

## A SPILOBLATTINID (HOLOPANDICTYOPTERA) HIND WING FROM THE CARBONIFEROUS OF SAN GIORGIO BASIN (SW SARDINIA): THE OLDEST FOSSIL INSECT FROM ITALY

ANGELO IANNI<sup>1</sup>, ANDRÉ NEL<sup>2</sup>, GIAN LUIGI PILLOLA<sup>3</sup>, MARCO ROMANO<sup>1</sup>  
& DANIEL ZOBOLI<sup>3,4\*</sup>

<sup>1</sup>Dipartimento di Scienze della Terra, Sapienza Università di Roma, Roma, Italy. E-mail addresses: ianni.1967264@studenti.uniroma1.it; marco.romano@uniroma1.it

<sup>2</sup>Institut Systématique Evolution Biodiversité (ISYEB), Museum National d'Histoire Naturelle, CNRS, Sorbonne Université, Université des Antilles, EPHE, 57 Rue Cuvier, CP 50, 75005 Paris, France. E-mail address: andre.nel@mnhn.fr

<sup>3</sup>Dipartimento di Scienze Chimiche e Geologiche, Università degli Studi di Cagliari, Cittadella Universitaria (Blocco A) - SS 554, 09042, Monserrato (CA), Italy. E-mail addresses: pillola.g@unica.it; danielc.zoboli@unica.it

<sup>4</sup>Direzione Qualità, Servizi bibliotecari e Attività museali, Museo Sardo di Geologia e Paleontologia "D. Lovisato", Università degli Studi di Cagliari, via Trentino 51, 09123, Cagliari, Italy

\*Corresponding Author.

Associate Editor: Matteo Montagna.

To cite this article: Ianni A., Nel A., Pillola G.L., Romano M. & Zoboli D. (2026) - A spiloblattnid (Holopandictyoptera) hind wing from the Carboniferous of San Giorgio Basin (SW Sardinia): the oldest fossil insect from Italy. . *Rivista Italiana di Paleontologia e Stratigrafia*, vol. 132(1): 1-8.

---

**Keywords:** Insecta; Blattodea; Holopandictyoptera; Pennsylvanian; Moscovian; Iglesias.

**Abstract.** In this contribution, we describe and figured a nearly complete and exquisitely preserved fossil hind wing of a roachoid insect (Holopandictyoptera) from the late Moscovian (Pennsylvanian, Carboniferous) of southwestern Sardinia. The specimen is characterised by distinctive darkened seams along the main veins and a fenestrate-type colour pattern, and can be tentatively attributed to the family Spiloblattnidae Handlirsch, 1906, a family known between the Moscovian and the Kungurian ( $315.2 \pm 0.2$  to  $274.4 \pm 0.4$  Ma) from China, Europe, North America, North Africa, and Southern Africa. At this stage, assignment at a generic level is not possible, due to the fragmentary nature of the fossil and the limited knowledge of hind wings within this group. The fossil was recovered from the carbon-rich lacustrine deposits of the San Giorgio Basin, a well-known continental Upper Carboniferous succession rich in ichnofossils and plant remains. This discovery represents, to date, the oldest fossil insect ever documented in Italy and the first formal record of an insect from Sardinia, also constituting the earliest occurrence of a spiloblattnid in the Italian Peninsula. Comparisons with other spiloblattnid and compsoblattid hind wings, including those from the Gzhelian and Permian of Europe and North Africa, support its assignment based on venation architecture, width of interveinal areas, and absence of reticulated cross venation. Our results demonstrate the considerable promise of integrative palaeontological research in Sardinia's Carboniferous strata and underline the need for sustained fieldwork and rigorous taxonomic study of the region's still poorly documented insect assemblages.

---

Received: August 6, 2025; accepted: November 28, 2025

## INTRODUCTION

Palaeozoic roachoids are mainly known and classified based on their forewings (e.g., Schneider 1983), while their hind wings are much less frequent and more poorly preserved and incomplete. It is also difficult to associate the fore- and hind wings with the same species or even genus because the specimens with the fore- and hind wings attached to the thorax generally have the hind wings hidden by the forewings, or the wings are isolated, detached from the body.

The roachoid family Spiloblattinidae Handlirsch 1906 is extensively present between the Moscovian and the Kungurian ( $315.2 \pm 0.2$  to  $274.4 \pm 0.4$  Ma). It is characterised by the presence of darkened bands along the main veins of the forewings. Schneider et al. (2013: fig. 4) used these insects and the changes in these patterns of colouration for stratigraphic purposes. Hind wings attributed to this family are quite infrequent.

Here, we describe a specimen from Sardinia representing the oldest known fossil insect from Italy. It is a well-preserved hind wing of a roachoid with colour pattern preserved, attributable to the family Spiloblattinidae. It is also the first representative of this family from Italy.

Some other Carboniferous roachoids are recorded from Italy, viz. in the Gzhelian of Tuscany (Canavari 1892; Cassinis 1997; Sabatini et al. 2021). These have never been described.

## GEOLOGICAL SETTING

In southwestern Sardinia, near Iglesias (Fig. 1), a limited exposure of Carboniferous (upper Moscovian) fluvio-lacustrine clastic deposits in the San Giorgio area is well known for its rich fossil assemblages (Cocozza 1967; Barca & Costamagna 2003; Zoboli 2023). These deposits have been attributed to the San Giorgio formation, an informal litho-stratigraphic unit first proposed by Del Rio et al. (2002). Since the late 19th century, this locality has yielded a variety of plant remains, sporomorphs, a few arthropods, and a moderately diverse ichnoassociation. Despite their limited present-day exposure, the Carboniferous deposits of Sardinia have consistently provided valuable new data on the late Palaeozoic continental biota of Italy (Gambera

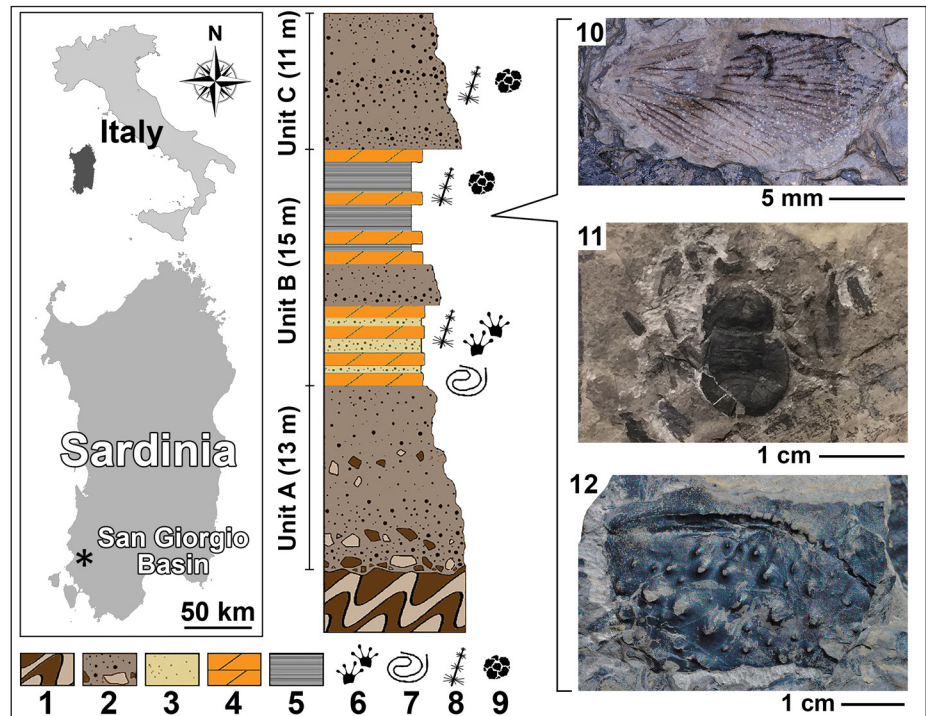
1897; Del Rio et al. 2002; Cleal et al. 2017; Marchetti et al. 2018, 2020; Pillola & Zoboli 2021).

The Carboniferous succession lies unconformably above the Cambrian-Ordovician metasiltites of the Cabitza Formation (Loi et al. 1996). Today, most outcrops are obscured by overburden resulting from historical mining activity (Pillola et al. 1998). The best-exposed continuous section, approximately 40 m thick, outcrops along an artificial drainage channel near a mining dump, which altered the course of the Rio San Giorgio (Del Rio et al. 2002). The first detailed stratigraphic and palaeontological description of these fluvio-lacustrine deposits was provided by Cocozza (1967). Subsequently, Barca & Costamagna (2003) provided new lithological and sedimentological data, interpreting the succession as consisting of debris and mass flow deposits resulting from rapid erosion of the adjacent Palaeozoic basement, interbedded with lacustrine sediments representing intervals of reduced subsidence.

Three units recognised within the formation are: i) bottom unit A (maximum thickness 13 m) represented by heterolithic breccias composed of angular, polygenic clasts (predominantly Cambrian limestones and dolostones) embedded in a grey dolomitic matrix; ii) intermediate unit B (maximum thickness 15 m) made by yellow-grey dolostones with local lenticular conglomerate bodies (containing well-rounded quartz pebbles), finely bedded breccias with dolomitic cement, grading into platy dolomites, dolomitic siltstones, and carbon-rich, finely laminated clays, topped by massive sandstones; iii) top unit C (maximum thickness 11 m), predominantly composed of polygenic heterolithic conglomerates interbedded with sandy, flat, lenticular deposits. Local concentrations of plant remains are present, including *Calamites* preserved in growth position.

The plant assemblage was first described by Cocozza (1967), who proposed a late Stephanian age, later corroborated by sporomorph and macrofloral data (Del Rio 1973; Del Rio & Pittau 2004). Further studies of the macroflora revealed a dominance of spheophytes, with subordinate pteridosperms, ferns, noeggerathians, and cordaitanthaleans, suggesting assignment to the upper part of the *Crenulopteris acadica* Zone or possibly the *Odontopteris cantabrica* Zone (late Asturian or Cantabrian = late Moscovian; Cleal et al. 2017).

Fig. 1 - Location of the Carboniferous San Giorgio Basin and synthetic stratigraphic column of the San Giorgio formation with maximum observed thickness of its informal units: 1, Palaeozoic basement; 2, heterometric breccias and conglomerates; 3, sandstones; 4, dolostones; 5, carbon-rich clays; 6, tetrapod footprints; 7, invertebrate traces; 8, macroflora; 9, microflora; 10, ? *Spiloblatinidae* hind wing; 11, trigonotarbid arachnid *Anthracomartus voelkelianus* Karsch, 1882; 12, incomplete right paratergite of *Arthropleura armata* Jordan, 1854.



A late Westphalian D age was also proposed based on tetrapod footprints from the lower part of the intermediate unit (Fondi 1980). More recently, Marchetti et al. (2018) conducted an ichnotaxonomic and palaeoecological analysis of newly discovered vertebrate and invertebrate trace fossils from the same unit. The tetrapod tracks were assigned to the ichnospecies *Batrachichnus salamandroides* (Geinitz, 1861), alongside indeterminate tracks possibly produced by small temnospondyls and/or lepospondyls. Invertebrate traces include locomotion traces (*Diplichnites* isp.), grazing traces such as *Cochlichnus anguineus* Hitchcock, 1858, and feeding structures including *Treptichnus bifurcus* Miller, 1889, and *Treptichnus* isp. The ichnoassemblage was interpreted using ichnofacies analysis, indicating a transitional *Scoyenia*–*Mermia* ichnofacies typical of alluvial plain to marginal lacustrine environments. Notably, the ichnoassociation from the San Giorgio Basin represents the oldest continental ichnofauna known from Italy (Marchetti et al. 2018, 2020).

The arthropod body fossils recovered from the carbon-rich clay horizons of unit B include a nearly complete trigonotarbid arachnid attributed to *Anthracomartus voelkelianus* Karsch, 1882 (Selden & Pillola 2009), a fragment of a paratergite referred to *Arthropleura armata* Jordan in Jordan & von Meyer, 1854 (Pillola & Zoboli 2021), and a roachoid hind wing, the subject of the present study,

previously reported by Del Rio et al. (2002), Pillola et al. (2004), and Zoboli (2023).

## MATERIAL AND METHODS

The hind wing venation terminology for roachoid used in this contribution follows the scheme of Schubnel et al. (2020) and Schubnel (2018, 2021), based on basivenale bullae from which the main veins emerge, rather than Li et al. (2018), who based their study on wing tracheation. The photograph of the fossil was taken using an Olympus DSX1000 digital microscope.

**Abbreviations for veins used in the text and figure are as follows:** C = costa; CuA = cubitus anterior; CuP = cubitus posterior; M = media; MA = media anterior; MP = media posterior; PCu = postcubitus; R = radius; RA = radius anterior; RP = radius posterior; ScP = subcosta posterior.

**Material:** PAS-GLP 0112 (a nearly complete and well-preserved hind wing with pattern of colouration well-preserved and posterior part of the anal area folded below the rest of the wing), stored at the Museo dei Paleoambienti Sulcitani - E.A. Martel of Carbonia.

**Age and outcrop:** San Giorgio Basin (Iglesias, SW Sardinia) (39°17'39.81"N - 8°31'11.74"E), San Giorgio formation (Carboniferous, Pennsylvanian, upper Moscovian).

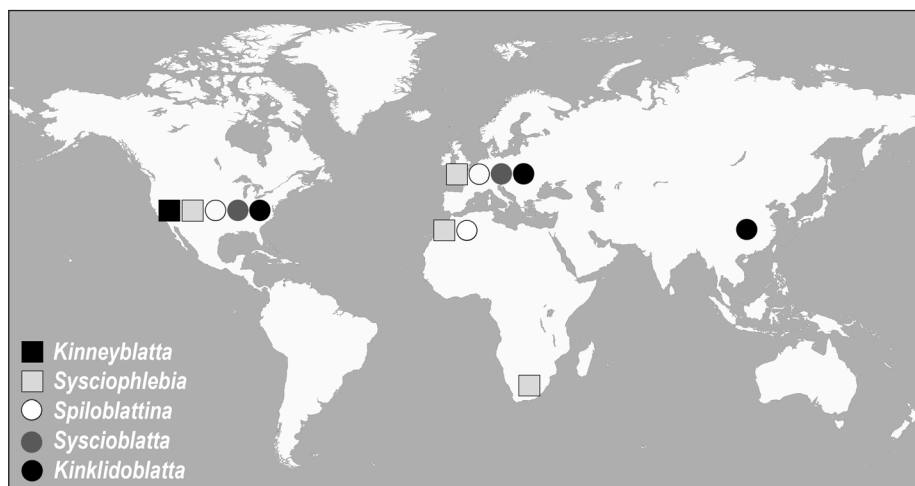


Fig. 2 - Distribution map of the Spiloblattinidae genera.

## SYSTEMATIC PALAEONTOLOGY

Superorder **Holopandictyoptera** Kluge, 2010  
(= total group of extant Dictyoptera Leach, 1815)  
Plesiomorphon Eoblattodea Laurentiaux, 1959  
(*sensu* Li, 2019)  
? Family Spiloblattinidae Handlirsch, 1906

**Included genera:** *Spiloblattina* Scudder, 1885 (North America, Europe, and Morocco), *Syscioblatta* Handlirsch, 1906 (North America and Europe), *Kinklidoblatta* Handlirsch, 1906 (China, North America, Europe), *Sysciophlebia* Handlirsch, 1906 (North America, Europe, Morocco, and South Africa), and *Kinneyblatta* Schneider et al., 2021 (North America) (Nel et al. 2022) (Fig. 2).

Genus and species undetermined

Fig. 3

**Remarks.** Kluge (2010: 32) defined Holopandictyoptera as follows: “Holopandictyoptera taxon nov. for the Pandictyoptera s.l. (including Palaeoblattariae with their long ovipositor and no outer genital chamber) and Cryptovipositoria taxon nov. for the Pandictyoptera s.str., with ovipositor reduced and hidden (completely or partly) in the outer genital chamber formed by the enlarged abdominal sternum 7. Thus, the name Dictyoptera and its monosemantic circumscriptional synonyms Panisoptera, Blattopteroidea and Isopteria are non-monosemantic circumscriptional synonyms of Holopandictyoptera and Cryptovipositoria”. Here, we consider that the Palaeozoic roachoids belong to the stem group of the extant Dictyoptera (Blattodea and Mantodea), because they share at least a unique synapomorphy in the strongly concave and curved forewing vein CuP (Prokop et al. 2014, 2023). The

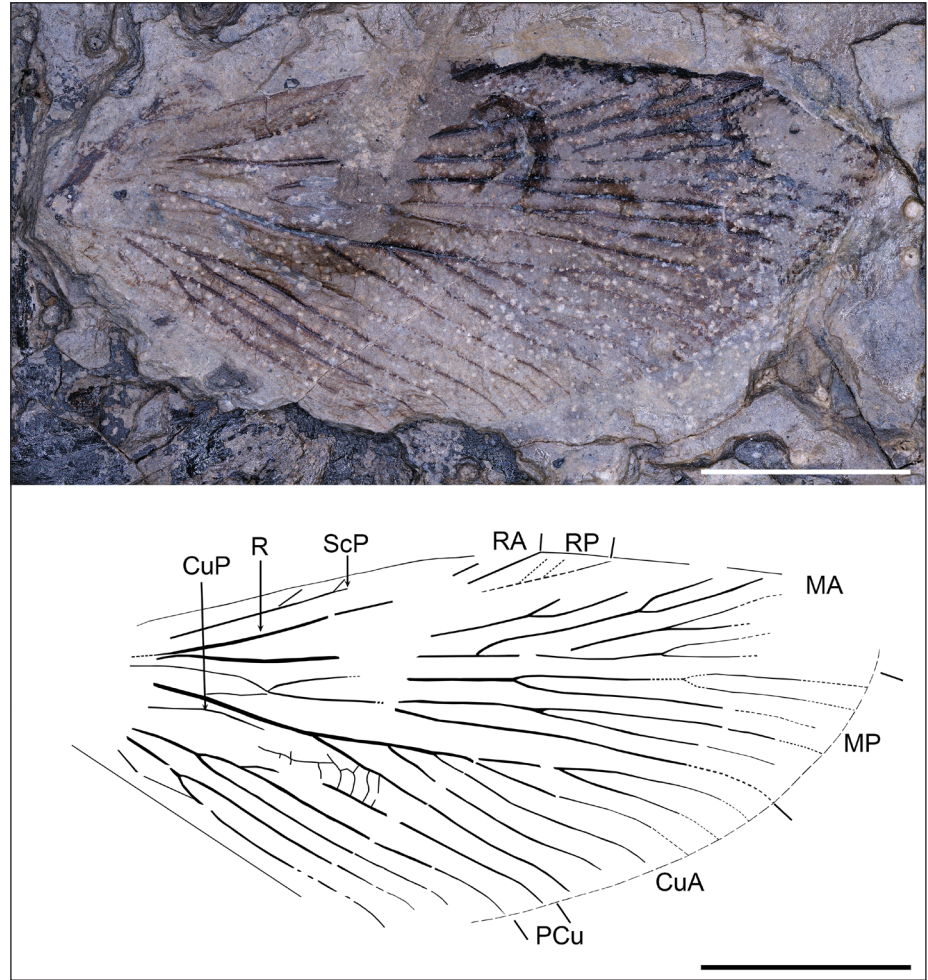
term Dictyoptera also corresponds to the Mantides Latreille 1802 *sensu* Vršanský 2024). Owing to this and other examples of nomenclatural duplication, it would be useful for the International Commission of the Code of Nomenclature to clarify, in the near future, the taxon names of high ranks.

**Description.** Pattern of colouration well visible, with darkened bands along all branches of main veins, these not being confluent anywhere; wing margin with a thin darkened band between the apex of RA and that of M (costal-maculae, R-maculae and CuA-maculae reduced); a transverse darkened zone crossing branches of MP and of CuA in middle of wing and a second one crossing branches of RP and of M near wing apex.

Wing base missing, fragment 19.5 mm long, probable wing length 21.3 mm, 9.4 mm wide at level of apex of anal area; area between ScP and C narrow 0.4 mm wide; area between ScP and R/RA 0.4 mm wide; area between R and MA 1.1 mm wide; area between MP and CuA 0.6 mm wide; radial area very narrow; median area very broad, broader than that of CuA; ScP long but weak, reaching level of mid-wing, anteriorly pectinate with few weak branches, simple and parallel; R stronger than ScP, RA and RP well-defined but short; RA apparently simple; RP with few anterior branches; MA and MP separated close to wing base, MA forked near mid wing, anterior branch with four branches; posterior branch with eight-nine branches, and reaching wing apex; MP weaker in its basal part than basal part of MA, with six branches reaching posterior margin of wing; stem of CuA slightly sigmoidally curved, without anterior branch, posteriorly pectinate, with six



Fig. 3 - ? *Spiloblattinidae* genus and species undetermined (PAS-GLP 0112). Photograph of the hind wing and drawing highlighting the venation pattern. See "Material and Methods" for abbreviations. Scale bars = 5 mm.



simple branches; CuP poorly preserved and weak, apparently simple; PCu regularly weakly curved; anterior branch of anal vein subdivided into four simple and nearly straight branches; posterior part of anal area folded below the rest of the wing and hardly discernible; no elongate intercalary longitudinal veins between main veins but a series of short oblique sigmoidal veinlets between MP and CuA.

**Discussion.** The zones between the main longitudinal veins and their branches are of fenestrate-type (fenestrater Typ *sensu* Schneider 1984: 9): ‘Zwischengeäder in dicht reticulate bzw. anastomisierend-striate Bereiche (sog. Säume) und nicht oder weitmaschig sehr fein reticulate Maculae aufgelöst’ (Taf. V, fig. 6): *Spiloblattinidae*, *Compsoblattidae*, *Subioblattidae*’ [Interveins divided into densely reticulate or anastomosing-striate areas (so-called seams) and not or widely reticulated very finely reticulated maculae (Pl. 5, fig. 6): *Spiloblattinidae*, *Compsoblattidae*, *Subioblattidae*]. The new fossil has exactly this pattern.

The hind wings in the Triassic family *Subioblattidae* Schneider, 1983 are very poorly known. Montagna et al. (2025: fig. 2) have figured a nearly complete specimen from the Triassic of Switzerland, but its hind wings are poorly preserved. Nevertheless, it does not show the seams along the main veins, especially in the distal half of the wing, while these are distinct in the new fossil. Also, Hinkelmann (2002: fig. 5) has shown that the *Subioblattidae* have supplementary longitudinal veins between the main veins and their branches in both fore- and hind wings.

Schneider et al. (2021) proposed the following emended diagnosis for the *Spiloblattinidae*: ‘Phyloblattid-like wing venation pattern but with a much lower number of veins and with extended fields between the main veins’... ‘Most diagnostic is a fenestrate colour pattern consisting of pale areas of various extent 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'. This pattern is present in the forewings of the Spiloblattinidae but can be present or absent in the hind wings of the same genus *Spiloblattina* Scudder, 1885, as figured by Belahmira et al. (2024: pl. 2, fig. 8, pl. 4, fig. 1, pl. 5, fig. 7, pl. 6, fig. 1).

But *Compsoblatta* Schlechtendal in Handlirsch, 1907 (unique genus of the Compsoblattidae Schneider 1978) also shows a similar pattern of pale areas of various extent between the main veins and their branches and dark seams along the veins, in both fore- and hind wings (Schneider 1983: pl. 3, fig. 7; Belahmira et al. 2019: 962): 'Hindwings of *Compsoblatta* are of similar size to those of *Phyloblatta* but would have a color pattern of similar design to the corresponding forewings (JWS personal observation)'. Belahmira et al. (2019: 962) also indicated that the 'family Compsoblattidae includes blattoids displaying an enigmatic mixture of a *Phyloblatta*-like venation pattern combined with a wing coloration comparable to the Spiloblattinidae'. But they added in the diagnosis of the Compsoblattidae that the 'general venation pattern is similar to that of *Phyloblatta*, but in contrast to this genus the crossvenation in the basal three quarters of the wings consists of seams formed by crossvein bases along the main veins and their branches; the remaining wing surface shows a delicate irregularly reticulated cross venation. 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 wing does not show any 'delicate irregularly reticulated cross venation' in its distal part. It also differs from the hind wing of *Phyloblatta* and probably *Compsoblatta* in the area between RP and M nearly as broad as those between RA and RP and between M and CuA vs much narrower in the latter (Belahmira et al. 2019: fig. 14.6-8). The specimen attributed to *Spiloblattina pygmaea* (Meunier, 1904) by Belahmira et al. (2024: pl. 6, fig. 1) shows similar rather broad areas between the main veins of the hind wing. Lastly the apical part of the new wing has a venation much less dense than in *Compsoblatta stelzneri* Deichmüller, 1882 (see Schneider 1978: pl. 46: figs 1a and 2a).

These three arguments (density of venation, widths of the areas between the main veins, and

pattern of areas between main veins) allow us to propose an attribution of the new fossil to the Spiloblattinidae. But this can only be tentative because of the current fragmentary knowledge on the hind wing of the Palaeozoic roachoids and also because the limits and monophyly of these families remain uncertain (Legendre et al. 2015). Schneider et al. (2004: 255) indicated that 'the Mesozoic blattids originated from Phyloblattidae and Spiloblattinidae (for details see Schneider 1984)', which clearly means that these authors considered these families as paraphyletic.

Any generic attribution remains impossible because the hind wings remain very poorly known in the different spiloblattinid genera.

## CONCLUSION

In this contribution, we describe a fossil hind wing from the upper Moscovian fluvio-lacustrine succession of the San Giorgio Basin (SW Sardinia), adding new data to our knowledge of Carboniferous insect diversity. On the basis of venation architecture, the characteristic fenestrate-type colour pattern, and the relative proportions of the interveinal areas, the specimen can be tentatively assigned to the family Spiloblattinidae Handlirsch, 1906. Although a more precise generic attribution remains impossible due to the limited comparative material of hind wings within this family, the combination of traits appears to align it with other spiloblattinid representatives from the late Palaeozoic, notably those from the Gzhelian and Permian deposits of Europe, North Africa, and North America. The absence of intercalary veins and the presence of darkened seams along the main veins seem to support such an attribution, representing characters that distinguish Spiloblattinidae from other contemporaneous blattodean families, including Compsoblattidae and Phyloblattidae.

This discovery represents the first fossil insect formally described from Sardinia and also constitutes the oldest known insect fossil from the Italian Peninsula, filling a significant paleobiogeographic gap in the record of Palaeozoic insect faunas in southern Europe. In addition, its exceptional preservation, which includes well-defined wing venation and distinct pigmentation patterns, underlines the taphonomic potential of the San Giorgio

formation for yielding exquisitely preserved terrestrial arthropods. This is further corroborated by the presence of other rare arthropods in the same stratigraphic section, represented by the trigonotarbid arachnid *Anthracomartus voelkelianus* and a fragment of *Arthropleura armata*.

From a stratigraphic perspective, this fossil provides an additional biostratigraphic marker within the San Giorgio formation, supplementing existing palaeontological data from palynology, plant macrofossils, and vertebrate/invertebrate ichnofossils. The presence of spiroblatinid insects in this context is consistent with other late Moscovian continental assemblages and suggests faunal connections with other regions, such as Central Europe and North Africa. Finally, this study reinforces the potential of integrated palaeontological investigations in the Carboniferous deposits of Sardinia, stressing the importance of continued exploration and systematic description of the largely unstudied insect material from the area.

**Data Availability Statement.** The data supporting the results of this research are available upon request. Interested researchers may contact the corresponding Author to obtain access.

**Acknowledgments:** The Editor Matteo Montagna and two anonymous reviewers are warmly thanked for their corrections and suggestions that improved an early version of the manuscript. We thank Dario Fancello for providing the photographs of the fossil.

#### REFERENCES

- Barca S. & Costamagna L.G. (2003) - The Upper Carboniferous S. Giorgio succession (Iglesiente, SW Sardinia): stratigraphy, depositional setting and evolution of a late to post-Variscan molassic basin. *Bollettino della Società Geologica Italiana*, 2: 89-98.
- Belahmira A., Schneider J.W. & Saber H. (2024) - Insect (Blattodea, Spiloblattinidae) biostratigraphy of the Pennsylvanian Souss basin, Morocco: a contribution to non-marine – marine correlation. *Newsletters on Stratigraphy*, 57(3): 299-322. DOI: 10.1127/nos/2024/0821
- 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(5): 945-965. DOI: 10.1017/jpa.2019.20
- Canavari M. (1892) - Insetti del Carbonifero di San Lorenzo nel Monte Pisano. Nota preventiva. *Atti della Società Toscana di Scienze Naturali, Processi Verbalì*, 8: 33-34.
- Cassinis G. (1997) - Review on continental Permo-Carboniferous deposits in Italy. *Geodiversitas*, 19(2): 203-216.
- Cleal C.J., Scanu G.G., Buosi C., Pittau P. & Kustatscher E. (2017) - Middle Pennsylvanian vegetation of the San Giorgio Basin, southern Sardinia (Italy). *Geological Magazine*, 154: 1155-1170. DOI: 10.1017/S0016756816000765
- Cocozza T. (1967) - Il Permo-Carbonifero del bacino di San Giorgio (Iglesiente, Sardegna sud-occidentale). *Memorie della Società Geologica Italiana*, 6: 607-642.
- Deichmüller J.V. (1882) - Über einiger Blattiden aus den Brand-schiefern der unteren Dyas von Weissing bei Pillnitz. *Sitzungsberichte und Abhandlungen der Naturwissenschaftlichen Gesellschaft Isis*, Dresden, 1882: 33-44.
- Del Rio M. (1973) - Palinologia di un livello “permo-carbonifero” di San Giorgio (Iglesiente, Sardegna sud-occidentale). *Bollettino della Società Geologica Italiana*, 93: 113-124.
- Del Rio M. & Pittau P. (2004) - The Upper Carboniferous San Giorgio Basin. In Barca S. & Cherchi A. (eds), 32nd International Geological Congress: Sardinian Palaeozoic basement and its Meso-Cainozoic covers (Italy). Field Trip Guide Book P39: 16-18.
- Del Rio M., Pillola G.L. & Muntoni F. (2002) - The Upper Carboniferous of the San Giorgio Basin. *Rendiconti della Società Paleontologica Italiana*, 1: 223-229.
- Fondi R. (1980) - Orme di microsauro nel Carbonifero superiore della Sardegna. *Memorie della Società Geologica Italiana*, 20: 347-356.
- Gambera V. (1897) - Sulla scoperta di nuove zone di Carbonifero e sulla stratigrafia dell'Iglesiente. 5 pp. Tipografia Commercianti, Cagliari.
- Geinitz H.B. (1861) - Dyas oder die Zechsteinformation und das Rothliegende, Heft II: Die Pflanzen der Dyas und Geologisches. Verlag Wilhelm Engelmann, Leipzig: 132-342.
- Handlirsch A. (1906) - Revision of American Paleozoic insects. *Proceedings of the United States National Museum*, 29: 661-820.
- Handlirsch 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.
- Hinkelman J. (2022) - A monospecific assemblage of cockroaches (Dictyoptera: Subioblattidae) from the Triassic of Kyrgyzstan. *PalZ*, 96(4): 781-793. DOI:10.1007/s12542-022-00617-7
- Hitchcock E. (1858) - Ichnology of New England: A report on the sandstone of the Connecticut Valley especially its fossil footmarks made to the Government of the Commonwealth of Massachusetts, W. White, Boston, 220 pp.
- Jordan F.W.H. & Meyer H. von (1854) - Ueber die Crustaceen der Steinkohlenformation von Saarbrücken. *Palaeontographica*, 4: 1-15.
- Kluge N.J. (2010) - Circumscriptional names of higher taxa in Hexapoda. *Bionomia* 1, 15-55. DOI: 10.11646/bionomia.1.1.3
- Latreille P.A. (1802) - Histoire naturelle, générale et particulière des Crustacés et des Insectes. Ouvrage faisant suite aux œuvres de Leclerc de Buffon et partie du cours complet d'Histoire naturelle rédigé par C.S. Sonnini. T. 3-4, an X. Familles naturelles et genres. Paris, Dufart: 1-467 and 1-387.
- Laurentiaux D. (1959) - La reproduction chez les insectes blattaires du Carbonifère, facteurs du panchronisme et classification naturelle de l'ordre. *Bulletin de la Société Géologique de France*, 7(7): 759-766.
- Leach W.E. (1815) - Entomology. In: Brewster, D. (ed.): The Edinburgh Encyclopaedia, Edinburgh, Blackwood, 9: 57-172.
- Legendre F., Nel A., Svenson G.J., Robillard T., Pellens R. &



- Grandcolas P. (2015) - Phylogeny of Dictyoptera: dating the origin of cockroaches, praying mantises and termites with molecular data and controlled fossil evidence. *Plos one*, 10(7): e0130127. DOI: 10.1371/journal.pone.0130127
- Li X.R. (2019) - Disambiguating the scientific names of cockroaches. *Palaeoentomology*, 2(4): 390-402. DOI: 10.11646/palaeoentomology.2.4.13
- Li X.R., Zheng Y.H., Wang C.C. & Wang Z.Q. (2018) - Old method not old-fashioned: parallelism between wing venation and wing-pad tracheation of cockroaches and a revision of terminology. *Zoomorphology*, 137(4): 519-533. DOI: 10.1007/s00435-018-0419-6
- Loi A., Pillola G.L. & Leone F. (1996) - La limite Cambrien-Ordovicien dans le SW de la Sardaigne: relations avec des événements eustatiques globaux. *Comptes rendus de l'Académie des Sciences Paris*, 323: 881-888.
- Marchetti L., Muscio G., Pillola G.L. & Zoboli D. (2020) - The Carboniferous tetrapod ichnoassociation from Italy. In: Romano M. & Citton P. (eds), Tetrapod ichnology in Italy: the state of the art. *Journal of Mediterranean Earth Sciences*, 12: 29-37. DOI: 10.3304/jmes.2020.16871
- Marchetti L., Petti F.M., Zoboli D. & Pillola G.L. (2018) - Vertebrate and invertebrate trace fossils in the Late Pennsylvanian (Carboniferous) fluvio-lacustrine San Giorgio Basin (South-West Sardinia): remarks on the oldest continental ichnoassociation of Italy. *Ichnos*, 25: 94-105. DOI: 10.1080/10420940.2017.1337572
- Meunier F. (1904) - Eine neue Blattinaria aus der Oberen Steinkohlenformation (Ottweiler Schichten, Rhenpreussen). *Jahrbuch der Königlich Preussischen Geologischen Landesanstalt und Bergakademie zu Berlin*, 23: 454-457.
- Miller A. (1889) - North American geology and palaeontology for the use of amateurs, students and scientists. Western Methodist Book Concern, Cincinnati, Ohio, 664 pp.
- Montagna M., Magnani F., Magoga G. & Nel A. (2025) - First subbiolattid roachoid (Insecta: Holopandictyoptera) from the Middle Triassic of Monte San Giorgio (Switzerland). *Swiss Journal of Palaeontology*, 144: 14. DOI: 10.1186/s13358-025-00354-9
- Nel A., Santos, A.A., Hernández-Orúe, A., Wappler, T. & Diez, J.B. (2022) - The first representative of the roachoid family Spiloblatinidae (Insecta, Dictyoptera) from the Late Pennsylvanian of the Iberian Peninsula. *Insects*, 13 (828): 1-14. DOI: 10.3390/insects13090828
- Pillola G.L., Leone F. & Loi A. (1998) - The Cambrian and Early Ordovician of SW Sardinia. *Giornale di Geologia, Special Issue, ECOS VII - Sardinia Guide-book*, 60: 25-38.
- Pillola G.L., Petti F., Sacchi E., Sergio Piras S., Zoboli D. & Nicosia U. (2004) - Tetrapod footprints and associated biota: new evidences from the Upper Carboniferous of Southwestern Sardinia. *Geological Society of America, Abstracts*, 36(4): 82.
- Pillola G.L. & Zoboli D. (2021) - First occurrence of *Arthropleura armata* (Myriapoda) in the Moscovian (Carboniferous) of SW Sardinia (Italy). *Bollettino della Società Paleontologica Italiana*, 60(1): 49-54. DOI: 10.4435/BSPI.2021.01
- Prokop J., Krzeminski W., Krzeminska E., Hörschemeyer 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(5): 601-622. DOI: 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. DOI: 10.1146/annurev-ento-120220-022637
- Sabatini F., Pandeli E. & Kustatscher E. (2021) - Carboniferous plant fossils from the San Lorenzo schists (Pisani mountains, Tuscany, Italy): a preliminary study of the palaeobotanical collection of the Museo Naturalistico Archeologico dell'Appennino Pistoiese. *Rivista Italiana di Paleontologia e Stratigrafia*, 127(2): 397-425. DOI: 10.13130/2039-4942/15843
- Schneider J.W. (1978) - Zur Taxonomie und Biostratigraphie der Blattodea (Insecta) des Karbon und Perm der D.D.R. *Freiberger Forschungshefte (C)*, 340: 1-152.
- Schneider J.W. (1983) - Die Blattodea (Insecta) des Paläozoikums, 1: Systematik, Ökologie und Biostratigraphie. *Freiberger Forschungshefte, (C)*, 382: 107-146.
- Schneider J.W. (1984) - Die Blattodea (Insecta) des Paläozoikums, 2: Morphogenese der Flügelstrukturen und Phylogenie. *Freiberger Forschungshefte, (C)*, 391: 5-34.
- Schneider J.W., Lucas S.G. & Barrick J.E. (2013) - The Early Permian age of the Dunkard Group, Appalachian basin, U.S.A., based on spiloblatinid insect biostratigraphy. *International Journal of Coal Geology*, 119: 88-92. DOI: 10.1016/J.COAL.2013.07.019
- 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. and 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., Scholze F., Ross A.J., Blake B.M.Jr & Lucas S.G. (2021) - Improved blattoid insect and conchostracan zonation for the late Carboniferous, Pennsylvanian, of Euramerica. *The Geological Society Special Publications*, 512: 1-27. DOI : 10.1144/SP512-2021-93
- Schubnel T. (2018) - Homologie de la nervation des ailes et phylogénie des Dictyoptera actuels et fossiles (Insecta). Master Thesis, MNHN – Sorbonne Université: 1-38 + annex.
- Schubnel T. (2021) - L'évolution des insectes passée aux rayons X: étude des homologies de nervation alaire via la  $\mu$ CT et le registre fossile. Unpublished PhD Thesis, Museum National d'Histoire Naturelle, Paris, 208 pp.
- 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. DOI: 10.1111/syen.12399
- Scudder S.H. (1885) - New genera and species of fossil cockroaches, from the older American rocks. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 37: 34-39.
- Selden P. & Pillola G.L. (2009) - A trigonotarbid arachnid from the Upper Carboniferous of the San Giorgio Basin, Sardinia. *Rivista Italiana di Paleontologia e Stratigrafia*, 115: 269-274.
- Vršanský P. (2024) - Late Mesozoic cockroaches s.l. from the Karabastau Formation in Kazakhstan. *Amba Projekty*, 14(1), 1-700.
- Zoboli D. (2023) - The Rich Palaeontological Heritage of SW Sardinia (Italy), a Possible Resource for a Geotourism Development. *Geoheritage*, 15: 41. DOI: 10.1007/s12371-023-00803-2