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New remains of the ankylosaurian dinosaur *Polacanthus* from the Lower Cretaceous of Soria, Spain

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Abstract

The Zorralbo locality of the eastern Cameros Basin, near Soria, Spain, has produced a diverse dinosaur assemblage from the Lower Cretaceous Golmayo Formation. Ankylosaurs are represented by dorsal vertebrae and ribs, a fragmentary sacrum and ilium, and several types of dermal armour. Most, if not all, of the material probably belongs to a single medium to large-sized adult individual. The Soria remains are referred to *Polacanthus* on the basis of the presence of conical, ungrooved presacral spines, a sacropelvic shield composed of irregularly arranged bosses and small tubercles, large spined plates, and hollow-based triangular caudal plates with an extended posterior basal edge and a pointed spine. *Polacanthus* is well known from the Wealden Group (Barremian-Aptian) of the Isle of Wight and from the Weald Clay Group of West Sussex (England). In addition, isolated remains have been reported from the penicontemporaneous formations of the Iberian Peninsula. The Soria outcrop is currently the most productive *Polacanthus* site outside England. Moreover, it has yielded the oldest record (late Hauterivian to basal Barremian according to charophyte association) of this ankylosaur known to date in Europe. Minor anatomic differences between the Soria material and the taxa *P. foxii* (type-species) and *P. rudgwickensis* suggest the presence of a third species of *Polacanthus* in the Iberian Peninsula, but additional material is needed to confirm this interpretation.

Keywords: Dinosauria; Thyreophora; Ankylosauria; *Polacanthus*; Early Cretaceous; Iberian Peninsula

1. Introduction

Two ankylosaurian dinosaurs have been recognized in the Lower Cretaceous formations of Europe: *Hylaeosaurus* (type species *H. armatus* Mantell, 1833) is known from the Grinstead Clay Formation of the Hastings Beds Group (Valanginian) of Sussex, England; and *Polacanthus* (type species *P. foxii* Owen, 1865 in Anonymous, 1865b) has been found in the Wealden Group (Barremian-lower Aptian) of the Isle of Wight, England (Blows, 1987, 1996, 1998; Pereda Suberbiola, 1993, 1994; Naish and Martill, 2001). The species *Polacanthus foxii* is known from several partial skeletons with dermal armour from the Wealden Group (both Wessex and Vectis formations; Barremian-lower Aptian) of the Isle of Wight (Hulke, 1882, 1888; Lydekker, 1891; Seeley, 1891; Nopcsa, 1905; Blows, 1983, 1987, 1998; Pereda Suberbiola, 1993, 1994). A second and more robust species of *Polacanthus*, *P. rudgwickensis*, was erected on the basis of a collection of postcranial bones with armour from the Weald Clay Group (Barremian) of West Sussex (Blows, 1996). A privately owned partial skeleton of *Polacanthus* is on display in a fossil shop at Black Gang Chine on the Isle of Wight, but remains undescribed (Naish and Martill, 2001). Additional material tentatively assigned to *Polacanthus* consists of isolated finds, including a braincase (Norman and Faiers, 1996), a tooth, postcranial bones and

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dermal armour from the Isle of Wight (Seeley, 1876; Blows, 1987; Pereda Suberbiola, 1994; Naish and Martill, 2001) and the English mainland (Devon – not Dorset –; see Blows, 1996). The Devon specimen (Blows, 1987: fig. 11) is probably not referable to *Polacanthus*. The stratigraphical range of *Polacanthus* in England is Barremian-Aptian.

Outside England, *Polacanthus* is poorly documented. Isolated remains have been found in the Iberian Peninsula, mostly consisting of dermal armour from the Barremian-Aptian of Burgos (Sanz, 1983; Pereda Suberbiola et al., 1999) and from the lower Aptian of Castellón (Gasulla et al., 2003). In North America, a few specimens from the Lower Cretaceous of South Dakota and Utah in the United States have been referred to *Polacanthus* (Blows, 1987; Pereda Suberbiola, 1991, 1994). However, the referral of these American specimens to *Polacanthus* is not supported by other authors (Coombs, 1995; Carpenter and Kirkland, 1998; Vickaryous et al., 2004).

Here new *Polacanthus* remains from the Lower Cretaceous of Soria, Spain, are described. The material, which consists of vertebrae, ribs, pelvic remains and abundant dermal armour, is the most diverse assemblage of *Polacanthus* currently found outside England.

Institutional abbreviations. BMNH, The Natural History Museum (formerly British Museum of Natural History), London, U.K.; GM, Gosport Museum, Hampshire, U.K.; HORSM, Horsham Museum, Horsham, Sussex, U.K.; MNS, Museo Numantino, Soria, Spain; PS, Museo de Dinosaurios (Paleontología), Salas de los Infantes, Burgos, Spain; USNM, National Museum of Natural History, Washington D.C., U.S.A.

2. Geological setting

The Zorralbo outcrop where the new ankylosaurian remains were discovered is located near the place known under the same name, in the township of Golmayo, west of the city of Soria in northern Spain (UTM coordinates: 30TWM394238, Mapa Topografico Nacional of Spain, 1:50000, sheet 342) (Fig. 1).

Geologically, the Zorralbo area lies within the eastern sector of the Cameros Basin (northwestern margin of the Iberian Ranges). The Cameros Basin (now 75 × 145 km in size) has been interpreted as an intraplate rift basin that developed during the Late Jurassic and the Early Cretaceous. It was filled by a thick succession of alluvial and lacustrine deposits, with only rare marine incursions (Alonso and Mas, 1993). The sedimentary succession can be divided into six main depositional sequences, which correlate with marine sequences (Mas et al., 1993; Mas and Salas, 2002). The 800 m thick Golmayo Formation consists of channel sandstones, micritic limestones, red lutites, and to a lesser extent siliciclastic and calcareous conglomerates. They were deposited in a fluvio/lacustrine environment (Clemente and Alonso, 1990). The Golmayo Formation, which is limited to the Soria region, extends from the eastern foothills of the Sierra de Cabrejas to the Sierra de San Marcos (both Upper Cretaceous), as a narrow strip of land extending from the west of the city of Soria to the NE-SW Cuevas de Soria fault. This fault delimits the base of the Golmayo Formation, which overlies the Hoya del Moro Formation (Tithonian-Berriasian). The Golmayo Formation is overlain by the Pantano de la Cuerda del Pozo Formation (middle Barremian). The Golmayo Formation of Soria is included in the upper Hauterivian-lower Barremian Depositional Sequence III (Clemente and Pérez-Arlucea, 1993; Mas et al., 1993; K1.4 sequence of Mas and Salas, 2002). The charophyte association found in this formation is characteristic of the Triqueta Biozone, Triqueta Sub-Biozone, which is considered to be latest Hauterivian to earliest Barremian (Martín-Closas and Alonso, 1998).

Excavation of the Zorralbo site was undertaken by several of us (the Meijide-Fuentes family) between 2000-2004. The fossiliferous beds are reddish mudstones (thickness between 0.4 and 1 m). About 100 m^2 were excavated and mapped using

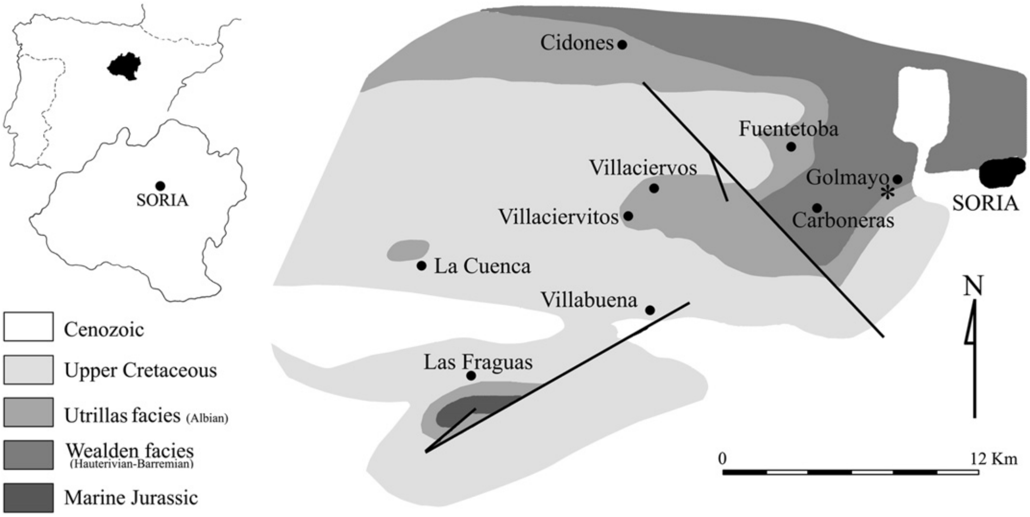

Fig. 1. Geological location map of the Zorralbo locality, Soria, Spain. Modified from the Mapa Geológico de España 1: 50 000, sheets 349 (Cabrejas del Pinar) and 350 (Soria), IGME, 1991. The Golmayo Formation is included in the "Wealden facies". The asterisk indicates the ankylosaur site.

a square-metre grid system. More than 4500 fossils were collected but only a fraction of the assemblage is identifiable. The site has yielded dinosaur, crocodilian, turtle and bivalve remains. Dinosaurs are represented in order of relative abundance by ornithopods (cf. *Iguanodon*), ankylosaurs (*Polacanthus*), sauropods (basal member of Titanosauriformes) and indeterminate theropods (Fuentes Vidarte et al., 2005).

3. Systematic palaeontology

Ornithischia Seeley, 1888
Thyreophora Nopcsa, 1915
Ankylosauria Osborn, 1923

Genus *Polacanthus* Owen, 1865 (in Anonymous, 1865a)

Euacanthus Tennyson, 1897
Polacanthoides Nopcsa, 1928 in part
Vectensia Delair, 1982

Type species. *Polacanthus foxii* Owen, 1865 (in Anonymous, 1865b; see also Fox, 1866); holotype: BMNH R175, a partial skeleton with vertebrae, pelvic girdle, hindlimb bones and dermal armour from the Wessex Formation (Barremian) of the Isle of Wight, England (Hulke, 1882, 1888; Nopcsa, 1905; Blows, 1987; Pereda Suberbiola, 1994).

Referred material. Most of the referred specimens come from the Wessex and Vectis formations (Barremian-lower Aptian) of the south-west coast of the Isle of Wight, e.g., BMNH R9293, a partial skeleton with skull fragments, vertebrae, ribs, pelvic remains and armour (Blows, 1987); BMNH R1006-1107, casts of a humerus and a tibia (part of the type of *Polacanthoides ponderous* Nopcsa, 1929; originals currently lost); BMNH R1926, fragmentary ilium with armour (type of *Polacanthus becklesi* Hennig, 1924); BMNH R643, dermal ossicle (Lee, 1843); GM 981.45, dermal spine (type of *Vectensia* Delair, 1982). Additional specimens of *P. foxii* are kept at London (BMNH), Cambridge (Sedgwick Museum, Cambridge University), Sandown (Museum of Isle of Wight Geology) and in private collections (see Blows, 1987; Pereda Suberbiola, 1994 for a complete listing of referred material).

Other species. *Polacanthus rudgwickensis* Blows, 1996; holotype: HORSM 1988.1546, fragmentary postcranial skeleton with armour from the Upper Weald Clay Formation (Barremian) of Rudgwick, West Sussex, England (Blows, 1996).

Diagnosis (modified from Pereda Suberbiola, 1994; Blows, 1996, 2001). Synsacrum composed of ten vertebrae, including five dorsosacrals, four sacrals and one sacrocaudal (only *Struthiosaurus languedocensis* has the same formula, but in the latter the presacral rod is proportionally longer); scapula with an acromial flange that is located closer to the dorsal edge than in *Hoplitosaurus* and not so extended toward the glenoid as is the case in *Gastonia*; horizontal preacetabular process of ilium scarcely divergent from the long axis of the vertebral column; tibia a third shorter than the femur; distinctive dermal armour, consisting of two cervical rings composed of separate, flat spines mounted on basal narrow bands of bone (larger and more pointed spines than in *Gastonia*), a cervicopectoral grooved spine with a deep keeled endodermal base; conical, ungrooved spines in the shoulder region (posteriorly grooved in *Gargoyleosaurus*, *Gastonia*, *Hoplitosaurus* and *Mymoorapelta*); a solid sacropelvic shield formed of a fused mosaic of round, oval bosses, low-keeled ossicles and small, polygonal tubercles (these elements are lower and more irregularly arranged in rows than in *Mymoorapelta*; there are no radial grooves around the margins as is the case in the large elements of *Gastonia*); large spined plates with a narrow base and a dorsal, pointed rod (as in *Hoplitosaurus*); triangular, laterally flattened, hollow-based anterior caudal plates (more extended posterior basal edge than in *Mymoorapelta*, more pointed spine than in *Gastonia*); oval, flat scutes and button-like ossicles on the posterior third of the tail (but no evidence of an incipient tail club).

Polacanthus sp.

Referred material. MNS 2002/95.109, 456, 614, dorsal vertebrae; MNS 2001/122.785, 2002/95.45, 61, 62, 65, 85, 139, 149, 176, 222, 270, 305, 385, 396, 635, 663, 713, 733-734, 735, 805, 895, fragmentary dorsal ribs; MNS 2002/95.608, fragment of sacrum and ilium; MNS 2002/95.110, 115, 2003/69.479, presacral spines; MNS 2002/95.132, presacral keeled scute; MNS 2002/95.261, 291, fragmentary presacral spines (?); MNS 2002/95.117bis, 118, 119, 120, 121, 122, 309, 609, 719, 734, fragments of sacropelvic shield; MNS 2002/95.10, plated spine; MNS 2002/95.49, 111, 112, 113, 116, 117, 245, 389, 744, 772, 870, caudal plates; MNS 2002/95.19, 124, 125, 228, 322, 481, isolated flat ossicles; MNS uncatalogued, many small fragments of armour.

Locality and age. Zorralbo locality, township of Golmayo, near Soria, Spain; Golmayo Formation (depositional sequence III of Clemente and Pérez-Arlucea, 1993; Mas et al., 1993; K1.4 sequence of Mas and Salas, 2002), uppermost Valanginian-lowermost Barremian (Triqueta-Triqueta charophyte Biozone; Martín-Closas and Alonso, 1998), eastern Cameros Basin, NW Iberian Ranges, Iberian Peninsula.

Taphonomic comments. More than 60 ankylosaurian postcranial bones, including vertebrae, ribs and numerous dermal elements have been found. Most of the remains were scattered over 8 m^2 of the approximately 100 m^2 excavated to date. Elements of the dorsal, sacropelvic and caudal regions are represented in the assemblage. Most of the material is presumed to come from one medium to large-sized individual because the remains are consistent in size, no elements are duplicated and the degree of ossification is coherent with an adult individual (about 5 m long). Nevertheless, a few fragments of large ribs (MNS 2002/95.45, 735, 895) could belong to a larger specimen, so the presence of a second individual in the assemblage cannot be definitively excluded.

4. Description and comparisons

See Table 1 for measurements.

4.1. Vertebral column

4.1.1. Dorsal vertebrae and ribs (Fig. 2)

A nearly complete dorsal vertebra and two fragmentary neural arches were found (MNS 2002/95.109, 456, 614; Fig. 2A-D). The anterior face of the centrum is slightly distorted due to crushing, and the top of the neural spine is missing. The articular surfaces are amphiplatyan to slightly amphicoelous. The length of the centrum is greater than its height or width. The anterior articular surface is situated ventral to the posterior one (Fig. 2A). The ventral side of the centrum is weakly keeled. The ventral part of the neural canal forms a V-shaped excavation into the dorsal part of the centrum, but the excavation is not as deep as is the case in some dorsal vertebrae of English *Polacanthus* specimens (Blows, 1987, 1996; Pereda Suberbiola, 1994). The transverse processes are directed dorsolaterally and form an angle of about 80° to each other, as in *Polacanthus* and *Sauropelta* (Ostrom, 1970). The neural pedicles are relatively tall. The neural canal is twice as high as it is wide; its posterior height is more than half the height of the centrum (Fig. 2B). The prezygapophyses are more prominent than the postzygapophyses. The articular surfaces of the prezygapophyses are subspherical and form an angle of about 95° to each other (Fig. 2C). In lateral view, the prezygapophyses extend anteriorly relative to the anterior face of the centrum, while the postzygapophyses extend posteriorly only slightly beyond the posterior face of the centrum. Based on these characteristics, this vertebra is identified as a posterior dorsal. In MNS 2002/95.456, the articular surfaces of the prezygapophyses and of a postzygapophysis are missing (Fig. 2D). The neural spine is a laterally compressed blade and appears to be very low.

Several fragments of dorsal ribs are present in the assemblage (MNS 2001/122.785, 2002/95.45, 61, 62, 65, 85, 139, 149, 176, 222, 270, 305, 385, 396, 635, 663, 713, 733-734, 735, 805, 895; Fig. 2E-H), but none preserves a complete articular region. Dorsally the ribs show a rough fibrous pattern, whereas the ventral surface is smooth. Proximally, the ribs are T-shaped in cross section, but they become flat toward the distal end. There is no evidence that the dorsal ribs were fused to the vertebrae as is typically the case in *Polacanthus* and in other ankylosaurs, but this may be due to the small size of the sample.

4.1.2. Sacral region (Fig. 3)

MNS 2002/95.608 is a fragmentary sacrum; it is much damaged because of crushing and deformation. Two sacral ribs and a fragment of a third one are preserved (Fig. 3). The sacral foramina, one of which is complete and two of which are incomplete, are oval (width: 95-100 mm; length: 30-40 mm). The size of the specimen is slightly smaller than that of the holotype synsacrum of *Polacanthus foxii* (Hulke, 1888; Pereda Suberbiola, 1994). A portion of the ilium (perhaps representing that part forming the border of the acetabulum) is apparently preserved fused to the sacrum, although the identification is difficult because of damage.

4.2. Dermal armour

Several types of armour are preserved (Figs. 4–8): high, pointed spines with a broad base; narrow, hollow-based triangular plates; plated spines with a cylindrical rod; low-keeled scutes and ossicles; and fragments of shield, including a mosaic of fused bosses and tubercles (terminology of Blows, 2001). Dermal elements from the presacral region, the sacropelvic shield and the tail are part of the assemblage.

4.2.1. Presacral spines (Fig. 4)

There are three nearly complete presacral spines (MNS 2002/95.110, 115, 2003/69.479), all of which have suffered some degree of deformation or compaction damage. They are tall (about 250 to 350 mm from the base to the tip), laterally compressed, conical spines. The asymmetrical, oval to roughly triangular base is excavated (MNS 2002/95.110; Fig. 4A-C) or nearly flat (MNS 2002/95.113, 2003/69.479; Fig. 4D-H). MNS 2002/95.110 is a narrow triangular spine, about three times higher than long. The base is well extended ventrally (Fig. 4A, C). On one side, the base is slightly convex, whereas on the other it appears to be flat to slightly concave (Fig. 4B). In MNS 2003/69.479, the dorsal point is strongly compressed laterally and well differentiated from the base (Fig. 4E, F). The basal region is oblique in profile and longer than wide (Fig. 4G). Although deformed, the anterior and posterior edges were probably straight (Fig. 4F, H). The apex of the spine extends posteriorly, so that it overhangs the posterior margin of the base. The third spine (MNS 2002/95.115. Fig. 4D) is much distorted; it is similar in shape to the preceding spine but slightly smaller. A small bone fragment may correspond to the distal point of a third presacral spine (MNS 2002/95.291).

In many respects, these spines look like the presacral spines of “polacanthid” ankylosaurs (Kirkland, 1998; Blows, 2001), but there are some differences. Firstly, the Soria spines are not grooved posteriorly, unlike the cervicopectoral or shoulder spines of *Polacanthus* (GM 981.45; Delair, 1982; Blows, 1987), *Hoplitosaurus* (Gilmore, 1914), *Mymoorapelta* (Kirkland and Carpenter, 1994), *Gastonia* (Kirkland, 1998) and *Gargoyleosaurus* (Kilbourne and Carpenter, 2005). Secondly, in contrast to the lateral cervical plates of *Polacanthus* and *Gastonia* (Blows, 2001), they lack a ventral keel. It is assumed that the spines were located in the shoulder region: the hollow based spine MNS 2202/95.110 probably extending laterally away from the body whereas the solid based spines MNS 2003/95.479 and 2002/95.115 were probably more erect and located medially on the trunk, near the animal’s vertebral column. In the Soria specimens the spines apex is curved posteriorly, in contrast to the presacral spines of *Polacanthus*, *Gastonia* and *Mymoorapelta*. Unlike *Gastonia* (Kirkland, 1998), there are no radial grooves at the base of the spines.

A fragmentary spine (MNS 2002/95.261), which preserves only the lateral or medial edge, may also come from the presacral region. It is approximately as long as the above described

Table 1
Measurements (in mm) of *Polacanthus* sp. remains from Zorralbo, Lower Cretaceous Golmayo Formation of Soria (Spain)

	L	W_p	H_p	W_p nc	H_p nc	Sp
Dorsal vertebrae						
MNS 2002/95.109, dorsal vertebra.	75	57	55	13	32	21 × 13
MNS 2002/95.456, dorsal neural arch.						23 × 17

	L	W
Dorsal ribs		
MNS 2001/122.785, fragment of dorsal rib.	+153	38
MNS 2002/95.45, fragment of dorsal rib.	+130	43
MNS 2002/95.61, fragment of dorsal rib.	+114	33
MNS 2002/95.62, fragment of dorsal rib.	+62	37
MNS 2002/95.65, fragment of dorsal rib.	+82	36
MNS 2002/95.85, fragment of dorsal rib.	+97	26
MNS 2002/95.139, fragment of dorsal rib.	+92	33
MNS 2002/95.149, fragment of dorsal rib.	+140	30
MNS 2002/95.176, fragment of dorsal rib.	+77	30
MNS 2002/95.222, fragment of dorsal rib.	+117	40
MNS 2002/95.270, fragment of dorsal rib.	+175	24
MNS 2002/95.305, fragment of dorsal rib.	+91	24
MNS 2002/95.385, fragment of dorsal rib.	+215	34
MNS 2002/95.396, fragment of dorsal rib.	+150	35
MNS 2002/95.635, fragment of dorsal rib.	+57	25
MNS 2002/95.663, fragment of dorsal rib.	+242	33
MNS 2002/95.713, fragment of dorsal rib.	+125	29
MNS 2002/95.733-734, fragment of dorsal rib.	+98	25
MNS 2002/95.735, fragment of dorsal rib.	+45	51
MNS 2002/95.805, fragment of dorsal rib.	+92	27
MNS 2002/95.895, fragment of dorsal rib.	+67	63

	L	W
Sacrum		
MNS 2002/95.608, fragmentary sacrum sf A	45	45
sf B	30	95
sf C		85

	L	H	W	D
Presacral armour				
MNS 2002/95.110, right? lateral shoulder spine.	130	350	37	155
MNS 2002/95.115, right medial shoulder spine.		∼25	35	∼140
MNS 2003/69.479, left medial shoulder spine.	80	335	37	170
MNS 2002/95.132, left low-keeled scute.	137	70	106	
MNS 2002/95.261, fragment of presacral spine?.	+148	+107		
MNS 2002/95.291, fragment of presacral spine?.	+71	+33		

	L	W	T
Sacropelvic shield			
MNS 2002/95.117bis, fragment of sacropelvic shield	+100	+35	
MNS 2002/95.118, fragment of sacropelvic shield	+164	+67	
MNS 2002/95.119, fragment of sacropelvic shield	+155	+80	
MNS 2002/95.120, fragment of sacropelvic shield	+140	+50	
MNS 2002/95.121, posterodorsal fragment of sacropelvic shield		+82	14
MNS 2002/95.122, fragment of sacropelvic shield	+110	+85	
MNS 2002/95.309, fragment of sacropelvic shield	30 × 29		
MNS 2002/95.609, fragment of sacropelvic shield	30 × 26		
MNS 2002/95.719, fragment of sacropelvic shield	38 × 34		
MNS 2002/95.734, fragment of sacropelvic shield	58 × 45		
MNS 2002/95.10, plated spine	+129	+260	36

	L	H	T_b
Caudal plates			
MNS 2002/95.49, fragmentary caudal plate	+92	115	
MNS 2002/95.111, incomplete caudal plate	+90	+170	
MNS 2002/95.112, left anterior caudal plate	129	187	20
MNS 2002/95.113, incomplete anterior caudal plate	+90	+223	

(*continued on next page*)

Table 1 (*continued*)

	L	H	T_b
MNS 2002/95.116, fragmentary caudal plate	+101	+72	
MNS 2002/95.117, left anterior caudal plate	150	207	25–30
MNS 2002/95.245, fragment of caudal plate	+46	+96	
MNS 2002/95.389, point of caudal plate?	+26	+43	
MNS 2002/95.744, fragmentary base of caudal plate	+75	+100	
MNS 2002/95.772; point of caudal plate	+25	+49	
MNS 2002/95.870, incomplete anterior caudal plate	+97	+115	
	L	W	
Other armour			
MNS 2002/95.19, peaked ossicle (boss?)	65	65	
MNS 2002/95.124, flat ossicle	+51	57	
MNS 2002/95.125, peaked ossicle (boss?)	+43	35	
MNS 2002/95.228, low-keeled ossicle	+78	55	
MNS 2002/95.322, peaked ossicle (boss?)	+65	50	
MNS 2002/95.481, peaked ossicle (boss?)	+49	32	

Abbreviations – Vertebrae and ribs: H_p, posterior height; sf, sacral foramen; L, length; nc, neural canal; Sp, articular surface of postzygapophysis; W, maximum width; W_p, posterior width; Armour: D, maximum basal diameter; H, distance from the base to apex; L, maximum anteroposterior length; T, maximum thickness; T_b , basal thickness; W, maximum width; +, as preserved (incomplete).

spines (as preserved, 145 mm). The external surface is remarkably concave and probably represents part of the basal region of a high spine.

MNS 2002/95.132 is a large oval scute with a low, asymmetrical keel that extends along the medial edge (Fig. 4I, J). It closely resembles a large presacral dorsal scute of *P. rudgwickensis* described by Blows (1996: figs. 7a-b) as the last spine in the bilateral presacral series, immediately anterior to the pelvis. Similar scutes, but lower, narrower and ventrally hollowed, are known in *P. foxii* (Blows, 1987, 1996). These keeled scutes were probably arranged in bands that extended laterally across the dorsal region of the body and were separated by rows of smaller scutes or ossicles, as in *Gastonia* and *Gargoyleosaurus* (Gaston et al., 2001).

4.2.2. *Sacropelvic shield (Fig. 5)*

At least five large pieces of the sacropelvic shield are known (MNS 2002/95.118, 119, 120, 121, 122). Additional remains might also belong to the dermal shield covering the synsacrum and pelvic girdle (MNS 2002/95.117bis, 309, 609, 719, 734). The shield fragments are preserved as irregular bands of roughly rectangular to polygonal armour; the surface of the largest piece (MNS 2002.95/118, 119) is about 0.1 m^2. The thickness of the fragments ranges from 11 to 19 mm. The shield is composed of a mosaic of fused elements forming a solid bony pavement, including bosses and small tubercles on the dorsal surface (Fig. 5A-E). The bosses consist of numerous rounded elements lacking ridges (about 20 to 35 mm in diameter) and a few oval low-keeled or peaked ossicles (up to 65 mm long); that of MNS 2002/95.121 apparently comes from the right posterolateral corner of the shield (Fig. 5D). These bosses were probably arranged in longitudinal and transverse rows (Fig. 5E), as in *Polacanthus* (Blows, 2001), *Mymoorapelta* (Kirkland et al., 1998) and *Gastonia* (Kirkland, 1998). The ornamentation is not as well preserved as in *P. foxii* (mainly BMNH R9293; see Blows, 1987; Naish and Martill, 2001) but is worn, and it is thus difficult to recognize the polygonal tubercles surrounding the large elements. The ventral surface of the shield exhibits the typical pattern of cross fibrous structure of ossified collagen fibres, with, in some areas, small pits (foramina for blood vessels) about 5 mm in diameter (Fig. 5F, G).

A dorsal sacropelvic shield is well known in *Polacanthus*, *Mymoorapelta* and *Gastonia* (Blows, 2001; Carpenter, 2001; Gaston et al., 2001). The shield is almost complete in the holotype of *P. foxii* forming a roughly rectangular structure of about 1 m^2 (900 mm long, 1080 mm wide; see Hulke, 1888; Pereda Suberbiola, 1994). The term "sacropelvic" is more accurate than the term "sacral" to describe the shield because it covers the pelvic bones and the synsacrum, including the presacral rod. The large individual elements of the sacropelvic shield of *Polacanthus* are lower than those of *Mymoorapelta*, and they are more irregularly organized in rows than in the latter taxon (Kirkland and Carpenter, 1994; Kirkland et al., 1998). Moreover, the bosses of *Polacanthus* lack a margin ornamented by radial ridges, in contrast to *Gastonia* (Kirkland, 1998).

MNS 2002/95.10 is interpreted as an incomplete plated spine ("splate" sensu Blows, 2001). If this is correct, the lower half of the spine is missing. It preserves a narrow, lateromedially compressed body with sharp anterior and posterior edges and a prominent cylindrical spine (Fig. 6A-B). In lateral view, one of the edges (anterior) is straight to very slightly convex, while the other edge is very slightly concave. This suggests that the spine was slightly inclined posteriorly. Although incomplete, it resembles the plates of *Polacanthus foxii* (Blows, 1987) and *Hoplitosaurus marshi* (Gilmore, 1914), but it is comparatively larger (preserved length 260 mm; 280 mm in the *P. foxii* specimen BMNH R9293; 380 mm in the *H. marshi* specimen USNM 4572). The plated spines were once thought to come from the anteriormost region of the tail, just posterior to the synsacrum (Blows, 1987; Pereda Suberbiola, 1994). However, it is more likely that they extended along the lateral edge of the sacropelvic shield (Carpenter and Kirkland, 1998; Blows, 2001) or just anterior to it (Kilbourne and Carpenter, 2005).

4.2.3. *Caudal plates (Fig. 7)*

There are at least eleven caudal plates, of which two are complete, four are incomplete and the remainder are fragmentary (MNS 2002/95.49, 111, 112, 113, 116, 117, 245, 389, 744, 772, 870. Fig. 7A-L). Some of them have been partially reconstructed. The subtriangular, hollow-based plates bear a posteriorly oriented spine. They are laterally flattened and have sharp edges. The anterior edge is convex and is longer than the moderately concave posterior one. The asymmetrical base is narrow and biconvex in cross-section. The best-preserved plates (MNS 2002/95.112, 117; Fig. 7A-G) exhibit a coral-like endodermal structure at the base consisting of numerous excrescences and rugosities for ligamentous attachment into the skin (Fig. 7D, G). Such structures are not commonly ossified in ankylosaurs. The blade-like caudal plates

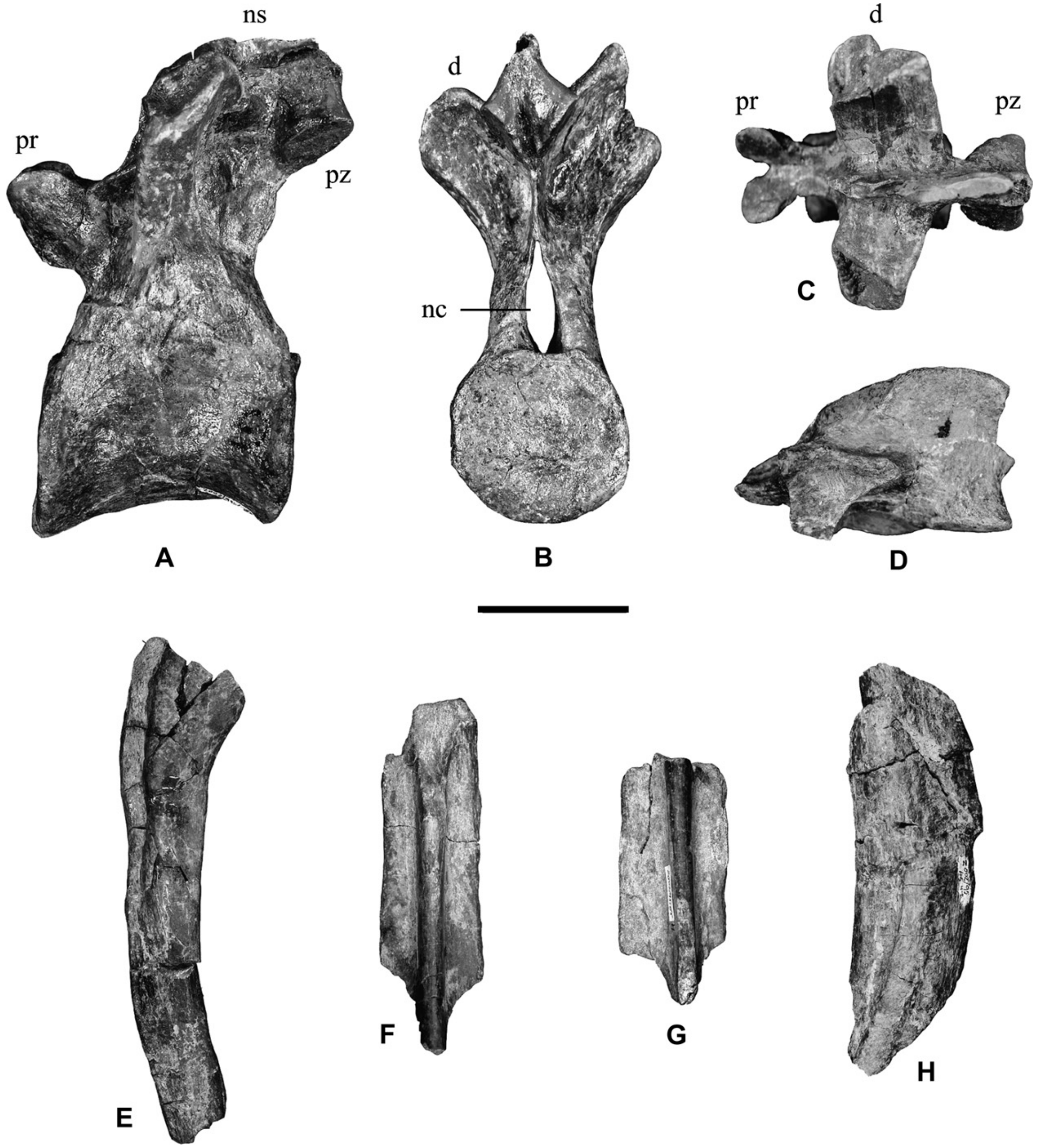

Fig. 2. *Polacanthus* sp. from the Lower Cretaceous of Soria, Spain. Dorsal vertebrae and ribs: A-C, dorsal vertebrae MNS 2002/95.109 in left lateral, posterior and dorsal views; D, dorsal vertebra MNS 2002/95.456 in left lateral view; E-H, dorsal ribs MNS 2002/95.270, 2002/95.61, 2002/95.65, 2002/95.45 in anterior (E, H) and ventral (F, G) views. Key: d, diapophysis; nc, neural canal; ns, neural spine; pr, prezygapophysis; pz, postzygapophysis. Scale line: 5 cm.

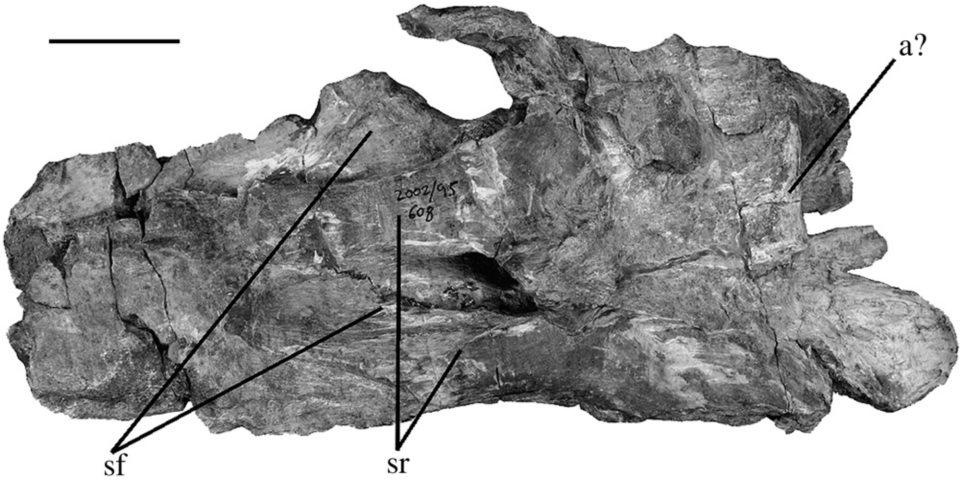

Fig. 3. *Polacanthus* sp. from the Lower Cretaceous of Soria, Spain. MNS 2002/95.608, fragmentary sacrum and pelvic girdle. Key: a, acetabulum?; sf, sacral foramen; sr, sacral rib. Scale bar: 5 cm.

probably projected laterally on each side of the tail (Kirkland, 1998; Gaston et al., 2001; Naish and Martill, 2001), and did not project dorsolaterally as reconstructed formerly. The size of the plates probably decreases posteriorly: the largest plates are assumed to be located more proximally along the tail. This armour arrangement would have been an effective defensive weapon as the tail was moved from side to side (Kirkland, 1998).

The Soria specimens resemble the caudal plates of *Polacanthus foxii* (Blows, 1987; Pereda Suberbiola, 1994) and other ankylosaurs, such as *Gastonia* (Kirkland, 1998), *Hoplitosaurus* (Gilmore, 1914; Pereda Suberbiola, 1994), *Mymoorapelta* (Kirkland and Carpenter, 1994; Kirkland et al., 1998), *Struthiosaurus* (Nopcsa, 1929; Pereda Suberbiola and Galton, 2001) and a large specimen from Utah tentatively referred to *Sauropelta* (Bodily, 1969; Carpenter et al., 1999). Nevertheless, the anterior caudal plates from Soria differ from those of *Sauropelta* in that they are wider (measured from the base of the tip of the triangle) than long (basal distance), and from those of *Struthiosaurus* in having a more concave posterior border. Compared with *Mymoorapelta*, they differ in having a greater basal length and in lacking a faintly fluted surface. Moreover, the spine tips do not extend beyond the posterior edges of the bases as they do in *Mymoorapelta*. On the other hand, the spine tips of the anterior caudal plates of *Polacanthus* are more pointed than in *Mymoorapelta* and *Gastonia*. Minor differences between the caudal plates of *P. foxii* (i.e., lateral width as compared to the overall length of the plate, relative size, and convexity of the anterior edge; BMNH R175, R9293, PS-FES 1) may represent individual variation, or even sexual dimorphism (Blows, 1996, 2001; Pereda Suberbiola et al., 1999).

In addition to the lateral triangular plates, *Gastonia* has been restored with paired, massive keeled scutes lying along the dorsal surface of the tail (Kirkland, 1998; Gaston et al., 2001). This type of armour has not been found at the Soria site. The holotype of *P. foxii* (BMNH R175) preserves a pair of flat, oval scutes and button-like ossicles associated with vertebrae and ossified tendons from the distal part (although not the end) of the tail, but there is no evidence of an incipient tail-club as in derived ankylosaurids (Pereda Suberbiola, 1994; Carpenter and Kirkland, 1998; contra Blows, 1987, 2001).

4.2.4. Other armour (Fig. 8)

Finally, there are a number of isolated flat ossicles in the assemblage (MNS 2002/95.19, 124, 125, 228, 322, 481; Fig. 8A-E). They are small (length 43 to 78 mm), oval to round solid-based elements that bear a blunt peak or a low-profile keel on the dorsal surface. The median keel extends axially in some ossicles, slightly obliquely in others. These ossicles were probably set as a mosaic between the large scutes and plates and small tubercles and arranged in rows along the trunk or the tail (Blows, 2001).

5. Discussion

The pervasive development of dermal armour is the most conspicuous synapomorphy of Ankylosauria (Coombs, 1978; Coombs and Maryanska, 1990; Vickaryous et al., 2004). The Soria ankylosaur shares with the "polacanthids" *Polacanthus*, *Mymoorapelta* and *Gastonia* the presence of a co-ossified sacropelvic shield and triangular caudal plates with asymmetrical hollow bases (Kirkland, 1998; Carpenter, 2001). Fusion of the sacropelvic armour also occurs in *Gargoyleosaurus* (Kilbourne and Carpenter, 2005), but the sacropelvic elements apparently do not fuse in other ankylosaurs, neither nodosaurids nor ankylosaurids. In addition, the Soria ankylosaur exhibits large spined plates, as do *Polacanthus* and *Hoplitosaurus* (Blows, 1987; Pereda Suberbiola, 1994; Carpenter, 2001).

In contrast to *Gastonia*, *Hoplitosaurus* and *Mymoorapelta*, the presacral spines of the Soria ankylosaur lack a groove along the posterior margin. This difference may indicate a distinct topographic position or be of taxonomic value. Grooved presacral spines are apparently absent in *Hylaeosaurus* (Mantell, 1833; Pereda Suberbiola, 1993). An isolated grooved spine is known in the armour assemblage of *Polacanthus* (described

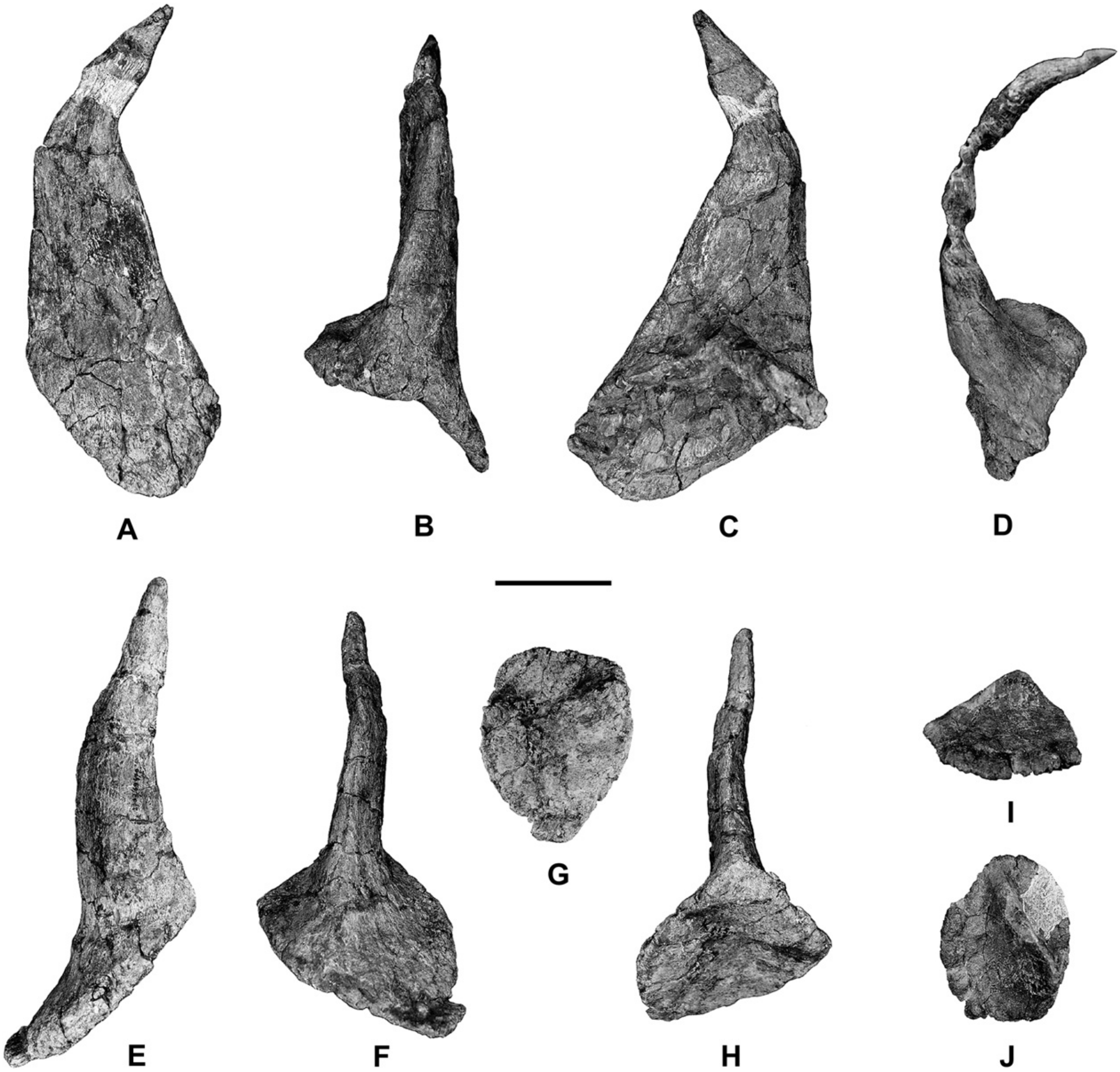

Fig. 4. *Polacanthus* sp. from the Lower Cretaceous of Soria, Spain. Presacral armour: A-C, MNS 2002/95.110, right? lateral shoulder spine in dorsal, anterior and ventral views; D, MNS 2002/95.115, right medial shoulder spine in anterior view. Note the damage because of deformation and faulting. E-H, MNS 2003/69.479, left medial shoulder spine in lateral, anterior, ventral and posterior views; I-J, MNS 2002/95.132, keeled scute in left lateral and dorsal views. Scale bar: 10 cm.

as *Vectensia* by Delair, 1982), and could correspond to the cervicopectoral region (Blows, 2001). It was probably situated near the neck because the spine has an endodermal basal keel coming out of the hollow base, as do the cervical spines of *Gastonia* (Kirkland, 1998; Blows, 2001).

The presacral spines of the Soria ankylosaur differ in some details from those of *Polacanthus*. These spines are here interpreted as coming from the shoulder region, including both lateral elements and spines placed close to the midline. Differences relative to the presacral spines of the *P. foxii* holotype could be due to a distinct topographic position. Assuming that the type specimen of *P. foxii* (BMNH R175) represents the posterior half of the animal's body, Carpenter and Kirkland (1998) interpreted these spines as projecting from the lateral margins of the sacropelvic shield. However, according to comparisons with the armour reconstruction of other ‘‘polacanthids’’, such as *Gastonia* (Kirkland, 1998; Gaston et al., 2001), these spines are more likely presacral elements. *Polacanthus* presumably combined bilateral rows of dorsolaterally placed conical, solid-based spines along the trunk with laterally projecting subtriangular, hollow-based spines. The taller elements were probably situated over the pectoral region and decreased in size posteriorly. The presacral spines from the Soria assemblage possibly correspond to the shoulder region, while those of the *P. foxii* holotype are regarded as posterior presacral spines, located just anterior to the sacropelvic shield. The apexes of the presacral spines from Soria are curved posteriorly whereas they tend to be straight in specimens of *Polacanthus*, *Gastonia* and *Mymoorapelta*. This may be autapomorphic for the Soria ankylosaur.

The sacropelvic dermal remains of the Soria ankylosaur resemble the shield of *Polacanthus foxii* in combining a mosaic of rounded to oval, ridged bosses and small, polygonal

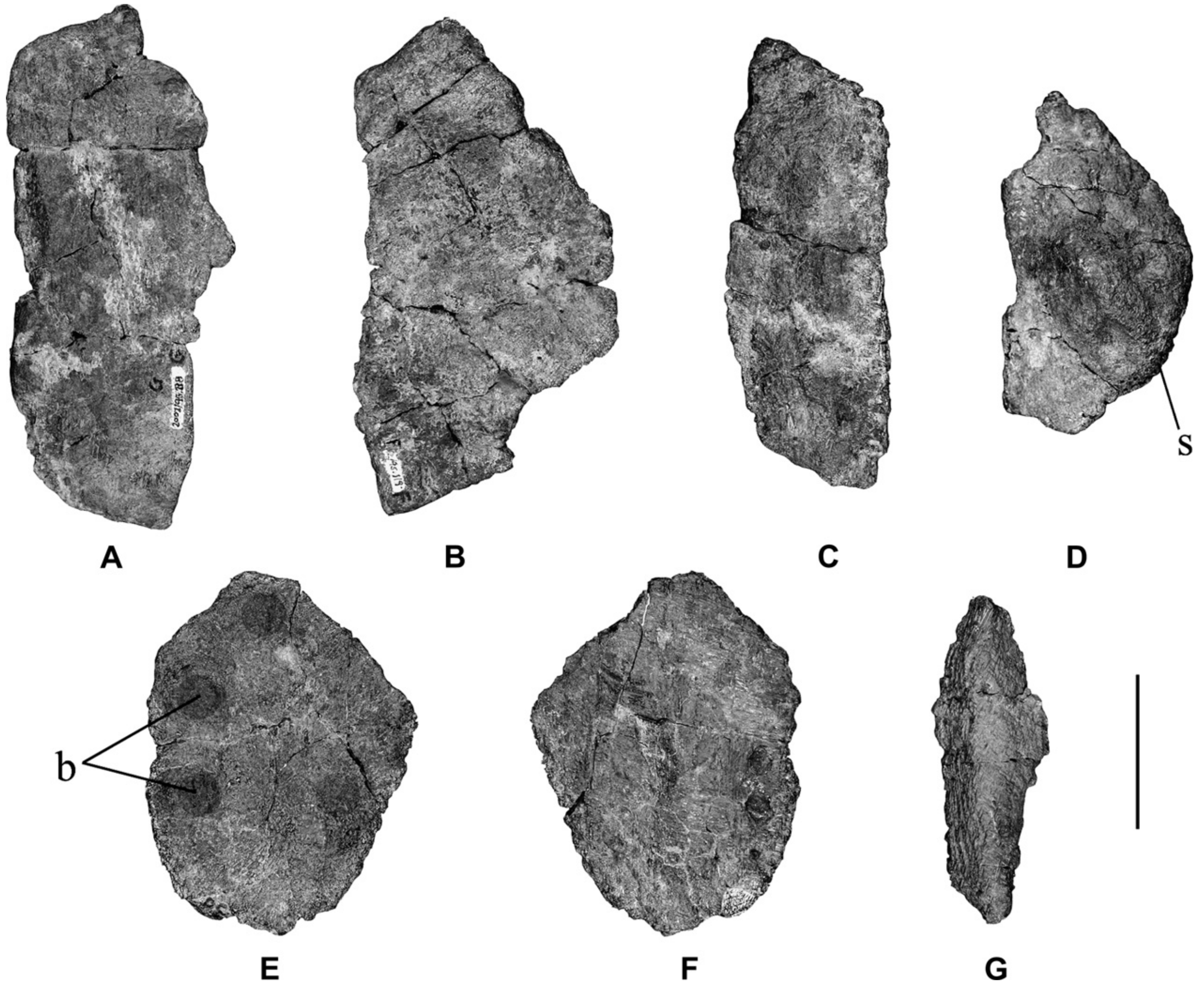

Fig. 5. *Polacanthus* sp. from the Lower Cretaceous of Soria, Spain. Sacropelvic shield remains: A-E, MNS 2002/95.118, 119, 120, 121, 122 in dorsal view, F-G, MNS 2002/95.122, 117bis in ventral view. Key: b, rounded boss; s, low-keeled scute. Scale bar: 5 cm.

tubercles (Hulke, 1888; Lydekker, 1891; Blows, 1987; Pereda Suberbiola, 1994). The bosses are arranged in transverse and longitudinal rows, with the largest, low-keeled elements located on the posterodorsal corners of the shield (Blows, 2001). A similar pattern can also be observed in the partial shields of *Mymoorapelta* and *Gastonia*, but the bosses are a different shape and appear to be more symmetrically distributed than in *Polacanthus* (Kirkland, 1998; Kirkland et al., 1998). When compared with *P. foxii*, the dorsal ornamentation of the sacropelvic shield remains of the Soria ankylosaur are nearly obliterated, and only the large elements can be easily recognized. The significance of this difference is not fully understood. It may be ontogenetic, but further material is needed to better understand the ontogeny of *Polacanthus*.

The hollow-based, triangular anterior caudal plates from Soria are similar to those of *Polacanthus foxii*, but differ in preserving a coral-like endodermal structure at their bases. These plates are wider transversely than long and bear a posteriorly pointed spine, as in the referred specimen BMNH R9293 (Blows, 1987). The anterior caudal plates of the *P. foxii* holotype (BMNH R175) follow this pattern, but the remaining plates are roof-shaped, being longer than wide (Pereda Suberbiola, 1994). According to Blows (1996), this difference is possibly sexual dimorphic. Another possibly dimorphic character in *Polacanthus* is the presence of a conspicuous convexity on the dorsal edge of the anterior caudal plates. This morphology, which is present in the anterior caudal plates referred to *Polacanthus* sp. from the Lower Cretaceous of Burgos (Pereda Suberbiola et al., 1999), is not present in the Soria material.

The dorsal vertebrae of the Soria ankylosaur resemble those of the holotype and referred material of *Polacanthus foxii* from the Isle of Wight in having transverse processes directed at about 90°, relatively high neural pedicles and a low neural spine (Blows, 1987; Pereda Suberbiola, 1994). They differ from those of *P. rudgwickensis* from West Sussex in that the centrum is smaller and more delicately proportioned when compared with the large, robust dorsal vertebrae with wide, round articular surfaces of *P. rudgwickensis* (Blows, 1996). On the other hand, the dorsal surface of the centrum MNS 2002/95.109 is moderately excavated by the neural canal and the ribs are not fused to the vertebra, unlike posterior dorsal vertebrae of both *P. foxii* and *P. rudgwickensis* (in which the centra show a deep V-shaped groove and the ribs are firmly co-ossified to the transverse processes).

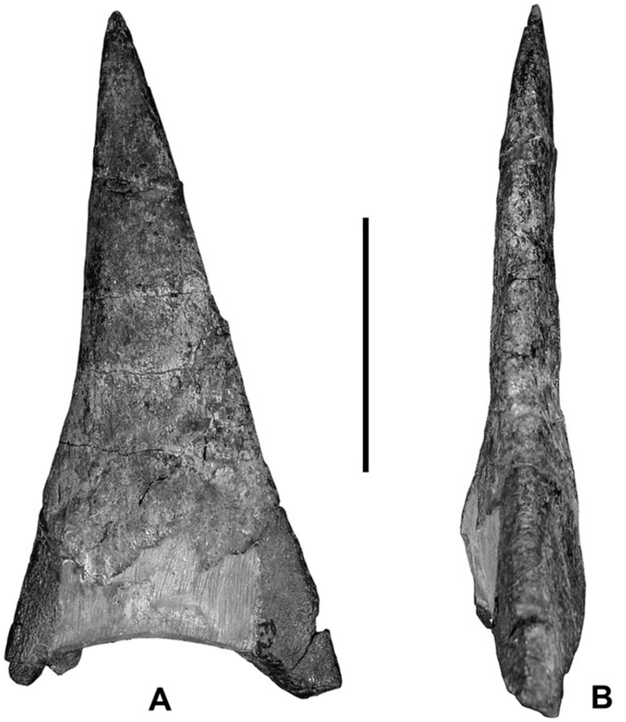

Fig. 6. *Polacanthus* sp. from the Lower Cretaceous of Soria, Spain. A-B, incomplete plated spine MNS 2002/95.10 in lateral? and posterior? views. Scale bar: 10 cm.

On the basis of armour features, the ankylosaur remains from the Lower Cretaceous of Soria are identified as *Polacanthus*. Differences between the Soria material and the species *P. foxii* and *P. rudgwickensis* (e.g., surface of dorsal centrum only moderately excavated by the neural canal; apex of the presacral spines curved posteriorly; partially obliterated dorsal ornamentation of the sacropelvic shield; rugose endodermal base in the anterior caudal plates), suggest the occurrence of a third species of *Polacanthus* in the Iberian Peninsula. Nevertheless, the morphological variability and growth processes of *Polacanthus* are not fully understood, so the possibility cannot be excluded that these osteological differences are due to individual variability and/or ontogenetic changes. Pending the discovery of new diagnostic material, the Soria remains are referred to *Polacanthus* sp.

6. Implications

The genus *Polacanthus* has been regarded as a junior synonym of *Hylaeosaurus* Mantell, 1833 (Coombs, 1978; Coombs and Maryanska, 1990), but there are significant anatomical differences between them (Blows, 1987; Pereda Suberbiola, 1993). In addition, their distribution provides further evidence to separate them: *Polacanthus* is known from the Weald Clay and Wealden groups (Barremian to possibly lower Aptian), whereas *Hylaeosaurus* occurs in the Hastings Beds Group (Valanginian). On the other hand, the phylogenetic position of *Polacanthus* is still controversial. *Polacanthus* has been referred to the Nodosauridae (Coombs, 1978; Blows, 1987; Pereda Suberbiola, 1994). Recent finds in North America have led to the erection of new taxa that seem closely related to *Polacanthus*. Kirkland (1998) grouped these taxa in the Polacanthinae, a clade that nests within Ankylosauridae. Similarly, Carpenter (2001) regarded the Polacanthidae (consisting of *Gargoyleosaurus*, *Hoplitosaurus*, *Hylaeosaurus*, *Gastonia*, *Mymoorapelta* and *Polacanthus*) as a distinct family and the sister group of Ankylosauridae. New phylogenetic analyses suggest that the Polacanthidae as defined by Carpenter is paraphyletic (or very weakly supported; see Parish, 2003), but support the idea that ‘‘polacanthids’’ are basal representatives of the Ankylosauridae (Vickaryous et al., 2001; Hill et al., 2003). In the most recent revision of the Ankylosauria, Vickaryous et al. (2004) classified *Gastonia* and *Gargoyleosaurus* as basal ankylosaurids, while *Polacanthus*, *Hylaeosaurus* and *Mymoorapelta* are referred to Ankylosauria *incertae sedis*. Ankylosaurid synapomorphies (most of which are cranial characters) listed by Vickaryous et al. (2004) cannot be tested in *Polacanthus*. Current evidence does not support the presence of an incipient tail club in *Polacanthus* (Pereda Suberbiola, 1994; Carpenter and Kirkland, 1998; contra Blows, 1987, 2001). To conclude, *Polacanthus* may be a basal member of Ankylosauridae, but only additional diagnostic material (especially skull bones) can confirm this interpretation.

If *Polacanthus* and *Hylaeosaurus* are eventually assigned to the Ankylosauridae, the distribution of European ankylosaurs should be revised. To date, only nodosaurids have been described in Europe, ranging in age from the Middle Jurassic to Late Cretaceous (e.g., Coombs, 1978; Galton, 1983; Coombs and Maryanska, 1990; Pereda Suberbiola, 1993). Galton (1983) assigned to the Nodosauridae several incomplete specimens from the Middle and Upper Jurassic of England (*Sarcolestes*, *Cryptosaurus*), from the Upper Jurassic or Lower Cretaceous of England (*Priodontognathus*), and from the Upper Jurassic of Portugal (*Dracopelta*). More recently, authors have cast doubt on the nodosaurid affinities - or even the valid status - of a number of these taxa (see Carpenter, 2001; Vickaryous et al., 2004; Pereda Suberbiola et al., 2005). Other nodosaurid records from the Lower to mid-Cretaceous of Europe are based on fragmentary or isolated remains (Pereda Suberbiola and Barrett, 1999; Weishampel et al., 2004). Only the juvenile *Anoplosaurus curtonotus* from the Albian of England possesses features typical of the Nodosauridae (Pereda Suberbiola and Barrett, 1999). On the other hand, nodosaurids are well represented in the Upper Cretaceous of Europe, with *Hungarosaurus* from the Santonian of Hungary (Ösi, 2005) and *Struthiosaurus* from the Campanian-Maastrichtian of Austria, Transylvania, Languedoc and the Iberian Peninsula (Pereda Suberbiola and Galton, 2001; Garcia and Pereda Suberbiola, 2003). The presence of ankylosaurids in the Upper Cretaceous of Europe is currently not supported.

7. Conclusions

Ankylosaur remains are recorded for the first time in the eastern sector of the Lower Cretaceous Cameros Basin (Zorralbo locality, Soria, Spain). They consist of dorsal vertebrae

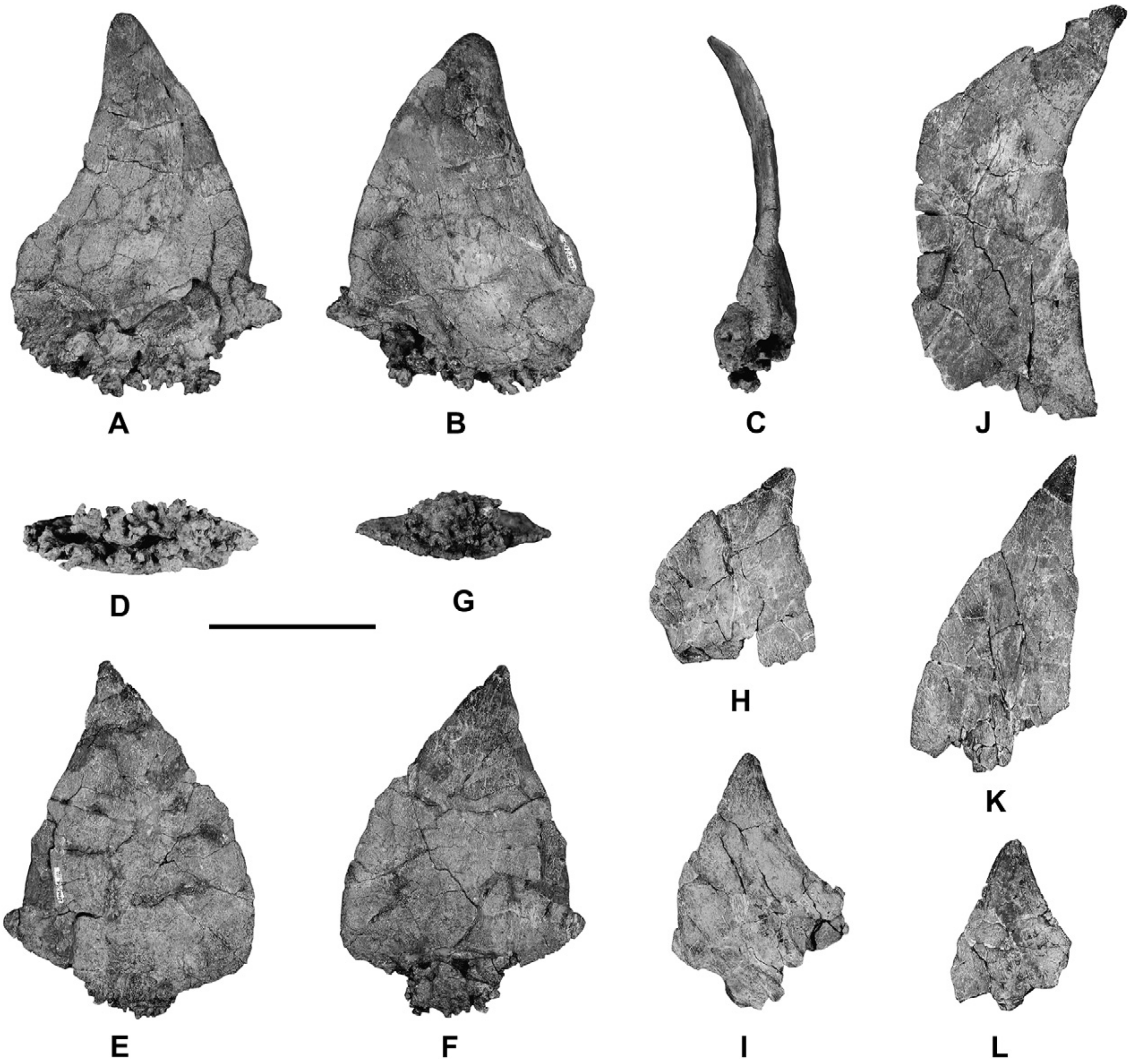

Fig. 7. *Polacanthus* sp. from the Lower Cretaceous of Soria, Spain. Caudal plates: A-D, MNS 2002/95.117, anterior left caudal plate in dorsal, ventral, anterior and proximal views; E-G, MNS 2002/95.112, anterior left caudal plate in dorsal, ventral and proximal views; H-L, MNS 2002/95.870, 49, 113, 111, 116, incomplete caudal plates in dorsal or ventral view. Scale bar: 10 cm.

and ribs, sacral and pelvic remains, and abundant dermal armour. Most (perhaps all) of the remains come from a single adult individual with a body length about 5 m. Based mainly on armour features, the Soria ankylosaur is identified as *Polacanthus*. This attribution is consistent with the equivalence in age of the outcrop (Golmayo Formation; upper Hauterivian to basal Barremian based on charophytes) to the Wealden Group and Weald Clay Group of England. Differences with

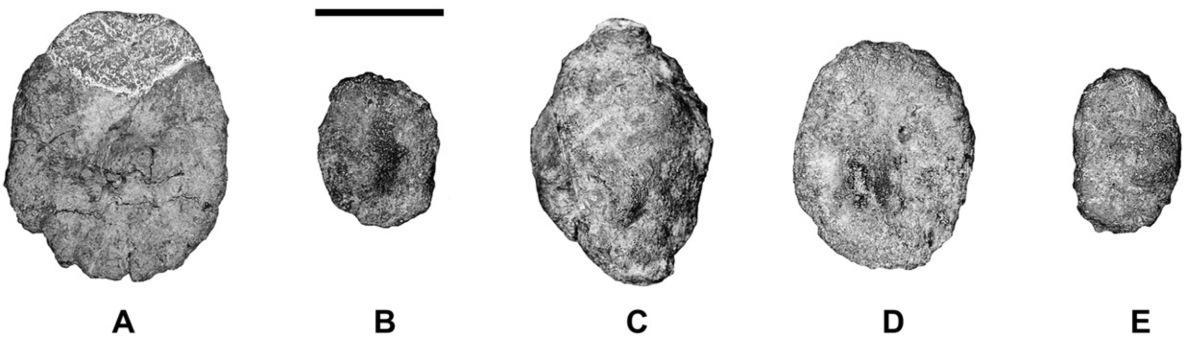

Fig. 8. *Polacanthus* sp. from the Lower Cretaceous of Soria, Spain. A-E, isolated ossicles MNS 2002/95.19, MNS 2002/95.125, MNS 2002/95.228, MNS 2002/95.322, MNS 2002/95.481 in dorsal view. Scale bar: 5 cm.

regard to *Polacanthus foxii* (the type-species of the genus) and *P. rudgwickensis* from England may indicate the presence of a third species of *Polacanthus* in the Iberian Peninsula. The affinities of *Polacanthus* within Ankylosauria are currently under debate: this genus was for a time referred to Nodosauridae, but new data suggests it may be a basal member of Ankylosauridae. If so, both nodosaurids and ankylosaurids are recorded in Lower Cretaceous formations of Europe.

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