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A new species of the 'protozygopteran' damselfly (Odonata: Permagrionidae) from the Lower-Middle Permian of Russia

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Abstract

The small Paleozoic protozygopteran family Permagrionidae comprises 11 described species in 5 genera from the Lower Permian Chekarda and Solikamsk localities in Russia (Zalessky, 1948; Nel *et al*., 2012) and Salagou Formation in France (Nel *et al*., 1999; Fate *et al*., 2013), the Middle Permian Soyana and Kargala localities in Russia (Martynov, 1932; Martynov, 1937; Nel *et al*., 2012), and the Upper Permian Bodie Creek Head locality in Malvinas Tillyard (1928). Here we describe the new species, *Epilestes rasnitsyni* **sp. nov.** from the Ufimian of Perm Territory, which is characterized by specific arrangement of veins in the petiole and the unique preservation of body structures.

Keywords: Protozygoptera, Ufimian, Permian, Russia, fossil, insect

Introduction

Permagrionidae is a small, extinct family of "protozygopteran" damselflies, comprising only 11 species in 5 genera (Tillyard, 1928; Martynov, 1932, 1937; Zalessky, 1948; Nel *et al*., 1999; Nel *et al*., 2012). Extinct members of the family were known from Permian deposits of Europe, Falkland Islands (Malvinas) and probably South Africa (Tillyard, 1928; Martynov, 1932, 1937; Zalessky, 1948; van Dijk & Geertsema, 1999; Nel *et al*., 1999; Nel *et al*., 2012). Permagrionids are characterized by having wings of moderate size with a distinct petiolate-like base; peculiar, heavily oblique nodal structures; strongly reduced longitudinal veins (AA and CuP) and, also, tetramerous tarsi. The last character differentiates them from more advanced archizygopterans and recent odonatans alike, which have trimerous tarsi Nel *et al*. (2012).

The type genus of the family, *Permagrion* Tillyard, 1928, from Wuchiapingian deposits of Falkland Islands (Malvinas) was studied at lesser extent, due to it being present as a single wing impression (Tillyard, 1928). The most abundant findings of permagrionids come from the Kungurian locality Chekarda (Perm Territory, Russia; Zalessky, 1948; Nel *et al*., 2012), Kazanian (ICC—Roadian), Soyana (Arkhangelsk region, Russia; Martynov, 1932; Nel *et al*., 2012), and Urzhumian (ICC—Wordian), Kargala (Orenburg region, Russia; Martynov, 1937).

In the present paper we describe a new species of *Epilestes* Martynov, 1937 from Ufimian deposits of Perm Territory. The wing venation of the new species is characterized by the specific arrangement of veins in the petiole, previously known in only a very few protozygopterans. In addition, this is the first representative of the *Epilestes* genus with a preserved body, which considerably expands our knowledge about non-wing related structures of protozygopterans.

Material and methods

The described material derived from the collection of Yu. M. Zalessky, which is deposited in the Vernadsky State Geological Museum, although it was not labeled as collected by him. The specimen was generously lent to us for describing and performing additional studies to determine its origin by the Vernadsky State Geological Museum senior curator Dr Iraida A. Starodubtseva. Yu. M. Zalessky worked at several Russian localities of Permian age and, to determine the origin of the aforementioned specimen, we produced thin lithological sections from the two most probable localities – Mogilnikovo (Vishera) and Tikhie Gory. Microtexture, granulometric composition and manganese inclusions correlated the placement of our specimen with the insectiferous deposits from Mogilnikovo locality (Vishera), Cherdynsky District, Perm Territory, Russia. In this case the material was probably collected by Zalessky in 1947.

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The specimen is represented by the body imprint of a damselfly with a partially preserved abdomen, detached legs and three wings of different preservation quality. The imprint is located on the surface of a large slab (21.0 × 20.5 × 2.5 cm) of thick, gray, platy limestone. Other associated organic remnants, except silty plant detritus, were not found.

The specimen is housed in the Vernadsky State Geological Museum (GGM), Russian Academy of Sciences and available for research.

The specimen was photographed in the Arthropod laboratory PIN RAS using a Leica M165C stereomicroscope with an attached Leica DFC425 digital camera and a Nikon D70 camera. Images were processed using Adobe Photoshop CS and Adobe Illustrator CC. Clarification of wing morphology and adjustment of line drawings were performed using a Olympus SZX10 stereomicroscope.

We follow the 'higher' taxa classification of the order Odonata based on the phylogenetic systematics of Bechly (1996, 2008). Interpretation of wing venation follows Riek & Kukalová-Peck (1984), as modified by Nel *et al*. (1993), Bechly (1996) and is used in the description.

Venation abbreviations are as follows: AA analis anterior; Arc arculus; Ax primary antenodal crossvein; C costa; Cr nodal cross-vein; CuA cubitus anterior; dc discoidal cell IR intercalary radial vein; MAa anterior branch of media anterior; MAb posterior branch of media anterior; m-cu concave vein between MP and CuA; MP media posterior; N nodus; Pt pterostigma; RA radius anterior; RP radius posterior; sdc subdiscoidal cell; Sn subnodal crossvein; ScP subcosta posterior.

Systematic palaeontology

'Protozygoptera' Tillyard, 1925
Family Permagrionidae Tillyard, 1928
Genus *Epilestes* Martynov, 1937

Type species. *Epilestes kargalensis* Martynov, 1937.

Other species. *Epilestes gallica* Nel *et al*., 1999, *E. angustapterix* Nel *et al*., 2012 and *E. rasnitsyni* **sp. nov.**

Emended diagnosis. Wings long but rather wide; Pt large, elongate and trapezoidal, base of IR1 lying one cell basal of Pt; main veins straight and long, without supplementary longitudinal veins between them; cubital area broad, with one or two rows of supplementary cells between CuA and posterior wing margin; crossvenation in distal part of wing very dense and straight.

Epilestes rasnitsyni sp. nov.
(Figs 1–3)

Material. Holotype specimen GGM-1844-02/BP-12885, imprint of a body in profile with legs, forewings and one hindwing not attached. Holotype deposited in the Vernadsky State Geological Museum, Russian Academy of Sciences, Russia.

FIGURE 1. *Epilestes rasnitsyni* **sp. nov.**, holotype GGM-1844-02/BP-12885. Photograph of habitus. Scale bar = 10 mm.

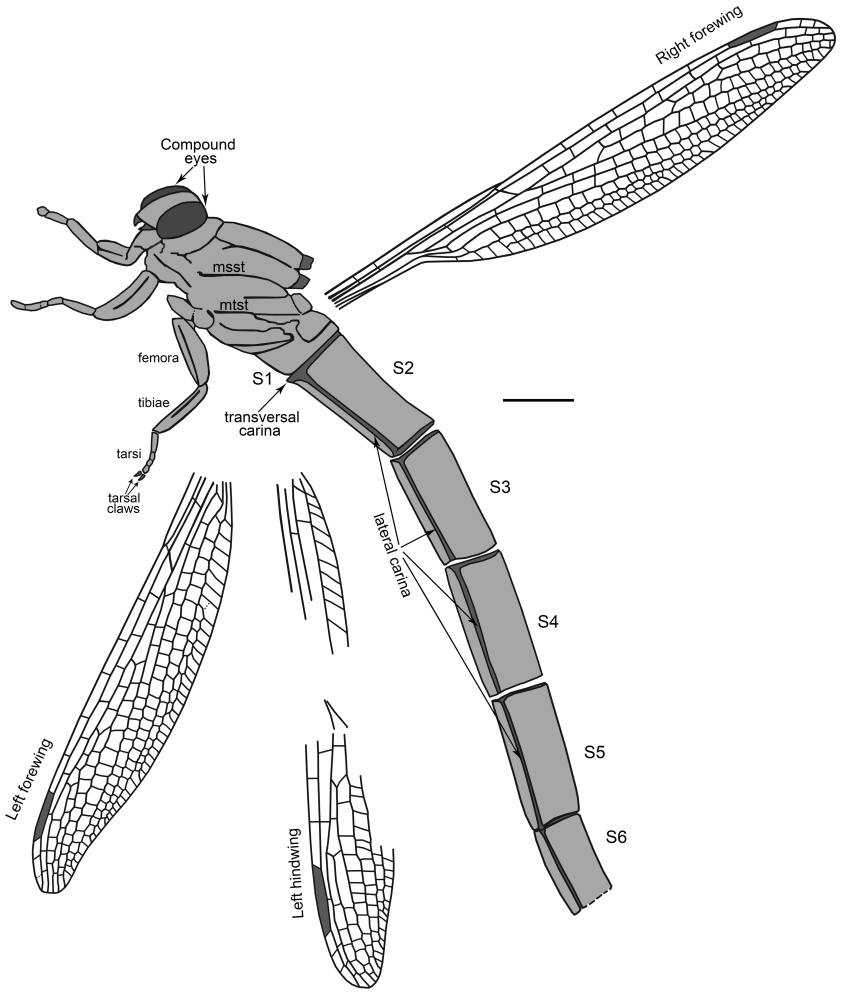

FIGURE 2. *Epilestes rasnitsyni* **sp. nov.**, holotype GGM-1844-02/BP-12885. Tracing of impression; S1–S6 = segments of abdomen, msst = mesopleural suture, mtst = metapleural suture. Scale bar = 10 mm.

Etymology. The specific name honours Professor Alexander P. Rasnitsyn, on his 85th birthday.

Diagnosis. Forewings: wing long and wide in middle part; strongly petiolate; Ax2 strongly basal of Arc. Five Pn and six or seven Psn. Pt trapezoidal, three underlying in interradial-area (between IR1 and RP1) cells long; m-cu lying distal of MAb; AA independent in basal half of petiole; cubital area broad, with one-supplement row of cells between CuA and posterior wing margin.

Locality and horizon. Mogilnikovo (Vishera), Cherdynsky District, Perm Territory; Solikamsk Formation, Solikamsk horizon; Ufimian Stage, Russia.

Description. Head in semi-profile position. Head is medium-sized, 5.5 mm long, 3.3 mm wide, with relatively small elliptical compound eyes, about 3.6 × 2.1 mm. Frons 2.8 × 0.9 mm, ocelli not visible. Antennae not preserved, mouthparts orthognathous, mandibles triangular, 1.7 mm long.

Thorax in profile. Prothorax is medium-sized; 4.1 mm long; part of prothorax is covered by a head. Pterothorax is strong, zygopteroid shape; mesopleural (msst) and metapleural (mtst) sutures are well distinguished and complete, msst 7.6 mm long, mtst 6.3 mm long; mesothorax 7.9 mm long, 3.4 mm wide, with visible mesipesternum and mesepimeron; metathorax with three distinguishable segments; metepisternum elongate, with rounded edges, 8.4 mm long, 2.6 mm wide; mesepimeron elongate, 7.0 mm long, 1.7 mm wide; the 3rd thorax sternite is poorly preserved, 3.4 mm long, 1.0 mm wide. Thorax skewness is pronounced (angle x – 43°; angle z – 44° *sensu* Needham & Anthony (1903)).

Legs of moderate length. Coxa not visible; trochanter preserved only on the left hind leg, 3.1 mm long, 0.9 mm wide; femora and tibiae are elongate, with equal length (about 5.0 mm), but the former are 3 times wider than the latter (1.5 mm and 0.5 mm respectively). Tarsi narrow and long, about 3.2 mm long, 0.3 mm wide, with two very strong claws; individual tarsal segments are poorly visible.

Abdomen in dorsal semi-profile, with six basal

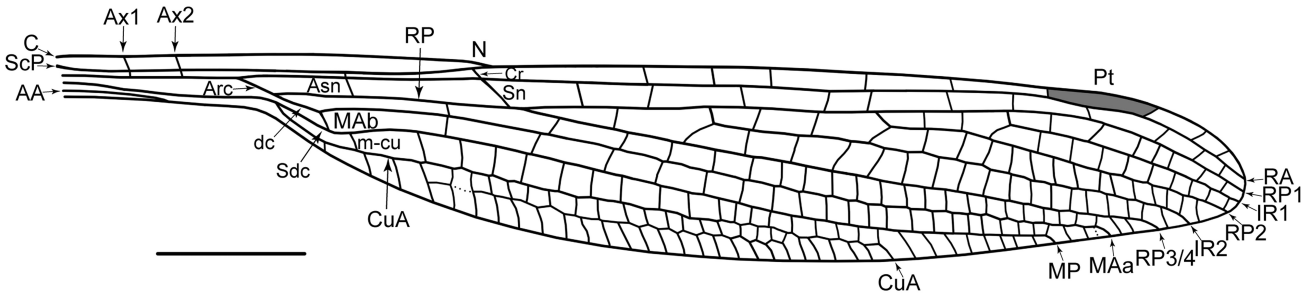

FIGURE 3. *Epilestes rasnitsyni* **sp. nov.**, holotype GGM-1844-02/BP-12885. Tracing of right forewing; Scale bar = 5 mm.

segments preserved. Lateral carina is clearly visible on 2–4 segments. The ratio of visible parts of sternite to tergite is 1 to 3. No trace of specialized genital structures on visible parts of the second and the third segments. Preserved part of abdomen is about 40.5 mm long, 3.9–5.1 mm wide. First segment shorter than others, 2.3 mm long, 5.1 mm wide.

Right forewing complete (Fig. 3). Wing length 42.3 mm, width at level of N 5.5 mm, maximum width, at level of base of IR3 6.8 mm; length from wing base to Arc 6.5 mm, from Arc to N 9.0 mm, from N to Pt 19.7 mm, from Pt to wing apex 3.5 mm. Two visible antenodal crossveins preserved, distance from wing base to Ax1 2.5 mm, from Ax1 to Ax2 1.8 mm, Ax2 2.0 mm basal of Arc. Subantenodal cross-vein (ASn), slightly oblique, oriented towards wing base, lying 9.9 mm distal of wing base and 5.0 mm basal of N. Nodus at basal third (about 37%) of wing length. Nodal structures strongly oblique, aligned with each other, Cr is half as long as Sn. Five postnodal crossveins not aligned with seven postsubnodal crossveins present in costal area between N and Pt. Two oblique postnodal crossveins not aligned with three postsubnodal crossveins lying distally Pt. Pt elongate and trapezoidal, thickened at the middle (maximum width, at the level of Pt brace 0.5 mm); costal side longer than others, 3.9 mm long; posterior (pterostigmal part of RA) side 3.3 mm long, basal part oblique, 0.3 mm long, distal part very oblique, 0.6 mm long. Pterostigmal brace oblique, oriented towards wing base, lying 1.4 mm distal of Pt base.

Petiole long and narrow; dc basally opened, elongate, distal edge of dc (MAb) 0.7 mm long. Subdiscoidal cell triangular, elongate, slightly curved; anterior part of Sdc 2.8 mm long, posterior part of Sdc 3.3 mm, distal edge (m-cu crossvein) 0.6 mm long. MAa and MAb separated 6.9 mm from base of RP; MAb 0.7 mm long; MP and CuA bifurcating opposite separation of RP and MA; AA independent, separated from AP at wing base, and ending in petiole 3.6 mm distal of wing base. CuP not visible in petiole.

Base of RP 1.3 mm distal to arculus; base of RP3/4 0.3 mm distal of Sn and 8.6 mm distal of base of RP; base of IR2 15.0 mm distal of RP origin, and 6.5 mm and two cells distal of base of RP3/4. Base of RP2 20.7 mm distal of RP origin, and 5.7 mm and three cells distal base of IR2. Base of IR1 25.2 mm distal of RP origin, 4.5 mm and three cells distal of base of RP2, 1.4 mm and one cell basal of Pt base. All radial and intercalary longitudinal veins are simple and straight, without visible longitudinal supplementary veins between them. Endings of radial and intercalary veins lying distal of Pt. MAa very weakly zigzagged in distal half, ending of MAa 4.5 mm basal of wing apex. MP simple and straight, ending 6.4 mm basal of wing apex, and 1.9 mm and three cells basal of ending of MAa. CuA weakly zigzagged and long, ending of CuA 12.0 mm basal of wing apex, and 5.7 mm and nine cells basal of ending of MP. Cubital area with one supplement row of cells on two thirds of its length.

Left forewing incomplete, wing base and apex not preserved. The length of preserved part 33.5 mm, width at level of N 5.3 mm, maximum width, at level of base of IR3 6.6 mm; length from N to Pt 20.1 mm.

Subantenodal cross-vein (ASn), slightly oblique, lying 4.2 mm basal of N. Cr aligned with Sn, Sn with stronger obliquity than Cr. Five postnodal crossveins not aligned with six postsubnodal crossveins before Pt. Only one visible postnodal crossveins not aligned with two postsubnodal crossveins present distal of Pt. Pt elongate and trapezoidal, maximum width, (in the distal quarter 0.5 mm); costal side 4.1 mm long; posterior (radial) side 3.3 mm long, basal part oblique, 0.4 mm long, distal part oblique, 0.6 mm long. Pterostigmal brace of inverted obliquity, lying 1.7 mm distal of Pt base.

Only distal parts of dc and Sdc preserved on indicated wing. Very oblique distal edge of dc (MAb) 1.0 mm long. Subdiscoidal cell slightly curved and elongate, with distal edge (concave m-cu crossvein) 0.8 mm long. MAa and MAb bifurcating 5.7 mm basal of N.

Base of RP3/4 0.6 mm distal of Sn; base of IR2 6.3 mm and two cells distal of base of RP3/4, and 7.1 mm distal of Sn. Base of RP2 5.6 mm and three cells distal

base of IR2, and 12.7 mm distal of Sn. Base of IR1 4.4 mm and three cells distal of base of RP2, and 17.1 mm distal of Sn, 1.0 mm and one cell basal of Pt base. No visible longitudinal supplementary veins between main radial and intercalary veins. RP1 and RP2 long and straight. IR1 and IR2 very weakly zigzagged in distal part. Ending of RP3/4 lying 1.2 mm and one cell distal of Pt edge. MAa and MP long and straight. Between endings of RP3/4 and MAa 2.5 mm and four cells; between the endings of MAa and MP 1.5 mm and three cells. Ending of MP lying at the level of basal edge of Pt. CuA very weakly zigzagged and long, ending of CuA 4.1 mm and eight cells basal of ending of MP. Cubital area with one row of cells to the level of N, with two rows more distally between level of N and the fourth postsubnodals, and again with one row near ending of CuA.

Left hindwing is poorly preserved and strongly deformed. The length of preserved part 31.6 mm, width at level of proximal edge of Pt 4.7 mm; Pt trapezoidal and elongate, with basal and distal edges of different obliquity. The length of the longest costal edge 4.3 mm, posterior (radial) edge 4.0 mm, maximum width of Pt 0.5 mm.

Discussion

Epilestes rasnitsyni **sp. nov.** is included in the family Permagrionidae on the basis of the following characteristics: presence of primary antenodals, aligned with underlying crossveins; rather long MAb of normal obliquity; presence of concave m-cu between MP and CuA; strong subantenodal cross-vein (ASn) in area between RA and RP at the distance from Arc to N; nodal Cr aligned with strong oblique Sn; sclerotized pterostigma with one hypostigmatic crossvein below it; and numerous cross-veins between main longitudinal veins Nel *et al*. (2012). Here we note that one character of the former familial diagnosis (AA fused with posterior wing margin) does not correspond to the new species petiole venation, and it is revised as follows: AA is independent of AP and posterior wing margin or fused with them.

The new species shares most of the typical characters of the genus *Epilestes*, including the elongate trapezoidal Pt; normal 'stepped' organization of bases of IR2 and RP2; presence of two rows of cells in the cubital area; and the absence of supplementary longitudinal veins between the main veins of median and radial areas. Based on the listed characters, we attribute the new species to the genus *Epilestes*.

Epilestes rasnitsyni **sp. nov.** differs from all known species of the genus in having the following characters: wing size is about 37–43 mm; Ax2 lying strongly basal of Arc; AA separates from AP at wing base and ends in the middle of petiole; CuP is not visible; Pt thickened at the middle, has a length of three underlying in interradial-area cells; at least five Pn not aligned with roughly six to seven Psn crossveins.

The new species differs from *E. kargalensis* in the longer and narrower wing, shorter Pt with more oblique basal and distal edges, and m-cu located distal of MAb. *Epilestes rasnitsyni* **sp. nov.** is similar to *E. angustapterix* in the width of the cubital area, but differs from it in the smaller Pt and narrower costal margin. Unlike *E. gallica*, the new species has a larger Pt, m-cu lying distal of MAb, and has only one supplement row of cells in the cubital area.

It should be noted that *E. rasnitsyni* **sp. nov.** is characterized by AA separated from AP and posterior wing margin in the petiole. That organization of the basal longitudinal veins is very rare and is currently known only in two species of protozygopterans, *Permepallage angustissima* Martynov, 1938 (fam. Permepallagidae) and *Kennedya azari* Nel *et al*., 2012 (fam. Kennedyidae), Nel *et al*. (2012).

Most descriptions of permagrionids were made on the basis of isolated wings. The single previously known specimen (Permagrionidae gen. and sp. indet., specimen PIN 1700/477) with a preserved thorax, legs and fragments of abdomen, was described in 2012 from the Chekarda locality Nel *et al*. (2012). Specimen GGM-1844-02/BP-12885 described herein shows well preserved body structures, which complements our knowledge about permagrionid morphology. It is noteworthy that the head of *E. rasnitsyni* **sp. nov.** bears fully separated ellipsoid compound eyes. They are significantly less convex and rounded than those of recent zygopterans. The thorax of *E. rasnitsyni* **sp. nov.** has the typical zygopteran appearance, with strong thorax skewness, which is of lesser degree than those of modern zygopterans (from ~50° on both angles in representatives of Epallaginae to 60–70° in Agrioninae), but notably stronger than in anisopterans (about 30–40° on 20–30°) sensu Needham & Anthony (1903). It should be noted, that the previously described permagrionid damselfly from Chekarda, had a larger pterothorax and overall "anisopteran appearance", manifested in lesser thorax skewness Nel *et al*. (2012). Regarding the leg morphology is the especially remarkable presence of distinctly thickened femora together with comparatively slender tibiae. Also, as in the previously described specimen from Chekarda (Nel *et al*., 2012: fig. 7, specimen PIN, No. 1700/477ab) there is an easily recognizable lateral carina in the middle part of abdomen of *E. rasnitsyni* **sp. nov.**, which seems to confirm the hypothesis about the independent appearance of this character in anisopterans and permagrionids Nel *et al*. (2012).

Conclusion

Representatives of *Epilestes* genus were known only from three specimens from Cisuralian – Guadalupian deposits of Russia and France. *Epilestes rasnitsyni* **sp. nov.** comes from boundary Kungurian-Roadian deposits (=Ufimian) of Perm Territory. This is the first finding of a damselfly of "protozygopteran appearance" from the Mogilnikovo locality, which is known for yielding numerous large meganeurids. Thanks to the exceptional preservation of this new specimen, it enriches our knowledge about *Epilestes* morphology and also expands data regarding permagrionid wing venation in general. The most important character of wing venation of the new specimen is the presence of an independent AA in the wing petiole; previously this condition was known only in several representatives of Kennedyidae and Permepallagidae (Nel *et al*., 2012).

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References

Bechly, G. (1996) Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata), unter besonderer Berücksichtigung der Phylogenetischen Systematik und des Grundplanes der Odonata. *Petalura*, 2, 1–402.

Bechly, G. (2008) Phylogenetic systematics of Odonata. Available from: https://bechly.lima-city.de/phylosys.htm (accessed 28 April 2021).

van Dijk, D.E. & Geertsema, H. (1999) Permian insects from the Beaufort Group of Natal, South Africa. *Annals of the Natal Museum*, 40, 137–171. https://hdl.handle.net/10520/AJA03040798_102

Martynov, A. (1932) New Permian Paleoptera with the discussion of some problems of their evolution. *Trudy Paleozoologicheskogo Instituta Akademii Nauk SSSR*, 1, 1–44 [In English, with Russian summary].

Martynov, A. (1937) Permian fossil insects from Kargala and their relationships. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR, Moscow–Leningrad*, 7, 8–92 [In Russian].

Needham, J.G. & Anthony, M.H. (1903) The skewness of the thorax in the Odonata. *Journal of the New York Entomological Society*, (3) 11, 117–125. https://www.jstor.org/stable/25003040

Nel, A., Martínez-Delclòs, X., Paicheler, J.C. & Henrotay, M. (1993) Les 'Anisozygoptera' fossiles. Phylogénie et classification (Odonata). *Martinia*, Numéro Hors Série 3, 1–311.

Nel, A., Gand, G., Garric, J. & Lapeyrie, J. (1999) The first recorded protozygopteran insects from the Upper Permian of France. *Palaeontology*, 42, 83–97. https://doi.org/10.1111/1475-4983.00063

Nel, A., Bechly, G., Prokop, J., Béthoux, O. & Fleck, G. (2012) Systematics and evolution of Paleozoic and Mesozoic damselfly-like Odonatoptera of the 'Protozygopteran' grade. *Journal of Paleontology*, 86, 81–104. https://doi.org/10.1666/11-020.1

Riek, E.F. & Kukalová-Peck, J. (1984) A new interpretation of dragonfly wing venation based upon early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings. *Canadian Journal of Zoology*, 62, 1150–1166. https://doi.org/10.1139/z84-166

Tillyard, R.J. (1928) A Permian fossil damselfly wing from the Falkland Islands. *Transactions of the Entomological Society of London*, 76, 55–63. https://doi.org/10.1111/j.1365-2311.1928.tb01187.x

Zalessky, G.M. (1948) Nasekomye iz permskih otlozheniï Solikamskogo i Cherdynskogo raïonov. *Voprosy Teoreticheskoï i Prikladnoï Geologii*, 5, 44–52.