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Large Chirotheriidae tracks in the Early Triassic of Wióry, Holy Cross Mountains, Poland

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ABSTRACT:

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Very large chirotheriid tracks have been discovered in the Early Triassic Wióry Formation (=Labyrinthodontidae and Hieroglyphic Beds), middle part of the Middle Buntsandstein, exposed at Wióry in the northeastern part of the Holy Cross Mountains (central Poland). Hitherto, six small and medium-sized chirotheriid tracks from the Wióry locality have been described. In the present paper two ichnotaxa are proposed: *Synaptichnium senkowiczowae* ichnosp. nov. and *Brachychirotherium kalkowensis* ichnosp. nov. Their presumed trackmakers, large Early Triassic (Olenekian) Archosauriformes (Proterosuchidae, Erythrosuchidae), about 5-7 m long, are unknown from the osteological record of this age worldwide. The newly described ichnotaxa represent the oldest known record of large chirotheriid tracks in the Middle Buntsandstein of Poland. The presence of large chirotheriid tracks in the upper part of the Early Triassic deposits is very important for the understanding of the evolution and radiation of early Archosauromorpha, as well as for reconstructing Early Triassic terrestrial palaeoecosystems.

Key words: Archosauromorpha, Vertebrate tracks, Chirotheriidae, Buntsandstein, Lower Triassic, Poland.

INTRODUCTION

The assemblage of vertebrate tracks from the Wióry tracksite, Holy Cross Mountains, Poland (Text-fig. 1) is the richest and most diverse in the Middle Buntsandstein of Europe (PTASZYŃSKI 2000a). Hitherto, it was the subject of two papers (FUGLEWICZ *& al.* 1990; PTASZYŃSKI 2000a) and three short communications (FUGLEWICZ *& al.* 1981; RDZANEK 1986; PTASZYŃSKI & NIEDŹWIEDZKI 2004c). Ichnotaxa identified at this site to date comprise eleven ichnospecies representing seven ichnogenera: *Capitosauroides* HAUBOLD, 1971; *Brachychirotherium* BAURLEN, 1950; *Isochirotherium* HAUBOLD, 1971; *Synaptichnium* NOPCSA, 1923; *Procolophonichnium* NOPCSA, 1923; *Rhynchosauroides* MAIDWELL, 1911; and *Prorotodactylus* PTASZYŃSKI, 2000. This paper contains a detailed study of the largest chirotheriid tracks ever found in the Wióry Formation. Hitherto, six small and medium-sized ichnospecies belonging to the ichnofamily Chirotheriidae have been described from Wióry: *Brachychirotherium hauboldi* (PTASZYŃSKI, 1990); *B. wiorense* PTASZYŃSKI, 2000; *Isochirotherium sanctacrucense* PTASZYŃSKI, 1990; *I. gierlinskii* PTASZYŃSKI, 2000; *Synaptichnium chirotheroides* PTASZYŃSKI, 1990; *S. kotanskii* PTASZYŃSKI, 2000.

The large exposure at Wióry resulted from the construction of the water barrage and reservoir on the Świślina River in 1979–2005. Vertebrate tracks were first discovered at this site by one of us (T.P.) in the autumn of 1980. Subsequent collections were made by Kazimierz RDZANEK and by both of us. The largest collection of tracks is deposited in the Museum of Nature and Technology at Starachowice. Smaller collections are also housed in other institutions (see PTASZYŃSKI & NIEDŹWIEDZKI 2004c). A number of specimens have been gathered by amateur geologists.

It has already been noted (FUGLEWICZ & *al.* 1990; PTASZYŃSKI 2000a) that the track assemblage from Wióry also contains rare, incomplete, deformed or poorly preserved tracks that are much larger than the largest well documented ichnospecies, *Brachychirotherium hauboldi* and *B. wiorense* (FUGLEWICZ & *al.* 1990, pls 5.3, 5.4; 10.2; 12.1). Some have been described in open nomenclature as *Isochirotherium* sp. (FUGLEWICZ & *al.* 1990) and ? *Isochirotherium* sp. (PTASZYŃSKI 2000a). They could also partly represent ichnospecies of *Brachychirotherium*. Other large specimens of tetrapod tracks, in part representing swimming traces, have also been observed (ichnogenus *Characichnos* WHYTE & ROMANO 2001).

The present paper supplements previous studies, providing a description of the paleoichnological collection deposited by Kazimierz RDZANEK at the Museum of Nature and Technology at Starachowice (abbreviated MPTS) and new material collected by the authors during the past seven years (deposited at the Museum of Nature and Technology in Starachowice, and the Geological Museum of the Holy Cross Branch of the Polish Geological Institute in Kielce – abbreviated Muz. PIG OS).

Measurements were made, with only few exceptions, on original specimens. The method of measurement corresponds to that in HAUBOLD (1971), DEMATHIEU (1985), LEONARDI (1987), and PTASZYŃSKI (2000a).

GEOLOGICAL SETTING

The geological succession exposed in Wióry is composed of sandstones, mudstones and clay-

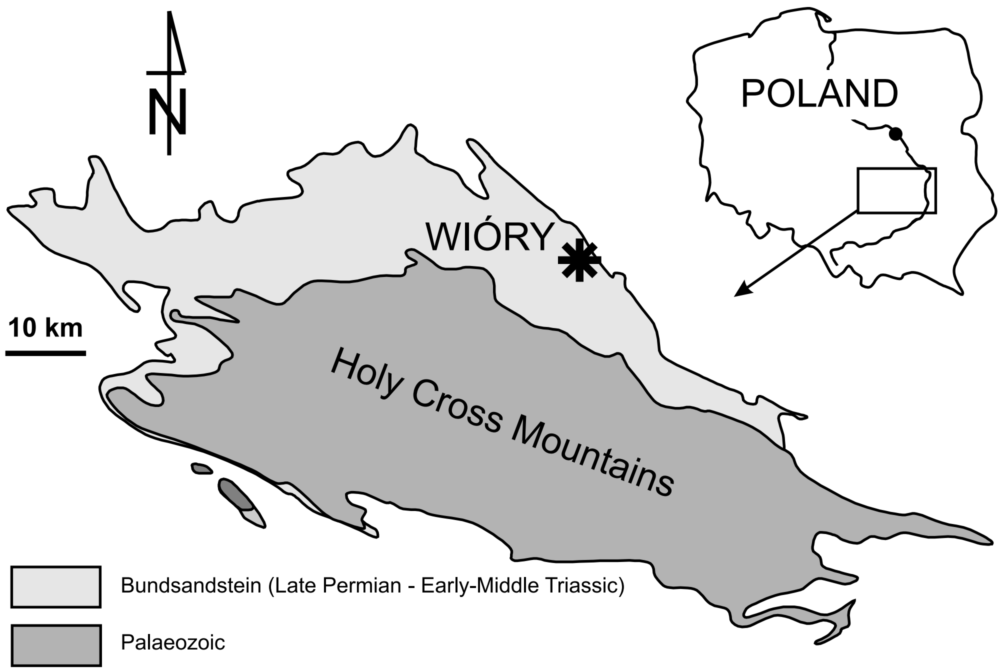


Fig. 1. Location of the Wióry tracksite in the Holy Cross Mountains, Poland

stones representing channel and floodplain braided/meandering river system (MADER & RDZANEK 1985; FUGLEWICZ & *al*. 1990). This succession, referred to as the Wióry Formation by KULETA & NAWROCKI (2000), consists of the Labyrinthodontidae and Hieroglyphic Beds (*sensu* SENKOWICZOWA 1970), which have been correlated with the so-called *Gervillia* Beds (Goleniawy Formation of KULETA & NAWROCKI 2000) of the lower Middle Buntsandstein in a regional lithostratigraphical scheme. The Wióry Formation yields numerous sedimentary structures, plant remains, isolated vertebrate bones (mostly temnospondyl remains), conchostracan carapaces, and diverse invertebrate trace fossils (MADER & RDZANEK 1985; MACHALSKI & MACHALSKA 1994; FUGLEWICZ & *al*. 1990; PTASZYŃSKI 2000a; RDZANEK 1999).

The identification of the conchostracan crustacean *Magniestheria deverta* (NOVOZHILOV, 1946) in mudstone and silstone intercalations allows the Wióry Formation to be assigned to the early Spathian of the Olenekian Stage (see BACHMANN & KOZUR 2004; KOZUR 2005; KOZUR & BACHMANN 2005 and earlier papers; see also PTASZYŃSKI & NIEDŹWIEDZKI 2002, 2004b, 2006).

The vertebrate ichnoassemblage described from the Wióry Formation is comparable with that known from the Detfurth Sandstein of the Detfurth Formation exposed near Wolfhagen (Germany, North-Hessen) and with that from the lower Hardegsen Formation (Hardegsen-Abfolge 1) cropping out near Gieselwerder (FICHTER & LEPPER 1997; FICHTER & KUNZ 2004); all also Spathian in age (BACHMANN & KOZUR 2004; KOZUR 2005; KOZUR & BACHMANN 2005).

PALAEONTOLOGICAL DESCRIPTION

Ichnofamily Chirotheriidae ABEL, 1935
Ichnogenus *Synaptichnium* NOPCSA, 1923

Synaptichnium senkowiczowae ichnosp. nov. (Text-figs 2, 3, ?6 B, E, H-J, L-O)

HOLOTYPE: MPTS 2612A, right pes imprint (Text-figs 2A, 3A)

TYPE LOCALITY: Wióry near Ostrowiec Świętokrzyski, northeastern margin of the Holy Cross Mountains, Poland.

TYPE HORIZON: Wióry Formation, lower part of the Middle Buntsandstein, Early Triassic, Olenekian, early Spathian.

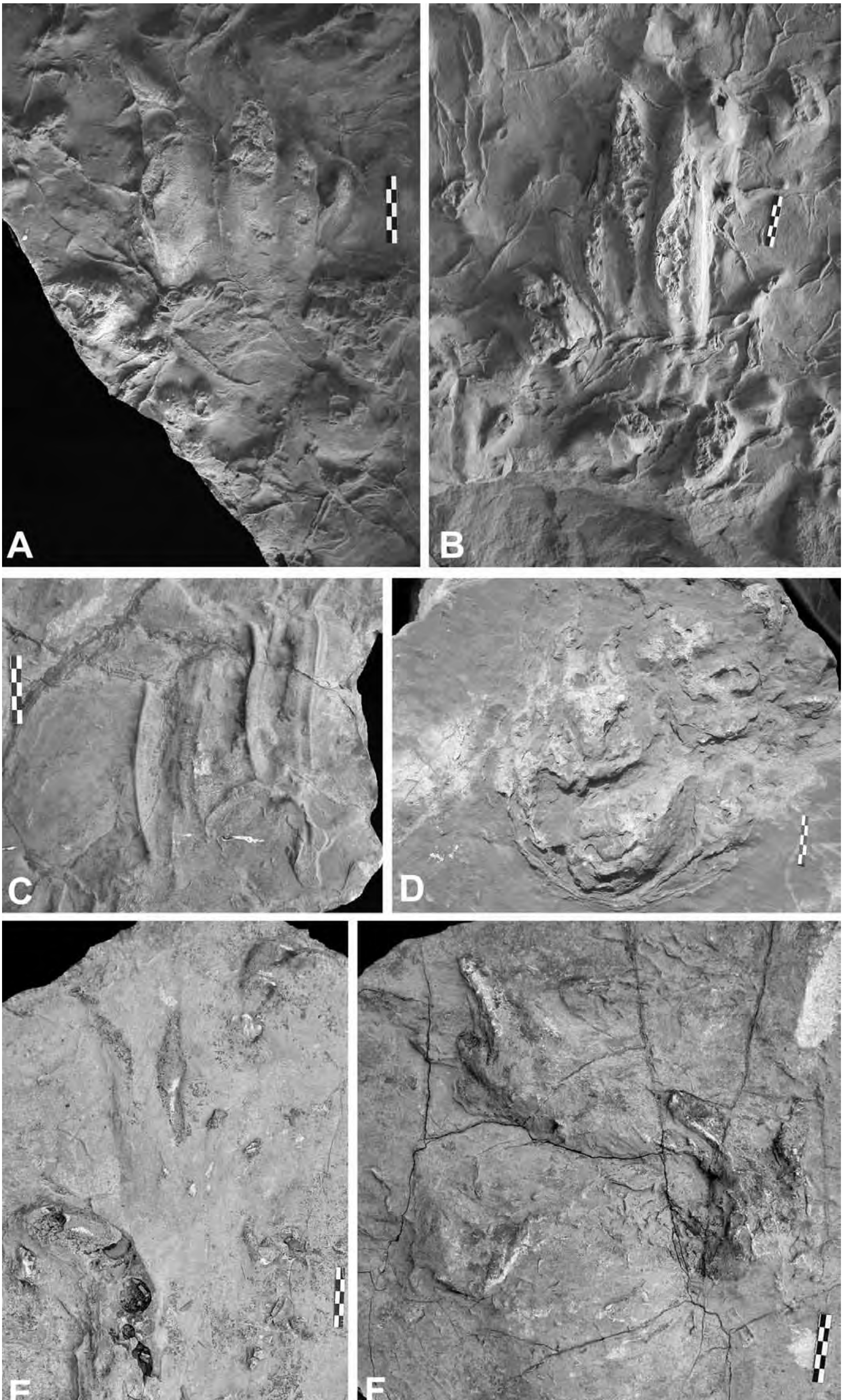
DERIVATION OF THE NAME: In honour of Professor Hanna Senkowiczowa, expert on the Polish Triassic.

DIAGNOSIS: Large, morphologically typical *Synaptichnium* with pes imprint up to 30 cm long. Pes digit proportions: IV>III>II>I (IV and III of similar length). Low value of the cross axis angle: 70°. Digit V relatively long and narrow. Manus imprints are 1.5 times smaller than pes ones (in the material studied the former are usually poorly preserved).

MATERIAL: MPTS 2611, fragmentary trackway (Text-fig. 2B – pes imprint from this trackway); MPTS 2612B, set of pes and manus imprints (Text-fig. 6N); MPTS 2613, left pes imprint (Text-figs 2D, 3B); Muz. PIG OS-220/256, left pes imprint (only digits I–IV visible, Text-fig. 6O); Muz. PIG OS-220/253 (plaster cast), specimen identified in a large slab with poorly preserved tracks (also with sets of pes and manus imprints – Text-figs 2F, 3D) forming possible fragmentary trackway (one of them – Text-figs 2C, 3C shows left pes features); Muz. PIG OS-220/255 (plaster cast), poorly preserved pes imprint (Text-fig. 6H); Muz. PIG OS-220/257, poorly preserved set of pes and manus imprints (Text-fig. 6J); MPTS 2614, right pes imprints (Text-fig. 6L); Muz. PIG OS-220/258 (plaster cast), left pes imprint (Text-fig. 6I); uncollected specimens, set of pes and manus imprints (Text-figs 2E, 3E). Poorly preserved material: uncollected specimens, partially preserved pes imprints (Text-fig. 6B, E, M).

DESCRIPTION

Trackway: Fragmentary and problematic trackways have been identified on slabs: MPTS 2611 and MPTS 2612B. A poorly preserved trackway, which was measured but not collected, was found on a slab in the field (Text-fig. 3F). A few sets of pes and manus imprints (Muz. PIG OS-220/257, and field observations) have also been found. Unfortunately, in most cases the trackway features are difficult to assess. The fragmentary trackway MPTS 2611, another fragmentary trackway MPTS 2612B, and the


A
B
C
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F

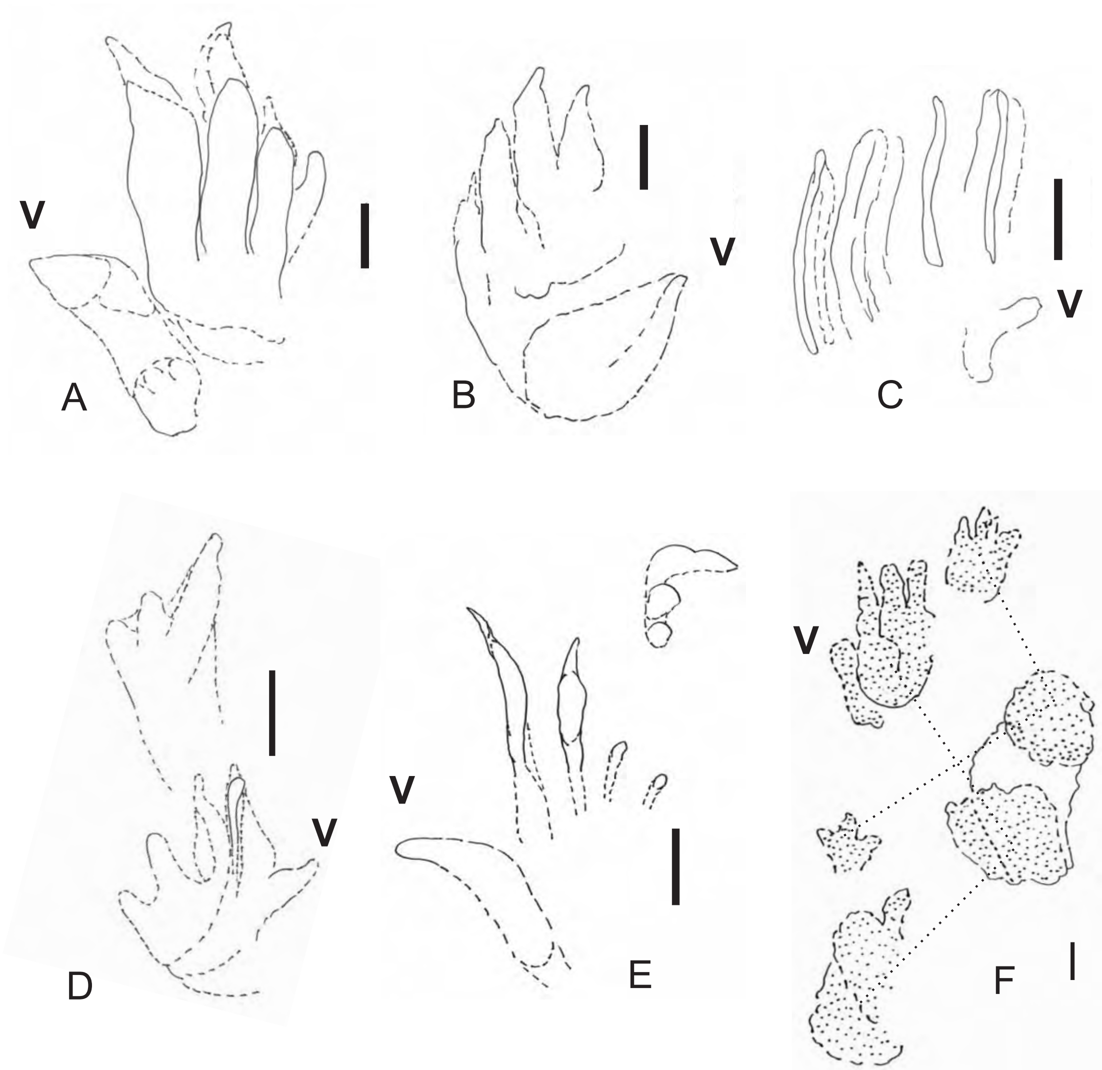


Fig. 3. *Synaptichnium senkowiczowae* ichnosp. nov. **A** – MPTS 2612A, holotype. **B** – MPTS 2613. **C.** Muz. PIG OS-220/253. **D**, **E** – Right and left set of pes and manus imprints (field observation). **F** – Fragmentary preserved trackway (field observation). Scale bars 5 cm

uncollected poorly preserved trackway (Text-fig. 3F) seem to have originated from the same track-bearing surface. In the uncollected trackway (Text-fig. 3F) the pes stride attains about 73 cm, oblique pace 53 and 52 cm, width of the trackway 36 cm, and the pace angulation about 88°. Similar values are found in the fragmentary trackway MPTS 2612B and MPTS 2611. Measurements of three imprints (possibly forming consecutive pes imprints of the same trackway) of MPTS 2611, show the stride 70 cm, oblique pace 58 cm and 46 cm, width of the trackway 38 cm, and pes pace angulation about 80°. The most characteristic features are the low value of the pace angulation and the large trackway width. The pes imprints diverge from the midline at a low angle. The manus axes are almost parallel to the pes ones.

Pes imprints: The most completely preserved specimen, the holotype MPTS 2612A (Text-figs 2A, 3A), is an imprint 29 cm long and 24 cm wide, only slightly deformed by the sliding movement (the largest imprint observed in the field was 33 cm long). The digit group I–IV, 20 cm long and 18 cm wide, shows digit length proportions IV>III>II>I. Of these,

Fig. 2. *Synaptichnium senkowiczowae* ichnosp. nov. (A – left and B-D – right pes imprints) E, F – set of pes and manus imprints). **A** – MPTS 2612A, holotype. **B** – MPTS 2611. **C** – Muz. PIG OS-220/253 (plaster cast). **D** – MPTS 2613. **E**, **F** – Uncollected material (field observation). Scale bars 5 cm

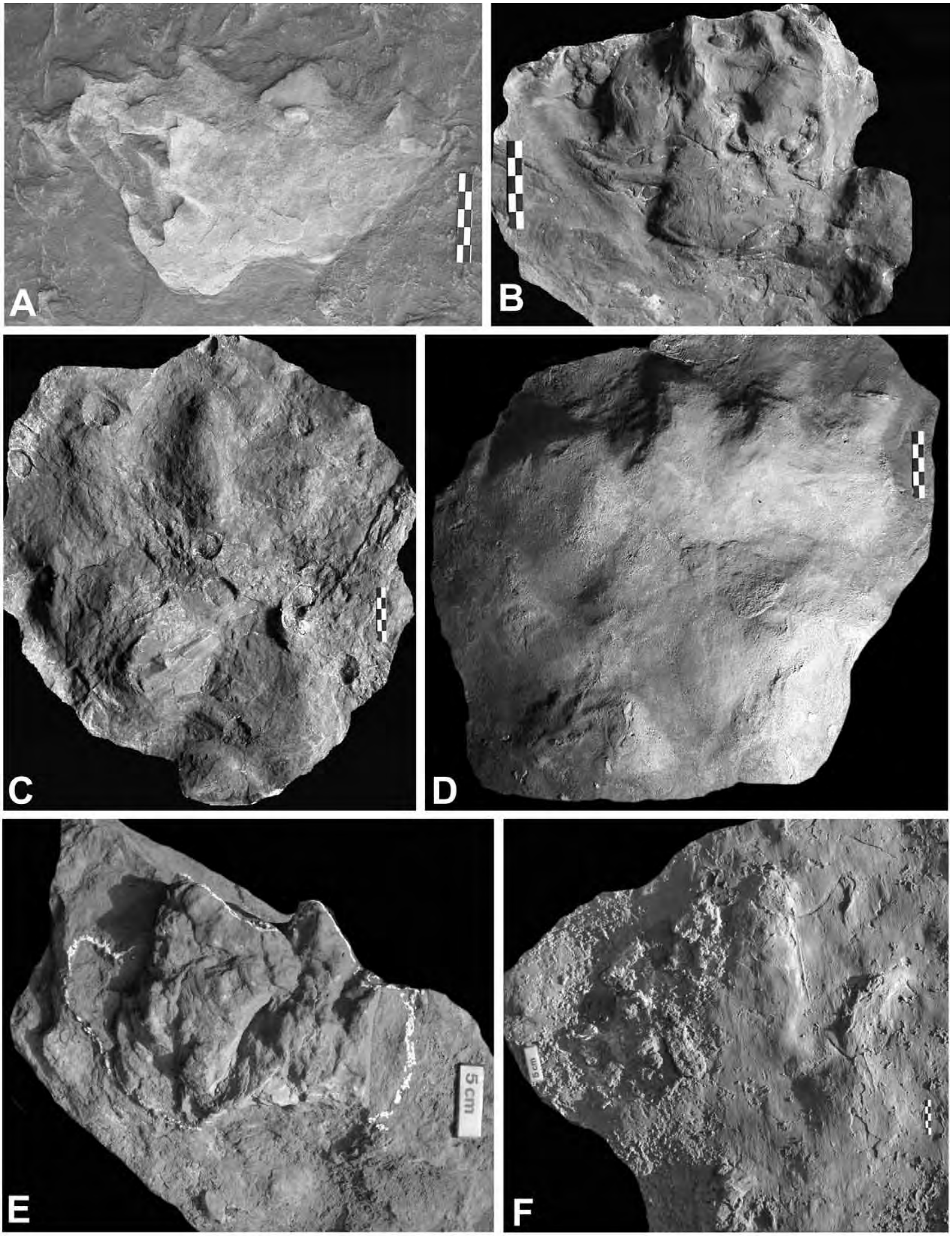


Fig. 4. *Brachychirotherium kalkowensis* ichnosp. nov. (A – ? right manus and pes imprints, B – left manus imprint, C, F – left pes imprints, D – right pes imprint, E – ? right pes imprint). **A** – Specimen not collected (field observation). **B** – Muz. PIG OS-220/250 (plaster cast). **C** – Muz. PIG OS-220/251, holotype (plaster cast). **D** – Muz. PIG OS-220/254 (plaster cast). **E** – Uncatalogued specimen deposited in the MPTS. **F** – MPTS 494A. Specimens B and C were identified on the same surface (specimens left in field). Scale bars 5 cm

digits IV and III are similar in length. Other imprints are only a little smaller: the width of the digit group I–IV in the specimen Muz. PIG OS-220/253 does not exceed 15.5 cm. In the specimen Muz. PIG OS-220/256 only digit group I–IV is preserved: it is 20 cm long and 17 cm wide. In this specimen the cross axis angle is the most clearly seen and attain 70°. Digits I, II, III and IV are 10, 12, 15 and 16 cm long respectively. In this specimen, digits I–IV diverge at a small angle, about 10°. In the holotype (Text-figs 2A, 3A), digits I–IV diverge at about 20°, and digits IV and V at 30°. The digit V imprint, clearly visible in specimen MPTS 2612A (holotype), is relatively long (about 17 cm). Its metatarsal pad is narrow, and indistinctly subdivided from the phalangeal portion.

Manus imprints: These are poorly and only incompletely preserved in the material investigated (Muz. PIG OS-220/257, MPTS 2612B, and field observations). In the fragmentary set of pes and manus imprints of Muz. PIG OS-220/255 the pes and manus digit groups I–IV are about 16 cm and about 12 cm wide respectively. In the poorly preserved set Muz. PIG OS-220/257 the pes and manus imprints are about 16 cm and 10.5 cm wide respectively. This gives an average pes to manus surface ratio of about 1.4-1.6, a range of values rather typical of representatives of *Synaptichnium* and *Brachychirotherium*.

COMMENTS: *Synaptichnium senkowiczowae* ichnosp. nov. shows the shape typical of representatives of the Chirotheriidae such as *Synaptichnium chi-*

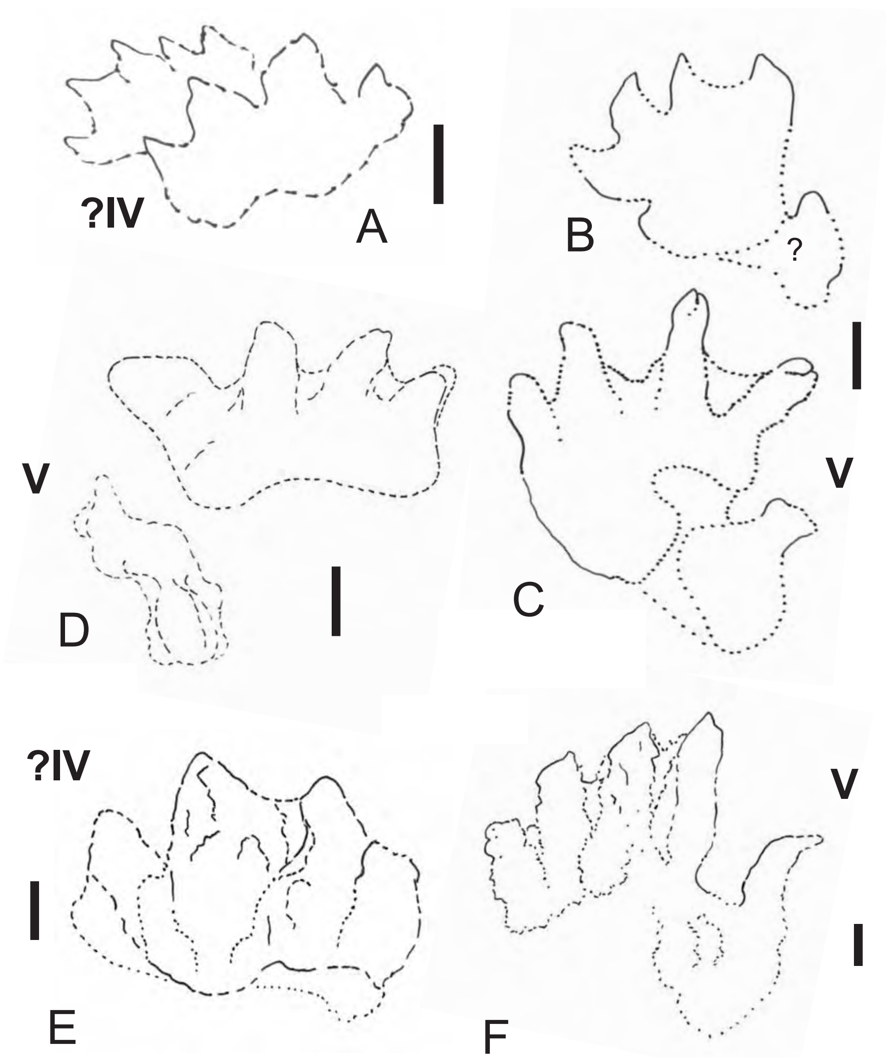


Fig. 5. *Brachychirotherium kalkowensis* ichnosp. nov. **A** – Specimen not collected (field observation). **B** – Muz. PIG OS-220/250. **C** – Muz. PIG OS-220/251, holotype. **D** – Muz. PIG OS-220/254. **E** – Uncatalogued specimen deposited in the MPTS. **F** – MPTS 494A. Scale bars 5 cm

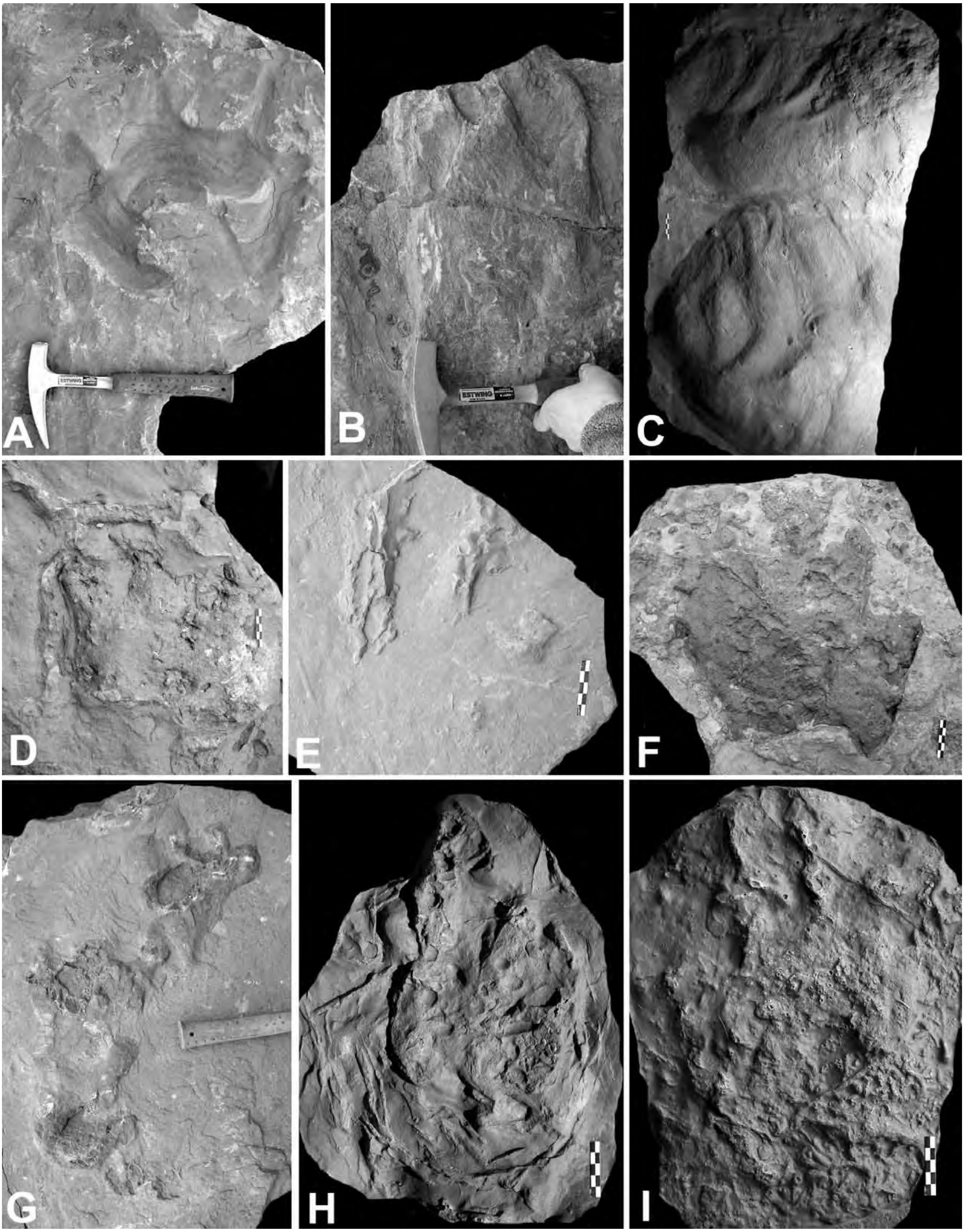


Fig. 6a, b. Poorly preserved large Chirotheriidae tracks. **A, C, D, F, G, K** – *Brachychirotherium kalkowensis* ichnosp. nov. **B**, **E**, **H-J**, **L-O** – *Synaptichnium senkowiczowae* ichnosp. nov. Scale: geological hammer – 27 cm and bars – 5 cm (**A**, **B**, **D-G**, **K**, **M** – field observations; **C** – plaster cast Muz. PIG OS 220/252; **H** – plaster cast Muz. PIG OS 220/255; **I** – plaster cast Muz. PIG OS 220/258; **J** – Muz. PIG OS-220/257; **L** – MPTS 2614; **N** – MPTS 2612B ; **O** – Muz. PIG OS-220/256) *rotherioides* PTASZYŃSKI, 1990 and, especially, *Synaptichnium primum* DEMATHIEU & HAUBOLD, 1982. The tracks assigned to this new ichnospecies are about twice as large as the largest chirotheriid tracks described to date from Wióry. The pes imprints of this ichnospecies are also larger than any other pes imprints from this locality. Hitherto, larger chirotheriid ichnospecies have been described only from much younger deposits (HAUBOLD 1984).

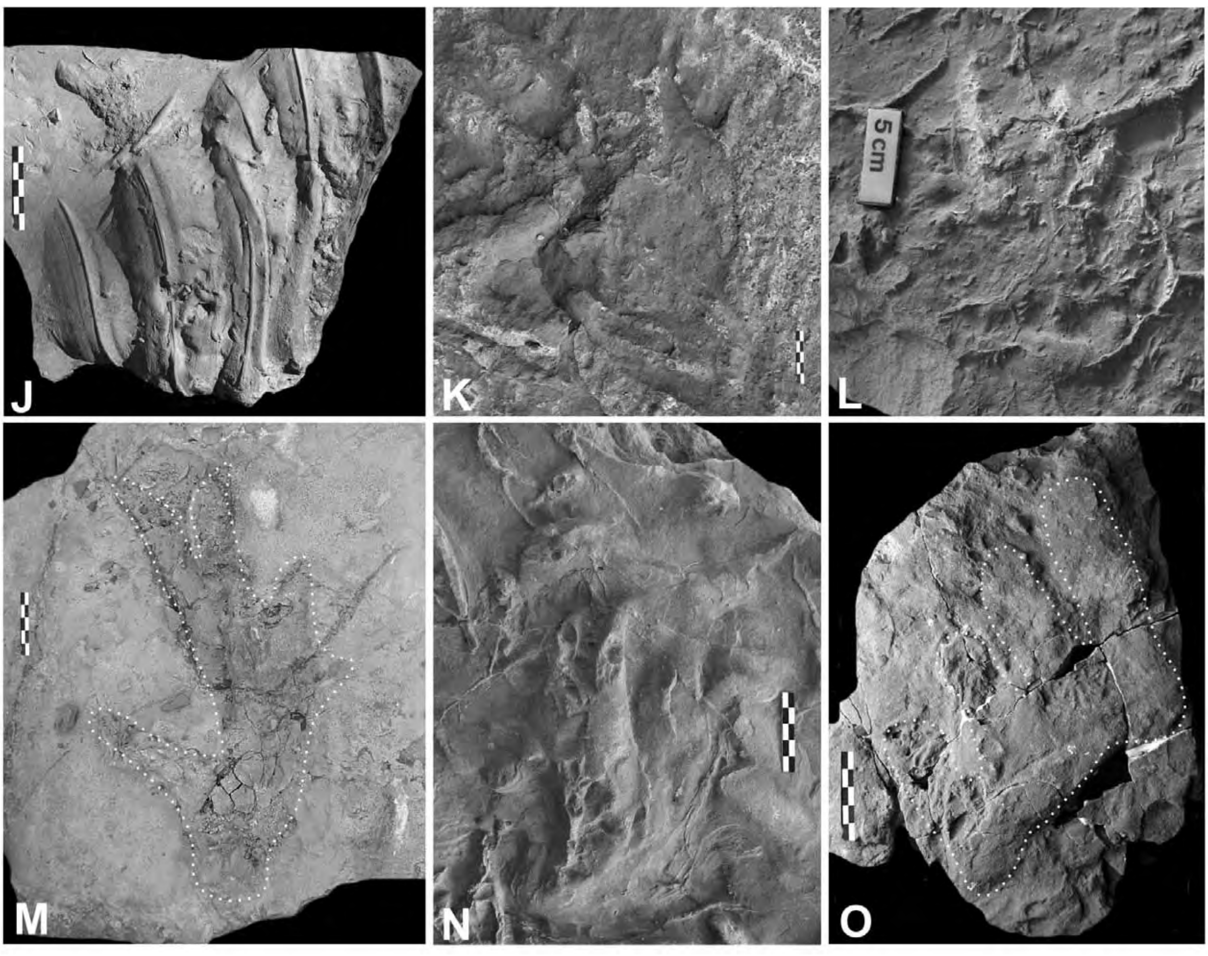
Ichnospecies similar to *S. senkowiczowae* ichnosp. nov. are *S. primum* DEMATHIEU & HAUBOLD, 1982 and *S. chirotherioides* PTASZYŃSKI, 1990. *S. senkowiczowae* ichnosp. nov. is distinctly larger than both these ichnotaxa, having a relatively shorter stride and a low value of pace angulation. *S. senkowiczowae* ichnosp. nov. differs from the *S. chirotherioides* in much larger size and a shorter stride in relation to the width of the trackway. In *S. chirotherioides*, the axes of the manus and pes diverge at a distinctly smaller angle than in *S. primum*. In *S. senkowiczowae* ichnosp. nov., the shape of the tracks shows no adaptations to carry a heavier body weight, apart from their large size. Such features as the 'lacertoid' digit group I–IV length proportions (I<II<III<IV), the lack of a distinct enlargement of the metatarsal portion of digit V and the generally narrow and elongated imprints, seem unusual for very large and heavy animals, distinguishing the new ichnospecies from other large representatives of the Chirotheriidae.

Ichnogenus *Brachychirotherium* BEURLEN, 1950

Brachychirotherium kalkowensis ichnosp. nov.
(Text-figs 4, 5, 6 A, C, D, F, G, K)

HOLOTYPE: Muz. PIG OS-220/251 (plaster cast; the original specimen was left in the field), left pes imprint (Text-figs 4C, 5C).

TYPE LOCALITY: Wióry near Ostrowiec Świętokrzyski, northeastern margin of the Holy Cross Mountains, Poland.



TYPE HORIZON: Wióry Formation, lower part of the Middle Buntsandstein, Early Triassic, Olenekian, early Spathian.

DERIVATION OF THE NAME: After the village of Kałków, where the first poorly preserved specimen of this ichnospecies was observed on a sandstone slab in the wall of a Catholic sanctuary (Sanktuarium Maryi Matki Boskiej z Ziemi Świętokrzyskiej).

DIAGNOSIS: Large *Brachychirotherium*-like track with low value of cross axis angle, about 70°. Pes digit group I–IV somewhat curved outwards (a feature clearly visible in specimen Muz. PIG OS-220/254). Ichnoform with relatively large manus (only 1.6 times shorter than pes). Pes digit length relations: I<II<III=IV (digits III and IV subequal in length, digit III longer than II).

MATERIAL: Muz. PIG OS-220/254 (plaster cast; the original specimen, preserved as a natural mould was left in the field), left manus imprint (Text-figs 4B, 5B); Muz. PIG OS-220/254 (plaster cast; the original specimen, preserved as a natural mould, was left in the field), right pes imprint (Text-figs 4D, 5D); MPTS 494A, left pes imprint (Text-figs 4F, 5F). Poorly preserved material: Muz. PIG OS-220/252 (plaster cast), ?set of pes and manus imprints (Text-fig. 6C); uncatalogued specimen deposited in the MPTS (Text-figs 4E, 5E); uncollected specimens, partially preserved pes imprints (Text-fig. 6A, D, F, G, K) and a set of pes and manus imprints (Text-figs 4A, 5A).

Description pes imprints: These are almost as long as wide. The holotype imprint (Muz. PIG OS-220/251) is 32 cm long and 27 cm wide (the largest specimens observed in the field were 36-40 and 38-42 cm long; specimen MPTS 494A is of a similar size – see Text-figs 4F, 5F). The cross axis angle in the holotype is 75°; in other specimens (Muz. PIG OS-220/254 and field observations), which are rather poorly preserved, it ranges from about 60 to 80° (70° on average). Pes digits are 1.4-1.5 times longer than the corresponding digits of the manus. Pes digit IV is the longest, digit I is the shortest, and digits III and IV are of similar length. The length of digits (measurements in the holotype): I = 9.5 cm; II = 12.5 cm; III = 13.5 cm; IV = 14 cm; V = 12.5 cm (length proportions of digits: I<II=V<III=IV). Digit V is distinctly separated from the digit group I-IV. Digit group I-V is 24.5 cm wide in the holotype. The digits of group I-IV are curved outwards; in some specimens the axes of digits IV and V are almost parallel. The axes of digits I-IV form a variable angle (60° in the holotype pes imprint; 40-50° in the other specimens). The angle between the individual digits (measurements from the holotype) are as follows: I-II = 12°; II-III = 14°; III-IV = 34°; IV-V = 12°; I-V = 72°. Claw marks are present at the tips of all five digits, but they are rather poorly preserved and not clearly visible in all the specimens recognized. Digit V is long, usually poorly preserved, with a large atypically formed metatarsal pad.

Manus imprints: These are wide and relatively large (the manus in the imprint Muz. PIG OS-220/250 is 21 cm wide and 17 cm long). All five digits have distinct claws and poorly preserved digital pad impressions. Digit I is the smallest and is distinctly separated from the digit group I-IV. Digit IV is the longest and is nearly subequal to digit III. The lengths of the digits (measurements from specimen Muz. PIG OS-220/250) are as follows: I = 6 cm; II = 8.5 cm; III = 9.5 cm; IV = 10 cm; V = 9 cm (length relations of digits: I<II<V<III=IV). Digit group I-IV is 17.5 cm wide. The relatively long digit V is distinctly separated from the digit group I-IV and turned outwards. The angles between the individual digits (measurements from the specimen Muz. PIG OS-220/250) are as follows: I-II = 35°; II-III = 12°; III-IV = 18°; IV-V = 28°; I-V = 93°. The manus surface is only 1.7 times smaller than that of the pes. The imprint of the palm area is relatively large (in the holotype it is 6 cm long and 8.5 cm wide).

COMMENTS: The morphology of *B. kalkowensis* ichnosp. nov. is somewhat similar to that of the following ichnotaxa: *Brachychirotherium kuhni* DEMATHIEU & HAUBOLD, 1982 from the Thuringian Chirotherian Sandstone, Solling Formation, of Germany; *Brachychirotherium wiorense* PTASZYŃSKI, 2000, from the Wióry Formation, and *Isochirotherium inferni* AVANZINI & LEONARDI, 2002, described from the lower beds of the Morbiac Dark Limestone of Italy (DEMATHIEU & HAUBOLD, 1982; FUGLEWICZ & *al.* 1990; PTASZYŃSKI 2000a; AVANZINI & LEONARDI 2002). Nevertheless, *B. kalkowensis* ichnosp. nov. is about 3.2 times longer than *B. kuhni* and 2.4 times longer than *B. wiorense* (Text-fig. 7). Moreover, pes digit I is shorter than digits II, III and IV. *B. kalkowensis* ichnosp. nov. is also similar to the enigmatic ichnospecies *Isochirotherium archaeum* DEMATHIEU & HAUBOLD, 1982 described on the basis of somewhat poorly preserved materials from the Solling Formation (DEMATHIEU & HAUBOLD 1982; LOCKLEY & MEYER 2000) and interpreted by its describers as two parallel trackways of a bipedal archosaur. Interestingly, *B. kalkowensis* ichnosp. nov. is similar in size to the largest known chirotheriid ichnotaxa of the latest Olenekian and early Anisian: *Isochirotherium herculis* (EGERTON, 1839), *Chirotherium rex* PEABODY, 1948, and *Ch. moquinense* PEABODY, 1948. In specimens representing this ichnospecies, clear adaptations to carry the heavy body of the animal are visible: all parts of the foot, including the sole and digits, are closely assembled, the feet imprints are nearly as long as wide and rather not elongated as in the smaller chirotheriid morphotypes. They also do not have not such a distinct metatarsal joint as is present in most of other chirotheriids. A similar, albeit extremely advanced, condition can be observed in the feet of sauropods and elephants.

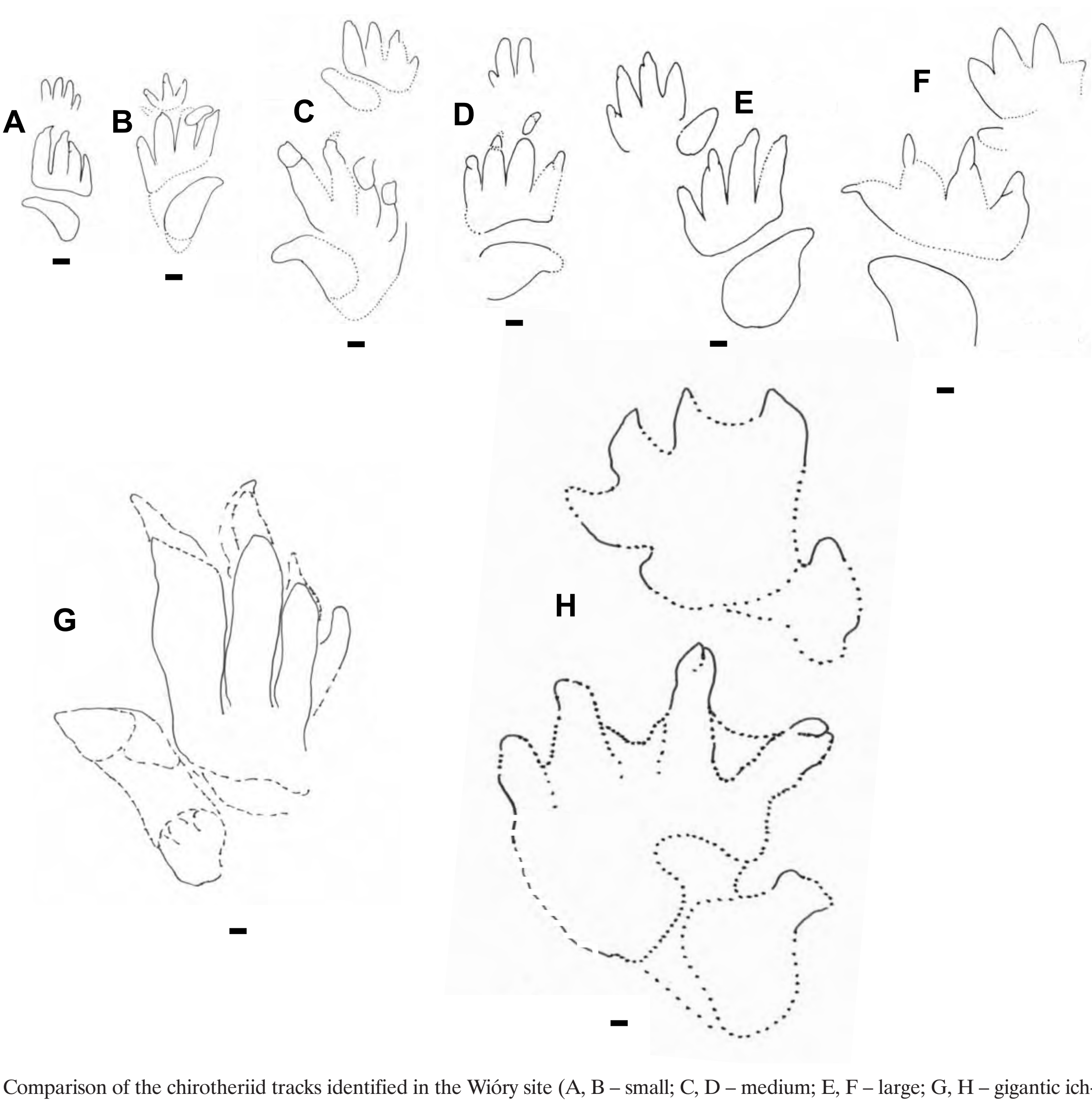
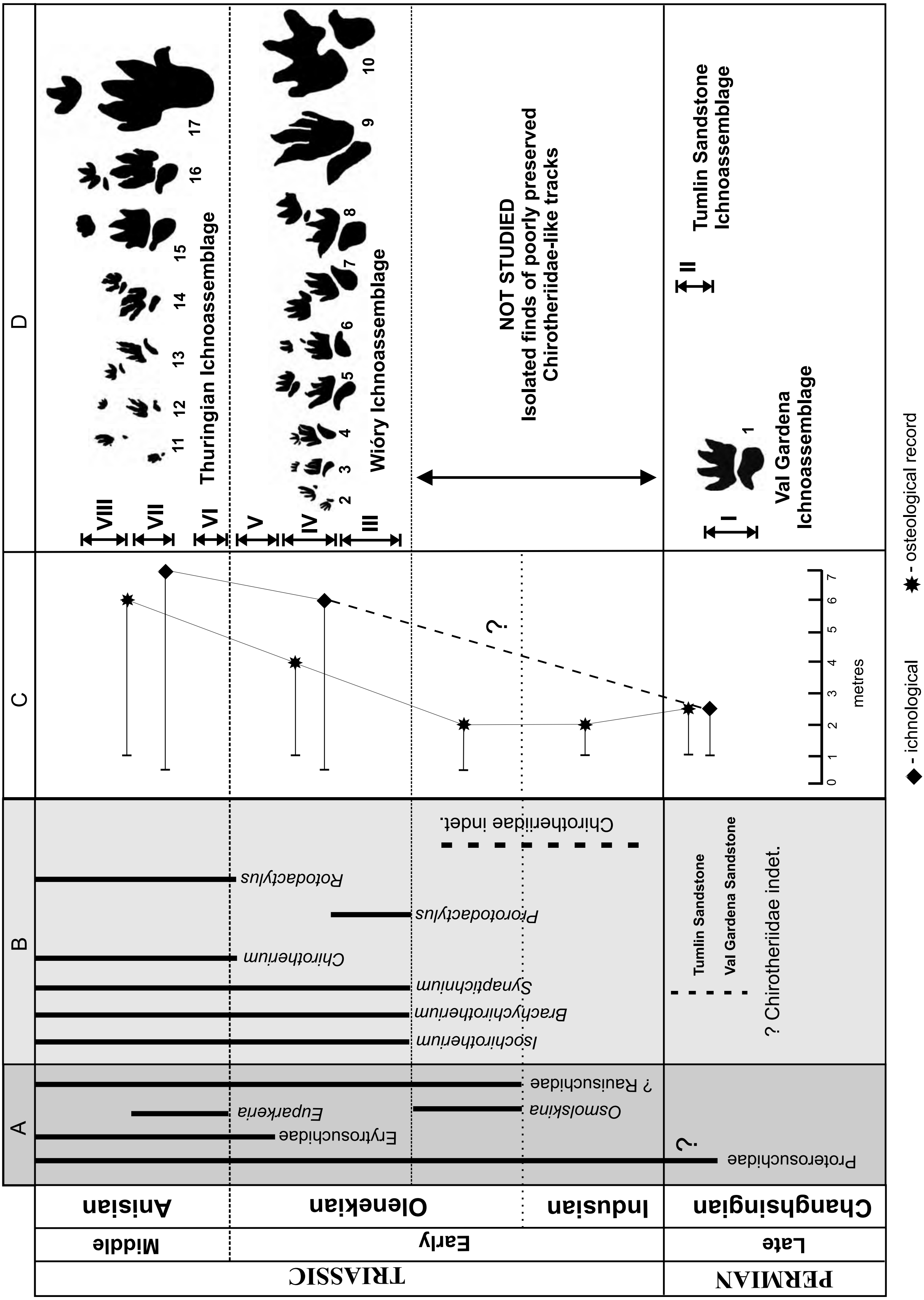


Fig. 7. Comparison of the chirotheriid tracks identified in the Wióry site (A, B – small; C, D – medium; E, F – large; G, H – gigantic ichnoforms; A-F, H – manus and pes imprints; G – pes imprint). **A** – *Synaptichnium kotanskii* PTASZYŃSKI, 2000; **B** – *Isochirotherium gierlinskii* PTASZYŃSKI, 2000; **C** – *S. chirotheroides* PTASZYŃSKI, 1990; **D** – *I. sanctacrucense* PTASZYŃSKI, 1990; **E** – *Brachychirotherium hauboldi* (PTASZYŃSKI, 1990); **F** – *B. wiorense* PTASZYŃSKI, 2000; **G** – *S. senkowiczowae* ichnosp. nov.; **H** – *B. kalkowensis* ichnosp. nov. Scale bar 1 cm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DISCUSSION

The megaichnofauna of the Wióry Formation represents the oldest known ichnological record of very large tetrapods in the Early Triassic (Text-fig. 8). We interpret their trackmakers as large Archosauromorpha (probably basal Archosauriformes *sensu* GAUTHIER, 1986), about 5-7 m long (see Text-figs 8, 9), for which there is no osteological record in deposits of this age worldwide (JUUL 1994; SENNIKOV 1995, 1996; LUCAS 1998; GOWER & SENNIKOV 2000a, b; BENTON & *al.* 2004; WARD & *al.* 2005a). The largest known Early Triassic land tetrapod is *Erythrosuchus africanus* BROOM, 1905, a predator with skull about 1 m long and total body length about 5 m (after SENNIKOV 1995). *E. africanus* has been identified in the upper part of the *Cynognathus* Assemblage Zone within the Burgersdorp Formation deposits of the Karoo Basin (see also KITCHING 1995). LUCAS (1998) proposed the term Nonesian Land Vertebrate Fauna for the time-equivalent of the *Cynognathus* Assemblage Zone vertebrate fauna and suggested an Olenekian age for this zone. According to OCHEV & SHISHKIN (1989), SHISHKIN & *al.* (1995), HANCOX (1998) and SHISHKIN (2005) only the lower *Cynognathus* Subzone is of late Olenekian age. Interestingly, BENTON & *al.* (2004) suggested that there was a lack of large tetrapods in the Early Triassic terrestrial ecosystems ("large herbivores and specialist top carnivores").

In the cladistic scheme, basal Archosauriformes include five possible clades: Proterosuchidae, Erythrosuchidae, *Osmolskina*, *Euparkeria*, and Proterochampsidae (GOWER & SENNIKOV 2000b; BORSUK-BIAŁYNICKA & EVANS 2003). Two of these could be possible trackmakers of the large tracks from Wióry: Proterosuchidae and Erythrosuchidae, which have been identified both in Laurasia (Russia) and Gondwana (Africa and China). Proterosuchids were small to medium-sized reptiles (body length 1-3 m), known from the Late Permian to the Middle Triassic (SENNIKOV 1995; GOWER & SENNIKOV 2000b). However, BENTON & *al.* (2004) and WARD & *al.* (2005a) suggested that the first proterosuchid remains were not older than earliest Triassic. The identification of the Late Permian *Archosaurus rossicus* TATARIANOV, 1960 as a proterosuchid archosaur, however, has apparently never been seriously questioned (GOWER & SENNIKOV, 2000b). Erythrosuchids were larger predators (body length 3-6 m) recorded from the late Olenekian to Ladinian (SENNIKOV 1995). SENNIKOV (1995), GOWER & SENNIKOV (2000b) and BENTON & *al.* (2004) also suggested the occurrence of some early possible rauisuchian (Rauisuchia) forms in the late Early Triassic of Russia.

The latest Permian paleoichnologic record of vertebrates in Europe starts with the Val Gardena ichnoassociation described from the Southern Alps, Italy (CONTI & *al.* 1977) and the somewhat younger Tumlin ichnoassociation from Poland (PTASZYŃSKI 2000b; PTASZYŃSKI & NIEDŹWIEDZKI 2004a). The last is also close to the lowermost Buntsandstein vertebrate ichnofauna recently studied by us (see PTASZYŃSKI & NIEDŹWIEDZKI 2002). Younger vertebrate track assemblages are well documented from the Early (but not earliest) Triassic of Poland and Germany – the Wióry ichnoassemblage (FUGLEWICZ & *al.* 1990; PTASZYŃSKI, 2000a; FICHTER & LEPPER 1997; FICHTER & KUNZ 2004). The paleoichnologic record of the earliest Triassic (Indusian and Early Olenekian) vertebrates is poor in this area (see HAUBOLD 1971; DEMATHIEU & HAUBOLD 1972; LEPPER & RÖHLING 1998) and needs additional

Fig. 8. Distribution of the basal Archosauriformes *sensu* GAUTHIER, 1986 (A – taxa ranges; C – sizes of animals) and archosauromorpha tracks (B – ichnotaxa ranges; C – sizes of animals estimated from track records; D – ichnoassemblages from the European tracksites) in the Late Permian and Early-Middle Triassic of Pangaea (data in A after SENNIKOV 1995; GOWER & SENNIKOV 2000a, b; BORSUK-BIAŁYNICKA & EVANS 2003; BENTON & *al.* 2004; WARD & *al.* 2005a; data in B, E after CONTI & *al.* 1977; CONTI & *al.* 2000; DEMATHIEU & HAUBOLD 1972, 1982; HAUBOLD 1971, 1983, 1984; FUGLEWICZ & *al.* 1990; FICHTER & LEPPER 1997; PTASZYŃSKI 2000a, b; PTASZYŃSKI & NIEDŹWIEDZKI 2002, 2004a; FICHTER & KUNZ 2004; see also BACHMANN & KOZUR 2004; KOZUR 2005; KOZUR & BACHMANN 2005). Vertebrate ichnoassemblage: I – Val Gardena Ichnoassemblage; II – Tumlin Ichnoassemblage; III – Wióry Ichnoassemblage; IV – Hessen Ichnoassemblage; V – Pałęgi Ichnoassemblage; VI – Thuringian Ichnoassemblage; VII – Plattensandstein Ichnoassemblage; VIII – Frankischer Ichnoassemblage. Vertebrate ichnotaxa: 1 – "*Chirotherium* sp."; 2 – *Prorotodactylus mirus*; 3 – *Synaptichnium kotanskii*; 4 – *Isochirotherium gierlinskii*; 5 – *S. chirotheroides*; 6 – *I. sanctacrucense*; 7 – *Brachychirotherium hauboldi*; 8 – *B. wiorense*; 9 – *S. senkowiczowae* ichnosp. nov.; 10 – *B. kalkowensis* ichnosp. nov.; 11 – *Rotodactylus matthesi*; 12 – *I. soergeli*; 13 – *Chirotherium sickleri*; 14– *B. praeparvum*; 15 – *I. hessbergense*; 16 – *Ch. barthii*; 17 – *I. herculis*

study and revision of the existing data (PTASZYŃSKI & NIEDŹWIEDZKI 2005). In the Holy Cross Mountains area, vertebrate tracks of this age are still unknown. Late Early Triassic and Middle Triassic vertebrate ichnoassociations have been known for over a hundred years from many European localities including Poland (KULETA & *al.* 2001, 2005a, b), but differ mainly at the ichnospecies level from the Wióry ichnoassociation. Although chirotheriid-like footprints have been reported from the Val Gardena Formation (CONTI & *al.* 1977; see also CONTI & *al.* 2000 and AVANZINI & *al.* 2001), their finds ("*Chirotherium* sp.") can be interpreted either as Chirotheriidae indet. or as representatives of the ichnogenus *Ichniotherium*. Other specimens that cannot be determined exactly ("*Synaptichnium* sp.", "? *Thecodontichnus* cf. *verrucae*", "Proterosuchia indet.") are similar to small chirotheriid tracks but could also represent tracks of large rhynchosauroids (CONTI & *al.* 2000). The essential difference between the Tumlin and the younger vertebrate ichnoassociations is the lack of any typical chirotheriid tracks in the Tumlin ichnoassociation, while in the Wióry ichnoassociation these already show a high diversity and represent the greatest number of large and medium-sized tracks. In the spring of 2005, two poorly preserved specimens of small- and medium-sized tracks were found by one of us (G. N.) in the Tumlin Sandstone Member at the Tumlin Gród quarry. Although poorly preserved, they show morphological features similar to those observed in the Chirotheriidae. KLEIN & HAUBOLD (2003) proposed two small lacertoid-like chirotheriid tracks: *Synaptichnium diabolense* (PEABODY, 1948) and *Brachychirotherium harrasense* (HAUBOLD, 1967), as a morphotype of basal (ancestral), primitive chirotherian forms, but these tracks are known only from the latest Olenekian–Anisian deposits, so they are much younger than the Val Gardena, Tumlin, and Wióry vertebrate ichnoassociations.

The highly diverse chirotheriid tracks observed in the Wióry ichnoassociation (eight ichnotaxa, see Text-fig. 8) provides a unique insight on the Olenekian, probably post-radiational or radiational fauna of the basal Archosauriformes.

Rapid evolutionary radiation could explain the unique ichnorecord of very large and diversified Archosauromorpha in the Olenekian compared to earlier periods. Increase in size and diversification, as an expression of evolutionary success of the makers of the chirotheriid tracks in the Early Triassic may be explained by an abrupt (in a geological sense) evolutionary response (probably in the late Indusian or early Olenekian) by basal Archosauriformes (which were small and not diversified during the latest Permian and Indusian: see SENNIKOV 1995, 1996; GOWER & SENNIKOV 2000b) to ecological release after the Late Permian–earliest Triassic gradual faunal turnover (ecosystem and faunal changes interpreted between the *Dicynodon* and *Lystrosaurus*, and the *Lystrosaurus* and *Cynognathus* Faunal "Zones" of South Africa and Vyatskian and the Vetlugian, Vetlugian and Yarenskian Faunal "Zones" of Eastern Europe; see MARSHALL 2005; WARD & *al.* 2005a, b; SHISHKIN 2005; BENTON & *al.* 2004; RETALLACK & *al.* 2003; MACLEOD & *al.* 2000; LUCAS 1998; SENNIKOV 1996). These ecological phenomena were probably induced by long-term global changes (for example climatic changes; see OCHEV, 1995) that spanned about ten million years and consisted of several phases – pre-Lopingian, end-Permian, and Early Triassic (HONGFU YIN 2005). Some authors have also interpreted the *Dicynodon-Lystrosaurus* faunal turnover as a terrestrial catastrophic extinction (SMITH & WARD 2001; BENTON & *al.* 2004).

On the other hand, the widespread appearance and differentiation of the makers of the chirotheriid tracks in the Late Olenekian and Anisian vertebrate ichnoassemblages need not necessarily require any extraordinary evolutionary or catastrophic phenomena. Even 'abrupt' changes (in a geological sense) in the occurrence of any faunal group in any area can be explained as resulting from gradual evolution, environmental and climatic changes, and migration. Climatic changes and evolution certainly took place during that time. The early presence of Archosauromorpha is known from different areas from the Late Permian (CHARIG & SUES 1976; SENNIKOV 1995, 1996; GOWER & SENNIKOV 2000b). The evolution of this group was probably much more intense that is apparent from the poor and fragmentary palaeontological and chronostratigraphical data. The first Archosauromorpha appeared in the Late Permian and diversification of this group could have begun at least as early as this. After the first, poorly known part of their history, the dominance of the Archosauromorpha in the Middle and Late Triassic terrestrial ecosystems is evidenced from both osteological and ichnological records (SENNIKOV 1996; LUCAS 1998; HAUBOLD 1984; LOCKLEY & MEYER 2000).

CONCLUSIONS

The largest chirotheriid tracks are not common in the fluvial deposits of the Wióry Formation. Hitherto, only a few pes and manus imprints of large *Synaptichnium senkowiczowae* ichnosp. nov. and *Brachychirotherium kalkowensis* ichnosp. nov. have been found in the relatively rich (eleven ichnotaxa; thousands of specimens) Wióry vertebrate ichnoassemblage. Their trackmakers were thus either rather rare in the Early Triassic environments of the Holy Cross Mountains or they did not frequently penetrate river bank habitats. The size of the animals (estimated from the tracks: see Text-fig. 9) suggests that they might have been the largest vertebrates (? top predators) of this ecosystem.

The new ichnotaxa described above represent the oldest known (Olenekian, early Spathian) record of very large chirotheriid tracks in Middle Buntsandstein deposits. A well documented record of large chirotheriid tracks (25-35 cm long) is known from the latest Early Triassic and Middle Triassic (Solling Formation – latest Olenekian–early Anisian) in the Germanic Basin, Middle Triassic (Richthofen Conglomerate and Morbiac Dark Limestone – Anisian) of northern Italy, Middle Triassic (Grès inférieurs du Lyonnais – Anisian–Ladinian) of France, latest Early Triassic–Middle Triassic (Moenkopi Formation – latest Olenekian–Anisian) of North America, and latest Early Triassic and Middle Triassic (Samsonów Formation – latest Olenekian; Baranów Formation – Anisian; Krynki Beds – Anisian) of Poland (PEABODY 1948; HAUBOLD 1971, 1984; DEMATHIEU 1985; AVANZINI & *al.* 2001; LUCAS & SCHOCH 2002; AVANZINI & LEONARDI 2002; PTASZYŃSKI & NIEDŹWIEDZKI 2002; KULETA & *al*. 2005a, b; see also BACHMANN & KOZUR 2004; KOZUR & BACHMANN 2005; KOZUR 2005). Interestingly, the Middle Triassic of Poland also yielded gigantic chirotheriid tracks with pes imprints up to 50 cm long (KULETA & *al.* 2005a).

Although we interpret *Synaptichnium senkowiczowae* ichnosp. nov. and *Brachychirotherium kalkovensis* ichnosp. nov. as chirotherian, there is another possible interpretation of these tracks (H. HAUBOLD, 2007 – personal communication). *Brachychirotherium kalkovensis* ichnosp. nov. shows features that are atypical of all other chirotheriid tracks. The lack of distinct imprint of metatarsal joint and the atypically-formed metatarsal pad of the fifth digit are not characteristic of most known chirotheriid tracks.

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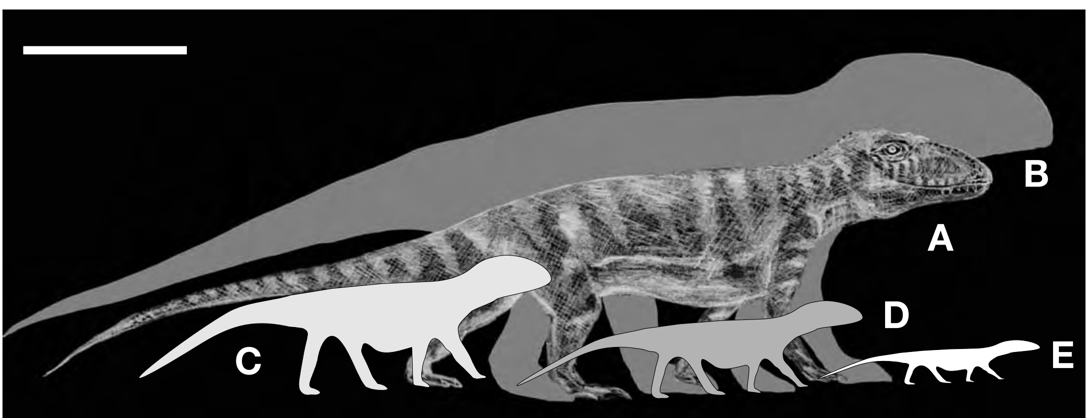

Fig. 9. Sizes of the largest (A, B), medium-, and small-sized (C-E) Archosauromorpha (probably basal Archosauriformes *sensu* GAUTHIER, 1986) from the Wióry Formation, trackmakers of *Synaptichnium senkowiczowae* ichnosp. nov. (A), *Brachychirotherium kalkowensis* ichnosp. nov. (B), *B. wiorense* PTASZYŃSKI, 2000 (C), *Isochirotherium sanctacrucense* PTASZYŃSKI, 1990 (D), and *Synaptichnium kotanskii* PTASZYŃSKI, 2000 (E); Scale bar 1 m

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