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RESEARCH ARTICLE

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Early Devonian non-trilobite arthropods from the Iberian Chains (North East, Spain)

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ABSTRACT

Slightly sclerotised arthropods are described from shales of the Early Devonian age of the Axial Depression of the Cámaras river in Northeast Spain. The oldest records represent eurypterid fragments assigned to indeterminate Pterygotidae. They have been found in the early Pragian Nogueras Formation associated with land plant remains and rare marine invertebrates. The other two correspond to the first report of the phyllocarid *Nahecaris* in Spain. *Nahecaris carlsi* n. sp. is represented by a single complete specimen from the Pragian Santa Cruz Formation and *Nahecaris* sp. by another specimen from the Emsian Mariposas Formation. Both are associated with a rich marine fauna of various invertebrate groups. Environmentally, these arthropods occupied different areas from marginal marine (Pterygotidae indet.) to more open marine conditions (*Nahecaris*). The discovery of slightly sclerotised arthropods in several levels informs about the potential of the area for such type of preservation.

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Introduction

The Lower Devonian of the Iberian Chains (NE Spain) has been of great interest for biostratigraphic and palaeogeographic purposes since the pioneering work of Carls (1965). The Devonian crops out in different areas (Figure 1), being the Axial Depression of the Cámaras River (ADRC) the most extensive outcrop (Carls & Valenzuela-Ríos, 2002a) (Figure 1). In this area, several fossil groups like conodonts, ostracods, trilobites and brachiopods have been studied in great detail from the biostratigraphic point of view (Carls, 1969, 1974, 1975, 1985, 1986; Carls & Gandl, 1969; Dojen, 2005; Dojen et al., 2004; Gandl, 1972). However, other groups such as crinoids (Ausich & Zamora, 2019), fish remains (Botella, 2005; Botella et al., 2006, 2014; Dupret et al., 2011; Martínez-Pérez et al., 2010), and plants (Cascales-Miñana et al., 2011, 2017) have received much less attention.

Arthropods (except ostracods and trilobites) are rare components in the fossil assemblages of the Devonian successions in the Iberian Chains and elsewhere. Carls (1965) and Carls and Valenzuela-Ríos (1999, 2002b) documented the presence of phyllocarids in several formations from the ADRC but without providing detailed descriptions and illustrations of these fossil remains (see Zamora, 2019 for a complete synthesis of fossils in different formations). Other Devonian arthropods from Spain include pterygotid eurypterids with Bohemian affinities from Catalonia (E Spain) reported from Lochkovian deep water successions (Chlupáč et al., 1997). These authors also mention the presence of phyllocarids in the same beds. In the palaeogeographically close Moroccan Anti-Atlas, phyllocarids are moderately common in the lower Emsian sediments (De Baets et al., 2010; Klug et al., 2010).

The aim of this work is to report the discovery of phyllocarid and eurypterid fossils in the Lower Devonian of the ADRC (Iberian Chains, Aragón, Spain), including two phyllocarids in two different levels in Pragian and Emsian successions (Santa Cruz and Mariposas formations), as well as Pragian eurypterid remains (Nogueras Formation). The description of these rare but important faunal components and some comments on the environmental conditions where those fossils occur will be provided. These new findings suggest a high potential of this area for the preservation of Devonian arthropods with only lightly sclerotised cuticles.

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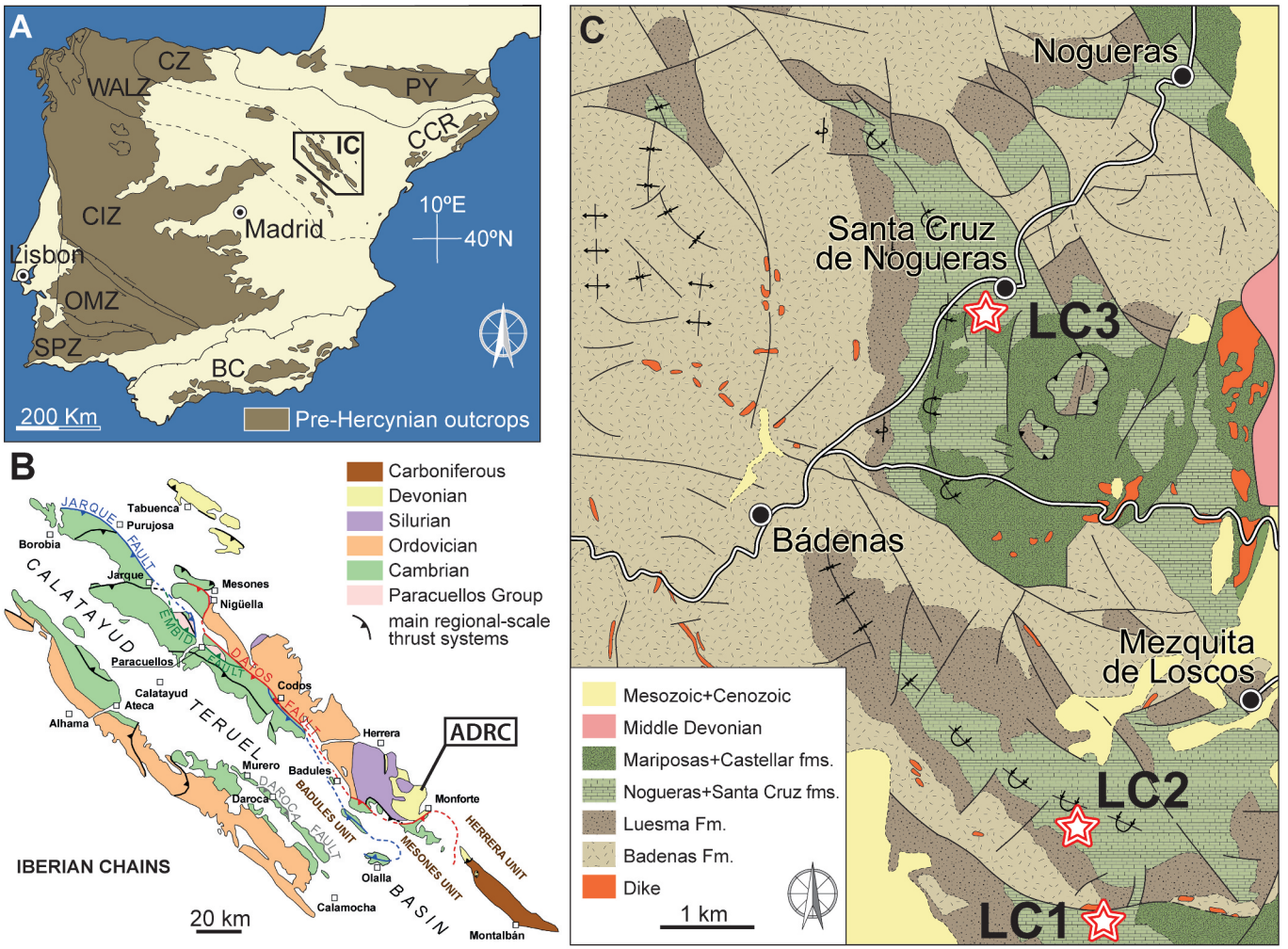

Figure 1. Localities yielding Devonian arthropods from Iberian Chains (NE Spain). (A) Map of Spain showing Pre–Hercynian outcrops and tectonostratigraphic zones. Zones: CZ, Cantabrian; CIZ, Central Iberian; WALZ, West Asturian–Leonese; OMZ, Ossa–Morena Zones; SPZ, South Portuguese; BC, Betic Cordillera; IC, Iberian Chains; PY, Pyrenees. (B) Geological map of the studied area with indication of Devonian outcrops and tectonostratigraphic units, after Álvaro et al. (2018). Note the position of the Axial Depression of the Río Cámaras (ADRC). (C) Detailed geological map of the ADRC with indication of the three studied localities (LC1 to LC3). After Zamora (2019).

Localities, age and stratigraphy

The Lower Devonian rocks that crop out in the Axial Depression of the Río Cámaras (ADRC) include different siliciclastic- and limestone-dominated formations (Figure 2). Most of these formations are fully marine, representing mostly shallow platform environments (Carls, 1988; Pérez-Pueyo et al., 2018). Nevertheless, the presence of complete plant remains preserving sporangia at some levels associated with a low diversity and number of marine taxa may point to freshwater influence in specific time intervals (Cascales-Miñana et al., 2017). This also shows that there were changes in the depositional depth and in palaeoenvironmental conditions within in these coastal to marine areas.

Earliest arthropods with poorly or unmineralised cuticles recovered from the Devonian of the ADRC are eurypterid remains (Figure 3(D)) collected from the Santo Domingo creek (Figure 3(A)) in the municipality of Mezquita de Loscos (Teruel) (LC1 in Figure 1). They occur in arenaceous shales from the so-called interval d2b of the Nogueras Formation (see LC1 in Figure 2) associated with plant remains (Figure 3(C)) and very rare invertebrates, mostly articulate brachiopods. The level corresponds to the fossil site Loscos 4, which is considered as located at the lower part of the Pragian (Cascales-Miñana et al., 2015, 2017).

The phyllocarid *Nahecaris carlsi* n. sp. (Figure 3(G)) occurs near the lowermost part of the Santa Cruz Formation (Pragian) in Terreros Creek (Mezquita de Loscos, Teruel) (LC2 in Figure 1) associated with trilobites (*Treveropyge wallacei procerospinosa* Gandl, 1972 and Homalonotidae indet.), brachiopods (*Ctenochonetes arenoricensis* Racheboeuf, 1976, *Hysterolites* sp. and *Plectodonta* sp.), the bivalve *Nuculoidea* sp., rare orthoceratids and indeterminate tabulate corals and ostracods. This level corresponds to the so-called interval d3aα of Carls (1988) (see LC2 in Figure 2).

The phyllocarid *Nahecaris* sp. (Figure 3(F)) was collected in the Mariposas Formation in Santa Cruz de Nogueras village (Teruel) in dark shales with an abundant benthic fauna, which corresponds to the so-called d4a interval described by Carls (1988), which is early

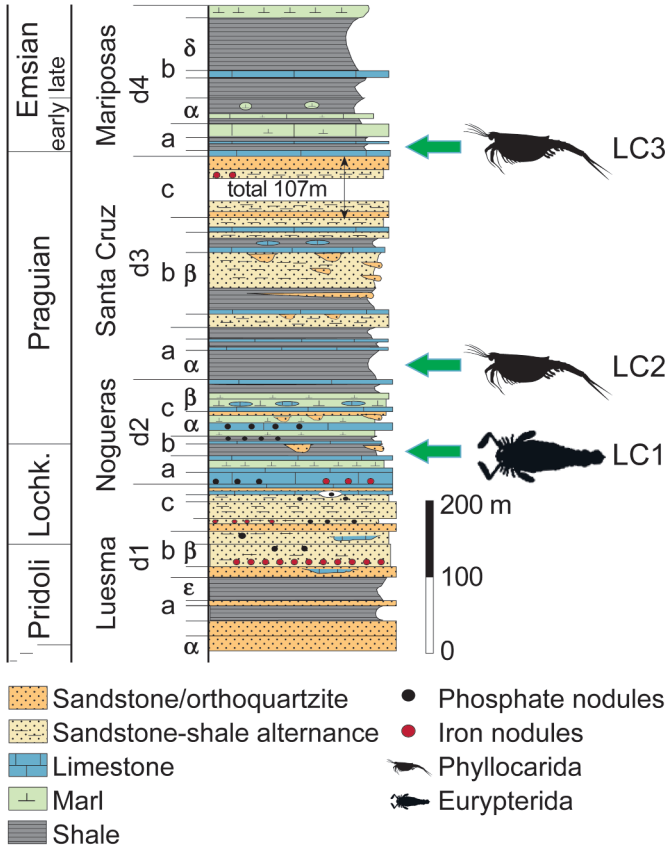

Figure 2. Stratigraphic log with the position of the beds containing arthropods. Lower level (LC1) corresponds to interval d2b of the Nogueras Formation in the Santo Domingo creek (Mezquita de Loscos, Teruel). Intermediate level (LC2) corresponds to interval d3aα of the Santa Cruz Formation (Pragian) in Terreros Creek (Mezquita de Loscos, Teruel). Upper level corresponds to d4a interval of the Mariposas Formation in Santa Cruz de Nogueras village (Teruel). Stratigraphy based on Carls and Valenzuela-Ríos (2002a).

Figure 3. Field photographs and fossil remains. (A) Barranco de Santo Domingo creek showing interval yielding eurypterid and plant remains. (B) Santa Cruz de Nogueras locality showing excavation yielding *Nahecaris* sp. (C) Plant remains of *Teruelia* sp. from Barranco de Santo Domingo locality. (D) Eurypterid fragment from the same locality showing lunate shape ornamentation. (E) Complete camerate undescribed crinoid from Santa Cruz de Nogueras locality. (F) *Nahecaris* sp. (G) *Nahecaris carlsi* n. sp.

Emsian in age (LC3 in Figures 1 and 2). The section was described by García-Alcalde et al. (in Villas et al., 2018) and crops out close to the ruins of an ancient mill, at the left bank of the Cámaras river, 500 m south west of Santa Cruz de Nogueras (Figure 3(B)). These strata are rich in brachiopods, solitary corals and crinoids (Figure 3(E)), thus indicating fully marine conditions.

Material and methods

Specimens are preserved as compressed fossils in shales with skeletons replaced by carbonaceous films (Figure 3(D,F)), rarely partially altered to iron oxides (Figure 3(G)). Eurypterid remains are mostly fragmented with no signs of articulation representing moults that were probably subjected to resedimentation for

a certain time before final burial. They appear to be associated with plant remains preserving sporangia in rare instances. The two phyllocarids are preserved in association with other marine fauna that appear articulated in many instances (e.g. trilobites and crinoids) suggesting rapid burial. In fact, one of the specimens (*Nahecaris carlsi* n. sp.) is preserved with the two valves in a butterfly position (Figure 3(G)) supporting high energy events and rapid burial of empty moults (exuviae) (*sensu* García-Bellido et al., 2009).

The specimens were prepared using a Micro Jack 2 air scribe (Paleotools; Brigham, UT, U.S.A.). Phyllocarids were casted using latex casts prior to photography. The specimens were then photographed dry and coated with ammonium chloride sublimate. Detailed photography of the carapace surfaces was made using a Nikon d7100 camera (Nikon, Tokyo, Japan) with a macro 60 mm-lens. Key aspects of the specimens are shown in Figures 4 and 5.

Specimens were collected with permission from the regional Government of Aragón (EXP: 350/2023).

Repository and institutional abbreviation.— All figured specimens are deposited in the Museo de Ciencias Naturales de la Universidad de Zaragoza (Zaragoza, Spain) under the acronyms MPZ2025/01–04.

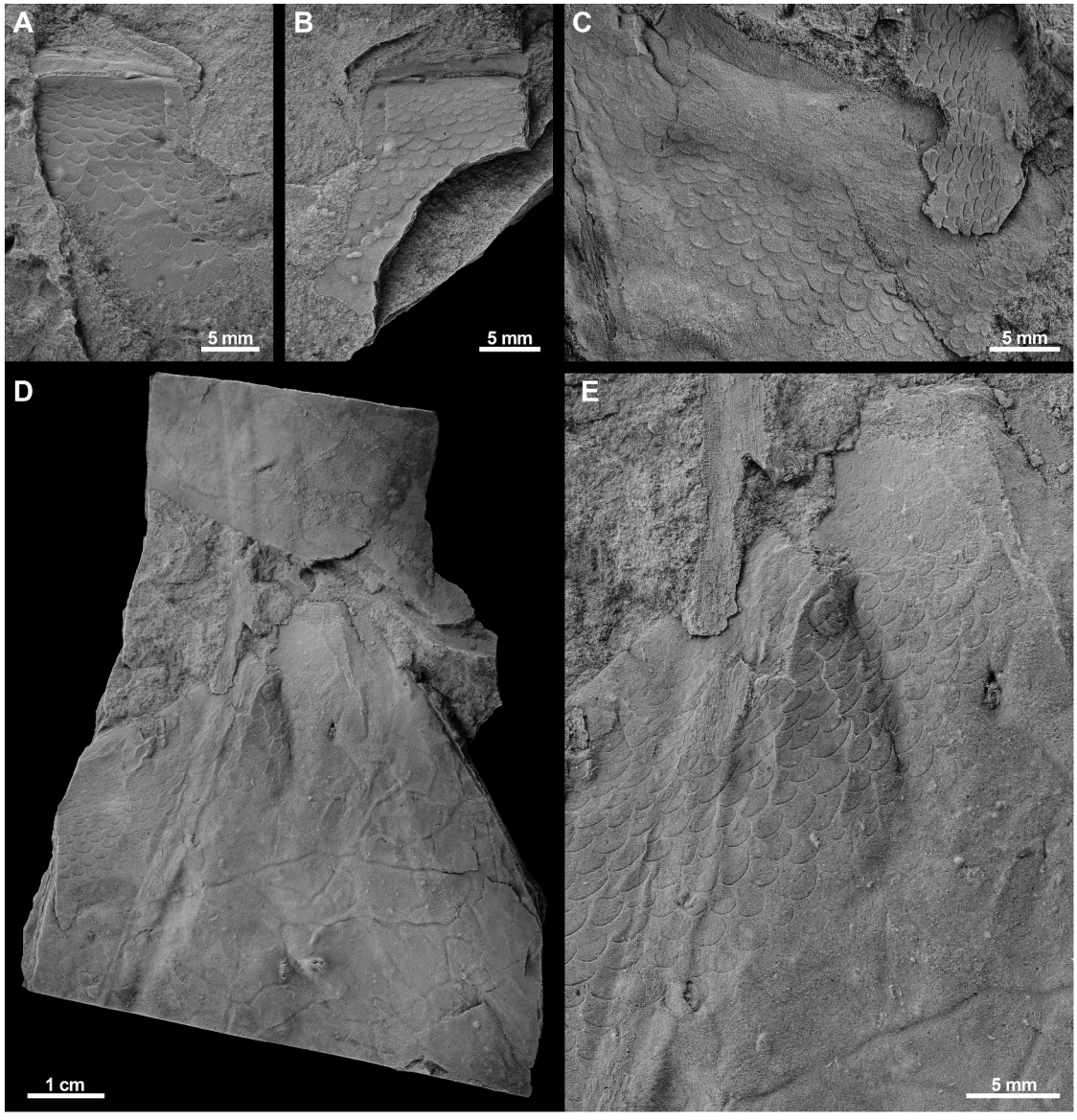

Figure 4. Eurypterid fragments assigned to Pterygotidae indet. From Nogueras Formation in the Santo Domingo creek (Mezquita de Loscos, Teruel). (A, B) Opisthosomal segment, most likely a mesosomal tergite (MPZ2025/01). (C–E) Fragments of cuticle with the distinctive broad lunules likely portions of opisthosomal segments (MPZ2025/02).

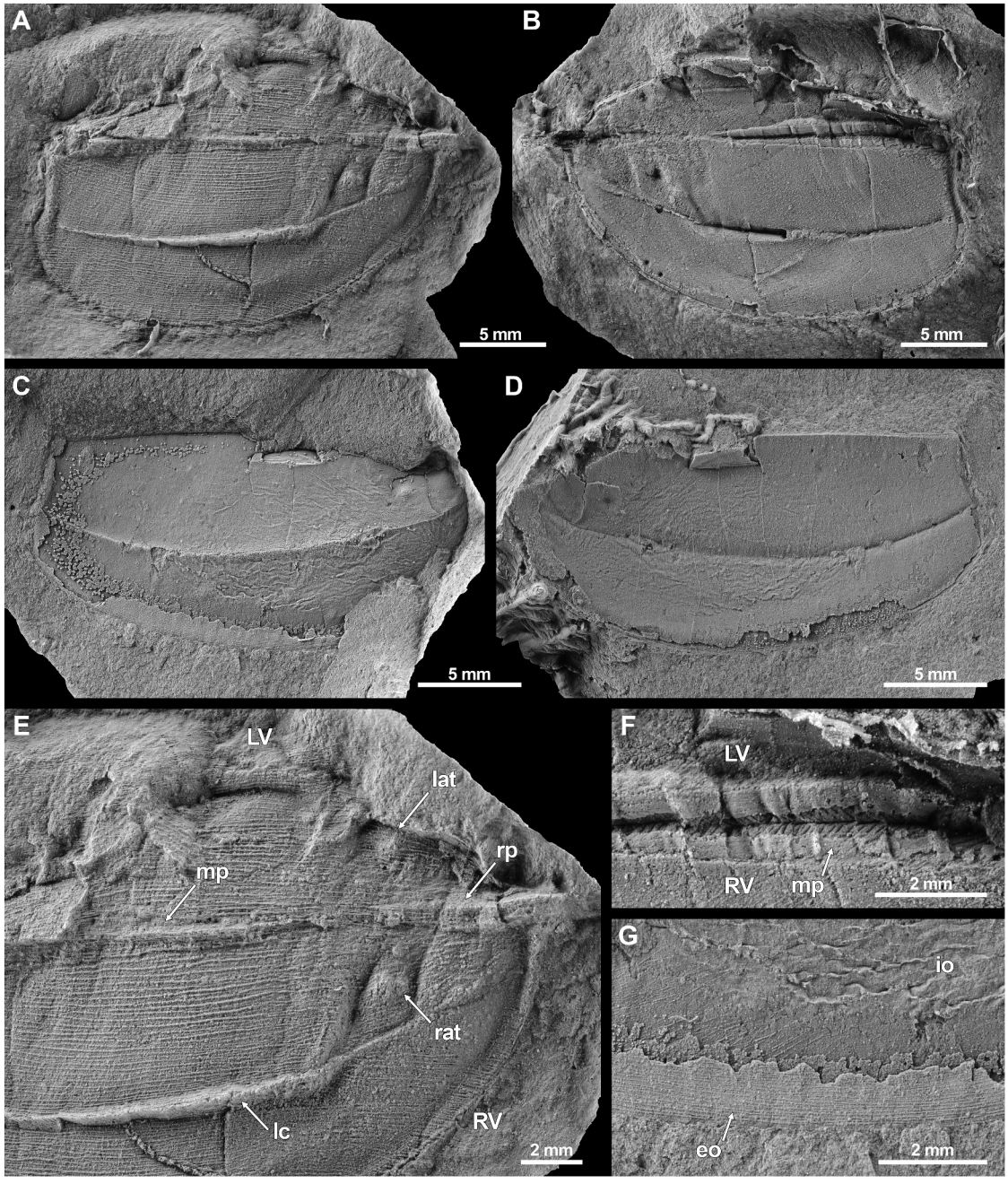

Figure 5. Phyllocarid carapaces from the Iberian Chains. (A, B, E, F) *Nahecaris carlsi* n. sp. from the Santa Cruz Formation (Pragian) in Terreros Creek (Mezquita de Loscos, Teruel). Specimen MPZ2025/03. (C, D, G) *Nahecaris* sp. from the Mariposas Formation in Santa Cruz de Nogueras village (Teruel). Specimen MPZ2025/04. (A, B) Complete specimen of *N. carlsi* n. sp. in a butterfly position part (A) and counter-part of the external view (B). (C) External view of *Nahecaris* sp. with the external ornamentation partially developed on the ventral part (G). (D) External view of the carapace in *Nahecaris* sp. (E) Anterior view of *N. carlsi* n. sp. (F) Detail of the median dorsal plate of *N. carlsi* n. sp. All specimens are latex casts whitened with ammonium chloride sublimated. Abbreviations: eo. external ornamentation, io. internal ornamentation, mp. median dorsal plate, lat. left anterior tubercle, lc. lateral carina, LV. left valve, rat. right anterior tubercle, rp. rostral dorsal plate, RV. right valve.

Systematic palaeontology

Terminology for *Nahecaris* follows the terminology in Brauckmann et al. (2002). Nomenclature for eurypterid remains follow Miller (2007) and Bicknell et al. (2020).

Phylum Arthropoda von Siebold, 1848
Subphylum Chelicerata Heymons, 1901
Order Eurypterida Burmeister, 1843
Suborder Eurypterina Burmeister, 1843
Family Pterygotidae Clarke & Ruedemann, 1912

Pterygotidae indet.
Figures 3(D) and Figures 4(A–E)

Material. MPZ2025/01, MPZ2025/02

Description of MPZ2025/01. Part (Figures 3(D) and 4(A)) and counterpart (Figure 4(B)) of a fragment of an opisthosomal segment, most likely a mesosomal tergite. Specimen dimensions are 13 mm × 21 mm. Anterior surface covered by broad lunules, getting larger posteriorly; posterior one-third smooth. Anterior margin bends sharply downwards at the front and then continues forward towards a thin marginal articular surface.

Description of MPZ2025/02. A 86 mm × 68 mm slab (Figure 4(D)) containing several fragments of cuticle with the distinctive broad lunules (Figure 4C(,E)). The largest fragment (Figure 4(C)) is 50 mm wide. Fragments are distorted, cracked and crossed by plant remains, hampering the identification of segmental boundaries. There is insufficient evidence to assign these to distinct regions of the body, but they are most likely portions of opisthosomal segments.

Discussion. The specimens have the characteristic broad and dense lunules of pterygotid eurypterids. However, the lack of phylogenetically informative features, such as chelicerae and telson, precludes a more definitive assignation. We therefore follow Bicknell et al. (2020), who worked with similar material, in designating this as Pterygotidae indet. Lamsdell and Legg (2010) pointed out serious concerns with a pterygotid classification, including the possibility of paraphyletic genera. Previously described fragments from elsewhere identified as *Pterygotus* sp. (Table 1) should probably be assigned only to the family. Specimen MPZ2025/01 can be compared to the large mesosomal tergite of *Pterygotus anglicus* Agassiz, 1844 illustrated in Woodward (1866–1878), plate II figure 2), which shows a similar pattern of lunules at the anterior margin.

Subphylum Crustacea Brünnich, 1772
Class Malacostraca Latreille, 1802
Subclass Phyllocarida Packard, 1879
Order Archaeostraca Claus, 1888
Suborder Rhinocarina Clarke in Zittel, 1900
Family Rhinocarididae Hall & Clarke, 1888
Genus *Nahecaris* Jaekel, 1921

Type species. *Nahecaris stuertzi* Jaekel, 1921

Diagnosis (after Poschmann, 2021). Rhinocaridid phyllocarid with a single mesolateral carina on each carapace valve, mesolateral carina extending from or almost from anterior to posterior carapace margin; each valve with anterior tubercle and dorsal depressions generally present, posterodorsal spine lacking; median dorsal plate ending posterior to anterior tubercle; cross section of carapace nearly trapezoidal; surface more or less largely covered by short striae, fine undulating and anastomosing ridges, or straight lines.

Age. Previous records included only Emsian occurrences, but the presence of one Pragian specimen in the Santa Cruz Formation expands the stratigraphic range into the Pragian-Emsian (Table 2).

Geographical occurrence. Harz Mountains, Hunsrück, Rhenish Slate Mountains, Eifel Mountains (Germany), Dra Valley and Tafilalt (Morocco), Réideschbaach (Luxembourg) Axial Depression of the Cámaras River (Spain). Included species are summarised in Table 2.

Nahecaris carlsi n. sp.
Figures 3G and 5(A,B,E,F)

Holotype. Specimen MPZ2025/03, which is a complete carapace in a butterfly position, preserving the complete right valve and a partial left valve.

Locus typicus. Los Terreros, Axial Depression of the Cámaras River, Mezquita de Loscos (Teruel, Spain).

Stratum typicum. d3aα of the Santa Cruz Formation, Pragian (Lower Devonian).

Material. Single specimen designed as the holotype.

Derivation of name. Honoring Peter Carls for his pioneering work in the area describing the Santa Cruz Formation in Los Terreros Creek for the first time.

Table 1. Previously described occurrences of pterygotid eurypterids from the Lochkovian and Pragian. Data from the paleobiology database.

Taxon	Age	Locality	Formation	Palaeoenvironment	Reference
Acutiramus sp.	Lochkovian	New York, USA	Manlius Formation	Lagoonal/Restricted shallow marine	Ciurca (1978)
Acutiramus sp.	Lochkovian	Catalonia, Spain	Olorda Formation	Offshore indet.	Chlupáč et al. (1997)
Acutiramus perneri	Lochkovian	Barrandian, Czech Republic	Lochkov Formation	Deep subtidal	Chlupáč (1994)
Acutiramus perneri	Lochkovian	Catalonia, Spain	Olorda Formation	Offshore indet.	Chlupáč et al. (1997)
Acutiramus bohemicus	Lochkovian-Pragian	Central Algeria	Idjerane Sandstone	Transition zone/lower shoreface	Legrand (1965); Berry and Boucot (1973)
Acutiramus cf. *bohemicus*	Pragian	Victoria, Australia	Wilson Creek Shale	Offshore	Bicknell et al. (2020)
Pterygotus sp.	Lochkovian	Poland (boreholes)	Bostów Formation	indet.	Tomczyk et al. (1977)
Pterygotus sp.	Lochkovian	Spitsbergen, Norway	Fraenkelryggen Formation	Marginal marine	Størmer (1934)
Pterygotus sp.	Lochkovian	Siberia, Russian Federation	Zub Formation	Paralic indet.	Marshall et al. (2014); Novožilov (1958)
Pterygotus anglicus	Lochkovian	Scotland, UK	Dundee Flagstone	Fluvial-lacustrine indet	Braddy (2000)
Pterygotus anglicus	Lochkovian	New Brunswick, Canada	Dalhousie Formation	Offshore	Copeland and Bolton (1960); Miller (1996)
Pterygotus cf. *barrandei*	Lochkovian	Catalonia, Spain	Olorda Formation	Marginal marine	Chlupáč et al. (1997)
Pterygotus vogti	Lochkovian	Spitsbergen, Norway	Fraenkelryggen Formation	Marginal marine	Størmer (1934)
Pterygotus wanggaii	Lochkovian	Yunnan, China	Xiaxishancun Formation	Marine indet.	Z. Ma et al. (2023)
Pterygotus wanggaii	Lochkovian-Pragian	Yunnan, China	Xitun Formation	Marine indet.	Z. H. Ma et al. (2025)
Pterygotus carmani	Lochkovian-Pragian	Ohio, USA	Holland Quarry Shale	Marginal marine indet	Kjellesvig-Waering (1961)
Pterygotus floridanus	Lochkovian	Florida, USA	Borehole – 'core 44'	indet.	Kjellesvig-Waering (1950); Pojeta et al. (1976)
Pterygotidae indet.	Lochkovian	Ardennes, France	Fépin Formation	Marginal marine	Blieck et al. (2013)
Pterygotidae indet.	Lochkovian	New South Wales, Australia	Muttama Creek Siltstone	Marginal marine indet.	Bicknell et al. (2020)
Pterygotidae indet.	Lochkovian	Victoria, Australia	Humevale Siltstone	Deep-water indet.	Bicknell et al. (2020)
Pterygotidae indet.	Lochkovian	Nova Scotia, Australia	Knoydart Formation	Non-marine	Copeland and Bolton (1960)
Erettopterus saetiger	Lochkovian-Pragian	Ohio, USA	Holland Quarry Shale	Marginal marine indet	Kjellesvig-Waering (1961)
Jaekelopterus cf. *howelli*	Pragian	Wyoming, USA	Beartooth Butte	Estuary/Bay	Lamsdell and Legg (2010)

Table 2. Devonian occurrences of the phyllocarid *Nahecaris*..

Species	Age	Locality	Reference
Nahecaris carlsi n. sp.	Praguian	Loscos, Teruel (Spain)	This work
Nahecaris sp.	Early Emsian	Santa Cruz de Nogueras, Teruel (Spain)	This work
Nahecaris jannae	Early Emsian	Tafilalt (Morocco)	Klug et al. (2008)
Nahecaris malvinae	Early Emsian	Draa Valley (Morocco)	Klug et al. (2008)
Nahecaris stuertzi	Early Emsian	Hunsrück (Germany)	Jaekel (1921)
Nahecaris sp.	Early Emsian	Réideschbaach site (Luxembourg)	Poschmann et al. (2024)
Nahecaris lata	Late Emsian	Rhenish Slate Mountains (Germany)	Traquair in Walther (1903)
Nahecaris sabineae	Late Emsian	Heckelmann Mill near Steinsberg, Rhineland-Palatinate (Germany)	Poschmann (2021)
Nahecaris frankei	Late Emsian	Western Eifel Mountains (Germany)	Brauckmann et al. (2002)

Diagnosis. Medium sized *Nahecaris* with prominent anterior tubercle on each carapace valve, moderately straight median dorsal plate and large rostral plate ending in a prominent process. Lateral carina crossing the whole valve being more prominent in the medial portion. Surface covered by thin parallel striation that covers the whole valve.

Description. Specimen MPZ2025/03 represents a complete carapace with both valves, although the left valve is slightly damaged due to compaction. Valves are sub-semi elliptical, subdivided by a mesolateral carina into a dorsal and ventral region (*sensu* Brauckmann et al., 2002). Maximum length is 25 mm, and maximum height is 10.5 mm. The length-to-height-ratio is about 2.4. Both valves with anteriorward ascending mesolateral carina with a chevron pattern in the posterior part. Carapace rim narrow, more marked posteriorly. Carapace with fine parallel ridges that become closely spaced ventrally. Rostral plate large ending in a rostral

spine. Median dorsal plate is thin. Anterior tubercle relatively large with two well-developed depressions (one anterior, one posterior).

Discussion. The described material agrees with the diagnosis proposed by Poschmann (2021) for the genus *Nahecaris* specially in the presence of a single mesolateral carina on each valve, extending from the anterior to the posterior carapace margin; presence of an anterior tubercle and dorsal depressions and ornamentation pattern. *Nahecaris carlsi* represents the oldest occurrence of the genus. Comparison of *Nahecaris carlsi* with the type species *Nahecaris stuertzi* is complicated due to different type of preservation, but in the former ornamentation consists mostly on parallel ridges all over the carapace while in the later ridges are short or interrupted, with the exception of some specimens (see Bergström et al., 1987, fig. 5). Anterior tubercle is poorly developed or lacking in *N. stuertzi* (*sensu* Brauckmann et al., 2002), while well developed and present in *N. carsli*. *N. carlsi* shows a prominent process in the rostral plate that is not preserved in some species (i.e. *Nahecaris lata* (Traquair in Walther, 1903), see Poschmann, 2021, fig. 4) and less developed in species like *N. sabineae* Poschmann, 2021. *N. frankei* Brauckmann et al., 2002 lacks such a process. The ornamentation in *N. carlsi* is similar to that of *Nahecaris malvinae* Klug et al., 2008, but the spacing between the lines in the latter is wider. *Nahecaris lata* has similar terrace lines as *N. carlsi*, but only between the carina and the base of the plate, while in *N. frankei*, lines are absent in the upper part of the valves, at least in the specimens figured by Brauckmann et al. (2002). *N. jannae* Klug et al., 2008 has strong tubercles on the surface, which might be a diagnostic character of that species. *N. sabineae* Poschmann, 2021 shows strong oblique terrace lines on the dorsal part of the valves.

Nahecaris sp.
Figures 3(F) and 5(C,D,G)

Material. A single specimen of a right valve preserving part of the ornamentation in the ventral side. MPZ2025/04.

Description. Specimen MPZ2025/04 represents only a right valve. The valve is sub-semi elliptical with a well-developed mesolateral carina that does not reach the anterior margin. Maximum length is 24 mm, and maximum height is 11 mm. Length-to-height ratio is about 2.2. Carapace with very thin parallel ridges ventrally, and corrugated rows internally developed. Anterior tubercle very small with no obvious associated depressions.

Discussion. The specimen is assigned to *Nahecaris* because of the presence of a single mesolateral carina extending from the anterior to the posterior carapace margin, the valve shape and the presence of an anterior tubercle. Ventral ornamentation consisting of parallel lines is similar to *Nahecaris malvinae* and *N. frankei* (Brauckmann et al., 2002; Klug et al., 2008). Its incomplete preservation precludes species assignation of this single right valve.

Discussion

Environmentally, the association of pterygotids with both land plants and brachiopods, suggesting a nearshore habitat, is consistent with previous interpretations of their broad environmental range, ranging from shallow to deep-water (Bicknell et al., 2020; Braddy, 2023; Plotnick, 1999; Plotnick & Baumiller, 1988). Early Devonian pterygotids are cosmopolitan (Table 1), with remains found in Europe, Algeria, China, Siberia, Australia, and North America. Overall diversity of Pterygotidae was already low by the Early Devonian, with extinction of the clade occurring during the Eifelian. This reflects an important part of the transition of eurypterids from mainly marine habitats in the Ordovician to the Early Devonian to almost exclusively freshwater from the Late Devonian onwards (Lamsdell & Selden, 2017).

Age, proportions, size and ornamentation as well as the clayey sedimentary facies of the host rock of the newly described phyllocarids from Lower Devonian strata of Spain correspond very well to the occurrences known from Morocco (De Baets et al., 2010; Klug et al., 2010). Additionally, the association with trilobites, brachiopods, palaeotaxodont bivalves, orthocerids, tabulate corals and ostracods is remarkably similar to the lower Emsian faunas of Morocco. This is not surprising, taking into account the palaeogeographical proximity of Spain and the Anti-Atlas in the Rheic Ocean at that time (Kocsis & Scotese, 2021). Of course, the faunal composition rather reflects a similar palaeoenvironment than only a geographic proximity. Pelagic elements such as cephalopods associated with the phyllocarids indicate open marine conditions and the palaeotaxodont bivalves point at soft sediments and at low oxygen levels in the sediment as well as in lower parts of the water column. Although the preservation is much better and the diversity is significantly higher (probably due to the much lower sampling effort in Morocco and Spain than in the German Hunsrück), both the Spanish and the

Moroccan faunas are reminiscent of the assemblages of the German Hunsrück Slate (e.g. Bartels et al., 2009).

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