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A new dustywing (Neuroptera: Coniopterygidae) from the Early Cretaceous amber of Spain

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Abstract

A new Cretaceous dustywing, *Soplaconis ortegablancoi* **gen. et sp. nov.** (Neuroptera: Coniopterygidae), is described from four specimens preserved in Early Cretaceous (Albian, ~105Ma) El Soplao amber (Cantabria, northern Spain). Two additional specimens are assigned to this new taxon. A crossvenational abnormality on an area of diagnostic significance from one of the holotype's forewings provides a reminder of the importance of not ruling out character plasticity or teratosis when evaluating palaeodiversity. A comment on the possible palaeoecological significance of the co-occurrence as syninclusions of plant trichomes with the holotype of *S. ortegablancoi* and seven of the eleven described Burmese amber dustywing species is provided.

Keywords: Coniopterygidae, Neuroptera, amber, Cretaceous, teratosis

Introduction

Dustywings (Coniopterygidae) comprise a relatively large neuropteran family with about 570 extant species described and a cosmopolitan distribution (Oswald & Machado, 2018; Engel *et al.*, 2018). Both adults and larvae are usually generalist predators that can be mostly found on bushes and trees, although some species are more commonly found in low vegetation feeding on minute, generally inactive arthropods such as aphids, coccids, and mites; some species appear to be associated with particular plant species, which suggests preference for certain food types (Meinander, 1972). Coniopterygids reach the smallest sizes within Neuroptera, which also translates into simplified wing venation patterns. The

group has been recovered as sister to the remaining neuropteran diversity in the latest phylogenetic studies (Winterton *et al.*, 2010, 2018; Wang *et al.*, 2017). Fossil coniopterygids are known since the Late Jurassic of Kazakhstan (Meinander, 1975), and currently comprise 25 Mesozoic and 16 Cenozoic species, mostly known from amber inclusions (Li *et al.*, 2019; Ružičková *et al.*, 2019).

Material and methods

The specimens described herein are provisionally housed at the Museo Geominero (IGME) in Valencia (Spain); their final deposition will be in the institutional collection of the El Soplao Cave (Government of Cantabria).

A Discovery.V12 Zeiss stereomicroscope, and two compound microscopes (an Olympus BX51 and a Zeiss AXIO) were used to study the specimens. Drawings were made using a camera lucida attached to the stereomicroscope and to the Olympus BX51 compound microscope. Photographs were taken using an Axiocam 105 colour digital camera attached to both the stereomicroscope and the Zeiss AXIO. Series of images were taken with the software ZenPro v.2.3 and then digitally stacked using the software Helicon Focus v.6.8.0. Measurements in the description are those of the holotype.

General terminology follows the monograph of Meinander (1972), with venational terminology updated after Breitkreuz *et al.* (2017). Abbreviations: A₁, A₂, anal veins; *dMs*, distal median seta; C, costal vein; CuA, cubital anterior vein; CuP, cubital posterior vein; e, ectoproct; hy,

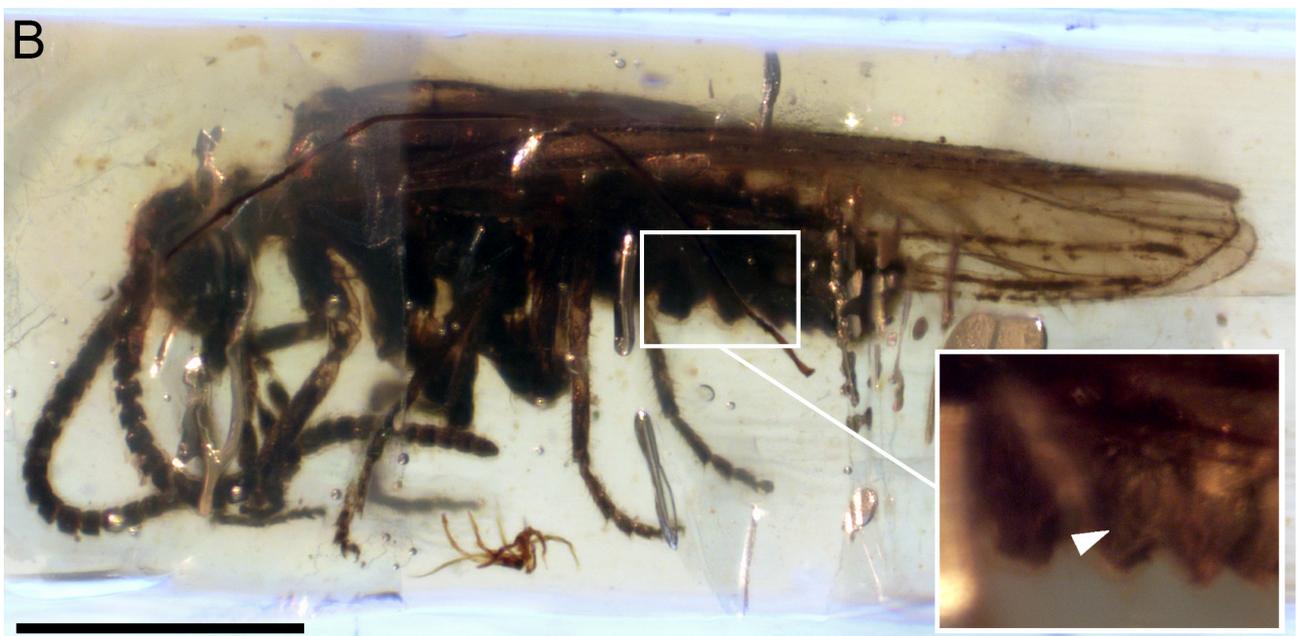


FIGURE 1. *Soplaoconis ortegablancoi* gen. et sp. nov. (Neuroptera: Coniopterygidae), habitus photographs from the holotype CES 348. **A**, Dorsal habitus. **B**, Lateral habitus. The bottom right inset shows the plicatura visible on sternite IV (arrowhead). Scale bars 0.5 mm.

hypandrium (terminal process); M, medial vein; *pMs*, proximal median seta; RA, radial anterior vein; RP, radial posterior vein; Sc, subcostal vein; rp-m, radial posterior-medial crossvein; posterior vein.

Systematic Palaeontology

Family Coniopterygidae Burmeister, 1839

Subfamily Aleuropteryginae Enderlein, 1905

Tribe Fontenelleini Carpentier & Lestage, 1928

Genus *Soplaconis* gen. nov.

Type species. *Soplaconis ortegablancoi* sp. nov.

Diagnosis. Antennae with 24 to 27 antennomeres; scape slightly longer than wide. Fontanelle extended posterolaterally, leaving a rather pronounced posteromedian frontal sclerotization. Forewing with basal abscissa of RP_2 elongate, slightly angled forwards at about its mid-length; RP_2 connected to MA_1 by a rp_2-ma_1 crossvein. Forewing media with three branches and two stiff setae inserted rather distally (distal median seta inserted after the $rp-m$ crossvein). Distalmost medio-cubital crossvein ($mp-cua$) present between MP and CuA. Hind wing media with three branches.

Etymology. The generic name is a combination of “El Soplao”, the name of the amber locality where the type specimens were recovered from, and the Greek term *konis*, meaning “dust”. The gender of the name is feminine.

Soplaconis ortegablancoi sp. nov.

Figs 1–4

Material. Holotype CES 348, male, a complete specimen preserved in a clear amber matrix prepared in a $23 \times 15 \times 2$ mm Epoxy resin prism. Preservation is good but wing venation is somewhat distorted. One young dendritic trichome (see Pérez-de la Fuente *et al.*, 2012) and likely spider web remains are preserved in the same preparation. The original inclusion belonged to an amber piece with 16 syninclusions that fragmented during preparation, including a partially preserved coniopterygid lacking wings (CES 352.4), six brachyceran dipterans (including the holotype of the zhangsolvid *Buccinatoromyia soplaensis* Arillo, Peñalver & Pérez-de la Fuente, 2015, CES 349.1, and a chimeromyiid), four hymenopterans (two platygastriids and one mymarommatid among them), a psylloid homopteran, and a psocopteran. Interestingly, the holotype displays a mismatch with the position of the rp_2-ma_1 crossvein between the two forewings (Fig. 3), the condition shown in the right wing being the abnormal state.

Three paratypes: CES 015.5, CES 459, and CES 460. The paratype CES 015.5 is a complete specimen of unknown sex prepared in a prism $15 \times 19 \times 6$ mm. Although wing venation is difficult to discern due to overlapping of all wings, all the diagnostic characters of

the new taxon but the two stiff setae on M are visible. Syninclusions: three dipterans, i.e., the almost complete paratype of the zhangsolvid *Buccinatoromyia magnifica* Arillo, Peñalver & Pérez-de la Fuente, 2015, CES 015.1, a forewing and a small portion of the thoracic cuticle of the holotype of *B. soplaensis*, CES 015.2 (see Arillo *et al.*, 2015), and an empidoid brachyceran, as well as a platygastriid wasp. CES 459 is an almost complete male prepared in a $22 \times 14 \times 1$ mm Epoxy prism, missing some wing parts. Wing venation as in the holotype, including diagnostic characters but the two stiff setae on M, which are not visible likely due to polishing of the wing near the surface of the preparation; the angulation of the basal abscissa of RP_2 is likely present but masked by a longitudinal fracture. CES 460 is a partially preserved specimen of unknown sex due to preservation (abdomen decayed by fungal hyphae), prepared in a $23 \times 14 \times 1$ mm Epoxy prism. Head not preserved but one antenna with at least 19 flagellomeres. All venational diagnostic characters are visible, including the two stiff setae on M.

Additional material: CES 392.4 and CES 476.5. CES 392.4 is a partial specimen of unknown sex preserving the body and the basal part of wings and legs prepared in a $30 \times 11 \times 8$ mm prism. Syninclusions: three dipterans (head remains from the holotype of *B. soplaensis*, CES 392.2; wing and body fragments from the paratype of the zhangsolvid *B. magnifica*, CES 392.3, see Arillo *et al.*, 2015; and one complete empidoid brachyceran), a platygastriid wasp, a micropterygid lepidopteran, a spider, and a mite. CES 476.5 is a male preserved in a fragment of a double stalactite-shaped amber piece, $13 \times 6 \times 3$ mm, together with the following syninclusions: two hymenopterans (one platygastriid among them), one nematoceran dipteran (a ceratopogonid?), one spider, and one badly-preserved neuropterid, possibly another coniopterygid. The specimen, which appears to be trapped in a spider web, seems complete but due to the position of the specimen in the amber piece, the head is not discernible and the proximal half of the body is hardly visible or not visible at all. The three branches of M in the forewing and the diagnostic elongate and angulate basal abscissa of RP_2 are visible in the specimen.

The holotype CES 348, the paratype CES 015.5 and the additional specimen CES 392.4 originally belonged to the same amber piece (Pérez-de la Fuente, 2012).

Diagnosis. As for the genus (see above) with the following addition: fore- and hind wing membranes hyaline, lacking fuscous spots or other maculations.

Description. *Male.* Total body length 1.33 mm.

Head. Cephalic capsule higher than long (0.38 mm high, 0.25 mm long); genae long, malar space very short. Compound eye 0.21 mm high, 0.12 mm long, (H/L= 1.75), height 0.55× that of head. Vertex swollen. Fontanelle present, relatively large, expanded posterolaterally, leaving

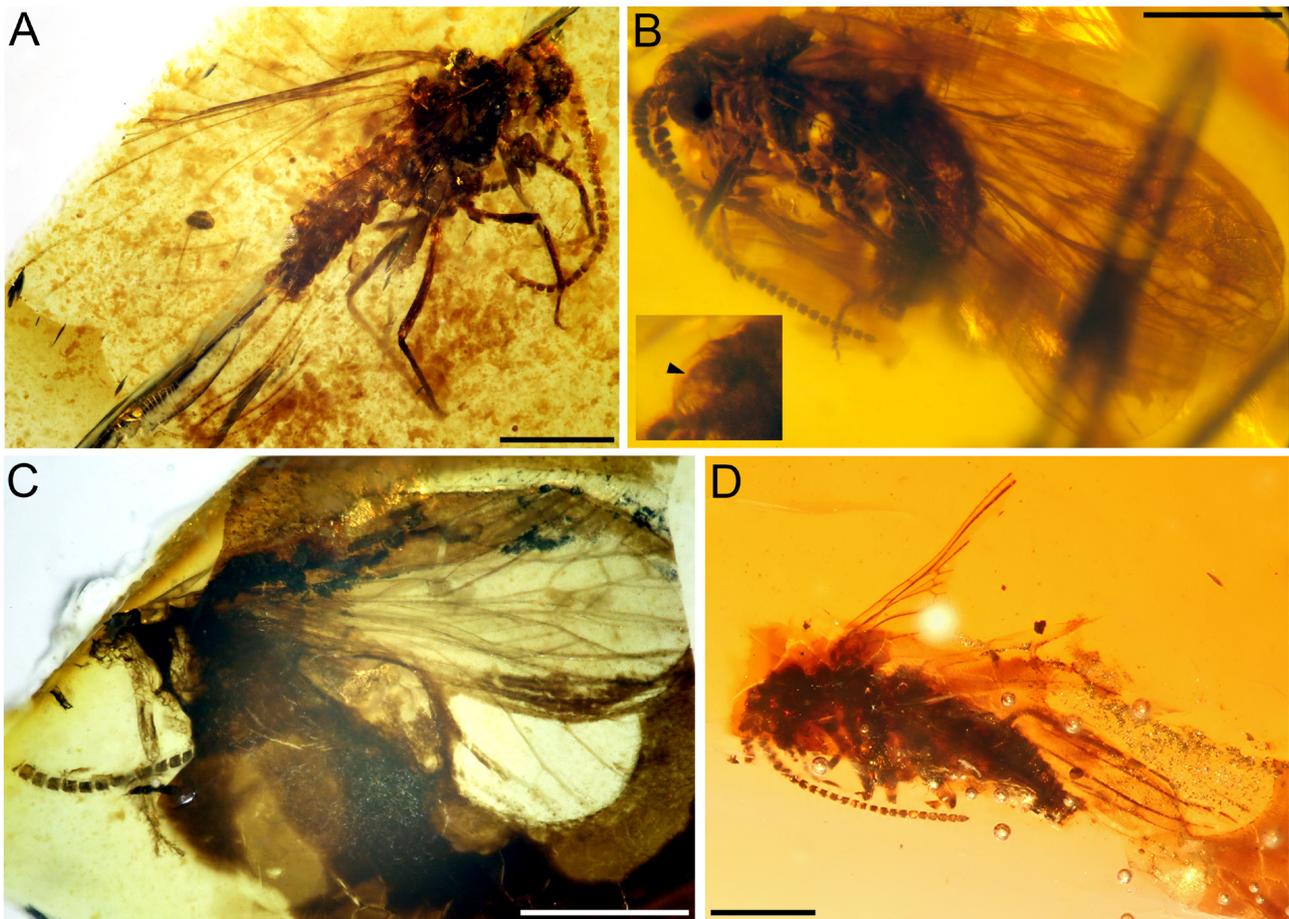


FIGURE 2. *Soplaoconis ortegablancoi* gen. et sp. nov. (Neuroptera: Coniopterygidae), habitus of paratypes and additional specimen. **A**, Dorsolateral habitus of paratype CES 459. **B**, Lateral habitus of paratype CES 015.5. Bottom left inset magnifies the proximal frons-vertex area, with arrowhead pointing at the posteromedian frontal sclerotization. **C**, Lateral habitus of paratype CES 460. **D**, Lateral habitus of additional specimen CES 392.4. All scale bars 0.5 mm.

a rather pronounced posteromedian frontal sclerotization (well visible in CES 015.5, Fig. 2B); full fontanelle shape unknown (frontal view not available for any specimen). Antennae 24–27 segmented, 1.01 mm long. Scape and pedicel relatively short. Scape expanded distally, slightly longer than wide, 0.08 mm long, 0.06 mm wide, separation between scapes not assessable. Pedicel slightly wider than long, 0.06 mm long, 0.07 mm wide. Antennae with 22–25 flagellomeres; flagellomere 1 bell-shaped, about as long as wide; flagellomeres 2–4 clearly transverse, 0.03 mm long, 0.05 mm wide, gradually lengthening distally, by flagellomere 10 clearly becoming about as long as wide, subquadrate; terminal flagellomere subconical. Maxillary palpus pentamerous, 0.36 mm long, with all palpomeres about twice as long as wide; palpomeres cylindrical but terminal palpomere, triangular in lateral view and with a flat mesal edge. Basigalea distinct (Fig. 4A), galea with distal digitation. Labial palpus trimerous, 0.17 mm long; terminal labial palpomere enlarged, fusiform, 0.10 mm long, 0.04 mm wide, inserted to palpomere 2 by its extero-proximal edge.

Thorax. Total length 0.51 mm. Legs slender, densely covered by microtrichia. All legs with minute spines along tibiae. Tarsi pentamerous. First tarsomere longest, as long as subsequent three tarsomeres on all legs. All fourth tarsomeres shorter than remaining tarsomeres, broad, dorsally slightly hollowed around base of fifth tarsomere, produced into two ventrodistal lobes (bilobed). Pretarsal claws minute, simple; arolium absent. Wing membranes hyaline, lacking fuscous spots. Wings with marginal fringe composed of minute setae; with particularly larger setae, almost spine-like, interspersed every 5–12 minute setae (Fig. 4E); fringe present on entire wing margin down to cubital/anal veins (Fig. 3A).

Forewing relatively narrow, 1.73 mm long, 0.55 mm wide ($L/W = 3.2$) (Fig. 3A, B). Two distinct costal crossveins proximally ($1c-sc_1$ and $2c-sc_1$) in costal area, separated by about $6\times$ their length. Sc_2 meeting RA strongly basad sc_2-rp_1 . Crossvein sc_2-rp_1 striking RP_1 distad fork of RP_1 and RP_2 . Basal abscissa of RP_2 (its stretch before rp_2-ma_1 crossvein) elongate, slightly angled forwards at about its midlength (Fig. 4C, D). Basal abscissa of RP_2

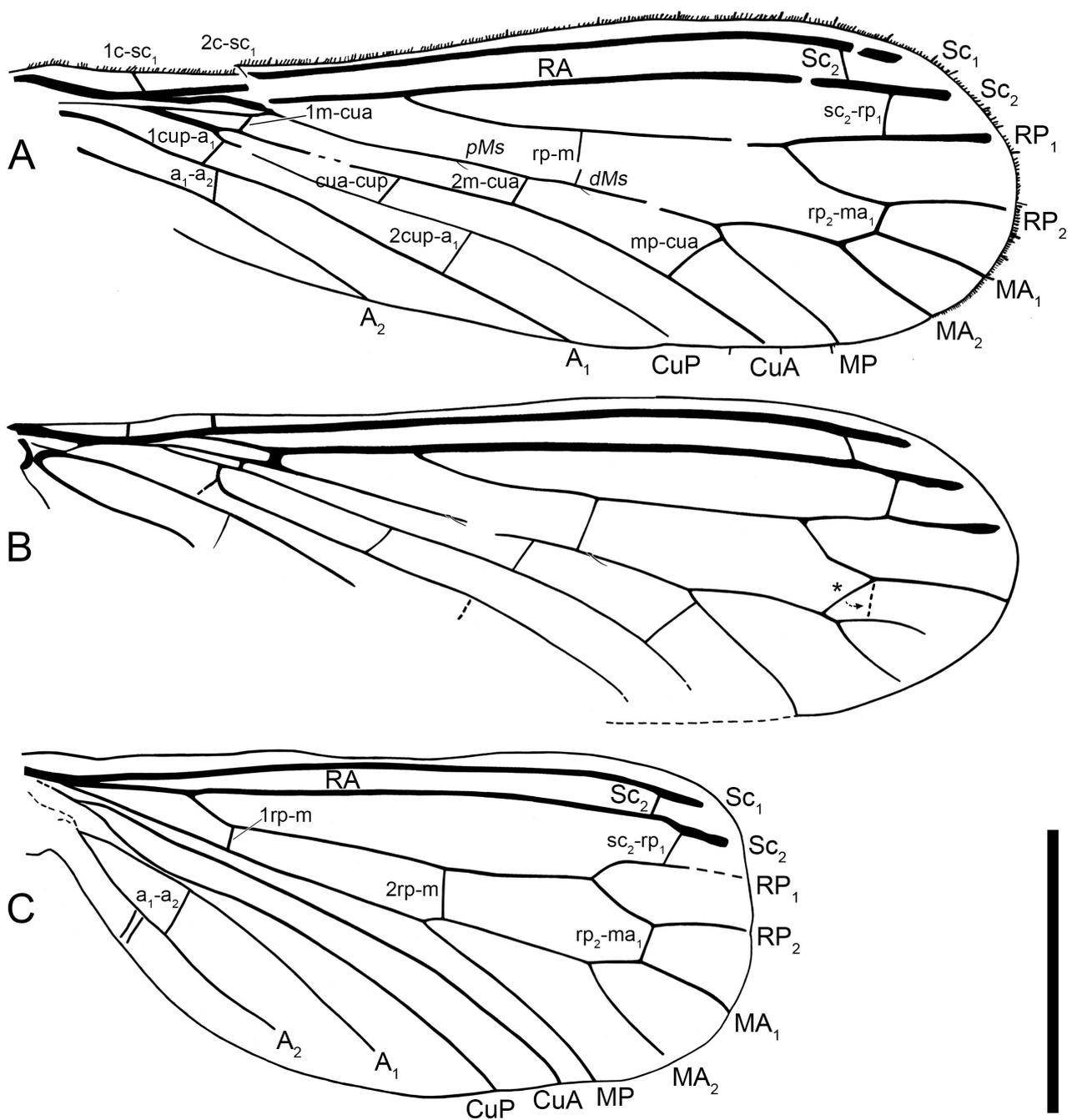


FIGURE 3. Camera lucida drawings of the wings of *Soplaoconis ortegablancoi* **gen. et sp. nov.** (Neuroptera: Coniopterygidae), holotype CES 348. **A**, Left forewing (mirrored), with venational nomenclature tagged. **B**, Right forewing. The asterisk marks an abnormal state of the rp_2 - ma_1 crossvein, with the dashed arrow showing its normal state. **C**, Right hind wing, with venational nomenclature tagged. The distal anterior part of the wing has been unfolded. Fringe of microsetae has only been depicted in A. All drawings to the same scale. Scale bar 0.5 mm.

nearly aligned with apical abscissa of RP_2 (not strongly angled at rp_2 - ma_1 crossvein). RP_2 not fused to MA_1 , both connected by a rp_2 - ma_1 crossvein. Crossvein rp - m near wing midlength, distad of $2m$ - cua . M vein with two stiff setae present (visible in both forewings of holotype and right forewing of paratype CES 460), apparently lacking insertion thickenings: proximal median seta (pMs) and distal median seta (dMs), rather distal in position, i.e.,

0.51 and 0.75 mm from M branching, respectively (Fig. 3); bases of setae separated by distance ~ 7 – $9\times$ length of setae. M with three branches, MP (i.e., posterior branch of M) branching off at distal third of wing. Distalmost medio-cubital crossvein (mp - cua) present between MP and CuA . Posteriormost anal region not visible in any forewings, so presence of crossvein between A_2 and wing margin unknown.

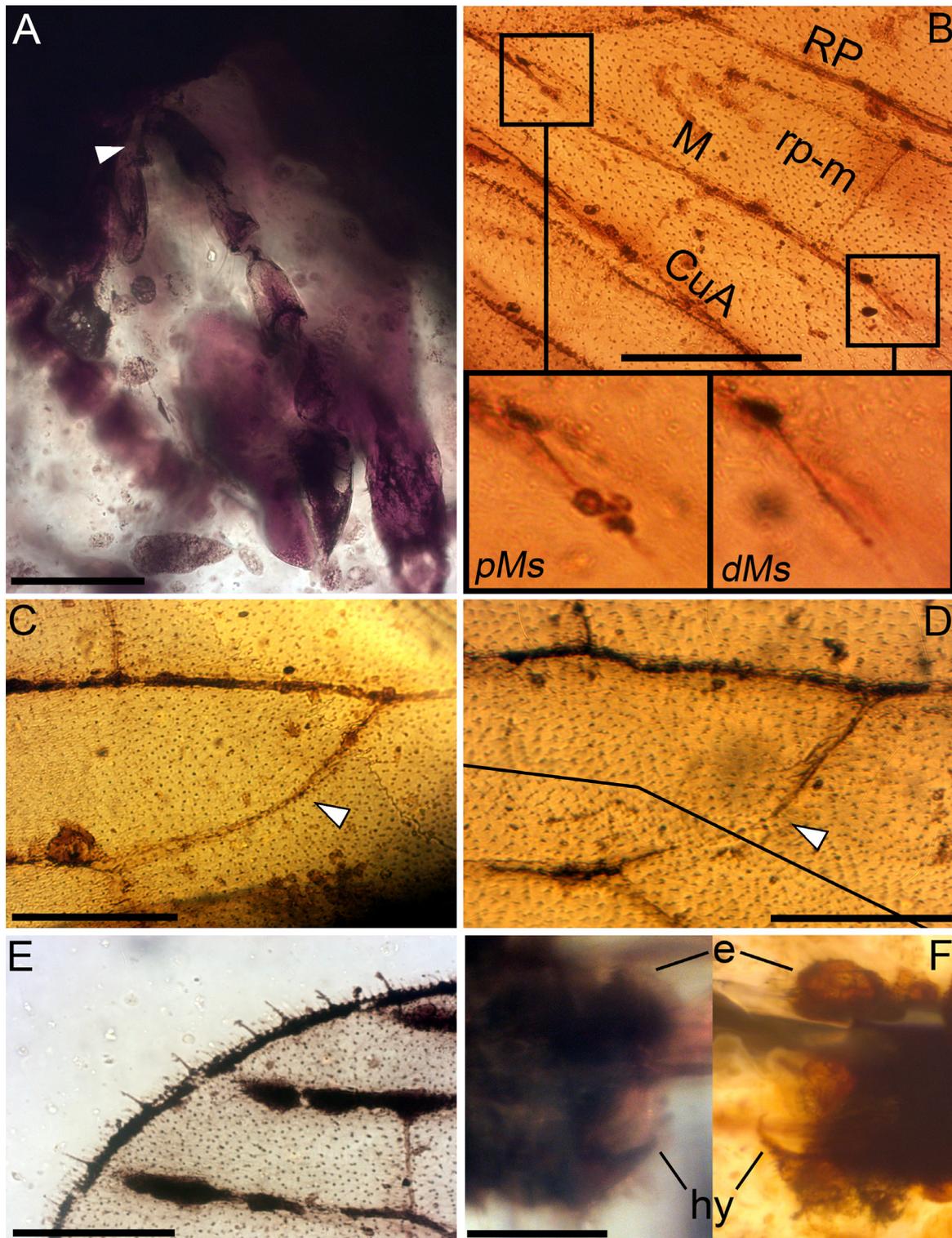


FIGURE 4. *Soplaoconis ortegablancoi* gen. et sp. nov. (Neuroptera: Coniopterygidae), detail photomicrographs taken from the paratype CES 459 (A, F) and the holotype CES 348 (B–F). **A**, Mouthparts, including left maxillary palpus and galea (arrowheads points to the basigalea). **B**, Central area of the right forewing, showing the proximal and distal median setae (*pMs* and *dMs*). **C**, Basal abscissa of RP_2 from left forewing. Image is a single shot photograph, i.e., not affected by wing folding nor depth distortion. Change of slope is marked by an arrowhead. **D**, Basal abscissa of RP_2 from right forewing (mirrored). Image composed by two single shot photographs separated by a black line, the latter following a moderate folding on the wing membrane. Change of slope is marked by an arrowhead. **E**, Wing margin of the right forewing showing fringe of minute setae interspersed with larger, spine-like setae. **F**, Terminalia in lateral view (left, holotype CES 348; right, paratype CES 459). Both images share the scale. All scale bars 0.1 mm.

Hind wing 1.30 mm long, about 0.57 mm wide ($L/W = 2.3$), slightly wider than forewing (Fig. 3C). RP branching at 0.31 mm of the wing base, i.e., at about $\frac{1}{4}$ of wing length. Bases of M and Cu running almost parallel and very close to each other for about basal third of their length. RP with two branches. Media with three branches. Three radio-medial crossveins present: 1rp-m present $2\times$ its length after branching of RP, 2rp-m right after branching of MP, and rp_2-ma_1 at about midlength of RP_2 . Anal region with two anal veins and two crossveins, an a_1-a_2 crossvein and a crossvein between A_2 and wing margin.

Abdomen. Total length 0.57 mm. Plicaturae visible on sternites III and IV (Fig. 1B), but number of pairs of abdominal plicaturae not entirely visible. Terminalia with ectoproct arched, moderately sized; caudal projections of gonarcus not discernible, not particularly developed if present; hypandrium protruding caudally, with terminal processes sharp and recurving mediodorsad (Fig. 4F).

Female. Unknown.

Locality and age. El Soplao amber outcrop (Rábago, Cantabria, northern Spain); middle Albian (ca. 105 Ma) (E. Barrón, pers. comm.), Early Cretaceous (Najjarro *et al.*, 2009, 2010).

Etymology. The specific epithet is a patronym honouring Dr. Jaime Ortega-Blanco, a good colleague, friend, and an important and dedicated scholar of Spanish amber.

Discussion

The suprageneric affiliations of the new genus and species within Coniopterygidae follow the classification of Meinander (1972). Assignment to the subfamily Aleuropteryginae is based on the dorsoventrally elongate head capsule in lateral view, with genae long; the galea with basigalea (Fig. 4A) and a terminal knob; the forewing having two radio-medial crossveins, two setae on M with more or less enlarged bases; the hind wing with RP branching off from R very near the base of the wing; and the presence of plicaturae, i.e., highly folded, oblong, membranous areas on the sternites of three to six abdominal segments (Fig. 1B) (see Tjeder, 1957). The new genus and species is assigned to the tribe Fontenelleini due to the presence of a large unsclerotised area on the frons (= fontanelle), wings with very short marginal fringes (Fig. 4E), RP of the forewing superficially resembling the anterior branch of M, and radial crossvein (= sc_2-rp_1) of hind wing striking RP on branch RP_1 and not on or before forking (Meinander, 1972).

The presence of two stiff setae on the forewing media is a character easy to overlook but it is clearly visible in

the two wings of the holotype (CES 348) as well as in the right wing of the paratype CES 460 (its other wing is folded). In both specimens, the setae on the media are not inserted in conspicuous vein thickenings as occurs in other species where this character is present such as in *Apoglaesoconis* Grimaldi, 2000, *Geroconiocompsa* Engel, 2010, *Garnaconis* Perrichot & Nel, 2014, or *Achlyoconis* Engel, 2016 (Grimaldi, 2000; Engel, 2010, 2016; Perrichot *et al.*, 2014), although this might be related to deficient preservation of the wings (venation has a somewhat distorted appearance in both specimens). Note that two setae on the media, although not figured or depicted, were also described from *Alboconis* Nel *et al.*, 2005.

The presence of three branches of the forewing media, a character unknown in modern representatives (Meinander, 1972; Engel, 2016), rules out the affiliation of the specimens described herein with the Cretaceous species having only two forewing media branches, i.e., *Burmaleuropteryx* Li *et al.*, 2019, *Cretaconiopteryx* Liu & Lu, 2017, *Garnaconis*, *Libanosemidalis* Azar *et al.*, 2000, *Mulleroconis* Ružičková *et al.*, 2019, *Paranimboa* Engel, 2016, and *Phthanoconis* Engel, 2004 (see remarks on *Alboconis* below), whereas the presence of setae on the forewing media in the new fossil species precludes assignment to the genera *Cycloconis* Li *et al.*, 2019, *Glaesoconis* Meinander, 1975, and *Libanoconis* Engel, 2002 (see Whalley, 1980; Azar *et al.*, 2000; Grimaldi, 2000; Engel, 2004, 2016; Nel *et al.*, 2005; Sziráki, 2016, 2017; Makarkin & Perkovsky, 2017, 2019; Li *et al.*, 2019). Other taxa possessing a forewing with three media branches and with setae on the media, as in the new genus and species, are classified in the genera *Achlyoconis*, *Apoglaesoconis*, and *Palaeoconis* Ružičková *et al.*, 2019. However, the two species within the genus *Achlyoconis*, i.e., *A. heptatrachia* Engel, 2016 and *A. jiae* Li *et al.*, 2019, have seven stiff setae along the entire forewing media's length (Engel, 2016), not two, whereas *Palaeoconis* has only one stiff seta on the media (Ružičková *et al.*, 2019). Moreover, in the four species classified in the genus *Apoglaesoconis*, the two median setae are more proximal in position, and RP_2 (= R_{4+5}) and MA_1 (= M_{1+2}) are partially fused (and therefore a distal radio-medial crossvein, rp_2-ma_1 , is absent) (Grimaldi, 2000; Engel, 2002). The latter condition was also reported from an *Achlyoconis heptatrachia* specimen (Li *et al.*, 2019: fig. 2E). Two further characters present in *S. ortegablancoi* **gen. et sp. nov.** are highly distinctive and allow to further distinguish it from the species classified within the genera *Apoglaesoconis*, *Achlyoconis*, and *Palaeoconis*. First, the shape of the basal abscissa of RP_2 in the forewing is highly characteristic of the new genus and species. It is not straight as in most other Cretaceous coniopterygids but changes its slope rather abruptly (angled) at about

its midlength anteriorly, similar to the condition present in *Achlyoconis*, although RP_2 is significantly more elongate (see Engel, 2016; Li *et al.*, 2019). And second, the presence of a distal medio-cubital crossvein (mp-cua) placed between the last branch of M (=MP) and CuA in the forewing is a character state absent from all other known Cretaceous amber coniopterygids but three: *Alboconis cretacica* Nel *et al.*, 2005, *Cretaconiopteryx grandis* Liu & Lu, 2017, and *Palaeoconis azari* Ružičková *et al.*, 2019. In *Burmaleuropteryx meinanderi* Li *et al.*, 2019 and *Phthanoconis burmitica* Engel, 2004, there is a rather distal medio-cubital crossvein but it precedes the basalmost branch of M. Furthermore, it is important to note that although *A. cretacica* (which possesses two stiff setae on the forewing's M rather basally as described by Nel *et al.*, 2005) was described as having two branches on the forewing's media, it could actually possess three, as the forewing's tips are missing from the specimen. Similarly, the shape of the basal abscissa of RP_2 is also unclear but it could resemble that of *S. ortegablancoi*, although it appears not to be clearly angulate in the photograph and drawing provided by Nel *et al.* (2005). In any case, *Alboconis* is herein considered distinct from *Soplaconis* **gen. nov.** in the presence of fuscous spots on the forewing and a remarkably lower number of flagellomeres (18), although these differences appear rather weak when considered alone and so further French and Spanish material could draw a narrower line between these two genera. It should be also noted that the exact number of flagellomeres is a character considered to show certain intraspecific variability (Meinander, 1972) and therefore unreliable for taxonomic purposes to a certain extent. For instance, the antennae of *Glaesoconis cretica* Meinander, 1975 were described as having 24 to 27 antennomeres, those of *G. balipteryx* Engel, 2004 as 27 to 29 (25 to 27 flagellomeres), and those of *G. nearctica* Grimaldi, 2000 with 27 to 32 antennomeres (25 to 30 flagellomeres) (Meinander, 1975; Grimaldi, 2000; Engel, 2004). The number of antennal articles in the new genus and species varies between 24 and 27 (23 to 25 flagellomeres): 25 antennomeres in the holotype, 27 in the paratypes CES 015.5 and CES 459 (head not preserved in the paratype CES 460), and 24 in the additional specimen CES 392.4. Anomalous, often intraindividual, venational features resulting in fluctuating asymmetry within a species' population have been long recognised in the modern insect fauna (Giard, 1896), and have been related to environmental 'stress' (Clarke, 1993; New, 1998). These abnormal conditions can be frequent in some groups, such as termites (Engel & Delclòs, 2010), and have also been detected in extinct insects. Among neuropterans, asymmetrical wing venation (usually altering crossvenation) has been reported in fossils belonging to several groups (Makarkin

& Perkovsky, 2009; Yang *et al.*, 2010; Makarkin *et al.*, 2016), including coniopterygids (Sziráki & Gröhn, 2015). In the holotype of the new species, whereas the rp_2 - ma_1 crossvein in the left forewing of the holotype is connected to MA after its bifurcation (normal state), that of the right forewing connects to MA before its bifurcation, and it is twice as long and markedly more oblique (Figs 1, 3). This represents yet another instance that highlights the need to consider character plasticity and/or abnormal conditions as potential sources of noise in fossil insect systematics and, more particularly, in those of fossil Coniopterygidae, since the forewing venation around the distal branches of RP and MA bears a high diagnostic significance.

It is not unusual for plant trichomes to be preserved in the close vicinity of the described Cretaceous coniopterygids from Spanish and Burmese ambers. Apart from the holotype of the new species (Fig. 1), and based on the published photographs, that is the case of seven specimens belonging to seven of the eleven species hitherto described from Burmese amber, i.e., the holotypes of *A. jiae*, *B. meinanderi*, *C. grandis*, *Mulleroconis hyalina* Ružičková *et al.*, 2019, *Paranimboa litotes* Engel, 2016, the paratype of *G. balipteryx*, and an additional specimen of *A. heptatrachia* (Engel, 2004, 2016; Liu & Lu, 2017; Li *et al.*, 2019; Ružičková *et al.*, 2019). In total, this represents almost a third of the described coniopterygid individuals from Spanish and Burmese ambers (eight out of 27 individuals), a number that would appear to be higher than that expected by chance. Some of the trichomes preserved together with the coniopterygids are clearly dendritic, show different maturity stages, and fit within the category recognised as belonging to ferns (see Pérez-de la Fuente *et al.*, 2012). If supported by a larger sample pool, the co-occurrence as proximity syninclusions of trichomes and dustywings in Spanish and Burmese ambers could indicate that these insects frequented trichome-producing vegetation (namely ferns) presumably to hunt on the herbivorous arthropods feeding there upon, such as mites or homopterans, a circumstance that takes place in modern ecosystems (Meinander, 1972; Oswald & Machado, 2018).

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