Notice of nodosaur (Dinosauria, Ankylosauria) remains from the mid-Cretaceous of Cambridge, England, with comments on cervical half-ring armour.

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Abstract.

Three pieces from cervical half-rings of an immature nodosaur, part of a nodosaurid presacral rod and some post-cranial osteoderms from the Cretaceous of Cambridge were studied at the Booth Museum of Natural History, Brighton, UK. Two of the three half-ring elements show dorsal ridge morphologies distinct from each other, and all three have unfused sutured lateral borders. It is possible they may be derived from the same animal. Comparison with other material from the Cretaceous of Europe, USA and Asia indicates the presence of a large nodosaurid in the Cambridge Greensand fauna, with cervical half-ring morphologies similar to North American taxa, but unlike any previously known from the European Cretaceous.

Key words: Ankylosaur, Nodosauridae, Armour, Cretaceous, Greensand, England

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1. Introduction

Ankylosaur remains are rare in England, particularly from the mid to late-Cretaceous (Albian to Maastrichtian). Some are recorded from the Cambridge Greensand of Cambridgeshire (basal Cenomanian)(Nopcsa, 1923; Seeley, 1879, Pereda-Suberbiola and Barrett, 1999). This material includes vertebrae, limb elements and dermal armour (osteoderms). Most of the osteoderms are single isolated ridged scutes probably from the animal's trunk and caudal regions. A few pieces of cervical armour also exist from the Cambridge Greensand, including some elements not previously described.

Ankylosaur cervical armour is rare worldwide, due in part because individual animals had fewer cervical elements than other osteoderms, and because cervical armour was frequently lost along with the skull after death. Differences in cervical armour morphology may have taxonomic significance, therefore all specimens should be recorded and described. The remains described here are part of a collection from the Cambridge Greensands of Cambridge present in the Booth Museum of Natural History, Brighton, Sussex. Who found the specimens and when is unknown, but Mr A. F. Griffith (1856-1933) became the owner. It is possible did not collected them himself. He was occasionally Chairman of the Booth Museum and a member of Brighton Corporation (now Brighton Council). In 1883 he presented a large collection of Cambridge Greensand fossils, including the nodosaur remains, to the Brighton Museum and Art Gallery. They were subsequently moved to the Booth Museum of Natural History in 1970 (Adams, 2011). The bones were in a collection of marine reptiles, and Mr Andrew Ottaway, a local amateur palaeontologist, recognised the specimens as being from an armoured dinosaur and suspecting they may not have been identified as such, brought them to the author's attention.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York; BGS GSM, British geological Survey, Keyworth, Nottingham; BMBG Booth Museum Brighton-Geology, Sussex; CEUM College of Eastern Utah, Prehistoric Museum, Price, Utah; CMN, Canadian Museum of Nature, Ottawa; FMNH Field Museum of Natural History, Chicago, Illinois; GI SPS Geological Institute Section of Palaeontology and Stratigraphy, Academy of sciences of the Mongolian people's Republic, Ulan Bator; KUVP University of Kansas, Museum of Natural History, Lawrence; NHMUK London Natural History Museum; PIUW Paläontologisches Institut der Universität Wien; ROM Royal Ontario Museum, Toronto; SMC, Sedgwick Museum, Cambridge University; USNM Nation Museum of Natural History (formerly United States National Museum), Washington DC; YPM, Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

2. Geological Setting

The Cambridge Greensand of Cambridgeshire is a marine stratigraphic unit at the base of the Chalk Marl of early Cenomanian age in the UK. The bed is derived from rock and fossil material, including dinosaur remains, eroded from an uplifting of the Gault at the end of the Albian. These late Albian fossils were redeposited during the Cenomanian in a matrix of sand and chalky marl with phosphatic nodules (Chatwin, 1961). As derived and redeposited material, lower Cenomanian UK dinosaur remains are relatively rare, fragmentary and often poorly preserved, but includes Sauropodomorpha, Ornithopoda (Seeley, 1876, 1879) and Ankylosauria (Pereda-Suberbiola and Barrett, 1999). Unwin (2001) gives an review of the Cambridge Greensand sedimentology and palaeontology and notes that important collections of these remanié fossils exist in a number of UK and European museums including the Booth Museum, Brighton.

3. Systematics

Ornithischia Seeley, 1887

Thyreophora Nopcsa, 1915 (sensu Norman 1984)

Ankylosauria Osborn, 1923

Family Nodosauridae Marsh, 1890

Nodosauridae Indet.

(Figs. 1 and 2)

3.1. Material

BMBG 004989 a cervical half-ring segment; BMBG 020531 a cervical half-ring segment; BMBG 020533 a cervical half-ring segment; BMBG 004992 the anterior-most vertebral centrum of the presacral rod (synsacrum); BMBG 020532 a post-cranial osteoderm and BMBG 004993 a small post-cranial dermal osteoderm.

3.2. Description

BMBG 004989 (Fig. 1A) is a dorso-ventrally flattened element with a raised dorsal ridge. It has two lateral unfused sutured edges (shown as "s" in Figure 1A). These sutured edges are set at an angle of about 40 degrees relative to each other. This gives the bone a wedge shape in dorsal view, and this suggests the element was positioned at a bend in the half-ring. One lateral edge is incomplete and the bone loss continues along the ?posterior edge. The natural maximum width, i.e. 85mm, is measured between the two suture surfaces. The dorsal ridge is a low, narrow raised keel, off-set to one side, being significantly closer and almost parallel to one of the lateral sutured edges. The ridge has no distinctive features that separate it from the basal bone, so it appears to arise directly from the basal bone. This ridge is 40mm long as preserved, the posterior end being eroded. The ?anterior end of the ridge is better preserved, with about 20mm of flat bone between the termination of the ridge and the ?anterior edge. The ventral surface is basically flat.

BMBG 020531 (Fig. 1B) is a dorso-ventrally flattened element with a tall robust dorsal spine-like ridge. The whole element is cranio-caudally longer (119mm) than wide (100mm), giving a slightly rectangular overall shape when viewed dorsally. The two suture edges are slightly angled from each other by about 10 degrees. One anterior corner is naturally curved inwards making the ?anterior edge narrower (50mm) than the ?posterior edge (94mm). The dorsal ridge is placed slightly off-set from centre between the two sutured lateral edges (marked "s" on Figure 1B). This ridge is 65mm long as preserved, and is positioned close to the ?posterior edge but separated from the ?anterior edge by 30mm of flat bone. The ridge is 106mm tall as preserved, the peak of the ridge is now eroded. This spine-like ridge has a step in the bone at the base marking the distinction between the ridge and the basal bone. The ventral surface is basically flat. The distinct differences in the morphology of the two elements BMBG 004989 and BMBG 020531 indicates they were not a matching pair, therefore they occupied different asymmetrical positions either within the same half-ring, or perhaps come from different half-rings.

BMBG 020533 (Fig. $1C_{1-2}$) is a dorso-ventrally flattened element with no dorsal ridges. It is laterally wider (100mm) than its cranio-caudal depth (63mm) giving it a rectangular shape when viewed dorsally or ventrally. There is only one suture edge (one of the short edges, shown as "s" on figure 1C). The other short edge, although being damaged, does not show any evidence of sutures, suggesting it may be the lateral-most terminal element.

BMBG 004992 is the anterior-most dorsal vertebral centrum of the presacral rod (the synsacrum)(Fig. $2A_{1-2}$). This specimen consists of most of the centrum broken off the synsacrum to which it was fused. It also lacks the neural arch and processes. The anterior articular end is almost round and flat. The lateral and ventral surfaces are also virtually flat, lacking the inward curvature seen in unfused dorsal vertebral centra. The specimen is 63mm long as preserved, but this is just the anterior end of a long synsacrum.

BMBG 020532 is a post-cranial osteoderm (Fig. $2B_{1\text{-}2}$) from the trunk or tail. The specimen has a tear drop shape in dorsal view. It has a centrally placed low dorsal keel dividing the specimen into two approximately equal halves. This keel extends posteriorly beyond the base and narrows to a point, which is missing from erosion. The interpretation that the point is posterior is based on similar osteoderms found in situ in some nodosaurs from the USA. Maximum length of the specimen measured along the keel is 102mm as preserved (tip missing) and the specimen has a maximum width of 89mm. The dorsal keel is distinguished from the base by a shallow step-like ridge which is typical of such dermal armour throughout the group.

BMBG 004993 is a smaller (75mm by 50mm) dermal osteoderm with a low dorsal keel leading to a posterior point that also overlaps the base.

4. Discussion

The two families of the Ankylosauria, i.e. the Nodosauridae and the Ankylosauridae (Coombs, 1978), had cervical and pectoral armour to protect the neck and shoulder regions. Cervical half-rings of osteoderms are synapomorphic for the Ankylosauria. They were positioned as a collar across the dorsal surface of the neck, and were curved to fit around the dorsal neck contours. The throat region of the animal was not protected, and the term half-ring is used to indicate that only the dorsal surface was thus covered. Typically, nodosaurids and ankylosaurids had two such cervical half-rings, one behind the other; i.e. half-ring 1 (h.r.1) which was positioned cranially to half-ring 2 (h.r.2). Half-ring 1 was usually smaller with either less or smaller bony elements than half-ring 2. Between the half-rings, and particularly between half-ring 1 and the skull, were bands of skin with very small granular armour, often called ossicles, which allowed flexibility of the neck, as seen in the two specimens with *in situ* armour, i.e. the nodosaurid *Edmontonia rugosidens* (AMNH

5665)(Matthew 1922) and the ankylosaurid *Scolosaurus cutleri* (NHMUK R5161)(Penkalski and Blows, 2013).

Several different types of cervical half-rings are known from a range of ankylosaur taxa, mostly from North American and Asian specimens. They consist of variations in a basal bone which forms a strip beneath a series of dorsal ridges and spines.

In some nodosaurids, e.g *Stegopelta, Silvisaurus* and *Sauropelta* (Fig. 3A-D) the half-ring consists of flat units, mostly three on each side, which are fused along their lateral edges creating a band (Carpenter and Kirkland, 1998). The two halves, i.e. the left and right quarter-rings, may not be fused along the midline (Fig. 3A-D). Each bone element bears a dorsally placed keeled spine or ridge of various morphologies. The most medially placed unit is usually small with a very low keeled spine. The central unit of the three is commonly larger usually with the tallest spine of the ring projecting dorsolaterally, and the lateral unit is intermediate in size with a large keeled spine projecting laterally (Fig. 3A-D). The dorsal spines may be developed from separate centres of ossification and fused to the basal bone (e.g. h.r.1 of *Euoplocephalus*), or they may appear to arise directly from the dorsal surface of the basal unit (as in the Bexhill specimens). The separate dorsal osteoderms may not fuse centrally to the basal bone but can be off-set so they overhang the boarder of the basal bone in some half-rings (as in YPM 5178 *Sauropelta*, Fig. 3E, Ostrom, 1970). A similar arrangement to *Silvisaurus* and *Sauropelta* occurs in the Jurassic nodosaur *Gargoyleosaurus* where the second half-ring is composed of two quarter-rings unfused along the mid-line. However, the first ring has two quarter-rings composed of two ridged units each, separated medially by a single, unfused, mid-line scute (Kilbourne and Carpenter, 2005).

Some taxa had unfused separate basal bone segments in mature animals. The individual segments are found separately and show no evidence of sutured edges. Each segment supports laterally flattened dorsal spines which collectively have profiles ranging from very low to very tall and peaked. This morphology is found in *Polacanthus* (e.g. NHMUK R9293, Blows 1987)(Fig. 3F) and *Gastonia* (e.g. CEUM 1215 and CEUM 1016, Kirkland, 1998; Blows, 2001). The anatomical location of each separate segment on the neck and shoulder regions is usually lost due to post-mortem displacement. The extent of fusion of nodosaurid half-rings in mature animals can vary, and there may be a gradient involving different degrees of fusion, from unfused to fully fused, in different taxa.

Edmontonia and *Panoplosaurus* are nodosaurids with cervical half-rings composed of three or four rectangular, sub-triangular or oblong osteoderms on each side supporting low dorsal ridges positioned approximately centrally on each osteoderm. The ridges are slightly peaked posteriorly in some, the orientation based on observation of the armour *in situ* in *Edmontonia rugosidens* (AMNH 5665, Fig. 4). *Edmontonia* had two cervical half-rings which are followed posteriorly over the root of the neck and shoulder region by a third large cervico-pectoral half-ring. In AMNH 5665 (Fig. 4) the first (1CR) and second (2CR) cervical half-rings are composed of bilateral medial, central and lateral elements which are flat, low ridged plates joined along their lateral borders. The lateral elements of the second half-ring (2CR) and the cervico-pectoral half-ring behind it bear large spines. These terminal spines were massive and tall, extending to varying distances either laterally or anteriorly, as part of a row of lateral spines protecting the shoulders and flanks on both sides of the animal. In *Panoplosaurus* the nature of the third half-ring is unclear due to poor preservation, but the large lateral spines typical of *Edmontonia* are absent in *Panoplosaurus* (Carpenter, 1990).

Ankylosaurids had two cervical half-rings consisting of a fused basal bone creating a band across the neck with low keeled scutes mounted on the dorsal surface. The North American *Euoplocephalus* (Fig. 5A) and the Asian *Saichania* (Fig. 5B) are the best known taxa with preserved half-rings. Penkalski (2001) identified two first half-ring classes (or morphotypes) and four or five distinct subtypes existing across the Ankylosauridae. The two classes are those with six dorsal osteoderms, and those with either two or four osteoderms. The dorsal osteoderm morphology varied consistently between the first (six osteoderm) and the second (two or four osteoderm) classes indicating that it was not just a distinction based on osteoderm number. Penkalski discussed the relationship between the two classes of half-ring and individual variation, sexual dimorphism, ontogeny and taxonomy, concluding that the differences are unlikely to be due to ontogeny or individual variation, but may be due to sexual dimorphism and taxonomy (Penkalski, 2001). Some of the specimens which are generally accepted as referable to *Euoplocephalus* may actually belong to new undescribed taxa, or may be referable to *Scolosaurus* (e.g. USNM 7943, Fig. 5C)(Penkalski, 2001, Penkalski and Blows 2013). The holotype of *Euoplocephalus* (CMN 0210, Fig. 5A, Lambe, 1902) has a first cervical half-ring with six scutes (only five are preserved): two medial, two dorsolateral, and two lateral. A very similar morphology is seen in the neck ring of the Asian ankylosurid *Saichania* (Fig.5B)(Maryańska, 1977). Ankylosaurid cervical half-rings are made from separate pieces of bone fused together by sutures to form a continuous band (Fig. 5C1, 6A). This feature is also shared with some nodosaurs (e.g. *Sauropelta*, Fig. 3E, Ostrom, 1970, Carpenter and Kirkland 1998). The two cervical half-rings of the North American ankylosaur *Scolosaurus cutleri* (Fig. 6B, 6C) are very different from *Euoplocephalus* (Penkalski and Blows, 2013). *Scolosaurus* half-rings have cranio-caudally broader basal bones with two dorsally mounted osteoderms which appear rounded in shape with low peaks, in particular in half-ring 2 (Fig, 6C) which is similar to Fig. 5C1. The lateral terminal units of these half-rings are large low-keeled spines with posteriorly projected peaks.

The three pieces of cervical half-rings described here (BMBG 004989, BMBG 020531 and BMBG 020533)(Fig. 1A-C) represent pieces of what could be the same cervical half-ring, or elements from either half-ring of the same animal. Comparing the general morphology of the three pieces within each quarter-ring of other taxa suggests that BMBG

004989 may have been placed medially, BMBG 020531 may be centrally placed within the quarter-ring and BMBG 020533 may have been the lateral terminal element, but these positions cannot be confirmed. The pieces do not directly fit together but the presence of non-fused natural suture edges on all three pieces indicates that they were from an immature animal, and it would have grown to a substantially larger size prior to complete fusion. If these pieces do represent parts of the same quarter-ring, it would have been at least twice the width (55cm) of the three pieces put together (27.5cm). When further growth into maturity is taken into account, these specimens are an indication of a very large animal. The angles set between the edges of BMBG 004989 particularly, but also BMBG 020531, indicates that the half-ring was bent at an angle. Such angles in neck rings are rare. The second half-ring of *Gargoyleosaurus* shows an angle of about 35 degrees (Kilbourne and Carpenter, 2005), and a sharper angle is seen in one half-ring of *Silivisaurus* (Eaton, 1960; Carpenter and Kirkland, 1998) and the European *Hungarosaurus* (Ősi, 2005).

Cervical ring elements of the mainland European nodosaur *Struthiosaurus* (Campanian to Maastrichtian) are known from various specimens, and consists of tall lateral spines on a basal bone strip which is dorsally ornamented with small low pointed elements medially (Fig. 7A). This is a very different morphology to the Booth Museum specimens, indicating further the absence of *Struthiosaurus* in the late Cretaceous of the UK.

Osteoderms from other UK nodosaur cervical half-rings (SMC B55522, B55523, B55525)(Fig. 7B) from the Cambridge Greensands are described by Pereda-Suberbiola and Barrett (1999). These are mostly low ridged osteoderms which are joined by their lateral borders to form parts of several half-rings. The neck ring element SCM B55525 shows an angle of about 70 degrees (Fig. 7B). The difference in morphology between the Sedgwick and Booth Museum specimens, notably the extent and directions of the dorsal ridges, suggest that they represent different nodosaur taxa. The dinosaur fauna of the Cambridge Greensand may have been diverse enough to include at least two different nodosaur taxa, possibly more.

The nodosaur remains from the Cambridge Greensand deposits have been referred to the taxa *Anoplosaurus curtonotus* (Seeley, 1879) and *Acanthopholis horridus* (Huxley, 1867). Although *Anoplosaurus* is regarded as a valid taxon (Pereda-Suberbiola and Barrett, 1999), there is no dermal armour recorded, therefore it is not possible to determine the nature of its cervical armour. Pereda-Suberbiola and Barrett (1999) identified the juvenile nature of the holotype of *Anoplosaurus* and discussed the absence of armour as an ontogenetic feature seen in the very early stages of nodosaur development. The Booth Museum specimens are also juvenile, but represent an ontogenetic stage later than that seen in the *Anoplosaurus* holotype. The Booth Museum armour may be from an *Anoplosaurus* older than the holotype, i.e. at the armour development stage, but this cannot be confirmed.

Acanthopholis is regarded as *nomen dubium* (Coombs, 1978; Suberbiola and Barrett, 1999) since it is based on fragmentary material with insufficient characters to determine its taxonomic status below family level. Unfortunately, the Booth Museum material is insufficient to resolve the problem of taxonomic status of these animals. However, it does indicate that a large nodosaur with a solid cervical half-rings, very similar to some North American taxa, was part of the mid-Cretaceous terrestrial fauna of the UK.

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Explanation of figures

Fig. 1. Nodosaur cervical armour fragments from the Cambridge Greensand of Cambridgshire: (a1-3) BMBG 004989 in (a1) dorsal view, (a2) ventral view, (a3) ? posterior view; (b1-4) BMBG 020531 in (b1) dorsal view, (b2) ventral view, (b3) ?posterior view, (b4) lateral view (sp = spine; bb = basal bone); (c1-2) BMBG 020533 in (c1) dorsal view, (c2) ventral view. "s" = unfused suture edge. Scale bar for a1, a2, b4, c1, c2 = 20mm, for a3, b1-b3 = 15mm.

Fig. 2. Nodosaur bones from the Cambridge Greensand of Cambridgeshire: (a1-2) BMBG 004992 anterior-most dorsal vertebral centrum of the presacral rod (anterior-most part of synsacrum) in (a1) semi-lateral view, (a2) anterior view; (b1-2) BMBG 020532 post-cranial osteoderm in (b1) dorsal view, (b2) lateral view showing spine over-hanging beyond the base. Scale bar for A = 25mm, B = 20mm.

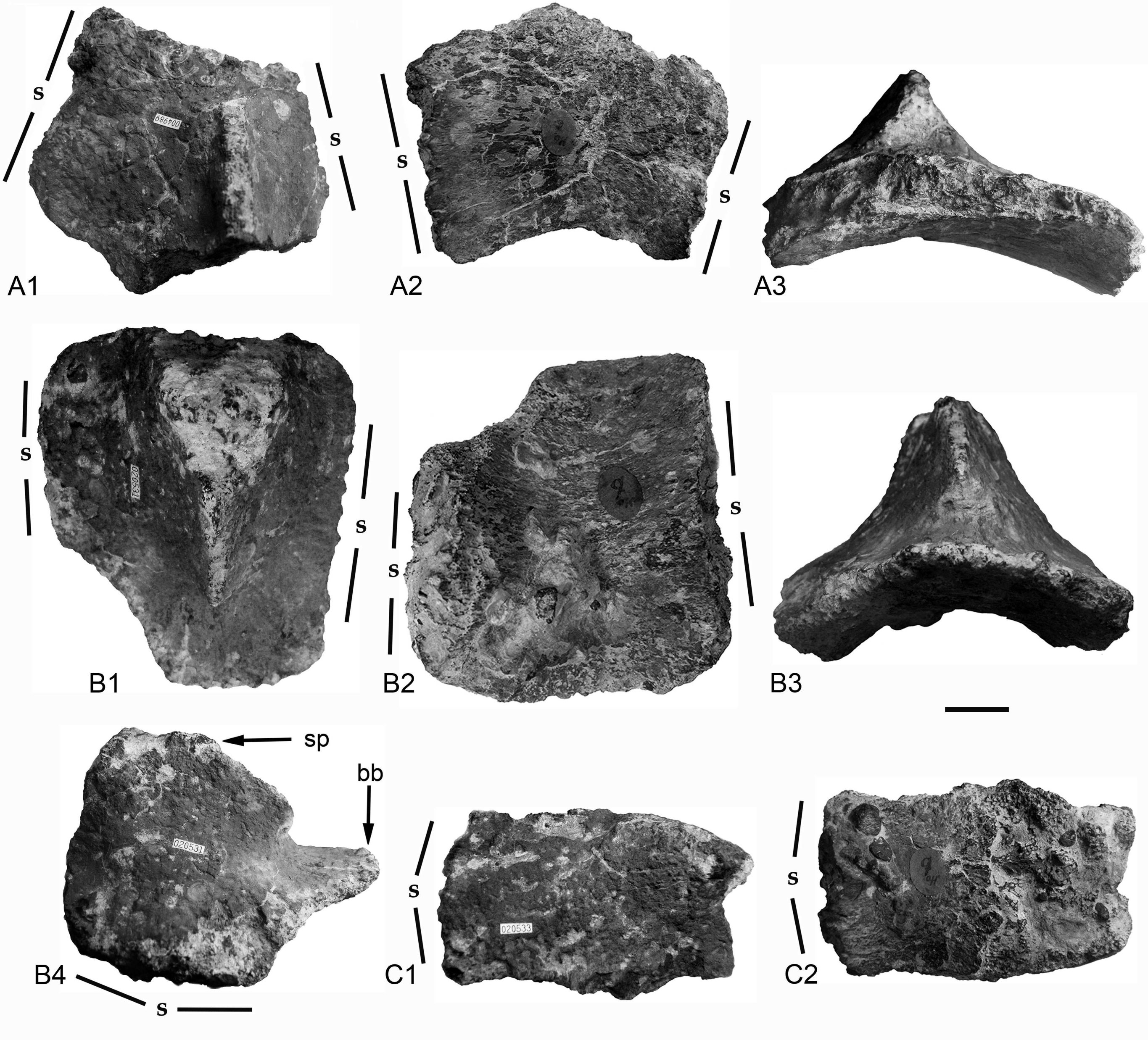
Fig. 3. Cervico-pectoral armour of Lower Cretaceous nodosaurid dinosaurs: (a) YPM 5178 *Sauropelta edwardsi* from Wyoming, USA, cervical half-ring in anterior view; (b) FMNH UR88 *Stegopelta landerensis* from Wyoming, USA, cervical half-ring in posterior view. (c) and (d) KUVP 10296 *Silvisaurus condrayi* from Kansas, USA, two cervical half-rings in anterior views; (e) YPM 5178 *Sauropelta edwardsi* cervical half-ring in ventral view to show large spines overlapping the edge of the basal bone; (f) NHMUK R9293 *Polacanthus foxii* cervico-pectoral spine from the Isle of Wight, UK. a-d redrawn from Carpenter and Kirkland 1998. Scale bar for a = 80mm, b = 50mm, for c, d, e = 40mm and for f = 30mm.

Fig. 4. AMNH 5665 *Edmontonia rugosidens* cervico-pectoral armour in situ from the Upper Cretaceous of Alberta, Canada, in dorsal view. Image # 310269 courtesy of American Museum of Natural History Library. Scale bar = 20mm.

Fig. 5. Cervical armour of Upper Cretaceous ankylosaurid dinosaurs from North America and Asia: (a) CMN 0210 Holotype cervical ring of *Euoplocephalus tatus* from Alberta, Canada, redrawn from Penkalski (2001) with one medial osteoderms replaced; (b) GI SPS 100/151 Holotype cervical ring of *Saichania chulsanensis* from the Gobi desert of Mongolia, in anterior view (redrawn from Maryańska 1977); (c1-2) USNM 7943 cervical half-ring from Montana, USA, usually referred to *Euoplocephalus* but may be *Scolosaurus* or an unnamed taxon in (c1) dorsal view showing two round osteoderms with central peaks on a basal bone, a similar arrangement to the second half-ring of *Scolosaurus* (Fig. 6c), (c2) ventral view of the basal bone. Scale bar for a = 50mm, for b = 70mm, for c = 30mm.

Fig. 6. Cervical armour of Upper Cretaceous ankylosaurid dinosaurs from North America: (a) ROM 5406 *Euoplocephalus tatus* cervical half-ring in dorsal view showing basal bone (bb) and osteoderms (os); (b) NHMUK R5161 *Scolosaurus cutleri*. B. First cervical half-ring in dorsal view; (c) Second cervical half-ring in dorsal view (pe 2nd cr = posterior edge of second cervical ring). Scale bar for a = 20mm, for b = 30mm, for c = 45mm.

Fig. 7. Cervical armour of Cretaceous European nodosaurs: (a) PIUW 2349/13 *Struthiosaurus austriacus* ornamented fragment of second half-ring from Austria, in dorsal view, redrawn after Seeley (1881); (b) SCM B55525 Indeterminate nodosaur from the Cambridge Greensand of Cambridgeshire, UK, in dorsal view showing a bend. Scale bar for a = 25mm, b = 10mm.



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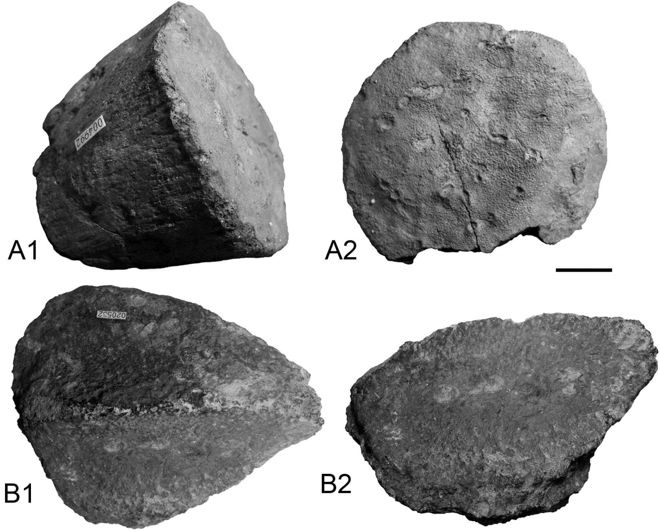
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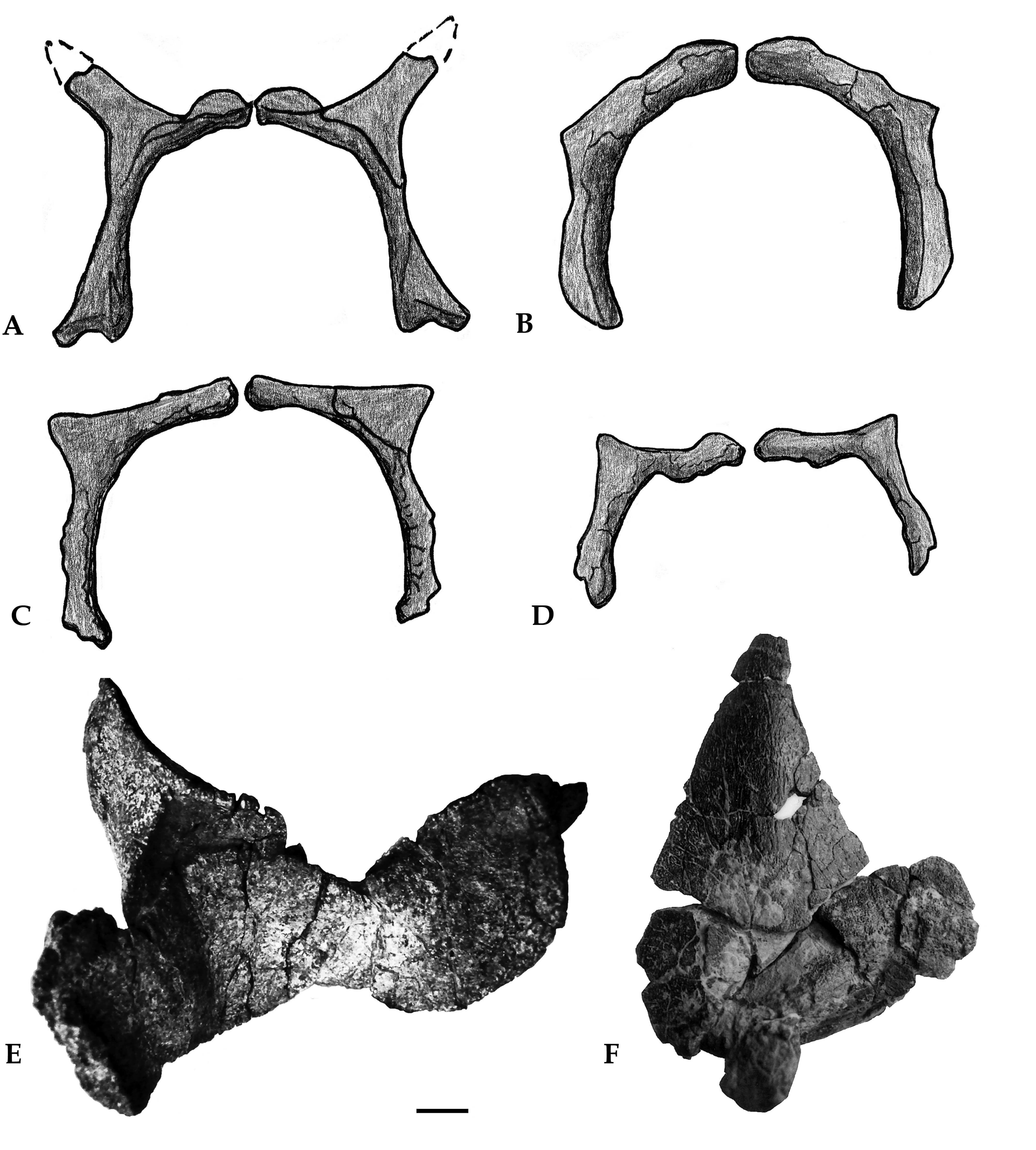
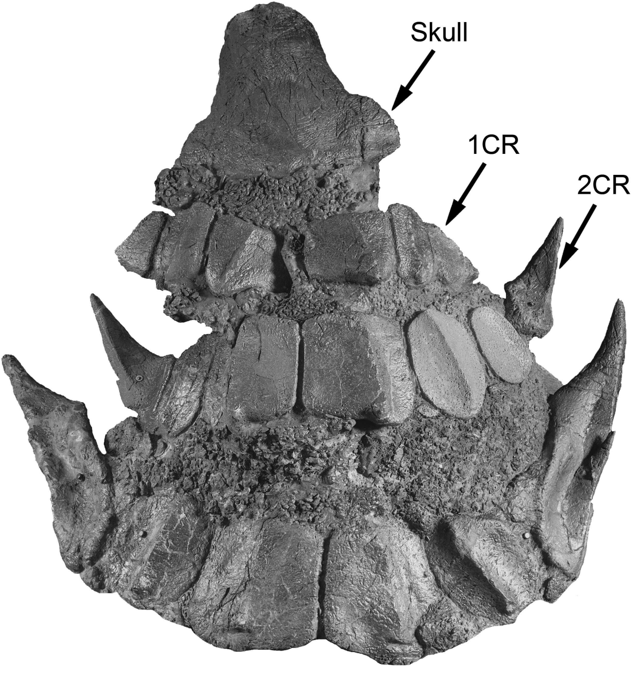
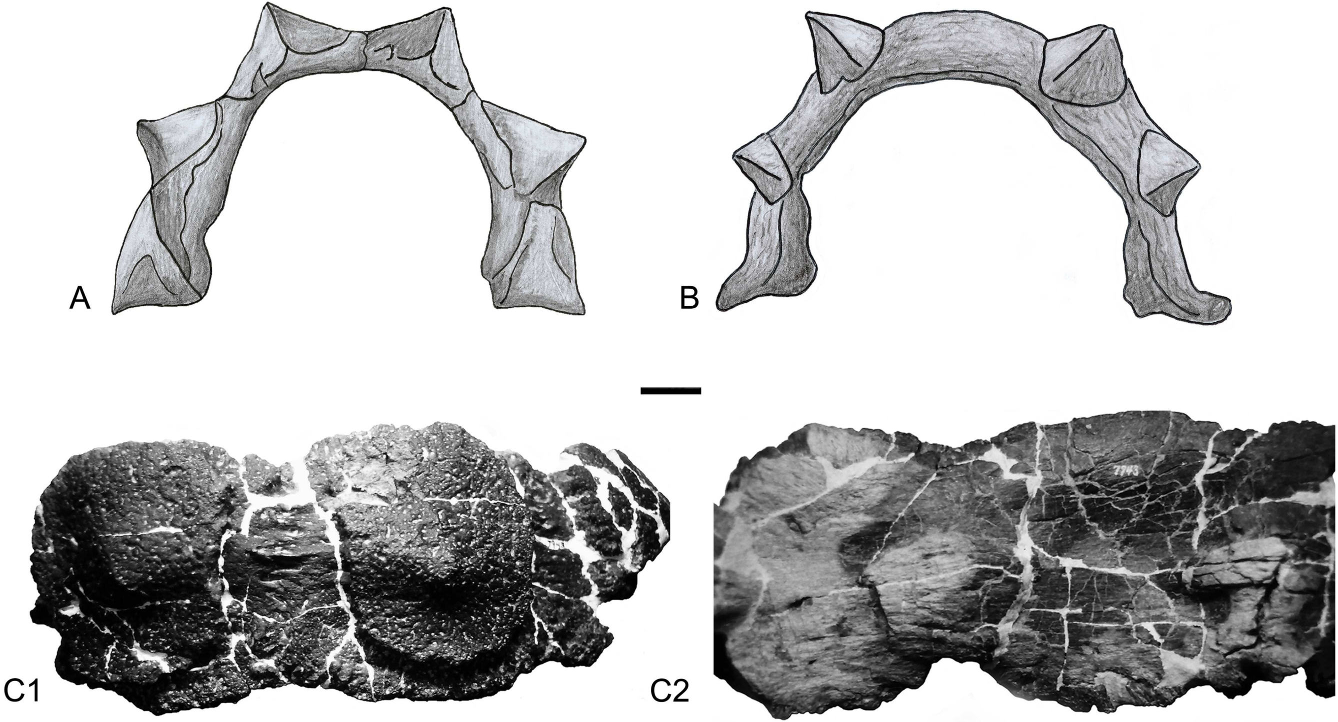
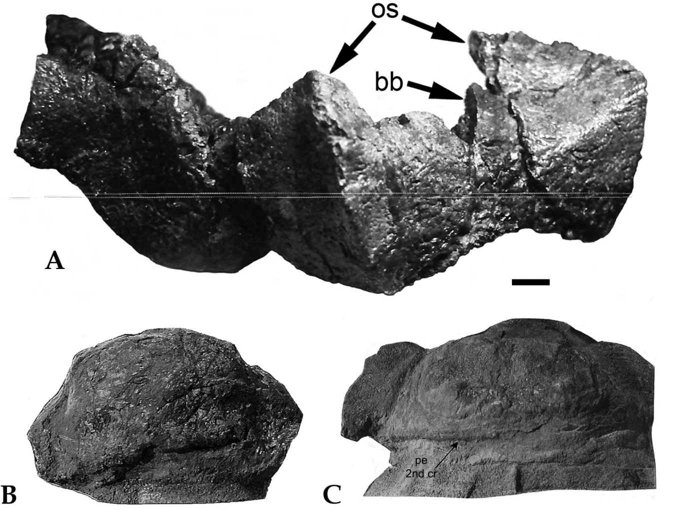
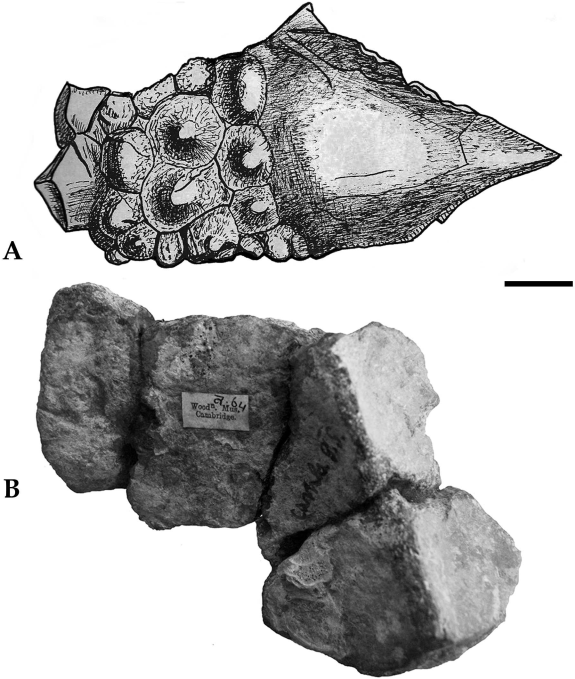
B1
B2


A
B
C
D
E
F


Skull
1CR
2CR


A
B
C1
C2


os
bb
A
B
pe
2nd cr
C


A
B
Woodⁿ. Mus.
Cambridge.