

Small theropod and ornithopod footprints in the Late Jurassic of Poland

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ABSTRACT:

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Late Jurassic material of small theropod and ornithopod dinosaur footprints are reported from the northeastern slope of the Holy Cross Mountains, Poland. The ichnites occur in five lithostratigraphical units of an epicontinental basin in central Poland. Small theropod tracks, *Wildeichnus* isp. and *Jialingpus* isp., came from the Bałtów Platy Limestones, Bałtów Coral Limestones and Wierzbica Oolite and Platy Limestones. Four specimens of small ornithopod footprints, assigned to *Dinehichnus* isp., were found in the Błaziny Oolite Limestones and Wierzbica Oolite and Platy Limestones. A medium-sized ornithopod footprint, identified as cf. *Dinehichnus* isp., was discovered in the Ożarów Oolite and Platy Limestones. The described footprints from the Upper Jurassic of Poland are smaller than similar types of ichnites from other parts of the world. The Polish Late Jurassic dinosaur community probably represented a diminutive insular fauna.

Key words: Dinosaur footprints; Late Jurassic; Holy Cross Mountains; Poland.

INTRODUCTION

Dinosaur footprints reported between 1991 and the present are well known from nine Early Jurassic sites in the Holy Cross Mountains of central Poland (e. g., Gierliński 1991, 1994, 1995, 1996a, 1997, 1999; Gierliński and Niedźwiedzki 2002c; Gierliński and Pieńkowski 1999; Gierliński and Sawicki 1998; Gierliński *et al.* 2001a, b, 2004; Niedźwiedzki 2003; Niedźwiedzki and Niedźwiedzki 2001, 2004; Niedźwiedzki and Pieńkowski 2004; Gierliński and Niedźwiedzki 2005). Subsequently, from 2001, dinosaur tracks were also reported in five Late Jurassic localities along the northeastern slope of the Holy Cross Mountains. Well preserved dinosaur footprints are found in Ożarów (Gierliński *et al.* 2001b), Bałtów (Gierliński and Sabath 2002), Błaziny (Gierliński and Niedźwiedzki 2002a, 2002b), and recently in Wierzbica

and Wólka Bałtowska (Text-fig. 1). The footprints occur in five lithostratigraphic units (Text-fig. 2) established by Gutowski (1992, 1998), and dated from the middle Oxfordian to the early Kimmeridgian on the basis of correlation with the ammonite zones of *Gregoryceras transversarium*, *Perisphinctes bifurcatus*, *Epipeltoceras bimammatum*, *Idoceras planula*, *Ataxioceras hypselocyclum*, and *Crussoliceras divisum*.

Extra-Carpathian/Sudetic Poland is mostly covered with thick Quaternary deposits and forested or adapted for farmland. This leaves only small windows into potentially track-bearing surfaces, resulting in a fragmented distribution of ichnological resources. Dinosaur footprints are usually found as isolated specimens on loose slabs in quarries, at the base of a section mined with the use of explosives, like at Ożarów, Błaziny, Wierzbica and Wólka Bałtowska. There is little chance of finding continuous surfaces with long

trackways or even of following the track-bearing surface *in situ*. Nevertheless, the study area has yielded abundant and well-preserved material.

Institutional abbreviations: CU-MWC, University of Colorado/Museum of Western Colorado Joint Collection, Denver, Colorado; MLP, Museo de La Plata, La Plata, Argentina; MPT (known also as MNTS), Museum of Nature and Technology (former Museum of History of Material Culture, MHKM) in Starachowice, Poland; Muz. PIG, Geological Museum of the Polish Geological Institute, Warsaw, Poland; OUM, Oxford University Museum, Oxford, United Kingdom.

SYSTEMATIC ICHNOLOGY

Superorder Dinosauria Owen, 1842

Order Saurischia Seeley, 1888

Suborder Theropoda Marsh, 1881

Ichnogenus *Wildeichnus* Casamiquela, 1964

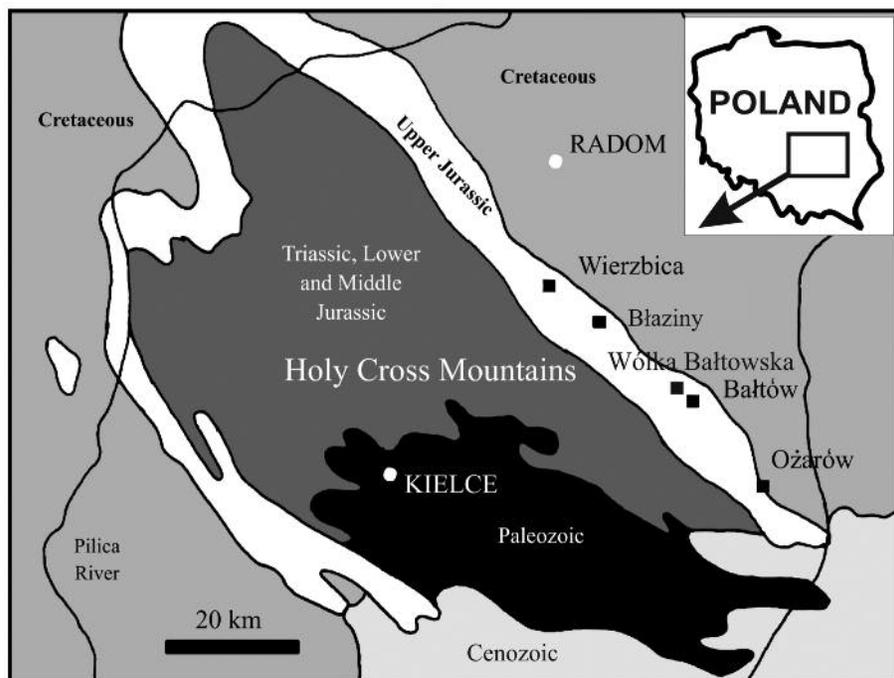
Wildeichnus isp.
(Text-fig. 3A, B)

MATERIAL: Two natural casts preserved in carbonates. The first one (Text-fig. 3A) was found in 2002, on the bottom surface of limestone layer at the base of the Devil's Foot near Bałtów, in the yellowish massive bio-

clastic limestone of the Bałtów Coral Limestones (latest middle Oxfordian). The original specimen is housed in the Bałtów theme park and its plaster cast is catalogued as MPT.P/121 (formerly GG/6). The second specimen, Muz. PIG 1663.II.4 (Text-fig. 3B), is preserved in grey platy limestone and was found in the Wierzbica Oolite and Platy Limestones (lower Kimmeridgian) of the Wierzbica mine.

DESCRIPTION: Tridactyl pes 3.5–3.7 cm long. Digit length ratios are: III/II = 1.33–1.46, III/IV = 0.97–1.00. The angles between the axes of digits II and III are between 9–21°, while the angles between the axes of digits III and IV are between 24–27°.

COMMENTS: Similar ichnites from the La Matilde Formation of the Santa Cruz Province, Argentina, have been described as *Wildeichnus naversi* Casamiquela, 1964 (Text-fig. 4A). The La Matilde Formation is Oxfordian, or Callovian according to the opinion of Leonardi (1994). The Polish specimens could thus be nearly the same age as *W. naversi* or slightly younger. Other small theropod footprints similar to these are younger and come from the Lower Cretaceous of Soria in Spain and the mid-Cretaceous of Lark Quarry in Queensland, Australia. Spanish specimens described as *Kalohipus bretunensis* Fuentes Vidarte and Meijide Calvo, 1998, are very similar to *Wildeichnus* and hence *Kalohipus* might be a junior synonym of *Wildeichnus*. The Australian ichnites, named *Skartopus australis* Thulborn and Wade, 1984 (Text-fig.



Text-fig. 1. Late Jurassic tracksites located along the northeastern flank of the Holy Cross Mountains

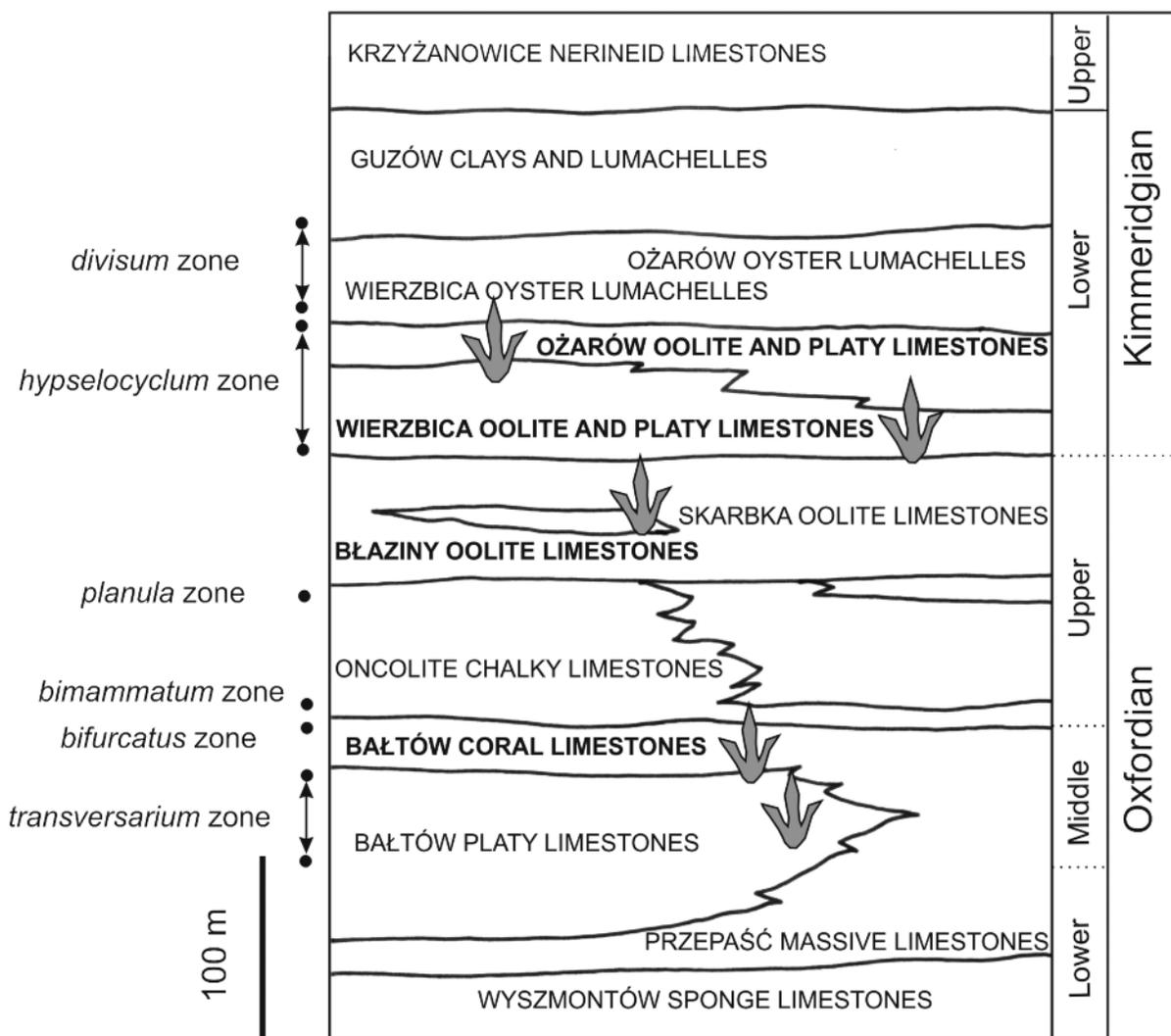
4B), differ from the Bałtów specimen in the lack of distinctly imprinted phalangeal pads. However, in the case of *Skartopus* tracks, produced by running trackmakers, the absence of morphological details such as phalangeal pads probably resulted from a dynamic interaction between foot and substrate and not from differences in the trackmaker's pedal morphology.

The specimens from Bałtów and Wierzbica are smaller than *Wildeichnus* and several *Skartopus* footprints, which possess the most proximal pads imprinted. The *Wildeichnus* footprints on the slab MLP 65-XI-12-1/2 are 5.5 cm long.

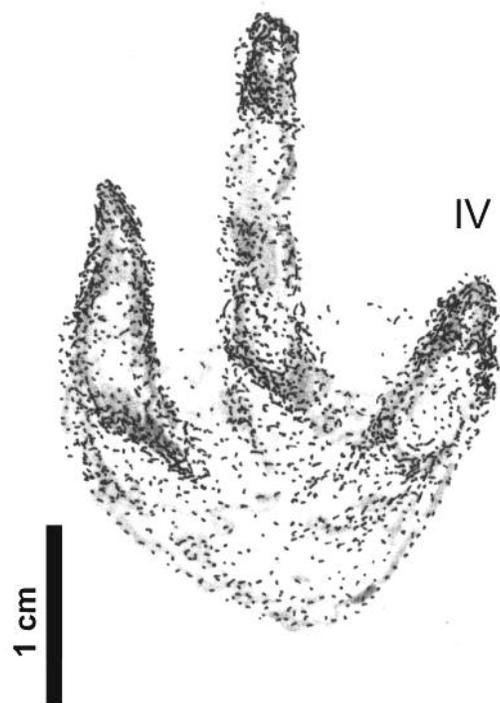
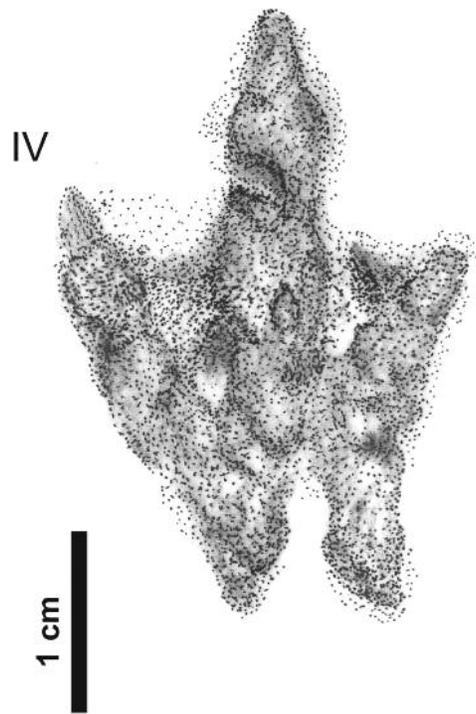
We suppose that our footprints, like several specimens of *Skartopus*, represent a subdigitigrade impression, which is shorter due to the lack of metatarsophalangeal pads. In several digitigrade dinosaur footprints, the metatarsophalangeal pads of the second and third

digits are absent, while those of the fourth digit are more clearly impressed and contribute to the asymmetric posterior outline of the footprint. In contrast, in the Polish specimen from Bałtów, the proximal phalangeal pad of digit II appears at the same level as digit IV.

The absence of the metatarsophalangeal pad of digit IV may not always indicate taxonomical differences. Among 1150 investigated footprints of living Eurasian otters, 61.1% were imprinted without the heel pad, 38.9% with that pad, and among those 38.9%, only 35% were, in fact, completely imprinted with the heel pad and both lateral digits (Reuther *et al.* 2000). It also seems that post-Liassic small theropods (possibly coelurosaurians), while running or just walking, showed a tendency towards subdigitigrade locomotion. Some of them revealed this tendency occasionally, others permanently, like the trackmakers of *Carmelopo-*



Text-fig. 2. Correlation of the lithostratigraphic units of the Upper Jurassic of the northeastern flank of the Holy Cross Mts., proposed by Gutowski (1992, 1998), showing stratigraphical position of the dinosaur footprints



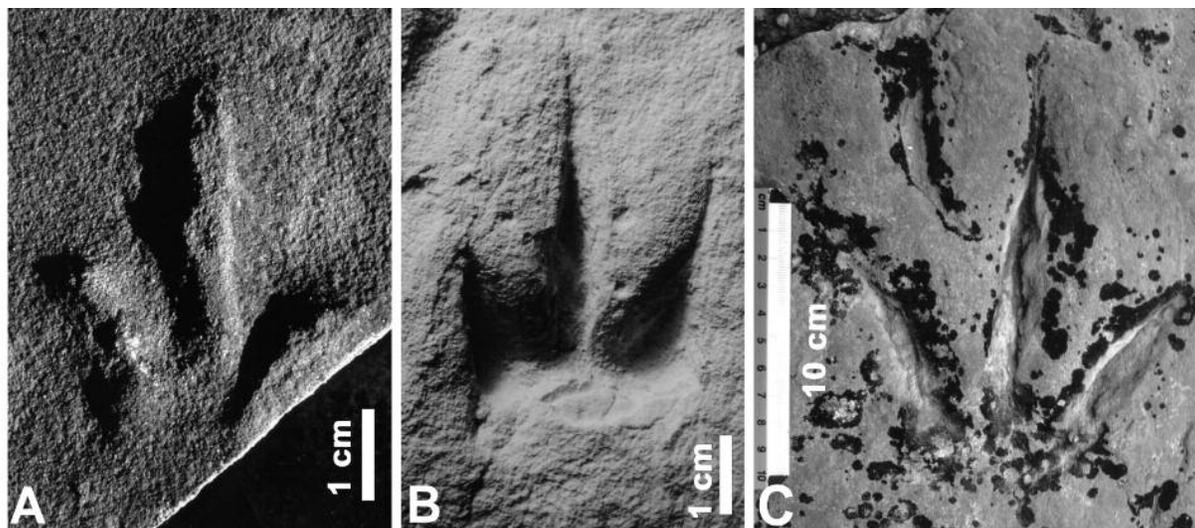
Text-fig. 3. Theropod footprints, *Wildeichnus* isp. **A** – MPT.P/121 from the Bałtów Coral Limestones, Bałtów; **B** – Muz. PIG 1663.II.4 from the Wierzbica Oolite and Platy Limestones, Wierzbica

us Lockley, Hunt, Paquette, Bilbey and Hamblin, 1998 (see Lockley *et al.* 1998a) from the Middle Jurassic of Utah and Wyoming, USA (Text-fig. 4C).

According to the method of Olsen *et al.* (1998), the lengths of the second and third digits, measured between the mid-points of the proximal phalangeal pads and the mid-points of the claw impressions, reflect the combined lengths of phalanges 2 and 3 of the trackmaker's digit II, and the combined lengths of phalanges 2, 3, and 4 of the trackmaker's digit III respectively. The length of the fourth digit, measured between the mid-point of its metatarsophalangeal pad and the mid-point of the claw impression, reflects the combined lengths of all the phalanges of the trackmaker's digit IV. However, in the case of the Polish specimens, where digit IV possibly lacks a metatarsophalangeal pad, the length of this digit may reflect only the combined lengths of phalanges 2, 3, 4, and 5 of the trackmaker's digit IV. With such a correction applied to comparison with the skeleton material, the Polish specimens fit the digit length ratios and the pes length of the type specimen of *Compsognathus longipes* Wagner, 1861 (BSPHG AS I 563). This specimen is considered to be a juvenile individual (Ostrom 1978). The BSPHG AS I 563 pedal digit ratios are: III/II = 1.40 and III/IV = 0.80 (= 1.00 excluding phalanx IV 1). The length of the phalangeal part of the BSPHG AS I 563 foot is 5.4 cm and, excluding phalanx IV 1, 4 cm.

Ichnogenus *Jialingpus* Zhen, Li and Zhen, 1983

cf. *Jialingpus* sp.
(Text-fig. 5A, B, C)

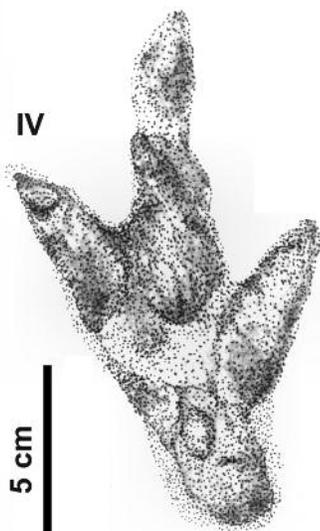


Text-fig. 4. Theropod footprints. A – *Wildeichnus* isp. from the Bonaparte's quarry, La Matilde Formation (Middle/Late Jurassic), Argentina; B – *Skartopus* isp. from the Lark Quarry, Winton Formation (Middle Cretaceous) of Australia; C – *Carmelopodus* isp. from Red Gulch Track site (Middle Jurassic) of Wyoming

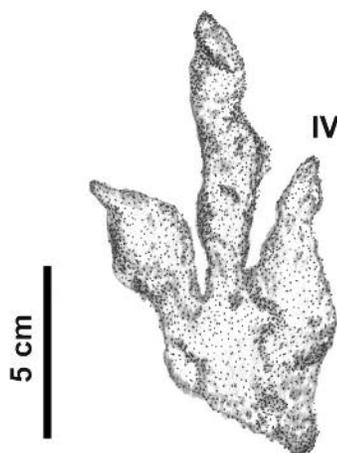
MATERIAL: Two natural casts of the left pedal print (Text-fig. 5B, C) and one right pedal imprint (Text-fig. 5A). The first specimen, MPT.P/138 (formerly MHKM GG/2), is from the slab found in 2001 near the post-office building in Bałtów (Text-fig. 5A). The slab belongs to the dolomitized upper part of the Bałtów Coral Limestones (late middle Oxfordian). The second specimen, Muz. PIG 1663.II.3 (Text-fig. 5B; plaster cast), was found in the Wierzbica Oolite and Platy Limestones (early Kimmeridgian) in 2006, at the southeastern exposure of the lower level in the Wierzbica quarry. The last specimen of *Jialingpus* reported herein (Text-fig. 5C) was found in 2006 at the Wólka Bałtowska quarry, where the Bałtów Platy Limestones are exposed.

DESCRIPTION: The pedal imprints are tridactyl and 13–15 cm long. Digit length ratios are: III/II = 2.10–2.42, III/IV = 0.98–1.23. The angles between the axes of digits II and III are 30°–37°, and between the axes of digits III and IV 19°–23°. The footprints are characterized by large elongate metatarsophalangeal pads on digit IV (this feature is especially well exhibited by MPT.P/138 and Muz. PIG 1663.II.3), which markedly extends the proximal (metatarsophalangeal) area of the footprint posteriorly. This so-called 'heel' area constitutes 40% of the footprint length in MPT.P/138.

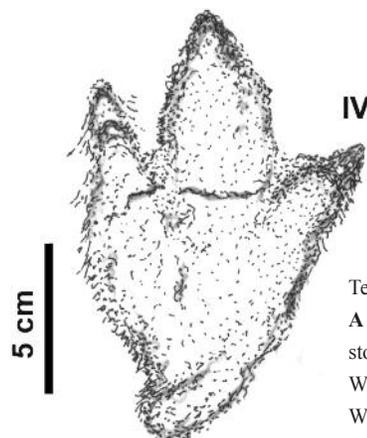
COMMENTS: *Jialingpus* Zhen, Li and Zhen, 1983, from the Late Jurassic Penglaizhen Formation of Sichuan Province in China, shows a morphological pattern (Text-fig. 6A) similar to our specimen. The Pol-

**A****IV**

5 cm

**B****IV**

5 cm

**C****IV**

5 cm

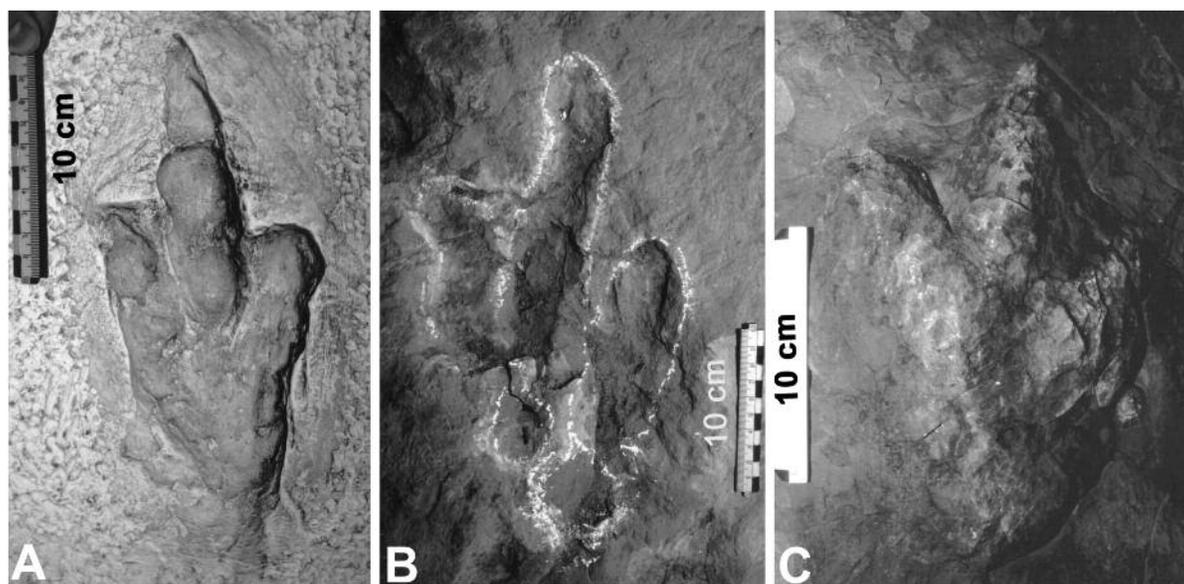
Text-fig. 5. Theropod footprints, *Jialingpus* isp. **A** – MPT.P/138 from the Bałtów Coral Limestones, Bałtów; **B** – Muz. PIG 1663.II.3 from Wierzbica Oolite and Platy Limestones, Wierzbica; **C** – Muz. PIG 1713.II.1. from Wólka Bałtowska Platy Limestones, Wólka Bałtowska

ish forms are approximately 25–35% smaller, with more widely divergent digits, than the Chinese type material of *Jialingpus*, but they correspond to *Jialingpus* in their digit length ratios and the distinctively swollen metatarsophalangeal pad of digit IV. As noted originally by Zhen *et al.* (1983), the characteristically large metatarsophalangeal pad of digit IV is a diagnostic feature of this ichnotaxon. Unfortunately, this information was not repeated later by Zhen *et al.* (1989), when the description of *Jialingpus* was repeated. Generally, the tulip-shaped *Jialingpus* footprints, with a strongly projected middle toe, greatly resemble the Early Jurassic ichnogenus *Grallator* Hitchcock, 1858. Contrary to the previous opinion suggesting an anomoeopodid affinity of *Jialingpus* (Zhen *et al.* 1983; Zhen *et al.* 1989), Gierliński (1994) treated *Jialingpus* as a junior synonym of *Grallator*.

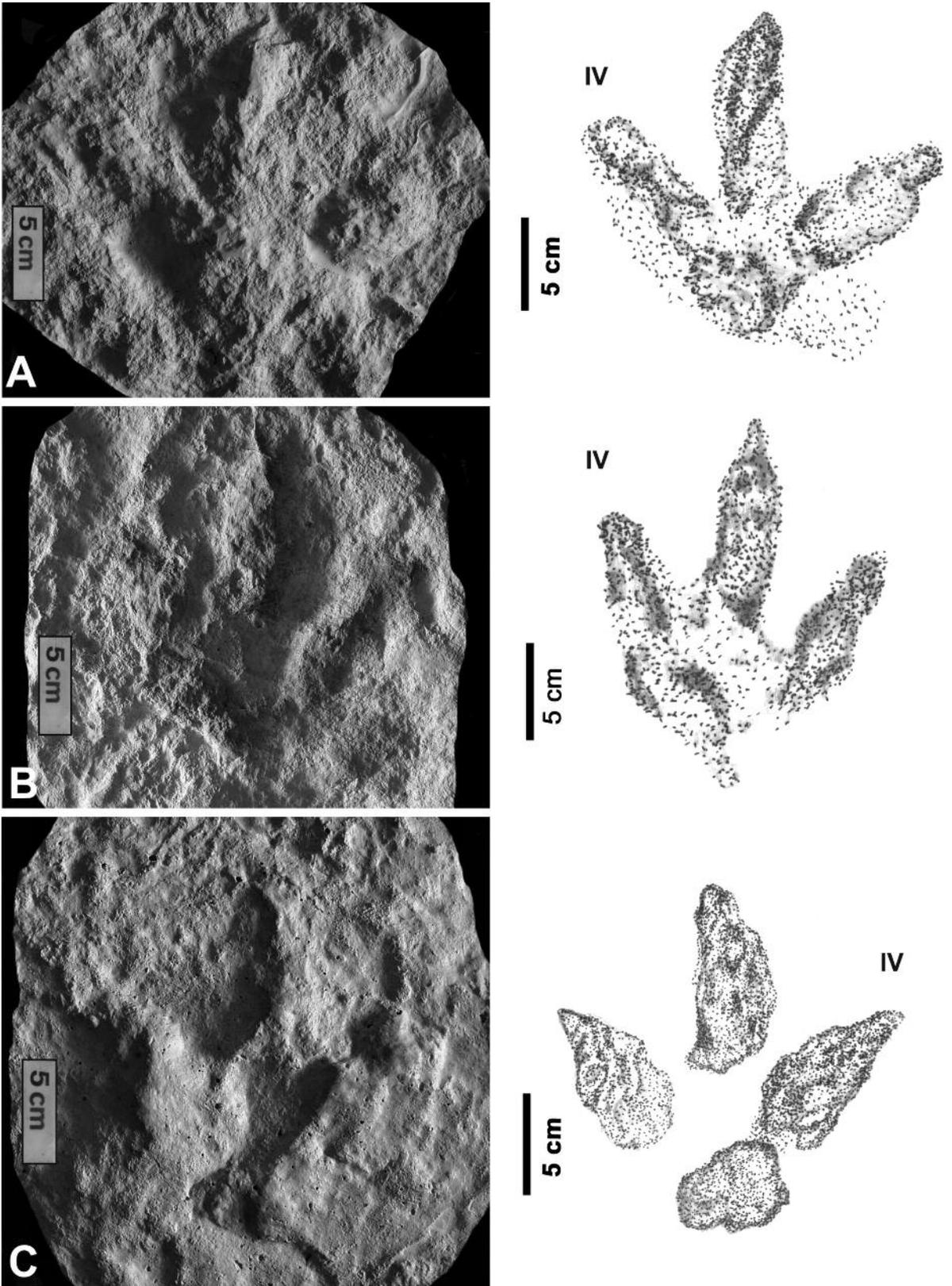
The presence of a metatarsal impression and hallux imprint in the *Jialingpus* type specimen BNHM-SCFP 24, and in an isolated anomoeopodid-like manual print, led Zhen *et al.* (1983) and Zhen *et al.* (1989) to the conclusion that the tracks were similar to the Early Jurassic ornithischian tracks of *Anomoepus* Hitchcock, 1848. The alleged manual print BNHM-SCFP 24 is not convincingly associated with any pedal print of *Jialingpus*, and it does not even look like a manus to us. The presence of the metapodium and the occurrence of the hallux imprint in the plantigrade footprint BNHM-SCFP 24 cannot prove its ornithischian origin, or its similarity to *Anomoepus*. Evidently several other theropod ichnites were also misinterpreted as ornithischian on the

basis of the metapodium trace (see Gierliński 1994, 1996b). In fact, theropods possessed a metapodium and were able to imprint it while sitting, travelling across the swamp, hiding in ambush, squatting at the carcass of prey, crouching during mating display, or possibly when injured (Lockley *et al.* 2003).

On the other hand, however, *Jialingpus* differs clearly from *Grallator* in having a distinctly larger “heel” area. If specimens of *Jialingpus* and *Grallator* of the same size are compared, the “heel” area in the Polish specimen constitutes 40% of the footprint length, while in the *Grallator* specimen AC 28/1 it constitutes 28%. Moreover, some *Jialingpus* specimens possess phalangeal portions of digit II that are extraordinarily short in comparison with the other digits. The digit length ratios of the *Jialingpus* specimen BNHM-SCFP 21 are III/II = 2.31, and III/IV = 1.50. Such digit length ratios are not observed among the Early Jurassic grallatorids (see Olsen *et al.* 1998), but they could have resulted from the lack of a fully impressed claw of digit II, whose anterior portion might not have touched the ground. The next interesting feature is that *Jialingpus* is V-shaped posteriorly. The fourth digit’s metatarsophalangeal pad is located below the middle toe. This may suggest an arctometatarsalian arrangement of the metatarsals. *Jialingpus*-like footprints (Text-fig. 6C) occur in the Kimmeridgian of Asturias, Spain (according to field observations by one of us). There are also some *Jialingpus*-like footprints in the Cretaceous, e.g. in the Berriasian-Valanginian of Germany (Text-fig. 6B).



Text-fig. 6. Theropod footprints, *Jialingpus* isp. **A** – BNHM-SCFP 21 from the Penglaizhen Formation of China; **B** – Specimen in field, Münchhagen Dinopark, Bückebug Formation (Berriasian-Valanginian) of Germany; **C** – Specimen in field, Tereñes Cliffs, Asturias, Tereñes Formation of Spain



Text-fig. 7. Ornithopod footprints, *Dinehichnus* isp. from the Blaziny Ooilte Limestones of Poland, Blaziny. A – MPT.P/135 (plaster cast), right pedal print; B – MPT.P/136 (plaster cast), right pedal print; C – MPT.P/137 (plaster cast), left pedal print

Order Ornithischia Seeley, 1888
Suborder Ornithopoda Marsh, 1871

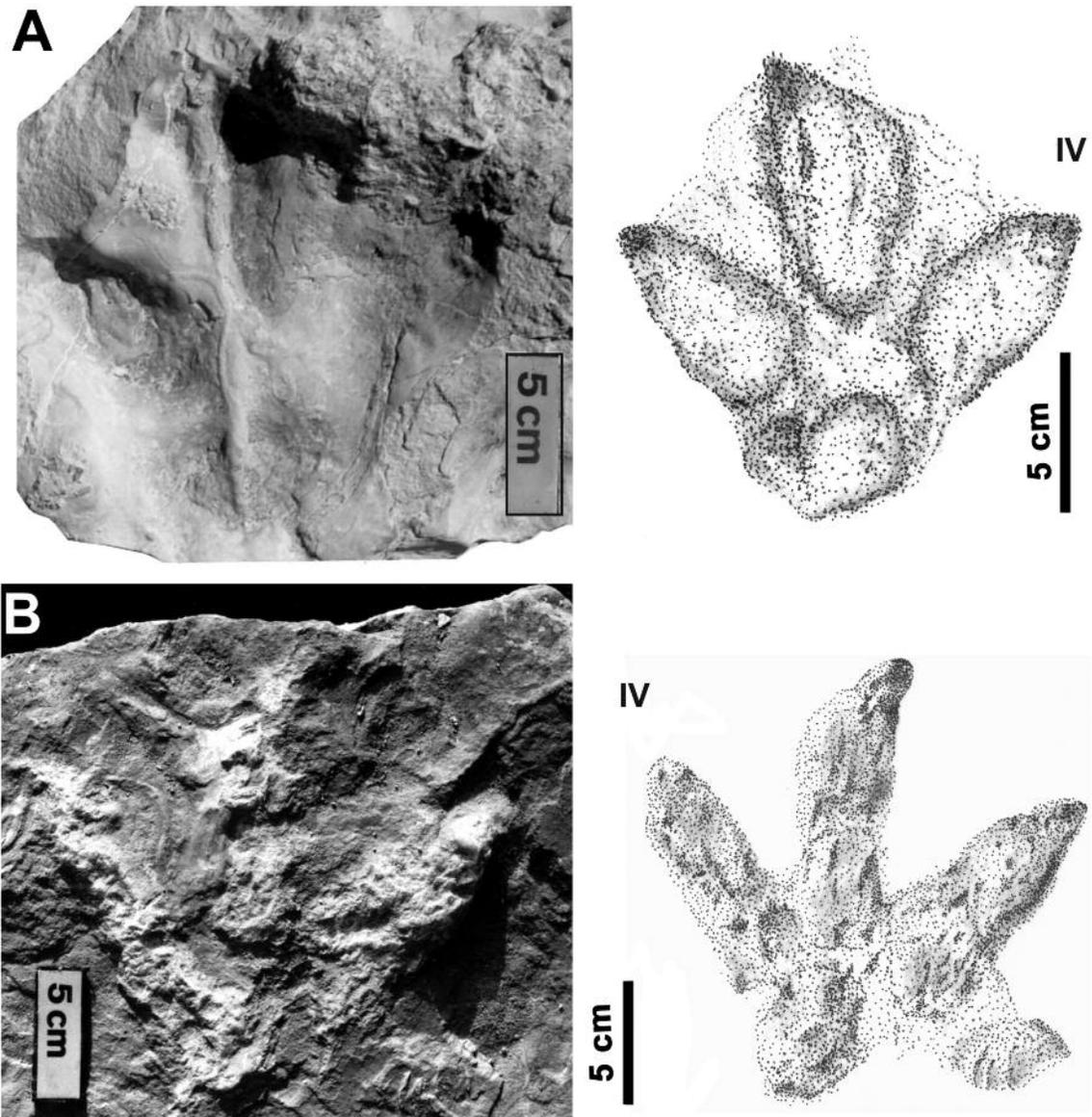
Ichnogenus *Dinehichnus* Lockley, Santos, Meyer
and Hunt, 1998

Dinehichnus isp.
(Text-fig. 7A-C, 8A)

MATERIAL: A right pedal print, Muz. FIG 1663.II.1 (Text-fig. 8A), from the Wierzbica Oolite and Platy Limestones (early Kimmeridgian), found in the south-eastern exposure of the lower level in the Wierzbica quarry. Plaster casts of right and left pedal prints,

MPT.P/135, 136, 137 (Text-fig. 7), originally preserved as natural casts in the bioclastic grainstone of the upper part of the Błaziny Oolite Limestones (Late Oxfordian), which is mined in the upper level of the Błaziny Quarry.

DESCRIPTION: Tridactyl quadripartite symmetric footprint about as wide as long. The specimen Muz. FIG 1663.II.1 is 12 cm long and 12.3 cm wide, while the specimens from Błaziny MPT.P/135, 136, 137 are 14–15 cm long and 14–15.5 cm wide. The digits lack distinctly imprinted phalangeal pads. The metatarsophalangeal pads of digits II and IV made a large isolated posterior impression, located centrally below

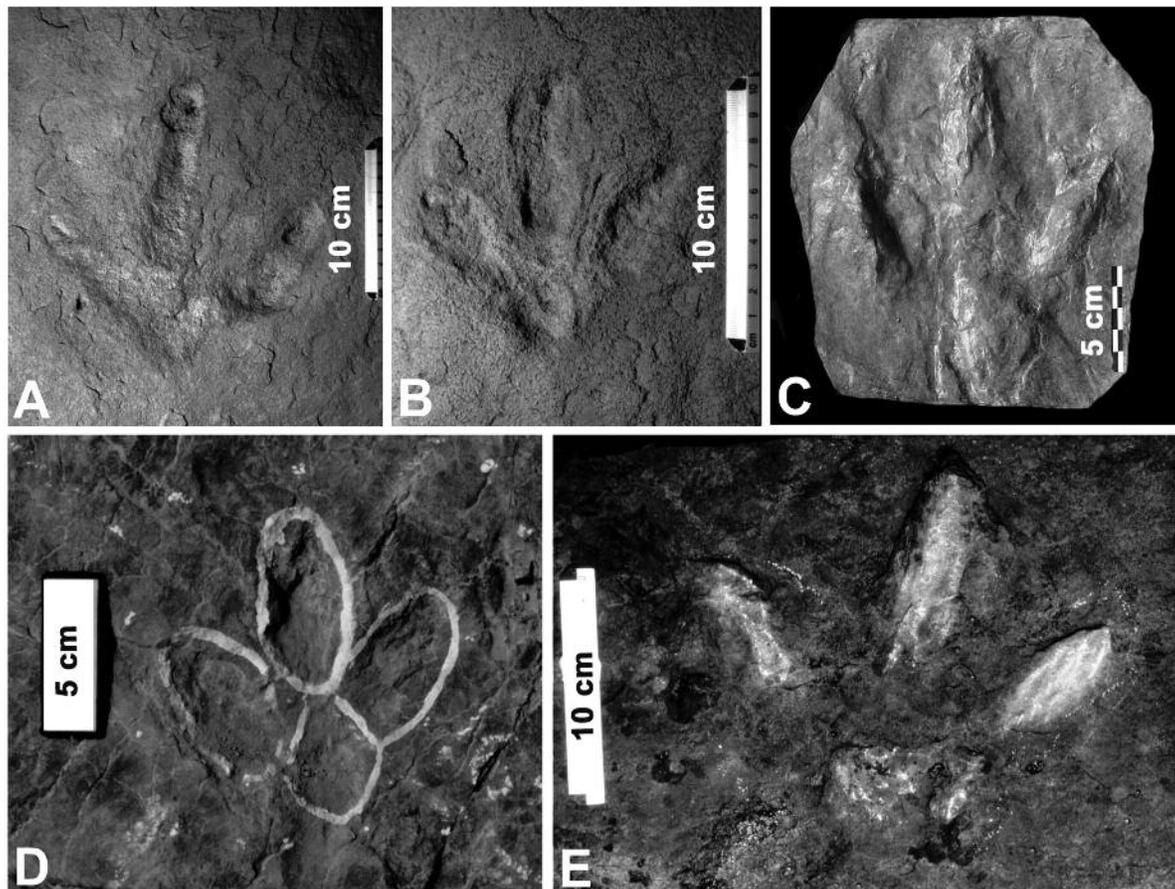


Text-fig. 8. Ornithopod footprints. A – *Dinehichnus* isp., Muz. FIG. 1663.II.1 from the Wierzbica Oolite and Platy Limestones, Wierzbica; B – cf. *Dinehichnus* isp., Muz. FIG 1663.II.2 from the Ożarów Oolite and Platy Limestones, Ożarów

digit III. Excluding the metatarsophalangeal pad of digit IV, the toes are subequal in length and widely divergent. In Muz. PIG 1663.II.1, the angle between the axes of digits II and III is 40° , and between the axes of digits III and IV 52° . The digits of specimen MPT.P/137 are slightly less divergent: the angle between the axes of digits II and III is 37° and between the axes of digits III and IV is 40° .

COMMENTS: In its general form, the footprints resemble Early Jurassic tracks of *Anomoepus* Hitchcock, 1848. However, the *Anomoepus* footprints are often narrower, with less divergent and thinner digits, which usually show well defined phalangeal pads. The footprints described by Lockley *et al.* (1998b) as *Dinehichnus socialis* (Text-fig. 9A, B) from the Salt Wash Member of the Morrison Formation (Kimmeridgian) of Utah, USA, are almost identical. Similarly the *Dinehichnus* footprint from the Tereñes Formation of Asturias, Spain (Text-fig. 9E), show a circular proximal node produced by the metatar-

sophalangeal pad of digit IV. In our specimens, two metatarsophalangeal pads have probably coalesced into the “heel” pad, which is oblong rather than circular. This also makes the Polish specimens different from the Early Cretaceous *Dinehichnus*-like footprints found in the Spanish tracksites of the Era del Peladillo, at site 5 (Text-fig. 9D), the Valdevajes site cited by Lockley *et al.* (1998b) and the Dakota Group of Colorado, USA (Text-fig. 9C). The Early Cretaceous specimens from Spain were supposedly of hypsilophodontid origin, while the Late Jurassic type material from Utah is suspected of dryomorph affinity (Lockley *et al.* 1998b; Gierliński *et al.* 2005). The size of the Polish specimens corresponds to the smallest *Dinehichnus* ichnites from Utah (Text-fig. 9B). The recently described hypsilophodontid footprints of *Hypsiloichnus* Stanford, Weems and Lockley, 2004, from the Lower Cretaceous of Maryland and Virginia, are clearly unlike the ichnites of the Late Jurassic *Dinehichnus*, and *Dinehichnus*-like forms from the Lower Cretaceous.



Text-fig. 9. Ornithomimid footprints. **A, B** – *Dinehichnus socialis* Lockley, dos Santos, Meyer and Hunt, 1998, Morrison Formation, Utah, USA; **C** – cf. *Dinehichnus* isp., Dakota Group, Colorado, USA; **D** – cf. *Dinehichnus* isp., Enciso Group, Era del Peladillo, Spain; **E** – cf. *Dinehichnus* isp., Tereñes Formation, Tereñes Cliffs, Spain. Scale: A, B, E = 10 cm; C, D = 5 cm

cf. *Dinehichnus* isp.
(Text-fig. 8B)

MATERIAL: Natural cast of a shallow left pedal print Muz. PIG 1663.II.2 (Text-fig. 8B) from the Ożarów Oolite and Platy Limestones (late early Kimmeridgian), found in an isolated block of micritic limestone below the northwestern front face of the Ożarów quarry.

DESCRIPTION: Functionally tridactyl, symmetric footprint about as long as wide, 18 cm long and 19 cm wide. The elongate oval digits show slightly visible phalangeal pads. The two distal pads on digit III are almost fused into one elongate pad. The metatarsophalangeal pad of digit IV constitutes a discrete proximal pad located almost below the third digit. There is a small impression of a medially directed hallux. All digits are widely divergent, with similar angles between their axes (I-II = 45°, II-III = 40°, III-IV = 41°). Digit length ratios are: III/II = 1.35 and III/IV = 0.75.

COMMENTS: The symmetric, broad footprint Muz. PIG 1663.II.2, is nearly as long as wide, with cigar-shaped, widely and equally divergent digits, and a discrete, oval proximal pad located almost centrally below the middle toe; these are all features that resemble those of *Dinehichnus* and are even more like those of *Anomoepus*. However, the presence of the hallux impression, together with slightly, but recognizably delineated phalangeal pads, and a proximal pad not “sufficiently well” separated from digit IV, make specimen Muz. PIG 1663.II.2 different from *Dinehichnus*. Footprints similar to the Polish specimen were also found in the Vega Beach, in the Upper Jurassic of Asturias, in Spain (Valenzuela *et al.* 1988, fig. 21), with the description suggesting an ornithopod origin. A similar footprint from the Morrison Formation of Wyoming, USA, was interpreted as belonging to a dryosaur by Bakker (1996).

The presence of a hallux imprint in the Polish specimen speaks against its dryosaur origin, suggesting rather a camptosaurid affinity for its trackmaker (Gierliński *et al.* 2001b). The footprint from the Morrison Formation illustrated by Bakker (1996, fig. 2) lacks a hallux impression, but it nevertheless possesses a footprint morphology and digit length ratios (III/II = 1.32 and III/IV = 0.78) close to those of Muz. PIG 1663.II.2. The digit length ratios of both footprints resemble the ratios of the pedal digit lengths of *Camptosaurus dispar* Marsh, 1879 (III/II = 1.33, III/IV = 0.76). According to the method of Olsen *et al.* (1998) of measuring the length of the phalangeal part of the trackmaker foot skeleton, the pedal imprint Muz. PIG

1663.II.2 seems to have been left by a pes about 33% smaller than that of *C. dispar*.

The total length of the footprint left by this American camptosaur might be estimated as about 26 cm, and thus even less than that of the largest ichnite (28 cm long) labelled as *Dinehichnus* by Lockley *et al.* (1998b).

Our observations allow us to conclude that the supposedly camptosaur tracks may represent a relatively gracile form similar to *Dinehichnus*. They will possibly be classified as a new ichnospecies of *Dinehichnus*, if the material is well enough preserved and sufficiently abundant. Our conclusion contrasts with the traditional vision of camptosaur tracks, seeking alleged camptosaur footprints among the larger and more robust Late Jurassic forms, 30–45 cm long, which are basically too large by camptosaur standards. The 45-cm long prints from the Morrison Formation of Colorado and the Summerville Formation of Oklahoma were originally supposed to be of camptosaur origin (Lockley 1986; Lockley *et al.* 1986). However, this interpretation was later revised and they are more recently considered as large theropod tracks (Prince and Lockley 1989; Lockley and Hunt 1995; 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. According to the osteological material presently known, there are no Late Jurassic ornithopods large enough to produce such large, robustly-shaped ichnites.

DISCUSSION

The footprints from the Upper Jurassic of Poland under discussion are smaller than similar types of ichnites from other parts of the world. The pedal print Muz. PIG 1663.II.2, cf. *Dinehichnus* isp., from the upper lower Kimmeridgian of Ożarów, as noted above, was left by a foot 33% smaller than that of the American *Camptosaurus dispar*, and it is even 36% smaller than the foot of the European *Camptosaurus prestwichii* Hulke, 1880 from the upper lower Kimmeridgian of England. Despite the European camptosaur being anatomically more gracile than the American form, it is not that much smaller, as shown by the specimen OUM J.3303. The size of the footprint Muz. PIG 1663.II.1, cf. *Dinehichnus* isp., from the lower Kimmeridgian of Wierzbica, fits the sizes of the smallest *Dinehichnus* specimens from the Kimmeridgian of Utah.

The *Jialingpus* footprint from Poland is consistent with the apparent size trend of the Polish Late Juras-

sic footprints, being 25–35% smaller than the Chinese type material of *Jialingpus*.

The *Wildeichnus* isp. from the Devil's Foot near Bałtów seems to be an exception to this size trend. It does fit the size of the German *Compsognathus longipes* from the Solnhofen Limestones, if the absence of its metatarsophalangeal pads is taken into account. However, Ostrom (1978) suggested that the German *Compsognathus longipes*, BSPHG AS I 563, was a juvenile specimen, while the adult version of this species came from the Tithonian of France and was originally described as *Compsognathus corallestris* Bidar, Demay, and Thomel, 1972. The French skeleton is about 50% larger than the German one, but it appears to be identical in all other respects (Norman 1990). On the other hand, Griffiths (1994) identified small circular objects spread near the abdominal region of *C. longipes* BSPHG AS I 563, as the eggs at an early stage of development, still lacking the eggshell and the elongate shape characteristic of theropod eggs. If this identification is correct, the German specimen may represent a mature individual of small size.

The Solnhofen paleoenvironment indicates a large inland sea with scattered islands. *Compsognathus* lived on islands along the shoreline of a slowly emerging central German swell (Haubold 1997). Many insular animals tend to evolve smaller body size than their mainland relatives. Given this possibility, the pattern of small tracks may be an indication of a dwarf fauna. Such changes are among the fastest evolutionary responses to varying environmental conditions. Body-size change may thus precede further modifications leading eventually to speciation. In our opinion, the German *Compsognathus* is a dwarf variant of the same species as the one from France, and not a juvenile specimen, as confirmed by the supposed eggs, indicating sexual maturity.

A question now arises: did the Polish Late Jurassic dinosaurs represent a diminutive insular fauna? We do not have enough material to support such an assumption so convincingly as in the case of the Croatian Cretaceous pygmy dinosaurs documented at the Istrian tracksites by their rich track assemblages (Dalla Vecchia *et al.* 2000, 2001; Dalla Vecchia 2003). However, the geological data do not discount the possibility that our dinosaurs lived on islands.

Liszkowski (1972) believed that the emersion resulted in the appearance of reef islands similar to those now present in the Indian and Pacific Oceans. The islands supported xerophyllous vegetation, sparse forests of conifers (Pinopsida) with an admixture of maidenhair trees (Ginkgopsida), cycads (Cycadophytina) and horsetails (Sphenophytina). From Wólka Bałtowska,

Liszkowski (1972) described Oxfordian horsetails, seed ferns, ginkgoes, conifers, and bennettites. He regarded the low species diversity, predominance of conifers, and minor contribution of other gymnosperm orders as an indication of climatic zonation and climate aridization. Analysis of the morphology and histology of the plant remains support this conclusion. The flora from Wólka Bałtowska reveals thickened cuticles covering the leaves, as well as stomatal structure typical of xerophytes. These features indicate very arid climatic conditions. The same is suggested by leathery leaves of Pteridospermales and scaly leaves of conifers. Warm arid conditions in this area are also predicted by numerical climate models for the Late Jurassic (e.g., More and Ross 1996). Such harsh environments (limited area of the island with limited productivity of a xerophyllous flora) might have been responsible for the strong dwarfism. Recently, dwarfism among sauropods was documented from the Kimmeridgian of northern Germany (Sander *et al.* 2006).

Gutowski (personal communication) rejects the possibility of small islands present in Central Poland in the Late Jurassic. During that time the Holy Cross Mts., as well as the surrounding regions of Poland, were predominantly covered by shallow epicontinental seas. The nearest lands were situated to the southeast (the Ukrainian shield), and to the north (the Baltic shield). The northeastern flank of the Holy Cross Mts. was located closer to the Ukrainian shield (Ziegler 1990). In Oxfordian-Kimmeridgian times, the Ukrainian land seems to have been nearly the size of the Great Britain (see, Golonka *et al.* 1996). Whether such a relatively large island might have induced dwarfism, probably depends on the environmental conditions of the island, and the periodicity and duration of its connection with larger land masses, possibly the Asian continent.

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