

Stegosaurian footprints from the Morrison Formation of Utah and their implications for interpreting other ornithischian tracks

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ABSTRACT - The supposed stegosaurian track *Deltapodus* Whyte & Romano, 1994 (Middle Jurassic of England) is sauro-pod-like, elongate and plantigrade, but many blunt-toed, digitigrade, large ornithopod-like footprints (including pedal print cast associated with the manus of *Stegopodus* Lockley & Hunt, 1998) from the Upper Jurassic of Utah, better fit the stegosaurian foot pattern. The Morrison Formation of Utah yielded other tracks fitting the dryomorph (camptosaur) foot pattern (*Dinehichnus* Lockley *et al.*, 1998) much better than *Stegopodus*. If the *Stegopodus* pedal specimen (we propose to shift the emphasis from the manus to the pes in the revised diagnosis of this ichnotaxon) and similar ichnites are proper stegosaur footprints, *Deltapodus* must have been left by another thyreophoran trackmaker. Other *Deltapodus*-like (possibly ankylosaurian) tracks include *Navahopus* Baird, 1980 and *Apulosauripus* Nicosia *et al.*, 1999. Heel-dominated, short-toed forms within the *Navahopus-Deltapodus-Apulosauripus* plexus differ from the gracile, relatively long-toed *Tetrapodosaurus* Sternberg, 1932, traditionally regarded as an ankylosaurian track. Thus, the original interpretation of the latter as a ceratopsian track might be correct, supporting early (Aptian) appearance of ceratopsians in North America.

Isolated pedal ichnites from the Morrison Formation (with a single tentatively associated manus print, and another one from Poland) and the only known trackways with similar footprints (Upper Jurassic of Asturias, Spain) imply bipedal gait of their trackmakers. Thus, problems with stegosaur tracks possibly stem from the expectation of their quadrupedality. Massive but short stegosaur forelimbs suggest primarily bipedal locomotion, and quadrupedal defense posture.

Key words: dinosaur footprints, ichnotaxonomy, Ornithischia, Thyreophora, Ornithopoda, Ceratopsia, Jurassic.

INTRODUCTION

The past decade of the dinosaur ichnology renaissance clearly revealed that the diversity of Early Jurassic dinosaur tracks exceeds the diversity of dinosaur taxa known from osteological remains of the same age. For Late Jurassic dinosaur faunas, on the contrary, the proportion seems reversed. The Morrison Formation of the western United States is one of the most famous dinosaur-bearing strata worldwide, but its track assemblages are still poorly recognized (see Lockley *et al.*, 1998b). Like in the case of the "Gobi Desert syndrome" (Ishigaki, 1999, Currie *et al.*, 2003), the ichnological material from the Morrison Formation stays in the shadow of the osteological material. From such bone rich localities as the Cleveland-Lloyd Dinosaurs Quarry in Utah, Como Bluff and Howe Quarry in Wyoming, dinosaur footprints were just vaguely reported or partially described (Lockley & Hunt, 1998; Nadon, 2001; Kvale *et al.*, 2004).

Thus, it is not surprising that tracks of such Late Jurassic Morrison ornithischians like *Camptosaurus* Marsh, 1885 and *Stegosaurus* Marsh, 1877 present a conundrum to dinosaur ichnology. Their supposed ichnites were long debated among the ichnologists, but mostly without the reference to material whose geographic and stratigraphic provenance allow one to expect camptosaur or stegosaur footprints. For instance, the first alleged camptosaur tracks were reported

by Casamiquela & Fasola (1968) from the Lower Cretaceous of Chile and by Lapparent & Davoudzadeh (1972) from the Lower Jurassic of Iran. A stegosaurian origin was first attributed to a pseudosuchian track of *Rigalites* Huene, 1931, from the Middle Triassic of Argentina, then to a synapsid-like footprint from the Lower Jurassic of Australia (Hill *et al.*, 1966) and then to an iguanodontoid track named *Carri-richnium* Leonardi, 1984 from the Lower Cretaceous of Brazil.

Leonardi's contribution to the search for stegosaurian tracks appears quite reasonable to us. He expected stegosaur trackmakers to leave digitigrade ornithopod-like pedal prints, while most later authors proposed different views. Thulborn (1990) proposed a conjectural reconstruction of stegosaur pedal footprints as narrow and plantigrade. Thulborn's reconstruction also had unusually long pedal digits, too long, in our opinion, for a plausible soft tissue arrangement around the short-toed stegosaur foot skeleton. Almost a decade later, a form similar to the Thulborn's reconstruction was found in the ichnological record at La Gironnette, Lower Jurassic of France (Le Loeuff *et al.*, 1999), but not from the post-Liassic strata. In post-Liassic deposits, in the Middle Jurassic of England, there occurs a short-toed variant of Thulborn's stegosaur footprint, *Deltapodus* Whyte & Romano, 1994, and indeed Whyte & Romano (2001) suggested its stegosaurian origin. Recently, a number of *Deltapodus*

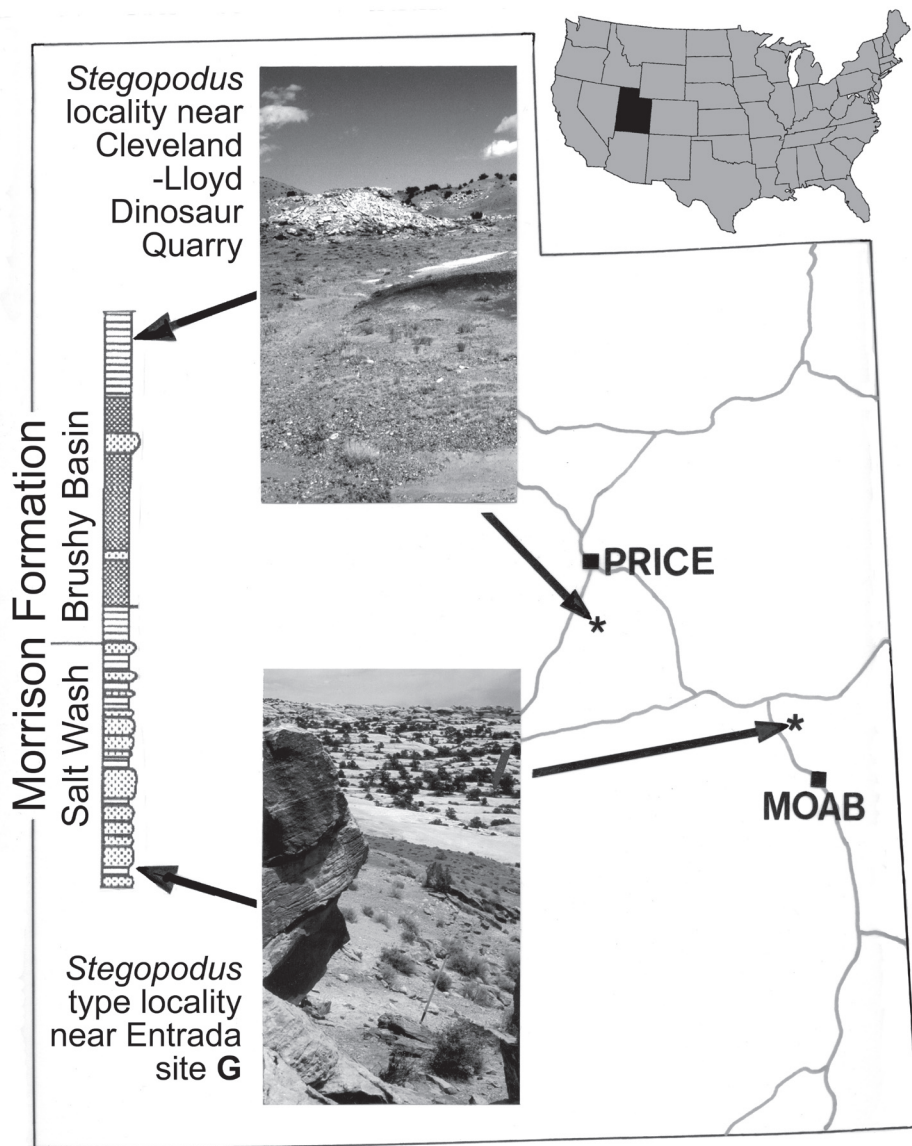


Figure 1 - Stratigraphic and geographic location of the stegosaurian tracks in the Morrison Formation (Upper Jurassic) of Utah.

footprints were found in the Late Jurassic of Asturias (Spain) where stegosaurian skeletal remains are also found (Lires et al., 2002; Garcia-Ramos *et al.*, 2006).

An alternative concept of stegosaur tracks, reminiscent to that of Leonardi (1984), was presented by Bakker (1996). He compared the stegosaur foot with a digitigrade, ornithopod-like footprint from the Morrison Formation and illustrated it with a mistaken caption pointing to Como Bluff in Wyoming as its source locality. Later Lockley & Hunt (1998) elucidated the specimen's actual provenance as the Cleveland-Lloyd Dinosaur Quarry in Utah (fig. 1). Five similar additional specimens were found by Gregory Nadon and John Bird in 1993. Those tracks, together with the sauropod pes-manus set left in the field (Nadon, 2001: fig. 27.6B) and two theropod footprints on the slab CEUM 93, were preserved as natural casts in the light, slightly pinkish sandstone just below the conglomerate bed and they were collected on

the slope, along the quarry road west from the visitor center.

According to Kantor (1995), Kantor et al. (1995) and Nadon (2001), the footprints came from the fluvial deposits of the upper unit of the Brushy Basin Member (Tithonian). Because of initial reports that the tracks, as loose specimens, came from the Cedar Mountain Formation, which overlies the Morrison Formation in that area and because of the *Iguanodon*-like track shape of those footprints, and their high position relative to the main bone-bearing zone of the Cleveland-Lloyd Dinosaur Quarry, Lockley & Hunt (1994, 1995a) supposed that the footprints were Early Cretaceous in age. However, Bilbey (1998) argued for their Morrison Formation provenance, because the track-bearing horizon still lies below the calcrete layer, forming the lower lithostratigraphic boundary of the Cedar Mountain Formation. Moreover, almost in concert with Bilbey's argumentation, in the same year, Lockley & Hunt (1998) published new

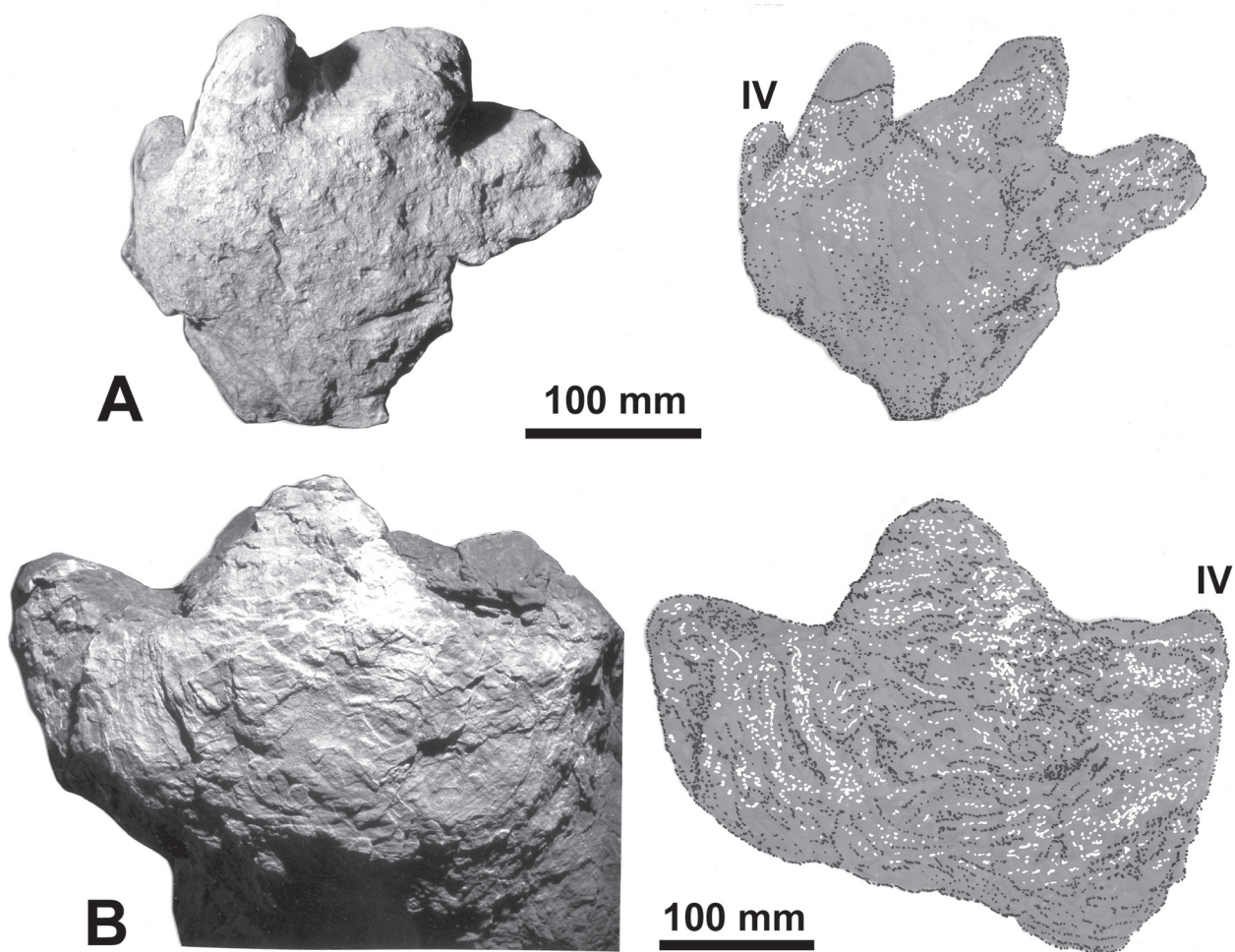


Figure 2 - Former and present type material of *Stegopodus czerkasi* from the Salt Wash Member (lower Morrison Formation) of Moab vicinity in Utah: the former holotype - manual specimen CU-MWC 195.1 (A) and the present holotype - pedal specimen CU-MW 195.2 (B). The specimens' photographs (left) and their interpretative drawings (right).

finds from the Morrison Formation of Utah: an isolated cast of manual imprint supposedly of stegosaurian origin, found near an isolated cast of a pedal print similar to those from the Cleveland-Lloyd Dinosaur Quarry. Both ichnites were discovered by Lockley in 1993, on a hill located north of the Entrada tracksite G, on the northern flank of the Salt Valley anticline near Moab (fig. 1).

The tracks came from the base of the alluvial Salt Wash Member, so their age seems to be early Kimmeridgian, according to Kowallis et al. (1998).

All these specimens show exaggerated iguanodontoid-like foot pattern characterized by short, blunt toes, which allowed us (Gierlinski & Sabath, 2002) to conclude that their trackmaker's feet should have possessed reduced, thick digits with broad hooves, and the only such hoofed animal presently known to live in the Late Jurassic (the Morrison times) were stegosaurs.

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History in New York, New York; CEUM, CEU Prehistoric Museum in Price, Utah; CU, University of Colorado at Denver, Colorado; CU-MWC, University of Colorado and Museum of Western Colorado joint collection; HMN, Humboldt Museum für Naturkunde in Berlin, Germany; MUJA, Museo del Jurásico de Asturias near Colunga, Spain; MNA, Museum of Northern Arizona in Flagstaff, Arizona; MNTS, Museum of Nature and Technology in Starachowice, Poland; MOR, Museum of the Rockies in Bozeman, Montana; Muz. PIG, Geological Museum of the Polish Geological Institute in Warsaw, Poland; NAMAL, North American Museum of Ancient Life in Lehi, Utah; TMP, Royal Tyrrell Museum of Palaeontology in Drumheller, Alberta; ZPAL, Institute of Palaeobiology of the Polish Academy of Sciences, in Warsaw, Poland.

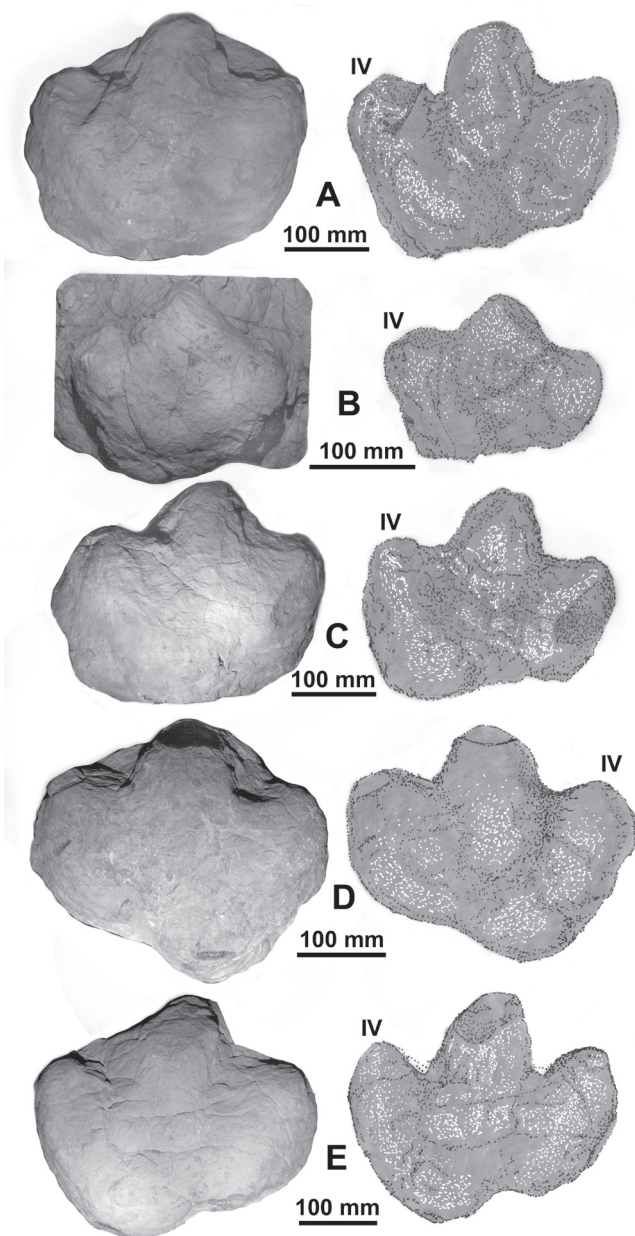


Figure 3 - Pedal specimens of *Stegopodus czerkasi* from the Brushy Basin Member (upper Morrison Formation) of Cleveland-Lloyd Dinosaur Quarry in Utah: (A) CEUM 8003, (B) CEUM 9071, (C) CEUM 20551, (D) CEUM 20571, and (E) CEUM 22577. The specimens' photographs (left) and their interpretative drawings (right).

SYSTEMATIC ICHNOLOGY

DINOSAURIA, Owen 1843
 ORNITHISCHIA Seeley, 1888
 THYREOPHORA Nopcsa, 1915
 EURYPODA Sereno, 1986
 STEGOSAURIA Marsh, 1877

Ichnogenus: *Stegopodus* Lockley & Hunt, 1998, emended herein

Type ichnospecies: *Stegopodus czerkasi* Lockley & Hunt, 1998, emended herein

Included ichnospecies: *Stegopodus czerkasi* Lockley & Hunt, 1998, emended herein

Referred material: CU-MWC 195.1 and 2 (fig.2) from the Morrison Formation of the Salt Valley area near Moab, Utah; CEUM 8003,9071 20551, 20571 and 22577 (fig. 3) from the Morrison Formation of the Cleveland-Lloyd Dinosaur Quarry the near Price, Utah; uncatalogued footprints from the Tereñes Formation (fig. 6) of the so-called "ornithopod tracksites" on Tereñes Cliff near Ribodesella, Spain; MNTS GG/2 from the Bałtów Coral Limestone of Bałtów, Poland.

Distribution: Upper Jurassic of North America and Europe.

Emended diagnosis: Medium to large, tridactyl blunt-toed pedal prints left by a digitigrade semibiped. Pedal digits are very short, broad and widely divaricated. Pedal digits barely project beyond the hypex. Pes is asymmetrical, with the proximal pad located posterolaterally. Manus is entaxonic and tetradactyl.

Comments: Originally the name *Stegopodus* was established to primarily denote the morphological pattern of manus ichnite CU-MWC195.1, supposedly of stegosaurian origin (Lockley & Hunt, 1998). The manus specimen (fig. 2A) indeed fits the conjectural reconstruction of stegosaur manual print proposed by Thulborn (1990).

The cast of pedal print CU-MWC 195.2 (fig. 2B) from the same locality was introduced in the *Stegopodus* diagnosis rather briefly, because the authors were not fully convinced that both ichnites were left by the same trackmaker. However, since the discovery of CU-MWC 195.1, no similar manual prints have been found anywhere in the Upper Jurassic, but numerous pedal prints resembling the one accompanying manual *Stegopodus* cast are known from other Upper Jurassic sites.

There are five specimens from the Cleveland-Lloyd Dinosaur Quarry in Utah (Fig 3), four trackways with similar footprints reported by Piñuela *et al.* (2002) as ornithopod tracks from Tereñes Cliffs in Spain (fig. 6B,D) and one specimen described as a probable stegosaurian track from Poland (Gierliński & Sabath, 2002). Lockley & Hunt (1998) appended their concept of *Stegopodus* tracks with an appeal that additional specimens should be sought to enable refining and emending the diagnosis and description. We believe that the aforementioned additional material means that time has come for such a revision, which would shift the focus from the manus to the pes (as discussed below in comments on the ichnospecies).

So far, *Stegopodus* is monospecific. However, after comparing available material from Spain and Poland with the American ichnofossils described here, we could already indicate future candidates for, at least, two new ichnospecies of *Stegopodus*. Spanish tracks exposed *in situ* on Tereñes

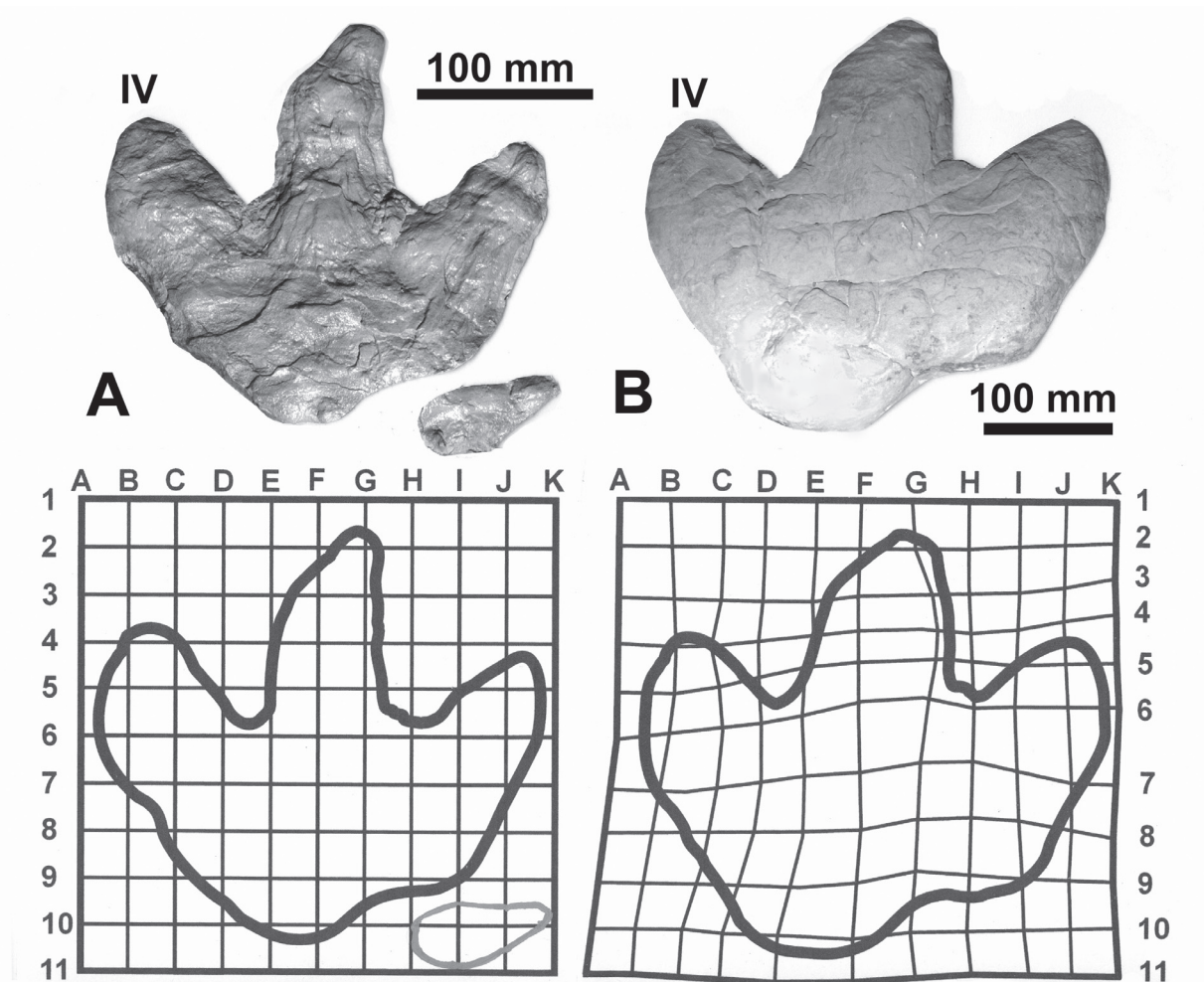


Figure 4 – Comparison of *Moyenisauropus karaszewskii*, Muz. PIG 1560.11.18 (A, C) from the Lower Jurassic of Poland with *Stegopodus czerkasi* CEUM 22577 (B, D) from the Upper Jurassic of Utah, with the Cartesian diagrams (C, D)

Cliffs (fig. 6B) are less asymmetrical, more crown-shaped, with digits more equal in length than those from Utah and Poland. On the other hand, the Polish specimen differs from the American and Spanish ones by being slightly longer than wide, with pedal digits II and III much larger than digit IV. Such high discordance of digit lengths results in its almost didactyl appearance. This footprint from Bałtów is also associated with a supposed manual print, which seems entaxonic, but in contrast to the specimen CU-MWC 195.1, seems rather tridactyl. Thus, the Spanish and Polish specimens help to show a range of morphological (at least, extramorphological) variation among the tracks of *Stegopodus*, but should not be included to *Stegopodus czerkasi*, which comprises very similar forms from the Morrison Formation.

Though *Stegopodus* pedal prints are seemingly iguanodontoid-like in general shape, under closer examination most of the tridactyl ornithischian ichnotaxa share different morphology. The tracks of Iguanodontoidea *seusu* Norman (2004), such as *Amblydactylus* Sternberg, 1932, *Carririchnium* Leonardi, 1984, *Iguanodontipus* Sarjeant,

Palais & Lockley 1998 and *Hadrosauropodus* Lockley, Nardon & Currie, 2004 (fig. 7D) show more prominent digit III (as observed by Martin Lockley, personal communication, 2005) and their metatarsophalangeal pads are well fused into a single proximal pad, which is located centrally and makes the entire footprint symmetrically shaped. This symmetry is also shown by the smaller ornithopod footprints like *Delatorrichus* Casamiquela, 1964 (fig. 8B) and *Dinehichnus* Lockley, Santos, Meyer & Hunt, 1998a (fig. 7B). In contrast, the *Stegopodus* pes is more asymmetrical. Its laterally placed proximal pad is developed on the swollen metatarsophalangeal pad of digit IV, which barely projects beyond the hypex and is slightly less divaricated from digit III than digit II.

Among the ornithischian ichnotaxa the most similar form is *Moyenisauropus karaszewskii* Gierliński, 1991 (fig. 4A) from the Lower Jurassic of Poland, a form attributed to a basal thyreophoran (Gierliński, 1999). This resemblance is evident from the comparison of Cartesian diagrams (fig. 4C, D) where the *Stegopodus* pes clearly appears as a derived “flattened” morphotype of *Moyenisauropus* Ellenberger,

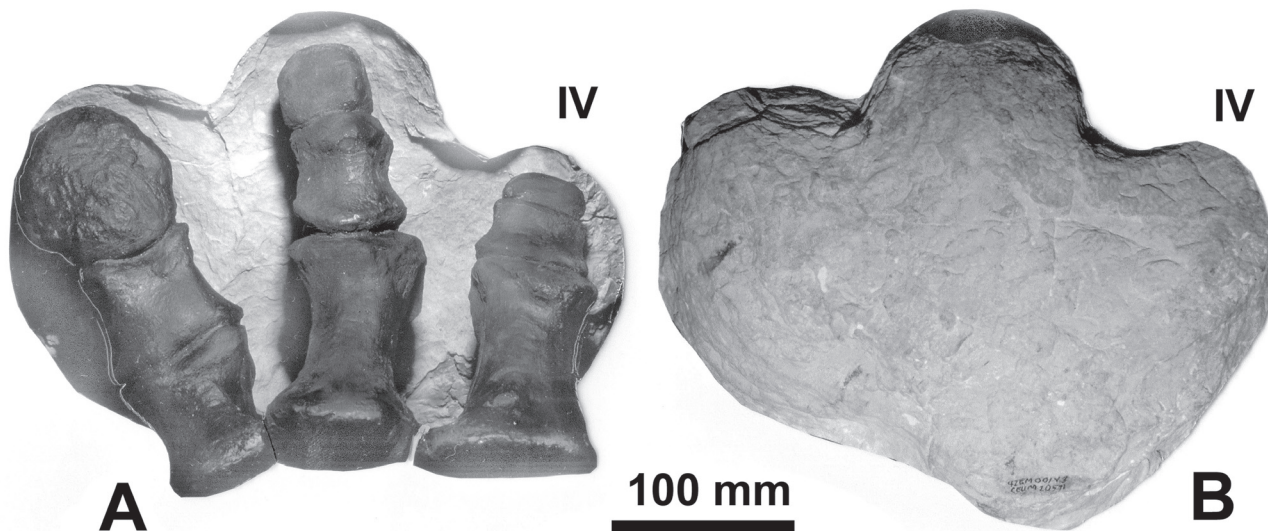


Figure 5 – The CEUM reconstruction of *Stegosaurus* foot skeleton (A) superimposed onto a mold of *Stegopodus czerkasi* specimen CEUM 20571 (B).

1974. Additionally, it supports the intermediate morphology of *Moyenisauropus*, placed between the gracile *Anomoepus* Hitchcock, 1848, and the robust *Stegopodus* pes. This disagrees with the synonymization of *Moyenisauropus* with *Anomoepus* postulated by Olsen & Rainforth (2003), that ignored the *Moyenisauropus* concept of Gierliński (1991, 1999) and was recently questioned by Lockley (2005), Lockley & Gierlinski (2006), and Gierlinski & Kowalski (2006).

Olsen and Rainforth (2003) did not support their ichnosystematic conclusion by examination of the original Ellenberger's material stored in the Montpellier University, nor the available Polish and French *Moyenisauropus* tracks. The French semibipedal *Moyenisauropus* trackway from La Girronette comprises digitigrade tracks very similar to those of the Polish *M. karaszewskii*, but also some semidigitigrade and plantigrade pedal prints, which are absent in the short Polish bipedal trackway Muz.PIG 1560.II.9. Interestingly, such occasional plantigrade pedal print from La Girronette (footprint A3 in Le Loeuff *et al.*, 1999) resembles the Spanish *Deltapodus* footprint MUJA JVLBS-62 of a possibly juvenile trackmaker from the Lastres Formation of Villaviciosa, which in turn may suggest that the *Moyenisauropus* morphotype may be ancestral for the derived Late Jurassic distinct forms of *Deltapodus* and *Stegopodus*.

Stegopodus czerkasi Lockley & Hunt, 1998, emended herein

Figs. 2B, 3, 4B D, 5B

1994 ornithopod tracks – Lockley & Hunt: fig. 5

1996 stegosaur footprint – Bakker: fig. 2A

1998 *Stegopodus czerkasi* – Lockley & Hunt: p. 334, fig. 1

Holotype: CU-MWC 195.2, natural casts in light, slightly brownish sandstone (fig. 2).

Type horizon: Lower Salt Wash Member of the Morrison Formation (Kimmeridgian).

Type locality: Northern flank of the Salt Valley, Grand County, Utah.

Hypodigm: CEUM 8003, 9071, 20551, 20571 and 22577 from the upper Brushy Basin Member of the Morrison Formation of Cleveland-Lloyd Dinosaur Quarry, Emery County, Utah (fig. 3).

Distribution: Morrison Formation (Upper Jurassic) of Utah, USA.

Emended diagnosis: Medium to large, tridactyl blunt-toed pedal prints left by a digitigrade trackmaker. Pes is wider than long, always asymmetrical, with the large proximal pad located posterolaterally. A single phalangeal pad, often not well defined, occurs on each pedal digit, but the swollen pad of digit II is wider than those on digits III and IV. Pedal digit IV is the longest, but barely projecting beyond the hypex. Digits II and III are relatively shorter but more projecting beyond the hypex than digit IV. The angle between the digits II and III is wider than between digits III and IV.

Description: Our measurements of the *Stegopodus czerkasi* former holotype, the manual specimen CU-MWC 195.1 (fig. 2A), partly differ from those given by Lockley & Hunt (1998). Following the method recommended by Leonardi (1987), the manus length measured parallel to the manus long axis (the third digit axis) equals 24 cm (not 21.5 cm as given by the original authors). However, the manus width measured parallel to the transverse axis (the axis perpendicular to the long axis) equals 26 cm., which is consistent with the data of Lockley & Hunt (1998). Manus shows the “heel”-

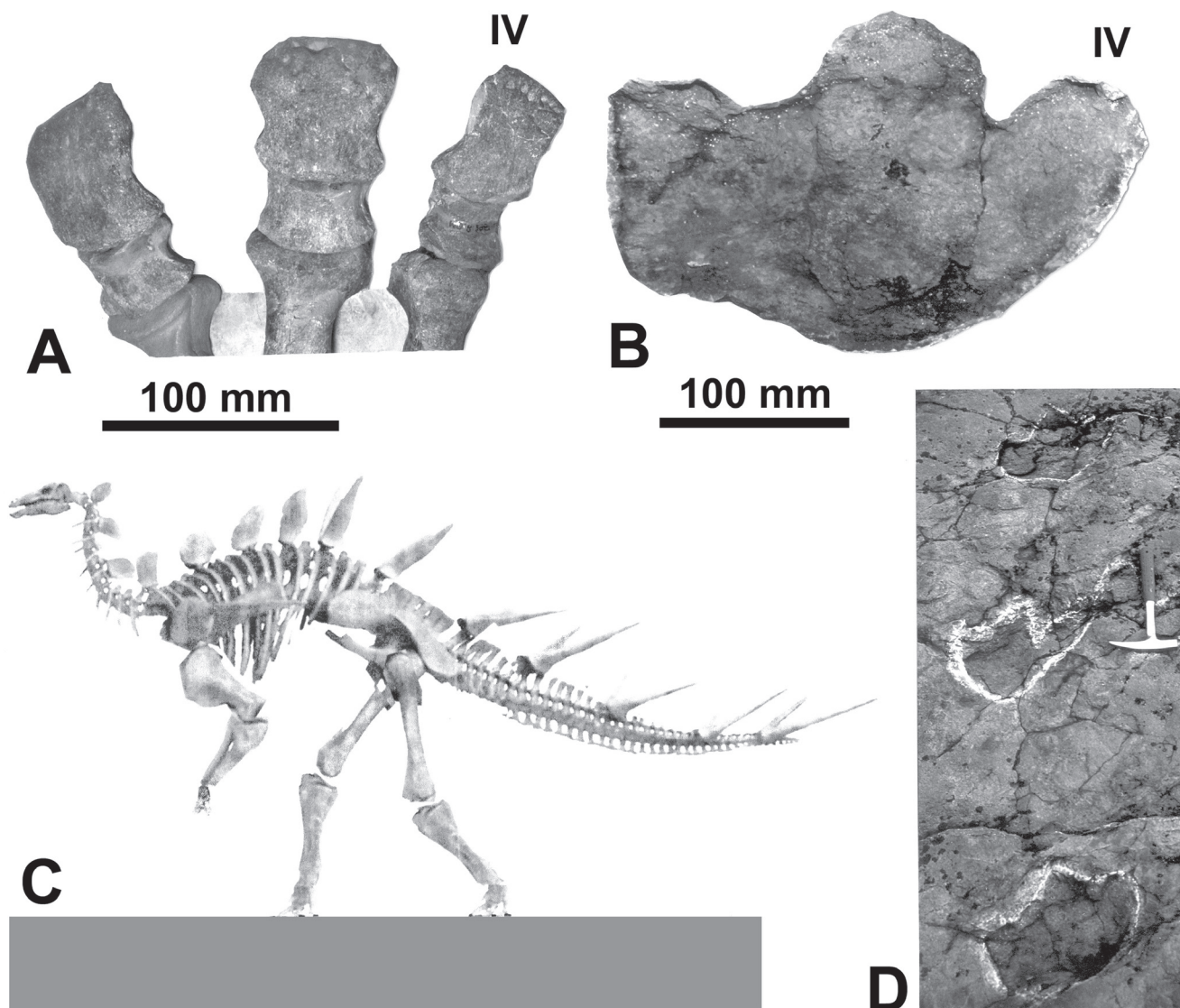


Figure 6 – The *Kentrosaurus* pes HMN MBR 2951 (A) from the Tendaguru Beds (Upper Jurassic) of Tanzania, in comparison with *Stegopodus* sp. (B) from the Tereñes Formation (Upper Jurassic) of Asturias, Spain. The HMN *Kentrosaurus* skeleton arranged in a bipedal posture (C) by K. Kuchnio and the bipedal trackway of *Stegopodus* sp. from the Tereñes Formation of Asturias (D).

dominated morphology, with a very large palm (15 cm long and 18 cm wide) and short, blunt digits. Manual digits increase in length in the formula of IV, III, II, I and the angles between their axes increase in the same way (IV–III = 12°, III–II = 17°, II–I = 30°). Our observations about this manual specimen are generally consistent with those provided by Lockley & Hunt (1998), while our view on the pedal specimen, the present holotype, is significantly different.

Contrary to previous authors, we interpret the pedal specimen CU-MWC 195.2 (fig. 2B) as a digitigrade, not a plantigrade footprint, thus, not longer than wide, but wider than long (26 cm long and 33 cm wide); we see it as a quite well preserved specimen sharing its distinctive morphology with the footprints from the Cleveland-Lloyd Dinosaur Quarry (fig. 3).

Digit length ratios of CU-MWC 195.2 are: IV/II = 1.17 and IV/III = 1.28. The angle between the axes of digits II and III is 28°, while the angle between the axes of digits III and IV equal 24°. The footprint is wider than long by 22%. Such measurement fit in within the range of those obtained from the pedal ichnites of the Cleveland-Lloyd Dinosaur Quarry. Their digit length ratios vary as follow: IV/II = 1.09–1.25 and IV/III = 1.25–1.39. The angles between the digit axes are: II–III = 25°–34° and III–IV = 14°–27°. The footprints are wider than long by 13% up to 25%.

The smallest footprint (CEUM 9071) is 15 cm long and 20 cm wide, while the largest one (CEUM 8003) is 28 cm long and 34 cm wide.

Comments: The type specimens of *S. czerkasi* were found as loose casts of manual and pedal imprints, weathered

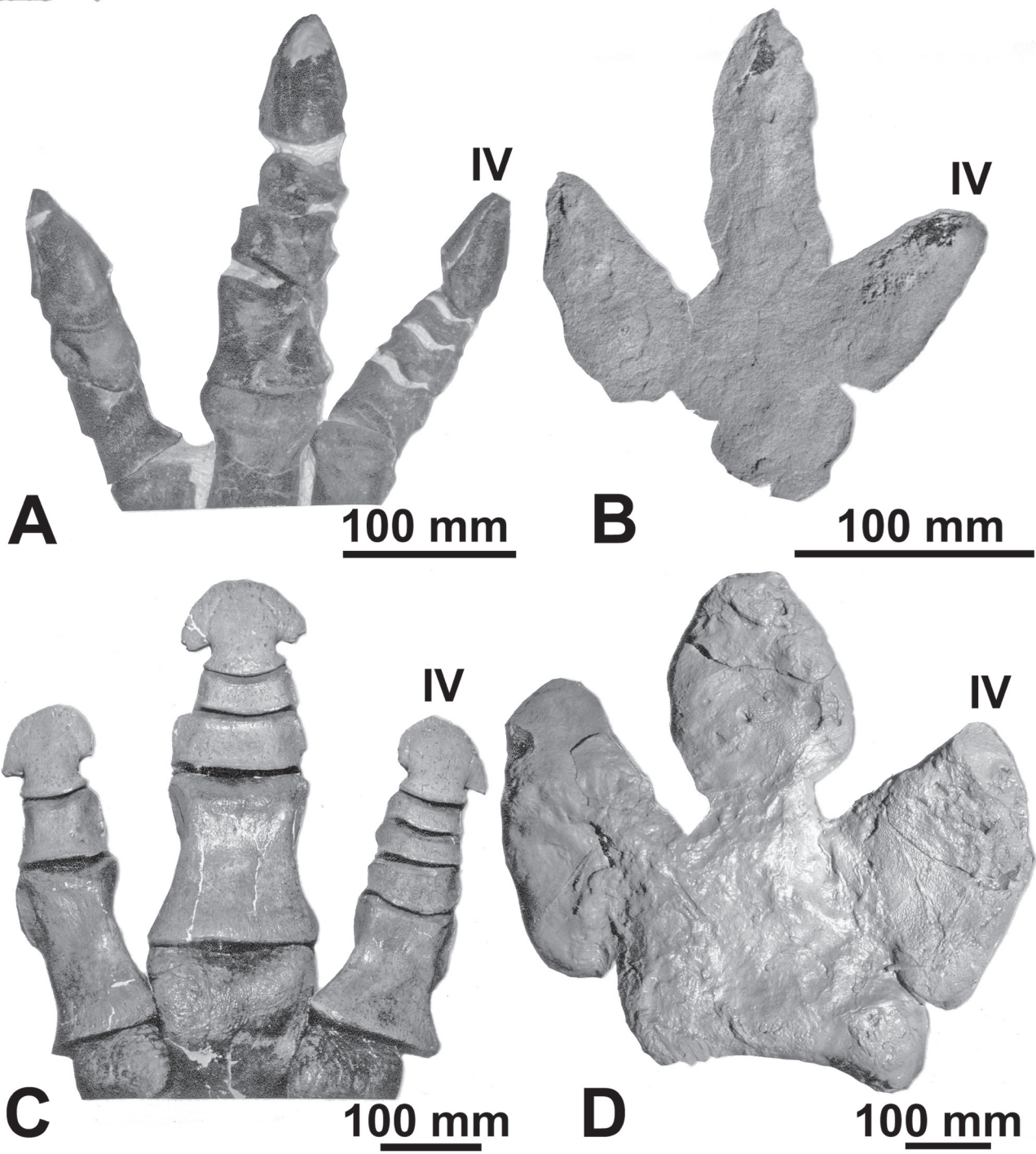


Figure 7 – Foot skeleton of basal (dryomorph) and derived (hadrosaurid) iguanodontians and their supposed footprints (interpretatively modified photographs): *Camptosaurus* pes NAMAL 102 (A) from the Morrison Formation (Upper Jurassic) of the Bone Cabin Quarry West in Wyoming and the large specimen CU-MWC 198.3 of *Dinehichmus socialis* (B) from the Morrison Formation of Boundary Butte in Utah; *Brachylophosaurus* pes MOR 794 (C) from the Judith River Formation (Upper Cretaceous) of Murphy hadro site in Montana and *Hadrosauropodus langstoni* TMP 87.76.6 (D) from the St. Mary River Formation (Upper Cretaceous) of St. Mary River Valley in Alberta, Canada.

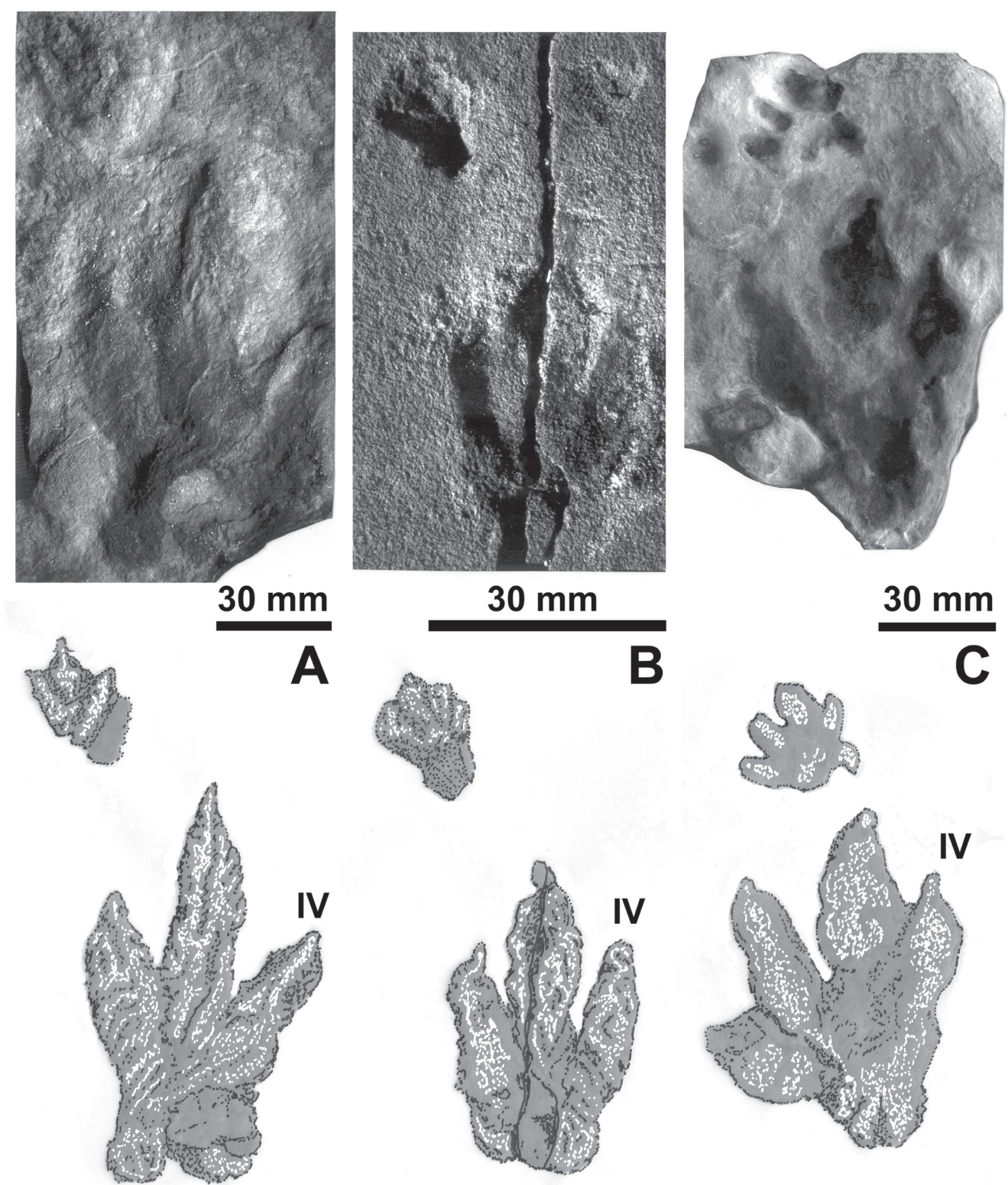


Figure 8 – Postulated basal ornithischian and basal ornithopod tracks: (A) *Atreipus* sp. from the upper Chinle Formation (Upper Triassic) of Utah, (B) *Delatorrichnus goyenechei* from the La Matilda Formation (Middle Jurassic) of Argentina, (C) type specimen CU-199.46 of *Hypsiloichnus marylandicus* from the Patuxent Formation (Lower Cretaceous) of Maryland. The specimens' photographs (top) and their interpretative drawings (bottom).

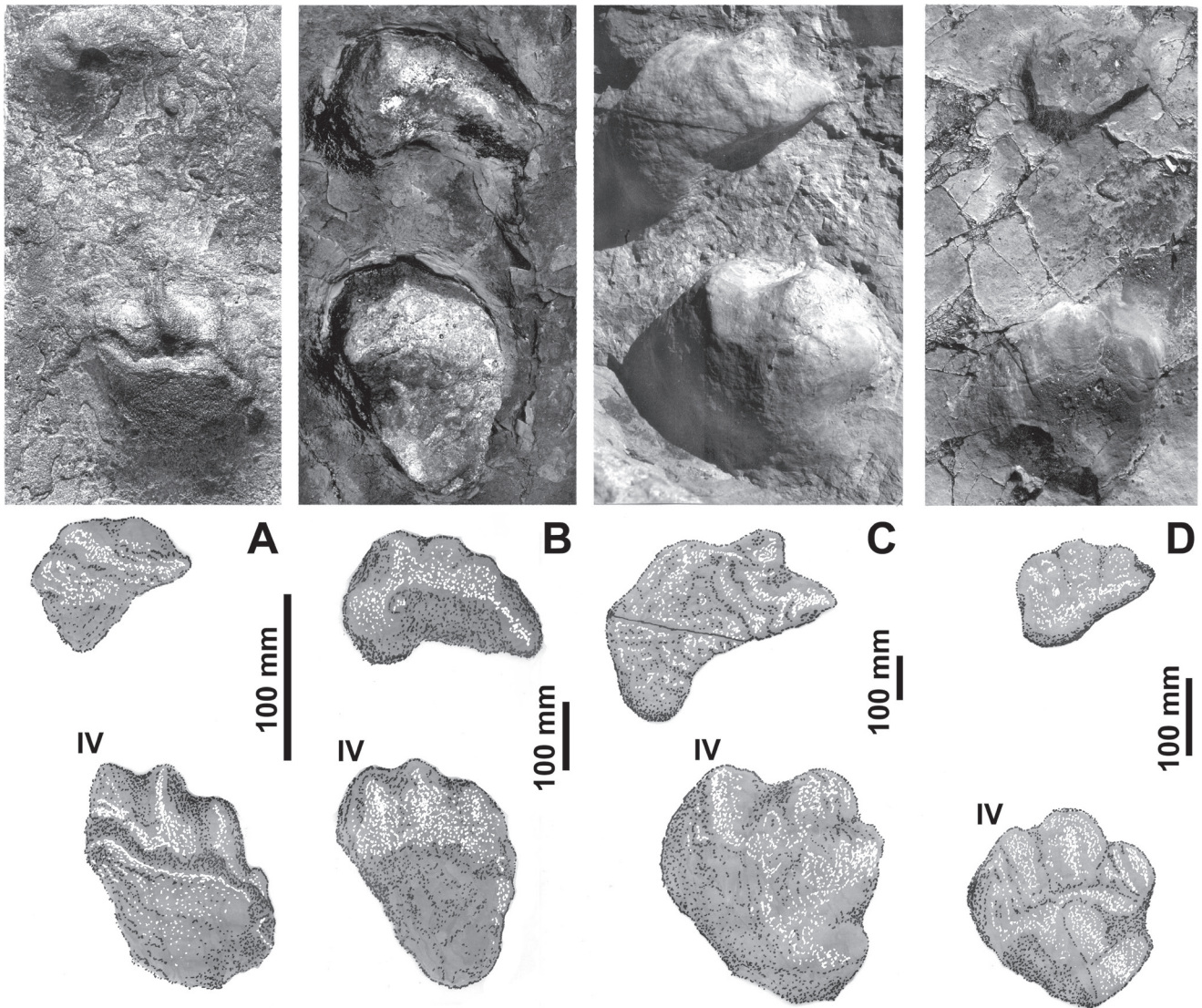


Figure 9 – Postulated ankylosaurian tracks: (A) type specimen MNA P3.339 of *Navahopus falcipollex* from the Navajo Formation (Lower Jurassic) of Kaibito Plateau in Arizona, (B) *Deltapodus* sp. from the Tereñes Formation (Upper Jurassic) of Asturias in Spain, (C) cf. *Apulosauripus* sp. from the Dakota Group (Middle Cretaceous) of Skyline Drive tracksite in Colorado, (D) *Apulosauripus federicianus* from the Altamura Limestone Formation (Upper Cretaceous) of Puglia in Italy. The specimens' photographs (top) and their interpretative drawings (bottom).

and displaced downslope for a distance of no more than two meters (Lockley & Hunt, 1998). Thus, it is possible to suppose that both ichnites came from the same level and belong to the same trackway. No other footprints were found nearby. Lockley & Hunt (1998) described those specimens mainly focusing on the cast of manus CU-MWC 195.1, treating the pes specimen CU-MWC 195.2 rather cautiously and superficially. They admitted that the relationship of the pes cast to the manus cast is uncertain. Indeed, we suppose that both casts do not represent a single manus-pes set. One is a cast of a right manual print, while the other seems to be a cast of a left pedal print (fig.2). However, we may suppose that both could have originated from the same trackway being eroded from the same small outcrop.

As mentioned earlier, while no more such manual prints have been found anywhere in the Upper Jurassic, there are examples of pedal prints similar to CU-MWC 195.2 known from the Cleveland-Lloyd Dinosaur Quarry.

Lockley et al. (1998b) stated that the pedal specimens from the Cleveland-Lloyd Dinosaur Quarry could not be assigned to the ichnogenus *Stegopodus* until a complete trackway showing the relationship between manus and pes, is found. We present a different point of view. The presence of the pedal ichnite CU-MWC 195.2 may support stegosaurian origin of manual imprint CU-MWC 195.1, which might have been weathered from the same trackway and was left just incidentally by a usually bipedal animal. We argue for a new concept of *Stegopodus* that recognizes the importance

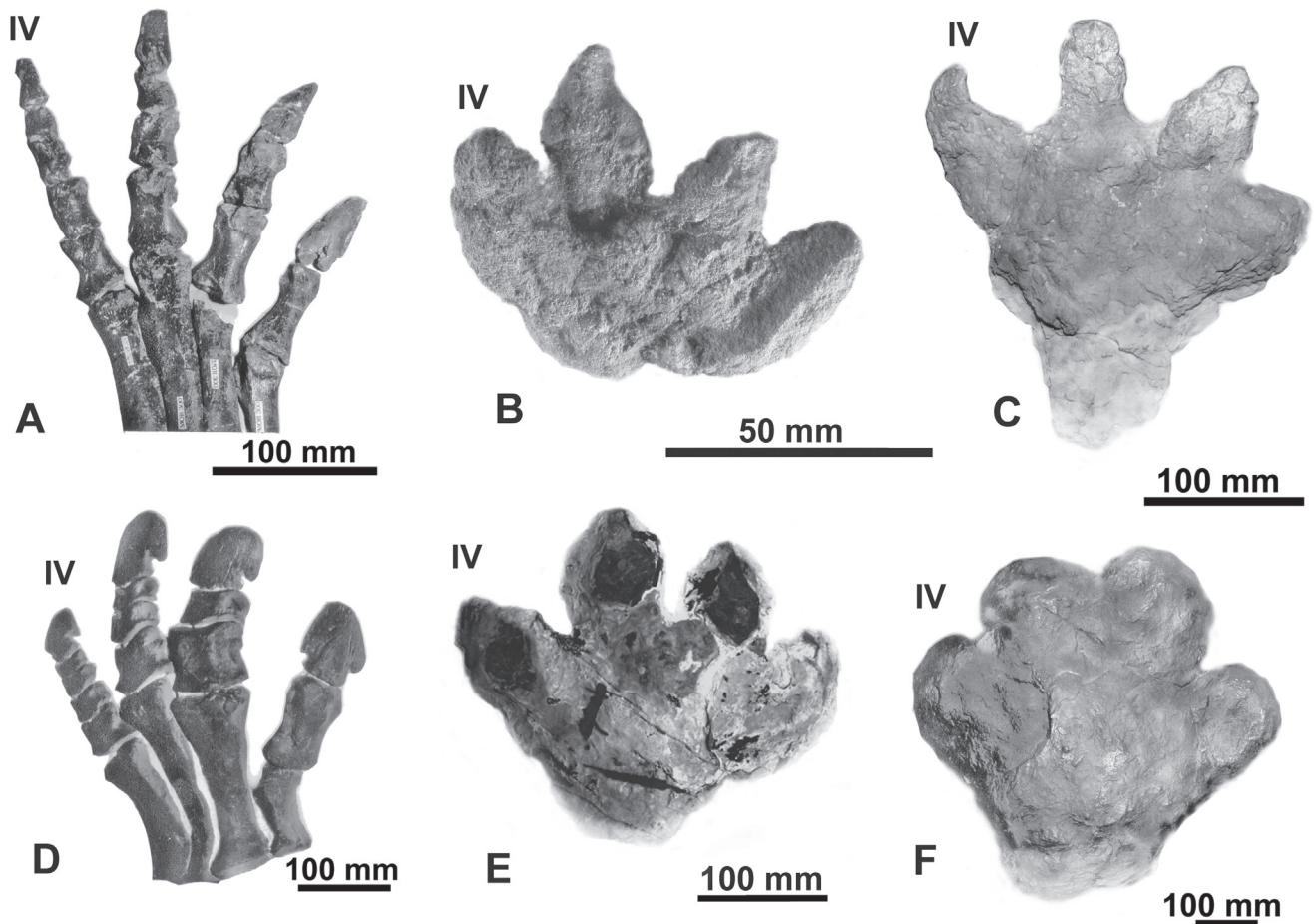


Figure 10 – Foot skeleton of basal and derived neoceratopsians and their supposed footprints (interpretatively modified photographs): *Cerasinops* pes MOR 300 (A) from the Two Medicine Formation (Upper Cretaceous) of Montana, *Protoceratops* footprint ZPAL MgD-II/3 (B) from the Djadokhta Formation (Upper Cretaceous) of Mongolia and *Tetrapodosaurus* CU-MWC 209.33 (C) from the Dakota Group (Middle Cretaceous) of Colorado; *Centrosaurus* pes AMHN 5351 (D) from the Dinosaur Park Formation (Upper Cretaceous) of Alberta, unnamed ceratopsian footprint CU-MWC 227.1 (E) from the Iron Springs Formation (Upper Cretaceous) of Utah and *Ceratopsipes goldensis* CU-MWC 220.516 (F) from the Laramie Formation (Upper Cretaceous) of Colorado.

of the pedal ichnites. However, there is no so easy way out of this taxonomic ambiguity.

Lockley & Hunt (1998) were, indeed, not fully convinced that both ichnites of pes and manus were left by the same trackmaker, so they mainly defined *S. czerkasi* on manual morphology, but they did include the pedal ichnite as the referred specimen of this ichnotaxon and they did mention pedal morphology in their diagnosis of *S. czerkasi*. Thus, *S. czerkasi* seems to be a valid name to label the pes ichnite, provided the diagnosis is emended as we propose here. Moreover, it is a fairly simple solution.

DISCUSSION

Lockley (1999) noticed a progressive trend in the evolution of foot shape which occurred convergently in different terrestrial vertebrates. He observed that the basal forms possessed elongate feet with relatively long digits,

while the foot of their advanced descendants became broad with relatively short, thick digits and large wide heel or metatarsophalangeal area. According to this scheme, the footprints described above clearly reflect an advanced pattern of morphology, whoever their trackmaker was.

Precisely, those Late Jurassic tracks look like a derived version of the Early Jurassic *Moyenisauropus karaszewskii* (fig. 4), which is supposed of basal thyreophoran origin (Gierliński, 1999).

Lockley & Hunt (1994, 1995a) and Kantor et al. (1995) attributed the specimens from the Morrison Formation of Cleveland-Lloyd Dinosaur Quarry to ornithopods. However, there were no known ornithopods in the Late Jurassic, that might have produced such robust footprints. A camptosaurus would be expected to leave more gracile footprints, with more elongate and pointed digits (Gierliński & Sabath, 2002).

Medium and large ornithopod footprints like *Dine-*

hichuus (fig. 7B), *Amblydactylus*, *Carririchnium* and *Hadrosauropus* (fig. 7D) exhibit characteristic quadripartite shape, accentuated by a relatively long digit III and nearly equal, wide angles between their digit axes, and by a centrally located proximal pad, reflecting the tightly packed metatarsals of their trackmakers' feet (fig. 7 A, C). In contrast, the broad *Stegopodus* pedal print is produced by thick, spread apart toes with an asymmetrically placed proximal pad. Such pattern clearly reflects wide arrangement of metatarsals in the *Stegopodus* trackmaker's feet, which match stegosaurian feet (figs. 5, 6A, B).

Stegopodus pedal material from the Morrison Formation of Utah is distinguished by the large digit II, always wider and rounder than the more elongate digits III and IV. Such a feature of *S. czerkasi* fits well with *Stegosaurus* pes ending with a very large hoof on the second digit (fig. 5), whereas the more even-sized pedal digits of *Kentrosaurus* Henning, 1915 better correspond with the pedal morphology of the footprints from the Tereñes Cliffs in Asturias, Spain (fig. 6A, B).

Basically, the only known trackways on the Tereñes Cliffs unquestionably demonstrate bipedal gait of the *Stegopodus* trackmaker (fig. 6D). It is less obvious in the case of the American material, which comprises isolated footprints and only the numerous pedal specimens in comparison with just one manual specimen may tentatively suggest their trackmaker's bipedality.

The stegosaurian bipedality is not a new idea. Bakker (1986: p. 187–192), presenting his own observations supporting adaptations of stegosaurs to a tail-supported tripod stance and thus high-browsing feeding specialisation, referred to the long history of the idea dating back to Marsh in the 19th century and to D'Arcy Thompson (1942), who in noted the mechanical similarity of the stegosaur vertebral spines to a suspension bridge (with the main support at the hips). Bipedal stegosaurs were also depicted in artistic restorations of that period; e.g. Murray Chapman portrayed a bipedal *Stegosaurus* in 1924 (his drawing was reproduced by Sarjeant (2001: fig. 33.8; the same figure shows another thyreophoran, *Scelidosaurus*, in a tripod kangaroo posture, as drawn by Lady Bray in 1921). More recently, in 2003, Polish paleoartist Krzysztof Kuchnio came to a similar conclusion, studying stegosaur anatomy, based on HMN specimen of *Kentrosaurus aethiopicus* Henning, 1915; he created a computer animation showing a bipedally walking *Kentrosaurus* skeleton (fig. 6c), and later sculpted its life restoration accordingly for a dinosaur theme park in Bałtów, Poland.

Despite the widely assumed quadrupedal stance of stegosaurs, arguments in favor of their bipedality or facultative bipedality are quite strong. In 2002, "T.R. Karbek" (anagram of R.T. Bakker) argued for bipedality of *Stegosaurus* and *Kentrosaurus*, using the following points: great contrast in hind and forelimb length, body proportions indicating that the center of gravity moved toward the hips, position of plates, enhancing agility in bipedal stance, as well as development of neural tissue near the propulsive hind limbs,

reducing time lag of neural reactions. All these adaptations might be explained as indicators of a lifestyle of an agile, cursorial biped. Naturally, it does not mean that stegosaurs did not stand on all fours. They have short (possibly too short for efficient walking or running), but heavily built forelimbs well designed to carry the body weight, paradoxically more massive than in quadrupedal ornithopods. Thus, the forelimbs were most probably important in the defense position to provide stability and leverage while the animal used its tail as weapon; in quadrupedal posture the fairly stiff tail could have been swung with greater force, by moving the whole body laterally with the use of forelimb muscles. Obviously, the forelimbs could have been used as support during feeding on low vegetation, but this does not explain their massive bones as well as their defense purpose does. Thus, stegosaurs were probably semibipedal, and might then occasionally left their manual imprints.

However, if those robust blunt-toed tridactyl footprints from the Upper Jurassic were left by bipedal stegosaurs, then where are the "true" camptosaurus tracks? Fortunately, two recent discoveries of the small euornithopod tracks of *Hypsiloichnus* Stanford, Weems & Lockley, 2004, from the Patuxent Formation of Maryland and Virginia, and the complete preserved *Camptosaurus* foot skeleton NAMAL 102 from the Morrison Formation of Bone Cabin Quarry in Wyoming may help to answer the question about the "missing" camptosaurus tracks. The Early Cretaceous *Hypsiloichnus* ichnites (fig. 8 C) possess the grallatorid-like pedal digit group II–IV with elongate toes and the third digit as the longest one, which is associated (contrary to *Grallator* Hitchcock, 1985) with the large functional hallux and the small mesaxonian manus. According to Stanford et al. (2004), their trackmakers were related to basal ornithopods like *Zephyrosaurus* Sues, 1980 and *Hypsilophodus* Huxley, 1869. In our opinion, the *Hypsiloichnus* morphotype resembles also the Late Triassic *Atreipus* Olsen & Baird, 1986 (fig. 8A), originally considered as a basal ornithischian track, and the Early to Middle Jurassic *Delatorrichnus* (fig. 8B) suspected of a basal ornithopod origin by Gierliński & Niedźwiedzki (2002). Thus, *Atreipus*–*Delatorrichnus*–*Hypsiloichnus* plexus seems to comprise tracks of basal ornithischians and basal ornithopods *sensu* Norman et al. (2004), which have theropod-like pes (despite the large hallux in *Hypsiloichnus*) and shows a tendency to quadrupedal gait. The bipedal *Dinehichnus* tracks, with the cigar-shaped, widely and equally divaricated digits, and the characteristic discrete oval proximal pad located centrally below the middle toe does not correspond closely with the *Hypsiloichnus* morphotype. Therefore, from among the two possible candidates for *Dinehichnus* trackmaker, *Hypsilophodon* and a dryosaur, which were discussed by Lockley et al. (1998a), the latter one might be preferred. However, a newly found complete skeleton of *Camptosaurus* foot from the Morrison Formation of Bone Cabin Quarry in Wyoming, the specimen NAMAL 102 (fig. 7A), fits well a large *Dineichnus* specimen CU-MWC 198.3 (fig. 7B). It does not exclude dryosaurid affinity of the track-

maker, but rather suggests that *Dinehichnus* may reflect, in general, the dryomorph (including dryosaur and camptosaur) foot pattern. The monospecific ichnoassemblage of Boundary Butte revealed *Dinehichnus* tracks ranging in length from 10 cm up to 28 cm. Thus, they might have been produced by a mixed-age camptosaur herd, or the camptosaur-dryosaur multispecies group. Examples of similar communities can now be found in the East African savanna, where mixed herds of different species of herbivorous ungulates travel together. Whichever interpretation is correct, we can conclude that the camptosaur tracks might correspond to relatively gracile forms like *Dinehichnus* from the Morrison Formation of Utah. Such conclusions contrast with the traditional view, seeking alleged camptosaur footprint among the more robust Late Jurassic footprints like those we attribute to stegosaurs, or even those made by large theropods. For instance, the 45 cm long prints from the Morrison Formation of Oklahoma were originally attributed to camptosaurus (Lockley, 1986; Lockley et al., 1986). Later, however, their interpretation was revised and they are regarded as large theropod tracks (Prince & Lockley, 1989; Lockley & Hunt, 1995a; Lockley et al., 2001). In our opinion, the same could also apply to the alleged large ornithopod pedal prints described by Harris (1998) from the Morrison Formation of Garden Park in Colorado. The osteological material presently known does not reveal any Late Jurassic ornithopods large enough to produce such large, robustly shaped ichnites.

The last problem to be solved to firmly establish our stegosaurian track concept, concerns *Deltapodus* and *Tetrapodosaurus* Sternberg, 1932. If the tracks similar to *Deltapodus* (fig. 9B) are of ankylosaurian, not stegosaurian origin (as we assume, and as McCrea et al., 2001, postulated earlier), then why is *Tetrapodosaurus* Sternberg, 1932, conventionally regarded as the ankylosaurian track morphotype, so different from *Deltapodus*? *Deltapodus* from the Middle Jurassic of England shares a more or less similar morphology with many other tracks ranging from the Early Jurassic to the Late Cretaceous of Europe, Asia and North America, while *Tetrapodosaurus* seems to be unique, even endemic, to the Mid-Cretaceous of North America.

The *Deltapodus* trackway is quadrupedal, very wide (pes angulation about 90°) and the pedal prints are anteriorly, or slightly outwardly directed. Pedal prints are longer than wide, with very large triangular heel area and thick, extremely short digits. The manus is relatively large, broader than long and semicircular in shape, located anteriorly or anterolaterally to the pes. Similar tracks were reported from the Upper Jurassic of Asturias in Spain (Lires et al., 2002) where they were interpreted as stegosaurian, and from the Lower and Upper Cretaceous of South Korea (Lim et al., 1995; Huh et al., 2003), described as the sauropod tracks, in accord with the original attribution of *Deltapodus* by Whyte & Romano (1994). Other Cretaceous *Deltapodus*-like prints of *Apulosauripus* Nicosia, Marino, Mariotti, Muraro, Panigutti, Petti & Sacchi, 1999 (fig. 9D) from the Altmura track-site in southern Italy, were previously identified as tracks of

quadrupedal hadrosaurids. However, *Apulosauripus* manual prints are much larger in comparison with the pedal prints (averagely half the pes size) than observed in the trackways of large quadrupedal ornithopods from the Cretaceous (see Lockley & Wright, 2001). The *Apulosauripus* trackway is clearly wide-gauge and the pace angulation of pes varies there from 88° to 120°, which seems too low for ornithopod standards. There is also no inward rotation of pes, so characteristic for quadrupedal and bipedal iguanodontian trackways. Dal Sasso (2003) noted the presence of ankylosaurian footprints in the Altamura tracksite, but in our opinion, all Altamura footprints, including *Apulosauripus*, were left by ankylosaurians. Tracks similar to *Apulosauripus* (tentatively attributed to *Tetrapodosaurus* by Kurtz et al., 2001a) are also known from the Dakota Group of Colorado, at the Skyline Drive site (fig. 9C). Those tracks, reported by Kurtz et al. (2001a,b) differ from *Deltapodus* only in having more or less clearly imprinted hallux, which is less obvious in the Italian material and better defined in the pedal specimens from Colorado. However the hallux presence or absence is not a diagnostic feature of ankylosaurian tracks, because their pedal digit count is variable. There are tridactyl feet in *Euoplocephalus* Lambe, 1910 and *Liaoningsaurus* Xu, Wang & You 2001, while tetradactyl feet occur in *Niobrariasaurus* Carpenter, Dilkes & Weishanpel, 1995, *Nodosaurus* Marsh, 1889, *Sauropelta* Ostrom, 1970 and *Talarurus* Maleev, 1952 (see Coombs, 1986; Xu et al., 2001; Carpenter et al., 1995; Lull, 1921; Maryńska, 1977; Vickaryous et al., 2004).

Disregarding the inconsistent tetradactyly, Early Jurassic strata also revealed footprints resembling *Deltapodus*, such as the unnamed tracks from the Calcari Grigi Formation of Sarca Valley in Italy (Avanzini et al., 2001) and a controversial tracks of *Navahopus* Baird, 1980 (fig. 9A) from the Navajo Formation of Kaibito Plateau in Arizona. The *Navahopus* was originally considered as quadrupedal prosauropod tracks distorted by slumped sand as the trackmaker progressed uphill (Baird, 1980). Later, Lockley et al. (1994) suggested their synapsid origin, but more recently Rainforth (2003) argued again for the prosauropod affinity of the *Navahopus* trackmaker. Her opinion seems to be also supported by *Lavinipes* Avanzini, Leonardi & Mietto 2003, large quadrupedal prosauropod tracks from the Lower Jurassic of the Italian Alps, which indeed might be *Navahopus*-like, if diminutive and deformed. However, Avanzini et al. (2003) stressed the differences rather than the similarities between *Lavinipes* and *Navahopus*. Recently, Hunt & Lucas (2006) returned to the “synapsid concept” and suggested that *Navahopus* represent an extramorphological variant of a large tritylodont trackway.

We believe that an early ankylosaurian is at least as plausible a candidate for the *Navahopus* trackmaker as a synapsid or a prosauropod.

The *Navahopus-Deltapodus-Apulosauripus* plexus is quite uniform morphologically. Its heel-dominated and short-toed pedal morphology (indeed sauropodomorph-like) corresponds well with that of “*Metatetrapous*” Nopcsa, 1923

– a purported ankylosaurian trackway from the Lower Cretaceous of Germany. However, we can only infer such resemblance from the illustration, not the original material. The “*Metatetrapous*” type material has not been seen for a long time. Haubold (1971) supposed that Nopcsa erected this ichnotaxon based only on the drawing provided by Ballerstedt (1922) and later nobody managed to relocate the actual specimen (Haubold, 1971; 1987), nor did we. Recently Hornung *et al.* (2007) reported the rediscovery of “*Metatetrapous*” type material, but without a new description, “*Metatetrapous*” still seems to be a nomen nudum. Probst & Windolf (1993) noted that the “*Metatetrapous*” manus is similar in shape to that of the “classic” ankylosaurian track of *Tetrapodosaurus*, but its pes is different by being narrower with pointed digits. Also the heel area is larger in “*Metatetrapous*” than in *Tetrapodosaurus*. *Tetrapodosaurus* shows a relatively gracile pedal structure with blunt-tip pad, but relatively long digits (fig. 10C). Such gracile morphology of *Tetrapodosaurus* has been demonstrated by McCrea (2000: fig. 6) referring to a particular footprint, possibly left on a drier and harder substrate than other tracks from the Gates Formation of Alberta in Canada. Paradoxically, McCrea (2000) persuaded by the morphology of that specimen and sharing the commonly held view on its ankylosaurian origin, questioned another common wisdom about the elephantine appearance of ankylosaurian feet, rather than simply consider a non-ankylosaurian affinity of the *Tetrapodosaurus* trackmaker. The belief in ankylosaurian origin of *Tetrapodosaurus* was strengthened by Carpenter (1984), who convincingly compared *Sauropelta* foot skeleton with *Tetrapodosaurus*. However, the foot skeleton of basal neoceratopsians also matches *Tetrapodosaurus* well (fig. 9A, B). Interestingly, Sternberg (1930) initially identified its trackmaker as an ancestral ceratopsian and it still seems reasonable to us.

McCrea *et al.* (2001) discussed the possible criteria for discriminating ankylosaurian tracks from those of ceratopsians. The authors noted that in the foot of the ceratopsid *Centrosaurus* Lambe, 1904 (fig. 10D) the hallux is not as short (reduced) in comparison with digits II–IV as it became in the *Sauropelta* pes. The *Centrosaurus* foot fits the pedal morphology of *Ceratopsipes* Lockley & Hunt, 1995b (fig. 10F) and unnamed ceratopsian track (fig. 10E) recently described by Milner *et al.* (2006), where digit I and IV are nearly equally developed. In contrast, our *Navahopus-Deltapodus-Apulasouripus* morphotype contains functionally tridactyl footprints, which lack a strong hallux, or have one that is clearly shorter than the main digit group II–IV. Thus, the definitely tetradactyl *Tetrapodosaurus* is closer to the ceratopsian type than to ankylosaurian skeletal pedal patterns, which may even be tridactyl. The first pedal digit was already well developed in the basal neoceratopsians, like *Protoceratops* Granger and Gregory, 1923 (see Brown & Schlaikjer, 1940), *Archaeoceratops* Dong & Azuma, 1997, *Montanoceratops* Brown & Schlaikjer, 1942 and *Cerasinops* Chinnery & Horner, 2007 (see fig. 10A). Moreover, such large hallux is present in the unquestionably basal neocer-

atopsian track from Mongolia (fig. 10B), which looks like a smaller and digitigrade version of a larger and semiplanigrade *Tetrapodosaurus*. This interesting footprint, directly associated with its trackmaker, was recently discovered by Tomasz Singer, while he was preparing the articulated *Protoceratops* skeleton ZPAL MgD-II/3, collected in Bayanzag by the Polish-Mongolian Expedition of 1962.

The *Navahopus-Deltapodus-Apulasouripus* plexus is widely distributed in the Jurassic and Cretaceous of Laurasia, while *Tetrapodosaurus* is restricted to the Middle Cretaceous (Aptian through Cenomanian) of Cordilleran North America. The first *Tetrapodosaurus* specimens were described from the Gething Formation (Aptian–Albian) of British Columbia (Sternberg, 1932), more recently it has been found in the Dunvegan Formation (Cenomanian) of British Columbia (Currie, 1989), the Gates Formation (Albian) of Alberta (McCrea and Currie, 1998; McCrea, 2000), the coal-bearing sequences of Ross River Block (Albian–Cenomanian) in Yukon Territory (Gonglott *et al.*, 2004) and the Dakota Group (Albian–Cenomanian) of Walsh area in Colorado (Lockley *et al.*, 2006). Thus, the *Tetrapodosaurus* occurrence supports the Aptian migrations of early neoceratopsians from Asia to North America postulated by Chinney *et al.* (1998).

Therefore, attributing the large, blunt-toed tridactyl footprints from the Morrison Formation to stegosaurian trackmakers results in a domino effect, leading to new (or resurrecting old) suggestions on the affinity of many other dinosaur ichnotaxa related to ornithischians ranging from ankylosaurians to ceratosaurs to dryomorph ornithopods.

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