

A new species of *Cretevania* (Hymenoptera: Evaniidae) preserved in Albian amber of El Soplao (Cantabria, Spain)

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Abstract

A new species of the diverse extinct genus *Cretevania* Rasnitsyn, 1975, *Cretevania orgonomecorum* Peñalver & Sánchez-García **sp. nov.**, is described from Spanish Lower Cretaceous (middle Albian) amber from El Soplao, based on a single, complete and well-preserved female. The new species is compared with other known species of the genus, mainly those with similar wing shape and venation, large body size, and those described from Albian Spanish amber. This new species is among the largest within the genus and similar in body length to *C. tenuis* from Cenomanian Kachin amber (Myanmar) and *C. pristina* from Barremian compression rocks of Beipiao (China). Its description and the revision of other species have led to the identification of previously unrecognized characters which may be useful in future taxonomic diagnoses. These results contribute to a more accurate understanding of interspecific differences and will help delimit species boundaries within a genus, proving increasingly diverse in the Cretaceous. The previously established synonymisation of the genus *Procretevania* as junior to *Cretevania* is also reviewed here. Palaeobiological comments are provided based on anatomical features of the genus.

Keywords: Insecta, ensign wasp, new taxon, wing venation, Mesozoic

Introduction

The extinct hymenopteran genus *Cretevania* Rasnitsyn,

1975 was erected in its own extinct family Cretevaniidae (Rasnitsyn, 1975) and later classified within the extant family Evaniidae (Basibuyuk *et al.*, 2002). The genus is diverse and currently encompasses 20 fossil species preserved in Cretaceous amber and compression deposits across Spain, the United Kingdom, Jordan, Lebanon, Myanmar, the Russian Federation, Mongolia and China (Rosse-Guillevic & Jouault, 2023: fig. 4). The genera *Procretevania* Zhang & Zhang, 2000, *Eovernevania* Deans, 2004 and *Dabburatypus* Kaddumi, 2005 are junior synonyms of *Cretevania* (Peñalver *et al.*, 2010; Li *et al.*, 2018). The species count above includes a new combination established in 2018, *Cretevania extincta* (Kaddumi, 2005), although the taxon was originally described without a diagnosis and the holotype specimen needs reevaluation and a new description.

Here, we present a new species of *Cretevania* from middle Albian amber of the El Soplao outcrop (Cantabria, Spain), within the Las Peñas Formation. This is the second species of the genus described from El Soplao amber and is based on a complete female specimen.

Material and methods

The specimen described herein is preserved in amber from the El Soplao outcrop, dated as middle Albian and located in the municipality of Herrerías (Rábago,

Cantabria, northern Spain). To date, this deposit has yielded approximately 1,550 bioinclusions, from which 30 species of arthropods have been described (Peñalver *et al.*, 2025). Discovered in 2005 during roadworks to improve access to El Soplao Cave, the first bioinclusions were identified in 2007 at the Geological Survey of Spain. The outcrop is located within the subsident Basque-Cantabrian Basin, which originated from extensional forces associated with a distensive rift setting along the northern Iberian margin. On the western margin of the basin, the El Soplao outcrop occurs within an Albian siliciclastic unit (Las Peñas Fm.) that represents a transition between continental and marine environments, positioned within a regressive-transgressive marine carbonate sequence spanning from the early Aptian to the Albian. The amber is found within the maximum regressive phase (Najarro *et al.*, 2009, 2010). For further details on the geology and research, see Peñalver *et al.* (2025). El Soplao amber outcrop is the type locality of three species of hymenopterans, and two other species are present as co-occurrences (Álvarez-Parra & Azar, 2024). The new species herein described increases the number of wasp species in Spanish amber to 52 (Álvarez-Parra & Azar, 2024).

The amber piece was encased in high-quality epoxy casting (Epo-Tek 301), following the protocols outlined in Corral *et al.* (1999) and Nascimbene and Silverstein (2000). This process enabled thin slicing and precise polishing of the amber pieces, allowing for optimal viewing of the inclusions near the surfaces. The holotype specimen is housed at the Institutional Collection from the El Soplao amber outcrop, El Soplao Cave facilities, Celis, Cantabria, Spain.

Taxonomic identification and investigation were conducted using an Olympus BX53 compound microscope (at IGME, CSIC, València, Spain) under both transmitted and reflected light. One general photograph was taken using a Canon EOS 650D digital camera with the software ‘Macrofotografía 1.1.0.5’ (IGME, CSIC, Madrid, Spain). The rest of the photographs were taken using the Olympus BX53 compound microscope equipped with a digital camera. Some photographs were created by stacking sequential images obtained at different focal planes. Photo-plates were processed and edited using Adobe Photoshop CS2 version 9.0. The specimen was illustrated with the aid of an Olympus U-DA drawing tube attached to the Olympus BX53 microscope.

Wing venation nomenclature follows Peñalver *et al.* (2010), basically that by Deans & Huben (2003).

Published work and nomenclatural acts are registered in ZooBank (<http://www.zoobank.org/>, last access: 11/08/2025), with the following LSID (reference): urn:lsid:zoobank.org:pub:E96EC2C0-03B7-4519-8E9A-69F45454FF7E

Systematic palaeontology

Order Hymenoptera Linnaeus, 1758

Suborder Apocrita Gerstaecker, 1867

Superfamily Evanioidea Latreille, 1802

Clade Neoevanioidea Engel, 2006

Family Evaniidae Latreille, 1802 (as Evaniales)

Genus *Cretevania* Rasnitsyn, 1975

Type species. *Cretevania minor* Rasnitsyn, 1975; by original designation from Late Santonian Yantardakh amber (Taimyr, Russia; see Zherikhin & Eskov, 1999).

Other species. See the list of the 20 described species in Rosse-Guillevic & Jouault (2023). One species described by Li *et al.* (2018) is inconsistently referred to as *C. venae* and *C. venata* in that paper; however according to the abstract, the Systematic Palaeontology section and the record in ZooBank, the correct name is *C. venae*. The total current number of recognised species, included the herein described, is 21.

Cretevania orgonomesorum Peñalver & Sánchez-García sp. nov.

(Figs 1–4)

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Material. Holotype CES 646 (female), housed at the Institutional Collection from the El Soplao amber outcrop located in the laboratory of the El Soplao Cave, Celis, Cantabria (Spain). The amber piece is 9 × 8 × 2 mm in size embedded into an epoxy resin prism of 19 × 14 × 2 mm. The specimen is complete, preserved in turbid amber and with some internal amber cracks which hinder the observation of some features, as the antennal insertions, eyes and ocelli. No syninclusions are present.

Etymology. The specific epithet is dedicated to the Orgonomesci people, who fought against Roman dominion and inhabited the Cantabrian area where the El Soplao outcrop is located. The name Orgonomesci derives from Celtic and can be translated to “bloodthirsty warriors”.

Diagnosis. Female. Large *Cretevania* species distinguished from the other species within the genus by the following combination of characters: (1) flagellum not broader distally, (2) 11 flagellomeres, (3) forewing apex rounded (*i.e.*, not pointed), (4) vein Sc+Rb as long as Sc+Ra, (5) pterostigma short and broad (less than 3 times longer than wide), (6) first submarginal cell ≈ 5.5 times longer than wide, (7) vein 2RS slightly curved, (8) first marginal cell ≈ 3.5 times longer than wide at base, (9) first discal cell slightly elongate, nearly squared, (10)

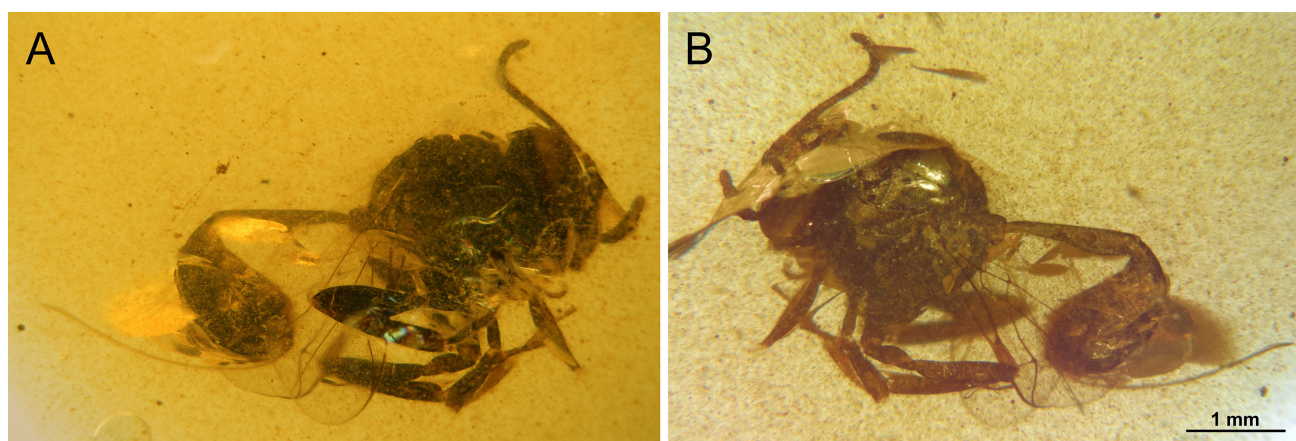


FIGURE 1. Holotype female of *Cretevania orgonomecorum* sp. nov. (Evaniidae), holotype CES 646, from middle Albian El Soplao amber, Herrerías-Rábago (Cantabria, Spain). **A**, Ventrolateral (left) view. **B**, Dorsolateral view. Both images at the same scale, composed from photographs taken at different focal planes.

1CU $\approx$ 2 times longer than 1m-cu, (11) 1r-rs straight (*i.e.*, not concave), (12) absence of a spectral vein rs-m, (13) complicated bulla forming a gap between each of 2RS+M, 2RS and 2M, (14) vein 2M nearly straight (*i.e.*, not concave subbasally), (15) vein 2CU+3CU steeply changing its slope distally, (16) vein 2cu-a strongly angled towards wing base, and (17) petiole $\approx$ 5 times longer than wide.

Locality and horizon. Middle Albian amber outcrop of El Soplao (near Rábago village, Herrerías municipality, Cantabria, northern Spain), Peñosas Fm. (Najarro *et al.*, 2009, 2010; Peñalver *et al.*, 2025).

Description. Female. Body (Figs 1, 4A) approximately 5 mm in length, including the petiole and gaster. Body shape rather robust, not gracile. Head large (0.68 long $\times$ 1.40 high mm in lateral view), with occipital carina lacking areolate sculpture. Eye large and ovoid, without setae, composed of numerous, minute ommatidia. Ocelli large (only two observed due to an internal crack in the amber piece). Antenna inserted on forehead, densely setose, with 11 flagellomeres, at least 2 mm long. Scape slightly broader and slightly expanded apically. Pedicel not expanded apically and small, subequal to flagellomere 1. Flagellomere 1 shorter than 2 ($\approx$ 0.8 the length of 2); flagellomere 11 rounded distally. Sensorial pits visible on several flagellomeres, elongate in the mid flagellum and circular on the distal flagellomere (Figs 2A, B, 4B). Flagellum uniformly thickened. Palpomeres obscured.

Mesosoma as high as long ($\approx$ 1.69 mm), with scarce sculpturing. Mesoscutum large and lacking notauli. Mesopleuron with areolate/polygonal sculpture at least on its ventral margin. Propodeum with scarce areolate sculpture close to hind coxa and at the posterior limits. Legs without sculpturing, setose, with conspicuous trochantellus and five tarsomeres. Fore and mid legs long

and thin, hind legs robust. Hind coxa very robust. Base of mid and hind coxae practically contiguous. Tibiae lack apical spurs and strongly sclerotized distal plates (unlike *C. alcalai*; see in Peñalver *et al.*, 2010), but the presence or absence of apical spurs in the fore tibiae has not been clearly observed, so this anatomical feature remains unresolved. Fore legs obscured, femur thin and constant in thickness throughout, 0.88 mm long. Fore tarsi not well visible. Mid leg 2.26 mm long, 2.62 mm including the trochanter; femur widened distally, 0.70 mm long, 0.21 mm at greatest width; tibia widened subdistally, 0.82 mm long, 0.14 mm wide distally; tarsus 0.74 mm long; tarsomere 1 of mid leg as long as the combination of ta2 to ta4. Hind leg 3.24 mm long, 3.76 mm including the trochanter; femur not widened basally or distally, 0.98 mm long, 0.18 mm at greatest width; tibia slightly widened distally, without a loose collection of spines along distal edge, 1.20 mm long, 0.18 mm wide distally; tarsus 1.07 mm long, approximately half as long as the mesosoma; tarsomere 1 of hind leg as long as combination of ta2 to ta5 (ta1 $\approx$ 3.5 times longer than ta2). Tarsal claws badly preserved.

Wings (Fig. 4C) hyaline, with abundant microtrichia. Forewing with apex rounded, without jugal lobe, 2.58 mm long, 1.44 mm at greatest width. Pterostigma dark brown, 0.33 mm long, 0.11 mm wide. Venation tubular, including 2M, 3M and 2CU+3CU. Vein 2CU+3CU extending to wing margin and arising directly from 1CU, steeply changing its slope distally. Vein 1CU $\approx$ 2 times longer than 1m-cu. Crossvein 1r-rs straight (Fig. 2F), near the pterostigma apex. Absence of a spectral vein rs-m. Vein 1RS short, strongly inclined towards wing base. Vein 1M slightly curved and longer than 1RS. Vein RS+M short. First marginal cell triangular and broad ($\approx$ 3.5 times longer than wide at base). Vein 3RS+4RS slightly curved. First

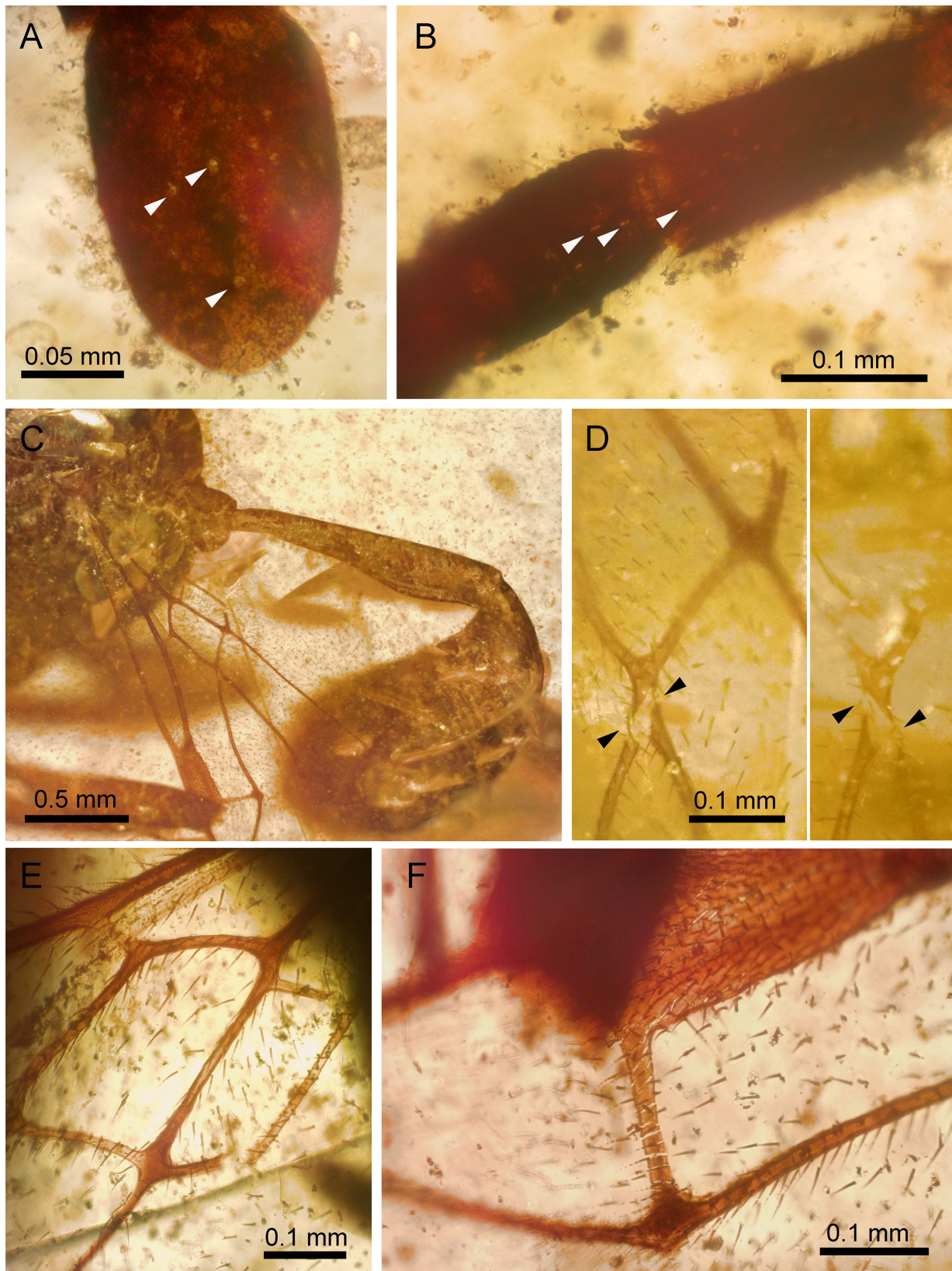


FIGURE 2. Antennae and forewing details of the holotype female of *Cretevania orgonomecorum* **sp. nov.** (Evaniidae), holotype CES 646, from middle Albian El Soplao amber, Herrerías-Rábago (Cantabria, Spain). **A**, Left distal flagellomere showing circular sensorial pits by transparency, some of them indicated with white arrowheads. **B**, Right middle flagellomeres showing elongated sensorial pits by transparency, some of them indicated with arrowheads. **C**, Metasoma in lateral view. **D**, Complicated bulla forming a gap between each of 2RS+M, 2RS and 2M (black arrowheads). **E**, Detail of the first discal and first subdiscal cells. **F**, Detail of the crossvein 1r-rs. Images composed from photographs taken at different focal planes, except **D** (left).

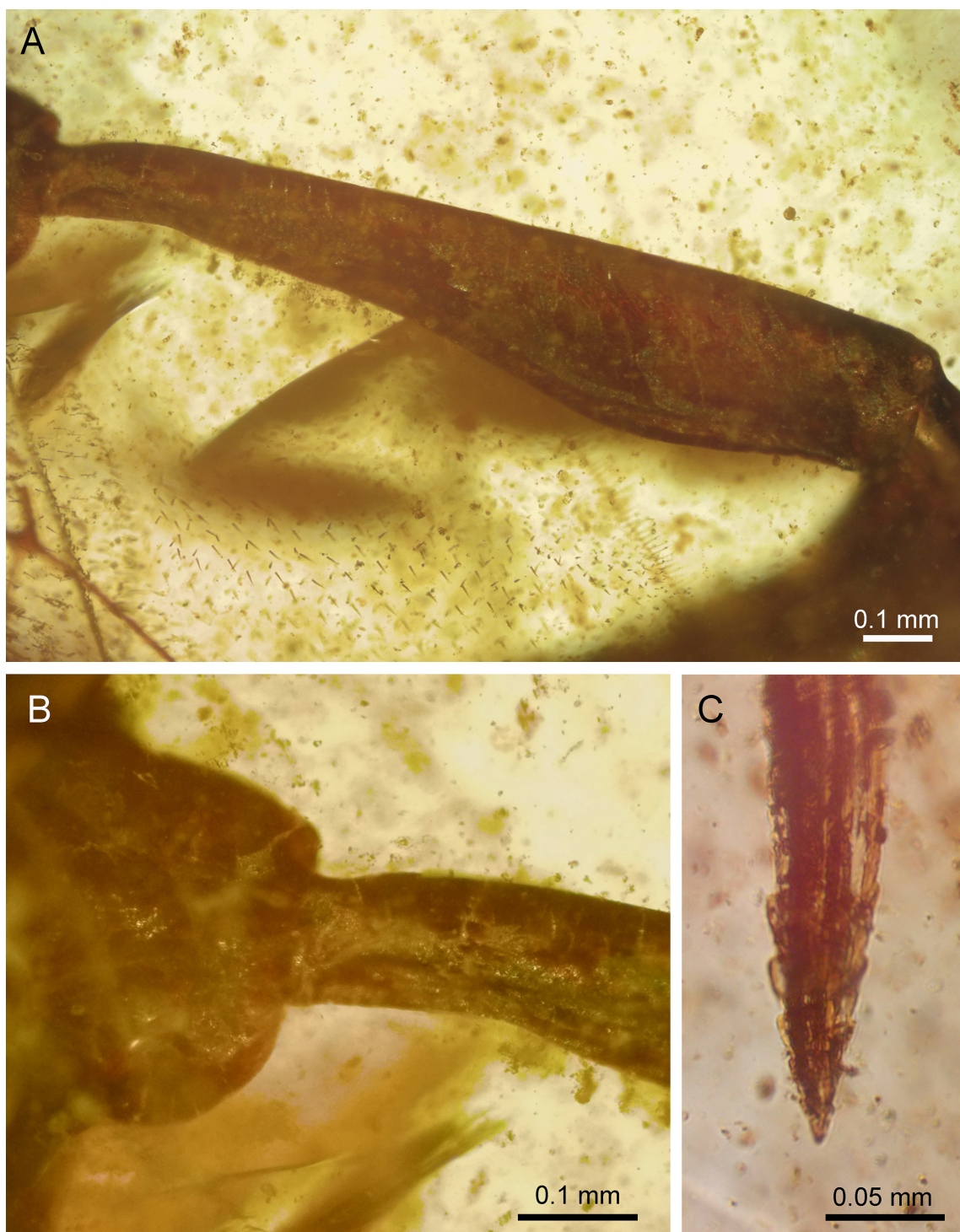


FIGURE 3. Metasomal details of the holotype female of *Cretevania orgonomecorum* **sp. nov.** (Evaniidae), holotype CES 646, from middle Albian El Soplao amber, Herrerías-Rábago (Cantabria, Spain). **A**, Petiole in lateral view. **B**, Articulation of the petiole with the mesosoma. **C**, Apex of the ovipositor showing annuli. Images composed from photographs taken at different focal planes.

submarginal cell broad (≈ 5.5 times longer than wide). First discal cell slightly elongate, nearly squared. First subdiscal cell elongate, narrow, smaller than first discal cell (Fig. 2E). Vein 2RS slightly curved. Complicated bulla forming a gap between each of 2RS+M, 2RS and 2M (Fig. 2D). Vein 2M nearly straight. Crossvein 1m-cu meets the vein M at the divergence of veins 2RS and 2M.

Crossvein 2cu-a aligned with 1m-cu. Vein 2cu-a strongly angled towards wing base. Crossvein 2m-cu absent. Hind wing with a strong costal vein and no other veins present.

Petiole (Figs 2C, 3A, B) subcylindrical, ≈ 5 times longer than wide (1.31 mm long, 0.27 mm at greatest width), with tergum and sternum fused, with distal half

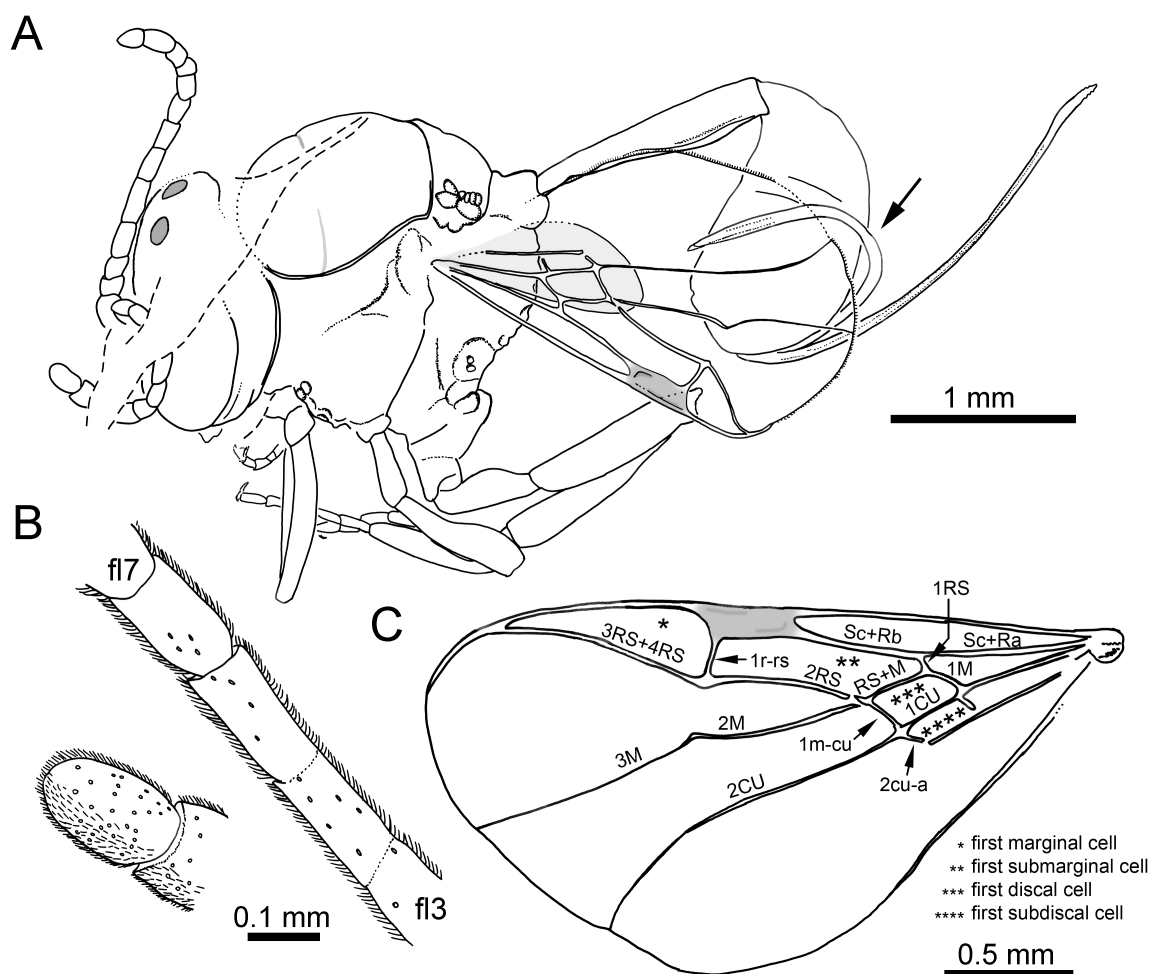


FIGURE 4. Camera lucida drawings of *Cretevania orgonomecorum* sp. nov. (Evaniidae), holotype CES 646, from middle Albian El Soplao amber, Herrerías-Rábago (Cantabria, Spain). **A**, Habitus in dorso-lateral view (hind wing coloured in grey; arrow indicates the ovipositor sheaths); the right legs and the right wings are not drawn. **B**, Sensorial pits on the antennae surfaces (details of the left distal flagellomere and right middle flagellomeres; flagellomere (fl) 3 to 7). **C**, Forewing reconstruction based on the two wings. Wing vein abbreviations: 1CU = first cubital; 1M = first medial; 1m-cu = first medial-cubital crossvein; 1RS = first radial sector; 1r-rs = first radial-radial sector crossvein; 2CU = second cubital; 2cu-a = second cubital-anal crossvein; 2M = second medial; 2RS = second radial sector; 3M = third medial; 3RS+4RS = third radial sector fused with fourth radial sector; RS+M = radial sector fused with medial; Sc+Ra = subcostal fused with the anterior branch of the radius; Sc+Rb = subcostal fused with the posterior branch of the radius.

expanded ventrally and a hump in the lower surface, not punctured, attached to dorsal surface of propodeum, and without ridges basally. Petiole meets propodeum much closer to metanotum than to hind coxae. Gaster (Fig. 2C) globe-shaped, 1.50 mm long, 0.81 mm wide. Ovipositor long, 2.46 mm long, exposed, curved and upturned, with the apex serrated corresponding to five annuli (Fig. 3C). The walls of the sheaths lack transverse narrow furrows and their apices are pointed and without setae.

Discussion

This is the second *Cretevania* specimen and species

described from the middle Albian El Soplao amber, following *C. soplaensis* Pérez-de la Fuente, Peñalver & Ortega-Blanco, 2012 (Pérez-de la Fuente *et al.*, 2012). The other four *Cretevania* species were described in slightly younger (upper Albian) Spanish ambers (Peñalver *et al.*, 2025): *C. alonsoi* Peñalver, Ortega-Blanco & Delclòs, 2010 from Peñacerrada I amber, *C. montoyai* Peñalver, Ortega-Blanco & Delclòs, 2010 and *C. alcalai* Peñalver, Ortega-Blanco & Delclòs, 2010 from San Just amber, and *C. rubusensis* Peñalver, Ortega-Blanco & Delclòs, 2010 from Arroyo de la Pascueta amber (Peñalver *et al.*, 2010).

The forewing of the new species is reminiscent of that of *C. alonsoi*. It differs from this species by having



FIGURE 5. Life reconstruction of the female of *Cretevania orgonomecorum* **sp. nov.** based on the holotype, and the silhouette of the male of *C. soplaensis* for size comparison; both species from El Soplao amber and both illustrations at the same scale. The body colouration is conjectural. Art by the co-author E.P.

a broader pterostigma, vein Sc+Rb as long as Sc+Ra, 2M ending distad to 2RS, vein 2cu-a strongly angled towards wing base, pedicel and flagellomere 1 subequal and absence of apical spurs in the tibiae (but not totally clear if the foretibiae lack apical spurs).

The differences between the new species represented by a female specimen and the male holotype of *C. soplaensis*, both from the same deposit, are more evident. *Cretevania orgonomecorum* **sp. nov.** is twice the size of *C. soplaensis* (Fig. 5), and its forewing differs by having a more elongate first marginal cell and by lacking the spectral vein rs-m. These differences are not attributable to sexual dimorphism, particularly since extant evaniids do

not appear to show sexual dimorphism in wing venation features or body size.

The holotype shows, through transparency, circular and elongate sensorial pits on some flagellomeres (Fig. 2A, B), a feature never observed in *Cretevania*. This interesting character has not been included in the diagnosis of *C. orgonomecorum* **sp. nov.** because it is very difficult to detect and largely depends on the fossilization features of each specimen, namely on whether light can pass through the flagellomeres. This feature will most likely be described in future species of the genus or noted in re-examinations of existing holotypes.

Another important anatomical feature of the new

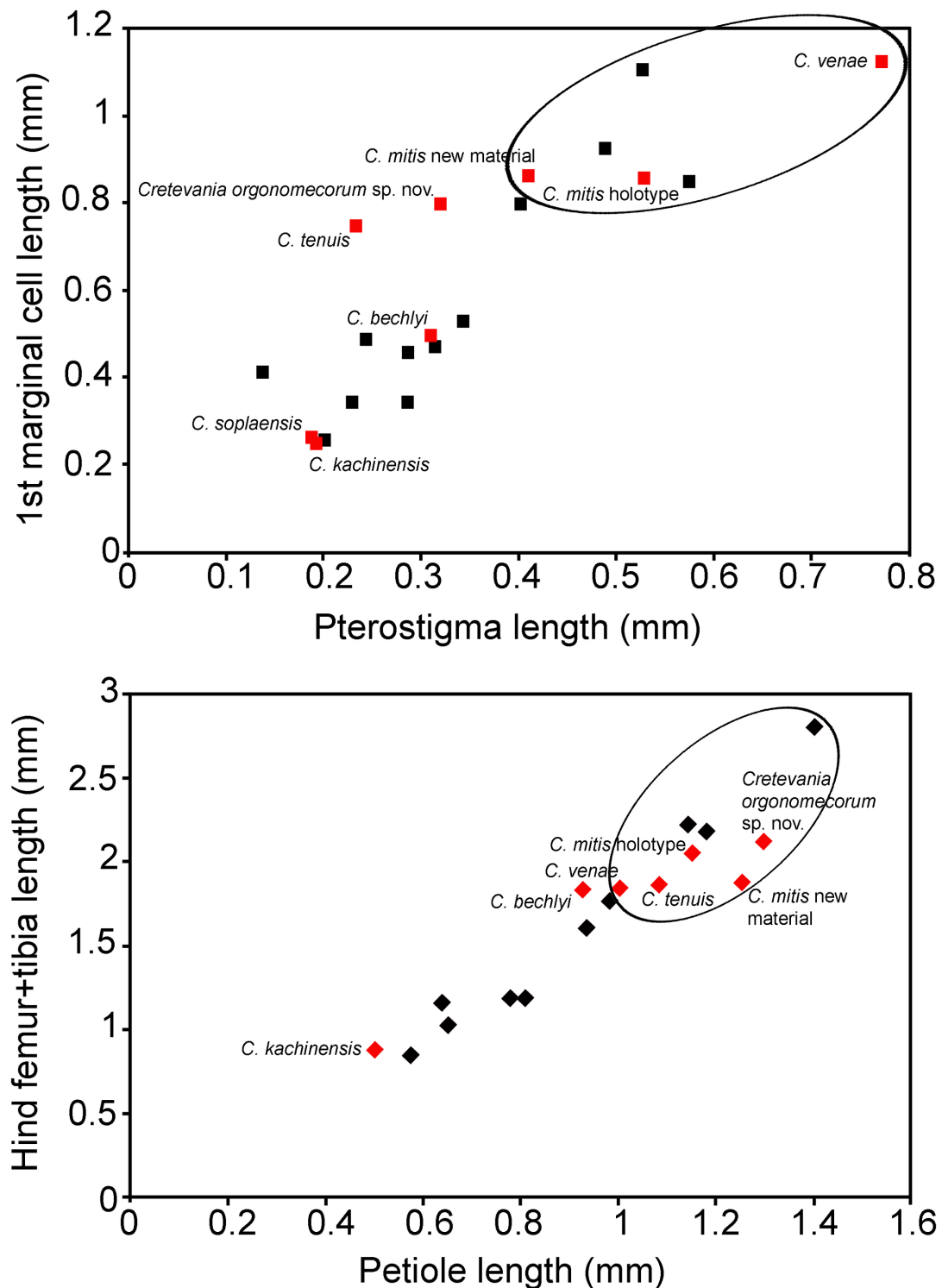


FIGURE 6. Plots of anatomical measurements for several *Cretevania* features, based on Figure 4 in Peñalver *et al.* (2010) (black) and new data from species described subsequently (red), only these last labelled. Pterostigma lengths were measured from the proximal margin to the intersection with the 1r-rs cross-vein. For species described with unsuitable or undetailed figures, measurements were taken from the descriptions when available (no suitable measurements exist for *C. extincta*; the upper plot excludes measurements for *C. alcalai*, and the lower plot excludes measurements for *C. concordia*, *C. meridionalis*, and *C. soplaensis*). For *C. mitis*, measurements are provided for the holotype (corrected) and a new specimen described four years later (Li *et al.*, 2014, 2018). The five large Chinese species preserved as compression fossils and previously classified (or that would have been classified in this genus if not previously synonymised) in the genus *Procretevania* are encircled. Note the position of the new species and *C. tenuis* (both preserved in amber), which fall close to or within the intraspecific variation of the larger species (the four Chinese species originally described in the synonymised genus *Procretevania* and also *C. venae*).

morphotype is a well-developed vein 2RS+M (not representing a simple point of contact), but not contiguous, lacking two small portions at the basal points of the veins 2RS and M. These two small portions that the vein 2RS+M lacks are not artefactual, since they are the same in both forewings and are specularly symmetrical between them. The exact same gaps are present in *C. kachinensis* Rosse-Guillevic & Jouault, 2023, although they were not depicted in the interpretative drawing of the original paper (Rosse-Guillevic & Jouault, 2023: fig. 3). A review of the holotypes of the Spanish amber species *C. montoyai* and *C. alcalai* revealed that the former does not show this feature, having a continuous and tubular vein in this region, whereas the latter clearly exhibits the characteristic small gaps in vein 2RS+M in both forewings. The review of the holotype of *C. rubusensis* was inconclusive because this part of the forewings is obscure. Although not previously detected, these small gaps in vein 2RS+M may represent a feature worth considering in future descriptions of *Cretevania* species. It is very likely that these gaps correspond to bullae, although no membrane folds associated with them could be detected in the present specimen—likely due to the inherent difficulty in recognizing such fine folds in fossil specimens. If present, these bullae would have presumably increased wing flexibility during flight.

Also distinctive of the new taxon are the antennae, which possess 11 flagellomeres. Only two species of *Cretevania* exhibit antennae with 10 flagellomeres, *C. kachinensis* (Rosse-Guillevic & Jouault, 2023) and *C. bechlyi* Jennings, Krogmann & Mew, 2013 (Jennings *et al.*, 2013), both from Burmese amber. The latter species also shows notauli, a feature not observed in any other *Cretevania* species. However, it seems that Rasnitsyn (1975: fig. 92) drew notauli in the interpretative drawing of the type species *C. minor*. Curiously, despite these two notable anatomical differences, the forewing of the new species is reminiscent of that of *C. bechlyi*.

The new species exhibits a similar body size to the three Chinese species, which were found as compression fossils and originally described within the genus *Procretevania*. These Chinese species are characterized by their large body size. Li *et al.* (2018) indicated that their newly described species, *C. tenuis* Li & Rasnitsyn, 2018 from Burmese amber, has a body length of around 5 mm, close to that of *C. pristina* Zhang & Zhang, 2000 (Zhang H.C. & Zhang J.F., 2000) from a compression deposit of the Yixian Fm. (Barremian, not Upper Jurassic), which was previously placed in the synonymised genus *Procretevania*. Consequently, Li *et al.* (2018) considered that these large-sized forms cannot be separated into a distinct genus, *Procretevania*, thus accepting the synonymisations proposed by Peñalver *et al.* (2010). The new species serves as another example supporting this view, because its total body length

considering the combined length of the petiole and gaster is approximately 5 mm, similar to that of the Cenomanian *C. tenuis*. This indicates that there are now two species preserved in amber with body sizes comparable to those previously classified within the genus *Procretevania* and found in compression deposits.

Cretevania mitis (Li, Shih & Ren, 2014), originally included in the genus *Procretevania*, was described based on a female holotype specimen from a Chinese compression deposit of the Yixian Fm. at Huangbanjigou Village, Beipiao City, western Liaoning Province (Li *et al.*, 2014). Four years later, Li *et al.* (2018) described a new, conspecific specimen from the same deposit. The holotype has a notably larger body size compared to other species of *Cretevania*, and surprisingly, the new conspecific specimen is half the body size of the holotype. It seems clear that the measurements of *C. mitis* in the original description, and even in its figures, are erroneous. The holotype measurements appear to be exactly half of those originally provided, suggesting that the scale bars were erroneously considered to represent 1 mm instead of 0.5 mm. This adjustment is also important for recognising intraspecific size variation in this *Cretevania* species (see Fig. 6), although based on only two specimens. With the addition of seven new species (and an additional specimen of one) into the plots published by Peñalver *et al.* (2010), which included some anatomical measurements for comparison (Fig. 6), it is clear that there is a general continuum of body sizes within the species of *Cretevania*, with the previously described species as compression fossils included in the genus *Procretevania* being some of the larger species.

The plots in Figure 6 show a few small gaps in the general continuum. Specifically, these gaps appear in the “1st marginal cell length” around 0.6 mm, “Hind femur + tibia length” around 1.5 mm and 2.5 mm, and “Petiole length” around 0.9 mm. These characters were originally selected based on the best represented in the available specimens for comparison. Certainly, other small gaps might be observed by plotting different characters. Given the clear trend of the last two decades, new species of *Cretevania* will likely be published in the coming years, which may fill these gaps. It is premature to consider these gaps as potential limits for separating the current *Cretevania* species into multiple genera. Similarly, it is too early to use them to define distinct groups within *Cretevania*, for example, in order to consider potential subgenera.

Five annuli, cuticular ridges laterally produced as dentitions (see Vilhelmsen, 2000), are visible in *C. orgonomecorum*'s ovipositor tip on each of the two valvulae. The same number of annuli appear to be present in *C. roblesi* (Peñalver *et al.*, 2010). In other parasitoid wasps, the presence and absence of annuli, as well as the

development of its sculpture, appear to be related to the type and hardness where oviposition occurs (Le Ralec *et al.*, 1996; Ernst *et al.*, 2013). This character appears to be largely neglected in descriptions of extant evaniids, preventing comparison with extant forms. Most likely, this feature is perceived as having low value, especially when considering that extant specimens display a plethora of anatomical features to discriminate taxa.

Conclusion

The species of the genus *Cretevania* exhibit considerable variation in body sizes and forewing features, among other anatomical differences. Some morphological features detected for the first time, namely antennal sensoria, small gaps in the forewing vein 2RS+M and presumed absence of tibial spurs, could be considered in the description of further species. Two additional characters recently described for *C. bechlyi* from Cenomanian Burmese amber (Jennings *et al.*, 2013), namely the presence of both 10-segmented antennae and notauli, notably increased the anatomical variation in this genus, and, in that regard, the considerations by Jennings *et al.* (2013) are especially interesting.

The genus *Cretevania* seems exclusive of Cretaceous deposits (*C. pristina* is Cretaceous, not Jurassic, in age), both amber and compression deposits. Apparently, it was very diverse in forested environments, some with continental body waters. The identification of *Cretevania* species could help in the dating of Cretaceous ambers. For instance, there are two known species in the middle Albian of El Soplao, two different species in the slightly younger upper Albian of San Just, and another two different species in Peñacerrada I and Arroyo de la Pascueta, of the same age as San Just, and so co-occurrences are lacking between any of these amber outcrops. Likewise, in non-Spanish amber localities, *Cretevania* species are known but do not co-occur across sites.

This iconic Cretaceous genus needs more research to consolidate the previous conclusions, but considering the increase in new species described over the last two decades and its presence in diverse localities around the world, it seems it could act as a “guide fossil” for the late Mesozoic. This possibility is based on the preservation potential of this genus, its species palaeodiversity in both amber and compression deposits, its temporal limit within the Cretaceous, its characteristic and easily recognised wing venation, and its rapid morphological change, which is evidenced by the exclusive presence of species in known Cretaceous localities.

Acknowledgments

We are grateful to Rafael López del Valle for the preparation of the amber piece. We thank the editor, Alexander Rasnitsyn, and an anonymous referee for their reviews which improved the manuscript. The *Gobierno de Cantabria* (Spain) and *EL SOPLAO S.L.* are thanked for kindly enabling access to the specimen. This work is a contribution to the project PID2022-137316NB, funded by MICIU/AEI/10.13039/501100011033 and by ERDF/EU, to the project CIGE/2023/86 funded by GE2024 programme of the *Conselleria de Educación, Cultura, Universidades y Empleo, Generalitat Valenciana*, and also to the *Consejería de Industria, Turismo, Innovación, Transporte y Comercio* of the *Gobierno de Cantabria* through the semi-public enterprise *EL SOPLAO S.L.* research agreements (Ref. VAPC 20225428 with IGME, CSIC, and #20963 with University of Barcelona). This research was presented at *The 9th International Conference on Fossil Insects, Arthropods and Amber*, in April 2024, Xi'an (China).

References

- Álvarez-Parra, S. & Azar, D. (2024) The wasps (Hymenoptera) from Lower Cretaceous Lebanese and Spanish ambers. *Fossil Studies*, 2 (2), 110–122.
<https://doi.org/10.3390/fossils2020005>
- Basibuyuk, H.H., Rasnitsyn, A.P., Fitton, M.G. & Quicke, D.L.J. (2002) The limits of the family Evaniidae (Insecta: Hymenoptera) and a new genus from Lebanese amber. *Insect Systematics and Evolution*, 33, 23–34.
<https://doi.org/10.1163/187631202X00037>
- Corral, J.C., López Del Valle, R. & Alonso, J. (1999) El ámbar cretácico de Álava (Cuenca Vasco-Cantábrica, norte de España). Su colecta y preparación. *Estudios del Museo de Ciencias Naturales de Álava*, 14 (Spec. No. 2), 7–21.
- Deans, A.R. & Huben, M. (2003) Annotated key to the ensign wasp (Hymenoptera: Evaniidae) genera of the world, with descriptions of three new genera. *Proceedings of the Entomological Society of Washington*, 105, 859–875.
- Engel, M.S. (2006) Two ensign wasps in Cretaceous amber from New Jersey and Myanmar (Hymenoptera: Evaniidae). *Polish Journal of Entomology*, 75, 443–454.
- Ernst, A., Miko, I. & Deans, A. (2013) Morphology and function of the ovipositor mechanism in Ceraphronoidea (Hymenoptera, Apocrita). *Journal of Hymenoptera Research*, 33, 25–61.
<https://doi.org/10.3897/jhr.33.5204>
- Gerstaecker, A. (1867) Ueber die Gattung *Oxybelus* Latr. und die bei Berlin vorkommenden Arten derselben. *Zeitschrift für die Gesamten Naturwissenschaften*, 30, 1–96.

- Jennings, J.T., Krogmann, L. & Mew, S.L. (2013) *Cretevania bechlyi* sp. nov., from Cretaceous Burmese amber (Hymenoptera: Evaniidae). *Zootaxa*, 3609 (1), 91–95.
<https://doi.org/10.11646/zootaxa.3609.1.7>
- Latreille, P.A. (1802) *Histoire Naturelle, Générale et Particulière des Crustacés et des Insectes*, volume 3. F. Dufart, Paris, 467.
<https://doi.org/10.5962/bhl.title.15764>
- Le Ralec, A., Rabasse, J.M. & Wajnberg, E. (1996) Comparative morphology of the ovipositor of some parasitic Hymenoptera in relation to characteristics of their hosts. *The Canadian Entomologist*, 128, 413–433.
<https://doi.org/10.4039/Ent128413-3>
- Li, L.F., Shih, C.K. & Ren, D. (2014) New fossil evaniids (Hymenoptera, Evanioidea) from the Yixian Formation of western Liaoning, China. *Cretaceous Research*, 47, 48–55.
<https://doi.org/10.1016/j.cretres.2013.10.006>
- Li, L.F., Rasnitsyn, A.P., Shih, C.K., Labandeira, C.C., Buffington, M., Li, D.Q. & Ren, D. (2018) Phylogeny of Evanioidea (Hymenoptera, Apocrita), with descriptions of new Mesozoic species from China and Myanmar. *Systematic Entomology*, 43, 810–842.
<https://doi.org/10.1111/syen.12315>
- Linnaeus, C. (1758) *Systema Naturae per Regna Tria Naturae, Secundum Clases, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis* (volume 1, ed. 10, Reformata). Salviae; Holmiae, Stockholm, 824.
<https://doi.org/10.5962/bhl.title.542>
- Najarro, M., Peñalver, E., Rosales, I., Pérez-de la Fuente, R., Daviero-Gomez, V., Gomez, B. & Delclòs, X. (2009) Unusual concentration of Early Albian arthropod-bearing amber in the Basque-Cantabrian Basin (El Soplao, Cantabria, Northern Spain): Palaeoenvironmental and palaeobiological implications. *Geologica Acta*, 7 (3), 363–387.
<https://doi.org/10.1344/105.000001443>
- Najarro, M., Peñalver, E., Pérez-de la Fuente, R., Ortega-Blanco, J., Menor-Salván, C., Barrón, E., Soriano, C., Rosales, I., López del Valle, R., Velasco, F., Tornos, F., Daviero-Gomez, V., Gomez, B. & Delclòs, X. (2010) Review of the El Soplao amber outcrop, Early Cretaceous of Cantabria, Spain. *Acta Geologica Sinica* (English Edition), 84 (4), 959–976.
<https://doi.org/10.1111/j.1755-6724.2010.00258.x>
- Nascimbene, P. & Silverstein, H. (2000) The preparation of fragile Cretaceous ambers for conservation and study of organismal inclusions. In: Grimaldi, D. (Ed.), *Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey*. Backhuys Publishers, Leiden, pp. 93–102.
- Peñalver, E., Arillo, A., López Del Valle, R. & Delclòs, X. (2025) Cretaceous Spanish amber: History, research and checklist of taxa. *Palaeoentomology*, 8 (2), 195–234.
<https://doi.org/10.11646/palaeoentomology.8.2.10>
- Peñalver, E., Ortega-Blanco, J., Nel, A. & Delclòs, X. (2010) Mesozoic Evaniidae (Insecta: Hymenoptera) in Spanish amber: Reanalysis of the phylogeny of the Evanioidea. *Acta Geologica Sinica* (English Edition), 84 (4), 809–827.
<https://doi.org/10.1111/j.1755-6724.2010.00257.x>
- Pérez-de la Fuente, R., Peñalver, E. & Ortega-Blanco, J. (2012) A new species of the diverse Cretaceous genus *Cretevania* Rasnitsyn, 1975 (Hymenoptera: Evaniidae) from Spanish amber. *Zootaxa*, 3514 (1), 70–78.
<https://doi.org/10.11646/zootaxa.3514.1.4>
- Rasnitsyn, A.P. (1975) Hymenoptera Apocrita of Mesozoic. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR (Academy of Sciences of the USSR Transactions of the Palaeontological Institute)*, 147, 1–134 + plates I–VIII. [In Russian]
- Rosse-Guillevic, S. & Jouault, C. (2023) A new species of *Cretevania* Rasnitsyn, 1975 (Hymenoptera: Evaniidae) from the mid-Cretaceous Kachin amber. *Palaeoentomology*, 6 (3), 242–249.
<https://doi.org/10.11646/palaeoentomology.6.3.6>
- Vilhelmsen, L. (2000) The ovipositor apparatus of basal Hymenoptera (Insecta): phylogenetic implications and functional morphology. *Zoologica Scripta*, 29 (4), 319–345.
<https://doi.org/10.1046/j.1463-6409.2000.00046.x>
- Zhang, H.C. & Zhang, J.F. (2000) A new genus and two new species of Hymenoptera (Insecta) from the Upper Jurassic Yixian Formation of Beipiao, western Liaoning. *Acta Micropalaeontologica Sinica*, 17, 286–290.
- Zherikhin, V.V. & Eskov, K.Y. (1999) Mesozoic and Lower Tertiary resins in former USSR. *Estudios del Museo de Ciencias Naturales de Álava*, 14 (Special publication, 2), 119–131.