



HAL
open science

New insects (Paoliida, Dictyoptera) from the Carboniferous outcrop of Tante Victoire in Var, France

André Nel, Romain Garrouste, Corentin Jouault

► To cite this version:

André Nel, Romain Garrouste, Corentin Jouault. New insects (Paoliida, Dictyoptera) from the Carboniferous outcrop of Tante Victoire in Var, France. *Alcheringa*, 2023, 47 (3), pp.305-314. 10.1080/03115518.2023.2258977 . insu-04260538

HAL Id: insu-04260538

<https://insu.hal.science/insu-04260538v1>

Submitted on 13 Dec 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

New insects (Paoliida, Dictyoptera) from the Carboniferous outcrop of Tante Victoire (Var, France)

André Nel, Romain Garrouste and Corentin Jouault

ABSTRACT

We introduce a novel paoliid, *Carbonidelia gallica* gen. et sp. nov., which may share close affinities with the ‘ideliid’ genus *Sojanidelia* Storozhenko, 1992. This new taxon is described from Gzhelian strata exposed at Tante Victoire (Var, France). Additionally, we present a remarkably well-preserved forewing from the same outcrop belonging to the phyloblattid genus and species *Anthracoblattina ensifer* cf. ‘variety *desguini*’. This species was previously known from the Gzhelian of Comentry (Allier, France). Therefore, this finding strengthens the Gzhelian age derived from the study of the palaeoflora at this outcrop. In this study, we also briefly delve into the inter- and intraspecific variability in the forewing venation of the ‘*Anthracoblattina gigantea-ensifera* group’. Furthermore, we challenge the classification of two Mesozoic roachoids, *Sobytie tungusicum* Vršanský, 2010 and *Pozabudnutie antiquorum* Hinkelman and Vršanský, 2022, which, in our view, do not belong to the Phyloblattidae family. Instead, they should be regarded as Dictyoptera of uncertain family affinities. A comprehensive revision of these species will be necessary to establish their precise taxonomic positions.

André Nel [anel@mnhn.fr], Romain Garrouste [romain.garrouste@mnhn.fr], Corentin Jouault [jouaultc0@gmail.com], Institut de Systématique, Évolution, Biodiversité (ISYEB) Muséum national d’Histoire naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, CP50, 57 rue Cuvier 75005, Paris, France; Univ. Rennes, CNRS, Géosciences

Rennes, UMR 6118, F-35000, Rennes, France; Institut des Sciences de l'Évolution (UMR 5554), Université de Montpellier, CNRS, F-34095 Montpellier, France.

KEYWORDS

Insecta; Polyneoptera; Paoliida; Phylloblattidae; Gzhelian; stratigraphy

THE CARBONIFEROUS is a key period for the evolution of insects, as it witnessed the diversification of all the major pterygote clades, including the Palaeoptera, Polyneoptera, Acercaria, and Holometabola (e.g., Misof *et al.* 2014; Tong *et al.* 2015; Montagna *et al.* 2019; Prokop *et al.* 2023). However, despite this importance, Carboniferous strata with diverse insect assemblages remain scarce (Schachat & Labandeira 2021: fig. 1). The discovery of new outcrops and deposits provides new perspectives to investigate and comprehensively document insect diversity during this critical period (Nel *et al.*, 2013). In France, there is a wealth of well-documented Carboniferous exposures teeming with fossils, including fossil insects (e.g., Nel & Roques 2021; Nel *et al.* 2023). The strata, where fossil insects are found, were typically associated with mining activities, and mainly located in the northeast and the central France (<https://paleobiodb.org/>). However, ongoing research suggests that the Provence-Alpes-Côte d'Azur may also host promising deposits.

In a recent effort aimed at cataloging newly found Carboniferous fossiliferous deposits in France and revisiting previously explored deposits, we conducted field research in the Var department. Our primary focus was on the small, historic iron quarry of Tante Victoire (Var department, France). This quarry had been initially investigated back in the 1990s, leading to the remarkable discovery of well-preserved preserved wings of Polyneoptera (Nel *et al.* 2022).

Herein, we describe two newfound fossils from this outcrop, which we recently linked to the laminated insectivorous layers. We identify these wings as a new genus and species of Paoliidae and to a phyloblattid roachoid used to precisely determine the age of the outcrop. We anticipate that forthcoming findings will further enrich the diversity of fossil insects documented from this promising locality. While studying these specimens, we have also identified some noteworthy discrepancies in the placement of some taxa within the family Phyloblattidae. In light of our understanding of the evolution of Dictyoptera, we provide commentary on these placements.

Material and methods

The new fossils were found during a recent field investigation in the ancient ironstone quarry of Tante Victoire, Six-Four-les-Plages, Var department. The specimens were photographed using a Canon 50D camera with an attached Canon 65 MPE camera lens and mounted on an automated stacking rail (StackShot), and all these images are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using Helicon Focus 6.7. The figures were composed with Adobe Illustrator CC2019 and Photoshop CC2019 software.

After the ‘Notice de la Carte Géologique à 1/5000, BRGM, France’ of Toulon, strata exposed in the small ancient iron quarry of Tante Victoire (Playes Massif, Six-Fours-les-Plages town, Var department) is of Gzhelian (late Stephanian) age. This age was deduced from studies of the palaeoflora, notably composed of *Pecopteris*, *Calamites*, *Walchia* and *Sigillaria*. The new fossils are stored in the Palaeontological collection of the Muséum National d'Histoire Naturelle (MNHN.F), Paris, France.

Wing venation nomenclature follows Schubnel *et al.* (2020), especially concerning the presence of a postcubital vein in Pterygota. Abbreviations are as follows: A anal vein(s); arc

arculus (i.e., reinforced oblique crossvein between M and CuA); C costal vein; CuA cubitus anterior; CuP cubitus posterior; M median vein; MA median anterior; MP median posterior; PCu postcubital vein; RA radius anterior; RP radius posterior; ScP subcostal posterior.

Published work and nomenclatural acts are registered in ZooBank (<http://zoobank.org/>, last access: 07/09/2023), with the following LSID (reference):
urn:lsid:zoobank.org:pub:8DFEA4D0-63A5-46AF-AD0B-B8F0F131E590.

Systematic palaeontology

ORDER PAOLIIDA Handlirsch, 1906

FAMILY PAOLIIDAE Handlirsch, 1906

Remarks

Storozhenko (1992, 1998) considered the family Ideliidae as a lineage of the ‘Grylloblattida’. However, Prokop *et al.* (2014) argued that some genera within the family Ideliidae were more appropriately classified within the family Paoliidae (order Paoliida). Consequently, the following genera were subsequently transferred: *Stenaropodites* Martynov, 1928, *Aenigmidelia* Sharov, 1961, *Archidelia* Sharov, 1961, *Sojanidelia* Storozhenko, 1992, *Micaidelia* Aristov, 2004, *Acropermula* Aristov & Storozhenko, 2011, *Mongoloidelia* Storozhenko, 1992, and *Sylvidelia* Martynov, 1940.

The ‘Ideliidae’ as defined by Storozhenko (1998) appears to encompass a group of taxa that is likely polyphyletic. Notably, genera such as *Ideliopsina* Storozhenko, 1996 differ greatly from *Sojanidelia* in their very broad costal area with very long veinlets *versus* a very narrow area with short veinlets (Storozhenko, 1998; Oyama *et al.*, 2023). The speciose genus *Sojanidelia* is, to date, only known from the Permian of the Russian Federation (Storozhenko, 1992, 1998; Krassilov & Rasnitsyn, 1996).

Recently, Oyama *et al.* (2023: 209) raised concerns regarding the attribution of some Ideliidae to the Paoliida, as proposed by Prokop *et al.* (2013). They argued against this attribution by stating that ‘the Paoliida are characterized by nearly identical fore- and hind wings. However, Ideliidae species for which hind wings are known, such as *Stenaropodites sojanensis* Storozhenko, 1992, *S. mistshenkoi* Storozhenko, 1992 and *Archidelia elongata* Sharov, 1961 (see original descriptions), possess a large plicatum’. However, it is worth noting that the challenge with this assertion lies in the fact that the hind wings attributed by Storozhenko (1992) or Sharov (1961: 173) to these species, are isolated ones. Their current attributions to the same species as the type forewings lack substantial evidence. Furthermore, the other Ideliidae that Prokop *et al.* (2013) attributed to the Paoliida, based on putative synapomorphies, are also represented by isolated forewings. Therefore, the argument of Oyama *et al.* (2023) in refutation to Prokop *et al.* (2013) appears to be somewhat inconclusive.

***Carbonidelia* gen. nov.**

urn:lsid:zoobank.org:act:443ED2CE-01AB-420B-B75A-B228BA3ED102

Type species

Carbonidelia gallica gen et sp. nov.

Diagnosis

Wing characters only. Costal area very narrow in distal half of wing; ScP and RA simple; all branches of R, M, and CuA very long, subparallel and nearly straight, except some sigmoidal branches of MA and MP; posterior branches of MP and CuA subparallel to posterior wing margin.

Etymology

The genus name is a neologism referring to the Carboniferous period, and the suffix ‘idelia’ commonly used for paoliid taxa. Gender feminine.

Carbonidelia gallica gen. et sp. nov.

(Fig. 1)

Diagnosis

As for the genus (*vide supra*). In addition, wing rather elongate and narrow, 11.6 mm wide and ca. 38 mm long.

Etymology

Named after the Latin adjective ‘*gallica*’ related to Gauls, medieval Franks, and by extension to France.

Holotype

MNHN.F.A71369 (part and counterpart of a wing, with base and extreme apex missing), stored at Muséum national d’Histoire naturelle, Paris, France.

Type locality and age

Tante Victoire, Var department, France, Gzhelian (Pennsylvanian), Carboniferous.

Zoobank

urn:lsid:zoobank.org:act:7B7D10E4-FFD9-4EAF-909C-4CEC37E7BC46

Description

Preserved part of wing 35.7 mm long and 11.6 mm wide; costal area very narrow, 0.8 mm wide, with a series of very numerous short crossveins between C and ScP (most perpendicular to ScP); ScP very long and simple, slightly curved; RA very long and simple, parallel to ScP, area between RA and ScP very narrow, 1.0 mm wide (both ScP and RA probably ending on costal margin close to wing apex); RP separating from RA close to wing base, with two very long branches parallel to RA (likely ending at wing apex); MA very long, divided into three very long branches, mostly parallel to RP but sigmoidal apically; MP base apparently directed towards MA base, forked basally into two main branches, anterior branch divided into three branches (the first two distally sigmoidal), posterior branch forked into two weakly curved parallel branches, the posterior-most one being closely parallel to wing margin; CuA1 with two long branches, also closely parallel to wing margin; CuA2 simple, closely parallel to wing margin, with its base strongly approximating CuA1 (probably emerging from a common stem with it); very numerous and short crossveins, all simple between longitudinal veins.

Remarks

This fossil is unmistakably a wing belonging to the Polyneoptera. The very narrow area along the posterior margin would argue for a forewing, and the short costal area would strengthen this attribution, albeit partially preserved. However, due to the poor preservation of the costal and the anal areas, it could also be a hind wing. It is important to note that all the veins have the same convexity, making it impossible to determine their exact nature on the basis of this criterion. The nature of the veins posterior to the anterior-most branch of M is based on our understanding of Polyneoptera wing venation.

The very long and simple ScP and a very narrow costal area exclude affinities with Dictyoptera (either fore- or hind wings). The very numerous short crossveins support affinities with some Archaeorthoptera, Paoliida, or 'Grylloblattida'. The fossil is unlikely an Archaeorthoptera because the posterior-most longitudinal veins (CuA1 and CuA2) do not approximate the median vein basally, unlike the situation in the latter superorder. The very distinctive shape of CuA, with a forked anterior branch and a simple posterior one, fits quite well with the pattern in many 'Grylloblattida' and Paoliida. Also, the character 'MP and CuA closely parallel to the posterior margin of the wing' is encountered only in a few 'Grylloblattida' or Paoliida, viz., the liomopterid *Mioloptera stuchenbergi* Riek, 1973, and the 'ideliids' *Sojanidelia kostinae* (Sharov, 1961) and *Sojanidelia lineata* (Storozhenko 1992).

The new fossil differs from *Mioloptera* (and the other Liomopteridae) in the narrow costal area and the absence of additional long branches of ScP and RA. On the other hand, *Sojanidelia kostinae* strongly resembles the new fossil in the narrow costal area, straight and simple ScP and RA, all longitudinal veins subparallel in the distal part of the wing, and the base of RP located in the basal third of the wing (Sharov 1961). The new fossil shares with *Sojanidelia longula* Storozhenko, 1992 a distally very narrow costal area, but differs from it because of its very long main vein branches and its veins closely parallel to the posterior wing margin in the posterior half of the wing.

Therefore, the new fossil can be fairly accurately attributed to the 'Ideliidae', because of its great similarities with *Sojanidelia kostinae* and *Sojanidelia longula*. *Sojanidelia* currently comprises taxa with very different forewing venations. For instance, *Sojanidelia kostinae* does not resemble *Sojanidelia makarkini* Storozhenko, 1992 or *Sojanidelia vorkutensis* Storozhenko, 1992 (see Storozhenko 1998). We consider that the monophyly of this genus is not certain.

Additionally, the new fossil differs from all species in *Sojanidelia*, except *S. fasciata* Storozhenko, 1992 because of its vein CuA1 having only two branches (*versus* at least three in the other species), and from all *Sojanidelia* species because its posterior branch of M is branched (*versus* simple). The new fossil has some sigmoidal branches of M whereas they are all nearly straight in *Sojanidelia*. We consider that this fossil corresponds to a new genus that we tentatively place in Paoliidae, probably close phylogenetically to the genus *Sojanidelia*, with which it shares a putative synapomorphy in the special shape of the posterior-most veins (MP and CuA) in the distal half of the wing.

Given the limited information available regarding the extreme base of the wing, it is conceivable that what we have interpreted as the costal margin could alternatively be the posterior margin and vice-versa. Under this hypothesis, the vein previously interpreted as the cubital vein would become the subcostal and the vein initially interpreted as the ScP might be a branch either of CuA or of M. In this scenario, the very broad subcostal area with multiple ScP branches would suggest affinities with the Dictyoptera. However several inconsistencies contradict this hypothesis: the cubital and median veins would then run towards the anterior margin of the wing, a highly unlikely arrangement in all Palaeozoic insects; the CuA would be reduced to a simple vein, a character never observed in fossil Dictyoptera; the presence of two simple parallel veins closely parallel to the posterior wing margin is unprecedented among Palaeozoic insects, especially within the Dictyoptera. Consequently, this interpretation would imply a completely unique wing venation pattern that does not correspond to any known precedent. Conversely, our interpretation aligns reasonably well with an attribution to a Paoliidae taxon close to *Sojanidelia*, also a more parsimonious scenario.

CLADE HOLOPANDICTYOPTERA Kluge, 2010

(= total group of extant Dictyoptera Leach, 1815)

PLESIOMORPHON EOBLATTODEA Laurentiaux, 1959 (*sensu* Li, 2019)

FAMILY PHYLOBLATTIDAE Schneider, 1983

Remark

The specimens of Carboniferous Phyloblattidae listed under and formerly housed in the collection of the 'Ecole des Mines de Paris' are now stored in the collection of Paleontology of the University of Lyon (curator Emmanuel Robert):

- Holotype of *Platyblattina ampla* Laurentiaux, 1950, (prov. Fontanes, Gard Basin; Coll. Grand'Eury) (Laurentiaux, 1950: 74, pl. 3, fig. 3a–b).
- Holotype of *Phyloblatta fontanensis* (Meunier, 1906) (prov. Fontanes, Gard Basin; Coll. Grand'Eury) (Laurentiaux, 1950: 70–71, pl. 2, fig. 1a–b).

Anthracoblattina Scudder, 1879

Anthracoblattina ensifer Brongniart, 1894, cf. 'variety *desguini* Meunier, 1921'

(Fig. 2)

Material

Specimen MNHN.F.A71368 (part and counterpart of a nearly complete forewing, only extreme base and extreme apex missing), stored at Muséum national d'Histoire naturelle, Paris, France.

Type locality and age

Tante Victoire, Var department, France, Gzhelian (Pennsylvanian), Carboniferous.

Description

Forewing *ca* 39.5 mm long, 12.5 mm wide; costal area 3.5 mm wide, strip-like, up to about 90% of forewing length; ScP anteriorly pectinate, with nearly all branches simple and ending at anterior wing margin; R slightly sigmoidal; RA and RP separating *ca* 17.7 mm distad wing base, slightly basad fork of M; RA with at least three weak branches likely terminating at anterior wing margin; RP likely ending at wing apex, with at least two branches; M not sigmoidal, with at least four apical branches, and covering a narrow area; CuA base located 4.4 mm distad wing base, CuA covering a broad area, with *ca* 12 branches; CuP weakly curved; veins in anal area parallel to CuP and ending at posterior margin of wing.

Remarks

The absence of an oblique crossvein between M and CuA (arculus) and the very long distal-most branch of ScP support affinities with the families Subioblattidae Schneider, 1983, Phyloblattidae Schneider, 1983, Compsoblattidae Schneider, 1978 and Spiloblattinidae Handlirsch, 1906, and exclude affinities with Archimylacridae Handlirsch, 1906, Gyroblattidae Durden, 1969, Necymylacridae Durden, 1969, Poroblattinidae Handlirsch, 1906 and Mylacridae Scudder, 1885 (Handlirsch 1906; Schneider 1983a, b; Schneider & Rößler 2023).

Affinities of the new fossil with Subioblattidae are excluded because its R does not curve strongly and its ScP is approaching the wing apex (Papier *et al.* 1994; Papier & Nel 2001).

Nel *et al.* (2022: 7) indicated that ‘the diagnoses of the three families Phyloblattidae, Compsoblattidae, and Spiloblattinidae are very similar and would hardly justify families’ separations’. This comment highlights the lack of apomorphy or characters to support these clades.

Belahmira *et al.* (2019) proposed the following diagnosis for the family Compsoblattidae (unique genus *Compsoblatta* Schlechtendal in Handlirsch 1906–1908): “elongate ellipsoidal forewings of about 20–35 mm in length. Costal field strip-like, up to about 60–70% of forewing length. ScP pectinate, branches about 45° inclined to the apex and ending at the anterior wing margin. R sigmoidal, R branches terminate at anterior wing margin. M sigmoidal, multiple forked, branches covering an area extending from the wing tip to the transition between wing tip and posterior wing margin. CuA strongly sigmoidal. First CuA twigs arise by branching from CuA stem and rarely forked; all further branches arise by furcation. CuP(+PCu) regularly bended”. The general venation pattern of *Compsoblatta* is similar to that of *Phyloblatta*, but contrasts with the latter genus in the cross-venation of the basal three-quarters of the wings composed of seams formed by crossvein bases along the main veins and their branches; the remaining wing surface shows a delicate irregularly reticulated crossvenation. In contrast to the spiloblattinids, which show similar crossvein seams, the areas between the main veins are not distinctly broadened, and the venation is generally denser in compsoblattids. The new fossil differs strongly from *Compsoblatta* as follows: forewing larger, up to 40 mm long; costal field strip-like, and up to 90% of forewing length; R weakly sigmoidal; only three weak R branches terminating at anterior wing margin; M not sigmoidal, not multi-forked, and covering a narrow area.

Schneider *et al.* (2021) proposed an emended diagnosis for Spiloblattinidae: “Phyloblattid-like wing venation pattern but with a much lower number of veins and with extended fields between the main veins. Subcostal field strip-like. ScP pectinate, branches end inclined at the anterior wing margin. R sigmoidal, often with distinct RA, R branches terminate at anterior wing margin. M sigmoidal, multiple-forked, often with distinct MA; M branches covering an area extending from the wing tip to the transition between the wing tip and posterior wing margin. CuA long sigmoidal. First CuA sigmoidal. CuA twigs arise by

branching from CuA stem and are rarely forked, all further branches arise by furcation. CuP regularly bent. Anal field with regularly spaced and bent An veins. Most diagnostic is a fenestrate colour pattern consisting of pale areas of various extents between the main veins and their branches. The pale areas do not display a distinct cross-venation. Cross-venation outside the pale areas consists of cross-vein stumps, forming seams along the veins, and in larger dark fields it consists of anastomosing-striate to irregularly reticulate cross veins". The new fossil does not show a particular pattern of coloration (problem of fossilization or uniform original coloration of the wing). As for the previous families, it differs from the Spiloblattinidae in the R and M not being sigmoidal; the R with at most very few and weak branches ending into the anterior margin of the wing; and the M covering a narrow area. The wing venation of the new fossil also differs from the old diagnosis of the Spiloblattinidae proposed by Vishniakova (1993).

Among the Phyloblattidae, Belahmira *et al.* (2019) proposed the following diagnosis for *Phyloblatta* Handlirsch, 1906: "elongate ellipsoidal forewings of about 10–35 mm in length. Costal field strip-like, up to about 70% of forewing length. ScP pectinate; branches end at the anterior wing margin. R sigmoidal; R branches terminate at anterior margin of wing. M sigmoidal, multiple-forked, branches covering an area extending from the wing tip to the transition between wing tip and posterior wing margin. CuA sigmoidal. First CuA twigs arise by branching from CuA stem and are rarely forked; all further branches arise by furcation. CuP(+PCu) regularly bent. Cross-venation (archedictyon) reticulate to anastomosing striate". In the new fossil, ScP covers up to 90% of the wing length; R and M are not sigmoidal but nearly straight; M covers a very small area; and only a few weak R branches terminate at the anterior margin of the wing, which excludes affinities with *Phyloblatta*. Affinities with *Kunguroblattina* Martynov, 1930, *Kashmiroblattina* Verma, 1967,

Aissoblatta Handlirsch, 1904, and *Xenoblatta* Handlirsch, 1906 are also excluded for the same reasons (see Schneider 1983a; Schneider *et al.* 2004).

The majority of the species of *Anthracoblattina* Scudder, 1879 also differ from the new fossil in the ScP reaching at most 70% of wing length and numerous branches of R terminating at the anterior margin of the wing. But some specimens currently attributed to *Anthracoblattina ensifer* Brongniart, 1894 from Commeny better fit with the new fossil in having a ScP reaching around 80–90% of wing length, a RA with only three-four anterior branches, a RP covering a narrow area and a M also covering a narrow area. These have been considered as varieties of *A. ensifer* by Meunier (1921), *viz.*, *A. ensifer desguini* Meunier, 1921 (ScP reaching more than 90% of wing length, RA with four branches) (Fig. 3A), *A. ensifer* var. 2 (Meunier, 1921: fig. 39), and *A. ensifer* var. 3 (Meunier, 1921: fig. 40), and *A. ensifer elegantissima* Meunier, 1921 (ScP reaching 80% of wing length and RA with three branches) (Fig. 3B), whereas the type of *A. ensifer ensifer* has a shorter ScP (reaching *ca* 75% of wing length), and RA with six anterior branches (Fig. 4). Thus, we could attribute the new fossil to *Anthracoblattina ensifer* possibly variety *desguini*. The wing dimensions also fit well with those of the *A. ensifer* specimens. Schneider (1983a-b) considered that *Anthracoblattina ensifer* can be grouped together with *A. gigantea* Brongniart, 1894 in the ‘*Anthracoblattina gigantea-ensifera*- Gruppe’, but the syntype of *A. gigantea* has a much shorter ScP, reaching only 75% of wing length, and a RA with six branches (Fig. 5). Nevertheless, the limits between the different ‘species’ or ‘varieties’ in this complex are very poorly grounded and would greatly benefit from a more comprehensive morphometric analysis of their venation. Therefore, attributing the new fossil to the specific ‘variety’ *desguini* is evidently tentative and carries limited significance.

Discussion

Systematic considerations on the family Phyloblattidae

The good delimitation of fossil clades is of primary importance in paleobiology. They are used to infer paleobiogeographic scenarios, dynamics of lineages, and interactions with their environment (e.g., Garrouste *et al.* 2016; Jouault *et al.* 2022a; Aria *et al.* 2023). However, many polyneopteran lineages are poorly defined in the Paleozoic because of the variability of their wing venation and of the limited number of available specimens (Béthoux 2005; Jouault *et al.* 2021).

Phyloblattidae are no exception to this observation and the attributions of several fossils to this group in the past decade are questionable. For instance, the genus and species *Sobytie tungusicum*, from the Permian-Triassic boundary, has a much-reduced ScP compared to those of the other Phyloblattidae, *plus* there are intercalaries between the branches of the main veins (Vršanský 2010). However, these characters are not present in the other representatives of the family, suggesting that the placement of this taxon in Phyloblattidae is questionable.

More recently, *Pozabudnutie antiquorum* was described from the mid-Cretaceous and attributed to Phyloblattidae (Vršanský *et al.* 2022). This placement is not supported by apomorphic characters but rather by a series of symplesiomorphies questioning its validity. It was also suggested that *Pozabudnutie* was an ootheca-producing Dictyoptera (such as modern Blattodea), but Phyloblattidae with preserved bodies have long ovipositors (e.g., Fig. 4, specimen of *Anthracoblattina ensifer* figured by Laurentiaux 1951). The attribution of *Pozabudnutie* to Phyloblattidae would imply that this family contains taxa using two types of oviposition and thus that the production of ootheca and the reduction of the ovipositor would not be apomorphies of the crown group of Blattodea, which is, *per se* not a problem, but would increase the complexity of our understanding of Dictyoptera evolution. This statement's second result will be to consider the Phyloblattidae not as a clade but as a grade

towards the Blattodea. Indeed the wing venation of *Pozabudnutie* differs strongly from those of the Palaeozoic Phylloblattidae.

Thus we consider that *Sobytie tungusicum* and *Pozabudnutie antiquorum* do not belong to the Phylloblattidae, and must be considered as Dictyoptera of uncertain families. Their revision will be necessary to precise their positions.

The Gzhelian age of the Tante Victoire locality

Some fossil insects are informative and used as additional evidence to clarify the age of a fossil deposit. In fact, the life spans of certain clades, when correctly delineated, can be used to add stratigraphic constraints on the age of a deposit (e.g., Jouault *et al.* 2022b; Park *et al.* 2022).

Dictyoptera have been used repeatedly for insect-based biostratigraphy (Jarzembowski & Schneider 2007; Schneider & Rößler 2023). Their complex wing venation, their abundance, and their good preservation in many Carboniferous deposits allowed us to understand the intraspecific variability of some species and led to the descriptions of ‘varieties’ (Schneider 1983a-b). Among the abundant and speciose Carboniferous-Permian Dictyoptera, the genus *Anthracoblattina* provides valuable stratigraphic information. For instance, the temporal ranges of some of its constitutive species are short (e.g., *Anthracoblattina ensifer*) allowing for age correlations between deposits. In the present study, we described a new specimen of *Anthracoblattina ensifer* tentatively referred to the variety *desguini*. This variety is also known from the uppermost Carboniferous of Commentry (303.4 to 298.9 Ma, Gzhelian, France) (Brongniart 1894), suggesting that the two deposits are of the age, and corroborating the dating obtained with the study of the paleoflora.

Conclusion

Our fieldwork research suggested that the locality of Tante Victoire is promising for future insect discoveries. We added to the biodiversity of this deposit by describing a new paoliid *Carbonidelia gallica* gen. et sp. nov., and a roachoid attributed to *Anthracoblattina ensifer* and possibly belonging to the variety *desguini*. This specimen provides additional evidence for the Gzhelian age of the Tante Victoire locality, which was initially estimated using paleofloral studies. This correlation also confirms that well-defined insect clades can be used for stratigraphic comparisons and suggests that Carboniferous Dictyoptera, such as Phylloblattidae, may provide valuable stratigraphic evidence when their limits will be clarified.

Acknowledgments

We thank an anonymous referee, Dr Andrew Ross, and Dr Benjamin Kear for their useful remarks on the first version of the paper. We sincerely thank the Père Michel Denis, curator of the Notre-Dame de Pépiole (Six-Four-les-Plages) to which the small ancient iron quarry belongs, for the authorisation to search after sediments and stratigraphy for future field works. We also thank Dr. Emmanuel Robert for giving us the information on the locations of two roachoids from the Gard Basin, and Dr. Antoine Mantilleri (MNHN) for the access to imaging facilities. We thank the Institut de Systématique, Évolution, Biodiversité (ISYEB, MNHN) for financially supporting our fieldwork. The digitalization of the specimens MNHN.F.R51426, MNHN.F.R51421, MNHN.F.R51422, and MNHN.F.R51423 was possible thanks to the project RECOLNAT (ANR-11-INBS-0004). This work forms a part of CJ's Ph.D.

ORCID

André Nel <https://orcid.org/0000-0002-4241-7651>

Romain Garrouste <https://orcid.org/0000-0002-0880-5781>

Corentin Jouault <https://orcid.org/0000-0002-3680-5172>

References

- ARIA, C., JOUAULT, C., PERRICHOT, V. & NEL, A., 2023. The megathermal ant genus *Gesomyrmex* (Formicidae: Formicinae), palaeoindicator of wide latitudinal biome homogeneity during the PETM. *Geological Magazine* 160, 187–197. <https://doi.org/10.1017/S0016756822001248>
- BELAHMIRA, A., SCHNEIDER, J.W., SCHOLZE, F. & SABER, H., 2019. Phyloblattidae and Compsoblattidae (Insecta, Blattodea) from the late Carboniferous Souss Basin, Morocco. *Journal of Paleontology* 93, 945–965. <https://doi.org/10.1017/jpa.2019.20>
- BÉTHOUX, O., 2005. Wing venation pattern of Plecoptera (Insecta: Neoptera). *Illiesia* 1, 52–81.
- BRONGNIART, C., 1894. Recherches pour servir à l'histoire des insectes fossiles des temps primaires, précédées d'une étude sur la nervation des ailes des insectes. *Bulletin de la Société d'Industrie Minérale de Saint-Etienne* (3) 7, 1–494.
- 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>
- HANLIRSCH, A., 1906-1908. Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein Handbuch für Paläontologen und Zoologen. Engelmann, V.W. publ., Leipzig, 1430 pp.
- GARROUSTE, R., HUGEL, S., JACQUELIN, L., ROSTAN, P., STEYER, J.-S., DESUTTER-GRANDCOLAS, L. & NEL, A., 2016. Insect mimicry of plants dates back to the Permian. *Nature Communications* 7, 13735. <https://doi.org/10.1038/ncomms13735>

- JARZEMBOWSKI, E. & SCHNEIDER, J., 2007. The stratigraphical potential of blattodean insects from the late Carboniferous of southern Britain. *Geological Magazine* 144, 449–456. <https://doi.org/10.1017/S0016756807003421>
- JOUAULT, C., LEGENDRE, F., CONDAMINE, F.L. & NEL, A., 2021. A new stonefly species (Plecoptera: Perlodidae) from Eocene Baltic amber and questions on the wing venation potential for species diagnostic of fossil Plecoptera. *Palaeoentomology* 4, 243–256. <https://doi.org/10.11646/palaeoentomology.4.3.12>
- JOUAULT, C., NAM, G.-S. & NEL, A., 2022b. *Koreaphlebia* gen. nov. (Odonatoptera: Triadophlebiomorpha): new evidence of a Triassic age for the Amisan Formation in Korea. *Historical Biology* <https://doi.org/10.1080/08912963.2022.2102492>
- JOUAULT, C., NEL, A., PERRICHOT, V., LEGENDRE, F. & CONDAMINE, F.L., 2022a. Multiple drivers and lineage-specific insect extinctions during the Permo–Triassic. *Nature Communications* 13, 7512. <https://doi.org/10.1038/s41467-022-35284-4>
- KRASSILOV, V.A. & RASNITSYN, A.P., 1996. Pollen in the guts of Permian insects: first evidence of pollinivory and its evolutionary significance. *Lethaia* 29, 369–372. <https://doi.org/10.1111/j.1502-3931.1996.tb01672.x>
- LAURENTIAUX, D., 1950. Les insectes des bassins houillers du Gard et de la Loire. *Annales de Paléontologie* 36, 63–84.
- LAURENTIAUX, D., 1951. Le problème des blattes paléozoïques à ovipositeur externe. *Annales de Paléontologie* 37, 187–196.
- MEUNIER, F., 1921. Nouvelles recherches sur les insectes houillers de Commentry (Allier). (troisième partie) Orthoptères Blattidae. *Annales de Paléontologie* 10, 59–168.
- MISOF, B., LIU, SHANLIN, MEUSEMANN, K., PETERS, R.S., DONATH, A., MAYER, C., FRANSEN, P.B., WARE, J., FLOURI, T., BEUTEL, R.G., NIEHUIS, O., PETERSEN, M., IZQUIERDO-CARRASCO, F., WAPPLER, T., RUST, J., the 1KITE consortium (83 other authors), WANG,

- J., KJER, K.M. & ZHOU, X., 2014. Phylogenomics resolves the timing and pattern of insect evolution. *Science* 346, 763–767. <https://doi.org/10.1126/science.1257570>
- MONTAGNA, M., TONG, K.J., MAGOGA, G., STRADA, L., TINTORI, A., HO, S.Y.W. & LO, N., 2019. Recalibration of the insect evolutionary time scale using Monte San Giorgio fossils suggests survival of key lineages through the End-Permian Extinction. *Proceedings of the Royal Society B* 286 (20191854), 1–9. <http://doi.org/10.1098/rspb.2019.1854>
- NEL, A. & ROQUES, P., 2021. A new family and two new genera from Avion, Northern France, confirm the high Moscovian (late Carboniferous) diversity of the insect superorder Archaeorthoptera. *Acta Palaeontologica Polonica* 66, 879–884. <https://doi.org/10.4202/app.00940.2021>
- NEL, A., GARROUSTE, R., PEÑALVER, E., HERNÁNDEZ-ORÚE, A. & JOUAULT, C., 2022. Discovery of the first blattinopsids of the genus *Glaphyrophlebia* Handlirsch, 1906 (Paoliida: Blattinopsidae) in the Upper Carboniferous of Southern France and Spain and hypothesis on the diversification of the family. *Diversity* 14, 1–14. <https://doi.org/10.3390/d14121129>
- NEL, A., ROQUES, P., NEL, P., PROKIN, A.A., BOURGOIN, T., PROKOP, J., SZWEDO, J., AZAR, D., DESUTTER-GRANDCOLAS, L., WAPPLER, T., GARROUSTE, R., COTY, D., HUANG, DIYING, ENGEL, M. & KIREJTSHUK, A.G., 2013. The earliest known holometabolous insects. *Nature* 503, 257–261. <https://doi.org/10.1038/nature12629>
- NEL, A., SANTOS, A.A., HERNÁNDEZ-ORÚE, A., WAPPLER, T. & DIEZ, J.B., 2022. The first representative of the roachoid family Spiloblattinidae (Insecta, Dictyoptera) from the Late Pennsylvanian of the Iberian Peninsula. *Insects* 13, 1–14. <https://doi.org/10.3390/insects13090828>

- NEL, A., VALLOIS, B., & DUQUESNE, H., 2023. A new archaeorthopteran family from the upper Carboniferous of La Mure (France). *Historical Biology* 35, 264–267. <https://doi.org/10.1080/08912963.2022.2034804>
- OYAMA, N., SINODA, K., TAKAHASHI, H., DOI, E. & BÉTHOUX, O., 2023. A new species of the Triassic genus *Ideliopsina* (Grylloblattida: Ideliidae) from the Ominé locality (Momonoki Formation, southwest Japan). *Palaeoentomology* 6, 205–213. <https://doi.org/10.11646/palaeoentomology.6.2.12>
- PAPIER, F., GRAUVOGEL-STAMM, L. & NEL, A., 1994. *Subioblatta undulata* n. sp., une nouvelle blatte (Subioblattidae Schneider) du Buntsandstein supérieur (Anisien) des Vosges (France). Morphologie, systématique et affinités. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 5, 277–290.
- PAPIER, F. & NEL, A., 2001. Les Subioblattidae (Blattodea, Insecta) du Trias d'Asie Centrale. *Paläontologische Zeitschrift* 74, 533–542. <https://doi.org/10.1007/BF02988160>
- PARK, T., KIM, D., NAM, G. & LEE, M., 2022. A new titanopteran *Magnatitan jongheoni* n. gen. n. sp. from southwestern Korean Peninsula. *Journal of Paleontology* 96, 1111–1118. <https://doi.org/10.1017/jpa.2022.30>
- PROKOP, J., KRZEMINSKI, W., KRZEMINSKA, E., HÖRNSCHEMEYER, T., ILGER, J.-M., BRAUCKMANN, C., 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>
- PROKOP, J., NEL, A. & ENGEL, M.S., 2023. Diversity, form, and postembryonic development of Paleozoic insects. *Annual Review of Entomology* 68, 401–429. <https://doi.org/10.1146/annurev-ento-120220-022637>

- SCHACHAT, S.R. & LABANDEIRA, C.C., 2021. Are insects heading toward their first mass extinction? Distinguishing turnover from crises in their fossil record. *Annals of the Entomological Society of America* 114, 99–118. <https://doi.org/10.1093/aesa/saaa042>
- SCHNEIDER, J.W., 1983a. Die Blattodea (Insecta) des Paläozoikums, 1: Systematik, Ökologie und Biostratigraphie. *Freiberger Forschungshefte (C)* 382, 107–146.
- Schneider, J.W. 1983b. Taxonomie, Biostratigraphie und Palökologie der Blattodea-Fauna aus dem Stefan von Commeny (Frankreich). Versuch einer Revision. *Freiberger Forschungshefte (C)* 384, 77–100.
- SCHNEIDER, J.W., LUCAS, S.G. & ROWLAND, J.M., 2004. The Blattida (Insecta) fauna of Carrizo Arroyo, New Mexico – Biostratigraphic link between marine and nonmarine Pennsylvanian/Permian boundary profiles. In: LUCAS, S.G. & ZEIGLER, K.E. (eds). Carboniferous-Permian transition at Carrizo Arroyo, Central New Mexico. *Bulletin of the New Mexico Museum of Natural History and Science* 25, 247–262.
- SCHNEIDER, J.W. & RÖBLER, R., 2023. The early history of giant cockroaches: gyroblattids and necmylacrids (Blattodea) of the Late Carboniferous. *Diversity* 15 1–41. <https://doi.org/10.3390/d15030429>
- SCHNEIDER, J.W., SCHOLZE, F., GERMANN, S. & LUCAS, S.G., 2021. The Late Pennsylvanian nearshore insect fauna of the Kinney Brick Quarry invertebrate and vertebrate fossil lagerstätte, New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 84, 255–285.
- SCHUBNEL, T., DESUTTER-GRANDCOLAS, L., LEGENDRE, F., PROKOP, J., MAZURIER, A., GARROUSTE, R., GRANDCOLAS, P. & NEL, A., 2020. To be or not to be: postcubital vein in insects revealed by microtomography. *Systematic Entomology* 45, 327–336. <https://doi.org/10.1111/syen.12399>

- SHAROV, A.G. 1961. [Order Plecoptera.] pp. 166–175. In: ROHDENDORF, B.B., BECKER-MIGDISOVA, E.E., MARTYNOVA, O.M. & SHAROV, A.G. (eds). Paleozoiskie nasekomye Kuznetskogo basseina [Paleozoic insects of the Kuznetsk basin.] *Trudy Paleontologicheskogo Instituta Akademii nauk SSSR* 85.
- STOROZHENKO, S.Yu., 1992. Permian fossil insects of North-East Europe – New and little-known Ideliidae (Insecta, Plecopteroidea, Grylloblattida). *Entomologica Fennica* 3, 21–39.
- STOROZHENKO, S.Yu., 1998. Sistematika, filogeniya i evolyutsiya grilloblattidovykh nasekomykh (Insecta: Grylloblattida) [Systematics, phylogeny and evolution of the grylloblattids (Insecta: Grylloblattida).] Dal'nauka, Vladivostok, 1–207. [in Russian]
- TONG, K.J., DUCHÊNE, S., HO, S.Y.W. & LO, N., 2015. Comment on “Phylogenomics resolves the timing and pattern of insect evolution”. *Science* 349, 487-b. <https://doi.org/10.1126/science.aaa5460>
- VRŠANSKÝ, P., 2010. A new genus and species of cockroach (Blattida: Phyloblattidae) from the Permian/Triassic boundary beds of Tunguska Basin in eastern Siberia, Russia. *Zootaxa* 2353, 55–61. <https://doi.org/10.11646/zootaxa.2353.1.5>
- VRŠANSKÝ, P., ARISTOV, D., HAIN, M., KÚDELOVÁ, T., KÚDELA, M., METSCHER, B., PALKOVÁ, H., KÁČEROVÁ, J. & HINKELMAN, J., 2022. Longest-surviving Carboniferous-family insect found in Mesozoic amber. *Biologia* 78, 1611–1626. <https://doi.org/10.1007/s11756-022-01192-7>

Figure 1. *Carbonidelia gallica* gen. et sp. nov., holotype MNHN.F.A71369. **A**, Photograph of part, light from above. **B**, Photograph of part, grazing light. **C**, Photograph of counterpart. **D**, Reconstruction. Scale bars represent 2 mm.

Figure 2. *Anthracoblattina ensifer* cf. *desguini* Meunier, 1921, specimen MNHN.F.A71368. **A**, Photograph of part. **B**, Photograph of counterpart. Scale bars represent 5 mm.

Figure 3. *Anthracoblattina ensifer* from Commentry. **A**, Photograph of *A. ensifer desguini* Meunier, 1921, specimen MNHN.F.R51426 (credits: RECOLNAT: Gaëlle Doitteau). **B**, Photograph of *A. ensifer elegantissima* Meunier, 1921, specimen MNHN.F.R51421 (credits: RECOLNAT: Gaëlle Doitteau). Scale bars represent 10 mm.

Figure 4. *Anthracoblattina ensifer ensifer* Brongniart 1894, specimen MNHN.F.R51422, Commentry (credits: RECOLNAT: Gaëlle Doitteau). Photograph. Scale bar represents 10 mm.

Figure 5. *Anthracoblattina gigantea* Brongniart 1894, specimen MNHN.F.R51423, Commentry (credits: RECOLNAT: Gaëlle Doitteau). Photograph. Scale bar represents 10 mm.