Zootaxa 2895: 47–57 (2011)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Nedubroviidae, a new family of Mecoptera: the first Paleozoic long-proboscid scorpionflies

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Abstract

Nedubroviidae **fam. nov.** consists of *Nedubrovia* **gen. nov.**, with *Nedubrovia shcherbakovi* **sp. nov.** as the type species, *N. deformis* **sp. nov.**, and *N. mostovskii* **comb. nov.**, originally described in *Mesopanorpodes*. The second genus of Nedubroviidae is *Paranedubrovia* **gen. nov.**, with *Paranedubrovia novokshonovi* **sp. nov.** as the type species, and including *P. minutissima* **sp. nov.** Of these five species, all originate from the Late Permian of European Russia except for the Early Triassic *N. mostovskii*. The wing venation of these species indicates membership in the long-proboscid mecopteran clade Aneuretopsychina. The body structure of one species, *N. shcherbakovi*, includes a long proboscis consistent with fluid feeding on contemporaneous plants.

Key words: Mecoptera, Aneuretopsychina, new family, long-proboscid insects, Late Permian, Early Triassic, Russia

Introduction

Novokshonov *et al.* (2004) described a new species of *Mesopanorpodes* Tillyard 1918, *M. mostovskii*, based on two isolated forewings from the basal Triassic of Russia. The taxonomic attribution of these fossils to a genus of Permochoristinae (Permochoristidae) was based mainly on the following venational characters (fig. 2A): long SC with a single fore-branch, two-branched RS and MA with equally short forks, and four-branched MP (venational terminology is discussed below). However, the authors did not consider the nature of the junction between the CuA and MP veins of *M. mostovskii*, which are in fact fused for a distance, with M_5 being reduced, a feature not previously noted in *Mesopanorpodes*. Newly discovered mecopteran fossils from the Upper Permian, which undoubtedly are closely related to *M. mostovskii*, reveal additional features that question its systematic position. Particularly, some of the new species demonstrate CuA fused with MP very basally and for a long distance.

Fusion of CuA and MP is not characteristic of Permochoristidae, except for a few Permian and Mesozoic Mesochoristini (e.g. *Baianochorista mongolica* (Novokshonov 1997b) and often as individual deviations in some Permian species), as well as in some Mesozoic "paratrichopteran"-like forms (e.g. *Choristopsyche tenuinervis* Martynov 1937 (Novokshonov & Sukacheva 2001) and *Mesageta* spp. (Novokshonov 1997c)), whose relationship to Permochoristidae is doubtful. The MP+CuA fusion is still less expected in Mesopsychidae, in which *Mesopanorpodes* is a likely subordinate taxon (Bashkuev, in prep.). This family demonstrates a contrary tendency, with the CuA base shifted far distad to M_5, accompanied by an opposite change in branching angle. Finally, the new material reveals a rather complete specimen showing the hind wings and the head with elongated proboscis, a feature implying quite different taxonomic affinities of the group under consideration. This evidence indicates that the group in question forms a taxon of its own, which is established herein as Nedubroviidae **fam. nov.**

Material and methods

Described material was collected from four localities in the continental Permian-Triassic sequences of north-central European Russia (Fig. 1). The Isady locality is a lens of fluvio-lacustrine deposits within the Sukhona River

Accepted by E. Bernard: 3 May 2011; published: 27 May 2011

section, Vologda Province, which corresponds to the lower part of Kalikino Member of the Poldarsa Formation. It is dated latest Severodvinian (correlated with the lower Wuchiapingian: Golubev 2012). Thirty-one specimens of *Nedubrovia shcherbakovi* were collected by the PIN RAS field trips of 2005–2010. The insect assemblage of Isady is one of the best known and most diverse of the Upper Permian, comprising over 2,500 specimens assigned to at least 23 insect orders.

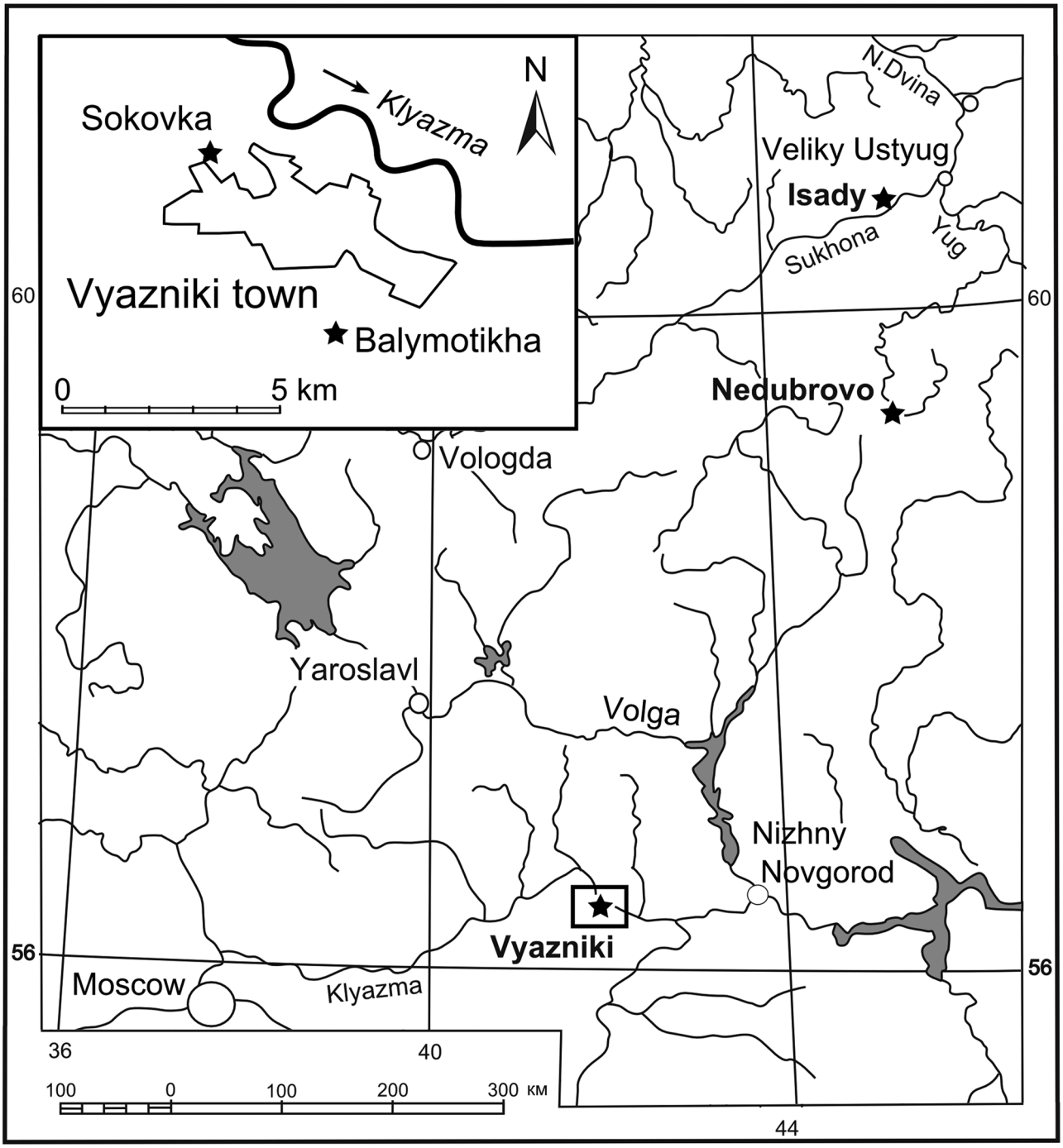

FIGURE 1. Map showing the general locations of collection sites.

The Balymotikha and Sokovka localities are two outcrops of laminated grey mudstone beds of Vyazniki Permian-Triassic sequence exposed at Vyazniki town, Vladimir Province. It is dated latest Vyatkian (Late Changhsingian), somewhat below the Permian-Triassic boundary (Newell *et al.* 2010). Four specimens of *Paranedubrovia* spp. and one specimen of *Nedubrovia deformis* were collected from Balymotikha and Sokovka, respectively.

The Nedubrovo site is located in the Kichmenga River basin (tributary of the Yug River), Vologda Province. Fossil insects occur in siltstones of lacustrine genesis assigned to the Nedubrovo Member of the Vokhmian Hori-

zon, Vetlugian Series. Nedubrovo is correlated immediately above the Permian-Triassic boundary (earliest Induan) (Krassilov & Karasev 2009). Two specimens of *Nedubrovia mostovskii* were described (as *Mesopanorpodes*) by Novokshonov *et al.* (2004).

The fossils were examined with a Leica M165C binocular microscope and photographed with an attached Leica DFC 425 digital camera. Images were digitally processed with Helicon Focus v. 5.1 and Adobe Photoshop CS3 graphic software. Line drawings were made with Inkscape v. 0.48 vector graphics editor.

All specimens are deposited in the Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia (PIN).

I follow the traditional (*sensu* Wootton 2003) venational terminology in the interpretation of Ponomarenko & Rasnitsyn (1974), Novokshonov (1997a, 2002), and Ren *et al.* (2009b) as applied to Mecopteroidea, wherein the RS of traditional terminology is referred to as RS+MA, and M as MP. Venation abbreviations are as follows (fig. 2A): C, costa; SC, subcosta; R, radius; RS, radial sector; MA, anterior medial; MP, posterior medial; M_5, posterior branch of posterior medial; CuA, anterior cubitus; CuP, posterior cubitus; A_1–A_3, anal veins; pt, pterostigma; th, thyridium; thl, thyridulum, a small desclerotized spot at the branching point of the RS and MA veins (Ren *et al.* 2009b).

Systematic paleontology

Order Mecoptera Packard, 1886

Family Nedubroviidae Bashkuev, fam. nov.

Type genus. *Nedubrovia* **gen. nov.**

Diagnosis. Small-sized insects (forewing length 3–5 mm). Head with prolonged proboscis. Setae on the legs not distinctly arranged in rings. Forewing tongue-shaped. SC long, reaching pterostigmal area, bearing a single short fore-branch at or before the level of RS+MA base. Subcostal space widened toward basal SC branch. Pterostigma distinct. Crossvein sc–r far proximad of pterostigma. RS and MA both 2-branched, with forks nearly equal, shorter than stems. MP 4-branched. CuA and MP fused for a distance, with M_5 lost and "Y-vein" not developed. Three simple anal veins. Crossveins not numerous. Hindwing shorter and wider than forewing, tending to a triangular shape. No pterostigma. Sc short, terminating before wing midlength into R, bearing only short basal branch. Venation pattern of RS+MA+MP repeating that of forewing. Three anal veins well-developed, anal area not expanded.

Included genera. *Nedubrovia* **gen. nov.**, *Paranedubrovia* **gen. nov.**

Genus *Nedubrovia* Bashkuev, gen. nov.

Mesopanorpodes: Novokshonov *et al.*, 2004, p. 214 (partim: quoad *M. mostovskii*).

Etymology. Derived from the Nedubrovo locality, where the first discovered species was found. Gender feminine.

Type species. *Nedubrovia shcherbakovi* **sp. nov.**

Diagnosis. Differs from *Paranedubrovia* **gen. nov.** in having forewing with CuA base oblique and curved, and CuA fused with MP for a shorter distance.

Included species. In addition to the type species, *N. deformis* **sp. nov.** and *N. mostovskii* **sp. nov.**

Nedubrovia shcherbakovi Bashkuev, sp. nov.

Figs. 2B, C; 3; 4; 6B–E.

Etymology. In honor of Dr Dmitry Shcherbakov, who led the first paleoentomological works at Isady.

Holotype. PIN, no. 3840/1337, nearly complete insect (part only). Forewings and abdomen partially overlapping and strongly distorted. Head with proboscis lacking distal part. Sex unknown.

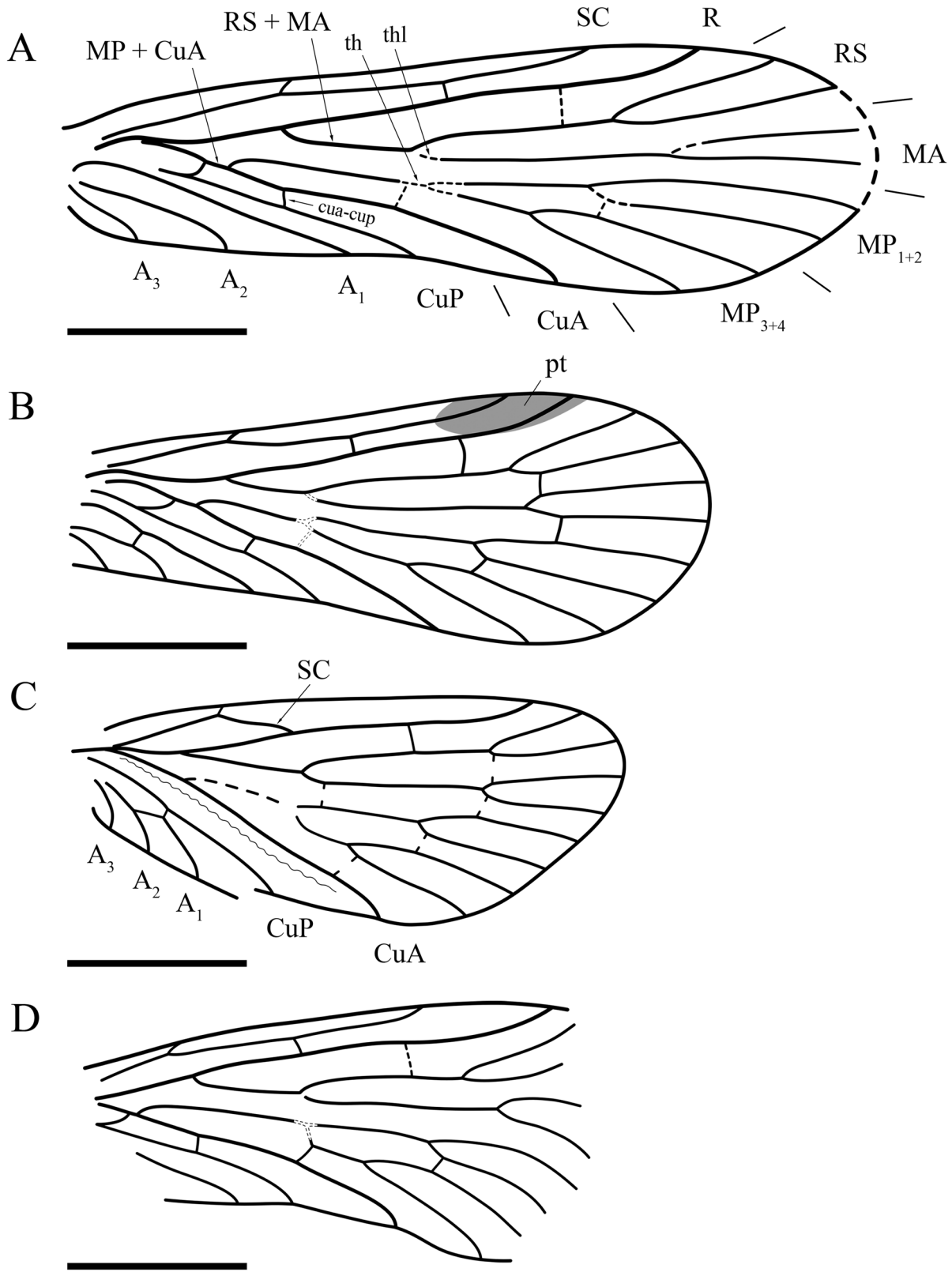

FIGURE 2. Wings of *Nedubrovia* **gen. nov. A**, *N. mostovskii* (Novokshonov, Sukacheva et Aristov, 2004), **comb. nov.**, holotype PIN, no. 4811/20, forewing. **B–C,** *N. shcherbakovi* **sp. nov. B**, paratype PIN, no. 3840/710, forewing. **C**, paratype PIN, no. 3840/229, hindwing. **D**, *N. deformis* **sp. nov.**, holotype PIN, no. 5102/8, forewing. Scale bar 1 mm.

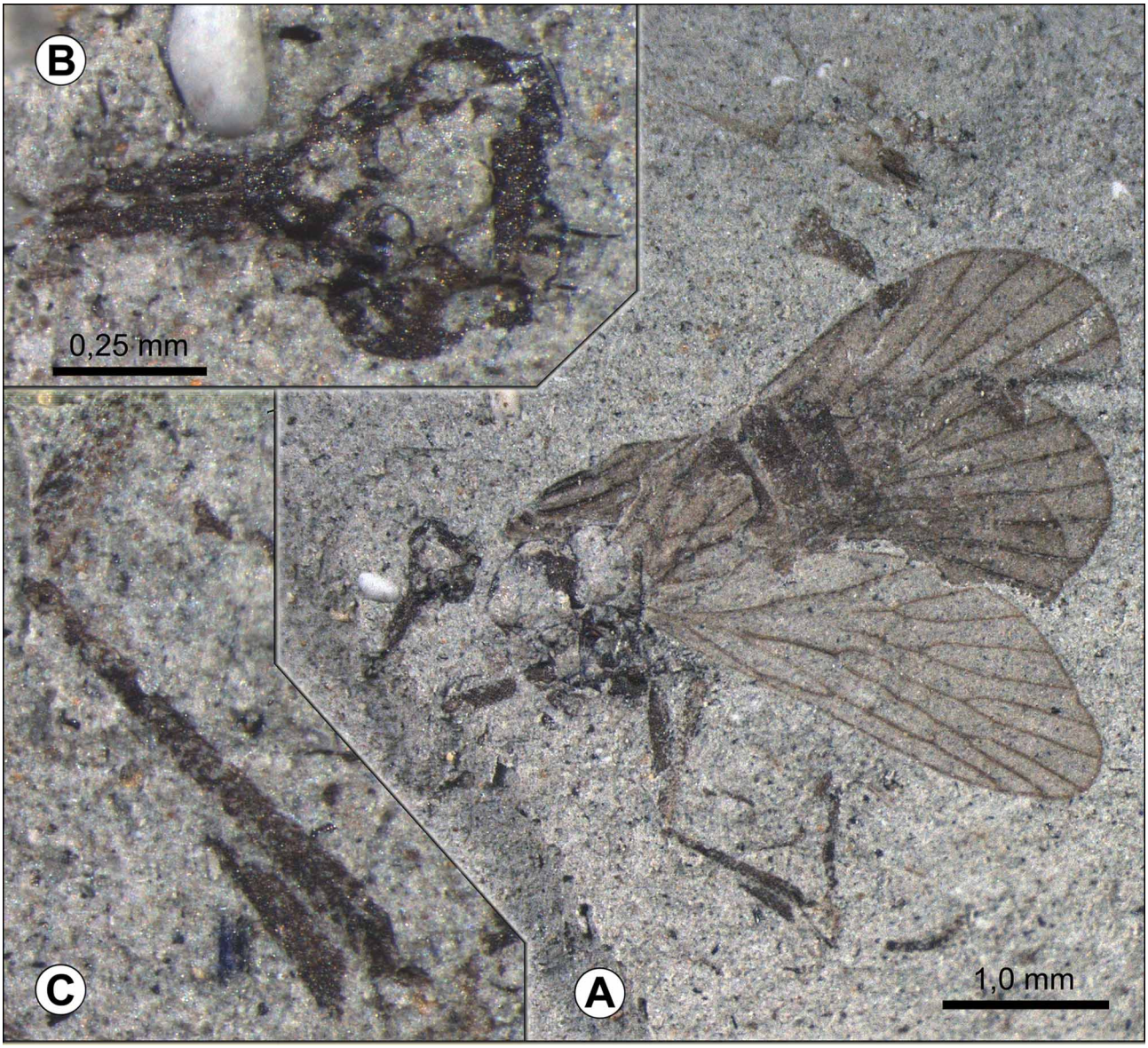

FIGURE 3. *Nedubrovia shcherbakovi*, holotype PIN, no. 3840/1337. **A**, general appearance. **B**, head with proboscis. **C**, details of hind leg.

Paratypes. PIN, no. 3840/73±, 75, 86±, 348±, 710±, 711, 712, 713, 714±, 715±, 1024, 1338, 1339±, 1340±, 1341±, 1342, 1343, 1344, 1345, 1346±, 2021A,B, 2022±, 2066, 2067, 2377±, forewings; PIN, no. 3840/229±, 312±, 1347, 1348±, hindwings.

Locality and Horizon. Isady locality, Vologda Province, North European Russia; Kalikino Member of the Poldarsa Formation, Upper Severodvinian, Upper Permian.

Diagnosis. Differs from both congeners in having distinctly shorter MP stem; from *N. mostovskii* also in having forewing shorter and wider; from *N. deformis* in forewing SC longer and MP separated from CuA distally.

Description. Head subtriangular in dorsal view, with prognathous, siphonate mouthparts (fig. 3B). Proboscis length 0.35 mm as preserved. Eyes apparently small, widely separated. Antennae not preserved. Pronotum not discernible, meso- and metanotum of about the same size, details of pterothorax obscure. Setal arrangement on legs not certain, apparently not annulate (fig. 3C).

Wings: Forewing (based mainly on paratypes PIN, no. 3840/710 (fig. 2B), 73, 1338, 1340) tongue-shaped, with nearly straight anterior margin and rounded apex. Forewing length 3.0–3.6 mm (holotype ~3.4 mm), width 1.2–1.4 mm. Pterostigma distinct, lanceolate. SC long, extending far deep into pterostigma, bending sharply backwards at anterior branch located at or somewhat before level of RS+MA base. Crossvein sc–r distal of RS+MA

fork. CuA and MP fused for a distance much shorter than that from MP+CuA fork to cua–cup crossvein. Free base of CuA long, strongly oblique, distinctly curved. Crossveins mostly weak or more likely desclerotized; mp–cua at or somewhat distal of MP fork (at thyridium). Wing membrane darkened, with discolored spots at crossveins (except for cua–cup and crossveins in anal area), the largest at thyridium + thyridulum area.

Hindwing (based on holotype and paratypes PIN, no. 3840/229 (fig. 2C), 1347, 1348) broad, subtriangular, with oblique posterior apical margin. Sc short, terminating before midlength of the wing into R. Length 2.9–3 mm, width 1.16–1.27 mm.

Remarks. The length of forewings of *N. shcherbakovi* varies from 3.0 (paratype PIN, no 3840/1340) to 3.6 mm, with most of them within the range of 3.4–3.6 mm.

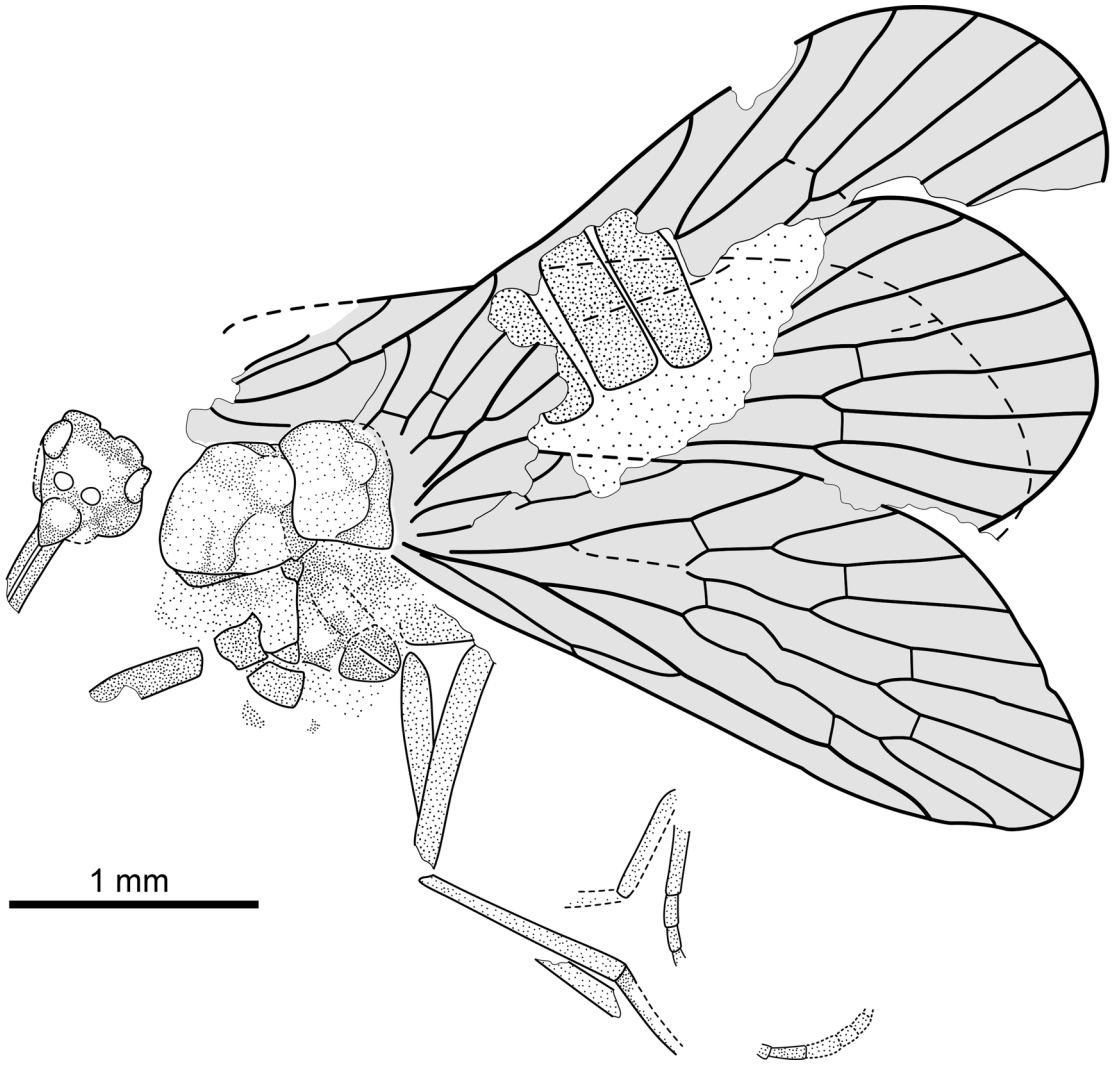

FIGURE 4. *Nedubrovia shcherbakovi*, line drawing of holotype.

***Nedubrovia deformis* Bashkuev, sp. nov.**
Figs. 2D; 6F, G.

Etymology. Derived from Latin *deformis*, "distorted".

Holotype. PIN, no. 5102/8; forewing (part and counterpart) distorted apically (apex missing).

Locality and Horizon. Sokovka locality, Vyazniki town, Vladimir Province, Central European Russia; uppermost Vyatkian, Upper Permian.

Diagnosis. Differs from congeners in having fore wings widened, MP+CuA fusion rather short due to early separation of MP, SC somewhat shortened, mp–cua crossvein located distal to thyridium.

Description. Forewing widened, with evenly convex anterior margin. Forewing length as preserved 2.82 mm, reconstructed, ~3.4 mm; width 1.45 mm. SC slightly shortened, apparently just reaching pterostigmal area, bending backwards at anterior branch located distinctly before level of RS+MA base. Crossvein sc–r located at level of RS+MA fork. RS, MA, and MP_{1+2} forks strongly distorted due to rock matrix deformation. CuA and MP fused for a short distance, MP separating from CuA quite basally. Free base of CuA strongly oblique, curved. Crossveins weak, mp–cua distal to MP fork (beyond thyridium). Pterostigma and color pattern not preserved.

Nedubrovia mostovskii (Novokshonov, Sukacheva & Aristov 2004), comb. nov.

Figs. 2A; 6A.

Mesopanorpodes mostovskii: Novokshonov, Sukacheva & Aristov, 2004, p. 214, fig. 1.

Holotype. PIN, no. 4811/20, forewing (part and counterpart).

Locality and Horizon. Nedubrovo locality, Vologda Province, North European Russia; Nedubrovo Member of Vokhmian Formation, Lower Induan, Lower Triassic.

Revised diagnosis. Forewing oblong, narrow, with ovoid apex, 4.7 mm long, ~1.4 mm wide. Anterior margin slightly convex in basal third. SC branch at level of RS+MA base. Crossvein sc–r distal to RS+MA fork. CuA and MP fused for a distance much shorter than that between MP+CuA fork and cua–cup crossvein. Free base of CuA oblique, distinctly curved. Crossvein mp–cua somewhat before MP fork (at thyridium).

Remarks. The pterostigma and color pattern as well as most of the crossveins are not traceable due to the poor state of preservation; only cua–cup and sc–r are visible.

Unfortunately, Victor Novokshonov did not have time to finish his work on *Mesopanorpodes mostovskii* from the Nedubrovo locality. The manuscript was prepared after his death by I.D. Sukacheva and D.S. Aristov, which resulted in a few flaws in the original description, corrected herein.

Paranedubrovia Bashkuev, gen. nov.

Etymology. Derived from Greek *para-*, "beside, nearby" and genus *Nedubrovia*. Gender feminine.

Type species. *Paranedubrovia novokshonovi* **sp. nov.**

Diagnosis. Differs from *Nedubrovia* in having forewing with the base of CuA transverse, and CuA fused with MP for a much longer distance.

Included species. In addition to the type species, *N. minutissima* **sp. nov.**

Paranedubrovia novokshonovi Bashkuev, sp. nov.

Figs. 5A, B; 6I, J.

Etymology. In honor of the late outstanding paleoentomologist and specialist on Mecoptera, Dr Victor Novokshonov.

Holotype. PIN, no. 5103/120, well-preserved forewing (part and counterpart).

Paratypes. Two well-preserved forewings, PIN, no. 5103/121 (fig. 5A), 5103/128.

Locality and Horizon. Balymotikha locality, Vyazniki town, Vladimir Province, Central European Russia; uppermost Vyatkian, Upper Permian.

Diagnosis. Differs from *P. minutissima* in being much larger.

Description. Forewing tongue-shaped, with convex anterior margin and rounded apex. Forewing measurements: holotype: length 4.2 mm, width 1.6 mm; paratypes: length 4.1–4.95 mm, width ~1.4–1.75 mm. Pterostigma distinct, ovate. CuA and MP fused for a distance much longer than that between MP+CuA fork and cua–cup crossvein. Free base of CuA nearly transverse, crossvein-like. Crossveins distinct; mp–cua distal of MP fork (beyond the thyridium). Coloration apparently absent, wing membrane covered uniformly with microtrichia.

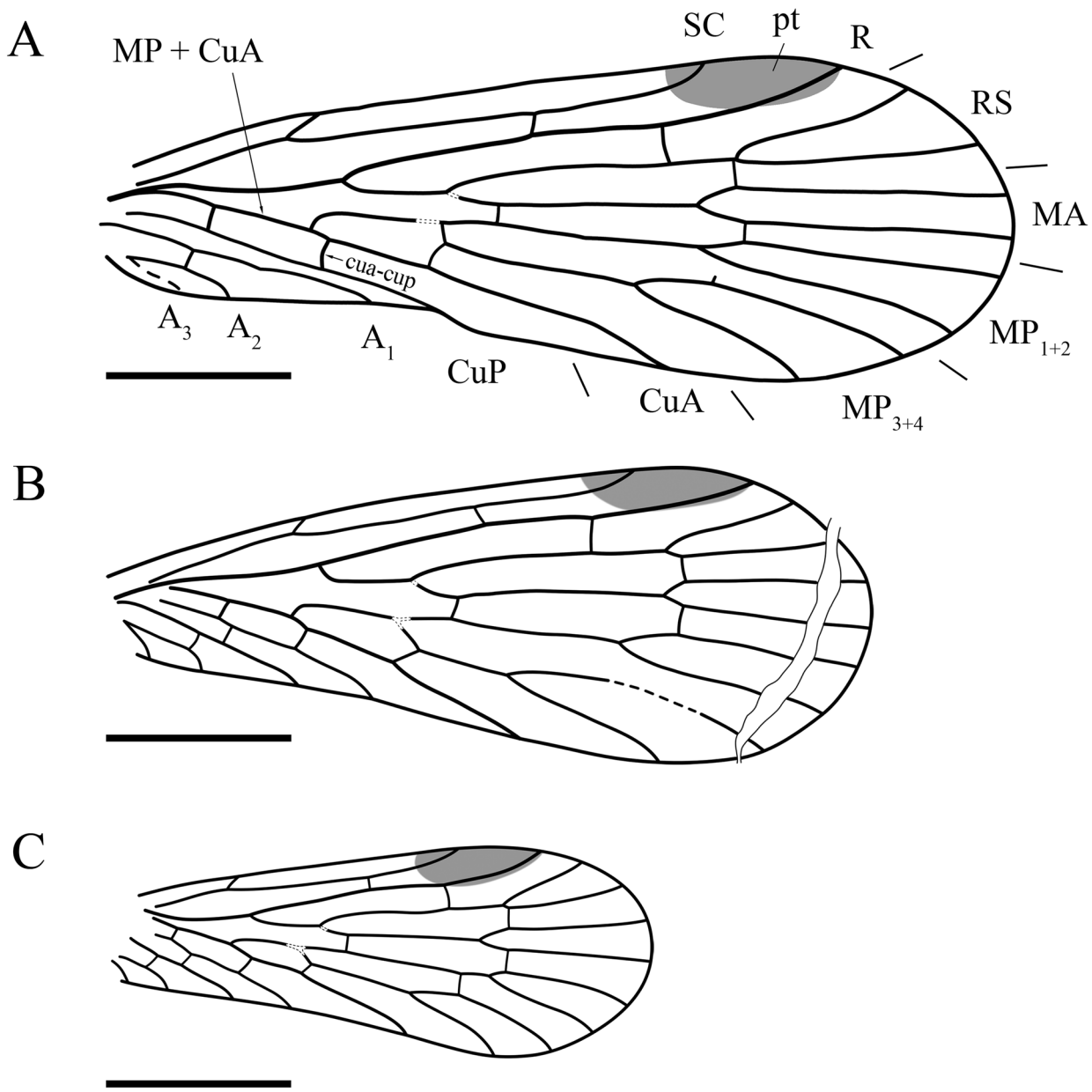

FIGURE 5. Forewings of *Paranedubrovia* **gen. nov. A–B**, *P. novokshonovi* **sp. nov. A,** paratype PIN, no. 5103/121. **B,** holotype PIN, no. 5103/120. **C**, *P. minutissima* **sp. nov.**, holotype PIN, no. 5103/284. Scale bar 1 mm.

***Paranedubrovia minutissima* Bashkuev, sp. nov.**
Figs. 5C; 6H.

Etymology. Derived from Latin *minutissimus*, "tiniest."

Holotype. PIN, no. 5103/284, well-preserved forewing (part and counterpart).

Locality and Horizon. Balymotikha locality, Vyazniki town, Vladimir Province, Central European Russia; uppermost Vyatkian, Upper Permian.

Diagnosis. Venationally similar to the type species but differing in being much smaller (about 0.6-0.7 times size of the type species).

Description. Forewing length 2.95 mm, width 1.16 mm.

Remarks. It cannot be excluded that the type is a dwarf specimen of *P. novokshonovi*. However, taking into consideration the comparatively low size variation of the latter, I prefer to consider them as distinct at the species level, and to wait for more material to test this hypothesis.

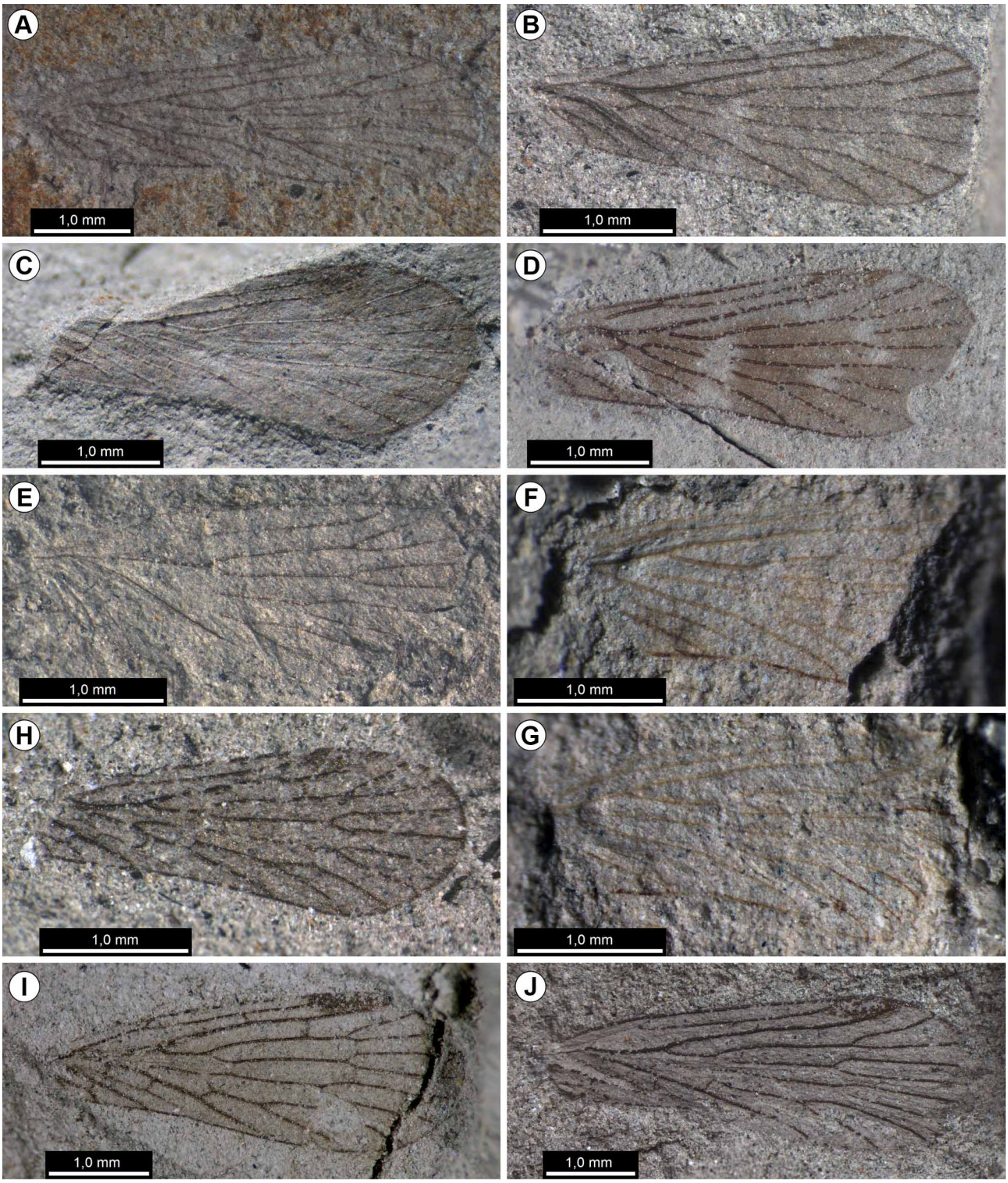

FIGURE 6. A, *Nedubrovia mostovskii* (Novokshonov, Sukacheva et Aristov, 2004), holotype. PIN, no. 4811/20. **B–E**, *N. shcherbakovi* **sp. nov. B**, paratype PIN, no. 3840/1338. **C–D**, paratype PIN, no. 3840/710, part and counterpart (mirrored). **E**, paratype PIN, no. 3840/229, hindwing (mirrored). **F–G**, *N. deformis* **sp. nov.**, holotype PIN, no. 5102/8, part (mirrored) and counterpart. **H**, *Paranedubrovia minutissima* **sp. nov.**, holotype PIN, no. 5103/284 (mirrored). **I–J**, *P. novokshonovi* **sp. nov. I**, holotype PIN, no. 5103/120 (mirrored). **J**, paratype PIN, no. 5103/121.

Discussion

Nedubroviidae represents a second clade of holometabolan long-proboscid insects in the Permian, besides the Kungurian *Tschekardithonopsis ?oblivius* Vilesov (Neuroptera: Permithonidae) as reinterpreted by Labandeira (2010). Possession of a siphonate proboscis is a particularly strong indication that Nedubroviidae belong to the Mesozoic clade Aneuretopsychina as defined by Ren *et al.* (2009a,b): that is, Mesopsychidae + Pseudopolycentropodidae + Aneuretopsychidae. This proposal makes the Aneuretopsychina scorpionflies currently the longest-ranging clade of long-proboscid insects, in existence from the Late Permian to the mid-Cretaceous (ca. 160 ma); i.e., as long as, or even longer than haustellate Lepidoptera. Besides Nedubroviidae, remains of Mesopsychidae are recorded in the same deposits, but there is no data yet available on their mouthparts (personal observation).

Extended siphonate mouthparts of Aneuretopsychina indicate they fed on external surface fluids, possibly secretions from reproductive organs of some gymnosperms (Ren *et al.* 2009a,b; Labandeira *et al.* 2007; Labandeira 2010). Among Permian seed plants, the enclosed ovuliferous organs (capsules), probably consistent with nonpenetrative fluid-feeding pollination by long-proboscid insects, are recorded in at least one advanced peltasperm lineage, Angaropeltaceae (= Cardiolepidaceae) (see for example, Naugolnykh & Oskolski 2010). Plant fossils, consisting mainly of dispersed cuticles and referable to this family, are quite common in all localities under discussion (Gomankov & Meyen 1986; Krassilov & Karasev 2009), but records in the same deposits of reproductive organs of these or any other peltasperms, which would strengthen evidence for entomophily and association with Nedubroviidae, are still unknown.

In venation pattern, and particularly in the character of SC, RS+MA, and MP, Nedubroviidae are similar to Mesopsychidae and some Permochoristinae (e.g. *Prochoristella* Riek, *Permeca* Novokshonov). This similarity suggests that Mesopsychidae and Nedubroviidae arose as a clade from a common permochoristid-like ancestor. At the same time, the character states of the junction between the CuA and MP, which are opposite in Nedubroviidae and Mesopsychidae, indicate basal divergence of these lineages. This inference is supported by co-occurrence of the oldest representatives of both families (*Nedubrovia* and true *Mesopanorpodes* in Isady, *Paranedubrovia* and *Mesopsyche* in Balymotikha (personal observation).

Late Permian *Neochoristella* Riek, 1953 and *Nannochoristella* Riek, 1953 from the Belmont fossil site, New South Wales, Australia, appear to be closely related to Nedubroviidae as well. These genera, believed earlier to be the oldest representatives of Nannochoristidae, were included by Novokshonov (1994, 1997a) in the permochoristid subfamily Pseudonannochoristinae, which was erected for two genera with oligomerous venation from the Middle Permian of the Kuznetsk Basin, *Pseudonannochorista* Novokshonov and *Miomeca* Novokshonov. The latter two genera are apparently true Permochoristidae, as indicated by SC bearing two anterior branches, long MA fork, and 5-branched MP. In contrast, the Australian genera show greater similarity to Nedubroviidae and differ from them only in reduced RS and MP_3 forks. The cladistic analysis by Ren *et al.* (2009a,b) based on the wing features suggested monophyly of Pseudonannochoristinae with the Aneuretopsychina, so the assumption of siphonate mouthparts in this taxon also was made. Therefore, it is possible that the two Australian genera belong to Nedubroviidae rather than to Pseudonannochoristinae in Permochoristidae. If correct, Nedubroviidae would be a widespread Pangaean taxon restricted to the Permian–Triassic boundary interval rather than endemic to European Russia. However, it does not seem appropriate to include *Neochoristella* and *Nannochoristella* in Nedubroviidae prior to re-examination of the Belmont type material. For the time being I regard them as questionable members of Pseudonannochoristinae (Permochoristidae).

Irrespective of the position of the two Australian genera, the Nedubroviidae appear to be a phylogenetically important group that casts light on the origin and evolutionary history of the clade Aneuretopsychina.

Acknowledgements

I would like to thank Alexandr Rasnitsyn, Dmitry Shcherbakov, Danil Aristov, and Serge Naugolnykh for useful comments and discussions. I also am grateful to Conrad Labandeira and Jörg Ansorge, who reviewed the paper and proposed valuable remarks. The research was supported by the Russian Foundation for Basic Research, projects N. , 10-04-01713, and 10-04-10032, and by the Program 15 of the Presidium of the Russian Academy of Sciences “The Origin of the Biosphere and Evolution of the Geo-Biosystems”.

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