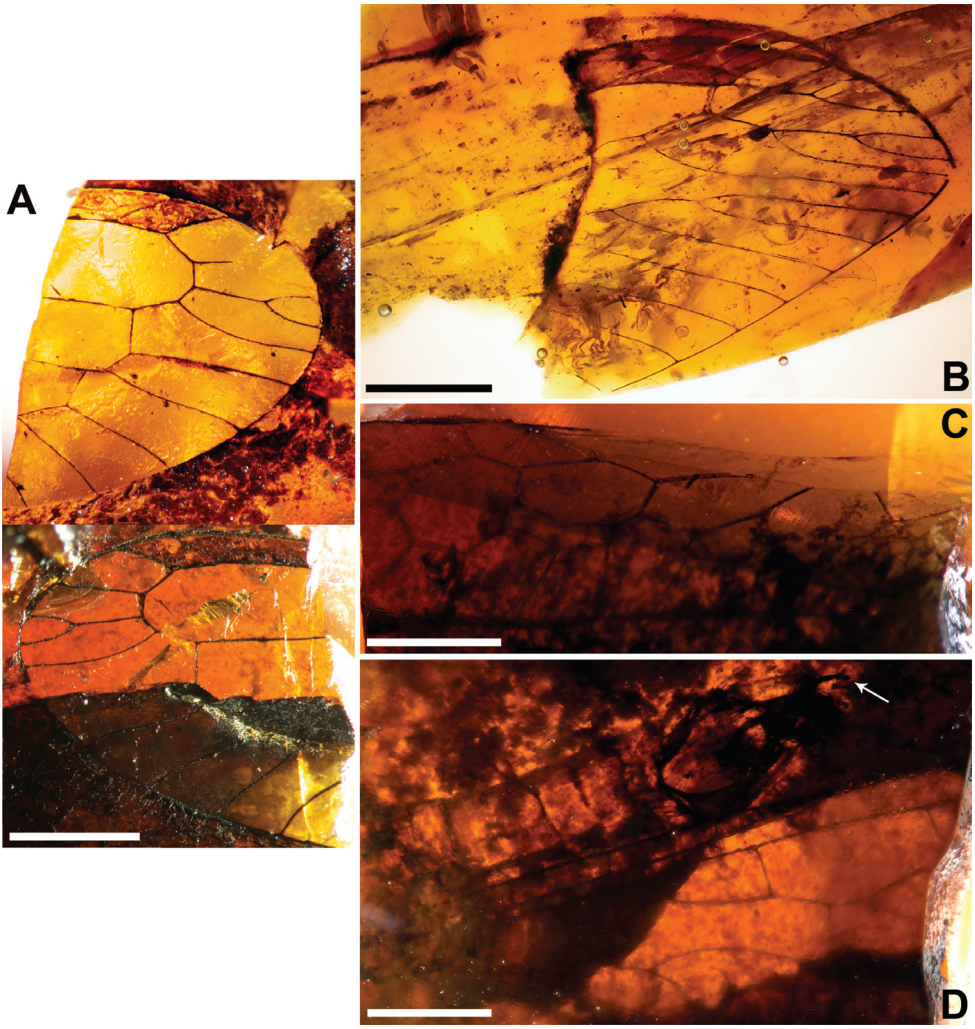

Figure 13. Fragmentary wing remains, genus and species indeterminate: CES 9218 part and counterpart (**A**), CES 376 (**B**), and MCNA 9316 (**C–D**). **A** distal part of a hind wing(?), part (above) and counterpart (below) **B** preserved distal wing fragments **C** preserved part of forewing **D** preserved part of hind wing and distal part of abdomen. Arrow points to the tip of right gonostylus 9. Scale bars = 1 mm.

Genus and species indet. 2

Figs 13B, 14B

Material. CES 376, from El Soplao amber; forewing apex and the area surrounding pterostigma from an additional wing. Some additional dorsoproximal parts of the wing are also present but with a very poor preservation, so just a few more characters can be elucidated. An indeterminate hymenopteran is present as a syninclusion.

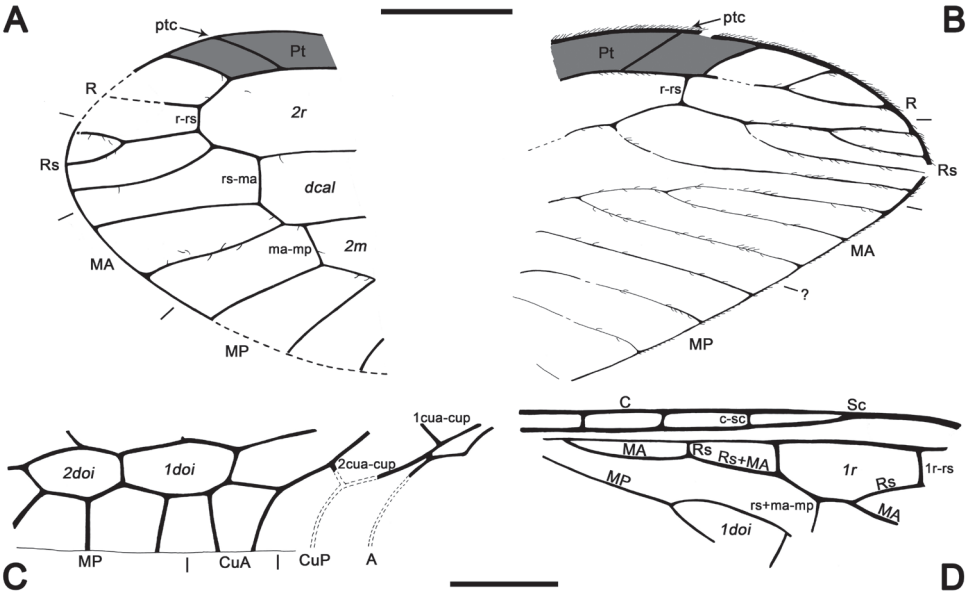

Figure 14. Drawings of fragmentary wing remains, genus and species indeterminate: CES 9218 counterpart (A), CES 376 (B), and MCNA 9316 (C–D). **A** distal part of hind wing(?) **B** best preserved distal wing fragment **C** preserved part of forewing **D** preserved part of hind wing; only the distalmost c-sc crossvein has been tagged; basalmost preserved c-sc crossvein not depicted. Scale bars = 1 mm (**A** and **B**; **C** and **D** at the same scale).

Descriptive notes. Length as preserved ca. 5.0 (wing well preserved only in 3.4 of that length), maximum width as preserved 2.7; wing apex pointed, positioned within Rs series; wing veins brown, meeting wing margins without bifurcating; veins with strong, short setae, especially abundant on C; Sc ending and proximal r-rs crossvein (1r-rs?; very faintly preserved) situated at about same wing length, pterostigma slightly widening distally, infumate; pterostigma with a very faint subdistal, rather straight (not conspicuously arcuate), strongly oblique crossvein; uncertain if pterostigmal division present; apical branches of Rs, MA and MP subparallel; two apical branches of R distal to pterostigma; Rs with four branches, posteriormost originating before distalmost r-rs crossvein (2r-rs?), separated from it by much more than its length; rs-ma and distalmost ma-mp crossveins lacking in preserved wing fragment, so most likely with a proximal position; MA most likely with three branches.

Comments. Despite the fact that CES 376 is distinct from the other taxa in Spanish amber, it is not named as its preserved parts are not enough to resolve its affinities. The wing fragments show a high resemblance with some mesoraphidiids such as *Mesoraphidia obliquivenatica* (Ren, 1994) and *Caloraphidia glossophylla*, both from the Cretaceous compression deposit of Liaoning (China), as long as all of them share the presence of a strongly oblique, rather straight pterostigmal crossvein in a

rather distal position and a distal portion of the wing with long apical branches and without crossveins other than the 2r-rs crossvein (Ren 1994: p. 134, fig. 4; 1997: p. 184, fig. 11). *Caloraphidia glossophylla* possesses subparallel apical branches of Rs, MA and MP, the Sc ending and the 1r-rs crossvein situated at about the same wing length, the 2r-rs crossvein closer to the end of the pterostigma than to the pterostigmal crossvein, and a pointed apex positioned within the Rs series, but in this species Rs has only three branches. By contrast, although *M. obliquivenatica* has Rs with four branches as in CES 376, the apical branches of Rs, MA and MP are not subparallel, the Sc ends in a more basal position than the 1r-rs crossvein, the 2r-rs crossvein is closer to the pterostigmal crossvein than to the end of the pterostigma, and the apex is more rounded and positioned between R and Rs. CES 376 is also quite similar to the wing apex of the compression fossil *Iberoraphidia dividua* Jepson, Ansorge and Jarzembowski, 2011, from El Montsec (Spain), Early Barremian in age, with its relatively simple venation, a Sc ending and a 1r-rs crossvein situated at about the same wing length, the 2r-rs, rs-ma and 2ma-mp crossveins not apically placed, the four branches of Rs, with the posteriormost branch of Rs originating before the 2r-rs crossvein, and the relatively simple apical fork of MA and MP (Jepson et al. 2011). CES 376 differs, however, in the presence of a pterostigmal crossvein (although in *I. dividua* the distal portion of the divided pterostigma could be basally closed by a crossvein), only two apical branches to R distal to the pterostigma (not three as in *I. dividua*), the posteriormost branch of Rs more proximally placed (separated from the distalmost r-rs by much more than its length, versus much shorter in *I. dividua*), and the more pointed wing apex which is positioned within the Rs series (rather than between R and Rs in *I. dividua*).

Genus and species indet. 3
Figs 13C–D, 14C–D

Material. MCNA 9316, from Peñacerrada I amber; fore- and hind wing fragments from the same side of the body and a poorly preserved part of the abdomen, although the genitalia is somewhat visible. The amber piece contains abundant organic remains. The specimen is preserved together with legs of a spider as syninclusions.

Descriptive notes. Male. Small size (inferred from preserved wing fragments). *Forewing.* Length as preserved about 4.5, maximum width not measurable. Two discoidal cells posterior to MP; posterior branch of MP unforked; M-CuA separation not preserved; 2A arcuate. *Hind wing.* Length as preserved about 4.7, maximum width not measurable. Costal field relatively narrow; four c-sc crossveins preserved; Sc ending into C at length of first radial cell's midlength; pterostigma not evidently infumate, not closed basally by a crossvein, at least proximally; first discoidal cell not especially small (or compact) (small in *Cantabroraphidia marcanoi*); rs+ma-mp crossvein present. *Abdomen.* Length as preserved (including genitalia) 3.8. Gonocoxites 9 with paired

basal inner tubercles with small dark teeth; gonocoxites 9 elongate, with very long, stiff setae distally; gonostyli 9 very elongate, slightly upcurved; parameres not conspicuous; tergite 10 (+11?) with distalmost two or three stripes of trichobothria.

Comments. The preserved characters of MCNA 9316 are not enough to create a new taxon. The combined presence of two discoidal cells posterior to MP as in *Cantabroraphidia* and *Amarantoraphidia* gen. n., and the lack of a crossvein closing the pterostigma basally in the preserved wing length as in *Necroraphidia* gen. n., *Ororaphidia*, and *Styporaphidia* (showing three discoidal cells), precludes assignment to any of these genera. The lack of a crossvein closing the pterostigma basally can mean that the base of the pterostigma may have been diffuse or that the pterostigma may have been placed in a more distal position, as occurs in some mesoraphidiids. However, the inferred size of MCNA 9316 would have not been as reduced as in the minute mesoraphidiids but would have better fit with that of those mesoraphidiids with a diffuse pterostigmal base (refer to comments for *Necroraphidia* gen. n.). Furthermore, the presence of a rs+ma-mp crossvein in the hind wing as occurs in MCNA 9316 is a very rare character among described Mesoraphidiidae but more common in modern snakeflies, although it is also present in *S. magia*. The morphology of the genitalia appear distinctive enough as to be recognizable in future findings. It is interesting to note that Aspöck and Aspöck (2004: figs 9, 10) used the presence of wartlike tubercles (covered with dark teeth) on the inner side of gonocoxite 9, larger but similar to those shown by MCNA 9316, as a diagnostic character for the inocelliid genus *Succinofibla* Aspöck & Aspöck, 2004 from Baltic amber. These authors also suggested that these tubercles could be related with the closing mechanism of the genitalia.

Dichotomous keys

The following keys include only those species sufficiently diagnostic to name. As such, the additional morphospecies are not considered here and so all new material should be cross-referenced with the above accounts on those more fragmentarily known taxa. Note that *Alavaraphidia imperterrita* sp. n. is absent from the first key given that the diagnostic parts of the forewings are not preserved.

Key to genera and species of Spanish amber Raphidioptera based on wings

1 Fore-/hind wing with pterostigmal crossvein **2**

– Fore-/hind wing without pterostigmal crossvein (Mesoraphidiidae) **4**

2 Fore-/hind wing with sparse or moderate crossvenation; at most with two radial cells, three medial cells, and three discoidal cells posterior to MP; often with no closed subradial cells (i.e., cells between Rs branches) (Mesoraphidiidae) **3**

– Fore-/hind wing with relatively rich crossvenation; with at least three radial cells, and numerous subradial, medial, and discoidal cells posterior to MP (Baissopteridae) .....***Baissoptera*? *cretaceoelectra* sp. n.**

3 Fore-/hind wing with a single pterostigmal crossvein; distalmost r-rs crossvein meeting R within pterostigma, Rs (proximally) forking before distalmost r-rs; rs-ma crossvein meeting MA before its distalmost fork..... ..... ***Necroraphidia arcuata* gen. et sp. n.**

– Hind wing with two pterostigmal crossveins; distalmost r-rs crossvein meeting R beyond pterostigma, Rs forking at r-rs crossvein; rs-ma crossvein meeting MA after its distalmost fork ..... ***Styporaphidia*? *hispanica* sp. n.**

4 Forewing with four c-sc crossveins; apicalmost branch of CuA forked near wing margin; M-CuA separation between 1cua-cup and 2cua-cup crossveins (closer to latter)..... ***Cantabroraphidia marcanoi* Pérez-de la Fuente et al., 2010**

– Forewing with six c-sc crossveins; apicalmost branch of CuA unforked; M-CuA separation at the 1cua-cup crossvein .... ***Amarantoraphidia ventolina* gen. et sp. n.**

Key to minute mesoraphidiid amber genera based on non-wing characters

1 Head not rhomboidal; compound eyes shorter, equal, or not much longer than head posterior to eyes; antennae with a low number of flagellomeres (≤ 26) **2**

– Head rhomboidal; compound eyes longer than head posterior to eyes; antennae very elongate, with a high number of flagellomeres (≥ 38) **5**

2 Head ovoid; compound eyes shorter or equal than head posterior to eyes; antennae with less than 26 flagellomeres **3**

– Head quadrangular; compound eyes slightly longer than head posterior to eyes;antennae with 26 flagellomeres .... ***Cantabroraphidia* Pérez-de la Fuente et al., 2010**

3 Compound eyes not distinctly shorter than head posterior to eyes; ocelli positioned between posterior half of compound eyes **4**

– Compound eyes distinctly shorter than head posterior to eyes; ocelli positioned between anterior half of compound eyes ..... ***Amarantoraphidia* gen. n.**

4 Compound eyes nearly equal than head posterior to eyes; antennae longer than head length; posterior border of head without a collar-like lip .... ***Nanoraphidia* Engel, 2002**

– Compound eyes apparently slightly longer or equal than head posterior to eyes; antennae shorter than head length; posterior border of head with a collar-like lip ..... ***Grimaldiraphidia* Bechly & Wolf-Schwenninger, 2011**

5 Compound eyes two times head posterior to eyes; clypeus short; antennae with around 38 flagellomeres; pronotum longer than head; bilobed extensions of third tarsomere lacking digitiform processes..... ..... ***Lebanoraphidia* Bechly & Wolf-Schwenninger, 2011**

– Compound eyes ca. 1.4 times head posterior to eyes; clypeus especially elongate; antennae with more than 38 flagellomeres; pronotum shorter than head; bilobed extensions of third tarsomere with distal digitiform processes..... ..... ***Alavaraphidia* gen. n.**

Discussion

Taxonomy

Recently, Bechly and Wolf-Schwenninger (2011) transferred several species of *Mesoraphidia* to the genus *Grimaldiraphidia*. Based on their study, these transfers were made to eliminate the putative paraphyly of *Mesoraphidia*, and the referred species were claimed to share the synapomorphic characters the authors used for their tribe Nanoraphidiini Bechly and Wolf-Schwenninger, 2011 (although recognition of this tribe leaves the remainder of their Mesoraphidiinae paraphyletic), i.e, "Rs distally unbranched or only with single apical fork, [ptero]stigma very long, postorbital margin region of head shortened, ovipositor short and conspicuosly strong (?), minute size of body and wings". While at least those few wing characters are correct for the combinations *G. mitchelli*, *G. parvula*, and *G. purbeckensis*, the transference of *M. durlstonensis* Jepson, Coram and Jarzembowski, 2009 and *M. heteroneura* Ren, 1997 to *Grimaldiraphidia* is in stark contradiction with some of these, as the holotype of *M. durlstonensis* has a forewing 10.6 long (Jepson et al. 2009), whereas *M. heteroneura* has a forewing with Rs forked twice and 10.5 long (Ren 1997). Moreover, the combination *Yanoraphidia gaoi* Ren in Ren et al., 1995 was restored in Pérez-de la Fuente et al. (2010) (it was previously transferred to *Mesoraphidia* by Engel in 2002) based on the distinctive pterostigma that goes up to the apex of R. By this reasoning, the transfer of this species by Bechly and Wolf-Schwenninger (2011) from the genus *Mesoraphidia* to the genus *Grimaldiraphidia* is not valid nor necessary. Accordingly, we formally return *M. gaoi* to *Yanoraphidia* (as done by Pérez-de la Fuente et al. 2010), and *G. durlstonensis* and *G. heteroneura* to *Mesoraphidia*, restoring the combinations *Yanoraphidia gaoi* Ren in Ren et al., 1995 stat. rest., *Mesoraphidia durlstonensis* Jepson, Coram and Jarzembowski, 2009 stat. rest., and *Mesoraphidia heteroneura* Ren, 1997 stat. rest. While we acknowledge that these last two species should perhaps be placed in a new genus on their own, if the criteria of Bechly and Wolf-Schwenniger (2011) were followed, herein we prefer to take a conservative stance as the genus *Mesoraphidia* is in need of serious revision and further subdivision or changes should be done in the context of such a comprehensive study.

Xylophilous mesoraphiidids

Seven larval mesoraphidiids have been described up to now from five Cretaceous amber localities around the world (Table 2). This circumstance contrasts with the lack

of larval records as compressions, mostly due to the decreased fidelity of preservation of the soft body tissues in such deposits. Taking into account that the larval record of the remainder of holometabolous orders is similarly not that abundant in Cretaceous ambers, the relatively high number of larval mesoraphidiids most likely indicates that at least some, if not all, were corticolous, i.e., they lived under bark, as is well known in extant snakeflies (Aspöck 2002). Therefore, one would expect that this ecological proximity to the resin sources, in addition to their active predatory behaviour, would have greatly increased the chances of larval mesoraphidiids to become embedded in resin. This inference is reinforced by the ovipositor structure in *Amarantoraphidia ventolina* sp. n. and *Alavaraphidia imperterrita* sp. n. Both show a dense annulation along the entire ovipositor (Fig. 7C), as occurs in Recent snakeflies (Mickoleit 1973), and which is an adaptation suitable for laying eggs deep inside irregular surfaces such as bark crevices. Today, whereas all known larval Inocellidae are corticolous, a significant number of Raphidiidae are terricolous as immatures, living in superficial layers of soil or detritus at the base of trees or shrubs (Aspöck 2002). The fact that the adult holotypes of *Cantabroraphidia marcanoi*, *Necroraphidia arcuata* sp. n., and *A. ventolina* have associated timber debris as syninclusions (especially abundant in the amber piece containing *C. marcanoi*, Fig. 12), most likely indicates xylophilous activity.

Uniqueness of the Spanish amber snakefly fauna

Like many moderate- to large-sized insects, snakeflies are difficult to find as amber inclusions, particularly complete specimens in Cretaceous ambers. It is not surprising that those individuals recovered as complete, or relatively complete, inclusions are among the smallest members of the order. Nonetheless, immatures and fragments of much larger snakefly species are also found as amber inclusions as evidenced by the rich Spanish fauna. What is more curious is that among the more abundant Cretaceous amber sources such as Lebanon, Myanmar, New Jersey, and Canada, the reported snakeflies remain relative rarities (Table 2; Engel pers. obs.), and the fragmentary remains of numerous, sometimes larger, species that are observed in the Spanish deposits are not seen in these other outcrops. Why should the Iberian fauna be so particularly rich? It is similarly enigmatic that as of yet the younger French ambers (late Albian to Cenomanian), with the exception of two larval head capsules from the late Albian Archingeay - Les Nouillers outcrop in southwestern France (Perrichot and Engel 2007), have not yielded significant raphidiopteran specimens despite the close geographic proximity of the sources. This dramatic faunal difference is seen in other groups. For example, ants are relatively diverse in French amber, but entirely absent in Spanish amber, while stigmaphronid wasps are most diverse in Spanish amber but missing from the deposits of France (Ortega-Blanco et al. 2011). These faunal singularities might have been caused by the insularity that the Iberian Plate had from the Early Jurassic to the Late Cretaceous (see Blakey 2011). However, whether these contrasting faunas are just a result of localized environmental differences or the younger age of the French deposits is not

entirely clear. The difference in age is not that great and given the similarities in some of the ant taxa between French and Burmese ambers, it is peculiar that there should not be greater similarity between the French and Spanish amber faunas. Furthermore, the amber of Archingeay - Les Nouillers, which is the richest French amber deposit from the Cretaceous, seems to be sampling a more litter fauna (Perrichot 2004), so it is plausible that in that particular case these observed faunal differences, to a greater or lesser extent, could be taphonomic in origin.

However, another hypothesis could explain the high abundance/diversity of snakeflies in Spanish amber, apart from its insularity. Perhaps this abundance is partly owing to the common occurrence of wildfires in the Spanish amber environment, inferred from evidence at several Spanish amber localities (see Najarro et al. 2010). The evidence of abundant charcoal associated with the Spanish ambers, the abundant amber masses with charcoalified plant fibers as inclusions (e.g., Fig. 4A), and the presence of gleicheniacean ferns remains, the last of which are primary succession pioneers following wildfires. After wildfires, there is abundant timber available for xylophagous or xylophilous insects, and resin production among surviving trees is greatly increased (e.g., Grimaldi 2000, Moretti et al. 2006, McKellar et al. 2011, Santolamazza-Carbone et al. 2011). As has been pointed out above, it seems most likely that mesoraphidiids had a xylophilous biology, adults laying their eggs under or in bark crevices (including dead timber), and both immatures and adults assuredly predators of xylophagous or xylophilous arthropods (analogous to living species which predate tree or shrub inhabiting insects). Thus, the combination of a xylophilous biology of adult and immature snakeflies and periodic wildfires might together result in greater resources for these species and at the same time a higher probability of them becoming ensnared in the increased resin flows. *Necroraphidia arcuata* and *Amarantoraphidia ventolina* are actually preserved with charcoalified plant fibers as syninclusions (see Figs 4A, 7A; Pérez-de la Fuente et al. 2012), highlighting that they were entrapped after an episode of burning. Nevertheless, wildfires seem unable to explain entirely the richness of the Spanish snakefly paleofauna, as these would have also been involved in the origin of the Turonian amber accumulation from New Jersey (Grimaldi et al. 2000).

Conclusions

The discovery of the first amber baissopterid is especially remarkable. Furthermore, the presence of the family in the Iberian territory during the Early Cretaceous completes the remarkable preexisting paleogeographic baissopterid hiatus between the Cretaceous localities from eastern Asia and Brazil.

With the fossils herein described, the Albian amber of Spain currently harbors the greatest abundance and diversity of snakeflies in Cretaceous resins. As is also suggested by other paleoentolomological records, this significant snakefly paleodiversity may reflect a faunistic singularity of the Iberian territory during the Albian perhaps as a consequence of its geographic isolation during the Jurassic and the Cretaceous, or a

combination of this with an environment resulting from episodic wildfires. Wildfires would have increased the availability of dead wood as a substrate for the xylophagous or xylophilous insects to develop, which, in turn, could have aided the increase in the xylophilous, predatory snakefly populations.

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RESEARCH ARTICLE

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First record of the genus *Bankisus* Navás, 1912 in China, with the description of a new species (Neuroptera, Myrmeleontidae)

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Abstract

A new species of *Bankisus* Navás, 1912, (*Bankisus sparsus* **sp. n.**) is described and illustrated with the genus newly recorded from China. A key to species of *Bankisus* is provided.

Keywords

Antlion, Myrmeleontiformia

Introduction

The genus *Bankisus* Navás, 1912 is a small genus of antlions included in the tribe Dendroleontini and occurs in Africa, Yemen and Oman (Stange 2004; Mansell 1985). It is characterized by lack of tibial spurs, long slender legs and hyaline wings with brown markings. Mansell (1985) reviewed the genus and recognized five species: *B. oculatus* Navás, 1912, *B. triguttatus* Navás, 1926, *B. carinifrons* (Esben-Petersen, 1936), *B. elegantulus* (Esben-Petersen, 1936), *B. maculosus* Hölzel, 1983. Recently, Ábrahám (2009) described a sixth species *B. antiatlasensis* from Morocco. Esben-Petersen (1936)

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placed two species (i.e. *B. carinifrons* and *B. elegantulus*) in his new genus *Navasius* which was subsequently synonymized with *Bankisus* by Markl (1954).

We herein describe the new species, *Bankisus sparsus* sp. n., from China. It is the first *Bankisus* species recorded from outside of Africa and its adjacent area (Yemen, Oman).

Material and methods

To examine the terminalia, the apex of the abdomen is treated with 10% KOH solution for five-six hours and then transferred to glycerine for further examination. Photographs of partial morphological characteristics were taken by a Canon® EOS 500D digital camera connected with Olympus® U-CTR30-2 microscope and UV-C (Application Suite) applied software by United Vision Ltd. Photographs of habitus were taken by a Nikon® COOLPIX4500 digital camera. All figures were processed in Adobe Photoshop® CS5. Terminology of wing venation follows Wang *et al.* (2003), while female terminalia terminology follows Stange (1994).

Taxonomy

***Bankisus* Navás, 1912**
http://species-id.net/wiki/Bankisus

Bankisus Navás, 1912: 45. Type species: *B. oculatus,* by original designation.
Navasius Esben-Petersen, 1936: 202. Synonymized by Markl, 1954: 221.

Diagnosis. Pronotum longer than broad. Wings hyaline with brown marks; Rs arises before CuA fork and three presectoral crossveins before origin of Rs in forewing. Lack of tibial spurs, long slender legs. Female anterior gonapophysis oval or absent.

Distribution. Africa, Oman, Yemen, China.

Key to species of *Bankisus*

1 Forewing 2A and 3A run parallel to each along length **2**
– Forewing 2A and 3A gradually approximate distally along length **4**
2 Anterior Banksian line distinct in both wings **3**
– Anterior Banksian line barely discernable in forewing, hindwing without anterior Banksian line ..... ***B. maculosus***
3 Female anterior gonapophysis absent, forewing with few large spots ..... ***B. carinifrons***
– Female anterior gonapophysis short with dense long brown setae, forewing with many small spots..... ***B. sparsus* sp. n.**
4 Thoracic tergites yellowish **5**

– Thoracic tergites reddish brown **6**
5 The spot proximal to hypostigmatic cell extending to costal area hindwing... ..... ***B. oculatus***
– The spot proximal to hypostigmatic cell small, not extending to costal area in hindwing ..... ***B. antiatlasensis***
6 Vertex reddish brown with a row of spots, forewing not much broader than hindwing ..... ***B. elegantulus***
– Vertex without a row of spots, hindwiwng much narrower than forewing..... ..... ***B. triguttatus***

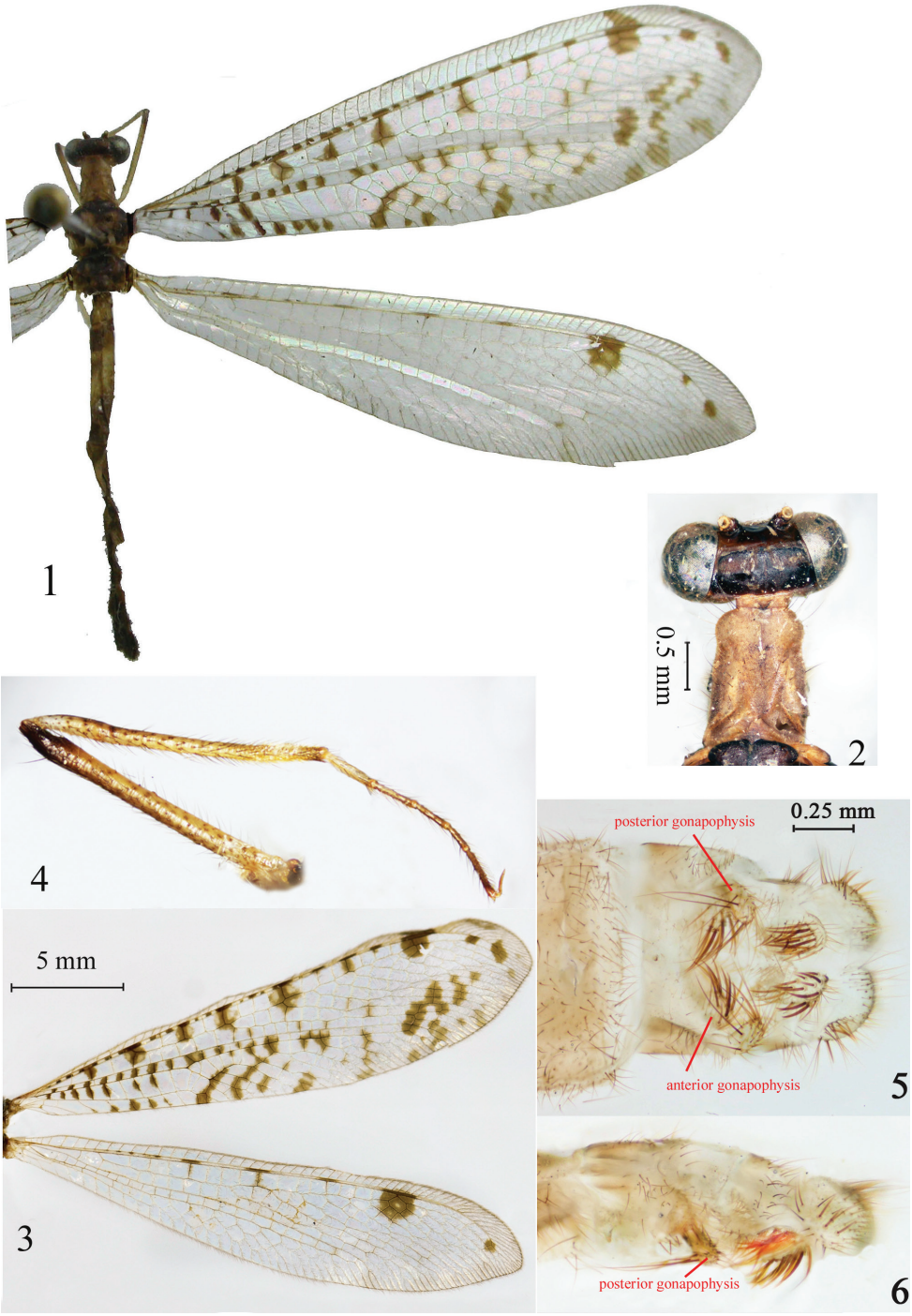
***Bankisus sparsus* sp. n.**
urn:lsid:zoobank.org:act:804E5172-AE3C-4B80-94E5-D7C1CF79852C
http://species-id.net/wiki/Bankisus_sparsus
Figure 1

Diagnosis. Pronotum yellowish, longer than broad. Wings hyaline with many brown marks, forewing with three presectoral crossveins before origin of Rs, about eight to ten branches of Rs; several discontinuous spots in subcostal area. In hindwing Rs arises before CuA fork, one presectoral crossvein before origin of Rs. Long slender legs, tibial spurs absent. Female terminalia: posterior gonapophysis developed with dense long brown setae; anterior gonapophysis short with dense long brown setae. Lateral gonapophysis developed with dense digging setae.

Material examined. Holotype, ♀, China, Guangxi Province, Xiangzhou (23°58.6'N, 109°42.3'E). IX-1980, Fashen Li leg. (CAU-N100208); **Paratype**, sex unknown (abdomen missing), Guangxi Province, Ningming, 180m, (22°07.2'N; 107°04.6'E). 24-V-1984, Fashen Li leg. (CAU-N100209)

The type specimens examined are deposited in the Insect Collections of China Agricultural University (ICCAU), Beijing, China.

Head (Fig. 2)**:** clypeus yellowish; labrum, maxillary and labial palpi yellow; compound eye dark with several black spots, antenna clavate, scape black; vertex inflated, dark with brown spots. ***Thorax*:** pronotum yellowish with several long setae, longer than broad; mesothorax and metathorax black with sparse white long setae. ***Wings*** (Fig. 3)**:** hyaline with many brown marks**,** with several disconnected spots in subcostal area in forewing, Rs arises before CuA fork, three presectoral crossveins and one spot before origin of Rs, about eight branches to Rs, sixteen cross-veins and five spots from origin of Rs to hypostigmatic cell; large brown spot in stigma area; anterior Banksian line discernible and without posterior Banksian lines; ten cross-veins in prefork area. 2A and 3A in the forewings run parallel to each other; a brown oblique stripe in rhegma area and anastomosis of CuA and CuP+1A; hindwing costal area is narrow, Rs arises before CuA fork, one presectoral crossvein before origin of Rs, about eight branches to Rs; anterior Banksian line discernible and without posterior Banksian line; a round spot proximal to hypostigmatic area. ***Legs*** (Fig. 4)**:** long and slender, yellow with black spots and dense



Figures 1–6. *Bankisus sparsus* sp.n. **1**. Habitus **2** Head and pronotum, dorsal view **3** Wings (Paratype) **4** Foreleg **5–6** Female *terminalia*, ventral and lateral view.

setae; claws bent back, sometimes straight. Foreleg: femur yellow brown with white and black bristles, distal part dark; tibia yellowish with dense setae. Tarsus yellow brown except the distal part dark; the first tarsomere long, the fifth slightly shorter; claws bent back; midleg with slightly expanded tibia and claws sometimes straight; hindleg similar to foreleg. ***Abdomen*:** shorter than hindwing, with yellow and black alternate banding. ***Female terminalia*** (Fig. 5-6)**:** ectoproct narrow with dense long setae; anterior gonapophysis short with dense long brown setae; posterior gonapophysis developed with dense long brown setae; lateral gonapophysis with dense digging setae.

Distribution. China (Guangxi Province).

Remarks. *Bankisus sparsus* sp.n. is similar to *B. maculosus* in appearance; however, it can be separated by following characters: forewing with several disconnected spots in subcostal area (*B. maculosus*: without several disconnected spots in subcostal area.); hindwing without spots except two spots at both side of hypostigmatic cell (*B. maculosus*: hindwing with several big spots at apical area).

Etymology. The species name is derived from the Latin *sparsus*, sprinkle; referring to the small spots in forewings.

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DATA PAPER

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Antarctic, Sub-Antarctic and cold temperate echinoid database

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Abstract

This database includes spatial data of Antarctic, Sub-Antarctic and cold temperate echinoid distribution (Echinodermata: Echinoidea) collected during many oceanographic campaigns led in the Southern Hemisphere from 1872 to 2010. The dataset lists occurrence data of echinoid distribution south of 35°S latitude, together with information on taxonomy (from species to genus level), sampling sources (cruise ID, sampling dates, ship names) and sampling sites (geographic coordinates and depth). Echinoid occurrence data were compiled from the Antarctic Echinoid Database (David et al. 2005a), which integrates records from oceanographic cruises led in the Southern Ocean until 2003. This database has been upgraded to take into account data from oceanographic cruises led after 2003. The dataset now reaches a total of 6160 occurrence data that have been checked for systematics reliability and consistency. It constitutes today the most complete database on Antarctic and Sub-Antarctic echinoids.

Keywords

Southern Ocean, echinoids, Antarctic species, Sub-Antarctic species, cold temperate species

Project details

Project title: Macroecology of Southern Ocean echinoids: Distribution, Biogeography and Ecological Niche Modelling.

Personnel: Pierrat Benjamin (collection identifier, data collector, data manager, data publisher), Saucede Thomas (collection identifier, data collector), Alain Festeau (computer specialist), David Bruno (collection identifier, general manager).

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Study area descriptions / descriptor. The study area covers the Southern Ocean, Sub-Antarctic and cold temperate areas, from the Antarctic continent to 35°S latitude. The aim of the project was to constitute the most complete and consistent echinoid dataset for the Southern Ocean, a vast ocean area that is known for suffering from under-sampling (Griffiths 2010), especially in sectors of East Antarctica, Amundsen and Bellingshausen Seas. The dataset latitudinal range (< 35°S) allows determining possible faunal connections between Antarctic seas and adjacent areas of South America, New Zealand and South Australia.

Design description: This dataset was developed to determine the current distribution patterns of Antarctic and Sub-Antarctic echinoid species at the scale of the whole Southern Ocean and to highlight the forcing factors that may control them. The ecological niche modelling (ENM) of 19 echinoid species showed that distribution is mainly structured according to two patterns: (1) a first one represented by species that are not limited to the south of the Polar Front and distributed from the Antarctic coasts to the Sub-Antarctic and cold temperate areas, and (2) a second one with species restricted to the Antarctic area.

In addition, a similarity analysis of echinoid fauna between bioregions of the Southern Ocean was performed at species and genus levels. The analysis reveals faunal connections between southern South America and Sub-Antarctic areas, interpreted as a result of echinoid paleobiogeographic and evolutionary history. Trans-Antarctic faunal connections were also demonstrated and interpreted as a result of West Antarctic Ice Sheet collapses and setting up of trans-Antarctic seaways during the Pleistocene.

Among the environmental parameters that may control echinoid distribution, three parameters seem to be the main forcing factors of echinoid distribution: depth, sea-ice cover and sea surface temperature. However, the respective contributions of these parameters vary among species. Differences are particularly emphasized in the case study of the genus *Sterechinus*, *S. neumayeri* being the species the most dependent on environmental conditions that prevail along the Antarctic coasts (sea surface temperature and sea-ice cover), while *S. antarcticus* does not seem to be so much under the control of these parameters. However, *S. antarcticus* is not present over the whole area of its potential distribution, what can be explained as the result of either (1) oceanographic factors (role of the Polar Front as a biogeographic barrier), (2) biotic interactions (inter-specific competition) or (3) temporal contingencies (ongoing range expansion).

Taxonomic coverage

General taxonomic coverage description: This database is devoted to all echinoid species inhabiting ocean areas south of 35S latitude (Echinodermata: Echinoidea). Echinoids are well represented in the Antarctic benthic communities in terms of frequency, abundance and species richness. They are frequently collected both at shallow depths

over the continental shelf and in deeper waters of the continental slope and ocean basins. With 82 species ever described that represent about 10% of echinoid species worldwide, the Southern Ocean is particularly rich in echinoid species. The Antarctic echinoid fauna is characterised by a relative high morphological diversity and high rate of endemism (66% of species - David et al. 2005b). It should be noticed that Antarctic echinoid diversity is represented by a few orders (7) among which the two orders Spatangoida and Cidaroida include 64.6% of Antarctic species. As a comparison, South Australian and New Zealand areas comprise 113 echinoid species, 62 genera and 12 orders, while southern South America only 36 species, 23 genera and 8 orders, and the Southern Ocean 82 species, 30 genera and 7 orders. Identifications and taxonomic accuracies were based on Mortensen (1928, 1935, 1943, 1950, 1951) and David et al. (2005b).

Taxonomic ranks

Kingdom: Animalia
Phylum: Echinodermata
Class: Echinoidea
Order: Arbacioida, Cassiduloida, Cidaroida, Clypeasteroida, Echinoida, Echinothurioida, Holasteroida, Pedinoida, Salenoida, Spatangoida, Temnopleuroida.
Family: Apatopygidae, Arachnoididae, Arbaciidae, Aspidodiadematidae, Asterostomatidae, Brissidae, Cidaridae, Clypeasteridae, Diadematidae, Echinidae, Echinolampadidae, Echinometridae, Echinothuriidae, Fibulariidae, Hemiasteridae, Laganidae, Loveniidae, Mellitidae, Palaeotropidae, Pedinidae, Phormosomatidae, Plexechinidae, Pourtalesiidae, Saleniidae, Schizasteridae, Spatangidae, Temnopleuridae, Toxopneustidae, Urechinidae.

Spatial coverage

General spatial coverage: The sampling area ranges from 35°S to 71°S latitude and from 180°W to 180°E longitude. The 35°S limit is coincident with the position of the Subtropical Convergence (Tchernia 1980; Knox 1983), which is considered to determine the limit between tropical and cold temperate marine species. The latter species were considered in the database, as they are likely to interact with Antarctic species in the future according to scenarii of forthcoming global climate change or to have interacted with them in the past.

Coordinates: 71°0'0"S and 35°0'0"S Latitude; 180°0'0"W and 180°0'0"E Longitude.

Temporal coverage

1872–2010.

Natural collections description

Parent collection identifier: Pierrat Benjamin, David Bruno, Saucede Thomas
Collection name: Antarctic, Sub-Antarctic and cold temperate echinoid database
Collection identifier: Pierrat Benjamin, David Bruno, Saucede Thomas
Specimen preservation method: Alcohol

Methods

Method step description: see sampling description above.

Study extent description: The study area includes the Antarctic, Sub-Antarctic and cold temperate regions. Five regions are particularly focussed on: (1) the Southern Ocean with the Antarctic Peninsula, the South Orkney Island, the Weddell Sea, Dronning Maud Land, Enderby Land, the Mawson Sea, Adelie Land, the Ross Sea, the Amundsen Sea and the Bellingshausen Sea, (2) the Sub-Antarctic Islands composed of Prince Edward, Crozet, Bouvet, Kerguelen and Heard Islands, (3) the South American coast, with the Argentinean coast, the Clilean coast and the Falkand Island, (4) the New Zealand coast and (5) the South Australian coast inclusive of Tasman coast.

Sampling description: Echinoids were collected during oceanographic cruises led in the Southern Ocean from 1872 to 2003. The database has been upgraded with data collected from 2003 to 2010. Sample depth ranges go from the shoreline to the deep sea. Sampling was performed with different protocols and different gears, specific to each cruise (Agassiz Trawl, Box Core, Beam Trawl, Epibenthic Sledge…). Each echinoid sample was separated at sea from other specimens of the macrofauna, then identified and fixed in formaldehyde for old samples, in 100% ethanol for recent ones.

Quality control description: Systematics reliability and consistency have been checked for by Bruno David, Thomas Saucède and Benjamin Pierrat, identification being based on species descriptions produced by Mortensen (1928, 1935, 1943, 1950, 1951) for Australian, New Zealand and South American species, on *Synopses of the Antarctic benthos* by David et al. (2005a) for Antarctic species.

Data resources: The data underpinning analyses of the paper are deposited at GBIF, the Global Biodiversity Information Facility, http://ipt.biodiversity.aq/resource.do?r=antarctic_subantarctic_and_cold_temperate_echinoid_database

Datasets

Dataset description: Our knowledge on Antarctic echinoids have been synthesized by David et al. (2005a) and led to constituting a first database: *Antarctic echinoids: an interactive database* (David et al. 2005b). This database listed echinoid samples collected during Antarctic cruises led before 2003 and counted 2029 occurrence records that ranged from 70°S to 45°S latitude. Research data to upgrade this first da-

tabase focused on different regions: (1) The Southern Ocean with samples collected during Antarctic cruises led after 2003, allowing the densification of data for under-sampled areas such as the eastern coast of Antarctica, the Bellingshausen and the Amundsen Seas (Griffiths 2010); (2) South America, with samples from Argentinian cruises housed at the Museo Argentino de Ciencas Naturales (Buenos Aires-ARG); (3) New Zealand and South Australia with samples from different collections (Australian Museum, Sydney, AUS; Melbourne Museum, Melbourne, AUS and NIWA, Wellington, NZ). Systematics has been checked for following Mortensen (1928, 1935, 1943, 1950, 1951) for Australian, New Zealand and South American species, and the *Synopses of the Antarctic benthos* by David et al. (2005a) for Antarctic species. All data are georeferenced (WGS1984).

Object name: Darwin Core Archive Antarctic, Sub-Antarctic and cold temperate echinoid database
Character encoding: UTF-8
Format name: Darwin Core Archive format
Format version: 1.0
Distribution: http://ipt.biodiversity.aq/resource.do?r=antarctic_subantarctic_and_cold_temperate_echinoid_database
Publication date of data: 2012-03-26
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RESEARCH ARTICLE

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Review of the *Eospilarctia yuennanica* group (Lepidoptera, Erebidae, Arctiinae) from the Indo – Himalayan region, with description of two new species and one subspecies

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Abstract

Two new *Eospilarctia* species and one new subspecies from China, Myanmar and Vietnam, respectively, are described. Superficially the new species *Eospilarctia maciai* **sp. n.**, *Eospilarctia naumanni* **sp. n.** and *Eospilarctia yuennanica fansipana* **ssp. n.** resemble related congeners but they can be distinguished by the differences in wing pattern, genitalia and distribution provided. *Eospilarctia yuennanica guangdonga* Dubatolov, Kishida & Wang, 2008 is upgraded to species level. A checklist of the genus *Eospilarctia* and a key to the *Eospilarctia yuennanica* (Daniel, 1943) species-group, based on external characters and male genitalia, is presented.

Keywords

Arctiinae, new species, new subspecies, China, Myanmar, Vietnam

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Introduction

The genus *Eospilarctia* Kôda, 1988 contains 13 species and two subspecies mainly distributed in China (ten species), Taiwan, Japan and Vietnam. All species of genus *Eospilarctia* have typical wings patterns concist from longitudinal white or yellowish streaks. Identification of species is available by compare genital structures of similar species. Comparisons of the genitalic structures of specimens found in the Zoologische Staatssammlung der Bayerischen Staaten (Munich, Germany)/Museum of Thomas Witt with *E. yuennanica* – cotype led to the description of the new species and subspecies.

Materials and methods

We examined specimens of *Eospilarctia* Kôda preserved in the Zoologische Staatssammlung der Bayerischen Staaten, Munich, Germany (ZSM) and the Museum of Thomas Witt (MWM). Examined specimens were collected in China, Myanmar and Vietnam using ultraviolet light traps. 31 genital slides were prepared and 124 photos were made. Reference to relevant literature (Freina de 1999, Fang 2000, Dubatolov, Kishida and Wang 2008; Dubatolov 2010) and consultation with expert taxonomists in addition to numerous genitalia dissections were used to resolve the taxonomy of *Eospilarctia yuennanica* species group.

Examination of morphology: after maceration, male and female genitalia were dissected and mounted in euparal on glass side. The abdominal integument was cut lengthwise, descaled, and mounted on the slide, dissection of genitalia follows Lafontaine (2004). Photos of genitalia where made using microscope Nikon SMZ745T and camera Moticam 2500.

Systematic accounts

Genus *Eospilarctia* Kôda, 1988
http://species-id.net/wiki/Eospilarctia

Eospilarctia Kôda, 1988. *Tyô to ga Zoologist* 39 (1): 39–45

Type species: *Seiarctia lewisii* Butler, 1885, by original designation.

Genus characteristic. Species of this genus typically have a medium wingspan, long bipectinate antennae, a red patagium, a narrow red abdomen, yellow tegulae, white or yellow longitudinal fascia transversing brown forewings, pale white or yellow-white hindwings with various sized brown spots in terminal and discal areas.

Male genitalia. Uncus massive, wide base abruptly narrowing at the tip; tegumen medium size; gnathos reduced; valvae simple with even edges but concave, rough or

rounded at the apex; juxta wide with wide excision; saccus short, semioval form; aedeagus straight, longer than valvae; vesica multiplex.

Female genitalia. Papilla analis massive; apophysis posterioris approximately 2.5 times shorter than apophysis anterioris; ductus short; bursa bisaccate, rounded, without signum.

Distribution. Fourteen species of *Eospilarctia* are distributed in China, Myanmar, Vietnam, Taiwan and Japan.

Key to *Eospilarctia* species related to *Eospilarctia yuennanica yuennanica* (Daniel, 1943) based on external characters

1 Forewings costal streak wide (Plate 1: fig. 3) **2**
– Forewings costal streak narrow (Plate 1: figs 1, 2, 4–6) **3**
2 Forewings costal streak extending from base to apical streak; postmedian streak short directed to costa (Dubatolov et al. 2008, fig. 7, p. 134)..... ..... ***E. guangdonga* (China: Guangdong)**
– Forewings costal streak extending from base to beginning, base of radial vein; postmedian streak short directed to termen (Plate 1: fig. 3)..... ..... ***E. yuennanica fansipana* ssp. n. (Vietnam: Fan-si-pan)**
3 Forewings pale light brown ... ***E. yuennanica yuennanica* (China: Sichuan)**
– Forewings highly contrasted (Plate 1: figs 4, 5) **4**
4 Forewings costal streak extending from base to apical streak (Plate1: fig. 5) .. .. ***E. naumanni* sp. n. (Myanmar: Kachin)**
– Forewings costal streak extending from base to beginning, base of radial vein (Plate 1: fig. 4) ..... ***E. maciai* sp. n. (China: Yunnan)**

Key to species *Eospilarctia* related to *Eospilarctia yuennanica yuennanica* (Daniel, 1943) based on male genital characters

1 Valva serrate at apex **2**
– Valva rounded or with one excavation at apex (Plate 2: figs 7, 8, 10, 11) **3**
2 Apical diverticulum of vesica near long as wide; subbasal diverticulum straight (Plate 2: fig. 3) ..... ***E. yuennanica yuennanica***
– Apical diverticulum of vesica narrow, about three time long as wide; subbasal diverticulum foot-shaped (Plate 2: fig. 6) .. ***E. yuennanica fansipana* ssp. n.**
3 Uncus two times longer than width (Plate 2: figs 7, 8; Plate 6: figs1, 2) .... ***E. maciai* sp. n.**
– Uncus same length as width (Plate2: figs 10, 11) **4**
4 Apex of valva deeply excavated; uncus cruciform Dubatolov et al. 2008, fig. 21, p. 136 ..... ***E. guangdonga***
– Apex of valva diagonally cuted, slightly sagged; uncus bulb-shaped (Plate 2: figs 10, 11; Plate 7: figs 1, 2) ..... ***E. naumanni* sp. n.**

Description of new taxa

***Eospilarctia yuennanica fansipana* ssp. n.**
urn:lsid:zoobank.org:act:C97E1B9C-F2DF-4329-9243-0143C22C99D6
http://species-id.net/wiki/Eospilarctia_yuennanica_fansipana
Plate 1: fig. 3, Plate 2: figs 4–6, Plate 5: figs 1–5

Type material. Holotype: male (Plate 1: fig. 3), northern Vietnam, Mt. Fan-si-pan, 1600-1800 m near Chapa 22°20"N, 103°40"E. Secondary forest, May 1995, leg. local collectors ex coll. A. Schintlmeister (slide No.OP1227), (deposited in ZSM/MWM).

Paratype: male, northern Vietnam, Mt. Fan-si-pan, Chapa, 1700 m NN (22°15"N, 103°46"E), June 1994, leg. Sinjaev & Einheim. Sammler (slide No.OP1226), (deposited in ZSM/MWM).

Diagnosis. The new subspecies is larger than other *Eospilarctia* species and nominate *E. yuennanica yuennanica* (Plates 3, 4). The pale yellow fascia of the forewings are much wider than in the nominate subspecies. Costal fascia of *E. yuennanica fansipana* ssp. n. extend to the middle of discal cell and the basal fascia ends in a sharp diagonal tip. *E. yuennanica yuennanica* is smaller (cotype forewing 28 mm, wingspan 59mm), forewing markings are similar except that the fascia are much narrower. In the male genitalia the valvae widen without a dorsal excision at apex; juxta with big lateral protrusions, subbasal diverticulum of the vesica has a simple mammilla form; median diverticulum is gently curved, wide.

Description. Male: Forewing length of holotype and paratype 33 mm, wingspan 66 mm. Wing pattern typical of genus; forewings' pale yellow fascia very wide; costal fascia reaching middle of medium cell; basal fascia with sharp diagonal tip.

Male genitalia (Plate 2: figs 4–6): valvae of the same type as the nominate subspecies, but dorsal margin near apex with big excision; oval juxta with wide excision at top, lateral arms very short; aedeagus longer than valvae, gently curved; vesica with footshaped subbasal diverticulum; median diverticulum long, narrow, strongly curved with short spines.

Female genitalia: unknown.

Bionomics and distribution. Known only from the Fan-si-pan mountains in far northern Vietnam. Two male specimens were attracted to light at the end of May at elevations ranging from 1600 to 1800 m.

Etymology. The specific name refers to the type-locality of the new subspecies.

***Eospilarctia maciai* sp. n.**
urn:lsid:zoobank.org:act:76553FDF-F6BC-4FC8-9BBC-92843706BAED
http://species-id.net/wiki/Eospilarctia_maciai
Plate 1: fig. 4, Plate 2: figs 7–9, Plate 6: figs 1–5

Holotype. ♂ (Plate 1: fig. 4, Plate 6: fig. 4), China, Yunnan prov. Dali Bai autonomy pref., Yulong county, Fengshuiuiny Mts., 2460 m., 13 km. N. of Coajian, 10–20 May

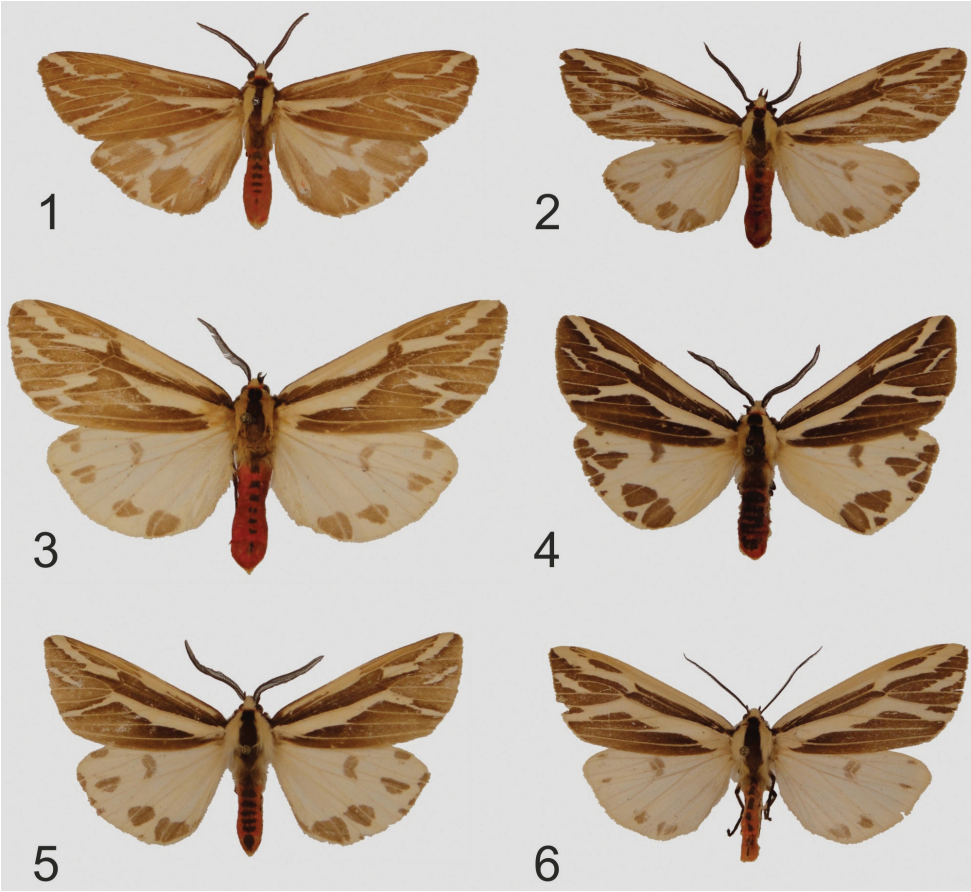

Plate 1, figures 1–6. *Eospilarctia* ssp. adults: **1** *E. yuennanica yuennanica,* ♂, cotype, China, Yunnan ZSM/MWM **2** *E. yuennanica yuennanica,* ♂, China, Yunnan ZSM/MWM **3** *E. yuennanica fansipana,* ♂, holotype, Vietnam, Mt. Fan-si-pan ZSM/MWM **4** *E. maciai,* ♂, holotype, China, Yunnan ZSM/MWM **5** *E. naumanni,* ♂, holotype, Myanmar, Kachin state, ZSM/MWM **6** *E. naumanni,* ♀, paratype, Myanmar, Kachin State ZSM/MWM.

1999, N25°46", E099°06", leg./ex.coll. Dr R. Brechlin (slide No.OP1225m), (deposited in ZSM/MWM).

Diagnosis. Externally the new species is most similar to the sibling species *Eospilarctia guangdonga* Dubatolov, Kishida & Wang, 2008 status n., *Eospilarctia yuennanica yuennanica* (Daniel, 1943) and *Eospilarctia naumanni* sp. n. In *E. guangdonga* (species was recently described and well illustrated (Dubatolov et al 2008)) the wing markings are noticeably paler and in the male genitalia the valvae do not widen at the excavated apex. The forewings of *E. yuennanica yuennanica* have more intensive brown markings, with fascia pale white, and the male valvae widen to rough-edged apex. In *E. naumanni*, the costal fascia from the forewing base do not extend to apex of medial cell. In the male genitalia the valvae are almost the same width as length,

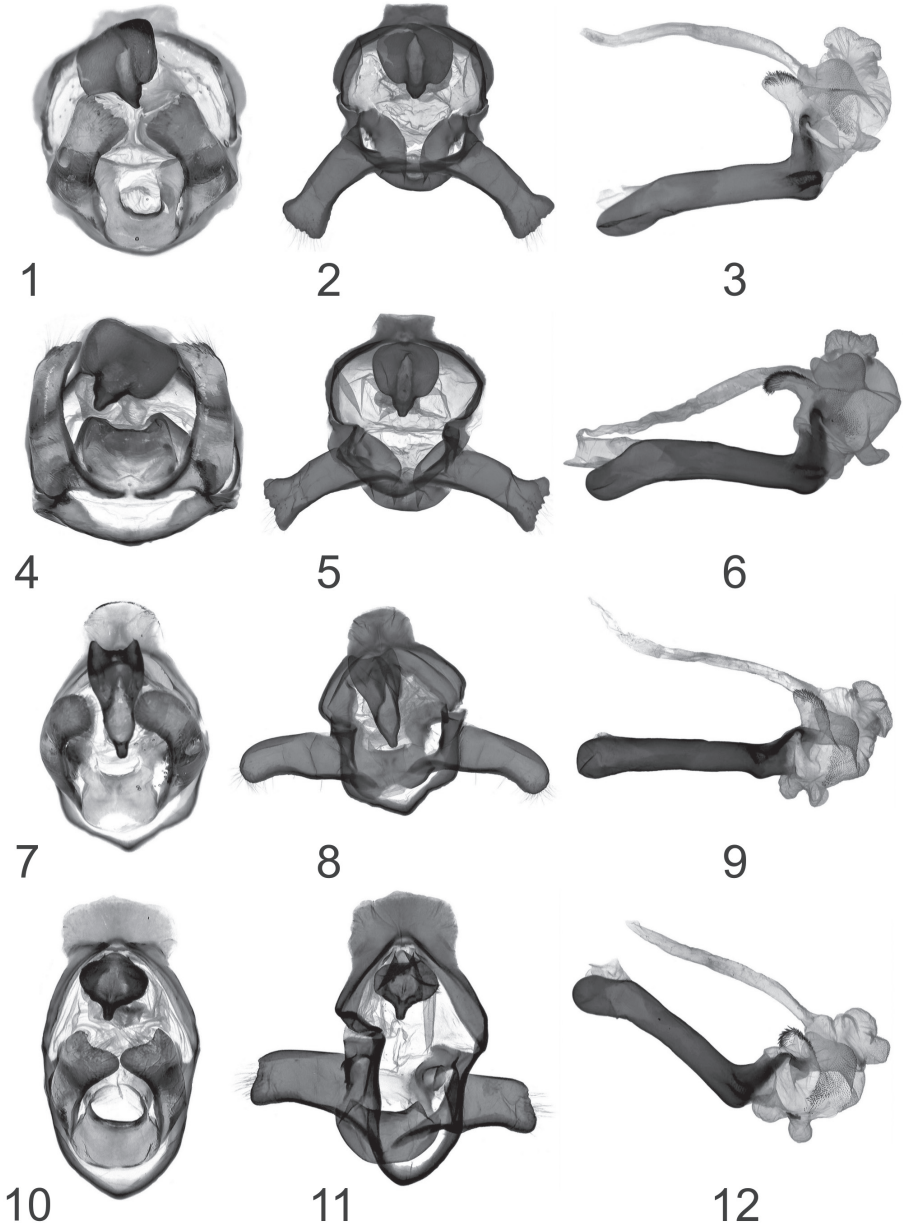

Plate 2, figures 1–12. *Eospilarctia* ssp. ♂ genitalia: **1** *E. yuennanica yuennanica,* ♂, cotype, clasping apparatus, prep. OP1223 **2** *E. yuennanica yuennanica,* ♂, cotype, clasping apparatus with opened valvae **3** *E. yuennanica yuennanica,* ♂, cotype, aedeagus **4** *E. yuennanica fansipana,* ♂, holotype, clasping apparatus, prep. OP1227 **5** *E. yuennanica fansipana,* ♂, holotype, clasping apparatus with opened valvae **6** *E. yuennanica fansipana,* ♂, holotype, aedeagus **7** *E. maciai,* ♂, holotype, clasping apparatus, prep. OP1225 **8** *E. maciai,* ♂, holotype, clasping apparatus with opened valvae **9** *E. maciai,* ♂, holotype, aedeagus **10** *E. naumanni,* ♂, holotype, clasping apparatus, prep. OP1228 **11** *E. naumanni,* ♂, holotype, clasping apparatus with opened valvae **12** *E. naumanni,* ♂, holotype, aedeagus.

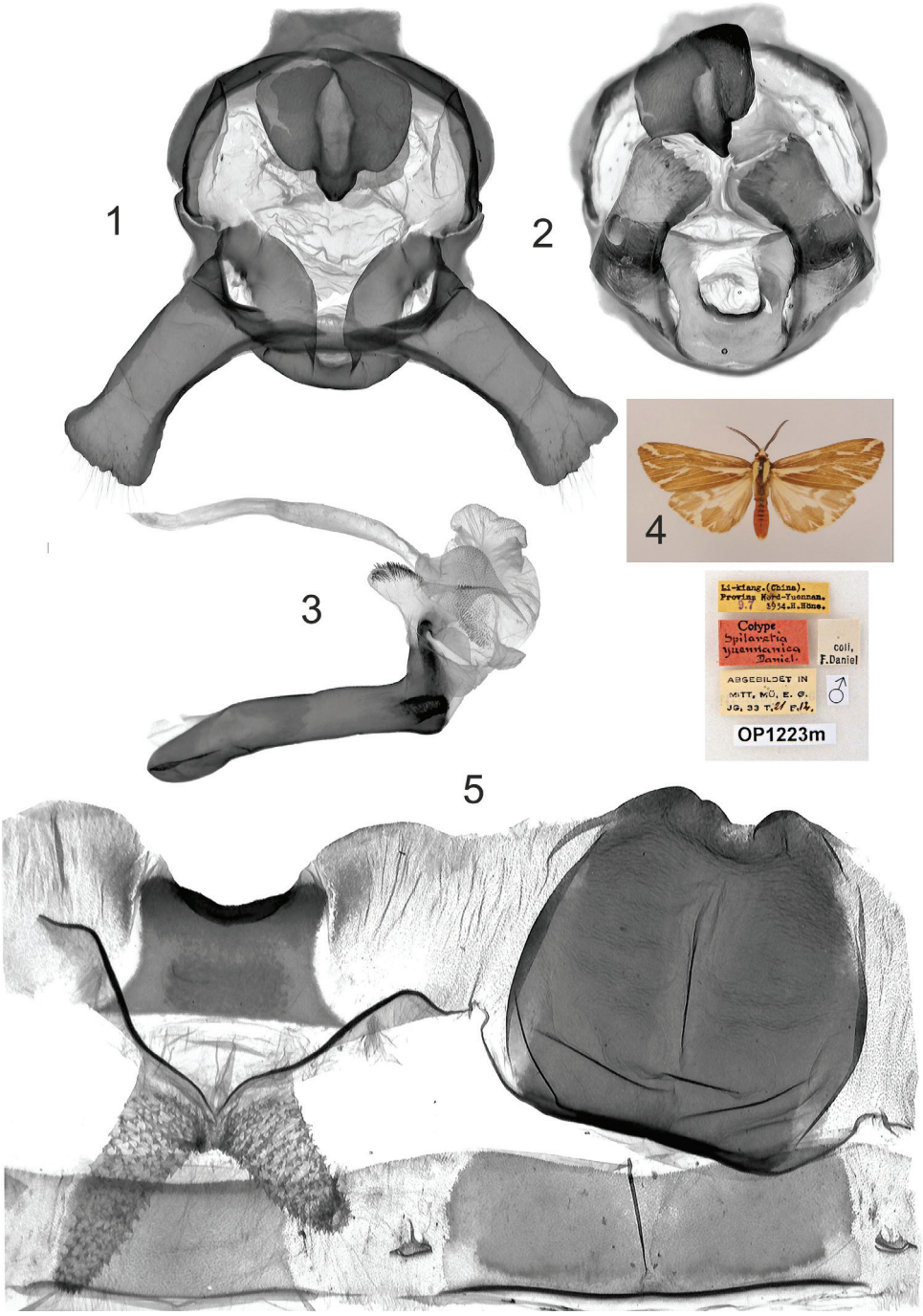

Plate 3, figures 1–5. *Eospilarctia yuennanica yuennanica,* ♂, cotype: **1** Clasping apparatus with opened valvae, prep. OP1223 **2** Clasping apparatus **3** Aedeagus **4** Adult 5 8th abdominal segment.

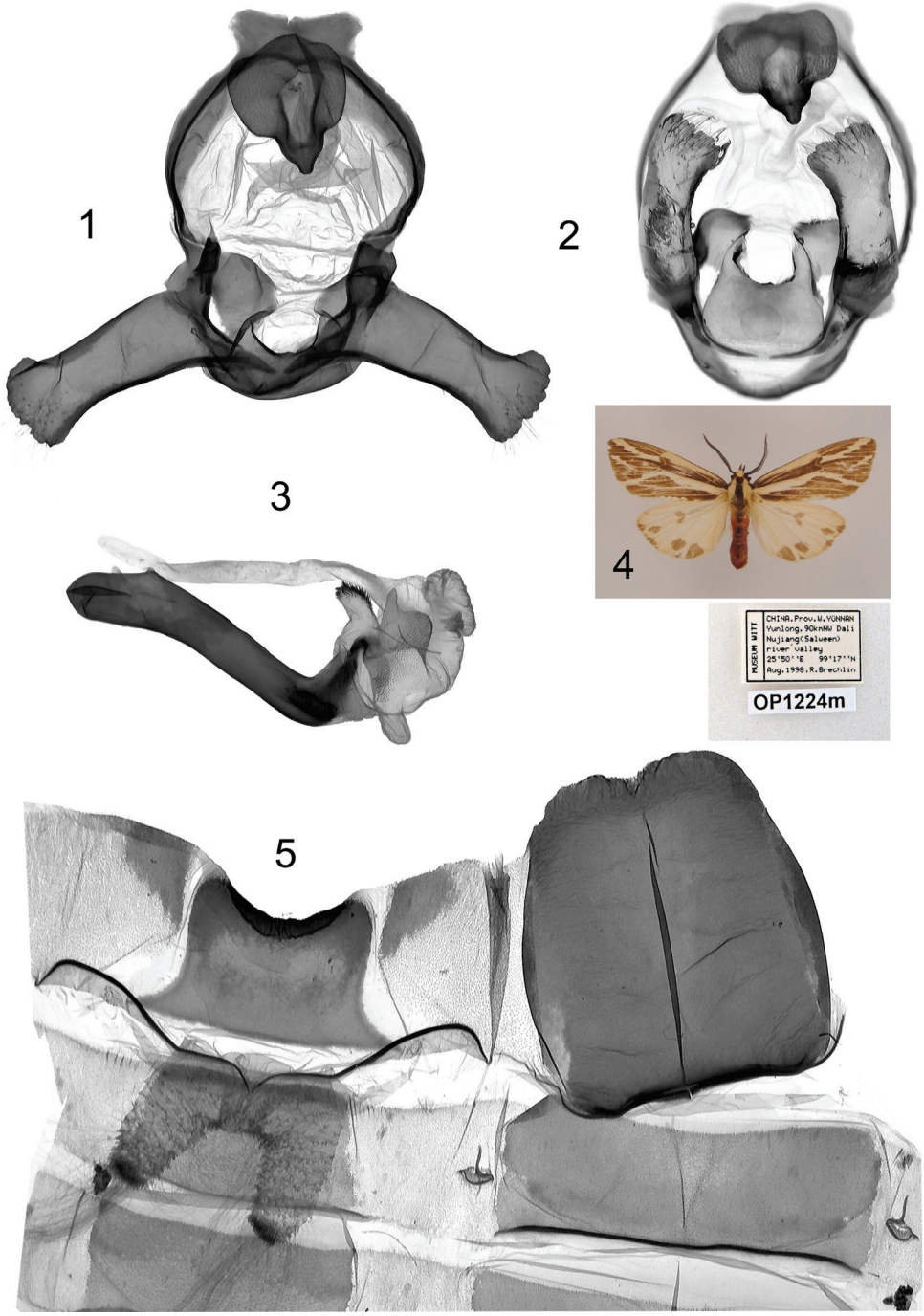

Plate 4, figures 1–5. *Eospilarctia yuennanica yuennanica*, ♂: **1** Clasping apparatus with opened valvae, prep. OP1224 **2** Clasping apparatus **3** Aedeagus **4** Adult **5** 8th abdominal segment.

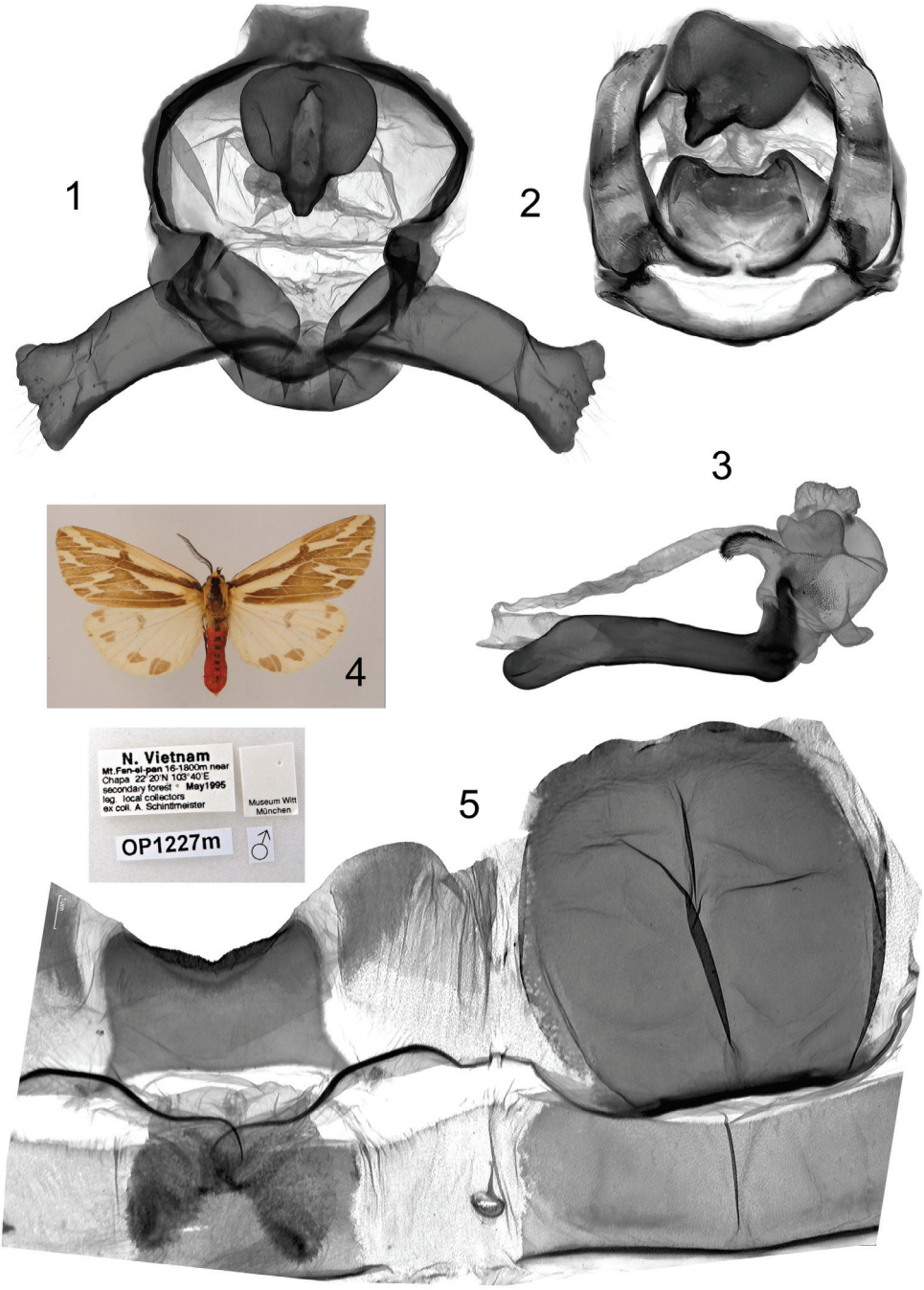

Plate 5, figures 1–5. *Eospilarctia yuennanica fansipana,* ♂, holotype: **1** Clasping apparatus with opened valvae, prep. OP1227 **2** Clasping apparatus **3** Aedeagus **4** Adult **5** 8th abdominal segment.

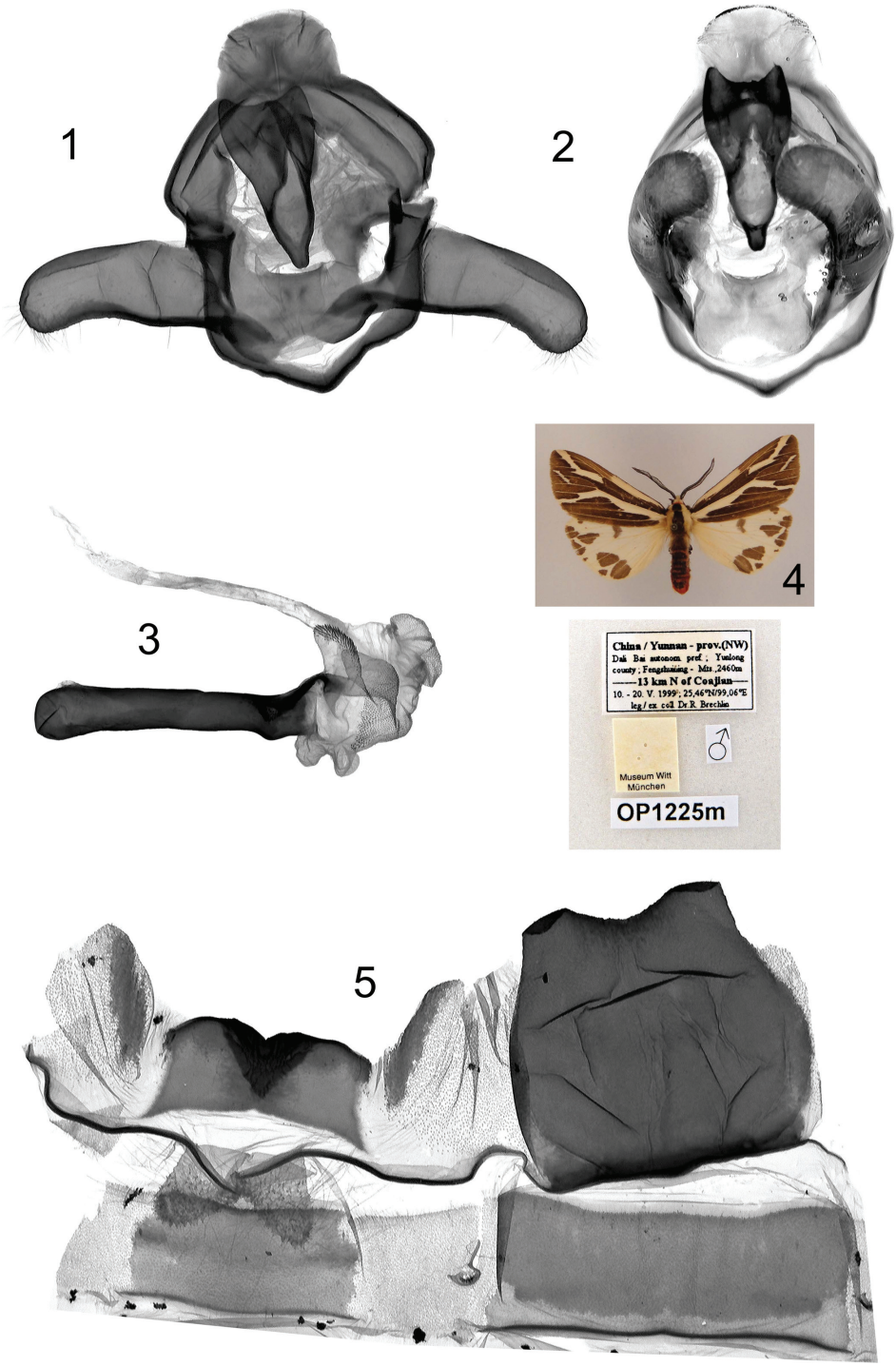

Plate 6, figures 1–5. *Eospilarctia maciai,* ♂, holotype: **1** Clasping apparatus with opened valvae, prep. OP1225 **2** Clasping apparatus **3** Aedeagus **4** Adult **5** 8th abdominal segment.

slightly curved at the middle and wide at tip; saccus massive, slightly narrowing with a blunt tip; juxta "X" shaped, top and bottom deep, juxta lateral sides with weak excavations; aedeagus straight, longer than valva, with visible bulge at ventral tip.

Description. Male: Forewing length of holotype 26 mm, wingspan 50 mm; antennae strongly bipectinate; ground color of forewings dark blackish brown, veins yellow, wing pattern typical of genus. Costal fascia from base not extending to M cell apex. Terminal streak from M2 straight, direct to termen at 45 degree angle crossing vein M1, narrow, with even edges. Hindwings whitish yellow, with brown patches, ventral pattern and color of wings similar to dorsal.

Male genitalia (Plate 2: figs 7–9, Plate 6: figs 1–3): Uncus severely narrowing to blunt tip; valvae almost the same width as length, slightly curved medially to the wide, oval apex; tegumen wide, narrowing; saccus massive, slightly narrowing to blunt tip; juxta wide at top and bottom deep, sides slightly excavated; aedeagus straight, longer than valvae, with ventral bulge at tip; vesica with two subbasal diverticula.

Female : unknown.

Bionomics and distribution. Known only from the Fengshuiuiny Shan Mountains in Yunnan province in southwest China, *Eospilarctia maciai* sp.n. is likely endemic to Yunnan, and the nearby regions of Myanmar. The single male specimen was attracted to light in mid-May at an elevation of 2500 m.

Etymology. The new species is named after Mr Ramon Macià Vilà (Barcelona, Spain), the famous Iberian Peninsula's Arctiidae specialist.

***Eospilarctia naumanni* sp. n.**
urn:lsid:zoobank.org:act:08D02B41-D6F3-4872-B2B2-1C9CB31A86D0
http://species-id.net/wiki/Eospilarctia_naumanni
Plate 1: fig. 5, 6, Plate 2: figs 10–12, Plate 7: figs 1–5, Plate 8: figs 1–5, Plate 9: figs 1, 2

Type material. Holotype: ♂ (Plate 1: fig. 5, Plate 7: fig. 4), Northeast Myanmar (Burma), Kachin state, road Chibwe - Pang Wah, 2 km N branch to Kanphant, 2180 m, N25.4251°, E98.5431°, 23 May, 2006 at light, leg. Stefan Naumann, Michael Langer, & Swen Löffler, ex. coll. Swen Löffler (slide No.OP1228) (deposited in ZSM/MWM).

Paratype: ♀ (Plate 1: fig. 6, Plate 8: fig. 1), Northeast Myanmar, road Kanphant – Mt. Inwa Bum, forest camp, 2440 m, N26.1608°, E98.35149°, 25 May, 2006, leg. S. Naumann, M. Langer, & S. Löffler, ex. coll. Swen Löffler (slide No.OP1229f), (pers. comm. S. Naumann) (deposited in ZSM/MWM).

Diagnosis. Externally the new species is most similar to sibling species *Eospilarctia guangdonga* Dubatolov, Kishida & Wang, 2008, *Eospilarctia yuennanica* (Daniel, 1943) and *Eospilarctia maciai* sp. n. In *E. guangdonga* the wing markings are noticeably paler and in its male genitalia the valvae are not widening at the apex, here with a noticeable excavation. *E. yuennanica* forewings are intense brown with pale white markings, in male genitalia the valvae are widening with cut and rough apex. In *E. maciai,* the forewing terminal streak from M_2 is straight, extending to termen at about a 45°

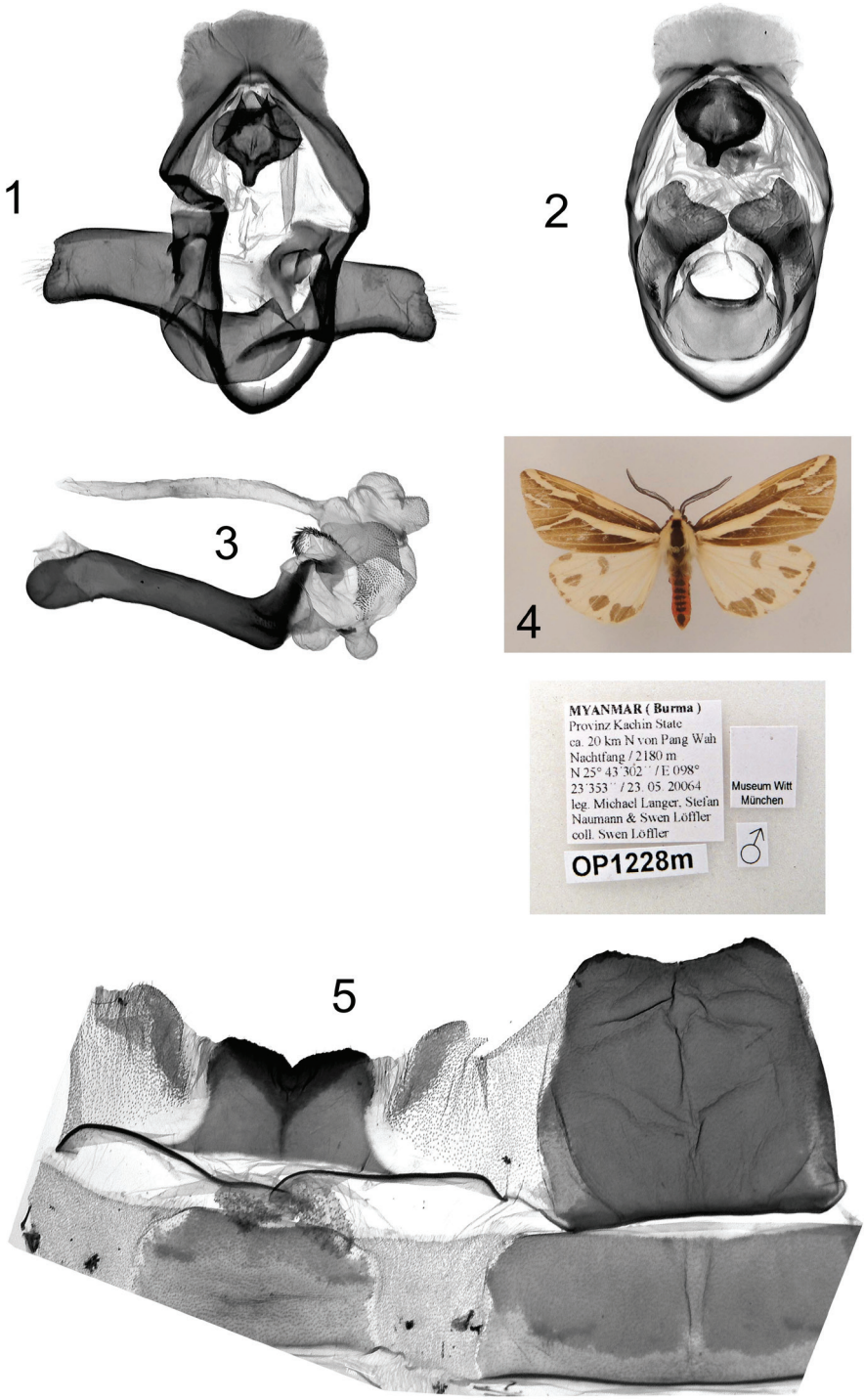

Plate 7, figures 1–5. *Eospilarctia naumanni,* ♂, holotype: **1** Clasping apparatus with opened valvae, prep. OP1228 **2** Clasping apparatus **3** Aedeagus **4** Adult **5** 8th abdominal segment.

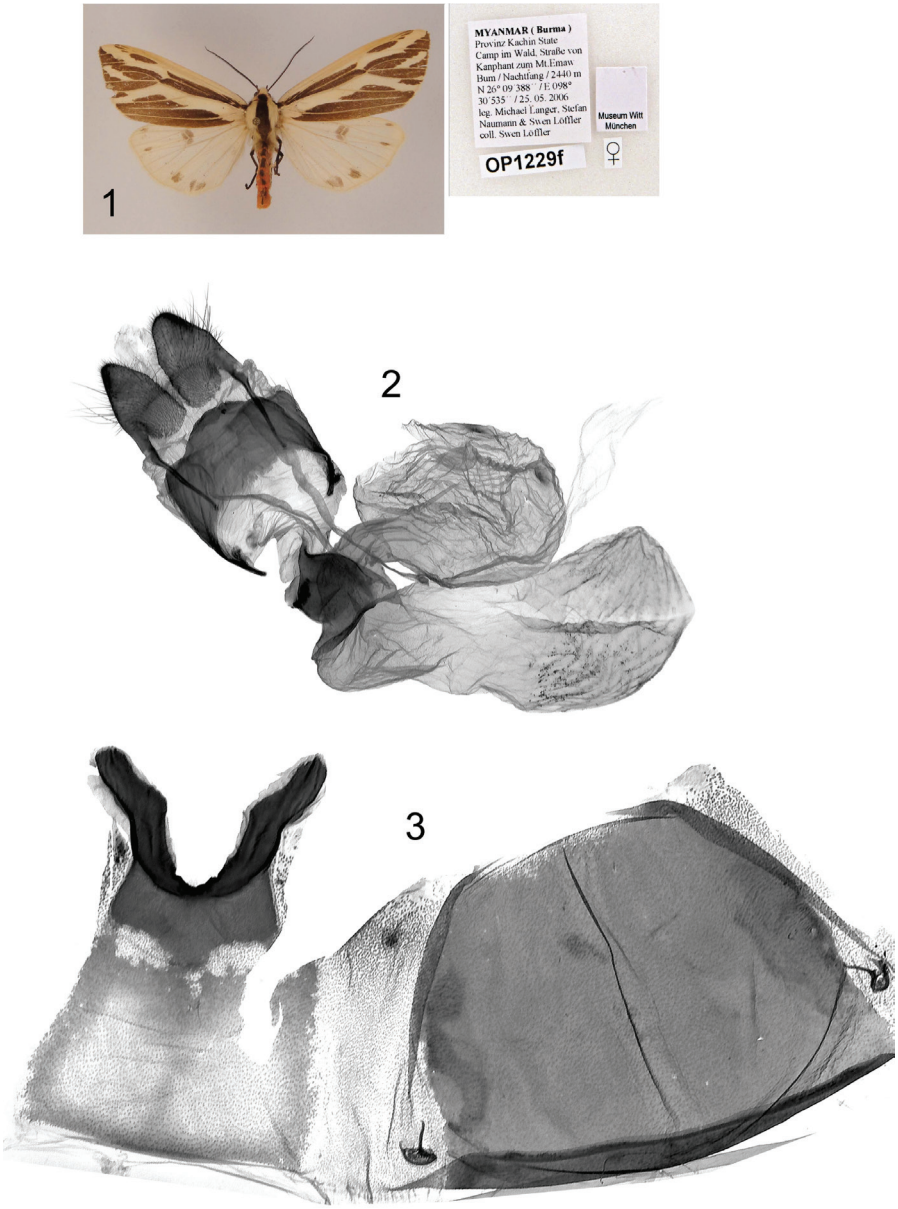

Plate 8, figures 1–5. *Eospilarctia naumanni,* ♀, paratype: **1** Adult **2** Ductus bursa, prep. OP1229 **3** 7th abdominal segment.

angle, crossing vein M_1, narrow, with even edges. The costal fascia does not extend to apex of the medial cell. In the male genitalia valvae almost the same width as long, in middle slightly curved, tip of valva wide, oval, tegumen wide narrowing, saccus with well visible blunt tip, juxta "X" form top and bottom wide deep, sides slightly excavated; aedeagus straight longer than valva, at the tip in ventral side with visible bulge.

1

2

Plate 9, figures 1, 2. *Eospilarctia naumanni,* type locality's: **1** Myanmar NE, Kachin state, road Chibwe – Pan Wah, 2 km N branch to Kanphant **2** Myanmar NE, Kachin state, road Kanphant – Mt. Inwa Bum.

Description. Male: Forewing length of holotype 26 mm, wingspan 54 mm; antennae strongly bipectinate; forewing veins yellow on brown background; wing pattern typical of genus. Yellow costal band extends from forewing basis to apical streak. Terminal streak from M_2 straight, direct to termen 35° angle, cross vein M1, narrow, with rough edges. Hindwing white yellow, with brown spots. Ventral wing pattern and color identical to upper side.

Female. Forewing length of paratype 27 mm; wingspan 55 mm; antennae weakly bipectinate; patches on hindwings very small; other morphological feature as in male.

Male genitalia (Plate 2: figs 10–12, Plate 7: figs 1–3)**.** Uncus bulbous; valvae short, almost the same width as length; slight curvature in mid-ventral portion of valve with tip transversely cut; tegumen narrow; saccus slightly narrowing without visible blunt tip; juxta wide, rounded, top deeply excavated; aedeagus straight, longer than valva, at the tip curved nearly 90°, vesica with two subbasal diverticula, one of them twice as wide as the other; median diverticulum short with short spines.

Female genitalia (Plate 8: figs 2, 3)**.** Papilla analis massive; apophysis posterioris about two and half times shorter than apophysis anterioris; ductus short; bursa bisaccate, rounded; eighth abdominal sternum with lateral sclerites; dorsum sclerotised, simple.

Bionomics and distribution. *Eospilarctia naumanni* sp.n. is known only from the Kachin region of northern Myanmar (Plate 9: figs 1, 2). The new species was collected in late May at elevations of 2200 to 3000 m in mountainous virgin mixed forest, with swampy and mossy meadows. The habitat dominated by various species of *Alnus*, *Prunus*, *Quercus*, *Rhododendron*, *Abies*, different species of small bamboos and other smaller shrubs and ferns. Specimens of the new species were attracted to light (pers. comm. S. Naumann).

Etymology. The new species is named after Mr Stefan Naumann (Berlin, Germany), a renowned Saturniidae specialist.

Dubatolov, Kishida and Wang (2008) described *Eospilarctia yuennanica guangdonga* as a new subspecies and included imago and male genitalia images, however we rise this taxa to species status, *E. guangdonga* stat. nov. The *E. guangdonga* forewing length is 31 mm compared to 28mm for *E. yuennanica yuennanica.* In *E. guangdonga* male genitalia the uncus is cruciform, valvae are not dilatable, tips of valvae are excavated, the juxta has short lateral protrusions, and aedeagus is shorter and stouter. In *E. yuennanica yuennanica* male genitalia the valvae widen without excision at dorsal side of the apex, the juxta have bigger lateral extensions, and aedeagus is longer and thinner.

Checklist of the genus *Eospilarctia*

Species distributions are given in Dubatolov (2010).

***Eospilarctia chuanxina* (Fang, 1982)**

Holotypus: Institute of Zoology, Academic Sinica (Beijing, China). Type locality: Sichuan. Distribution: China: Sichuan.

Eospilarctia fangchenglaiae **Dubatolov, Kishida & Wang, 2008**

Holotypus: Siberian Zoological Museum (Novosibirsk, Russia). Type locality: "Vietnam, cao Bang, Mt. Pia Oac, h=1700 m". Distribution: Northern Vietnam (Lao cai, Cao Bang); China: Sichuan, Yunnan, Guangdong, Zhejian, Jiangxi, Shaanxi, Hubei, Hunan.

Eospilarctia formosana **(Rothschild, 1933)**

Holotypus: Natural History Museum (London, UK). Type locality: "Rantaizan, Arizan"[Taiwan]. Distribution: Taiwan.

Eospilarctia guangdonga **Dubatolov, Kishida & Wang, 2008, stat. n.**

Holotypus: South China Agricultural University (Guangzhou, China). Type locality: Guangdong, China. Distribution: China: Guangdong.

Eospilarctia huangshanensis **Fang, 2000**

Holotypus: Institute of Zoology, Academic Sinica (Beijing, China). Type locality: "Anhui, Huangshan" [China]. Distribution: China: Anhui, Huangshan.

Eospilarctia lewisii **(Butler, 1885)**

Holotypus: Natural History Museum (London, UK). Type locality: [Japan]. Distribution: Japan: Honshu, Shikoku, Kyushu, Tsushima.

Eospilarctia maciai **sp. n.**

Holotypus: Zoologische Staatssammlung der Bayerischen Staaten (Munich, Germany)/Museum of Thomas Witt. Type locality: Yunnan prov. Dali Bai autonomy pref., Yulong county, Fengshuiuiny Mts., 2460 m (China). Distribution: China: Yunnan.

Eospilarctia naumanni **sp. n.**

Holotypus: Zoologische Staatssammlung der Bayerischen Staaten (Munich, Germany)/Museum of Thomas Witt. Type locality: Northeast Myanmar (Burma), Kachin state, road Chibwe - Pang Wah. Distribution: Myanmar: Kachin.

Eospilarctia nehallenia nehallenia **(Oberthür, 1911)**

Holotypus: Natural History Museum (London, UK). Type locality: "Tâ-tsien-Lou" [China: Sichuan]. Distribution: China: Sichuan, Shaanxi, Yunnan.

Eospilarctia nehallenia baibarensis **(Matsumura, 1930)**

Holotypus: National Science Museum (Tokyo, Japan). Type locality: "Formosa at Baibara near Horisha" [Taiwan]. Distribution: Taiwan.

***Eospilarctia neurographa* (Hampson, 1909)**
Holotypus: Natural History Museum (London, UK). Type locality: "Formosa, Kagi distr." [Taiwan]. Distribution: Taiwan.

***Eospilarctia pauper* (Oberthür, 1911)**
Holotypus: Natural History Museum (London, UK). Type locality: "Siao-Lou" [China: Sichuan]. Distribution: China: Sichuan, Yunnan.

***Eospilarctia taliensis* (Rothschild, 1933)**
= *jordansi* (Daniel, 1943)
Cotypus: Zoologische Staatssammlung der Bayerischen Staaten (Munich, Germany)/ Museum of Thomas Witt. Type locality: "Tali Haut, Yunnan" [China]. Distribution: China: Yunnan, Sichuan (?), Shaanxi.

***Eospilarctia yuennanica yuennanica* (Daniel, 1943)**
Cotypus: Zoologische Staatssammlung der Bayerischen Staaten (Munich, Germany)/ Museum of Thomas Witt. Type locality: "Li-kiang (Nord Yuennan)" [China]. Distribution: China: Sichuan, Yunnan.

***Eospilarctia yuennanica fansipana* ssp.n**
Holotypus: Zoologische Staatssammlung der Bayerischen Staaten (Munich, Germany)/Museum of Thomas Witt. Type locality: northern Vietnam, Mt. Fan-si-pan, 1600–1800 m near Chapa. Distribution: Vietnam: Chapa, Mt. Fan-si-pan.

Acknowledgements

The authors are grateful to Stefan Naumann (Berlin, Germany) for *Eospilarctia naumanni* sp.n. habitat photos, valuable information, Svitlana Pekarska (Budapest, Hungary) for genitalia photos. Many thanks to Robert Borth (Milwaukee, United States) for taxonomical and grammar suggestions and two anonymous reviewers for valuable comments and proposals.

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RESEARCH ARTICLE

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A new species of *Chalicodoma* from Saudi Arabia with modified facial setae (Hymenoptera, Megachilidae)

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Abstract

Some bees and pollen wasps have independently evolved simple, stiff, erect, apically-curved, curly or hooked facial setae as adaptations to collect pollen from nototribic flowers. A distinctive new species of *Chalicodoma* Lepeletier de Saint Fargeau subgenus *Pseudomegachile* Friese from Saudi Arabia with such morphological adaptations, *C. riyadhense* **sp. n.**, is described and figured. The species was captured visiting flowers of *Blepharis ciliaris* (L.) (Acanthaceae). The occurrence of modified facial setae is documented and discussed for the first time in eight other species of *Pseudomegachile*, and a key to the genera and subgenera of Megachilini currently confirmed for Saudi Arabia is provided.

Keywords

Apoidea, Anthophila, bees, *Blepharis ciliaris*, Megachilinae, Megachilini, taxonomy, nototribic flowers

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Introduction

The presence of erect or proclinate, stiff, apically curly or hooked setae on certain areas of the face of some bees and pollen wasps (Vespidae: Masarinae) is related to pollen-collecting behavior from nototribic flowers, or bilateral flowers in which filaments and styles are located on the adaxial side or top of the flower, particularly in the families Lamiaceae, Fabaceae, and Plantaginaceae (Müller 1996; Thorp 2000; Michener 2007). In some species, such as *Anthophora walteri* Gonzalez and *Anthidium rodriguezi* Cockerell, the areas of the face covered by these setae are also sometimes distinctly flat to nearly depressed, with the integument dull, coarsely and sparsely punctate (Brooks 1988; Michener et al. 2003; Gonzalez and Chavez 2004; Gonzalez and Griswold in prep.). Such morphological adaptations occur across multiple genera from different families (e.g., Thorp 2000; Michener 2007; Rightmyer et al. 2011). The modified setae vary among taxa in terms of the shape, length, thickness, orientation, and distribution. In some species they are short and erect and are found on the entire face (e.g., *Osmia calaminthae* Rightmyer et al.), in others they are rather long, apically curved or cork-screw shaped, and are present on the clypeus and supraclypeal area only; they can also be proclinate and form a basket on the vertex and frons, as in *O. brevis* Cresson (Tepedino et al. 1999; Rightmyer et al. 2011). In several *Anthophora* Latreille, in addition to the apically curved setae, there is a distinct row of stout, blunt setae across the base of the clypeus known as the pecten (Brooks 1988). Such a variation may indicate degrees of specialization on host plants, but observations are lacking.

Little is known about the foraging behavior of these bees on nototribic flowers but scant observations suggest some behavioral adaptations in how they harvest the pollen from the flower and remove it from the body, especially for those that exhibit modifications on both the facial setae and the integument (e.g., Müller 1996; Gonzalez et al. 2006). Although some of these morphological variations as well as the foraging behavior of bees were described in detail by Müller (1996) for 13 central European species (seven genera and three families), and have been sporadically mentioned in the literature from largely anecdotal observations, they remain to be thoroughly documented and studied across the Apoidea.

In this paper, we describe a distinctive new species of *Chalicodoma* Lepeletier de Saint Fargeau subgenus *Pseudomegachile* Friese from Saudi Arabia with modified facial setae. To date, the only other known *Chalicodoma* having similar setae is *Chalicodoma* (*Chalicodoma*) *albocristata* (Smith) from the western Palearctic (Müller 1996). Also, based on the study of specimens from more than half of the species-diversity of the subgenus, we document and discuss the occurrence of modified facial setae in eight other species of *Pseudomegachile*. Herein, *Chalicodoma* is recognized in a narrower sense than that of Michener (1962, 1965), and presently includes eight subgenera (*Alocanthedon* Engel and Gonzalez, *Callomegachile* Michener, *Cestella* Pasteels, *Chalicodoma* s.str., *Cuspidella* Pasteels, *Gronoceras* Cockerell, *Largella* Pasteels, and *Pseudomegachile*). *Pseudomegachile* is as highly diverse and morphologically heterogeneous as *Callomegachile*. It is widespread in the Eastern Hemisphere, across

the Palearctic and Oriental regions but *C. lanata* (Fabricius) has been introduced to Florida, USA and the West Indies and *C. ericetorum* (Lepeletier de Saint Fargeau) to Canada (Michener 2007; Sheffield et al. 2010).

Material and methods

Material considered herein is deposited in the King Saud University Museum of Arthropods, Plant Protection Department, College of Food and Agriculture Sciences, King Saud University, Riyadh, Kingdom of Saudi Arabia (KSMA) and Division of Entomology (Snow Entomological Collections), University of Kansas Natural History Museum, Lawrence, Kansas, USA (SEMC). Morphological terminology follows that of Engel (2001) and Michener (2007), except for torulus herein used instead of antennal alveolus, while the format for the description is largely based on that of Gonzalez et al. (2010) and Engel and Gonzalez (2011). Photomicrographs were prepared using a Canon 7D digital camera attached to an Infinity K-2 long-distance microscope lens. Measurements were made with an ocular micrometer attached to an Olympus SZX-12 stereomicroscope. To explore and document the occurrence of modified facial setae in *Pseudomegachile*, we examined specimens of 43 species deposited in SEMC that occur across the distribution range of the subgenus.

Systematics

Genus *Chalicodoma* Lepeletier de Saint Fargeau
Subgenus *Pseudomegachile* Friese

***Chalicodoma* (*Pseudomegachile*) *riyadhense* sp. n.**
urn:lsid:zoobank.org:act:FBCBB044-B2EA-47AC-BC4B-D68EFAE56B9C
http://species-id.net/wiki/Chalicodoma_riyadhense
Figs 1–17

Holotype. ♀, Saudi Arabia, Riyadh, Al Amariah, [Mazra'ah] Majra Al-Gasim [farm], 23-v-2011 [23 May 2011], M.A. Hannan // at flowers of *Blepharis ciliaris* [(L.) Acanthaceae] (KSMA).

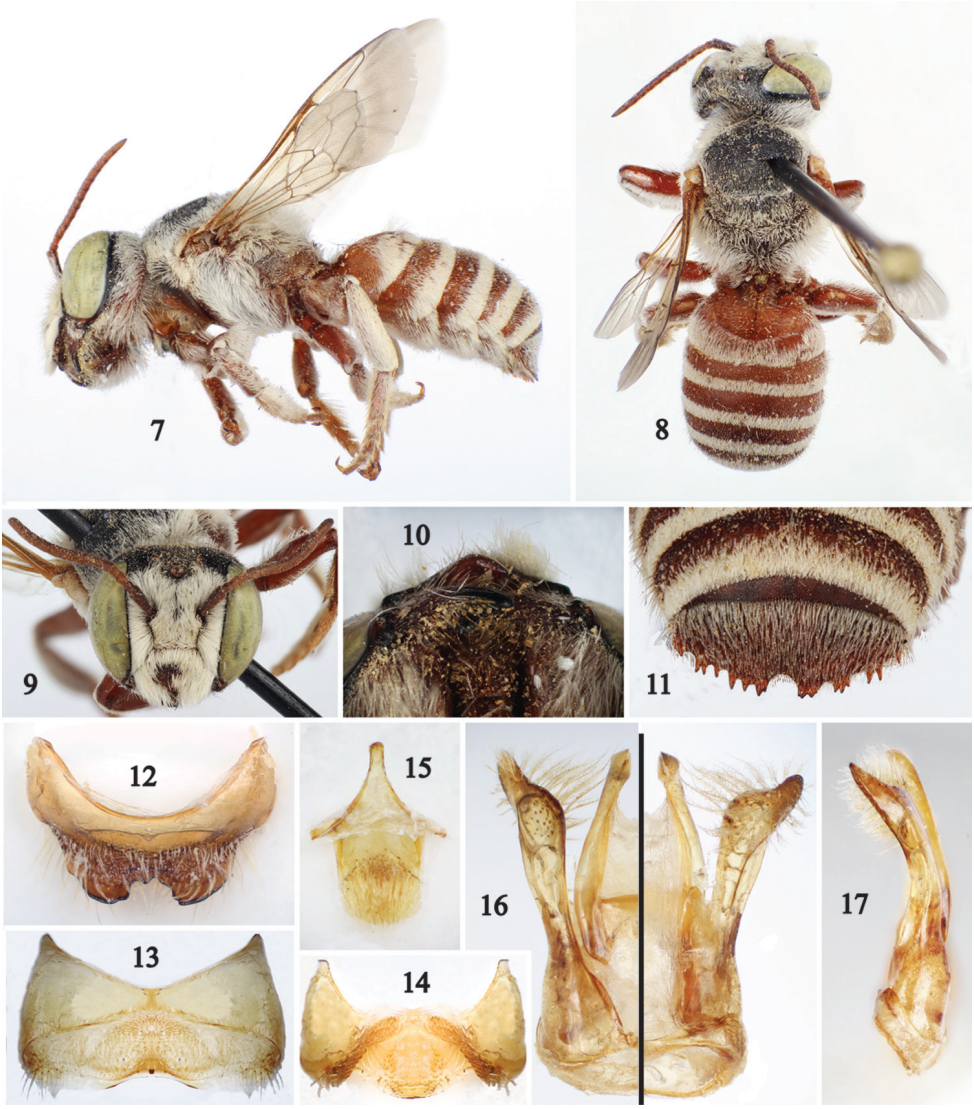
Paratypes. 1♂, 1♀, with the same data as the holotype (SEMC); 2♂♂, same data as holotype except 31-v-2011 [31 May 2011], I. Naser // at *Blepharis ciliaris* (SEMC & KSMA); 1♂, same data as holotype (KSMA); 1♂, same data as holotype except 17-v-2011 [17 May 2011] (KSMA).

Diagnosis. The female of this species can be recognized easily by the following combination of characters: body light reddish brown contrasting with dense, minutely-branched white setae on the body (Figs 1, 2); preoccipital border distinctly concave in dorsal view; clypeus, supraclypeal area, frons, and upper paraocular area with

Figures 1–6. Photomicrographs of female holotype (KSMA) of *Chalicodoma* (*Pseudomegachile*) *riyadhense* sp. n. **1** Lateral habitus **2** Dorsal habitus **3** Facial view **4** Detail of clypeus **5** Detail of mandibles **6** Detail of mesoscutal integument.

modified facial setae; and clypeus with distal margin distinctly impunctate and swollen medially (Figs 4, 5). In addition to the body coloration and pubescence (Figs 7, 8), which are similar to those of the female, the male can be recognized by the following combination of characters: clypeus distinctly pointed on distal margin (Fig. 10); mandible without inferior process; tarsi of all legs unmodified but with small dark spot on inner surface of probasitarsus; sixth metasomal tergum horizontal in profile, and seventh tergum with strong, transverse preapical carina deeply notched medially (Fig. 12).

The reddish body coloration contrasting with the white dense pubescence of *C. riyadhense* resemble some Palearctic and Oriental species, such as *C. flavipes* (Spinola), *C. rubripes* (Morawitz), and *C. xanthocneme* (Alfken), but it is easily separated from those and any other known species of *Pseudomegachile*, including those with modified facial setae, by the distinctive clypeus in both sexes. Furthermore, the male of *C. riyadhense* is also unique in having a seventh metasomal tergum with strong, medially notched preapi-



Figures 7–17. Photomicrographs of male paratype (SEMC) of *Chalicodoma* (*Pseudomegachile*) *riyadhense* sp. n. **7** Lateral habitus **8** Dorsal habitus **9** Facial view **10** Ventral view of head **11** Apex of sixth metasomal tergum **12** Seventh tergum **13** Fifth metasomal sternum **14** Sixth sternum **15** Eighth sternum **16** Genital capsule (dorsal left, ventral right) **17** Lateral aspect of genital capsule.

cal carina. Except for some species, such as *C. kigonserana* (Friese) and *C. nigrocaudata* (Friese), most *Pseudomegachile* males have a seventh tergum with a complete or medially pointed preapical carina. However, those males with similar bilobed preapical carina are much larger in size (18–20 mm in body length), have very long procoxal spines, strongly modified protarsi, and a different color pattern of the pubescence (head and mesosoma covered with black setae contrasting with ferruginous setae on the metasoma).

Description. *Female*. Body length 10.4 mm; forewing length (measured from apex of humeral sclerite to wing margin) 6.4 mm. Head 1.1 times broader than long; inner orbits of compound eyes parallel-sided; intertorular distance 2.2 times torulorbital distance; interocellar distance 3.2 times median ocellar diameter, 1.7 times ocellocular distance; ocelloccipital distance 1.7 times median ocellar diameter; torular process reduced, barely visible; vertex rounded in frontal view (Fig. 3); preoccipital border rounded, distinctly concave in dorsal view (Fig. 2); compound eye about 2.3 times longer than wide; gena slightly narrower (0.8x) than compound eye in profile, narrowest dorsally; mandible with four teeth, apical two longer and broader than basal two (Fig. 5); clypeus about 1.7 times broader than long, with epistomal sulcus gently convex basally, well projected over clypeal-labral articulation, elevated along midline on disc, distinctly swollen on distal margin medially (Figs 4, 5); supraclypeal area slightly elevated along midline; frons convex in profile, not flat; scape about 3 times longer than broad, not reaching lower margin of median ocellus in repose, pedicel about as long as broad, first flagellomere about as long as broad, about equal to pedicel length, 1.5 times longer than second flagellomere, subsequent flagellomeres progressively increasing in length towards apical flagellomeres, distalmost flagellomere longest. Omaulus rounded; pronotal lobe carinate; mesoscutum gently convex in profile; mesoscutellum flat on disc; pretarsal claws simple, basally with two unmodified simple setae, basal seta shortest; pro- and mesotibiae distally with angled medial projection on outer surfaces, not forming distinct spinose process. Second to fifth metasomal terga with elevated discal areas (i.e., premarginal lines distinct); sixth tergum straight in profile.

Body color light reddish brown except dark brown to black as follows: mandible distally, clypeal margin, epistomal sulcus, vertex, antenna (darker on outer surfaces of scape and pedicel), and mesoscutum and mesocutellum with faint spots on discs (Figs 2, 6). Tegula and humeral sclerite yellowish; wings hyaline, darker distally, veins yellowish basally (including pterostigma), dark brown distally.

Integument smooth and shiny between punctures except strongly imbricate on basal area of propodeum and weakly imbricate on metasomal sterna and terga. Face finely and closely punctate, nearly contiguous except on distal margin of clypeus medially smooth and shiny, punctures smaller on supraclypeal area; gena with shallower punctures than on face. Mesoscutum and mesoscutellum with punctures coarser and larger than on head (Fig. 6), those on mesoscutellum larger than on mesoscutum; mesepisternum with larger and coarser punctures than on metepisternum and sides of propodeum, punctures shallow on metepisternum; basal area of propodeum weakly striate basally. Metasomal terga finely punctate, punctures not contiguous, smaller than on mesoscutum; sterna with punctures coarser, sparser than on terga.

Pubescence white, unless indicated otherwise. Following areas with dense (integument obscured or barely visible among setae), minutely-branched, appressed or semierect setae: mandible basally, lower and middle paraocular areas, gena, pronotum, pronotal lobe, anterior half of tegula, humeral sclerite, margins of mesoscutum, mesoscutellum, metanotum, propodeum, remaining areas of mesosoma laterally, coxae, trochanters, posterior surfaces of pro- and mesofemora, anterior surface of metatibia,

outer surfaces of tibiae, outer surfaces of pro- and mesobasitarsi, first metasomal tergum entirely, depressed marginal areas of second to fourth terga (apical fasciae), fifth tergum entirely, distal margin of first sternum, sides of second to fourth sterna, and entire distal margin of fifth sternum; setae longer on head and mesosoma than on metasoma (Figs 1, 2). Clypeus, supraclypeal area, frons, and upper paraocular area with simple, stiff, apically-curved yellowish setae (at most as long as median ocellar diameter) sparsely covering integument (Fig. 3). Lower margin of mandible and gena inferiorly with long (about two times median ocellar diameter), erect, yellowish simple setae. Second to sixth metasomal sterna with yellowish scopal setae, shorter on sixth sternum.

Male. As described for female except for usual secondary sexual characters and following: Body length 11.6 mm; forewing length 6.4 mm. Head 1.2 times broader than long; inner orbits of compound eyes slightly converging below; intertorular distance 1.8 times torulorbital distance; interocellar distance 2.1 times median ocellar diameter, 1.8 times ocellocular distance; ocelloccipital distance 1.4 times median ocellar diameter; vertex slightly flat medially in frontal view (Fig. 9); preoccipital border not as distinctly concave as in female; compound eye about 2.6 times longer than wide; mandible with four teeth, without inferior process; clypeus more convex than in female, with distal margin distinctly projecting over clypeal-labral articulation, so that triangular in ventral view; scape 2.7 times longer than broad, reaching lower margin of median ocellus in repose, second to eleventh flagellomeres longer than broad. Procoxal spine small, about half length of median ocellar diameter as measured in profile; tarsi of all legs unmodified, but probasitarsus with inner surface asetose, with small dark spot; pretarsal claws cleft, inner ramus shorter than outer. Sixth metasomal tergum horizontal or nearly so in profile, without lateral projection on distal margin, transverse preapical carina strong, irregularly toothed, with broad median emargination (Fig. 11); seventh tergum with transverse preapical carina strongly projected, with deep median emargination thus forming a distinct lateral lobe (Fig. 12); fifth to eighth sterna (seventh sternum obsolescent in Megachilini) and genital capsule as in figures 13–17; volsella with apex distinctly notched or bilobed.

Body color slightly lighter than female but with frons, vertex, gena dorsally, mesoscutum, and mesoscutellum black (Figs 7, 8).

Pubescence in general longer and denser than female, particularly on discs of mesoscutum, mesoscutellum, and metasomal terga; clypeus, supraclypeal area, paraocular area, and frons densely covered by setae (integument obscured); procoxa with dense patch of short ferruginous setae above spine, coxa otherwise sparsely covered with branched setae. Fifth metasomal sternum with spatulate setae midbasally on postgradular area, setae otherwise minutely branched, except apicolaterally with long, simple setae; sixth sternum with dense spatulate setae basolaterally on postgradular area forming distinctive patch, otherwise setae apically flattened and curved; sternum eight without setae on or near lateral margin but ventrally with dense, minutely-branched setae on disc (Fig. 15).

Etymology. The specific epithet refers to the greater Riyadh area in Saudi Arabia, and from where the species was collected.

Host plant. The species was captured visiting flowers of *Blepharis ciliaris* (L.) (Acanthaceae), locally known as "Saha" or "Naqie" (Figs 18–20). The plant is a perennial herb, usually about 20 cm in height (10–30 cm), growing in small patches with small blue to light violet flowers and easily found in the area of Al Amariah, approximately 25 km northwest of Riyadh, from early April through early June. The species prefers the silt bottoms of rocky wadi basins. *Blepharis ciliaris* is a good source of nectar, particularly in the southwest and in years following a good rainy season. Regional beekeepers sometimes produce "Saha honey".

Figures 18–20. Photographs of *Blepharis ciliaris* (L.) (Acanthaceae) in Saudi Arabia. **18** Entire plant in lateral view **19** Detail of flowers **20** Entire plant as viewed from above (photographs by A.S. Alqarni).

Key to genera and subgenera of Megachilini of Saudi Arabia

Records of the occurrence of several megachiline species in Saudi Arabia remain to be confirmed and a key to species is therefore not presented at this time. The following key, which is modified from Michener (2007), will assist in the identification of the megachiline genera and subgenera that are presently confirmed to occur in Saudi Arabia.

1 Females **2**
– Males **6**

2(1) Scopa absent; metasoma tapering from near base to narrow, apex often acutely pointed; cleptoparasite ..... ***Coelioxys* (*Allocoelioxys*)**

– Scopa present on metasomal sterna two through five or six; metasoma not distinctly tapering throughout its length; free living..... **3**

3(2) Sixth metasomal sternum with a fringe of branched setae on or near apical margin; mandible with cutting edge in at least one interspace, sometimes hidden behind margin of interspace **4**

– Sixth metasomal sternum without apical fringe of branched setae; mandible without cutting edges between teeth **5**

4(3) Mandible five- or six-toothed, teeth (except first) similar and with similarly-shaped, incomplete cutting edges in second and third (and sometimes fourth) interspaces; apices of mandibular teeth roughly equidistant from nearest neighbors; preapical transverse mandibular groove distinct and filled with short, fine, pale setae ..... ***Megachile* (*Creightonella*)**

– Mandible four- to five-toothed, teeth above first of different shapes and cutting edges often of different shapes; apices of mandibular teeth commonly separated from nearest neighbors by different distances; preapical transverse mandibular groove, if present, not filled with short, pale setae .... ***Megachile* (*Eutricharaea*)**

5(3) Distal margin of clypeus irregularly rounded (rarely weakly emarginate medially), usually strongly crenulate, produced well over base of labrum, not thickened; mandible usually slender with apical margin strongly oblique; head little developed posteriorly, ocelloccipital distance thus not greater than interocellar distance ..... ***Chalicodoma* (*Chalicodoma*)**

– Distal margin of clypeus truncate, not crenulate, often not much produced over base of labrum, but if rounded and somewhat crenulate, then margin thickened and impunctate; head usually much developed posteriorly, ocelloccipital distance thus greater than interocellar distance ..... ***Chalicodoma* (*Pseudomegachile*)**

6(1) Sixth metasomal tergum with multispinose preapical carina, with two pairs of long, preapical spines, each spine of upper pair sometimes divided into two, or crenulate, rounded, or fused to other spine of pair; cleptoparasite..... ..... ***Coelioxys* (*Allocoelioxys*)**

– Sixth metasomal tergum with preapical carina not as above, often crenulate, medially emarginate, or sometimes reduced to two spines; free living **7**

7(6) Fifth and sometimes sixth metasomal sterna exposed and generally similar to preceding sterna (sometimes fifth sternum largely hidden but sixth sternum exposed); lateral extremity of carina of sixth tergum directed basad, away from apical margin of tergum ..... ***Megachile* (*Creightonella*)**

– Fifth and sixth metasomal sterna retracted, variously modified, less sclerotized, less punctate, and less setose than first to fourth sterna; lateral extremity of carina of sixth tergum absent or directed toward lateral extremity of apical margin of tergum..... **8**

8(7) Eighth metasomal sternum without marginal setae but discal setae sometimes extending beyond margin laterally; metasoma usually less strongly convex and usually less than twice as long as wide ..... ***Megachile*** **(*Eutricharaea*)**

– Eighth metasomal sternum *often* with lateral marginal setae; metasoma commonly strongly convex and twice as long as wide or more..... **9**

9(8) Toothed margin of mandible (three- to four-toothed) strongly oblique, nearly as long as distance from upper tooth to mandibular base; seventh metasomal tergum with narrow, median, apically-truncate projection extending well beyond teeth of sixth tergal carina; apex of gonostylus asetose or with very short, poorly-branched to simple setae..... ***Chalicodoma*** **(*Chalicodoma*)**

– Toothed margin of mandible (three-toothed) less oblique, much shorter than distance from upper tooth to mandibular base; seventh metasomal tergum a low sclerite largely hidden behind sixth tergum, sometimes produced to small median spine; apex of gonostylus often with long, densely-branched setae on medial margin..... ***Chalicodoma*** **(*Pseudomegachile*)**

Discussion

The bee fauna of Saudi Arabia is rich but relatively little known biologically and taxonomically. Already several new species and new records are accumulating from the material collected by the authors (e.g., Alqarni et al. 2012; Engel et al. in press), and further accounts of this fauna will be forthcoming (ASA, MAH, MSE in prep., unpubl. data). Thus, the new species described herein is a small contribution toward this larger effort to elucidate the Arabian melittological fauna.

Including the species described herein, we found nine species of *Pseudomegachile* with modified facial setae (Table 1). Hitherto, the only known species of *Chalicodoma* with modified facial setae was *C. albocristata* (Müller 1996). In all *Pseudomegachile* species, the modified setae consisted of simple, stiff, erect or proclinate, apically-curved setae. They were often found on the clypeus and supraclypeal area, and in some species also on the frons, as is the case for *C. riyadhense*. No modifications of the integument or in the areas of the face covered by these setae were observed. That is, in all species the integument was shiny and densely punctate, and the clypeus, supraclypeal area, and frons were not distinctly flat or depressed. Although we examined more than half of the known species of *Pseudomegachile*, these observations are doubtless preliminary. The desert plant species on which the new bee species was collected, *B. ciliaris*, has nototribic flowers, thus agreeing with the modified facial setae found on *C. riyadhense*. This suggests that *C. riyadhense* may be a regular visitor of this plant but it would be interesting to know to what extent it contributes to the pollination of *B. ciliaris* and how much it specializes on it. However, we hope to draw more attention to and encourage melittologists to document these morphological adaptations as well as the floral associations and foraging behavior of the bees that have them.

Table 1. Species of *Chalicodoma* Lepeletier de Saint Fargeau subgenus *Pseudomegachile* Friese with modified facial setae for pollen collection from nototribic flowers. Modified setae refer to simple, erect or proclinate, apically curved setae. Plus (+) and dash (–) symbols indicate presence or absence of a character; * = not distinctly modified. In *C. riyadhense* sp. n. the modified setae are also found on the upper paraocular area. The locality corresponds to the areas where the examined specimens were collected, not the total distribution of those species. It must be noted that *Chalicodoma* (from Gr. χάλιξ, χάλιχος, calx + δωμα, domus) is of neuter gender, and all names now referred to that genus have been made to conform. The derivation of the name was indicated by Brullé (1832), who gave: "*nom tiré de l'habitude de l'insecte, qui construit son nid avec de petits cailloux, comme Réaumur nous l'a fait connaître dans ses intéressants mémoires*". However, only those names which are latinized adjectival or participial species-group names are adjusted in gender (ICZN 1999: Art. 34.2), which means that the forms "angonicum", "farinosum", and "kigonseranum" which have appeared in various sources are all improper emendations.

Species	Modified setae			Locality
	Clypeus	Supraclypeal area	Frons	
C. angonica (Cockerell)[1]	+	+	+	Zambia [N.E. Rhodesia]
C. cinnamomeum (Alfken)	+	–	–	Morocco, United Arab Emirates
C. farinosa (Smith)	+	+	–	Greece
C. kigonserana (Friese)	+	–	–	Tanganyika, Democratic Republic of Congo [Belgian Congo], Zambia [N. Rhodesia], Malawi
C. lualabae (Cockerell)[2]	+	+	+	Zambia [N.E. Rhodesia]
C. marshalli (Friese)	+	+	+	Tanganyika, Zambia [N. Rhodesia]
C. riyadhense sp. n.	+	+	+	Saudi Arabia
C. seraxense (Radoszkowski)	+	+	+	S. India
C. transgrediens (Rebmann)	+	+*	–	Turkey

[1] Note that *C. angonica* was erroneously synonymized by Pasteels (1965) with *C. kigonserana*.

[2] Note that this species is possibly a junior synonym of *C. angonica*.

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