

New insects from the Permian of Catalonia (Spain) predate the early diversification of Triassic clades adapted to arid environments (Grylloblattodea, Probnidae, Dictyoptera)

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Abstract

Probnis sauvanyaensis sp. nov., the first representative of the ‘grylloblattodean’ family Probnidae from the Iberian Peninsula, is described from the middle to ?upper Permian outcrop of Sauvanya in the Catalan Pyrenees. The family is otherwise represented by two additional species of *Probnis* from the ?middle Permian of the USA and by a single genus and species from the ?Lower Triassic of Ukraine. As is known from outcrops with rather extreme climates, the family may have survived the global warming of the Permian–Triassic crisis. We also describe a roachoid of the family Spiloblattidae from the same outcrop as the second representative of this family from the Iberian Peninsula.

Key Words

Insecta, Polyneoptera, Spain, adaptations to arid environments, Permian–Triassic

Introduction

The ‘Grylloblattodea’ is a surprising insect group mostly represented today by the wingless and large-headed Grylloblattidae, commonly known as ice crawlers because they are adapted to extreme climatic conditions. Even if this group may have emerged from the winged ‘Grylloblattida’ during the late Carboniferous (Cawood et al. 2022), its evolution is poorly understood and its current classification remains obscure because its monophyly has not been demonstrated yet. Nevertheless, some families of ‘Grylloblattodea’ are well defined, especially

those with few taxa and obvious unique derived characters or autapomorphies. This is the case of the Probnidae Sellards, 1909, a family well characterized by putative synapomorphies, viz., narrow forewings, simple RP, M with very few branches, CuA with a long anterior branch, posteriorly pectinate and parallel to the posterior margin of the wing (Storozhenko 1998). This clade gathers three small-sized species: two from the Permian of the USA and one from the Triassic of Ukraine (Tillyard 1937; Rasnitsyn et al. 2004; Aristov 2005). Thus, the family crossed the Permian–Triassic mass extinction event and provides interesting information on the survival of these

miniaturized forms. Miniaturization is sometimes considered as a process favoring the survival during crises of diversity (Gall 1972; He et al. 2007; Thuy et al. 2022).

Here we describe the first representative of Probnidae from the middle-?upper Permian of the Catalan Pyrenees (NE Iberian Peninsula), on the basis of a nearly complete small forewing found at the Sauvanyà red bed outcrop.

Otherwise, we also describe and discuss the position of a roachoid tegmen from the same locality, unfortunately too incomplete to be attributed to a precise genus and species. These insects are the first ones from the Permian of Catalonia, enlarging the distribution of the group in this region of Pangaea.

Geological setting

Sauvanyà, a fossil site nearby a village with the same name, is included in the generally red bed successions of Permian age from the Catalan Pyrenees (NE Iberian Peninsula), in the southeastern area of the Pyrenean range. During the late Paleozoic and early Mesozoic, the southern Pyrenean area was a rift system in a generally strike-slip tectonic setting, constituting the so-called Pyrenean Basin (Gisbert 1981; Speksnijder 1985; Gretter et al. 2015; Mujal 2017). This basin is generally regarded as a semi-graben with west-east extension, and it contained several depocenters that constituted sub-basins within the whole rift system (e.g., Speksnijder 1985; Saura and Teixell 2006; Mujal 2017). The succession, including the Sauvanyà fossil site, is found in the western area of the Cadí sub-basin (Fig. 1), relatively close to other Permian as well as Triassic fossil localities within the same (Mujal et al. 2016, 2017) and other (De Jaime-Soguero et al. 2023) sub-basins.

The red bed succession of Sauvanyà corresponds to the depositional unit (*sensu* Gisbert 1981) known as the Upper Red Unit (URU), and more specifically, to its upper portion (upper URU), as described by Mujal et al. (2017). The geological succession stratigraphically below that of Sauvanyà corresponds to the lower URU, characterized by reddish-brownish floodplain mudstones with occasional fine-grained sandstones with erosive bases corresponding to relatively small fluvial channel deposits. The topmost part (ca. 2–3 m thick) of the lower URU consists of the same mudstones with large (5 to 20 cm in diameter) septariform nodules, clearly delimiting the boundary between the two subunits of the URU (e.g., Mujal et al. 2017). The upper URU is overlain by the Buntsandstein facies unit, which is of Triassic age and in the area is in angular unconformity with the Permian unit (Fig. 1B, C). The lowermost part of the Buntsandstein is composed of conglomerates composed of well-rounded, quartz-dominated pebbles with a matrix of red sandstones, generally corresponding to braided fluvial deposits; these are succeeded by fluvial red sandstones.

The sedimentary deposits of the upper URU at Sauvanyà consist of relatively thick (ca. 60–100 cm thick) and massive reddish mudstones cyclically

alternating with intervals composed of thin layers (2–5 cm thick) of greyish-bluish very fine-grained carbonate sandstones (Fig. 1C, D). These intervals usually contain multiple layers (variable in number, generally from one to ten layers) with the same reddish mudstones separating each layer (Fig. 1D), which are usually finely laminated (with either parallel or cross lamination) and display prominent desiccation cracks on their top surfaces. Such cyclic succession has been described in detail in nearby areas by Gisbert (1981), Speksnijder (1985), Gretter et al. (2015), and Mujal et al. (2017). The area of Sauvanyà is affected by multiple small-scale normal faults, hampering a detailed measurement of the thickness of the whole succession. Nevertheless, considering the different successions measured in detail in surrounding outcrops (Gisbert 1981; Speksnijder 1985; Mujal et al. 2017), the upper URU at Sauvanyà is ca. 80–100 m thick.

The greyish-bluish carbonate sandstone layers contain all fossils so far identified in the area, whereas the reddish mudstones are apparently barren. Besides the insects reported in this work, which are found in the mid-upper portion of the sedimentary unit, within the whole succession in the Sauvanyà area, these layers contain sparse indeterminate tetrapod footprints (identified only on one layer), plant debris, vertical cylindrical invertebrate burrows, and casts of potential bivalves (the latter accumulated at the bottom of incised micro-channel deposits or rills).

Generally, the cyclical alternation of lithologies, together with the localized (and limited) presence of fossils, as well as the mud cracks on the thin layers, indicates a strong seasonality (although generally semi-arid to arid conditions) within an ephemeral lacustrine setting. This paleoenvironmental interpretation agrees with that from other successions within the Pyrenean Basin (Gisbert 1985; Gretter et al. 2015; Mujal et al. 2017; De Jaime-Soguero et al. 2023). The age of the upper URU at the Sauvanyà area still has some degree of uncertainty, considering that this unit is probably diachronous throughout the whole Pyrenean Basin (e.g., De Jaime-Soguero et al. 2023; see also Speksnijder 1985), but the unit likely corresponds to the middle Permian (Guadalupian), even if a Lopingian age cannot be completely ruled out.

Materials and methods

The holotype of the new species of Probnidae and the roachoid were collected by first author RG and the team during 2019 fieldwork. The field campaign was performed with the legal permits issued by the Departament de Cultura of the Generalitat de Catalunya (Catalan Government) and the Serra del Cadí-Moixeró Natural Park. The photographs were taken with a Nikon Z7II camera attached to a Nikon SMZ25 stereomicroscope. Photographs were exported in NEF format and processed using Nikon NX Studio and DXO Lab 8 software. Imaging was realized in the Biophotonics 2D/3D Lab of the ISYEB institute.

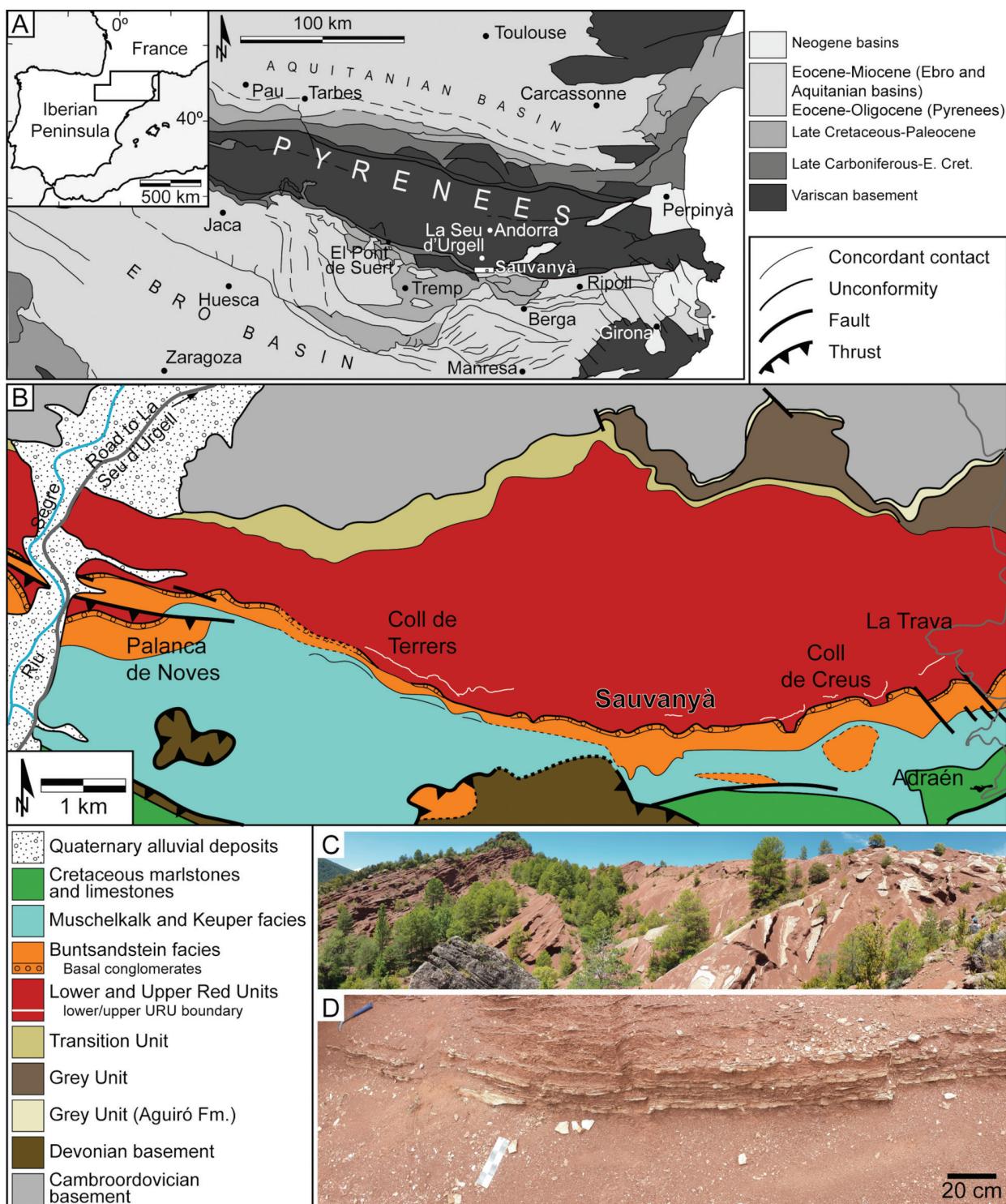


Figure 1. Geological setting. **A.** Location in Europe and regional geology of the Pyrenees, with study area (Sauvanyà) marked with a white rectangle; Pyrenean map modified from Vergés (1993); **B.** Geological map of the study area; modified from Mujal et al. (2017) (original map updated from Gisbert, 1981); **C.** Panoramic view of the outcrops of the upper Upper Red Unit in Sauvanyà; the hilltop on the left side of the photograph corresponds to the Buntsandstein deposits; **D.** Detail of an interval composed of multiple thin, very fine-grained layers; note the thickened lowermost layer at the left of the photograph, corresponding to a small channel deposit (rill).

Wing venation terminology follows the scheme of Schubnel et al. (2020) and Schubnel (2021), based on basivenale bullae from which the main vein emerges, rather than Li et al. (2018), who erroneously based their study on wing tracheation. Wing venation

nomenclature: C costal vein; CuA1 anterior-most branch of cubitus anterior; CuA2 posterior-most branch of CuA; CuP+PCu cubitus posterior plus postcubitus; M median vein; RA radius anterior; RP radius posterior; ScP subcostal posterior.

Institutional abbreviations

IPS, Institut Català de Paleontologia Miquel Crusafont (formerly Institut de Paleontologia de Sabadell), Sabadell, Catalonia, Spain.

Systematic paleontology

Class INSECTA Linnaeus, 1758

‘Order’ ‘GRYLLOBLATTODEA’ Brues & Melander, 1932 (sensu Storozhenko 1998)

Family PROBNIDAE Sellards, 1909

Included genera. *Probnis* Sellards, 1909 (Permian of North America and Spain), *Triassoprobnis* Aristov, 2005 (Late Triassic of Ukraine).

Genus *Probnis* Sellards, 1909

Type species. *Probnis speciosa* Sellards, 1909 (Permian of Kansas and Oklahoma).

Other species. *Probnis fossor* Aristov in Rasnitsyn et al. (2004) (Permian of New Mexico), *Probnis sauvanyaensis* sp. nov. (Permian of Spain, Guadalupian–?Lopingian).

Probnis sauvanyaensis sp. nov.

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Fig. 2

Material. Holotype IPS125664 (part and counterpart of a nearly complete forewing), stored at the Institut Català de Paleontologia Miquel Crusafont, Sabadell, Catalonia, Spain.

Etymology. Named after the type locality, Sauvanya.

Age and outcrop. Guadalupian–?Lopingian, upper Upper Red Unit, Sauvanya, Catalonia, Spain.

Diagnosis. A narrow area between RA and RP; base of RP basal of mid-wing level, area covered by CuA1 rather broad, broader than that of M; CuA1 branched far from its base; comb of branches of CuA1 not reaching wing apex.

Description. Forewing small, 5.7 mm long, 1.1 mm wide; no trace of coloration preserved; area between C and ScP very narrow, 0.2 mm wide; ScP simple, 3.7 mm long, closely parallel to R; R straight, with RP simple, branching at ca. 2.5 mm from wing base, nearly at level of mid-wing, closely parallel to RA; convex RA simple; neutral M basally separated from R and distally from RP, with two long branches; Cu separating into CuA and CuP; CuA basally separated into a straight and simple CuA2 and a curved and distally straight CuA1, distally parallel with posterior margin of wing and pectinate into a series of parallel branches, and well separated from M; area between CuA and CuP very narrow; CuP+PCu nearly straight; parallel to CuA2, reaching level of mid-wing; area between CuP+PCu and posterior wing margin narrow and elongate with one curved anal vein; no crossvein visible.

Remarks. The shape of the cubito-anal area, ScP and radial vein, and the weak corrugation of the veins indicate that it is a neopteran forewing. Affinities with the Acercaria or the Archaeorthoptera are excluded because of the common stem of CuA with CuP in the new fossil. Affinities with Holometabola are unlikely because of the absence of crossveins in the costal area and of specialized cells in the cubito-anal area. Affinities with the Dictyoptera are excluded because of the nearly straight and weakly concave CuP. The Paoliida would be excluded because the area between CuA and CuP is very narrow and there are no particular anterior branches of CuA. The remaining option is an attribution to the poorly defined group ‘Grylloblattodea,’ which means little, as the monophylies of this set of taxa and of the families inside are still not demonstrated.

Within the ‘Grylloblattodea,’ the new fossil fits well with the Permian genus *Probnis* (Probnidae), sharing a small and narrow forewing, a simple and long ScP, a narrow costal area, a simple RP closely parallel to RA, a narrow median area, no reticulation in the wing membrane, and a CuA basally separated from M and distally parallel with posterior margin of wing and pectinate into a series of parallel branches. The Tillyardiidae Zalessky, 1938, Phenopteridae Carpenter, 1950, and Aaliculidae Storozhenko, 1997 also have a long distal part of CuA parallel to posterior margin of wing but differ from the new fossil in the presence of broader areas between RP, M, and CuA (Storozhenko 1998). The Protembidiidae Tillyard, 1937 (*Protembia* Tillyard, 1937) also have a distal part of CuA parallel to posterior margin of wing, but it is shorter than in the new fossil, and they have a vein M with more branches (Carpenter 1950; Storozhenko 1998). Note that Tillyard (1937) also added the genus *Telactinopteryx* Tillyard, 1937, in the Probnidae, but Carpenter (1950) put it in synonymy with *Protembia*.

Probnis speciosa shares with the new fossil a narrow area between RA and RP but differs from the new fossil in the base of RP basad mid-wing level and the narrower area covered by CuA1, even if this structure is highly variable in *P. speciosa* (see Tillyard 1937: fig. 1). *Probnis fossor* has a broader area between RA and RP than in the new fossil, a base of RP in a more basal position than in the new fossil, and a rather broad area covered by CuA1. The forewings of the *Probnis speciosa* and *P. fossor* are longer than that of the new fossil (10 to 14 mm long vs. 5.7 mm) (Tillyard 1937; Rasnitsyn et al. 2004). The Triassic *Triassoprobnis humilis* Aristov 2005 has CuA1 branched more proximally, and the comb of branches of CuA1 almost reaching the wing apex, unlike in the new fossil and *Probnis* (Aristov 2005).

Superorder ‘HOLOPANDICTYOPTERA Kluge, 2010’ (= total group of extant Dictyoptera Leach, 1815)

Plesiomorphon EOBLATTODEA Laurentiaux 1959, (sensu Li 2019)

Remarks. Kluge (2010, p. 32) defined Holopandictyoptera as follows: “HOLOPANDICTYOPTERA taxon nov. for the Pandictyoptera s.l. (including Palaeoblattariae with

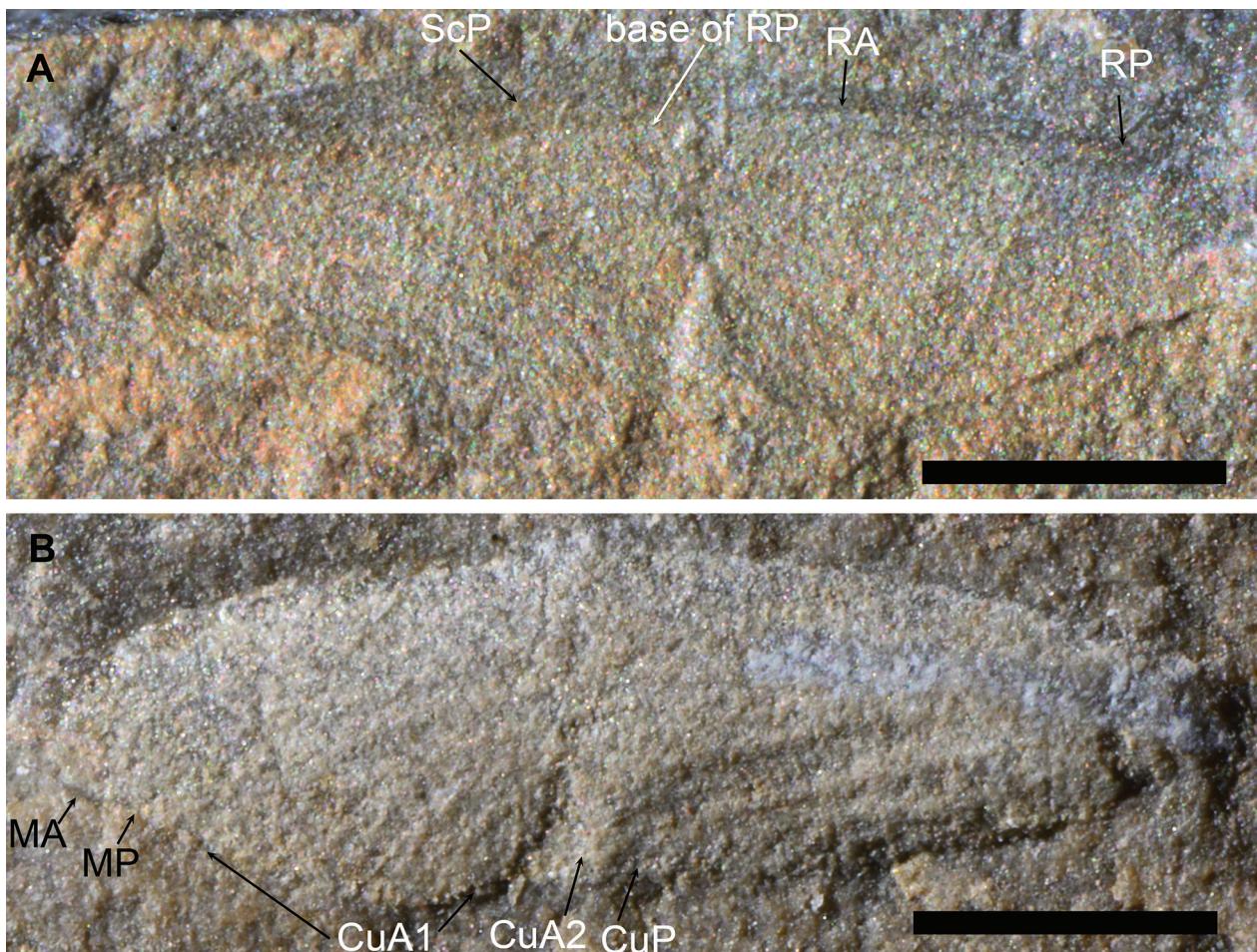


Figure 2. *Probnis sauvanyaensis* sp. nov., holotype IPS125664. Forewing photographs. A, Part. B, Counterpart. Scale bars: 1 mm.

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 Isoptoria are non-monosemantic circumscriptional synonyms of Holopandictyoptera and Cryptovipositoria. Holopandictyoptera and Cryptovipositoria.” Here, we consider that the Paleozoic roachoids belong to the stem group of the extant Dictyoptera (Blattodea and Mantodea) because they share at least one unique synapomorphy in the strongly concave and curved forewing vein CuP (Prokop et al. 2014).

Family SPILOBLATTINIDAE Handlirsch, 1906

Genus and species undetermined

Fig. 3

Material. Specimen IPS125659 (part and counterpart of the distal two-thirds of a forewing), stored at the Institut Català de Paleontologia Miquel Crusafont, Sabadell, Catalonia, Spain.

Age and outcrop. Guadalupian–?Lopingian, upper Upper Red Unit. Sauvanya, Catalonia, Spain.

Description. An incomplete tegmen, preserved part 12.5 mm long, 4.2 mm wide, with faint traces of coloration; area between C and RP 1.5 mm wide; area between R/RP and M/MA 0.3 mm wide; area between M/MP and CuA 0.4 mm wide; median area wider than that of RP; area of CuA slightly narrower than median area; RP regularly anteriorly pectinate; MA forked nearly at mid-wing level; MP regularly anteriorly pectinate, some of its branches forked again, reaching wing apex; CuA with a faint anterior branch, otherwise posteriorly pectinate, with all branches simple except the forked penultimate one; R, M, and CuA weakly sigmoidal; CuP(+PCu) regularly curved; seven simple and curved veins in anal area, parallel to CuP(+PCu).

Remarks. Although incompletely preserved, this roachoid tegmen could fall in one of the three families Phylloblattidae Schneider, 1983, Spiloblattinidae Handlirsch, 1906, or Subioblattinidae Schneider, 1983, because of the anteriorly and regularly pectinate RP and M (see Schneider 1983). The Subioblattinidae are characterized by sigmoidal main vein stems of R, M, and CuA, and often undulating branches of main veins (Papier and Nel 2001; Hinkelman 2022). The new fossil has a vein M that is rather sigmoidal, but it is not the case for veins R and CuA. Secondarily, the Subioblattinidae are currently known by Triassic taxa, but this is not a real argument against the presence of a taxon of this family

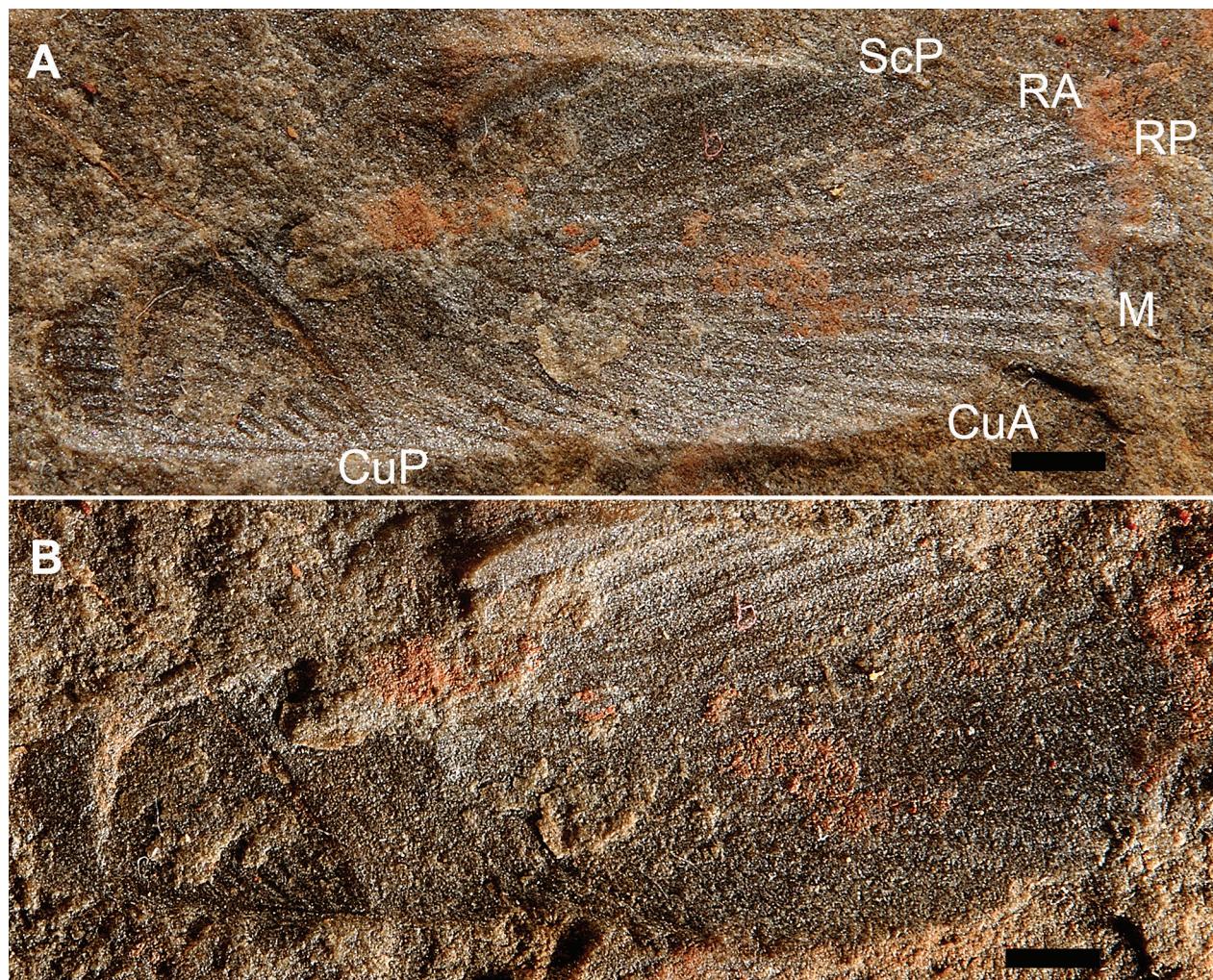


Figure 3. Spiloblattinidae, genus and species undetermined, specimen IPS125659. Forewing photographs. A, Part; B, Counterpart, mirrored. Scale bars: 1 mm.

in the Permian. Schneider et al. (2021: 268) proposed an emended diagnosis for the Spiloblattinidae, separating this family from the Phylloblattidae as follows: the Spiloblattinidae have a ‘phyloblattid-like wing venation pattern but with a much lower number of veins and with extended fields between the main veins [present in the fossil]. Subcostal field strip-like. ScP pectinate, branches end inclined at the anterior wing margin [unknown in the fossil]. R sigmoidal, often with distinct RA [unknown in the fossil]. R branches terminate at anterior wing margin [present in the fossil]. M sigmoidal, multiple-forked [present in the fossil], 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 [present in the fossil]. CuA long sigmoidal [present in the fossil]. First, CuA sigmoidal [present in the fossil]. CuA twigs arise by branching from CuA stem and are rarely forked; all further branches arise by furcation [present in the fossil]. CuP(+PCu) regularly bent [present in the fossil]. Anal field with regularly spaced and bent anal veins [present in the fossil]. Thus, the new fossil fits well with this diagnosis for the Spiloblattinidae.

Nevertheless, the current diagnosis of the Compsoblattidae (unique genus *Compsoblatta* Schlechtendal in Handlirsch,

1906–1908) (after Belahmira et al. 2019: 962) is nearly the same as that of the Spiloblattinidae, with the following differences: ‘The general venation pattern is similar to that of *Phylloblatta*, but in contrast to this genus, the cross-venation 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. These differences are so faint that they would hardly justify a genus separation among modern Blattodea and certainly not a separation between families. In the new fossil, the area covered by the vein RP seems to be less extended distally than in *Compsoblatta* (see Schneider 1983: pl. 3, fig. 7). Also, the area between RP and M is broader in the new fossil than in *Compsoblatta*.

Schneider et al. (2021) added that the ‘most diagnostic [character of the Spiloblattinidae] is a fenestrate color pattern consisting of pale areas of various extent between the main veins and their branches.’ But *Compsoblatta* also shows such a fenestrate pattern of coloration. Also, it is quite uncertain to base the diagnosis of a roachoid family

on such pattern of coloration because similar patterns of coloration are present in some extant taxa of the family Ectobiidae but clearly not all of them (see discussion in Nel et al. 2022). There is no clear pattern of coloration preserved in the new fossil.

On the basis of the venation, we tentatively attribute the new fossil to the Spiloblattinidae rather than Compsoblattidae. The Spiloblattinidae sensu Schneider et al.'s (2021) point of view currently comprises the genera *Spiloblattina* Scudder, 1885, *Syscioblatta* Handlirsch, 1906, *Kinklidoblatta* Handlirsch, 1906, *Sysciophlebia* Handlirsch, 1906, and *Kinneyblatta* Schneider et al. 2021. Nel et al. (2022) and Garrouste et al. (2025) compared the diagnoses of these genera and indicated that the differences are very faint, mainly based on the color patterns. As these are unavailable in the new fossil, it is not possible to attribute it to a precise genus.

Discussion and conclusion

With occurrences in the Permian of the USA and Spain, the genus *Probnis* is recorded in outcrops near the paleo-equatorial zone in the eastern and western margins of central Pangea, under arid and warm paleoclimates; Ukraine was also under a dry and warm climate during the Triassic (see the PALEOMAP Project site at <http://www.scotese.com/climate.htm>). Thus, being probably adapted to rather extreme climates and thanks to their small sizes compared to the other Permian Grylloblattodea, the family was able to survive the global warming of the Permian–Triassic crisis (Chen et al. 2022; Gliwa et al. 2023). Unfortunately, nothing is known about the biology of these insects. It is not surprising to find a Spiloblattinidae in the Permian of the Iberian Peninsula, as Nel et al. (2022) already described one from the upper Carboniferous in its northwestern region. Numerous Permian representatives of this family are already known in other countries.

These new fossil insects are the first ones from the Permian of the Iberian Peninsula. They are attributed to Grylloblattodea and Dictyoptera and therefore enlarge the distribution of these groups in time and space. They also contribute to our knowledge of the rich Permian faunal assemblage of the Catalan Pyrenees, which is already known by scarce vertebrate bones and more abundant ichnofossils (e.g., Fortuny et al. 2011; Mujal et al. 2016, 2017; De Jaime-Soguero et al. 2023).

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References

Aristov DS (2005) New grylloblattids (Insecta, Grylloblattida) from the Triassic of Eastern Europe, Eastern Kazakhstan and Mongolia. Paleontological Journal 39(2): 173–177.

Belahmira A, Schneider JW, Scholze F, Saber H (2019) Phylobattidae and Compsoblattidae (Insecta, Blattodea) from the late Carboniferous Souss basin, Morocco. Journal of Paleontology 93 (5): 945–965. <https://doi.org/10.1017/jpa.2019.20>

Carpenter FM (1950) The Lower Permian insects of Kansas. Part 10. The order Protorthoptera: the family Liomopteridae and its relatives. Proceedings of the American Academy of Arts and Sciences 78: 185–219. <https://doi.org/10.2307/20023577>

Cawood R, Nel A, Garrouste R, Moyo S, Villet MH, Prevec R (2022) The first ‘Grylloblattida’ of the family Liomopteridae from the middle Permian in the Onder Karoo, South Africa (Insecta, Polyneoptera). Comptes Rendus Palevol 21(22): 451–461. <https://doi.org/10.5852/cr-palevol2022v21a22>

Fortuny J, Bolet A, Sellés AG, Cartanyà J (2011) New insights on the Permian and Triassic vertebrates from the Iberian Peninsula with emphasis on the Pyrenean and Catalonian basins. Journal of Iberian Geology 37(1): 65–86. https://doi.org/10.5209/rev_JIGE.2011.v37.n1.5

Gall J-C (1971) Faunes et paysages du Grès à Voltzia du Nord des Vosges. Essai paléocologique sur le Buntsandstein supérieur. Mémoires du Service de la Carte géologique d'Alsace-Lorraine 34: 1–318.

De Jaime-Soguero C, Mujal E, Oms O, Bolet A, Dinarès-Turell J, Ibáñez-Insa J, Fortuny J (2023) Palaeoenvironmental reconstruction of a lower to middle Permian terrestrial composite succession from the Catalan Pyrenees: implications for the evolution of tetrapod ecosystems in equatorial Pangaea. Palaeogeography, Palaeoclimatology, Palaeoecology 632: 111837. <https://doi.org/10.1016/j.palaeo.2023.111837>

Garrouste R, Boderau M, Nel A (2025) New roachoids (Dictyoptera, Spiloblattinidae) from the ‘red’ Permian of Gonfaron (Southern France). Historical Biology. <https://doi.org/10.1080/08912963.2025.2472158>

Gisbert J (1981) Estudio geológico, petrológico del Estefaniense-Pér-mico de la Sierra del Cadí (Pirineo de Lérida): Diagénesis Y Sedimentología. Universidad de Zaragoza, Spain. PhD Thesis.

Gretter N, Ronchi A, López-Gómez J, Arche A, De la Horra R, Barrenechea JF, Lago M (2015) The late Palaeozoic-early Mesozoic

from the Catalan Pyrenees (Spain): 60 Myr of environmental evolution in the frame of the western peri-Tethyan palaeogeography. *Earth Science Review* 150: 679–708. <https://doi.org/10.1016/j.earscirev.2015.09.001>

Gliwa J, Wiedenbeck M, Schobben M, Ullmann CV, Kiessling W, Ghaderi A, Struck U, Korn D (2022) Gradual warming prior to the end-Permian mass extinction. *Palaeontology* 65(5): e12621. <https://doi.org/10.1111/pala.12621>

Handlirsch A (1906–1908) Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein Handbuch für Paläontologen und Zoologen. Engelmann, V.W. publ., Leipzig, 1–1430. <https://doi.org/10.5962/bhl.title.34145>

He W, Shi GR, Feng Q, Campi M (2007) Brachiopod miniaturization and its possible causes during the Permian-Triassic crisis in deep water environments, South China. *Palaeogeography Palaeoclimatology Palaeoecology* 252(1): 145–163. <https://doi.org/10.1016/j.palaeo.2006.11.040>

Hinkelman J (2022) A monospecific assemblage of cockroaches (Dictyoptera, Subioblattidae) from the Triassic of Kyrgyzstan. *PalZ* 96(4): 781–793. <https://doi.org/10.1007/s12542-022-00617-7>

Kluge NJ (2010) Circumscriptional names of higher taxa in Hexapoda. *Bionomina* 1: 15–55. <https://doi.org/10.11646/bionomina.1.1.3>

Li X-R (2019) Disambiguating the scientific names of cockroaches. *Palaeoentomology* 2(4): 390–402. <https://doi.org/10.11646/palaeoentomology.2.4.13>

Li X-R, Zheng YH, Wang CC, Wang ZQ (2018) Old method not old-fashioned: parallelism between wing venation and wing-pad tracheation of cockroaches and a revision of terminology. *Zoomorphology* 137(4): 5198533. <https://doi.org/10.1007/s00435-018-0419-6>

Mujal E (2017) Registre sedimentari i icnològic del fini-Carbonífer, Permià i Triàsic continentals dels Pirineus Catalans: Evolució i crisi paleoambientals a l'equador de Pangea. Universitat Autònoma de Barcelona, Spain, PhD Thesis.

Mujal E, Gretter N, Ronchi A, López-Gómez J, Falconnet J, Diez JB, De la Horra R, Bolet A, Oms O, Arche A, Barrenechea JF, Steyer JB, Fortuny J (2016) Constraining the Permian/Triassic transition in continental environments: Stratigraphic and paleontological record from the Catalan Pyrenees (NE Iberian Peninsula). *Palaeogeography, Palaeoclimatology, Palaeoecology* 445: 18–37. <https://doi.org/10.1016/j.palaeo.2015.12.008>

Mujal E, Fortuny J, Pérez-Cano J, Dinarès-Turell J, Ibáñez-Insa J, Oms O, Vila I, Bolet A, Anadón P (2017) Integrated multi-stratigraphic study of the Coll de Terrers late Permian-early Triassic continental succession from the Catalan Pyrenees (NE Iberian Peninsula): a geologic reference record for equatorial Pangaea. *Global and Planetary Change* 159: 46–60. <https://doi.org/10.1016/j.gloplacha.2017.10.004>

Nel A, Santos AA, Hernández-Orúe A, Wappler T, Diez JB (2022) The first representative of the roachoid family Spiloblattinidae (Insecta, Dictyoptera) from the Late Pennsylvanian of the Iberian Peninsula. *Insects* 13: 828. <https://doi.org/10.3390/insects13090828>

Papier F, Nel A (2001) Les Subioblattidae (Blattodea, Insecta) du Trias d'Asie Centrale. *Paläontologische Zeitschrift* 74(4): 533–542. <https://doi.org/10.1007/BF02988160>

Prokop J, Krzemiński W, Krzemińska E, Hörschemeyer T, Ilger J-M, Brauckmann C, Grandcolas P, Nel A (2014) Late Palaeozoic Paoliiida is the sister group of Dictyoptera (Insecta, Neoptera). *Journal of Systematic Palaeontology* 12(5): 601–622. <https://doi.org/10.1080/14772019.2013.823468>

Rasnitsyn AP, Aristov DS, Gorochov AV, Rowland JM, Sinitshenkova ND (2004) Important new insect fossils from Carrizo Arroyo and the Permo-Carboniferous faunal boundary. In: Lucas SG, Zeigler KE (eds). *Carboniferous-Permian transition at Carrizo Arroyo, Central New Mexico*. Bulletin of the New Mexico Museum of Natural History and Science 25: 215–246.

Saura E, Teixell A (2006) Inversion of small basins: effects on structural variations at the leading edge of the Axial Zone antiformal stack (Southern Pyrenees, Spain). *Journal of Structural Geology* 28(11): 1909–1920. <https://doi.org/10.1016/j.jsg.2006.06.005>

Speksnijder A (1985) Anatomy of a strike-slip fault controlled sedimentary basin, Permian of the Southern Pyrenees, Spain. *Sedimentary Geology* 44: 179–223. [https://doi.org/10.1016/0037-0738\(85\)90014-4](https://doi.org/10.1016/0037-0738(85)90014-4)

Schneider JW (1983) Die Blattodea (Insecta) des Paläozoikums, 1: Systematik, Ökologie und Biostratigraphie. *Freiberger Forschungshefte (C)* 382: 107–146.

Schneider JW, Scholze F, Ross AJ, Blake BM Jr, Lucas SG (2021) Improved blattoid insect and conchostracan zonation for the late Carboniferous, Pennsylvanian, of Euramerica. *The Geological Society Special Publications* 512: 1–27. <https://doi.org/10.1144/SP512-2021-93>

Schubnel T (2021) L'évolution des insectes passée aux rayons X: étude des homologies de nervation alaire via la µCT et le registre fossile. *Museum National d'Histoire Naturelle*, Paris, PhD Thesis.

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>

Scudder SH (1895) Revision of North American fossil cockroaches with descriptions of new forms. *Bulletin of the United States Geological Survey* 124: 1–176. <https://doi.org/10.3133/b124>

Sellards EH (1908) Cockroaches of the Kansas coal measures and of the Kansas Permian. *The University Geological Survey of Kansas* 9(11): 501–541.

Storozhenko SYu (1998) Sistematika, filogeniya i evolyutsiya grilloblattidovkh nasekomykh (Insecta, Grylloblattida) [Systematics, phylogeny and evolution of the grylloblattids (Insecta, Grylloblattida)]. Dal'nauka, Vladivostok, 1–207. [in Russian]

Thuy B, Eriksson M., Kutscher M., Lindgren J, Lea D, Numberger-Thuy LD, Wright DF (2022) Miniaturization during a Silurian environmental crisis generated the modern brittle star body plan. *Communication Biology* 5: 14. <https://doi.org/10.1038/s42003-021-02971-9>

Tillyard RJ (1937) Kansas Permian insects. 19. The order Protopleraria. The family Probnisidae. *American Journal of Science* 33(5): 401–425. <https://doi.org/10.2475/ajs.s5-33.198.401>

Vergés J (1993) Estudi geològic del vessant sud del Pirineu oriental i central. Evolució cinemàtica en 3D. Universitat de Barcelona, Barcelona, PhD Thesis.