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A probable stegosaurian track from the Late Jurassic of Poland

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Elusive tracks of stegosaurs have been long searched for by ichnologists, and various purported stegosaur imprints have recently been reported. A fragmentary trackway of a large, quadrupedal ornithischian dinosaur was found on an isolated slab of Oxfordian dolomite, on the northeastern slope of Holy Cross Mountains, Poland. The track is similar to large, blunt-toed Late Jurassic ichnites from North America. The footprints show a distinctive morphology, which fits the stegosaurian foot. The newly described ichnites from the Upper Jurassic of Poland provide the second ichnological evidence of the Late Jurassic dinosaurs in this country; numerous rich dinosaur footprint assemblages were previously known only from the Lower Jurassic outcrops.

Introduction

Stegosaurian tracks present a conundrum to ichnologists. Skeletal remains of stegosaurs are well documented in several Late Jurassic and Early Cretaceous deposits where footprints are also preserved, like the Morrison Formation of the western USA and the Spanish Weald. However, no stegosaur tracks were convincingly recognized until 1996. The first reliable identifications of the elusive footprints comprised Late Jurassic finds from Utah (Bakker 1996; Lockley and Hunt 1998).

Contrary to a conjectural reconstruction of stegosaur footprints as plantigrade impressions, proposed by Thulborn (1990), Bakker (1996) suggested a stegosaur origin for a digitigrate pedal print with extremely short toes, found in the Cleveland Lloyd Dinosaur Quarry. This specimen, from the Upper Jurassic Morrison Formation, was originally illustrated by Bakker (1996) with a mistaken caption pointing to Como Bluff as its source locality (Lockley and Hunt 1998). Another purportedly stegosaur ichnite was described and named *Stegopodus czerkasi* by Lockley and Hunt (1998). This is a natural cast of a manual imprint, associated with a cast of a pedal imprint, which was not included in the type, and which remains unnamed, because the authors were not fully convinced that both ichnites were left by the same trackmaker. Recently, *Deltapodus brodricki* Whyte and Romano, 1994, from the Middle Jurassic Saltwick Formation of Yorkshire, England, described originally as a sauropod trackway, has been also reconsidered as stegosaurian in origin (Whyte and Romano 2001). The tracks from Yorkshire are more robust than those from the Morrison Formation, and comprise large plantigrade pedal imprints and manual impressions resembling those of sauropods. These features reveal substantial morphological differences between supposed stegosaurian tracks from Yorkshire and Utah.

In the opinion of McCrea et al. (2001), the lack of inward rotation of the *Deltapodus* pedal imprints and the bluntness of the digits are more reminiscent of ankylosaurian tracks rather than the purported stegosaurian ones from Utah. We can add similar observations regarding Early Jurassic thyreophoran footprints *Anomoepus pienkovskii* Gierliński, 1991, also showing ankylosaurian-like track pattern. Interestingly, those medium-sized, quadrupedal tracks from the late Hettangian of Poland occur in association with large blunt-toed and bipedal footpints of *Moyenisauropus karaszevskii* Gierliński, 1991. The latter tracks have recently been inferred to be stegosaurian in origin (Le Loeuff et al. 1998, 1999; Gierliński 1999; Lockley and Meyer 2000). The co-occurrence of both types of tracks suggests that the stegosaurian lineage might have diverged from the ankylosaurian one as early as in the earliest Jurassic. Such timing is supported also by a phylogenetic analysis based on skeletal fossils (Carpenter 2001).

Recently, a large blunt-toed tridactyl ornithischian footprint has been discovered in the Upper Jurassic of Poland (Gaździcka et al. 2001). In May 2001, amateur fossil collector Artur Gołasa noticed an isolated slab of a yellowish gray dolomite with brown cherts, lying on the southern slope of the Larch Nature Preserve near the newly constructed post office building in Bałtów, a village northeast of the town of Ostrowiec Świętokrzyski, in the Holy Cross Mountains. The isolated slab most probably belongs to the dolomitized and chert-enriched upper part of the local unit recognized by Gutowski (1998) as the Bałtów Coral Limestones. Thus, according to the latter author, the specimen could be dated to the latest middle Oxfordian. However, the exact lithostratigraphical correlation of the slab will require future field research in the Bałtów area. The research may prove difficult, because there is no available outcrop in the vicinity of the find (the slab might have been excavated during construction work at the post office site).

The slab bears at least four impressions, including a left manus-pes set (Fig. 1A, B), and partial right pes imprint (Fig. 1C) of the same large ornithischian trackmaker. There is also a small theropod footprint, 15 cm long (Fig. 1D), similar to *Jialingpus* Zhen, Li, and Zhen, 1983 from the Late Jurassic of China, originally attributed to an ornithischian, and subsequently assigned to a theropod trackmaker (Gierliński 1994).

The newly described ichnites from Bałtów provide the second ichnological evidence of Late Jurassic dinosaurs in Poland; preceded by an ornithopod footprint (Fig. 2B) from the Kimmeridgian of Ożarów (Gierliński et al. 2001).

Institutional abbreviations—HMN, Humboldt Museum für Naturkunde, Berlin, Germany; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing, China; MHKM, Museum of Material Culture History, Starachowice, Poland; Muz.PIG, Geological Museum of the Polish Geological Institute, Warsaw, Poland; PMA, Provincial Museum of Alberta, Edmonton, Canada; PMP Prehistoric Museum at Price, Utah, USA, USNM, United States National Museum, Washington, DC, USA.

Description of the ornithischian trackway

Fragmentary wide-gauge ornithischian trackway with a left manus-pes set and a part of the right pes is preserved as natural mold on the slab MHKM GG/2 (Fig. 1A–C).

Blunt-toed tridactyl pes (Fig. 1A) is slightly longer than wide (27 cm long and 24 cm wide). Digit IV barely projects beyond the hypex, while digits II and III are better defined. Digits II and III are more strongly impressed (about 4–5 cm deep) than digit IV (1–2 cm deep). Digits diverge widely, but the angles between their axes are relatively

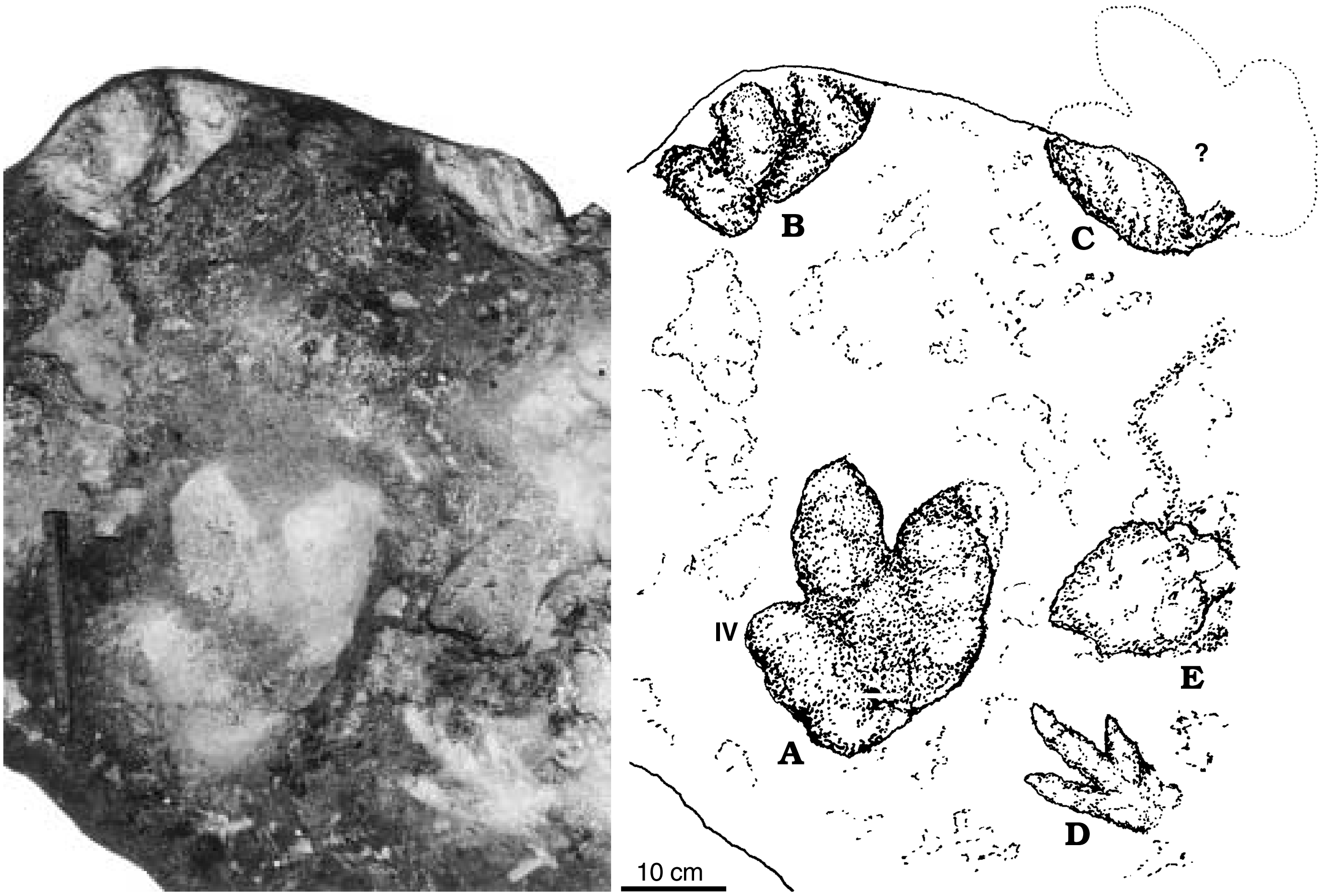

Fig. 1. **A**–**D**. The slab MHKM GG/2 from the Oxfordian of Bałtów, Poland, with footprints of a large ornithischian (**A**–**C**) and of a small theropod (**D**). **A**, **B**, left pes-manus set; **C**, fragment of right pedal imprint. **E**. Eroded part of the surface.

low (II–III = 8°, II–IV = 22°). Almost the entire surface of lateral digits together with the metatarsophalangeal pad of the middle toe constitute a broad "heel" area. The metatarsophalangeal pad of the fourth digit is, however, distinctly pointed, and is the most posteriorly located part of the footprint. The proximal portion of the imprint, the so-called "heel" area, equals 62% of the footprint length.

Despite such "heel-dominated" morphology, digital nodes are discernible, thus providing the opportunity to apply the osteometric method of digit length measurements. Following the method of Olsen et al. (1998), digit length ratios are: III/II = 0.98, III/IV = 1.09.

The manual imprint (Fig. 1B) is less informative than the pedal one. The ichnite is more a manual drag mark than a regular impression of the hand. It is situated anteriorly to the pes, and is slightly wider (25 cm) than the pedal impression. The manus is wider than long (length 17 cm) and slightly wider than the pedal imprint. The first, blunt digit made a moon-shaped trace, the second and third digits produced shorter elongate imprints. Although the manual morphology is distorted, it is possible to conclude that the print has been left by a relatively large, entaxonic digitigrade manus.

Discussion

The pedal print from Bałtów differs from comparably large ornithopod tracks by having an asymmetrically located proximal pad. The proximal pad of our specimen is mainly developed on the swollen metatarsophalangeal pad of digit IV. In contrast, the large ornithopod footprints such as *Gypsichnites* Sternberg, 1932, *Amblydactylus* Sternberg, 1932 (Fig. 2C), and *Caririchnium* Leonardi, 1984 (originally misinterpreted as stegosaur track), show more distinctively imprinted digits, while their metatarsophalangeal pads are well fused into a single proximal pad. This so-called "heel" is located centrally, below the toes, and makes these footprints symmetrically shaped. Most importantly however, there is no osteological evidence from the Upper Jurassic to confirm the presence of such large ornithopods with pedal digits ending in broad hooves. The only hoofed animals presently known to live in the Late Jurassic and to have feet able to produce such large, blunt-toed footprints are stegosaurs.

This track resembles specimens from the Morrison Formation of Utah: one reported by Bakker (1996) as a stegosaur track (Fig. 2A), and another, a pedal ichnite associated with a tetradactyl manual imprint named *Stegopodus czerkasi* Lockley and Hunt, 1998. The manual imprint from Bałtów differs from *Stegopodus* in being tridactyl and lacking a metacarpal proximal pad, present in *Stegopodus*. Consequently, our specimen cannot be assigned to *Stegopodus czerkasi*. Further comparison of *Stegopodus* and the Bałtów footprints will remain difficult until *Stegopodus* is found with an unquestionably associated pedal print.

Digital length ratios of the pes from Bałtów (III/II = 0.98, III/IV = 1.09) fit well within the range for stegosaur feet (*Stegosaurus* Marsh, 1877, USNM 4280: III/II = 1.00, III/IV = 1.16; *Kentrosaurus* Hennig, 1915, HMN Ki112: III/II = 0.92, III/IV = 1.05). The values of digit length ratios for *Kentrosaurus* are calculated for a properly oriented foot. The foot of *Kentrosaurus aethiopicus* Hennig, 1915, specimen HMN Ki112, has been repeatedly illustrated mislabeled as the right pes (e.g., Galton 1982: pl. 5:1, 2; Thulborn 1990: fig. 6.38). In fact, it is the left foot

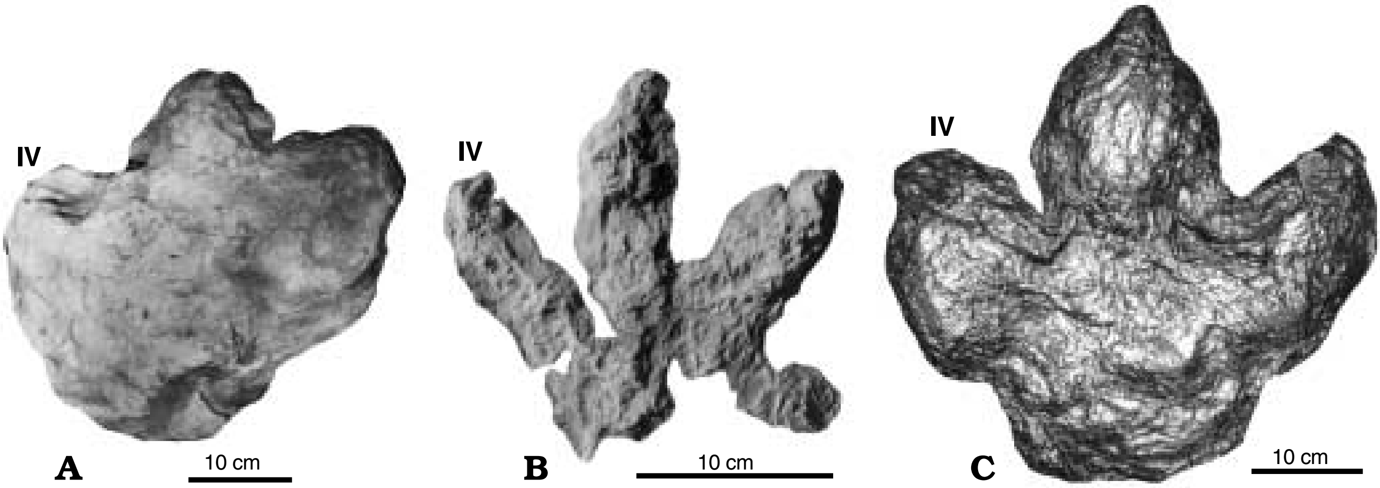

Fig. 2. Three major morphological patterns of large ornithischian footprints from the Late Jurassic and Early Cretaceous. **A**. Specimen reported by Bakker (1996) as a stegosaur footprint from the Morrison Formation (exhibit on display at PMP). **B**. cf. *Dinechichninus* sp., a probable camptosaur print from the Ożarów Oolite and Platy Limestone of Poland (Muz.PIG. 1663.II.3). **C**. Iguanodontid ichnite *Amblydactylus kortmeyeri* Currie and Sarjeant, 1979, from the Gethring Formation of British Columbia (holotype, PMA P76.11.11).

(Hennig 1925: 222, fig. 49a, b). The mistaken reconstruction can be traced to mislabeling of digits in fig. 50 in Hennig (1925): the caption states that this is the left foot; moreover, in the text the author mentions that the lower half of metatarsal II is missing. However, the digit starting from the metatarsal with dotted, reconstructed distal part is labeled as IV on the drawing. Later authors evidently copied this reversed scheme.

Characteristically, the second digit of stegosaurian foot is the longest, and ends with the largest ungual phalanx, while the fourth digit is the smallest one (Fig. 3). The ichnite from Bałtów described here perfectly reflects such a pattern.

We believe the manual trace (Fig. 1B) is almost complete, thus morphologically distinct from the pedal one (Fig. 1A). Moreover, the track-bearing slab from Bałtów had possibly preserved another manual print, a right one, that later eroded badly (Fig. 1E). However, other interpretations do exist. James O. Farlow (written communication 2001) proposed that the manual print (Fig. 1B) might in fact represent a left pedal imprint truncated by the edge of the slab, and both left tracks represent two successive impressions of the left pes. Thus, all three impressions (Fig. 1A–C) would have been produced by a biped taking short steps.

Generally, the existence of bipedal stegosaur trackways may be accounted for in several ways. The most obvious possibility to consider would be that at least some stegosaurs were bipeds or facultative bipeds, an idea discussed by Gierliński (1999, 2001) and Lockley and Meyer (2000). The ichnological data suggest that the stegosaurian ancestors could have been semibipedal thyreophorans that left distinctive tracks known as *Moyenisauropus karaszevskii* Gierliński, 1991 (Le Loeuff et al. 1998, 1999, Gierlinski 1999, Lockley and Meyer 2000). In the opinion of Galton (1982), the ancestor of Stegosauridae *sensu* Galton (1990) was probably an Early Jurassic form resembling the Middle Jurassic *Lexovisaurus* Hoffstetter, 1957. *Lexovisaurus* appears to have been a bipedal or semibipedal form, having a relatively large pelvis, strong and long hind limbs, and very short forelimbs.

A second possibility is that some trackmakers have overprinted their manual prints by their feet (Paul 1991; Lockley 1998). Such a gait might be expected in the case of short-bodied *Stegosaurus* Marsh, 1877. It is easy to imagine that this stegosaur would step with its feet onto the handprints, thus creating an apparently bipedal trackway.

The "bipedal" trackways of quadrupedal stegosaurs could also be attributed to the "undertrack syndrome". Undertracks occur as a result of deformation of deeper layers of the substratum, beneath the actually trampled surface (see e.g., Lockley 1991). The center of gravity in *Stegosaurus* seems to have been located quite far posteriorly, near the pelvic area. This was discussed by Bakker (1986: 187–192) in the context of high-browsing adaptations, and is a century-old observation dating back to Marsh. Thus, the *Stegosaurus* forefeet would exert much lesser pressure onto the substrate, and only the heavily pressed hindfeet would leave impressions in the underlayers, then preserved as undertracks. In some instances, for example, where skin impressions are preserved, distinguishing real tracks from undertracks is fairly easy. In most cases, however, when dealing with naturally exposed track-bearing surfaces, we have no idea how many of the impressions are in fact undertracks (Lockley 1989).

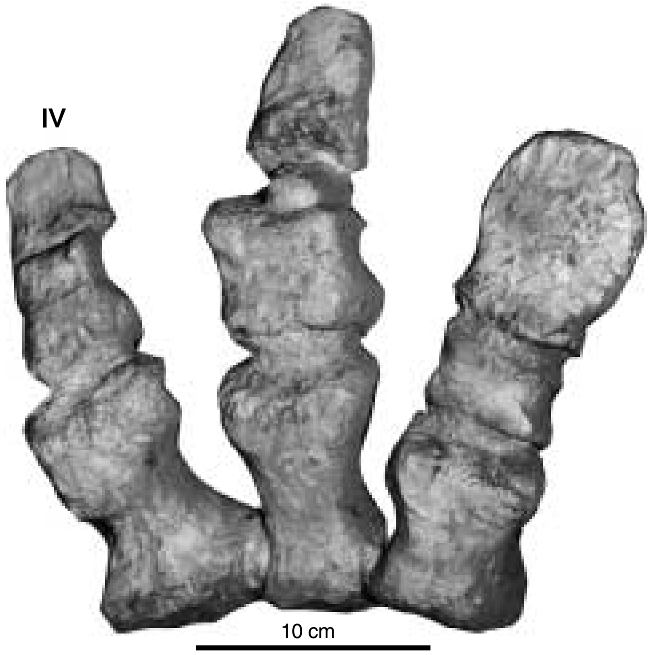

Fig. 3. Stegosaur right foot skeleton in ventral view, exemplified by *Tuojiangosaurus multispinus* Dong, Li, Zhou, and Chang, 1977 from the Upper Shaximiao Formation of China (display mount at the IVPP).

There was extensive morphological diversity among stegosaurs, so that variation in their trackway patterns may be expected. The large, short-bodied *Stegosaurus* could produce bipedal or seemingly bipedal tracks. However, the wide and quadrupedal trackway from Poland was probably been left by a smaller, *Kentrosaurus*-like trackmaker with a body more elongated than in *Stegosaurus*.

A final argument in favor of the interpretation that the track is stegosaurian in origin, is that no large tridactyl ornithopod, or ornithopod-like tracks, similar to those found in the Late Cretaceous and attributed to iguanodontids or hadrosaurs, have yet been found in the Late Jurassic, even though possible candidates, the camptosaurs—have been considered.

The camptosaur foot skeleton suggests that the tracks should be smaller, and the toe imprints should be more pointed than in the supposed stegosaurian ichnites. Occasionally, the hallux imprint might be also preserved. Such a pattern is visible in a footprint from the Morrison Formation, originally attributed to a dryosaur (Bakker 1996: fig. 2) and in an ichnite reported by Gierliński et al. (2001) from the Kimmeridgian of Poland and identified as cf. *Dinehichnus* sp. (Fig. 2B). The best candidates for dryosaur footprints are indeed the largest specimens of *Dinehichnus socialis* Lockley et al., 1998, from the Morrison Formation of Utah, while the smaller *Dinehichnus* and/or *Anomoepus*-like tracks might in fact be of hypsilophodontid origin. Thus, all dominant ornithischians of the Morrison times appear to have been preserved in the ichnological record.

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