

## One of the earliest stem-Plecoptera reassessed as a Blattinopsidae (Insecta)

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# One of the earliest stem-Plecoptera reassessed as a Blattinopsidae (Insecta)

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## ABSTRACT

In addition to their significance for ancient biogeography, the earliest occurrences of extant insect groups have gained particular importance over the past decade, as they are critical for temporally calibrating phylogenetic trees. In this context, the robustness of taxonomic assignments is crucial. The earliest fossil record of putative stoneflies (Plecoptera), from the Pennsylvanian, is based on a very limited number of species. The assignment of one of them, *Gulou oudardi* Schubnel, Perdu, Roques, Garrouste & Nel, 2019, from the Avion locality (Nord-Pas-Calais basin; France) and known from a single wing, is here reconsidered. Concordant evidence, including the presence of intercalary veins in the apical and postero-apical areas, and a CuA preserved as a concave groove, indicates that the specimen is not a stonefly forewing, but rather a hindwing of the Palaeozoic insect family Blattinopsidae (which ordinal affinities remain uncertain). More specifically, this hindwing can be confidently linked to a species known from a single forewing, also from the Avion locality, which constitutes the holotype of *Avionblattinopsis oudardi* Quispe, Roques, Garrouste & Nel, 2022. The two species are therefore synonymized as *Avionblattinopsis oudardi* (Schubnel, Perdu, Roques, Garrouste & Nel, 2019), n. comb.

## KEY WORDS

Blattinopsidae,  
Fossil insect,  
Carboniferous,  
Pennsylvanian,  
Avion,  
reflectance transforming  
imaging,  
new combination.

## RÉSUMÉ

*Un des premiers Plécoptères-souches réévalué comme un Blattinopsidae (Insecta).*

Outre leur portée en paléobiogéographie, les premières occurrences de groupes d'insectes actuels ont acquis une importance particulière au cours de la dernière décennie, car elles sont essentielles pour calibrer temporellement les arbres phylogénétiques. Dans ce contexte, la robustesse des attributions taxonomiques est cruciale. Le plus ancien enregistrement fossile de plécoptères (Plecoptera) supposés, du Pennsylvanien, est basé sur un nombre très limité d'espèces. L'attribution de l'une d'entre elles, *Gulou oudardi* Schubnel, Perdu, Roques, Garrouste & Nel, 2019, provenant de la localité d'Avion (bassin du Nord-Pas-Calais; France) et connue d'une seule aile, est ici réexaminée. Des critères concordants, notamment la présence de nervures intercalaires dans les zones apicale et postéro-apicale, et une CuA préservée sous la forme d'un sillon concave, indiquent que le spécimen n'est pas une aile antérieure de plécoptère, mais plutôt une aile postérieure de la famille d'insectes paléozoïques Blattinopsidae (dont les affinités ordinales restent incertaines). Plus précisément, cette aile postérieure peut être reliée avec assurance à une espèce connue à partir d'une seule aile antérieure, également de la localité d'Avion, qui constitue l'holotype d'*Avionblattinopsis oudardi* Quispe, Roques, Garrouste & Nel, 2022. Les deux espèces sont donc synonymisées comme *Avionblattinopsis oudardi* (Schubnel, Perdu, Roques, Garrouste & Nel, 2019), n. comb.

## MOTS CLÉS

Blattinopsidae,  
insecte fossile,  
Carbonifère,  
Pennsylvanien,  
Avion,  
imagerie de  
transformation par  
réflectivité,  
combinaison nouvelle.

## INTRODUCTION

The earliest fossil representatives of certain insect groups have drawn increased attention over the past decade, as they are essential for temporally calibrating phylogenetic trees – an approach that, in turn, enables the investigation of diversification patterns. Since the milestone contribution by Wolfe *et al.* (2016), efforts have intensified to identify robust calibration points for insects, as poor choices can significantly impact evolutionary inferences (among others, see Kohli *et al.* 2021). Earliest occurrences are also informative for reconstructing the area of origin of a given group.

In this context, a potentially important taxon is *Gulou oudardi* Schubnel, Perdu, Roques, Garrouste & Nel, 2019, from the Moscovian (Middle Pennsylvanian) Avion locality (France; Schubnel *et al.* 2019), originally identified as part of the stem-group of Plecoptera Burmeister, 1839 (i.e. a stem-stonefly). According to its original systematic placement, it is closely affiliated to *Gulou carpenteri* Béthoux, Cui, Kondratieff, Stark & Ren, 2011, known from the latest Bashkirian to middle Moscovian Xiaheyan locality (China; Béthoux *et al.* 2011a, Trümper *et al.* 2020). Therefore, the two sub-contemporaneous species were discovered in different paleogeographic areas, suggesting a wide distribution, during the Pennsylvanian, of these insects. Renewed interest in stonefly ancient evolutionary history (Sroka *et al.* 2025, Wang *et al.* 2025; among recent accounts) led me to reconsider the original material of *G. oudardi*, displaying several features seemingly inconsistent with a placement as stem-Plecoptera. New observations now support a different taxonomic assignment.

## MATERIAL AND METHODS

### FOSSIL MATERIAL

The two specimens investigated in this account belong to the Palaeontology collection of the Muséum national d'Histoire naturelle (Paris, France; acronym, MNHN.F).

### DATA ACQUISITION AND PREPARATION

Specimens were documented using Reflectance Transforming Imaging (RTI). The corresponding files are publicly available from Appendix 1. Each file was derived from a set of 42 photographs obtained using: 1) a digital camera Canon 5DS coupled to a Canon MP-E 65 mm macro lens (all Canon, Tokyo, Japan); and 2) a light dome of about 30 cm in diameter (courtesy of FlyDome, Paris, France). Both the camera and light dome were driven by a control box. For each set, obtained images were batch-optimized using Adobe Photoshop CS6 and then compiled into an RTI file using the RTI Builder software v.2.0.2 (HSH fitter; software freely available from Cultural Heritage Imaging). Interpretative drawings were then made using Adobe Illustrator CS6 (Adobe Systems, San Jose, CA, U.S.A.) based on a working document composed of several images extracted from the RTI files and composing distinct layers (the primary data being the 'normals view', on which each pixel is color-coded according to the orientation of the

vector perpendicular to the plane tangent to the corresponding point). Photographs reproduced on Fig. 1B, D are based on RTI extracts which were then specifically optimized using Adobe Photoshop CS6; and the photograph reproduced on Fig. 1D is a combination of extracts from both the positive and negative imprints. On drawings, reconstructed portions appear faded.

### WING VENATION TERMINOLOGY AND HOMOLOGIES

Herein I follow the serial insect wing venation ground-plan (Lameere 1922, 1923). Within this framework, particular aspects of the wing venation of Blattinopsidae Bolton, 1925 are to be considered. In representatives of this family, it is often the case that R emits a posterior branch basal to a stronger fork, itself interpreted as the RA/RP fork. The basal 'posterior branch' has been regarded as either an early branch of RP, or as part of the median system (among others, see Bolton 1925; Hörschemeyer & Stapf 2001). Based on my observation of the specimen MNHN.FA71321 (see below), and on reported cases of pectinate fusion of RP onto RA (i.e. successive origins of RP branches along the RA stem; Béthoux 2012; Carpenter 1940), herein I assume that the median system is independent from the radial one in Blattinopsidae. Also, there is no convex branch that can be decisively identified as the anterior sector of the Media. Consequently, I will not distinguish median sectors and instead consider the Media as a whole. These appreciations have no implications on conclusions regarding the taxonomic assignment of *G. oudardi*. Adopted abbreviations are repeated for convenience.

### Abbreviations

AA	anterior analis;
CuA	anterior cubitus;
CuP	posterior cubitus;
M	media;
RA	anterior radius;
RP	posterior radius;
ScP	posterior subcosta.

### Remark on abbreviations

On Fig. 1, to ease the identification of main vs intercalary veins between RA and CuP, they are indicated by grey dots and circles, respectively. I follow the convention by Cui *et al.* (2011) for describing branching patterns, as follows: for a given vein, in the annotation '(a,b)', 'a' indicates the number of terminal branches of the anterior branch, while 'b' indicates the number of terminal branches of the posterior branch.

### COMPARATIVE ANALYSIS

It will prove useful to first consider the specimen MNHN.FA71321, holotype of *Avionblattinopsis oudardi* Quispe, Roques, Garrouste & Nel, 2022 (see Quispe *et al.* 2022; Fig. 1A, B), assigned to the Palaeozoic insect family Blattinopsidae. Several observations reported in the original description could not be corroborated. Whether ScP reaches the anterior margin or RA cannot be clearly established, because both potential endings of this vein sector are equally strong. A conservative stand is, therefore, to consider that, as

in other Blattinopsidae, ScP reaches the anterior wing margin. The same comment applies to a presumed common stem formed by R and M, which cannot be confirmed (R overlaps ScP and may well overlap M as well). The strong m-cua cross-vein (i.e., the ‘arculus’) could not be observed because the corresponding area is missing. The same comment applies to the angle formed by R/RA at the origin of RP (reported as ‘pronounced’ in the original description). The vein M has a (2,1) branching pattern, instead of a (2,2) pattern (a convex intercalary vein may have been interpreted as a branch of M in the original description; and see below). The vein CuA has no anterior concave branch.

Conversely, the original description does not report the occurrence of strong and convex intercalary veins in the apical and postero-apical areas (grey circles on Fig. 1A). More specifically, a single intercalary vein can be clearly identified in each of the inter-veinal areas between RA and the anterior-most branch of CuA. That these structures do not belong to the main vein system is revealed by (i) their elevation, decidedly convex, whereas branches of RP and M are concave (with the exception of the terminal portion of the posterior-most branch of M, turning convex); and (ii) the Y-shaped origin of many of them. Judging from published data (Aristov & Rasnitsyn 2021, Carpenter 1966, Dvořák *et al.* 2023, Hörnschemeyer & Stapf 2001; among others), such structures are common in Blattinopsidae but have been usually interpreted as part of the main vein system (but see Bolton 1925). Also, in the specimen, CuA ‘emits’ several posterior veinlets before forming a more obvious fork (orange arrow on Fig. 1A). It is conceivable, and assumed thereafter, that the ‘posterior veinlets’ of CuA are derived from cross-venation (i.e. are intercalary veins; and see below). Then, judging from the distance between main vein branches along the posterior wing margin, CuA is likely forked, with an intercalary vein between its branches (and an aborted intercalary offshoot). Finally, the posterior-most branch of M, from its origin to its mid-length, is strongly desclerotized.

Likewise, several observations made by Schubnel *et al.* (2019) on the specimen MNHN.FA70112 (holotype of *Gulou oudardi*; Fig. 1C, D) could not be corroborated. The vein sector ScP reaches the anterior wing margin instead of RA; the stem of M can be distinguished from that of R; the vein M has 2 terminal branches instead of 4 (convex intercalary veins seem to have been interpreted as a genuine branch of M in the original description; and see below); and, finally, a strong m-cua cross-vein (i.e., the ‘arculus’) could not be observed. Conversely, as in the previously examined case, the original description omitted several important features. Notably, strong and convex intercalary veins occur in the apical and postero-apical areas. They are best visible on the negative imprint, preserving the apical part of the wing (Fig. 1D, right side). As with the previous case, a single intercalary vein occurs in each of the inter-veinal areas between the anterior-most branch of RP and the posterior-most branch of CuA. Another relevant point is the elevation of CuA. Instead of being convex, it is preserved as a concave, sharp groove (on an elevated portion). Such attribute is not totally unexpected, as it has been

described in fossilized hindwings of some polyneopteran taxa, including stem-dictyopterans (see Béthoux *et al.* 2011b) and stem-grylloblattodeans (see Béthoux & Beckemeyer 2007; among others), and also in hindwings of Blattinopsidae (Aristov & Rasnitsyn 2021). Altogether: 1) the occurrence of intercalary veins allows reconsidering the ‘stem-Plecoptera hypothesis’, as this trait has never been reported in this group; and 2) the concave CuA indicates that the specimen is unlikely a forewing, as posited in the original description, but more likely a hindwing.

Based on these new observations, the specimens MNHN.FA71321 and MNHN.FA70112 happen to share several features, as follows: occurrence of intercalary veins in the apical and postero-apical area; area between CuA and CuP with veinlets / longitudinal elements derived from cross-venation. It is then plausible that the specimen MNHN.FA70112 is a Blattinopsidae hindwing. Albeit limited, our current knowledge on hindwing morphology in this group (see Aristov & Rasnitsyn 2021) corroborates this view: notably, the plicatum is reduced, at least in the genus *Glaphyrophlebia* Handlirsch, 1906, a trait consistent with what is visible of the specimen MNHN.FA70112. Further similarities between the two specimens encompass the number of terminal branches of RP, M and CuA (respectively, 5-branched, 3- vs 2-branched, and 2-branched), the density and shape of cross-veins, and their total size (10.6 and 9.8 mm in length, respectively). Furthermore, compared to other forewings of Blattinopsidae (see, among others, Aristov *et al.* 2021; Aristov & Rasnitsyn 2022; Hörnschemeyer & Stapf 2001), the specimen MNHN.FA71321 is distinctive in displaying a relatively broad area between CuP and the first AA vein (but see Dvořák *et al.* 2023), a trait shared with the specimen MNHN.FA70112; whereas, in one of the few Blattinopsidae species known from both fore- and hindwing, this area is narrow in both wing pairs (see Aristov & Rasnitsyn 2021). Finally, the two specimens were collected from the same locality.

In summary, concordant evidence indicate that the specimens MNHN.FA71321 and MNHN.FA70112 belonged to individuals of the same Blattinopsidae species. *Avionblattinopsis oudardi* Quispe, Roques, Garrouste & Nel, 2022 is therefore a junior synonym of *Gulou oudardi* Schubnel, Perdu, Roques, Garrouste & Nel, 2019; while the latter can no longer be maintained in the genus *Gulou* Béthoux, Cui, Kondratieff, Stark & Ren, 2011. A formal systematic treatment follows.

## SYSTEMATIC IMPLICATIONS

Class INSECTA Linnaeus, 1758

Order uncertain

Family BLATTINOPSIDAE Bolton, 1925

## REMARKS

The relationships of the Blattinopsidae with the remaining neopteran insects are not settled. Among recent accounts, Prokop *et al.* (2014), followed by Quispe *et al.* (2022), assigned the family to the order Paoliida Rohdendorf, 1977, itself

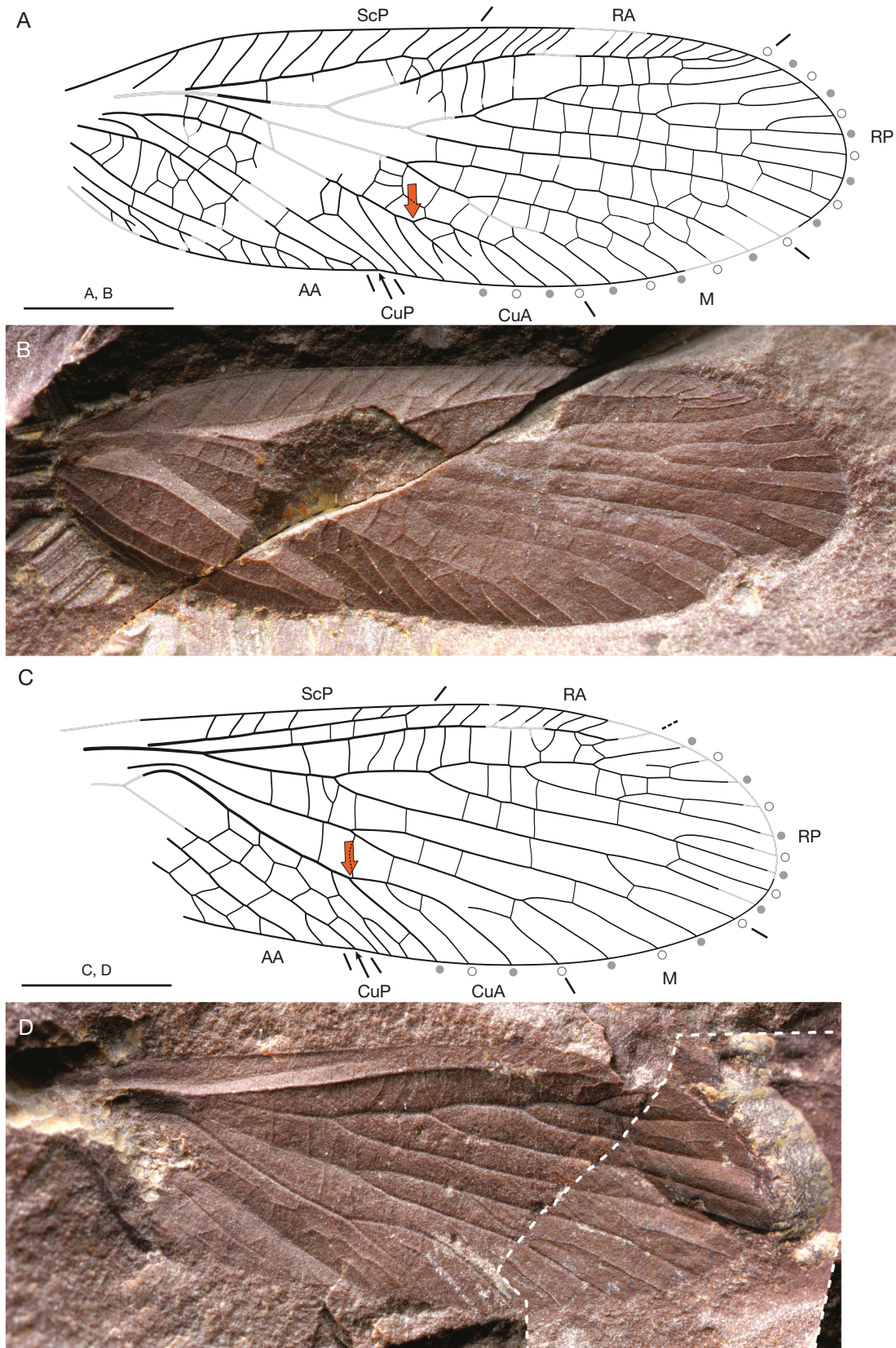


FIG. 1. — *Avionblattinopsis oudardi* (Schubnel, Perdu, Roques, Garrouste & Nel, 2019), n. comb.: **A, B**, specimen MNHN.F.A71321 (holotype of *Avionblattinopsis oudardi* Quispe, Roques, Garrouste & Nel, 2022), left forewing; **A**, interpretative line drawing (large orange arrow, main fork of CuA; grey dot, ending of a main vein; grey circle, ending of an intercalary vein); **B**, photograph [positive imprint, flipped horizontally, extracted from RTI file [light source coordinates x:-0.27, y:0.86]]. **C, D**, specimen MNHN.F.A70112 (holotype), left hindwing; **C**, interpretative line drawing (arrow and dots, as in **A**); **D**, combination of photograph of both imprints, delimited by a dashed line (left side, positive imprint, flipped horizontally, extracted from RTI file [light source coordinates x:-0.48, y:0.78]; right side, negative imprint, light-mirrored, extracted from RTI files [light source coordinates x:0.31, y:-0.66]). Scale bars: 2 mm.

regarded as closely related to dictyopterans (i.e. cockroaches, termites and mantises) by the former authors. On the other hand, Aristov & Rasnitsyn (2021), following Rohdendorf (1977), considered the family as the sole member of the order Blattinopsida Rohdendorf, 1977 (also spelled 'Blattinopseida' in the literature), itself understood as representing a remote stem-relative of one the three major neopteran lineages, or a combination of them. In regard of these controversies and of the fact that our knowledge on this group is actually very limited, I am in favour of adopting a cautious stand on the phylogenetic position of these insects.

Genus *Avionblattinopsis*  
Quispe, Roques, Garrouste & Nel, 2022

TYPE SPECIES. — *Avionblattinopsis oudardi* Quispe, Roques, Garrouste & Nel, 2022, thereafter regarded as a junior synonym and junior homonym of *Avionblattinopsis oudardi* (Schubnel, Perdu, Roques, Garrouste & Nel, 2019), n. comb.

SPECIES INCLUDED. — Type species only.

DIAGNOSIS. — By monotypy, same as for the type species.

*Avionblattinopsis oudardi*  
(Schubnel, Perdu, Roques, Garrouste & Nel, 2019),  
n. comb.  
(Fig. 1)

*Golou oudardi* Schubnel, Perdu, Roques, Garrouste & Nel, 2019: 431, fig. 1.

*Avionblattinopsis oudardi* Quispe, Roques, Garrouste & Nel, 2022: 388, fig. 3; n. syn., n. hom.

TYPE MATERIAL. — **Holotype. France** • 1 specimen (hindwing); Hauts-de-France, Pas-de-Calais, Avion, Terril n°7 (also known as 'Terril n°76, 7 de Liévin'); 50°24'00"N, 2°49'07"E; Pas-de-Calais basin; Carboniferous, Middle Pennsylvanian, Moscovian; Patrick Roques leg.; MNHN.FA70112 (Roques coll.; Fig. 1C, D).

ADDITIONAL MATERIAL. — **France** • 1 specimen (forewing); same data as for the holotype; MNHN.FA71321 (holotype of *Avionblattinopsis oudardi* Quispe, Roques, Garrouste & Nel, 2022; Roques coll.; Fig. 1A, B).

TYPE LOCALITY AND STRATIGRAPHY. — 'Terril n°7', Avion, Pas-de-Calais, France; Moscovian (Middle Pennsylvanian, Carboniferous).

DIAGNOSIS. — **In both fore- and hindwing:** first fork of M in a basal position, opposite (or nearly opposite) the first fork of RP (commonly located in a distal position, or even absent, in Blattinopsidae); area between CuP and the first AA vein comparatively broad (narrow in *Glaphyrophlebia* spp. and *Blattinopsis* spp.); occurrence of a single, well-delimited intercalary vein in each inter-veinal area between the anterior-most branch of RP and the posterior-most branch of CuA (a trait putatively shared with most *Glaphyrophlebia* spp. and *Stephanopsis* spp.). **Forewing:** ScP-R/RA area not particularly broad (commonly broad in other Blattinopsidae); RA-RP area broad (commonly narrow in other Blattinopsidae); longitudinal furrows between RP and M branches absent (present in at least some *Glaphyrophlebia* spp.); area between the first and second AA veins very broad. **Hindwing:** CuA with a clear, deep fork; RP, from its origin to its first fork, long.

#### REMARKS

The hindwing morphology of Blattinopsidae is incompletely documented yet. Therefore, character states proposed as specifically diagnostic of this organ should be regarded as tentative. As already pointed out by Quispe *et al.* (2022), the unusual combination of features displayed by the species justifies assigning it to a distinct genus. A species overall similar to *Avionblattinopsis oudardi* n. comb. is *Stephanopsis testai* Dvořák, Krzemiński & Prokop, 2023 (see Dvořák *et al.* 2023), known from a forewing from the Moscovian Mazon Creek locality. The two species differ in the width of the RA-RP area, of the areas between AA veins, and in the shape of the apex.

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#### REFERENCES

- ARISTOV D. S. & RASNITSYN A. P. 2021. — New and little known Blattinopsidae (Insecta: Blattinopsida) from the Middle Permian of Russia. *Paleontological Journal* 55: 288-293. <https://doi.org/10.1134/S0031030121030059>
- ARISTOV D. S. & RASNITSYN A. P. 2022. — New Blattinopsidae (Insecta: Blattinopsida) from the Middle Permian of European Russia. *Paleontological Journal* 56: 187-193. <https://doi.org/10.1134/S0031030122020034>
- ARISTOV D. S., RASNITSYN A. P. & NAUGOLNYKH S. V. 2021. — New Blattinopsidae (Insecta: Blattinopsida) in the Permian of the Pechora Basin (Komi Republic, Russia) in the context of landscape and vegetation evolution. *Paleontological Journal* 55: 641-649. <https://doi.org/10.1134/S0031030121060022>
- BÉTHOUX O. 2012. — King crickets, raspy crickets & weta, their wings, their fossil relatives. *Journal of Orthoptera Research* 21: 179-225. <https://doi.org/10.1665/034.021.0206>
- BÉTHOUX O. & BECKEMEYER R. J. 2007. — New and rare insect species from the Wellington Formation (Orthoptera, Grylloblattida; Lower Permian, USA). *Alavesia* 1: 49-61.
- BÉTHOUX O., CUI Y., KONDRATIEFF B., STARK B. & REN D. 2011a. — At last, a Pennsylvanian stem-stonefly (Plecoptera) discovered. *BMC Evolutionary Biology* 11: 248. <https://doi.org/10.1186/1471-2148-11-248>
- BÉTHOUX O., SCHNEIDER J. W. & KLASS K.-D. 2011b. — Redescription of the holotype of *Phylloblatta gaudryi* (Agnus, 1903) (Pennsylvanian; Commentry, France), an exceptionally well-preserved stem-dictyopteran. *Geodiversitas* 33 (4): 625-635. <https://doi.org/10.5252/g2011n4a4>. <https://sciencepress.mnhn.fr/fr/periodiques/geodiversitas/33/4/redescription-de-l-holotype-de-phyloblatta-gaudryi-agnus-1903-pennsylvanien-commentry-france-un-dictyoptere-souche-exceptionnellement-bien-preserve>
- BURMEISTER H. C. C. 1839. — *Handbuch der Entomologie. Zweiter Band. Besondere Entomologie. Zweite Abtheilung. Kaukerfe Gymnognatha. (Zweite Hälfte. vulgo Neuroptera)*. Enslin, Berlin, 1050 p. <https://www.biodiversitylibrary.org/page/8223115>
- BOLTON H. 1925. — *Insects from the Coal Measures of Commentry*. Trustees of the British Museum, London, 56 p.

- CARPENTER F. M. 1940. — A revision of the Nearctic Hemerobiidae, Berothidae, Sisyridae, Polystoechotidae and Dilaridae (Neuroptera). *Proceedings of the American Academy of Arts and Sciences* 74: 193-280. <https://doi.org/10.2307/20023398>
- CARPENTER F. M. 1966. — The Lower Permian insects of Kansas. Part 11: The orders Protorthoptera and Orthoptera. *Psyche* 73: 46-88. <https://doi.org/10.1155/1966/47172>
- CUI Y., BÉTHOUX O. & REN D. 2011. — Intraindividual variability in Sinonamuropteridae forewing venation (Grylloblattida; Late Carboniferous): taxonomic and nomenclatural implications. *Systematic Entomology* 36: 44-56. <https://doi.org/10.1111/j.1365-3113.2010.00545.x>
- DVOŘÁK T., KRZEMIŃSKI W. & PROKOP J. 2023. — New stem-dictyopteran insects from the Pennsylvanian deposits at Mazon Creek and Sosnowiec (Insecta: Polyneoptera). *Historical Biology* 32, 2334-2339. <https://doi.org/10.1080/08912963.2022.2140423>
- HANLIRSCH A. 1906. — Revision of American Paleozoic insects. *Proceedings of the United States National Museum* 29: 661-820. <https://doi.org/10.5479/si.00963801.29-1441.661>
- HÖRNSCHEMEYER T. & STAFF H. 2001. — Review of Blattinopsidae (Protorthoptera) with description of new species from the Lower Permian of Niedermoschel (Germany). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 221: 81-109. <https://doi.org/10.1127/njgpa/221/2001/81>
- KOHLI M., LETSCH H., GREVE C., BÉTHOUX O., DEREGNAUCOURT I., LIU S., ZHOU X., DONATH A., MAYER C., PODSIADŁOWSKI L., GUNKEL S., MACHIDA R., NIEHUIS O., RUST J., WAPPLER T., YU X., MISOF B. & WARE J. 2021. — Evolutionary history and divergence times of Odonata (dragonflies and damselflies) revealed through transcriptomics. *iScience* 24: 103324. <https://doi.org/10.1016/j.isci.2021.103324>
- LAMEERE A. 1922. — Sur la nervation alaire des insectes. *Bulletin de la Classe des Sciences de l'Académie royale de Belgique* 8: 138-149.
- LAMEERE A. 1923. — On the wing-venation of insects. *Psyche* 30: 123-132. <https://doi.org/10.1155/1923/16920>
- LINNAEUS C. 1758. — *Systema nature per regna tria natura, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Laurentius Salvius, Stockholm, 824 p. <https://doi.org/10.5962/bhl.title.542>
- PROKOP J., KRZEMIŃSKI W., KRZEMIŃSKA E., HÖRNSCHEMEYER T., ILGER J.-M., BRAUCKMANN B., GRANDCOLAS P. & NEL A. 2014. — Late Palaeozoic Paoliida is the sister group of Dictyoptera (Insecta: Neoptera). *Journal of Systematic Palaeontology* 12: 601-622. <https://doi.org/10.1080/14772019.2013.823468>
- QUISPE L., ROQUES P., GARROUSTE R. & NEL A. 2022. — Carboniferous Blattinopsidae: revision of *Klebsiella* and new genus and species from Avion (Insecta, Paoliida). *Historical Biology* 34: 383-389. <https://doi.org/10.1080/08912963.2021.1916817>
- ROHDENDORF B. B. 1977. — O ratsionalizatsii nazvaniy taksonov vysokogo ranga v zoologii. *Paleontologicheskii Zhurnal* 1977: 14-22.
- SCHUBNEL T., PERDU L., ROQUES P., GARROUSTE R. & NEL A. 2019. — Two new stem-stoneflies discovered in the Pennsylvanian Avion locality, Pas-de-Calais, France (Insecta: 'Exopterygota'). *Alcheringa* 43: 430-435. <https://doi.org/10.1080/03115518.2019.1569159>
- SROKA P., ROSOVÁ K., LEIPNER A. & PROKOP J. 2025. — Early evolution of the stonefly lineage (Insecta, Plecoptera) revealed by a new diversity of Carboniferous stem-group species. *BMC Ecology and Evolution* 25: 107. <https://doi.org/10.1186/s12862-025-02411-w>
- TRÜMPER S., SCHNEIDER J. W., NEMYROVSKA T., KORN D., LINNEMANN U. G., REN D. & BÉTHOUX O. 2020. — Age and depositional environment of the Xiaheyan insect fauna, embedded in marine black shales (Early Pennsylvanian, China). *Palaeogeography, Palaeoclimatology, Palaeoecology* 538: 109444. <https://doi.org/10.1016/j.palaeo.2019.109444>
- WANG Y., YANG X., ENGEL M. S., HUO Q.-B., DU Y.-Z. & CAI C. 2025. — Reconstructing the evolutionary history of stoneflies: Phylogenetic insights and temporal dynamics. *iScience* 28: 113614. <https://doi.org/10.1016/j.isci.2025.113614>
- WOLFE J. A., DALEY A. C., LEGG D. A. & EDGEcombe G. D. 2016. — Fossil calibrations for the arthropod Tree of Life. *Earth-Science Reviews* 160: 43-110. <https://doi.org/10.1016/j.earscirev.2016.06.008>

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