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Dermal armor of plated ornithischian dinosaur *Stegosaurus* from Morrison Formation (Upper Jurassic) of Colorado and Wyoming (based mostly on bones collected in 1877-1889 for O. C. Marsh), and Utah

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Abstract

Most of the important specimens with dermal armor are illustrated for the plated dinosaur *Stegosaurus* from the Morrison Formation (Upper Jurassic). These include specimens from Garden Park, Colorado and Como Bluff, Wyoming, collected in 1877-89 for O. C. Marsh, and from Utah. The holotype articulated skeleton from Garden Park of the neotype species of *Stegosaurus* Marsh, 1877, *S. stenops* Marsh, 1887, is a mostly complete articulated skeleton with all 17 dermal plates preserved. A set of 17 dermal plates (missing plates 3 and 5) and 2 pairs of tail spines from one individual of *S. stenops* from Como Bluff, is reassembled from three sets of adjacent osteoderms catalogued as separate specimens. An associated specimen from near Shell, Wyoming had 18 dermal plates, not 19 as reconstructed. Other non-Marsh specimens showing overlapping plates include another almost complete articulated specimen from Garden Park and partial skeletons from near Jensen, Utah and Grand Junction, Colorado. The form of the four pairs of terminal tail spines of the syntype of *S. ungulatus* Marsh, 1879 from Como Bluff represent two individuals, the larger spine pairs 1 and 3 and the smaller pairs 2 and 4. However, the flat distal tail spines, which were probably arranged dorsally as four pairs, are diagnostic. The anterior pair of tail spines are extremely massive in *S. sulcatus* Marsh, 1887 from Como Bluff. The spines with four subequal bases are extremely slender and elongate in *S. longispinus* Gilmore, 1914 from near Alcova, Wyoming, the type species of *Alcovasaurus* Galton & Carpenter, 2016 as *A. longispinus* (Gilmore, 1914), that was recently referred to *Miragaia* Mateus *et al.,* 2009 from western Europe as *M. longispinus* (Gilmore, 1914). The different form of nuchal, dorsal and distal caudal plates from Utah indicate a possible new species of *Stegosaurus*.

A cuirass of small throat ossicles is known only for *S. stenops* and one contains an embedded carnivorous theropod tooth. An isolated and dorsally incomplete “shoulder plate” from Como Bluff, which supposedly resembled some of the scutes of basal thyreophorans, is reoriented as an anterior dorsal plate with an extremely large base.

The first published restoration showing the paired and alternating arrangement of the plates was by C. R. Knight in Lucas (1901a, b; four pairs of tail spines so referable to *S. ungulatus*). However, Lucas/Knight statuettes with this arrangement and two pairs of tail spines, so referable to *S. stenops*, still exist from 1899, 1903 and 1904. Lucas (1910a) was the first to publish evidence for such an arrangement. A detailed summary is provided of the subsequent discussion supporting a single median row versus two rows in pairs or as alternating plates. Chirality or external mirror asymmetry occurred in *S. stenops* with plate 14, the largest, directed towards the right or to the left, but the dermal plates do not exhibit the sexual dimorphism present in *Hesperosaurus*, another Morrison stegosaur.

The proposed functions for the dermal osteoderms of stegosaurs are discussed. These include lateral display for species recognition and sexual interactions, with the plates also involved in different degrees of thermoregulation. In *Stegosaurus* the tail was held high, so parallel to the ground, and it bore tail spines that were directed laterally and only slightly dorsally so they could function better as defensive and offensive weapons. Spines of juvenile to adult individuals of *Stegosaurus* retain the plesiomorphic histology with a thin cortex and thick cancellous bone, which was suitable for display but not useful as a weapon. However, the spines of old adult individuals, with a thick cortex and a large central canal, made excellent weapons. Isolated stegosaur tail spines are from old adult individuals, the thick cortex of which favoured preservation.

Keywords

Dinosauria, Ornithischia, Stegosauria, *Stegosaurus*, Upper Jurassic, USA, osteoderms.

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Contents

1. INTRODUCTION

Field parties of Professor Othniel Charles Marsh (1831-1899; biography by Schuchert & LeVene, 1940; Colbert, 1968) 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 near Morrison and Garden Park near Cañon City in Colorado and at Como Bluff in eastern Wyoming (Schuchert & LeVene, 1940; Ostrom & McIntosh, 1966, 1999; McCarren, 1993; Breithaupt, 1998; Wallace, 1999; Foster, 2007; Rieppel, 2015).

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; Maidment, 2010; Galton, 2012). The best known genus is *Stegosaurus* Marsh, 1877 from the Morrison Formation (Late Jurassic, Kimmeridgian-Tithonian; Trujillo & Kowallis, 2015) of western USA. The original type species, *S. armatus* Marsh, 1877, the "armored roof reptile" from near Morrison, Colorado (map, Ostrom & McIntosh, 1966, 1999, fig. 1), was so named because the body was protected by large and supposedly procumbent bony dermal plates over a meter in length (Fig. 1Z). The very incomplete holotype skeleton (YPM VP 1850) of *Stegosaurus armatus* is in a very resistant sandstone so discoveries in softer rocks from the Morrison Formation of Garden Park near Cañon City, Colorado and Como Bluff, Wyoming took priority for preparation, that was much faster, and illustration. The unfigured holotype was eventually illustrated by Carpenter & Galton (2001; also Galton, 2010).

YPM VP 1853 was part of a shipment, YPM Accession Number [1271], which contained bones excavated from Reed's YPM Quarry 12 at Como Bluff in eastern Wyoming (map, Ostrom & McIntosh, 1966, 1999, fig. 3), and received at Yale College in New Haven on Sept. 10th 1879. *Stegosaurus ungulatus* Marsh, 1879 was erected and briefly described in December (paper dated Nov. 18), with the species name a reference to the terminal phalanges that are "short, broad, and obtuse, as in some ungulate mammals" (Marsh, 1879, p. 504). This material (mostly YPM VP 1853) was described and illustrated (armor, Figs 1A-U) in March as *S. ungulatus* by Marsh (1880; paper dated Feb. 18), who erected the Stegosauridae for it. This extreme rapidity of publication was necessitated by the intense, bitter and contentious rivalry with Edward Drinker Cope (1840-1897; biography by Osborn, 1931a; Colbert, 1968) of the Academy of Natural Sciences in Philadelphia. The infamous "Cope-Marsh Dinosaur War" ("Fossil Feud", "Bone War") started in 1869 and lasted until 1897 with the death of Cope. During this period, dinosaurs were hunted, dug up (often as complete skeletons) and described on an unprecedented scale (see Plate, 1964; Ostrom & McIntosh, 1966, 1999; Wallace, 1999).

From the structure of the well-preserved large dermal plates of *Stegosaurus ungulatus* (Figs 1G-L), Marsh (1880) concluded that the bases were set into the flesh along the mid-line and that they were held vertically rather than horizontally (Fig. 2A). The postcranial anatomy of *Stegosaurus*, as described and illustrated by Marsh (1879, 1880, 1881a, b, 1887, 1891a, b, 1892, 1896, 1897), was largely based on the specimens (Fig. 4; mostly YPM VP 1853, 1858) of *S. ungulatus* from the Morrison Formation of Como Bluff, Wyoming. An incomplete skeleton with a pair of very large anterior dermal tail spines (Figs 1V-X; USNM V 4937) from Como Bluff was made the holotype of *S. sulcatus* Marsh, 1887 and the distal tail of a juvenile individual of *Stegosaurus* (Fig. 1Y; USNM V 4288) was illustrated by Marsh (1887). The almost complete holotype skeleton (USNM V 4634, Fig. 2G, see Gilmore, 1914) of *S. stenops* Marsh, 1887 from Garden Park near Cañon City, Colorado (map, Ostrom & McIntosh, 1966, 1999, fig. 2) was used for the skull, the throat ossicles and the erect orientation of the plates in the skeletal reconstruction of *S. ungulatus* in which the plates are arranged as a single median row (Figs 2A, 3A; Marsh, 1891a, b, 1896, 1897). However, except for the skull (Marsh, 1887, 1896) and the lower surface of the block (cf. Figs 8A, B; Gilmore, 1914, pl. 4), USNM V 4634 was mostly unprepared in Marsh's lifetime (Gilmore, 1914). Incidentally, *Stegosaurus* is the state fossil for Colorado. A flesh restoration by C. R. Knight in Lucas (1901a, b) restored the plates as two rows of alternating plates (Fig. 28E), evidence for which was given by Lucas (1910a). However, Lull (1910a, b, 1912), who supervised the erection of the YPM mounted skeleton of *Stegosaurus* based on many of the bones described by O. C. Marsh (mostly YPM VP 1853, 1858; Fig. 4D), argued for two rows with the plates arranged as pairs (Fig. 4A).

The holotype of *S. stenops* (USNM V 4934) was well illustrated in the monographic description of *Stegosaurus* in 1914 by Charles W. Gilmore (1874-1946; biography by Lewis, 1946; see Colbert, 1968; Sues & Marsh, 2015), along with additional specimens from YPM Quarry 13 at Como Bluff. He presented arguments for the alternating arrangement of the plates that convinced Lull (1919a, b), who in 1924 rearranged the plates on the YPM mounted skeleton (Figs 4B-D). *S. longispinus* Gilmore, 1914 was erected for a partial skeleton with two pairs of extremely long subequal tail spines (Figs 23a-f) from Alcova, Wyoming. Gilmore (1914) included most of the line drawings of *S. ungulatus* from Marsh (1896) plus 10 unpublished lithographic plates prepared for Marsh in the 1880s (Gilmore, 1914, as pls 7-10, 12, 13, 15-18), including six of the dermal armor. The sauropod and

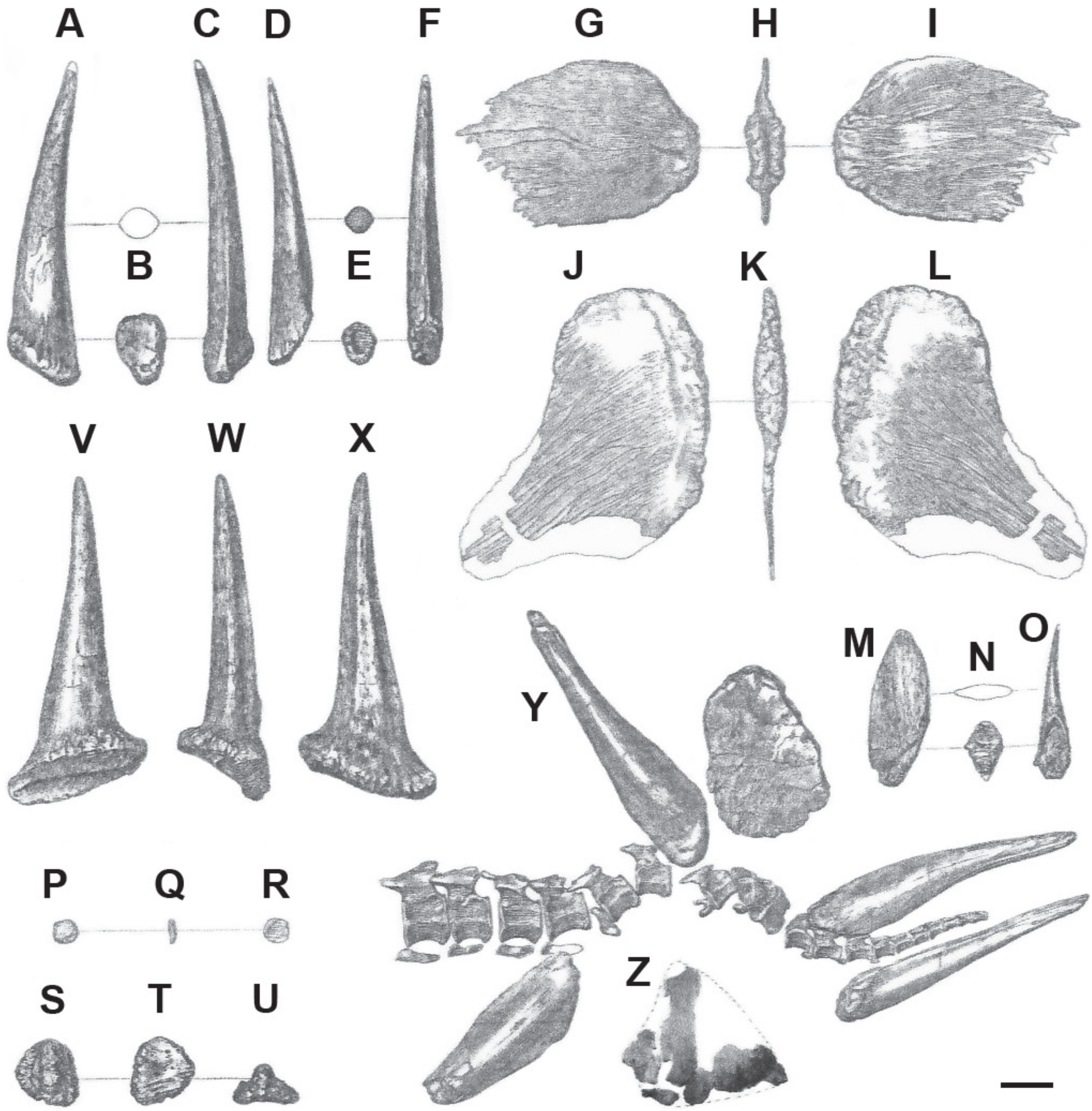

Fig. 1: A-Y: Dermal armor of *Stegosaurus* from Morrison Formation (Upper Jurassic) of Como Bluff, Wyoming as illustrated by Marsh (1880; A-U) and Marsh (1887; V-Y) and all reproduced again in 1896. A-U: *S. ungulatus* Marsh, 1879, part of YPM VP 1853, a syntype: A-F: anterior right (A-C) and posterior right (D-F) tail spines in A, D, side; B, E, cross-sectional with ventral, C, anterior and F, posterior views; G-I: plate 7 or 8 (transitional plate, dorsal plate 2 or 3), in G, I, side and H, ventral views. J-L: posterior dorsal or anterior caudal plate in J, L, side and K, ventral views; M-O: flat caudal spine in M, side (with cross-sectional); N, ventral and O, posterior views; P-R: gular or throat ossicle in P, superior; Q, side and R, inferior views; S-U: "tubercular spine" in S, superior; T, inferior and U, anterior or posterior views. V-X: *S. sulcatus* Marsh, 1887, part of holotype USNM V 4937, left anterior caudal spine in V, medial; W, posterior and X, lateral views. Y, *S. stenops*, referred specimen USNM V 4288, a juvenile individual in left lateral view as preserved, distal tail with last dermal plate and anterior and posterior pairs of tail spines. Z, *S. armatus* Marsh, 1877, part of YPM VP 1850, the holotype from Morrison, Colorado, incomplete dorsal or caudal plate in side view. Scale bar = 100 mm (A-X), 50 mm (Y) and 200 mm (Z).

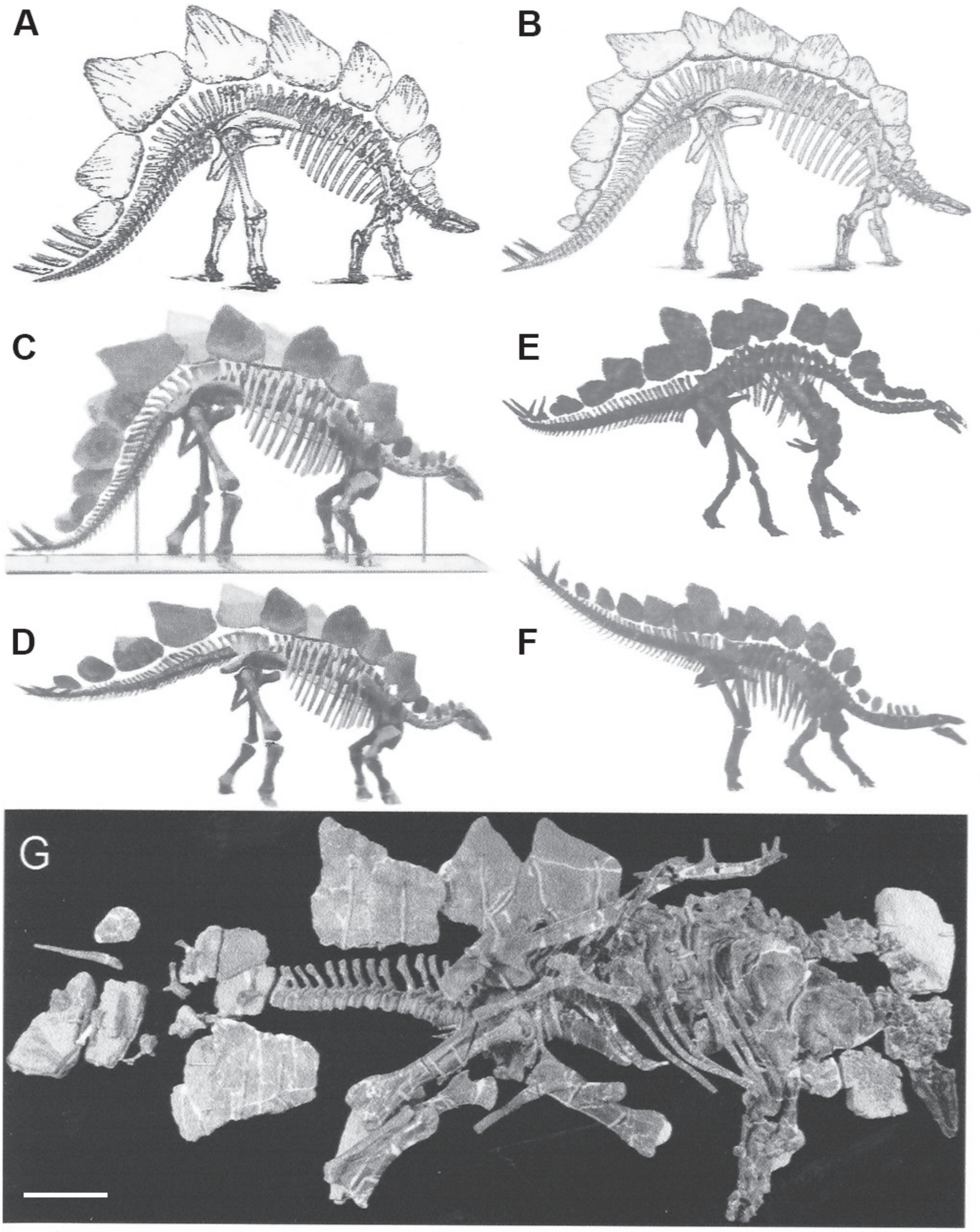

Fig. 2: A-F: Restored (A, B) and mounted skeletons (C-F) of Morrison species of *Stegosaurus* in right lateral view (reduced to ~uniform length) A, *S. ungulatus* from Marsh (1896) (reversed); B, *S. stenops*, from Romer (1933) "modified from Marsh and Gilmore" - modified from A by reducing proportional size of osteoderms with addition of plates anteriorly and posteriorly and an overlap between adjacent plates, outlines of plates after Gilmore (1914), and reduction of tail spines from four to two pairs. C-G: *S. stenops*, C-D, from YPM Quarry 13, Como Bluff, Wyoming, composite skeletal reconstruction (USNM V 8612): C, as mounted by Gilmore (1918), who lists field and catalogue numbers of bones used (from R. Purdy), and D, as exhibited in 2019 using casts of bones in C (from M. Brett-Surman); E-F: from near Shell, Wyoming, first mount based on bones from a single individual using: E, casts, SMA RCR0603, from Siber & Möckli (2009) and F, the bones, NHMNUK PV R36730, from Maidment *et al*. (2015). G, USNM V 4934, holotype of *S. stenops* Marsh, 1887, neotype species of *Stegosaurus* Marsh, 1877, upper surface of block as further prepared and exhibited in 2019 (cf. Fig. 8C; from T. Jorstadt). Lengths of skeletons: ~5.7 m (A, B), ~4.5 m (C, D) and ~5.6 m (E, F). Scale bar = 500 mm (G).

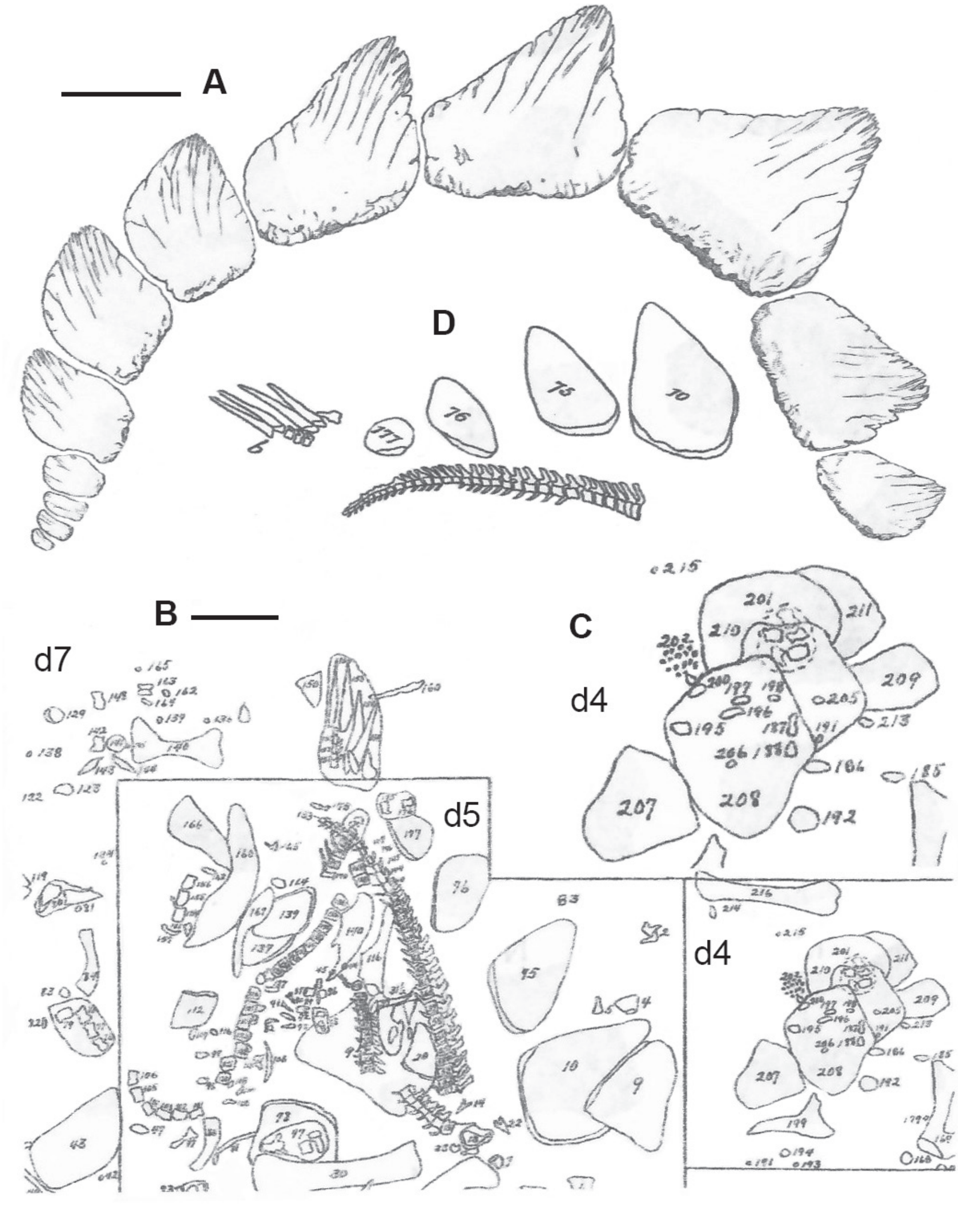

Fig. 3: A, dermal plates of *Stegosaurus* in left lateral view as reconstructed by Marsh (1891). B, distal portion of tail with plates 13 to 17 (field bone numbers 9, 10, 95, 96, 197) and tail spines of USNM V 4714 as found at Como Bluff, Wyoming in YPM Quarry 13 along with other bones in the area, adapted from parts of diagrams 4, 5 and 7 (d4, d5, d7) of map by Fred Brown in Gilmore (1914, pl. 37) with original quarry bone numbers and C, enlarged part of diagram 4. D, USNM V 4714, articulated distal caudal vertebrae, dermal plates 14 to 17 (field bone numbers 10, 95, 96, 197), and distal caudal spines as preserved, from Gilmore (1914, fig. 58) after diagrams 5 and 7 in B. Scale bars = 50 cm (A) and 100 cm (B).
Field numbers for anterior 13 plates used as bones in original mounted skeleton (USNM V 8612; Figs 2C, 10A, replaced by casts in 2019, Fig. 2D): USNM V 7615: gular ossicles (not used): d4, b202 (Figs 9H-I); plate 1: d4, b197 (Figs 11A1, 11B1); plate 2: d4, b196 (Figs 11A2, 11B2); plate 3: d4, b185 (Figs 11A3, 11B3); plate 6: d4, b211 (Figs 10A-E); plate 7: d4, b212 (Figs 10A, F-I); plate 8: d4, b209 (Figs 10A, J-M); plate 9: d4, b208 (Figs 10A, N-P); plate 10: d4, b210 (Figs 10A, Q, R); as plate 12: d4, b207 (12[11], Figs 10A, T, U) but actually plate 11 in series.

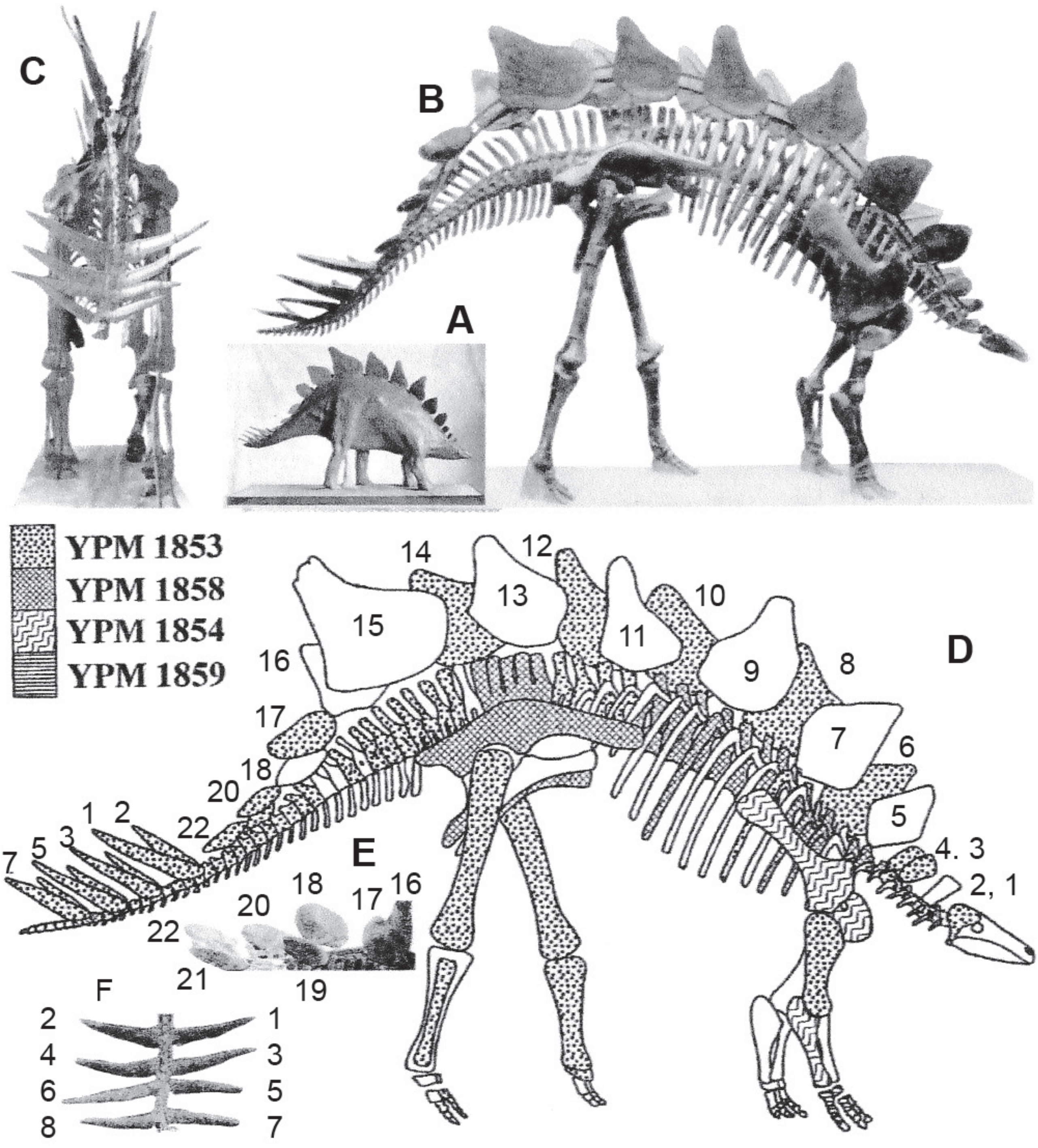

Fig. 4: YPM mounted skeleton using bones of *Stegosaurus* from YPM quarries at Como Bluff, Wyoming (mostly Quarries 11 and 12), all of dermal armor is from the syntype of *S. ungulatus*, YPM VP 1853, other bones as indicated are mostly from YPM VP 1853, 1858 plus 1854, 1859 (see D) in right lateral (A, B, D), posterior (C) and dorsal (F) views. A, life sculpture by Lull (1910a) with double row of paired plates. B-C, skeleton (5.7 m total length) as remounted in 1924 with paired alternating or staggered plates (from Lull, 1929); D, diagram of C for specimen numbers of the bones used (but YPM VP 1853 for both pubes and ischia) and the numbers used in this paper for the plates and caudal spines (modified from Carpenter & Galton, 2001); E, detail of plates on distal part of tail (cf. Fig. 20A) and F, tail spines (cf. Fig. 25C).

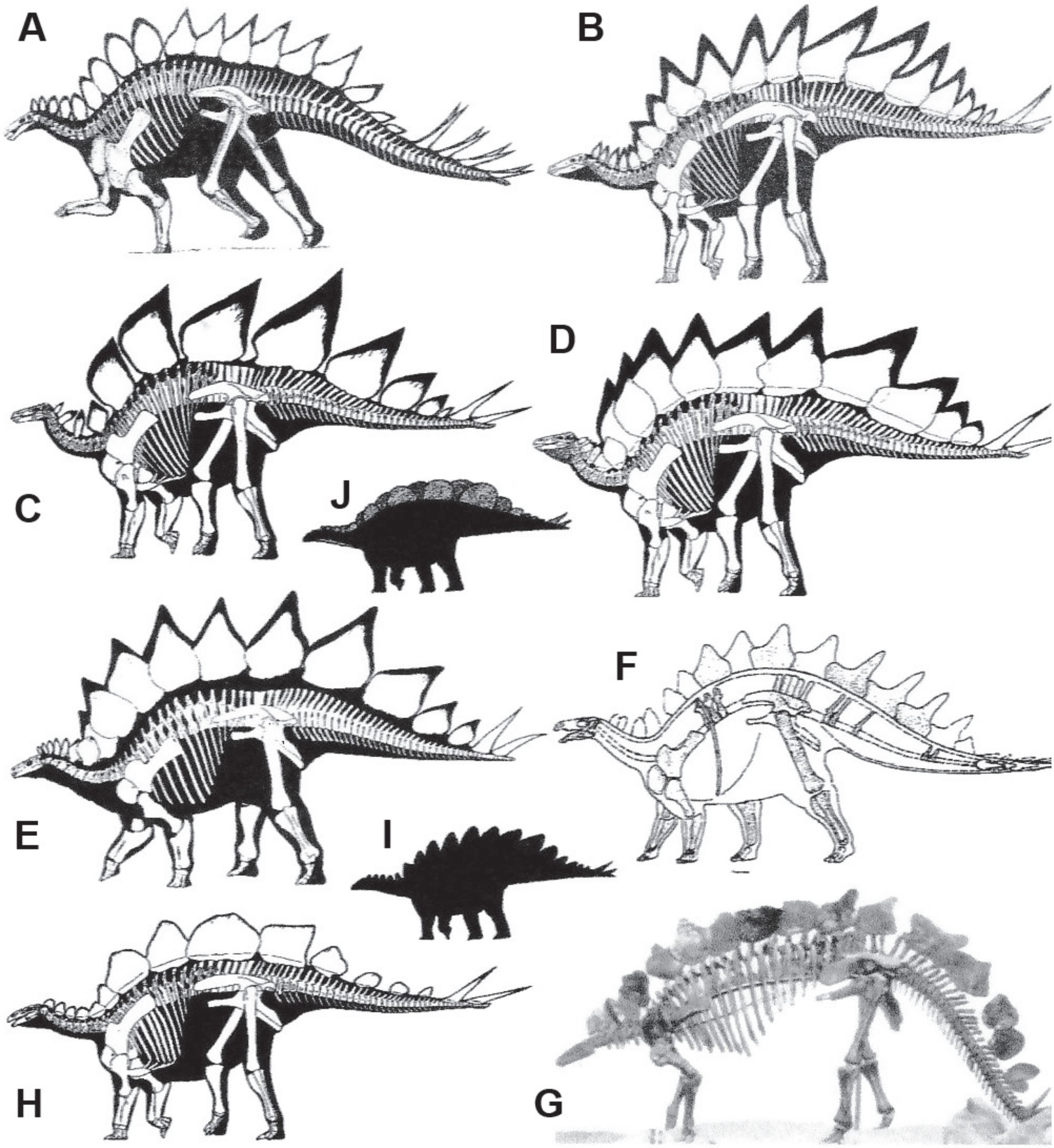

Fig. 5: Skeletal (A-H, reduced to ~uniform body length with A, G, H printed in reverse) and flesh (I, J) reconstructions in left lateral view of Morrison stegosaurs with paired alternating plates (A, B, D, F-H), paired plates (C) and a single median row with overlap of wider parts of plates (E). A-B, *Stegosaurus ungulatus*, based mostly on YPM VP 1853 (dermal armor, syntype, see Fig. 4D) from YPM Quarry 12, Como Bluff, Wyoming) and YPM VP 1858 (YPM Quarry 11, Como Bluff, Wyoming); C-E, *S. stenops* based mostly on USNM V 4934 (holotype, YPM Quarry 1, Garden Park, Colorado) and USNM V 4714 (YPM Quarry 13, Como Bluff, Wyoming); F-G, *Stegosaurus* sp. from Carnegie Museum Quarry at Dinosaur National Monument, Vernal, Utah; and H-J, *Hesperosaurus mjosi*, H, based on specimens from Howe-Scott Quarry on western slope of Big Horn Mountains, Wyoming at SMA (see Siber & Möckli, 2009); I-J, outline reconstructions of presumed female (I) and male (J), from E. Saitta. A from Bakker (1986), B from Paul (2010), C from Paul (1987) with paired plates, D revised reconstruction from Paul (1992) with alternating plates, E from Czerkas (1987) with a single median row of plates, F from Olshevsky & Ford (1995) based on bones on DNM cliff face at DINO, G composite mounted partial skeleton UNSM 53192 (ex CM 11372: DNM 39/60 and other material not recorded; McIntosh, 1981), H from Paul (2016). Body lengths: ~7 m (A, B), ~6.5 m (C-E, H), ~ 6 m (F), and ~ 5 m (G).

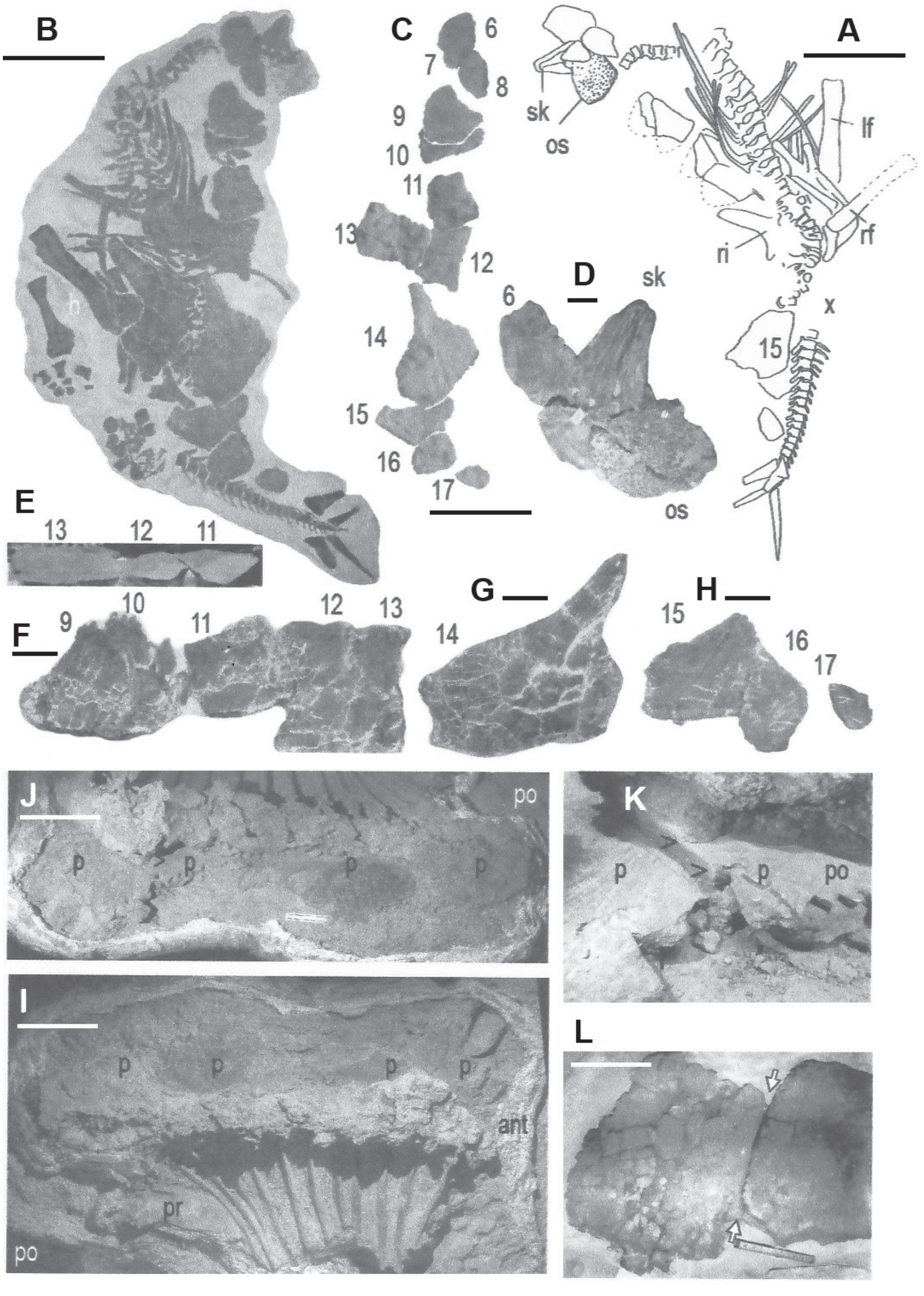

Fig. 6: Recently excavated specimens of *Stegosaurus* with overlapping plates. A-H: the "Small" *Stegosaurus stenops* skeleton, DMNH 2818, from close to type horizon and locality of holotype of *S. stenops* (USNM V 4934) in Garden Park near Cañon City, Colorado. A-B, complete skeleton: A, as exposed in quarry in right side view (modified from Carpenter, 1998) and B, as exhibited showing left side view; C-H, dermal plates visible in left side (C, D, F-H) and distal (E) views: C, sequence as preserved (plates 1-5 buried near skull); D, skull and throat ossicles; E, plates 13 to 11 to show overlap with matrix between the plates; F, plates 9 to 13 to show overlap; F, plate 14 and H, plates 15 to 17. I-K, "McStegosaur" from near Jensen, Utah, FHPR 572: I, the main block with 11 left dorsal ribs articulated with transversely sectioned centra of dorsal vertebrae and the preacetabular process of the left ilium in ventral view, plus the bases of four plates in right side view; J, bases of four incomplete dorsal plates in right side view (note that view rotated 180 degrees relative to I), and K, the two more anterior overlapping bases in right side-distal view to show matrix between the plates. L, the "Bollan stegosaur" from Rabbit Valley near Grand Junction, Colorado, MWC 81, two plates showing overlap in side view. Abbreviations: ant, anterior; os, dermal throat ossicles; p, ventral part of plates; po, posterior; pr, preacetabular process of left ilium; sk, skull; lf, left femur, li, left ilium; po, posterior; pr, preacetabular process of left ilium; rf, right femur; x, break in tail; 6-17, dermal plates 6 to 17; >, line of overlap between plates. B, C, E from K. Carpenter, D, F-H from O. Mateus, I-K from S. Sroka. Scale bars = ~1 m (A-C), 100 mm (D, F-H) and 300 mm (I, J, L).

stegosaur plates of O. C. Marsh were finally published by Ostrom & McIntosh (1966, 1999). Gilmore (1915) illustrated his bronze statuette of *S. stenops* with alternating plates (Fig. 27F) and in 1918 (also 1920) illustrated a composite mounted skeleton based on specimens from YPM Quarry 13, Como Bluff (Fig. 2C). The excavation of numerous dinosaur skeletons, including mostly disarticulated remains of *Stegosaurus* (see Section 7.4), occurred from 1909 to 1923 at the Carnegie Quarry near Jensen in northeastern Utah (McIntosh, 1977; McGinnis, 1982). In 1915 the quarry with 80 adjacent acres was designated as Dinosaur National Monument, with an enlargement in 1938, and the Visitor Center was opened in 1958 (see Section 4.5). Digging at the Cleveland-Lloyd Dinosaur Quarry in north-central Emery County started in 1929 and it was designated a National Monument in 1967 (Stokes, 1985; Miller *et al.,* 1996; see Section 4.6). Over 10,000 mostly isolated bones were recovered, the majority of which were from the theropod dinosaur *Allosaurus* (Madsen, 1976), along with some of *Stegosaurus* (see Section 7.4). Hotton (1963) suggested that the plates of *Stegosaurus* were used for display and thermal regulation, two functions that are still the subject of discussion (see Section 9.1).

Juvenile specimens of *Stegosaurus*, including one with caudal spines (Figs 22G-O), were described by Galton (1982). A second articulated skeleton of *S. stenops* (Figs 6A-H) from close to the type horizon and locality in Garden Park was briefly described by Carpenter (1998, 2007). A fairly complete skeleton from near Buffalo, Wyoming was described as *Hesperosaurus mjosi* Carpenter *et al*., 2001 in which the dorsal plates are longer than tall (Fig. 5H), the reverse of the situation in *Stegosaurus* (Figs 1J, 2, 5A-F). A partial skeleton of *Stegosaurus* cf. *ungulatus* was described from the Upper Jurassic of Portugal but the only preserved osteoderm is a nuchal plate (see Escaso *et al*., 2007, fig. 2m; similar to plate 6, Figs 10B-E).

Maidment *et al*. (2008), who reviewed all the species and most specimens of stegosaurs, recognized only three species of *Stegosaurus, S. armatus* Marsh, 1877 and *S. mjosi* (Carpenter *et al*., 2001) from the Morrison Formation and *S. hohmeni* (Dong, 1973) for *Wuerhosaurus hohmeni* Dong, 1973 (also Dong, 1990), represented by a partial postcranial skeleton and one low elongate dorsal plate (but incomplete dorsally, Maidment *et al*., 2015) from the Lower Cretaceous of Wuerho, Xinliang, China.

Siber & Mockli (2009) describe four mounted skeletons from the Morrison Formation on the western slopes of the Big Horn Mountains near Shell, Wyoming, each of which includes cranial material and dermal armor. Three were described as cf. *Hesperosaurus mjosi* and the fourth, the most complete skeleton ("Sarah" SMA RCR0603; Figs 2E, 7) which lacks only the proximal ~14 caudal vertebrae and the left forelimb, was described as cf. *Stegosaurus armatus*. Maidment (2010) gave a historical review by geographical regions of the species and specimens of stegosaurs. Carpenter (2010) discussed the species concept in dinosaurs and listed numerous differences in the anatomy of *S. stenops* and *Hesperosaurus mjosi* to demonstrate the validity of *Hesperosaurus*. Based on the characters of the dermal armor, Galton (2010) recognized several Morrison species of *Stegosaurus*, viz., *S. ungulatus* Marsh, 1879, *S. stenops* Marsh, 1887, *S. sulcatus* Marsh, 1887 and *S. longispinus* Gilmore, 1914. He discussed the inadequate nature of the holotype (YPM VP 1850) of *S. armatus* Marsh, 1877 as the type species of *Stegosaurus* Marsh, 1877. He suggested that *S. stenops* Marsh, 1887, based on the almost complete and articulated skeleton USNM V 4934 (Fig. 2G), 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).

Maidment *et al*. (2015) provide an excellent detailed and very well illustrated description as *S. stenops* for the bones of the associated, almost complete skeleton (Figs 2F, 7; "Sophie" NHMUK VP R36730; previously "Sarah") from the Morrison Formation near Shell, Wyoming.

Saitta (2015) described a sexual dimorphism (Figs 5I, J) based on differences in the shape of the dermal plates in specimens referred to *Stegosaurus mjosi* from the Morrison Formation near Shell (Siber & Möckli, 2009) and Como Bluff, Wyoming plus others from near the Grass Range, Montana. However, *Hesperosaurus* is recognized as a valid genus by Raven & Maidment (2017) *contra* Maidment *et al*. (2008). A partial skeleton with one dermal plate from near Livingston, Montana is described by Maidment *et al*. (2018) as *Hesperosaurus*. They rediagnosed this genus by a combination of seven plesiomorphies and two autapomorphies, one of which is that the dorsal dermal plates are longer than tall (Fig. 5H). They show from comparative histological studies that *Hesperosaurus mjosi* may have been a smaller species as an adult than *Stegosaurus stenops* and possibly occupied more arid environments than *Stegosaurus.*

The purpose of this paper is:

1. To provide a well-illustrated description of the dermal armor of the specimens of *Stegosaurus* collected for O. C. Marsh from Como Bluff, Wyoming and Garden Park, Colorado, as a supplement to the excellent monograph of Gilmore (1914), and to briefly describe the osteoderms of other important specimens of *Stegosaurus* from the Morrison Formation of these states and Utah.
2. To document the various reconstructions of the osteoderms of *S. ungulatus* and *S. stenops* and the evidence used to support the different arrangements proposed for the plates and spines.
3. To summarize the evidence for and against the different functions proposed for the plates and spines of *Stegosaurus*.

2. MUSEUM ABBREVIATIONS

AMNH, American Museum of Natural History, New York, USA; **BMNH**, British Museum (Natural History), London, England (now NHMUK); **CEUM**, Prehistoric Museum, Utah State University Eastern (formerly College of Eastern Utah Museum), Price, Utah, USA; **CLDQ**, Cleveland-Lloyd Dinosaur Quarry, Emery County, Utah, USA; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; **DINO**, Dinosaur National Monument, Vernal, Utah, USA; **DMNH**, Denver Museum of Nature and Science (formerly Denver Museum of Natural History), Colorado, USA; **DNM**, original bone numbers for bones on cliff face at DINO; **LACM**, Los Angeles County Museum, Los Angeles, California, USA; **FHPR**, Utah Field House of Natural History State Park Museum (formerly Field House Parks and Recreation), Vernal, Utah, USA; **MWC**, Museum of Western Colorado, Grand Junction, Colorado, USA; **NHMUK,** Natural History Museum, London, UK (formerly BMNH); **ROM**, Royal Ontario Museum, Toronto, Ontario, Canada; **SMA,** Sauriermuseum Aathal, Switzerland; **UMMP-NH**, University of Michigan Museum of Paleontology - Natural History, Ann Arbor, Michigan, USA; **UMNH**, Utah Museum of Natural History (formerly UUVP), Salt Lake City, Utah, USA; **UNSM**, University of Nebraska State Museum, Lincoln, Nebraska, USA; **USNM**, National Museum of Natural History (formerly United States National Museum), Washington DC, USA; **UUVP**, University of Utah Vertebrate Paleontology (now UMNH), Salt Lake City, Utah, USA; **WPL**, Western Paleontological Laboratories, Lehi, Utah, USA; and **YPM VP**, Division of Vertebrate Paleontology, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA.

3. THE MARSH LITHOGRAPHS

A set of 150 lithographic plates were prepared in the 1880s, under the direction of O. C. Marsh, by illustrator F. Berger and lithographer E. Crisand. Lithographs of two of the tails of *Stegosaurus stenops* from YPM Quarry 13 were prepared (Figs 22A, E) but only that of USNM V 4288 was published as a line engraving (Fig. 1Y) by Marsh (1887, pl. 9, 1896, pl. 51); a copy of the original lithograph (Fig. 22E) is in Gilmore (1914, pl. 16) but not in Ostrom & McIntosh (1966, 1999). The lithograph of the distal part of the tail of USNM V 4714 (Fig. 22A) was also published by Gilmore (1914, pl. 15).

The lithographs were printed for planned monographic volumes on the Stegosauria, Sauropoda and Brontotheridae (large Eocene mammals) at a cost then of over $40,000 ($1,014,423 in 2020; http://www.in2013dollars.com) to the US Geological Survey (Ostrom & McIntosh, 1966, 1999). However, these volumes were never written and the large dinosaur paper of Marsh (1896) is basically a slightly modified collation of his earlier papers. It included engraved line drawing versions of some of the figures in the lithographic plates. The three sets of Marsh's plates were later distributed to libraries at universities and museums by Osborn (1931b).

Copies of the sauropod and stegosaur lithographic plates of Marsh, except tail with spines (Fig. 22E, USNM V 4288, as Gilmore, 1914, pl. 16), were finally published in book form, with retention of the original plate numbers, by Ostrom & McIntosh (1966). Most of the copies of the plates were printed at the same size or slightly reduced compared to the originals. However, stegosaur plates 1, 21, 33, 42, 47, 48, 49, 55, 60, 63 are larger and, as they were to be folded to fit the US Geological Survey Monograph format (9" x 11.5"), they were printed at a greater degree of reduction. Dermal osteoderms are figured by O. C. Marsh in Ostrom & McIntosh (1966, 1999, plates, pls 61-64, see Figs 12I, K, M, 14D-F, 15E-H; and spines, pls 54-60, see Figs 19, 22A, 23X-Z, 24A-K, 26A, C, D, F).

Ostrom & McIntosh (1966, p. 362) noted that a skeletal reconstruction "was never completed as a lithograph. Marsh planned to duplicate plate 52 [Fig. 2A] from his" 1896 paper as plate 65 in the *Stegosaurus* monograph. However, when first published Marsh (1891a, p. 385, pl. 11) noted that this plate, "one thirtieth natural size, is reduced from a larger restoration, one-tenth natural size, made for a lithographic plate to accompany the monograph of the *Stegosaurus*." This scale may be incorrectly given because in the USNM archives there is a very large reconstruction of *Stegosaurus* in ink and wash (x 0.25, on heavy paper ~2 m long) but there is no evidence for a derived lithographic plate.

Ostrom & McIntosh (1966, 1999) provided captions and complimented the plates with a historical introduction to collecting at Morrison, Cañon City and Como Bluff, copies of watercolor paintings by Arthur Lakes of the Como area and quarries (1966 frontpiece in color, reprinted 1999 in black and white), a list of the Marsh quarries with the fauna for each, and a bibliography with the specimen numbers indicated for type and illustrated specimens in the main papers on the Marsh vertebrates up to 1961 (with an account of subsequent field work in 1999 reprint).

4. DISCOVERY AND OCCURRENCES

The extensive Morrison depositional basin in the Rocky Mountains was on the western margin of Laurasia. The Morrison Formation consists of non-marine sediments that were deposited across a broad, comparatively flat land that was formerly covered by the Middle to early Late Jurassic Sundance Seaway. The north-eastward withdrawal of this seaway coincided with subduction and uplift to the west, which was accompanied by volcanism that spread ash downwind. Radiometric dates from the ashes range from 156.84 ± 0.59 to 150.0 ± 0.52 Ma age for the Morrison Formation (Trujillo & Kowallis, 2015). The axis of the Morrison depositional basin extended across 12° to 15°, extending south of latitude 40°N and north of latitude 50°N (Carpenter & Galton, 2018, fig. 1). It largely represents semi-arid fluvio-lacustrine floodplains (Turner & Peterson, 2004), with generally seasonal drier conditions to the south and wetter conditions to the north (Demko *et al*., 2004). It preserves a diverse assemblage of dinosaurs, pterosaurs, crocodilians, turtles, mammals and other vertebrates, invertebrates, fungi, Protista, plants, pollen and trace fossils (list of taxa in Chure *et al*., 2006). For the dinosaurs (see Farlow, 2007; Carpenter & Galton, 2018 for bipedal ornithischians) and mammals, these represent the best known members of their respective clades for any Upper Jurassic formation anywhere in the world (Ostrom & McIntosh, 1966, 1999; Foster, 2003, 2007).

Como Bluff is a topographic feature just north of US Route 30/287 near the long gone Como Station that was on a former track of the Union Pacific Railroad. The quarries are on the north face of the gently dipping south limb of an east-west trending asymmetrical anticline (see Ostrom & McIntosh, 1966, 1999, fig. 3 for map, fig. 13 for panoramic photo). The following details on the four YPM quarries are mostly taken from Carpenter & Galton (2001).

4.1. *Stegosaurus ungulatus* Marsh, 1879 and Reed's YPM Quarry 12, Wyoming

Stegosaurus ungulatus Marsh, 1879 was named for material (YPM VP 1853) collected at YPM Quarry 12 (type incorrectly included in the faunal list for Quarry 13, Gilmore, 1914, p. 4), which was discovered on August 6, 1879 by Edward Ashley near Robber's Roost at Como Bluff (West Como Ridge, now Como Ridge) in Carbon County, Wyoming. This quarry is in the middle part of the upper or Brushy Basin Member equivalent of the Morrison Formation (Turner & Peterson, 1999, as WY-29 in fig. 7, ~149 ± 0.5 Ma). The site is at the extreme western end of the Como anticline and in the upper line of quarries, near the nose of the plunge where the beds dip steeply toward the north (Kohl & McIntosh, 1997, pp. 132, 136, 137; map Ostrom & McIntosh, 1966, 1999, fig. 3). Arthur Lakes continued to work YPM Quarry 12 throughout the winter of 1879 until March 20, 1880, when he left to join the faculty at the School of Mines in Golden, Colorado. William H. Reed stopped all work after a cave-in of the quarry walls but six years later, Fred Brown reopened the quarry, with the assistance of William Beck and Henry Kessler, and it was finally abandoned in August 1886. The additional material (as USNM V 7414; a syntype of *S. ungulatus*) collected includes nine pieces of ribs (cervicals and/or dorsals), nine incomplete caudal vertebrae, and a large dermal plate (Figs 14A, B; maximum length, 655 mm; width, 415 mm; maximum thickness of base, 70 mm).

The bones were mostly scattered but with some distinct clusters. Plates and spikes coexist with the bones (Carpenter & Galton, 2001, fig. 4.10), demonstrating minimal transport of bones, possibly because the sediments, a carbonaceous shale or mudstone, indicate a swampy site where water flow was minimal. The assemblage appears to be partially attritional and partially a non-catastrophic mass mortality (see Evanoff & Carpenter, 1998). These bones represent the syntypes of *Stegosaurus ungulatus* and include a partial skull (Galton, 2001), vertebrae, right humerus, ischia, left femur, tibia, fibula, distal tarsals and metapodial, an ungual phalanx, and dermal armor consisting of small to large plates, flat distal tail spines and terminal tail spines (Figs 1A-U, 4B-F, 12, 16, 19, 20, 24, 25; Ostrom & McIntosh 1966, 1999, pls 15, 16, 25-27, 29, 33, 43, 46, 48, 55, 56, 59, 60, 62, 63).

Isolated non-stegosaurian dinosaurian bones, especially teeth, were also recovered at Quarry 12, including bones from the sauropods *Camarasaurus* and *Diplodocus*, the theropods *Allosaurus* and *Coelurus*, the ornithischian *Nanosaurus agilis* (as *Laosaurus*, see Carpenter & Galton, 2018) plus the crocodile *Goniopholis* and a turtle cf. *Glyptops* (Ostrom & McIntosh, 1966, 1999).

4.2. *Stegosaurus duplex* Marsh, 1887 and Reed's YPM Quarry 11, Wyoming

Edward Ashley discovered YPM Quarry 11 in Albany County on July 31, 1879 near the famous mammal quarry, YPM Quarry 9 (see map in Ostrom & McIntosh, 1966, 1999, fig. 3). The site was worked sporadically (as were most of the Como Bluff quarries) by William Harlow "Bill" Reed (1848-1915, biography by Breithaupt, 1990), aided by Frederick Brown and Ashley, until April 21, 1880, when it was deemed played out. The quarry, which is in the middle part of the upper Brushy Basin Member equivalent (Turner & Peterson, 1999, as WY-18 in fig. 7, ~149 ± 0.5 Ma), is situated in mudstone and the preservation of the bone is very good. Based on all the maps made by Lakes and Reed, the composite map of the quarry given by Carpenter & Galton (2001, fig. 4.6) indicates that the holotype of *Stegosaurus duplex* Marsh, 1887 (YPM VP 1858) was originally a widely scattered and completely disarticulated skeleton. It includes a few cervical and dorsal vertebrae, ribs, the sacroiliac block, mid-caudal vertebrae, pubes, ischia, left femur, right coossified tibia, fibula, astragalus and calcaneum, and a few phalanges (see Ostrom & McIntosh, 1999, pls 8, 17, 18, 20, 21, 28, 42, 45, 47, 49). Many of these bones were included in the composite YPM mounted skeleton (Figs 4B-D).

Other specimens from the site include the holotype of the sauropod dinosaur *Apatosaurus amplus* (Marsh, 1881b) and an unidentified mammal tooth (Ostrom & McIntosh, 1966, 1999).

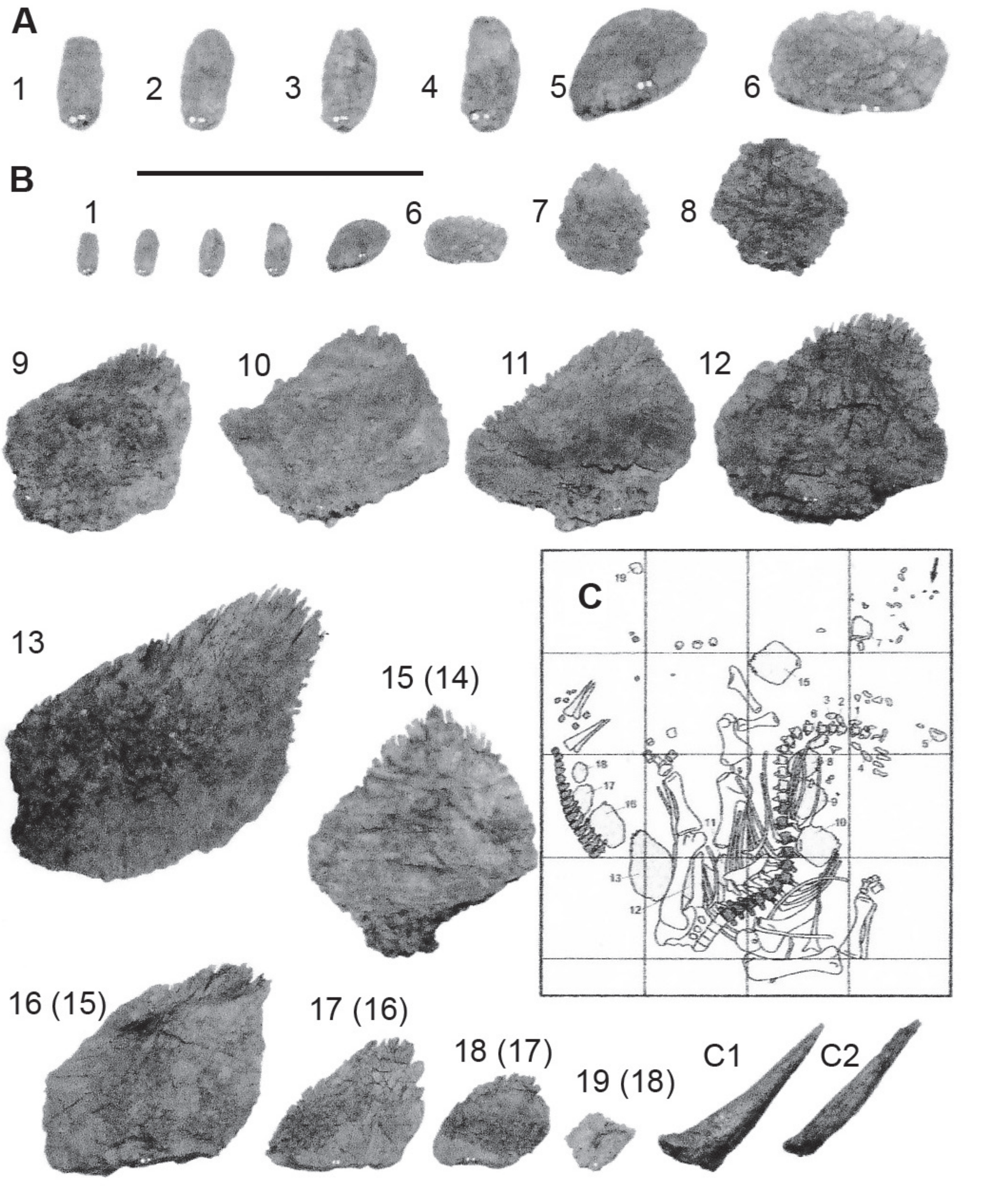

Fig. 7: A-B: Dermal armor from a single individual of *Stegosaurus stenops* from Morrison Formation (Upper Jurassic) near Shell, Wyoming, modified from Siber & Möckli (2009, pp. 44-45 with reorientation of plate 14, see Section 5.5) as SMA RCR0603 (now NHMNUK PV R36730). A, plates 1 to 6 in left side view; B, plates 1 to 19 in left side view (with numbers 1 to 19 as described by Maidment *et al.,* 2015) and left caudal spines (C1, C2) in side view, additional plate 14 was probably never present so total count actually 18 as preserved so (14) to (18) indicates revised position in series (see Section 5.5); C, quarry map drawn during excavation of SMA RCR0603, from Maidment *et al*. (2015) who modified it from Siber & Möckli (2009) by providing a meter grid and the plate numbers used in both papers. Scale bar = 250 mm (A) or 500 mm (B).

4.3. *Stegosaurus* spp. Marsh, 1887 and Reed's YPM Quarry 13, Wyoming

The discovery of YPM Quarry 13 was reported in a letter to Marsh from William Harlow "Bill" Reed on September 4, 1879 (quoted in Ostrom & McIntosh, 1966, 1999; Carpenter & Wilson, 2008). This was one of the most productive quarries at Como Bluff as regards to dinosaurs (Foster, 2007, faunal list p. 88), with the excavation of at least 14 individuals of *Stegosaurus* and 17 of the large bipedal ornithopod dinosaur *Camptosaurus* (Foster, 2007; see Carpenter & Galton, 2018). 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 (Ostrom & McIntosh, 1966, 1999, fig. 3).

YPM Quarry 13 produced the greatest numbers of *Stegosaurus* specimens that today are split between the YPM, for specimens collected prior to 1882, and after that to the USNM when US Government funding was utilized for collecting while Marsh was the Vertebrate Paleontologist for the US Geological Survey. Although the quarry was worked by Reed (1880-1882) and Kenney (1883), only the maps of Brown were compiled into a single map by Gilmore (1914, fig. 2, pl. 37; bone identifications pp. 5-24). Fortunately, maps for some of the missing areas exist in the letters of Reed and Kenney, and Reed records the first articulated tail and associated spikes found there (Carpenter & Galton, 2001, fig. 4.12). Over the next seven years, no fewer than five articulated tails with an associated two pairs of spikes were collected. Lithographs of two of these tails were prepared by Marsh for his planned monograph on the Stegosauria (see Carpenter & Galton, 2001, figs 4.13A, B) with one (USNM V 4288) published as a line engraving (Fig. 1Y) by Marsh (1887, pl. 9, 1896, pl. 51); a copy of the original lithograph (Fig. 22E) is in Gilmore (1914, pl. 16) but not in Ostrom & McIntosh (1966, 1999). The lithograph of the distal part of the tail of USNM V 4714 (Fig. 22A) was published by Gilmore (1914, pl. 15) and in Ostrom & McIntosh (1966, pl. 54).

Gilmore (1914, p. 4) lists *Stegosaurus ungulatus* and *Dryosaurus altus* as occurring in YPM Quarry 13 but these are not the holotypes as incorrectly indicated with an asterisk; these came from YPM Quarries 12 and 5, respectively. However, Gilmore (1914, p. 8) referred a tail with four spikes (part of composite skeleton AMNH FARB 650, see Brown, 1932; Colbert, 1962, pl. 66) from YPM Quarry 13 to *Stegosaurus ungulatus* (Carpenter & Galton, 2001, fig. 4.14; see Section 7.5), as well as a partial skeleton (USNM V 6646, Gilmore, 1914, p. 83). Gilmore (1914, p. 4) also records *S. stenops*, *Diracodon laticeps* Marsh, 1881 [holotype maxillae of Marsh (1881, 1896) and Gilmore (1914) are actually a pair of dentaries, YPM VP 1885, see Carpenter & Galton (2001, figs 4.18, 4.17)] and *S. sulcatus* Marsh, 1887 (holotype a partial skeleton USNM V 4937 which includes a massive anterior pair of tail spikes, Figs 1V-X, 26A-O) as coming from YPM Quarry 13.

4.4. *Stegosaurus stenops* Marsh, 1887 and Felch's YPM Quarry 1, Colorado

The site of Felch's YPM Quarry 1 was originally discovered by Henry Felch in 1869 or 1870 at Garden Park in Fremont County, north of Cañon City, Colorado (Hatcher, 1901; Gilmore, 1914; Evanoff & Carpenter, 1998; map, Ostrom & McIntosh, 1966, 1999, fig. 1), but it was not until 1877 that the quarry was opened by Benjamin Mudge (Evanoff & Carpenter, 1998) for less than three months before closure because of the discouraging results. Marshall Felch reopened the quarry at Marsh's request in the spring of 1882 and, as the quarry proved to be so productive, it was worked until 1889, making it one of the longest quarry operation for O. C. Marsh (Evanoff & Carpenter, 1998). This quarry is equivalent to the lower or Salt Wash Member based on radiometric date in Garden Park (K. Carpenter, pers. comm., 2019; Turner & Peterson, 1999, as CO-3 in fig. 7, 150 Ma). The holotype (Fig. 2G; USNM V 4934) of *Stegosaurus stenops* Marsh, 1887 was collected between 1885 and 1887 by M. Felch. He recorded the skeleton of *S. stenops* in his letters as it was found (Carpenter & Galton, 2001, fig. 4.15) and later in a composite quarry map. The skeleton was remarkably complete and articulated (Figs 2G, 8A-C; see Gilmore, 1914). Bones at the quarry occur partially as lag deposits in lenticular, coarse to conglomeratic sandstones, and partially in coarse to medium grained lateral accretion sediments (Evanoff & Carpenter, 1998). The site is the result of attritional and noncatastrophic mass mortality, with the articulated *S. stenops* skeleton possibly the result of a drought fatality (Evanoff & Carpenter, 1998).

Of the specimens available to Marsh (1891a, b) for his skeletal reconstruction of *Stegosaurus*, *S. stenops* was the most complete, being an articulated skeleton (Figs 2G, 8A-C; see Gilmore, 1914). Remarkably, Marsh did not use this skeleton for the core skeleton of his reconstruction, but only for the skull, throat ossicles and the erect arrangement of the plates on the back and tail (Figs 2A, 3A). Gilmore (1914) noted that, for reasons known only to Marsh, little of the skeleton was prepared during his lifetime. However, this was probably because the rock is extremely hard and Marsh would rather have his people work on easier specimens to maximize specimens time (K. Carpenter, pers. comm., 2019). After Marsh's death in 1899, the specimen was transferred from the YPM to the USNM, where most of the preparation of the upper side occurred (Gilmore, 1914) (see Section 5.2).

4.5. Carnegie Quarry at Dinosaur National Monument, Utah

Earl Douglass (1862-31; biography by Holland, 1931; Colbert, 1968; Douglass, 2009) of the Carnegie Museum of Natural History, Pittsburgh in 1909 was prospecting for dinosaurs in the area north of Jensen in Uintah County, north-eastern Utah. On August 17, while walking up a ridge of Morrison sandstone, he came across an articulated series of eight well preserved caudal vertebrae of a sauropod dinosaur. Further excavation showed that the vertebrae continued in both directions and, before this remarkably complete skeleton of *Apatosaurus* was fully exposed, another was encountered, and this continued for 13 years until 1922. The bones occur in an indurated, fine-grained lens of cross bedded sandstone, 2.4 to 3.6 m in thickness and about a mile (1.6 km) long, which formed as a river sand bar in the upper or Brushy Basin Member. Fortunately, there is good clevage between the bone and the extremely hard sandstone, which could be excavated as large blocks thanks to the softer underlaying stratum. In all, the Carnegie Museum removed 23 mountable skeletons, many of which have been exchanged with other museums. The CM mounted skeletons include those of the sauropods *Apatosaurus, Camarasaurus* and *Diplodocus,* the theropod *Allosaurus*, the ornithopods *Camptosaurus* and *Dryosaurus*, and the plated dinosaur *Stegosaurus* [photographs, McGinnis (1982); also details for non-CM mounts, Chure & McIntosh (1990); catalogue of specimens in CM collection, McIntosh (1981); map of CM excavation (plus current cliff face) and list of bones from Douglass, 1909-1923, Record Book in Carpenter (2013, fig. 10, appendix 1); for web sites to access quarry maps for all excavations and current DNM cliff face, see Esplin (2017)].

In October, 1915 the quarry with 80 adjacent acres was designated as Dinosaur National Monument, and in 1938 it was enlarged to include the scenic canyons of the Green and Yampa Rivers in Colorado. The 67 degree dip of the fossiliferous beds made it perfect for display, so a 55.75 m long by 10.5 m tall part of it with 1400 *in situ* bones exposed in relief formed the back wall to the Visitor Center (McIntosh, 1977). This opened in 1958 but, because of structural problems resulting from the unstable bed rock, a new enclosure building for the cliff face was opened in 2011 (see Carpenter, 2013 for history, sedimentary and taphonomy of quarry).

The varying degree of disarticulation suggest that the bones were the result of non-catastrophic mass mortality during extreme droughts (Carpenter, 2013). A minimum number of 10 individuals of *Stegosaurus* are represented based on right scapulae (Esplin, 2017). Although *Stegosaurus* is the second most common dinosaur in the quarry, it is represented mostly by isolated elements such as plates, spines, girdle and limb bones and vertebrae (including an articulated neck and sacra with ilia), and the greater part of a single individual has not been found in association (White, 1964; but see Section 5.6). Based on unspecified differences in the form of the radius and ulna, McIntosh (1981) recognised two species of *Stegosaurus* from this quarry, *S. ungulatus* and *S. stenops*.

4.6. Cleveland-Lloyd Dinosaur Quarry, Utah

The Cleveland-Lloyd Dinosaur Quarry (CLDQ), which is in north-central Emery County approximately 16 km (10 mi) east of Cleveland and 32 km (20 mi) south-southeast of Price, was declared a US National Monument in 1967. The fossils occur in a 1 m thick fine-grained calcareous mudstone in the lower portion of the Brushy Basin Member. The site was first excavated by parties from the University of Utah in 1929 and from Princeton University in 1939-1941, as reported by Stokes (1945; for history see Stokes, 1985). There were further excavations by the University of Utah (1960-1966, occasionally through 1985), the Utah Division of State History (1975-1980) and Brigham Young University (1986-1890) (Miller *et al*., 1996). It is the densest deposit of Jurassic theropod dinosaur bones discovered to date, with an unusual unbalanced ratio of carnivores to herbivores at 3:1. Approximately 10,000 disarticulated bones have been collected that represent a minimum of 70 individuals, representing a minimum of nine genera. At least 46 of the individuals are referred to the theropod dinosaur *Allosaurus fragilis* with over 85% representing juvenile/subadult individuals (Madsen, 1976). Other finds include two species of *Ceratosaurus* (Madsen & Welles, 2000), several genera of small theropods, the sauropod *Camarasaurus* and a sauropod indet., the ornithopods *Camptosaurus* and *C.* sp., an ankylosaur and *Stegosaurus* cf. *stenops* and *S*. sp. The bones represent an attritional assemblage in a poorly drained overbank deposit, with the totally disarticulated bones introduced post-mortem into an ephemeral pond during flood conditions (Peterson *et al*., 2017).

The cost of excavation and preparation of the bones was beyond the means of a single institution so in 1960 W. L. Stokes and J. H. Madsen, Jr. created the University of Utah Cooperative Dinosaur Project (Madsen, 1976, 1987; Stokes, 1985). The participating institutions (list with femur size in Madsen, 1976, pp. xi-xii; longer list in Stokes, 1985, p. 25) that contributed funds subsequently received at least one composite mounted skeleton of *Allosaurus fragilis* consisting of a mix of matching sized bones and casts (Madsen, 1973, 1976).

A minimum of five individuals of *Stegosaurus*, 7% of the total fauna, are known for CLDQ (Peterson *et al*., 2017) and skeleton kits of *Stegosaurus* were also sent out and mounted by Jim Madsen (list in 1976). Real bones from the CLDQ were included only in the mounted skeletons at the LACM (no bony osteoderms, L. Chiappe, pers. comm., 2019) and the CEUM (see Section 7.4).

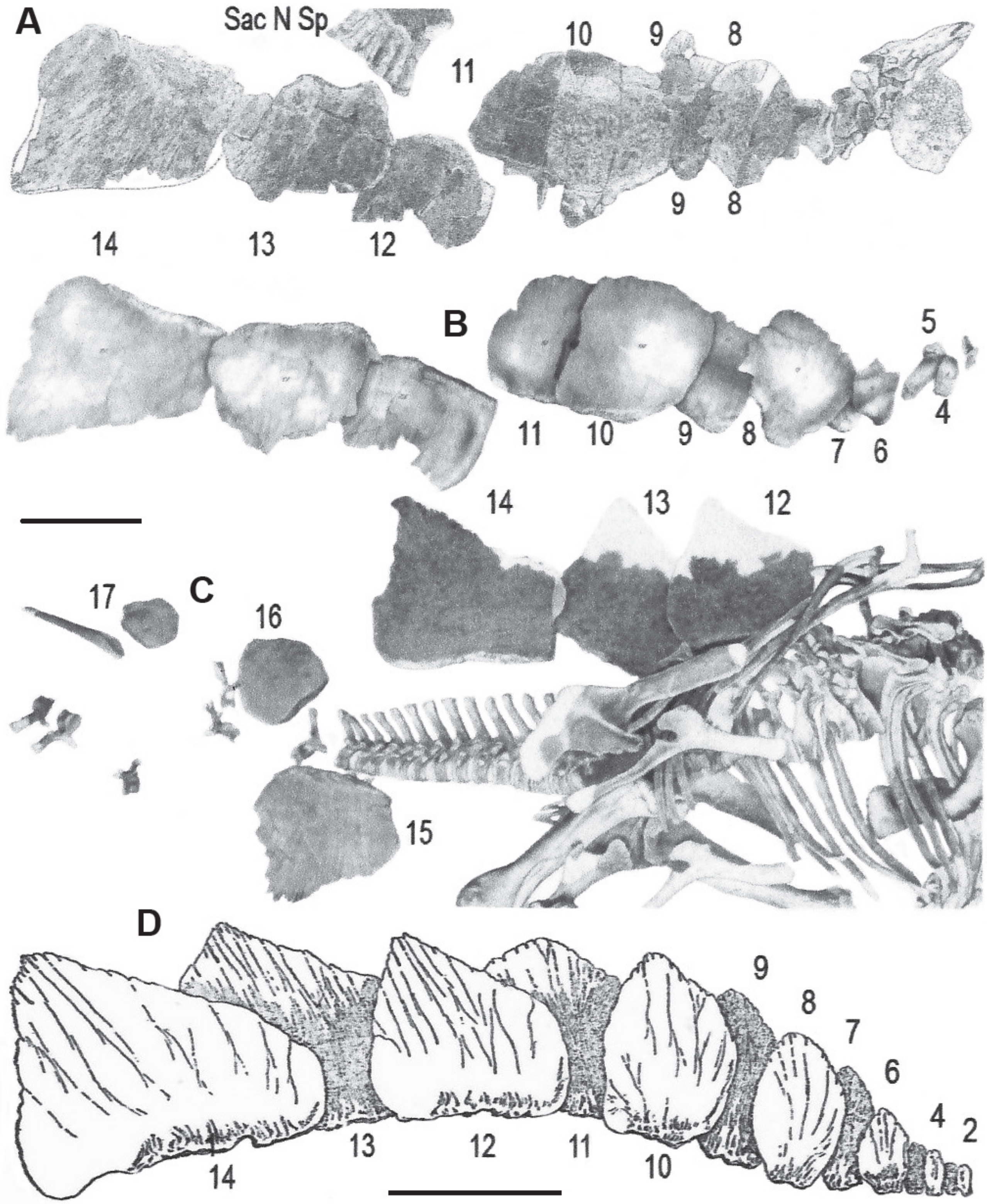

Fig. 8: Drawings of dermal plates of *Stegosaurus stenops*, holotype USNM V 4934, from Garden Park, Colorado: A-B: plates 1 to 14 as exposed (mostly under direction of O. C. Marsh, see Section 5.2) showing left side of skeleton on lower side of block (note even numbers on right side of midline, odds on left), drawings under supervision of A: C. W. Gilmore and B: F. A. Lucas by George E. Roberts (for details of smaller anterior plates, see Figs 9C-E); C, bones as exposed under direction of C. W. Gilmore on upper exhibited right side of block to show plates 12 to 17 and a dermal spine (cf. Fig. 2G); D, reconstruction of dermal plates 2 to 14 in right side view, drawing done under direction of F. A. Lucas. A-C from Gilmore (1914), D from Gilmore (1915); abbreviations: Sac N Sp, neural spines of sacral vertebrae; 2-17, plate positions in series, even numbers on right side of body, odd numbers on left side. Scale bars = 250 mm.

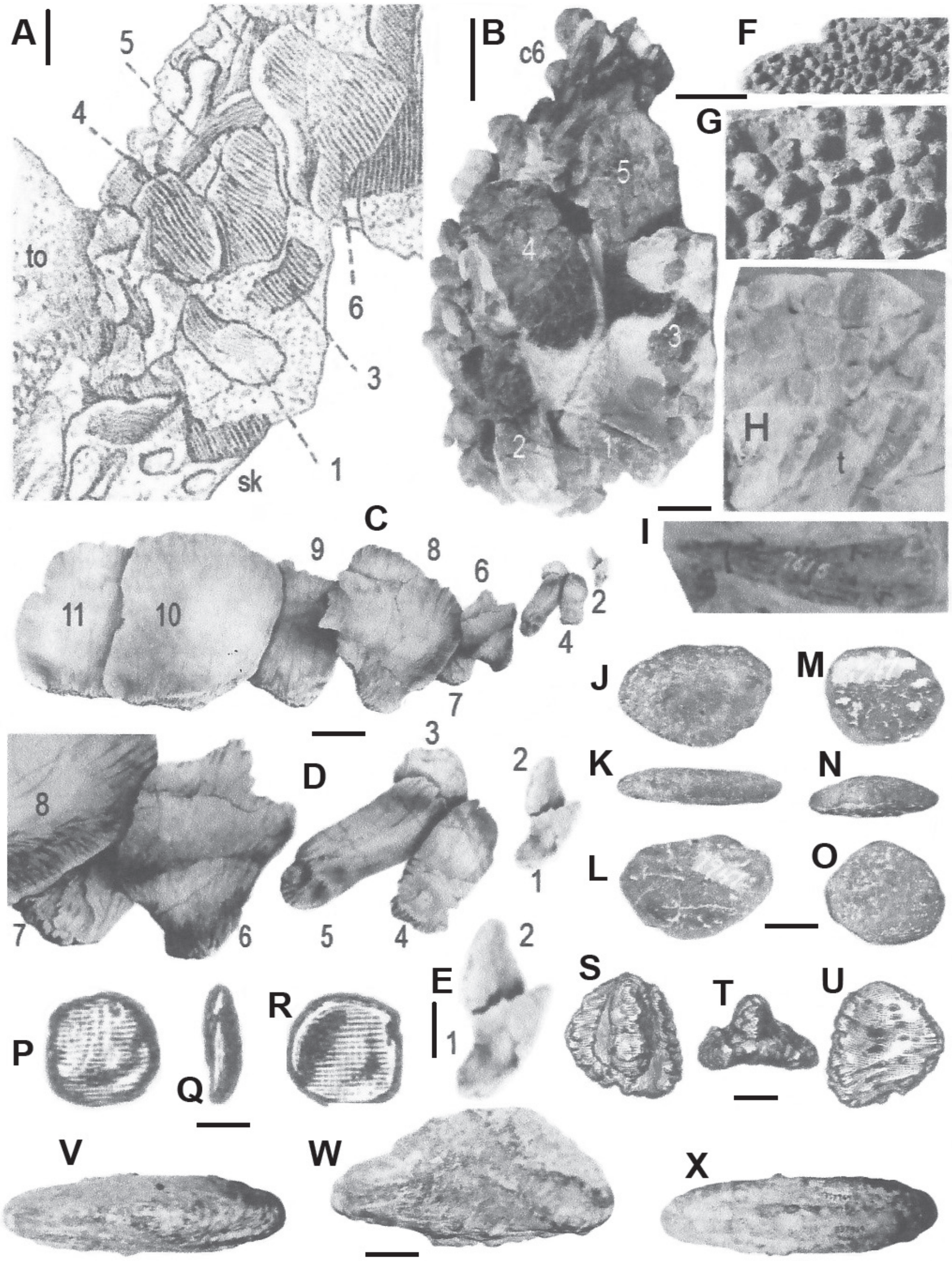

Fig. 9: Anterior dermal armor. A-O: *Stegosaurus stenops*, A-G: holotype USNM V 4934 from Garden Park, Colorado: A-E: nuchal (1-5) and transitional (6-9; dorsals 1-4) plates: A-B, as preserved; C-E: enlarged parts of drawing (Fig. 8B) prepared by G. E. Roberts under direction of F. A. Lucas in Gilmore (1914), C, plates 1-11; D, plates 1-8 and E, plates 1 and 2. F-G, part of cuirass-like arrangement of throat ossicles in internal view (see also Gilmore, 1914, pl. 22, fig. 3). H-O: specimens from YPM Quarry 13, Como Bluff, Wyoming: H-I: USNM V 7615, throat ossicles of cuirass in external view (see Gilmore, 1914, pl. 22, fig. 2 for another part of cuirass) and with a theropod tooth (detail in I). J-O: USNM V 7947, a smaller (J-L) and a larger (M-O) throat ossicle in J, M, external; K, N, edge on and L, O, internal views. P-U: from YPM Quarry 12, Como Bluff, *S. ungulatus,* YPM V 1853, since lost, P-R, throat ossicle and S-T, "tubercular spine" (incomplete nuchal plate) in P, S, external; Q, T, edge on and R, U, internal views. V-X, lateral bony scute of a polacanthid ankylosaur from YPM Quarry 13, USNM V 337969, in V, dorsal; W, side and X, ventral views. A-E modified from Gilmore (1914), J-O, V-X from M. Brett-Surman, P-U from Marsh (1880); abbreviations: c6, cervical vertebra 6; sk, skull; t, theropod tooth; to, throat ossicles; 1-11, plate numbers 1-11. Scale bars = 50 mm (A, B, D, E), 80 mm (C), 25 mm (F, P-U), 20 mm (G), 30 mm (H, J-O, V-X), and 15 mm (I).

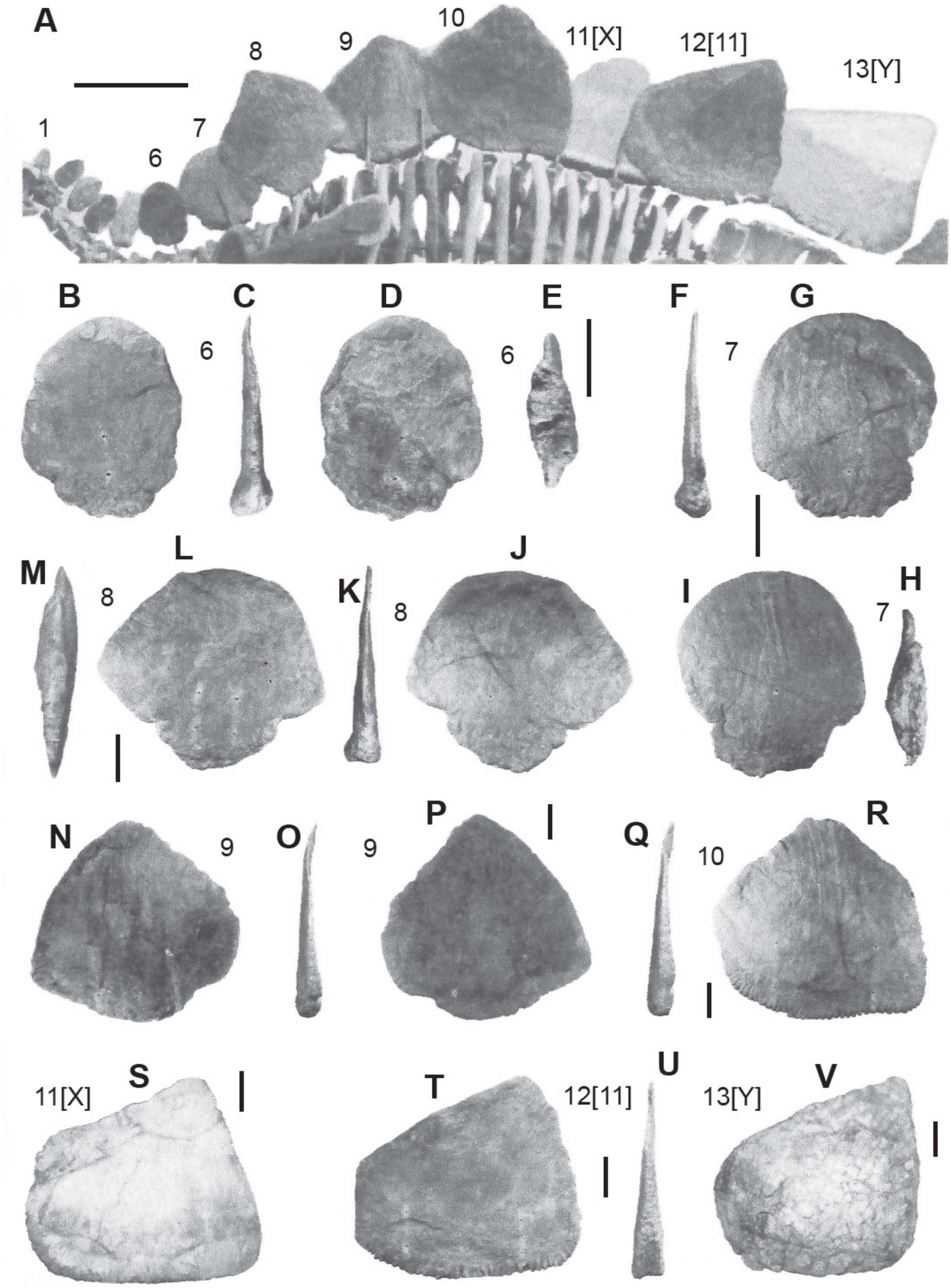

Fig. 10: Dermal plates of *Stegosaurus stenops* from YPM Quarry 13 at Como Bluff, used on the mounted skeleton USNM V 8612 by Gilmore (1918). A, plates 1 to 13 in left side view on mounted skeleton (Fig. 2C) to show relative proportions: plates 1, 2, 4 - USNM V 7615; plate 3 - USNM V 7383 (for plates 1-4 see Figs 11A, B); plate 5 - plaster; plates 6-10 and 12 (actually plate 11 of series, hence 12 [11], plate 11 [X] is a duplicate d5, b9, specimen number unknown, see Section 5.4); plate 13 (Y) another unknown specimen (see Section 5.4). B-E: plate 6 (mounted on left side) showing B, lateral; C, posterior; D, medial and E, ventral surfaces. F-I: plate 7 (on right side) showing F, posterior; G, medial; H, ventral and I, lateral surfaces. J-M: plate 8 (on left side) showing J, medial; K, anterior; L, lateral and M, ventral surfaces. N-P: plate 9 (on right side) showing N, lateral; O, posterior and P, medal surfaces. Q-R: plate 10 (on left side) showing Q, anterior and R, lateral surfaces. S, plate 11 [X] (on right side) showing medial surface. T-U: plate 12 [11] on left side) showing T, lateral and U, anterior surfaces. V: plate 13 [Y] (on right side) showing medial surface. B-V from M. Brett-Surman. Scale bars = 40 cm (A) and 100 mm (B-V).

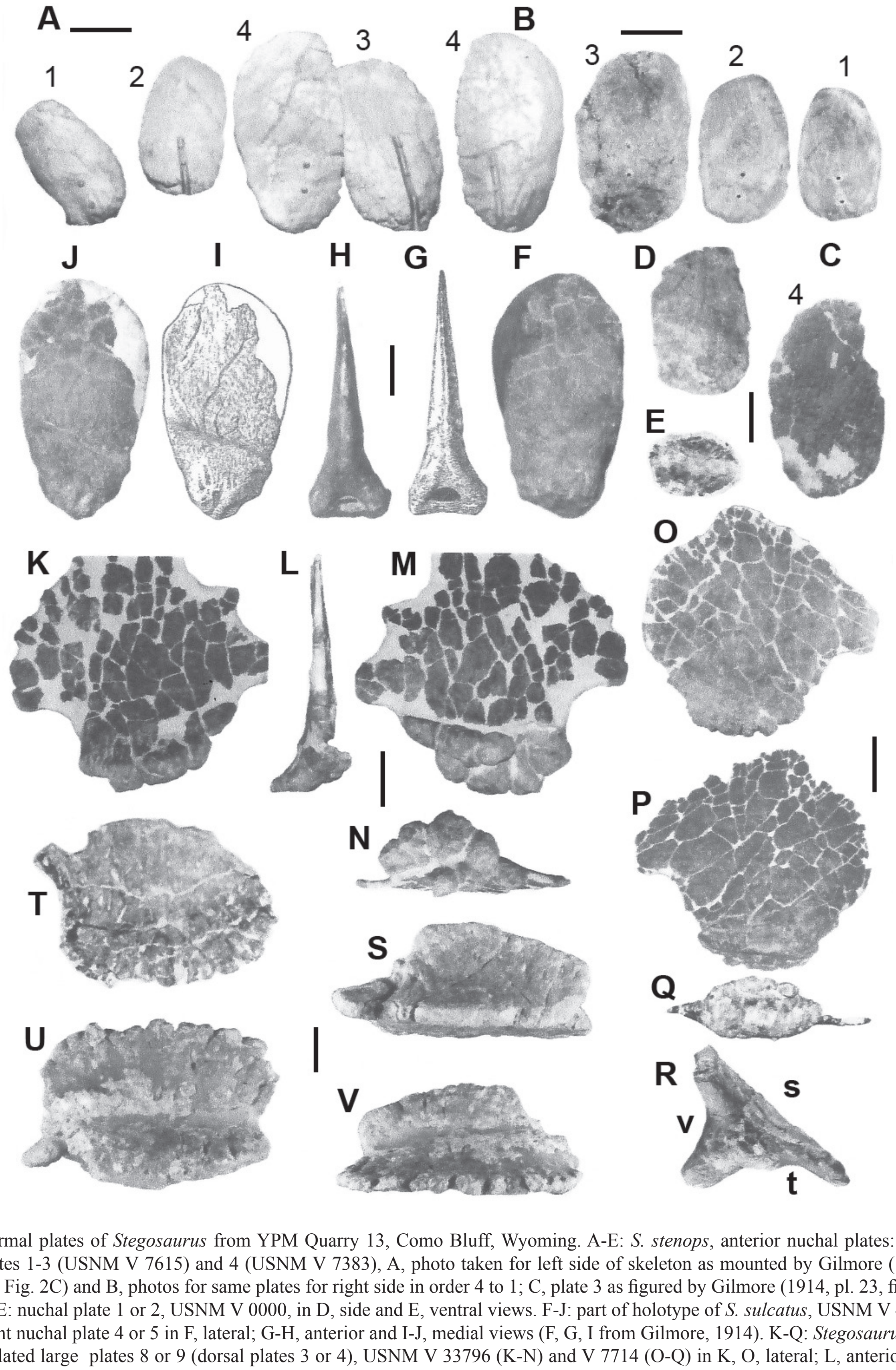

Fig. 11: Dermal plates of *Stegosaurus* from YPM Quarry 13, Como Bluff, Wyoming. A-E: *S. stenops*, anterior nuchal plates: A-B: plates 1-3 (USNM V 7615) and 4 (USNM V 7383), A, photo taken for left side of skeleton as mounted by Gilmore (1918; see Fig. 2C) and B, photos for same plates for right side in order 4 to 1; C, plate 3 as figured by Gilmore (1914, pl. 23, fig. 2). D-E: nuchal plate 1 or 2, USNM V 0000, in D, side and E, ventral views. F-J: part of holotype of *S. sulcatus*, USNM V 4937, right nuchal plate 4 or 5 in F, lateral; G-H, anterior and I-J, medial views (F, G, I from Gilmore, 1914). K-Q: *Stegosaurus* sp., isolated large plates 8 or 9 (dorsal plates 3 or 4), USNM V 33796 (K-N) and V 7714 (O-Q) in K, O, lateral; L, anterior; M, P, medial and N, Q, proximal views. R-V, Stegosaur indet., USNM V 7585, shoulder plate of Main *et al*. (2005, fig. 2F), R, identified as anterior view for a right plate and this end indicated by * in S, medial; T, ventral; U, dorsal and V, lateral views. Abbreviations: s, t, v surfaces shown in S, T and V, 1-4, cervical or nuchal plates 1 to 4. B, D, E, J-V from M. Brett-Surman. Scale bars = 50 mm (A-E, R-V), 40 mm (F-J), 100 mm (K-Q).

5. ASSOCIATED SERIES OF OSTEODERMS FOR SINGLE INDIVIDUALS

5.1. YPM VP 1853

The syntype of *Stegosaurus ungulatus* Marsh, 1879 (Fig. 4) from YPM Quarry 12 at Como Bluff, Wyoming includes a neck ossicle (Figs 1P-R, 9P-R, since lost), a "tubercular spine" (base of a nuchal plate, Figs 1S-U, 9S-U, since lost), 2 nuchal plates (Figs 1G-I, 12A-H), 1 anterior dorsal or transitional plate (Figs 12I-P), 6 dorsal to proximal caudal plates (Figs 1J-L, 14A-F, 16; plus an incomplete broken up plate, photograph from A. Heimer, pers. comm., 2018), 3 distal caudal flat spines (Figs 1M-O, 19A-J, N, 20; fourth lost, Figs 19K-M), and 4 pairs of terminal tail spines (Figs 1A-F, 24, 25; but probably from two individuals, Carpenter & Galton, 2001; see Section 7.6). However, the original positions of the osteoderms of YPM P 1853 is not known.

5.2. USNM V 4934

Gilmore (1914, p. 106) noted that this specimen was shipped to New Haven "where it was partially assembled and the rock covering was removed from what was the lower side in the quarry, as shown in plate 4 [part as Fig. 6A]. The skull was the only part worked out free of matrix." The material collected using government funds was shipped to the USNM during 1898-1899 but only "a very small part of the Stegosaurian material was in condition for study" (Gilmore, 1914, p. 1). Gilmore (1914, p. 106) noted that in "1904, under the direction of Mr. A. Lucas, the specimen was unpacked and sufficiently assembled for the life restoration made in that year by Mr. C. R. Knight" (Fig. 28E; also drawings of dermal plates made at same time, Fig. 8B, and probably the reconstruction, Fig. 8D). However, the life restoration was published in Lucas (1901a, b) and the 1899 photo of Knight working on his model of *Stegosaurus* (Fig. 28C) indicates that the reassembly must have occurred in 1899 soon after the arrival of the specimen. Further preparation of USNM V 4934 started in 1911 (Gilmore, 1914, p. 106) so the same information was available to O. C. Marsh and F. A. Lucas.

The holotype of *Stegosaurus stenops* Marsh, 1887 from YPM Quarry 1 at Garden Park near Cañon City, Colorado has nearly all of the dermal osteoderms found mostly in natural articulation (Figs 2G, 8A-C), viz., the throat ossicles (Figs 9F, G; Gilmore, 1914, pl. 22, fig. 3), plates 1-17 (Figs 2G, 8A-C, 9A-E, 14G-O) and a posterior tail spine (Figs 14M, 23S), with only three tail spines missing. These osteoderms were described by Gilmore (1914), who supplemented them with those from a few specimens from YPM Quarry 13 at Como Bluff. These included most of the tail (44 vertebrae with only proximal three missing, Gilmore, 1914, p. 58) of USNM V 4714, a slightly larger individual with plates 12 to 17 (Figs 3C, D, 15A-M) that correlated closely with the preserved parts of USNM V 4934 (Figs 8A-C, 9A-G, 14G-O; plate measurements for 4714 and 4934 in Gilmore, 1914, p. 94). It confirmed that the largest plate was over the base of the tail (Fig. 2C), as per Marsh (1891a, b, 1896, 1897; Fig. 2A), rather than over the sacrum (Figs 4A, 28E, F, H). Gilmore (1914, p. 98) noted that comparisons showed "that there were only three plates posterior to the largest of the series, or six for the two rows" for USNM V 4934. It also showed that the distal half of the tail is missing as noted by Gilmore (1918, p. 387), not 5 to 7 proximal caudal vertebrae (Gilmore, 1914, p. 93), with 22 preserved out of a total of ~47 (Gilmore, 1914, p. 58).

5.3. DMNH 2818

An excellent articulated skeleton (Figs 6A-E, Carpenter, 1998, 2007), lacking the forelimbs and girdles, was found near the type horizon and locality of *Stegosaurus stenops* in Garden Park, Colorado. Saitta (2015) gives the dermal plate count as 16, citing Paul (1992) and Carpenter (1998, 2007), but these papers do not give a plate count. The anterior plates are bunched together so their number is unclear but, assuming that the largest one of the series is plate 14, then there are 17 as in USNM V 4934 (K. Carpenter, pers. comm., 2019).

5.4. USNM V 4714/7584/7615

An almost complete series of dermal osteoderms (only plates 3 and 5 missing) from one individual of *Stegosaurus stenops* can be assembled based on bones from these specimens found in YPM Quarry 13 at Como Bluff, Wyoming. In diagram 5 for YPM Quarry 13 of F. Brown (in Gilmore, 1914, pl. 37; as Figs 3B, C), 44 caudal vertebrae, plates 13 to 17 (Figs 15B-M), and two pairs of tail spines (Figs 22A-D), are catalogued as USNM V 4714. In addition, bone 78 in diagram 5 (Fig. 3B) is also part of USNM V 4714 and it probably represents plate 12 (Fig. 15A cf. plate 12 of USNM V 4934, Figs 8, 9J).

Very close to plates 13 to 17 of USNM V 4714 is a group of six plates that are shown in diagram 4 as bones 207 to 212 (Figs 3B, C). These plates were placed on the USNM mounted skeleton (Figs 2C, 10A) as plates 6 to 10 (Figs 10B-R) and 12 (actually 11, Figs 10A, T, U) with field numbers b211, b212, b209, b208, b210 and b207, respectively (Figs 3B, C; Gilmore, 1918, p. 389). Given their close proximity and relative sizes, these plates are presumably from the same individual as USNM V 4714 but Gilmore (1914, p. 11, 1918, p. 389) catalogued them as USNM V 7584. Gilmore (1918, p. 389) mounted bone "d5, b9" of USNM V 7584 as plate 11 (as 11 [X] in Figs 10A, S) and this field number is inscribed in red ink on the plate (M. Carrano, pers. comm., 2019). However,

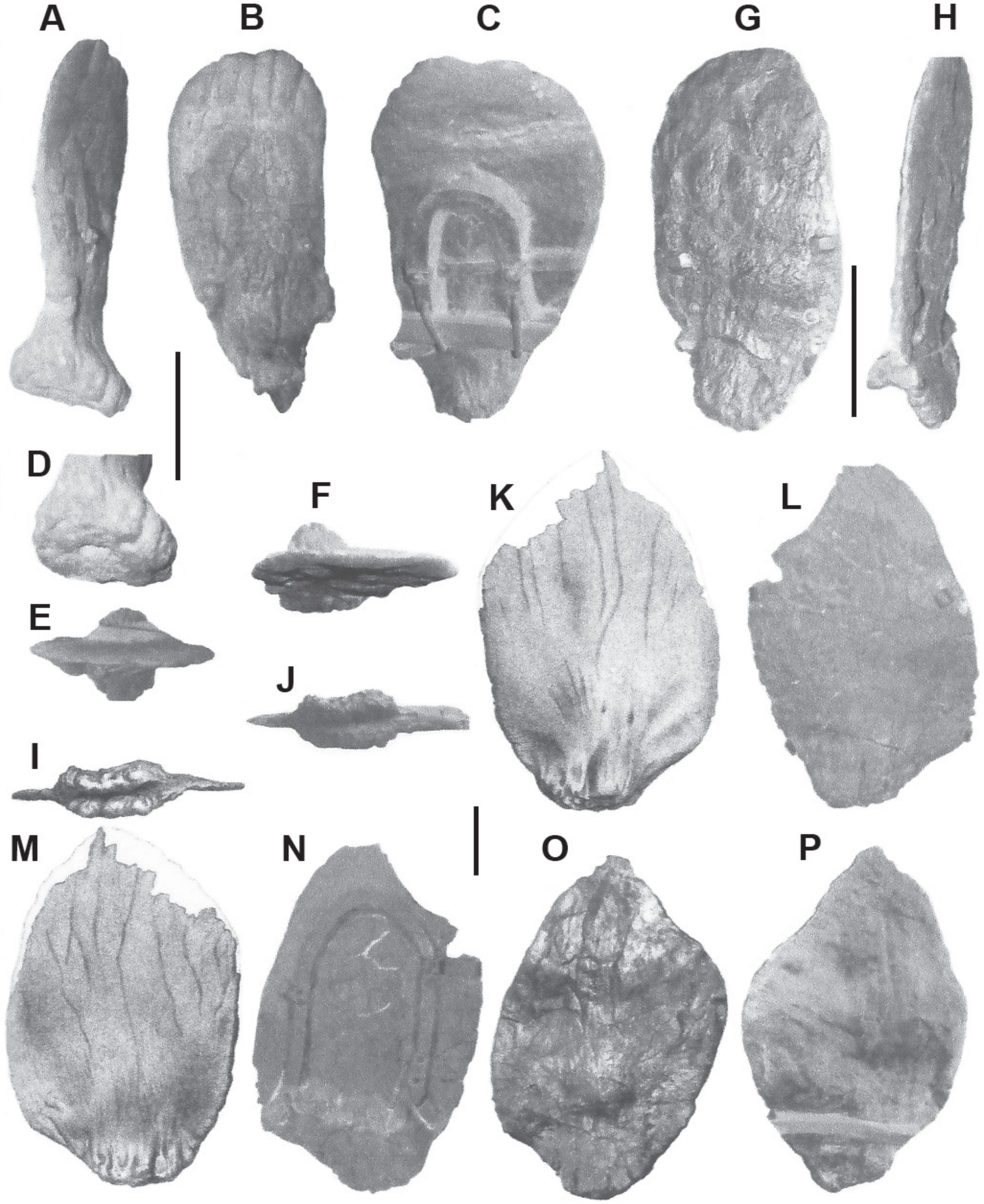

Fig. 12: Dermal plates of *Stegosaurus ungulatus* Marsh, 1879 from YPM Quarry 12 at Como Bluff, Wyoming, part of syntype YPM VP 1853. A-H, Nuchal plates: A-E: left plate 3 (mounted on right side, see Fig. 4D) showing A, anterior; B, lateral; C, medial; D, antero-ventral and E, dorsal views. F-H: left plate 4 (mounted on left side) showing F, dorsal; G, lateral and H, anterior views; I-P: mounted as left plate 6 (on left side) but probably plate 7 or 8 (transitional dorsal plate 2 or 3): I, K, M as figured by Marsh (cf. Figs 1G-I); J, L, N probably the same plate that was not used when skeleton was remounted in 1924 and O-P, plaster cast used on mounted skeleton in 1924 showing I, J, ventral; K, L, P, lateral and M-O, medial views. I, K, M from Ostrom & McIntosh (1966). Scale bars = 100 mm.

this bone was not part of the group (Fig. 3C) located in diagram 4 and this field number was also used for another plate. Gilmore (1914, pl. 13; incorrectly as bone "95" on p. 94, and in caption to pl. 23, fig. 6) correctly referred the other "d5, b9" plate to USNM V 4714. It was originally found overlapping bone 10 (Figs 3B, 15G-J) of USNM V 4714 (i.e., plate 14, Figs 3B, 15J), so this bone 9 is definitely plate 13 of USNM V 4714. It is in the collection, where I photographed it (Figs 15B-D) in the early 1980s, and this plate was not used as plate 11 when the skeleton was mounted in 1918 by C. W. Gilmore. The mounted plate 11 (11 [X] in Figs 10A, S) is probably not part of USNM V 7584 and, although it has "d5 b9" inscribed on it in red paint (M. Carrano, pers. comm., 2019), this field number is probably incorrect. However, whatever the correct field bone number, this bone was not part of the sequence of neck plates of USNM V 7584 located in diagram 4 (Fig. 3C). Mounted plate 13 (13 [Y] in Figs 10A, V) was referred to USNM V 4714 but, from the field number cited (d7, b43 in Gilmore, 1918, p. 389; Fig. 3B), this referral is probably incorrect (probably not referable to USNM V 7584 either). However, this bone has no red field number (M. Carrano, pers. comm., 2019) so the correct specimen number cannot be determined. Mounted plate 14 is a cast of plate 14 (d5, b10) of USNM V 4714 (Figs 15G-J).

Throat ossicles (Figs 9H, I; Gilmore, 1914, pl. 22, fig. 2; not used on mount) and mounted plates 1, 2 and 4 are catalogued as USNM V 7615 (Figs 10A, 11A-C; note plates 3 and 4 reversed on mount, Figs 10A, 11A).

These plates were collected as bone numbers 202, 197, 194 and 185, respectively (in diagram 4, Fig. 3C; Gilmore, 1918, p. 389) and, as they were found mixed in with (197, 194) or adjacent (202, 185) to the plates of USNM V 7584, they probably came from the same individual. Mounted plate 3 (Figs 11A3, 11B3) is USNM V 7383 (d7, b47, Gilmore, 1914, p. 389, pl. 37), and plate 5 is restored in plaster.

Thus, an almost complete series of osteoderms, with only plates 3 and 5 missing and belonging to one individual, is represented by bones catalogued as parts of three specimens found adjacent to each other (Figs 3B, C):

1. **USNM V 7615** for:
   Throat ossicles, d4, b202 (Fig. 9H; Gilmore, 1914, pl. 22, fig. 2; not used on mount),
   Plate 1, d4, b197 (Figs 11A1, 11B1; Gilmore, 1914, pl. 23, fig. 3, not 1 as in caption),
   Plate 2, d4, b196 (Figs 11A2, 11B2; Gilmore, 1914, pl. 23, fig. 2) and
   Plate 4, d4, b185 (Figs 11A4, 11B4, incorrectly mounted as plate 3).
2. **USNM V 7584** for:
   Plate 6, d4, b211 (Figs 10A-E; correlated with plate 6 of USNM V 4934 by Gilmore, 1914, pl. 23, fig. 5, not 4 as in caption),
   Plate 7, d4, b212 (Figs 10F-I),
   Plate 8, d4, b209 (Figs 10J-M; correlated with plate 8 of USNM V 4934 by Gilmore, 1914, pl. 23, fig. 4, not 5 as in caption),
   Plate 9, d4, b208 (Figs 10N-P),
   Plate 10, d4, b210 (Figs 10Q, R),
   Plate 11, d4, b207 (Fig. 10T; 11 [12] as mounted as plate 12, Fig. 9A).
3. **USNM 4714**, plates 13 to 17 were correlated with plates 13-17 of USNM V 4934 (Fig. 8) by Gilmore (1914, p. 93, fig. 58, pls 14, 23, fig. 6, 24):
   Plate 12, d5, b78 (Fig. 15A; cf. plate 12 of USNM 4934, Figs 8, 14J),
   Plate 13, d5, b9 (Figs 15B-F; Gilmore, 1914, pl. 12, pl. 23, fig. 6; Ostrom & McIntosh, 1999, pl. 61),
   Plate 14, d5, b10 (Figs 15G-J; cast mounted as plate 14; Gilmore, 1914, pl. 13, pl. 24, fig. 4, 1918; Ostrom & McIntosh, 1999, pl. 64),
   Plate 15, d5, b95 (Fig. 15K; Gilmore, 1914, pl. 24, fig. 3),
   Plate 16, d5, b96 (Fig.15L; Gilmore, 1914, pl. 24, fig. 2),
   Plate 17, d5, b197 (Fig. 15M; Gilmore, 1914, pl. 24, fig. 1) and
   Two pairs of tail spines (anterior, d7: b158, 159) and posterior (d7: b156, b157, Figs 22A-D; Gilmore, 1914, pl. 15; Ostrom & McIntosh, 1999, pl. 54).

5.5. NHMUK PV R36730

"Sophie/Sarah", from Morrison Formation near Shell, Wyoming is referred to *Stegosaurus stenops*. Siber & Möchli (2009, pp. 38-49, 53) give color photos of the mounted skeleton as cf. *S. armatus* based on casts, the first to be based mostly on bones from a single individual (Fig. 2E), overall layout views of the actual bones of the complete skeleton from both sides, and also just the dermal armor from both sides (see Figs 7A, B). These photos were taken when the bones were prepared as "Sarah" (SMA RCR0603) at the Sauriermuseum Aathal in Switzerland. The bones of "Sophie" (NHMUK PV R36730) are exhibited as a mounted skeleton (Fig. 2F), the first based mostly on actual bones from a single individual. They are illustrated as a layout of the right side in mostly lateral view and each dermal plate and spine is illustrated individually from both sides in color, described in detail, and compared with those of other stegosaurs by Maidment *et al*. (2015).

Both mounted skeletons have 19 plates, with only plate 14 restored, and the plates are arranged in the same order (Figs 2E, F, 7). However, Siber & Möchli (2009, pp. 40-41) note that there is a chance that one plate got lost when the shovel of the bulldozer hit the specimen and the untreated bone immediately disintegrated. Maidment *et al*. (2015, p. 107) note that "when the specimen was discovered, there was a space above the proximal portion of the tail [Fig. 7C] suggesting that another plate was originally present but became disarticulated post-mortem and was not preserved," so there were probably 19 plates. Saitta (2015, pp. 12-13, fig. S21), who regarded the 18 plates preserved (Fig. 7B) as representing the complete series, reassigned plate 5 from the neck to the tail (as plate 18) and plate 15 from the tail to the dorsal section (as plate 11). However, Maidment *et al*. (2015) noted that plate 5 was found adjacent to the neck (Fig. 7C), rather than near the tail, but did not comment on plate 15, the original identification of which seems to be correct. From the quarry map (Fig. 7C) plates 11 to 18 were preserved in a U-shaped curve as a continuous series except for a gap between preserved plates 13 and 16. The gap between these plates was filled by Maidment *et al*. (2015) with plate 15 that was found about 2 m to the south of the tail (Fig. 7C). Consequently, a reconstructed plate 14 is not needed and the preserved 18 plates represent the complete series (Fig. 7B).

Siber & Möckli (2009, fig. p. 45) note that plate 13 "should be rotated and oriented horizontally [as shown in Fig. 7B], rather than vertically" and this plate is incorrectly oriented in both mounted skeletons (Figs 2E, F). Maidment *et al*. (2015, p. 98) note that the anterior margin of plate 13 "is missing and a considerable part is reconstructed in plaster. As a result, it has an elongate, elliptical outline, although originally it was probably more similar in shape to Pl. 11 or 12," so it was even larger than shown (Figs 2E, F, 7B).

5.6. UMMP-NH 118201

This partial skeleton from DINO was displayed as a slab mount, originally mounted in 1969, that was recently dismantled and the plaster removed from the bones that were exchanged to the UMMP by the late Jim Madsen (UUVP). These resulted from the University of Utah excavations in 1923-24, initially led by Earl Douglass while on leave from the Carnegie Museum, and then by Golden York, retired curator of the Museum of Earth Sciences (see Esplin, 2017, p. 3). This undescribed partial skeleton (Fig. 17M) includes poorly preserved cervical and dorsal vertebrae, 33 mostly complete caudal vertebrae, and a left pectoral girdle, humerus (maximum length 540 mm) and partly restored bones, the left ilium and the right radius and ulna of UUVP quarry specimen #402. The well preserved last dorsal, dorsosacral, sacrals 1 to 4, sacrocaudal and the first caudal vertebra are from specimen #409/B. The former specimen is extremely important because 13 osteoderms are based on real bone, with plates 9 to 12 and 16 to 18 as mounted plus the right anterior tail spine from UUVP #402, plates 5 and 14 plus the left anterior tail spine from UUVP #340, and plates 4 and 8 from somewhere in the 1923-24 excavation site (UMMP-NH Archives). The plates of #402 are tentatively identified as plate 8 (Fig. 13f; UMMP-NH 118201.9), plate 9 (Fig. 13i; UMMP-NH 118201.10), plate 10 (Fig. 13j-l; UMMP-NH 118201.17), posterior dorsal (plates 11-13) or caudal 2 (plate 15) (Figs 17N-P; UMMP-NH 118201.12, 16), and an anterior flat distal tail spine (Figs 21C-E; UMMP-NH 118201.18). Plate UMMP-NH 118201.11 is indeterminate and appears to be mostly plaster (needs to be X-rayed as bone shows through in places), and there is a right anterior tail spine (Fig. 17M). Plates from #340 are the 7th (Figs 13X-Z; UMMP-NH 118201.5) and 14th (caudal 1, Fig. 17Q; UMMP-NH 118201.14) plus a left anterior tail spine (Fig. 17M). Those lacking field data are the 6th (Figs 13X-Z; UMMP-NH 118201.4) and a duplicate 8th plate (Figs 13e; UMMP-NH 118201.8).

6. DESCRIPTION OF DERMAL OSTEODERMS OF *STEGOSAURUS STENOPS*

6.1. Throat ossicles

Marsh (1880, pl. 101, figs 1a-c; 1887, 1896) illustrated a small dermal ossification of *Stegosaurus ungulatus* (Figs 1P-R, 9P-R; YPM VP 1853, since lost), with many of them shown below the skull (Fig. 2A; Marsh, 1891a, pl. 9). Gilmore (1914, pls 2-4, 22, fig. 3) described patches of scattered small (width up to 35 mm), depressed, angularly rounded ossicles with the smooth internal surfaces exposed near the skull in *S. stenops* (USNM V 4934; Figs 8A, 9F, G). In USNM V 7615 the rugose dorsal surfaces are exposed (Fig. 9H; Gilmore, 1914, pl. 22, fig. 2). With the latter there is an isolated carnivorous theropod tooth (Figs 9H, I) that was presumably shed during an attack on the vulnerable throat area. Two of the throat ossicles of USNM V 7947 are shown in three views (Figs 9J-O). In DNMH 2818 the cuirass of small, roughly hexagonal shaped ossicles are arranged in a rosette pattern and are preserved adjacent to the throat region (Figs 6A, B, D; Carpenter, 1998, figs 2, 6), rather than some of them being displaced close to the anterior part of the neck as in USNM V 4934 (Gilmore, 1914).

Czerkas (1987, p. 94) noted that "clusters of ossicles… have been found in association with other parts of the body as well as the neck" but this is not the case (Carpenter, 1998). The few scattered ossicles found adjacent to vertebrae 10, 11, 16 and plate 10 (Gilmore, 1914, p. 91) of USNM V 4934 were probably dispersed by currents from the main concentrations near the skull and neck. Comparable throat ossicles are not known in any other stegosaur.

Carpenter & Small (1993, p. 29A) noted for DNNH 2818 that "small keeled discs of bone (2.5 cm) were also found with the new *Stegosaurus* specimen" from Garden Park, Colorado. However, this was based on the cross-section of a broken rib that was pushed into the intercostal space between the parallel ribs of the opposite side (K. Carpenter, pers. comm., 2018).

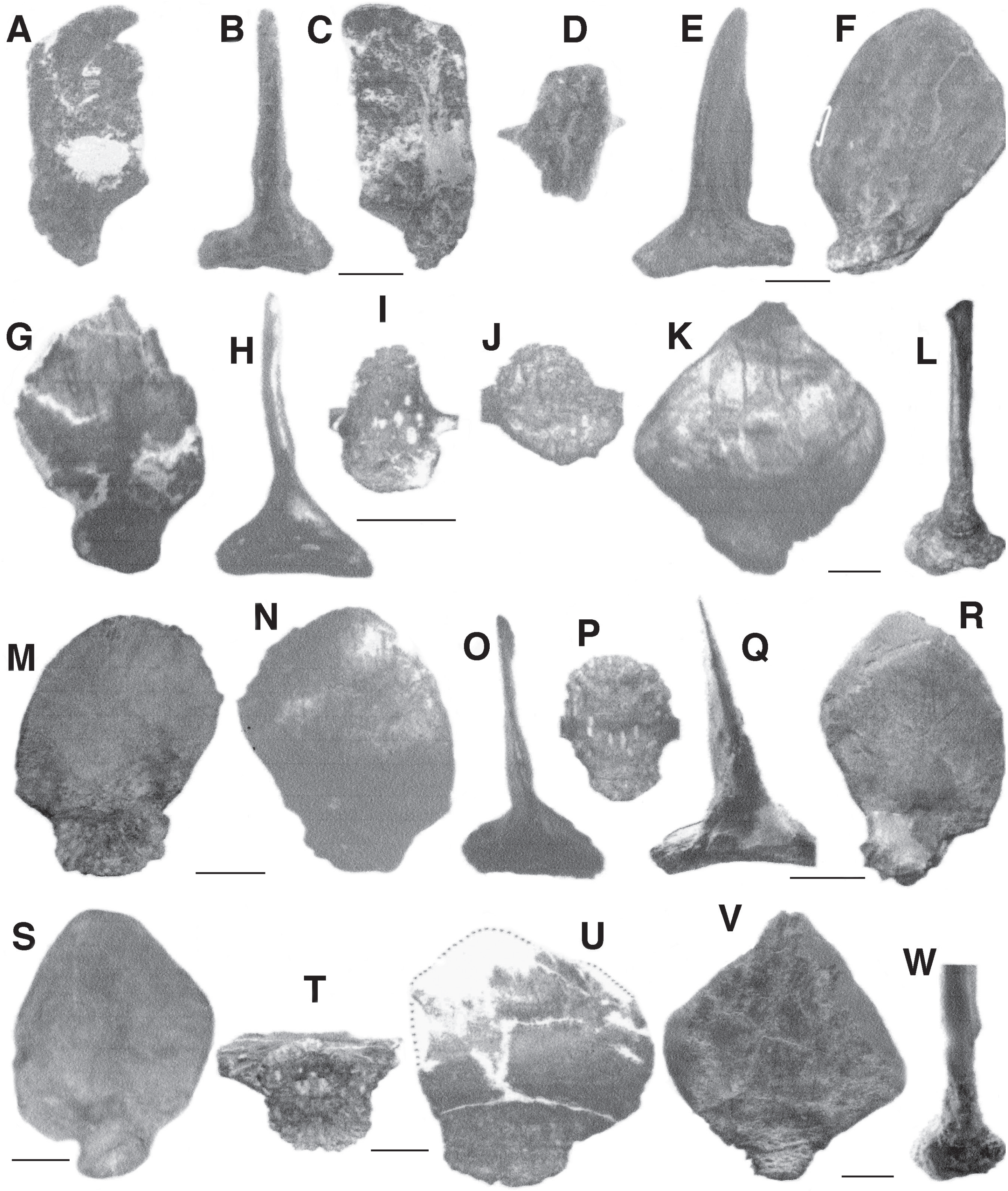

Fig. 13: Nuchal or neck plates (1-5) and transitional (6-9, dorsal plates 1-4) with transversely expanded bases from Morrison Formation of Utah, all reduced to unit height. A-W, from Cleveland-Lloyd Dinosaur Quarry, Emery County. A-D, nuchal plate 1, A, C, as bone, UMNH VP 9731 (UUVP 4502) and B, D, as a cast, UMMP NH 118201.1 in A, C, side; B, anterior and D, ventral or basal views. E-W, CEUM 1717, a collective number for all bones and casts from CLDQ, none of which were associated, E-F, nuchal plate ~2 as a cast (original UUVP bone not located) in E, anterior and F, side views; G-I, nuchal plate ~4 in G, side; H, anterior and I, ventral views; J-L, plate ~8 (dorsal or transitional plate 3) in J, ventral; K, side and L, anterior views; M-P, plate ~6 (dorsal or transitional plate 1) in M, N, side; O, anterior and P, ventral views; Q-R, nuchal plate ~5 in Q, anterior and R, side views; S, cast of nuchal plate ~3 in side view (original UUVP bone not located); T-U, plate ~7 (dorsal or transitional plate 2) in T, ventral and U, side views and V-W, plate 9 (dorsal or transitional plate 4) in V, side and W, anterior views.

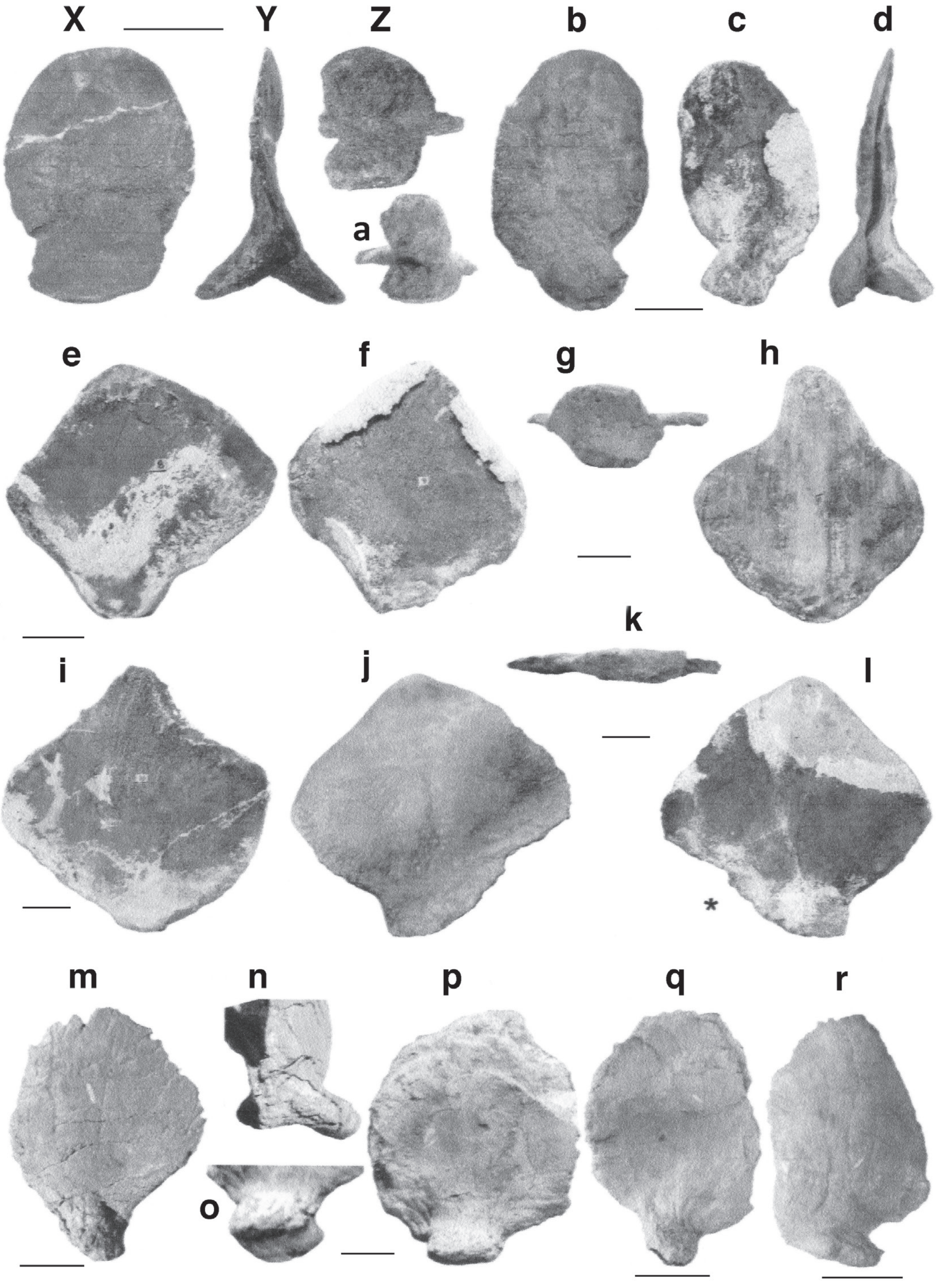

Fig. 13: (Continued). X-r, from Carnegie Quarry at Dinosaur National Monument near Jensen, Utah, X-l, UMMP-NH 118201 from dismantled slab mount (Fig. 17M), X-Z, dorsal (transitional) plate 1 (UMMP-NH 118201.4) in X, side; Y, anterior and Z, ventral views; a-d, dorsal (transitional) plate 2 (UMMP-NH 118201.5, UUVP #340/28) in a, ventral; b-c, side and d, anterior views; e, dorsal (transitional) plate 3 (UMMP-NH 118201.8) in side view; f-g, dorsal (transitional) plate 3 (UMMP-NH 118201.9, UUVP #402/11) in f, side and g, ventral views (side edges of base incomplete in g); h, indeterminate plate in side view, bone covered with plaster so X-rays needed to help identify it; i, dorsal (transitional) plate 4 (UMMP-NH 118201.9, UUVP #402/23) in side view; j-l, UMMP-NH 118201.17, UUVP #402/29), dorsal plate 5 in j, l, side and k, ventral views (* indicates edge shown in k). m-r, nuchal and anterior dorsal plates on DNM cliff face at DINO, m-n, DINO 4299 (DNM 588), anterior nuchal plate of juvenile individual in m, side and n, oblique anterior views (black area in n is shadow); o-p, DINO 4353 (DNM 727), dorsal (transitional) plate ~4 in o, oblique ventral (of ventral part) and p, side views; q, DINO 3749 (DNM 80) in side view and r, DINO 4194 (DNM 547) in side view. Photos A, C from Levitt-Bersian; B, D, X-i, k, l from A. Rountrey; E-W from K. Carpenter; and m-o from R. Hunt-Foster. Scale bars = 50 mm (A-F, S) and 100 mm (G-R,T-r).

6.2. Tall narrow plates 1 to 5 - nuchals

Gilmore (1914) described the nuchal plates of *Stegosaurus stenops* based on those of the holotype (USNM V 4934; Figs 9A-E; Garden Park, Colorado) plus USNM specimens from YPM Quarry 13, Como Bluff, Wyoming with V 7615 (Figs 11A1, 2, 4, 11B1, 2, 4) for plates 1, 2 and 4 and V 7383 (Figs 11A.3, 11B.3) for plate 3 plus an isolated plate 5 of the holotype of *S. sulcatus,* a larger individual (V 4937, Figs 11F-J).

The first five plates are small, vertically oriented, and taller than long antero-posteriorly (Gilmore, 1914, pls 2, 3, 14) with a progressive increase in height (Figs 8, 9A-E, 11A, B). They are small and thin, flattened on the external side and slightly convex antero-posteriorly medially, with roughened basal ends that are little expanded transversely and bear a single large vascular foramen (Figs 11G, H). About a third of plate 5 was inserted into the skin as shown by a constriction, above which there are vascular grooves, whereas below it the surface is roughened (Figs 11F, I, J). As K. Carpenter (pers. comm., 2019) notes, the significance of this is that it provides a minimum thickness for the skin on the neck of *Stegosaurus* (similarly, the base of back plates for back skin). This inferred thickness is remarkably thicker than the skin of an elephant. Thick skin has not been considered before as an important defence for *Stegosaurus* (and probably also for most dinosaurs).

On the mounted skeleton of *S. ungulatus* (Figs 4C, D; YPM VP 1853, YPM Quarry 12, Como Bluff) nuchal plates 3 and 4 are real bone (Figs 12A-H). Plate 3 has a single large basal foramen (Fig. 12D). The bases of these plates are proportionally more expanded transversely, so transverse width and anteroposterior length are subequal, and the blades antero-posteriorly than are those of *S. stenops*. However, this is probably a function of the larger size of YPM VP 1853.

The base of nuchal 3 from DINO is more expanded transversely than long anteroposteriorly (Figs 13m, n), as in plates 6 and 7 (Figs 13X-d), so this may have the case for all the nuchals. The bases of nuchal plates 1 to 5 (Figs 13A-I, P, Q, S) and of the transitional plates (Figs 13J-O, Q, R, T-W) from CLDQ have the same proportions.

Marsh (1891a, b, 1896, p. 195) mentioned that, in addition to the series of vertical plates, “there was a pair of small plates just behind the skull, which served to protect this part of the neck.” These elements cannot be located but were possibly the pair of proatlases which, although not known for Stegosauria, do occur in the euornithopod dinosaur *Hypsilophodon* (Galton, 1974, figs 18C, G).

6.3. Transitional plates 6-9 – dorsals 1-4

Gilmore (1914, p. 92) described plates 6 to 9 (dorsals 1 to 4, here termed the transitional plates) of *Stegosaurus stenops* based on those of the holotype (USNM V 4934; Figs 8, 9C, D). These are vertically oriented and sub-oval plates that become progressively larger. The outer surface of the plate is flattened whereas the medial surface is slightly convex antero-posteriorly. The bases have a median cleft and are slightly expanded transversely but are short compared to the fore and aft expansion of the more distal part. Gilmore (1914) suggested that the increased width of the base provided for more stability whereas the shortness allowed for more mobility. The bases are equally rugose laterally and medially but slightly asymmetrical, resulting in the plates being inclined slightly outwards with respect to the skin.

In USNM V 7584 (Figs 10A-P) from YPM Quarry 13, plates 6 to 9 are similar but the bases are less expanded transversely and lack the median groove; the length of the base of plate 9 is not restricted anteriorly (Figs 10N-P).

Two isolated incomplete and poorly preserved larger transitional plates (USNM V 53796, Figs. 11K-N; USNM V 7714, Figs 11O-Q) from Quarry 13 each probably represent plate 8 or 9. The bases are proportionally larger transversely (but still less than the length) and much more rugose than are those of other examples of these plates from Como Bluff and Garden Park.

Plate 6 on the mounted skeleton of *S. ungulatus* (YPM VP 1853; Quarry 12, Como Bluff; Lull, 1910a, 1912) is a plaster cast (Figs 12O, P) that in 1924 presumably replaced the bony plate on the original 1910 mount. This plate (Figs 12J, L, N), which still has the original iron work attached and was probably plate 7 or 8, is in the YPM VP basement and it matches the illustrations (Figs 1G-I, 12I, K, M) of Marsh (1880, pl. 10, figs 2a-c, 1887, 1896; Ostrom & McIntosh, 1966, 1999, pl. 62, figs 1-3). The rugose base is longer than transversely wide, rather than roughly subequal in the more anterior plates (Figs 12I, J cf. Figs 12E, F).

Transitional plates 6 and 7 from DINO (Figs 13X-d) have a base that is considerably wider transversely than long anteroventrally. Although the reverse is true for plate 9 and these measurements are subequal in plate 8 (Figs 13f, g, k), it is true for plates 6 to 9 from CLDQ (Figs 13J-O, TW; see Section 7.8).

6.4. Plates 10 to 17 – dorsal, sacral and caudal plates

Plates 10 to 17 of USNM V 4934 (Figs 2G, 6, 10G-O), the holotype of *Stegosaurus stenops*, were illustrated and described by Gilmore (1914, pp. 92-93, pls 2-4, 14), as were those of USNM V 4714 (Figs 11A-M; Gilmore, 1914, fig. 58, pls 13, 14, 23, figs 4, 24, figs 1-4; also Ostrom & McIntosh, 1966, 1999, pls 61, 64 for plates 13 and 14). Plates 10 to 14 (Figs 2G, 8) show a progressive increase in size with plate 14 as the largest over the base of the tail (Figs 8, 14G, H, J), whereas plates 14 to 17 show a progressive decrease in size (Figs 8C, 14H, K, M). This is also the case for these plates in DMNH 2818

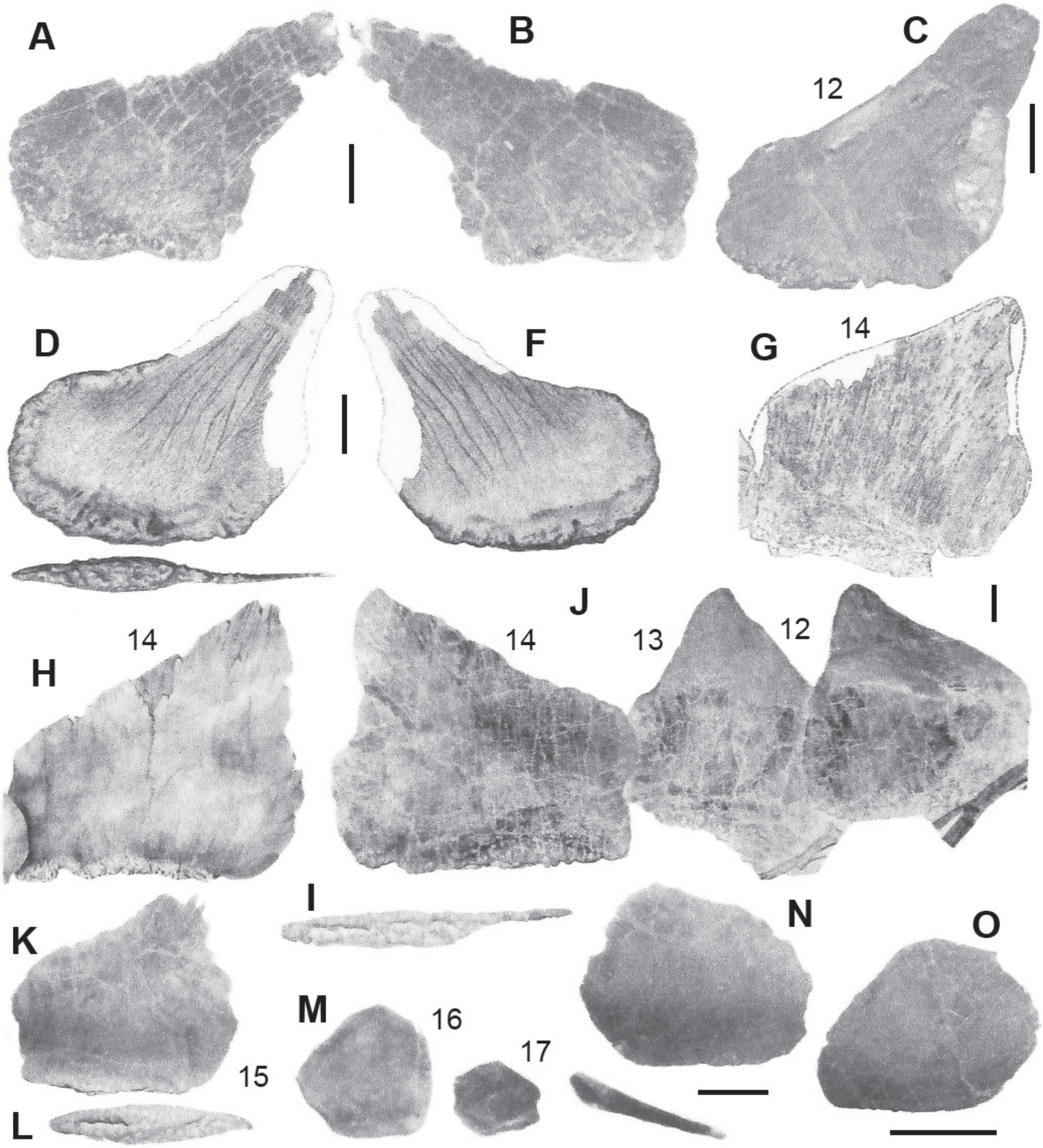

Fig. 14: Dermal plates of *Stegosaurus*. A-F: *S. ungulatus* Marsh, 1879 from YPM Quarry 12, Como Bluff, Wyoming, large posterior dorsal or anterior caudal plates, syntypes USNM V 7414 (A, B) and YPM VP 1853 (C, plate 12, Figs 4D, 16A, E); D-F, as figured by Marsh in Ostrom & McIntosh (1966) (cf. Figs 1J-L): A, C, D, plates showing left side; B, F, right side and E, ventral surfaces. G-O: *S. stenops* Marsh, 1887, holotype USNM V 4934 from Garden Park, Colorado, G-H, plate 14 (on right side of body, cf. Fig. 8A, B) showing medial surface; I, plate 14 in ventral view (with respect to 14 in J). J-M: plates 12-17 and posterior caudal spine as preserved on right side of block, at same scale of reduction (cf. Fig. 8C). J, plates 12-14; K-L, plate 15 in K, side and L, ventral views; M, plates 16, 17 and caudal spine; N, O, plates 16 and 17 at larger scale in side view. D-F from Ostrom & McIntosh (1966), G, H from Gilmore (1914); 12 to 17, plate positions in series, even numbers on right side of body, odd numbers on left side. Scale bars = 100 mm.

(Figs 6A-C, F-H), USNM V 4714/7584/7615 (Figs 3B, D, 10, 15), USNM V 6531 (Figs 18A, H) and NHMUK PV R36730 (Figs 2E, F, 7B; but plate 13 the largest and plates 13-18 diminish in size). However, three distal caudal plates of USNM V 2274 are subequal in size (Figs 18I-K).

Gilmore (1914) notes that plates 10 and 11 have a subrectangular outline (Figs 8B, 9C) but the rugose base has little transverse thickening. It is not cleft longitudinally, except in young individuals, and these are followed by thin, subtriangular plates 12 to 14 of the sacral and anterior caudal region (Figs 8A-C, 14G-J, 15A-J). Gilmore (1914) was unable to find differences in the latter plates that would distinguish the exterior from the interior surfaces because the bases are symmetrical (Figs 15 B-D), both surfaces being equally rugose and evenly covered with vascular grooves.

The original sequence for the seven dorsal to anterior caudal plates preserved in *S. ungulatus* (Figs 4B, D, 14A-C, 16; seventh incomplete and broken up) is not known and the distal flat caudal spines, which probably formed four pairs, are unique (Figs 19, 20; see Section 7.2).

The dorsal part of plate 14, the largest of the series, is more constricted dorsally in DMNH 2818 (Figs 6B, C, G), so the ventral part is more square and the dorsal part pointed and narrower than in other specimens of

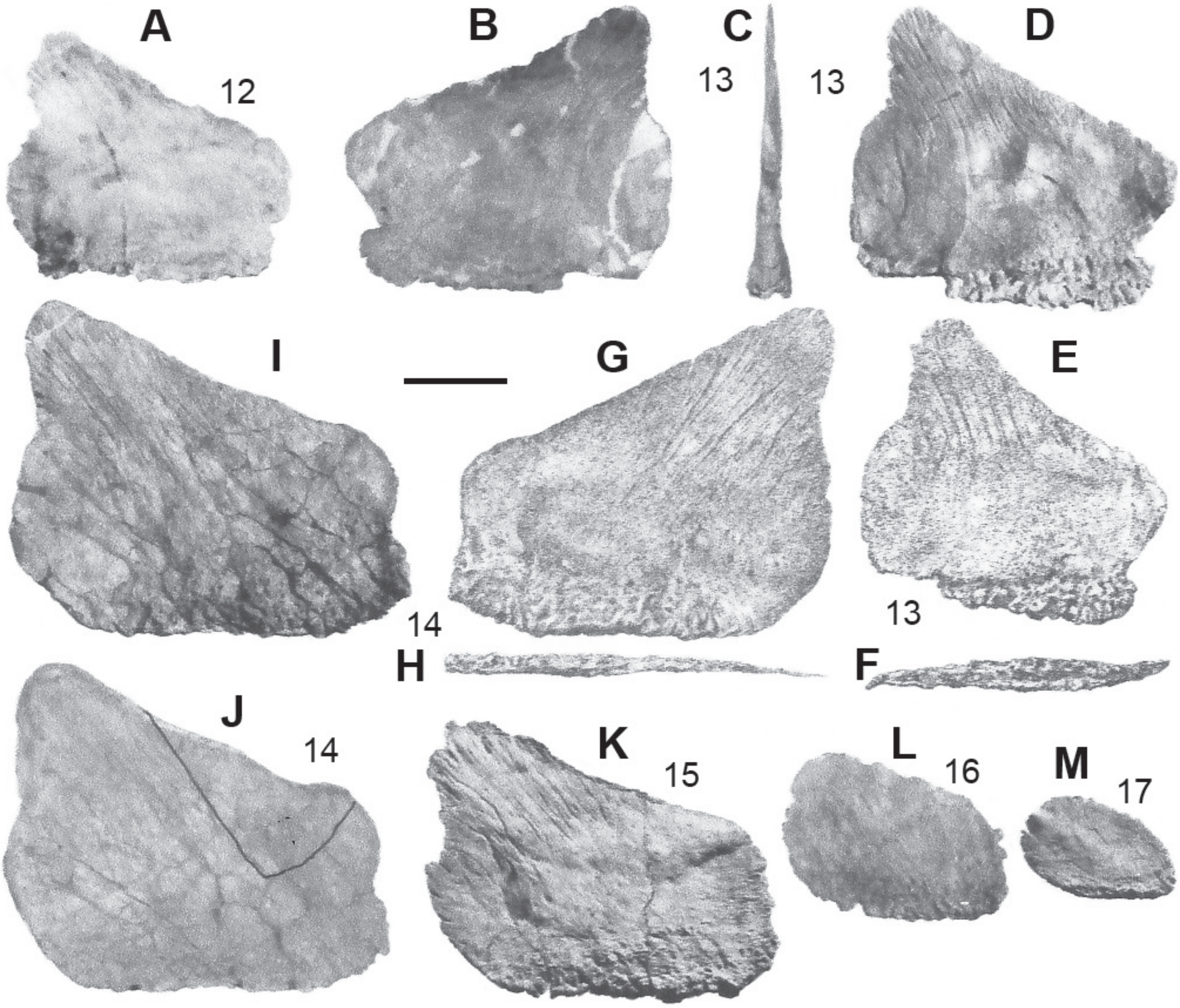

Fig. 15: Dermal plates from YPM Quarry 13, Como Bluff, Wyoming, diagram and field bone numbers (d, b) from Brown's map (see Figs 3C, D) in Gilmore (1914). A-M, series of dermal plates from one individual at same scale of *Stegosaurus stenops*, USNM V 4714, A, probable left plate 12 (d5, b78) showing lateral surface; B-F: right plate 13 (d5, b9) showing B, medial; C, anterior; D-E, lateral and F, ventral surfaces. G-J: left plate 14 (d5, b10) showing G, lateral; H, ventral and I-J, medial surfaces (with J showing area overlapped by plate 13, cf. Fig. 3B). K, right plate 15 (d5, b75) showing lateral surface. L, left plate 16 (d5, b76) showing medial surface. M, right plate 17 (d5, b177) showing lateral surface. E-H from Ostrom & McIntosh (1966), I, K-M from Gilmore (1914); abbreviations: 12 to 17, plate positions in series. Scale bar = 200 mm.

S. stenops, viz*.,* USNM V 4934 (Figs 8, 14G, H, J) and USNM 4714 (Figs 15G, I, J). In this respect it is similar to plates of *S. ungulatus* (Figs 1J, L, 16) and those from DINO (Figs 17A-G, N, Q) and CLDQ (Figs 17R-U).

Plates 8 to 10 from DINO have a similar roughly square shape (Figs 13f, i, j, l) but 8 and 9 were inserted into the skin by the lower apex (Fig. 13g) whereas in 10 most of the adjacent posterior surface was also inserted into the skin (Fig. 13k).

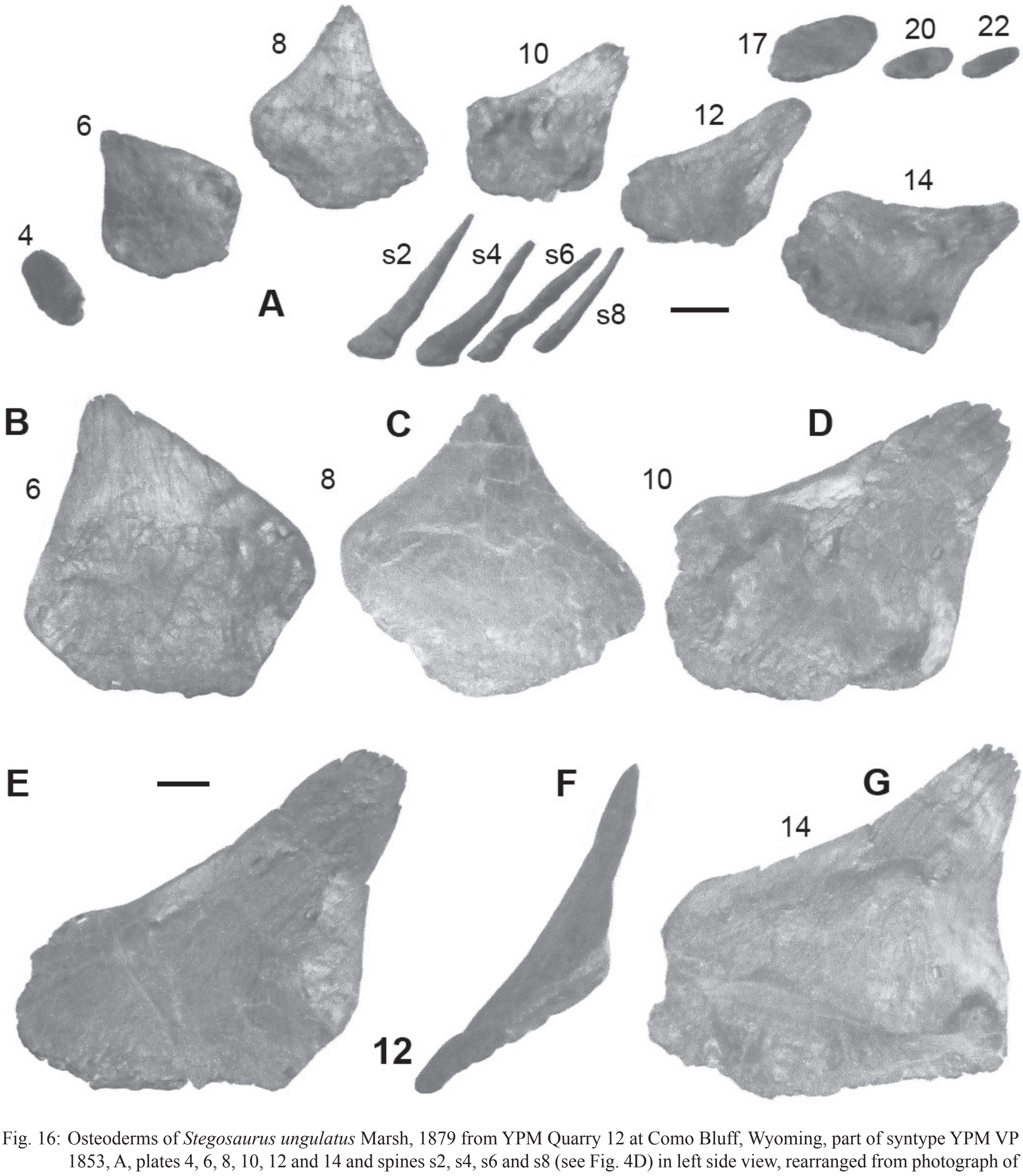

Fig. 16: Osteoderms of *Stegosaurus ungulatus* Marsh, 1879 from YPM Quarry 12 at Como Bluff, Wyoming, part of syntype YPM VP 1853, A, plates 4, 6, 8, 10, 12 and 14 and spines s2, s4, s6 and s8 (see Fig. 4D) in left side view, rearranged from photograph of complete skeleton, to show relative proportions. B-G, left osteoderms in side (A-E, G) and posterior (F) views: plates: B, 6; C, 8; D, 10; E-F, 12 and G, 14. Abbreviations: 4-22, plate positions as mounted, s2-s8, spine positions as mounted (see Fig. 4D). Scale bars = 200 mm (A) and 100 mm (B-G).

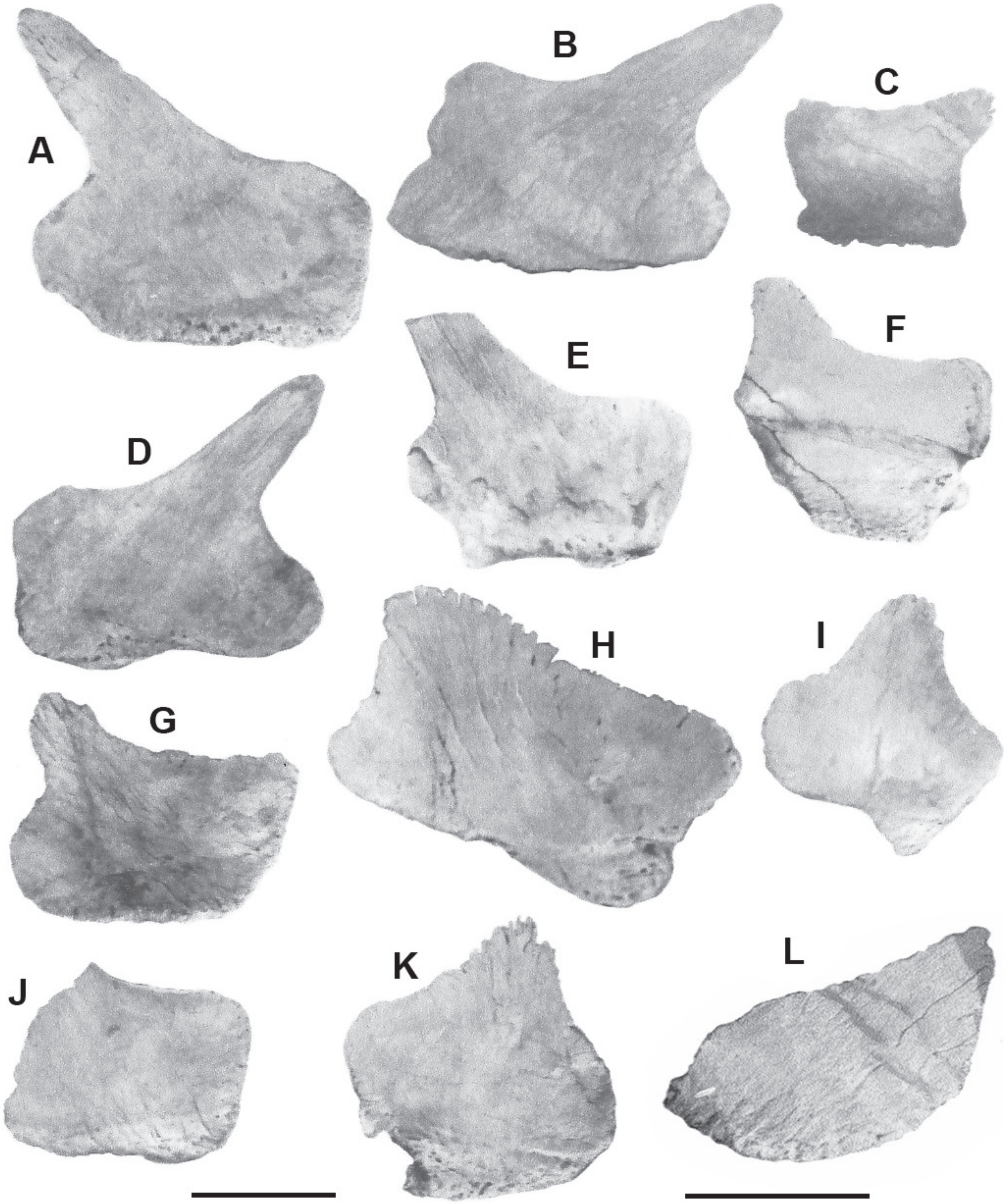

Fig. 17: A-L, Isolated mid-dorsal to anterior caudal (A-K) and posterior caudal (L) dermal plates in side view of *Stegosaurus* sp. from the Carnegie Quarry at Dinosaur National Monument, Jensen, Utah, still *in situ* (A, B, D-L) and removed from cliff face (C). A, DINO 3978 (DNM 309, maximum antero-posterior width or w 655 mm); B, DINO 4019 (DNM 351, w 635 mm); C, DINO 1105 (DNM 1105, w 408 mm); D, DINO 3980 (DNM 311, w 665 mm); E, DINO 4348 (DNM 722, w 626 mm); F, DINO 3866 (DNM 198, w 623 mm); G, DINO 4144 (DNM 478, w 596 mm); H, DINO 4076 (DNM 404, w 575 mm); I, DINO 3874 (DNM 206, w 517 mm); J, DINO 77B (DNM 94, w 485 mm); K, DINO 4107 (DNM 440, w 576 mm); L, DINO 4851 (DNM 1286, maximum length 515 mm).

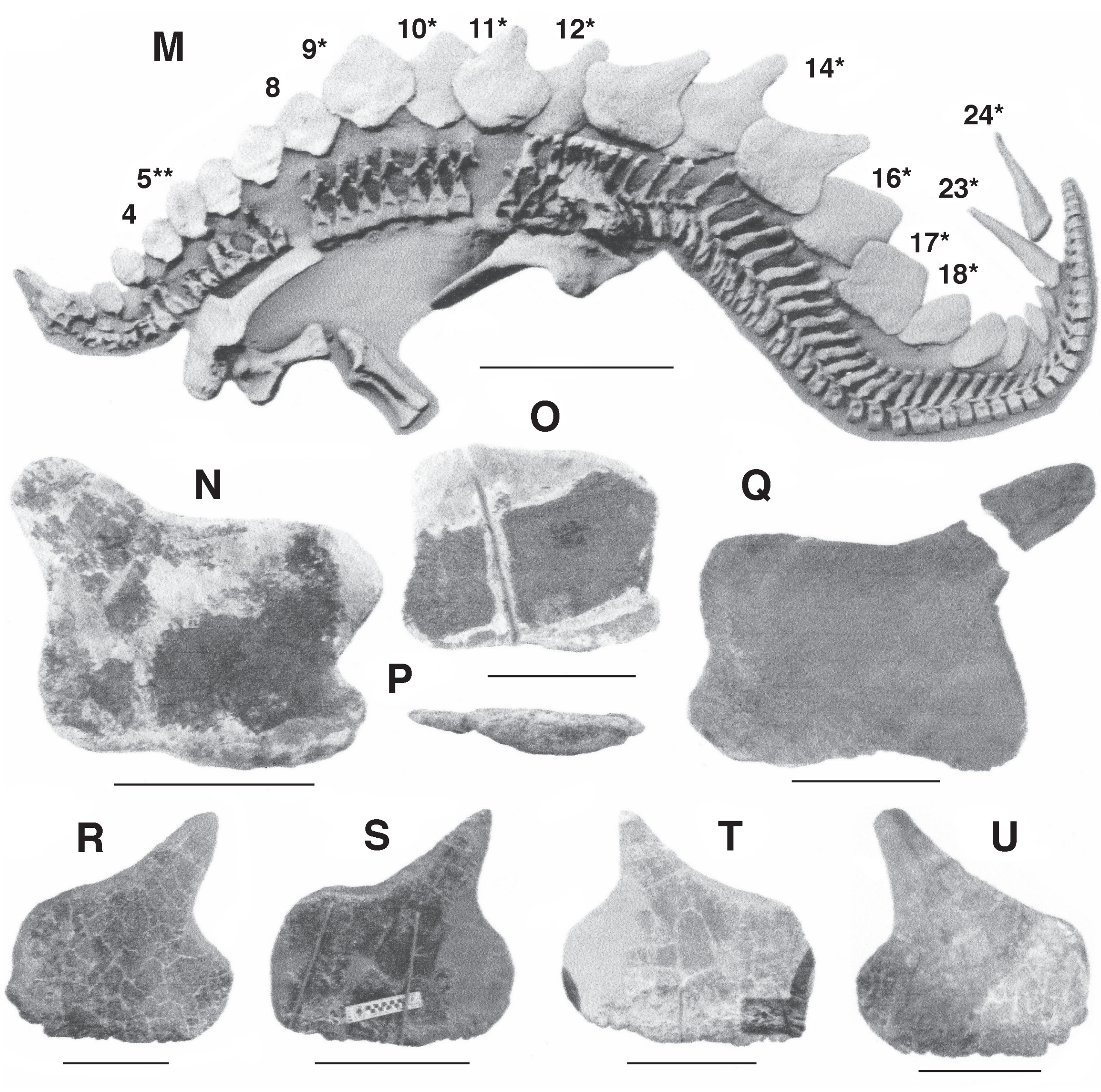

Fig. 17: (Continued) M-Q, partial skeleton from 1923-24 UUVP excavation at DINO (see Section 5.6), M, mounted as a slab mount, UMMP-NH 118201 (since dismantled), to show position of osteoderms on mount (basis for each bone ID number), for those based on bones, plates with an * (9-12, 16-18, 24) are part of main skeleton (UUVP DNM #402), those with ** (5, 14, 23) are part of #340, other plates (4, 8) are from unknown area(s) of 1923-24 excavation, and the remaining plates are plaster. From A. Rountrey, an orthographic rendering produced from a photogrammetric 3D model. Rendered in Blender v2.82 image courtesy of UMMP. N-Q, plates in side (N, O, Q) and ventral (P) views. N, posterior dorsal UMMP-NH 118201.12; O-P, dorsal plate UMMP-NH 118201.16 and Q, plate 14, first caudal plate, UMMP-NH 118201.14 (for other plates see Figs 13X-l, 21C-E). R-U, four non associated mid-dorsal plates in side view, CEUM 1717, from CLDQ. Scale bars = 300 mm (A-K, N-U), 200 mm (L) and 1 m (M).

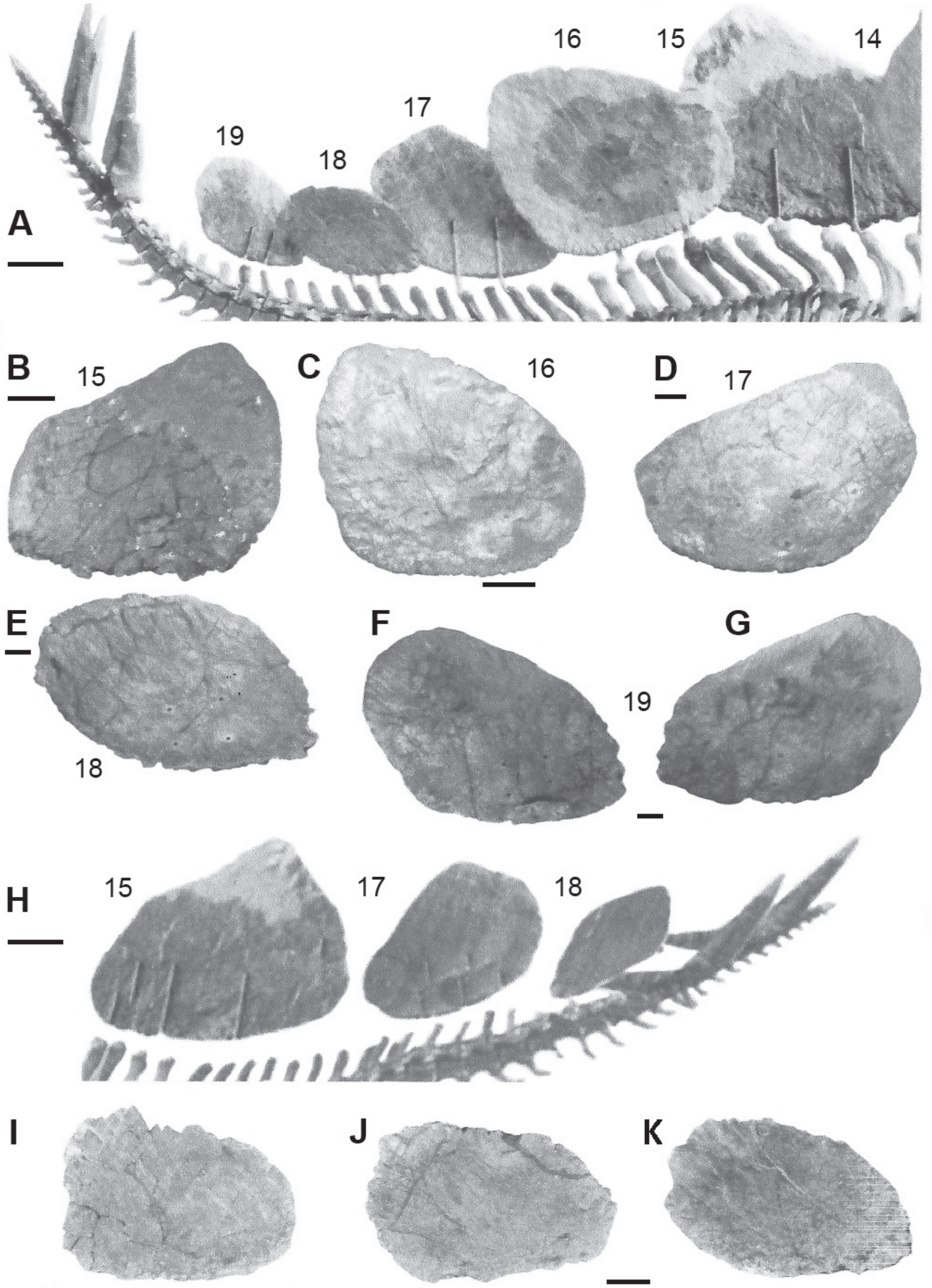

Fig. 18: Dermal plates of *Stegosaurus stenops* from YPM Quarry 13, Como Bluff: A-H, distal caudal plates 15 to 19 and tail spines of USNM V 6531: A, as mounted by Gilmore (1918) in right side view (plate 14 is plaster, cf. Figs 2C, D, 10A for rest of armor of USNM V 8612 as mounted). B, left plate 15 in medial view; C, right plate 16 in lateral view; D, left plate 17 in medial view; E, right plate 18 in lateral view; F-G: left plate 19 in F, medial and G, lateral views. H, distal caudal plates and tail spines of USNM 6531 as remounted in 2019 (Fig. 2D). I-K: USNM V 2274, distal most caudal plates, in side view, I, d5, b69; J, d5, b79, and K, d5, b77. A from R. Purdy, B-G from M. Brett-Surman. Scale bars = 100 mm.

6.5. Two pairs of terminal caudal spines

On the basis of an articulated tail of *Stegosaurus stenops* with distal caudal spines (USNM V 4714, Figs 22A-D; Ostrom & McIntosh, 1966, 1999, pl. 54; also juvenile individual USNM V 4288, Figs 1Y, 22E, F; Carpenter & Galton, 2001, figs 4.13A, B), Gilmore (1914, pls 15, 16) noted that the first or anterior pair of spines typically have broad bases and the posterior pair have narrow, more steeply angled bases. The anterior pair of spines of USNM V 4714 have anterior and posterior crests, probably the result of preservational crushing in soft sediments (also in USNM V 6531, Figs 23M, N), and these crests are not present in other terminal caudal spines (Figs 22G-Q, 23A-L, R-Z).

7. OTHER TYPES OF OSTEODERMS OF MORRISON STEGOSAURS

7.1. Absence of lateral body scutes – *Stegosaurus ungulatus and S. stenops*

Basal Thyreophora are characterised by the development of lateral body scutes as seen in the Lower Jurassic *Scutelosaurus* (Arizona, USA), *Emuasaurus* (Germany) and *Scelidosaurus* (England) or in ankylosaurs (Galton, 2019; Paul, 2016). The "tubercular spine" for *Stegosaurus ungulatus* of Marsh (1880, pl. 10, figs 1a-c, 1887, 1896; Figs 1S-U, 9S-U, YPM VP 1853, since lost) was re-identified by Czerkas (1987) as the severed base of a posterior nuchal plate.

No lateral dermal scutes are present in the articulated skeletons from Garden Park (USNM V 4934, DMNH 2818) and, despite the abundance of stegosaurian remains from YPM Quarry 13 (USNM, YPM), only one lateral scute was located. This is small, transversely narrow, sub-semicircular in side view with a gently convex top (Figs 9V-X, USNM V 337969). The ventral surface (Figs 9X) is only gently concave transversely, not markedly so as in lateral scutes of the basal Lower Jurassic thyreophorans *Scutelosaurus* (Arizona, USA), *Emuasaurus* (Germany) and *Scelidosaurus* (England) (Galton, 2019). However, this is the lateral plate of a polacanthid ankylosaur such as the Morrison genera *Gargoyleosaurus* or *Mymoorapelta* (K. Carpenter, pers. comm., 2019; Kirkland *et al*., 1998; Kirkland & Carpenter, 1994), the first record of an ankylosaur from Quarry 13.

7.2. Isolated "shoulder plate" from Como Bluff

Main *et al*. (2005, p. 297, fig. 2F) described USNM V 7617 from YPM Quarry 13 at Como Bluff as a shoulder plate of *Stegosaurus* sp. and it was figured "in lateral view (ventral side to right edge [lower edge, Fig. 11U]). This plate morphology is unusual because the keel is not as high as in most plates, the base is bilaterally expanded, and the proximal surface is concave; in these respects the plate resembles scutes of more basal thyreophorans and the intermediate condition of a moderately pronounced keel is evident. Note the many pits and channels on the [lateral] surface."

With reference to what is probably the anterior end of the plate (Fig. 11R), the "lateral" view is a proximal or ventral view. This gently concave surface is on the transversely expanded and elongate base, that is longer than wide, and it has many pits and channels (Fig. 11T). The thick fairly complete lateral edge of the base is extremely rugose (Figs 11T-V) and the thin medial edge, although less complete, was probably as rugose (Figs 11R-U). The lateral surface is strongly concave vertically (Figs 11R, V) whereas the dorsomedial surface is almost flat (Figs 11R, S). As only the proximal part of the plate or keel is preserved (Figs 11R, S, V), its height is indeterminate rather than being intermediate.

This plate does not resemble scutes of the three best known basal thyreophorans that are from the Lower Jurassic. In *Scutellosaurus* (Arizona) the entire scute is thin walled, like a conical water cup, and the surfaces are rugose and pitted (Colbert, 1981; Galton, 2019, figs 4S-U), as is also the case in *Emausaurus* (Germany; Haubold, 1990; Galton, 2019, figs 4P-R). In *Scelidosaurus* (England) the transversely compressed scutes are hollow based (Owen, 1863; Carpenter, 2001, fig. 21.4A; Galton, 2019, figs 4E-K).

A synapomorphy for Ankylosauria is the retention laterally of the hollow based trunk, sacral and caudal plates of basal thyreophorans which are lost in Stegosauria (Thompson *et al*., 2012, ESM: 23-4). In Polacanthidae these lateral plates are slightly recurved and the ventral edge is concave to a varying degree and may often be sinuous in side view (Thompson *et al*., 2012; for figures see Ford, 2000; Paul, 2016). Plates of this form occur in the Upper Jurassic polacanthids, viz., *Dracopelta* from Portugal (Galton, 1980, 1983) and for the Morrison Formation of western USA: *Gargoyleosaurus* (Carpenter, 2001, fig. 21.4B; Kilbourne & Carpenter, 2005; Galton, 2016, figs 2J-M) and *Mymoorapelta* (Kirkland *et al*., 1998, fig. 7; Galton, 2016, figs 4V, W), as well as in *Gastonia* (Carpenter, 2001, fig. 21.4C; Lower Cretaceous, Utah, USA), a basal ankylosaurid in cladogram of Arbour & Currie (2016) but described as a polacanthid by Kinneer *et al*. (2016). There is also no match for the Morrison "shoulder plate" USNM V 7617 in Cretaceous ankylosaurs in which the dermal armor is well represented (see Ford, 2000; Paul, 2016).

Histological sections should help to identify USNM V 7617 because the internal anatomy of the plates of *Stegosaurus* is distinctive (Buffrénil *et al*., 1986), as is the case for each of the three groups of ankylosaurs, the Polacanthidae, Nodosauridae and Ankylosauridae (see Scheyer & Sander, 2004; Hayashi *et al*., 2010; Burns & Currie, 2014). USNM V 7617 (Figs 11R-V) is a unique piece of dermal armor that, although not matched in any Morrison stegosaur, is tentatively identified as Stegosauria indet. Given the markedly varying proportions of the base of the transitional plates 6 to 9 in *Stegosaurus* (Figs 10B-P, 11K-Q, 12, 13), this plate might be a transitional plate.

7.3. Paired flat distal tail spines - *Stegosaurus ungulatus*

A possible autapomorphy for *Stegosaurus ungulatus* is the form of the small flat spines on the distal part of the tail, each of which has an obliquely inclined base and was posterodorsally oriented (Figs 1M-O, 19, 20; Ostrom & McIntosh, 1966, 1999, pls 59, 60). Ford (2006) identified one of them (Fig. 19M) as an anterior cervical plate. However, nuchal plates are known for *S. ungulatus* (Figs 12A-H) and, as they are similar to the nuchal plates of *S. stenops* (Figs 11A-E) and *S. sulcatus* (Figs 11F-J), this identification is incorrect. Marsh (1891a, p. 181) mentioned four flat spines, noting with reference to *S. ungulatus* that they "were probably in place below the tail, but as this position is somewhat in doubt, they are not in the present restoration" (Fig. 2A). He previously figured one of them as a "flat dermal spine" (Figs 1M-O; Marsh, 1880, pl. 10, figs. 3a-d) and it was referred to as a "dorsal spine" (Marsh, 1887, pl. 8, fig. 1, 1896, pl. 50, figs. 1a-d). Lull (1910a, p. 204) mentioned "three odd, sharp-edged, spine-like plates, one of which is so much larger than the other two that it seems to imply that at least one intervening size is missing" and, subsequently, as three pairs of plates that are "sharp-edged, pointed and bent backward" (Lull, 1910b, p. 368). Marsh (in Ostrom & McIntosh (1966, 1999, pls 59, 60) illustrated four of these spines (Fig. 19).

In the YPM skeleton (Figs 4B-E) as remounted in 1924, there are five (with two in plaster) alternating low elongate flat spines placed just anterior to the tail spikes (Fig. 20; Lull, 1929, pl. 13; Carpenter & Galton, 2001, figs 4.2, 4.3). Paul (1987, p. 34) noted that "a pair of virtually identical plates in the holotype *Stegosaurus ungulatus* [YPM VP 1853, Ostrom & McIntosh, 1999, pls 59-1, 60] suggests that the plates were paired." These plates, the two largest ones of the four mentioned by Marsh (1891a), are shown (Figs 19K-N) and are almost identical in size when the larger side view of one (Fig. 19N) is reduced to the same scale of reduction as the second one (Fig 19M, since lost; Galton, 2010, figs 3n, r). They are almost identical in outline but not in form, being mirror images with the former as a right and the latter as a left. There is no match for this series of three (or probably four) paired and postero-dorsally inclined flat distal caudal spines in *S. stenops,* that has three (USNM V 4934, Figs 8C, 14K, M, plates 15-17; USNM V 4714, Figs 15K-M; DMNH 2818, Figs 6A-C, H) or four (NHMUK PV R36730, Figs 2E, F, 7B) non-paired thin vertical plates in this region.

Flat distal caudal spines are also known from Utah at CLDQ (Figs 21D, H-S) and DINO (Figs 21E-G), where there is a flatter plate of similar form (Fig. 17L).

7.4. Dermal plates from Utah

White (1964) noted that the greater part of a single individual has not been found in association at DINO. Several of the mounted skeletons based on DINO specimens are composite with unknown quarry locations for the dermal plates. Most of the one in Toronto (ROM, ex. CM 88 + others; Fastovsky & Weishampel, 2005, fig. 6.2) came from Quarry D, Sheep Creek, Albany County, Wyoming, not DINO (McIntosh, 1981, p. 37). Isolated plates from DINO were used for the 1940 Carnegie Museum mounted skeleton of *Stegosaurus ungulatus* (CM 11341, mostly DNM 350 and 39/60AA; McIntosh, 1981, p. 35, fig. 17; also Kay, 1940; McGinnis, 1982, fig. p. 78). However, originally the top parts of all the plates were missing, being rather crudely restored, so they were given a more realistic shape in the 1980s by D. Pickering (pers. comm., 2019). The 1946 mounted skeleton in Lincoln, Nebraska (Fig. 5G; UNSM 53192, ex. CM 11372, DNM 39/60 + others) has plates that are better preserved but from unknown DNM specimens. Thus the 1989 Ann Arbor, Michigan skeleton, UMMP-NH 118201, is the only specimen with any associated osteoderms from DINO (Fig. 17M, for details see Section 5.6).

As discussed in detail by Carpenter & Wilson (2008, pp. 228-230, 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). As a reflection of this age difference, the two larger genera of Morrison ornithopod dinosaurs are now referred to different species based on a combination of different plesiomorphic and autapomorphic characters (see Carpenter & Galton, 2018; Carpenter & Lamanna, 2015). Thus, *Camptosaurus* Marsh, 1885 is represented by *C. dispar* (Marsh, 1879) versus *C. aphanoecetes* Carpenter & Wilson, 2008 at DINO, and *Dryosaurus* Marsh, 1894 is represented by *D. altus* (Marsh, 1878) versus *D. elderae* Carpenter & Galton, 2018 at DINO.

Olshevsky & Ford (1993, fig. 21, 1995, p. 54, fig. 41) suggested that the stegosaur bones *in situ* on the cliff face at DNM represent a new species (Fig. 5F) because the dorsal plates "are strongly pinched and pointed at their tips" (Ford, 2006, figs 1E, 2D). Dorsal plates exposed on the cliff face are shown (Figs 17A-L) and most fit this description (Figs 17A-G, I, J). However, others do not (Figs 17H, L), and one (Fig. 17H) is very different from those of other Morrison stegosaurs (cf. Figs 2, 5, 6A-H, 8; Saitta, 2015). Two of the dorsal plates of UMMP-NH 118201 are strongly pinched dorsally and pointed at their tips (Figs 17N, Q), as is also the case for a few dorsal plates on the Lincoln skeleton (Fig. 5G; UNSM 53192). However, this morphology is also shown by plate 14 of the second articulated specimen of *S. stenops* from Garden Park (Figs 4B, C, G; DMNH 2818) and, in addition, there are indications of it in some of the dorsal plates of *S. ungulatus* (Figs 14A-F, 16A, D, E, G).

Although not well preserved, posterior nuchal and/or anterior dorsal plates on the DNM cliff face have bases that appear to be widened transversely (Figs 13m-r), and in two plates the base appears to be wider than long (Figs 13n, o), the reverse of the usual form of any other plates of *Stegosaurus* (Figs 8, 9C-E, 10, 11, 12). This is certainly the case for plates ~6 and ~7 of UMMP-NH 118201 (Figs 13X-d; 4, 5** in Fig. 17M). In *S. ungulatus* the width and length of the bases of nuchals 3 and 4 are subequal (Figs 12A-H) but the length is greater than the width in plate 7 (Figs 12I, J), as is also the case for isolated large transitional plates from Como Bluff (Figs 11K-Q).

There are flat caudal spines from DINO comparable to

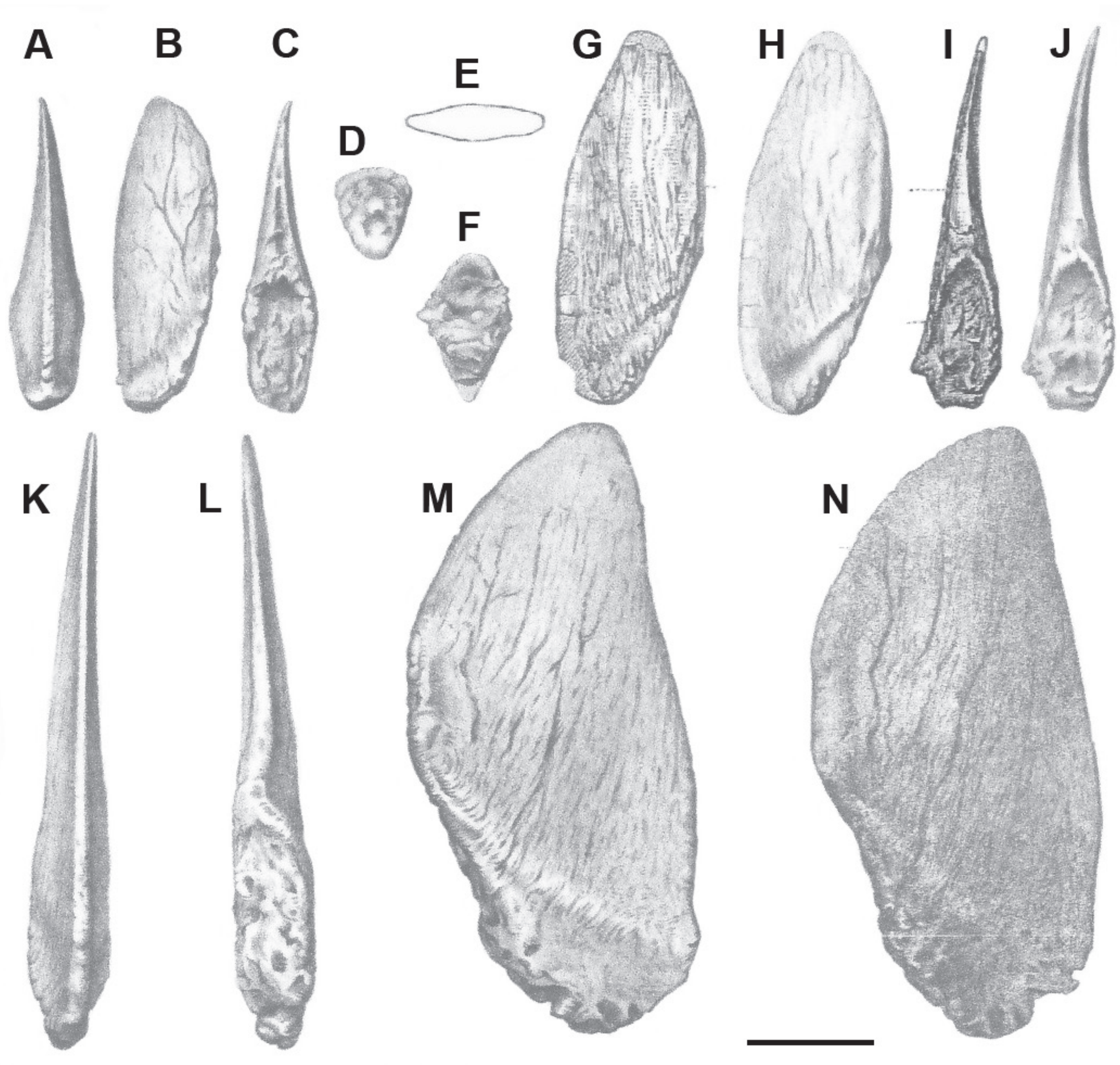

Fig. 19: Flat distal tail spines of *Stegosaurus ungulatus*, Marsh, 1879 from YPM Quarry 12 at Como Bluff, Wyoming, part of syntype YPM VP 1853 as illustrated by Marsh (1880) (G, I) and in Ostrom & McIntosh (1966, 1999) (A-F, H, J-N), reduced to same scale (x 0.2). A-D: smallest (most posterior, number 22 mounted as a left, Figs 20A, G-I) right flat spine in A, anterior; B, medial; C, posterior and D, proximal views; E-J: middle sized right flat spine (number 20 mounted as a left, Figs 20A, D-F) in E, cross-sectional; F, proximal; G-H, medial and I-J, posterior views. K-M: largest (most anterior; lost) right flat spine in K, anterior; L, posterior and M, medial views. N, pair to K-M, left plate spine (number 17 mounted as a right, Figs 20A-C) in medial view. Scale bar = 100 mm.

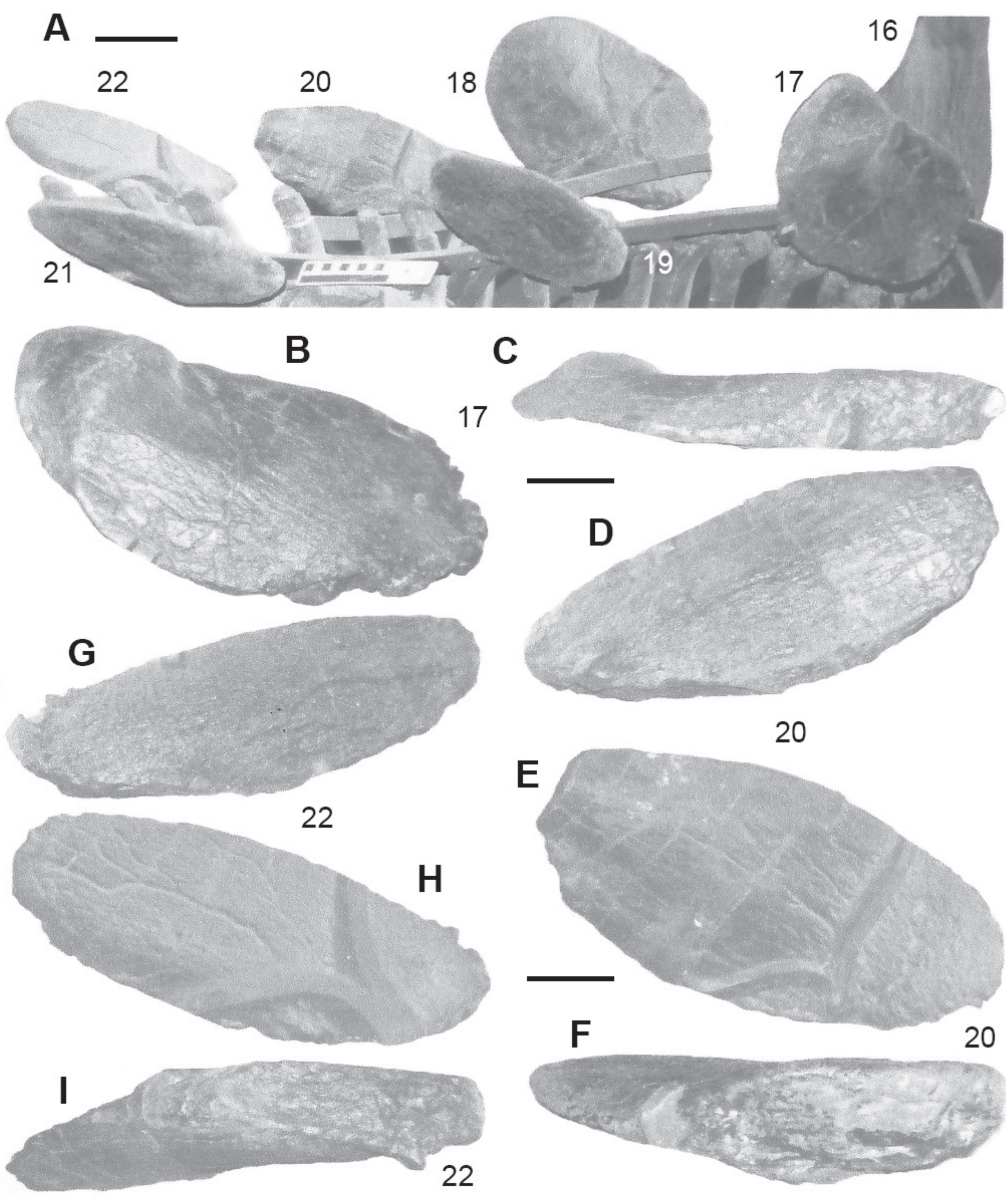

Fig. 20: Flat distal tail spines of *Stegosaurus ungulatus*, Marsh, 1879, part of syntype YPM VP 1853 from YPM Quarry 12 at Como Bluff, Wyoming. A, part of distal tail of mounted skeleton in right side and slightly dorsal view showing plates 17 to 22 (cf. Figs 4C-E; plates 17, 20, 22 real bone; plates 18, 19, 21 plaster). B-C: left (mounted as a right, number 17, cf. Fig. 19N) in B, medial and C, ventral views. D-F: right plate spine (mounted as a left, number 20) in D, medial; E, lateral and F, ventral views (cf. Figs 19E-J). G-I: right plate spine (mounted as a left, number 22) in G, medial; H, lateral and I, ventral views (cf. Fig. 19A-D). Scale bars = 100 mm (A-D) and 50 mm (E-I).

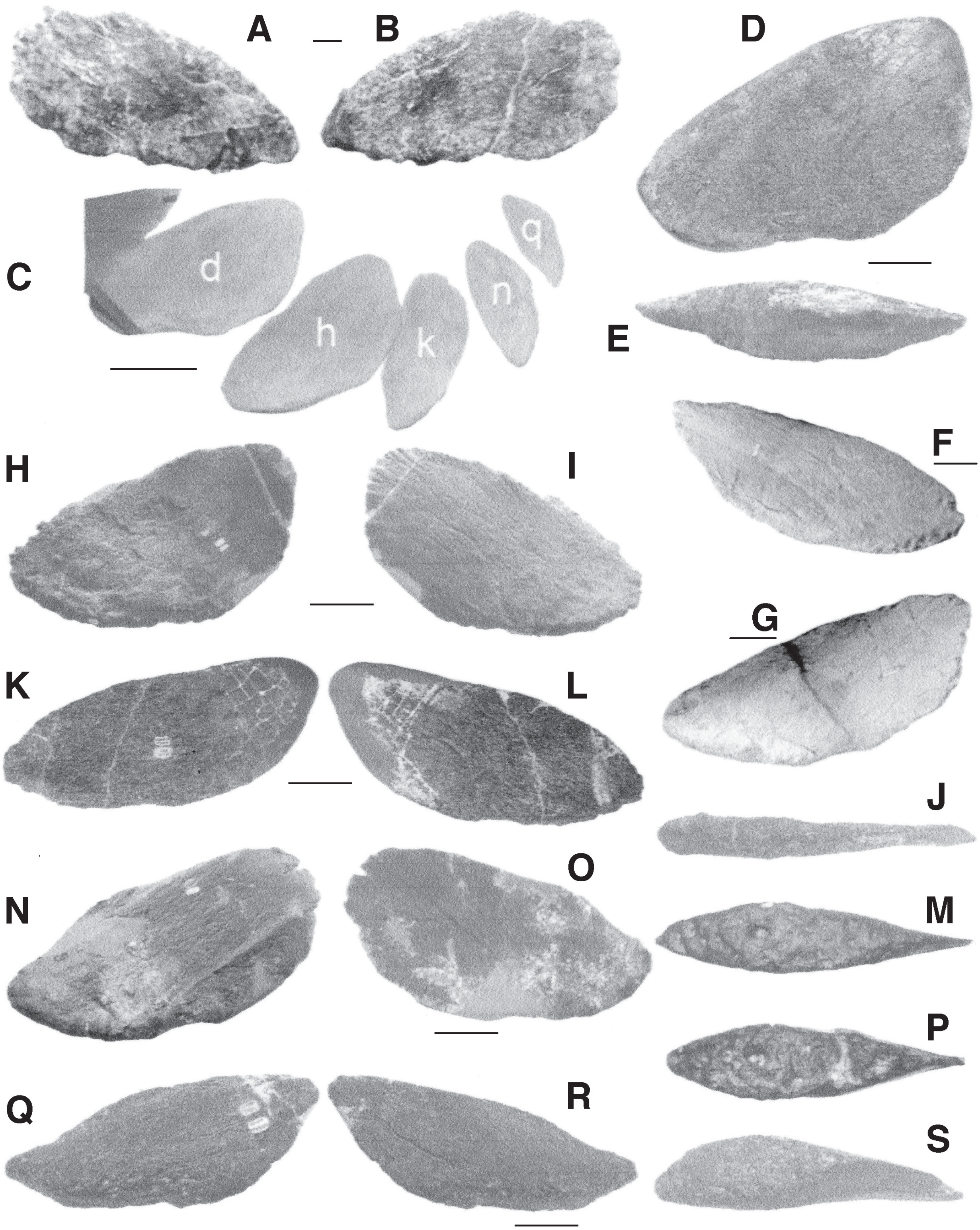

Fig. 21: Dermal osteoderms of *Stegosaurus* from Quarry 13, Como Bluff (A-B), Carnegie Quarry, DINO (C-G) and CLDQ (H-S). A-B, distal caudal plate in side view, USNM V 6135. C, bone (d) and casts (h, k, n, q) of five distal flat caudal spines in left side view of *Stegosaurus*, UMMP-NH 118201 (Fig. 17M), put together by Jim Madsen (UUVP), the real bones shown in H, K, N and O are basis for h, k, n and o; D-E, UMMP-NH 118201.18 (18*, Fig. 17M, formerly UUVP DNM 403/29), anterior flat distal tail spine in D, side and E, ventral view; F-G, flat distal tail spines on cliff face in side view, F, DINO 4121 (DNM 455) and G, DINO 3945. H-S, original non associated bones, basis for casts shown in C, in left side (H, K, N, Q), right side (I, L, O, R) and ventral views (J, M, P, S): H-J, N-P, CEUM 1717; K-M, UMNH VP 5997 and Q-S, UMNH VP 5500. Scale bars = 50 mm (A, B, D-S) and 100 mm (C).

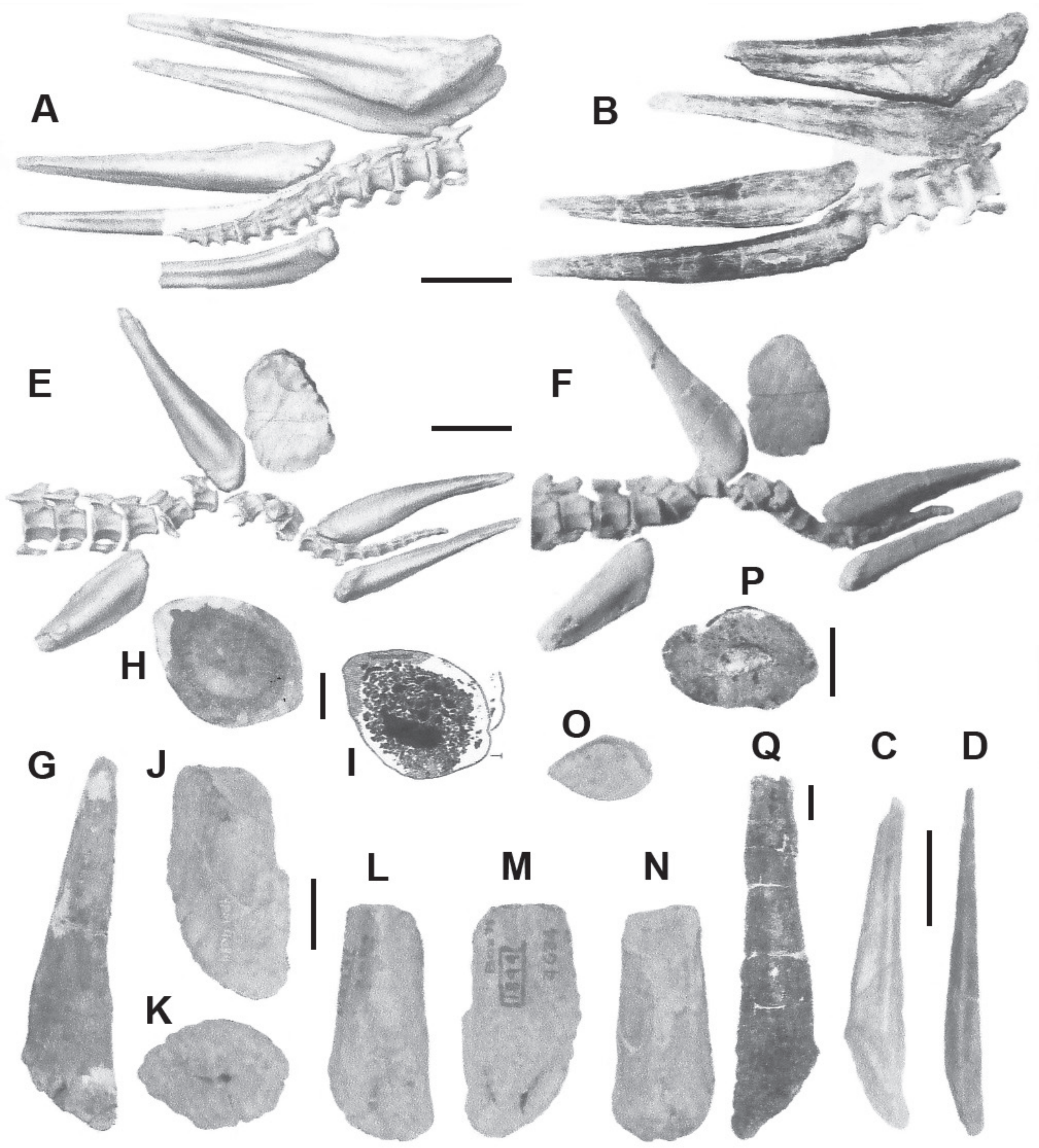

Fig. 22: Dermal tail spines of *Stegosaurus stenops* from Morrison (Upper Jurassic) of Wyoming (A-O; YPM Quarry 13, Como Bluff, Wyoming) and Garden Park, Colorado (P, Q). A-D: USNM V 4714, A-B, distal end of tail with anterior and posterior caudal spine pairs in right side view: A. with proximal part of right anterior spine moved to show terminal caudal vertebrae and B, as preserved; C-D: right spines in lateral view: C, anterior and D, posterior. E-F: USNM V 4288, distal end of tail with paired spines and displaced most posterior plate of a juvenile individual as preserved in left side view (cf. Fig. 1Y; shown in reverse by Galton & Carpenter, 2016, figs 5C, D). G-O: YPM VP 4634, tail spines of a subadult individual, G-I: larger anterior spines, G, right in lateral view and H, I, left in cross-sectional view and J-O: partial right smaller posterior spine in J, lateral; K, proximal; L, anterior; M, medial; N, posterior and O, distal views (see Galton, 1982, figs 5, 6A-L for photographs of appendicular skeleton). P-Q: DMNH 2418, left posterior spine of an old adult individual in P, cross-sectional and Q, lateral views (for photographs of mounted skeleton see Reinheimer, 1939). A from Ostrom & McIntosh (1966), E from Gilmore (1914), H, I, P, Q from Hayashi *et al*. (2012), G, J-O from Aly Heimer. Scale bars = 50 mm (A-F), 100 mm (G, P), 10 mm (H-I), 25 mm (J-O) and 20 mm (Q).

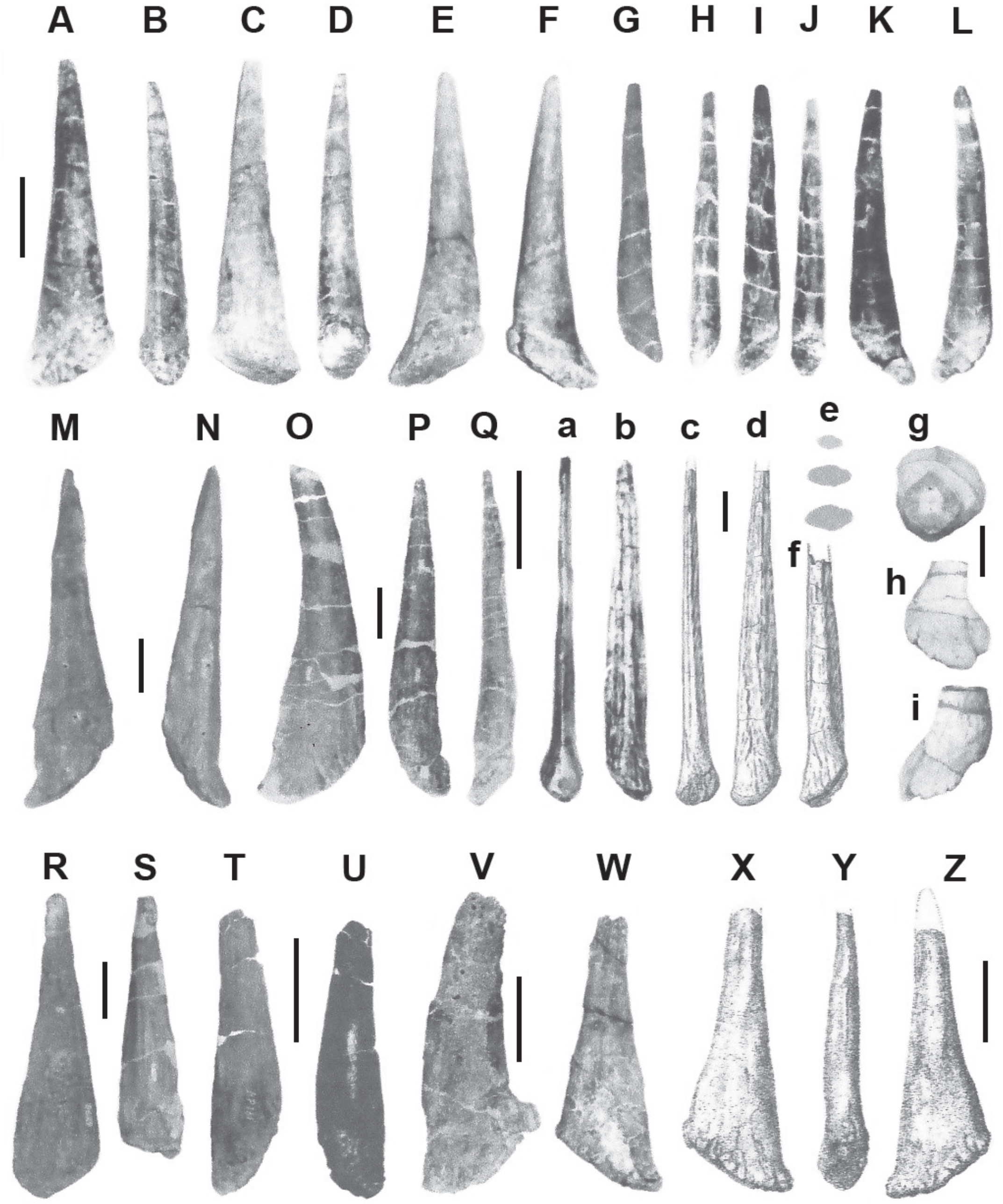

Fig. 23: Terminal tail spines from Morrison Formation, Wyoming: *Stegosaurus* from YPM Quarry 13, Como Bluff, Wyoming (A-Z) and *Miragaia longispinus* (Gilmore, 1914) from near Alcova (a-f) and at Como Bluff (g-i). A-L: USNM V 6099, A-F: right (A-D) and left (E, F, distal 60% restored) anterior tail spines in A, E, lateral; B, anterior; C, F, medial and D, posterior views; G-L: right (G-J) and left (K, L) posterior tail spines in G, L, lateral; H, anterior; I, K, medial and J, posterior views. M-N: USNM V 6531, tail spines in lateral view, M, anterior left and N, posterior right (also Figs 18A, H). O-P: USNM V 7413, tail spines in lateral view, O, anterior left and P, posterior right. Q, part of USNM V 4934, holotype of *S. stenops* Marsh, 1887, smaller posterior spine in side view (see Figs 8C, 14M). R-U: tail spines of juvenile individuals in R, T, anterior and S, U posterior views: R-S: USNM V 6629c and T-U: USNM V 7359. V, USNM V 6646, *S. ungulatus* from YPM Quarry 13, described by McWhinney *et al*. (2001, fig. 7.1C, details fig. 7.6), pathological right anterior spine in lateral view, broken in life and showing remodelling of the broken bone surface. W-Z: USNM V 6135, right anterior spine in W, X, medial; Y, posterior and Z, lateral views. a-f: *Miragaia longispinus* (see also Galton & Carpenter, 2016, fig. 8): a, b, holotype tail spines UW 20503 (formerly D54) of type species *Stegosaurus longispinus* Gilmore, 1914 and c-f, USNM V 8036, casts, a-f: left (a-e) and right (f) posterior pair of tail spines in a, anterior; b, f, medial; c, posterior, d, lateral and e, cross-sectional views. g-i: cf. *Miragaia longispinus* from near Bone Cabin Quarry, Como Bluff, proximal end of right larger anterior spine (WPL, lost, K. Carpenter, pers. comm., 2016) in g, distal (with cross-section), h, anterior and i, lateral views (also Ford, 2006, fig. 3e with 4 views). A-W, a, b, e from M. Brett-Surman, X-Z from Ostrom & McIntosh (1966), c, d, f from Gilmore (1914), g-i from K. Carpenter. Scale bars = 150 mm (A-L), 100 mm (M-Q, T-Z) and 25 mm (R, S).

those of *Stegosaurus ungulatus* (Figs 19, 20), with two on the cliff face (Figs 21F, G), a slightly more anterior one with UMMP-NH 118201 (Figs 21C-E), and a possibly even more anterior plate with a similar shape on the cliff face (Fig. 17L).

It is concluded that the stegosaur from DINO is characterized by a combination of derived characters in the dermal armor, viz., nuchal and transitional (anterior dorsal) plates with a base that is wider transversely than long (Figs 13X-g, m-r), dorsal plates that are strongly pinched dorsally with a pointed tip (Figs 17A-G, N, Q), and the presence of flat distal caudal spines (Figs 17L, 21F, G). Other suggested characters include a proportionally shorter skull than in *Stegosaurus stenops*, based on the DINO mandible described by Berman & McIntosh (1986; CM 41681, not CM 41691 as cited by Olshevsky & Ford, 1993, 1995), and a broader pelvic girdle than in other species of *Stegosaurus* (based on DINO 4069 ex. DNM 402; see Olshevsky & Ford, 1993, fig. 40n, 1995, fig. 52N).

The dermal plates from CLDQ are similar to those from DINO so they may represent the same or a closely related species. In addition to the transitional (dorsals 1 to 4) plates, all the nuchals plates have a base that is wider transversely than long (Fig. 13). Some of the dorsal plates are strongly pinched dorsally with pointed tips (Figs 17R-U) and there are flat distal caudal spines (Figs 21H-S).

7.5. Four pairs of terminal tail spines - *Stegosaurus ungulatus*

In the skeletal reconstructions of Marsh (1891a, b, 1896, 1897) and Lull (1910b, 1912, 1929) (Figs 2A, 4, 24L, 25A-E), four pairs of tail spines are shown (also in Young, 1950, fig. 246; Bakker, 1986, figs pp. 226, 348, see Fig. 5A), a number long thought to be diagnostic for *Stegosaurus ungulatus* (YPM VP 1853). However, Lucas (1900-1904) suggested that the four pairs of spines of *S. ungulatus* represented two individuals. Caudal spines were found in four different areas of YPM Quarry 12

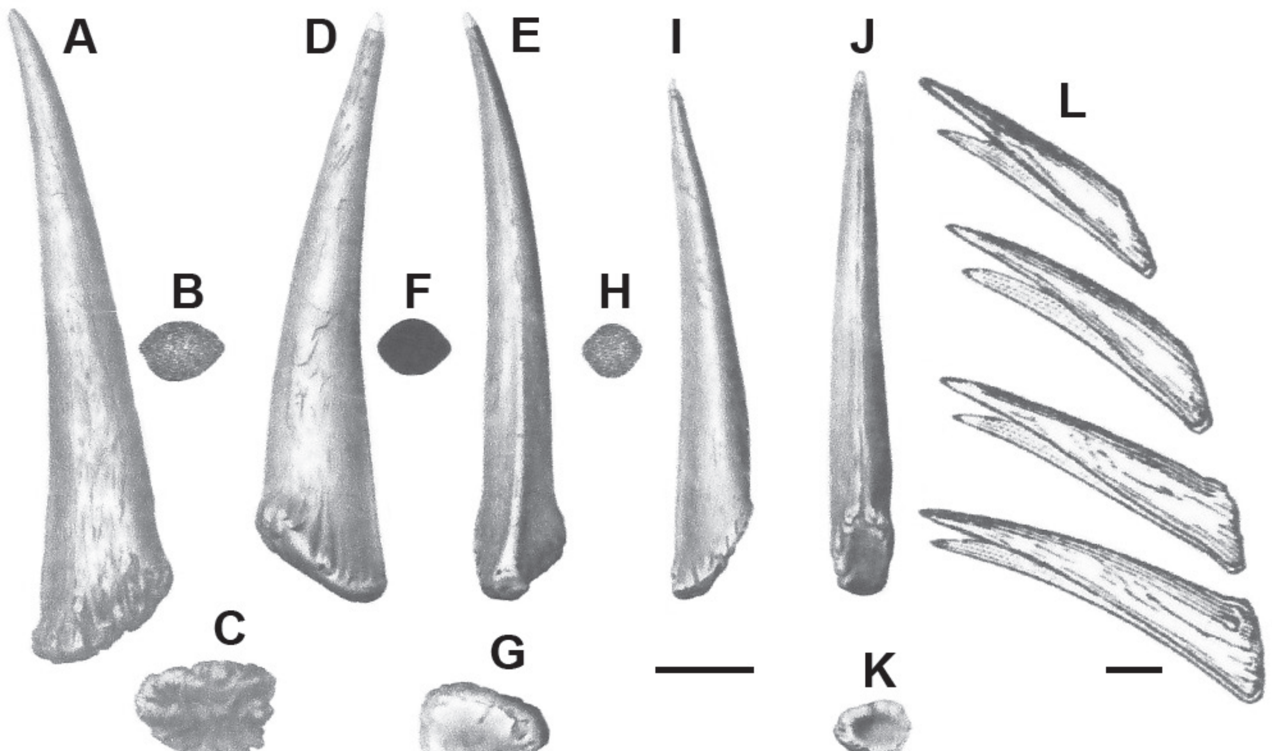

Fig. 24: Terminal caudal dermal spines of *Stegosaurus ungulatus*, Marsh, 1879 from YPM Quarry 12 at Como Bluff, Wyoming, part of syntype YPM VP 1853 (cf. Figs 1A-F from Marsh, 1880): A-C, left larger anterior spine (number 2, Figs 4D, F, 25B, C, E, N, O) in A, lateral (with distal cross-section); B, mid-cross sectional and C, ventral views; D-G, right smaller anterior spine (number 3, Figs 4D, F, 25A, C, D, H, I) in D, lateral; E, anterior; F, mid cross-sectional, and G, ventral views; H-K, left smaller posterior spine (number 8, Figs 4D, F, 25B, C, E, T, U) in H, mid cross-sectional; I, lateral; J, posterior and K, ventral views; L, reconstructed set of tail (cf. Figs 2A, 4D, F, 25A-D for numbers) spines based on two anterior spines (numbers 1, 2) from a larger individual, two anterior spines (numbers 3, 4) from a smaller individual, two posterior spines (numbers 5, 6) from a larger individual, and two posterior spines (numbers 7, 8) from a smaller individual. A-K from Ostrom & McIntosh (1966), L from Marsh (1891a). Scale bars = 100 mm.

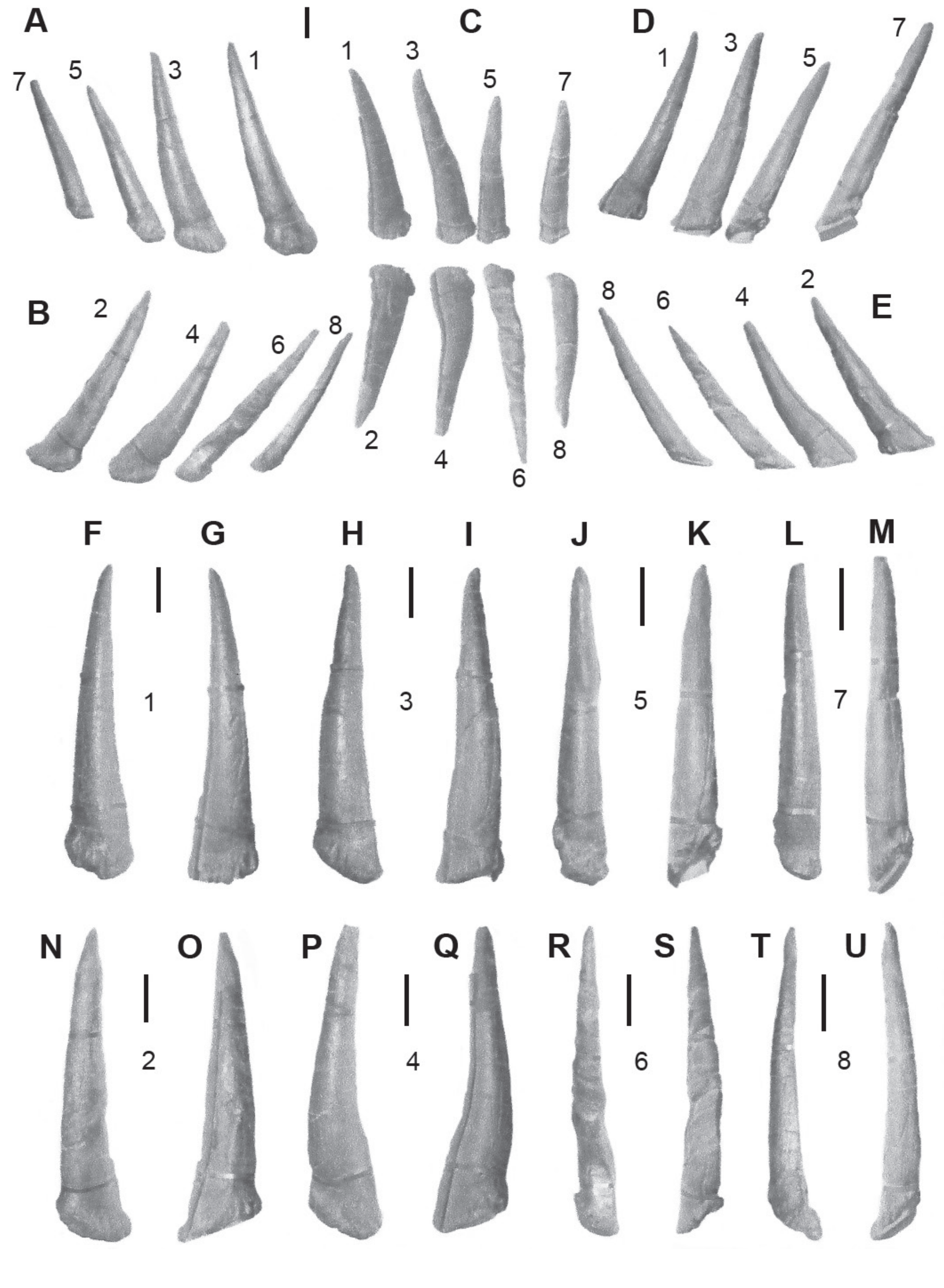

Fig. 25: Caudal dermal spines of *Stegosaurus ungulatus*, Marsh, 1879 from YPM Quarry 12 at Como Bluff, Wyoming, part of syntype YPM VP 1853: A-E, four pairs of spines as mounted on YPM skeleton (see Figs 4B-D, F): A-B, right spines in A, lateral and B, medial views; C, spine pairs in dorsal view (cf. Fig. 4F) and D-E, left spines in D, lateral and E, medial views. F-U, spines reduced to unit length in lateral (F, H, J, L, O, Q, S, U) and medial (G, I, K, M, N, P, R, T) views: F-M: right spines: F-G, larger anterior spine, number 1; H-I, smaller anterior spine, number 3; J-K, larger posterior spine, number 5; L-M, smaller posterior spine, number 7; N-U: left spines: N-O, larger anterior spine, number 2; P-Q, smaller anterior spine, number 4; R-S, larger posterior spine, number 6; T-U, smaller posterior spine, number 8. Scale bars = 100 mm.

(Carpenter & Galton, 2001, fig. 4.11), with two clusters (I and III) containing distal caudal vertebrae and III also containing four spikes. That two clusters of distal caudals occur in the quarry suggests that two animals, not one, may be present.

On the basis of an articulated tail of *Stegosaurus stenops* with spines (Figs 22A-D; Ostrom & McIntosh, 1966, 1999, pl. 54; also USNM V 4288, Figs 1Y, 22E, F; Gilmore, 1914, pls 15, 16), Gilmore (1914) noted that the first, or anterior, larger pair of spikes typically have broad bases and the posterior pair have narrow, more steeply angled bases. Other examples of associated anterior and posterior tail spines with these characters are shown (Figs 22G-O, 23A-U).

The tail of the skeleton of *S. ungulatus* as reconstructed by Marsh (1891a, b, 1896, 1897; Figs 2A, 24L) and mounted by Lull (1910a, b, 1912; Figs 4B-D, F, 25A-E) anteriorly has two pairs of moderately angled, broad-based anterior spines (one shown in Figs 1A-C, from Marsh 1891, 1896; two shown in Figs 24A-H, from Ostrom & McIntosh, 1999, pls 55, 56, figs 1-3; spine numbers 1-4, Fig. 25) and posteriorly there are two pairs of more steeply angled, narrow-based posterior spines (one shown in Figs 1D-F, from Marsh 1891a, 1896; Figs 24I-K, from Ostrom & McIntosh, 1999, pl. 56, figs 4-6; spine numbers 5-8, Fig. 25). This duplication indicates that the mounted tail is a combination of caudal spines from two individuals, one larger (spines 1, 2, 5, 6) than the other (spines 3, 4, 7, 8). The absence of duplicate limb elements may be due to an incomplete overlap of two skeletons in the quarry, but these may be found if YPM Quarry 12 is ever reopened.

Gilmore (1914, p. 8) referred a tail with two pairs of spikes from YPM Quarry 13 to *Stegosaurus ungulatus* (Carpenter & Galton, 2001, fig. 4.14). This specimen is now incorporated into a mounted skeleton of *Stegosaurus* at the AMNH (see Brown, 1932, fig. p. 495; Colbert, 1962, pl. 66; AMNH FARB 650). Although no reasons were given for assigning this tail to *S. ungulatus*, this identification is almost certainly correct. As Carpenter & Galton (2001) note, the deeply bifurcated neural spines on the anterior caudal vertebrae and the tall dorsal processes on the caudal ribs are characteristic of *S. ungulatus*. Gilmore (1914, p. 83 for 1,200 mm long femur) also referred USNM V 6646 (Fig. 23V for anterior tail spine), a partial skeleton of a large individual from YPM Quarry 13, to *S. ungulatus*.

7.6. Large anterior pair of terminal tail spikes - *Stegosaurus sulcatus*

Gilmore (1914, pp. 109-110, fig. 65, pl. 18, measurements p. 111; USNM V 4937) described the spines of *Stegosaurus sulcatus.* He regarded the very large spikes (Figs 26A-O; Ostrom & McIntosh, 1966, 1999, pl. 58) as being equivalent to the broad based anterior pair of the articulated tails referred to *S. stenops* (Figs 18A, H, 22A, B, E, F, 23A-U). However, the "diagnostic" anterior and posterior grooves are present on the medial surface of the left spike (Figs 26A-C, F, M) but not on the right one (Figs 26G, H, M). The posterior pair of slender based spines are also preserved (Figs 26K, L, P; Gilmore, 1914, pl. 25, fig. 3). Based on the associated postcrania (Figs 11F-J), Gilmore (1914, fig. 38, pl. 20, figs 3A, 4A, 21, fig. 2 for radius, ulna, manus) considered USNM V 4937 to represent a very large and old individual of *S. ungulatus*. However, the humerus with a length of 609 mm is about the same length as that of *S. ungulatus* (YPM VP 1853; Ostrom & McIntosh, 1999, pl. 33).

Bakker (1988, p. 22, fig. 9) considered that, although the terminal set of spines of USNM V 4937 were a good fit over caudal vertebra 35 in anterior view, the ventral curvature of the bases of the anterior spikes "is far too gentle to fit around the distal tail but would fit the curvature over the shoulder or at the neck base" (Fig. 26M). However, Paul (1996a, fig. p. 63) restored the large spikes as the anterior pair of the two distal pairs of tail spines (Figs 26K, L) as per Gilmore (1914). The proximal parts of a comparable pair of massive anterior caudal spikes are referred to *Dacentrurus armatus* (Figs 26Q-S; Upper Jurassic, England; Galton, 1985; as *Omosaurus hastiger*, Owen, 1877). As regards the possible presence of large spikes near the end of the tail in *Stegosaurus sulcatus*, this certainly occurs in *Chungkingosaurus jiangbeiensis* (Middle Jurassic, China, referral by Maidment & Wei 2006). Dong *et al*. (1983, p. 137, fig. 102; Dong, 1990, fig. 19.14) illustrated an articulated distal tail with three pairs of spines, the anterior two pairs being massive, and noted that "the specimen was associated with a total of four pairs of caudal spines, the most anterior of which were lost due to weathering."

7.7. Two pairs of elongate subequal terminal tail spines - "*Stegosaurus*" *longispinus*

Stegosaurus longispinus Gilmore, 1914 was based on a rather incomplete skeleton from near Alcova in central Wyoming, most of which was destroyed by flooding while on exhibition. Only the femur (UW 20503, formerly D54, maximum length 1082 mm) survived, along with casts of the pair of extremely elongate anterior caudal spines (USNM V 8036; Figs 23a-f). However, based on archival photos of the sacrum and spines taken *in situ* in the quarry and of spines and vertebrae as exhibited, plus the drawings, photos and casts of the spines, Galton & Carpenter (2016) made *Stegosaurus longispinus* Gilmore, 1914 the type species of *Alcovasaurus* Galton & Carpenter, 2016 as *A. longispinus* (Gilmore, 1914). The caudal spines were described by Gilmore (1914, p. 112, fig. 65), who noted that the longest of the four preserved spines had an estimated length of 985 mm. He characterized the unique form of the spines by "the long,

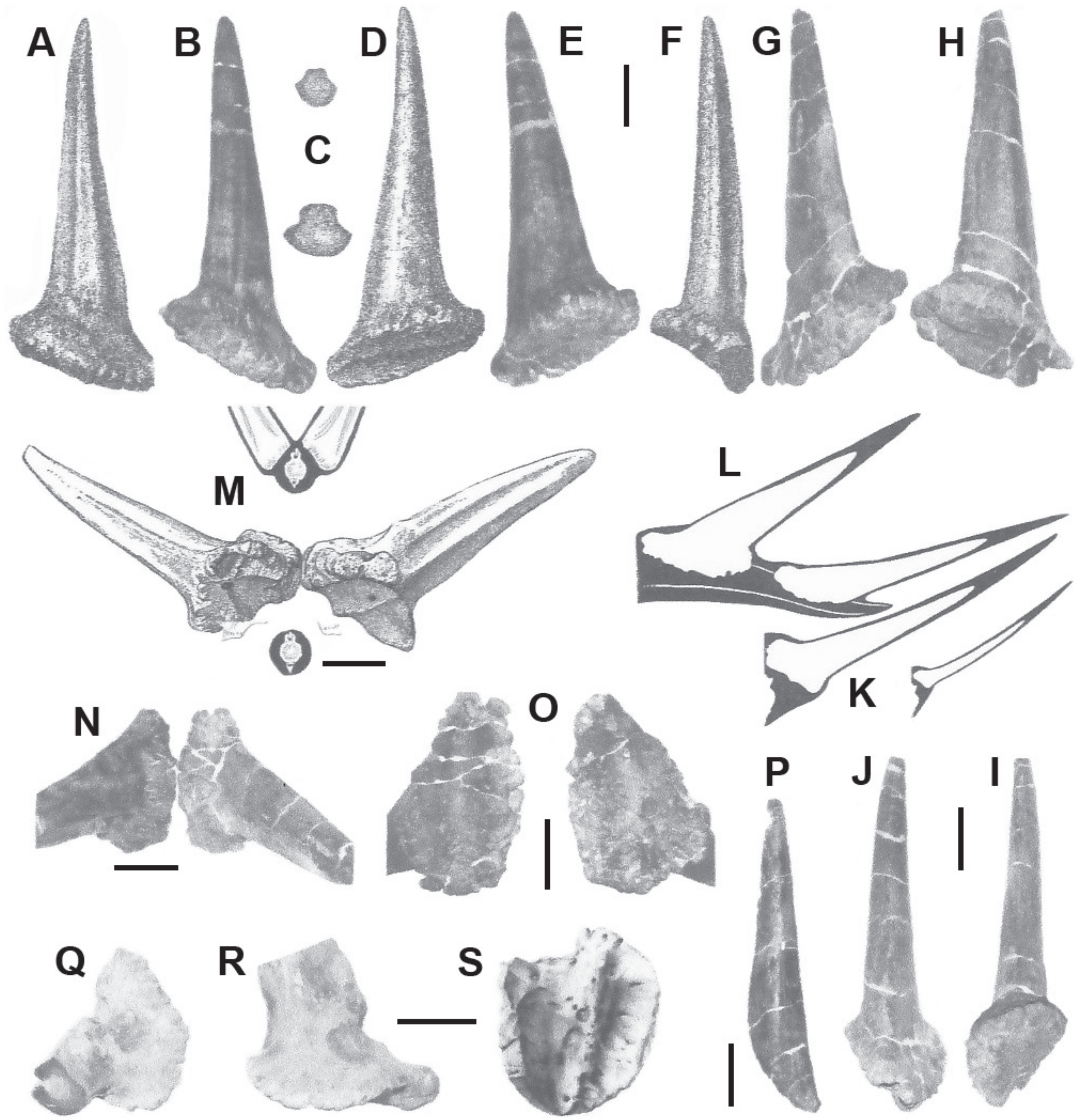

Fig. 26: Dermal tail spines of stegosaurs from Upper Jurassic: A-P: from YPM Quarry 13, Como Bluff, Wyoming, dermal tail spines of *Stegosaurus sulcatus* Marsh, 1887, part of holotype USNM V 4937 (see Figs 1V-X, from Marsh, 1887): A-J: left (A-F) and right (G-J) large anterior spines in A, B, G, medial; C, two cross-sectional; D, E, H, lateral; F, I, posterior, I, dorsal and J, anterior views; K-M, anterior and posterior spines in K, anterior; L, right lateral and M, posterior views (with caudal vertebra 35 in M). N-O, bases of large posterior spines in N, dorsal and O, ventral views. P, right small posterior spine in lateral view. Q-S, *Dacentrurus armatus* from Swindon, England, NHMUK PV OC46013, holotype of *Omosaurus hastiger* Owen, 1877, large right (Q, R) and left (S) anterior spines in Q, dorsal; R, medial and S, ventral views. A, C, D, F from Ostrom & McIntosh (1966), K, L from Paul (1996b) and M from Gilmore (1914) and Bakker (1988), S from Owen (1877). Scale bars = 100 mm.

slender, flattened shaft with sharp edges; the constriction of the shaft above the bases; and the uniformity in the development of the base of the spine series" with the four bases varying by only a few millimeters. The cladistic analysis of Raven & Maidment (2017) demonstrates that this is a valid taxon. The proximal end of a very large spine from near Bone Cabin Quarry, Como Bluff was referred to *A. longispinus* by Galton & Carpenter (2016, figs 8V, W; Ford 2006, fig. 3E; Galton, 2016, figs 3I-L; WPL, original mislaid, Figs 23g-i, cast as DMNH 3341). Based on the form of the distal caudal vertebra, the absence of the distal articular surface on the anterior surface of the femur, and of form of the tail spines, this species was recently referred by Costa & Mateus (2019) to the genus *Miragaia* Mateus *et al*., 2009 (Upper Jurassic, western Europe) as *M. longispinus* (Gilmore, 1914).

8. RECONSTRUTIONS OF *STEGOSAURUS*

8.1. Procumbent plates, possibly movable

Marsh (1877) initially suggested that *Stegosaurus armatus,* the "armored roof reptile", was aquatic and that the body was protected by large procumbent bony dermal plates that were over a meter in length (Fig. 1Z). These were supposedly supported in part by the elongate neural spines of the caudal vertebrae, somewhat like those of the plastron of the Late Cretaceous giant aquatic turtle *Protostega* (western USA; see reconstructions of protostegid *Archelon* in Romer, 1956, fig. 216; 1966, fig. 168). The permanent procumbent pose is shown (but with numerous spines incorrectly placed between the plates) in a flesh reconstruction drawn by Frank Bond in 1899, under the direction of Dr. W. O. Knight at the University of Wyoming, Laramie, and first published by Gilmore (1914, pl. 33, lower fig.; also in Colbert, 1962; Czerkas, 1987). However, as Gilmore (1914, p. 98) noted, the plates were not permanently procumbent because both surfaces of the plates are "covered with blood-vessel impressions and no indication of either having been in contact with the creature's flesh" and that the rugose base is the only part adapted for insertion into the skin.

Large procumbent plates, that could be moved to the vertical position, were shown in a reconstruction (Fig. 27H) by Winsor McCay (the animator for "Gertie the Dinosaur") in Ballou (1920; see Switek, 2012), who made the outlandish suggestion that they were used in the former pose as planes for gliding like a flying squirrel.

It has been suggested that the plates of *Stegosaurus* were normally held horizontally but that they could be suddenly erected by skin muscles (Hotton, 1963; Halstead, 1975; Bakker, 1986, pp. 231-233, fig. p. 231). Alternatively, this movement was caused by modified epaxial muscles, the tendons of which insert on the osteoderms in Crocodilia (Seidel, 1979). However, studies of the histology of the plates of *Stegosaurus* by Buffrénil *et al*. (1986) suggest that this kind of plate mobility, that would require the evolution of new transverse back muscles to pull the plates upright, is very unlikely. Surface markings on the basal third of the plate indicate that it was embedded symmetrically in the thick, tough skin. Histological studies by Buffrénil *et al*. (1986, p. 466, fig. 7) show that "the system of Sharpey's fibers (which establish connections between primary bone tissues and non-mineralized connective tissues, notably dermis, tendons, and ligaments) in the basal third of the plate is symmetrical relative to the sagittal plane of the plate [and this] supports the classic, vertical orientation of the plates and falsifies the horizontal, recumbent or movable orientation hypotheses."

8.2. A single row of vertical plates

Marsh (1891a, b, 1896, 1897) restored the complete skeleton of *Stegosaurus ungulatus* (Fig. 2A) based on the skull of *S. stenops* (USNM V 4934), the postcranial bones mostly on *S. ungulatus* (YPM VP 1853, 1858), the placement of the dermal armor on USNM V 4934, and four pairs of tail spines on *S. ungulatus* (YPM VP 1853). The plates are shown vertical, but not paired as in USNM V 4934, and Czerkas (1987, p. 86) noted that they "are drawn from the *S. stenops*, USNM 4934." However, Marsh (1891a, b, 1896, p. 195) omitted "four flat spines, which were probably in place below the tail" of YPM VP 1853 because "their position is somewhat in doubt."

This skeletal reconstruction was followed by two flesh reconstructions the next year, one by Carl Dahlgren for *Californian Magazine* (Fig. 27G) and the other (Fig. 27A) by Joseph Smit in Hutchinson (1892; slightly modified in 1893, see Gilmore, 1914, pl. 32, lower fig.; Colbert, 1962; Czerkas, 1987). These reconstructions show a single row of plates, as do two showing a more upright limb posture by Charles R. Knight in 1897 that appeared in *McClure's Magazine* (Fig. 28A) and in *Century Magazine* (Fig. 28B). The former shows a body covering of dermal armor, comparable to that of a crocodile, for which there is no evidence, and the latter shows four pairs of nuchals and five pairs of spines (see also Figs 27C, D; Section 8.3). As discussed below, Czerkas (1987) argued for a single row of vertical dermal plates in *Stegosaurus* (Fig. 5E, see Section 8.4).

8.3. Early reconstructions with double row of plates

A second reconstruction by J. Smit was in Kulpe (1905; also in Hutchinson, 1912 as cited by Gilmore, 1914; Colbert, 1962; Czerkas, 1987) and it clearly shows two rows of alternating or staggered plates but the middle third of the tail lacks plates (Fig. 27B). A restoration (Fig. 27C) by an unknown artist in Lancaster (1905), modified slightly from that of C. R. Knight (Fig. 28B), was adapted (Fig. 27D) for the 1912 novel "The Lost World" by Sir Arthur Conan Doyle. These three restorations show a double row of plates arranged as pairs for just the first four pairs of small anterior nuchal plates. This possibility was suggested by Marsh (1887, 1896) but was not shown in his reconstruction (Fig. 2A). However, Czerkas (1987, p. 86) notes that in an earlier version of this reconstruction (in USNM Archives), four pairs of nuchal plates are shown but the matching plates of one row were erased and did not appear in the published version.

Frederic A. Lucas (1852-1929; Fig. 28I; biography by Townsend, 1930; Anon, 2019; see also Lucas, 1933) from 1900 to 1904, while Curator of Comparative Anatomy and Acting Curator of Vertebrate Fossils at the USNM, supervised three flesh reconstructions showing the plates of *Stegosaurus*, two as paintings with two rows of plates, each adjacent to the mid-line, rather than the single median row of O. C. Marsh. The first, by Charles R. Knight (1874-1953; Fig. 28C; biography by Czerkas & Glut, 1982; Paul, 1996b; Milner, 2012), has four pairs of terminal tail spines (Fig. 28E), so it represents *S. ungulatus* (Lucas, 1901a, fig. 24; 1901b, pl. 4). Lull (1910b, p. 372, 1912, p. 373, 1919a, b; also Gilmore, 1914, p. 123; Colbert, 1962, p. 155; Czerkas, 1987, p. 87) noted that in this reconstruction the plates are paired but not alternating. George E. Roberts, who drew a figure of plates 1-14 of USNM V 4934 as preserved on the lower surface of the block (Fig. 8B; Gilmore, 1914, pl. 14), is credited by Gilmore (1914, p. 123) for the second 1901 flesh reconstruction (Fig. 27E) that was first published in Geare (1910, fig. p. 4; in caption as C. R. Knight but signed G. E. Roberts). According to Gilmore (1914, p. 123; also Colbert, 1962, p. 155) this second reconstruction of 1901 was supposedly the earliest illustration to, firstly, show alternating plates (also Czerkas, 1987, p. 83), and, secondly, to represent *S. stenops* because there are two pairs of tail spines. Lucas (1901a, p. 107; 1901b) noted that, while the dermal plates were originally figured as a single series down the back, "it seems much more probable that they formed parallel rows" and subsequently that they "appear to have been arranged alternately and not in pairs" (Lucas, 1902, p. 171, but no illustration). This is clearly shown by a figure of plates 2 to 14 of *S. stenops* (Fig. 8D, USNM V 4934) reproduced by Gilmore (1915, fig. 1), who noted that it was probably prepared under the supervision of F. A. Lucas while he was studying *Stegosaurus* (i.e., 1900-1904).

Czerkas & Glut (1982; also Paul, 1996b) reproduce a photograph taken in 1899 showing C. R. Knight sculpting a *Stegosaurus* model (Fig. 28C) for the AMNH with two rows of plates, some of which are clearly alternating or staggered, and two pairs of tail spines (so is *S. stenops*). Although not readily apparent from the copy of the 1901 painting in Gilmore (1914, pl. 33, lower fig.), many of the plates of the right row are visible in the gaps between the plates of the left row so they were not paired but alternating or staggered. This is clearly shown in the model sculpted by C. R. Knight for this painting (Figs 28C, D) and in the color version of the painting in Czerkas & Glut (1982, fig. 88; see Fig. 28E).

The painting (Fig. 28E) by C. R. Knight in Lucas (1901b; listed in Lucas, 1933, p. 54 as publication # 203 versus # 210 for Lucas, 1901a) is the earliest published reconstruction showing the alternating or staggered arrangement of the plates of *Stegosaurus* (but with four pairs of tail spines so is *S. ungulatus*). The 1899 sculpture and the 1901 painting both show more detail on the armor than was available in Marsh (1891a, b, 1896, 1897) or at the AMNH, so they were presumably both done under the direction of F. A. Lucas, who got to use a copy of the painting (Lucas, 1901a, b). This is confirmed by Gilmore (1914, p. 106), who noted that "in 1904, under the direction of Mr. F. A. Lucas, the specimen [USNM V 4934] was unpacked and sufficiently assembled to obtain the necessary data for the life restoration made in that year [1904] by Mr. C. R. Knight" (Fig. 28E). However, this reconstruction is in Lucas (1901a, b) and it, along with the 1899 photograph of Knight working on his statuette of *Stegosaurus* (Fig. 28C), indicates that F. A. Lucas assembled the specimen soon after its arrival in Washington from New Haven, which occurred sometime in 1898 or 1899 (Gilmore, 1914, p. 1). Interestingly, the 1899 Knight model and the text in Lucas (1901a, b) both indicate two pairs of tail spines but the 1901 painting shows four pairs.

Statuettes of *Stegosaurus stenops* showing alternating plates and two pairs of tail spines, prepared by C. R. Knight under the supervision of F. A. Lucas, still exist from 1899 (Figs 28C, D), 1903 (Fig. 28F; one tenth life size; cited by Lull, 1910b, 1912), and 1904 (Fig. 28H). The 1903 model (Fig. 28F), along with a life-sized sculpture of the head and neck in plaster (Fig. 28G), were the basis for a full-scale sculpture made in clay at the Milwaukee Papier Mâché Works, Inc. Once it was approved by F. A. Lucas, a mould of it was then used for a cast in papier mâché (Fig. 28H). Only one painted papier mâché cast was made from the single mold of the clay sculpture as per the original contract (mold sent to USNM; sculpture to St. Louis in 1904, total cost F.O.B. $950.00, Rye, 2014; worth $27,612 in 2020; www.in2013dollars.com). The life size model was part of the USNM exhibit at the "World's Fair" (Louisiana Purchase International Exposition) in St. Louis in 1904 (for photographs see Smith Woodward, 1909, fig. opposite p. 84; Rye, 2014, fig. p. 2), the Lewis and Clark Centennial and American Pacific Exposition and Oriental Fair of 1905 in Portland, Oregon, and as part of the hall of fossil vertebrates at the USNM (Gilmore, 1918, pl. 62) until 2014 (Fig. 28H). It is now exhibited at the Paleontological Research Institution's Museum of the Earth in Ithica, NY (for photographs and details on the papier mâché sculpture, see Rye, 2014).

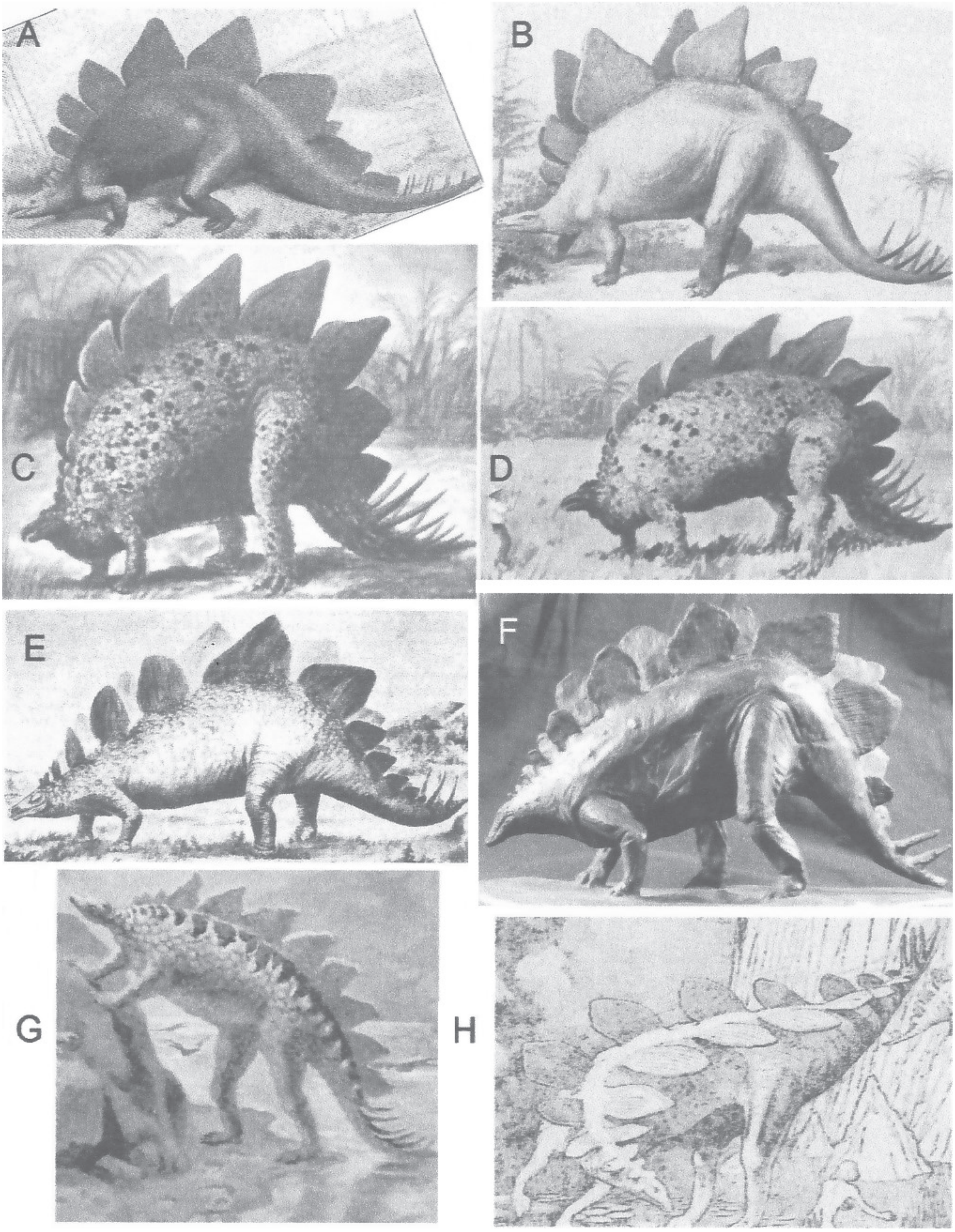

Fig. 27: Flesh reconstructions in left lateral view of Morrison species of *Stegosaurus*: *S. ungulatus* (A, B, G, with 4 pairs of tail spines, C, D, with 4 pairs of nuchal plates and 5 pairs of tail spines, based on Fig. 28B) and *S. stenops* (E, F, H; with 2 pairs of tail spines). A, by Joseph Smit (1836-1924) in 1892, printed in reverse, from Hutchinson (1897); B, by J. Smit in Kulpe (1905; also in Hutchinson, 1911); C, by an unknown artist in Lancaster (1905); D, by the fictitious artist "Maple White" in *The Lost World* by Sir Arthur Conan Doyle (1912); E, by George E. Roberts under direction of Frederic A. Lucas in 1901, in Geare (1910); F, a small bronze sculpture (USNM V 8368) by Charles W. Gilmore, in Gilmore (1915), from M. Brett-Surman; G, by Carl Dahlgren (1847-1920) in 1892 in *Californian Magazine*, also in Dahlgren (1920); H, by Winsor McCay in Ballou (1920, also in Switek, 2012).

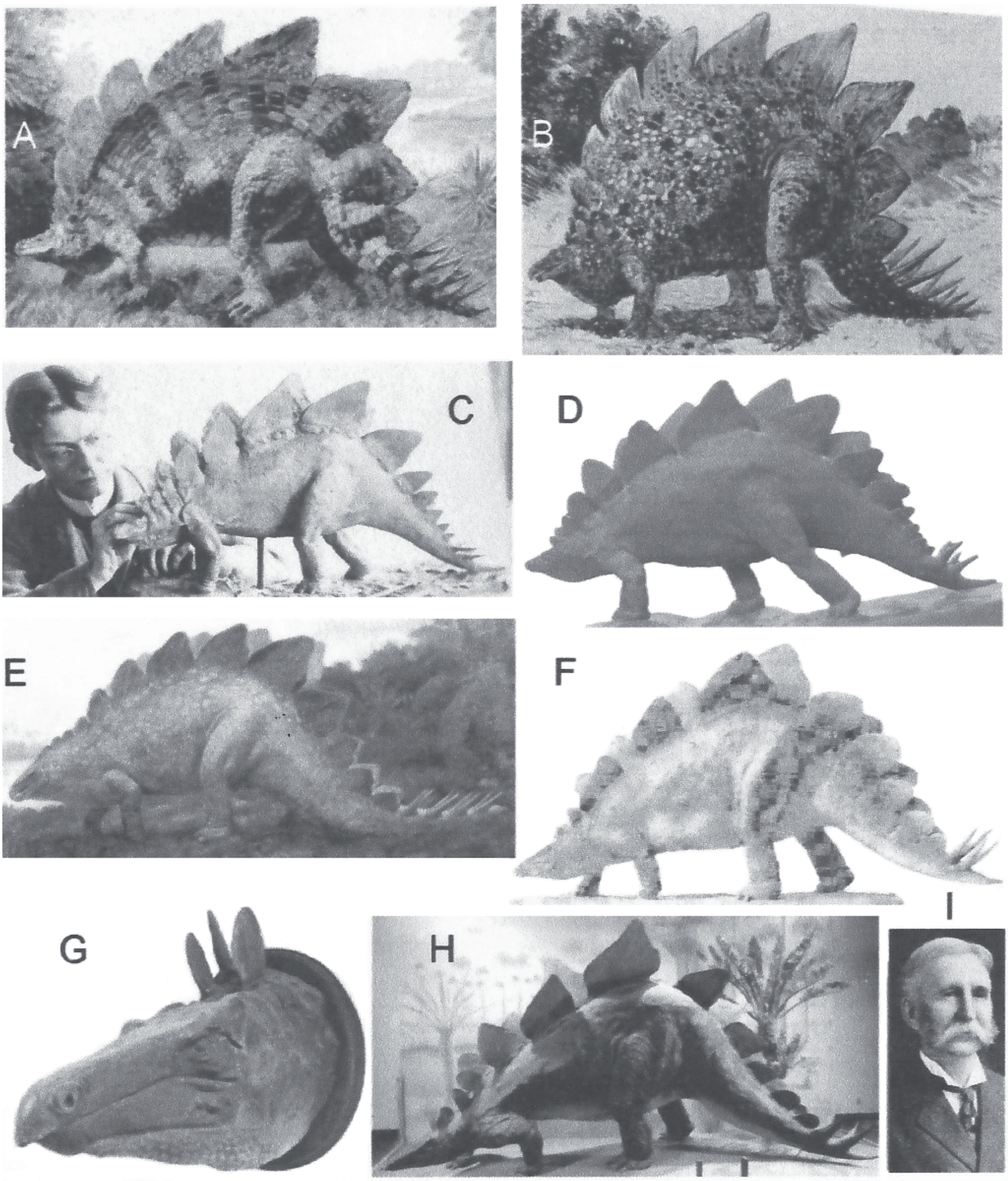

Fig. 28: A-H, Flesh reconstructions in left lateral view of *Stegosaurus ungulatus* (A, E, with 4 pairs of tail spines; B with 4 pairs of nuchal plates and 5 pairs of tail spines) and *S. stenops* (C, D, F, H, with 2 pairs of tail spines): A-B, by Charles R. Knight in 1897: A, for *McClure's Magazine* and B, for *Century Magazine* (printed in reverse); C-H, by C. R. Knight under direction of Frederic A. Lewis: C, photograph of Knight working on study sculpture in 1899 for the AMNH and D, the study sculpture (printed in reverse), still exhibited at the AMNH, that was used for restoration in E, painting for AMNH, copy published by Lewis (1901a, b); F-G, study sculptures prepared in 1903: F, x 1/10 model (USNM V 5794) and G, life size model of head for H, a life size model in papier mâché exhibited at the Louisiana Purchase Exposition (St. Louis World's Fair) in 1904 and later at the USNM (as V 5796; see Section 8.4). I, portrait of Frederic A. Lewis in 1911. C, E from G. Raml, D from C. Manning, G from T. Jorstad, H from Brett-Surman, and I from Anon (2019).

8.4. Evidence for alternating versus paired plates

Lucas (1900-1904, 1910a, b) argued that the plates were arranged as two rows because in USNM V 4934 (Fig. 8) the combined length of the plates is twice that of the underlying vertebrae, or something like 16 to 8 feet (incorrectly given as 40 versus 20 feet by Lucas, 1910a). In addition, none of the plates has a symmetrical base and in all cases there is a slight transverse slope to the vertical axis in one direction or the other, so the plates did not rest squarely on the body along the midline. Lucas (1910a, p. 73) noted that, although logically they should be arranged in pairs, this was not the case because:

1. Alternating double row arrangement present for some of the plates in one articulated specimen [USNM V 4934; Figs 2G, 8A-C],
2. Absence of any matching pairs of plates for any USNM specimen. "No pairs of plates has ever been found and, making the greatest allowance possible for individual variation, it seems incredible that differences of several inches should exist between the plates from the two sides of the body, if they were arranged in symmetrical pairs."

Richard Swan Lull (1867-1957; biography by Gregory, 1957; Colbert, 1968) oversaw the construction of the first mounted skeleton of *Stegosaurus*, that of *S. ungulatus* (Lull, 1910a, b, 1912). This involved many of the YPM bones illustrated by Marsh (1880, 1881, 1887, 1891a, b, 1896, 1897). As evidence for the upright posture of the plates, Lull (1910a, p. 208, 1912) cited USNM V 4634 (Figs 2G, 8A-C) in which the three plates over the sacral region (12-14), "lie as though they had fallen to the right, the anterior ones to the left, a thing manifestly impossible in plates naturally procumbent on either side." In the mounted skeleton the dermal plates were arranged dorsally in matching pairs (see sculpture, Fig. 4A), being angled dorsally and slightly laterally on either side of the midline (Lull, 1910a, b, 1912; Gilmore, 1914, pl. 35). However, most of the plates of the right side were plaster restorations of the "missing" mates to the preserved bones of the left side (Fig. 4D). Lull (1910a, b, 1912) provided cross-sections through the neck, trunk, and proximal tail of YPM VP 1853 to show the relationship of the paired plates to the underlying vertebrae (Figs 29A-C). Lull (1910a, p. 206, 1912) disagreed with the staggered arrangement of the plates shown in the 1903 Lucas/Knight one tenth size statuette (Fig. 28F), noting that:

1. No known reptile has alternating dermal elements,
2. "The series of plates of one side [of USNM V 4934] might easily have shifted forward or backward slightly during maceration or in the subsequent movement of the rocks, as an oblique crushing of fossil bones is a very familiar phenomenon" and
3. The slight disparity of size and shape of two plates in a pair is not surprising when considering that the hypertrophy involved is in itself abnormal. This hypertrophy is comparable to the growth of the large antlers of deer, notably in the Caribou, where those of one individual differ in size, weight, form and even in the number of points (the tines).

Gilmore (1912, 1914, 1915) discussed the arrangement of the plates in articulated specimens of *S. stenops*, especially USNM V 4934 and V 4714, and concluded that they were arranged close together on either side of the midline as two rows, as per Lull (1910a, b, 1912; Lucas, 1900-1904; also 1910a, b *that were not cited* by Gilmore, 1912, 1914, 1915; by Lull, 1910a, 1912; or by Czerkas, 1987), but with the two rows staggered, so there is a slight amount of overlap between adjacent plates, as per Lucas (1900-1904, 1910a, b). Gilmore (1914) modified the cross-sections (Figs 29D-F) given by Lull (1910a, 1912). In addition to points 1 and 2 of Lucas (1900-1904, 1910a), Gilmore (1914, p. 97) noted that:

1. "There is no evidence for forward or backward shifting of the plates – plates 2, 4 and 14 [?2 to 11, Figs 8A-C] fell to the left and lie under the body, whereas the posterior plates [12-14] are approximately in position above the pelvic region, yet both sections show the same alternating arrangement."
2. "There is a remarkable uniformity of the overlapping plates of one side upon those of the opposite row – that is, the middle point of the underlying plates, taken longitudinally, is, in nearly all instances, in the center of the interspace between the plates of the uppermost series. This exact spacing of the plates would indicate that they remained attached to the skin until becoming fixed in the position in which we now see them. If this be true, it is difficult to explain the possibility of bringing the plates of opposite sides into alignment, since in order to do so, it would be necessary to shift the small anterior ones only a few inches, while the larger plates would need to be moved a foot or more. Certainly, if remaining attached to the skin in sequential order, as the evidence appears to show, had the plates of one side shifted, all would have moved in the same direction and approximately similar distances."
3. The suggestion that the shift in the plates resulted from movement of the rock is absolutely untenable because there is no indication of lateral shearing in the specimen or in the attached rock.

Gilmore (1918) illustrated the exhibits of *Stegosaurus* at the USNM that included the 1904 Lucas/Knight life sized model (Fig. 28H), the holotype skeleton of *S. stenops* (Fig. 2G), the 1915 Gilmore model (Fig. 27F) and a newly mounted skeleton (Fig. 2C; latter two also in Gilmore, 1920). The mounted composite skeleton (Fig. 2C; USNM V 8612), based mostly on the bones of USNM V 6531 from YPM Quarry 13, most of which are located in diagram 13 in Gilmore (1914, pl. 37). These included most of the vertebral column, a few dorsal ribs, the pelvic girdle, dermal plates 15 to 19 and two pairs of caudal spines (Fig. 18A). These were supplemented with other YPM Quarry 13 bones that were selected based on the relative proportions of these bones in USNM V 4934 (see Gilmore, 1918, table pp. 388-389 for full list of bones, * indicates bones illustrated in Gilmore, 1914). Gilmore (1918) noted that this reconstruction (Fig. 2C) showed several differences from previous ones (Figs 2A, 28H). These included a shorter body so that the fore and hind limbs were closer together, 19 erect dermal plates were required to complete the two rows, and the placement of the largest plate 14 over the base of the tail rather than over the hips. The mount was renovated and exhibited in 2019, using casts of the bones, and the plate count was reduced to 17 (Fig. 2D).

Lull (1919a, p. 237, 1919b) acknowledged that Gilmore (1914) "demonstrates pretty conclusively that in *S. stenops*, at least, there were but twenty alternating flat plates, the largest of which was situated over the base of the tail," and that the tail was terminated by two pairs of spines. Lull used the alternating arrangement of the plates, but retained the four pairs of terminal spines, when the YPM skeleton was remounted in 1924 for exhibition in the new museum building (Figs 4B, C; see Lull, 1929, pl. 13; Carpenter & Galton, 2001, fig. 4.3B).

The skeletal reconstruction of *Stegosaurus* (Fig. 2B) in the textbook of vertebrate paleontology by Romer (1933, fig. 183) was "modified after Marsh and Gilmore". The single row of 12 large plates of Marsh (1891a, b, 1896, 1897) was replaced by a double row of 19 proportionally smaller alternating plates (after figures in Gilmore, 1914), with the largest one over the base of the tail, and the four pairs of large tail spines were replaced by two pairs of smaller spines, the pattern seen in *S. stenops* (Figs 18A, H, 22A-F). The skull was slightly redrawn and the cuirass of small ossicles was omitted but the remainder of the skeleton was essentially unchanged from that of Marsh (1891a, b, 1896, 1897). This hybrid reconstruction was widely seen, appearing also in Romer (1945, 1956, 1966), and similar reconstructions appeared in Young (1950, fig. 246, "modified after various authors", but with four pairs of spines), Carroll (1988, fig. 14.44, "redrawn from Gilmore, 1914"), and Benton (1990, fig. 7.18, "after Gilmore 1914").

In the 1980s several researchers such as Czerkas (1987) and Paul (1987) drew the bones of *Stegosaurus*, rather than relying on the illustrations of O. C. Marsh and C. W. Gilmore, and provided more dynamic poses, such as the reconstructions of *S. ungulatus* (Fig. 5A) by Bakker (1986; also flesh reconstruction fig. p. 348 plus fig. p. 188 for *S. stenops*). Czerkas (1987) notes that the assertion by Lull (1910a, p. 206, 1912) that no known reptile has alternating dermal armor is true for crocodiles and gavials. However, "in reptiles that possess a single, median row of dermal elements (e.g., [the lizard] *Cyclura cornuta*) it is not uncommon for the smaller, initially symmetrical elements to develop asymmetry as they enlarge in growth, often alternating in opposing directions" (Czerkas, 1987, p. 93, fig. 16). Czerkas (1987) measured the vertebrae and dermal armor of USNM V 4934 and V 4714 and demonstrated that there was room for the plates to be arranged as a single row along the midline over the neural spines (Figs 29G-I), being angled slightly outwards so there was only overlap of the wider more distal parts of the plates situated above the cervical and dorsal vertebrae (Fig. 5E). However, Carpenter (1998) noted that in the Garden Park specimens (USNM V 4934, Figs 8A-C; DMNH 2818, Figs 6A-H) there is matrix between the bases of adjacent overlapping plates (Fig. 6E), indicating that the plate rows were separate and not diverging from a single row as suggested by Czerkas (1987).

Paul (1987) noted that at least some of the plates of *S. ungulatus* were paired because a pair (i.e., left and right) of virtually identical plates (Figs 19M, N) were figured for YPM VP 1853 by O. C. Marsh in Ostrom & McIntosh (1966, 1999, pl. 59, fig. 1, pl. 60; Galton, 2010, figs 3n, r). Paul (1987) restored two rows of paired plates for *S. stenops* (Fig. 5C; also shown in dorsal and anterior views plus a side view with restoration of superficial muscles), based on USNM V 4934 and 4714. Paul (1992, also 2010, 2016) provided a revised reconstruction of *S. stenops* with alternating plates (Fig. 5D; USNM V 4934 and 4714), with conformational information provided by the new Garden Park specimen (DMNH 2818, Figs 6A-H; Carpenter, 1998, 2007), and for *S. ungulatus* with two pairs of tail spines (Fig. 5B; Paul, 2010, 2016).

In addition to the holotype of *S. stenops* (USNM V 4934, Figs 2G, 8, 9A-E) from Garden Park near Cañon City, Colorado, there are several other specimens that show evidence of overlapping plates. DMNH 2818 was found near the type horizon and locality and it is a nearly complete skeleton that probably has 17 plates, several of which are overlapping (Figs 6A-H; Carpenter, 1998, 2007).

Although not indicated by Gilmore (1914, fig. 58; Fig. 4D), the original quarry map for USNM V 4714 from Como Bluff (Fig. 4B) shows bone 9 overlapping bone 10 (i.e., plate 13 overlapping 14; Gilmore, 1914, pl. 37), with the medial surface of plate 14 showing the area of overlap (Figs 15I, J). The "Bollan stegosaur" (MWC 81; Bollan, 1991), found 25 feet (7.6 m) above the base of the Brushy Basin Member in Rabbit Valley, about 25 miles (40 km) west of Grand Junction, western Colorado, has about 75% of the skeleton that includes two overlapping anterior dorsal plates (Fig. 6L). Bilbey & Hamblin (1992) reported on about 30% of an articulated skeleton from the Salt Wash Member east of Jensen, Utah. The "McStegosaur" (FHPR 572) consists of limb bones plus the articulated left half of the upper torso with the preacetabular process of the ilium, a poorly preserved dorsal vertebral column represented by damaged centra, and 12 dorsal ribs in ventral view (Figs 6I, J). There are four dorsal plates, not five as originally reported by Bilbey & Hamblin (1992), aligned vertically as two parallel rows along the vertebrae, with the anterior two overlapping and staggered with matrix in between (Figs

6J, K), whereas the posterior two plates are not clearly overlapping (Bilbey & Hamblin, 1992).

8.5. *Hesperosaurus* and two morphs for plates

The basal Morrison stegosaur *Hesperosaurus mjosi* Carpenter *et al*., 2001 from near Buffalo, Wyoming, has low dorsal plates with the height less than the length (Fig. 5H), the reverse of the situation in *Stegosaurus* (Figs 2, 5A-G). Saitta (2015) documented two morphs for the dermal plates of *S. mjosi*, one with wide, oval plates (Fig. 5J) 45% larger in surface area than the tall, narrow plates of the other morph (Fig. 5I), with this variation possibly representing a sexual dimorphism with the former morph possibly representing males. *Hesperosaurus* is considered to represent a valid genus by Raven & Maidment (2017; new diagnosis by Maidment *et al*., 2018), as maintained by Carpenter (2010), rather than a separate species of *Stegosaurus* (as *S. mjosi*, see Maidment *et al*., 2008). A comparable plate dimorphism has not been described for the plates of *Stegosaurus*.

8.6. Chirality of plates for *Stegosaurus stenops*

Plate 14 of the holotype of *Stegosaurus stenops* (USNM V 4934) is the largest of the series and it tilts slightly to the right (Figs 8, 29O). However, because of this geometrical asymmetry, it could theoretically tilt slightly to the left in another individual (Fig. 29P). This external mirror asymmetry or chirality is quite common in animals, occurring in snails, fiddler crabs, flounders, narwhals and crossbills amongst others (Neville, 1976) and could, potentially, result in two forms of *S. stenops*. These are designated (R) *S. stenops* and (L) *S. stenops* (Figs 28O, P) by Cameron *et al*. (2015, p. 2, 2016), who correctly determined that the holotype USNM V 4934 (Fig. 8) is a (R) *S. stenops* (Cameron *et al*., 2016, fig. 1). They also state without discussion that USNM V 4714 is a (R) *S. stenops* and this agrees with Gilmore (1918, pls 57-63), who mounted a cast of plate 14 on the right side of the mounted skeleton (Fig. 2C). However, quarry diagrams by F. Brown (in Gilmore, 1914, pl. 37, diagram 5) show that bone 9 (i.e. plate 13) overlapped the right (medial) side of bone 10 (i.e. plate 14) (Fig. 7B) that was on the left side, and this line of overlap is indicated on plate 14 (Fig. 15J). Consequently, USNM V 4714/7584/7615 is a (L) *S. stenops*.

Based on the quarry map (Fig. 6B; Carpenter, 1998, fig. 2), the Small skeleton from near Cañon City (DMNH 2818) is cited by Cameron *et al*. (2015) as a (L) *S. stenops*, thus proving that chirality existed in *S. stenops*, but as a (R) *S. stenops* by Cameron *et al*. (2016). Plate 15 is a right (Fig. 6H) with 14 as a left so DNMH 2818 is a (L) *S. stenops*.

Cameron *et al.* (2015, fig. 4) note that in the mounted skeleton NHMUK PV R36730 (Figs 2E, F, 7B) the largest plate is on the right side so it is a (R) *S. stenops* but this is plate 13, not 14 as in the other individuals.

9. FUNCTIONS OF OSTEODERMS

9.1. Plates

The overall pattern of the plates and spines is characteristic for each species of stegosaur (see skeletal reconstructions in Olshevsky & Ford, 1995; Paul, 2016), so it was probably important for the recognition of other individuals of the same species and for sexual displays. Davitashvili (1961) suggested that this was probably the original function of the erect osteoderms and, as noted by Spassov (1982), the armor of all stegosaurs is ideally arranged for maximum effect during a lateral display.

It has been suggested that the plates of *Stegosaurus* were normally procumbent, being held horizontally, to provide a flank defense, with the largest plates over the vulnerable hindlimb. However, the plates could supposedly be suddenly erected by skin muscles to startle and deter an attacker, or to ward off attack from above (Hotton, 1963; Halstead, 1975; Bakker, 1986, pp. 231-233, fig. p. 231). Hotton (1963; also Seidel, 1979) suggested that this change in orientation was for display or thermoregulatory purposes. However, histological studies by Buffrénil *et al*. (1986, p. 466, fig. 7) support the classic, vertical orientation of the plates and falsifies the horizontal, recumbent or movable orientation hypotheses (see Section 8.1). Furthermore, the plates of *Stegosaurus* are unlikely to have functioned as armor because they consist of cancellous bone with a thin cortex (Buffrénil *et al*., 1986; Main *et al*., 2005), not thick compact bone like the terminal pairs of tail spines of old adult individuals (see Section 9.3.1).

Apart from any use in sexual display, the plates could have functioned in temperature regulation. In an alternating arrangement, the plates could have worked well as a forced convection fin to dissipate heat, and possibly as heat absorbers from solar radiation (Farlow *et al*., 1976; Buffrénil *et al*., 1986). The plates would have formed a scaffolding for the support of a richly vascularized skin which would have acted as an efficient heat exchange structure. A heat-absorbing role for the plates would be useful if *Stegosaurus* was an ectotherm (“cold-blooded”), whereas heat loss by radiation or forced convection would help if *Stegosaurus* was ectothermic or to any degree endothermic (“warm-blooded”; Buffrénil *et al*., 1986). These conclusions would also probably apply to the similarly large, thin dorsal plates of *Hesperosaurus* (Fig. 5H) and of *Loricatosaurus* (Middle Jurassic, England; Galton, 1985, 2016), but in other stegosaurs with smaller plates display was probably their main function.

Main *et al*. (2005) question the thermoregulatory function of the vertical plates of *Stegosaurus*, which are not present in most stegosaurs, and favor a display

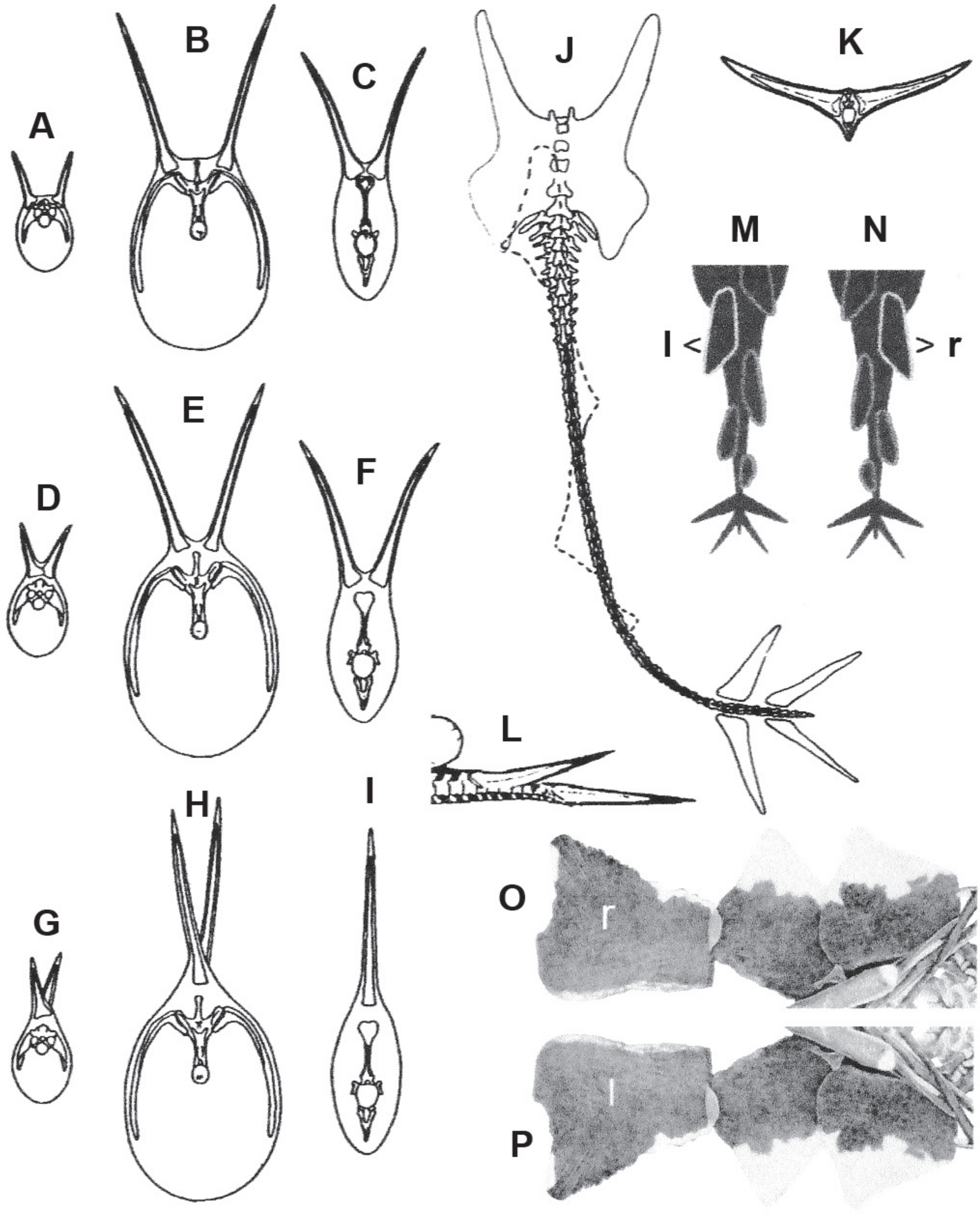

Fig. 29: *Stegosaurus stenops*. A-I: Cross-sections of neck (A, D, G), trunk (B, E, H) and proximal caudal (C, F, I) vertebrae to show postulated positions of dermal plates. A-C, the paired arrangement of Lull (1910a); D-F, as modified for a staggered arrangement by Gilmore (1914) and G-I, as modified for a single row of plates by Czerkas (1987). J-L, orientation of tail spines: J, in dorsal view with tail vertebrae and sacrum, plates (dashed lines) restricted motion of tail proximally so greatest bending movement is in distal third; K, cross-section of tail in posterior view to show lateral projection of spines and L, left lateral view to show more horizontal orientation of tail spines. M-P: chirality or a sense of handiness for plates of *S. stenops*: M-N: the largest plate 14 can tilt to the left (M) or to the right (N) to give (L) *S. stenops* or (R) *S. stenops* and O-P, *S. stenops*: O: in USNM V 4934 plate 14 tilts to the right (cf. Figs 2G, 8C for more complete views of specimen) so it is (R) *S. stenops* whereas in P, the mirror image, plate 14 would tilt to the left so it represents (L) *S. stenops*. A-I from Czerkas (1987), J-K from Carpenter (1998), L from Carpenter (2010), M-N from Cameron *et al*. (2015), and O-P from Gilmore (1914).

and recognition function analogous to the varied cranial characters developed in other ornithischian groups. Their comparative histological studies show that the mostly thin parasagittal vertical plates and spikes of *Stegosaurus* grew mainly by basal osteogenesis, with some lateral periosteal deposition, and extensive internal remodelling, so the plates "evolved" by hypertrophic growth of the parasagittal keel of the basal thyreophoran scute. Internal "pipes" and external groves are often present in broad, flat bones, including the cranial frills of ceratopsian dinosaurs, as well as the horns of artiodactyls, structures that do not seem to be primarily for thermoregulation. They conclude that these vascular and histological features are best regarded as constructional artifacts, a reflection of the processes and modes of bone growth. Surface vascular features on the plates probably also provided the blood supply to a keratinous covering so, like the tail spikes, they were probably covered by horn, as suggested for *Stegosaurus* by Gilmore (1914; Horner & Marshall, 2002).

Hayashi *et al*. (2009), who identified four histological changes that occurred during the development of the bones of *Stegosaurus*, determined that these changes occurred later in the plates and spines than in the long bones. Thus a juvenile *Stegosaurus* already has well-developed dorsal plates. In addition, the osteoderms maintained faster growth than the other bones for a longer period of time after the maturity of the skeleton, resulting in the uniquely large size of the plates. In contrast, the small-plated and/or spiked Upper Jurassic stegosaurs *Miragaia* (western Europe) and *Kentrosaurus* (East Africa) show a developmental delay of osteoderms with respect to the body skeleton as occurs in living alligators (Hayashii *et al*., 2014).

Based on infrared thermographic imaging of basking Caimans, Farlow *et al*. (2010, p. 173) provided evidence for the possibility of heat exchange with the external environment as a result of the vascularity of the osteoderms. They noted that in *Stegosaurus* "the potential thermoregulatory role of the plates may have been greater than in other thyreophorans by virtue of their extensive external and internal vascularity, their large size, thin cross-sections above the plate base, dorsal position, and alternating arrangement."

Anduza & Lombardo (2018) created 3D models to demonstrate a significant difference in the plate surface area and body volume between numerous taxa of stegosaurs that, along with the diversity of plate size and form, argues against a primary thermoregulatory function for the plates. They demonstrated that a staggered plate arrangement, an unusual and selectively unexplained arrangement for an otherwise bilaterally symmetrical animal can, with appropriate coloration, produce a "motion dazzle" effect similar to the stripes on a modern Zebra. In conjunction with the defensive role of the tail spines, this effect would have acted as a warning to predators.

9.2. Tail spines

9.2.1. For display and defense

The horn-covered terminal tail spines of *Stegosaurus* and other stegosaurs would have been formidable weapons. Bakker (1986) suggested that the loss of ossified tendons in stegosaurs was correlated with increased flexibility of the tail. He visualized *Stegosaurus* using the strong shoulder muscles to pivot its body on the very tall hind limbs (also Lull, 1910b), the main weight supporters, as it arched and twisted its tail so the spines were driven into the body of an attacker. In lateral view the tail spines of *Stegosaurus* were usually reconstructed pointing postero-dorsally and slightly laterally at the end of a drooping tail (Figs 2A-C, 5G, 18A). However, the distal pair of tail spines in *Kentrosaurus* (Upper Jurassic, Tanzania) are preserved along the sides of the distal caudal vertebrae and extend well beyond the end of the tail (Galton, 1982, pl. 4, figs 20-23). Olsevsky & Ford (1993, 1995; Ford, 1997) argue that the tail and its spines were held more horizontally (Figs 2D, 5F, H, 18H, 29J-L). As Carpenter (1998) notes, the tail was held high in the air and mostly parallel to the ground (see Figs 2D-F, 5A-E) because, as in the sauropod dinosaur *Diplodocus* (Gilmore, 1932), the posterior surface of the last sacral centrum faces upwards and the centrum of the first caudal centrum is wedge shaped in side view. The more horizontal orientation of the spines (Figs 5F, 18H) enhanced their role as weapons (Figs 29J-L) and the expanded, bifid neural spines provided additional attachment surface for the supraspinous and interspinous ligaments that helped to maintain the horizontal posture without muscular effort. The horizontal posture was also aided by the bases of the large plates that effectively "locked" segments of vertebrae together. This was also true for lateral motion of the tail but, because the small amount of motion between vertebrae was cumulative, the posterolaterally directed terminal tail spikes acted as a weapon that could be projected a little more than perpendicular to the long axis of the body (Figs 29J-L; Carpenter, 1998).

Gilmore (1914) observed that the larger anterior of the two pairs of tail spines of *Stegosaurus* were more deeply embedded by their bases in thick skin and more prone to injury and fracture than the posterior pair. McWhinney *et al*. (2001) found that ~10% (5 out of 51) of tail spines examined showed broken tips with trauma-induced bone fractures and remodelling of broken bone surfaces, indicating survival after injury (Fig. 23V; Carpenter *et al*., 2005, figs 17.3A, B). The remodeling implies that the spines were broken well before death and that the horny sheath probably protruded less than 1 cm beyond the bony tip, otherwise the horny sheath would have broken off rather than the bony spine. They concluded that the dermal tail spines of *Stegosaurus* were primarily used in active defensive and offensive posturing in interspecific and intraspecific combat. In addition, an isolated first caudal vertebra of the theropod dinosaur *Allosaurus fragilis* has an opening in the transverse process that matches the cross-section of the proximal part of a tail spine of *Stegosaurus* (Carpenter *et al*., 2005, figs 17.1, 17.2).

The forces developed during defensive and offensive movements of the tail of *Stegosaurus stenops* with the spines held at an angle of 45 degrees are analysed by Gertsch (1994), for a more horizontal posture (Figs 5F, 18H) by Carpenter *et al*. (2005), and in more detail for *Kentrosaurus* (Upper Jurassic, Tanzania) by Mallison (2011).

In *Stegosaurus* the throat ossicles and dermal plates retain the plesiomorphic histology for Thyreophora (Scheyer & Sander, 2004; Main *et al*., 2005). However, Hayashi *et al*. (2008) pointed out that the dermal tail spines of *Stegosaurus* and *Dacentrurus* (Fig. 26Q; Upper Jurassic, England) have thick compact bone, lacking prominent collagen fibers, and a well-defined medullary cavity, whereas those of ankylosaurs have a unique structure of supporting collagen fibers. Consequently, the two groups used different strategies to develop defensive weapons. Hayashi *et al*. (2012) later studied the ontogenetic changes exhibited by the spines of a juvenile, a subadult, a young adult and five old adult individuals of *Stegosaurus.* The tail spines of the stages up to young adult have a thin cortex and thick cancellous bone without a central canal (Figs 22G-I), so they were presumably used for display rather than defence. Only the caudal spines of old adults have a thick cortex and a large central channel (Figs 22P, Q; also true for old adults of Morrison *Hesperosaurus mjosi*, Hayashi *et al*., 2012; Saitta, 2015, fig. S19; *Dacentrurus armatus,* Fig. 26Q, Upper Jurassic, England, Owen, 1875, 1877). Hayashi *et al*. (2012) suggest that this change indicates that the tail spines of *Stegosaurus* acquired a weapon function for defence ontogenetically late; this was presumably also the case for *Hesperosaurus* and *Dacentrurus*.

9.2.2. Preservation of isolated tail spines

Stegosaurian spines and spikes are preserved as isolated finds from the Upper Jurassic of England and Portugal and the Lower Cretaceous of Spain (Galton, 2016, figs 1U-X, 3M-U, 4A-K). These spines have a cross-sectional gross histology corresponding to that of old adult individuals of *Stegosaurus* as determined by Hayashi *et al*. (2012), viz., a very thick cortex and a prominent central canal (Figs 22P, Q; Galton, 2016, figs 1T, X, 3S-U, 4B, C, J). Such a cross-section is shown by the isolated dermal tail spine tentatively referred to the Morrison stegosaur *Miragaia* (as *Alcovasaurus*) *longispinus* (Figs 23g-i; Upper Jurassic, USA; Galton & Carpenter, 2016, fig. 3I-L), so this is from an old adult individual. This contrasts with the thin cortex with cavernous bone and no central canal that occurs in juvenile, subadult and young adult individuals of *Stegosaurus* (Figs 22H, I), the plesiomorphic condition for dermal armor in Thyreophora (Hayashi *et al*., 2012). Hayashi *et al*. (2012) suggest that, in addition to their display functions in juvenile, subadult and adult individuals, the more resistant structure of tail spines of old adult individuals also reflects a defensive function. Although based on a small sample size, a bias favoring preservation of isolated spines and spikes from old adult individuals is not unexpected.

9.2.3. Preservation of spines as a pair

Gilmore (1914, p. 110, fig. 65) figured a very rugose distal medial basal surface on the very large anterior pair of tail spikes in *Stegosaurus sulcatus* (Figs 26D, E, N, O) that he suggested was for cartilage uniting the adjacent bases (Fig. 26M). The preservation together in isolation of a pair of spines of *Miragaia* (*Alcovasaurus*) *longispinus* (Galton & Carpenter, 2016, figs 1E, 2A, 8A-J) and of ?*Dacentrurus* (Upper Jurassic, Spain; Company *et al*., 2010; Galton, 2016, figs 3W-Z) indicate that the bases were probably bound together by ligaments. Other evidence for such a binding is provided by the bases of each pair of dermal spines being preserved close together in articulated distal tails preserved either on their side (Figs 22A, B, posterior pair Figs 22E, F; *Chungkingosaurus jianbeinsis*, Dong *et al*., 1983; Dong, 1990; Upper Jurassic, China) or horizontally, in which case the spines together form a V in ventral view as seen in *Miragaia* (*Alcovasaurus*) *longispinus* (Galton & Carpenter, 2016, fig. 1E).

SUMMARY

Many specimens of the plated dinosaur *Stegosaurus* were collected between 1877 and 1889 for O. C. Marsh of New Haven College, Connecticut from the Morrison Formation (Upper Jurassic) of Western USA. Most of the important specimens of dermal armor are illustrated for this material, which came from Garden Park, Colorado and Como Bluff, Wyoming, and also for specimens from Utah from the Carnegie Quarry of Dinosaur National Monument and the Cleveland-Lloyd Dinosaur Quarry; and information is provided about the six quarries involved. The holotype (USNM V 4934) of the neotype species of *Stegosaurus* Marsh, 1877, *S. stenops* Marsh, 1887, is a mostly complete articulated skeleton from Garden Park with all 17 dermal plates and 1 of 4 tail spines preserved. An almost complete series of 17 dermal plates (only plates 3 and 5 missing) and 2 pairs of tail spines from one individual of *S. stenops* (USNM V 4714/7584/7615, YPM Quarry 13, Como Bluff) is reassembled from three sets of osteoderms that, as shown by quarry maps, were found close together. An associated specimen (NHMUK PV R36730, "Sophie/

Sarah" from near Shell, Wyoming) probably had 18 dermal plates, rather than 19 as reconstructed. Other illustrated non-Marsh specimens include a second almost complete articulated specimen from Garden Park, the "Small *Stegosaurus*" (DNMH 2818). Two others, the "McStegosaur" (FHPR 572, from near Jensen, Utah) and the "Bollan stegosaur" (MWC 81, from near Grand Junction, Colorado) also show an overlap of some of the plates. The form of the four pairs of terminal tail spines of the syntype of *S. ungulatus* Marsh, 1879 (YPM VP 1853, YPM Quarry 12, Como Bluff) indicates that these are from two individuals, the larger one for spine pairs 1 and 3 and the smaller one for pairs 2 and 4. However, the flat distal tail spines, which were probably arranged as four pairs, are diagnostic. Isolated spines of this form also occur in Utah at the Carnegie Quarry and at the Cleveland-Lloyd Dinosaur Quarry. The distinctive form of the terminal tail spines supports the validity of two of the species of Morrison stegosaurs. The anterior pair are extremely massive in *S. sulcatus* Marsh, 1887 (USNM V 4937, YPM Quarry 13, Como Bluff) and both pairs are extremely slender and elongate in *S. longispinus* Gilmore, 1914 from near Alcova, Wyoming. This is the type species of *Alcovasaurus* Galton & Carpenter, 2016 as *A. longispinus* (Gilmore, 1914). However, based on the form of the distal articular surface of the femur, of the distal caudal vertebra, and of the tail spines, this species was recently referred by Costa & Mateus (2019) to the genus *Miragaia* Mateus *et al*., 2009 (Upper Jurassic, western Europe) as *M. longispinus* (Gilmore, 1914). The possibility of a new species of *Stegosaurus* from the Carnegie Quarry is indicated by the base of the nuchal and anterior dorsal plates being transversely wider than long, by several other dorsal to anterior caudal plates that are strongly pinched in dorsally with pointed tips, and by flat distal tail spines. These three types of osteoderms also occur in the Cleveland-Lloyd Dinosaur Quarry.

A cuirass of small throat ossicles is known only for *S. stenops*, being well preserved in the two articulated skeletons from Garden Park (USNM V 4934, DNMH 2818); in USNM V 7615 (YPM Quarry 13, Como Bluff) a carnivorous theropod tooth is preserved between the ossicles. No lateral body scutes are preserved in the two skeletons from Garden Park and the lost "tubercular spine" of *S. ungulatus* (YPM VP 1853) is the severed base of a nuchal plate. The isolated and dorsally incomplete "shoulder plate" (USNM V 7617, YPM Quarry 13), which supposedly resembled some of the scutes of basal thyreophorans, is reoriented and it may be an anterior dorsal plate with a uniquely large base. A low, sub-semicircular and transversely narrow oval scute (USNM V 337464), that lacks any ventral excavation, is the only lateral body scute from YPM Quarry 13 but it is from a polacanthid ankylosaur.

Marsh (1891a, b) showed the plates as a single median row and four pairs of tail spines in his skeletal restoration of *S. ungulatus*. The history of subsequent restorations is discussed and illustrated. The first published restoration showing the paired and alternating arrangement of the plates was by C. R. Knight in Lucas (1901a, b; four pairs of tail spines so are of *S. ungulatus*). Lucas/Knight statuettes with this arrangement and two pairs of tail spines, so are of *S. stenops*, still exist from 1899, 1903 and 1904. Lucas in 1900-1904 illustrated plates 6 to 14 of the holotype of *S. stenops* as being paired and alternating as preserved (figure in Gilmore, 1914) and as reconstructed for plates 2 to 14 (figure in Gilmore, 1915), and Lucas (1910a) was the first to publish evidence for such an arrangement. A detailed summary of the subsequent discussion supporting paired alternating plates versus two rows in pairs or as a single median row with longer plates overlapping distally is provided.

There is no evidence in *S. stenops* for a sexual dimorphism of the plates as described for the Morrison stegosaur *Hesperosaurus mjosi*. However, there is evidence for external mirror asymmetry or chirality in which the largest plate of the series, usually the 14th, tilts either to the right or to the left. The holotype is a (R) *S. stenops*, as are DMNH 2818 and NHMUK PV R36730 (but with plate 13 as the largest) whereas USNM V 4714/7584/7615 is a (L) *S. stenops.*

Histological changes in the bones of *Stegosaurus* occurred later in the osteoderms than in the long bones. In addition, the osteoderms maintained faster growth than the other bones for a longer period of time after the maturity of the skeleton, resulting in the uniquely large size of the plates. In contrast, the small-plated and/or spiked Upper Jurassic stegosaurs *Miragaia* (western Europe) and *Kentrosaurus* (East Africa) show a developmental delay of osteoderms with respect to the body skeleton as occurs in living alligators.

The proposed functions for the dermal osteoderms of stegosaurs are discussed. For plates and tail spines these include lateral display for species recognition and sexual interactions, with the plates also involved in different degrees of thermoregulation. In *Stegosaurus* the tail was held high, so parallel to the ground, and it bore tail spines that were directed laterally and only slightly dorsally (rather than dorso-laterally as usually shown) so they could function better as defensive and offensive weapons. This has been documented histologically for the spines of old adult individuals of *Stegosaurus, Hesperosaurus*, and *Dacentrurus* (Upper Jurassic, England), in which there is a thick cortex and a large central canal. Spines of juvenile to adult individuals of *Stegosaurus* retain the plesiomorphic histology with a thin cortex and thick cancellous bone, which was suitable for display but not useful as a weapon. Stegosaur tail spines represented by isolated finds from the USA and Western Europe are from old adult individuals, the thick cortex of which favoured preservation.

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REFERENCES

Anduza D. & Lombardo M. D. 2018. Stegosaur plate function: thermoregulation vs. display and a novel new hypothesis. *Society of Vertebrate Paleontology, Program and Abstracts*, 2018: 81-82.

Anon 2019. Frederic Augustus Lucas. https://en.wikipedia.org/Frederic_Augustus_Lucas

Arbour V. M. & Currie P. J. 2016. Systematics, phylogeny and palaeobiogeography of the ankylosaurid dinosaurs. *Journal of Systematic Palaeontology*, 14(5): 385-444.

Bakker R. T. 1986. *The Dinosaur Heresies. New Theories Unlocking the Mystery of the Dinosaurs and their Extinction*. William Morrow & Co., Inc., New York, 482 pp.

Bakker R. T. 1988. Review of the Late Cretaceous nodosauroid Dinosauria. *Denversaurus schlessmani*, a new armor-plated dinosaur from the latest Cretaceous of South Dakota, the last survivor of the nodosaurians, with comments on stegosaur-nodosaur relationships. *Hunteria*, 1(3): 1-23.

Ballou W. H. 1920. The aeroplane dinosaur of a million years ago. *The Ogden Standard Examiner*, Sunday Morning, Ogden, Utah, August 15: 8.

Benton M. J. 1990. *Vertebrate Palaeontology*. Unwin Hyman, London, xii + 377 pp.

Berman D. S. & McIntosh J. S. 1986. Description of the lower jaw of *Stegosaurus* (Reptilia, Ornithischia). *Annals of the Carnegie Museum*, 55: 29-40.

Bilbey S. A. & Hamblin A. H. 1992. An articulated partial skeleton of *Stegosaurus* from the Salt Wash Member of the Morrison Formation near Jensen, Utah. *Geological Society of America Meeting, Rocky Mountain Section, Abstracts with Program*, 24(6): 4.

Bollan H. R. 1991. The Bollan *Stegosaurus*. *Guidebook for Dinosaur Quarries and Tracksite Tour: Western Colorado and Eastern Utah*. Geological Society, Grand Junction: 53-54.

Breithaupt B. H. 1990. Biography of William Harlow Reed: the story of a frontier fossil collector. *Earth Sciences History*, 9(1): 6-13.

Breithaupt B. H. 1998. Railroads, blizzards, and dinosaurs: A history of collecting in the Morrison Formation of Wyoming during the nineteenth century. *Modern Geology*, 23: 441-463.

Brown B. 1932. A spine-armored saurian of the past. *Natural History*, 32(6): 493-496.

Buffrénil V. de, Farlow J. O. & Ricqlès A. de. 1986. Growth and function of *Stegosaurus* plates: evidence from bone histology. *Paleobiology*, 12(4): 459-473.

Burns M. E. & Currie P. J. 2014. External and internal structure of ankylosaur (Dinosauria, Ornithischia) osteoderms and their systematic value. *Journal of Vertebrate Paleontology*, 34(4): 835-841.

Cameron R. P., Cameron J. A. & Barnett S. M. 2015. Were there two forms of *Stegosaurus*? *arXiv:1508.03729v1*

Cameron R. P., Cameron J. A. & Barnett S. M. 2016. *Stegosaurus* chirality. *arXiv:1611.08760*

Carpenter K. 1998. Armor of *Stegosaurus stenops*, and the taphonomic history of a new specimen from Garden Park, Colorado. *Modern Geology*, 23: 127-144.

Carpenter K. 2001. Phylogenetic analysis of the Ankylosauria. *In*: Carpenter K. (Ed.), *The Armored Dinosaurs*. Indiana University Press, Bloomington: 455-483.

Carpenter K. 2007. How to make a fossil: Part 1. Fossilizing bone. *Journal of Paleontological Sciences*, 2007(1): 1-10.

Carpenter K. 2010. Species concepts in North American stegosaurs. *Swiss Journal of Geosciences*, 103(2): 155-162.

Carpenter K. 2013. History, sedimentology, and taphonomy of the Carnegie Quarry, Dinosaur National Monument, Utah. *Annals of Carnegie Museum*, 81: 153-232.

Carpenter K. & Galton P. M. 2001. Othniel Charles Marsh and the myth of the eight-spiked *Stegosaurus*. *In*: Carpenter K. (Ed.), *The Armored Dinosaurs*. Indiana University Press, Bloomington: 76-102.

Carpenter K. & Galton P. M. 2018. A photo documentation of bipedal ornithischian dinosaurs from the Upper Jurassic Morrison Formation, USA. *Geology of the Intermountain West*, 5: 167-207.

Carpenter K. & Lamanna M. C. 2015. The braincase assigned to the ornithopod dinosaur *Uteodon* McDonald, 2011, reassigned to *Dryosaurus* Marsh, 1894 - implications for iguanodontian morphology and taxonomy. *Annals of the Carnegie Museum*, 83: 149-165.

Carpenter K. & Small B. 1993. New evidence for plate arrangement in *Stegosaurus stenops* (Dinosauria). *Journal of Vertebrate Paleontology*, 13 (Supplement to number 3): 28A-29A.

Carpenter K. & Wilson Y. 2008. A new species of *Camptosaurus* (Ornithopoda: Dinosauria) from the Morrison Formation (Upper Jurassic) of Dinosaur National Monument, Utah, and a biomechanical analysis of its forelimb. *Annals of Carnegie Museum*, 76: 227-263.

Carpenter K., Miles C. A. & Cloward K. 2001. New primitive stegosaur from the Morrison Formation, Wyoming. *In*: Carpenter K. (Ed), *The Armored Dinosaurs*. Indiana University Press, Bloomington: 55-75.

Carpenter K., Sanders F., McWhinney L. A. & Wood L. 2005. Evidence for predator-prey relationships. Examples for *Allosaurus* and *Stegosaurus*. *In:* Carpenter K. (Ed.), *The Carnivorous Dinosaurs*. Indiana University Press, Bloomington: 325-350.

Carroll R. L. 1988. *Vertebrate Paleontology and Evolution*. Freeman & Co., New York, xiv + 698 pp.

Chure D.J., Litwin R., Hasiotis S.N.T., Evanoff E. & Carpenter K. 2006. The fauna and flora of the Morrison Formation: 2006. *New Mexico Museum of Natural History and Science Bulletin*, 36: 233-249.

Chure D. J. & McIntosh J. S. 1990. Stranger in a strange land: A brief history of the paleontological operations at Dinosaur National Monument. *Earth Sciences History*, 9(1): 34-40.

Colbert E. H. 1962. *Dinosaurs. Their Discovery and Their World*. Hutchinson & Co., Ltd., London, 288 pp.

Colbert E. H. 1968. *Men and Dinosaurs. The Search in Field and Laboratory*. E. P. Dutton & Co., Inc., New York, xviii + 283 pp.

Colbert E.H. 1981. A primitive ornithischian dinosaur from the Kayenta Formation of Arizona. *Museum of Northern Arizona Press Bulletin Series*, 33: vii + 61.

Company J., Pereda Suberbiola X. & Ruiz-Omeñaca J. I. 2010. New stegosaurian (Ornithischia, Thyreophora) from Jurassic-Cretaceous transition beds of Valencia province (Southwestern Iberian Range, Spain). *Journal of Iberian Geology*, 36: 243-252.

Costa F. & Mateus O. 2019. Dacentrurine stegosaurs (Dinosauria): A new specimen of *Miragaia longicollum* from the Late Jurassic of Portugal resolves taxonomical validity and shows the occurrence of the clade in North America. *PLos ONE*, 14(11):e0224263. https://doi.org10.1371/journal.pone.0224263

Czerkas S. A. 1987. A reevaluation of the plate arrangement on *Stegosaurus stenops*. *In*: Czerkas S. J. & Olson E. C. (Eds), *Dinosaurs Past and Present, Volume 2*. University of Washington Press, Seattle: 83-99.

Czerkas S. J. & Glut D. F. 1982. *Dinosaurs, Mammoths, and Cavemen. The Art of Charles R. Knight*. E. P. Dutton. Inc., New York, 120 pp.

Dahlgren C. 1920. *Dinosaurs and Prehistoric Animals* (not seen).

Davitashvili L. 1961. [*The Theory of Sexual Selection*.] Izdatel'stvo Akademia Nauk SSSR, Moscow. (In Russian)

Demko T. M., Currie B. S. & Nicoli K. A. 2004. Regional paleoclimatic and stratigraphic implications of paleosols and fluvial/overbank architecture in the Morrison Formation (Upper Jurassic), Western interior, USA. *Sedimentary Geology*, 167(3): 115-135.

Dong Z.-M. 1973. [Dinosaurs from Wuerho.] *Institute of Paleontology and Paleoanthropology Memoir*, Beijing, 11: 45-52. (In Chinese)

Dong Z.-M. 1990. Stegosaurs of Asia. *In*: Carpenter K. & Currie P.J. (Eds), *Dinosaur Systematics: Approaches and Perspectives*. Cambridge University Press, Cambridge: 255-268.

Dong Z.-M., Zhou S.-W. & Zhang X. 1983. [Dinosaurs from the Jurassic of Sichuan.] *Palaeontologica Sinica,* Beijing, 162 (C23): 1-151. (In Chinese with English summary)

Doyle A. C. 1912. *The Lost World*. Hodder & Stoughton, New York: 319 pp.

Douglass G. E. 2009. *Speak to the Earth and it will teach you: The Life and Times of Earl Douglass, 1862-1931*. BookSurge Publishing, Charleston: 449 pp.

Escaso F., Ortega F., Dantas P., Malafaia E., Pimentel N. L., Pereda Suberbiola X., Sanz J. L., Kullburg J. C., Kullburg M. C. & Barriga F. 2007. New evidence of shared dinosaur across Upper Jurassic Proto-North Atlantic: *Stegosaurus* from Portugal. *Naturwissenschaften*, 94: 367-374.

Esplin R. 2017. Digitizing Dinosaur National Monument's Carnegie Quarry. *All Theses and Dissertations, Brigham Young University*, 6647: 1-45. https//scholarsarchive.byu.edu/etd/6647

Evanoff E. & Carpenter K. 1998. History, sedimentology, and taphonomy of Felch Quarry 1 and associated sandbodies, Morrison Formation, Garden Park, Colorado. *Modern Geology*, 22: 145-169.

Farlow J. O. 2007. A speculative look at the paleoecology of large dinosaurs of the Morrison Formation, or, life with *Camarasaurus* and *Allosaurus*. *In*: Kvale E. P., Brett-Surman M. K. & Farlow J. O. (Eds), *Dinosaur Paleoecology and Geology: The Life and Times of Wyoming's Jurassic Dinosaurs and Marine Reptiles*. GeoScience Adventures Workshop, Shell, Wyoming: 98-151.

Farlow J. O., Thompson C. V. & Rosner D. E. 1976. Plates of the dinosaur *Stegosaurus*: forced convection heat loss fins? *Science*, 192: 1123-1125.

Farlow J. O., Hayashi S. & Tattersall G. J. 2010. Internal vascularity of the dermal plates of *Stegosaurus* (Ornithischia, Thyreophora). *Swiss Journal of Geosciences*, 103: 173-185.

Fastovsky D. E. & Weishampel D. B. 2005. *The Evolution and Extinction of the Dinosaurs*. Second Edition. Cambridge University Press, New York: xiii + 485 pp.

Ford T. L. 1997. How to draw dinosaurs. *Stegosaurus*. *Prehistoric Times*, 22: 22-23.

Ford T. L. 2000. A review of ankylosaur osteoderms from New Mexico and a preliminary review of ankylosaur armor. *New Mexico Museum of Natural History and Science Bulletin*, 17: 157-176.

Ford T. L. 2006. How to draw dinosaurs. Stegosaurs: plates, splates and spikes, Part 2. *Prehistoric Times*, 77: 20-21.

Foster, J. R. 2003. Paleoecological analysis of the vertebrate fauna of the Morrison Formation (Upper Jurassic), Rocky Mountain region, USA. *New Mexico Museum of Natural History and Science Bulletin*, 23: 1-95.

Foster J. R. 2007. *Jurassic West. The Dinosaurs of the Morrison Formation and their World*. Indiana University Press, Bloomington, 387 pp.

Galton P. M. 1974. The ornithischian dinosaur *Hypsilophodon* from the Wealden of the Isle of Wight. *British Museum (Natural History) Geology, Bulletin*, 25(1): 1-152c.

Galton P. M. 1980. Partial skeleton of *Dracopelta zbyszewskii* n. gen. and n. sp., an ankylosaurian dinosaur from the Upper Jurassic of Portugal. *Géobios*, 13: 451-457.

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: 1-25.

Galton P. M. 1985. British plated dinosaurs (Ornithischia, Stegosauridae). *Journal of Vertebrate Paleontology*, 5: 211-254.

Galton P. M. 2001. Endocranial casts of the plated dinosaur *Stegosaurus* (Upper Jurassic, Western USA): A complete undistorted cast and the original specimens of Othniel Charles Marsh. *In*: Carpenter K. (Ed.), *The Armored Dinosaurs*. Indiana University Press, Bloomington: 455-484.

Galton P. M. 2010. Species of plated dinosaur *Stegosaurus* (Morrison Formation, Late Jurassic) of western USA: new type species designation needed. *Swiss Journal of Geosciences*, 103: 187-198.

Galton P. M. 2011. Case 3536. *Stegosaurus* Marsh, 1877 (Dinosauria, Ornithischia): proposed designation of *Stegosaurus stenops* Marsh, 1887 as the type species. *Bulletin of Zoological Nomenclature*, 68(2): 127-133.

Galton P. M. 2012. Stegosaurs. *In*: Brett-Surman M. K., Holtz T. R. Jr. & Farlow J. O. (Eds), *The Complete Dinosaur.* 2nd ed., Indiana University Press, Bloomington: 482-504.

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, Abhandlung*, 282(1): 1-25.

Galton P. M. 2019. Earliest record of an ankylosaurian dinosaur (Ornithischia: Thyreophora): Dermal armor from Lower Kota Formation (Lower Jurassic) of India. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlung*, 291(2): 205-219.

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, Abhandlung*, 279(2): 185-208.

Galton P. M. & Upchurch P. 2004. Stegosauria. *In*: Weishampel D. B., Dodson P. & Osmólska H. (Eds), *The Dinosauria,* 2nd ed., University of California Press, Berkeley: 343-362.

Geare R. I. 1910. Some extinct animals. *Outdoor Life*, Winter Park, Florida, 25(1): 6-11.

Gertsch L. 1994. Dinosaur tail dynamics. *Wyoming Geological Association Annual Field Conference Guidebook*, 44: 25-38.

Gilmore C. W. 1912. Remarks on the skeleton of the dinosaur, *Stegosaurus*. *Science*, 35(912): 972.

Gilmore C. W. 1914. Osteology of the armoured Dinosauria in the United States National Museum, with special reference to the genus *Stegosaurus*. *United States National Museum, Bulletin*, 89: 1-143.

Gilmore C. W. 1915. A new restoration of *Stegosaurus*. *United States National Museum, Proceedings*, 49(2110): 355-357.

Gilmore C. W. 1918. A newly mounted skeleton of the armored dinosaur, *Stegosaurus stenops*, in the United States National Museum. *United States National Museum, Proceedings*, 54(2211): 383-390.

Gilmore C. W. 1920. Reptile reconstructions in the United States National Museum. *Smithsonian Institution*, *Annual Report,* 1918: 271-280.

Gilmore C. W. 1932. On a newly mounted skeleton of *Diplodocus* in the United States Museum. *United States National Museum, Proceedings*, 81(8): 1-21.

Gregory J. T. 1957. Richard Swan Lull. Vertebrate paleontologist. *Science*, 126: 604-605.

Halstead L. B. 1975. *The Evolution and Ecology of Dinosaurs*. Peter Lowe, London.

Hatcher J. B. 1901. The Jurassic dinosaur deposits near Garden Park, Colorado. *Annals of the Carnegie Museum*, 1: 327-341.

Haubold H. 1990. En neuer Dinosaurier (Ornithischia, Thyreophora) aus dem Unteren Jura des Nordlichen Mitteleuropa. *Revue de Paléobiologie*, 9(1): 149-177.

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. & Suzuki D. 2009. Different growth patterns between the skeleton and osteoderms of *Stegosaurus* (Ornithischia: Thyreophora). *Journal of Vertebrate Paleontology*, 29(1): 123-131.
Hayashi S., Carpenter K., Watabe M., Scheyer T. M. & Suzuki D. 2010. Function and evolution of ankylosaur dermal armor. *Acta Palaeontologica Polonica*, 55(2): 213-228.
Hayashi S., Carpenter K., Watabe M. & McWhinney L. A. 2012. Ontogenetic histology of *Stegosaurus* plates and spikes. *Palaeontology*, 55(1): 145-161.
Hayashi S., Redelstorff R., Mateus O., Watabe M. & Carpenter K. 2014. Gigantism of stegosaurian osteoderms. *Society of Vertebrate Paleontology, Program and Abstracts,* 2014: 145.
Holland W. J. 1931. Earl Douglass. A sketch in appreciation of his life and work. Carnegie Museum Annals, 20: 279-292.
Horner J. R. & Marshall C. 2002. Keratinous covered dinosaur skulls. *Journal of Vertebrate Paleontology,* 22 (Supplement to no. 3): 67A.
Hotton N. III. 1963. *Dinosaurs*. Pyramid Publications, New York.
Hutchinson H. N. 1892. *Extinct Monsters*. Chapman & Hall, London, 1st ed: xv + 270 pp.
Hutchinson H. N. 1893. *Extinct Monsters*. Chapman & Hall, London, 2nd ed: xv + 270 pp.
Hutchinson H. N. 1897. *Extinct Monsters*. Chapman & Hall, London, 5th ed: xxii + 270 pp
Hutchinson H. N. 1911. *Extinct Monsters and Creatures of Other Days.* Chapman & Hall, London, New ed: xiv + 329 pp.
ICZN 2013. Opinion 2320 (Case 3536) *Stegosaurus* Marsh, 1877 (Dinosauria, Ornithischia): type species replaced with *Stegosaurus stenops* Marsh, 1887. *Bulletin of Zoological Nomenclature*, 70(2): 129-130.
Kay J. L. 1940. Behold the mighty dinosaur. *The Carnegie Magazine*, 14: 211-215.
Kilbourne B. & Carpenter K. 2005. Redescription of *Gargoyleosaurus parkpinorum*, a polacanthid of Albany County, Wyoming. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlung*, 237(1): 111-160.
Kinneer B., Carpenter K. & Shaw A. 2016. Redescription of *Gastonia burgei* (Dinosauria: Ankylosauria, Polacanthidae), and description of a new species. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlung*, 262(1): 37-80.
Kirkland J. I. & Carpenter K. 1994. North America's first pre-Cretaceous ankylosaur (Dinosauria) from the Upper Jurassic Morrison Formation of eastern Colorado. *Brigham Young University Geological Studies*, 40: 25-42.
Kirkland J. I., Carpenter K., Hunt A. P. & Scheetz R. D. 1998. Ankylosaur (Dinosauria) specimens from the Upper Jurassic Morrison Formation. *Modern Geology*, 23: 145-177.
Kohl M. F. & McIntosh J. S. 1997. *Discovering Dinosaurs in the Old West. The Field Journals of Arthur Lakes*. Smithsonian Institution Press, Washington DC: xvii + 198 pp.
Kulpe H. R. 1905. *Nebula to Man*. Dent & Co., London: vii + 251 pp.
Lancaster E. R. 1905. *Extinct Animals*. Henry Holt & Co., New York: xxiii + 331 pp.
Lewis G. E. 1946. Memorial to Charles Whitney Gilmore. *Proceedings of the Geological Society of America*, 1945: 235-243.
Lucas F. A. 1900-1904. *Stegosaurus*. 36 pp., Unpublished MS in USNM Archives (also in YPM VP Archives, received 1907).
Lucas F. A. 1901a. *Animals of the Past*. McClure, Phillips & Co., New York: xx + 258 pp.
Lucas F. A. 1901b. The dinosaurs or terrible lizards. *Annual Report of the Board of Regents of the Smithsonian Institution*, 1901: 641-647.
Lucas F. A. 1902. *Animals before Man in North America. Their Lives and Times*. Appleton & Co., New York: vii + 291 pp.
Lucas F. A. 1910a. The armour of *Stegosaurus*. *Nature*, London, 85: 73.
Lucas F. A. 1910b. Arrangement of plates in *Stegosaurus*. *Science Progress in the Twentieth Century*, London, 5: 682 (short abstract of 1910a).
Lucas F. A. 1933. *Fifty Years of Museum Work. Autobiography, Unpublished Papers, and Bibliography*. American Museum of Natural History, New York: x + 81 pp.
Lull R. S. 1910a. The armor of *Stegosaurus*. *American Journal of Science*, (4) 29: 201-210.
Lull R. S. 1910b. *Stegosaurus ungulatus* Marsh, recently mounted at the Peabody Museum of Yale University. *American Journal of Science*, (4) 30: 361-377.
Lull R. S. 1912. The armored dinosaur *Stegosaurus ungulatus*, recently restored at Yale University. *Verhandlungen des VIII Internationalen Zoologen-Kongresses zu Graz vom 15-20 August 1910*: 672-681.
Lull R. S. 1919a. Review of Gilmore (1914, 1918). *American Journal of Science*, (4), 47: 236-238.
Lull R. S. 1919b. Review of Gilmore (1914, 1918). *Nature*, 95: 276-277.
Lull R. S. 1929. *Organic Evolution*. Macmillan, New York, 2nd ed: xiv + 743 pp.
Madsen J. H., Jr. 1973. On skinning a dinosaur. *Curator*, 16(3): 225-266.
Madsen J. H., Jr. 1976. *Allosaurus fragilis*. A revised osteology. *Utah Geological and Mineral Survey, Bulletin*, 109: xii + 50 pp.
Madsen J. H., Jr. 1987. The dinosaur department store. *In*: Averett W. R. (Ed.), *Paleontology and Geology of the Dinosaur Triangle, Guidebook for Field Trip*, Museum of Western Colorado, Grand Junction: 65-74.
Madsen J. H., Jr. & Welles S. P. 2000. *Ceratosaurus* (Dinosauria, Theropoda). A revised osteology. *Utah Geological Survey, Miscellaneous Publication,* 00-2: 1-80.
Maidment S. C. R. 2010. Stegosauria: a historical review of the body fossil record and phylogenetic relationships. *Swiss Journal of Geosciences*, 103: 199-210.
Maidment S. C. R. & Wei G. 2006. A review of the Late Jurassic stegosaurs (Dinosauria, Stegosauria) from the People's Republic of China. *Geological Magazine*, 143: 621-634.
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., Brassey C. & Barrett P. M. 2015. The post-cranial skeleton of an exceptionally complete individual of the plated dinosaur *Stegosaurus stenops* (Dinosauria: Thyreophora) from the Upper Jurassic Morrison Formation of Wyoming, U.S.A. *PloS ONE* 10(10):e0138352. doi:10.1271/journal.pone.0138352

Maidment S. C. R., Woodruff C. D. & Horner J. R. 2018. A new specimen of the ornithischian dinosaur *Hesperosaurus mjosi* from the Upper Jurassic Morrison Formation of Montans, U.S.A., and implications for growth and size in Morrison stegosaurs. *Journal of Vertebrate Paleontology*, DOI: 10.1080/02724634.2017.1406366.

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: 291-314.

Mallison H. 2011. Defensive capabilities of *Kentrosaurus aethiopicus* Hennig 1915. *Palaeontologia Electronica*, 14(2) 10A: 25 pp.

Marsh O. C. 1877. A new order of extinct Reptilia (Stegosauria) from the Jurassic of the Rocky Mountains. *American Journal of Science*, (3) 14: 34-35.

Marsh O. C. 1878. Principle characters of American dinosaurs, Part I. *American Journal of Science*, (3) 16: 411-416.

Marsh O. C. 1879. Notice of new Jurassic reptiles. *American Journal of Science*, (3) 18: 501-505.

Marsh O. C. 1880. Principal characters of American Jurassic dinosaurs. Part III. *American Journal of Science*, (3) 19: 253-259.

Marsh O. C. 1881a. Principal characters of American Jurassic dinosaurs. Part VI: Spinal cord, pelvis, and limbs of *Stegosaurus*. *American Journal of Science*, (3) 21: 167-170.

Marsh O. C. 1881b. Principal characters of American Jurassic dinosaurs. Part V. *American Journal of Science*, (3) 21: 417-423.

Marsh O. C. 1885. Names of extinct reptiles. *American Journal of Science*, (3) 29: 169.

Marsh O. C. 1887. Principal characters of American Jurassic dinosaurs. Part IX: The skull and dermal armor of *Stegosaurus*. *American Journal of Science*, (3) 34: 413-417.

Marsh O. C. 1891a. Restoration of *Stegosaurus*. *American Journal of Science*, (3) 42: 179-181, pl. 9.

Marsh O. C. 1891b. Restoration of *Stegosaurus*. *Geological Magazine*, (3) 8: 385-387, pl. 11.

Marsh O. C. 1892. Notes on Mesozoic vertebrate fossils. *American Journal of Science*, (3) 44: 171-176.

Marsh O. C. 1894. The typical Ornithopoda of the American Jurassic. *American Journal of Science*, (3) 48: 85-90.

Marsh O. C. 1896. The dinosaurs of North America. *United States Geological Survey 16th Annual Report*, 1894-95: 133-244.

Marsh O. C. 1897. Vertebrate fossils of the Denver Basin. *United States Geological Survey Monograph*, 27: 473-527.

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,* B, 276: 1815-1821.

McCarren M. J. 1993. *The Scientific Contributions of Othniel Charles Marsh. Birds, Bones and Brontotheres*. Peabody Museum of Natural History, Yale University, New Haven: 66 pp.

McGinnis H. J. 1982. *Carnegie's Dinosaurs*. Carnegie Institute, Pittsburgh: 120 pp.

McIntosh J. S. 1977. *Dinosaur National Monument*. Constellation Phoenix, Inc., Phoenix (no pagination).

McIntosh J. S. 1981. Annotated catalogue of the dinosaurs (Reptilia, Archosauria) in the collections of Carnegie Museum of Natural History. *Bulletin of Carnegie Museum of Natural History*, 18: 1-65.

McWhitney L. A., Rothchild B. M. & Carpenter K. 2001. Posttraumatic chronic osteomyelitis in *Stegosaurus* dermal plates. *In*: Carpenter K. (Ed.). *The Armored Dinosaurs*. Indiana University Press, Bloomington: 141-156.

Miller W. E., Horrocks R. D. & Madsen J. H., Jr. 1996. The Cleveland-Lloyd Dinosaur Quarry, Emery County, Utah: A U.S. natural landmark (including history and a quarry map). *Brigham Young University Geology Studies*, 41: 3-24.

Milner R. 2012. *Charles R. Knight: The Artist who saw through Time*. Abrams, New York: 180 pp.

Neville A. C. 1976. *Animal Asymmetry*. Edward Arnold Publishers, London: 60 pp.

Olshevsky G. & Ford T. L. 1993. [The origin and evolution of the stegosaurs.] *Kyoryugaku Saizensen* (*Dino-Frontline*), Gakken Mook, Tokyo, 4: 65-103. (In Japanese)

Olshevsky G. & Ford T. L. 1995. The origin and evolution of the stegosaurs. *Historical Dinosaurology*, Publications Requiring Research, Buffalo, 1: 1-121.

Osborn H. F. 1931a. *Cope: Master Naturalist*. University of Princeton Press, Princeton: xvi + 741 pp.

Osborn H. F. 1931b. United States Geological Survey unpublished lithographic plates of vertebrate fossils for distribution. *Science*, 74 (1906): 43-44.

Ostrom J. A. & McIntosh J. S. 1966. *Marsh's Dinosaurs. The Collections from Como Bluff*. Yale University Press, New Haven: xvi + 388 pp.

Ostrom J. A. & McIntosh J. S. 1999. *Marsh's Dinosaurs. The Collections from Como Bluff. With a New Forward by Peter Dodson and a Historical Update by Clifford A. Miles and David W. Hamblin*. Yale University Press, New Haven: xxxii + 388 pp.

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.

Owen R. 1877. A monograph on the fossil Reptilia of the Mesozoic formations: part three. *Omosaurus* (continued). *Palaeontological Society Monographs*, 31: 95-97.

Paul G. 1987. The science and art of restoring the life appearance of dinosaurs and their relatives. A rigorous how-to guide. *In*: Czerkas S. J. & Olson E. C. (Eds), *Dinosaurs Past and Present, Volume 2*. University of Washington Press, Seattle: 4-49.

Paul G. 1992. The arrangement of the plates in the first complete *Stegosaurus*, from Garden Park. *Tracks in Time*, Garden Park Paleontological Society, 3(1): 1-2.

Paul G. S. 1996a. *The Complete Illustrated Guide to Dinosaur Skeletons*. Gakken, Tokyo: 100 pp.

Paul G. S. 1996b. The art of Charles R. Knight. *Scientific American*, 274(6): 76-81.

Paul G. 2010. *The Princeton Field Guide to Dinosaurs.* Princeton University Press, Princeton, 1st ed.: 320 pp.

Paul G. 2016. *The Princeton Field Guide to Dinosaurs.* Princeton University Press, Princeton, 2nd ed.: 320 pp.

Peterson J. E., Warnock J. P., Eberhart S. L., Clawson S. R. &

Noto C. R. 2017. New data towards the development of a comprehensive taphonomic framework for the Late Jurassic Cleveland-Lloyd Dinosaur Quarry, Central Utah. *Peer J*. 5:e3368. DOI 10.7717/peerj.3368

Plate R. 1964. *The Dinosaur Hunters Othniel C. Marsh and Edward C. Cope*. David McKay Co., Inc., New York: vi + 281 pp.

Raven T. J. & Maidment S. C. R. 2017. A new phylogeny of Stegosauria (Dinosauria, Ornithischia). *Palaeontology*, 60(3): 401-408.

Reinheimer P. 1939. Vertebrate paleontology. *Annual Report of the Colorado Museum of Natural History*, 1939: 33-35.

Rieppel L. 2015. Prospecting for dinosaurs on the mining frontier: The value of information in America's Gilded Age. *Social Studies of Science,* 2015: 1-26.

Romer A. S. 1933. *Vertebrate Paleontology.* University of Chicago Press, Chicago, 1st ed: vii . 491 pp.

Romer A. S. 1945. *Vertebrate Paleontology.* University of Chicago Press, Chicago, 2nd ed.: x + 687 pp.

Romer A. S. 1956. *Osteology of the Reptiles*. University of Chicago Press, Chicago: xxi + 772 pp.

Romer A. S. 1966. *Vertebrate Paleontology.* University of Chicago Press, Chicago, 3rd ed.: x + 468 pp.

Rye R. 2014. A *Stegosaurus* built to last. *Digging the fossil record: Paleobiology at the Smithsonian:* 1-7. http:/nmnh.typepad.com/Smithsonian_fossils/2014/06/a-stegosaurus-built-to-last.html

Saitta E. T. 2015. Evidence for sexual dimorphism in the plated dinosaur *Stegosaurus mjosi* (Ornithischia, Stegosauria) from the Morrison Formation (Upper Jurassic) of western USA. *PLoS ONE*, 10(4): e0123503. doi:10.1371/journal.pone.0123503

Scheyer T. M. & Sander P. M. 2004. Histology of ankylosaur osteoderms: Implications for systematics and function. *Journal of Vertebrate Paleontology*, 24(4): 874-893.

Schuchert C. & LeVene C. M. 1940. *O. C. Marsh: Pioneer of Paleontology*. Yale University Press, New Haven: 541 pp. [Reprint 1978, Arno Press, New York]

Seidel M. R. 1979. The osteoderms of the American Alligator and their functional significance. *Herpetologica*, 35(4): 375-380.

Siber H. J. & Möckli U. 2009. *The Stegosaurs of the Sauriermuseum Aathal*. Sauriermuseum Aathal, Aathal: 58 pp.

Smith Woodward A. 1909. The relations of paleontology to other branches of science. *International University Lectures at the Congress of Arts and Science, Universal Exposition*, *Saint Louis, 1904*, 5: 81-102.

Spassov N. B. 1982. The bizarre dorsal plates of *Stegosaurus*: Ethological approach. *Comptes Rendus de l'Académie Bulgare des Sciences*, 35(3): 367-370.

Stokes W. L. 1945. A new quarry for Jurassic dinosaurs. *Science*, 101: 115-117.

Stokes W. L. 1985. *The Cleveland-Lloyd Dinosaur Quarry - Window to the Past*. U.S. Government Printing Office, 1985-0-576-423, 27 pp.

Sues H. & Marsh D. 2015. Charles Whitney Gilmore - the forgotten "Dinosaur hunter". http//paleobiology.si.edu/history/Gilmore.html

Switek B. 2012. The fastastic gliding *Stegosaurus*. www.smithsonianmag.com/science-nature/the-fantastic-gliding-stegosaurus-107838cience

Thompson R. S., Parish J. C., Maidment S. C. R. & Barrett P. M. 2012. Phylogeny of the ankylosaurian dinosaurs (Ornithischia: Thyreophora). *Journal of Systematic Palaeontology*, 10(2): 301-312.

Townsend C. H. 1930. In memoriam: Frederick Augustus Lucas. Born March 25, 1852 - died February 9, 1929. *The Auk*, 47: 147-158.

Trujillo K. C. & Kowallis B. J. 2015. Recallibrated legacy 40Ar/39Ar ages for the Upper Jurassic Morrison Formation, Western Interior, USA. *Geology of the Intermountain West*, 2: 1-8.

Turner C. E. & Peterson F. 1999. Biostratigraphy of dinosaurs in the Upper Jurassic Morrison Formation of the western interior, U.S.A. *Utah Geological Survey Miscellaneous Publication*, 99-1: 77-114.

Turner C. E. & Peterson F. 2004. Reconstruction of the Upper Jurassic Morrison Formation extinct ecosystem - a synthesis. *Sedimentary Geology*, 204: 309-355.

Wallace D. R. 1999. *The Bonehunters' Revenge. Dinosaurs, Greed, and the Scientific Feud of the Golden Age*. Houghton Mifflin Co., New York: xiv + 366 pp.

White T. E. 1964. The dinosaur quarry. *Thirteenth Annual Field Conference, Intermountain Association of Petroleum Geologists*, Tulsa: 21-28.

Young J. Z. 1950. *Life of the Vertebrates*. Clarendon Press, Oxford, 1st ed: xvi + 767 pp.