

New Teeth of Nodosaurid Ankylosaurs from the Lower Cretaceous of Southern England

Authors: Blows, William T., and Honeysett, Kerri

Source: *Acta Palaeontologica Polonica*, 59(4) : 835-841

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2012.0131>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

New teeth of nodosaurid ankylosaurs from the Lower Cretaceous of Southern England

WILLIAM T. BLOWS and KERRI HONEYSETT



Blows, W.T. and Honeysett, K. 2014. New teeth of nodosaurid ankylosaurs from the Lower Cretaceous of Southern England. *Acta Palaeontologica Polonica* 59 (4): 835–841.

We present new nodosaurid teeth from the Valanginian of Bexhill, Sussex and the Barremian of the Isle of Wight, the first from the Lower Cretaceous of the United Kingdom. Teeth found during the mid-1800s from the Valanginian and ascribed to the nodosaurid *Hylaeosaurus* are probably from sauropod dinosaurs. The Isle of Wight tooth could possibly be referred to *Polacanthus foxii*, the teeth of which are unknown. These new English nodosaurid teeth are similar to those of North American and European Jurassic to Late Cretaceous nodosaurids, especially the American *Gastonia*, *Texasetes*, *Mymoorapelta*, *Gargoyleosaurus*, and the European *Hungarosaurus*.

Key words: Dinosauria, Nodosauridae, *Polacanthus*, ankylosaur, Valanginian, Barremian, Cretaceous, England.

William T. Blows [w.t.blows@city.ac.uk], School of Health Sciences, City University, London, EC1A 7QN, UK;

Kerri Honeysett [kerrihoneysett@googlemail.com], 10 Camperdown Street, Bexhill on Sea, East Sussex, TN39 5BE, UK.

Received 8 November 2012, accepted 11 March 2013, available online 13 March 2013.

Copyright © 2014 W.T. Blows and K. Honeysett. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

There are few skull and tooth remains of armoured dinosaurs (Thyreophora) from the Jurassic and Cretaceous of the United Kingdom. Some partial skull elements have been referred to ankylosaurs, including the maxilla of *Priodontognathus phillipsii* Seeley, 1875, which may be Jurassic or Early Cretaceous (CAMSM B53408, see Galton 1980b); the holotype left mandible with teeth of the nodosaurid *Sarcolestes leedsi* from the Middle Jurassic of Fletton, Cambridgeshire (NHMUK R2682; Lydekker 1893); a single nodosaurid tooth from the Berriasian of Dorset (NHMUK R2940; Galton 1980a, 1983a); a neurocranium fragment of ?*Polacanthus* from the Lower Cretaceous of Southern England (CAMSM X26242; Norman and Faiers 1996); skull material that is part of the holotype of the nodosaurid *Hylaeosaurus armatus* (NHMUK R3775; Carpenter 2001); and a small incomplete left dentary without teeth, one of the paralectotypes of the nodosaurid *Anoplosaurus curtonotus*, from the upper Albian (CAMSM B55670; Seeley 1879; Pereda-Suberbiola and Barrett 1999). The only teeth found with these skull elements are the crowns of a few unerupted teeth in *Priodontognathus* (Galton 1980b) and *Sarcolestes* (Galton 1983b). All these taxa are referable to the Nodosauridae.

It is surprising that teeth were not found in association with the partial nodosaurid skeletons referred to *Polacanthus* and *Hylaeosaurus* (Blows 1998; Pereda-Suberbiola

1993). Isolated teeth from the same strata as *Hylaeosaurus* (NHMUK 2310, NHMUK 3326, NHMUK R739, BMBG 004179, BMBG 013516) were tentatively assigned to *Hylaeosaurus* by Mantell (1841) and Owen (1857). Mantell's illustration (1841: pl. 6: 9–11) is a single tooth subsequently destroyed by lapidary. Mantell (1841) labels this as “The tooth of an unknown reptile, probably referable to the *Hylaeosaurus*”, but the illustration suggests this referral was inaccurate. Owen's illustrations (1857: pl. 8: 6–9) are of three similar teeth “In the British Museum”. Owen did not give museum registration numbers, so it is not possible to match these illustrations with specimens, except NHMUK 2310 (possibly Owen 1857: pl. 8: 9). All these teeth generally show no ankylosaur characters and are now referred to the sauropod taxon *Pleurocoelus* (Upchurch et al. 2011).

Lower Cretaceous nodosaurid teeth are also rare in the rest of Europe despite the presence of postcranial remains of *Polacanthus* from the uppermost Valanginian to Barremian of Spain (Pereda-Suberbiola et al. 2007). Two teeth of an indeterminate nodosaurid from deposits of Hauterivian to Barremian age in Spain were described by Canudo et al. (2004, 2010).

Some nodosaurid teeth are known from the Albian to Maastrichtian of England and elsewhere in Europe. There are three isolated teeth (BGS GSM 109045, 109046 in part, 109051) from the Lower Chalk (Cenomanian) of Folkestone, Kent, UK. These were formerly referred to the nodosaurid *Acanthopholis horridus* (Huxley, 1867), as were other frag-

mentary armoured dinosaur remains from the same location. However, this taxon is now considered to be a *nomen dubium* (Pereda-Suberbiola and Barrett 1999) and therefore this material, along with the teeth, is referred to as *Nodosauridae* indeterminate. From various Late Cretaceous localities in Europe some teeth have been referred to the small nodosaurid dinosaur *Struthiosaurus* Bunzel, 1870, e.g., three isolated teeth (UM2 OLV-D18–20 CV) from the lower Campanian of Southern France (Garcia and Pereda-Suberbiola 2003). Finally, the holotype of the nodosaurid *Hungarosaurus tormai* Ősi, 2005 from the upper Santonian western Hungary comprises 21 teeth, with cranial and postcranial remains.

The new teeth (Figs. 1, 2) are a single almost complete tooth from the Barremian of the Isle of Wight (IWCMS 5390) and two complete teeth and a crown of a third tooth from the Valanginian of Bexhill, Sussex (BEXHM 2008.16, 2008.16.2, 2008.16.1). They were found in the 1990s. Although these isolated teeth are regarded as nodosaurid, they cannot currently be assigned with certainty to any of the UK Lower Cretaceous nodosaurids *Polacanthus*, *Hylaeosaurus*, or *Priodontognathus* until more complete remains with associated dentition are found.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; BEXHM, Bexhill Museum, Bexhill-on-Sea, Sussex, UK; BGS GSM, British Geological Survey, Keyworth, Nottingham, UK; BMBG, Booth Museum Brighton-Geology, Sussex, UK; CAMSM, Sedgwick Museum, Cambridge University, Cambridge, UK; CEUM, College of Eastern Utah Prehistoric Museum, Price, USA; DMNH, Denver Museum of Natural History, USA; GI SPS Geological Institute Section of Palaeontology and Stratigraphy, Academy of Sciences of the Mongolian People's Republic, Ulaan Bator, Mongolia; IWCMS, Isle of Wight Council Museum Service, Dinosaur Isle, Sandown, Isle of Wight, UK; IVPP Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China; MCNA, Museo de Ciencias Naturales de Alava/Arabako Natur Zeintzen Museum, Vitoria-Gasteiz, Spain; MPZ, Museum of Paleontology of the University of Zaragoza, Zaragoza, Spain; NHMUK, Natural History Museum, London, UK; NMC, Canadian Museum of Nature, Ottawa, Canada; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; UM2, Université des Sciences et Techniques du Languedoc, Montpellier, France; USNM, United States National Museum (National Museum of Natural History), Washington, USA; ZIN PH, Paleoherpétological Collection, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

Other abbreviations.—PDB, plant debris bed.

Geological setting

The tooth from the Isle of Wight (Fig. 1) comes from a plant debris bed (PDB) in the Sudmoor Point Sandstone Member

of the Wessex Formation (Barremian, Lower Cretaceous) exposed as sea cliffs at Sudmoor Point, east of Brook Chine, Isle of Wight (Naish and Martill 2001). PDBs may be the product of flooding across a flat terrestrial plain creating a debris flow (Sweetman and Insole 2010). The debris is a mixture of large quantities of surface plant detritus, and the remains of vertebrate and invertebrate animals, and it is transported by water before being deposited in depressions.

The other teeth (BEXHM 2008.16, 2008.16.1, 2008.16.2; Fig. 2) were found in 1997 in Pevensy Pit, Ashdown Quarry, Bexhill, East Sussex by David Brockhurst, an employee of Ashdown Quarry and notable amateur palaeontologist. These teeth come from conglomerate approximately mid-way within the Wadhurst Clay Formation (Valanginian, Hastings Beds). The layer is 60 mm thick at its maximum, and often occurs in lenses. This bed has also yielded remains of the fish *Hybodus* and *Lepidotes*, and of various reptiles, including small dinosaurs and the crocodile *Goniopholis* (Austen et al. 2010).

Systematic palaeontology

Ornithischia Seeley, 1887

Thyreophora Nopcsa, 1915 (sensu Norman 1984)

Ankylosauria Osborn, 1923

Family Nodosauridae Marsh, 1890

Nodosauridae indet.

Figs. 1, 2.

Material.—IWCMS 5390, one tooth from the Barremian of the Isle of Wight, UK; BEXHM 2008.16, 2008.16.1, 2008.16.2, two complete teeth and one crown from the Valanginian of Bexhill, Sussex, UK.

Description.—IWCMS 5390 (Fig. 1) consists of a nearly complete, well preserved and largely unworn tooth crown, with most of the root attached. The total preserved height is 17 mm, the maximum width at the crown base is 6 mm,

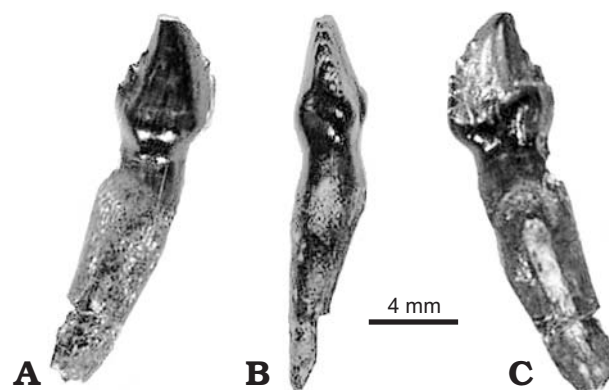


Fig. 1. Three views of a nodosaurid (possibly *Polacanthus*) tooth, IWCMS 5390, from the Barremian (Lower Cretaceous) Wessex Formation, Isle of Wight, UK. In ?labial (A), distal (B), and ?lingual (C) views.

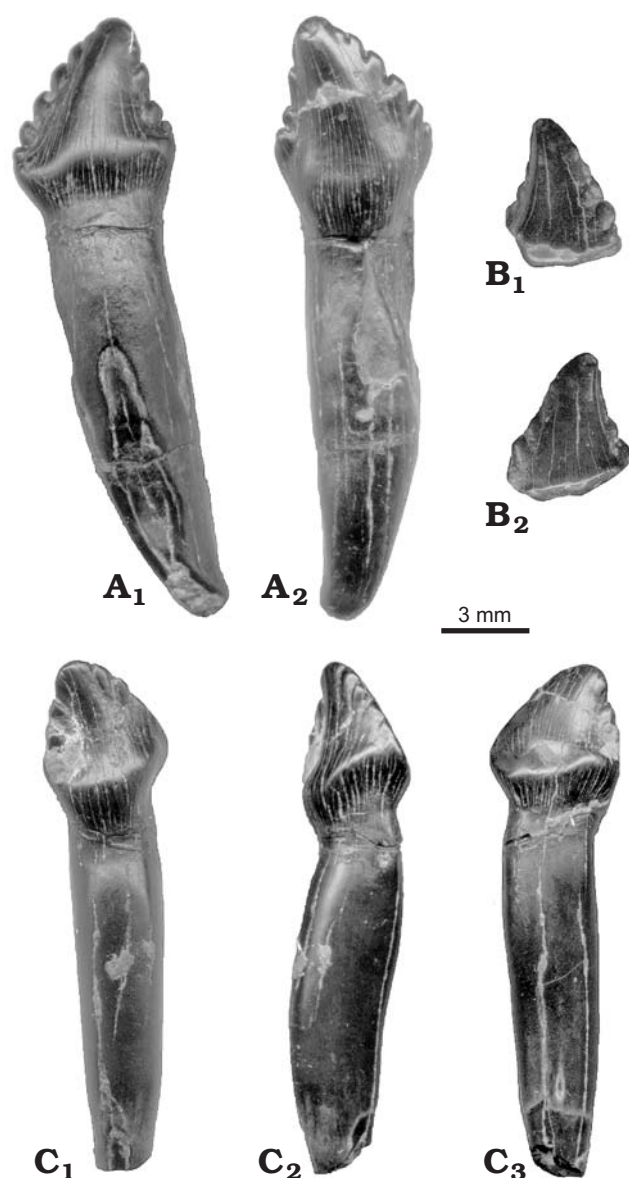


Fig. 2. Nodosaurid teeth from the Valanginian (Lower Cretaceous) Wadhurst Clay Formation, Sussex, UK. A. BEXHM 2008.16, complete tooth in ?lingual (A₁) and ?labial (A₂) views. B. BEXHM 2008.16.1, crown of tooth shown in opposite sides (B₁ and B₂). C. BEXHM 2008.16.2, complete tooth in ?lingual (C₁), distal (C₂), and ?labial (C₃) views.

and the crown height is 7 mm. The labial and lingual crown surfaces are smooth and swollen around the base. There is a smooth raised crown base on the ?labial side (Fig. 1A) and a cingulum similar to teeth of other nodosaurids on the ?lingual side (Fig. 1C). The swollen crown walls on both sides form a wide central ridge extending towards the apex. The anterior and posterior carinae bear a series of denticles. The secondary ridges (or fluting) that support the denticles do not extend down the crown faces towards the cingulum as they do in many stegosaurs (e.g., *Stegosaurus*, *Kentrosaurus*, *Huayangosaurus*; Galton and Upchurch 2004) and many Late Cretaceous nodosaurids such as *Edmontonia*. The tip is slightly eroded but the apex was probably pointed. The crown is slightly recurved posteriorly, with five denticles decreasing

in size towards the apex on the leading (mesial) carina (Fig. 1B), and three on the posterior (distal) carina. The crown surfaces appear smooth. There is a constriction just below the crown, and below this the root widens slightly before tapering and narrowing distally. The root is straight and approximately circular in cross section and there is a fracture on one side of the root that reveals a hollowed interior (Fig. 1C).

BEXHM 2008.16 (Fig. 2A) is 20.5 mm long, with a maximum width across the crown base of 5 mm and a crown height of about 7 mm. The crown is slightly recurved posteriorly, with five denticles on the leading (mesial) carina, the first in line with the crown base, and a poorly developed sixth close to the apex. The posterior (distal) carina has three distinct denticles and a poorly developed fourth denticle close to the apex. The crown base is swollen, with a weak cingulum on both sides, and the base is continuous, with a broad ridge that extends vertically to form the apex. This vertical ridge narrows towards the apex, and is more distinct on the ?lingual surface (Fig. 2A₁) than the ?labial surface (Fig. 2A₂). The tip of the apex is slightly worn. The crown surfaces are smooth, apart from some post-mortem vertical cracking, with no evidence of fluting. The root's original shape and cross section is now distorted.

BEXHM 2008.16.1 (Fig. 2B) is a crown broken off above the crown base. It is 5 mm in height as preserved, 4 mm wide and 2 mm thick. Only three denticles are preserved on each carina edge, and any further denticles that occurred below this are now missing. The apex is slightly recurved and pointed and the crown surfaces are smooth.

BEXHM 2008.16.2 (Fig. 2C) is 17 mm in preserved height, with a crown that is 5 mm high (reduced height due to apical wear) and 4 mm across the crown base. The crown is slightly recurved, with two identifiable denticles and the a third denticle nearest to the crown base on the mesial edge, but this denticle may be worn, and is obscured by a small area of matrix. The posterior edge has three identifiable denticles, but the lowest is also obscured by a combination of erosion and matrix. The crown base is swollen, with a ridge-like cingulum, and is continuous with the vertical ridge forming the apex. The apex is rounded by wear or erosion, but must have been more pointed. The root is straight, 3 mm wide and 12 mm long, but the shape appears to have been distorted by compression.

Discussion

Thyreophoran tooth morphology is well known from North American and Asian materials (Coombs 1978; Vickaryous et al. 2004). Stegosaurian and ankylosaurian teeth are generally small in proportion to body size. The crowns are broadly leaf-shaped, and labiolingually compressed, with various arrangements of denticles along the anterior and posterior carinae. The single straight roots are cylindrical and taper slightly.

Teeth of the basal thyreophoran *Scelidosaurus harrisoni* from the Lower Jurassic have tall crowns with many small

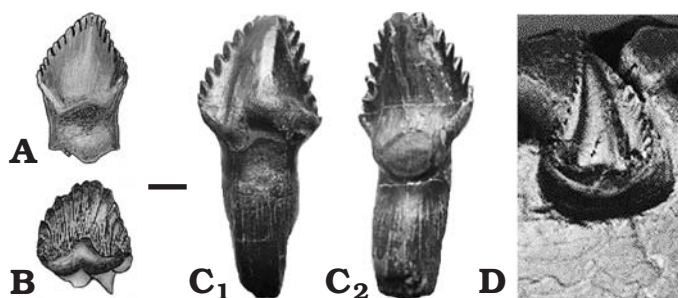


Fig. 3. Thyreophoran dinosaur teeth. **A.** Maxillary tooth of the basal thyreophoran dinosaur *Scelidosaurus harrisoni* Owen, 1861 from the Lower Jurassic of Dorset, UK, NHMUK R1111 in lingual view (drawn after Barrett 2001). **B.** Stegosaurid tooth from Middle Jurassic of Russia, ZIN PH2/117 in ?buccal view (drawn from Averianov and Krasnolutsii 2009). **C.** Nodosaurid tooth from the ?Lower Cretaceous of Dorset, UK, NHMUK R2940 in ?labial (**C₁**) and ?lingual (**C₂**) views. **D.** Tooth of the nodosaurid dinosaur *Sarcolestes leedsi* Lydekker, 1893 from the Middle Jurassic of Fletton, Cambridgeshire, UK, NHMUK R2682, holotype in medial view. Scale bar: A–C, 10 mm; D, 3 mm.

denticles on each carina, no crown surface fluting and a distinct cingulum on the lingual surface (Fig. 3A). There are six premaxillary teeth, 17 maxillary teeth and 16 dentary teeth. Premaxillary teeth are lacking in most stegosaurs and ankylosaurs. The few exceptions are the Chinese Jurassic stegosaur *Huayangosaurus*, which has seven teeth in each premaxilla (Galton and Upchurch 2004), and the North American Cretaceous nodosaurids *Silvisaurus condrayi*, *Pawpawsaurus campbelli*, and *Gargoyleosaurus parkinorum*, which have eight (Eaton 1960; Carpenter and Kirkland 1998), four (Lee 1996), and eight (Carpenter et al. 1998, Kilbourne and Carpenter 2005) teeth respectively in each premaxilla.

The absence of stegosaur teeth from the UK Lower Cretaceous coincides with the very rare, fragmentary and isolated nature of other stegosaur remains. The few available pieces are mostly postcranial and possible dermal armour elements (Blows 2001). The only cranial piece is a dentary fragment (NHMUK 2422) of the stegosaur *Regnosaurus northamptoni* (Mantell, 1848) from Cuckfield, Sussex, which has only tooth roots and alveoli preserved (Barrett and Upchurch 1995; Barrett and Maidment 2011a).

Stegosaur cheek teeth from the Jurassic (Fig. 3B) have asymmetrical crowns with a ring-like horizontal cingulum around the crown base. Multiple rounded denticles are mounted along the carinae. In most taxa, there are vertical grooves of varying extent down both crown faces, from between the denticles to the cingulum. A few stegosaurian taxa, e.g. the South African *Paranthodon* (Galton and Coombs 1981) and the Chinese stegosaurs *Huayangosaurus* (Zhou 1984) and *Tuojiangosaurus* (Dong 1977), have a central ridge from the cingulum to the crown apex that divides the denticulate part of the crown into two portions (Galton and Upchurch 2004). The new UK teeth can be distinguished from stegosaurian teeth by having crowns with a more pointed apex and sharper pointed denticles than in stegosaurs. They also have a cingulum that is less pronounced than in stegosaur teeth (Fig. 3B). They lack the ridges or grooves that extend down the

crown surfaces of most stegosaur teeth from the denticles to the cingulum. Unlike most stegosaurs, the crown surfaces of the new nodosaur teeth are swollen and smooth, forming a tapering ridge from the base to the apex which separates the denticles on both carinae.

The Isle of Wight tooth and the three Sussex teeth are referred to the Nodosauridae on the basis of general resemblance. They are laterally compressed but have a flatter, smoother cingulum, unlike some other nodosaurids (e.g., *Edmontonia*) and stegosaurs (e.g., *Stegosaurus*) in which the cingulum is more pronounced, or is frequently absent as in the teeth of most ankylosaurids. Nodosaurid and ankylosaurid teeth have rounded, swollen crown bases, but some nodosaurid teeth such as *Edmontonia* lack the distinct, broad, smooth, central ridge extending up to the crown apex seen in the UK teeth and the nodosaurids *Texasetes* (Coombs 1995), *Gargoyleosaurus* (Kilbourne and Carpenter 2005) and *Gastonia* (Kirkland 1998).

Comparative teeth include two ankylosaur specimens known from the pre-Valanginian beds of the UK, which are similar to the teeth described here. NHMUK R2940 is an unnamed isolated tooth (Fig. 3C) recorded as coming from the Purbeck Limestone Group of Lulworth Cove, Dorset, although its actual provenience is unknown (Norman and Barrett 2002); it could come from the lowest Cretaceous at Purbeck. This tooth was described by Galton (1980b, 1983a) and was considered to be nodosaurid by Norman and Barrett (2002) and ankylosaur by Barrett and Maidment (2011b). NHMUK R2682, is the holotype of *Sarcolestes leedsi* (Lydekker, 1893), a left mandibular fragment with replacement teeth, from the Lower Oxford Clay, Middle Jurassic (middle Callovian) of Fletton, Cambridgeshire, near Peterborough (Fig. 3D). Galton (1983b) recognised the ankylosaur affinities of the *Sarcolestes leedsi* mandible, placing this taxon within the Nodosauridae. Both NHMUK R2940 and NHMUK R2682 show ankylosaur dental features very similar to the Early Cretaceous teeth—a crown base with weak smooth cingulum, no crown face fluting (NHMUK R2682) or weak fluting on one face (NHMUK R2940), a broad central ridge extending vertically from base to apex on one face, and denticles confined along both carina edges. The denticle numbers vary, with 7 denticles on each carina in NHMUK R2940, and many small denticles in *Sarcolestes leedsi*.

North American nodosaurid teeth resemble the UK teeth. *Gastonia* teeth (Fig. 4A–C) are very similar to the UK teeth, and to the maxillary teeth of *Gargoyleosaurus*, but differ by the size and numbers of denticles. *Gastonia* has 6 to 9 small denticles along both carinae, a total of 12 or more denticles per crown. *Gastonia* has 15–16 maxillary teeth, but the dentary count is unavailable because there are no mandibles. The maxillary teeth of *Gargoyleosaurus* (Fig. 4D) are similar to the UK teeth, the main difference being the number and size of the denticles, i.e., 16 to 17 small denticles in total for *Gargoyleosaurus*, compared with 8 larger denticles in total for the UK teeth (Kilbourne and Carpenter 2005). The teeth

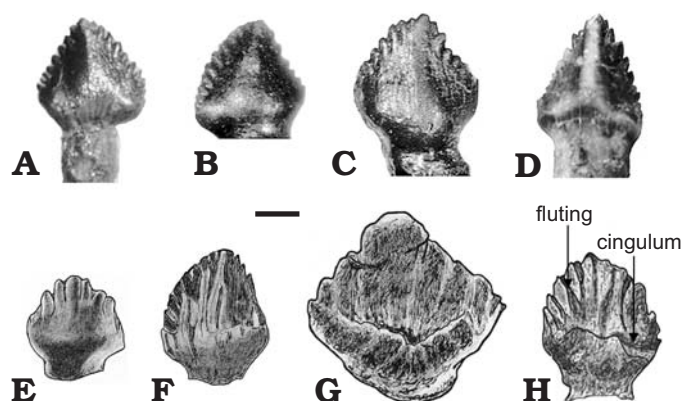


Fig. 4. Teeth of nodosaurid dinosaurs. **A–C.** Three teeth of the holotype (CEUM 1307) of *Gastonia burgei* Kirkland, 1998 from Lower Cretaceous of Utah, USA (photographs courtesy of James Kirkland). **A.** First tooth in ?lingual view. **B.** Second tooth in ?lingual view. **C.** Third tooth in ?buccal view. **D.** *Gargoylesaurus parkpinorum* Carpenter, Miles, and Cloward, 1998 from the Upper Jurassic of Wyoming, USA (photograph courtesy of K. Carpenter), DMNH 27726, holotype in ?lingual view. **E.** Unnamed nodosaurid from the Lower Cretaceous of Spain, MPZ 2002/926 in labial view (drawn after Canudo et al. 2004). **F.** *Acanthopholis horridus* Huxley, 1867 from the Upper Cretaceous of England, BGS GSM 109045 in ?lingual view (drawn after Pereda-Suberbiola and Barrett 1999). **G.** *Struthiosaurus languedocensis* Garcia and Pereda-Suberbiola, 2003 from the Upper Cretaceous of Southern France, UM2 OLV-D18 CV in ?lingual view (drawn after Garcia and Pereda-Suberbiola 2003). **H.** *Edmontonia rugosidens* (Gilmore, 1930) from the Upper Cretaceous of USA, NMC 8531 in lingual view (drawn after Barrett 2001). Scale bar: A, B, D, F–H, 3 mm; C, 2 mm; E 1.5 mm.

of *Texasetes* (Coombs 1995) are similar to the UK teeth, with no fluting on the crown faces. In *Texasetes*, *Gargoylesaurus* and *Gastonia* the tooth apex is either upright or slightly recurved posteriorly, and the crown base is swollen, with a cingulum that is similar to the new UK teeth, i.e., less distinct, being flatter and smoother than in other nodosaurids. *Mymoorapelta* has few known teeth, but they are very similar to *Gargoylesaurus* (Kirkland et al. 2010).

Early Cretaceous teeth from mainland Europe are very rare. Two teeth of an indeterminate nodosaurid from the Hauterivian to Barremian of Spain (Canudo et al. 2004, 2010; Fig. 4E) are significantly different from the UK teeth in having very rounded swollen crown bases, no cingulum, and a few large denticles each side of the low apex. Despite wide variation in the teeth of a single ankylosaur taxon (Coombs 1990), the differences between the English and Spanish teeth must indicate that they come from different taxa.

Nodosaurid teeth are also known from the post-Barremian Cretaceous of Europe, including the UK. Three nodosaurid teeth (BGS GSM 109045, 109046 in part, 109051), collected along with other nodosaurid remains including a skull fragment and dermal armour, from the Lower Chalk (Lower Cenomanian) of Folkestone, Kent, were named by Huxley (1867) as *Acanthopholis horridus* and redescribed by Pereda-Suberbiola and Barrett (1999) as *Nodosauridae* incertae sedis. The best preserved crown (BGS GSM 109045; Fig. 4F) compares closely with the new teeth except for a

rather more distinct cingulum and no smooth swollen ridge extending centrally from the base up to the crown apex.

The nodosaurid, *Struthiosaurus austriacus* (Bunzel, 1871), known from various Campanian to Maastrichtian strata across Spain, France, Austria, and Romania (Nopcsa 1915; Pereda-Suberbiola and Galton 1994, 1997; Pereda-Suberbiola et al. 1995), includes a few teeth from the late Campanian to early Maastrichtian of the Iberian Peninsula (Pereda-Suberbiola 1999), and three teeth (UM2 OLV-D18-20 CV) from the lower Campanian of southern France referred to *S. languedocensis* (Fig. 4G). This tooth has a crown that is wider than tall, with broadly fluted asymmetric faces and a very distinct cingulum on both sides. This tooth is more similar to a stegosaur tooth than to the Wealden teeth. The maxillary and dentary alveolar count for European ankylosaurs remains largely unknown. Pereda-Suberbiola et al. (1995) report a near complete mandible of *Struthiosaurus* (MCNA L1.B.110) as having 19, perhaps 20 empty alveoli.

Twenty-one teeth were found as part of the holotype of the nodosaurid *Hungarosaurus tormai* Ősi, 2005, from the Upper Cretaceous Santonian of western Hungary. The teeth are remarkably similar to the new UK teeth in having a crown with pointed apex, a low, ridged cingulum, denticles on both mesial and distal edges of the crown (about 16 in total), and a long, peg-like root with a slight swelling below the crown-root junction. A central ridge extends from cingulum to apex and separates the lingual crown surface into two parts. The crown surfaces do not appear to be fluted (Ősi 2005: fig. 4E–G). The UK teeth also lack the crown fluting extending from the carina towards the cingulum that is seen in *Euoplocephalus*, some nodosaurids (e.g., *Edmontonia*; Fig. 4H) and stegosaur teeth (e.g., *Stegosaurus*). The fluting pattern is unique in *Euoplocephalus* (Vickaryous and Russell 2003; Fig. 5A) but other North American ankylosaurids had smoother crowns without fluting (e.g., *Ankylosaurus*; Fig. 5B). In the best known Asian ankylosaurids the crowns had fluting and a cingulum, e.g., *Saichania* (Fig. 5C) and *Pinacosaurus* (Fig. 5D).

The location of the new teeth in the jaws is hard to determine. Because they are not conical they are unlikely to be premaxillary. However, it is not possible to say if they are maxillary or mandibular teeth because both have very similar morphology (Coombs 1990). Nor is it possible to identify whether these UK teeth are from *Hylaeosaurus* or

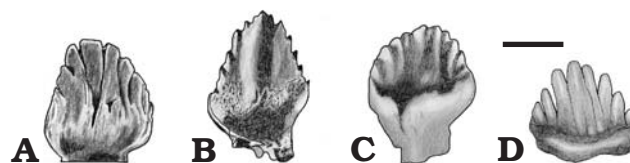


Fig. 5. Teeth of ankylosaurid dinosaurs from the Upper Cretaceous of North America (**A, B**) and Asia (**C, D**). **A.** *Euoplocephalus tutus* Lambe, 1910, TMP 87.36.99 in ?lingual view (drawn after Vickaryous and Russell 2003). **B.** *Ankylosaurus magniventris* Brown, 1908, AMNH 5214 in ?lingual view (drawn after Coombs 1990). **C.** *Saichania chulsanensis* Maryańska, 1977, GI SPS 100/151 in lingual view (drawn after Maryańska 1977). **D.** *Pinacosaurus grangeri* Gilmore, 1933, TVPP V16283 in lingual view (drawn after Burns et al. 2011). Scale bar: A, B, 4 mm; C, 5 mm; D, 2 mm.

Polacanthus, or from an unnamed taxon. IWCMS 5390 is illustrated by Naish and Martill (2001) and they refer it to “possible *Polacanthus*”, probably because of its discovery in the Barremian of the Isle of Wight. However, they also note its similarity to some troodontid theropods. The characters that suggest it is ornithischian rather than theropod are a distinct leaf-shaped crown, a swollen crown base separated from the root by a constriction, and different lingual and labial surfaces. There is currently no evidence of *Hylaeosaurus* from the Barremian of the UK; it is restricted to the Valanginian, which suggests that this tooth might come from *Polacanthus*. The identity of the Bexhill teeth is even more problematic, because both *Polacanthus* and *Hylaeosaurus* are recorded from the Wadhurst Clay Formation of Pevensey Pit at Bexhill (Austen et al. 2010).

Acknowledgements

We thank Julian Porter (Curator of the Bexhill Museum, Sussex, UK) and Steven Hutt (former Curator of the Museum of Isle of Wight, Sandown, UK) for permission to study and publish on specimens in their care; James Kirkland (Utah Geological Survey, Salt Lake City, USA) and Kenneth Carpenter (Denver Natural History Museum, Denver, USA; now at Utah State University-Eastern, Prehistoric Museum, Price, USA) for photographs and for their advice on North American nodosaurid teeth; Sandra Chapman (NHMUK) for access to specimens; Paul Barrett (NHMUK), Peter Galton (University of Bridgeport, Bridgeport, Connecticut), Javier Pereda-Suberbiola (University of the Basque Country, Leioa, Spain), and Paul Penkalski (The Geology Museum, Madison, Wisconsin, USA) for their valuable comments on the paper; Latinka Hristova (Sofia Natural History Museum, Bulgaria) for her help with the figures; David Brockhurst (Ashdown Quarry, Bexhill-on-Sea, UK), collector of the Bexhill teeth, for his advice on the discovery site, and Steve Chapman (manager of the Ibstock-Ashdown Works, Bexhill-on-Sea, UK) for his co-operation in allowing collection of fossils from the quarry.

References

- Austen, P., Brockhurst, D., and Honeysett, K. 2010. Vertebrate fauna from Ashdown Brickworks, Bexhill, East Sussex. *Wealden News* 8: 13–23.
- Averianov, A.O. and Krasnolutsii, S.A. 2009. Stegosaur remains from the Middle Jurassic of west Siberia. *Proceedings of the Zoological Institute RAS* 313: 153–167.
- Barrett, P.M. 2001. Tooth wear and possible jaw action of *Scelidosaurus harrisoni* Owen and a review of feeding mechanisms on other thyrophan dinosaurs. In: K. Carpenter (ed.), *The Armored Dinosaurs*, 25–52. Indiana University Press, Bloomington.
- Barrett, P.M. and Maidment, S. 2011a. Armoured Dinosaurs. In: D.J. Batten (ed.), *English Wealden Fossils*, 391–406. The Palaeontological Association, London.
- Barrett, P.M. and Maidment, S. 2011b. Dinosaurs of Dorset: Part III, the ornithischian dinosaurs (Dinosauria, Ornithischia) with additional comments on the sauropods. *Proceedings of the Dorset Natural History and Archaeological Society* 132: 145–163.
- Barrett, P.M. and Upchurch, P. 1995. *Regnosaurus northamptoni*, a stegosaurian dinosaur from the Lower Cretaceous of southern England. *Geological Magazine* 132: 213–222.
- Blows, W.T. 1998. A review of Lower and Middle Cretaceous dinosaurs of England. In: S.G. Lucas, J.I. Kirkland, and J.W. Estep (eds.), *Lower and Middle Cretaceous Terrestrial Ecosystems. New Mexico Museum of Natural History and Science Bulletin* 14: 29–38.
- Blows, W.T. 2001. Possible stegosaur dermal armor from the Lower Cretaceous of Southern England. In: K. Carpenter (ed.), *The Armored Dinosaurs*, 130–140. Indiana University Press, Bloomington.
- Brown, B. 1908. The Ankylosauridae, a new family of armored dinosaurs from the Upper Cretaceous. *Bulletin of the American Museum of Natural History* 24: 187–201.
- Bunzel, E. 1870. Notice of a fragment of a reptilian skull from the Upper Cretaceous of Grünbach. *Quarterly Journal of the Geological Society* 26: 394.
- Bunzel, E. 1871. Die Reptilfauna der Gosauformation in der Neuen Welt bei Wiener-Neustadt. *Abhandlungen der Geologischen Reichsanstalt* 5: 1–18.
- Burns, M.E., Currie, P.J., Sissons, R.L., and Arbour V.M. 2011. Juvenile specimens of *Pinacosaurus grangeri* Gilmore, 1933 (Ornithischia: Ankylosauria) from the Late Cretaceous of China, with comments on taxonomy of *Pinacosaurus*. *Cretaceous Research* 32: 174–186.
- Canudo, J.I., Ruiz-Omeñaca, J.I., and Cuenca-Bescós, G. 2004. Los primeros dientes de anquilosaurio (Ornithischia: Thyreophora) descritos en el Cretácico Inferior de España. *Revista Española de Paleontología* 19: 33–46.
- Canudo, J.I., Gasca, J.M., Aurell, M., Badiola, A., Blain, H.-A., Cruzado-Caballero, P., Gómez-Fernández, D., Moreno-Azanza, M., Parrilla, J., Rabal-Garcés, R., and Ruiz-Omeñaca, J.I. 2010. La Cantalera: an exceptional window onto the vertebrate biodiversity of the Hauterivian–Barremian transition in the Iberian Peninsula. *Journal of Iberian Geology* 36: 205–224.
- Carpenter, K. 2001. Skull of the polacanthid ankylosaur *Hylaeosaurus armatus* Mantell, 1833, from the Lower Cretaceous of England. In: K. Carpenter (ed.), *The Armored Dinosaurs*, 169–172. Indiana University Press, Bloomington.
- Carpenter, K. and Kirkland, J.L. 1998. Review of Lower and Middle Cretaceous ankylosaurs from North America. In: S.G. Lucas, J.L. Kirkland, and J.W. Estep (eds.), *Lower and Middle Cretaceous Terrestrial Ecosystems. New Mexico Museum of Natural History and Science, Bulletin* 14: 249–270.
- Carpenter, K., Miles, C., and Cloward, K. 1998. Skull of a Jurassic ankylosaur (Dinosauria). *Nature* 393: 782–783.
- Coombs, W.P. 1978. The families of the ornithischian dinosaur Order Ankylosauria. *Palaeontology* 21: 143–170.
- Coombs, W.P. 1990. Teeth and taxonomy in ankylosaurs. In: K. Carpenter and P. Currie (eds.), *Dinosaur Systematics Approaches and Perspectives*, 269–279. Cambridge University Press, Cambridge.
- Coombs, W.P. 1995. A new nodosaurid ankylosaur (Dinosauria: Ornithischia) from the Lower Cretaceous of Texas. *Journal of Vertebrate Paleontology* 15: 298–312.
- Dong, Z.M. 1977. On the dinosaurian remains from Turpan, Xinjiang [in Chinese, with English summary]. *Vertebrata Palasiatica* 15: 59–66.
- Eaton, T.H. 1960. A new armored dinosaur from the Cretaceous of Kansas. *The University of Kansas Paleontological Contributions, Vertebrata* 25: 1–24.
- Galton, P.M. 1980a. Armoured dinosaurs (Ornithischia: Ankylosauria) from the Middle and Upper Jurassic of England. *Geobios* 13: 825–837.
- Galton, P.M. 1980b. *Priodontognathus phillipsii* (Seeley), and ankylosaurian dinosaur from the Upper Jurassic (or possibly Lower Cretaceous) of England. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1980 (8): 477–489.
- Galton, P.M. 1983a. Armoured dinosaurs (Ornithischia: Ankylosauria) from the Middle and Upper Jurassic of Europe. *Palaeontographica, Abteilung A* 182: 1–25.
- Galton, P.M. 1983b. *Sarcolestes leedsi* Lydekker, an ankylosaurian dinosaur from the Middle Jurassic of England. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1983 (3): 141–155.
- Galton, P.M. and Coombs, W.A. 1981. *Paranthodon africanus* (Broom), a stegosaurian dinosaur from the Lower Cretaceous of South Africa. *Geobios* 14: 299–309.

- Galton, P.M. and Upchurch, P. 2004. Stegosauria. In: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, 2nd edition, 343–362. University of California Press, Berkeley.
- García, G. and Pereda-Suberbiola, X. 2003. A new species of *Struthiosaurus* (Dinosauria: Ankylosauria) from the Upper Cretaceous of Villeveyrac (southern France). *Journal of Vertebrate Paleontology* 23: 156–165.
- Gilmore, C.W. 1930. On dinosaurian reptiles from the Two Medicine Formation of Montana. *Proceedings of the United States National Museum* 77 (16): 1–39.
- Gilmore, C.W. 1933. Two new dinosaurian reptiles from Mongolia with notes on some fragmentary specimens. *American Museum Novitates* 679: 1–20.
- Huxley, T.H. 1867. On *Acanthopholis horridus*, a new reptile from the Chalk Marl. *Geological Magazine* 4: 65–67.
- Kilbourne, B. and Carpenter, K. 2005. Redescription of *Gargoylesaurus parkpinorum*, a polacanthid ankylosaur from the Upper Jurassic of Albany County, Wyoming. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 237: 111–160.
- Kirkland, J.I. 1998. A polacanthine ankylosaur (Ornithischia: Dinosauria) from the Early Cretaceous (Barremian) of eastern Utah. In: S.G. Lucas, J.I. Kirkland, and J.W. Estep (eds.), *Lower and Middle Cretaceous Terrestrial Ecosystems. New Mexico Museum of Natural History and Science Bulletin* 14: 271–281.
- Kirkland, J.I., Hunt-Foster, R.K., Foster, J.R., and Loewen, M. 2010. Newly recovered skeletal elements of the Late Jurassic dinosaur *Mymoorapelta* from its type locality in the Morrison Formation permits re-evaluation of ankylosaur phylogeny. *Journal of Vertebrate Paleontology* 30: 116A.
- Lambe, L.M. 1910. Note on the parietal crest of *Centrosaurus apertus* and a proposed new generic name for *Stereosphenus tutus*. *The Ottawa Naturalist* 24: 149–151.
- Lee, Y.-N. 1996. A new nodosaurid ankylosaur (Dinosauria: Ornithischia) from the Paw Paw Formation (late Albian) of Texas. *Journal of Vertebrate Paleontology* 16: 232–245.
- Lydekker, R. 1893. On the jaw of a new carnivorous dinosaur from the Oxford Clay of Peterborough. *Quarterly Journal of the Geological Society* 49: 284–287.
- Mantell, G.A. 1833. Observations of the remains of the *Iguanodon*, and other fossil reptiles, of the strata of Tilgate Forest in Sussex. *Proceedings of the Geological Society of London* 1: 410–411.
- Mantell, G.A. 1841. Memoir on a portion of the lower jaw of the *Iguanodon*, and on the remains of the *Hylaeosaurus* and other saurians, discovered in the strata of Tilgate Forest, in Sussex. *Philosophical Transactions of the Royal Society of London* 131: 131–151.
- Mantell, G.A. 1848. On the structure of the jaws and teeth of the *Iguanodon*. *Philosophical Transactions of the Royal Society of London* 138: 183–202.
- Marsh, O.C. 1890. Additional characters of the Ceratopsidae, with notice of new Cretaceous dinosaurs. *American Journal of Science, series 3* 39: 418–426.
- Maryńska, T. 1977. Ankylosauridae (Dinosauria) from Mongolia. *Palaeontologia Polonica* 37: 85–151.
- Naish, D. and Martill, D.M. 2001. Armoured Dinosaurs: Thyreophorans. In: D.M. Martill and D. Naish (eds.), *Dinosaurs of the Isle of Wight. Field Guides to Fossils*, 10, 147–184. The Palaeontological Association, London.
- Nopcsa, F. 1915. Die Dinosaurier der siebenbürgischen Landesteile Ungarns. *Mitteilungen aus dem Jahrbuche der königlich ungarischen Geologischen Reichsanstalt, Budapest* 23: 1–26.
- Norman, D. 1984. A systematic reappraisal of the reptile order Ornithischia. In: W.-E. Reif and F. Westphal (eds.), *Proceedings of the Third Symposium on Mesozoic Terrestrial Ecosystems*, 157–162. Attempto Verlag, Tübingen.
- Norman, D. and Barrett, P.M. 2002. Ornithischian dinosaur from the Lower Cretaceous (Berriasian) of England. *Special Papers in Palaeontology* 68: 161–189.
- Norman, D. and Faiers, T. 1996. On the first partial skull of an ankylosaurian dinosaur from the Lower Cretaceous of the Isle of Wight, Southern England. *Geological Magazine* 133: 299–310.
- Osborn, H.F. 1923. Two Lower Cretaceous dinosaurs of Mongolia. *American Museum Novitates* 95: 1–10.
- Ösi, A. 2005. *Hungarosaurus tormai*, a new ankylosaur (Dinosauria) from the Upper Cretaceous of Hungary. *Journal of Vertebrate Paleontology* 25: 370–383.
- Owen, R. 1857. Monograph on the fossil Reptilia of the Wealden and Purbeck Formations. Part IV, Dinosauria (*Hylaeosaurus*). *Palaeontographical Society of London Monographs* 10: 1–26.
- Owen, R. 1861. Monographs on the British fossil Reptilia from the Oolitic Formations. Part I, *Scelidosaurus harrisonii* and *Pliosaurus grandis*. *Palaeontographical Society of London Monographs* 13: 1–16.
- Pereda-Suberbiola, J. and Galton, P.M. 1994. A revision of the cranial features of the dinosaur *Struthiosaurus austriacus* Bunzel (Ornithischia: Ankylosauria) from the Late Cretaceous of Europe. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 191: 173–200.
- Pereda-Suberbiola, X. 1993. *Hylaeosaurus*, *Polacanthus*, and the systematics and stratigraphy of Wealden armoured dinosaurs. *Geological Magazine* 130: 767–781.
- Pereda-Suberbiola, X. 1999. Ankylosaurian dinosaur remains from the Upper Cretaceous of Lano (Iberian Peninsula). In: H. Astibia, J.C. Corral, X. Murelaga, X. Orue-Etxebarria, and X. Pereda-Suberbiola (eds.), *Geology and Palaeontology of the Upper Cretaceous Vertebrate-Bearing Beds of the Lano Quarry (Basque-Cantabrian region, Iberian Peninsula). Estudios del Museo de Ciencias Naturales de Alava* 14: 273–288.
- Pereda-Suberbiola, X. and Galton, P.M. 1997. Armoured dinosaurs from the Late Cretaceous of Transylvania. *Proceedings of the Mesozoic Vertebrate Faunas of central Europe Symposium, Museul Civilizatiei Dacice si Romane, Deva. Sargetia, Scientia Naturae* 17: 203–217.
- Pereda-Suberbiola, X. and Barrett, P.M. 1999. A systematic review of ankylosaurian dinosaur remains from the Albian–Cenomanian of England. *Special Papers in Palaeontology* 60: 177–208.
- Pereda-Suberbiola, X., Astibia, H., and Buffetaut, E. 1995. New remains of the armoured dinosaur *Struthiosaurus* from the Late Cretaceous of the Iberian peninsula (Laño locality, Basque-Cantabric Basin). *Bulletin de la Société Géologique de France* 166: 207–211.
- Pereda-Suberbiola, X., Fuentes, C., Meijide, M., Meijide-Fuentes, F., and Meijide-Fuentes, M., Jr. 2007. New remains of the ankylosaurian dinosaur *Polacanthus* from the Lower Cretaceous of Soria, Spain. *Cretaceous Research* 28: 583–596.
- Seeley, H.G. 1875. On the maxillary bones of a new dinosaur (*Priodontognathus phillipsii*), contained in the Woodwardian Museum of the University of Cambridge. *Quarterly Journal of the Geological Society* 31: 439–443.
- Seeley, H.G. 1879. On the Dinosauria of the Cambridge Greensand. *Quarterly Journal of the Geological Society* 35: 591–635.
- Seeley, H.G. 1887. On the classification of the fossil animals commonly called Dinosauria. *Proceedings of the Royal Society, London* 43: 165–171.
- Sweetman, S.C. and Insole, A.N. 2010. The plant debris beds of the Early Cretaceous (Barremian) Wessex Formation of the Isle of Wight, Southern England: their genesis and palaeontological significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* 292: 409–424.
- Upchurch, P., Mannion, P.D., and Barrett, P.M. 2011. Sauropod dinosaurs. In: D.J. Batten (ed.), *English Wealden Fossils*, 476–525. The Palaeontological Association, London.
- Vickaryous, M.K. and Russell, A.P. 2003. A redescription of the skull of *Euplocephalus tutus* (Archosauria: Ornithischia): a foundation for comparative and systematic studies of ankylosaurian dinosaurs. *Zoological Journal of the Linnean Society* 137: 157–186.
- Vickaryous, M.K., Maryanska, T., and Weishampel, D.B. 2004. Ankylosauria. In: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, 2nd edition, 363–392. University of California Press, Berkeley.
- Zhou, S. 1984. *The Middle Jurassic Dinosaurian Fauna from Dashanpu, Zigong, Sichuan. Vol. 2, Stegosaurus* [in Chinese, with English summary]. 51 pp. Sichuan Science and Technology Publishing House, Chengdu.