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LOWER TRIASSIC FOOTPRINTS FROM THE ŚWIĘTOKRZYSKIE (HOLY CROSS) MOUNTAINS, POLAND

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A tetrapod footprints assemblage from the Middle Buntsandstein labyrinthodontid beds, NE Świętokrzyskie Mts, appears to be the oldest known from the Triassic of Europe. It comprises 8 taxa: cf. *Capitosauroides* sp., *Chirotherium haubold*i sp.n., *Isochirotherium sanctacrucense* sp.n., *Isochirotherium* sp., *Brachychirotherium kuhni* Demathieu et Haubold, 1982, *Synaptichnium chirotherioides* sp.n., *Rhynchosauroides brevidigitatus* sp.n. and *R. polonicus* sp.n. Footprints are preserved chiefly as casts on the sole surfaces, rarely as imprints on the upper surfaces of sandstones. Skin textures of chirotheriids have been noticed. Formation and preservation of prints as well as their relationship to facies are discussed. Mode and direction of motion of trackmakers and general characteristics of the environment in which their activity took place are reconstructed. Age and tectonic framework of the labyrinthodontic beds formation are briefly discussed.
Key words: tetrapods, footprints, parataxonomy, taphonomy, stratigraphy, Lower Triassic, Poland.

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INTRODUCTION

Wióry in the Świętokrzyskie Mts is the easternmost vertebrate footprints locality in the European Buntsandstein Basin.

Up to the present, vertebrate footprints were occasionally reported from a few stratigraphic formations of the Middle and Upper Buntsandstein in that region: prints from the Tumlin Sandstone (Gradziński *et al.* 1979), a pair of footprints from the Röt of Witulin (Senkowiczowa 1982) and isolated footprints from the sandstone with Labyrinthodontidae (Samsonowicz 1929), from the Lower Triassic of the Wióry area (Senkowiczowa and Ślączka 1962), and the Röt of the Kosowice—Jarugi sections (Samsonowicz 1929, 1934, Karaszewski 1966, 1976, also cited by Senkowiczowa 1970). A few footprints were also collected from the Röt and unsubdivided Lower Triassic in NE Świętokrzyskie Mts during preparation of the master degree theses (unpubl. M.Sc. Thesis of Rdzanek 1977, cited in Rdzanek 1984, and unpubl. M. Sc. Thesis of Ptaszyński 1979).

In vast exposures of the Buntsandstein, made in 1980 in connection with construction works of a water barrage and reservoir at Wióry near Ostrowiec Świętokrzyski (fig. 1) two slabs with footprints were discovered by T. Ptaszyński. Subsequent exploration gave rich paleontological material. Preliminary ichnological and sedimentological data have been presented up to now in Fuglewicz *et al.* (1981), Mader and Rdzanek (1985) and Rdzanek (1986).

The sequence from Wióry is assigned to the labyrinthodontid beds (Mader and Rdzanek 1985; Rdzanek 1986), the local lithostratigraphic unit in the margin of the Świętokrzyskie Mts (Senkowiczowa and Ślączka 1962: Labyrinthodontidae beds). The Wióry sequence displays features typical of these beds: alternations of sandstones-siltstones and claystones, calcareous cement in sandstones, red coloration, and rare, scattered vertebrate bones. The labyrinthodontid beds were tentatively correlated (Rdzanek 1984) with the upper oolitic beds, the unit distinguished by Fuglewicz (1973, 1979, 1980) in the Middle Buntsandstein of the Polish Lowlands.

In this study, the stratigraphy is by the late R. Fuglewicz of the Institute of Geology of the Warsaw University, the taxonomy — by T. Ptaszyński, and the taphonomic interpretation of footprints — by K. Rdzanek. The studied footprints were collected by the two latter authors who also made latex casts. Plaster casts were made by T. Ptaszyński while K. Rdzanek took the field photodocumentation and is responsible for organizational matters.

Labelling of specimens consists of an acronyme of the collection and a number of the slab and of the footprint on this slab. For example, MWGUW 01141: 3.20 means, that the footprint no. 20 on the slab no. 3 is stored at the Museum of the Faculty of Geology, Warsaw University, under the catalogue number 01141. Each footprint on the slab is numbered; the trackway consisting of several footprints is marked by a sequence of numbers, for example: 3.29-30-17-13-14. Lack of the acronyme means, that the original specimen was destroyed and only its photographs or plaster casts exist. A small part of the specimens is housed at the Museum of the Faculty of Geology, Warsaw University (MWGUW) and the rest belongs to K. Rdzanek (KR) and T. Ptaszyński (TPW) private collections.

Acknowledgements. — Warm thanks are due to Dr. H. Haubold (Halle) for critical comments on the manuscript and advice in taxonomical studies of the footprints. Dr. D. Mader (Frankfurt a. Main) for help in sedimentological studies, Dr W. R. Kowalski for assistance in preparation of fig. 14, Mr. S. Kolanowski and his team of the Photographic Laboratory of the Institute of Geology, Warsaw University for the illustrations, and Dr. B. Jendryka-Fuglewicz for editorial work on the first draft of manuscript prepared by her late husband. K. Rdzanek expresses his special thanks to M. Sc. eng. C. Kowalski, M. Sc. eng. Z. Held and M. Sc. eng. A. Sokoliński of the Board of Directors of the Regional Water Management in Warsaw, for a friendly athmosphere and an understanding for his scientific aspirations.

AGE AND TECTONIC FRAMEWORK OF THE LABYRINTHODONTID BEDS FORMATION

At the margin of the Świętokrzyskie Mts the Buntsandstein is generally represented by sediments of marginal facies of the central European Basin. It is characterized by high share of fluvial material, reflected by high frequency of conglomerates and sandstones, marked predominance of red colours, and exceptional scarcity of fossils. This strongly impedes stratigraphic analysis of these rocks and their correlation with Buntsandstein rocks of the Polish Lowlands which differ in lithology. Therefore, litho- and chronostratigraphy of the rocks from the margin of the Świętokrzyskie Mts and correlation with complete sequences remain debatable. However, new paleontological and geological data gathered in the last years made it possible to characterize the Buntsandstein of that area anew and to establish correlation with the sequences of classic German area.

It is widely assumed after Samsonowicz (1929) that the Zechstein/ /Buntsandstein boundary may be drawn in the Świętokrzyskie Mts region on the basis of appearance of quartz pebbles in sediment. These pebbles mark a stage of fluvial sedimentation, characteristic of the Buntsandstein. In the Czerwona Góra section Samsonowicz (1929) has drawn lower boundary of the Buntsandstein at the base of beds subsequently named (Senkowiczowa and Ślączka 1962) as the Czerwona Góra beds. Different point of view was presented by Senkowiczowa and Ślączka (1962) and Senkowiczowa (1970) who ascribed a transitional nature of strata underlaying the Czerwona Góra conglomerates and assigned these Zechstein-Buntsandstein transitional beds to basal part of the Lower Buntsandstein. The recent data (Rościszewski 1985 and this paper) confirm the interpretation of Samsonowicz (1929). He connected the origin of conglomerates of the "transitional beds" with the Zechstein Sea and degradation of the Paleozoic sockle of the Świętokrzyskie Mts. The Czerwona Góra conglomerates were due according to this author to transport of quartz pebbles from outside the Świętokrzyskie Mts by rivers. Differences in conditions of sedimentation of Zechstein and Buntsandstein conglomerates and the lack of sedimentary continuity between them in the Permo-Triassic section of the Piekoszów Basin were also emphasized by Pawłowska (1978).

Samsonowicz (1929), Senkowiczowa and Ślączka (1962) and Senkowiczowa (1970), considered that all the Buntsandstein substages are represented in the Świętokrzyskie Mts area. However, the latest palynological analyses shown that Middle and Upper Buntsandstein have spores are the oldest microfossils recorded in both, direct neighbourhood of the Paleozoic sockle (Dybova-Jachowicz and Laszko 1980; Rdzanek 1981,

1984) and areas somewhat distant from the sockle. The assemblage characteristic of the Lower Buntsandstein, known from complete and well-documented Buntsandstein sections of the Fore-Sudetic Monocline and Kujawy (Fuglewicz 1977, 1979, 1980; Orłowska-Zwolińska 1984), was not recorded here. This agrees with results of the present analysis of vertebrate footprints, as the recorded taxa were reported from France and Germany from higher parts of Middle and Upper Buntsandstein only (fig. 2). It follows that there is no paleontological record which would

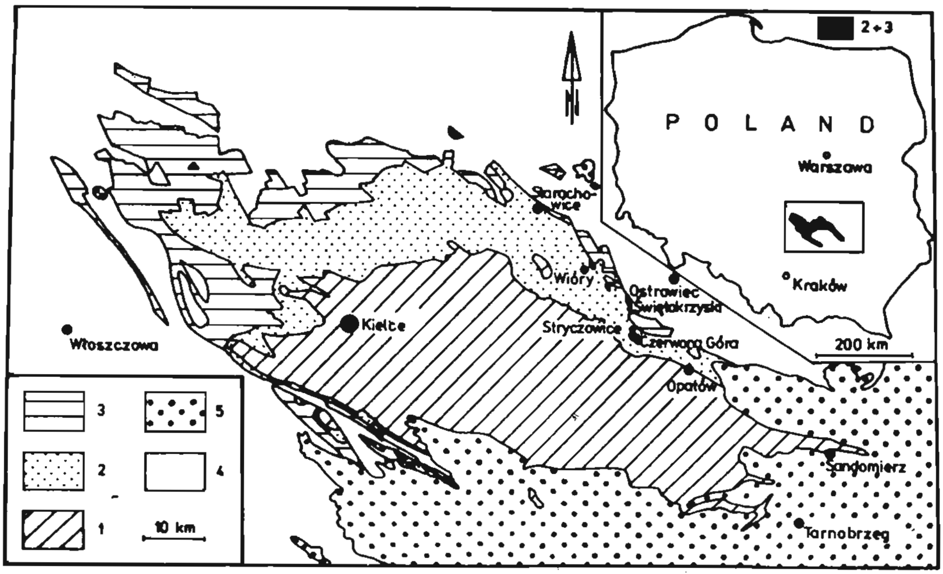

Fig. 1. Geological sketch map of the Świętokrzyskie (Holy Cross) Mountains, Poland (after Rühle *et al.* 1977). 1 Palaeozoic basement, 2 Buntsandstein, 3 Muschelkalk, 4 Jurassic and Cretaceous, 5 Tertiary, Quaternary removed, tectonics not respected.

indicate the occurrence of the Lower Buntsandstein at the margin of the Świętokrzyskie Mts.

The Gervilleia beds, known from the borehole Radoszyce 3 (Dembowska 1954; Senkowiczowa and Ślączka 1962; Senkowiczowa 1970), are used as a marker in regional correlations of the Buntsandstein of the NW margin of the Świętokrzyskie Mts. The beds yield marine fauna represented by *Avicula* (*Gervilleia*) *murchisoni* (Geinitz), a bivalve characteristic of the Middle Buntsandstein. In the section of the NE margin the role of marker is played by the labyrinthodontid (Labyrinthodontidae beds in Senkowiczowa and Ślączka 1962) beds with vertebrate footprints discussed in this paper. The beds represent an equivalent

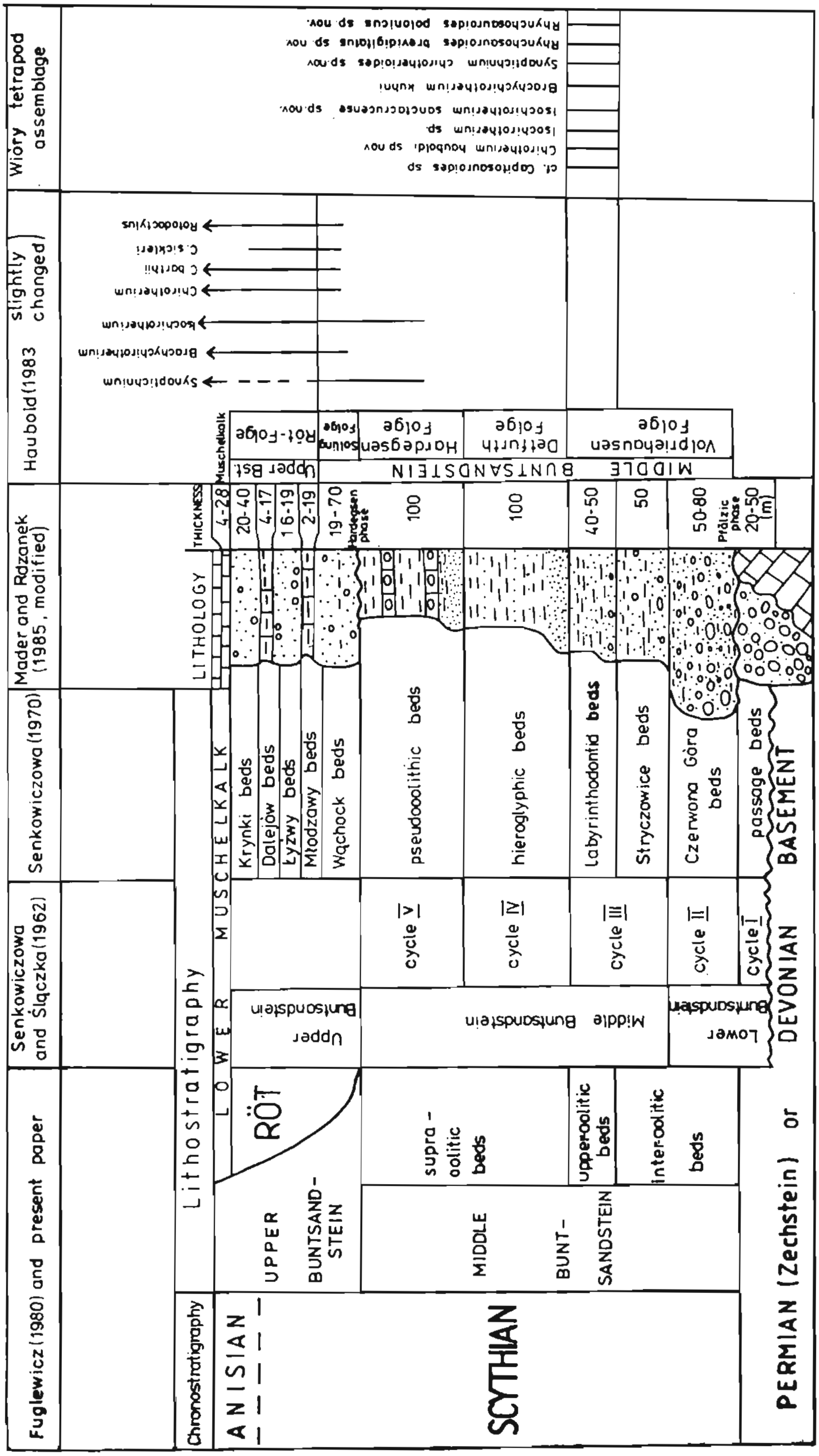

Fig. 2. Stratigraphy of the Buntsandstein in the northern margin of the Świętokrzyskie Mts and its correlation with German division.

of those with *Avicula* (*Gervilleia*) *murchisoni* (Senkowiczowa and Ślączka 1962) and are correlatable with the upper oolite beds in subdivision of the Buntsandstein of the Polish Lowlands (Fuglewicz 1980) and upper part of the Volpriehausen-Folge series in the German subdivision (Fuglewicz 1977). Thus the coarse-clastic rocks underlying the labyrinthodontid beds (i.e. the Czerwona Góra and Stryczowice beds) should be treated as corretable with the inter-oolite beds and identically developed lower part of the Volpriehausen-Folge series in the German subdivision (fig. 2). The series belongs to the Middle Buntsandstein so it means that sedimentation also started in the Middle Buntsandstein at the margin of the Świętokrzyskie Mts.

The analysis of complete and well documented sections from the Polish Lowlands shows that the Lower Buntsandstein is present only in sections with complete Zechstein, representing the same regressive sedimentary cycle determined by sedimentation under the same tectonic and paleogeographic conditions. Therefore the Lower Buntsandstein coincides in extent with the uppermost Zechstein. In the Świętokrzyskie Mts only lower parts of the Zechstein occur (Kowalczewski 1978). They are represented by mainly coarse-clastic rocks (Zygmuntówka conglomerate), deposited in the Zechstein sea. A new sedimentary cycle began with sedimentation of the Czerwona Góra beds in the Middle Buntsandstein, after Palatinian movements. The Czerwona Góra conglome-

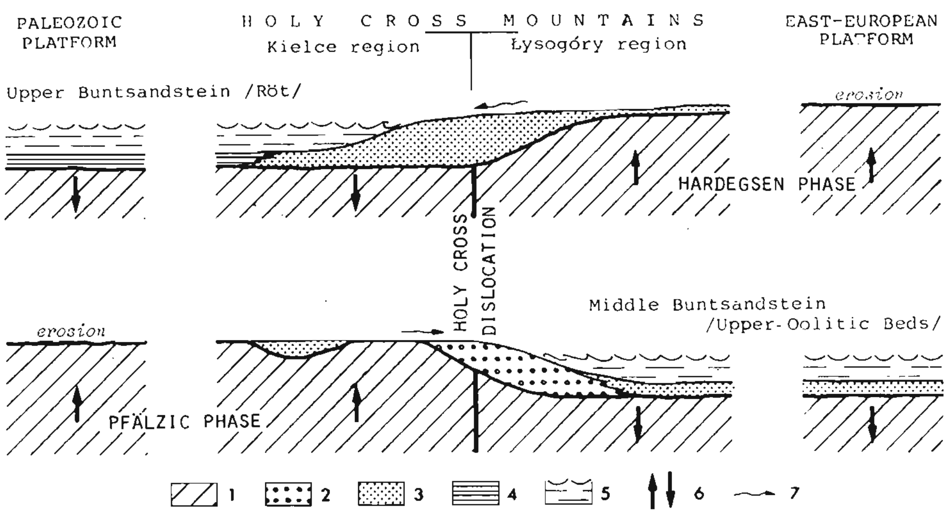

Fig. 3. Łysogóry region and Kielce region interrelationships, and sedimentation of the Buntsandstein in the margin of the Świętokrzyskie Mts. *1* basement, *2* conglomerates, *3* sandstones, *4* marls and carbonate rocks, *5* sea, *6* directions of epeirogenic movements, *7* directions of transport of detrital material.

rates are locally underlain by mudstones discordantly resting on an older basement.

The above presented paleontological and geological data are indicative of a stratigraphic gap between rocks of lower part of the Zechstein and the Czerwona Góra beds. The gap comprises upper part of the Zechstein and Lower Buntsandstein.

Sedimentation of the Buntsandstein was determined by tectonic movements of the Palatinian and Hardegsen phases in the whole central European Basin, including the area of the Świętokrzyskie Mts (fig. 3; Fuglewicz 1980). The position of the Świętokrzyskie Mts at the contact of two major tectonic units, old Precambrian and young Paleozoic platforms, was here of special importance. The northern (Łysogóry) and southern (Kielce) regions were separated by the Świętokrzyski Fraction and the former was connected with the East-European Precambrian Platform while the latter with the Paleozoic Platform. Similarly as these two platforms, the regions were subjected to different tectonics regimes which was the reason for different developments of the Buntsandstein. In result of the Palatinian phase (Middle Buntsandstein), the Paleozoic Platform became uplifted and fluvial transport generally from the South northwards was initiated both in Poland (Senkowiczowa and Ślączka 1962, Fuglewicz 1967, Mader and Rdzanek 1985) and Germany (Wurster 1965, Mader 1983). In connection with subsidence of the East--European Platform the northern region also began to sink and intensely covered with terrigenous material supplied from the South. This explains why Middle Buntsandstein packet is here the thickest. Further subsidence of the East-European Platform resulted in transgression of the Boreal sea, which sediments (upper oolite beds) are known from vast areas (Fuglewicz 1980). In times of sedimentation of the upper oolite beds, the Świętokrzyskie Mts area was a coastal plain sloping to the North and West and with well-developed fluvial system (Mader and Rdzanek 1985). The labyrinthodontid beds rich in vertebrate remains and footprints and, locally, flora, originated under these conditions. Warm and humid climate and immediate proximity of the upper oolite sea clearly created favorable conditions for organic world. This sedimentary cycle was broken by Hardegsen movements, marking the Middle/Upper Buntsandstein boundary (fig. 3). The phase also resulted in reversal of movement of the platforms and, therefore, break of connections with the Boreal Sea and transgression of the Röt sea, reaching the northern (Łysogóry) region only in some times. Therefore, deltaic sequences of the Upper Buntsandstein still formed in that region at the beginning of the Middle Triassic (Ptaszyński 1979, 1981). Material transported by rivers to that region was coming from the North, that is from the opposite direction than during the Middle Buntsandstein.

FOOTPRINT DESCRIPTIONS

REMARKS ON THE MATERIAL

Footprints occur mostly as casts on the sole surfaces of sandstones beds (convex hyporelief) and, in some cases as imprints on the upper surfaces (concave epirelief). On many slabs, footprints are numerous, made in several generations, overlapping and defacing one another. Numerous footprints are poorly recorded and preserved, being frequently destroyed by weathering. On the other hand, some of them display fine details, e.g. a skin texture with granular scales (Chirotheriidae), and shape of small claws (*Rhynchosauroides*). Because of large dimensions, numerous slabs were not collected but only documented by photographs, plaster and latex casts. Till now, only small slabs and a large one (MGUW 01141), were collected. Some of the slabs left in the field have already been lost, being used by country people as building stones.

Measurements, if possible, were made on the original slabs except for some cases when authors disposed only of the plaster casts and photographs (slabs No 2 and 5). Measurements of some poorly preserved specimens, in which distances and angles could be only estimated, are marked with (e.). In tables, these values are given in brackets. The accepted scheme of measurements is after Haubold (1971).

Class **Amphibia** Linné, 1758
Subclass **Labyrinthodontia** H.v. Meyer, 1842
Order **Temnospondyli** Zittel, 1887—1890
Superfamily **Capitosauroidea** Romer, 1947
cf. *Capitosauroides* sp.
(pl. 1: 1—4; fig. 4: 1—9)

Material. — 1.1-2-3-4-5-6-7-8-9-10-11-12-13 — irregular, well preserved trackway consisting of 4 imprints of left pes, 5 imprints of left manus and 4 imprints of right pes; TPW 1: 1.1; TPW 2: 1.2; TPW 3: 1.3, TPW 4: 1.4; TPW 5: 1.5; TPW 6: 1.6; TPW 7: 1.7; TPW 8: 1.9 (plaster casts).

Description. — Trackway. The trackway shows the following irregularities: (1) in the right pes, divarication of digit III from the midline is larger than in the left pes, (2) the oblique pace length measured from the imprint of right pes to that of the left pes is larger than the length measured from the left pes imprint to the right one; (3) the imprints of left manus are in a larger distance from the midline than those of the left pes; (4) imprints of the right manus lack in that trackway (for measurements see Table 1).

Pes. All imprints of pes are well preserved. Tips of digits I—V are well preserved and they form an arc the radius of which is about 30 mm. Neither in the pes nor manus imprints, there is the metapodial joint marked. Digits III and IV are the longest; the imprint of digit IV seems to be somewhat wider than

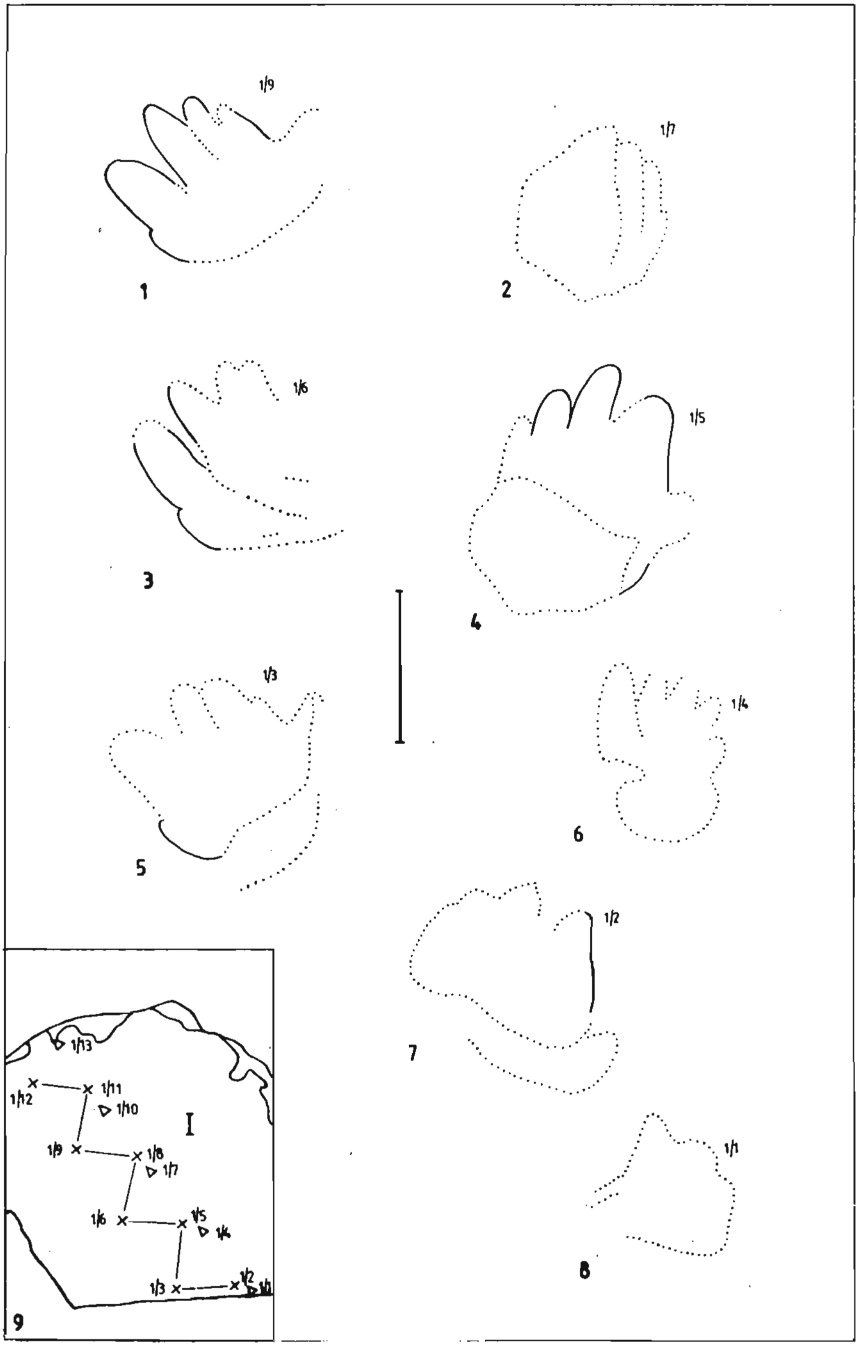

Fig. 4. cf. *Capitosauroides* sp. 1 Imprint of the right pes, TPW 8: 1.9; 2 Imprint of the left manus, TPW 7: 1.7; 3 Imprint of the right pes, TPW 6: 1.6; 4 Imprint of the left pes, TPW 5: 1.5; 5 Imprint of the right pes, TPW 3: 1.3; 6 Imprint of the left manus, TPW 4: 1.4; 7 Imprint of the left pes, TPW 2: 1.2; 8 Imprint of the left manus, TPW 1: 1.1; 9 Trackway, slab No. 1. Preservation state as in 1981. Crosses — pes imprint; triangles — manus imprint. 1—8: scale = 5 cm; 9: scale = 10 cm.

others; distance between tips of digits III and IV is somewhat larger than that between tips of digits I, II and III; digit V is slightly posterior to the group of digit I—IV, but it does not differ in the shape from other digits.

Manus. Manus imprints are poorly preserved. They are somewhat smaller than those of the pes. Arrangement of the five digits is similar to that in the pes.

Table 1

Measurements of *Capitosauroides bernburgensis* Haubold, 1971 (after Haubold, 1971) and cf. *Capitosauroides* sp. from Wióry (in millimetres and degrees).

Measurement		*Capitosauroides bernburgensis* Haubold, 1971		cf. *Capitosauroides* sp. from Wióry
		Type HF-24	Paratype HF-25	
Stride length	manus	372	422	380
	pes	373	428	390 ... 420
Oblique pace length	manus	202 ... 240	234, 254	—
	pes	234	239	300 ... (350) LR* 270 ... 290 RL
Width of trackway	manus	108 ... 132	112, 130	—
	pes	143	111	210 ... 230
Divarication of digit III from midline	manus	0 ... −14	0 ... −5	(−15), (−17)
	pes	−19 ... −35	−15 ... −26	(−35), (−38)
Pace angulation	manus	114	120	—
	pes	105	126	82 ... 87
Manus — pes distance		35 ... 45	45 ... 57	105 ... 120
Glenoacetabular distance		230	265	—
Pes length		45	55	(53) ... (57)
Pes width		(60)	67	(52) ... (60)
Manus length		32	40	(45)
Manus width		45	52	(50)
Divarication of digits I—IV	manus	108, 118	94, 102	—
	pes	112, 118	100, 104	—
Stride: pes length ratio		8.2:1	7.8:1	(7.4:1)
Stride: glenoacetabular distance		1.62:1	1.62:1	—

* L left pes. R right pes
(see aslo the text, p. 116).

Discussion. — Size of the trackway, the shape of footprints, the number and arrangement of digits, the lack of claws and imprint of the metapodial joint conform to the diagnosis of *Capitosauroides* Haubold, 1970 (Haubold 1971). Differences concern the larger width of the trackway and the occurrence of overstepping of the manus imprints by those of the pes. They cause that, at present, the above described trackway, which conforms to *Capitosauroides*, can only be determined in the open nomenclature.

Class **Reptilia** Linné, 1758
Subclass **Archosauria** Cope, 1891
Order **Thecodontia** Owen, 1859
Suborder **Pseudosuchia** Zittel, 1887—1890
Family **Chirotheriidae** Abel, 1935
Genus *Chirotherium Kaup*, 1835
Chritherium lauboldi Ptaszyński sp. n.

(pl. 2: 1—3; pl. 3: 1—4; pl. 4: 1, 2; pl. 10: 2; pl. 11: 1; fig. 5: 1—6; fig 6: 1—4, 8, 9; fig. 7: 6)

Syntypes: KR 5: 8.1 — deeply impressed, somewhat damaged imprint of right pes, pl. 3: 1; fig. 5: 3; KR 9: 14.1 — imprint of right pes with partly preserved digit V, pl. 2: 1, fig. 5: 1; KR 1: 56.1 — imprint of right pes, pl. 3: 3, fig. 5: 4; MWGUW 01139: 16.1-2 set of right manus-pes imprints somewhat deformed by a sliding movement, pl. 2: 2, fig. 5: 2.

Type locality: Wióry near Ostrowiec Świętokrzyski, Świętokrzyskie Mts., Poland.

Type horizon: Labyrinthodontid beds, Middle Buntsandstein, Lower Triassic.

Derivation of the name: In honour of Dr. Hartmut Haubold, the investigator of fossil vertebrate tracks.

Diagnosis. — Medium sized *Chirotherium* with relatively short and wide digit group I—IV. Metatarsal joint in form of an arc with large radius and slightly bent forward. Cross axis in pes is estimated for 61—76 degrees. Pedal digit III only somewhat shorter than width of the digit group I—IV.

Referred material. — MWGUW 01141: 3.6-5-4 — three successive pes-manus-pes imprints; MWGUW 01141: 3.12-28-25-19-24-20-21-23 — irregular trackway; 11.1-2 — set of left pes-manus imprints; TPW 9: 12.1 (plaster cast) — imprint of right pes associated with tail impression; TPW 10: 12.24 (plaster cast) — imprint of left pes: TPW 11: 12.80 (plaster cast) — imprint of right pes; KR9: 14.2 — partial imprint of left pes, probably of the same trackway as the syntype KR 9: 14.1. Here should be probably referred also a trackway 12.36-37-42-43-55-56-78 — three successive sets of imprints of manus and pes plus a problematic footprint described as Chirotheriidae indet. (fig. 6: 5, 6, 7). For trackway measurements see Table 7.

Description. — Trackway. Most of the trackway measurements may be only estimated because of the lack of longer sections of regular trackways. Oblique pace length is, as estimated, 325—415 mm up to 430 mm (MWGUW 01141: 3.6-5-4, fig. 6: 9); these values correspond to the stride length about 600—700 mm. Pace angulation was not measured in the regular trackway; basing on the slab MWGUW 01141: 3, it might attain about 140 degrees. The distance between footprints KR 9: 14.1 and 14.2 (interpreted as width of the trackway) is 160 mm (pl. 2: 1, fig. 5: 5). Estimated divarication of pedal digit III from the midline is 7 degrees (MWGUW 01141: 3.6 and 3.4) up to 35 degrees (KR 9: 14.1 and 14.2;

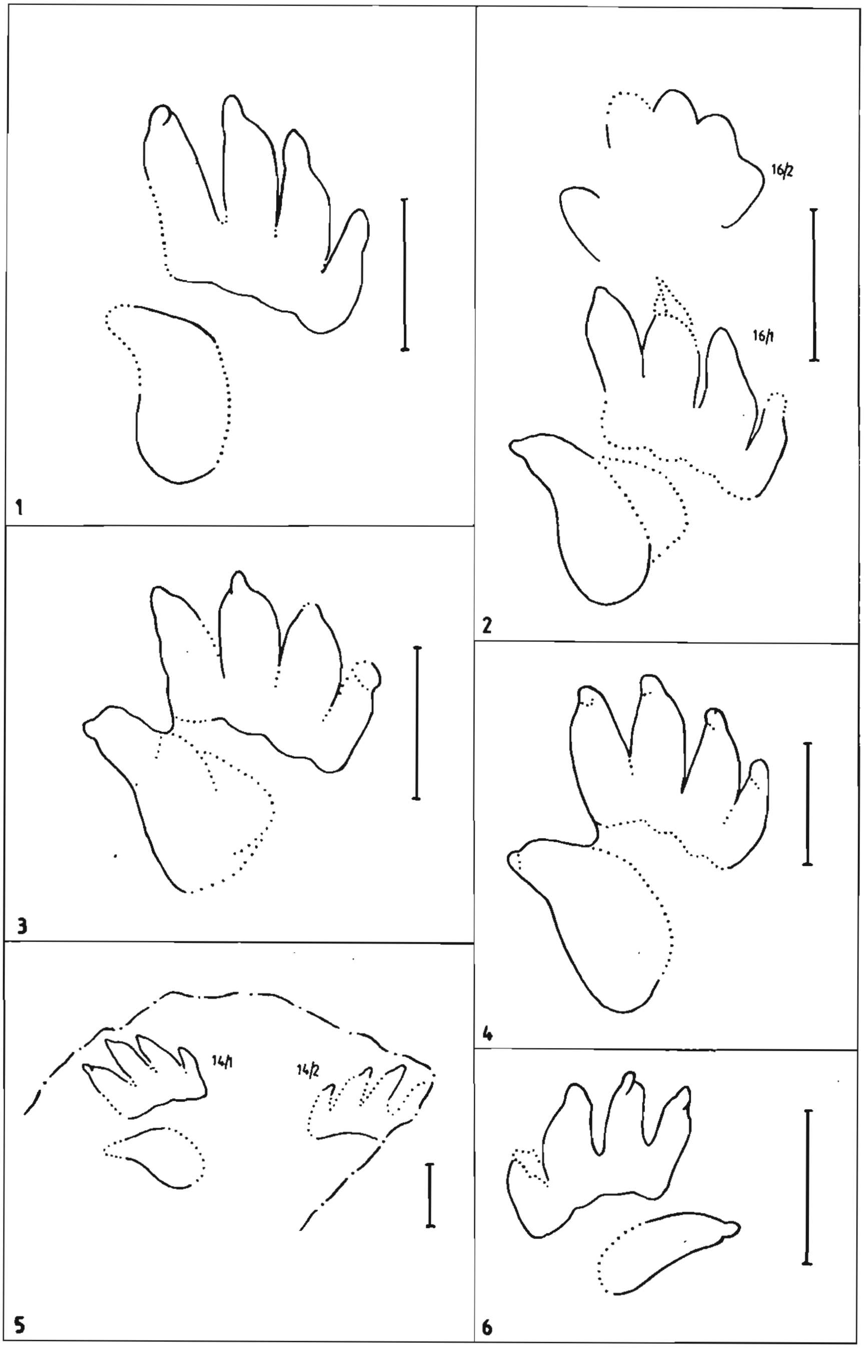

Fig. 5. *Chirotherium hauboldi* sp.n. 1 Imprint of the right pes, syntype, KR-9: 14.1; 2 Set of right pes and manus imprint, syntype, MWGUW 01139: 16.1-2; 3 Imprint of the right pes, syntype, KR 5: 8.1; 4 Imprint of the right pes, syntype, KR 1: 56.1; 5 Sketch of the slab KR 9: 14 with left and right pest imprint, KR 9: 14.1 and 14.2, made by standing (?) animal; 6 Imprint of the left manus, MWGUW 01141: 3.20. 1 — 6: scale = 5 cm.

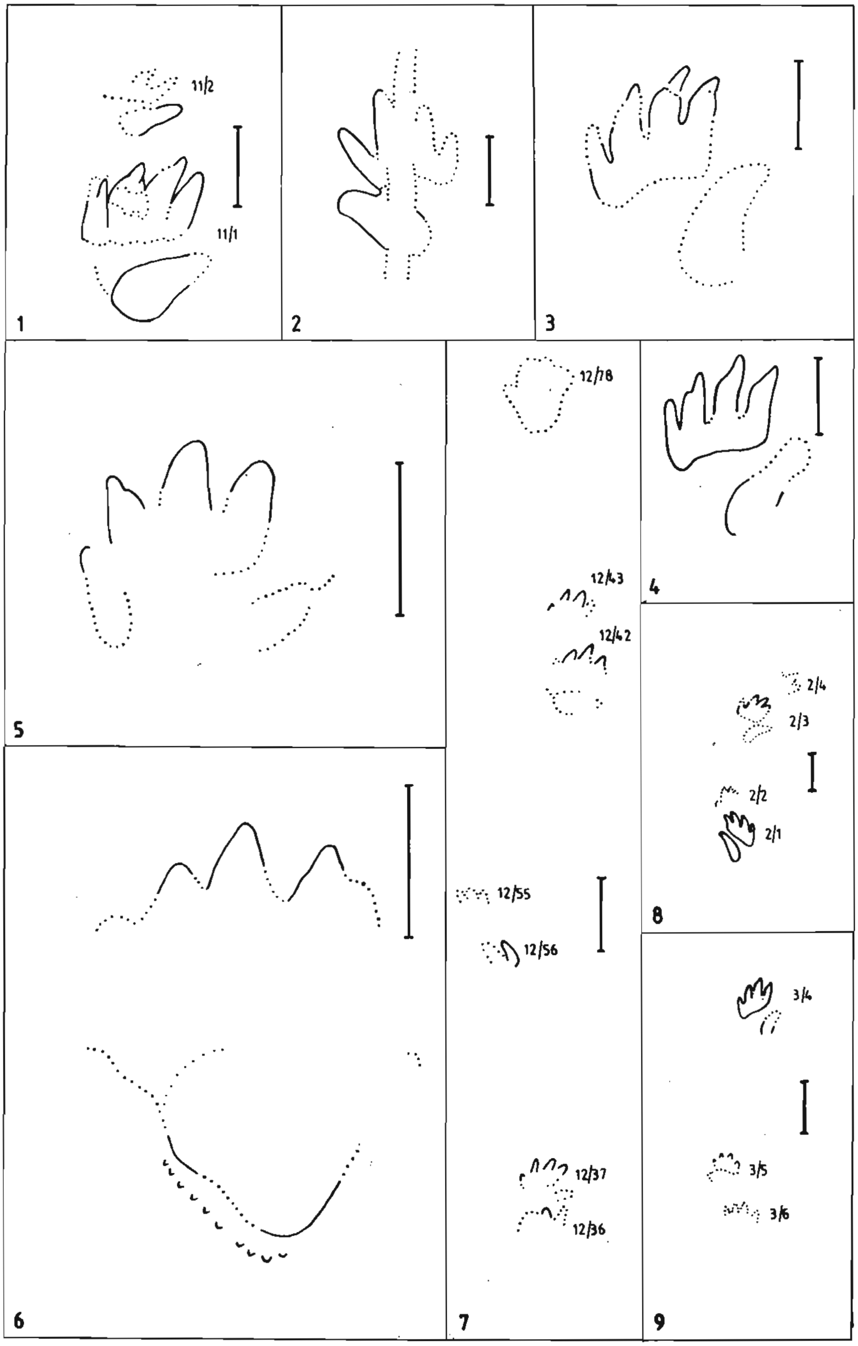

Fig. 6.1 *Chirotherium hauboldi sp.n.*, set of left pes and manus imprint 11.1-2; 2 *Chirotherium hauboldi sp.n.*, imprint of the right pes, TPW 9: 12.1; associated with the tail mark; 3 Chirotheriidae indet., left pes imprint, 2.3; 4 *Chirotherium hauboldi* sp.n., left pes imprint, MWGUW 01141: 3.4; 5, 6 Chirotheriidae indet., left manus and left pes imprint, TPW 40: 12.37. plaster cast; and TPW 41: 12.42 plaster cast; the best preserved imprint from the trackway of relatively large individual, probably *Chirotherium hauboldi* sp.n.; 7 Chirotheriidae indet., trackway: 12.36-37-42-43-55-56-78; 8 Chirotheriidae indet., 2.1-2-3-4; four consecutive pes and manus imprint; 9 *Chirotherium hauboldi* sp.n., three consecutive pes and manus imprint of running (?) individual, MWGUW 01141: 3.6-5-4; 1—6: scale = 5 cm; 7—9: scale = 10 cm.

Table 2

Measurements of pes and manus imprints of *Chirotherium hauboldi* sp. n. (in millimetres and degrees).

Designates of specimens		pes										manus		
				S					S	S	S			S
		2.3	3.4	8.1	11.1	12.1	12.24	12.80	14.1	16.1	56.1	3.19	3.20	16.2
Length of digits	I	(40)	47	39	43	(43)	42	43	44	38	51	(23)	29	23
	II	56	62	48	52	(55)	(60)	56	58	(47)	60	(37)	40	30
	III	64	69	57	57	(65)	66	72	67	(62)	70	—	41	34
	IV	55	57	48	51	(50)	56	(60)	58	(50)	58	(36)	38	33
	V	73	(75)	63	(63)	(78)	(74)	(78)	82	(60)	84	(48)	49	(45)
Footprint	length	(123)	—	114	108	(128)	122	135	134	(108)	137	—	76	59
	width	(104)	(98)	98	(88)	107	(96)	100	(98)	92	110	(73)	76	68
Set of digits I—IV	length	(86)	82	(74)	(66)	(84)	(80)	89	82	77	85	(52)	55	47
	width	(72)	72	70	(68)	78	80	67	71	60	82	(55)	59	50
Divarication I—IV		(33)	25	34	(23)	48	(37)	(23)	32	28	28	(33)	30	(45)
Divarication IV—V		(20)	(22)	20	26	20	(28)	20	(26)	19	24	(55)	48	(34)
Cross axis		(61)	68	61	68	74	(76)	63	65	67	68	(70)	74	68

S — syntypes

MWGUW 01141: 3.24 and 3.21). This angle was obtained as a half of the angle between digits III of two successive pes imprints. Measured according to the same method, divarication of the manual digit from the midline equals 25 degrees (MWGUW 01141: 3.19 and 3.20). The manus-pes distance is 90—135 mm (e.). The ratio stride length/pes length is estimated between 5:1 and 6:1. It is assumed that the irregular, not well preserved trackway MWGUW 01141: 3.12-28-25-19-24-20-21-23 was made by a walking animal which stopped for a moment (pl. 11:1, fig. 7: 6; cf. Peabody 1948: fig. 31 B). A long trackway 12.36-37-42-43-55-56-78 is made by relatively large individual. The poor state of preservation makes impossible the specific determination of this form. The length and width of the best preserved pes impression, 12.42, is 140 mm by 110 mm, respectively.

Pes. Digit III is the longest and digits II and IV are about equal in the length; digit I is the shortest (Table 2). Digits I—IV end in strong, triangular in outline, sharp claws. The value of the cross axis is low, 61—76 degrees (e.). Digits I—IV diverge at 23—36 degrees, except of footprints TPW 9: 12.1 in which they diverge at 47 degrees. Digit V is relatively large, in a distance from digit group I—IV. In the well preserved fooprints, there are visible a large, elongated metatarsal pad and a more slender, curved somewhat outward phalangeal part of this digit. In the best preserved deeply impressed footprints, the tip of digit V ends with a structure which may be interpreted as the print of a short, blunt claw (KR 5: 8.1; KR 1: 56.1; MWGUW 01139: 16.1; pls 2: 2; 3: 1, 3, fig. 5: 2—4).

Manus. Digit group I—IV is relatively short and wide; digit III is the longest while digits II and IV are equal. Digits I—IV diverge at about 30—45 degrees. All the digits had shorter claws than those of the pedal digits, but of the similar shape.

Tail. The print of tail is visible associated with the footprints on the slab No. 12 (TPW 9: 12.1, pl. 4: 2, fig. 6: 2). In cross section, it is a barrel-like structure, about 20 mm wide. It cuts the pes imprint between digits II and III and in the hind part of digit V.

Discussion. — *Chirotherium hauboldi* sp.n. is a primitive chirotheriid with relatively short and wide digit group I—IV. Low value of the cross axis is similar to that in representatives of *Synaptichnium* Nopcsa, 1923 and *Brachychirotherium* Beurlen, 1950. Pedal digits length relations are typical of *Chirotherium* Kaup, 1835: III>IV≥II>I. The new ichnospecies is similar to *Brachychirotherium gallicum* (Willruth, 1917) but differs from it in other length relations among digits I—IV, smaller dimensions and a digit V more distant from digit group I—IV. (cf. Demathieu 1974, 1984). It should be mentioned that the assignment of the above described form to a new ichnospecies was suggested (basing on the photograph) by Dr. H. Haubold (1982 personal communication).

Genus *Isochirotherium* Haubold, 1971

Isochirotherium sanctacrucense Ptaszyński sp.n.

(pl. 4: 1, 3, 4; pl. 11: 1; fig. 7: 3, 4, 5, 7)

Holotype: MWGUW 01141: 3.29 — complete imprint of right pes, slightly deformed by a sliding movement, pl. 4: 1, 3, fig. 7: 3.

Paratype: MWGUW 01140: 13.7 (plaster cast) well preserved (except of digit IV) imprint of left pes, pl. 4: 4, fig. 7: 4.

Type locality: Wióry near Ostrowiec Świętokrzyski, Świętokrzyskie Mts, Poland.

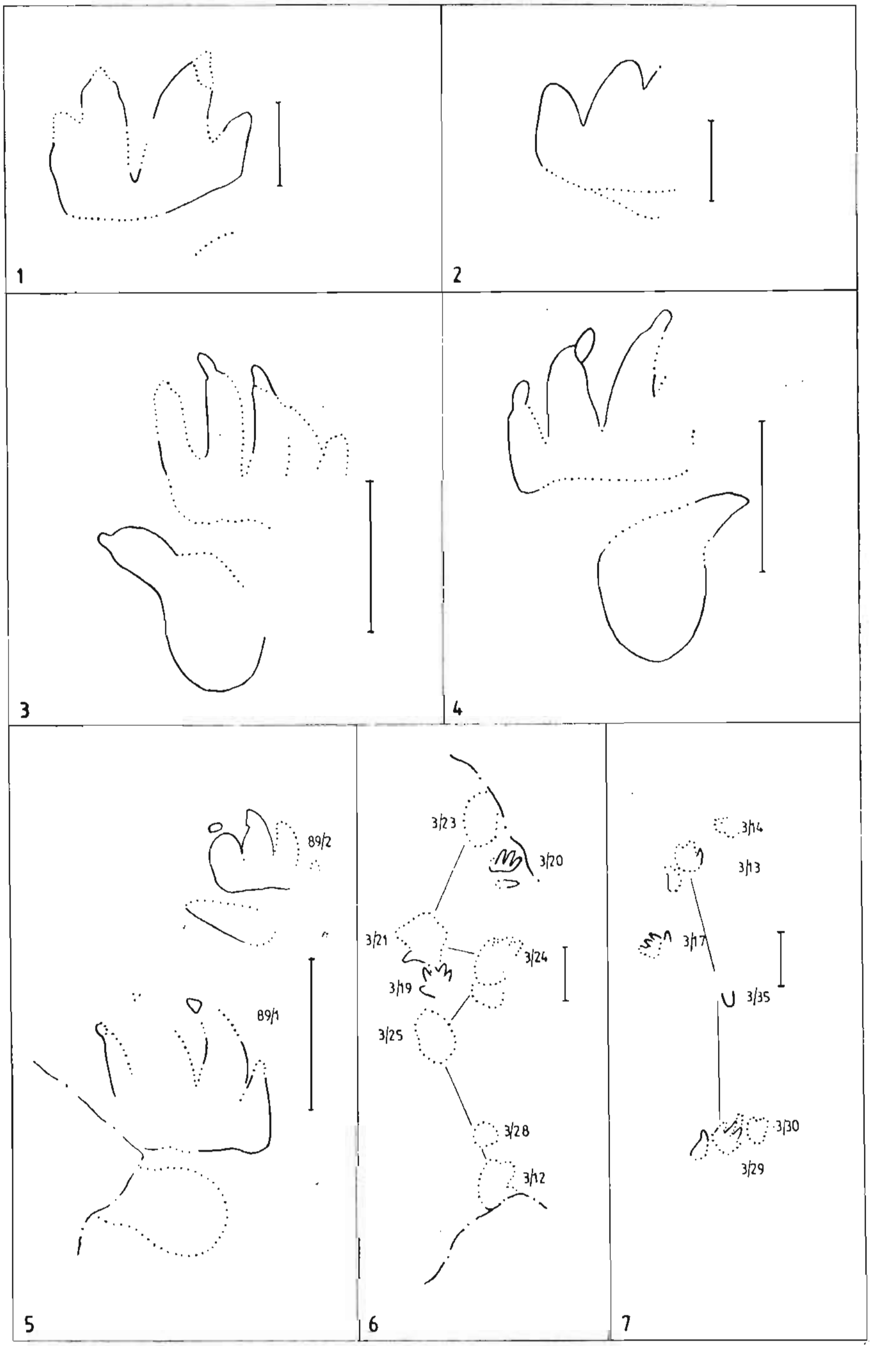

Fig. 7. 1 *Isochirotherium* sp., digit group I—IV of the left pes imprint, 2.5; 2 *Isochirotherium* sp., imprint of a partly preserved right pes digit group I—IV, TPW 14: 30.1; 3 *Isochirotherium sanctacrucense* sp.n., imprint of the right pes, holotype, MWGUW 01141: 3.29; 4 *Isochirotherium sanctacruense* sp., imprint of the left pes, paratype, MWGUW 01140: 13.7 plaster cast; 5 *Isochirotherium sanctacrucense* sp.n., set of right pes and manus imprint, TPW 12: 89.1-2; 6 *Chirotherium hauboldi* sp.n., irregular trackway showing a differentiated speed of the individual, MWGUW 01141: 3.12-28-25-19-24-21-20-23; 7 *Isochirotherium sanctacrucense* sp.n., irregular trackway: MWGUW 01141: 3.29-30-35-17-13-14. 1—5: scale = = 5 cm; 6—7: scale = 10 cm.

Type horizon: Labyrinthodont beds, Middle Buntsandstein, Lower Triassic.

Derivation of the name: after the Latin name of the Świętokrzyskie (Holy Cross) Mountains.

Diagnosis. — Medium sized *Isochirotherium* with relatively short digit group I—IV, the width of which almost equals the length. Pedal digit IV shorter than digit II, but distinctly longer than digit I; digit V somewhat longer than digit III.

Material referred. — MWGUW 01141: 3.30-35-17-13-14 (with the holotype) — irregular, partly and poorly preserved trackway; TPW 12: 89.1-2 — set of right manus-pes imprints; TPW 13: 13.17 (plaster cast) — partly and poorly impressed imprint of right pes, probably made by the same animal as the paratype. For measurements of trackway MWGUW 01141: 3.29-30-35-17-13-14 see table 7.

Description. — Trackway. The trackway is not regular, therefore its measurements cannot be considered as representative of this ichnospecies (fig. 7: 7). Distance between footprints MWGUW 01140: 13.7 and TPW 13: 13.17 (i.e. the oblique pace length) equals 248 mm. Pedal digit III deviates about 30 degrees from the midline. Manus-pes distance between footprints TPW 12: 89.1 and 89.2 equals 90 mm.

Pes. Digit III is the longest within digit group I—IV; digit IV is distinctly shorter than digit II, but much longer than digit I (Table 3). Claws relatively long and narrow and their imprints are well visible on tips of the first four digits. Metatarsal joint is nearly straight, only slightly bent forward. Cross axis equals 75—80 degrees (e.). Digits I—IV diverge at about 22—24 degrees. Digit V is more proximally placed in respect to digit group I—IV than in *Chirotherium hauboldi* sp.n. It displays a large, ovoid metatarsal pad and a phalangeal part which is distinctly defined, narrow and curved outward. Tip of digit V ends with a structure which is interpreted as the imprint of a short, blunt claw (pl. 4: 3, fig. 7: 3).

Manus. Footprints TPW 12: 89.2 and MWGUW 01141: 3.17 are the best preserved although somewhat deformed by a sliding movement. Claws are present on tips of the all five digits. Manus imprints are about three times smaller than those of the pes.

Discussion. — The relatively large manus imprint and long pedal digit IV in *Isochirotherium sanctacrucense* sp. n., similar to those in *I. archaeum* Demathieu et Haubold, 1982, prove that our ichnospecies is very primitive. The large value of cross axis and the pedal digit length relations, III>II>IV>I, are typical of *Isochirotherium*. Among the known species, *I. sanctacrucense* is most similar to *I. soergeli* (Haubold, 1967) but differs from the latter in a relatively larger manus imprint and longer digits IV and V.

Isochirotherium sp.
(pl. 5: 3, 4; fig. 7: 1, 2)

Material. — 2.5 poorly preserved imprint of left pes; TPW 14: 30.1 (plaster cast) — imprint of right pes with digits III, IV and a part of digit II.

Description. — It is the largest form in the investigated material (Table 3). Digit III is the longest and digit IV the shortest; digit II is longer than digit I. Digits II and III end with claws. Cross axis is 75 degrees (e.). In the footprint 2.5, there is indistinctly visible digit V (pl. 10: 2).

Discussion. — The imprints are most similar to *Isochirotherium hessbergense* (Haubold, 1970) with regard to the size, shape and digit length relations (digit IV is the shortest). The form is too imperfecly known to allow any specific assignment.

Table 3

Measurements of pes and manus imprints of *Isochirotherium* sp., *Isochirotherium sanctacrucense* sp. n., *Brachychirotherium kuhni* Demathieu and Haubold, 1982 and *Synaptichnium chirotherioides* sp. n. (in millimetres and degrees).

Designates of specimens		*Iso.* sp.		*Isochirotherium sanctacrucense*						*Brachychirotherium kuhni*					*Synaptichnium chirotherioides*				
		pes		pes				manus		pes				manus	pes			manus	
				H		P									S	S			
		2.5	30.1	3.29	3.13	13.7	89.1	3.17	89.2	5.1	13.14	39.1	57.1	57.5	13.6	48.2	12.18	13.8	13.9
Length of digits	I	(60)	—	(42)	(40)	38	(38)	—	—	(49)	(52)	(49)	(40)	—	(38)	46	(39)	—	(22)
	II	90	—	(56)	—	59	(50)	(30)	(22)	(55)	(63)	(60)	55	(37)	(54)	63	(56)	(34)	(36)
	III	(98)	(95)	58	—	60	(53)	(36)	26	(64)	(66)	62	(62)	(42)	65	72	(61)	(42)	(41)
	IV	(50)	(58)	(47)	—	—	(46)	(28)	25	—	(54)	56	(46)	(27)	56	57	55	(33)	—
	V	—	—	(68)	(58)	64	—	(31)	29	—	—	(80)	(77)	—	—	(66)	—	—	—
Footprint	length	—	—	113	112	114	(90)	(58)	46	—	—	121	125	—	—	(118)	—	—	—
	width	—	—	(86)	87	87	—	(59)	46	—	—	124	97	—	—	94	—	—	—
Set of digits I—IV	length	(98)	—	(68)	—	64	61	(40)	(32)	(93)	(82)	(83)	86	—	(73)	83	(67)	(49)	(50)
	width	(96)	—	(62)	(59)	(61)	54	(47)	35	—	(85)	(90)	76	—	(64)	63	64	44	(50)
Divarication I—IV		(24)	—	(24)	—	(22)	(23)	—	—	—	(50)	(47)	(30)	—	(35)	(30)	(35)	(18)	—
Divarication IV—V		—	—	(16)	—	(16)	—	(50)	(60)	—	—	(0)	(10)	—	—	(20)	—	—	—
Cross axis		(75)	(76)	(77)	—	80	(75)	(80)	(85)	(40)	(55)	(50)	(40)	—	(68)	68	65	(70)	(65)

H — holotype
P — paratype
S — syntypes

Genus *Brachychirotherium* Beurlen, 1959

Brachychirotherium kuhni Demathieu et Haubold, 1982

(pl. 5: 1, 2; pl. 6: 1; pl. 10: 3; fig. 8: 1—4)

1982. *Brachychirotherium kuhni* sp. n.: Demathieu et Haubold, 106—107, photo 4; Abb. 2d.
1983. *Brachychirotherium kuhni*; Haubold: 127—128, fig. 2f.
1984. *Brachychirotherium kuhni*; Haubold: Abb. 95.1.

Material. — 5.1 partly preserved imprint of left pes; TPW 15: 13.14 (plaster cast) — imprint of left pes digit group I—IV; TPW 16: 39.1 — imprint of right pes; TPW 17: 57.1; TPW 18: 57.5 (plaster casts) — set of right manus-pes imprints; KR 12: 44.1-2 — poor, partly preserved set of manus-pes imprints.

Description. — There is no trackway in the investigated material. In two known cases, the manus-pes distance equals 80 and 120 mm (e.).

Pes. Width of the footprint almost equals the length. The same is true for the digit group I—IV. Digit III is the longest and digit I the shortest; digit II is distinctly longer than digit IV. Digits I—IV have enlarged polsters and long, narrow claws (pl. 5: 1, fig. 8: 3, 4). Digit V is subparallel to digit IV, has relatively wide metatarsal pad and distinctly separated phalangeal portion (pl. 5: 2, fig. 8: 1, 2). Value of the cross axis is low, 40—50 degrees (e.). Divarication of digits I—IV is between 30 and 50 degrees (e.).

Manus. Imprints of the manus are too poorly preserved to be studied.

Discussion. — Footprints of *Brachychirotherium kuhni* from Wióry are somewhat larger (Table 3) than the type, which was described from the stratigraphically younger deposits (Solling Folge. Harmuthshausen in Hessen, BRD) but otherwise they are identical. Difference in the size may be due to the state of preservation.

Genus *Synaptichnium* Nopcsa, 1923

Synaptichnium chirotherioides Ptaszyński sp.n.

(pl. 6: 2, 3, 4; fig. 8: 5—7)

? 1982. *Synaptichnium* sp.: Demathieu et Haubold: 105—106; photo 3: Abb. 2c.
? 1983. *Synaptichnium* sp.; Haubold: 126, fig. 2c.
? 1984. *Synaptichnium* sp.; Haubold: Abb. 94. 3.

Syntypes: MWGUW 01142: 13.6 (plaster cast) — imprint of left pes digit group I—IV, pl. 6: 2, fig. 8: 7; TPW 19: 48.2 (plaster cast) — shallow, but complete imprint of left pes, pl. 6: 3, fig. 8: 6.

Type locality: Wióry near Ostrowiec Świętokrzyski, Świętokrzyskie Mts. Poland.

Type horizon: Labyrinthodontid beds, Middle Buntsandstein, Lower Triassic.

Derivation of the name: similar to representatives of *Chirotherium*.

Diagnosis. — Relatively large *Synaptichnium*. Pedal digit III the longest, digit IV somewhat shorter but distinctly longer than digit II, digit V relatively small and placed in a distance to digit group I—IV. The latter relatively narrow posteriorly.

Material referred. — 12.4-18-41-49 fragmentary trackway (TPW 20: 12.4; TPW 21: 12.18; TPW 22: 12.41; TPW 23: 12.49; all plaster casts), TPW 24: 13.8 and TPW 25: 13.9 (plaster casts) — imprints of left and right manus, probably associated with syntype MWGUW 01142: 13.6; TPW 26: 48.3 (plaster cast) — very poorly preserved imprint of left manus, probably associated with syntype TPW 19: 48.2 in the same set.

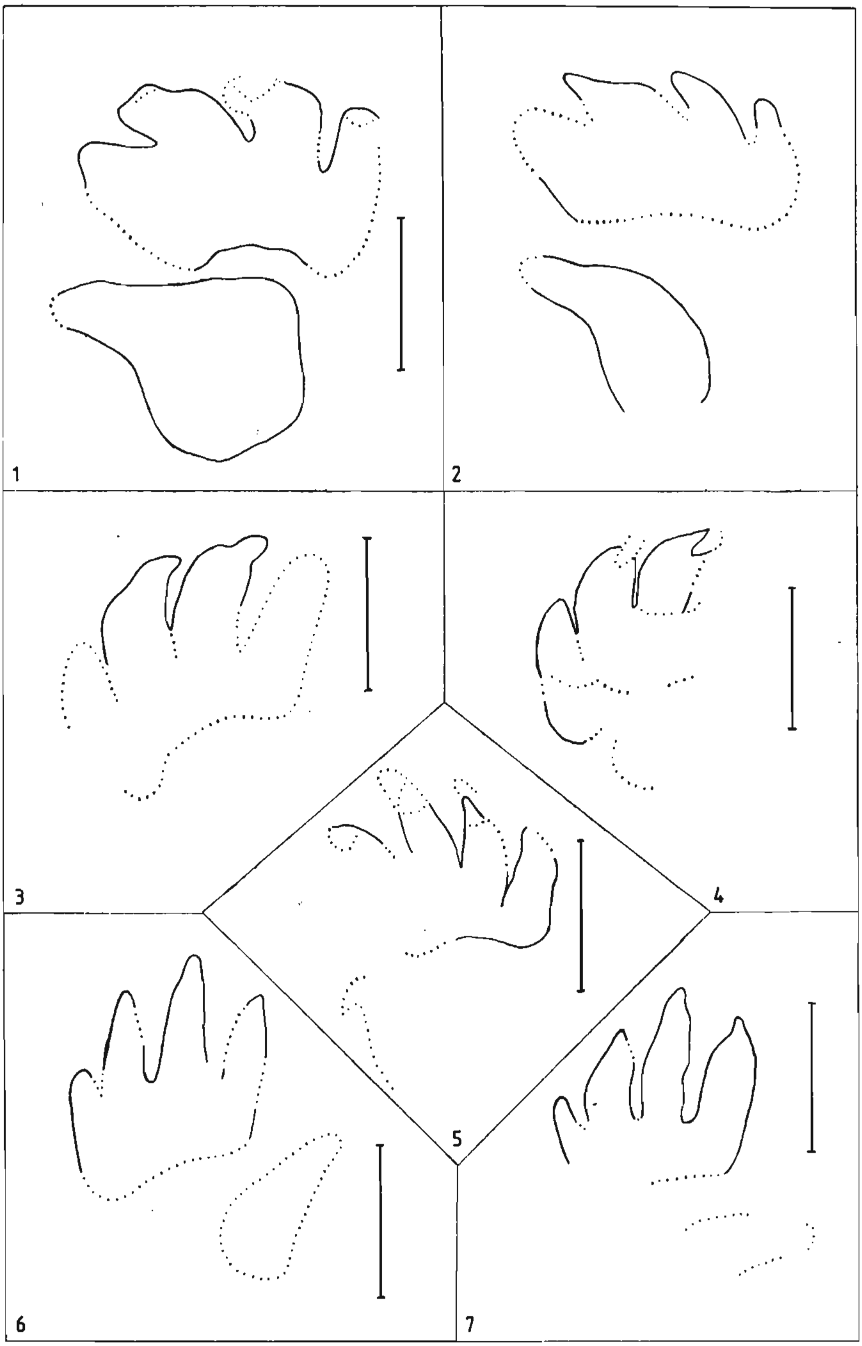

Fig. 8. *Brachychirotherium kuchni* Demathieu et Haubold, 1982. 1 Imprint of the right pes, TPW 16: 39.1; 2 Imprint of the right pes, TPW 17: 57.1 plaster cast; 3 Imprint of the left pes digit group I—IV, TPW 15: 13.14 plaster cast; right pest, TPW 16: 39.1; 2 Imprint of the right pes, TPW 17: 57.1 plaster cast; 3 Imprint of the left pes digit group I—IV, TPW 15: 14.14 plaster cast; 4 Imprint of a partly preserved left pes, 5: 1; *Synaptichnium chirotherioides* sp.n. 5 Imprint of the right pes, TPW 21: 12.18 plaster cast; 6 Imprint of the left pes, syntype, TPW 19: 48.2 plaster cast; 7 Imprint of the left pes, syntype, MWGUW 01142: 13.6 plaster cast; 1—7: scale = 5 cm.

For measurements of trackway 12.4-18-41-49 see Table 7.

Description. — Trackway. Pace angulation was indirectly measured and its value might attain about 150 degrees. For other trackway measurements see Table 7. Manus-pes distance between footprints TPW 19: 48.2 and TPW 26: 48.3 equals 120 mm.

Pes. Digit group I—IV is dictintly longer than wide being relatively narrow at the basal portion. Long and narrow claws are present on tips of the first four digits (MWGUW 01142: 13.6). Digit III is the longest and digit IV is longer than digit II. Digit I—IV diverge at 30—35 degrees (e.). In all so far known footprints of this ichnospecies, digit V was not recorded, while in our print TPW 19: 48.2 it is impressed, relatively short, narrow and placed in a distance from digit group I—IV. Cross axis is 65—68 degrees (Table 3).

Manus. Imprints of manus are not well preserved. Long and narrow claws are present on the tips of all five digits (TPW 24: 13.8 and TPW 20: 12.4). The manus-pes size relation cannot be determined. For measurements see Table 3.

Discussion. — The present author had at his disposal only the photographs of the footprints described by Demathieu and Haubold (1982) as ?*Synaptichnium* sp., which display similar length relations between pedal digits II, III, IV. There seem to be no differences between the footprints from Wióry and the latter ones, except for the larger size and a somewhat larger value of the cross axis of the Wióry prints.

Synaptichnium chirotherioides spn. is somewhat smaller than *Chirotherium hauboldi* sp.n. and additionally differs from that ichnospecies in relatively longer pedal digit IV, the narrower posterior portion of digit group I—IV, the more digitigrade pes imprints and the smaller, pedal digit V more distantly placed from digit group I—IV.

In the atypical length of pedal digit IV in respect to digit III, the above described ichnospecies differs from all other representatives of *Synaptichnium* (except for those recorded in the synonymy).

Subclass **Lepidosauria** Dumeril et Bibron, 1839
Family **Rhynchosauroidae** Haubold, 1966
Genus *Rhynchosauroides* Maidwell, 1911
Rhynchosauroides brevidigitatus Ptaszyński sp.n.

(pl. 7: 1—4; pl. 8: 3; pl. 10: 3; fig. 9: 1—4, 11, 12; fig. 10: 2)

Holotype: MWGUW 01144: 5.2 (plaster cast) — complete imprint of left pes, pl. 7: 4, fig. 9: 1.

Paratypes: KR 11: 4.16 — imprint of left pes, pl. 8: 3; fig. 9: 3;TPW 27: 60.2 — imprint of right pes, pl. 7· 2, fig. 9: 2; TPW 28: 111.1-2 — two successive imprints of pes, pl. 7: 1, fig. 9: 4.

Type locality: Wióry near Ostrowiec Świętokrzyski, Świętokrzyskie Mts., Poland.

Type horizon: Labyrinthodontid beds, Middle Buntsandstein, Lower Triassic.

Derivation of the name: because of the relatively short digit group I—IV.

Diagnosis. — Medium sized *Rhynchosauroides* with relatively short digit group I—IV, with digit II not shorter than half of the length of digit IV, digit V somewhat wider than others with its tip on the level of basal part of digit IV.

Material referred. — KR 11: 4.5-4 — set of imprints of right pes and manus; KR 11: 4.22-24-21-13 (with paratype KR 11: 4.16) — group of poorly preserved imprints of manus and pes, representing probably and incomplete trackway; KR 11:

Table 4

Measurements of pes and manus imprints of *Rhynchosauroides brevidigitatus* sp. n. (in millimetres and degrees).

Designates of specimens		*Rhynchosauroides brevidigitatus*											
		pes										manus	
		H 5.2	P 4.16	P. 60.2	3.37	5.3	4.5	6.3	12.62	111.1	111.2	4.4	4.10
Length of digits	I	—	—	—	—	—	—	—	—	—	—	—	—
	II	9	8	8	(7)	(9)	—	(7)	(9)	10	(11)	—	—
	III	13	12	12	(10)	—	—	—	—	(16)	15	(7)	(8)
	IV	15	(13)	(16)	(12)	—	—	—	—	(16)	17	(8.5)	(9)
	V	(8.5)	—	—	—	—	—	—	—	—	—	(4)	(4)
Footprint	length	22	—	—	—	—	—	—	—	—	—	(11.5)	(12.5)
	width	18	—	—	—	—	—	—	—	—	—	(13)	(13.5)
Set of digits I—IV	length	17	—	—	—	—	—	—	—	—	—	—	—
	width	15	—	—	—	—	—	—	—	—	—	(10)	—
Set of digits II—IV	length	16	(15)	(17)	(15)	—	—	—	—	(18)	20	(9)	(9)
	width	12	12	11	12	(12)	(12)	(11)	(11)	13	13	(9)	(11)
Divarication II—IV		(12)	19	(22)	(27)	(17)	—	(19)	—	(30)	(30)	(21)	(28)
Divarication IV—V		(12)	—	—	—	—	—	—	—	—	—	—	—

H — holotype
P — paratypes

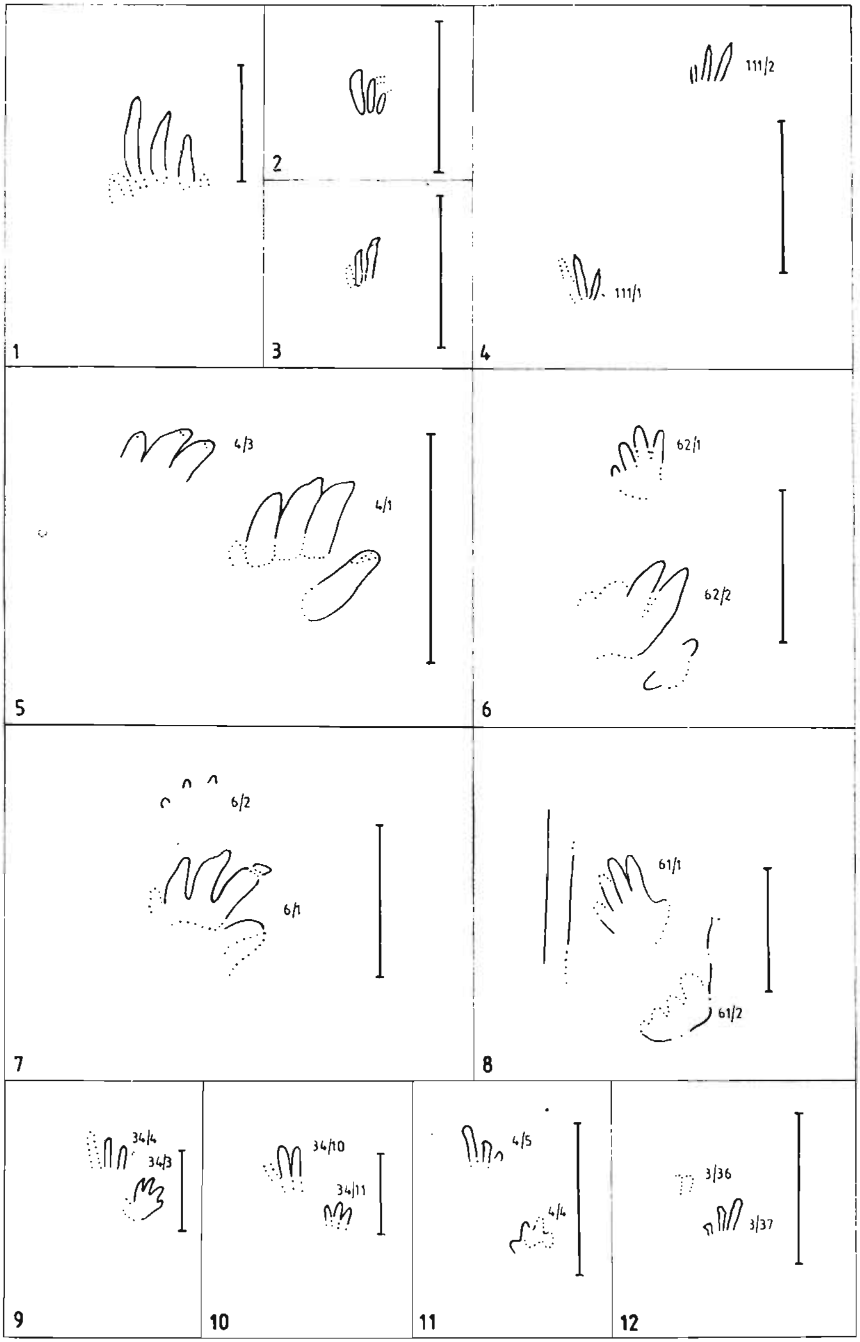

Fig. 9. *Rhynchosauroides brevidigitatus* sp.n. 1 Imprint of the right pes, holotype, MWGUW 01444: 5.2; 2 Imprint of the right pes, paratype, TPW 27: 60.2; 3 Imprint of the left pes, paratype, KR 11: 4.16; 4 Two consecutive pes imprint, paratypes, TPW 28: 111.1-2; *Rhynchosauroides polonicus* sp.n.; 5 Set of left pes and manus imprint, holotype, KR 11: 4.1 and 4.3; 6 Set of right pes and manus imprint on the upper side of sandstone bed, KR 4: 62.2-1; 7 Set of left pes and manus imprint, KR 2: 6.1-2; 8 Set of left manus and pes imprit associated with the tail mark (?), TPW 37: 61.1-2; 9, 10. Two imprint sets of manus overstepped by pes, TPW 36: 34.4-3 and TPW 36: 34.10-11; *Rhynchosauroides brevidigitatus* sp.n.; 11 Set of right manus overstepped by the pes, KR 11: 4.5—4; 12 Set of the pes behind the manus imprint, MWGUW 01141: 3.37-36; 1: scale = 2 cm; 2—12: scale = 5 cm.

Table 5

Measurements of pes and manus imprints of *Rhynchosauroides polonicus* sp. n. (in millimetres and degrees).

Designates of specimens		*Rhynchosauroides polonicus*											
		pes					manus						
		H 4.1	4.6	6.1	34.4	62.2	4.9	4.7	4.3	6.2	34.3	61.1	62.1
Length of digits	I	7	—	(10)	—	—	—	—	—	—	(12)	(10)	—
	II	16	—	20	18	—	—	(7)	—	—	(17)	(19)	(14)
	III	18	(17)	26	(24)	(33)	—	(11)	—	—	(20)	(21)	(17)
	IV	19	(19)	28	—	(34)	—	(12)	—	—	(20)	(20)	(16)
	V	20	—	(35)	—	—	—	(14)	—	—	(12)	(19)	—
Footprint	length	32	—	46	—	—	—	—	—	—	31	(38)	—
	width	32	—	39	—	(40)	—	—	—	—	23	(31)	—
Set of digits I—IV	length	27	(27)	35	—	—	—	—	—	—	(23)	(31)	(24)
	width	22	(24)	31	—	—	—	—	—	(24)	17	25	20
Set of digits II—IV	length	24	(24)	28	(30)	—	—	(15)	—	—	(21)	(24)	(24)
	width	19	(18)	27	22	(25)	(12)	(15)	17	(19)	15	20	17
Divarication II—IV		23	(21)	35	(12)	—	(34)	(29)	(24)	—	26	(17)	(40)
Divarication IV—V		20	—	(13)	—	(7)	—	—	—	—	(50)	(44)	—

H — holotype

4.10 isolated imprint of manus; KR 2: 6.3-4 — set of left manus-pes imprints; MWGUW 01141: 3.37-36 — set of imprints of left pes and manus; TPW 29: 5.3 (plaster cast) — isolated imprint of pes. Numerous rhynchosauroid footprints are present also on slabs: TPW 27, TPW 30—35. The prints are mostly incompletely impressed, only digits II—IV or their tips are visible. However, most of them represents probably this species.

Description. — Trackway. For the measurements of the only known incomplete trackway see Table 6; for measurements of the manus and pes see Table 4.

Pes. In the majority of footprints, only the digits or digit tips I—IV are preserved, except for MWGUW 01144: 5.2 which displays all five digits impressed. Digit group II—IV is somewhat longer than wide. Relatively narrow digits II—IV have long, sharp claws; digit I is poorly impressed, short digit V is broader than others and subparallel to digit group II—IV, its tip leveling the distal end of digit IV.

Manus. Imprints of manus are relatively wide and have best impressed digits II—V, with digit IV somewhat longer than digit III; digit V is rather short. Claws are not visible in the investigated footprints.

Discussion. — In regard to the size, position of pedal digit V, the shape and known features of the trackway, *Rhynchosauroides brevidigitatus* sp.n. is most similar to *R. bornemanni* Haubold, 1966. The distinct differences concern the length relation of digits II—IV, especially digit II which is very long in respect to the remaining two. The new ichnospecies differs from *R. articeps* (Owen, 1842) in the wider and shorter digit group II—IV, the smaller size and not parallel digits II—IV. From pedal imprints of *R. petri* Demathieu, 1966 described from the Middle Triassic of France, the new species differs in the smaller size and the broader, relatively short digit IV, which in the France footprint is more than twice longer than digit II.

Rhynchosauroides polonicus Ptaszyński sp.n.

(pl. 8: 1—4; pl. 9: 1; pl. 10: 1; fig. 9: 5—10; fig. 10: 1)

Holotype: KR 11: 4.1 — complete imprint of left pes, pl. 8: 1, fig. 9: 5.

Type locality: Wióry near Ostrowiec Świętokrzyski, Świętokrzyskie Mts., Poland.

Type horizon: Labyrinthodontid beds, Middle Buntsandstein, Lower Triassic.

Derivation of the name: known from Poland.

Diagnosis. — Large *Rhynchosauroides* with relatively short digit group I—IV and nearly equally long digits III and IV; tip of digit V on the level of half the length of digit IV.

Material referred. KR 11: 4.19-9-6-7-3 (with the holotype) — imprints of manus and pes, forming a short but well preserved trackway; KR 2: 6.1-2 — set of left manus — pes imprints; KR 4: 62.2-1 — set of right manus — pes imprints; TPW 36: 34.3-4 (latex cast) — set of left manus — pes imprints; TPW 36: 34.10-11 (latex cast) — set of left manus — pes imprints; TPW 37: 61.1-2 — set of left manus — pes imprints associated with a tail (?) mark. Numerous footprints representing probably this species occur on slab No. 34.

Description. — Trackway. There is only one known trackway (KR 11: 4.19-9-6-7--1-3, pl. 8: 3, fig. 10: 1; for measurements see Table 6). In this trackway, probably not a straight one, divarication of pedal and manual digits III from the midline is variable and thus may be only estimated. E.g., divarication of pedal digit III

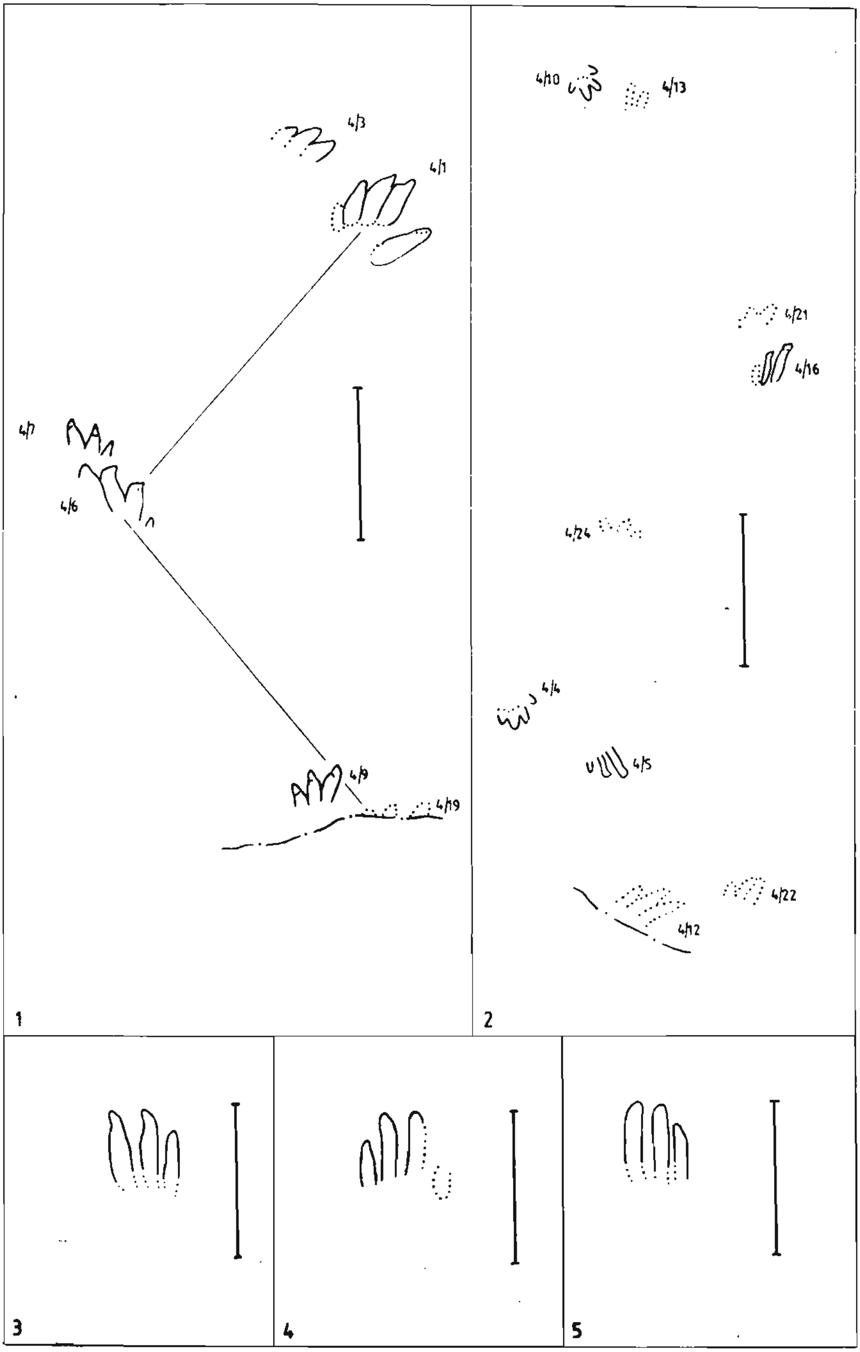

Fig. 10. 1 *Rhynchosauroides polonicus* sp.n. trackway, KR 11: 4.19-9-6-7-1-3; 2 *Rhynchosauroides brevidigitatus* sp.n., association of pes and manus imprints redrawn from the slab KR 11: 4; specimens: 4.22; 4.24; 4.16 (paratype); 4.21 and 4.13; may represent poorly recorded trackway; 3, 4, 5 Typically recorded rhynchosauroid footprints (only digits II, III and IV impressed) representing probably *Rhynchosauroides polonicus* sp.n., TPW 36: 34.1; 34.2; 34.6. 1—5: scale = 5 cm.

Table 6

Trackway measurements of *Rhynchosauroides brevidigitatus* sp. n. and *Rhynchosauroides polonicus* sp. n. (in millimetres and degrees).

Measurement		*Rhynchosauroides brevidigitatus* sp. n.		*Rhynchosauroides polonicus* sp. n.	
		specimens 111.1, 111.2	other specimens	The trackway with the holotype, 4.1	other specimens
Stride length	manus	—	(123)	220	—
	pes	—	176?; 158?	(213)	—
Oblique pace length	manus	—	86?; 57?	125; 140	—
	pes	82	87?; 99?	130, (142)	—
Width of trackway	manus	—	34?	72	—
	pes	—	47?; 46?	(86)	—
Divarication of digit III from midline	manus	—	—	+9; −40; +10	—
	pes	−10	−4	−20; −28	—
Divarication of manus and pes digits III		—	0	−10; +26	+23 ... +40
Pace angulation	manus	—	120?	115	—
	pes	—	120?	(102)	—
Manus-pes distance		—	13 ... 28	34, 23, (28)	(30) ... (58)
Glenoacetabular distance		—	(76)? (estimated)	128	—
Stride: pes length ratio		—	(11.0:1)?	(6.8:1)	—
Stride: glenoacetabular distance ratio		—	(2.2:1)?	1.7:1	—

? — measurements from problematical tracks (slabs with numerous but poorly preserved footprints; slab No. 4 — cf. fig. 8:2).

Table 7

Trackway measurements of Chirotheriidae (in millimetres and degrees).

Measurement	*Chirotherium hauboldi* sp. n., MWGUW 01141: 3.12-28-25-19-24-20-21--23	Chirotheriidae indet. 12.36-37-42-43-55-56-78	*Isochirotherium sanctacrucense* sp. n. MWGUW 01141: 3.29-30-35-17-13-14	*Synaptichnium chirotherioides* sp. n., 12.4--18-41-49
Oblique pace length (pes) (manus)	310 190 160 260	400 430	303 206 244	370
Stride length	415 190 300	800	535	740 (e.)
Pace angulation (pes) (manus)	115 75 90	147 154	240 232	
Width of trackway (pes)	130	110		90 (e.)
Manus — pes distance	90 115 190	90 110 90	105 132 77	85
Glenoacetabular distance	370	455	320	
Divarication of pes digit III from the midline		15		9 16
Divarication of manus digit III from the midline		23 25 47		18 27(e.)

from the midline is about 25 degrees and manual digit is inclined to the midline at 0—10 degrees. Divarication of the manual and pedal digits III from one another in the same sets increases in some cases, e.g. between 25 and 40 degrees (e.). In the above mentioned trackway, pes imprints are placed laterally to manus imprints or slightly behind. In other cases, pes imprints are more or less distinctly posterior to those of the manus (pls. 8: 2, 4; 10: 1, fig. 9: 6, 7, 8) or in front of them (fig. 9: 9, 10). These differences may result from speed differences of individuals.

The problematic tail mark (TPW 37: 61.1-2, pl. 8: 2, fig. 9: 8) is a structure barrel-like in cross section, flattened and 9 mm wide.

Pes. Digit group I—IV is relatively short and wide. Digit IV is the longest but only slightly longer than digit III; digits II—IV end with wide, sharp claws of triangular shape; digit I is rarely and poorly preserved; digit V (completely impressed in the holotype and the footprint KR 2: 6.1) is relatively long and diverges at 20 degress from digit IV its tip being on the level of a half the length of digit IV. It was probably provided with a claw (pl. 8: 1). For measurements see Table 5.

Manus. In all footprints, digits I—IV are well preserved, digit V is only occasionally impressed (TPW 37: 61.1; TPW 36: 34.3) placed backward in respect to digit group I—IV. Digits III and IV are almost equal in the length. Claws are similar to those of pes and are best preserved in footprint KR 11: 4.7.

Discussion. — *Rhynchosauroides polonicus* sp.n. is most similar to the large representatives of the rhynchosauroides, *R. schochardti* (Rühle v. Lilienstern, 1939), *R. moenkopiensis* Haubold, 1970 and to the Late Triassic ichnospecies *R. brunswickii* (Ryan et Willard, 1974). From the latter our species differs in a smaller divarication of manual digit I and in divarication of manual and pedal digits III from one another. The new species is smaller than *R. schochardti* and *R. moenkopiensis* but displays the relatively larger pace angulation, the smaller stride length/glenoacetabular length ratio as well as the larger width of the trackway of manus imprints in respect to that of the pes. Additionally, *R. polonicus* differs from *R. schochardti* in the shorter pedal digit group I—IV. Divarication of pedal digit III from the midline is not as large in *R. polonicus* as it is in *R. schochardti* but also this digit is not parallel to the midline as is the case in *R. moenkopiensis*.

TAPHONOMY OF FOOTPRINTS

GEOLOGIC CONTEXT

Occurrence and collecting of footprints

The studied footprints occur at sole and top surfaces of sandstone layers in a sequence of thin- and thick-bedded sandstones intercalated by silt or clay. The sandstone layers are often very thin (about 1 cm thick) and easily break into slabs not large enough to display more than one ichnotaxon. Slabs displaying more ichnotaxa come as a rule from thicker layers. For example, slab no. 12 with at least 4 ichnotaxa represented by over 80 footprints, was derived from a layer about

1.2 m thick. The exception is here slab np. 34 (cast TPW 34), derived from a layer only 20 cm thick and displaying at least 2 ichnotaxa represented by about 200 footprints. So high concentration of traces makes it difficult to decipher to which trail individual footprints belong (pl. 9: 1—2).

The sandstone layers are separated by unlithified clay and/or silty intercalations which tightly adhere to freshly excavated sandstones and obscure their surface. Cleaning of the surface of such slabs becomes much easier when subjected to weathering for a few months. It should be noted that search for footprints does not become easier when surface of a slab is wet.

Excavation of the material often resulted in mechanical damage of the footprints, especially in the course of dumping (slabs MWGUW 01141, KR 2—3, KR 5, KR 7).

Diagenesis and weathering

Desiccation of sediments lead to deformation of clay layers (see p. 139). Chemical processes, oxidation including, causing pigmentation of the sediments covering the footprints, are highly complex but of minor importance for preservation of the footprints (cf. Haubold and Katzung 1978). Red sandstone of the sequence examined is quite often characterized by a willow green colour at the contact with underlying clays which explains fairly common greenish colour of footprint casts (e.g., slabs MWGUW 01139, KR 1, KR 2, KR 6—9, TPW 80, TPW 82, TPW 113).

Lithification of the sediments was connected with formation of authigenic quartz, neoformation of iron oxides and cementation with carbonates (Mader and Rdzanek 1985). Carbonate cement was found in a number of slabs (e.g., KR 9, KR 11, TPW 61, TPW 75, TPW 81, TPW 89, TPW 93—94, TPW 99, TPW 117) but it often appears to be absent from the lower part of a layer (slabs KR 2, TPW 34, TPW 82, TPW 94) or limited to some horizons only (slabs TPW 95, TPW 124). Natural casts cemented in such a way display higher resistance to mechanical destruction.

Lithified sandstones from the Wióry locality were subjected to tectonic compression in at least two phases. Older fractures are usually narrow and scarred (e.g., slabs TPW 64, TPW 76, TPW 81, TPW 95) and the younger — wide and causing desintegration of layers into blocks. However, it should be noted that the network of the fractures is not dense enough to lead to significant destruction of biogenic traces.

Clay-carbonate and clay-iron incrustations and crusts formed at the surface of beds during weathering often obscure the footprints (e.g., slabs MWGUW 01141, KR 11, TPW 93, TPW 114, TPW 117—118).

Selective disintegration leads to removal of obscuring clay or to destruction of the prints when mold-forming sandstone is rich in easily weathering mud flakes (e.g., slabs 12, MWGUW 01141, KR 5, TPW 94). In proximity of tectonic fractures, and sometimes at the contact of layers, carbonate cement became remobilized and removed, causing increase of porosity and decrease of compactness of sandstones. As a result of weathering imprints are either missing or strongly corroded on slabs situated near the surface (slab TPW 77).

Syndepositional deformations and erosion

Footprints from the labyrinthodontid beds are often deformed in result of superimposition on one another, especially when their concentration is high (slabs MWGUW 01141, Kr 4, KR 6, KR 9, KR 11, TPW 104, TPW 139). But, superimposition can also give profitable results. The footprint *Chirotherium hauboldi* sp.n. on the slab KR 1 (pl. 3: 3) is one of the best preserved imprints of pes. In front part of that footprint, an older imprint is marked of toe tips with a pit after a washed out mud flake. It is fairly possible that the younger footprint was impressed so accurately because the sediment became more plastic owing to formation of the older trace (tixotropy effect). In turn, the specimen KR 100 (pl. 13: 1) may serve as an example of two manus prints superimposed on one another and looking like an imprint of foot with eight digits.

Several slabs with footprints display deformations by mud cracks (eg. slab 5, pl. 5: 1; slab TPW 40, pl. 14: 2, and slabs 12, KR 5, KR 12, TPW 99, TPW 113, TPW 125, TPW 130) or syneresis cracks (slabs KR 4, TPW 61, TPW 96, TPW 123, TPW 125, TPW 131). Mud cracks do not deform usually the footprints which suggests that the cracks were formed before the footprints. This phenomenon is typical of the European Triassic (Müller 1954).

Moreover, some thin beds with footprints display effects of early diagenetic bending (e.g. slab TPW 81).

Relation between preservation of footprints and erosion may be observed in the labyrinthodontid beds (Rdzanek 1986). The most clear erosional surfaces were found in sandstones (fig. 11) and sometimes (when are uneven and covered with different sediment) in claystones and siltstones. In fine-grained sediments, the surfaces are usually untraceable and their occurrence may be inferred indirectly from the lack of parent sandstone layer over mud crack molds “hanging” in claystone layer, or (according to Mader in: Mader and Rdzanek 1985) from erosional lack of bioturbations in the top of clay-silt layer. A lack of *in situ* calcrete type soils, combined with their repeated occurrence in the form of redeposited material indicates an extensive erosion (Mader and Rdzanek 1985). The commonness of erosion further supports the assumption that surfaces with footprints were originally much frequent than it can be inferred from the preserved records in the Wióry section.

Major mechanisms of erosion of the horizons with footprints seem to be related to common autocyclic redeposition of fluvial sediments. Chances for escaping erosion are the lowest in the case of footprints formed in active river channels, and increase for those formed outside the channels (see Maulik and Chaudhuri 1983, Pieńkowski 1985).

It should be also noted that despite of the commonness of erosion the surfaces with footprints from Wióry display neither traces of current marks nor flow marks. This may be explained as due to quiet deposition of covering sand (see p. 143) and early-diagenetic consolidation of substratum leading to its increasing resistance to scouring. This consolidation could be mainly due to drying (e.g. Richter 1928), or, among others, to water draining of the sediment by underlying sands (compare Roniewicz 1965, Crimes 1975).

The subaqueous prints could be also protected by stagnant water dissipating energy of a new sand-supplying flood (Rdzanek 1986). However, it is widely assumed that preservation of footprints in subaqueous conditions is poorer than those left on land (Sarjeant 1975). This is probably due to the fact that footprints were frequently formed in shallow pools, through which land vertebrates were often passing (compare Lehmann 1978, Gand 1986). Foot set pushfully splashes water and forms radial furrows which obliterate imprint outline (Lotze 1928). In turn, quick withdrawal of the foot results in locally strong turbulence due to a rapid invading of water into the empty space. Moreover, a trace on the bottom also acts as an obstacle and causes turbulence of flow and/or deflects currents streams. This may lead to its modification or even complete obliteration. Slab 19 displays a special case of strongly advanced modification: footprints of a single trackway, measuring originally about a dozen cm in size, deformed and elongated (?) about three times (pl. 12: 1).

Erosional modifications of footprints are as a rule difficult to distinguish from alterations of other types. Therefore, contribution of erosion in modification of traces may be often underestimated. Nevertheless, it may be stated that erosion was of minor importance as far as modification of imprints is concerned but highly important as a process leading to their complete destruction in the course of sedimentation of the labyrinthodontid beds.

Burial

The footprints examined most often occur as convex hyporelief at a sole of sandstone layer, i.e. in the form of casts, and rarely on an upper surface in the form of concave epirelief. General sedimentary conditions of deposition of the beds predicated a fairly quick covering of footprints (Rdzanek 1986). The analysis of the mode of burial confirmed this conclusion. The mode of burial could be reconstructed with reference to grain size of the beds bearing hyporeliefs and sedimentary structures, geometry and thickness of these beds.

Among the slabs examined fine grained and mixed fine- and medium-grained sandstones predominate over coarse-grained ones. Within 130 samplings the share of grain fractions is as follows:

fine-grained sandstones	69%
mixed fine- and medium-grained sandstones	18%
medium-grained and mixed with coarse-grained sandstones .	11%
coarse-grained sandstones (traces poorly preserved) . . .	2%

Sedimentary structures observed here include cross-bedding and horizontal parallel and often wavy lamination; some slabs do not display any lamination.

The cross-bedding was not subdivided into subtypes (tabular lamination, trough lamination) as the available slabs are too small (e.g., a slab representing lower part of a layer of unknown thickness) and a few larger ones had underwent destruction before detail analysis could be made. Nevertheless, individual laminasets appear rather thin and it is possible to assume that the cross-bedding was due to migration of ripples of various size. The wavy lamination also appears related to ripples.

Horizontal parallel lamination at Wióry is observed in thin (up to 3 cm thick) interbeddings of fine-grained sandstones. Small thickness and fine grain fraction exclude any relation of this bedding to plane beds (compare Allen diagram 1968: fig. 6.9). Horizontal parallel lamination is reported from the end of ephemeral stream sequences as related to vanishing currents (Picard and High 1973). It is also present in sediments considered as deposits of a transition zone between stagnant water and small-ripples-forming current (Doktor and Gradziński 1985: facies H2). However, in the present case the horizontal lamination is confined to sediment of grain size larger than clay and silt fractions, corresponding to that of the wavy lamination, and it occurs in separate thin layers. Therefore, its origin is explained as due to weak but steady current in moderately shallow water, forming small ripples. Each of them left its basal lamina in passing further.

Layers looking structureless can be regarded as deposited from suspension.

Table 8

<table>
<tr><td colspan="12">SAND COVERING OF FOOTPRINTS</td></tr>
<tr><td colspan="9">by rhytmic transportation
96%</td><td colspan="3" rowspan="2">from suspension?
4%</td></tr>
<tr><td colspan="9">BEDDING RELATED TO</td></tr>
<tr><td colspan="6">small-scale ripples
62%</td><td colspan="3">large-scale ripples
34%</td><td colspan="3"></td></tr>
<tr><td colspan="12">TYPES OF BEDDING</td></tr>
<tr><td colspan="3">horizontal parallel lamination
13%</td><td colspan="3">wavy lamination
45%</td><td colspan="3">cross-bedding
38%</td><td colspan="3">structureless?
4%</td></tr>
<tr><td>D</td><td>P</td><td>M</td><td>D</td><td>P</td><td>M</td><td>D</td><td>P</td><td>M</td><td>D</td><td>P</td><td>M</td></tr>
<tr><td>%</td><td>%</td><td>%</td><td>%</td><td>%</td><td>%</td><td>%</td><td>%</td><td>%</td><td>%</td><td>%</td><td>%</td></tr>
<tr><td>13</td><td>–</td><td>–</td><td>45</td><td>–</td><td>–</td><td>4</td><td>21</td><td>13</td><td>2?</td><td>2?</td><td>–</td></tr>
<tr><td colspan="12">flow energy →</td></tr>
</table>

Table 8 presents types of bedding recognized in slabs examined, and their frequency and relationship with subfacies of the fluvial environment (see fig. 11): main channel bar sediments (M), sediments of proximal part of crevasse-splays (P) and sediments of distal part of crevasse-splays (D) (classification using the criteria of Mader and Rdzanek 1985: table 1, and Doktor and Gradziński 1985). The results are probably overestimated in the case of the subfacies D in result of disintegration of slabs (see p. 137).

The bulk of footprints were preserved due to covering by sediment of small-scale ripple lamination (62%), especially that of wavy type (45%) formed in distal parts of crevasse-splays. Almost all of the remaining footprints were covered by large ripples (medium- to large-scale cross-lamination) and only 4% of the footprints were covered with material deposited probably from suspension. It should be emphasised that 96% of the imprints were covered with sediments from rhythmic transport (i.e. form-drag bedding comprising the above mentioned horizontal parallel, horizontal wavy and cross-lamination, compare Jopling 1966; the bedding mentioned is common in sediments covering the traces, compare Osgood 1970, Haubold and Katzung 1978). Such transport may be supposed to create best conditions for burial of the footprints. This is possibly due to the mode of deposition: grains freely rolling down downstream slope of ripples and gently covering the prints. Such quiet burial is the main prerequisite for preservation of footprints. However, it should be noted that, under certain conditions, the prints may be also preserved despite of a high dynamics of covering. The sole of slab KR 12 with fine-grained wavy lamination displays a cast of print of *Brachychirotherium kuhni* infilled with large fragments of intraformational breccia. This imprint acted as a trap for material dragged (or rolled) along the bottom. It is verisimilar that there a higher dynamics occurred at the very beginning of covering prints with sediment.

PALEOENVIRONMENTAL AND PALEOBIOLOGICAL INTERPRETATION

Substratum

Footprints made in clay or silt, i.e. plastic substratum, predominate in the labyrinthodontid beds. Their preservation indicates variable degree of consolidation and diverse thickness of plastic layer. Footprints very deep and difficult to identify because of deformation (e.g. TPW 110, pl. 13: 4) form in thick layers of soft clay and silt (Haubold and Katzung 1978), and recent observations of the author). Deformations may be due to extreme upwards bending of digits (TPW 104; cf. Winkler 1886). As a rule, digits I—IV come close to one another in very deep imprints as well as some shallower ones (KR 101, pl. 13: 3) but in the latter toes are simultaneously strongly bent to one side, outside the trackway. Such footprints could originate in clay or clay-rich substratum under conditions of high water content (Atterberg limits: Casagrande 1948). When water content is too high, the footprints slump and become deformed (e.g., Tucker and Burchette 1977: squalch marks). Soft clay stuck to foot may be the reason why traces fail to reflect foot shape (cf. Winkler 1886). Experiments of Fichter (1982b) show that when substratum is too soft, angle between toes decreases, a trend to parallel orientation of medial toes is clearly marked, and imprints of some toes "vanish" (pl. 13: 4), and a furrow between foot sole and toes appears.

In the substratum characterized by physical properties suitable for origin of undeformed footprints (sometimes even with skin texture preserved: pl. 3: 4, pl. 4: 1), feet of large animals sunk to the depth of 0.8 to 2.0 cm (pl. 2: 2, pl. 3: 1—4), and those of small animals to the depth of 0.3 to 0.8 cm (pl. 8). Shallower imprints were formed when substratum was more firm (pl. 2: 1, pl. 4: 4, pl. 5: 3—4, pl. 6: 1, 2, 4). Along with advancement of consolidation (e.g. desiccation) the substratum is becoming more and more firm, footprints of younger generation appear incomplete and less clear (Lapparent 1962, Lehmann 1978). After some consolidation of sediment, imprints could be left by very heavy animals only (Boy and Fichter 1982).

In the material from Wióry, traces made by light animals are represented by prints of toes I—IV only (pl. 7: 2, pl. 8: 3). This may be explained by small weight combined with swift motion and the type of substratum. An experiment with a lizard, *Lacerta agilis*, allowed the author to observe how the footprints of a small tracemaker are formed. Moving quickly on a thin (up to 2 mm thick) layer of soft mud spread on hard sandstone layer, the lizard left very small footprints (three pits 2—3 mm in diameter). Footprints reflecting true size of its feet formed only when the lizard walked slowly or took a rest (pl. 14: 1). Running, the animal moved on toes or even on their tips penetrating thin mud layer and bounding off the sandstone "bedrock". Without such firm support its feet would sink deeper (see above) and would result in prints of the whole toes or even the whole feet. It may be expected that footprints of other light animals, running on toes over consolidated mud and compact sand, should be similar. Some analogies may be found in imprints *Rhynchosauroides brevidigitatus* sp.n. Also the maker of *R. polonicus* sp.n. who formed complete prints of the hind foot, left in the same trackway the prints of the toes alone (slab KR 11), may be due to more advanced consolidation of substratum in that place (compare Tucker and Burchette 1977). It should be also noted that both species did not leave complete prints of manus. This means that smaller weight was put on front legs due to body shape (compare Fichter 1982a, 1983a, b) and that possibly the motion was swift. In any case, a substratum soft enough for origin of the pes prints was too hard for those of manus. It cannot be excluded that in some cases the animal used its front limbs to test firmness of substratum. As even small zones of quaggy mud could act as a trap for small animals, they avoid such dangerous sites (compare behaviour of recent birds: Trusheim 1929) and chose more firm substrate. Among others, this could be the reason, why footprints of small animals preserved as concave epirelief are much more frequent in sandstones than those of Chirotheriidae (TPW 34, pl. 9: 1, 2, KR 4, pl. 10: 1), despite of smaller weight of the former.

Epirelief from a sandstone layers shows that footprints could also arise in sand but their preservation is much less satisfactory. This requires wet (Brand 1979, Gradziński *et al.* 1979: pl. 19) and loose, unconsolidated sand (Peabody 1948). Loose consistency of the sand made possible its compaction under the foot pressure (Wasmund 1936, Linck 1954) which is reflected by bending of laminae under the print (margin of plate KR 4). Clay, clayey silt or clayey sand behaved differently in such a situation. In comparison with pure sand, such sediment did not become compact immediately, but thanks to its plasticity displaced to the sides beneath

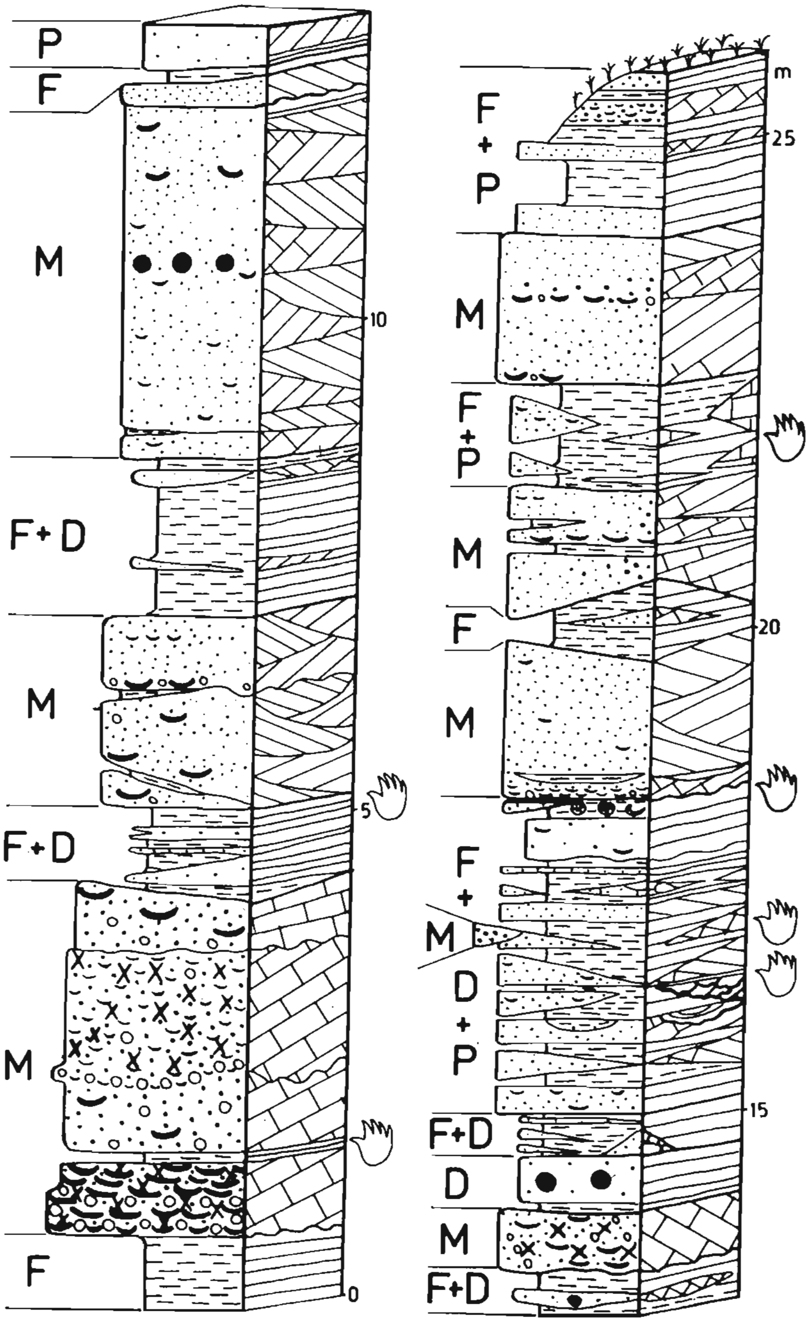

Fig. 11. Lithofacies log (columnar section) of the labyrinthodontid beds exposed at Wióry (after Mader and Rdzanek 1985, slightly modified) with situation of tetrapod footprints. *A* main channel deposits, *P* proximal part of crevasse sediments, *D* distal part of crevasse deposits, *F* flood-plain suspension sediments (detailed explanations cf. Mader and Rdzanek 1985: 295).

the pressing foot. This is well shown by a simple experiment with variously coloured clay placed in a transparent container. When pressed from above with a piston narrower than the container diameter, the clay "flows" to the sides and upwards around it. *Brachychirotherium kuhni* imprint on the slab TPW 40 may serve as a fossil example of this phenomenon. In that case, the foot pressure of the maker resulted in tilting the sand-infilling mud crack from the vertical (fig. 12, pl. 14: 2). Convexities (concavities on the molds) of surface around imprints (pls 3: 1 and 5: 2) may be also related to squeeze out of a plastic substratum (Lapparent and Montenat 1967: bourrelets de vase; Gand 1986: bourrelets

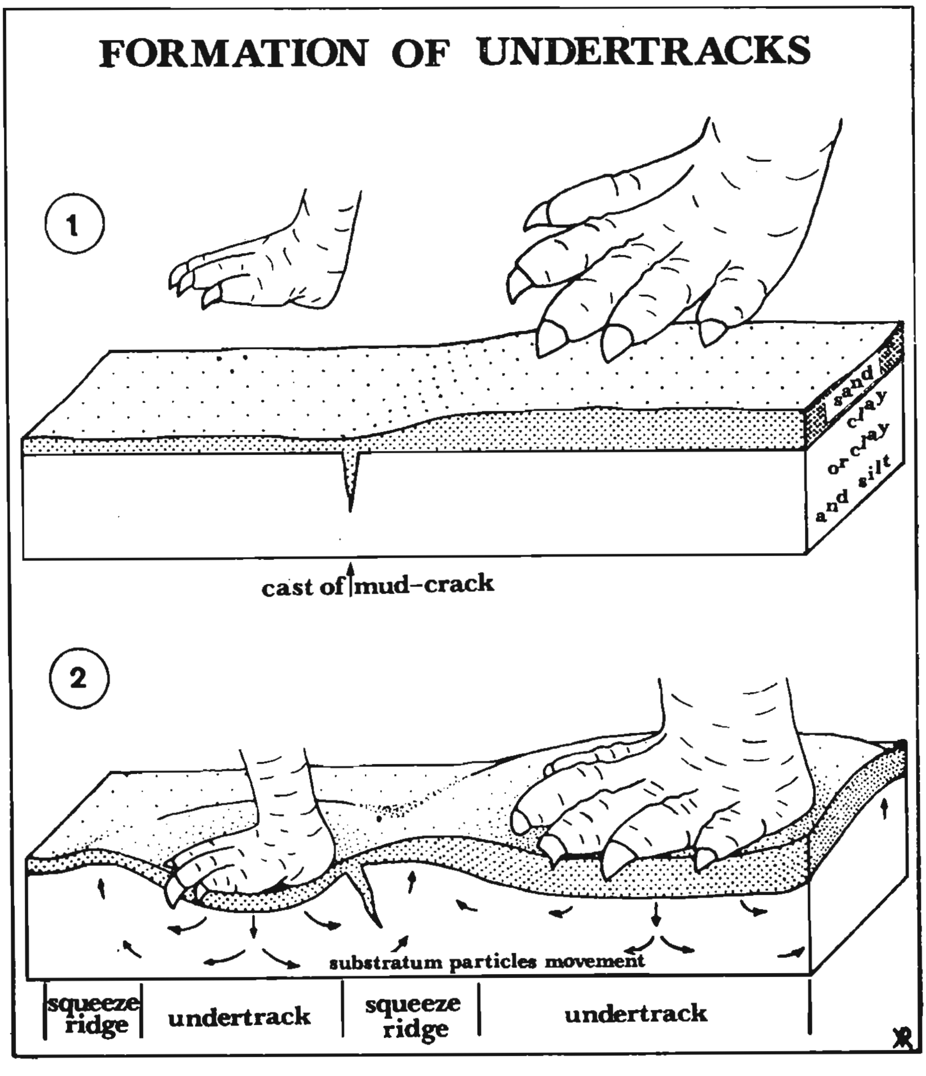

Fig. 12. Origin of undertracks: *1* prerequisities, *2* track formation; the thinner sand sheet, the deeper and sharper the undertrack. See also pl. 14: 2.

de refoulement). It follows that the squeeze ridge may serve as an indicator whether substratum was plastic or loose.

The above mentioned slab TPW 40 is an example of a peculiar type of footprint, which is quite common in the studied section. This is an undertrack, i.e. a trace formed in clay substratum covered with thin sandy layer and regarded as one of more common forms in the fossil record by Seilacher (1953a, b). Undertracks made by invertebrates were often cited. The specimens from Wióry support the opinion (Demathieu and Oosterink 1988) that such traces could be also made by tetrapods. In the present case (fig. 12), sand layer resting on clay was 0.5 cm thick beneath manus enabling its penetration by claws and, therefore, formation of a rather distinct imprint. In turn, the sand layer was about 1.0 cm thick beneath pes, so the undertrack is less clear and with only one and poorly marked print of claw (pl. 14: 2).

Place of footprint formation

The nature of substratum, its variability, the hazard of destruction and other factors determining preservation of footprints depend on facies as well as position of a given locality within the facies. The labyrinthodontid beds may serve as an example of location favourable for both origin and preservation of footprints. The general tectonic and paleogeographic setting is characterized elsewhere (p. 111—115). Here, it should be noted that in the regional geological sequence (fig. 2) the footprints appear to be related to a packet of alternating sandstones, siltstones and claystones. The sedimentary environment of the labyrinthodontid beds was discussed in detail in Mader and Rdzanek (1985), and its reconstruction is presented herein in fig. 14. The places of formation of the prints coincide with areas repeatedly flooded and emerging from beneath water.

In the labyrinthodontid beds, formation of footprints was related to water both at the stage of imprinting (wet sediment) and burial (fluvial transport). The covering layer has preserved shape of footprint and numerous other informations concerning the nature of habitat and mode of life of trackmakers. A preliminary paleoecological analysis involved a comparison of directions of animals movement in relation to those of currents responsible for burial of the footprints.

A question of the time span between formation and burial of footprints arises in the case of footprints from a sole of a layer. The footprints were made earlier, not on the covering layer which provides the record of current direction but on an older one, formed when the direction could be different (compare Peabody 1948). However, it seems that "choice" of direction by the current responsible for deposition of the covering layer was determined by the same peleorelief on which trackmaking animals moved. Therefore, the author's working hypothesis assumes that direction of motion of the animals was also determined by the paleorelief. The hypothesis, assuming a relation between directions of the animals movement and currents bringing sediment preserving the footprints, is verifiable statistically.

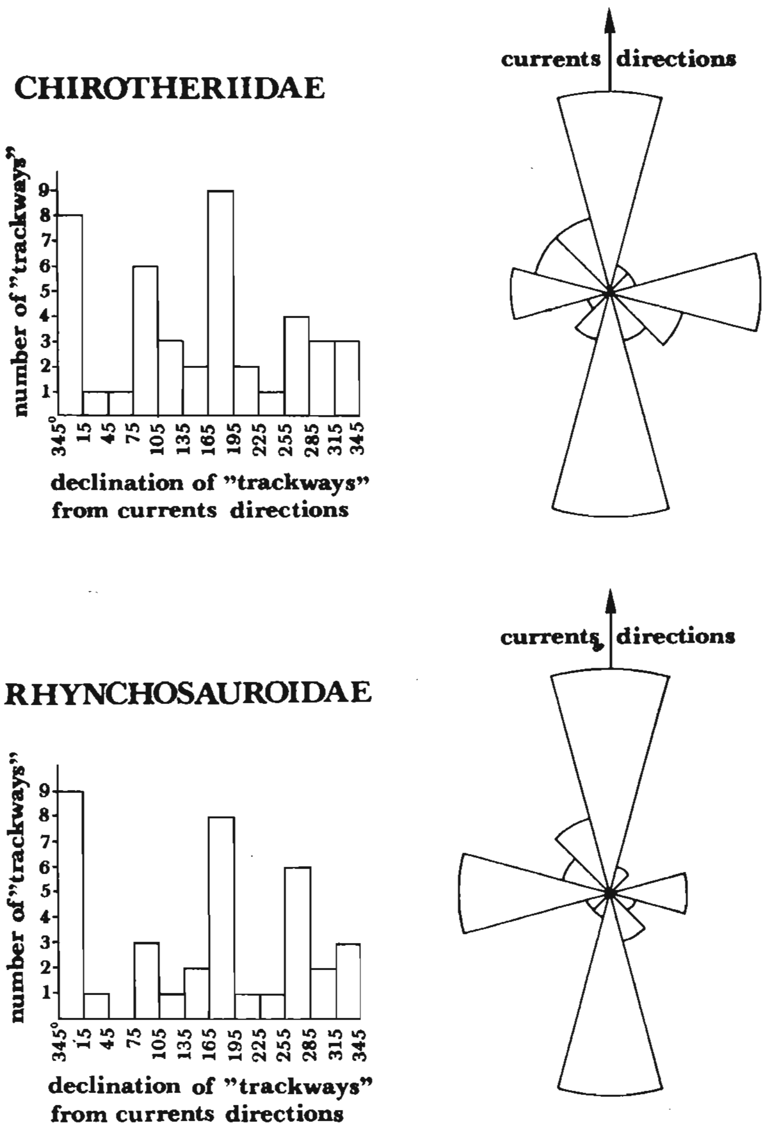

Fig. 13. Relationship between footprint routes (courses of animals motion) and directions of water currents depositing the cover of the footprints. The term "trackway" means the set of consecutive prints and the isolated ones.

Table 9

RELATION OF ICHNOTAXA TO FLUVIAL SUBFACIES and INTEGRATION LEVEL OF ICHNOCOENOSIS

depositional subfacies:
- M main channel
- P proximal part of crevasse-splay
- D distal part of crevasse-splay

[box] total number of trackways preserved on the sole of facially classified slabs

	C. hauboldi	*R. brevidigitatus*	*S. chirotherioides*	*I. sanctacrucense*	*B. kuhni*	*R. polonicus*	cf. *Capitosauroides* sp.	*Rhynchosauroides* spp.	*Chirotheriidae* indet.	I Number of ichnotaxa "trackways" in the three fluvial subfacies			II	III Number of concurrent ichnotaxa in:			IV Number of concurrent "trackways" in:		
										M	P	D	total	M	P	D	M	P	D
Chirotherium hauboldi	5M 6P	2M	2M	2M	1M 2P			3M	2M 1P	5	6		4	4	1		10	2	
Rhynchosauroides brevidigitatus	5M	2M 7P 10D		2M	1D	2P		2M 2P 2D	2M	2	7	10	4	2	1	1	9	2	1
Synaptichnium chirotherioides	2M		3M	1M	2M			2M	3M	3			4	4			7		
Isochirotherium sanctacrucense	4M		2M	3M	1M			1M	4M	3			4	4			8		
Brachychirotherium kuhni	1M 1P	1D	3M	1M	2M 2P 5D			2M 1D	3M	2	2	5	4	4	1	1	7	1	2
Rhynchosauroides polonicus		7P				2P		1P			2		1		1			7	
cf. *Capitosauroides* sp.							1M			1									
Rhynchosauroides spp.	5M	2M 1P 7D	3M	3M	2M 1D	1P		5M 4P 13D	7M 1P 1D	5	4	13	4	4	1	1	20	1	2
Chirotheriidae indet.	4M 1P	2M	3M	2M	2M			3M 3P 3D	10M 11P 4D	10	11	4	1	1	1	1	5	3	3

As one direction of movements ("trackway") is regarded every sequence of footprints (trackway *sensu stricto*) and each isolated footprint, considering average deviation of footprint from the midline for a given taxon. Current directions were reconstructed basing on the cross-bedding, current ripples and other current marks. The directions were, however, impossible to decipher for some cases as stratifications close to horizontal are very common here. Therefore, the compiled histograms and rose diagrams of directions of animals movement (fig. 13) do not show the directions in particular subfacies (insufficient number of observations) but a summary for all the environments, which gives statistically significant picture. The obtained results are further confirmed by similar share of opposite directions, as on the assumption that a number of "trackways" in one direction should be essentially similar to that of "trackways" leading back. The numbers perfectly coincide after summing up both rose diagrams of directions of movement.

Distribution obtained for two taxonomic groups, chirotheriids and rhynchosauroids, appears bimodal but not equal. Directions parallel to those of currents predominate whereas perpendicular ones are scarcer. The share of intermediate directions appears fairly high, especially in the case of large footprints (chirotheriids). Trackways of Chirotheriidae from the Moenkopi formation (Peabody 1948) were also found to follow a river. However, it should be noted that there were also reported reptilian trackways oriented towards a reservoir (Demathieu 1985, Gand 1986), or randomly oriented due to dense spacing of minor reservoirs (Tucker and Burchette 1977).

Relation of the identified ichnotaxa and the fluvial subfacies M, P and D was also analysed. The analysis was made assuming a relation between the sedimentary and ecological conditions and relief of terrain surface. Table 9 shows data for footprints from the sole surface only. The imprints *Isochirotherium* sp. were omitted in that analysis as the relevant slabs were destroyed before a detailed study. The data presented in the first part of that table (diagonally arranged rectangles) and in column I suggest some relation between the recorded taxa and environment. *Chirotherium hauboldi* sp.n. occurs in zones which were early covered with sediments of the main channel facies (M) and those of proximal part of crevasse-splays (P). *Synaptichium chirotherioides* sp.n. and *Isochirotherium santacrucense* sp.n. were found at the sole of main channel sediments only. *Brachychirotherium kuhni* occurs in all the subfacies, being most common in areas of sedimentation of distal parts of crevasse-splays (D), situated far from river channels. Distribution of *Rhynchosauroides brevidigitatus* appears similar to that of *B. kuhni*. In the case of the remaining taxa, the available data are too scarce to draw any general conclusions. It may be only noted here that *R. polonicus* was found twice at the sole of proximal part of crevasse-splays and once in large numbers at the top of layer of the same subfacies (TPW 34) and at the top of distal part of crevasse-splay (KR 4).

Taking into account the above data and those for specimens not identified at the specific level, it may be stated that the near-channel zone was favourable for formation of footprints of large animals (Chirotheriidae, compare Peabody 1948), whereas footprints of small ones (Rhynchosauroidae) were mainly formed in the floodplains, far from strong currents. The conclusions are similar to those concerning the Middle Triassic assemblage from the Massif Central (Demathieu 1977).

Co-occurrence of several taxa on the same slab gave some additional data which were compiled in the remaining columns of table. 9. The data in column II indicate that all common taxa frequently occur together. Taking into account a short time span of susceptibility of the substratum to formation of footprints (see p. 152), it may be stated that the time intervals between formation of individual ichnotaxa were short and the trackmakers were meeting one another in their biotope. Therefore, the biocoenosis may be treated possibly as quite well integrated (in the sense of Demathieu 1977) and all its elements (except for cf. *Capitosauroides* sp. and, perhaps, *R. polonicus*) played equal role in the integration.

The data in column III indicate that representatives of diverse species most often met one another in area of deposition of the main channel sediments. This was area of interference of fields of motion shown in column I. The data in column IV give further support to this conclusion, showing that various animals used to appear in that area not accidentally, but rather repeatedly.

In analyses such as the above presented it is necessary to take into account some "informational noise" caused by the preservational state of the material analysed: as slabs of channel facies sandstones (M) are generally larger than those of distal parts of crevasse-splays (D), chances of preservation of footprint associations markedly increase in the former. However, this factor does not seem to be important in the case of this study as frequencies of occurrence of taxa on also large slabs of rocks of the facies P appear to be different. Moreover, it is very difficult to expect high co-occurrence of taxa in the zone D because of scarcity of chirotheriids in this facies.

To sum up, it should be emphasized that the taphonomical studies have to be based on slabs representing complete thickness of a layer. Only material collected in such a manner may preserve the whole paleontological value of ichnological data.

It is necessary to mention objective limitations of the taphonomic method. For example, the opinion on the limitation of paleobiotopes to the immediate neighbourhood of the water zone, based on findings of the footprints exclusively in these area may be often unsubstantiated.

Taphonomic studies of the footprints indicate that many animals could penetrate vast areas, including eolian ones, whereas the ichnological record of their migration is confined to zones of sediments favourable for their formation and fossilization (fig. 14). Similarly as in paleontological studies of body fossils, mainly limited by taphonomic processes responsible for decay of soft parts, partitioning, redeposition, dissolution of skeletons, etc., the ichnological analyses are limited by taphonomic reasons — the lack of suitable conditions for formation and/or fossilization of footprints in some areas. In both cases we are using a kind of taphonomic "windows" in paleontological reconstructions.

Time of footprints formation

If an erosion of footprints in their preburial state is taken into account, it may be assumed that formation of footprints must be a fairly common process during sedimentation of the labyrinthodontid beds. Figure 14 presents a tentative reconstruction of the environment for the time span of sedimentation of individual layer in the section. The reconstruction is based on results of taphonomic analysis of the footprints.

This scheme assumes alternations of two states of the environments, with time intervals difficult to evaluate. A state of high water level (upper part in fig. 14) is simultaneously an initial stage, at which substratum for footprints originates, and a final one, at which erosional modification and burial of the footprints formed previously take place. In turn, low water level (lower part in fig. 14) made possible formation of footprints by exposing fresh sediments and consolidation, e.g. desiccation of sediments with imprints. Optimum time for formation of the prints correlates with a quite narrow time span between partial evaporation and complete drying of sediments (Peabody 1948, Tucker and Burchette 1977). Low water is the most important stage in formation of footprints. This is the stage of action of a biological factor and initiation of a long process leading to their fossilization.

The labyrinthodontid beds originated in the middle of a sedimentary megacycle (fig. 2), at a transitional stage between the initial sandy phase and the final clayey one (Mader and Rdzanek 1985). This transitional stage created the best taphonomic conditions for formation and preservation of footprints (alternating lithology, optimum substratum, protective cover, etc.).

In relation to a distrophic movement (see p. 115), the labyrinthodontid beds were deposited in a period of subsidence of continental areas. This agrees with a general rule of formation and fossilization of traces in times of origin of molasse basins and tectonic troughs (Seilacher 1954, 1959, Haubold 1984).

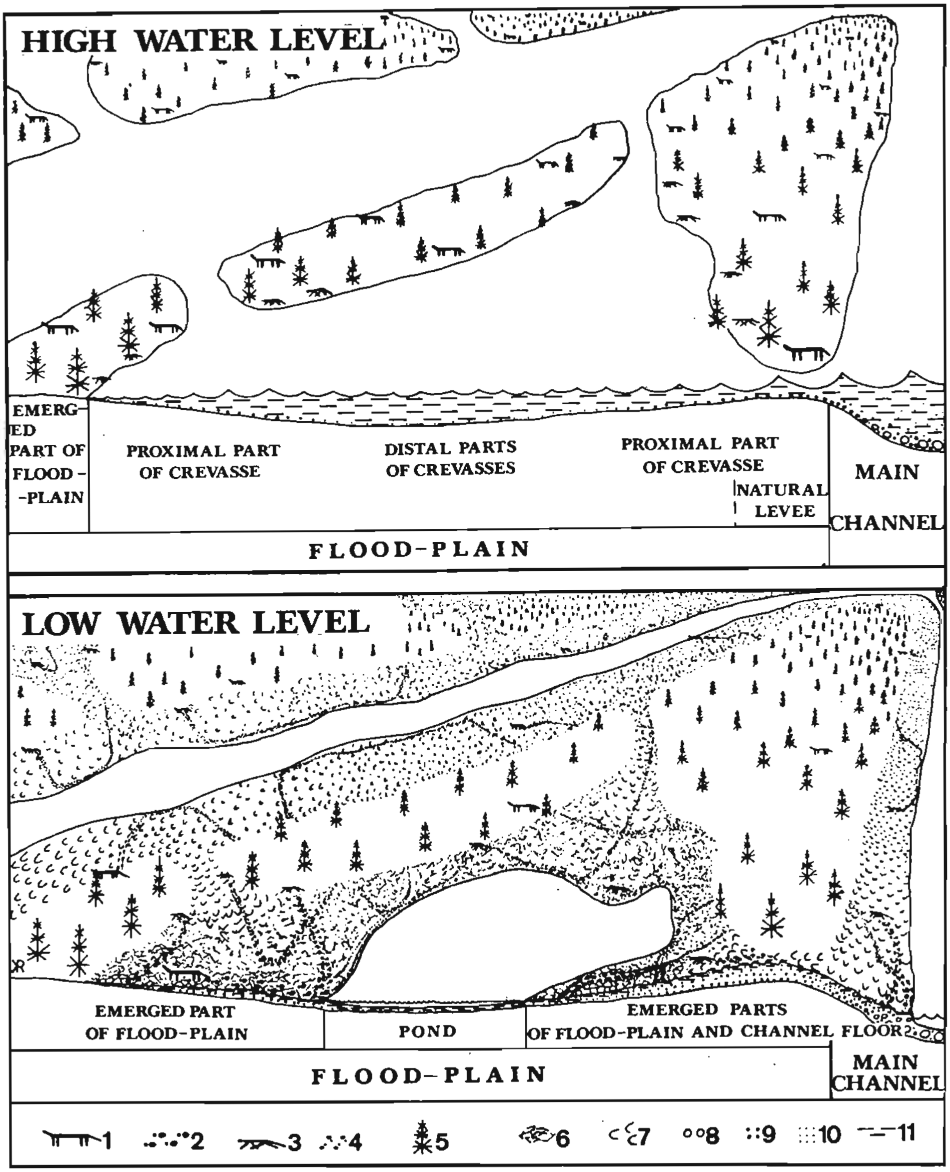

Fig. 14. Lower Triassic biotope of tetrapods of the labyrinthodontid beds. Conditions of footprints origin and their covering (burying) with sediment: extensive flood causes fragmentation of the biotope and concentration of animals on narrow land patches (*above*); numerous footprints impressed in muddy sediment during the low-water period (*below*) are to be subsequently covered by sand during the following flood. *1* Chirotheriidae makers, *2* their footprints, *3* Rhynchosauroidae makers, *4* their footprints, *5* plants, mainly horsetails, *6* clay (mud), locally with desiccation cracks, *7* current ripples with clay (mud) veneer, *8* gravel, *9* coarse sand, *10* fine sand, *11* silt and clay.

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ŚLADY TETRAPODA Z DOLNEGO TRIASU GÓR ŚWIĘTOKRZYSKICH

Streszczenie

W pracy przedstawiono pierwsze monograficzne opracowanie najstarszego w triasie europejskim zespołu śladów Tetrapoda z pstrego piaskowca środkowego, z okolic miejscowości Wióry koło Ostrowca Świętokrzyskiego (figs. 1, 11). Ślady Tetrapoda o zbliżonym składzie rodzajowym znane były do tej pory głównie z osadów pstrego piaskowca górnego z obszaru Niemiec i Francji (fig. 2).

W zespole śladów z Wiór zdecydowanie dominują ślady gadów (pls. 2—14, figs. 5—10). Stwierdzono także trop płaza cf. *Capitosauroides* sp. (pl. 1, fig. 4), należącego do podgromady Labyrinthodontia. Wśród śladów gadów największymi rozmiarami wyróżniają się odlewy stóp Archosauria, z rodziny Chirotheriidae (5 taksonów). Małych rozmiarów są dość częste ślady Lepidosauria z rodzaju *Rhynchosauroides* (2 gatunki). W zespole liczącym 8 taksonów opisano 5 nowych gatunków: *Chirotherium hauboldi, Isochirotherium sanctacrucense, Synaptichnium chirotherioides, Rhynchosauroides brevidigitatus* i *R. polonicus.* Wyróżniono ponadto *Isochirotherium* sp. i *Brachychirotherium kuhni* Demathieu et Haubold, 1982.

Dla zachowania pełnej wartości paleontologicznej ślady muszą być kolekcjonowane z całą miąższością ławicy (płyty) i przechowywane w pomieszczeniach. Towarzyszące wydobyciu składowanie płyt na hałdach powoduje liczne uszkodzenia śladów. Stopień rozdrobnienia płyt może mieć wpływ na wyniki badań ilościowych.

Do pierwotnych zmian tafonomicznych należą deformacje. Częstą ich przyczyną było następowanie zwierząt na już istniejące ślady. Pokrycie śladów zachodziło dość szybko dzięki rytmicznemu (tabela 7) transportowi osadu, którym był głównie piasek drobnoziarnisty (69%). Erozja, mniej znacząca dla modyfikacji kształtu, odegrała wielką rolę w całkowitym niszczeniu śladów. Na kształt śladów i stopień ich kompletności, różny dla kończyn przednich i tylnych, oprócz zróżnicowania plastyczności podłoża wpływały różnica w obciążeniu przedniej i tylnej kończyny i tempo ruchu. O plastycznym charakterze podłoża informują wałki wypierania osadu wokół śladu. Przy pokryciu mułu cienką warstewką piasku powstawały undertracks (fig. 12). Miejsce tworzenia śladów zostało określone przez ich związek z kierunkami prądów (fig. 13) oraz z subfacjami sedymentacyjnymi (tabele 8, 9). Ślady powstawały na obszarach zalewanych przez okresowe powodzie. Czas tworzenia zachowanych śladów przypadał na okres niskich wód (fig. 14); w skali megacyklu — na okres przejściowy pomiędzy sedymentacją piaszczystą i ilastą (fig. 2).

Ichnocenoza z Wiór ma praktycznie tylko jeden wspólny gatunek z zespołami

zachodnioeuropejskimi, t.j. *Brachychirotherium kuhni*. Odrębność tego zespołu wynika prawdopodobnie z różnicy wiekowej między nimi.

Najstarszymi skamieniałościami w pstrym piaskowcu obrzeżenia Gór Świętokrzyskich, zarówno w bliskim sąsiedztwie trzonu paleozoicznego, jak i na obszarach nieco oddalonych od trzonu, są mega i miospory pstrego piaskowca środkowego i górnego (Rdzanek 1981, 1984; Dybova-Jachowicz i Laszko 1980). Nie stwierdzono tu zespołu spor charakteryzujących pstry piaskowiec dolny, występujących w kompletnych, udokmentowanych profilach pstrego piaskowca na obszarze monokliny przedsudeckiej i w strefie kujawskiej (Fuglewicz 1977, 1979, 1980; Orłowska-Zwolińska 1984). Fakt ten wskazuje na niepełność profilu pstrego piaskowca w Górach Świętokrzyskich.

Analiza diastrofizmu na przełomie permu i triasu oraz korelacja pstrego piaskowca Gór Świętokrzyskich z obszarem Niemiec również prowadzą do wniosku, że pomiędzy osadami niższego cechsztynu a osadami reprezentującymi początek sedymentacji triasowej — warstwami z Czerwonej Góry — występuje luka stratygraficzna obejmująca wyższy cechsztyn i pstry piaskowiec dolny, oraz że początek sedymentacji utworów pstrego piaskowca w obrzeżeniu Gór Świętokrzyskich przypada na pstry piaskowiec środkowy. Zmienia to dotychczasowy pogląd na kompletność profilu pstrego piaskowca w Górach Świętokrzyskich (por. Samsonowicz 1929; Senkowiczowa i Ślączka 1962; Senkowiczowa 1970) oraz pozycję tzw. warstw przejściowych (por. Senkowiczowa i Ślączka 1962; Senkowiczowa 1970).

Sedymentacja pstrego piaskowca w obrzeżeniu Gór Świętokrzyskich, podobnie jak w całym basenie środkowo-europejskim była uzależniona od ruchów tektonicznych fazy palatyńskiej i fazy hardegseńskiej (fig. 2, 3; Fuglewicz 1980). Rozwój sedymentacji przebiegał odmiennie na obszarze północnym (łysogórskim) i południowym (kieleckim). Było to uwarunkowane sytuacją paleogeograficzną i tektoniczną Gór Świętokrzyskich, które położone na pograniczu dwóch wielkich platform — starej platformy wschodnioeuropejskiej i platformy paleozoicznej podlegały kontrastowemu reżimowi tektonicznemu platform. Region południowy (kielecki) wykazuje identyczny rytm tektoniczny i sedymentacyjny z leżącym na SW obszarem platformy paleozoicznej, natomiast region północny (łysogórski) ma zupełnie odmienny rozwój sedymentacyjny i tektoniczny, analogiczny do obszaru platformy wschodnioeuropejskiej (szczególnie do regionu radomsko-lubelskiego). Podnoszeniu się i erozji jednej platformy towarzyszyło obniżanie się i akumulacja na obszarze drugiej platformy (fig. 3). Rozłam świętokrzyski stanowił prawdopodobnie granicę tektoniczną między nimi.

EXPLANATION OF PLATES 1—14

All specimens are from the labyrinthodontid beds, Middle Buntsandstein, Lower Triassic; Wióry quarry, 14 km West of Ostrowiec Świętokrzyski, northeastern margin of the Świętokrzyskie (Holy Cross) Mountains, Poland.

Photographs taken by:

Kazimierz Rdzanek: pl. 1: 1—4; pl. 2: 1, 3; pl. 3: 2, 4; pl. 4: 1—4; pl. 5: 1, 3, 4; pl. 6: 1, 2, 4; pl. 7: 3; pl. 9: 1, 2; pl. 10: 2, 3; pl. 11: 1, pl. 12: 1, 3; pl. 14. 1.

Stanisław Kolanowski: pl. 2: 2; pl. 3: 1, 3; pl. 5: 2; pl. 6: 3; pl. 7: 1, 2, 4; pl. 8: 1—4; pl. 10: 1; pl. 13: 1, 3, 4; pl. 14: 2.

Stanisław Skompski: pl. 12: 2.

Stanisław Ulatowski: pl. 13: 2.

Scale in cm.

Plate 1

cf. *Capitosauroides* sp.

1. Trackway. Preservation state as in 1981. Specimens 1.1 to 1.13; designates see text — fig. 2: 9.
2. Imprint of the left manus, 1.7.
3. Imprint of the right pes, 1.9.
4. Set of left pes and manus imprints, 1.5-4.

Plate 2

Chirotherium hauboldi sp.n.

1. Imprint of the right pes, syntype, KR 9: 14.1 and partly preserved imprint of the left pes, 14.2; track of standing (?) animal.
2. Set of right pes and manus imprint, syntype, MWGUW 0113 9: 16. 1—2.
3. Set of left pes and manus imprints, 11.1—2.

Plate 3

Chirotherium hauboldi sp.n.

1. Imprint of the right pes, syntype, KR 5: 8.1.
2. Imprint of the pes of running (?) animal with poorly recorded digit V, MWGUW 01141: 3.4. Enlarged from plate 11: 1.
3. The largest known, well preserved right pes imprint, syntype, KR 1: 56.1.
4. Imprint of the left manus with granular structure of the skin, MWGUW 01141: 3.20. Enlarged from plate 11: 1.

Plate 4

1. *Chirotherium hauboldi* sp.n., a part of the irregular trackway, specimens: MWGUW 01141: 3.19; 3.24; 3.20 and 3.21. In the right upper corner visible imprint of the left pes of *Isochirotherium sanctacrucense* sp.n., MWGUW 01141: 3.29; holotype. Enlarged from plate 11: 1.
2. *Chirotherium hauboldi* sp.n., imprint of the right pes associated with the tail mark, 12.1.

3. *Isochirotherium sanctacrucense* sp.n., imprint of the left pes, holotype, MWGUW 01141: 3.29; slightly deformed by sliding movement, and fragmentary preserved left manus imprint MWGUW 01141: 3.30. Enlarged from plate 11: 1.
4. *Isochirotherium sanctacruense* sp.n., imprint of the left pes, paratype, 13.7.

Plate 5

Brachychirotherium kuhni Demathieu et Haubold, 1982

1. Imprint of the partly preserved left pes, 5.1.
2. Imprint of the right pes, TPW 16: 39.1.

Isochirotherium sp.

3. Partly preserved imprint of the right pes, 30.1.
4. Imprint of the left pes, 2.5. Enlarged from plate 10: 2.

Plate 6

1. *Brachychirotherium kuhni* Demathieu et Haubold, 1982; imprint of the left pes digit group I—IV, 13.14.
2. *Synaptichnium chirotherioides* sp.n., imprint of the pes digit group I—IV, syntype, 13.6. Enlarged from plate 6: 4.
3. *Synaptichnium chirotherioides* sp.n., imprint of the left pes, syntype, TPW 19: 48.2 plaster cast.
4. A part of the slab No. 13 with footprints of *Synaptichnium chirotherioides* sp.n.: syntype, 13.6 (uppermost part of the photograph) and two manus imprints left and right, 13.8 and 13.9, made probably by the same animal (left lower part of the photograph).

Plate 7

Rhynchosauroides brevidigitatus sp.n.

1. Two consecutive pes imprints TPW 28: 111.1-2; paratypes.
2. The slab TPW 27: 60 with association of pes and manus imprints of *R. brevidigitatus* sp.n., in the central part the paratype, TPW 27: 60.2.
3. Set of right pes and manus imprints, KR 11: 4.5-4.
4. Imprints of the right pes, holotype, MWGUW 01144: 5.2 plaster cast; with all five digits recorded.

Plate 8

Rhynchosauroides polonicus sp.n.

1. Set of pes and manus imprints, holotype, KR 11: 4.1 and 4.3. Enlarged from plate 8: 3.
2. Set of left pes and manus imprints, TPW 37: 61.1-2; associated with the tail mark (?).

3. Trackway: KR 11: 4.19-9-6-7-1-3; isolated manus and pes of *R. brevidigitatus* sp.n. are visible, among others the paratype, KR 11: 4.16.
4. Set of left pes and manus imprints, KR 2: 6.1-2.

Plate 9

1. *Rhynchosauroides* sp. A part of the slab No. 34 (upper side of the sandstone layer, concave epirelief) with many footprints, most of them probably represent *R. polonicus* sp.n. 2. Rhynchosauroid footprints. TPW 36: 34.1 and 34.2. Enlarged from plate 9: 1.

Plate 10

1. *Rhynchosauroides polonicus* sp.n., set of right pes and manus imprints on the upper side of sandstone layer, KR 4: 62.2-1.
2. The slab No. 2 with *Isochirotherium* sp., 2.5 (at the left upper corner of the photograph) and many other indeterminated specimens.
3. The slab No. 5 with many *Rhynchosauroid* footprints, among others *R. brevidigitatus* sp.n., holotype, 5.2 and 5.3. In the upper part of the photograph imprint of the left pes of *Brachychirotherium kuhni* Demathieu et Haubold 1982, 5.1.

Plate 11

1. Irregular trackways of *Chirotherium hauboldi* sp.n.: MWGUW 01141: 3.12-28-25--19-24-20-21-23 and *Isochirotherium sanctacrucense* sp.n.: MWGUW 01141: 3.29-30--35-17-13-14. Designates of footprints are on the photograph.

Plate 12

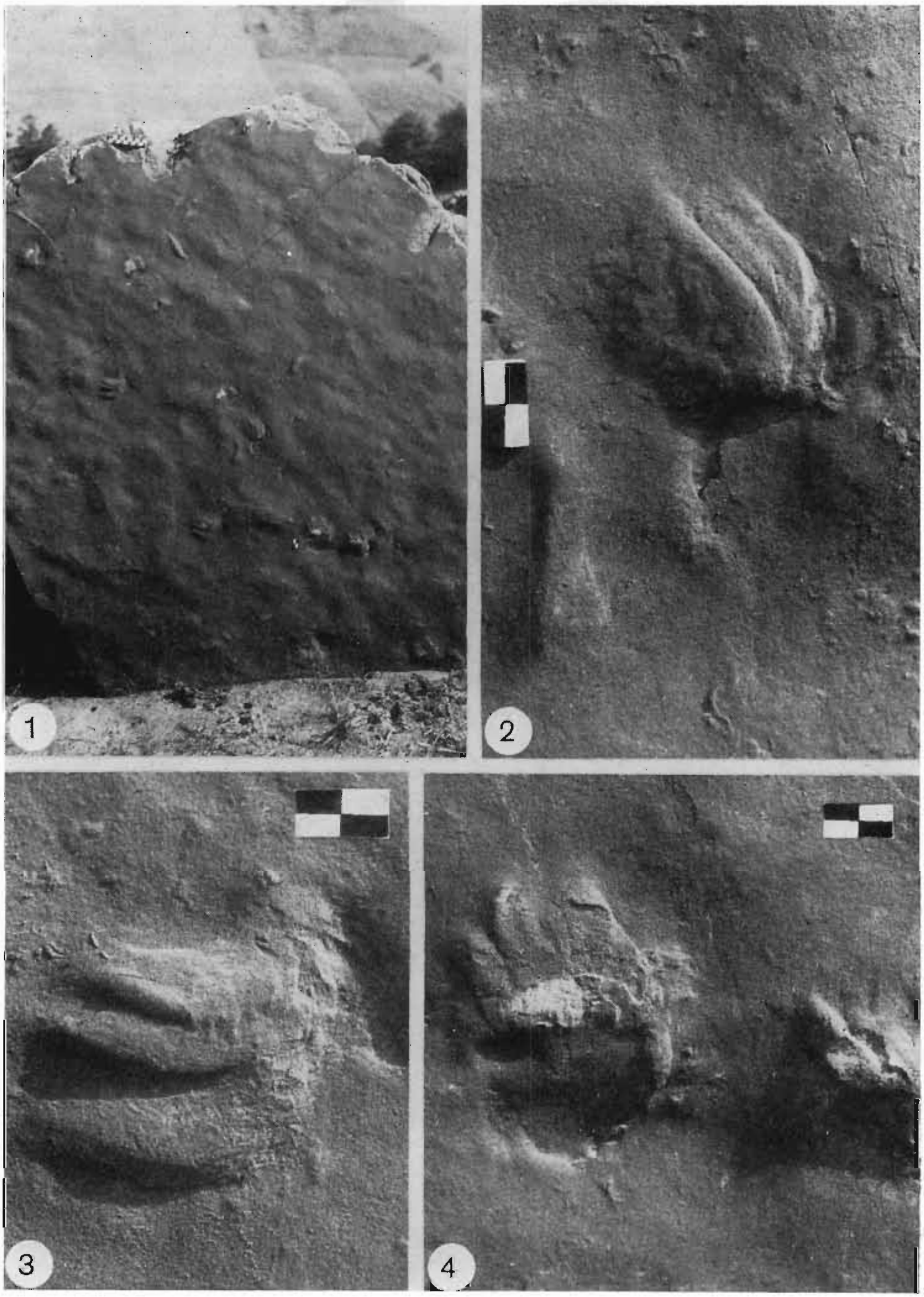
1. Problematical structures, probably footprints enlarged and deformed by current activity, slab No. 19.
2. Indeterminated footprints, deeply but poorly recorded, deformed by sliding? movement; slab No. 25.
3. Chirotheriidae indet., slab No. 57.

Plate 13

1. "Eight-digit" cast: deformation of a footprint by another one; KR 100: 108.1.
2. Effects of a change of illumination and covering with ammonium chloride, cf. pl. 2: 2 particularly the digit I of pes and the digit V of manus. *Chirotherium hauboldi* sp.n.; MWGUW 01139: 16.1-2.
3. Warped, 4 cm deep imprint of ?*Chirotherium hauboldi* sp.n., made in slushy mud. Specimen KR 101: 73.1.
4. Very deep footprint, beyond taxonomic determination, made in slushy and thick mud, TPW 38: 110.1.

Plate 14

1. Digit- and footprints of present-day lizard *Lacerta agilis* in thin (up to 2 mm) layer of mud, spread on a hard sandstone slab. Running gait — the smallest imprints (2—3 mm), rest traces — the largest ones.
2. The undertrack of *Brachychirotherium kuhni* Demathieu et Haubold, 1982; cf. fig. 12. Note two manus claws, one of pes and the distorted cast of the desiccation crack; TPW 39: 40.1-2.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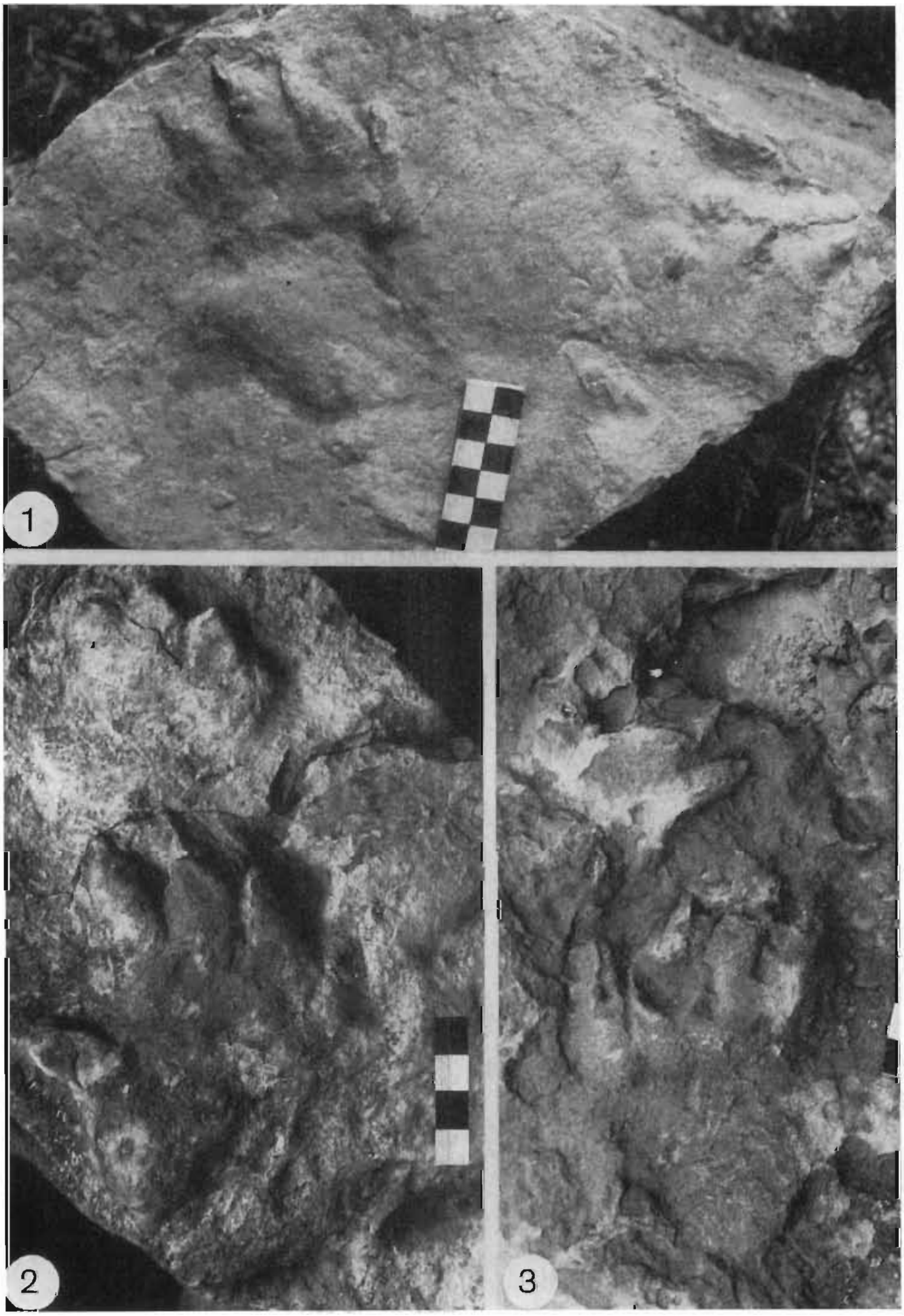
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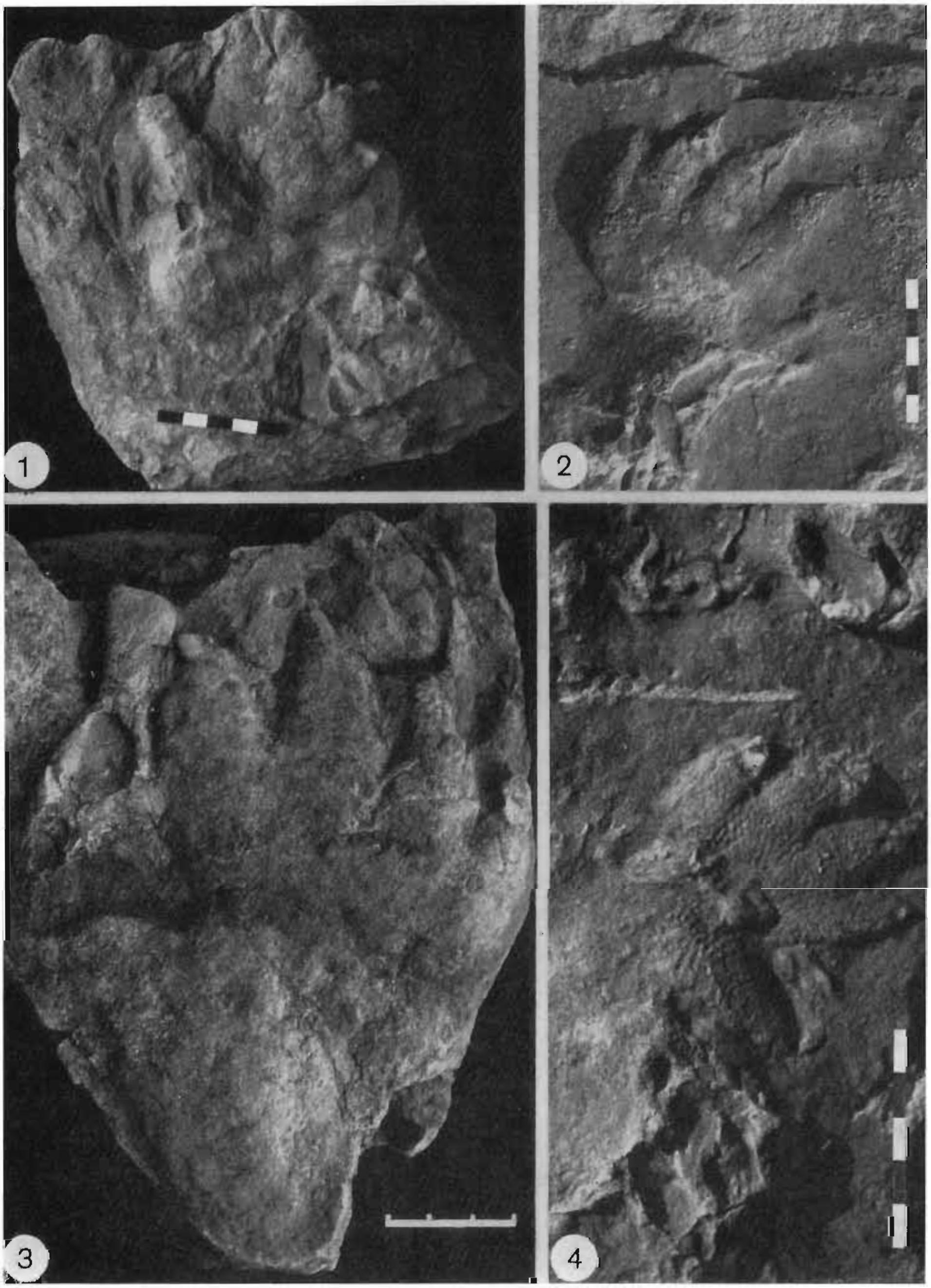
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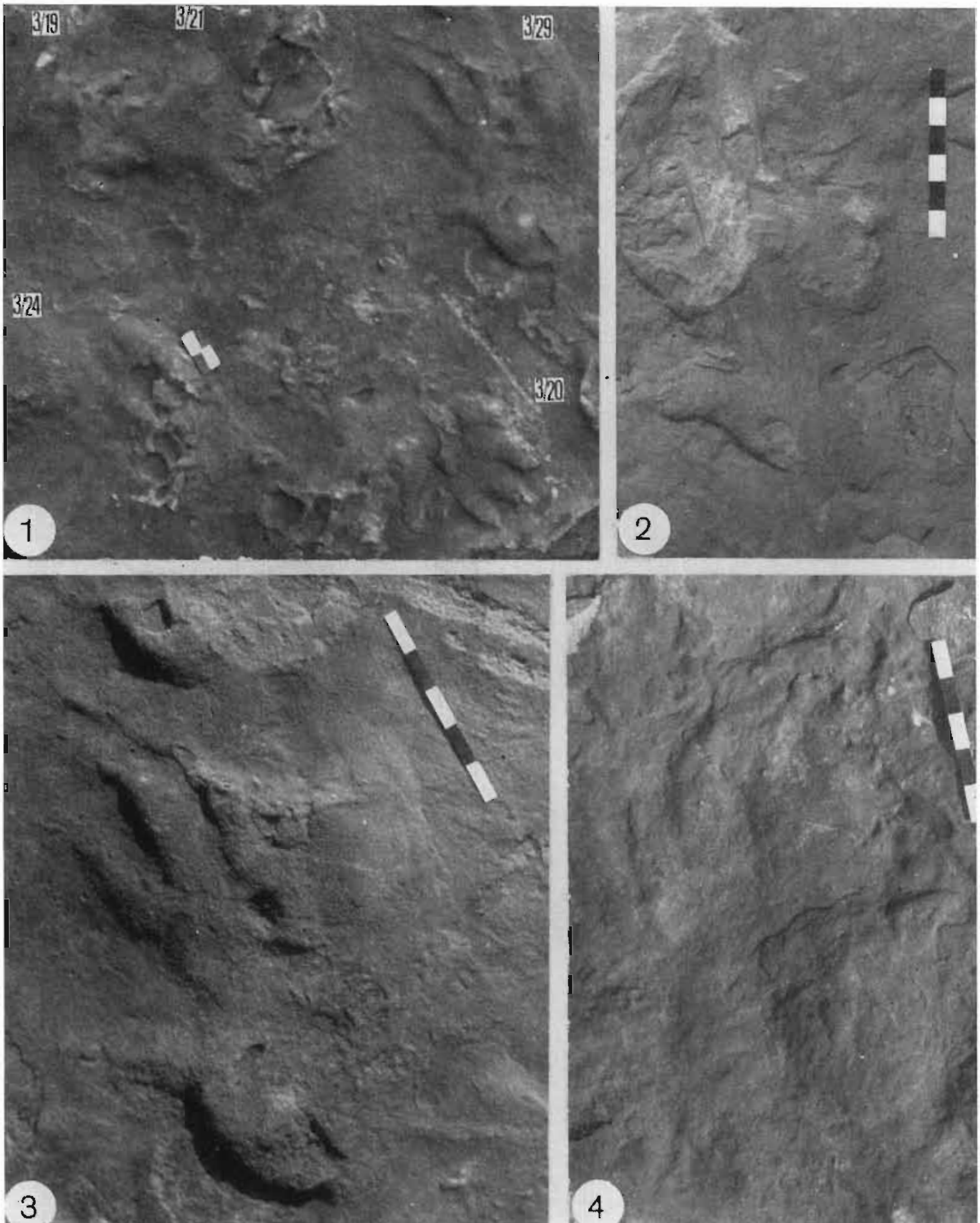

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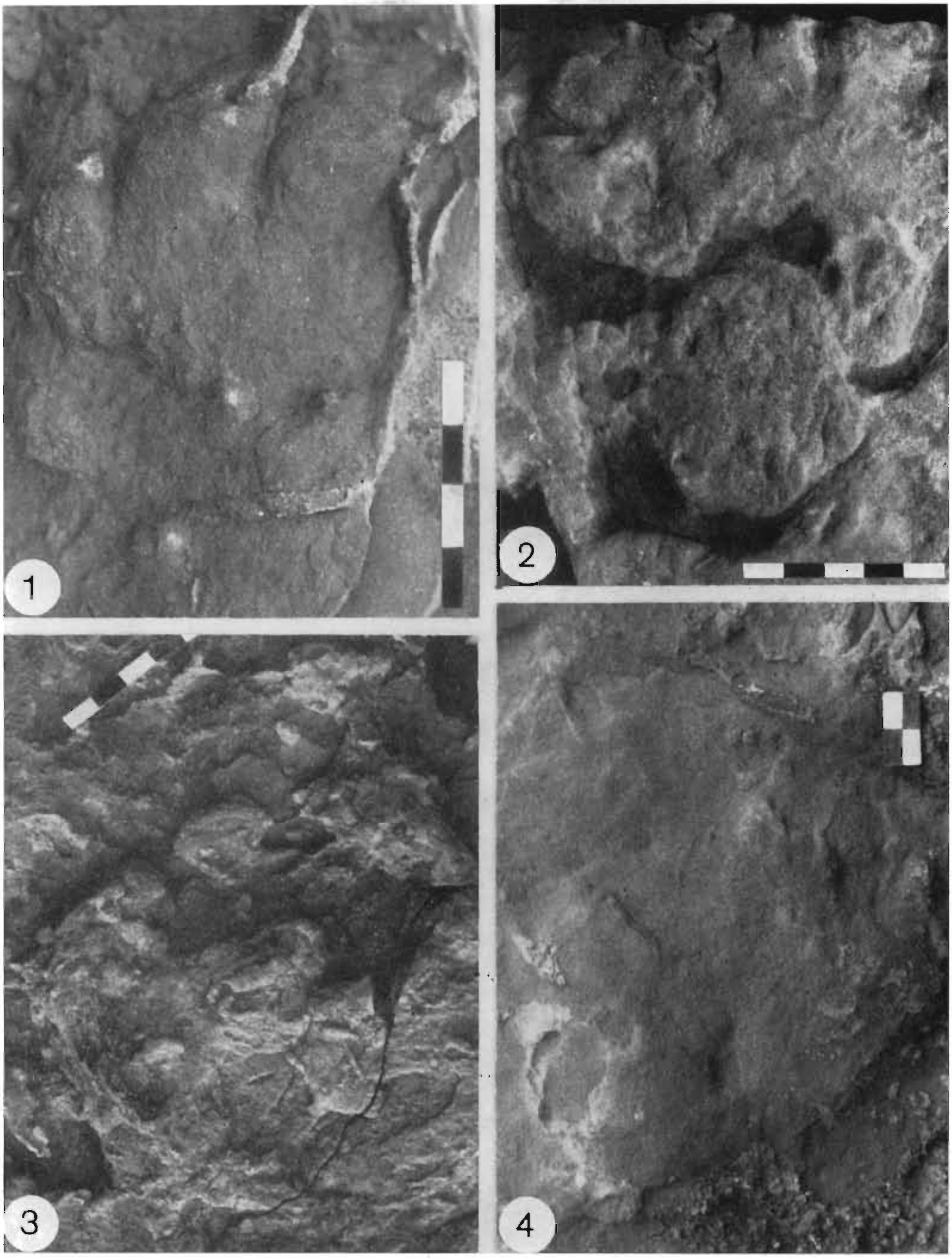
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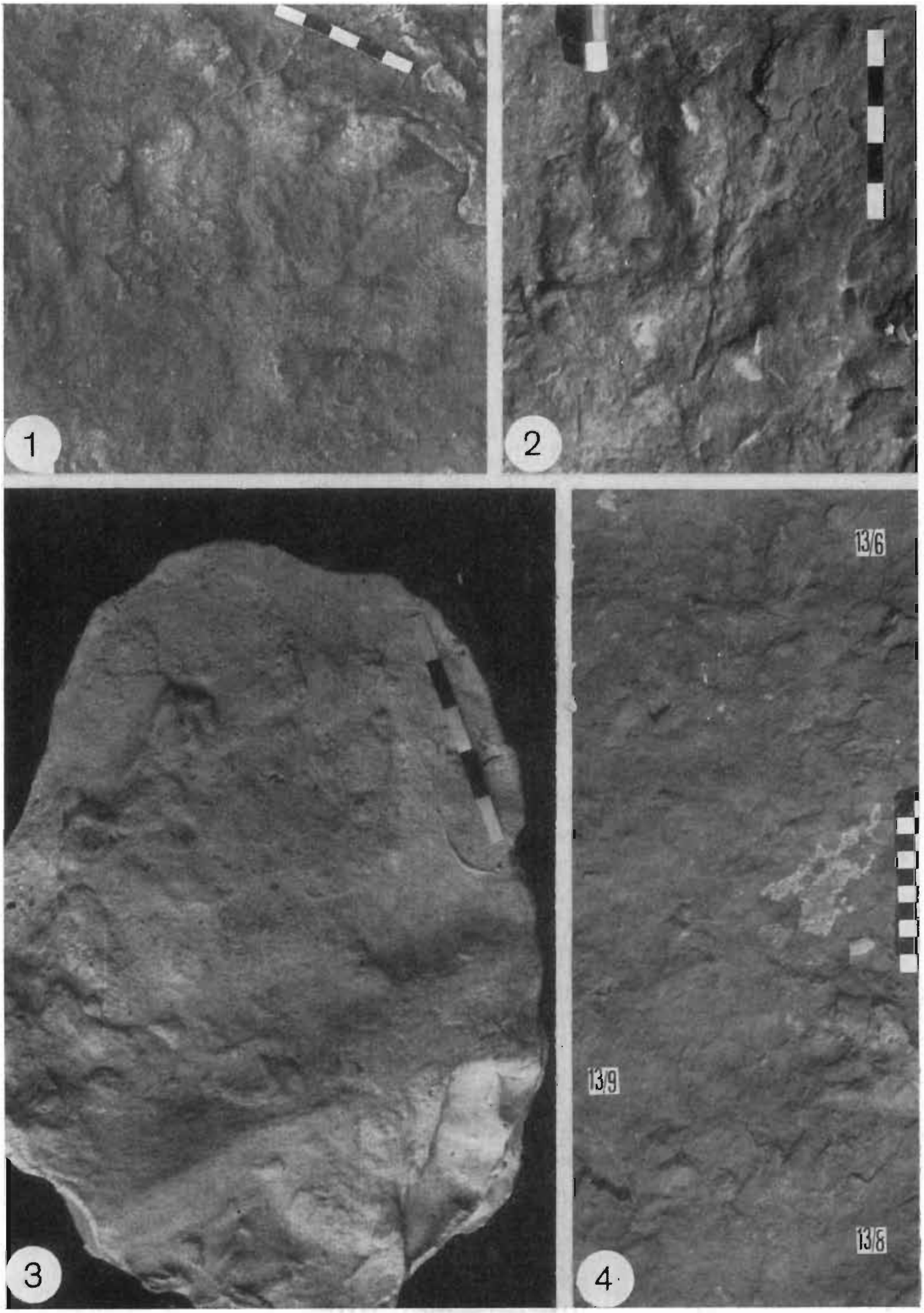
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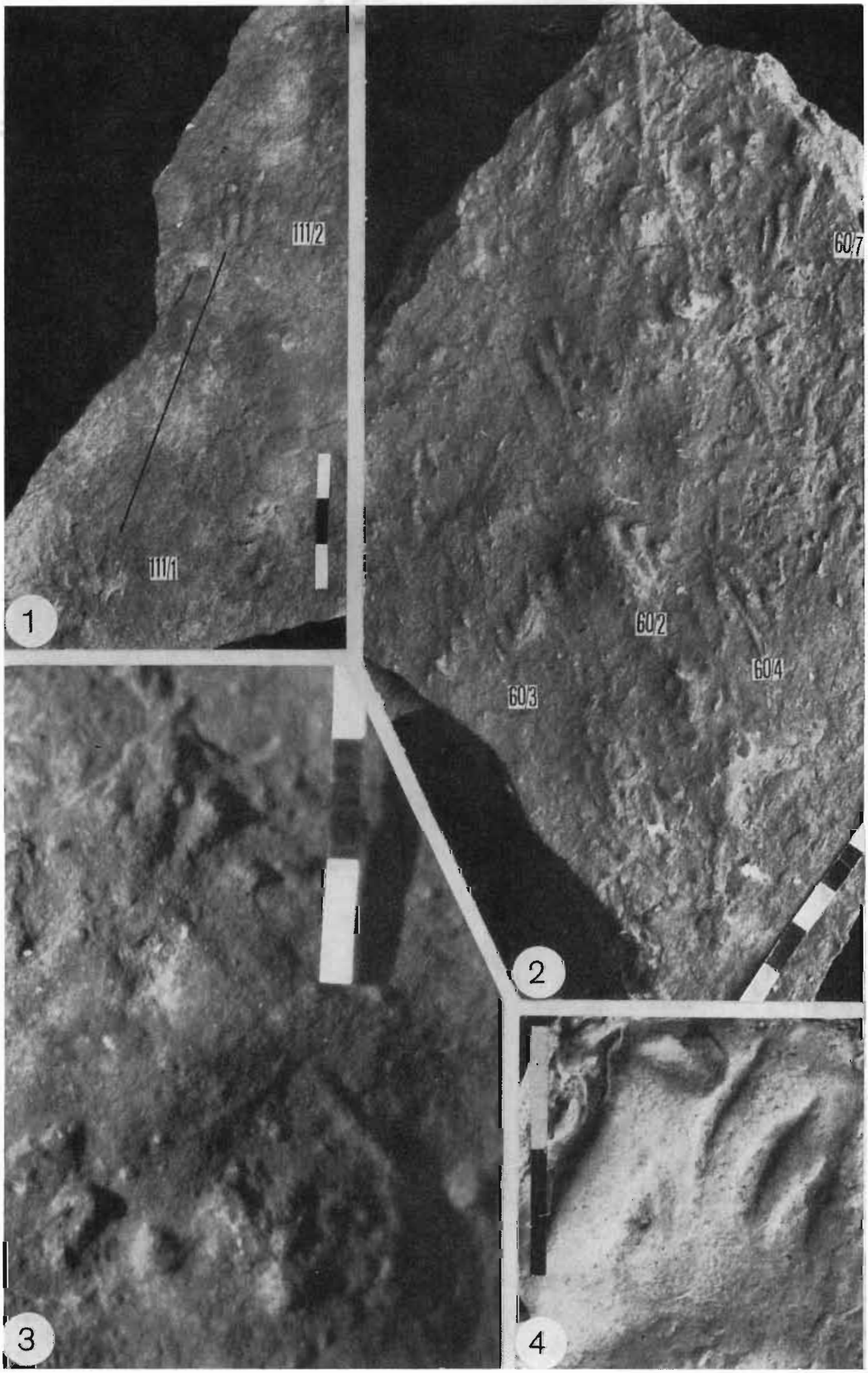
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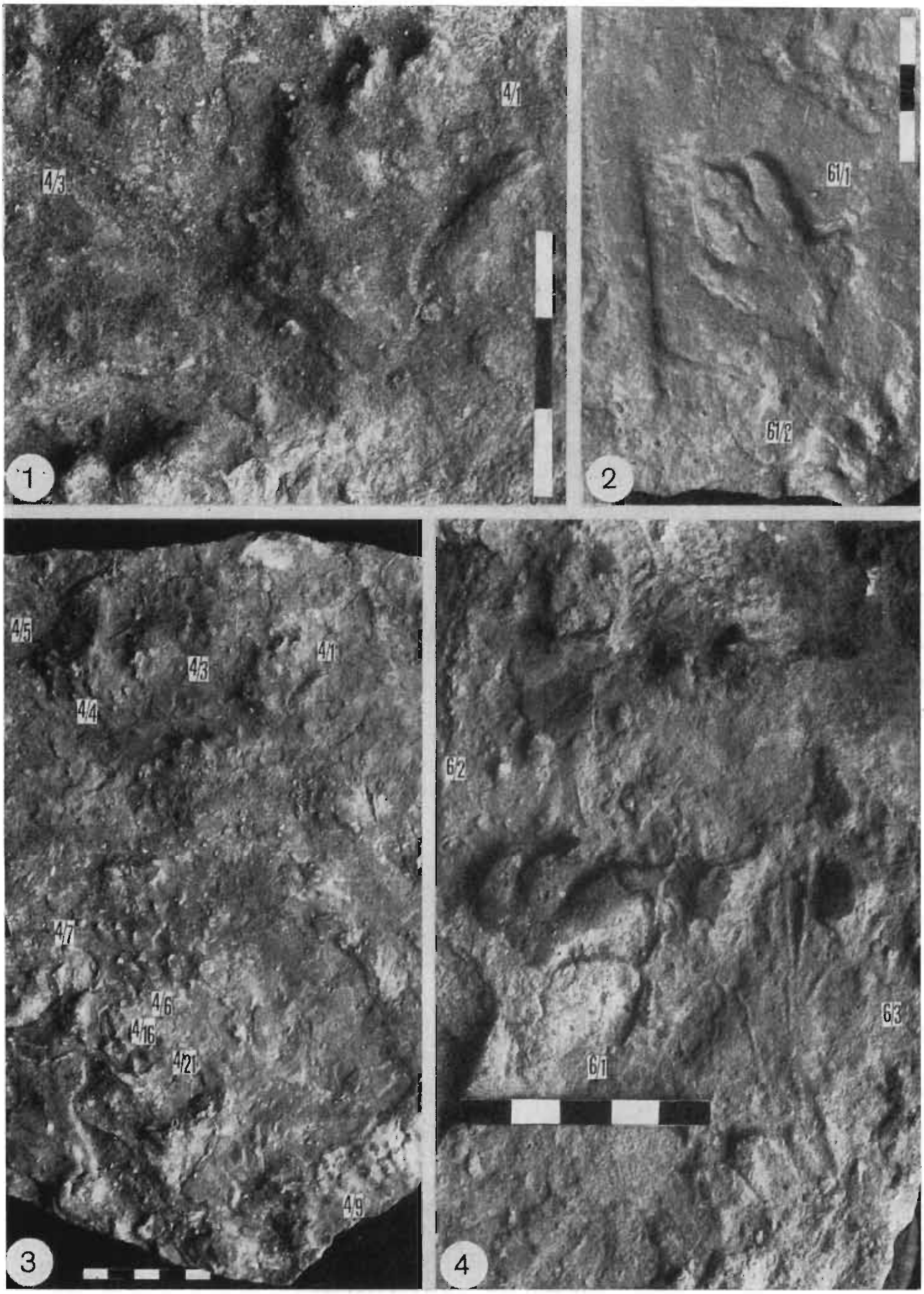
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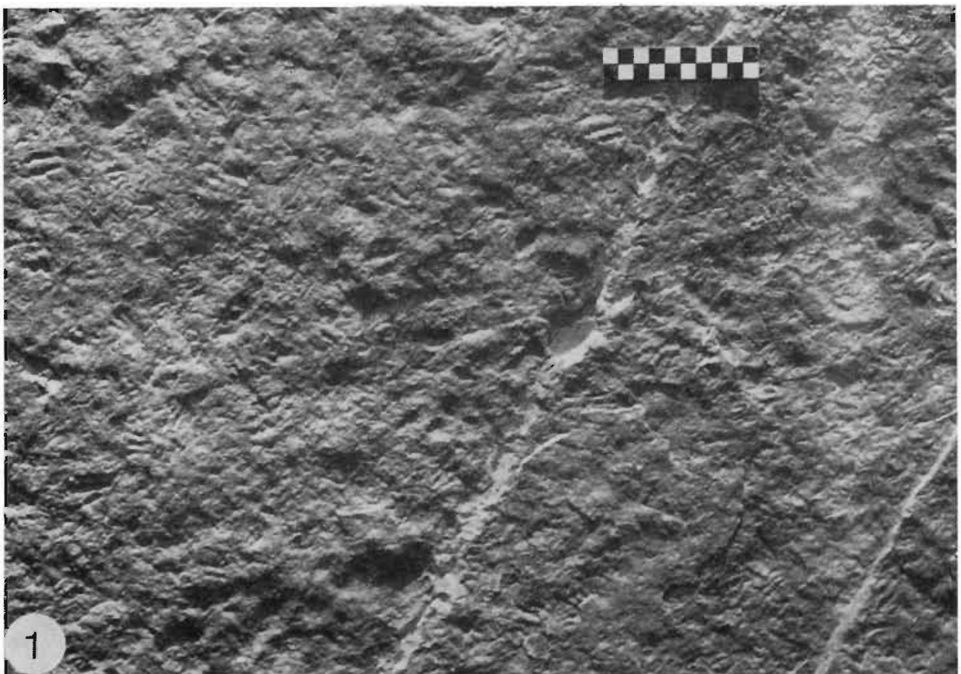
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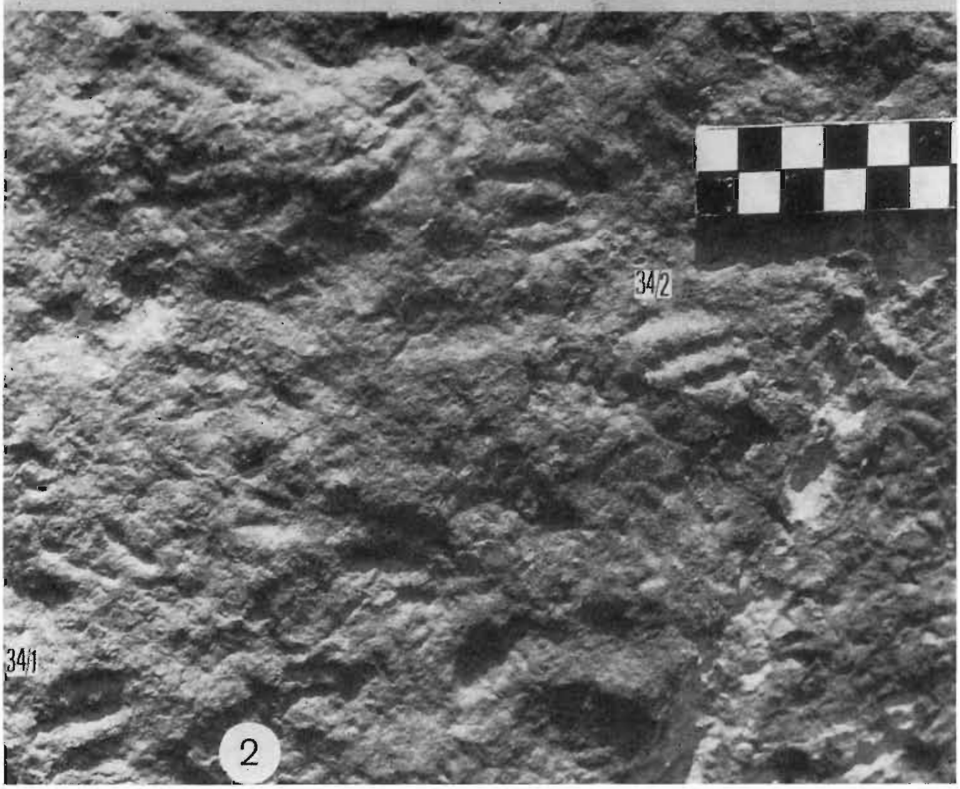
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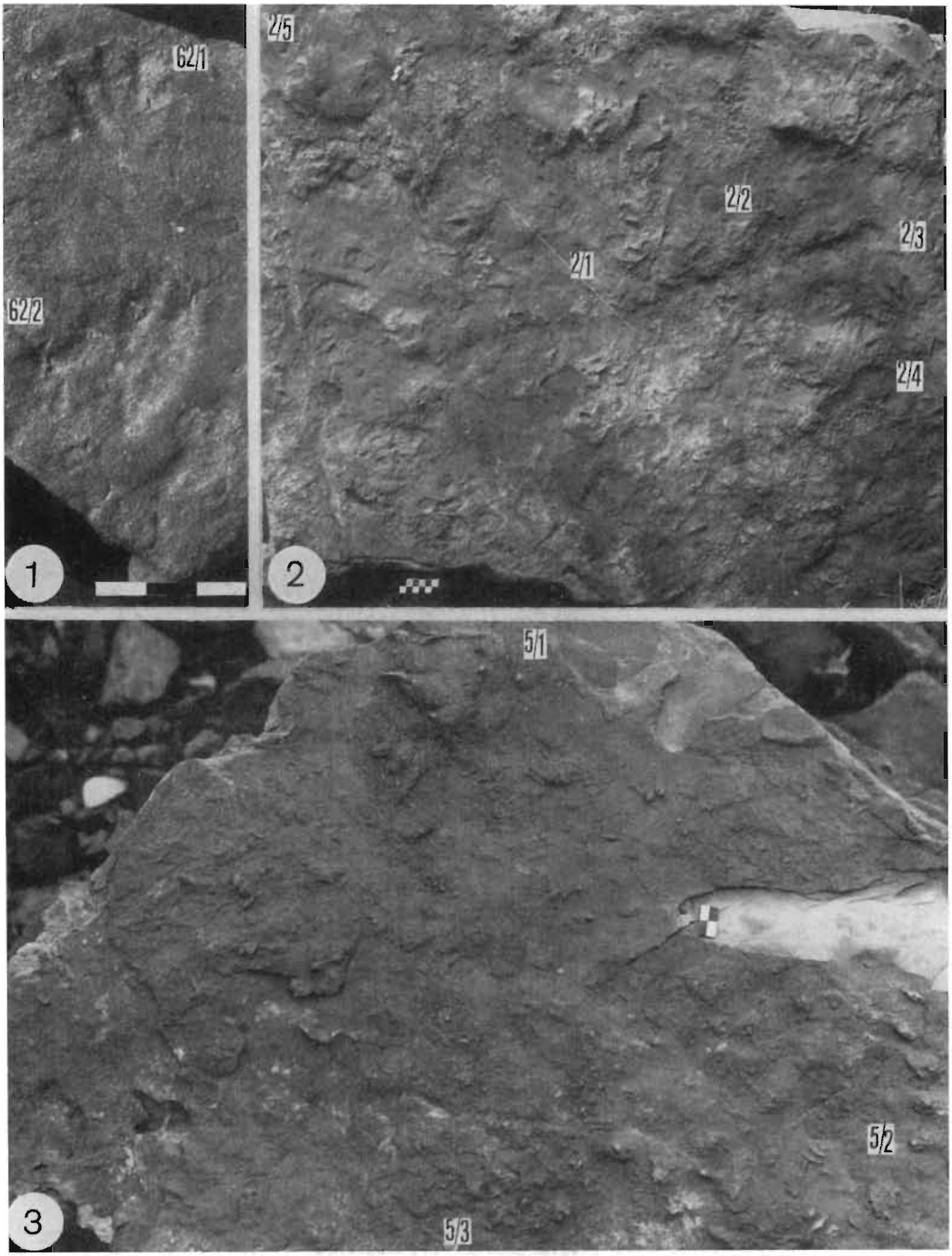
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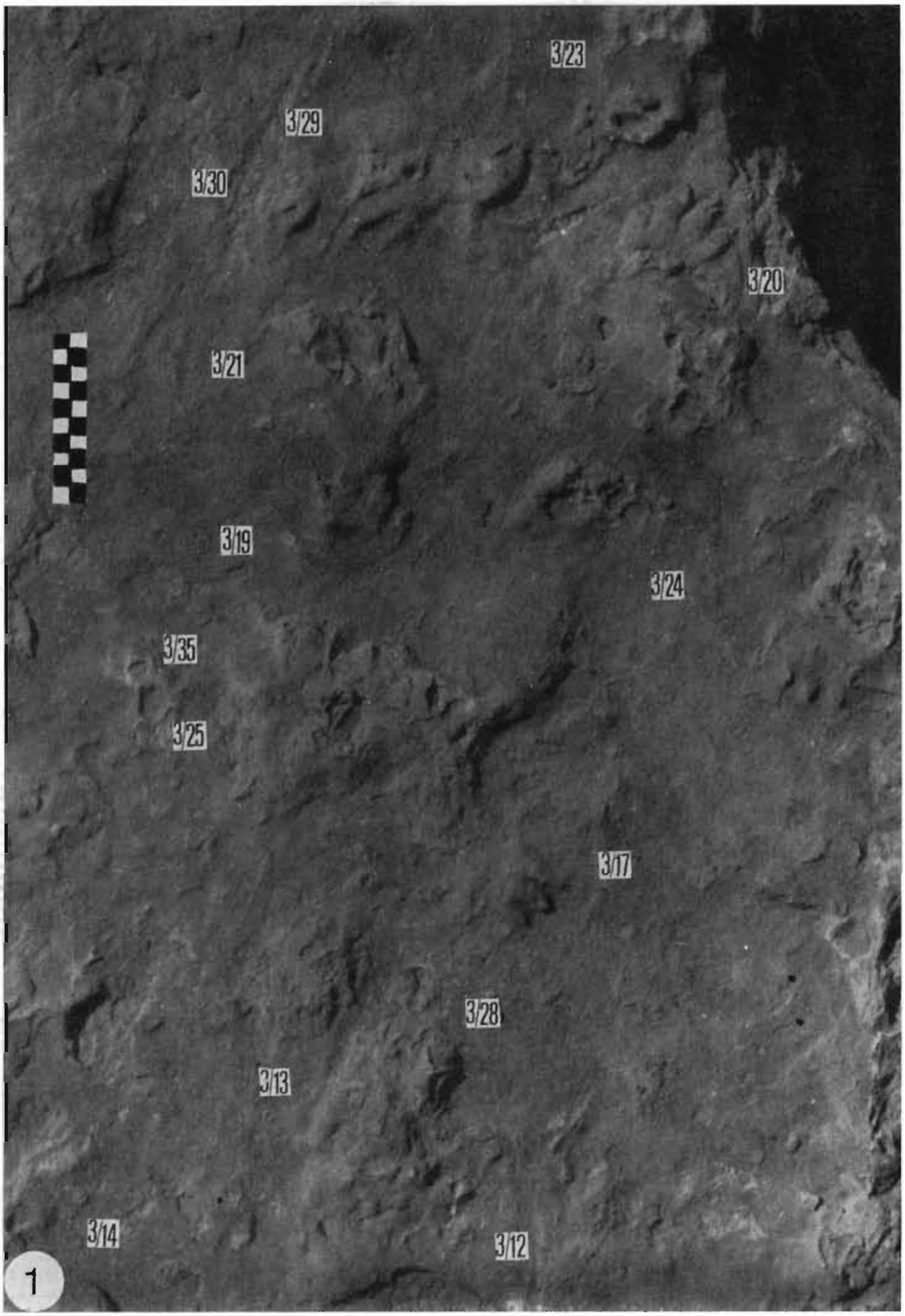
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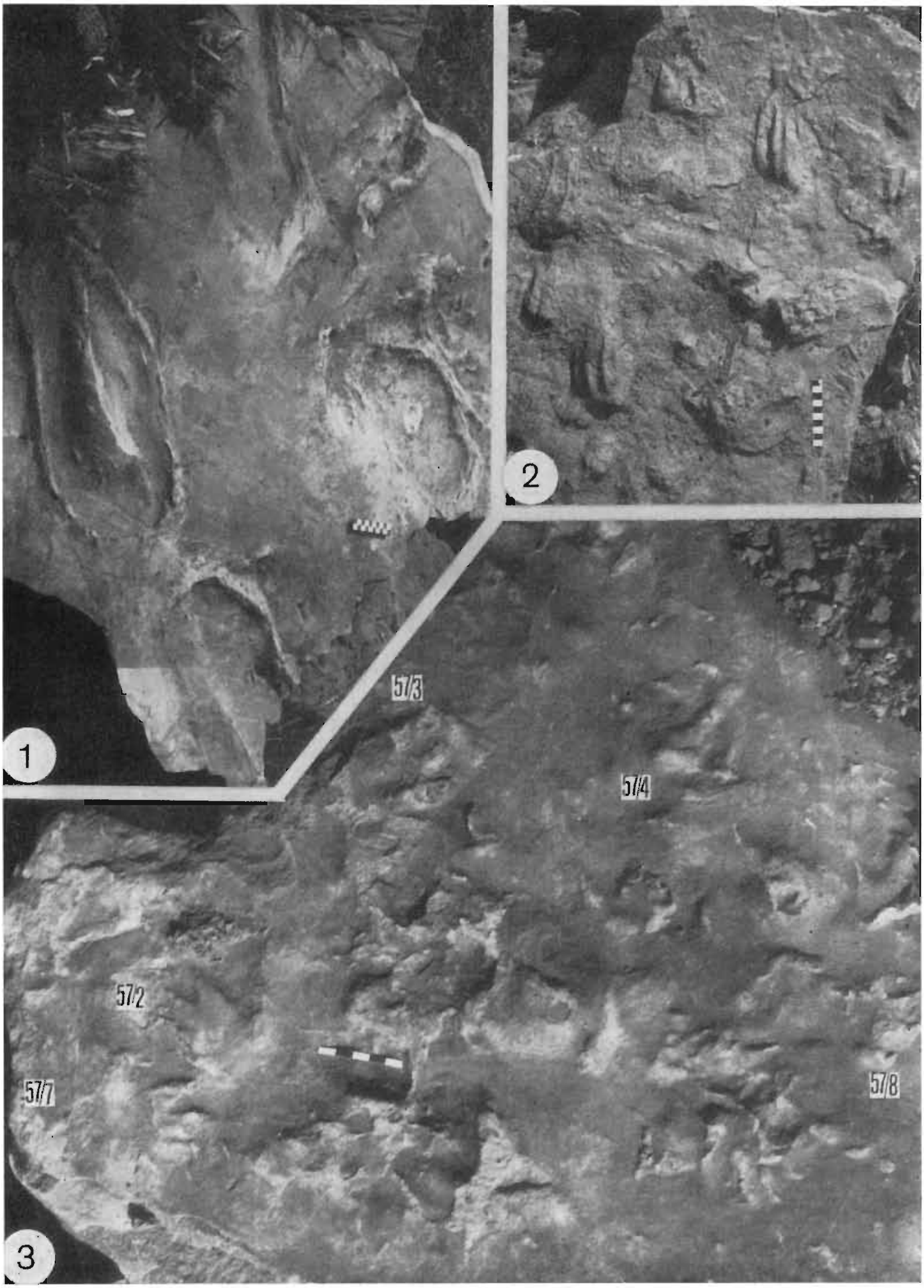
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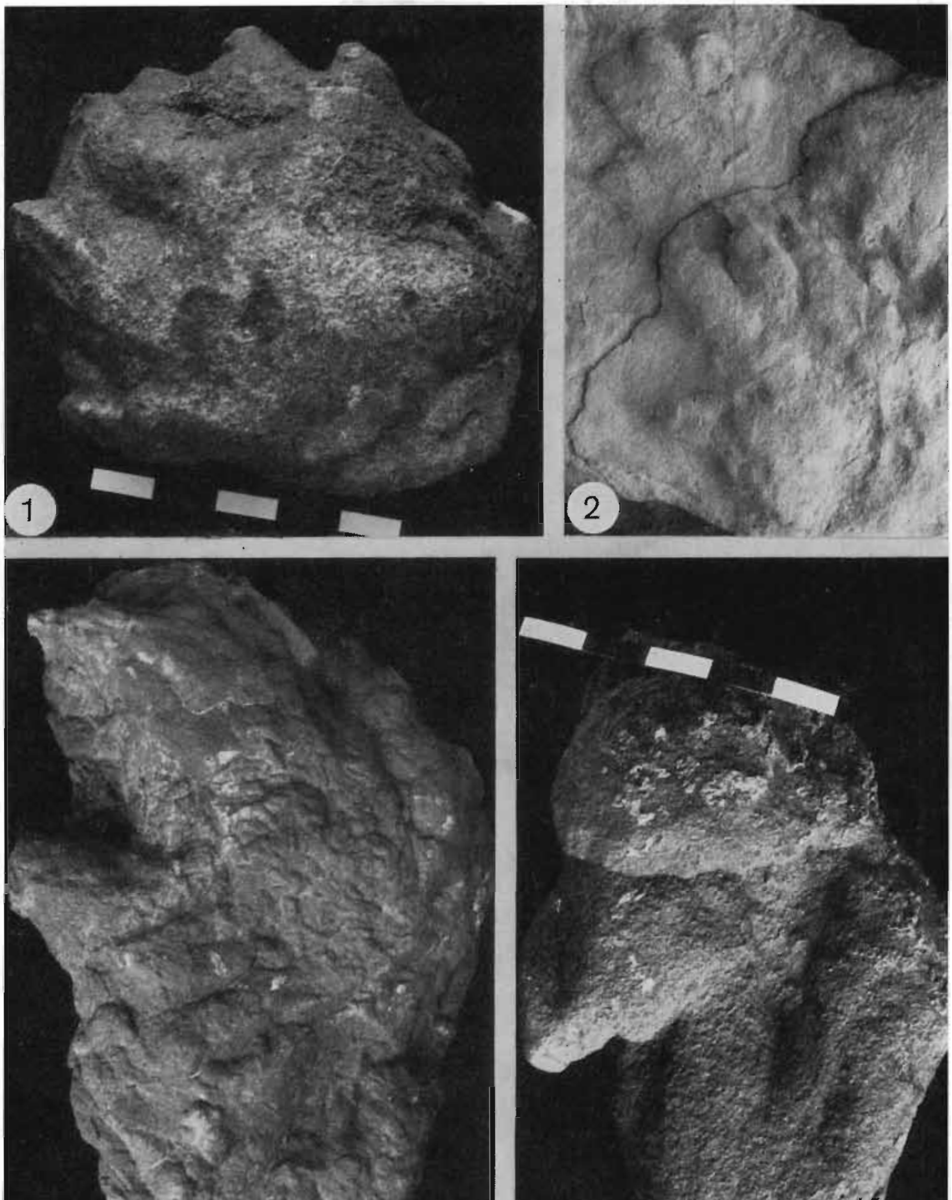
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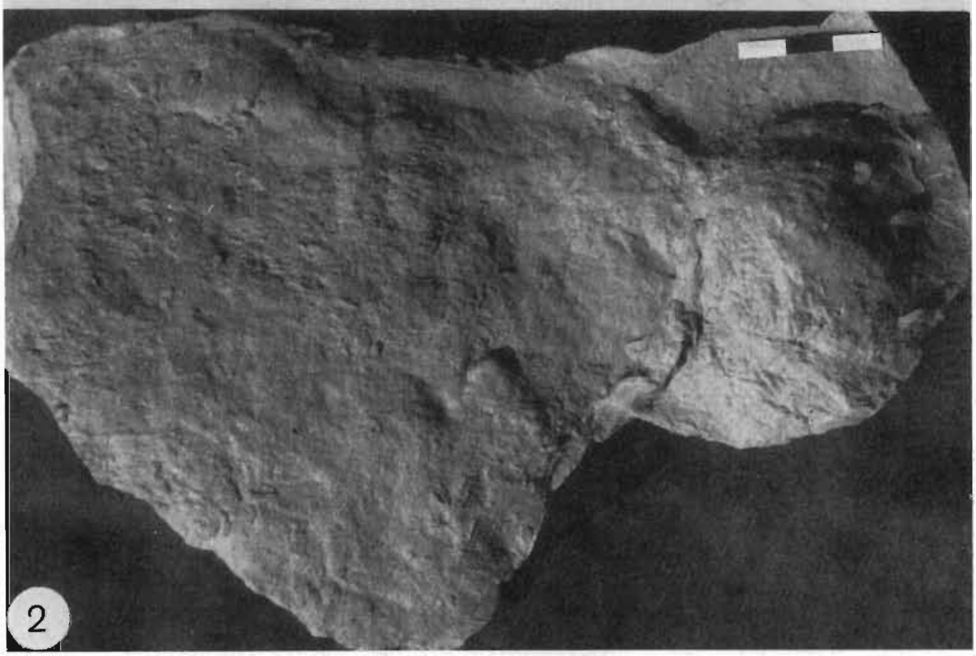
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