

Purported earliest bones of a plated dinosaur (Ornithischia: Stegosauria): a “dermal tail spine” and a centrum from the Aalenian-Bajocian (Middle Jurassic) of England, with comments on other early thyreophorans

Peter M. Galton

With 2 figures

Abstract: The supposed base of a slender dermal tail spine from the Inferior Oolite Group (shallow marine deposit, early Middle Jurassic, Aalenian-Bajocian) of Dorset, England, previously reported as “*Stegosaurus*” and *Thyreophora* indet., is a half centrum of a caudal vertebra, Archosauria indet. A dorsally and ventrally incomplete vertebra from the same locality has a low centrum that is slightly wider transversely than it is long and, as there is a parapophysis anteriorly, it is part of a cervical vertebra. However, it does not match those of marine reptiles from the Middle Jurassic (Callovian) of England in which the cervical centra are elongate in crocodylomorphs, plate-like in ichthyosaurs, and short and wide in some sauropterygians (plesiosaurs and pliosaurs) but the parapophysis is mid-ventrally situated. The Dorset centrum does not correspond to those of most contemporaneous dinosaurs, viz. theropods, basal sauropodomorphs, basal sauropods and ornithopods. However, it proportions correspond to posterior neck vertebrae of the basal thyreophoran *Scelidosaurus* (Lower Jurassic, England) and those of eurypod thyreophorans, the dacentrurine stegosaur *Dacentrurus* (described as *Miragaia*, Upper Jurassic, Portugal) and the nodosaurid ankylosaur *Mymoorapelta* (Upper Jurassic, USA), so the Dorset centrum is tentatively identified as *Thyreophora* indet. The earliest skeletal records for armored dinosaurs are from the Middle Jurassic: for Euryopoda a proximal ulna from the early Bajocian of Scotland, for Stegosauria two large sub-vertically plates from the earliest Bathonian of England, and for Ankylosauria the ?Bathonian-Callovian of China or the early middle Callovian of England. However, the stegosaurian footprint taxon *Deltapodus brodricki* (Aalenian) of England pushes the origin of Stegosauria (and sister group Ankylosauria) down into the Early Jurassic.

Key words: Thyreophora, Euryopoda, Stegosauria, Ankylosauria, *Deltapodus*, Sauropterygia, Jurassic, England, Portugal, USA, bones, footprints.

1. Introduction

The Stegosauria of MARSH (1877) is a clade of quadrupedal graviportal herbivorous ornithischian dinosaurs with a bizarre array of dermal plates and spines arranged as two rows along the top of the body from the neck to the end of the tail. The group is represented by bones from the Middle Jurassic to the Late Cretaceous

and from all continents except Antarctica and Australia (GALTON & UPCHURCH 2004; MAIDMENT et al. 2008; MAIDMENT 2010; GALTON 2012).

BENTON & SPENCER (1995: 125) listed “*Stegosaurus*” spines from a shallow marine deposit in the Inferior Oolite Group (Aalenian-Bajocian, early Middle Jurassic) of Bradford Abbas (National Grid Reference SY 5915) near Yeovil in Dorset, southern England.

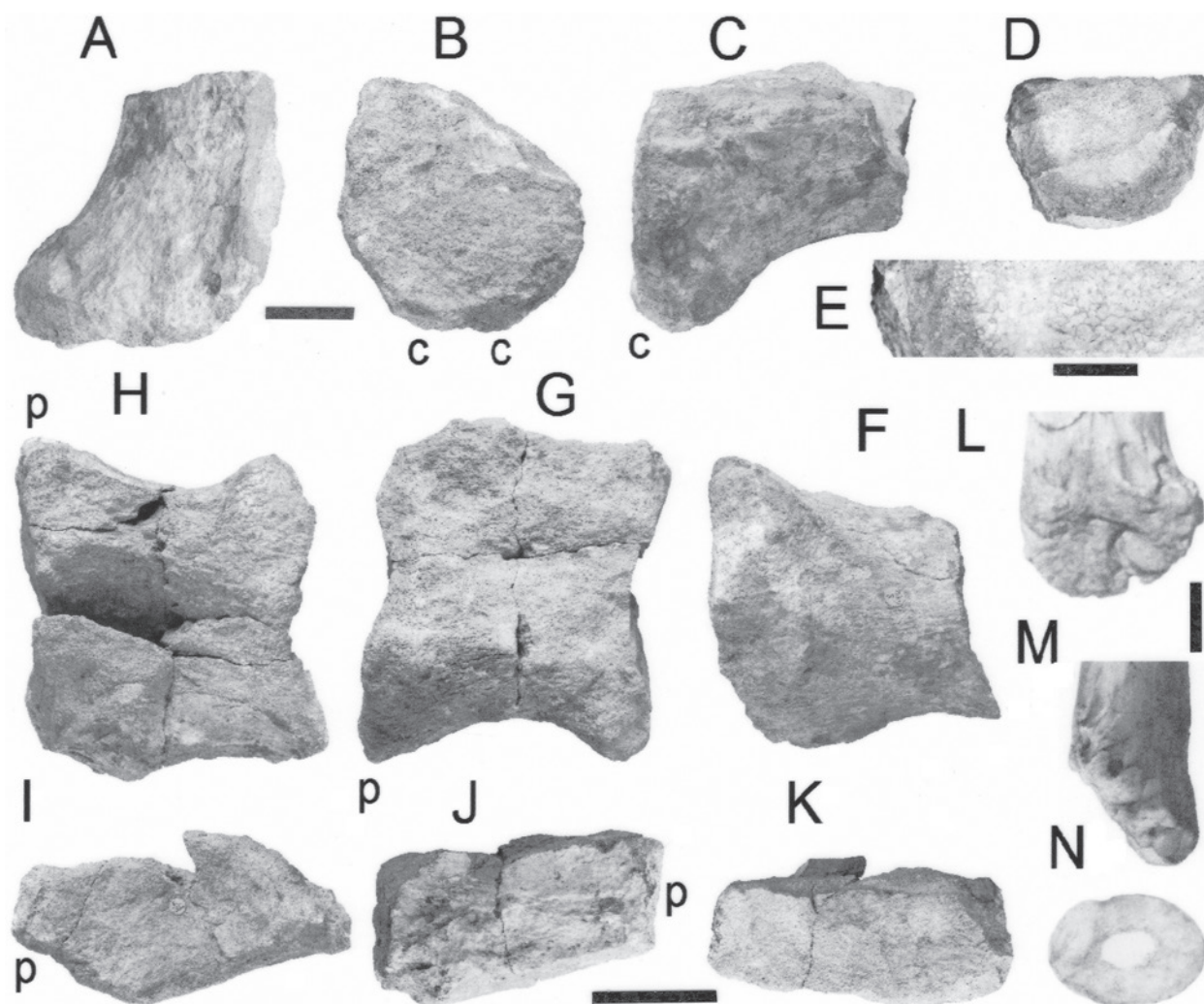


Fig. 1. A–K – Incomplete bones from Inferior Oolite Group (Aalenian–Bajocian, early Middle Jurassic) from Bradford Abbas near Yeovil, Dorset, England. A–F, purported “*Stegosaurus*” dermal tail spine, NHMUK PV R.6334, oriented as a spine (A) and as a half centrum of a caudal vertebra, Archosauria indet. (B–F), in A, C, lateral; B, articular end on (or proximal for spine) views; D–E, cross-sectional (with detail E) and F, ventral (or anterior for spine) views. G–K, incomplete posterior cervical vertebra, mostly centrum, Thyreophora indet., ?Euryopoda indet., NHMUK PV R.6336, in G, ventral; H, dorsal; I, anterior; J, right lateral and K, posterior views (J, K lit from above). L–N – Stegosaur *Dacentrurus armatus* (Upper Jurassic, England), holotype NHMUK PV OR46013, proximal end of left dermal spine in L, proximal; M, medial and N, cross-sectional views M, N from OWEN 1875). Abbreviations: c, facet for chevron; p, parapophysis; scale lines = 50 mm (A–D, F–N) and 10 mm (E).

These bones were cited as stegosaurian by NAISH & MARTILL (2008: 616), so this would be the earliest record for stegosaur bones, but MAIDMENT et al. (2008) re-identified the spine as Thyreophora indet.; they also mentioned a fragmentary vertebral centrum and two indeterminate fragments.

These bones were collected and subsequently donated in 1951 to the NHMUK by DAVID MEREDITH SEARES WATSON (1886–1973), a distinguished vertebrate paleontologist and professor at University College of Lon-

don University from 1921 to 1951 (see PARRINGTON & WESTOLL 1974). There is no information on the position of these bones as found and they are the only ones in the WATSON Collection from this locality (S.D. CHAPMAN, pers. comm. 2016). The results of an examination of these potentially important but previously unillustrated bones is given here.

Institutional abbreviations: CAMSM, Sedgwick Museum, Cambridge University, England; CV, Chongqing Museum of

Natural History, People's Republic of China; EGSUS, Palaeoecological Collection, Environmental and Geological Sciences, University of Sheffield, England; MB, Museum für Naturkunde, Berlin, Germany; ML, Museu da Lourinhã, Portugal; MWC, Museum of Western Colorado, Grand Junction, Colorado, USA; NHMUK PV: Division of Vertebrate Palaeontology, Natural History Museum, London, England; SDM, Stroud and District Museum, Stroud, England; SGDS: St. George Dinosaur Discovery Site at Johnson Farm, St. George, Utah, USA; SM, Staffin Museum, Isle of Skye, Scotland; USNM, National Museum of Natural History [formerly United States National Museum], Smithsonian Institution, Washington DC, USA.

2. Description and comparisons

The bone fragments of BENTON & SPENCER (1995) were identified as NHMUK PV R.6333-36 by MAIDMENT et al. (2008: 386, but incorrectly cited as from *Lower Jurassic*) as follows: “R.6334 is a small fragment of a dermal spine. It is expanded slightly at the base and appears to be rounded in cross-section. R.6336 may be a partial vertebral centrum, although (it) is extremely fragmentary. R.6333 and R.6335 are indeterminate bone fragments. Just a small part of the dermal spine is present, and morphologically it could be referable to either Ankylosauria or Stegosauria. These elements are therefore regarded as *Thyreophora* indet.”

NHMUK PV R.6334 (Fig. 1A-F): as shown (Fig. 1A) it looks like a stegosaurian dermal caudal spine but it differs from those of the stegosaur *Dacentrurus* (Fig. 1L-N; Upper Jurassic, England; OWEN 1875; GALTON 1985, 2016) and *Stegosaurus* (Upper Jurassic, USA; GALTON 2016). The proximal surface is smooth (Fig. 1B), rather than being very irregular with foramina (Fig. 1L), and the rim is smooth rather than being indented by numerous grooves. The distal broken cross-section (Fig. 1D, E) lacks a thick outer layer of compact bone bordering a well-defined central cavity as in *Dacentrurus* (Fig. 1N) and old adult individuals of *Stegosaurus* (Upper Jurassic, USA; MAIN et al. 2005; HAYASHI et al. 2008, 2012). Instead it resembles the dermal spines of juvenile to young adult individuals of *Stegosaurus* and those of ankylosaurs in having a thin outer layer of compact bone bordering cancellous bone, with no well-defined central cavity (HAYASHI et al. 2010, 2012). Proximally this spine differs from those of nodosaurid ankylosaurs from the Upper Jurassic of the USA in which this surface is markedly concave (“hollow”) with smoothly rounded edges (KIRKLAND & CARPENTER 1994; KIRKLAND et al. 1998; GALTON 2016).

The cross-section of the broken end is roughly U-shaped (Fig. 1D), rather than sub-circular to oval (Fig. 1N), so the presumed posterior outline is indeterminate. Because the cited histology (Fig. 1D, E) matches that of a vertebral centrum, as does the morphology, R.6334 is re-identified as the half centrum of a caudal vertebra (Fig. 1B-F). The form of the articular end surface corresponds to that of a centrum and the oblique ventral surface (Fig. 1C) has facets for a chevron (Fig. 1B). In ventral view (Fig. 1F) the sides initially converge but then diverge, as do the sides of a centrum, rather than continuing to converge distally as on a stegosaurian dermal spine (Fig. 1L, M; GALTON 2016). The original length of this centrum was at least twice its height (Fig. 1C), quite unlike the proportionally short caudal centra of stegosaurs in which the height exceeds the length except in the most distal part of the tail (GILMORE 1914; ZHOU 1984). More elongate caudal centra occur in many groups of dinosaurs (WEISHAMPEL et al. 2004) and in marine crocodylomorphs (ANDREWS 1913), so this half centrum is tentatively identified as *Archosauria* indet.

NHMUK PV R.6336 (Fig. 1G-K): this is a ventrally incomplete vertebral centrum and, from the presence of a parapophysis anterodorsally (Fig. 1G-J), it is from a cervical vertebra. The centrum is slightly asymmetrical in ventral view and amphicoelous (gently concave at both ends), with the maximum anterior width greater than the length (Fig. 1G, H). Originally the centrum was low, being wider than high (Fig. 1G, J), and it probably came from the posterior part of the neck.

The Inferior Oolite Group (Middle Jurassic) of England is a marine deposit but the remains of marine reptiles from it are rather limited, consisting mostly of isolated bones and teeth of crocodylomorphs, plus fragments of ichthyosaurs, plesiosaurs and pliosaurs (BENTON & SPENCER 1985). These groups are very well represented in the more recent marine Peterborough Member of the Oxford Clay Formation (basal middle Callovian, Middle Jurassic) of Fletton near Peterborough, England (ANDREWS 1910, 1913). The crocodylomorphs do not have short cervicals. The ichthyosaurs have extremely short centra that are thick plate-like discs. Short wide cervical centra occur in some sauropterygians (plesiosaurs and pliosaurs) but the parapophysis is situated ventrally at mid-length, with the diapophysis sometimes fused to it dorsally (ANDREWS 1910, figs. 50, 51, pl. 3, fig. 4; ANDREWS 1913, figs. 17-19). The proportions of the caudal centra of some plesiosaurs, such as in some elasmosaurids (ANDREWS 1910, figs. 58, 85), resemble R.6336 in being wider transversely than long.

However, the base of the transverse process originates from the middle of the centrum that is longitudinally symmetrical in ventral view with paired chevron facets at both ends.

The most common terrestrial tetrapod remains from the English Inferior Oolite are isolated teeth and jaws of the tetanuran theropod dinosaur *Megalosaurus* (BENTON & SPENCER 1985). Only an incomplete cervical vertebra is described for *Megalosaurus bucklandii* (Middle Jurassic, Bathonian; BENSON 2010) from near Oxford, England. However, posterior cervicals are known for the megalosaurids *Eustreptospondylus* (Middle Jurassic, middle Callovian, England; SADLEIR et al. 2008) and *Torvosaurus* (Upper Jurassic, USA; BRITT 1987). In these taxa the cervical centra are very different from R.6336 (Fig. 1G-K), being very strongly opisthocoelous (articular surfaces strongly convex anteriorly and concave posteriorly) with well-developed lamellae bordering prominent lateral fossae or pleurocoels (side cavities) for pneumatic diverticular for extensions of the air sacs (BRITT 1997). Cervical vertebrae are not known for the ceratosaurian theropod *Sarcosaurus* (Lower Jurassic, England; ANDREWS 1921) but in the ceratosaurian *Dilophosaurus* (Lower Jurassic, USA; WELLES 1984) the centra are similar to those of megalosaurids but only weakly opisthocoelous. The same is true for the proportionally more elongate centra of the sauropod dinosaur *Cetiosaurus* (Middle Jurassic, Bajocian, England) in which the parapophysis is on the anteroventral corner and the fossae and lamellae are very prominent (UPCHURCH & MARTIN 2002).

As BRITT (1997) notes, the interior of the centra of most saurischian dinosaurs, i.e., theropods and sauropod sauropodomorphs, contain sizable cavities that were filled with marrow and fatty tissues or, if connected to the outside by a large pneumatic foramen, then with air as part of a pneumatic diverticulum. In underrived or camerate vertebrae, as occur in sauropods and non-tetanuran theropods (includes Ceratosauria, e.g., *Ceratosaurus* Upper Jurassic, USA; MADSEN 1976, fig. 26B), the walls are relatively thick with several large internal chambers. In derrived or camellate vertebrae, as occur in tetanuran theropods (most theropods, e.g., *Allosaurus*, Upper Jurassic, USA; MADSEN 1976, fig. 26A; includes Megalosauridae), the walls are thin with supernumerary, small internal chambers. However, the Dorset centrum shows no evidence of any internal cavities or lateral foramina (Fig. 1G, J), as is also true for all ornithischian dinosaurs including ornithomorphs (e.g., NHMUK PV R.2477, *Hypsilophodon*, Lower Cretaceous, England; HULKE 1882, pl. 76, fig. 2), basal thyreophorans (e.g., NHMUK PV R.1111, *Scelidosaurus*; Lower Jurassic, England; OWEN 1863, pl. 1, fig. 4), stegosaurs (e.g., NHMUK PV OC46013, *Dacentrurus*; OWEN 1875, pl. 22, fig. 1; GALTON 1985, fig. 3M), and ankylosaurs (*Europelta*, Lower Cretaceous, Spain; KIRKLAND et al. 2013, fig. 12).

The cervical centra of the ornithomorph dinosaur *Camptosaurus* (Upper Jurassic, England and USA) are longer than wide and weakly opisthocoelous (GILMORE 1909; GALTON & POWELL 1980), as is the cervical centrum of the small basal thyreophoran *Scutellostaurus*

Fig. 2. A-H – Centra of posterior cervical vertebrae of thyreophoran dinosaurs in anterior (A, C, E, G) and ventral (B, D, F, H) views: **A-D**, basal thyreophoran *Scelidosaurus harrisonii* (Lower Jurassic, England), **A-B**, NHMUK PV R.1111 and **C-D**, juvenile individual CAMSM X.39256; **E-F**, dacentrurine stegosaur *Miragaia longicollum* (Upper Jurassic, Portugal; may be *Dacentrurus longicollum*, see COBOS et al. 2010), ML 433; **G-H**, nodosaurid ankylosaur *Mymoorapelta maysi* (Upper Jurassic, USA), MWC. **I-M** – Thyreophoran left ulnae (I, L incomplete) in lateral view of: **I**, Eurypoda indet., SM 1977,1997.1, from middle Bajocian (Middle Jurassic) of Isle of Skye, Scotland; **J**, nodosaurid ankylosaur *Mymoorapelta maysi* (Upper Jurassic western USA); **K**, stegosaur *Stegosaurus sulcatus*, USNM V 4937 (Upper Jurassic, western USA) and **L-M**, basal thyreophorans from Lower Jurassic: **L**, *Scutellostaurus lawleri* from western USA and **M**, *Scelidosaurus harrisonii* from England, SGDS 1311, a cast of skeleton in collection of DAVID SOLE in England. **N** – Outline of track as left manus-pes couple preserved in reverse as positive hypichnia (natural casts, holotype EGSUS F00768) of stegosaurian ichnite taxon *Deltapodus brodricki* from Saltwick Formation (Middle Jurassic, Aalenian) near Whitby, Yorkshire, England. **O-V** – Upright dermal plates from the Chipping Norton Formation (basal *Parkinsonia convergens* subzone of Lower Bathonian) of the New Park Quarry in Longborough near Stow-on-the-Wold, Gloucestershire, England, the earliest skeletal record for the group, **O-R**, SDM 44.41 and **S-V**, NHMUK PV R.5938 in **O, R, S, U**, side (lateral or medial), **P, V**, proximal (basal, ventral), and **Q, T**, edge on (anterior or posterior) views. A, B modified from OWEN (1863), I from CLARK (2001), J reversed from KIRKLAND & CARPENTER (1994), L from COLBERT (1981), N from WHYTE & ROMANO (1995) and O, U from REYNOLDS (1939; for photographs see GALTON & POWELL 1983, pl. 1, figs. 12, 15; GALTON 1985, fig. 21P, T; LAMAX & TAMURA 2014, fig. 151A, B but for A rotate 135° so base is horizontal). Abbreviations: p, parapophysis; 1, 4, digits 1 and 4; scale lines = 10 mm (A-D, G, H, L), 25 mm (E, F), 50 mm (I, J, M) and 100 mm (K, N-U).

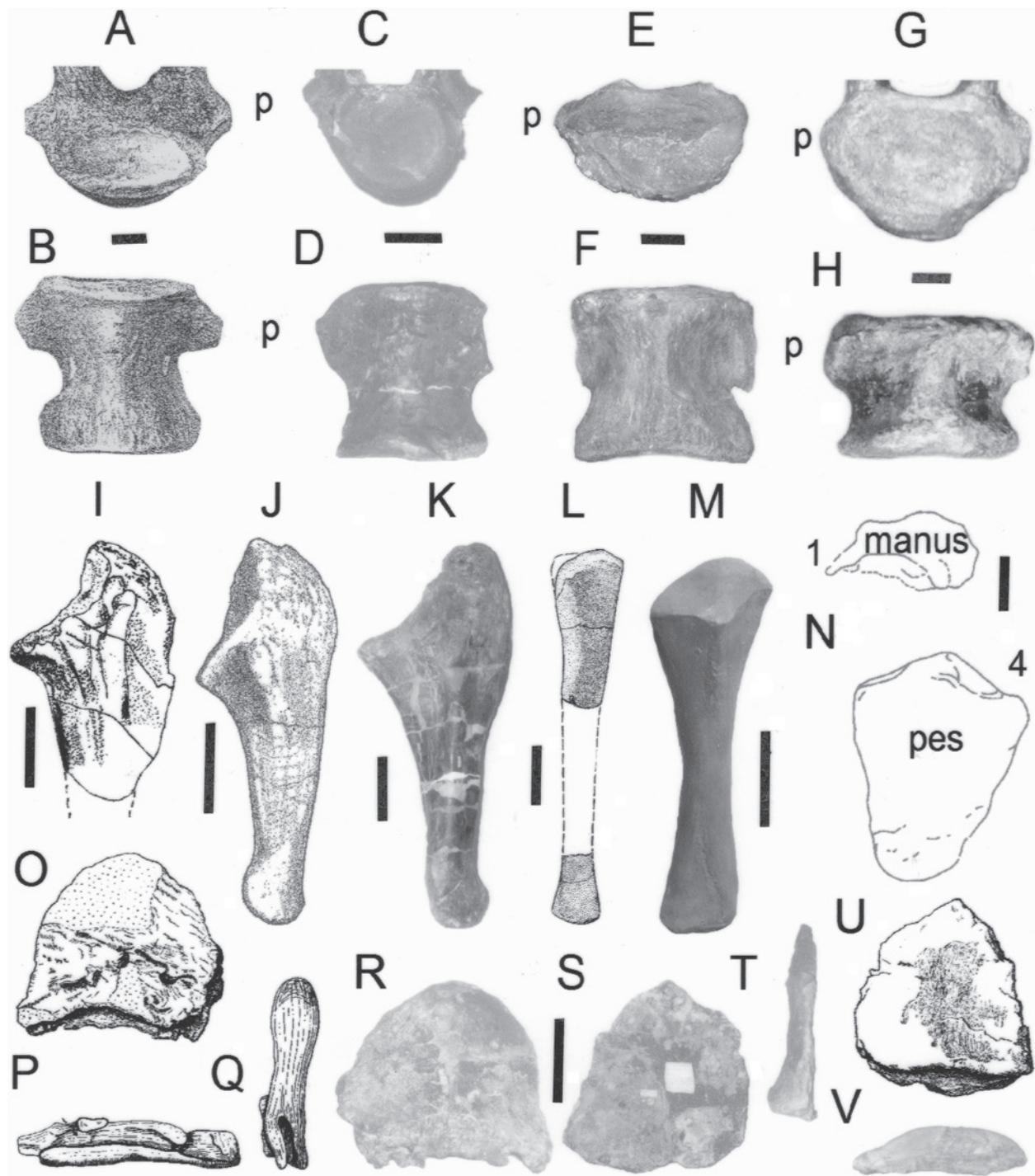


Fig. 2.

(Lower Jurassic, USA; COLBERT 1981, fig. 12A, B). For the large basal thyreophoran *Scelidosaurus harrisonii* (Lower Jurassic, England), OWEN (1863) illustrated the ?sixth cervical vertebra of the holotype in which the

centrum is wider than long (NHMUK PV R.1111; Fig. 2A, B). This vertebra cannot be located and most of the neck no longer exists (S. CHAPMAN, pers. comm. 2016). However, in the eighth cervical (cervicodorsal) centrum

of a partial skeleton of a juvenile individual (CAMSM X.39256; see LOMAX & TAMURA 2014, fig. 117), these dimensions are subequal (Fig. 2C, D; also true for CD 7, NORMAN, pers. comm. 2017). In the holotype of the stegosaur *Dacentrurus armatus* (Upper Jurassic, England) the dorsal centra are weakly amphicoelous, low and diagnostically wider than long (GALTON 1985). The posterior cervicals are not well preserved but those of *Dacentrurus lennieri* (Upper Jurassic, France) also have these proportions (NOPCSA 1911; GALTON 1991), as does cervical 16 of the dacentrurine *Miragaia longicollum* (Fig. 2E, F; Upper Jurassic, Portugal; MATEUS et al. 2009, ESM fig. S2, lower set for all five views; ?*Dacentrurus longicollum* of COBOS et al. 2010). These proportions are also present in the nodosaurid ankylosaur *Mymoorapelta maysi* KIRKLAND & CARPENTER, 1994 (Fig. 2G, H; Upper Jurassic, USA; cervical vertebrae recently recovered from type locality, KIRKLAND et al. 2010). The centra of these thyreophorans have a prominent rugose ventral keel (Fig. 2B, D, F, H) but this region is not preserved in the Dorset centrum (Fig. 1G, I-K) that, because of its proportions, is identified as *Thyreophora* indet.

3. Discussion

The large thyreophoran centrum NHMUK PV R.6336 (Fig. 1G-K) from the Aalenian-Bajocian (early Middle Jurassic, 174.1-168.3 Ma; ages from ICS 2015; see COHEN et al. 2013) of England predates the earliest bones of Stegosauria and Ankylosauria:

Earliest bones of Stegosauria: Very large (estimated original length ~1000 mm), columnar partial femoral shafts from the Upper Triassic (Rhaetian) of Avon, England were tentatively referred to the Stegosauria by GALTON (2005). However, REDELSTORFF et al. (2014) concluded that they are probably dinosaurian, as indicated by the presence of fibrolamellar bone, and represent an unknown lineage of the Sauropodomorpha or, alternatively, they represent an unknown pseudosuchian lineage that independently evolved fibrolamellar bone as an adaptation for reaching giant size.

Articulated skeletons of the basal stegosaur *Huayangosaurus taibaii* are from the Bathonian-Callovian (168-164 Ma) of China (ZHOU 1984; SERENO & DONG 1982; MAIDMENT et al. 2006). There are isolated remains from the Bathonian (168-166 Ma) of West Siberia, Russia (AVERIANOV & KRASNOLUTSKII 2009) and from the upper Bathonian of southern England (GALTON

& POWELL 1983; GALTON 1985; MAIDMENT et al. 2008: 384; LOMAX & TAMURA 2014, figs. 157D-F, 159, 160; incorrectly tabulated as *middle* Bathonian in ULANSKY 2014). Two large upright dermal plates from the Hook Norton Member of the Chipping Norton Formation (*Parkinsonia convergens* subzone at base of lower Bathonian; incorrectly tabulated as *middle* Bathonian in ULANSKY 2014) of Longborough near Stow-on-the-Wold in Gloucestershire, England were described by REYNOLDS (1939) as stegosaurian (Fig. 2O, U). HOFFSTETTER (1957) noted that these plates were more similar to those of Cretaceous ankylosaurs but they were described as stegosaurian by GALTON & POWELL 1983; also GALTON 1985; SDM 44.41, Fig. 2O-R; NHMUK PV R.5938, Fig. 2S-V; LOMAX & TAMURA 2014, fig. 151; maximum length, height and thickness in mm: 270, 335; 280, 275; 30-40, 50-60). MAIDMENT et al. (2008: 385) noted that “the plates are quite robust and have the plate-like spine morphology that is common to many genera of stegosaurs, including *Dacentrurus* (NHMUK PV OC46013 [GALTON 1985]), *Kentrosaurus* (MB [GALTON 1982]) and *Chungkingosaurus* (CV 206 [DONG et al. 1983]).” They referred the plates to Stegosauria gen. et sp. indet., so these represent the oldest skeletal record of the Stegosauria; a possible autapomorphy for one of the plates is the transverse swelling of its more distal part (Fig. 2Q).

Earliest bones of Ankylosauria. NATH et al. (2002) described jaw bones, a few vertebral centra, fragments of scapula and ilium, and dermal armor from the Lower Jurassic of southern India and referred this material to the Ankylosauria. However, the jaws are crocodylomorph and the rest of the bones represent a basal thyreophoran (see GALTON & CARPENTER 2016: 208). The mandible of *Sarcolestes leedsi* from the basal middle Callovian of Fletton near Peterborough, England (GALTON 1983) is recognized as the oldest valid genus but it is Ankylosauria *incertae sedis* (VICKARYOUS et al. 2004). *Tianchisaurus nedegoapeferima* DONG, 1993 (a *nomen dubium*, VICKARYOUS et al. 2004) may be older; it consists of a partial skeleton from the Middle Jurassic (Bathonian-Callovian; EBERTH et al. 2001) of China.

Earliest bones of Eurypoda. A massive proximal ulna (Fig. 2I; with proximal radius) from the Bearraig Sandstone Formation (middle Bajocian, early Middle Jurassic, 170.3-168.3 Ma) of Bearraig Bay near Staffin, Isle of Skye, Scotland (CLARK 2001; LOMAX & TAMURA 2014, fig. 147) is very similar to the ulnae of the nodosaurid ankylosaurs *Mymoorapelta maysi* (Fig.

2J; Upper Jurassic, USA; KIRKLAND & CARPENTER 1994; ulna length 200 mm) and *Sauropelta edwardsorum* (Lower Cretaceous, USA; OSTROM 1970; VICKARYOUS et al. 2004; ulna 445 mm, femur 765 mm). However, it is also similar to the ulna of *Stegosaurus unguatus* (Fig. 2K; Upper Jurassic, USA; GILMORE 1914; ulna 594 mm), so CLARK (2001) identified the Skye ulna more closely with the Eurypoda (Stegosauria + Ankylosauria) than with basal Thyreophora. The comparison for basal Thyreophora was made with the ulna of *Scutellosaurus lawleri* (Fig. 2L; Lower Jurassic, USA), but this is a small dinosaur (femur 114 mm, COLBERT 1981). Comparisons were not made with the much larger basal thyreophoran *Scelidosaurus harrisonii* (Lower Jurassic, England) because only the proximal end of the ulna is preserved in the holotype skeleton (OWEN 1863, pl. 3 as bone 33; femur 444 mm; skeleton LOMAX & TAMURA 2014, fig. 116A). However, the ulna is also slender in a referred skeleton (Fig. 2M; ulna ~190 mm; femur ~550 mm; skeleton in private collection of DAVID SOLE, see LOMAX & TAMURA 2014, fig. 119). This contrasts with the massiveness of the Skye ulna that still identifies more closely with the Eurypoda as per CLARK (2001). However, it is a *left* ulna, not a *right*, that is illustrated in medial and lateral views (CLARK 2001, fig. 2b, c; in lateral view fig. 3b and in fig. 4a along with other thyreophoran left, not right, ulnae as fig. 4b-e).

Earliest footprint record of Stegosauria. *Deltapodus brodricki* WHYTE & ROMANO, 1995, which was based on a supposed sauropod dinosaur trackway (Fig. 2N) from the basal Middle Jurassic (Aalenian, 174–170 Ma) of Yorkshire, England, was re-identified as representing the prints of a three toed stegosaur like *Stegosaurus* by WHYTE & ROMANO (2001, table 1 for details; for photographs *in situ* as preserved, see WHYTE & ROMANO 1993, fig. 3 for holotype, figs. 4, 7 for trackway; LOMAX & TAMURA 2014, figs. 130A, B, 131A, B). The quadrupedal trackway shows several distinctive characters, viz., for manus prints (m, Fig. 2N): arcuate (transversely wide so arc shaped), entaxonic (medial digits more strongly developed), pollex (digit I) print evident, and digit prints indistinct; for pes prints (pes, Fig. 2N): triangular with elongate heel, digitigrade, three very wide blunt digits not separated by well-developed hypicies (angles), weakly mesaxonic (digit III only slightly longer than II and IV), and toes radiating (WHYTE & ROMANO 2001; LI et al. 2012). These characters agree with the foot skeleton and anticipated footprints of a quadrupedal stegosaur such as *Stegosaurus* (see GILMORE 1914) and not with those of other potentially contemporaneous

dinosaurs (see WHYTE & ROMANO 2001, table 1). This referral is supported by subsequent studies (MILAN & CHIAPPE 2009; COBOS et al. 2010; MATEUS et al. 2011; PASCUAL et al. 2012; LI et al. 2012; XING et al. 2013; ROMANO & WHYTE 2015; LOCKLEY et al. 2017). As MATEUS et al. (2011: 656) noted, the “occurrence of *Deltapodus* in the Aalenian of England and its confirmation as a stegosaur implies an earlier cladogenesis for the Stegosauria, than the Bajocian or Bathonian age implied by the skeletal record.” This earlier origin is also true for the sister group, the Ankylosauria, with both groups probably originating sometime in the Early Jurassic at the latest.

Acknowledgments

For their assistance with specimens under their care, I thank M. BRETT-SURMAN (USNM) and especially S.D. CHAPMAN (NHMUK), who also provided information and arranged for specimens to be photographed by H. TAYLOR and J. JACKSON (NHMUK Image Resources; Fig. 1A-K). Other photographs were kindly supplied by J.D. HARRIS (Dixie State University, St. George, Utah, USA; Fig. 2M), J.I. KIRKLAND (Utah Geological Survey, Salt Lake City, USA; Fig. 2G, H), O. MATEUS (ML; Fig. 2E, F), and D.B. NORMAN (CAMSM; Fig. 2C, D). The copyright for all the photographs is retained by the housing institutions. The original MS benefitted from the constructive comments of K. CARPENTER (Utah State University – Eastern, Price, USA) and an anonymous reviewer and O. MATEUS.

References

- ANDREWS, C.W. (1910): A Descriptive Catalogue of the Marine Reptiles of the Oxford Clay. Based on the LEEDS Collection in the British Museum (Natural History), London. Part I. – xvii + 205 pp.; London (British Museum).
- ANDREWS, C.W. (1913): A Descriptive Catalogue of the Marine Reptiles of the Oxford Clay. Based on the LEEDS Collection in the British Museum (Natural History), London. Part II. – xix + 206 pp.; London (British Museum).
- ANDREWS, C.W. (1921): On some remains of a theropodous dinosaur from the Lower Lias of Barrow-on-Soar. – *Annals and Magazine of Natural History*, (9), 8: 570–576.
- AVERIANOV, A.O. & KRASNOLUTSKII, S.A. (2009): Stegosaur remains from the Middle Jurassic of West Siberia. – *Proceedings of the Zoological Institute of the Russian Academy of Sciences*, **313** (2): 153–167.
- BENSON, R.B.J. (2010): A description of *Megalosaurus bucklandii* (Dinosauria: Theropoda) from the Bathonian of the UK and the relationships of Middle Jurassic theropods. – *Zoological Journal of the Linnean Society of London*, **58**: 882–877.
- BENTON, M.J. & SPENCER, P.S. (1995): Fossil Reptiles of Great Britain. – *Geological Conservation Review Series*, **10** (4):

- 1-386.
- BRITT, B.B. (1987): Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic, Colorado), with emphasis on the osteology of *Torvosaurus tanneri*. – *Geology Studies of Brigham Young University*, **37**: 1-72.
- BRITT, B.B. (1997): Postcranial pneumaticity. – In: CURRIE, P.J. & PADIAN, K. (Eds.): *Encyclopedia of Dinosaurs*: 590-593; New York (Academic Press).
- CLARK, D.L. (2001): A thyreophoran dinosaur from the Early Bajocian (Middle Jurassic) of the Isle of Skye, Scotland. – *Scottish Journal of Geology*, **37** (1): 19-26.
- COBOS, A., ROYO-TERRES, R., LUQUE, L., ALCALÁ, L. & MAMPEL, L. (2010): An Iberian stegosaurs paradise: The Villard et Arzobispo Formation (Tithonian-Berriasian) in Teruel (Spain). – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **293**: 223-236.
- COHEN, K.M., FINNEY, S.C., GIBBARD, P.L. & FAN, J.-X. (2013): The ICS International Chronostratigraphic Chart. – *Episodes*, **36** (3): 199-204.
- COLBERT, E.H. (1981): A primitive ornithischian dinosaur from the Kayenta Formation of Arizona. – *Bulletin Series of the Museum of Northern Arizona Press*, **33**: vii + 61 pp.
- DONG, Z. (1993): An ankylosaur (ornithischian dinosaur) from the Middle Jurassic of the Junggar Basin, China. – *Vertebrata Palasiatica*, **31**: 258-266.
- DONG, Z.-M., ZHOU, S.-W. & ZHANG, X. (1983): [Dinosaurs from the Jurassic of Sichuan]. – *Palaeontologica Sinica*, **162** (C23): 1-151 (In Chinese with English summary).
- EBERTH, D.A., BRINKMAN, D.B., CHEN, P.-J., YUAN, F.-T., WU, S.-Z., GANG, I.Z. & CHENG, X.-S. (2001): Sequence stratigraphy, paleoclimate patterns and vertebrate fossil preservation in Jurassic-Cretaceous strata of the Junggar Basin, Xinjiang Autonomous Region, Peoples' Republic of China. – *Canadian Journal of Earth Sciences*, **38**: 1627-1644.
- GALTON, P.M. (1982): The postcranial anatomy of stegosaurian dinosaur *Kentrosaurus* from the Upper Jurassic of Tanzania, East Africa. – *Geologica et Palaeontologica*, **15**: 139-160.
- GALTON, P.M. (1983): Armored dinosaurs (Ornithischia: Ankylosauria) from the Middle and Upper Jurassic of Europe. – *Palaeontographica (A)*, **182** (1-3): 1-23.
- GALTON, P.M. (1985): British plated dinosaurs (Ornithischia, Stegosauridae). – *Journal of Vertebrate Paleontology*, **5** (3): 211-254.
- GALTON, P.M. (1991): Postcranial remains of the stegosaurian dinosaur *Dacentrurus* from the Upper Jurassic of France and Portugal. – *Geologica et Palaeontologica*, **25**: 299-327.
- GALTON, P.M. (2005): Bones of large dinosaurs (Prosauropoda and Stegosauria) from the Rhaetic Bone Bed (Upper Triassic) of Aust Cliff, southwest England. – *Révue de Paléobiologie*, **24** (1): 51-74.
- GALTON, P.M. (2012): Stegosauria. – In: BRETT-SURMAN, M.K., HOLTZ, T.R., Jr. & FARLOW, J.O. (Eds.): *The Complete Dinosaur* (2nd edition): 482-504; Bloomington (Indiana University Press).
- GALTON, P.M. (2016): Notes on plated dinosaurs (Ornithischia: Stegosauria), mostly on dermal armor from Middle and Upper Jurassic of England (also France, Iberia), with a revised diagnosis for *Loricatosaurus priscus* (Callovian, England). – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **282** (1): 1-25.
- GALTON, P.M. & CARPENTER, K. (2016): The plated dinosaur *Stegosaurus longispinus* GILMORE, 1914 (Dinosauria: Ornithischia; Upper Jurassic, western USA), type species of *Alcovasaurus* n. gen. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **279** (2): 185-208.
- GALTON, P.M. & POWELL, H.P. (1980): The ornithischian dinosaur *Camptosaurus prestwichii* from the Upper Jurassic of England. – *Palaeontology*, **23** (2): 411-443.
- GALTON, P.M. & POWELL, H.P. (1983): Stegosaurian dinosaurs from the Bathonian (Middle Jurassic) of England, the earliest record of the family Stegosauridae. – *Géobios*, **16** (2): 219-229.
- GALTON, P.M. & UPCHURCH, P. (2004): Stegosauria. – In: WEISHAMPEL, D.B., DODSON P. & OSMÓLSKA, H. (Eds.): *The Dinosauria* (2nd edition): 343-362; Berkeley (University of California Press).
- GILMORE, C.W. (1909): Osteology of the Jurassic reptile *Camptosaurus*, with a revision of the species of the genus, and a description of two new species. – *Proceedings of the United States National Museum*, **36**: 197-332.
- GILMORE, C.W. (1914): Osteology of the armoured Dinosauria in the United States National Museum, with special reference to the genus *Stegosaurus*. – *Bulletin of the United States National Museum*, **89**: 1-143.
- HAYASHI, S., CARPENTER, K., SCHEYER, T.M., WATABE, M. & SUZUKI, D. (2010): Function and evolution of ankylosaur dermal armor. – *Acta Palaeontologica Polonica*, **55** (2): 213-228.
- HAYASHI, S., CARPENTER, K., WATABE, M., MATEUS, O. & BARSBOLD, D. (2008): Defensive weapons of thyreophoran dinosaurs: histological comparisons and structural differences in spikes and clubs of ankylosaurs and stegosaurs. – *Journal of Vertebrate Paleontology*, **28** (Supplement to number 3): 89A-90A.
- HAYASHI, S., CARPENTER, K., WATABE, M. & McWHINNEY, L.A. (2012): Ontogenetic histology of *Stegosaurus* plates and spikes. – *Palaeontology*, **55** (1): 145-161.
- HOFFSTETTER, R. (1957): Quelques observations sur les stégosaurinés. – *Bulletin du Muséum National d'Histoire Naturelle, Paris*, **29**: 537-547.
- HULKE, J.W. (1882): An attempt at a complete osteology of *Hypsilophodon foxii*, a British Wealden dinosaur. – *Philosophical Transactions of the Royal Society of London*, **172**: 1035-1062.
- ICS (2015): International Commission on Stratigraphy: International Chronostratigraphic Chart v2015/01 – <http://www.stratigraphy.org/index.php/ics-chart-timescale>
- KIRKLAND, J.L., ALCALÁ, L., LOEWEN, M.A., ESPÍLEZ, E., MAMPEL, L. & WIERSMA, J.P. (2013): The basal nodosaurid ankylosaur *Europelta carbonensis* n. gen., n. sp. from the Lower Cretaceous (Lower Albian) Escucha Formation of northeastern Spain. – *PloS ONE*, **8** (12): e80405. DOI:10.1371/journal.pone.0080405
- KIRKLAND, J.I. & CARPENTER, K. (1994): North America's first pre-Cretaceous ankylosaur (Dinosauria) from the Upper Jurassic Morrison Formation of Western Colorado. – *Geology Studies of Brigham Young University*, **40**: 25-42.
- KIRKLAND, J.L., CARPENTER, K., HUNT, A.P. & SCHEETZ, R.D.

- (1998): Ankylosaur (Dinosauria) specimens from the Upper Jurassic Morrison Formation. – *Modern Geology*, **23**: 145-177.
- KIRKLAND, J.I., HUNT-FOSTER, R., FOSTER, J.R. & LOEWEN, M. (2010): Newly recovered skeletal elements of the Late Jurassic dinosaur *Mymoorapelta maysi* from its type locality in the Morrison Formation permits reevaluation of ankylosaur phylogeny. – *Journal of Vertebrate Paleontology* for 2010, Supplement: Program and Abstracts: 116A.
- LI, J., LOCKLEY, M.G., ZHANG, Y., HU, S., MATSUKAWA, M. & BAI, Z. (2012): An important ornithischian tracksite in the Early Jurassic of the Shenmu Region, Shaanxi, China. – *Acta Geologica Sinica*, **86** (1): 1-10.
- LOCKLEY, M., GIERLINSKI, G., MATTHEWS, N., KING, L., FOSTER, J. & CART, K. (2017): New dinosaur track occurrences from the Upper Jurassic Salt Wash Member (Morrison Formation) of southwestern Utah: Implications for thyreophoran trackmaker distribution and diversity. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **470**: 116-121.
- LOMAX, D.R. & TAMURA, N. (2014): *Dinosaurs of the British Isles*. – 414 pp.; Manchester (Siri Scientific Press).
- MADSEN, J.H., Jr. (1976): *Allosaurus fragilis*: a revised osteology. – *Bulletin of the Utah Geological and Mineralogical Survey*, **109**: xii + 50 pp.
- MAIDMENT, S.C.R. (2010): Stegosauria: a historical review of the body fossil record and phylogenetic relationships. – *Swiss Journal of Geosciences*, **103** (2): 199-210.
- MAIDMENT, S.C.R., NORMAN, D.B., BARRETT, P.M. & UPCHURCH, P. (2008): Systematics and phylogeny of Stegosauria (Dinosauria: Ornithischia). – *Journal of Systematic Palaeontology*, **6**: 367-407.
- MAIDMENT, S.C.R., WEI, G. & NORMAN, D.B. (2006): Redescription of the postcranial skeleton of the Middle Jurassic stegosaur *Huayangosaurus taibaii*. – *Journal of Vertebrate Paleontology*, **26** (4): 944-956.
- MAIN, R.P., RICQLÈS, A. DE, HORNER, J.R. & PADIAN, K. (2005): The evolution and function of thyreophoran dinosaur scutes: implications for plate function in stegosaurs. – *Paleobiology*, **31** (2): 291-314.
- MARSH, O.C. (1877): A new order of extinct Reptilia (Stegosauria) from the Jurassic of the Rocky Mountains. – *American Journal of Science*, (3) **14**: 513-514.
- MATEUS, O., MAIDMENT, S.C.R. & CHRISTIANSEN, N.A. (2009): A new long-necked “sauropod-mimic” stegosaur and the evolution of the plated dinosaurs. – *Proceedings of the Royal Society of London, (B)*, **276**: 1815-1821. DOI:10.1098/rspb.2008.1909
- MATEUS, O., MILAN, J., ROMANO, M. & WHYTE, M.A. (2011): New finds of stegosaur tracks from the Upper Jurassic Lourinhã Formation, Portugal. – *Acta Palaeontologica Polonica*, **56** (3): 651-658.
- MILAN, J. & CHIAPPE, L.M. (2009): First American record of the Jurassic ichnospecies *Deltapodus brodricki* and a review of the fossil record of stegosaurian footprints. – *Journal of Geology*, **117**: 343-348.
- NAISH, D. & MARTILL, D.M. (2008): Dinosaurs of Great Britain and the role of the Geological Society of London in their discovery: Ornithischia. – *Journal of the Geological Society of London*, **165**: 613-623.
- NATH, T.T., YADAGIRI, P. & MOITRA, A.K. (2002): First record of armoured dinosaurs from the Lower Jurassic Kota Formation, Pranhita Valley, Andhra Pradesh. – *Journal of the Geological Society of India*, **59**: 575-577.
- NOPCSA, F. (1911): *Omosaurus lennieri*, un nouveau dinosaurien du Cap de la Hève. – *Bulletin de Société Géologique de Normandie*, **30**: 23-42.
- OSTROM, J.A. (1970): Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Montana and Wyoming. – *Bulletin of the Peabody Museum of Natural History*, **35**: 1-234.
- OWEN, R. (1863): A monograph on the fossil Reptilia of the Liassic formations. Part II. A monograph of a fossil dinosaur (*Scelidosaurus harrisonii*) of the Lower Lias. – *Palaeontographical Society Monographs*, **14**: 1-26.
- OWEN, R. (1875): A monograph on the fossil Reptilia of the Mesozoic formations: part two. (Genera *Bothriospondylus*, *Cetiosaurus*, *Omosaurus*). – *Palaeontographical Society Monographs*, **29**: 15-94.
- PARRINGTON, F.R. & WESTOLL, T.S. (1974): DAVID MEREDETH SEARES WATSON. 1886-1973. – *Biographical Memoirs of Fellows of the Royal Society of London*, **20**: 482. (<http://dx.doi.org/10.1098%2Frsbm1974.0021>)
- PASCUAL, C., CANUDO, J.I., HERNANDEZ, N., BARCO, J.L. & CASTANERA, D. (2012): First record of stegosaur dinosaur tracks in the Lower Cretaceous (Berriasian) of Europe (Oncala Group, Soria, Spain). – *Geodiversitas*, **34** (2): 297-312.
- REDELSTÖRFF, R., SANDER, P.M. & GALTON, P.M. (2014): Unique bone histology in partial large bone shafts from Upper Triassic of Aust Cliff, England: An early independent experiment in gigantism. – *Acta Palaeontologica Polonica*, **59** (3): 607-615.
- REYNOLDS, S.H. (1939): On a collection of reptilian bones from the Oolite of Stow-on-the-Wold, Gloucestershire. – *Geological Magazine*, **76**: 193-214.
- ROMANO, M. & WHYTE, M.A. (2015): Could stegosaurs swim? Suggestive evidence from the Middle Jurassic tracksite of the Cleveland Basin, Yorkshire, UK. – *Proceedings of the Yorkshire Geological Society*, DOI: 10.1144/pygs2015-354
- SADLEIR, R., BARRETT, P.M. & POWELL, H.P. (2008): The anatomy and systematics of *Eustreptospondylus oxoniensis*, a theropod dinosaur from the Middle Jurassic of Oxfordshire, England. – *Palaeontographical Society Monographs*, **160** (627): 1-82.
- SERENO, P.C. & DONG, Z. (1992): The skull of the basal stegosaur *Huayangosaurus taibaii* and a cladistic analysis of Stegosauria. – *Journal of Vertebrate Paleontology*, **12** (3): 318-343.
- ULANSKY, R.E. (2014): Dinosaur classification. Basal Thyreophora & Stegosauria. – *Dinologia*, 8 pp.
- UPCHURCH, P. & MARTIN, J. (2002): The Rutland *Cetiosaurus*: the anatomy and relationships of a Middle Jurassic British sauropod dinosaur. – *Palaeontology*, **45** (6): 1049-1074.
- VICKARYOUS, M.K., MARYAŃSKA, T. & WEISHAMPEL, D.B. (2004): Ankylosauria. – In: WEISHAMPEL, D.B., DODSON, P. & OSMÓLSKA, H. (Eds.): *The Dinosauria* (2nd edition): 363-392; Berkeley (University of California Press).
- WEISHAMPEL, D.B., DODSON, P. & OSMÓLSKA, H. (2004): *The Dinosauria* (2nd edition): xviii + 861 pp.; Berkeley (Uni-

- versity of California Press).
- WELLES, S.P. (1984): *Dilophosaurus wetherilli* (Dinosauria, Theropoda) osteology and comparisons. – *Palaeontographica*, (A), **185** (4-6): 85-180.
- WHYTE, M.A. & ROMANO, M. (1993): Footprints of a sauropod dinosaur from the Middle Jurassic of Yorkshire. – *Proceedings of the Geologists' Association*, **104**: 195-199.
- WHYTE, M.A. & ROMANO, M. (1995): Probable sauropod footprints from the Middle Jurassic of Yorkshire, England. – *Gaia*, **10**: 15-26.
- WHYTE, M.A. & ROMANO, M. (2001): Probable stegosaurian dinosaur tracks from the Saltwick Formation (Middle Jurassic) of Yorkshire, England. – *Proceedings of the Geologists' Association*, **112**: 45-54.
- XING, L., LOCKLEY, M.G., MCCREA, R.T., GIERLINSKI, G.D., BUCKLEY, L.G., ZHANG, J., QI, L. & JIA, C. (2013): First record of *Deltapodus* tracks from the Early Cretaceous of China. – *Cretaceous Research*, **42**: 55-65.
- ZHOU, S. (1984): [The Middle Jurassic dinosaurian fauna from Dashanpu, Zigong, Sichuan, Volume 2: Stegosaur]. – 52 pp.; Sichuan (Sichuan Scientific and Technological Publishing House) (In Chinese with English summary).

Manuscript received: March 25th, 2016.

Revised version accepted by the Stuttgart editor: May 11th, 2017.

Address of the author:

Dr. PETER M. GALTON, Professor Emeritus, University of Bridgeport, Bridgeport, Connecticut, USA; Curatorial Affiliate, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA. Present address: 1065 Vintage Drive, Rio Vista, California 94571, USA; e-mail: pgalton@bridgeport.edu