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"Carbonífero de Puertollano" Natural Monument (Puertollano basin, Spain): a window for the knowledge of Early Vertebrates

Monumento Natural "Carbonífero de Puertollano" (cuenca de Puertollano, España): una ventana al conocimiento de los Vertebrados Primitivos

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Abstract: Coal mining at the Puertollano Carboniferous basin has led to the discovery and study of numerous fossiliferous layers, rich in chondrichthyan, actinopterigyan and tetrapod remains. The end of the mining operations and closure of the mines could also represent complete cease of palaeontological prospections and field work at the Puertollano basin. Fortunately, three quarries, called María Isabel, La Extranjera and La Tejera, have been declared a Natural Monument. Consequently, they are protected by law and reserved for geological and palaeontological scientific research. In this paper, we describe the geology of the Natural Monument and its vertebrate fossil record. The outcrops of the three quarries show the most superficial part of the stratigraphic series so that they inform about the latest stages of the sedimentological and palaeogeographical evolution of the Puertollano basin. The actual coal basin appears to represent a remnant of a much larger basin which opened eastward to the Palaeo-Tethys. The diverse chondrichthyan assemblage (acanthodians, xenacanths and euselachians) and euryhaline actinopterygians, and the presence of tidal rhythmites, indicate an estuarine-deltaic environment. Future sedimentological and palaeontological studies at the Natural Monument will inform about the degree of marine influence in the basin and the changes of the vertebrate communities.

Resumen: La minería del carbón en la cuenca carbonífera de Puertollano, ha permitido el descubrimiento y estudio de numerosos niveles fosilíferos ricos en restos de condrictios, actinopterigios y tetrápodos. El final de la explotación del carbón y el cierre o restauración de las minas, pudo suponer la eliminación de toda posibilidad de futuras prospecciones paleontológicas. Afortunadamente, tres minas a cielo abierto, María Isabel, La Extranjera y La Tejera, han sido declaradas Monumento Natural y, por lo tanto, son áreas protegidas, reservadas para la investigación geológica y paleontológica. En este trabajo describimos la geología de las tres localidades del Monumento y estudiamos el contenido en vertebrados. En las tres minas afloran los niveles más superficiales de la cuenca, dando información de los momentos finales de sedimentación y evolución paleogeográfica de la cuenca de Puertollano. La cuenca carbonífera actual sería un resto de una cuenca mucho mayor conectada hacia el este con el Paleo-Tetis. La abundancia de condrictios (acantódidos, xenacántidos y euseláceos) y actinopterigios eurihalinos, y la existencia de ritmitas mareales, indica un ambiente de tipo estuarino-deltaico. Futuros estudios sedimentológicos y paleontológicos en el Monumento Natural informarán sobre el grado de influencia marina en la cuenca y los cambios de las comunidades de vertebrados.

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INTRODUCTION

The Puertollano coal and oil shale field presents a wide fossil record including flora and fauna. Extensive coal mining led to detailed palaeontological investigations, mainly floral biostratigraphy with a direct application in the correlation of coal-bearing strata. Since its discovery in 1873, the Puertollano basin was well known by the plants remains (see Wagner & Álvarez-Vázquez, 2010, 2015 for recent taxonomical and palaeoenvironmental reviews) but detailed prospection and excavations in the coal mines also provided very important information about faunal contents. Invertebrate skeletal remains are rare and belong only to several groups of arthropods (Wagner, 1985; Castro, 1997; Soler-Gijón, 1993a, 1997c). By contrast, the vertebrate remains are very common and represent elements of three main groups: chondrichthyans (acanthodians, xenacanths and euselachians), actinopterygians (palaeonisciforms) and temnospondyl amphibians.

Alvarado and Menéndez Puget (1931) gave the first description of vertebrate remains in the basin and referred them to the palaeonisciform *Amblypterus angustus* and other ganoid fish similar to *Eurynotus crenatus* from the Upper Coal Measures of Scotland. Many years later, Forey and Young (1985) published the first detailed description of vertebrates and identified the material as xenacanths ("*Diplodus*"-type teeth corresponding to *Orthacanthus*), acanthodians (articulated specimens of *Acanthodes* sp.) and palaeonisciforms (articulated specimens assigned to the new genus *Puertollanichthys*, and other material belonging to *Elonichthys* and *Amblypterus*). During the last 30 years several papers have studied the taxonomy/systematics, development, evolution and palaeoecology of the carboniferous vertebrates of Puertollano (see Soler-Gijón, 1990, 1993a, 1993b, 1994, 1995, 1997a, 1997b, 1997c, 1999a, 1999b, 2000, 2004; Schultze, 2009, 2013; Soler-Gijón & Moratalla, 2001; Laurin & Soler-Gijón, 2001, 2006, 2010; Schultze & Soler-Gijón, 2004; Schneider *et al*., 2000).

The vertebrates come from mudstone/siltstone and black shales layers associated to coal seams exploited in four coal mines: the Calvo Sotelo deep mine, and the Emma, María Isabel and La Extranjera opencast mines. The Calvo Soleto mine was closed in 1966 and the Emma mine, the largest and most important quarry because of its palaeontological record, has been restored in order to avoid the environmental impact of the mining works. Fortunately, María Isabel and La Extranjera mines are still accessible for geological and palaeontological studies. In addition, the former clay quarry La Tejera, immediately south of Puertollano, also exposes carboniferous layers. Since 2021, these three quarries are protected by law and declared a Natural Monument (Monumento Natural "Carbonífero de Puertollano").

The main goals of our contribution are to 1) describe the geographical and geological features of the Natural Monument with special emphasis in the fossiliferous levels with early vertebrates, 2) describe the vertebrate fossil record of the Natural Monument and to compare it with the complete fossil record of the basin, and 3) indicate the importance of the Natural Monument in the knowledge of the evolution of habitats and biotic communities during the Late Carboniferous, as recorded in the Puertollano coal basin, a model of Stephanian paralic basin (Schultze, 2009).

GEOLOGICAL SETTING. LOCALITIES OF THE NATURAL MONUMENT

The Stephanian Puertollano basin is approximately 15 km long and 4.3 km wide. It is located in the province of Ciudad Real in southern Spain. It consists of a shallow syncline in the western part and two synclines in the eastern part ("Óvalo Norte" and "Óvalo Sur"), separated by the Ojailén river anticline (Fig. 1A).

The Carboniferous strata rest on Ordovician (Llandeilo) quartzites and are overlain by Miocene and Quaternary deposits. The Carboniferous section mainly consits of conglomerates (extremely rare), sandstones, siltstones, claystones, siderite carbonates, volcanic material (tuffite), and coal. Siderite appears as nodules and continuous layers. There are eight principal coal seams, which are numbered 0, 1, 1bis and 2-6 in descending order. Four bituminous layers also occur: layer "Emma" (above coal seam 3) and layers A, B and C (located between coal seams 4 and 5) (Wagner, 1985).

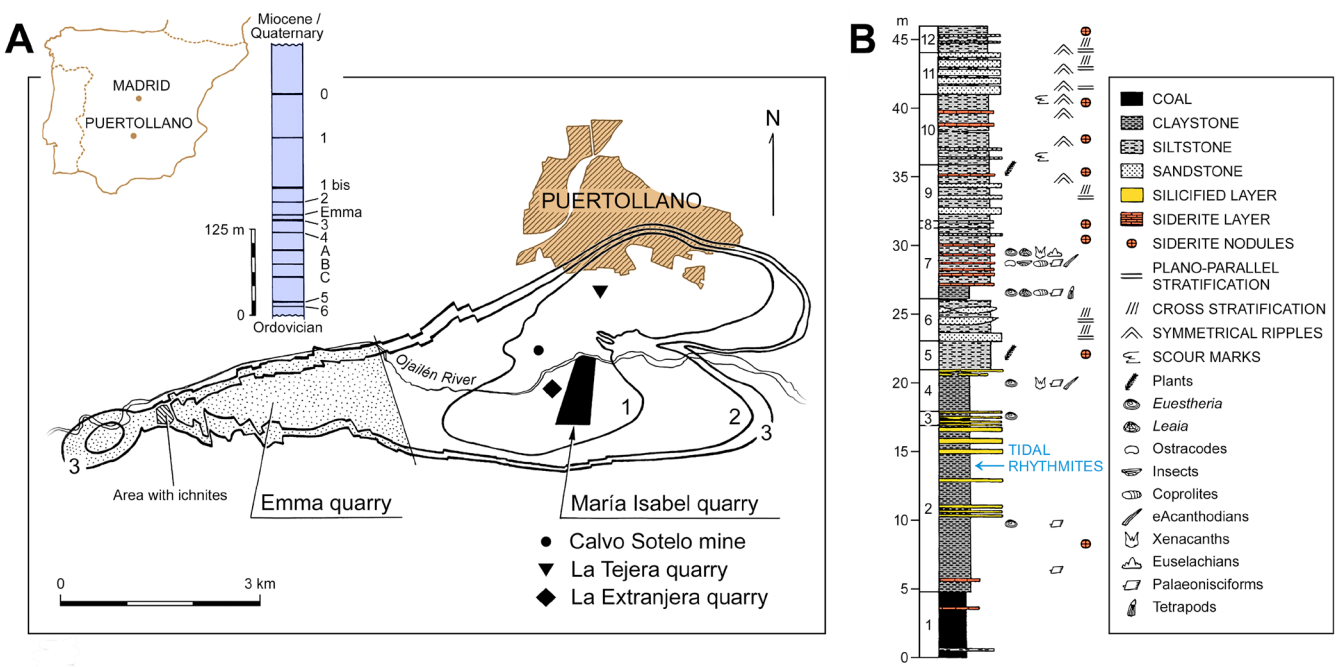


Figure 1. A, Map of the Puertollano basin with the location of María Isabel, La Extranjera and La Tejera quarries; a simplified stratigraphic column of the basin (upper left in the figure) indicates the position of coal seams and bituminous layers (after Soler-Gijón & Moratalla, 2001); **B,** measured stratigraphic section above coal seam 1 as exposed in María Isabel opencast mine (after Soler-Gijón, 1997c).

The quarries María Isabel, La Extranjera and La Tejera expose part of the stratigraphic succession overlying coal seam 1 (Fig. 1).

María Isabel quarry

Soler-Gijón (1993a, 1997c) and Soler-Gijón and López-Martínez (2008) provided the most detailed descriptions of the stratigraphy and sedimentology of that succession as observed in the María Isabel quarry. The authors distinguished 12 stratigraphical beds forming two coarsening-upward sequences of claystone, siltstone and sandstone. The lower sequence overlies coal seam 1 (bed 1) and extents to the basal part of bed 6; the upper sequence overlies a thin coal layer at the top of bed 6 and extents to bed 12 (Fig. 1B). Both sequences exhibit numerous layers rich in fossil remains and sedimentary structures. In this respect, we have to point out the tidal rhythmites found in the laminated claystones of bed 2 (see Soler-Gijón & López-Martínez, 2008 and Supplementary Fig. 1) and the siltstone/sandstone layers with cross stratification and ripple marks (Supplementary Figs. 2–4).
Recently, additional sedimentological and palaeontological data from the María Isabel quarry have been obtained by the detailed examination of blocks displaced from their original location in the stratigraphical succession. Fallen blocks coming probably from beds 6 and 11 (see Fig. 1B) present a heterolithic structure with rhythmic alternations of fine-grained sandstone and siltstone layers. These blocks also exhibit numerous sedimentary features usually described in tidal environments such as flaser, wavy and lenticular bedding, herringbone stratification and load casts structures (Tessier, 1993). Traces of bivalves (resting, equilibrium and escape traces) are common. Bivalve and annelid locomotion traces are also present.

La Extranjera quarry

The correlation of the coal and sedimentary layers of La Extranjera quarry with those from the María Isabel quarry is particularly difficult because of the fluvio-estuarine features of the stratigraphic succession above the main coal seam 1. A coal layer which is visible as two thin sublayers in several areas of La Extranjera quarry appears correlate with the coal layer at the top of bed 6 in María Isabel quarry. A thick bed of mudstone with sideritic intercalations (continuous layers and nodules) and vertebrates remains is located above the coal in a fashion similar to that in María Isabel quarry (Supplementary Fig. 5).
Below the coal, siltstone/sandstone beds with plant remains are found. A sandstone bed exhibiting a large surface with wave ripples is located several meters below the coal (Supplementary Fig. 6). The wave ripples exhibit concave eroded crests, a feature interpreted as indication of the development of microbial mats in tidal enviroments (see Bottjer & Hagadorn, 2007). Laminated sandtone at the top of the ripples also suggests an inter-supratidal location (Archer, 2013).

La Tejera quarry

La Tejera quarry exposes a large lithosome (about 4 meters thick), composed by conglomerates, sandstones and mudstones, which overlie a relatively thin bed of claystone with a intercalation of sandstone. This sucession is stratigraphically positioned in the interval between the coal seams 0 and 0bis and represents a period of fluvial sedimentation. The lithosome, interpreted as a channel filling of meandering river (Wagner, 1985), presents a complex structure with a fining-upward sedimentary pattern typical of river point-bar with tidal influence (see Archer, 2013 and references therein). Sigmoidal cross-stratified sandstone bodies are overlain by a heterolithic sucession of sandstone and mudstone layers. The claystone bed cut by the lithosome is very rich in fossil plants (Álvarez-Vázquez *et al*., 2022); a single specimen of arthropleurid and an insect wing are also documented (Wagner, 1985). Sandstone layers also exhibit plants remains and numerous external casts of unidentified invertebrates (probably bivalves) (Supplementary Fig. 7).

VERTEBRATE PALAEONTOLOGICAL RECORD

The vertebrate remains come from five main fossiliferous levels: 1) bituminous bed B above coal seam 5 (Calvo Sotelo deep mine), 2) amphibian bed above the coal seam 3 (Emma opencast mine), 3) bituminous bed "Emma" above the coal seam 3 (Emma opencast mine), 4) bed 7 above the coal seam 1 (María Isabel opencast mine; Natural Monument) and 5) mudstone/Siltstone layers above coal seam 1 (La Extranjera opencast mine; Natural Monument) (see Tab. 1).

Table 1. Vertebrate taxa and fossiliferous levels at the Puertollano basin. **1,** Bituminous bed B above the coal seam 5 (Calvo Sotelo deep mine); **2,** amphibian bed above the coal seam 3 (Emma opencast mine); **3,** bituminous bed "Emma" above the coal seam 3 (Emma opencast mine); **4,** bed 7 above the coal seam 1 (María Isabel opencast mine; Natural Monument); **5,** mudstone/siltstone layers above coal seam 1 (La Extranjera opencast mine; Natural Monument) (Data from Forey & Young, 1985; Soler-Gijón, 1990, 1993a, 1993b, 1997a, 1997b, 1997c, 1999a, 1999b; Soler-Gijón & Moratalla, 2001; Laurin & Soler-Gijón, 2001, 2006).

I. CHONDRICHTHYANS	
ACANTHODIANS	
Acanthodids	
Acanthodes sp.	(1-5; Fig. 4A)
XENACANTHS	
Xenacanthids	
Orthacanthus meridionalis	(1-5; Fig. 4B-4G)
Triodus nov. sp.	(2-5)
EUSELACHIANS	
Sphenacanthids	
Sphenacanthus carbonarius	(4-5; Fig. 4H-4K)
Lonchidiids	
Lissodus lopezae	(4-5; Fig. 4L-4O)
Lissodus cf. *L. zideki*	(2-3)
Lissodus sp.	(2-3)

II. ACTINOPTERYGIANS	
Palaeonisciforms	
Amblypterids	
Amblypterus angustus	(1)
Elonichthyds	
Elonichthys sp.	(1-5; Fig. 5)
Aeduellids	
Puertollanichthys ritchiei	(1)
Bourbonella ? sp.	(2)
Pygopterids	
Progyrolepis speciosus	(4-5)
Paramblypterids	
Paramblypterus sp.	(2-3)
Palaeoniscids	
Palaeoniscum cf. *P. freieslebeni*	(4-5)
Platysomids	
Platysomidae indet.	(3)
III. TETRAPODS	
Temnospondyls	
Iberospondylus schultzei	(2-5; Fig. 6)
Temnospondyl indet.	(4-5)

Skeletal remains

The skeletal vertebrate remains exhibit a wide range of preservational features from nearly complete and articulated specimens preserved in bituminous shales (Fig. 2) to disarticulated elements in "bone beds". Hard tissues (dentine, bone and calcified cartilage) present an excellent preservation allowing to detailed anatomical and histological studies (Fig. 3).

Three main groups of vertebrates are represented in the basin: Chondrichthyans (Acanthodians, Xenacanths and Euselachians), Actinopteryginas (Palaeoniscirforms) and Tetrapods (temnospondyls) (see Tab. 1). The acanthodians are represented by the genus *Acanthodes* (Fig. 4A). It is recorded as complete skeletons in bituminous layer B (Calvo Sotelo mine; see Forey & Young, 1985; Soler-Gijón, 1999b) and as isolated remains (fin spines, gill-rakers, scales and bones)

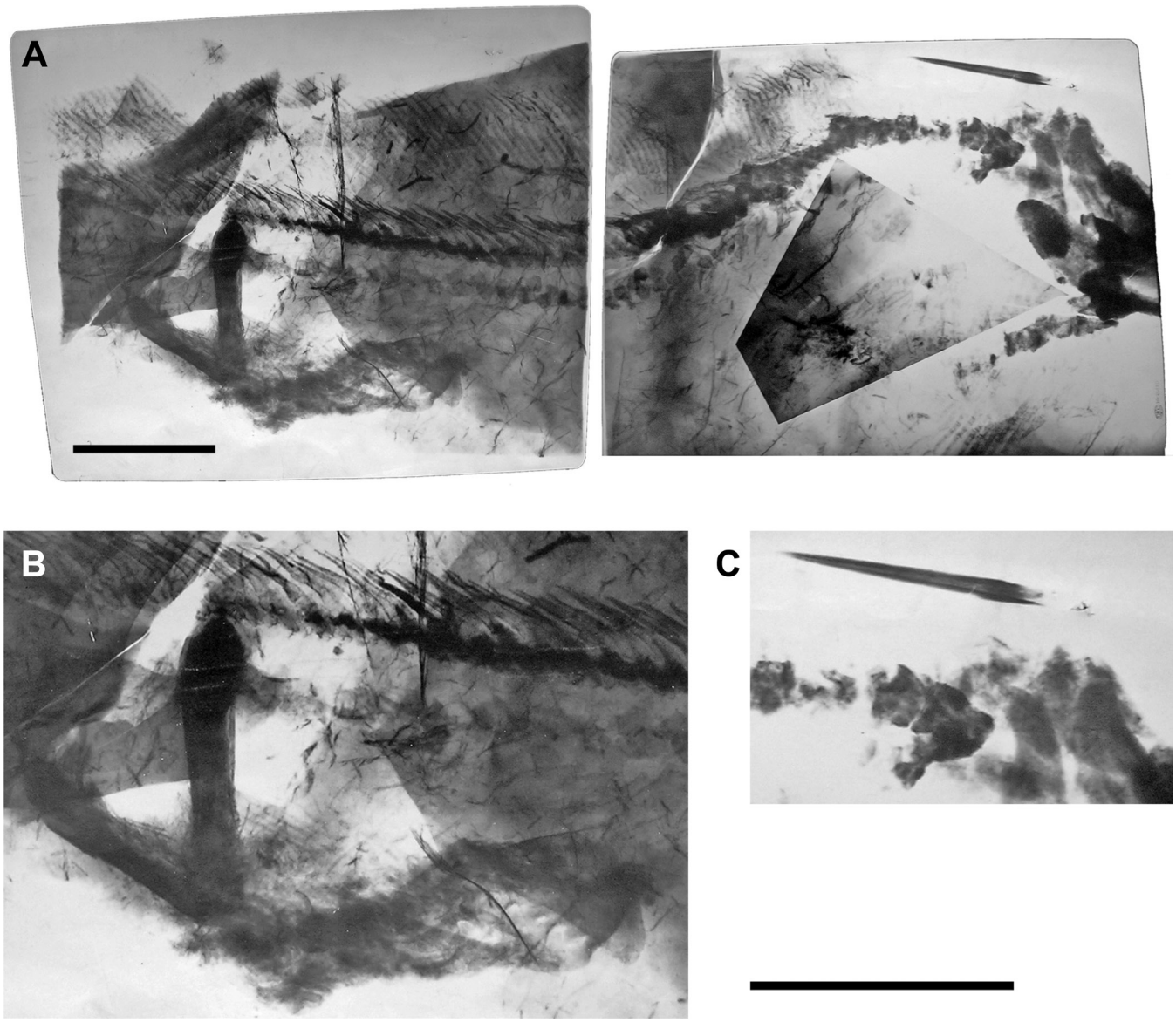


Figure 2. *Orthacanthus meridionalis*, articulated skeleton of a mature male (X-ray picture); Calvo Sotelo mine. **A,** General view; **B,** detail of pelvic area with pelvic girdle, fins and claspers; **C,** detail of dorsal fin spine, located along the cervical vertebral column. Specimen colleted by Dr A. Ritchie in 1966 and currently housed in the Australian Museum Sydney. X-ray pictures courtesy of Drs S. Turner, and R. Jones (Australian Museum); scale bars = 10 cm.

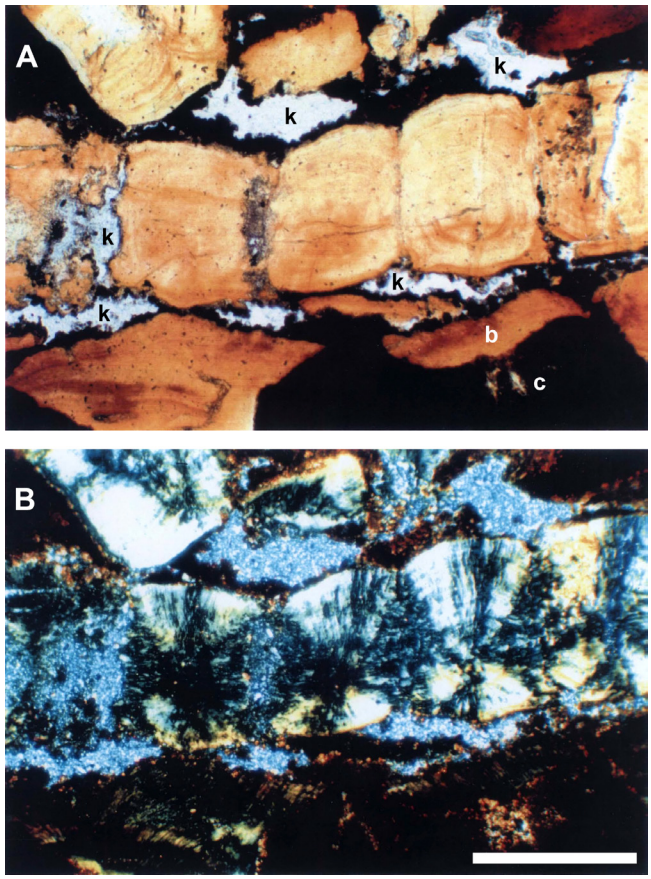


Figure 3. *Sphenacanthus carbonarius*, PU-SP79; María Isabel opencast mine. Vertical section of fin showing endoskeleton (a layer of prismatic calcified cartilge) and exoskeleton (scales in life position; note the orientation of basal plate and crown). **A,** Normal transmitted light; **B,** cross-polarized light. Note the tesserae with Liesegang rings. During early fossildiagenesis the secondary porosities were filled by kaolinite. **PU-SP,** Departamento de Paleontología, Universiad Complutense Madrid; **PU,** Puertollano; **SP,** sphenacanthids. **c,** crown; **b,** base; **k,** kaolinite; scale bar = 0.5 mm (after Soler-Gijón, 1993a).

in numerous mudstone/siltstone layers associated to coal seams 1 and 3. *Acanthodes* exhibits a long slender eel-shaped body, a single dorsal fin located at the level of the anal fin, and a heterocercal caudal fin. Long fin-spines appear in front of the dorsal, pectoral, pelvic and anal fins. Teeth are absent. Large fin spines from Puertollano (Fig. 4A) point to animals up to 1 m in complete length, which could represent the maximum size for the genus (Zajíc, 1998, 2005). The large branchial region of *Acanthodes* with strong gill-rakers suggests a microphagous diet based on small invertebrates (*e.g.*, conchostracan crustaceans and ostracods) with sporadic processing of larger preys such as small palaeonisciforms (Burrow, 2021).

The xenacanth sharks from Puertollano, *Orthacanthus meridionalis* (Fig. 4B–4G) and a new species of *Triodus* (Soler-Gijón, 1999b, fig. 6) are mainly recorded as isolated teeth and dorsal fin spines in several mudstone/siltstone layers above coal seams 1 and 3. Articulated, nearly complete skeletons of *O. meridionalis*, have also been reported from bituminous layer B at Calvo Sotelo mine (see Beck *et al*., 2016 and Fig. 2). The xenacanth sharks present an eel-shaped body with a cervical fin spine in front of an elongated dorsal fin, two anal fins and a pseudo-diphycercal caudal fin. *Orthacanthus* was a very large predator which could reach 2.5 to 3 m in total length in contrast to *Triodus*, a relatively small xenacanth, usually less than 1 m long (Soler-Gijón, 2004). The xenacanths were top predators feeding on all other vertebrates including other xenacanths (Soler-Gijón, 1995; Ó Gogáin *et al*., 2016).

The euselachians are represented by *Sphenacanthus carbonarius* and several species of *Lissodus* (*L. lopezae* and *L.* cf. *L. zideki*) (Fig. 4H–4O). These taxa are mainly recorded as isolated skeletal elements (teeth, scales and dorsal fin spines). Disarticulated and partially complete cartilages from *Sphenacanthus* have also been found in mudstone/sideritic layers at María Isabel and La Extranjera opencast sites. Complete skeletons from other european localities shows the typical phalacanthous morphology in *Sphenacanthus* and *Lissodus*: two dorsal fins with fin-spines in their leading margins and a heterocercal caudal fin. *Sphenacanthus* had a moderate size ranging from 0.5 to 1.5 m in length as suggest the comparison of their fin spines and those in closely related palaeozoic phalacanthous known by complete skeletons (Maisey, 1982; Coates & Gess, 2007; Ginter, 2021). *Lissodus* was a dwarf shark never longer than 30 cm (Soler-Gijón *et al*., 2016). These sharks could swim close to the bottom and fed mainly on invertebrates such as bivalves and crustaceans.

The palaeonisciforms are very diverse and represented in the basin by seven families: Amblypteridae, Elonichthydae, Aeduellidae, Pygopteridae, Paramblypteridae, Palaeoniscidae and Platysomidae (Fig. 5). Articulated and nearly complete specimens of the aeduellid *Puertollanichthys ritchiei* have been reported from bituminous layer B at Calvo Sotelo mine (Forey & Young, 1985). Paramblypterids (*Paramblypterus*) and aeduellids (probably *Bourbonella*) were found in mudstone and bituminous layers above coal seam 3 at the Emma opencast mine. Recently, numerous articulated specimens of elonichthyds (probably *Elonichthys*) and associated remains of the large pygopterid *Progyrolepis speciosus* have been reported from several mudstone/siltstone layers above coal seam 1 in María Isabel and La Extranjera opencasts (Fig. 5). Isolated palaeonisciform remains (teeth, scales, dermal fin-rays and bones) are very common in "bone beds", sometimes associated to sideritic layers and coprolites. With the exception of Pygopteridae and Palaeoniscidae, the palaeonisciforms are relatively small fishes, about 10–20 cm in total length. All those families, except Platysomidae, comprise fishes with a fusiform body. Progyrolepids (up to 60 cm total length) and elonichtids developed large conical teeth and hunted other fishes, amphibians and insects. In contrast, paramblypterids and aeduellids developed a tubular dentition adapted to feed on small planktonic or benthonic invertebrates

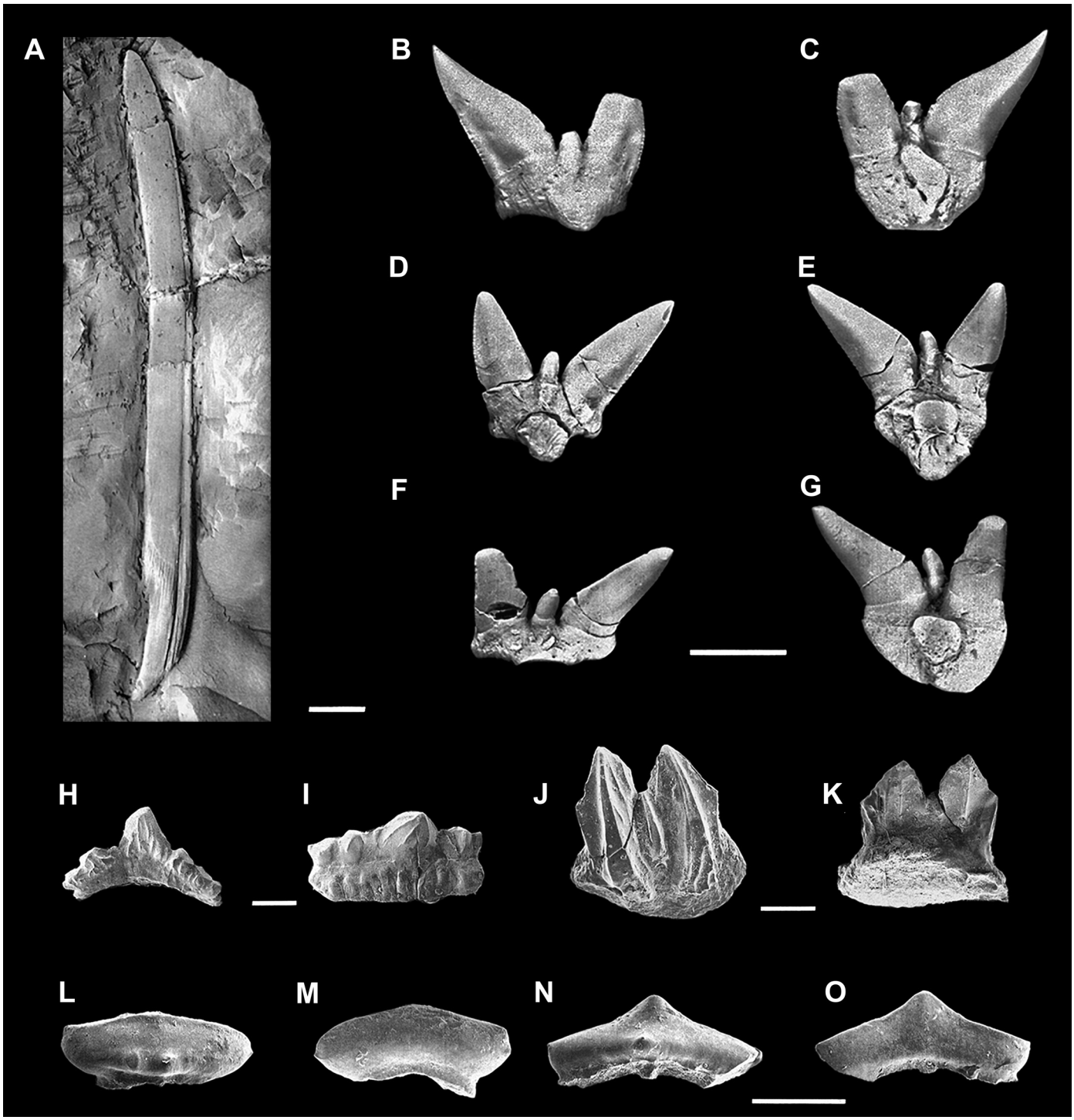


Figure 4. Chondrichthyans. **A,** *Acanthodes* sp., Emma opencast mine, large pectoral fin spine (uncatalogued specimen); **B**–**G,** *Orthacanthus meridionalis*, teeth; **B**–**E,** María Isabel opencast mine; **B**–**C,** PU-XE19, lateral tooth in labial (**B**) and lingual (**C**) views; **D**–**E,** PU-XE73, lateral tooth in labial (**D**) and lingual (**E**) views; **F**–**G,** Emma opencast mine, PU-XE28, lateral tooth in labial (**F**) and lingual (**G**) views; **H**–**K,** *Sphenacanthus carbonarius*, teeth and scale, María Isabel opencast mine; **H**–**I,** teeth; **H,** PU-SP121, anterolateral tooth in labial view; **I,** PU-SP118, lateral tooth in occluso-lingual view; **J**–**K,** scale; **J**–**K,** PU-SP90, scale in anterior (**J**) and posterior (**K**) views; **L**–**O,** *Lissodus lopezae*, teeth, María Isabel opencast mine; **L**–**M,** PU-HI77, mesial tooth in labial (**L**) and lingual (**M**) views; **N**–**O,** PU-HI78, lateral tooth in labial (**N**) and lingual (**O**) views. **PU-XE, PU-SP and PU-HI** indicate catalogued specimens housed in Departamento de Paleontología, Universidad Complutense Madrid; **PU,** Puertollano; **XE,** xenacanths; **SP,** sphenacanthids; **HI,** hybodont sharks; scale bars = 1 cm for A, 0.5 cm for B–G, 1 mm for H–K and 0.5 mm for L–O (after Soler-Gijón, 1993a).

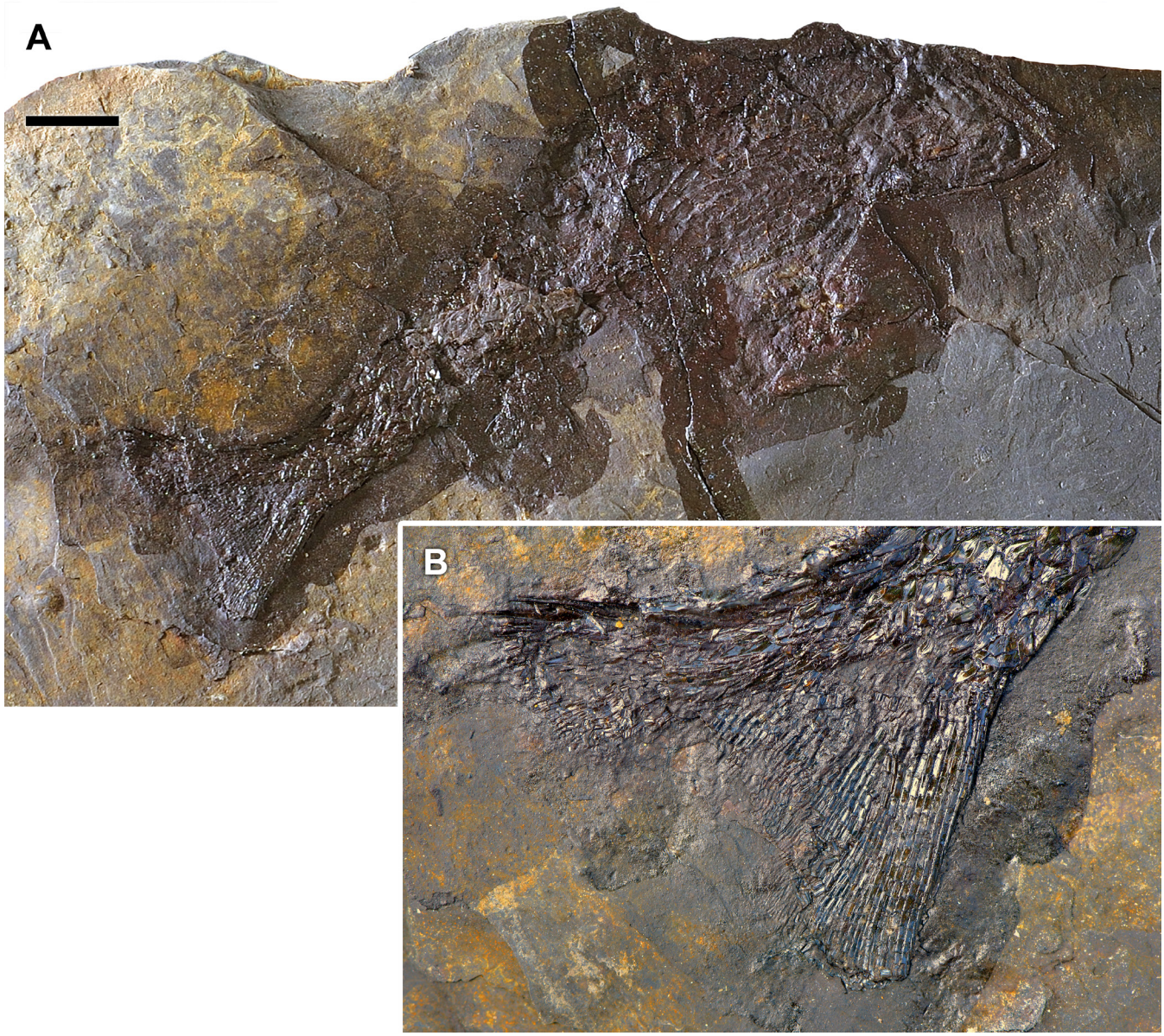


Figure 5. Actinopterygian palaeonisciform. cf. *Elonichthys*, nearly complete and articulated specimen, María Isabel opencast mine (uncatalogued specimen currently housed in Museo de la Minería y el Carbonífero, Puertollano). **A,** General view; **B,** detail of the caudal fin; scale bar = 1 cm.

such as conchostracan crustaceans (Štamberg, 2020). The temnospondyl amphibians are mainly represented by *Iberospondylus schultzei* (Fig. 6A). The taxon was originally described from articulated specimens from the mudstone and bituminous layers above coal seam 3 at Emma opencast (Laurin & Soler-Gijón, 2001, 2006). Recently, partially articulated cranial remains of *Iberospondylus* (probably *I. schultzei*) have also been found in sideritic layers, above coal seam 1 (María Isabel and La Extranjera opencast mines) (Fig. 6B). *Iberospondylus schultzei* could reach 1 m in length and developed a large skull, triangular in outline, and strong jaws with numerous (labyrinthodont) teeth. *Iberospondylus* was an euryhaline temnospondyl, top predator of the estuarine/deltaic coastal areas, preying on fishes (actinopterygians and acanthodians) and other tetrapods (Laurin & Soler-Gijón, 2010).

Trace fossils

Soler-Gijón and Moratalla (2001) described fish and tetrapod traces from a single siltstone horizon of the "amphibian bed", above coal seam 3 (Emma quarry). The fish traces, assigned to the ichnogenus *Undichna* (*U. britannica* and *U. unisulca*) were produced by the xenacanth *Orthacanthus merdionalis*, swimming very close to the bottom. The tetrapod traces, both track-ways of the ichnogenus *Puertollanopus* (*P. microdactylus*) and resting traces, were produced by a small terrestrial animal, a microsaur amphibian or small reptile. Numerous invertebrate traces, provisionally assigned to *Planolites* (Soler-Gijón & Moratalla, 2001, p. 1) occur associated to the vertebrate traces in the same bedding plane of the "amphibian bed"; this material, not yet described in detail, exhibits many

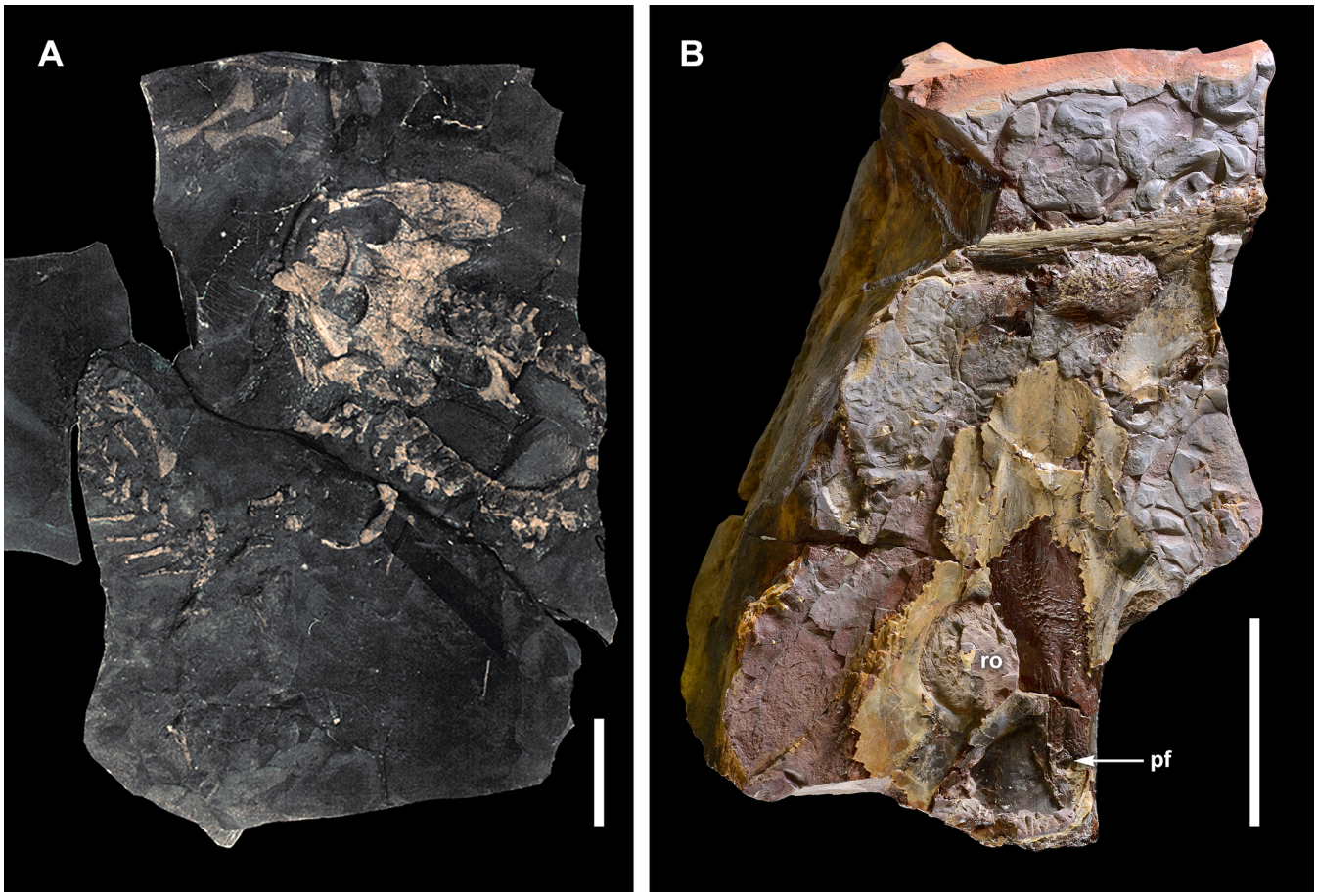


Figure 6. Tetrapods. **A,** *Iberospondylus schultzei*, PU-ANF2, Emma opencast mine (after Soler-Gijón, 1993a; Laurin & Soler-Gijón, 2006); **B,** *Iberospondylus* cf. *I. schultzei*, cranial remains, María Isabel opencast mine (uncatalogued specimen currently housed in Museo de la Minería y el Carbonífero, Puertollano). **PU-ANF,** Departamento de Paleontología, Universidad Complutense, Madrid; **PU,** Puertollano; **ANF,** amphibians; **pf,** pineal foramen; **ro,** right orbit; scale bars = 5 cm.

features of grazing and locomotion traces (*e.g.*, *Gordia*) probably produced by several groups of invertebrates.

Recently, new invertebrate and vertebrate trace assemblages have been found in sandstone and siltstone layers above coal seam 1 at La Extranjera and María Isabel quarries. Soler-Gijón *et al*. (2022) described the fish trace *Undichna* associated to traces of terrestrial arthropods (*e.g.*, *Diplichnites* and *Diplopodichnus* produced by small juvenile arthropleurids) in a dump slab coming from the fossiliferous layers of La Extranjera quarry.

A rich assemblage of tetrapod traces similar to the synapsid trace *Dimetropus* has been found in a fallen sandstone/siltstone slab located in the south part of La Extranjera quarry (Fig. 7). The tetrapod traces, preserved as convex hyporelief, appear associated to numerous circular imprints interpreted here as gas-escape structures. Nearly identical circular imprints has usually been identified as rain-prints (see for example, Voigt *et al*., 2011 who also describe *Dimetropus*). However, experimental and sedimentological studies (Rindsberg, 2005; Bartley & Gilliland, 2021) pointed out that some of those imprints could be the consequence of gas bubbles production in a wet or submerged surfaces, rejecting the traditional interpretation of raindrop impact on subaerial surfaces. Interestingly, the presence of gas-escape structures in La Extranjera is in agreement with the evidences of microbial mat in the layer with wave ripples (see Supplementary Fig. 6).

The ichnogenus *Dimetropus* is described in many late Carboniferous and early Permian localities and related to several non-therapsid synapsids (edaphosaurids, sphenacodontids, ophiacodontids and caseids) (see Calábková *et al*., 2023 and references therein). In Spain, this ichnite is only reported from the early Permian of Pyrenees and Mallorca basins (Mujal *et al*., 2016; Matamales-Andreu *et al*., 2021). If our identification is confirmed in future detailed studies, the Carboniferous traces found in the Natural Monument could represent the oldest Spanish record of *Dimetropus* and the first (indirect) evidence of synapsid tetrapods in the Puertollano basin.

Bromalites

The majority of bromalites found in Puertollano are spiral coprolites (Fig. 8). Heteropolar spiral coprolites, very common, appear in all the fossiliferous levels with vertebrate skeletal remains. In addition, amphipolar spiral coprolites are also reported from the bed 7 in María Isabel quarry. Regurgitalites are rare.

Figure 7. Fallen sandstone/siltstone slab showing a rich assemblage of tetrapod ichnites similar to the synapsid trace *Dimetropus*; La Extranjera opencast mine. Note that the traces are preserved as convex hyporeliefs. Well-preserved manus (**m**) and pes (**p**) are pointed out in the right side of the picture (compare with Matamales-Andreu *et al*., 2021, fig. 5). Although the weathered slab does not allow to recongnize trackways with the usual manus-pes paired sets, the orientation of the preserved traces indicate the direction of movement of, at least, four trackmakers (see arrows); **gb** refers to the large surface with numerous circular imprints, preserved in convex hyporelief, which represent gas escape structures (cf. Bartley & Gilliland, 2021); scale bar = 10 cm.

In general, the coprolites from Puertollano present a good preservation. Cross sections show their internal structure of spirally coiled fecal ribbons. The fossilized fecal ground mass appears as amorphous phosphatic matter (probably carbonate fluorapatite) which contains numerous palaeonisciform scales and skeletal debris of unidentified organisms. A rare specimen of regurgitalite or coprolite contains a fragmentary insect wing.
Soler-Gijón (1993a, 1994) described and illustrated in first time the coprolites from the Puertollano basin, mainly coming from the Emma quarry but also from the María Isabel quarry, now a part of the Natural Monument. The coprolite record from Puertollano is unique in the whole Spanish Carboniferous localities. In fact, no Spanish locality is cited by Hunt and Lucas (2013) in their recent review of the Carboniferous and Permian coprofaunas. Next field trips at the Natural Monument will make special emphasis in the systematic prospection and detailed study of the bromalites from María Isabel and La Extranjera quarries.

The spiral coprolites from Puertollano probably correspond to chondrichthyans (xenacanths and euselachians) with different sizes and morphologies of the valvular intestine (Hunt & Lucas, 2021). According to Byrne *et al*. (2022), the acanthodians, as stem-chodrichthyans could also developed a spiral gut valve and consequently spiral faeces, but lacking the abundant hard inclusions typical of predators.
Future studies of the diverse coprolites from Puertollano can provide information about other groups of vertebrates not yet reported from their skeletal remains (*e.g*., non-tetrapod sarcopterygians). As Byrne *et al*. (2022) demonstrated for Tournaisian deposits of East Greenland, the detailed analyses of bromalites can inform about the true vertebrate diversity, higher than expected, with the inclusion of "transient faunal elements within an open system".

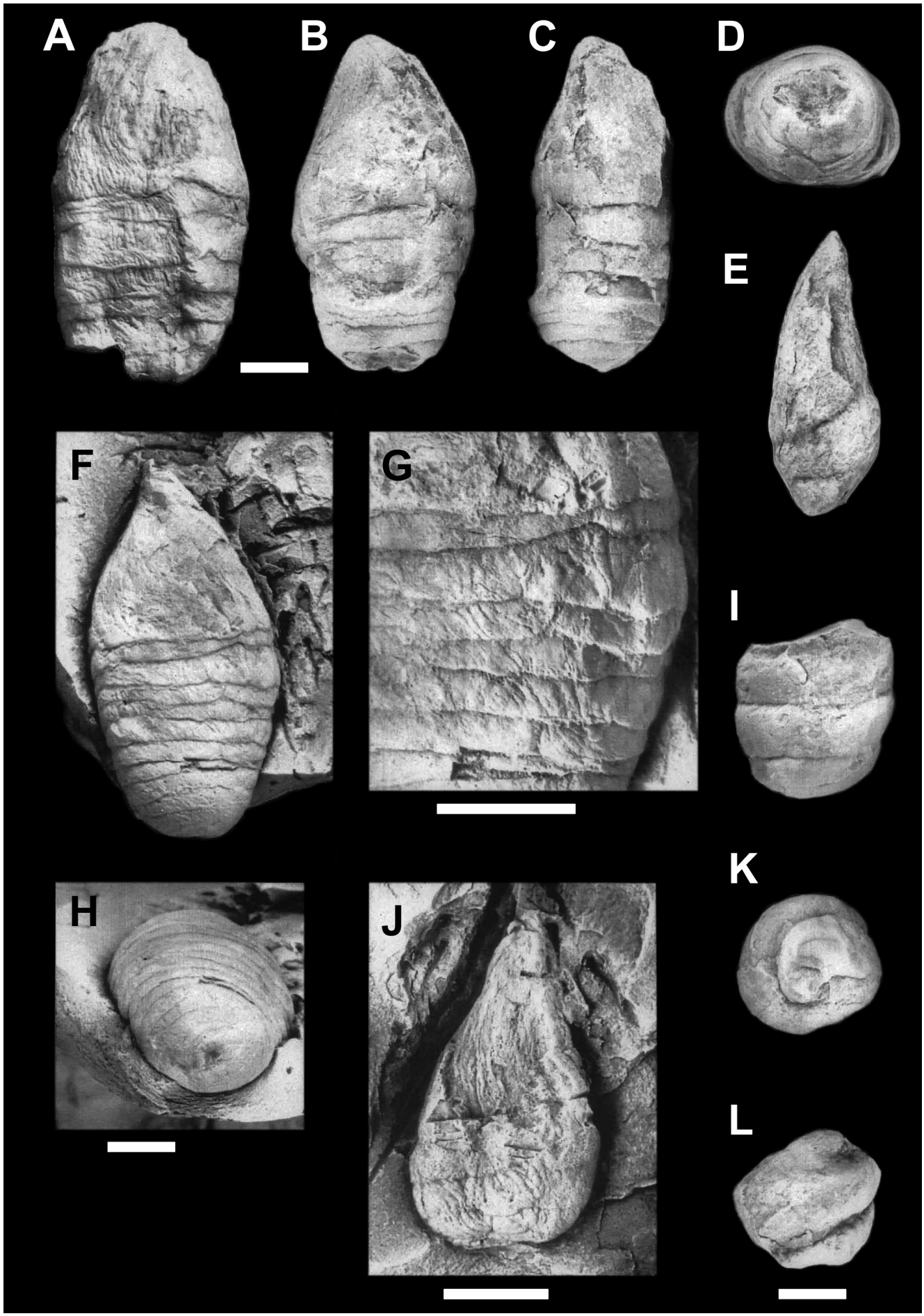
DISCUSSION

Geochronology

During the last decades the Puertollano basin has been dated as late Stephanian B (Wagner, 1985), late Stephanian B and/or early Stephanian C (Wagner, 1989) and Stephanian C (= lower Autunian) (Soler-Gijón, 1997c; Wagner, 1999; Wagner & Álvarez-Vázquez, 2010; Álvarez-Vázquez *et al*., 2018). Recently, U-Pb radiometric dating of two ash-fall tuff associated to the coal seams 2 and 3 (Emma quarry) has given an absolute age of approximately 303 My (Knight *et al*., 2023). Importantly, this radiometric dating allows to assign a precise age to the fossiliferous layers associated to coal seam 3 (*e.g*., "The amphibian bed" and "the bituminous bed Emma", both above coal seam 3). The rich assemblages of vertebrates are now referred to the early Gzhelian (= early Saberian) (see Opluštil *et al*., 2021; Knight *et al*., 2023). The absence of volcanic material above coal seam 1 will force to conduct very detailed sedimentological and biostratigraphical studies in order to date the fossiliferous layers shown at the Natural Monument.

Palaeoenvironmental significance

The Puertollano basin was traditionally interpreted as an endorheic, fluvial-lacustrine basin (Wagner, 1985 and references therein). However recent sedimentological, geochemical and palaeontological studies indicate a paralic environment (coastal, estuarine or lagoonal). The coal and bituminous deposits of the actual Puertollano basin appear to represent a remnant of a much larger basin which opened eastwards in direction to the Palaeo-Tethys Ocean (Wagner, 1989, 1999; Wagner *et al*., 2003; Wagner & Álvarez-Vázquez, 2010, 2015; Knight *et al*., 2023).
Cyclic tidal sediments (tidal rhythmites) are exposed in the mudstone/siltstone layers above coal seam 1 in María Isabel and La Extranjera quarries. Two scales of lamination strongly suggest tidal processes in the basin (Soler-Gijón & López-Martínez, 2008). Dark and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light bands observed in Puertollano are interpreted as deposits of neap and spring tides, respectively. The tidal rhythmites from Puertollano indicate a high sedimentation rate, high concentration of suspended sediment and the deposition in a protected environment allowing the preservation of the delicate lamination. These necessary conditions point to an upper/middle estuarine area or proximal part of bay (see Tessier, 1993; Archer, 2013).

The co-occurrence (superposition) of traces of the large xenacanth shark *Orthacanthus* and a small terrestrial tetrapod in the same bedding plane of the "amphibian bed", above coal seam 3 (see Soler-Gijón & Moratalla, 2001), also points to an intertidal situation in agreement with the geochemical analyses (García-Molla, 1994; Alastuey *et al*., 2001) which detected aliphatic hydrocarbons and high content of boron, proofs of marine influence. In addition, a rich assemblage of acritarchs, dominated by leiosphaerids, has been reported in the Puertollano basin, indicating a marginal-marine depositional setting (Fonollá, 1988; Soler-Gijón, 1997c).

The presence of the same euryhaline fish fauna (*e.g*., xenacanths, *Sphenacanthus carbonarius*, *Lissodus zideki*, *Progyrolepis speciosus* and aeduellids) in Puertollano and other Permo-Carboniferous localities of Europe (*e.g*., localities from Saar-Nahe and Saale basins; see Boy & Schindler, 2000) and in North America (Dunkard basin, Pennsylvania; Peru, Nebraska; see Ginter, 2021) indicate marine dispersal between open basins (Schneider *et al*., 2000; Schultze & Soler-Gijón, 2004; Schultze, 2009, 2013; Laurin & Soler-Gijón, 2010; Ó Gogáin *et al*., 2016; Ginter, 2021).

Fischer *et al*. (2013) analyzed the oxygen and strontium isotopic composition of biogenic fluorapatite of teeth of *Orthacanthus meridionalis* from the bituminous bed Emma ("Emma" quarry). The authors obtained $^{87}Sr/^{86}Sr$ ratios in the shark teeth more radiogenic than $^{87}Sr/^{86}Sr$ of contemporaneous seawater and high ^{18}O and concluded that the xenacanths were stenohaline freshwater organisms living in an endorheic fluvio-lacustrine environment with high evaporation due to a warm and dry climate. We agree with the non-marine feature in the Puertollano basin as indicated by the strontium signature (*i.e*., absence of normal salinity). However, the obtained values do not automatically exclude the possibility of brackish conditions expected in transitional environments such as estuaries and bays (Carpenter *et al*., 2011; Gierlowski-Kordesch & Cassle, 2015; Ó Gogáin *et al*., 2016). In addition, the co-existence of sphenopsids, ferns and pteridosperms in the fossiliferous layers of the "Emma" quarry indicate humid environment (Álvarez-Vázquez *et al*., 2018); consequently, the high ^{18}O agrees with brackish conditions. Interestingly, a seasonal and drier climate is suggested for the stratigraphical succession above coal seam 1 where the conifers are very common (Álvarez-Vázquez *et al*., 2018, 2022). Finally, we have to remark here that the isotopic signature registered in the teeth corresponds to a very short temporal interval of mineralization in the dental hard tissue (few days or weeks); we have to use dorsal spines, which document the complete life of the shark in order to analyse the possible movements of the animals between different environments (Soler-Gijón, 1999a; Beck *et al*., 2016).

CONCLUSIONS

The Natural Monument "Carbonífero de Puertollano" includes three quarries (María Isabel, La Extranjera and La Tejera) which represent unique protected areas for the geological and palaeontological investigations of the Puertollano coal basin. The outcrops exhibit the sequence of coal, mudstone/siltstone, sideritic and conglomerate/sandstone layers above coal seam 1, at the end of the stratigraphical series of the basin. Consequently, the Natural Monument offers the opportunity to study in detail the latest palaeogeographical stages of the basin and to compare with the information of deeper layers in the serie in order to analyze the evolution of the habitats and biotic communities, during the complete time recorded in the Puertollano basin.

The Natural Monument presents a remarkable record of new vertebrate taxa which never before were described in the rest of the basin: the euselachians *Sphenacanthus carbonarius* and *Lissodus lopezae* and the palaeonisciforms *Progyrolepis speciosus* and *Palaeoniscum* cf. *P. freieslebeni*. Other taxa recorded in the three protected quarries, also found in the lower part of the stratigraphical section, are the acanthodian *Acanthodes*, the xenacanth sharks (*Orthacanthus meridionalis* and *Triodus*), the palaeonisciform *Elonichthys* and the temnospondyl *Iberospondylus*. There is no evidence yet of several groups of palaeoncisciforms (amblypterids, aeduellids, paramblypterids, platysomids) described above coal seam 3 (Emma quarry).

Tidal rhythmites and the diverse assemblage of euryhaline vertebrates, recorded in the Natural Monument, indicate an estuarine-deltaic environment. The new data support the model of the actual Puertollano coal basin as a remnant of a much larger basin open to the Palaeo-Tethys. Future sedimentological and palaeontological studies will provide detailed information about the palaeoenvironmental (*i.e*., marine influence) and palaeoclimatic changes explaining the unique faunal and floral assemblages at the end of the Stephanian sedimentation in the Puertollano basin.

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Figure 8. Coprolites. **A**–**H, J,** Heteropolar spiral coprolites from the Emma opencast mine and Calvo Sotelo deep mine (**E**); **A,** PU-COP1; **B**–**D,** PU-COP2; **E,** PU-COP3; **F**–**H,** PU-COP4; **J,** PU-COP5; **I, K**–**L,** amphipolar spiral coprolites from the María Isabel opencast mine; **I,** PU-COP6; **K**–**L,** PU-COP7. **PU-COP,** Departamento de Paleontología, Universidad Complutense, Madrid; **PU,** Puertollano; **COP,** coprolites; scale bars = 0.5 cm (after Soler-Gijón, 1993a, 1994).

Supplementary information. Detailed geological graphic information is included as Supplementary Figures, available at the Spanish Journal of Palaeontology web-site (https://sepaleontologia.es/spanish-journal-palaeontology/) linked to the corresponding contribution. The information provided by the authors has not being copy edited or substantially formatted.

Author contributions. RS-G and ADR conceived the study, analysed the data, and wrote the manuscript.

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