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A dinosaur track assemblage from the Upper Hettangian (Lower Jurassic) marginal-marine deposits of Zapniów, Holy Cross Mountains, Poland

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Upper Hettangian (Lower Jurassic) marginal-marine Przysucha Ore-bearing Formation exposed at Zapniów mine and clay-pit (northwestern part of the Holy Cross Mountains area, central Poland) revealed an interesting assemblage of dinosaur tracks. Although mostly yielding poorly preserved and isolated tracks probably left in shallow water conditions, the site nevertheless indicates a diversity of early saurischian (theropods and sauropodomorphs) and ornithischian (thyreophorans) dinosaur trackmakers. This new assemblage is partly consistent with the Lower-Middle Hettangian ichnorecord from the same region. The tracks are preserved in sediments of a barrier-foreshore origin within a barrier/lagoonal depositional system, belonging to the highstand systems tract, located below a marked erosional surface (sequence boundary), which is associated with a substantial fall in sea level at the end of Hettangian times. Here we described all previously and newly collected or observed in the field dinosaur tracks from both surface and underground exposures at Zapniów. Four ichnospecies: *Grallator* isp., *Anchisauripus* isp., cf. *Tetrasauropus* isp., and cf. *Anomoepus* isp. were identified. The theropod and ornithischian tracks show distinct similarities to those described from the richest in this region and most famous Gliniany Las dinosaur track assemblage, in age approximately coeval to Zapniów. Two sizes of theropod tracks (small and medium) indicate the presence of two different size classes or species of predators in this area. The described cf. *Tetrasauropus* isp. from Zapniów is the first unquestioned evidence of basal sauropodomorphs in the Upper Hettangian of the Holy Cross Mountains and first record of this ichnotaxa in the Lower Jurassic of Poland. Additionally, two theropod trackways (*Anchisauripus* isp.) show evidence for trotting. The new finds suggest similarities between marginal-marine environments (delta-plain and foreshore-barrier/lagoon lithofacies) association of dinosaurs containing low-browsing thyreophorans accompanied by small or juvenile sauropodomorphs and small to medium sized theropods. Presence of the ornithischian footprints suggests their prominent role as a major component in Middle-Upper Hettangian dinosaur faunas in marginal-marine environments dominating in the region.

Key words: dinosaur tracks, Przysucha Ore-bearing Formation, Upper Hettangian, Lower Jurassic, Holy Cross Mountains, Poland.

INTRODUCTION

Trace fossils provide unparalleled information about the behaviour of extinct animals in the environments in which they lived. One of the aims of vertebrate palaeoichnological studies must be the reconstruction of the animal communities represented by the trace fossils. Research of the dinosaur ichnofauna of the Lower Jurassic of the Holy Cross Mountains in Poland illustrates some of these possibilities (Gierliński and Pieńkowski, 1999; Gierliński et al., 2004). The information that can be deduced from Holy Cross Mountains ichnofaunas is particularly vital for our understanding of the Early Jurassic tetrapod community ecology, because of the scarcity of skeletal remains of this age (e.g., Shubin and Sues, 1991; Sues et al., 1994; Irmis, 2005; Smith et al., 2007). Globally, Early Jurassic tetrapod assemblages are remarkably homogeneous, rather dominated by dinosaur taxa and it is well-visible in body and trace fossil record (e.g., Olsen and Galton, 1977, 1984; Attridge et al., 1985; Sues and Reisz, 1995; Olsen et al., 1998; Irmis, 2004).

The Lower Jurassic tetrapod track record is widespread throughout large area of the northern Mesozoic margin of the Holy Cross Mountains (see Niedźwiedzki et al., 2009). First dinosaur footprints in the Holy Cross Mountains were discovered in the Upper Hettangian deposits of Gliniany Las (Karaszewski, 1969, 1975). Subsequently, they were identified in numerous horizons of terrestrial and marginal-marine Lower Jurassic formations in localities such as: Sołtyków, Zapniów, Jakubów, Śmiłów, Idzikowice, Gromadzice A and B (lower and upper), Podole, Śmiłów, Kontrewers, Paszkowice, Starachowice,

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Szwarszowice, Chyby, Żarnów, Bielowice, Szydłówek (Gierliński and Potemska, 1987; Pieńkowski and Gierliński, 1987; Gierliński and Sabath, 1998; Gierliński and Sawicki, 1998; Gierliński, 1990, 1991, 1994, 1995a, b, 1996, 1997, 1999, 2004; Gierliński and Pieńkowski, 1999; Niedźwiedzki, 2003, 2006, 2011; Gierliński et al., 2001a, b, 2004, 2005, 2009; Niedźwiedzki and Niedźwiedzki, 2001, 2004; Gierliński and Niedźwiedzki, 2002, 2005; Niedźwiedzki and Pieńkowski, 2004, 2014; Niedźwiedzki et al., 2005, 2006, 2008a, b, 2009; Niedźwiedzki and Remin, 2008). This ichnofauna is important for several reasons. Firstly, this is one of the richest record of post-extinction, end-Triassic extinction, earliest Jurassic tetrapod ichnofauna in Europe and one of the few records of very large Early Hettangian theropod tracks worldwide (Gierliński et al., 2001b; Pieńkowski et al., 2014). Secondly, vertebrate ichnofauna from the Holy Cross Mountains area shows a unique early ornithischian trace fossil diversity (Gierliński, 1999; Gierliński and Pieńkowski, 1999).

Dinosaur trace fossils from Hettangian (Zagaje, Skłoby and Przysucha Ore-bearing) formations include material from a variety of theropod, sauropodomorphs and basal ornithischians. However, still there were some gaps of knowledge concerning dinosaur ichnofaunas from the Upper Hettangian of the Holy Cross Mountains due to sparse outcrops. The only site containing numerous and well-preserved dinosaur tracks have been known from the Upper Hettangian strata, upper part of the Przysucha Ore-bearing Formation, exposed at Gliniany Las. Few dinosaur tracks have been reported also from the same formation exposed at Zapniów (Pieńkowski and Gierliński, 1987; Gierliński, 1995b; Gierliński and Niedźwiedzki, 2005), but this tracksite has never been well-studied in terms of tracks, lacking detailed descriptions and figures. However, this site is significant also for its palaeoenvironmental and palaeoecological context. During the Early-Middle Hettangian brackish sea invaded the Holy Cross Mountains area (Pieńkowski, 2004) and this general change of Hettangian environment had a profound impact on dinosaur faunal composition (Gierliński and Pieńkowski, 1999).

Between 2003 and 2005, new dinosaur tracks were found in the Zapniów mine and clay-pit near Przysucha (51°18’53"N, 20°34’27"E), located in the northern margin of the Holy Cross Mountains area (Fig. 1). Hitherto, only a poorly preserved isolated ornithischian (originally described as *Moyenisauropus* isp.) track and numerous theropod tracks (*Anchisauripus* isp.) were reported from this locality (Pieńkowski and Gierliński, 1987; Gierliński, 1995a, b; Gierliński and Niedźwiedzki, 2005). Newly discovered material consists of small and medium sized theropod tracks, medium sauropodomorph manus and pes tracks, and also two isolated tracks of medium-sized early ornithischians (possibly thyreophorans). This new material from the Zapniów mine and clay-pit had never been adequately examined before.

The Zapniów underground mine and clay-pit (both now disused and closed) are situated on the edge of the Mazowieckie voivodship (province), near the border with the Świętokrzyskie voivodship. The mine was established in 1975 and exploited high-quality ceramic claystone (kaolinite rich intervals of the Przysucha Ore-bearing Formation), until it was closed in 2010. The underground excavations reached a depth of 55 m and consisted of several kilometres long system of tunnels. Currently (2011–2015), the clay-pit and underground mine are flooded and there is no access to track-bearing deposits in all described tracksites (A–D).

The first dinosaur track was found at Zapniów (tracksite A; 51°18’80"N, 20°34’30"E) in 1985 (Pieńkowski and Gierliński, 1987; Muz. PIG 1572.II.2, specimen of ornithischian track previously described as *Moyenisauropus* isp. – and herein as cf. *Anomoepus* isp.). In 1993, was discovered isolated and poorly preserved medium-sized theropod tracks [*Anchisauripus* isp.; Muz. PIG 1560.II.35; originally described as *Grallator* (*Grallator*) *tenuis*] in area located close to the tracksite B (51°18’83"N, 20°34’32"E; see Gierliński, 1995b).

After many years of research on the dinosaur tracks from Hettangian and collecting new important material from the Przysucha Ore-bearing Formation exposed at Zapniów, systematization, update and summary of hitherto published results are needed. The new material presented here was discovered in four places named as tracksite A–D, during occasional visits in the Zapniów mine and clay-pit. Some of these specimens (tracksite C) were briefly described by Gierliński and Niedźwiedzki (2005), but other tracks (tracksite A, B, D) have not been previously published. The surface from the tracksite C had been reburied in 2006 with rock debris to prevent the many tracks that were there from being damaged by clay-pit vehicles. We have identified the tracks to the ichnogeneric level and emphasized identifying individual.

This paper contributes to the knowledge on Hettangian dinosaur ichnofaunas of the Holy Cross Mountains and their relations with environment, as well as to the knowledge on an Early Jurassic evolution of dinosaurs.

GEOLOGICAL AND PALAEOENVIRONMENTAL BACKGROUND

The Lower Jurassic dinosaur tracks of the northern margin of the Holy Cross Mountains occur within the six Lower Jurassic lithoformations (Fig. 2; Pieńkowski, 2004; Niedźwiedzki et al., 2009). The Early Jurassic epoch represents more than 25 Myr long period of alternating non-marine and marginal-marine deposition in the northern margin of the Holy Cross Mountains. During this time the area was occupied by several floras (Barbacka et al., 2010, 2014; Pacyna, 2013) and faunas, composition of which was strictly controlled by marine transgressions and climatic changes (Gierliński et al., 2004; Hesselbo and Pieńkowski, 2011; Pieńkowski et al., 2012).

The most diversified dinosaur track assemblages from this region are mostly Hettangian and Late Pliensbachian in age, because outcrops of continental or marginal-marine deposits of Sinemurian or Toarcian age are very rare (Gierliński, 1995b; Niedźwiedzki et al., 2009). Herein, we describe dinosaur footprints coming from the Late Hettangian (ca. 199.5 Ma – Cohen et al., 2015) upper part of the Przysucha Ore-bearing Formation (Fig. 2). Lithofacies and sedimentary cyclicity development, which was observed in the Zapniów exposure is also known from fully-cored boreholes (Fig. 1). The nearest, reference one is Gródek OP-2 (Fig. 1), in which the interval 135–150 metres corresponds to Zapniów section (see Pieńkowski, 2004; http://www.pgi.gov.pl/docman-tree/publikacje-2/special-papers/ /12/1546-sp12-figury/file.html). The data from boreholes and outcrops allowed high-resolution lithological, biostratigraphical and sequence stratigraphy correlation of the Hettangian strata (Pieńkowski, 2004).

Hettangian section in northern slopes of the Holy Cross Mountains is expanded, exceeding in the depocentre 300 m. It is composed of three formal lithoformations: Zagaje Formation, it’s the lowermost part of which comprise also some deposits of the Rhaetian age, Skłoby Formation and Przysucha Ore-bearing Formation, approximately corresponding to the Hettangian depositional sequence – numbered as the sequence I (Pieńkowski, 2004). Continental Zagaje Formation and deltaic/brack-

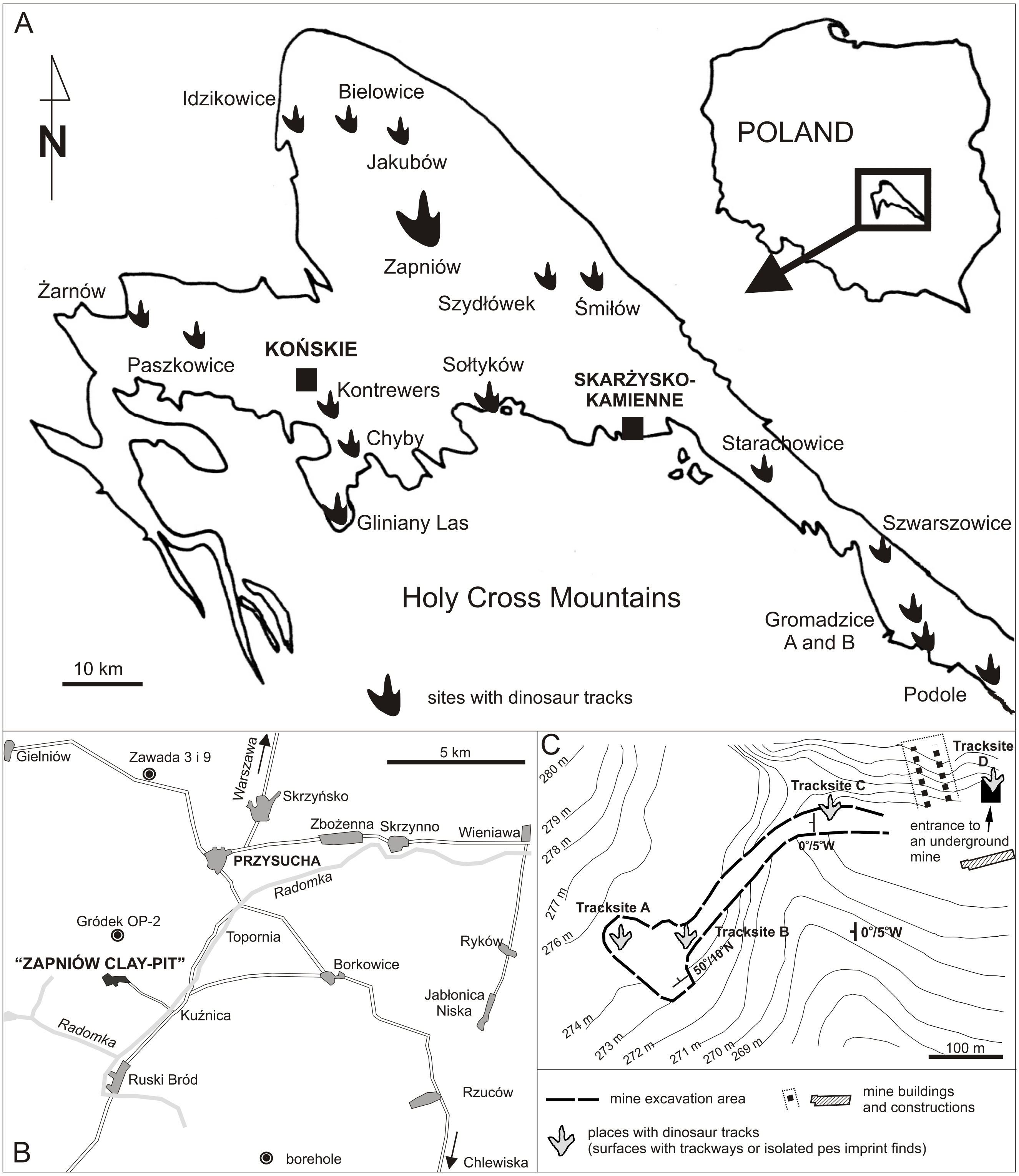

Fig. 1A – location of sites with the Lower Jurassic dinosaur tracks in the Holy Cross Mountains, Poland; B – a sketch map showing location of the Zapniów mine and clay-pit near Przysucha; C – detailed map of the Zapniów mine and clay-pit area with positions of dinosaur track-bearing surfaces

ish-marine Skłoby Formation are of Lower-Middle Hettangian age and represent the transgressive systems tract (TST). The maximum transgressive surface occurs in the Middle Hettangian Skłoby Formation and its uppermost part, along with the overlying Przysucha Ore-Bearing Formation, represent the progradational, highstand systems tract (HST). The end of progradational sedimentation at the top of Przysucha Ore-Bearing Formation is marked by the regional erosion surface (Fig. 2). In most places, erosion removed sediments of the underlying parasequences. Based on comparison to the more complete succession revealed at the nearby Gródek OP-2 borehole, at least 4 m or more metres of sediments of the uppermost parasequence were removed at the erosional sequence boundary at Zapniów. This erosional surface is associated with a sub-

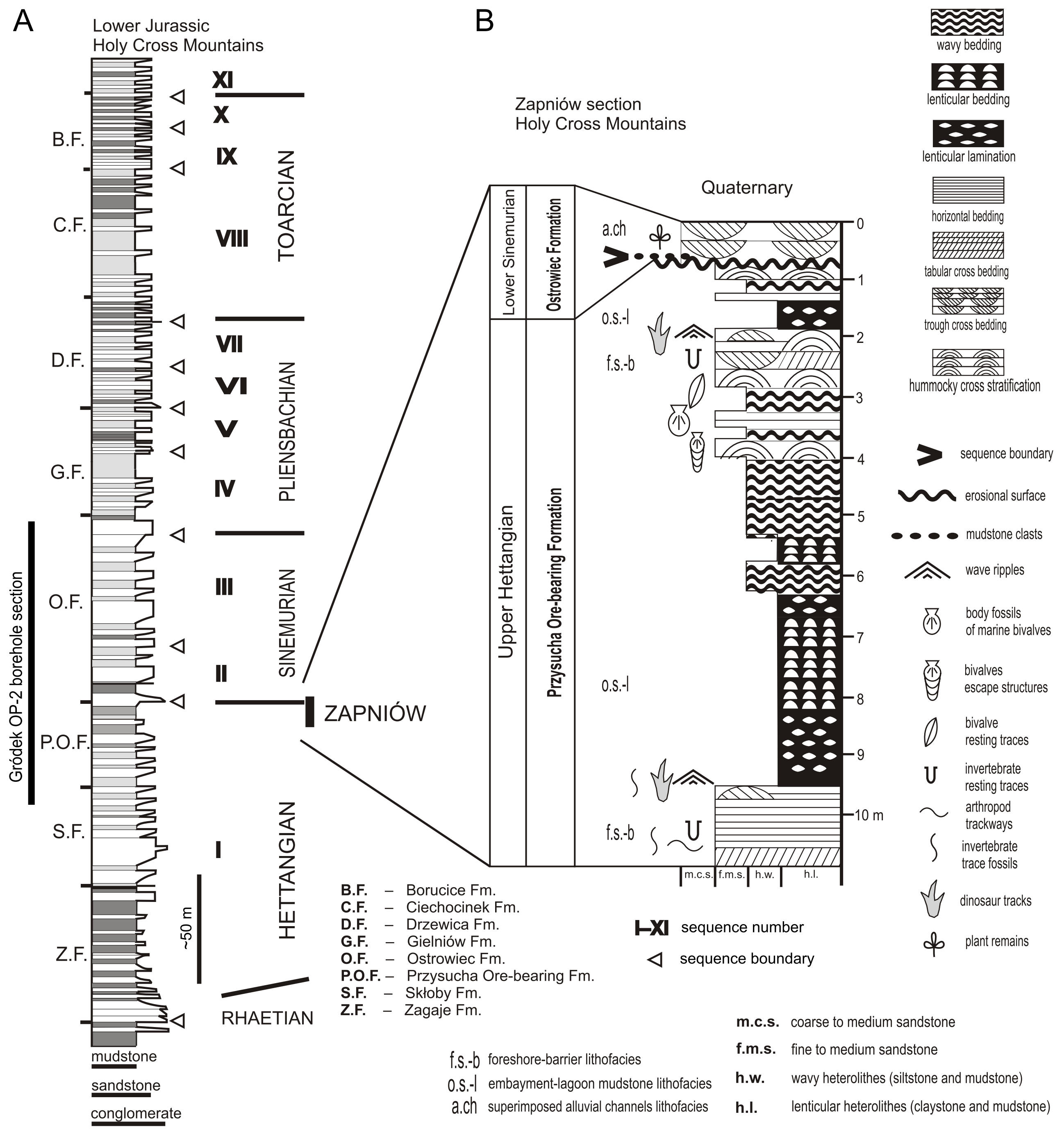

Fig. 2A – overall section of the Lower Jurassic of the Holy Cross Mountains with position of Zapniów section; for more detailed section (135–150 m) in the reference Gródek OP-2 borehole see Pieńkowski (2004); http://www.pgi.gov.pl/docman--tree/publikacje-2/special-papers/12/1546-sp12-figury/file.html; B – lithostratigraphical-log of the Zapniów mine and clay-pit section, showing occurrences of some fossils, sedimentary structures and horizons from where dinosaur tracks have been in situ recorded (profiles after Pieńkowski, 2004, modified)

stantial fall in sea level and it forms a typical sequence boundary, ending progradational HST and commencing the TST belonging to the next sequence II of a Lower Sinemurian age. Character of clay mineralogy, palynomorphs, rare plant macroremains and also some invertebrate body and trace fossils point to warm and rather humid climate in the area studied, in the Late Hettangian times (Pieńkowski, 1985, 2004; Pacyna, 2013).

The Late Hettangian Przysucha Ore-bearing Formation and corresponding HST is composed of increasingly prograding parasequences, pointing to progradational, regressive trend (Pieńkowski, 1983, 1991, 2004). Barrier-lagoon depositional cycles dominate (like in the Zapniów exposure, Figs. 2 and 3A), but also fluvial-dominated deltaic cycles are common. Within the Polish Basin, this formation occurs only in the Holy Cross Mountains region, thus pointing to a specific character of this part of basin in the Late Hettangian times. Particularly characteristic are lagoonal deposits, represented by sideritic clays and mudstones forming characteristic "ore-bearing" horizons. Lagoons were broad but shallow and are often associated with marsh deposits with palaeosol horizons. Vast marsh/swampy areas developed around lagoon coasts provided high quantities of iron. In the Holy Cross Mountains subbasin, there are usually three ore-bearing horizons, corresponding to three episodes of widespread development of lagoon depositional subsystem. Towards the basin centre, which was located in the NE Poland, connections with the open basin were wider which led to formation of more open embayments and migrating barriers, such as in Zapniów (Fig. 4). The land rimmed by a delta system, was located further to the N–NE, beyond the Nowe Miasto-Iłża Fault Zone (Fig. 4), which formed the northern tectonical frame of the Early Jurassic basin in the Holy Cross Mountains area (Pieńkowski, 2004). Embayment located at Zapniów was opening to the NW, towards the more open brackish basin, extending to the Central Poland and further to Pomerania, north Germany and Denmark, where it merged with the open boreal sea (Pieńkowski, 2004). Barrier deposits at Zapniów are built of well-sorted quartz sandstones (arenites) and form two conspicuous layers, separated by lagoonal deposits (Fig. 3A). The barriers were flat, of a low-relief character. The lack of aeolian deposits and traces of vegetation, abundance of wave ripple marks (Fig. 3B) and invertebrate trace fossils, including *Skolithos*, *Monocraterion*, *Calycraterion*, *Lockeia*, *Cochlichnus* (Fig. 3C), point to their partly submerged/temporarily emerged character. Measurements of azimuths of wave ripple crests at the top of the lower barrier sandstone (ranging between 100 and 125 degrees), allowed for approximate estimation of the barrier shoreline orientation, which was roughly parallel to the WWN–EES direction.

Temporarily emerged barriers provided good environment both for dinosaur penetration and preservation of their tracks. The *Anomoepus–Moyenisauropus–Anchisauripus–Grallator* track association was defined as a typical dinosaur track association for this kind of environment (Gierliński and Pieńkowski, 1999). Dinosaur footprints in Zapniów come entirely from the upper surfaces of two barrier systems where they were left. Most of the tracks were found on the top of the lower barrier level (Fig. 2). Tracks were quickly filled with fine-grained lagoonal deposits, which protected them from erosion.

MATERIAL AND METHODS

Dinosaur tracks found at Zapniów are preserved as true tracks (concave epireliefs), undertracks and also as natural casts on the bottom surfaces of fine-grained, clayish or siderite-rich sandstone. They show different states of preservation. Some tracks contain anatomically controlled structures (e.g., claw or pad impressions), other are without such characters.

In June 2002 and May 2003, a track-bearing surface (tracksite C; 51°18’92"N, 20°34’42"E) was exposed. Once the tracksite C, measuring 28 m^2, was fully exposed (Fig. 5C), the footprints were identified and the surface was mapped onto a graph paper. Seven specimens of *Anchisauripus* isp. footprints were preserved on exposed *in situ* sandstone surface in the mine driveway leading to the front face of the Zapniów clay-pit (Gierliński and Niedźwiedzki, 2005). In 2004, the authors found the surface with two isolated theropod dinosaur tracks (*Anchisauripus* isp.) in the underground part of the Zapniów mine (tracksite D; level mining 2, –12 m, tunnel B, about 23 m from the intersection with main tunnel). Both footprints were left in the place of the discovery (in the floor of mining tunnel), but their pictures and clay casts were taken.

The most numerous is medium-sized theropod track *Anchisauripus* isp., occurring mainly in the form of true tracks or in part undertracks in two horizons of the section in Zapniów (Figs. 2 and 5–7). Four specimens have been found *ex situ* in

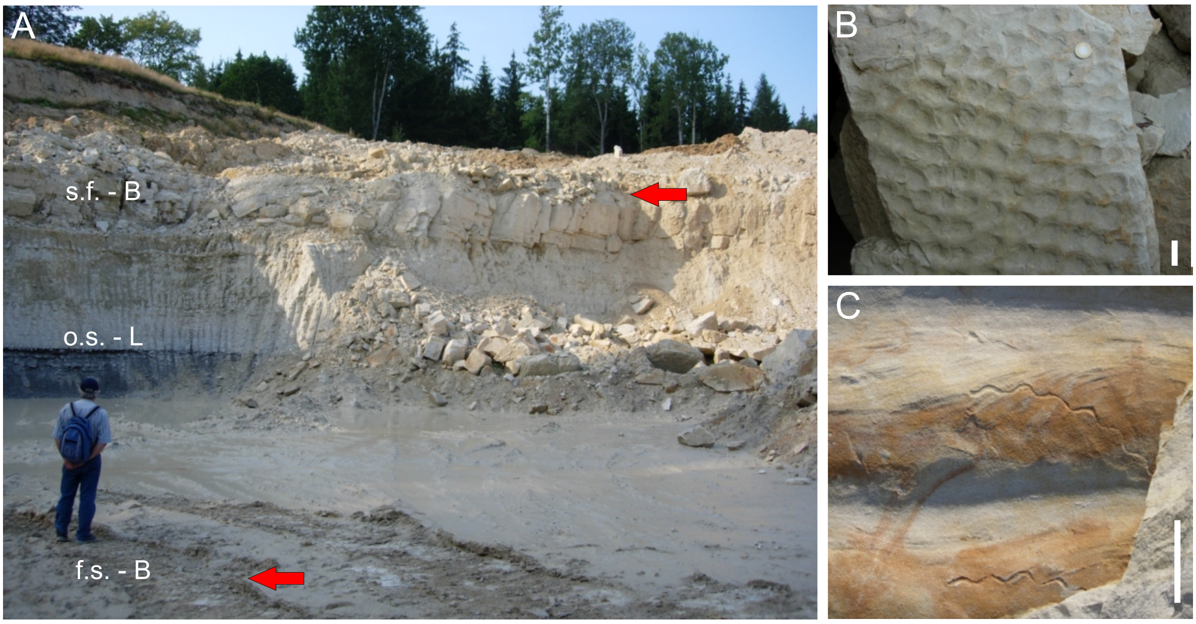

Fig. 3A – deposits of the barrier-lagoon-embayment depositional system from the Zapniów exposure near Przysucha (Late Hettangian, Przysucha Ore-bearing Formation); B – surfaces with wave ripple marks; C – *Cochlichnus* isp., sinusoidal invertebrate traces

Red arrows – footprint-bearing horizons; f.s. – B – foreshore-barrier lithofacies with *Anchisauripus* isp. tracks; o.s. – L – embayment-lagoon mudstone lithofacies; s.f. – B – shoreface heterolith-sandstone lithofacies with record of temporal emersions marked with dinosaur tracks; scale bar – 3 cm

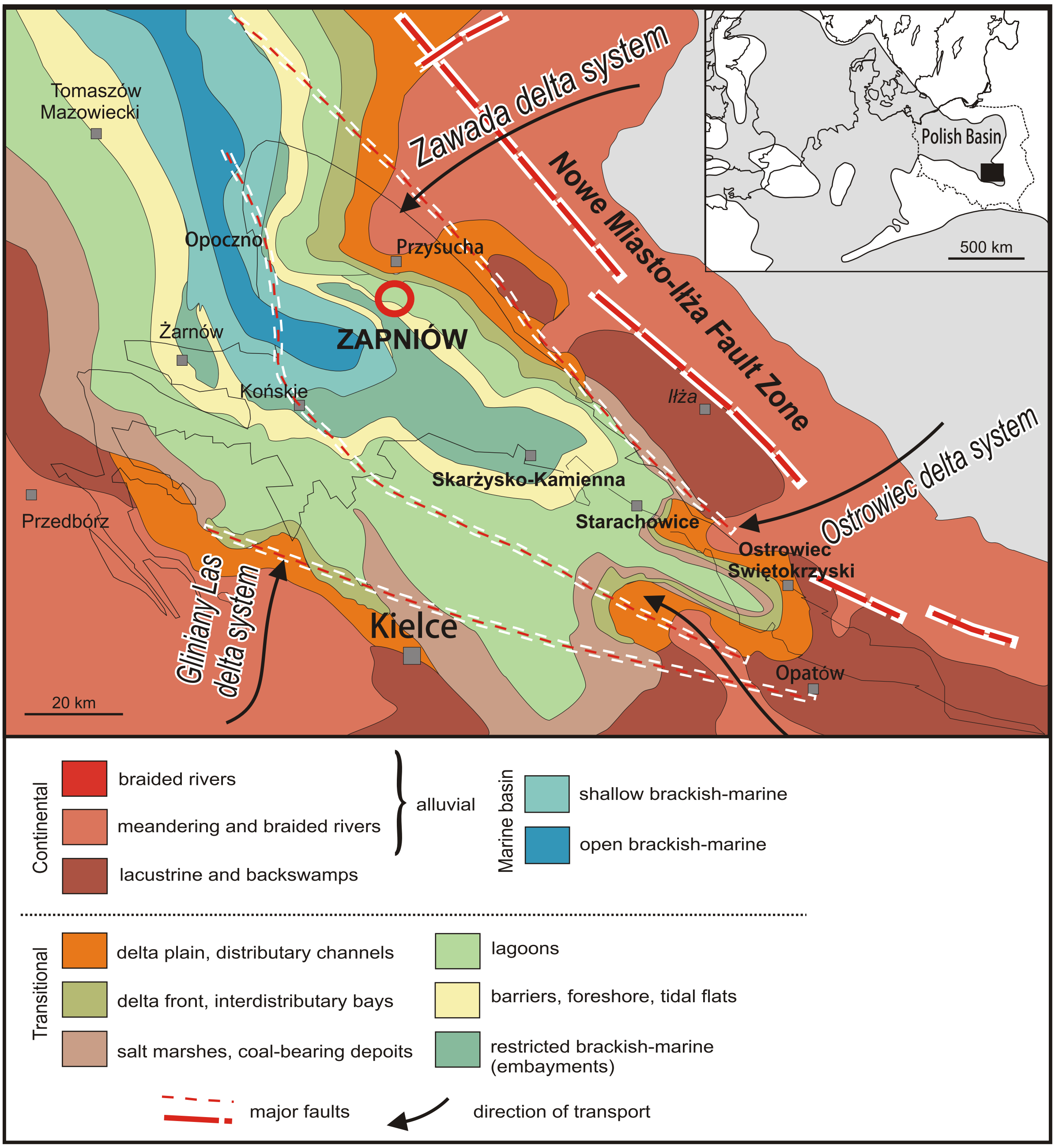

Fig. 4. Location of the Zapniów mine and clay-pit in the northern margin of the Holy Cross Mountains area on the palaeogeographical background during Late Hettangian; inset – general palaeogeographical extent of the Early Jurassic epicontinental basins in Europe (after Pieńkowski, 2004, modified)

loose sandstone blocks with record of ripplemarks (Figs. 6B, D, E), numerous invertebrate bioturbation (Fig. 8A, C) or in the siderite-rich sandstone surface (Fig. 6C). Other specimens have been found *in situ* (Figs. 6A, 7 and 8B, D). Photographs were taken under natural light in the field and museum (Geological Museum, Polish Geological Institute – National Research Institute, Warsaw). Measurements were taken on the original material or casts (Table 1) following the methods of Leonardi (1987) with measurements of tridactyl footprints digit ratios [L/W, L/III, III/II, III/IV, te/fw, (fl-te)/fw] after Weems (1992) and Olsen et al. (1998). The ichnological terminology used in this paper for the description of these dinosaur tracks mainly follows the works of Thulborn (1990).

Two calculations were made from the measurements. First, we calculated the hip height of the *Anchisauripus* trackamker using the morphometric ratios suggested by Thulborn (1990) as follows: $h \approx 4.5$ x footprint length (formula for footprints smaller than 25 cm). Second, a hip height was used to estimate speeds using an equation developed by Alexander (1976). The equation for speed is:

$$v = 0.25\, g^{0.5}\, \lambda^{1.67}\, h^{-1.17}$$

where: v – represents velocity, g – is the acceleration due to free fall, λ – represents stride length, h – represents height of the animal at the hip).

Fig. 5. Discoveries of dinosaur tracks in Zapniów mine and clay-pit, Przysucha Ore-bearing Formation (Upper Hettangian), Holy Cross Mountains, Poland

A – tracksite C; two tracks of *Anchisauripus* isp. left on the top of lower barrier deposits (photo. G. Gierliński); **B** – tracksite C; excavation of the surface with numerous *Anchisauripus* isp. tracks (Zapniów, 2003; photo. G. Gierliński); **C** – tracksite C; mapping of the surface with numerous *Anchisauripus* isp. tracks (Zapniów, 2003; photo. G. Gierliński); **D** – tracksite D; examination of two *Anchisauripus* isp. tracks preserved on the top of sandstone (arrow) exposed in underground mine (Zapniów, 2004); **E** – tracksite D; surface with *Anchisauripus* isp. tracks (arrows) preserved as true tracks (Zapniów, 2004)

Original specimen or plaster casts of some specimens from Zapniów are housed in the Geological Museum of the Polish Geological Institute – National Research Institute in Warsaw, Poland (abbreviation: Muz. PIG) and the Museum of Nature and Technology (former Museum of History of Material Culture) in Starachowice (abbreviation: MPT).

DESCRIPTION OF DINOSAUR TRACKS

THEROPOD TRACKS

Ichnofamily: Grallatoroidae Lull, 1904
Ichnogenus: *Grallator* Hitchcock, 1858
Grallator isp. (Fig. 6D, E)

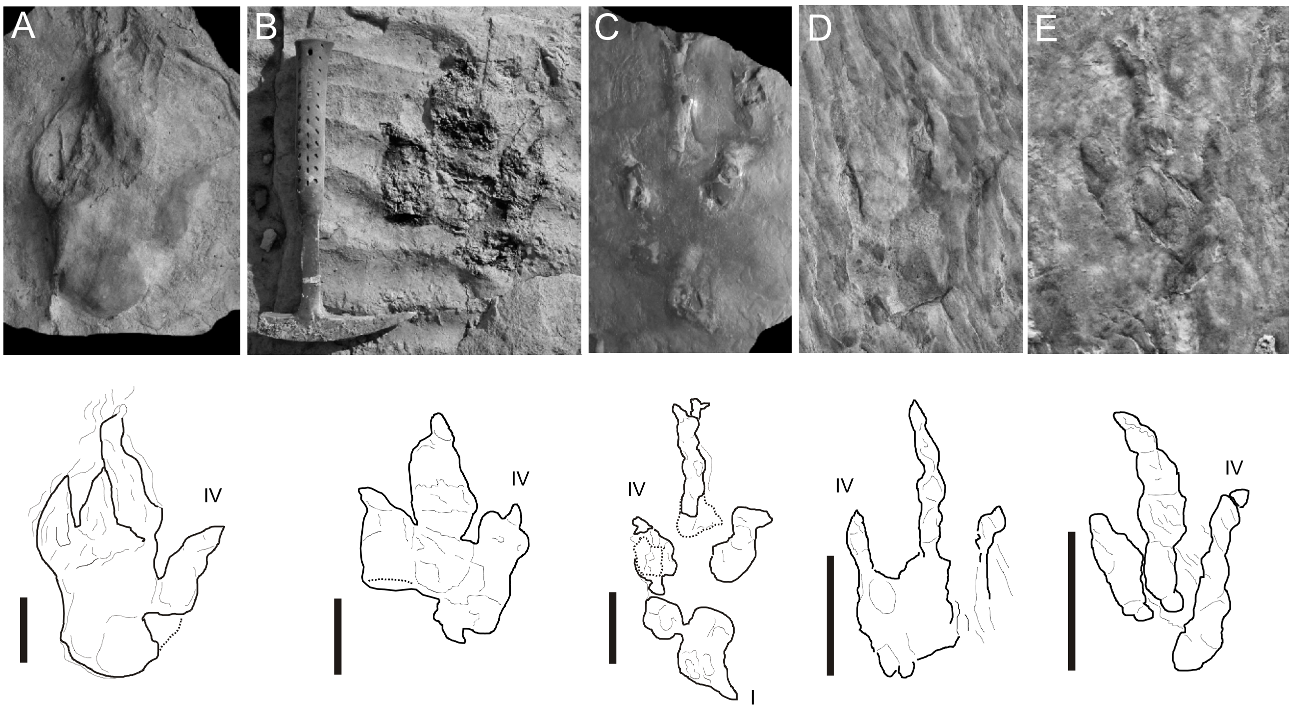

Fig. 6. Theropod tracks from Zapniów mine and clay-pit near Przysucha, Przysucha Ore-bearing Formation (Upper Hettangian), northern margin of the Holy Cross Mountains, Poland (photographs and schematic drawings; IV – position of the digit number four)

A–C – *Anchisauripus* isp. (A – clay cast, unregistered, deposited in the Geological Museum, Polish Geological Institute – National Research Institute, Warsaw, specimen from tracksite D; B – specimen found *ex situ* and left in the field on the loose sandstone; C – Muz. PGI 1560.II.35, specimen from tracksite A); **D, E** – *Grallator* isp., both specimens were found *ex situ* and left in the field on loose sandstone slabs; scale bar – 5 cm

M a t e r i a l. – Two uncollected slab with isolated pes imprints preserved on the surface with ripplemarks and observed in the tracksite A (original specimens left in field; 51°18'82"N, 20°34'28"E).

D e s c r i p t i o n. – Small sized (up to 120 mm long), digitigrade and functionally tridactyl pedal imprints preserved as natural casts. The pedal digit ratios are: III/II = 1.52–1.73 and III/IV = 1.05–1.12; L/III = 1.37–1.53; te/fw = 0.56–0.67; (fl-te)/fw = 0.89–1.01.The total length to total width ratio is 1.75–1.87. The digit II is shorter than IV, but both are shorter than III. Impressions of two phalangeal pads are visible in digit II, three in digit III (Fig. 6E) and digit IV contains more than three phalangeal pads. Divarication angle of outer digits is narrow: 30 and 35°.

D i s c u s s i o n. – Here we use the term *Grallator* in the traditional, restricted, ichnotaxonomic sense, only to describe small, tridactyl footprints that show strong similarity to various Newark Supergroup material (Olsen et al., 1998). The *Grallator* ichnogenus is widely distributed in the Lower to Upper Hettangian of the Holy Cross Mountains (Gierliński and Pieńkowski, 1999; Niedźwiedzki, 2011). Very similar small theropod tracks have been described from the Przysucha Ore-bearing Formation exposed at Gliniany Las (Gierliński, 1996). The narrow divarication angle is typical of *Grallator* described by Olsen et al. (1998). *Grallator* is also a long-ranging dinosaur ichnotaxon and therefore of little biostratigraphic utility. Tracks in the Zapniów ichnoassemblage have a mean foot length and width of 98 and 51 mm respectively. Most authors agree that *Grallator* represents a theropod dinosaur, possibly a small theropod similar to *Coelophysis* and *Megapnosaurus* (Colbert, 1989; Irmis, 2004). The mean sizes of all *Grallator* footprints collected from the Przysucha Ore-bearing Formation (Gliniany Las = 2, Paszkowice = 1, Zapniów = 2) sample are around 15–20% larger than those recorded from some classical Upper Triassic site of North America (e.g., Lockley and Eisenberg, 2006; Lockley and Gierliński, 2009). This suggests that there are some differences between the Late Triassic and Early Jurassic representatives of the *Grallator* ichnogenus.

Grallator footprints are relatively rare in the Lower Jurassic of Europe (Lockley and Meyer, 2000). What seems to be interesting is a common and rather widespread ichnogenus in the Middle-Upper Triassic of Germany and France (Haubold, 1984; Klein and Lucas, 2010). This is consistent with the high diversity Hettangian ichnofaunas from Poland with rare *Grallator* and suggests that typical *Grallator*-dominated assemblages disappeared in this part of the world across the Triassic-Jurassic boundary.

Ichnofamily: Grallatoroidae Lull, 1904
Ichnogenus: *Anchisauripus* Lull, 1904
Anchisauripus isp. (Figs. 6A–C and 7)

M a t e r i a l. – One collected pes specimen (Fig. 6C; Muz. PGI 1560.II.35) from tracksite A; three plaster cast (Fig. 7B, Muz. PGI 1688.II.1; Fig. 7D, MPT.P/6 and unregistered cast deposited in the Polish Geological Institute – National Research Institute, Warsaw) of the pes specimens from the tracksite C (specimens *in situ*); clay cast (unregistered, deposited in the Polish Geological Institute – National Research Institute, Warsaw) of the pes specimen from underground mine (tracksite D,

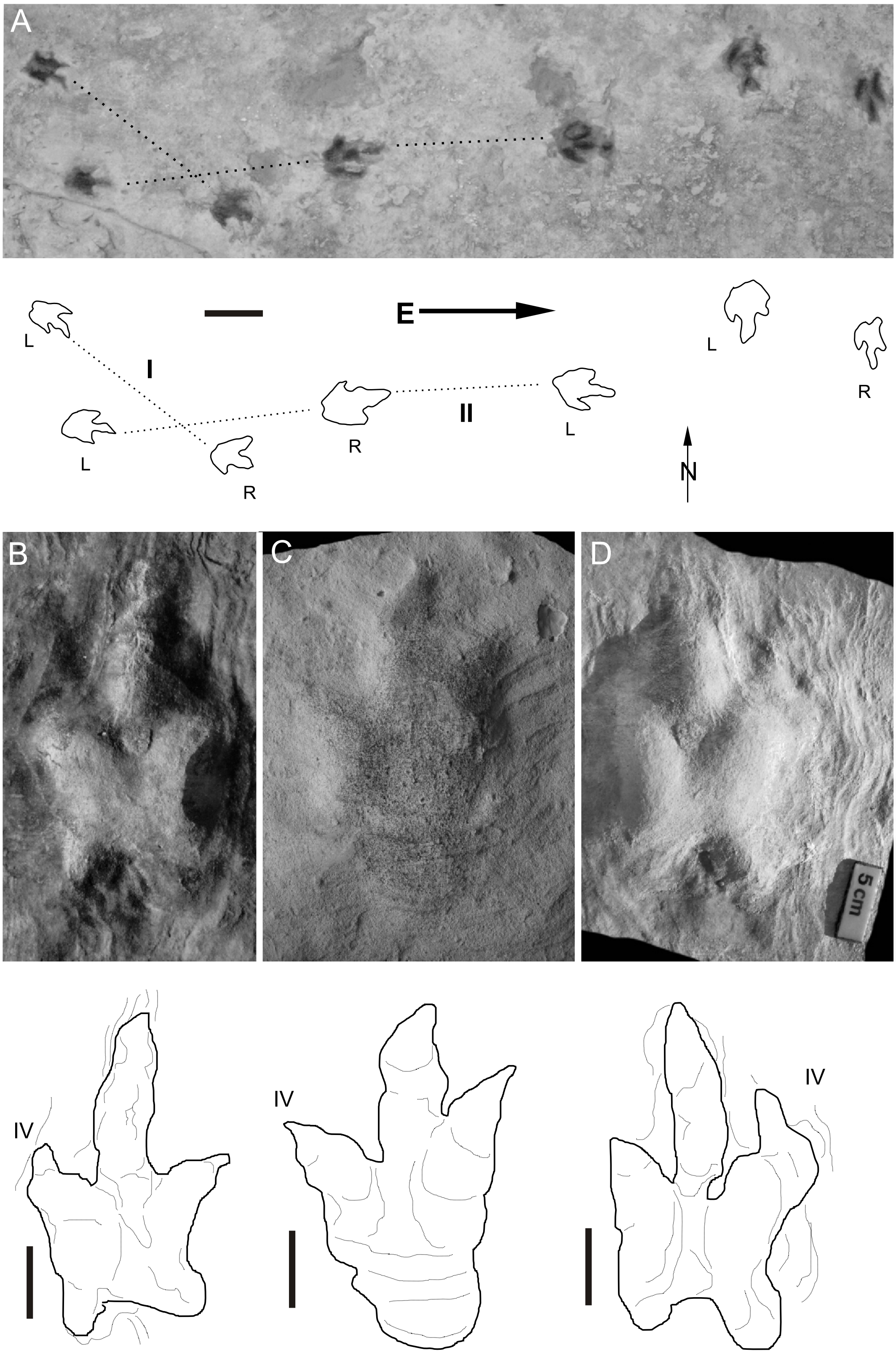

Fig. 7. Theropod tracks from Zapniów mine and clay-pit near Przysucha, Przysucha Ore-bearing Formation (Upper Hettangian), northern margin of the Holy Cross Mountains, Poland (photographs and schematic drawings; IV – position of the digit number four)

A – surface with numerous *Anchisauripus* isp. tracks and map of the surface with marked trackways (R – right, L – left imprint); note approximately W–E direction of the trackways, which is approximately parallel to the shoreline direction, inferred from azimuths of wave ripples; **B–D** – plaster casts of selected *Anchisauripus* isp. tracks from the surface exposed at tracksite C (B – Muz. PGI 1688.II.1, plaster cast; C – plaster cast, unregistered; D – MPT. P/6, plaster cast); scale bar – 5 cm

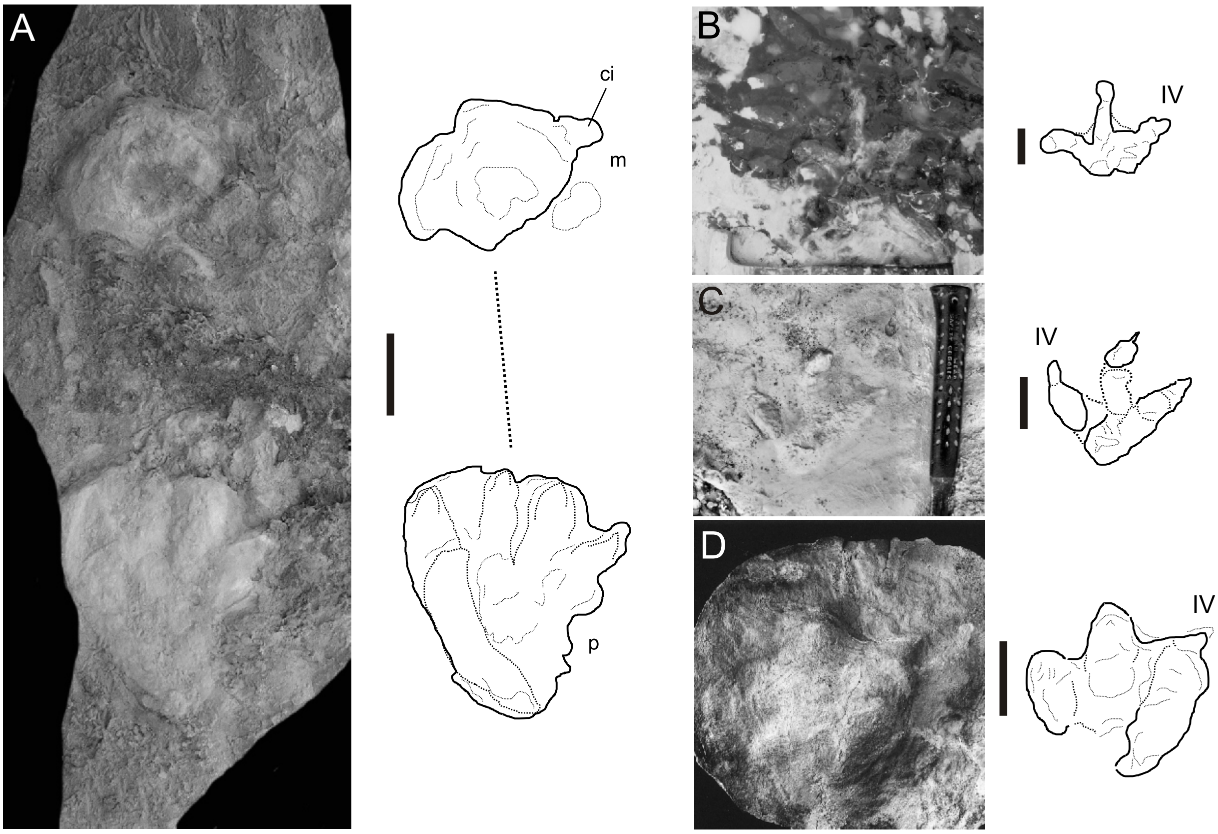

Fig. 8. Sauropodomorph and ornithischian tracks from Zapniów near Przysucha, Przysucha Ore-bearing Formation (Upper Hettangian), northern margin of the Holy Cross Mountains, Poland (photographs and schematic drawings; IV – position of the digit number four; ci – claw impression)

A – cf. *Tetrasauropus* isp., juvenile or small sauropodomorph tracks, manus (m) and pes (p) tracks (specimen left in the field); **B–D** – cf. *Anomoepus* isp., an early ornithischian tracks (B, C – specimens left in the field; D – Muz. PGI 1572.II.2, plaster cast); scale bar – 5 cm

specimen preserved *in situ*) (Fig. 6A); isolated pes (not collected) preserved *in situ* in tracksite D (not illustrated); slab with isolated pes preserved on surface with ripplemarks and observed in the tracksite A (Fig. 6B; original specimen left in field; 51°18'86"N, 20°34'40"E); four pes specimens (not collected) preserved *in situ* on surface in the tracksite C (Fig. 7A).

D e s c r i p t i o n. – Medium sized (up to 235 mm long), digitigrade and functionally tridactyl pedal imprints preserved as true tracks or undertracks (Figs. 6A, B and 7) and natural cast (Fig. 6C). The pedal digit ratios are: III/II = 1.54–1.65 and III/IV = 1.10–1.16; L/III = 1.67–1.83; te/fw = 0.52–0.62; (fl-te)/fw = 1.13–1.32. The digit II is shorter than IV, but both are shorter than III. The total length to total width ratio is 1.70–1.82. Divarication angle of outer digits is narrow: 35–55°. The surface with *Anchisauripus* isp. from tracksite C (Fig. 7A and Table 1) shows seven footprints (trackway I with two steps is 96 cm long; trackway II with three steps is 193 cm long; two isolated footprints), representing probably four animals (see Table 1). Both trackways (I and II; Fig. 7A) trend approximately towards the E–EESast; interestingly, this direction is roughly parallel to the WWN–EES direction of palaeoshoreline, which was inferred from azimuths of wave ripples. It should be noted that the difference in depth and morphology of these trackways suggests that they were made at different times. Two shallower footprints (first from trackway I, and one isolated footprint) have indications of pad and claw impressions (Fig. 7B, C). Other footprints show little more than the outline of the foot.

D i s c u s s i o n. – These medium-sized and relatively narrow forms can be assigned to *Grallator* Hitchcock, 1858, following grallatorid designation concept of Lockley and Hunt (1995), or to the ichnogenus *Anchisauripus sensu* Olsen et al. (1998). The pes measurement ratios of these specimens correspond also to the ratios of *Grallator tuberosus sensu* Weems, 1992. Olsen et al. (1998) diagnosed this type of footprint (medium sized and narrow pes about length between 15 and 25 cm) as ichnogenus *Anchisauripus*. In *Anchisauripus* the digit III projects relatively further anteriorly than in small specimens of *Eubrontes* and *Kayentapus*, but not as far as in *Grallator*. We believe that the classification of Olsen et al. (1998) better reflects diversity of the Lower Jurassic theropod ichnotaxa. As has been previously reported (Niedźwiedzki and Pieńkowski, 2004) in comparison to frequencies of other theropod ichnotaxa a medium-sized theropod footprints (*Anchisauripus*) are generally rare in the Lower Jurassic dinosaur track assemblages of Poland (Gierliński, 1995a, b; Niedźwiedzki, 2011; Niedźwiedzki and Niedźwiedzki, 2001, 2004; Gierliński and Niedźwiedzki, 2005). Newly described *Anchisauripus* specimens from the Zapniów slightly increase a generally low frequency of these ichnotaxa occurrences in the Lower Jurassic of the Holy Cross Mountains area. Ichnogenus *Anchisauripus* represents a theropod dinosaur, possibly a medium sized *Coelophysis*-like theropod.

Two *Anchisauripus* isp. trackways from the tracksite C, indicate trotting behaviour. Both trackways, have stride to hip

Table 1

Measurements (in cm) of dinosaur tracks from Zapniów mine and clay-pit

Specimen	Ichnotaxa	TR	TL	TW	TD	Pa	λ	h	v
Left in the field	*Grallator* isp.	A	11.9	5.9	30	–	–	53.5	–
Left in the field	*Grallator* isp.	A	9.5	5.6	35	–	–	42.7	–
Unregistered, clay cast	*Anchisauripus* isp.	D	21.1	12.5	42	–	–	94.9	–
Left in the field	*Anchisauripus* isp.	D	19.2	13.1	35	–	–	86.4	–
Muz. PGI 1688.II.1, plaster cast	*Anchisauripus* isp.	C (TR I)	22.8	12.5	39	77	154*	102.6	3.5
Left in the field	*Anchisauripus* isp.	C (TR I)	21.5	11.8	55			96.7	
Left in the field	*Anchisauripus* isp.	C (TR II)	22.5	13.6	47	96	174	101.2	3.9
Unregistered, plaster cast	*Anchisauripus* isp.	C (TR II)	22.3	14.8	36			100.3	
MPT.P/6, plaster cast	*Anchisauripus* isp.	C (TR II)	23.1	12.5	39	78		103.9	
Left in the field	*Anchisauripus* isp.	C	23.5	14.2	42	–	–	105.7	–
Left in the field	*Anchisauripus* isp.	C	23.2	13.5	39	–	–	104.4	–
Muz. PGI 1560.II.35	*Anchisauripus* isp.	A	17.2	10.2	46	–	–	77.4	–
Left in the field	*Anchisauripus* isp.	A	20.5	12.8	42	–	–	92.2	–
Left in the field	cf. *Tetrasauropus* isp. manus (pes)	A	13.4 (31.7)	20.4 (24.9)	–	–	–	155.3	–
Left in the field	cf. *Anomoepus* isp.	A	14.1	17.5	74	–	–	63.4	–
Left in the field	cf. *Anomoepus* isp.	B	13.3	12.7	68	–	–	59.8	–

TR – trackway, TL – total length, TW – total width, TD – total divarication, Pa – pace, λ – stride, h – height at hip, * – stride that was determined by multiplying a single pace by two, *v* – velocity in m/s

height ratios close to the trot (data included in Table 1) and this indicates that both trackmakers were running. The evidence from the tracksite C at Zapniów is in agreement with observations made by other workers (e.g., Thulborn, 1989, 1990; Irby, 1996; Getty, 2005) in that dinosaurs using a trotting or running gait were small- to medium-sized animals.

SAUROPODOMORPH TRACKS

Ichnofamily: Navhopodidae Olsen and Galton, 1984
Ichnogenus: *Tetrasauropus* Ellenberger, 1972
cf. *Tetrasauropus* isp. (Fig. 8A)

M a t e r i a l. – Uncollected slab with manus and pes imprints preserved on the surface with numerous invertebrate trace fossils and observed in the tracksite A (original specimen left in field; 51°18'85"N, 20°34'39"E).

D e s c r i p t i o n. – Natural cast of the pes-manus set of quadrupedal dinosaur, plantigrade, with a tetradactyl pes. The pes is asymmetrical. The pes is tetradactyl and elongated, 317 mm long, 249 mm wide anteriorly and 115 mm wide posteriorly. The posterior part of pes shows heel-like area. Divarication between pes digits is low. Digit I lies posteriorly with respect to digits II–IV. Digit III extended forward more than the others. Manus smaller then pes, semicircular, 204 mm wide and 134 mm long. The manus is situated anteromedially to the pes. The ratios of the pes length to manus length equal 3.01; pes width to manus width equals 2.37; pes length to pes wide (anteriorly) equals 1.36.

D i s c u s s i o n. – The ichnogenus *Tetrasauropus* Ellenberger, 1972 was described for the first time from the Late Triassic-Early Jurassic ichnofauna of southern Africa (Lesotho). The ichnogenus was revised by D'Orazi Porchetti and Nicosia (2007) and considered as monotypic with *T. unguiferus* as the only valid type ichnospecies. The presence of *Tetrasauropus* outside Lesotho has often been inferred, especially in North America (e.g., Lockley and Hunt, 1993, 1995; Lockley et al., 2001; Gaston et al., 2003) but footprints resembling *Tetrasauropus* were described from from the Upper Triassic (Norian–Rhaetian) of Switzerland (Furrer, 1993), Upper Triassic (Norian–Rhaetian) of Greenland (Jenkins et al., 1994; Lockley and Meyer, 2000; Sulej et al., 2014), Upper Triassic of of South Wales (Lockley et al., 1996), Upper Triassic (Carnian) Portezuelo Formation of Argentina (Marsicano and Barredo, 2004), Upper Triassic (Norian) of Poland (Gierliński, 2007). The only report about occurrence of *Tetrasauropus* in Early Jurassic strata (Corniola Formation) from Central Italy (Arduini, 1996) has already been questioned (Manni et al., 1999). However, in the Lower Jurassic strata of northern Italy there were sauropodomorph tracks reported (named as *Lavinipes cheminii* Avanzini, Leonardi et Mietto 2003), whose characteristics are comparable with those of *Tetrasauropus* (D'Orazi Porchetti and Nicosia, 2007).

Cf. *Tetrasauropus* isp. from Zapniów shows several distinctive features (Fig. 9). Manus was resting on the ground, in an anterior and external position – with respect to the pes. Asymmetrical pes and manus exhibit a definite heteropody. Manus digit I mainly shows an imprint of a large, bent claw. Ichnogenus *Tetrasauropus* is a record of a large quadruped and the calculated height at the hip of this trackmaker is about 2 metres, a total body length is about 10 metres (D'Orazi Porchetti and Nicosia, 2007). Since first reported, the ichnogenus has been referred both to dinosaurian taxa and to non-dinosaurian groups (see D'Orazi Porchetti and Nicosia, 2007).

Ellenberger et al. (1969, 1970) and Ellenberger (1970) suggested a large melanorosarid sauropodomorph as a supposed trackmaker. Baird (1980), Olsen and Galton (1984), Haubold (1984), Thulborn (1990), Anderson et al. (1998) and Lockley and Meyer (2000) referred *Tetrasauropus* to a prosauropod (= sauropodomorph). Lockley et al. (2001) proposed a sauropodan affinity for the North American *Tetrasauropus* which, as we note, are apparently somewhat different from the South African type material. Rainforth (2003) considers *T. unguiferus* from Lesotho as a poorly preserved *Brachychirotherium*, and implicitly as a non-dinosaurian track. Recently, D'Orazi Porchetti and Nicosia (2007), based on direct comparison of footprints and manus and pes osteology, suggested *Yunnanosaurus* sauropodomorph from the Early Jurassic of China as the best candidate to be the *Tetrasauropus* trackmaker.

THYREOPHORAN TRACKS

Ichnofamily: Anomoepodidae Lull, 1904
Ichnogenus: *Anomoepus* Hitchcock, 1848
cf. *Anomoepus* isp. (Fig. 8B–D)

M a t e r i a l. – Uncollected slab with pes imprint preserved on the surface with invertebrate trace fossils (Fig. 8C) and observed in the tracksite A (original specimen left in field; 51°18'83"N, 20°34'37"E); uncollected pes imprint preserved on the surface with ripplemarks (Fig. 8B) in the tracksite B (original specimen left in field; 51°18'83"N, 20°34'32"E); plaster cast (Fig. 8D; Muz. PGI 1572.II.2) of the pes specimens discovered in 1985 in the tracksite A (specimens was found *in situ*).

D e s c r i p t i o n. – Three isolated small to medium sized (130–160 mm long and 105–125 mm wide) tridactyl pes imprints, preserved as natural moulds (Fig. 8B, D) or natural cast (Fig. 8C). All pes specimens are slightly longer than wide by 5–10%. The projection of the third digit beyond the lateral digits varies from 12–25% of the whole pes length. All specimens show wide digit divarication: II–III = 35–40°, III–IV = 30–34°, II–IV = 65–74°. Digits III and IV are subequal in length with small claw imprints (Fig. 8C), but in poorly preserved specimen (Muz. PGI 1572.II.2) the fourth digit is the longest. Digit II is clearly shorter than III and IV. Digit III is slightly curved in the end in two observed specimens (Fig. 8B, C). All ichnites show two poorly preserved phalangeal pads on digit III.

D i s c u s s i o n. – The two footprints (Fig. 8B, C) show an anomoepodid pattern and typical functionally tridactyl pes with relatively short digits and also typical *Anomoepus* sizes (Gierliński, 1991; Thulborn, 1994; Lockley and Gierliński, 2006). However, the specimen Muz. PGI 1572.II.2 shows also some specific morphological aspects (blunted digits, short digit II, long digit IV), characteristic for ichnogenus *Moyenisauropus* Ellenberger, 1974. Two described specimens (Fig. 8B, C) show features identified in the Early Jurassic ichnospecies *Anomoepus pienkovskii* Gierliński, 1991, such as its size, proportions of digit length and relatively narrow digits. Some authors considered Ellenberger's *Moyenisauropus* as a junior synonym of *Anomoepus* (Olsen and Galton, 1984; Thulborn, 1994). Recently, Lockley and Meyer (2000), Olsen and Rainforth (2003) contended that all ichnospecies of *Moyenisauropus* (except *Moyenisauropus karaszevskii* Gierliński, 1991) should be transferred to *Anomoepus* – however, further debate on these taxonomical questions would be beyond scope of this paper.

Pieńkowski and Gierliński (1987) proposed a hypothetical "wading and swimming scenario" to explain the origin of the first anomoepodid specimen discovered in the Zapniów (Fig. 8D; *Moyenisauropus* isp. here in redescribed as cf. *Anomoepus* isp.). 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. According to Gierliński and Pieńkowski (1999) the "undertracks scenario" is unlikely, because the tracks are preserved on two corresponding slabs: as a mould (slab Muz. PGI 1560.II.9A), and as a cast (slab Muz. PGI 1560.IL9B). 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.

DISCUSSION

The Upper Hettangian marginal marine sediments in Zapniów mine and clay-pit are not rich in fossils but nevertheless yield quite diversified dinosaur track assemblage (Fig. 10). The dinosaur ichnofauna described from Zapniów comprises

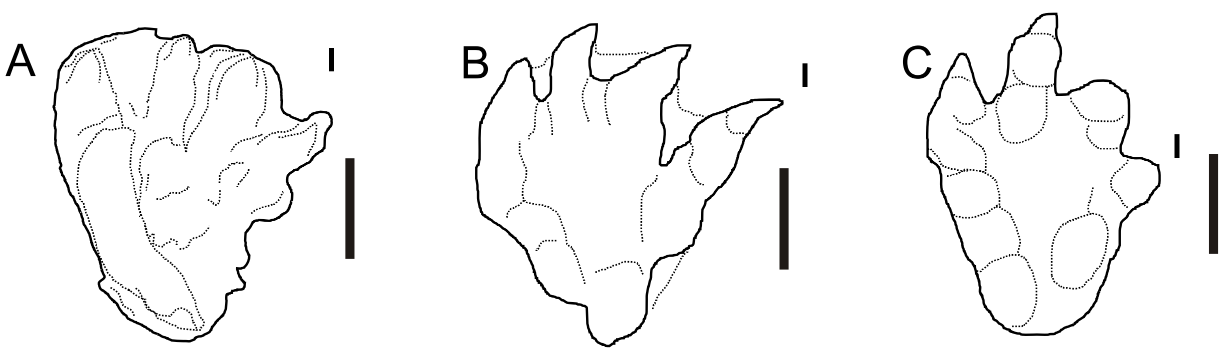

Fig. 9. Comparative silhouettes of sauropodomorph pes tracks (I – first digit)

A – cf. *Tetrasauropus* isp. from the Upper Hettangian of Poland; **B** – *Tetrasauropus* Ellenberger, 1972 from the Late Triassic–Early Jurassic of southern Africa (Lesotho); **C** – *Lavinipes* Avanzini, Leonardi et Mietto, 2003 from the Lower Jurassic of northern Italy; scale bar – 10 cm (modified from Ellenberger, 1972; Avanzini et al., 2003) tracks of small and medium theropods (*Grallator* isp., *Anchisauripus* isp.), large basal sauropodomorph (cf. *Tetrasauropus* isp.) and an ornithischian dinosaur (cf. *Anomoepus* isp.), which probably represent early thyreophorans. No typical swimming traces (scratches) from either dinosaurs, crocodiles, turtles or fishes have so far been found in the Zapniów exposure.

During Late Hettangian times, the area represented marginal marine settings, located between the emerged land and the shallow epicontinental sea (Fig. 4). It was area with shallow lagoons, marshes, barriers and other ecosystems of marginal-marine coastal plain and attracted the dinosaur biota. In the Zapniów section dinosaur tracks occur in foreshore – barrier lithofacies, which probably represented a environment frequented by these animals for communication (likely long-shore wandering) and feeding opportunities. However, as has been demonstrated above, the more detailed study of these tracks presents some difficulties linked to the preservation of individual tracks and longer trackways.

Relatively short, less than 2 Myr (Cohen et al., 2015) Hettangian age is important in terms of dinosaur evolution as the beginning of this age was associated with a rapid radiation of this group. Numerous workers (e.g., Benton, 1986; Hunt, 1991; Olsen et al., 2002; Brusatte et al., 2008, 2010) have drawn attention to a relatively sudden increase in dinosaur abundance, diversity and body size during the latest Triassic-earliest Jurassic and this event is geographically widespread and not lithofacies correlated, so probably it is a record of evolutionary events connected with terminal Triassic extinction of therapsid-pseudosuchian faunas on the lands. Indeed, the Hettangian track assemblage from the Holy Cross Mountains (Fig. 11) reflects notable dinosaur diversity (Gierliński and Pieńkowski, 1999; Niedźwiedzki, 2011; Pieńkowski et al., 2014), both in continental and marginal-marine settings. Moreover, the rich dinosaur track assemblages register an earlier appearance of certain dinosaur groups and more rapid dinosaur evolution than it was believed, based on North American reports (i.e., Lucas, 1996; Lockley et al., 1998; Padian, 1989 – see discussion in Gierliński and Pieńkowski, 1999). Markedly, alluvial plain and barrier-lagoon, deltaic environments registered different dinosaur track assemblages (Fig. 11). Both large early sauropods and giant theropods are missing in the latter (Gierliński and Pieńkowski, 1999), although bit smaller basal sauropodomorphs (trace-makers of cf. *Tetrasauropus* isp.) and theropods (not bigger than *Dilophosaurus*) as well as juvenile sauropods (Gierliński, 1997; Niedźwiedzki and Pieńkowski, 2004) could occasionally invade these marginal-marine plains. Discerning factor was substrate stability, discouraging bigger and heavier animals, and low-rise vegetation, favouring specialized, low browsing ornithischians (early thyreophorans), which were trace-makers of *Anomoepus* and *Moyenisauropus* tracks. Small to medium-sized theropods would follow these herbivorous dinosaurs, leaving *Anchisauripus* and *Grallator* tracks. Interestingly, the earliest Hettangian tetrapod assemblages of the Holy Cross Mountains contain, besides the most common dinosaur tracks, ichnites of basal crocodylomorphs, early mammals and other small reptiles (probably lepidosauromorphs), while marginal-marine plains with deltas, barrier-lagoon environments are dominated by dinosaur tracks. This showing wide environmental adaptation of dinosaurs in their early evolutionary history. No tracks from large theropod dinosaurs have so far been found at the Zapniów locality, but tracks from relatively large theropods (*Kayentapus* isp.) are known from the nearby Gliniany Las tracksite of a similar geological age (Gierliński and Niedźwiedzki, 2005), and it is likely that larger theropod tracks will turn up during future research and excavations in the Przysucha Ore-bearing Formation sites located near Zapniów.

This diversity of early dinosaur tracks in the Hettangian formations of the Holy Cross Mountains reflects a diverse fauna,

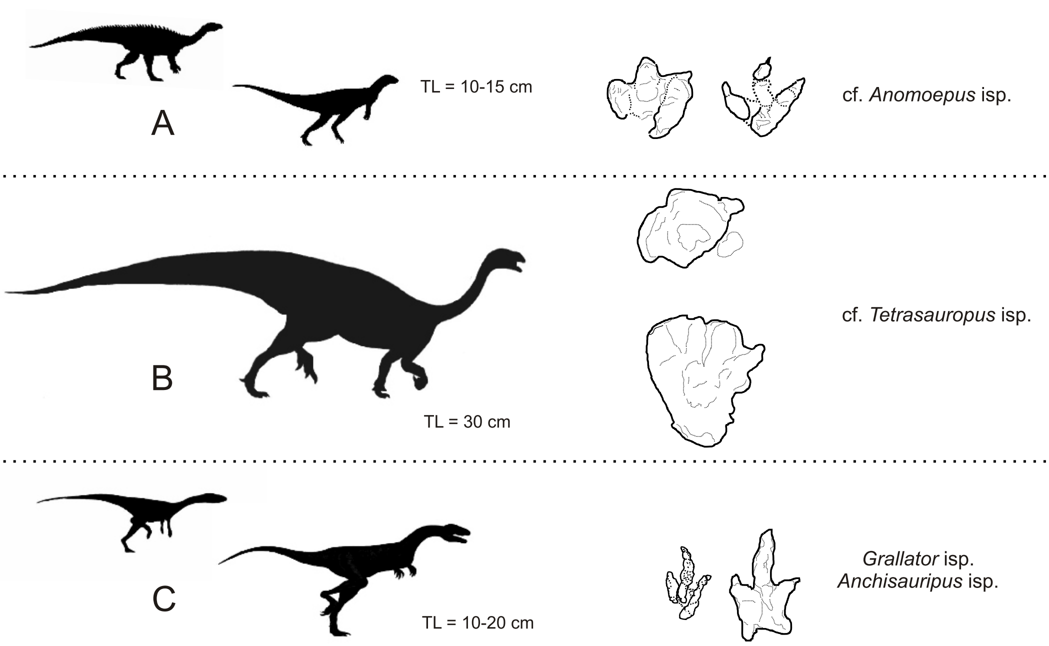

Fig. 10. Dinosaur ichnotaxa of the Przysucha Ore-bearing Formation (Upper Hettangian) of Zapniów, Holy Cross Mountains, Poland

Trackmakers: **A** – early ornithischians (possibly thyreophorans), **B** – sauropodomorph, **C** – small to medium-sized theropods; TL – total length of tracks

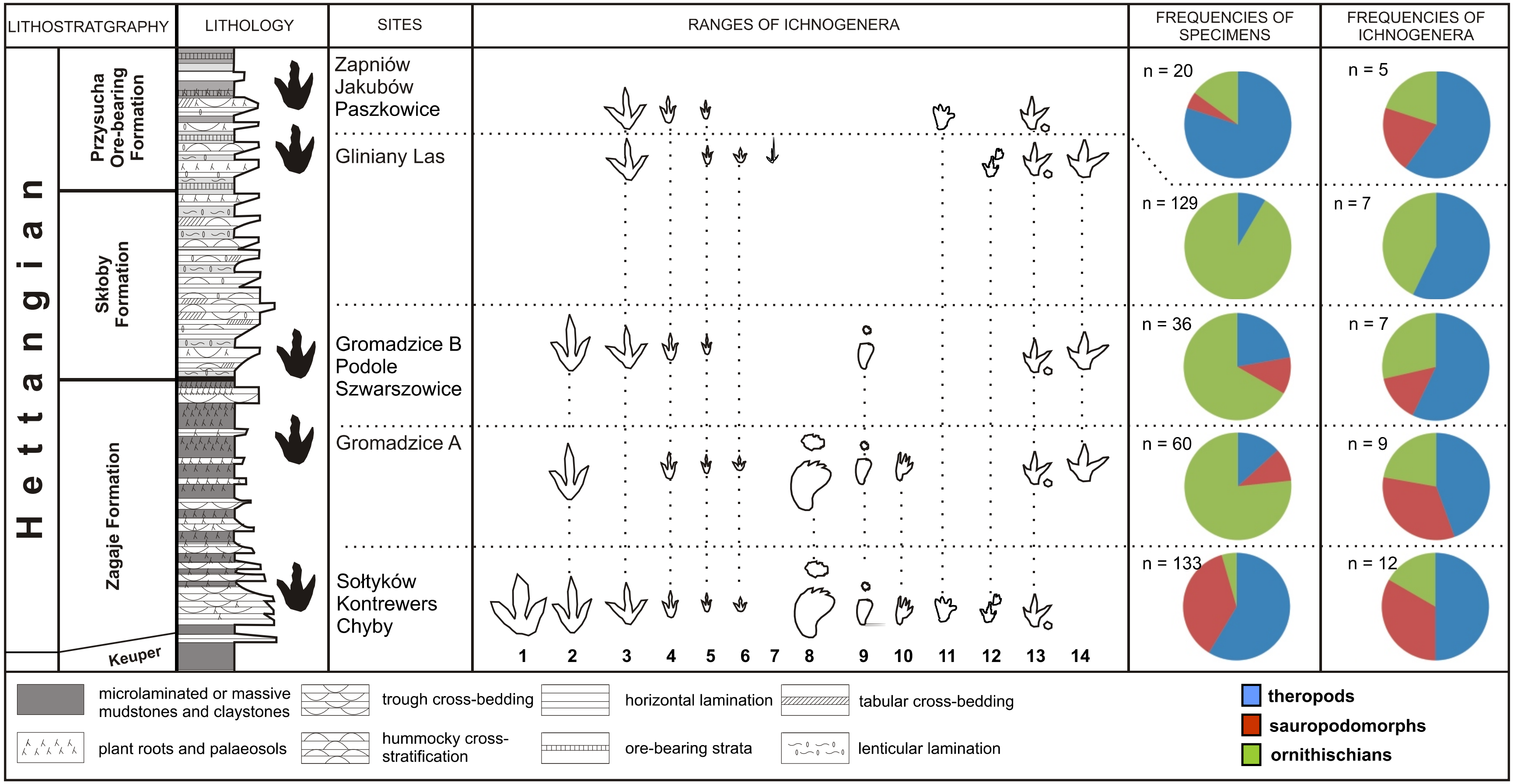

Fig. 11. Stratigraphic positions, ranges and frequencies of dinosaur tracks in the generalized lithological profile of the Lower to Upper Hettangian (Lower Jurassic) of the Holy Cross Mountains, Poland (based on Pieńkowski, 2004; Niedźwiedzki et al., 2009; Niedźwiedzki, 2011)

1 – gigantic theropod tracks cf. *Megalosauripus* isp.; 2 – large theropod tracks cf. *Eubrontes* isp./cf. *Kayentapus* isp.; 3 – large theropod tracks *Kayentapus* isp.; 4 – medium-sized theropod tracks *Anchisauripus* isp.; 5 – small theropod tracks *Grallator* isp.; 6 – cf. *Stenonyx* isp.; 7 – small bird-like tracks *Plesiornis* isp.; 8 – large sauropodomorph tracks; 9 – small sauropodomorph tracks; 10 – sauropodomorph tracks cf. *Otozoum* isp.; 11 – sauropodomorph tracks cf. *Tetrasuropus* isp.; 12 – small ornithischian tracks cf. *Delatorrichnus* isp.; 13 – medium-sized ornithischian dinosaur tracks *Anomoepus* isp./*Moyenisauropus* isp.; 14 – large-sized ornithischian dinosaur tracks *Moyenisauropus* isp.

which is still poorly known based on osteological discoveries (see Niedźwiedzki, 2011). This makes the ichnoassemblage from the Przysucha Ore-bearing Formation an important window into the Hettangian dinosaur-dominated ecosystem.

CONCLUSIONS

The combined dinosaur ichnofauna of Zapniów consists of tracks of at least two theropods, a sauropodomorph and early ornithischian, possibly thyreophoran. This site reveals a coastal dinosaur track assemblage and confirms the existence of the characteristic Lower Jurassic dinosaur ichnofacies (Gierliński and Pieńkowski, 1999; Niedźwiedzki and Pieńkowski, 2004), dominated by small-medium sized theropods and ornithischians. Palaeoecologically the occurrence of cf. *Anomoepus* isp. in marginal marine strata supports former hypotheses (Gierliński and Pieńkowski, 1999; Gierliński et al., 2009) that ornithischian dinosaurs preferred coastal environments and low-rise vegetation. In addition, *Anchisauripus* isp. trackways from tracksite C indicating trotting gaits of medium-sized theropods. The Zapniów ichnoassemblage enriches our knowledge about dinosaur communities in the Late Hettangian, adding medium-sized sauropodomorph as a further component. These finds confirm a high phylogenetical diversity of dinosaurs, reached as early as in the Hettangian age. The Late Hettangian dinosaur communities were well established and determined by environmental factors.

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