

Shedding light on the enigmatic extinct insect order Glosselytrodea: new diversity and key morphological insights into non-tegmenized Permian forms

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Abstract: Glosselytrodeans are enigmatic extinct (Permian–Jurassic) insects classified in their own order. The monophyly of Glosselytrodea is not universally accepted and its large-scale relationships remain problematic, namely because its diversity is largely known from hardened (i.e. tegmenized/‘elytrized’) forewings of allegedly derived forms. Thus, new data on the group’s early diversity and/or complete specimens are critical. Herein we describe the oldest glosselytrodean known, *Moscheloptera phantasma* gen. et sp. nov. (Permoberothidae), based on a forewing from the Niedermoschel black shale (Germany; early Permian). The holotype of *Permoberotha villosa* Tillyard (Permoberothidae) (a forewing) and a previously described complete conspecific specimen, both from Elmo (USA; early Permian), are reassessed and photographically figured for the first time. A new, complete *P. villosa* specimen from Elmo preserves body structures hitherto not reported among glosselytrodeans, including complex pretarsal claws and detailed male genitalia. The holotypes of two further species,

Sylvaelytron latipennatum Novokshonov (herein transferred to Permoberothidae) and *Archoglossopteron shoricum* Martynova (Archoglossopteridae), are also reassessed and figured. An emended diagnosis and an updated catalogue of the Glosselytrodea are provided. *Glossopteron* Sharov is returned to its own family: Glossopteridae Sharov. Our findings substantially expand the knowledge of the Permoberothidae, which is the earliest glosselytrodean lineage and lacks sclerotization-related forewing specializations. Although the exact phylogenetic position of glosselytrodeans is still unresolved, the female and male terminalia described herein almost certainly support them as early holometabolan insects, possibly closer to the mecopterid rather than the neuropteroid lineage. Shedding light on Glosselytrodea improves our understanding of the early evolution of the Holometabola.

Key words: Glosselytrodea, extinct insects, early Holometabola, Permoberothidae, Permian, tegmenized wings.

GLOSSELYTRODEA Martynov, 1938 (= Jurinida Zalessky, 1929) is an extinct insect order known from the early Permian to the Middle Jurassic. It is probable that the group was widespread across Pangaea at least by the late Permian, given that it has been described from Eurasia, America and Australia, and was putatively present in the Triassic of South Africa (Anderson *et al.* 1998; Nicholson *et al.* 2015) (Appendix S1). Significantly more glosselytrodean species have been described from the Permian than from the Mesozoic (37 vs 9, respectively) (Appendix S1). Although this difference could be bias related (e.g. collection, preservation), the effect of the Permo-Triassic mass extinction event needs to be

determined in the group. Most of the glosselytrodean diversity is known from isolated wings, particularly forewings due to their greater degree of sclerotization. Only a few body fossils have been described and/or figured (Martynov 1938; Martynova 1961; Sharov 1966; Novokshonov 1998; Rasnitsyn 2002). Because of these, it is known that glosselytrodeans were mandibulate, hypognathous to opisthognathous, had long wings in proportion to the body, and possessed cursorial legs, among other features.

Glosselytrodea was until recently divided into four families: Archoglossopteridae Martynova, 1958, Glosselytridae Martynov, 1938, Jurinidae Zalessky, 1929 and the oldest family, Permoberothidae Tillyard, 1932, which was hitherto

exclusively known from the Artinskian, lower Permian (Rasnitsyn & Aristov 2013). This taxonomic arrangement was deduced from a hypothesized process of forewing sclerotization that glosselytrodeans seemingly went through (Rasnitsyn & Aristov 2013). Recently, the family Polycyttellidae Martynova, 1952 was restored based on a single diagnostic character, the area anterior to RA and opposite the end of ScP large (accounting for approximately one-quarter of the wing width); the group as currently understood is restricted to Gondwanan forms (Béthoux & Anderson 2021). The phylogenetic position of glosselytrodeans has always been and remains controversial. The group has been previously regarded as orthopteroid (Martynov 1938; Béthoux *et al.* 2001), belonging to the clade Eumetabola [= Acercaria + Holometabola] (Béthoux *et al.* 2007) or as holometabolans, with the current trend leaning towards deeming them as neuropterans (Tillyard 1932; Carpenter 1992) or, at least, neuropterids (Sharov 1966; Rasnitsyn & Aristov 2013). Glosselytrodea as a group has even been regarded as unnatural, with the Permoberothidae considered to be either stem-group or crown-group Neuropterida (as stem-group Eidoneuroptera), and the rest of the families, that is, the ‘Glosselytrodea s.s.’, viewed as an assemblage of contentious phylogenetic position, perhaps orthopteroid (Grimaldi & Engel 2005; Engel *et al.* 2018). The lack of data on the structures from their extreme wing base and the body structure, particularly the genitalia, has contributed to their disputed position.

In this work we describe the oldest glosselytrodean currently known and assign it to the family Permoberothidae. We also reassess the type and additional specimens from other species either previously or herein classified in Permoberothidae, as well as holotypes from other Glosselytrodea, figuring them as photographs for the first time. Overall, the data herein presented significantly advance the knowledge on the earliest lineage known of the Glosselytrodea, and provide key morphological information for reassessing matters such as the integrity of the group or their wide phylogenetic relationships.

GEOLOGICAL SETTING

The genus *Permoberotha* Tillyard, 1932, with its type and only species *P. villosa* Tillyard, 1932, is the type genus of the family Permoberothidae. The holotype of this species, as well as the two additional conspecific specimens figured and (re)described herein, are from the locality of Elmo, c. 5.5 km south-east from the unincorporated town of Elmo, Banner Township, Dickinson County, Kansas, USA (Dunbar 1924; Beckemeyer 2007). This locality, early Permian in age (Artinskian), belongs to the Wellington

Formation (= Fm.), which ranges from north-central Kansas to north-central Oklahoma (Dunbar 1924; Beckemeyer & Hall 2007). The site represents one of the most prolific localities for Permian insects worldwide (Grimaldi & Engel 2005). The fossil insects are preserved in a light grey argillaceous limestone layer overlying a black carbonaceous clay shale level with *in situ* tree stumps and abundant plant remains (Dunbar 1924). The palaeontomological specimens are preserved as impressions or, more rarely, compressions with a certain relief. The latter can show a high quality of morphological detail (RPF, pers. obs.), as shown by the new *P. villosa* specimen figured herein. The Elmo deposit has been reconstructed as corresponding to freshwater bodies set in a coastal environment (Dunbar 1924; Beckemeyer & Hall 2007).

The new glosselytrodean species described herein, *Moschelopectera phantasma*, is preserved in blue-grey, slightly contact-metamorphic, silty claystone from a road-cut east of Niedermoschel/Rhineland-Palatinate, the type locality of the Niedermoschel black shale (*sensu* Schindler 1997). This lithostratigraphical unit is restricted to the north-east of the Saar-Nahe Basin in south-west Germany. Stratigraphically, it belongs to the Jeckenbach Member, Meisenheim Fm., Lower Rotliegend Group, lower Permian, Asselian–?Sakmarian (cf. Boy *et al.* 2012; Schneider *et al.* 2020). The Niedermoschel black shale was deposited in the profundal zone of an ancient freshwater lake in an intramontane setting. It yielded an abundance of plant remains, aquatic arthropods such as diplostracans, syncaridans and xiphosurans, as well as fishes and a few branchiosaurs (Poschmann *et al.* 2021). Most remarkable are the abundance and the diversity of insects, which suggest that the Niedermoschel black shale may be one of the most important fossil insect-bearing units from the early Permian (Nel & Poschmann 2021; Poschmann & Nel 2021; Poschmann *et al.* 2021).

MATERIAL AND METHOD

Specimens

The holotype of *Permoberotha villosa* Tillyard, 1932, YPM IP 005426p/cp, and the conspecific specimen YPM IP 015592p/cp were photographed at the YPM with a Leica M205 C stereo microscope and Leica DMC 4500 camera attachment running the Leica Application Suite X software, version 3.0.7.19082, 2018. The new complete specimen of *P. villosa*, MCZ-ENT-PALE-5852a/b, was found among the Elmo MCZ’s holdings lacking identification during the digitization of the museum’s fossil insect collection (i.e. the Frank M. Carpenter Collection) back in 2015. This specimen was photographed with a

Canon EOS 6D equipped with an MP-E 65 mm macro lens with a low focal depth setting to increase image sharpness; stacks of photographs were mounted using the software Helicon Focus Pro 6.0 (HeliconSoft Ltd). The holotype of *Moscheloptera phantasma*, NHMMZ PE 2020/5005-LS, was examined using a Leica MZ 7.5 stereomicroscope both dry and immersed in alcohol. Photographs were taken with the specimen under isopropanol using a Canon EOS 600D SLR camera equipped with a Canon MP-E 65 mm macro lens. Photographs were processed using the image-editing software Adobe Photoshop. Drawings were made from enlarged photographs. The holotypes PIN 966/1 of *Archoglossoptera shoricum* Martynova, 1958 and PIN 1700/1701 of *Sylvaelytron latipennatum* Novokshonov, 1998 were photographed at the PIN, Moscow using a Leica M165C stereomicroscope with a Leica DFC 420 camera.

Nomenclature

We generally follow the wing venation nomenclature proposed by Béthoux *et al.* (2007) (updated by Béthoux & Anderson 2021, such as the use of CuAant and CuApost), after Kukalová-Peck & Lawrence (2004). In particular, Béthoux *et al.* (2007) showed that the vein between CuA and RP is concave in *Eoglosselytrum perplexum* (Riek, 1953) and corresponds to MP, while the first branch of RP is convex and corresponds to MA. Thus, we consider that MA is basally fused to RP into an RP + MA and separates again distally, while MP would appear to be independent of RP + MA in the Glosselytrodea. This wing venation pattern corresponds to that proposed by Shi *et al.* (2012) for the Neuropterida on the basis of the relative convexity or concavity of the veins; while Breitkreuz *et al.* (2017) proposed a different interpretation based on the wing tracheation pattern in which MA is completely separated from RP and has a long basal free stem with MP. Because the affinities of the Glosselytrodea are still contentious and tracheation patterns can be misleading (e.g. Schubnel *et al.* 2020), for now we prefer to use the basic wing venation nomenclature adopted by Béthoux *et al.* (2007). Nevertheless, after the recognition herein of a faint yet allegedly true vein interpreted as MP between the axial veins, at least in Permoberothidae, we differ from Béthoux *et al.* (2007) in considering the posterior axial vein as the anteriormost branch of CuA instead of MP, a stance coincident with other authors such as Martynova (1952) or Rasnitsyn & Aristov (2013). Additionally, we recognize the presence of a PCu vein after Schubnel *et al.* (2020). Terminalia nomenclature follows that of Mickoleit (1973) (updated by Grimaldi & Engel 2005) for female specimens and that of Boudinot (2018) for male specimens.

Anatomical abbreviations. A, anal vein(s); a, antenna; ar, arolium; BCu, bulla of cubitus vein; BPCu, bulla of posterior cubitus vein; C, costal vein; ce, cercus; cl, clypeus; CuA, cubitus anterior vein; CuAant, anteriormost branch of cubitus anterior vein; CuApost, posteriormost branch of cubitus anterior vein; CuP, cubitus posterior vein; e, compound eye; fw, forewing; gap, gonapophysis 8 (female); gcx, gonocoxite 9 (male/female); gst, gonostylus 9 (male, female; also termed 'gonoplacs' in the female); hw, hind wing; lb, labium; lc, lacinia; m, mandible; MA, media anterior vein; MP, media posterior vein; mstl, mesothoracic leg; mttl, metathoracic leg; pca, 'precostal' area; PCu, postcubital vein; ptl, prothoracic leg; RA, radius anterior vein; RP, radius posterior vein; ScA, subcostal anterior vein; ScP, subcostal posterior vein; tVIII–XI, tergites VIII–XI.

Institutional abbreviations. MCZ-ENT-PALE, Palaeontological Collection; Museum of Comparative Zoology, Harvard University, Cambridge MA, USA; NHMMZ, State Collection of Natural History of Rhineland-Palatinate at the Museum of Natural History, Mainz, Germany; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; YPM IP, Division of Invertebrate Paleontology, Yale Peabody Museum, New Haven CT, USA.

SYSTEMATIC PALAEOLOGY

Order GLOSSELYTRODEA Martynov, 1938
[= JURINIDA Zalesky, 1929]

Revised diagnosis. (Only wing venation characters) (cf. Carpenter 1992; Rasnitsyn 2002; Béthoux *et al.* 2007). Fore and hind wings: RA very long, running parallel to the course of C until, at least, being close to the wing tip; RP and MA fused basally, separated distally; RA and RP closely running subparallel to each other for most of the wing's length; RP single or divided into a few pectinate, rather long branches; radial area with numerous cells that are variably dense; MA convex (+), straight or weakly zigzagged, very long; axial veins (i.e. anterior axial vein = MA, and posterior axial vein = CuAant) running parallel to each other for most of the wing's length, well-separated to closely spaced (sometimes seemingly fusing), roughly dividing the wing in two longitudinal halves, with no or few crossveins between them; a faint concave (–) vein (interpreted as MP) present or apparently absent (allegedly fused with either MA or CuAant), when present simple, emerging very close to base of RP + MA; stem of Cu divided into CuA and CuP near wing base; CuA convex, single or divided into a few pectinate branches; cubital area narrow basally and more or less broadened distally, with numerous cells that are variably dense; PCu and anal veins (up to three) straight, subparallel and simple; anal area independent of cubital veins.

Forewing: suboval to lanceolate in outline. Area between C and ScP moderately to greatly broadened, with simple veinlets (which can show a few crossveins between them) or a few to multiple rows of cells (= 'precostal' area); CuApost straight or variably extended to follow the wing margin, in the most

extreme degree seemingly meeting an extended RA at the wing tip to form a continuous border (the so-called complete ambient vein).

Hind wing: suboval in outline, with anal lobe typically distinct. Slightly smaller than forewing. Area between C and ScP narrow, constant in width, bearing parallel, simple and short crossveins perpendicular to ScP (i.e. 'precostal' area always lacking); ScP very short to relatively long, ending on RA at or before the basal third of the wing's length; CuApost straight, not extending to follow the wing margin.

Remarks. *Stephanastus* (belonging to Skleroptera, putatively sister to the Coleoptera) has a superficial similarity to some representatives of Glosselytrodea. However, among other differences, *Stephanastus* lacks axial veins, with a concave M and a convex CuA that run alongside but in a curved fashion, not straight, and seemingly meeting basally, in contrast to the straight, convex MA and CuAant in Glosselytrodea that are fully separated down to the wing base (Nel *et al.* 2013; Kirejtshuk & Nel 2013, 2019).

Family PERMOBEROTHIDAE Tillyard, 1932

Type genus. *Permoberotha* Tillyard, 1932.

Other genera included. *Sylvaelytron* Novokshonov, 1998; *Moschelloptera*.

Emended diagnosis. (Only wing venation characters.) Fore and hind wings with: (1) veins MA and CuAant (= axial veins) widely separated (i.e. medially, about 2/3 of the space between CuAant and the immediately posterior CuA branch); (2) a faint vein running between MA and CuAant (preferentially interpreted as MP), emerging rather basally; (3) cells in radial and cubital areas comparatively large and low in number, equally developed in both wings. Forewing: (4) with 'precostal' area not differentiated; and (5) lacking a complete ambient vein, with CuApost not even partially developed, straight. (6) Hind wing with ScP relatively long, reaching beyond the basal third of the wing's length.

Remarks. Note that the character considered as characteristic of Permoberothidae by Rasnitsyn & Aristov (2013, p. 696) of 'a long Sc of ordinary appearance' in the forewing is not included in the emended diagnosis because a shorter ScP is present in *Moschelloptera phantasma*.

Genus PERMOBEROTHA Tillyard, 1932

1937 *Dictyobiella* Tillyard, p. 104.

Type & only species. *P. villosa* Tillyard, 1932 (early Permian, Artinskian, Elmo, USA).

Emended diagnosis. Forewing with costal area relatively narrow; ScP long, ending beyond the wing midlength; RP with branches running parallel to each other; CuA with pectinate branch between CuAant and CuApost bifurcating once; anal lobe moderately developed, as wide as costal area. Forewing with dense setation on longitudinal veins and crossveins; setae with well-marked insertion sockets. Both wings with radial and cubital areas subequally developed (reaching the same maximum width).

Remarks. The genus *Permoberotha*, and its type and only species *P. villosa*, can be distinguished from the other two genera herein classified in the Permoberothidae (i.e. *Sylvaelytron* and *Moschelloptera*; both also monospecific) by having at least the forewing with radial and cubital areas reaching the same maximum width (the radial area is more developed than the cubital area in *Sylvaelytron*, particularly that of the hind wing, whereas the opposite occurs in *Moschelloptera*) and having the anal lobe moderately developed (vs poorly developed, posteriorly straight, in both *Sylvaelytron* and *Moschelloptera*). *Permoberotha* further differs from *Moschelloptera* in the forewing with a narrower costal area, longer ScP, RP with branches running parallel to each other (not zigzagging), and CuA with the pectinate branch between the anteriormost and posteriormost CuA branches (CuAant and CuApost) bifurcating once (instead of twice at least in *Moschelloptera*).

Permoberotha villosa Tillyard, 1932

Figures 1–4

1937 *Dictyobiella nervosa* Tillyard, p. 105

1937 *Permoberotha convergens* Tillyard, p. 109

Holotype. Specimen YPM IP 005426p/cp (part and counterpart), isolated forewing (counterpart originally described as *P. convergens* by Tillyard 1937) (see Carpenter 1943), from the lower Permian (Artinskian) of Elmo, Wellington Fm., Kansas, USA. Holotype (both part and counterpart) herein figured as photographs for the first time.

Additional material examined. Two specimens from the same locality as the holotype. Specimen YPM IP 015592p/cp, complete specimen preserved in lateral view with overlapping fore and hind wing from one side of the body plus the hind wing from the opposite body side exposed, originally described as the holotype and only specimen of *Dictyobiella nervosa* by Tillyard (1937) and later regarded as a junior synonym of *P. villosa* by Carpenter (1943); specimen herein figured as photographs for the first time. The specimen possesses one prothoracic leg extended, whereas the meso- and metathoracic legs are folded upon their respective pair. Specimen MCZ-ENT-PALE-5852a/b (part and counterpart), new specimen virtually complete, remarkably well preserved as a compression with slight relief, and in probable ventral view (although dorsal view is not ruled out). The configuration of the anterior part of the body, including the head and prothorax, is challenging to ascertain in the specimen based on the fossilization position. Although eyes

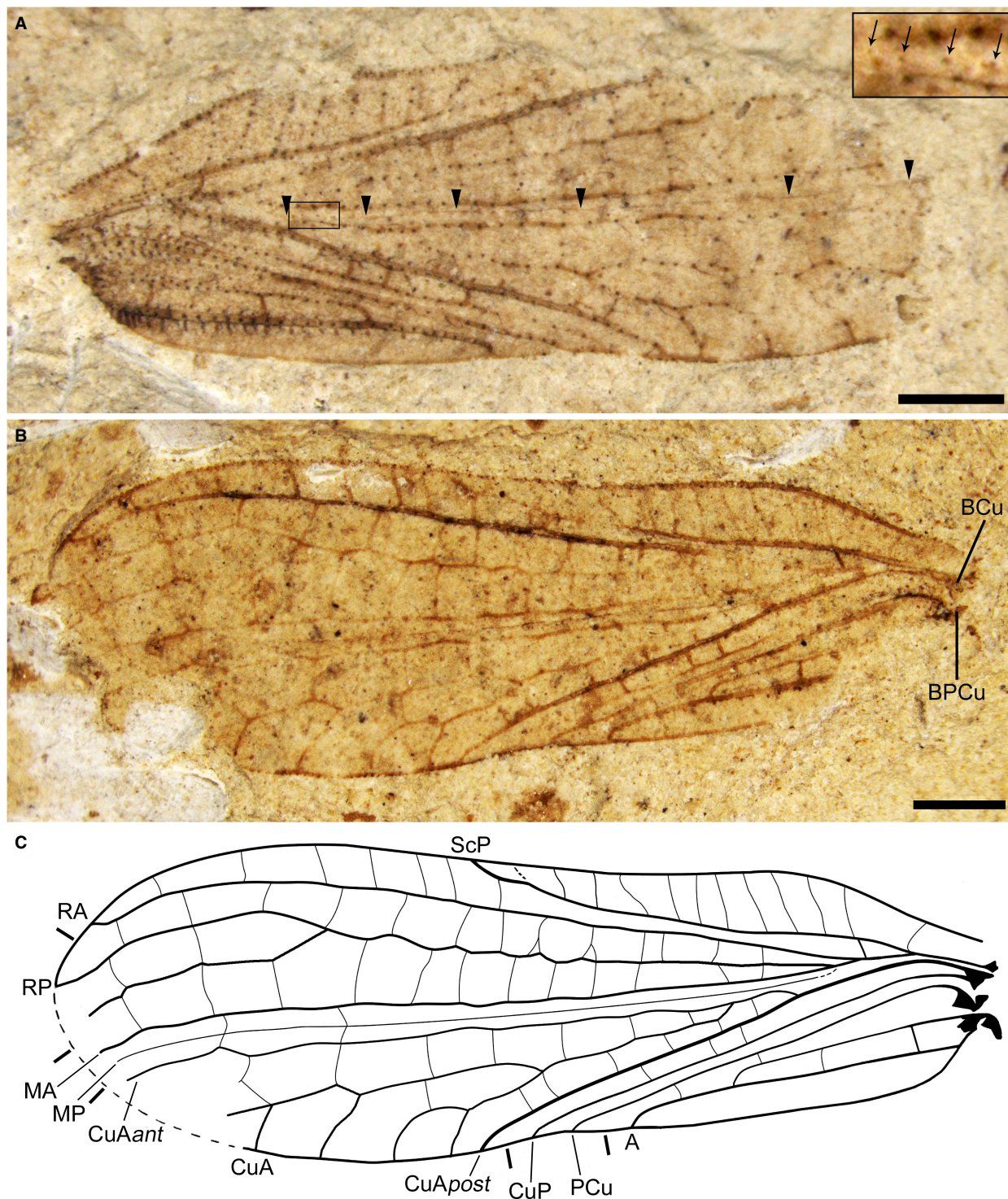


FIG. 1. *Permoberothena villosa* Tillyard, 1932 (Glosselytrodea, Permoberothidae), holotype YPM IP 005426, forewing from the lower Permian of Elmo, USA. A, photograph of part; arrowheads follow the course of the weak vein between the axial veins (interpreted as MP), with the top right inset showing macrosetal insertions (arrows) near the base of this vein. B–C, counterpart: B, photograph; C, drawing with some areas completed from the part. *Abbreviations:* A, anal vein(s); BCu, bulla of cubitus vein; BPCu, bulla of posterior cubitus vein; CuA, cubitus anterior vein; CuAant, anteriormost branch of cubitus anterior vein; CuApost, posteriormost branch of cubitus anterior vein; CuP, cubitus posterior vein; MA, media anterior vein; MP, media posterior vein; PCu, postcubital vein; RA, radius anterior vein; RP, radius posterior vein; ScP, sub-costal posterior vein. Scale bars represent 0.75 mm. Photographs by Susan Butts, Division of Invertebrate Paleontology, Yale Peabody Museum.

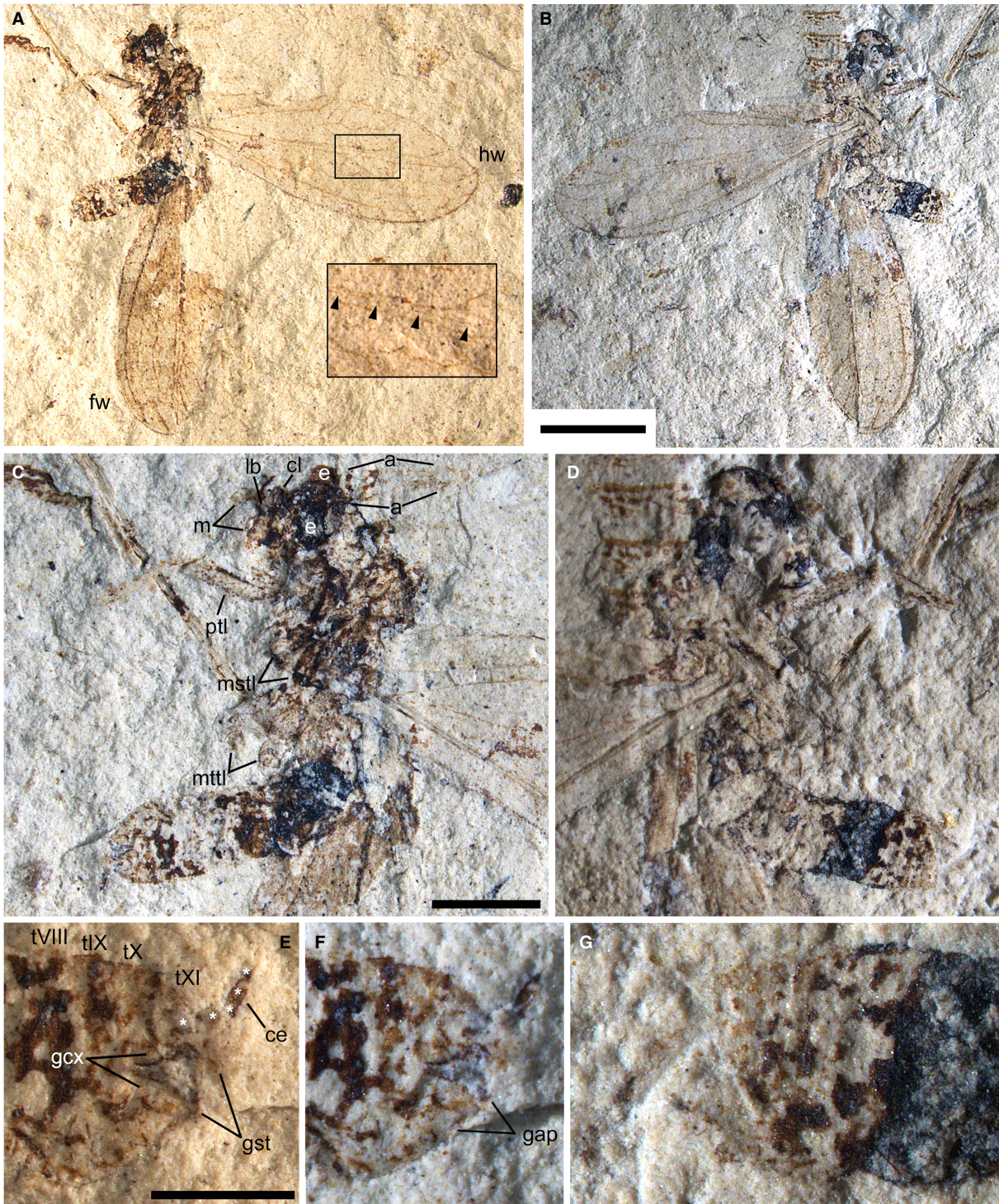


FIG. 2. *Permoberotha villosa* Tillyard, 1932 (Glosselytrodea, Permoberothidae), YPM IP 015592p/cp, complete female from the lower Permian of Elmo, USA. A–B, lateral habitus (part and counterpart, respectively), arrowheads in inset show the weak vein between the axial veins (interpreted as MP) in the hind wing. C–D, detail of body, in lateral view (part and counterpart, respectively). E–G, detail of distal abdomen, in lateral view and with dorsal side at the top of the image (E–F, part under different light settings; G, counterpart); cercomeres marked with asterisks. *Abbreviations:* a, antenna; ce, cercus; cl, clypeus; e, compound eye; fw, forewing; gap, gonapophysis 8; gcx, gonocoxite 9; gst, gonostylus 9; hw, hind wing; lb, labium; m, mandible; mstl, mesothoracic leg; mttl, metathoracic leg; ptl, prothoracic leg; tVIII–XI, tergites VIII–XI. Scale bars represent: 2 mm (A, B, same scale); 1 mm (C, D, same scale); 0.5 mm (E–G, same scale). Photographs by Susan Butts, Division of Invertebrate Paleontology, Yale Peabody Museum.

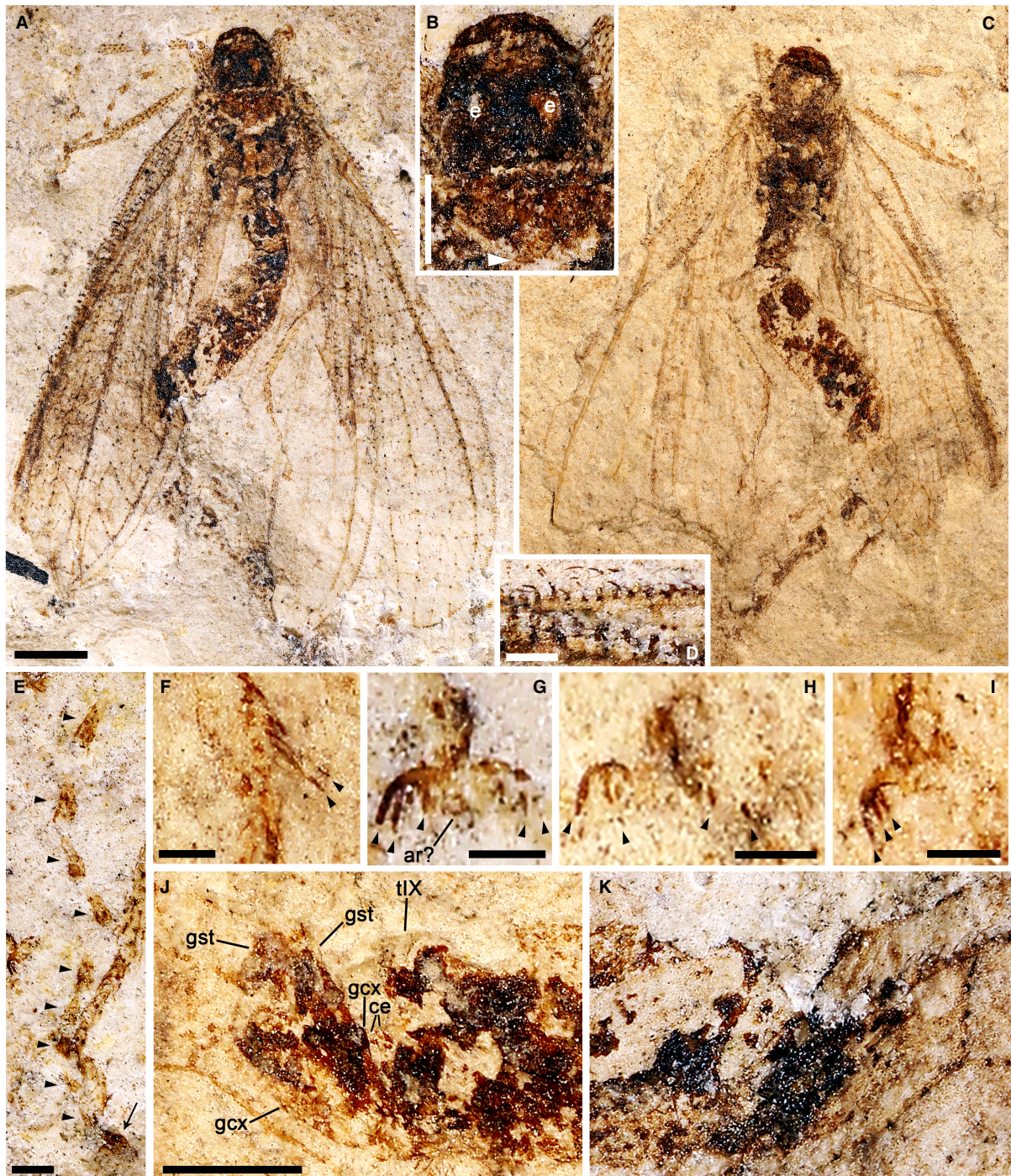


FIG. 3. *Permoberotha villosa* Tillyard, 1932 (Glosselytrodea, Permoberothidae), new specimen MCZ-ENT-PALE-5852a/b, complete male from the lower Permian of Elmo, USA. A, habitus (part). B, detail of the head (part); mouthparts not defined well enough to provide a convincing interpretation (arrowhead pointing to possible tip of left mandible). C, habitus (counterpart). D, detail of specialized setae on the costal margin (part). E, visible antennal flagellomeres, marked with arrowheads, with the last visible flagellomere marked by an arrow. F, tibio-tarsal articulation of metathoracic leg (counterpart), showing paired metatibial spurs (arrowheads). G–H, pretarsal claws, probably from prothoracic leg, showing teeth (arrowheads): G, part; H, counterpart. I, pretarsal claws from metathoracic leg (counterpart). J–K, genitalia in lateral view: J, counterpart; K, part. *Abbreviations:* ar, arolium; ce, cercus; e, compound eyes; gcx, gonocoxite 9; gst, gonostylus 9; tIX, tergite IX. Scale bars represent: 1 mm (A, C, same scale); 0.5 mm (B, J–K same scale); 0.2 mm (D, E); 0.1 mm (F–I). All images are ©President and Fellows of Harvard College.

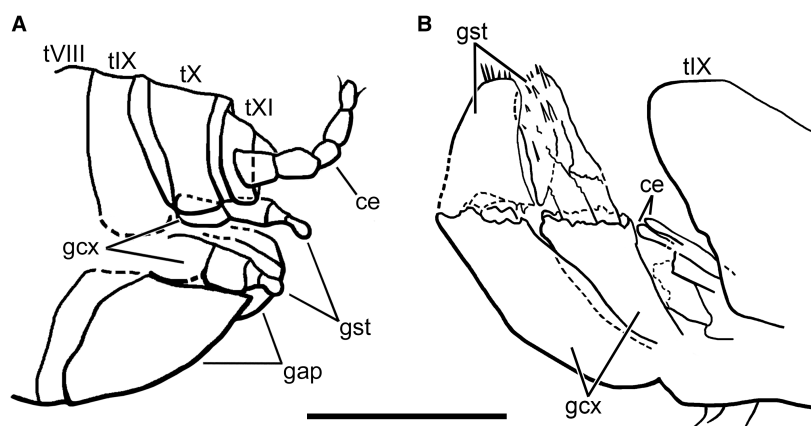


FIG. 4. Terminalia interpretations for the two *Permoberotha villosa* Tillyard, 1932 (Glosselytroidea, Permoberothidae) specimens preserved as full bodies reported herein. A, female terminalia of YPM IP 015592p/cp. B, male terminalia of MCZ-ENT-PALE-5852a/b. *Abbreviations:* ce, cercus; gap, gonapophysis 8; gcx, gonocoxite 9; gst, gonostylus 9; tVIII–XI, tergites VIII–XI. Scale bar represents 0.5 mm.

appear to be overlapping, this is also likely to be due to positioning.

Emended diagnosis. As for the genus (*vide supra*).

Redescription

Body. Length c. 5.50 mm.

Head. Sub-hypognathous (Fig. 2C, D). Compound eyes large; ovoid, c. 0.60 mm long, 0.43 mm wide; well separated, probably by a distance at least as wide as their own width. Vertex moderately pronounced. Ocelli, if present, not visible. Clypeus wide. Antennae relatively long, c. 3.30 mm long as preserved; inserted between compound eyes (in YPM IP 015592p/cp); scape and pedicel structure unclear but apparently longer and thicker than flagellomeres (YPM IP 015592p/cp); visible antenna with 10 preserved flagellomeres (in MCZ-ENT-PALE-5852a/b), each flagellomere narrower proximally and distally expanded (Fig. 3E); flagellomeres decreasing in length distally along the antennal length, with basalmost visible flagellomere more than 3× as long as wide. Labrum an apparently triangular sclerite. Mandibles well developed, at least 0.40 mm long, with incisor edge apparently sharp, at least one tooth probably present, other details unclear.

Thorax. Prothorax subquadrate, about as long as compound eyes, covering most of the sub-hypognathous head dorsally; meso- and metathorax well developed. All legs setose, setae up to 0.12 mm. Coxae (at least procoxae) well developed. Metatibiae bearing two moderately developed ventral spurs (Fig. 3F), not distinct in other legs. Tarsi five-segmented; tarsomeres 1–4 with particularly strong setae along plantar surfaces, the distal-most ones distinctly larger. All pretarsal claws complex, equal, widely separated from one another; each distally subdivided into at least two (possibly three) teeth (Fig. 3G–I) and probably bearing additional shorter teeth basally, teeth arrangement uncertain,

that is, pretarsal claws either bifid or trifold (with teeth subequal in length) or pectinate (with teeth progressively decreasing in length proximally); arolium apparently present, at least in the probable prothoracic leg, moderately enlarged (in MCZ-ENT-PALE-5852a/b) (Fig. 3G).

Forewing. (Measurements taken from the holotype, with the two remaining specimens assessed falling in the same size ranges) (Figs 1, 2A, B, 3A, C). Elongate and relatively narrow, 7.8 mm long, 2.6 mm maximum width (reached by the wing's distal third); crossvenation not dense, all veins (including most crossveins) highly setose, setae up to c. 0.13 mm, with setal insertions well marked; setae preserved in the costal margin with a thick straight base and a distal region thin and abruptly bent forwards (Fig. 3D). Costal space moderately broadened, with at least 11 visible simple veinlets. ScP ending on C beyond the wing's mid-length. Basal ScP-R crossvein present immediately before the origin of RP + MA. RA simple, straight until the wing's distal 1/5, then slightly bent downwards following the wing's tip, with seven visible veinlets, all simple; RP + MA arising at c. 1.1 mm from wing base; RP with two branches (three in MCZ-ENT-PALE-5852a/b) splitting beyond the wing's distal third (before mid-wing in YPM IP 015592p/cp, MCZ-ENT-PALE-5852a/b, and other material described by Carpenter 1943), with RP1 slightly bent downwards; MA straight until the wing's distal 1/5, then slightly bent downwards; a weak vein interpreted as MP arising at an indeterminate point slightly beyond the fusion of RP and MA; MA and CuA_{ant} (= axial veins) running parallel until the wing's midlength, then slightly diverging to become subparallel, with a few distal crossveins apparently present between them; vein between axial veins (alleged MP) equidistant from MA and CuA_{ant} along all its length; cubital bulla visible, with CuA and CuP separation very basal; CuA base highly curved, split beyond the branching of RP + MA into two principal branches, CuA_{ant} and CuA_{post}, the latter particularly thick (about as much as RA), straight and reaching the wing margin slightly beyond the wing's midlength, beyond the ending of ScP; a pectinate CuA branch bifurcated once between CuA_{ant} and

CuApost; CuP straight, parallel to CuApost; PCu arising from a pronouncedly curved bulla, straight, running closely parallel to CuP; anal lobe moderately developed; anal veins simple, with a few crossveins between them; A1 approximating PCu gradually, then abruptly downcurving to end in A2 distad to the wing margin; A2 well developed, mostly straight.

Hind wing. (Fig. 2A, B) Elongate and relatively narrow, more oval than forewing in outline, 7.6 mm long, 2.4 mm maximum width (reached between mid-wing and the wing's distal third), crossvenation not dense, all veins (including most crossveins) highly setose, with setal insertions well marked although apparently not as much as in forewing. ScP running closely parallel to RA, meeting RA well beyond the wing's basal third, at c. 2.8 mm from wing base. Venational structure of radiomedial and cubital areas as in the forewing, including the presence of a weak vein (interpreted as MP) between the axial veins, roughly as in forewing; branching point of intermediate branch of CuA not visible; anal veins barely discernible.

Abdomen. Length c. 3.50 mm, less than half of the forewing's length. Female terminalia (YPM IP 015592p/cp; Figs 2E–G, 4A) with 11 visible segments. Segment VIII lacking visible ovipositor ventrodistally but with gonapophyses 8 probably present, basally wide and narrowing distally (Fig. 2F). Segment IX ventrally bearing gonocoxites and gonostyli (gonoplacs), the latter probably with at least two segments, the terminal one knob-shaped. Segment XI with cerci subterminal, multisegmented (at least four-segmented, probably five-segmented), c. 0.40 mm as preserved (Fig. 2E, F); other structures not evident (few of these abdominal structures are evident in the counterpart; Fig. 2G). Male terminalia (MCZ-ENT-PALE-5852a/b; Figs 3J–K, 4B) with nine visible segments. Gonocoxites massive, slightly expanding medially in lateral view, c. 0.80 mm long, 0.23 mm wide, fully independent and (allegedly) mobile, attached ventrally, positioned at about a 40° angle relative to the remaining abdomen; gonocoxites bearing irregular serrations in distal border. Gonostyli narrower than gonocoxites, tapering apically; exact shape unclear, apparently bearing spine-like setae. Paired small, simple, spoon-shaped structures interpreted as cerci present.

Remarks. Re-interpretation of the forewing venation of *P. villosa* is based on the holotype and its counterpart (Fig. 1), which show the base of the wing (including the vein bullae) remarkably well preserved. The preserved basal structures identified as bullae are interpreted as such because the longitudinal veins appear to emerge directly from them and a more proximal position for median plates or axillary sclerites would be expected. The basal bulla of PCu (interpreted as A1 by Tillyard 1932) is characterized by its pronounced curved shape (see Schubnel et al. 2020). The weaker vein immediately anterior to PCu has to correspond to CuP, and the vein anterior to CuP corresponds to CuA; the bulla of the cubital vein (BCu) is also visible (Fig. 1B), showing that the separation of CuA and CuP occurs very close to the wing base. CuA has a strong stem (the posteriormost) running straight to the wing margin and two anterior branches. Anterior to CuA and posterior to MA, emerging from an indeterminate area probably after the branching of R and M, there is a straight vein,

clearly weaker than MA and CuA, that we interpret as MP (Fig. 1; see Discussion).

Attribution of the specimen YPM IP 015592p/cp to *P. villosa* and its synonymy with *Dyctiobiella nervosa* done by Carpenter (1943) are herein supported. The forewings of both YPM IP 015592p/cp and MCZ-ENT-PALE-5852a/b show the same characters as those from the holotype except for the branching of RP taking place at about the wing's midlength instead of beyond the wing's distal third. Additionally, the forewing's RP of MCZ-ENT-PALE-5852a/b has three principal branches instead of two, the anteriormost RP branch briefly bifurcating near the wing's tip. These differences are regarded as intraspecific variability. Carpenter (1943) also noted some variability in the forewing pattern in the material that he examined and assigned to *P. villosa*. Setational differences apparently existing between the assessed forewings could be related to poor preservation and are, therefore, not reliable. Aside from wing characters, the remaining features (including size) between specimens YPM IP 015592p/cp and MCZ-ENT-PALE-5852a/b, accounting for putative preservational biases and terminalic differences, are compatible with their conspecificity. The body characters visible in YPM IP 015592p/cp are generally consistent with those described by Tillyard (1937) (see Discussion), who provided only descriptive notes and a drawing of the putative cercus. Although the author mentioned that two forewings and a hind wing were visible from the specimen, only one forewing overlapping with the hind wing is evident, given that the other visible exposed wing corresponds to the hind wing (Fig. 2A, B).

Genus SYLVAELYTRON Novokshonov, 1998

Type & only species. *Sylvaelytron latipennatum* Novokshonov, 1998.

Emended diagnosis. Forewing with costal area relatively narrow; ScP long, ending beyond the wing midlength; anal lobe weakly developed, narrower than costal area. Both wings (particularly the hind wing) with the radial area more developed than the cubital area (reaching a greater maximum width).

Remarks. In spite of the faint preservation of the wing venation in this species, the genus *Sylvaelytron*, and its type and only species *S. latipennatum*, can be separated from *Permoberotha* and *Moschelopectera* by at least the forewing having the radial area more developed (i.e. reaching a greater maximum width) than the cubital area (the opposite in *Moschelopectera*, subequally developed in *Permoberotha*). Other visible differences regarding *Permoberotha* include the less developed anal lobe in the forewing, whereas *Sylvaelytron* further differs from *Moschelopectera* in the narrower costal area and the longer ScP.

Sylvaelytron latipennatum Novokshonov, 1998

Figure 5

Holotype. Specimen PIN 1700/1701, from Chekarda (Koshelevka Fm.), Middle Urals, Russian Federation; Kungurian, early Permian (Zhuzhgorova et al. 2015); a complete yet faintly preserved specimen in lateral habitus showing one forewing and one hind wing exposed.

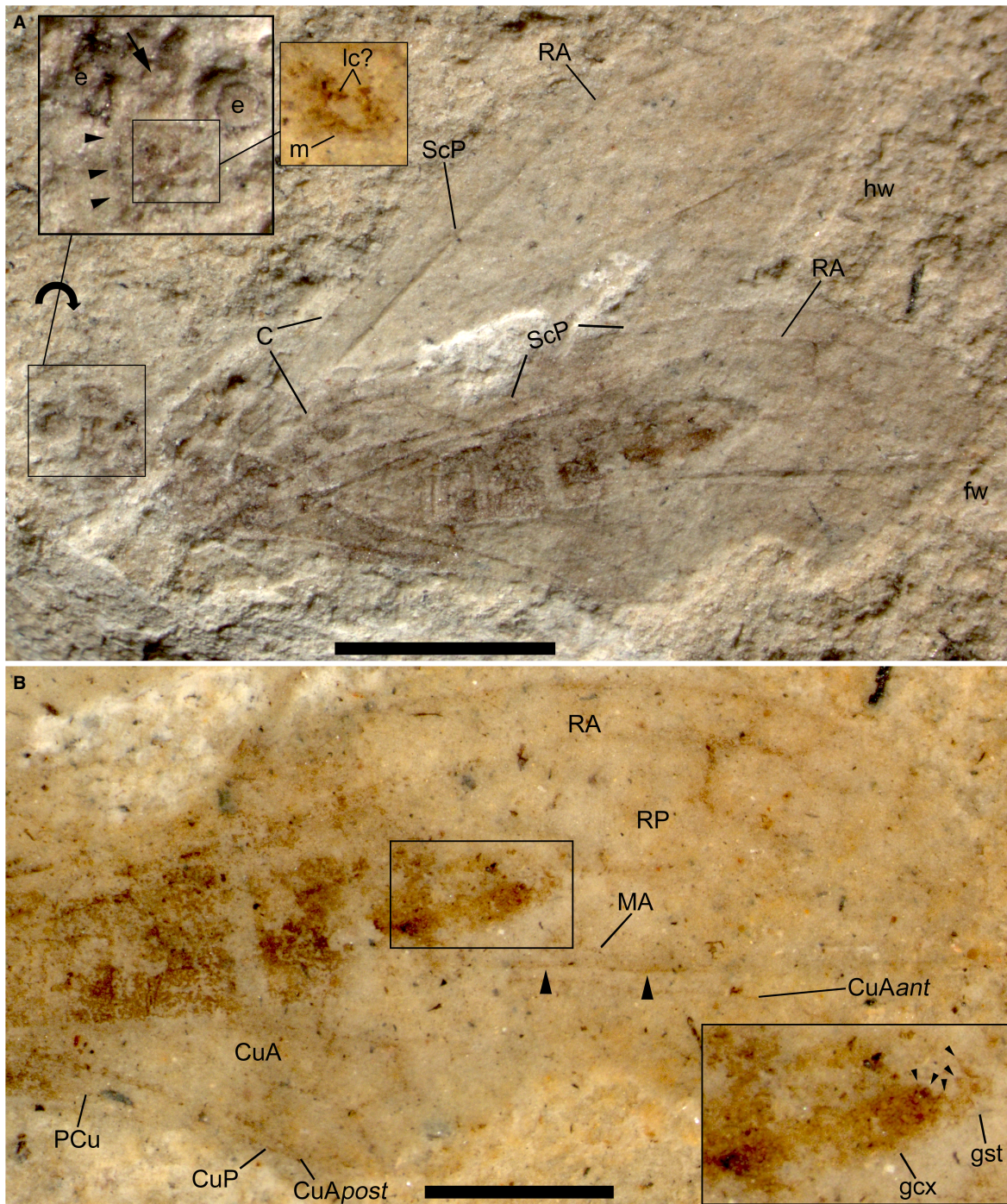


FIG. 5. *Sylaelytron latipennatum* Novokshonov, 1998 (Glosselytroidea, Permoberothidae), holotype PIN 1700/1701, complete specimen (interpreted as male) from the lower Permian of Chekarda, Russian Federation. A, habitus; inset shows head (rotated 180°) with a different light orientation; arrow points to the right antennal insertion, with arrowheads showing the course of visible proximal antennal segments; mandibles (and possibly laciniae) shown on the right under alcohol. B, forewing distal half and abdomen, under alcohol; arrowheads follow the course of the weak vein between the axial veins (interpreted as MP); the right inset shows detail of the male terminalia, with arrowheads marking serrations on the inner side of narrow gonostyli. *Abbreviations:* C, costal vein; CuA, cubitus anterior vein; CuAant, anteriormost branch of cubitus anterior vein; CuApost, posteriormost branch of cubitus anterior vein; CuP, cubitus posterior vein; e, compound eye; fw, forewing; gcx, gonocoxite 9; gst, gonostylus 9; hw, hind wing; lc, lacinia; m, mandible; MA, media anterior vein; PCu, postcubital vein; RA, radius anterior vein; RP, radius posterior vein; ScP, subcostal posterior vein. Scale bars represent: 2 mm (A); 1 mm (B). Photographs by Dmitry Vasilenko, Paleontological Institute, Russian Academy of Sciences.

Emended diagnosis. As for the genus (*vide supra*).

Remarks. The specimen is herein identified as male due to the presence of enlarged, broad gonocoxites bearing narrower gonostyli, the latter probably movable, concave, incurved distally; both the distal end of the gonocoxites and the inner side of the gonostyli appear to bear serrations (see inset in Fig. 5B).

Genus MOSCHELOPTERA nov.

LSID. urn:lsid:zoobank.org:act:0E8B9F40-60B6-4D92-844B-FF02BF65C8AA

Type & only species. *Moscheloptera phantasma* sp. nov.

Derivation of name. Named after the Moschel, a small creek and fourth-order tributary to the Rhine river close to the type locality, and *-optera*, a suffix referring to winged insects. Gender feminine.

Diagnosis. Forewing with costal area broad; ScP short, ending before the wing midlength; RP with branches zigzagging distally; cubital area well developed, reaching a greater maximum width than radial area; CuA with pectinate branch between CuAant and CuApost bifurcated twice at least; anal lobe poorly developed, narrower than costal area, posteriorly straight; anal margin bearing a fringe of distinctive thick setae.

Remarks. *Moscheloptera*, and its type and only species *M. phantasma*, can be distinguished from *Permoberotha* and *Sylvaelytron* by the forewing with a broader costal area, a shorter ScP, a cubital area that is more developed than the radial one, and zigzagging RP branches. Differences only with *Permoberotha* include forewing CuA with the branch between CuAant and CuApost bifurcated twice at least (bifurcated only once in *Permoberotha*) and the absence of a developed anal lobe. Also, although both *Permoberotha* and *Moscheloptera* appear to share the specialized forewing setae, these were present in *Moscheloptera* along the posterior wing margin, in the anal area, whereas they appear to be absent in that region in *Permoberotha*.

Moscheloptera phantasma sp. nov.

Figure 6

LSID. urn:lsid:zoobank.org:act:7D8C98C2-F231-4501-990C-C4E5CF62D91B

Derivation of name. From the Latin word *phantasma*, meaning ‘phantom, ghost’ and referring to the shadow-like appearance of the holotype in the rock matrix.

Holotype. Specimen NHMMZ PE 2020/5005-LS (former collector’s number 1344-P); a complete forewing largely preserved as an imprint in black shale from Niedermoschel, stored in the State Collection of the Natural History of Rhineland-Palatinate at the Museum of Natural History, Mainz, Germany.

Occurrence. Roadcut east of Niedermoschel/Rhineland-Palatinate, the type locality of the Niedermoschel black shale (*sensu* Schindler 1997; see Poschmann *et al.* 2021 for further information), Saar-Nahe Basin, Germany; Jeckenbach Member, Meisenheim Formation, Lower Rotliegend Group, lower Permian, Asselian–?Sakmarian (cf. Boy *et al.* 2012; Voigt *et al.* 2019; Schneider *et al.* 2020).

Diagnosis. As for the genus (*vide supra*).

Description. Forewing suboval, 9.9 mm long, 3.6 mm maximum width reached at 2/3 of wing length; wing membrane with apparent maculations, in the radial and cubital areas roughly adjusting to the area within most of the cells; C bearing a distinctive dense fringe of well-developed setae; costal area broad, abutting, 0.7 mm maximum width, with c. 13 costal veinlets, apparently all simple; ScP relatively short, ending before wing midlength, at 4.2 mm from wing base, mostly straight and gently upcurving distally; branching of RA and RP + MA not discernible but rather basal; RA mostly straight, parallel to anterior wing margin after meeting point between C and ScP, distally curved following C but not reaching the wing tip; RP and MA probably separating at c. 1.9 mm from the wing base; RP with three branches, distally zigzagged; at least seven visible crossveins between RA and RP; MA straight; base of vein interpreted as MP not visible, but possibly arising between branching of RP + MA and that of MA; vein between axial veins (interpreted as MP) very weak, barely visible, discernible subdistally running closely parallel to MA; CuAant and CuApost forking at c. 0.6 mm from wing base; cubital region reaching a greater maximum width than radial region, CuA well developed, with a branch between CuAant and CuApost bifurcated at least twice; CuAant running parallel to MA, subsequent CuA branches distally downcurving towards wing margin; CuApost very gently downcurved; CuP weakly downcurved and closely parallel to CuApost; one PCu vein and one anal vein visible, details not assessable; anal area relatively narrow, slightly narrower than costal area; anal margin with a series of thick setae with a straight base and a distal region abruptly bent forwards.

Remarks. The broad costal area and ScP meeting C (instead of RA) indicate that NHMMZ PE 2020/5005-LS represents a forewing. Note that *Moscheloptera phantasma* is not the first Glosselytrodea known from Germany, given that Bashkuev *et al.* (2012, p. 176) indicated the presence of a ‘Glosselytrodea: Jurinidae (*s.l.*) gen. et sp.’ from the early Anisian of Franconia. The series of peculiar setae along the anal margin of *M. phantasma* could have played a role in the attachment of the fore and hind wings, although this remains conjectural at present.

DISCUSSION

The family Permoberothidae: diagnostic characters and current composition

The wing characters used as diagnostic for the family Permoberothidae Tillyard, 1922 and their comparison with the remaining Glosselytrodea are discussed in detail

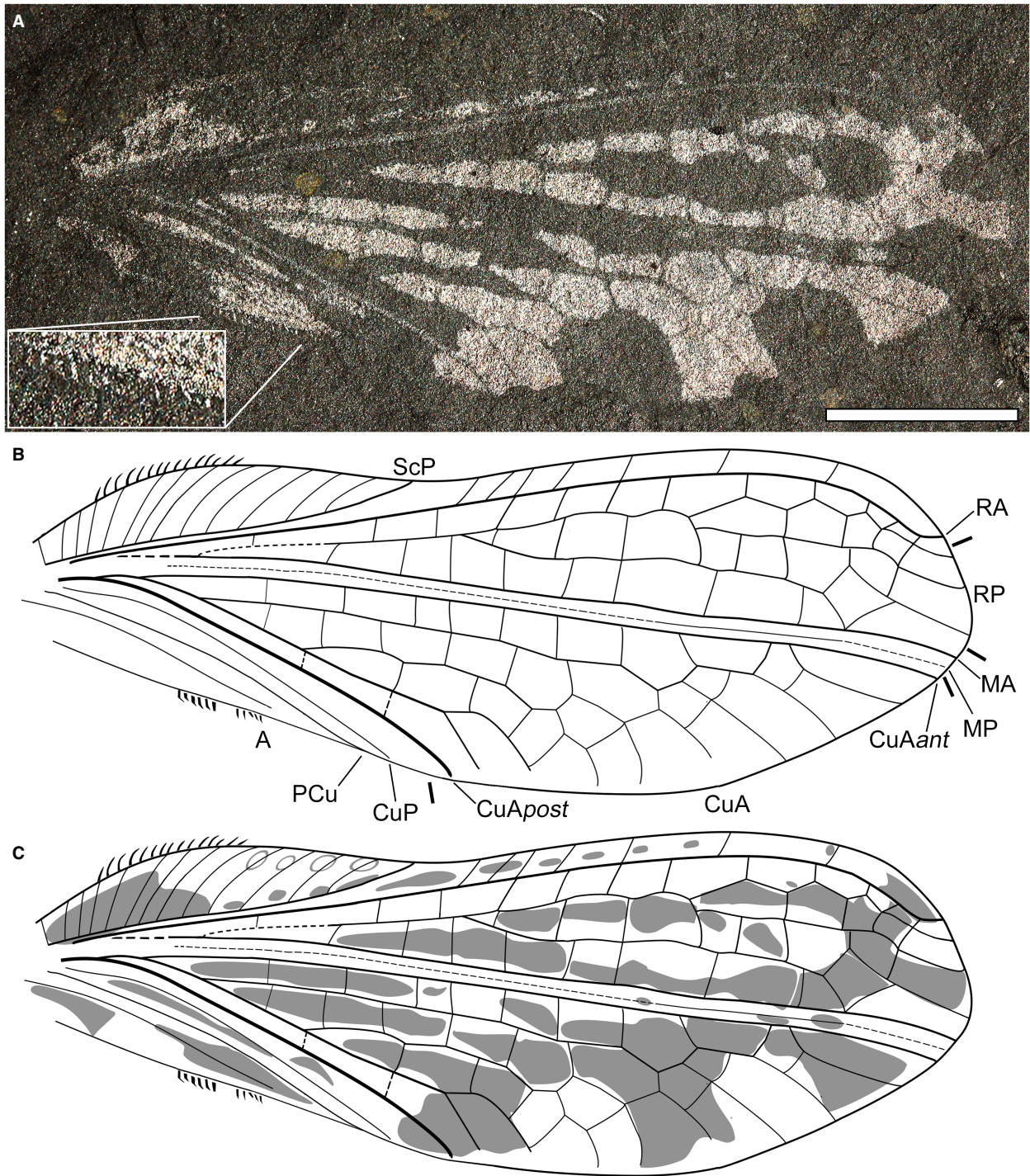


FIG. 6. *Moschelopectera phantasma* gen. et sp. nov. (Glosselytrodea, Permoberothidae), holotype NHMMZ PE 2020/5005-LS, forewing from the lower Permian of Niedermoschel/Rhineland-Palatinate, Germany. A, photograph under alcohol. B, wing venation reconstruction, with longitudinal veins tagged. C, same as B, with maculated areas shown as observed in the fossil. *Abbreviations:* A, anal vein(s); CuA, cubitus anterior vein; CuAant, anteriormost branch of cubitus anterior vein; CuApost, posteriormost branch of cubitus anterior vein; CuP, cubitus posterior vein; MA, media anterior vein; MP, media posterior vein; PCu, postcubital vein; RA, radius anterior vein; RP, radius posterior vein; ScP, subcostal posterior vein. Scale bar represents 2 mm.

below. The degree of separation between the forewing veins MA and CuAant (i.e. the axial veins, putatively synapomorphic for Glosselytrodea) is variable across the order, ranging from a relatively wide separation in Permoberothidae and *Archoglossopterus* Martynova, 1958 (family diagnostic character 1) (Figs 1–3, 5–7) to a narrow separation (e.g. *Eoglosselytrum* Martynova, 1952, *Glossopterus* Sharov, 1966, *Mongolourina* Ponomarenko, 1988) (Martynova 1952, 1961; Ponomarenko 1988, 2000; Novokshonov 1998), to even (allegedly) complete fusion (e.g. *Argentinoglosselytrina* Martins-Neto & Gallego, 2001, *Karajurina* Novokshonov & Vilesov in Vilesov & Novokshonov, 1994, *Polycytella* Tillyard, 1922) (Vilesov & Novokshonov 1994; Martins-Neto & Gallego 2001; Béthoux & Anderson 2021). The alleged complete fusion of the axial veins might imply that the weakened vein (interpreted herein as MP) present between them at least in Permoberothidae and *Archoglossopterus* is no longer present or visible, not even as a trace. Rasnitsyn & Aristov (2013) proposed that the axial veins are also fused in *Isadelytron planum* Rasnitsyn & Aristov, 2013 and *Karajurina desperata* Rasnitsyn & Aristov, 2013, although these taxa are based on poorly preserved material. *Polycytella* was originally considered in a separate family, Polycytellidae Martynova, 1952, synonymized with the Glosselytridae Martynov, 1938 by Rasnitsyn & Aristov (2013), and then classified back to Polycytellidae together with *Argentinoglosselytrina* and *Moltenourina* Béthoux & Anderson, 2021 by Béthoux & Anderson (2021). The character ‘complete fusion of the alleged vein MP with either MA or CuAant’ could constitute a putative synapomorphy for the species classified in these three genera but it could also constitute a synapomorphy for those classified in *Karajurina*.

A weak vein running between MA and CuAant in both the fore and hind wings (diagnostic character 2 for Permoberothidae) had originally been overlooked in *Permoberotha villosa* Tillyard, 1932, for which only a ‘groove or furrow’ was described in this position (Tillyard 1932, 1937, p. 105; Carpenter 1943, fig. 4). Later, Carpenter (1992, p. 537) noted that this groove was ‘apparently bearing a spurious vein’. *Permoberotha villosa* clearly possesses a continuous yet weak vein between the axial veins, as the images from the holotype and additional conspecific specimens herein show (Figs 1–3). The same vein was drawn from *Sylvaelytron latipennatum* Novokshonov, 1998 but overlooked in the description (Novokshonov 1998); the reassessment of its holotype also shows the presence of this weak vein running between the axial veins (Fig. 5). *Archoglossopterus shoricum* Martynova, 1958 also appears to possess this character, although its course cannot be fully resolved due to preservation artefacts (Fig. 7). We interpret this structure quite confidently as a vein as opposed to a flexion line. Although the

permoberothid wing might have been folded to a certain degree longitudinally along the space between the axial veins (including the vein in between) in some permoberothid taxa as already noted by Tillyard (1937), the possibility that this longitudinal vein was merely a flexion line in the wing membrane of some Glosselytrodea such as Permoberothidae is considered unlikely due to the presence of a few macrosetal insertions preserved close to the base of this vein in *P. villosa* (see inset in Fig. 1A), and because it seems implausible that flexion lines would fossilize in the same way that veins do in fossils at least partly preserved as impressions. In the *Permoberotha* (and *Sylvaelytron*, to a lesser degree) specimens preserved as impressions herein presented, the putative MP veins have a similar appearance to the remaining veins, although they are clearly weaker, both having left a dark carbonaceous residue of cuticle. Furthermore, although we prefer to tentatively interpret the weakened longitudinal vein between the axial veins in *Permoberotha*, *Sylvaelytron* and *Archoglossopterus* (barely discernible in *Moscheloptera*) as MP, the lack of an apparent connection of its base with RP + M in these taxa, if not regarded as preservational, also enables the alternative interpretation that it could represent an intercalary vein (a fact that would render the medial vein simple following our present venational approach). This hypothesis seems less plausible because intercalary veins typically appear in multiple numbers, not single, along contiguous sets of principal veins across diverse insect lineages, and would appear to be less prone to bearing macrosetae. It is important to note that Martynova (1958, 1961) interpreted the vein MA of *Archoglossopterus* as being MP basally fused to RP. Likewise, in both Glosselytridae and Jurinidae Zalesky, 1929 the anterior axial vein had been interpreted as MP (Martynov 1938; Martynova 1952, 1961; Rasnitsyn & Aristov 2013). We propose that this vein can be homologized with that of Permoberothidae and *Archoglossopterus*, and therefore it actually corresponds to MA, with a putative MP absent due to reduction or complete loss (allegedly concomitant with the narrowing of the space between axial veins) during the process of forewing sclerotization in Glosselytrodea. Future findings should be able to shed light on these and other matters concerning the wing venation interpretation in glosselytrodeans.

Permoberothidae (and *Archoglossopterus*) have larger cells in the radial and cubital areas when compared with most of the remaining glosselytrodean diversity (family diagnostic character 3), particularly Glosselytridae and Polycytellidae. Moreover, their cells are of equal size and morphology between the fore and hind wings, something that would not appear to be the case outside the group, as shown by *Eoglosselytrum* and *Jurina* Zalesky, 1929, where radial and cubital cells tend to be larger in the hind wing than in the forewing (Martynov 1938; Martynova

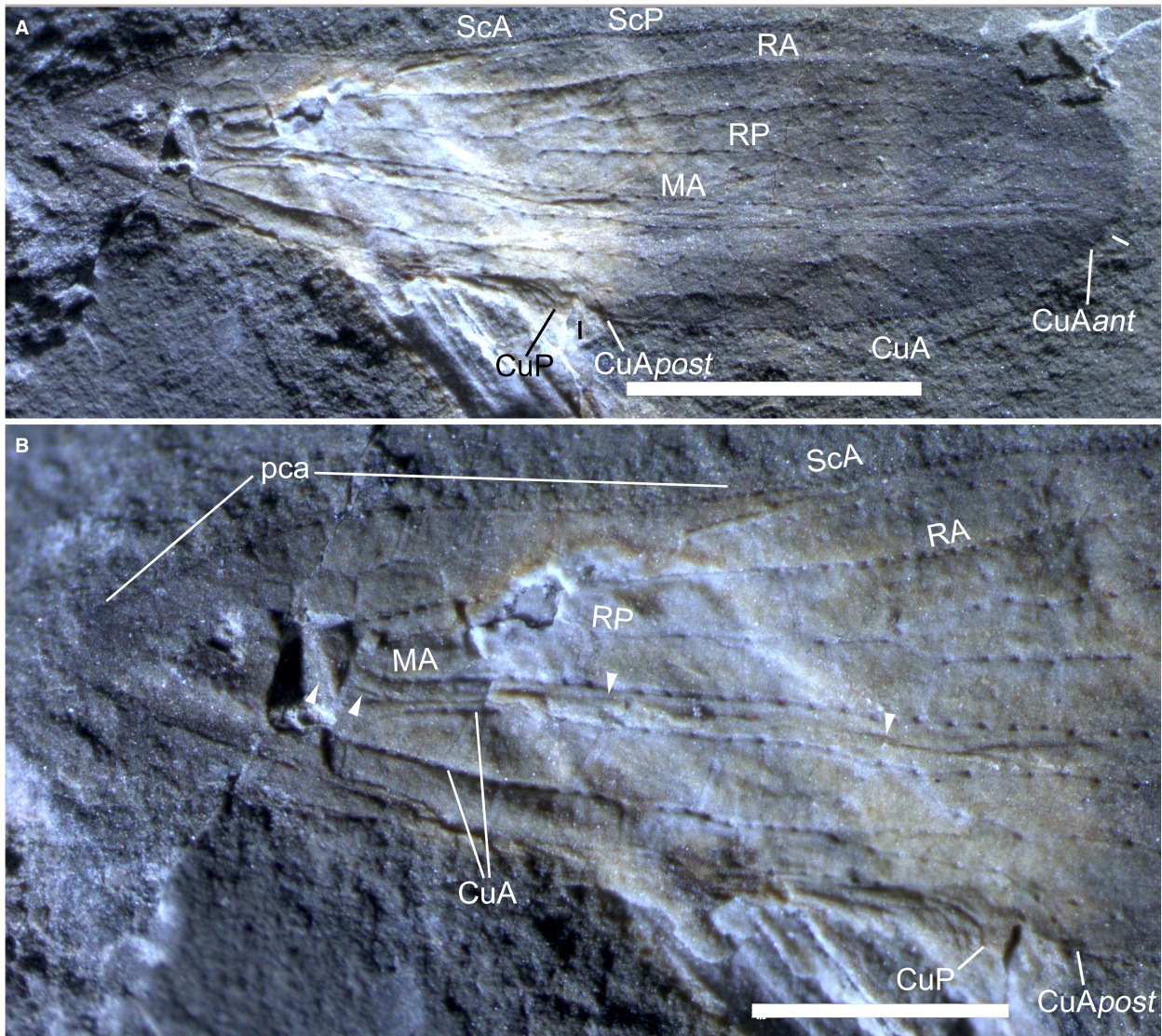


FIG. 7. *Archoglossopterus shoricum* Martynova, 1958 (Archoglossopteridae), holotype PIN 966/1, forewing from the middle Permian of Kaltan (outcrop 1300), Russian Federation. A, habitus. B, detail from basal half of the wing; arrowheads following alleged course of the weak vein between the axial veins (interpreted as MP), distally unclear due to poor preservation. Abbreviations: CuA, cubitus anterior vein; CuAant, anteriormost branch of cubitus anterior vein; CuApost, posteriormost branch of cubitus anterior vein; CuP, cubitus posterior vein; MA, media anterior vein; pca, 'precostal' area; RA, radius anterior vein; RP, radius posterior vein; ScA, subcostal anterior vein; ScP, subcostal posterior vein. Scale bars represent: 2 mm (A); 1 mm (B). Photographs by Dmitry Vasilenko, Paleontological Institute, Russian Academy of Sciences.

1952; Vilesov & Novokshonov 1994). Furthermore, permoberothids lack the development in their forewing of the so-called 'precostal' area (family diagnostic character 4), whereas other glosselytrodeans (including *Archoglossopterus*) show a development of this region that is variable in shape (abutting to lanceolate) and venation, with the alleged development of ScA and abundant crossvenation between branches of ScA and ScP, which form multiple rows of cells.

In glosselytrodeans the term 'ambient' is used to describe an apparently continuous vein that creates a ledge along the forewing margin. This ambient vein is

actually composed of two veins, RA anteriorly and CuApost (also interpreted as CuP by some authors) posteriorly (cf. *Eoglosselytrum*, *Surijoka* Martynova, 1958, *Protojurina* Martynova, 1958), which showed different degrees of development throughout evolution and met at the wing tip as an alleged derived scenario according to Rasnitsyn & Aristov (2013). Although virtually all glosselytrodean wings have an RA that follows the course of C until, at least, being close to the wing tip, only some taxa have an RA that is fully extended following the course of C and which reaches the wing tip to apparently meet with CuApost. This condition occurs in all Glosselytridae and

Polycyttellidae; in the Jurinidae a fully ambient vein is present in, at least, *Mesojurina* Martynova, 1943, *Shaanxiglosselytron* Hong, 2007 and *Sinoglosselytron* Hong, 2007 (Martynov 1938; Martynova 1943; Ponomarenko 1988; Vilesov & Novokshonov 1994; Martins-Neto & Gallego 2001; Hong 2007; Huang *et al.* 2007; Béthoux & Anderson 2021). The vein CuApost, however, is always straight, not even partially ambient, in the forewings of Permoberothidae (family diagnostic character 5) (Figs 1–6) and *Archoglossopteryx* (see vein re-interpretation in Fig. 7), as well as those of *Glossopteryx*. In the glosselytrodean hind wing (see below) RA and CuApost never form an ambient vein, their structure being very similar to those of the permoberothid forewing, that is, R following the course of C until being close to the wing tip but not reaching the median veins, and CuApost straight, not following the course of C (Tillyard 1937; Martynov 1938; Carpenter 1943; Martynova 1952; Vilesov & Novokshonov 1994; Béthoux *et al.* 2007). In contrast, the two species classified within the genus *Glossopteryx*, *G. sharovi* Novokshonov, 1998 and *G. martynovae* Sharov, 1966, lack any development whatsoever of an ambient vein in the forewing (nor anteriorly or posteriorly, given that RA ends in the wing margin at a point similar to Permoberothidae and CuApost is fully straight as well), although an ambient vein is present in the Glosselytridae, Polycyttellidae and Jurinidae. Therefore, there is no strong argument to maintain the genus *Glossopteryx* in the Glosselytridae at present; it was transferred therein by Rasnitsyn & Aristov (2013). At the same time, *Glossopteryx* cannot be accommodated into the Permoberothidae or the Archoglossopterygidae due to the axial veins narrowly separated, the conspicuously denser cells in radial and cubital areas, and forewing with a distinct ‘precostal’ area with more than two cell rows. Thus, we transfer the genus *Glossopteryx* and its two species back to its own family, Glossopterygidae Sharov, 1966 stat. rest., acknowledging that future material should clarify the status of this taxon.

Hind wings are known only in the following glosselytrodean taxa: *Permoberotha villosa*, *Sylvaelytron latipennatum* (Permoberothidae) (Tillyard 1937; Martynov 1938; Vilesov & Novokshonov 1994) (Figs 2, 5), *Eoglosselytrum kaltanicum* Martynova, 1952, *E. kondomense* Sharov, 1966, *E. perplexum* (Riek, 1953), *E. zalesskyi* Novokshonov & Vilesov in Vilesov & Novokshonov, 1994 and *Jurina sojanensis* Martynov, 1938 (Jurinidae) (Martynov 1938; Martynova 1952; Vilesov & Novokshonov 1994; Béthoux *et al.* 2007). Two hind wings assigned to *Eoglosselytrum* were also described by Martynova (1961). Note that the hind wings of Glosselytridae, Polycyttellidae, *Archoglossopteryx* and *Glossopteryx* remain unknown. All of the known glosselytrodean hind wings lack an ambient vein, with CuApost being straight (Martynova 1952; Vilesov &

Novokshonov 1994; Béthoux *et al.* 2007). Whereas the permoberothid hind wings (*Permoberotha* and *Sylvaelytron*) possess an ScP reaching beyond the proximal wing’s third (Permoberothidae diagnostic character 6) (Tillyard 1937; Martynov 1938; Vilesov & Novokshonov 1994), that vein is always shorter in the jurinid hind wings (*Eoglosselytrum* and *Jurina*). Although ScP is particularly long in the hind wing assigned to *E. perplexum* by Béthoux *et al.* (2007), it still does not reach the wing’s proximal third. Note that Vilesov & Novokshonov (1994) depicted the hind wing of *Eoglosselytrum zalesskyi* as possessing an alleged groove (marked with a discontinuous line as in Tillyard 1932, 1937 and Carpenter 1943) between the axial veins, but confirmation of the absence of a true yet weak vein (an alleged MP) cannot be provided at this time. Despite the differences noted above, the scenario of the hind wings assigned to Jurinidae actually belonging to Permoberothidae is deemed unlikely, given that no permoberothid forewings have been described from any locality in which hind wings assigned to Jurinidae are known, that is, Karaungir-II in Kazakhstan, Letopala River and Kaltan (outcrop 1300) in the Russian Federation, and Warner’s Bay in Australia (Appendix S1).

The genera *Sylvaelytron* and *Moscheloptera* are herein added to the Permoberothidae, a family that up to now was composed only of *Permoberotha* and its type and only species, *P. villosa*. *Sylvaelytron latipennatum* was originally placed in the family Glossopterygidae Sharov, 1966 but was transferred into the Glosselytridae by Rasnitsyn & Aristov (2013). This species is here tentatively transferred to the Permoberothidae based on all of the diagnostic characters of the family except character 4 (i.e. the lack of a ‘precostal’ area in the forewing), which is not clear due to poor preservation (Fig. 5). The assignment of *Sylvaelytron* to Permoberothidae was already suggested by Béthoux *et al.* (2001), who preferred to wait until re-examination of the holotype was possible. In contrast, *Archoglossopteryx shoricum* fulfils at least half of the diagnostic forewing characters of Permoberothidae (i.e. characters 1, 3 and 5 for certain). A faint vein between the axial veins (character 2) is probably present, although following its course is hampered by poor preservation (Fig. 7). However, this species presents a distinctly developed ‘precostal’ area, albeit consisting only of two rows of cells. For that reason, in line with Rasnitsyn & Aristov (2013), we prefer to keep this species in its own family for now, Archoglossopterygidae Martynova, 1958, acknowledging that this taxon probably forms a grade with the taxa classified in the Permoberothidae. Note that, although Martynova (1958, 1961) depicted the vein CuApost (CuP for that author) as partly ambient (i.e. following the course of the wing margin) in *A. shoricum*, our interpretation shows that the alleged distal part of that vein probably

represents a deformation of the rock, and that *CuApost* actually ends on the wing margin much more basally than originally recognized (Fig. 7).

The body structure of Glosselytrodea

Information on the glosselytrodean body structure is scarce and has hindered the understanding of the relationships outside of and within the order. Body structure has been reported only in the families Jurinidae and (to a lesser extent) Permoberothidae. For the Jurinidae, body structures have been described and figured from *Eoglosselytrum kondomense*, *E. perfectum* Martynova, 1961, *Jurina marginata* Martynov, 1938, *J. reducta* Martynov, 1938 and *J. sojanensis* (Martynov 1938; Martynova 1961; Sharov 1966). An additional, undescribed, complete jurinid was figured by Rasnitsyn (2002). Moreover, *Glossopterum martynovae* and *G. sharovi* were described based on complete specimens (Sharov 1966; Novokshonov 1998; Rasnitsyn 2002; Zhuzhgova *et al.* 2015). Based at least on this evidence, non-permoberothid glosselytrodeans had a hypognathous to opisthognathous head, compound eyes well separated, antennae moniliform; thorax with movable prothorax, pronotum well developed, meta- and metathorax of subequal size and structure; legs cursorial, with well-developed coxae and five-segmented tarsi; wing position at rest roof-like; and abdomen narrow, much shorter than the wings (abdomen ending at about 2/3 of forewing length), bearing apparently one-segmented cerci (adapted from Rasnitsyn 2002). A reconstruction of *Glossopterum* by A.G. Ponomarenko was provided by Rohdendorf & Rasnitsyn (1980) (re-figured by Rasnitsyn 2002).

Data on the body parts of permoberothid glosselytrodeans are even scarcer. It was hitherto based on only two specimens: the specimen YPM IP 015592p/cp originally described as the type of *Dictyobiella nervosa* Tillyard, 1937; and the holotype of *Sylvaelytron latipennatum* (Tillyard 1937; Novokshonov 1998). A new complete individual is herein added: the specimen MCZ-ENT-PALE-5852a/b. Details of these three specimens are provided below.

YPM IP 015592p/cp. The photographs of this specimen, provided herein for the first time, enable us to reassess several structures. Tillyard (1937, p. 105) described the specimen's head as having 'large and apparently strongly projecting compound eyes separated from one another by a space about equal to their own width', which are visible in the photographs (Fig. 2C, D). The clypeus was deemed as 'a clear, somewhat projecting plate', and he added that 'only the scape of one antenna can be seen'. The clypeus, indeed, appears to be well developed, but the scapes of

both antennae, the pedicels, and a significant part of each flagellum (full antennal length not evident) are also visible (Fig. 2C, D). Additionally, the head is clearly subhypognathous, and at least the mandibles appear to be discernible as well (Fig. 2C, D). Tillyard (1937, p. 105) described the thorax as 'short and stout, the prothorax apparently small, the meso- and metathorax well developed; the femur and tibia of one foreleg are visible, each about as long as the head is wide', characters that seem to be present based on the photographs, and he added 'the femur not very stout, fusiform, and carrying many stiff hairs', which is visible in Figure 2C, D. All the remaining legs are preserved, but retracted and folded upon the body. Last, Tillyard (1937, p. 106) described the abdomen of YPM IP 015592p/cp as 'short, only about half as long as the forewing', this also being evident from our photographs. The author added 'the last segment shows, in the obverse only, a terminal triangular notch or incision, suggestive of a division into paired male genitalia of the hemerobioid type, closely appressed to the last segment on either side'. Indeed, this 'notch' is visible only in the part, probably due to the arrangement of the two structures interpreted herein as the gonocoxites + gonostyli 9 (Fig. 2E, F). Contrary to Tillyard (1937), we have interpreted the genitalia of this specimen as female. Tillyard (1937, p. 106) described and drew from the last abdominal segment a 'short, very pointed process, black at apex and ending in a stiff bristle, which I take to be one of a pair of reduced cerci'. Carpenter (1943) stated that Tillyard's interpretation was wrong due to the fossil not being completely exposed, and that both cerci were longer than originally interpreted (having four or five segments), and lacked a terminal bristle. Based on the photographs provided herein, five segments appear to be visible for the only visible structure interpreted as a cercus (Figs 2E, F, 4A).

PIN 1700/1701. Although Novokshonov (1998) recognized the composite eyes, the mandibles and the possible laciniae in his drawings of the holotype of *S. latipennatum*, these are photographically figured herein for the first time (Fig. 5). The right antennal insertion and the basal stretch of said antenna also appear to be preserved. Moreover, the presence of enlarged gonocoxites inserted ventrally and bearing distal teeth-like projections (as in *Permoberotha villosa*) and narrower gonostyli, the latter probably concave, incurved distally, and with visible inner serrations, is herein reported, enabling us to regard the specimen as male.

MCZ-ENT-PALE-5852a/b. The new *Permoberotha villosa* specimen from Elmo is remarkably well preserved, and provides additional data on the body parts of Permoberothidae, namely on the fine structure of the pretarsal

claws and the male terminalia. The pretarsal claws, apparently in all legs, are complex, that is, they bear multiple teeth, although their specific arrangement is challenging to discern (Fig. 3G–I). Complex tarsal claws have evolved independently among a wide range of insects, also encompassing the majority of holometabolous lineages (e.g. McAlpine *et al.* 1981, 1987; Goulet & Huber 1993; Sattler & Wojtusiak 1999; Leschen *et al.* 2010; Leschen & Beutel 2014; Beutel & Leschen 2016), including both Neuroptera (Lambkin 1986) and Mecoptera (Beutel & Gorb 2001; Grimaldi & Johnston 2014). Therefore, this character, or at least the present understanding of it, does not seem to be informative when aiming to elucidate the relationships of Glosselytrodea. Moreover, the terminalia of this specimen is consistent with those of *S. latipennatum* (see above), showing the development of massive, independent, and ventrally inserted gonocoxites 9 bearing irregular teeth-like projections distally, to which relatively smaller, narrower, incurved gonostyli apparently bearing spine-like setae are articulated (Figs 3J, K, 4B). The serrations and/or spine-like setae in the dorsal and inner surfaces of gonocoxites and gonostyli in male permoberothids (as evidenced by *P. villosa* and *S. latipennatum*) are likely to have increased the grasping ability of these structures during nuptial and/or copulatory phases. Other structures visible in the new *P. villosa* male specimen from Elmo include apparently one-segmented cerci (Figs 3J, K, 4B). Rasnitsyn (2002, p. 191) stated that the glosselytrodean male genitalia was ‘rather small, symmetrical, with ovoid gonocoxa and small articulated gonostylus’, which was based on an interpretation of the holotype of *Glossopterus martynovae* (A.P. Rasnitsyn pers. comm. 2021). Although that assessment is compatible with our interpretation of the genitalia of *P. villosa* and *S. latipennatum*, these structures would appear to be relatively large in these species.

The contentious phylogenetic relationships of Glosselytrodea

The glosselytrodean wing venation patterns have not been able to shed light on the phylogenetic position of the group. Glosselytrodeans have a stem of Cu distinctly separated from that of R and M. That rules out affiliation to the polyneopteran superorder Archaeorthoptera *sensu* Béthoux & Nel (2002), given that in Archaeorthoptera the CuA is fused with M at the very base of the wing (Béthoux & Nel 2002; Béthoux *et al.* 2007). Similarly, attribution of this order to the superorder Acercaria is unlikely because CuA is not fused to R + M at the wing base (Nel *et al.* 2012). On the contrary, a stem of Cu independent from those of R and M is present in the Palaeodictyoptera (Prokop *et al.* 2018), the non-archaeorthopteran Polyneoptera and the Holometabola, this condition probably being symplesiomorphic. In any case, there is no clear putative

synapomorphy for supporting the attribution of the Glosselytrodea to the Holometabola based on wing venation characters. However, Beutel & Gorb (2001) proposed to support the Holometabola on the basis of a five-segmented tarsus, a character present in the Glosselytrodea, but also present in several non-holometabolous groups (e.g. Mantophasmatodea, stem Odonatoptera).

Assignment of the Glosselytrodea to the Neuroptera based on venation characters is hardly justified despite having been the general trend. Veins ScP and R/RA running closely parallel are not only present in Neuroptera, but also in other groups such as the superorder Mecopterida (= Amphimesenoptera + Antliophora). The shape of the anal veins in the Glosselytrodea and Neuroptera is different, with rather simple parallel veins in the former clade. Although the general pattern of venation in Permoberothidae is reminiscent of that of Neuroptera, especially in the veins MA and MP running closely parallel, the shape of the cells in the distal half of the wing, and that of the branches of RP, these characters could be the result of convergence. In Glosselytrodea it is still uncertain whether R and M have a common stem or separate ones running closely parallel to each other.

The terminalia characters described from the complete permoberothids figured herein offer new data to assist the elucidation of the broader relationships of Glosselytrodea. In the Polyneoptera, the female gonostyli are either lost or strongly reduced, rendering an affinity of glosselytrodeans to this group based on this character highly unlikely. The female terminalic conformation of the *P. villosa* specimen YPM IP 015592p/cp appears to differ from both the neuropteroid and the mecopterid ground plans, and is instead compatible with that closer to the hypothesized holometabolous ancestral structure in which the ovipositor has been reduced (therefore unable to insert eggs in the substrate) but gonapophyses 8 are still well developed, gonocoxites and gonostyli 9 are present, even if reduced, and multisegmented cerci have been retained (Mickoleit 1973; Grimaldi & Engel 2005; Hünefeld *et al.* 2012). Moreover, according to Hünefeld *et al.* (2012) the groundplan condition for the female postabdomen of the Mecopterida is telescoping, which is not apparent in the specimen. Note that the configuration of the female terminalia of YPM IP 015592p/cp is very similar to the structures sketched by Sharov (1966) from a specimen assigned to *Eoglosselytrum kondomense* Martynova, 1952 (Jurinidae) by Martynova (1961). In contrast, the male terminalia in the *P. villosa* specimen MCZ-ENT-PALE-5852a/b would appear to be closer to that of the antliophoran type, or at least plesiomorphic when compared with that of Neuroptera, due to the presence of massive, independent gonocoxites 9 inserted ventrally, which are primarily reduced and integrated with the remaining abdomen in neuropterids (Aspöck & Aspöck 2008).

The inclusion of Permoberothidae within the Glosselytrodea does not appear to be universally accepted. *Permoberotha* remained separated from the other Glosselytrodea (Tillyard 1932, 1937; Carpenter 1943) until Martynova (1961) (as corroborated by Sharov 1966) indicated a relationship of this taxon with the remaining glosselytrodeans. Later, Rohdendorf & Rasnitsyn (1980) and Carpenter (1992, p. 357) adopted that stance, the latter simply stating ‘It now seems certain that the Permoberothidae are, in fact, members of the Glosselytrodea’, without providing references. Béthoux *et al.* (2001) considered the Permoberothidae as a separate lineage from Glosselytrodea *s.s.* and classified within the Neuropterida. Although Rasnitsyn (2002) did not question the glosselytrodean status of permoberothids, Grimaldi & Engel (2005, p. 332) considered that glosselytrodeans ‘may be an unnatural group, consisting on the one hand of the Early Permian Permoberothidae and on the other hand as an assemblage of Late Permian and Triassic–Jurassic families’. Later, Béthoux *et al.* (2007) assigned *Permoberotha* to Glosselytrodea, listing several potentially synapomorphic characters, and so did Rasnitsyn & Aristov (2013). However, more recently, Engel *et al.* (2018) included only the Permoberothidae in a phylogeny of Neuropterida. The data discussed herein support permoberothids and the remaining glosselytrodeans as having a very similar body structure, and reinforce the idea that they belong to the same lineage. At present there are no strong arguments to support the view that the two groups are not closely related phylogenetically. A difference between Permoberothidae and the remaining Glosselytrodea would include the development of the cerci, which are multisegmented in Permoberothidae but apparently one-segmented or at least less developed in other Glosselytrodea. Besides the similar body structure of permoberothids and the remaining glosselytrodeans, their significant differences in forewing structure can be interpreted as resulting from a sclerotization process, with taxa (*Archoglossopteron* or *Glossopteron*) showing morphologies apparently bridging the two (Rasnitsyn & Aristov 2013).

Forewing sclerotization in Glosselytrodea

The sclerotization of the forewings is a process that has taken place multiple times across neopterans to increase the protection offered to both the hind wings and the abdomen when the former are kept retracted upon the latter. Sclerotized forewings include diverse tegmina present across several polyneopteran groups (e.g. dermapterans, dictyopterans, orthopterans), the hemipteran hemelytra, and the coleopteran elytra (Grimaldi & Engel 2005). Other instances are known in a few Psocodea (Lienhard 2005) and the Mecoptera, that is, in the only extant species of the relictual Eomeropidae, *Notiothauma reedi* MacLachlan, 1877 (Crampton 1930; Mickoleit 1971).

It has been posited that the glosselytrodeans also underwent a general trend of forewing sclerotization (i.e. tegmenization or ‘elytrization’ in its widest sense) and an increase in the protective role of forewings throughout their evolutionary history (Rasnitsyn & Aristov 2013), although the mode and tempo of such a process still need to be elucidated. Interestingly, most (if not all) of the forewing diagnostic characters of Permoberothidae can be interpreted in the context of absence of forewing sclerotization and, thus, they are putatively plesiomorphic: axial veins well separated (far from being fused) with a faint vein retained in between, low vein/cell density, ‘precostal’ (and anal) areas not (or barely) differentiated, and ambient veins absent. Although most of these characters are also present in *Archoglossopteron shoricum*, the presence of a ‘precostal’ area in this species (Fig. 7) appears to be a step closer towards forewing sclerotization.

CONCLUSION

The oldest known Glosselytrodea, *Moschelopectera phantasma* gen. et sp. nov., is described from the lower Permian of Germany, and classified in the family Permoberothidae together with *Permoberotha villosa* and *Sylvaelytron latipennatum*. The genus *Glossopteron* is excluded from the Glosselytridae and classified in its own family, Glossopteridae Sharov, 1996 stat. rest. Glosselytrodean diversity is currently classified into six families (Appendix S1). The permoberothid body structure, the knowledge of which has been significantly expanded with the new data presented herein, is consistent with that known from other glosselytrodeans, supporting the integrity of the ‘Glosselytrodea *s.l.*’ (i.e. including Permoberothidae) as a natural group. Body structures herein figured and described with the greatest detail thus far in the group, such as the pretarsal claws and both the female and male terminalia, increase the characters able to assist the elucidation of the obscure phylogenetic relationships of glosselytrodeans. Although it would currently seem certain that glosselytrodeans are early holometabolous insects, their affiliations are still doubtful and require further morphological data. One option, given the seemingly plesiomorphic nature of the holometabolous male terminalia of *P. villosa* and *S. latipennatum*, with independent gonocoxites and movable gonostyli, and the very reduced ovipositor in female specimens, is that glosselytrodeans could be stem-aparaglossatans, that is, sister to the clade consisting of Holometabola excluding Hymenoptera (e.g. Song *et al.* 2016). The permoberothid male terminalia presented herein, however, appear to bear a greater resemblance to those of the antliophoran lineage (Mecoptera, Diptera) rather than to the neuropterid one

(Raphidioptera, Megaloptera, Neuroptera), the lineage to which glosselytrodeans have been most frequently related to in the last decade. In any case, a phylogenetic analysis of the whole order Glosselytrodea is necessary to clarify both its large-scale relationships, the tegmenization/‘elytrization’ hypothesis that allegedly drove the evolution of the group, and the limits of the currently accepted families. For this goal, it is necessary to continue to increase the diversity of glosselytrodeans, particularly that of permoberothids due to their putative ‘plesiomorphic’ status, as well as to expand the knowledge on their body structures. By doing so not only the origins of this enigmatic extinct order, but probably also the early evolutionary history of the entire Holometabola, will be one step closer to resolution. Improving the known glosselytrodean diversity will also lead to a better understanding of their diversity trends through time, including assessing potential impacts of the Permo-Triassic mass extinction event.

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DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: <http://zoobank.org/References/1218890B-4A73-4DD2-9506-EDF67082C7D8>

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1111/pala.1452>):

Appendix S1. List of described Glosselytrodea.

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