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Evidence for a sauropod-like metacarpal configuration in stegosaurian dinosaurs

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The stegosaurian forelimb is usually portrayed with the metacarpals slanted and distally spread. However, manual manipulation of stegosaurian metacarpals reveals that in that configuration they do not articulate with each other nor with the rest of the forelimb. Rather, they do articulate with each other and with the rest of the forelimb when posed vertically and arranged in a compact, semi-tubular configuration, as in sauropods. This configuration agrees with data from articulated specimens and trackways. As with sauropods, this metacarpal configuration makes retention of phalanges awkward for locomotion and may be functionally related to the vestigiality of the manual phalanges of the outer digits.

Key words: Dinosauria, Ornithischia, Stegosauria, forelimb, functional morphology.

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Introduction

The metacarpals in the hands of most dinosaurs articulate in a shallow arc in proximal view (Norman 1980; Sereno 1993; Senter 2007a; Carpenter and Wilson 2008). In contrast, the metacarpals of sauropod dinosaurs articulate in a tight curve that in proximal view is a nearly complete circle in derived sauropods and a semicircle in basal sauropods, so that the hand skeleton forms a vertical tube in the former and a vertical half-tube in the latter (Bonnar 2003) (Fig. 1A). Until now such a tubular skeletal configuration of the hand has not been reported in Ornithischia. Here I show that this configuration is present in the ornithischian taxon Stegosauria.

In 1891 Marsh reconstructed the skeleton of *Stegosaurus* with the metacarpals slanting and somewhat spread distally (Marsh 1891). This portrayal was continued by Gilmore (1914) and later authors (Galton and Upchurch 2004). At first glance these illustrations seem to show the metacarpals posed with their long axes vertical, an illusion that is caused by a combination of the squat shapes of the bones and the perspective from which they are drawn. However, if one manually arranges the bones in the same pose and observes them in proximal and oblique views it is clear that they are slanted and that their distal ends are spread apart. In such a pose the proximal ends of the metacarpals have no bony support from beneath, necessitating the presence of a palmar pad of soft tissue to support them, as hypothesized by Abel (1912). In contrast, the metacarpals form a vertical semi-tube as found in situ in USNM 4934 (Gilmore 1914), a specimen of *Stegosaurus armatus* Marsh, 1877 (Maidment et al. 2008) (Fig. 1C). In that specimen there is slight disarticulation of the metacarp-

als, but they are nonetheless articulated enough to confirm that their configuration resembles that found in CM 11338, an articulated specimen of the sauropod *Camarasaurus lentus* Marsh, 1889 (Gilmore 1925) (Fig. 1B). This suggests that, as in some sauropods, the articulated stegosaurian metacarpus formed a vertical semi-tube. In such a configuration the metacarpals do not require a soft-tissue pad for support because they are vertical.

To determine the correct metacarpal configuration I treated the slanting and spreading configuration and the vertical semi-tubular configuration as competing hypotheses, each with a set of testable predictions. Each hypothesis of metacarpal configuration in stegosaurs predicts that the configuration: (1) is allowed by the shapes of the metacarpals, (2) provides a better fit between the metacarpals than the competing hypothesis, (3) provides sufficient support for and does not disarticulate the more proximal forelimb bones, (4) does not compromise the goodness of fit between the metacarpals and the phalanges, (5) is not contradicted by specimens articulated in situ, and (6) agrees with ichnological evidence.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York City, USA; CM, Carnegie Museum of Natural History, Pittsburgh, USA; USNM, United States National Museum, Washington, USA; YPM, Yale Peabody Museum, New Haven, USA.

Tests of the hypotheses

Prediction 1, that the shapes of the metacarpals allow the configuration, is satisfied for both hypotheses, as is illus-

trated by USNM 4937, the specimen upon which Gilmore (1914) based his reconstruction of the manus. This specimen is the holotype of *Stegosaurus sulcatus* Marsh, 1887 and is currently catalogued under that taxonomic name. Galton (1990) and Galton and Upchurch (2004) considered *S. sulcatus* a junior synonym of *Stegosaurus armatus*, but Maidment et al. (2008) considered USNM 4937 a stegosaur of indeterminate genus and species. According to a new review of stegosaurs from the Morrison Formation, USNM 4937 is a specimen of *Stegosaurus*, most likely *S. sulcatus* (Galton in press). The metacarpals and carpals of the specimen are free from matrix but are currently stored in articulation, supported from beneath by a plaster stand that keeps them in approximately the configuration illustrated by Gilmore (1914). In this configuration the metacarpals do not interfere with each other (Fig. 1E, F). Nor do they interfere with each other when removed from the stand and posed vertically in a sandbox. Such posing shows that their shapes allow them to articulate into a semi-tube (Fig. 2). In this pose the distal ends of metacarpals II–V are separated from each other only by miniscule gaps at points at which the smoothness of the surface texture of the bone is reduced, suggesting the presence of syndesmotomic ligaments.

Prediction 2, that the configuration provides a better fit between the metacarpals than does the other configuration, is satisfied for the vertical semi-tube hypothesis and falsified for the slanted and spreading hypothesis. The metacarpals of USNM 4937 are wedge-shaped in proximal view so that when articulated in contact with each other proximally they fit tightly together in a vertical semi-tube with no gaps between their proximal ends (Fig. 2). In contrast, the slanted and spreading configuration leaves gaps between the proximal ends of the metacarpals (Gilmore 1914), necessitating the presence of a soft-tissue support not only beneath them (Abel 1912) but also between metacarpals II and III and between III and IV (Fig. 1F). Simply put, when slanted the metacarpals just do not fit each other.

The proximal ends of the metacarpals of the stegosaur *Kentrosaurus aethiopicus* Hennig, 1915 are also wedge-shaped (Hennig 1925). These bones cannot be examined directly because they were destroyed or misplaced during World War II (Galton 1982), but Hennig (1925) illustrated the shapes of their proximal ends. Manipulation of the proximal ends of the metacarpals in his figure shows that when articulated in contact they form a semicircular arc with no gaps between the metacarpals, which is consistent with a semi-tubular configuration (Fig. 1D). Isolated metacarpals of other stegosaurs are also wedge-shaped in proximal view (Galton 1985), which is consistent with articulation into a tight arc.

Prediction 3, that the configuration provides sufficient support for and does not disarticulate the more proximal forelimb bones, is satisfied for the vertical semi-tube hypothesis and falsified for the slanted and spreading hypothesis. The proximal ends of the metacarpals of USNM 4937 form a flat table that supports the block-like carpal bones like pillars

supporting a ceiling, and the anterior circumference of the metacarpal arc matches the anterior curvature of the edge of the carpus with only metacarpal V left uncovered (Fig. 2). In contrast, in the slanted and spreading configuration the anterior edges of the proximal ends of the metacarpals do not conform to the anterior curvature of the pair of carpals; parts of the proximal ends of metacarpals II–V protrude beyond the anterior margins of the carpals (Fig. 1G). More importantly, in this configuration the proximal surfaces of the metacarpals do not form a horizontal table to support the flat distal surfaces of the carpals but instead slant such that the palmar half of each carpal hangs off the edge of the metacarpus and is unsupported from beneath (Fig. 1H). Furthermore, the proximal surfaces of the carpals in this configuration are too strongly slanted support the radius and ulna from beneath. In contrast, with the metacarpals articulated in a vertical semi-tube the proximal surface of the carpus forms a horizontal table that correctly articulates with the distal antebrachium if the antebrachium (though not the humerus) is held vertically as in quadrupedal ceratopsians (Fujiwara 2009). In this configuration the carpals articulate tightly, closely matching the complementary distal ends of the radius and ulna and requiring the distal ends of the radius and ulna to tightly articulate with each other. The skeletal mount of AMNH 650, a specimen of *Stegosaurus armatus* (Maidment et al. 2008), shows the distal ends of the radius and ulna articulating in exactly this manner (Fig. 1D); the goodness of fit between these two bones proximally and distally, as well as the goodness of fit between them and the humerus, shows that this configuration is an anatomically feasible configuration for the humerus, radius, and ulna. Simply put, when slanted the metacarpals do not fit the rest of the forelimb, but in a vertical semi-tube they do.

Prediction 4, that the configuration does not compromise the goodness of fit between the metacarpals and the phalanges, is satisfied for both hypotheses. Neither configuration results in interference among phalanges within or between fingers because both configurations are digitigrade. As in sauropods the articular surface for the proximal phalanx is located on the extensor surface of each metacarpal rather than on the distal surface, so that with a vertical metacarpus the finger is perpendicular to the metacarpal and parallel to the ground (Fig. 2). The phalanges of the thumb are less horizontal than the other fingers, but the slant of the thumb can be accommodated with a vertical metacarpus because metacarpal I is shorter than the middle three metacarpals so that the proximal end of metacarpal I is held off the ground.

Prediction 5, that the configuration is not contradicted by articulated specimens, is satisfied for the vertical semi-tube hypothesis and falsified for the slanted and spreading hypothesis. The only known stegosaurian metacarpus that is articulated in situ, that of USNM 4934, a specimen of *Stegosaurus armatus* (Maidment et al., 2008), exhibits a vertical semi-tubular configuration (Gilmore 1914) (Fig. 1C). The carpus and metacarpals I–III were discovered in semi-articulation in USNM 7401 (Gilmore 1914), a juvenile stegosaur

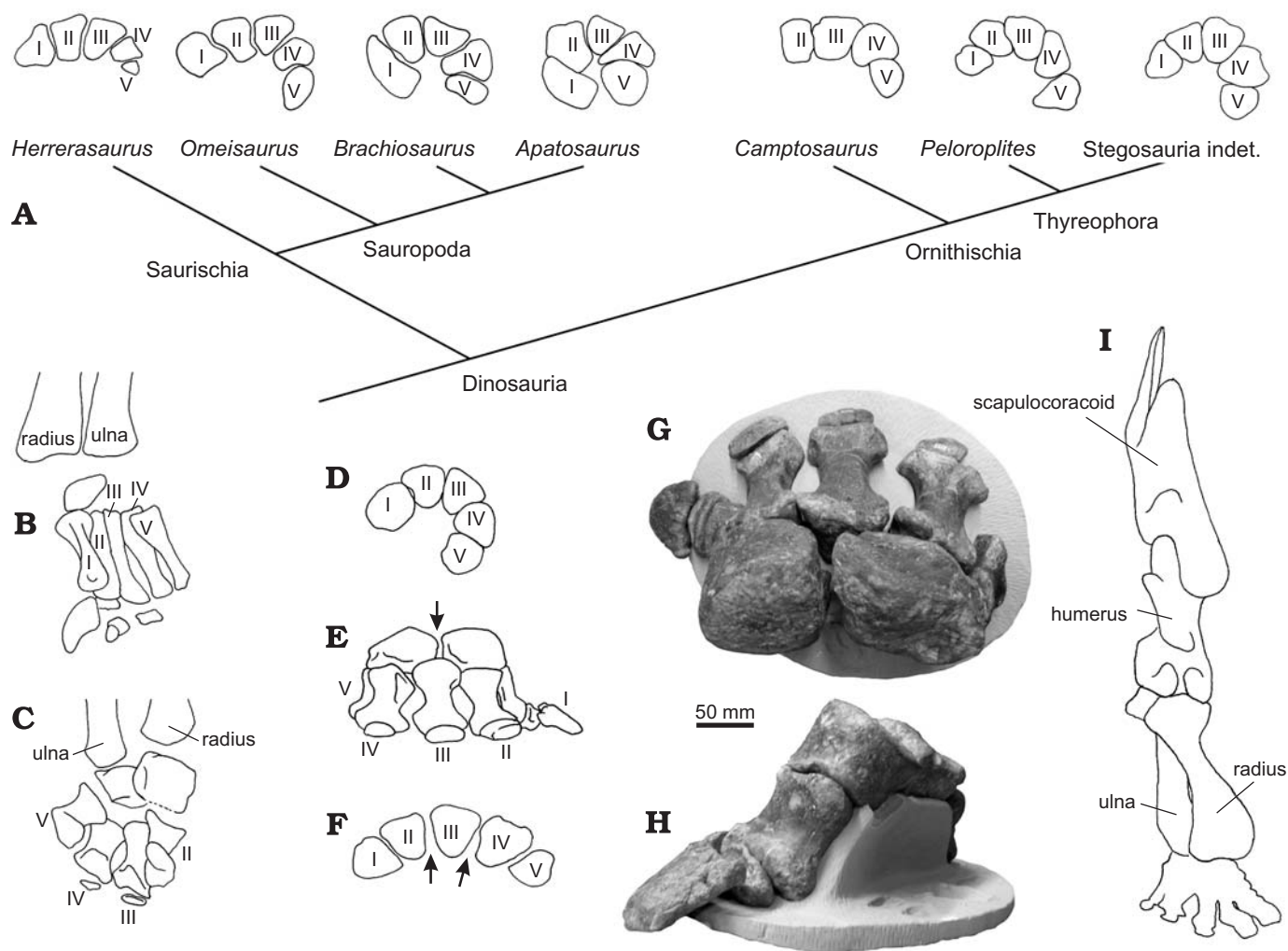


Fig. 1. Manual skeletal configuration in stegosaurs and other dinosaurs. **A.** Cladogram of Dinosauria with proximal views of metacarpals, showing convergent evolution of tightly curved metacarpal arc in Sauropoda and Thyreophora; *Herrerasaurus* after Sereno (1993), sauropods after Bonnan (2003), *Camptosaurus* after Carpenter and Wilson (2008), and *Peloroplites* after Carpenter et al. (2008). **B.** Articulated manus of the sauropod *Camarasaurus lentus*, CM 11338 (after Gilmore 1925). **C.** Articulated manus of the stegosaur *Stegosaurus armatus*, USNM 4934 (right, after Gilmore 1914) as found in situ, showing that the metacarpals form a vertical tube (*C. lentus*) or semi-tube (*S. armatus*). **D.** Articulated metacarpals of the stegosaur *Kentrosaurus aethiopicus* in proximal view (modified from Hennig 1925). **E.** Previous, incorrect reconstruction of the manus of USNM 4937 (Gilmore 1914), a stegosaur of indeterminate genus and species (Maidment et al. 2008), in cranial view, showing unnatural gap between carpals (arrow) (likely *Stegosaurus sulcatus*, Upper Jurassic, USA; see text). **F.** Previous, incorrect reconstruction of the manus of USNM 4937 (Gilmore 1914) in proximal view, showing unnatural gaps between metacarpals (arrows). **G.** Incorrectly articulated right hand of the stegosaur USNM 4937 viewed from above. **H.** Incorrectly articulated right hand of the stegosaur USNM 4937 viewed from obliquely behind and to the left. **I.** Cranial view of mounted right forelimb of *Stegosaurus armatus* AMNH 650, showing distal contact between radius and ulna; carpus and manus are cast from a different specimen. Scale bar applies to photographs only; line illustrations not to scale. Roman numerals refer to digit number.

of indeterminate genus and species (Maidment et al. 2008) that does not show a semi-tubular metacarpal configuration as preserved. However, the gap between the carpus and metacarpus and between the proximal ends of metacarpals I and II (Gilmore 1914) show that, as found, these bones were not in their original positions relative to each other. The carpal bones of USNM 7401 and of USNM 7403, another juvenile stegosaur of indeterminate genus and species (Maidment et al. 2008), were articulated with each other in situ and were in contact (Gilmore 1914), which is consistent with the contact between the carpals that occurs with the metacarpals configured into a vertical semi-tube.

Prediction 6, that the configuration agrees with ichnological evidence, is satisfied for the vertical semi-tube hypothesis and falsified for the slanted and spreading hypothesis. In *Deltapodus brodricki* White and Romano, 1994, an ichnospecies attributed to stegosaurs, the distal metacarpus forms a semicircle. A palmar pad, which would have been necessitated by a slanting and spreading metacarpal configuration (Abel 1912), is absent (Whyte and Romano 2001; Milàn and Chiappe 2009). This is consistent with the vertical semi-tube hypothesis but not with the slanted and spreading hypothesis.

Interestingly, while a palmar pad is absent, a distal pad for metacarpal I appears to be present. As mentioned above, the

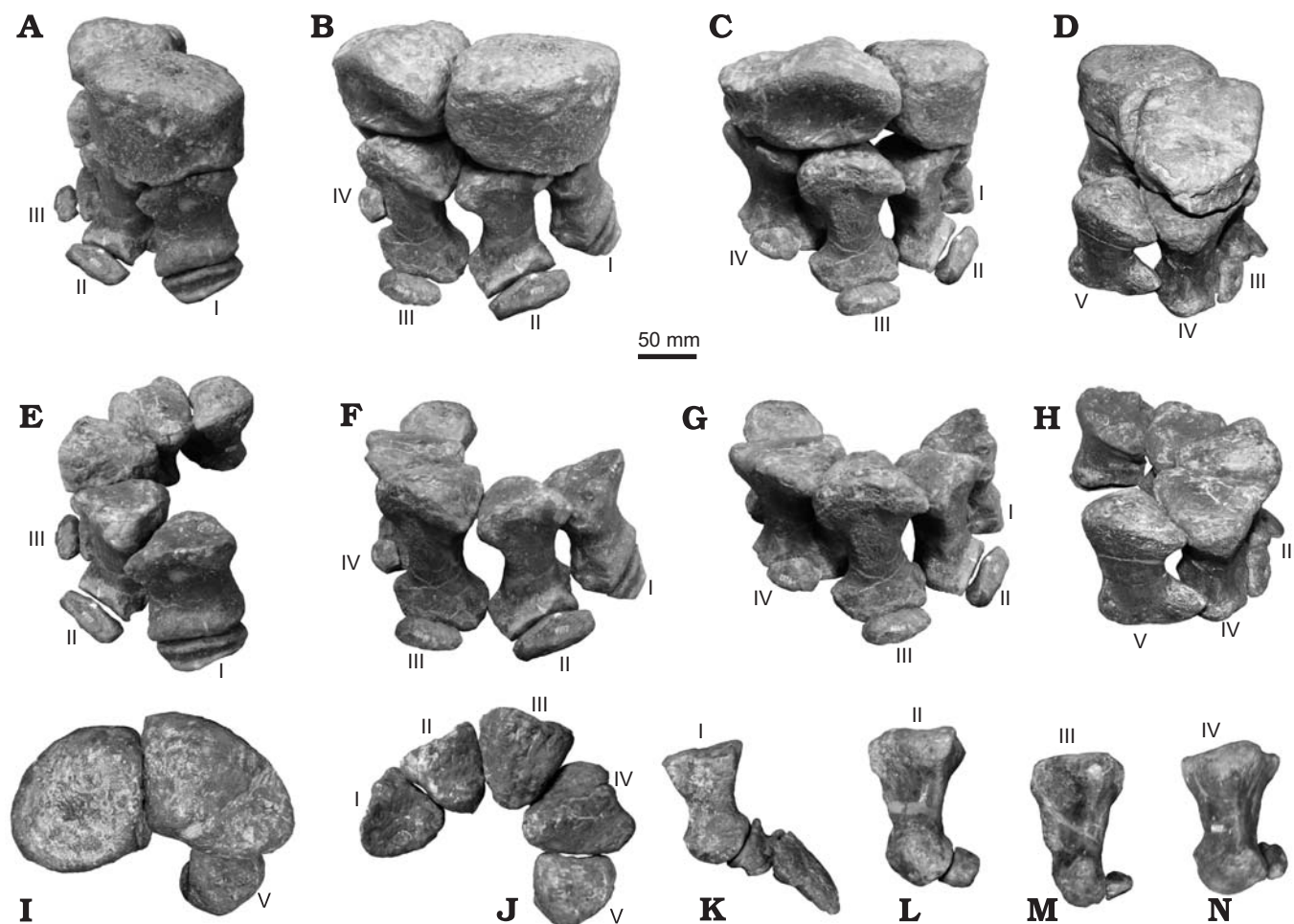


Fig. 2. Correctly articulated (vertically oriented, based on the results of this study) right manual skeleton of the stegosaur *Stegosaurus sulcatus*, from the Upper Jurassic of Wyoming, USA USNM 4937, shown in four oblique views with (A–D, I) and without (E–H, J) carpals, and with each metacarpal shown individually in lateral view with its associated phalanx or phalanges correctly articulated (K–N). Roman numerals refer to digit number.

distal end of this metacarpal is higher above the ground than the distal ends of metacarpals II–IV. A gap would therefore be present in the manus print distal to metacarpal I if a distal pad were not present on the tip of this metacarpal. The lack of such a gap in the manus prints (Whyte and Romano 2001; Milàn and Chiappe 2009) suggests the presence of a distal pad for this metacarpal.

Stegopodus czerkasi Lockley and Hunt, 1998 and an unnamed ichnospecies from Australia, both of which have been attributed to stegosaurs, exhibit a palmar pad. However, stegosaurs probably did not make those two track types, because both ichnospecies exhibit four well-defined fingers (Milàn and Chiappe 2009), whereas no stegosaur is known to have had more than two (Galton and Upchurch 2004).

Conclusion

All predictions of the vertical semi-tube hypothesis of metacarpal configuration in stegosaurs are supported by available data, whereas four of the predictions of the hypothesis of a

slanted and spreading metacarpal configuration in stegosaurs are falsified. The latter hypothesis is therefore falsified, and the former is supported.

Final remarks

This finding adds important details to existing knowledge of functional morphology in stegosaurs. Because of its contact with the ground, the distal metacarpus must have been used to push off during each step. Propulsion with the distal metacarpus instead of the fingers has two important consequences for finger evolution. First, it requires that the fingers remain out of the way of the metacarpus so as not to interfere with its contact with the ground. In both sauropods and stegosaurs this is accomplished by the repositioning of the fingers on the extensor surfaces of the metacarpals instead of on their distal surfaces as is usual for most dinosaurs and other tetrapods. Second, it renders fingers unnecessary for locomotion and therefore allows them to become vestigial or lost. In both sauropods and stegosaurs the lateral fingers are vestigial, with the distal pha-

langes lost and the distalmost remaining phalanges reduced to tiny nubbins or lost (Janensch 1922; Gilmore 1925; Zhang 1988; Galton and Upchurch 2004). In titanosaurian sauropods the fingers are lost altogether (Apesteguía 2005).

Ankylosauria is the sister taxon to Stegosauria (Butler et al. 2008). I did not examine ankylosaurs to test for a sauropod-like metacarpal configuration, but such a configuration is consistent with data that have been collected on the ankylosaur manus. In a manus of the ankylosaur *Saichania chulsanensis* Maryańska, 1977 that was found in articulation the metacarpals are parallel to each other instead of distally divergent, and they are figured and described as forming “an arch with metacarpal V shifted distinctly backward” (Maryańska 1977: 130). The metacarpals of the ankylosaur *Peloroplites cedrimontanus* Carpenter, Bird, Bartlett, and Barrick, 2008 were found disarticulated but when posed in articulation they form a semi-circular arc (Carpenter et al. 2008) (Fig. 1A). Ankylosaur manus prints only include impressions of phalanges and the distal metacarpus, the latter of which exhibits tight curvature, and a palmar pad impression is absent (McCrea et al. 2001). These data suggest that ankylosaurian metacarpals were also configured in a vertical semi-tube, which is consistent with the shapes of ankylosaurian manus prints (Carpenter 1984). Interestingly, the metacarpals were vertical—although in a broad curve rather than a semi-tube—in quadrupedal members of another ornithischian taxon: Ceratopsia (Senter 2007a; Fujiwara 2009).

The appearance of the vertical metacarpal tube in Sauropoda appears to be the result of developmental “dragging” of the metacarpus by the radius as it was reoriented to a more medial position than is usual in other dinosaurs (Bonnar 2003). That evolutionary event facilitated sauropod manual propulsion by causing the palm to face caudally, whereas it plesiomorphically faced medially (Sereno 1993; Bonnar and Senter 2007; Senter 2007b). It is possible that such an evolutionary event happened in the common ancestor of Stegosauria and Ankylosauria also, but a test of that possibility awaits further investigation.

The stegosaurian metacarpus is often mounted in an incorrect slanting and spread configuration (e.g., at the AMNH and the USNM) despite that in this configuration the metacarpals fit neither with each other nor with the rest of the forelimb and that arranging them so that they do fit together produces a vertical semi-tube. This underscores the need to challenge long-standing habits in dinosaur reconstruction with direct, manual manipulation of fossil bones.

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