First Iberian aspidothoracid megasecopteran insect and associated plants evidencing herbivory in a tropical Carboniferous forest from León, Spain

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We describe *Aspidothorax hispanicus* sp. nov. from Gzhelian, Pennsylvanian strata of León, Spain, representing the first occurrence of Aspidothoracidae in the Iberian Peninsula. This discovery expands the paleogeographical range of the family, previously known only from the Russian Federation and France. The new insect is preserved in close association with foliar remains of medullosan (*Alethopteris zeilleri*) and callistophytalean (*Pseudomariopteris cordato-ovata*) seed-ferns whose environmental preferences suggest that the new insect species inhabited humid tropical forests. The fossil leaves bear six types of damage, probably produced by insects, belonging to three functional feeding groups: margin feeding, hole feeding, and piercing and sucking. This diversity of interactions highlights varied feeding strategies, including chewing, piercing and sucking behaviors, evidencing a more complex range of herbivory in the area than previously known. The stylet mouthparts of Megasecoptera make these insects strong candidates for producing the piercing and sucking damage on the associated plants. The presence of dark patches and spots on the fossil wing, probably represents a camouflage strategy against predators, such as Palaeodictyoptera and other active hunters. The dark wing apex might also reflect the presence of sexual dimorphism or courtship behavior. This new assemblage of insects, in addition to plants and plant-insect interactions, contributes to a broader paleoecological understanding of the Carboniferous forests of the La Magdalena Coalfield.

Key words: Insecta, Megasecoptera, Paleoptera, plant-insect interactions, tropical paleoecosystem, Gzhelian, Carboniferous, León Province, Spain.

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Introduction

Megasecoptera, an order of insects within the superorder Palaeodictyopterida, is common in Carboniferous and Permian entomofaunas worldwide (Prokop et al. 2016; Pecharová et al. 2020). This superorder is distinguished by its piercing and sucking mouthparts, likely used for feeding on the inner tissues of various vascular plants (Kukalová-Peck 1991b; Labandeira and Phillips 1996; Engel et al. 2013; Pecharová et al. 2020). However, most research on

Table 1. List of Carboniferous Megasecoptera recorded from the Iberian Peninsula; modified from Santos et al. (2023).

Family	Species	Age	Locality	References
Anchineuridae	*Anchineura hispanica* Carpenter, 1963	"Saberian", Gzhelian, Late Pennsylvanian	Garaño, La Magdalena Coal-field,León Province, Spain	Carpenter 1963; Brauckmann 1993
Corydaloididae	*Corydaloides leonensis* Santos et al., 2023	Stephanian B, Gzhelian, Late Pennsylvanian	Tremor de Arriba, El Bierzo Coalfield, León Province, Spain	Santos et al. 2023
Mischopteridae	*Mischoptera bergidensis* Santos et al., 2023	Stephanian B, Gzhelian, Late Pennsylvanian	Santa Marina de Torre, El Bierzo Coalfield, León Province, Spain	Santos et al. 2023
Aspidothoracidae	*Aspidothorax hispanicus* sp. nov.	"Saberian", Gzhelian, Late Pennsylvanian	Carmen mine, La Magdalena Coalfield, León Province, Spain	this study

Megasecoptera has focused on the taxonomy of fossils, leaving their paleoecology, paleohabitats, and feeding strategies largely unexplored. Therefore, clarifying both the taxonomy and lifestyles of these insects and their host plants (Santos et al. 2022, 2023, 2024; Garrouste et al. 2024) is crucial for resolving the paleoenvironments and paleoecological interactions in Carboniferous equatorial forests.

The rich Pennsylvanian (late Carboniferous) entomofaunas of the United Kingdom, Germany, and France are well known, in contrast to those of the Iberian Peninsula. However, recent investigations in Portugal and Spain have helped to fill this gap, with the descriptions of new specimens of Palaeodictyopterida (Palaeodictyoptera, Megasecoptera), Odonatoptera (Meganisoptera), Archaeorthoptera (Orthoptera, Caloneurodea), Dictyoptera and its sister order Paoliida (see Santos et al. 2023: table 1, and references therein). Recently described Iberian megasecopterans are the anchineurid *Anchineura hispanica* Carpenter, 1963, the corydaloidid *Corydaloides leonensis* Santos et al., 2023, and the mischopterid *Mischoptera bergidensis* Santos et al., 2023 (see Table 1 for details on previous Megasecoptera occurrences in the Iberian Peninsula).

Here, we describe the fourth Iberian representative of this order and the first record of Aspidothoracidae Handlirsch, 1919, from Spain, this family was previously known only from the Pennsylvanian of France and the Permian of the Russian Federation. We also describe and identify various plant fossils closely associated with this new megasecopteran. The plant fossils were also analyzed for plant-insect interactions which are identified and discussed in this work.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in ZooBank: urn:lsid:zoobank.org:pub:D50E4135-5AC0-4A32-8499-EF0085141FC3.

Institutional abbreviations.—MUPE, Museo Paleontológico de Elche, Elche, Alicante, Spain.

Other abbreviations.—C, costa; CuA: cubitus anterior; CuP, cubitus posterior; DTs, Damage Types; FFGs, Functional Feeding Groups; MA: median anterior; MP, median posterior; m-cua, basalmost crossvein between M and CuA; PCu, postcubital vein; RA, radius anterior; RP, radius posterior; rp-ma: basalmost crossvein between RP and MA.

Material and methods

The insect wing described herein, co-occurring with various plant fossils, was collected by José Luis Garrido (Elche, Alicante, Spain) close to the Carmen mine (Fig. 1), within the upper part of La Magdalena Coalfield succession (Castro 2005a). The stratigraphic position and paleoflora favor a "Saberian" (Gzhelian) age (Santos et al. 2023).

Vein terminology for the insect wing (Fig. 2) follows that of Schubnel et al. (2020).

The fossil plants (Fig. 3) were identified using the extensive literature on Carboniferous floras from the region (Wagner 1968; Krings and Kerp 2000; Castro 2005b). We also analyzed the associated plant fossils for plant-arthropod interactions using the classification scheme developed by Labandeira et al. (2007) to categorize damage features. This framework classifies interactions on fossil leaves into various stereotypical morphotypes, referred to as Damage Types (DTs), each assigned an identifying number. Most DTs are associated with specific Functional Feeding Groups (FFGs). Furthermore, each DT is linked to a specific level of specialization, determined by its occurrence on various host plants (Labandeira et al. 2007).

The specimen is housed at the Museo Paleontológico de Elche (MUPE) provisionally labeled as MUPE-IWC-01.

Geological setting

La Magdalena Coalfield is located in northwestern Spain, in the north of León Province. This is one of the most studied post-Asturian coalfields in the Cantabrian region of the Iberian Peninsula and its paleoflora is one of the richest and best preserved in the district (Castro 2005a).

Based on plant fossils identified in previous studies, strata in La Magdalena Coalfield have been assigned to the *Alethopteris zeilleri* Megafloral Zone dated as "Saberian", which in the northwestern Iberian Peninsula corresponds to the earliest part of the Gzhelian (Knight et al. 2023).

During the Gzhelian, the Cantabrian continental basins were located less than 5° south of the equator (Scotese and Golonka 1992). They were adjacent to the Paleotethys Sea and formed in the foreland of the Hercynian mountain range (Wagner and Castro 2011) during the peak of Southern Hemisphere glaciation at a time of stregthened latitudinal

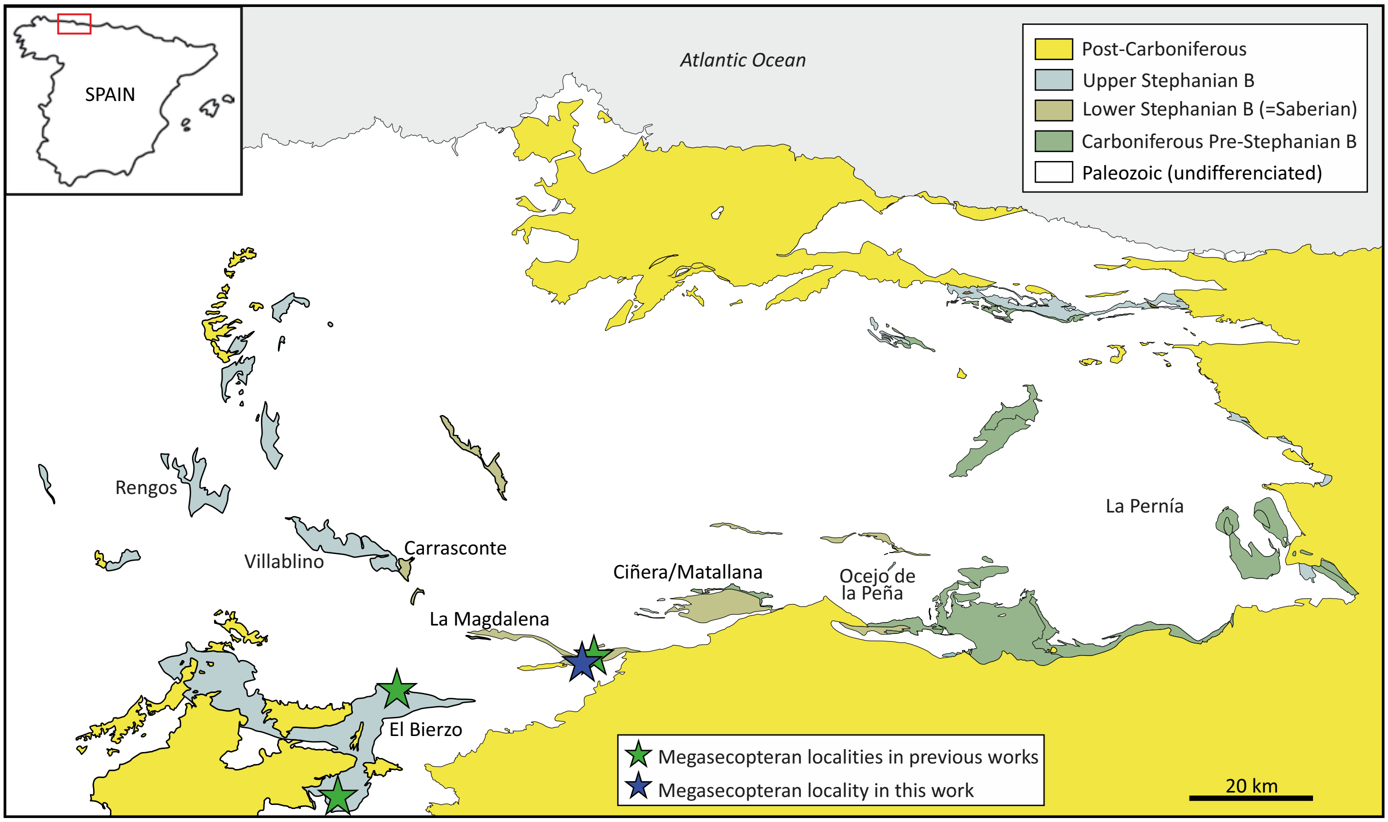

Fig. 1. Geological sketch map showing the La Magdalena Coalfield (León Province, NW Spain) and other coalfields previously yielding Carboniferous Megasecoptera in the northwestern Iberian Peninsula (see Table 1 for previous records).

climatic and floristic gradients (McLoughlin 2001; Gastaldo et al. 2020). This region experienced a tropical, humid climate, which gradually became more arid as it transitioned into the Permian (Tabor and Poulsen 2008).

Strata within La Magdalena Coalfield have been subjected to facies analyses resulting in two broad interpretations of the depositional setting. Heward (1978) considered that mass flow deposits typical of alluvial fans were the most important facies in the succession. Heward (1978) differentiated conglomerates of proximal areas, sandy and conglomeratic lobes of middle fan regions, alluvial fan channels, associations of interlobes and interchannels, distal fans and lacustrine facies. Alternatively, Colmenero et al. (1996) argued that alluvial fan processes were restricted to areas flanking the mountains and breaches of some river levees, and that deposition occurred primarily in braided and meandering rivers. Bashforth et al. (2010) also interpreted most of the deposits as fluvial, but indicated that deposits in proximal areas derived from debris flows.

The studied sample was recovered from near the Carmen mine, from strata unassigned to a formal lithostratigraphic unit but corresponding to the uppermost parts of the La Magdalena succession (Castro 2005a). These beds were laid down during the most stable fluvial phases, with development of mire environments favoring the accumulation of coal.

Systematic palaeontology

Phylum Arthropoda Gravenhorst, 1843

Class Insecta Linnaeus, 1758

Superorder Palaeodictyopterida Bechly, 1996

Order Megasecoptera Brongniart, 1885

Family Aspidothoracidae Handlirsch, 1919

Genus *Aspidothorax* Brongniart, 1894

Type species: *Aspidothorax triangularis* Brongniart, 1894 (original designation) from Gzhelian (Pennsylvanian, Carboniferous) strata of Commentry, France.

Included species: *Aspidothorax permianus* Sinitshenkova & Aristov in Sinitshenkova et al., 2020, from Kazanian, Permian; Perm Region, Russian Federation, and *Aspidothorax hispanicus* sp. nov., from Gzhelian, Pennsylvanian, Carboniferous of Spain.

Aspidothorax hispanicus sp. nov.

Fig. 2.

Zoobank LSID: urn:lsid:zoobank.org:act:158B10CA-E6B4-40C1-8376-6C724E66DB68.

Holotype: MUPE-IWC-01, well-preserved distal two-thirds of a wing co-preserved with *Alethopteris zeilleri* and *Pseudomariopteris cordato-ovata* plant fragments.

Type locality: Outcrop near Carmen mine, La Magdalena Coalfield, León Province, Spain (Fig. 1).

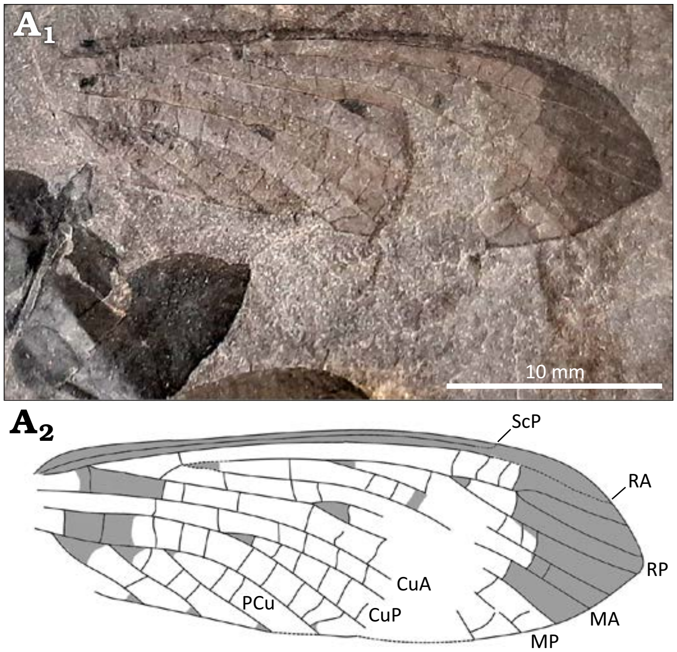

Fig. 2. Aspidothoracid megasecopteran insect *Aspidothorax hispanicus* sp. nov. holotype (MUPE-IWC-01) from mine heap near Carmen mine, La Magdalena Coalfield, León Province, Spain, "Saberian": Gzhelian; A_1, photography of the specimen, note fossils of the gymnosperm *Pseudomariopteris cordato-ovata* (Weiss, 1869) Gillespie et al., 1978 ex Krings et Kerp, 2000, with evidence of herbivory; A_2, line drawing of wing venation.

Type horizon: Un-named "Saberian", Gzhelian, upper Carboniferous beds.

Diagnosis.—Wing characters only. RP with four branches; CuP and MP veins each with long fork; area between PCu and posterior wing margin broad, with five–six rows of cells in-between.

Description.—Wing hyaline except for darkened costal area, apex, and small spots at forks of RP, MP, and CuP; wing apex pointed; preserved part 29.6 mm long, wing 10.2 mm wide; costal area very narrow, 0.2 mm wide; ScP close to R/RA and terminating at C 8.5 mm from wing apex; R/RA weakly curved, with apical part of area between it and C slightly widened, with few weak and short crossveins; base of RP 22.5 mm from wing apex; RP posteriorly pectinate, with four main branches, all simple; base of M 26.9 mm basal to that of RP; base of MA 3.6 mm distally; RP and MA touching at one point near base of RP; MA simple, MP with two long branches; a strong crossvein m-cua between base of M and CuA; CuA simple; bases of CuA and CuP not preserved; CuP with two long branches; PCu posteriorly pectinate, with four branches preserved; five–six rows of cells between PCu and posterior margin of wing.

Remarks.—The new insect fossil is similar to the wings of megasecopterans belonging to Aspidothoracidae Handlirsch, 1919, and Bardohymenidae Zalessky, 1937. Owing to the lack of phylogenetic analyses of Megasecoptera, we compare the new fossil with all megasecopteran families.

Representatives of Protohymenidae Tillyard, 1924, have a very narrow area between C and RA and a very distinctive posterior branch of RA near its apex (Huang et al. 2021), unlike the new fossil. Mischopteridae Handlirsch, 1906, Foriidae Handlirsch, 1919, and Aspidohymenidae Martynov, 1930, have distinctive wing shapes, and the distal crossveins are arranged in several lines as in extant Chrysopidae (order Neuroptera). Representatives of Moravohymenidae Kukalová-Peck, 1972, have a broader area between RA and RP than the new fossil, and MA, MP and branches of RP slightly curve anteriorly in their distal portion. Anchineuridae Carpenter, 1963, Hanidae Kukalová-Peck, 1975, Caulopteridae Kukalová-Peck, 1975, Arcioneuridae Kukalová-Peck, 1975, Engisopteridae Kukalová-Peck, 1975, and Ancopteridae Kukalová-Peck, 1975, have many more veins and crossveins than the new fossil (Kukalová-Peck 1975, 1991a). Members of Alectoneuridae Kukalová-Peck 1975, have MA touching RP at only one point (Carpenter 1963; Kukalová-Peck 1975). Scytohymenidae Martynov, 1937, Aykhalidae Sinitshenkova, 1993, Sphecopteridae Carpenter, 1951, Brodiopteridae Carpenter, 1963, and Brodiidae Handlirsch, 1906, have a relatively simplified venation with very few crossveins (Carpenter 1992; Pecharová et al. 2015a; Prokop et al. 2017). Representatives of Xenopteraidae Ross et al. 2013 (replacement name for Xenopteridae Pinto, 1986) have a MA connected to RP (Pinto 1986; Pecharová et al. 2015b). Vorkutiidae (*Vorkutia* Rohdendorf, 1947, *Siberiohymen* Rohdendorf, 1961, and *Fragmohymen* Novokshonov, 1995) seem to constitute a composite group with taxa having varied venation styles, based on incomplete wings. Nevertheless, they all differ from the new fossil by the ScP ending in RA at the midwing (Rohdendorf 1947, 1961; Novokshonov 1995). Corydaloididae Handlirsch, 1906 (*Corydaloides* Brongniart, 1885), Sphecorydaloididae Pinto, 1994 (*Sphecorydaloides* Pinto, 1994) and Ischnoptilidae Carpenter, 1951 (*Ischnoptilus* Brongniart, 1894) have a MA that anastomoses with RP, and a CuA anastomosing with M for some distances, unlike in the new fossil.

The new fossil shares with Aspidothoracidae and Bardohymenidae the characters of vein MA not touching RP and CuA not touching M. Pecharová et al. (2020: 10) proposed the following emended diagnosis for Aspidothoracidae: "The fore and hindwings homonomous, venation nearly the same, wings narrowing gradually basally, not petiolate. The apex distinctly pointed. ScP terminates near RA. ScP and RA very close together, connected to costal margin; stem of M very close to, but separate from base of RA + RP; MA free from RP and not diverging towards it, connected by strong cross vein rp-ma; stem of Cu basally very close to M, but not connected to it; CuA not diverging towards MP, connected by a strong cross vein (m-cua); one anal vein A1 [PCu]. Cross veins numerous and nearly evenly distributed over the wing". All the preserved characters of the new fossil conform well to this diagnosis, except for the presence of a strong crossvein rp-ma.

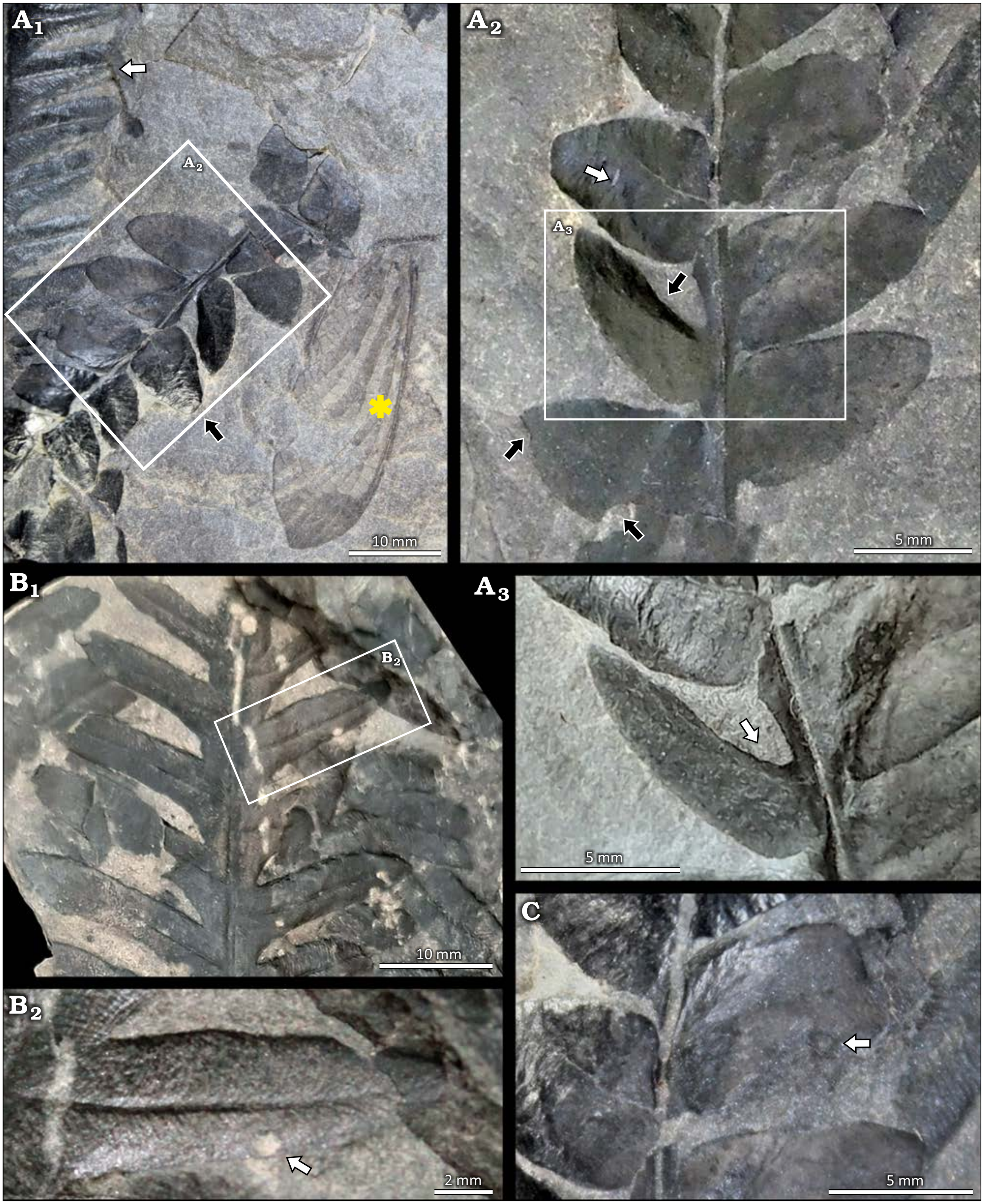

Fig. 3. Plant fossils associated with *Aspidothorax hispanicus* sp. nov. (MUPE-IWC-01, marked as yellow asterisk) from La Magdalena Coalfield, Spain; Gzhelian, upper Carboniferous. **A**. MUPE-IWC-01b; A_1, evidence of medullosan *Alethopteris zeilleri* Ragot, 1955 ex. Wagner, 1965 (white arrow), and the callistophytalean *Pseudomariopteris cordato-ovata* (Weiss, 1869) Gillespie et al., 1978 emend. Krings and Kerp 2000 (black arrow), note that the white arrow also denotes insect damage (margin feeding DT013) in the apical part of a pinnule; A_2, detail of *P. cordato-ovata* with evidence of plant-insect interactions, including hole feeding (DT007, white arrow) and margin feeding (DT012, black arrows); A_3, detail showing margin feeding (DT012) with reaction rim on a *P. cordato-ovata* pinnule (white arrow). **B**. MUPE-IWC-01c; B_1, specimen of *A. zeilleri* hosting hole feeding (DT001); B_2, detail of the hole feeding (DT001) on a pinnule of *A. zeilleri*. **C**. MUPE-IWC-01d, detail of a pinnule of *P. cordato-ovata*, the white arrow shows piercing and sucking damage (DT046).

Pecharová et al. (2020: 2) proposed the following emended diagnosis for the Bardohymenidae: "Fore and hind wings subequal in length and shape (nearly homonomous), petiolate, similar in venation; CA+CP flattened and wide, running close to ScA+ScP (costal space narrow); ScP distinguishable as a separate vein only in proximal part of wing; distally continues along RA, RA connected with CA+CP and ScA+ScP except in the distal part of wing; RA diverging from CA+CP + ScA+ScP and forming an apical cell; RP originating at about midwing, gives rise to 2–5 branches, M lies close to RA+RP basally, but separate from it, diverging away from RA+RP in the second quarter of wing; M dividing into simple MA and MP near to the point at which RP separates from RA; MA connected to RP by a strong cross vein; Cu at the base connected with the stem of M; CuA connected to M by a strong cross vein, one long anal vein with posterior branches; cross veins usually arranged in 2 staggered rows".

The new fossil shares the presence of more crossveins not arranged in two rows with Aspidothoracidae, in contrast to all taxa of Bardohymenidae. However, it shares the character of area between C and RA broadened apically and having some very short intervening crossveins with Bardynohymenidae. This broadening is similar to that of *Aspidothorax triangularis* Brongniart 1894, but is much weaker in the new fossil than in all Bardohymenidae (Pecharová et al. 2020: fig. 7). Thus, we assign the new fossil to Aspidothoracidae. *Aspidothorax permianus* differs from the new fossil in its simple CuP and MP vs with a long fork (Sinitshenkova et al. 2020). *Aspidothorax triangularis* differs from the new fossil in having a narrower area between PCu and the posterior wing margin, with one–two rows of intervening cells vs five–six (Carpenter 1992).

Stratigraphic and geographic range.—Known only from type locality and horizon.

Associated plants and plant-insect interactions

Preserved on the same bedding plane and almost overlapping the insect wing are several plant fossils (Fig. 3). The medullosan gymnosperm *Alethopteris zeilleri* Ragot, 1955 ex. Wagner, 1965 (Fig. 3A_1, B) is widely distributed in Stephanian and lower Permian strata of tropical Laurasia (Wagner 1968; Zodrow 2007). The new specimens of *A. zeilleri* consist of typical alethopteroid pinnae with well-separated pinnules 7–22 mm long and of fairly constant (4–5 mm) width in the middle part of the pinnules. Pinnules are ovate to lorate, clearly confluent at the base and broadly attached to the rachis with subsidiary veins on both sides of the midvein (Fig. 3B). Pinnules are alternate with variable angles of insertion (40–80°) on the rachis. These specimens have a strong and distinctive midvein that extends about 4/5 of the pinnule length. Secondary veins are relatively dense (35–40 veins/cm measured), perpendicular to the pinnule margins.

Some compressed pinnae fragments in this assemblage can be assigned confidently to the callistophytalean gymnosperm *Pseudomariopteris cordato-ovata* (Weiss, 1869) Gillespie et al. 1978 emend. Krings and Kerp 2000 (Figs. 2, 3A, C). *Pseudomariopteris* is common in late Carboniferous and early Permian floras of Europe and North America (Krings and Kerp 2000). Representatives of this genus have been interpreted to possess liana-like growth habits in forested areas (Krings and Kerp 2000). The new specimens have typical slightly asymmetrical oblong mariopterid pinnules that are 5–9 mm long, 4–5 mm wide, with entire margins, slightly pointed apices and a vaulted limb. Pinnules are inserted at 30–50° to the rachis, broadly attached, but slightly constricted at the base with the basiscopic side decurrent under the constriction and extending as a narrow flange down the rachis. The midvein is decurrent, extending about two-thirds of the pinnule length. The secondary veins are indistinct owing to poor preservation, but are bifurcated. Cuticle details were not recoverable.

Several herbivory features were identified on these plant remains and are referable to six DTs belonging to three FFGs. These FFGs are margin feeding (DT012, DT013), hole feeding (DT001, DT003, DT007) and piercing and sucking damage (DT046). *Alethopteris zeilleri* hosts evidence of margin feeding and hole feeding (DT012, DT001, and DT013; Fig. 3A_1, B). *Pseudomariopteris cordato-ovata* has a greater number and diversity of interactions, including margin feeding (DT012; Fig, 3A_2, A_3), and elliptical hole feeding with a weakly developed reaction rim (DT003; Fig. 3A_2); the reaction rims observed in these interactions reflect a well-developed plant response to the damage, indicating that the plant was alive when the damage occurred. Finally, *P. cordato-ovata* also hosts a more specialized damage type (DT046; Fig. 3C) consisting of an isolated, slightly concave, styletal puncture into the leaf tissue, 0.6–0.7 mm in diameter and characterized by dark carbonized material with a central depression. These piercing and sucking marks were probably caused by insects with stylet-like mouthparts.

Discussion

Previous studies have indicated that the diversity of Carboniferous insects in the Iberian Peninsula was relatively low compared to other parts of Europe (Carpenter 1992; Santos et al. 2023). Nevertheless, renewed interest in the study of Paleozoic insects and plant-arthropod interactions from the Iberian Peninsula in the past few years has revealed numerous new fossils, suggesting that insect occurrence and diversity in these deposits is much greater than previously recognized (Correia et al. 2020, 2021; Nel et al. 2022a, b; Santos et al. 2022, 2023, 2024). This renewed focus has

Fig. 4. Reconstruction of megasecopteran insect *Aspidothorax hispanicus* sp. nov. on leaves of *Pseudomariopteris cordato-ovata* and *Alethopteris zeilleri* with evidence of herbivory in a tropical late Carboniferous forest of Iberia. Reconstruction by Pollyanna von Knorring, Swedish Museum of Natural History, Stockholm.

opened new lines of research in the relationships between Paleozoic tropical plants and insects. The identification of *Aspidothorax hispanicus* sp. nov. in close association with herbivore-damaged gymnosperms (see reconstruction in Fig. 4) expands the complexity of Iberian Gzhelian terrestrial ecosystems.

Both plant species found associated with the new insect wing, *Alethopteris zeilleri* and *Pseudomariopteris cordato-ovata*, have features that are informative of the climate and local vegetation structure. Based on the pinnules of *A. zeilleri* being coriaceous, with inrolled margins, thick cuticles with upper surface hairs, and deeply sunken stomata restricted to the lower surfaces, Šimůnek (1989), Kerp and Barthel (1993), and Zodrow (2007), interpreted the parent plant to be mesophytic, growing on the margin of peat-forming areas. DiMichele et al. (2006) pointed out that, in the Upper Pennsylvanian of Texas, *A. zeilleri* locally occurs in shales associated with organic accumulations, but tends to be more common in less organic-rich deposits. Bashforth and Zodrow (2007) reported this species in Middle Pennsylvanian deposits of Nova Scotia in non-peat-forming habitats but in proximity to swamps, where they may have been exposed to intense sunlight or wind. Further, Bashforth et al. (2010), in their work on the vegetation of La Magdalena, cited *Alethopteris* and *Pseudomariopteris* as typical of non-peat-forming communities located in marginal wetlands and interfluve wetlands. These authors noted that both genera had a clear preference for disturbed sites, closer to rivers, in interfluve wetlands over other "seed-ferns". The co-occurrence of *A. zeilleri* and *P. cordato-ovata* indicates that *Aspidothorax hispanicus* likely lived in humid environments in alluvial settings, perhaps close to rivers in communities of arborescent Medullosales (*A. zeilleri*) and climbing/scrambling (liana-like) Callistophytales (*P. cordato-ovata*). Despite the Megasecoptera wing being disarticulated, it lacks abrasion or other evidence of transport, as do the plant remains. Thus, this assemblage seems to reflect minimal transport.

Several of the damage types observed on the studied plant remains have been found in other Carboniferous assemblages of northwestern Spain (Santos et al. 2022). However, we report damage types DT046, DT013, DT003, and DT007 for the first time in the Carboniferous of Spain. This diversity of interactions is indicative of a diverse and well-established entomofauna in the area, and is consistent with previous interpretations that the Carboniferous insect diversity from this region was much higher than recorded so far (Santos et al. 2022, 2023). Linking the damage to specific families or genera of insects is challenging, especially when the damage is very generalized, as is the case for DT012, DT001 or DT003, which could have been produced by several types of insects or other arthropods with chewing mouthparts. The more specialized piercing and sucking scars were probably made by insects with stylet mouthparts. Megasecoptera are strong candidates for this kind of damage, as insects of this group possessed piercing and sucking mouthparts (Prokop et al. 2016), probably to penetrate and feed on the inner tissues of various vascular plants (Kukalová-Peck 1991b; Labandeira and Phillips 1996; Engel et al. 2013; Prokop et al. 2016; Pecharová et al. 2020). Diverse genera of Megasecoptera were present in the region based on several records from Carboniferous deposits, including species of Anchineuridae (Carpenter 1963; Brauckmann 1993), Corydaloididae (Santos et al. 2023), Mischopteridae (Santos et al. 2023), and Aspidothoracidae; (Table 1). Future studies on the entomofauna and plant-insect interactions in the region may help to link insects with some interactions.

The new herbivorous species *Aspidothorax hispanicus* likely fed on the vegetation of the Carboniferous tropical forests of the area, which also provided shelter and protection from predators. Notably, *A. hispanicus* possessed patterning traits that may have helped avoid or deter predators. Dark patches and spots similar to those on the new species have been observed on other members of the genus, such as *A. triangularis*, for which this disruptive coloration was interpreted as a camouflage mechanism (Pecharová et al. 2020). The dark patch on the wings of *A. hispanicus* likely also served as effective camouflage, allowing the insect to blend into a dappled-light background. This camouflage would have offered protection from predators, such as griffinflies (Meganisoptera) (Nel et al. 2009; Pecharová et al. 2020), large damselfly-like species in the "Protozygopteran" group of Odonatoptera (Nel et al. 2012, 2018), and potentially even vertebrate predators. Disruptive color patterns in flight are commonly present in both modern and fossil odonates (Jouault et al. 2022), typically as transverse bands and spots on the wings, much like those in *A. hispanicus*. However, the distinct dark area at the wing apex might also have played a role in sexual display or courtship, similar to the color variations in the pterostigmata of male and female *Sympetrum* species. Although we agree with Pecharová et al. (2020) that the spots' most likely function was camouflage, the dark wing apex may have played an additional role in sexual dimorphism and courtship behavior.

Conclusions

The discovery of *Aspidothorax hispanicus* sp. nov. in Gzhelian, Pennsylvanian, deposits of León marks the first record of Aspidothoracidae in the Iberian Peninsula. This newly described species, found in close association with several plant remains, expands the distributions of this family and genus, which were previously identified only in France and the Russian Federation. The fossil represents the fourth megasecopteran species described from the Iberian Peninsula, contributing significantly to our understanding of the regional Carboniferous insect diversity.

The association of *Aspidothorax hispanicus* with gymnosperms, namely *Alethopteris zeilleri* and *Pseudomariopteris cordato-ovata*, suggests that these insects inhabited forested communities that included climbing plants/ground covers of humid alluvial environments. The presence of six damage types belonging to three functional feeding groups including margin feeding (DT012, DT013), hole feeding (DT001, DT003, DT007), and piercing and sucking (DT046), indicates diverse insect feeding strategies in the area during the Carboniferous. It also suggests the presence of chewing and piercing and sucking insect herbivores. The stylet mouthparts of Megasecoptera make insects of this order good candidates for the production of piercing and sucking damage found in the associated plants. *Aspidothorax hispanicus* sp. nov. probably used the vegetation for both nourishment and protection. Its wing markings, having coloration that likely served as camouflage, helped it blend into its environment and avoiding predators, such as griffinflies and damselfly-like species. The dark wing apex may also indicate the presence of sexual dimorphism or courtship behavior. These findings provide valuable insights into the habitats and ecological conditions in the area at that time, adding new information on Carboniferous tropical terrestrial environments of Spain.

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