Cretaceous Research 142 (2023) 105372

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

A cranefly rendezvous: The highest known Mesozoic diversity of Tipulidae (Insecta: Diptera) in the Lower Cretaceous Crato Formation of NE Brazil

Daubian Santos [a, *], Ismar de Souza Carvalho [b, c], Guilherme Cunha Ribeiro [a]

[a] Universidade Federal Do ABC (UFABC), Centro de Ciências Naturais e Humanas, Santo André, São Paulo, Brazil
[b] Universidade Federal Do Rio de Janeiro, Departamento de Geologia, CCMN/IGEO, 21.949-900, Cidade Universitária – Ilha Do Fundão, Rio de Janeiro, Brazil
[c] Universidade de Coimbra, Centro de Geociências, Rua Sílvio Lima, 3030-790, Coimbra, Portugal

ARTICLE INFO

Article history:
Received 24 June 2022
Received in revised form
22 September 2022
Accepted in revised form 22 September 2022
Available online 28 September 2022

Keywords:
Fossil insects
Gondwana
Leptotarsus
New species

ABSTRACT

The genus *Leptotarsus* (Tipulomorpha: Tipulidae) is one of the oldest lineages of the family Tipulidae known from the Early Crataceous to the present. Most *Leptotarsus* fossils are from the Cretaceous period, and the Crato Formation of the Lower Cretaceous of NE Brazil is notable for bearing the greatest known Mesozoic diversity of the genus. This study describes twelve new species of the genus: *Leptotarsus acciolii* sp. nov., *L. alemaoi* sp. nov., *L. bonifacioi* sp. nov., *L. capanemai* sp. nov., *L. coutoi* sp. nov., *L. feijoi* sp. nov., *L. ferreirai* sp. nov., *L. lagosi* sp. nov., *L. lemesi* sp. nov., *L. pereirai* sp. nov., *L. petrii* sp. nov. and *L. velosoi* sp. nov. With the new taxa described herein, a total of 21 *Leptotarsus* species are now recorded from the Crato Formation. An updated identification key for all Cretaceous *Leptotarsus* species of the world is provided.

1. Introduction

The fossil record of the megadiverse insect order Diptera is extensive (Kovalev, 1990; Krzeminski and Ansorge, 1995; Krzeminski, 1992a,b; Krzeminski et al., 2000; Krzeminski and Krzeminska, 2003; Rasnitsyn and Quicke, 2002; Grimaldi and Engel, 2005; Blagoderov et al., 2007; Lukashevich, 2009; Ponomarenko et al., 2014; Ribeiro and Lukashevich, 2014; Kopeć, 2017; Kopeć et al., 2018; Lukashevich and Ribeiro, 2019; Kopeć et al., 2021; Krzemiński et al., 2021). The oldest known representatives of the Diptera come from the Middle Triassic in northeastern France (242–247 Ma) (Krzeminski et al., 1994; Lukashevich and Ribeiro, 2019). Among these early lineages, there are extinct genera of the superfamily Tipuloidea (a clade formed by the families Pediciidae, Limoniidae, Cylindrotomidae and Tipulidae) (Ribeiro 2008; Petersen et al., 2010; Zhang et al., 2016; Kang et al., 2017; Lukashevich and Ribeiro, 2019). The systematic position of the Triassic members of the clade implies a minimum age of the Tipulomorpha (Trichoceridae + Tipuloidea) also in the Triassic period, although members of the families Trichoceridae, Pediciidae, and Tipulidae do not appear in the fossil record until the Early, Middle, and Late Jurassic, respectively. The oldest described representatives of Cylindrotominae are only known from the Paleogene (Kania-Kłosok et al., 2021). However, the presence of its sister group, the Tipulidae, in the Late Jurassic (the Jurassic genus *Tipunia* Krzeminski & Ansorge, 1995 appears well nested within the Tipulidae in the phylogenetic study of Lukashevich & Ribeiro, 2019) implies the same minimum age for the Cylindrotomidae as well.

With over 4000 recent species, the Tipulidae is known in the fossil record mostly from Cenozoic deposits, with only two Mesozoic genera of Tipulidae being recorded so far (Table 1).

Knowledge of the diversity of Mesozoic tipulids has increased significantly in recent years with the description of many new taxa from the Early, middle, and Late Cretaceous. In this context, the Crato Formation of northeastern Brazil (Araripe Basin) is notable for bearing most of the world's Mesozoic tipulid diversity. In addition to the 9 species already described, an even greater diversity of tipulids from the Crato Formation is revealed herein with the description of twelve new species of the genus *Leptotarsus*.

The extant fauna of *Leptotarsus* includes over 300 species in 20 subgenera. Dobrotworsky (1968) revised the characteristics of the genus *Leptotarsus*. Most characters refer to features that usually are

* Corresponding author.
E-mail address: daubians@gmail.com (D. Santos).

https://doi.org/10.1016/j.cretres.2022.105372
0195-6671/

not preserved in compression fossils. Nevertheless, there are features typical of the genus which can be seen in Crato fossils, such as a rostrum as long as the remainder of the head; front usually with distinct tubercle or gibbosity above antennae (as seen, for instance, in *L. grimaldii* Ribeiro & Lukashevich, 2014); wings with Sc1 present (as in Crato fossils) (some extant members of the genus may have it atrophied); abdomen usually shorter than wing, robust, (as in Crato specimens) (some extant species have the abdomen slender and about as long as wing); and conical gonocoxites (as in L. grimaldii Ribeiro & Lukashevich, 2014). The very long and filiform antenna, seen in many Crato specimens, is also typical of the genus. In addition, some wing features typical of *Leptotarsus* species include the short and normally acuated Rs, originating at the level of the base of m-cu or posterior to this point, and vein Sc complete and long, reaching C at the level of the mid-length of the discal cell.

Ribeiro et al. (2015) and Ribeiro et al. (2021a) have detailed why the assignment of the Mesozoic fossil *Leptotarsus* to any of the extant subgenera cannot be satisfactorily made, given that various combinations of wing traits (the primary source of information for the diagnosis of compression-fossil taxa) can occur among members of the same subgenus, and there are no apparent differences between the wings of some subgenera. Much probably, many of the subgenera may not constitute monophyletic units (Young and Geuhaus, 1992; Gelhaus and Young, 1995; Gelhaus, 2009).

The extant diversity of the genus is concentrated in the Southern Hemisphere, with only 9 *Leptotarsus* species present in the entire Holarctic region. It is in the Australasian (with 162 species), Neotropical (with over 90 species), Afrotropical (47 species), and Oriental (11 species) regions that the bulk of the diversity of the group is found (Oosterbroek, 2022). Besides the Mesozoic occurrences, fossils of *Leptotarsus* are known from the Oligocene of France and the late Eocene Isle of Wight, England (Krzemiński et al., 2019).

To commemorate the 200th anniversary of Brazil's independence (1822−2022), eleven of the twelve new specific names pay homage to the pioneers of the exact sciences and of nature in Brazil. The addition of scientific knowledge of these researchers made possible new political and economic strategies that contributed to the identity of the territory and Brazilian nationality. Through the pioneering work of these scientists, it was possible to identify new animal and plant species, alongside the detection of new minerals and anthropological aspects of the indigenous populations. Also, we name one species after Professor Setembrino Petri (1922 -) in honor of the 100th anniversary of the life of the most important geoscientist dedicated to the geological history of the Brazilian Cretaceous.

2. Geological setting

The geology and paleontology of the Crato Formation were revised in detail by Martill (2007) and Ribeiro et al. (2021b). The Crato Formation is one of the stratigraphic units that constitute the Santana Group of the Araripe Basin (Fig. 1). The Santana Group consists of the Barbalha, Crato, Ipubi, and Romualdo formations. The age of the Crato Formation is considered to be upper Aptian (Lower Cretaceous) (Heimhofer and Hochuli, 2010).

The specimens analyzed in this study occur in the lower carbonate succession of the upper Aptian age (Crato Formation), which comprises one of the most important Cretaceous Lagerstätten. Large numbers of invertebrate, vertebrate, and plant fossils from the Crato Lagerstätte show exquisite soft tissue preservation and it is the best-known Mesozoic Lagerstätte of Gondwana (Agnolin

Table 1
Mesozoic fossil species of Tipulidae.

Mesozoic fossil species of Tipulidae		
Species	Horizon	Locality
Genus *Tipunia* Krzemiński and Ansorge 1995		
T. austeni Jarzembowski, 1991	Lower Cretaceous (Valanginian)	Weald Clay Formation, UK
T. intermedia Krzemiński and Ansorge 1995	Upper Jurassic (Tithonian)	Altmühltal Formation, Germany
T. jorgi Lukashevich 2009	Upper Jurassic (Tithonian)	Ulan Malgait Formation, Mongolia
T. undata Lukashevich 2009	Upper Jurassic (Tithonian)	Ulan Malgait Formation, Mongolia
Genus *Leptotarsus* Guerin-Meneville, 1831		
L. andradei Ribeiro, Santos and Santos, 2021	Lower Cretaceous (Aptian)	Crato Formation, Brazil
L. burmica Men & Hu, 2021	Mid-Cretaceous (Cenomanian)	Hukawng Valley, Myanmar
L. buscalioniae Ribeiro & Lukashevich, 2014	Lower Cretaceous (Barremian)	La Huérguina Formation, Spain
L. contractus Ribeiro & Lukashevich, 2014	Lower Cretaceous (Barremian)	La Huérguina Formation, Spain
L. cretaceus Ribeiro & Lukashevich, 2014	Lower Cretaceous (Aptian)	Crato Formation, Brazil
L. eva (Krzeminski, 1992a)	Upper Cretaceous (Cenomanian)	Upper Burneya, Khabarovsky Kray, Russia
L. gelhausi Ribeiro, Santos and Santos, 2021	Lower Cretaceous (Aptian)	Crato Formation, Brazil
L. grimaldii Ribeiro & Lukashevich, 2014	Lower Cretaceous (Aptian)	Crato Formation, Brazil
L. ibericus Ribeiro & Lukashevich, 2014	Lower Cretaceous (Barremian)	La Huérguina Formation, Spain
L. ivoneae Ribeiro, Santos and Santos, 2021	Lower Cretaceous (Aptian)	Crato Formation, Brazil
L. lemeae Ribeiro, Santos and Santos, 2021	Lower Cretaceous (Aptian)	Crato Formation, Brazil
L. lukashevishae Ribeiro, Santos & Nicolau, 2015	Lower Cretaceous (Aptian)	Crato Formation, Brazil
L. martinsnetoi Ribeiro & Lukashevich, 2014	Lower Cretaceous (Aptian)	Crato Formation, Brazil
L. primitivus Shih, Dong, Kania, Liu, Krzeminski & Ren, 2015	Lower Cretaceous (Aptian)	Yixian Formation, China
L. riberoi Krzeminski, Kopec and Kania, 2017	Lower Cretaceous (Aptian)	Crato Formation, Brazil
L. acciolii sp. nov.	Lower Cretaceous (Aptian)	Crato Formation, Brazil
L. alemaoi sp. nov.	Lower Cretaceous (Aptian)	Crato Formation, Brazil
L. bonifacioi sp. nov.	Lower Cretaceous (Aptian)	Crato Formation, Brazil
L. capanemai sp. nov.	Lower Cretaceous (Aptian)	Crato Formation, Brazil
L. coutoi sp. nov.	Lower Cretaceous (Aptian)	Crato Formation, Brazil
L. feijoi sp. nov.	Lower Cretaceous (Aptian)	Crato Formation, Brazil
L. ferreirai sp. nov.	Lower Cretaceous (Aptian)	Crato Formation, Brazil
L. lagosi sp. nov.	Lower Cretaceous (Aptian)	Crato Formation, Brazil
L. lemesi sp. nov.	Lower Cretaceous (Aptian)	Crato Formation, Brazil
L. pereirai sp. nov.	Lower Cretaceous (Aptian)	Crato Formation, Brazil
L. petrii sp. nov.	Lower Cretaceous (Aptian)	Crato Formation, Brazil
L. velosoi sp. nov.	Lower Cretaceous (Aptian)	Crato Formation, Brazil

et al., 2020; Barling et al., 2015; Carvalho et al., 2015a,b, 2019, 2021; Dias and Carvalho, 2020, 2022; Catto et al., 2016; Maldanis et al., 2016; Martill, 2007; Warren et al., 2017; Varejão et al., 2019; Iniesto et al., 2021; Ribeiro et al., 2021a,b; Santos et al., 2020, 2021; Cincotta et al., 2022).

According to Ribeiro et al. (2021b), the fossil-rich interval of the formation — the "Crato Konservat-Lagerstätte" or CKL —, consisted of a semi-arid seasonal lacustrine wetland, in which a shallow water body was succeeded up-landward by neighboring mesophytic ecotones, periodically flooded, besides outer xeric habitats. Trophic structure analysis and details of the putative food web that took place within the Crato Ecosystem are provided by Mendes et al. (2020).

3. Material and methods

The studied specimens belong to the following collections:

1. Centro de Ciências Naturais e Humanas, Universidade Federal do ABC, Santo André, São Paulo, Brazil: CCNH 83; CCNH 374; CCNH 417.
2. Laboratório de Paleontologia, Departamento de Geologia, Universidade Federal do Ceará, Fortaleza, Ceará, Brazil: LP/UFC CRT 2707; LP/UFC CRT 1229; LP/UFC CRT 1365b; LP/UFC CRT 2420.
3. Coleção de Macrofósseis da Universidade Federal do Rio de Janeiro (UFRJ), Rio de Janeiro, Brazil: UFRJ-DG 75Ins; UFRJ-DG 865Ins; UFRJ-DG1100Ins; UFRJ-DG1107Ins; UFRJ-DG1552Ins.

Photographs were obtained with digital cameras attached to stereomicroscopes. Illustrations of wing venation were made using photographs as templates. Measurements were taken with Carl Zeiss AxioVision software. Descriptive terminology follows, with minor changes, the terminology adopted in the Manual of Afrotropical Diptera (Cumming and Wood, 2017; Jong, 2017). The final artwork of the illustrations was made using Adobe Photoshop software. The illustrations of the wings were based on information from both wings (when preserved), always from the holotype specimen. Measures of the specimens were made with the software Carl Zeiss AxioVision. Wing length, width, and proportions for all Cretaceous *Leptotarsus* species are provided in Table 2.

4. Results

4.1. Taxonomy

Family Tipulidae

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

Leptotarsus acciolii sp. nov (Fig. 2)
urn:lsid:zoobank.org:act:FD3A37FF-E877-4927-B515-A88F51068962

Type material. Holotype: Male. CCNH 417. NE Brazil, Crato Formation, Aptian, Lower Cretaceous. Housed at collection of the Centro de Ciências Naturais e Humanas, Universidade Federal do ABC, CCNH — UFABC), Brazil.
Etymology. This species is named after José de Sá Bittencourt e Accioli (1755—1828). Accioli was a mineralogist who was engaged in prospecting minerals such as saltpeter, an important ore in 19th century Brazil, and in studies of climatology. He was associated with the Royal Academy of Sciences of Lisbon. Later accused of trying to make gunpowder for independence movements, was exiled to Angola.
Diagnosis. The species is defined by the combination of m-cu attached at the fork of M_{3+4} and Rs as long as R_{2+3+4}.
Description. Wing length 1.3× the length of thorax and abdomen combined. Antenna long, ca. 2× the body length. Scape 3× longer than wide. Head without rostrum ca. 2× longer than rostrum. There is a nasus in the rostrum, 1.5× times shorter than rostrum. Abdomen ca. 2.5× longer than thorax. Thorax 1.3× longer than head. Wing transparent, but with an evident pterostigma. Vein Sc reaching the wing margin distal to the fork of Rs. Cross-vein sc-r branching distal to the level of the fork of Rs. Rs as long as R_{2+3+4}. R_1 reaching the wing margin distal to the level of the fork of R_{2+3+4}. R_{2+3+4} slightly arched, R_3 shorter than R_{2+3+4}. R_{2+3} 4× shorter than R_2 and 5× shorter than R_3. R_4 straight. Basal deflection of R_5 ca. 1.6× the length of r-m, R_5 slightly curved downwards on the distal third of its length, basal deflection of M_{1+2} ca. 2.5× longer than r-m. Medial M_{1+2} (the segment between the insertion of cross-veins r-m and m-m) ca. 1.9× longer than distal M_{1+2} (the segment between the insertion of m-m and the fork of M_{1+2}). M_4 reaching the wing margin more proximal than the insertion of m-m on M_3, m-cu attached at the fork of M_{3+4}.
Measurements. Wing length/width: 12.2 mm/3.3 mm.
Remarks. The holotype is the only known specimen. This species has wing proportions equal to *L. pereirai* sp. nov. (described below in this paper). It differs from *L. pereirai* sp. nov. mainly in the attachment of m-cu, shape of the discal cell, shape of M_4, and R_2.

Leptotarsus alemaoi sp. nov (Fig. 3)
urn:lsid:zoobank.org:act:03B7FE7E-9A0F-4256-8EA2-07C077F00071

Type material. Holotype: Female. LP/UFC CRT 2707. NE Brazil, Crato Formation, Aptian, Lower Cretaceous. Housed at collection of Universidade Federal do Ceará (UFC), Brazil.
Etymology. This species is named after Francisco Freire Alemão (1797—1874). Alemão was a botanist, member of the Brazilian Historic and Geographic Institute and founder and president of the Velosian Natural Science Society of Rio de Janeiro. He was Head of the Department of Botany of the Scientific Commission of Exploration of the Northern Provinces, the first scientific expedition formed by Brazilians in the 19th century.
Diagnosis. The species is defined by the combination of r-m aligned with the basal defection of R_5 and a straight M_4.
Description. Wing length 1.2× longer than the length of thorax and abdomen combined. Cervix as long as head without rostrum. Rostrum half the length of the remainder of the head. There is a small nasus in the rostrum. Palpi ca. 2× the length of the head, length of the first palpomere twice than the second one. Antenna short, flagellomeres ovoid. Abdomen ca. 3× longer than thorax. Thorax ca. 1.5× longer than head. Wing transparent, but with an evident pterostigma. Vein Sc reaching the wing margin distal to the fork of Rs. Rs longer than R_{2+3+4}. R_1 reaching the wing margin at the level of the fork of R_{2+3+4}. R_3 shorter than R_{2+3+4}. R_{2+3} 3.5× shorter than R_2 and 5.5× shorter than R_3. R_4 straight. Basal deflection of R_5 ca. 1.5× longer than the length of r-m, r-m aligned with the basal defection of R_5. R_5 slightly curved downwards on the distal third of its length. Basal deflection of M_{1+2} ca. 2.5× longer than r-m. Medial M_{1+2} ca. 2× longer than distal M_{1+2}. Basal deflection of M_3 as long as M_{3+4}. M_4 reaching the wing margin more proximal than the insertion of r-m. Cross-vein m-cu less inclined, m-cu attached on M_4.
Measurements. Wing length/width: 11 mm/2.7 mm.
Remarks. The holotype is the only known specimen. This species has wing length similar to *L. andradei* Ribeiro, Santos and Santos,

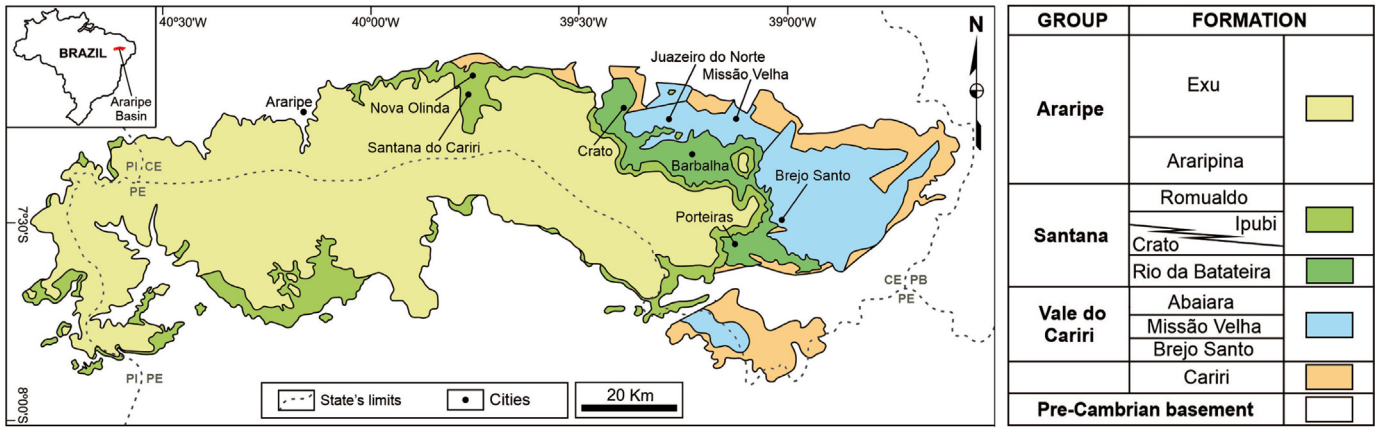

Fig. 1. Map of the Araripe Basin in northeastern Brazil, showing outcrops of Crato and Romualdo formations and a simplified stratigraphic section of the Araripe Basin (modified from Dias and Carvalho 2020, 2022).

2021. It differs from *L. andradei* mainly by the inclination of R_{2+3}, shape of m-cu, and by the distance between M_3 and M_4.

Leptotarsus bonifacioi sp. nov (Fig. 4)
urn:lsid:zoobank.org:act:215D292A-3390-440C-B4C1-3772D1F8915A

Type material. Holotype: Sex unknown. LP/UFC CRT 1229. NE Brazil, Crato Formation, Aptian, Lower Cretaceous. Housed at Universidade Federal do Ceará (UFC), Brazil.
Etymology. This species is named after José Bonifácio de Andrada e Silva (1763–1838). Known as José Bonifácio, he was one of the most important mineralogists of the 19th century. He played an important role as statesman, minister and adviser to the prince Regent and future Emperor D. Pedro I. He encouraged the monarch to proclaim the Independence of Brazil in 1822 and incorporated the first squadron of leaders of the new Nation.
Diagnosis. The species is defined by a strongly curved R_2. Also, this species is defined by the combination of r-m half than the basal deflection of R_5 and a tiny R_{2+3+4}.
Description. Wing length 1.1× the length of thorax and abdomen combined. Cervix very short. Antenna long, not entirely preserved. Abdomen ca. 2× longer than thorax. Thorax 2× longer than head without rostrum. The dorsolateral preservation preserves the curvature of scutum. Wing transparent, but with an evident pterostigma. Vein Sc reaching the wing margin distal to the fork of Rs. Rs longer than R_{2+3+4}. R_1 reaching the wing margin more distal than the level of the fork of R_{2+3+4}. R_3 shorter than R_{2+3+4}. R_{2+3} 8× shorter than R_2 and 10.5× shorter than R_3. R_4 straight. Basal deflection of R_5 2× the length of r-m, R_5 slightly curved downwards on the distal third of its length. Basal deflection of M_{1+2} ca. 4× longer than r-m. Medial M_{1+2} ca.1.5× longer than distal M_{1+2}. Basal deflection of M_3 as long as M_{3+4}. M_4 reaching the wing at the level

Table 2
Measures and proportions of the wing of cretaceous *Leptotarsus*.

Measures and proportions of the wing of cretaceous *Leptotarsus*			
Species	Length (mm)	Width (mm)	Length/width ratio (L/W)
L. burmica Men & Hu, 2021	6.1	1.5	4.08
L. grimaldii Ribeiro & Lukashevich, 2014	6.8	1.8	3.78
L. eva (Krzeminski, 1992a)	7.5	2.3	3.26
L. riberoi Krzeminski, Kopec and Kania, 2017	7.6	2.1	3.62
L. buscalioniae Ribeiro & Lukashevich, 2014	8.5	2.8	3.04
L. ivoneae Ribeiro, Santos and Santos, 2021	8.6	2.4	3.58
L. contractus Ribeiro & Lukashevich, 2014	8.9	1.8	4.94
L. feijoi sp. nov.	9	2.2	4.1
L. petrii sp. nov.	9.8	2.8	3.5
L. cretaceus Ribeiro & Lukashevich, 2014	9.9	2.5	3.96
L. gelhausi Ribeiro, Santos and Santos, 2021	10.1	2.9	3.48
L. andradei Ribeiro, Santos and Santos, 2021	11	2.8	3.93
L. alemaoi sp. nov.	11	2.7	4.07
L. lukashevishae Ribeiro, Santos & Nicolau, 2015	11.5	3.1	3.71
L. capanemai sp. nov.	11.5	2.8	4.11
L. ibericus Ribeiro & Lukashevich, 2014	11.7	2.6	4.5
L. lemeae Ribeiro, Santos and Santos, 2021	11.7	3.5	3.34
L. martinsnetoi Ribeiro & Lukashevich, 2014	11.8	2.9	4.07
L. velosoi sp. nov.	11.9	3.3	3.6
L. acciolii sp. nov.	12.2	3.3	3.7
L. pereirai sp. nov.	12.2	3.3	3.7
L. lemesi sp. nov.	12.5	3.1	4.1
L. ferreirai sp. nov.	12.7	3.4	3.8
L. bonifacioi sp. nov.	12.8	3.2	4
L. coutoi sp. nov.	12.9	3.6	3.5
L. lagosi sp. nov.	13.9	3.5	3.97
L. primitivus Shih, Dong, Kania, Liu, Krzeminski & Ren, 2015	16.8	4.5	3.73

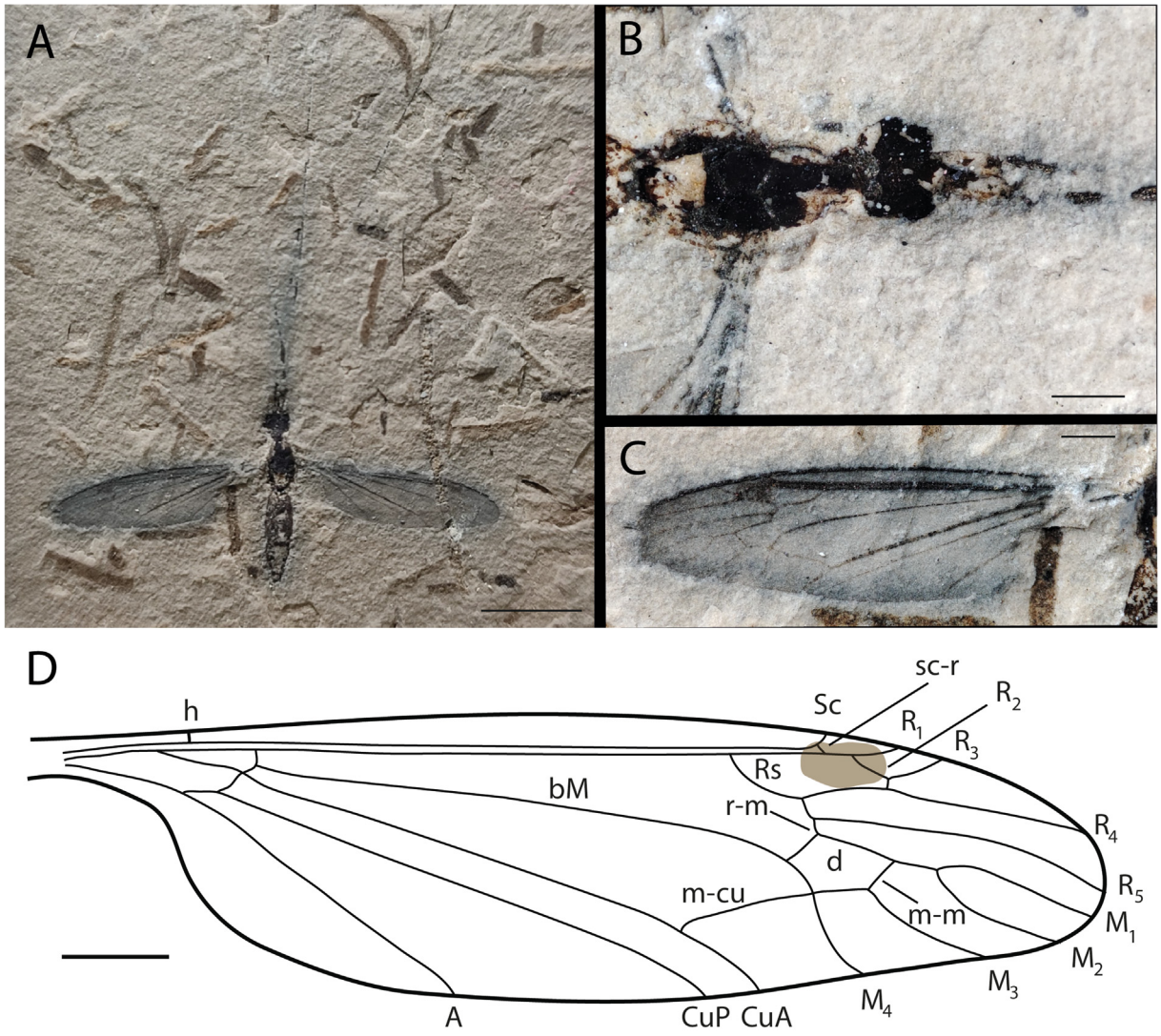

Fig. 2. *Leptotarsus acciolii* sp. nov. Holotype CCNH 417. A-habitus; B-head and thorax; C-left wing; D-illustration of wing venation (scale bar = 5 mm for A, and 1 mm for B, C and D).

of the tip of Sc. Cross-vein m-cu slightly sinuous, m-cu attached on M_4.

Measurements. Wing length/width: 12.8 mm/3.2 mm.

Remarks. The holotype is the only known specimen. This species is similar in length to *L. ferreirai* sp. nov. (described below in this paper) and to *L. coutoi* sp. nov. (described below in this paper). It differs from *L. ferreirai* sp. nov. mainly in size, shape of the discal cell, shape of M_3, and R_2. It differs from *L. coutoi* sp. nov. mainly in size, the attachment of m-cu, length of r-m, shape of Rs, and R_2.

Leptotarsus capanemai sp. nov (Fig. 5)
urn:lsid:zoobank.org:act:13BBB13F-5373-4278-A4C6-967AE17D490D

Type material. Holotype: Female. LP/UFC CRT 1365b. NE Brazil, Crato Formation, Aptian, Lower Cretaceous. Housed at Universidade Federal do Ceará (UFC), Brazil.

Etymology. This species is named after Guilherme Schüch (1824–1908). Known as Baron of Capanema, he was a naturalist and the engineer responsible for installing the first telegraph line in Brazil. As a member of the Velosian Natural Science Society of Rio de Janeiro, he was Head of the Department of Botany of the Scientific Commission of Exploration of the Northern Provinces, the first scientific expedition formed by Brazilians in the 19th century.

Diagnosis. The species is defined by the combination of basal deflection of M_{1+2} as long as M_{3+4} and m-cu attached at the fork of M_{3+4}.

Description. Wing length 1.2× longer than the length of thorax and abdomen combined. Although damaged, cervix long, ca. as long as head without rostrum. Head without rostrum c.a 1.5× longer than rostrum. Palpi as long as head, first palpomere twice in length than the second one. Abdomen ca. 2.5× longer than thorax. Thorax 1.5× longer than head. Wing transparent, but with an evident pterostigma. Vein Sc reaching the wing margin distal to the fork of Rs. Rs longer than R_{2+3+4}. R_1 reaching the wing margin at the level of the fork of R_{2+3+4}. R_3 shorter than R_{2+3+4}. R_{2+3} 3× shorter than R_2 and 7.5× shorter than R_3. R_4 straight. Basal deflection of R_5 1.5× longer than the length of r-m, R_5 curved downwards on the distal third of its length. Basal deflection of M_{1+2} ca. 2.5× longer than r-m. Medial M_{1+2} ca. 2× longer than distal M_{1+2}. Basal deflection of M_3 as long as M_{3+4}. M_4 reaching the wing at the level of the tip of Sc. Cross-vein m-cu straight, m-cu attached at the fork of M_{3+4}.

Measurements. Wing length/width: 11.5 mm/2.8 mm.

Remarks. The holotype is the only known specimen. This species has measurements similar to *L. lukashevishae* Ribeiro, Santos & Nicolau, 2015. It differs from *L. lukashevishae* mainly by the

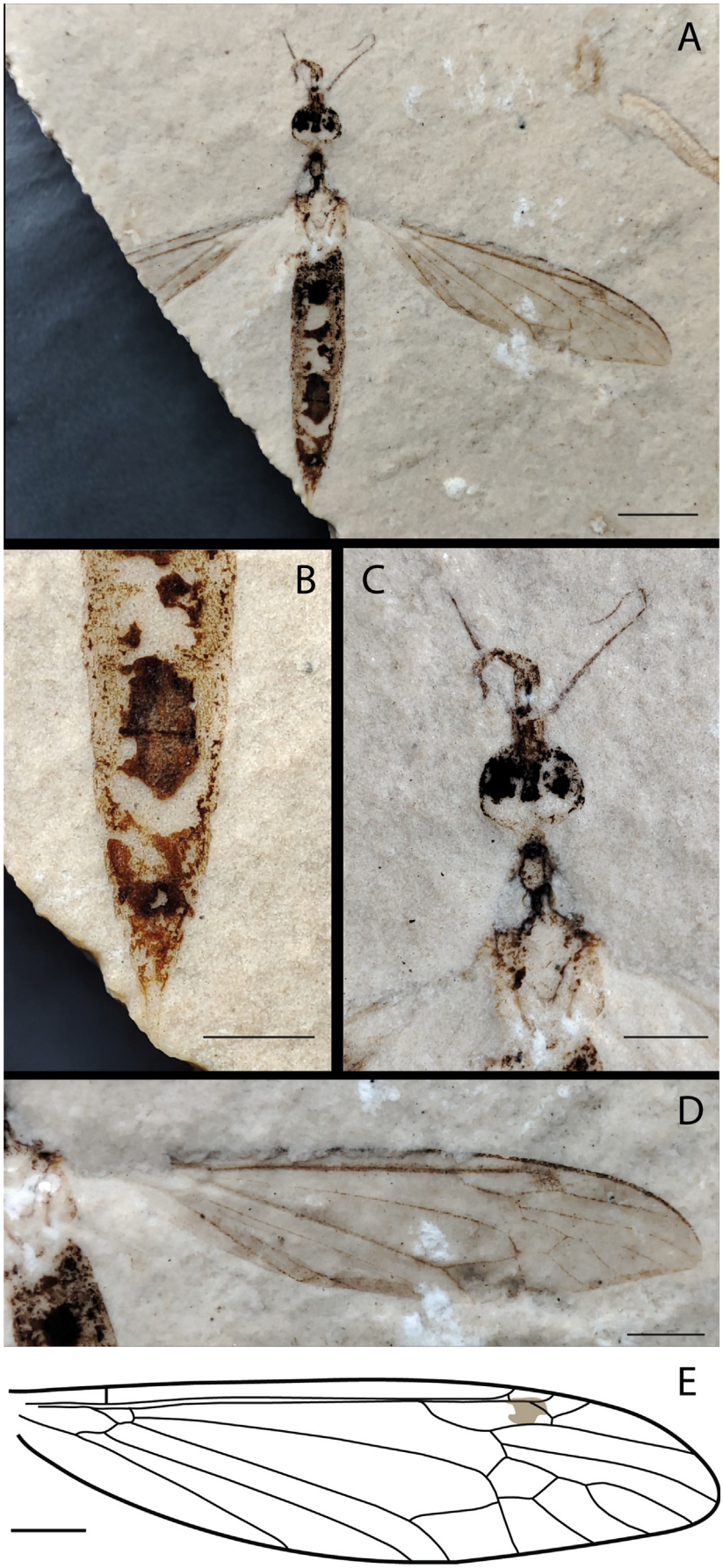

Fig. 3. *Leptotarsus alemaoi* sp. nov. Holotype LP/UFC CRT 2707. A-habitus; B-female terminalia; C-head and thorax; D-right wing; E-illustration of wing venation (scale bar = 2 mm for A, and 1 mm for B, C, D and E).

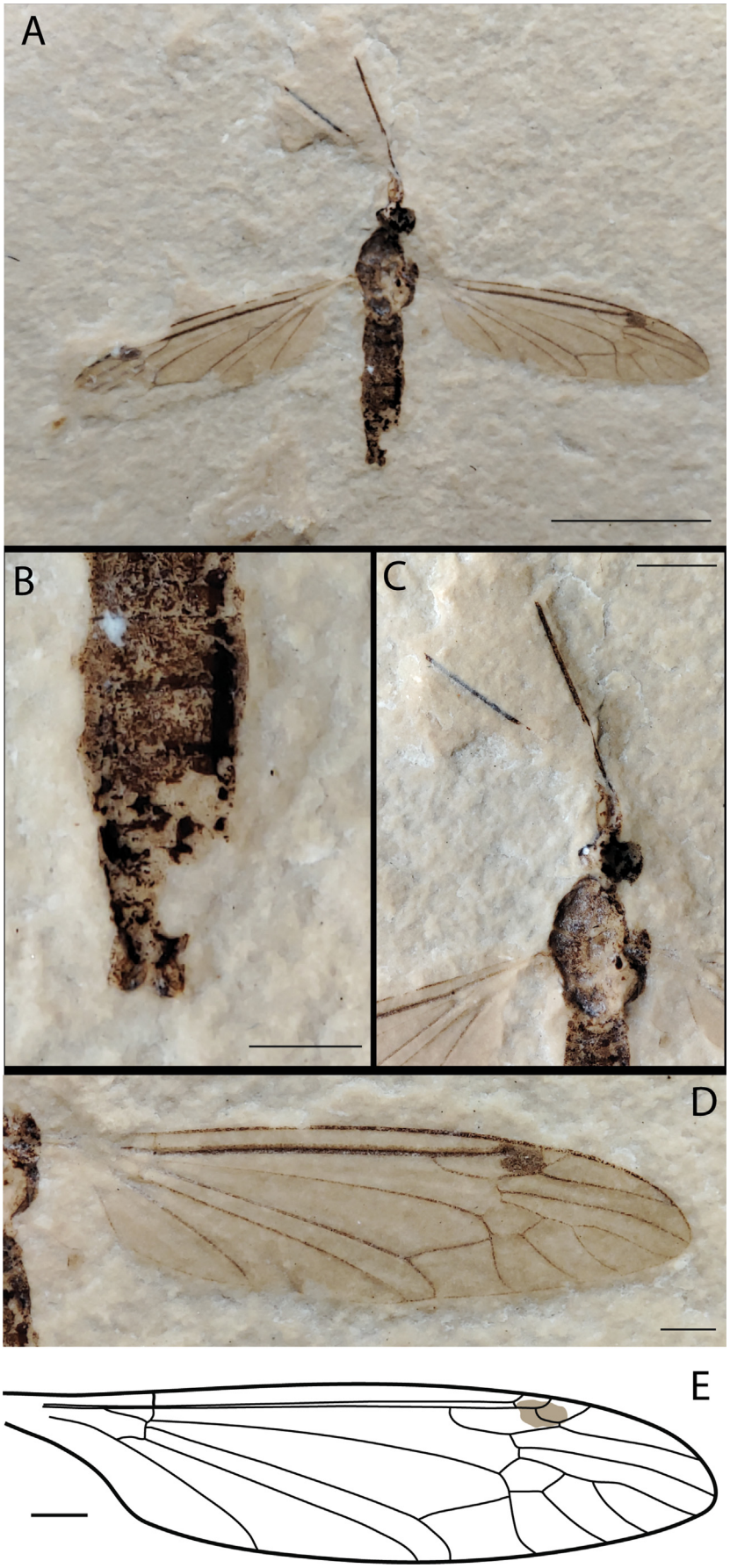

Fig. 4. *Leptotarsus bonifacioi* sp. nov. Holotype LP/UFC CRT 1229. A-habitus; B-male terminalia; C-head and thorax; D-right wing; E-illustration of wing venation (scale bar = 5 mm for A, 1 mm for B, D and E, and 0.5 for C).

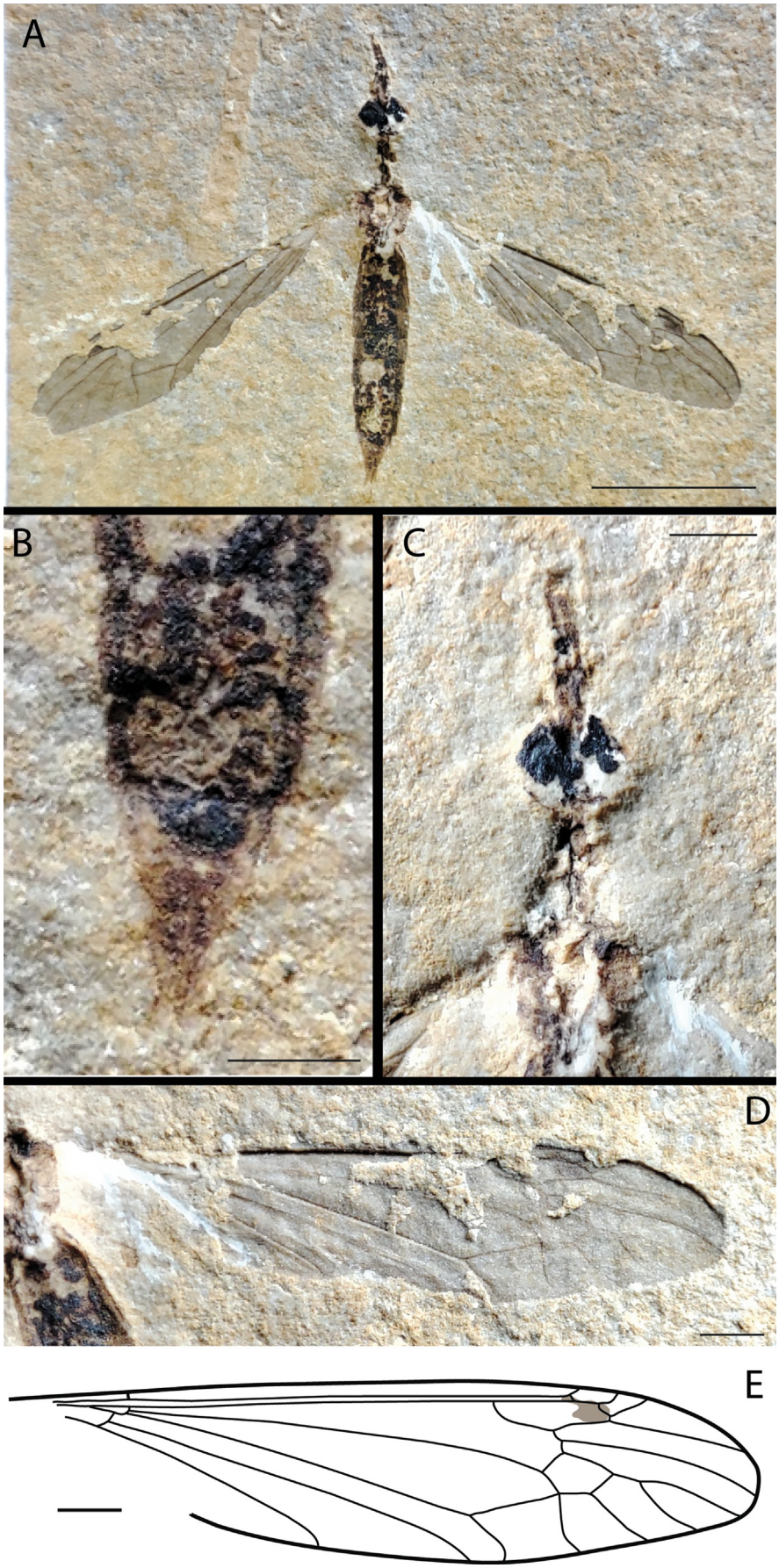

Fig. 5. *Leptotarsus capanemai* sp. nov. Holotype LP/UFC CRT 1365b. A-habitus; B-female terminalia; C-head and thorax; D-right wing; E-illustration of wing venation (scale bar = 5 mm for A, and 1 mm for B, C, D, and E).

attachment of m-cu, basal deflection of R_5, and shape of pterostigma.

Leptotarsus coputoi sp. nov (Fig. 6)
urn:lsid:zoobank.org:act:A1FE7506-8945-4D81-98D3-F7099BF5306F

Type material. Holotype: Sex unknown. UFRJ-DG 1107Ins. NE Brazil, Crato Formation, Aptian, Lower Cretaceous. Housed at the collection of Universidade Federal do Rio de Janeiro (UFRJ), Brazil.

Etymology. This species is named after José Vieira Couto (1752–1827). He was a mineralogist who contributed to social and economical development in the 18th and 19th centuries, through the reform of education in Portugal and the implementation of new mining and smelting techniques in Brazil and in Portugal to optimize the use of ores.

Diagnosis. The species is defined by the combination of r-m longer than the basal deflection of R_5 and m-cu attached at the fork of M_{3+4}.

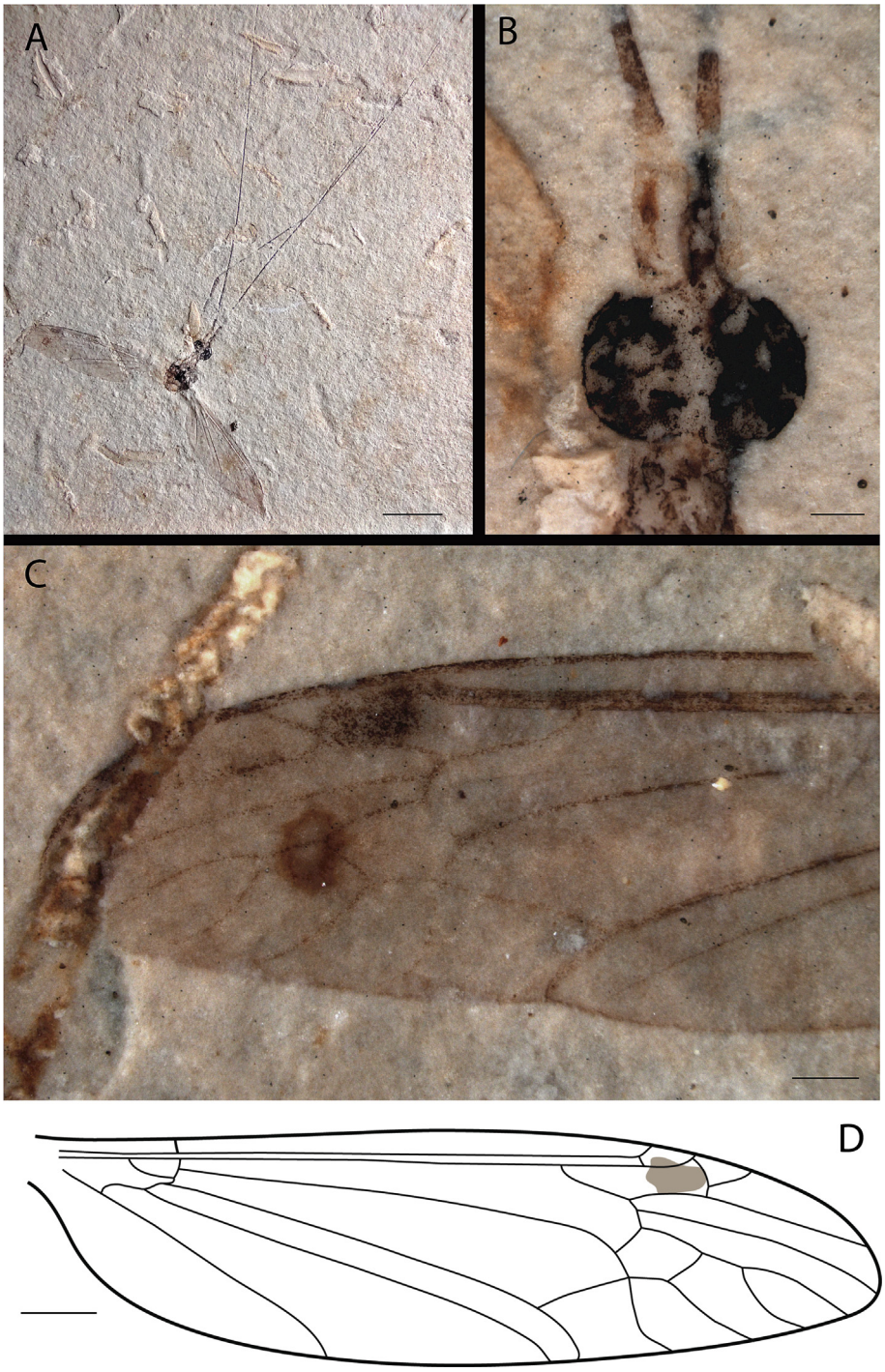

Fig. 6. *Leptotarsus coutoi* sp. nov. Holotype UFRJ-DG 1107ins. A-habitus; B-head; C-left wing; D-illustration of wing venation (scale bar = 5 mm for A, 0.5 mm for B and C, and 1 mm for D).

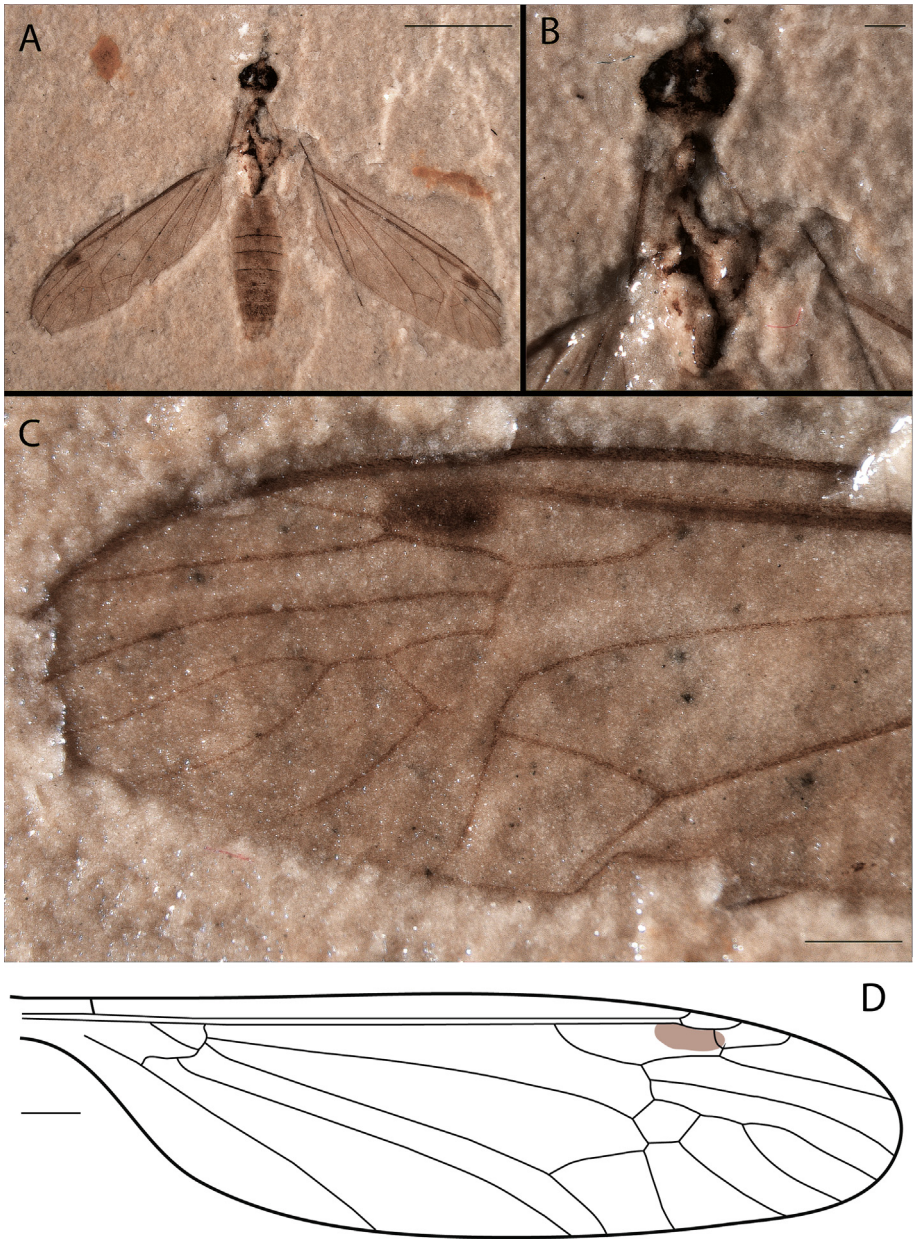

Fig. 7. *Leptotarsus feijoi* sp. nov. Holotype UFRJ-DG 1407ins. A-habitus; B-head and thorax; C-left wing; D-illustration of wing venation (scale bar = 5 mm for A, 1 mm for B and D, and 0.5 mm for C).

Description. Wing length ca. 4× the length of thorax. Cervix wide, half in wideness than head. Cervix as long as head. Antenna very long, ca. 6.5× the length of the thorax and head combined. Scape twice longer than wide, pedicel globular, flagellomeres cylindrical. Thorax 2× longer than head. Wing transparent, but with an evident pterostigma. Vein Sc reaching the wing margin distal to the fork of Rs. Rs as long as R_{2+3+4}. R_3 shorter than R_{2+3+4}. R_{2+3} 3× shorter than R_2 and 4× shorter than R_3. R_2 reaching R_1 almost at its end. Basal deflection of R_5 ca. 2× shorter than the length of r-m. Basal deflection of M_{1+2} ca. 2× longer than r-m. Medial M_{1+2} ca. 1.5× longer than distal M_{1+2}. Basal deflection of M_3 1.3× shorter than M_{3+4}. M_4 reaching the wing distal than the level of the tip of Sc. Tip of M_4 angled forward. Cross-vein m-cu attached on M_{3+4}.Tip of Cu curved downwards.

Measurements. Wing length/width: 12.9 mm/3.6 mm.

Remarks. The holotype is the only known specimen. This species is similar in length to *L. bonifacioi* sp. nov. (described below in this paper) and to *L. lagosi* sp. nov. (described below in this paper). It differs from *L. bonifacioi* sp. nov. mainly in size, the attachment of m-cu, length of r-m, shape of Rs, and R_2. It differs from *L. lagosi* sp. nov. mainly by the attachment of m-cu, length of R_2, and the shape of M_4.

Leptotarsus feijoi sp. nov (Fig. 7)
urn:lsid:zoobank.org:act:6FFADCB5-FC90-48B7-989D-4ADFD6824ED1

Type material. Holotype: Male. UFRJ-DG 1407ins. NE Brazil, Crato Formation, Aptian, Lower Cretaceous. Housed at the collection of Universidade Federal do Rio de Janeiro (UFRJ), Brazil.

Etymology. This species is named after João da Sylva Feijó (1760–1824). Feijó was sergeant major of the militias of the captaincy of Ceará, with the task of enabling the economic exploitation of local nature, seeking saltpeter deposits in particular. He was the first naturalist to recognize the fossils from the Araripe Basin.

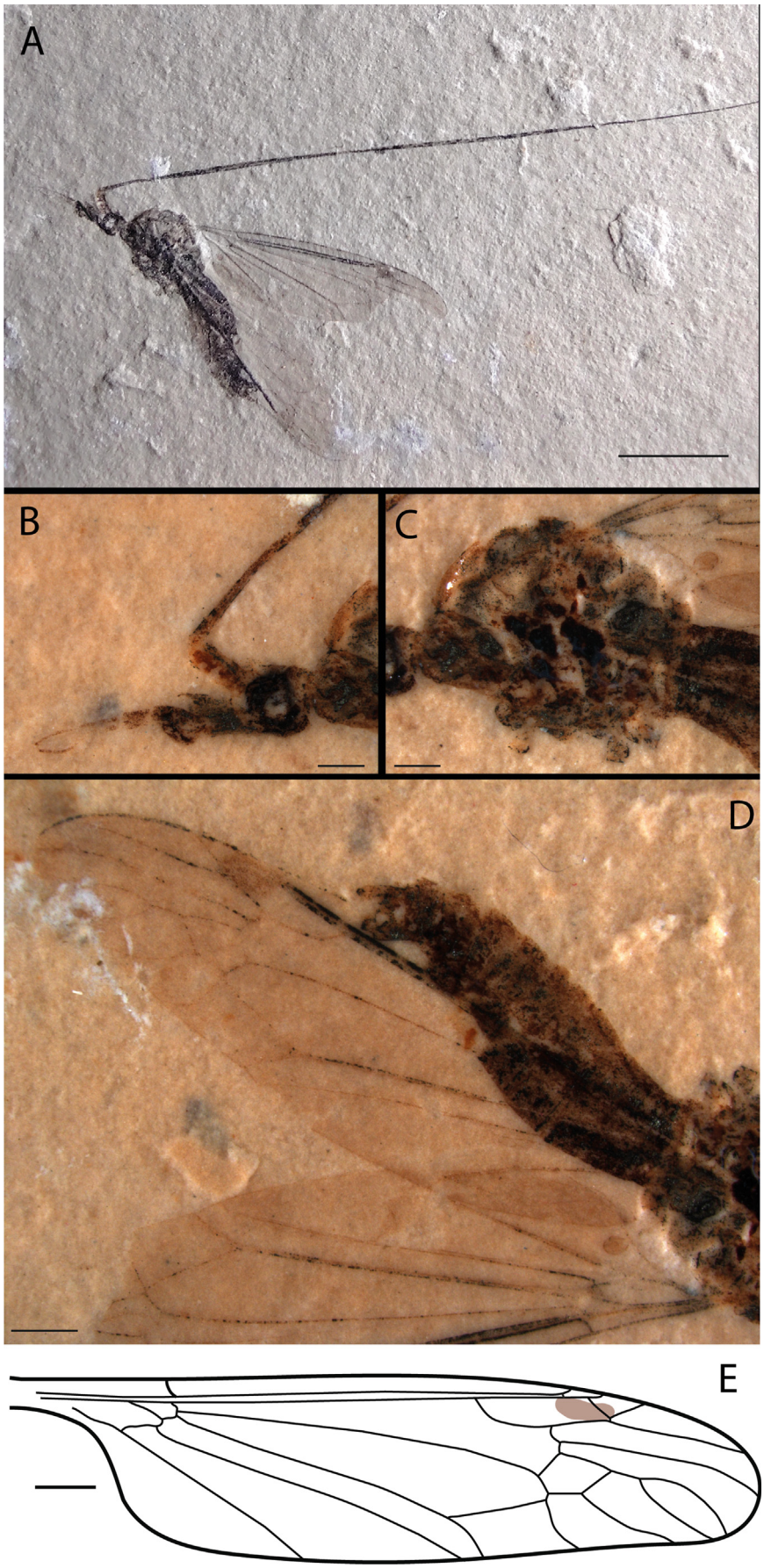

Fig. 8. *Leptotarsus ferreirai* sp. nov. Holotype UFRJ-DG 1100Ins. A-habitus; B-head; C-thorax; D-left wing; E-illustration of wing venation (scale bar = 5 mm for A, 0.5 mm for B and C, and 1 mm for D and E).

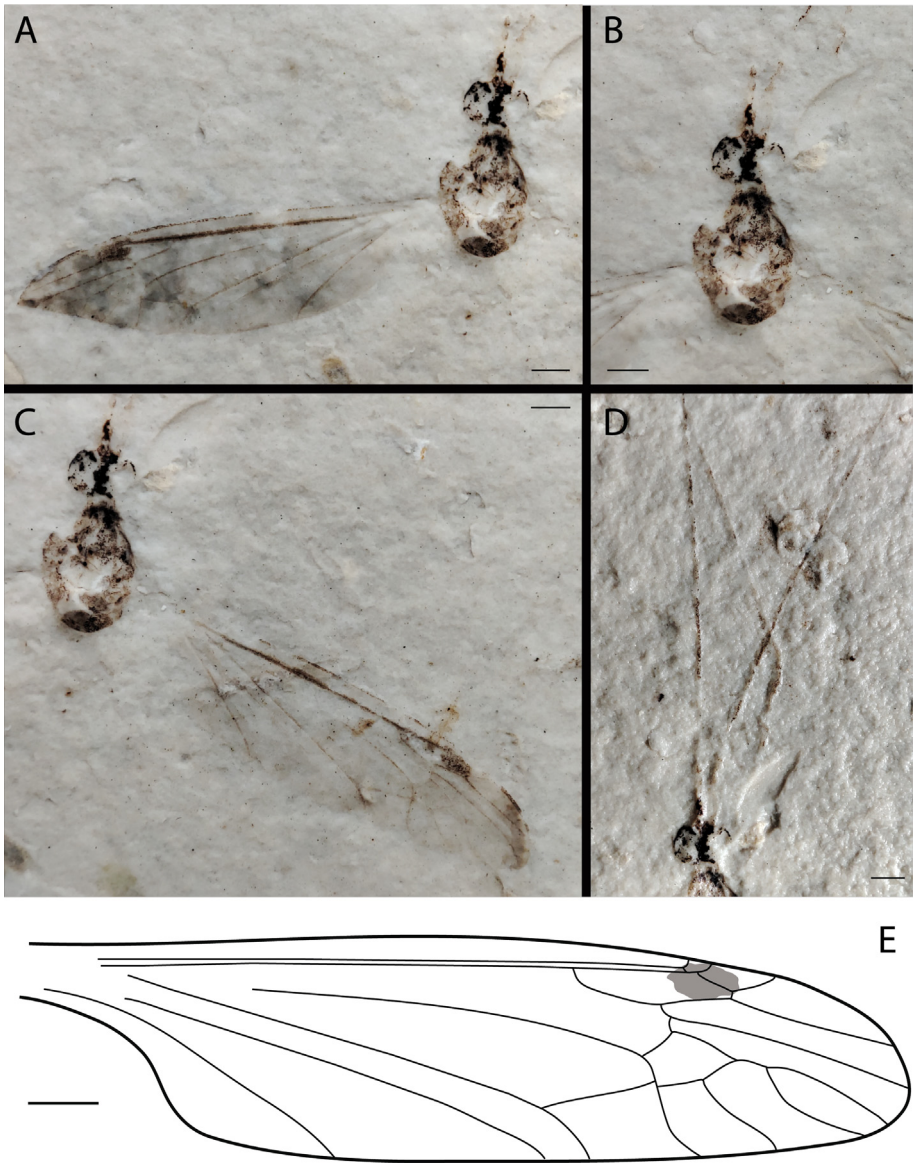

Fig. 9. *Leptotarsus lagosi* sp. nov. Holotype LP/UFC CRT 2420. A-left habitus; B-head and thorax; C-right habitus; D-antenna; E-illustration of wing venation (scale bar = 1 mm).

Diagnosis. The species is defined by M_{3+4} simultaneously longer than the basal deflection of M_3 and as long as the basal deflection of M_{1+2}.

Description. Wing as long as thorax and abdomen combined. Cervix 4× times shorter than the length of head without rostrum, cervix half in wideness than head. Head without rostrum c.a 2× longer than rostrum. There is a small nasus in the rostrum. Abdomen ca. 2× longer than thorax. Thorax ca. 2× longer than head. Wing transparent, but with an evident pterostigma. Vein Sc reaching the wing margin distal to the fork of Rs. Rs longer than R_{2+3+4}. R1 reaching the wing margin distal than the level of the fork of R_{2+3+4}. R_3 shorter than R_{2+3+4}. R_{2+3} 4× shorter than R_2 and 12× shorter than R_3. R_2 slightly curved. R_4 straight. Basal deflection of R_5 1.5× shorter than the length of r-m, R_5 curved downwards on the distal third of its length. Basal deflection of M_{1+2} ca. 1.5× longer than r-m and as long as M_{3+4}. Medial M_{1+2} as long as distal M_{1+2}. Tips of M_1 and M_2 parallels. Basal deflection of M_3 ca. 1.3× shorter than M_{3+4}. M_4 reaching the wing proximal than the level of the tip of Sc. Cross-vein m-cu attached on M_4.

Measurements. Wing length/width: 9 mm/2.2 mm.

Remarks. The holotype is the only known specimen. This species is similar in length to *L. petrii* sp. nov. (described below in this paper) and to *L. contractus* Ribeiro & Lukashevich, 2014. It differs from *L. petrii* sp. nov. mainly in the shape of discal cell and M_{1+2}, and lengths of r-m and R_3. It differs from *L. contractus* Ribeiro & Lukashevich, 2014 mainly in shape of discal cell, shape of M_{3+4}, and level of insertion of Sc.

Leptotarsus ferreirai sp. nov (Fig. 8)
urn:lsid:zoobank.org:act:58DAEFE0-038B-4022-82C1-BA8FDF133727

Type material. Holotype: Male. UFRJ-DG 1100Ins. NE Brazil, Crato Formation, Aptian, Lower Cretaceous. Housed at the collection of Universidade Federal do Rio de Janeiro (UFRJ), Brazil.

Etymology. This species is named after Alexandre Rodrigues Ferreira (1756–1815). He was a botanist who toured vast areas of the interior of the Brazilian Amazon, between 1783 and 1792. He described aspects of the agriculture of Indigenous people, fauna, flora and anthropological aspects of the regions he visited.

Diagnosis. The species is defined by the combination of r-m half than basal deflection of M_{1+2} and a tiny R_{2+3}.

Description. Wing length ca. 1.2× longer than the length of thorax and abdomen combined. Although damaged, cervix very short. Head without rostrum as long as rostrum. There is a evident nasus, 3× shorter than rostrum. Palpomeres well preserved, the first half in length than the second one, the third one as long as the fourth one. Palpi as long as head. Antenna very long, ca. 3× the body length. Scape 3× longer than wide, pedicel globular, flagellomeres cylindrical. Thorax 1.5× longer than head. Thorax 1.25 longer than tall. Abdomen ca. 1.5× longer than thorax. Male terminalia preserved with clasper and lobe of gonostylus observable. Wing transparent, but with an evident pterostigma. Vein Sc reaching the wing margin distal to the fork of Rs. Rs longer than R_{2+3+4}. R_1 reaching the wing margin at the level of the fork of R_{2+3+4}. R_3 half than R_{2+3+4}. R_{2+3} 6× shorter than R_2 and 7.5× shorter than R_3. R_4 straight. Basal deflection of R5 1.5× shorter than the length of r-m, R_5 curved downwards on the distal third of its length. Basal deflection of M_{1+2} ca. 2× longer than r-m. Medial M_{1+2} ca. 1.8× longer than distal M_{1+2}. Basal deflection of M_3 1.3× longer than M_{3+4}. Tips of M_1 and M_2 convergent, tip of M_3 curved forward. M_4

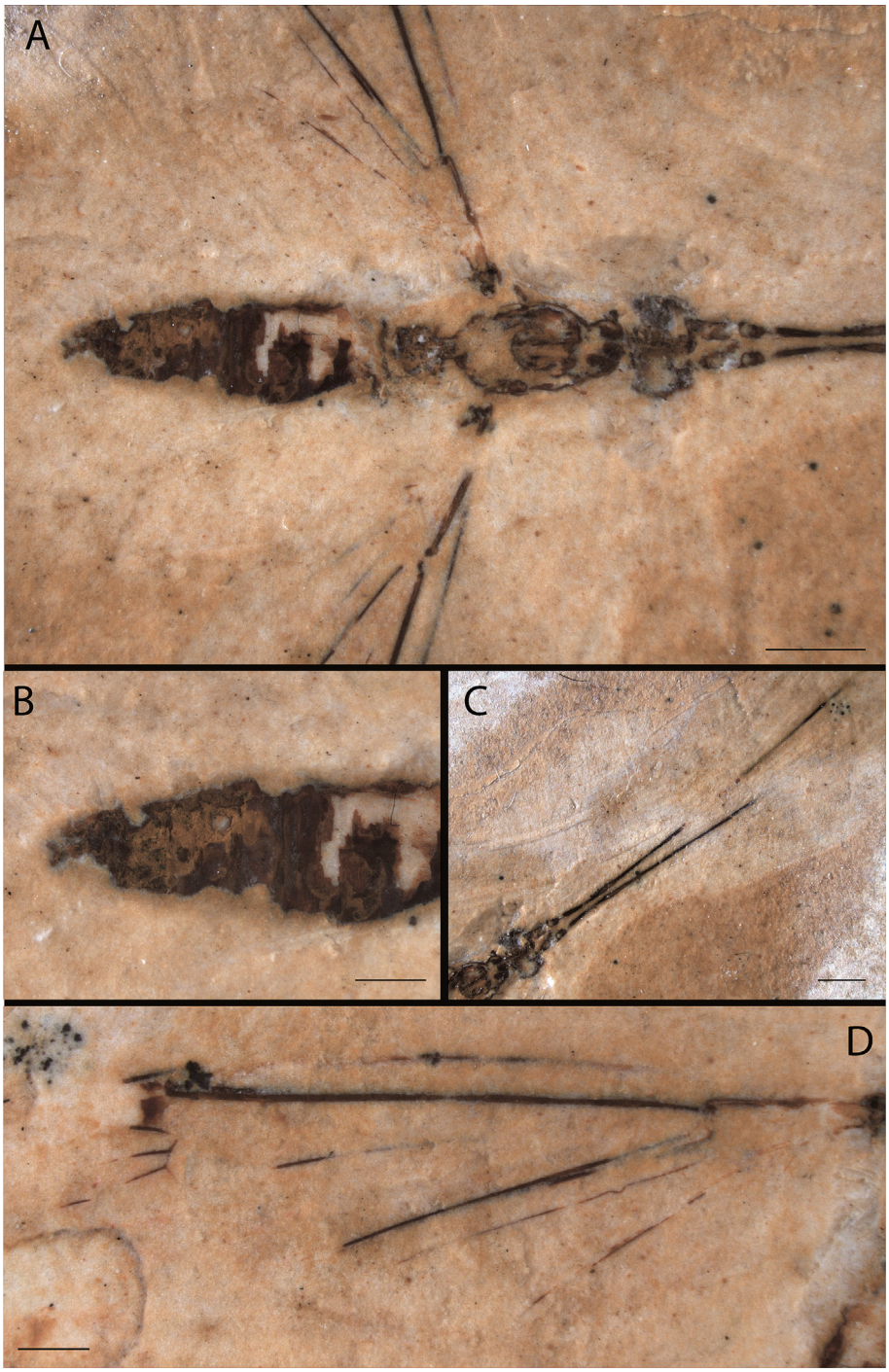

Fig. 10. *Leptotarsus lagosi* sp. nov. Paratype UFRJ-DG 75Ins. A-habitus; B-male terminalia; C-head and antenna; D-left wing (scale bar = 1 mm).

reaching the wing near the level of the tip of Sc. Cross-vein m-cu straight, m-cu attached on M_4.
Measurements. Wing length/width: 12.7 mm/3.4 mm.
Remarks. The holotype is the only known specimen. This species is similar in length to *L. bonifacioi* sp. nov. and to *L. lemesi* sp. nov. (described below in this paper). It differs from *L. bonifacioi* sp. nov. mainly in size, shape of the discal cell, shape of M_3, and R_2. It differs from *L. lemesi* sp. nov. mainly in size, shape of Rs, length of R_2, shape of Rs and of the basal deflection of M_{1+2}.

Leptotarsus lagosi sp. nov (Figs. 9–10)
urn:lsid:zoobank.org:act:A1E5A5F6-F2E3-437D-92A2-1A2C61A7FFD7

Type material. Holotype: Sex unknown. LP/UFC CRT 2420. NE Brazil, Crato Formation, Aptian, Lower Cretaceous. Housed at collection of Universidade Federal do Ceará (UFC). Paratype: Male. UFRJ-DG 75Ins. NE Brazil, Crato Formation, Aptian, Lower Cretaceous. Housed at Universidade Federal do Rio de Janeiro (UFRJ), Brazil.
Etymology. This species is named after Manuel Ferreira Lagos (1816–1871). Physician and naturalist, he was director of the Department of Zoology and Comparative Anatomy of the National Museum and was part of the Scientific Commission of the Empire that organized the first exhibition on natural history and ethnography of the State of Ceará.
Diagnosis. The species is defined by m-cu attached in M_{3+4}.
Description. Wing length ca. 3.5× the length of thorax. Cervix short. Antenna very long, ca. 6× the length of thorax, flagellomeres cylindrical. Thorax 2× longer than head. Wing transparent, but with an evident pterostigma. Vein Sc reaching the wing margin distal to the fork of Rs. Rs longer than R_{2+3+4}. R_1 reaching the wing margin more proximal than the level of the fork of R_{2+3+4}. R_3 shorter than R_{2+3+4}. R_{2+3} 6× shorter than R_2 and 8× shorter than R_3. Basal deflection of R_5 as long as r-m. Basal deflection of M_{1+2} ca. 2× longer than r-m. Medial M_{1+2} ca. 2× longer than distal M_{1+2}. Basal deflection of M_3 as long as M_{3+4}. M_4 reaching the wing at the level of the tip of Sc. Cross-vein m-cu sinuous, m-cu attached on M_{3+4}.
Measurements. Wing length/width: 13.9 mm/3.5 mm.
Remarks. This species is the largest *Leptotarsus* of Brazil and the second largest of the Mesozoic. The differences of this species with the largest *Leptotarsus* (*L. primitivus* Shih, Dong, Kania, Liu, Krzeminski & Ren, 2015) are mainly in size, proportions of discal cell, length of R_{2+3}, and the attachment of m-cu. The species with more comparable size in the Crato formation is *L. coutoi* sp. nov. It differs from *L. coutoi* sp. nov. mainly by the attachment of m-cu, length of R_2, and the shape of M_4. The specimen MP/3554 was designated by Krzemiński et al. (2017) as *L. martinsnetoi*. However, this specimen is another exemplar of *L. lagosi* sp. nov.

Leptotarsus lemesi sp. nov (Fig. 11)
urn:lsid:zoobank.org:act:DC641016-9026-4919-8250-19905D0821CB

Type material. Holotype: Male. UFRJ-DG 865ins. NE Brazil, Crato Formation, Aptian, Lower Cretaceous. Housed at the collection of Universidade Federal do Rio de Janeiro (UFRJ), Brazil.
Etymology. This species is named after Antônio Pires da Silva Pontes Lemes (1750–1805). Lemes was a mathematician who worked in expeditions for delimitation of the Brazilian borders in the 1780s and 1790s. He was a corresponding member of the Royal Academy of Sciences of Lisbon. As a politician, he became governor of the captaincy of Espírito Santo.
Diagnosis. The species is defined by the combination of r-m half than the basal deflection of R_5 and the basal deflection of M_3 longer than M_{3+4}.
Description. Wing length ca. 1.2× longer than the length of thorax and abdomen combined. Cervix as long as head without rostrum, cervix as wide as head. Head without rostrum c.a 1.5× longer than rostrum. There is a small nasus in the rostrum. Thorax ca. 2× longer than head. Abdomen ca. 2× longer than thorax. Gonocoxite observable. Wing transparent, but with an evident pterostigma. Vein Sc reaching the wing margin distal to the fork of Rs. Rs longer than R_{2+3+4}. R_1 reaching the wing margin at the level of the fork of R_{2+3+4}. R_3 shorter than R_{2+3+4}. R_{2+3} 2.5× shorter than R_2 and 5.5× shorter than R_3. R_4 straight. Basal deflection of R_5 2× the length of r-m, R_5 curved downwards on the distal third of its length. Basal deflection of M_{1+2} curved and ca. 4× longer than r-m. Medial M_{1+2} ca. 2.5× longer than distal M_{1+2}. Basal deflection of M_3 ca. 1.2× longer than M_{3+4}. M_4 reaching the wing at the level of the tip of Sc. Cross-vein m-cu attached on M_4.
Measurements. Wing length/width: 12.5 mm/3.1 mm.
Remarks. The holotype is the only known specimen. This species is similar in length to *L. ferreirai* sp. nov. and to *L. pereirai* sp. nov. (described below in this paper). It differs from *L. ferreirai* sp. nov. mainly in size, shape of Rs, length of R_2, shape of Rs and the basal deflection of M_{1+2}. It differs from *L. pereirai* sp. nov. mainly in size, length of r-m, shape of Rs and of the basal deflection of M_{1+2}.

Leptotarsus pereirai sp. nov (Fig. 12)
urn:lsid:zoobank.org:act:A152FC54-815B-40D1-8E30-DAF78DC2E937

Type material. Holotype: Male. UFRJ-DG 1552Ins. NE Brazil, Crato Formation, Aptian, Lower Cretaceous. Housed at the collection of Universidade Federal do Rio de Janeiro (UFRJ), Brazil.
Etymology. This species is named after João Manso Pereira (? 1750–1820). He was a teacher of humanities disciplines and a self-taught scientist, dedicated to mineralogy and chemistry. He was also an entrepreneur of products such as clays for porcelain and processing of ores found in the Brazilian territory, through techniques developed by himself.
Diagnosis. The species is defined by the basal deflection of M_3 simultaneously shorter than m-m and as long as M_{3+4}.
Description. Wing length ca. 3.5× longer than thorax. Cervix as long as head without rostrum. Thorax ca. 4× longer than head, ca. 2× longer than tall. Wing transparent, but with an evident pterostigma. Vein Sc reaching the wing margin distal to the fork of Rs. Rs longer than R_{2+3+4}. R_1 reaching the wing margin more proximal than the level of the fork of R_{2+3+4}. R_3 shorter than R_{2+3+4}. R_{2+3} 6.5× shorter than R_2 and 9.5× shorter than R_3. R_4 straight. Basal deflection of R_5 1.5× longer than the length of r-m. Basal deflection of M_{1+2} ca. 2.5× longer than r-m. Medial M_{1+2} ca. 2.5× longer than distal M_{1+2}. Basal deflection of M_3 as long as M_{3+4}. M_4 reaching the wing at the level of the tip of Sc. Tip of M_4 curved forward. Cross-vein m-cu straight, m-cu attached on M_4.
Measurements. Wing length/width: 12.2 mm/3.3 mm.
Remarks. The holotype is the only known specimen. This species has wing proportions equal to *L. acciolii* sp. nov. It differs from *L. acciolii* sp. nov. mainly in insertion of m-cu, shape of the discal cell, shape of M_4, and R_2.

Leptotarsus petrii sp. nov (Fig. 13)
urn:lsid:zoobank.org:act:97F86EC5-7B8B-40FA-AB86-AB7F1E615818

Type material. Holotype: Male. CCNH 374. NE Brazil, Crato Formation, Aptian, Lower Cretaceous. Housed at Centro de Ciências Naturais e Humanas, Universidade Federal do ABC, CCNH – UFABC), Brazil.
Etymology. This species is named after Setembrino Petri (1922 -) in honor of his 100th anniversary. Setembrino Petri is the most important geoscientist dedicated to the geological history of the Brazilian Cretaceous. In his centenary, Setembrino Petri is the

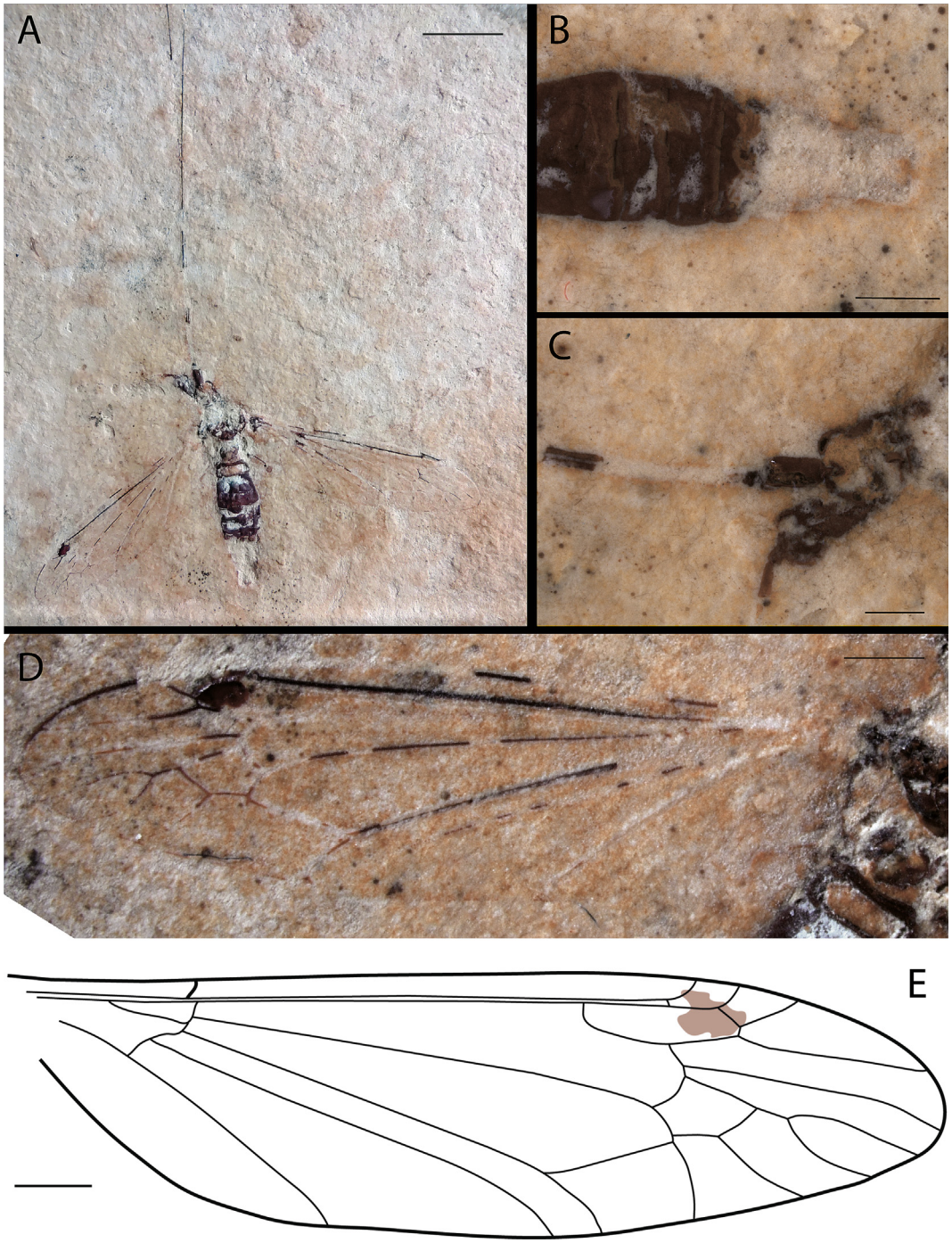

Fig. 11. *Leptotarsus lemesi* sp. nov. Holotype UFRJ-DG 865Ins. A-habitus; B-male terminalia; C-head; D-left wing; E-illustration of wing venation (scale bar = 5 mm for A, 1 mm for B, C, D, and E).

synthesis of the determination of Brazilian scientists in building scientific knowledge.

Diagnosis. The species is defined by the combination of basal deflection of M_{1+2} sinuous.

Description. Wing length ca. 1.2× longer than the length of thorax and abdomen combined. Cervix short. Thorax ca. 3× longer than head. Abdomen ca. 2× longer than thorax. Wing transparent, but with an evident pterostigma. Vein Sc reaching the wing margin distal to the fork of Rs, crossvein sc-r close from the tip of Sc. Rs longer than R_{2+3+4}. R_1 reaching the wing margin at the level of the fork of R_{2+3+4}. R_3 1.1× shorter than R_{2+3+4}. R_{2+3} ca. 3× shorter than R_2 and 4× shorter than R_3. R_4 straight and inclined downwards. Basal deflection of R_5 2 times longer than the length of r-m, R_5 curved downwards on the distal third of its length. Basal deflection of M_{1+2} sinuous, ca. 5× longer than r-m. Medial M_{1+2} ca. 2× longer than distal M_{1+2}. M_{3+4} curved. Basal deflection of M_3 1.2× longer than M_{3+4}. Tip of M_4 straight. Cross-vein m-cu attached on M_4.

Measurements. Wing length/width: 9.8 mm/2.8 mm.

Remarks. The holotype is the only known specimen. This species is similar in length to *L. feijoi* sp. nov. and to *L. cretaceus* Ribeiro &

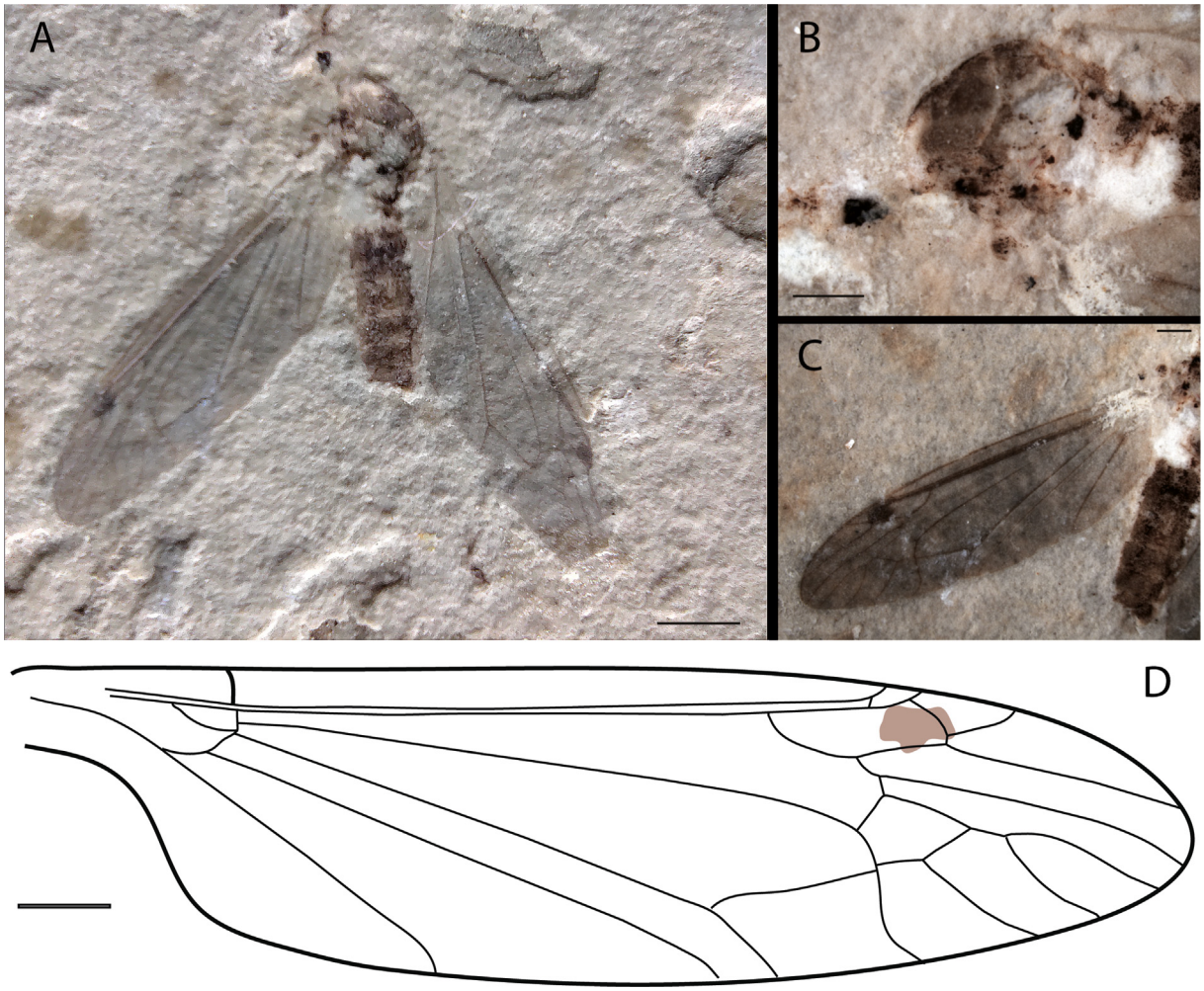

Fig. 12. *Leptotarsus pereirai* sp. nov. Holotype UFRJ-DG 1552Ins. A-habitus; B-head and thorax; C-left wing; D-illustration of wing venation (scale bar = 2 mm for A, 1 mm for B, C and D).

Lukashevich, 2014. It differs from *L. feijoi* sp. nov. mainly in the shape of discal cell and M_{1+2}, and lengths of r-m and R_3. It differs from *L. cretaceus* mainly in the shape of discal cell and M_{3+4}, length of r-m, and inclination of R_{2+3}.

Leptotarsus velosoi sp. nov (Fig. 14)

urn:lsid:zoobank.org:act:09A38A40-5514-431D-9454-BB1B0244718A0

Type material. Holotype: Male. CCNH 83. NE Brazil, Crato Formation, Aptian, Lower Cretaceous. Housed at Centro de Ciências Naturais e Humanas, Universidade Federal do ABC, CCNH – UFABC), Brazil.

Etymology. This species is named after José Mariano da Conceição Veloso (1742–1811). Veloso was a missionary, teacher, and botanist. He collected animal, plant and mineral specimens in the then province of Rio de Janeiro, which were later presented in his work *Flora Fluminensis*. He collaborated with the collection of specimens of flora and fauna for the Royal Museum and Botanical Garden of Ajuda, in Lisbon (Portugal).

Diagnosis. The species is defined by sc-r more proximal than the origin of Rs.

Description. Wing length ca. 1.3× longer than the length of thorax and abdomen combined. Although damaged, cervix short. Antenna very long, flagellomeres cylindrical. Although damaged, length of antenna ca. 1.7× the body length. Thorax ca. 3× longer than head. Abdomen ca. 1.3× longer than thorax. Wing transparent, but with an evident pterostigma. Vein Sc reaching the wing margin proximal to the fork of Rs, crossvein sc-r far from the tip of Sc. Rs longer than R_{2+3+4}. R_1 reaching the wing margin at the level of the fork of R_{2+3+4}. R_3 1.2× shorter than R_{2+3+4}. R_{2+3} ca. 5× shorter than R_2 and 9× shorter than R_3. R_4 straight and inclined downwards. Basal deflection of R_5 1.5× shorter than the length of r-m, R_5 curved downwards on the distal third of its length. Basal deflection of M_{1+2} ca. 1.5× longer than r-m. Medial M_{1+2} ca. 1.8× longer than distal M_{1+2}. Basal deflection of M_3 1.3× longer than M_{3+4}. Cross-vein m-m sinuous. Tip of M_4 curved forward. Cross-vein m-cu slightly sinuous, m-cu attached on M_4.

Measurements. Wing length/width: 11.9 mm/3.3 mm.

Remarks. The holotype is the only known specimen. This species is similar in length to *L. acciolii* sp. nov. and to *L. martinsnetoi* Ribeiro & Lukashevich, 2014. It differs from *L. acciolii* sp. nov. mainly in insertion of m-cu, shape of the discal cell, shape of M_4, and R_5. It differs from *L. martinsnetoi* mainly in the tip of Sc, shape of M_4, and length of r-m.

Identification key to Cretaceous species of Leptotarsus

1) Sc ending closer to the origin of Rs than the fork of Rs ….. 2
Sc ending closer to the fork of Rs than the origin of Rs ……..3

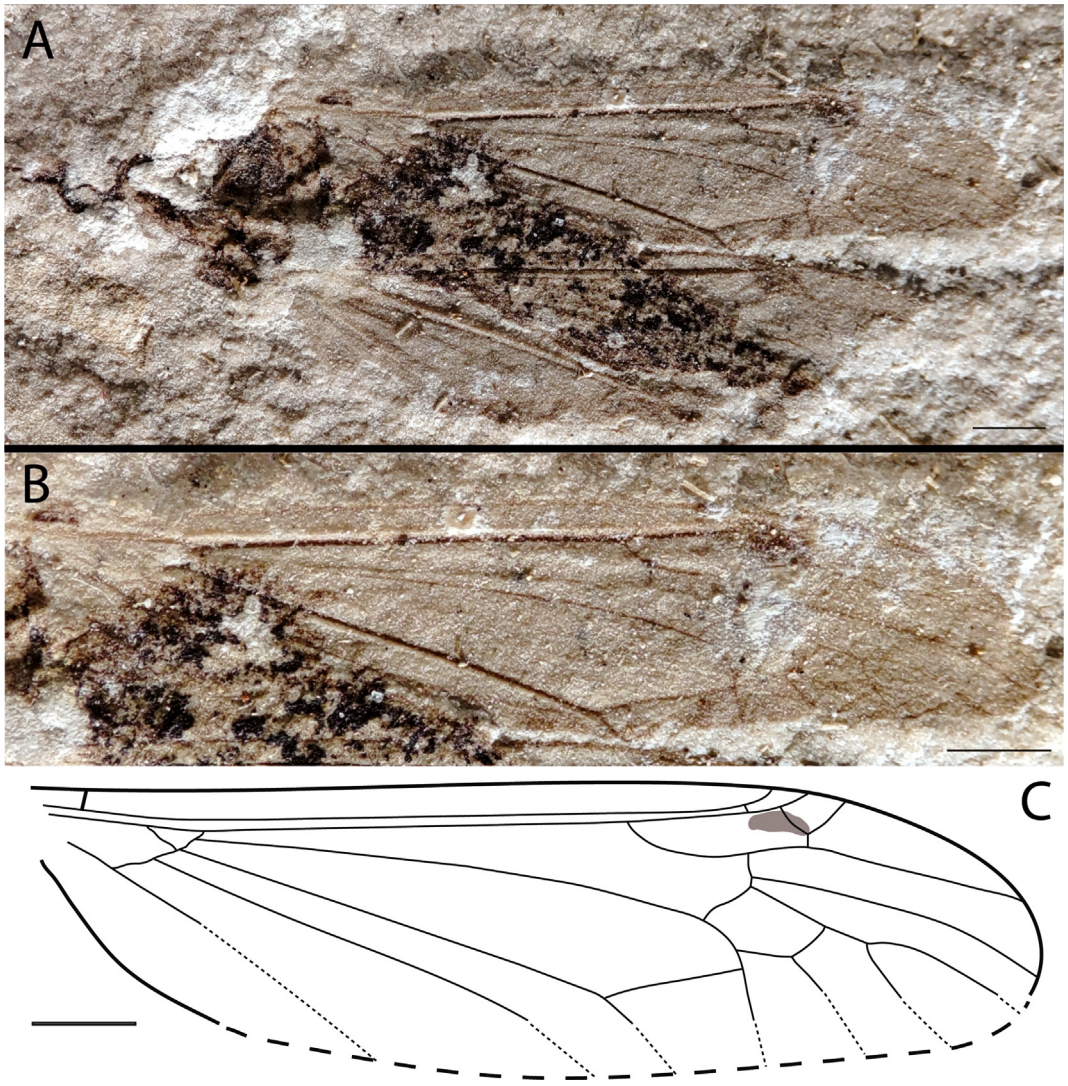

Fig. 13. *Leptotarsus petrii* sp. nov. Holotype CCNH 374. A-habitus; B-right wing; C-illustration of wing venation (scale bar = 1 mm).

2) Cross-vein sc-r far from the tip of Sc; R_{2+3} ca. 5× shorter than R_2 (Fig. 14D) … *L. velosoi* sp. nov. (Crato Formation, Brazil).
Cross-vein sc-r close to the tip of Sc; R_{2+3} ca. 2× shorter than R_2 (Fig. 15F) … *L. eva* (Krzeminski, 1992a) (Kyndaly Formation, Russia).
3) M_{3+4} aligned with the axis of bM ……...4
M_{3+4} unaligned with bM, inclined downwards ……6
4) Darkened costal field; R_3 aligned with R_{2+3}; length of R_{2+3} about half of R_2; basal deflection of M_3 unaligned with M_{3+4} …….. 5
Clear costal field; R_3 unaligned with R_{2+3}; R_{2+3} longer than half of R_2; basal deflection of M_3 aligned with M_{3+4} (Fig. 15E) …*L. cretaceus* Ribeiro and Lukashevich, 2014 (Crato Formation, Brazil).
5) R_3 is 3 times longer than R_2; Rs origin more proximal than the connection of m-cu and Cu (Fig. 15D)…*L. contractus* Ribeiro and Lukashevich, 2014 (La Huerguina Formation, Spain).
R_3 is less than 2 times longer than R_2; Rs origin near the level of connection of m-cu and Cu (Fig. 15C) … *L. buscalioniae* Ribeiro and Lukashevich, 2014 (La Huerguina Formation, Spain).
6) Cross-vein m-cu attached at the fork of M_{3+4} or on M_{3+4} …..7
Cross-vein m-cu attached on M_4 ……..12
7) Cross-vein m-cu attached at the fork of M_{3+4}; distal section of M_{1+2} straight ……...…8
Cross-vein m-cu attached on M_{3+4}; distal section of M_{1+2} curved (Fig. 9E) … *L. lagosi* sp. nov. (Crato Formation, Brazil).
8) Basal deflection of M_{1+2} shorter than M_{3+4}; tip of M_4 straight …….. 9
Basal deflection of M_{1+2} longer or equal than M_{3+4}; tip of M_4 curved……..10
9) R_{2+3+4} curved; Sc ending more distal than the level of r-m (Fig. 15G) … *L. gelhausi* Ribeiro, Santos and Santos, 2021 (Crato Formation, Brazil).
R_{2+3+4} straight; Sc ending more proximal than the level of r-m (Fig. 15O) … *L. ribeiroi* Krzeminski, Kopec and Kania, 2017 (Crato Formation, Brazil).
10) Distal section of M_{1+2} shorter than m-m; tip of Cu curved backwards ……..11
Distal section of M_{1+2} longer than m-m; tip of Cu straight (Fig. 2D) … *L. acciolii* sp. nov. (Crato Formation, Brazil).
11) R_3 similar in length to R_2; Rs longer than R_{2+3+4} (Fig. 6D) … *L. coutoi* sp. nov. (Crato Formation, Brazil).

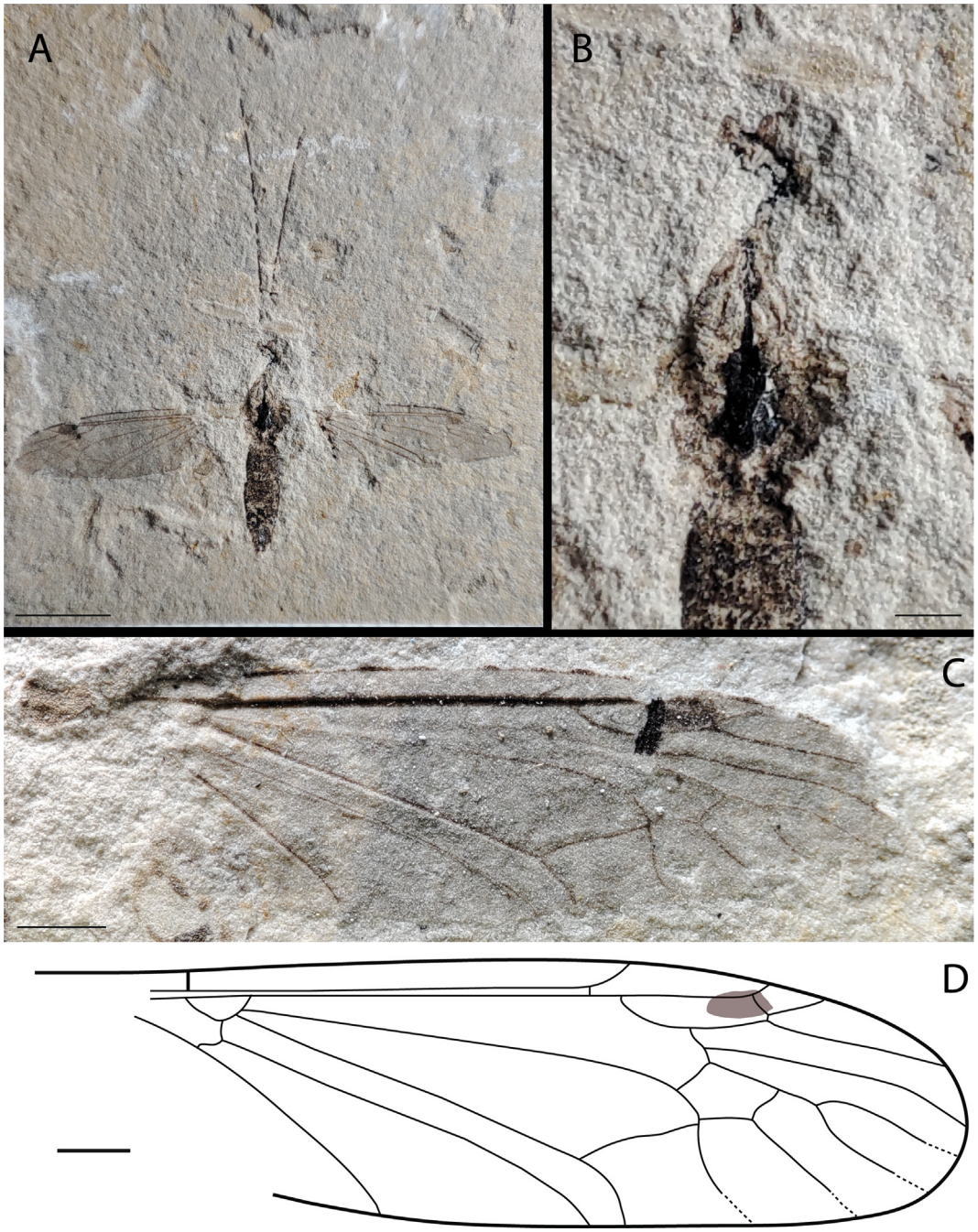

Fig. 14. *Leptotarsus velosoi* sp. nov. Holotype CCNH 83. A-habitus; B-head and thorax; C-right wing; D-illustration of wing venation (scale bar = 5 mm for A, and 1 mm for B, C and D).

R_3 at least 2 times longer than R_2; Rs similar in length to R_{2+3+4} (Fig. 5E) … *L. capanemai* sp. nov. (Crato Formation, Brazil).

12) Cross-vein m-m at least 4 times longer the length of the distal section of M_{1+2} ……13
Cross-vein m-m shorter than 4 times the length of the distal section of M_{1+2} ……..……...…14

13) Clear costal field; Basal deflection of M_3 curved; length of r-m similar to basal deflection of M_{1+2} (Fig. 15I) … *L. ibericus* Ribeiro and Lukashevich, 2014 (La Huerguina Formation, Spain).
Darkened costal field; Basal deflection of M_3 straight; length of r-m half than basal deflection of M_{1+2} (Fig. 15J) … *L. ivoneae* Ribeiro, Santos and Santos, 2021 (Crato Formation, Brazil).

14) R_3 similar in length to R_2; r-m unaligned with basal deflection of R_5 ……...15
R_3 at least 1.5 times longer than R_2; r-m unaligned with basal deflection of R_5 … 16

15) Tips of M_1 and M_2 divergent; M_{3+4} as long as basal deflection of M_3 (Fig. 12D) … *L. pereirai* sp. nov. (Crato Formation, Brazil).

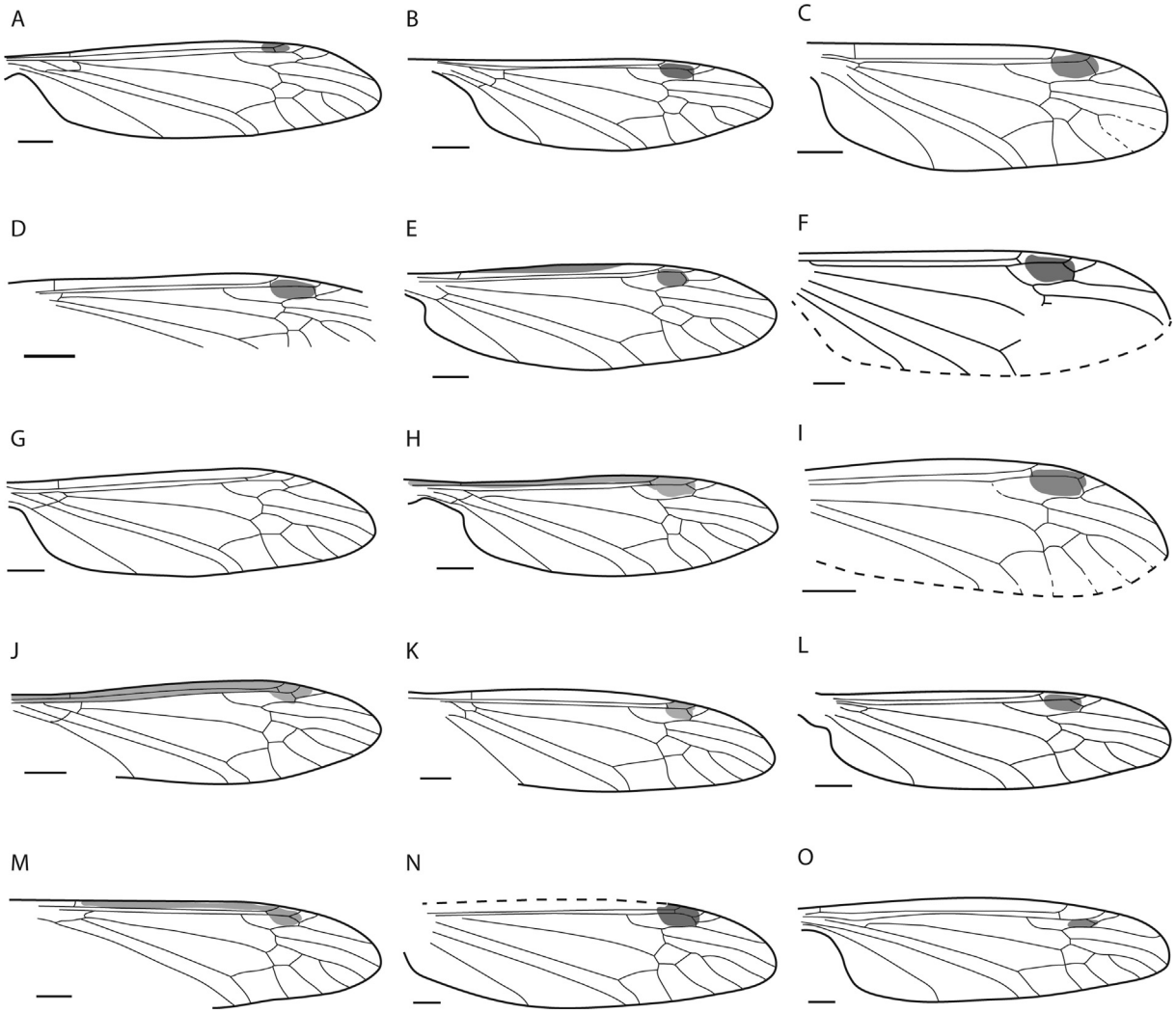

Fig. 15. Described *Leptotarsus*. A) *L. andradei* (adapted from Ribeiro, Santos and Santos, 2021); B) *L. burmica* (adapted from Men & Hu, 2021); C) *L. buscalioniae* (adapted from Ribeiro & Lukashevich, 2014); D) *L. contractus* (adapted from Ribeiro & Lukashevich, 2014); E) *L. cretaceus* (adapted from Ribeiro & Lukashevich, 2014); F) *L. eva* (adapted from Krzeminski, 1992a); G) *L. gelhausi* (adapted from Ribeiro, Santos and Santos, 2021); H) *L. grimaldii* (adapted from Ribeiro & Lukashevich, 2014); I) *L. ibericus* (adapted from Ribeiro & Lukashevich, 2014); J) *L. ivoneae* (adapted from Ribeiro, Santos and Santos, 2021); K) *L. lemeae* (adapted from Ribeiro, Santos and Santos, 2021); L) *L. lukashevishae* (adapted from Ribeiro, Santos & Nicolau, 2015); M) *L. martinsnetoi* (adapted from Ribeiro & Lukashevich, 2014); N) *L. primitivus* (adapted from Shih, Dong, Kania, Liu, Krzeminski & Ren, 2015); O) *L. ribeiroi* (adapted from Krzeminski, Kopec and Kania, 2017). Scale bar = 1 mm.

Tips of M_1 and M_2 convergent; M_{3+4} shorter than basal deflection of M_3 (Fig. 8E) … *L. ferreirai* sp. nov. (Crato Formation, Brazil).

16) Medial section of M_{1+2} longer than distal section of M_{1+2}; M_{3+4} shorter than basal deflection of M_3 ……..17
Medial section of M_{1+2} shorter or equal to distal section of M_{1+2}; M_{3+4} longer or equal to basal deflection of M_3 …….. 18

17) Distal M_{1+2} curved; length of M_{3+4} 2× longer than the basal deflection of M_4 (Fig. 15N) … *L. primitivus* Shih, Dong, Kania, Liu, Krzeminski and Ren, 2015 (Yixian Formation, China).
Distal M_{1+2} straight; length of M_{3+4} 4× longer than the basal deflection of M_4 (Fig. 3E) … *L. alemaoi* sp. nov. (Crato Formation, Brazil).

18) Tips of M_3 and M_4 divergent; basal deflection of M_{1+2} as long as M_{3+4}; clear costal field; tip of Sc ending more distal than the level of the fork of Rs (Fig. 7D) … *L. feijoi* sp. nov. (Crato Formation, Brazil).
Tips of M_3 and M_4 parallel; basal deflection of M_{1+2} shorter than M_{3+4}; darkened costal field; tip of Sc ending near at the level of the fork of Rs (Fig. 15H) … *L. grimaldii* Ribeiro and Lukashevich, 2014 (Crato Formation, Brazil)

19) Distal section of M_{1+2} longer than m-m; M_{3+4} curved …… 20
Distal section of M_{1+2} shorter or equal to m-m; M_{3+4} straight … 21

20) Basal deflection of M_{1+2} sinuous; basal deflection of R_5 verticalized (Fig. 13C) … *L. petrii* sp. nov. (Crato Formation, Brazil).
Basal deflection of M_{1+2} curved; basal deflection of R_5 inclined (Fig. 11E) … *L. lemesi* sp. nov. (Crato Formation, Brazil).

21) Distance between tips of M_3 and M_4 longer or equal than that between tips of M_4 and Cu … 22
Distance between tips of M_3 and M_4 shorter than that between tips of M_4 and Cu … 24

22) R_2 at least 3 times longer than R_{2+3}; m-m straight …… 23
R_{2+3} similar in length to R_2; m-m curved (Fig. 15B) … *L. burmica* Men & Hu, 2021 (Burmese amber, Myanmar).

23) Tip of Sc ending near at the level of the fork of Rs; R_2 curved; basal deflection of R_5 longer than r-m (Fig. 15L) … *L.*

lukashevichae Ribeiro, Santos and Nicolau, 2015 (Crato Formation, Brazil).

Tip of Sc ending more distal than the level of the fork of Rs; R_2 straight; basal deflection of R_5 as long as r-m (Fig. 4E) … *L. bonifacioi* sp. nov. (Crato Formation, Brazil).

24) Darkened costal field; Length of the basal deflection of M_3 similar to m-m and to M_{3+4} (Fig. 15M) … *L. martinsnetoi* Ribeiro and Lukashevich, 2014 (Crato Formation, Brazil).

Clear costal field; Basal deflection of M_3 longer than m-m and longer than M_{3+4} 25

25) Length of the basal deflection of the vein R_5 similar to r-m; Length of the basal deflection of the vein M_{1+2} twice than r-m (Fig. 15K) … *L. lemeae* Ribeiro, Santos and Santos, 2021 (Crato Formation, Brazil).

Basal deflection of the vein R_5 longer than r-m; Length of the basal deflection of the vein M_{1+2} is ca. 1.5 times longer than r-m (Fig. 15A) … *L. andradei* Ribeiro, Santos and Santos, 2021 (Crato Formation, Brazil).

5. Discussion

With 21 species of *Leptotarsus*, the Crato Formation is the richest known assemblage of Mesozoic Tipulidae.

Even though few specimens (or, in many instances, a single specimen) are known from each of the described species of the Crato fauna, each one can be recognized by unique combinations of characters. Extant species of Tipuloidea are normally distinguished by differences in wing features and dimensions, and also by remarkable differences in coloration and the structure of male and female terminalia. Detailed comparisons of wing features, dimensions, and proportions are also useful for distinguishing among fossil species, and these are in fact the only information for all fossil taxa described here (Table 2).

As discussed elsewhere (e.g., Gelhaus, 2009; Ribeiro & Lukashevich, 2014) *Leptotarsus* is probably a non-monophyletic unit, including representatives of early lineages of the family Tipulidae. Not much is known about the biology and environmental requirements of *Leptotarsus* species, and it is not easy to understand the reasons for such high biodiversity in the Crato Formation. To gain insight into the problem, we reviewed the literature and reviewed the type of biome in which the extant species of the genus are found. The biology of the immature stages is largely unknown, but according to Alexander (1920), the Nearctic species of the subgenus *L.* (*Longurio*) are semiaquatic, with aquatic larvae and terrestrial pupae. As pointed out by Gelhaus and Young (1995), the habitats in which the larvae live can vary considerably, from dry soil, forest leaf litter, rotting wood, and spring runs.

The adult forms of some species occur at the transition between forest and scrubland, such as *L.* (*L.*) spinosus (Wood, 1952) at Meiringspoort, South Africa (Geldenhuys, 1997). In South Africa, *L.* (*L.*) *stuckenbergi* (Alexander) has been directly associated with a stream in the Renosterveld vegetation, a type of open scrubland (Alexander, 1964). *Leptotarsus* (*L.*) *goyazanus* (Alexander, 1940) is known from the tropical savannah (Cerrado) in Brazil. Despite these few examples, the vast majority of species are associated with humid forests.

According to the reconstruction by Ribeiro et al. (2021b), the ecosystem of the Crato Formation at the time of its deposition consisted of a semi-arid, seasonal, shallow wetland. Fossils were preserved in a shallow deposit system that was subject to regular flooding over large areas. This scenario is corroborated by an abundance of diverse fossil plants, contemporary relatives of which inhabit transitional environmental gradients, such as hydrophytes (indicating fully aquatic habitats), helophytes, and amphiphytes (representing flooded transitional vegetation with dry herbaceous vegetation). The insect assemblage of the Crato Formation, on the other hand, suggests the division of the paleoenvironment into terrestrial habitats with well-developed vegetation (i.e., forests), fully aquatic habitats, and transition zones between terrestrial and aquatic habitats. Here, there are taxa typically associated with semi-aquatic and shallow water vegetation, and taxa with immature aquatic stages and terrestrial adults.

Therefore, it appears that the different types of vegetation – ranging from dry scrubland to mesophytic, helophytic, and aquatic ecotones – that were present in close proximity to the depositional environment allowed for a large concentration of Tipulidae. It must also be noted that this high concentration of well-preserved fossils would be very unlikely to occur unless these individuals were autochthonous. The adults of Tipulidae are extremely fragile insects, and the extremely fragile antenna preserved in many specimens suggests little or no transport from the place of death to the place of preservation.

Most of the *Leptotarsus* species described from Crato are known from a single specimen, or in some cases from very few specimens. It probably reflects the fact that in the Crato wetland, home to a large number of species, the preservation of many individuals of the same species was less likely to happen compared to individuals of different species. Furthermore, neither species should stand out enough in terms of relative abundance or population density to make it appear more frequently than the others in the Crato paleontological record.

6. Conclusions

Twelve new species of *Leptotarsus* are described from the Lower Cretaceous Crato Formation of Brazil. Today, the Crato Beds, with 21 known species, are by far the most diverse Mesozoic fossil site for this early lineage of the family Tipulidae. It shouldn't be a surprise if many more new species become known in the future as collection efforts progress.

Acknowledgments

We thank the Brazilian National Mining Agency (Agência Nacional de Mineração), through the geologists José Artur Ferreira Gomes Andrade and Irma T. Yamamoto, for collecting permits to GCR and ISC. To Jaime Joaquim Dias for the support with the geological map of Araripe Basin. This research was financially supported by a grant from FAPESP (grant number 2020/02844-5) to Guilherme Cunha Ribeiro. Daubian Santos reports financial support provided by State of Sao Paulo Research Foundation. This study was also supported by Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (Proc. E-26/200.828/2021, Brazil) and by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 303596/2016–3, Brazil) to Ismar de Souza Carvalho. Financial support for Daubian Santos was provided by FAPESP (grant number 2017/16305-6). We are gratefull to Ewa Krzeminska and an anonymous reviewer for the many corrections and suggestions to the first version of the manuscript.

References

Agnolin, F., Carvalho, I.S., Aranciaga Rolando, A.M., Novas, F.E., Xavier-Neto, J., Andrade, J.A.F.G., Freitas, F.I., 2020. Early Cretaceous neobatrachian frog (Anura) from Brazil sheds light on the origin of modern anurans. Journal of South American Earth Sciences 101, 102633. https://doi.org/10.1016/J.JSAMES.2020.102633.

Alexander, C.P., 1920. The Crane-flies of New York. Part II. Biology and Phylogeny, vol. 38. Cornell University Agricultural Experiment Station Memoir, pp. 691–1133.

Alexander, C.P., 1940. Records and descriptions of Brazilian Tipulidae (Dipt.). Part VI. Revista de Entomologia 11, 382–397.
Alexander, C.P., 1964. Diptera (Nematocera): Tanyderidae, Ptychopteridae, Tipulidae. South African Animal Life 10, 229–441.
Barling, N., Martill, D.M., Heads, S., Gallien, F., 2015. High fidelity preservation of fossil insects from the Crato Formation (lower cretaceous) of Brazil. Cretaceous Research 52, 602–622.
Blagoderov, V., Grimaldi, D.A., Fraser, N.C., 2007. How time flies for flies: diverse Diptera from the Triassic of Virginia and early radiation of the order. American Museum Novitates 2007 (3572), 1–39. https://doi.org/10.1206/0003-0082(2007)509[1:HTFFFD]2.0.CO;2.
Carvalho, I.S., Novas, F.E., Agnolín, F.L., Isasi, M.P., Freitas, F.I., Andrade, J.A., 2015a. A Mesozoic bird from Gondwana preserving feathers. Nature Communications 61 (6), 1–5. https://doi.org/10.1038/ncomms8141.
Carvalho, I.S., Novas, F.E., Agnolín, F.L., Isasi, M.P., Freitas, F.I., Andrade, J.A., 2015b. A new genus and species of enantiornithine bird from the Early cretaceous of Brazil. Brazilian Journal of Geology 45, 161–171. https://doi.org/10.1590/2317488920150002000l.
Carvalho, I.S., Agnolin, F., Aranciaga Rolando, M.A., Novas, F.E., Xavier-Neto, J., Freitas, F.I., Andrade, J.A.F.G., 2019. A new genus of pipimorph frog (Anura) from the Early cretaceous Crato Formation (Aptian) and the evolution of South American tongueless frogs. Journal of South American Earth Sciences 92, 222–233. https://doi.org/10.1016/J.JSAMES.2019.03.005.
Carvalho, I.S., Leonardi, G., Rios-Netto, A.M., Borghi, L., Freitas, A.P., Andrade, J.A., Freitas, F.I., 2021. Dinosaur trampling from the Aptian of Araripe Basin, NE Brazil, as tools for paleoenvironmental interpretation. Cretaceous Research 117, 104626. https://doi.org/10.1016/j.cretres.2020.104626.
Catto, B., Jahnert, R.J., Warren, L.V., Varejao, F.G., Assine, M.L., 2016. The microbial nature of laminated limestones: Lessons from the Upper Aptian, Araripe Basin, Brazil. Sedimentary Geology 341, 304–315. https://doi.org/10.1016/j.sedgeo.2016.05.007.
Cincotta, A., Nicolaï, M., Campos, H.B.N., McNamara, M., et al., 2022. Pterosaur melanosomes support signalling functions for early feathers. Nature 1–5. https://doi.org/10.1038/s41586-022-04622-3.
Cumming, J.M., Wood, D.M., 2017. Adult morphology and terminology. In: KirkSpriggs, A.H., J Sinclair, B. (Eds.), Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families. Suricata 4. South African National Biodiversity Institute, Pretoria, pp. 89–133.
Dias, J.J., Carvalho, I.S., 2020. Remarkable fossil crickets preservation from Crato Formation (Aptian, Araripe Basin), a Lagerstätten from Brazil. Journal of South American Earth Sciences 98, 102443. https://doi.org/10.1016/J.JSAMES.2019.102443.
Dias, J.J., Carvalho, I.S., 2022. The role of microbial mats in the exquisite preservation of Aptian insect fossils from the Crato Lagerstätte, Brazil. Cretaceous Research 130, 105068. https://doi.org/10.1016/J.CRETRES.2021.105068.
Dobrotworsky, N.V., 1968. The Tipulidae (Diptera) of Australia. I. A review of the genera of the subfamily Tipulinae. Australian Journal of Zoology 16, 459–494. https://doi.org/10.1071/ZO9680459.
Geldenhuys, C.J., 1997. Composition and biogeography of forest patches on the inland mountains of the southern Cape. Bothalia 27 (1), 57–74. https://doi.org/10.4102/abc.v27i1.660.
Gelhaus, J.K., 2009. Tipulidae (Crane Flies, Tipulidos). In: Brown, B.V., Borkent, A., Cumming, J.M., Wood, D.M., Woodley, N.E., Zumbado, M. (Eds.), Manual of Central American Diptera, Vol. 1. NRC Research Press, pp. 193–236.
Gelhaus, J.K., Young, C.W., 1995. Pupae of the crane fly genus Leptotarsus (Diptera: Tipulidae) in the New World, with discussion of the monophyly of the genus. Annals of Carnegie Museum 64, 135–145. https://doi.org/10.5962/p.226635.
Grimaldi, D., Engel, M.S. (Eds.), 2005. Evolution of the Insects. Cambridge University Press, Cambrigde.
Guérin-Méneville, F.E., 1831. Insectes, plates 20-21. In: Duperrey, L.I. (Ed.), Voyageautour du monde, execute par ordre du Roi, sur la corvette de samajeste La Coquille etc. Histoire naturelle, zoologie. Atlas, Paris plates, pp. 1–21.
Heimhofer, U., Hochuli, P.A., 2010. Early Cretaceous angiosperm pollen from a low-latitude succession (Araripe Basin, NE Brazil). Review of Palaeobotany and Palynology 161 (3–4), 105–126. https://doi.org/10.1016/j.revpalbo.2010.03.010.
Iniesto, M., Gutiérrez-Silva, P., Dias, J.J., Carvalho, I.S., Buscalioni, A.D., López-Archilla, A.I., 2021. Soft tissue histology of insect larvae decayed in laboratory experiments using microbial mats: Taphonomic comparison with cretaceous fossil insects from the exceptionally preserved biota of Araripe, Brazil. Palaeogeography, Palaeoclimatology, Palaeoecology 564, 110156.
Jarzembowski, E.A., 1991. New insects from the Weald Clay of the Weald. Proceedings of the Geologists' Association 102 (2), 93–108. https://doi.org/10.1016/S0016-7878(08)80069-7.
Jong, H. de, 2017. Limoniidae and Tipulidae (crane flies). In: Kirk-Spriggs, A.H., Sinclair, B.J. (Eds.), Manual of Afrotropical Diptera, vol. 2. South African National Biodiversity Institute, Pretoria, pp. 427–477. Suricata 5.
Kania-Kłosok, I., Nel, A., Szwedo, J., Jordan-Stasiło, W., Krzemiński, W., 2021. Phylogeny and biogeography of the enigmatic ghost lineage Cylindrotomidae (Diptera, Nematocera). Scientific Reports 11 (1), 1–13. https://doi.org/10.1038/s41598-021-91719-w.
Kopeć, K., 2017. The genera Architipula Handlirsch, 1906 and Grimmenia Krzemiński and Zessin, 1990 (Diptera: Limoniidae) from the Lower Jurassic of England. Palaeontologia Electronica 20 (1.15 A), 1–7.
Kopeć, K., Ansorge, J., Soszyńska-Maj, A., Krzemiński, W., 2018. revision of the genus Mesotipula Handlirsch, 1920 (Diptera, limoniidae, Architipulinae) from the lower Jurassic of northeast germany. Historical Biology 32 (4), 500–507. https://doi.org/10.1080/08912963.2018.1503257.
Kopeć, K., Soszyńska-Maj, A., Kania-Kłosok, I., Coram, R.A., Krzemiński, W., 2021. Morphology of the oldest fossil subfamily of Limoniidae (Diptera, Architipulinae) in the light of exceptionally preserved Mesozoic material. Scientific Reports 11 (1), 1–11.
Kovalev, V.G., 1990. Dvukrylye. Muscida [Flies. Muscida]. In: Rasnitsyn, A.P. (Ed.), Pozdnemezozoiskie nasekomye Vostochnogo Zabaikal'ya [Late Mesozoic insects of eastern Transbaikalia], vol. 239. Transactions of the Paleontological Institute of the USSR Academy of Sciences, pp. 123–177.
Krzeminski, W., 1992a. Tipula (s. lato) eva n. sp. from cretaceous (East Asia) - the oldest representative of the family Tipulidae (Diptera, Polyneura). Acta Zoologica Cracoviensia 35 (1), 43–44.
Krzeminski, W., 1992b. Triassic and Lower Jurassic stage of Diptera evolution. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 65, 39–59.
Krzeminski, W., Ansorge, J., 1995. New Upper Jurassic Diptera (Limoniidae, Eoptychopteridae) from the Solnhofen Lithographic Limestone (Bavaria, Germany). Stuttgarter Beiträge zur Naturkunde - Serie B 221, 1–7.
Krzeminski, W., Krzeminska, E., 2003. Triassic Diptera: descriptions, revisions and phylogenetic relations. Acta Zoologica Cracoviensia 46 (Suppl. l), 153–184.
Krzeminski, W., Krzeminska, E., Papier, F., 1994. *Grauvogelia arzvilleriana* sp. n., the oldest Diptera species (Lower/Middle Triassic of France). Acta Zoologica Cracoviensia 37, 95–99.
Krzeminski, W., Evenhuis, N.L., Papp, L., Darvas, B., 2000. Review of Diptera palaeontological records. In: Contributions to a Manual of Palaearctic Diptera, vol. 1, pp. 535–564.
Krzeminski, W., Kopec, K., Kania, I., 2017. New and little known species from the genus Leptotarsus Guerin-Meneville, 1831 (Diptera: Tipulidae) from the Lower cretaceous of Northern Brazil. Cretaceous Research 78, 103–108. https://doi.org/10.1016/j.cretres.2017.05.032.
Krzemiński, W., Blagoderov, V., Dany, A.Z.A.R., Lukashevich, E., Szadziewski, R., Wedmann, S., Nel, A., Collomb, F.-M., Waller, A., Nicholson, D.B., 2019. True flies (Insecta: Diptera) from the late Eocene insect limestone (Bembridge Marls) of the Isle of Wight, England, UK. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 110 (3–4), 495–554.
Krzemiński, W., Kania-Kłosok, I., Krzemińska, E., Ševčík, J., Soszyńska-Maj, A., 2021. Fossils shed a new light on the diversity and disparity of the Family Limoniidae (Diptera, Nematocera). Insects 12 (3), 206.
Kang, Z., Zhang, X., Ding, S., Tang, C., Wang, Y., de Jong, H., Cameron, S.L., Wang, M., Yang, D., 2017. Transcriptomes of three species of Tipuloidea (Diptera, Tipulomorpha) and implications for phylogeny of Tipulomorpha. PLoS One 12 (3), e0173207.
Lukashevich, E.D., 2009. Limoniidae (Diptera) in the Upper Jurassic of Shar Teg, Mongolia. Zoosymposia 3 (1), 131–154. https://doi.org/10.11646/zoosymposia.3.1.12.
Lukashevich, E.D., Ribeiro, G.C., 2019. Mesozoic fossils and the phylogeny of Tipulomorpha (Insecta: Diptera). Journal of Systematic Palaeontology 17 (8), 635–652. https://doi.org/10.1080/14772019.2018.1448899.
Maldanis, L., Carvalho, M., Almeida, M.R., Freitas, F.I., Andrade, J.A.F.G., Nunes, R.S., Rochitte, C.E., Poppi, R.J., Freitas, R.O., Rodrigues, F., Siljeström, S., Lima, F.A., Galante, D., Carvalho, I.S., Perez, C.A., Carvalho, M.R., Bettini, J., Fernandez, V., Xavier-Neto, J., 2016. Heart fossilization is possible and informs the evolution of cardiac outflow tract in vertebrates. Elife 5, e14698. https://doi.org/10.7554/eLife.14698.
Martill, D.M., 2007. The age of the cretaceous Santana Formation fossil Konservat Lagerstätte of north-east Brazil: a historical review and an appraisal of the biochronostratigraphic utility of its palaeobiota. Cretaceous Research 28, 895–920. https://doi.org/10.1016/j.cretres.2007.01.002.
Men, Q., Hu, Z., 2021. Leptotarsus (Longurio) burmica sp. nov.–The first species of Tipulidae (Diptera) from the mid-cretaceous Burmese amber. Cretaceous Research 121, 104723. https://doi.org/10.1016/j.cretres.2020.104723.
Mendes, M., Bezerra, F.I., Adami, K., 2020. Ecosystem structure and trophic network in the Late Early Cretaceous Crato Biome. Brazilian Paleofloras: From Paleozoic to Holocene. Springer, Cham, pp. 1–19.
Oosterbroek, P., 2022. Catalogue of the Craneflies of the World (Insecta, Diptera, Nematocera, Tipuloidea) [WWW document]. Available from: https://ccw.naturalis.nl/index.php/. (Accessed 10 May 2022).
Petersen, M.J., Bertone, M.A., Wiegmann, B.M., Courtney, G.W., 2010. Phylogenetic synthesis of morphological and molecular data reveals new insights into the higher-level classification of Tipuloidea (Diptera). Systematic Entomology 35, 526–545.
Ponomarenko, A.G., Aristov, D.S., Bashkuev, A.S., Gubin, Yu M., Khramov, A.V., Lukashevich, E.D., Popov, Yu A., Pritykina, L.N., Sinitsa, S.M., Sinitshenkova, N.D., Sukatsheva, I.D., Vassilenko, D.V., Yan, E.V., 2014. Upper Jurassic Lagerstatte Shar Teg, southwestern Mongolia. Paleontological Journal 48, 1573–1682. https://doi.org/10.1134/S0031030114140160.
Rasnitsyn, A.P., Quicke, D.L.J. (Eds.), 2002. History of Insects. Kluwer, Dordrecht. https://doi.org/10.1007/0-306-47577-4.
Ribeiro, G.C., 2008. Phylogeny of the Limnophilinae (Limoniidae) and early evolution of the Tipulomorpha (Diptera). Invertebrate Systematics 22, 627–694.

Ribeiro, G.C., Lukashevich, E.D., 2014. New Leptotarsus from the Early Cretaceous of Brazil and Spain: the oldest members of the family Tipulidae (Diptera). Zootaxa 3753 (4), 347–363. https://doi.org/10.11646/zootaxa.3753.4.4.

Ribeiro, G.C., Santos, D., Nicolau, R.C.R., 2015. A new species of Leptotarsus (Diptera: Tipulidae) from the Lower Cretaceous Crato Formation of Brazil. Cretaceous Research 56, 244–249. https://doi.org/10.1016/j.cretres.2015.05.005.

Ribeiro, G.C., Reis Santos, R. dos, Santos, D., 2021a. Four new species of the genus Leptotarsus Guerin-Meneville, 1831 (Insecta: Diptera: Tipulidae) from the Lower cretaceous Crato Formation of Brazil. Cretaceous Research 123, 1–11. https://doi.org/10.1016/j.cretres.2021.104776.

Ribeiro, A.C., Ribeiro, G.C., Varejão, F.G., Battirola, L.D., Pessoa, E.M., Simões, M.G., Warren, L.V., Riccomini, C., Poyato-Ariza, F.J., 2021b. Towards an actualistic view of the Crato Konservat-Lagerstätte paleoenvironment: A new hypothesis as an Early Cretaceous (Aptian) equatorial and semi-arid wetland. Earth-Science Reviews 216, 103573. https://doi.org/10.1016/j.earscirev.2021.103573.

Santos, Â.C.S., Guerra-Sommer, M., Degani-Schmidt, I., Siegloch, A.M., Carvalho, I.S., Mendonça Filho, J.G., Mendonça, J.O., 2020. Fungus–plant interactions in Aptian Tropical Equatorial Hot arid belt: White rot in araucarian wood from the Crato fossil Lagerstätte (Araripe Basin, Brazil). Cretaceous Research 114, 104525. https://doi.org/10.1016/J.CRETRES.2020.104525.

Santos, Â.C.S., Siegloch, A.M., Guerra-Sommer, M., Degani-Schmidt, I., Carvalho, I., 2021. Agathoxylon santanensis sp. nov. from the Aptian Crato fossil Lagerstätte, Santana Formation, Araripe Basin, Brazil. Journal of South American Earth Sciences 112, 103633. https://doi.org/10.1016/J.JSAMES.2021.103633.

Shih, C., Dong, F., Kania, I., Liu, L., Krzeminski, W., Ren, D., 2015. A new species of Tipulidae (Diptera) from the Lower Cretaceous Yixian formation of Liaoning, China. Evolutionary implications. Cretaceous Research 54, 98–105. https://doi.org/10.1016/j.cretres.2014.12.009.

Varejão, F.G., Warren, L.V., Simões, M.G., Fürsich, F.T., Matos, S.A., Assine, M.L., 2019. Exceptional preservation of soft tissues by microbial entombment: insights into the taphonomy of the Crato Konservat-Lagerstätte. PALAIOS 34, 331–348. https://doi.org/10.2110/PALO.2019.041.

Warren, L.V., Varejão, F.G., Quaglio, F., Simões, M.G., Fürsich, F.T., Poiré, D.G., Catto, B., Assine, M.L., 2017. Stromatolites from the Aptian Crato Formation, a hypersaline lake system in the Araripe Basin, northeastern Brazil. Facies 631 (63), 1–19. https://doi.org/10.1007/S10347-016-0484-6, 2016.

Wood, H.G., 1952. The crane-flies of the South-West Cape (Diptera, Tipuloidea). Annals of the South African Museum 39, 1–327.

Young, C.W., Gelhaus, J.K., 1992. Leptotarsus (Longurio) byersi, a new flightless crane fly from Ecuador (Diptera: Tipulidae). Acta Zoologica Cracoviensia 35, 97–105.

Zhang, X., Kang, Z., Mao, M., Li, X., Cameron, S.L., de Jong, H., Wang, M., Yang, D., 2016. Comparative Mt genomics of the Tipuloidea (Diptera: Nematocera: Tipulomorpha) and its implications for the phylogeny of the Tipulomorpha. PLoS One 11 (6), e0158167.