



Tracks of a large thyreophoran dinosaur from the Early Jurassic of Poland

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The origin of a large ornithischian track *Moyenisauropus karaszewskii* Gierliński, 1991, from the Hettangian of the Holy Cross Mountains of Poland, needs reappraisal. Hitherto, this taxon was difficult to compare with any known Liassic ichnotaxon from the Northern Hemisphere. Its previous taxonomic assignment is controversial as well. *M. karaszewskii* has been previously considered as a track of some unknown earliest iguanodontian, despite the lack of a supporting osteological record nor phylogenetic inferences based on timing and evolutionary patterns in advanced ornithopods. Thus, a new interpretation is proposed: this footprint may fit the foot of a basal thyreophoran such as *Scelidosaurus harrisonii* Owen, 1861 or a more stegosaur-like form. Also, the problematic Early Jurassic tracks *Moyenisauropus natator* Ellenberger, 1974 and *Anomoepus pienkovskii* Gierliński, 1991, appear to be intermediate forms between the basal ornithischian tracks of *Anomoepus* Hitchcock, 1848 and the early advanced thyreophoran track of *M. karaszewskii*.

The ichnogenus *Moyenisauropus* Ellenberger, 1974 has remained one of the most problematic ichnotaxa among the Early Jurassic tridactylous tracks. Ellenberger (1974) erected the ichnogenus *Moyenisauropus* to comprise eight ichnospecies of the Liassic ornithischian ichnites from Lesotho: *Moyenisauropus natator*, *M. minor*, *M. vermivorus*, *M. dodai*, *M. natatilis*, *M. levicauda*, *M. longicauda* and *M. minimus*. Subsequent authors considered *Moyenisauropus* as junior synonym of *Anomoepus* Hitchcock, 1848 (Olsen & Galton 1984; Thulborn 1994). There are indeed no morphological differences between *Anomoepus* and most ichnospecies of *Moyenisauropus* to distinguish them at the ichnogenetic level. However, *Moyenisauropus natator* (the type ichnospecies of *Moyenisauropus*) is different from any anomoepodid tracks. In *M. natator* the length ratio (*sensu* Olsen *et al.* 1998) of digit III/IV equals 0.66, which is below the value typical for anomoepodid tracks. Such ratios measured in the pes of supposed Early Jurassic anomoepodid trackmakers (*Lesothosaurus*, *Scutellosaurus*, *Heterodontosaurus*) are never lower than 0.7, according to Olsen *et al.* (1998: table 3).

Moreover, *M. natator* demonstrates a feature unusual among Liassic tridactylous tracks: it has only two phalangeal pads on digit III. This may have been caused either by having only two phalangeal joints on that digit, or three joints, if the penultimate phalanx was so short that the two distal joints correspond to one distal pad. As exemplified by lateral toes of extant *Rhea americana* (Farlow & Chapman 1997: fig. 36.11), very short distal non-ungual phalanges of the iguanodontid and scelidosaurid pedal digit III may have been covered by a single distal phalangeal pad on that digit, actually corresponding to more than one terminal phalangeal joint.

Distinctive features of *Moyenisauropus natator* are even more expressed in *Moyenisauropus karaszewskii* Gierliński, 1991 from the late Hettangian of Gliniany Las, Poland (Fig. 1C–F). The Polish form is more robust, with phalangeal pads much wider than those of *M. natator*. The metatarsal-phalangeal pads of *M. karaszewskii* are almost fused into a large swollen proximal pad, a so-called heel pad. The track length reaches 25 cm, being markedly larger than anomoepodids, whose pedal imprints are usually about 10 cm long. Thus, the size (pedal length about 20 cm) and shape of *M. natator* seem to be morphologically intermediate between *Anomoepus* and *M. karaszewskii*.

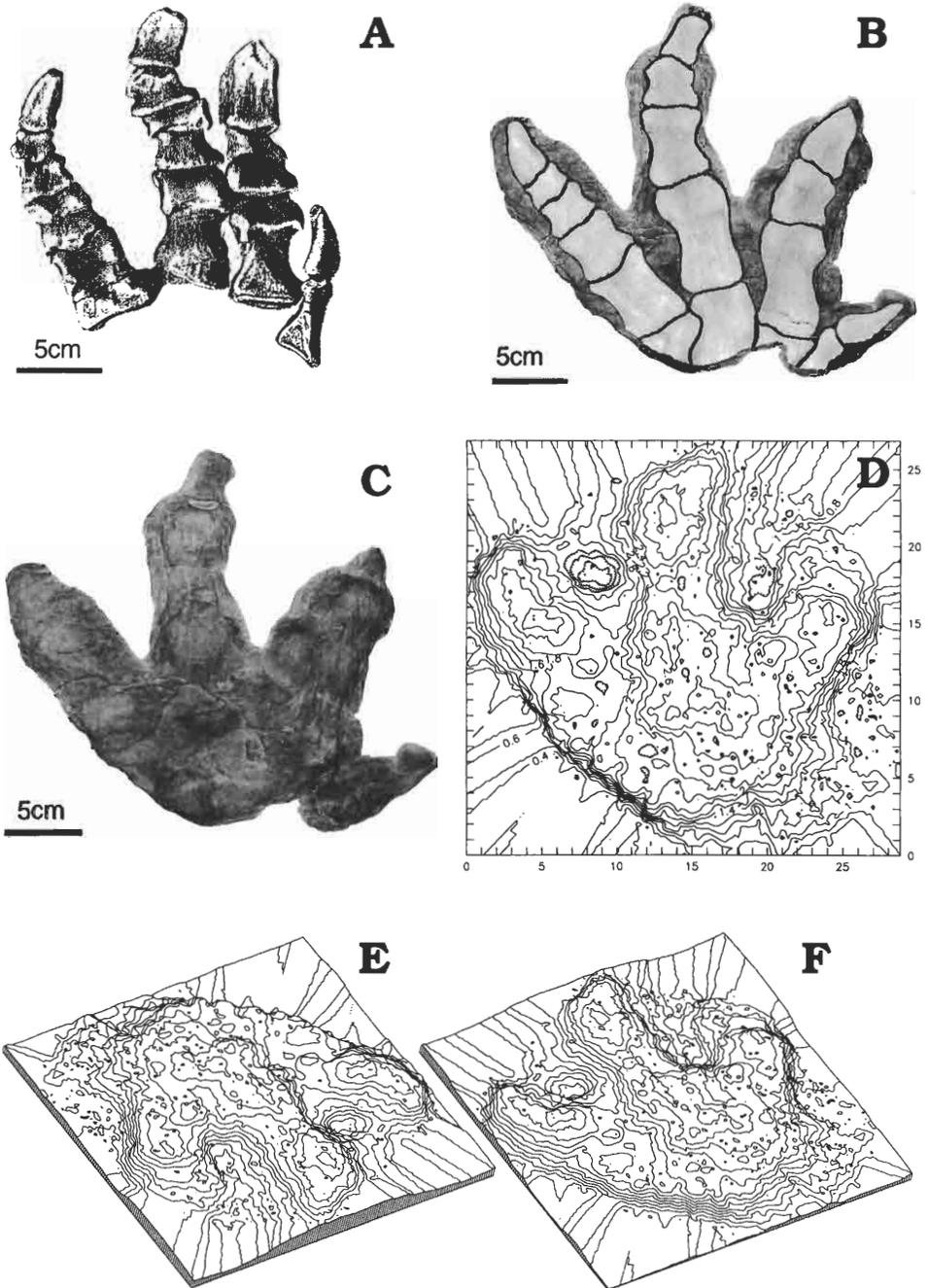


Fig. 1. **A.** Pes of *Scelidosaurus harrisonii* Owen, 1861 (from Owen 1863) superimposed (**B**) onto *Moyenisauropus karaszewskii* Gierliński, 1991 from the late Hettangian of Gliniany Las, Poland (**C**). **D–F.** Computer-generated topographic maps of the *M. karaszewskii*, digitized by J.O. Farlow in 1995. The illustrated track owned by author; its plaster cast ZPAL z.p.R.II/1 is housed in the Institute of Palaeobiology of the Polish Academy of Sciences.

M. karaszewskii has been previously considered as an ichnite of some unknown early iguanodontid (Gierliński 1991). However, no Early Jurassic remains of such purported trackmaker are known. New evidence pertaining to the identity of the *M. karaszewskii* trackmaker appeared with the recent discovery of similar, if not conspecific, footprints from the Hettangian of Dordogne, France. The French tracks led Le Loeuff *et al.* (1998, 1999) to conclude of a basal thyreophoran affinity for their trackmaker. Their conclusion was mainly supported by the features predicted for stegosaur tracks. Contrary to the Polish bipedal trackway, the French one contains manual imprints, which resemble a manus impression of *Stegopodus czerkasi* Lockley & Hunt, 1998, a Late Jurassic track from Utah attributed to a stegosaur.

However, the stegosaur-like affinity suggested for the French and Polish tracks is not the only available interpretation. The presence of hallux imprints in these tracks is discrepant with the strictly tridactyl pes of stegosaurs. The phalangeal pad formula 1-2-2-2-0 (metatarsal-phalangeal pads not included in the count) of the tracks in question does not fit the stegosaurian foot pattern well (*contra* Le Loeuff *et al.* 1999). The primitive stegosaurian phalangeal formula 0-2-3-3-0 in *Huayangosaurus* is reduced to 0-2-2-2-0 in the more advanced forms like *Stegosaurus* (Galton 1990). Thus, the phalangeal pads, if they correspond to the phalangeal joints, constitute a formula 0-1-2-2-0 for primitive stegosaurs, and 0-1-1-1-0 for the advanced ones. So, conceivably, the advanced stegosaur foot pattern might have produced an iguanodontid-like track, with single phalangeal pads on each toe (see Bakker 1996).

In my opinion, the pedal morphology and the Hettangian age of both Polish and French tracks speak in favor of a pre-stegosaurian trackmaker. The foot of the basal thyreophoran *Scelidosaurus harrisonii* Owen, 1861 shows a phalangeal formula of 2-3-4-5-0 (Fig. 1A). Extremely short distal phalanges of *Scelidosaurus* digit III and IV may have resulted in the reduction of pad numbers in these digits. Consequently, a foot of *Scelidosaurus* superimposed onto the footprint of *Moyenisauropus karaszewskii*, fits quite well (Fig. 1B). Alternatively, *M. karaszewskii* may represent pedal morphology linking the scelidosaurid foot pattern with the derived stegosaurian pattern (with reduced phalangeal count in digits III and IV). In this case, the *Scelidosaurus* foot would be expected to produce a more anomoeopodid-like track than the stubby moyenisauropodid one. Then, another ichnotaxon from the Gliniany Las, *Anomoepus pienkovskii* Gierliński, 1991, is worth mentioning here. This unusual anomoeopodid, with pedal digit ratios close to those of *M. natator* and the two distal pads on the digit III almost fused, is another candidate for a track of scelidosaurid origin (an idea considered by Gierliński 1995b). Differences between *A. pienkovskii* and *M. karaszewskii* may represent either low-level taxonomic, or ontogenetic variation (*A. pienkovskii* is 14 cm long, while *M. karaszewskii* reaches 25 cm; estimated length of a digitigrade footprint of *S. harrisonii* would be intermediate between the two).

These data require a reappraisal of the interpretation of *Otozoum* Hitchcock, 1847 as a scelidosaurid-like thyreophoran track (Gierliński 1995a). *Otozoum*, characterized by three well developed phalangeal pads on digit III, does not fit the above scenario, where the shortening of basal thyreophoran phalanges is reflected in reduction of the number of digital nodes. As recently noted by Martin Lockley (written communication 1998), *Otozoum* is marked by a highly segmented pattern of the foot which is much more theropod-like than in any configuration seen in large ornithischian tracks. Moreover, the *Otozoum* hallux is a little too long for *Scelidosaurus* (Gierliński 1995a). Finally, new comparisons (Olsen *et al.* 1998) of the digit length ratios of prosauropod feet with those of *Otozoum* support its traditional attribution to prosauropod origin (e.g., Lull 1953; Haubold 1971; Lockley & Hunt 1995).

Additionally, the interpretation of *Moyenisauropus karaszewskii* as a scelidosaurid track suggests occasionally bipedal gait in these thyreophorans. Moreover, if Le Loeuff *et al.* (1998, 1999) are right about the stegosaurian nature of the trackmaker, such an early stegosaurian might also walked bipedally, as did possibly later forms. If so, tracks of later, at least facultatively bipedal, stegosaurs would be difficult to discern from bipedal iguanodontian tracks (especially the most robust thick-toed forms) in the Late Jurassic and Early Cretaceous track assemblages.

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