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Dinosaur track assemblages from the Hettangian of Poland

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Almost all dinosaur tracks in Poland come from three lowermost formations of the Lower Jurassic in the Holy Cross Mountains: Zagaje Formation, Skłoby Formation and Przysucha Ore-Bearing Formation. Floristic remains and sequence stratigraphy correlation indicate the Hettangian age of all three formations. They represent various continental and marginal-marine environments. Fluvial and lacustrine sediments dominate in the continental Zagaje Formation, while the nearshore and deltaic facies are dominant in the two overlying formations. Various ornithischian, sauropod and theropod tracks occur in these sediments. Parallel sauropod trackways reported herein are the earliest record of sauropod gregarious behavior. Moreover, the present paper summarises and systematises the whole existing material, addressing the ichnosystematic and preservational aspects. Dinosaur tracks assemblages are assigned to three parts of the lithostratigraphical succession in which they occur and are discussed against their palaeoenvironmental background. Two general assemblages are distinguished: lower Zagaje assemblage of an inland, humid habitat with both low- and high-growing vegetation, dominated by high browsing herbivores (sauropod trackmakers of *Parabrontopodus*) and medium- to large-sized predators (theropod trackmakers of *Anchisauripus* and *Kayentapus*), and upper Zagaje–Skłoby–Przysucha assemblage, representing deltaic plain-shoreline habitats with low, dense vegetation, dominated by low browsing herbivores (ornithischian trackmakers of *Anomoepus* and *Moyenisauropus*), associated by small- to medium-sized predators (theropod trackmakers of *Grallator* and *Anchisauripus*). Dinosaur ichnofauna from Poland rather poorly reflects biostratigraphical vertebrate faunal change in Early Jurassic time, but it does reflect environmental and biogeographical differences quite well. The discussed data imply also a high dinosaur phylogenetical diversity as early as in the Hettangian age.

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Key words: Poland, Early Jurassic, dinosaur tracks, ichnotaxonomy, palaeoenvironmental background.

INTRODUCTION

Dinosaur tracks in Poland occur in the Early Jurassic deposits of the Holy Cross Mountains (Fig. 1). For the first time they have been described by W. Karaszewski (1969, 1975), and then the research continued in the eighties and nineties (G. Gierliński, 1990, 1991, 1994, 1995*a, b*, 1996*c*, 1997*a*, 1999; G. Gierliński, A. Potemska, 1987; G. Gierliński, K. Sabath, 1998; G. Gierliński, G. Sawicki, 1998; G. Pieńkowski, G. Gierliński, 1987; G. Pieńkowski, 1998). As a result, a number of new forms have been described, some of them new to science. After many years of research on the dinosaur tracks of Poland and collecting new important material, a systematisation, update and summary of hitherto published results are needed. The Polish material has been compared to specimens from other parts of the world to resolve systematical dilemmas. Dinosaur tracks from Poland are mostly Hettangian in age, although potentially dinosaur-bearing strata occur in the whole Early Jurassic of Poland, but outcrops of continental deposits of Sinemurian, Pliensbachian or Toarcian age are very rare. Single theropod track is known from the late Toarcian (G. Gierliński, 1995*b*). The present paper presents Hettangian dinosaur tracks against the palaeoenvironmental background. Interpretation of sedimentary environments is based on detailed sedimentological studies from the previous papers (G. Pieńkowski, 1981, 1983, 1985, 1991*a*, 1997, 1998; G. Pieńkowski, G. Gierliński, 1987) and new data discussed herein. Hettangian dinosaur ichnofacies from Poland are fairly rich and in many ways unique, arousing ichnotaxonomical and palichnostratigraphical questions. This paper contributes to the knowledge on Early Jurassic dinosaurs and their relations with environment, as well as to the knowledge on an early speciation rate of thyreophoran dinosaurs.

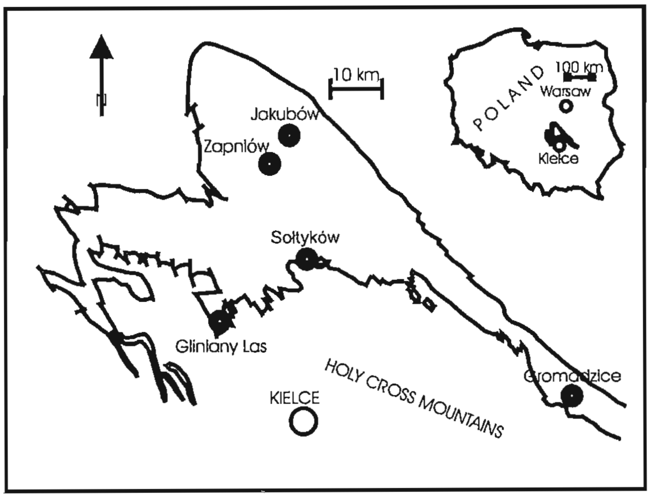

Fig. 1. Hettangian dinosaur tracksites in the northern slope of the Holy Cross Mountains superimposed onto the extent of the exposed Early Jurassic deposits, or covered by Quaternary deposits

STRATIGRAPHY AND SEDIMENTOLOGY OF THE HETTANGIAN SEDIMENTS IN THE HOLY CROSS MTS.

In the Hettangian time the terrigenous, continental and nearshore deposition was taking place in the Holy Cross Mountains area, which constituted the southeasternmost ending of the large, epeiric basin along the Teisseyre-Tornquist line between Denmark–South Sweden and SE Poland (Fig. 1). Earliest Jurassic (Hettangian) sediments are subdivided into three formations: the lowermost, entirely continental Zagaje Formation, transgressive, brackish-marine (nearshore and deltaic) Skłoby Formation and regressive, lagoonal, deltaic and fluvial Przysucha Ore-Bearing Formation (Fig. 2). Also the lowermost, fluvial complex of the overlying Ostrowiec Formation is assigned to the Hettangian. The siliciclastic Hettangian sediments do not contain fully-marine fossils. Some brackish marine bivalves, foraminifera and worms occurring in the Skłoby and Przysucha Ore-Bearing Formations do not provide good stratigraphical datum. Therefore, stratigraphy is based on floristic remains. Megaspore *Nathorstisporites hopliticus* which occurs in the Zagaje, Skłoby, Przysucha and lower Ostrowiec Formations (T. Marcinkiewicz, 1971) is characteristic for Hettangian and early Sinemurian. Moreover, miospores *Aratrisporites minimus, Pinuspollenites minimus* and *Zebraisporites* sp. occurring in these sediments (W. Karaszewski, 1974; M. Waksmundzka, pers. comm.) are characteristic for Hettangian. Sedimentation and sequence stratigraphy in this basin were described by G. Pieńkowski (1983, 1985, 1991*a*, *b*, 1997). A reliable correlation between the relative sea level in the Polish-Swedish basin and the eustatic curve proposed by the Exxon Production Research Group = EPR curve (B. Haq *et al.*, 1988), as well as by A. Hallam (1988) could be worked out (G. Pieńkowski, 1991*a*, 1997). Such correlation follows the principles of sequence stratigraphy and is largely based on the transgressive-regressive cycles, following the concept of D. Emery, K. J. Myers (1996). Hettangian sedimentation, representing a whole type II sequence and beginning of the next sequence of the same type, can be summarised as follows (Fig. 2):

1. Erosional surface at the base of the Zagaje Formation corresponding to the uppermost Rhaetian shelf margin wedge system tract (SMW).

2. Continental Zagaje Formation, corresponding to an initial phase of the world-wide *planorbis* and *liassicus* transgressive system tract (TST), which initiated backstepping of sedimentary package reflected by the succession of the braided river regime–meandering river regime–lacustrine regime in the synthetic profile of the Zagaje Formation. Such a backstepping sedimentary package, connected with approaching transgression, but actually located below the transgressive surface, can be called a pre-transgressive systems tract (G. Pieńkowski, 1997). In its uppermost part, it can also include delta plain sediments, which is the case observed in the lower Gromadzice outcrop. Zagaje Formation represents most probably the lowermost *planorbis* Zone.

3. Transgressive surface occurs at the base of the brackish-marine Skłoby Formation and corresponds to the lower part of the *planorbis* Zone.

4. Transgressive systems tract (continuation) encompasses transgressive Skłoby Formation, characterised by gradual intensification of brackish-marine influences towards the uppermost part of this formation, culminating in the maximum flooding surface, which corresponds to the middle part of the *liassicus* Zone and world-wide maximum flooding surface on the EPR curve.

5. Highstand systems tract (HST) is represented by regressive Przysucha Ore-Bearing Formation. This HST corresponds to the topmost part of the *liassicus* and *angulata* Zones.

6. Erosional surface at the top of the Przysucha Ore-Bearing Formation, commencing the next type II sequence, corresponds to the SMW dated at the upper part of the *angulata* Zone.

7. Fluvial sediments of the lowermost part of the Ostrowiec Formation representing the initial phase of the next TST (backstepping of sedimentary package — pre-transgressive systems tract), corresponding to the uppermost *angulata* Zone and lowermost *bucklandi* Zone (Sinemurian). Sinemurian ammonites occur some 20 m above this transgressive surface in southern Sweden (Scania), and they represent the next *semicostatum* Zone (R. A. Reyment, 1959), which consequently dates the previously deposited sediments in the Polish-Swedish basin as older than the *semicostatum* biochronozone (G. Pieńkowski, 1991*a, b*).

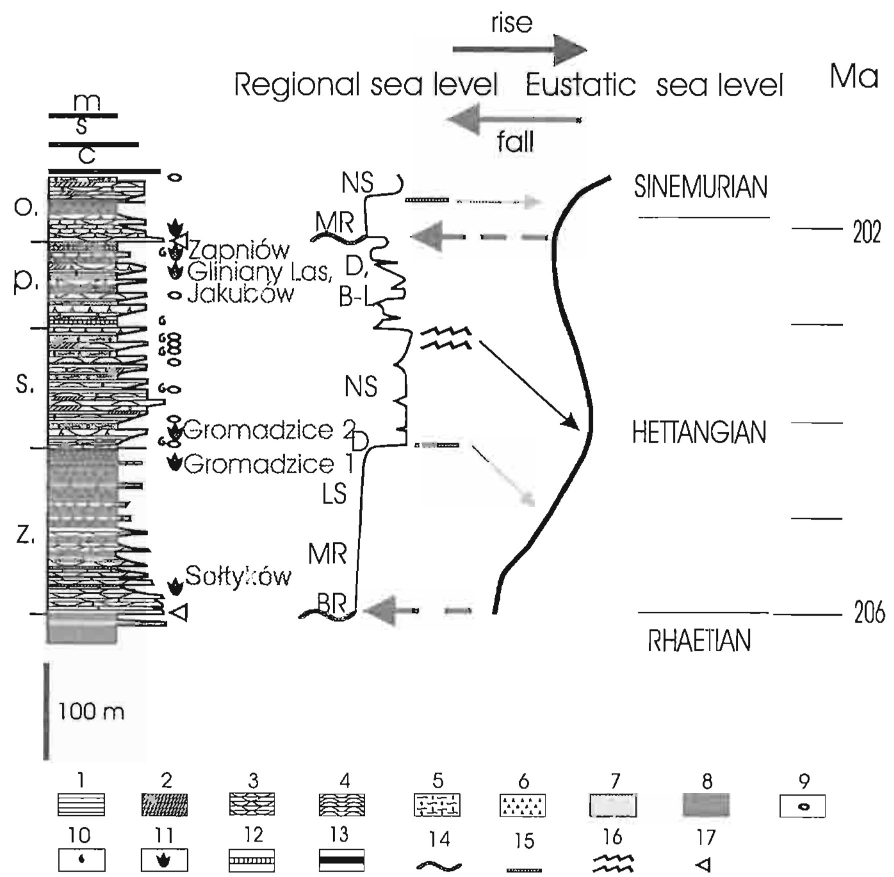

Fig. 2. Sedimentological-stratigraphical profile of the Hettangian deposits on the northern slope of the Holy Cross Mountains showing the stratigraphical and palaeoenvironmental position of the dinosaur tracksites

z. — Zagaje Formation; s. — Skłoby Formation; p. — Przysucha Ore-Bearing Formation; o. — Ostrowiec Formation; **bars above the profile**: C — conglomerates, S — sandstones, m — mudstones; **sedimentary palaeoenvironments and facies**: BR — braided rivers, MR — meandering rivers, LS — lacustrine-swamps, D — deltas, B–L — barrier-lagoon, NS — nearshore; **dominating sedimentary structures and other explanations**: 1 — parallel lamination, 2 — tabular cross-bedding, 3 — trough cross-bedding, 4 — hummocky cross stratification, 5 — heteroliths with trace fossils, 6 — plant roots and palaeosols, 7 — brackish-marine mudstones, 8 — lacustrine mudstones, 9 — brackish-marine bivalves, 10 — brackish-marine foraminifera, 11 — dinosaur tracks, 12 — siderites, 13 — coal seams, 14 — regional erosional surfaces, 15 — transgressive surfaces, 16 — maximum flooding surfaces, 17 — sequence boundaries; eustatic curve after A. Hallam (1988)

LOWER ZAGAJE TRACK ASSEMBLAGE

GEOLOGICAL SETTING

In the Sołtyków outcrop (abandoned clay pit, now nature reserve, known also as the Odrowąż outcrop), meandering river plain deposits embracing laterally accreting channels, flood plain/lacustrine deposits with numerous crevasse sediments are visible (Fig. 3). Sediments exposed in the Sołtyków outcrop belongs to the lowermost part of the Zagaje Formation (Figs. 2, 3), dominated by fluvial deposits. The borehole situated in Sołtyków revealed some 8–10 m thick sequence of low-sinuosity river sediments underneath the deposits visible in the outcrop. The earliest Liassic age of the sediments in the outcrop (*Thaumatopteris* Zone) is confirmed by the well-preserved floristic remains (E. Wcisło-Luraniec, 1991) and by the sequence stratigraphy correlation (G. Pieńkowski, 1991*a*, 1997, 1998). Detailed description of the whole Sołtyków profile was given by G. Pieńkowski, G. Gierliński (1987) and G. Pieńkowski (1998). The latter paper describes structures tentatively interpreted as dinosaur nests and post-egg structures.

Newly exposed, track-bearing surface of some 100 m^2 (constituting a fragment of much larger, but hitherto unexcavated surface of about 1000 m^2) belongs to the lower part of the outcrop, dominated by flood plain (lacustrine) muds with palaeosols and crevasse splays associated with small-scale fan deltas, levee deposits and channel deposits (G. Pieńkowski, 1998, fig. 2). The newly exposed surface trampled by dinosaurus (Fig. 4; Pl. I, Fig. 1) represents a top surface of about 20 cm thick bed showing a persistent lateral extension. The bed is built of poorly sorted, fine-grained quartz wacke, cemented by ferruginous minerals (primary siderite replaced

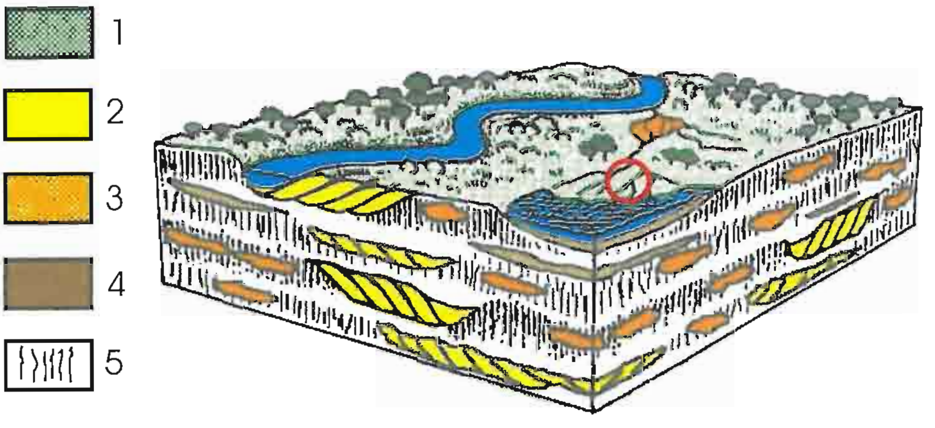

Fig. 3. Spatial reconstruction of the facies and palaeoenvironments of the Sołtyków outcrop; position of the bed with sauropod and theropod trackways is marked with the red circle; the bed belongs to a distal crevasse-lacustrine fan delta subenvironment on a floodplain of meandering river

1 — floodplain with a low-growing vegetation, high-growing vegetation occurs on a higher ground; 2 — laterally accreting river channels; 3 — crevasse splays; 4 — lacustrine facies; 5 — floodplain muds with distal crevasses and palaeosols

by iron hydroxides) and silica. Siderite spherulites, up to 1 mm in diameter, are very frequent, marking (along with abundant plant roots) a pedogenic horizon within this bed (Pl. I, Fig. 2). The bed reveals parallel lamination and sometimes inconspicuous trough cross bedding, or is structureless. This bed represents a distal crevasse splay/lacustrine fan delta environment, situated on a floodplain of a meandering river, covered with a low-rise, dense vegetation (Fig. 3; Pl. I, Fig. 2). Nearby, on a higher ground, conifer forests comprised 6 m high trees of *Hirmerella* (G. Pieńkowski, G. Gierliński, 1987; E. Wcisło-Luraniec, 1991). Palaeoenvironmental setting of this bed is shown in the Figure 3, against the background of a spatial sedimentary architecture and a reconstruction of landscape.

THEROPOD TRACKS

The track-bearing strata in Sołtyków outcrop comprise medium and large grallatorid tracks. The medium-sized and relatively narrow form (Pl. II, Fig. 1) can be assigned to *Grallator* Hitchcock, 1858, following grallatorid designation concept of M. G. Lockley, A. P. Hunt (1995), or to the ichnogenus *Anchisauripus sensu* P. E. Olsen *et al.* (1998). Large Sołtyków grallatorids, with highly divergent toes were assigned to *Kayentapus soltykovensis* (Gierliński, 1991) Gierliński, 1996*a* (Pl. II, Fig. 3), an ichnospecies recognised also in the Hettangian of Sweden (G. Gierliński, A. Ahlberg, 1994) and Hungary (G. Gierliński, 1996*a*).

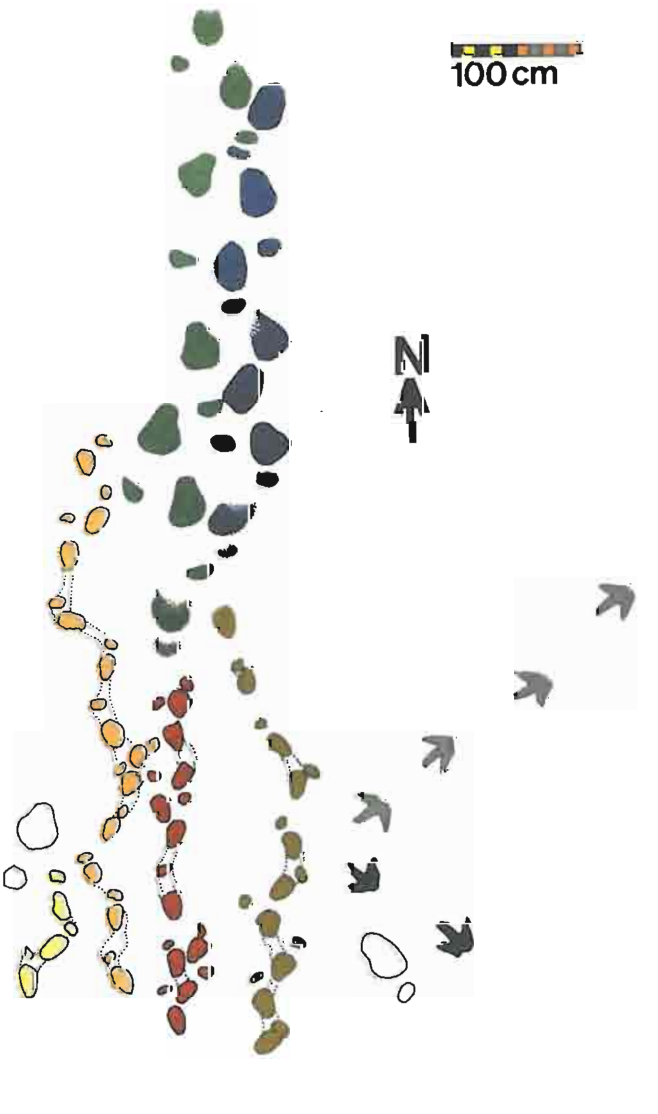

Fig. 4. Map of the area excavated in Sołtyków in June 1999

Theropod tracks *Kayentapus soltykovensis* (Gierliński, 1991) Gierliński, 1996*a* marked in grey and black; juvenile sauropod tracks *Parabrontopodus* sp. marked in yellow, orange, red and brown; adult sauropod track *Parabrontopodus* sp. marked in green and blue

SAUROPOD TRACKS

Until November 1998, no exposed surface with more than three-step dinosaur trackway was known in Poland. All previously described specimens were found on loose slabs. The new Sołtyków assemblage is the large, track-bearing surface discovered *in situ* (Pl. I, Fig. 1). The recently excavated area in June 1999 revealed two parallel trackways of large sauropods (Fig. 4, green and blue trackways), heading south. In 1998, only a part of the "green" trackway was excavated and described by G. Gierliński and G. Sawicki (1998). The area excavated nearby contains also four parallel juvenile sauropod trackways, heading north (Fig. 4, yellow, orange, red and brown) and the *Kayentapus* Welles, 1971 tracks oriented south-west and north-west.

All sauropod trackways show a narrow-gauge pattern *sensu* J. O. Farlow (1992), which corresponds to the ichnogenus *Parabrontopodus* Lockley, Farlow et Meyer, 1994. The lengths of pedal impressions in the small sauropod trackways are 19–25 cm. According to M. G. Lockley (1994) the small sauropod trackmakers from Sołtyków, which pedal lengths equal 45–55% of the pedal length of the large ones, would probably have been no more than one, and maximum two years old.

Trackways of the small individuals represent the second European example of herding among juvenile sauropods, after the Portugal tracksite (M. G. Lockley *et al.*, 1994); they also seem to record the oldest known evidence of such sauropod behaviour.

Contrary to the regular gait of associated theropods, the sauropod trackways indicate irregular gait. Generally, the steps of juvenile trackmakers become longer along the exposed stretch of trackways and they all clearly turned north-west. It is tempting to suggest that the group of juveniles escaped from the large theropod (Fig. 4, black trackway), which moved towards the north-west. Tracks of another theropod (Fig. 4, grey trackway) are very shallowly impressed and might not have been left at the same time. The same is true for adult sauropod trackways, which become shallower towards south and disappear in the area trampled by juveniles. The same happens with the tracks of juveniles, but in the opposite direction. This may suggest that substrate condition could have been different at that time when both juveniles and adults were passing across the area.

Ratio of stride length to pes length in the juvenile sauropod trackways increases from 1.80 to 4.50. The same ratio in the associated theropod trackways of *Kayentapus soltykovensis* equals 4.80–5.30. According to the original formula $V = 0.25\ g^{0.5}\ SL^{1.67}\ h^{-1.17}$ (V — velocity of the animal, g — acceleration due to gravity, SL — stride length, h — hip height, estimated as four times footprint length) developed by R. Mc N. Alexander (1976), disregarding its later modifications (e.g. R. A. Thulborn, 1990), the speed of juvenile trackmakers increased from 0.66 to 3.34 km/h, while the theropod speed might be estimated at about 5 km/h.

PROBABLE ORNITHISCHIAN TRACK

The isolated and poorly preserved, 55 mm long *Anomoepus*-like footprint (Pl. II, Fig. 2), has been found in loose slab in the lower part of Sołtyków outcrop.

UPPER ZAGAJE AND SKŁOBY TRACKS ASSEMBLAGE

GEOLOGICAL SETTING

LOWER OUTCROP IN GROMADZICE (GROMADZICE 1, UPPER PART OF THE ZAGAJE FORMATION)

The upper part of the Zagaje Formation is dominated by lacustrine sediments in the central part of the basin of the Holy Cross Mountains, and meandering river/floodplain sediments in the marginal parts of the basin. The first outcrop in Gromadzice, on the bank of a Kamionka River, situated in the marginal part of the sedimentary basin, represents the uppermost part of the Zagaje Formation and reveals typical meandering river deposits with lenticular, incised channels and overbank mudstones rich in drifted flora and *in situ* plant roots (Pl. I, Fig. 2). In the upper part of the outcrop the lithological and sedimentological features are somewhat different. Lenticular lithosomes are replaced by more continuous, much less incised sandstone layers, scale of sedimentary structures is generally smaller and palaeocurrents velocity was significantly lower in comparison to the lower part of the outcrop. Consequently, the outcrop shows an upward decreasing of energy of sedimentary processes.

The newly discovered ornithischian tracks are known from a layer in the middle part of the upper part of the Gromadzice, the first outcrop. The upper part of this outcrop was previously assigned to a deltaic plain environment, basing on higher boron content, more numerous trace fossils (*Palaeophycus* sp., *Helmiuthopsis* sp.) and few bivalves resembling brackish-marine specimens (G. Pieńkowski, 1981). Later, this view was abandoned, largely because of inconclusive character of the bivalve fossils, and the fact that the transgressive surface is situated above the alleged brackish-marine (deltaic) sediments. Consequently, the whole outcrop has been included to the fluvial, meandering river facies of the uppermost Zagaje Formation. At present we could partly return to the second author's original view, claiming that the upper part of this outcrop may represent an upper part of a deltaic plain. The retrogradational trend, observed in the lower Hettangian of the Polish-Swedish basin, may have begun in the upper part of the fluvial Zagaje Formation, as the continental sequence is characterised by a gradual reduction in the depositional energy through time. Even beyond the direct influence of a transgressing sea, rising base level caused a fluvial regime to be replaced by a lacustrine regime (G.

Table 1

Digit length ratios of the ornithischian tracks discussed in text in comparison with digit length ratios obtained from the osteological material

Anomoepus curvatus (MUZ PIG 1560.II.21) III/II* = 1.65 III/IV*= 0.83	*Lesothosaurus*** phalanx III2+III3+III4/phalanx II2+II3 = 1.64 phalanx III2 + III3/digit IV = 0.83
*Anomoepus scambus*** (AC 37/10) III/II* = 1.52 III/IV* = 0.72	*Sculetosaurus*** phalanx III2+III3+III4/phalanx II2+II3 = 1.50 phalanx III2 + III3/digit IV = 0.73
Anomoepus pienkovskii (MUZ PIG 1560.II.20) III/II* = 1.15 III/IV* = 0.67	
*Moyenisauropus natator**** III/II* = 1.16 III/IV* = 0.66	
Moyenisauropus karaszevskii (MUZ PIG 1560.II.9B) III/II*= 1.10 III/IV* = 0.65	*Scelidosaurus***** phalanx III2+III3+III4/phalanx II2+II3 = 1.11 phalanx III2 + III3/digit IV = 0.63

* — digit length ratio *sensu* P. E. Olsen *et al.* (1998); ** — measurements given by P. E. Olsen *et al.* (1998); *** — based on material illustrated by P. Ellenberger (1974, pl. D); **** — measurements given by R. Owen (1863)

Pieńkowski, 1991*a*). Such a process is clearly visible in the lower Gromadzice outcrop, where clearly channelled, fluvial deposits are replaced by lower-energy deposits of broader, shallow channels, which might represent distributaries of crevasses. These lower-energy deposits contain numerous mudstone bands of overbank/lacustrine origin. Plant roots are very abundant within this part of the section. Slightly higher boron content may indicate some influence of brackish water. Therefore, the upper part of this outcrop probably represents a landward part of the deltaic/fluvial plain.

This more-or-less gradual process was interrupted by a distinct, relatively short-lived and widespread event, during which the transgressing sea quickly submerged the whole sedimentary basin at the base of the Skłoby Formation. The transgressive sediments occur several metres above the Gromadzice lower outcrop, where one can find typical nearshore deposits, representing the first parasequence of transgressive systems tract of the Skłoby Formation (early-mid Hettangian). The transgressive surface and subsequent parasequences were recognised in details in the nearby Miłków borehole (G. Pieńkowski, 1991*a*).

UPPER OUTCROP IN GROMADZICE (GROMADZICE 2, SKŁOBY FORMATION)

Some 15–20 m above the transgressive surface, within the next parasequences, one can observe typical deltaic cycles with well-developed rim of near-deltaic barrier-lagoonal sediments (G. Pieńkowski, 1991*b*). Deltaic cycles with distributary facies represent upper, regressive parts of parasequences occurring within the transgressive systems tract of the Skłoby Formation in Gromadzice. Small sauropod tracks were found in loose blocks, which come from the distributary channel facies. One should note that the current energy in those channels was rather low, which is indicated by fine- and very fine-grained sandstones and abundant small-scale sedimentary structures (ripple-drift cross lamination).

ORNITHISCHIAN TRACKS

The medium-sized semibipedal ornithischian tracks (Pl. II, Figs. 5, 6) in the lower Gromadzice outcrop of the uppermost Zagaje Formation have been discovered and subsequently collected by G. Niedźwiedzki, in the spring of 1999. Two of these specimens, MUZ PIG 1651.II.3 and 4, are stored in the museum. Pedal imprints are 16–18 cm long, while the pentadactyl manus is 10 cm long, being more than half the size of the pes. Pedal impressions are usually associated with the relatively large hallux imprints (Pl. II, Fig. 6). Hitherto, such a relatively large manus was known only in *Anomoepus pienkovskii* Gierliński, 1991. However, *A. pienkovskii* is a more gracile form. Similarly to *Moyenisauropus sensu* Gierliński (1991), the ichnites show two phalangal pads on digit III, because two distal pads are almost fused on that digit (Pl. II, Fig. 5), but they differ from the Polish large tracks of *Moyenisauropus karaszevskii* Gierliński, 1991 by being smaller and having well segmented digit IV, which appeared clearly in the shallow impressions (Pl. II, Fig. 5). The pedal digit length ratios (digit lengths measured as shown on Fig. 5) of the Gromadzice specimens are: III/II = 1.12–1.37 and III/IV = 0.61–0.66. Such a wide range of calculated values partially overlaps those of *A.pienkovskii* and *M.karaszevskii.* The morphometrics of the Gromadzice material resemble most closely the *Moyenisauropus natator* Ellenberger, 1974, a moyenisauropodid from the Early Jurassic of Lesotho (see Table 1).

According to the measurements method of P. E. Olsen *et al.* (1998) (Fig. 5), *A. pienkovskii* seems to has been left by a trackmaker with the foot pattern intermediate between basal thyreophoran one and *Scelidosaurus* one (Table 1). The Gromadzice tracks already show digit length ratios very close to those of the *Scelidosaurus* pes. Their pedal lengths fit almost perfectly the 15 cm long phalangal part of the foot of *Scelidosaurus harrisoni* Owen, 1861.

SAUROPOD TRACKS

First dinosaur tracks of Gromadzice have been reported in the Skłoby Formation from the upper Gromadzice outcrop by G. Gierliński (1997*a*). The relatively small sauropod tracks (Pl. II, Fig. 7), with pes 24.5–30.5 cm long, might have been left by a diminutive or juvenile sauropod. Those ichnites provided also the first record of sauropod tracks in the Early Jurassic of Poland. Their presence in deltaic environment is probably connected with their small size. Larger sauropod tracks are absent from this locality.

PRZYSUCHA TRACK ASSEMBLAGE

GEOLOGICAL SETTING

Most of known dinosaur footprints of the late Hettangian Przysucha Ore-Bearing Formation come from a small farmer quarry situated near the village of Gliniany Las. The first ever Polish dinosaur tracks were described from here (W. Karaszewski, 1969). Sandstones with mudstone intercalations occurring in this quarry have been assigned to the upper part of the Przysucha Ore-Bearing Formation (or more precisely, to a sedimentary package separating the middle and upper siderite-bearing horizons). In the past, they were some controversies concerning the geological setting of this outcrop. W. Karaszewski (1975), contrary to his own previous view (W. Karaszewski, 1969), claimed that the sediments in this quarry should represent the lowermost part of the overlying Ostrowiec Formation. However, one can not find equivalents of those sediments in the nearby borehole within the Ostrowiec Formation profile. Therefore, we accept the previous view of W. Karaszewski (1969) and W. Karaszewski, J. Kopik (1970), that this outcrop belongs to the upper Przysucha Ore-Bearing Formation. Gliniany Las outcrop has been described by G. Pieńkowski (1981, 1985). Profile included in the present paper show the same profile, with some modifications and marked position of dinosaur tracks (Fig. 6). The sediments visible in the profile represents part of a larger deltaic-barrier-lagoon sequence recognised in the nearby borehole. The outcrop reveals a regressive sequence showing a near-deltaic barrier with superimposed backbarrier/shallow lagoon deposits, covered by deltaic/fluvial sediments (Fig. 6). Most of

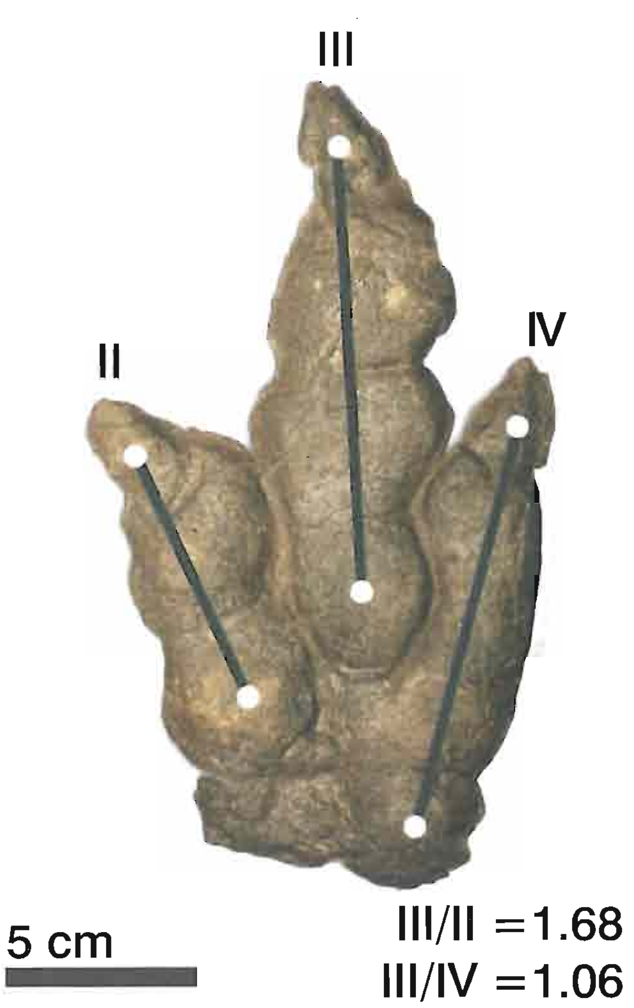

Fig. 5. Lengths of the phalangeal portion of digits measured according to the method of P. E. Olsen *et al.* (1998), exemplified on *Anchisauripus* track UR 260 from the Early Jurassic of Connecticut, stored in the Field Museum of Natural History; the second and the third digit length measured between mid-point of the proximal phalangeal pad and mid-point of the claw impression may reflect combined length of phalanx 2 and 3 of the trackmaker digit II and combined length of phalanx 2, 3 and 4 of the trackmaker digit III; the fourth digit length measured between mid-point metatarsal-phalangeal pad and mid-point of the claw impression may reflect combined length of all phalanges of the trackmaker digit IV

the dinosaur tracks come from two (1–3 cm thick) sandstone beds of back-barrier origin, several centimetres above the top of barrier sandstone (Fig. 6). Tracks occur as moulds on one bed and as casts on the bottom surface of the overlying bed. Presence of numerous perfectly preserved dinosaur tracks in these particular beds was probably caused by very favourable preservational conditions.

Outcrops in Jakubów and Zapniów (both are situated in the vicinity of Przysucha) represent a geological setting similar to that of the Gliniany Las, i.e. barrier-lagoonal/deltaic sediments belonging to the Przysucha Ore-Bearing Formation.

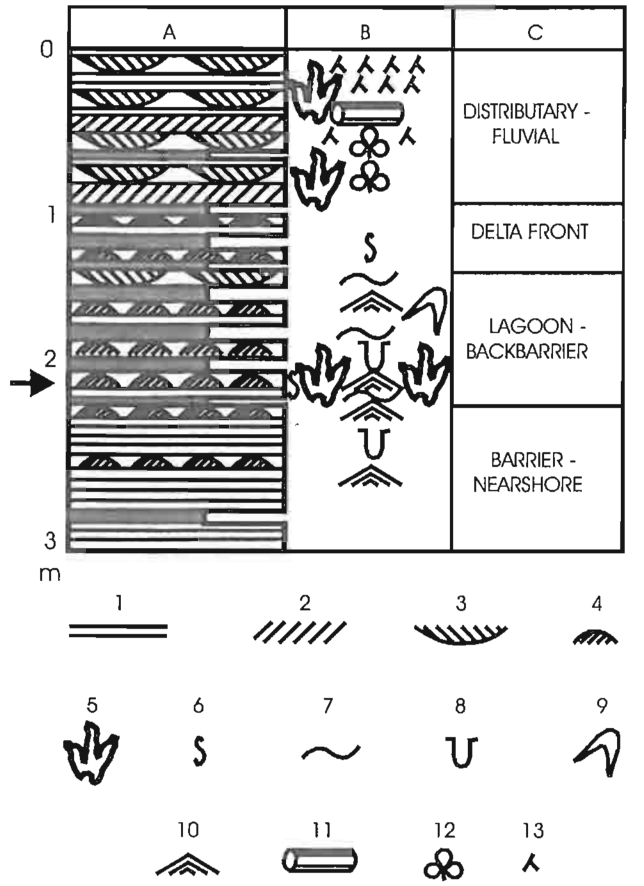

Fig. 6. Profile of the Gliniany Las outcrop (Przysucha Ore-Bearing Formation), showing a regressive sequence with position of the dinosaur tracks indicated

A — lithological and sedimentological profile — sandstones are marked in white, mudstones are marked in grey: 1 — horizontal lamination, 2 — tabular cross-bedding, 3 — trough cross-bedding, 4 — ripple-drift cross lamination; arrow marks the beds of backbarrier-lagoonal origin with abundant dinosaur tracks; B — trace fossils, sedimentary structures and plant remains: 5 — dinosaur tracks, 6 — invertebrate feeding traces, 7 — invertebrate crawling traces, 8 — invertebrate dwelling structures, 9 — ?fish marks, 10 — oscillation ripples, 11 — large pieces of wood, 12 — drifted flora, 13 — plant roots; C — palaeoenvironmental interpretation; after G. Pieńkowski (1985), appended and modified

NONAVIAN THEROPOD TRACKS

Theropod tracks in the Przysucha Ore-Bearing Formation are relatively rare. A small theropod track (12.5 cm long) from Gliniany Las (Pl. III, Fig. 1) has been identified as *Grallator tenuis* Hitchcock, 1858 by G. Gierliński (1995*a*). This footprint shows digit length ratios (III/II = 1.61, III/IV = 0.92) close to those given by P. E. Olsen *et al.* (1998) for *Syntarsus*, but not so close to those of *Grallator parallelus* Hitchcock, 1858, the type ichnospecies of *Grallator*, revised by P. E. Olsen *et al.* (1998). Although its designation as *G.tenuis* (based on formula by R. E. Weems, 1992) may be valid, it seems reasonable to use only ichnogeneric level nomenclature, until all ichnospecies belonging to *Grallator*, *Anchisauripus* and *Eubrontes* shown by P. E. Olsen *et al.* (1998) as poorly defined, are thoroughly revised.

Ichnotaxonomical designation of medium-sized (23 cm long) grallatorid from the Przysucha Ore-Bearing Formation of Jakubów (Pl. III, Fig. 2; Fig. 7.4) should be also revised. This track has been previously described according to the geometrical-numerical method of R. E. Weems (1992) as *Eubrontes minusculus* (Hitchcock, 1858) Weems, 1992 by G. Gierliński (1995*b*), the same as the famous E. Hitchcock's specimen AC 1/7 (G. Gierliński, 1996*b*, 1997*b*; K. Sabath, 1997; K. Sabath, G. Gierliński, 1998). However, the Jakubów track and AC 1/7 from the Early Jurassic of Massachusetts (Fig. 7.3) do not correspond to the morphology of AC 16/1 (Fig. 7.1) being a holotype of *E. minusculus* (*Brontozoum minusculum* after E. Hitchcock, 1858; *Anchisauripus minusculus* after R. S. Lull, 1904; and *Grallator minusculus* after G. R. Demathieu, 1990). Another E. Hitchcock's specimen AC 13/6 (Fig. 7.2), regarded by him as *Brontozoum minusculum*, seems to be rather a fine specimen of *Kayentapus* track. The holotype of *E. minusculus* (AC 16/1) actually shows a robust *Eubrontes*-like pattern, with the digit length ratios: III/II = 1.50 and III/IV = 0.80. In contrast, the AC 1/7 and the Jakubów track (MUZ PIG 1560.II.36) are the smaller forms fitting the *Anchisauripus* track size range (length 15–25 cm), and they also have digit length ratios closer to those of *Grallator* and *Anchisauripus*. The digit length ratios of the MUZ PIG 1560.II.36 (III/II = 1.71, III/IV = 1.06) and the AC 1/7 (III/II = 1.65, III/IV = 1.04) are quite similar to those of *Anchisauripus exsertus* (Hitchcock, 1858) Lull, 1904 — the specimen UR 260 stored in the Field Museum of National History in Chicago (Fig. 5). Therefore we should name both discussed specimens as *Grallator* sp., according to the point of view presented by M. G. Lockley and A. P. Hunt (1995), or as *Anchisauripus* sp., following the concept of P. E. Olsen *et al.* (1998).

There are also some tracks regarded as theropod ichnites from the Przysucha Ore-Bearing Formation of Gliniany Las (MUZ PIG 1560.II.19) and Przysucha–Ostrowiec Formation of Zapniów (MUZ PIG 1560.II.35). Identification of the specimen MUZ PIG 1560.II.19 is rather tentative. This specimen described by G. Gierliński (1990) as *Grallator* (*Eubrontes*) sp. may have been a large theropod track, or poorly preserved footprint of *Moyenisauropus karaszevskii* Gierliński, 1991. The specimen MUZ PIG. 1560.II.35 assigned as *Grallator* (*Grallator*) *tenuis* according to the method of R. E. Weems (1992) by G. Gierliński (1995*b*), actually represents a medium-sized *Anchisauripus*-like form.

PROTOAVIAN TRACK

Plesiornis pilulatus Hitchcock, 1858, a very small track (46 mm long) from Gliniany Las (Pl. III, Fig. 3; Pl. IV, Fig. 1), is one of the most intriguing dinosaur ichnites in the Hettangian of Poland. The specimen displays such avian features as a reversed hallux and swollen proximal pad of the third digit. The track is perfectly, evenly impressed and no associated disturbance structures are observed (Pl. IV, Fig. 1). This excludes the possibility that the imprint described in our specimen as the imprint of a reversed hallux might represent a disturbance structure (e.g. a drag mark or a structure left by metapodium) like those described by S. M. Gatesy *et al.* (1999). In the opinion of R. E. Weems, P. G. Kimmel (1993), G. Gierliński (1996*c*) and G. Gierliński, K. Sabath (1998), the *Plesiornis* trackmaker might have been of an avian affinity.

ORNITHISCHIAN TRACKS

Track-bearing strata of Przysucha Ore-Bearing Formation is dominated by various ornithischian tracks. The smallest one (11.4 cm long) from Gliniany Las (Pl. III, Fig. 4) fits well into the *Anomoepus* pattern. Among the morphologically related forms it is clearly distinguished by relatively less divaricated digits (total divarication equals 53°) and in being more slender. Thus, it resembles *Anomoepus curvatus* Hitchcock, 1865. Digit length ratios of this track (MUZ PIG 1560.II.21) fit well those of *Lesothosaurus* (Table 1).

Gliniany Las track assemblage comprises also the medium-sized quadrupedal *Anomoepus pienkovskii* Gierliński, 1991 (Pl. III, Fig.6) and the large bipedal *Moyenisauropus karaszevskii* Gierliński, 1991 (Pl. III, Fig. 5), both recently supposed to be of thyreophoran origin (G. Gierliński, 1999). The intermediate pedal pattern of *A. pienkovskii* (see, the discussion on ornithischian tracks from Gromadzice and Table 1) allowed to search for its trackmaker among the moderate-sized proto-scelidosaurid thyreophorans such as *Emausaurus* Haubold, 1990. However, the pes of *Emausaurus* is unknown and so no pedal osteometric data are available for comparison. It seems also a bit unclear if *Anomoepus pienkovskii* should be classified to the ichnogenus *Anomoepus* or *Moyenisauropus*. G. Gierliński (1995*a*) considered also an idea that *A. pienkovskii* might have been left by the juvenile trackmakers of *M. karaszevskii.*

In the opinion of J. Le Loeuff *et al.* (1998, 1999), *Moyenisauropus karaszevskii* is so distinctive that it should not be assigned to the ichnogenus *Moyenisauropus.* However, even if *M. karaszevskii* would fall into a different ichnogenus, the ichnogenus *Moyenisauropus* would be valid to comprise intermediate forms between the gracile *Anomoepus* and the robust *M. karaszevskii.* Such intermediate forms are represented by *M. natator* and possibly *A. pienkovskii.*

The digit length ratios of *Moyenisauropus karaszevskii* fit well those of *Scelidosaurus* (Table 1), but the footprint size of *M. karaszewskii* and almost identical tracks from Hettangian of France (J. Le Loeuff *et al.*, 1998, 1999) allow estimation of the lengths of their trackmakers as being near 5 m, which is significantly larger than the length of *Scelidosaurus harrisonii* (3.5 m long). J. Le Loeuff *et al.* (1998, 1999) suggest even the stegosaurian origin for *M. karaszevskii.* Such an early stegosaurian appearance may be supported by the stegosaur presence in the Middle Jurassic of China. The Central Asia became isolated near the beginning of Middle Jurassic, so stegosaurs might have already existed and migrated there before that time (D. A. Rusell, J. F. Bonaparte, 1997).

A poorly preserved *Moyenisauropus*-like track was also reported from the beds from transition between Przysucha Ore-Bearing Formation and Ostrowiec Formation of Zapniów (G. Pieńkowski, G. Gierliński, 1987).

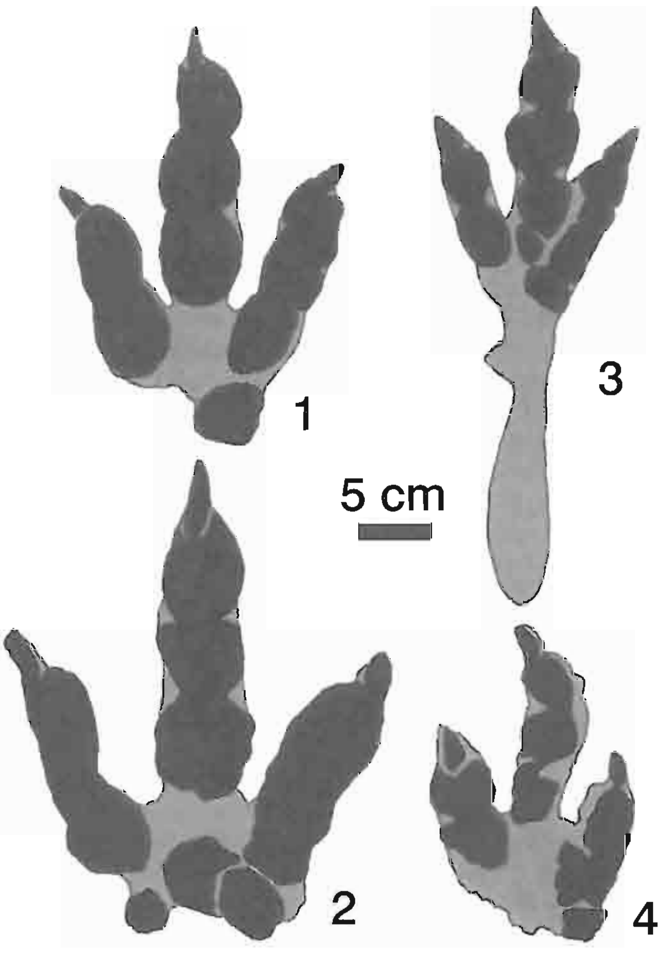

Fig. 7. The holotype of *Eubrontes minusculus* (Hitchcock, 1858) Weems, 1992 from the Early Jurassic of Massachusetts (1) in comparison with the tracks previously assigned to *E. minusculus* — from the Early Jurassic of Massachusetts (2, 3) and from the late Hettangian of Jakubów, Poland (4)

1 — AC 16/1, the holotype of *E.minusculus;* 2 — AC 13/6 regarded herein as *Kayentapus* track; 3 — AC 1/7, *Anchisauripus* sp., originally assigned by E. Hitchcock (1858) to *"Anomoepus major"*; 4 — MUZ PIG 1560.II.36 (plaster cast), *Anchisauripus* sp. previously described as *E. minusculus*

PROBLEMATIC SUBDIGITIGRADE TRACKS

Subdigitigrade tracks reflect the condition when only the distal part of the digits appears in the impression (G. Leonardi, 1987). Such theropod ichnites have been recently described as *Carmelopodus untermannorum* M. G. Lockley *et al.* (1998), from the Carmel Formation of northeastern Utah. A similar Polish form from the Przysucha Ore-Bearing Formation of Gliniany Las was named *"Grallator (Grallator) zvierzi"* Gierliński, 1991 (Pl. III, Fig. 7).

In the light of subdigitigrade theropod tracks distinguished on ichnogeneric level as *Carmelopodus*, the ichnospecies "*G.* (*G.*) *zvierzi*", recognised on ichnospecific level, for the same reason could not be valid any more.

The association of ornithischian subdigitigrade tracks similar to *Wintonopus* Thulborn et Wade, 1984 with *G.* (*G.*) *zvierzi* on the same slabs: MUZ PIG 1560.II.9A (Pl. IV, Fig. 2) and 1560.II.9B (the slabs comprise also a holotype of *M. karaszevskii*), allowed the conclusion that all subdigitigrade imprints should be assigned as cf. *Wintonopus* sp. (G. Gierliński, 1995*a*, *b*, 1996*c*). However, such generalisation seems to be incorrect if we examine the specimens more carefully. The tracks previously named "*G.* (*G.*) *zvierzi*" are 9–12.6 cm long, sharply pointed, with the angle between digits II and IV ranging from 18 to 37°. Tracks similar to *Wintonopus* are nearly of the same length, but much wider, with the angle between digits II and IV of about 50°. Besides, they have rounded digital tips.

As yet, we have no good idea how to satisfactory explain origin of these tracks. Once we have tentatively proposed (G. Pieńkowski, G. Gierliński, 1987) a hipothetical "wading and swimming scenario" to explain their origin. M. G. Lockley (1991) proposed his "undertracks scenario" instead, reasoning that there were no continuous trackways showing transition from complete to incomplete tracks, left by an animal progressing into deeper water. However, the "undertracks scenario" is unlikely, because the tracks are preserved on two corresponding slabs: as a mould (slab MUZ PIG 1560.II.9A (Pl. IV, Fig. 2), and as a cast (slab MUZ PIG 1560.II.9B). On both track-bearing sides one can observe the same morphological pattern of the same tracks and there are neither tracks nor undertracks on the opposite sides of these relatively thin slabs.

Basically, subdigitigrade tracks are expected to be left by trotting or running animals (R. A. Thulborn, 1990). However, in the case of *Carmelopodus* tracks, M. G. Lockley *et al.* (1998*b*) supposed that they originate directly from the trackmaker, which particular type of foot was morphologically predisposed to produce such characteristic footprints.

CONCLUSIONS

As far as the world-wide stratigrapical correlations of dinosaur ichnotaxa are concerned, the Polish track assemblages apparently do not fit well to the Hettangian age referred to the upper Zagaje, Skłoby and Przysucha Ore-Bearing Formations. Lower Zagaje track assemblage of Sołtyków actually corresponds to the Hettangian assemblage of Lavini di Marco, Italy. The Italian assemblage comprises narrow-gauge sauropod trackways associated with medium-sized and large theropod tracks (M. Lanzinger, G. Leonardi, 1991; F. M. Dalla Vecchia, 1994; G. Leonardi, M. Avanzini, 1994; G. Leonardi, 1996; M. Avanzini, 1997; M. Avanzini *et al.*, 1997).

However, the upper Zagaje–Skłoby assemblage of Gromadzice comprises moyenisauropodid tracks similar to those reported from the Kayenta–Navajo transition zone in southern Utah (M. G. Lockley *et al.*, 1998*a*). This zone is usually considered as not older than Sinemurian (e.g. M. G. Lockley, A. P. Hunt, 1995, figs. 3.27 and 4.2). We suppose *Scelidosaurus* origin of Gromadzice ornithischian tracks, and the *Scelidosaurus* remains were also reported from the Kayenta Formation of northern Arizona (K. Padian, 1989). Moreover, *Scelidosaurus* is regarded as an index fossil of the *Scelidosaurus* biochron, which corresponds to the Sinemurian age (S. G. Lucas, 1996). Thus, basing on those views, one might assign the upper Zagaje Formation to the Sinemurian age. Skłoby Formation revealed small sauropod tracks and the remains of European Liassic diminutive sauropod *Ohmdenosaurus* Wild, 1978 came from the Toarcian of Germany. Moreover, if the supposition of stegosaurian origin of *Moyenisauropus karaszevskii* is correct, then it would not be surprising, if Przysucha Ore-Bearing Formation would represent the latest Early Jurassic, or even Middle Jurassic.

However, the geological and stratigraphical data firmly proved the Hettangian age of Zagaje, Skłoby and Przysucha Ore-Bearing Formations. Even the lowermost part of the Ostrowiec Formation may be still of the Hettangian age. Consequently, the Polish dinosaur track assemblages poorly reflect faunistic change during the Early Jurassic, but they do reflect ecological, environmental and biogeographical differences in the Early Jurassic time. We distinguish two general environmental realms in the Hettangian of Poland, which reveal two different track assemblages:

1. The first assemblage is represented by the lower Zagaje assemblage from the Sołtyków outcrop. These deposits represent palaeoenvironment of inland, warm, humid habitat with low- and high-growing vegetation (G. Pieńkowski, G. Gierliński, 1987; E. Wcisło-Luraniec, 1991; G. Pieńkowski, 1998). High browsing herbivores (sauropod trackmakers) and medium- to large-size predators (theropod trackmakers of *Anchisauripus* and *Kayentapus*) roamed this habitat.

2. The second assemblage is represented by footprints from Gromadzice (upper Zagaje and Skłoby Formations), Gliniany Las, Jakubów and Zapniów (Przysucha Ore-Bearing Formations). All those deposits represent deltaic-lagoonal shoreline habitat with low and dense vegetation (G. Pieńkowski, G. Gierliński, 1987) invaded by low browsing herbivores such as ornithischian trackmakers of *Anomoepus* and *Moyenisauropus*, and small- to medium-sized predators, such as theropod trackmakers of *Grallator* and *Anchisauripus*. Presence of some small sauropod tracks in this assemblage reminded that small (dimunitive or juvenile) sauropods might have been, in fact, the low browsing, until they were small and were travelling separately from adults. Large sauropod tracks are absent from this assemblage.

The discussed data imply a high phylogenetical diversity of dinosaurus, reached as early as in the Hettangian age. The earliest Jurassic dinosaur communities were well established, clearly determined by environmental factors.

Abreviations of cited repositories: AC — Pratt Museum of Natural History, Amherst College, Amherst, Massachusetts, USA; MUZ PIG — Geological Museum of the Polish Geological Institute, Warsaw, Poland.

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ZESPOŁY ŚLADÓW DINOZAURÓW Z HETTANGU POLSKI

Streszczenie

Ślady dinozaurów w Polsce są do tej pory znane tylko z Gór Świętokrzyskich. Inne odsłonięcia utworów lądowych wczesnej jury (pliensbachu i późnego toarku) w innym obszarze ich występowania na powierzchni (Jura Krakowsko-Wieluńska) mogą też zawierać ślady dinozaurów, ale dotychczas nie zostały one znalezione, co jest przede wszystkim związane z fragmentarycznością i złym stanem tych odsłonięć. Niemal wszystkie ślady dinozaurów znane z północnego obrzeżenia Gór Świętokrzyskich pochodzą z trzech najniższych formacji: zagajskiej, skłobskiej i przysuskiej rudonośnej

reprezentujących hettang. Taki wiek tych osadów wynika z danych makro- i mikroflorystycznych oraz z korelacji opartej na stratygrafii sekwencyjnej. Pojedyncze ślady znaleziono też w najniższej, lądowej części formacji ostrowieckiej (również najprawdopodobniej reprezentującej najpóźniejszy hettang) oraz w utworach lądowych późnego toarku w okolicach Opoczna (jeden bardzo dobrze zachowany ślad teropoda).

Formacja zagajska, skłobska i przysuska rudonośna reprezentują różnorodne środowiska kontynentalne i marginalnomorskie. W najniższej formacji, zagajskiej występują utwory związane ze środowiskiem lądowym, rzecznym i jeziorno-bagiennym, w samym stropie mogącym reprezentować już środowisko równi deltowej, związanej ze zbliżającą się transgresją. Z transgresją wczesnego hettangu związana jest nadległa formacja skłobska, w której dominują środowiska przybrzeżne, na peryferiach basenu deltowe.

Następna, przysuska formacja rudonośna ma względem formacji skłobskiej charakter regresywny, dominują w niej osady płytkich, rozległych zatok i lagun rozdzielone piaszczystymi osadami delt, barier i rzek. Kulminacją regresji jest regionalna powierzchnia erozyjna w jej stropie, nad którą występuje pakiet fluwialny zaliczany do formacji ostrowieckiej. W utworach tych występują zróżnicowane ślady wczesnych dinozaurów ptasiomiednicznych, zauropodów i teropodów, które opisano z poszczególnych odcinków profilu utworów hettangu.

Z utworów najwcześniejszego hettangu (dolna część formacji zagajskiej), z odsłonięcia w Sołtykowie, pochodzi unikatowa powierzchnia z tropami dorosłych i młodych zauropodów. Jest to najstarszy znany dowód stadnego życia tych dinozaurów. Oszacowano wzajemne kierunki i prędkość poruszania się zwierząt, a także wiek młodych osobników (1–2 lata). Konieczne było też usystematyzowanie i podsumowanie wszystkich dotychczas zebranych danych pod względem ichnotaksonomicznym.

Zebrany i opracowany materiał ichnologiczny pozwolił też na wyodrębnienie dwóch zasadniczych zespołów śladów. Pierwszy zespół, charakterystyczny dla dolnej części formacji zagajskiej, jest związany z typowo lądowym środowiskiem równi rzecznych, porośniętych zarówno nisko-, jak i wysokopienną roślinnością. Dominują w nim twórcy śladów — *Parabrontopodus* (zauropody), wyspecjalizowani w żerowaniu na wysokopiennej, drzewiastej roślinności, oraz średnie i duże drapieżniki, teropody, twórcy śladów — *Anchisauripus* i *Kayentapus*. Drugi zespół, typowy dla najwyższej części formacji zagajskiej, formacji skłobskiej i przysuskiej formacji rudonośnej, jest związany ze środowiskami równi deltowych i przybrzeżnych porośniętych gęstą, niskopienną roślinnością. Dominują w nim twórcy śladów — *Anomoepus* i *Moyenisauropus*, a więc dinozaury ptasiomiedniczne wyspecjalizowane w żerowaniu na niskopiennej roślinności, wraz z małymi lub średnimi drapieżnymi teropodami — twórcami śladów — *Grallator* i *Anchisauripus*. Obecność śladów niewielkich (karłowatych lub młodych) zauropodów w tym drugim zespole nie zakłóca całego podziału — mogły się w nim pojawiać również małe zauropody, gdyż ich pożywieniem mogła być z powodzeniem roślinność niskopienna.

Omawiane tropy dobrze odzwierciedlają związek ze środowiskiem i czynnikami paleobiogeograficznymi. Uzyskane wyniki wyraźnie wskazują też na silne zróżnicowanie filogenetyczne dinozaurów w najwcześniejszej jurze, a także na to, że już w tym czasie stanowiły one dobrze wykształcone zespoły, determinowane przez czynniki ekologiczne.

EXPLANATIONS OF PLATES

PLATE I

Fig. 1. *Parabrontopodus* sp., four parallel trackways of the juvenile sauropods. The Sołtyków tracksite, as it has been excavated by June 1999, viewed from the south

Fig. 2. Cross-section of the upper part of the dinosaur track-bearing layer of the Sołtyków tracksite. Fine grained quartz wacke with numerous plant roots (arrow) and very abundant siderite spherulites (small dots)

PLATE II

Fig. 1. *Anchisauripus* sp.
Sołtyków, MUZ PIG 1651.II.1 (plaster cast)

Fig. 2. ?*Anomoepus* sp.
Sołtyków, MUZ PIG 1560.II.39

Fig. 3. *Kayentapus soltykovensis* (Gierliński, 1991) Gierliński, 1996
Sołtyków, MUZ PIG 1560.II.10

Fig. 4. Juvenile sauropod track from Sołtyków, found on the isolated slab out of the trampled surface mapped herein
MUZ PIG 1651.II.2

Figs. 5, 6. *Moyenisauropus* cf. *natator* Ellenberger, 1974
Gromadzice; Fig. 5 — MUZ PIG 1651.II.3; Fig. 6 — MUZ PIG 1651.II.4

Fig. 7. Juvenile or diminutive sauropod track from Gromadzice
MUZ PIG 1560.II.61

PLATE III

Fig. 1. *Grallator* sp.
Gliniany Las, MUZ PIG 1562.II.33

Fig. 2. *Anchisauripus* sp.
Jakubów, MUZ PIG 1560.II.36 (plaster cast)

Fig. 3. *Plesiornis pilulatus* Hitchcock, 1858
Gliniany Las, MUZ PIG 1560.II.38

Fig. 4. *Anomoepus curvatus* Hitchcock, 1865
Gliniany Las, MUZ PIG 1560.II.21

Fig. 5. *Moyenisauropus karaszevskii* Gierliński, 1991
Gliniany Las, MUZ PIG 1560.II.9B

Fig. 6. *Anomoepus pienkovskii* Gierliński, 1991
Gliniany Las, MUZ PIG 1560.II.20

Fig. 7. cf. *Carmelopodus* sp.
Gliniany Las, MUZ PIG 1560.II.9B

Fig. 8. cf. *Wintonopus* sp.
Gliniany Las, MUZ PIG 1560.II.9B

PLATE IV

Fig. 1. Trackway of *Plesiornis pilulatus* Hitchcock, 1858
Gliniany Las, MUZ PIG 1560.II.38

Fig. 2. Part of the slab MUZ PIG 1560.II.9A, Gliniany Las
1 — cf. *Carmelopodus*, the specimen previously regarded as the holotype of "*Grallator* (*Grallator*) *zvierzi*" Gierliński, 1991; 2 — cf. *Wintonopus* sp.

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Fig. 1

Fig. 2

Gerard GIERLIŃSKI, Grzegorz PIEŃKOWSKI — Dinosaur track assemblages from the Hettangian of Poland


LOWER ZAGAJE FM.
IV
1
IV
2
IV
3
4
10 cm
UPPER ZAGAJE and SKŁOBY FM.
IV
5
6
V
IV
7

PRZYSUCHA FM.

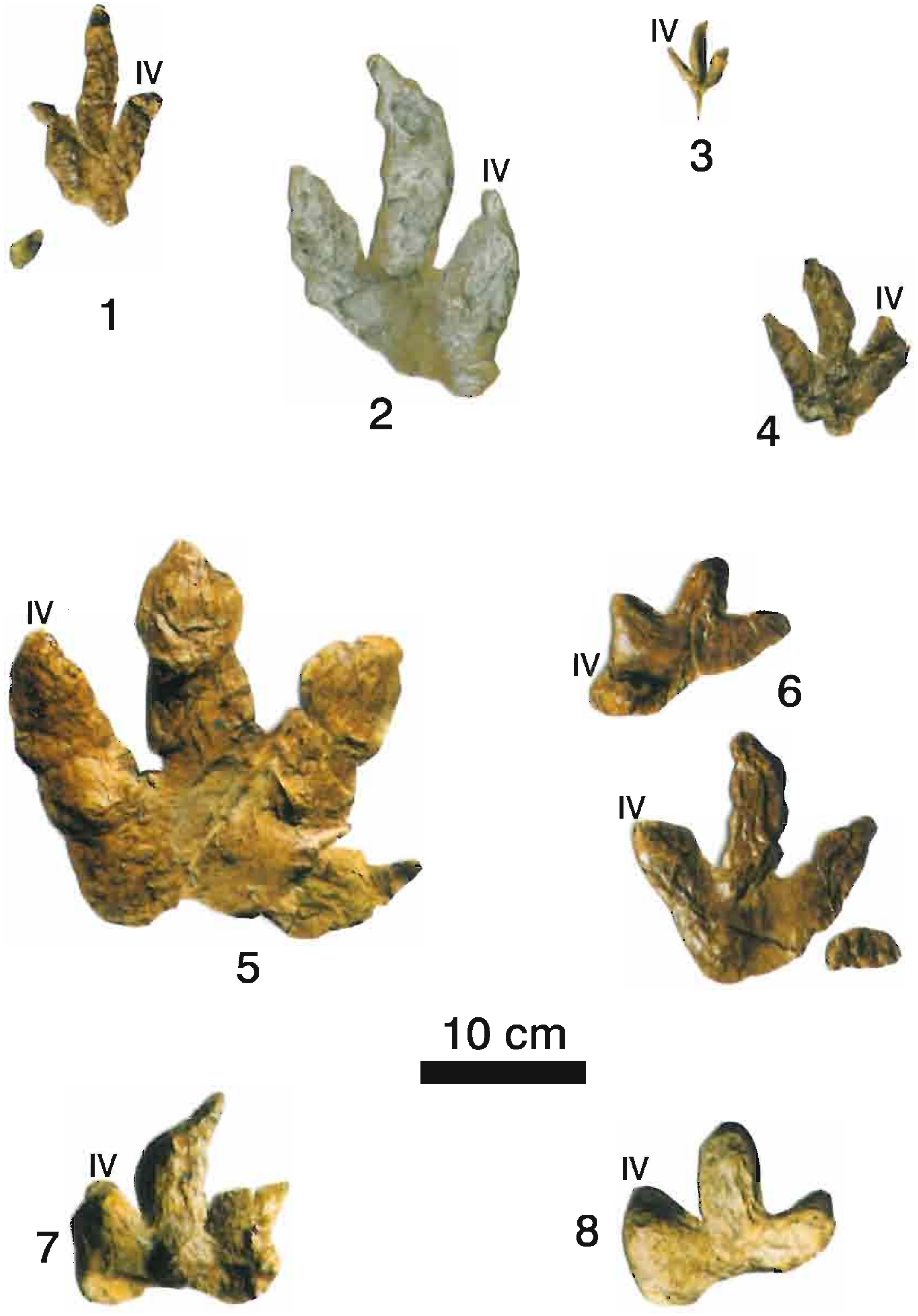

Fig. 1

Fig. 2