

Research Paper

The oldest Gondwanan non-biting midge (Diptera, Chironomidae, Podonominae) sheds light on the historical biogeography of the clade

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ARTICLE INFO

Keywords:

Biogeography
Diptera
Podonominae
Jurassic
Gondwana

ABSTRACT

Podonominae, a group of non-biting midges within the Chironomidae family, serves as an important biogeographical model. For a long time, it was believed that Podonominae originated in Northern Gondwana and later spread to Laurasia. However, because the oldest known fossils of this group come from the Jurassic period in Eurasia more recent interpretations have suggested a Laurasian origin.

We present the oldest record of Podonominae from Gondwana, specifically from the Tithonian age (Jurassic) in Australia. This discovery is also the oldest Chironomidae fossil found in the Southern Hemisphere and suggests that Podonominae likely originated in Gondwana. The new fossil represents a highly specialized form of Podonominae, adapted to living in the littoral zones of large lakes. It has adaptations to this environment that are unique amongst Podonominae, and similar to those found in some modern marine Chironomidae species such as Telmatogetoninae.

1. Introduction

Non-biting midges have long been used as a model system for understanding historical biogeography, providing a means to describe and interpret general patterns in distribution and origin of the biological diversity (Matzke, 2014). Of particular importance was the pioneering work by Brundin (1966) that focused on the similarities and differences in a specific clade of the non-biting midge fauna (Chironomidae, Podonominae) in the southern Hemisphere. This work suggested that the modern patterns in diversity resulted from vicariance as the continents separated. Podonominae is a group of Chironomidae with a worldwide distribution (albeit mostly bipolar-disjunct one) that is an important clade to examine historical biogeography. The highest richness of extant species is recorded in the higher latitudes of the Southern Hemisphere, with lower diversity occurring in the high latitudes of the Northern Hemisphere, and few species known from equatorial areas (Ashe and O'Connor, 2009). In fact, 133 species of Podonominae are found in the Southern Hemisphere, and only 37 species in the Northern

Hemisphere (Roque and Trivinho-Strixino 2004, Ashe and O'Connor, 2009, Rodríguez et al., 2009, Siri and Donato 2012, Siri and Brodin 2014, Siri et al., 2024, Cranston and Krosch 2015, Pinho and Shimabukuro 2018, Luo and Tang, 2023, Shimabukuro et al., 2023).

Brundin (1966) interpreted the spatial distribution and phylogenetic relations within Podonominae as best being explained by vicariance driven by continental drift in the Mesozoic. Brundin (1966, 1976) thought that Podonominae as a group, most probably originated in Northern Gondwana, and then dispersed to Laurasia. This hypothesis, in Brundin's opinion, was corroborated by the discovery of *Libanochlites neocomicus* Brundin, 1976, at the northern edge of Gondwana. This fossil in Lebanese amber (ca. 125 MYA) represented at that time the oldest known Podonominae. A Gondwanan origin of Podonominae was also considered consistent with the fact that the center of extant species richness is in the Southern Hemisphere.

Since Brundin's original writings, numerous fossils tentatively considered to be representatives of Podonominae have been uncovered from Jurassic Oxfordian sediments in Siberia, Mongolia, and China (15

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<https://doi.org/10.1016/j.gr.2025.09.001>

Received 22 May 2025; Received in revised form 15 September 2025; Accepted 16 September 2025

Available online 8 October 2025

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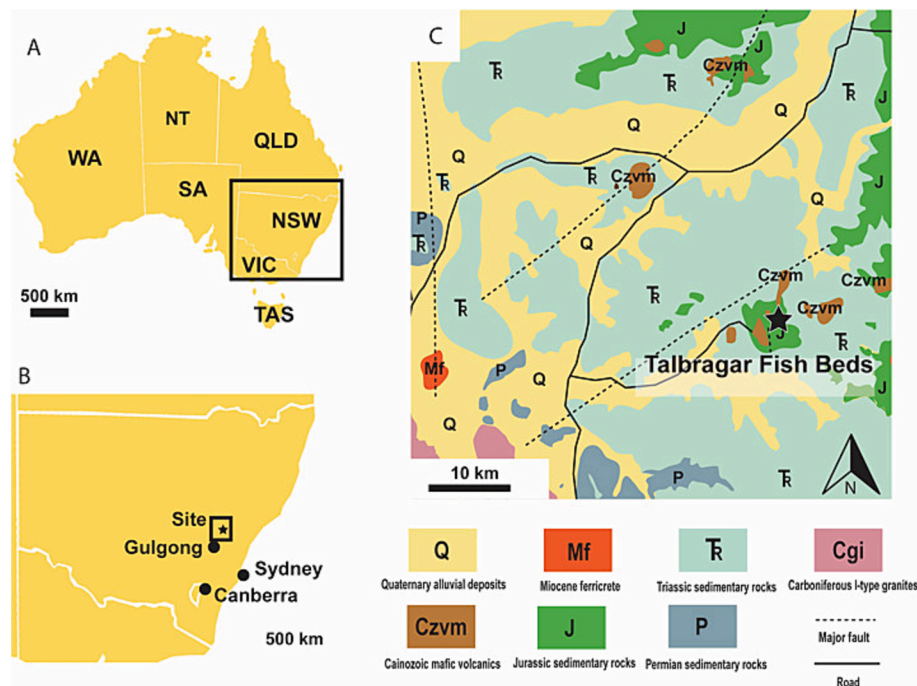


Fig. 1. (A and B) Location of the site in New South Wales, Australia. (C) Local geology near the site showing Miocene ferricrete and extensive Mesozoic bedrock. - Adapted from Fig1 in the McCurry et al. 2022.

MYA) (Kalugina, 1980, Kalugina, 1985, Lukashevich, 2012, Lukashevich and Przhiboro, 2018, Ashe et al., 2024). These records cast doubt on the Gondwanan origin of the group. Taking into account a foundational role of the Brundin's (1966) original research in the development of the modern historical biogeography, reappraising the geographical history of this group is very important. Analysis using molecular data largely corroborated Brundin's original hypothesis, suggesting a Laurasian-Gondwanan split in Podonominae around 133 MYA (Cranston et al 2010).

Unfortunately, the lack of the Mesozoic Chironomidae fossils, and in particular Podonominae, from the Southern Hemisphere has severely limited capacity to test alternative biogeographic models. The majority of available chironomid fossils from the Early Mesozoic come from Eastern Asia with records from Siberia, China and Mongolia (Ansoerge, 1999, Armitage et al., 1995, Ashe et al., 2024, Azar et al., 2008, Baranov et al., 2014, Giřka et al., 2019, Krzeminski and Jarzembowski, 1999, Kalugina, 1980, 1985, 1993, Lukashevich, 2012, 2020, Lukashevich and Ansoerge, 2024, Lukashevich and Przhiboro, 2011, 2012, 2018, Veltz et al., 2007). Many of these were initially regarded as Podonominae (Kalugina, 1985). Few pre-Cretaceous fossils of non-biting midges are known from the Southern Hemisphere. In fact, the presence of Chironomids from the Talbragar fish beds (Tithonian, 149–145 MYA) of New South Wales, Australia (Beattie and Avery, 2012) is one of the only indications of Southern Hemisphere Jurassic records of the group. No Mesozoic records of Podonominae exist from the Southern Hemisphere, and only two Cenozoic records of this group are known from former components of erstwhile Gondwana (both of them adult midges in amber). One unidentified Eocene Podonominae from Australia (Blake et al., 2024) and one *Paraboreochlus* sp. specimens from Paleocene-Eocene of India (Stebner et al., 2017). Despite a variety of well-preserved insects being described from Talbragar fish beds, material from this deposit representing non-biting midges remains largely unstudied in detail (Frese et al., 2017).

In this communication we describe fossil chironomids from the Talbragar fish beds that represent the oldest direct evidence of Chironomidae in Gondwana. All new fossil specimens studied are pupae and pharate adults. We critically re-evaluate the historical biogeography of

Podonominae based on phylogenetic re-analysis of the group in light of these fossils.

2. Methods

2.1. Geological setting

Talbragar Fossil Fish Bed is a formal geological unit located approximately 30 km Northeast of Gulgong, NSW, Australia (Fig. 1A-C). The deposit is a part of the Purlawaugh Formation within the Surat Basin. The fossiliferous strata are composed of fine-grained tuffaceous siltstones and mudstones (Bean 2006). The bed has been estimated to be of Late Jurassic age Kimmeridgian–Tithonian (Late Jurassic) based on SHRIMP (sensitive high-resolution ion microprobe) analysis of the zircons (Chen et al., 2019).

The palaeoenvironment at the fossil site has been interpreted as a large lake based on the sedimentology and fauna (Beattie and Avery 2012). Fauna from the site include a variety of fish, the most abundant of which is *Cavenderichthys talbragarensis* (Woodward 1895, Bean 2006). A temnospondyl tooth has also been described from the site (Hart et al 2021). Arthropods described from the site include a spider (Aranea, Uloboridae), beetles (Coleoptera, Staphylinidae, Elateridae, Nemonychidae, Hydrophilidae), Cicada (Auchenorrhyncha, Palaeontinidae) a dragonfly (Odonata: Anisoptera), flies (Diptera: Athericidae, Archisargidae) a wasp (Hymenoptera, Praeaulacidae) and a stonefly (Plecoptera, Notonemouridae) (Selden and Beattie, 2013, Oberprieler and Oberprieler 2012, Nel et al 2017, Oberprieler et al., 2012, Cai et al. 2013, Chen et al 2019, Li et al 2022). Flora from the site includes conifers *Agathis jurassica* and *Rissikia talbragarensis* among other plants (White 1981).

Fossil material. We examined six specimens of fossil Chironomidae pupae and pharate adults from Talbragar fish beds, housed in the palaeontology collection of the Australian Museum, Sydney.

Extant comparative material (*Tanytus* sp. and *Parochlus araucanus* Brundin, 1966) were sourced from the collection of the Bavarian State Collection for Zoology (ZSM), with no accession numbers available.

2.2. The morphological terminology

Terminology is based on Sæther (1980), Marshall et al. (2017) and Borkent and Sinclair (2017), and specifically follows Borkent (2012) for culicomorphan pupae anatomy. The following keys and papers were used: Ansoerge, 1999, Armitage et al., 1995, Azar et al., 2008, Baranov et al., 2014, Gilka et al., 2019, Krzeminski and Jarzembowski, 1999, Kalugina, 1980, 1985, 1993, Lukashevich, 2012, 2020, Lukashevich and Ansoerge, 2024, Lukashevich and Przhiboro, 2011, 2012, 2018, Veltz et al., 2007).

Nomenclature: The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN). Manuscript to be reviewed and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix <https://zoobank.org/>. The LSID for this publication is: urn:lsid:zoobank.org:pub:63EE417B-2AEA-478E-B653-8A1DEB0D18A7.

2.3. Imaging

Specimens were imaged using either a Canon EF-S 18–55 mm macro lens or a Canon MP-E 65 mm f/2.8 1–5x macro lens. Exact methods follow those of Haug et al. (2011). Images were taken with additional light-polarized illumination, with a Canon Eos Rebel Canon EOS 5D MKIII camera on a repro-stand. All images were assembled into vertical stacks and horizontal panoramas, using PICOLAY open stacking software (Picolay, 2025) and AutoStitch (2025) panorama software respectively. Morphometry of the specimens was conducted using photos of the object micrometers and specimens photographed at the same magnifications, whence the image of the micrometer was used to set scale in ImageJ (Schindelin et al., 2012).

2.4. Phylogenetic analysis (morphological matrix)

A morphological matrix was compiled from published data and examination of the actual specimens in the collection of the Zoological State Collection, Munich. A full list of characters and sources is provided in the Supplementary Files <https://zenodo.org/records/15191920>. Out of 174 characters used, 106 were unordered, while for 68 characters where clear consensus on the state polarity exists, we have ordered them (Sæther, 1977, Cranston and Edward, 1998, Silva and Ekrem, 2016). Characters were sampled from the larvae, pupae and adult males and females where available. Fossil taxa of course were underrepresented in terms of characters available for observation (see <https://zenodo.org/records/15191920>). The morphological matrix contains data for 57 species, 19 of which are represented by fossils. The character matrix for phylogenetic analysis was built using nexus data editor v.0.5.051. We obtained branch support with the ultrafast bootstrap 10000 (Hoang et al., 2018) implemented in the IQ-TREE 1.6.12 software (Minh et al., 2020), using the MK + ASC substitution model.

We did not combine molecular and morphological matrices or include fossils as tips into the BEAST2 chronogram. The combination of an incomplete current understanding of Chironomidae morphology that limits confident exclusion of homoplasies, and an unbalanced molecular data set lacking information for taxa represented by fossils would lead to unmeasurable uncertainty (Wiens, 2003). Inclusion of the fossil data into the morphological matrices seems to mostly improve phylogenetic analysis (Mongiardino-Koch et al., 2021). This however comes with a caveat that most of the fossil tips should have most of the characters coded (Wiens, 2003, Mongiardino-Koch et al., 2021). In case of Chironomidae it is very hard to do, as informative characters and

synapomorphies are distributed across three life stages and two sexes (larvae, pupae and adult males/females), and most of the fossil species are known from a single life stage/sex (Ashe et al., 2024). Thus, from our experience nodes containing Diptera fossils with many missing characters can present very weak or no support (Baranov et al., 2016).

2.5. Phylogenetic analysis (molecular matrix)

DNA sequences for the phylogenetic analysis were selected from published data available through GenBank are based on the dataset from (Cranston et al., 2010, 2012, Krosch et al., 2022). The assembled molecular dataset representing 37 species was a 2399 bp alignment consisting of 662 bp of the mitochondrial protein coding gene cytochrome oxidase subunit I (COI), 627 bp of the nuclear protein coding gene CAD3, 708 bp of ribosomal RNA 18 s and 402 bp of the ribosomal RNA LSU (28S) (Table 2, and accession numbers at <https://zenodo.org/records/15191920>). Sequences for each gene fragment were aligned in Geneious Prime (Geneious Prime 2023.1.1), using Multiple align functionality and verified by eye. Each gene alignment was treated with Gblocks (Talavera and Castresana, 2007) to remove poorly aligned and hypervariable regions and then the four were concatenated into a single alignment. In addition to representatives of Chironomidae we include homologous data for an outgroup comprising Ceratopogonidae representatives (genera *Brachypogon* and *Atrichopogon*) (Cranston et al., 2010). Analysis of the matrix was performed with Bayesian mixed-model approach, using one Markov chain Monte Carlo (MCMC) running for 100.000.000 million generations, with trees sampled every 1000 generations, following approach used by Cranston originally with this dataset (Cranston et al., 2010). We have permitted a higher number of runs to allow a tree comparable with the one used in the BEAST2 analysis of the divergence times, which required a higher number of runs, to reach acceptable ESS.

2.6. Estimation of divergence times

We conducted an estimation of times to the most recent common ancestor (*t*_{mrc}) in BEAST ver 2.7.6 (Bouckaert et al., 2019), using molecular dataset as described above (COI + 28 s + 18 s + CAD3). We used the Yule model for the reconstruction. We used Gamma variation model for all partitions, with estimated shape parameters for molecular partitions, as well as Relaxed Clock Log Normal model for a clock model. We accessed convergence of runs using Tracer 1.7.2 (Rambaut et al., 2018).

We applied *Grauvogelia arzwilleriana* Krzeminski, Krzeminska et al., 1994—the oldest confirmed Diptera fossil (Krzeminski et al., 1994)—as a dating for the Diptera root node, using exponential prior, with zero offset of 247 MYA and mean of 10 MYA. We have applied *Aenne triassica* (Krzeminski and Jarzembowski 1999) – oldest confirmed Chironomid fossil – as a calibration to the root node of Chironomidae, using exponential prior, with zero offset of 203 MYA and mean of 15 MYA. We have used the oldest Podonominae fossil – *Oryctochlus* from Siberia (Lukashevich, 2012), we applied exponential prior, with zero offset of 155 MYA and 5 MYA of mean. *Oryctochlus* was used to date the node of all Podonominae. Finally, we have used *Telmatomyia*, to date the base node for all “Boreochlini” we have used exponential prior, with zero offset of 149 MYA and 1 MYA of mean. In all four cases offset was based on the fossil’s age, while mean was based on extrapolation of the existing dated phylogenies of Diptera, onto a maximal age of the node (Ansoerge, 1999, Krzeminski et al., 1994, Lukashevich, 2012, Beattie and Avery, 2012). We applied only four calibrations, as adding additional calibrations was leading to the lower ESS in many parameters, due to overparametrization of the analysis. We have run 100 000 000 of the permutations, with 10 % burnin. Estimated sample size (ESS) of all the relevant statistics was greater than 200. Chronogram was produced from a stationary distribution, using TreeAnnotator v2.7.6 (Rambaut et al., 2018).

2.7. BioGeoBEARS models

We used the BEAST chronogram to conduct an ancestral range estimation analysis using *BioGeoBEARS* (Matzke, 2014) R package in the R version 4.2.3 (15 March 2023 UCRT) — ‘Shortstop Beagle’ (R Core Team, 2023). We specifically test Brundin’s (1976) hypothesis that Podonominae originated in the Northern Gondwana. We ran BioGeoBEARS analysis with a binary distribution (Gondwana-Laurasia) to test the vicariance hypothesis founded on the separation by continental drift of freshwater habitats associated with the palaeo-landscapes of Gondwana and Laurasia. Details of the former ranges of extinct species that are represented by a small number of fossils, are not known. We therefore selected this simplified dichotomous approach for Podonominae to minimize distribution uncertainty.

Dispersal distances: we built a distance matrix using straight line, minimal distance between the “Gondwana” and “Laurasia” through the time we have used “global_paleogeographic_n.kmz” plugin in Google Earth, and its embedded paleogeographic maps.

See supplementary files and code <https://zenodo.org/records/15191920>. We collated minimal distances between the regions at the following time intervals – End Permian, projected oldest Diptera (254 MYA); Cretaceous, breakup of Gondwana intensifies (105 MYA); Paleocene, former Gondwanan landmass are still situated close by, ice free Antarctica (50 MYA); Mid- Eocene, landmasses that once formed Laurasia and Gondwana are drifting further apart; Miocene- starting of the short lasting warm global episode (Middle Miocene climate optimum) (23 MYA); Late Miocene, end of ice-free Antarctica (15 MYA); modern day (0.1 year ago, as BioGeoBEARS does not accept “0” values) (Sýkora et al., 2023).

Dispersal multipliers were set as follows – land masses modelled as being connected directly during the given period, were assigned multiplier “1”. Areas considered to have been without direct contact (i.e. separated by oceans) were given lower values: where a multiplier of “0.5” in the direction of the hypothesized west wind drift, and “0.1” in the opposite direction (Sanmartin et al., 2007). Areas separated by the vast swath of the oceans without dominant, migration-assisting winds, are given a reciprocal multiplier “0.1” (See supplementary files and code <https://zenodo.org/records/15191920>).

2.8. Setting up BioGeoBEARS analysis

The analysis was set up following the phylowiki tutorial for the biogeographic analysis in the package. We implemented DEC, DIVALIKE and BAYAREALIKE models (Matzke 2014). We also ran more structured models, where “jump” between the distribution areas (relative per-event weight of jump dispersal) was allowed as an additional parameter – DEC + J, DIVALIKE + J and BAYAREALIKE + J (Matzke, 2014, 2022). We kept free parameters “d” – anagenesis: rate of ‘dispersal’ (range expansion) and “e” – anagenesis: rate of ‘extinction’ (range contraction) at their default values. Max numbers of the areas allowed for the case distribution case “1” was four regions, and for the case “2” – Gondwana-Laurasia, we have allowed a maximum of two distribution areas.

2.9. Accessibility of the data

Fossil specimens used in this study are housed in the collection of Australian museum, under the following accession numbers: Holotype AM F145999 (female pupa), Paratypes: AM F137133 (female pupa) and AM F141772 (pupa). Other material: AM F 141771, AM F 137130, AM F 137136, AM F 146000. Material representing extant species used for comparison purposes in this paper is housed in the Zoological State Collection, Munich (Zoologische Staatssammlung München, ZSM). In particular: *Thalassomyia frauenfeldi* Schiner, 1856 (w/o number), slide mounted pupal exuviae; *Telmatogeton torrenticola* (Terry, 1913) (w/o number), slide mounted pupal exuvium; *Telmatogeton japonicus* Tokunaga, 1933 (w/o number), slide mounted pupal exuvium; *Trichotanypus*

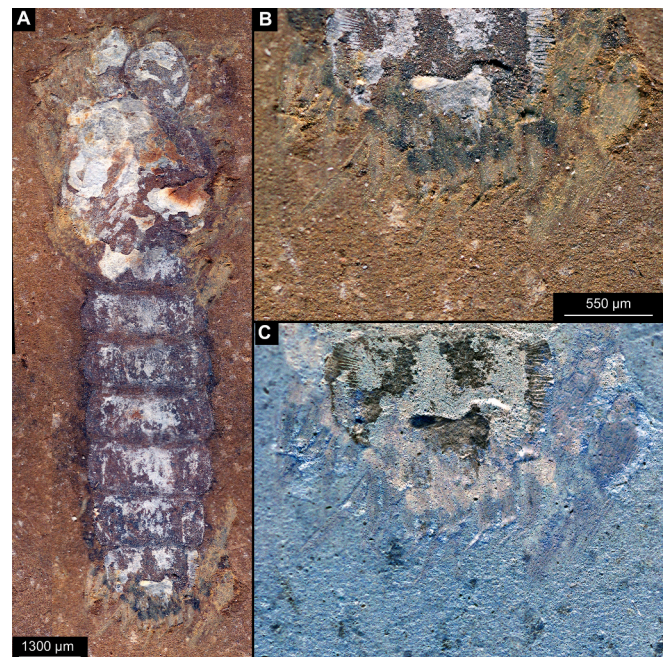


Fig. 2. *Telmatomyia talbragarica* (AM F141771), female pupa. A) Habitus B) Terminal disk; C) Terminal disk, with enhanced contrast.

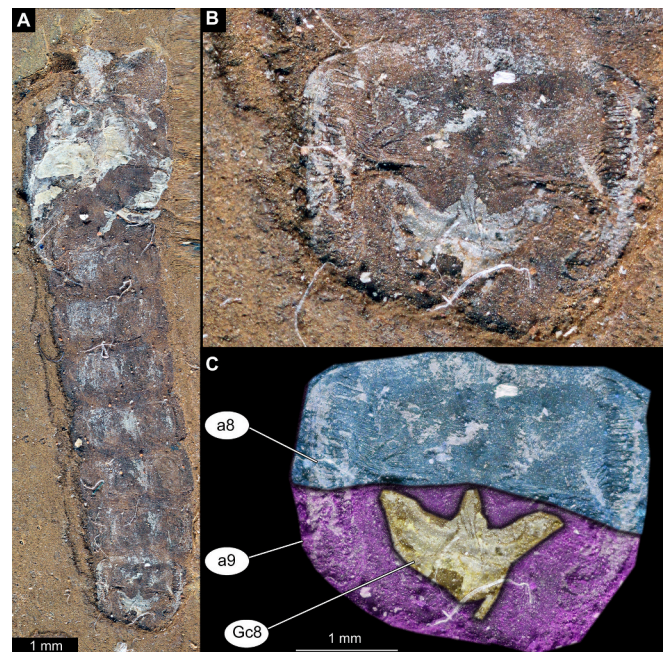


Fig. 3. *Telmatomyia talbragarica*, Holotype (AM F145999), female pupa. A) Habitus; B) Terminal disc, unmarked; C) Terminal disc, marked. Abbreviations: a8, a9 – abdominal segments 8 & 9; Gc8 – female gonocoxite 8.

posticalis (Lundbeck, 1898) (w/o number), pupa in ethanol; *Tanytus* sp. (w/o number), pupa in ethanol; *Parochlus araucanus* Brundin, 1966 w/o number), pupa in ethanol.

3. Results

3.1. Systematic palaeontology

Chironomidae (Newman, 1834).

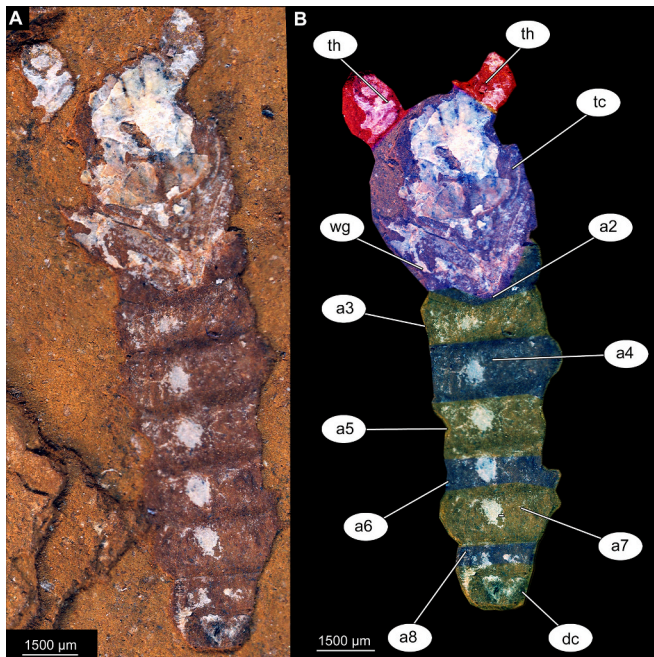


Fig. 4. *Telmatomyia talbragarica*, Paratype (AM F141772), female pupa. A) Habitus, unmarked; B) Habitus, marked. Abbreviations: a2-a8 – abdominal segments 2–8; dc – terminal disc/abdominal segment 9; tc – thorax; th – thoracic horn; wg – wing (pads).

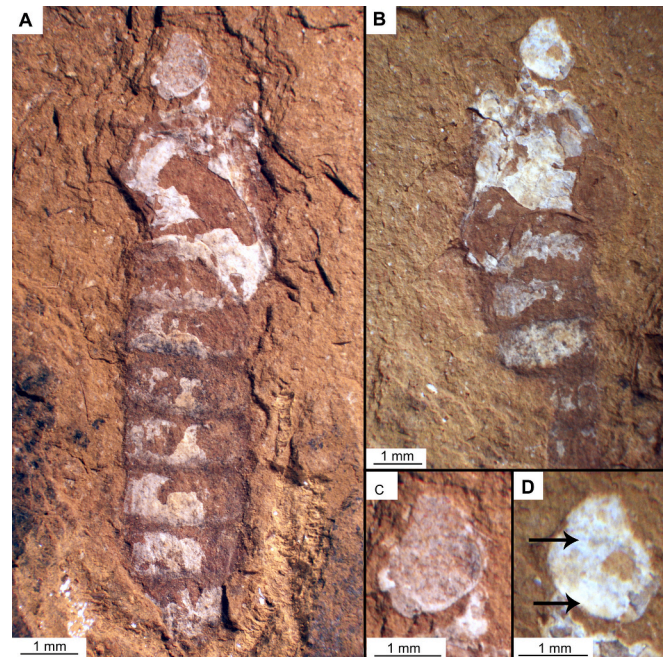


Fig. 6. *Telmatomyia talbragarica*, Paratype (AM F137133/ 137134), female pharate pupa. A) Part, AM F137133, habitus; B) Counterpart, AM F137134; habitus; C) Thoracic horn, AM F137133; D) Thoracic horn, AM F137134, upper arrow marks presumed plastron of the thoracic horn, while lower arrow marks presumed stalk.

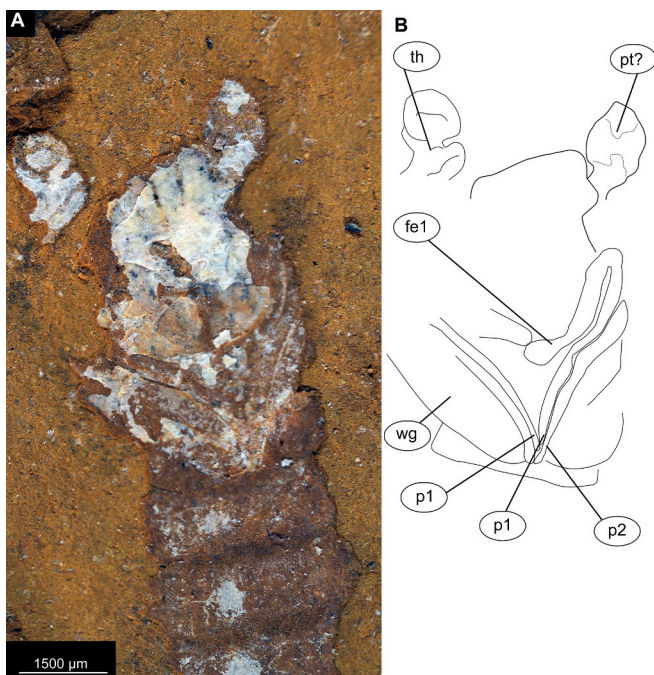


Fig. 5. *Telmatomyia talbragarica*, Paratype (AM F141772), female pupa. A) Thorax, unmarked; B) Thorax, linedrawing. Abbreviations: fe1 – femora, foreleg; p1 – foreleg; p2 – midleg; pt? – plastron (of thoracic horn); th – thoracic horn; wg – wing (pads).

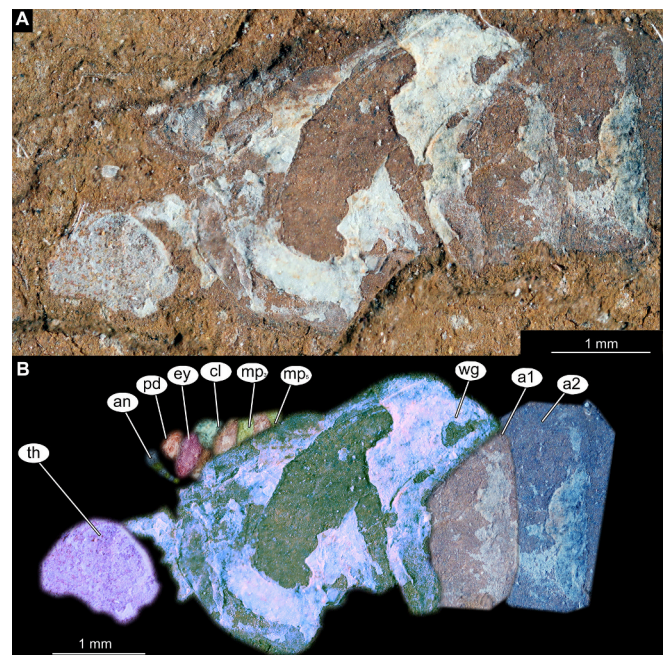


Fig. 7. *Telmatomyia talbragarica*, Paratype (AM F137133), female pharate pupa. A) Thorax, unmarked; B) Thorax, marked. Abbreviations: a1-a2 – abdominal segments 1 & 2; an – antenna; cl – clypeus; ey – eye; mp – maxillary palp; pd – pedicillus; th – thoracic horn; wg – wing (pads).

Podonominae Thienemann and Edwards in Thienemann, 1937.
Telmatomyia gen. nov. (Fig. 2 A-C; 3 A-B; 4 A-B; 5 A-D; 6 A-B; 7 A-C; 8 A, B).
 Zoobank: urn:lsid:zoobank.org:act:E0BC02B4-9AF4-4201-A573-9D17DFA84E10.
 Differential diagnosis.

Diagnosis. *Pupa*: can be distinguished from any other representative of Chironomidae by its very large size (> 9 mm), almost round thoracic horns with plastron occupying about 70 %–80 % of it, and uniquely modified abdominal segments 8 and 9, which form an oval terminal disc with a suture like articulation between the segments, wider than long, apparently without fringe of terminal setae (although there are setae

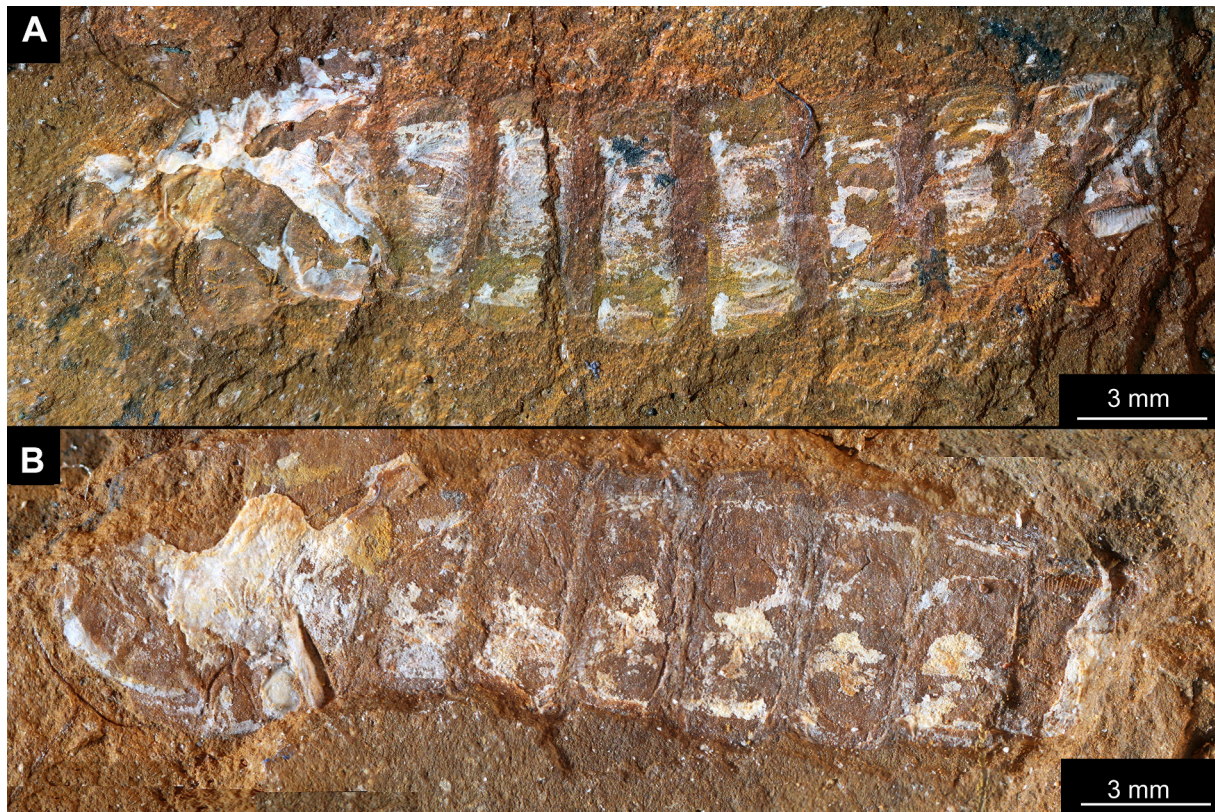


Fig. 8. Habitus of additional specimens of *Telmatomyia talbragarica* (all female pupae). A) AM F109731; B) AM F137130. (Note that areas of matrix in the top right corners of image B have been edited with rock texture from the same photograph to cover empty space; the area including the specimen is not affected).

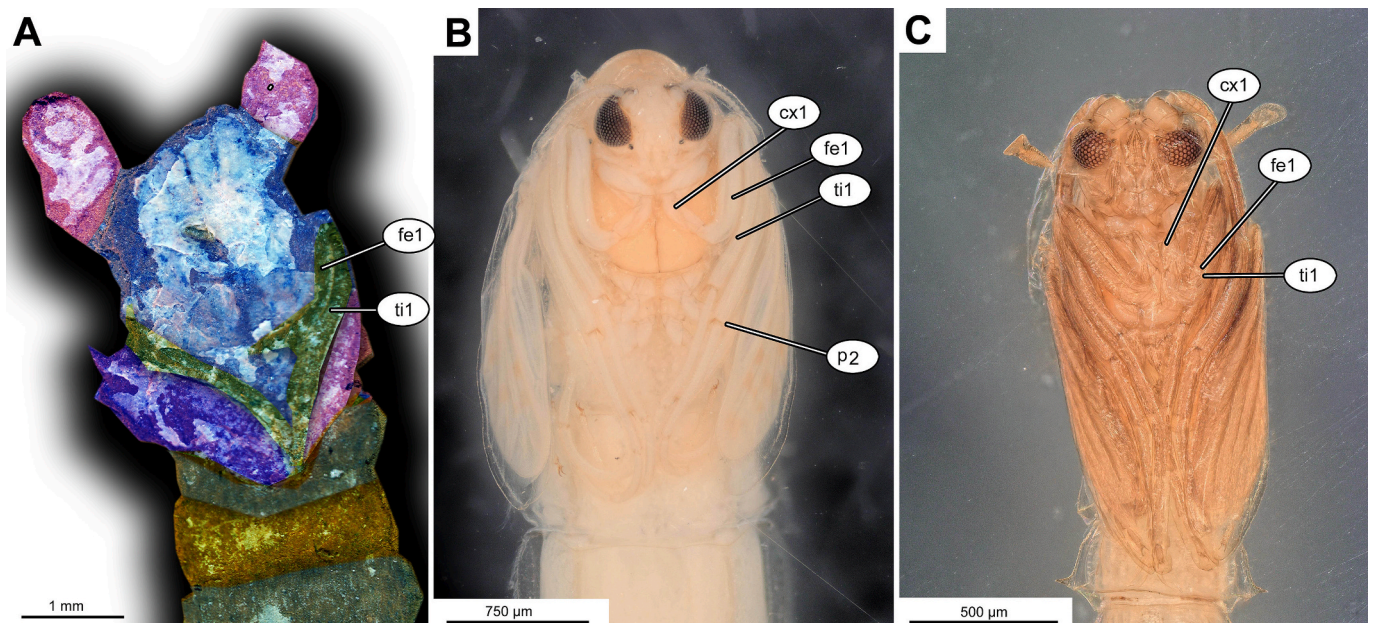


Fig. 9. Comparison of the leg sheath arrangement on the pupae of *Telmatomyia talbragarica* (AM F141772) (A), *Tanypus* sp. (B) and *Parochlus araucanus* (C). Abbreviations: cx1- coxa of the foreleg; fe1 – femora, foreleg; p2 – midleg; ti1 – tibia of the foreleg.

looking marks around the terminal disk.

Etymology: *Telmatomyia*, is from the Greek “*Telmato-*” adjective, “of stagnant water” reflecting the lacustrine nature of the habitat at Talbragar, and “*myia*” – Greek for “fly”.

Description: see “*Telmatomyia talbragarica* sp.nov.”.

Telmatomyia talbragarica sp.nov. (Fig. 2A-C, Fig. 3A-C, Fig. 4A, B,

Fig. 5A, B, Fig. 6A-D; Fig. 7A, B, Fig. 8A; B).

Material: Holotype AM F145999 (female pupa), Paratypes: AM F137133 (female pupa) and AM F141772 (pupa). Other material: AM F141771, AM F137130, AM F137136, AM F146000.

Zoobank: urn:lsid:zoobank.org:act:ADAA375B-4445-4048-A3E7-5C348290DF58.

Table 1
Measurements of the thoracic horns of the *T. talbragarica*.

Specimen	Length of TH	Width of TH	L/W ratio
AM F137133	1.6 mm	1.4 mm	1.14
AM F141772	1.5 mm	1.2 mm	1.25
AM F141771	1.5 mm	1.3 mm	1.15
AM F141771	1.9 mm	1.6 mm	1.18

Table 2
Characteristics of the different partitions in the phylogenetic analysis.

Partition	Taxa	GC content	Base Pairs
COI	38	32.8 %	662
28 s	36	44.6 %	402
18 s	37	42.2 %	708
CAD3	31	38.9 %	627

Differential diagnosis: as for genus.

Etymology: from Talbragar formation.

4. Description

Pupa. Habitus. Body length 9–14.4 mm ($n = 6$). Body, wide and stocky, with length to max abdomen width (at abdominal segment 4) is 3.9 ($n = 4$).

The body differentiated into presumably 20 segments, ocular segments plus 19 post-ocular segments (Fig. 2A-C, Fig. 3A-C, D, Fig. 4A, B); anterior part of the body composed of head and thorax, visible as a single semi-circular structure; thorax with wings and ambulatory appendages (legs) (Fig. 4A, B, Fig. 5A, B); ocular segment and post-ocular segments 1–5 (presumably) forming a distinct capsule (head capsule); gnathal

appendages (“mouthparts”) located ventrally and thus not available for observation. Antenna visible on the pharate adult specimens; sheath of maxillary palps perpendicular to the axis of the pupa’s body; maxillary palp with 5 palpomeres (Fig. 6A, B, Fig. 7A, B). Wingpads are very short, barely reaching to the second segment of the abdomen (Fig. 2 A-C, Fig. 3A-C, Fig. 4A, B).

Thoracic segments forming a single semi-globose structure closely enveloping the head of the pupa. Prothorax bears thoracic horns (Fig. 7A, B). Surface of the thoracic horn seem to be sculptured. Thoracic horns are widely oval to round, measurements of the thoracic horns as in the Table 1 ($n = 4$) (Fig. 7A, B). Thoracic horn with apical papilla (Fig. 7A, B). Plastron appears to be very large and reticulate, occupying about 70 to 80 % of the total thoracic horn area (Fig. 7A, B). Pupal leg sheaths of fore- and midlegs make a 45° angle at the point where femorae join tibiae, then extending straight towards the abdomen, along the midline of the body, ending between the edges of the wing pads (Fig. 4 A, B, Fig. 5 A, B). Forelegs are located more medially than midlegs. Hind Legs are curved beneath the wing pads, with tips of the leg sheath meeting at the tips of the wings. Leg sheath tips do not all end at the same level, with the tips of the forelegs being the most antero-medial.

Abdomen (posterior trunk) (Fig. 2A-C, Fig. 3A-C, Fig. 4A, B). Setae of abdominal segments not preserved. Ventral lamella lacking/ not preserved. Traces of lateral setae on abdominal segments are not discernible either. Segments II-VII broadly rectangular. Abdominal segment 8 fused with segment 9 into the terminal disc. Disc formed by the reduction and fusion of the segments 8 and 9 and seem to be oriented dorsally. The disc carries numerous muscle marks, distributed around the surface of the disc.

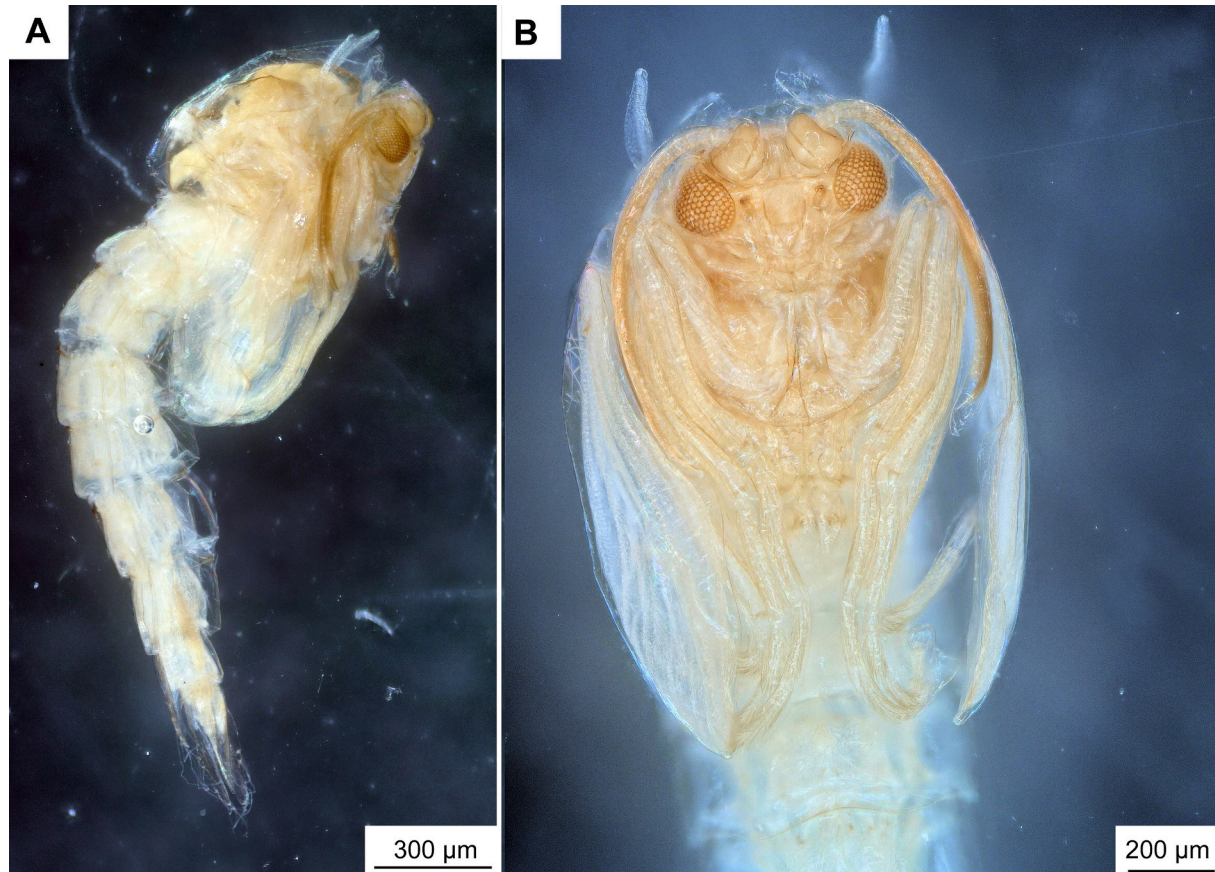


Fig. 10. *Trichotanypus posticalis* (Lundbeck, 1898), male pupa. A) Habitus, lateral view; B) Leg sheaths arrangement on the thorax, ventral view.

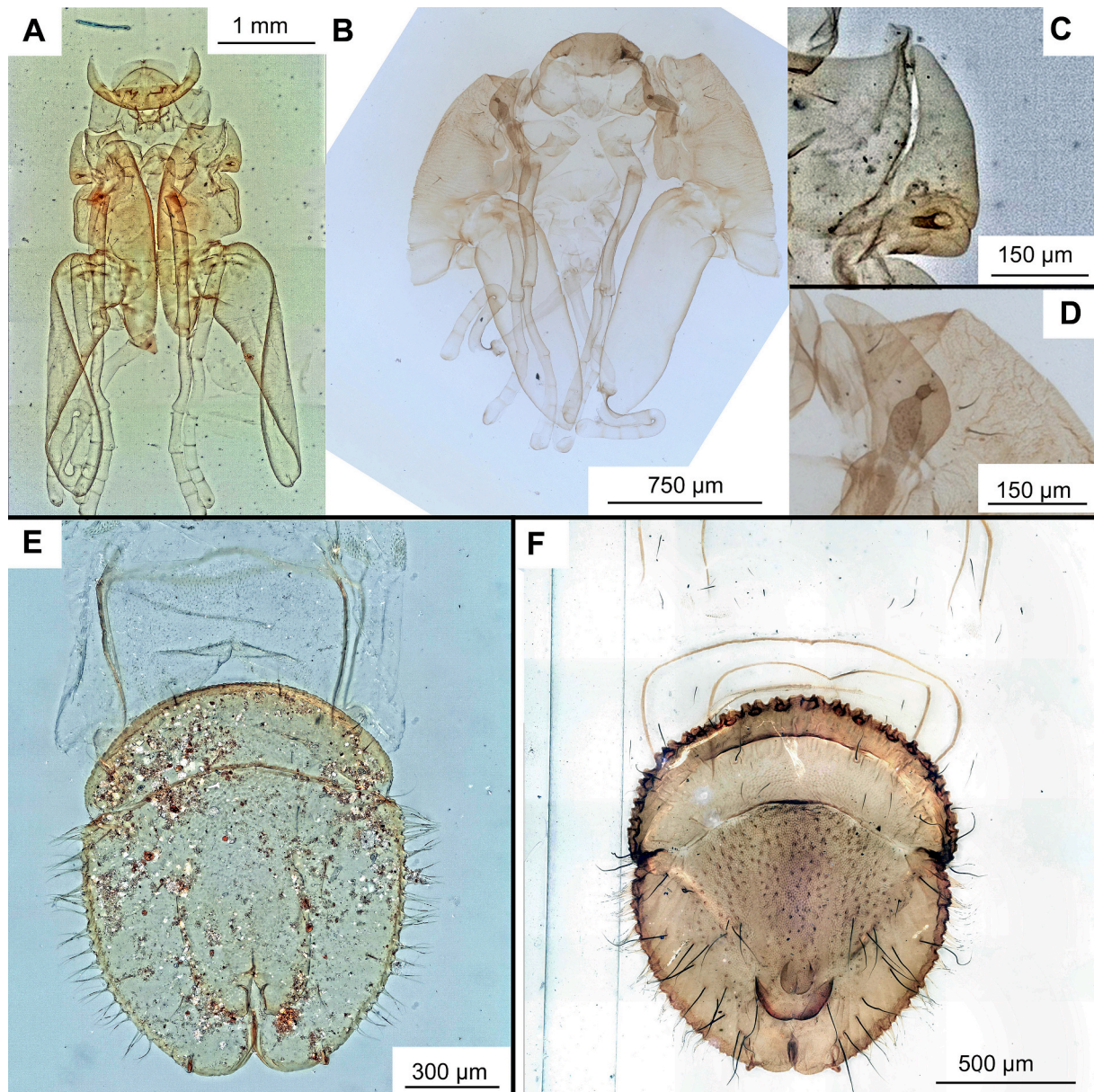


Fig. 11. Telmatogetoninae pupal structures. A, C, E – *Thalassomyia frauenfeldi*; B, D – *Telmatogeton japonicus*; F – *T. torrenticola*. A-B) Pupal cephalothorax; C-D) Thoracic horns; E-F) Terminal discs of the abdomen.

4.1. Taxonomic attribution

We classified these specimens as Chironomidae based on the following combination of pupal characters: thoracic horn with strong plastron plate; terminus of trunk with non-articulated rounded anal lobe (Fig. 2A-C, Fig. 3A-C, Fig. 4A, B) (Borkent, 2012). Within Chironomidae, this morphotype falls within the Podonominae based on the following combination of characters: thoracic horn well developed, with prominent distal plastron; leg sheath of hind and midlegs straight, ending medially between the median edges of wingpads, sheath of hind legs curved beneath the wing pads (Fig. 5 A, B) (Brundin, 1966). Within Podonominae, this new species may be related *Jurochilus*, based on the combination of naked eyes, five-palpomeres maxillary palps (Fig. 7A, B), thorax short, postnotum short/ narrow and strap-like, pupae with ovoid thoracic horns and large plastron occupying around 80 % of thoracic horns, fore and midlegs with a sharp bend, hind legs ending curved anteriorly in the direction of the head under the wing pads, running in parallel to the fore and midlegs, wingpads very short, barely reaching

the second abdominal segment. Abdominal segments II-VII quadrangular, wider than long, anal lobes absent, segments 8 and 9 are modified into the terminal disc, oval in shape (Fig. 2A-C, Fig. 3A-C, Fig. 4A-B).

4.2. Remarks

Placement of the new species into the Podonominae is based on the combination of the large thoracic horns with strong plastron only occurring in some Tanypodinae and Podonominae, and since we cannot access setation of the abdomen, which contains characters which are autapomorphies of Podonominae (such as presence of wavy setae on the abdominal segments VIII and IX), we had to rely on the positions of leg sheaths to verify the subfamily affinities of the species. In most Podonominae fore- and midlegs going straight down the middle of the body and ending between the wingtips, and hindlegs distal tarsomers curved under the wing (Brundin, 1966, 1975). We have however conducted extensive comparison of the leg sheath position in the modern representatives of Podonominae and Tanypodinae (Fig. 9A-C), and it appears

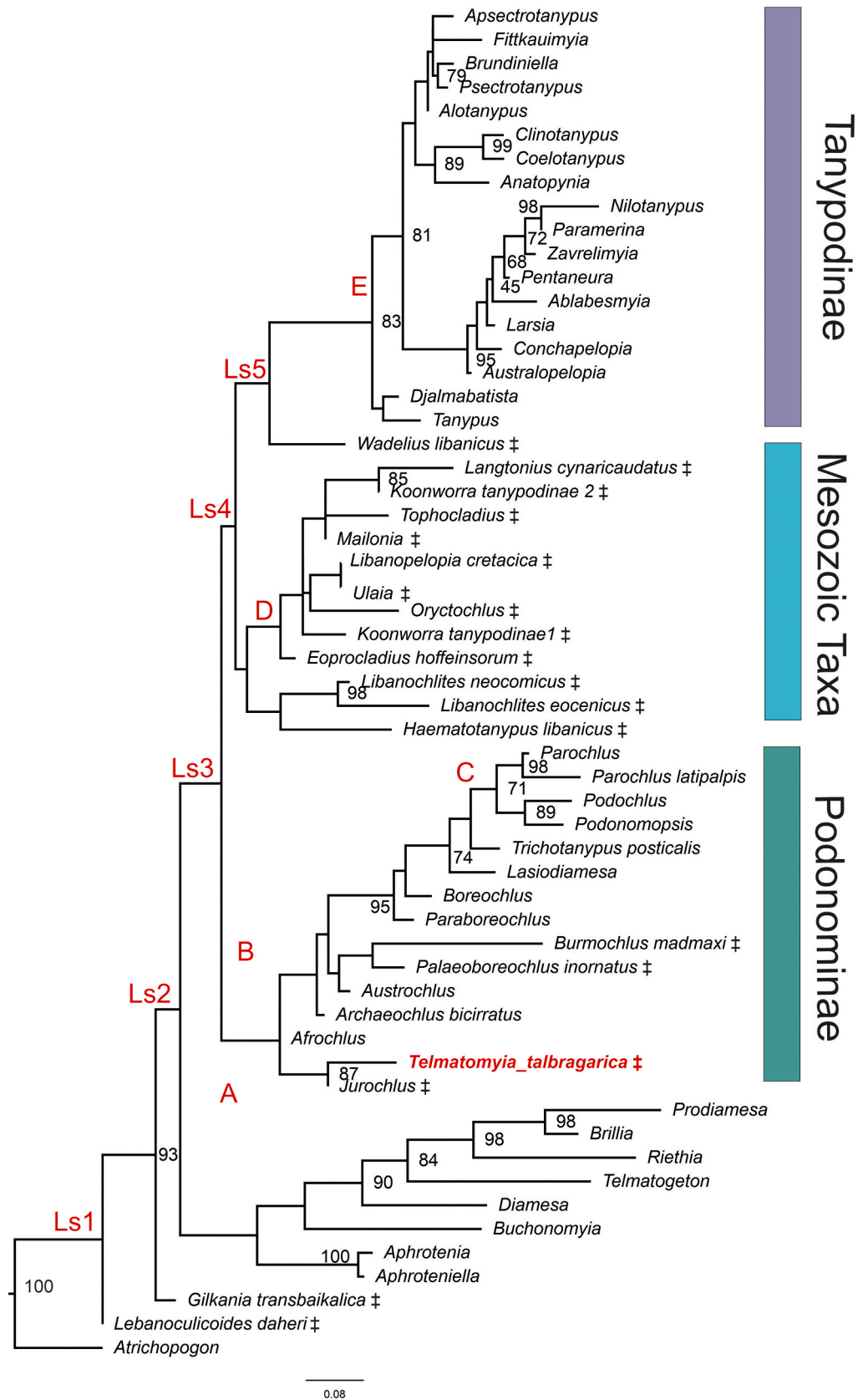


Fig. 12. Maximum likelihood tree, morphological dataset (38 spp, 88 characters). Support values for the maximum likelihood, in %, are provided below the nodes (values below 70 % are not shown). Fossil taxa marked with “†” symbol. Nodes: “A”- *Telmatomyia* + *Jurochilus*, “B” – crown-group Podonominae, “C” – *Parochlus*, “D” – mesozoic taxa adjacent to Tanypodinae, “E” – crown-group Tanypodinae; “Ls1”-” Ls5” – nodes containing fossils with support less than 70 %.

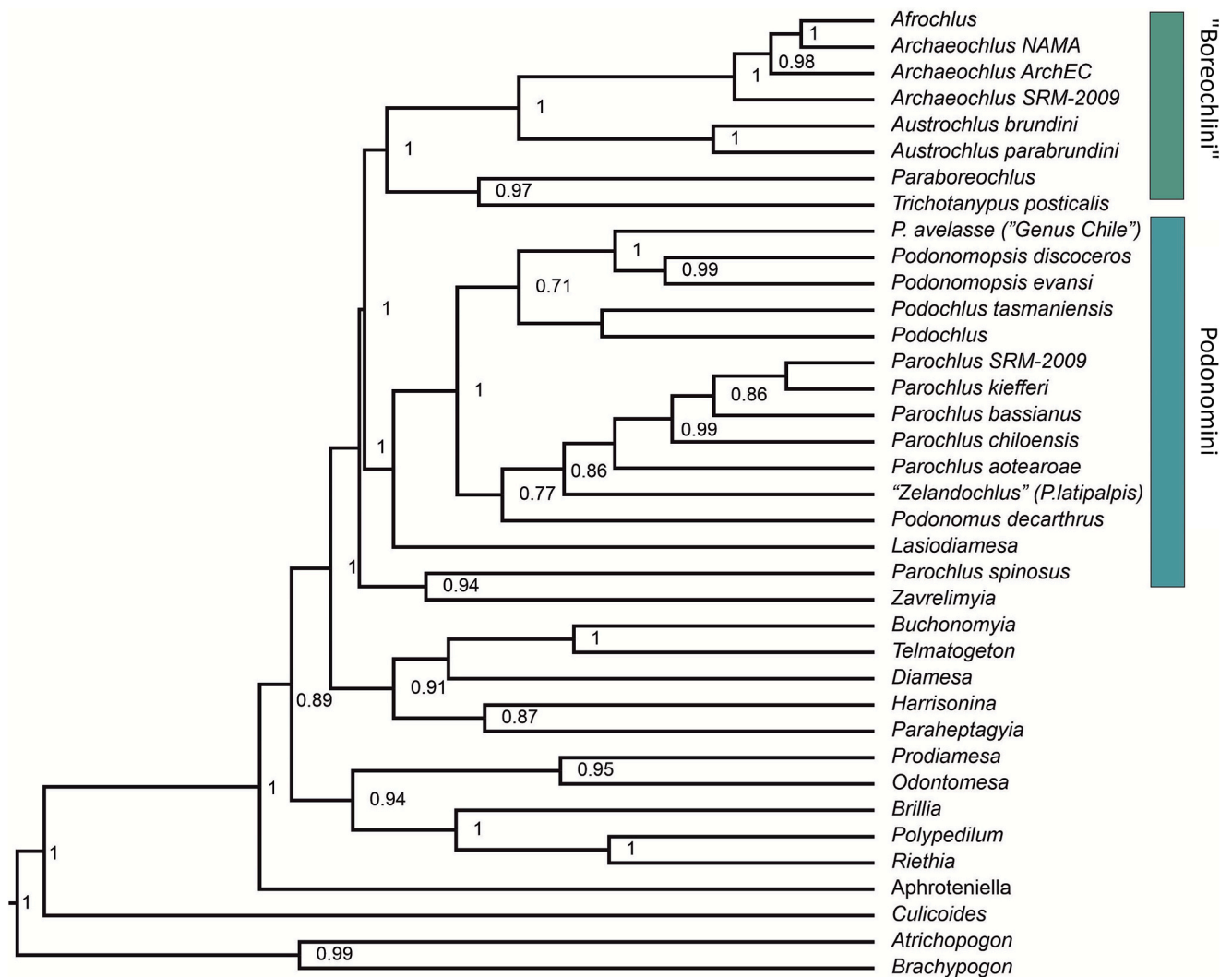


Fig. 13. Bayesian inference (100.000.000 runs), molecular dataset (COI + 28 s + 18 s + CAD3). Support values provided are posterior probabilities (probabilities below 0.7 are not shown).

that in most of the Podonominae analyzed (except *Trichotanyptus*, Fig. 10A, B) their fore and mid leg tips rest straight between the wing pads, while in all the Tanypodinae representatives examined, tips of all legs have been curved under the wing pads at least slightly. Additionally, tibia and femora of all Podonominae pupae examined, formed a sharper angle, around 40–45° while in most Tanypodinae there fewer sharp angles in the leg sheath, with leg elements mostly transitioning into one another through the sweeping curves. Therefore, leg position of the *T. talbargarensis* provides a strong corroboration for its affinity with Podonominae. Of course, the most notable feature of this new species is a composite terminal disc, made up of segments 8 and 9 of the abdomen. In the extant chironomid fauna, such character is considered to be an autapomorphy of the Telmatogetoninae (Sæther, 1977). We have compared the fossils of *T. talbargarensis* with the pupae of the extant Telmatogetoninae, and it is apparent that the pupae of the Telmatogetoninae are quite different from the new species (Fig. 11A–F). Most importantly, leg sheath of the hindlegs of the Telmatogetoninae are looping under the wing sheath, before exiting again distally from the wing pads, which is not the case for the *T. talbargarensis* (Fig. 5A, B). Also, on the leg sheaths of the Telmatogetoninae, delimitations of the tarsomeres 1–5 are clearly visible, which is not the case either in the new fossil nor in the extant Podonominae (Fig. 5A, B, Fig. 9A–C, Fig. 11A–F). Additionally, thoracic horns of the Telmatogetoninae have a distinct, anvil-shape, very different from *T. talbargarica* (Fig. 6C, D, Fig. 11C, D).

4.3. Phylogenetic position of the new species and related taxa (morphology-based)

Maximum likelihood phylogenetic analysis of the position of the new species, have putatively corroborated its affinity with Podonominae. Most of the nodes containing fossils have got support below 70 %, due to unavailability of the most characters for the fossil taxa (see methods).

Most of the tested fossils, that have previously been interpreted as members of Podonominae, (Kalugina, 1980, 1985, 1993, Lukashevich, 2012, 2020, Lukashevich and Ansoerge, 2024, Lukashevich and Przhiboro, 2011, 2012, 2018), were resolved as members of Tanypodinae or groups sister to Tanypodinae and Podonominae (see node D) (Fig. 12). For example, genera *Libanochilites*, *Tophocladus* and *Langtonius* have all fallen into the clade aggregating sister-taxa to Tanypodinae (node D). *Gilkania transbaicalica* Lukashevich, 2020 was resolved as a sister group to the rest of Chironomidae, which probably was an artefact of most of the characters missing in this particular taxon, due to an only partial preservation of the available specimens (Lukashevich, 2020). The node containing all the monophyletic Tanypodinae also includes a sister group to the rest of Tanypodinae (node E), made up of Cretaceous and Jurassic fossils Chironomidae. Including both species of *Libanochilites* (Brundin, 1976, Baranov et al., 2019), *Langtonius* (Lukashevich and Przhiboro, 2018), *Wadelius* (Azar et al., 2008), *Haematotanyptus* (Azar et al., 2008) and "Koonworra tanypodinae 2" (Jell and Duncan, 1986).

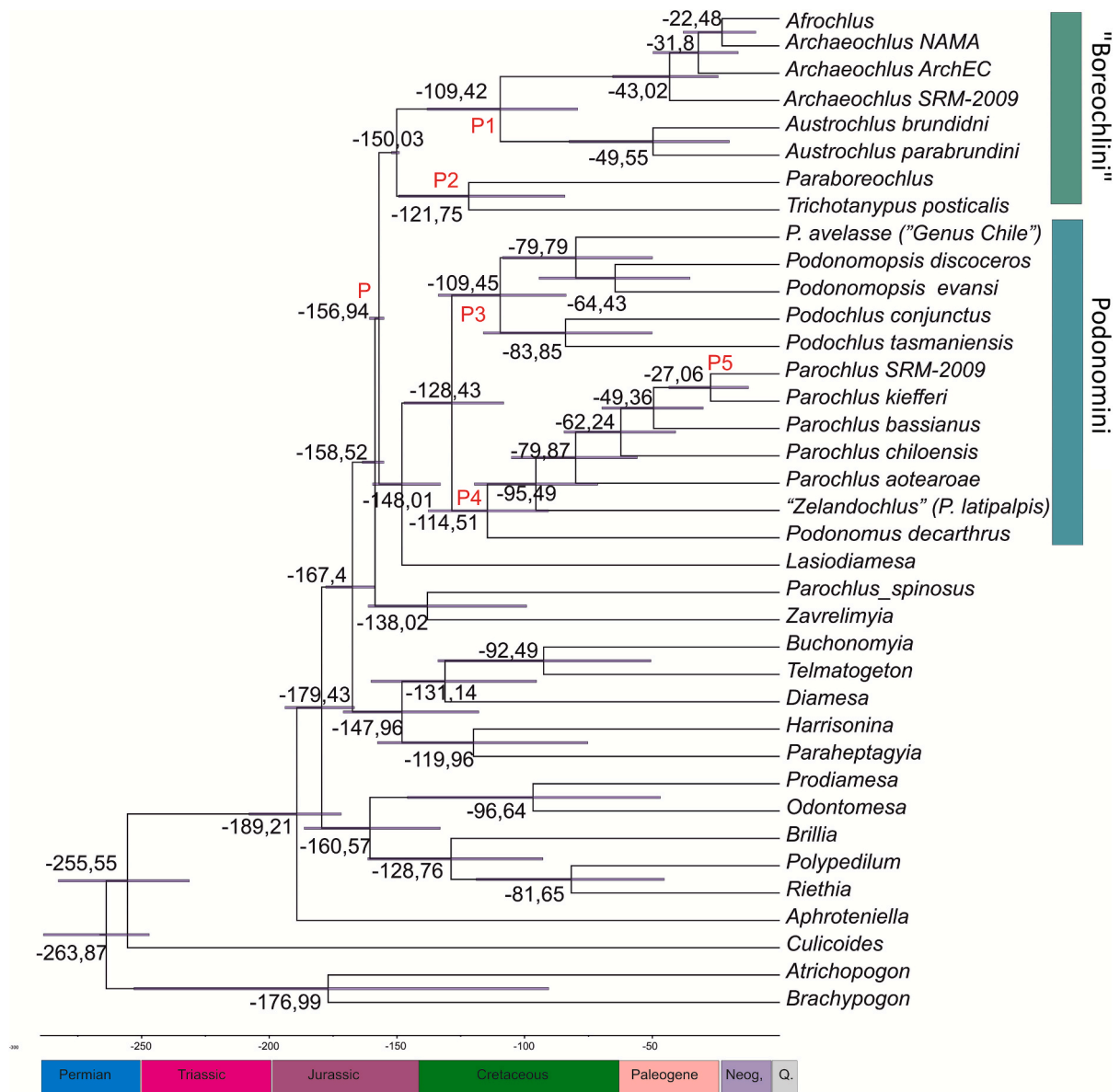


Fig. 14. Estimated divergence times of Podonominae and Tanypodinae based on molecular sequence data (same as tree at the Fig. 12). Nodes on the phylogram represent means of the probability distributions for node ages, with time intervals for 95 % probability of actual age represented as broad bars. Mean age of the node is provided as a number as well. Nodes names: “P”-Podonominae, “P1” – Gondwana “Boreochlini”; “P2”- Laurasia “Boreochlini”; “P3” – Podonomopsis + *Podochlus*, “P4”- *Parochlus*, “P5” – Holarctic *Parochlus*.

Fossil genera *Oryctochnus*, *Mallonina*, *Ulaia* and *Tophocladius* were recovered as sister groups to the rest of Tanypodinae, which were recovered as a monophyletic group (node D).

Palaeoboreochlus inornatus + *Burmochlus madmaxi* were recovered as a sister to the “Boreochlini”+ *Telmatomyia talbragarica* were recovered as a sister group to the rest of Podonominae.

4.4. Estimation of the divergence time

Our phylogenetic analysis of 2399 bp of DNA sequence data(CO1 + 18 s + 28 s + CAD) recovered monophyly of Podonominae (Figs. 13, 14 node P) as previously reported (Cranston et al., 2010, 2011, Krosch et al., 2022). In particular, the age of the monophyletic Podonominae is median of 158 Mya (CI 125–160.5 MYA). “Boreochlini” latest common

Table 3
Comparison of the BioGeoBEARS models, likelihoods and parameters.

Model	LnL	numparams	d	e	j
DEC	-31.93083	2	0.01924212	0.0001661174	0.0
DEC + J	-31.93083	2	0.01924212	0.0001661174	0.0
DIVALIKE	-31.04323	2	0.02032326	1e-12	0.0
DIVALIKE + J	-30.0214	3	0.01728081	1e-12	0.17291101
BAYAREALIKE	-38.14484	2	0.01843613	0.001298042	0.0
BAYAREALIKE + J	-35.57228	3	0.01471662	0.00081542	0.02874386

Table 4a

Comparison of the BioGeoBEARS models, AIC: Log-Likelihood and Degrees of Freedom.

alt	null	LnLalt	LnLnull	DFalt	DFnull	DF	Dstatistic	pval
DEC + J	DEC	−31.93	−31.93	3	2	1	0	1
DIVALIKE + J	DIVALIKE	−30.02	−31.04	3	2	1	2.04	0.15
BAYAREALIKE + J	BAYAREALIKE	−35.57	−38.14	3	2	1	5.15	0.023

Table 4b

Comparison of the BioGeoBEARS models, AIC: Test Statistics and AIC Weights.

test	tail	AIC1	AIC2	AICwt1	AICwt2	AICweight_ratio_model1	AICweight_ratio_model2
DEC + J chi2	one-tailed	69.86	67.86	0.27	0.73	0.37	2.72
DIVALIKE + J chi2	one-tailed	66.04	66.09	0.51	0.49	1.02	0.98
BAYAREALIKE + J chi2	one-tailed	77.14	80.29	0.83	0.17	4.82	0.21

ancestor is aged about 150 MYA (Node P1, P2) (CI 152–155.7 MYA). Podonomini's latest common ancestor is ca. 128 MYA (nodes P3–P5) (CI 150–110 MYA). (Fig. 14).

4.5. Ancestral range estimation

We ran 6 models for BiogeoBEARS for binary distribution “Gondwana-Laurasia” for all the taxa. Best performing model in “Gondwana-Laurasia” binary model was a BAYAREALIKE + J model (Tables 3, 4a, 4b). Overall both BAYAREALIKE + J were suggesting an origin of the Podonominae in Gondwana, with some clades of the group migrating to the Northern Hemisphere by 150 MYA (Fig. 15). Divergence of the Gondwanan and Laurasian “Boreochlini” had occurred around 150 MYA (Fig. 14, Fig. 15), whilst divergence between (mostly) Gondwanan Podonomini and Laurasian *Lasiodiamesa* has occurred around 148 MYA (Fig. 13, Fig. 14). Divergence between *Parochlus* representatives of the Southern Hemisphere, and *Parochlus kiefferi* –group – only representative of Podonomini *s.str* in the Northern Hemisphere has occurred around 27 MYA (Fig. 13, Fig. 14, node P5).

5. Discussion

Jurassic Podonominae fossils discovered over the last decade have led to suggestions that the subfamily originated in Laurasia in the Jurassic. Here we describe the oldest record of Gondwanan Podonominae that reveals the group either originated in Gondwana or in Laurasia much earlier than previously thought. This new species with its unique adaptation for the turbulent habitats shows that these traits are not only characteristic of marine tidal taxa but also those that occur in large freshwater lakes.

5.1. Phylogenetic position of the new species and related taxa

The Podonominae have long been recognized as the sister group to Tanypodinae+(Diamesinae+(Orthocladiinae + Chironominae)) – based on the molecular data (Ashe and O'Connor, 2009, Cranston et al., 2012). However, our phylogenetic analysis of the available morphological data casts new light on the recent assertion by the Lukashevich (2012), Lukashevich and Przhiboro (2012) that fossil taxon *Oryctocheilus* is a member of the Podonominae.

Most of the fossils that initially hypothesized as members of Podonominae (Kalugina, 1985; Lukashevich, 2012, 2020; Lukashevich and Ansoorge, 2024, Lukashevich and Przhiboro, 2011, 2012, 2018) were resolved in our analysis as members of Tanypodinae or a sister group to Tanypodinae and Podonominae (Fig. 12, Fig. 13, Fig. 14, Fig. 15). For example, the genera *Libanochchilites*, *Tophocladius* and *Langtonius* all aggregate in the clade sister to Tanypodinae. We recovered *Gilkania transbaicalica* Lukashevich, 2020 as sister to the Aphroteniinae, but this is probably an artifact of partial preservation of the available specimens that means most characters are missing in this particular taxon

(Lukashevich, 2020).

Extant Podonominae and related fossil taxa formed a monophyletic group. In addition to extant Podonominae this node includes several fossils; *Palaeoboreochlus inornatus* Baranov and Andersen, 2014, *Burmochlus madmaxi* Giitka et al., 2019, *Jurochilus* spp and *Telmatomyia talbragarica* gen. et sp. nov.

Palaeoboreochlus inornatus + *B. madmaxi* form a group sister to the other Podonominae representatives. Topology of these nodes was highly congruent with previous studies (Cranston et al., 2010, 2012, Siri and Brodin, 2014, 2024).

Representatives of Cretaceous Chironomidae including both species of *Libanochchilites* (Brundin, 1976, Baranov et al., 2019), *Langtonius* Lukashevich and Przhiboro, 2018, *Wadelius* Azar et al., 2008, *Haematotanypus* Azar et al., 2008 and “Koonworra tanypodinae 2” (Jell and Duncan, 1986) formed group sister to the extant Tanypodinae, which were recovered a monophyletic group.

Many nodes containing fossils were recovered with low support values, due to the lack of information about morphological characters across the life stages (Ls1–Ls5, Fig. 12). This is a common problem in the phylogenetic analyses of insects that include fossils (Klopfstein and Spasojevic, 2019).

5.2. Estimation of most recent common ancestor

Using molecular data and fossil calibration the common ancestor of the Podonominae and its Tanypodinae has previously been estimated to be around 135 MYA (Cranston et al. 2010). Utilizing recently described fossils including *Telmatomyia talbragarica* gen. et sp. nov. To help constrain node age we inferred an earlier age of 158 ± 3 MYA for their most recent common ancestor (Fig. 14).

Our phylogenetic analysis recovered monophyly of both Tanypodinae and Podonominae, following previous analysis by (Cranston et al., 2010, 2012, Krosch et al., 2022). In particular, the crown age of the Podonominae has a median of 150 Mya (CI 110–190 MYA). Within Podonominae the most recent common ancestor of “Boreochlini” is aged about 100 MYA (CI 140–55 MYA) and tribe Podonomini is ca. 55 MYA (CI 75–35 MYA) (Fig. 14). Monophyly of the Tanypodinae was confirmed with their latest common ancestor at about 100 MYA (CI 150–75 MYA).

5.3. Specialized adaptations of the new species

Some extant chironomids have become highly specialized in their lifestyle, living as commensals of sponges (Fusari et al., 2008) and bivalves (Gordon et al., 1978), xylophages of the waterlogged wood (Cranston and McKie, 2006), or as ectoparasites of other insects and fishes (Armitage et al., 1995, Ashe and O'Connor, 2002).

Some aspects of lifestyle can be preserved in the fossil record (Baranov et al., 2023). Among the most extreme specializations exhibited by chironomids are adaptations to life in the intertidal zone

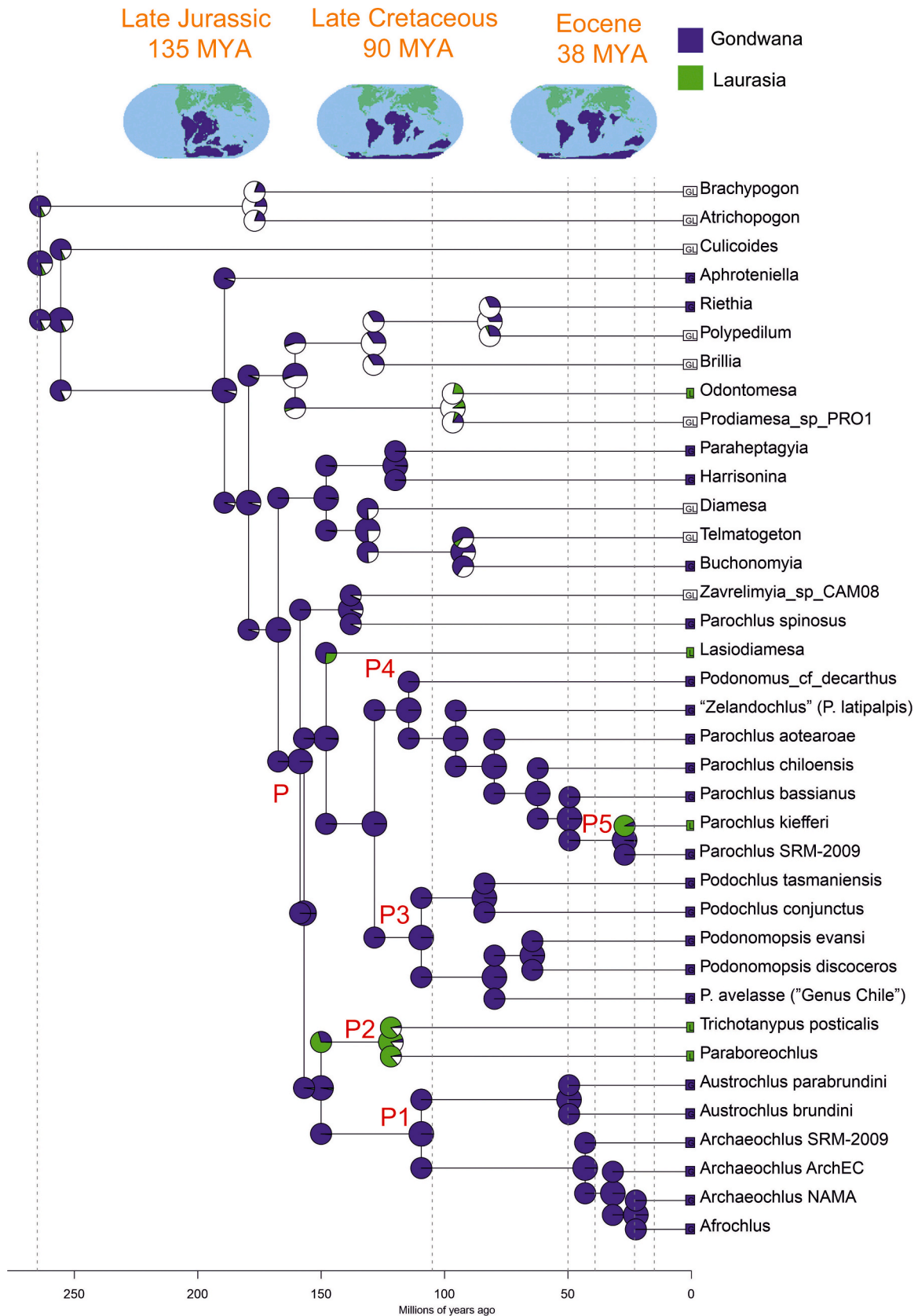


Fig. 15. Ancestral range estimation in BioGeoBEARS: best fitting model, BAYAREALIKE + J for the binary Laurasia-Gondwana distribution. Blue colour stands for Gondwana, green for Laurasia, white - distribution at both landmasses/ uncertain ancestral state. Nodes names: "P"-Podonominae, "P1" – Gondwana "Boreochlini"; "P2"- Laurasia "Boreochlini"; "P3" –*Podonomopsis* + *Podochlus*, "P4"- *Parochlus*, "P5" – Holarctic *Parochlus*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Fig. 16. Reconstruction of the lake shore of Talbragar Fossil Fish Bed, depicting several *T. talbragarica* pupae attached to a rock underwater. Pair of Orthognikleithridae fishes are patrolling the waters of the lake, while *Rhoetosaurus browni* is approaching the lakeshore, by the grove of “*Agathis*” *jurassica*. Artwork by Valentyna Inshyna, used with permission.

(Tang et al., 2023). Representatives of Telmatogetoninae (Chironomidae) in particular, have become so specialized for marine environments, that it was for a long time doubted that they were chironomids (Sæther, 1977). These adaptations mostly manifest as a drastic reduction and transformation of the anal lobes into a single pupal disc, and generally robust habitus with short, stocky legs and reduced wings in adults (Armitage et al., 1995). Until now, similar adaptations have never been observed in non-marine Chironomidae (Ferrington, 2008).

No marine chironomids have been recorded in the fossil record (Ashe et al., 2024). That being said, *Hintelmaniella noncatafractata* Baranov et Haug, 2022, shows surface-skimming adaptations, characteristic of some marine chironomids such as *Pontomyia* (Tang et al., 2023). In the case of *H. noncatafractata*, we are however sure that it was inhabiting freshwater habitat (Baranov et al., 2022).

Available evidence suggests that the Talbragar Fish Beds represent a large freshwater lake, housing a diverse fish community, and freshwater insects, most notably Plecoptera, which exclusively occur in the freshwater habitats (Beattie and Avery, 2012). It thus appears that the *Telmatomyia talbragarica* gen. et sp. nov. and other members of this lineage developed Telmatogetoninae-like adaptations in freshwater habitat. It is believed that extant Telmatogetoninae use the terminal disc to close the opening of the larval tube in which pupation occurs, preventing negative impacts of wave action and sedimentation on the pupal development (Langton, 1995). Another hypothesis proposes that extant Telmatogetoninae use the disc to prevent aggressive takeover of the larval tube by other Telmatogetoninae pupae vying for a more advantageous position (Langton, 1995). Finally, it is possible that pupae of the species used the disc to attach themselves to the substrate (Fig. 16), as disc it carries numerous muscle marks that suggest that it might have been used for suction (Fig. 3B).

5.4. Historical biogeography of Podonominae

Podonominae have been extremely important for the development of biogeographical models and historical biogeography theory as the focus of Brundin’s (1966) monograph on the nature of transantarctic relations. Brundin (1966) used early interpretation of Hennig’s phylogenetic systematics (1966) and newly emerging plate tectonic theory, to explain north north–south Hemisphere disjunction in Podonominae. He built a broad argument on the role of vicariance in formation of the distribution patterns in Podonominae in the southern Hemisphere, best explained in Brundin’s opinion by the breakup of Gondwana (Brundin, 1966).

Analyzing the distribution of the fossil Podonominae, Brundin

(1976) came to a conclusion that the subfamily likely originated on the northern edge of Gondwana. This was based on the presence of mid-Cretaceous *Libanochilites neocomicus* fossils in Lebanese amber (125 MY) from sediments that were at that time accumulating north of Gondwana (Brundin, 1976). Later discoveries in Russia, such as *Oryctocheilus* (Kalugina, 1985, Lukashovich, 2012, Lukashovich and Przhiboro, 2012) suggest instead that Podonominae originated in Laurasia, and this poses an interesting conundrum for Brundin’s original interpretation.

If indeed the center of Podonominae origin was in the southern Hemisphere, it is hard to explain away oldest northern Hemisphere fossils predating oldest southern Hemisphere ones by more than 20 MY (Brundin, 1966, 1976, Kalugina, 1985). It is important to note that the fossil record is strongly biased in terms of numbers towards the Northern Hemisphere, for reasons of land area (land mass area is smaller in the Southern Hemisphere) and historical and socio-cultural differences (Raja et al., 2022). It is possible, even probable, that older fossils of the Podonominae exist in the Southern Hemisphere but are yet to be found. In particular Antarctica has so far yielded almost no terrestrial arthropod fossils, most probably due to taphonomic reasons and the adversities associated with excavation in Antarctica, rather than due to the absence of such animals.

6. Conclusions

Currently available data on the historic biogeography of Podonominae can be explained by two possible hypotheses:

- A) Podonominae did originate in Gondwana, but their fossil record is lacking due to the taphonomic and study bias in fossils of the Southern Hemisphere.
- B) Podonominae did originate in Laurasia in the Early to Mid-Jurassic and have dispersed into Gondwana by mid-Jurassic, where some highly specialized forms emerged by Tithonian age of the Jurassic (such as *Telmatomyia talbragarica*), with their continuing radiation leading to the current, higher diversity of Podonominae in the Southern Hemisphere.

The first hypothesis is hard to test, barring emergence of the new fossils, but it is currently supported by the BioGeoBears-based ancestral range estimation, with BAYarea-like + J analysis having a largest likelihood (Table 3). BAYarea-like analysis normally models dispersal between two large, continuous areas, and provides much lower likelihoods for the models dealing with the biogeography of the terrestrial animals (Matzke, 2014). In the case of Podonominae, better performance of the BAYarea-like + J model makes sense, in the context of them moving between two large landmass-blocks – Gondwana and Laurasia. New discovery of Jurassic, highly specialized Podonominae from Australia, further supports Gondwana origins of the group.

7. Data Availability

All data and code used for the analyses are available at the Zenodo repository: <https://zenodo.org/records/15191920>.

CRedit authorship contribution statement

Viktor Baranov: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Matthew R. McCurry:** Writing – review & editing, Writing – original draft, Visualization, Resources, Methodology. **André P. Amaral:** Methodology. **Robert Beattie:** Writing – review & editing, Methodology, Conceptualization. **Steven A. Treweek:** Writing – review & editing, Writing – original draft, Software, Methodology, Investigation, Formal analysis.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

VB's work was supported by Ramon y Cajal 2021 Grant RYC2021-032144-I funded by MCIN/AEI/10.13039/501100011033 and by 'European Union NextGenerationEU/PRTR'. He was also supported by the LMU Excellence Initiative during the early stages of work on the manuscript. The work of VB at the Australian Museum was supported by The Australian Museum Foundation. MRM was funded through an ARC Linkage Grant (LP210301049). We acknowledge support for the publication fee by the CSIC Open Access Publication Support Initiative through its Unit of Information Resources for Research (URICI). VB is grateful to Joachim Haug (LMU) for his help with plates assembly, image processing, general discussion, and years of fruitful cooperation in general, Martin Spies, and Dieter Doczkal from the Zoologische Staatssammlung München (ZSM) for their invaluable help with the ZSM collection and literature searches. We thank Nigel McGrath and Lyn and Geoff Gale for generosity and help in accessing the site; Matt Hensley for assistance in excavating the site. Peter Cranston and Nick Matzke provided advice and constant support during the project. We are grateful to the Handling editor – Prof. Ian Somerville and two anonymous reviewers for their efforts in improving this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gr.2025.09.001>.

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