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Species of plated dinosaur *Stegosaurus* (Morrison Formation, Late Jurassic) of western USA: new type species designation needed

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Abstract *Stegosaurus armatus* Marsh 1877, based on a partial tail and a very large dermal plate from the Morrison Formation (Late Jurassic) of Morrison, Wyoming, USA, is a *nomen dubium*. Valid Morrison stegosaur species (with possible autapomorphies, dermal "armor" considered if present), with most holotypes consisting of a disarticulated partial postcranial skeleton at most, include: *Hypsirhophus discurus* Cope 1878 (characters of incomplete vertebrae, a dorsal and a caudal; Garden Park near Cañon City, Colorado); *Stegosaurus ungulatus* Marsh 1879 (half skeleton with partial skull; three pairs of small flat dermal spines adjacent to terminal tail spikes; Quarry 12, Como Bluff near Como station, Wyoming; syntype is holotype of *S. duplex* Marsh 1887, half skeleton lacking armor; Quarry 11, Como Bluff); *Diracodon laticeps* Marsh 1881b (just partial dentaries with few teeth, diastema between predentary and tooth 1; Quarry 13, Como Bluff); *Stegosaurus sulcatus* Marsh 1887 (pair of ?tail spikes with greatly enlarged base; Quarry 13, Como Bluff); *S. longispinus* Gilmore 1914 (characters of distal caudal vertebrae, tail spikes: two pairs, sub-equal bases, transversely flattened, very elongate; Alcova, Wyoming); and *Hesperosaurus mjosi* Carpenter, Miles & Cloward, 2001 (?*Stegosaurus mjosi*; partial articulated skeleton with skull, no limbs, several plesiomorphic and autapomorphic characters, dorsal plates longer than tall; Wyoming). However, the well known valid nominal species, *S. stenops* Marsh 1887 (12 autapomorphies, three alternating flat plates adjacent to terminal tail spikes; Garden Park), is based on a virtually complete articulated skeleton lacking only the terminal caudal vertebrae and first pair of tail spikes. It includes 17 dermal plates, is still exposed as preserved on the block, and is the current basis for *Stegosaurus*. The International Commission on Zoological Nomenclature (ICZN) will be petitioned to designate *S. stenops* Marsh 1887 as the new type species of *Stegosaurus* Marsh 1877 in order to conserve Stegosauria Marsh 1877 and Stegosauridae Marsh 1880 (also Stegosauroidea, Stegosaurinae).

Keywords Ornithischia · Stegosauria · *Stegosaurus* · *Hesperosaurus* · Late Jurassic · Taxonomy

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Institutional abbreviations

AMNH	American Museum of Natural History, New York, USA
DMNH	Denver Museum of Nature & Science (formerly Denver Museum of Natural History), Colorado, USA
HMNH	Hayashibara Museum of Natural History, Okayama, Japan
MNHM	Morrison Natural History Museum, Morrison, Colorado, USA
SMA	Sauriermuseum Aathal, Switzerland
USNM	National Museum of Natural History (formerly United States National Museum), Washington DC, USA
UW	Department of Geology and Geophysics, University of Wyoming, Laramie, USA

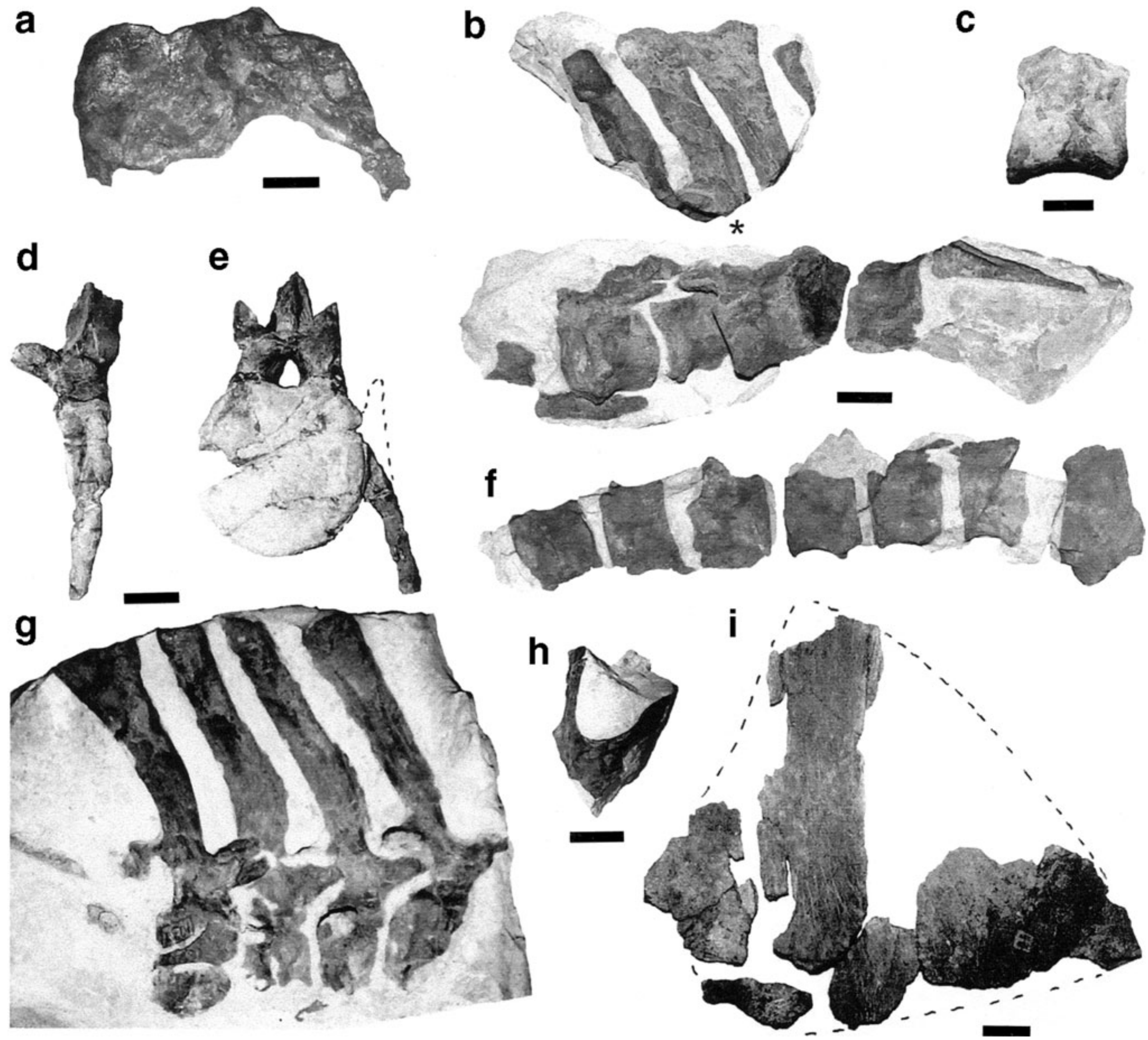


Fig. 1 *Stegosaurus armatus* Marsh 1877, part of holotype YPM 1850, from the Morrison Formation (Kimmeridgian–Tithonian) of Wyoming, USA. Vertebrae from proximal half of tail (order passing distally: **a**, **d**, **e**, **g**, **b**, **f**), dorsal vertebrae (**c**, **h**), and a large dermal plate (**i**). **a** First or second caudal vertebra. **b** Caudals with neural spines and centra, some with chevrons, in right lateral view, * indicates where these two blocks fit together (M.T. Mossbrucker, pers. comm. 2009). **c** Partially prepared dorsal centrum in lateral view. **d**, **e** Caudal in left lateral (**d**) and anterior (**e**) views. **f** Caudal centra in left lateral view. **g** Four almost complete caudals in right lateral view. **h** Partial neural spine and transverse process of a dorsal vertebra in anterior or posterior view. **i** Fragments of a large dermal plate, probably from above the pelvic region or at base of tail. Modified from Carpenter and Galton (2001). *Scale bars* 10 cm

YPM Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA

Introduction

Stegosauria is a clade of quadrupedal, herbivorous ornithischian dinosaurs with a bizarre array of dermal plates and spines extending along the body from the neck to the end of the tail (Galton 1990; Sereno and Dong 1992; Galton and Upchurch 2004; Maidment et al. 2008). The best known genus is *Stegosaurus* Marsh 1877 from the Morrison Formation (Late Jurassic, Kimmeridgian–Tithonian; Turner and Peterson 1999; Foster 2007) of western USA, the basis for Stegosauria Marsh 1877, Stegosauroidea (Marsh 1880) Hay 1902, Stegosauridae Marsh 1880, and Stegosaurinae (Marsh 1880) Abel 1919. However, the

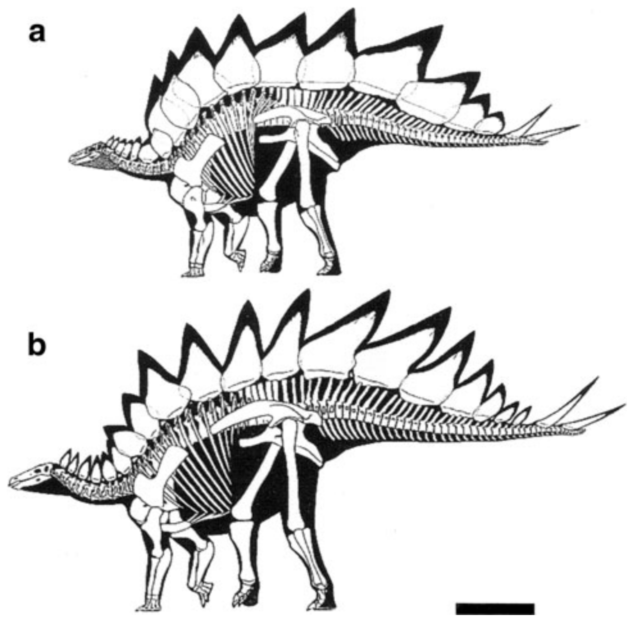


Fig. 2 Skeletal reconstructions of two *Stegosaurus* species (at same scale of reduction) from the Morrison Formation (Kimmeridgian–Tithonian), USA. **a** *Stegosaurus stenops* Marsh 1887, based on holotype USNM 4934 from Colorado and referred specimen USNM 4714 from Wyoming (see Figs. 3s, t; 4). **b** *Stegosaurus ungulatus* Marsh 1879, mostly based on syntypes YPM 1853 and 1858 from Wyoming (see Carpenter and Galton 2001 for details). *Courtesy* of Gregory Paul (who retains the copyright). *Scale bar* 100 cm

type species, *S. armatus* Marsh 1877, is based on a very incomplete holotype specimen that was first figured by Carpenter and Galton (2001).

Specimens from outside of North America have recently been included in *Stegosaurus* with Escaso et al. (2007) referring a partial skeleton, from the Late Jurassic of Portugal, to *S.* cf. *ungulatus*. Also Maidment et al. (2008) referred *Wuerhosaurus homheni* Dong 1973 (Early Cretaceous, Wuerho, China; Dong 1973, 1990) to *Stegosaurus*, as *S. homheni* (Dong 1973), a referral disputed by Carpenter (2010). However, these referrals are beyond the scope of this paper that will briefly review the holotypes of the Morrison stegosaurian species. The purpose is to show that, firstly, *S. armatus* Marsh 1877 is a *nomen dubium* and, secondly, that
S. stenops Marsh 1887 is the most suitable taxon to be designated as the new type species of *Stegosaurus* Marsh 1877.

Systematic palaeontology: review of the holotypes of the Morrison stegosaurian species

Stegosaurus armatus Marsh 1877 (Fig. 1)

The holotype of *Stegosaurus armatus*, YPM 1850, was found in an extremely hard rock layer at Lake's YPM Saurian Quarry 5 near the base as exposed of the type section for the Morrison Formation north of Morrison, Colorado. The stratigraphical position and age for most of the quarries that produced the holotypes of the Morrison stegosaurs are indicated by Turner and Peterson (1999, fig. 7). YPM 1850 was first described by Carpenter and Galton (2001, pp. 81–85; figs. 4.4, 4.5), who provided details on the discovery, occurrence and bones). It includes an anterior caudal vertebra (Fig. 1d, e), but the "several fragmentary vertebrae" of Maidment et al. (2008, p. 11; Carpenter and Galton 2001 was not cited by Maidment et al. 2008) are two incomplete dorsal vertebrae (Fig. 1c, h), a first or second caudal (Fig. 1a), and several blocks containing 17 incomplete articulated caudal vertebrae from the proximal half of the tail (Fig. 1b, f, g). In addition, there is a partial proximal right ischium, a partial femoral shaft, and a fragmentary large dermal plate (Fig. 1i, tallest piece 414 mm), the basis for the species name *armatus* (for details on discovery, occurrence and bones, see Carpenter and Galton 2001, pp. 81–85; figs. 4.4, 4.5). Incomplete bones are exposed on the broken surfaces of numerous small pieces of the extremely hard matrix, the result of reducing the size of larger blocks using dynamite. Consequently, preparation ceased once more complete bones were discovered in much softer rocks in quarries at Garden Park near Cañon City, Fremont County, Colorado and, in particular, at Como Bluff near the old Como station, Albany County, Wyoming (for details on history and quarries see Ostrom and McIntosh 1999; Carpenter and Galton 2001).

Stegosaurus is not the only dinosaurian taxon represented in Quarry 5. Other finds include a series of associated but isolated maxillary teeth of the sauropod *Diplodocus lacustris* (YPM 1922, Marsh 1884; originally referred to *Stegosaurus armatus* by Marsh 1877, 1880), an ungual phalanx of the sauropod *Apatosaurus ajax* (M.T. Mossbrucker, pers. comm. 2009), other bones of sauropods, and an incomplete theropod tibia (Carpenter and Galton 2001).

One result of further preparation of the blocks of YPM 1850 at the MNHM is that two of the blocks now fit together (Fig. 1b; M.T. Mossbrucker, pers. comm. 2009). In addition, the MNHM has recently recovered many large blocks that originally came from the bone-bearing layer (M.T. Mossbrucker, pers. comm. 2009).

Based on a cladistic analysis of all stegosaurian species considered by them to be valid, Maidment et al. (2008, p. 377) diagnosed *Stegosaurus* by the following autapomorphies:

1. Quadrate-squamosal-paroccipital process articulation overhangs the retroarticular process of the lower jaw;
2. Postzygapophyses on posterior cervical vertebrae are elongated posteriorly and overhang the back of the centrum;

3. Transverse processes on anterior caudal vertebrae (except for caudals one and two) project ventrally rather than laterally;
4. Large, rectangular acromial process of the scapula;
5. Supra-acetabular process diverges at an angle of 90° from the anterior process of the ilium;
6. Medial process present on the posterior iliac process of the ilium;
7. Alternating rows of dermal armor down the midline (Maidment et al. 2008, p. 404).

Maidment et al. (2008, p. 378) further noted that *Stegosaurus armatus* differs from all other stegosaurs in having:

8. An edentulous portion of the dentary anterior to the tooth row and posterior to the predentary;
9. Dorsally elevated postzygapophyses of cervical vertebrae;
10. Bifurcated summits of neural spines of the anterior and middle caudal vertebrae;
11. Unexpanded posterior end of the pubis;
12. Dermal ossicles embedded in the skin on the underside of the cervical region.

Maidment et al. (2008) regarded *S. armatus* as a species showing a wide range of variation postcranially. However, this is not supported by the variation within the next best-represented stegosaurian species, *Kentrosaurus aethiopicus* Hennig 1915 from the Tendaguru Formation (Late Jurassic) of Tanzania (Hennig 1915, 1925; Galton 1982; Mallison 2010).

Maidment et al. (2008) regarded most of the valid species from the Morrison Formation as junior synonyms of *Stegosaurus armatus* Marsh 1877, with 11 of the 12 characters based on referred specimens, not the holotype. The holotype (YPM 1850) only exhibits character 3 (Figs. 1d, e), an autapomorphy of *Stegosaurus*, so the genus is valid only if it is monospecific. However, Maidment et al. (2008) recognized *Stegosaurus* (*Hesperosaurus*) *mjosi* (Carpenter, Miles & Cloward 2001), which also has character 3 (Carpenter et al. 2001, fig. 3.6K). Consequently, *Stegosaurus armatus* Marsh 1877 is a *nomen dubium*, and *Stegosaurus* is not available as a genus or as the basis for the Stegosaurinae, Stegosauridae, Stegosauroidea or Stegosauria of Marsh (1880), Hay (1902) and Abel (1919). This would also be the case if, as argued by Carpenter (Carpenter et al. 2001; Carpenter 2010), *Hesperosaurus* represents a separate genus from *Stegosaurus*, character 3 being common to both genera.

Maidment et al. (2008, p. 383), with reference to *Stegosaurus longispinus*, discounted characters of the plates and spines as autapomorphies for species of *Stegosaurus* because "dermal armour is likely to be extremely variable depending on age, size and the sex of the animal that bore it." However, one of the autapomorphies listed by Maidment et al. (2008, p. 379) for *Stegosaurus* (*Hesperosaurus*) *mjosi* is "dorsal dermal plates longer anteroposteriorly than tall dorsoventrally". In addition, they diagnosed *Gigantspinosaurus sichuanensis* Ouyang 1992 (Late Jurassic, Zigong, China) by one autapomorphy, the possession of a "parascapular spine that is at least twice the length of the scapula" (Maidment et al. 2008, p. 377; fig. 6B; see Ouyang 1992; Peng et al. 2005). Also one of the autapomorphies used to diagnose the stegosaur *Miragaia longicollum* Mateus, Maidment & Christiansen 2009 (Late Jurassic, Portugal) is "paired, slightly outwardly convex, triangular cervical dermal plates with a notch and projection on the anterodorsal margin" (Mateus et al. 2009, p. 3).

The overall pattern of the bizarre array of plates and spines along the back is presumably characteristic for each species of stegosaur, so it was probably important for the recognition of other individuals of the same species and for sexual display (Carpenter 1998a). Davitashvili (1961) suggested that this was probably the original function of the erect osteoderms and this is supported by the histological studies of Main et al. (2005). The dorsal plates of all stegosaurs are ideally arranged for maximum effect during a lateral display (Spassov 1982). Consequently, differences in form should provide autapomorphic characters for the different species of stegosaurs. However, the possibility of a sexual dimorphism in the form of the plates should not be overlooked.

The other species of Morrison stegosaurs are reconsidered below, within the framework provided by Maidment et al. (2008), and in the chronological order of their erection. When applicable, the dermal plates and spines are also considered for possible autapomorphic characters.

Hypsirophus discurus Cope 1878

The holotype of *Hypsirophus discurus*, AMNH 5731, was excavated from Cope's Quarry 3, Garden Park near Canõn City, Colorado. It consists of a partial middle (Carpenter 1998b, figs. 5A, B, D) or posterior dorsal vertebra [Maidment et al. 2008, fig. 9 as *H. discursus* (*sic*)], a rib fragment, two anterior caudal neural arches (one including neural spine and postzygapophyses, Carpenter 1998b, fig. 5C; other top of a neural spine), and two distal caudal centra. A theropod femur was originally described as part of the same individual (Cope 1878).

Carpenter (1998b, p. 415) noted several differences from dorsal vertebrae of *Stegosaurus stenops*:

1. Circular fossa between postzygapophyses *versus* vertical groove;

2. Median ridge extending from base of postzygapophyses to neural canal *versus* no ridge [a groove in *S. ungulatus* (as *S. armatus*)];
3. In cross-section of pedicel, the anterior surface is convex *versus* being concave (Carpenter 1998b, figs. 5D, E); posterior surface concave in both.

Maidment et al. (2008), who did not cite Carpenter (1998b), referred *Hypsirophus discurus* to *Stegosaurus armatus* because they considered that all characters of the dorsal vertebra lie within the range of variation seen in other specimens of *S. armatus*. The two caudals were not mentioned by Maidment et al. (2008, p. 15) but only character 10 listed above for *S. armatus* is exhibited by *Hypsirhophus discurus* (Carpenter 1998b, fig. 5C). Carpenter (1998b) tentatively accepted *Hypsirophus discurus* Cope 1879 as a valid genus and Maidment et al. (2008) regarded it as a junior synonym of *Stegosaurus armatus*, so both agreed that *discurus* is a valid species.

Hypsirophus seeleyanus Cope 1879

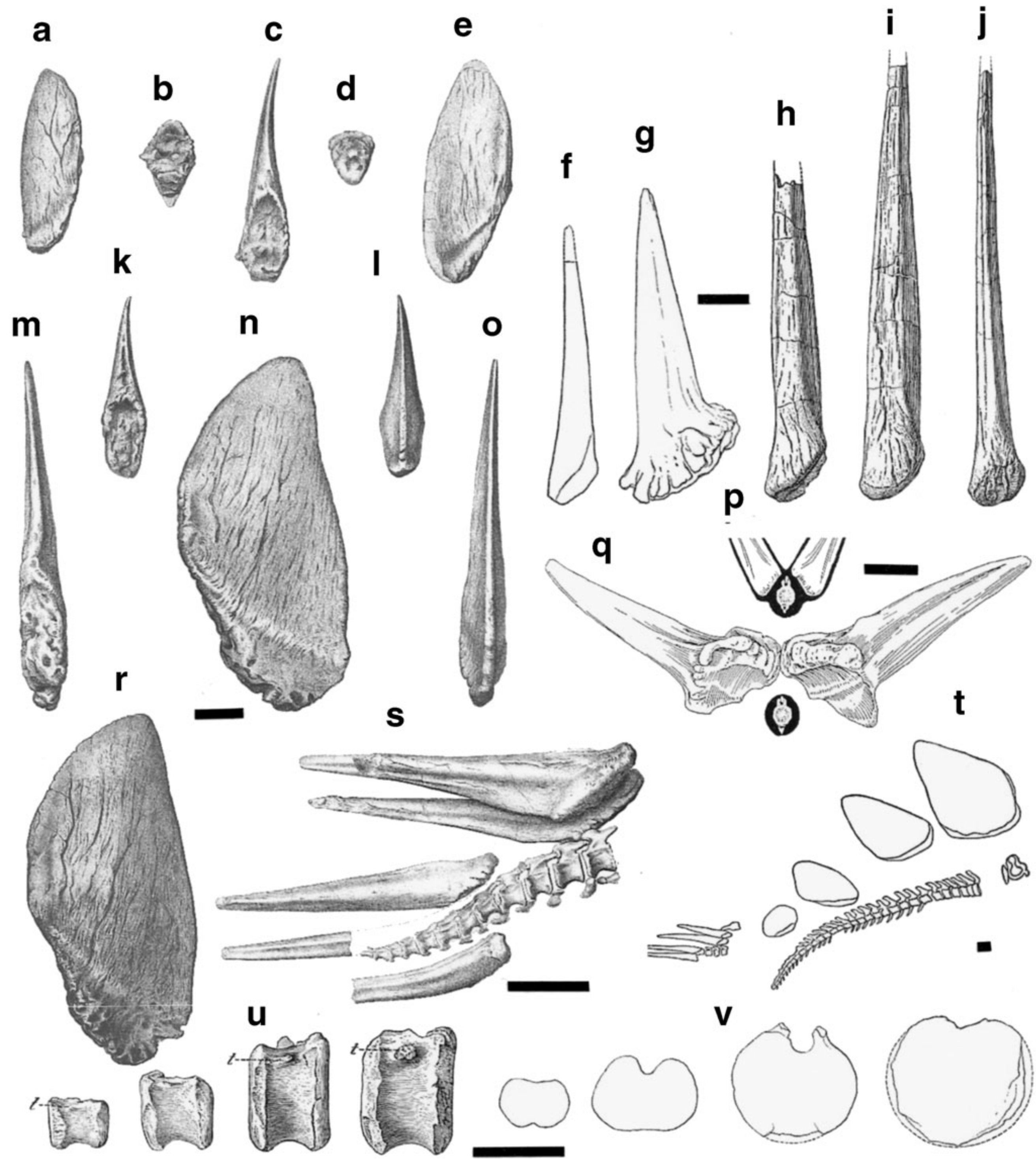
Hypsirophus seeleyanus, based on unillustrated and lost dorsal and caudal vertebrae and a distal femur (theropod teeth also included by Cope 1879), presumably from Colorado, is a *nomen nudum* (Gilmore 1914; Maidment et al. 2008).

Stegosaurus ungulatus Marsh 1879
(Figs. 2b; 3a–e, k–o, r)

Stegosaurus ungulatus is based upon two syntypes (YPM 1853 from Reed's YPM Quarry 12; YPM 1858 from Reed's YPM Quarry 11; both from Como Bluff; for details see Carpenter and Galton 2001, pp. 84–90; figs. 4.6–12; table 4.1). The paralectotype (YPM 1853) includes the posterior part of the skull with an endocranial cast (Galton 2001), dorsal and caudal vertebrae, right humerus, ischium, both femora, tibia, fibula, phalanges of pes, 12 plates and 8 tail spikes (see Marsh 1896; Gilmore 1914; Ostrom and McIntosh 1999). Brown, Beck and Kessler in 1886 excavated other parts of the same individual as YPM 1853 (Carpenter and Galton 2001). USNM 7414 includes rib pieces, a few incomplete caudal vertebrae and a large dermal plate (plate, Carpenter and Galton 2001; another photo including caudals in Glut 1997, p. 845).

The two partial skeletons (YPM 1853, 1858) were combined to form most of the skeleton of the reconstruction of *Stegosaurus ungulatus*: as a drawing in Marsh (1891, 1896; skull from USNM 4934, *S. stenops* holotype) and as the YPM mounted skeleton (Lull 1910a, b; see Carpenter and Galton 2001, figs. 4.2, 4.3; table 4.1 for bones involved including other YPM specimens). In both reconstructions four pairs of tail spikes are shown (also in Bakker 1986, p. 228), long thought to be diagnostic for *S. ungulatus* (YPM 1853). However, there are no field records from other quarries for such a tail, only tails with two pairs of spikes, so YPM 1853 may include the tail spikes from two different individuals (Carpenter and Galton 2001). Although there is no duplication of bones for YPM 1853 and USNM 7414, these may be found if Quarry 12 is ever reopened. YPM 1853 has characters 1, 3, 7, 9 and 10, as listed above for *Stegosaurus* and *S. armatus,* and it represents a valid species (Gilmore 1914; Galton 1990; Galton and Upchurch 2004; Maidment et al. 2008).

The skeletal reconstruction of *Stegosaurus ungulatus* (YPM 1853, 1858, etc.) by Paul has two pairs of tail spikes (Fig. 2b). Note various differences, including the proportionally long ilium and femur and the shape of the dorsal, sacral and caudal plates, that indicate that *S. ungulatus* and *S. stenops* represent separate species (Fig. 2). Here one possible autapomorphy for *S. ungulatus* is discussed, the form of the small flat posterior spines, each with an obliquely inclined base (Figs. 3a–e, k–o, r). Marsh (1891, 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." He previously figured one of them (Marsh 1880, pl. 10, figs. 3a–d as "flat dermal spine"; Marsh 1887, pl. 8, fig. 1 as "dorsal spine"; also Marsh 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). In the current YPM skeleton (remounted in 1925), there are five (with two in plaster) alternating low elongate spines placed just anterior to the tail spikes (Lull 1929, pl. 13; Carpenter and 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 1853, Ostrom and McIntosh 1966, pls. 59-1, 60) suggests that the plates were paired." These plates, the two largest ones of the four (Fig. 3a–e, k–o, r) mentioned by Marsh (1891) are shown and they are almost identical in size when the much more greatly magnified one (Fig. 3r) is reduced to the same scale of reduction as the other one (Fig. 3n). However, they are not identical in shape but mirror images with the former being the right and the latter the left. There is no match for this series of three (or possibly four) flat paired and posterodorsally inclined spines in *S. stenops* (Fig. 2a), either in the tail (Figs. 2a, 3t, 4, see below) or in the neck. Nuchal plates 1–5 of *S. stenops* are small, vertically oriented, and taller than long anteroposteriorly (USNM 4934; Gilmore 1914, pls. 2, 3, 14). Plate 6 is larger but also vertically



oriented with a very short base relative to the size of the plate. A nuchal plate of this form is also present in YPM 1853 (see Marsh 1880, pl. 10, figs. 2a–c; Marsh 1896, pl. 50, figs. 2a–c; Ostrom and McIntosh 1999, pl. 62, figs. 1–3).

Stegosaurus affinis Marsh 1881a

Marsh (1881a) did not figure the inadequately described, unfigured and lost holotype pubis of *Stegosaurus affinis* (Reed's YPM Quarry 13 W, Como Bluff; Ostrom and

◀ **Fig. 3** Dermal spines and plates (**a–t**) and distal caudal vertebrae (**u**, **v**) of *Stegosaurus* from the Morrison Formation (Kimmeridgian–Tithonian), USA. **a–e, k–o, r** *Stegosaurus ungulatus* Marsh 1879, holotype YPM 1853, four flat posterior dermal tail plates at same scale of reduction, from right (**a**, **d**, **k**, **l**; **b**, **c**, **e**, **r**) and left (**m–o**) side, in medial (**a**, **e**, **n**), posterior (**c**, **k**, **m**), anterior (**l**, **o**), ventral (**b**, **d**) and lateral (**r**) views. **f–j** *Stegosaurus* tail spikes at same scale of reduction: *S. stenops*, holotype USNM 4934, right posterior tail spike in medial view (**f**); *S. sulcatus* Marsh 1887, holotype USNM 4937, anterior right tail spike in medial view (**g**); *S. longispinus* Gilmore 1914, holotype UW 20503 (formerly UW D54), pair of anterior spikes (**h–j**), in left lateral (**h**), right medial (**i**) and posterior (**j**) views. **p**, **q** Bases of anterior pair of spikes in anterior view, fitted onto distal tail section at caudal 35 (the position where these spikes occur in USNM 4714, see **s**, **t**), in *S. stenops*, USNM 4934 (**p**) and *S. sulcatus*, USNM 4937 (**q**). **s**, **t** *Stegosaurus stenops*, USNM 4714, in right lateral view, detail of end of tail with tail spikes, basal half of posterior right spike displaced ventrally to show underlying vertebrae (**s**) and distal half of tail as preserved (**t**). **u**, **v** *Stegosaurus longispinus*, holotype UW 20503 (formerly D54), four of 10 preserved distal caudal vertebrae in right lateral (**u**; **t**: transverse process) and anterior or posterior (**v**) views. **a–e**, **k–o**, **r**, **s** from Ostrom and McIntosh (1999), **f–j**, **t–v** from Gilmore (1914) and **p**, **q** from Bakker (1988). *Scale bars* 10 (**a–r**; **u**, **v**) and 5 (**s**, **t**) cm

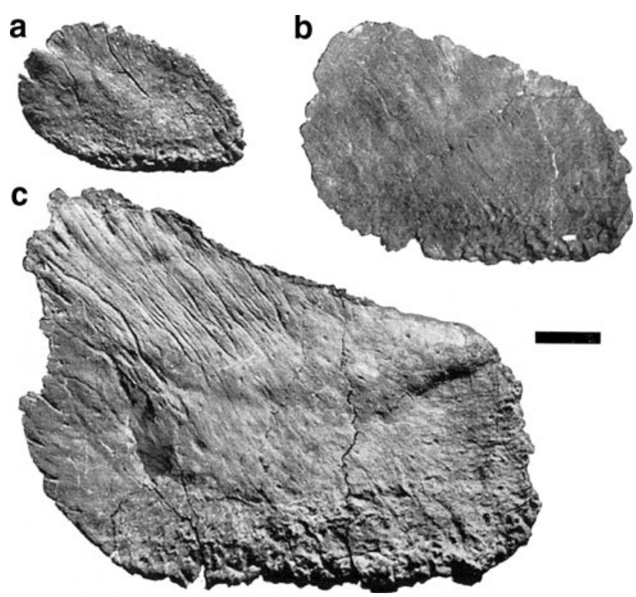


Fig. 4 *Stegosaurus stenops*, referred specimen USNM 4714, from Morrison Formation (Kimmeridgian–Tithonian) of Quarry 13, Como Bluff, Wyomong, USA: last three caudal plates, numbers 15 (**a**), 16 (**b**) and 17 (**c**), viewed from right side (see Fig. 3t), from Gilmore (1914). *Scale bar* 8 cm

McIntosh 1999). No other YPM or USNM specimens were referred to this taxon so it is a *nomen nudum* (Gilmore 1914; Maidment et al. 2008).

Diracodon laticeps Marsh 1881b

The holotype, YPM 1885, was discovered in Reed's YPM Quarry 13W, Como Bluff (Carpenter and Galton 2001). Gilmore (1914, pp. 104, 108, 109) suggested that *Diracodon laticeps* was probably a juvenile individual of *Stegosaurus stenops.* Bakker (1986, figs. on p. 188, 227) resurrected *Diracodon laticeps* for flesh reconstructions based on specimens representing a growth series from Quarry 13 (see Gilmore 1914), a topotypic series he considered diagnosed the taxon, and USNM 4934 (holotype of *S. stenops*). He regarded *Stegosaurus stenops* as a junior synonym of *Diracodon laticeps* with *S. ungulatus* as a valid species (R.T. Bakker, pers. comm. 1987). Galton (1990; also Galton and Upchurch 2004) tabulated *Stegosaurus stenops* Marsh 1887 as including *Diracodon laticeps* Marsh 1881a. Maidment et al. (2008) regarded *Diracodon laticeps* Marsh 1881b as a junior synonym of *Stegosaurus armatus* Marsh 1877. The two incomplete holotypic tooth-bearing bones, the maxillae of Marsh (1881b, 1896; also Gilmore 1914), are actually a pair of dentaries that were first illustrated by Carpenter and Galton (2001). Only character 8 listed above for *S. armatus* is exhibited by YPM 1885 (Carpenter and Galton 2001). However, they considered it to be a valid species (as did Bakker 1986; Galton 1990; Galton and Upchurch 2004; Maidment et al. 2008).

Stegosaurus stenops Marsh 1887
(Figs. 2a; 3f, p, s, t; 4)

The holotype skeleton of *Stegosaurus stenops,* USNM 4934, excavated from Felch's YPM Quarry 1 at Garden Park (Carpenter 1998a), was the subject of a detailed monograph by Gilmore (1914). Gilmore (1914, pls. 2-4; also Czerkas 1987, figs. 2, 3) illustrated the upper and lower surfaces of the block containing the almost complete skeleton as it is still preserved. The bones and the 17 dermal plates are in almost natural articulation, with only five to seven of the most distal caudal vertebrae and three tail spikes missing. Gilmore (1914) described and figured the skull (also Huene 1914; reconstructions in Galton 1990; Sereno and Dong 1992; Ostrom and McIntosh 1999; Galton and Upchurch 2004) and individual postcranial bones.

Maidment et al. (2008, pp. 381–382) discussed the characters proposed by Gilmore (1914) and Galton and Upchurch (2004) to separate *Stegosaurus stenops* from the other species of *Stegosaurus*. They concluded that, as it has no autapomorphies, it is a junior subjective synonym of *S. armatus*. However, characters 1–12 listed above for *Stegosaurus* and *S. armatus* are all present in USNM 4934, the only holotype with characters 8 and 12, and it is considered as a valid species (Gilmore 1914; Galton 1990; Galton and Upchurch 2004; Maidment et al. 2008).

In addition to USNM 4934, there are two other almost complete referred skeletons that, along with the holotype, are stratigraphically from within 10 m of each other (Carpenter 1998a). One of these, DMNS 2818 (excavated in 1992 at Garden Park), has a complete skull and a few of the 17 plates are preserved overlapping each other (for bones as exposed in quarry, see Carpenter 1998a, fig. 2; for other side, Carpenter 2007, fig. 2); it exhibits characters 1, 2, 5, 7, 8 and 12.

Gilmore (1914) equated the five preserved plates of USNM 4714 (Figs. 3t, 4; Quarry 13, Como Bluff, Wyoming; Gilmore 1914, fig. 58, pl. 23, fig. 6, pl. 24, figs. 1–4) with plates 13–17 of USNM 4934 (Gilmore 1914, pls. 2–4). The largest, most anterior plate of the series, 14, is situated over the base of the tail. In both specimens the last three transversely flat plates, unpaired and presumably alternating, show a marked and progressive decrease in size (Figs. 2a, 3t, 4). The tail of DMNS 2818 (Carpenter 1998a, fig. 2; 2007, fig. 2) confirms the correctness of the reconstruction of the tail of *S. stenops* using USNM 4714 (Figs. 2a, 3t). These three flat non-paired plates of *S. stenops* contrast with the three paired flat caudal spines of *S. ungulatus* (Figs. 2b, 3a, e, n, r; YPM 1853).

Stegosaurus sulcatus Marsh 1887 (Fig. 3g, q)

The holotype of *Stegosaurus sulcatus,* USNM 4937, was excavated from Reed's YPM Quarry 13 Middle, Como Bluff (Gilmore 1914; Ostrom and McIntosh 1999; Carpenter and Galton 2001). Marsh (1887, 1896; also in Ostrom and McIntosh 1999, pl. 58, figs. 1–5) figured one large tail spike. Illustrations of this spike, its antimere, a nuchal plate, and the right radius, ulna, and manus were provided by Gilmore (1914, figs. 38, 39, 41.2, 57, 65, pl. 18, pl. 20, figs. 3A, 4A, pl. 21, fig. 2, pl. 25, fig. 3). The manus is described in detail by Senter (2010), who concludes that the metacarpals were posed vertically in a compact semicircular arrangement as in sauropods. The holotype also includes several vertebrae (3 cervical neural arches, 8 cervical centra, 7 dorsal centra, 1 caudal centra), portions of both scapulae (left fused to partial coracoid), right humerus, left radius and partial manus, parts of ischium, femora and fibula, and a mid-dorsal plate (Gilmore 1914).

The spike figured by Marsh (1887, 1896) has two very prominent grooves or sulci along the inner face of the spike, hence the specific name (Fig. 3q). This spike has a very massive base with a very rugose sutural surface medially for the opposite tail spike (Fig. 3g, q). Gilmore (1914, fig. 65) illustrated it in articulation with its antimere that lacks the supposedly diagnostic prominent longitudinal grooves (Fig. 3q; photo, both spikes in Glut 1997, p. 847). He noted that a pair of posterior tail spikes of normal proportions (Gilmore 1914, pl. 25, fig. 3; antimere not illustrated) indicated that the very large spikes could represent the more anterior of the distal tail spikes.

In an articulated tail referred to *Stegosaurus stenops* (USNM 4714; Fig. 3s, t; Gilmore 1914), the anterior pair of spikes fit over caudal vertebra 35 (Fig. 3p). However, Bakker (1988) showed that the curvature of the very large bases of the anterior pair of spikes of *S. sulcatus* was too shallow to occupy this position (Fig. 3q). Consequently, he concluded that the large pair of spikes occupied the base of the neck-shoulder region, but they could equally well be more distally placed nearer to the sacrum. Either way, these spikes do not fit into the pattern of plates and spikes well established for *Stegosaurus stenops* on the basis of articulated specimens (Fig. 2a; USNM 4934, USNM 4714, DMNH 2818).

Because of the greater size of USNM 4937, Gilmore (1914) considered that the differences between *Stegosaurus sulcatus* and *S. ungulatus* were age-related, with the former representing an old individual of the latter species. Maidment et al. (2008) noted that USNM 4937 bears no synapomorphies that allow it to be referred to any of the species of *Stegosaurus* and, as no unique characters or character combinations were identified, they considered *S. sulcatus* to be a *nomen dubium* with USNM 4937 as Stegosauria indet. However, USNM 4937 exhibits character 4 in the *Stegosaurus* list given above and the greatly enlarged base of the "anterior pair of tail spikes" (Fig. 3g, q) is a possible autapomorphy for *Stegosaurus sulcatus* Marsh 1887. Consequently, this taxon is considered to be a valid species.

Stegosaurus duplex Marsh, 1887 (Fig. 2b)

The holotype of *Stegosaurus duplex***,** YPM 1858, was excavated from Reed's YPM Quarry 11, Como Bluff (Carpenter and Galton 2001). It consists of vertebrae from all regions of the column (including the sacrum) plus the ilia, left pubis and ischium, femur, tibia and fibula (Carpenter and Galton 2001, figs 4.1–3; table 4.1; Marsh 1896; Gilmore 1914; Ostrom and McIntosh 1999); it shows characters 2, 5, 6, 9, 10 and 11 in the *Stegosaurus* and *S. armatus* list given above.

Lull (1910a, b), who included both specimens in the same mounted skeleton (Carpenter and Galton 2001, figs. 4.2, 4.3), and Gilmore (1914) both considered *Stegosaurus duplex* to be a junior objective synonym of *S. ungulatus*. This was because the specimen used as the holotype of *S. duplex* had previously been described by Marsh (1879, 1880a, 1891, 1896) as one of the two syntypes of *S. ungulatus.* This interpretation is followed here (Fig. 2b), as it was by Galton and Upchurch (2004) and Maidment et al. (2008), and this species is a valid taxon.

Stegosaurus longispinus Gilmore 1914 (Fig. 3h–j, u, v)

The holotype of *Stegosaurus longispinus*, UW 20503 (Foster 2007, formerly D54, was collected in 1908 by Reed and Dart, from Alcova (near present-day Alcova Reservoir, Foster 2007), Natrona County, Wyoming, and described by Gilmore (1914). He noted that it consisted of 42 vertebrae from all parts of the column (including fragmentary sacrum and 10 caudals, Gilmore 1914, fig. 67; Fig. 3u, v), plus the ischia (Gilmore 1914, pl. 25, fig. 4), part of a pubis, the right femur (Gilmore 1914, figs. 45.2, 68; photo in Foster 2007: fig. 6.33F) and four tail spikes, two of which were fairly complete (Gilmore 1914, figs. 60A, 66; Figs. 3h–j). Based on a photograph taken of UW 20503 as originally exhibited (J.S. McIntosh, pers. comm. 1988), it showed characters 3, 5 and 10 in the list given above. However, most of the specimen was destroyed when the museum's overhead water pipes burst in the early 1920s (Southwell and Breithaupt 2007). Only the femur remains, but other bones may be in boxes still to be sorted (B. Breithaupt, pers. comm. 2009). There are also plaster casts of the figured pair of very elongate tail spikes (UW 20503, USNM 8036; Gilmore 1914, figs. 60A, 66; photo in Glut 1997, p. 848). Gilmore (1914) noted that the elongated tail spikes (Fig. 3h–j), with the most complete at 860 mm (originally ~985 mm), are readily distinguished from those of other species of *Stegosaurus* (Figs. 2, 3f, g, q, s, t). Cited characters include:

1. Long slender shafts transversely flattened throughout their entire length *versus* a circular to oval cross section;
2. Constriction of the shaft above the base so widest part is ~225 mm above the basal end (Fig. 3h, i) *versus* a gradual taper from the base to apex in other *Stegosaurus* tail spikes (Fig. 3f, g, q, s);
3. Uniform size of the bases of the spikes (longest one: anteroposterior diameter 145 mm, transverse diameter 110 mm; comparable measurements of other three spikes within 5 mm). The bases of the anterior pair of spikes of the other species (Figs. 2, 3g, q, s) are considerably larger than those of the posterior pair (Gilmore 1914, table on p. 111 for *S. stenops*).

Gilmore (1914) noted that the 10 distal caudal centra (Fig. 3u, v), that undoubtedly belonged to the holotype skeleton because no bones of other animals were found in the quarry (Reed in Gilmore 1914), were easily distinguished from those of other species of *Stegosaurus* because they:

1. Were vertically compressed, so vertical height equals or exceeds transverse diameter (Fig. 3v), *versus* transversely compressed;
2. Were rounded in anterior and posterior views (Fig. 3v) *versus* hexagonal in outline;
3. Bore transverse processes (Fig. 3u) *versus* being absent, disappearing at about caudal 17 or 18 in USNM 4934 (Fig. 2a; Gilmore 1914).

Maidment et al. (2008) noted that if vertebral characters "2 and 3 are correct, then these may be valid autapomorphies for *S. longispinus*, however, because the holotype specimen is lost, the characters cannot be confirmed and *S. longispinus* is considered to be a *nomen dubium*." In addition, S.C.R. Maidment (pers. comm. 2010) suggested that the vertebrae are mid-caudals, and therefore the same as the mid-caudals of every other stegosaur, rather than being special and unique distal caudals. However, this re-identification would only eliminate character 3 but, judging from the change in height of the centra, this would result in a very foreshortened tail. As distal caudals, the continuation of the transverse processes almost to the end of the tail correlates well with the much longer tail spikes. These additional processes would have provided for a greater lateral tail muscle mass superior (*m. longissimus caudalis superior*) and inferior (*m. caudi-femoralis longus*, *m. iliocaudalis*) to them. This extra muscle mass would have enhanced the effectiveness of the tail spikes as weapons, a role demonstrated for the tail spikes of *Stegosaurus* (Carpenter et al. 2005).

Based on the unique form of the distal caudal vertebrae and of the two pairs of tail spikes, *S. longispinus* Gilmore 1914 is regarded as a valid species.

Hesperosaurus mjosi Carpenter, Miles & Cloward 2001

The holotype, HMNH 001 (cast as DMNH 29431), was excavated from 5 m above the base of the Morrison Formation (so in the Salt Wash Member) in Johnson County, Wyoming, and a quarry map documents the original position of the bones (Carpenter et al. 2001, fig. 3.1). The skeleton includes a nearly complete, disarticulated skull, complete vertebral column, partial left scapula and coracoid, ilia, ischia, pubes, 11 dermal plates and four tail spikes (see Carpenter et al. 2001; Carpenter 2010, fig. 7b; for several photos of holotype in matrix and of articulated bones, see Glut 2003, pp. 354–359). This species was referred to *Stegosaurus* as *S. mjosi* (Carpenter, Miles & Cloward 2001) by Maidment et al. (2008). However, Carpenter et al. (2001; also Carpenter 2010, fig. 7) considered that there are too many differences between the skeletons of *S. stenops* and *Hesperosaurus mjosi* to support referral to the same genus.

Maidment et al. (2008) referred three partial skeletons from the Howe Ranch Quarries, near Shell, Wyoming (Ayer 2000; updated specimen numbers H.J. Siber, pers. comm. 2009): SMA 0092 ("Lilly"), SMA 0018 ("Victoria") and SMA 3074-FV01 ("Moritz") to *H. mjosi* (for details see Siber and Möckli 2009). These specimens are being described by O. Mateus (pers. comm. 2009) and, if the referrals are correct, then these specimens should provide much additional information concerning the anatomy of this taxon.

Maidment et al. (2008, p. 379) noted that *Hesperosaurus* (as *Stegosaurus*) *mjosi* (see Carpenter et al. 2001; Carpenter 2010, fig. 7b) is a valid species that differed from *S. armatus* "as the former possesses the following primitive characters: atlas neural arches not fused to intercentrum in ontogenetically mature individuals, postzygapophyses not elevated significantly on posterior cervical vertebrae, neural arches of dorsal vertebrae not elongated above the neural canal, ossified epaxial tendons present, ribs distally expanded, caudal neural spines not bifurcated, enlargement of the distal end of the pubis. It also has the following autapomorphies: 11 dorsal vertebrae, fourth sacral vertebra not fused to sacrum, dorsal dermal plates longer anteroposteriorly than tall dorsoventrally. This combination of autapomorphies and retained plesiomorphies is not seen in any other stegosaur." Using the SMA specimens noted above, Carpenter (2010) provides an updated diagnosis for *Hesperosaurus mjosi* and Billon-Bruyat et al. (2010) provides details on the teeth of *Hesperosaurus*.

Discussion and conclusion: need for new type species for *Stegosaurus* Marsh 1877

Maidment et al. (2008) regarded all the species of Morrison stegosaurs that they considered valid, with the exception *Stegosaurus mjosi*, as junior synonyms of *Stegosaurus armatus* Marsh 1877. Maidment et al. (2008) listed 12 autapomorphic characters for *Stegosaurus* and *S. armatus*. However, the holotype (YPM 1850) has only character 3, an autapomorphy for *Stegosaurus* only if *S. mjosi* is included in the genus (if not then no autapomorphic characters for *Stegosaurus*). Based on the holotype, there are no autapomorphies for the species *armatus* so, even within the framework of Maidment et al. (2008), *Stegosaurus armatus* Marsh 1877 is a *nomen dubium*.

Other than *Stegosaurus stenops* Marsh 1887, each of the holotypes of the Morrison species of *Stegosaurus* consists of a partial disarticulated skeleton or less (see above for details). Also, apart from *S. mjosi* (if referral correct), there are no quarry drawings to indicate the original relationships of the bones and, if preserved, of the dermal armor. On the basis of differences in the dermal armor discussed above, there may be four or five Morrison species of *Stegosaurus*: *S. ungulatus* Marsh 1879 with three pairs of small flat dermal spines immediately anterior to the tail spikes (Figs. 2b, 3a–g, k–o, r), *S. stenops* Marsh 1887 with three larger alternating unpaired flat plates immediately anterior to the tail spikes (Figs. 2a, 3t, 4), *S. sulcatus* Marsh 1887 with a very large-based spike that was possibly placed more proximally on the tail or on the shoulder (Fig. 3g, q), *S. longispinus* Gilmore 1914 with two pairs of extremely elongate tail spikes (Fig. 3h–j), and *Stegosaurus* (*Hesperosaurus*) *mjosi* Carpenter, Miles & Cloward 2001 (if correctly referred) with dorsal plates that are longer anteroposteriorly than tall dorsoventrally (see Carpenter 2010, fig. 7b).

There are possibly up to four or five species of *Stegosaurus* based on differences in the form of the dermal plates and spikes. This is too many to be explained by sexual dimorphism, especially as all the holotypes were found at different stratigraphic horizons (see Turner and Peterson 1999, fig. 7). This may seem to represent a high taxonomic diversity but the Morrison Formation is ~180 m thick, lasted from about 154.8 to 148 Ma (but most occurrences of bones between ~61 and 168 m; Turner and Patterson 1999, fig. 10), and other Morrison herbivorous dinosaurs are also diverse. Thus the ornithopods include *Othnielosaurus, Dryosaurus* and *Camptosaurus* (2 species) and the other group of large herbivorous dinosaurs exhibits an extremely high diversity, viz., the Sauropoda, with *Amphicoelias, Apatosaurus* (5 species), *Barasaurus, Brachiosaurus, Camarasaurus* (4 species), *Diplodocus* (2 or 3 species), *Haplocanthosaurus* (2 species), *Seismosaurus* and *Suuwassea* (see Foster 2007).

With four or five other valid species of *Stegosaurus, S. armatus* is definitely a *nomen dubium*. As a consequence, the generic name *Stegosaurus*, and the derived higher taxonomic levels Stegosaurinae, Stegosauridae, Stegosauroidea, and Stegosauria of Marsh (1877, 1880), Hay (1902) and Abel (1919) are not available.

Hypsirophus Cope 1878, *Diracodon* Marsh 1881b and *Hesperosaurus* Carpenter, Miles & Cloward 2001 are based on valid species and are available as replacement generic names for the species of Morrison plated dinosaurs. However, both older genera are based on fragmentary and inadequate holotypes that were only recently described, *Hypsirophus* by Carpenter (1998b) and *Diracodon* by Carpenter and Galton (2001; resurrection by Bakker 1986 based on referred specimens). In addition, there is no associated dermal armor so these taxa would be indeterminate relative to the four species with armor. *Hesperosaurus mjosi* Carpenter, Miles & Cloward 2001 is based on good material but it may (Maidment et al., 2008) or may not (Carpenter et al. 2001; Carpenter 2010) be referable to the same genus as *ungulatus* and *stenops.*

As noted above, USNM 4934, the holotype of *Stegosaurus stenops* Marsh 1887, has all 12 autapomorphies listed by Maidment et al. (2008) for "*Stegosaurus*" and "*S.*" *armatus* and, in addition, it is the only holotype with characters 8 and 12. Only the most distal caudal vertebrae and the anterior pair of tail spikes are not represented in this almost complete articulated skeleton. Much of the skeleton is still in matrix, so the original relationships of the bones and dermal armor are preserved, and it is now the universal image for *Stegosaurus* (Fig. 2a; Czerkas 1987; Paul 1987, 1992; Galton 1990, 1997; Sereno and Dong 1992; Galton and Upchurch 2004). In addition, there are two other referred articulated skeletons, with one from the type area in Garden Park (DMNH 2818, has characters 1, 2, 5, 7, 8, 12), and all three skeletons were found stratigraphically within 10 m of each other (Carpenter 1998a). Consequently, the ICZN will be petitioned to designate *S. stenops* Marsh 1887 as the new type species for *Stegosaurus* Marsh 1877 to replace *S. armatus* Marsh 1877; this would also conserve the higher categories Stegosaurinae, Stegosauridae, Stegosauroidea and Stegosauria.

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References

Abel, O. (1919). *Die Stämme der Wirbeltiere* (914 pp.). Berlin & Leipzig: De Gruyter.

Ayer, J. (2000). *The Howe Ranch Dinosaurs. Die Howe Ranch Dinosaurier* (96 pp.). Aathal: Sauriermuseum Aathal.

Bakker, R. T. (1986). *The dinosaur heresies. New theories unlocking the mystery of the dinosaurs and their extinction* (482 pp.). New York: Morrow & Co., Ltd.

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

Billon-Bruyat, J.-P., Mazin, J.-M. & Pouech, J. (2010). A stegosaur tooth (Dinosauria, Ornithischia) from the Early Cretaceous of southwestern France. *Swiss Journal of Geosciences, 103* (this volume). doi:10.1007/s00015-010-0028-y.

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

Carpenter, K. (1998b). Vertebrate biostratigraphy of the Morrison Formation near Cañon City, Colorado. *Modern Geology, 23*, 407–426.

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

Carpenter, K. (2010). Species concept in North American stegosaurs. *Swiss Journal of Geosciences, 103* (this volume). doi: 10.1007/s00015-010-0020-6.

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

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

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

Cope, E. D. (1878). A new genus of Dinosauria from Colorado. *American Naturalist, 12*, 181.

Cope, E. D. (1879). New Jurassic Dinosauria. *American Naturalist, 13*, 402–404.

Czerkas, S. A. (1987). A reevaluation of the plate arrangement on *Stegosaurus stenops*. In S. J. Czerkas & E. C. Olson (Eds.), *Dinosaurs past and present* (Vol. 2, pp. 83–99). Seattle: University of Washington Press.

Davitashvili, L. (1961). *The theory of sexual selection* (538 pp.). Moscow: Izdatel'stvo Akademia Nauk SSSR (In Russian).

Dong, Z. (1973). Dinosaurs from Wuerho. *Institute of Paleontology and Paleoanthropology Memoir, 11*, 45–52 (In Chinese).

Dong, Z. (1990). Stegosaurs of Asia. In K. Carpenter & P. J. Currie (Eds.), *Dinosaur systematics* (pp. 255–268). Cambridge: Cambridge University Press.

Escaso, F., Ortega, F., Dantas, P., Malafaia, E., Pimentel, N. L., Pereda-Suberbiola, X., et al. (2007). New evidence of shared dinosaur across Upper Jurassic Proto-North Atlantic: *Stegosaurus* from Portugal. *Naturwissenschaften, 94*, 367–374.

Foster, J. (2007). *Jurassic West: The dinosaurs of the Morrison Formation and their world* (389 pp.). Bloomington: Indiana University Press.

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. (1990). Stegosauria. In D. B. Weishampel, P. Dodson, & H. Osmólska (Eds.), *The Dinosauria* (1st ed., pp. 435–455). Berkeley: University of California Press.

Galton, P. M. (1997). Stegosaurs. In J. A. Farlow & M. K. Brett-Surman (Eds.), *The complete dinosaur* (pp. 291–306). Bloomington: Indiana University Press.

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 K. Carpenter (Ed.), *The armored dinosaurs* (pp. 455–484). Bloomington: Indiana University Press.

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

Gilmore, C. W. (1914). Osteology of the armored Dinosauria in the United States National Museum, with special reference to the genus *Stegosaurus*. *United States National Museum Bulletin, 89*, 1–143.

Glut, D. F. (1997). *Dinosaurs. The encyclopedia* (1088 pp.). London: McFarland & Co., Inc.

Glut, D. F. (2003). *Dinosaurs. The encyclopedia. Supplement 3* (726 pp.). London: McFarland & Co., Inc.

Hay, O. P. (1902). Bibliography and catalogue of the fossil Vertebrata of North America. *United States Geological Survey, Bulletin, 179*, 1–495.

Hennig, E. (1915). *Kentrosaurus aethiopicus*, der Stegosauride des Tendaguru. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, 1915*, 219–247.

Hennig, E. (1925). *Kentrosaurus aethiopicus*. Die Stegosaurier-Funde vom Tendaguru, Deutsch-Ostafrika. *Palaeontographica Supplement, 7*(1), 101–254.

Lull, R. S. (1910a). The armor of *Stegosaurus*. *American Journal of Science,* Series 4, *29*, 201–210.

Lull, R. S. (1910b). *Stegosaurus ungulatus* Marsh, recently mounted at the Peabody Museum of Yale University. *American Journal of Science,* Series 4, *30*, 361–377.

Lull, R. S. (1929). *Organic evolution* (729 pp.). Macmillan: New York.

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.

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. (2010). CAD assessment of the posture and range of motion of *Kentrosaurus aethiopicus* Hennig 1915. *Swiss Journal of Geosciences, 103* (this volume). doi:10.1007/s00015-010-0024-2

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

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

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

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

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

Marsh, O. C. (1884). Principal characters of American Jurassic dinosaurs. Part VII: Diplodocidae, a new family of the Sauropoda. *American Journal of Science,* Series 3, *27*, 160–168.

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

Marsh, O. C. (1891). Restoration of *Stegosaurus. American Journal of Science,* Series 3, *42*, 179–181.

Marsh, O. C. (1896). The dinosaurs of North America. In: United States Geological Survey 16th annual report 1894–95 (pp. 133–244).

Mateus, O., Maidment, S. C. R., & Christiansen, N. A. (2009). A new long-necked 'sauropod-mimic' stegosaur and the evolution of the plated dinosaurs. *Proceedings of the Royal Society of London B, 276*, 1815–1821.

Ostrom, J. A., & McIntosh, J. S. (1966). *Marsh's dinosaurs. The collections from Como Bluff* (1st ed., 388 pp.). New Haven: Yale University Press.

Ostrom, J. A., & McIntosh, J. S. (1999). *Marsh's dinosaurs. The collections from Como Bluff* (2nd ed., 388 pp.). New Haven: Yale University Press.

Ouyang, H. (1992). [Discovery of *Gigantspinosaurus sichuanensis* and its scapular spine orientation.] *Abstracts and summaries for youth academic symposium on new discoveries and ideas in stratigraphic paleontology* (pp. 47–49), December 1992 (in Chinese).

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

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

Peng, G., Ye, Y., Gao, Y., Shu, C., & Jiang, S. (2005). *Jurassic dinosaur faunas in Zigong* (236 pp.). Zigong: Sichuan Scientific and Technological Publishing House (In Chinese, English summary).

Senter, P. (2010) Evidence for a sauropod-like metacarpal configuration in stegosaurian dinosaurs. *Acta Palaeontologica Polonica, 55* (in press).

Sereno, P. C., & Dong, Z.-M. (1992). The skull of the basal stegosaur *Huayangosaurus taibaii* and a cladistic diagnosis of Stegosauria. *Journal of Vertebrate Paleontology, 12*, 318–343.

Siber, H. J., & Möckli, U. (2009). *The Stegosaurs of the Sauriermuseum Aathal* (56 pp.). Aathal: Sauriermuseum Aathal.

Southwell, E., & Breithaupt, B. (2007). The tail of the lost *Stegosaurus longispinus* tail. *Journal of Vertebrate Paleontology, 27*(Suppl. to no. 3), 150A–151A.

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

Turner, C. E., & Peterson, F. (1999) Biostratigraphy of dinosaurs in the Upper Jurassic Morrison Formation of the western interior, U.S.A. In: D. D. Gillette (Ed.), *Vertebrate paleontology in Utah* (pp. 77–114). Utah Geological Survey Miscellaneous Publication 99-1.

von Huene, F. (1914). Über die Zweistämmigkeit der Dinosaurier, mit Beiträgen zur Kenntnis einiger Schädel. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilageband, 37*, 577–589.