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Pterosaur tracks from the early Kimmeridgian intertidal deposits of Wierzbica, Poland

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In the early Kimmeridgian (*hypselocyclum* Zone) tidal flat carbonate deposits cropping out in the large Wierzbica quarry at northern slope of the Holy Cross Mountains (20 km south of the town of Radom), characteristic *Pteraichnus* sp. tracks have been found. These tracks are assigned to pterosaurs and represent the first pterosaur ichnites found in Poland. Seven specimens of pterosaur tracks (*pes* and *manus* prints) are described, although no trackway can be observed. The manual prints are asymmetric, digitigrade and tridactyl. The pedal prints are elongate, symmetrical, plantigrade and functional-tetradactyl. Presence of pterosaur tracks point to subaerial conditions and supports the view that the Late Jurassic land, situated in Ukraine and Eastern Poland, temporarily extended to the northern part of the Holy Cross Mountains area.

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INTRODUCTION

The subject of this paper is one of the most recent discoveries from the Wierzbica quarry in the northern slope of the Holy Cross Mountains, Poland (Fig. 1), where seven specimens of Pteraichnidae *manus* and *pes* prints have been found. Current discovery in Wierzbica adds to the recent years expansion of the vertebrate tracks finds in the Late Jurassic carbonates of the Holy Cross Mts. region, summarized by Gierliński (2004).

Stokes (1957) described the first pterosaur trackways from the Middle-Late Jurassic marine coastal deposits of Arizona, assigned to the Salt Wash Member of the Upper Jurassic Morrison Formation. Padian and Olsen (1984) disputed Stokes' interpretation and argued that the trackways were made by a small crocodilian (see also Padian, 2003).

New discoveries of the Middle-Late Jurassic and Cretaceous *Pteraichnus*-like tracks (Lockley and Hunt, 1995; Lockley *et al*., 1995, 1996, 1997, 2001; Mazin *et al*., 1995; Lockley and Mickelson, 1997; Wright *et al*., 1997; Calvo and Moratalla, 1998; Lockley, 1999; Meijide-Calvo and Fuentes Vidarte, 1999; Garcia-Ramos *et al*., 2000, 2001; Lockley and Meyer, 2000; Pascual Arribas and Sanz Perez, 2000; Calvo and Lockley, 2001; Meijide-Calvo *et al*., 2001; Rodriguez de la Rosa, 2001; Hwang *et al*., 2002; Li *et al*., 2002; Stanford and Lockley, 2002; Mickelson *et al*., 2004) are now clearly interpreted as pterosaurian, not crocodilian (see also Bennett, 1997; Unwin, 1997, 2003). All these new finds provide evidence that pterosaur tracks are more abundant as ichnofossils in Jurassic and Cretaceous deposits than previously believed before and those tracks are often associated with the marine coastal palaeoenvironment.

So far, three ichnogenera of pterosaur tracks have been distinguished. *Pteraichnus* (*P. saltwashensis*) was proposed by Stokes (1957) for tracks from the Upper Jurassic Morrison Formation (Salt Wash Member) in the Carrizo Mountains, Arizona. Lockley *et al.* (1995) named a second ichnospecies, *P. stokesi* from the Jurassic Sundance Formation at Alcova Lake, Wyoming, and proposed also new ichnofamily, Pteraichnidae, later revised by Lockley *et al.* (2001). Since 1995 several other ichnospecies of *Pteraichnus* have been named (Pascual Arribas and Sanz Perez, 2000; Meijide-Calvo *et al*., 2001). Second and third ichnogenera were added to this ichnofamily with the identification of *Purbeckopus* (*P. pentadactylus*) from the Early Cretaceous Purbeck Limestone Formation of Dorset (Wright *et al*., 1997) and *Haenamichnus*

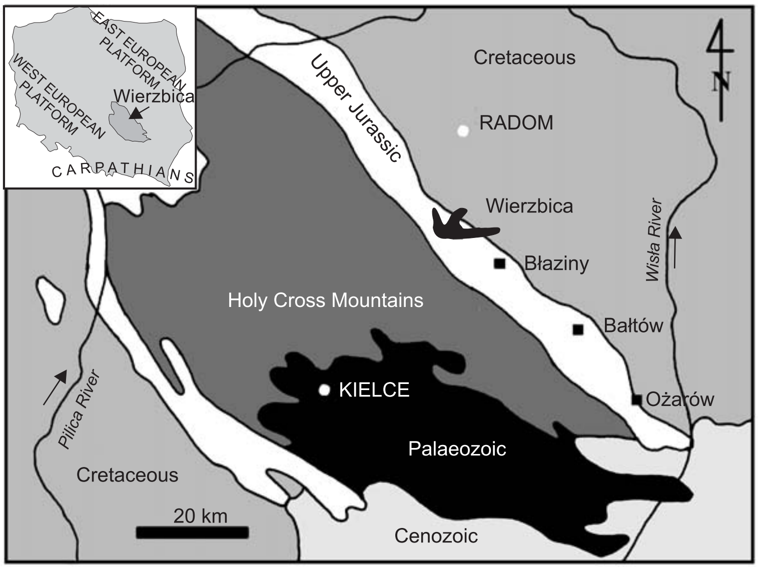

Fig. 1. Locality of Wierzbica quarry against a general geological background

The Late Jurassic tracksites of Wierzbica, Błaziny, Bałtów and Ożarów are marked

(*H. uhangriensis*) from the Late Cretaceous Uhangri Formation of South Korea (Hwang *et al.*, 2002). Other pterosaur footprints, such as those from Crayssac (Mazin *et al.*, 1995), may differ from *Pteraichnus*, *Purbeckopus* and *Haenamichnus* but have yet to be formally named either at the ichnogenus or ichnospecies level.

GEOLOGICAL AND PALAEOENVIRONMENTAL BACKGROUND

In the abandoned Wierzbica quarry, situated 20 km south of town of Radom (Fig. 1), about 60 m of early Kimmeridgian carbonate rocks is exposed. These carbonates have been described by Gutowski (1998, 2004) as the Wierzbica Oolite and Platy Limestones (informal lithostratigraphic unit). According to Gutowski (2004), this succession represents a shallowing upward sedimentary cycle deposited on a carbonate ramp that developed on the SW margin of the East European Platform. The shallowing upward succession represents (from the bottom to the top): open shelf (open ramp) deposits, oolitic barrier, protected bay, hypersaline lagoon and tidal flat (Gutowski, 2004). This succession is capped by the hardground surface, which ends the sedimentary cycle. Overlying marls, limestones and coquina beds represent the beginning of the next cycle associated with a rise in relative sea level (Gutowski, 2004). The pterosaur footprints occur in tidal flat deposits, in the uppermost part of the sedimentary cycle (Fig. 2).

Shallowing-upward oolitic sedimentary cycles are common in ancient and recent carbonate shelf successions (Powers, 1962; Bishop, 1968; Purser, 1972; Wright and Burchette, 1996; Gutowski, 1998, 2004; Pieńkowski and Gutowski, 2004). The succession of tidal flats (interpreted by Gutowski, 2004), capping the shallowing-upward cycle, has been studied in details (Fig. 2A). Five facies associations have been distinguished:

(1) grey laminated marls — attributed to the lagoonal/lower tidal flat facies, above 2 m thick;

(2) white/grey heteroliths (flaser, wavy and lenticular bedding) composed of micritic limestones/marls (slack water conditions) and predominantly oolitic-organodetrital grainstones (current conditions; Fig. 2B, D), attributed to a mixed tidal flat/intertidal environment, thickness about 2 m;

(3) laminated grey/brownish clayey marls. Micropalaeontological investigations (J. Smoleń, pers. comm.) revealed strongly impoverished microfauna, composed of scarce foraminifera (*Spirilina* sp. and *Lenticulina* sp.), rare ostracods and broken echinoid spikes. Additionally, coated grains and plant debris have been found. Collectively, these finds point to an extremely shallow, restricted, turbulent environment, which is in perfect accordance with an intertidal environment (Fig. 2E), the upper tidal flat, thickness 0–0.2 m;

(4) cross-bedded, greenish/grey grainstones with redeposited shells, glauconite, arenaceous grains concentrated at the bottom and large floral debris (Fig. 2C, F), attributed to the tidal channel, thickness 0–1.1 m;

(5) white, pelitic limestones and marls with disturbed bedding, numerous *Spongeliomorpha* (= *Thalassinoides*) burrows, rhizoids, representing the tidal flat deposits, eroded from the top and capped with hardground surface, thickness 0–3 m.

The palaeoenvironmental interpretation of facies association (2) as tidal flat (Gutowski, 2004) is further confirmed by presence of vertically accreted tidal bundles (Kreisa and Moiola, 1986), each representing deposition in one tidal cycle. These bundles are not always regular, but in places their internal structure can be recognized. A tidal bundle is usually a several-centimetre thick couplet of oolitic-organodetrital limestone with cross lamination, resulting from the deposition of one ripple train. This grainstone is capped by a 1 mm to few centimeters thick marly drape (Fig. 2B, D), in which sometimes a more discrete fine-grained grainstone bed can be observed when the tidal bundle is thick enough. This feature indicates tidal dynamics characterized by a dominant current. Moreover, in the tidal complex (2) one can distinguish vertical repetition of bundles (wavy- and flaser-bedded), where thicker mud components seem to repeat regularly (Fig. 2D). Such “rhythms” are about 20 cm thick. Number of bundles in each rhythm is not easy to count precisely due to amalgamation and irregularities of many individual bundles, but one can count approximately about twenty–thirty bundles per rhythm. This would correspond to astronomical cyclicity of tides (neap–spring–neap tidal cyclicity; Fig. 2D). Neap tides are weaker, thus containing relatively more muddy (marly) components. Thicker tidal bundles with more oolitic-organodetrital limestones would correspond to spring periods. Similar tidal cyclicity was described by Tessier and Gigot (1989) in Miocene tidal deposits of Haute Provence (France).

Above these “rhythmites” a 20 cm thick, laterally discontinuous grey/brownish laminated marl layer (3) occurs (Fig. 2E). This layer is interpreted as an upper tidal flat deposit. Pterosaur footprints were left at the top this marl layer.

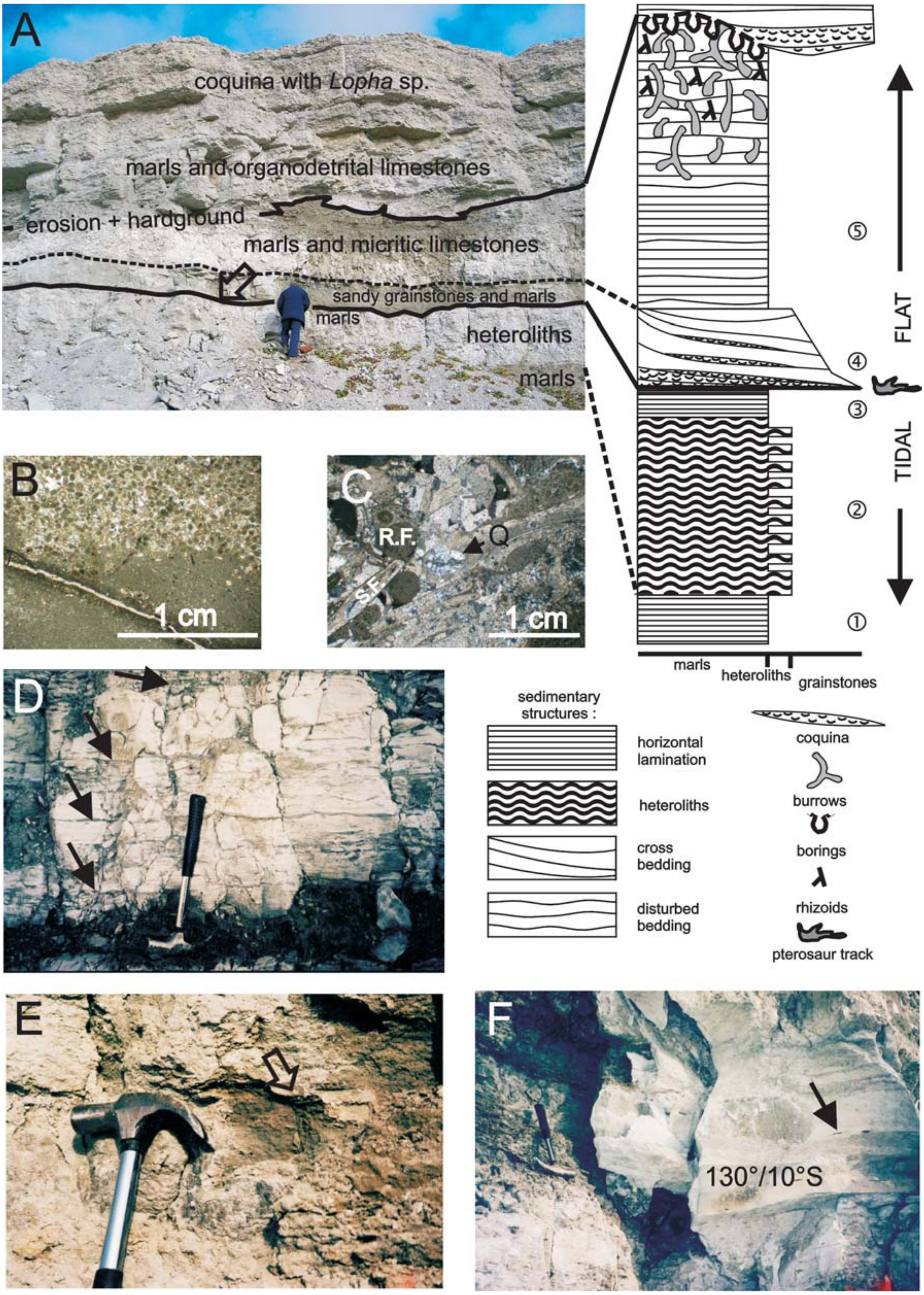

Fig. 2. The early Kimmeridgian Oolite and Platy Limestones exposed at the Wierzbica quarry, showing detailed geological section of tidal flat succession and consecutive succession of facies associations (1–5) with position of the pterosaur tracks marked at the bottom of facies association (4)

A — general view showing main lithofacies and boundaries; locality of pterosaur tracks is marked with arrow; **B** — microphotograph showing heterolithic facies association (2) and two subordinate microfacies: oolitic-organodetrital grainstone (upper part) representing current stage and marl representing slack water stage (lower part), note a more discrete fine-grained grainstone laminae can be observed within the marl; **C** — microphotograph showing grainstone of facies association (4), Q — quarts or quartzite grain, R.F. — carbonate rock fragment, S.F. — oyster shell fragment; **D** — detail of facies association (2) showing rhythmical sedimentation with repeating more abundant marly component (arrowed); **E** — marl layer of facies association (3) topping the heterolithic unit (2), the pterosaur tracks were left on top of this layer (arrowed); **F** — channelized facies association (4) represented by glauconitic, cross-bedded grainstones with plant debris (arrowed), strike and dip of dominating cross bedding set is 130°/10°S, pointing to the tidal channel ebb flow directed to SW

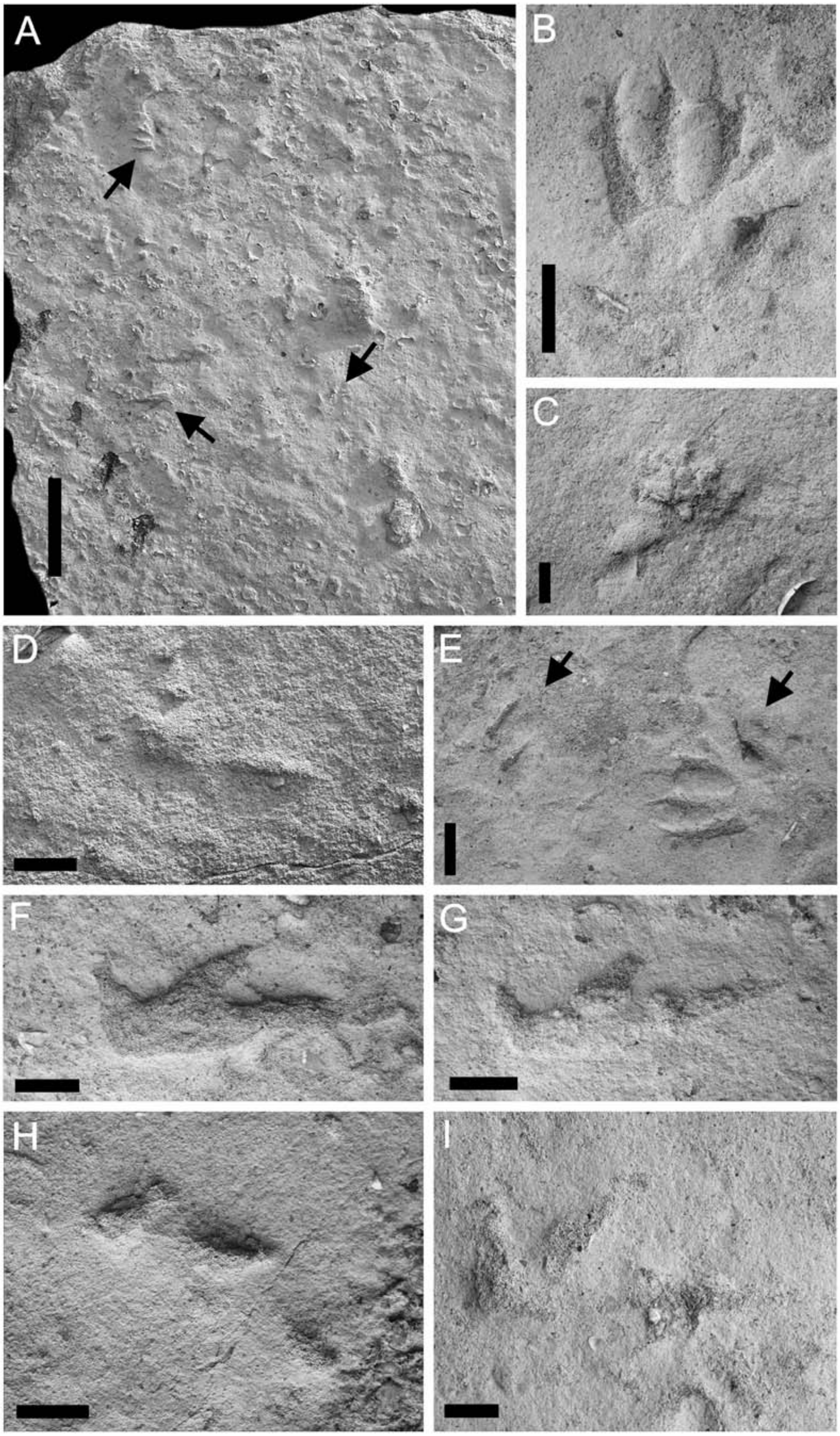

Fig. 3. ***Pteraichnus*** **sp. (pterosaur tracks) from the early Kimmeridgian Oolite and Platy Limestones, Wierzbica quarry**

A–**G** — specimen MP-Z KG/1, surface with tracks; **H**, **I** — uncollected specimens; **B**, **C**, **E** — casts of pedal prints with claw marks; **D**, **F**–**I** — casts of manual prints; scale bar: A — 10 cm; B, C, E — 1.5 cm; D, F–I — 1 cm (see also Fig. 4)

The footprints have been preserved as a positive hyporelief at the bottom of tidal channel deposits, which form the next facies (4). This facies was described by Gutowski (2004) as a wedging out layer of organodetritic marls with shell debris, quartz grains, carbonate rock fragments, glauconite and floral debris (Fig. 2A, F). The term "marl" can be assigned only to the uppermost part of the layer, while for the most part, particularly in the lower section of the layer, this rock should be assigned to grainstone composed of shell debris, quartz or quartzite grains and carbonate rock fragments (Fig. 2C). Gutowski (2004) noted that some of the floral remains (represented by cycadacean trunks) are up to 3 metres long and 40 cm in diameter. Cross bedding resulting from migration of sand waves and sand ripples, and channel fill is conspicuous: prevailing transport directions point to SW (about 130° strike, average 10–15° dip). This facies association (4) shows numerous internal erosional surfaces marked with shell debris, which are concentrated at the lower part. In the upper part of this complex the grain size diminishes and erosional features are rare. Interpretation of sedimentary processes for this upper part is that migration of bottom bed forms, associated with suspension fallout, prevailed. This clearly points to upward-diminishing energy of sedimentary processes. The whole facies association (4) represents a composite layer, resulting from channel migration, with upward decrease of current velocities. The channelized facies association (4) is situated within tidal flat deposits, which points to its tidal channel origin. Assuming a general palaeogeographical situation (with the sea located generally to the west and the land to the east), transport direction pointing to the SW allows interpretation of these channels as dominated by ebb currents.

The next facies association (5) is represented by white, pelitic limestones and marls with disturbed bedding, and is interpreted as a tidal flat system due to presence of rhizoids (Gutowski, 2004), and reveals of dinosaur footprints *Dinehichnus* sp. (Gierliński, 2004). Crustacean burrows *Spongeliomorpha* (= *Thalassinoides*) are common in this complex (for systematics see Fürsich, 1973; Schlirf, 2000). The whole facies association (5) is eroded from the top-creating erosional channels up to 1.5 m deep. The upper boundary of the complex is a hardground surface with numerous borings, except for the bottom of eroded channels (Gutowski, 2004). The hardground surface represents an erosion or non-deposition period in sedimentation.

DESCRIPTION OF PTEROSAUR FOOTPRINTS

Ichnofamily **Pteraichnidae** Lockley, Wright, Langston and West, 2000

Pteraichnus sp.

(Figs. 3 and 4)

Material. — Specimen MP-Z KG/1 (Fig. 3A), limestone slab from Wierzbica with five isolated natural casts of three *manus* and two *pes* prints, which is housed in geological collection of the town Przysucha; uncollected limestone slab from Wierzbica with two isolated natural casts of *manus* prints (specimen left in field).

Description. — *Pes* (Figs. 3B, C, E; 4A, B): *Pes* prints are longer than wider (prints are 35–45 mm long and 20–25 mm wide), symmetrical, plantigrade and functional-tetradactyl. Separation of the digits is conspicuous. *Pes* digit III is the longest, digit I is the shortest, and II and IV digits are intermediate and have a similar length. The length of digits are: I = 12–18 mm; II = 14–19 mm; III = 22–28 mm; IV = 20–24 mm (length relations of digits: I < II = I V < III). The angle between axes of digits I–IV is small (about 15–19°); also angle between axes of digits III–IV is relatively small (about 4–7°). The angle between digits: I–II = 5–7°; II–III = 4–5°; III–IV = 4–7°. Very small and thin claw marks are present at the tips of digits II–IV, and are well-preserved and clearly visible in specimens MP-Z KG/1A. The print of the sole area is relatively large and elongate, but in the studied specimens is poorly preserved.

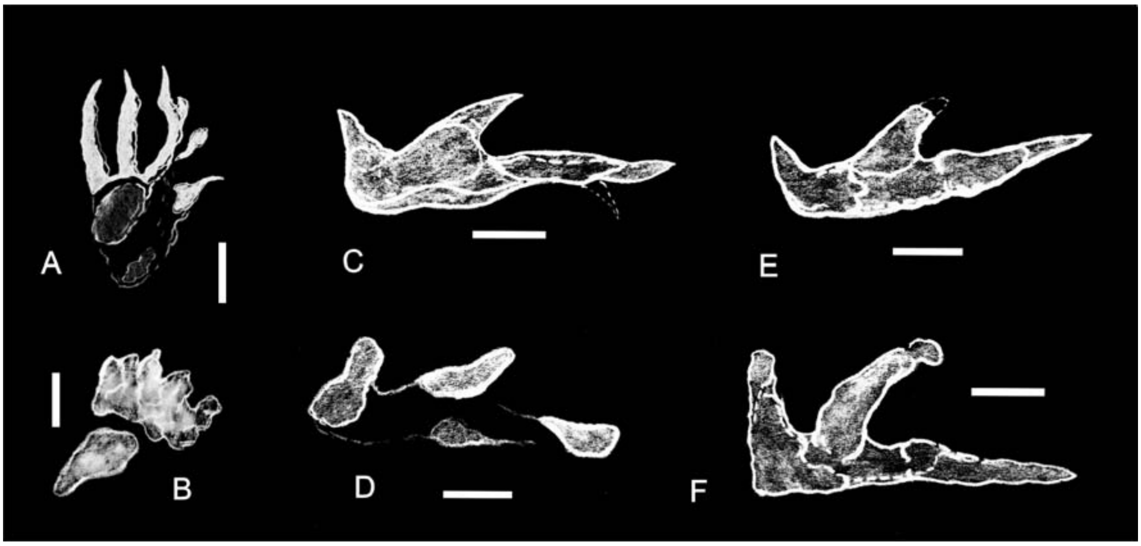

Fig. 4. ***Pteraichnus*** **sp. from the early Kimmeridgian Oolite and Platy Limestones in Wierzbica quarry**

A–**C**, **E** — specimen MP-Z KG/1; **D**, **F** — uncollected specimen; **A**, **B** — casts of the pedal prints; **C**–**F** — casts of the manual prints; scale bar: A, B — 1.5 cm; C–F — 1 cm

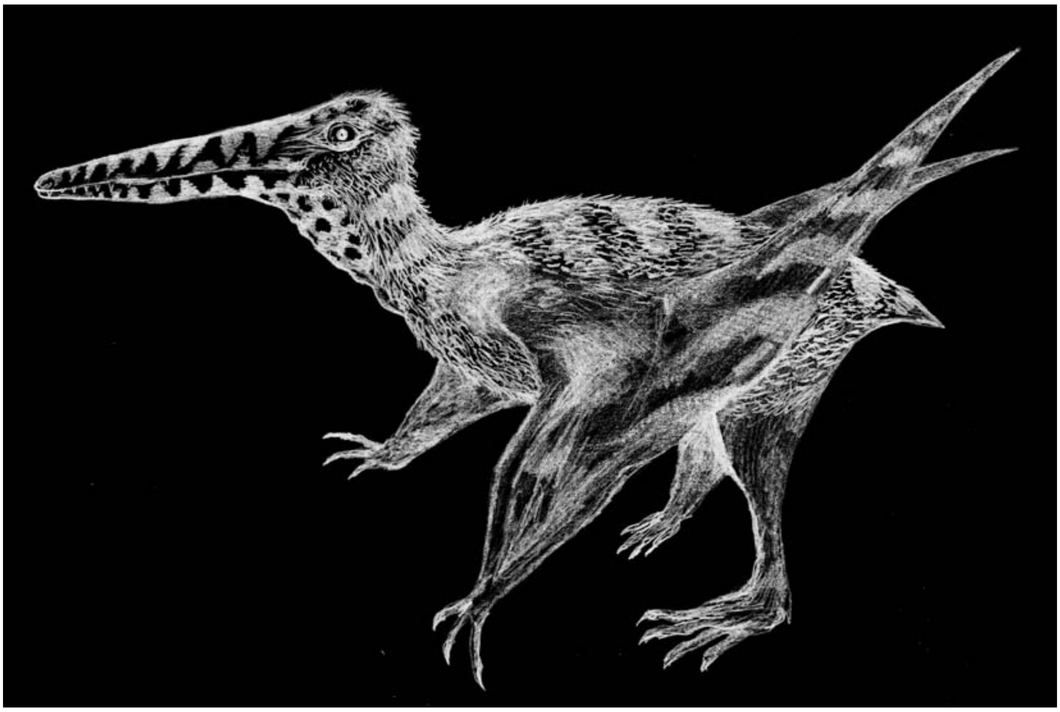

Fig. 5. Reconstruction of pterosaur posture while making the tracks (after Unwin, 1997, modified)

Manus (Figs. 3D, F–I; 4C–F): *Manus* prints are asymmetric, functional-tridactyl. Print of the *manus* specimen MP-Z KG/1C is 42 mm long and 25 mm wide. All three digits have very thin claw prints. The relatively short digit I is separated from digits II–III and turned outwards. Digit III is the longest. The length of digits: I = 6–12 mm; II = 8–20 mm; III = 10–25 mm (length relations of digits: I < II < III). The width of the digit group I–III equals 27–45 mm. The angle between the digits: I–II = 65–75°; II–III = 30–40°. The *manus* surface is about 2 times smaller than that of *pes*. The imprint of palm area is poorly preserved but is relatively large (in specimen MP-Z KG/1D it is 4 mm wide and 7 mm long). As argued by Unwin (1997, 2003), pterosaurs moved in quadrupedal plantigrade fashion (Fig. 5) and despite the apparent awkwardness of this type of gait it was reasonably efficient concerning terrestrial ability of pterosaurs.

CONCLUSIONS

Pteraichnus sp. tracks found in Wierzbica quarry show distinct pterosaur affinity. This find is coupled with detailed sedimentological studies, which proves that the imprints were left on a tidal flat. Most likely, this was one of environments frequented by pterosaurs. Similar behaviour is observed in modern birds, finding favourable feeding opportunities in this environment, as well as the safe resting places. Well documented association of described herein pterosaur tracks with the tidal flat deposits confirm supposed pterosaur preferences, which are shown by many other pterosaur tracks occurrences, where they are clearly associated with marine coastal facies (Lockley *et al*., 1996). On the other hand, the muddy-carbonate surface of the upper tidal flat provided an excellent medium for precise imprinting of delicate tracks made by a light animal. Even minute details of tracks, such as minute claw marks are visible, although postcontemporaneous erosion has slightly diminished the quality of imprints. A further favourable factor increasing tracks preservation potential was a quick burial of the imprints underneath tidal channel sediments. Most likely these tracks were left by a small pterodactylid or rhamphorhynchoid pterosaur, with wingspans of about 0.5 to 1 m.

Presence of subaerial structures, like rhizoids, pterosaur tracks and dinosaur footprints (Gierliński *et al*., 2001; Gierliński, 2004) in the lower Kimmeridgian strata of the northern slope of the Holy Cross Mountains clearly points to emersions at that time. The East European Land must have periodically extended far to the west, which was postulated by Gutowski (2004). Naturally, pterosaurs could leave their tracks anywhere on dry land, also on ephemeral shoals in the sea too. However, presence of detrital quartz and quartzite fragments, large wood fragments, as well as occurrence of dinosaur footprints in Wierzbica and Ożarów quarry situated some 75 km to the SE (Gierliński *et al*., 2001; Gierliński, 2004), prove that the discussed pterosaur tracks were rather left on a shore the East European Land.

Abbreviations. MP-Z KG — Museum of Przysucha, Geological Collection at Zapniów.

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