Phylogeny and biogeography of the enigmatic ghost lineage Cylindrotomidae (Diptera, Nematocera)

Iwona Kania-Kłosok1, André Nel2, Jacek Szwedo3, Wiktoria Jordan-Stasiło1 & Wiesław Krzemiński4

Ghost lineages have always challenged the understanding of organism evolution. They participate in misinterpretations in phylogenetic, clade dating, biogeographic, and paleoecologic studies. They directly result from fossilization biases and organism biology. The Cylindrotomidae are a perfect example of an unexplained ghost lineage during the Mesozoic, as its sister family Tipulidae is already well diversified during the Cretaceous, while the oldest Cylindrotomidae are Paleogene representatives of the extant genus Cylindrotoma and of the enigmatic fossil genus Cyttaromyia. Here we clarify the phylogenetic position of Cyttaromyia in the stem group of the whole family, suggesting that the crown group of the Cylindrotomidae began to diversify during the Cenozoic, unlike their sister group Tipulidae. We make a comparative analysis of all species in Cyttaromyia, together with the descriptions of the two new species, C. gelhausi sp. nov. and C. freiwaldi sp. nov., and the revision of C. obdurescens. The cylindrotomid biogeography seems to be incongruent with the phylogenetic analysis, the apparently most derived subfamily Stibadocerinae having apparently a ‘Gondwanan’ distribution, with some genera only known from Australia or Chile, while the most inclusive Cylindrotominae are Holarctic.

Cylindrotomidae Schinner, 18631 together with Limoniidae Speiser, 19092, Pediciidae Osten-Sacken, 18603, and Tipulidae Latreille, 18024 sensu stricto are classified within Tipuloidea Latreille, 18024, group of insects present in the fossil record since at least 220 Ma (Triassic)5. With only 71 extant6 and 16 extinct7 species, this smallest family within Tipuloidea is divided into two subfamilies Cylindrotominae, represented mainly in Holarctic Region, and Stibadocerinae with an example of vicariant distribution with a sister-group relationship between South American and East Asian taxa, supporting hypothesis an ‘ancestral’ trans-Pacific biota8.

According to phylogenetic synthesis based on combined morphological characters of adult, larvae and pupae, together with nuclear gene sequence data as 28S rDNA or CAD, the Cylindrotomidae are found as a sister group of Tipulidae (both being treated as subfamilies in Tipulidae in Ref.9. This group of insects is generally indicated as a sister group or being closely related to the Tipulidae by other authors10–20. But, within Cylindrotomidae21, only the representatives of subfamily Cylindrotominae are known from fossil record. The oldest described representatives of Cylindrotominae are only known from the Paleogene (56.0–47.8 Ma) by the extant genera Cylindrotoma Macquart, 183422 and Diogma Edwards, 193823–33, plus the extinct genus Cyttaromyia Scudder, 187734, while the oldest crown Tipulidae are Jurassic and the oldest stem Tipulidae are Cretaceous35–37. Thus, the Cylindrotomidae can be considered as a typical ghost lineage during the Mesozoic.

This phytophagous group of craneflies, which immatures lives among mosses and herbaceous plants. The Cylindrotomidae (Supplementary Data S1) probably knew a period of diversification during the Eocene, sufficient to become frequent enough to be found as fossils. Most of the fossil Cylindrotomidae are
know from the Middle Eocene Baltic amber\cite{31,32,38,39} and the Late Eocene Florissant Formation in USA\cite{24,30}. Three species of *Cylindrotoma* are known from impressions of the Ypresian Fur Formation; two species from the Ølst Formation of Denmark were described within *Cyttaromyia*\cite{29} (Supplementary Table S1). Four species of *Cyttaromyia* were described from the Eocene Green River Formation USA, the other were described from Florissant Formation and Kishenehn Formation in USA, Middle Salt Formation in Alsace (France), Biamo Formation in Russia, and from Baltic amber\cite{24,27,28,30,31,40}. Here we propose a morphological phylogenetic analysis to define the relationships between extinct genus *Cyttaromyia* and the other taxa in the family. We also describe two new species of *Cyttaromyia* on the basis of new fossils from the same Formation, and new techniques of research give us possibility to redescribe *Cyttaromyia obdurescens* Cockerell, 1924\cite{27}.

**Results**

**Systematic paleontology.**

Order Diptera Linnaeus, 1758\cite{32}
Infraorder Tipulomorpha Latreille, 1802\cite{4}
Family Cylindrotomidae Schinner, 1863\cite{1}
Subfamily Cylindrotominae Schinner, 1863\cite{1}
Genus *Cyttaromyia*

Type species: *C.yttaromyia fenestrate* Scudder, 1877\cite{34}, by monotypy.

Key to species of the genus *Cyttaromyia* Scudder, 1877\cite{34}

1. Wings without distinct patterning………………………………………………………………………………………..3.
   – Distinct patterns of coloration on wings…………………………………………………………………………2.

2. Rs longer than _R_23+4 and _R_3+4 combined………………………………………………………………………………..Cyttaromyia vahldieki Freiwald, 1991\cite{29}
   Denmark/Ølst Formation
   – Rs shorter than _R_23+4 and _R_3+4 combined…………………………………………………………………………Cyttaromyia rayona Freiwald & Krzemiński, 1991\cite{30}
   Russia/Biamo Formation

3. Wings hyaline…………………………………………………………………………………………………………………………4.
   – Wings pale brownish without conspicuous markings with end of marginal cell apically somewhat clouded (Cockerell, 1924)…………………………………………………………………………………..Cyttaromyia reclusa Cockerell, 1924\cite{26}
   USA/Green River Formation/Roan Mountains/Colorado

4. Vein _R_1 well-developed……………………………………………………………………………………………………5.
   – Vein _R_1 reduced…………………………………………………………………………………………………………..7.

5. Crossvein m-cu situated beyond bifurcation of Mb on _M_1+2 and _M_3+4; Sc terminating in C far beyond fork of Rs……………………………………………………………………………………………………6.
   – Crossvein m-cu situated at bifurcation of Mb on _M_1+2 and _M_3+4; Sc terminating in C just beyond fork of Rs……………………………………………………………………………………………………………..Cyttaromyia gelhausi sp. nov.
   USA/Green River Formation

6. Crossvein sc-r one of its length before tip of Sc; A1 tip before tip of Sc level………………………………………………Cyttaromyia obdurescens Cockerell, 1925\cite{27}
   USA/Green River Formation/Roan Mountains/Colorado
   – Crossvein sc-r at least two of its length before tip of Sc; _A_1 tip beyond _e_ tip of Sc level………………………………………………………………………………………………………………Cyttaromyia princetoniana Scudder, 1894\cite{38}
   USA/Green River Formation

7. Sc elongate, terminating in C well beyond level of fork of Rs………………………………………………………………8.
   – Sc short, terminating in C before level of fork of Rs…………………………………………………………………Cyttaromyia freiwaldi sp. nov.
   USA/Green River Formation
8. Crossvein m-cu situated at most or before fork of Mb on M1+2 and M3+4.  
   - Crossvein m-cu situated beyond fork of Mb on M1+2 and M3+4.  
   \[Cyttaromyia frelloi\] Krzemiński, 1998  
   Baltic amber

9. Vein r–r (R3) terminating before level of r′–m′, before level of m–m.  
   - Vein r–r (R3) terminating at level of r′–m′, behind level of m–m.  
   \[Cyttaromyia fenestrata\] Scudder, 1877  
   USA/Green River Formation

10. d′-cell as long as d-cell or shorter.  
   - d′-cell longer than d-cell.  
   \[Cyttaromyia lynnae\] De Jong, 2019  
   USA/Kishenehn Formation.

11. M3+4 bifurcation on M3 and M4 approximately at level of m–m; d-cell 2× as long as M4; m–m beyond level of tip of r–r (R3).  
   - M3+4 bifurcation on M3 and M4 before level of m–m; d-cell 1.5× as long as M4; m–m approximately at level of tip of r–r (R3).  
   \[Cyttaromyia fuscula\] Cockerell, 1921  
   USA/Green River Formation

12. Fork of Mb at level of fork of Rs; d′-cell narrowed at base.  
   - Fork of Mb before level of fork of Rs; d′-cell narrow, but not narrowed at base.  
   \[Cyttaromyia quievreuxi\] Séguy, 1934  
   Alsace, France/Middle Salt Formation.

13. Tip of r–r (R3) beyond level of tip of fork of M3+4 on M3 and M4; Rs at 2× as long as R2+3+4.  
   - Tip of r–r (R3) before level of tip of fork of M3+4 on M3 and M4; Rs at approximately as long as R2+3+4.  
   \[Cyttaromyia rossi\] Krzemiński, 2019  
   UK/Isle of Wight/Bembridge Marl

\[Cyttaromyia obdurescens\] Cockerell, 1925  
(Fig. 1).

Material examined. Holotype No. 26284 (AMNH) (female); American Museum National History; Green River Formation USA, Eocene.

Emended diagnosis. Wing without color spots; Sc elongate, terminating in C well beyond level of fork of Rs, beyond r–m level but far before m–m and r′–m′ level; opposite approximately half the length of Rs; R1 well-developed; R2+3+4 longer than half length of Rs; d′-cell longer than d-cell, narrowed at its base; crossvein m-cu positioned beyond fork of Mb on M1+2 and M3+4; apical section of M3 almost as long as d-cell; A1 tip positioned near apex of wing, far behind level of Mb bifurcation on M1+2 and M3+4, before r–m level.

Comparison. \[Cyttaromyia obdurescens\] differs from \[C. fenestrata\], \[C. freiwaldi\] sp. nov., \[C. frelloi\], \[C. lynae\], \[C. quievreuxi\], \[C. scudder\], and \[C. vahldeki\] by a well-developed vein r–r (R3). Wing of \[C. obdurescens\] is without spot. \[C. rayona\] and \[C. vahldeki\] have different patterning of wings. In contrast to \[C. gelhausi\] sp. nov., crossvein m-cu is situated beyond Mb, while in \[C. gelhausi\] sp. nov., it is located at Mb bifurcation, in \[C. frelloi\] just before Mb bifurcation. In \[C. obdurescens\], vein sc-r is located one of its length from tip of Sc, tip of A1 is located before tip of Sc, while in \[C. princeotoniana\] vein sc-r is located at least two of its length before the tip of Sc, A1 tip is located beyond level of tip of Sc. In \[C. obdurescens\] crossvein m-cu is positioned beyond fork of Mb measured from base of wing, while in \[C. rossi\] m-cu is distinctly before fork of Mb.

\[Cyttaromyia gelhausi\] sp. nov.  
\[http://zoobank.org/URN: lsid:zoobank.org:act:9165E3D2-514B-4524-9F85-A9895CBF2A31.  
(Figs. 2, 3).
Material examined. Holotype MNHN.FA71341 (18a, male); additional material 18b, female; 18c, female (on the same slab with holotype); Muséum national d'Histoire naturelle (MNHN), Paris; Green River Formation USA, Eocene.

Figure 1. *Cyttaromyia obdurescens* Cockerell, 192527, holotype No. 26284 (AMNH) (female): (A) habitus, lateral view; (B) apex of wing; (C) head and thorax, enlarged lateral view; (D) haltera; (E) apex of wing, drawing; (F) wing; C. terminal part of abdomen with *ovipositor* visible. *cp, capitellum, pd, pedicellus of haltera, oc, ocellus, ped, pedicellus, pr, pronotum.*
**Etymology.** The specific name is given to honor Doctor John Gelhaus (Academy of Natural Sciences of Drexel University), the eminent specialist on extinct and extant insects.

**Diagnosis.** Flagellomeres short and relatively wide; wing without color spots; Sc not very elongate, terminating in C just beyond level of fork of Rs, opposite level of crossvein r–m; opposite approximately 1/10 length of R2+3+4; vein r–r (R2) terminating far before r′–m′ and just before m–m level, at level of basal part of M3; R1 well-developed; R2+3+4 longer than half length of Rs; d′-cell longer than d-cell, narrowed at its base; crossvein m-cu positioned at fork of Mb on M1+2 and M3+4; apical section of M3 almost as long as d-cell.

**Comparison.** Cyttaromyia gelhausi sp. nov. has no distinct color patterning of the wings in contrast to C. vahldieki and C. rayona. The wing of C. reclusa is pale brownish without conspicuous markings, but the end of the marginal cell and the veins bounding the discal cell apically are somewhat clouded. The body length of C. gelhausi sp. nov. is at most 6.83 mm, wing length 7 mm, while the body length of C. reclusa is 13.5 mm and wing length 12 mm. In C. gelhausi sp. nov. tibial spurs are absent while pattern of tibial spurs of C. frelloi is 1:1:2. Vein R1 is well-developed in C. gelhausi sp. nov., while in C. freiwaldi sp. nov., C. frelloi, C. fuscula, C. lynnae, C. quievreuxi, C. rossi, C. scudder, C. vahldieki R1 is reduced. In C. gelhausi sp. nov. Sc is very elongate, terminating in C just beyond level of fork of Rs, opposite level of crossvein r–m, while in C. fenestrata, C. frelloi, C. fuscula, C. lynnae, C. obdurescens, C. princeontiana, C. quievreuxi, C. rayona, C. scudder, and C. vahldieki, it is terminating far beyond level of Rs. In C. freiwaldi sp. nov. Sc terminating in C before Rs level. In C. fenestrata and C. vahldieki, Sc is very elongated, terminating in C opposite basal part of M3. Crossvein m-cu is positioned...
at fork of Mb on M_{1+2} and M_{3+4}; while in other fossil species of the genus *Cyttaromyia* this vein is situated beyond fork of Mb; in *C. frelloi* this vein is located before fork of Mb. Moreover, in *C. vahldieki* and *C. fenestrata* vein r–r (R_{2}) terminating in R_{3+4} beyond d‘ level, far beyond the level of basal part of M_{3}; in *C. gelhausi* sp. nov. this vein is terminating at the level of d’, at the level of basal part of M_{3}.

**Cyttaromyia freiwaldi** sp. nov.  (Figs. 4, 5).

http://zoobank.org/urn:lsid:zoobank.org:act:DB604450-AD47-4644-82E0-A33FEAEB7157.

**Material examined.** Holotype MNHN.FA71342 (70A, part/68, counterpart, female), additional material 70B, female, on the same slab as holotype), Muséum national d'Histoire naturelle (MNHN), Paris; Green River Formation USA, Eocene.

**Etymology.** The new species is dedicated to the German eminent researcher Doctor Andre Freiwald (Institut für Paläontologie, Universität Erlangen).

**Diagnosis.** Wing without color spots; Sc short, terminating in C before level of fork of Rs, far before level of crossvein r–m; vein r–r (R_{3}) terminating far before r’–m’ level and at m–m level, just beyond level of basal part of M_{3}; R_{1} atrophied; R_{2+3+4} longer than half length of Rs; d’–cell shorter than d-cell, narrowed at its base; crossvein m–cu positioned beyond fork of Mb on M_{1+2} and M_{3+4}; M_{3} shorter than d-cell.
Comparison. *Cyttaromyia freiwaldi* sp. nov. has no distinct patterning of the wings in contrast to *C. vahldieki* and *C. rayona*. In contrast to *C. reclusa*, the body length of *C. freiwaldi* sp. nov. is at most 4.8 mm, wing length 6.22 mm, while the body length of *C. reclusa* is 13.5 mm and wing is 12 mm long with the end of the marginal cell and the veins bounding the discal cell apically are somewhat clouded. *C. freiwaldi* sp. nov. differs from other

**Figure 4.** *Cyttaromyia freiwaldi* sp. nov. No. MNHN.F.A71342 (70A, part, female), (holotype): (A) habitus, dorsal view; (B) head, dorsal view; (C) ovipositor, dorsal view, (D) wing venation, (E) wing venation, drawing.
fossil species especially by point of termination of Sc. In C. freiwaldi sp. nov. vein Sc terminating in C before fork of Rs while in other fossil species, excluding C. reclusa\(^2\), Sc terminating in C just beyond or far beyond bifurcation of Rs. Moreover, in contrast to C. gelhausi sp. nov., C. obdurescens, C. princetoniana, and C. rayona, the vein R\(_1\) in C. freiwaldi sp. nov. is reduced. Vein r–r (R\(_2\)) of C. freiwaldi is terminating in R\(_{3+4}\) at d-cell level while in C. fenestrata and C. rayona beyond this level, in C. vahldieki even beyond d`-cell level (Supplementary Data S2).
Phylogenetic position of Cyttaromyia within Cylindrotomidae. The parsimony analysis yielded three equally most parsimonious cladograms, 53 steps long, with consistency index CI = 62, RI = 66. Their consensus majority rule cladogram is shown in Fig. 6A. The Cylindrotomidae clade is supported by six synapomorphies: presence of petiole (character 15, state 0), relationship of R₃ and R₄ (character 17, state 1), position of crossvein m-cu relative to the bifurcation of M₁₄ (character 18, state 1), shape of d-cell (character 20, state 1), position of tip of A₂ (character 25, state 0), morphology of aedeagus (character 28, state 2). Cyttaromyia is supported on consensus tree by the ‘presence of supernumerary crossvein connecting vein R₇⁻₈, with M₁ near its origin, to produce two discal cells’ (character 16, state 1). The clade (Cylindrotominae + Stibadocerinae (Hennig, 1973)) is supported by two synapomorphies, relationship of M₃ and M₄ (character 14, state 1), position of tip of A₃ (character 26, state 0). The clade [Phalacrocorica replicata Linnaeus, 1758 + (Liogma nodicornis Osten Sacken, 1865 + Triogma triscutala Shummel, 1829)] is supported by one synapomorphy, viz. position of crossvein m-cu relative to the bifurcation of Mb (character 19, state 1). Triogma triscutala appears as the sister-group to Liogma nodicornis, the clade (Liogma nodicornis + Triogma triscutala) being supported by three synapomorphies: shape of flagellomeres (character 2, state 1), position of R₃ (character 13, state 1), degree of reduction of crossvein r–m (character 24, state 1). The clade Stibadocerinae [= (Stibadocerodes australiensis Alexander, 1922 + (Stibadocera bullans Enderlein, 1912 + (Stibadocerella pristina Brunetti, 1918 + Stibadocerina chilensis Alexander, 1928)))] is supported by two synapomorphies: the number of branches of Rs reaching wing margin (character 9, state 1), relationship of R₃ and R₄ (character 17, state 2) (Supplementary Data S3).

Discussion
The subfamily Cylindrotominae currently contains more species and genera, compared to the Stibadocerinae. The oldest record of the extinct genus Cyttaromyia is Paleogene, as for the genus Cylindrotoma. The fossil record of the Cylindrotominae dated back to at least 56.0 Ma, with no evidences on older occurrences. Other representatives of Cylindrotominae are known in the Eocene, but most of them are strictly modern (Supplementary Figs. S1, S2).

According to our parsimony analysis (consensus tree), Cyttaromyia falls as sister group of all the extant genera of Cylindrotomidae, and thus belongs to the stem group of the family, and could correspond to a different subfamily. Also, the extant Cylindrotominae appear paraphyletic in respect to the Stibadocerinae because the two genera Cylindrotoma and Diogma fall in an unresolved polytomy with this subfamily plus a clade that contains the other cylindrotomine genera. Nevertheless, these results are preliminary and would need to be completed by the addition of characters, in particular molecular.

The Cylindrotominae (and also Cyttaromyia) have a Holarctic distribution, while the Stibadocerinae have a more disjunctive distribution in Indo-Malaysia, Australo-Papua and Southern Neotropics (Taiwan, China, Indonesia, Malaysia, India, Papua New Guinea, Philippines, Australia, and Chile). Such distribution resembles that of an ancient Gondwana group, with ‘relic’ taxa in Australia and Chile; but the present phylogenetic analysis would contradict this hypothesis, as the only known stem representative of the family is also Holarctic. Further analyses together with discoveries of fossil Cylindrotomidae in the Southern Hemisphere shall be necessary to clarify this complex, strange situation.

From a taxonomic point of view, Architipula is characterized by the occurrence of vein Sc tip beyond fork of Rs level, subequal to or a little shorter than veins R₁₃ and R₄ combined, distinctly inclined crossvein m-m relative to the bifurcation of Mb (character 19, state 1). Triogma triscutala appears as the sister-group to Liogma nodicornis, the clade (Liogma nodicornis + Triogma triscutala) being supported by three synapomorphies: shape of flagellomeres (character 2, state 1), position of R₃ (character 13, state 1), degree of reduction of crossvein r–m (character 24, state 1). The clade Stibadocerinae [= (Stibadocerodes australiensis Alexander, 1922 + (Stibadocera bullans Enderlein, 1912 + (Stibadocerella pristina Brunetti, 1918 + Stibadocerina chilensis Alexander, 1928)))] is supported by two synapomorphies: the number of branches of Rs reaching wing margin (character 9, state 1), relationship of R₃ and R₄ (character 17, state 2) (Supplementary Data S3, S4).

Conclusion
The revision of Cyttaromyia obdurescens and the description of two new species Cyttaromyia gelhausi sp. nov. and Cyttaromyia freiwaldi sp. nov., allowed us to propose a key to the species of this genus. We have also made the first morphological phylogenetic analysis of the Cylindrotomidae, with the in the rather surprising result of the putative paraphyly of the Cylindrotominae and a position of Cyttaromyia in the stem group of this family.

Material and methods
The study was based on material from the collection of the Muséum national d’Histoire naturelle (MNHN), Paris (five specimens) and American Museum National History (AMNH) (one specimen). The imprints from sediments of Green River Formation USA (age 50.3–46.2 Ma) were studied using a Nikon SMZ 1500 stereomicroscope equipped with a Nikon DS–Fi1 camera in University of Rzeszów. The microphotographs and measurements were taken with NIS–Elements D 3.0 software. Drawings were completed by tracing the photographs, nomenclature of wing venation was used.

The Eocene Green River Formation USA (50.3–46.2 Ma) is one of the most famous Eocene palaeontological sites of the World. The sediments include mainly calcium carbonate, calcite and aragonite. The occurrence of different types of sludge varies with the geological levels. Tipton Shale Member in Greater Green River Basin is the oldest rock formation of the Green River.

Placement of the genus Cyttaromyia within Cylindrotomidae was tested with the use of Maximum Parsimony (MP) criterion, implemented in TNT 1.5 software package, with the ‘Traditional Search’ options, with memory to store 99,999 trees, 10,000 replications, with 100 trees to save per replication; utilizing
Figure 6. (A) Consensus relationships tree of genera of subfamily Cylindrotominae. Filled circles indicate synapomorphies or autapomorphies; open circles indicate plesiomorphies. Number of character given above circles, states of characters below circles; (B) Wing venation of fossil Cylindrotominae with chronostratigraphic distribution view; (C) Wing venations of representatives of genera: Cylindrotoma, Cyttaromyia, Diogma, represented in fossil record. Wing venation redrawing24,25,27–29,31,34,42,50. Stratigraphic chart according to International Stratigraphic Chart, International Commission of Stratigraphy (v. 2021/05) https://stratigraphy.org/chart.
tree-bisection-reconnection (TBR) algorithm and collapsing zero length branches. The type species of extinct and extant genera of family Cylindrotomidae were included in the analysis. *Architipula seebachi* (Geinitz, 1884)—type species of the genus *Architipula* Handlirsch, 1906—was selected as outgroup because the *Architipulae* are closely related to Cylindrotominae. *Tipula oleracea* Linnaeus, 1758—was used as a type species of the genus *Tipula*, in the family Tipulidae, currently considered as the sister family of the Cylindrotomidae. The morphological data to the matrix were compiled in the Nexus file using Mesquite v. 3.61 build 927 57. All 28 characters of the imagoes used in the analysis were treated as unordered and unweighted (Supplementary Table S2). Equal weighting analysis (EW) was performed 58; the trees received were viewed and their features studied using WinClada 1.00.08 and ASADO 1.61, with Unambiguous Changes Only, Fast Optimization (ACC TRAN) and Slow Optimization (DELTRAN) options 57–59. Tree files received were adjusted using Corel Draw X3 and Photo-Paint Software. The 28 morphological characters of the imago observed in the fossil and recent material and used for analysis are listed below. The data matrix given is partly based on used morphological features 4,8,21,34,41,43–45,50,56.

Received: 28 January 2021; Accepted: 31 May 2021
Published online: 06 July 2021

References

1. Schiner, J. R. Vorlaufiger Commentar zum dipterologischen Theile der Fauna austriaca. V [concl.]. *Wiener Entomologische Monatschrift* 7, 217226 (1863).
2. Speiser, P. A Orthorapha. Orthorapha Nematocera. *Wissenschaftliche ergebnisse der Schwedischen zoologischen expedition nach dem Kilimandjaro, dem Meru und den umgebenden Massaisstappen Deutsch-Ostafrikas 1905–1906*, unterleitung von prof. dr. Ynge Sjostedt. *Diptera* 10, 31–65 (1909).
3. Osten Sacken, C. R. New genera and species of North American Tipulidae with short palpi, with an attempt at a new classification of the tribe. *Proc. Acad. Nat. Sci. Phila.* 1859, 197–254 (1860).
4. Latreille, P. A. Histoire naturelle, generale et particuliére, des Crustaces et des Insectes. Tome troisiéme. Ouvrage faisant suite a la histoire naturelle generale et particuliére, composee par Leclerc de Buffon, et redigée par C.S. Sonnini, membre de plusieurs societés savantes. *Familles naturelles des genres, Paris*, 13–467. I–xii (1802).
5. Krzemiński, W. *Tipula* (s. lato) eva n. sp. from Cretaceous (East Asia)—The oldest representative of the family Tipulidae (Diptera, Polyneura). *Acta Zool. Crac.* 35, 43–44 (1992).
6. Oosterbroek, P. Catalogue of the Crane–flies of the World. (Diptera: Tipulidae: Pedicidae, Limoniidae, Cylindrotomidae, Tipulidae). [https://ccw.naturalis.nl/](https://ccw.naturalis.nl/) Accessed 28 May 2020 (2020).
7. Evenhuis, N. L. Catalog of the fossil flies of the world (Insecta: Diptera). Version. 2.0. [http://hbs.bishopmuseum.org/fossilloci/](http://hbs.bishopmuseum.org/fossilloci/) Accessed 13 Feb 2014 (2014).
8. Ribeiro, G. C. The Neotropical genus Stibadocerina Alexander and its phylogenetic relationship to other Stibadocerinae genera: Further evidence of an ancestral trans-Pacific biota (Diptera: Cylindrotomidae). *Syst. Entomol.* 34, 324–333 (2009).
9. Petersen, M. J., Bertone, M. A., Wiegann, B. M. & Courtney, G. W. Phylogenetic synthesis or morphological and molecular data reveals new insights into the higer level classification of Tipulodidae (Diptera). *Syst. Entomol.* 35, 526–545 (2010).
10. Alexander, C. P. Notes on the genus *Dicanotypha* Osten Sacken (Tipulidae, Diptera). *Entomol. News* 30, 19–22 (1919).
11. Alexander, C. P. New or little-known Tipulidae (Diptera). III. Ethiopian species. *Ann. Mag. Nat. Hist.* 9(5), 465–472 (1920).
12. Savchenko, E. N. *Tipulidae. Fauna Ukrainy* 14, 1–551 (1966).
13. Savchenko, E. N. Limonideae of South Primorye. *Akademii Nauk Ukrainskoy SSR*, Kiev 1–156 (1983).
14. Brodo, F. A revision of the subfamily Cylindrotominae in North America (Diptera: Tipulidae). *Bull. U. S. Geol. Geogr. Surv. Territ.* 126 (1), 103–107 (2000).
15. Oosterbroek, P. & Theowald, B. Phylogeny of the Tipuloida based on characters of larvae and pupae (Diptera, Nematocera), with an index to the literature except Tipulidae. *Tidsskrift for Entomologie* 134, 211–267 (1991).
16. Stary, J. Phylogeny and classification of Tipulomorpha, with special emphasis on the family Limonideae. *Acta Zool. Crac.* 35, 11–36 (1992).
17. Ribeiro, G. C. The phylogeny of the Limnophilinae (Limoniidae) and the early evolution of the Tipulomorpha (Diptera). *Invertebr. Syst.* 22, 627–694 (2008).
18. Zhang, X. et al. Comparative Mt genomics of the Tipulodidae (Diptera: Nematocera: Tipulomorpha) and its implications for the phylogeny of the Tipulomorpha. *PLoS ONE* 11(6), 1–20 (2016).
19. Lukashchev, E. D. & Ribeiro, G. C. Mesozoic fossils and the phylogeny of Tipulomorpha (Insecta: Diptera). *J. Syst. Paleontol.* 17, 635–652 (2019).
20. Kang, Z., Zhang, X. & Yang, D. Characterization of the complete mitochondrial genome of the snow crane-fly *Chionea crusipes gracilistyla* (Diptera, Tipulidae, Limoniidae) with phylogenetic analysis. *Mitochondrial DNA (B)* 4, 2662–2663 (2019).
21. Osten Sacken, C. R. *Monographs of the Diptera of North America. Part IV*. Smithson. Misc. Collect. 8(219), 345 (1869).
22. Macquart, P. J. M. Histoire naturelle des insectes. Tome première. *N.E. Boret Paris. 578* (1834).
23. Edwards, E. W. On the British Lestremiinae, with notes on exotic species—3. (Diptera, Cecidomyiidae). *Proc. R. Entomol. Soc. Lond. (B)* 7, 102–108 (2009).
24. Scudder, S. H. Tertiary Tipulidae, with special reference to those of Florissant, Colorado. *Proc. Am. Philos. Soc.* 32, 163–245 (1894).
25. Cockerell, T. D. A. Eocene insects from the Rocky Mountains. *Proc. U.S. Natl. Mus.* 57, 233–260 (1921).
26. Cockerell, T. D. A. Fossil insects in the United States National Museum. *Proc. U.S. Natl. Mus.* 64(13), 1–15 (1924).
27. Cockerell, T. D. A. Plant and insect fossils from the Green River Eocene of Colorado. *Proc. U.S. Natl. Mus.* 66(19), 1–13 (1925).
28. Séguy, E. Un nouveau Cylindrotomine fossile (Tipulidae). *Encycl. Entomol. (B)* 17(7), 47–48 (1934).
29. Freiwald, A. Insekten aus der Fur-Formation von Dänemark (Moler, oberes Paleozän/ unteres Eozän). 5. Cylindrotomidae (Diptera: Tipulomorpha). *Meyniana* 43, 97–123 (1991).
30. Freiwald, A. & Krzemiński, W. Cylindrotomidae (Diptera, Tipulomorpha) from the Paleogene of Bohlsyama Svetlovodnaya (eastern Asiatic USSR). *Palaontol. Z.* 65, 339–344 (1991).
31. Krzemiński, W. *Cytatromyia frellii* sp. n., the first representative of the family Cylindrotomidae in Baltic amber (Diptera: Tipulomorpha). *Polskie Pismo Entomologiczne* 67, 303–308 (1998).
32. Podenas, S. A new species of *Diogma* Edwards, 1938 (Diptera, Cylindrotomidae) from Baltic amber (Eocene). *Trans. Am. Entomol. Soc.* 126(1), 103–107 (2000).
33. Brodo, F. A review of the subfamily Cylindrotominae in North America (Diptera: Tipulidae). *Univ. Kansas Sci. Bull.* 47, 71–115 (1967).
34. Scudder, S. H. The first discovered traces of fossil insects in the American territories. *Bull. U.S. Geol. Geogr. Surv. Territ.* 3, 741–762 (1877).
35. Krzemiński, W. & Ansorge, J. New Upper Jurassic Diptera (Limoniiidae, Eoptychopteridae) from the Solnhofen lithographic limestone (Bavaria, Germany). Stuttgarter Beiträge zur Naturkunde (B) 221, 1–7 (1995).
36. Lukashevich, E. D. Limoniidae (Diptera) in the Upper Jurassic of Shar Teg, Mongolia. Zoosynopsis 3, 131–154 (2009).
37. Krzemiński, W., Kopeć, K. & Kania, I. New and little known species from the genus Leptotarsus Guérin-Méneville, 1831 (Diptera: Tipulidae) from the Lower Cretaceous of Northern Brazil. Cretac. Res. 78, 103–108 (2017).
38. Loew, H. Über den Bernstein und die Bernsteinfauna. Programm der K. Realschule Meseritz 1–44 (1850).
39. Krzemiński, W. Revision of the fossil Cylindrotomidae (Diptera, Nematocera) from Florissant and White River, USA. Palaeontol. Z. 65, 333–338 (1991).
40. Krzemiński, W. et al. True flies (Insecta: Diptera) from the late Eocene insect limestone (Bembridge Marl) of the Isle of Wight, England, UK. Earth Environ. Sci. R. Soc. Edinb. 110, 495–554 (2019).
41. Linnaeus, C. Systema Naturae per Regna tria Naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. T. 1. Holmiæ: Impensis Direct. Laurentii Salvii. 800 (1758).
42. Greenwalt, D. E. et al. Diptera of the middle Eocene Kishenehn Formation. I. Documentation of diversity at the family level. Palaeontol. Electron. 22, 1–56 (2019).
43. Hennig, W. Flügelgeäder und System der Dipteren unter Berücksichtigung der aus dem Mesozoikum beschriebenen Fossilien. Beiträge zur Entomologie 4, 245–388 (1973).
44. Osten Sacken, C. R. Description of some new genera and species of North American Limnobiina. Part I. Proc. Entomol. Soc. Phila. 4, 224–241 (1865).
45. Schummel, T. E. Beschreibung der in Schlesien einheimischen Arten einiger Dipteren-Gattungen 1 Limnobia. Meigen. Beiträge zur Entomologie, besonders in Bezug auf Schlesien, Breslau 1, 97–201 (1829).
46. Alexander, C. P. New or little-known Tipulidae (Diptera) IX. Australasian species. Ann. Mag. Nat. Hist. 9(9), 297–315 (1922).
47. Enderlein, G. Ueber den Bernstein und die Bernsteinfauna. Zeitschrift der Deutschen Geologischen Gesellschaft 36, 566–583 (1884).
48. Brunetti, E. Revision of the Oriental Tipulidae with descriptions of new species. Part II. Rec. Indian Mus. 15, 255–344 (1918).
49. Alexander, C. P. Diptera. Fam. Tipulidae. Subfam. Cylindrotominae. Genera Insectorum. 187 (1927), 1–16 (1928).
50. Meigen, J. W. Systematische Beschreibung der bekannten europäischen zweiflügeligen Insecten. I. Friedrich Wilhelm Farstmann, Aachen, i–xxxvi+1–332+[1] (1818).
51. Kopć, K., Krzemiński, W., Skowron, K. & Coram, R. The genera Architipula Handlirsch, 1906 and Grammenia Krzemiński & Zessin, 1990 (Diptera: Limoniiidae) from the Lower Jurassic of England. Palaeontol. Electron. 20.1.15A, 1–7 (2017).
52. Self, J. G., Johnson, R. C., Brownfield, M. E. & Mercier, T. J. Stratigraphic cross sections of the Eocene Green River Formation in the Piceance Basin, northwestern Colorado. U.S. Geol. Surv. Digit. Data Ser. DDS-69-Y 5, 7 (2010).
53. Goloboff, P. A., Farris, J. & Nixon, K. TNT, a free program for phylogenetic analysis. Cladistics 24, 774–786 (2008).
54. Goloboff, P. A. & Catalano, S. TNT version 1.5, including a full implementation of phylogenetic morphometrics. Cladistics 32, 221–238 (2016).
55. Geinitz, F. E. Über die Fauna des Dobbertiner Lias. Zeitschrift der Deutschen Geologischen Gesellschaft 36, 566–583 (1884).
56. Handlirsch, A. Die fossilen Insecten und die Phylogenie der rezent Formen. Engelmann, Leipzig, (1906–1908).
57. Maddison, W. P. et al. Cladistic analysis of the Piceance Basin, northwestern Colorado: US. Geol. Surv. Digit. Data Set. DDS-69-Y 5, 7 (2010).
58. Nixon, K. C. WinClada ver. 1.00.08 Published by the author, Ithaca, New York (2002).
59. Nixon, K. C. ASADO, version 1.85 TNT-MrBayes Slaver (vl 5.30). Published by the author, Ithaca, New York (2004).

Acknowledgements
We would like to acknowledge for financial support of these research by JM Rector of University of Rzeszów (Al. Rejtana 16c, 35–601 Rzeszów). We would like to thanks two anonymous Reviewers for valuable comments and remarks.

Author contributions
I.K.-K. conceived and designed the study, lead and performed the data analysis, interpretations and writing, making photographs, graphical figures, analysis; correspondence. A.N. writing and corrections of the manuscript. J.S. corrections of phylogenetic analysis methods. W.J.-S. making photographs and drawing, graphical figures, analysis. W.K. corrections of the manuscript.

Funding
Open Access funding enabled and organized by the University of Rzeszów.

Competing interests
The authors declare no competing interests.

Additional information
Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-021-91719-w.

Correspondence and requests for materials should be addressed to I.K.-K.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher’s note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.
