



Triassic iotacyphids shed light on the venation of crown Thysanoptera and their stem relatives (Condylognatha: Holothysanoptera)

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Abstract

We report the discovery of the first Triassic ‘shielded thrips’ of the family Iotacyphidae, represented by two species: *Triassocypha prima* **gen. et sp. nov.** and *T. secunda* **sp. nov.** The species are described and illustrated, and comparisons are made with other stem-Thysanoptera lineages. The unique wing venation of Iotacyphidae and related families is reinterpreted in the light of these new fossils. The venation pattern supports the diagnosis of the family, as well as of higher clades within the broader lineage that includes both thrips and their extinct relatives (in the total group Holothysanoptera, formerly Thripida), and contributes to clarifying the systematics of thrips.

Keywords

Acercaria, classification, ‘Lophioneurida’, Middle Triassic, Monte San Giorgio, wing venation

1. Introduction

Extant thrips (Thysanoptera) are minute insects with exceptionally narrowed wings, with reduced venation and fringed margins. The mouthparts are asymmetrical and, like Hemiptera, form a sucking apparatus to feed on plant fluids or fungal spores (Heming 1993). Although modern thrips are easily characterized and distinctive, there is a

rich fossil record of stem groups (‘protolithrips’) forming a grade leading to crown-Thysanoptera and extending back to the Paleozoic. Most of these stem groups are diverse during the Early Mesozoic (from the Triassic through the Early Cretaceous), with more modern-appearing thrips dominating from the Early Cretaceous to the late

Cenozoic, and largely preserved as inclusions in amber (PBDB: <https://paleobiodb.org>). The stem-group lineages are, however, crucial for understanding the character transformations that progressively gave rise to the suite of synapomorphies we today understand as distinguishing modern thrips from their many relatives (Nel et al. 2014).

One of the more diverse groups among stem-Thysanoptera is the family Lophioneuridae Tillyard, 1921 (here-in classified as comprising two distinct families, below). These fossils, preserved largely as compressions but also including some inclusions in mid-Cretaceous amber, are vital for elucidating early relationships and homologies within Condylgnatha. Here we report the discovery of a lineage of stem-Thysanoptera from the Middle Triassic of Switzerland, previously known only from mid-Cretaceous amber of northern Myanmar. These insects significantly expand our knowledge of the “Lophioneurida”, extending their distribution into the Triassic of Europe, and allowing us to provide a reinterpretation of venational homologies across living and fossil relatives of the Thysanoptera.

2. Material and methods

Monte San Giorgio’s Middle Triassic carbonate succession is a UNESCO World Heritage site (Switzerland-Italy) famous for its well-preserved fossil fishes and marine reptiles (e.g., Rieppel 2019). In recent years, Monte San Giorgio has gained significant importance for fossil insects, revealing an exceptionally diverse and well-preserved assemblage (Montagna et al. 2024a, 2024b). The unique sedimentary conditions were the result of a long-term transgression and dysoxic to anoxic bottom waters (e.g., Bernasconi 1994; Stockar et al. 2013). Fossils were collected during the excavation led by the Museo cantonale di storia naturale (MCSN) in 2020 at the Val Mara VM 12 site (DMS geographical coordinates: 45°53’26’’N; 8°56’49’’E; valley of the Gaggiolo River, Fig. 1A), west of Meride village (Monte San Giorgio, Switzerland) (Montagna et al. 2024a). The fossil-bearing strata, which preserve the insect fauna, belong to the upper “Kalkschieferzone” (Senn 1924), dated to the late Ladinian (~239 Ma; Stockar et al. 2012) (Fig. 1B). These strata consist of alternating thin-bedded laminated limestones and marly limestones, with subordinate marlstones and calcareous marlstones, reflecting a shallow lagoon environment with seasonal salinity variations (Tintori 1990). During the Ladinian, the region experienced monsoonal circulation (Preto et al. 2010), leading to seasonal variations and density stratification in the hypersaline lagoon (Furrer 1995).

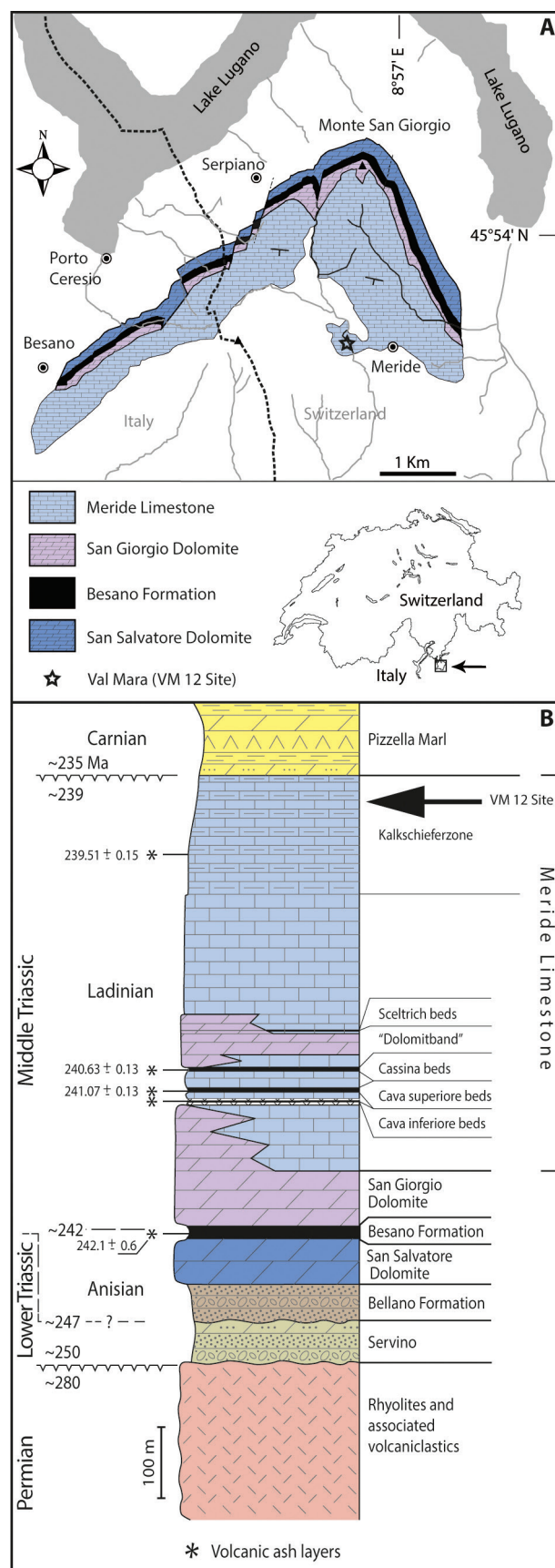


Figure 1. Location of Monte San Giorgio (Italy-Switzerland) UNESCO World Heritage and stratigraphic section of the Middle Triassic sediments. **A** Map with Monte San Giorgio, showing the carbonate Anisian–Ladinian sequence, the star indicates the location of the Val Mara VM12 excavation site. **B** Stratigraphic column of the Monte San Giorgio, the black arrow indicates the VM12 strata that yielded the here described specimens. Commissione scientifica transnazionale (after Stockar et al. 2012).

The fossils were prepared using a steel needle under a stereomicroscope, and high-quality images were captured using an Olympus SZX 12 microscope coupled with an Olympus UC50 camera and KEYENCE VHX-X1F digital microscope with VHX-7020 camera with VH-Z20T zoom lens. Post-processing of images was performed using Adobe Photoshop CS2. Venation terminology follows Nel et al. (2012) for the Acercaria, modified by Schubnel et al. (2020) to consider the presence of a postcubital vein (see also alternative hypotheses in interpretation presented in the Discussion, below). Vein names between brackets, e.g., ‘CuA’ or ‘M’, are those proposed by Cumming et al. (2024); those without brackets are newly accepted herein. Abbreviations for veins and crossveins are:

A anal vein; **C** costa; **Cu** cubitus; **CuA** cubitus anterior; **CuP**, cubitus posterior; **cua-cup** specialized crossvein between CuA and CuP; **M** median vein; **MA** media anterior; **MP** media posterior; **PCu** postcubitus; **R** radius; **RA** radius anterior; **RP** radius posterior; **ScP** subcosta posterior.

3. Results

Systematic palaeontology

Cohort Acercaria Börner, 1904

3.1. Superorder Holothysanoptera Engel, Montagna, Boderau, P. Nel, & A. Nel nov.

(Carboniferous Westphalothripidesidae P. Nel, Azar, Prokop, Roques, Hodebert, & A. Nel, 2012 to crown-Thysanoptera) (= “Thripida Fallén, 1814” sensu P. Nel et al. 2014)

Diagnosis. Left mandibular stylet, right absent; piercing lacinial stylets; pretarsus with eversible arolium; pretarsal claws reduced in adults; wings with fringe of long setae and CuA simple.

Included clades. Westphalothripidesidae, Lophioneroptera (spectral and shielded thrips), Betathysanoptera Engel (Zoropsocidae Tillyard, 1935, beta thrips), Thysanoptera (true thrips).

3.2. Clade Lophioneroptera Engel, Montagna, Boderau, P. Nel, & A. Nel nov.

(= “Lophioneurida Tillyard, 1921” sensu auctorum)

Remarks. We reject the name “Lophioneurida” as applied to this clade on the grounds that it and other names

like it above the family group, represent an attempt to impose a rogue nomenclatural system by way of changes to the Principle of Coordination relative to the ICZN family-group series. In brief, there is no such thing as “Lophioneurida Tillyard, 1921” as names above the family group are not coordinate with the family-group series of names. Tillyard (1921) established a family-group name, Lophioneuridae, based on the type genus *Lophioneurina* Tillyard, 1921 and therefore his name is coordinate throughout the ICZN-regulated family group (ICZN 1999), but not further through names outside of the family group. Efforts to either typify and/or make names above the level of the family group coordinate with those of families (e.g., Rohdendorf 1977; Rasnitsyn 1982) have never been adopted nor sanctioned by the ICZN (1999). Accordingly, such efforts to make them part of the natural coordination and typification of family-group names are operating outside of the bounds of the ICZN (1999). We therefore reject the use of “Lophioneurida” and other rogue attempts to circumvent the ICZN and force typified coordination of family-group names with those clearly outside of the ICZN-regulated system of names. The same problem applies to the family-group name Thripidae Fallén, 1814 as extended to a superorder as “Thripida”.

Diagnosis. Forewing with CuA re-emerging orthogonally from R+M+CuA.

Included families. Lophioneuridae Tillyard, 1921 (spectral thrips) and Iotacyphidae Shcherbakov, Bashkuev, & Shmakov, 2024 (shielded thrips).

3.3. Family Iotacyphidae Shcherbakov, Bashkuev, & Shmakov, 2024, stat. nov.

Iotacyphinae Shcherbakov, Bashkuev, & Shmakov, 2024: 416. Type genus: *Iotacypha* Shcherbakov, Bashkuev, & Shmakov, 2024.

Diagnosis. These insects are well characterized by the synapomorphic presence in the forewing of large median cells and strong angles in the courses of R and M, all absent in the Lophioneuridae (sensu Nel et al. 2012, 2014) and Moundthripidae Nel, Azar, & Nel, 2007. These three families have a CuA re-emerging first from R+M+CuA but CuA is not orthogonal to R+M in the Moundthripidae versus orthogonal in Iotacyphidae and Lophioneuridae (see below).

Included genera. *Burmacypha* Zherikhin, 2000 (mid-Cretaceous Kachin amber); *Iotacypha* Shcherbakov, Bashkuev, & Shmakov, 2024 (mid-Cretaceous Kachin amber); *Retiptera* Cumming, Engel, Lian, & Ulietzka, 2024 (mid-Cretaceous Kachin amber); *Triassocypha* gen. nov. (Middle Triassic, Monte San Giorgio, Switzerland).

3.4. *Triassocyphinae* subfam. nov.

<https://zoobank.org/BC3F6D67-3CC8-41E0-BC21-1E75C7D7B857>

Type genus. *Triassocypha* gen. nov.

Diagnosis. Two closed cells between R and M and a closed cell between the branches of M.

3.5. *Triassocypha* gen. nov.

<https://zoobank.org/F19D8697-6BE5-473B-A616-09FB13D-9CC0F>

Type species. *Triassocypha prima* sp. nov.

Etymology. The name is an artificial combination of Triassic, referring to period from which the fossils originate, and the Ancient Greek adjective κῦφός (kūphós, meaning, “bent forward” or “curved”; feminine κῦφή). The gender of the name is feminine.

Diagnosis. Forewing ScP re-emerging from R as a short, straight veinlet perpendicular to C; a closed cell between MA and MP; two longitudinal cells between R and M/MA; CuP+PCu well separated from A.

Included species. *Triassocypha prima* sp. nov. and *T. secunda* sp. nov., both from the Triassic of Monte San Giorgio.

3.6. *Triassocypha prima* sp. nov.

<https://zoobank.org/393685B4-0B19-4461-93FA-78D75D123F11>

Figures 2A, B, D, 3A

Material. Holotype, MCSN 8715 (a body with two forewings and one hind wing, legs, and one antenna apparently complete), stored in Museo cantonale di storia naturale, Lugano, Switzerland.

Locality and horizon. Upper Kalkschieferzone member of Meride Limestone (transition interval to Archelaus and Regoledanus Ammonoid Zones, upper Ladinian), Middle Triassic; VM12 site (DMS geographical coordinates: 45°53'26"N; 8°56'49"E), Val Mara near Meride, Monte San Giorgio, Switzerland.

Etymology. The specific epithet is the Latin adjective primus, meaning, “first” or “early”, and refers to this as the first described species of the genus.

Diagnosis. Forewing characters only: ma-mp longer than r-ma; distal-most cell between R and MA three times as long as wide.

Description. Body 1.3 mm long, presence of long macrosetae on the thorax and some wing veins. **Head:** head apparently orthognathous to prognathous, with a relatively long buccal cone; compound eyes rounded with diameter 0.1 mm; antenna elongate, with flagellomeres elongate, distal most flagellomeres shorter than other flagellomeres, scape large, pedicel apparently small. **Thorax:** thorax 0.5 mm long; all legs preserved and of similar shapes, apparently only two tarsomeres, basal one light brown and distal one dark brown. **Abdomen:** abdomen elongate and broad, 0.7 mm long, 0.55 mm wide; cerci absent. **Forewing venation:** forewing 1.6 mm long, 0.6 mm wide, pear-shaped, rounded apically, narrow basally; a common stem ScP+R+M+CuA from which CuA separates 0.2 mm from wing base, perpendicular to ScP+R+M and short before cua-cup terminates into vein; cua-cup 0.07 mm long, straight, aligned with distal part of CuA; CuA simple and curved distally, ending at wing margin 0.5 mm from wing base; CuP+PCu straight, well separated from A; A short, weakly curved; ScP re-emerging from R 0.8 mm from wing base, perpendicular to C and R, straight, 0.12 mm long; M separating from R 0.1 mm distal of base of CuA; stem of M curved, 0.25 mm long, separating into MA and MP and delimiting a broad elongate closed cell, 0.5 mm long, 0.2 mm wide; both MA and MP with a strong angle distally and ending on posterior margin at right angle; a long ma-mp perpendicular to MA and MP; two elongate, broad cells between R and MA, separated by r-ma perpendicular to R and MA, basal-most cell 0.35 mm long, 0.07 mm wide; distal-most cell 0.6 mm long, 0.2 mm wide; R forming an angle distal of ScP and straight distally; separating into RA and RP 0.45 mm distal of ScP; RA straight, short, rather oblique, nearly orthogonal with RP; RP forming a strong angle and reaching wing apex; straight, elongate rp-ma, 0.1 mm long.

3.7. *Triassocypha secunda* sp. nov.

<https://zoobank.org/A658AE57-4368-406E-9706-25E54BA181E2>

Figures 2C, E, 3B

Material. Holotype MCSN 8689 (a body with two forewings and fragments of legs), stored in Museo cantonale di storia naturale, Lugano, Switzerland.

Locality and horizon. Upper Kalkschieferzone member of Meride Limestone (transition interval to Archelaus and Regoledanus Ammonoid Zones, upper Ladinian), Middle Triassic; VM12 site (DMS geographical coordinates: 45°53'26"N; 8°56'49"E), Val Mara near Meride, Monte San Giorgio, Switzerland.

Etymology. The specific epithet is the Latin numeral secundus, meaning “second”, and refers to this as the second described species of the genus.

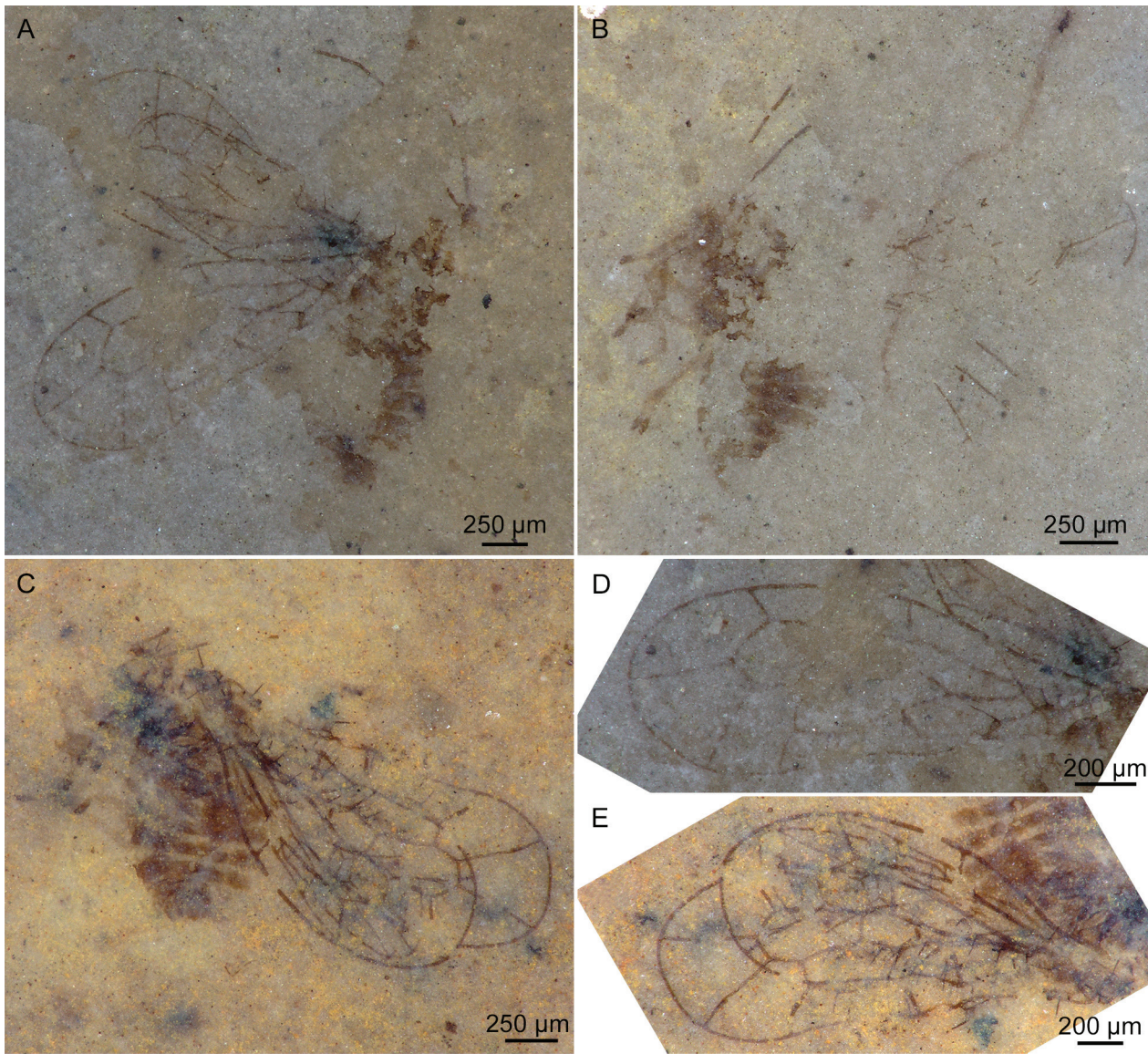


Figure 2. Habitus and forewing details of *Triassocypha* gen. nov. (Lophioneuroptera: Iotacyphidae) species. **A, B, D** *Triassocypha prima* sp. nov., holotype MCSN 8715 imprint (**A, D**) and counterimprint (**B**). **C, E** *Triassocypha secunda* sp. nov. holotype MCSN 8689.

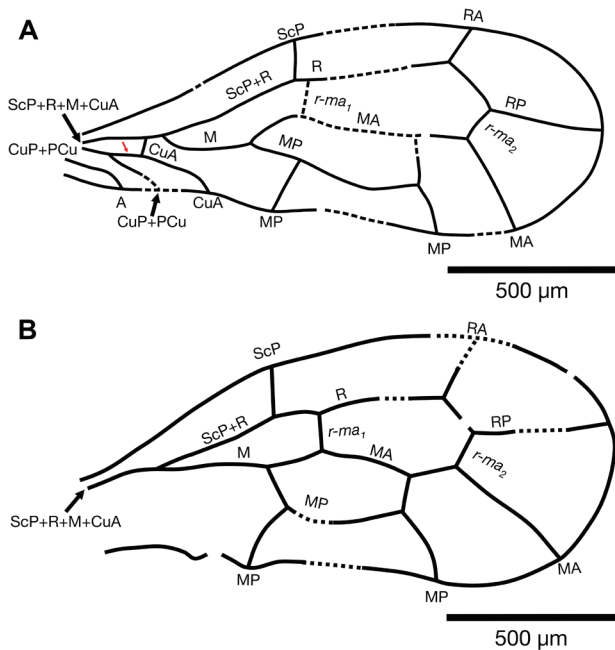


Figure 3. Forewing reconstructions of *Triassocypha* gen. nov. (Lophioneuroptera: Iotacyphidae) species. **A** *Triassocypha prima* sp. nov., holotype MCSN 8715. **B** *Triassocypha secunda* sp. nov. holotype MCSN 8689. The small red arrow indicates the cua-cup crossvein. Abbreviations: A = anal vein; Cu = cubitus; CuA = cubitus anterior; CuP = cubitus posterior; M = media vein; MA = media anterior; MP = media posterior; PCu = post-cubitus; R = radius; RA = radius anterior; RP = radius posterior; ScP = subcosta posterior.

Diagnosis. Forewing characters only: ma-mp as long as r-ma; distal-most cell between R and MA two times as long as wide.

Description. Body 1.4 mm long, presence of long macrosetae on the head, thorax, and some wing veins. **Head:** head apparently orthognathous to prognathous, with a relatively long buccal cone; compound eyes rounded with diameter 0.1 mm; [antenna not preserved]. **Thorax:** 0.37 mm long, 0.4 mm high; legs partly preserved. **Abdomen:** broad, 0.9 mm long, 0.7 mm wide; cerci absent. **Forewing venation:** forewing 1.7 mm long, 0.8 mm wide, pear-shaped, rounded apically, narrow basally; a common stem ScP+R+M+CuA; CuA, cua-cup, and CuP not visible; ScP re-emerging from R 0.8 mm from wing base, perpendicular to C and R, straight, 0.15 mm long; M separating from R 0.6 mm distal of base of CuA; stem of M curved, 0.5 mm long, separating into MA and MP and delimiting a broad elongate closed cell, 0.4 mm long, 0.19 mm wide; both MA and MP with a strong angle distally and ending on posterior margin at right angle; a long ma-mp perpendicular to MA and MP; two elongate, broad cells between R and MA, separated by r-ma perpendicular to R and MA, basal-most cell 0.4 mm long, 0.15 mm wide; distal-most cell 0.46 mm long, 0.23 mm wide; R forming an angle distal of ScP and straight distally, separating into RA and RP 0.5 mm distal of ScP; RA straight, short, rather oblique, nearly orthogonal with RP; RP forming a strong angle, reaching wing apex; straight, elongate rp-ma, 0.12 mm long.

4. Discussion

4.1. Untangling Lophoneuroptera systematics and wing venation homologies

Since both fossils exhibit remarkably similar forewing venation, it is most appropriate to place them within the same genus. They differ in the lengths of the cell between ScP and RA, that of the distal cell between R and MA, and of the cell between branches of M. Collectively, their venation is quite particular, with large polygonal cells and main veins forming pronounced angles. This kind of venation is encountered in some other Acercaria, such as Sphaeropsocidae (Psocodea) or some Hemiptera (e.g., Coleorrhyncha, Heteroptera: Schizopteridae). Regardless, the two new fossils differ greatly from Hemiptera in the simple CuA, a synapomorphy of the Holothysanoptera, versus with an areola postica present in Hemiptera and the Tetrastigmoptera (= 'Permopsocida', Permopsocoptera) (Huang et al. 2016). The Sphaeropsocidae have an entirely different pattern of venation (see Smithers 1990: fig. 121; Grimaldi and Engel 2006), except for the early Cretaceous *Asphaeropsocites neli* Azar, Engel, & Grimaldi, 2010. The latter genus shares with the new fossils veins ScP and RA reemerging as short veinlets from

ScP+R, a simple CuA, and three large polygonal cells medially in the forewing, but not homologous, with two between R and M; and the third one between M and CuA (Azar et al. 2010: Fig. 2) rather than between MA and MP in the two new fossils.

The forewing venations of the two new fossils are most similar to those of the Iotacyphidae (originally proposed as a subfamily but herein accorded familial rank), a small clade currently placed in the holothysanopteran lineage as related to Lophoneuridae, and which comprises the genera *Iotacypha*, *Burmacypha*, and *Retiptera*, all from mid-Cretaceous Kachin amber. Zherikhin (2000), Cumming et al. (2024), Shcherbakov et al. (2024), and Shcherbakov and Shmakov (2024) did not justify the attribution of the Iotacyphidae to Holothysanoptera and its subclade Lophoneuroptera. Nel et al. (2012) discussed the position of *Burmacypha* and suggested that it could belong to the Holothysanoptera based on the simple forewing CuA but also that it is difficult to determine the exact nature of the venation and body structures in the available material of that genus. *Iotacypha* and *Retiptera* have elongate mouthparts without any visible mandibles, unlike Psocodea and Tetrastigmoptera, suggesting that these are internalized. Additionally, the distal part of the labrum of *Retiptera brennae* Cumming, Engel, Lian, & Ulitzka, 2024 has a labral pad partly enclosed in the pair of elongate paraglossae of the labium (Cumming et al. 2024: fig. 4D). This complex structure probably guided the stylets of the laciniae and mandible(s), in the same manner as in extant thrips (Chistolm and Lewis 1984: Fig. 1D,F; Hunter and Ullman 1989: fig. 1B). The presence of a labral pad is also attested in the lophoneuropteran Moundthripidae *Moundthrips beatificus* P. Nel, Azar, & A. Nel, 2007 (P. Nel et al. 2025), and represents probably a synapomorphy of the Holothysanoptera. Unfortunately, the new fossils do not show clearly the head structures, but both seem to have a buccal cone (Fig. 2), a labral pad, and no strong mandibles that would be visible laterally, and collectively these character states suggest a position in Holothysanoptera.

Cumming et al. (2024: fig. 3) interpreted the forewing venation of Iotacyphidae as follows: CuA and M are basally fused with R and distally reemerge from it, and there is a specialized cua-cup between CuP and R+M+CuA, or M+CuA, or CuA (both synapomorphies of the Acercaria, sensu A. Nel et al. 2012). Based on a comparison of the current fossils, Iotacyphidae, Lophoneuridae, and other holothysanopterans we offer a different interpretation of some details as pertain the interpretations of Cumming et al. (2024), Shcherbakov et al. (2024), and Shcherbakov and Shmakov (2024) regarding CuA, CuP, and 1A.

If we follow the wing venation pattern of the Neoptera as proposed by Schubnel et al. (2020), a supplementary longitudinal main vein is present between the cubital and the anal veins, viz. the postcubital vein PCu. In the Acercaria, this vein is especially important as it is partly or totally fused with CuP. In the photograph of forewing base of *Iotacypha zherikhini* Shcherbakov, Bashkuev, & Shmakov, 2024 (figured in Cumming et al. 2024: figs 1D, 2A, 3D) and in photographs of the same species in

Shcherbakov et al (2024: figs 1–3), a straight, white (desclerotized?), and oblique structure is clearly visible in the area between ‘CuP’ and ‘1A’. This structure merges at the extreme wing base with the vein termed ‘1A’ by these authors. This ‘1A’ emerges from a curved basivenale bulla that has the typical shape of that of the vein PCu. The vein interpreted as the basal part of ‘CuP’ vanishes in the extreme basal part of the area between R+M+CuA and the ‘straight, white (desclerotized?), and oblique structure’. Given that it does not extend more proximally than the bulla, we therefore do not believe that this is CuP. Accordingly, we reinterpret the venation of *I. zherikhini* as follows: there is a basal fusion of R with M and with CuA in a common stem; CuP is independent of the stem R+M+CuA and corresponds to the ‘straight, white (desclerotized?), and oblique structure’; the vein interpreted as ‘1A’ is PCu and is basally touching CuP, as in many Neoptera, and especially Acercaria; the anal vein is reduced to the basal part of the posterior margin of the wing, note that in Neoptera the extreme base of the anal vein is well separated from the base of Cu and of PCu; cua-cup is the vein interpreted as the basal part of ‘CuP’ by Cumming et al. (2024); CuA emerges first and separately from R+M. CuA emerging first and orthogonal to R+M is interpreted as a putative synapomorphy of the clade Lophioneoptera (‘Lophioneurida’ sensu P. Nel et al. 2014: fig. 11), this CuA is simple; the vein interpreted as ‘CuA’ by Cumming et al (2024: fig. 2B) is likely M, it is not perpendicular to the radial vein but instead oblique. Its interpretation as ‘CuA’ is not congruent with an attribution of these insects as lophioneuropterans; the vein interpreted as ‘M’ in Cumming et al. (2024: fig. 2B) is RP and the vein interpreted as ‘MP’ is MA, while the vein interpreted as ‘MP+CuA’ is likely MP. It is quite unusual that a vein ‘MP’ would have a reversed course, directed towards the wing base; but if interpreted as MA, then its direction is more ‘usual’.

The fact that the character ‘CuA emerges first and separately from R+M’ is a putative synapomorphy of the clade Lophioneoptera is not obvious and could be contradicted by its presence in the Tetrastigmoptera, sister group of the Holothysanoptera + Hemiptera (Huang et al. 2016). This would suggest that it is a plesiomorphy or much more likely independently derived and simply a convergence. The relative positions of the re-emergences of CuA and M are highly variable within the Hemiptera: basal to, at the same point as, or distal to M+CuA. The character at least tacitly supports Lophioneoptera despite its more homoplastic occurrence in a more global phylogenetic distribution.

Based on our reinterpretation (see Fig. 4), in *R. brennae* the vein ‘CuP’ sensu Cumming et al. (2024: fig. 2C) should be CuA merging distally with CuP+PCu; there is a short common stem M+CuA separating from R, and from which CuA emerges perpendicularly; ‘CuA’ would be M, while ‘M’ should be a crossvein between MA and RP; ‘Rs+M’ should be RP, ‘MP+CuA’ is MP, and ‘MP’ would be MA. Likewise, in *Burmacypha longicornis* Zherikhin, 2000, there would be a longer common stem of M+CuA than in *Retiptera*, ‘Cu’ should be M+CuA, separating

into CuA (‘CuP’), perpendicular to M (‘CuA’), this CuA merges distally with CuP+PCu+1A (posterior margin of wing), M separates into MA (‘MP’) and MP (‘MP+CuA’), ‘M’ is a crossvein between MA and RP; ‘Rs+M’ would be RP. Forewing ScP is fused basally with R+M+CuA in *Retiptera*, *Iotacypha*, and *Triassocypha* and re-emerges distally as a curved vein in the two former and as a straight veinlet in the latter. In *Burmacypha*, the vein interpreted as ‘RA’ is in exactly the same position as in *Triassocypha*, supporting the hypothesis that it is also the re-emergence of ScP and that ScP basally is fused with R+M+CuA at wing base (and not separated from it).

Our current reinterpretation of the venation of these insects is congruent with the presence of a CuA that is simple (synapomorphy of Holothysanoptera), and perpendicular to R+M or to M (putative synapomorphy of the Lophioneoptera, but see below), and with the presence of a PCu (a character of the wing venation ground-

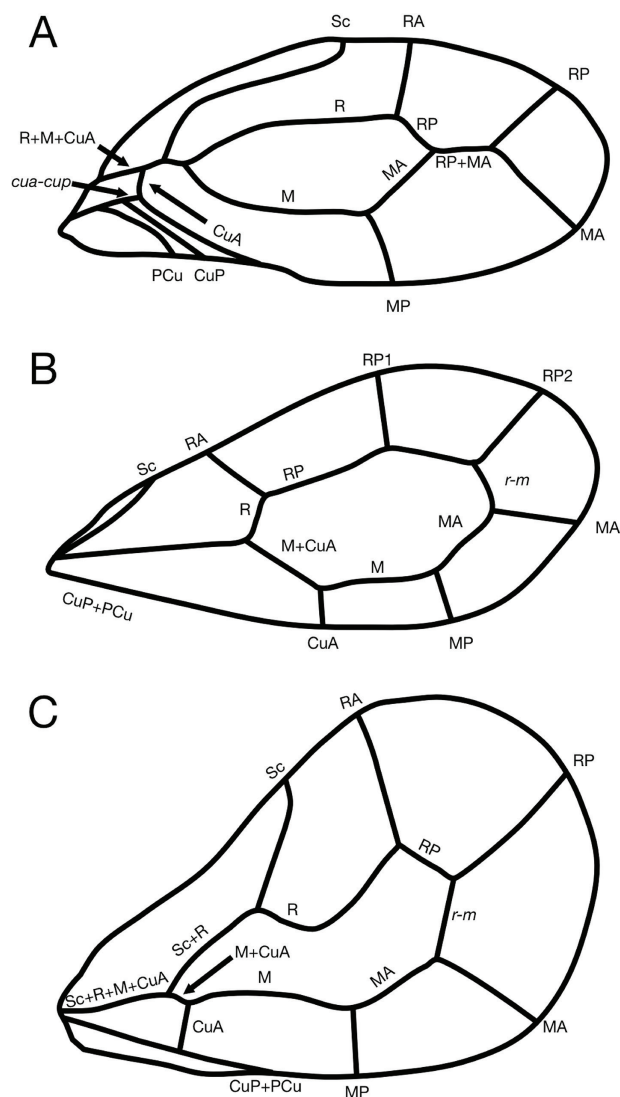


Figure 4. Kachin amber Iotacyphidae, reinterpretation of forewing venation. **A** *Iotacypha zherikhini* Shcherbakov, Bashkuev, & Shmakov, 2024. **B** *Burmacypha longicornis* Zherikhin, 2000; **C** *Retiptera brennae* Cumming, Engel, Lian, & Ullitzka, 2024 (redrawn after Cumming et al. 2024). Abbreviations as in Fig. 3.

plan of Neoptera). The reduction of CuA to a short vein in *Iotacypha* and *Burmacypha* is also congruent with the general tendency to the reduction of this vein in the Holothysanoptera, CuA perhaps being totally absent in extant Thysanoptera (but see discussion, below, on the absence of CuA in crown-Thysanoptera). Regardless, our interpretation of the venation supports an attribution of these clades to the Holothysanoptera and to the Lophioneuroptera. The new fossils differ from *Iotacypha*, *Burmacypha*, and *Retiptera* in the presence of two closed cells between R and M and a closed cell between the branches of M, versus only one cell between R and M and no closed cell between the branches of M (Fig. 4).

4.2. Presence or absence of an independent re-emergence of CuA in crown-Thysanoptera

Nel et al. (2012) interpreted the venation of the extant thrips as having no CuA re-emerging from R+M+CuA due to the exceedingly narrow wing and reduced venation. Nevertheless, another interpretation is possible. In the forewing of extant Aeolothripidae, the thrips family with the most complete venation and a wingspan suitable for studying basal venation structures, CuP is fused basally with PCu in a large basivenale bulla, common in all neopteran lineages (Schubnel et al. 2020), and distally separates from it in a longitudinal vein '1' that makes a strong angle and proceeds to the posterior margin as a short veinlet (Fig. 5). At that point, there is a vein that continues the basal part of CuP and ends into a vein '2' that posteriorly emerges from R+M+CuA (Fig. 5). The vein '1' has the same pattern of ornamentation as vein

'2', as frequently happens for the cua-cup of Hemiptera. One interpretation is that '1' is cua-cup, and then, vein '2' is M+CuA in which cua-cup terminates. Under this interpretation, CuA would merge with M, and the first short veinlet between M+CuA and the posterior wing margin could be CuA (vs. M2 as proposed by P. Nel et al. 2012). According to this, M would be simple in crown-Thysanoptera and, following this hypothesis, the synapomorphy of crown-Thysanoptera would be that M is simple vs CuA absent as previously proposed by P. Nel et al. (2012). In the representatives of stem-group Thysanoptera, M is forked and CuA remains present. This interpretation is certainly consistent with all observations.

The hypothesis about a re-emergence of CuA from M+CuA is tentative because it is not possible to distinguish the shape and color between the two distal branches of M+CuA. In Thripidae there is no short vein between M+CuA and the posterior wing margin, thus CuA (or M2) is absent as an independent vein. For now, we tentatively consider the hypothesis identifying a cua-cup vein and a re-emergence of M+CuA from R+M+CuA as stronger given the ornamentation of the veins and the position and nature of cua-cup as a crossvein between CuP and CuA (or M+CuA) more widely in the Acercaria. But we do note that the two interpretations of a re-emergence of CuA vs. M2 are challenging to distinguish amongst, and future work is needed in a broader sampling of fossil Holothysanoptera to properly elucidate the situation for crown-Thysanoptera. Furthermore, new comparative anatomical studies based on basivenal bullae and microtomography data (Schubnel et al. 2023) may allow a more accurate identification of the main veins in Thysanoptera, thereby helping to clarify whether the re-emergence of CuA has occurred.

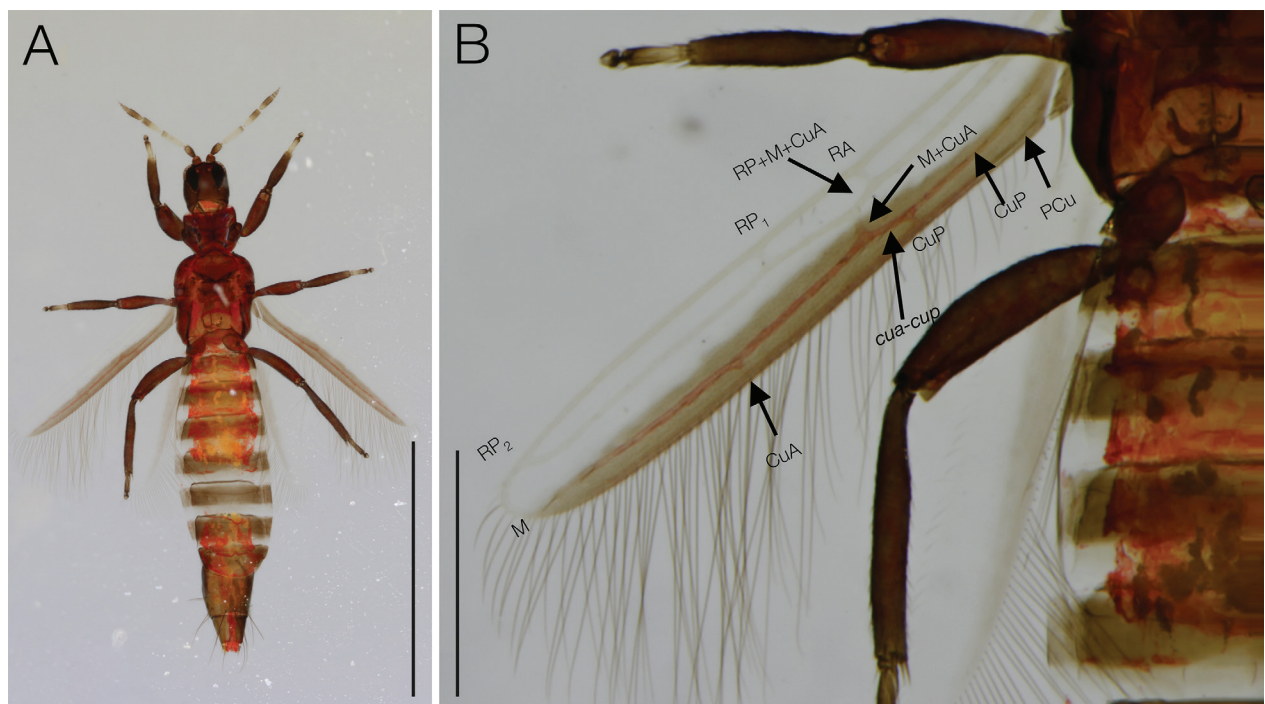


Figure 5. *Aeolothrips vittatus* Haliday, 1836 (Thysanoptera: Aeolothripidae). **A** General habitus (scale bar = 1 mm), **B** forewing details (scale bar = 250 μ m).

5. Declarations

Authors' contributions. Conceptualization: MB, MM, MSE, PN, AN. Data Curation: MM, FM, GM. Formal analysis: MB, MM, FM, GM, AS, MSE, PN, AN. Investigation: MB, MM, MSE, PN, AN. Supervision: MM, MSE, AN. Writing—original draft: MB, MM, MSE, AN. Writing—review and editing: MB, MM, FM, GM, AS, MSE, PN, AN.

Competing interests. The authors declare no competing interests.

Ethical aspects. Fossils were collected in Switzerland in accordance with national legal requirements and ethical standards.

Permissions. All fossils were collected under excavation permits granted to the Museo cantonale di storia naturale of Lugano, in accordance with Swiss legal requirements.

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