

The first unique-headed bug (Hemiptera, Enicocephalomorpha) from Cretaceous Iberian amber, and the Gondwanan connections of its palaeontomological fauna

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Typescript received 11 September 2023; accepted in revised form 21 December 2023

Abstract: Enicocephalomorpha, also known as unique-headed bugs, are a seldom-collected infraorder of heteropteran insects whose evolutionary relationships have puzzled entomologists for more than a century. Unique-headed bugs are exceptionally rare in the fossil record, which hinders our understanding of the morphological transformations of the lineage across time and also affects the calibration of molecular clock estimates used to date the origins of the infraorder. Here, we report the discovery of *Enicocephalinus ibericus* sp. nov. from Iberian amber in the Ariño deposit in Spain, early Albian (Early Cretaceous) in age. The new species represents the second oldest fossil enicocephalomorphan to date, and the second record of this infraorder from European deposits. Remarkably, the closest relative of *E. ibericus* is the congeneric *E. acragimaldii* Azar from Lebanese amber

that is *c.* 20 myr older (Barremian), indicating a long-term persistence of the *Enicocephalinus* lineage across geological time. A review of the existing literature enabled us to record a total of 20 congeneric insect species that have been found in both Lebanese and Iberian ambers, suggesting the existence of previously underappreciated entomofaunal connections between southern Laurasia (the European archipelago) and northern Gondwana during the Cretaceous. We show that the palaeontomological record holds remarkable potential for elucidating the faunistic exchanges and palaeobiogeographical patterns in the peri-Tethyan region during the Cretaceous.

Key words: palaeobiogeography, Iberia, Maestrazgo Basin, Teruel, Lebanese amber, Albian.

ENICOCEPHALOMORPHA Stichel, 1955, also known as the unique-headed bugs, are among the most elusive of all heteropteran infraorders (Schuh & Weirauch 2020). All Enicocephalomorpha live in protected and humid habitats such as leaf litter, under rocks or bark (Wygodzinsky & Schmidt 1991). Due to their secretive habits, Enicocephalomorpha are seldom collected, with *c.* 430 species known to science, which are subdivided into two families: the Aenictopecheidae Usinger, 1932 (11 genera, 22 spp.) and the Enicocephalidae Stål, 1860 (42 genera, *c.* 410 spp.) (Schuh & Weirauch 2020). However, the actual diversity of the group may double the number of described taxa, with hundreds of undescribed taxa in collections, and many more awaiting discovery in the field (Baňář & Davranoglou, pers. obs.) Despite this paucity of information, Enicocephalomorpha display intriguing behaviours and morphological adaptations. Many, possibly most, winged Enicocephalomorpha form nuptial

swarms of hundreds, perhaps thousands of individuals (Schuh 1970), and all species appear to have the capacity to communicate with chemical signals (Davranoglou *et al.* 2017). The genus *Probosciodipirates* Villiers, 1958 may represent one of the few cases of thelytokous Heteroptera (Baňář *et al.* 2015), while *Phallopirates* Štys, 1985 is characterized by needle-like detachable genitalia that may be involved in traumatic insemination or as mating plugs (Štys 1985). As for the systematic affinities of Enicocephalomorpha, a sister-group relationship to litter bugs (Dipsocoromorpha) is supported by both morphological (Miyamoto 1961) and molecular data (Wang *et al.* 2016, 2019; Johnson *et al.* 2018; Weirauch *et al.* 2019). However, the internal phylogeny of Enicocephalomorpha has not been investigated in detail. Regarding the deep-time origins of unique-headed bugs, phylogenomic estimates suggest that the common ancestor of the Enicocephalomorpha–Dipsocoromorpha clade lived

approximately between 262 and 191 Ma (Wang *et al.* 2016, 2019; Johnson *et al.* 2018), although the infraorder Enicocephalomorpha itself may be considerably younger, with an origin in the Early Cretaceous (133–113 Ma) (Wang *et al.* 2016, 2019). However, these dates should be treated with caution, given that derived enicocephalomorphans are known from 130-Myr-old Lebanese amber (Azar *et al.* 1999), suggesting that the infraorder appeared earlier.

Enicocephalomorphans are also highly unusual in the fossil record. In terms of past enicocephalomorphans diversity, 15 fossil species in nine genera have been described (for a recent review, refer to Luo *et al.* (2021) and Luo & Xie (2022)), the oldest one being *Enicocephalinus acragimaldii* Azar *et al.*, 1999 from Lower Cretaceous Lebanese amber (Azar *et al.* 1999). Other fossil enicocephalomorphans have been described from mid-Cretaceous Burmese and Miocene Dominican ambers, as well as from the lower Eocene London Clay Formation at Paddy's Point, Isle of Sheppey (Luo *et al.* 2021). It is evident that the remarkable morphological and temporal disparity in the fossil record of Enicocephalomorpha presents challenges for dating the origins of the infraorder and reconstructing its internal phylogeny, for mapping the morphological transformations that led to the unique adaptations found in extant species, and for elucidating the historical biogeography of the group.

Based on the fossil record of terrestrial vertebrates and other organisms such as charophytes, it is well known that the circum-Mediterranean region represented an area of intermittent organismal interchange between Gondwana (namely Africa) and Laurasia throughout the Cretaceous (Gheerbrant & Rage 2006; Martín-Closas & Wang 2008; Fanti 2012). However, the palaeobiogeography of other terrestrial organisms represents a largely untapped resource in that area and elsewhere. Despite the staggering diversity and disparate dispersal abilities of insects, their use in palaeobiogeography (particularly at a more regional scale) has been hampered by the relative scarcity of localities preserving fossil taxa, which are often Konservat-Lagerstätten. It is in this context that increased discovery and study of amber localities can lead to the elucidation of palaeobiogeographical patterns, due to the high degree of morphological fidelity that characterizes amber inclusions, resulting in greater taxonomic precision.

Few studies have provided faunistic comparisons from a biogeographical standpoint using the Cretaceous palaeoentomological record from Iberia. Peris *et al.* (2016) assessed the known composition of coleopteran families between Spanish (Iberian), Lebanese, Burmese and French ambers and found a greater similarity between Iberian (namely Albian) and Lebanese (Barremian) ambers than between Iberian and either French or Burmese (Cenomanian) ambers, despite the much closer geographical position (and age, generally) of the Iberian and French

ambers. Similarly, Álvarez-Parra *et al.* (2023) compared psocodean taxa of different ranks among Cretaceous ambers and found a higher resemblance between Iberian, Lebanese and Burmese ambers than between Iberian and French ambers. In contrast, Buscalioni & Poyato-Ariza (2016) provided palaeobiogeographical insights based on the fossil record (including the entomofauna) preserved in the finely laminated limestones from Las Hoyas, of Barremian age, from Cuenca (central Spain). Some insect groups from Las Hoyas show affinities with taxa from the Crato Formation, Aptian of Ceará (NE Brazil); the dispersive model for these lineages was hypothesized to be from Eurasia to Gondwana through the Central Tethyan archipelago (Buscalioni & Poyato-Ariza 2016). These insect taxa include chrysopoid Neuroptera, aeshnidid Odonata and tipulid Diptera (Fleck & Nel 2003; Nel *et al.* 2005; Ribeiro & Lukashevich 2014).

In this work, we present the discovery of an enicocephalomorph from the Ariño outcrop in eastern Spain (early Albian, *c.* 110 Ma), making this the first fossil record of the infraorder in Iberia, and the second in Europe, represented only by an Eocene pyritized fossil (Štys 2010). The new species, *Enicocephalinus ibericus*, is significant because it is among the oldest enicocephalomorphans known (second to a species described from Lebanese amber) and represents a remarkable instance of palaeofaunistic and biogeographical connections between southern Laurasia and northern Gondwana during the Cretaceous, which we discuss in detail. To further our understanding on the systematic affinities of the genus *Enicocephalinus*, we examined a suite of modern Enicocephalomorpha using scanning electron microscopy (SEM) and state-of-the-art synchrotron x-ray micro-computed tomography.

GEOLOGICAL SETTING

The Ariño deposit is located in an open-pit coal mine in the Ariño municipality, Teruel Province, eastern Spain. The deposit is part of the Oliete Sub-basin of the Maestrazgo Basin (Salas & Guimerà 1996). Stratigraphically, the deposit is found in the Escucha Formation, representing transitional environments that included flood-tidal deltas (Rodríguez-López *et al.* 2009). More particularly, the level that has yielded the amber, AR-1, is composed of marls rich in organic matter, at times in the form of coal, and has been dated as early Albian (*c.* 110 Ma; Alcalá *et al.* 2012; Tibert *et al.* 2013; Villanueva-Amadoz *et al.* 2015; Álvarez-Parra *et al.* 2021). This amber is highly unusual because it is associated with a bonebed that includes bone concentrations of dinosaurs, crocodiles and turtles, as well as ostracods, charophytes and abundant palynological content (Álvarez-Parra *et al.* 2021). Strictly *in situ* amber derived from resin produced by

roots was also reported from this locality preserved in a 'root level', overlaid by a 'litter layer' containing a high quantity of aerial amber that had undergone low-grade transport. The aerial amber of Ariño is particularly rich in bioinclusions compared with other ambers known worldwide, with 145 bioinclusions per kg of aerial amber reported (Álvarez-Parra *et al.* 2021; Álvarez-Parra 2023).

MATERIAL AND METHOD

The amber fragment containing the specimen was prepared in epoxy resin. The specimen was photographed using an Axiocam 105 colour digital camera attached to a Discovery.V12 Zeiss stereomicroscope and a Zeiss AXIO compound microscope. Serial images were taken using ZenPro v.2.3 software and stacked with Helicon Focus v6.8.0. SEM photographs of extant enicocephalomorphans (Aenictopsechidae: *Lomagostus jeanneli* Villiers, 1958; *Ulugurocoris grebennikovi* Štys & Bañar, 2013; Enicocephalidae: *Probosciodopirates rugulosus* Bañar & Štys, 2015 in Bañar *et al.* 2015) were taken with a JEOL JSM-6380 LV at the Laboratory of Electron Microscopy, Faculty of Science, Charles University, Prague, Czech Republic. Confocal images of the amber specimen were taken with an Olympus FV1000, at a laser wavelength of 488 nm at the Dunn School of Pathology, University of Oxford. To visualize the three-dimensional (3D) mid-tarsal morphology of extant Enicocephalomorpha, we used synchrotron radiation micro-computed tomography at the TOMCAT beamline, Swiss Light Source (SLS), Paul Scherrer Institut, Switzerland, using an ethanol-preserved male specimen of *Cocles* sp. (Enicocephalidae). We scanned the specimen at a beam energy of 15.99 keV, which gave a final pixel size of 1.625 µm. 3D reconstruction was carried out using Amira 6.1 software (Mercury Systems). Image brightness adjustment and labelling were performed in Adobe Photoshop CS6 (Adobe Systems) and Adobe Illustrator CC/CS6 (Adobe Systems), respectively. All drawings were generated in Adobe Illustrator CC/CS6.

SYSTEMATIC PALAEOLOGY

Order HEMIPTERA Linnaeus, 1758
 Suborder HETEROPTERA Latreille, 1810
 Infraorder ENICOCEPHALOMORPHA Stichel, 1955
 Family INCERTAE SEDIS
 Genus *Enicocephalinus* Azar *et al.*, 1999

Type species. *Enicocephalinus acragrimaldii* Azar *et al.* 1999.

Emended diagnosis. Pronotum compact, indistinctly subdivided into three lobes (i.e. collar, anterior and posterior pronotal lobes); forewing with long basal cell and a distinct costal fracture

(both not visible in *E. ibericus*); apicitibial armature simple, comprising solely one group of sclerotized spine-like setae; all tarsi one-segmented; fore tarsus with two spiniform setae; parameres probably mobile; phallus distinctly visible (genital features not visible in *E. ibericus*).

Enicocephalinus ibericus sp. nov.

Figures 1–5

LSID. <https://zoobank.org/nomenclaturalActs/9B37B6BD-8FAB-418C-9296-88F2160A7080>

Derivation of name. Named after the Iberian Peninsula, where the type locality is located.

Holotype. Specimen AR-1-A-2019.55 from Ariño amber, housed at Fundación Conjunto Paleontológico de Teruel-Dinópolis, Teruel, Spain. Largely complete individual (Fig. 1), except for most of the head beyond the anteocular lobe and part of the right side of the posterior pronotal lobe, which are missing (Figs 1–3). Most of the specimen is in poor condition and not visible due to amber opacity (Fig. 1), with only the right foreleg (Figs 1, 4A–E), the apical portions of the mid and hind tarsi (Fig. 5A–C), and the left forewing (Fig. 2) being well preserved. No syninclusions visible. Dimensions of amber piece 3.8 mm (width) × 2.4 mm (length) × 1.25 mm (height). The amber piece was prepared in a prism of epoxy resin.

Differential diagnosis. The new species differs from *E. acragrimaldii* in the following features: pronotal lobe 1.3-fold wider than long (at least 1.5-fold in *E. acragrimaldii*, based on the measurable pronotal portion); apicitibial armature consisting of four thick spiniform setae (seven in *E. acragrimaldii*); inner pre-tarsal claw as long as tarsus; apex of hind tibia with two pairs of spines (three pairs in *E. acragrimaldii*).

Type locality. Found in the Ariño amber-bearing outcrop, Teruel Province, eastern Spain, dated as early Albian (c. 110 Ma; Alcalá *et al.* 2012; Tibert *et al.* 2013; Villanueva-Amadoz *et al.* 2015; Álvarez-Parra *et al.* 2021). The palaeoenvironment of the Ariño outcrop has been reconstructed as a subtropical swamp (Álvarez-Parra *et al.* 2021).

Description

Structure & vestiture. Probably male, with hemelytra significantly surpassing abdominal apex (Fig. 1; hemelytra smaller in female specimens of *E. acragrimaldii*; Azar *et al.* 1999). Small and delicate enicocephalomorph (Fig. 1), inferred body size of c. 1.87 mm from level of eyes to abdominal apex, and 2.6 mm from the former to the wing apex. Body surface smooth, devoid of distinct microsculpture, covered by dense layer of short, adpressed setae, including on veins.

Head. Left compound eye large, about as wide as long (Fig. 1), with many ommatidial facets (Fig. 3A–C); ocelli present (Fig. 2), positioned on a distinct ocellar lobe (Fig. 3A, B, D), almost

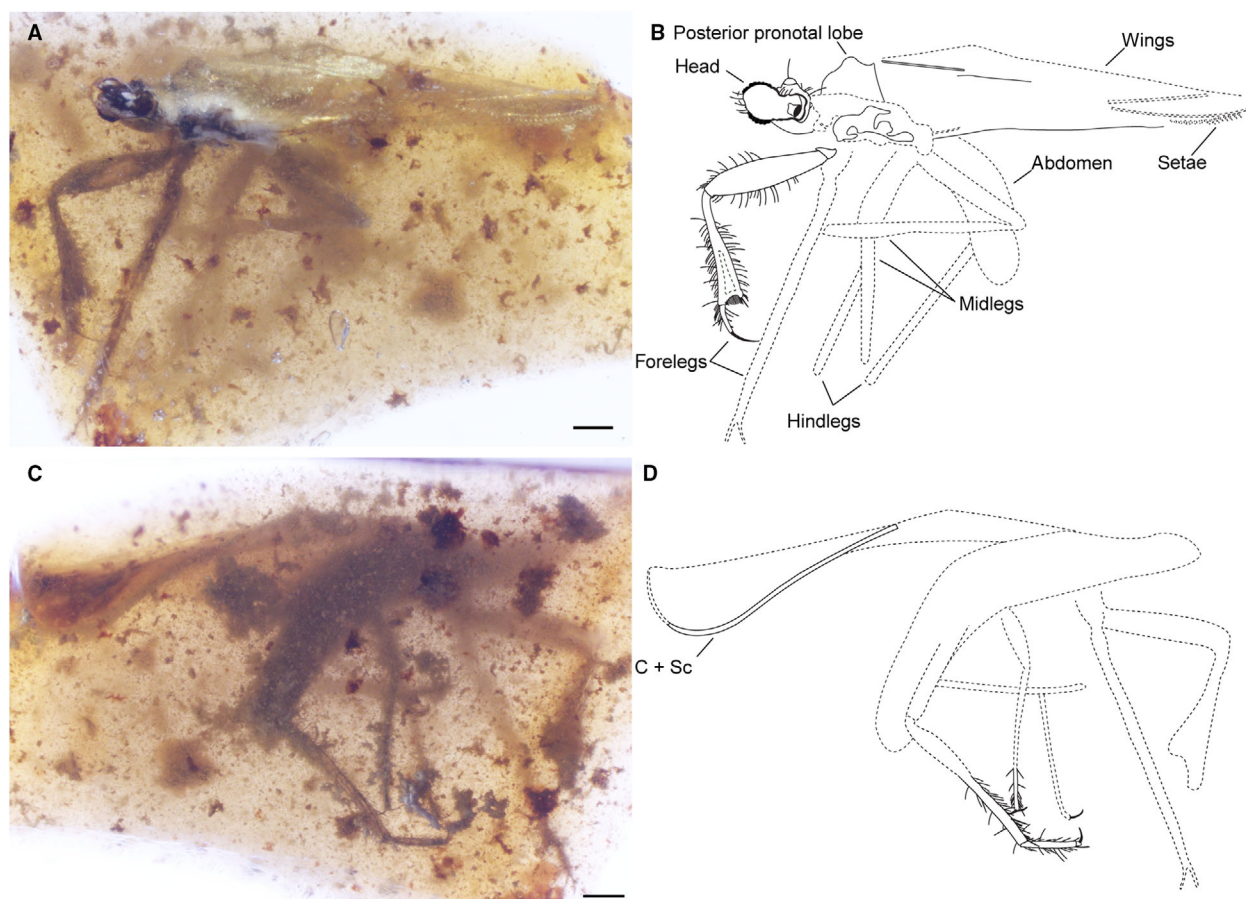


FIG. 1. Habitus of the holotype of *Enicocephalinus ibericus* sp. nov. (Enicocephalomorpha) (AR-1-A-2019.55) from Iberian Lower Cretaceous Ariño amber. A–B, photograph and interpretation of the lateral habitus. C–D, photograph and interpretation of the opposite lateral habitus. Scale bars represent 200 μ m.

touching posterior margin of eye; right eye and remaining portion of postocular lobe missing (Fig. 2). Antennae, mouthparts and other head structures not preserved.

Thorax. Pronotum compact (Fig. 2), c. 1.3-fold wider than long, subdivided into three indistinct lobes; collum distinctly visible (Fig. 2); external margin of pronotum slightly concave at mid-length (Fig. 2B), posterior margin slightly convex; mesoscutellum, acetabula and coxae not visible. Fore femur stout, 4.3-fold as long as wide, widest in distal third (Figs 1A, 4A–B); fore tibia fourfold as long as wide, widest at distal apex, with six distinctly erect and long setae (Figs 1A, 4A–B); apicitibial armature comprising four thick spiniform setae (tss), bristle comb (cmb) with c. 18 spiniform bristles (Figs 1A, 4A–D; sps); fore tarsus clavate, 2.6-fold longer than maximum width, provided with two spiniform setae (Fig. 4D); fore pretarsal claws asymmetrical, inner pretarsal claw (ic) about as long as fore tarsus (Fig. 4E); dorsal surface of fore tarsus with at least one long and erect seta (Fig. 4B, D; es). Ventral surface of hind tibial apex bearing two pairs of spines (Fig. 5A–C; spn); mid and hind tarsi one-segmented, inner pretarsal claw longer than the outer one (Fig. 5A–C). Venation of hemelytra incomplete, costal fracture and basal cell not visible, observable forewing veins include R

and M (Fig. 2B); proportions and shape of veins distorted by folding; hind wing venation reduced, namely consisting of R and M meeting beyond the wing mid length.

Abdomen. Largely not visible, slender in shape.

Measurements. L = maximum length, W = maximum width. Eye W = 0.06 mm, L = 0.06 mm. Pronotum L = 0.26 mm, W = 0.34 mm. Forewing L = 1.9 mm. Right foreleg: femur L = 0.65 mm, W = 0.15 mm; tibia L = 0.56 mm, W = 0.14 mm; tarsus L = 0.12 mm, W = 0.05 mm. Hind tibia L = 0.77 mm. Hind tarsus L = 0.3 mm. Abdomen L = 1.2 mm, W = 0.2 mm.

DISCUSSION

The systematic position of Enicocephalinus

The following diagnostic characters of the previously described species *E. acragrimaldii* are visible in the new enicocephalomorphan: compact pronotum with indistinct anterior and posterior lobes (Fig. 2), simplified apicitibial

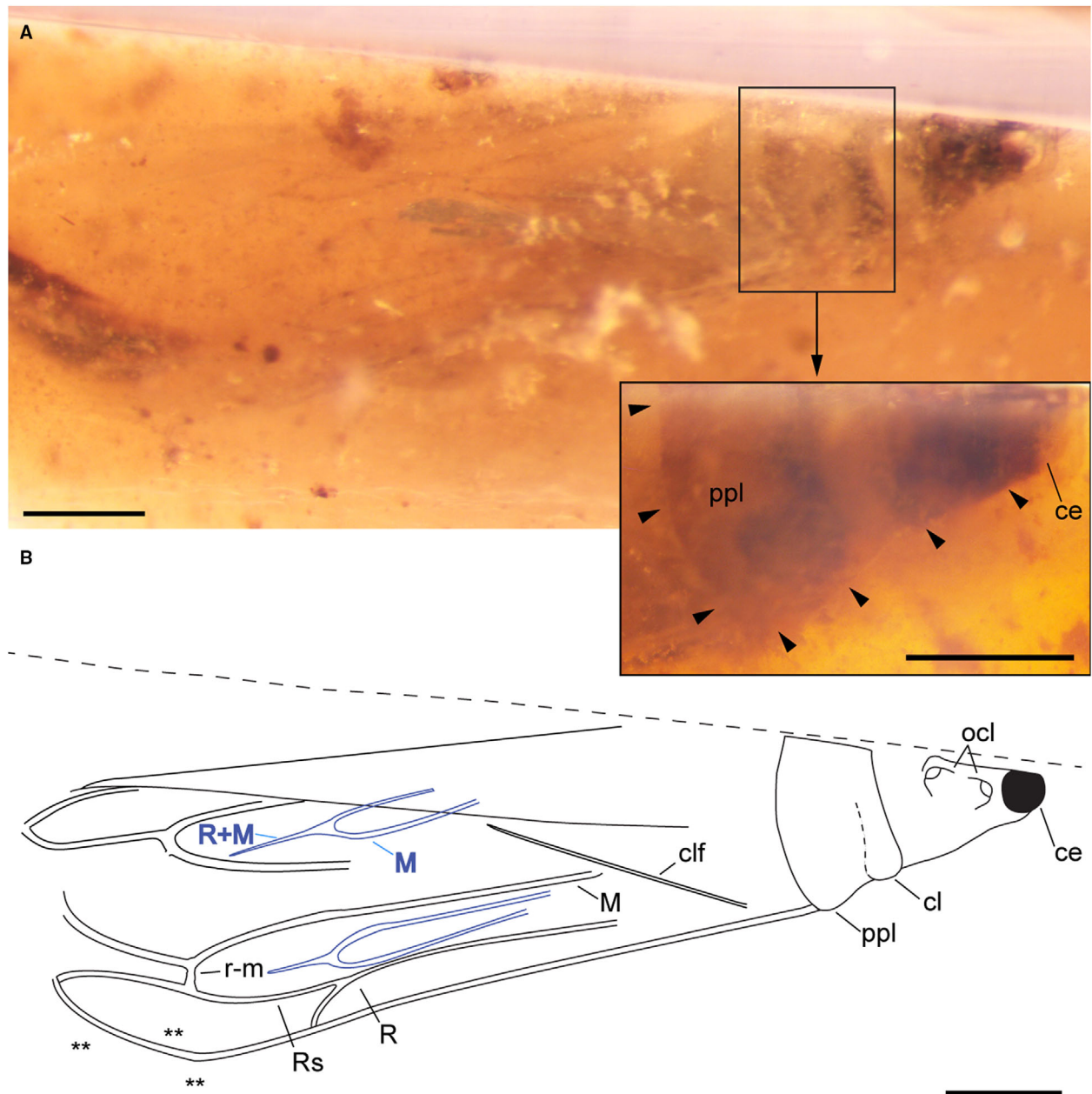


FIG. 2. Dorsal view of the holotype of *Enicocephalinus ibericus* sp. nov. (Enicocephalomorpha) (AR-1-A-2019.55). A, photomicrograph, with inset showing pronotal outline. B, interpretation; hind wing shown in blue. The double asterisks (**) mark strong wing folding. Abbreviations: ce, compound eye; cl, collum; clf, claval fracture; M, media vein; ocl, ocelli; ppl, posterior pronotal lobe; R, radius vein; Rs, radius sector vein; r-m, radiomedial cross-vein. Scale bars represent 100 μm .

armature consisting only of a few spines (tss; Figs 1A, 4A–D), and all tarsi one-segmented (Figs 4, 5) (Azar *et al.* 1999). These authors also considered the two spines on the ventral surface of the fore tarsus of *E. acragrimaldii* to be distinctive, ‘instead of four as in all known New World Enicocephalidae except *Brevadorsus*’; given that this condition is also present in the new species (Fig. 4D), this character has been added to the diagnosis of

Enicocephalinus. Although some important features are not visible in the new species (external male genitalia, large parts of wing venation, head), we are confident that the above features are distinctive enough to conform with the diagnosis of the morphologically aberrant unique-headed bug of the genus *Enicocephalinus*.

Enicocephalinus ibericus differs from the type species in the proportions of the pronotum, the smaller number of

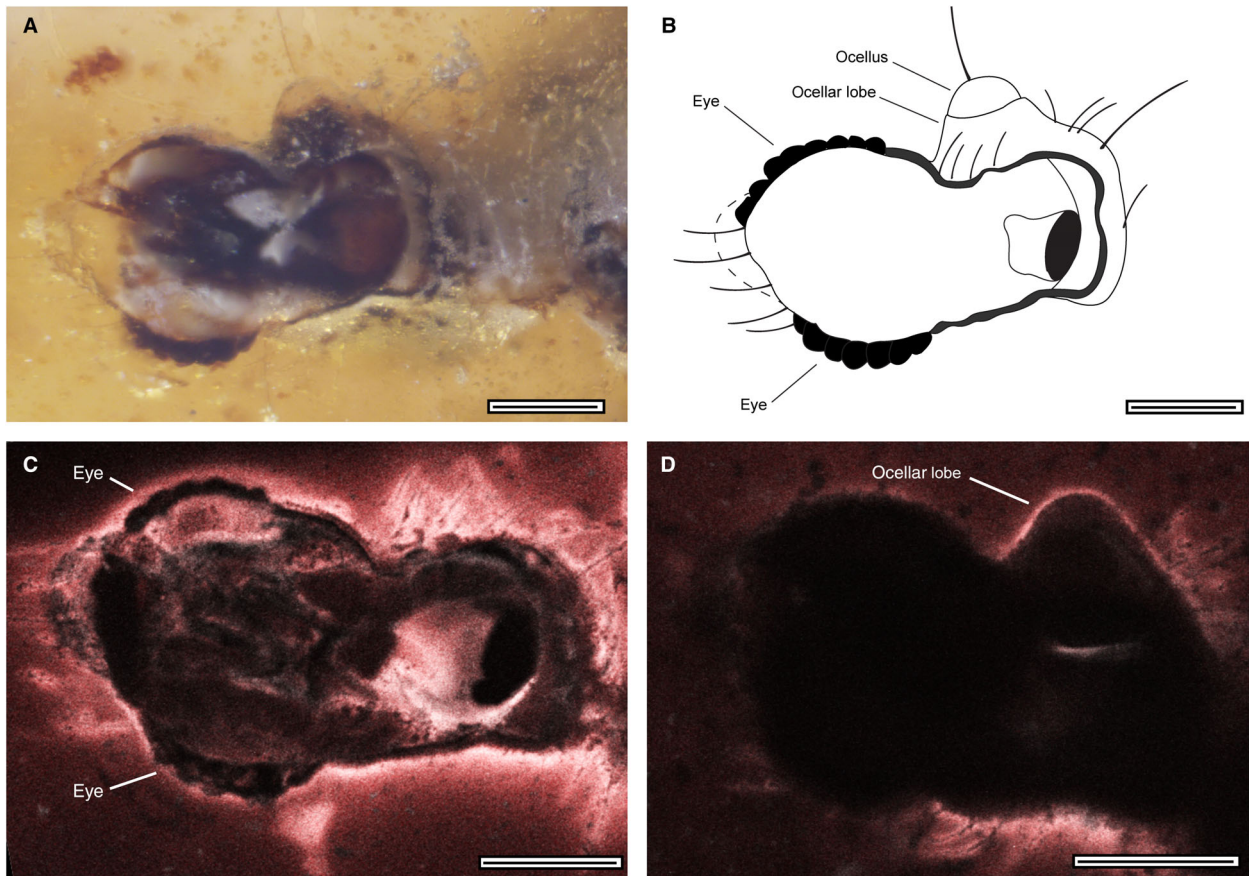


FIG. 3. Detailed head morphology of the holotype of *Enicocephalinus ibericus* sp. nov. (Enicocephalomorpha) (AR-1-A-2019.55). A–B, photomicrograph and interpretation of frontal oblique view of head. C–D, head imaged with confocal laser scanning microscopy focusing on: C, the compound eye and the internal morphology of the head capsule; D, the ocellar lobe. Scale bars represent 100 μm .

thick spiniform setae on the fore tibial armature (Figs 1A, 4A–D), and the presence of only two pairs of spines in the hind tibial apex (Fig. 5A–C). Both the tarsus and the pretarsal claw from the prothoracic leg appear to be more elongated in *E. ibericus* than in *E. acragrimaldii* (with pretarsus about threefold longer than broad at base and with propretarsal claw about sixfold longer than broad at base), although measurements of these structures were not provided for the described specimens assigned to the latter species (Grimaldi *et al.* 1993; Azar *et al.* 1999) and, thus, we have refrained from including these characters in the diagnosis of the new species. In any case, we should note that the intraspecific variation of the abovementioned characters in Enicocephalomorpha has not been quantified, nor were they studied in the original description of *E. acragrimaldii*, despite more than 70 specimens being available for study (Azar *et al.* 1999). Lebanese amber has been dated as Barremian, most probably early Barremian (*c.* 130 Ma) (Maksoud *et al.* 2017), rendering *E. ibericus* roughly up to 20 myr younger than the type species, suggesting remarkable morphological conservatism over that

time. Given the geographical distance (Fig. 6) and the chronological gap between the two species, our identification of *E. ibericus* as a new taxon is further justified.

A cladistic analysis based on 14 characters recovered *Enicocephalinus* as the sister-group to Enicocephalinae (Enicocephalidae) (Azar *et al.* 1999). Recently, Luo & Xie (2022) suggested that *Enicocephalinus* should be moved to Aenictopecheidae based on the following characters: (1) compact pronotum; (2) forewing with short costal fracture; (3) ventral margin of mid and hind tibia with pairs of spines; and (4) pygophore and phallus well developed, mobile. We note that pairs of spines in the mid and hind tibia are common in Enicocephalidae (Fig. 5D), while the modified genitalia that define Enicocephalidae clearly represent a derived condition, which might have not evolved yet in possible now extinct sister-group taxa such as *Enicocephalinus*. Furthermore, the slender forelegs of *Enicocephalinus* are nearly identical to those of extant Enicocephalidae (Fig. 4G), and strongly dissimilar to the extremely stout fore femora of Aenictopecheidae (Fig. 4F). Asymmetric fore pretarsal claws

characterize both families (Fig. 4H), while a departure from the general two-segmented tarsus on the mid and hind tibia (Fig. 5D) is developmentally malleable (especially in paedomorphic or brachypterous taxa; Wygodzinsky & Schmidt 1991; Davranoglou 2014), and therefore likely to be homoplastic. Until a more comprehensive phylogenetic analysis becomes available, we prefer to treat *Enicocephalinus* as *Enicocephalomorpha incertae sedis*.

As the oldest enicocephalomorphans, species classified in the genus *Enicocephalinus* are of considerable systematic significance. Phylogenomic estimates recover *Enicocephalomorpha* as having evolved in 130 Ma (Wang *et al.* 2016, 2019), which is highly unlikely because *Enicocephalinus* is dated to the same time interval and possesses all derived traits of *Enicocephalomorpha*, which are likely to have evolved much earlier. The temporal origins of *Enicocephalomorpha* therefore remain an open question.

Palaeoecological insights and biogeographical implications

The discovery of *E. ibericus* in Iberian amber is remarkable due to the scarcity of enicocephalomorphans in the fossil record. Indeed, c. 4000 inclusions in Iberian ambers have been identified in more than 25 years of study, yielding only the single enicocephalomorph reported herein. Given that extant enicocephalomorphans are characterized by cryptic habits such as living in leaf litter, under stones, and in decaying bark (Wygodzinsky & Schmidt 1991), if their Cretaceous relatives had a similar ecology, that would have significantly decreased the chances of fossilization, at least that in resin, consistent with actinotaphonomic studies that have demonstrated a clear entrapment bias of different groups of arthropods in modern resins (Solórzano Kraemer *et al.* 2018).

The finding of more than 70 enicocephalomorph individuals from the amber locality of Hammana/Mdeyriy in Lebanon is exceptional, and might be related to the behaviour of forming mating swarms (Schuh 1970), although no data on syninclusions were reported; in other Lebanese amber localities, *E. acragrimaldii* was noted as being quite rare (Azar *et al.* 1999). The climate in both Ariño and the Lebanese outcrops has been described as warm subtropical (Azar *et al.* 2003; Álvarez-Parra *et al.* 2021), a climate preference maintained by a large number of extant *Enicocephalomorpha* (Štys 2008; Schuh & Weirauch 2020).

Aside from *Enicocephalinus*, 19 other insect lineages comprise congeneric species that have been found in both Iberian and Lebanese ambers, half of which are exclusively present in these two localities (Table 1). These include Diptera, Hymenoptera, Coleoptera, Psocodea, Thysanoptera, and now Hemiptera (Table 1). This

geographical pattern also applies to an archaeognathan genus (A. Sánchez-García, pers. comm. 2023) and *Eophlebotomus* (Diptera, Psychodidae), both of which are currently unpublished and have therefore been excluded from Table 1. Despite Lebanese and Iberian ambers being separated by a significant temporal gap of up to 20–25 myr, our findings strongly support closer biogeographical connections than currently recognized between southern Laurasia and northern Gondwana during the Barremian–Albian based on the Cretaceous palaeontological record (Buscalioni & Poyato-Ariza 2016; Peris *et al.* 2016; Álvarez-Parra *et al.* 2023).

The palaeontological pattern described herein further corroborates previously characterized connections of the Iberian vertebrate fauna with both Laurasia and Gondwana during the Cretaceous, which are especially pronounced in dinosaurs (Canudo *et al.* 2009; Torices *et al.* 2012). Similar patterns have also been described by palaeobotanical studies that identified a primarily Laurasian affinity for the Early Cretaceous Iberian flora, albeit with the presence of northern Gondwanan influences (e.g. García Esteban *et al.* 2006; Mohr *et al.* 2006; Villanueva-Amadoz *et al.* 2010; Mendes *et al.* 2022; Barrón *et al.* 2023). Although Iberia was the closest continental mass to Gondwana during the beginning of the Cretaceous (Fig. 6; Ziegler 1988; Dercourt *et al.* 2000; Scotese 2021) and was once assumed as the point at which an intermittent land connection between Gondwana and Laurasia was established (Galton 1977; Sereno *et al.* 1994), abundant geological data have shown the development of a deep pelagic furrow between southern Iberia and northwestern Africa during that time (e.g. Dercourt *et al.* 2000; Scotese 2021). Therefore, evidence for intercontinental bridges in that region is currently lacking.

Conversely, the currently favoured interpretation postulates a direct trans-Tethyan biogeographical connection between Laurasia and Gondwana through the establishment of land ‘bridges’ in the peri-Adriatic (including the Apulian) region. This hypothesis is supported by structural, sedimentological, stratigraphic and palaeontological evidence, including the presence of dinosaur footprints (Bosellini 2002; Gheerbrant & Rage 2006; Petti *et al.* 2020; Randazzo *et al.* 2021). These data indicate that such a bridge was composed of carbonate platforms exposed due to sealevel changes during the Early to mid-Cretaceous, and that the bridge gradually fragmented during the Late Cretaceous (Randazzo *et al.* 2021). Given that the dispersal ability of extant enicocephalomorphans is considered low due to the concealed habitats they typically inhabit (Wygodzinsky & Schmidt 1991), it is likely that the *Enicocephalinus* lineage may have utilized the peri-Adriatic land bridge to colonize northern Gondwana and southern Laurasia; at least across a time interval of 20–25 Ma.

Overall, the insights presented herein represent a first step towards understanding the palaeobiogeographic processes that shaped the Iberian Cretaceous entomofauna. The sampling of additional localities and palaeoclimatic-

palaeobiogeographic analyses are likely to elucidate whether the Early Cretaceous entomological assemblages of Iberia and the southern Cretaceous European archipelago can be understood as having an endemic 'core' that

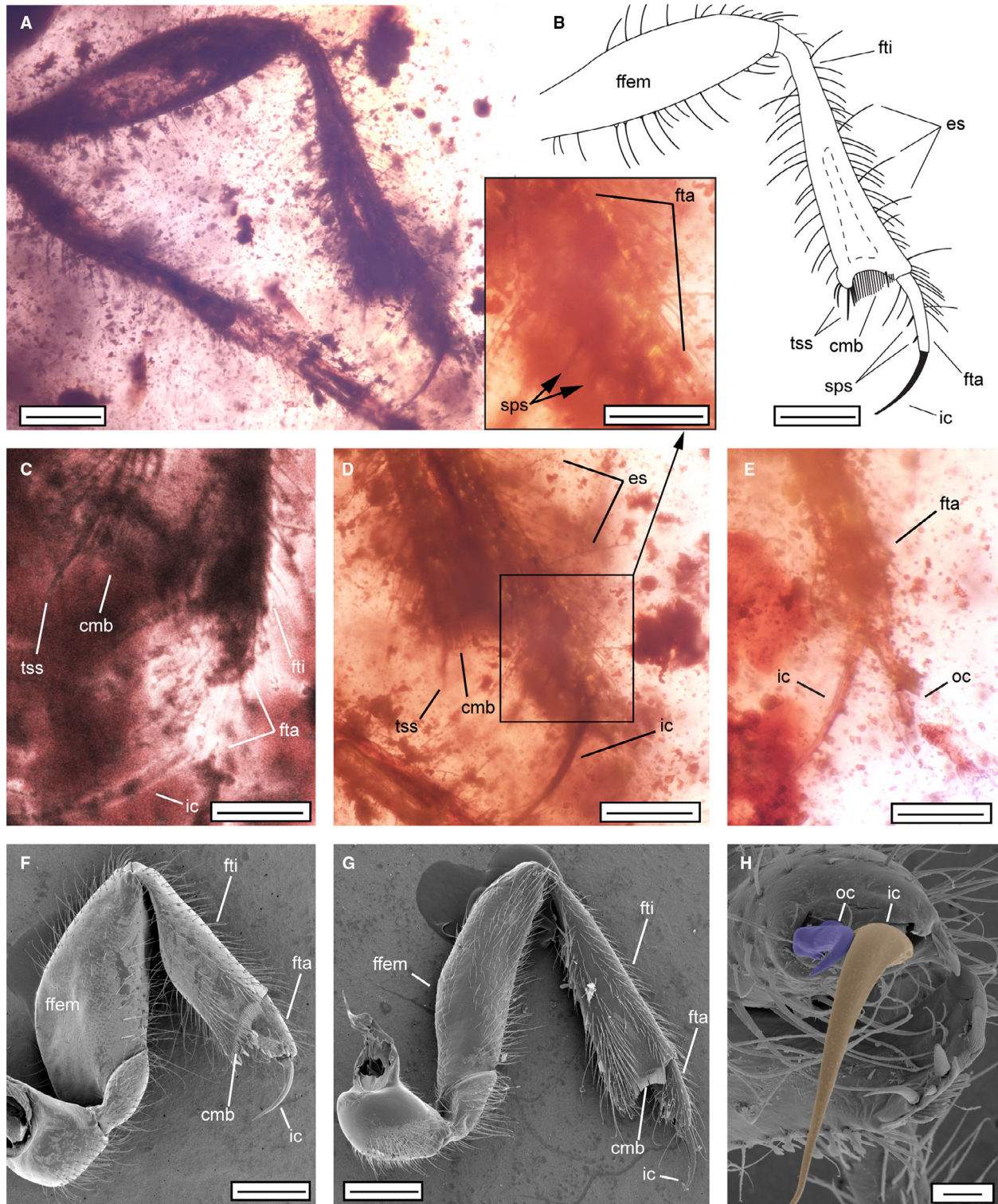


FIG. 4. Foreleg morphology of the holotype of *Enicocephalinus ibericus* sp. nov. (Enicocephalomorpha) (AR-1-A-2019.55) (A–E) and selected extant Enicocephalomorpha (F–H). A–B, photomicrograph and interpretation of right foreleg. C, apex of right fore tibia and tarsus, imaged with confocal laser scanning microscopy. D, photomicrograph of the same area with emphasis on tibial structure and armature; enlargement shows tarsal outline and spines. E, left fore tarsus, photomicrograph. F, SEM image of left foreleg of *Lomagostus jeanneli* Villiers, 1958 (Aenictopecheidae). G, SEM image of left foreleg of *Proboscidopirates rugulosus* Baňář & Štys, 2015 in Baňář *et al.* (2015) (Enicocephalidae). H, false-colour SEM image of fore tarsus of *Ulugurocoris grebennikovi* Štys & Baňář, 2013 (Aenictopecheidae), highlighting the asymmetric pretarsal claws. *Abbreviations:* cmb, bristle comb; es, erect setae; ffem, fore femur; fta, fore tarsus; fti, fore tibia; ic, inner pretarsal claw; oc, outer pretarsal claw; sps, spiniform bristles; tss, thick spiniform setae. Scale bars represent: 100 μ m (A, B, D enlargement); 50 μ m (C, D, E); 200 μ m (F, G); 20 μ m (H).

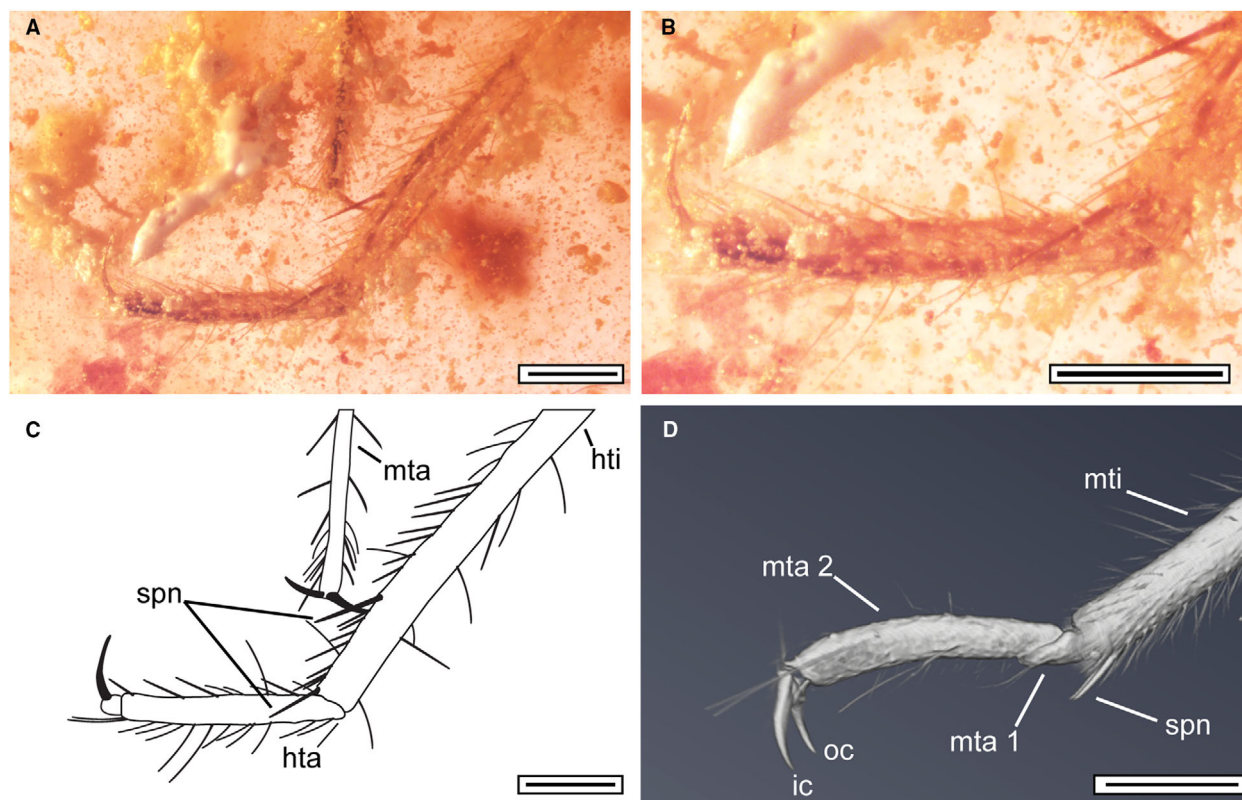


FIG. 5. Mid and hind legs of *Enicocephalinus ibericus* sp. nov. (AR-1-A-2019.55) and a selected extant enicocephalid (*Cocles* sp.). A–C, photomicrograph, close-up and interpretation of the hind tarsus. D, 3D volumetric reconstruction of synchrotron x-ray micro-computed tomography images of *Cocles* sp. mid tibia (<https://doi.org/10.17602/M2/M599154>). *Abbreviations:* hta, hind tarsus; hti, hind tibia; ic, inner pretarsal claw; oc, outer pretarsal claw; mta, mid tarsus; mti, mid tibia; spn, spine. Scale bars represent: 100 μ m (A–C); 250 μ m (D).

was supplemented by immigration waves as posited based on the vertebrate and botanical fossil record (Csiki-Sava *et al.* 2015), or whether the entomofaunal biogeographic dynamics followed a different pattern, perhaps influenced by the dispersal capacity of different cohorts of insects that exploited currents, both oceanic or wind-based, or vertebrate hosts (Osborne *et al.* 2002; Gillespie *et al.* 2012). Although the use of palaeoentomology in regional palaeobiogeographic studies is still scant due to the more limited nature of its geographical and stratigraphic

record, we show that it has the potential to further elucidate the influence of vicariance, extinction and dispersal on the palaeobiogeographical dynamics between Laurasia and Gondwana during the Cretaceous.

CONCLUSION

Here we describe *Enicocephalinus ibericus* from the Ariño outcrop in eastern Spain (*c.* 110 Ma), rendering the new

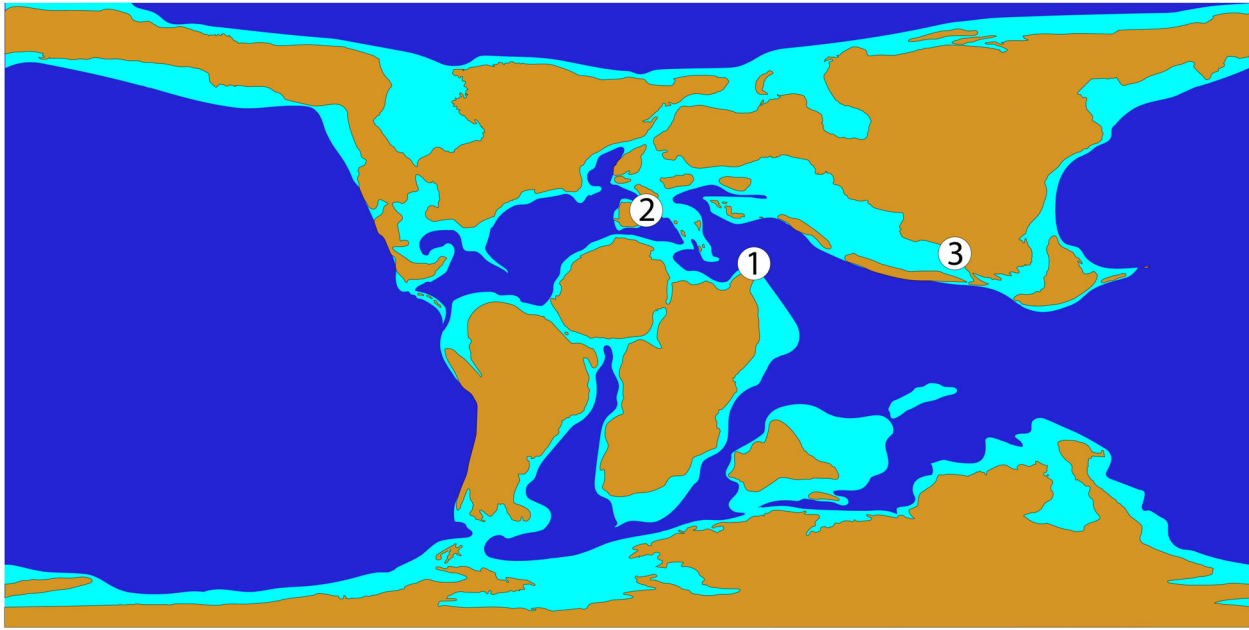


FIG. 6. Cretaceous distribution of described Enicocephalomorpha (Hemiptera, Heteroptera). The paleogeographical map (redrawn from Scotese 2021) corresponds to the middle Albian (105 Ma). Occurrences: 1, Lebanese amber (Hammana/Mdeyrij locality; early Barremian, *c.* 130 Ma), *Enicocephalinus acragrimaldii* (Azar *et al.* 1999); 2, Iberian amber (Ariño locality, early Albian, *c.* 110 Ma), *Enicocephalinus ibericus* sp. nov. (AR-1-A-2019.55); 3, Burmese (Kachin) amber (early Cenomanian, 99 Ma), *Allocephalocoris zhengi* (Luo *et al.* 2021), *Cretocephalus stysi* (Luo & Xie 2022), *Disphaerocephalus constrictus* (Cockerell 1917), *D. swinhoei* (Cockerell 1917), *D. macropterus* (Cockerell 1917), *Paenicotechys fossilis* (Cockerell 1916).

TABLE 1. Shared insect taxa at the genus level between Iberian and Lebanese ambers.

Taxa (genus)	Family	Order	References
<i>Archaeotropos</i>	†Empheriidae	Psocodea	Baz & Ortuño 2000; Azar & Nel 2004
<i>Archiaustroconops</i>	Ceratopogonidae	Diptera	Szadziewski 1996; Szadziewski & Arillo 1998; Borkent 2000; Pérez-de la Fuente <i>et al.</i> 2011; Choufani <i>et al.</i> 2015a
<i>Austroconops</i>	Ceratopogonidae	Diptera	Szadziewski 1996; Borkent 2000; Pérez-de la Fuente <i>et al.</i> 2011
<i>Chimeromyia</i>	†Chimeromyiidae	Diptera	Grimaldi & Cumming 1999; Grimaldi <i>et al.</i> 2009
<i>Creteamma</i>	†Gallorommatidae	Hymenoptera	Ortega-Blanco <i>et al.</i> 2011a; Rasnitsyn <i>et al.</i> 2022
<i>Cretevania</i>	Evaniidae	Hymenoptera	Deans <i>et al.</i> 2004; Peñalver <i>et al.</i> 2010; Pérez-de la Fuente <i>et al.</i> 2012
<i>Enicocephalinus</i>	<i>Incertae sedis</i>	Hemiptera	Azar <i>et al.</i> 1999; this paper
<i>Gerontodacus</i>	Ceratopogonidae	Diptera	Szadziewski 1996; Szadziewski & Arillo 1998; Borkent 2000; Pérez-de la Fuente <i>et al.</i> 2011; Choufani <i>et al.</i> 2015a; Borkent & Dominiak 2020
<i>Gonomyia</i>	Limoniidae	Diptera	Kania <i>et al.</i> 2015; Kania-Kłosok <i>et al.</i> 2022
<i>Helius</i>	Limoniidae	Diptera	Kania <i>et al.</i> 2013, 2016, 2017; Krzemiński <i>et al.</i> 2014; Kania-Kłosok <i>et al.</i> 2021
<i>Lebanoculicoides</i>	Ceratopogonidae	Diptera	Szadziewski 1996; Pérez-de la Fuente <i>et al.</i> 2011; Choufani <i>et al.</i> 2015a, 2015b
<i>Leptoconops</i>	Ceratopogonidae	Diptera	Borkent 2001; Szadziewski & Arillo 2003; Azar <i>et al.</i> 2010
<i>Libanoglaris</i>	†Empheriidae	Psocodea	Perrichot <i>et al.</i> 2003; Azar & Nel 2004; Álvarez-Parra <i>et al.</i> 2022
<i>Libanophron</i>	†Stigmaphronidae	Hymenoptera	Engel & Grimaldi 2009; Ortega-Blanco <i>et al.</i> 2011b
<i>Microserphites</i>	Dolichopodidae	Diptera	Hennig 1971; Grimaldi & Cumming 1999; Arillo <i>et al.</i> 2008
<i>Microserphites</i>	†Serphitidae	Hymenoptera	Kozlov & Rasnitsyn 1979; Ortega-Blanco <i>et al.</i> 2011c; Rasnitsyn <i>et al.</i> 2022
<i>Mymaropsis</i>	†Spathiopterygidae	Hymenoptera	Engel <i>et al.</i> 2013; Krogmann <i>et al.</i> 2016
<i>Prosolierius</i>	Staphylinidae	Coleoptera	Thayer <i>et al.</i> 2012; Peris <i>et al.</i> 2014
<i>Rhizophytoma</i>	Monotomidae	Coleoptera	Kirejtshuk <i>et al.</i> 2009; Kirejtshuk & Azar 2013; Peris & Delclòs 2015
<i>Tethysthrips</i>	Thripidae	Thysanoptera	Nel <i>et al.</i> 2010

Taxa exclusively described from the two ambers considered herein are shown in **bold**.

species as the second oldest fossil enicocephalomorph known to date, after a previously described congener dating to *c.* 130 Ma. The new species adds to further evidence that Enicocephalomorpha were already diverse during the Early Cretaceous, indicating that current molecular divergence estimates that have recovered an origin for the infraorder at 130 Ma may need to be reconsidered.

By comparing its morphology with that of other fossil and extant Enicocephalomorpha, we suggest that the genus *Enicocephalinus*, recently ascribed to Aenictopecheidae, possesses traits more similar to Enicocephalidae, in agreement with a previous cladistic study (Azar *et al.* 1999). Given that the internal phylogeny of Enicocephalomorpha is poorly resolved, we recommend placing the genus *Enicocephalinus* as *incertae sedis* within the infraorder.

The discovery of *Enicocephalinus* in Iberian and Lebanese ambers, together with newly presented evidence for 19 other insect lineages that are shared in both locations, indicates the existence of biogeographical connections between Laurasia and Gondwana during the Barremian–Albian. This finding is in agreement with the trans-Tethyan bridge hypothesis, which suggests that faunal movements between Laurasia and Gondwana may have utilized land bridges in the peri-Adriatic region. Our study showcases the importance of Cretaceous entomofauna for disentangling the intricacies of animal dispersal on Laurasia–Gondwana, thereby opening up exciting research avenues in the field of palaeobiogeography.

Acknowledgements. L-RD acknowledges the Leverhulme Trust Early Career Fellowship grant (ECF-2021-199) for funding this research. The authors are grateful to Sergio Álvarez-Parra for directing excavations in Ariño, and for preparing and databasing the amber inclusions. We are grateful for the collaboration of the SAMCA Group and Fundación Conjunto Paleontológico de Teruel–Dinópolis during fieldwork at Ariño, and for the support of the Dirección General de Patrimonio Cultural del Gobierno de Aragón (Spain) in granting the excavation permit 201/10 2019. L-RD thanks Xavier Delclòs for facilitating the study of the examined material while it was deposited at the University of Barcelona. We acknowledge the Paul Scherrer Institut, Villigen, Switzerland for provision of synchrotron beam time at the TOMCAT beamline X02DA of the SLS. This work is a contribution to the project PID2022-137316NB funded by the 10.13039/501100011033 – Agencia Estatal de Investigación and the European Regional Development Fund (ERDF/FEDER) scheme. Two anonymous referees commented on an earlier draft of this manuscript.

Author contributions. **Conceptualization** L-R Davranoglou (LRD); **Data Curation** LRD; **Formal Analysis** LRD; **Funding Acquisition** LRD, E Peñalver (EP), R Pérez-de la Fuente (RPF); **Investigation** LRD, P Bañar (PB), RPF; **Methodology** LRD, PB, RPF; **Project Administration** LRD; **Resources** LRD, EP,

PB, RPF; **Visualization** LRD, PB, RPF; **Writing – Original Draft Preparation** LRD, RPF; **Writing – Review & Editing** LRD, EP, PB, RPF.

DATA ARCHIVING STATEMENT

The tomographic dataset of the extant enicocephalomorph (*Cocles* sp.) that was used in this work is part of an ongoing study (led by LRD and PB) and is archived in MorphoSource (<https://doi.org/10.17602/M2/M599154>) and available upon request. This published work and the nomenclatural act it contains, have been registered in ZooBank: <https://zoobank.org/References/520BFD8C-AC2A-43B7-B0E0-72B62CBB0078>

Editor. Conrad Labandeira

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