Revue de Paléobiologie, *Genève* (janvier 2023) 42 (1): 129-141 ISSN 0253-6730

A sternal bone of plated ornithischian dinosaur *Stegosaurus* (Upper Jurassic, Utah), the first for Stegosauria, and the enigmatic "sternal bones" of Gilmore (1914)

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Abstract

Associated with a right scapula-coracoid of *Stegosaurus* from the Morrison Formation (Upper Jurassic) of the Carnegie Quarry, Dinosaur National Monument, Utah, is a right sternal bone, so identified by comparison with sternals of other ornithischian dinosaurs. Comparisons show that the three "sternal bones" of *Stegosaurus* identified by Gilmore (1914) from the Morrison of Como Bluff, Wyoming do not match sternals of any dinosaur. They are tentatively re-identified as the anterior half of the right ischium of a nodosaurid ankylosaurian dinosaur and a right and a left proatlas from a very large sauropod dinosaur. A sternal bone from the Cleveland-Lloyd Dinosaur Quarry, Utah is from a large non-*Camptosaurus,* non-*Dryosaurus* Morrison ornithopod dinosaur.

Keywords

Dinosauria, Ornithischia, *Stegosaurus*, Ornithopoda, Ankylosauria, Sauropoda, Upper Jurassic, USA, osteology.

1. INTRODUCTION

Stegosauria Marsh, 1877 is a clade of quadrupedal graviportal herbivorous ornithischian dinosaurs with a bizarre array of vertical dermal plates and distal tail spines. This armor extended out dorsally and slightly laterally from close to the midline along the top of the body from the neck to the end of the tail. The group is known from the Middle Jurassic to the Late Cretaceous and from all continents except Australia and Antarctica (Olshevsky & Ford, 1995; Galton & Upchurch, 2004; Maidment *et al*., 2008; Galton, 2012; Paul, 2016). The best known genus is *Stegosaurus* Marsh, 1877 from the Morrison Formation (Late Jurassic, Kimmeridgian-Tithonian; Trujillo & Kowallis, 2015) of western USA. The very incomplete holotype skeleton (YPM VP 1850) of *Stegosaurus armatus* Marsh, 1877 from Morrison, Wyoming remained unfigured until it was described by Carpenter & Galton (2001). Galton (2010) suggested that *S. stenops* Marsh, 1887, based on the almost complete and only slightly disarticulated holotype skeleton USNM V 4934 (see Gilmore, 1914; Galton, 2020) from Garden Park near Cañon City, Colorado, would make a much better neotype species for *Stegosaurus* Marsh, 1877. Galton (2011) petitioned for this change which was accepted by the International Commission on Zoological Nomenclature (ICZN, 2013).

Field parties of Professor Othniel Charles Marsh (1831-1899) from the Peabody Museum of Natural History of Yale College in New Haven, Connecticut, USA, excavated dinosaur bones from the Morrison Formation (Upper Jurassic). They worked from 1877 to 1889 in western USA, including near Morrison and in Garden Park near Cañon City in Colorado and at Como Bluff in eastern Wyoming (Schuchert & LeVene, 1940; Ostrom & McIntosh, 1999; Galton, 2020; Foster, 2020). YPM Quarry 13 was one of the most productive quarries at Como Bluff as regards to ornithischian dinosaurs (Foster, 2020, faunal list p. 466), with the excavation of at least 14 individuals of *Stegosaurus* (Gilmore, 1914, 1918; Galton, 2020) and 17 of the large bipedal ornithopod dinosaur *Camptosaurus* (Foster, 2020; see Gilmore, 1909, 1912). The quarry is in the upper part of the lower or Salt Wash Member equivalent (Turner & Peterson, 1999, as WY-46 in fig. 7; 156 Ma, Carpenter & Wilson, 2008) near the eastern end of Como Bluff (East Como Ridge, now Pine Tree Ridge) in Albany County, Wyoming (Ostrom & McIntosh, 1999, fig. 3). The maps of the excavations by Fred Brown were compiled into a single map by Gilmore (1914, fig. 2, pl. 37; bone identifications pp. 5-24).

Submitted February 2022, accepted June 2022
Editorial handling: L. Cavin
DOI: 10.5281/zenodo.7446065

Gilmore (1914, 1918) described and illustrated the bones of *Stegosaurus* from Garden Park and Como Bluff.

A large number of dinosaur bones, many as articulated skeletons representing a variety of different genera, were excavated from the Morrison Formation at the Carnegie Quarry of Dinosaur National Monument in Vernal, eastern Utah (McIntosh, 1977; McGinnis, 1982; Carpenter, 2013; Foster, 2020). These include skeletons that are mounted at the Carnegie Museum in Pittsburgh of the sauropods *Apatosaurus, Camarasaurus* and *Diplodocus*, the theropod *Allosaurus*, the ornithopods *Camptosaurus* and *Dryosaurus*, and *Stegosaurus* (McGinnis, 1982). About 2000 bones were left in place and prepared in relief on the 67 degrees inclined bedding plane, which forms a cliff that is surrounded by a permanent exhibition building. The dinosaur bones on the cliff include those of *Stegosaurus* (see Galton, 2020 for dermal armor) with bones from a minimum of 10 individuals based on the number of right scapulae (Esplin, 2017). As discussed in detail by Carpenter & Wilson (2008, fig. 2), preliminary indications suggest that the bones from YPM Quarry 13 at Como Bluff in Wyoming are significantly older (>156 Ma) than those on the Colorado Plateau including DINO (150.91±0.43 Ma ~1 m below quarry, Trujillo & Kowallis, 2015).

A right sternal bone is described in association with a right scapula and coracoid of *Stegosaurus* (Figs 1A, B) from the Carnegie Quarry. This throws doubt on the identification by Gilmore (1914: 65-66, figs 32, 33) of a very different looking isolated bone (Figs 2A-G) from YPM Quarry 13 at Como Bluff as a sternal bone of *Stegosaurus*.

MUSEUM ABBREVIATIONS

AMNH, American Museum of Natural History, New York, USA; **CEUM**, Prehistoric Museum, Utah State University Eastern (formerly College of Eastern Utah Museum), Price, Utah, USA; **CM**, Carnegie Museum, Pittsburgh, Pennsylvania, USA; **DINO CL**, specimens on cliff of Carnegie Dinosaur Quarry at Dinosaur National Monument, Vernal, Utah, USA; **DNM**, original specimen numbers for bones at DINO; **HMN**, Humboldt Museum fur Naturkunde, Berlin, Germany; **IGM**, Institute of Geology, Mongolian Academy of Sciences, Ulaan Baatar, Mongolia; **ISI,** Indian Statistical Institute, Calcutta, India; **KUVP**, Kansas University, Vertebrate Paleontology, Lawrence, Kansas, USA; **MWC**, Museum of Western Colorado, Grand Junction, Colorado, USA; **NHMUK,** Natural History Museum, London, UK; **SMA**, Sauriamuseum Aathal, Switzerland; **UMNH**, Utah Museum of Natural History, Salt Lake City, Utah, USA; **UO**, University of Oklahoma, Norman, Oklahoma, USA: **USNM**, National Museum of Natural History (formerly United States National Museum) of the Smithsonian Institution, Washington DC, USA; **UUVP**, University of Utah, Vertebrate Paleontology, specimens now catalogued in UMNH; and **YPM VP**, Division of Vertebrate Paleontology, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA.

Fig. 1: Sternal bones of ornithischian dinosaurs. **A-B,** *Stegosaurus* sp. from Morrison Formation (Upper Jurassic) of the Carnegie Quarry at Dinosaur National Monument, Vernal, Utah, A, incomplete right scapula and coracoid DINO CL 4357 (was DNM CL731) in lateral view with sternal bone DINO CL4349 (was DNM 723) in dorsal view and B, right sternal bone DINO CL 4349 in dorsal view. **C-D,** nodosaurid ankylosaurs from Lower Cretaceous of western USA, C, *Silvisaurus condrayi* from Kansas, left sternal bone KUVP 10296 in dorsal (visceral) view. D, *Gastonia burgei* from Utah, sternal plate CEUM 1495 in dorsal (visceral) view. **E-U,** ornithopod dinosaurs, E-K, Ankylopollexia, E-H, *Camptosaurus* sp. from Morrison Formation of Cleveland-Lloyd Dinosaur Quarry, Utah, right sternal plate UMNH VP 16497 (was UUVP 5701) in E, dorsal; F, medial; G, ventral and H, lateral views; I-K, *Camptosaurus dispar*, right sternal bone from YPM Quarry 13 at Como Bluff, Wyoming, USNM V 5473 in I, lateral; J, ventral and K, posterior views. L, left sternal plate of *Tenontosaurus* from Lower Cretaceous of Wyoming, UO 11, in ventral view. M-N, *Camptosaurus dispar* from Morrison Formation (Upper Jurassic) of YPM Quarry 13 at Como Bluff, Wyoming, YPM VP 1880 (part of holotype of *C. medius* Marsh, 1894) in M, ventral and N, dorsal (visceral) views. O-P, large non-*Camptosaurus,* non-*Dryosaurus* ornithopod, left sternal bone from Cleveland-Lloyd Dinosaur Quarry, Wyoming, UMNH VP 16493 (was UUVP 4822), in O, dorsal and P, ventral views. Q-R, *Iguanodon* from Lower Cretaceous of Belgium, Q, *I. atherfieldensis*, right sternal bone in ventral view and R, *I. bernisartensis*, sternal region as preserved in ventral view. S, *Hypsilophodon foxii* from Lower Cretaceous of England, NHMUK VP R196, sternum as preserved in dorsal view with associated left sternal ribs. T-U, hadrosaurid *Anatosaurus annectens* from Upper Cretaceous of Wyoming, left sternal bone in T, dorsal and U ventral views. The correctness of the apposition of the medial edges is shown by the articulated sternal plates of the mummified skeleton of *A. annectens*, AMNH FARB 5060 (Osborn, 1912, fig. 1, pl. 5). Abbreviations: co, coracoid; iso, intersternal ossification; ste, sternal bone; 1-4, sectioned left dorsal ribs or associated sternal ribs in ventral view. C from Carpenter & Kirkland (1998), D from Kinneer *et al.* (2016), I-L from Dodson & Madsen (1981), Q from Norman (1980), R from Norman & Weishampel (1990), S from Galton (1974) and T, U from Marsh (1896), scale bars = 10 cm (A, B, R, T-U), 5 cm (C-Q), and 1 cm (S).

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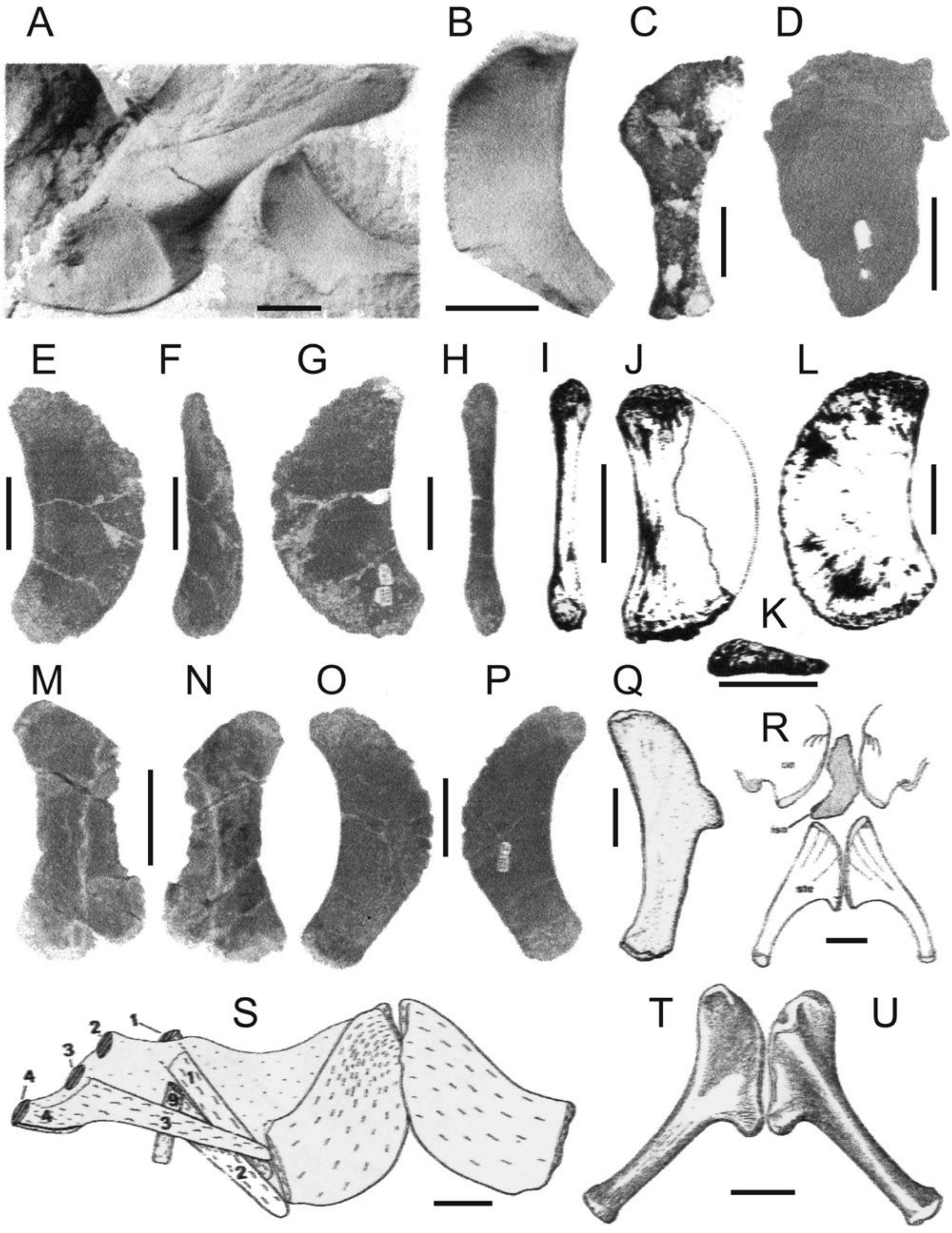
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2. RESULTS

2.1. Sternal bones of *Stegosaurus* from Carnegie Quarry, Utah

An incomplete and fused right scapula and coracoid (DINO CL4357, was DNM 0731; Fig. 1A) of *Stegosaurus* are preserved in lateral view at the top of the quarry face near the eastern end (in Sector G-1). Jim Adams (1976 pers. comm. from his index card catalogue) noted that the postero-ventral part of the scapula (length ~785 mm) and the posterior part of the coracoid are missing. The antero-dorsal margin of the blade of the scapula is overlain by rock and then by a bone (DINO CL4349, was DNM 0723) identified as the ischium of the sauropod dinosaur *Camarasaurus*. However, comparisons of this bone (Figs 1A, B) with figures of the ischium of *Camarasaurus* (Ostrom & McIntosh, 1999, pl. 68 for YPM VP 1905 as *Morosaurus*) show that this bone is not the ischium of a sauropod or, for that matter, any other bone of a sauropod (see Ostrom & McIntosh, 1999, pls 1-90; Tschopp & Mateus, 2012). From comparisons with the sternal bones of other dinosaurs - ornithischians (Figs 1C-U), sauropods (Figs 3B-G) and theropods - DINO CL4349 (Fig. 1B) is tentatively identified as a right sternal plate of *Stegosaurus* in dorsal (visceral) view. The sub-rectangular shaped proximal region is gently concave both antero-posteriorly and transversely with a thickened and rugose anterior edge, which becomes thin but still rugose on the medial part. This region corresponds to most of the sternal plate in *Camptosaurus*, *Tenontosaurus* and *Hypsilophodon* (Figs 1B, E, G, J, L-N, S). The rounded, smooth and gently concave lateral edge continues onto the postero-laterally directed process that is strongly developed in *Iguanodon* and hadrosaurids (Figs 1Q, R, T, U).

2.2. "Sternal bones of *Stegosaurus*" from Como Bluff, Wyoming

Gilmore (1914: 65-66, figs 32.1, 2; see Figs 2B, D) identified and described USNM V 7620 (Figs 2A-G, L) from the Morrison Formation of YPM Quarry 13 at Como Bluff as a sternal bone of *Stegosaurus*. He noted that the wide anterior end (Figs 2A, B, D-F, identified by comparisons with the sternal bone of the hadrosaurid dinosaur *Anatosaurus* as *Trachodon,* Figs 1T, U), "is truncated with a comparatively thin but roughly rugose border. On the inner side the anterior third presents a thickened area which looks upward and inward (Figs 2D-G) and doubtless represents the median union of the plates of opposite sides (Figs 2L, M). The ventral surface is slightly convex transversely (Figs 2A, B), and the dorsal or visceral surface is concave (Figs 2D, E). Both surfaces are comparatively smooth with the exception of roughened areas (r, Figs 2B, C) which probably represent the points of attachment of the sternal ribs. The outer border is somewhat thickened and rounded (Fig. 2C), while the inner thins out to a sharp edge (Fig. 2G). Both borders are slightly concave from end to end. Articulated, the broad truncated ends probably meet the anterior (*sic*., posterior) border of the coracoids, and the elements of opposite sides join on the median line (Figs 2L, M) at the thickened and rugose surface described above. The pointed ends would be directed backward and outward (Figs 2L, M) as in *Trachodon* (now *Anatosaurus*, Figs 1T, U). Although these bones were found widely separated in the quarry and none of the three can be definitely associated with any of the surrounding specimens, yet a comparison of these elements with those of *Trachodon* (now *Anatosaurus*, compare Figs 2B, D, L, M with Figs 1T, U) show such close general resemblances that there appears to be but little doubt of their correct identification." Although not mentioned, this bone is a left (Figs 2B, D, L). Gilmore (1914: 66) gave the maximum

Fig. 2: **A-M,** bones of *Stegosaurus* sp. from Morrison Formation (Upper Jurassic), YPM Quarry 13, Como Bluff, Wyoming, identified by Gilmore (1914) as: A-G, a left sternal bone USNM V 7620 (bone #d7b157) and H-K, a right sternal bone USNM V 7619 (#d7b121) in ventral (A, B, H), lateral (C, K), dorsal (D, E, J) and anterior (F) views. L-M, sternal bone USNM V 7620 (L) and USNM V 7618 (M) in dorsal view in pose suggested by Gilmore (1914, fig. 33); **N-Q,** same bones restored in ventral view with USNM V 7620 as a left proatlas (O) and as a right proatlas (P). If USNM V 7620 may be a right proatlas (see text), in which case these bones are in dorsal (A, B, H), lateral (C, K), ventral (D, E, J), anterior (F) and medial (G, I) views. **R-V,** USNM V 7619, right sternal bone of Gilmore (1914) reidentified as a right ischium of a nodosaurid ankylosaurian dinosaur in R, medial; S, anterior; T, V, lateral and U, posterior views. **W-A'**, right ischia (W, X, Z as left in reverse) in lateral view of nodosaurid (W-Y) and ankylosaurid (Z, A') ankylosaurian dinosaurs: W, *Mymoorapelta* from Morrison Formation (Upper Jurassic) of Colorado, MWC 4027; X, *Edmontonia* from Upper Cretaceous of Montana, USNM V 11868; Y, *Gastonia burgei* from Lower Cretaceous of Utah, CEUM 5351, ischium of *G. lorriemcwhinneyae* from same bone bed is extremely similar to that of *Edmontonia* (Fig. 1X; see Kinneer *et al*., 2016, fig. 16J); Z, *Saichania* from Upper Cretaceous of Mongolia, IGM 100/1305 and A', *Ankylosaurus* from Upper Cretaceous of Montana, AMNH FARB 5214. Abbreviation: a, medial wall of acetabulum; i, iliac peduncle with facet for ilium; p, pubic peduncle with facet for pubis; r, articulation area for sternal parts of most anterior dorsal ribs; s, rugose sutural area. B, D from Gilmore (1914), X from Gilmore (1930), Y from Kinneer *et al.* (2016), Z from Carpenter *et al.* (2011), A' from Coombs & Maryanska, 1990; scale bars = 5 cm (A-V) and 10 cm (W-A').

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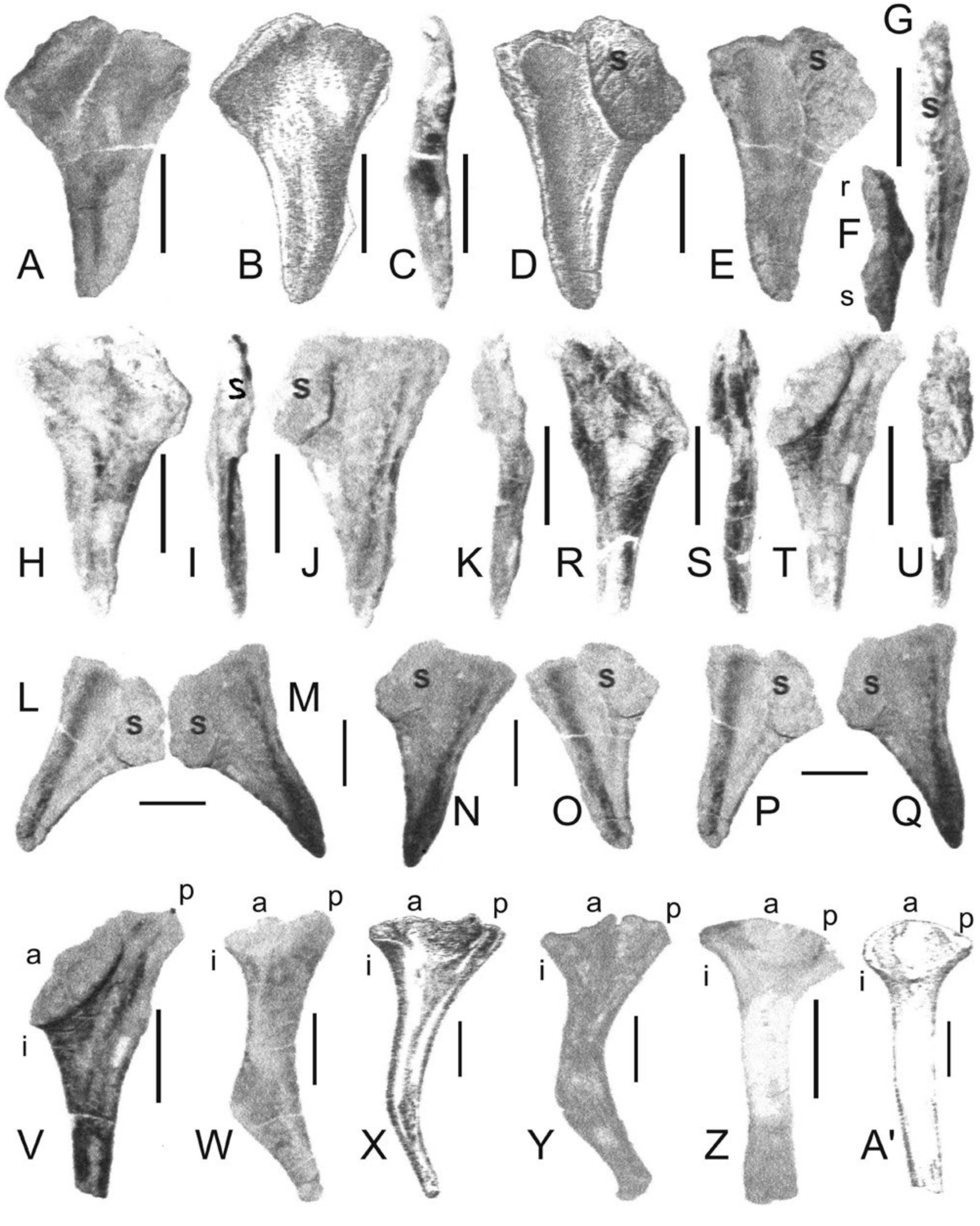
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length and transverse width of USNM V 7620 as 156 and 65 mm, with the corresponding measurements for two slightly larger but less well preserved and undescribed right sternal bones (USNM V 7618, Figs 1H-K, M and USNM V 7619, Figs 1R-V), as 170 and 85 mm and 178 and ? mm. USNM V 7620 is bone 157 from diagram 7, with V 7619 as bone 124, whereas V 7618 is bone 99 from diagram 5 (see Gilmore, 1914: 13, 17, 18, fig. 2, pl. 37).

Apart from differences in preservation, the result of a slight amount of crushing, the right sternal bone (USNM V 7618, Figs 2H-K, M) is very similar to the slightly smaller left one (Figs 2A-G, L) described by Gilmore (1914). Consequently, they are arranged as a pair in dorsal (visceral) view (Figs 2L, M), in a pose that matches those of the hadrosaurid *Anatosaurus* (Figs 1T, U), as suggested by Gilmore (1914, fig. 33).

From comparisons with the sternal bones of dinosaurs (see Section 6) – ornithischians (Fig. 1), sauropods (Figs 3B-G) and theropods – it is evident that the identification of these two bones from Quarry 13 (Figs 2A-M) as sternals is probably incorrect. In dorsal or ventral views (Figs 2B, D, H, K-M) these supposed sternals differ from those of other ornithischian dinosaurs in being roughly triangular in shape, tapering distally and twisting slightly to end in a blunt point. An additional difference is the presence of a large rugose sutural area antero-medially on the dorsal surface (s, Figs 2L, M). This area was illustrated (Fig. 2D) but not mentioned by Gilmore (1914), and it is not present on any sternal bone.

2.3. Ischium of ankylosauria

USNM V 7619, which differs from the other two bones identified by Gilmore (1914) as sternal bones (cf. Figs 2R-V with Figs 2A-M), is possibly the anterior half of the right ischium of a nodosaurid ankylosaurian dinosaur (cf. Figs 2W-Y). In particular, the slightly eroded anterior end (p, Fig. 2V) is identified as the pubic peduncle, the anterior surface of which would have sutured with the pubis. Posterior to this is the posterior part of the medial wall of the acetabulum and then the iliac peduncle for articulation with the ilium (a, i, Fig. 2V). For comparisons, figures are given of the right ischium for the nodosaurids *Mymoorapelta* (Fig. 1W, Morrison Formation, Colorado, Kirkland *et al*., 1998; ischium not known for *Gargoyleosaurus* from Morrison of Utah, Kilbourne & Carpenter, 2005), *Edmontonia* (Fig. 1X, Upper Cretaceous of Montana, Gilmore, 1930; ischium of *Gastonia lorriemcwhinneyae* from Lower Cretaceous of Utah is extremely similar, see Kinneer *et al*., 2016, Figs 16G-K), and *Gastonia burgei* (Fig. 2Y, Lower Cretaceous, Utah; Kinneer *et al*., 2016). Figures of the right ischium of ankylosaurid ankylosaurians, in which the anterior end is not obliquely inclined to the long axis of the bone and there is no bend at mid-shaft as in nodosaurids (Figs 2W-Y), are given for *Saichania* (Fig. 2Z; Upper Cretaceous, Mongolia) and *Ankylosaurus* (Fig. 2A', Upper Cretaceous, Alberta.

2.4. Sternal bones of other dinosaurs

2.4.1. Ornithopoda

The numerous remains of the large ornithopod dinosaur *Camptosaurus dispar* are known from YPM Quarry 13 in the Morrison at Como Bluff (Gilmore 1909, 1912), being the other abundant dinosaur with 17 individuals represented versus 14 for *Stegosaurus* (Foster, 2020). However, the sternal plates of *Camptosaurus dispar* were unknown until described by Dodson & Madsen (1981). The sternal bone of USNM V 5473 (Figs 1I-K) comes from YPM Quarry 13 at Como Bluff, as does that of YPM VP 1880 (Figs 1M, N), part of the holotype of *Camptosaurus medius* Marsh, 1894. These bones with lengths of 176 and 139 mm are comparable in size to USNM V 7620 at 155 mm (Figs 2A-G) but the form is very different (cf. Figs 2A-N with Figs 1E-K, also Figs 1M, N), whereas that of DINO CL4349 (Fig. 1B) is similar.

A more complete sternal plate of *Camptosaurus* (UMNH VP 16497, was UUVP 5701, Figs 1E-H) was described by Dodson & Madsen (1981, fig. 4A) from the Morrison of the Cleveland-Lloyd Dinosaur Quarry (CLDQ) in central Utah (Miller *et al*., 1996). The sternal bone of *Camptosaurus dispar* (Figs 1E-K, M, N) is a mostly a thin plate with a gently convex ventral surface and a gently concave dorsal or visceral surface. The thick anterior and posterior ends are rugose, the convex lateral border is thick and smooth, and most of the edge of the thin convex medial border is rugose.

A left sternal plate (Figs 1O, P; UMNH VP 16497, was UUVP 4822) from the CLDQ was incorrectly identified as a right and as probably that of *Camptosaurus* by Dodson & Madsen (1981, fig. 4B, inverted). When correctly orientated, there is a short postero-lateral process on this left sternal bone that resembles the much longer one, the handle of the hatchet-shaped sternal bone of *Iguanodon* (Figs 1Q, R; Norman, 1980) and hadrosaurids (Figs 1T-U). The sternal bones of *Dryosaurus* (CM 11340), the other large Morrison ornithopod, are similar to those of *Camptosaurus* (see Gilmore, 1925; Carpenter, 1994; also Janensch, 1955, fig. 33 for dryosaurid *Dysalotosaurus*, Upper Jurassic, Tanzania; for discussion as a probable junior synonym of *Dryosaurus,* see Carpenter & Lamanna, 2015). Consequently, this sternal bone (Figs 1O, P) probably indicates the presence of another large ornithopod in the Morrison that is distinct from *Camptosaurus* and *Dryosaurus*.

Sternal bones are preserved in several ornithopods from the Lower Cretaceous such as *Hypsilophodon* (Fig. 1S, England; preserved in articulation with the sternal ribs of both sides, Galton, 1974, figs 37A-E), *Tenontosaurus* (Fig. 1L; Wyoming; Ostrom, 1970; Dodson & Madsen, 1981, figs 1A, 2A, B), *Ouranosaurus* (sternal bone similar to *Iguanodon*, Niger; Taquet, 1976, fig. 49), and *Iguanodon* (Figs 1Q, R; Belgium; preserved in articulation with coracoids, Norman, 1980, figs 54-56, 1986, figs 45, 46). The ornithopod sternal bones illustrated (Figs 1E-U) show various degrees of similarity to the sternal bone DINO CL4349 (Fig. 1B) but none to the Quarry 13 bones (Figs 2A-M).

2.4.2. Ankylosauria

Several genera of nodosaurid ankylosaurs are known from the Upper Jurassic including *Dracopelta* from Portugal (Galton, 1980; Russo & Mateus, 2021) and the Morrison genera *Gargoyleosaurus* (Wyoming; Kilbourne & Carpenter, 2005; Foster, 2020) and *Mymoorapelta* (Colorado; Kirkland *et al*., 1998; Foster, 2020), but no sternal bones are described. The sternal bone of the nodosaurid *Sauropelta* (Lower Cretaceous, Wyoming and Montana; Ostrom, 1970) figured by Coombs & Maryanska, (1990, fig. 22.9D; also Vickaryous *et al*., 2004, fig. 17.17D) is probably a sacral rib (Ken Carpenter, pers. comm., 2021). The sternal bone of the nodosaur *Silvisaurus* (Fig. 1C; Lower Cretaceous, Kansas; Carpenter & Kirkland, 1998) and the fused plates of *Gastonia* (Fig. 1D, Lower Cretaceous, Utah; Kinneer *et al*., 2016, fig. 13O) do not resemble the bones in question (Figs 2A-M).

2.4.3.Theropoda

Sternal bones are unknown in the two common and well represented large Morrison theropods (Foster, 2020): *Allosaurus* (Gilmore, 1920; Madsen, 1976) and *Ceratosaurus* (Gilmore, 1920; Madsen & Welles, 2000). Holtz *et al*. (2004: 88) note that "at present there are no confirmed examples of unquestionable ossified sternal elements within the Tetanurae outside the coelurosaurian clade Maniraptoriformes." The sternal plates in this clade are either unfused or fused (Zheng *et al*., 2012, fig. 5) and do not resemble the bones in question (Figs 1B, 2A-M).

2.4.4. Sauropoda

The sternal bones of sauropods are shield-like flat oval or reniform shallow bowl-like plates (Figs 3B-G) with dorsal and ventral surfaces that are respectively gently concave and convex longitudinally and transversely. The plates vary in shape (McIntosh, 1990, figs 16.9A-L; Upchurch *et al*., 2004, figs 13.11A-K), but none resembles the bones in question (Figs 1B, 2A-M).

2.5. Ribs, and other bones of the sauropod chest region

Because of the lack of sternal bones in USNM V 4934 (Gilmore, 1914; Galton, 2020) and NHMUK PV R36730 (Maidment *et al*., 2015), the two most complete articulated specimens of *Stegosaurus stenops* known, Maidment *et al*. (2015: 72) concluded that "ossified sternals were absent in *Stegosaurus* and that the element illustrated by Gilmore (1914, fig. 32) pertains to a different genus. Based on its morphology and size, it is possible the latter is an atlantal rib of a sauropod." However, the atlantal rib of sauropods (Figs 3H-K), like that of the crocodile (Mook, 1921, fig. 2C), is a slender element that is nothing like the supposed sternal bones (Figs 2A-M). There are no rib structures resembling these bones (Figs 2A-M) from any other region of the vertebral column of Morrison and Tendaguru sauropods, viz., the posterior dorsals, the sacrals, and the anterior caudals (Hatcher, 1901; Holland, 1906; Gilmore, 1936; Janensch, 1929, 1950; Osborn & Mook, 1921; Tschopp & Mateus, 2017). Other bones of the chest region of sauropods, the clavicles, interclavicles, sternal ribs and gastralia, are all elongate slender bones (Figs 3A, B; Tschopp & Mateus, 2012).

2.6. Proatlas of sauropod dinosaurs

The proatlases (as post-occipitals) of the Morrison sauropod *Camarasaurus* (as *Morosaurus*) were described by Marsh (1883: 83; for USNM V 5384, but no figure, see Figs 3L-P) as paired bones that "are attached to the occiput just above the foramen magnum, and extend backward and outward, overlapping the lateral pieces of the atlas, thus protecting the spinal cord at this point, which would otherwise be much exposed. These bones are short, flattened, and slightly curved, resembling somewhat a riblet. The anterior end is thickened and rugose for attachment to a rugose surface on the exoccipital just above and outside the foramen magnum. The shaft is flattened from above downward, and gradually converges to a thin posterior end. In *Camarasaurus* (as *Morosaurus*) *grandis* these bones (YPM VP 1905, Figs 3Q, R) are about 65 mm in length, and 30 mm along the surface which joins the occiput." The proatlases were illustrated (without description) in articulation on the occiput of *Camarasaurus agilis* (*, Fig. 3O) by Marsh (1889, fig. 3, 1896, pl. 30, fig. 1). Gilmore (1907: 157-158, figs 1, 4a, b, pl. 12) noted that in lateral view (Figs 3L, N) these proatlases "in profile are subtriangular, flattened, and somewhat curved antero-posteriorly. The anterior ends (Fig. 3M) are greatly thickened and somewhat concave transversely, to better fit the posterior surfaces of the exoccipital with which they articulate. A notch and groove on the anterior end and side (Fig. 3L) appear to indicate the course of a nerve. The internal surface of this bone is gently concave antero-posteriorly." *Camarasaurus* *agilis* Marsh, 1889 was made the type species of the new dicraeosaurid sauropod genus *Smitanosaurus* by Whitlock & Wilson Mantilla (2020). They illustrated the right proatlas *in situ* as well as the facet for the proatlas (**, *, Fig. 3P), a raised elliptical surface shown on the left side of the supraoccipital. They noted that the anterior part of the proatlas, which has a trapezoidal cross-section (Fig. 3M), tapers posteriorly to an elongate, blade-like process (Figs 3N, P). For a sauropod braincase from the Upper Cretaceous of central India, Berman & Jain (1982: 412) noted that on the exoccipitals "on either side of the foramen magnum (there) is a circular, boss-like protuberance that was undoubtedly the site of articulation of the vertebral proatlas" (*, Fig. 3Y).

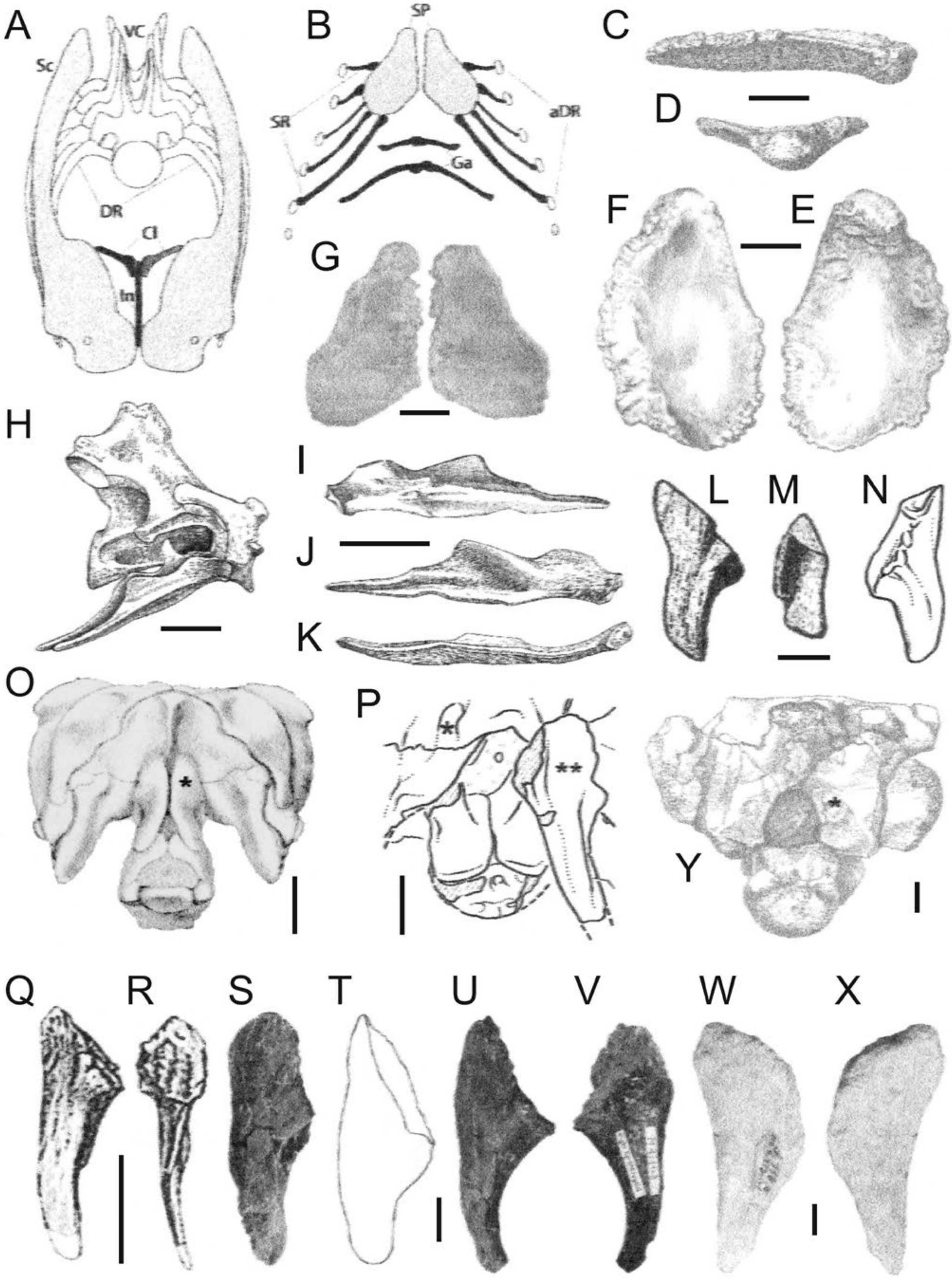
Two of the "sternal bones" of *Stegosaurus* (Figs 2A-M) are quite like the proatlas of the sauropod *Smitanosaurus agilis* (Figs 3L-P). In dorsal and ventral views, both are subtriangular in shape with a broad anterior end that tapers and twists slightly as a slender blade-like process with a rounded posterior end that is not sutured to an adjacent bone. The pair are shown in ventral view with USNM V 7620 as a left proatlas (Figs 2N, O) and as a right proatlas (Figs 2P, Q). The latter identification is more probable because the curves of the bone match those of the articulated proatlas (cf. Figs 2N, O and 3O, P) and the rugose area (s, Figs 2D, G, I, K-Q) for the supraoccipital is closer to the foramen magnum (cf. Figs 3P, Y).

If correctly identified then, with the lengths of USNM V 7620 and 7619 at 156 and 176 mm, respectively, these bones would be from extremely large sauropod skulls with very long bodies.

The lengths of the proatlas, skull and body length are known for several sauropod dinosaurs [although the proatlases are less similar (Figs 3Q-X) to the bones in question (Figs 2A-Q)], and the increased size factor for USNM V 7620 and 7619 are indicated. For *Camarasaurus grandis* (YPM VP 1905) these lengths are ~65 mm for the proatlas (Figs 3Q, R; Marsh, 1883), ~500 mm for the skull (Madsen *et al.*, 1995, fig. 1A) and 14 m for the body (Paul, 2016). With size factors of x2.4 and x2.7, this would give skull lengths of ~1200 mm and ~1350 mm whereas the longest skull figured for *Camarasaurus* is ~670 mm (DNM 975, *C. lentus*, Madsen *et al.*, 1995, fig. 1F; DNM 975).

For sauropods from the Morrison of the Big Horn Basin, Wyoming, these lengths for *Kaatedocus siberi* are ~50 mm (Figs 3S, T; SMA 004, Tschopp & Mateus, 2013), ~300 mm and 17 m (H. J. Siber, pers. comm. 2022), with size factors of x3.1 and x3.7 so skull lengths would be ~930 mm and ~1110 mm; and for *Galeamopus pabsti* (SMA 11; Tschopp & Mateus, 2017, figs 17A, B) they are 65 mm (proatlas, Figs 3U, V) and ~466 mm, with size factors of x3.1 and x3.5 so skull lengths would be ~1445 mm and ~1631 mm. For the brachiosaurid *Giraffatitan* Paul, 1988 (HMN SII, holotype of type species *Brachiosaurus brancai*, see Taylor, 2009, Upper Jurassic, Tanzania), these lengths are ~88 mm (proatlas Figs 3W, X; Janensch, 1950, fig. 6), ~540 mm (Janensch, 1935, fig. 56) and 23 m for body length (Janensch, 1961; Paul, 2016, fig. p. 228), so with size factors of x1.56 and x1.76 the skull lengths would be ~840 mm and ~954 mm and body lengths of ~36 m and ~40 m. Paul (1988: 7) notes that the largest specimen of *Giraffatitan*, the fibula HMN XV2 (Janensch, 1950, 1961), is 13% larger than HNM SII. Given the lengths relative to HMN SII, USNM

Fig. 3: Saurischia, sauropod dinosaurs from the Upper Jurassic (A-X) Morrison Formation of western USA (A-V), the Tendaguru of Tanzania, East Africa (W, X) and the Upper Cretaceous of central India (Y). **A-B,** reconstructions of the pectoral girdle of a diplodocid sauropod in A, anterior and B, of the thoracic region in ventral view. **C-G,** sauropod sternal plates: C-F, *Brontosaurus excelus* (incorrectly referred to *Apatosaurus*, see Tschopp *et al.*, 2015) from YPM Quarry 10, Como Bluff, Wyoming, YPM VP 1980, left sternal bone in C, medial; D, anterior; E, ventral and F, dorsal (visceral) views. G, diplodocid *Diplodocus carnegii* from the Carnegie Quarry, Dinosaur National Monument, Jensen, Utah, sternal plates of CM 84 in dorsal (visceral) view; **H,** reconstruction of atlas and axis of CM 84 with ribs from AMNH FARB 969 in right lateral view (ribs now *Galeamopus* sp., see Tschopp *et al.*, 2015) from Bone Cabin Quarry near Como Bluff, Wyoming; **I-K,** *Galeamopus* sp., AMNH FARB 969, right rib of atlas in I, medial; J, lateral and K, ventral views. **L-P,** dicraeosaurid *Smitanosaurus* (*Camarasaurus*) *agilis,* from Garden Park near Cañon City, Colorado, USNM V 5384, right proatlas in L, lateral; M, anterior and N, medial views; O, proatlases shown in articulation on skull in occipital view (right indicated by *) and P, right proatlas in articulation (*) and elliptical raised sutural area for proatlas shown on left side of supraoccipital (*). **Q-X**, left (Q-T, W, X) and right (U, V) proatlases: Q-R, *Camarasaurus grandis*, YPM VP 1905, Ostrom & McIntosh, 1999, pl. 3) in Q, medial and R, ventral views; S-V, from the Howe-Scott Quarry, Bighorn Basin, Wyoming: S-T, dicraeosaurid ?*Kaatedocus* SMA P29-1, now on mounted head and neck SMA 357; in S, dorsal and T, medial views; U-V, diplodocid *Galeamopus pabsti* SMA 0011 in U, lateral and V, medial views; V-W, *Giraffatitan* (*Brachiosaurus*) *brancai*, HMN Fund SII in W, dorsal and X, ventral views. Y, titanosaurid braincase ISI R-199, in occipital view, right boss-like protuberance for proatlas indicated by (*). Abbreviations: aDR, anterior dorsal ribs; Cl, clavicles; Co, coracoid; DR, dorsal ribs; Ga, gastralia; Sc, scapula; SP, sternal plates; SR, sternal ribs; VC, vertebral column. A, B from Tschopp & Mateus (2012), C, D from Ostrom & McIntosh (1999), E, F from Marsh (1896), G from Hatcher (1901), H-K from Holland (1906), scale lines based on Hatcher (1901, fig. 6), L, M from Gilmore (1907), N, P from Whitlock & Wilson Mantilla (2020, see figs 6A, B for stereo photograph and outline drawing of complete occiput with left sutural area and right proatlas), O from Marsh (1896), Q, R from Madsen *et al.* (1995) based on Ostrom & McIntosh (1999, pl. 3) as postfrontal, S provided by H. K. Siber, T from Tschopp *et al.* (2015), U, V from Tschopp & Mateus (2017), W, X provided by E. Schopp, and Y from Berman & Jain (1982). Scale bars = 100 mm (C-G), 50 mm (H-K), 10 mm (L-N, P, S-Y), and 25 mm (O, Q, R). ►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V 7620 (Figs 2A-G, O, P) and USNM V 7618 (Figs 2H-K, N, Q) are tentatively identified as the right and a left proatlas of a sauropod dinosaur (Figs 2P, Q).

3. SUMMARY

In close proximity to a right scapula-coracoid of the ornithischian plated dinosaur *Stegosaurus* from the Morrison Formation (Upper Jurassic) of the Carnegie Quarry, Dinosaur National Monument, Utah is a right sternal bone (Figs 1A, B), so identified by comparison with the sternal bones of ornithopod dinosaurs (Figs 1E-U). This casts doubts on the identification of the three bones (Figs 2A-M) described by Gilmore (1914) as sternal bones of *Stegosaurus* from the Morrison of Como Bluff, Wyoming, especially as they do not resemble the sternal bones of any dinosaur (Figs 1, 3C-G; see Section 5).

One bone (USNM V 7619) is tentatively re-identified as the anterior half of the right ischium of a nodosaurid ankylosaurian dinosaur (Figs 2R-U) that, anterior to the acetabular region, has a slightly eroded process for the pubis (Fig. 2V cf. 2W-Y).

Maidment *et al.* (2015: 72) suggested that *Stegosaurus* lacked ossified sternals and that the element illustrated by Gilmore (1914, fig. 32) was possibly the atlantal rib of a sauropod. However, this rib of sauropods (Figs 3H-K), like that of the crocodile (Mook, 1921, fig. 2C), is a slender element that is nothing like the supposed sternal bones (Figs 2A-M). There are no rib structures resembling these bones (Figs 2A-M) from any other region of the vertebral column of Morrison and Tendaguru sauropods. Other bones of the chest region of sauropods, the clavicles, interclavicles, sternal ribs and gastralia, are all elongate slender bones (Figs 3A, B; Tschopp & Mateus, 2012).

The other two “sternal bones” of *Stegosaurus* (Figs 2A-M) are quite similar to the proatlas of the sauropod *Smitanosaurus* (Figs 3L-P). In dorsal and ventral views, both are subtriangular in shape with a broad anterior end from which the bone tapers and twists slightly as a slender blade-like process with a free ending rounded posterior end. The “pair” are shown in ventral view with USNM V 7620 as a left proatlas (Figs 2N, O) and as a right proatlas (Figs 2P, Q). The latter identification is probably correct because the curves of the bone then more closely correspond to those of an articulated proatlas and the raised sutural area (s) is closer to the foramen magnum (cf. Figs 2N, O and Figs 3P, Q).

If USNM V 7620 and 7619 are correctly identified as proatlases then, with lengths of 156 and 176 mm, respectively, these bones would be from extremely large sauropods. The largest proatlas described to date is that of the brachiosaurid *Giraffatitan* Paul, 1988 (HMN SII, holotype of type species *Brachiosaurus brancai*, see Taylor, 2009, Upper Jurassic, Tanzania; the fibula HMN XV2 represents a specimen 13% larger than HMN SII (Paul, 1988: 7). Here the lengths are ~88 mm (Figs 3W, X) for the proatlas (Janensch, 1950, fig. 6), 540 mm for the skull (Janensch, 1935, fig. 56) and 23 m or 72 ft for the skeleton (Janensch, 1961; Paul, 2016, fig. p. 228). With size factors of x1.56 and x1.76, the skull lengths would be ~840 mm and ~954 mm and the body lengths would be ~36 m and ~40 m. USNM V 7620 (Figs 2A-G, P) and USNM V 7618 (Figs 2H-K, Q) are tentatively identified as a right and a left proatlas (Figs 2P, Q) of a sauropod dinosaur.

An isolated left sternal bone (Figs 1O, P) from the Cleveland-Lloyd Dinosaur Quarry, Utah is from a large non-*Camptosaurus,* non-*Dryosaurus* Morrison ornithopod dinosaur.

ACKNOWLEDGEMENTS

I thank the following people for all their assistance at: DINO: Dan Chure and most recently ReBecca Hunt-Foster. I am extremely grateful to Jim Adams who, during several visits to the DNM in the mid-1970s to the mid-1980s, operated the system of pulleys moving girders on rails to bring the work platform (see photo in McIntosh, 1977) close to the specimens of *Stegosaurus* on the cliff face so I could safely photograph them, and for a copy of his card catalogue of these specimens on the cliff face. Unfortunately, this system was discarded in the new building because the bones are fully prepared; USNM: the late Nick Hotton, III, Robert Purdy, Matt Carrano, and especially Michael Brett-Surman from 1979 to 2018; and YPM VP: the late John Ostrom, Jacques Gauthier and especially Daniel Brinkman since July 2001. I thank Ken Carpenter (University of Colorado Museum, Boulder, Colorado, USA) for all his assistance with this paper and a pers. comm. I am extremely grateful for the following people who kindly provided photographs during the difficult times of the Covid-19 crisis: Ken Carpenter (Figs 1C, D, 2L, M, V, Y, Z); Matt Carrano (Figs 2A, E, F; USNM); Jim Kirkland (Fig. 2W; Utah Geological Survey, Salt Lake City, Utah, USA); Carrie Levitt-Bussian (Figs 1E-H, O, P; UMNH); Andy McDonald (Figs 1M, N; Western Science Center, Hemet, California, USA), H. J. “Kirby” Siber (Fig. 3S; SMA), and Emanuel Tschopp (Figs 3U-X; University of Hamburg, Germany). The remaining photographs were taken by the author and the copyright for all the photographs is retained by the housing institutions. This research was started while in receipt of USA NSF grants DEB 77-24088 and BSR 85-00342. I thank the reviewer Eric Buffetaut (CNRS, Paris, France) for his comments on the MS, and the editor Lionel Cavin for improvements in the figures.

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