



Trigonotarbids (Arachnida) hidden in plant debris from a Late Pennsylvanian tropical forest at El Bierzo, Castilla y León, Spain

Artai A. Santos¹ · Jason A. Dunlop² · Antonio Hernández-Orúe³ · Paul A. Selden^{4,5} · José B. Diez⁶ · Stephen McLoughlin¹

Received: 17 October 2024 / Accepted: 2 August 2025

© The Author(s) 2025

Abstract

Two new fossils belonging to the extinct arachnid order Trigonotarbida are described from uppermost Carboniferous (Gzhelian, Upper Pennsylvanian) strata of the Villablino and El Bierzo basins (Castilla y León; NW Spain). These discoveries represent the second and third Spanish records of this arachnid order and are among the oldest arachnid records known from the Iberian Peninsula. They also represent the first evidence of arachnids from the Villablino and El Bierzo basins. One fossil consists of an almost complete individual including the prosoma, opisthosoma, legs and pedipalps but its preservation in ventral view makes unequivocal identification difficult. Comparison with other material favours its assignment to *Aphantomartus* sp. (Aphantomartidae). The second specimen consists of a prosoma and opisthosoma preserved in dorsal view and is assigned to *Aphantomartus areolatus*. These two arachnids were preserved alongside several plant remains referable to ferns (*Polymorphopteris polymorpha*, *Polymorphopteris integra*, *Nemejcopteris feminaeformis* and *Oligocarpia leptophylla*), seed-ferns (*Neuropteris ovata*) and lycophytes (*Cyperites bicarinatus*). The abundance and diversity of co-occurring plant remains are consistent with the other known Spanish *Aphantomartus* record, which is also preserved in association with several plant fossils. Based on the new occurrences, we infer that *Aphantomartus* favoured humid, broad-leafed, evergreen forest habitats that provided a diverse array of food and shelter.

Keywords Arachnids · Aphantomartidae · *Aphantomartus* · Palaeobotany · Plant-arthropod interactions · Gzhelian

Handling Editor: Ulrich Kotthoff.

✉ Jason A. Dunlop
Jason.dunlop@mf.n.berlin

¹ Department of Palaeobiology, Swedish Museum of Natural History, Box 50007, 104 05 Stockholm, Sweden

² Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity, Humboldt University Berlin, Berlin, Germany

³ Independent researcher, Álava, Spain

⁴ Department of Geology, University of Kansas, Lawrence, KS, USA

⁵ Natural History Museum, London, UK

⁶ Departamento de Xeociencias Mariñas e Ordenación do Territorio, Facultade de Ciencias do Mar, Universidade de Vigo, 36310 Vigo, Spain

Introduction

Trigonotarbids (Arachnida: Trigonotarbida) are an extinct order of arachnids recorded from the late Silurian to the early Permian (Dunlop, 1996, 2010; Dunlop & Rößler, 2013; Dunlop & Selden, 2004; Dunlop et al., 2008; Poschmann & Dunlop, 2010). Most are of late Carboniferous age and are particularly concentrated in the former coal mining districts of Great Britain through to central Europe (Table 1; Dunlop & Rößler, 2013; Fig. 6; Dunlop et al., 2008). By contrast, trigonotarbid fossils from the Iberian Peninsula are very scarce (Table 1). Selden and Romano (1983) reported *Aphantomartus areolatus* Pocock, 1911 (Aphantomartidae) from the Prado Formation (mid-Cantabrian, i.e., lower Kasimovian) of the Guardo Coalfield in León Province, northwestern Spain (Knight et al., 2023). Correia et al. (2013) reported *Aphantomartus pustulatus* Scudder, 1884 from lower Gzhelian strata of the São Pedro da Cova region of northwestern Portugal and commented on the biogeographical implications of their discovery.

Table 1 Trigonotarbida records from the Iberian Peninsula, including the two new specimens

Order and family	Species	Stage	Locality, basin and country	References
Trigonotarbida (Aphantomartidae)	<i>Aphantomartus areolatus</i>	mid-Cantabrian (lower Kasimovian)	Guardo Coalfield (León, Spain)	Selden and Romano (1983)
Trigonotarbida (Aphantomartidae)	<i>Aphantomartus pustulatus</i>	lower Gzhelian	São Pedro da Cova (Portugal)	Correia et al. (2013)
Trigonotarbida (Aphantomartidae)	<i>Aphantomartus</i> sp.	upper Stephanian B (Gzhelian)	Chuchú-Navaleo section in El Bierzo Coalfield (León, Spain)	This study
Trigonotarbida (Aphantomartidae)	<i>Aphantomartus areolatus</i>	upper Stephanian B (Gzhelian)	Calderón Group, Villablino Coalfield (León, Spain)	This study

Note that the ages of all occurrences were recalibrated according to stratigraphical data from Wagner and Álvarez-Vázquez (2010) and Knight et al. (2023)

Superficially, trigonotarbids resemble spiders, to which they are closely related. However, trigonotarbids are characterised by an opisthosoma divided dorsally into rows of three or five plates. More than seventy species are currently recognised in nine families (Garwood & Dunlop, 2010; Jones et al., 2014), seven of which are known from the Carboniferous.

Isolated and cryptic arthropod remains associated with fossil vegetation and the damage features that these invertebrates inflicted upon plants provide insights into the biodiversity, ecological interactions and energy flow within late Palaeozoic forest ecosystems—most of which have no close modern analogues to extant communities. Historically, very few studies have focused on the arthropods and putative plant–arthropod interactions from the Carboniferous of Spain (see Santos et al., 2023, Table 1). However, several recent works have provided insights into the diversity of arthropods in this region and their possible palaeoecological relationships with plants in the Pennsylvanian ecosystems of Iberia (Santos et al., 2024; Nel et al., 2022a, 2022b; Santos et al., 2022, 2023). These studies have focused mostly on fossil insects and plant–insect interactions, but insights into the taxonomy and palaeoecology of arachnids that cohabited these Carboniferous forests are lacking. In order to advance palaeoecological interpretations of these ancient terrestrial ecosystems, we report two new Gzhelian (Late Pennsylvanian) arachnid occurrences from the Villablino and El Bierzo coalfields (León Province, NW Spain). We aim to: (1) describe and identify the new trigonotarbid fossils; (2) identify the plant remains associated with the arachnids; and (3) evaluate the palaeoecological and palaeobiogeographic implications of the fossil assemblages.

Geological setting and palaeoenvironments

The slabs hosting the new arachnid fossils were recovered from two localities in León Province, Spain: the Chuchú-Navaleo section in the Bierzo Coalfield and the Calderón

interval in the Villablino Coalfield (Fig. 1). Both sites expose Stephanian B strata sensu Wagner and Álvarez-Vázquez (2010). Based on correlations by Knight et al. (2023) this “substage” corresponds to the middle–upper Gzhelian (Upper Pennsylvanian: dated to ca. 300 Ma).

The studied region has complex geology resulting from deformation during the final phases of the Hercynian Orogeny. At the end of the Carboniferous, following predominantly marine deposition, sediments laid down in the Rheic Ocean were uplifted and began to emerge above sea level. In the mid-late Barruelian (late Kasimovian), the Asturian phase of tectonic uplift (Stille, 1920; Wagner, 1957, 1965), produced sediments that were deposited in several coal basins, including the Villablino and El Bierzo basins (= coalfields) (Wagner & Álvarez-Vázquez, 2010). To the east (e.g., Picos de Europa), the post-Asturian terrestrial deposits are locally intercalated with marine facies (Wagner & Martínez-García, 1998; Merino-Tomé et al., 2006). By contrast, sedimentation in the western areas was predominantly continental. Although no fully marine deposits have been identified, bivalves recovered from Sabero, Ciñera-Matallana, and La Magdalena indicate the presence of paralic or brackish depositional environments (Eagar, 1985; Eagar & Weir, 1971; Knight, 1971). This marine influence is corroborated by the discovery of a pygidium belonging to the trilobite (or trilobite derivative?) *Cinerana matallanensis* Gandl, 2021, in Ciñera-Matallana (Gandl, 2021; Wagner & Castro, 2011).

Despite the current isolation of post-Asturian sedimentary succession outliers, it is estimated that at least some of them, especially the westernmost ones, originally formed a single foreland basin with sediments sourced from the mountains to the north and west and drainage towards the Palaeotethys Ocean in the east (Wagner & Castro, 2011). This basin accumulated terrigenous sediments in paralic successions alternating with marine platform carbonate deposits, and turbidite or olistolith accumulations (Knight & Álvarez-Vázquez, 2021). The interpretation of a formerly

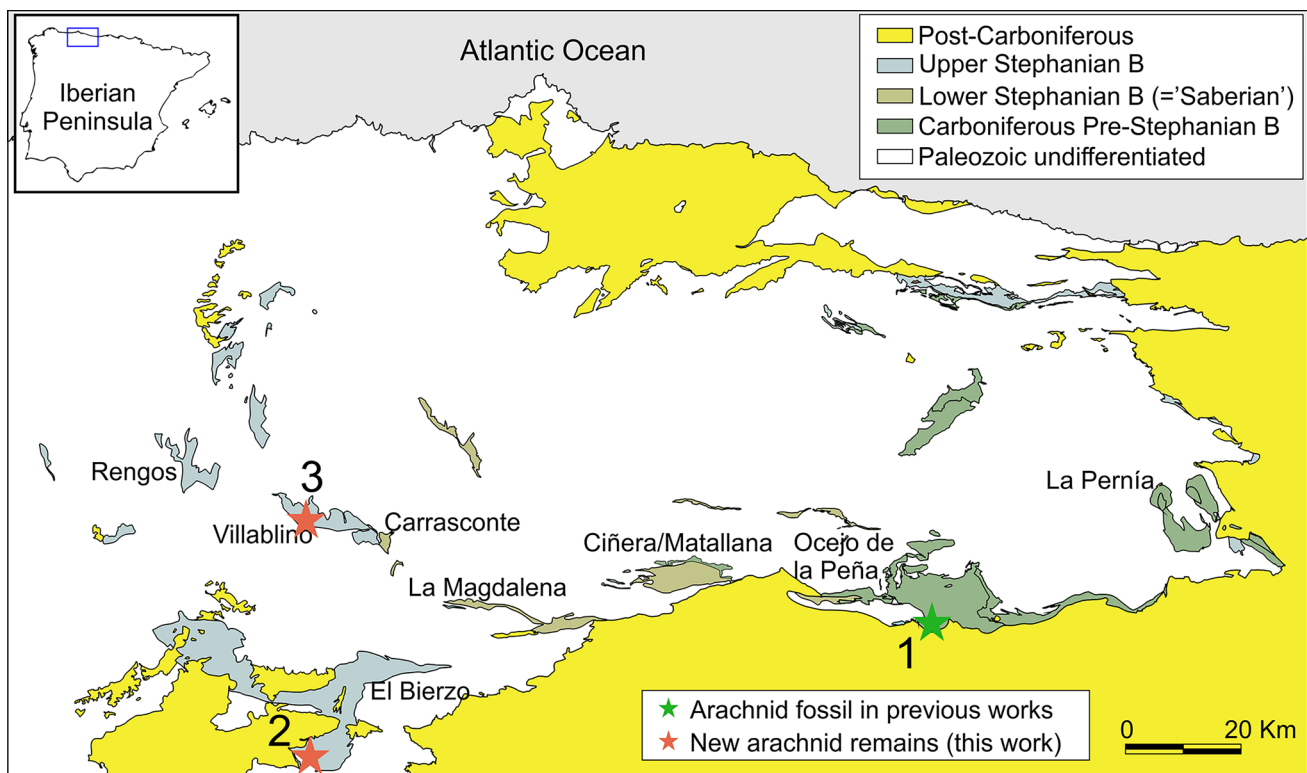


Fig. 1 Geographical and geological map of the Palaeozoic deposits of the northern Iberian Peninsula. Modified from Santos et al. (2022). The red stars indicate the deposits and position in which the arachnids AF/0127 and MCNA-15041 were collected. 1: *Aphantomartus*

areolatus in Selden and Romano (1983) from the Guardo Basin; 2: *Aphantomartus* sp. (AF/0127) from the El Bierzo Basin; 3: *Aphantomartus areolatus* (MCNA-15041) from the Villablino Basin

extensive sedimentary basin is supported by the presence of large braided fluvial channel deposits (Bashforth et al., 2010; Colmenero et al., 1996), which are more typical of basins with a significant spatial extent (Bashforth et al., 2010).

This single post-Asturian basin expanded westward during the late Stephanian as the mountains became eroded, although Wagner and Castro (2011) argued that simultaneous eastward encroachment cannot be excluded. These authors noted that this westward expansion of the basin is particularly recorded in the succession of the aligned basins of Sabero, Ciñera-Matallana, La Magdalena and Carrasconte/Villablino (with a possible continuation to those of Rengos, Cangas del Narcea, Tineo, and Arnao) and, perhaps, also in the aligned basins of Canseco, Rucayo, and Puerto Ventana. However, Knight et al. (2023) indicated that apart from the succession represented in the Sabero and Ciñera-Matallana basins, the remaining isolated exposures are less obviously related in the absence of correlatable lithologies. Therefore, although the two Trigonotarbida specimens in this study are described from different outcrops, we cannot exclude the possibility that they derive from a formerly contiguous sedimentary basin.

The Carboniferous coalfields of León have yielded various terrestrial arthropod fossils, but these are mostly insect

remains including Palaeodictyoptera (Santos et al., 2023), Megasecoptera (Brauckmann, 1993; Carpenter, 1963; Santos et al., 2023), Archaeorthoptera (Brauckmann et al., 2001; Santos et al., 2023), Paoliida (Santos et al., 2023), Caloneurodeia (Santos et al., 2024) and Dictyoptera (Álvarez-Ramis, 1990; Álvarez-Ramis et al., 1986; Brauckmann, 1993; Iwaniw, 1985; Nel et al., 2022b). Plant–arthropod interactions were also reported from this area (Santos et al., 2022). As noted above, the only trigonotarbid found previously in Spain (one of only two from the Iberian Peninsula), derives from León and was assigned to *Aphantomartus areolatus* by Selden and Romano (1983) more than 40 years ago.

Materials and methods

The new material consists of two arachnid specimens found in different lithologies at two localities in León (Spain) by Don José Vicente Casado. Specimen AF/0127, the ventral surface of an arachnid with legs and pedipalps (Fig. 2a, b) is preserved as a compression with a red–orange patina in grey siltstones. Specimen MCNA-15041 is the mould of the dorsal surface of an arachnid lacking appendages (Fig. 3c) preserved in dark grey siltstones. Both specimens

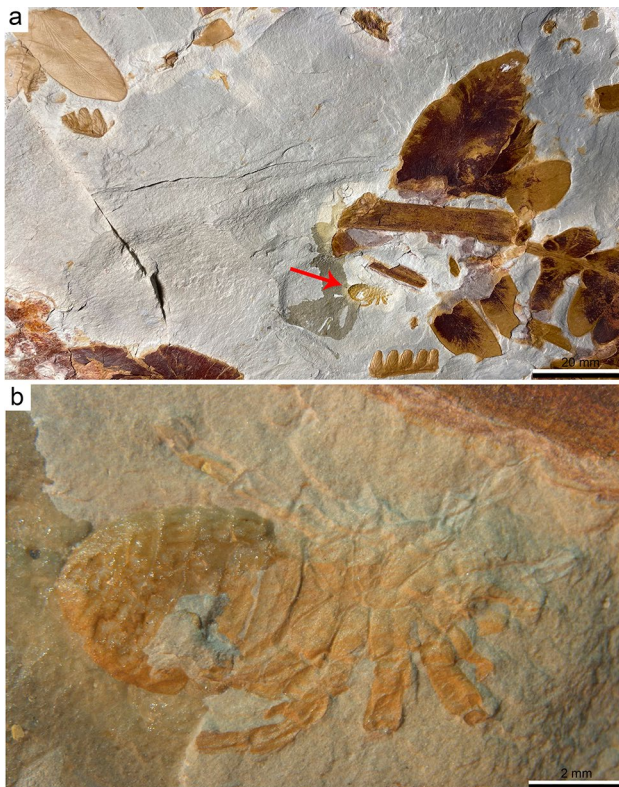
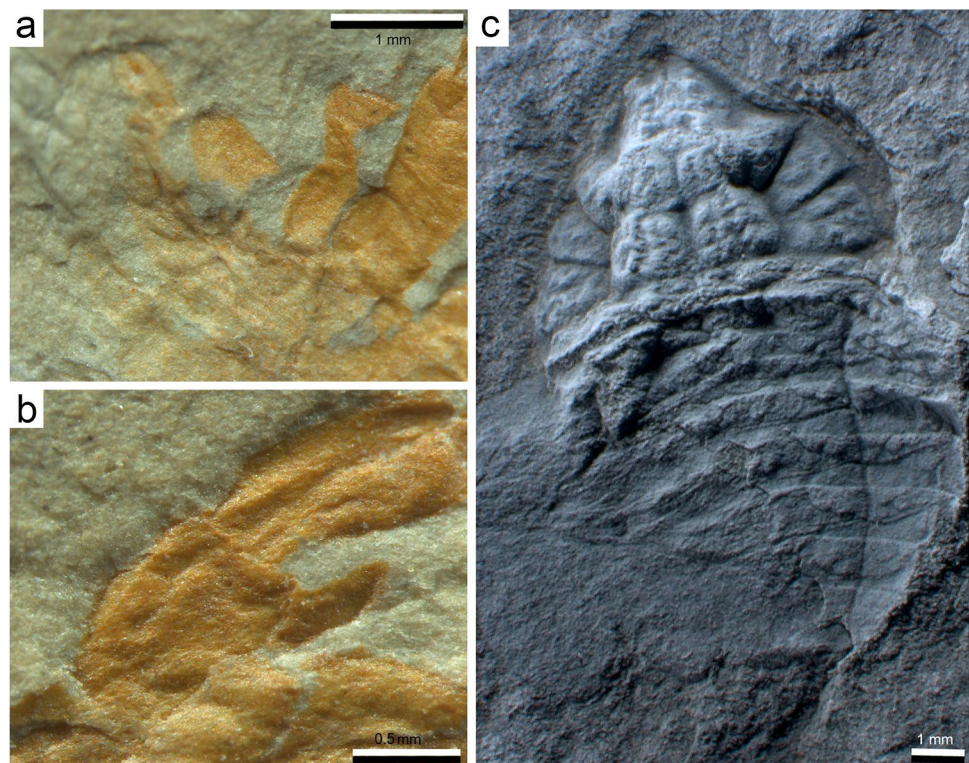


Fig. 2 **a** General view of the slab bearing the arachnid AF/0127 (red arrow) in association with debris of *Neuropteris ovata* and *Nemejopteris feminaeformis*; Scale=20 mm. **b** Details of the ventral side of the trigonotarbid AF/0127; Scale=2 mm

Fig. 3 **a** Details of the mouthparts of *Aphantomartus* sp. (specimen AF/0127); Scale=1 mm. **b** Detail of the grappling or fighting spine on one of the legs (specimen AF/0127). Scale=500 μ m. **c** View of impression of dorsal surface of *Aphantomartus areolatus* (Specimen MCNA-15041); Scale=1 mm



were carefully prepared using needles, brushes and air scribes. Specimen AF/0127 was photographed, both dry and immersed in alcohol, with a Leica MC170-HD camera attached to a Leica M205-C stereomicroscope at the Laboratory of Palaeobotany (Universidade de Vigo). Photographs of specimen MCNA-15041 were taken with an Olympus Tough TG-5 camera using natural sunlight at the Museum of Natural Sciences of Álava, Vitoria, Spain. Line drawings of the specimens (Fig. 4) were compiled using a camera-lucida and retraced in Adobe Photoshop CS6 and Adobe Illustrator. Photographs of associated plants were taken with an Olympus Tough TG-5 and Leica MC170-HD camera attached to a Leica M205-C stereomicroscope. The plants (Figs. 5, 6) were identified using specific palaeobotanical literature from the region (e.g., Castro, 2005; Hernández-Orúe, 2024 and references herein). The fossils are stored in the Museo del Alto Bierzo, in Bembibre (AF/0127) and the Museum of Natural Sciences of Álava, in Vitoria (MCNA-15041). Detailed information on the sources of the fossils can be obtained from the respective institutions by bona fide researchers. Morphological terminology for trigonotarbids follows that of Dunlop (1996).

Systematic palaeontology

Subphylum **Chelicerata** Heymons, 1901

Class **Arachnida** Lamarck, 1801

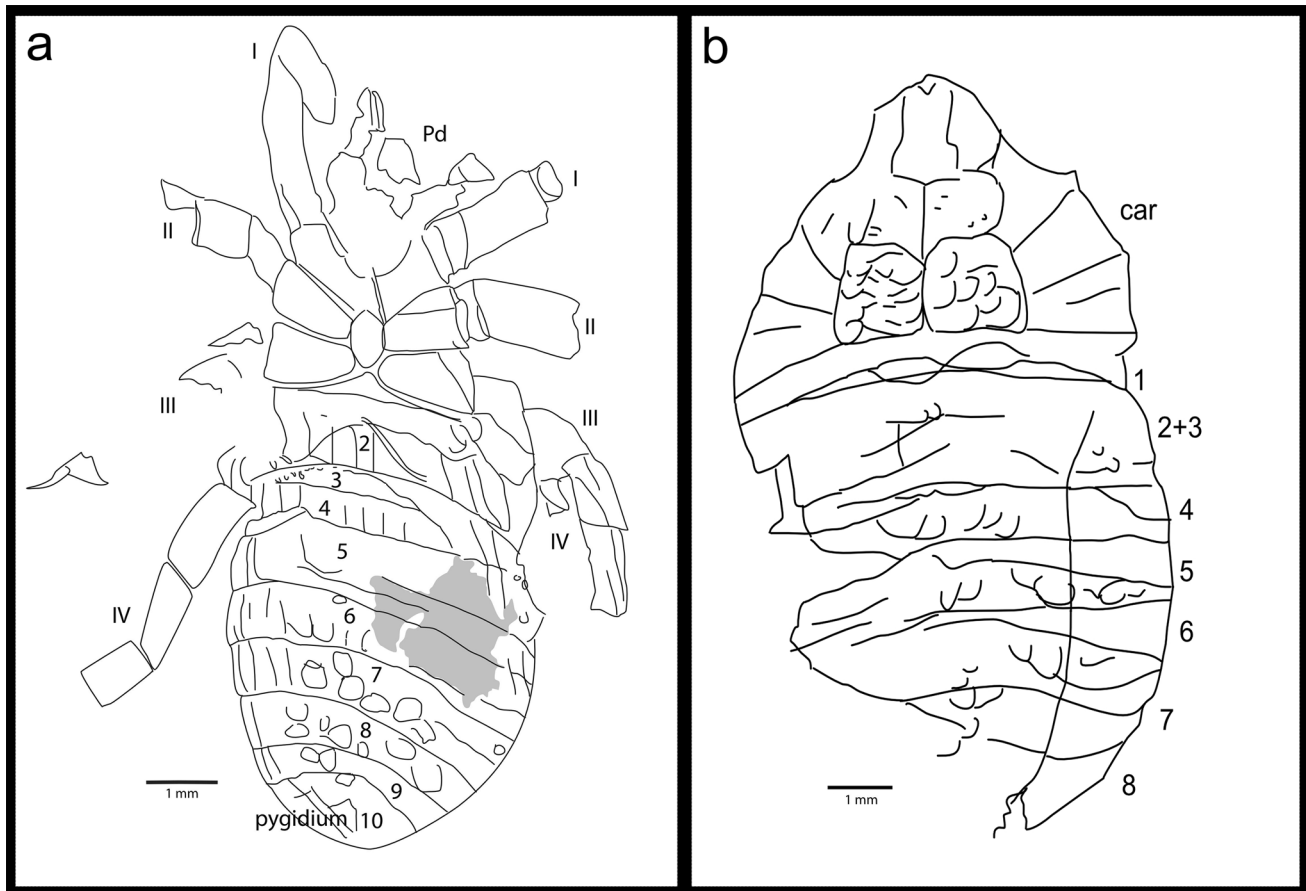


Fig. 4 **a** Drawing of the ventral view of specimen AF/0127 (*Aphantomartus* sp.); Scale=1 mm. **b** Drawing of the dorsal view of specimen MCNA-15041 (*Aphantomartus areolatus*); Scale=1 mm

Order **Trigonotarbida** Petrunkevitch, 1949
 Family **Aphantomartidae** Petrunkevitch, 1945
 (= **Trigonomartidae** Petrunkevitch, 1949)
 Genus *Aphantomartus* Pocock, 1911
 Species *Aphantomartus* sp.
 Figures 2, 3a, b and 4a

Material. Sample AF/0127; orange-red body compression with limbs preserved in grey siltstone associated with several plant remains (see Fig. 2); stored at Museo del Alto Bierzo (Bembibre, León Province, Spain).

Age, stratigraphy and locality. Stephanian B (Gzhelian, Late Pennsylvanian); Chuchú-Navaleo section in the Bierzo Coalfield, Santa Marina de Torre, León Province, Castilla y León, northern Spain (Fig. 1).

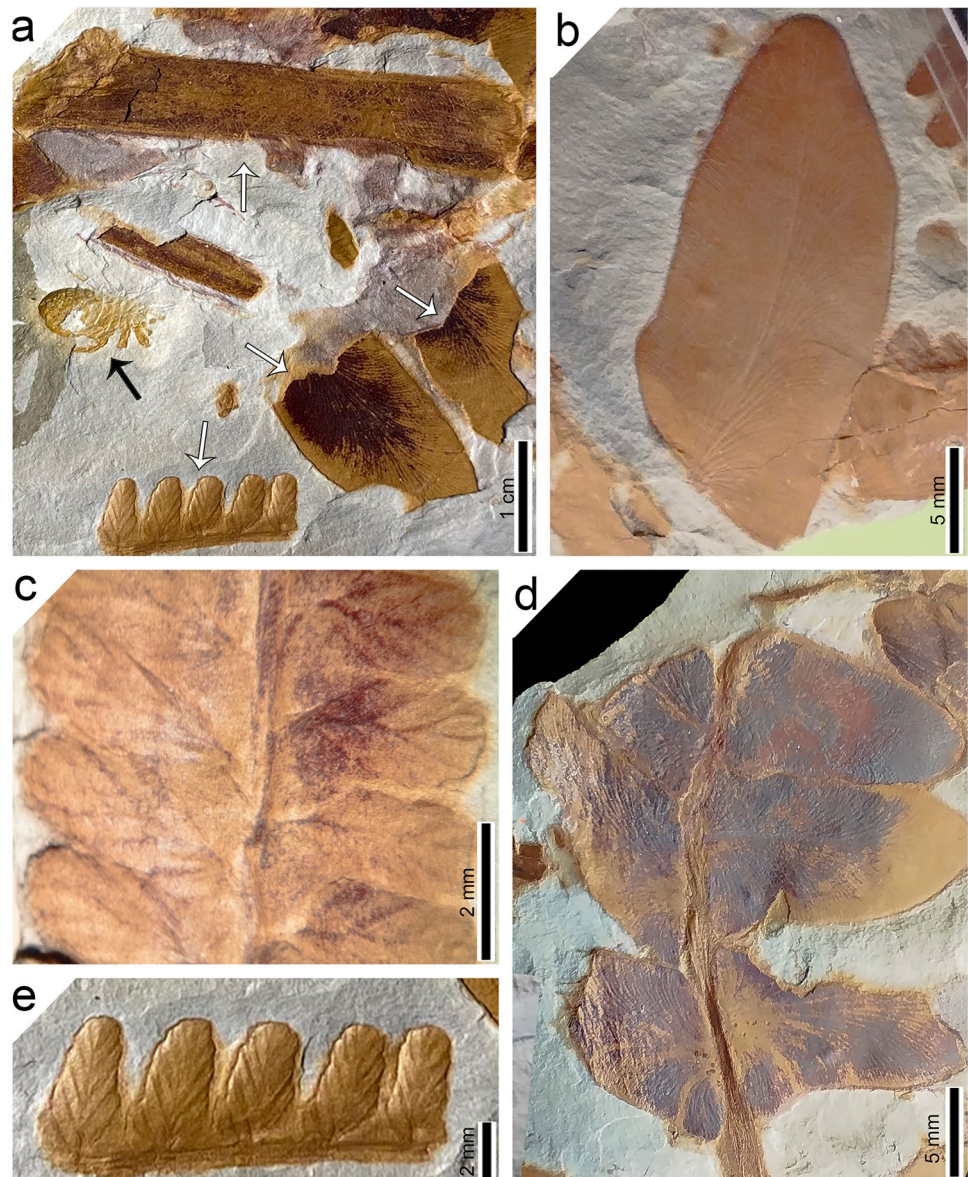
Description. Ventral surface of prosoma and opisthosoma (possibly with superimposed dorsal opisthosomal features) with partial preservation of the legs, pedipalps and pygidium. Relatively small aphantomartid, 11.7 mm long and 8.9 mm wide, subtriangular with oval to circular clypeus in ventral view. Clypeus 1.6 × 1.2 mm; prosoma 4.3 mm long,

2.9 mm wide; opisthosoma 6.2 mm long, 4.4 mm wide. Opisthosoma almost oval in ventral outline and tuberculate; tubercles slightly longer in the tergal region, smaller towards the lateral sides. Ten segmental elements evident, with pygidium partially preserved towards the posterior end, again suggesting the presence of both dorsal and ventral opisthosomal features.

All four leg pairs partially preserved; generally robust, with maximum preserved leg lengths of 4.1 mm. In some cases, (e.g., pair IV, fine preservation reveals anatomical details of the legs including the femur, patella, tibia, metatarsus and tarsus. A spine approximately 0.5 mm long is preserved at the base of leg III (Fig. 3b). Robust trochanter present on anterior legs. Pedipalps c. 0.6 mm long with a pediform structure.

Remarks. The specimen is preserved in ventral view anteriorly, but apparently with a combination of dorsal and ventral elements posteriorly, perhaps due to post-mortem compression of the opisthosoma. Its habitus is consistent with it being a member of the Trigonotarbida. The well-developed sternum is surrounded by leg coxae, as in spiders,

Fig. 5 Plants found in association with the new *Aphantomartus* sp. in sample AF/0127. **a** *Aphantomartus* sp. (black arrow) associated with *Neuropteris* sp., *Nemejcopteris feminaeformis*, and unidentified roots and stems (white arrows). Scale = 1 cm. **b** *Neuropteris* sp. Scale = 5 mm. **c** *Nemejcopteris feminaeformis*. Scale = 2 mm. **d** *Neuropteris ovata*. Scale = 5 mm. **e** *Nemejcopteris feminaeformis*. Scale = 2 mm



but the legs are robust (rather than gracile as would be more typical for spiders) and there is no evidence of spinnerets. The opisthosomal cuticle is also heavily ornamented (granular), which is typical of the dorsal surface of more derived trigonotarbid families. Assignment to a particular family of trigonotarbids is challenging in the absence of dorsal prosomal features, but an oval opisthosoma, which is of similar length to the carapace, is consistent with it being a member of Aphantomartidae. In other highly ornamented Carboniferous families, such as Eophrynidae and Kreischeriidae, the opisthosoma tends to be more circular and is usually noticeably larger than the carapace (Jones et al., 2014, Fig. 1).

Carboniferous Aphantomartidae are represented by the recently described *Doubravartarus* Hradská et al. (2022), which differs from the studied specimen on account of its fairly gracile legs and the presence of small marginal spines

on the opisthosoma. The studied specimen is more consistent with *Aphantomartus* Pocock 1911 based on the body proportions of other members of this genus; see especially comparative images by Rößler (1998). Three species of *Aphantomartus* are currently recognised, but the ventral surface is not well documented in the two most common taxa, *A. pustulatus* Scudder, 1884 and *A. areolatus* Pocock, 1911, which differ primarily in their patterns of dorsal tuberculation. Since it is not entirely clear whether the observed granulation is dorsal or ventral in the new fossil, we provisionally assign it to *Aphantomartus* sp.

Associated plant remains. The sample bearing this arachnid also hosts the remains of typical Late Pennsylvanian plants, including foliar fragments of *Neuropteris* sp., *Neuropteris ovata* Hoffman, 1826, *Nemejcopteris feminaeformis* (Schlotheim, 1820) Barthel, 1968, *Pecopteris*

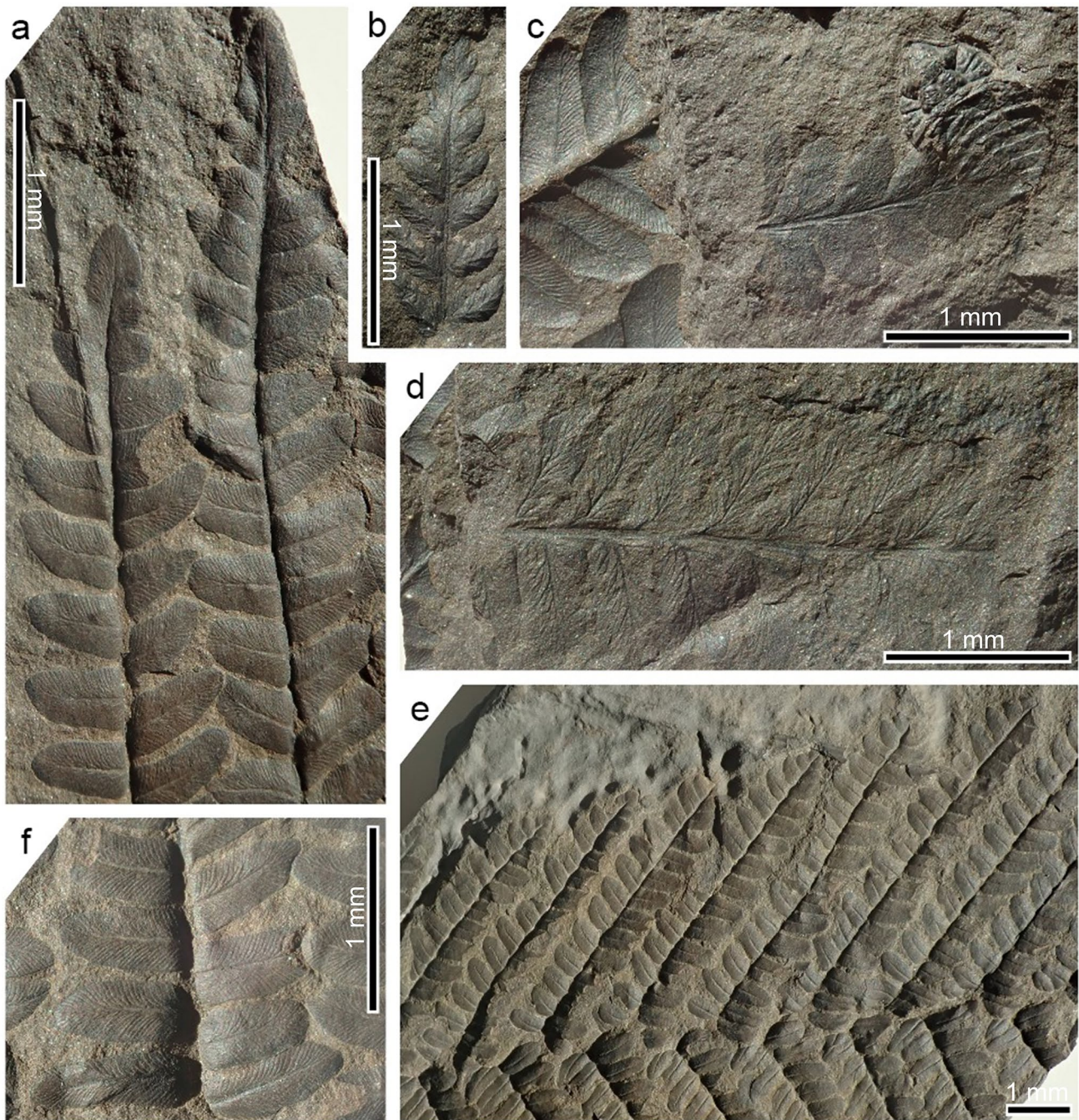


Fig. 6 Plants found in association with *A. areolatus* in sample MCNA-15041. **a** *Polymorphopteris polymorpha*. **b** *Oligocarpia leptophylla*. **c** *Polymorphopteris integra*, *Polymorphopteris polymorpha*

and the new trigonotarbid *Aphantomartus areolatus*. **d** *Polymorphopteris integra*. **e** *Polymorphopteris polymorpha*. **f** Detail of *Polymorphopteris polymorpha*. Scales = 10 mm

sp., and *Cyperites bicarinatus* Lindley & Hutton, 1832, in addition to other unidentifiable vegetative remains, such as roots and wood (Figs. 2a, 5).

Species *Aphantomartus areolatus* Pocock, 1911
 Figures 3c, 4b and 6c

Material. Sample MCNA-15041 (Museum of Natural Sciences of Álava, Vitoria-Gasteiz, Basque Country, Spain); External mould of an arachnid dorsal surface preserved in dark grey siltstone with several plant fragments (see Fig. 6c).

Age, stratigraphy and locality. Stephanian B (Gzhelian, Late Pennsylvanian); Calderón deposits in Villablino Coalfield, León Province, Castilla y León, northern Spain.

Description. Incomplete trigonotarbid retaining prosoma and opisthosoma. Legs, pedipalps, and (ventral) pygidium not preserved. Relatively small trigonotarbid, 11.5 mm long, 6.2 mm wide. Carapace subtriangular and clypeus oval in dorsal view. Clypeus 1.5 × 1.8 mm; carapace 3.9 mm long, 6.2 mm wide; opisthosoma elliptical, 7.5 mm long, 6.2 mm wide. Eight tergites evident in the opisthosoma. Tubercles of various sizes present on almost all tergites; larger in the middle part and smaller towards the lateral margins.

Remarks. The anatomy of this specimen is clearly consistent with Trigonotarbida. It has tergites divided into median and lateral plates and an ornamented opisthosomal dorsal cuticle bearing variably sized tubercles, which is characteristic of the more derived trigonotarbids. Its systematic placement within Trigonotarbida is constrained by possession of an elliptical to oval opisthosoma with granular tuberculation, which is of similar length to the prosoma. These features are typical of members of Aphantomartidae.

The absence of small marginal spines on the opisthosoma of the new fossil excludes affinities with *Doubravatarbus* Hradská et al. (2022), and the size and habitus of the new fossil are more consistent with *Aphantomartus* Pocock, 1911; see, e.g., comparative images by Rößler (1998). Three species of *Aphantomartus* are currently recognised: *A. pustulatus* Scudder, 1884 and *A. areolatus* Pocock, 1911 are the most common and are also known from the Iberian Peninsula (Table 1). The tuberculation on the tergites with somewhat larger individual tubercles is consistent with that described for *A. areolatus* (Selden & Romano, 1983), hence, we assign the new specimen to that species. In *A. pustulatus*, the dorsal surface tends to be more granular, with smaller individual tubercles.

Associated plant remains. The slab bearing *A. areolatus* also hosts foliar remains of *Oligocarpia leptophylla* (Bunbury in Ribeiro, 1853) Grauvogel-Stamm & Doubinger, 1975, *Polymorphopteris polymorpha* (Brongniart, 1834) Wagner, 1959 ex Knight, 1985 (\equiv *Acitheca polymorpha* (Brongniart, 1834) Schimper, 1879) and *Polymorphopteris integra* (Andrae in Germar, 1849) Wagner, 1999 (Fig. 6).

Discussion

Implications of the new trigonotarbids

Trigonotarbids were a diverse group of arachnids during the Paleozoic, with more than 70 species described (Dunlop et al., 2008)—most from the Carboniferous of north and central Europe (Dunlop & Rößler, 2013; Dunlop et al., 2008). As noted above, fossils of this group from the

Iberian Peninsula are remarkably scarce (Table 1). Notable finds include *Aphantomartus areolatus* from the mid-Cantabrian (= lower Kasimovian) of northwestern Spain (Selden & Romano, 1983) and *Aphantomartus pustulatus* from lower Gzhelian strata of northwestern Portugal (Correia et al., 2013). This scarcity of arachnids in general from the Carboniferous of Spain might result from: 1, a genuine low abundance of this group in the Paleozoic ecosystems of Iberia; 2, taphonomic biases inhibiting preservation in these Carboniferous deposits; or 3, low sampling intensity and targeting of trigonotarbids, together with the small size of these remains in comparison to other fossils. Similar challenges in interpreting invertebrate fossil records, including issues of preservation, sampling effort, and morphological inconspicuousness, have been discussed more broadly by Whitaker and Kimmig (2020).

The new fossils documented in this paper have doubled the record of this group in the Iberian Peninsula from two to four, suggesting that scarcity in the Carboniferous ecosystems and taphonomical biases are unlikely to explain their poor record in Iberia. The discovery of several other small arthropods (mainly insects) with similar chitinous composition in the same coalfields (see Table 1 in Santos et al., 2023) suggests that taphonomic biases resulting in trigonotarbids being more difficult to preserve in these deposits are unlikely. Therefore, the small size of these fossils, usually concealed among the remains of fossil plants, together with the lack of targeted sampling by palaeoarachnologists in Spain and Portugal, seems a more likely explanation for the sparse representation of arachnids in this area. They may have been relatively abundant in the terrestrial ecosystems of Iberia, but their fossils have likely been overlooked in past fieldwork and studies of collections.

The new fossils derive from two localities in northwestern Spain which have not previously yielded trigonotarbids. This study thus expands the group's known geographic range in the Carboniferous, but no increase in taxon diversity was detected; i.e., there is no evidence that they represent new genera or species. It seems that the diversity of trigonotarbids was low in the Iberian region as in other regions of Laurussia (e.g., UK and Central Europe; Dunlop et al., 2008). In general, *Aphantomartus* is a genus with a wide distribution and a long stratigraphic range (Rößler, 1998, Fig. 17). Alongside *Trigonotarbus* and *Anthracomartus*, it is one of only three trigonotarbid genera known so far from the Gzhelian (Dunlop & Rößler, 2013, Fig. 5), with *Aphantomartus* also extending its range into the Early Permian, a time period which has yielded only one other genus: *Permotarbus*. In this context, *Aphantomartus* appears to have survived the so-called Carboniferous Rainforest Collapse during the Kasimovian (ca. 305 Ma) and may thus represent one of the most successful and durable trigonotarbid lineages.

The presence of a spine on the base of leg pair III (Fig. 3b) is of interest as it has not been reported in other specimens of *Aphantomartus* (cf. Rößler, 1998) or other trigonotarbids in general. However, spinose structures have been described on other parts of these animals, such as on the margins of the opisthosoma of some species of Eophrynidae. Marginal spines probably provided protection against attack from the rear or the sides, and presumably made these trigonotarbids less palatable to predators (Dunlop & Garwood, 2014). Nevertheless, the presence of this spine on the inner part of the III walking leg of *Aphantomartus* sp. does not seem especially defensive or ornamental. It might have functioned as a grappling structure, as it has a similar architecture to the grappling spines on legs of other arthropods. Spines on the legs of some arachnids may have a grappling function that helps with the capture or immobilization of prey (Dunlop et al., 2007). Alternatively, some modern laniatorean harvestmen use spines on their hind legs as weapons during antagonistic male–male competition (e.g., Willemart et al., 2009). A reproductive role, such as assisting in immobilizing the female during copulation, cannot be excluded, though this remains speculative in the absence of clear criteria for sex determination in the trigonotarbid fossils.

The feeding preferences of trigonotarbids remain obscure. Most euchelicerate groups are inferred to have been predatory (Haug, 2018). The predatory behaviour of *Aphantomartus* sp. is supported by the relatively well-developed pedipalps (the first pair of appendages; Fig. 3a) that may have helped grab and process prey items. In this sense, the well-developed spine might have been an additional weapon for this trigonotarbid to immobilize prey. It is difficult to infer which animals were the typical prey of trigonotarbids, but several groups of insects occur in the same stratigraphic levels of the El Bierzo Basin (viz., Megasecoptera, Dictyoptera and Panorthoptera; Santos et al., 2023). Nevertheless, the relatively large size of most of these insects makes them unlikely to be the predation targets of these smaller arachnids, at least as adults. Small roachoids or juveniles of other insects might have been the typical prey for trigonotarbids in this region. It is also possible that there is a lack of information regarding smaller species and that only the more conspicuous individuals have been identified in the fossil record.

A rich entomofauna with various herbivorous strategies inhabited the Pennsylvanian forests of northern Spain (Santos et al., 2022, 2023, 2024). The interactions of these insects with plants probably made these richly vegetated areas prime habitats for trigonotarbids to feed and shelter.

Paleobotanical and palaeoenvironmental setting

Sample AF/0127 (*Aphantomartus* sp.) comes from the El Bierzo Coalfield, an area characterized by peat bog, fluvial channels, and sporadic lake and floodplain swamp

environments (Fernández-García et al., 1984). These conditions were periodically disrupted by subsidence phases, leading to the establishment of higher energy braided fluvial systems. This alternation of lacustrine, swamp, and fluvial channel depositional environments resulted in a cyclical sedimentation pattern (Fernández-García et al., 1984). According to Colmenero et al. (1996), the beds containing *Aphantomartus* sp. represent palaeoenvironments with anastomosing and meandering fluvial channels, transitioning laterally and vertically into floodplain deposits. In distal areas, these deposits were occupied by ephemeral lakes, marshes, and swamps. By contrast, sample MCNA-15041 derives from the Calderón site in the Villablino Coalfield. This basin contains lithologies similar to those found at El Bierzo, with Stephanian sediments laid down in short-transport fluvial systems with episodic high flow rates (Corrales & Peláez-Pruneda, 1958). These deposits also constitute repetitive successions of sandstones, shales and coal (Corrales, 1971), indicative of fluvial, lacustrine and swampy sedimentary systems. Palaeontological data based on plant and animal fossils further support these palaeoenvironmental interpretations for both the El Bierzo and Villablino basins (Álvarez-Vázquez & Wagner, 2014; Santos et al., 2023; Wagner & Álvarez-Vázquez, 2010).

We identified a diverse and well-preserved fossil plant assemblage closely associated with the trigonotarbids. The plant remains, particularly those associated with specimen MCNA-15041, are well preserved reflecting limited transport before burial. Previous studies of Gzhelian–Asselian successions have linked the fossil plant taxa to various climatic and environmental conditions providing information on the broader palaeohabitats and palaeoclimates occupied by the trigonotarbids (Fig. 7).

Sample AF/0127 (*Aphantomartus* sp.) is dominated by *Neuropteris ovata* (Fig. 2a), which is associated with a broad range of habitats, including peat bogs, alluvial plains, and clastic swamps (Bashforth et al., 2010; DiMichele et al., 2013; Donovan et al., 2021). This species is accompanied by *Nemejcopteris feminaeformis* (Fig. 2a), found in similar palaeoenvironments (Barthel, 1968, 1976, 2001, 2005, 2016; Bashforth et al., 2010; Martín-Closas & Martínez-Roig, 2007; Reichel & Schauer, 2006; Rößler & Barthel, 1998; Schneider & Barthel, 1997). However, Rößler and Barthel (1998) and Barthel (2016) suggested that, in some areas, this species may have also grown in hygrophilous/mesophilous, species-rich pteridosperm-coenopterid-fern communities on well-drained mineral soils. These environments, characterized by microtopographic and edaphic variability, likely supported a mosaic of vegetation types, with better-drained or drier sites above the groundwater level dominated by pteridosperms and ferns, fringing swamp vegetation.

An accompanying species, *Cyperites bicarinatus*, is represented by long, narrow leaves of various arborescent

Sample	Climatic adaptations	Rheophyte	Hydrophyte	Hygrophyte		Mesophyte	Xerophyte	
	Plant / Environment	Riparian	Peatbog	Swampy forest	Wetlands and Floodplains	Mesophyle	Xerophyle	
AF/0127 <i>Aphantomartus</i> sp.	<i>Neuropteris ovata</i>			Bashforth et al. (2010)				
				DiMichele et al. (2013)				
				Donovan et al. (2021)				
	<i>Nemejcopteris feminaeformis</i>				Barthel (1968, 1976, 2001)			
					Barthel (2005)	Rössler & Barthel (1998)		
					Barthel (2016)			
					Schneider & Barthel (1997); Reichel & Schauer (2006)			
	<i>Cyperites bicarinatus (Sigillaria brardi)</i>				Bashforth et al. (2010)			
					Martín-Closas & Martínez-Roig (2007)			
				Martín-Closas & Galtier (2005); Martín-Closas & Martínez-Roig (2007)	Barthel (2001, 2003)		Schneider & Barthel (1997)	
				Rössler & Barthel (1998)				
			Bashforth et al. (2010)					
		Tosal et al. (2022)						
MCNA-15041 <i>A. areolatus</i>	<i>Polymorphopteris polymorpha</i>			Barthel (2016)				
				Barthel (2005)				
		Martín-Closas & Martínez-Roig (2007)		Martín-Closas & Galtier (2005); Martín-Closas & Martínez-Roig (2007); Tosal et al. (2022)				
	<i>Oligocarpia leptophylla</i>			Barthel (2001)	Rössler & Barthel (1998); Reichel & Schauer (2006); Barthel (2016)			
			Bashforth et al. (2010)		Schneider & Barthel (1997)			

Fig. 7 Chart showing the environmental affinities and climatic adaptations of the plants associated with the trigonotarbid of northwestern Spain based on published studies. Note that all the associated species occur in hygrophilous vegetation

lycopsids, such as *Sigillaria*, *Lepidodendron*, *Lepidophloios*, *Omphalophloios* and *Polysporia* (Álvarez-Vázquez & Wagner, 2014). We consider *Sigillaria brardii* to be the primary candidate for the parent plant of these dispersed leaves in the Bierzo coalfield. This species, with its *Stigmariopsis*-type root system, could exploit deeper groundwaters and withstand changes in water availability (Pfefferkorn & Wang, 2009). Consequently, it likely thrived in diverse environments, ranging from riparian (Tosal et al., 2022) to hygrophilous or hydrophilous mires (Barthel, 2001, 2003; Bashforth et al., 2010; Martín-Closas & Galtier, 2005; Martín-Closas & Martínez-Roig, 2007) and even mesophilous environments hosting the previously mentioned species (Barthel, 2016; Rössler & Barthel, 1998). Reviewing the data published by Bashforth et al. (2010) on the palaeovegetation of La Magdalena, the three plant species mentioned above have been found together in interfluvial non-peat-forming wetlands distant from braided channels. In summary, the plant species associated with the *Aphantomartus* sp. specimen suggest that its original ecosystem likely ranged between hygrophyte swamp forests, interfluvial wetlands, and floodplains, with a mosaic of hygrophilous/mesophilous vegetation. Organic mires (*sensu* Moore, 1989) are excluded as a possible habitat due to the fossils being found in clastic sedimentary rocks.

Sample MCNA-15041 hosting *Aphantomartus areolatus* also primarily contains two species of *Polymorphopteris* (see the artistic reconstruction in Fig. 8).

Polymorphopteris polymorpha has been found predominantly in hygrophilous environments, such as swamp forests, interfluvial wetlands and floodplains (Barthel, 2005, 2016; Bashforth et al., 2010; Martín-Closas & Galtier, 2005; Martín-Closas & Martínez-Roig, 2007). Additionally, Martín-Closas and Martínez-Roig (2007) reported its presence in fluvial channels in the Gzhelian of Surroca-Ogassa. Although abundant in Gzhelian strata of NW Spain, *Polymorphopteris integra* is rarely mentioned in palaeoecological studies (we did not use in our discussion the identification by Tosal et al., 2022, of *P. cf. integra*, because their illustration in Fig. 11E seems to correspond with *P. polymorpha*). It typically occurs in clastic deposits not associated with peatlands and is accompanied by other hygrophilous species. Finally, *Oligocarpia leptophylla* has been identified in hygrophilous and mesophilous environments by Schneider and Barthel (1997), Rössler and Barthel (1998), Barthel (2001, 2016), Reichel and Schauer (2006) and Bashforth et al. (2010). In summary, the new *Aphantomartus areolatus* fossil likely inhabited environments very similar to the new *Aphantomartus* sp. specimen, including hygrophylous forests, interfluvial wetlands, floodplains, and hygrophilous/mesophilous vegetation mosaics.

Both of the new trigonotarbid derive from low-palaeolatitude settings close to the peak of the Late Paleozoic Ice Age, when coal-forming and humid forest communities of the palaeotropics contracted geographically (Gastaldo

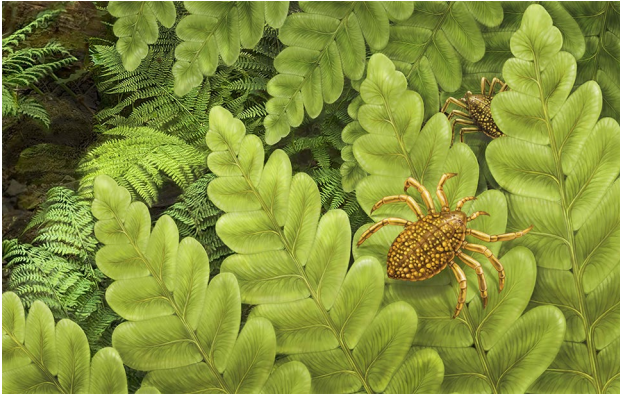


Fig. 8 Reconstruction of the Spanish trigonotarbids *Aphantomartus areolatus* and *Aphantomartus* sp. on the fern *Polymorphopteris polymorpha* in the Carboniferous tropical forest of León (NW Spain). Scientific illustration: Pollyanna von Knorring (Swedish Museum of Natural History)

et al., 2020a, 2020b). The broadleaved, evergreen, humid forests in actively subsiding basins of Iberia and western Europe may have acted as palaeotropical refugia for this group of arachnids at the close of the Carboniferous.

Conclusions

The discovery of two new Trigonotarbida fossils from Pennsylvanian deposits of El Bierzo and Villablino doubles the representation of this arachnid order in the Iberian Peninsula. We suggest that the scarcity of trigonotarbid fossils in Iberia is likely due to sampling biases rather than a genuine scarcity. The presence of other small arthropods with chitinous exoskeletons in the same coalfields supports this conclusion. Therefore, trigonotarbids were likely abundant in the Carboniferous forests of Iberia, but have been overlooked due to their modest size and the lack of targeted searches.

The new fossils are assigned to *Aphantomartus* sp. and *Aphantomartus areolatus*, and extend the known geographical distribution of trigonotarbids in northern Spain during the Pennsylvanian. The singular presence of a proximal spine on the hindleg of the El Bierzo specimen might indicate a specialized function related to grappling or fighting.

Paleobotanical remains associated with *Aphantomartus* sp. and *Aphantomartus areolatus* imply that these arachnids inhabited palaeotropical humid vegetated areas dominated by pteridophytes, reinforcing the previously established relationship between these animals and plants. The close co-occurrence of the Iberian *Aphantomartus* with medullosan gymnosperms, ferns and lycopsids, such as *Neuropteris ovata*, *Cyperites bicarinatus*, *Polymorphopteris polymorpha*, *Polymorphopteris integra*, *Nemejcopteris feminaeformis* and

Oligocarpia leptophylla, further suggests that these arachnids lived in hygrophilous to mesophilous vegetation typical of swamp forests, interfluvial wetlands, and floodplains. These Carboniferous forests hosted a diverse entomofauna, providing a rich source of potential food, with the forest habitat presumably offering shelter for these trigonotarbids.

Acknowledgements We thank Juan Manuel Rincón Rivero, director of the “Museo del Alto Bierzo” for the management of the studied specimen and the “Asociación Aragonito Azul” for the help in the storage of the fossil. We also thank Jesús Alonso and Carmelo Corral, former director and current curator of the Museum of Natural Sciences of Álava, Vitoria-Gasteiz, for their assistance. Additionally, we thank José Vicente Casado for the discovery and donation of both specimens. Thanks also to the scientific artist Pollyanna von Knorring (NRM) for the illustration provided in this work. This research also represents a contribution to the Médulas-Telmo UNESCO Global Geopark project. Artai Santos was supported by a postdoctoral fellowship from UNAM-DGAPA 2023–2024 and a subsequent postdoctoral fellowship funded from the Swedish Research Council Grant VR 2022-03920 to Stephen McLoughlin. We are grateful to the editor and to the reviewers, Dr. Valérie Ngô-Muller and Dr. Julien Kimmig, for their valuable and constructive comments, which have improved the manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL.

Data availability Data will be made available on request.

Declarations

Conflict of interest The authors have no competing interests to declare.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Álvarez-Ramis, C., Gómez-Porter, P., & Lanzarote, D. (1986). *Phylloblatta monubilis* Meunier, forma spathulata Bolton del Estefaniense superior de la Cuenca de Villablino (León). In *II Jornadas de Paleontología. Resumen de las Comunicaciones* (p. 57). Sociedad Española de Paleontología.
- Álvarez-Ramis, C. (1990). Présence de restes de Blattidae dans le faisceau Carrasconte du bassin stéphanien de Villablino (Léon, Espagne). *Bulletin De La Société D’histoire Naturelle D’automne*, 131, 7–10.
- Álvarez-Vázquez, C., & Wagner, R. H. (2014). Lycopsida from the lower Westphalian (Middle Pennsylvanian) of the Maritime Provinces, Canada. *Atlantic Geology*, 50, 167–232. <https://doi.org/10.4138/atlgeol.2014.011>

- Barthel, M. (1968). 'Pecopteris' *feminaeformis* (Schlotheim) Sterzel und 'Araucarites' *spiciformis* Andrae in Germar-Coenopterideen des Stephans und Unteren Perms. *Paläontologische Abhandlungen, Abteilung B*, 2, 727–742.
- Barthel, M. (1976). Die Rotliegendflora Sachsens. *Abhandlungen des Staatlichen Museums Für Mineralogie und Geologie Zu Dresden*, 24, 1–190.
- Barthel, M. (2001). Pflanzengruppen und Vegetationseinheiten der Manebach-Formation. *Beiträge Zur Geologie Von Thüringen, N.f.*, 8, 93–123.
- Barthel, M. (2003). Die Rotliegendflora des Thüringer Waldes. Teil 1: Einführung und Keilblattpflanzen (Sphenophyllales). *Veröffentlichungen Naturhist. Museum Schleusingen*, 18, 3–16.
- Barthel, M. (2005). Die Rotliegendflora des Thüringer Waldes. Teil 3: Farne. *Veröffentlichungen Naturhist. Museum Schleusingen*, 20, 27–56.
- Barthel, M. (2016). The Lower Permian (Rotliegend) flora of the Döhlen Formation. *Geologica Saxonica*, 61(2), 105–238.
- Bashforth, A. R., Falcon-Lang, H. J., & Gibling, M. R. (2010). Vegetation heterogeneity on a late Pennsylvanian braided-river plain draining the Variscan Mountains, La Magdalena Coalfield, northwestern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 292(3–4), 367–390.
- Brauckmann, C. (1993). Notiz über Insekten-Reste aus dem Oberkarbon in Spanien. *Jahresberichte des Naturwissenschaftlichen Vereins in Wuppertal*, 46, 115–119.
- Brauckmann, C., Arillo, A., & Ortuño, V. M. (2001). A new Geraridae (Insecta, hemipteroid stem assemblage) from the Upper Carboniferous of La Magdalena (León, northern Spain). *Boletín Geológico y Minero*, 112, 57–62.
- Carpenter, F. M. (1963). A megasecopter from upper Carboniferous strata in Spain. *Psyche*, 70, 44–49.
- Castro, M. P. (2005). La flora estefaniense B de La Magdalena (León, España), un referente europeo. Tomo II: Descripción sistemática de las Gimnospermas. *Cuadernos del Museo Geominero*, 4, 1–229. Instituto Geológico y Minero de España, Madrid.
- Colmenero, J. R., Bahamonde, J. R., & Barba, P. (1996). Las facies aluviales asociadas a los depósitos de carbón en las cuencas estefanienses de León (borde sur de la Cordillera Cantábrica). *Cuadernos De Geología Ibérica*, 21, 71–92.
- Corrales, I. (1971). La sedimentación durante el Estefaniense B-C en Cangas de Narcea, Rengos y Villablino (MW de España). In R. H. Wagner (Ed.), *The Carboniferous of Northwest Spain* (pp. 69–73). Trabajos de Geología, 3(1). Facultad de Ciencias, Universidad de Oviedo.
- Corrales, I., & Peláez-Pruneda, J. R. (1958). La sedimentación marginal en la cuenca estefaniense de Villablino (León). *Brevioria Geologica Asturica*, 10(1), 33–54.
- Correia, P., Murphy, J. B., Sá, A. A., Domingos, R., & Flores, D. (2013). First Paleozoic arachnid from Portugal and implications for Carboniferous palaeobiogeography. *Geological Journal*, 48, 101–107.
- DiMichele, W. A., Wagner, R. H., Bashforth, A. R., & Álvarez-Vázquez, C. (2013). An update on the flora of the Kinney Quarry of Central New Mexico (Upper Pennsylvanian), its preservational and environmental significance. In S. G. Lucas et al. (Eds.), *Carboniferous-Permian Transition in Central New Mexico* (pp. 289–325). *New Mexico Museum of Natural History and Science, Bulletin*, 59.
- Donovan, M. P., DiMichele, W. A., Lucas, S. G., & Schneider, J. W. (2021). Atlas of selected Kinney Quarry plant fossils, Late Pennsylvanian, Central New Mexico. In S. G. Lucas, W. A. DiMichele, & B. D. Allen (Eds.), *Kinney Brick Quarry Lagerstätte* (pp. 153–183). *New Mexico Museum of Natural History and Science Bulletin*, 84.
- Dunlop, J. A., Menon, F., & Selden, P. A. (2007). Arachnida: Spiders, scorpions and allies. In *The Crato Fossil Beds of Brazil: Window into an ancient world* (pp. 103–131).
- Dunlop, J. A. (1996). A trigonotarbid arachnid from the Upper Silurian of Shropshire. *Palaeontology*, 39, 605–614.
- Dunlop, J. A. (2010). Geological history and phylogeny of Chelicerata. *Arthropod Structure and Development*, 39(2–3), 124–142.
- Dunlop, J. A., Penney, D., Tetlie, O. E., & Anderson, L. I. (2008). How many species of fossil arachnids are there? *The Journal of Arachnology*, 36(2), 267–272.
- Dunlop, J. A., & Rößler, R. (2013). The youngest trigonotarbid *Permotarbus schuberti* n. gen., n. sp. from the Permian Petrified Forest of Chemnitz in Germany. *Fossil Record*, 16, 229–243.
- Dunlop, J. A., & Selden, P. A. (2004). A trigonotarbid arachnid from the Lower Devonian of Tredomen, Wales. *Palaeontology*, 47(6), 1469–1476.
- Eagar, H. M. C., & Weir, J. (1971). Some Spanish Upper Carboniferous non-marine bivalve faunas: A preliminary statement with emphasis on facies in North-west Spain and in Britain. In R. H. Wagner (Ed.), *The Carboniferous of Northwest Spain* (pp. 87–99). Trabajos de Geología, 3(1). Facultad de Ciencias, Universidad de Oviedo.
- Eagar, H. M. C. (1985). The non-marine bivalves of the succession of Stephanian B age in the Ciñera-Matallana Coalfield. In M. J. Lemos de Souza & R. H. Wagner (Eds.), *Papers on the Carboniferous of the Iberian Peninsula* (pp. 5–14). *Anais Faculdade de Ciências*, Supplement volume 64. Universidade do Porto.
- Fernández-García, L. G., Moro-Gómez, C., Gómez-Prieto, J. A., & Álvarez del Campo, C. (1984). Revisión y síntesis geológico-minera de la cuenca carbonífera de "El Bierzo" (León). Informe interno n° 11101. IGME, Madrid.
- Gandl, J. (2021). Die Karbon-Trilobiten des Kantabrischen Gebirges (NW-Spanien), 6. Trilobiten des tieferen Stephan. *Abhandlungen der Senckenberg Gesellschaft Für Naturforschung*, 576, 1–99.
- Garwood, R. J., & Dunlop, J. A. (2010). Fossils explained 58. Trigonotarbids. *Geology Today*, 26, 34–37.
- Garwood, R. J., & Dunlop, J. (2014). Three-dimensional reconstruction and the phylogeny of extinct chelicerate orders. *PeerJ*, 2, Article e641.
- Gastaldo, R. A., Bamford, M., Calder, J., DiMichele, W. A., Iannuzzi, R., Jasper, A., Kerp, H., McLoughlin, S., Opluštil, S., Pfefferkorn, H. W., Roessler, R., & Wang, J. (2020a). UNIT 12: The Icehouse-Hothouse of the Late Paleozoic Ice Age, coal-forming environments, and their non-analog vegetation. In E. Martinetto, E. Tschopp, & R. A. Gastaldo (Eds.), *Nature through time* (pp. 291–316). Springer.
- Gastaldo, R. A., Bamford, M., Calder, J., DiMichele, W. A., Iannuzzi, R., Jasper, A., Kerp, H., McLoughlin, S., Opluštil, S., Pfefferkorn, H. W., Roessler, R., & Wang, J. (2020b). UNIT 13: The coal farms of the late Paleozoic. In E. Martinetto, E. Tschopp, & R. A. Gastaldo (Eds.), *Nature through time* (pp. 317–343). Springer.
- Haug, C. (2018). Feeding strategies in arthropods from the Rhynie and Windyfield cherts: Ecological diversification in an early non-marine biota. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1739), 20160492.
- Hernández-Ortúe, A. (2024). *Revisión de los géneros de Pecopterídeas Post-Astúricas del NW de la Península Ibérica*. Ph.D. thesis. Departamento de Geología. Universidad del País Vasco/Euskal Herriko Unibertsitatea (UPV/EHU).
- Hradská, I., Opluštil, S., Selden, P. A., & Dunlop, J. A. (2022). A new species of trigonotarbid arachnid from the Pilsen Basin of the Czech Republic. *Bulletin of Geosciences*, 97(2), 261–268.
- Iwaniew, E. (1985). Floral palaeoecology of debris flow dominated valley-fill deposits in the Lower Cantabrian of NE León, NW Spain. In M. J. Lemos de Souza & R. H. Wagner (Eds.), *Papers on*

- the Carboniferous of the Iberian Peninsula (pp. 283–357). Anais Facultade de Ciências.
- Jones, F. M., Dunlop, J. A., Friedmann, M., & Garwood, R. J. (2014). *Trigonotarbus johnsoni* Pocock, 1911, revealed by X-ray computed tomography, with a cladistic analysis of the extinct trigonotarbid arachnids. *Zoological Journal of the Linnean Society*, 172, 49–70.
- Knight, J. A. (1971). The sequence and stratigraphy of the eastern end of the Sabero Coalfield (León, N. W. Spain). In *The Carboniferous of Northwest Spain* (pp. 193–229). Trabajos de Geología, 3. Facultad de Ciencias, Universidad de Oviedo.
- Knight, J. A., Cleal, C. J., & Álvarez-Vázquez, C. (2023). The challenge of relating the Kasimovian to West European chronostratigraphy: A critical review of the Cantabrian and Barruelian substages of the Stephanian Stage. In S. G. Lucas, W. A. DiMichele, S. Opluštil, & X. Wang (Eds.), *Ice Ages, Climate Dynamics and Biotic Events: The Late Pennsylvanian World* (pp. 1–23). Geological Society, London, Special Publications, 535.
- Knight, J. A., & Álvarez-Vázquez, C. (2021). A summary of upper Pennsylvanian regional substages defined in NW Spain: The chronostratigraphic legacy of Robert H. Wagner. *Newsletters on Stratigraphy*, 54, 75–300.
- Martín-Closas, C., & Galtier, J. (2005). Plant taphonomy and paleoecology of Late Pennsylvanian intramontane wetlands in the Graissessac-Lodève Basin (Languedoc, France). *Palaios*, 20, 249–265. <https://doi.org/10.2110/palo.2003>
- Martín-Closas, C., & Martínez-Roig, D. (2007). Plant taphonomy and palaeoecology of Stephanian limnic wetlands in the eastern Pyrenees (Catalonia, Spain). *Comptes Rendus Palevol*, 6, 437–449.
- Merino-Tome, O., Villa, E., Bahamonde, J. R., & Colmenero, J. R. (2006). Fusulinoidean characterization of the uppermost Moscovian-Gzhelian (upper Pennsylvanian) synorogenic depositional sequences from northern Picos de Europe Unit (Spain). *Facies*, 52, 521–540.
- Moore, P. D. (1989). The ecology of peat-forming processes: A review. *International Journal of Coal Geology*, 12, 89–103.
- Nel, A., Garrouste, R. E., Peñalver, E., Hernández-Orúe, A., & Jouault, C. (2022a). 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(12), 1129. <https://doi.org/10.3390/d14121129>
- Nel, A., Santos, A. A., Hernández-Orúe, A., Wappler, T., Diez, J. B., & Peñalver, E. (2022b). The first representative of the roachoid family Spiloblattinidae (Insecta, Dictyoptera) from the Late Pennsylvanian of the Iberian Peninsula. *InSects*, 13(9), 828. <https://doi.org/10.3390/insects13090828>
- Perrier, V., & Charbonniere, S. (2014). The Montceau-les-Mines Lagerstätte (late Carboniferous, France). *Comptes Rendus Palevol*, 13, 353–367. <https://doi.org/10.1016/j.crpv.2014.03.002>
- Pfefferkorn, H. W., & Wang, J. (2009). *Stigmariopsis*, *Stigmaria asiatica*, and the survival of the *Sigillaria brardii-ichthyolepis* group in the tropics of the late Pennsylvanian and early Permian. *Palaeoworld*, 18(2–3), 130–135.
- Poschmann, M., & Dunlop, J. A. (2010). Trigonotarbid arachnids from the Lower Devonian (Lower Emsian) of Alken an der Mosel (Rhineland-Palatinate, SW Germany). *Paläontologische Zeitschrift*, 84, 467–484.
- Reichel, W., & Schauer, M. (2006). Das Döhlener Becken bei Dresden: Geologie und Bergbau. *Bergbau in Sachsen*, 12, 1–343.
- Rößler, R. (1998). Arachniden-Neufunde im mitteleuropäischen Unterkarbon bis Perm – Beitrag zur Revision der Familie Aphantomartidae Petrunkevitch 1945 (Arachnida, Trigonotarbida). *Paläontologische Zeitschrift*, 72, 67–88.
- Rößler, R. (2021). The most entirely known Permian terrestrial ecosystem on earth—Kept by explosive volcanism. *Palaeontographica B*, 303(1–3), 1–75. <https://doi.org/10.1127/palb/2021/0072>
- Rößler, R., & Barthel, M. (1998). Rotliegend taphocoenoses preservation favoured by rhyolitic explosive vulcanism. *Freiberger Forschungshefte, C* 474, 59–101.
- Santos, A. A., Diez, J. B., & Nel, A. (2024). *Wappleria tremoris* gen. et sp. nov., the first representative of the insect order Caloneuroidea in Spain (León, NW Spain) found in a Late Carboniferous forest. *Historical Biology*. <https://doi.org/10.1080/08912963.2024.2344799>
- Santos, A., Hernández-Orúe, A., Wappler, T., & Diez, J. B. (2022). Plant-insect interactions from the Late Pennsylvanian of the Iberian Peninsula (León, northern Spain). *Review of Palaeobotany and Palynology*, 301(104658), 1–10.
- Santos, A. A., Hernández-Orúe, A., Wappler, T., Peñalver, E., Diez, J. B., & Nel, A. (2023). Late Carboniferous insects from the Iberian Peninsula: State of the art and new taxa. *Palaeontographica Abteilung A*, 326(1–6), 1–27.
- Schneider, J. W., & Barthel, M. (1997). Eine Taphocoenose mit Arthropodura (Arthropoda) aus dem Rotliegend (? Unterperm) des Döhlen-Becken (Elbe-Zone, Sachsen). *Freiberger Forschungshefte*, 466, 183–223.
- Selden, P. A., & Romano, M. (1983). First Palaeozoic arachnid from Iberia: *Aphantomartus areolatus* Pocock (basal Stephanian; prov. León, N.W. Spain), with remarks on aphantomartid taxonomy. *Boletín Del Instituto Geológico y Minero De España*, 94, 106–112.
- Slater, B. J., McLoughlin, S., & Hilton, J. (2012). Animal-plant interactions in a Middle Permian permineralised peat of the Baimmedart Coal Measures, Prince Charles Mountains, Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 363, 109–126. <https://doi.org/10.1016/j.palaeo.2012.08.018>
- Slater, B. J., McLoughlin, S., & Hilton, J. (2015). A high-latitude Gondwanan lagerstätte: The Permian permineralised peat biota of the Prince Charles Mountains, Antarctica. *Gondwana Research*, 27, 1446–1473. <https://doi.org/10.1016/j.gr.2014.01.004>
- Stille, H. (1920). Alter und Art der Phasen variscischer Gebirgsbildung. *Nachrichten Von der Gesellschaft der Wissenschaften Zu Göttingen, Mathematisch-Physikalische Klasse*, 1920, 218–224.
- Tosal, A., Pàmies, J., & Martín-Closas, C. (2022). Plant taphonomy and palaeoecology of Upper Carboniferous wetlands from the Erillcastell Basin (central Pyrenees, Catalonia). <https://doi.org/10.2139/ssrn.4084650>
- Wagner, R. H. (1957). Nota sobre la estratigrafía del terreno hullero de Sabero (León). *Estudios Geológicos “Lucas Mallada”*, 13(35–36), 229–239. Lám. XXXII–XXXV.
- Wagner, R. H. (1965). Palaeobotanical dating of upper Carboniferous folding phases in NW Spain. *Memorias Del Instituto Geológico y Minero De España*, 66, 1–169.
- Wagner, R. H., & Álvarez-Vázquez, C. (2010). The Carboniferous floras of the Iberian Peninsula: A synthesis with geological connotations. *Review of Palaeobotany and Palynology*, 162, 239–324.
- Wagner, R. H., & Castro, M. P. (2011). Compositional changes in a mid-Stephanian (Kasimovian) flora in relation to alluvial plain deposits derived from westward-receding mountains and bordered by the Paleotethys: La Magdalena Coalfield, Northwestern Spain. *Palaios*, 26(1), 33–54.
- Wagner, R. H., & Martínez-García, E. (1998). Floral remains from the highest Valdeón Formation, a marine Stephanian unit south of the Picos de Europa, and comparisons with eastern Asturias, NW Spain. *Revista Española De Paleontología*, 13(1), 93–106.
- Whitaker, A. F., & Kimmig, J. (2020). Anthropologically introduced biases in natural history collections, with a case study on the invertebrate paleontology collections from the middle Cambrian Spence Shale Lagerstätte.

Willemart, R. H., Osses, F., Chelini, M. C., Macías-Ordóñez, R., & Machado, G. (2009). Sexually dimorphic legs in a neotropical harvestman (Arachnida, Opiliones): Ornament or weapon? *Behavioural Processes*, 80(1), 51–59.