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New *Leptotarsus* from the Early Cretaceous of Brazil and Spain: the oldest members of the family Tipulidae (Diptera)

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Abstract

New species of *Leptotarsus* (Tipulidae *s.str.*) are described from the Early Cretaceous beds of Brazil (Santana Fm. Aptian/Albian, ca. 112 Mya) and Spain (La Huérguina Fm., Late Barremian, ca. 126 Mya), vis. *L. grimaldii* **sp. nov**., *L. cretaceus* **sp. nov**., *L. martinsnetoi* **sp. nov.**, *L. buscalioniae* **sp. nov**., *L. ibericus* **sp. nov**. and *L. contractus* **sp. nov**. Males of three species possess extremely long antennae. The fossils are the oldest representatives of the genus *Leptotarsus*, and the oldest known members of the family Tipulidae.

Key words: *Leptotarsus*, Early Cretaceous, new species, Santana, Las Hoyas

Introduction

The Tipulomorpha—crane flies—is one of the largest groups of the order Diptera. The group has a worldwide distribution, and includes over 15000 extant species (Oosterbroek 2013). Only one tipulomorphan family, the Limoniidae, is well represented in the fossil record since the early Middle Triassic (ca. 240 million years in age, Mya), being the most ancient living family of the order Diptera (Shcherbakov *et al.* 1995; Krzemiński & Evenhuis 2000; Krzemiński & Krzemińska 2003; Blagoderov *et al*. 2007). The family Tipulidae, however, does not appear in the geologic record until the mid-Cretaceous: *Tipula eva* Krzemiński, 1992 (Krzemiński 1992), described on the basis of a single wing fragment, stands alone as the oldest know representative of the family and the only species so far described for the Mesozoic. The fossil came from the Upper Bureya depression, Khabarovsk Krai, Russia, Kyndaly Formation, which age has been referred to as Albian–Cenomanian (Stratigraphic Dictionary of the USSR 1979). However, based on plant megafossils and palynomorphs, this formation has been dated as Albian (ca. 105 Mya; Krassilov 1973; Markevich & Bugdaeva 2009).

Leptotarsus is a large genus of the family Tipulidae, comprising over 300 extant species in 20 subgenera (Oosterbroek 2013). Though *Leptotarsus* species occur in all the world's biogeographic regions, it is in the Southern Hemisphere that the bulk of the diversity of the genus is found, with only seven species of subgenus *Longurio* Loew occurring in the Northern Hemisphere. No extant species of the genus are known to occur in West Palaearctic, and only three East Palaearctic species are known (from China and Japan) (Oosterbroek 2013). The most species-rich regions are the Neotropical and Australian. The fossil record of the genus *Leptotarsus* is much reduced, and extinct species were recorded only from Europe and only from the Cenozoic: two species placed in the subgenus *Macromastix* (*bornhardti* Meunier, 1917 and *cladoptera* Cockerell et Haines, 1921) were described respectively from the Eocene Baltic amber and Eocene/Oligocene of England (Tertiary of France was stated erroneously for the former in Evenhuis 1994).

In this paper, six new fossil species of the genus *Leptotarsus* are described from two Early Cretaceous outcrops: Santana (Crato) Formation of Brazil and Las Hoyas (La Huérguina Formation) of Spain. These are the oldest records of the genus, and also the oldest occurrences of the family Tipulidae.

The laminated limestone of the Santana (Crato) Formation in Northeastern Brazil, considered to be of Aptian/

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Albian age (ca. 112 Mya), is famous for the exquisite level of preservation of its fossils. The first records of crane flies from this locality were provided by Grimaldi (1990), who figured some specimens of Limoniidae, but did not provide formal descriptions with names. At the moment, the only formally named species were described by Ribeiro & Martins-Neto (1999) and Ribeiro & Krzemiński (2000), all belonging to the Limoniidae.

The laminated limestone of the La Huérguina Formation, east-central Spain, considered to be of Late Barremian age (ca. 126 Mya), is famous for the quality of preservation of soft-bodied organisms. No crane fly species have been hitherto described or mentioned for Las Hoyas.

Both localities are among the most important Early Cretaceous *Konservat-Lagerstätten* in the world, and they have revealed a great diversity of Mesozoic fossil insects (for further details see Martill *et al.* 2007 and Buscalioni & Fregenal-Martínez 2010). The dipteran faunae from the Santana Formation as well as from the La Huérguina Formation are very distinctive compared to that of other diverse Cretaceous insect *Lagerstätten*, the most significant aspect being their relative rarity. Santana fossil Diptera comprise merely 2% of all insect specimens (Martill *et al*. 2007). A similar proportion is found in collections of Las Hoyas fossils. The second author examined a small Diptera collection housed in the Museum of Science of Castilla–La Mancha in Cuenca numerically: among about 3000 total insects only several dozen of dipteran impressions were collected during two decades of excavations (excluding numerous poorly preserved larvae of Chaoboridae). The reasons of such rarity are not clear.

Material and methods

The specimens from the Santana Formation of Brazil are housed in the collections of the Division of Invertebrate Zoology, American Museum of Natural History (AMNH), New York, USA and Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); the specimens from the La Huérguina Formation of Spain are in the collections of Museo de las Ciencias de Castilla–La Mancha (LH).

Photographs of AMNH specimens were prepared with Microptics image system (www.visionarydigital.com). Images of MZUSP material were obtained with a Nikon DS-Ri1 digital camera attached to Nikon SMZ1000 stereoscopic microscope. LH specimens were photographed with a Nikon D3100 digital camera attached to Nikon stereoscopic microscope. Illustrations were made with a drawing tube attached to a stereoscopic microscope. Measurements were taken with a digital stage micrometer (AMNH specimens), and with Carl Zeiss AxioVision software (MZUSP specimens), and are given in millimeters.

Descriptive terminology follows mostly McAlpine (1981). Terminology for male terminalia and wing venation are in accordance with that used by Ribeiro (2006, 2008). The vein nomenclature differs from the system adopted by most authors (e.g., Alexander & Byers 1981; Starý 1992; Shcherbakov et al. 1995; Lukashevich 2009), in which the vein treated here as a true cross-vein r-r is considered as R_2.

Systematics

Family Tipulidae

Genus *Leptotarsus* Guérin-Méneville, 1831

Leptotarsus Guérin-Méneville, 1831: pl. 20, fig. 1 [1838: 286].
Type species *Leptotarsus macquarti* Guérin-Méneville, 1831, by monotypy.

Key to Early Cretaceous species *of Leptotarsus*

1 (6) Wing transparent except for dark pterostigma and costal field
2 (3) Distal sections of veins M_3 and M_4 parallel. . . . . ***L.grimaldii* sp. nov.**
3 (2) Distal sections of veins M_3 and M_4 divergent
4 (5) Discal cell twice longer than wide . . . . . ***L. cretaceus* sp. nov.**
5 (4) Discal cell as long as wide . . . . . ***L. martinsnetoi* sp. nov.**

6 (1) Wing transparent except for dark pterostigma
7 (10) Rs origin at the level of connection of m-cu and Cu
8 (9) Cross-vein m-m subequal to distal section of M_{1+2}; distal sections of veins M_3 and M_4 strongly divergent . . . . . ***L. buscalioniae* sp. nov.**
9 (8) Cross-vein m-m longer than distal section of M_{1+2}; distal sections of M_3 and M_4 almost parallel . . . . . ***L. ibericus* sp. nov.**
10 (7) Rs origin proximal to connection of m-cu and Cu . . . . . ***L. contractus* sp. nov.**

***Leptotarsus grimaldii* sp. nov.**
(Figs 1, 2, 10–13)

Type material. *Holotype*: AMNH SA 46358 (entire male specimen, preserved in dorsal view; preserved structures include the long antennae, left front leg and terminalia). *Paratype:* AMNH SA 46366 (entire male specimen, preserved in lateral view; preserved structures include head with mouthparts, the long antennae, and middle legs). NE Brazil, Santana Fm., Aptian/Albian, Early Cretaceous. Both housed in the Division of Invertebrate Zoology, American Museum of Natural History, New York, USA.

Etymology. The species is named after Dr. David Grimaldi, curator at the American Museum of Natural History in New York, for his great contribution to the paleontology of insects.

Diagnosis. This species differs from the other Cretaceous species mostly by having the distal sections of veins M_3 and M_4 very similar in length and shape, running parallel to each other.

Description. Male. *Head.* Head capsule with an anterodorsal protuberance; antenna long and slender, bearing long and slender flagellomeres (total number of flagellomeres unknown); scape stout and long, ca. 3.5x longer than pedicel; nasus distinct; rostrum ca. 0.5x the total length of head. *Thorax* stout, ca. 1.8x longer than wide and almost as long as high. *Wing* transparent except for dark pterostigma and costal field. Sc reaching wing margin at the level of first bifurcation of Rs and beyond the level of the tip of Cu; sc-r present, positioned near the tip of Sc; Rs curved, subequal in length with R_{2+3}; R_1 reaching wing margin at the level of bifurcation of R_{2+3}; r-r oblique, linking R_1 to R_2; R_2 oblique; medial vein four-branched; discal cell small, ca. 1.23 to 1.5x longer than wide; veins M_3 and M_4 running parallel to each other, very similar in length and shape; m-cu linking Cu to the base of M_4. *Abdomen* stout, ca. 1.7x longer than thorax; gonocoxite conical, ca. 2.4x longer than wide; gonostylus divided with clasper of gonostylus slightly longer than the lobe of gonostylus.

Measurements. Male. Antenna length, at least 16.49. Body length, ca. 7.2. Wing length/width ca. 6.9/ 1.78–1.89.

***Leptotarsus cretaceus* sp. nov.**
(Figs 3, 14, 15)

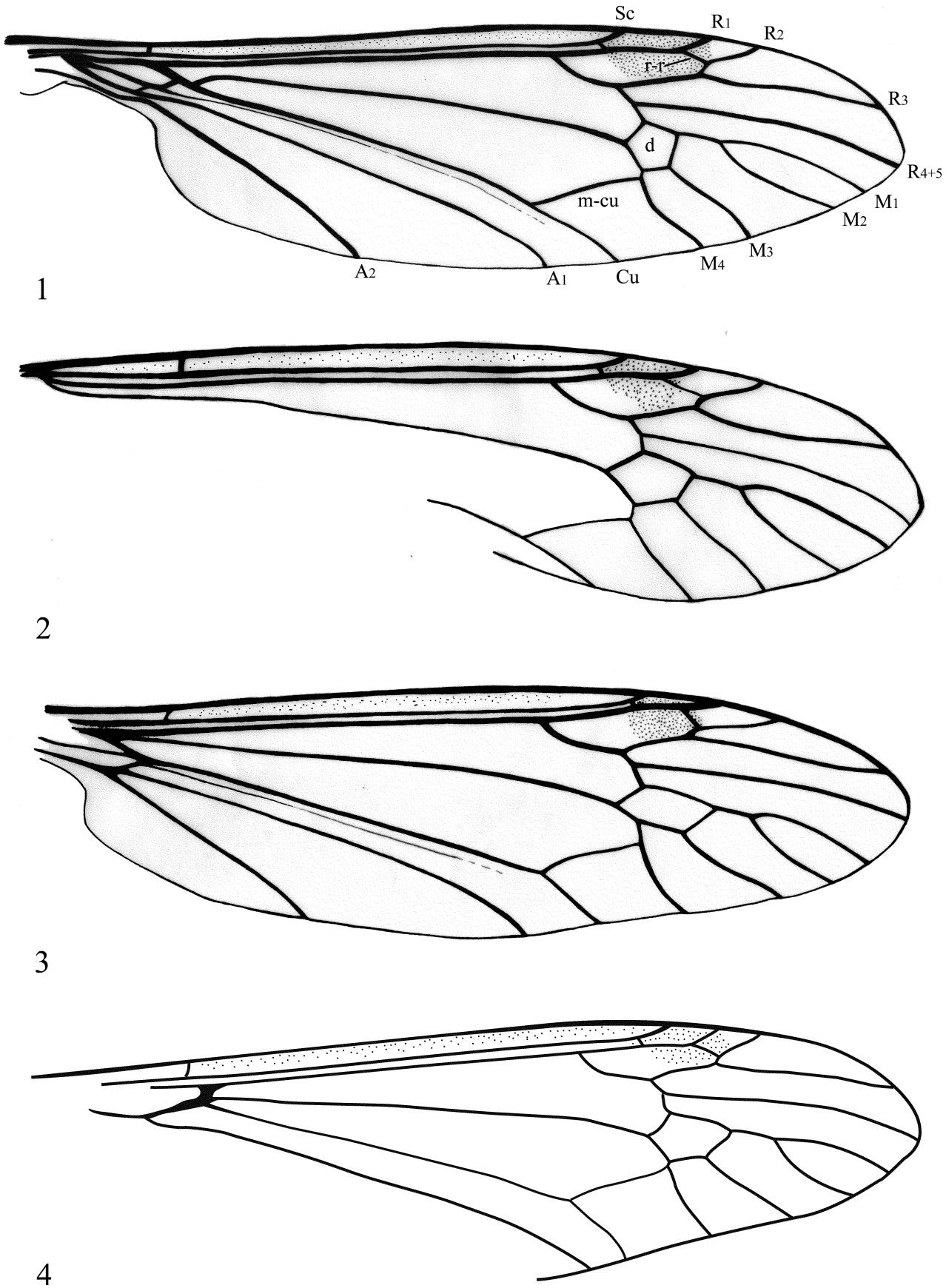
Type material. *Holotype*: AMNH SA 46354 (entire female specimen, preserved in dorsal view; preserved structures include the basal portions of antennae and head with mouth parts). NE Brazil, Santana Fm., Aptian/ Albian, Early Cretaceous. Housed in the Division of Invertebrate Zoology, American Museum of Natural History, New York, USA.

Etymology. From Latin, “chalky”. Named in reference to the Cretaceous Period.

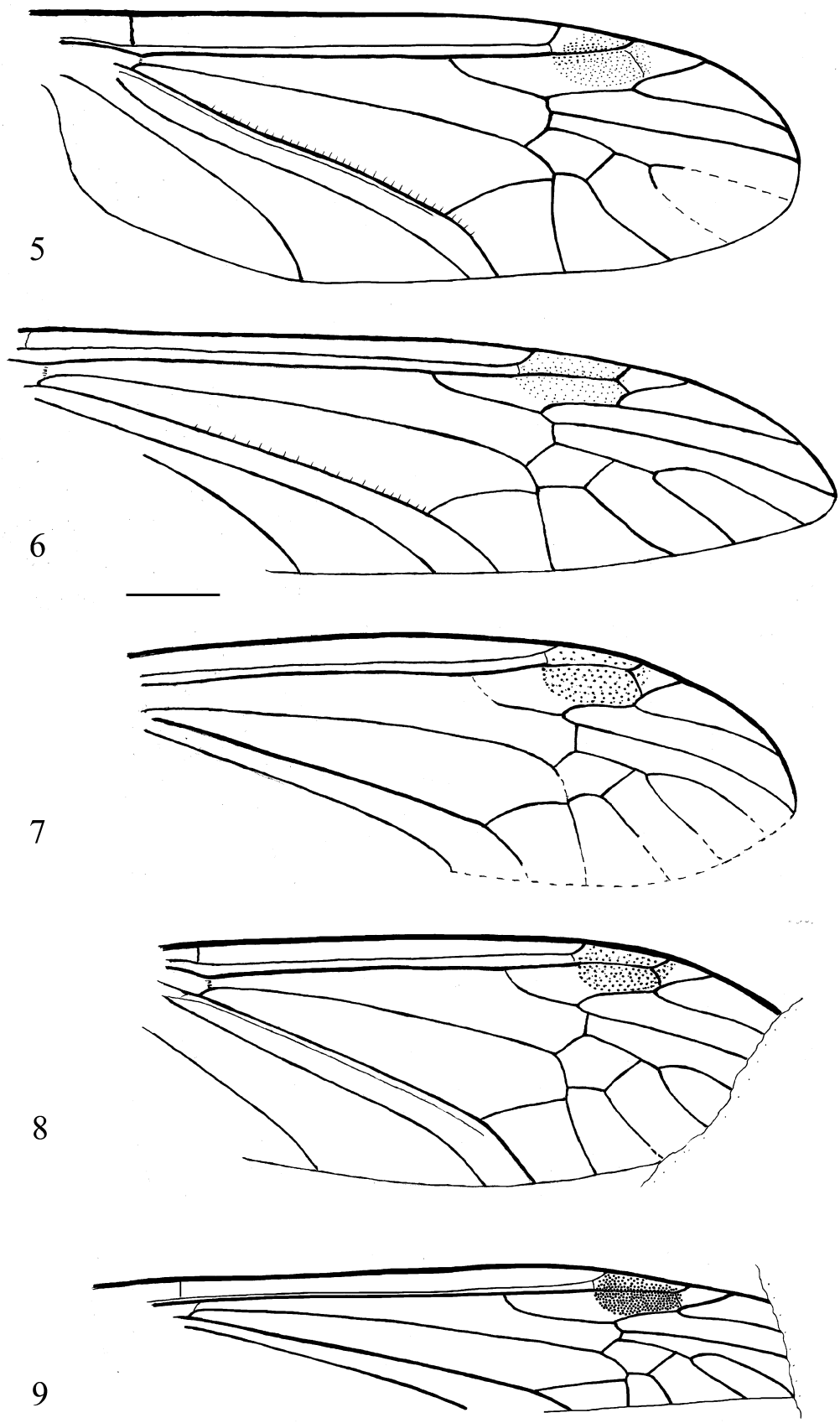
Diagnosis. This species differs from the other Cretaceous species by its dark costal field, narrower parallelogram-shaped discal cell and veins M_3 and M_4 divergent and dissimilar in shape.

Description. Female. *Head.* Antenna with short flagellomeres, first flagellomere shorter than remaining; scape stout and long, about 4x longer than pedicel; rostrum ca. 0.5x the total length of head. *Thorax* stout, ca. 1.7x longer than wide. *Wing* transparent except for dark pterostigma and costal field. Sc reaching wing margin shortly beyond the level of first bifurcation of Rs and beyond the level of the tip of Cu; sc-r present, positioned very near the tip of Sc; Rs curved, slightly shorter than R_{2+3}, R_1 reaching wing margin beyond the level of bifurcation of R_{2+3}; r-r oblique, linking R_1 to R_2; R_2 oblique; medial vein four-branched; parallelogram discal cell relatively large, ca. 2.1x longer than wide; M_3 and M_4 divergent toward wing margin; M_3 sinuous; M_4 arcuated; m-cu linking Cu to the base of M_4. *Abdomen* stout, ca. 1.8x longer than thorax.

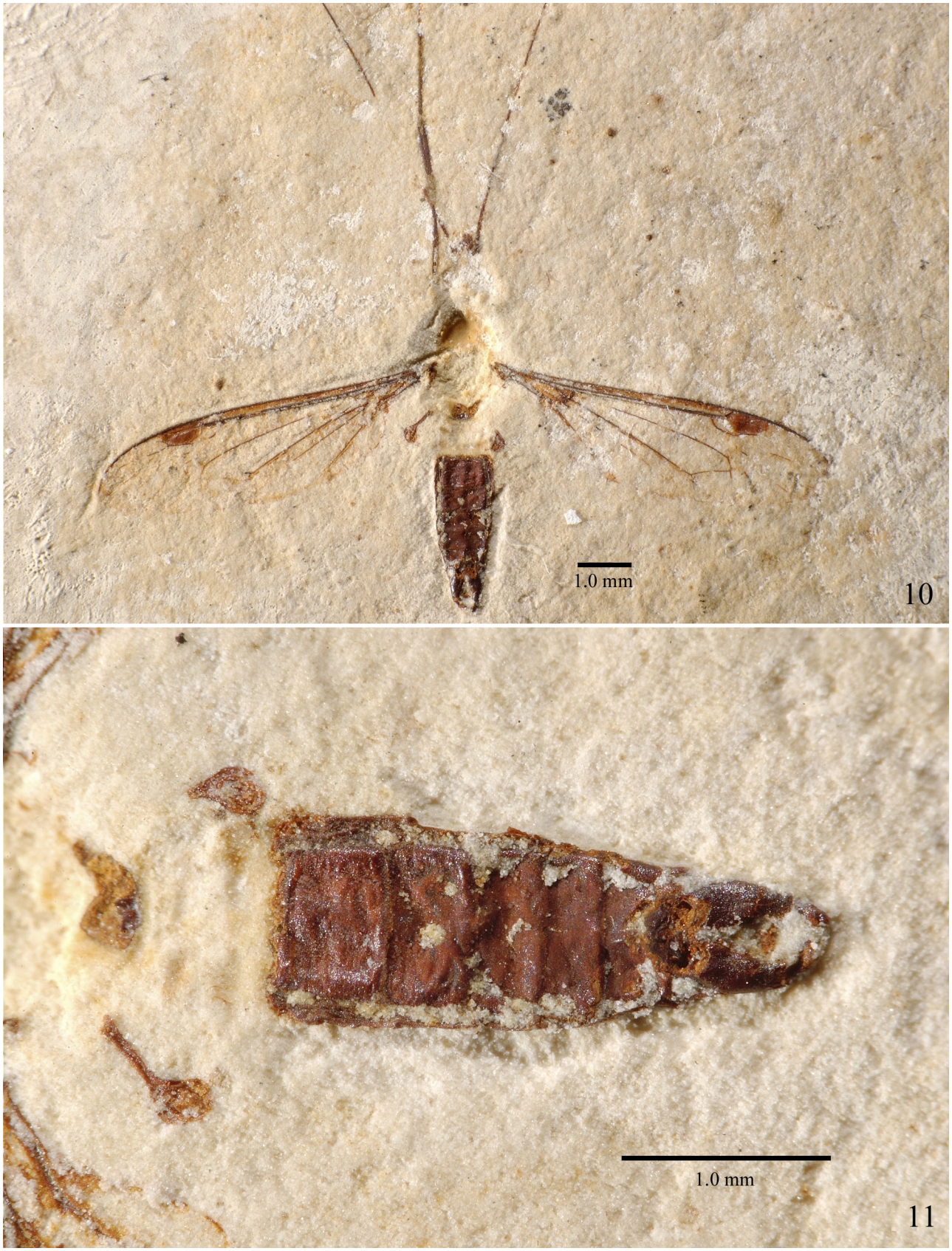
Measurements. Head length, 1.99. Body length, ca.12.3. Wing length/width ca. 9.8/2.8.



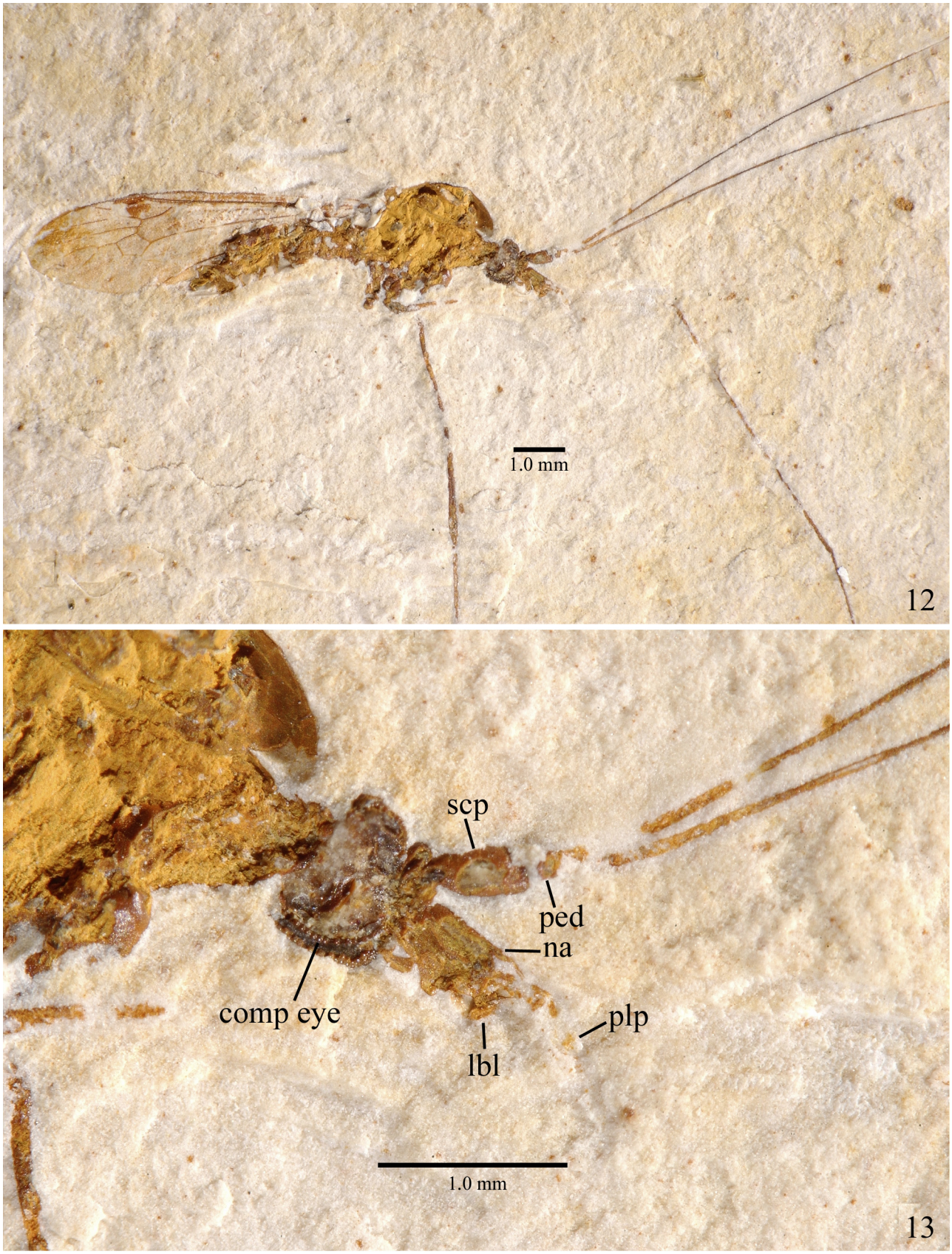
FIGURES 1–4. Wing venation of *Leptotarsus* spp. from Santana Formation, Early Cretaceous, Brazil. 1—*L. grimaldii* **sp. nov.**, holotype AMNH SA 46358, right wing. 2—*L. grimaldii* **sp. nov.**, paratype AMNH SA 46366, left wing. 3—*L. cretaceus* **sp. nov.**, holotype AMNH SA 46354, right wing. 4—*L. martinsnetoi* **sp. nov.**, holotype MZUSP1580, left wing.



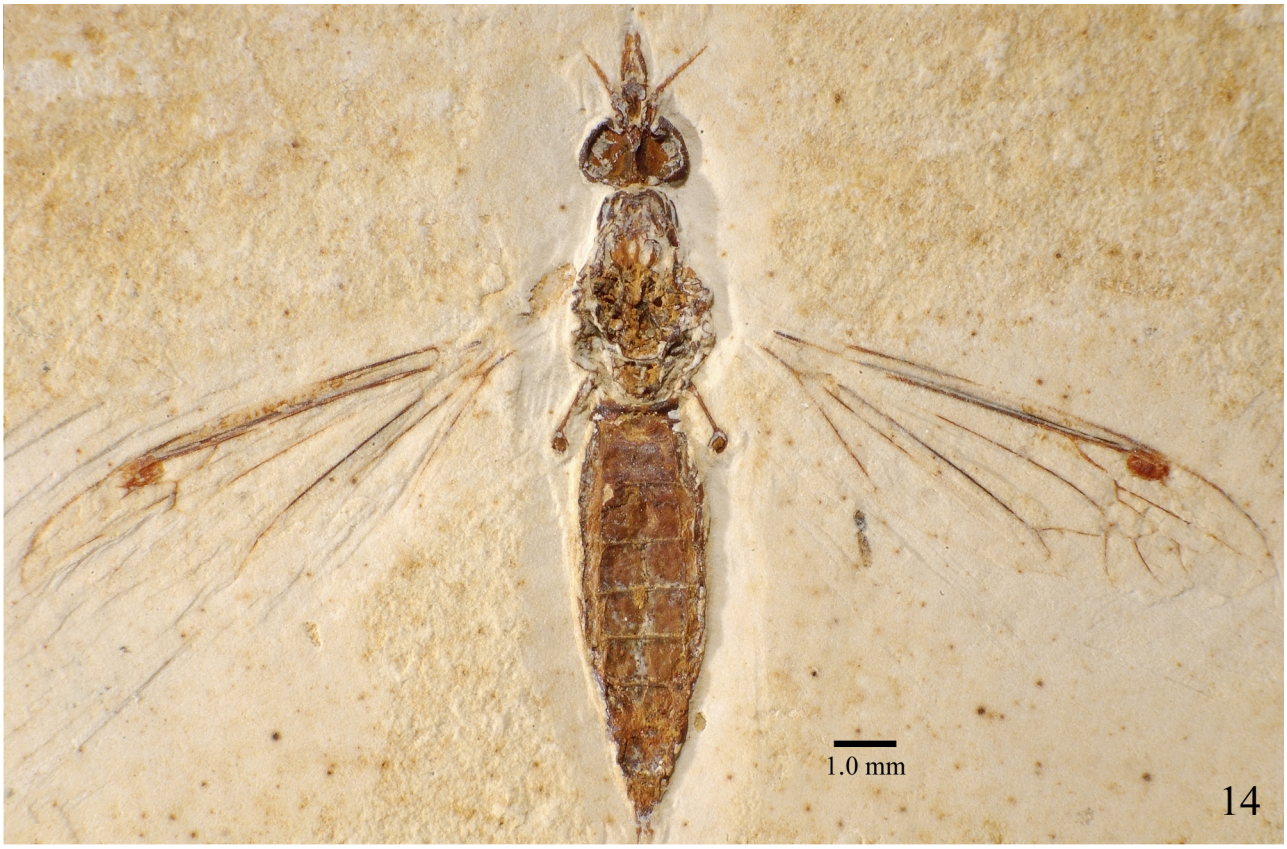
FIGURES 5–9. Wing venation of *Leptotarsus* spp. from Las Hoyas, Early Cretaceous, Spain. 5—*L. buscalioniae* **sp. nov.**, holotype LH 35088, right wing. 6—*L. buscalioniae* **sp. nov.**, holotype LH 35088, left wing. 7—*L.ibericus* **sp. nov.**, holotype LH 28206. 8—*L.ibericus* **sp. nov.**, paratype LH 29995. 9—*L.contractus* **sp. nov.**, holotype LH 15419. Scale bar 1 mm.

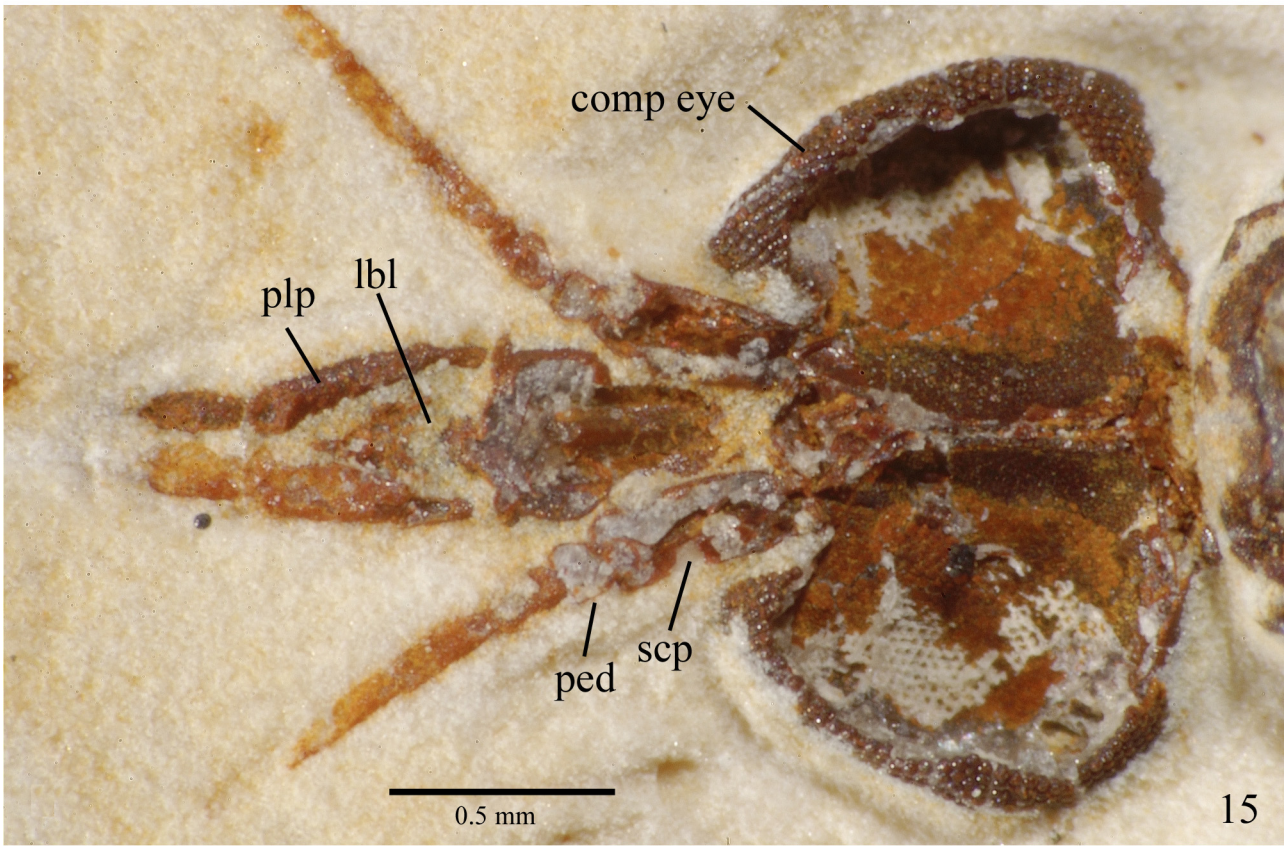


FIGURES 10–11. *Leptotarsus grimaldii*, **sp. nov.**, from Santana Formation, Early Cretaceous, Brazil, holotype AMNH SA 46358. 10—Total view. 11—Detail of abdomen and genitalia.

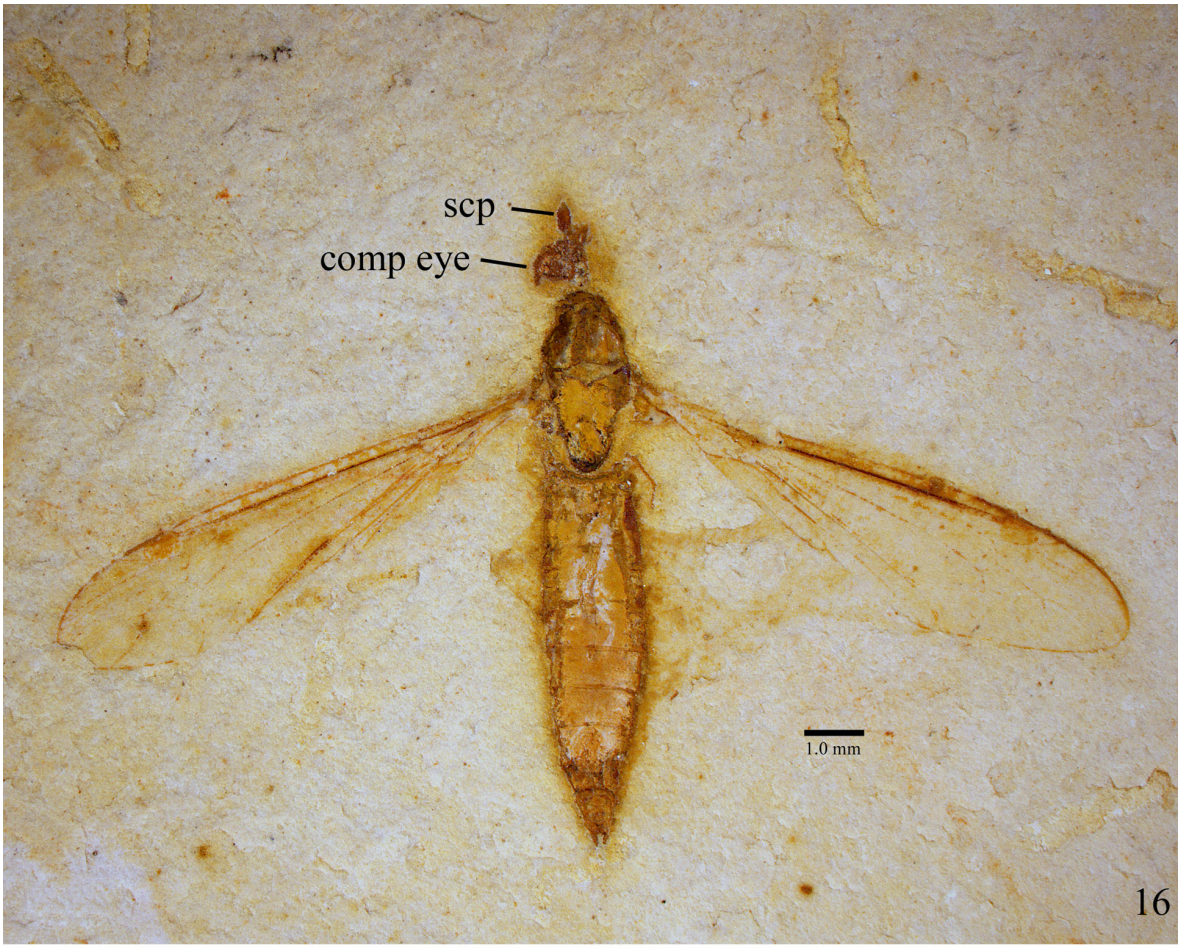


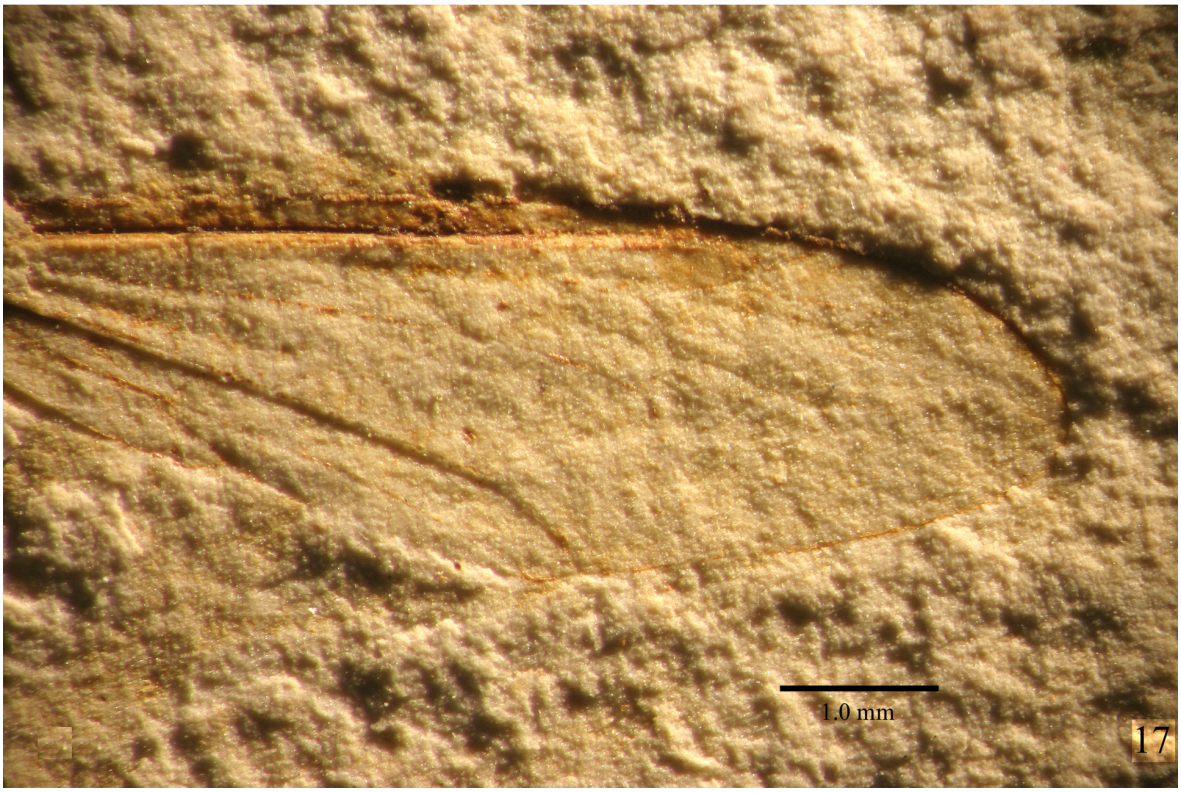
FIGURES 12–13. *Leptotarsus grimaldii*, **sp. nov.**, from Santana Formation, Early Cretaceous, Brazil, paratype AMNH SA 46366. 12—Total view. 13—Detail of head. Abbreviations: comp eye: compound eye; lbl: labella; na: nasus; ped: pedicel; plp: palpus; scp: scape.





FIGURES 14–15. *Leptotarsus cretaceus*, **sp. nov.**, from Santana Formation, Early Cretaceous, Brazil, holotype AMNH SA 46354. 14—Total view. 15—Detail of head. Abbreviations: comp eye: compound eye; lbl: labella; ped: pedicel; plp: palpus; scp: scape.





FIGURES 16–17. *Leptotarsus martinsnetoi*, **sp. nov.**, from Santana Formation, Early Cretaceous, Brazil, holotype (part) MZUSP1580. 16—Total view. 17—Detail of right wing. Abbreviations: comp eye: compound eye; scp: scape.

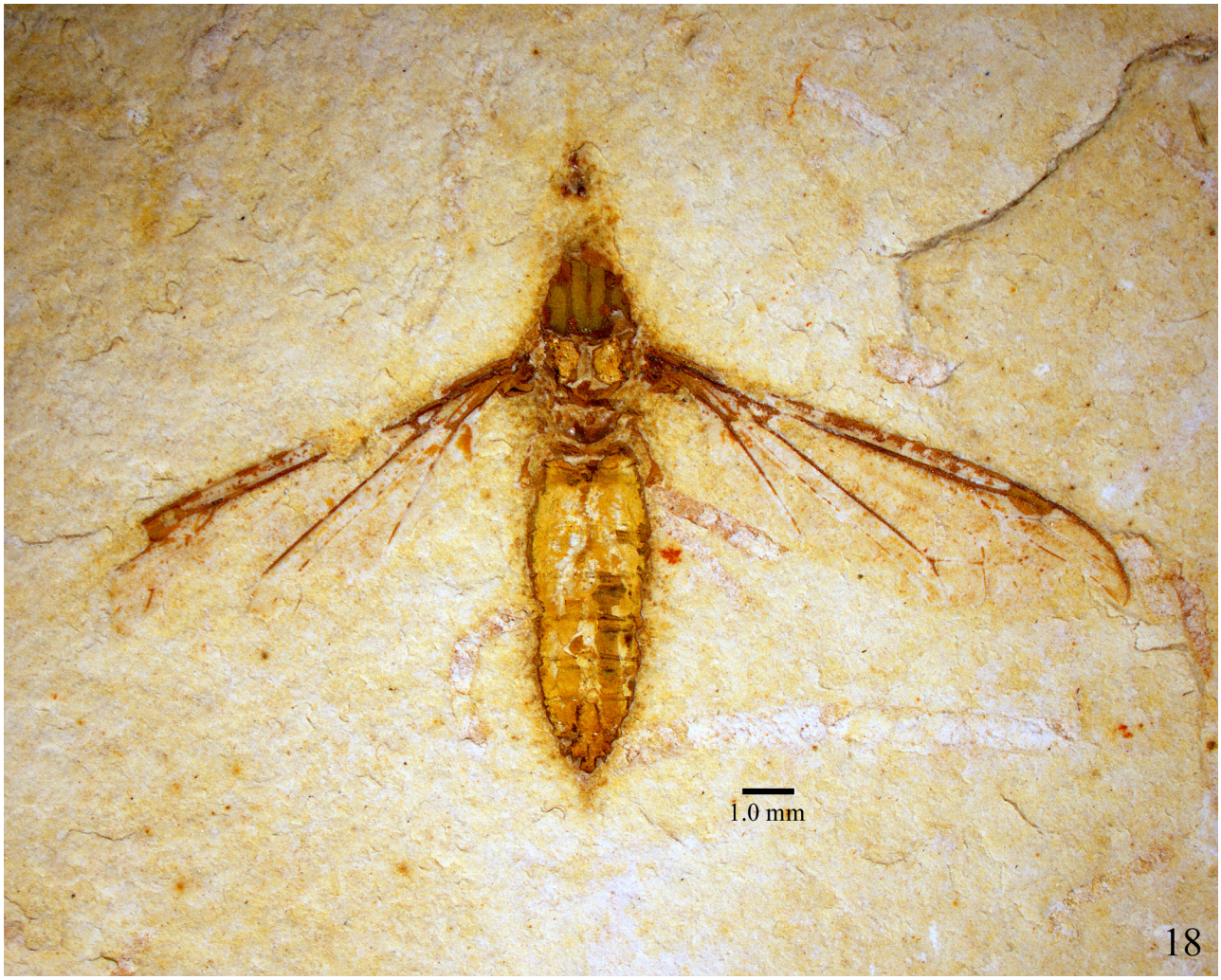


FIGURE 18. *Leptotarsus martinsnetoi*, **sp. nov.**, from Santana Formation, Early Cretaceous, Brazil, paratype MZUSP1581, total view.

***Leptotarsus martinsnetoi* sp. nov.**
(Figs 4, 16–18)

Type material. *Holotype*: MZUSP1580 (part and counterpart of entire female specimen, preserved in dorsal view; head partially preserved. *Paratype*: MZUSP1581 (entire female specimen, preserved in dorsal view; head poorly preserved). NE Brazil, Santana Fm., Aptian/Albian, Early Cretaceous. Both specimens are housed in the Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP).

Etymology. The species is named after Dr. Rafael Gioia Martins-Neto (1954–2010), Brazilian paleontologist, collector of the MZUSP specimens.

Diagnosis. This species differs from the other Cretaceous species by its dark costal field, wide small discal cell and veins M_3 and M_4 divergent.

Description. *Head.* Scape stout and long, about 2.4x longer than wide. *Thorax* stout, ca. 2.1x longer than wide. *Wing* transparent except for dark pterostigma and costal field. Sc reaching wing margin shortly beyond the level of first bifurcation of Rs and near the level of the tip of M_4; sc-r present, positioned near mid-point between origin of Rs and tip of R_1; Rs curved, slightly longer than R_{2+3}; R_1 reaching wing margin at the level of bifurcation of R_{2+3}; r-r oblique, linking R_1 to R_2; R_2 oblique; medial vein four-branched; discal cell ca. 1.63x longer than wide; M_3 and M_4 divergent toward wing margin, similar in shape; m-cu linking Cu to the base of M_4. *Abdomen* stout, ca. 2.0x longer than thorax; ovipositor with short, stout cerci.

Measurements. Body length, 10.7–11.9. Wing length/width, 8.9–10.5/2.4–2.8.

Note. The holotype is a bit smaller than the paratype, but since the two specimens have basically the same pattern of wing venation, they are treated here as belonging to the same species.

***Leptotarsus buscalioniae* sp. nov.**
(Figs 5, 6, 19–21)

Type material. *Holotype*: LH 35088± (part and counterpart of entire male specimen; preserved structures include the long antenna and terminalia). East-central Spain, Las Hoyas; La Huérguina Limestone Formation, Late Barremian, Early Cretaceous. Housed in Museo de Ciencias de Castillia–La Mancha.

Etymology. The species is named after Dr. Angela Buscalioni, the main organizer and motor of the excavation in Las Hoyas for many years.

Diagnosis. This species differs from all known Cretaceous species by relatively long abdomen. It differs from other species of *Leptotarsus* from the Early Cretaceous of Spain by long distal section of vein M_{1+2} and distal sections of veins M_3 and M_4 strongly divergent, and from Brazilian species by absence of dark costal field.

Description. *Head.* Antennae long and slender, bearing long and slender flagellomeres (total number of flagellomeres unknown); rostrum ca. 0.5x the total length of head. *Thorax* stout, as long as wide. *Wing* transparent except for dark pterostigma; Sc reaching wing margin at the level of first bifurcation of Rs and beyond level of the tip of Cu; sc-r present, positioned near the tip of Sc; Rs 1.2–1.4 times longer than R_{2+3} stem; R_1 reaching wing margin distal to the level of R_{2+3} bifurcation; r-r oblique, linking R_1 to R_2; R_2 oblique; medial vein four-branched; discal cell as long as wide; M_3 and M_4 strongly divergent; M_3 sinuous; M_4 arcuated and shorter; long m-cu linking Cu to the base of M_4. *Abdomen* stout, ca. 3.0x longer than thorax; gonocoxite conical, as long as wide.

Measurements. Antenna length, at least 10.2. Body length, ca. 9.5. Wing length/width, 9.4–10.0/2.2–2.7.

Note. In the holotype, one wing is longer and narrower than the other (proportions of length to width about 1:4.5 and 1:3.5 respectively). This shows clearly that the original proportions of the wings have been distorted. Therefore, one must be careful when comparing proportions of wings in Las Hoyas fossil insects.

***Leptotarsus ibericus* sp. nov.**
(Figs 7, 8, 22–25)

Type material. *Holotype*: LH 28206± (part and counterpart of entire male specimen; preserved structures include the long antenna and terminalia). *Paratypes:* LH 29995± (part and counterpart of isolated wing) and LH 18122± (part and counterpart of adult). East-central Spain, Las Hoyas; La Huérguina Limestone Formation, Late Barremian, Early Cretaceous. Housed in Museo de Ciencias de Castillia–La Mancha.

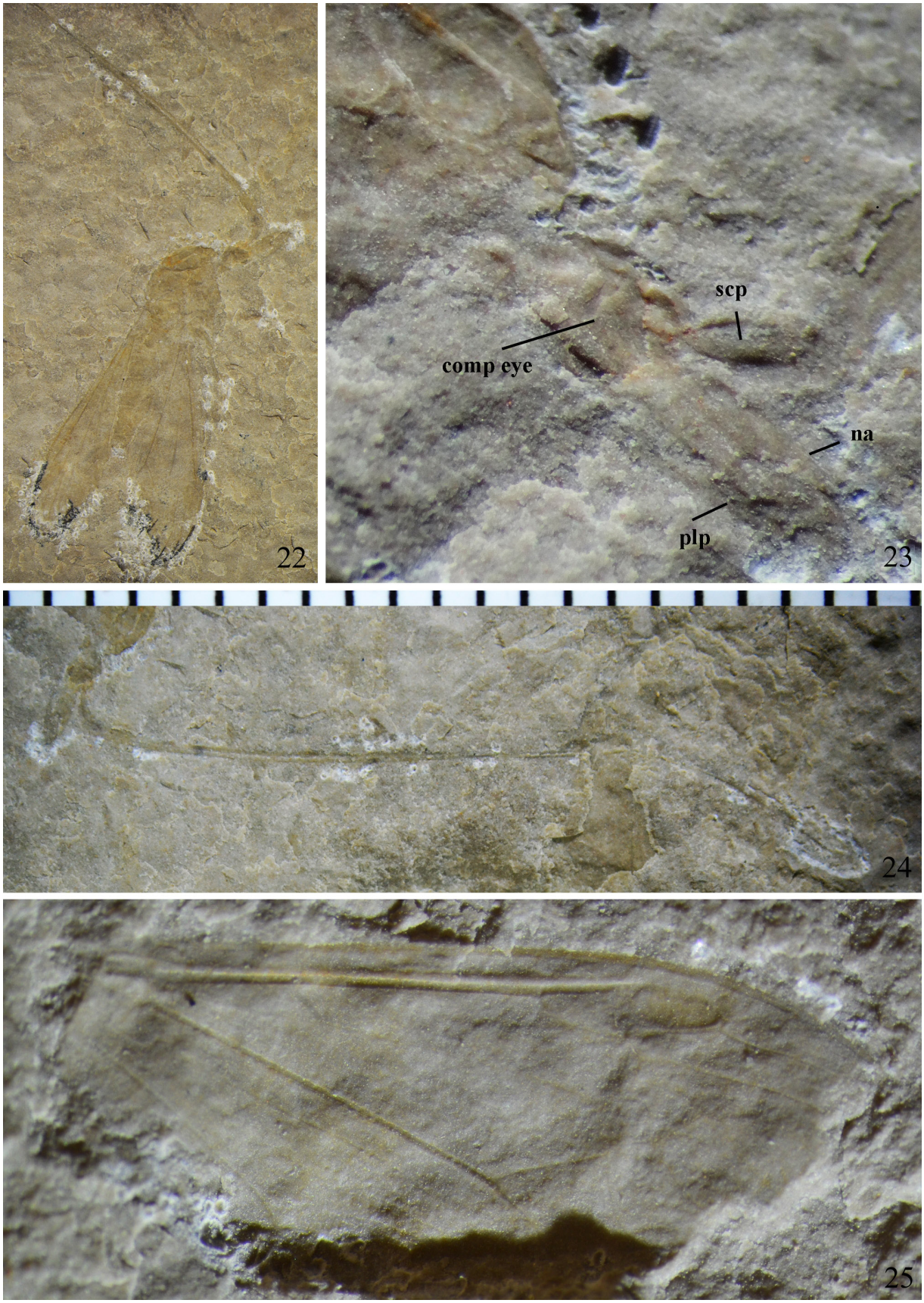
Etymology. Named after Iberian Mountain Range.

Diagnosis. This species differs from species of *Leptotarsus* from the Cretaceous of Brazil by absence of dark costal field, and from *L. buscalioniae* **sp. nov.** by the shorter distal section of M_{1+2} and distal sections of veins M_3 and M_4 almost parallel.

Description. *Head.* Head capsule with an anterodorsal protuberance; antennae long and slender, bearing long and slender flagellomeres (total number of flagellomeres unknown); scape stout and long, swollen in middle, 3x longer than pedicel; vestiture of flagellar segments long, delicate and abundant, without visible verticils, length of macrosetae ca. 4.0x the diameter of flagellomere (visible on short portion of antenna); nasus distinct, rostrum ca. 0.5x the total length of head. *Thorax* stout, as long as wide; transverse suture distinct; praescutal longitudinal stripes clearly delimited. *Wing* transparent except for dark pterostigma. Sc reaching wing margin at the level of first bifurcation of Rs and beyond level of the tip of Cu; sc-r present, positioned near the tip of Sc; Rs subequal to R_{2+3} stem; R_1 reaching wing margin distal to the level of R_{2+3} bifurcation; r-r oblique, linking R_1 to R_2, R_2 oblique; medial vein four-branched; discal cell wide; distal sections of veins M_3 and M_4 subparallel, subequal; long m-cu linking Cu to the base of M_4. *Abdomen* stout, ca. 1.5x longer than thorax; gonocoxite probably conical, as long as wide.

Measurements. Antenna length, 19.4. Body length, 7.8. Wing length/width, 6.9–7.9/2.1–2.5.

FIGURES 19–21. *Leptotarsus buscalioniae* **sp. nov.**, from Las Hoyas, Early Cretaceous, Spain, holotype LH 35088. 19—Total view (part). 20—Forebody (counterpart). 21—Distal portion of wing (part).



FIGURES 22–25. *Leptotarsus ibericus* **sp. nov.**, from Las Hoyas, Early Cretaceous, Spain: 22—Holotype LH 28206, total view (antenna truncated). 23—Holotype LH 28206, detail of head. 24—Holotype LH 28206, head with antennae. 25—Paratype LH 29995. Abbreviations: comp eye: compound eye; na: nasus; plp: palpus; scp: scape.

***Leptotarsus contractus* sp. nov.**
(Figs 9, 26)

Type material. *Holotype:* LH 15419± (part and counterpart of male without head). East-central Spain, Las Hoyas; La Huérguina Limestone Formation, Late Barremian, Early Cretaceous. Housed in Museo de Ciencias de Castillia—La Mancha.

Etymology. From the Latin *contractus* (tightened) in reference to unusually narrow shape of wing.

Diagnosis. This species differ from all Cretaceous species by longer Rs (Rs origin proximal to connection of *m-cu* and Cu) and narrower wing.

Description. *Thorax* stout, as long as wide, transverse suture distinct, praescutal longitudinal stripes clearly delimited. *Wing* transparent except for dark pterostigma. Sc reaching wing margin at the level of first bifurcation of Rs and beyond level of the tip of Cu; sc-r present, positioned near the tip of Sc; Rs 1.8 times longer than R_{2+3}; R_1 reaching wing margin distal to level of R_{2+3} bifurcation; r-r oblique, linking R_1 to R_2, R_2 oblique; medial vein four-branched; discal cell narrowed; distal sections of veins M_3 and M_4 subparallel, subequal; long m-cu linking Cu to the base of M_4. *Abdomen* stout, ca. 1.5x longer than thorax; gonocoxite conical, probably as long as wide.

Measurements. Body length, 7.1. Wing length/width, 7.1–7.4/1.6.

Note. One of the wings is probably distorted judging by the shape of second wing with unclear venation. The virtually straight vein m-cu (Fig. 9) is also suggestive of such distortion. In Tipulidae in general, m-cu is not straight but curved.

FIGURE 26. *Leptotarsus contractus* **sp. nov.**, from Las Hoyas, Early Cretaceous, Spain, holotype LH 15419, total view.

Discussion

The genus *Leptotarsus*, including over 300 species in 20 subgenera, is a morphologically diverse group. Alexander (1969) considered the presence of spine-like setae in the clasper of gonostylus the main defining character of the genus, but noted that this feature is not exclusive of the group. Such morphological details are impossible to see in the Mesozoic fossils described here. Nevertheless, considering other anatomical aspects, they fit well within the morphological variation found in extant representatives of the genus. For instance, two of the Mesozoic species described here, *L. grimaldii* **sp. nov.** and *L. ibericus* **sp. nov.**, have head capsule morphologies identical with what is found in some Neotropical living species, such as *L.* (*Longurio*) *goyazanus* (Alexander) and *L.* (*Longurio*) *brasiliae* (Alexander) (personal observation of the first author, based on the primary types of both species housed in MZUSP). In all these taxa, the male antenna is very long (a condition found in several Neotropical species in the

subgenus *Longurio,* and also present in some species of *Araucomyia* Alexander, *Macromastix* Osten Sacken and *Habromastix* Skuse, as discussed below), with long and narrow individual flagellomeres. The scape is stout, long, and much developed compared with the pedicel. An anterodorsal protuberance of the head is present, and the rostrum is well developed (about half the length of the entire head) and bears a distinct, well visible nasus. These features also occur in *Leptotarsus* species from other regions, such as in the Australian species *Leptotarsus* (*Macromastix*) *costalis* (Sweredus) (see Dobrotworsky 1968).

The wing morphology of the new Mesozoic fossils described here are also typical of *Leptotarsus* species. The darker costal field as found in the Santana fossil specimens is typical of several Neotropical and Australian living species. The dark pterostigma is a fairly common feature of the genus. As in *Leptotarsus* species in general, the vein Sc is long and reach the wing margin beyond the midlength of wing, distal to or near the level of the first bifurcation of Rs. Vein Rs is typically short in the genus, and is similar in length with R_{2+3}. Vein R_2 is typically inclined upwards and shorter than R_3.

Other similarities of the new fossils with extant *Leptotarsus* species lie in the morphology of the male genitalia. The cone-shaped gonocoxite, clearly visible in some of the fossils described here, is a typical feature (although not exclusive) of *Leptotarsus*.

Many of the *Leptotarsus* characters mentioned above are clearly plesiomorphic in comparison with the conditions found in most other Tipulidae genera. For instance, the long veins Sc and R_1 are similar with the condition found in the Limoniidae. The same holds for the morphology of the male genitalia. In most Tipulidae, the gonocoxite is a semi-globular structure, whereas in *Leptotarsus*, the gonocoxite is a cone-shaped structure (Oosterbroek 1980). This is clearly a plesiomorphic condition for crane flies in general, and *Leptotarsus* appear as a basal branch in the Tipulidae clade in the study of Ribeiro (2008). In this regard, the occurrence of the genus as the oldest known Tipulidae is consistent with its suggested phylogenetic position near the base of the Tipulidae tree.

The monophyly of the genus *Leptotarsus* has been questioned by several authors (e.g., Young & Gelhaus 1992; Gelhaus & Young 1995; De Jong 1989). Also, the interrelationships among the various subgenera are unknown. The status of most subgenera as monophyletic units is also very doubtful.

As noted by Alexander (1969), in most subgenera of *Leptotarsus* the antennae in both sexes are very short, but some species occur where the males have this organ excessively elongated, such as *Araucomyia*, *Macromastix*, *Habromastix* and *Longurio*. The long male antenna is clearly an apomorphic condition. It is unclear if this derived character state has appeared independently in different subgenera, as suggested by current taxonomy. Alternatively, this character could be evidence of a single clade within the genus. Only a comprehensive revision of the group could throw some light into the evolutionary significance of this derived feature, which nevertheless has evolved in the genus at least since the Early Cretaceous. There seems to be certain plasticity in this character, and the antennae are occasionally extremely long in males of some extant species of Limoniidae (*Hexatoma* Latreille, *Rhabdomastix* Skuse, *Tasiocera* Skuse). In Tipulidae, long antennae in males are recorded only within three tipulid genera, namely subgenus *Megistomastix* Alexander of *Dolichopeza* Curtis, *Megistocera* Wiedemann, and *Leptotarsus* (Savchenko 1983, 1986).

Given the problems exposed above, no subgeneric rank is attributed to any of the new *Leptotarsus* species described here. For the time being, is seems preferable to let this refinement as an open question for future studies.

On the enigmatic genus *Tipunia*, and the age of the family Tipulidae

Krzemiński and Ansorge (1995) described the genus *Tipunia*, from the Lower Tithonian (Hybonotum zone) of Solnhofen lithographic limestone (Late Jurassic). Already in the original description of the first discovered species, *Tipunia intermedia* Krzemiński et Ansorge, 1995, the authors mentioned that some of its wing characters, such as r-r almost parallel to costal wing margin and very broad cu cell, were typical features of the Tipulidae. On the other hand, vein Sc terminating on the wing margin and relatively long R_2 (R_3 in their paper) are typical features of the Limoniidae. Although the genus was tentatively positioned in the Limoniidae, due to lack of information on the morphology of rostrum, palpi and antennae in the Solnhofen specimen, the authors raised questions about the family-level affinities of the new genus, so "transitional" name was chosen for it. Despite of the discovery of additional species of *Tipunia*, described later by Lukashevich (2009), all these characters as well as the male genitalia remain unknown till now.

Some of the characters of *Tipunia*, mentioned in the original diagnosis (Sc terminating in C; distal part of d cell

widened, m-cu long and almost parallel to the wing margin) are known in Early Cretaceous and extant members of *Leptotarsus.* The long Sc vein typical of most Limoniidae, but also found in basal Tipulidae lineages such as *Leptotarsus* and *Brachypremna* Osten-Sacken, is clearly a plesiomorphic feature (see ground-plan reconstruction of Tipulomorpha in Ribeiro 2008: 661), and therefore should not be used for the establishing of family-level relationships. However, the "tipulid-like" shape of the medial veins of *Tipunia*, which includes a long vein m-cu, may well be a synapomorphy of the Tipulidae, and this genus may represent, in fact, the earliest lineage of the family. Nevertheless, until further morphological evidence is discovered, we prefer to maintain *Tipunia* within the Limoniidae.

Although the wing venation of the new *Leptotarsus* species described here resemble that of *Tipunia*, there are important differences. In *Tipunia*, the stem of vein Rs is longer than (and plesiomorphic relative to) the condition found in *Leptotarsus*, in which the stem of Rs is subequal in length with R_{2+3}. Also, in *Tipunia* species (e.g., *Tipunia undata* Lukashevich and *Tipunia jorgi* Lukashevich), the vein R_2 is not so much inclined as in *Leptotarsus* species. The veins R_2 and R_3 in *Tipunia* run more or less parallel to each other, and are only slightly divergent towards the wing margin. This is a plesiomorphic feature for Tipulomorpha, and the very inclined vein R_2, typical of most *Leptotarsus* and present in the Cretaceous species of the genus is more apomorphic (Ribeiro 2008).

In conclusion, until additional light is shed on the family-level relationships of *Tipunia*, the Early Cretaceous *Leptotarsus* species described here are not only the oldest representatives of the genus, but also the oldest undisputed members of the family Tipulidae.

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