Lower Triassic vertebrate footprints from Wióry, Holy Cross Mountains, Poland

TADEUSZ PTASZYŃSKI

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Vertebrate footprints occur in the Middle Buntsandstein (Lower Triassic) Labyrinthodontidae Beds exposed at Wióry in the northeastern margin of the Holy Cross Mountains (Poland). They represent the richest footprint assemblage from the Middle Buntsandstein in Europe known to date. This assemblage comprises 11 ichnospecies representing seven ichnogenera attributable to amphibians and reptiles. The following new ichnotaxa are erected: Prorotodactylidae ichnofam. n., *Prorotodactylus mirus* ichnogen. et ichnosp. n., *Capitosauroides fuglewiczi* ichnosp. n., *Brachychirotherium wiorense* ichnosp. n., *Isochirotherium gierlinskii* ichnosp. n., *Synaptichnium kotanskii* ichnosp. n., and *Rhynchosauroides rdzaneki* ichnosp. n. The *Prorotodactylus* trackmakers possibly represent a systematic group close to that from which the *Rotodactylus* trackmakers and dinosaurs originated.

Key words: Footprints, ichnotaxonomy, Buntsandstein, Lower Triassic, Poland.

Tadeusz Ptaszyński, ul. Strońska 1 m. 12, PL-01-461 Warszawa, Poland.

Introduction

Vertebrate footprints are rare in Lower and Middle Buntsandstein (Lower Triassic) deposits, being commoner and more diversified in the Upper Buntsandstein (Haubold 1971a; Ptaszyński 1996). The footprint assemblage from Wióry, Holy Cross Mountains, Poland (Fig. 1) is the richest and most diverse in the Middle Buntsandstein known to date (Fuglewicz *et al.* 1981, 1990). The present paper supplements a previous study by Fuglewicz *et al.* (1990), and offers a partial reinterpretation of material recorded earlier as well as a description of new material collected during the past ten years.

The large outcrop at Wióry resulted from the water barrage and reservoir construction in 1979–1980. Vertebrate tracks, discovered at this site by the author in the autumn of 1980, were subsequently collected by the author and Kazimierz Rdzanek, founder of the Ichnological Museum at Wióry. Thanks to efforts of the latter, particu-

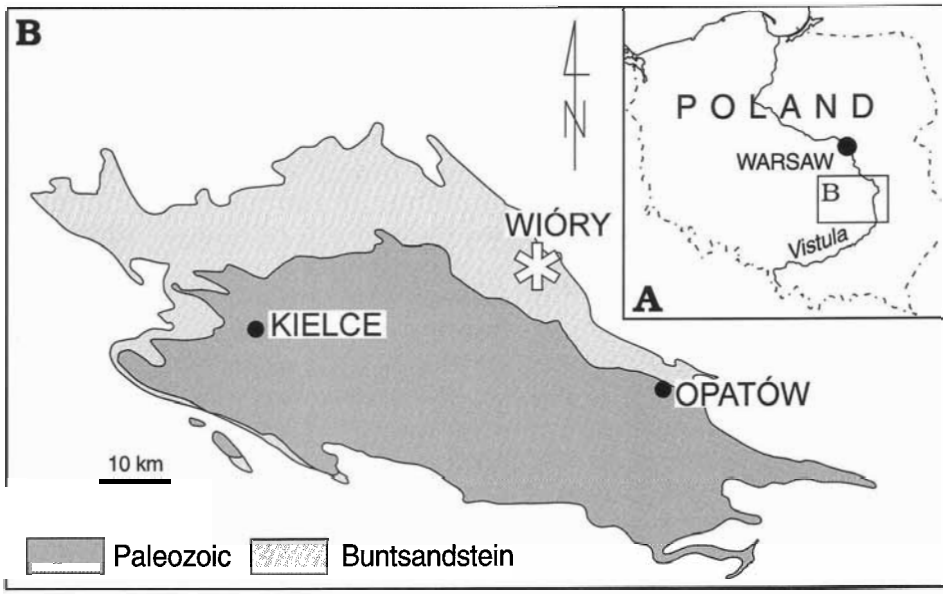


Fig. 1. Location of the Wióry site in Poland (**A**) and in Holy Cross Mountains (**B**) (after Fuglewicz *et al.* 1990, slightly simplified). Quaternary removed, tectonics not respected.

larly during the past seven years when the construction works of the water barrage were resumed after ten years of interruption, most of the important material could be salvaged.

Specimens described in this paper are deposited in the following collections: (1) Institute of Palaeobiology of the Polish Academy of Science, Warszawa (abbreviated ZPAL); (2) Tadeusz Ptaszyński private collection, ul. Strońska 1 m. 12, Warszawa (abbreviated TP); (3) Kazimierz Rdzanek private collection, ul. Muszlowa 3 m. 55, Warszawa (abbreviated KR); (4) Museum of the Faculty of Geology, University of Warsaw (abbreviated MWGUW).

Some slabs bearing the prefix TP have not been recovered but are documented only by photographs, plaster casts and measurements. Some of them are still accessible in the field (TP 620), other have been damaged as a result of quarrying activity (TP 11, TP 294). The three original slabs TP 1, TP 50 and TP 223 were recovered by Kazimierz Rdzanek and are now housed at the Ichnological Museum at Wióry (under construction).

Geological setting

The ichnological material described in the present paper comes from a single outcrop situated on the right bank of the Świślina River valley on the water barrage construction site near the village of Wióry, 14 km north-west of the town of Ostrowiec Świętokrzyski in the northeastern margin of the Holy Cross Mountains (Fig. 1).

The lithologic sequence exposed at Wióry comprises of sandstones, siltstones and claystones of fluvial origin, about 40–50 meters thick (Mader & Rdzanek 1985: fig. 2; Fuglewicz *et al.* 1990: fig. 2). These strata are assigned to the Labyrinthodontidae Beds of the Middle Buntsandstein in a local lithostratigraphic scheme (Senkowiczowa & Ślączka 1962), and originated in channels and floodplains of a braided river system (Mader & Rdzanek 1985; Fuglewicz *et al.* 1990). The Labyrinthodontidae Beds are correlated with the Upper Oolithic Beds of the Polish Lowland, which show some marine incursions (Senkowiczowa & Ślączka 1962; Fuglewicz *et al.* 1990). Palynostratigraphic (Fijałkowska 1994) and magnetostratigraphic (Nawrocki 1997) studies allow to precise the age of the Labyrinthodontidae Beds as Dienerian.

Footprints occur mainly in the middle and upper part of the section. The sequence yields numerous sedimentary structures, rare plant remains, reptilian and labyrinthodont amphibian bones and phyllopod carapaces. In addition to the trace fossils of vertebrate origin, there are numerous invertebrate tracks (Mader & Rdzanek 1985). Arthropod tracks of possibly notostracan origin, determined as '*Diplichnites*' *triassicus* (Linck, 1943), from the Labyrinthodontidae Beds at a locality nearby (Stryczowice) were described by Machalski & Machalska (1994).

Methods

Labels with single imprints consist of number of slab and imprint. Labels with tracks comprise, in addition to number of slab, also numbers of all preserved imprints. For example, the single footprint ZPAL R.7/31: 21 belongs to the track numbered ZPAL R.7/31: 14–30. Measurements were made, with only few exceptions, on original specimens (Tables 1–6). The method of measurements corresponds to that in Haubold (1971a), Demathieu (1985) and Leonardi (1987). Tables with full numerical and statistical data of all specimens studied are available from the author and from the Library of the Institute of Palaeobiology of the Polish Academy of Science.

Descriptions

Ichnogenus *Capitosauroides* Haubold, 1971

Capitosauroides fuglewiczi ichnosp. n.

Figs. 2A, B, 3A–D, 4A–D; Tables 1, 2.

cf. *Capitosauroides* sp.; Fuglewicz *et al.* 1990: pl. 1: 1–4; fig. 4.

Holotype: The second pair of imprints of left pes (plaster cast ZPAL R.7/1: 5, Figs. 3D, 4B) and manus (plaster cast ZPAL R.7/1: 4, Fig. 4B) imprints preserved in track TP 1: 1–13 (Figs. 2A, 4A), composed of nine consecutive pes and left manus imprints, also referred to in Fuglewicz *et al.* (1990: pl. 1: 1–4, fig. 4: 1–9) and now housed in the Ichnological Museum at Wióry (under construction).

Type locality: Wióry near Ostrowiec Świętokrzyski, Holy Cross Mts, Poland.

Type horizon: Labyrinthodontidae Beds, Middle Buntsandstein, Lower Triassic.

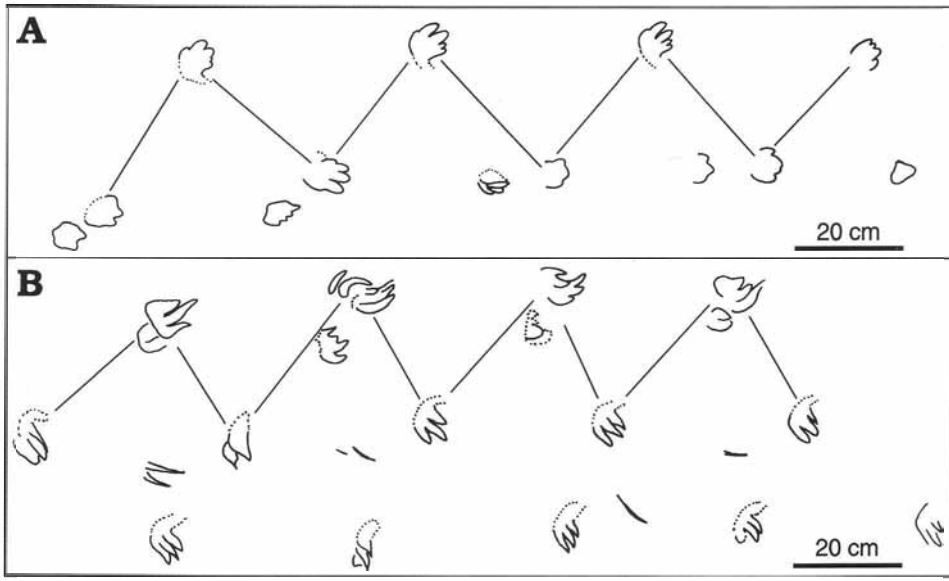


Fig. 2. *Capitosauroides fuglewiczi* ichnosp. n. **A**. Track TP 1: 1–13. **B**. Two incomplete tracks TP 223: 1–13 and TP 223: 14–18.

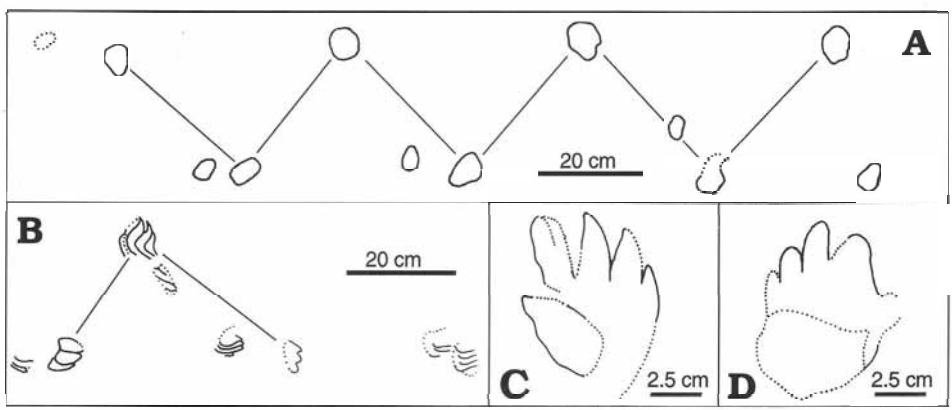


Fig. 3. *Capitosauroides fuglewiczi* ichnosp. n. **A**. Track TP 620: 1–11. **B**. Track TP 294: 1–8. **C**. Isolated imprint ZPAL R.7/2: 1, see Fig. 4C. **D**. Holotype, left pes imprint TP 1: 5 (plaster cast ZPAL R.7/1: 5), see Fig. 4B.

Derivation of the name: In honour of the late Ryszard Fuglewicz, the co-author of the first paper on the Wióry ichnofauna.

Diagnosis. — Medium-sized *Capitosauroides* with low pace angulation 74–89° (82° on average). Angles between pes digit axes I–IV and I–V low, about 25 and 47°, respectively. Pes imprints distinctly longer than wide.

Material. — In addition to the holotype the following specimens have been studied: TP 620: 1–11, distinct track, although no details are visible (Fig. 3A); TP 223: 1–13, TP 223: 14–18, two incomplete, parallel tracks (Fig. 2B); TP 294: 1–8, a short track with imprints of all four feet

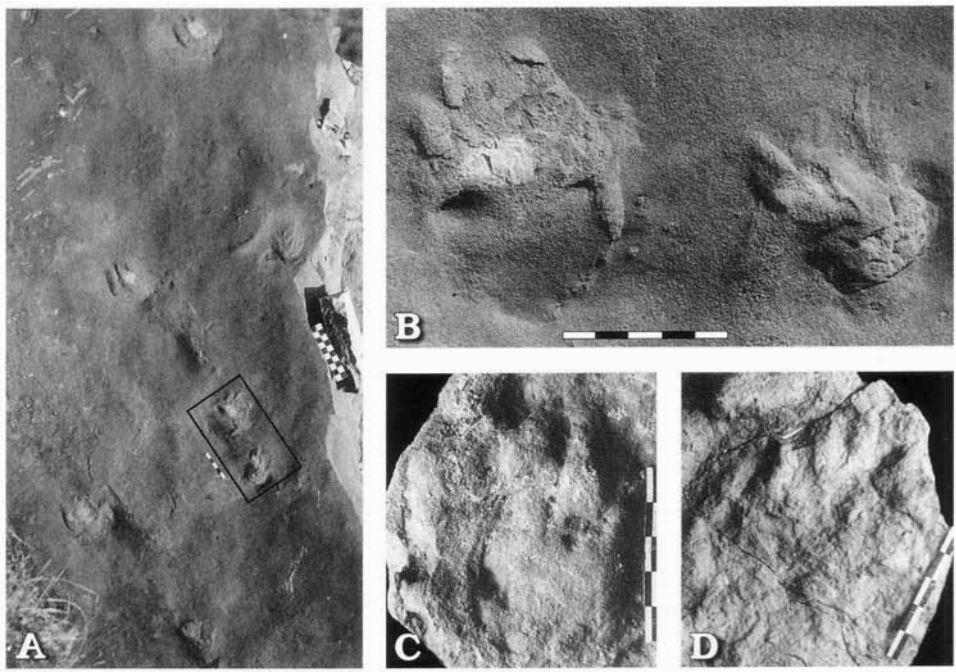


Fig. 4. *Capitosauroides fuglewiczi* ichnosp. n. **A.** Track TP 1: 1–9, in rectangle shown the holotype TP 1: 5, 4. **B.** Set of left pes and manus imprints, holotype TP 1: 5, 4 (plaster casts ZPAL R.7/1: 5 and ZPAL R.7/1: 4), enlargement of the area rectangled in A, see also Fig. 3D. **C.** Possible pes imprint ZPAL R.7/2: 1; see also Fig. 3C. **D.** Isolated imprint ZPAL R.7/3: 1. Scale in cm.

preserved (Fig. 3B); ZPAL R.7/2, ZPAL R.7/3, small slabs with isolated imprints preserved as natural casts (Figs. 3C, 4C, D).

Description. — Track. TP 1: 1–13 shows the following irregularities (see Fuglewicz *et al.* 1990): measurements of the oblique pace from left to right pes are lower than those from right to left, divarications of the left pes imprints from midline are smaller than those of right pes imprints, manus imprints are present on only one (left) side of the track. The pes pace angulation is low and constant, 86–87°. The stride in TP 1: 1–13 is 408 mm on average; oblique pace measured from left to right pes imprints is 280–290 mm while that feature measured from right to left attains 300–335 mm. Both measured right pes imprints diverge out from the midline at 35 and 38°, while that of the left one at only 16°. The pes width of pace is about 220 mm. In the track TP 620: 1–11 values of oblique pace measured from left to right pes imprints are smaller than those measured from right to left, in contrast to the track TP 223: 1–13 in which those values measured from left to right pes imprints are greater than those from right to left. In none of the tracks are both values equal.

In all tracks described pace angulation varies between 73 and 89°. There appear imprints of four (Fig. 3B), three (Fig. 2A), or even one limb (Fig. 2B). Manus imprints, if present, occur regularly mostly on one side of the track (Figs. 2A, 3A, 4A) and are overstepped by those of the pes. In TP 294: 1–8 (Fig. 3B), the width of pes and manus pace are almost equal.

Pes. Pes imprints do not show neither metapodial joint nor claw imprints. Details of imprints are well visible in the holotype ZPAL R.7/1: 5 and in isolated imprints ZPAL R.7/2: 1 and ZPAL R.7/3: 1, 2 (Figs. 3C, 4C, D). Digit tips I–V form an arc with a radius of about 30 mm.

Table 1. Footprint measurements of holotypes and some other specimens. Abbreviations: I, II, III, IV, V, lengths of digits; L, footprint length; b, footprint width; M, length of the digit group I–IV; m, width of the digit group I–IV; t(2/4), t'(1/4), f(1/5), angles between the corresponding digits measured along axes of these digits; q, cross axis.

Name of the ichnospecies	Specimen		Characters												
			I	II	III	IV	V	L	b	M	m	t (2/4)	t' (1/4)	f (1/5)	q
Capitosauroides fuglewiczi ichnosp. n.	pes	ZPAL R.7/1:5	21	32	46	47		80	67	54	55				
	pes	ZPAL R.7/2:1	32	34	37	41	47	75	67	54	60	12	25	47	
Brachychirotherium hauboldi (Ptaszyński, 1990)	pes	TP 569:1	47	58	67	58	72	118	98	80	67	23	38	51	68
	manus	TP 569:2	30	38	45	42	35	62	69	55	58	20	42	80	70
Brachychirotherium wiorense ichnosp. n.	pes	ZPAL R.7/6:1	39	56	59	55	64	121	117	85	99	54	70	67	60
	manus	ZPAL R.7/6:2	32	41	46	43		75	82	56	70	16		105	70
Isochirotherium gierlinskii ichnosp. n.	pes	ZPAL R.7/10:1	33	37	40	36	49	88	54	46	46	26	30	45	70
	manus	ZPAL R.7/10:2	14	17	19	16	18	35	36	24	31	43	52	80	70
Isochirotherium sanctacrucense Ptaszyński, 1990	pes	ZPAL R.7/16:1	38	55	62	41	44	108	70	69	58	16	19		81
	manus	ZPAL R.7/16:2		24	26					29	34				
Synaptichnium chirotherioides Ptaszyński, 1990	pes	ZPAL R.7/4:12	38	51	62	56	59	106	90	74	60	17	32	46	68
	manus	ZPAL R.7/4:13		35	45	38		59	64	59	49	26	29	66	63
Synaptichnium kotanskii ichnosp. n.	pes	ZPAL R.7/21:11	23	34	37	35	33	64	39	42	33	5	13	47	70
	manus	ZPAL R.7/21:13	14	20	22	19	15	31	26	25	23	23	40	77	77
Procolophonichnium polonicum (Ptaszyński, 1990)	pes	ZPAL R.7/26:1	10	12	16	17	18			23	24	43	56	83	65
	pes	ZPAL R.7/27:1		16	20	24	13	32	30	32	23	23	41	73	
Rhynchosauroides brevidigitatus (Ptaszyński, 1990)	pes	ZPAL R.7/29:9	4	8	12	15		18	16			38			
	manus	ZPAL R.7/29:10		6	7	8	5	13	11			52			
Rhynchosauroides rdzaneki ichnosp. n.	pes	ZPAL R.7/30a:3	13	21	32	33				48	28	24	40		
	pes	ZPAL R.7/30b:3	14	28	35	38	19	50	41	46	30	22	28	72	
	pes	ZPAL R.7/30a:9	15	22	28	32	20	43	32	39	26	26	40	53	
	pes	ZPAL R.7/11:7		15	22	25						28			
	manus	ZPAL R.7/11:10	12	13	16	18	15	29	22	28	18	26	39	72	
Prorotodactylus mirus ichnosp. n.	pes	ZPAL R.7/31:21	9	17	24	27				32	23	23	36		73
	manus	ZPAL R.7/31:22	9	12	15	13	10	23	18	19	15	18	32	70	66
	pes	ZPAL R.7/31:7	11	22	28	31				38	24	7	7		
	manus	ZPAL R.7/31:6	8	11	16	14	8	22	16	17	13	18	31	92	
	pes	ZPAL R.7/31:38		16	27	32	12	38	25		22	7			
	manus	ZPAL R.7/31:41	10	15	18	17	10	24	19	19	15	11	11	76	
	pes	ZPAL R.7/31:42	13	24	26	29	12	47	28	39	23	8	13	23	67
	pes	ZPAL R.7/31:44		20	28	31		46	29	33	24	7			70

Table 2. Track features of *Capitosauroides fuglewiczi* ichnosp. n. Abbreviations: Sp, stride pes; Sm, stride manus; Pp, oblique pace pes; Pm, oblique pace manus; PAp, pace angulation pes; PAm, pace angulation manus; Wp, width of pace pes; Wm, width of pace manus; MP, manus-pes distance (*sensu* Haubold 1984); Dp3, divarication of pes from midline; Dm3, divarication of manus from midline Dpm, divarication of pes and manus digits III one from another. L/R, R/L, measurements from left to right and from right to left imprint, respectively.

Trackway	Sm	Sp	Pm		Pp		PAm	PAp	Wm	Wp	MP	Dp3
			L/R	R/L	L/R	R/L						
TP 1: 1–13 with the holotype, TP 1: 5, 4 (ZPAL R.7/1: 5, 4)	380 390	395 400 435 400			290 280 290	300 335		87 87 86 86		210 230	115 105 80	-35 -38 -16
TP 620: 1–11	455 435	460 465 480 465 450			310 310 320	340 370 355		87 89 83 87 88		240 240 230		
TP 223: 1–13	360 410 380	420 395 360 390 410 350 390			340 365 370 350	280 290 270 280		86 73 69 74 76 76 68		250		
TP 294: 1–8	357 357	375 312	277	165	227	326	102	87	116	196	83 120 95 58	

The distance between the tips of digits III and IV is slightly larger than that between I, II and III (Figs. 3C, D, 4B, C). Digits I–IV and I–V diverge at relatively small angles – in specimen ZPAL R.7/2: 1 they attain 25 and 47°, respectively). Digit V is more posterior and lateral to digits I–IV.

Manus. Manus imprints are slightly smaller than those of the pes, similar in shape but are all poorly preserved (Figs. 3B, 4B).

Discussion. — *Capitosauroides fuglewiczi* ichnosp. n. may be attributed to amphibians. It is abundant in the material studied, occurring mostly in main channel facies deposits.

Vertebrate tracks possibly made by amphibian trackmakers are known from the Lower Triassic of North America (Peabody 1948) and Europe (Haubold 1971a). They are mostly poorly preserved and show few diagnostic features. *Capitosauroides fuglewiczi* ichnosp. n. is somewhat larger in size than the only previously described congeneric form *C. bernburgensis* Haubold, 1971 and differs from that also in smaller pace angulation (< 90° in all tracks described; 105 and 126° in two measured specimens of *C. bernburgensis*, see Haubold 1971a). Moreover, pes imprints in *C. fuglewiczi* are much more elongated and digits I–IV and I–V have less divergent axes.

The following features of the tracks indicate that these were formed mostly under water by half-swimming animals: (1) Overstepping of manus by pes imprints, a feature not typical of amphibian tracks (Haubold 1971a); (2) Presence of tracks of aquatic invertebrates and subaqueous sedimentary structures on *Capitosauroides*-bearing surfaces, not yielding any other vertebrate footprints; (3) The 'asymmetry' of tracks (different divarication of left and right pes imprints from the midline, and different oblique pace measured from left to right and from right to left imprints in the same track); (4) The presence of incomplete tracks with preserved imprints of fe-

Table 3. Track features of *Brachychirotherium hauboldi*, *B. wiorense* ichnosp. n., *Isochirotherium sanctacrucense*, and *Isochirotherium gierlinskii* ichnosp. n. For abbreviations see Table 2.

Track	Sm	Sp	Pm	Pp	PAm	PAp	Wm	Wp	MP	Dp3	Dm3	Dpm
Brachychirotherium hauboldi ZPAL R.7/4: 1–11	448 570 687	610 610 645 673	208 238 334 353	338 280 340 335 350	180 191 169	163 161 150 154	10 28 40	50 50 87 70	235 92 80 70 97	-28 -32 -22 -26 -26 -40 -50	-42 -9 -13 -3	6 24 23
Brachychirotherium hauboldi ZPAL R.7/21: 76-83	760	750	345 330	360 330	148	138	92	125	115 105 110	-29 -21 -32	-18 -22 -16	7 7 11
Brachychirotherium wiorense ichnosp. n. ZPAL R.7/9: 1–7	405	390 380	270 175	230 230	128	120 107	100	120 145	55 105 75	-48	-38 0 0	24
Isochirotherium gierlinskii ichnosp.n. ZPAL R.7/10: 1, 2									38			16
Isochirotherium gierlinskii ichnosp.n. ZPAL R.7/11: 1–4			157	180							-19	
Isochirotherium gierlinskii ichnosp.n. ZPAL R.7/14: 1–3				183					46			
Isochirotherium gierlinskii ichnosp.n. ZPAL R.7/13: 1–5		340	185	170 193		132	(38)	70	38 46	-33	-17	
Isochirotherium sanctacrucense ZPAL R.7/17: 1–5		330	168	193		140?	55?	75?	71 95	-25	-20	5
Isochirotherium sanctacrucense ZPAL R.7/16: 1–4	327	320							80 80			0 7

ver than four feet (Figs. 2A, B, 3A, B, 4A). Such traces are best explained as left by animals partially buoyant and touching the bottom only occasionally (Brand & Tang 1991); (5) The common occurrence of distinct, S-shaped scratches (Figs. 2A, B, 3B, 4A). These are typical swimming traces like those described by Lockley & Hunt (1995).

The Wióry locality has yielded slabs with numerous, mostly indeterminable footprints due to slipping movements of their makers (Mader & Rdzanek 1985). Many of these so-called 'swim traces' (Lockley & Hunt 1995), but not all, were made by *Capitosauroides fuglewiczi* ichnosp. n. trackmakers. Some of them have no doubt been produced by other, possibly reptilian trackmakers.

Ichnofamily Chirotheriidae Abel, 1935

Ichnogenus *Brachychirotherium* Beurlen, 1959

Brachychirotherium hauboldi (Ptaszyński, 1990)

Figs. 5A–C, 6A–C; Tables 1, 3.

Chritherium lauboldi Ptaszyński sp. n. (sic!); Fuglewicz *et al.* 1990: pls. 2: 1–3, 3: 1–4, 4: 1, 11: 1; figs. 5: 1, 3–6, 6: 1, 4.

Material. — KR 5 8: 1 (plaster cast ZPAL R.7/32), isolated right pes imprint (Fuglewicz *et al.* 1990: pl. 3: 1; fig. 5: 3, syntype); KR 9 14: 1, 2, two pes imprints of probably standing animal

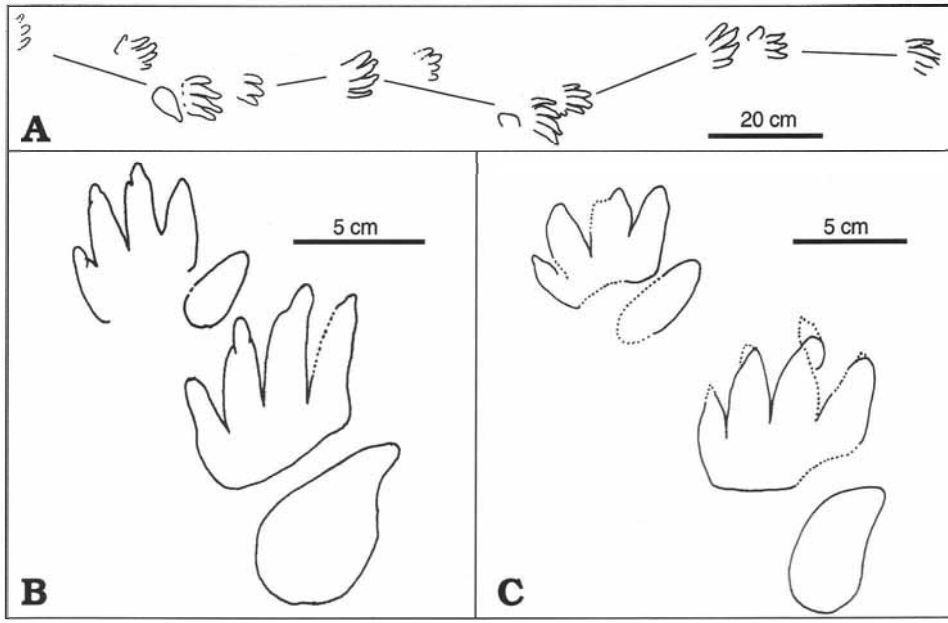
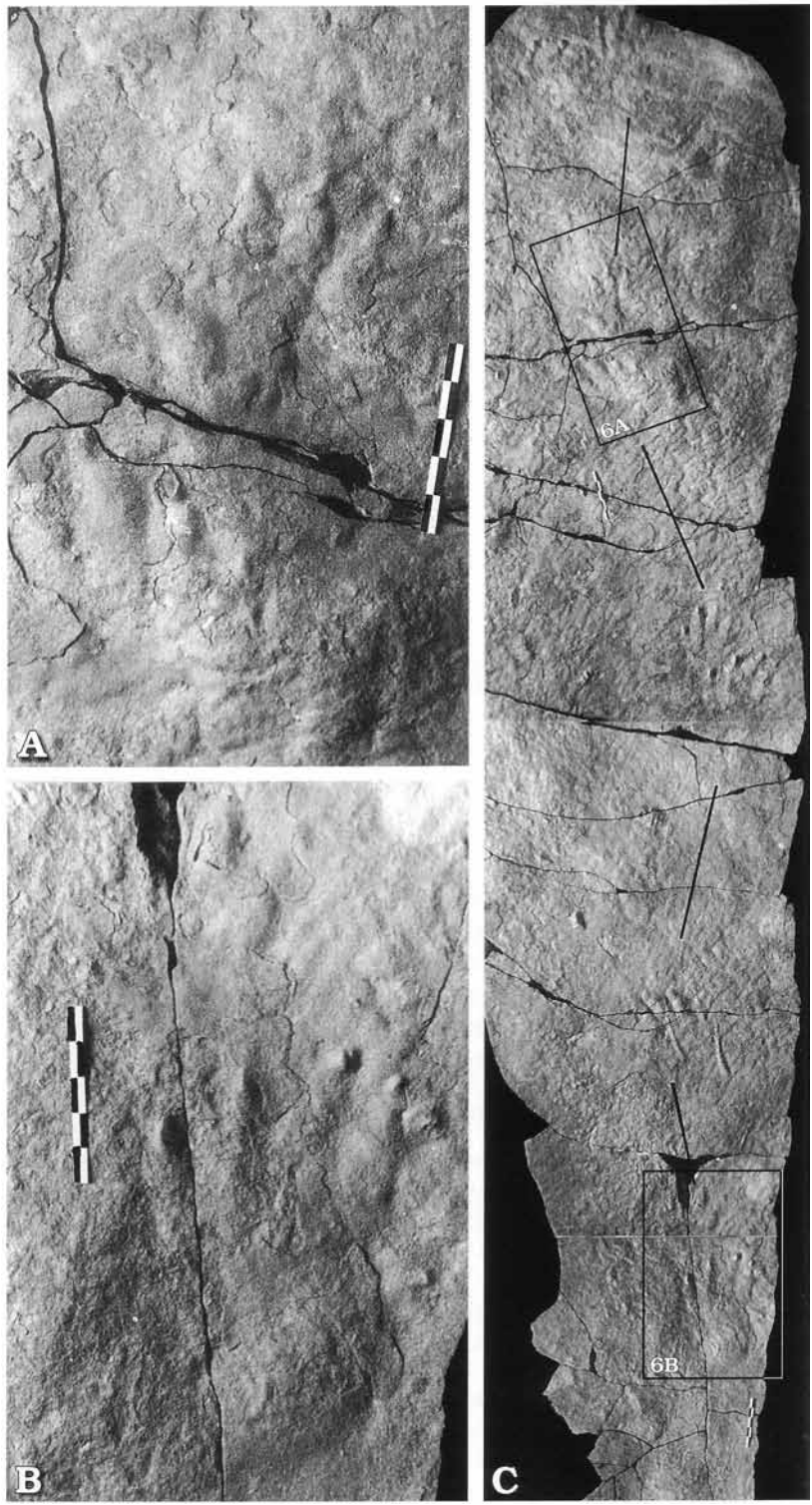


Fig. 5. *Brachychirotherium hauboldi* (Ptaszyński, 1990). **A**. Track ZPAL R.7/4: 1–11. **B**. Set of pes and manus compiled from incomplete imprints ZPAL R.7/4: 3, 4, 9, 10. **C**. Isolated set of pes and manus imprints ZPAL R.7/5: 1, 2.

(Fuglewicz *et al.* 1990: pl. 2: 1, fig. 5: 1, 5) of which specimen KR 9 14: 1 (plaster cast ZPAL R.7/33) is designed syntype; KR 1 56: 1 (plaster cast ZPAL R.7/35), isolated pes imprint (Fuglewicz *et al.* 1990: pl. 3: 3, fig. 5: 4, syntype). Tracks: MWGUW 001141 3: 12-28-25-19-24-20-21-23, track made by a walking animal which stopped for a moment (Fuglewicz *et al.* 1990: pl. 11, figs. 5: 6, 7: 6); MWGUW 001141 3: 6-5-4, fragmentary track (Fuglewicz *et al.* 1990: pl. 3: 2, fig. 6: 4); TP 12: 36-37-56-55-42-43-78, regular but only partially preserved track (Fuglewicz *et al.* 1990: fig. 6: 7); ZPAL R.7/4: 1–11, well preserved, almost regular track with imprints of all four feet visible although not all completely impressed (Figs. 5A, 6A–C); ZPAL R.7/76–83, track with shallow imprints, made by a large individual. Isolated sets of pes and manus imprints: TP 11: 1, 2, not collected (Fuglewicz *et al.* 1990: pl. 2: 3; fig. 6: 1); TP 234: 1, 2; TP 279: 1, 2; TP 463: 1, 2; ZPAL R.7/5: 1, 2 (Fig. 5C); TP 565: 1, 2; TP 569: 1, 2. Isolated pes imprints: TP 12: 24; TP 12: 80; TP 239: 1; TP 468: 1; TP 476: 1; TP 485: 1; TP 574: 1; TP 587B: 1; TP 589: 1.

Remarks. — *Chirotherium hauboldi* Ptaszyński, 1990 is reassigned here to the ichnogenus *Brachychirotherium* on account of the relatively large size of the manus (which is only 1.8 times smaller than the pes) and relatively large size of the pes digit I. In *Chirotherium* species such as *Ch. barthii* Kaup, 1835 and *Ch. sickleri* Kaup, 1835 the pes digit I is rather small in relation to digits II–IV.

Brachychirotherium hauboldi is abundant at Wióry. This ichnospecies was originally described on the basis of four syntypes which showed distinct details. One of them, a set of pes and manus imprints MWGUW 001139 16: 1–2 (Fuglewicz *et al.*1990: pl. 2: 2, fig. 5: 2) was deformed by a slipping movement of the animal. This deformation caused enlongation of the imprint of digit IV in relation to II and placement of the imprint of digit V more outwardly of digit group I–IV, as in *Synaptichnium chirotherioides* Ptaszyński, 1990. It is worth mentioning the presence of a claw on digit V, clearly visible in some specimens (Fuglewicz *et al.* 1990), a fea-


A
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6A
6B

ture regarded as primitive among Chirotheridae (Haubold 1971a). After publication of Fuglewicz *et al.*'s 1990 paper, an almost regular track was found, ZPAL R.7/4: 1–11 (Figs. 5A, 6C). The stride (pes) in this track is 610 to 673 mm; pace angulation 150–163°; oblique pace 280–350 mm. The respective values for manus are: 448–687 mm, 156–162° and 208–353 mm. The manus and pes width of pace attain 26 mm and 64 mm, on average. In the most regular part of this track, pes digit III diverges from the midline at 27° on average, whereas manus digit III diverges from the midline at about 8°.

Among other members of the ichnogenus, *B. hauboldi* is the most similar to the Middle Triassic *B. gallicum* (Willruth, 1917), but differing in smaller size and in having pes digit II almost equal to digit IV whereas in *B. gallicum* digit II is significantly longer than IV. Pes digit V of *B. hauboldi* is much shorter in relation to the digit group I–IV than in *B. gallicum*.

Brachychirotherium wiorense ichnosp. n.

Figs. 7A–C, 8A–C, 9A, 10A; Tables 1, 3.

Brachychirotherium kuhni Demathieu & Haubold, 1982; Fuglewicz *et al.* 1990: pls. 5: 1, 2; 6: 1; 10: 3; fig. 8: 1–4.

Holotype: ZPAL R.7/6: 1, 2 – set of right pes and manus imprints (Figs. 7A, 8B).

Type locality: Wióry near Ostrowiec Świętokrzyski, Holy Cross Mts, Poland.

Type horizon: Labyrinthodontidae Beds, Middle Buntsandstein, Lower Triassic.

Derivation of the name: after the village of Wióry, type locality of the species.

Diagnosis. — Large *Brachychirotherium* with low value of cross axis angle, about 50°. Digit group I–IV strongly curved outwards. Pes digit length relations: III>II>IV>I; digits II and IV are approximately equal in length and digit III is distinctly longer than II. Divarication of manus digits I–V axes attains 102–105°.

Material. — Fragments of a single track: ZPAL R.7/7a: 1 (right manus imprint) and ZPAL R.7/7b: 2, 3 (left set of pes and manus imprints), and ZPAL R. 7/7c: 1 (right pes imprint) (Figs. 7B, C, 8A); TP 50: 1–7 (plaster cast ZPAL R.7/9: 1–7), partly destroyed, irregular track composed of right pes imprint and three consecutive sets of pes and manus imprints (Fig. 9A). Sets of imprints and isolated imprints: TP 5: 1 (not collected), partially preserved imprint of left pes (Fuglewicz *et al.* 1990: pl. 5: 1, fig. 8: 4); plaster cast ZPAL R.7/47, isolated left pes digit group I–IV imprint (Fuglewicz *et al.* 1990: pl. 6: 1, fig. 8: 3); ZPAL R.7/43, isolated imprint of right pes (Fuglewicz *et al.* 1990: pl. 5: 2, fig. 8: 1); plaster casts ZPAL R.7/48: 1, 2, set of right pes and manus imprints (Fuglewicz *et al.* 1990: fig. 8: 2); TP 261: 1, 2, partially preserved set of right pes and manus imprints; ZPAL R.7/8: 1, 2, set of right pes and manus imprints (Figs. 8C, 10A); ZPAL R.7/13: 6, 7, poorly preserved set of left pes and manus imprints. Specimens TP 261 and ZPAL R.7/8: 1, 2 were collected from the same surface as ZPAL R.7/7 and may represent other parts of the same track, damaged by exploitation.

Description. — Track. Track features of *Brachychirotherium wiorense* ichnosp. n. are poorly known. The irregular track ZPAL R.7/9: 1–7 (Fig. 9A) suggests a pes width of pace of 120 to 145 mm, and that of manus, 100 mm. The pace angulation of pes is low, 107 to 120°. The single measured manus pace angulation equals 128°. Stride and oblique pace of pes are 380–390 mm and 230 mm, respectively. Stride and oblique pace of manus imprints are 405 mm and 175–270 mm, respectively. In the holotype ZPAL R.7/6: 1, 2 axes of pes and manus are parallel. In the specimen ZPAL R.7/7b: 2, 3 the angle between pes and manus axes is 22° wheras in the specimen ZPAL R.7/8: 1, 2 it is 28°. In track ZPAL R.7/9: 1–7, the divarication of pes from the track midline equals 48°; three manus imprints in this track diverge from the midline between 0 and 38°.

Fig. 6. *Brachychirotherium hauboldi* (Ptaszyński, 1990). **A**. Set of pes and manus imprints ZPAL R.7/4: 9, 10. **B**. Set of pes and manus imprints ZPAL R.7/4: 3, 4. **C**. Track ZPAL R.7/4: 1–11, in rectangles shown A, B, see also Fig. 5C. Scale in cm.

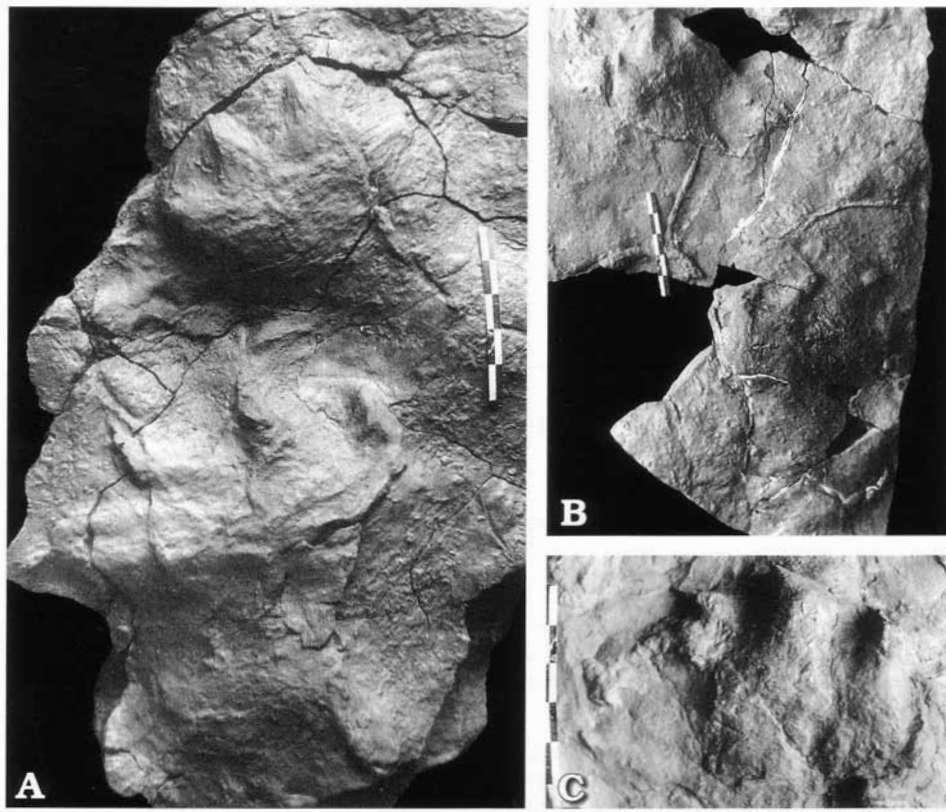


Fig. 7. *Brachychirotherium wiorense* ichnosp. n. **A**. Set of right pes and manus imprints, holotype ZPAL R.7/6: 1, 2 see also Fig. 8B. **B**. Set of left pes and manus imprints ZPAL R.7/7b: 2, 3. **C**. Right manus imprint ZPAL R.7/7a: 1. Scale in cm.

Pes. Pes imprints are almost as long as wide. In the holotype, the pes imprint ZPAL R.7/6: 1 is 121 mm long and 117 mm wide. Claws are present at tips of all five digits, those of the first three digits being large and distinct. The claw of digit IV is narrower (Figs. 7A, 8B). Indistinctly impressed claw is also present at the tip of the large and massive digit V. Pes digit III is the longest of the group I–IV; digit II is longer than IV which is slightly longer than I. The digit group I–IV is strongly curved outwards; axes of digits V and IV are almost parallel. The difference in angles between digit axes I–IV and I–V is about 9° on average. The axes angle of digits I–IV is relatively large at 56°. Cross axis angle in the holotype equals 60°; in other specimens, often poorly preserved, it ranges from 40 to 62° (56° on average). Pes digits I–IV are 1.3–1.4 times longer than the corresponding digits of manus.

Manus. Manus imprints are wide and relatively large. All five digits have distinct, sharp claws. The relatively long digit V is distinctly turned outwards in comparison to digit group I–IV. Digit I is distinctly separated from the digit group I–IV (Fig. 7C). Digits I–V axes diverge between 102 and 105°.

Discussion. — *Brachychirotherium wiorense* ichnosp. n. is rare in the material studied. The only ichnospecies comparable to that from Wióry, is *B. kuhni* Demathieu & Haubold, 1982 from Lower Triassic Solling Folge deposits (Demathieu & Haubold 1982; Fuglewicz *et al.* 1990).

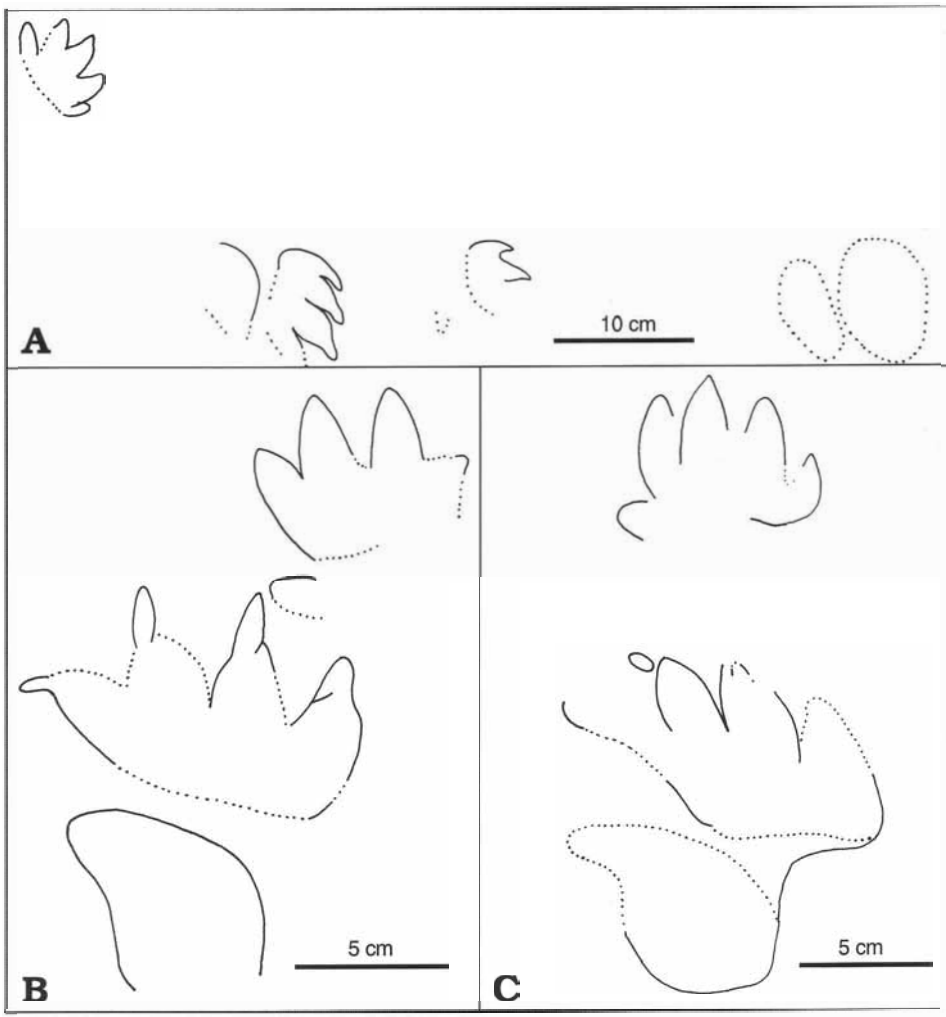


Fig. 8. *Brachychirotherium wiorense* ichnosp. n. **A**. Fragmentary track containing specimens ZPAL R.7/7a: 1, ZPAL R.7/7b: 2, 3, and ZPAL R.7/7c: 1. **B**. Set of pes and manus imprints, holotype ZPAL R.7/6: 1, 2. **C**. Set of pes and manus imprints ZPAL R.7/8: 1, 2.

Isolated footprints of *B. wiorense* ichnosp. n. from Wióry were at first identified as *B. kuhni* Demathieu & Haubold, 1982 (Fuglewicz *et al.* 1990) because of their similarity to that ichnospecies. *B. wiorense* ichnosp. n. is much larger than *B. kuhni*, has longer pes digit IV in relation to I, II and III, and more divergent pes and manus digits I–IV and manus digits I–V. Its pes digit III is distinctly longer than II, being almost equal to the II in *B. kuhni*. *B. wiorense* ichnosp. n. shows a lesser length relation between respective pes and manus digits I–IV in comparison to *B. kuhni*. The pes digit group I–IV in *B. wiorense* ichnosp. n. is almost as long as wide, similar to the whole pes imprint, in contrast to the relatively wide digit group I–IV and much narrower whole pes imprint of *B. kuhni*. The manus width of pace in *B. wiorense* ichnosp. n. is approximately equal to that of pes. In *B. kuhni* the manus width of pace seems to be distinctly larger than that of pes (compare Demathieu & Haubold 1982: photo 4, p. 102).

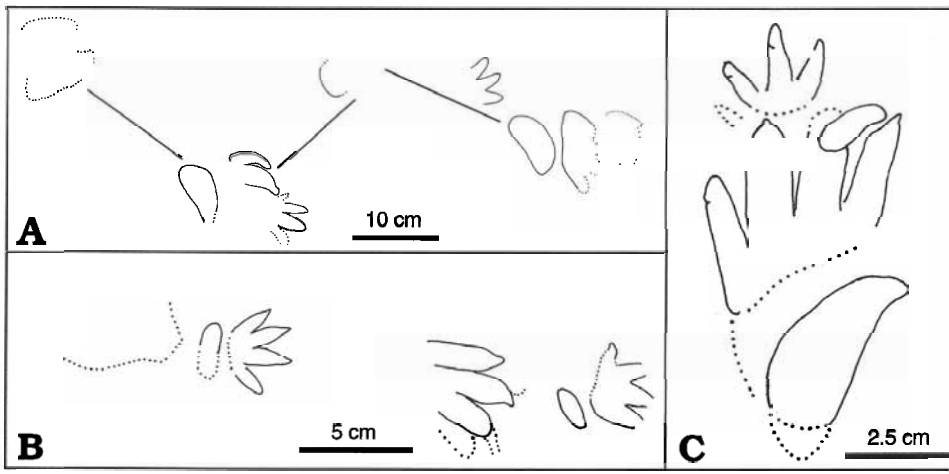


Fig. 9. **A.** *Brachychirotherium wiorense* ichnosp. n.; fragmentary track ZPAL R.7/9: 1–7. **B, C.** *Isochirotherium gierlinskii* ichnosp. n. **B.** Two consecutive sets of imprints ZPAL R.7/11: 1–4; see also Fig. 10D. **C.** Set of pes and manus imprints, holotype ZPAL R.7/10: 1, 2; see also Fig. 10B.

B. wiorense ichnosp. n. differs from *B. hauboldi* in having the digit group I–IV curved strongly outwards, digit IV almost parallel to the V, almost twice greater angle between digits I and IV, more divergent manus digits I–V, and low pace angulation.

Genus *Isochirotherium* Haubold, 1971

Isochirotherium gierlinskii ichnosp. n.

Figs. 9B, C, 10B–E, 11A–C; Tables 1, 3.

Holotype: ZPAL R.7/10: 1, 2, set of left pes and manus imprints (Figs. 9C, 10B) forming a natural cast of the specimen ZPAL R.7/13: 1, 2.

Type locality: Wióry near Ostrowiec Świętokrzyski, Holy Cross Mts, Poland.

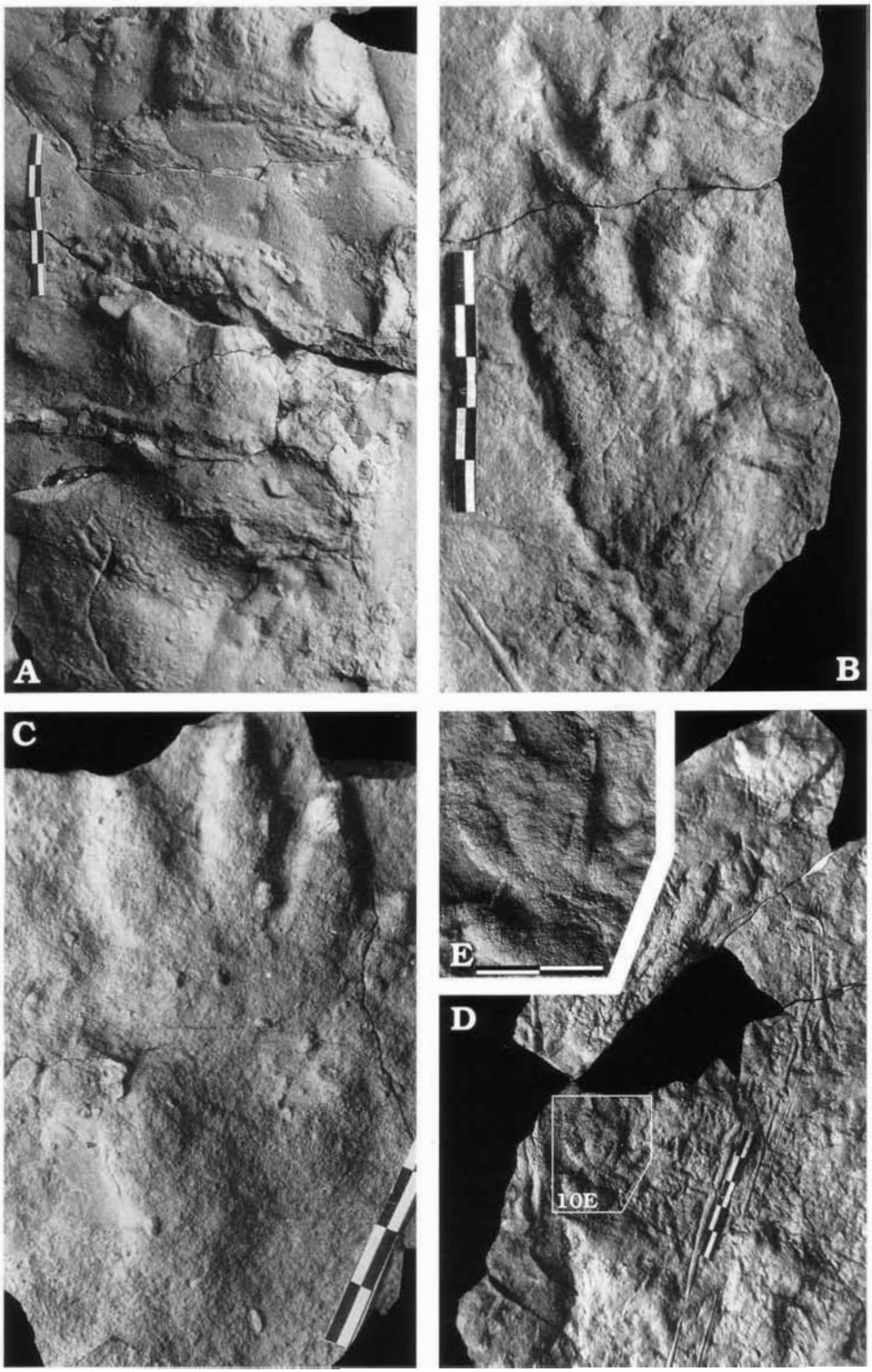
Type horizon: Labyrinthodontidae Beds, Middle Buntsandstein, Lower Triassic.

Derivation of the name: In honour of Gerard Gierliński, researcher of Mesozoic vertebrate footprints.

Diagnosis. — Small *Isochirotherium* with first four pes digits subequal in length but having typical length relations III>II>IV>I. Pes digit V relatively long, diverging from the digit group I–IV under low angle, 15°. Manus imprints small, more than twice shorter than those of pes. Manus surface is about four times smaller than that of pes. The divarication of manus digits I–IV high, up to 84°; that of I–V ranges between 80 and 120°. Cross axis angle 70°.

Material. — ZPAL R.7/11: 1–4, two consecutive sets of pes and manus imprints (Figs. 9B, 10D, E); ZPAL R.7/14: 1–3, set of pes and manus and next consecutive pes imprints (Fig. 11B); ZPAL R.7/45: 2 isolated pes imprint; ZPAL R.7/13: 1–5, track consisting of two sets of pes and manus and the next consecutive pes imprint (Fig. 11A) preserved on the upper side of a sandstone layer, of which the natural casts of imprints ZPAL R.7/13: 1, 2, num-

Fig. 10. **A.** *Brachychirotherium wiorense* ichnosp. n.; set of right pes and manus imprints ZPAL R.7/8: 1, 2. **B–E.** *Isochirotherium gierlinskii* ichnosp. n. **B.** Set of left pes and manus imprints, holotype ZPAL R.7/10: 1, 2; see also Fig. 9C. **C.** Isolated pes imprint ZPAL R.7/12: 1, see also Fig. 11C. **D.** Two consecutive sets of pes and manus imprints ZPAL R.7/11: 1–4; see also Fig. 9B. **E.** Manus imprint ZPAL R.7/11: 2, enlargement of the area marked in D. Scale in cm.


A
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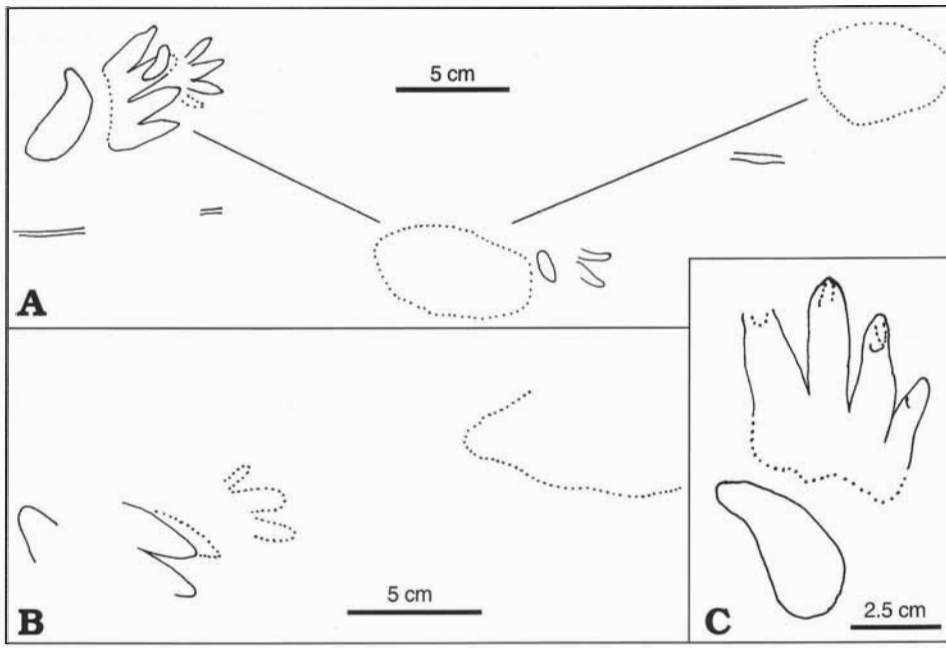


Fig. 11. *Isochirotherium gierlinskii* ichnosp. n. **A**. Short, incomplete track with tail mark ZPAL R.7/13: 1–5. **B**. Two consecutive pes and one manus imprints ZPAL R.7/14: 1–3. **C**. Isolated pes imprint ZPAL R.7/12: 1.

bered ZPAL R.7/10: 1, 2, are designated holotype; ZPAL R.7/12:1, isolated pes imprint (Figs. 10C, 11C).

Description. — Track. Fragmentary tracks ZPAL R.7/13: 1–5, ZPAL R.7/14: 1–3, ZPAL R.7/10: 1, 2 and ZPAL R.7/11: 1–4 are from a single track bearing surface and may have been produced by the same individual. The stride pes of this relatively small animal attains 340 mm; pace angulation is relatively low, 132°; the relation of stride to pes length ratio equals 4.1. The pes width of pace is about 70 mm, the oblique pace ranges from 170 up to 195 mm (Figs. 9B, 10D, 11A).

Pes. Pes imprints of this ichnospecies, and of *Synaptichnium kotanskii* ichnosp. n. (see below) are the smallest among the Chirotheriidae from Wióry. The best preserved specimen, holotype ZPAL R.7/10: 1, 2 is 88 mm long and 54 mm wide. The width of digit group I–IV equals its length. Length relations of digits I–IV are III>II>IV>I. Digits are more equal in length than in other ichnospecies from Wióry: digit III is only 1.34 times longer than I, and digit IV is only slightly shorter than II. The first four digits have relatively large claws. The first three digits are more deeply impressed than the fourth. Long and strongly developed pes digit V (49 mm in length) also ends with a claw (Figs. 9C, 10B, C). Cross axis angle is low, 70°.

Manus. Manus imprints are relatively small; the imprint of the holotype manus is 35 mm long and 36 mm wide. All five digits, slender in outline, have distinct claws. Characteristic is the strong inclination of digit I towards the midline, high divarication of digits I–IV, 52 up to 84° (70° on average), and that of digits I–V, ranging between 80 and 120°. Digit V is relatively small; it is similar in size and outline to the first four digits (Fig. 10B, E). The manus surface is about four times smaller than that of pes. In the holotype the posterior portion of the manus imprint is overlapped by that of the pes, which is an unusual feature among Chirotheriidae (Figs. 9C, 10B).

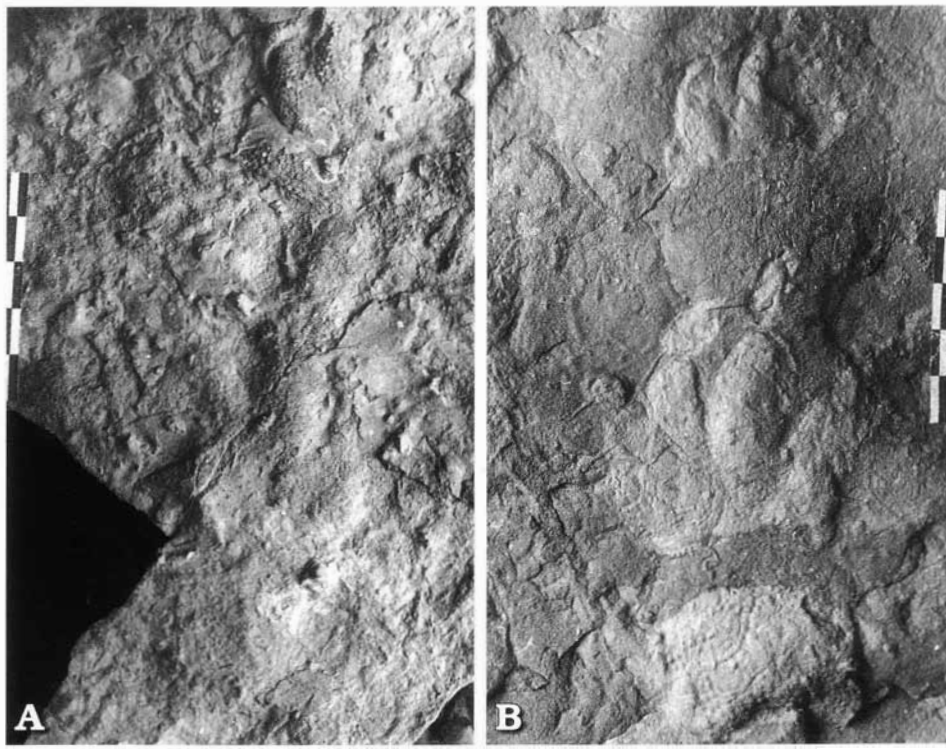


Fig. 12. *Isochirotherium sanctacrucense* Ptaszyński, 1990. **A**. Set of right pes and manus imprints ZPAL R.7/15: 1, 2, see also Fig. 13A. **B**. Set of left pes and manus imprints ZPAL R.7/16: 1, 2; see also Fig. 13B. Scale in cm.

Discussion. — *Isochirotherium gierlinskii* ichnosp. n. differs significantly from other Chirotheriidae from Wióry in having subequal pes digits I–IV and in the general structure of the relatively small manus imprints with slender digits and widely expanded manus digits I–V axes.

Isochirotherium gierlinskii ichnosp. n. reveals features typical of *Isochirotherium*: small size of manus imprints in relation to those of pes, digits I–IV length proportions, and relatively large pes digit V. The cross axis angle is exceptionally small thus resembling small *Brachychirotherium* such as *B. paeneparvum* Demathieu & Leiz, 1982 and *B. hessei* (Soergel, 1925).

In comparison with *I. santacrucense*, *I. gierlinskii* ichnosp. n. has a slender outline of all five manus digits, larger angles between their axes, longer pes digit V, more than two times exceeding the length of the digit group I–IV, and a low value of cross axis angle.

Isochirotherium sanctacrucense Ptaszyński, 1990

Figs. 12A, B, 13A–C; Tables 1, 4.

Isochirotherium sanctacrucense Ptaszyński sp. n.; Fuglewicz *et al.* 1990: pls. 4: 1, 3, 4; 11; fig. 7: 3, 4, 5, 7.

Isochirotherium sanctacrucense Ptaszyński, 1990; Fichter & Lepper 1997: figs. 2–4.

Material. — MWGUW 001141 3: 29-30-35-17-13-14, irregular track including the holotype MWGUW 001141 3: 29 (plaster cast of holotype ZPAL R.7/36) (Fuglewicz *et al.* 1990: pl. 4: 1, 3; fig. 7: 3, 7); ZPAL R.7/17: 1–5, fragmentary track consisting of two sets and next

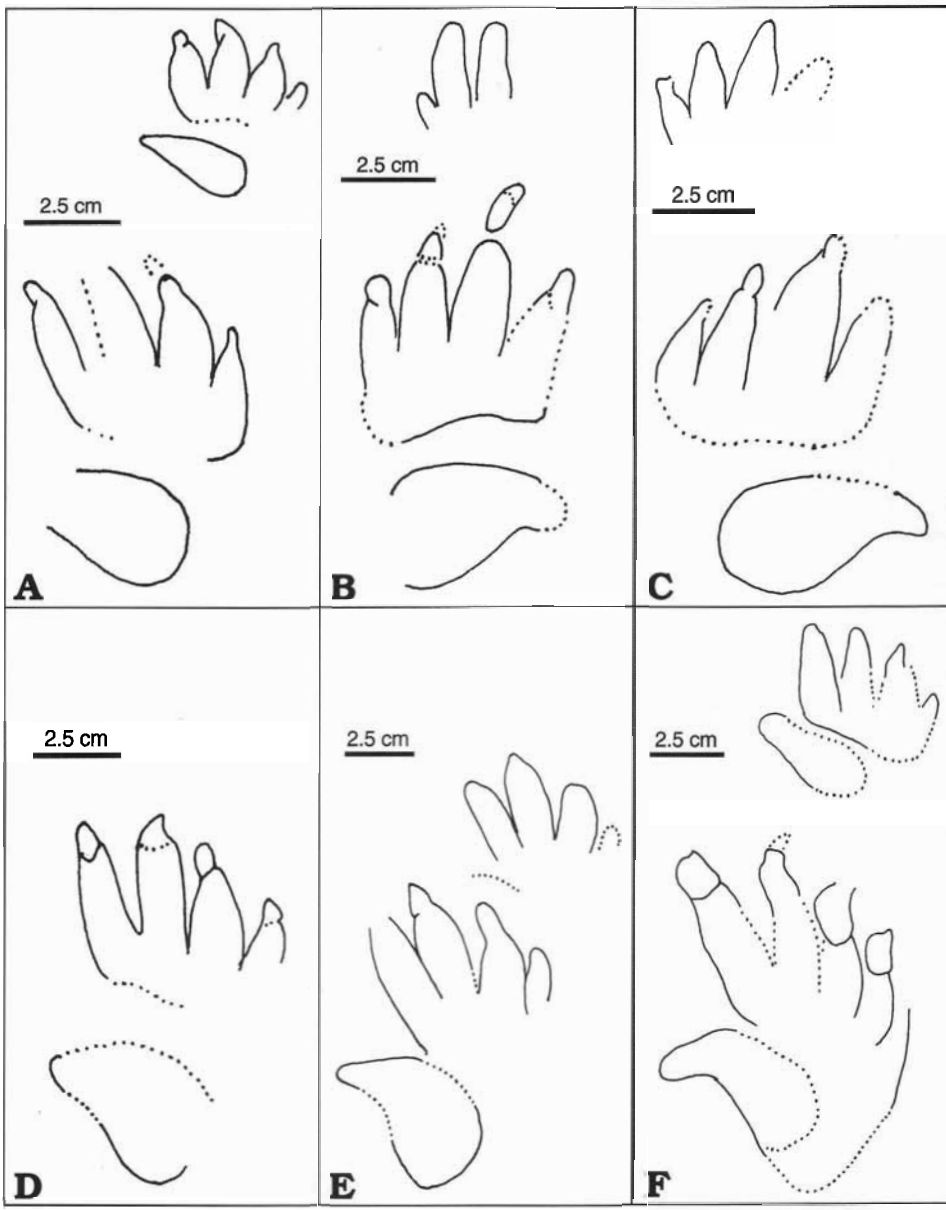


Fig. 13. **A–C.** *Isochirotherium sanctacrucense* Ptaszyński, 1990. **A.** Set of right pes and manus imprints ZPAL R.7/15: 1, 2. **B.** Set of left pes and manus imprints ZPAL R.7/16: 1, 2. **C.** Set of left pes and manus imprints ZPAL R.7/17: 3, 4. **D–F.** *Synaptichnium chirotherioides* Ptaszyński, 1990. **D.** Right pes imprint ZPAL R.7/18: 1. **E.** Set of right pes and manus imprints ZPAL R.7/12, 13. **F.** Set of right pes and manus imprints ZPAL R.7/19: 1, 2.

consecutive pes imprint mostly partially and shallowly impressed, poorly preserved (Fig. 13C); MWGUW 001140 13: 7 (plaster cast ZPAL R.7/37), specimen described as paratype (Fuglewicz *et al.* 1990: pl. 4: 4; fig. 7: 4); ZPAL R.7/15: 1, 2, isolated set of right pes and

Table 4. Track features of *Synaptichnium chirotherioides* and *S. kotanskii* ichnosp. n. For abbreviations see Table 2.

Synaptichnium chirotherioides	Sm	Sp	Pm	Pp	PAm	PAp	Wm	Wp	MP	Dp3	Dm3	Dpm
ZPAL R.7/4:12–15			408	400					67 85	-17		0 10
Synaptichnium kotanskii ichnosp. n.	Sm	Sp	Pm	Pp	PAm	PAp	Wm	Wp	MP	Dp3	Dm3	Dpm
ZPAL R.7/21: 1–13	317 311 293 308	316 314 314 295 320	153 157 171 151	167 171 158 155 180 154	140 143 139	140 133 141 141 138	52 55 49	64 55 53 67 57	72 62 51 68 66 65	-8 -20 -12	0	
ZPAL R.7/21: 14–19		358		195 175		163		30	76	-17 -5	-4 -2	
ZPAL R.7/21: 20–26		460 385		270 215		156		53	100	-13 -15	-4	
ZPAL R.7/21: 33–39	375	375 390	205 200	190 220 200	140	136 143	65	75 70	55 60 68	-13 -12	-3	
ZPAL R.7/21: 40–45		530 524	258 292	270		153	67		45 53	-16	-11 -18	
ZPAL R.7/21: 53–56		362		185				67	77	-20		9
ZPAL R.7/21: 46–52		405 383		185 193 225		145 145		56		-22		

manus imprints (Figs. 12A, 13A; Fuglewicz *et al.* 1990: fig. 7: 5); ZPAL R.7/16: 1–4, fragmentary track conwsisting of two consecutive sets of shallow imprints with the scaly skin surface visible (Figs. 12B, 13B).

Remarks. — *Isochirotherium sanctacrucense* Ptaszyński, 1990 is rare in the material studied. The original description of this ichnospecies was based upon an irregular track containing the holotype, deformed by the sliding movement, and incompletely preserved paratype (see Fuglewicz *et al.* 1990). Between 1985 and 1995, two fragmentary tracks and some isolated sets of imprints were found. In the fragmentary track ZPAL R.7/1–4 the stride pes is only 330 mm, much less than in MWGUW 001141 3: 29-30-35-17-13-14 (see Fuglewicz *et al.* 1990); oblique pace of pes and manus equals 193 and 168 mm, respectively. Pace angulation of pes is about 140°. The width of pace for pes and manus equals approximately 75 and 55 mm; the best preserved imprint of pes diverges out from the midline at 25°; the same feature for the manus attains 20°. The well-preserved specimen ZPAL R.7/16: 1 (Figs. 12B, 13B) distinctly shows the most characteristic features of this ichnospecies: the whole imprint of digit IV being distinctly shorter than II and only slightly longer than I; high value of the cross axis angle, 81°, and digit V behind the digit group I–IV. Dermal scales imprints are visible on the latter. Pes digit length relations are typical of *Isochirotherium* representatives: III>II>IV>I.

Isochirotherium sanctacrucense is a primitive form with a relatively long pes digit IV. However, it is much shorter than II and relatively small, but large in relation to other *Isochirotherium* manus imprints. Together with *Brachychirotherium hauboldi* and *Synaptichnium chirotherioides*, it represents one of three similarly sized ichnospecies belonging to three different ichnogenera of Chirotheriidae present at Wióry.

Fichter & Lepper (1997) have recently described a specimen assigned to *I. sanctacrucense* from the Middle Buntsandstein of Germany.

?Isochirotherium sp.

Isochirotherium sp.; Fuglewicz *et al.* 1990: pls. 5: 3, 4; 10: 2; fig. 7: 1, 2.

Remarks. — The footprint assemblage from Wióry contains rare tracks which are much larger than the largest known *Brachychirotherium hauboldi* and *B. wiorense* ichnosp. n. They are poorly preserved, incomplete or deformed, and therefore not identifable. The only known well-preserved specimen TP 2: 5 (not collected) is assigned to *Isochirotherium* sp. (Fuglewicz *et al.* 1990: fig. 7: 1; pl. 5: 4 and pl.10: 2 left upper corner of the photograph) is longer there, having been damaged by quarrying. Other specimens, in part representing 'swim traces', have been observed on slabs TP 48, TP 227, TP 291, TP 386 and TP 714. The large tracks from Wióry may either represent extremely large representatives of one of the *Brachychirotherium* ichnospecies or belong to *Isochirotherium.*

Ichnogenus *Synaptichnium* Nopcsa, 1923

Synaptichnium chirotherioides Ptaszyński, 1990

Figs. 13D–F, 14A–D; Tables 1, 4.

Synaptichnium chirotherioides Ptaszyński ichnosp. n.; Fuglewicz *et al.* 1990: pl. 6: 2, 3, 4; fig. 8: 5, 6, 7.

Material. — Tracks: TP 12: 4-18-41-49, fragmentary track (Fuglewicz *et al.* 1990: fig. 8: 5); ZPAL R.7/4: 12–15, two consecutive sets of imprints (Figs. 13E, 14C); MWGUW 001142 13: 6 (plaster cast ZPAL R.7/39), syntype (Fuglewicz *et al.* 1990: pl. 6: 2, 4). Isolated specimens: ZPAL R.7/20: 2, 3, set of left pes and manus (barely visible) imprints, syntype (Fig. 14A) and Fuglewicz *et al.* 1990: pl. 6: 3; fig. 8: 6); TP 13: 8, 9, imprints of left and right manus, probably associated with syntype MWGUW 001142 13: 6 (Fuglewicz *et al.* 1990: pl. 6: 4); TP 431: 1, isolated left pes imprint; ZPAL R.7/19: 1, 2, set of right pes and manus imprints (Figs. 13F, 14D); ZPAL R.7/18: 1, isolated right pes imprint with scaly skin surface visible (Fig. 14B).

Remarks. — *Synaptichnium chirotherioides* is a relatively large form with pes digit length relations III>IV>II>I. Fragmentary tracks and isolated footprints found during the past ten years have made it possible to observe complete footprint and track features. With regard to the size and general shape, *S. chirotherioides* may be compared with the large-sized ichnospecies *S. primum* Demathieu & Haubold, 1982. In *S. chirotherioides* pes digit IV is only slightly longer than II, in contrast to *S. primum* in which pes digit IV length exceeds that of II more than 1.5 times (Demathieu & Haubold 1982: table 1). In *S. chirotherioides,* divarications of pes digits I–IV, II–IV and I–V attain higher values than those in *S. primum.* Pes imprints of *S. chirotherioides* are shorter and wider than those of *S. primum.*

Synaptichnium kotanskii ichnosp. n.

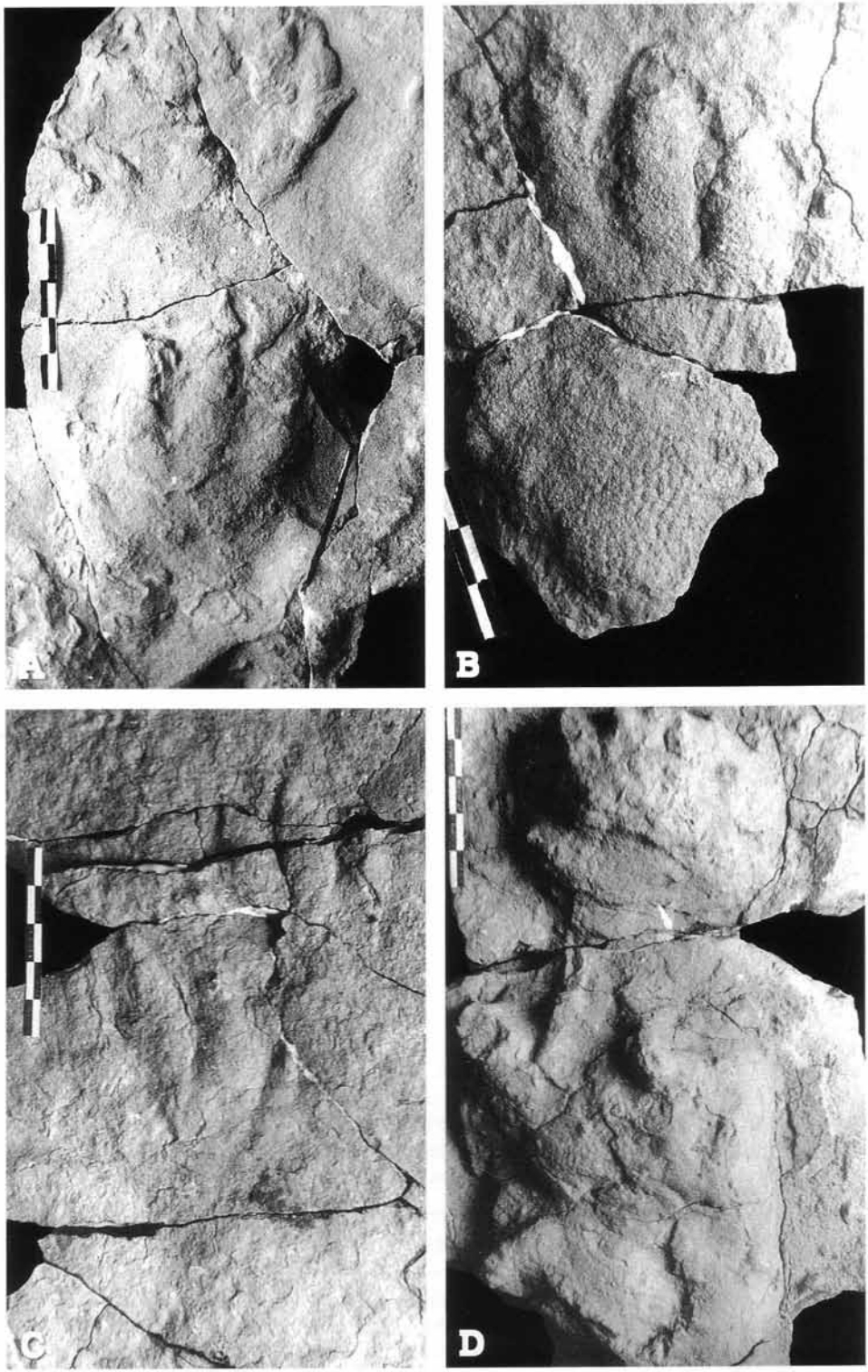
Figs. 15A–C, 16A–D, 17A, B, 18A–F, 19A; Tables 1, 4.

Holotype: ZPAL R.7/21: 11, left pes imprint (Figs. 16A, 17A, 18A), and ZPAL R.7/21: 13, the best impressed and preserved right manus (Figs. 16B, 17A, 18B), both from the regular track ZPAL R.7/21: 1–13.

Type locality: Wióry near Ostrowiec Świętokrzyski, Holy Cross Mts, Poland.

Type horizon: Labyrinthodontidae Beds, Middle Buntsandstein, Lower Triassic.

Fig. 14. *Synaptichnium chirotherioides* Ptaszyński, 1990. **A.** Set of left pes and just visible manus imprints ZPAL R.7/20: 2, 3, syntype (see Fuglewicz *et al.* 1990: pl. 6: 3, fig. 8: 6). **B.** Right pes imprint ZPAL R.7/18: 1. **C.** Set of right pes and manus imprints ZPAL R.7/12, 13. **D.** Set of right pes and manus ZPAL R.7/19: 1, 2. Scale in cm.


A
B
C
D

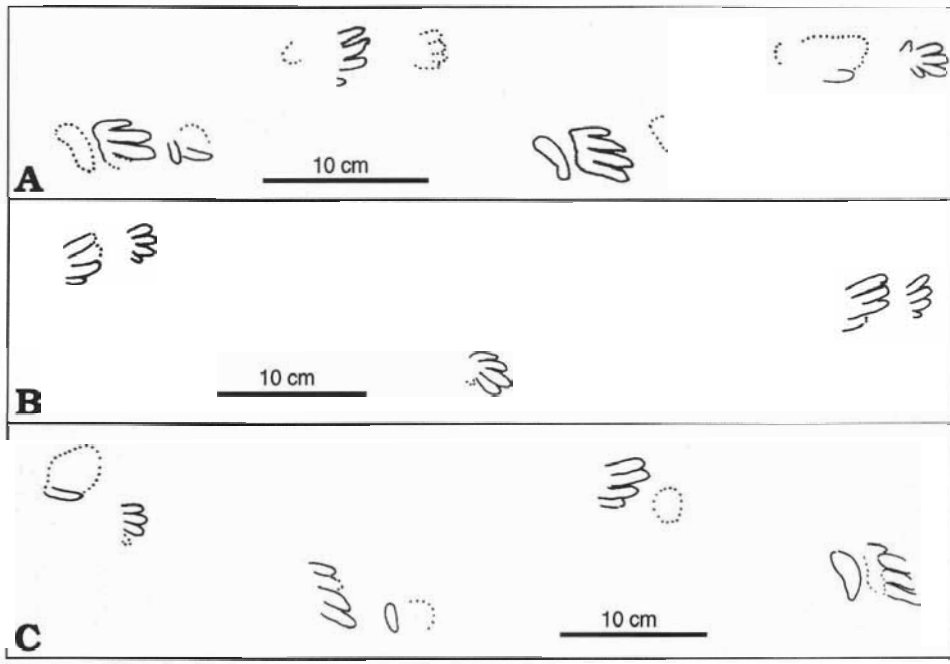


Fig. 15. *Synaptichnium kotanskii* ichnosp. n. **A**. Track ZPAL R.7/21: 7–13. **B**. Track ZPAL R.7/21: 40–44. **C**. Track ZPAL R.7/21: 33–39.

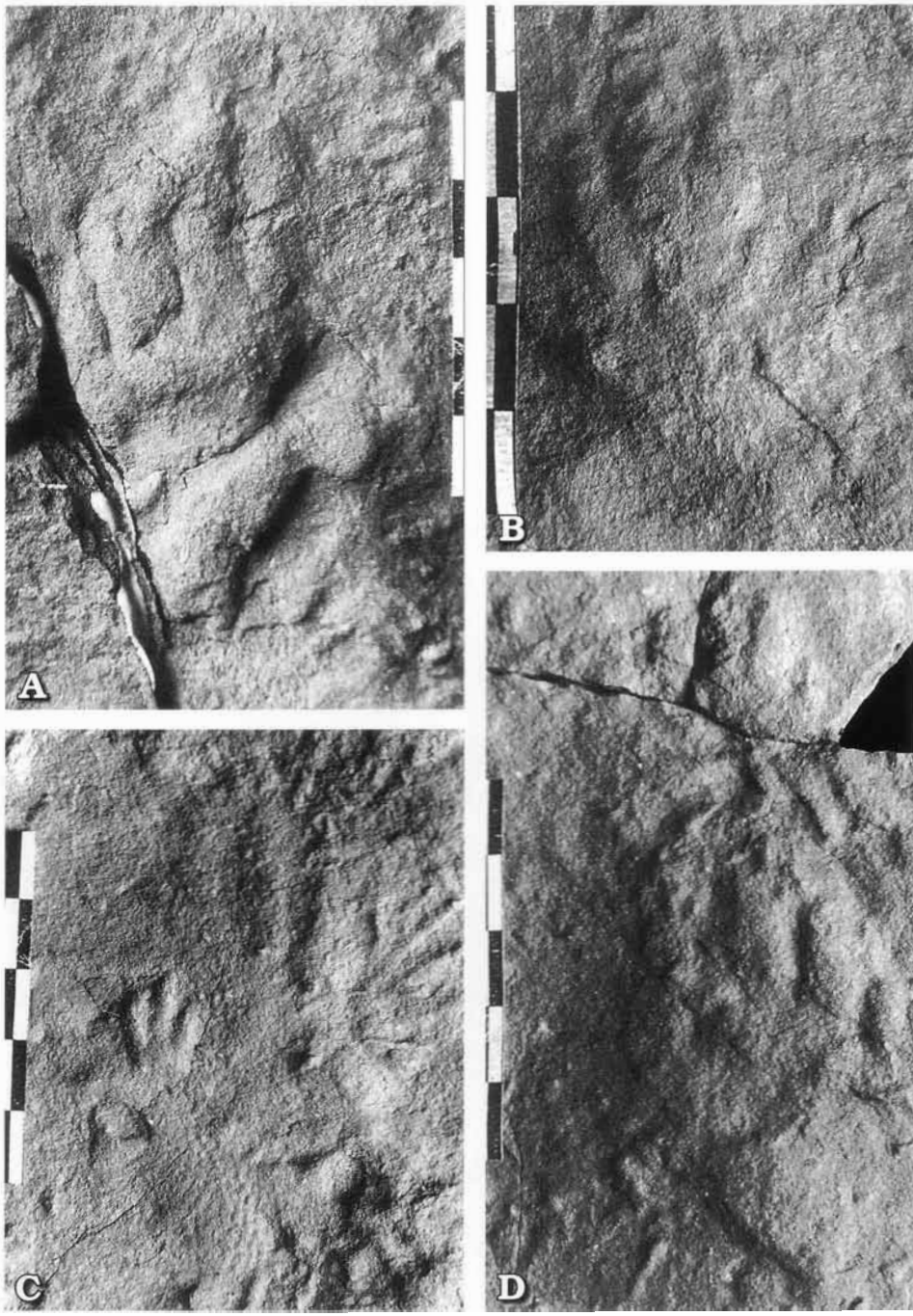
Derivation of the name: In honour of Professor Zbigniew Kotański, expert of the Polish Triassic.

Diagnosis. — Small *Synaptichnium* with pes digits III and IV equal in length, and relatively long digit II. Both pes and manus digits II–IV are subparallel. Manus digit III longer than IV. Divarications of pes digits I–IV and II–IV are low, 10 and 6°, respectively.

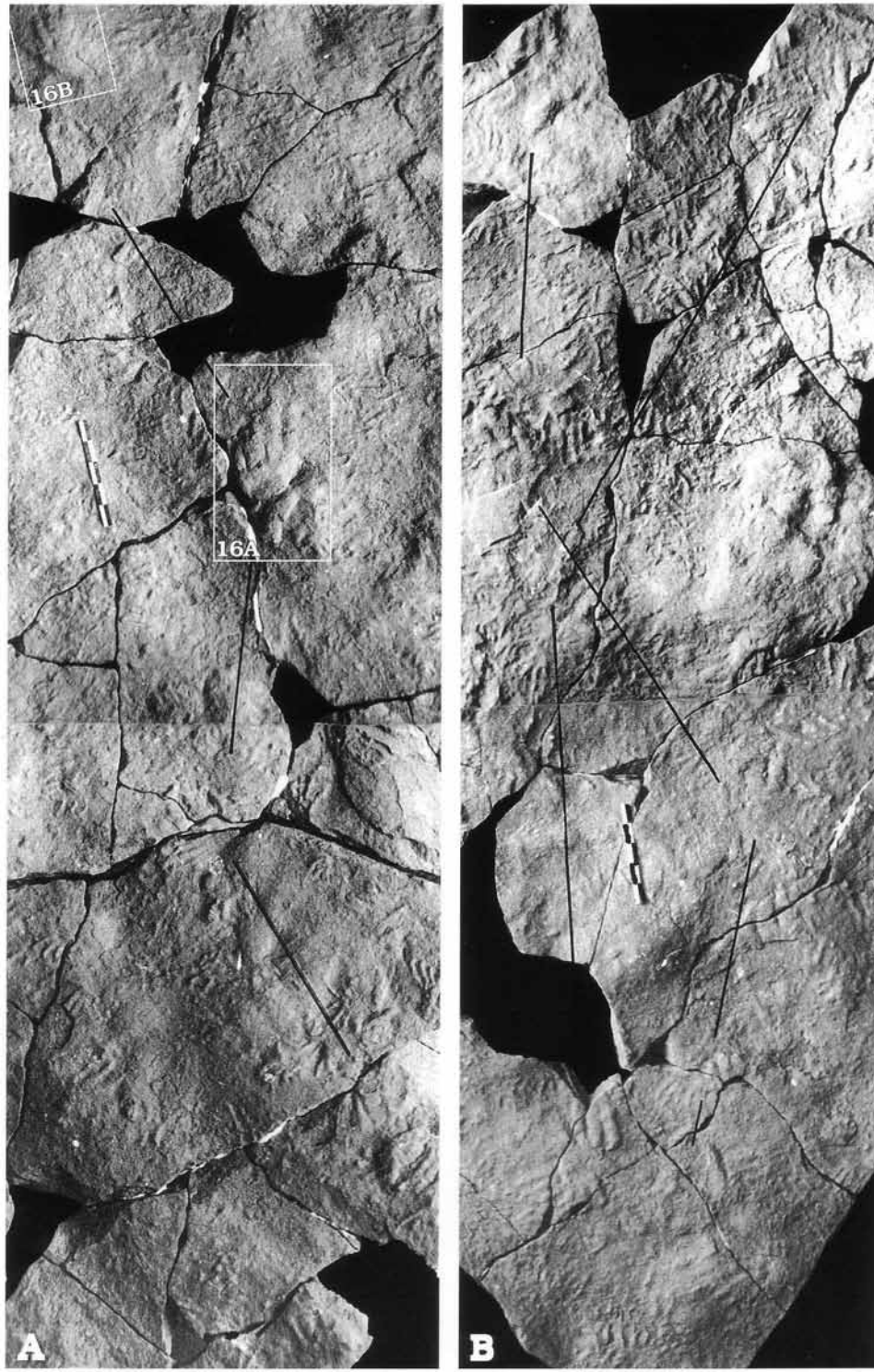
Material. — ZPAL R.7/21: 1–13, regular track consisting of 7 consecutive sets of pes and manus imprints representing various degrees of impression and state of preservation (Figs. 15A, 17A), containing specimens ZPAL R.7/21: 11 (left pes imprint) and ZPAL R.7/21: 13 (right manus imprint) designated holotype; footprints ZPAL R.7/21: 94–96 belong possibly to the same track; ZPAL R.7/21: 14–19 and ZPAL R.7/21: 90–93, two parts of the same, incomplete track (Fig. 18C, D); ZPAL R.7/21: 20–26, partially preserved track (Figs. 16D, 18E); ZPAL R.7/21: 27–32, incomplete and poorly preserved track of animal which possibly stopped for a moment; ZPAL R.7: 33–39, incomplete track which may have been left by the same individual as ZPAL R.7/21: 20–26 (Figs. 15C, 17B); ZPAL R.7/21: 40–45, short track with unusually long stride (running gait?) (Figs. 15B, 17B); ZPAL R.7/21: 46–52 and ZPAL R.7/21: 53–56, two tracks intersecting, incomplete (Figs. 16C, 18F); ZPAL R.7/24: 1, 2, set of left pes and manus imprints (Fig. 19A). Incomplete, shallowly impressed or isolated imprints and fragmentary tracks of the new ichnospecies are also present on slabs ZPAL R.7/17 and ZPAL R.7/31.

Description. — Track. A few reguarly developed tracks are known from the large slab ZPAL R.7/21. Stride of the track containing holotype equals from 295 up to 320 mm. Pes pace →

Fig. 16. *Synaptichnium kotanskii* ichnosp. n. **A**. Left pes imprint, holotype ZPAL R.7/21: 11, enlargement of the area rectangled in Fig. 17A; see also Fig. 18A. **B**. Right manus imprint ZPAL R.7/21: 13 from the same track as specimen ZPAL R.7/21: 11, enlargement of the area rectangled in Fig. 17A; see also Fig. 18B.



C. Shallow imprint of right pes with granular skin texture ZPAL R.7/21: 55; see also Fig. 18F. Before the V digit tip there is a deep manus imprint of *Prorotodactylus mirus* ichnosp. n. ZPAL R.7/21: 61 with only three digits II–IV visible. **D**. Set of right pes and manus imprints ZPAL R.7/21: 25, 26; see also Fig. 18E. Scale in cm.


16B
16A
A
B

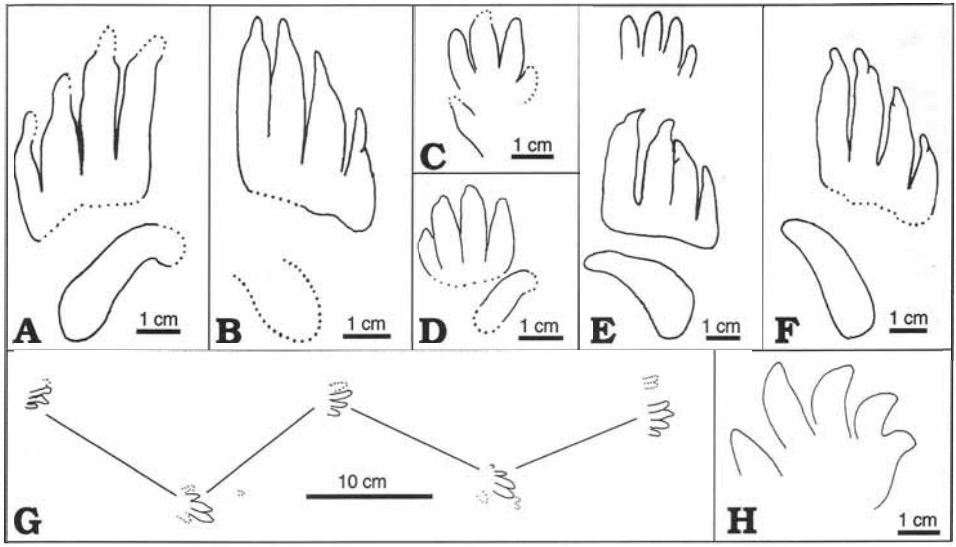


Fig. 18. **A–F.** *Synaptichnium kotanskii* ichnosp. n. **A.** Left pes imprint, holotype ZPAL R.7/21: 11. **B.** Right pes imprint ZPAL R.7/21: 14. **C.** Right manus imprint ZPAL R.7/21: 13, the best preserved manus imprint from the track containing the holotype. **D.** Left manus imprint ZPAL R.7/21: 19, the best preserved imprints from the track ZPAL R.7/21: 14–19. **E.** Set of right pes and manus imprints ZPAL R.7/21: 25, 26 from the track ZPAL R.7/21: 20–26. **F.** Right pes imprint ZPAL R.7/21: 55. **G, H.** *Procolophonichnium polonicum* (Ptaszyński, 1990). **G.** Semibipedal track with unusually high pace angulation and problematical manus imprints ZPAL R.7/22: 1–9. **H.** Large right pes imprint ZPAL R.7/23: 1; see also Fig 20F.

angulation is 133–141°. The width of pace pes is only slightly larger than that of manus (59 and 52 mm on average, respectively). Unusual is the track ZPAL R.7/21: 40–45 with high values of stride 530 and 524 mm, and oblique pace 258 and 292 mm, in contrast to average values of stride (382 mm) and oblique pace (195 mm) of all remaining referred tracks made by animals of similar size. This track may have been produced by a running animal. Pes imprints diverge from the midline at a small angle (14° on average), still exceeding that of manus imprints (6° on average).

Pes. In the holotype, pes imprint is 64 mm long and 39 mm wide. Digit group I–IV is narrow, having 42 mm in length and 33 mm in width. Digits III and IV are of equal length. Their average length is 38 and 37.6 mm, respectively. Claws visible on tips of digits I–IV are long and narrow. Digit V, slightly shorter than III, is behind the digit group I–IV and ends with a structure probably representing a large, blunt claw (Figs 16A, C, D). The angle between digits I–IV and II–IV is low; the first four digits are subparallel. In specimen ZPAL R.7/21: 49, the scaly texture of the plantar surface is visible (Fig. 16C).

Manus. In the holotype, manus imprint is 30 mm long and 27 mm wide. The digit group I–IV, is 26 mm long and 21mm wide. Digit III is longer than IV. As in pes imprints, the angle between digits I–IV and II–IV is relatively low, 26 and 18° on average. Claws are developed on the tips of all five digits (Fig. 16B).

Discussion. — *Synaptichnium kotanskii* ichnosp. n. belongs to a group of small *Synaptichnium* ichnospecies, which is represented by poorly documented (see Haubold 1971a) *S. pseudo-*

Fig. 17. *Synaptichnium kotanskii* ichnosp. n. **A.** Track ZPAL R.7/21: 7–13, in rectangles shown Fig.16A and B; see also Fig. 15A. **B.** Two tracks ZPAL R.7/21: 33–39 and ZPAL R.7/21: 40–45 crossing one another; see also Fig. 15B, C. Scale in cm.

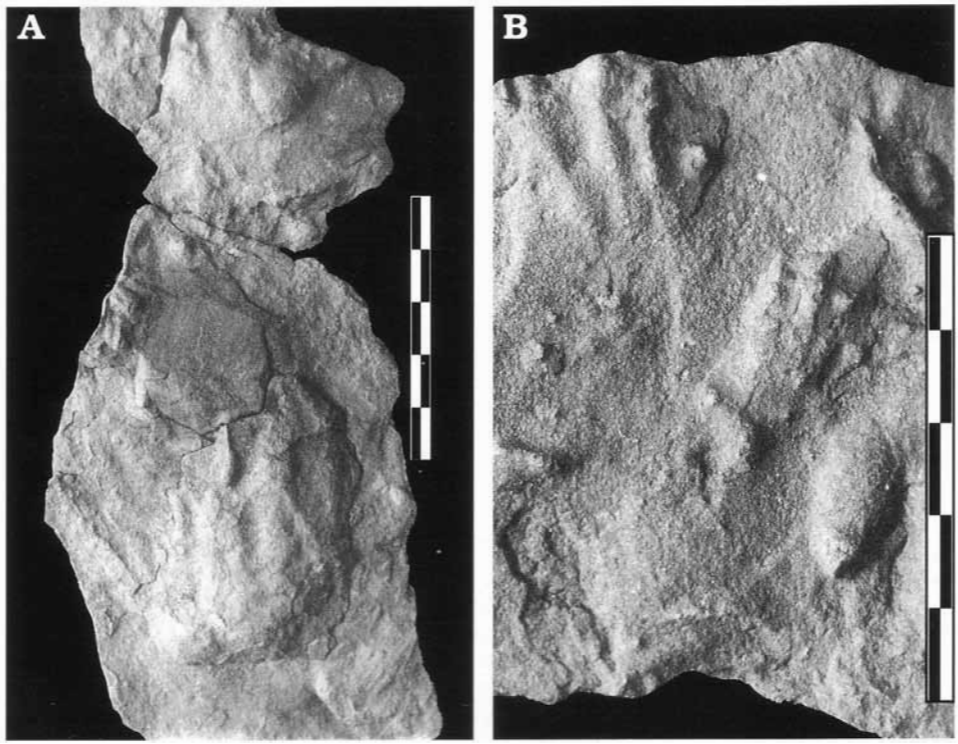


Fig. 19. **A**. *Synaptichnium kotanskii* ichnosp. n. Set of left pes and manus imprints ZPAL R.7/24: 1, 2. **B**. *Prorotodactylus mirus* ichnosp. n. Set of right pes and manus imprints ZPAL R.7/25: 1, 2; see also Fig. 29E. Scale in cm.

suchoides Nopcsa, 1923, first described and illustrated by Woodward (1902). *S. diabloense* (Peabody, 1948) and *S. cameronense* (Peabody, 1948) are two other small species from the Triassic Moenkopi Formation of North America. Moreover, from the Buntsandstein of Germany are known *S. cf. pseudosuchoides* Demathieu & Haubold,1982 and *S. hildburghausense* (Rühle von Lilienstern, 1939); from the Middle Triassic of France – *S. priscum* Demathieu, 1970 and some specimens not identified to ichnospecies (Demathieu & Leitz 1982; Gand 1975; Demathieu & Haubold 1982). Demathieu & Haubold (1982) described as *S.* cf. *pseudosuchoides* a form very close to *S. pseudosuchoides*.

Synaptichnium kotanskii ichnosp. n. differs from *S.* cf. *pseudosuchoides* in being larger, with much more elongated, slender digit group I–IV and the whole pes imprint in general, and with the length of digit II exceeding that of digits III and IV. Divarications of pes digits I–IV and II–IV are smaller in value than those of *S.* cf. *pseudosuchoides*. Equal length of pes digits III and IV differentiates *S. kotanskii* ichnosp. n. from *S. pseudosuchoides* Nopcsa, 1923, the pes of the latter being much narrower (Woodward 1902; Haubold 1971a). Moreover, in *S. pseudosuchoides* digit V in both pes and manus imprints are situated more posteriorly of digit I–IV group.

S. kotanskii ichnosp. n. is of a much larger size than *S. diabloense*. Its pes digits I and II are shorter than III and IV, but not to the degree seen in *S. diabloense* (Peabody 1948: table 7). *S. kotanskii* ichnosp. n. differs from both *S.cameronense* and *S. hildburghausense* in size, divarication of the first four pes digits as well as in shape and position of the digit V (compare Peabody 1948).

Table 5. Track features of *Procolophonichnium polonicum*, *Rhynchosauroides brevidigitatus*, and *R. rdzaneki* ichnosp. n. For abbreviations see Table 2.

Procolophonichnium polonicum	Sm	Sp	Pm	Pp	PAm	PAp	Wm	Wp	MP	Dp3	Dm3	Dpm
ZPAL R.7/1-9		246 245 260		160 143 147 145		108 113 130		93 78 63		-22 -15 -13		
Rhynchosauroides brevidigitatus	Sm	Sp	Pm	Pp	PAm	PAp	Wm	Wp	MP	Dp3	Dm3	Dpm
TP 100: 1–4			71	84					15 17	-8	3	
ZPAL R.7/29: 11–16	107	108 107							10 11	-8 -5 0	27	36
ZPAL R.7/29: 1–10	130	150 140 143 143	82 63	95 85 84 81 92	137	131 120 113 117	30	39 42 46 50	11 9 15	0 0 5 -8 -10	30	30
Rhynchosauroides rdzaneki ichnosp. n.	Sm	Sp	Pm	Pp	PAm	PAp	Wm	Wp	MP	Dp3	Dm3	Dpm
ZPAL R.7/11: 5–14	312 300	3 18 301 302	180 170 180	214 222 213 211	156 150	93 90 93	65 84	146 154 143	48 52 41 45	-14 -20 -26 -14 -25	3 1 14	16 23 19
TP 442ab: 1–7 and ZPAL R.7/11: 15–21	270 243 235	258 238 215	150 128 135 130	170 177 175 173	143 154 148	96 90 80	45 52 56	110 120	30 43 34	-20	-6 -5 0 16	15 9
ZPAL R.7/21: 84–89	212	197		147 149		85	65	105	32	-17 -10 -14	16 17	31
ZPAL R.7/30b: 1–5		303 275		186 208 210		87 95		140 138	26	-8 -25 4 -32		
ZPAL R.7/30a: 1–8		340 370	193	225 219 215		113 107	83	132 124	33	-6 -13 -10 -14	13	31
ZPAL R.7/30b: 6–10		352		221 218		107	74	138	40 30 32	-25 -25		

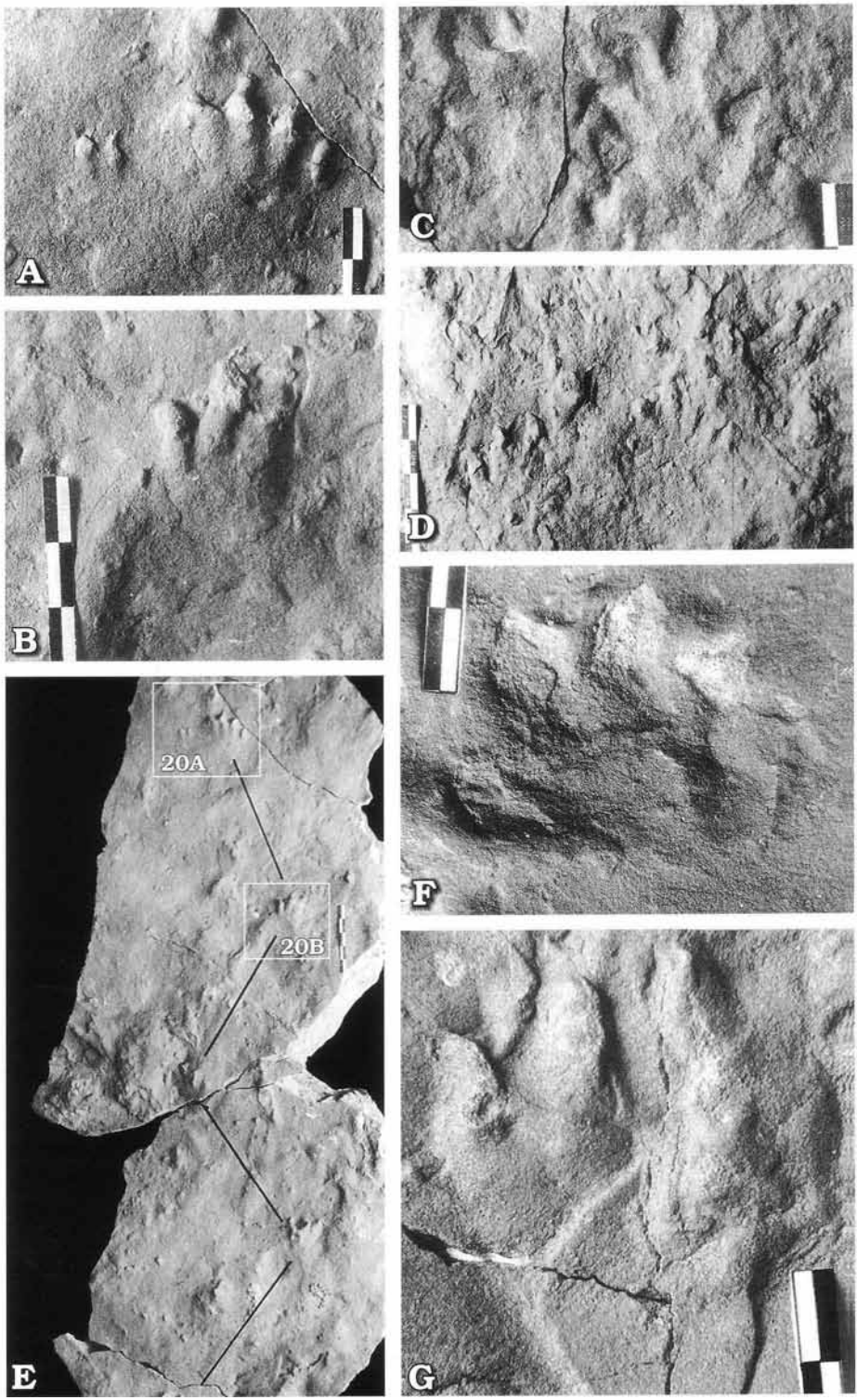
Ichnogenus *Procolophonichnium* Nopcsa, 1923

Procolophonichnium polonicum (Ptaszyński, 1990)

Figs. 18G, H, 20A–G; Tables 1, 5.

Rhynchosauroides polonicus Ptaszyński sp. n.; Fuglewicz *et al.* 1990: pls. 8: 1, 3, 4; 10: 1; fig. 9: 5, 6, 7.

Material. — KR 11 4: 19-9-6-7-1-3, short track, containing the holotype KR 11 4: 1, 3 (plaster cast ZPAL R.7/40: 1) (Fuglewicz *et al.* 1990: pl. 8: 1, 3; figs. 9: 5, 10: 1); KR 2 6: 1, 2 (plaster cast


A
B
C
D
E
20A
20B
F
G

ZPAL R.7/46), set of pes and manus imprints (Fuglewicz *et al.* 1990: pl. 8: 4; fig. 9: 7); KR 4 62: 2, 1, set of left pes and manus imprints (Fuglewicz *et al.* 1990: fig. 9: 6); ZPAL R.7/22: 1–9, semibipedal track consisting of five pes and four problematical poorly preserved manus imprints (Figs. 18G, 20A, B, E); ZPAL R.7/23: 1, 2, two large, consecutive pes imprints (Figs. 18H, 20F, G); ZPAL R.7/26: 1, isolated pes imprint (Fig. 20C); ZPAL R.7/27: 1, 2, isolated imprints with accompanying tail drag mark (Fig. 20D). Representatives of this ichnospecies occur on many other slabs mostly as isolated footprints; tracks are noted on slabs TP 586, TP 12 and TP 463.

Remarks. — *Procolophonichnium polonicum*, previously described as *Rhynchosauroides polonicus* (see Fuglewicz *et al.* 1990) is frequent in the material studied. This ichnospecies should be included in ichnogenus *Procolophonichnium* on account of presence of a long pes digit V imprint situated closely to the digit group I–IV. Digit group I–IV is short and wide; the pes width of pace, except for the unusual track on slab ZPAL R.7/22 discussed below, is close to that of manus, as in other ichnospecies of *Procolophonichnium*. Moreover, in all known cases manus imprint is anterior of or almost in line with the pes.

Interesting is the irregular track ZPAL R.7/22: 1–9 (Figs. 18G, 20E) showing variable high pes pace angulation, from 108 up to 130°. Poorly and fragmentarily preserved imprints interpreted as manus imprints, are situated irregularly, partially much further from the midline than pes imprints (Fig. 20A). Such a track may have been produced by a running animal.

ZPAL R.7/23: 1, the largest known, well-preserved pes imprint attributed to this ichnospecies, is 40 mm long by 44 mm wide (Figs. 18H, 20F).

Some specimens identified previously as *Rhynchosauroides polonicus* with overstepping of manus by pes imprints (Fuglewicz *et al.* 1990: pl. 9: 1, 2; fig. 9: 8, 9, 10) should be regarded as indeterminate. They may in part represent *Rhynchosauroides rdzaneki* ichnosp.n. described below.

In recent years, *Procolophonichnium jageri* and *P. winterswijkense* have been described from the Lower and Middle Triassic of Europe, respectively. In comparison with those ichnospecies, *P. polonicum* is the largest in size. Its pes digits III and IV are almost equal in length, whereas in *P. jageri* pes digit IV is distinctly longer than III. *P. polonicum* differs from both ichnospecies in having less divaricated pes digits I–IV, II–IV and I–V. In the new ichnospecies, the length of digit group I–IV almost equals the width; in *P. winterswijkense* this digit group is broader in relation to its length. The fifth digit of *P. polonicum* is much longer in comparison with digits I–IV, than in *P. winterswijkense* and *P. jageri*. *Procolophonichnium* sp. described by Haubold (1971a: table III, fig. 1) most closely resembles *P. jageri*. A comparison of *P. polonicum* with the small species, *Procolophonipus vonhuenei* Bock, 1952 is impossible due to the poor preservation of the latter (see Bock 1952); the same goes for *Procolophonipus acutus* and *Procolophonipus mülleri* which have track features quite different from those of *P. polonicum* and which would certainly represent separate ichnospecies (see Haubold 1971a).

Ichnofamily Rhynchosauroidae Haubold, 1966
Ichnogenus *Rhynchosauroides* Maidwell, 1911
Rhynchosauroides brevidigitatus Ptaszyński, 1990

Figs. 21A–E, 22B–G; Tables 1, 5.

Rhynchosauroides brevidigitatus Ptaszyński sp. n.; Fuglewicz *et al.* 1990: pls. 7: 1–4; 8: 3; 10: 3; figs. 9: 1–4; 10: 2, 11, 12.

Fig. 20. *Procolophonichnium polonicum* (Ptaszyński, 1990). **A**. Right pes with problematical, unusually situated manus imprint ZPAL R.7/22: 5, 9, enlargement of the area rectangled in E. **B**. Left pes imprint ZPAL R.7/22: 4, enlargement of the area rectangled in E. **C**. Isolated footprint ZPAL R.7/ 26: 1. **D**. Isolated imprints ZPAL R.7/27: 1, 2 with accompanying tail drag mark. **E**. Semibipedal track with barely visible, problematical manus imprints ZPAL R.7/22: 1–9, in rectangles shown A and B; see also Fig. 18G. **F**. Right pes imprint ZPAL R.7/23: 1, see also Fig. 18H. **G**. Left pes imprint ZPAL R.7/ 23: 2. Scale in cm.

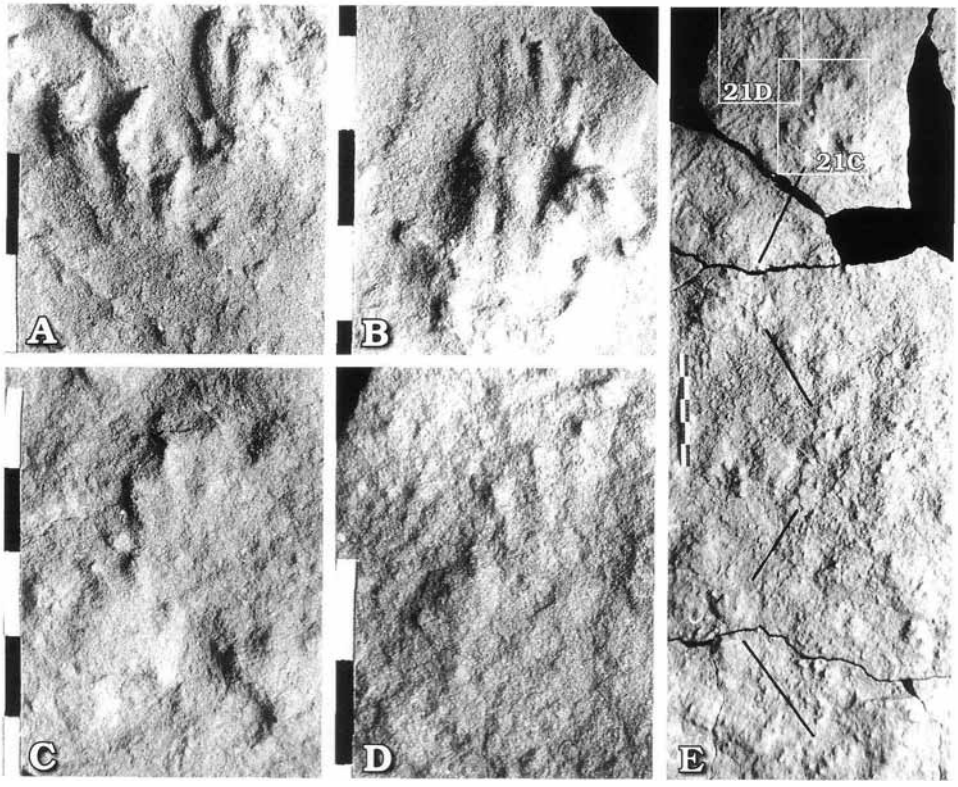


Fig. 21. *Rhynchosauroides brevidigitatus* Ptaszyński, 1990. **A, B**. Two consecutive right sets of footprints of the same track ZPAL R.7/28: 1, 2 and ZPAL R.7/28: 3, 4, respectively; see also Fig. 22C, D. **C**. Set of left pes and manus imprints ZPAL R.7/29: 9, 10, enlargement of the area rectangled in E; see also Fig. 22F. **D**. Set of left pes and manus imprints ZPAL R.7/29: 17,18, enlargement of the area rectangled in E; see also Fig. 22E. **E**. Track ZPAL R.7/29: 1–10, in rectangles shown C and D; see also Fig. 22B. Scale in cm.

Material. — MWGUW 001144 5: 2 and ZPAL R.7/41, plaster casts of the holotype, a complete left pes imprint (Fuglewicz *et al.* 1990: pl. 7: 4; fig. 9: 1); KR 11 4: 16, paratype, imprint of left pes (Fuglewicz *et al.* 1990: pl. 8: 3; fig. 9: 3); ZPAL R.7/42: 2, paratype, right pes imprint (Fuglewicz *et al.* 1990: pl. 7: 2; fig. 9: 2); TP 100: 1–4, two consecutive sets of pes and manus imprints; TP 100: 5-7, fragmentary track; ZPAL R.7/29: 1–10, long track (Figs. 21C, E, 22B, F); ZPAL R.7/29: 11–16, fragmentary track; ZPAL R.7/29: 17,18, isolated set of imprints (Figs. 21D, 22E); ZPAL R.7/28: 1–4, fragmentary track (Figs. 21A, B, 22C, D); ZPAL R.7/28: 5–8, fragmentary track; ZPAL R.7/44: 1, 2, two successive pes imprints (Fuglewicz *et al.* 1990: pl. 7: 1; fig. 9: 4); KR 11 4: 5, 4, set of right pes and manus imprints; KR 11 4: 22-24-21-13 (containing paratype 4: 16), group of manus and pes imprints probably representing an incomplete track; KR 11 4: 10, isolated imprint of manus; KR 2 6: 3, 4, set of left pes and manus imprints; MWGUW 001141 3: 37, 36, set of left pes and manus imprints; plaster cast TP 5: 3, isolated pes imprint. Isolated footprints of *R. brevidigitatus* occur abundantly on many slabs, e.g. TP 189, TP 513 and TP 224.

Remarks. — The original description of *Rhynchosauroides brevidigitatus* Ptaszyński, 1990 was based mainly upon isolated imprints and fragmentary tracks. Extensive material obtained during the past ten years has allowed the author to define track features and collect more data on this species. Most characteristic is the position of pes and manus imprints of the same set.

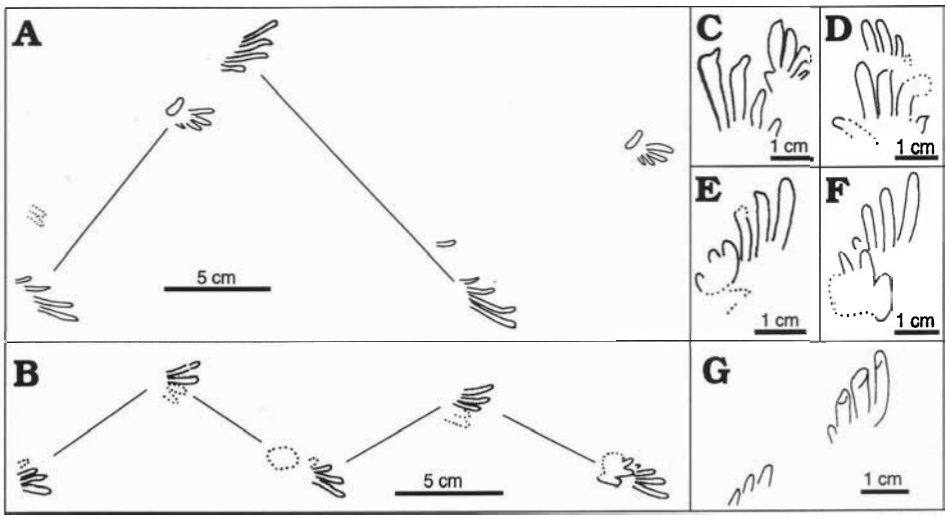


Fig. 22. **A**. *Rhynchosauroides rdzaneki* ichnosp. n.; track ZPAL R.7/21: 84–89. **B–G**. *Rhynchosauroides brevidigitatus* Ptaszyński, 1990. **B**. Track ZPAL R.7/29: 1–10. **C, D**. Two consecutive sets of the manus and pes imprints in the same track ZPAL R.7/28: 1, 2 and ZPAL R.7/28: 3, 4. **E**. Set of left pes and manus imprints ZPAL R.7/29: 17, 18. **F**. Set of left pes and manus imprints ZPAL R.7/29: 9, 10. **G**. Set of left pes and manus imprints ZPAL R.7/ 28: 9, 10.

Manus imprints may occur in front of the pes (Figs. 21A, B; 22C, D) or may be overstepped by the latter (Figs. 21C, D, 22E, F). In the digit group I–IV in both pes and manus imprints, IV is the longest. Digit I is small and its imprint has never been fully recorded in the material studied. In the longest known track, ZPAL R.7/29: 1–10, pace angulation pes attains from 113 up to 131°, stride 140–150 mm and oblique pace 81–95 mm. Pes imprints diverge from the midline at 0–10°, about 5° on average.

Rhynchosauroides rdzaneki ichnosp. n.

Figs. 22A, 23A–C, 24A–D, 25A, B, 26A–C; Tables 1, 5.

Holotype: Set of pes and manus imprints ZPAL R.7/30a: 3, 4 (Figs. 23A, 24D).

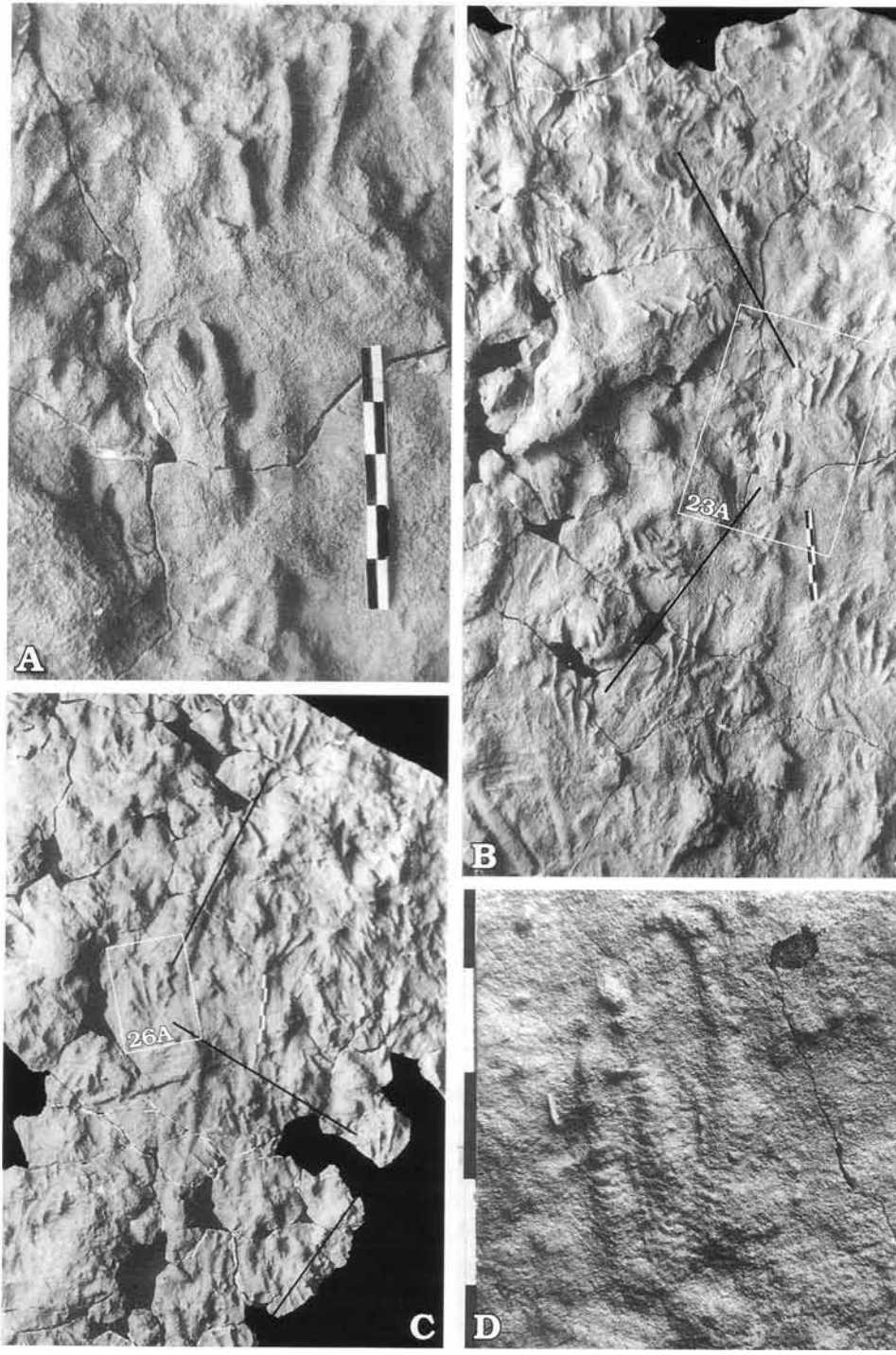
Type locality: Wióry near Ostrowiec Świętokrzyski, Holy Cross Mts, Poland.

Type horizon: Labyrinthodontidae Beds, Middle Buntsandstein, Lower Triassic.

Derivation of the name: In honour of Kazimierz Rdzanek, co-author of the first description of vertebrate footprints from Wióry.

Diagnosis. — *Rhynchosauroides* with typical pes digit length relations: IV>III>II>I; pes length up to 5 cm. Manus width of pace equals approximately one half of that of pes; pes pace angulation ranges between 80 and 113° (94° on average). In tracks, pes diverge from the midline from about 16 (average value of all six referred tracks) to 25°. Manus imprints show an increase in length from digit I to IV and are inclined to the midline at 6° on average. Digits I–IV diverge of about 40° on average; the divarication of digits I–V is about 82°.

Material. — ZPAL R.7/30a: 1–8, track composed of 4 sets of consecutive pes and poorly preserved manus imprints; of these, ZPAL R.7/30a: 3, 4 was designated as a holotype (Figs. 23A, B, 24D, 25A); ZPAL R.7/30b: 1–5, track composed of four consecutive pes imprints and one manus (Figs. 23C, 24A, C); ZPAL R.7/30b: 6–10, fragmentary track; ZPAL R.7/30A: 9,10, isolated set of pes and manus imprints; ZPAL R.7/21: 84–89, a short track (Figs. 22A, 26B); TP 442ab: 1–7 and ZPAL R.7/11: 15–21, part and counterpart of the same track (Figs. 24B, 26C); ZPAL R.7/11:


A
B
23A
C
26A
D

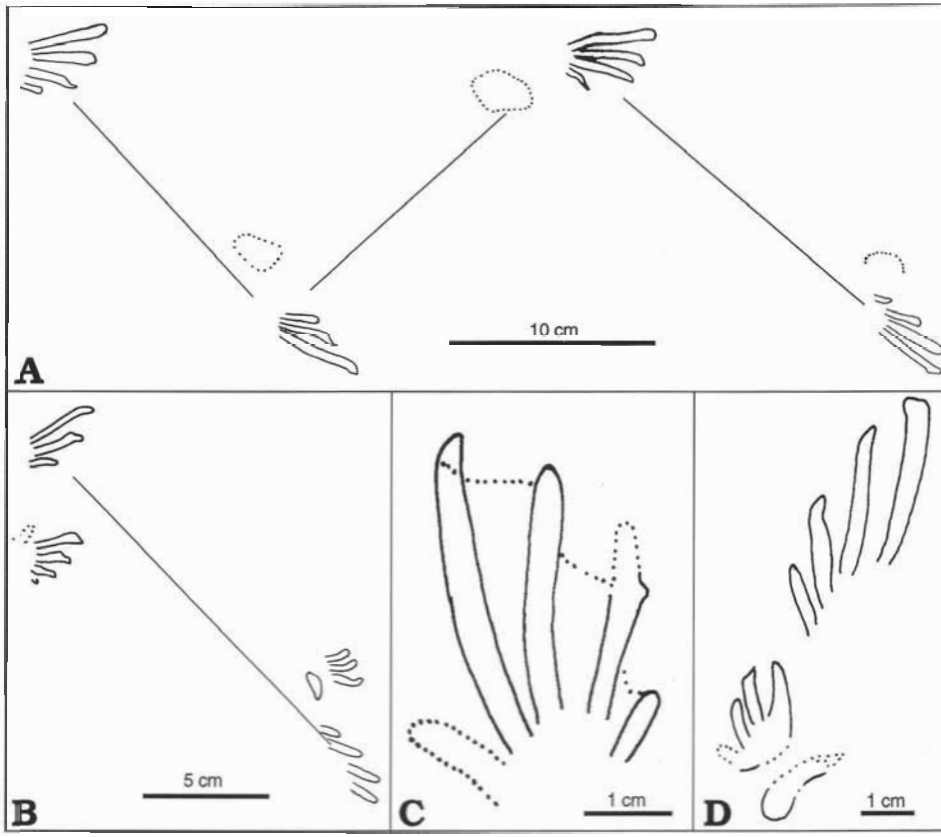


Fig. 24. *Rhynchosauroides rdzaneki* ichnosp. n. **A**. Track ZPAL R.7/30b: 1–5. **B**. Two consecutive sets of pes and manus imprints ZPAL R.7/11: 18–21. **C**. Complete imprint of the right pes ZPAL R.7/30b: 3 with a web-like structure made by claw trails. **D**. Set of left pes and manus imprints, holotype ZPAL R.7/30a: 3, 4.

5–14, shallow, complete track consisting of five consecutive sets of pes and manus imprints (Fig. 25B). Footprints assigned to this ichnospecies occur on many other slabs, but are mostly incomplete and isolated or preserved in fragmentary tracks.

Description. — Track. In all tracks known, manus imprints are overstepped by those of pes. The width of pace manus equals approximately half of that of pes; pace angulation ranges between 80 and 113° (94° on average). In the track ZPAL R.7/30a: 1–8, containing the holotype, pes imprints diverge from the midline at about 11° on average; the average value of all 6 referred tracks equals 16°. Pes pace angulation is 107 and 113°, slightly more than in other tracks. Manus imprints are slightly inclined to the midline at 6° on average.

Pes. In the most cases, only the first three or four digits are impressed. All four digits, of which IV is the longest, end in distinct, sharp claws. The length of digits I–IV decreases from IV

Fig. 23. **A–C**. *Rhynchosauroides rdzaneki* ichnosp. n. **A**. Set of left pes and manus imprints, holotype, ZPAL R.7/30a: 3, 4, enlargement of the area rectangled in B; see also Fig. 24D. **B**. Track ZPAL R.7/30a: 1–6, in rectangle shown A, see also Fig. 25A. **C**. Track ZPAL R.7/30b: 1–5 in rectangle shown Fig. 26A; see also Fig. 24A. **D**. *Prorotodactylus mirus* ichnosp. n.; left pes imprint ZPAL R.7/21: 74 with scaly skin texture visible. Scale in cm.

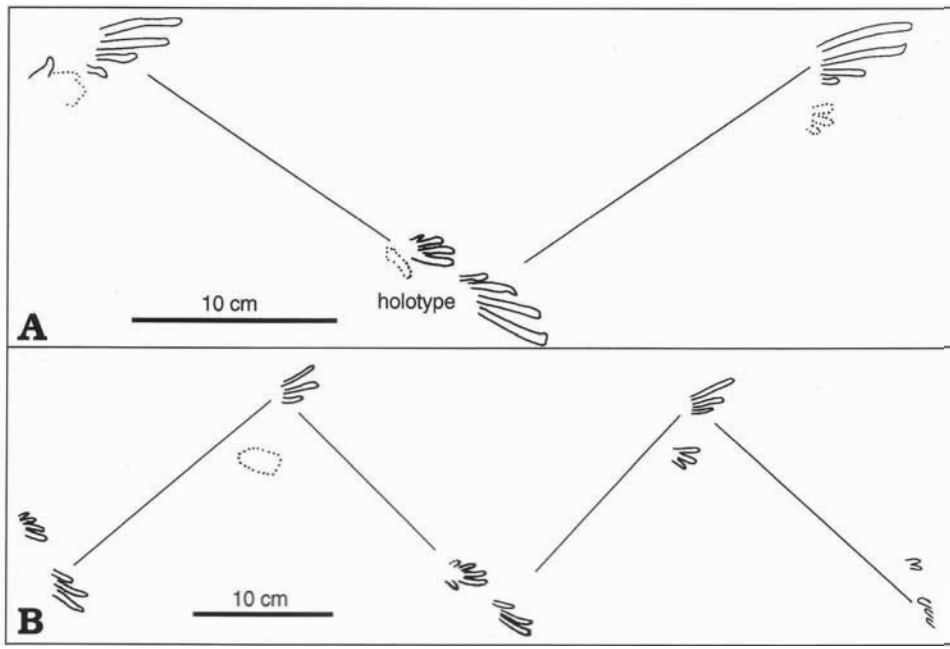


Fig. 25. *Rhynchosauroides rdzaneki* ichnosp. n. **A**. Part of the track ZPAL R.7/30a: 1–8 containing the holotype ZPAL R.7/30a: 3, 4; see also Fig. 24D. **B**. Track ZPAL R.7/11: 5–14.

to I, like in other representatives of *Rhynchosauroides*. The fifth digit, when visible, is placed laterally and somewhat posterior of digit group I–IV (Figs. 24C, 26A), as in many other ichnospecies of *Rhynchosauroides*. In some imprints on slabs ZPAL R.7/30b and ZPAL R.7/30a (Figs. 24C, 26A), there are structures between the distal parts of digits I–IV, which resemble those described by some authors as the edge of a web (Beasley 1905; Maidwell 1911, 1914; see also Haubold 1971a). These structures are here interpreted as drag marks left by the claws of a walking animal. On other specimens these structures are missing.

Manus. As in pes imprints, digit IV is the longest; digits III, II, and I are consecutively shorter. Digit V is situated outward and slightly posterior of this group.The average divarication of digits I–IV and I–V is 40 and 82°, respectively. All five digits have distinct claws. Digits I–IV are often slightly curved medially.

Discussion. — Digit length relations of both manus and pes imprints are typical of *Rhynchosauroides*: IV>III>II>I. *R. rdzaneki* ichnosp. n. may be compared with such large Triassic *Rhynchosauroides* representatives as *R. schochardti* (Rühle von Lilienstern, 1939), *R. rectipes* Maidwell, 1911, *R. hyperbates* Baird, 1957, *R. peabodyi* (Faber, 1958), *R. palmatus* (Lull, 1942) and *R. moenkopiensis* Haubold, 1971. *R. rdzaneki* ichnosp. n. differs distinctly from *R. palmatus* and *R. schochardti* in smaller divarication of manus digits I–IV and I–V, and smaller divarication of pes and manus digits III (see Haubold 1971a). Characteristic is the position of pes digit V of *Rhynchosauroides rdzaneki* ichnosp. n., less posterior and more lateral in relation to group I–IV than in *R. peabodyi* and *R. hyperbates*. Digits II–IV of *R. rdzaneki* ichnosp n. diverge at about 19° whereas in *R. hyperbates* they are almost parallel (Haubold 1971a). Its pes axis is not parallel to the midline contrary to pes axes of *R. hyperbates* and *R. moenkopiensis*. Manus imprints of *R. rdzaneki* are less inclined to the midline than those of *R. moenkopiensis* (see Haubold 1971a: p. 434).

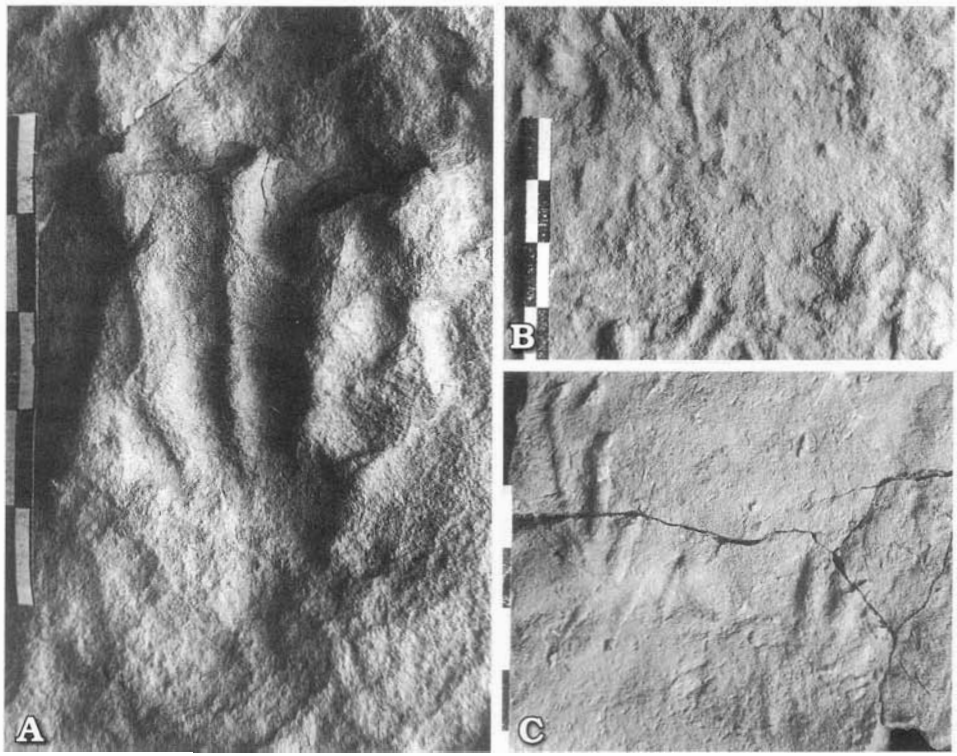


Fig. 26. *Rhynchosauroides rdzaneki* ichnosp. n. **A**. Right pes imprint ZPAL R.7/30b: 3, enlargement of the area rectangled in Fig. 23C, see also Fig. 24C. **B**. Set of right pes and manus imprints ZPAL R.7/21: 85, 86. **C**. Set of right pes and manus imprints ZPAL R.7/11: 18, 19. Scale in cm.

According to the diagnosis given by Haubold (1971a), in the type of *R. rectipes* (illustrated in Maidwell 1911: pl. 4: 1 and Beasley 1905: pl. 4: 1) pes and manus digits III are almost parallel. This information is inconsistent with the illustrations (see Beasley 1905: pl. 4: 1; Haubold 1971a: fig. 10a) which show the angle between pes and manus digits III to be about 20°, being close to that of *Rhynchosauroides rdzaneki* ichnosp. n. According to Haubold (1971a: p. 429), the track of *R. rectipes* is not known. However, Maidwell (1911: fig. 5) figured a track, which he named *R. rectipes*.

The manus width of pace in *R. rdzaneki* is smaller than that of pes, wheras in *R. rectipes* these values are almost equal. Moreover, the latter differs from *R. rectipes* in the smaller angle between axes of manus digits I–IV. It should be noted here that a detailed comparison of those two species is currently impossible due to the poor data available for *R. rectipes*. The Rhynchosauroidae of the British Isles certainly are in need of a revision; it is possible that specimens described as *R. rectipes* and. *R. membranipes* Maidwell, 1911 may in part represent the ichnogenus *Procolophonichnium*.

Prorotodactylidae ichnofam. n.

Derivation of the name: After the name of *Prorotodactylus* ichnogen. n.

Diagnosis. — Long-striding tracks of small animals. Manus imprints are overstepped by those of pes or placed on the same line. Pes first four digits, of which IV is the longest, end in distinct,

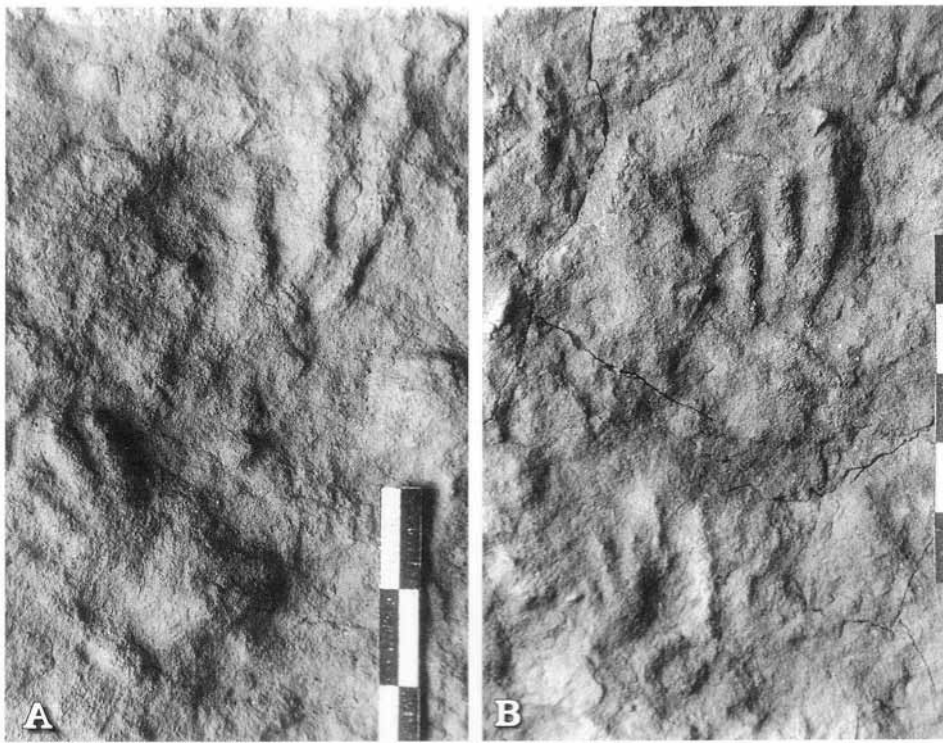


Fig. 27. *Prorotodactylus mirus* ichnosp. n. **A**. Set of left pes and manus imprints, holotype ZPAL R.7/31: 21, 22, enlargement of the area rectangled in Fig. 30A; see also Fig. 28C. **B**. Set of left pes and manus imprints ZPAL R.7/31: 5, 6, enlargement of the area rectangled in Fig. 30A; see also Fig. 28E. Scale in cm.

sharp claws. Digits II–IV diverge at a low angle. Posterior ends of digits, close to each other, form a distinct straight metatarsal-phalangeal joint. Imprints of pes digits V occur only occasionally, situated slightly posteriorly and outwards of the digit group I–IV. Manus imprints are most typical. Digit V is distinctly straight and separated from digit group I–IV, situated behind and slightly outwards of this group. In group I–IV, digit III is the longest. Digit I is distinct although being the shortest.

Remarks. — The main difference between Prorotodactylidae ichnofam. n. and Rotodactylidae Peabody, 1948 is the lack of any rotation in digits V of both manus and pes imprints. The configuration of manus digits in Prorotodactylidae ichnofam. n. is different from that in Rhynchosauridae, resembling that in pes imprints of Chirotheridae Abel, 1835.

Prorotodactylus ichnogen. n.

Type ichnospecies: *Prorotodactylus mirus* ichnosp. n.

Derivation of the name: Alluding to features close to *Rotodactylus*, but found in older deposits and therefore possibly left by ancestors of the *Rotodactylus* trackmakers.

Diagnosis. — See ichnofamily Prorotodactylidae (monogeneric).

Other ichnospecies. — *Prorotodactylus lutevensis* (Demathieu, 1984) described from the Middle Triassic of France as *Rhynchosauroides lutevensis* (see Demathieu 1984) is also placed here. The general structure of manus imprints, such as length relations of the first four digits and arrangement of the fifth suggest that this ichnospecies is a member of the ichnogenus *Prorotо-*

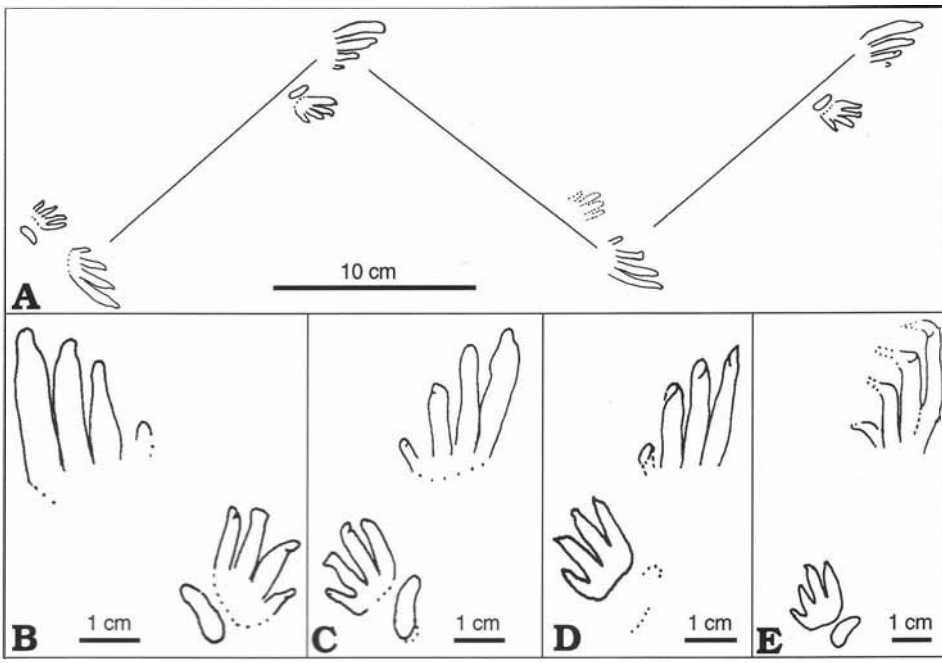


Fig. 28. *Prorotodactylus mirus* ichnosp. n. **A**. Track ZPAL R.7/31: 21–27 including the holotype ZPAL R.7/31: 21, 22. **B**. Set of right pes and manus imprints ZPAL R.7/31: 23, 24. **C**. Set of left pes and manus imprints, holotype ZPAL R.7/31: 21, 22. **D**. Set of left pes and manus imprints ZPAL R.7/31: 18, 19. **E**. Set of left pes and manus imprints ZPAL R.7/31: 5, 6.

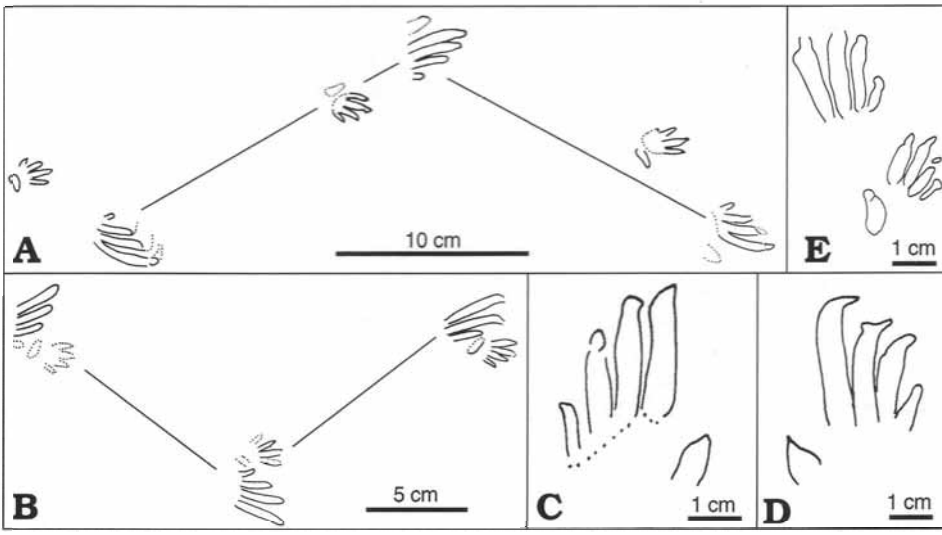


Fig. 29. *Prorotodactylus mirus* ichnosp. n. **A**. Track ZPAL R.7/31: 5–10. **B**. Track ZPAL R.7/31: 32–37. **C**. Isolated, complete left pes imprint ZPAL R.7/31: 42. **D**. Isolated, complete right pes imprint ZPAL R.7/31: 44. **E**. Set of right pes and manus imprints ZPAL R.7/25: 1, 2.

Table 6. Track features of *Prorotodactylus mirus* ichnofam., ichnogen. et ichnosp. n. For abbreviations see Table 2.

Track	Sm	Sp	Pm	Pp	PAm	PAp	Wm	Wp	MP	Dp3	Dm3	Dpm
ZPAL R.7/31:1–13	311	320	158	170	154	126	34	82	38	-8	12	19
	323	356	156	190	151	121	38	89	43	-9	8	17
	322	328	170	182	160	123		91	46	-7	16	19
	312	328	161	186		122		88	50	-12	4	21
		318		182		123			46	-8	4	12
				190					50	-8	6	15
									48			
ZPAL R.7/31:14–30	241	280	132	153	120	96	73	106	23	-23	11	26
	266	282	146	168	138	103	53	104	22	-18	21	38
	266	263	144	167	139	111	53	94	25	-22	9	31
	265	245	142	166	142	103	43	104	32	-14	11	22
		262	142	167		105		102	30	-13	14	26
		260	138	166		112		85	27	-13	17	25
		268		162					30	-7	16	22
				155					15		9	
ZPAL R.7/31–41	227	236	122	150	130	112	52	80	28	-19	3	24
	243	252	135	140	140	122	42	70	20	-21	10	26
			124	152					22	-7		15
									15			
ZPAL R.7/21: 57–65	360	373	215	220	148	125	50	95	55	-14	13	18
	342	371	163	204	142	123	58	103	67	-4	18	23
		361	203	210		131		88	62	-6	17	24
				200						-3		
										-8		
ZPAL R.7/21: 66–72		343	186	195				95	50	-7	10	18
									48	-7		18

dactylus. Interestingly, manus imprints of *Rotodactylus mckeei* Peabody, 1948 show a similar general pattern of the manus imprint, with digit V not rotated posteriorly, except for digit IV distinctly longer than III (Peabody 1948). On the other hand, *Rotodactylus matthesi* Haubold, 1967 has manus digit V distinctly rotated posteriorly and manus digit III longer than IV or being of the same length (Haubold 1967).

Prorotodactylus mirus ichnosp. n.

Figs. 16C, 19B, 23D, 27A, B, 28A–E, 29A–E, 30A–D, Tables 1, 6.

Holotype: Set of left pes and manus imprints, ZPAL R.7/31: 21, 22 (Figs. 27A, 28C)

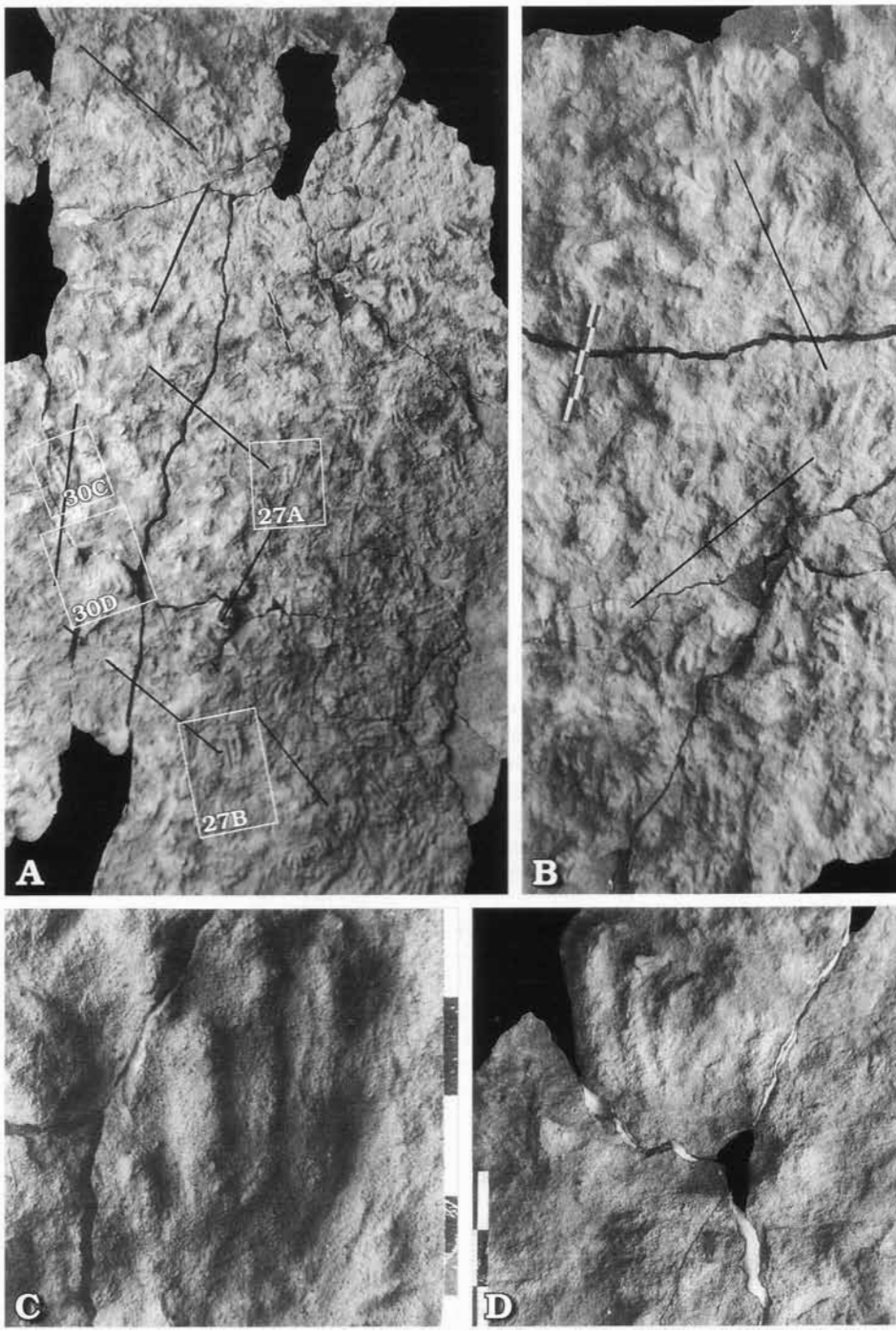
Type locality: Wióry near Ostrowiec Świętokrzyski, Holy Cross Mts, Poland.

Type horizon: Labyrinthodontidae Beds, Middle Buntsandstein, Lower Triassic.

Derivation of the name: latin *mirus* strange, because of the unusual manus imprint features.

Diagnosis. — Medium-sized *Prorotodactylus*. Average pes angulation varies in different tracks between 106 and 126°. Divarication of pes digits II–IV is 10° on average. Divarication of pes digits III from the midline is 18°. Manus imprints inclined to the midline at 11°. Of the manus digit group I–IV, digit III is the longest. Manus digits I–V and I–IV diverge at about 82°and 28°, respectively.

Fig. 30. *Prorotodactylus mirus* ichnosp. n. **A.** Two tracks: ZPAL R.7/ 31: 5–9 and ZPAL R.7/31: 18–28, in rectangles shown Figs. 27A, B, 30C, D; see also Figs. 28A, 29A. **B.** Track ZPAL R.7/31: 32–37; see also Fig. 29B. **C.** Isolated pes imprint ZPAL R.7/31: 42 with all five digits visible, enlargement of the area →



rectangled in A; see also Fig. 29C. **D**. Isolated pes imprint ZPAL R.7/31: 44 with all five digits visible, enlargement of the area rectangled in A; see also Fig. 29D. Scale in cm.

Material. — ZPAL R.7/31: 1–13, long track consisting of 7 consecutive sets of imprints; the sixth one of pes has no accompanying manus because of damage of the slab at this place (Figs. 27B, 28E, 29A, 30A); ZPAL R.7/31: 14–30, long track consisting of 9 sets; the fifth of them ZPAL R.7/31: 21, 22 being designated holotype (Figs. 27A, 28A–D, 30A); ZPAL R.7/31: 31–41, track consisting of six sets of imprints, interpreted as the result of slow gait (Figs. 29B, 30B); ZPAL R.7/21: 57–65, track consisting of four consecutive sets and fifth pes imprint; ZPAL R.7/21: 66–72, incomplete and irregular track; ZPAL R.7/21: 73–75, fragmentary track containing left pes imprint ZPAL R.7/21: 74 showing fine details of scaly skin surface (Fig. 23D); ZPAL R.7/25: 1, 2, isolated set of right pes and manus imprints (Figs. 19B, 29E); ZPAL R.7/31: 42 and ZPAL R.7/31: 44, isolated, complete pes imprints with all five digits visible (Figs. 29C, D, 30A, C, D).

Description. — Track. In known tracks, the manus imprints are distinctly overstepped by those of pes except for the track ZPAL R.7/31: 31–41 which shows pes and manus imprints at almost the same line, with relatively low pace angulation (117° on average). The known track patterns differ to a certain extent. Pes pace angulation in the track ZPAL R.7/31: 1–13 exceeds 120°, reaching a maximum of 131°. Manus pace angulation in the latter exceeds 150°. In the track ZPAL R.7/31: 31–41 interpreted as the result of slow gait, these average values attain 105 and 135°, respectively. The average divarication of digit III from the midline is 18°. Manus imprints are inclined to the midline at about 11°.

Pes. Digits I–IV end in distinct claws, increasing in length from I up to IV. Digits II–IV are distinctly subparallel and close together. Their proximal ends are placed along an almost straight line. Some footprints display much shorter digit I imprints, slightly separated from the group II–IV, and inclined more inwardly. Imprints of digits V, occasionally present, show mostly their distal portions preserved only in isolated, deep imprints ZPAL R.7/31: 42 and ZPAL R.7/31: 44 (Figs. 29C, D, 30C, D), and are placed slightly posteriorly and outwards of digit group I–IV. No claws on their tips have been observed.

Manus. The manus is relatively narrow. Digits of the group I–IV are almost straight; they have sharp claws of moderate size. Digit III is the longest. Digit V is distinctly separated from the digit group I–IV; situated posteriorly of digit group I–IV and ending with a claw similar in shape to those of first four digits. Sometimes, when I and V digit impressions are lacking, such incomplete manus imprints show a close resemblence to pes imprints of three-toed dinosaurs (Fig. 16C). The posterior ends of the first four digits are placed along a distinct, almost straight line. Manus digits I–V and I–IV diverge at about 82 and 28°, respectively. An imprint of skin scales was found in pes imprint ZPAL R.7/31: 74 (Fig. 23D). In this specimen complete imprints of digits II, III and IV are visible. The scaly pattern consists of scutes or scales partly arranged in parallel rows perpendicular to digit axes, reminiscent of transversely elongated scales known in representatives of *Rotodactylus* (Peabody 1948; Demathieu 1984). This arrangement of scales is different from the known texture of wart-like scales in *Rhynchosauroides peabodyi* (Faber, 1958) as described by Demathieu & Oosterink (1983) with no row arrangement visible, and from small scales distributed on the whole footprint surfaces of different chirotheriid ichnogenera (Soergel 1925; Peabody 1948; Demathieu 1984; Fuglewicz *et al.* 1990; Figs. 12B, 16C).

Discussion. — In comparison with *Prorotodactylus lutevensis* (Demathieu, 1984), *P. mirus* ichnosp. n. is slightly larger and shows a relatively higher pes pace angulation angle (average values in various tracks of *P. mirus* are 123, 105, 117, and 126° in comparison to 96° in *P. lutevensis*).

Systematic remarks. — The most characteristic features of the *Prorotodactylus* ichnogen. n. manus imprints are the length of digit III which exceeds that of IV, the position of V digit set posteriorly of digit group I–IV and the relatively long and distinct digit I imprint. The length of the pes digit IV is typical of lacertoid footprints, like in *Rhynchosauroides,* or

Rotodactylus. Subparallel positioning of digits II–IV and arrangement of their proximal ends close to each other along almost straight line, suggest a close and parallel arrangement of the distal parts of metatarsals, as in *Rotodactylus* footprints. Most of the track and footprint features are similar in representatives of *Rotodactylus* and *Prorotodactylus*, suggesting that their trackmakers were closely related groups. The occasional presence in tracks of only the distal part of the fifth pes digit imprint indicates that it did not perform a significant function in locomotion.

The unique feature of *Rotodactylus* – presence of the posteriorly reversed rotated V digits – should not only be considered a result of fifth digit reduction but regarded as an important adaptive feature. I doubt the interpretation of this character as an aid in elevating the metapodium off the ground (Peabody 1948; Thulborn 1990). A prop directed posteriorly would rather impede running movement of an agile terrestrial animal. Functionally reversed digits are found in several animal taxa. Various birds (e.g., Psittaciformes, Piciformes, Strigiformes, Acipenseriformes, Passeriformes) have one or two reversed toes. They are adapted to perching on branches or to grasping prey. Some wading birds (e.g. heron) use a well developed, reversed digit I to enlarge the foot surface, which is helpful when walking on a muddy substrate. The length of digit I in the flightless birds is highly reduced and their feet are functionally tridactyl or even didactyl (e.g., ostrich). Some quadrupeds with extremely specialized grasping limbs (chameleons, arboreal marsupials and primates) have more or less opposable digits in both manus and pes, in due to the arboreal adaptation. Similarity of manus and pes structure in *Rotodactylus* suggests a functional similarity of fore- and hind limbs of the trackmakers. The animals were able to run occasionally bipedally, but only to the same degree as Chirotheriidae trackmakers or extant basilisk lizards and crocodiles, being however functionally quadrupedal. Thus, the author regards them as an arboreal, side branch of specialized archosaurs. Characteristic differences between fore- and hind limb imprints in *Prorotodactylus* reflecting different manus and pes structure may result from their different specialization. Forelimbs became adapted to grasping or manipulating function or were used for digging or hunting. Contrary to the typical lacertoid pattern, manus digit III is clearly longer than IV, and their relatively strong digit I evokes a similar trend in early dinosaurs, which also have the inner fingers more strongly developed than the outer ones. At the same time, with forelimbs acquiring their new functions, a tendency towards bipedal gait could have resulted in a gradual increase of pace angulation, still low in *Prorotodactylus*. Closer position of distal parts of metatarsals was beneficial for the metatarsus acting as another lever, besides that of stylo- and zeugopodium.

Dinosaurs (and probably their avian relatives) originated in the Triassic. Dinosaurs, whose tracks are known since the Middle Triassic (Gand 1975; Courel & Demathieu 1976), show advanced, differentiated specialization of feet. *Prorotodactylus* trackmakers could well represent a taxon close to the ancestors of those groups of animals.

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Tropy kręgowców z dolnego triasu Wiór, Góry Świętokrzyskie

TADEUSZ PTASZYŃSKI

Streszczenie

Tropy kręgowców są rzadko spotykane w utworach dolnego i środkowego pstrego piaskowca stając się częstymi i zróżnicowanymi skamieniałościami śladowymi dopiero w jego górnej części. Opisany w tej pracy materiał ichnologiczny pochodzi z pojedyńczego, dużego odsłonięcia znajdującego się w prawym zboczu doliny Świśliny koło wsi Wióry, 14 km na północny zachód od Ostrowca Świętokrzyskiego na północno-wschodnim obrzeżeniu Gór Świętokrzyskich (Fig. 1) i jest najbogatszym znanym zespołem tropów kręgowców ze środkowego pstrego piaskowca (Fuglewicz *et al.* 1981, 1990).

Odsłonięcie w Wiórach powstało w związku z budową zapory i zbiornika wodnego dla Ostrowca Świętokrzyskiego w latach 1979–1980. Występują tu przeławicające się piaskowce, mułowce i iłowce systemu kanałów oraz równi zalewowych rzek roztokowych o łącznej miąższości 40–50 m (Mader & Rdzanek 1985; Fuglewicz *et al.* 1990). Są to warstwy labiryntodontowe środkowego pstrego piaskowca (dolny trias) korelowane z górnymi warstwami oolitowymi Niżu Polskiego (Senkowiczowa & Ślączka 1962; Fuglewicz *et al.* 1990). Badania palinostratygraficzne (Fijałkowska 1994) oraz magnetostratygraficzne (Nawrocki 1997) pozwalają zaliczyć warstwy labiryntodontowe do dieneru. Warstwy labiryntodontowe odsłonięte w Wiórach zawierają liczne struktury sedymentacyjne, szczątki roślin, kości kręgowców, a także odciski pancerzyków esterii oraz liczne i zróżnicowane ślady bezkręgowców (Mader & Rdzanek 1985; Fuglewicz *et al.* 1990).

Istniejący opis paleontologiczny zespołu ichnofauny z Wiór (Fuglewicz *et al.* 1990) został uzupełniony i częściowo zrewidowany w rezultacie badań prowadzonych w ciągu ostatnich dziesięciu lat. Tropy kręgowców odkryte w tym miejscu po raz pierwszy przez autora jesienią 1980 r., były zbierane i zabezpieczane przed zniszczeniem przez autora tej pracy oraz Kazimierza Rdzanka, organizatora Muzeum Ichnologicznego w Wiórach.

Rozpoznany dotychczas zespół śladów kręgowców z Wiór zawiera 11 ichnogatunków przypisywanych płazom i gadom, należących do siedmiu ichnorodzajów: *Capitosauroides*, *Brachychirotherium*, *Isochirotherium*, *Synaptichnium*, *Rhynchosauroides*, *Procolophonichnium* oraz nowego ichnorodzaju *Prorotodactylus* reprezentującego nową rodzinę

Prorotodactylidae. Opisano 6 ichnogatunków proponowanych tu jako nowe: *Capitosauroides fuglewiczi* ichnosp. n., *Brachychirotherium wiorense* ichnosp. n., *Isochirotherium gierlinskii* ichnosp. n., *Synaptichnium kotanskii* ichnosp. n., *Rhynchosauroides rdzaneki* ichnosp. n. i *Prorotodactylus mirus* ichnosp. n. Ichnogatunek *Chirotherium hauboldi* uznany został za reprezentanta ichnorodzaju *Brachychirotherium*; *Rhynchosauroides polonicus* włączono do ichnorodzaju *Procolophonichnium*. Okazy opisane poprzednio (Fuglewicz *et al.* 1990) z Wiór jako *Brachychirotherium kuhni* Demathieu & Haubold, 1982 uznane zostały za przedstawicieli nowego ichnogatunku *Brachychirotherium wiorense* ichnosp. n.

W dyskusji dotyczącej zwierząt będących twórcami tropów *Prorotodactylus* zwrócono uwagę, w oparciu o morfologię tropów, na możliwy związek z formami, z których powstały dinozaury oraz z twórcami tropów *Rotodactylus*.