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A new lace bug from Lower Cretaceous Spanish amber informs the evolution of forewing venation in Tingidae

Leonidas-Romanos Davranoglou[1,2*†], Dolev Fabrikant[1†], Enrique Peñalver[3], Ricardo Pérez-de la Fuente[2], Sergio Álvarez-Parra[3], Xavier Delclòs[4,5]

[1]The Steinhardt Museum of Natural History, Tel Aviv University, 12 Klausner Street, Tel Aviv, Israel

[2]Oxford University Museum of Natural History, University of Oxford, Parks Road, Oxford, OX1 3PW UK

[3]Museo Geominero, Instituto Geológico y Minero de España (IGME), CSIC, C/Cirilo Amorós 42, 46004 Valencia, Spain

[4]Department of Earth and Ocean Dynamics, Faculty of Earth Sciences, University of Barcelona, Barcelona, 08028, Spain

[5]Biodiversity Research Institute (IRBio), University of Barcelona, Barcelona, 08028, Spain

[*]leonidasdav@tauex.tau.ac.il; leonidas-romanos.davranoglou@oum.ox.ac.uk

[†]Joint first co-authors

Abstract

A new lace bug, ***Paleoanomala decapitata*** **sp. nov. (Tingidae: Tingiometrinae)**, is described from Lower Cretaceous (upper Albian) amber of Peñacerrada I (Burgos, Spain). The genus *Paleoanomala* was previously known only from Cenomanian Kachin amber of Myanmar, and the discovery of this new species significantly expands

its palaeogeographical range as well as the known diversity of lace bugs from Spanish amber deposits. Furthermore, the description of the new species urged us to undertake a reinterpretation of forewing venation in early lace bugs, finding nearly identical venation patterns in the extinct genera *Paleoanomala* and *Tingiometra* (Tingiometrinae), and *Hispanocader* (Hispanocaderidae). Based on this revised interpretation and other shared morphological characters, the extinct tingid subfamily Tingiometrinae and the family Hispanocaderidae are synonymised with Ebboidae, which is here treated as the subfamily **Ebboinae stat. nov.** within Tingidae. Additionally, ***Paleoanomala aptenus* Poinar & Vega, 2020** is recognised as a junior synonym of ***Tingiometra yuripopovi* Golub & Heiss, 2020**, and the latter species is transferred to *Paleoanomala* as ***Paleoanomala yuripopovi* comb. nov.** The affinities of the male paratype previously assigned to this species remain uncertain and it is tentatively treated as **Ebboinae indet**. Finally, a synthesis of the palaeobiogeographical affinities of arthropods from Iberian Cretaceous amber suggests extensive faunal connections between Iberia, Myanmar, and the Middle East during the Early Cretaceous, reflecting the widespread distribution of resiniferous forest ecosystems across Laurasia.

Keywords: Heteroptera, Cimicomorpha, Tingidae, lace bug, fossil, Cretaceous, amber, Spain, Iberia, Burmite, Kachin.

Introduction

The true bug family Tingidae, commonly known as lace bugs, comprises a diverse group (ca. 2,600 species) of phytophagous Heteroptera characterised by their reticulate hemelytra and pronotal expansions (Schuh & Weirauch, 2020). Lace bugs are represented by three families, the extinct Hispanocaderidae and Ignotingidae, and the

extant Tingidae (Zhang et al., 2005; Golub, Popov & Arillo, 2012). Another family, Ebboidae, comprising the monotypic genus *Ebboa* Perrichot, Nel, Guilbert & Didier (2006), was considered to be close to Tingidae (Perrichot et al., 2006), but was later reassessed as pertaining to Microphysidae or Plokiophilidae (Golub & Popov, 2008).

Extant representatives of the family Tingidae are classified into three subfamilies: Vianaidinae, Cantacaderinae, and Tinginae (Guilbert et al., 2014; Schuh & Weirauch, 2020). Fossil relatives of tingids are known from the Upper Jurassic to the Miocene, with about 50 genera and more than 80 described species (Du & Yao, 2018; Wang et al., 2021; Kaulfuss & Heiss, 2023; Mu et al., 2024; Ross, 2024). The earliest definitive record of the family Tingidae includes *Sinaldocader* from the Zaza Formation of Baissa in Transbaikalia, Russia (Golub & Popov, 2008), dated to the Valanginian–Hauterivian or Aptian ages (Zhang et al., 2023), while *Archetingis ladinica* Montagna et al., 2018, from the Middle Triassic of Monte San Giorgio in Switzerland has been classified into this family, but its placement remains controversial (Wang et al., 2021).

Extinct relatives of tingids, which belong to the broader superfamily of Miroidea, reveal considerable morphological disparity in pronotal structures, venation, and wing development, suggesting independent evolutionary trajectories for traits such as the hood, carinae, and paranota (Du & Yao, 2018). Furthermore, the extinct genus *Tingiometra*, belonging to the currently monotypic tingid subfamily Tingiometrinae and known exclusively from Cenomanian Kachin amber (Myanmar), is equipped with an aberrant, hydrometrid-like head and unusual wing venation that sets them apart from all living representatives (Heiss, Golub & Popov, 2015; Golub & Heiss, 2020; Poinar & Vega, 2020; Mu et al., 2024). Based on the above, lace bug morphological diversity may have been considerably more diverse in the Cretaceous than it is today (Golub & Heiss, 2020).

In Spain, the Lower Cretaceous (Albian) amber of Peñacerrada I (Moraza, Burgos Province) has produced one of the most diverse assemblages of fossil insects from this period (Alonso et al., 2000; Delclòs et al., 2007; Peñalver et al., 2025). Among Miroidea, the monotypic family Hispanocaderidae was described from this deposit, represented by *Hispanocader lisae* Golub, Popov & Arillo, 2012. This taxon exhibits a suite of distinct morphological traits, including a rudimentary ostiolar-stenocostal system without stenocostal area, large, ventrally faceted eyes, and unfused hemelytral veins, which were interpreted by Golub, Popov & Arillo (2012) as significant enough to justify the creation of a new family related to the tingid branch of Miroidea. However, as we show in subsequent sections of this manuscript, the extinct tingid subfamily Tingiometrinae (Heiss, Golub & Popov, 2015) is characterised by similar venation patterns.

Examination of additional material from the same deposit has revealed a new specimen pertaining to the Miroidea, with distinct morphological features not attributable to the genus *Hispanocader* but consistent with the genus *Paleoanomala* Poinar & Vega, 2020, so far known exclusively from Cretaceous Myanmar amber (Poinar & Vega, 2020). This specimen is described herein, thereby contributing to our understanding of Early Cretaceous diversity of lace bugs and their extinct relatives. The discovery of this new species prompted us to revise the morphology and taxonomy of several Cretaceous lace bugs and to examine the biogeographical affinities of arthropods known from Iberian amber.

Material and Methods

Geological Context

The amber-bearing strata of Peñacerrada I are located on the eastern margin of the Basque-Cantabrian Basin in northern Spain and belong to the "Utrillas Group" (Barrón et al., 2015, 2023; Peñalver et al., 2025). The amber occurs within organic-rich, feldspathic sandstones and shales related to a paralic deltaic environment (Martínez-Torres et al., 2003) during the upper Albian (Lower Cretaceous), approximately 103 million years ago. Although the Peñacerrada I outcrops were originally dated to the Aptian–Albian and assigned to the Nograro Formation (Alonso et al., 2000), they were later considered part of the Escucha Formation (Martínez-Torres et al., 2003). Palynological data subsequently refined their age to the upper Albian and led to their current placement at the base of the aforementioned "Utrillas Group" (Barrón et al., 2015). The amber is interpreted to derive from araucariacean conifers, probably related to the genus *Agathis*, based on its geochemical composition and the abundance of associated inaperturate pollen grains attributable to Araucariaceae (Chaler & Grimalt, 2005; Barrón et al., 2015; Menor-Salván et al., 2016).

Peñacerrada I and Peñacerrada II amber deposits are renowned for their exceptional preservation of biological inclusions, which number over 2,455 specimens, of which 106 are holotypes (Delclòs et al., 2007; Peñalver et al., 2025). These inclusions represent a remarkably diverse assemblage of terrestrial and also included a few aquatic arthropods, including representatives of at least 17 hexapod orders (Peñalver et al., 2025). Notably, the amber has yielded early representatives of lace bugs and their allies, such as the previously mentioned *Hispanocader lisae* (Golub, Popov & Arillo, 2012).

Specimen Information and Terminology

The specimen described herein is catalogued as MCNA-9548 and housed in the Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, Álava Province, Spain). The specimen

originates from Peñacerrada I, in the village of Moraza (Burgos Province, Spain). It is preserved as an inclusion in amber and exhibits excellent morphological detail. However, the head, prothorax, and all leg segments other than the metacoxae are missing. To ensure its long-term preservation, the piece of amber was embedded in epoxy resin (Epotek 301; Corral et al., 1999). The morphological terminology used in the study is primarily based on Drake & Davis (1960) and forewing area designation is based on Lis (1999), while the nomenclature on forewing wing venation is based on the standard pattern in Heteroptera (Schuh & Weirauch, 2020), which we implemented in our revised terminology of the relevant wing veins.

Microscopy

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. Image brightness adjustment was performed in Adobe Photoshop CS6 (Adobe Systems), while drawings were generated in Adobe Illustrator CS6.

Results

Systematic Palaeontology

Suborder Heteroptera Latreille, 1810

Infraorder Cimicomorpha Leston, Pendergrast & Southwood, 1954

Superfamily Miroidea Hahn, 1833

Family Tingidae Laporte, 1832

Subfamily Ebboinae Perrichot, Nel, Guilbert & Didier, 2006 (emended classification, previously ranked as family)

Genus *Paleoanomala* Poinar & Vega, 2020 (emended classification, previously assigned to Tingiometrinae)

Type species. *Paleoanomala yuripopovi* (Golub & Heiss, 2020) (new combination after synonymy with *P. aptenus*)

Paleoanomala decapitata Davranoglou & Fabrikant sp. nov. (Fig. 1)

LSID. https://zoobank.org/NomenclaturalActs/7f8f7151-d161-4aeb-856a-40553c249910

Derivation of name: The second epithet of the species name, *decapitata*, is derived from the Latin adjective *decapitatus*, meaning "beheaded" or "headless," in reference to the absence of the head in the holotype specimen. The genus *Paleoanomala* is feminine.

Diagnosis: Forewings submacropterous, membrane completely reduced; costal area narrow with basal thickening; subcostal area with at most a single transverse vein; discoidal area split by M, and four crossveins into six large cells; posterior medial discoidal cell relatively small; veins Sc, R, M and CuA basally separate, fusing only at apex; claval furrow reduced; claval area not reaching mid-length of hemelytron; A1(?) vein sinuate; abdomen short and broad.

Material examined: Holotype female (specimen code MCNA-9548) included in upper Albian amber, embedded in a block of transparent epoxy resin, and deposited at the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz (Basque Country), Spain. Head, pronotum, and legs are absent, except for the metacoxae. No syninclusions were observed.

Description: Holotype. Body oval, rounded (Fig. 1A). Hemelytral surface covered by small rows of areolate microsculpture. Wings submacropterous, only slightly surpassing abdominal apex (Fig. 1A); hemelytral sutural area reduced. Rich hemelytral

venation compared to modern relatives (Fig. 1A, B); veins R and M and CuA separate for the entire length of hemelytra, only fusing near apex; no distinct furrow between clavus and corium; ventral surface of hemelytral base with short transverse groove extending from scent gland pore to costal area (Fig. 1C); costal area proximally bulbous, narrow for most of its length, separated from the remainder of the hemelytra by vein Sc (= C+Sc), composed of a single row of small, punctiform areolae along its entire length, expanding basally to accommodate 2–3 areolae.

Subcostal area broad, bordered by veins Sc and R, containing 5–6 rows of areolae throughout its length; a transverse vein (or thickened areola) interrupts the area medially, subdividing it into two halves.

Discoidal area delimited by vein R (separating it from the subcostal area) and vein CuA (separating it from the sutural area); discoidal area divided by vein M and four crossveins into six large cells, three anterior cells (basal, medial, and apical) bordering the subcostal area and three posterior cells (basal, medial, and apical) bordering the sutural area and clavus (corresponding to areolae described by Golub, Popov & Arillo, 2012 for *Hispanocader lisae*); anterior basal cell with 5–6 rows of small areolae at its widest point; anterior medial cell with 4–5 rows of areolae; posterior basal, medial, and apical cells contain 9–11, 4–5, and 5–6 rows of small areolae, respectively. Sutural area open, bordered by vein CuA and wing margin; veins M and CuA unite near apex of hemelytron.

Metasternum produced into a short xyphus (Fig. 1C). Abdomen rounded; outline of apex smooth, suggesting that the specimen is female (Fig. 1D).

Measurements: Each hemelytron is 0.5 mm wide and 1.3 mm long.

A reconstruction of *P. decapitata* is provided in Fig. 2, with head and leg structures being derived from previously known *Paleoanomala*.

Morphological insights

Evolution of forewing venation in lace bugs

The forewing of extant and most extinct Tingidae is covered in dense areolae and displays three distinct veins, conventionally identified as Sc, R+M, and CuA, which divide the forewing into the costal, subcostal, discoidal, and sutural (membrane) areas, with an additional subdivision, the stenocostal area, so far unique to Cantacaderinae, which is delimited by a prominent costal carina (Drake, & Davis, 1960; Lis, 1999). On the other hand, Cretaceous fossil lace bugs assigned to Hispanocaderidae and Tingiometrinae exhibit an expanded venation pattern that is different from all other extant or extinct lace bugs, consisting of four (rather than three) distinct veins interconnected by crossveins. Elucidating the identity of these veins provides further information on the evolution of tingid tegminal venation more broadly (Pericart, 1983; Golub, Popov & Arillo, 2012).

The identity of forewing veins in fossil lace bugs attributed to Hispanocaderidae and Tingiometrinae has been subject to varying interpretations, with most studies generally following Shcherbakov's (1996) scheme, who suggested that the anteriormost tegminal vein in Heteroptera is the costa (Zhang, 2005; Golub, Popov & Arillo, 2012; Heiss, Golub & Popov, 2015).

Golub, Popov & Arillo (2012) attempted to implement this scheme when describing the family Hispanocaderidae. However, while trying to reconcile the expanded venation in these fossils, Golub, Popov & Arillo (2012) confused the otherwise synonymous sutural area and membrane as distinct areas, and further complicated the interpretation

by an impossible placement of the anal vein on the corium, thus deviating from all previous conventions of tingid wing venation.

To resolve these issues, we opted to follow the conventional interpretation of Heteroptera venation, which is generally accepted to consist of the Subcosta (synonymous with C+Sc) at the anterior margin, followed by the radial (R), medial (M), and cubital anterior (CuA) veins on the corium and anal (A) veins on the clavus (Betts, 1986; Wooton et al., 1986; Lis, 1999; Schuh & Weirauch, 2020;). Under this interpretation, no heteropteran group displays a distinct costal vein, with a possible exception of partial separation in Enicocephalomorpha (Schuh & Weirauch, 2020), which of course could represent a secondary reversal.

As such, we reinterpret the four distinct forewing veins present in *Paleoanomala*, *Hispanocader*, and *Tingiometra* to represent Sc (= C+Sc), R, M, and CuA on the corium and A on the clavus (Fig. 3). Those veins in turn separate the forewing into the costal, subcostal, discoidal, claval, and sutural areas, respectively (Figs. 1B, 3).

Among extant tingids, the only venation pattern that approximates the condition observed in *Hispanocader*, *Paleoanomala*, and *Tingiometra* is to be found in Cantacaderinae (Fig. 3E), and allows us to unambiguously identify and compare homologous veins. Our review has revealed a discordance between the commonly accepted venation pattern of Tingidae (Sc, R+M, CuA) to these three genera which we propose to unite under Ebboinae stat. nov. (see below). The secure position of all veins, as based on the standard interpretation of the heteropteran wing plan, along with the placement of the free CuA vein in Ebboinae stat. nov. clearly illustrate that in all other tingids the vein previously labelled as R+M is in fact R, that CuA is M, and that CuA

is reduced and fuses with M at the apex (Fig 3E). This reinterpretation is consistent with the standard designation of forewing areas in tingids (Lis, 1999).

We suggest that the venation of lace bugs has undergone a process of simplification. In the first stage, the base of CuA shifted towards the claval furrow, becoming indistinct from the corial margin of the claval furrow, with CuA emerging at the apex of the clavus to reach the tip of the forewing and join apically with M. This state is characteristic of Ebboinae stat. nov.

In Cantacaderinae, the fusion point of M and CuA approaches much closer to the wing base, leaving only a small portion of CuA free. This state is exemplified by Cantacaderinae: *Stenocader* (Fig 3E). Subsequently several lineages of Tingidae continued the simplification with the clavus being reduced, and with M approaching the posterior wing margin; this is exemplified by Ceratocaderini and Tinginae (Fig. 3F).

Taxonomic changes in Ebboidae, Hispanocaderidae and Tingiometrinae

Based on our re-evaluation of the wing venation in early diverging lace bugs, we propose the following taxonomic changes in Ebboidae, Hispanocaderidae and Tingiometrinae:

(i) **Ebboidae, Hispanocaderidae and Tingiometrinae belong to the same lineage of early diverging lace bugs, the Ebboinae stat. nov.:** The genera *Hispanocader*, *Paleoanomala*, and *Tingiometra* share a series of diagnostic characters not found in any other lace bug lineage, extant or extinct. Species in these three genera exhibit much more complex venation than any other lace bug lineage, including separate R, M, and CuA, all of which reach the wing apex and form a very wide discoidal area bearing at least five cells (Fig. 3A–D). The venation could not be studied for Ebboidae, as the

wings are damaged in the type material (Perrichot et al., 2006; Néraudeau et al., 2020). Furthermore, the genera *Ebboa*, *Hispanocader*, *Paleoanomala*, and *Tingiometra* exhibit the following unique combination of diagnostic traits: (1) head elongate, devoid of spines; (2) postocular area enlarged; (3) clypeus apically bulbous, shield-like in frontal view; (4) eyes positioned far from pronotum; (5) ocelli present (absent in all other lace bugs); (6) anteocular portion of head long or very long (also in Cantacaderinae and Vianaidinae); (7) second antennal segment longest (unique among lace bugs, where it is very short with the exception of the Mesozoic *Ignotingis* Zhang et al. 2005, *Burmacader* Souma et al. 2021 and the relict Vianaidinae where it is also somewhat elongate); (8) pronotum simple, with a single medial carina, narrow paranota, and concave posterior margin of pronotum (also concave in *Eocader* Drake & Hambleton, 1934 and some Vianaidinae; Guidoti et al. 2020); (9) (meso) scutellum large, fully visible (lack of posterior pronotal process – also in Cantacaderinae); (10) stenocostal area absent (unique to Cantacaderinae); and (11) ventral base of costal area displaying rudimentary ostiolar-stenocostal system (without a stenocostal area), consisting of a short transverse groove connected to the scent gland peritreme (Golub, Popov & Arillo 2012). The genera *Ebboa* and *Tingiometra* are unique in that they possess three-segmented tarsi – a condition found in no other lace bug lineage. Although *Tingiometra* was described as having two-segmented tarsi (Heiss & Golub, 2015; Golub & Heiss, 2020), our examination of three undescribed species (Davranoglou & Fabrikant, personal observation) show that they clearly have three tarsal segments; so does *Ebboa*, as can be seen in Fig. 8A1, A3 of Neraudeau et al. (2020). The number of tarsal segments is not able to be determined in Hispanocader, although specimens morphologically similar to this genus and *P. yuripopovi* indet.

also possess three-segmented tarsi (L.-R. Davranoglou & D. Fabrikant, pers. obs.

2026).

Based on the above it is evident that Ebboidae, Hispanocaderidae and Tingiometrinae share several putative synapomorphies that are found nowhere else in the lace bug lineage. We therefore unite these genera under Ebboidae, the earliest described group, with Hispanocaderidae and Tingiometrinae becoming the junior synonyms of the latter.

However, despite their morphological differences from present-day lace bugs, the genera *Ebboa*, *Hispanocader*, *Paleoanomala* and *Tingiometra* are most similar to Tingidae (and specifically to Cantacaderinae) than any other lineage of Miroidea and likely represent the sister-group to all lineages of present-day tingids, or the sister-group to Cantacaderinae. Although a sister-group relationship with all tingids could be used to support the familial rank of Ebboidae, it is our view that taxonomic ranks should aim towards simplicity and propose that Ebboidae should be downgraded to subfamily rank, with Ebboinae stat. nov. being the new combination, which comprises the genera *Ebboa*, *Hispanocader*, *Paleoanomala*, and *Tingiometra*.

We should mention that Golub & Popov (2008) rejected the placement of *Ebboa* within Tingidae, noting that *"the markedly convex dorsum, much elongated head with very small eyes, antennal bases set much anterior to eyes, long 2nd antennomere, small pronotum, large scutellum, 3(?)-segmented tarsi, and also the venation of areolate hemelytra, much differing from that of all known fossil and recent tingoids, preclude allocation of E. areolata to Tingidae"* (Golub & Popov, 2008). However, Golub, Popov & Arillo (2012) subsequently established the subfamily Tingiometrinae within Tingidae, a group characterised by the exactly the same suite of morphological traits. Ergo, our interpretation of *Ebboa* as a core member of the *Hispanocader-Paleoanomala-Tingiometra* should be uncontroversial.

As each newly described species of Ebboinae contributes additional morphological information that may affect the delimitation of genera, we refrain from providing an identification key at this stage. Instead, we summarise the characters that currently appear to distinguish the four recognised genera of Ebboinae in Table 1.

Table 1. Diagnostic differences among genera of Ebboinae.

Character	***Tingiometra***	***Hispanocader***	***Paleoanomala***	***Ebboa***
Anteocular	Very elongate; laterally flattened (hydrometrid-like)	Shorter	Shorter	Shorter
Postocular	Bulges adjacent to eyes	Bulges separated from eyes by constriction	Bulges separated from eyes by constriction	Not specified
Vertex	Smooth	Medial longitudinal depression extending from interocular area to postocular	Medial longitudinal depression extending from interocular area to postocular	Smooth
Pronotal callus	Without punctures	Punctate	Without punctures	Not discernible
Hind femur length	Reaches apex of abdomen	Shorter	Shorter	Shorter

Character	***Tingiometra***	***Hispanocader***	***Paleoanomala***	***Ebboa***
Costal area	Uniformly narrow	Widened near wing base	Widened near wing base	Uniformly narrow
R and M veins	Fused into common stem at wing base	Separate, fork at wing base	Separate, fork at wing base	Fused into common stem at wing base (?)
Tarsi	3-segmented	2-segmented (?)	2-segmented (?)	3-segmented

Based on our revised classification, lace bugs now comprise two families, Tingidae and Ignotingidae. The extinct family Ignotingidae are likely more closely related to extant tingids than to Ebboinae stat. nov., as they do not share the distinct suite of venational and cephalic characters of the latter. Since we have not examined any ignotingid material we refrain from changing its current classification at present, although we caution that it can likely be considered as part of Tingidae.

(ii) **Synonymy of *Tingiometra yuripopovi* Golub & Heiss, 2020 and *Paleoanomala aptenus* Poinar & Vega, 2020.**

Tingiometra yuripopovi Golub & Heiss, 2020 (published 29 April 2020) and *Paleoanomala aptenus* Poinar & Vega, 2020 (published 1 June 2020) are considered conspecific. Both taxa share identical morphology and proportions of the head, thorax, and abdomen, as well as forewing venation. Under the principle of priority, the earlier name must be retained. The following synonymy is therefore established:

Tingiometra yuripopovi Golub & Heiss, 2020

= *Tingiometra aptenus* (Poinar & Vega, 2020), syn. nov.

(iii) **Transfer of the female of *Tingiometra yuripopovi* Golub & Heiss, 2020 to *Paleoanomala*.**

Our reinterpretation of early tingid wing venation indicates that the female specimen originally described as *Tingiometra yuripopovi* belongs to the genus *Paleoanomala*. This placement is strongly supported by several morphological characters. The postocular portion of the head is broader than the anteocular portion and bears distinctly separated lateral bulges behind the eyes, whereas in *Tingiometra* the portion is uniformly bulging. The vertex bears a longitudinal medial furrow, while in *Tingiometra* it is convex. The eyes are small, in contrast to the larger eyes present in *Tingiometra* and *Hispanocader*, and the legs are shorter and stouter. The forewing structure and venation are also essentially identical to those of *Paleoanomala*, with the wing being submacropterous, the veins R and M arising separately, the base of the costal area widened, the claval furrow reduced, CuA markedly sinuate, and the anterior apical cell of the discoidal area small (Fig. 3A). On the basis of these characters, the female specimen of *T. yuripopovi* is transferred to *Paleoanomala* as *Paleoanomala yuripopovi* comb. nov (Golub & Heiss, 2020).

The affinities of the male paratype specimen assigned to *T. yuripopovi* are puzzling, as its venation is clearly different to all other *Tingiometra* (Fig. 3B) and *Paleoanomala*. Despite the stark morphological discordance from *P. yuripopovi*, it was presumed conspecific by Golub & Heis (2020) (Fig. 3D). This specimen appears to be most similar to *Hispanocader* with the following distinct combination of traits: postocular portion of head with distinct lateral protrusions separated from the eyes with a constriction (lobes touching the eyes in *Tingiometra*); medial furrow running from base

of head to eye level (uniformly convex in *Tingiometra*); laterally expanded mandibular plates (laterally flattened in *Tingiometra*); large eyes (diminutive eyes in *Paleoanomala*); callus punctate (devoid of punctures in *Paleoanomala* and *Tingiometra*), forewing with claval furrow (reduced claval furrow in *Paleoanomala*), R and M veins fork near forewing base (share stem R+M in *Tingiometra*). However, it differs from the type specimen of *Hispanocader* by the narrower and shorter subcostal area and differing cell proportions in the discoidal area (Fig. 3B, C).

Based on these observations, we hypothesise that the male paratype of *T. yuripopovi* may represent the first known male of *Paleoanomala*, which would imply an extreme degree of sexual dimorphism (with no parallel in any Tingidae, to our knowledge). Indeed, the male specimen does possess certain shared traits with the female of *P. yuripopovi*, namely: smaller body size compared to *Tingiometra* males (less than 2.4 mm), postocular portion of head broader than the anteocular one, distinct tubercles behind eyes, and antennae rather short. Furthermore, all *Paleoanomala* specimens (including at least three more specimens we have examined from Kachin amber) are female (Davranoglou & Fabrikant, personal observation).

However, we cannot exclude that the male specimen assigned to *P. yuripopovi* is an aberrant member of *Hispanocader*, or possibly even a representative of an undescribed genus. Such morphological discordance cannot be attributed to differences between male and female *Tingiometra*, as females of *Tingiometra* are already known and do not exhibit significant morphological divergence from their male counterparts (Heiss & Golub, 2015). If *Paleoanomala yuripopovi* is indeed strongly sexually dimorphic and the male is congeneric with *Hispanocader*, it would also raise the possibility that the newly described *Paleoanomala decapitata* could represent the female of *Hispanocader lisae*. However, this hypothesis cannot presently be substantiated due to the absence of

additional comparative material that might reveal further morphological diversity in Ebboinae. Moreover, *P. decapitata* is significantly smaller than *H. lisae*, which further complicates this interpretation.

In light of these uncertainties, we tentatively treat the male specimen as Ebboinae *incertae sedis*, while acknowledging that its taxonomic placement requires further revision.

Nomenclatural note on gender agreement. The type species of the genus Paleoanomala, originally described as *Paleoanomala aptenus* Poinar & Vega 2020, requires correction of the species name to reflect gender agreement. The genus name *Paleoanomala* is feminine, given that it is derived from the Greek adjective an_omalos (ἀmώlakoς), feminized to anomala. The prefix 'Paleo-' does not affect grammatical gender (ICZN Art. 30.1.2). The species epithet *aptenus* is derived from the Greek adjective *aptenos* (ἄpsemoς), meaning 'wingless' or 'unable to fly', and is adjectival in nature, as indicated by both its etymology and descriptive usage in the original publication. Given that there was no indication that the epithet was intended as a noun in apposition, it must agree in gender with the genus name (ICZN Art. 31.2). Consequently, the correct spelling of the type species is *Paleoanomala aptena*, with *aptenus* representing an incorrect original spelling subject to mandatory correction under ICZN Article 34.2.

Taxonomic affinities of *Paleoanomala decapitata* sp. nov.

The wing venation of *P. decapitata* is nearly identical to *Paleoanomala yuripopovi* comb. nov. (Golub & Heiss, 2020; Poinar & Vega 2020), which until now was the only known species of the genus, found exclusively in Cenomanian Kachin amber and assigned to the extinct tingid subfamily Tingiometrinae (Golub & Heiss, 2020; Poinar & Vega, 2020). The major differences we could identify, based on the original articles

describing *P. yuripopovi*, are listed as follows: the presence of ca. seven crossveins on the subcostal area of *P. yuripopovi* – there is at most one transverse vein in *P. decapitata* (Fig. 1); posterior medial cell of the discoidal area relatively small (clearly larger in *P. yuripopovi*); claval area shorter than midlength of hemelytron (reaches midlength in *P. yuripopovi*), and CuA vein more sinuate (narrower in *P. yuripopovi*). Based on their morphological similarity, we propose that the two species are closely related, despite their large temporal (ca. 4 million years) and considerable geographical distance. As such, *P. decapitata* represents a valuable addition to the fossil record of lace bugs and highlights the palaeobiological richness of the Peñacerrada I amber deposit.

Palaeobiogeography of Cretaceous Iberian amber fauna

The discovery of *Paleoanomala decapitata* in Lower Cretaceous Peñacerrada I amber significantly expands our understanding of the biogeographical connections of tingids and their extinct relatives in Iberia. Prior to this study, the genus *Paleoanomala* was known exclusively from Cenomanian Kachin amber (Golub & Heiss, 2020; Poinar & Vega, 2020). Its occurrence in Spain, separated by thousands of kilometres, suggests that lineages of Tingidae and closely related groups were widely distributed across Laurasia from the Albian to the Cenomanian periods, potentially reflecting the connectivity of forested ecosystems across northern Gondwanan and southern Laurasian margins.

Another hemipteran, the enicocephalomorphan genus *Enicocephalinus* provides a complementary perspective on these patterns. Like *Paleoanomala*, *Enicocephalinus* demonstrates close biogeographical affinities between Spanish amber with geographically distant Barremian deposits from Lebanon (Azar et al., 1999;

Davranoglou et al., 2024; Azar and Maksoud, 2025). The presence of *Enicocephalinus* in both Iberian and Lebanese deposits highlights repeated examples of genus-level continuity across widely separated palaeobiogeographical regions (Peris et al., 2016; Álvarez-Parra et al., 2023; Davranoglou et al., 2024;). Together with *Paleoanomala*, these findings underscore that certain insect lineages were able to maintain broad ranges across Laurasia and northern Gondwana, either through dispersal along connected forested ecosystems or by persistence in ecologically similar habitats. To substantiate this hypothesis, we undertook a comprehensive analysis of the palaeobiogeographic affinities of all arthropods known from Iberian amber deposits.

Of the 53 arthropod genera documented from Albian Spanish amber (Table 2), 29 also occur in Myanmar (Cenomanian), 21 in Lebanon (Barremian), 15 in Russia (Turonian?), 10 in the Nearctic (Turonian to Campanian), and only 9 in neighbouring France (Albian–Cenomanian). These shared faunal affinities indicate that a substantial fraction of the Iberian amber fauna had close biogeographical connections with contemporaneous biotas across Eurasia and into northern Gondwana. Although Myanmar amber has been more extensively collected and studied than other Cretaceous ambers, thereby introducing an inevitable sampling bias, these patterns nonetheless suggest the existence of a broadly distributed biogeographical realm characterised by similar floral and faunal assemblages. The relatively low faunistic match between Spanish and French amber faunas, the two closest temporally and geographically, is puzzling and more data is required in order to understand its causes (Peris et al., 2016).

Indeed, the widespread occurrence of resin-producing trees, likely Araucariacea such as *Agathis*-like species, supports the notion that similar resiniferous forest ecosystems extended across large parts of the northern and southern hemispheres during the Early Cretaceous (Chaler & Grimalt, 2005; Barrón et al., 2015; Delclòs et al., 2023). These

forests would have provided both the ecological context and taphonomic conditions necessary for the formation of amber and the exceptional preservation of arthropod inclusions. The shared occurrence of genera across Spanish, Myanmar, and Lebanese amber deposits implies that this biome was extensive, spanning Europe, the Middle East, and Southeast Asia, with minor geographic differentiation, possibly driven by latitudinal climatic gradients or regional floral compositions.

Conclusion

The Iberian Cretaceous amber fauna demonstrates that Early Cretaceous resiniferous forests supported a remarkably similar component of their insect assemblages across wide geographic distances. The presence of *Paleoanomala* in both Iberia and Burma Terrane exemplifies this biogeographical continuity, highlighting the potential for broad dispersal of small, likely phytophagous insects within connected resin-producing forest ecosystems. However, assessments on the proportion of endemic taxa of each amber fauna (taking into account current biases in our understanding) should complement data on faunistic overlap in order to elucidate how truly similar roughly coetaneous insect assemblages were across wide geographical distances.Regarding the taxonomic findings of our study, the discovery of *Paleoanomala decapitata* sp. nov. from Albian Spanish amber extends the geographical and temporal range of the genus and adds to the diversity of Early Cretaceous lace bugs. Our reinterpretation of forewing venation reveals a shared wing ground plan among the genera *Paleoanomala*, *Tingiometra*, *Hispanocader* and *Ebboa*, supporting the synonymization of Tingiometrinae and Hispanocaderidae with Ebboinae stat. nov. Our results indicate that wing venation in Tingidae evolved through progressive simplification from a more complex ancestral condition. The revised classification clarifies the relationships of

several enigmatic Cretaceous taxa and provides a new framework for understanding early lace bug evolution.

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Author contributions. **Conceptualization** Leonidas-Romanos Davranoglou (L-RD); **Data Curation** L-RD, Ricardo Pérez-de la Fuente (RPF), Sergio Álvarez-Parra (SA-P), Enrique Peñalver (EP); **Funding Acquisition** L-RD; **Investigation** L-RD, Dolev Fabrikant (DF), RPF, SA-P, EP, Xavier Delclòs (XD); **Project Administration** L-RD; **Resources** L-RD; **Visualization** L-RD, DF; **Writing – Original Draft** L-RD, EP, RPF, SA-P, DF, XD; **Writing – Review & Editing** L-RD, EP, RPF, SA-P, DF, XD.

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