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Redefining the extinct orders Miomoptera and Hypoperlida as stem acercarian insects

Jakub Prokop1, Martina Pecharová1, Romain Garrouste2, Robert Beattie3, Ioana C. Chintauan-Marquier2† and André Nel2*†

Abstract

Background: The systematic positions of the extinct insect orders Hypoperlida, Miomoptera and Permopsocida were enigmatic and unstable for nearly a century. The recent studies based on new material, especially from the Cenomanian Burmese amber, shed light on evolutionary history of Acercaria resolving Permopsocida as the stem group of Condylognatha. However, the knowledge of the remaining two orders differs significantly.

Results: In this study, we describe new specimens and evaluate morphology of various structures with emphasis on the mouthparts and wing venation. Our results are primarily based on revisions of the type specimens with a proper delimitation of taxa Hypoperlida and Miomoptera followed by their significance for the evolutionary history of Acercaria. Three new genera as Belmomantis gen. nov., Elmomantis gen. nov., and Mazonopsocus gen. nov. are designated as members of Palaeomanteidae. The Pennsylvanian Mazonopsocus provides a minimum age for calibration, in accordance to the presence of crown acercarians during the late Carboniferous.

Conclusions: This contribution demonstrates that Hypoperlida and Miomoptera are stem groups of Acercaria. The putative clade (Hypoperlida + Miomoptera) is appearing as potential sister group of (Psocodea + (Permopsocida + (Thripida + Hemiptera))).

Keywords: Insecta, Acercaria, Late Palaeozoic, Mesozoic, Evolutionary history, Wing venation

Background

The Hypoperlida are an extinct order proposed by Martynov [1] for several enigmatic Permian insects. Since this date several authors placed many Paleozoic taxa in this order, on the basis of wing venation and mouthpart structures, even if the type genus and species Hypoperla elegans Martynov, 1928 [1] is based on isolated wings. The Hypoperlida are currently considered as a crucial order that would link the palaeopteran group Palaeodictyopterida with the neopteran clade Acercaria ([2]), under a general scheme of classification that refutes the division of pterygote insects into Palaeoptera and Neoptera, preferring a subdivision into Scara-baeones and Gryllones. Huang et al. [3]) made a revision of the acercarian order Permopsocida, as sister group of the clade (Thripida + Hemiptera). These results were confirmed by Yoshizawa & Lienhardt [4] who used different set of characters like wing base articulations. In the same paper of Huang et al. [3], the type family Hypoperlidae of the Hypoperlida was also revised. The wing venation of Hypoperla and related genera showed the acercarian synapomorphies as defined by Nel et al. [5]. Thus the family Hypoperlidae was falling as sister group of all other acercarian insects (Psocodea + (Permopsocida + (Thripida + Hemiptera))), even if they have retained the plesiomorphic condition of the presence of one-segmented cerci, unlike the orders of the crown group Acercaria. Thus the order ‘Hypoperlida’ has to be considered as belonging to the stem group of Acercaria. It remains that ca. fourteen fossil families are currently considered in Hypoperlida. Their positions need to be reconsidered.

The Miomoptera were another extinct order lacking clear synapomorphy to define it [5]. We had recently the opportunity to restudy the type species of the order Miomoptera, and describe new Carboniferous
and Permian miomopterans from Mazon Creek (USA), Elmo (USA), and Belmont (Australia). These fossils show wing venation patterns typical of the Acercaria and few differences with the Hypoperlidae. Therefore a revision of both Miomoptera and Hypoperlida is necessary.

**Results**

Superorder Clareocercaria (= Acercaria Börner, 1904 [6] sensu lato) (as pan group).

Etymology. Named after Clareo and cercaria pointing out that the presence or absence of cerci play important role in evolution.

Included orders. Miomoptera Martynov, 1927 [7] sensu nov.; Hypoperlida Martynov, 1928 [1] sensu nov. (as stem groups); Acercaria sensu stricto (crown group), comprising Psocodea Hagen, 1865 [8], Permopsocida Tillyard, 1926 [9] (sensu Huang et al., 2016 [3]), Thripida Fallen, 1814 [10], Hemiptera Linné, 1758 [11].

Diagnosis. Huang et al. [3] listed a series of body and wing venation synapomorphies for the crown group of Acercaria. Only the following wing venation synapomorphies are present in Hypoperlidae and Miomoptera too: a common stem R + M + CuA, M + CuA separating from R distally; convex CuA immediately emerging from M + CuA (three characters also present in the Archaeorthoptera sensu Béthoux and Nel [12]; long crossvein M + CuA (three characters also present in the Archaeorthoptera sensu Tillyard, 1926 [9] (sensu Huang et al., 2016 [3]), Thripida Fallen, 1814 [10], Hemiptera Linné, 1758 [11].

Remarks. The Miomoptera appear as a set of taxa currently supported by no clear synapomorphy. The presence of long cerci in the Palaeomanteidae suggests that it is in more ‘basal’ position than the Hypoperlida (Hypoperlidae) that have very short one-segmented cerci.

The Miomoptera have also been named Palaeomanteida Handlirsch, 1906 [21]. The other families currently considered as Miomoptera are here excluded from this order.

Type genus and species. *Palaeomantis schmidtii* Handlirsch, 1904 [22].

Age range. Late Carboniferous to Middle Permian.

**Remarks.** The Miomoptera appear as a set of taxa currently supported by no clear synapomorphy. The presence of long cerci in the Palaeomanteidae suggests that it is in more ‘basal’ position than the Hypoperlida (Hypoperlidae) that have very short one-segmented cerci.

The Miomoptera have also been named Palaeomanteida Handlirsch, 1906 (see Zhuzhgova et al. [23]). The Palaeomanteidae and the Hypoperlidae share two synapomorphies, viz. presences in the fore- and hindwings of darkened pterostigmata covering the area between C and anterior branch of RP (including the apex of RA) (see discussion below).

**Palaeomanteidae are stem acercarians**

The structure of the basal parts of the median and cubital veins is rather poorly known in the Palaeomanteidae, even if in general, the median vein is considered to be basally fused with radius (or very strongly approximate). In Elmomantis gen. nov., *Perunopterum* Kulakova, 1963 [24], *Permodelopterum* Kulakova, 1963 [24], *Archisialis* Martynov, 1933 [25], *Delopsocus* Tillyard, 1928 [26], *Miomatanoea* Martynov, 1927 [7] (note that Martynov [1927; 7]) gave two names for this genus: *Minomatoneura* and *Miomatanoea*) [27], *Palaeomantina* Rasnitsyn, 2004 [14], and some *Palaeomantis* species (e.g., the type species *P. schmidtii* Handlirsch, 1904 [22], *P. laeta* Novokshonov and Zhuzhgova, 2002 [28]), a vein that corresponds to the crossvein cua-cup of the Acercaria, is clearly present between CuP and M + CuA [24, 25, 26, 28].
More precisely, in *Palaeomantis laeta*, the basal part of Cu is concave together with the vein that Novokshonov and Zhuzhgova [28] considered as CuA. Thus this alleged concave ‘CuA’ cannot be CuA but either a branch of CuP (as in Archaeorthoptera) or a cross-vein. In *Palaeomantis schmidtii* Handlirsch, 1904 and *Elmomantis engeli* sp. nov., this vein is concave in its part near concave CuP and more convex near the convex M + CuA. This situation is exactly identical to what can be observed in extant Acercaria [5].

Previous authors that studied the Palaeomanteidae did not consider the relative convexity vs. concavity of the veins to homologize them, but only their relative positions. The situation is the same for the numerous taxa that are currently included in the Hypoperlida (see below the discussion on these taxa).
Unfortunately this vein between CuP and M + CuA seems to be not preserved in *Palaeomantis sylvensis* Martynov, 1940 [29], *P. apicalis* Rasnitsyn, 2004 [14], *P. ostertalis* (Guthörl, 1962) [30], *P. hangardi* (Guthörl, 1962) [30], but the other forewing veins of these taxa correspond to the same pattern present in the other species of *Palaeomantis* [14, 22, 28, 31].

All these fossils have forewing venations typical of Acercaria sensu Huang et al. [3], with the following synapomorphies: a common stem R + M + CuA; a faint crossvein cu-a-cup; an areola postica; RP and M with few branches; few crossveins. They share with the Hypoperlidae (sensu Huang et al. [3]) the presence of a pterostigmal zone around apex of RA extending below RA, a character absent in all other Acercaria, appearing as a potential synapomorphy of the Hypoperlidae, plus the three-branched RP. They differ from the Hypoperlidae in the median vein separating from CuA very far from their common re-emergence from R + M + CuA. This character is typical to the Palaeomanteidae Handlirsch, 1906 [21], and more precisely to the genera *Palaeomantis* Handlirsch, 1904 [22], *Pernodelopterum* Kukalová, 1963 [24], and *Perunopterum* Kukalová, 1963 [24] (Fig 1c, f). They also share the following characters: RP with 3–4 branches, and areola postica elongate.

In conclusion, we consider the Paleomanteidae as representatives of the stem group of the Acercaria, with one important difference with the Hypoperlidae, cerci long, probably two-segmented (Figs 1a-b, 1e); plus a less significant difference, longer stem M + CuA re-emerging from R + M + CuA. Whether Palaeomanteidae and Hypoperlidae are sister groups, as in our phylogenetic analysis (see below), or not is still an opened question because there are not enough characters to decide this important point.

Martynov [7] considered the Palaeomantidae as the type family of the Miomoptera Martynov, 1927 [7]. The Miomoptera have to be considered as belonging to the superorder Acercaria, and should comprise only the family Palaeomanteidae.

The other families currently included in the Miomoptera sensu Carpenter [32], viz. Archaemiopteridae Guthörl, 1939 [33] and Metropatoridae Handlirsch, 1906 [21], are based on incomplete wings (*Miomina* Martins-Neto and Gallego, 1999 [34], *Metropator* Handlirsch, 1906 [21], *Saaromioptera* Guthörl, 1963 [35], *Archaemioptera* Guthörl, 1939 [33]) with crucial structures of wing base not preserved, or wings that have not the acercarian characters (*Tychtodelopterum* Martynova, 1958 [36]) [32, 34, 37], or even as pinnule of fern (*Eodelopterum* Schmidt, 1962 [38]).
Thus we exclude them from the Miomoptera and consider them as Insecta: Neoptera of uncertain affinities. Nov., after Rasnitsyn [39]. This last author included the families Palaeomantiscidae and Permosialidae in the Miomoptera. After Storozhenko and Novokshonov [40], the Permosialidae have no cua-cup, thus they are probably not related to the Acercaria and to the Palaeomanteidae. The type genus of the Palaeomanticidae, *Palaeomantisca* Martynov, 1940 [29] was synonymized with the palaeomanteid *Sellardsioptis* Zalessky, 1939 [39, 41, 42].

Family Palaeomanteidae Handlirsch, 1906 [21].

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**Fig. 3** *Delopterum minutum* Sellards, 1909 (Miomoptera), Early Permian, Elmo, Kansas, USA. (a) photograph of neotype No. MCZ 3295b; (b) photograph of forewing venation No. MCZ 3203b; (c) photograph of forewing venation No. MCZ 3206; (d) photograph of No. MCZ 3209b; (e) photograph of No. MCZ 3201a; (f) photograph of forewing venation specimen No. MCZ 3296; (g) photograph of specimen No. MCZ 13311 (scale bars represent 1 mm). Abbreviations: ce – cerci, fl – flagellum, mp – maxillary palpus, pe – pedicelus, pt – pterostigma, sc – scapus, sm – sockets of macrotrichia, ts – tarsi.
Rasnitsyn, 2004 [14]) also proposed a key to the genera and species of this family.

Other genera accurately attributable to the Paleomanteidae, for the veins CuP cua-cup, M and CuA visible with their relative convexity: *Belmomantis* gen. nov., *Elmomantis* gen. nov., *Mazonopocus* gen. nov. *Perunopterus* Kukalová, 1963 [24], *Permodelopterus* Kukalová, 1963 [24] (Dostál [44] provided photographs showing the acercarian pattern of venation and especially the relative convexity of the basal veins of these two latter taxa), *Delopsocus* Tillyard, 1928 [26: Fig. 6].

Some genera are maintained in the Palaeomanteidae for their general wing venations very similar to that of *Palaeomantis*, and with veins CuP, cua-cup, M and CuA visible even if their relative convexities are unknown and should be verified: *Miomatoneurites* Martynova, 1958 [36], *Miomantisca* Zalessky, 1956, while *Permonia* Rohdendorf [48] did not consider in the Palaeomanteidae the three genera *Deloperiella* Zalessky, 1956, *Miomantiscia* Zalessky, 1956, and *Miomatoneurites* Zalessky, 1956, which were originally put in the Palaeomanteidae [49]. Carpenter [32] synonymized them with *Palaeomantis*. The basal parts of the wings of these taxa are unknown but they all have a long fusion of M with CuA and the veins ScP, RA and RP as in the other Palaeomanteidae [49]. *Miomantiscia* has a short ScP, ending on costa at the level of the base of RP, unlike *Palaeomantis schmidti*. These taxa should be revised.

Genus *Palaeomantis* Handlirsch, 1904 [22].

Type species *Palaeomantis schmidti* Handlirsch, 1904 [22].

(Fig. 2a-b).

Material. Handlirsch [22] based his description on the print and couterprint of a forewing overlying a hindwing plus what he considered as a hindwing. Lectotype specimen 5323–5 (182/2), paralecotype specimen 5320–5321. Palaeontological Institute of Russian Academy of Science collection (Moscow, Russia).

Age and outcrop. Middle Permian, Guadalupian, Roadian, lagoonal claystone, Baitugan Formation, Tikhie Gory, Russian Federation.

Redescription. Martynov [7] redescribed this species but he made several errors. Lectotype. A complete isolated forewing, maybe covering a second wing as some veins seem to be double, wing 6.8 mm long, 2.2 mm wide, no trace of coloration preserved, but apparently hyaline; ScP progressively diverging from radius, ending on costa 4.05 mm from wing base, with two oblique crossvein between it and costa; RA with distal fork; RP diverging from RA 2.4 mm from wing base; RP forked 1.3 mm distally, with anterior and posterior branches forked again 1.9 mm and 1.3 mm respectively distally; a common stem R + M + CuA, with M + CuA separating from R 1.6 mm from wing base; a faint transverse sigmoidal vein cua-cup between CuP and ending on M + CuA far from the base of this vein, with its part close to CuP concave and its part close to CuA convex;
relatively neutral M and convex CuA separating 0.9 mm from their common base; M with a deep fork; CuA with a clear areola postica, distinctly longer than high; CuP concave simple; two convex anal veins, first one simple, second with a small crossvein between it and first anal vein.

Paralectotype very similar to the lectotype, thus probably also a forewing, 7.3 mm long, 2.3 mm wide. 

**Belmomantis gen. nov.**

Type species. *Belmomantis azari* sp. nov.

Eymology. Named after Belmont, type locality, and Mantis, as for many Palaeomanteidae.

**Diagnosis.** As for the genus.

**Description.** A nearly complete isolated forewing, with only basal part of anal area not preserved, wing 5.7 mm long, 1.6 mm wide, apparently hyaline but with a darker elliptical pterostigmal zone around apex of RA extending below RA; ScP progressively diverging from radius, touching costa 0.4 mm distal of base of RP, 2.0 mm from wing base, and apparently ending on RA distally as a transverse vein between costa and RA; absence of crossveins between main veins; CuA with only one fork; cua-cup sigmoidal and ending on M + CuA far from the base of this vein; RP three-branched; a distinct pterostigma; stem of M long; absence of a crossvein below pterostigma between RA and RP.

**Belmomantis engeli** sp. nov.

**Material.** Holotype specimen USNM without number, Smithsonian Institution, National Museum of Natural History, Washington, USA.

**Diagnosis.** ScP touching C and apparently ending on RA distally as a transverse vein between costa and RA; absence of crossveins between main veins; CuA with only one fork; cua-cup sigmoidal and ending on M + CuA far from the base of this vein; RP three-branched; a distinct pterostigma; stem of M long; absence of a crossvein below pterostigma between RA and RP.

**Material.** Holotype AM F.142068 (part) and AM F.142069 (c/part), stored in the collection of The Australian Museum, Sydney (New South Wales).

**Diagnosis.** As for the genus. 

**Description.** As for the genus.

**Belmomantis azari** sp. nov.

**Material.** Holotype AM F.142069 (c/part), stored in the collection of The Australian Museum, Sydney (New South Wales).

**Diagnosis.** ScP touching C and apparently ending on RA distally as a transverse vein between costa and RA; absence of crossveins between main veins; CuA with only one fork; cua-cup sigmoidal and ending on M + CuA far from the base of this vein; RP three-branched; a distinct pterostigma; stem of M long; absence of a crossvein below pterostigma between RA and RP.

**Elmomantis engeli** sp. nov.

**Material.** Holotype specimen USNM without number, Smithsonian Institution, National Museum of Natural History, Washington, USA.

**Diagnosis.** As for the genus.

**Description.** A nearly complete isolated forewing, with only basal part of anal area not preserved, wing 5.7 mm long, 1.6 mm wide, apparently hyaline but with a darker elliptical pterostigmal zone around apex of RA extending below RA; ScP progressively diverging from radius, touching costa 0.4 mm distal of base of RP, 2.0 mm from wing base, and apparently ending on RA distally as a transverse vein between costa and RA; absence of crossveins between main veins; CuA with only one fork; cua-cup sigmoidal and ending on M + CuA far from the base of this vein; RP three-branched; a distinct pterostigma; stem of M long; absence of a crossvein below pterostigma between RA and RP.

**Elmomantis azari** sp. nov.

**Material.** Holotype AM F.142069 (c/part), stored in the collection of The Australian Museum, Sydney (New South Wales).

**Diagnosis.** As for the genus.

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**Diagnosis.** As for the genus.

**Description.** As for the genus.

**Belmomantis azari** sp. nov.

**Material.** Holotype AM F.142068 (part) and AM F.142069 (c/part), stored in the collection of The Australian Museum, Sydney (New South Wales).

**Diagnosis.** As for the genus.

**Description.** As for the genus.
between the main veins, CuA with only one fork, RP three-branched, a distinct pterostigma. In the key to Palaeomanteidae of Rasnitsyn (in [14]), Elmomantis would fall near Stigmodeleptopterum pterostigmalis Rasnitsyn, 2004 (in [14]), from which it differs in the longer stem of M and absence of a crossvein below pterostigma between RA and RP. Note that the structure of ScP is unknown in between RA and RP. Stigmodeleptopterum pterostigmalis is unknown in between RA and RP. Note that the structure of ScP is unknown in between RA and RP. Note that the structure of ScP is unknown in between RA and RP. Note that the structure of ScP is unknown in between RA and RP. Note that the structure of ScP is unknown in between RA and RP. Stigmodeleptopterum pterostigmalis is unknown in between RA and RP. Note that the structure of ScP is

Delopsocus elongatus Tillyard, 1928. Other species. Delopsocus fasciatus Tillyard, 1928, Delopsocus furcatulus (Martynov, 1930), Delopsocus kamensis (Martynov, 1938), Delopsocus kansanum (Carpenter, 1939), Delopsocus lepidus (Kukalová, 1963), Delopsocus sinuosus (Kukalová, 1963), Delopsocus stenopterus Rasnitsyn, 2004, Delopsocus latus (Sellards, 1909).

**Remark.** Carpenter [32] synonymized the genus Delopsocus with Palaeomantis. Rasnitsyn (in [14]) considered them as different genera but without formally restoring the genus Delopsocus. We restore the genus Delopsocus because the type species *D. elongatus* differs from the type species of *Palaeomantis* in two important characters: ScP is emitting a posterior branch (or strong crossvein) towards RA at its apex in the former while it is absent in the latter; vein cua-cup is in a very basal position in the former while it is distinctly more distal in the latter. Both these characters are present in the majority of the species currently included in *Delopsocus*.*D. stenopterus* is based on an incomplete wing, with basal structures and apex of ScP missing [14].

**Delopsocus latus** (Sellards, 1909) [originally *Delopterum latum* Sellards, 1909].

Material. Holotype 94 (hindwing) in Sellards’ collection. Redescribed and figured by Tillyard [26: fig. 8], who listed several other specimens. Here we redescribe the specimen YPM 5384A–B (part and counterpart) in Yale Peabody Museum collection.

**Age and outcrop.** Elmo Limestone member of the Wellington Formation, Lower Permian, Elmo, Kansas, USA.

**Description of specimen No. YPM 5384.**

Body not well preserved, head only partly visible; apical part of an antenna with ca. five short flagellomeres visible; thorax 1.65 mm long, 1.25 mm wide; legs not visible; abdomen 2.46 mm long, 1.09 mm wide; cerci partially preserved, probably two-segmented, 0.39 mm long.

Forewing 5.65 mm long, 1.82 mm wide; ScP 2.37 mm long, with an apical fork, anterior branch ending on C while posterior one ends on RA; R divided into RA and RP 1.80 mm from wing base; RA simple; RP with three branches; M and CuA basally fused with R, separating again 2.09 mm from wing base in a widened part of R; R + M + CuA, R, RA, and M + CuA distinctly convex; a faint vein cua-cup between concave CuP and point of re-emergence of M + CuA, convex near M + CuA and vanishing near CuP (preservation of absence of connection with CuP as in many Hemiptera?); M and CuA separating 0.78 mm from their connection to R; M with two branches; CuA with two branches (areola postica longer than wide); CuP simple; claval furrow well discernable running close and parallel to CuP (see Fig. 1i); anal area poorly preserved, but with only convex A1 discernable, a crossvein between CuA1 and M2, one between M1 and RP; veins R, RA, M + CuA, and CuP with large insertions of basal sockets of macrotrichia, Hindwings partly preserved, of same sizes as forewings; preserved veins identical to those of forewings; a dark zone around apex of RA (either a pterostigma or just dense pattern of microtrichia).

**Remark.** The redescription of this fossil confirms the attribution of *Delopsocus* to the acercarian stem group (typical wing venation), together with the presence of presumably two-segmented cerci in the Palaeomanteidae. Moreover, the pattern of prominent basal sockets of macrotrichia on main longitudinal veins R, M + CuA (Fig. 1i) also occurs in other members of Acercaria, like a hemipteran *Mundus nodosus* Becker-Migdisova, 1960 and many extant psocopterans, e.g. [51]. Another important point is the presence of claval furrow (cf) medi ally running closely parallel to CuP. This character is also present in *Perinopterum peruni* Kukalová, 1963 where it is apically diverging from CuP (see Fig. 1c).

**Delopterum Sellards, 1909.**

Type species. *Delopterum minutum* Sellards, 1909. Other species. *Delopterum anale* Martynov, 1928, *Delopterum candidum* Zhuzhova, 2002, *Delopterum commune* Rasnitsyn, 2004, *Delopterum iljinskiense* Martynova, 1961, *Delopterum incertum* Martynov, 1928, *Delopterum insigne* Martynov, 1928, *Delopterum kaltanicum* Martynova, 1961, *Delopterum latum* Sellards, 1909, *Delopterum pantherinum* Rasnitsyn, 2004, *Delopterum radschenkoi* Martynova, 1961, *Delopterum ransitsyni* Novokshonov, 2000, *Delopterum truncatum* Kukalová, 1963, *Delopterum zonatum* Rasnitsyn, 2004. A revision of the different species in this genus will be necessary to verify their value.

**Delopterum minutum** Sellards, 1909.

**Remark.** The holotype of *D. minutum* No. MCZ 3979 is lost, after Carpenter [52], who designated a neotype the specimen MCZ 3295a, b (Fig. 3a). The original type shows remarkably well preserved cerci [15: pl. 2, fig. 3]. He also studied several other specimens, also from the Museum of Comparative Zoology at Harvard, USA. We restudy some of them of great interest for the wing venation and other body structures of this genus.

**Descriptions.**
Specimen 3203a, b (Fig. 3b). Although this fossil is an incomplete forewing, it shows the acercarian pattern of venation, viz. ScP reaching costal margin in proximal third of wing with one oblique crossvein; CuA is basally fused with M and R in a convex vein; between concave CuP, there is a faint vein cua-cup that ends in M + CuA at its point of separation with R, which is basally concave and distally convex. Otherwise, forewing 1.2 mm wide; R divided into RA and RP 1.1 mm from wing base; R + M + CuA, R, RA, and M + CuA distinctly convex; RA simple; M and CuA separating again 0.5 mm from wing base in a widened part of R; M and CuA separating 0.7 mm from their common base; M with two branches; CuA with two branches (areola postica longer than wide); concave CuP simple; anal area with only A1 and A2, a crossvein between A1 and A2; no visible crossvein between CuA1 and M2 or between M1 and RP; veins R, RA, M + CuA, and CuP with large insertions of macrotrichia; surface of wing covered with microtrichia; a darkened zone (pterostigma?) surrounding apex of RA.

Specimen 3206 (complete forewing) (Fig. 4c). Wing 4.75 mm long, 1.49 mm wide; ScP 1.70 mm long, with a humeral crossvein perpendicular to it and to C, and a distal fork, anterior branch ending in C and posterior branch ending in RA; RA apparently simple; RP with three branches; M with two branches; areola postica longer than wide; pattern of veins at wing base identical to that of specimen 3203, with a cua-cup basally concave and distally convex, aligned with distal part of M + CuA; a darkened zone (pterostigma?) surrounding apex of RA, poorly visible.

Specimen 3209 (body with two wings) (Fig. 3d). This specimen is of interest for the very clear pterostigma covering all the area around the apex of RA (apparently simple) and the most anterior branch of RP; general shape of venation identical to that of 3206, but basal part of wing rather poorly preserved, although cua-cup
is poorly preserved. Their distal two-thirds. Unfortunately, the wing bases have the same venation as the forewings, at least in (Fig. 3a). This specimen shows the hindwings that segments.

**Specimen 3295** (neotype, body with four wings) (Fig. 3a). This specimen shows the hindwings that have the same venation as the forewings, at least in their distal two-thirds. Unfortunately, the wing bases are poorly preserved.

**Specimen 3201a, b** (body with a forewing clearly visible in its distal half) (Fig. 3e). The interest of this fossil is the clearly visible distal fork of RA at the level of pterostigma. This fork is not visible in the previous specimens, probably due to a problem of preservation. The distal two-thirds of the venation is the same as in other specimens. The legs are visible. Carpenter [52] counted four posterior tarsomeres, but he has confused the long tibia with a basal tarsomere (hindleg). There are three basal tarsomeres of the same length, obliquely ‘cut’ at their apices plus two cylindrical apical tarsomeres, narrower than the basal ones, two claws and an arrolium between them; one strong seta at apex of posterior tibia. Foreleg with basal long three segments.

**Specimen 3296** (complete wing) (Fig. 3f). This wing also shows a distal fork of RA.

**Specimen 13,311** (body with poorly preserved wings) (Fig. 3g). The interest of this fossil is the presence of the curved cerci, longer than in the Hypoperlidae.

Remark. Delopterum minutum shares with Delopsocus the very basal position of cua-cup. It differs from Delopsocus lattus at least in the distally forked RA, larger pterostigma, presence of a basal crossvein perpendicular to C and ScP, absence of a crossvein between RP and M1, and absence of a crossvein between M2 and areola postica.

**Mazonopsocus gen. nov.**

Type species. Mazonopsocus testai sp. nov.

Etymology. Composite name after Mazon Creek (type locality) and Psocus (genus name).

Diagnosis. Wings elongated, ScP ending on Costa behind midwing, RA simple, RP with three or four branches, M and CuA basally fused with R, distinctly convex M + CuA diverging from R; a faint vein cua-cup between concave CuP and point of re-emergence of M + CuA, convex near M + CuA and concave near CuP; M with two branches; CuA with two branches (areola postica); faint CuP simple, anal area with two convex veins as A1 and A2.

**Mazonopsocus testai** sp. nov.

Material. Holotype FM TVT1991a (part) and FM TVT1991b (c/part), stored in the collection of The Field Museum, Chicago (Illinois, USA), originally from Thomas V. Testa collection.

Specimen 3206 and 3203. This fossil also shows an antenna with at least six flagellomeres, slightly longer than wide and scape and pedicel broader than flagellomeres; maxillary palp with three visible segments.

**Specimen 3295** (neotype, body with four wings) (Fig. 3a). This specimen shows the hindwings that have the same venation as the forewings, at least in their distal two-thirds. Unfortunately, the wing bases are poorly preserved.

**Specimen 3201a, b** (body with a forewing clearly visible in its distal half) (Fig. 3e). The interest of this fossil is the clearly visible distal fork of RA at the level of pterostigma. This fork is not visible in the previous specimens, probably due to a problem of preservation. The distal two-thirds of the venation is the same as in other specimens. The legs are visible. Carpenter [52] counted four posterior tarsomeres, but he has confused the long tibia with a basal tarsomere (hindleg). There are three basal tarsomeres of the same length, obliquely ‘cut’ at their apices plus two cylindrical apical tarsomeres, narrower than the basal ones, two claws and an arrolium between them; one strong seta at apex of posterior tibia. Foreleg with basal long three segments.

**Specimen 3296** (complete wing) (Fig. 3f). This wing also shows a distal fork of RA.

**Specimen 13,311** (body with poorly preserved wings) (Fig. 3g). The interest of this fossil is the presence of the curved cerci, longer than in the Hypoperlidae.

Remark. Although the common stem M + CuA is relatively shorter than in some other Palaeomanteidae, the cua-cup is ending into this stem, unlike in the Hypoperlidae in which it ends into CuA or very close to it. Thus this fossil is attributable to the former family. It corresponds to the oldest record of the Mimoptera sensu nov., in the late Carboniferous. Rasnitsyn [39: fig. 214] noted another formerly undescribed specimen from the same locality attributable to Palaeomanteidae with poorly preserved wing bases. Oudard [53: figs 14, 17] also figured some forewings from the Gzhelian of Montceau-les-Mines with all the distal structures of venation typical of the Palaeomanteidae, including the long stem M + CuA and the areola postica.

Order Hypoperlida Martynov, 1928 [1] (sensu nov.).

Type family. Hypoperlidae Martynov, 1928 [1]. All the other families currently in the Hypoperlidae are here excluded from this order (see below).
Diagnosis. Wing venation very similar to those of the Palaeomanteidae, except mainly in the shorter stem M + CuA. Cerci one-segmented and very short, unlike the long cerci of the Palaeomanteidae.

Family Hypoperlidae Martynov, 1928 [1] (= Kaltanelmoaidae Rohdendorf, 1961 [48]).

Type genus. Hypoperla Martynov, 1928 [1] (four species: H. elegans Martynov, 1928 [1], H. grata Novokshonova, 1998 [54], H. nobilis Novokshonov, 1995 [55], and H. vaulevi Novokshonov, 2001 [56]).

Age range. Permian.

Other genera Kaltanelmoa Rohdendorf, 1961 [48] (single species: K. sibrica Rohdendorf, 1961 [48]), Boreopsocus Schcherbakov, 1994 [57] (two species: B. danksae Schcherbakov, 1994 [57] and B. ficticius Novokshonov, 1995 [55]), Onthomastax Rasnitsyn & Aristov, 2013 [45] (single species: O. coprinus Rasnitsyn & Aristov, 2013 [45]), and possibly some of the species previously attributed to the genus Idelopsocus Zalessky, 1929 [58], viz. I. galinae Novokshonov, 2001 [56], I. incommensatus Novokshonov et al., 2002 [59], I. levis Novokshonov, 1995 [55], I. mutovinus Rasnitsyn and Aristov, 2013 [45], and I. splendens (Zalessky, 1948) [60], but maybe not Idelopsocus diradiatus Rasnitsyn, 1996 [in 61], Idelopsocus tartaricus Zalessky, 1929 [58], and Idelopsocus arcuatus (Martynov, 1928) [1] (see below).

Position of the Hypoperlidae in Acercaria. Rasnitsyn [43] included seven genera in Hypoperlidae: Hypoperla, Hypoperlopsis Zalessky, 1948 [60], Martynopsocus Karny, 1930 [62], Kaltanelmoa Rohdendorf, 1961 [48], Fatjanoptera Martynova, 1961 [63], Tshunicala Rasnitsyn, 1977 [43], and Tshekarodobia Rasnitsyn, 1977 [43]. The latter three genera are discussed below. Schcherbakov [57] restricted the Palaeozoic Hypoperlidae to embrace only the four genera Hypoperla, Idelopsocus Zalessky, 1929 [58], Kaltanelmoa, and Boreopsocus Schcherbakov, 1994 [57].

Martynov [1] erected the family Dinopsocidae for the genus Dinopsocus Martynov, 1928 [1]. Karny [62] proposed the new names Martynopsocus for the genus and Martynopsocidae because of the existence of a psocid genus Dinopsocus Banks, 1920. Laurentiaux [64] listed the Martynopsocidae in the Permopsocida. Rasnitsyn [45] synonymized the Martynopsocidae with the Hypoperlidae. The type species is Martynopsocus arcuatus (Martynov, 1928) [1]. Martynov [1] suggested that Idelopsocus and Dinopsocus could be the same genus. Laurentiaux [63] included the genus Idelopsocus (type species I. tartaricus Zalessky, 1929 [58]) in the Martynopsocidae. Carpenter [32] proposed the generic synonymy of Idelopsocus Zalessky, 1929 [58] with Martynopsocus, but did not take into account the date priority of Idelopsocus on Martynopsocus. Therefore the valid genus name is Idelopsocus.

The venation of Hypoperla elegans (type species of Hypoperlidae, type family of the order Hypoperlida) is typical for Acercaria by having a common stem R + M + CuA; M + CuA separating from R distally; convex CuA immediately emerging from M + CuA; long crossvein cu-a-cup between concave CuP and CuA, which is concave near CuP and convex near CuA; CuA with an areola postica (see Fig. 5c-d). Nevertheless, Hypoperla elegans differs from the Permopsocida in several important plesiomorphies: RP with a series of parallel posterior branches instead of a single fork, as in modern Acercaria and Permopsocida (a likely plesiomorphy because numerous posterior branches of RP are known in the ground plans of polyneopterous orders and in Neuropterida and Panorpida); no distinct angle of radius at base of M + CuA; pterostigma more ‘rudimentary’ and consisting of a darker zone covering apical parts of ScP, RA, and apical part of area between RA and RP not delimited posteriorly by RA. The same pattern of venation occurs in Hypoperla grata and Hypoperla vaulevi.

The venation of Idelopsocus tartaricus is clearly of acercarian type, showing a convex CuA emerging with concave M from a common stem with R, a long brace cu-a-cup between concave CuP and CuA, concave near CuP and convex near CuA, and two convex simple anal veins. The CuA of I. tartaricus is simple, concave ScP ends on RA, and concave RP and M both have three branches with few crossveins [58]. This venation is closer to modern Acercaria than to that of Hypoperla. It differs from the Permopsocida in lacking a strong angle between RA and basal stem R + M + CuA, and not having a sclerotized pterostigma.

The venations of I. arcuatus strongly resembles that of I. tartaricus from which it differs in the presence of an areola postica (CuA forked) [1].

Idelopsocus diradiatus also has a venation closer to non-hypoperlidan Acercaria in that the RP only has two branches, and M with only three branches, but lacking any angle in the course of R at the base of M + CuA [65]. Idelopsocus diradiatus has a forked CuA, unlike I. tartaricus. Idelopsocus tartaricus and I. incommensatus share similar venation characters except for presence of an areola postica [66]. The venation appears somewhat variable among the species currently placed in Idelopsocus, especially in the number of main vein branches. Unlike Hypoperla, where only the distal parts of the wings have darkened membranes, species of Idelopsocus possess sclerotized pterostigmata in fore- and hind wings (Fig. 5e-f) [1], not homologous to that of Permopsocida because the pterostigmata cover a zone crossing the distal area between the anterior wing margin and RA and part of the area between RA and RP. In Permopsocida, the pterostigmata are delimited posteriorly by RA. Idelopsocus mutovinus is probably also a Hypoperlidae,
Fig. 5 Hypoperlida: (a-d), *Hypoperla elegans* Martynov, 1928: (a) Holotype PIN 2050/17 (Late Permian, Soyana River, Archangelsk Region, Russia), photograph of forewing venation (scale bar represents 2 mm); (b), PIN No. 3353/415 (Late Permian, Soyana River, Archangelsk Region, Russia), photograph of body with fore- and hindwings venation, specimen. (c), PIN No. 117/968 (Late Permian, Soyana River, Archangelsk Region, Russia), photograph of forewing, specimen; (d), PIN No. 3353/471 (Late Permian, Soyana River, Archangelsk Region, Russia), photograph of hindwing, specimen. e-j ‘Idelopsocus’ sp., (e) ‘Idelopsocus’ cf. *splendens*, PIN 1700/3298, photograph of habitus; (f) *Idelopsocus* sp., PIN 1700–3257 (Early Permian, Tshekarda, Russia), habitus in dorsal view; (g) *Idelopsocus* sp. PIN 124–118 (Early Permian, Tshekarda, Russia), habitus in lateral view; (h) *Idelopsocus* sp., PIN 1700/479 (Early Permian, Tshekarda, Russia), habitus in dorsolateral view; (i) PIN 1700/3298 (Early Permian, Tshekarda, Russia), lateral view of head with maxillary palps; (j) ‘Idelopsocus’ *splendens* PU 2/129 (Early Permian, Tshekarda, Russia), apex of abdomen with one segmented cerci (scale bars represent a, c, d, f-h = 2 mm, b, e = 5 mm, i, j = 0.5 mm). Abbreviations: ce – cerci, mp – maxillary palps, pt – pterostigma
although the basal part of the vein CuA is not clearly discernable [45]. *Idelopsocus diradiatus* and *Idelopsocus splendens* have five-segmented tarsi (specimens PIN 1700/3298 or PU 2/129 attributed to *I. splendens* by Novoskshonov [56] and Rasnitsyn [2]); while the type specimen of *I. splendens* is an isolated wing originally described as *Hypoperlopsis splendens* [60]. This tarsal formula is a plesiomorphy in Acercaria and most insects.

Boreoposocus has a venation most suggestive to that of Permopsocida, with RP having a distal fork, pterostigma in fore- and hind wings delimited by a posterior curve of RA, with a crossvein below it and RP (but narrower than in Permopsocida, except *Stenopsocidium*). Unlike Permopsocida [23, 57], it lacks an angular R, and possesses five-segmented tarsi. *Kaltanelmoa sibirica* (based on the basal two-thirds of an isolated wing) also has a venation typical of Acercaria (courses of M and cubital veins, simple fork of CuA). RP and M in this species appear to be simply forked, as in modern acercarians and Permopsocida, but R lacks an angle in its course distal to base of M. The area of the putative pterostigma is hardly preserved [48].

In summary, the family Hypoperlidae *sensu* Scherbakov [57] appears to be a 'group' of acercarian genera, but they lack a clear apomorphy that could support them as a clade. They may represent a paraphyletic 'evolutionary grade' (with regard to wing venation and number of tarsomeres) from *Hypoperla* to Boreoposocus, the latter is sharing several apomorphies with Permopsocida (similar pterostigma and venation). The venations of the *Idelosocus* species could represent 'intermediate' stages, having reduced branchings in RP and M, compared to the situation observed in *Hypoperla*, but with a particular pterostigma different from Boreoposocus and Permopsocida. Interestingly, a strikingly similar phenomenon happened during the evolution of the odonatopteran pterostigmata: the basal clades (Geroptera Brodsky, 1994 [67], Meganisoptera Martynov, 1932 [68]) have no pterostigma, whereas Odonata have a pterostigma delimited posteriorly by RA [69]. The pterostigma in the 'intermediate' clade Protanisoptera Carpenter, 1931 [70] is almost identical in shape and position to that of *Idelopsocus* [71].

**Phylogenetic analysis of the Acercaria sensu lato**

Huang et al. [3] proposed a phylogenetic analysis of the Acercaria sensu stricto in which the Hypoperlidae falls as sister group of the crown group. We use the same set of 63 characters as in Huang et al. [3] supplementing the set of taxa by a representative of the Miomoptera (*Palaeomantis aestiva*) (see matrix of characters in Additional files 1, 2 and 3). Using maximum parsimony (MP), we have obtained nine equally most parsimonious cladograms, length = 90 steps; consistency index CI = 0.8111; CI excluding uninformative characters = 0.8023; RI = 0.8859; RC = 0.7186. The Acercaria sensu lato are monophyletic, supported by the wing venation characters only, and appear as sister group of the Holometabola (Fig. 6). The hierarchy of the crown group Acercaria sensu stricto is the same as in Huang et al. [3], supported by the same set of synapomorphies. The two groups Hypoperlidae and Miomoptera fall together in the same clade, but with a trichotomy, supported by the characters '47, state 1' and '48, state 1' that concern the particular shape of the pterostigma. The polytomy is due to the absence of data on the character '56' ( cerci) for *Hypoperla*.

Using a Bayesian analysis, we obtained 75,000 cladograms, with a topology of the 50% consensus (see Additional file 4) very close to that of the MP strict consensus cladogram. The unique difference is *Hypoperla* as sister group of crown Acercaria and (*Idelopsocus + Palaeomantis*) as sister group of (*Hypoperla + crown Acercaria*). This second analysis shows that the relative positions of the Miomoptera and Hypoperlidae are uncertain. The Miomoptera are likely to be the sister group of the Hypoperlidae, or the sister group of the (Hypoperlidae + crown Acercaria), or even the two groups are paraphyletic.

Nevertheless, the difference in the structure of the cerci (one-segmented vs. pluri-segmented) between the Hypoperlidae and the Miomoptera is sufficient to distinguish the two groups at this stage of knowledge. Thus we keep the two orders Miomoptera and Hypoperlidae separately.

Whether they can still be considered as separate orders is another question that will need further discoveries of more complete specimens to be solved. The problem is similar to the situation between the Timemoea and the Euphasmatodea in Phasmatoidea [72].

**Discussion**

**Limits of the Hypoperlida**

As the Hypoperlidae, type family of the Hypoperlida, are Acercaria, we have to determine if the other taxa currently considered as Hypoperlida are also related to the Acercaria.

Scherbakov [57] divided the Hypoperlida into the suborders Hypoperlinea ['ancestral to Psocida (and other Acercaria)', with the two families Hypoperlidae Martynov, 1928 [1] and Ampelipteridae Haupt, 1941 [73], and Strephecladinia. Later, Rasnitsyn [1] considered this group to consist of three suborders: Hypoperlina (viz. Hypoperlidae Martynov, 1928 [1], Ampelipteridae Haupt, 1941 [73], see below), Strephecladinia Martynov, 1938 [74], and Perieletrina Zallesky, 1948 [60] (*Perieletrony* Zallesky, 1948 [60]).

Recently, Emeljanov [75] stated 'When considering the characteristic and description of the order Hypoperlida' in the Historical Development of the Class Insecta (1980) [76] and the History of Insects (2002) [1], one
gets the impression that this order includes two different groups: Hypoperlida proper (= Hypoperlina) and Strephocladina; the latter should instead be treated as an order within Dictyoneuridea’ (= ‘Pseudorhynchota’ sensu Emeljanov [75], also = Palaeodictyopteroidea). Note that the name Pseudorhynchota was preoccupied by the Pseudorhynchota Cholodkovsky 1903 [77], a junior synonym of the Anoplura Leach, 1815 [78].

Remark. Rasnitsyn [2: p. 115] indicated that the three Palaeozoic genera Rhipidioptera Brongniart, 1893 [79], Psoroptera Carpenter, 1976 [80], and Homoeodictyon Martynov, 1937 [81] ‘may belong to Hypoperlida, though their position there is tentative at best’. Aristov [82] placed Psoroptera and the Psoropteridae Carpenter, 1976 [80] in the Cnemidolestida. Homoeodictyon has a dense venation with archeaictyon and the basal part of wing missing, so that it is certainly not related to the Aceraria [81]. Hörnschemeyer and Stapf [83] placed Rhipidioptera in the Blattinopsidae, a family not related to the Hypoperlidae or the Aceraria at all [84].

Problem of the Perielytrina

Perielytron mirabile Zalessky, 1948 [60] is an enigmatic Permian insect having sclerotized forewing with poorly known venation, and lacking synapomorphies with Aceraria [1, 60]. We consider it as a ‘Neoptera incertae sedis’.

Problem of the Strephocladina

Strephocladina sensu Rasnitsyn [1] comprise the Palaeozoic families Synomaloptilidae Martynov, 1938 [74], Tococladidae Carpenter, 1966 [82, 85, 86, 87], Heteroptilidae Carpenter, 1976 [80], Nugonioneuridae Carpenter, 1976 [80], and Anthracoptilidae Handlirsch, 1922 [88], the Strephocladidae being a junior synonym of this last family [89]. The Tococladidae are Archaeorthoptera [90], a clade with a wing venation different from those of the Aceraria (see above). Anthracoptilidae belongs to Paoliida [89], a clade related to Dictyoptera. Thus, the group Strephocladina is polyphyletic and should be abandoned as currently defined.
Anthracoptilidae, Heteroptilidae, and Nugonioneuridae have CuA emerging from a common stem with CuP [80]. This character excludes them from having any closer affinities with Pan Acercaria and Hypoperlidae (see diagnosis of the Acercaria).

Thus, the wing venation of all these ‘Strephocladina’ greatly differs from the acercarian type.

The family Anthracoptilidae (= ‘Strephocladidae’) is not related to the Palaeodictyoptera, refuting Emeljanov [75]’s hypothesis of a link between Strephocladina and ‘Dictyoneuridea’.

The Synomaloptilidae currently comprise the three genera Synomaloptila Martynov, 1938 [73], Rhinomaloptila Rasnitsyn, 1977 [43], and Mycteroptila Rasnitsyn, 1977 [43]. Carpenter [32] included Synomaloptila in the Caloneuroidea but Béthoux et al. [91] excluded this taxon from this group. The wing venations of Rhinomaloptila and Mycteroptila are very incompletely known, and do not allow a correct placement of these genera [43, 92]. Synomaloptila should be revised before its placement.

Some ‘Strephocladina’ (e.g. Synomaloptila) have an elongate head with apparently beak-like mouthparts. Such superficial similarities do not support a phylogenetic relationship of these insects and Acercaria. As modern Psocodea lack such elongate mouthparts, this character is clearly not a ground plan autapomorphy of Acercaria. Also, Palaeodictyoptera have elongate sucking-piercing mouthparts, which is clearly a convergent character with Hemiptera (see below).

**Problem of the Hypoperlina**

Shcherbakov [56] divided the Hypoperlina (his Hypoperlida) into two Paleozoic families, Hypoperlidae and Ampelipteridae (a family he synonymized with the Protoprosbolidae Laurentiaux, 1952 [93] and the Fatjanopteridae Martynova, 1961 [63]. The same author also listed within Ampelipteridae the genera Tshunicola Rasnitsyn, 1977 [43] and Tshekardobia Rasnitsyn, 1977 [43] [Rasnitsyn 2: fig 120] confirmed these placements but included the latter genus in Hypoperlidae. Rasnitsyn [1] added the Carboniferous genera Limburgina Laurentiaux, 1950 [94], Aenigmatodes Handlirsch, 1906 [21], Gyrophlebia Handlirsch, 1906 [21], Protopachytylopsis Laurentiaux and Laurentiaux-Vieira, 1981 [95], Anthraconeura Laurentiaux and Laurentiaux-Vieira, 1980 [96], and, preliminarily, Mixotermes Sterzel, 1881 [97], Pruvostra Bolton, 1921 [98], and Boltonocosta Carpenter, 1986 [99] in Hypoperlina.

The Protoprosbolidae were recently revised, restored, and re-transferred to Hemiptera [5, 100], Ampeliptera limburgica Pruvostr, 1912 [101], type species of Ampelipteridae, has been placed in Archaeorthoptera [12, 73]. Fatjanoptera mnemonica Martynova, 1961 [63], type of Fatjanopteridae, is an enigmatic taxon strongly differing from Ampeliptera. Unlike Ampeliptera, Fatjanoptera possesses a net of cells between the main wing-veins, and, more notably, Fatjanoptera has a convex CuA and a concave CuP, emerging from a common stem (see Huang et al. [3]: Figs S9B, S9E), dissimilar to venation in acercarian orders and Archaeorthoptera. Fatjanoptera also possesses at least three anal veins, unlike Acercaria and Hypoperlidae. Fatjanopteridae should be restored as a separate family, and placed outside of Archaeorthoptera, Acercaria, and ‘Hypoperlida’ (see below for venation of the Hypoperlidae). Fatjanoptera was originally considered to be in Holometabola, related to Raphidiordera [63]. Some aspects of the wing venation in Fatjanoptera are reminiscent to those of Holometabola in the distal fusion of ScP with RA and the presence of a pterostigma-like zone, defined by small veinlets between RA and the costa. Nonetheless, placement of Fatjanoptera will remain uncertain until discovery of fossils preserving its body structures.

Béthoux and Nel [12] placed Protopachytylopsis in Panorthoptera, unrelated to Ampeliptera. Béthoux [102] revised Anthraconeura, transferring it to Archaeorthoptera. The description of Limburgina was based on the distal two-thirds of its fore (?) wing. However, the bases of the cubital veins are not preserved [94] in its type specimen, thus preventing the distinction between archaeorthopteran or acercarian venation patterns. We consider Limburgina as Neoptera incertae sedis.

The basal portions of the wings (especially the bases of CuA and CuP) of Boltonocosta splendens Bolton, 1912 [103], Mixotermes lugauensis Sterzel, 1881 [97], and Aenigmatodes danielsi Handlirsch, 1906, are not well preserved in their respective type specimens [21, 97, 103]. Thus, the taxonomic affinities of these fossils cannot be firmly established. Nevertheless, available wing venation patterns of these specimens lack any of the synapomorphies to place them in Acercaria. Béthoux [102] indicated that the type specimen of Gyrophlebia longicollis Handlirsch, 1906 is poorly preserved and its taxonomic placement cannot be correctly determined. Pruvostra spectabilis Bolton, 1921 has a venation typical of Anthracoptilidae [98], with a convex CuA having three, clearly concave anterior branches, and CuA and CuP having a common stem. Tshunicola carbonarius and the five species of Tshekardobia have a wing venation similar to Acercaria in having a reduced number of branches of main veins and few crossveins. But, the organization of the cubital veins in these taxa requires reexamination.

Novokshonov [104] and Rasnitsyn [2] added the Permian Asiuropaideae Novokshonov, 1997 [104] (single genus Asiuropa Novokshonov, 1997 [104]) to Hypoperlida. Asiuropa uralensis Novokshonov, 1997 [104] superficially resembles some Acercaria by having few
crossveins between RA and RP and other main veins. However, _A. uralensis_ differs from _Hypoperla_ and other acercarian-like insects by possessing numerous branches of CuA. The organization of the basal parts of veins R, M, CuA, and CuP is not known. A revision of the type material will be necessary to determine if its venation is of acercarian type.

Rasnitsyn [2] added the Permian _Letopalopteridae_ Martynova, 1961 (with two genera _Letopaloptera_ Martynova, 1961 [63] and _Permindigena_ Novokshonov, 1998 to _Hypoperlina_ [63, 92]. Novokshonov and Willmann [105] revised _Letopaloptera_ and retained it in _Hypoperlida_. But, Aristov and Rasnitsyn [106] synonymized _Letopalopteridae_ with _Permindibiidae_ Tillyard, 1937 [107] and transferred this family into the extinct order _Miomopteridae_ (see above). The wing venation of these insects greatly differs from those of _Hypoperlidae_ and _Acercaria_, most importantly in the presence of a common stem of CuA with CuP.

Rasnitsyn and Aristov [in 47] placed the Ichstoneuridae (and the genus _Ichstoneura_ Brongniart, 1893 [79]) in the _Hypoperlina_. Béthoux and Nel [108] considered that this taxon belongs to the Archaeorthoptera, confirmed in [89].

All of the aforementioned fossils, previously considered as _Hypoperlina_, are not closely related to _Acercaria_ or to _Hypoperlidae_ (see below). Therefore, we exclude them from _Hypoperlida_. We consider that the _Hypoperlida_ are reduced to the sole _Hypoperlidae._

Remark. The enigmatic Permian fossils _Sojanopus festivum_ Novokshonov, 2002 [59] (unique representative of the family _Sojanoperidae_ Novokshonov, 2002 [59]) and _Montanuralia aeria_ Novokshonov, 1998 [54] (unique representative of the family _Montanuraliidae_ Novokshonov, 1998 [92]), have been considered as possible _Hypoperlidae_ [59, 92]). They share with _Acercaria_ the CuA basally fused with R + M and re-emerging distally, with a cu-a-cup between it and the concave CuP. But their wing venations are highly simplified without other crossveins. _Montanuralia aeria_ has five tarsomeres, suggesting a very basal position in this clade. Their exact relationships with the other _Acercaria_ remain uncertain.

Aristov [87] considered the monospecific family _Permetatoridae_ Novokshonov, 1999 as belonging to the _Hypoperlida_. He erroneously attributed this position to Novokshonov [86] who considered this family as ‘Ordinis incertis’. The wings of _Permetator semitritus_ are incompletely preserved. Novokshonov [86] considered that this taxon had a common stem Cu of CuA and CuP and a ‘M5’ between M and CuA, but he did not precise the convexity of these veins, so that only a revision of the type material would allow to determine if his ‘M5’ and his ‘CuA’ are convex or concave, which would completely change the position of this taxon. Nevertheless, the presence of numerous crossveins in all wings, and especially in the area between C and ScP put serious doubts on an attribution close to the _Hypoperlidae_ and the _Acercaria._

### Relationships between _Miomoptera_, _Acercaria_, and _Palaeodictyopterida_

The ‘_Hypoperlida_’ sensu Rasnitsyn [2] is considered as paraphyletic group giving rise to ‘_Dictyneuridea_, _Psocidea_ and _Cimicidea_’ (respectively _palaeodictyopteridan_ and _acercarian_ orders). The proposed ‘clade’ (Hypoperlida + Palaeodictyopterida + _Acercaria_) is allegedly supported by the presence of ‘maxilla with lacinia rod- or stylet-like’. This character, in most cases, is not visible in compression fossils and also difficult to discern in amber material. Even it is absent in the _Hypoperlidae_.

The _Palaeodictyopterida_ have either been considered as member of _Palaeoptera_ or as sister group of _Neoptera_ (Sroka et al. [109], but certainly do not nest within _Neoptera_, while _Acercaria_ is a subgroup of crown group _Neoptera_. The fact that _Palaeodictyopterida_ and _Acercaria_ are not closely related is strongly supported by morphological analyses [110].

Rasnitsyn [2] considered the piercing rostrum of _Palaeodictyoptera_ and _Hemiptera_ as homologous and derived from a _hypoperlidan_ ancestor. Kukalová-Peck [111] presented a detailed reconstruction of _palaeodictyopteroid_ mouthparts, with structures (lacinia, anteclypeus, mandibular condyles, etc.) generally unavailable for observation in fossils, or undissected modern insects. Other interpretations by Kukalová-Peck [112], Laurentiaux [93], or even Dohrn [113], remain more reasonable, describing very long stylet-like mandibles, and long maxillary palps, but without information on other parts such as laciniae. Prokop et al. [114] demonstrated these parts with microstructures by the use of ESEM on _Brodoptera sinensis_ (Megasecoptera) bearing presumably shorter labium that consists of a pair of lobes. Even though these structures are reminiscent of those of _Hemiptera_ (except presence of maxillary palps), they are certainly the result of convergence as already proposed by Laurentiaux [64] and Emeljanov [115], and are not synapomorphies with those _Acercaria_ with piercing mouthparts. All other structures (especially the wing venation) exhibit no synapomorphies between _Palaeodictyopterida_ and _Acercaria_.

The wing venations of _Hypoperlidae_ and _Palaeomanteidae_ lack any synapomorphy with the _palaeodictyopteridan_ groups (Dictyneuridea _sensu_ Rasnitsyn [2]). In particular the common stem R + M + CuA, present in the _Hypoperlidae_ and the _Acercaria_, is absent in _palaeodictyopteridan_ orders. Also, _Hypoperlidae_ has only two convex simple anal veins, identical to _Acercaria_, but different from the anal veins of _Palaeodictyoptera_, where
there are numerous anal veins reinforced by a prominent anal ridge (the so-called ‘anal brace’). These neopteran families cannot be considered as members of a grade that would have given rise to any palaeopterous insects.

Rasnitsyn [2] considered the mouthparts as diagnostic characters for the order Hypoperlida. He described them as ‘chewing though often beak-like elongate, with lacinia rod- or styletlike, clypeus convex indicating strong cibarial muscles, or, if flat, mandibles and lacinia long, jointly forming short beak’. Such structures are barely visible in the few described Hypoperlidae with preserved bodies. In fact, the mouthparts of *Idelopsocus splendens* (specimens PIN 1700/3298 and PU 2/129), *Idelopsocus diradiatus*, and *Idelopsocus galinae* are not particularly elongate and resemble the mouthparts of Psocodea, especially in the entire gena [56, 61].

**Conclusions**

The direct re-exam of the type material of *Hypoperla* and *Palaeomantis*, and the study of new specimens allows us to restrict the limits of the two orders Hypoperlida and Miomoptera to the sole type families, to consider them as Acercaria sensu lato on the basis of clearly defined synapomorphies, and to exclude all the other families previously included in these orders. We also exclude any affinities between the Hypoperlida and the Palaeodictyopterida, and affinities between the Miomoptera sensu stricto and the Holometabola.

**Methods**

**Wing venation terminology and abbreviations**

Venation nomenclature is following the concept of Nel et al. (2012) [5]. Wing venation abbreviations: (ScP—subcosta posterior, RA/RP—radius anterior/posterior, M—indistiguishable polarity of median vein, CuA/CuP—cubitus anterior/posterior, A1/A2—first/second anal vein; pt—pterostigma; cf—claval furrow; cua-cup—specialized cross-vein proximally concave and distally convex between CuP and CuA).

**Line drawings and photographs**

The venation patterns were drawn directly using a camera lucida. Photographs were taken with digital camera Canon D550 with reverse lens MP-E 65 mm. Original photographs were processed using the image-editing software Adobe Photoshop CS4, and for some images were processed by the focus-stacking software Helicon Focus Pro. Scanning electron micrographs of *Delopsocus latus* were taken by an environmental electron microscope Hitachi S-3700 N in the National Museum in Prague.

**Phylogenetic analysis**

The phylogenetic analysis was performed using the software Win-Paup4b10 [116], Bandb option. The matrix was established using Mesquite 3.03 [117]. The characters are equally weighted and unordered. The chosen outgroups are: *Periplaneta* sp. (Dictyoptera), *Eusthenia* sp. (Plecoptera) and *Xylea* sp. (Holometabola: Hymenoptera).

The Bayesien analyses were conducted using the Mk model of discrete character evolution, as suggested by Wright and Hillis [118], with MrBayes 3.1.2 [119]. We ran the analyses for 50 millions of generations with the command stoprule = yes, sampling tree every 500 generations. We used Tracer 1.5 [120] to check that our effective sample size was large enough for a meaningful estimation of parameters and to assess the burn-in. Finally, we checked for convergence of our results ensuring that the potential scale-reduction factor approached 1.0 for all parameters.

**Additional files**

- **Additional file 1:** Phylogenetic analysis and list of characters. (DOC 81 kb)
- **Additional file 2:** Coding of characters and list of taxa used in this study. (XLS 100 kb)
- **Additional file 3:** Nexus file used for the phylogenetic analysis. (NEX 9 kb)
- **Additional file 4:** Bayesian 50% consensus tree. (TIFF 788 kb)

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**Availability of data and materials**

All relevant data are available from the authors.

**Fossil material**

Specimens from the following institutional collections were examined: AM – The Australian Museum, Sydney, New South Wales, Australia; FMNH – The Field Museum, Chicago, USA; MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, USA; PIN – Paleontological Institute of Russian Academy of Sciences, Moscow, Russia; PU – Perm State University, Perm, Russia; UK – Charles University, Faculty of Sciences, Prague, Czech Republic; USNM – Smithsonian Institution, National Museum of Natural History, Washington, USA; YPM – Yale Peabody Museum, New Haven, USA.
Nomenclatural acts
This published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature (ICZN). The registration numbers are indicated for each new species.

Authors' contributions
AN conceived the initial idea and designed the project; JP and AN wrote the paper with the help of MP, RG, ICC-M and RB; JP and MP produced the figures and illustrations. ICC-M made the Bayesian phylogenetic analyses. AN and RB conceived the initial idea and designed the project; JP and AN wrote the paper with the help of MP, RG, ICC-M and RB; JP and MP produced the figures and illustrations. ICC-M made the Bayesian phylogenetic analyses.

Ethics approval and consent to participate
Not applicable

Consent for publication
All authors consent to publication.

Competing interests
All authors declare that they have no competing interests.

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