

Species concept in North American stegosaurs

Kenneth Carpenter

Received: 14 July 2009 / Accepted: 25 May 2010 / Published online: 21 August 2010
© Swiss Geological Society 2010

Abstract The plated thyreophoran or stegosaurian dinosaur *Stegosaurus armatus* was named in 1877 by Marsh for fragmentary remains from the Morrison Formation (Upper Jurassic) of Colorado, USA. Subsequent discoveries from the same formation in Wyoming and Colorado (USA) have been assigned to separate stegosaurian genera and species, but most of these are no longer considered valid. More recently, a partial stegosaurian skeleton from Wyoming was named *Hesperosaurus mjosi*. However, the validity of this genus has been questioned recently, raising the question: how much osteological difference among stegosaur taxa is needed to separate genera from species? The question is examined vis-à-vis species and genus recognition in other dinosaurs, including iguanodonts, lambeosaurine iguanodontids, chasmosaurine ceratopsians, tyrannosaurid theropods, and diplodocid sauropods. The basis for taxonomic distinction is largely philosophical: if the species are morphologically distinct enough, they should be treated as separate genera. Based on these criteria, *Hesperosaurus mjosi* is a distinct taxon.

Keywords *Stegosaurus* · *Hesperosaurus* · Morrison Formation · Late Jurassic · Palaeontological species · Taxonomy

Institutional abbreviations

| | |
|------|--|
| DMNH | Denver Museum of Natural History (now the Denver Museum of Nature & Science), Denver, CO, USA |
| HMNH | Hayashibara Museum of Natural History, Okayama, Japan |
| SMA | Sauriermuseum Aathal, Switzerland |
| USNM | United States National Museum (now the National Museum of Natural History, Smithsonian Institution), Washington, DC, USA |
| YPM | Yale Peabody Museum of Natural History, New Haven, CT, USA |

Introduction

The stegosaurid *Hesperosaurus mjosi* CARPENTER, MILES & CLOWARD (2001), was named for a nearly complete skeleton from very low in the Morrison Formation in north-central Wyoming, USA. Carpenter and Galton (2001) reviewed the species of *Stegosaurus* named by Marsh and concluded that *S. armatus* could not be diagnosed at the species level with the available material, although two species (*S. stenops*, *S. unguulates*) were valid (*S. longispinus* was not considered). Maidment et al. (2008) challenged these conclusions, considering *Hesperosaurus mjosi* as a species of *Stegosaurus* (as *S. mjosi*), along with *S. armatus* from North America, and *S. homheni* (for *Wuerhosaurus homheni*) from China. They noted that *Stegosaurus mjosi* 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,

Editorial handling: Jean-Paul Billon-Bruyat & Daniel Marty.

K. Carpenter (✉)
Prehistoric Museum, Utah State University-College of Eastern
Utah, 155 Main Street, Price, UT 84501, USA
e-mail: ken.carpenter@ceu.edu

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.” (Maidment et al. 2008, p. 379).

The number of North American stegosaur genera and species raises the age old question of the species concept in palaeontology. The subject for dinosaurs was addressed in Carpenter and Currie (1990), and more recently by Paul (2008) for iguanodontids. The argument for species recognition in palaeontology is mostly philosophical because species recognition is limited to only a portion of the entire biological system, namely the hard parts, which among vertebrates is the skeleton (Raup and Stanley 1978; Donoghue 1985; see also Ereshefsky 2001). The application of the species concept in palaeontology, including dinosaurs, has long struggled with what criteria to use in taxonomy.

Early palaeontologists, especially Marsh and Cope, are frequently derided today for naming taxa based on scrappy, fragmentary material. For example, Marsh (1889) named *Triceratops galeus* for a nasal horn core collected from the Late Cretaceous near Denver, CO, USA. Leidy (1856) named four species of dinosaurs from among a hand-full of teeth surface collected by Hayden in the Late Cretaceous badlands along the Judith River of Montana (Leidy 1859). Then, of course, there is *Iguanodon* named by Mantell (1825) for teeth discovered by his wife. Some of the fragmentary materials named by these pioneers are borderline as to whether they are sufficiently unique for the name to be valid. For example, Cope (1876) named *Monoclonius crassus* for material collected along the Judith River. Dodson (1996) accepted the taxon as valid, whereas Sampson et al. (2008) did not.

It is easy today to ridicule these pioneers for naming taxa from scrappy material. However, we need to view their actions in the light of the times. The 1800s is when the natural world was just beginning to be studied scientifically. The large majority of the animals and plants we know today were given their scientific names during this time. The principles of zoological and plant nomenclature, roughed out previously by Linnaeus (1735), were being utilized in scientific descriptions. It is important to consider that many of these early palaeontological pioneers in dinosaurs also described modern organisms. Cope is especially noted for his work on reptiles, amphibians and fishes (Osborn 1931). Thus, these early workers had an understanding of modern organisms and the methodology for describing them. It was with this concept of organisms that they drew upon when faced with fragmentary specimens. These specimens became less fragmented once techniques were developed for hardening crumbly fossils

and encasing larger ones in plaster of Paris jackets. Regardless, these pioneers were faced with fossils of organisms unlike anything living today. Clearly, the organisms were morphologically different and hence, to their thinking, warranted a distinct name; this same philosophy holds today in the naming of specimens as is evidenced by the “diagnosis.”

It was inevitable that the principles of taxonomy as applied to vertebrate fossils in the 1800s and early 1900s would be questioned as specimens accumulated. Much of this questioning came during the 1930s to 1940s, and again in the 1960s, by such workers as Simpson, Dobzhansky and Mayr, and it has been revived yet again with the expanded use of cladistics (e.g. Wheeler and Meier 2000). The problem, of course, is due to the limitations of only having hard parts, usually fragmented and incomplete, and which are often distorted due to crushing during sediment compaction. It is the unfortunate nature of vertebrate fossils, particularly dinosaurs, that does not allow the use of modern techniques to identify species, including molecular, colour or scale patterns of skin, behaviour, reproductive potential, vocalizations, etc. Therefore, all methodologies for the identification of dinosaur species must rely upon skeletal differences. But how much difference must two specimens show or have to warrant separation at the species level, let alone at the generic level? Unfortunately, there is no consensus to this conundrum (i.e. the species problem in palaeontology). As Raup and Stanley (1978) noted, sibling species differ very slightly from one another, whereas other species are so very different that their separation is obvious. But what level of “obvious” is acceptable? Barrett et al. (2005) diagnosed two small ornithischians from China, each with a single autapomorphy: *Hexinlusaurus multidentis* (“marked concavity that extends over the lateral surface of the postorbital”) and *Xiaosaurus dashanpensis* (“proximally straight humerus”). Are these single autapomorphies sufficient? If so, then the situation is as Raup and Stanley (1978, p. 108) stated: “A species is a species if a competent specialist says it is.” This use of only autapomorphies to diagnose taxa may work some of the time, but other times it may not. For example, Farke (2007: 253) noted that “few characters are truly unique to the species *T[orosaurus] latus*, but the combination of characters *is* unique. Only the *combination* of features diagnoses the taxon” (emphasis by Farke 2007).

Lessons learned from species concept in dinosaur palaeontology

There is little question that *Tyrannosaurus rex* is a distinct taxon from *Allosaurus fragilis* because each can be identified based on very distinct morphological (typological)

criteria. However, such a distinction is less apparent among several other different groups of dinosaurs. As Sampson et al. (2008) have noted, ceratopsid taxa are notoriously conservative in their postcrania, with almost all of the generic and specific criteria being based on differences in the skull architecture (Fig. 1); this point has been also noted by Dodson (1996) and Paul (2007, 2008), among

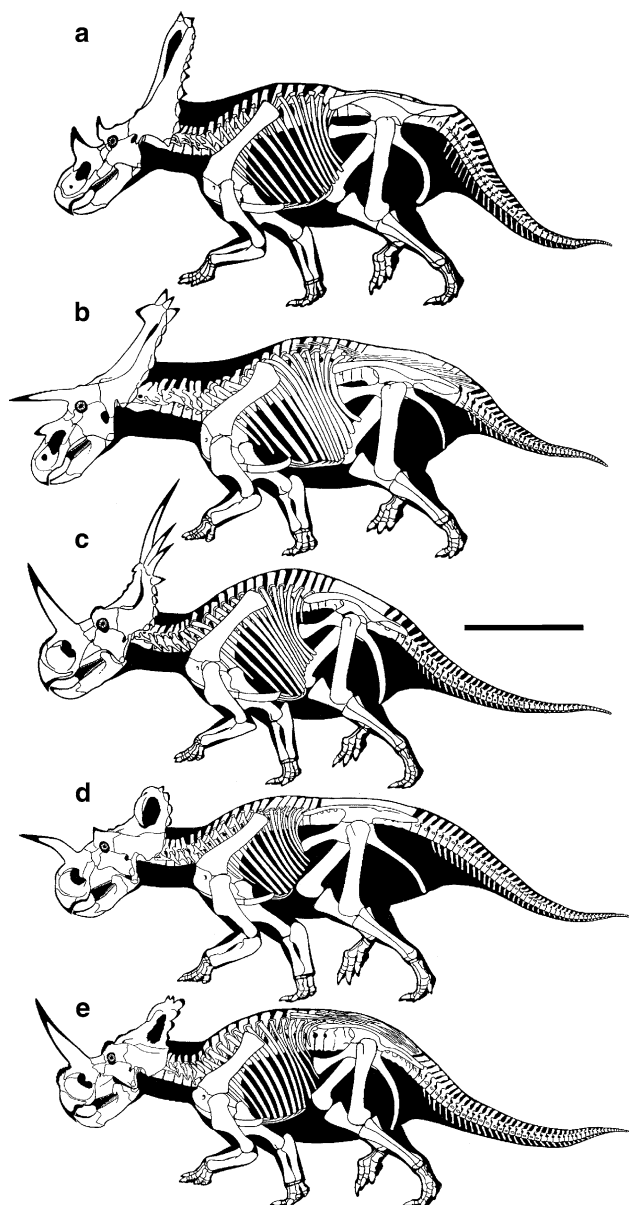


Fig. 1 Example of ceratopsians in which the similarities are greater than the differences. Two genera of long faced chasmosaurines *Chasmosaurus belli* (a) and *Anchiceratops* (b) versus two genera of short faced centrosaurines *Styracosaurus ovatus* (c) and *Centrosaurus apertus* (d). Compare with the two species of *Centrosaurus*: *Centrosaurus apertus* (d) and *Centrosaurus nasicornis* (e). The two *Centrosaurus* species are linked by the hook-like process over the frill fenestra, and are separated in part by the nasal horn. Courtesy of Gregory S. Paul. Scale bar 1 m

others. Lambeosaurine hadrosaurs are also conservative in their postcrania, with the biggest differences also occurring in the skull (Fig. 2; Dodson 1975; Paul 2007, 2008); even the well known tyrannosaurids are remarkably similar (Fig. 3). The reverse may also be true where the skull is conservative, with the biggest differences in the postcrania. Such a situation is seen in *Apatosaurus* and *Diplodocus* (Fig. 4), which led to the skull of *Apatosaurus* being unrecognized for over 50 years (Fig. 5; Berman and McIntosh 1978).

Species recognition in dinosaurs is even more difficult because one person's species is another person's genus. A case in point is the skull Marsh (1894) referred to *Campotossaurus amplus*, a name long accepted until Brill and Carpenter (2007) renamed the specimen *Theiophytalia kerri*. Besides morphological differences, they also noted that the skull actually came from the Lower Cretaceous Lytle Formation, not the Upper Jurassic Morrison Formation. This recognition of two genera from what had previously been one also occurred with the separation of *Mantellisaurus* from *Iguanodon* by Paul (2007; see Fig. 6).

More recently, parsimony analysis of specimens (rather than taxa) has been used to cluster them into possible species (e.g. Yates 2003; Upchurch et al. 2004). However, assigning genus or species names to clusters, especially to "sister clusters", will always be philosophical, and hence

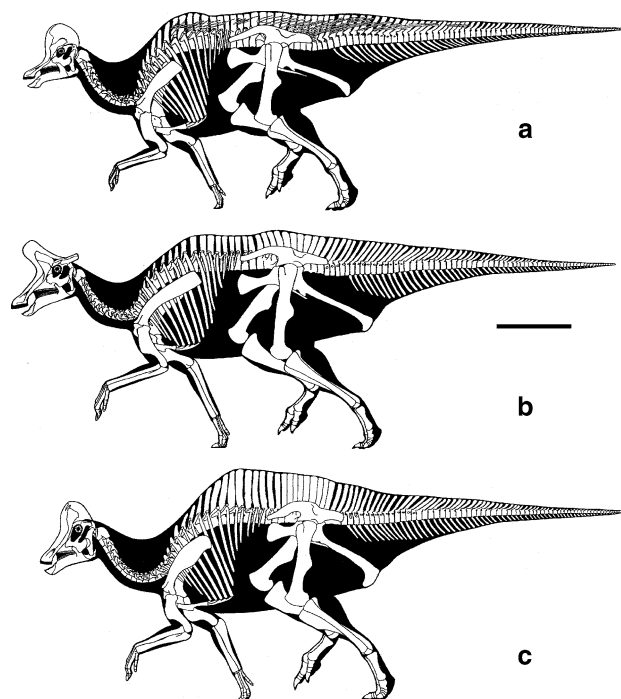


Fig. 2 Comparison of lambeosaurine hadrosaurs: *Corythosaurus casuarius* (a), *Lambeosaurus lambei* (b) and *Hypacrosaurus stebingeri* (c). Cranial differences are in the crest, whereas most postcranial differences are in the neural spine height. Other differences are minor. Courtesy of Gregory S. Paul. Scale bar 1 m

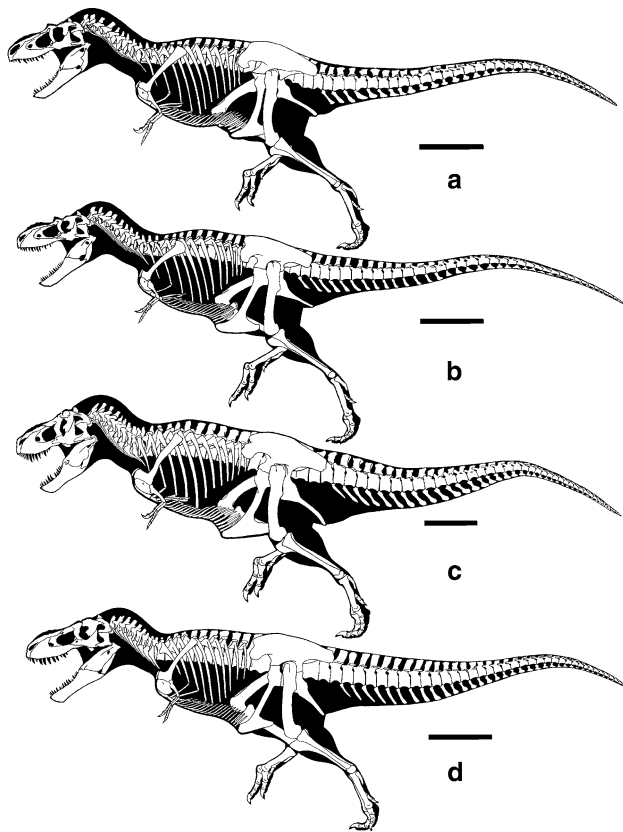


Fig. 3 Comparison of various adult tyrannosaurids: *Gorgosaurus libratus* (a), *Albertosaurus sarcophagus* (b), *Tyrannosaurus rex* (c) and *Tarbosaurus bataar* (d). Differences are minor at the generic level. Courtesy of Gregory S. Paul. Scale bars 1 m

the subject of debate. It may be a more useful tool for determining what taxon a particular specimen belongs to.

The species concept in *Stegosaurus*

The genus *Stegosaurus* was established by Marsh (1877) for very scrappy material collected approximately in the middle of the Morrison Formation (Turner and Peterson 1999). Named *S. armatus*, the morphology of the caudal vertebrae and large plate-like osteoderms define the genus, species and family. Unfortunately, in the context of considerably more material, including nearly complete skeletons, it is debatable whether the material is diagnostic at the species level (Carpenter and Galton 2001). A similar situation exists with *Titanosaurus indicus* as noted by Wilson and Upchurch (2003), who discussed the concept of ‘historical obsolescence’, that is characters once thought to be unique were later found to be more widely distributed through the discovery of new and better specimens.

In making their diagnosis of *Stegosaurus*, Maidment et al. (2008) did not base it on the holotype material, YPM

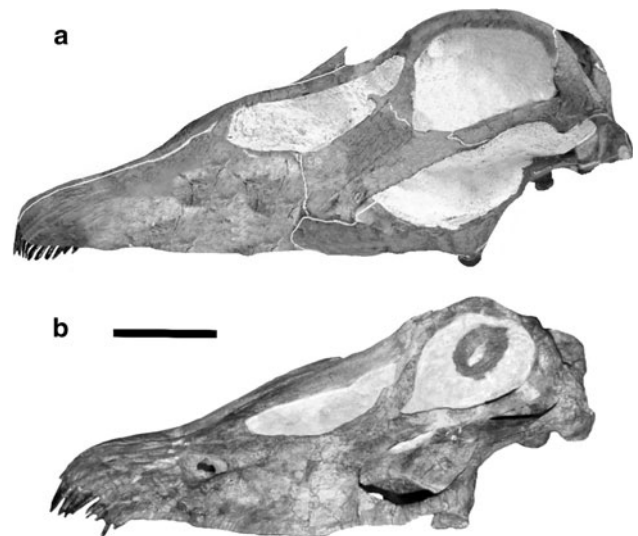


Fig. 4 The skulls of *Apatosaurus louisae* (CM 11162) (a) and *Diplodocus* sp. (CM 11161) (b), showing how similar they are and why it took over 50 years for them to be separated. Scale bar 10 cm

1850, but rather on a composite of various specimens that were assumed by them to be of a single species showing a wide range of non-ontogenetic variation throughout the skeleton. However, the variation cannot be replicated in other large samples of stegosaurids (e.g. *Kentrosaurus aethiopicus*), making the validity of the variations suspect. Furthermore, some characters stated by Maidment et al. (2008) to be variable in *S. armatus* are used to diagnose other taxa. For example, the enormously long and slender osteoderm spines of *S. longispinus* are “not considered a valid autapomorphy as dermal armour is likely to be extremely variable depending on age, size and the sex of the animal that bore it” (Maidment et al. 2008, p. 17). Yet *Gigantospinus sichuanensis* is diagnosed from a single autapomorphy: “possessing a parascapular spine that is at least twice the length of the scapula” (Maidment et al. 2008, p. 11). Based on the ontogenetic changes known to occur in the osteoderms of stegosaurs (Hayashi et al. 2009), and acknowledged by Maidment et al. (2008), dismissal of spine size leaves *G. sichuanensis* without any diagnostic features, and must by conditions advocated by Maidment et al. (2008) be considered a *nomen dubium*. Clearly characters dismissed in the diagnosis of one taxon, must also hold true for another.

In other instances, the statements used to justify synonymies are clearly in error. For example, *Wuerhosaurus hemheni* is placed in the genus *Stegosaurus* as a new combination *S. hemheni* because “the elements preserved are identical in most aspects to those of *Stegosaurus armatus*” (Maidment et al. 2008, p. 14). Except for the general features that unite all stegosaurs, this statement is misleading. The pelvis as illustrated has a very short

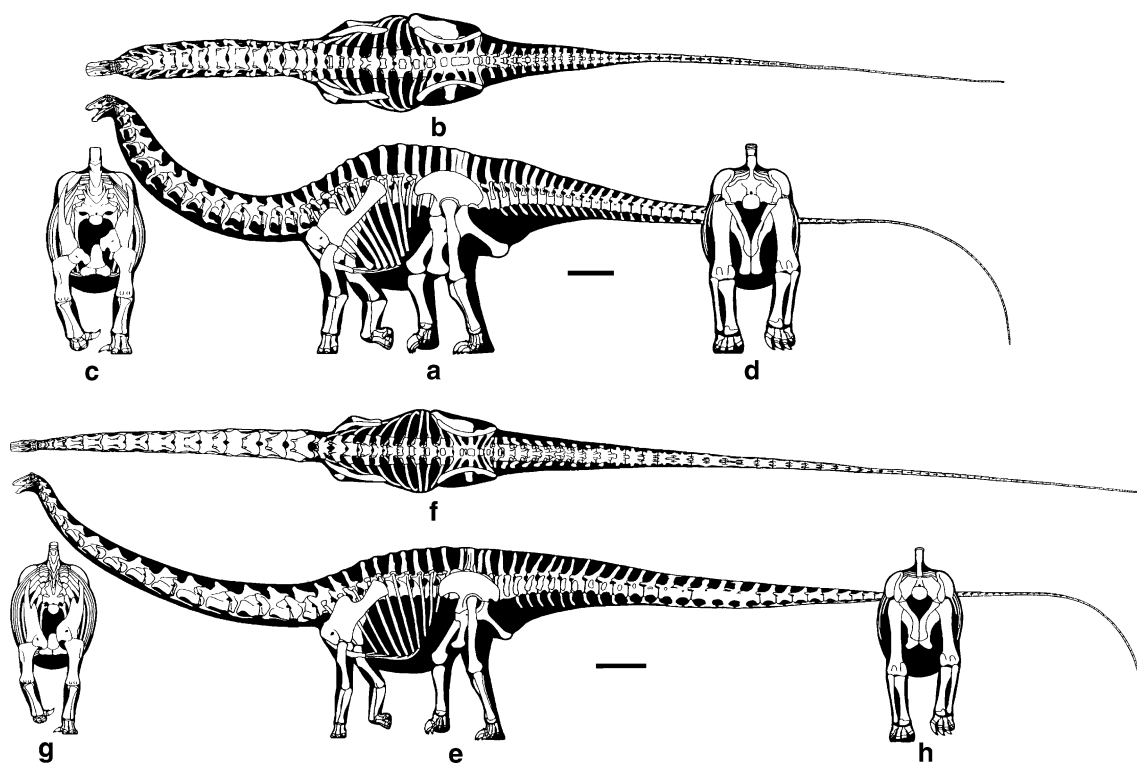


Fig. 5 Although the skulls of *Apatosaurus* and *Diplodocus* are very similar (cf. Fig. 4), their postcranial skeletons differ considerably. *Apatosaurus louisae* (CM 3018 and CM 11162) in left lateral (a), dorsal (b), anterior (c, without cervicals), and posterior (d, without

caudals). *Diplodocus carnegie* (CM 84 and CM 94) in left lateral (e), dorsal (f), anterior (g, without cervicals), and posterior (h, without caudals). Courtesy of Gregory S. Paul. Scale bars 1 m

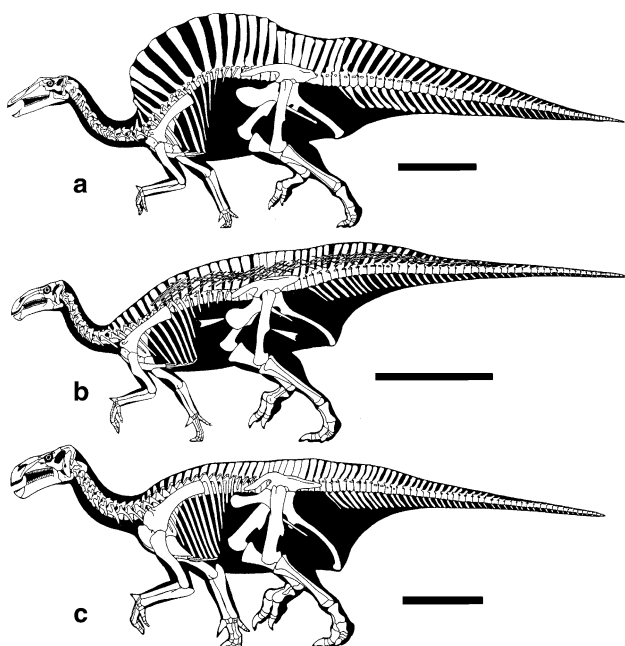


Fig. 6 Generic differences between iguanodontids is readily apparent among *Ouranosaurus nigeriensis* (a), *Mantellisaurus atherfieldensis* (b) and *Iguanodon bernissartensis* (c), yet only recently was *Mantellisaurus* separated from *Iguanodon* by Paul (2007). Courtesy of Gregory S. Paul. Scale bars 1 m

preacetabular process, unlike the long process in *Stegosaurus* (compare Maidment et al. 2008: Figs. 8C and 2B). *S. armatus* lacks the deep fossa above the neural canal on the posterior side, which Maidment et al. used to diagnose *S. hemheni* from the Early Cretaceous of China (Dong 1973). The dorsal plate is totally unlike those of *Stegosaurus armatus* (as defined by Maidment et al. 2008). These differences argue for *Wuerhosaurus hemheni* being a distinct genus from the Late Jurassic *Stegosaurus*.

With regards to *Stegosaurus armatus*, I agree with the proposal of Galton (2010) to petition the International Zoological Commission to suppress *Stegosaurus armatus* and establish *S. stenops*, USNM 4934, as the name-bearing type. Doing this eliminates the assumed wide range of variation claimed by Maidment et al. (2008) and allows separation of *S. stenops* and *S. unguulatus* as advocated by Carpenter et al. (2001) and Carpenter and Galton (2001). This separation places *Hesperosaurus msoji* outside the morphological range seen by *Stegosaurus* as first advocated by Carpenter et al. (2001; see Figs. 7, 8). As Maidment et al. (2008, p. 13) noted, “*Hesperosaurus* has autapomorphies and retained plesiomorphies not seen in other stegosaurs [i.e., *Stegosaurus*].” Furthermore as Mateus et al. (2009) admit, *Hesperosaurus* is closely related to

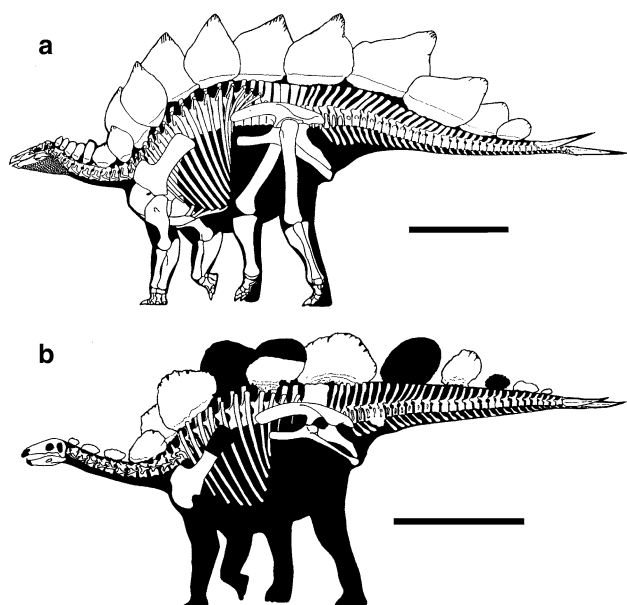


Fig. 7 Comparisons of the skeletons of *Stegosaurus stenops* (USNM 4934) (a) and the holotype of *Hesperosaurus mjosi* (HMNH 001) (b). Based upon the criteria used to separate other dinosaurs, these two warrant separation at the genus level. a is courtesy of Gregory S. Paul. Scale bars 1 m

Dacentrurus, which only strengthens the separation of *Hesperosaurus* from *Stegosaurus*.

The distinction of *Hesperosaurus* is heightened by the discovery of several additional specimens low in the Morrison Formation near the Howe Ranch on the west side of the Big Horn Mountains, Wyoming (first-hand obs. 2009; Siber and M \ddot{o} ckli 2009). The most important of these are SMA 3074-FV01 (“Moritz”) and SMA 0018 (“Victoria”). Incorporating data from these specimens allows for a revised diagnosis of *Hesperosaurus mjosi*.

Revised diagnosis: Antorbital fenestra large versus very small in *Stegosaurus stenops*; maxilla short and deep, height equal to half of length, unlike *S. stenops* where height equals one-third of length; basisphenoid short, long

Fig. 8 Pelvis of *Hesperosaurus mjosi* holotype (HMNH 001) (a) and *Stegosaurus stenops* (DMNH 1483) (b). The preacetabular process is strongly divergent in *H. mjosi*, less so in *S. stenops*. Scale bars 10 cm



in *S. stenops*; long-necked stegosaur with 13 cervicals versus 10 in *S. stenops*; short bodied with 13 dorsals versus 17 in *S. stenops*; neural arch of mid-dorsals low as in *Huayangosaurus taibaii*, not tall as in *S. stenops*; cervical ribs expanded distally, not expanded in *S. stenops*; tops of neural spines of proximal caudals rounded, not bifurcated as in *S. stenops*; dorsal edge of scapular blade with distinct step mid-length, no step (margins parallel) in *S. stenops*; preacetabular process strongly divergent, less so in *S. stenops*; distal end of prepubic process expanded vertically, unexpanded in *S. stenops*; distal end of postacetabular process swollen into knob-like structure, unswollen in *S. stenops*. Mid-dorsal to anterior caudal osteoderm plates vertically low and oval in shape, rather than tall and triangular as in *S. stenops*.

Conclusions

The palaeontological concept of species is problematic because it is based on osteological characters. The situation is made worse by the fragmentary nature of most specimens. It is no wonder then that there is no agreement as to whether a particular taxon is a valid species, let alone a valid genus. Certain dinosaur taxa currently accepted as valid genera (e.g. *Lambeosaurus*, *Corythosaurus* and *Hypacrosaurus*) could arguably be considered different species of the same genus (G. S. Paul, pers. comm. 2009). However, other taxa are so different that they warranted separation, as recently occurred by the separation of *Mantellisaurus* from *Iguanodon* by Paul (2008). The Stegosauria is osteologically a conservative group and this makes taxonomic distinctions problematic. Philosophically, it has been argued by some that *Stegosaurus* consists of two species in North America, *S. mjosi* and *S. armatus*, the latter of which is exceptionally variable. Such a wide range of variability is unique among the Dinosauria, except in waste-basket taxa (e.g. *Megalosaurus*), and for that reason

is rejected. Finally, as Maidment et al. (2008, p. 379) acknowledged, *Hesperosaurus mjsi* has a unique “combination of autapomorphies and retained plesiomorphies”. I consider that this unique combination warrants recognition of the taxon as a separate genus, as originally proposed by Carpenter et al. (2001). Furthermore, *Stegosaurus armatus* should be considered a *nomen dubium* as advocated by Galton (2010) and replaced with *S. stenops*. Even with these recommended changes, I have no doubts that this is not the last word on the subject.

Acknowledgments First, special thanks to Peter Galton for numerous email exchanges regarding his thoughts and observations on stegosaurs. These exchanges, plus review comments, helped me formulate the revision of the manuscript. I also thank Gregory Paul for discussions over the years about dinosaur species recognition and the associated problems. We have not always agreed on whether a particular taxon should be recognized at the species or genus level, but the discussions have been fruitful nonetheless. I have borrowed freely from these discussions, and acknowledge that Greg has published more on the subject than me, most recently in his review of iguanodonts (Paul 2008). I thank him for providing the skeletal reconstructions used in the figures. I also thank Hans Jakob “Kirby” Siber for the invitation of submit a manuscript to the Symposium on Stegosauria, and for hosting my visit to the Sauriermuseum Aathal, Switzerland where several new specimens of *Hesperosaurus* are exhibited. Finally, thanks for Paul Upchurch for his insightful review comments, as well as those of an anonymous reviewer.

References

- Barrett, P. M., Butler, R. J., & Knoll, F. (2005). Small-bodied ornithischian dinosaurs from the Middle Jurassic of Sichuan, China. *Journal of Vertebrate Paleontology*, 25, 823–834.
- Berman, D. S., & McIntosh, J. S. (1978). Skull and relationships of the Upper Jurassic sauropod *Apatosaurus* (Reptilia, Saurischia). *Bulletin of the Carnegie Museum of Natural History*, 8, 1–35.
- Brill, K., & Carpenter, K. (2007). A description of a new ornithopod from the Lytle Member of the Purgatoire Formation (Lower Cretaceous) and a reassessment of the skull of *Camptosaurus*. In K. Carpenter (Ed.) *Horns and beaks: ceratopsian and ornithopod dinosaurs* (pp. 49–67). Bloomington: Indiana University Press.
- Carpenter, K., & Currie, P. J. (1990). Introduction: on systematic and morphological variation. In: K. Carpenter, & P. J. Currie (Eds.), *Dinosaur systematics: approaches and perspectives* (pp. 1–8). Cambridge: Cambridge University Press.
- Carpenter, K., & Galton, P. (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.
- Cope, E. D. (1876). Description of some new vertebrate remains from the Fort Union Beds of Montana. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 28, 248–261.
- Dodson, P. (1975). Taxonomic implications of relative growth in lambeosaurine hadrosaurs. *Systematic Zoology*, 24, 37–54.
- Dodson, P. (1996). *The horned dinosaurs* (p. 346). Princeton: Princeton University Press.
- Dong, Z. (1973). Dinosaurs from Wuerho. *Memoirs of the Institute of Vertebrate Paleontology and Paleoanthropology*, 11, 45–52.
- Donoghue, M. J. (1985). A critique of the biological species concept and recommendations for a phylogenetic alternative. *The Bryologist*, 88, 172–181.
- Ereshefsky, M. (2001). *The poverty of the Linnaean hierarchy: a philosophical study of biological taxonomy* (328 pp). New York: Cambridge University Press.
- Farke, A. A. (2007). Cranial osteology and phylogenetic relationships of the chasmosaurine ceratopsid *Torosaurus latus*. In: K. Carpenter (Ed.), *Horns and beaks: ceratopsian and ornithopod Dinosaurs* (pp. 235–257). Bloomington: Indiana University Press.
- 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. doi:10.1007/s00015-010-0022-4.
- Hayashi, S., Carpenter, K., & Suzuki, D. (2009). Differential growth patterns between the skeleton and osteoderms of *Stegosaurus* (Ornithischia: Thyreophora). *Journal of Vertebrate Paleontology*, 29, 123–131.
- Leidy, J. (1856). Notices of the remains of extinct reptiles and fishes, discovered by Dr F.V. Hayden in the badlands of the Judith River, Nebraska Territory. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 8, 72–73.
- Leidy, J. (1859). Extinct vertebrata from the Judith River and Great Lignite Formations of Nebraska. *American Philosophical Society Transactions*, 11, 139–154.
- Linnaeus, C. (1735). *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Netherlands, 11 pp.
- 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.
- Mantell, G. (1825). Notice on the *Iguanodon*, a newly discovered fossil reptile, from the Sandstone of Tilgate Forest, in Sussex. *Philosophical Transactions of the Royal Society of London*, 115, 179–186.
- Marsh, O. C. (1877). New order of extinct Reptilia (Stegosauria) from the Jurassic of the Rocky Mountains. *American Journal of Science*, 114, 513–514.
- Marsh, O. C. (1889). Notice of new American dinosaurs. *American Journal of Science*, 137, 334–336.
- Marsh, O. C. (1894). The typical Ornithopoda of the American Jurassic. *American Journal of Science*, 148, 85–90.
- 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.
- Osborn, H. F. (1931). *Cope: Master Naturalist* (740 pp). Princeton: Princeton University Press.
- Paul, G. S. (2007). Turning the old into the new: a separate genus for the gracile iguanodont from the Wealden of England. In K. Carpenter (Ed.), *Horns and beaks: ceratopsian and ornithopod Dinosaurs* (pp. 69–77). Bloomington: Indiana University Press.
- Paul, G. S. (2008). A revised taxonomy of the iguanodont dinosaur genera and species. *Cretaceous Research*, 29, 192–216.
- Raup, D. M., & Stanley, S. M. (1978). *Principles of paleontology* (481 pp). San Francisco: W. H. Freeman & Co.
- Sampson, S. D., Ryan, M. J., & Tanke, D. H. (2008). Craniofacial ontogeny in centrosaurine dinosaurs (Ornithischia: Ceratopsidae): taxonomic and behavioral implications. *Zoological Journal of the Linnean Society*, 121, 293–337.

- Siber, H.J., & Mockli, U. (2009). The Stegosaur of the Sauriermuseum Aathal. Aathal, 56 pp.
- Turner, C. E., & Peterson, F. (1999). Biostratigraphy of dinosaurs in the Upper Jurassic Morrison Formation of the Western Interior, USA. In D. Gillette (Ed.) *Vertebrate Paleontology in Utah* (pp. 77–114) Utah: Utah Geological Survey Miscellaneous Publication 99-1.
- Upchurch, P., Tomida, Y., & Barrett, P. M. (2004). A new specimen of *Apatosaurus ajax* (Sauropoda, Diplodocidae) from the Morrison Formation (Upper Jurassic) of Wyoming, USA (pp. 1–118) Tokyo: National Science Museum, Tokyo Monographs 26.
- Wheeler, Q. D., & Meier, R. (2000). *Species concepts and phylogenetic theory: a debate* (256 pp). New York: Columbia University Press.
- Wilson, J. A., & Upchurch, P. (2003). A revision of *Titanosaurus* Lydekker (dinosauria–sauropoda), the first dinosaur genus with a ‘Gondwanan’ distribution. *Journal of Systematic Palaeontology*, *1*, 125–160.
- Yates, A. M. (2003). The species taxonomy of the sauropodomorph dinosaurs from the Lowenstein Formation (Norian, Late Triassic) of Germany. *Palaeontology*, *46*, 317–337.