Citation: Blows, W. & Honeysett, K. (2014). First Valanginian Polacanthus foxii (Dinosauria, Ankylosauria) from England, from the Lower Cretaceous of Bexhill, Sussex. Proceedings of the Geologists' Association, 125(2), pp. 233-251. doi: 10.1016/j.pgeola.2014.01.002

First Valanginian *Polacanthus foxii* (Dinosauria, Ankylosauria) from England, from the Lower Cretaceous of Bexhill, Sussex.

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ABSTRACT.

A new partial skeleton of the armoured ornithischian dinosaur *Polacanthus* found in the Wadhurst Clay Formation (Valanginian stage) of Bexhill, Sussex is the oldest recorded occurrence of this taxon. Previous discoveries suggested that at least two armoured ornithischians occur in the Wealden succession: *Polacanthus*, which was mostly restricted to the Barremian, and *Hylaeosaurus*, which was recorded as present only in the Valanginian. The new discovery extends the stratigraphic range of *Polacanthus* into the Valanginian. Although these two taxa appear to be closely similar anatomically, their osteology now suggests they are not synonymous. The new specimen includes the first known jugal as well as a comparatively rare polacanthid plate/spine (splate) which probably comes from the shoulder (pectoral) area of these animals.

Key *words*: *Polacanthus*, *Hylaeosaurus*, Valanginian, Barremian, Wealden, Cretaceous.

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1. Introduction

We describe here a partial skeleton of *Polacanthus* collected from Bexhill, Sussex. The Lower Cretaceous sediments of southern England yield a dinosaur fauna that is dominated by iguanodontian ornithopods. By comparison armoured orninithischians (ankylosaurs) are rare. *Hylaeosaurus armatus* Mantell, 1833 and *Polacanthus foxii* (attributed to Owen in Anonymous, 1865) are the two principal armoured taxa known from this area. Little additional material of *Hylaeosaurus* has been found since the 19th century because the original quarries in the Tilgate Forest area have been closed and back-filled. *Polacanthus* was founded upon a more complete skeleton discovered on the Isle of Wight, and in recent decades more material has been discovered and described (Blows, 1987; Norman and Faiers, 1996; Pereda-Suberbiola et al., 2007, Barrett and Maidment, 2011).

Institutional abbreviations: BEXHM Bexhill Museum, Bexhill-on-Sea, Sussex; CAMSM Sedgwick Museum, University of Cambridge, Cambridge; CEUM College of Eastern Utah Prehistoric Museum; GM Gosport Museum, Hampshire; HORSM Horsham Museum, West Sussex; IWCMS Isle of Wight Council Museum Service, Dinosaur Isle, Sandown, Isle of Wight; MNS Museo Numantino, Soria, Spain; NMW National Museum of Wales, Cardiff; NHMUK, Natural History Museum, London, UK; NMC National Museum of Canada, Ottawa; MWC Museum of Western Colorado, Colorado; ROM Royal Ontario Museum, Toronto, Canada; USNM United States National Museum, Washington.

2. Geological Setting

The Bexhill skeleton (BEXHM) was found in the Pevensey Pit at Ashdown Quarry, Bexhill, East Sussex. The Pevensey Pit exposes a sequence of the Wadhurst Clay Formation, which is comprised of upper and lower units, both argillaceous in origin. The units are separated by an arenaceous sandstone (Naish and Sweetman, 2011, p. 465), known locally as the Northiam Sandstone) (see Fig. 1). The remains were found in the upper clay unit approximately 11 meters above the top of this sandstone. The Wadhurst Clay Formation has proved very productive in terms of vertebrate remains, notably crocodiles, turtles, fish and thirteen species of dinosaur. However it is only the horizon known locally as the '*Polacanthus* bed' (which is between 45 and 60 cm thick) that has produced the remains of *Polacanthus* (Austen et al., 2010, p.13., Naish and Sweetman, 2011, p. 465). The '*Polacanthus* bed' has also produced substantial remains of Iguanodontian ornithopods.

The Wadhurst Clay Formation is part of the Hastings Beds, which is part of the Wealden sub-basin. The lithology consists of alternating argillaceous and arenaceous beds. The argillaceous beds are thought to have been deposited in lakes, channels, lagoons and mudflats of low salinity, whereas the arenaceous beds may be the result of meander plain to bridal plain and fan environments (Radley 2006, p.110, Radley and Allen 2012, pp. 256-257).

3. Systematics

Ornithischia Seeley, 1887

Thyreophora Nopcsa, 1915 (sensu Norman, 1984)

Ankylosauria Osborn, 1923

Family Polacanthidae Wieland, 1911 (sensu Carpenter, 2001)

Genus: *Polacanthus* (Owen in Anon., 1865)

Type species: *Polacanthus foxii* (Owen in Anon., 1865)

Holotype: NHMUK R175 a posterior partial skeleton lacking the skull, forelimbs and some anterior armour (Fox collection).

Type geology and locality: From a plant debris bed in blue shale of the Wessex Formation, Lower Cretaceous Barremian, east of Barnes Chine, south coast of the Isle of Wight, England (Hulke, 1881).

Referred specimens: NHMUK R9293 a partial skeleton with armour and three small possible skull fragments (Blows, 1987), and a privately held specimen lacking skull material, both from the Barremian Wessex Formation of the Isle of Wight; BEXHM 1999.34.1-BEXHM 1999.34.15; BEXHM 2002.34.2; BEXHM 2002.50.23; BEXHM 2002.50.52; BEXHM 2002.50.55-BEXHM 2002.50.70; BEXHM 2002.50.75-BEXHM 2002.50.79; BEXHM 2002.50.81-BEXHM 2002.50.92; BEXHM 2002.50.96; BEXHM 2002.50.98-BEXHM 2002.50.107; BEXHM 2002.50.110-BEXHM 2002.50.122; BEXHM 2002.50.125-BEXHM 2002.50.131; BEXHM 2003.70-BEXHM 2003.70.1; BEXHM 2009.4-BEXHM 2009.4.7; BEXHM 2011.3-BEXHM 2011.4; BEXHM 2011.22-BEXHM 2011.23.1 all parts of a single skeleton with armour and a right jugal from the Wadhurst Clay Formation (Valanginian) of Ashdown Quarry, Bexhill, Sussex, (the multiple numbers are due to collection, donation and accession over two decades, 1990-2010); numerous other isolated bones and armour from the Barremian of both England and Spain (see lists in Blows 1987, Pereda-Suberbiola 1993 and Pereda-Suberbiola et al., 2007).

Tentatively referred specimens: A partial neurocranium CAMSM X26242 (Norman and Faiers, 1996) from the Barremian of the Isle of Wight; one almost complete tooth from the Barremian of the Isle of Wight MIWG 5390 (Blows and Honeysett, in press). A second neurocranium NHMUK R16495 (Barrett and Maidment, 2011) from the Valanginian of Fairlight Cove, Sussex could be *Polacanthus*.

Other species. Polacanthus rudgwickensis Blows, 1996; holotype: HORSM 1988.1546, incomplete post-cranial skeleton with armour from the Weald Clay Formation (Barremian) of Rudgwick, West Sussex, England (Blows, 1996).

Differential Diagnosis: (modified from Blows, 1987, 1996; Pereda-Suberbiola, 1993, 1994; Pereda-Suberbiola et al., 2007; Barrett and Maidment, 2011). Moderate to large ankylosaur, 5 metres in mature body length; synsacrum of five dorsosacrals, four sacral, and one sacrocaudal vertebrae; caudal vertebral transverse processes as far as distal one-third of the tail; caudal vertebrae with unfused haemal arches; scapulae with fused coracoid in mature animals (separate in *Hylaeosaurus*); acromion forms a ridge arising from, and remaining close to, the dorsal edge of the scapula (located more centrally towards the glenoid in *Hylaeosaurus* and *Gastonia*); preacetabular process of the ilium short and minimally divergent, about 15^o; distinct lesser trochanter near mid-length of the femur; tibia 63% the length of the femur; cervical half-ring armour of separate basal bones each bearing a medium to large, triangular flattened spine (significantly larger than *Gastonia*); large flattened splates (shared character with *Hoplitosaurus* but not currently known in any other armour dinosaur); large (one metre square) sacral shield composed of a mosaic of fused small tubercles surrounding larger laterally and posteriorly placed bosses (mosaic pattern different in *Gastonia*, unknown in *Hylaeosaurus*); caudal armour of bilateral rows of tall, laterally flattened plates with narrow hollowed bases extending into the plate, decreasing size distally to small low keeled scutes.

Known biogeographic distribution. *Polacanthus* is known currently from England and Spain, (Pereda-Suberbiola, 1991, 1994).

Known biostratigraphy. The first appearance datum (FAD) of *Polacanthus* is the Valanginian (Wadhurst Clay Formation) of England. The last appearance datum (LAD) is Barremian (see discussion).

Material: BEXHM 1999.34.1 - BEXHM 1999.34.15; BEXHM 2002.34.2; BEXHM 2002.50.23; BEXHM 2002.50.52; BEXHM 2002.50.55 - BEXHM 2002.50.70; BEXHM 2002.50.75 - BEXHM 2002.50.79; BEXHM 2002.50.81 - BEXHM 2002.50.92; BEXHM 2002.50.96; BEXHM 2002.50.98 -BEXHM 2002.50.107; BEXHM 2002.50.110 - BEXHM 2002.50.122; BEXHM 2002.50.125 - BEXHM 2002.50.131; BEXHM 2003.70 - BEXHM 2003.70.1; BEXHM 2009.4 - BEXHM 2009.4.7; BEXHM 2011.3 - BEXHM 2011.4; BEXHM 2011.22 - BEXHM 2011.23.1 a single partial skeleton consisting of a right jugal, cervical, dorsal and caudal vertebrae, ribs, pelvic and pectoral fragments, limb elements and dermal armour.

Description: The remains were disarticulated but are considered to be parts of the same animal as they were found at the same site within close proximity to each other, with no duplication of elements. Preservation of the individual bones is quite good, indicating that post-mortem dispersal and erosion was limited, although disarticulation was complete. Other than this one site, armoured dinosaur remains to date are very rare in this quarry.

Skull: BEXHM 2002.50.98 (Fig. 2) is a right jugal with a ventral coronux (terminology sensu Blows, 2001) fused to the outer surface. The bilateral jugals extend below the orbit to form the ventrolateral rims of the orbit (Fig. 2A). Posteriorly they fuse with the postorbital to form the post-ocular shelf. As preserved, the Bexhill specimen has overall measurements of 54 mm anteroposteriorly, 50 mm dorsoventrally and 48 mm laterally. It is gently curved in lateral view to match the lower curvature of the orbit (Fig. 2A). The depth of this rim is 33 mm at the posterior end, narrowing anteriorly (Fig. 2D). The ventral coronux lies exclusively on the jugal, a character of the Polacanthidae (Kirkland et al., in press). The coronux has a wide base which is curved to match the curvature of the jugal and extends anteriorly. It is cone-shaped, slightly compressed laterally, arriving at a rounded apex (Fig. 2A, C). This apex has an asymmetric relationship with the base, i.e. the peak of the coronux occurs off-centre to the base and as a result is angled posteriorly. It is slightly smaller than the coronux in *Gastonia*, but a natural unfused articular surface, 18 mm by 33 mm, for attachment to the postorbital at the posterior end of the bone suggests the skull was not fully mature, and may have grown slightly larger (Fig. 2A, C, D).

Axial skeleton: The full vertebral count for *Polacanthus* is unknown, since no complete sequence of vertebrae has been found. The vertebrae found with the Bexhill specimen have some features in common, notably amphiplatyan centra, and some show a central raised notochordal bump on both articular faces. This bump is common amongst ankylosaurian taxa and some non-dinosaurs, and it is individually variable. The prezygapophyseal articular surfaces are angled upwards throughout the vertebral series. In cervical vertebrae the angle is about 25 degrees from the horizontal (Fig. 3G) and about 45 to 50 degrees from the horizontal in the dorsal (Fig. 4A, C) and early caudal vertebrae (Fig. 5A, C), becoming 75 degrees in the middle and late caudal vertebrae (Fig. 5G). The postzygapophyseal articular surfaces are similarly angled. All these features are common amongst other ankylosaurs.

BEXHM 2002.50.84 (Fig. 3A, B, C) is the centrum of a cervical vertebra about equal in length and width (approximately 60 mm). The articular ends are oval to slightly heart-shaped (Fig.3A, C), a typical ankylosaur morphology. The parapophyses are located on the lateral wall against the anterior end at the top of the centrum. This, and the long centrum indicates the specimen is an early cervical vertebra, possibly C3 or C4. In later vertebrae, the parapophyses remain against the anterior border but migrate down towards the base.

BEXHM 2002.50.99 (Fig. 3D, E, F, G) is the almost complete left side of a cervical vertebra with the parapophyses close to the base of the centrum, indicating it occupied a central position in the cervical row. The neural canal is well exposed and dorso-ventrally wide, showing a ventral V-shaped excavation into the centrum. The pre- and postzygapophyses both overhang the borders of the centrum, the prezygapophyses by a very small margin (similar to NHMUK R9293, Fig. 3I), and the postzygapophyses by a wide margin (unlike NHMUK R9293). Since these variations can be attributed to the different positions these vertebrae occupied in the series, they generally compare favourably with the Barremian example (NHMUK R9293)(Fig. 3H-J). The centrum was approximately 40 mm long as estimated from what remains of the centrum.

BEXHM 2002.50.78a is the right side of a cervical vertebral arch with only the neural canal lateral wall, right prezygapophysis and top of the centrum preserved. The neural canal is dorso-ventrally wide and the base shows a V-shaped excavation.

BEXHM 2002.50.87 (Fig. 4A-D) is a nearly complete dorsal vertebra. The right transverse process is almost complete and angles upwards from the horizontal by at least 40^{o}. The height without the neural spine is 115 mm and length of the centrum is 68 mm. The prominent parapophyses are positioned high on the lateral walls of the neural arch immediately beneath the transverse process, as in Barremian *Polacanthus* and other ankylosaur dorsal vertebrae (Fig. 4E-G). The floor of the neural canal is excavated into the centrum by a few millimetres. The pre and postzygapophyses overhang the centrum by a small margin. The centrum is cylindrical with rounded ends (Fig. 4A, C), the anterior end being slightly taller (65 mm) than the posterior end (58 mm). The neural arch slopes anteriorly from the posterior end of the centrum up to the parapophysis when viewed laterally (Fig. 4B). The anterior end of the centrum supports a shorter and shallower posteriorly directed slope of the neural arch to the parapophysis. This morphology matches closely the lateral profile of Barremian *Polacanthus* dorsal vertebrae (Fig. 4F, G).

The synsacrum, sacrum and sacral ribs are very poorly preserved. BEXHM 2011.3 is part of the anterior portion of the synsacrum (the presacral rod), which is made from modified posterior dorsal vertebrae fused together. This specimen is composed of two fused posterior dorsal vertebral centra, one slightly larger than the other. The neural arch is missing. Both centra have a flat base which narrows from the larger of the two centra to the smaller. The neural canal also has a flat base and neural foramen on each side at the point where the two centra join. This junction is marked around the two sides and the base by a slightly raised ridge of bone.

BEXHM 2009.4.4 is a fragment of sacrum. BEXHM 2002.50.119 and BEXHM 2002.50.96 are sections of the neural arch from the presacral rod, and BEXHM 1999.34.8 may be another smaller fragment of this neural arch. BEXHM 2002.50.101 is possibly a fragment of a sacral rib, 55 mm long as preserved.

Five well preserved caudal vertebrae are present in the Bexhill specimen. BEXHM 2002.50.88 (Fig. 5A, B) is a nearly complete anterior caudal vertebra with an overall height of 145 mm, the centrum being 55 mm in height and 65 mm in width. The neural spine is laterally compressed and widens gradually towards the top to form a broad termination, similar to NHMUK R9293 (Fig. 5C). The pre- and postzygapophyses both extend beyond the centrum, and have articular faces angled at about 60 degrees from the horizontal. The left lateral process is a long cylindrical rod which normally extends straight out laterally from the upper half of the centrum, but is ventrally depressed in this specimen due to tectonic pressure. The centrum is nearly circular on both faces, The heamal arch facets occur on the posterior ventral border of the centrum.

BEXHM 2002.50.85 (Fig. 5G, H) is a mid-caudal vertebra . The neural process base is preserved along with the postzygapophyses which have strongly inclined articulation faces angled at about 75 degrees from the horizontal. The prezygapophyses are similarly angled. Both the pre and postzygapophyses extend beyond the ends of the centrum. The lateral processes extend directly out from the mid line of the centrum as slender rods. The anterior face of the centrum is almost circular, the posterior face being very similar except the ventral edge is flattened to accommodate the haemal arch facets. As preserved, the total height is 120 mm, the centrum measures 56 mm long and 62 mm wide.

BEXHM 2002.50.23 (Fig. 5I-J) is a nearly complete mid-caudal vertebra. The neural process is laterally flattened, widening slightly at the termination. The pre and postzygapophyses articular faces are steeply inclined at about 75 degrees from the horizontal.

Both pre and postzygapophyses extend beyond the ends of the centrum. The transverse processes extend as a dorsoventrally flattened rod from a position half-way down the lateral wall of the centrum. The centrum is round on both articular faces and is 63 mm wide, 53 mm in height and 58 mm long. Haemal arch facets are more prominent on the posterior ventral border of the centrum that the anterior border.

BEXHM 2002.50.86 (Fig. 5K) is a mid-caudal vertebra. The neural process is laterally flattened with some lateral displacement caused by tectonic pressures. This caudal is otherwise similar to BEXHM 2002.50.23, although the prezygapophyses articular faces do not angle upward quite as steeply. The centrum width is 68 mm and height 55 mm. As preserved, the total height is 125 mm.

BEXHM 2011.4 (Fig. 5D) is an almost complete mid- caudal vertebra. The prezygapophyses articular faces angle upwards at about 55 degrees above the horizontal, and they extend significantly beyond the centrum. The centrum is elongate, being 65 mm in length, 42 mm in height and 52 mm maximum width. The lateral transverse processes are located midway along the lateral centrum wall, half-way between the base and the neural canal in line with a pronounced longitudinal ridge. This ridge divides the centrum lateral wall into an upper and lower half which are slightly angled from each other. The end articular faces of the centrum are generally round but they reflect the lateral ridges by bulging slightly on the lateral edges. They also have a rough and flattened area of the ventral edges as part of the haemal arch facets at both ends. These facets are large, especially at the posterior end of the centrum. The ventral surface of the centrum is concaved.

Two haemal arches, BEXHM 2002.50.82 (Fig. 5E) and 2002.50.81 (Fig. 5F) are Y-shaped with broad double headed articular surfaces, as seen in other ankylosaurs. The articular surfaces are almost flat and round in proximal view, being 22 mm in diameter each. The haemal canal is oval measuring about 12 mm to 15 mm deep and 7 mm wide. The twin halves fuse below the canal to form a single inferiorly directed rod. BEXHM 1999.34.11 and BEXHM 1999.34.15 are two further haemal arch fragments.

Sequencing of the caudal vertebrae is possible because of changes in both the overall size, the haemal arch articulation facets, and the location of the lateral (transverse) processes. Anterior caudal vertebrae (e.g. BEXHM 2002.50.88 and NHMUK R9293) are the largest caudal vertebrae with shallow haemal arch facets and lateral (transverse) processes mounted high on the lateral centrum adjacent to the neural arch. The dorsal surface of these processes blends with the neural arch forming a ridge, a development that is prominent in *Polacanthus rudgwickensis* (HORSM 1988.1546; Blows, 1996). Progressing posteriorly, the vertebrae become more medium sized with moderate haemal arch attachments. At the mid-caudal sequence (e.g. BEXHM 2002.50.86) the lateral process has migrated downwards towards the mid-line of the centrum. The dorsal surface of the process becomes progressively more detached from the neural arch. By the late caudal sequence (e.g. BEXHM 2011.4), the vertebral centrum is reduced in height being longer than tall, with large haemal arch facets. The transverse process is mounted on the midline of the centrum. This midline becomes progressively more distinct, through the posterior half of the tail, by the development of a longitudinal ridge which ultimately divides the centrum into an upper and lower segment. The transverse processes are significantly reduced in thickness, their dorsal surface at this point having lost all contact with the neural arch above. In very late (distal) vertebrae, the transverse process and haemal arch facets are lost.

Numerous rib pieces were found with the Bexhill *Polacanthus*. Ribs connect to the vertebrae via a tuberculum articulating with the diapophysis of the lateral process, and a capitulum which articulates below with the parapophysis. Since no complete *Polacanthus* cervical rib is known, the two cervical rib fragments from the Bexhill *Polacanthus* cannot be identified as either the capitulum or the tuberculum. They are long and narrow with approximately circular articular (proximal) ends. BEXHM 1999.34.13 has a preserved length of about 52 mm, and a diameter 14 mm at the articular end. BEXHM 2009.4.1 is a very similar process of a cervical rib with a preserved length of 110 mm and cross sectional diameter at the articular end of about 30 mm.

Dorsal ribs of *Polacanthus* and many other ankylosaurs are typically T-shaped in cross section, with a flat horizontal, usually rugose upper surface and a vertical supportive, usually smooth ridge of varying depths and widths placed ventrally. The tuberculum is reduced to a flat facet on the upper surface. This raises the upper surface of the rib to a level in line with the diapophysis on the lateral process, and from here the rib gradually curves away laterally. . BEXHM 2002.50.92 is a 185 mm length of rib close to the head (proximal) end. The upper surface has a flattened but rugosed oval shaped tuberculum, and from this point the capitulum curves downwards. The proximal end is missing. BEXHM 2002.50.91 is a gently curved 210 mm mid-section of a rib just lateral to the tuberculum. The ventral ridge is narrow and deep (30 mm) proximally, becoming wider and more shallow (20 mm) distally. BEXHM 2002.50.128 is the proximal end of a rib with similar morphology. BEXHM 2009.4.2 is a fragmented section of a robust rib close to the head end. The ventral ridge is deep (40 mm) and the approximately length, as preserved, is 100 mm. BEXHM 2002.50.79a (Fig. 4H, I) is an unusual proximal end of a robust posterior rib (65 mm length, 40 mm depth) with a prominent concave tuberculum on the dorsal border. It has a 7-shaped cross section creating a concavity beneath the tuberculum. This concavity narrows sharply medially down what remains of the capitulum. The ventral ridge thickens along the inferior border, which is rounded. Only a short section of the dorsal border exists but this shows that it is wider than the inferior border. A similar rib morphology is described from *Gargoyleosaurus* (Kilbourne and Carpenter, 2005). Other rib fragments include BEXHM 2011.23.1, BEXHM 2002.50.130,

BEXHM 2002.50.129, BEXHM 1999.34.10, BEXHM 2002.50.107 and BEXHM 2002.50.77a.

Appendicular skeleton: Very little of the pelvis exists in the Bexhill specimen. BEXHM 1999.34.1.2 and BEXHM 1999.34.1 (Fig. 6A, B) are two irregular fragments of the ilium which fit together. The united fragment is part of the lateral border of the preacetabular process. It is gently domed into a shallow arch shape. The ventral surface is gently concave, forming a smooth curve. The dorsal surface is rough and gently undulating. It is crossed by several transverse, irregularly placed and approximately parallel shallow grooves (Fig. 6B). The nature and cause of these grooves is considered in the discussion along with similar grooves on the dorsal surface of the holotype ilium of *Mymoorapelta* (MWC 1815, Fig. 6C)(Kirkland et al., 1998). Part of the natural lateral border is preserved in BEXHM 1999.34.1, and the fragment thins gradually towards this border. Another small piece of ilium bearing dorsal grooves does not attach directly to the large fragment. There is no evidence of the ischia or pubis.

BEXHM 2009.4 is the cranial (proximal) end of the right scapula with part of the anterior scapular blade (Fig. 7A-C). The coracoid is missing. The preserved length is 215 mm and the maximum depth at the proximal end is 150 mm. The dorsal edge of the scapula is wider than the ventral edge. The acromion occurs along the dorsal edge and is joined by a low ridge from the body of the scapular blade below the acromion. The acromion is eroded at the proximal end involving loss of most or all of the coracoid articular surface, so the extent of coracoid fusion with the scapula is impossible to assess. There is also surface erosion of the glenoid facet, but between these two areas of bone loss, immediately above the glenoid, there is about 20 mm of intact non-eroded edge. This natural edge shows no evidence of fusion with the coracoid, suggesting that either the scapula and coracoid were not fused in this animal, or possibly the fusion occurred above this intact edge. This bone loss also makes it difficult to assess the extent by which the acromion is folded towards the glenoid, but there is no evidence of any such encroachment towards the glenoid from what is preserved, contrary to *Hylaeosaurus* (see discussion).

BEXHM 2002.50.55 is a left scapula mid-blade fragment that narrows distally and has a matching morphology to BEXHM 2009.4. The acromion is largely missing but enough is present to indicate that it arose along the dorsal edge. About 130 mm of it is preserved.

No complete front limb for *Polacanthus* has been found. All the front limb elements are missing in the holotype of *Polacanthus*, and there are only isolated and often fragmentary front limb pieces in referred specimens. The holotype of *Polacanthus* includes hind limb bones, but pes and manus remains are still largely unknown. This makes it difficult to assign any new limb material accurately.

BEXHM 1999.34.5 (Fig. 8E) is a proximal end fragment of a humerus. As preserved, it is approximately half the width of the proximal epiphysis plus only a short section of shaft; the remainder of the bone is missing. It has a rounded, roughened articular surface for cartilage.

BEXHM 1999.34.3 is the epiphysis of a long bone. It has a subtriangular diaphyseal cross section with a small marrow cavity. The articular surface is longer (65 mm) than wide (30 mm), and forms a rounded ridge which is roughened for articular cartilage attachment. One side is compressed, the other side is centrally ridged. The entire epiphysis is curved in such manner that the articular end faces approximately 40 degrees away from the line of the shaft.

BEXHM 2002.50.89 (Fig. 8F- I) is a complete fibula 300 mm long. The proximal end is broad (75 mm) and flat (28 mm thick) with a large, slightly depressed, rough area extending down the medial side about 70 mm for cartilaginous articulation with the tibia. The distal end is flat (30 mm thick) but slightly narrower (65 mm) than the proximal end and has a similar roughened cartilaginous articulate surface extending 60 mm down the medial side. One edge of the distal epiphysis is narrow whilst the other is broader, forming a triangular shaped profile for the distal end (Fig. 8I). The diaphysis is about 38 mm in width and shows a mid-shaft muscle scar on the lateral surface. The shaft is twisted through approximately 45 degrees along its length, so the two ends are offset by this amount relative to each other.

BEXHM 1999.34.4 is the proximal epiphysis and BEXHM 2002.50.90 is 150 mm (as preserved) of the diaphysis of the second fibula. They appear to have once fitted together. They have very similar morphology and measurements to BEXHM 2002.50.89.

BEXHM 2003.70.1 (Fig. 8A-D) is a metapodial. It is nearly complete with rounded and eroded epiphyses. These ends show convex articular surfaces as preserved, likely due to some bone loss around the perimeters (Fig. 8C and D). The diaphysis is well preserved, being convex on one surface and slightly concave on the opposing surface. The bone is 153 mm long and tapered, being 60 mm wide at the proximal end and 45 mm wide at the distal end. It is not possible to state the anatomical location of this bone, but metacarpals (notably no. IV) and metatarsals (notably no. III) of the ankylosaurid *Pinacosaurus* also show convex and concave dorsal and plantar surfaces. However, the *Pinacosaurus* bones are shorter with broader epiphyses than in BEXHM 2003.70.1 (see Currie et al., 2011). The *Polacanthus foxii* holotype NHMUK R175 (Fig. 8J-L) includes a block of two associated metatarsals with an attached tarsal bone. The designation of metatarsals (pes) for this specimen is based on the fact that hind limb material is present in the holotype, but forelimb bones are absent. They were previously described by Hulke (1881) who also identified them as metatarsals. The two are attached together, metatarsal A (MTA) being larger and longer than metatarsal B (MTB) (Fig. 8K). MTA is strongly narrowed centrally forming a tapering shaft with broad proximal and distal ends which are twisted at an angle to each other (Fig. 8L). MTB is shorter, straight and less narrowed centrally. A tarsal (T) appears to be covering part of proximal surface, fused across both metatarsals (Fig. 8J). BEXHM 2003.70.1 is similar to the holotype in having a tapering diaphysis with one flattened surface, but the diaphysis does not twist in the Bexhill specimen. Despite some erosion, the ends do not show the expansion in width seen in NHMUK R175, and it may therefore be a metacarpal.

BEXHM 2003.70 (Fig. 9A, B) is a nearly complete metapodial, 75 mm in length, 53 mm proximal width and 40 mm distal width. The proximal epiphysis is broader than the distal epiphyses, but some bone loss at both ends prevents a full assessment of the articular faces.

BEXHM 2002.50.70 (Fig. 9C, D) is a nearly complete metapodial with some crushing and erosion of the proximal end. It is 55 mm long and 40 mm wide at the distal end. The distal articular end is strongly rounded on one side, the other side being reduced in size from bone loss. What remains of the proximal articular face slopes downwards in lateral and inferior views. The diaphysis is broad in antero-posterior views, but narrow in lateral views, especially immediately above the distal epiphysis.

BEXHM 2009.4.5 (Fig. 9E) is another nearly complete metapodial, 61 mm long and 35 mm wide at the end with the least bone loss, i.e. probably the distal end. The other end, which is probably the proximal end, has significant bone loss, so its not possible to determine the full extent of the articular surface.

BEXHM 2002.50.68 is a complete small phalanx, 32 mm long and 37 mm wide at the proximal end, 28 mm wide at the distal end.

BEXHM 2002.50.69 is the proximal end of a terminal (ungual) phalanx (Fig. 9H, I). The distal half of the bone is distorted and partly lost due to pathological bone loss during life. Such pathology is seen in other ankylosaur and ceratopsian unguals, and it may be due to bone infection following trauma to the anterior end of the bone, or possibly from parasitic infection (D. Tanke, pers. comm. 2013). The proximal end has an almost intact articular surface which is smooth and concave, the dorsal margin of which extends proximally as a V-shape. The dorsal surface of the phalanx is rugose, probably for the anchorage of a keratin claw.

BEXHM 2002.50.120 (Fig. 9F, G) is a complete terminal phalanx, probably from the pes. The total length as preserved is 90 mm (just the tip is eroded). It is 72 mm wide as preserved at the proximal end and tapers strongly from there to the tip when viewed dorsally or ventrally. The proximal articular surface is complete and slightly concave. This surface can be seen from the ventral view, but not from the dorsal view because the dorsal border extends posteriorly in a curve whilst the ventral border is less well developed in this way. The bone surface is slightly rugose, but not to the same extent as in BEXHM 2002.50.69. BEXHM 2002.50.120 compares well with a terminal phalanx of the *P. foxii* holotype (Fig. 9J, K) which has very similar morphology. However, these specimens are unlike the terminal phalanx collected as part of the *Polacanthus* referred specimen (NHMUK R9293) (Fig. 9L), which is smaller and narrower, with a flatter base, and has a bony flange around the mid region of the bone. NHMUK R9293 does not appear to be pes, but may be from the manus.

Armour: Dermal armour is commonly found associated with most ankylosaur discoveries, including this partial skeleton. There are many pieces of armour present in the Bexhill specimen, from near complete elements down to small fragments. We concentrate on those elements which are either almost complete or constitute important pieces.

Polacanthus armour falls into the following categories:

1. Cranial armour: In the absence of a complete skull, the cranial armour of *Polacanthus* is mostly unknown except for a few fragments (see discussion), including the jugal coronux (BEXHM 2002.50.98) described above (Fig. 2).

2. Cervical spines: BEXHM 1999.34.2 (Fig. 10A-C) is the complete cervical basal bone with some of the lower spine attached. It is 102 mm in length measured along the keel axis, and 80 mm maximum height as preserved; the entire top of the spine is missing. The

spine is laterally compressed and shows remnants of a sharp edge to the keel at both ends. The base is the widest part of the spine which narrows towards the apex. A distinct step in the bone marks the junction between the spine and the basal bone below. The curved basal bone is off-set from the spine and extends laterally beyond the spine on both sides. On one side the extension occurs towards the end of the spine, on the other it occurs midway along the spine. This arrangement of curvature and offset mounting of the spine on the basal bone allows for its accommodation on the neck as part of the cervical armour series. This is seen in the corresponding bones from NHMUK R9293 *Polacanthus* (Fig. 13A) and NHMUK OR3775 *Hylaeosaurus* (Fig. 13C). BEXHM 2002.50.66 and BEXHM 2002.50.67 are fragments of the basal region of other cervical spines.

3. Splates: probably part of the pectoral armour: BEXHM 2009.4.6 (Fig. 11A-C) is a nearly complete splate 215 mm maximum width, and 333 mm in height as preserved (the tip is missing). An encompassing ventral rugose ridge indicates a maximum dermal insertion depth of 65 mm at a point midway along the base directly below the spine. It is laterally flattened in the lower half (the "plate" segment) creating rounded "wings" at each end of the keel. Rising out of this plate segment is a cylindrical process (the "spine" segment) which apexes at a point. The spine tapers gradually towards the apex and is supported by a ridge of thicker bone extending down across the plate on both sides. The spine inclines at about 70 degrees from a line running across the junction with the dermal insertion at both ends. The base is elongate, solid and thick centrally, thinning towards the ends. The dermal insertion creates a ridge offset from a central position (Fig. 11C). This specimen compares well with the same element in the referred *Polacanthus* (NHMUK R9293; Fig. 11D), and *Hopiltosaurus marshi* (USNM 4752; Fig. 11E) but not with any known dermal element from *Hylaeosaurus*. The American *Gastonia* (CEUM 1307; see Blows, 2001, Fig. 17.3) had much smaller modified versions of this element.

4. Presacral spines: BEXHM 2002.50.83 (Fig. 10 I-K) is one of the smaller pre-sacral dorsal spines with a flat, solid, oval shaped base and a low, laterally displaced dorsal keel peaking at one end. The top of the spine is missing but was unlikely to have extended beyond the border of the base. The dorsal keel has a sharp edge throughout its length. Being displaced towards one side, this keel divides the upper surface into two unequal segments when viewed dorsally. It is 120 mm in length and 85 mm maximum width. BEXHM 2002.50.126 is the top of a spine with matrix containing *Lepidotus* scales. BEXHM 2002.50.112, BEXHM 2002.50.113 and BEXHM 2009.4.7 are short fragments from below the apex of large presacral spines.

5. Ossicles: There are numerous ossicles associated with the Bexhill specimen, as there are with other *Polacanthus* discoveries, e.g. NHMUK R9293 (Blows 1987). Most ossicles are small to moderate in size, round or oval with a mix of concave and ridged dorsal surface, the solid base being either flat or domed. Most ossicle dorsal ridges occupy the long axis of the oval ossicles, but in some cases the ridge is at right angles to the long axis. They mostly have a flat, cross-hatched patterned base. BEXHM 2002.50.65 (Fig. 10F) is a nearly complete oval ossicle, 60 mm long and 47 mm maximum width. It has a round area of bone missing from one edge creating a notch, sometimes known as a "resorption pit". This may be due to secondary bone resorption following infection or parasitic infestation (D. Tanke pers. comm. 2013). BEXHM 1999.34.6, BEXHM 1999.34.7, BEXHM 2002.59, BEXHM 2002.50.60 to BEXHM 2002.50.64 are other small to medium size (15 mm to 60 mm diameter) ossicles. BEXHM 2002.50.103 is a small collection of three ossicle fragments.

6. Sacral shield: The Bexhill *Polacanthus* includes a few larger sacral shield pieces and some smaller fragments. BEXHM 2002.50.58 (Fig. 10D, E) is a fragment of shield, 110 mm by 55 mm as preserved, with all the edges broken. The dorsal surface shows a mosaic pattern of large and small, fused tubercles with shallow groves between them. The ventral

surface shows the characteristic cross-hatching of ossified fibrous tissue. BEXHM 2002.50.102 (Fig. 10G, H) is another shield piece, 80 mm by 50 mm as preserved, with one naturally intact edge. The dorsal and ventral surfaces have very similar patterns to that of 2002.50.58. BEXHM 2002.50.131 is a sacral shield fragment including a complete, rounded, low peaked boss. BEXHM 2002.50.104 is another sacral shield fragment.

7. Caudal plates: BEXHM 2002.50.122 (Fig. 12A, B, C) is a large, nearly complete plate from the mid-caudal sequence. It is 210 mm long, 150 mm in height (as preserved) and 30 mm wide at the base. It is laterally flattened with a symmetrical central peak. The base is hollowed through most of its length, but one end (possibly the posterior) is not hollowed. The hollowing becomes progressively more shallow as this end is approached. The solid end usually occurs beneath the direction the apex of the spine points in (Fig. 12D-F). The keel edges are mostly intact, sharp and almost straight. BEXHM 2002.50.56 is a caudal plate basal fragment and 2002.50.57 is a large fragment of a mid-caudal plate. BEXHM 2002.50.58 is a fragment of the solid (possibly posterior) section from a caudal plate. The intact edge reaches a height of 60 mm. BEXHM 2011.22 is a fragment of the hollowed section from the base of a tall caudal plate. BEXHM 2002.50.121 is the basal fragment from the anterior end of a caudal plate. About 50 mm of the anterior plate edge and the ridge indicating dermal insertion are preserved.

4. Discussion

4.1. The distinction between *Polacanthus* and *Hylaeosaurus*.

The holotypes of *Hylaeosaurus* (NHMUK OR3775, Fig. 13G) and *Polacanthus* (NHMUK R175), have very few bones in common with each other. *Hylaeosaurus* is represented by the anterior half of the animal and *Polacanthus* is represented by the posterior half. Possibly the only bones in common between the two holotypes are a few dorsal vertebrae. Coombs (1978) synonymised these two taxa by making *Polacanthus* (Anon. 1865) a junior synonym of *Hylaeosaurus* (Mantell, 1833). This synonymy was unsafe because the two holotypes could not be compared directly, and because at that time they were separated by a significant age gap; *Hylaeosaurus* was late Valanginian and *Polacanthus* was Barremian. Retaining them as separate taxa until new material was available was a safer option. The discovery of a new Barremian *Polacanthus* (NHMUK R9293) in 1979 (Blows, 1987) included for the first time some anterior skeletal elements, notably cervical vertebrae and cervico-pectoral armour. This armour indicated that the two taxa were probably distinct.

The cervical armour in *Polacanthus* (NHMUK R9293) consisted of half-rings made from separate units (Blows, 2014), i.e. not a fused together (Fig. 13A and B). Each unit has a medium or large flat triangular or curved spine fused to a curved basal bone. These half-ring elements are now known from the holotype of *Hylaeosaurus* (NHMUK OR3775; Fig. 13C) although damage prevents the overall shape of the dorsal spine from being determined. It would appear that NHMUK OR28681 is also a cervical spine of *Hylaeosaurus* (Mantell, 1850, Owen, 1857). Therefore separate unfused units of the cervical half-rings are found in both taxa, unlike the fused half-rings seen in most other ankylosaurian taxa (Blows, 1987, 2014).

The pectoral armour in *Hylaeosaurus* (Fig 13G) consisted of a bilateral row of long, flat, narrow, posteriorly projecting spines on narrow bases which are similar to, but flatter than, the long pectoral spines of *Sauropelta* and *Edmontonia*. This spine type is not seen in *Polacanthus* which had splates and posteriorly grooved triangular spines. These are shorter and stouter than the pectoral spines of *Hylaeosaurus*, and they have large bases with deep dermal insertions, unlike anything seen in *Hylaeosaurus*. Whilst the exact anatomical location of the splates in *Polacanthus* remains unknown, a process of elimination leads to the conclusion that they were pectoral in origin. Ossicles occur in both taxa, but in *Polacanthus* they range from small and round to larger variously shaped elements, whilst they are smaller and oval in *Hylaeosaurus*.

Barrett and Maidment (2011) noted a feature in *Polacanthus,* a V-shaped dip of the neural canal into the dorsal surface of the centrum in all presacral vertebrae. This feature can now be identified in at least one dorsal vertebra of the *Hylaeosaurus* holotype (NHMUK OR3775) and can also be traced through the cervical vertebrae series in *Scelidosaurus* (NHMUK R12019). Whilst not present in all ankylosaur taxa, it may be a feature more commonly found in the Ankylosauria than previously thought.

The characters that distinguish *Hylaeosaurus* from *Polacanthus* that can be established at this time, are: 1. Coracoid and scapula remains unfused in mature specimens of *Hylaeosaurus* (Fig. 13D, E and F), but are fused in *Polacanthus*; 2. A large robust acromion of the scapula directed downwards towards the glenoid in *Hylaeosaurus* (Fig. 13D-F), and a smaller, narrow ridged acromion remaining close to the dorsal edge of the scapula in *Polacanthus* (Figs. 7); 3. The variations in the pectoral armour morphology between the two taxa (as noted above) including the presence of splates and posteriorly grooved triangular spines with deep dermal insertions in *Polacanthus* and *Hoplitosaurus*, unknown in *Hylaeosaurus*; 4. The apparent absence of a sacral shield in *Hylaeosaurus*, but present in all the *Polacanthus* discoveries (Barrett and Maidment, 2011); 5. The presence of tall, robust, flat based presacral dorsal spines in *Polacanthus* which are unknown in *Hylaeosaurus*; 6. The differences in ossicle morphology. Unfortunately, neither taxa has satisfactory skull material to allow a comparison, or to add anything to the diagnoses. We consider these characteristics to be of taxonomic status, not ontogenetic or due to sexual dimorphism. Both holotypes, *Polacanthus* and *Hylaeosaurus*, appear to be of approximately equal growth stages (sub-adult). Blows (1996) identified three possible characters which may be indicative of sexual dimorphism in *Polacanthus*, using NHMUK R175 and NHMUK R9293, i.e. variations in anterior caudal vertebrae, anterior caudal plates and ischium morphology. Unfortunately, these characters cannot be tested directly in *Hylaeosaurus*.

The referral of the Bexhill Museum specimen to *Polacanthus* rather than *Hylaeosaurus* was made based on the following: pectoral and presacral dorsal spines are of the *Polacanthus* morphology, including the presence of splates seen in the Barremian *Polacanthus* (NHMUK R9293), but not seen in *Hylaeosaurus*; the scapula acromion (although eroded) suggests it was of the *Polacanthus* morphology; the armour included several fragments of sacral shield (absent from all the *Hylaeosaurus* discoveries); ossicles of the *Polacanthus* morphology type are present. There are no other characters which could distinguish it from *Polacanthus*. Unfortunately, the main piece of scapula is eroded just short of the coracoid articulation, and the coracoid is missing; therefore the status of the fusion between the scapula and coracoid cannot be determined.

Hylaeosaurus and *Polacanthus* are both placed within the Polacanthidae by Carpenter (2001). This clade is supported by new skull features (Kirkland 2013 pers. comm.) including a ventral coronux that exists entirely within the jugal, a feature now demonstrated in *Polacanthus*.

4.2. *Polacanthus* and *Hylaeosaurus* biostratigraphy

Until now, the majority of UK and Spanish specimens of *Polacanthus* were known only from the Barremian period. There are some isolated ankylosaur remains known from Aptian and Albian sediments of the UK, but amongst these only the taxon *Anoplosaurus* is considered to be valid (Carpenter 2001, Vickaryous et al., 2004); the remainder are from indeterminate ankylosaurs. Kirkland et al. (2013) discuss the replacement of the polacanthids in Europe with a new monophyletic clade of nodosaurids, the Struthiosaurinae, during the mid-Cretaceous. This coincides with a similar replacement of the polacanthids by nodosaurids in North America at about the same time. The European Struthiosaurinae includes the UK taxon *Anoplosaurus curtonotus* Seeley 1879. Evidence for the presence of ankylosaurs in general, and *Polacanthus* in particular, during the post-Barremian Cretaceous of the UK remains mostly indeterminate, due to changes to marine conditions (Pereda-Suberbiola and Barrett, 1999). The last appearance datum (LAD) of *Polacanthus* is therefore Barremian. The first appearance datum (FAD) of *Polacanthus* was the Golmayo Formation of Spain (uppermost Valanginian or lowermost Barremian) (Pereda-Suberbiola et al., 2007). This is now extended back earlier into the Valanginian, (Wadhurst Clay Formation) as a result of the Bexhill specimen.

Hylaeosaurus appears to be restricted to the Cuckfield Stone Bed (containing the Tilgate Stone) of the Tunbridge Wells Sand Formation, Grinstead Clay Member, of late Valanginian age. The extension of the FAD of *Polacanthus* distribution into the Valanginian Wadhurst Clay Formation contradicts previous the hypothesis that these two taxa occupied non-overlapping biostratigraphical ranges (Norman, 1987), as noted by Barrett and Maidment (2011). There appears to have been sympatric populations of both taxa for at least a period of time during the Valanginian.

4.3. Grooves on the ilia.

The grooves on the dorsal surface of the ilium (BEXHM 1999.34.1.2 / BEXHM 1999.34.1) are probably not predatory theropod tooth marks because the surface bone within the grooves appears evenly compressed to a shallow depth. They are not irregular deep incisions into the bone, or the bone surface breached to varying depths, as would be expected from indiscriminate damage caused by sharp teeth applied with force. The dorsal surface of the ilia in *Polacanthus* was covered in life by a dermal plate (the sacral shield) approximately one metre square. This was separated from the ilia by 1 mm to 10 mm of probably connective tissue (measured in the uncrushed pelvis NHMUK R1926) (Lydekker, 1891). Predators would have had to penetrate this sacral shield, and the tissue below would provide little bulk or nutrition as it was not muscle. The grooves on the ilium also show evidence of branching (Fig. 6B) which is unlikely with predatory tooth marks. Britt et al. (2009) provide illustrations and discussion of marks on dinosaur bone, and the tooth marks illustrated in their Fig. 13B, C and D are deep, intermittent incisions into the bone, unlike the Bexhill ilium grooves which are shallow and continuous. A better comparison can be made with the "trample marks" (illustrated in Fig. 13A of Britt et al., 2009). However, it is unlikely this is the cause of the Bexhill specimen ilium grooves because trampling is indiscriminate, with further marks occurring on other bones. Moreover, similar marks are found on the dorsal ilium of another armoured dinosaur, the North American Jurassic ankylosaur *Mymoorapelta* (Fig. 6C) (MWC 1815, Kirkland et al., 1998). These two specimens (MWC 1815 and BEXHM 1999.34.1.2 / BEXHM 1999.34.1), are separated by about 15 million years, and exist several thousand miles apart, yet both have very similar grooves on the dorsal ilium, with no other bones involved. We suggest that these grooves are a normal anatomical feature, not a post-mortem artefact. It is possible they may be related to the overlying sacral shield in some way. In the holotype of *Polacanthus* both ilia have the sacral shield in anatomical position which hides the dorsal surface of the ilia, so this hypothesis cannot be tested in this specimen. There is a fragment of ilium of *Polacanthus* without sacral shield as part of NHMUK R9293, but the dorsal surface is covered in a fine layer of matrix

4.4. Armour in *Polacanthus*.

The armour arrangement on *Polacanthus* is now generally understood. However, there are many details missing, including the full skull armour, and the exact location of the splates and the pre-sacral spines.

A complete skull of *Polacanthus* is unknown, but some fragments have been found. NHMUK R16495 is a neurocranium which is under study elsewhere. It comes from the beach at Hastings, Sussex, and is probably Valanginian. It may be *Polacanthus* or *Hylaeosaurus*

(Barrett and Maidment 2011). The skull roof appears to be covered by armour several millimetres thick. A partial neurocranium (CAMSM X26242; Norman and Faiers, 1996) from the Barremian of the Isle of Wight, and tentatively referred to *Polacanthus,* has fused flat dermal ossifications across the preserved portion of the frontal bone. The origin of skull armour in ankylosaurs is not entirely clear. It is probable that skull armour was the result of two processes happening simultaneously. One was the remodeling and elaboration of the bone surface, seen in the quadratojugal, squamosal, supraorbital and perhaps elsewhere. The other process was the fusion of dermal armour to the bone surface (Vickaryous et al., 2001; Carpenter 2001; Vickaryous et al., 2004).

An unfused left angular, part of NHMUK R9293 from the Barremian of the Isle of Wight, was described by Blows (1987) who noted the dermal ossification on the outer surface (Fig. 14B-D). The total length of the angular is 85 mm. It is boat shaped, narrow with one well preserved edge. The dermal ossification is elongate (maximum length 47 mm, maximum width 31 mm) and has a rugose surface with a low longitudinal ridge. Burns et al. (2011) indicate that the mandibular osteoderm in *Pinacosaurus* began development in juveniles on the angular and grew forward onto the dentary, ultimately obliterating the dentary-angular suture. This may be true for *Polacanthus* because the osteoderm remains entirely within the angular which is unfused and separated from the dentary. Blows (1987) recognised the separate sutures of the skull and atlas vertebra in NHMUK R9293 and considered the specimen a sub-adult. Maturation differences in *Polacanthus* appears to occur on each side of the atlas-axis articulation, with the skull and 1st cervical vertebra (neural arch) remaining unfused for some time after the remaining skeleton has matured. It would appear that the limited growth and development of the mandibular osteoderm in NHMUK R9293, entirely within the borders of the angular, supports the sub-adult status of this animal.

The ventral coronux (BEXHM 2002.50.98, Fig. 2) is mounted entirely on the jugal and is one of a pair of cone-shaped armour elements on each side of the skull, the dorsal and ventral coronuces (or "caudolateral horns"), positioned above and below the orbital rim (Blows, 2001, p. 371). An unfused junction between the jugal and post-orbital in the Bexhill specimen, with the post-cranial remains showing complete fusion (e.g. dorsal and caudal vertebral arches), also indicates the dichotomy between the cranial and post-cranial maturity, and the sub-adult status of the Bexhill Valanginian *Polacanthus.*

The cervical armour spines (Fig. 10 A-C) are medium to large spines surrounding the dorsal aspect of the neck. They have flattened dorsal keels rising to a pointed apex, and solid curved bases to accommodate the curvature of the neck. The arrangement of these spines over the cervical region is currently unknown in *Polacanthus*. This armour occurs in separate units, not as a fused half-ring as in other nodosaurs and ankylosaurs (Blows, 2014). BEXHM 1999.34.2 (Fig. 10A-C), NHMUK R9293 *Polacanthus* (Fig. 13A, B) and NHMUK OR3775 *Hylaeosaurus* (Fig. 13C) all had half-rings consisting of separate units. This morphology differs slightly from the cervical ring elements seen in the American polacanthid *Gastonia* (Kirkland, 1998) which are smaller and form quarter-rings, i.e. two separate units which remain unfused medially. The primitive but unique triradiate elements of the Early Jurassic *Scelidosaurus* occur as separate units (Norman et al., 2004).

Polacanthus is known to have splates and triangular posteriorly-grooved spines with deep dermal insertions. Splates are rare - only three complete splates (shown in Fig. 11), one partial splate (MNS 2002/95.10, see Table 1 and Fig. 6 in Pereda-Suberbiola et al., 2007) and a few fragments are known, all from the Lower Cretaceous. Two of the complete splates are from the UK (NHMUK R9293 and BEXHM 2009.4.6) and the third is from the American *Hoplitosaurus* (USNM 4752). The anatomical position of splates is currently unknown since they are rare and no splates have been found in their natural position. Their deep dermal insertion base suggests a pre-caudal location since caudal armour has hollowed bases. The absence of a distinct, curved basal bone precludes them from the cervical half-rings, and the presacral dorsal spines had flat bases, which excludes splates from this position. Small plates with spines have been found in association with pectoral armour in *Gastonia*, and this may ultimately prove to be the position of these larger elements in *Polacanthus*.

A spine (GM 981.45, Delair 1982), was assigned to *Polacanthus* by Blows (1987). The anatomical position is unknown, but it is probably from the pectoral region, as suggested by the groove along the posterior edge and deep ventral dermal insertion. A similar spine, without the ventral insertion, is known from *Hoplitosaurus* (USNM 4752). The arrangement of splates and posterior grooved spines over the pectoral area of *Polacanthus* must have been complex.

The presacral trunk spines (Fig. 10 I-K) are small to large upright solid spines with flat, slightly asymmetrical, solid bases. They extended in a double row along the dorso-lateral aspect of the trunk. The holotype (NHMUK R175) was mounted with the tallest spines anterior of the mid-point along the row, and the lowest immediately anterior of the sacral shield. It is not known if William Fox found them in this position when excavating the holotype, so this arrangement remains to be confirmed in *Polacanthus*.

The sacral shield (Fig. 10 D-E, G-H) was a sheet of fused bone approximately a metre square covering the ilia and sacrum. It was about 10 mm thick and lay above the ilia with a slight gap in between, as described above (NHMUK R1926). The shield consists of interlocking, fused, small bony tubercles surrounding larger flat, keeled or pointed bosses (the coossified rosettes of Arbour et al., 2011). Distinct anterior-posteriorly aligned rows of these bosses can be traced across the dorsal surface of the shield, with the largest occurring along the lateral and posterior borders, the smallest occurring medially (Hulke, 1887). Arbour et al., (2011) placed this rosette-type morphology into Category 2, the second of three categories of sacral shield morphology. Category 2 shields supports the clade Polacanthidae (Arbour et al., 2011) for which they list the same taxa identified by Carpenter (2001) as the Polacanthidae (i.e. *Gargoyleosaurus*, *Gastonia*, *Mymoorapelta*, *Hylaeosaurus* and *Polacanthus*). The inclusion of *Hylaeosaurus* in Category 2 is problematic. There appears to be no evidence in the specimens of *Hylaeosaurus* for a sacral shield. The nature of *Hylaeosaurus* sacral armour remains unknown. Arbour et al. (2011) plotted the three categories of sacral shield morphology stratigraphically and found that dinosaurs with Category 2 shields were restricted to the late Jurassic and early to mid Cretaceous of Europe and the USA, and this supports Kirkland et al. (2013) that the Polacanthidae were replaced by nodosaurs bearing mostly Category 3 sacral shields by the mid Cretaceous in Europe. Arbour et al. (2011) also point out that one of the reasons for the failure of some ankylosaur analyses (e.g. Vickaryous et al., 2004) to recover the clade Polacanthidae may be the lack of armour characteristics used, in particular the sacral shield data.

Caudal plates (Fig. 12) are a double row of long, tall-peaked and laterally flattened dermal plates with asymmetric hollow-chambered bases. The hollow bases extend deep into the taller plates, the upper segment being solid. The plates are tallest at the tail root immediately behind the pelvis and descend in height and size along the length of the tail. These plates were laterally placed along the tail in some taxa where they are preserved *in situ* (e.g. *Dyoplosaurus,* Arbour et al., 2009) and this may have been the positioning of the plates in *Polacanthus*.

Acknowledgements.

We thank Julian Porter, Curator of Bexhill Museum for access to the specimen in his care; Sandra Chapman of the Natural History Museum, London, for access to specimens; David Brockhurst, finder of the Bexhill remains, for his advice on the discovery site, and

Steve Champan, works manager of the Ibstock-Ashdown Works, Bexhill on Sea for his co-operation in allowing collection of fossils from the quarry. Photographs by courtesy of Julian Porter, Dr. James Kirkland, and the London Natural History Museum.

Thanks also to Dr Latinka Hristova for her assistance with the figures, also Peter Austen and Marianne Hopwood for their assistance with Figure 1, and Paul Penkalski for reviewing the manuscript.

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Figure captions:

Fig. 1. Divisions of the Lower Cretaceous, showing the English Wessex and Wealden sub-basins, the ‘Bexhill *Polacanthus* Site’, the Isle of Wight *Polacanthus* sites and the *Hylaeosaurus* sites in their relative stratigraphical placement. Adapted from Rasnitsyn et al. (1998), Thomas and Batten (2001), Watson and Sincock (1992), Rawson et al. (1978). NS - Northiam Sandstone.

Fig. 2. BEXHM 2002.50.98 right jugal with ventral coronux of *Polacanthus foxii* from the Lower Cretaceous Valanginian of Bexhill, Sussex: (A) lateral view (showing location of orbit); (B) anterior view; (C) ventral view; (D); dorsal view; ant. – anterior; post – posterior; s - suture line. Scale bar is 10 mm.

Fig. 3. *Polacanthus foxii* cervical vertebrae from the Lower Cretaceous of the UK. A-C BEXHM 2002.50.84 a cervical centrum: (A) anterior view; (B) left lateral view; (C) posterior view; D-G BEXHM 2002.50.99 the left half of a cervical vertebra: (D) medial view; (E). detail of D, showing neural canal floor dipping into the centrum; (F) left lateral view; (G) anterior view; A-G from the Valanginian of Bexhill, Sussex; H-J NHMUK R9293 cervical vertebra: (H) anterior view; (I) right lateral view; (J) ventral view from the Barremian of the Isle of Wight. Scale bar is 30 mm.

Fig. 4. Dorsal vertebrae and rib of *Polacanthus foxii* from the Lower Cretaceous of the UK. A-D BEXHM 2002.50.87: (A) anterior view; (B) right lateral view; (C) posterior view; (D) dorsal view, from the Valanginian of Bexhill, Sussex; E-G NHMUK R9293: (E) anterior view; (F) right view; (G) left lateral view of different vertebrae, from the Barremian of the Isle of Wight; H-I Two views of a rib section, from the Valanginian of Bexhill, Sussex. Scale bar is 50 mm.

Fig. 5. Caudal vertebrae and haemal arches of *Polacanthus foxii*, A, B. BEXHM 2002.50.88 anterior (proximal) caudal vertebra: (A) posterior; (B) lateral views; (C) NHMUK R9293 anterior caudal vertebra in anterior view from the Barremian of the Isle of Wight; (D) BEXHM 2011.4 mid-caudal vertebra in right lateral view; (E) BEXHM 2002.50.82; (F) BEXHM 2002.50.81 two caudal haemal arches; G-H BEXHM 2002.50.85 mid-caudal vertebra: (G) anterior view; (H) left lateral view; I-J BEXHM 2002.50.23 mid-caudal vertebra: (I) posterior view; (J) right lateral view; K BEXHM 2002.50.86 mid-caudal vertebra in posterior view. All specimens except C. are from the Lower Cretaceous Valanginian of Bexhill, Sussex. Scale bar is 50 mm.

Fig.6. Ilia of polacanthid dinosaurs showing grooves on the dorsal surface: (A) BEXHM 1999.34.1.2 and BEXHM 1999.34.1 dorsal views of conjoining ilium fragments of *Polacanthus foxii* from the Lower Cretaceous Valanginian of Bexhill, Sussex; (B) Detail view of grooves shown in A; (C) MWC 1815 holotype ilium of *Mymoorapelta maysi* from the Upper Jurassic Morrison Formation of Colorado, USA. Scale bar is 50 mm.

Fig. 7. BEXHM 2009.4 anterior end of the right scapula of *Polacanthus foxii* from the Lower Cretaceous Valanginian of Bexhill, Sussex: (A) lateral view; (B) anterior (cranial) view; (C) medial view. a - eroded acromion, g - eroded glenoid, ne - non-eroded intact edge. Scale bar is 100 mm.

Fig. 8. Appendicular remains of *Polacanthus foxii* from the Lower Cretaceous of the UK. A-D BEXHM 2003.70.1 metapodial: (A, B). two lateral/medial views; (C) proximal end view; (D) distal end view; E. BEXHM 1999.34.5 proximal fragment of a humerus. F-I . BEXHM 2002.50.89 fibula: (F) lateral view; (G) medial view, (H) proximal end view; (I) distal end view; J-L. NHMUK R175 metatarsal block, (J) proximal end; (K, L) anterior/posterior views; from the Barremian of the Isle of Wight. MTA - metatarsal A; MTB - metatarsal B; T - tarsal

bone. A-I from the Valanginian of Bexhill, Sussex. Scale bar is 100 mm for A-E; H-L; for F-G it is 150 mm.

Fig. 9. Bones of the manus and pes of *Polacanthus foxii* from the Lower Cretaceous of the UK: A, B - BEXHM 2003.70 metapodial: (A) ventral view; (B) dorsal view; C, D - BEXHM 2002.50.70 metapodial: (C) ventral view; (D) lateral view; E - 2009.4.5 metapodial in dorsal view; F, G - BEXHM 2002.50.120 terminal phalanx: (F) dorsal view; (G) ventral view; H, I - BEXHM 2002.50.69 terminal phalanx: (H) dorsal view; (I) ventral view, showing pathological erosion of bone; J-K - NMHUK R175 terminal phalanx: (J) dorsal view; (K) ventral view; (L) NHMUK R9293 terminal phalanx in dorsal view. A-I from the Valanginian of Bexhill, Sussex; J-L from the Barremian of the Isle of Wight. Scale bar is 50 mm

Fig. 10. Pre-caudal armour of *Polacanthus foxii* from the Lower Cretaceous Valanginian of Bexhill, Sussex. A-C BEXHM 1999.34.2 base of a cervical spine, part of the half-ring: (A) lateral or medial view to show spine above and the basal bone below extending ventrally beyond the spine; (B) ventral (basal) view; (C) anterior or posterior view showing the basal bone curving downwards in both lateral and medial directions; D-E BEXHM 2002.50.58 a sacral shield fragment: (D) ventral view; (E) dorsal view; (F) BEXHM 2002.50.65 ossicle (scute) in dorsal view showing "reabsorption pit" in upper margin (see text for details); G-H BEXHM 2002.50.102 a sacral shield fragment: (G) dorsal view; (H) ventral view; I-K BEXHM 2002.50.83 presacral spine: (I) dorsal view; (J) lateral view; (K) ventral view. Scale bar is 50 mm.

Fig. 11. Splates of Lower Cretaceous armoured dinosaurs, A-C. BEXHM 2009.4.6 large splate of *Polacanthus foxii*: (A) lateral view; (B) medial view; (C) ventral view; from the Valanginian of Bexhill, Sussex; (D) - NHMUK R9293 a large splate of *Polacanthus foxii*

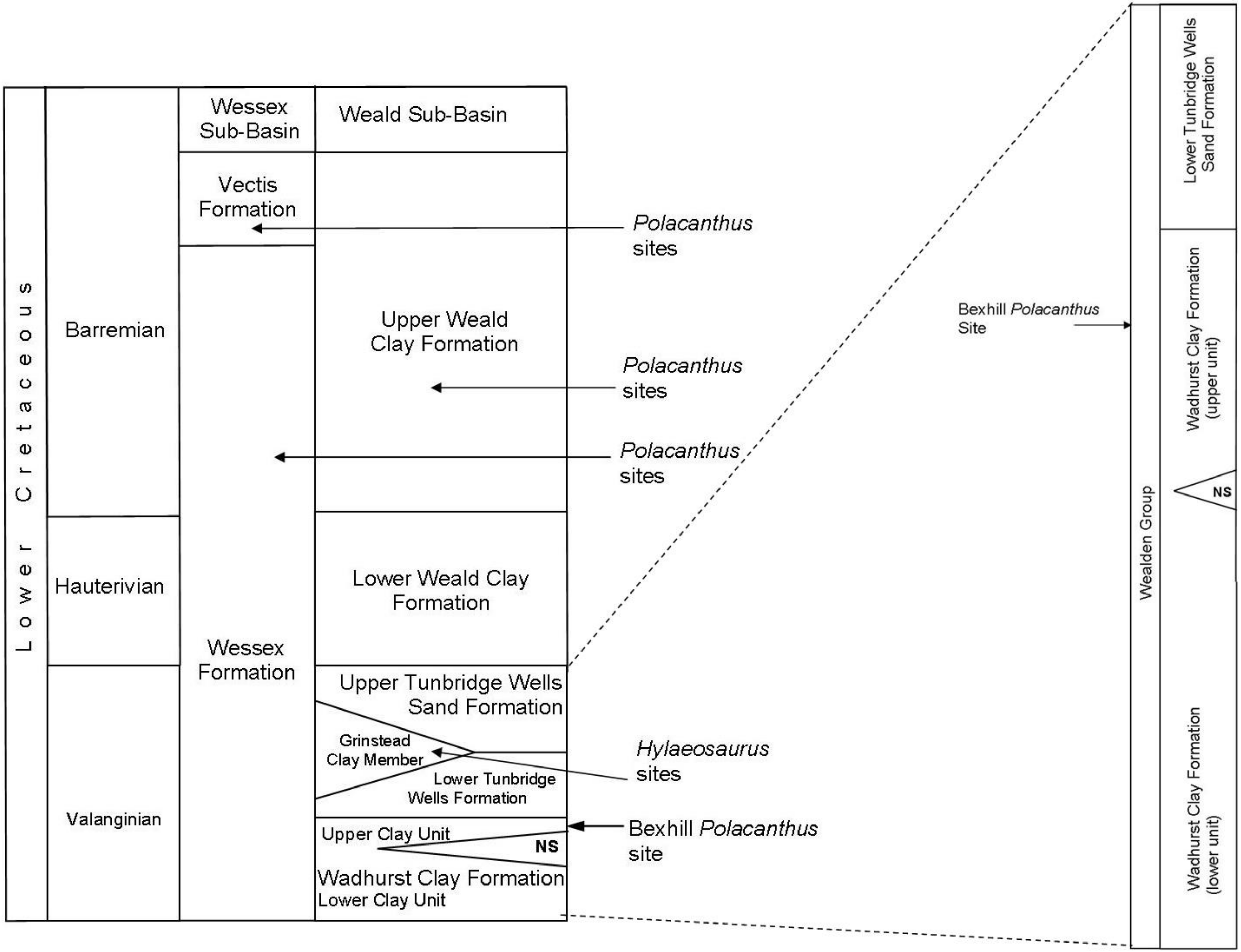
from the Barremian of the Isle of Wight; (E) - USNM 4752 a large splate of *Hoplitosaurus marshi*, from the Lakota Formation of South Dakota, USA. Scale bar is 100 mm.

Fig. 12. Caudal armour of *Polacanthus foxii* from the Lower Cretaceous of the UK; A-C. BEXHM 2002.50.122 a mid-caudal plate: (A) lateral view; (B) medial view; (C) ventral view, from the Valanginian of Bexhill, East Sussex; D-F. NHMUK R9293 proximal (anterior) caudal plates from the Barremian of the Isle of Wight: (D) medial view; (E) ventral view of one plate; (F) possible medial view of a second plate. Scale bar is 100 mm.

Fig. 13. Features of *Polacanthus* and *Hylaeosaurus* from the Lower Cretaceous of the UK (see text for details). A-B. NHMUK R9293 Separate cervical-ring spine of *Polacanthus*: (A) lateral view, showing basal bone extending down below the spine; (B) ventral view; (C) NHMUK OR3775 Holotype of *Hylaeosaurus* separate cervical neck-ring spine showing basal bone extending down below the spine; (D) NHMUK OR3775 Holotype of *Hylaeosaurus* detail of left scapula-coracoid articulation; (E) NHMUK 2602a proximal end of scapula of *Hylaeosaurus* showing large acromion (above) and unfused coracoid articulation surface; (F) NHMUK 2584 proximal end of scapula of *Hylaeosaurus* showing large acromion (to the right); (G) NHMUK OR3775 Holotype of *Hylaeosaurus* sketch of anterior skeleton and armour in situ; c coracoid, ca cervical armour, cv cervical vertebrae, pa pectoral armour, r ribs, s scapula and sk skull fragment. Scale bar is 100 mm for A to F and 300 mm for G

Fig. 14. Angular with dermal ossification in armoured dinosaurs: (A) NMHUK cast of ROM 1215 *Edmontonia* mature mandible from the Upper Cretaceous of Alberta, Canada, to show extent and size of the dermal ossification (Russell 1940); (B) NHMUK R9293 *Polacanthus* immature angular to same scale as A to show external dermal ossification; C-D. NHMUK R9293 *Polacanthus* angular in detail, (C) ventral view and (D) medial view (i.e. the surface

that attaches to the jaw), from the Lower Cretaceous Barremian of the Isle of Wight. Scale bars A, B is 50 mm, C, D is 20 mm.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Upper Tunbridge Wells Sand Formation
Grinstead Clay Member
Lower Tunbridge Wells Formation
Upper Clay Unit
NS
Wadhurst Clay Formation
Lower Clay Unit
Polacanthus sites
Polacanthus sites
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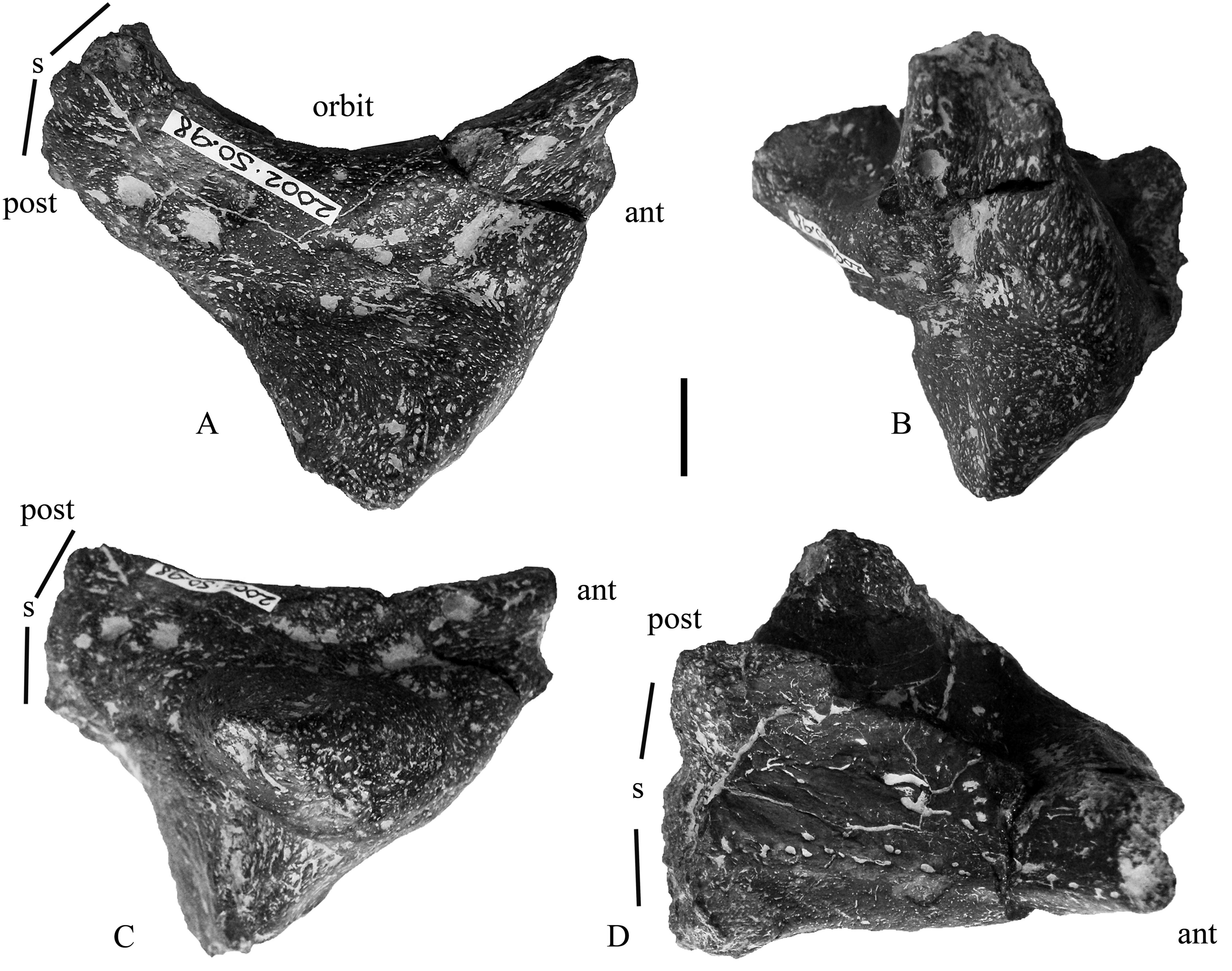
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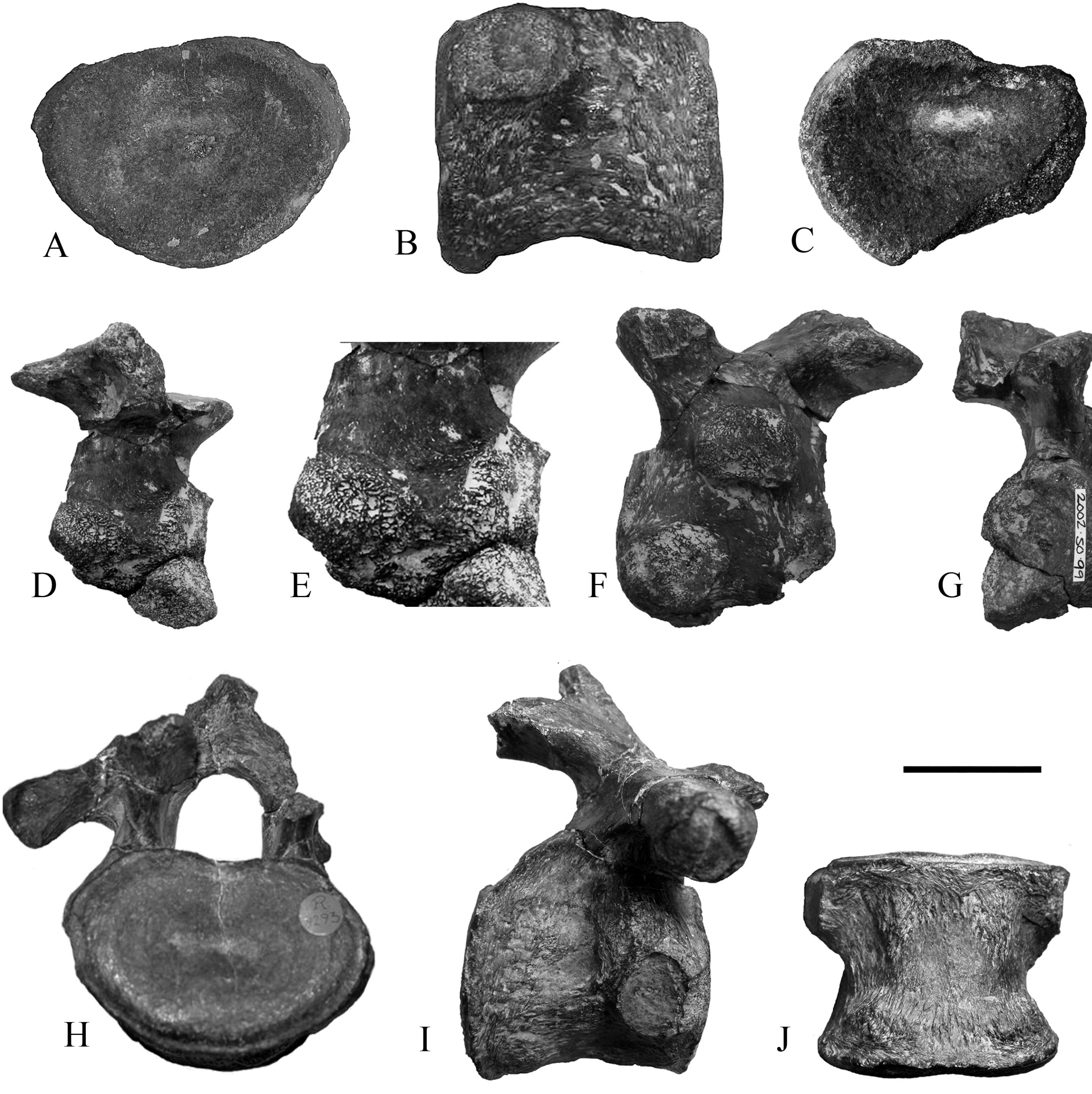
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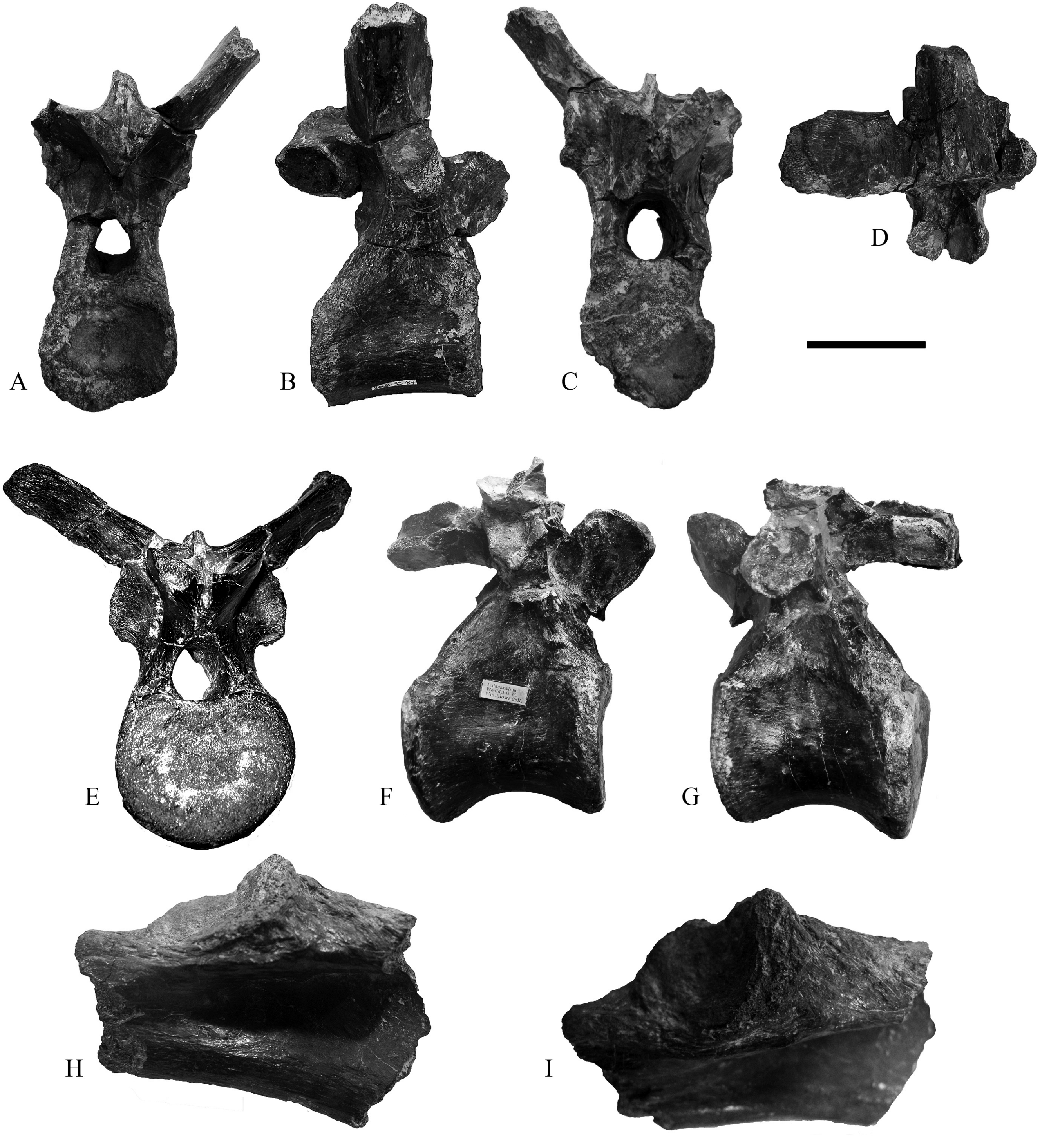
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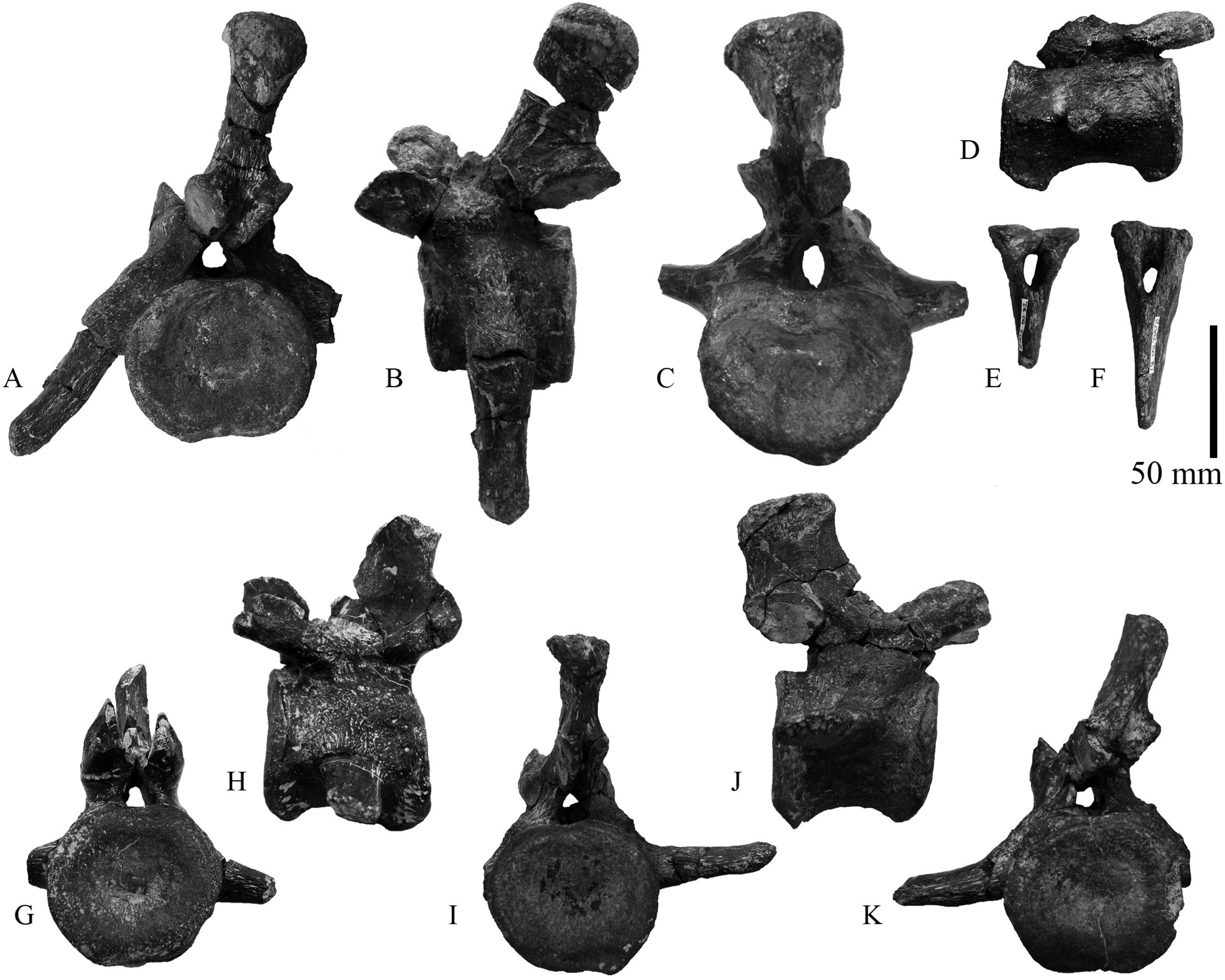
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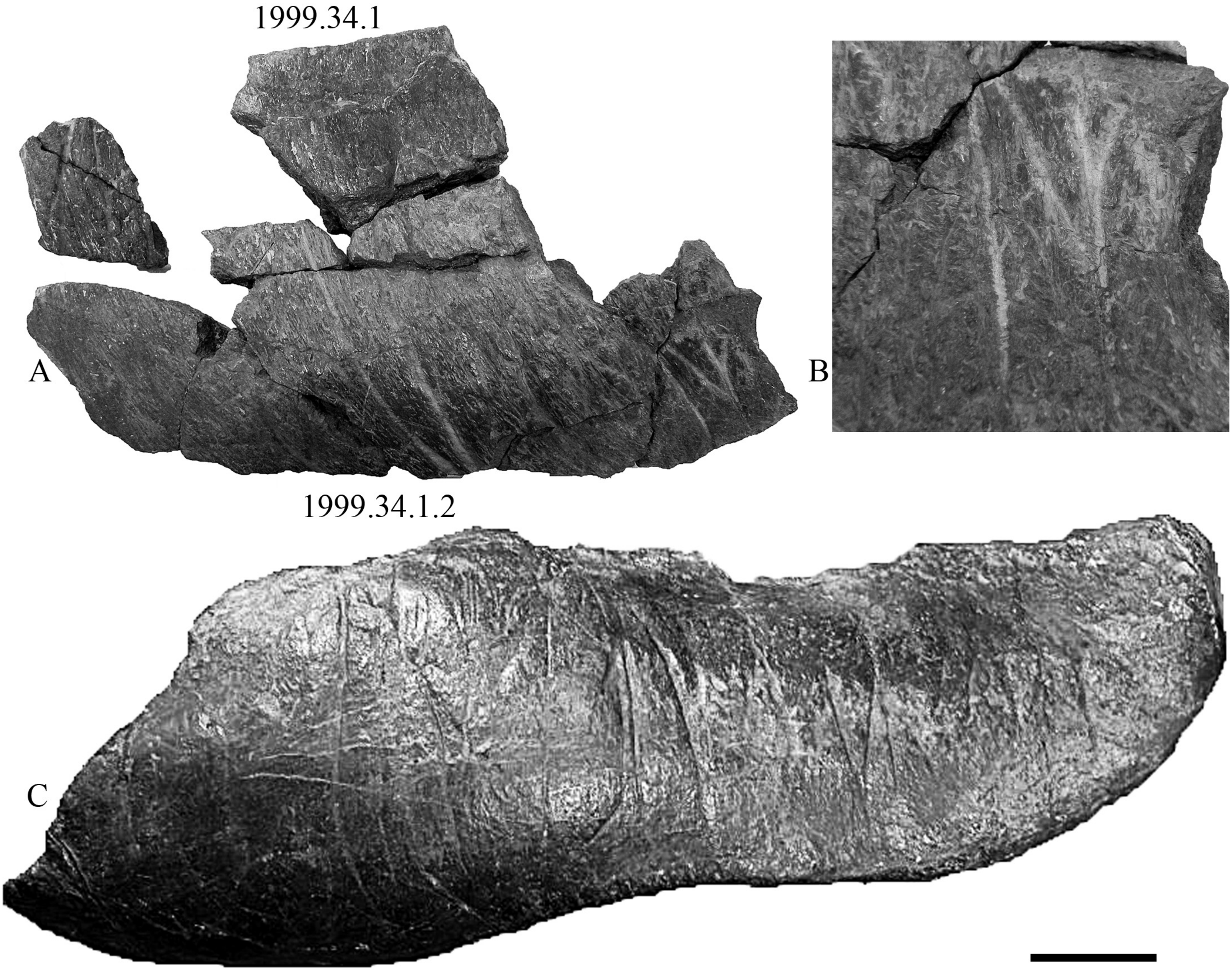
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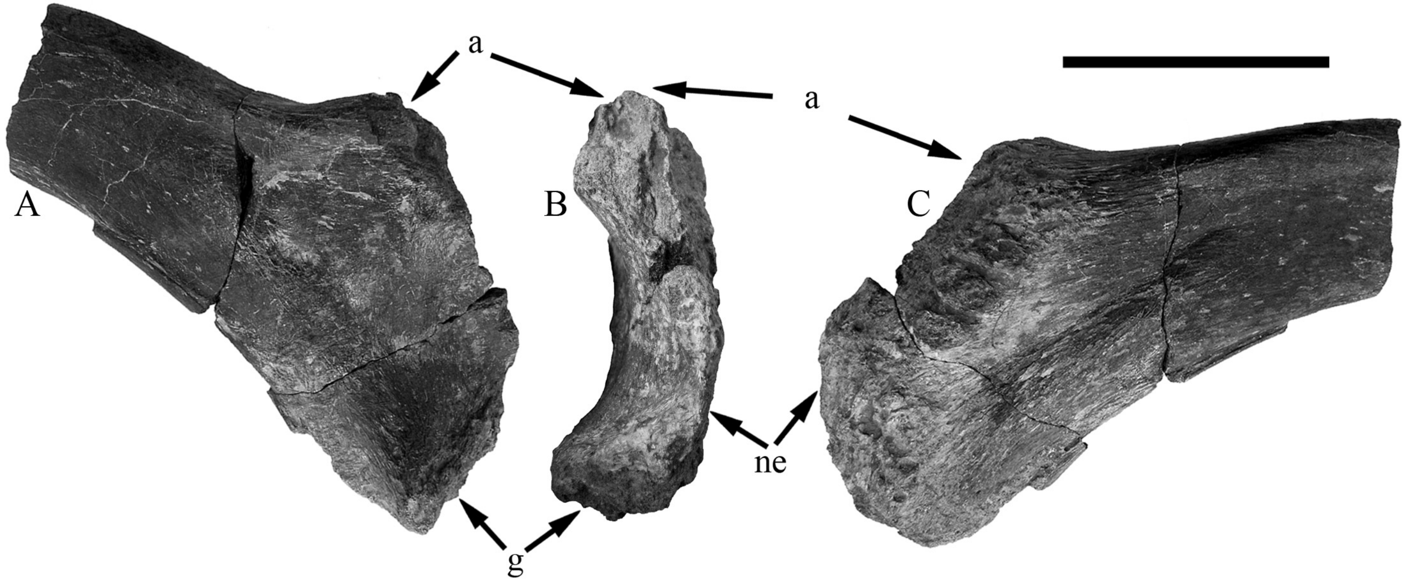
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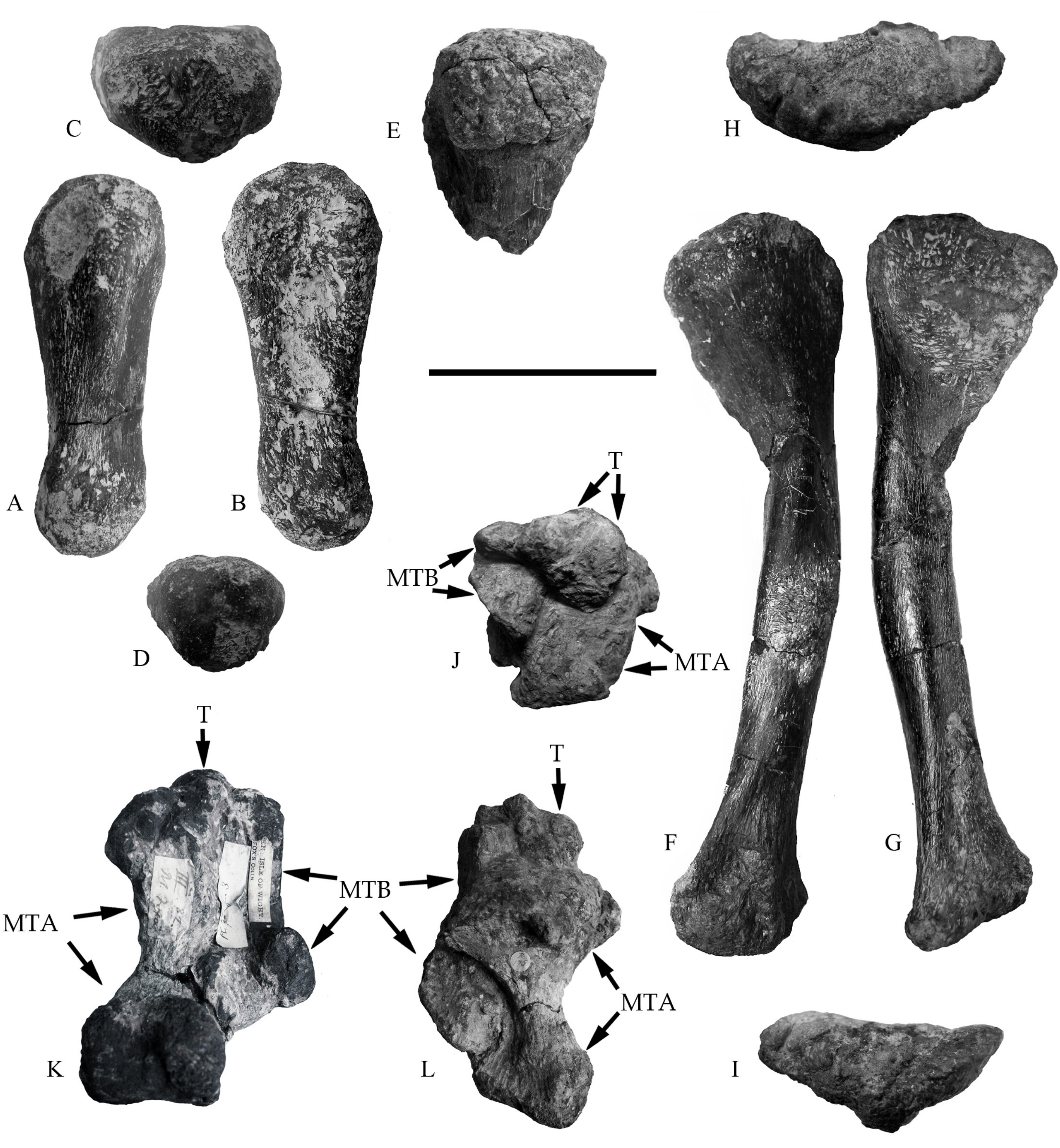
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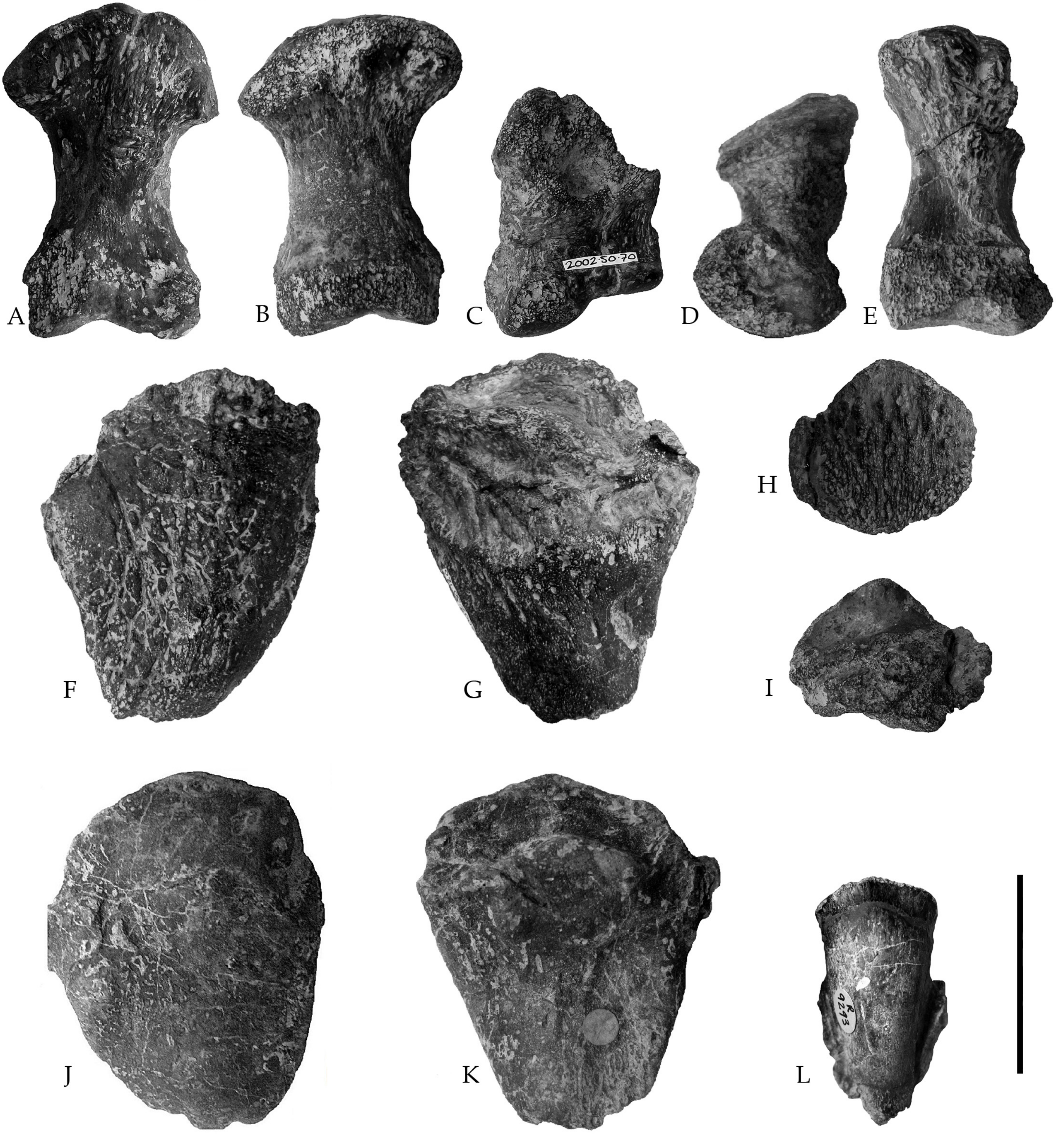
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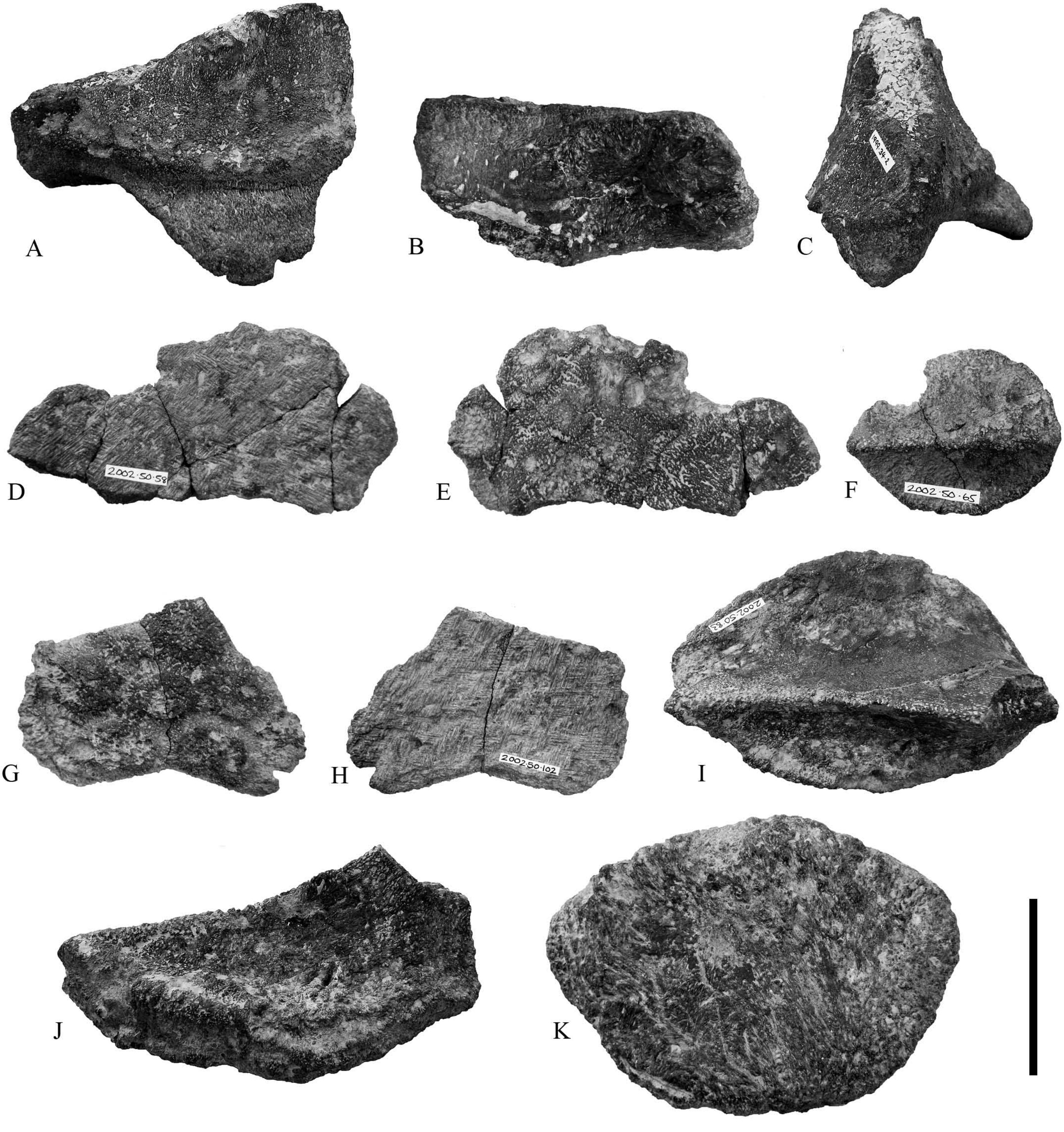
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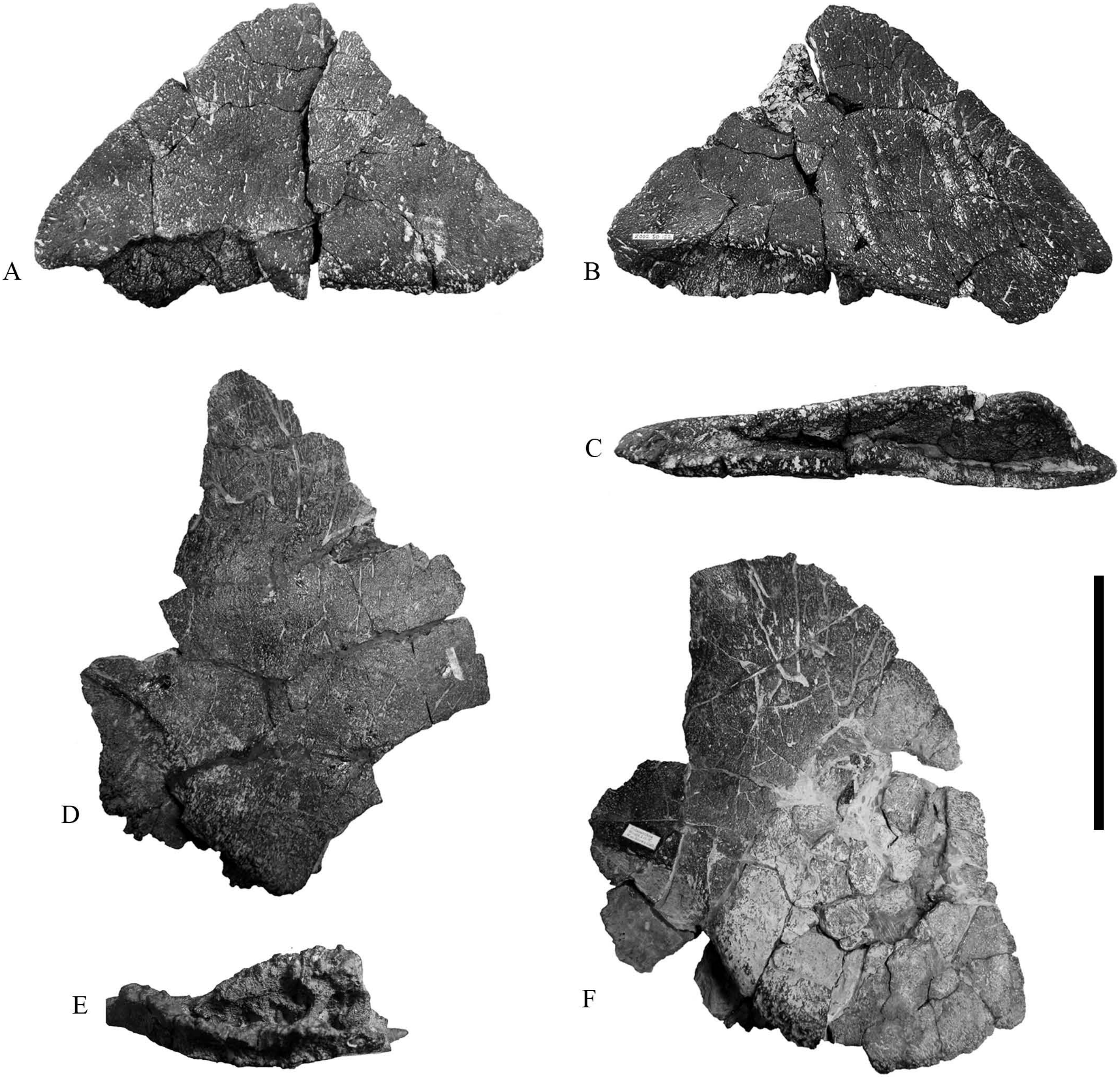
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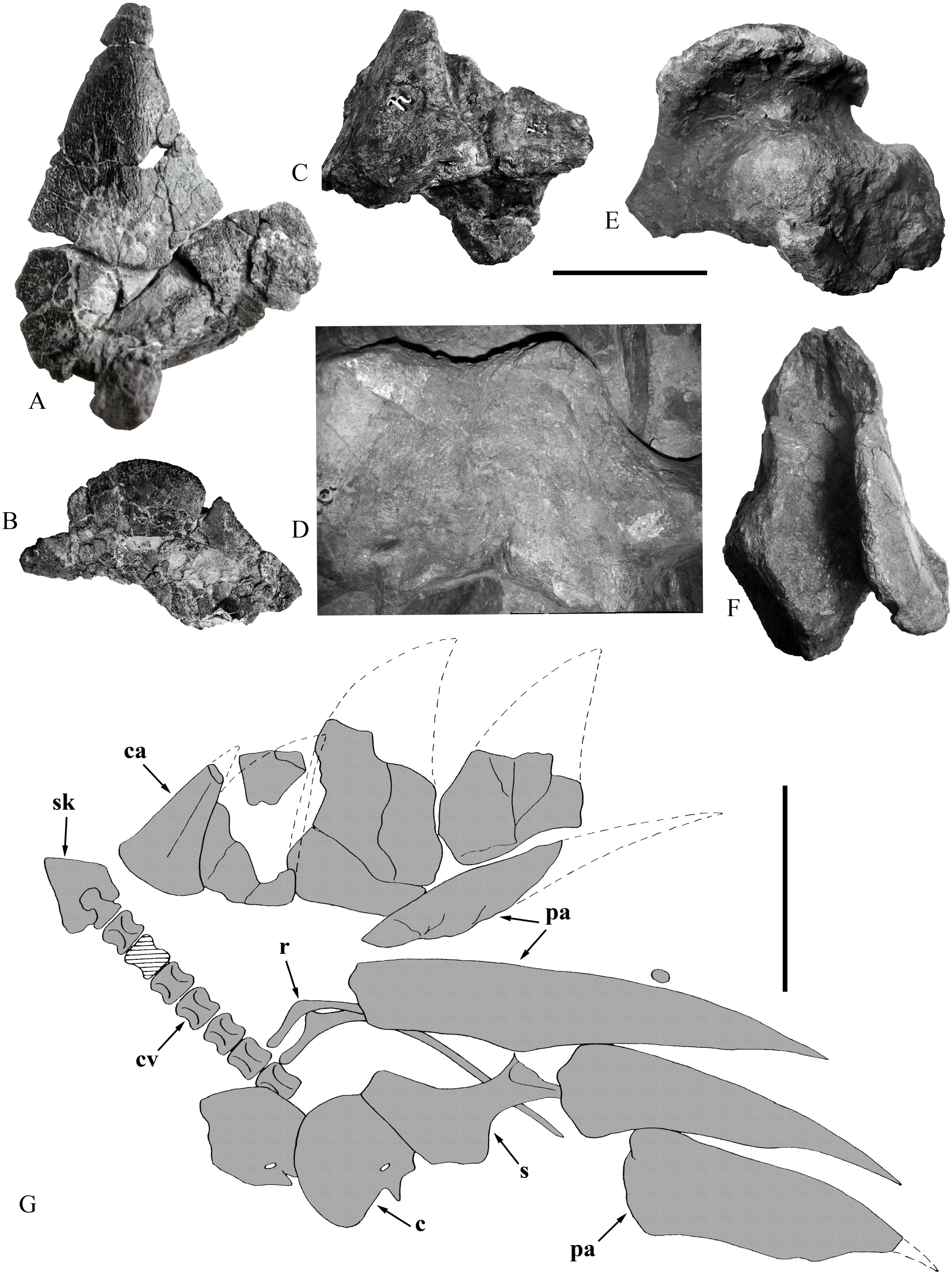
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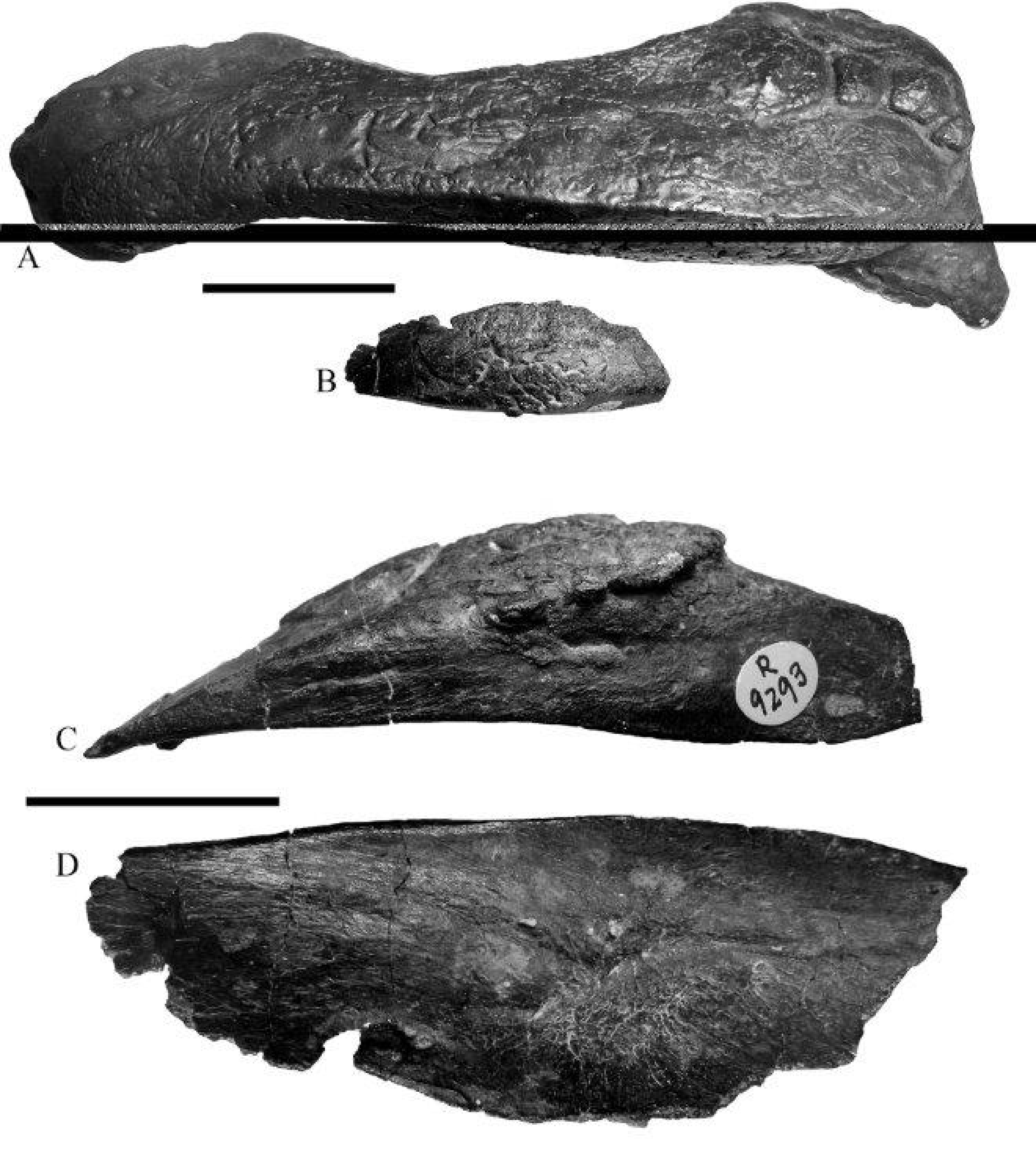
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