

The oldest Gondwanan fossil of Leiinae (Diptera, Mycetophilidae): Phylogenetic and evolutionary implications

Dalton de Souza Amorim^a , Sarah Siqueira Oliveira^b ,
Daniel Dias Dornelas do Carmo^a  and Guilherme Cunha Ribeiro^{c*} 

^aDepartamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Av. Bandeirantes 3900, 14040-901, Ribeirão Preto, SP, Brazil; ^bDepartamento de Ecologia, Universidade Federal de Goiás, Campus II, Instituto de Ciências Biológicas, prédio ICBI, sala 124. CEP 74001-970, Goiânia, Goiás, Brazil; ^cCentro de Ciências Naturais e Humanas, Universidade Federal do ABC, Santo André, São Paulo, Brazil

Accepted 16 October 2022

Abstract

A fossil Mycetophilidae from the Aptian Crato Formation—*Cretomanota gondwanica* gen. nov., sp. nov.—is described, which is the first mycetophilid from the Crato Formation and corresponds to the oldest known fossil leiine and only the second Gondwanan fossil mycetophilid described so far. *Cretomanota gondwanica* and both species of *Alavamanota* Blagoderov and Arillo were added as terminals to the data matrix of a general phylogenetic analysis of the Mycetophilidae, and both fit into the Leiinae. *Alavamanota* is monophyletic, sister to the clade composed by *Cretomanota* and the extant genus *Manota* Williston. The biology of the extant members of this fungivorous family corroborates the reconstruction of the Crato palaeoenvironment as including woodlands with humid habitats and microhabitats. The presence of a Cretaceous member of the tribe Manotini at low latitudes in South America reinforces the hypothesis that the clade with all manotines except *Leiella* Edwards corresponds to a Lower Cretaceous offshoot from a group in southern Gondwana expanding its distribution to more northern areas into the Gondwana and into Laurasia.

© 2022 Willi Hennig Society.

Introduction

Diptera has an extensive fossil record in the Mesozoic, from the late Triassic to the late Cretaceous (Kovalev, 1990; Krzeminski, 1992a, b; Krzeminski and Ansoerge, 1995; Krzeminski and Evenhuis, 2000; Rasnitsyn and Quicke, 2002; Krzeminski and Krzeminska, 2003; Grimaldi and Engel, 2005; Blagoderov et al., 2007; Lukashevich, 2008, 2009; Ponomarenko et al., 2014; Ribeiro and Lukashevich, 2014; Kopeć, 2017; Lukashevich and Ribeiro, 2019; Kopeć et al., 2020, 2021; Krzeminski et al., 2021). Despite being the dominant group of insects in many Mesozoic deposits (Kalugina, 1980; Kalugina and Kovalev, 1985; Jell and Duncan, 1986; Han et al., 2019), dipterans are

poorly represented and rare in the Lower Cretaceous beds of the fossil-rich Crato Formation (an important Gondwanan Konservat-Lagerstätten; Martill et al., 2007; Moura-Júnior et al., 2018)—accounting for merely 4% of the described species diversity of the palaeontomofauna (Ribeiro et al., 2021). Recent studies have considerably increased our knowledge of the fly diversity of the Crato Formation, not only for the lower dipteran clades (Ribeiro and Lukashevich, 2014; Ribeiro et al., 2015, 2021; Lukashevich et al., 2021), but also for brachycerans (Carmo et al., 2022; Lamas et al., 2022).

The Mycetophilidae (extant representatives are shown in Figs 1a, b, and c) include over 4200 described extant species in almost 150 genera, distributed in six subfamilies—Sciophilinae, Tetragoneurinae, Leiinae, Gnoristinae, Mycomyiinae and Mycetophilinae (Oliveira and Amorim, 2021). Although many of the genera in the family are worldwide in distribution, the generic composition

*Corresponding author:
E-mail address: guilherme.ribeiro@ufabc.edu.br

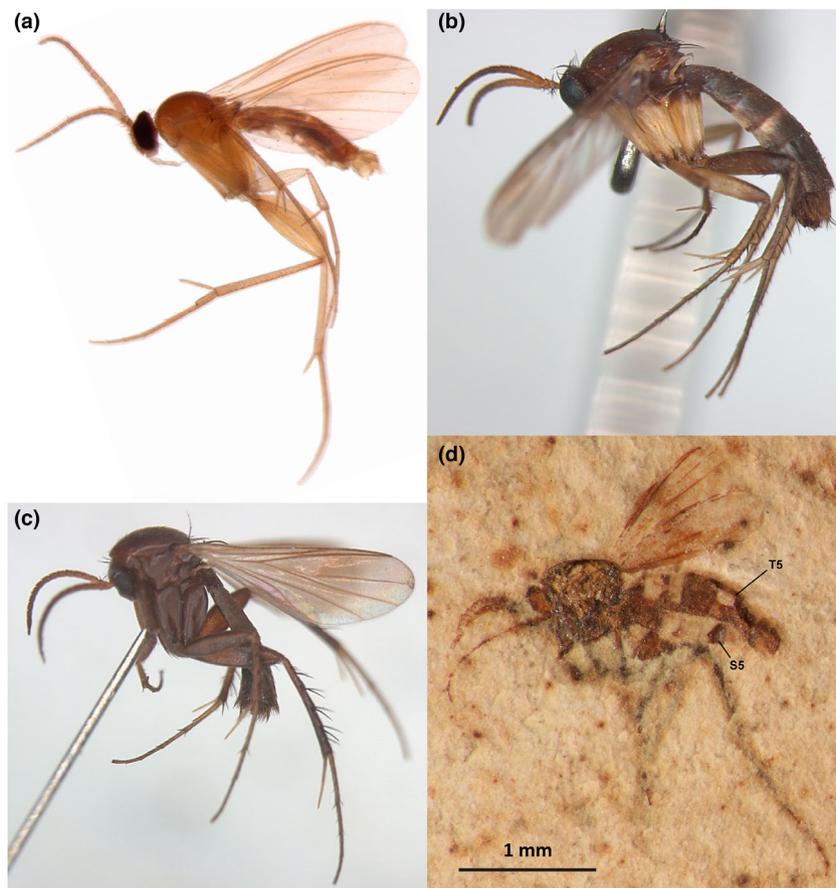


Fig. 1. a–d. Habitus of males of leinine genera. a. *Manota palpalis* Lane (male, Brazil, State of São Paulo, São Luis do Paraitinga, Parque Estadual da Serra do Mar, Núcleo Santa Virgínia, 23°19'27.1" S, 45°05'38.4" W, 22.x.2010, Malaise trap, Ponto #6, N.W. Perioto and team cols., MZUSP). b. *Allactoneura argentosquamosa* (Enderlein) (male, Madagascar, 9-23xi1957, NMSA). c. *Leiella ochreocalcar* Enderlein (male, Brazil, State of Santa Catarina, Nova Teutonia, ix.1971, Fritz Plaumann, MZUSP). d. *Cretomanota gondwanica* sp. nov. (holotype) (LP-UFC). Abbreviations: S, sternite; T, tergite.

of the family in tropical and temperate environments is remarkably different. The Mycomyiinae and Mycetophilinae are known only from Cenozoic records (Evenhuis, 2014), while the Sciophilinae, Tetragoneurinae and the Gnoristinae have Cretaceous fossils and sciophilines are known from Valanginian Baisa deposits, very early in the Cretaceous (Blagoderov, 1995, 1997, 1998). The earliest known leinines so far are from Alava (Spain) Lower Cretaceous amber and from the Mid-Cretaceous Myanmar amber (Blagoderov and Arillo, 2002; Blagoderov and Grimaldi, 2004; Oliveira and Amorim, 2021). Oliveira and Amorim (2021) carefully revisited all Cretaceous fossils of Mycetophilidae and discussed those that could fit at given nodes in the phylogeny of the Leininae. *Alavamanota* Blagoderov and Arillo was assumed to be possibly related to the extant genus *Manota* Williston.

The geology and palaeontology of the Crato Formation were revised in detail by Martill et al. (2007) and Ribeiro et al. (2021). The Crato Formation is one of the stratigraphic units of the Santana Group, Araripe

Basin, which, from the base to the top, includes 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).

According to Ribeiro et al. (2021), the palaeoenvironment of the fossil-rich interval of the formation—the ‘Crato Konservat-Lagerstätte’ (or CKL)—consisted of a semi-arid seasonal lacustrine wetland with a shallow water body. A diversified aquatic fauna and flora was present as an integral part of this biome, succeeded up-landward by neighbouring mesophytic ecotones (including woodlands) that were periodically flooded, surrounded by outer xeric habitats. A trophic structure analysis detailing the putative food web that took place within the Crato Ecosystem was provided by Mendes et al. (2020).

Among a large number of insects of different orders from the Crato Formation in collections not assessed before, we found a male mycetophilid. The species is

described here and its phylogenetic position is investigated. The implications of this new fossil for the tempo and mode of Mycetophilidae evolution are discussed, as well as its relevance as evidence for our understanding of the Crato Formation palaeoenvironment.

Material and methods

The specimen studied in this paper belongs to the collection of the Laboratório de Paleontologia, Universidade Federal do Ceará, Fortaleza, Brazil. The specimen was collected at the Três Irmãos quarry in Nova Olinda, Ceará, northeastern Brazil.

Owing to the small size of the specimen, we used a compound microscope Nikon Eclipse 80i with adapted incident lights, equipped with a Nikon DS-R1i digital camera to take the photographs. Photos were stacked using the Combine ZP software edited with Adobe Photoshop CC. Plates were prepared using Adobe Illustrator CC.

The morphological nomenclature follows Cumming and Wood (2017), particularly for homology and terminology of the wing venation, as well as Söli (1997, 2017) for structures typical of mycetophilids. Wing vein abbreviations are used as in Cumming and Wood (2017).

Cretomanota gondwanica (herein described), *Alavamanota hispanica* Blagoderov and Arillo, 2002 (Early Aptian–Middle Albian, Spain—Alonso et al., 2000) and *A. burmitina* Blagoderov and Grimaldi, 2004 (Cenomanian, Myanmar—Shi et al., 2012) were added to the data matrix used in Oliveira and Amorim (2021) as new terminal taxa. That is the most updated and comprehensive study of the internal relationships of the subfamily Leiinae. Minor modifications were made in the matrix to a few wing vein features: in characters 95 and 100 of the original datamatrix, Oliveira and Amorim (2021) considered the r-m vein absent in *Manota* Williston. Vein r-m is actually present in the wing, but it is not possible to determine its precise length (in *Manota* and *Paramanota* Tuomikoski) owing to the absence of the base of M_{1+2} . We changed the codification of characters 95 and 100 for the terminals *Manota* sp. and *Paramanota peninsulæ*: the former character from ‘—’ to ‘0’ (r-m vein straight), the latter character from ‘—’ to ‘1’ (base of vein M_{1+2} , obsolete, not reaching R_s).

The data matrix has a wide taxonomic sampling of non-leiine mycetophilids and is rooted on a species of keroplatid. It includes nine species of sciophilines, six species of gnoristines, two species of mycomyiines, four species of mycetophilines and 18 species of tetragoneurines, besides all 32 genera of Leiinae, 18 of which have more than one species. The matrix was built using WinClada (version 1.89, Nixon, 1999–2004) and characters were treated as unordered; unobserved states and inapplicable data were coded respectively as ‘?’ and ‘—’ (Appendix S1).

The phylogenetic position of the fossil species was assessed with two different optimality criteria, i.e. parsimony and Bayesian Inference. Bayesian Inference—with MRBAYES 3.2.7 (Ronquist et al., 2012)—was used to check if the analytical approach using parsimony was bringing any bias to the topology. The parsimony analysis was performed using TNT (Tree Analysis Using New Technologies—Willi Hennig Society Edition; Goloboff et al., 2008) with New Search Technology (Goloboff, 1999; Nixon, 1999; Goloboff et al., 2008). The following parameters were used: *Max. trees* 10 000; *Random seed* 0; *Random addition sequences* 200, *Sectorial search*; *Ratchet* 200 interactions; and *Tree fusing* 5 cycles (following Oliveira and Amorim, 2021). The strict consensus was done in WinClada (version 1.89). For the Bayesian inference analyses, we used the standard MK model, as proposed by Lewis (2001). For modelling character rate variation, we used a lognormal distribution with

four categories (Wagner, 2012). We ran the analysis with two simultaneous runs, with four chains each containing 13 million generations of the mcmc chain. To achieve convergence, it was necessary to run the analysis for additional 7 million generations; trees were sampled every 1000 generations and the burn-in cutoff was set at 25%. We checked convergence by the standard deviation of the sample splits and by examining ESS values and trace plots using Tracer 1.7 (Rambaut et al., 2018). The standard deviation splits were below 0.01 (0.007) and the trace plots reached stationarity.

Acronyms used in the text:

AMSA—Australian Museum, Sydney, Australia.

ANIC—Australian National Insect Collection, Canberra, Australia.

CEUA—Colección de Entomología of the University of Antioquia, Colombia.

CNC—Canadian National Collection of Arachnids, Nematodes and Insects, Ottawa, Canada.

INPA—Instituto Nacional de Pesquisas Amazônicas, Manaus, Brazil.

LP/UFC—Laboratório de Paleontologia da Universidade Federal do Ceará, Fortaleza, Brazil.

MZUSP—Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.

NMSA—KwaZulu–Natal Museum South Africa, Pietermaritzburg, South Africa.

Family Mycetophilidae Newman, 1834

Subfamily Leiinae Edwards, 1925

Tribe Manotini Edwards, 1925

Genus *Cretomanota* Amorim and Oliveira gen. nov.

Type species: *Cretomanota gondwanica* sp. nov. (by present designation).

Etymology. The generic name makes reference to the fact that the fossil represents a Cretaceous stem species connected to the extant genus *Manota* Williston.

Figs 1d, 2a, 3, 4e, 5c

Zoobank: [Urn:Lsid:zoobank.org:Act:71B6DB20-9C0D-4EFE-AD30-84702CE586BC](https://zoobank.org/Act:71B6DB20-9C0D-4EFE-AD30-84702CE586BC)

Diagnosis. C extending well beyond tip of R_5 ; first sector of R_s short, perfectly transverse, second sector running very close to R_1 and to C; r-m longitudinal, perfectly aligned with second sector of R_s and bM. M_{1+2} apparently not produced, M_1 complete, running close to R_5 , M_2 slightly convex in relation to wing anterior margin. CuA almost straight, no sinuosity on posterior half (Figs 3 and 4e).

***Cretomanota gondwanica* Amorim and Oliveira sp. nov.**

Type-material. Holotype, male, LP/UFC CRT 1381. NE Brazil, Crato Formation, Aptian, Lower Cretaceous. Housed in the Laboratório de Paleontologia, Universidade Federal do Ceará, Fortaleza, Brazil (LP/UFC).

Etymology. The specific epithet makes reference to the Gondwana, the supercontinent where the species originated. It also makes reference to the region of origin of *Manota* Williston before its worldwide radiation.

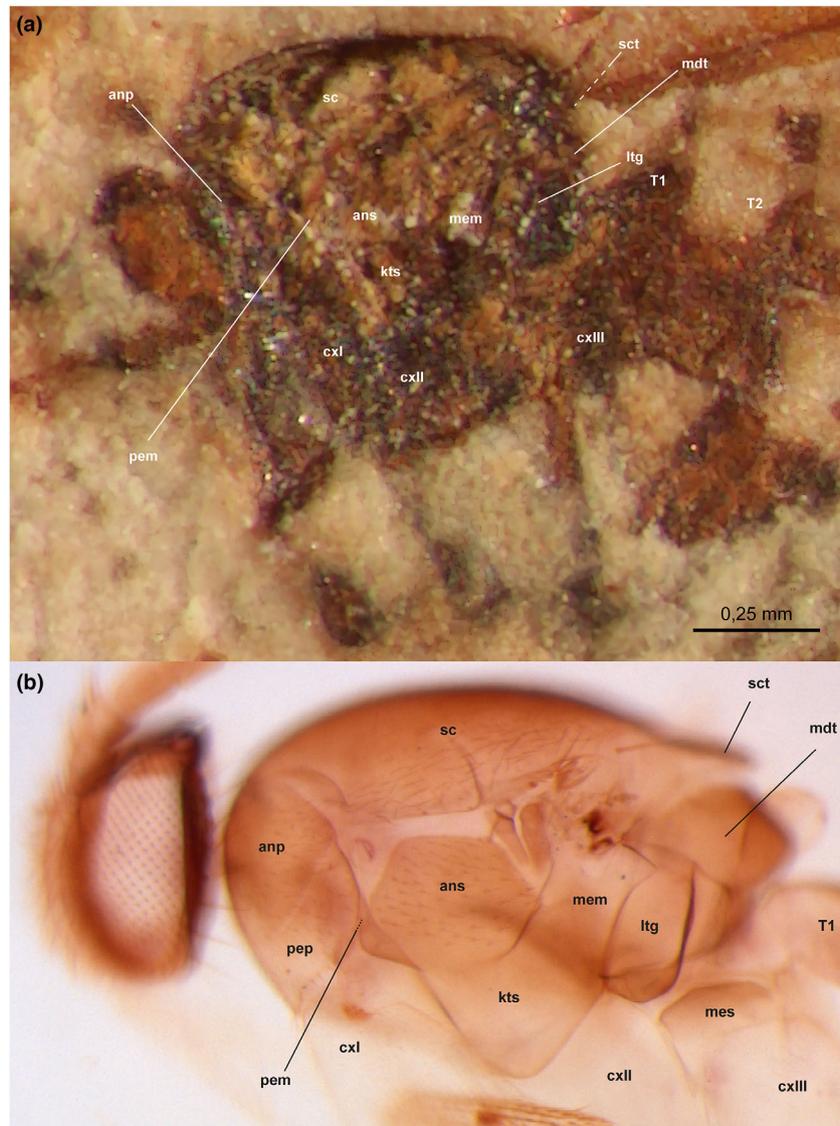


Fig. 2. a and b. Thorax pleural sclerites of leine genera. a. *Cretomanota gondwanica* sp. nov. (holotype) (LP-UFC). b. *Manota* sp. (male, BRAZIL, State of Amazonas, Barcelos, Rio Paduari, Com. Ararinha, Malaise trap, 5-8.vi.2010, INPA). Abbreviations: anp, antepronotum; ans, anepisternum; cxI, fore coxa; cxII, mid coxa; cxIII, hind coxa; kts, katepisternum; ltg, laterotergite; mem, mesepimeron; mes, metepisternum; mtg, mediotergite; pem, proepimeron; sc, scutum; sct, scutellum; T, tergite.

Figs 1d, 2a, 3, 4e, 5c.

Zoobank: [Urn:Lsid:zoobank.org:Act:E1239B99-8D9C-4598-90E0-190D4F88A3F1](https://zoobank.org/Act:E1239B99-8D9C-4598-90E0-190D4F88A3F1)

Diagnosis. As for the genus.

Description. Body length, 1.89 mm; wing length, 1.19 mm; width, 0.38 mm. **Male. Head** (Figs 1d, 2a). Oval, top of vertex slightly lower than scutum. Occiput is very slender posteriorly to the eye in lateral view. Antenna filiform, shorter than head and thorax together, flagellomeres cylindrical, slightly longer than wide. **Thorax** (Fig. 2a). Scutum dorsoventrally compressed. Pronotum ovoid, not shield-like. Mesepimeron reaching ventral end of thorax. Anepisternum is apparently separated from katepisternum by a suture,

katepisternum triangular. Laterotergite with longer axis inclined, slightly projected. Coxae elongate, apparently dark on dorsal end, lighter more distally, femora, tibiae and tarsi dark. **Wing** (Figs 3, 4e). No evidence of macrotrichia on wing membrane; C clearly extending beyond the apex of R_5 . R_1 reaching C more basally than two-thirds of wing length; R_5 reaching C more basally than the tip of M_2 , running very close to C, slightly curved posteriorly near apex; r-m strictly aligned to bR and R_5 , running parallel and close to bR; M_{1+2} and anterior end of M_1 absent, projected point of origin of medial fork slightly more basal than tip of R_1 , M_1 and M_2 sclerotized, running mostly parallel to each other along most of their length, M_1 quite

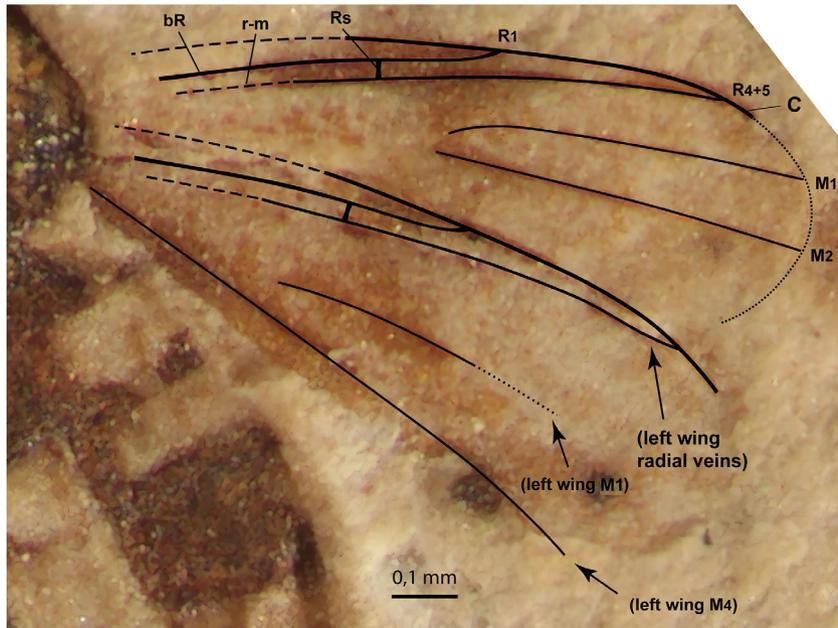


Fig. 3. Interpretation of the vein pattern of the overlapped wings of the holotype of *Cretomanota gondwanica* sp. nov.

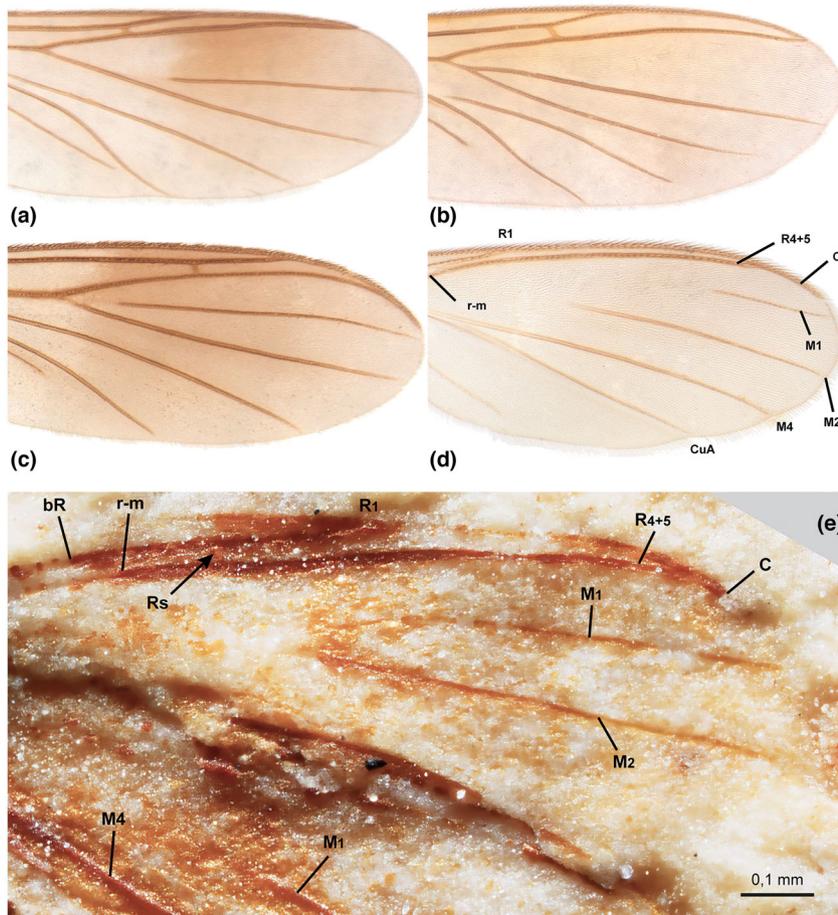


Fig. 4. a–e. Detail of venation at distal end of wing of leine genera. a. *Leiella ochreocalcar* Enderlein (same as Fig. 3c). b. *Sticholeia cheesmanae* Söli (Australia, N.T., Baroalba Ck., Springs, 19 km NE by E of Mt Cahill, 17.xi.1972, D.H. Colless, ANIC). c. *Eumanota* sp. (female, Papua-New Guinea, Oomsis lae, 25.vii.2000, AMSA). d. *Manota* sp. (same as Fig. 3f). e. *Cretomanota gondwanica* sp. nov. (holotype) (LP-UFC).

approximated to R_5 , M_2 slightly convex in relation to anterior margin (M_4 and CuA not particularly clear because of wing overlap). **Abdomen** (Fig. 1d). Abdomen tergites wider than long, tergites 1 and 4 dark, tergites 2, 3 and 5 with a wide light band along anterior two thirds, sternites 3 and 4 mostly light, sternites 4 and 5 with a lighter band on anterior half, dark on the posterior half. **Terminalia** (Fig. 5c). Apparently a large gonocoxite, terminalia rotated 180°.

Remarks. Both wings of the fossil overlap and the impression of anterior veins of the right wing overlaps the area of M_4 and CuA of the left wing. This means that we have to be careful about the interpretation of the venation of the posterior half of the wing. There is no question that the specimen described here is a mycetophilid—sciarids (and some cecids) also have a longitudinal r-m aligned with the second sector of R_s (Figs 3, 4e), but other wing, thorax and head features

in the fossil definitely do not match these groups. Within the Mycetophilidae (see, e.g., Söli, 1997, 2017; Oliveira and Amorim, 2021), the rather short R_1 and r-m aligned to the second sector of R_s is basically found in leiines (as in *Mohelia* Matile, some Cycloneurini, and some Manotini). Among the leiines, very few genera have M_{1+2} incomplete or missing. *Leiella* and *Eumanota* Edwards have M_1 detached from M_{1+2} , but M_{1+2} present. *Cretomanota* differs from *Alavamanota* because in this later genus R_4 is present, the medial fork is complete and the distal end of M_{1+2} is present. As discussed below, some but not all of the diagnostic features of *Manota* are present in *Cretomanota*. The holotype of *Cretomanota gondwanica* is in lateral view (Ribeiro et al., 2021, p. 18, Fig. 16h), with the head, thorax, wing, front leg, part of mid leg and hind leg, abdomen and terminalia preserved and visible, antennal scape and pedicel, mouthparts and ocelli not

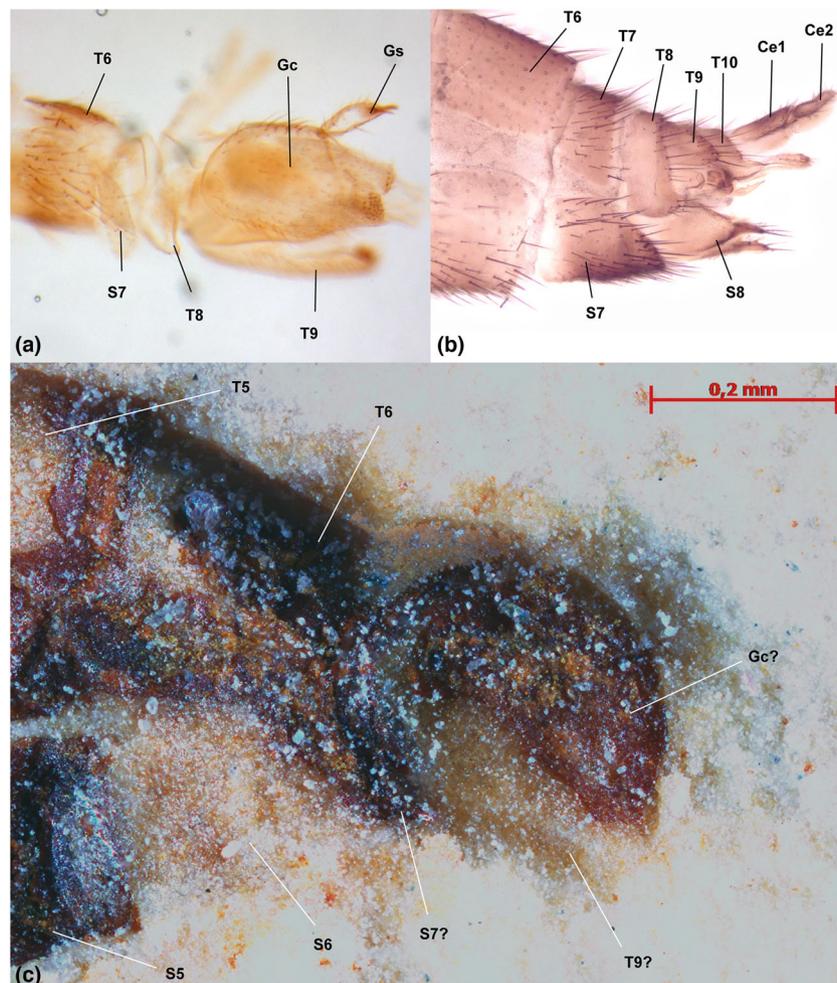


Fig. 5. a–c. Tip of abdomen of leiine genera. a. Male, *Promanota malaisei* Tuomikoski (male, Thailand, 29.vi–2.vii.2006, MZUSP). b. Female, *Eumanota wolffae* Amorim, Oliveira & Henao-Sepulveda (female, Colombia, Antioquia, Envigado, Loma del Escobero, Parcelación Nubarrones, 6°13'97" N, 75°55'54" W, Malaise trap, Bosque, 29.i–11.ii.2017, M. Wolff and c. H.-Sepúlveda cols., CEUA). c. *Cretomanota gondwanica* sp. nov. (holotype) (LP-UFC). Abbreviations: ce1, first cercomere (female); ce2, second cercomere (female); gcx, gonocoxite; gs, gonostyle; S, sternite; T, tergite.

visible. There are cases of compression fossils in which colour patterns are artefacts. The abdomen of the holotype has light areas in tergites 2, 3 and 5, and sternites 3, 4, 5 and 6, contrasting with other abdominal sclerites (Figs 1d, 5c). We assume that these lighter areas were yellowish in the original specimen and are not artefacts. The main reason is that other leiines typically have abdominal colour patterns with yellowish and brown tergites and sternites. Additional specimens should test this assumption.

Discussion

Phylogenetic position of Cretomanota gen.nov. and of Alavamanota

From the point of view of Gondwanan terranes, the lygistorrhinid *Lebanognoriste* Blagoderov and Grimaldi (Blagoderov and Grimaldi, 2004) was described from Lebanese amber and the unplaced mycetophilid *Microntos philadilphiaensis* Kaddumi (Kaddumi, 2005) was described from Jordanian amber. This makes *Cretomanota gondwanica* the second species of Mycetophilidae from Gondwana. Grimaldi (1990) refers to a macrocerine keroplatid and a couple of specimens that may correspond to mycetophilids from the Crato Formation, but they are not well preserved and could not be described. There are big hopes for what is going to be found in the Mesozoic deposits from Australia (Stilwell et al., 2020) as a means to understand the evolution of the Gondwanan insect fauna, including the fungus gnats. At this stage, the leiine species described in this paper is the only fossil of the subfamily to be formally described from Cretaceous Gondwanan deposits.

The parsimony analysis of the data matrix including *Cretomanota gondwanica* and both species of *Alavamanota* yielded seven most parsimonious trees, of which the strict consensus is shown in Fig. 6. The topology recovered by the Bayesian Inference (along with the posterior probabilities) is shown in Fig. 7.

The results of the parsimony analysis in this paper are largely identical to those obtained by Oliveira and Amorim (2021). This means that the addition of *Cretomanota* and *Alavamanota* to the data matrix of the parsimony analysis did not affect the relationships along the backbone of the Leiinae obtained by Oliveira and Amorim (2021), despite the presence of a considerable amount of missing data in the new terminal taxa.

The results of the parsimony and Bayesian inference analyses in this paper are very congruent with each other. The main differences between the results are that in the latter: (1) *Trichoterga* Tonnoir & Edwards and *Gracilileia* Matile, rogue terminals in Oliveira and

Amorim (2021), are together in a small clade in a polytomy with all leiine tribes except the Selkirkiini; (2) *Paracycloneura* Tonnoir and Edwards, another rogue genus in the original analysis, is included in the Megophthalmidiini; (3) the genera of Cycloneurini are dispersed in a large polytomy together with the tribes of the higher leiines; and (4) the genus *Leiella* is in this same polytomy, not with the remainder of Manotini.

Both analytical approaches, among other points, agree about three key aspects of the evolution of mycetophilids: the monophyly of the leiines without Tetrageurinae; the Manotini deeply nested within the Leiinae (see the morphological similarities in Figs 1–5, 8, 9); and *Cretomanota* and *Manota* as sister genera, which together are sister to *Alavamanota*. The strong affinity of the Manotini with the leiines, obtained with morphological data, conflicts with published results in which the manotine genera correspond to an early divergence in the evolution of mycetophilids (e.g. Kasprák et al., 2019). Other molecular reconstructions (e.g. Burdíkova et al., 2019; Mantić et al., 2020) also do not strictly corroborate the results of Kasprák et al. (2019) and there is a full range of morphological characters of different body parts shared by manotines and other leiines at different nodes along the phylogeny of the subfamily. This could suggest that long-branch attraction may be affecting the position of the higher manotines in molecular analyses.

Most evidence that *Alavamanota* is sister to (*Cretomanota* + *Manota*) comes from wing characters (using the character numbers of Oliveira and Amorim (2021); Fig. 10):

- long C beyond the tip of R₅ (ch. 82:2), shared with higher manotines, except *Alavamanota burmitina*;
- short R₁ (ch. 87:2), reaching C at the basal third of the wing, a synapomorphy of (*Cretomanota* + *Manota*);
- perfectly transverse first sector of Rs (ch. 91:1), shared with higher manotines;
- short R₅ (ch. 93:1), shared with manotines, except *Sticholeia*;
- R₅ following the wing curvature (ch. 94:0), shared with manotines and other leiines;
- perfectly longitudinal r-m (ch. 95:0), aligned with bM and with the second sector of R₅, a synapomorphy of (*Alavamanota* (*Cretomanota* + *Manota*)), homoplastic with *Paramanota* Williston;
- M₁₊₂ obsolete, not reaching Rs (ch. 100:1), shared by higher manotines, except with *Promanota* Williston;
- M₁ not sclerotized at proximal end (ch. 102:1), a synapomorphy of the higher manotines (except *Alavamanota burmitina*, with a secondary, complete M₁).

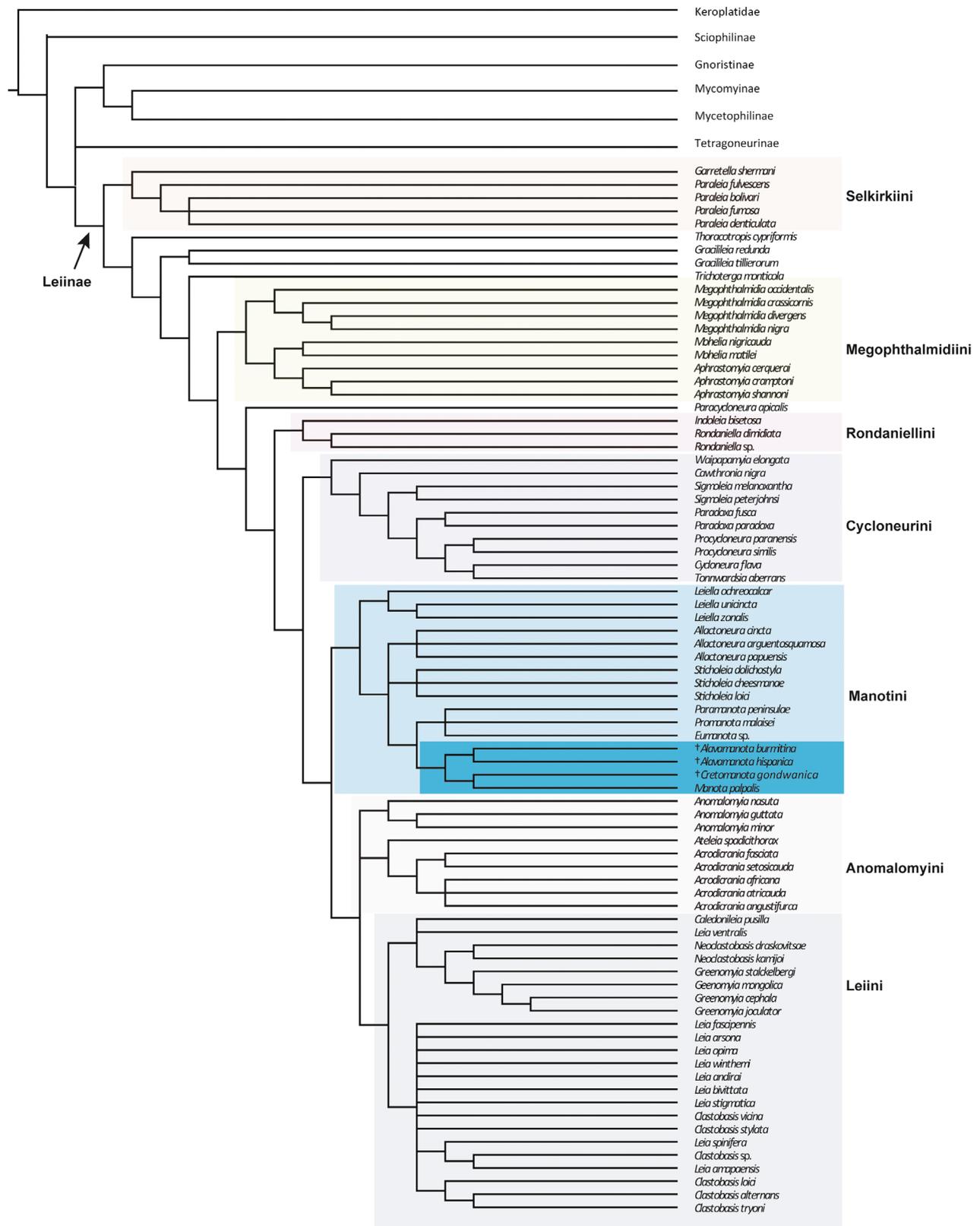


Fig. 6. Strict consensus of the parsimony analysis of the data matrix in Oliveira and Amorim (2021) with the addition of *Cretamanota gondwanica* sp. nov., *Alavamanota burmitina* Blagoderov and Grimaldi and *Alavamanota hispanica* Blagoderov and Arillo. Topology simplified, with non-leiines genera collapsed into subfamilies. Highlighted in light blue, the Manotini; in darker blue, the clade (*Alavamanota* + (*Cretamanota* + *Manota*)).

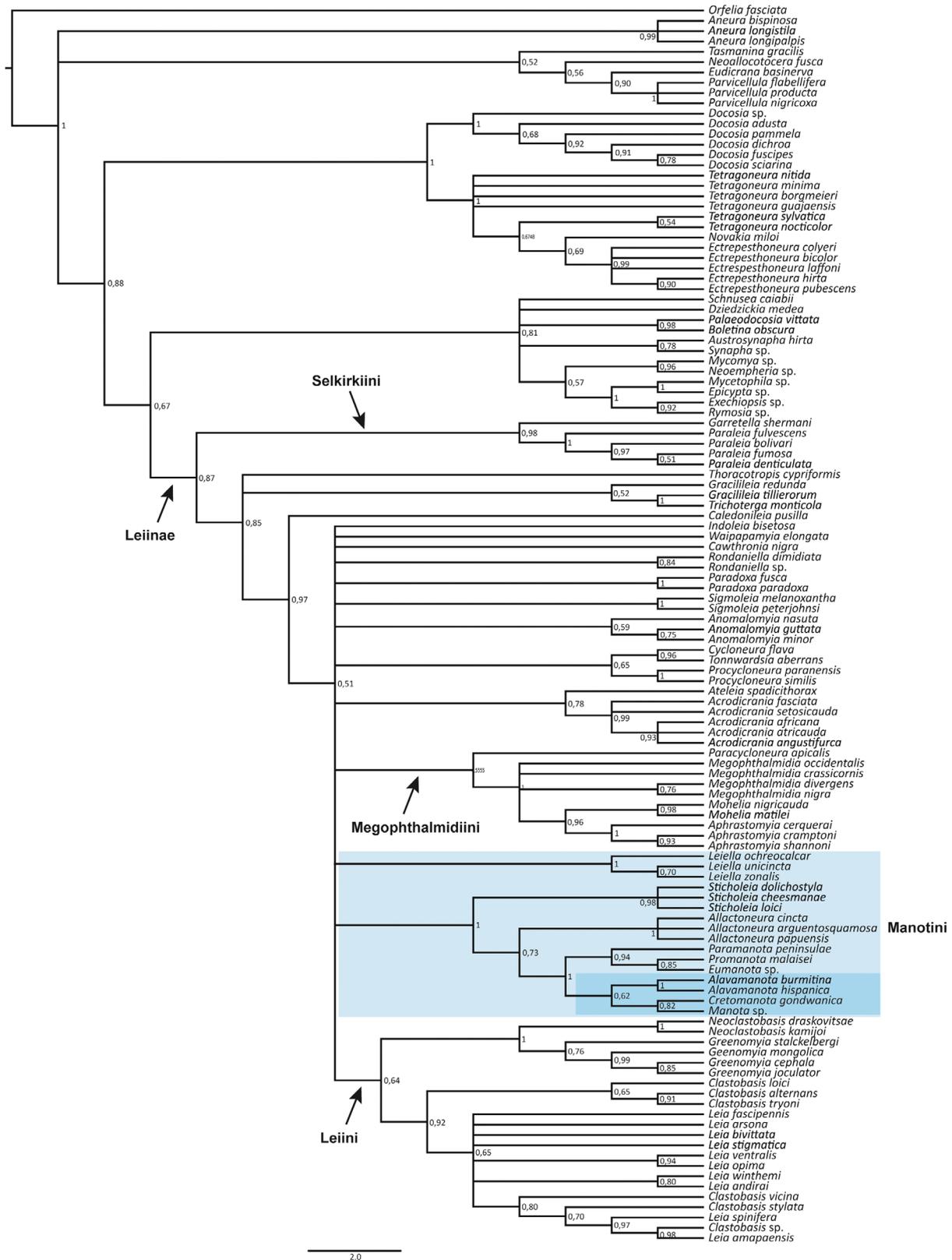


Fig. 7. Bayesian Inference of the data matrix in Oliveira and Amorim (2021) with the addition of *Cretomanota gondwanica* sp. nov., *Alavamanota burmitina* Bladoderov and Grimaldi and *Alavamanota hispanica* Blagoderov and Arillo. Highlighted in light blue, the Manotini; in darker blue, the clade (*Alavamanota* + (*Cretomanota* + *Manota*)). Numbers within clades are posterior probabilities.

There are also some head and thorax features that, as the wing vein characters, are consistent with the hypothesis of (*Alavamanota* + (*Cretomanota* + *Manota*)) nested within the leiines. In the thorax (Figs 8 and 2), the compressed scutum (ch. 36:2) and the pronotum, wide medially with tapered ends (ch. 42:2), are shared with the higher manotine genera, and in the head (Fig. 2) the depressed occiput (ch. 6:1) is an apomorphy shared with higher manotines and *Allactoneura* de Meijere. Additional specimens of *Cretomanota* with information on other body parts may bring corroboration to the hypothesis of a sister-group relationship with *Manota*.

Two diagnostic features of *Manota* as a genus— M_1 displaced to a more anterior position at the wing and M_2 slightly convex in relation to the wing anterior margin, parallel to M_1 (see fig. 5f, not as characters in Oliveira and Amorim, 2021)—are shared with *Cretomanota* and *Alavamanota*. One of the species of *Alavamanota*, *A. burmitina* has a complete medial fork, with the distal part of M_{1+2} sclerotized and a complete M_1 (see Blagoderov and Grimaldi, 2004, p. 23, fig. 25). It is noteworthy that the wing venation of *Cretomanota* and *Alavamanota* shows character states that correspond to intermediate conditions between leiines

with a more plesiomorphic wing pattern and the derived condition of the wing seen in *Manota*. This points to *Cretomanota* and *Alavamanota* as typically Cretaceous stem clades of the extant genus *Manota*. The small size of the holotype of *Cretomanota gondwanica* (Fig. 1d) in a certain way agrees with the condition in *Manota*, one of the smallest extant known leiines.

Cretomanota, *Alavamanota* and the evolution of the leiine mycetophilids

The present knowledge on Mesozoic insect fossils has a strong bias towards northern hemisphere deposits. *Cretomanota gondwanica* is the first mycetophilid formally described from the Crato Formation, the oldest known fossil leiine and the second Gondwanan fossil mycetophilid described so far. The study of the evolution of the Leiinae mycetophilids in Oliveira and Amorim (2021) shows that the group originally had a wide distribution in southern Gondwana—the recent fauna including nine genera endemic to New Zealand and several other lineages endemic to southeast Australia and in southern South America.

Seven Leiinae clades, however, in the diversification of the subfamily, expanded their distribution from austral temperate areas to the northern hemisphere or to tropical areas in the southern hemisphere (Oliveira and Amorim, 2021). One of these clades corresponds to the Manotini except *Leiella* Enderlein. This group includes: (1) *Sticholeia* Söli, exclusive of the Vanuatu archipelago; (2) *Allactoneura* de Meijere, with an Afro-Australian-Oriental distribution in the extant fauna and a Cenozoic fossil from France; (3) *Paramanota* and *Promanota* Tuomikoski, basically Oriental but also including *Paramanota grandaeva* Hippa, from Eocene Baltic amber; (4) *Eumanota*, mostly Oriental but with one species from Colombia; and (5) *Manota*, worldwide in distribution (with Cenozoic fossils from different deposits). The presence of the stem *Manota* Cretaceous clades *Cretomanota* and *Alavamanota* at lower latitudes in Gondwanan terranes and in Laurasian terranes respectively corroborates this clade as being already ‘out of southern Gondwana’ in the early Cretaceous (Fig. 11). This was assumed by Jaschhof et al. (2011, p. 63), who considered that the ‘Manotinae’ would have a southern origin and that the Holarctic species of *Manota* would be a northern offshoot of a group with Gondwanan origin in the Cretaceous, reaching a worldwide extant distribution. One of the most immediate implications of the discovery of *Cretomanota* is to push the diversification of the higher manotines deeper into the lower Cretaceous (Fig. 11).

A number of cases of extant intercontinental transtropical disjunctions in plants and animals earlier considered to be potentially Gondwanan in origin are



Fig. 8. a–b. Detail of head and thorax of leiine genera. a. *Leiella ochreocalcar* Enderlein (same specimen of Fig. 1c). b. *Allactoneura argentosquamosa* (Enderlein) (same specimen of Fig. 1b).

actually too young to correspond to Jurassic or Cretaceous clades. In the case of the Manotini genus *Eumanota* Edwards, for example, present in northern South America and in the Oriental region, the disjunction can be better explained as a case of pseudocongruence, with early Cenozoic vicariance in tropical Laurasian terranes, later expanding southward, with late Cenozoic extinction in North America and Europe (Amorim et al., 2018). The cases of *Cretomanota* and *Alavamanota*, however, are different. The Crato Formation record of *Cretomanota* should correspond to a truly Gondwanan element in South America, disjunct from the Laurasian stem corresponding to *Alavamanota*.

A species with a fungivorous larva in the Crato palaeoenvironment

Most extant sciaroids, including the Mycetophilidae, are strongly associated with humid environments. There are some cases of mycetophilids known from

open environments, but most extant members of the family are known from woodlands. Mycetophilid larvae in most cases are associated with fungi, found under brackets, in old tree trunks and in some cases with decaying plants (Søli, 2017). The larvae of the Mycetophilinae attack mostly soft fungi, but the remaining subfamilies are more diversified, with larvae associated to fungi or bark, with some few cases of specialized biologies (Søli, 2017). There is information on the biology of only a couple of species of *Manota*, despite over 300 species now having been described worldwide (Kurina and Hippa, 2021). Zaitzev (1990) described the immatures of *M. unifurcata* Lundström, with illustrations of the body and head capsule of the larva, as well as the adult morphology. One larva was reared on the surface of very moist, rotten birch wood covered with a greyish coat of an unidentified fungus. A larva has been found in rotten beech wood bearing an unidentified myxomycete (Chandler, 1978 *apud* Jakovlev and Penttinen, 2007).

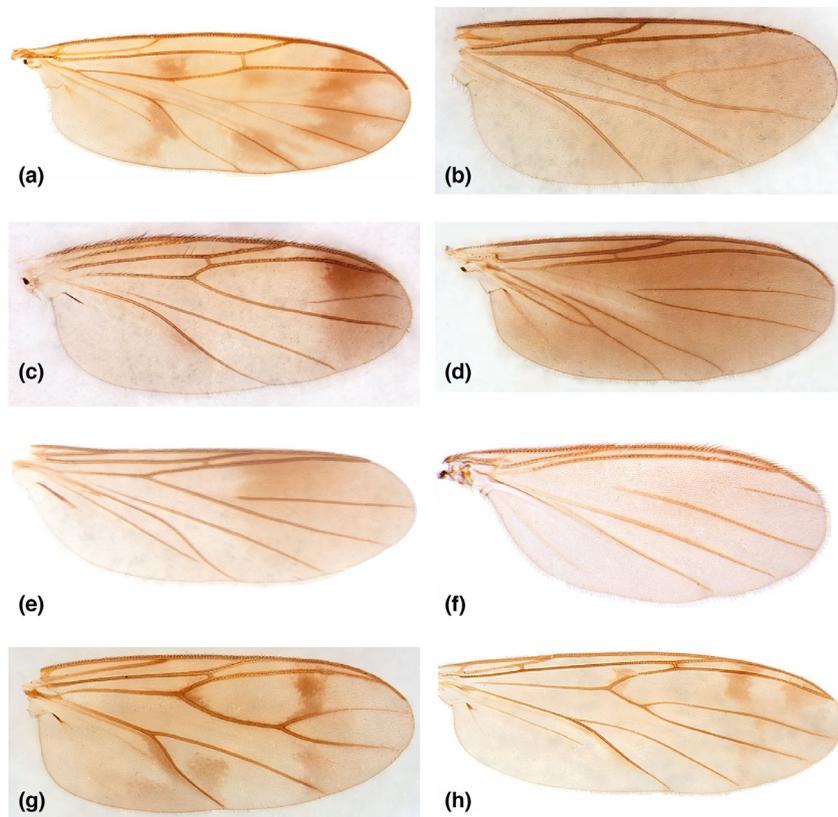


Fig. 9. a–h. General wing venation patterns of leine genera. a. *Paraleia nubilipennis* (Walker) (male, CHILE, Osorno, Argallanes, Monte Alto, Puyehue, J.P. Duret leg., MZUSP). b. *Megophthalmidia nigra* Freeman (male, CHILE, Estera la Jaula, Curico, i.1964, *Nothofagus* forest, L.E. Peña col., CNC). c. *Rondaniella dimidiata* (Meigen) (male, CANADA, NB, Kouchibouguac National Park, 5.vii.1977, J.R. Vockeroth leg., Code 5486Z, CNC). d. *Paradoxa paradoxa* Jaschhof (female, South Africa, natal, 75 km WSW Estcourt Cathedral Peaks for Stn. 1500 m, 7–31.xii.1979, S. and J. Peck, CNC). e. *Leiella ochreocalcar* Enderlein (Brazil, State of Santa Catarina, Nova Teutônia, 27°11' S, 52°23' E, ix.1971, Fritz Plaumann leg, MZUSP). f. *Manota pseudoiota* Kurina, Hippa & Amorim (Brazil, State of Santa Catarina, São Bento do Sul, Rugendas, Malaise trap, 13–16.Oct.2001, M.V. Yamada leg., MZUSP). g. *Anomalomyia guttata* (Hutton) (New Zealand, Kanaeranga Vly., Malaise trap, 23.i.1970, H.A. Oliver col, ANIC). h. *Leia winthemi* Lehmann (Norway, EIS 38 HES, Kongsvinger, Abborhogda, 10.vii–06.ix.2003, Karsten Sund leg. MZUSP).

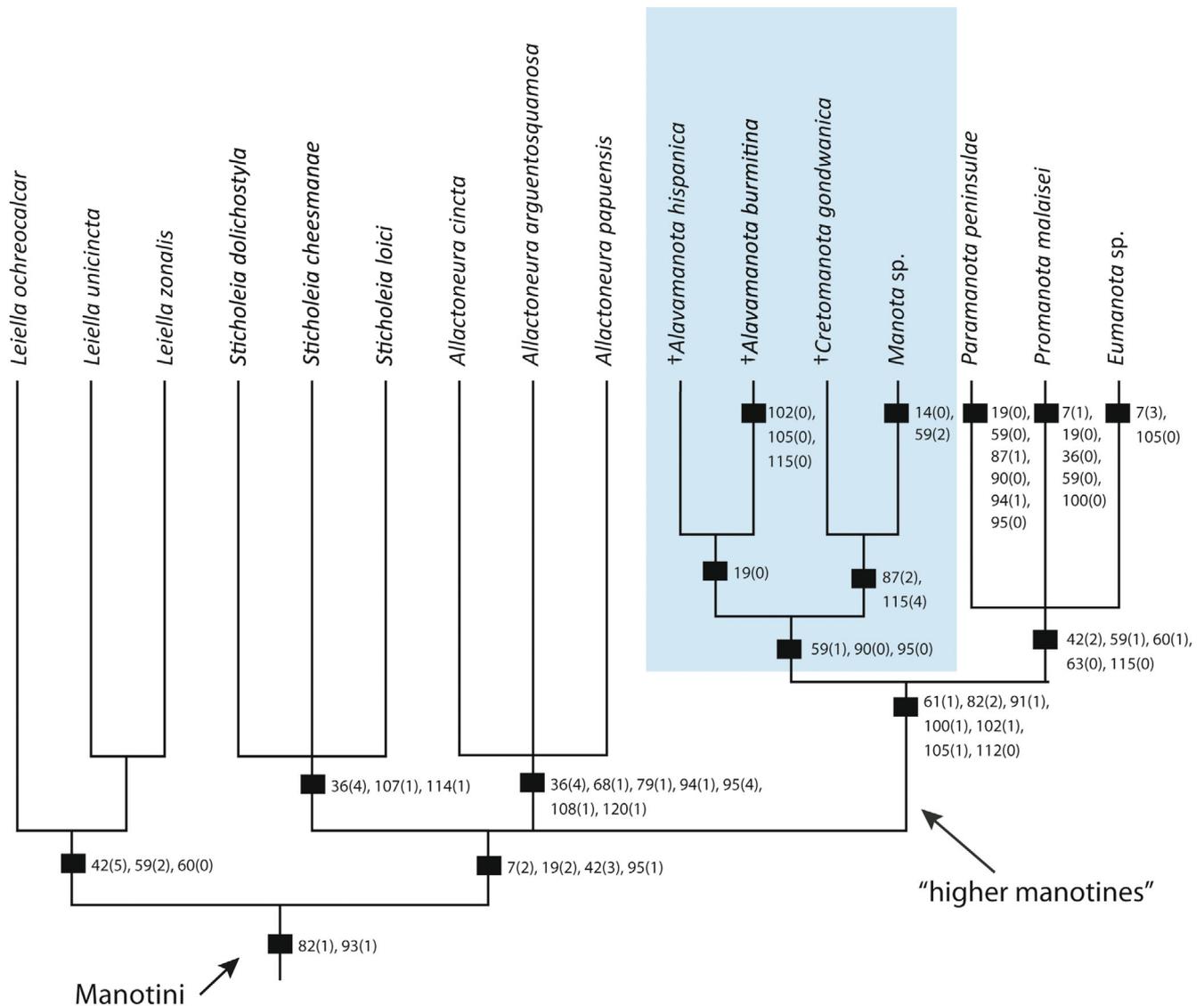


Fig. 10. Relationships between the genera of Manotini, nodes with selected characters that can be observed in *Cretomanota gondwanica* sp. nov. (modified from Oliveira and Amorim, 2021, fig. 107). Some characters were optimized with ACCTRAN, some characters with DELTRAN. List of characters from Oliveira & Amorim (2021, Appendix I).

The evidence assembled by Ribeiro et al. (2021) with respect to the palaeoenvironment of the Crato Formation indicates that it consisted of a huge wetland with shallow aquatic environments surrounded by helophytic and mesophytic ecotones, further surrounded by a xeric ecotone. Also, evidence from the insect fauna preserved in the fossil assemblage suggests that the mesophytic ecotone must have been in part constituted of a well-developed forest. Seasonal variation on the water level accounted for a dynamic system, with countless opportunities for moist microhabitats to develop. The presence in the Crato Formation of *Cretomanota gondwanica* is an important corroboration of Ribeiro et al.'s (2021) reconstruction. Like its recent relatives of the genus *Manota*, they

were probably feeding on fungus covering rotten wood and other decomposing plant tissues along the humid microhabitats of the Crato wetland—from which even a well preserved mushroom is known (Heads et al., 2017).

The known flora of the Crato Formation, synthesized by Kunzmann et al. (2021), includes, besides ferns, conifers and gnetophytes, an impressive diversification of angiosperms, including species of Nymphaeales, Magnoliales, Laurales, Piperales, different monocots, Ranunculales and Proteales. Some of these groups of seed plants were present certainly as broad-leaved trees, supporting the idea of a mesophytic forest with associated fungi. The floristic composition of the Crato Formation already demonstrates a pretty early

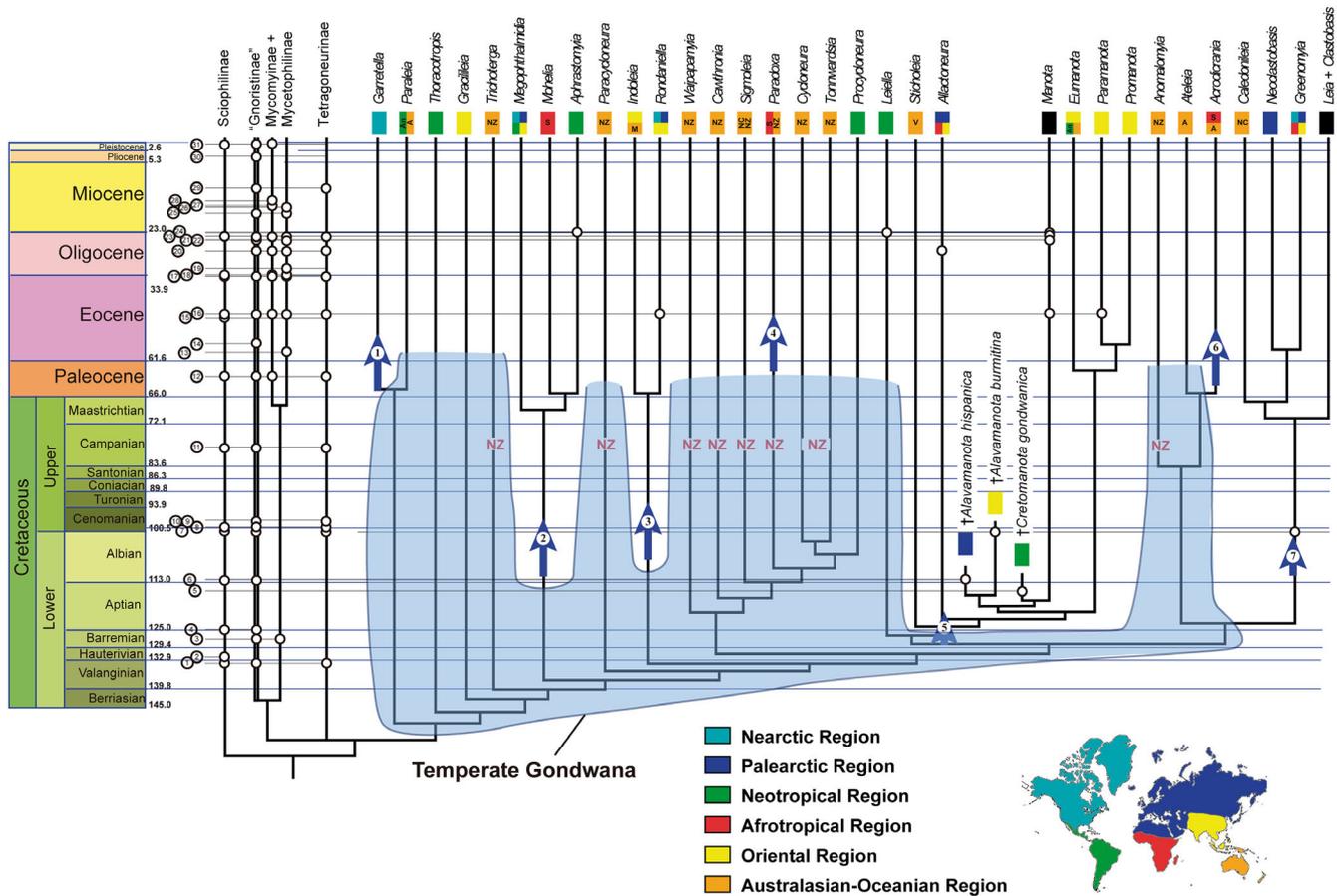


Fig. 11. Mycetophilid phylogeny (genera of all subfamilies except Leiinae collapsed into a single terminal) overlapped with information about all known mycetophilid fossils (updated from Oliveira and Amorim, 2021, fig. 107), with the addition of *Cretomanota gondwanica* sp. nov., *Alavamanota hispanica* Blagoderov and Grimaldi and *Alavamanota burmitina* Blagoderov and Arillo as terminals. Fossils of the same clade from the same deposit indicated as a single mark along the phylogeny. Geographical distribution of each Leiinae genus at the tip of terminals (A = Australia; An = Andes; M = Maluku Islands; NC = New Caledonia; NZ = New Zealand; S = South Africa; V = Vanuatu). Hypothesis of leiine nodes with temperate gondwanan distribution indicated with light blue; events of expansion of clade distribution to more northern terranes indicated with numbered dark blue arrows. Details on the deposit numbers (at left) in the Appendix S2. *Microntos philadelphiaensis* Kaddumi, from Jordan amber (Kaddumi, 2005) is unplaced at the subfamily level and cannot be included in this illustration.

‘crucial developmental stage in the evolution of flowering plants’ (Kunzmann et al., 2021), along the turnover from gymnosperm-dominated forests to modern, angiosperm-dominated forests. Indeed, forests, their associated terrestrial fungi and the corresponding Mesozoic fungivorous fauna of sciaroids evolved together (Oliveira and Amorim, 2021), but the details of the turnover of these three elements together along the Jurassic/Cretaceous are still poorly understood.

Conclusion

There is a growing amount of information on the Crato Formation palaeoentomofauna providing complementary information on the Aptian palaeoenvironment in northeastern South America—then still connected to Africa. The mycetophilid species

described here, of an extant group obviously connected to fungi and to humid environments, supports the interpretation that at least part of the insect fossils of the Crato Formation belong to an autochthonous fauna connected to a mesophytic ecotone. The fact that there is a formal prior phylogenetic analysis of the Leiinae allowed the described species, *Cretomanota gondwanica* and both Cretaceous species of *Alavamanota*, to be precisely placed into the system of the leiines as stem members of the megadiverse extant genus *Manota*. This fossil present at low latitudes in Gondwanan terranes corroborates the interpretation of Oliveira and Amorim (2021) that this clade of manotines already had expanded in the Aptian northwards from the southern Gondwanan original area of distribution of the leiines. It also pushes the origin of the Manotini still further back into the first half of the Lower Cretaceous.

Acknowledgements

We are grateful to Dr Márcio Mendes, Universidade Federal do Ceará, Fortaleza, Brazil, for the loan of the studied specimen. We thank the Brazilian National Mining Agency (ANM) for the fossil collecting permits. DSA had financial support from CNPq (grant #440549/2015-9) and from FAPESP (#2016/50369-9 and 2021/08713-2). SSO had support from CNPq (#308298/2021-7), DDDC from CNPq (#151205/2021-3) and GCR from FAPESP (#2020/02844-5).

Conflict of interest

None declared.

References

- Alonso, J., Arillo, A., Barrón, E., Carmelo Corral, J., Grimalt, J. et al., 2000. A new fossil resin with biological inclusions in Lower Cretaceous deposits from Alava (northern Spain, Basque-Cantabrian Basin). *J. Paleol.* 74, 158–178.
- Amorim, D.S., Oliveira, S.S. and Henao-Sepulveda, A.C., 2018. A new species of *Eumanota* Edwards (Diptera: Mycetophilidae: Manotine) from Colombia: Evidence for a pseudogondwanan pattern. *Am. Mus. Novit.* 3915, 1–19.
- Blagoderov, V.A., 1995. Fungus gnats of the tribe Sciophilini (Diptera, Mycetophilidae) from the Early Cretaceous of Transbaikalia. *Paleontologica Journal* 29, 72–83.
- Blagoderov, V.A., 1997. Fungus gnats of the tribe Gnoristini (Diptera, Mycetophilidae) from the Lower Cretaceous of Transbaikalia. *Paleontological Journal* 31, 609–615.
- Blagoderov, V.A., 1998. Fungus gnats of the tribe Gnoristini and Leiini (Diptera, Mycetophilidae) from the Lower Cretaceous of Transbaikalia. *Paleontological Journal* 32, 58–62.
- Blagoderov, V.A. and Arillo, A., 2002. New Sciaroidea (Insecta: Diptera) in Lower Cretaceous amber form Spain. *Stud. Dipterol.* 9, 3–12.
- Blagoderov, V.A. and Grimaldi, D.A., 2004. Fossil Sciaroidea (Diptera) in Cretaceous ambers, exclusive of Cecidomyiidae, Sciaridae, and Keroplatidae. *Am. Mus. Novit.* 3433, 1–76.
- Blagoderov, V.A., Grimaldi, D.A. and Fraser, N.C., 2007. How time fly for flies: Diverse Diptera from the Triassic of Virginia and early radiation of the order. *Am. Mus. Novit.* 3572, 1–39.
- Burdíková, N., Kjørandsen, J., Lindemann, J.P., Kaspárk, D., Tóthová, A. and Ševčík, J., 2019. Molecular phylogeny of the Paleogene fungus gnat tribe Exechiini (Diptera: Mycetophilidae) revisited: Monophyly of genera established and rapid radiation confirmed. *J. Zool. Syst. Evol. Res.* 57, 806–821. <https://doi.org/10.1111/jzs.12287>.
- Carmo, D.D.D., Lamas, C.J.E. and Ribeiro, G.C., 2022. The oldest fossil stiletto fly: A new genus and species from the Lower Cretaceous Crato formation of Brazil (Diptera: Therevidae). *Cretac. Res.* 130, 105039. <https://doi.org/10.1016/j.cretres.2021.105039>.
- Chandler, P.J., 1978. Association with plants. Fungi. In: Stubbs, A. and Chandler, P.I. (Eds.), *A Dipterist's Handbook*. Amateur Entomologist 15. The Amateur Entomologist's Society, Middlesex, pp. 199, 255–211.
- Cumming, J.M. and Wood, D.M., 2017. Adult morphology and terminology. In: Kirk-Spriggs, A.H. and Sinclair, B.J. (Eds.), *Manual of Afrotropical Diptera*. Introductory chapters and keys to Diptera families, Vol. 1. South African National Biodiversity Institute, Pretoria, pp. 89–133.
- Edwards, F.W., 1925. British fungus-gnats (Diptera, Mycetophilidae). With a revised generic classification of the family. *Trans. R. Entomol. Soc. Lond.* 1924, 505–670.
- Evenhuis, N.L., 2014. Family Mycetophilidae. In: *Catalog of the fossil flies of the world (Insecta: Diptera)*. website. Online resource (<http://hbs.bishopmuseum.org/fossilcat/fossmyceto.html>), accessed 1 September 2019.
- Goloboff, P.A., 1999. Analyzing large data sets in reasonable times: Solutions for composite optima. *Cladistics* 15, 415–428.
- Goloboff, P.A., Farris, J.S. and Nixon, K.C., 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24, 774–786.
- Grimaldi, D. and Engel, M.S., 2005. *Evolution of the insects*. Cambridge University Press, Cambridge, p. 772.
- Grimaldi, D.A., 1990. Insects from the Santana formation, Lower Cretaceous, of Brazil. *Bull. Am. Mus. Nat. Hist.* 195, 1–191.
- Han, Y., Ye, X., Feng, C., Zhang, K., Shih, C. and Ren, D., 2019. Chapter 23: Diptera – true flies with two wings. In: Ren, D., Shih, C.K., Gao, T., Yao, Y. and Wang, Y. (Eds.), *Rhythms of Insect Evolution: Evidence from the Jurassic and Cretaceous in Northern China*. John Wiley & Sons Ltd, New York, NY, pp. 497–553.
- Heads, S.W., Miller, A.N., Crane, J.L., Thomas, M.J., Ruffatto, D.M. et al., 2017. The oldest fossil mushroom. *PLoS ONE* 12, e0178327. <https://doi.org/10.1371/journal.pone.0178327>.
- Heimhofer, U. and Hochuli, P.-A., 2010. Early Cretaceous angiosperm pollen from a low-latitude succession (Arapari Basin, NE Brazil). *Rev. Palaeobot. Palynol.* 161, 105–126.
- Jakovlev, E.B. and Penttinen, J., 2007. *Boletina dispectoides* sp. n. and six other species of fungus gnats (Diptera: Mycetophilidae) new to Finland. *Entomol. Fenn.* 18, 211–217.
- Jaschhof, M., Jaschhof, C. and Kjaerandsen, J., 2011. New records of *Manota* Williston (Diptera: Mycetophilidae) in Europe and North America, including a redescription of *Manota unifurcata* Lundström and pointers towards the interrelationships among Palaeartic species. *Stud. Dipterol.* 17, 55–66.
- Jell, P.A. and Duncan, P.M., 1986. Invertebrates, mainly insects, from the freshwater Lower Cretaceous, Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria. *Memoir of the Association of the Australasian Palaeontologists* 3, 111–205.
- Kaddumi, H.F., 2005. *Amber of Jordan: the Oldest Prehistoric Insects in Fossilized Resin*. Published by the author, Amman, p. 168.
- Kalugina, N.S., 1980. Cretaceous Aphroteniinae from North Siberia (Diptera, Chironomidae), *Electrotentia brundini* gen. nov., sp. nov. *Acta Univ. Carol. Biol.* 1978, 89–93.
- Kalugina, N.S. and Kovalev, V.G., 1985. Dipterous Insects of Jurassic Siberia. *Paleontological Institute, Akademia Nauk, Moscow*, p. 198 [In Russian].
- Kaspárk, D., Kerr, P.H., Sýkora, V., Tóthová, A. and Ševčík, J., 2019. Molecular phylogeny of the fungus gnat subfamilies Gnoristinae and Mycomyinae, and their position within Mycetophilidae (Diptera). *Syst. Entomol.* 44, 128–138.
- Kopec, K., 2017. The genera *Architipula* Handlirsch, 1906 and *Grimmia* Krzemiński and Zessin, 1990 (Diptera: Limoniidae) from the Lower Jurassic of England. *Palaeontologia Electronica* 20(1.15 A), 1–7.
- Kopec, K., Ansoerge, J., Soszyńska-Maj, A. and Krzemiński, W., 2020. Revision of the genus *Mesotipula* Handlirsch, 1920 (Diptera, Limoniidae, Architipulinae) from the Lower Jurassic of Northeast Germany. *Hist. Biol.* 32, 500–507. <https://doi.org/10.1080/08912963.2018.1503257>.
- Kopec, K., Soszyńska-Maj, A., Kania-Kosok, I., Coram, R.A. and Krzemiński, W., 2021. Morphology of the oldest fossil subfamily of Limoniidae (Diptera, Architipulinae) in the light of exceptionally preserved Mesozoic material. *Sci. Rep.* 11, 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, Moscow, 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 Zool. Cracov.* 35, 43–44.
- Krzeminski, W., 1992b. Triassic and Lower Jurassic stage of Diptera evolution. *Mitt. Schweiz. Entomol. Ges.* 65, 39–59.
- Krzeminski, W. and Ansoerge, J., 1995. New Upper Jurassic Diptera (Limoniidae, Eoptychopteridae) from the Solnhofen lithographic limestone (Bavaria, Germany). *Stuttg. Beitr. Naturkd. B* 221, 1–7.
- Krzeminski, W. and Evenhuis, N., 2000. Review of Diptera palaeontological records. In: Papp, L. and Darvas, B. (Eds.), *Contributions to Manual of Palaearctic Diptera*, Vol. 1. Science Herald, Budapest, pp. 535–564.
- Krzeminski, W. and Krzemińska, E., 2003. Triassic Diptera: Descriptions, revisions and phylogenetic relations. *Acta Zool. Cracov.* 46, 153–184.
- Krzemiński, W., Kania-Kosok, I., Krzemińska, E., Ševčík, J. and Soszyńska-Maj, A., 2021. Fossils shed a new light on the diversity and disparity of the family Limoniidae (Diptera, Nematocera). *Insects* 12, 206.
- Kunzmann, L., Coiffard, C., Westerkamp, A.P.A.O., Batista, M.E.P., Uhl, D. et al., 2021. Crato Flora: A 115-Million-Year-Old Window into the Cretaceous World of Brazil. In: Iannuzzi, R. and Rößler, R. (Eds.), *Lutz Kunzmann, Brazilian Paleofloras: from Paleozoic to Holocene*. Springer, Dordrecht, pp. 1–40.
- Kurina, O. and Hippa, H., 2021. Additions to the knowledge of *Manota* Williston (Diptera: Mycetophilidae) from the Neotropical region, with description of four new species. *Zootaxa* 4938, 85–100.
- Lamas, C.J.E., Sampronha, S. and Ribeiro, G.C., 2022. A new robber fly from the Lower Cretaceous (Aptian) Crato formation of NE Brazil (Insecta: Diptera: Asilidae). *Cretac. Res.* 131, 105114. <https://doi.org/10.1016/j.cretres.2021.105114>.
- Lewis, P.O., 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. *Syst. Biol.* 50, 913–925.
- Lukashevich, E.D., 2008. Ptychopteridae (Insecta: Diptera): History of its study and limits of the family. *Paleontol. J.* 42, 66–74.
- Lukashevich, E.D., 2009. Limoniidae (Diptera) in the Upper Jurassic of Shar Teg, Mongolia. *Zoosymposia* 3, 131–154. <https://doi.org/10.11646/zoosymposia.3.1.12>.
- Lukashevich, E.D. and Ribeiro, G.C., 2019. Mesozoic fossils and the phylogeny of Tipulomorpha (Insecta: Diptera). *J. Syst. Palaeontol.* 17, 635–652. <https://doi.org/10.1080/14772019.2018.1448899>.
- Lukashevich, E.D., Amorim, D.D.S. and Ribeiro, G.C., 2021. A Gondwanan record of the extinct genus *Cretobibio* (Diptera: Bibionidae). *Palaeontomol.* 4, 468–474. <https://doi.org/10.11646/palaeontomol.4.5.13>.
- Mantič, M., Sikora, T., Burdíkóvá, N., Blagoderov, V., Kjaerandsen, J., Kurina, O. and Ševčík, J., 2020. Hidden in plain sight: Comprehensive molecular phylogeny of Keroplatidae and Lygistorrhinidae (Diptera) reveals parallel evolution and leads to a revised family classification. *Insects* 11, 348. <https://doi.org/10.3390/insects11060348>.
- Martill, D.M., Bechly, G. and Loveridge, R.F., 2007. *The Crato Fossil Beds of Brazil: Window into an Ancient World*. Cambridge University Press, Cambridge, p. 625.
- Mendes, M., Bezerra, F.I. and Adami, K., 2020. Ecosystem structure and trophic network in the Late Early Cretaceous Crato Biome. In: Iannuzzi, R., Rößler, R. and Kunzmann, L. (Eds.), *Brazilian Paleofloras*. Springer, Cham.
- Moura-Júnior, D.A., Scheffler, S.M. and Fernandes, A.C., 2018. A Paleontomofauna Brasileira: Cenário Atual, vol. 41. *Anuário do Instituto de Geociências – UFRJ, Rio de Janeiro*, pp. 142–166.
- Newman, E., 1834. Attempted division of British insects into natural orders. *Entomological Magazine* 2, 379–431.
- Nixon, K.C., 1999. The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics* 15, 407–414.
- Nixon, K.C., 1999–2004. *Winclada* (BETA) ver. Asado 1.89. Published by the author, Ithaca, NY.
- Oliveira, S.S. and Amorim, D.S., 2021. Phylogeny, classification, Mesozoic fossils, and biogeography of the Leinae (Diptera, Mycetophilidae). *Bull. Am. Mus. Nat. Hist.* 446, 1–108.
- Ponomarenko, A.G., Aristov, D.S., Bashkuev, A.S., Gubin, Y.M., Khranov, A.V. et al., 2014. Upper Jurassic Lagerstätte Shar Teg, southwestern Mongolia. *Paleontol. J.* 48, 1573–1682, 1682. <https://doi.org/10.1134/S0031030114140160>.
- Rambaut, A., Drummond, A.J., Xie, D., Baele, G. and Suchard, M.A., 2018. Posterior summarization in Bayesian Phylogenetics using tracer 1.7. *Syst. Biol.* 67, 901–904. <https://doi.org/10.1093/sysbio/syy032>.
- Rasnitsyn, A.P., Quicke, D.L.J. (Eds.), 2002. *History of insects*. Kluwer Academic Publisher Dordrecht, XII + 517 pp., 503 figures, ISBN 1-4020-0026-X.
- Ribeiro, A.C., Ribeiro, G.C., Varejão, F.G., Batriolla, L.D., Pessoa, E.M. et al., 2021. Towards an actualistic view of the Crato Konservat-Lagerstätte paleoenvironment: A new hypothesis as an Early Cretaceous (Aptian) equatorial and semi-arid wetland. *Earth Sci. Rev.* 216, 103573. <https://doi.org/10.1016/j.earscirev.2021.103573>.
- Ribeiro, G.C. and Lukashevich, E.D., 2014. New Leptotarsus from the early cretaceous of Brazil and Spain: The oldest members of the family Tipulidae (Diptera). *Zootaxa* 3753, 347–363.
- Ribeiro, G.C., Santos, D. and Nicolau, R.C.R., 2015. A new species of *Leptotarsus* (Diptera: Tipulidae) from the Lower Cretaceous Crato formation of Brazil. *Cretac. Res.* 56, 244–249. <https://doi.org/10.1016/j.cretres.2015.05.005>.
- Ronquist, D., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. and Huelsenbeck, J.P., 2012. MrBayes 3.2. Efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* 61, 539–542.
- Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J. et al., 2012. Age constraint on Burmese amber based on UePb dating of zircons. *Cretac. Res.* 37, 155–163.
- Søli, G.E.E., 1997. The adult morphology of Mycetophilidae (s. str.), with a tentative phylogeny of the family (Diptera, Sciaroidea). *Entomol. Scand. Suppl.* 50, 5–55.
- Søli, G.E.E., 2017. 20. Mycetophilidae (Fungus Gnats). In: Kirk-Spriggs, A.H. and Sinclair, B.J. (Eds.), *Manual of Afrotropical Diptera*. Vol. 2. Nematocera and Lower Brachycera. SANBI Publishing, Pretoria, pp. 533–555.
- Stilwell, J.D., Langendam, A., Mays, C., Sutherland, L.J.M., Arillo, A. et al., 2020. Amber from the Triassic to Paleogene of Australia and New Zealand as exceptional preservation of poorly known terrestrial ecosystems. *Sci. Rep.* 10, 5703. <https://doi.org/10.1038/s41598-020-62252-z>.
- Wagner, P.J., 2012. Modelling rate distributions using character compatibility: Implications for morphological evolution among fossil invertebrates. *Biol. Lett. Paleont.* 8, 143–146.
- Zaitzev, A.I., 1990. The immature stages of *Manota unifurcata* Lundst. and position of the subfamily Manotinae in the system of Diptera. *Mycetophiloidea. Biol. Sci.* 3, 63–71 [in Russian].

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Data matrix.

Appendix S2. Age and location of mycetophilid amber and compression fossil sites (Fig. 11).