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Evidence for a sauropod-like metacarpal configuration in ankylosaurian dinosaurs

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Ankylosaurian dinosaurs are armored, quadrupedal members of the ornithischian clade Thyreophora. Ankylosaurs are typically portrayed with the metacarpals slanted and distally divergent, with their proximal ends arranged in a shallow arc, both in the literature (Matthew 1922; Gaston et al. 2001; McCrea et al. 2001; Vickaryous et al. 2004) and in museum mounts (Fig. 1). In contrast, Carpenter (1984) illustrated the metacarpals of the ankylosaur *Sauropelta edwardsorum* Ostrom, 1970, from the Lower Cretaceous Cloverly Formation of Wyoming and Montana, with their proximal ends arranged in a tight, semicircular arc, but even in that depiction the metacarpals were slanted and distally divergent. Members of the thyreophoran clade Stegosauria, the sister taxon to the Ankylosauria (Butler et al. 2008), have also typically been portrayed with slanted and distally divergent metacarpals (Marsh 1891; Gilmore 1914; Galton and Upchurch 2004). Some researchers expressed the opinion that stegosaur metacarpals were held vertically, not distally divergent, with their proximal ends arranged in a tight, semicircular arc, so that the metacarpus formed a vertical half-tube (von Huene 1931; Thulborn 1990; Christiansen 1997) such that flexion of digit I would move it toward digit V. Manual manipulation of stegosaurian metacarpals has since confirmed that this is the correct configuration of the stegosaurian metacarpus (Senter 2010). Here I investigate the possibility that the ankylosaurian metacarpus exhibited a similar configuration.

As in the previous study on stegosaurs (Senter 2010), I treat 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 ankylosaurs predicts that the configuration (1) is allowed by the shapes of the metacarpals, (2) provides a better fit (alignment and contact of opposing articular surfaces) between the metacarpals than the competing hypothesis, (3) does not compromise the goodness of fit between the metacarpals and the phalanges, (4) is not contradicted by articulated specimens, and (5) agrees with ichnological evidence. In the previous study on stegosaurs I included an additional prediction: that the configuration provides sufficient support for and does not disarticulate the more proximal forelimb bones. Here, that prediction is omitted, because the ankylosaurian carpus is unknown (Vickaryous et al. 2004) except for a single carpal described by Maleev (1954).

Institutional abbreviation.—CEUM, College of Eastern Utah Prehistoric Museum, Price, Utah.

Tests of the hypotheses

I tested the first three predictions by manually posing the metacarpals and phalanges of the left manus of the ankylosaur *Peloroplites cedrimontanus* Carpenter, Bartlett, Bird, and Barrick, 2008, a member of the Nodosauridae from the Lower Cretaceous Cedar Mountain Formation of Utah (Carpenter et al. 2008). The bones are all from the same individual, but each has a different accession number. The accession numbers are CEUM 12187–12193, 12218–12223 (Carpenter et al. 2008). The specimen is missing the distal phalanges of the second and fourth digits and all phalanges (if there were any) of the fifth digit.

Prediction 1, that the shapes of the metacarpals allow the configuration, is satisfied for both hypotheses. The metacarpals do not interfere with each other in either pose (Figs. 1–3).

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 *P. cedrimontanus* are wedge-shaped in proximal view so that when articulated in proximal contact with each other, with opposing articular surfaces aligned, they fit tightly together in a vertical semi-tube with no gaps between their proximal ends and with their proximal surfaces together forming a subhorizontal surface, approximately parallel to the ground (although not a perfectly planar surface), as in sauropods (Bonnan 2003) and stegosaurs (Senter 2010). In contrast, when the metacarpals are posed in a slanting and spreading configuration and arranged in a shallow arc in proximal view, there are gaps between the palmar extremities of the proximal ends of the metacarpals (Fig. 2A). It is possible to pose the metacarpals in a slanting and spreading configuration and arranged in a tight arc in proximal view to articulate their beveled proximal shapes (Fig. 3B–F), but in this pose the proximal surfaces of the metacarpals do not form a neat horizontal surface, and the opposing articular surfaces between metacarpals I and II, between III and IV, and between IV and V are misaligned (Fig. 3B–F).

Prediction 3, 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 (Figs.

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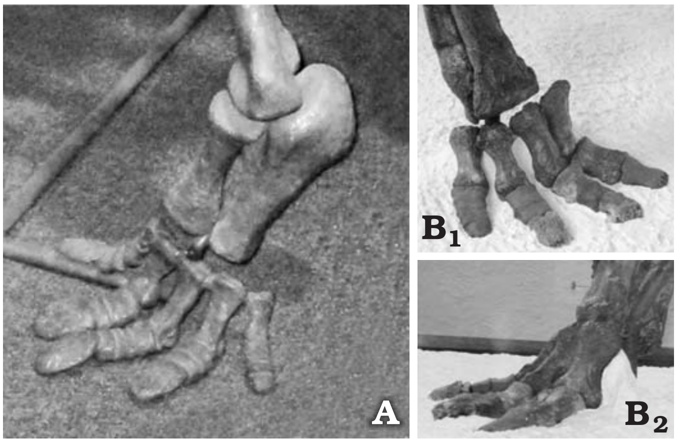

Fig. 1. The manus in mounted skeletons of ankylosaurs, showing metacarpals incorrectly configured in a shallow arc with their shafts slanted and their distal ends divergent. **A**. *Gastonia burgei* Kirkland, 1998 from Cedar Mountain Formation, Utah, USA; College of Eastern Utah Prehistoric Museum, Price, Utah, in oblique dorsolateral view. **B**. *Edmontonia rugosidens* Gilmore, 1930 from Dinosaur Park Formation, Alberta, Canada; American Museum of Natural History, New York City, New York, USA, in oblique dorsolateral (B_1) and medial (B_2) views.

1, 3B–F). As in sauropods and stegosaurs the articular surface for the proximal phalanx is located on the extensor surface of each metacarpal rather than on the distal surface (Fig. 3A), so that with a vertical metacarpus the finger is perpendicular to the metacarpal and parallel to the ground (Fig. 3B–F). As in stegosaurs (Senter 2010) the phalanges of the thumb are less horizontal than those of the other fingers. However, as in stegosaurs the slant of the thumb can be accommodated with a vertical metacarpus because metacarpal I is shorter than metacarpals II–IV so the distal end of metacarpal I is held off the ground (Fig. 3A).

Prediction 4, 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. Only one known ankylosaurian metacarpus is articulated in situ, that of a specimen of the ankylosaurid *Saichania chulsanensis* Maryańska, 1977, from the Upper Cretaceous Barun Goyot Formation of Mongolia. In that specimen the long axes of the metacarpals are parallel to each other and form an arc in proximal view (Maryańska 1977). Measured along the palmar surfaces of the proximal ends of the metacarpals in proximal view, the arc is nearly a semicircle (Fig. 4). Its shallower appearance is an optical illusion caused by enlargement of the proximal end of the first metacarpal (Fig. 4).

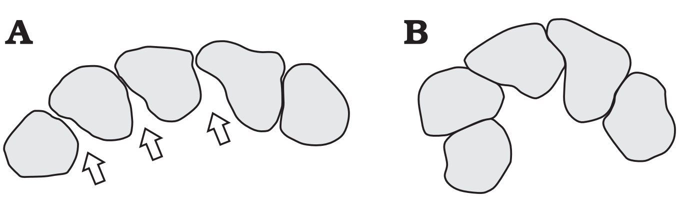

Fig. 2. Proximal view of left metacarpals of the ankylosaur *Peloroplites cedrimontanus* from Cedar Mountain Formation, Utah, USA; with digit I to the right, incorrectly configured in a shallow arc (**A**) and correctly configured in a semicircle (**B**). Note the presence of gaps (arrows) between the metacarpals in A and their closure in B.

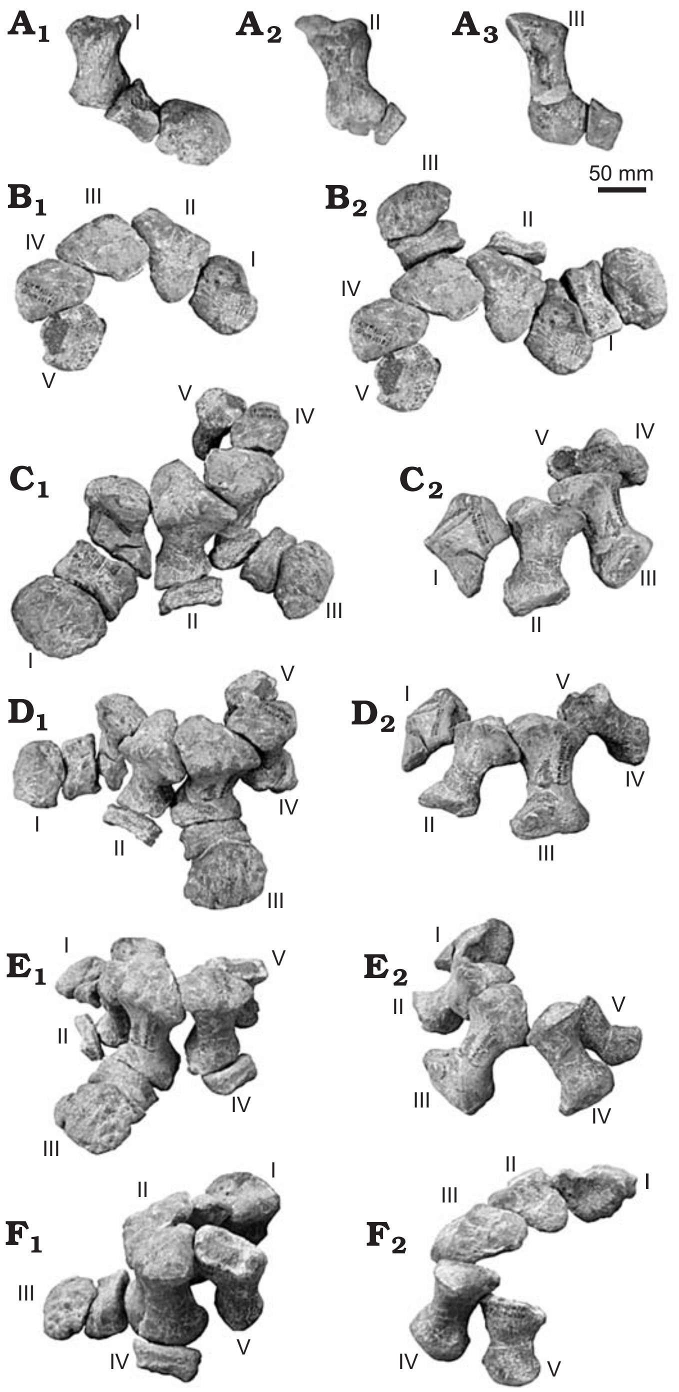

Fig. 3. Left manual skeleton of the ankylosaur *Peloroplites cedrimontanus* Carpenter, Bartlett, Bird, and Barrett, 2008 from Cedar Mountain Formation, Utah, USA (CEUM 12187–12193, 12218–12223); articulated correctly and incorrectly. **A**. Metacarpals in pollucal view, correctly articulated with phalanges: I (A_1), II (A_2), and III (A_3). **B**. Metacarpals in proximal view, correctly articulated without (B_1) and with (B_2) available phalanges. **C**–**F**. Correctly (C_1–F_1) and incorrectly (C_2–F_2) articulated metacarpals shown in four oblique views with (C_1–F_1) and without (C_2–F_2) available phalanges. **C**. Craniodorsal view, centered on digit II. **D**. Craniodorsal view, centered on digit III. **E**. Laterodorsal view, centered between digits III and IV. **F**. Caudodorsal view, centered between digits IV and V. In both configurations the metacarpals are arranged in a tight arc, but they are vertical and parallel to each other in the correct configuration, whereas they are slanted and distally divergent in the incorrect configuration. Roman numerals refer to digit number.

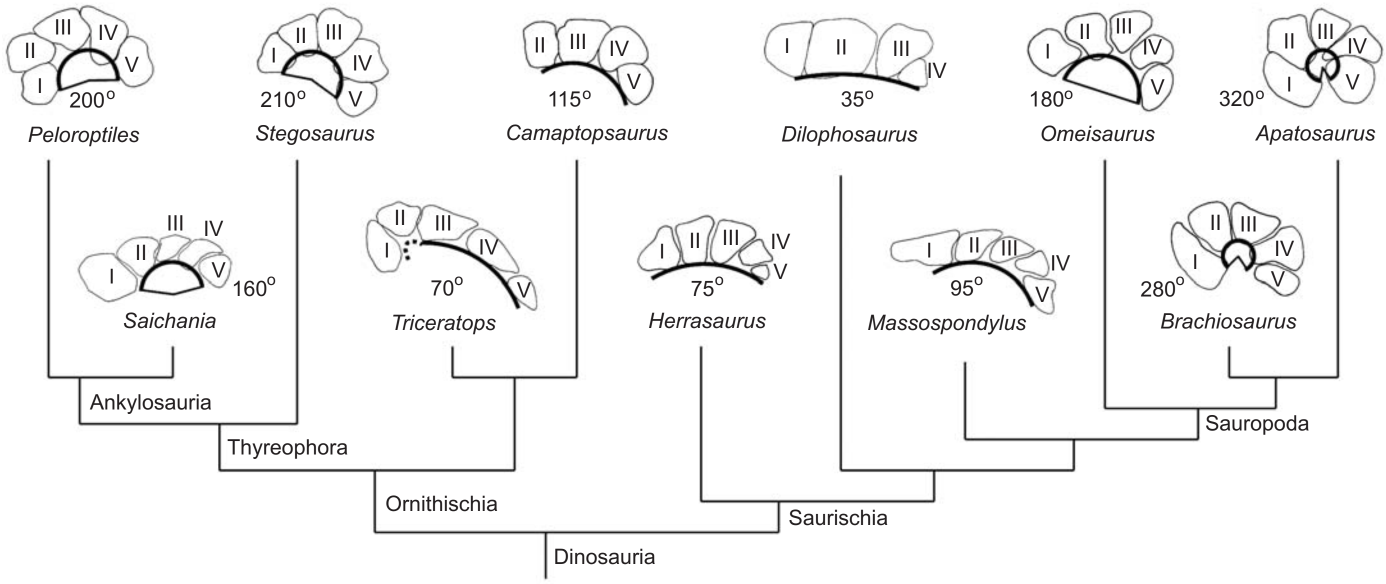

Fig. 4. Proximal views of the metacarpus in the Dinosauria, showing that a semicircular configuration is present only in the Thyreophora and basal Sauropoda. Sources of drawings are as follows: *Saichania*, Maryańska (1977); *Stegosaurus*, Senter (2010); *Triceratops*, Fujiwara (2009); *Camptosaurus*, Carpenter and Wilson (2008); *Herrerasaurus*, *Massospondylus*, *Omeisaurus*, *Brachiosaurus*, and *Apatosaurus*, Bonnan (2003); *Dilophosaurus*, modified from photo by author. Roman numerals refer to digit number.

Prediction 5, that the configuration agrees with ichnological evidence, is satisfied for the vertical semi-tube hypothesis and falsified for the slanted and spreading hypothesis. North American and European ankylosaur manus tracks form a semicircular arc with no impression of a palmar pad (McCrea et al. 2001). A palmar pad to support the metacarpals from beneath is expected for metacarpals that slant, as has previously been pointed out (Senter 2010). The manus prints exhibit a distal pad for metacarpal I, bridging the gap between this short metacarpal and the ground, as in stegosaurs (Senter 2010). Bolivian dinosaur tracks that have been attributed to ankylosaurs exhibit manus impressions that lack an arced shape, indicating that the distal ends of the metacarpals were in a line rather than an arc (McCrea et al. 2001). However, these tracks are probably not ankylosaurian, because both the manus prints and the pes prints are dissimilar to ankylosaur tracks from elsewhere.

Conclusion

All predictions of the vertical semi-tube hypothesis of metacarpal configuration in ankylosaurs are supported by available data, whereas three of the predictions of the hypothesis of slanted and spreading metacarpal configuration are falsified. The latter hypothesis is therefore falsified, and the former is supported.

Discussion

The Ankylosauria are the sister taxon to the Stegosauria (Butler et al. 2008). The two share a vertical, semi-tubular metacarpal configuration that is absent in other ornithischians (Norman 1980; Senter 2007; Carpenter and Wilson 2008; Fujiwara 2009), suggesting the possibility that they inherited this configuration from a common ancestor. In other ornithischians and in saurischians other than sauropods, the metacarpals are arranged in a shallow arc. In those dinosaurs the arc is less than 120°, and usually less than 100°, when measured along the palmar edges of the proximal ends of the metacarpals in proximal view (Fig. 4), although it should be noted that in ceratopsids this arc is disrupted by palmar displacement of the first metacarpal. The proximal metacarpal arc is closer to a semicircle in the Thyreophora, as in basal sauropods such as *Omeisaurus* (Fig. 4). In later sauropods the proximal metacarpal arc far exceeded this curvature and came closer to forming a closed circle (Fig. 4). The absence of a semicircular proximal metacarpus in other ornithischians and in saurischians other than basal sauropods (Sereno 1993; Bonnan 2003; Senter 2006) indicates that its common presence in the Thyreophora and basal Sauropoda is an example of convergent evolution.

As is the case with stegosaurs, the ankylosaur manus is often incorrectly portrayed with distally divergent metacarpals (Matthew 1922; Carpenter 1984; Gaston et al. 2001; McCrea et al. 2001; Vickaryous et al. 2004) (Fig. 1). The results of this study underscore the need to test long-standing habits in dinosaur reconstruction with direct, manual manipulation of fossil bones.

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