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AVIALIAN THEROPOD TRACKS FROM THE EARLY JURASSIC STRATA OF POLAND*

Gerard Gierliński**

RESUMEN

Las primeras huellas de Plesiornis pilulatus *se describieron en depósitos del Hetangiense Superior de las Montañas de Santa Cruz. Los especímenes de Polonia están tan bien conservados que de ellos se deducen datos importantes de la forma del pie y del parentesco del autor de la huella.*

Plesiornis, *como las pisadas de aves del Mesozoico Superior y Cenozoico, tiene la almohadilla falangiana del tercer dedo muy desarrollada y no tiene almohadillas falangianas no metatarsales en los dedos laterales –lo contrario que en las huellas dinosaurias tridáctilas no aviformes–. Parece que esto es una estructura clave para distinguir marcas aviformes de las de terópodos no aviformes. Si esto es así, hay impresiones liásicas consideradas aviformes* –Trisauropodiscus–, *que no son tan seguras. Los trisauropodíscidos (sensu Lockley et al., 1992) se parecen más a* Anomoepus *(pisadas ornitisquias primitivas) que a icnitas de ave.*

La forma Plesiornis *es intermedia entre* Grallator *y las huellas de ave posteriores. Los parámetros de sus estructuras son iguales a los del pie de* Archaeopteryx. Plesiornis *se debe considerar la señal aparentemente de ave más antigua de las que se conocen; es 50 m.a. anterior a los primeros huesos fósiles de ave encontrados de estos animales. Por otra parte, los datos mencionados suponen que los animales aviformes que vivieron cerca del límite Triásico-Jurásico no habían evolucionado filogenéticamente tanto como había sugerido la interpretación cuestionada de los restos llamados* Protoavis.

Palabras clave: Pisadas, Theropoda, Avialae, Hetangiense, Polonia

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** Geological Museum of the Polish Geological Institute, ul. Rakowiecka 4, 00-975 Warszawa, Poland.

The first tracks of Plesiornis pilulatus *are reported from the Late Hettangian deposits of the Holy Cross Mountains. The perfect preservation of the Polish specimen allows for significant conclusions on the trackmaker's pedal morphology and its affinity.*

Contrary to the nonavialian tridactyl dinosaur footprints, Plesiornis *like the Late Mesozoic and Cenozoic bird tracks, has the third digit metatarsal - phalangeal pad strongly developed and no metatarsal - phalangeal pads of the lateral toes. This seems also to be a key feature to distinguish avialian tracks from those of the nonavialian theropods. If this is indeed the most distinctive characteristic of the avialian pes type, then other Liassic tracks identified as avialian* –Trisauropodiscus–, *become discussable. Trisauropodiscids (sensu Lockley et al., 1992) bear a resemblance rather to* Anomoepus *(early ornithischian tracks) than to the bird ichnites.*

Plesiornis *shows the transitional pedal morphology between* Grallator *and later bird tracks. Its pes parameters correspond to the* Archaeopteryx *pes structure.* Plesiornis *could be therefore treated as the oldest known sign of the bird appearance, which is preceding the osteological record by more than 50 Ma. On the other side, however, the above mentioned data suggest that avialians near the Triassic - Jurassic boundary were not as much advanced phylogenetically as the recently questioned interpretation of the remains named* Protoavis, *has previously suggested.*

Key words: Footprints, Theropoda, Avialae, Hettangian, Poland.

0. INTRODUCTION

The described specimen came from the historically first and still the richest Polish dinosaur tracksite of Gliniany Las, near Mniów (Karaszewski, 1969, 1975a, b; Gierliński and Potemska, 1987; Gierliński, 1990, 1991, 1995a). During the last years, four new localities of So3tyków, Zapniów, Jakubów and Idzikowice have been recognized (Pieñkowski and Gierliński, 1987; Gierliński, 1991, 1995a,b). Among them, however, it is the Gliniany Las site that revealed the most interesting material. Hitherto described dinosaur ichnospecies of Gliniany Las, comprised *Grallator tenuis* ó small nonavialian theropod tracks, *Anomoepus pienkovskii* ó possibly heterodontosaurid tracks, and the intriguing ichnotaxon of *Moyenisauropus karaszevskii*, regarded as the earliest iguanodontid footprints (Gierliński, 1991, 1995a). The fourth ichnospecies ó *"Grallator (Grallator) zvierzi"*, has been recently reidentified as similar to *Wintonopus* ó produced by small running ornithopods (Gierliński, 1995a).

The Gliniany Las exposure shows a regressive sequence of the upper part of the Przysucha Formation (Pieńkowski, 1985). Numerous ichnites have been found preserved as natural casts on the bottom surface of certain sandstone layer, which is considered as sediment of the barrier - lagoon transitional environment (Gierliński, 1991). Dinosaurs left there approximately twelve tracks per square meter. Most of them are morphologically close to *Wintonopus*, while the least numerous are those of theropods, including avialian ichnites described herein.

Pieńkowski and Gierliński (1987) have suggested bridge - like function for the barrier. The Gliniany Las prominents ó various - sized herbivores (trackmakers of *Wintonopus, Anomoepus* and *Moyenisauropus*), could just had used it to travel between their main terrestial biotopes, or occasionally, as a route of their seasonal migrations (Gierliński, 1995a). Whereas, in the case of small predators, the barrier - lagoon environment seems to be a permanently favourable. Track - bearing stratum contains large number of the invertebrate crawling, dwelling and feeding traces (Pieńkowski, 1985). Similarly, avialian tracks occur often in association with invertebrate traces in several other localities (Lockley *et al.*, 1992).

Following Gauthier (1986), the term Avialae is used herein for the traditional taxon Aves. Avialae is treated as a clade within Theropoda.

I. SYSTEMATIC ICHNOLOGY

THEROPODA Marsh 1881
AVIALAE Gauthier 1986
Ichnofamily: Plesiornithidae n. ichnofam.
Type genus: *Plesiornis* Hitchock 1858

Occurrence: Upper Triassic to Lower Jurassic: Newark Supergroup of eastern North America and Przysucha Formation of Poland.

Diagnosis. Bipedal. In the trackway, the pes is directed forward. Small tracks with a broad U - shaped contour. Pes functionally tridactyl with hallux also imprinted. The third digit is longest. Digits are thin, relatively long with no phalangeal pads clearly marked. The third digit metatarsal - phalangeal pad is well traced, whereas metatarsal - phalangeal pads of the lateral toes are not impressed.

Remarks: The plesiornithid pes impressions reflect a mixture of grallatorid and the exact bird tracks traits. Forwardly directed pes in the trackway, the pes longer than wide with the longest digit III, while the lateral ones are nearly equal in length; all bear a resemblance to the ichnogenus *Grallator sensu* Olsen, 1980, and Gierliński, 1994. However, such features as the absence of the lateral digits metatarsal - phalangeal pads, deeply impressed metatarsal - phalangeal pad of digit III, highly divaricated and slender digits, hallux impression strongly opposite, located just below the third digit, closely to the most proximal pad, are all indicative of bird tracks.

Plesiornis shows a transitional morphology between the Grallatoridae and the Cretaceous bird tracks grouped in the ichnofamily of Ignotornidae (Lockley *et al.*, 1992). Consequently, I propose to distinguish *Plesiornis* morphological type on the higher ichnosystematic level, erecting the monogeneric ichnofamily of Plesiornithidae.

Ichnogenus *Plesiornis* Hitchcock 1858.

Plesiornis pilulatus Hitchcock 1858.

Material: Muz. PIG 1560.II.38. Trackway preserved as a natural cast, found in Gliniany Las, Poland: upper part of the Przysucha Formation (Upper Hettangian).

Description: Ratio of the pes width to external trackway width 1:1.4. Ratio of the pes length (excluding hallux) to pace 1:1.5. Pes directed forward. Track length (including hallux) accounts for 46 mm. Following Demathieu (1990) statistical method, the pes measurement ratios are: the third digit length (excluding metatarsal - phalangeal pad) to the first digit lenght (III/I) = 3.00, third digit length to the second one (III/II) = 1.26, third to fourth one (III/IV) = 1.18, fourth to second one (IV/II) = 1.06, third digit length to the third digit projection value (III/D) = 2.03, pes length to pes width (L/W) = 1.08, and the pes length to third digit length (L/III) = 1.24. The angles between the digit axes are:I-II = 141°-144°, II-III = 25°-53°, III-IV = 31°-39°. The total divarication (II-IV) varies from 61° to 92°.

Remarks: Lull (1953) has mentioned five ichnospecies of *Plesiornis* ó *Plesiornis pilulatus, P. aequalipes,P. mirabilis, P. giganteus* and *P. quadrupes*. However, he has also noted that the only *P. pilulatus* could stand as the separate ichnotaxon, while others could be refferable

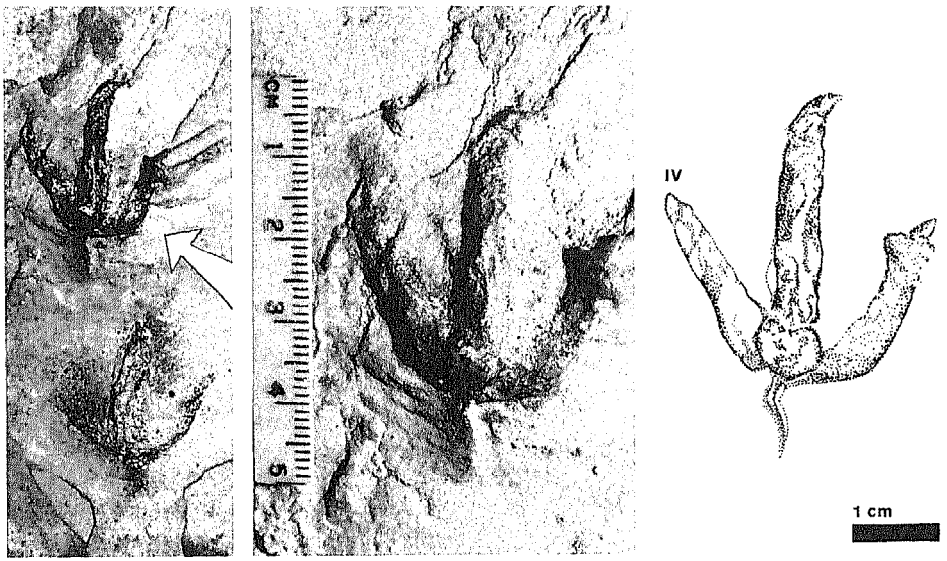

Fig. 1. Plesiornis pilulatus *(Muz. PIG 1560.II.38), from Gliniany Las near Mniów, Poland (Upper Hettangian).*

to different genera. In agreement with his opinion, *Plesiornis* is considered herein as a monospecific genus, represented by *P. pilulatus.*

The Polish specimen bears a strong resemblance to the *P. pilulatus* holotype. The hallux of the Polish sample, however, is much clearer traced than in the holotype, which makes it comparable to the *P. pilulatus* from Virginia (Weems and Kimmel, 1993).

2. DISCUSSION

Lull (1953) considered *Plesiornis* as a theropod track.

According to the theropod tracks classification method of Weems 1992, *Plesiornis* fits the pes proportion ratios of typically large sized grallatorid ó *Kayentapus soltykovensis* (Gierliński 1991) Gierliński 1996. A very small size of *Plesiornis* makes then possible to suppose that was left by a juvenile of the *Kayentapus soltykovensis* trackmaker. However, two important features of *Plesiornis* clearly discord with *Kayentapus soltykovensis* and any other early nonavialian theropod tracks.

Among the Late Triassic and Early Jurassic tridactylous ichnotaxa, the unusual possition of the hallux and metatarsal - phalangeal node, are the most distinguishing features of *Plesiornis. Plesiornis* has no metatarsal - phalangeal pads of the lateral digits, while that of the middle toe is well visible, being the deepest impressed part of the footprint. Other dinosaur tracks have often the fourth digit metatarsal - phalangeal pads impressed. When they got all of them impressed, then metatarsal - phalangeal pads are rather distinct, usually with the priority for the fourth one to be traced strongest.

The above mentioned feature has also been discussed by Padian and Olsen (1989). In their opinion, the absence of the lateral toes' metatarsal - phalangeal pads is related to bird hind-limb anatomical specificity, sligthly different from those of the nonavialian theropods (exclu-

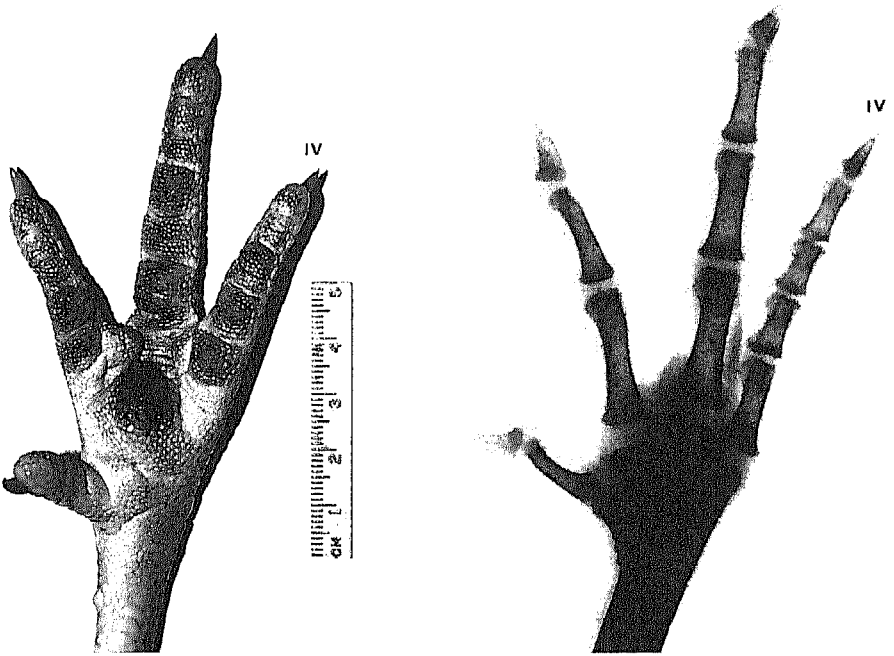

Fig. 2. The pes of a living avialian Gallus domesticus *and its X-ray photograph.*

ding ornithomimosaurians). Whatever the reason, the *Plesiornis* third digit seems to be the main weight - bearing axis of its trackmaker pes. The same pattern characterized birds, where the only one supporting metatarsal - phalangeal pad occurs ó that of the inner toe (Fig. 2).

The second avialian feature of *Plesiornis* concerns its hallux possition. In the numerous early nonavialian theropod tracks, even if the subreduced hallux is imprinted, usually its trace is left just by the hallux tip, which sank into the substrate leaving there the posteromedial mark, far away from the entire pes impression (Fig. 3). Such type of impression has been caused by the fact that nonavialians usually had the first metatarsal shorter than the second, third and fourth. Therefore, only the claw of the posteriorly oriented hallux was sometimes able to rearch the ground. The bird foot shows usually a different pattern, having hallux as the functionally opposite digit. Metatarsals from I to IV are usually subequal in length, lying closely to each other in the early avialians (Fig. 4), or being fused in the later forms. The type of a hallux impression in *Plesiornis* (Fig. 1) clearly corresponds to the avialian pattern.

However, the *Plesiornis* hallux is less developed than in the later birds' tracks of *Ignotornis* and *Jindongornipes* (Lockley *et al.*, 1992). The *Plesiornis* hallux length is only one-third of the third digit length, which resembles the length ratio between the pedal digit I and III of *Archaeopteryx lithographica* (following the measurements given by Wellnhofer, 1974). Foot of the next advanced avialian after *Archeopteryx* ó that of *Sinornis*, (Sereno and Rao, 1992) became functionally tetradactyl, having hallux of nearly half the third digit length.

Consequently, if the hallux enlargement reflects an adaptational trend in the early avialian evolution, than functionally tridactyl pes of *Plesiornis* with just slightly avialian - like modified hallux, seems to be left by a trackmaker not more advanced than *Archaeopteryx.*

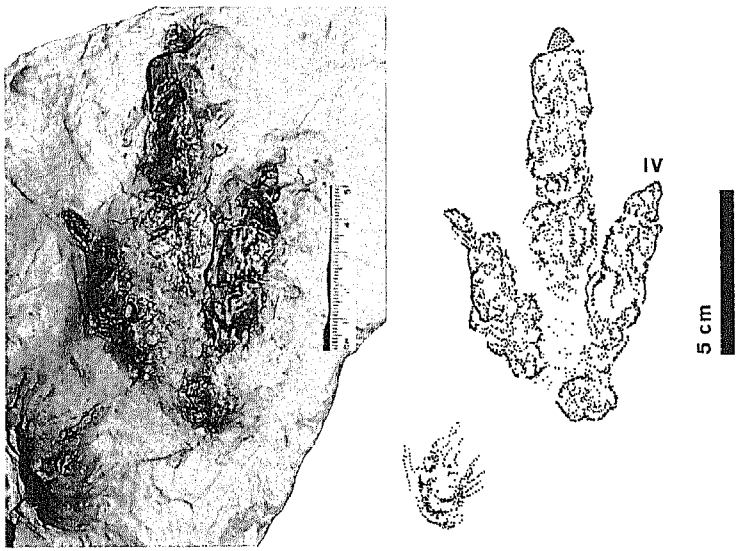

Fig. 3. Grallator tenuis *(Muz. PIG 1569.II.33), from Gliniany Las, near Mniów, Poland (Upper Hettangian).*

Assuming the avialian affinity of the modern bird - like shaped tracks of *Trisauropodiscus* (Lockley *et al.*, 1992), there was some avialian trackmaker more advanced than that of *Plesiornis*, near the Trassic - Jurassic boundary. In my opinion, however, *Trisauropodiscus* tracks (especially *T. moabensis*) bear a strong resemblance to the well known Liassic ornithischian footprints of *Anomoepus* (Lull, 1953; Olsen, 1980).

Lockley *et al.*, (1992) noted that *Trisauropodiscus* is distinguished by the wide divarication between digits II and IV (total divarication), in the range of 90° to 120°. However, Thulborn (1990) disagrees with the traditional opinion that the wide digit divarication is the discriminating parameter of bird tracks. He has pointed out that also some dinosaur (= nonavialian dinosaur) tracks may have a total divarication much greater than 90°. It seems to be especially true for the typically bird - like shaped tracks of early ornithischians. For instance, total divarication of the pes impressions in the *Anomoepus* specimen from Massachusetts ó AC 50/I (Fig.5), varies from 50° up to 100°. One of the *Anomoepus* trackway from the Lisbon oilfield site in Utah (Lockley and Hunt, 1995), shows the digit total divarication of 100° - 105°. In another North American *Anomoepus* trackway (YPM 5910), the total divarication reaches 120°. Moreover, *Trisauropodiscus* does not show the characteristicly swelled pad below the third digit. Conversely, *Trisauropodiscus moabensis* seems to have the fourth digit metatarsal - phalangeal pad imprinted, similarly to anomoepodid tracks and several other nonavialian dinosaur footprints.

To summarize, three main conclusions could be traced. Firstly, the excessive development of the third digit metatarsal - phalangeal pad together with the absence of the lateral digits' proximal pads, appears to be the best criterion for avialian track recognition. Such recognition would be however possible only on the basis of well preserved specimens.

Secondly, avialian tracks are rare near the Trassic - Jurassic boundary. There are no other ichnites from that time, except *Plesiornis*, which could be treated as unquestionably

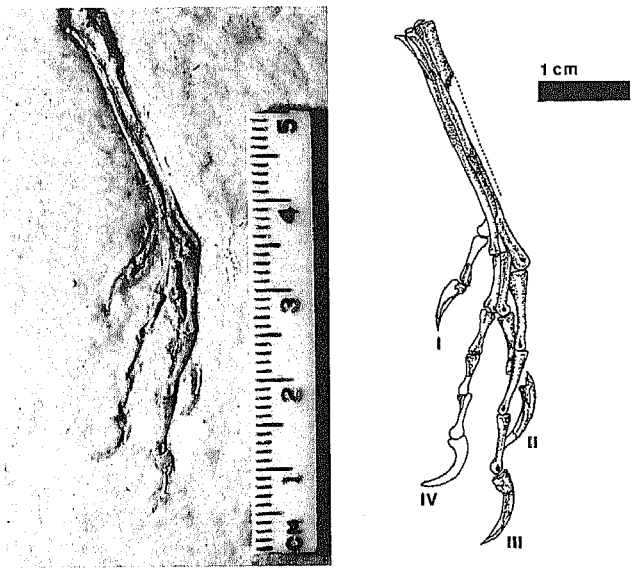

Fig. 4. Archaeopteryx lithographica, *left pes of the Eichstätt specimen, after Wellnhofer, 1974.*

avialian. The avialian affinity of the Liassic tracks ó *Masitisisauropus*, suggested by Ellenberger (1974), has been later questioned. Feather - like impressions around these footprints are considered as the invertebrate traces (Molnar, 1985). *Masitisisauropus* tracks seem to me to be partially resembling *Grallator*, and partially *Anomoepus*.

Thirdly, the *Plesiornis* stratigraphical location implicates the avialian appearance 50 Ma earlier than osteological record indicated. The Late Triassic remains, named *Protoavis* (Chatterjee, 1991), to which Weems and Kimmel (1993) referred *Plesiornis* tracks, are questioned as the remains of avialian origin (Ostrom, 1991; Sereno and Rao, 1992; Chiappe, 1995).

3. ABBREVIATIONS OF CITED REPOSITORIES

AC ó Pratt Museum of Natural History, Amherst College, Amherst, Massachusetts, U.S.A.; Muz. PIG ó Geological Museum, Polish Geological Institute, Warsaw, Poland; YPM ó Peabody Museum of Natural History, Yale University, New Haven, Connecticut, U.S.A.

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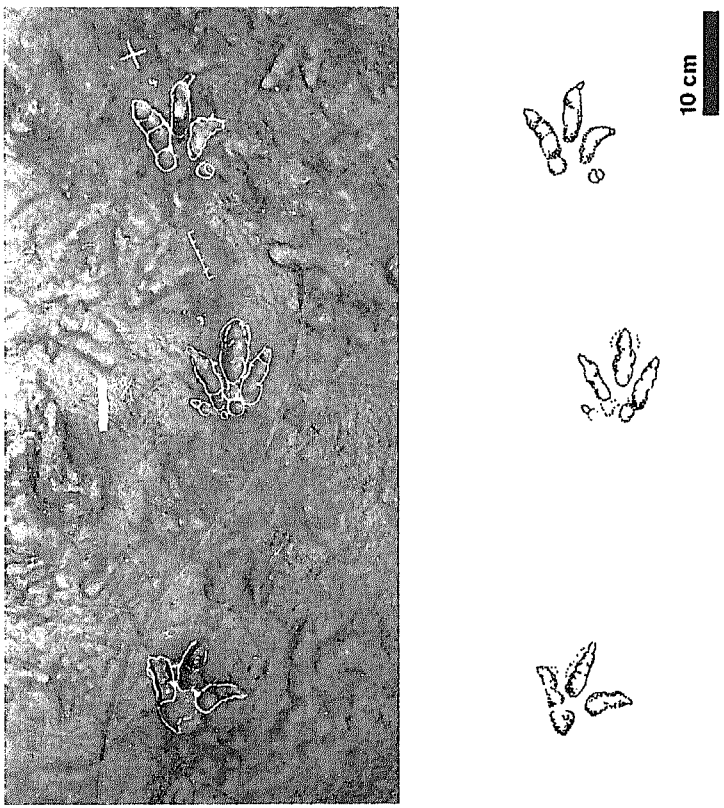

Fig. 5. The Anomoepus *trackway (AC 50/I) from Turners Falls, Massachusetts, U.S.A. (Lower Jurassic).*

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