Late Permian vertebrate tracks from the Tumlin Sandstone, Holy Cross Mountains, Poland

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Ptaszyński, T. and Niedźwiedzki, G. 2004. Late Permian vertebrate tracks from the Tumlin Sandstone, Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica* 49 (2): 289–320.

This paper describes the vertebrate ichnofauna from the Tumlin Sandstone (Buntsandstein) of the Holy Cross Mountains in Poland. The footprint assemblage has previously been regarded as Early Triassic in age; however, ichnogenera characteristic of the Late Permian are now recognized. Lack of representatives of the ichnofamily Chirotheriidae, characteristic of continental Triassic sediments worldwide, also indicates a Permian rather than a Triassic age for the studied assemblage. Three ichnogenera (*Batrachichnus*, *Limnopus*, and *Amphisauropus*) produced by amphibians are recognized, the remainder (*Varanopus*, *Chelichnus*, *Dimetropus*, *Rhynchosauroides*, *Palmichnus*, *Paradoxichnium*, and *Phalangichnus*) being of reptilian origin. *Batrachichnus* cf. *salamandroides* (Geinitz, 1861), *Limnopus* cf. *zeilleri* (Delage, 1912), *Amphisauropus* cf. *latus* Haubold, 1970, *Varanopus* aff. *microdactylus* (Pabst, 1896), *Chelichnus* cf. *duncani* (Owen, 1842), and *Dimetropus* sp. are recorded in the Lower Buntsandstein for the first time. The following new ichnospecies are erected: *Rhynchosauroides kuletae* ichnosp. nov., *Palmichnus lacertoides* ichnosp. nov., *Paradoxichnium tumlinense* ichnosp. nov., *Phalangichnus gradzinskii* ichnosp. nov., and *Phalangichnus gagoli* ichnosp. nov.

Key words: Vertebrate footprints, ichnotaxonomy, Lower Buntsandstein, Tumlin Sandstone, Permian, Holy Cross Mountains, Poland.

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Introduction

Vertebrate footprints were first reported from the Buntsandstein of the Holy Cross Mountains (Góry Świętokrzyskie), Poland by Samsonowicz (1929). However, until the first palaeontological description of the vertebrate ichnofaunal assemblage from Wióry (Fuglewicz et al. 1990), they were the subject of few reports and communications (see Fuglewicz et al. 1981, 1990). Subsequent studies (Ptaszyński 1996, 2000a, b; Kuleta et al. 2001; Ptaszyński and Niedźwiedzki 2002) confirmed the presence of vertebrate footprints throughout most of the Buntsandstein section in the Holy Cross Mountains.

In the Tumlin Sandstone vertebrate tracks were first discovered by Gradziński et al. (1979) at Tumlin Gród quarry, and subsequently at Sosnowica Hill quarry (Gradziński and Uchman 1994). Footprints were initially identified by Ptaszyński (2000b). The ichnological material described below comes mainly from a single well-known outcrop situated at Tumlin Gród, 11 km northwest of the town of Kielce. Many specimens have also been found at Sosnowica Hill quarry 8 km north of Kielce, and we have observed indeterminable tracks at Ciosowa quarry (Fig. 1). The vertebrate ichnocoenosis from Tumlin Sandstone is especially important for an understanding of vertebrate evolution around the Permian/Triassic boundary.

All specimens described in this paper are housed in the collection of the Holy Cross Branch of the Polish Geological Institute, Kielce (abbreviated Muz. PIG OS).

Geological setting and age

The Tumlin Sandstone, a part of Tumlin Sandstone Member (Kuleta and Nawrocki 2000), is also informally called the Tumlin beds. This lithostratigraphic unit is restricted to a relatively short and narrow outcrop belt in the western part of the Holy Cross Mountains (Gradziński et al. 1979), and is exposed in a few quarries: Tumlin Gród, Sosnowica Hill, Pieniężna, Wykień, and Ciosowa Hill (Fig. 1). In the Radoszyce borehole, 25 km NW of Tumlin, the Tumlin Sandstone attains a thickness of 105 m (Gradziński et al. 1979). In other boreholes on the NW margin of the Holy Cross Mountains the so-called "complex C", distinguished on the basis of sedimentary/petrographical features (Kuleta 1985, 1990), contains mostly sandstone deposited in dune and inter-dune areas as well as in braided river or periodic stream channels. It is 52.0–151.7 m thick (Fijałkowska 1994). In adjacent areas of the Holy Cross Mountains, the Tumlin Sandstone is correlated with the Stryczowice Beds and with the upper part of the Baltic Formation (Senkowiczowa 1970; Szyperko-Teller et al. 1997). Lithologically, the Tumlin Sandstone mostly comprises thick sandstone bodies, deposited as dunes, and thinly-bedded sandstone with siltstone and claystone intercalations, interpreted by Gradziński et al. (1979) and Gradziński and Uchman (1994) as the interdune deposits of periodic streams, lakes and ponds. Interdune sequences contain numerous sedimentary structures and invertebrate trace fossils butno body

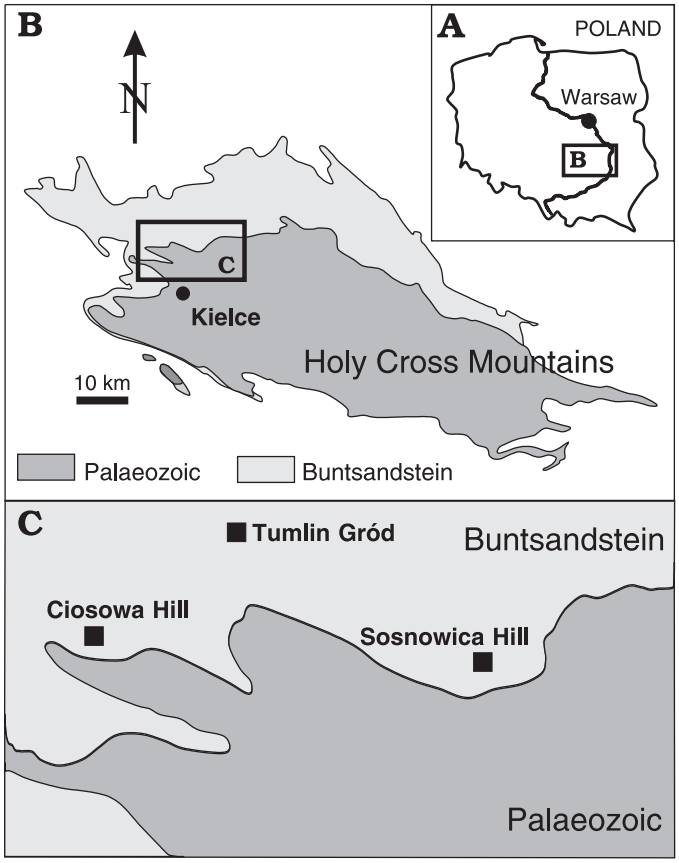

Fig. 1. Location of the Tumlin Sandstone vertebrate tracksites in Poland (**A**) and in Holy Cross Mountains (**B**, **C**). Quaternary removed, tectonics not respected (modified from Ptaszyński and Niedźwiedzki 2002).

fossils. The Tumlin Sandstone has been variously attributed to the Lower (Fijałkowska 1994), Middle (Senkowiczowa and Ślączka 1962; Senkowiczowa 1970; Gradziński et al. 1979; Szyperko-Teller and Moryc 1988) or partly Lower and partly Middle (Szyperko-Śliwczyńska 1980) Buntsandstein of the Holy Cross Mountains. Following Fijałkowska (1992, 1994; see also Kuleta and Nawrocki 2000), we here regard the Tumlin Sandstone as the uppermost member of the Lower Buntsandstein of the Holy Cross Mountains (Fig. 2).

The age of the Buntsandstein in Poland has traditionally been regarded as Early Triassic (since Alberti 1834), with its lower boundary believed to represent the chronostratigraphic base of the Triassic. Later work interpreted the base of the Triassic in Poland to lie close to the lithostratigraphic lower boundary of the Buntsandstein which commences with transgressive sediments thought to have been deposited during the postulated worldwide transgression at the beginning of the Triassic (Wagner 1988, 1994; Pieńkowski 1989, 1991). However, some doubts have remained about this interpretation (Wagner et al. 1978; Wagner 1988). Magnetostratigraphic investigations are consistent with these age determinations (Nawrocki et al. 1993; Nawrocki 1995; Kuleta and Nawrocki 2000; Nawrocki et al. 2003), even though the evidence is equivocal given the nature of palaeomagnetic data (see Szulczewski 1986; Lozovsky 1997). The age of the Tumlin Sandstone has therefore been generally accepted as Early Triassic by most authors. To date only Fuglewicz (1980, 1987) and Kozur (1993b) have suggested a Late Permian age for considerable parts of the Lower Buntsandstein in Poland.

The lower biostratigraphic limit of the Tumlin Sandstone is determined relative to borehole sections-based lithostratigraphic correlation (see Fijałkowska 1992, 1994) by the *Lundbladispora obsoleta–Protohaploxypinus pantii* Assemblage Zone (Fig. 2). This is correlated with the Boreal *Otoceras* fauna and *Protohaploxypinus* association from East Greenland, referred to the earliest Triassic, Induan: Griesbachian (Orłowska-Zwolińska 1984, 1985; Fijałkowska 1992, 1994; Marcinkiewicz 1992; Wagner 1994; see also Szyperko-Teller et al. 1997). The Tumlin Sandstone is also older than the *Densoisporites nejburgii* Assemblage Zone from the lower and middle part of the Middle Buntsandstein which is of Early Triassic age, Induan (Fuglewicz 1987): upper Griesbachian to Dienerian (Fijałkowska 1994) or early Olenekian (see Kozur 1998c). Unfortunately, the Tumlin Sandstone does not contain any microflora ("barren interval", Fijałkowska 1994; see also Fig. 2B).

According to recent data concerning the Permian–Triassic boundary (Kozur 1978, 1988a, b, 1998a, b, c, 2001, and personal communication 2003), this is defined by the lower limit of the *Hindeodus parvus* Zone.

The *Hindeodus parvus* Zone corresponds possibly to at least a considerable part of the *Lundbladispora obsoleta–Protohaploxypinus pantii* Assemblage Zone, which correlates with the *Otynisporites eotriassicus* Zone in the Lower Buntsandstein. On the other hand, at least a part of the *Otynisporites eotriassicus* Zone is correlated with the Boreal *Otoceras boreale* Zone with *Protohaploxypinus* association, of uppermost Permian–Dorashamian age (Fuglewicz 1980, 1987; Kozur 1988b, 1994, 1998a, b; Ptaszyński and Niedźwiedzki 2002). This is also confirmed by the presence of *Tympanicysta* (Fijałkowska 1992, 1994) in strata containing the *Lundbladispora obsoleta–Protohaploxypinus pantii* microfloral assemblage, which is abundant only in the uppermost Permian and becomes rare towards the Permian/Triassic boundary (Kozur 1998a, b; for the detailed discussion see Kozur 1978, 1988a, b, 1990, 1993a, 1994, 1998a, b, c). The *Lundbladispora obsoleta–Protohaploxypinus pantii* assemblage also shows a close similarity to the uppermost Permian *Lundbladispora obsoleta–Lunatisporites noviaulensis* assemblage from the Lower Buntsandstein of the German Basin (Kozur 1990, 1994). Thus, the *Lundbladispora obsoleta–Protohaploxypinus pantii* Assemblage Zone may not be of Early Triassic age, but represent the uppermost Permian–lowermost Triassic span. This is confirmed by newest studies of the Central European Basin where the Permian–Triassic boundary is found within Lower Buntsandstein sections (Roman 2004; Szurlies et al. 2003).

The majority of vertebrate footprints from the Tumlin Sandstone contains representatives of ichnogenera known to occur only in Permian deposits. The only exception is *Rhyn-*

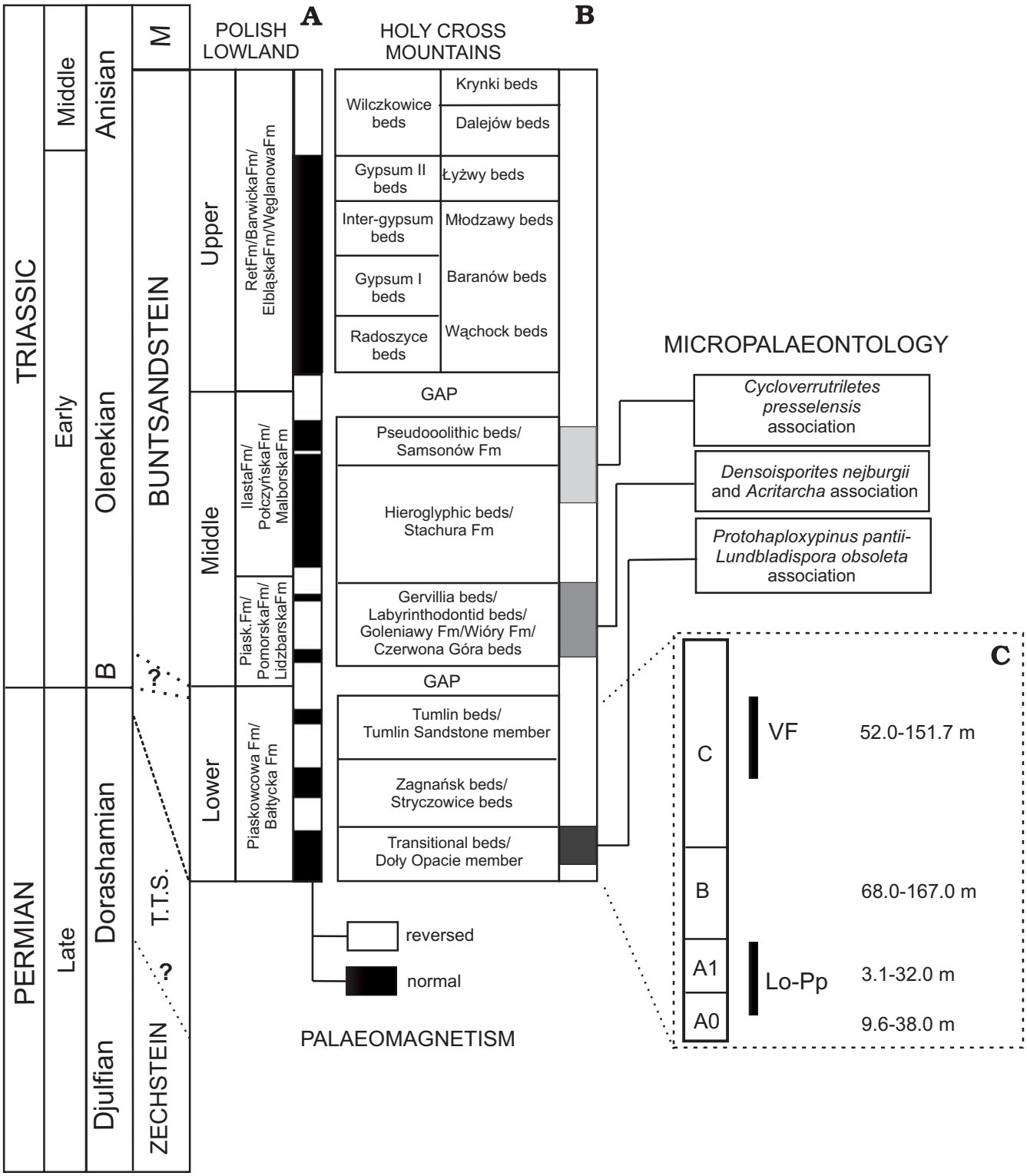

Fig. 2. Stratigtraphic scheme of the Buntsandstein in the NW and N margin of the Holy Cross Mountains (modified from Kuleta and Nawrocki 2000; with data from Barczuk 1979; Fijałkowska 1994; Fuglewicz 1973, 1980, 1987; Fuglewicz et al. 1990; Kozur 2003 personal communication; Kuleta 2002 personal communication; Mader and Rdzanek 1985; Nawrocki 1995; Ptaszyński 2000b; Ptaszyński and Niedźwiedzki 2002; Rdzanek 1984; Senkowiczowa 1970; Szyperko-Teller et al. 1997). **A**. Lithostratigraphic and magnetostratigraphic scheme of the Polish Lowland Buntsandstein and of the Holy Cross Mountains (T.T.S., Top Terrigenous Series; B, Brahmanian; M, Muschelkalk). **B**. Real occurrence of Lower and Middle Buntsandstein microflora associations in the lithostratigraphic section of the NW margin of the Holy Cross Mountains (after Fijałkowska 1994). **C**. Occurrence of the *Lundbladispora obsoleta–Protohaploxypinus pantii* association (Lo-Pp) and Tumlin sandstones vertebrate ichnoassemblage (VF) in the Lower Buntsandstein profile of the NW margin of the Holy Cross Mountains (thickness from boreholes after Fijałkowska 1994). A0, A1, B, C, petrographic complexes after Kuleta (1990) and Kuleta and Nawrocki (2000).

chosauroides known from both the Late Permian and Triassic. Therefore the age of the Tumlin Sandstone is determined here as the latest (uppermost) Permian (Dorashamian), very close to the Permian–Triassic boundary (Fig. 2). The status of the *Lundbladispora obsoleta–Protohaploxypinus pantii* Assemblage Zone supports this interpretation (Ptaszyński and Niedźwiedzki 2002). This also allows us to assign a Late Permian age to the considerable part of the Lower Buntsandstein (in the sense of Kuleta and Nawrocki 2000, see also Ptaszyński and Niedźwiedzki 2002) outcropping in the Holy Cross Mountains.

Remarks on the palaeoenvironment

Vertebrate tracks from the Tumlin Sandstone occur almost exclusively in interdune deposits of periodic fluvial, lacustrine, and pond origin. Footprint-bearing surfaces often show mud cracks, rain drops, differentiated ripplemarks and numerous invertebrate tracks. They have been preserved because of the presence of thin mud intercalations between sandstone layers. We found no trackways associated with dune slopes, except for a single, hardly determinable trackway (possibly *Amphisauropus*) observed at Sosnowica Hill quarry (Ptaszyński and Niedźwiedzki 2002: fig. 10). In many cases tracks, if present, are abundant, often consisting of numerous specimens of a single ichnospecies. This may be caused by the gregarious behaviour of the trackmakers or by their different habitat preferences. A similar mass occurrence of tracks of mostly one ichnotaxon on track bearing surfaces has been observed in the Early Triassic footprint assemblage at Wióry (Fuglewicz et al. 1990; Ptaszyński 2000a). Interestingly, in all dune and interdune structures investigated we have found no trackways with asymmetric footprints like those described from the Coconino Sandstone, Arizona, USA and other localities (see Brand and Tang 1991). Such asymmetric footprints in trackways have been observed in the Labyrinthodontidae Beds at Wióry where *Capitosauroides* trackways are interpreted as having been made by partly buoyant swimming animals that touched the bottom occasionally (Ptaszyński 2000a). Despite the scarcity of trackways preserved on dune slope surfaces, we believe that unusual trackways similar to those found in the Coconino Sandstone are better explained by the underwater buoyancy rather than the subaerial dune slope hypothesis (see Haubold et al. 1995; Haubold 1996).

Methods

Specimen numbers are made up of an abbreviation of the collection, the number of the slab, and the number of the imprint. Trackway labels comprise an abbreviation of the collection, the number of the slab and all of the numbers of the imprints comprising the trackway. Footprints in trackways are marked on photographs and drawings by connecting the bases of the imprints of pedal digit III with lines.

Measurements were taken from original specimens and plaster casts. Some photographs show convex plasticine replicas made from concave moulds of imprints. The method of measurement corresponds to that of Haubold (1971b), Leonardi (1987), and Ptaszyński (2000a). Many slabs have not been recovered, but only documented in situ by photographs, plaster casts and measurements before being destroyed during quarrying. Such material, if included in descriptions, has also been given a number even though the original slabs have not been collected. Plaster casts of parts of these slabs are included in the ichnological collection.

Descriptions

Amphibian ichnotaxa

Ichnogenus *Batrachichnus* Woodworth, 1900

(= *Saurichnites* Geinitz, 1851; *partim*)
(= *Anthichnium* Nopcsa, 1923)

Batrachichnus cf. *salamandroides* (Geinitz, 1861)

Figs. 3A–D, 5B, C.

Material.—Tumlin Gród quarry: Muz. PIG OS-220/41 thin sandstone slab with many poorly preserved natural casts of imprints on its bottom side; Muz. PIG OS-220/42 (Fig. $3A_1$, A_2); Muz. PIG OS-220/43 (Fig. 3B); Muz. PIG OS-220/51 three slabs representing the same track-bearing surface with imprints on the bottom side of the layer with ripple marks; Muz. PIG OS-220/48, Muz. PIG OS-220/49, Muz. PIG OS-220/50 slabs with moulds on upper sides, representing the same track-bearing surface as Muz. PIG OS-220/41; Muz. PIG OS-220/44: 1, 2, 3 (Figs. $3C_1$, C_2, C_3, 5B, C) slab with relatively well preserved imprints; Muz. PIG OS-220/45 (Fig. 3D), Muz. PIG OS-220/46 thin slabs with poorly preserved footprints and invertebrate tracks on their bottom sides; Muz. PIG OS-220/47 slab with poorly preserved imprints. Small, poorly preserved imprints have been found also at Sosnowica Hill quarry.

Description.—In Tumlin Gród quarry small structures occur which can be identified as very small vertebrate footprints. No trackways were observed, only isolated imprints or sets have been found (Figs. $3C_3$, 5B). They are mostly poorly preserved, often visible only as small hollows on sandstone layers. Similar state of preservation is known from other localities (Gand and Haubold 1984: fig. 12).

Pes.—Pentadactyl pedal imprints, with length equal width about 12 mm (Figs. $3C_3$, 5B). The digit group I–IV is 11 mm long by 12 mm wide. Digits I–IV diverge at about 30°. They increase in length from I to IV; the IV is almost equal in length to the III (Figs. $3C_2$, 5C). Digit V, situated somewhat behind the digit group I–IV, is 6 mm long. Digits I–V diverge

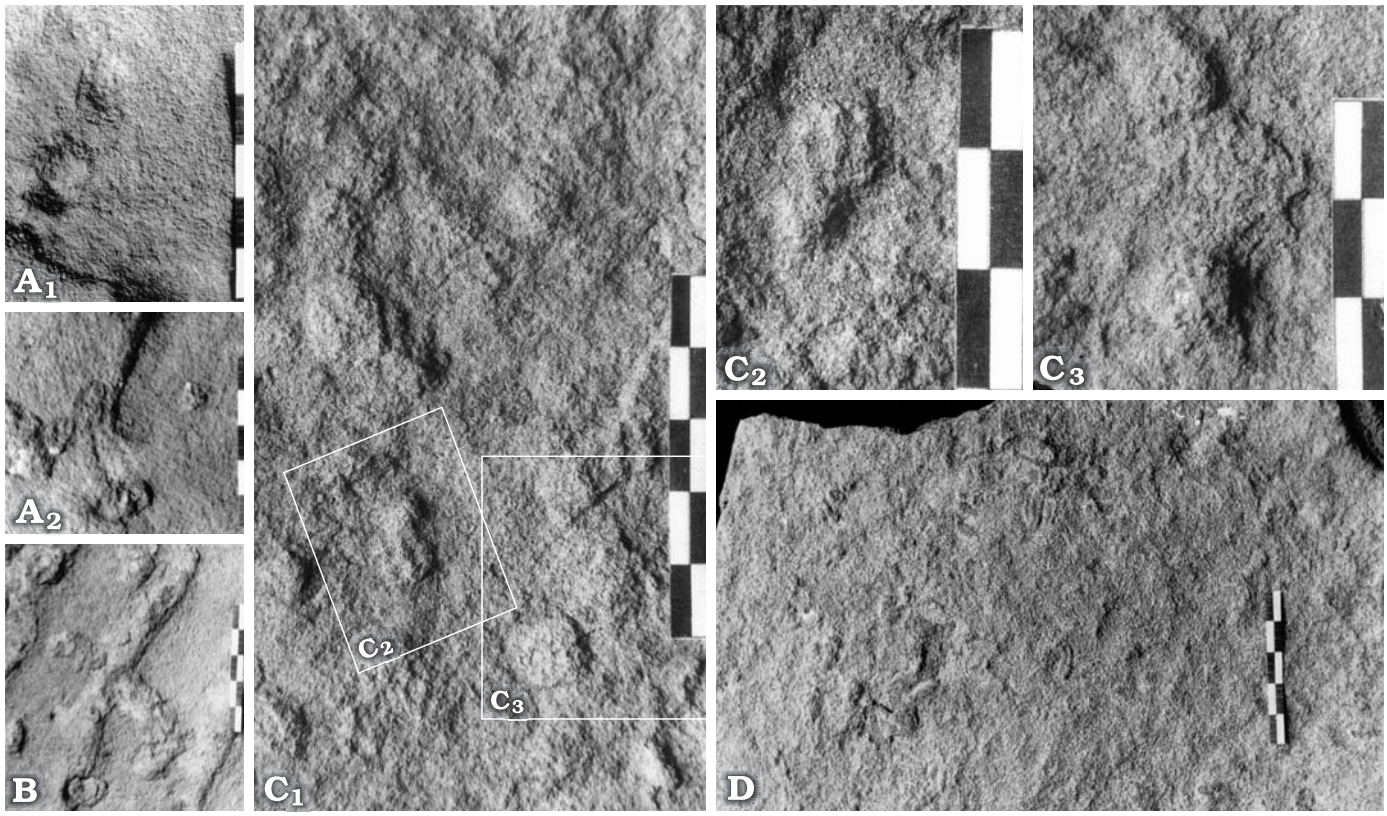

Fig. 3. *Batrachichnus* cf. *salamandroides* (Geinitz, 1861). **A_1**, **A_2**. Muz. PIG OS-220/42 poorly preserved imprints. **B**. Muz. PIG OS-220/43 poorly preserved imprints. **C_1**. Muz. PIG OS-220/44 isolated, well preserved imprints. **C_2**. Muz. PIG OS-220/44: 3 left pedal imprint. **C_3**. Muz. PIG OS-220/44: 1, 2 right set of pedal and manual imprints (in the middle and upper part of the photograph). **D**. Muz. PIG OS-220/45 problematic imprints with accompanying invertebrate tracks. Scale bars: A–C_1, D, 5 cm; C_2, C_3, 3 cm.

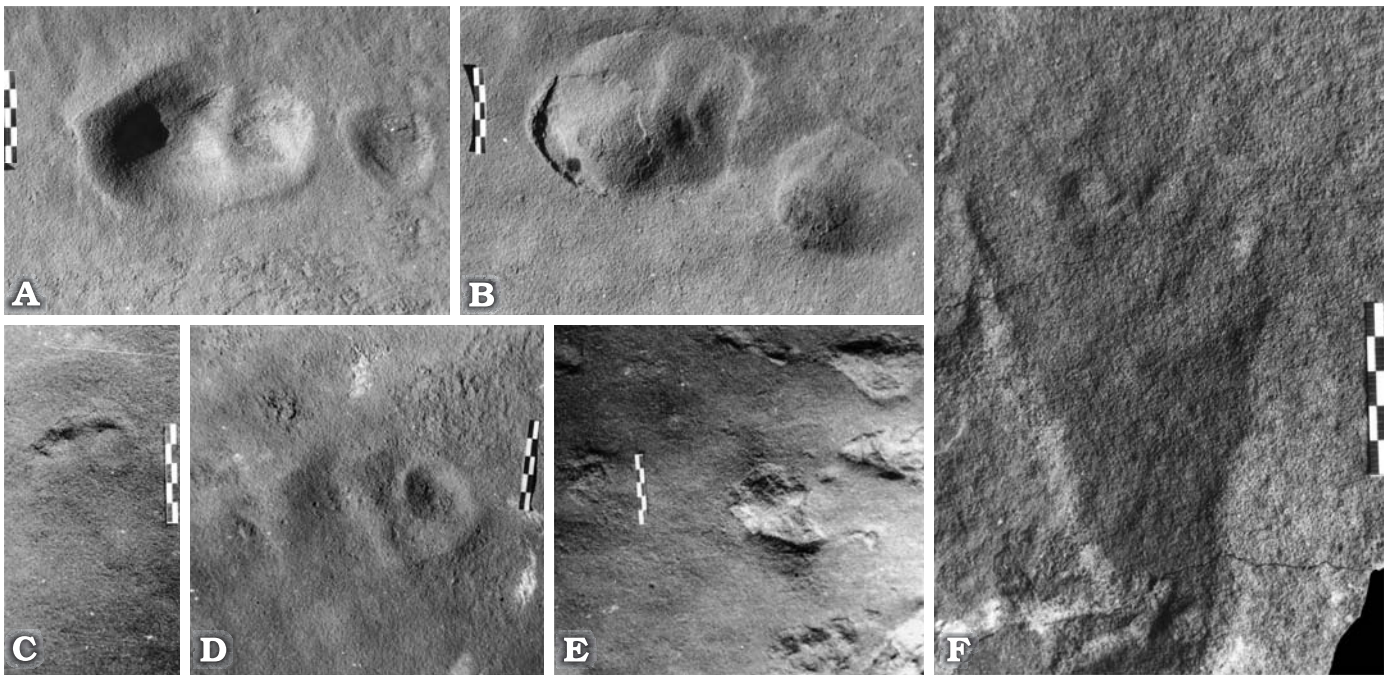

Fig. 4. *Limnopus* cf. *zeilleri* (Delage, 1912). **A**, **B**, **D**. Fragmentary imprints from the track bearing surface from the middle part of the Tumlin Gród quarry section (specimens not collected). **C**, **E**. Fragmentary imprints (only digit tips visible) from the upper part of the Tumlin Gród quarry section (specimens not collected). **F**. Muz. PIG OS-220/31B: 1 left manual imprint, natural cast of Muz. PIG OS-220/31A: 1. Scale bars 5 cm.

at about 100°. Digit tips are distinctly impressed, but no claw marks are discernible.

Manus.—Supposed manual imprints are somewhat smaller than pedal ones (Figs. $3C_3$, 5B). Manual digits I–IV increase in length, like in pedal ones. The manus is probably tetradactyl; digit V was not observed.

Remarks.—Lack of trackway features, incompleteness, poor preservation and uncertain number of manual digits make determination of these tracks somewhat difficult. Small size of imprints, their shape, angles between digits and digit length proportions allow determination of these footprints as representatives of *Batrachichnus* Woodworth, 1900. There are no visible differences between the imprints described above and specimens described by many authors as *Anthichnium salamandroides* or *Batrachichnus salamandroides*. Nevertheless, the material of very small footprints accounted to ichnogenera *Batrachichnus*, *Anthichnium*, *Saurichnites* and many others, often fragmentarily and poorly preserved, needs revision (see Holub and Kozur 1981, Fichter 1983a, Gand and Haubold 1988). Trackmakers of those footprints may represent different and systematically distant groups of animals.

Ichnogenus *Limnopus* Marsh, 1894
Limnopus cf. *zeilleri* (Delage, 1912)

Figs. 4A–F, 5A.

Material.—Muz. PIG OS-220/31A: 1, slab with moulds on the upper surface of the sandstone slab and Muz. PIG OS-220/31B: 1, with their natural casts showing left manual imprint, with other accompanying poorly preserved imprints (Figs. 4F, 5A); Muz. PIG OS-220/50: 1 isolated, poorly preserved (?) left pedal imprint. Many incompletely preserved, not catalogued and not numbered imprints (Fig. 4A–E) representing this ichnogenus have been found on two track-bearing surfaces in the upper and in the middle part of the Tumlin Gród quarry section.

Description.—Poorly preserved material did not allow recognition of any trackway pattern or even a fully impressed footprint, despite their common presence. Imprints are incomplete, composed mostly of the rounded imprints of digit tips preserved as concave, shallow hollows being concave moulds on the upper side of the layer, or natural casts on the bottom side (Fig. 4A–E). Digit tip imprints are differentiated in size, placed along arcs, showing no claw marks (Figs. 4A–F, 5A). Except for digit tips, other parts of imprints are usually not observed, except for the specimen Muz. PIG OS-220/31A: 1 and Muz. PIG OS-220/31B: 1, the mould and its natural cast (Figs. 4F, 5A), fully preserved manual imprint. This imprint shows the presence of only four digits. The rounded digit I tip imprint is the largest, about 20 mm in diameter. Other digit tip imprints are 11–14 mm. The width of the digit group I–IV is 87 mm; its length attains about 70 mm. In other, partial imprints on the same slab, the length of the arc formed by digit tips attains up to 100 mm. No metapodial joint has been observed.

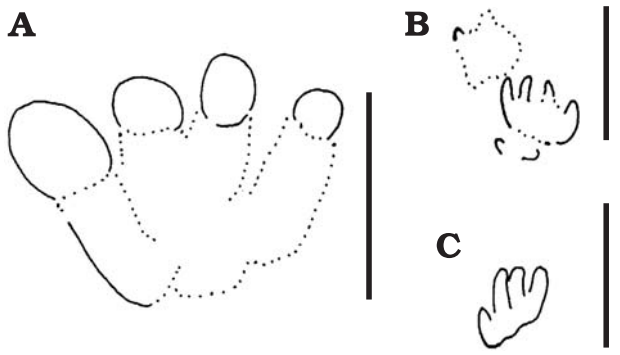

Fig. 5. **A**. *Limnopus* cf. *zeilleri* (Delage, 1912); Muz. PIG OS-220/31A: 1, left pedal imprint. **B**, **C**. *Batrachichnus* cf. *salamandroides* (Geinitz, 1861). **B**. Muz. PIG OS-220/44: 1, 2, right set of pedal and manual imprints. **C**. Muz. PIG OS-220/44: 3, left pedal (?) imprint. Scale bars: A, 5 cm; B, C, 2 cm.

Remarks.—The shape, size, mode of preservation, number of manual digits, rounded digit tips, lack of claw marks and the absence of a metapodial joint allow recognition of these footprints as amphibian *Limnopus* tracks. Similarly preserved tracks, often with enlarged I digit tip imprint (see Haubold 1971b: 17) of the same size and shape were observed in the Permian of France (Gand and Haubold 1984; Gand 1985, 1987, 1991, 1993; Demathieu et al. 1992; Gand et al. 1997), attributed mostly to the ichnospecies *Limnopus zeilleri* (Delage, 1912). Specimens from Tumlin Gród are similar to this ichnospecies and to *Limnopus* sp. representatives from Val Gardena Sandstone (Conti et al. 1977).

Ichnogenus *Amphisauropus* Haubold, 1970
Amphisauropus cf. *latus* Haubold, 1970

Figs. 6A–C, 7A–I, 8A–F.

Material.—Tumlin Gród quarry: Muz. PIG OS-220/26: 6, 7 two consecutive left pedal imprints (Figs. 7A, 8E); Muz. PIG OS-220/35: 1 left pedal imprint (Figs. 7B, 8A); Muz. PIG OS-220/37: 1 left pedal imprint (Fig. 7C); Muz. PIG OS-220/52: 1 left pedal imprint (Figs. 7D, 8B); Muz. PIG OS-220/34: 1–11 fragmentary trackway (Figs. 6C, $8F_2$); Muz. PIG OS-220/34: 20 complete pedal imprint with the next, but poorly preserved set of imprints (Figs. 6B, C, 7E, 8C); Muz. PIG OS-220/34: 12–19 fragmentary trackway (Figs. 6A; $8F_1$); Muz. PIG OS-220/36: 1–3 fragmentary trackway composed of left manual and next set of pedal and manual imprints (Figs. 7F, 8D); Muz. PIG OS-220/54: 12 right pedal imprint (Fig. 7G); Sosnowica Hill quarry: Muz. PIG OS-220/5A: 1, 2 left set of pedal and manual imprints (Fig. 6H); Muz. PIG OS-220/5B: 1 isolated, possibly manual imprint; Muz. PIG OS 220/11 left pedal imprint (Fig. 7I).

Description.—Trackway. Despite the relatively common presence of *Amphisauropus* imprints on some track-bearing surfaces, only poor and fragmentary, irregular trackways have been found (Figs. 6A–C, 8F). The trackway Muz. PIG OS-220/34: 2–11 shows the following pedal trackway features: stride length 290–310 mm; oblique pace 180–200 mm;

width of pace 110 mm; pace angulation 115°. Respective manual values are 290–320 mm, 200–230 mm, 150 mm and 83°. Pedal digit III diverges from the midline at about –20°. The stride exceeds the total pedal length (about 60 mm) approximately three times. Another fragmentary trackway: Muz. PIG OS-220/26: 6, 7 shows the pedal stride length of 250 mm with the stride to pedal length ratio 3.7. Digits III diverge from the midline at –14° and –9°. Poorly and only fragmentary preserved trackway: Muz. PIG OS-220/34: 12–19 (Figs. 6A, 8F$_1$) shows the following pedal trackway features: stride 195, 160 mm; oblique pace 145, 150, 150 mm; width of pace 118 mm; pace angulation 78°. The pedal width of the digit group I–IV is 49 mm; divarication of digit III from the midline equals –15°. The manual oblique pace in the specimen Muz. PIG OS-220/36: 1–3 attains 115 mm; digits III are inclined to the midline at +25° on average.

Pes.—Both pes and manus are pentadactyl, similar in shape and show no visible metapodial articulations. Even in deep imprints digit tips are usually distinctly rounded (Fig. 7D, F, I) or if somewhat sharpened in shape (Fig. 7A, C, G), show no presence of claw marks. Pedal imprints are relatively wide. Their total length ranges from about 40 mm (specimens Muz. PIG OS-220/35: 1 and Muz. PIG OS-220/11; Fig. 7B, I), 50 mm (specimen Muz. PIG OS-220/36: 2; Fig. 7F) up to 68 mm (Muz. PIG OS-220/26: 7; Fig. 7A). Their total width ranges from 45 to 60 mm, somewhat less than the length. In measured footprints, the digit group I–IV is 37–52 mm long and 38–45 mm wide. The length of digits I–IV increases from I to IV: 18–25, 22–28, 27–35, and 30–38 mm, respectively. Digits I–IV diverge at 30–54°. Digit V is directed somewhat laterally and posteriorly from the digit group I–IV (Fig. 7A, C–G). Divarication of digits I–V varies from 70° up to 92°. Digit V is relatively long, may be longer than digit IV (in specimen Muz. PIG OS-220/26: 7 it's length is 41 mm). Shallow imprints show only proximal digit end imprints (Fig. 7B, D, E); in deep ones is visible also a sole, being long as like as the palm (Fig. 7C, E–G).

Manus.—Manual imprints are similar in shape to pedal ones being somewhat smaller, and therefore difficult to distinguish in isolated imprints (Fig. 7F, H). Digit lengths increase, as with pedal imprints from I to IV; digit III may be equal to digit IV (specimen Muz. PIG OS-220/5A: 2, Fig. 7H). Digits I–V in the well and completely preserved specimen Muz. PIG OS-220/36: 3 (Figs. 7F, 8D) are 12, 17, 19, and 21 mm long (respectively) being only somewhat shorter than respective pedal ones: 21, 23, 26, 27, and 28 mm. The whole manual imprint of this set is 32 mm long by 47 mm wide, and its digit group I–IV is 30 mm long and 35 mm wide. Divarications of digit axes I–IV and I–V attain 65 and 125°, respectively.

Remarks.—*Amphisauropus latus* Haubold, 1970 is possibly a younger synonym of "*Ichnium" pachydactylum* Pabst, 1900 and "*Saurichnites" intermedius* Fritsch, 1895 (see Haubold 1971a; Holub and Kozur 1981). Revision of all the synonymy concerning this ichnotaxon exceeds the scope of this present work.

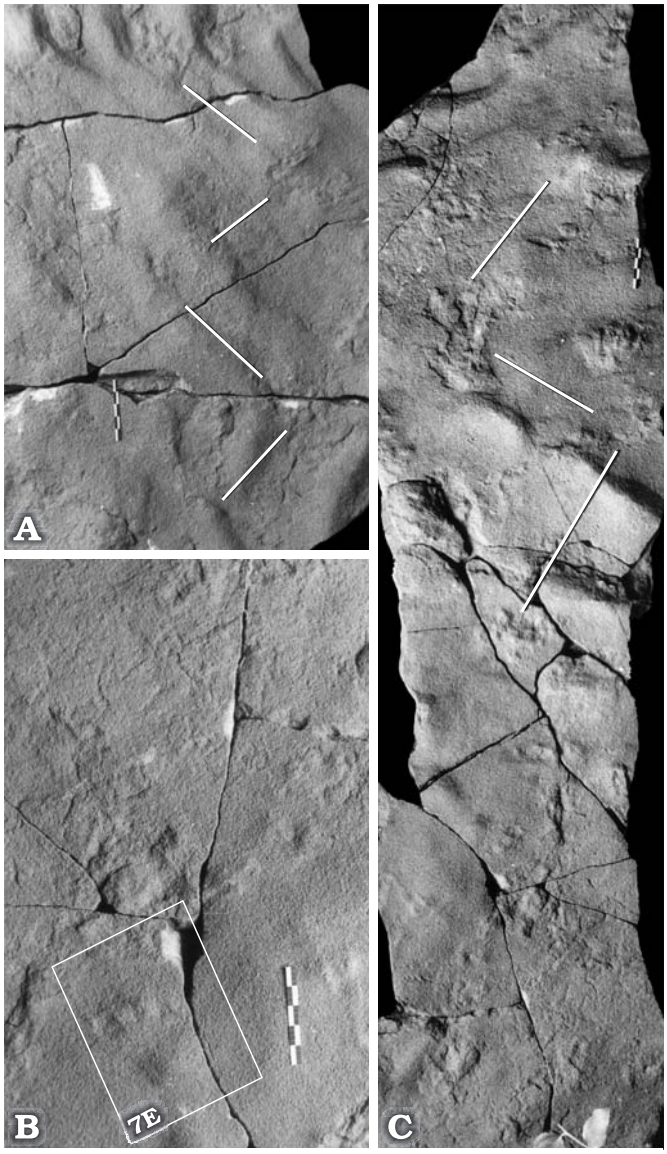

Fig. 6. *Amphisauropus* cf. *latus* Haubold, 1970. **A**. Muz. PIG OS-220/34: 12–19 poorly preserved trackway. **B**. Muz. PIG OS-220/34: 20 complete pedal imprint with the consecutive next, poorly preserved set of imprints. **C**. Muz. PIG OS-220/34: 2–11 fragmentary trackway. Scale bars 5 cm.

Reptilian ichnotaxa

Ichnofamily Rhynchosauroidae Haubold, 1966

Small and middle sized tracks of lacertoid animals. Pedal pace width is usually larger than manual one. Pedal pace angulation ranges from about 70° up to 135°. Manual imprints are situated variously in relation to pedal ones: in front, at the same line, or may be overstepped by them, depending on the speed of movement. Both pes and manus have five, clawed digits. Digits V are situated laterally and somewhat posteriorly to the group I–IV. The size and shape of pedal

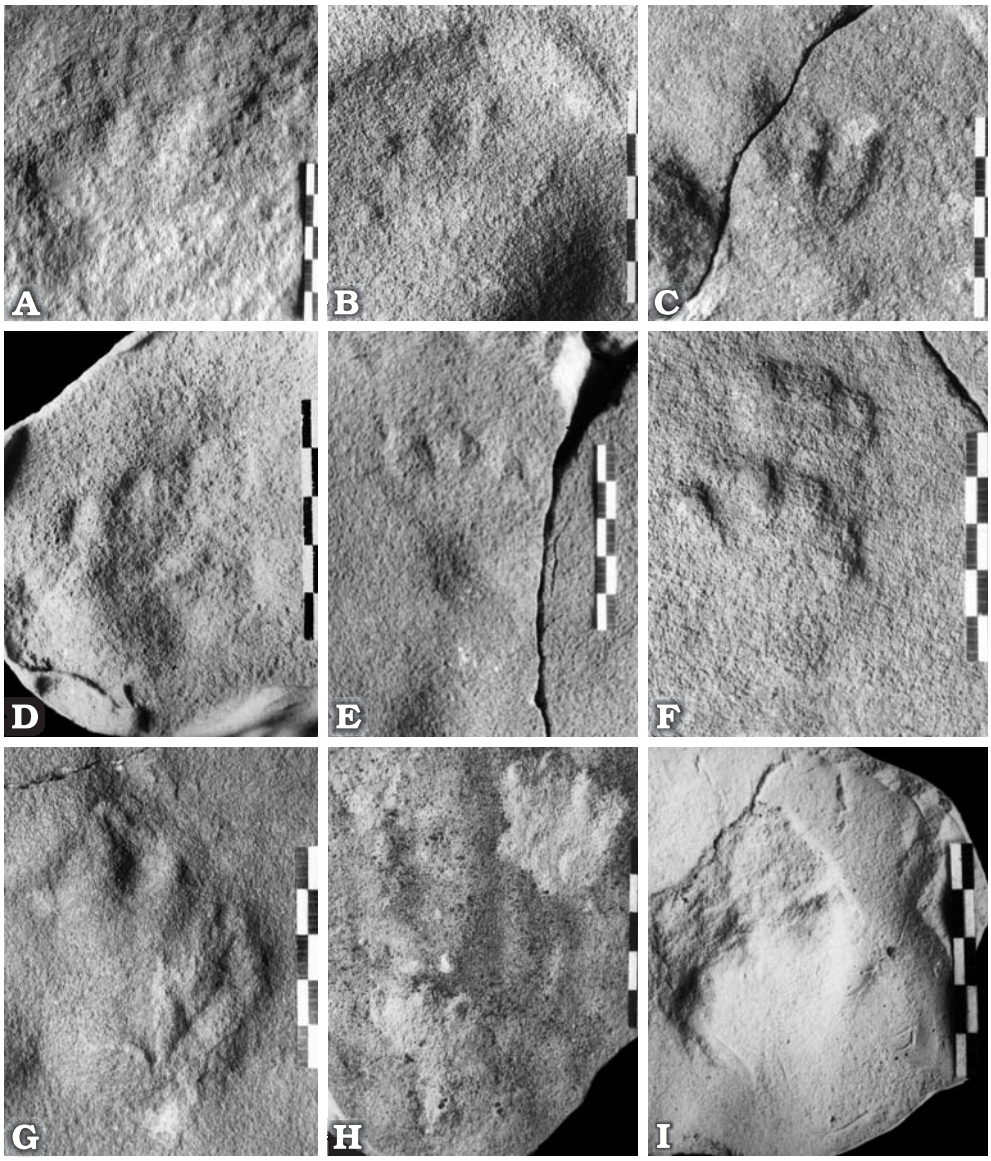

Fig. 7. *Amphisauropus* cf. *latus* Haubold, 1970. **A**. Muz. PIG OS-220/26: 7 left pedal imprint. **B**. Muz. PIG OS-220/35: 1, left pedal imprint. **C**. Muz. PIG OS-220/37: 1 left pedal imprint. **D**. Muz. PIG OS-220/52: 1 right pedal imprint. **E**. Muz. PIG OS-220/34: 20 right pedal imprint. **F**. Muz. PIG OS-220/36: 2, 3 set of right pedal and manual imprints. **G**. Muz. PIG OS-220/54: 12 right pedal imprint. **H**. Muz. PIG OS-220/5A: 1, 2 set of left pedal and manual imprints (plaster cast). **I**. Muz. PIG OS-220/11 left pedal imprint (plaster cast). Scale bars 5 cm.

and manual imprints are differentiated. Pedal imprints are narrow, digitigrade. Digits I–IV increase in length from I to IV; III and IV may be equal in length. The digit V may be as long as digit III (*Rhynchosauroides, Paradoxichnium*) or much shorter (*Phalangichnus*). Manual imprints are more plantigrade, with digit I–IV length ratios similar to pedal ones. Digits I and V may be absent from shallow tracks.

The ichnofamily Rhynchosauroidae includes ichnogenera: *Rhynchosauroides* Maidwell, 1911; *Paradoxichnium* Müller, 1959; *Palmichnus* Schmidt, 1959; *Phalangichnus* Schmidt, 1959; *Dromopus* Marsh, 1894.

Remarks.—Ichnofamily Rhynchosauroidae was described as monogeneric, comprising lacertoid footprints derived at first from Triassic sediments. Later, representatives of the ichnogenus *Rhynchosauroides* were found in the Upper Permian Val Gardena Sandstone (Conti et al. 1977; Ceoloni et al. 1988). The ichnogenera: *Paradoxichnium* Müller, 1959; *Palmichnus* Schmidt, 1959 and *Phalangichnus* Schmidt, 1959 have been documented from the latter, Cornberg Sandstone and "Terrestrischer Zechstein" (Müller 1959). These ichnogenera resemble *Rhynchosauroides*, showing varied situation of manual and pedal imprints in trackways and differentiated pedal and manual pace width. This ichnofamily may also include the questionable and poorly documented (see Haubold et al. 1995; Haubold 1996; Haubold and Stapf 1998) and therefore problematic ichnogenus *Anhomoiichnium* Dozy, 1935.

We regard the trackmakers of those ichnogenera as taxonomically close animals and agree with suggestion of Haubold (1971b), that they all represent lacertoid type of imprints.

The problem of formal presence of lacertoid vertebrate ichnogenera *Palmichnus* and *Phalangichnus* (compare: Haubold et al. 1995; Haubold 1996; McKeever and Haubold 1996; Haubold and Stapf 1998) in the ichnological nomenclature should be once again revised with support of existing materials and new finds from the Holy Cross Mountains. Un-

satisfactory preservation (lack of details) in many cases makes their precise recognition impossible. Possibly many of specimens assigned to the ichnogenus *Chelichnus* (in the sense of Haubold et al. 1995; Haubold 1996; McKeever and Haubold 1996; Haubold and Stapf 1998) have been made by Rhynchosauroidae trackmakers.

We suggest also a reinterpretation of *Phalangichnus simulans* Schmidt, 1959 and *P. perwangeri* Conti et al., 1977. Both trackway descriptions are based on poorly preserved material made, possibly, by more than one trackmaker, and therefore trackway features of these ichnospecies have been erroneously interpreted.

Here we accept the existing formal nomenclature of ichnogenera *Paradoxichnium* Müller, 1959; *Palmichnus* Schmidt, 1959 and *Phalangichnus* Schmidt, 1959.

Ichnogenus *Rhynchosauroides* Maidwell, 1911

Remarks.—From the Late Permian deposits there are two similar ichnospecies that are described as typical *Rhynchosauroides* representatives: *Rhynchosauroides pallinii* Conti et al., 1977 and *Rhynchosauroides kuletae* ichnosp. nov. Specimens from the Val Gardena Sandstone attributed to the ichnospecies *R. palmatus* (Lull, 1942) by Conti et al. (1977) may represent *Varanopus* aff. *microdactylus* (Pabst, 1896) described below. The ichnofaunal list from Val Gardena Formation (Ceoloni et al. 1988) also contains *Rhynchosauroides schochardti* (Rühle von Lilienstern, 1939).

Rhynchosauroides kuletae ichnosp. nov.

Figs. 9A–C, 10A–D, 11A, B, 12A–D.

Rhynchosauroides cf. *pallinii* Conti et al., 1977; Ptaszyński 2000b: fig. 2, trackway described in this paper as Muz. PIG OS-220/26: 1–5.

Holotype. Set of left pedal and manual imprints Muz. PIG OS-220/27: 11, 12 (Figs. $9A_1$, $10\ A_1$, $11A_1$, $12A_1$).

Type locality: Tumlin Gród quarry, 11 km NW of Kielce, Holy Cross Mts., Poland.

Other localities: Sosnowica Hill quarry, 8 km N of Kielce, Holy Cross Mts., Poland.

Type horizon: Tumlin beds, Lower Buntsandstein, uppermost Permian.

Derivation of the name: In honour of Maria Kuleta, researcher and expert of the Holy Cross Mountains Buntsandstein lithostratigraphy and sedimentary environment.

Material.—Tumlin Gród quarry: Muz. PIG OS-220/26: 1–5 trackway consist of two sets and the next consecutive manual imprint; Muz. PIG OS-220/27: 1–14 seven sets of imprints (Figs. $9A_1$, $10A_1$, A_2, $11A_1$, $12A_1$), among them the fifth, left set of pedal and manual imprints (Muz. PIG OS-220/27: 11, 12 is designated as the holotype); Muz. PIG OS-220/27: 15–31 nine consecutive sets of imprints (Figs. $9A_2$, $10A_3$, A_4, $11A_2$, $12A_3$); Muz. PIG OS-220/27: 119–136 nine consecutive sets of imprints; Muz. PIG OS-220/28: 1–11 six consecutive sets of imprints, the second represented only by manual imprint (Figs. 9B, 10C, 11B, 12B); Muz. PIG OS-220/29: 1 isolated left pedal imprint; Muz. PIG OS-220/73: 1–26 eleven consecutive sets of pedal and manual imprints (Figs. 9C, $12C_2$); Muz. PIG OS-220/73: 27–31 three consecutive sets of pedal and manual imprints; Muz. PIG OS-220/73: 88, 89 set of right pedal and manual imprints, the largest specimen accounted to this ichnospecies (Figs. 10B, $12C_1$); Muz. PIG OS-220/73: 33–38 three consecutive sets of imprints; Muz. PIG OS-220/73: 39–41 right pedal imprint and the next (left) set of imprints; Muz. PIG OS-220/27: 76, 77 isolated set of right pedal and manual imprints (Fig. $12A_2$); Muz. PIG OS-220/27: 84, 85 isolated set of imprints; Muz. PIG OS-220/27: 78, 79 isolated set of imprints. Sosnowica Hill quarry: Muz. PIG OS-220/1 set of right pedal and manual imprints; Muz. PIG OS-220/6: 1, 2 set of left pedal and manual imprints (Figs. 10D, 12D).

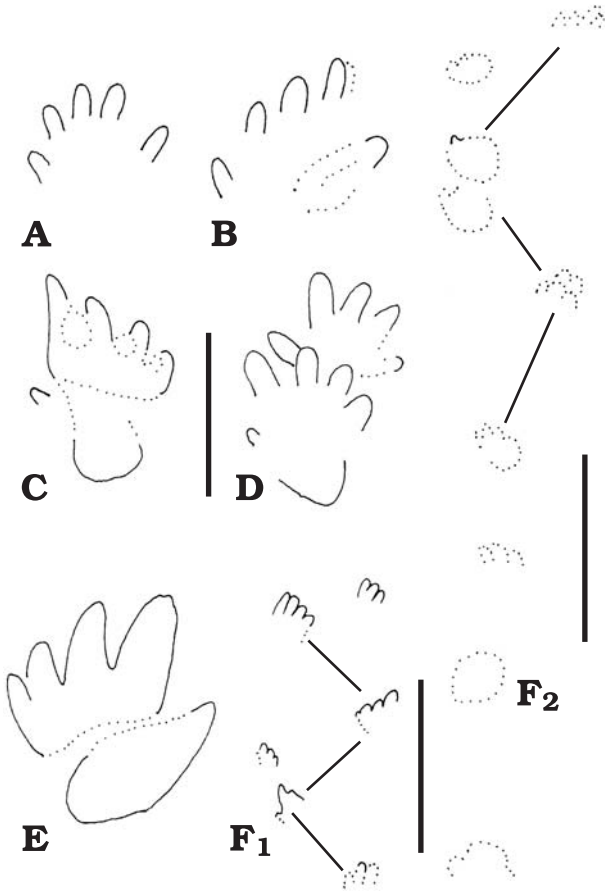

Fig. 8. *Amphisauropus* cf. *latus* Haubold, 1970. **A**. Muz. PIG OS-220/35: 1 left pes imprint. **B**. Muz. PIG OS-220/52: 1 right pedal imprint. **C**. Muz. PIG OS-220/34: 20 right pedal imprint. **D**. Muz. PIG OS-220/36: 2, 3 set of right pedal and manual imprints. **E**. Muz. PIG OS-220/26: 7 left pedal imprint. $\mathbf{F_1}$. Muz. PIG OS-220/34: 12–19 fragmentary trackway. $\mathbf{F_2}$. Muz. PIG OS-220/34: 4–11 fragmentary trackway. Scale bars: A–E, 5 cm; F, 20 cm.

Diagnosis.—Large *Rhynchosauroides* with a total pedal length of about 60 mm. Pedal pace angulation ranges from about 100° up to 111–116°. Both pedal and manual digit V is relatively long and distinct. The pedal axis diverges from the midline at –4°, while manual one is inclined to the midline at about +23°. Divarication of manual digits I–V about 90°. The stride/pedal length ratio attains 7.2.

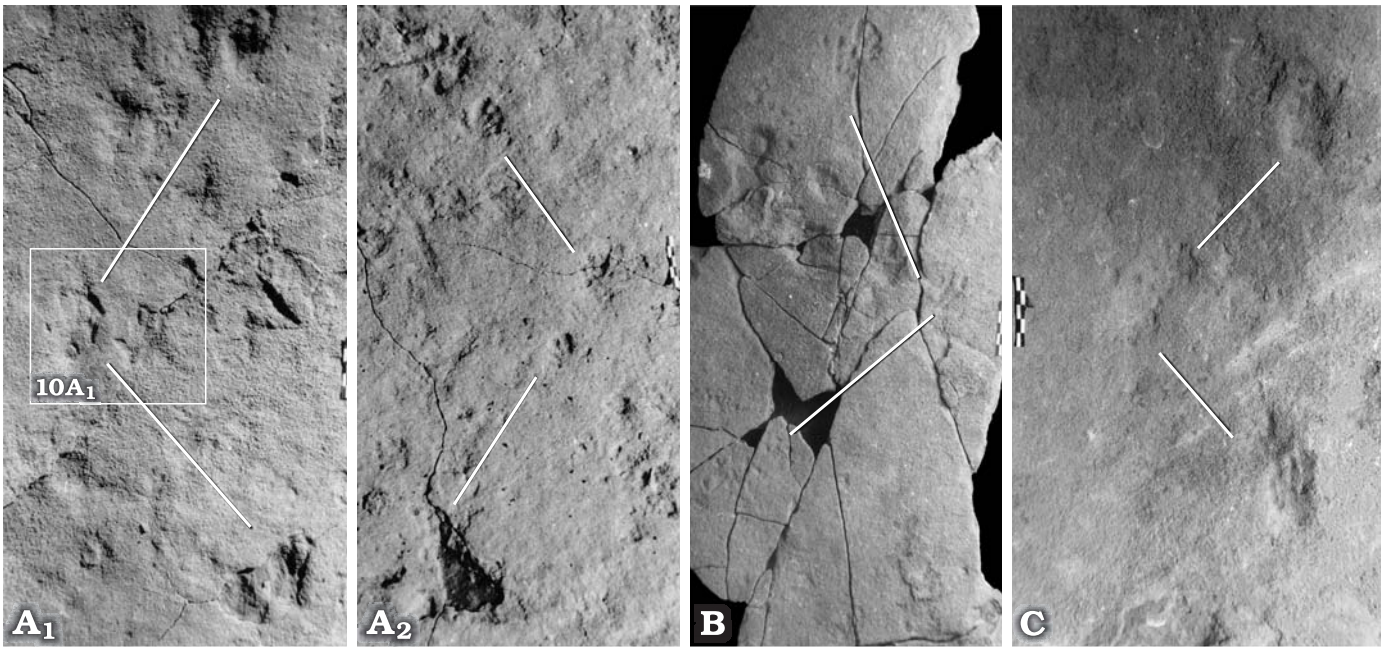

Fig. 9. *Rhynchosauroides kuletae* ichnosp. nov. **A$_1$**. Muz. PIG OS-220/27: 9–14 trackway; the second set is designed as the holotype. **A$_2$**. Muz. PIG OS-220/27: 17–21 trackway. **B**. Muz. PIG OS-220/28: 4–11 four consecutive sets of imprints. **C**. Muz. PIG OS-220/73: 1–6 trackway. Scale bars 5 cm.

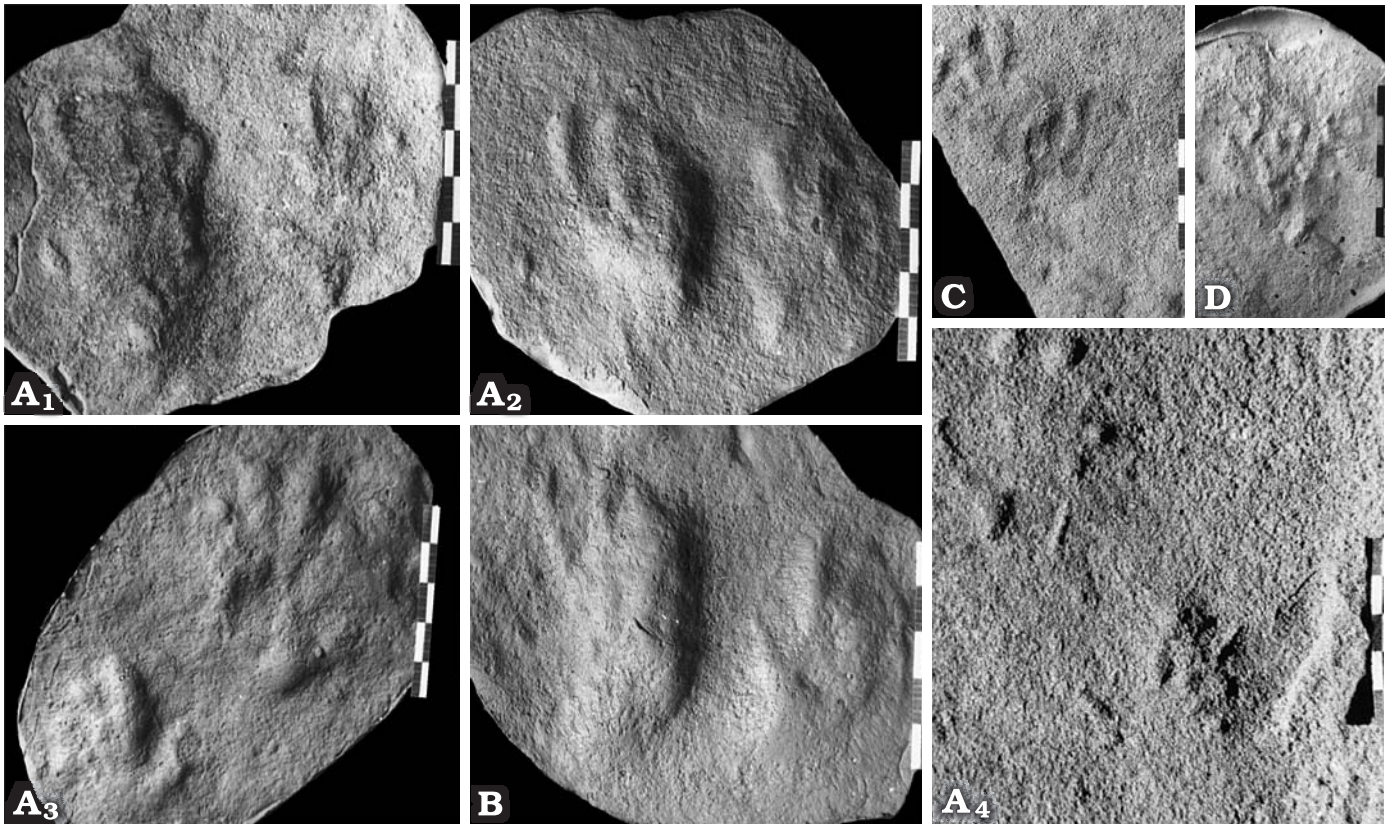

Fig. 10. *Rhynchosauroides kuletae* ichnosp. nov. **A$_1$**. Muz. PIG OS-220/27: 11, 12 set of left pedal and manual imprints, holotype. **A$_2$**. Muz. PIG OS-220/27: 13, 14 set of right pedal and manual imprints. **A$_3$**. Muz. PIG OS-220/27: 20, 21 set of left pedal and manual imprints. **A$_4$**. Muz. PIG OS-220/27: 30, 31 set of left pedal and manual imprints. **B**. Muz. PIG OS-220/73: 88, 89 set of right pedal and manual imprints. **C**. Muz. PIG OS-220/28: 1, 2 set of right pedal and manual imprints. **D**. Muz. PIG OS-220/6: 1, 2 set of left pedal and manual imprints. Scale bars 5 cm.

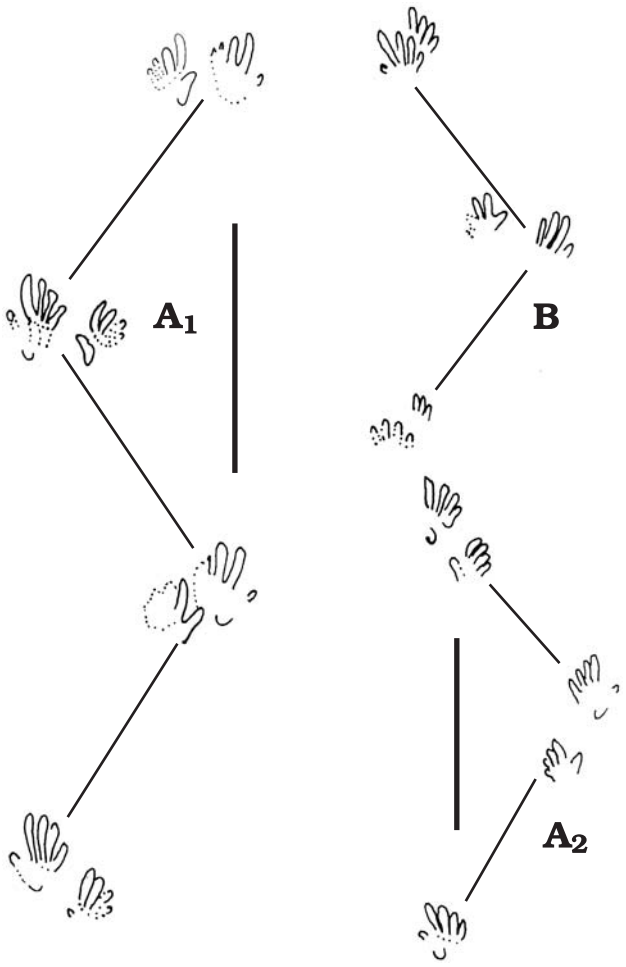

Fig.11. *Rhynchosauroides kuletae* ichnosp. nov. **A_1**. Muz. PIG OS-220/27: 7–14 trackway; the third set is designed as the holotype. **A_2**. Muz. PIG OS-220/27: 17–21 trackway. **B**. Muz. PIG OS-220/28: 6–11 trackway. Scale bars 20 cm.

Description.—Trackway. Trackway features typical of the ichnogenus *Rhynchosauroides*. The relative position of manus and pes in the same set varies in known trackways. Pedal imprints may distinctly overstep manual ones (Muz. PIG OS-220/27: 15–31); both may be on the same line (Muz. PIG OS-220/27: 1–14, Figs. $9A_1$, $11A_1$) or manual imprints may be situated before pedal ones (Muz. PIG OS-220/28: 1–11, Figs. 9B, 11B); Muz. PIG OS-220/73: 1–26, Fig. 9C). Pedal axes diverge slightly from the midline at about –4° on average; the average inclination to the midline of manual axes is +23°. The length of stride ranges from 340 mm up to 447 mm. In all known trackways pedal and manual pace angulation attain 100–116° and 117–153°, respectively. The stride/pedal length ratio is high, up to 7.2.

Pes.—The length of pedal imprints is about 60 mm. The largest known specimen shows a pes length of about 65 mm (Muz. PIG OS-220/73: 88, 89, Figs. 10B, $12C_1$). There are specimens from Sosnowica Hill quarry (Muz. PIG OS-220/1: 1, 2 and Muz. PIG OS-220/6: 1, 2; Figs. 10D, 12D) with pedal imprints only 40 mm long. The digit group I–IV is relatively short and wide, with typical digit length ratios of *Rhynchosauroides*, I<II<III<IV: 23, 29, 32, and 34 mm in the holotype. Divarications of digits II–IV and I–IV are 22 and 33° on average, respectively. The digit V, distinctly visible in most of known specimens (Figs. 10A, B, D, 12A, B, C_1, D), as long as digit III or IV, diverges from digit I at about 64°. Deep imprints show its whole shape, as like as the whole pedal imprint; in some shallower imprints only a proximal, rounded pad and the distal part of the digit, with a distinct, big claw mark is visible (Figs. $10A_1$, A_2, A_4, $12A_1$–A_3).

Manus.—Manual imprints are relatively large (Figs. $10A_1$, B, C, $12A_1$, A_2, B, C_1). Digits I–IV increase in length from I to IV: 14, 21, 24, 28 mm in the holotype. The digit group I–IV is 32.4 mm long by 34.1 mm wide, on average. Digit V is as long as digit III, diverge from digit I at 75–90°; this value does not exceed the right angle. All digits have claw marks.

Discussion.—*Rhynchosauroides kuletae* ichnosp. nov. shows similarity to *Rhynchosauroides pallinii* Conti et al., 1977, and is also of the same size. *Rhynchosauroides kuletae* ichnosp. nov. however differs from the latter as it has higher pace angulation and a relatively bigger digit V, both in pedal and

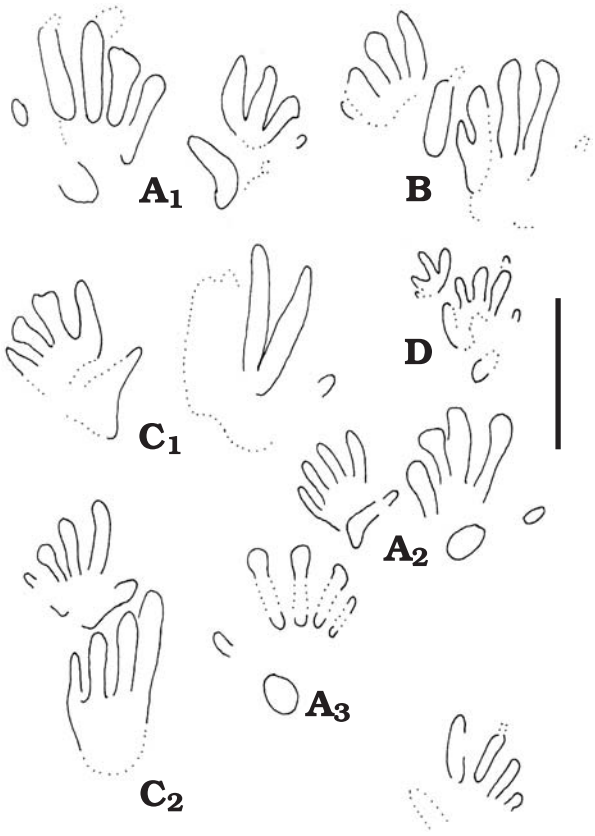

Fig. 12. *Rhynchosauroides kuletae* ichnosp. nov. **A_1**. Muz. PIG OS-220/27: 11, 12 set of left pedal and manual imprints, holotype. **A_2**. Muz. PIG OS-220/27: 76, 77 set of right pedal and manual imprints. **A_3**. Muz. PIG OS-220/27: 30, 31 set of left pedal and manual imprints. **B**. Muz. PIG OS-220/28: 1, 2 set of right pedal and manual imprints. **C_1**. Muz. PIG OS-220/73: 88, 89 set of right pedal and manual imprints. **C_2**. Muz. PIG OS-220/73: 7, 8 set of right pedal and manual imprints. **D**. Muz. PIG OS-220/6: 1, 2 set of left pedal and manual imprints. Scale bar 5 cm.

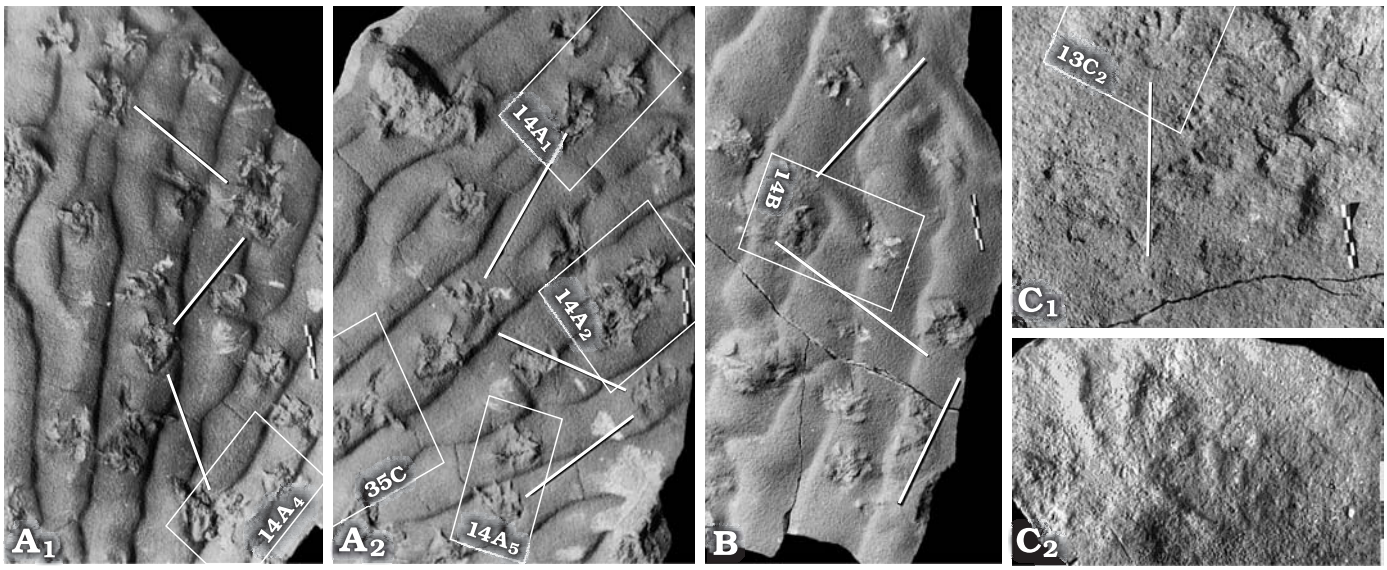

Fig. 13. *Palmichnus lacertoides* ichnosp. nov. **A_1**. Muz. PIG OS-220/55: 1–7 trackway with the holotype, Muz. PIG OS-220/55: 6, 7. **A_2**. Muz. PIG OS-220/55: 8–14 trackway. **B**. Muz. PIG OS-220/54: 1–7 trackway, other isolated sets of imprints Muz. PIG OS-220/54: 8, 9 and Muz. PIG OS-220/55: 10, 11 are also visible. **C_1**. Muz. PIG OS-220/27: 32, 33, and 34, 35 two sets of right pedal and manual imprints. **C_2**. Muz. PIG OS-220/27: 34, 35 set of right pedal and manual imprints. Scale bars 5 cm.

manual imprints. Its manual digit V diverges from the digit IV at smaller angle, being perpendicular not to the digit IV as in *R. pallinii,* but to digit I.

Ichnogenus *Palmichnus* Schmidt, 1959

Remarks.—Medium-sized Rhynchosauroidae representatives. The manual pace width is close to the pedal one. Pace angulation about 90° or more. Manual imprints situated before those of pes or on the same line. The pedal digit V is as long as digit III. In both pedal and manual imprints digits diverge at high angles; that of digits I–V attains 90° in pedal imprints and much more in those of manus. Stride/pedal length ratio is relatively low, and does not exceed 5. Except for *Palmichnus tambachensis* Haubold, 1970 considered (Haubold 1998) as synonym of *Varanopus microdactylus*, there are only two known ichnospecies representing this ichnogenus: *Palmichnus renisus* Schmidt, 1959 and *Palmichnus lacertoides* ichnosp. nov.

Palmichnus lacertoides ichnosp. nov.

Figs. 13A–C, 14A–C, 15A–C, 16A–D, 34C_1, 35B, C.

Palmichnus sp. Ptaszyński 2000b: fig. 4 (upper part of the photograph), specimens described in this paper as Muz. PIG OS-220/33: 5–8 fragmentary trackway.

Holotype: Muz. PIG OS-220/55: 6, 7 right pedal and manual imprints (Figs. 13A_1, 14A_1, 15A, 16A_2).

Type locality: Tumlin Gród quarry, 11 km NW of Kielce, Holy Cross Mts., Poland.

Type horizon: Tumlin beds, Lower Buntsandstein, uppermost Permian.

Derivation of the name: After the similarity of pedal imprints to *Rhynchosauroides* representatives.

Material.—Muz. PIG OS-220/54: 1–7 four consecutive (partly incomplete) sets of pedal and manual imprints (Fig. 13B); Muz. PIG OS-220/54: 8, 9 isolated set of right pedal and manual imprints (Fig. 13B); Muz. PIG OS-220/54: 10, 11 isolated set of right pedal and manual imprints (Figs. 13B, 14B, 16B); Muz. PIG OS-220/55: 1–7 trackway consist of four consecutive sets of pedal and manual imprints (Figs. 13A_1, 14A_1, A_2, A_4, 15A, 16A_1, A_2, A_4); the fourth set of them, Muz. PIG OS-220/55: 6, 7 right pedal and manual imprints are designed as the holotype (Figs. 14A_1, 16A_2); Muz. PIG OS-220/55: 8–14 four (partly incomplete) sets of pedal and manual imprints (Figs. 13A_2, 14A_5, 15B, 16A_5); Muz. PIG OS-220/55: 15–20 three sets (Figs. 15C, 16A_3); Muz. PIG OS-220/55: 21–25 three sets of pedal and manual imprints (Fig. 14A_3); Muz. PIG OS-220/55: 26–31 (Fig. 35C); Muz. PIG OS-220/56: 1–4 and Muz. PIG OS-220/56: 5–7 fragmentary trackways; Muz. PIG OS-220/27: 32, 33 and 34, 35 two consecutive right sets of pedal and manual imprints (Figs. 13C, 16C); Muz. PIG OS-220/33: 5–8 fragmentary trackway (Ptaszyński 2000b: fig. 4, upper part of the photograph); Muz. PIG OS-220/29: 2, 3 left and right, isolated pedal imprints (Figs. 14C, 16D); Muz. PIG OS-220/39: 7–12 three consecutive sets of imprints (Fig. 34C_1). Many other isolated imprints occur on slabs Muz. PIG OS-220/54, Muz. PIG OS-220/55, Muz. PIG OS-220/56, Muz. PIG OS-220/57, Muz. PIG OS-220/58, Muz. PIG OS-220/59, Muz. PIG OS-220/60 and Muz. PIG OS-220/72 from the same footprint-bearing surface with mass occurrence of *Palmichnus lacertoides* ichnosp. nov. Other, isolated or poorly preserved, unnumbered specimens were found on slabs Muz. PIG OS-220/27, Muz. PIG OS-220/28, Muz. PIG OS-220/73 and Muz. PIG OS-220/28.

Diagnosis.—Middle sized *Palmichnus* with manual imprints strongly inclined towards the midline; manual pace width slightly narrower than pedal width.

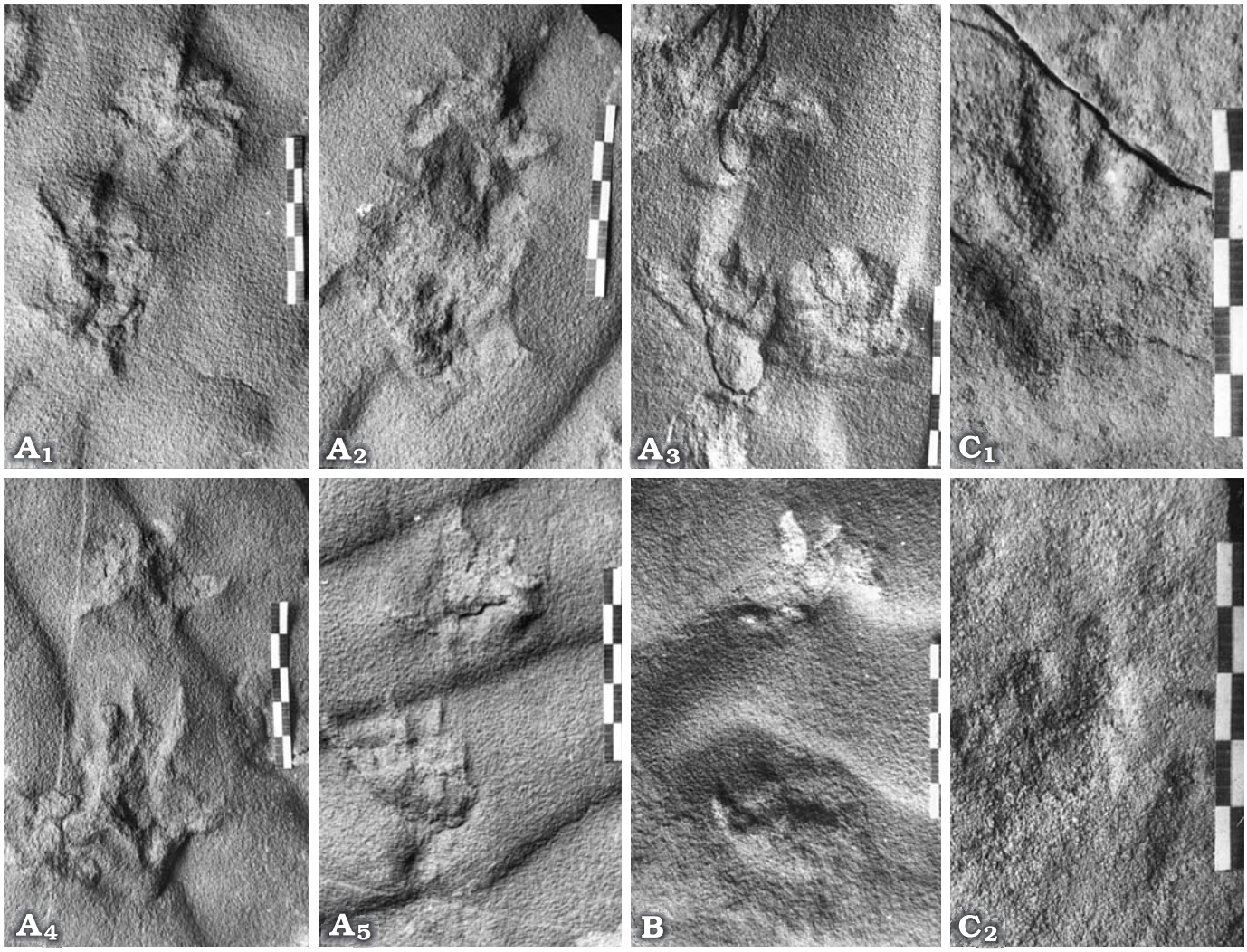

Fig. 14. *Palmichnus lacertoides* ichnosp. nov. **A_1**. Muz. PIG OS-220/55: 6, 7 set of right pedal and manual imprints, holotype. **A_2**. Muz. PIG OS-220/55: 4, 5 set of left pedal and manual imprints. **A_3**. Muz. PIG OS-220/55: 23, 24 set of right pedal and manual imprints. **A_4**. Muz. PIG OS-220/55: 1, 2 set of left pedal and manual imprints. **A_5**. Muz. PIG OS-220/55: 8, 9 set of right pedal and manual imprints. **B**. Muz. PIG OS-220/54: 10, 11 set of right pedal and manual imprints. **C_1**. Muz. PIG OS-220/29: 2 left, isolated pedal imprint. **C_2**. Muz. PIG OS-220/29: 3 right isolated pedal imprint. Scale bars 5 cm.

Description.—Trackway. In all known trackways manual imprints are situated more or less before pedal ones (Figs. 13A, B, 15A–C, 34C_1), or almost on the same line (Muz. PIG OS-220/27: 32–35, Figs. 13C, 16C) but have never been observed overstepped by them. The pedal pace width is only somewhat greater than manual one, which causes similar pace angulation angle. The direction of trackway Muz. PIG OS-220/55: 1–7, containing the holotype (Muz. PIG OS-220/55: 6, 7) is slightly turned right (Figs. 13A_1, 15A), therefore pedal pace angulation about 120 and 88° and manual ones about 94°. The same concerns partly other pedal trackway features: stride 275, 230 mm; oblique pace 170, 160, 175 mm; width of pace 97, 80 mm and manual ones: stride 290 mm; oblique pace 170 mm; width of pace 107 mm. In the trackway representing slow gait, Muz. PIG OS-220/55: 8–14 (Figs. 13A_2, 15B) the pedal pace width: 145–130 mm clearly exceeds manual one: 110 mm. The pedal digit III is inclined somewhat out the midline at –3 to –10°. The inclination of manual axes to the midline attains +25° up to +56°. The precise measurement of its value is impossible because of their strong bend inward the trackway. In sets Muz. PIG OS-220/27: 32, 33, and 34, 35 the inclination of manual digit III does not exceed +8°, but the trackway is only fragmentary (Figs. 13C_1, 16C).

In all measured trackways, pedal stride varies between 170 and 275 mm, oblique pace attains 145 to 180 mm; width of pace 80–145 mm; 88–120°. These respective manual values are 215–290 mm; 150–170 mm; 107–110 mm and 80–103°. The stride/pedal length ratio is about 4.2.

Pes.—Pedal imprints are 55 mm long (holotype) and 44 mm wide. Digit V, in many imprints, is relatively strongly impressed (Figs. 14A_1, A_4, C, 16A_1, A_2, A_4, C, D_1), is as long as digit III, diverging from digit I at a relatively high angle, about 78–85°. In digit group I–IV, 37 mm long and 35 mm wide, digits I–IV diverge of about 40°; that value of digits II–IV attains 30–35°. Digits I–IV increase in length from I to

IV attaining about 18, 22, 29, and 32 mm, respectively. Specimen Muz. PIG OS-220/27: 33 shows the lengths of digits I–IV: 18, 23, 26, 30 mm and the divarication of digits I–IV: 44°. All digits from this group have distinct claw marks. In many of imprints, even completely preserved, the sliding movement of digit tips causes their imprints to be more parallel or elongated than on an ever surface (Fig. 14A$_4$).

Manus.—Manual imprints are the most characteristic of this ichnospecies, 34 mm long and 35 mm wide. The length of digits I–IV increases (in the holotype) from I to IV: 15, 18, 19, 23 mm (respectively), in most cases deformed by the sliding movement. Digit V at 22 mm is as long as digit IV. Divarication of manual digits I–V is very high, ranging from 135 to 155°, much more than in other ichnospecies found at Tumlin Gród (Figs. 14A, B, 16A$_1$–A$_3$, A$_5$, B, C). This feature in clearly impressed specimen Muz. PIG OS-220/27: 35 equals 125°. This imprint shows digit lengths increasing from I to V: 11, 14, 16, and 19 mm, and divarications I–IV: 65°; I–V: 127°; II–IV: 35°.

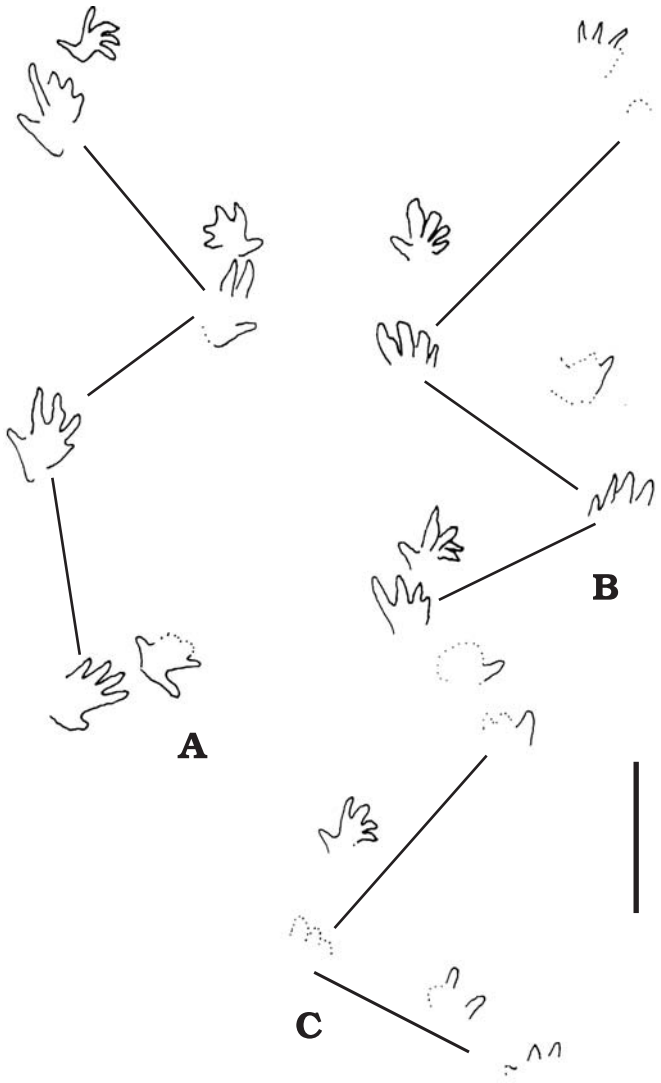

Fig. 15. *Palmichnus lacertoides* ichnosp. nov. **A**. Muz. PIG OS-220/55: 1–7 trackway with the holotype, Muz. PIG OS-220/55: 6, 7. **B**. Muz. PIG OS-220/55: 8–14 trackway. **C**. Muz. PIG OS-220/55: 15–20 trackway. Scale bar 10 cm.

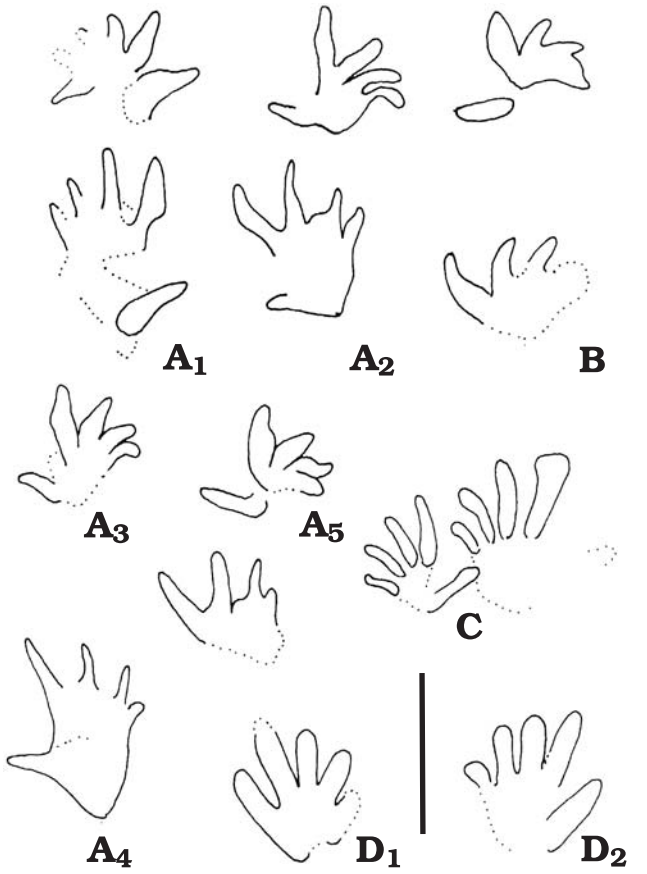

Fig. 16. *Palmichnus lacertoides* ichnosp. nov. **A$_1$**. Muz. PIG OS-220/55: 1, 2 set of left pedal and manual imprints. **A$_2$**. Muz. PIG OS-220/55: 6, 7 set of right pedal and manual imprints; holotype. **A$_3$**. Muz. PIG OS-220/55: 18 isolated right manual imprint. **A$_4$**. Muz. PIG OS-220/55: 7 right pedal imprint. **A$_5$**. Muz. PIG OS-220/55: 8, 9 set of right pedal and manual imprints. **B**. Muz. PIG OS-220/54: 10, 11 set of right pedal and manual imprints. **C**. Muz. PIG OS-220/27: 34, 35 set of right pedal and manual imprints. **D$_1$**. Muz. PIG OS-220/29: 2 isolated left pedal imprint. **D$_2$**. Muz. PIG OS-220/29: 3 right pedal imprint. Scale bar 5 cm.

Discussion.—*Palmichnus lacertoides* ichnosp. nov. differs distinctly in size from *P. renisus* by having a smaller manual pace width than pedal width and a strong inclination of manual axis to the midline. Other, smaller ichnospecies, *Palmichnus tambachensis* was recognised by Haubold (1998) as a synonym of *Varanopus microdactylus*.

Poorly preserved, incomplete specimens or those deformed by the sliding movement resemble *Chelichnus* (Fig. 35B; Muz. PIG OS-220/33: 5–8 fragmentary trackway; Ptaszyński 2000b: fig. 4, upper part of the photograph) or *Anhomoiichnium* (Fig. 35C) imprints. It is possible, that a part of materials from other localities described erroneously as *Chelichnus* may represent *Palmichnus* trackways.

Ichnogenus *Paradoxichnium* Müller, 1959

Remarks.—Middle-sized lacertoid tracks with manual imprints situated before pedal ones or on the same line. Manual

pace width is much narrower than that of the pes; similarly difference concerns pace angulations. Pedal digits I–V and manual digits I–IV diverge at low angles and are not strongly differentiated in length. Except for *Paradoxichnium radeinensis* Ceoloni et al., 1986 uncertainly attributed to the ichnogenus *Paradoxichnium* (Ceoloni et al. 1986), the only *Paradoxichnium* representatives described are *P. problematicum* Müller, 1959 and *Paradoxichnium tumlinense* ichnosp. nov. Ichnogenus *Paradoxichnium* Müller, 1959 is known from the Late Permian deposits (Müller 1959; Ceoloni et al. 1986).

Paradoxichnium tumlinense ichnosp. nov.

Figs. 17A, B, 18A, B, 19A–E, 20A, B, 21A, B, 29C, $35A_2$.

Holotype: Set of right pedal and manual imprints, Muz. PIG OS-220/27: 44, 45 (Figs. 17A, B, 19C, $20A_1$).

Type locality: Tumlin Gród quarry near the village Tumlin, 11 km NW of Kielce, Holy Cross Mts., Poland.

Type horizon: Tumlin beds, Lower Buntsandstein, uppermost Permian.

Derivation of the name: From the name of the village of Tumlin, the type locality.

Material.—Muz. PIG OS-220/27: 36–55 ten consecutive sets of imprints (Figs. 17A, B, 18A, 19A, $20A_1$, A_2, A_4, $21A_1$); the fifth of them is designed as the holotype, Muz. PIG OS-220/27: 44, 45 (Figs. 19C, $20A_1$); Muz. PIG OS-220/27: 139–146 four consecutive sets of pedal and manual imprints (Figs. 19B, $21A_2$); Muz. PIG OS-220/27: 82, 83 isolated set of imprints; Muz. PIG OS-220/39: 13–18 three consecutive sets of pedal and manual imprints (Figs. 18B, 21B); Muz. PIG OS-220/27: 167–178 six consecutive sets of pedal and manual imprints (Fig. $35A_2$).

Diagnosis.—Relatively small *Paradoxichnium* with a pedal imprint of about 50 mm length. Pedal pace angulation is 106–118°; that of manual ranges 151–167°. Divarication of pedal digit III from the midline is about –14°, when manual imprints are strongly inclined to the midline at about +38°. Pedal digits I–V diverge at about 40°.

Description.—Trackway. In the trackway Muz. PIG OS-220/27: 36–55 (Figs. 17A, B, 18A, 19A, $20A_4$, $21A_1$, with the holotype, Muz. PIG OS-220/27: 44, 45) the pedal stride is 270–325 mm; that of manus attains 290–315 mm. In this trackway, interpreted as result of fast movement, manual imprints are situated on the same level as pedal ones. The pedal pace width (90–105 mm) and that of manus (15–40 mm) differ greatly, as do the respective pace angulations, 106–118° and 151–167°. This great difference is caused by an unusually narrow manual pace width. While pedal imprints diverge from the midline at –14° on average, manual imprints are inclined strongly to the midline at average angle +38°. In trackway, Muz. PIG OS-220/27: 167–178 (Fig. $35A_2$) interpreted as result of slow gait, manual imprints are situated slightly before pedal ones. In this trackway, pedal pace angulation reaches only 102°, and manual one 128°. The stride ranges 250–260 mm, while the pedal and manual width of pace equals 100 mm and 60 mm, respectively. The trackway of a slowly moving animal, Muz. PIG OS-220/27:

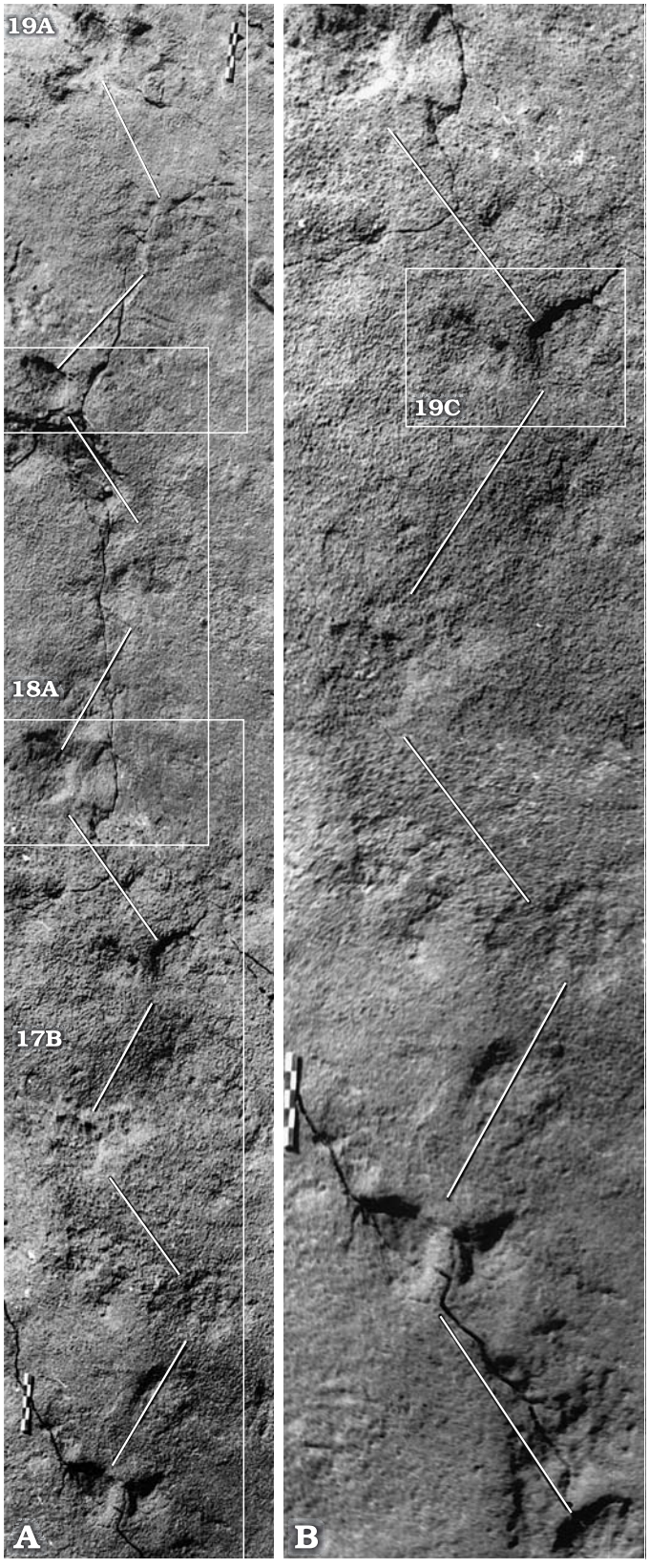

Fig. 17. *Paradoxichnium tumlinense* ichnosp. nov. **A**. Muz. PIG OS-220/27: 38–55 trackway with the holotype, Muz. PIG OS-220/27: 44, 45. **B**. Muz. PIG OS-220/27: 36–47 trackway with the holotype, Muz. PIG OS-220/27: 44, 45. Scale bars 5 cm.

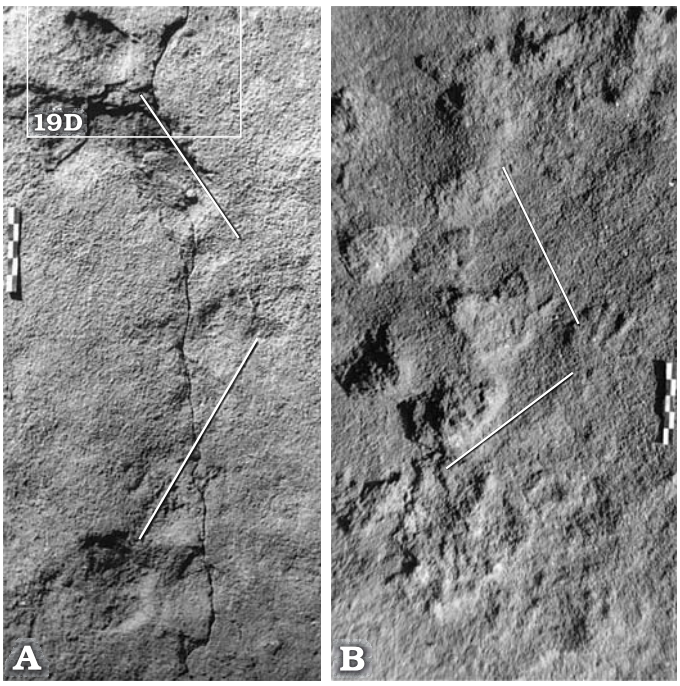

Fig. 18. *Paradoxichnium tumlinense* ichnosp. nov. **A**. Muz. PIG OS-220/27: 46–51 trackway. **B**. Muz. PIG OS-220/39: 13–18 trackway. Scale bars 5 cm.

139–146 (Figs. 19B, $21A_2$) shows pedal and manual pace angulations 90° and 123° (respectively). Manual imprints are strongly inclined towards the midline at +40°, situated in slow gait slightly before pedal ones (Muz. PIG OS-220/27: 167–178, Muz. PIG OS-220/27: 139–146, Muz. PIG OS-220/39: 13–18, Figs. 18B, 19B, $21A_2$, B, $35A_2$) or on the same line (Muz. PIG OS-220/27: 36–55, Figs. 17A, B, 18A, 19A, $20A_4$, $21A_1$). Animals of similar size made all known trackways.

Pes.—Pedal imprints in trackway Muz. PIG OS-220/27: 36–55 are 50 mm long by 46 mm wide. In the digit group I–IV, 45 mm long by 38 mm wide, with greatest load on digits I–III, the digit IV is the longest. Digits I–IV diverge of 26–30°; the angle between axes of digits I and V is low, 62–64°. Digits increase in length from I to IV attaining 23, 28, 32, 34 mm (respectively). Digit V, often visible, is long as like as digit IV, 34 mm, diverging from digit I at 35–48°. Pedal imprints shows the greatest load on digits I–III. All five digits have claw marks (Figs. 19C, E, $20A_1$–A_3).

Manus.—Manual imprints are 40 mm long by 30 mm wide. Digit group I–IV is 29 mm long and 26 mm wide. Digits I–IV are relatively narrow and not strongly differentiated in length, increasing from I to IV: 16, 20, 23, 27 mm, respectively. Digit I-IV have relatively small, but distinct claw

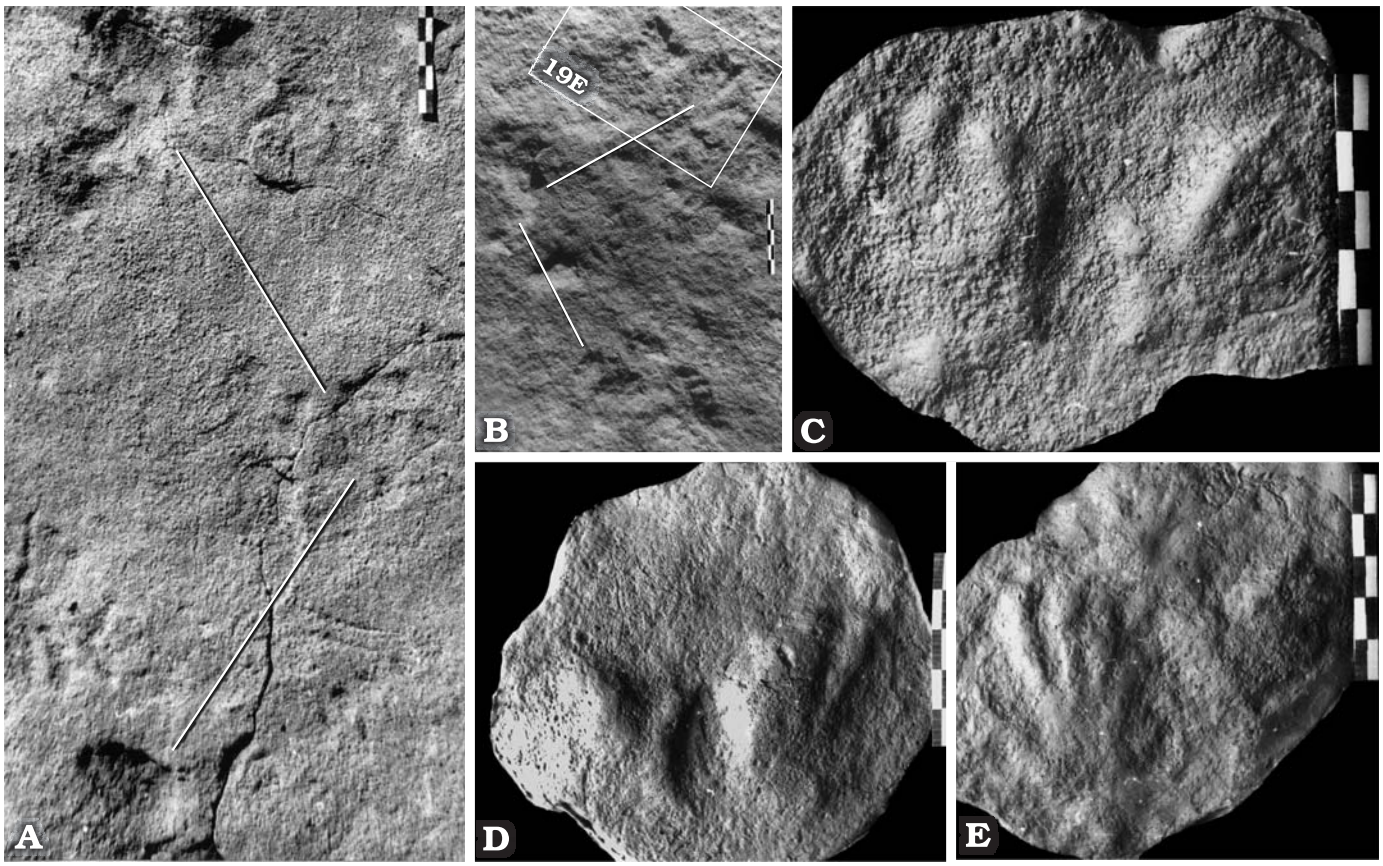

Fig. 19. *Paradoxichnium tumlinense* ichnosp. nov. **A**. Muz. PIG OS-220/27: 50–55 trackway. **B**. Muz. PIG OS-220/27: 139–144 trackway. **C**. Muz. PIG OS-220/27: 44–45 set of right pedal and manual imprints, holotype. **D**. Muz. PIG OS-220/27: 50, 51 set of left pedal and manual imprints. **E**. Muz. PIG OS-220/27: 143, 144 set of right pedal and manual imprints. Scale bars 5 cm.

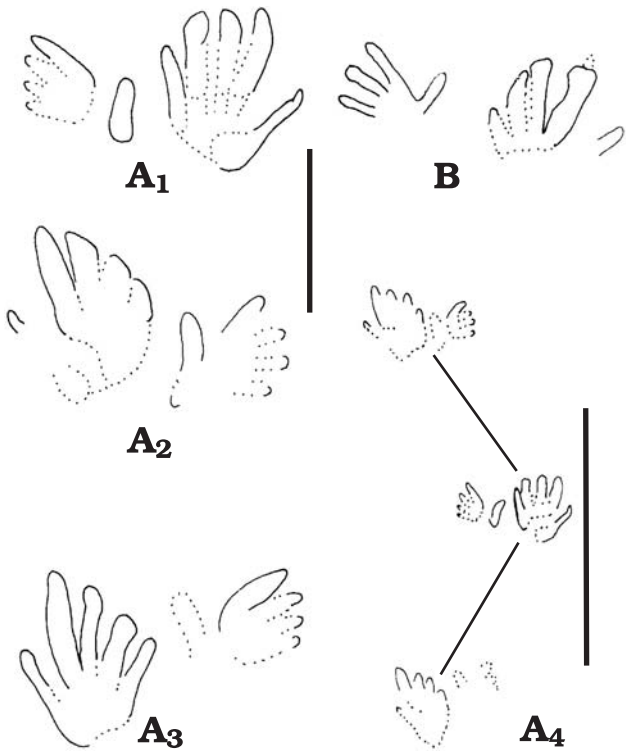

Fig. 20. *Paradoxichnium tumlinense* ichnosp. nov. **A_1**. Muz. PIG OS-220/27: 44, 45 set of right pedal and manual imprints, holotype. **A_2**. Muz. PIG OS-220/27: 46, 47 set of left pedal and manual imprints. **A_3**. Muz. PIG OS-220/27: 143, 144 set of right pedal and manual imprints. **A_4**. Muz. PIG OS-220/27: 42–47. **B**. Muz. PIG OS-220/39: 15, 16 set of left pedal and manual imprints. Scale bars: A_1, A_2, A_3, B, 5 cm, A_4, 20 cm.

marks. Digit V, 22 mm long, is much stronger imprinted than the first four digits. It is somewhat bent, enlarged on its proximal and distal end, showing distinct claw mark. It diverges from digit IV at the relatively large angle of 47°, while divarication of digits I–IV attains only 25°.

Discussion.—*Paradoxichnium tumlinense* ichnosp. nov. is about two times smaller than *Paradoxichnium problematicum* Müller, 1959. It shows larger pace angulation on both manual and pedal imprints, larger divarication of pedal digits I–IV and I–V, much narrower manual width of pace in respect to the pedal one and a stronger inclination of the manual axes to the midline. In comparison with *Paradoxichnium radeinensis* Ceoloni et al., 1986, ichnospecies questionably accounted to this ichnogenus, *Paradoxichnium tumlinense* ichnosp. nov. shows much narrower manual width of pace which is almost equal to pedal one in *Paradoxichnium radeinensis*. In contrast with the latter, *Paradoxichnium tumlinense* ichnosp. nov. shows pedal axes inclined outside the midline, and larger divarication of pedal and manual axes. Moreover, its pedal digit group I–IV is narrower, than that relatively short and wide in *P. radeinensis*.

Ichnogenus *Phalangichnus* Schmidt, 1959

Remarks.—Small to medium-sized Rhynchosauroidae representatives. The manual pace width is equal or smaller to pedal pace width. The pedal digit V is relatively small, as long as digit I or II. Pedal digit IV is longer than digit III or may be equal in length to it. Pace angulation ranges from somewhat less than 90° up to 120°, depending on the gait. The stride/pedal length ratio is up to 8. Ichnogenus *Phalangichnus* shows similarity to the ichnogenus *Rhynchosauroides* (see Haubold 1971b), from which it differs mainly in the shape of pedal imprint and the length and position of the pedal digit V. Incomplete pedal imprints may show digit tips marked on the same line, being the motivation of the name *Phalangichnus* (Fig. 34A, B), although treated in this paper as "not exactly determinable". This position of digit tips imprints is highly unusual for *Rhynchosauroides* tracks.

Phalangichnus was first described by Schmidt (1959) with two new ichnospecies: *Phalangichnus alternans* and *Phalangichnus simulans* from the Cornberger Sandstone. Later, Conti et al. (1977) described *Phalangichnus perwangeri* from the Val Gardena Sandstone. Fichter (1983b) considered *Phalangichnus simulans* as a synonym of *P. alternans*. Haubold (1995) and Haubold et al. (1995) considered both *Phalangichnus* ichnospecies together with *Harpagichnus, Akropus diversus* (= *Anhomoiichnium diversum*) and many other specimens as synonyms of *Chelichnus* or not determinable specimens (Haubold and Stapf 1998, see below).

Investigation of *Phalangichnus* tracks from the Tumlin beds may help to resolve some doubts concerning the possible erroneous interpretation of these trackways. Those de-

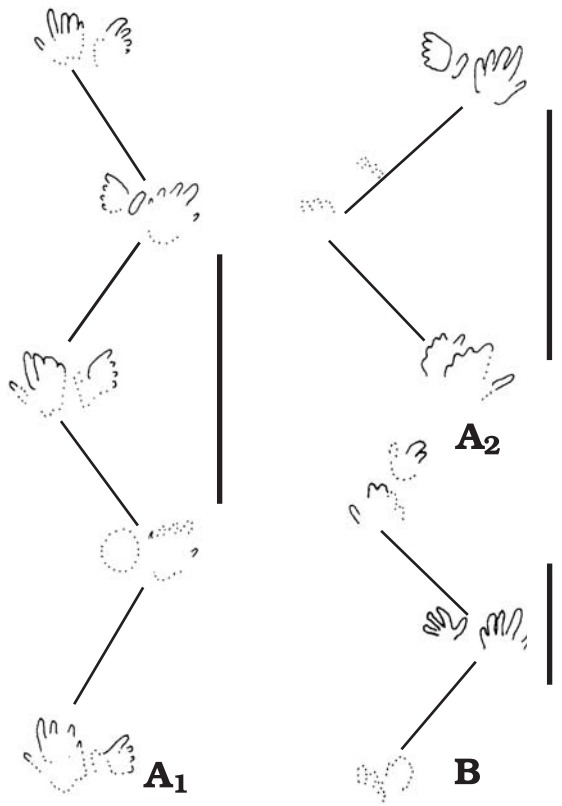

Fig. 21. *Paradoxichnium tumlinense* ichnosp. nov. **A_1**. Muz. PIG OS-220/27: 46–55 trackway. **A_2**. Muz. PIG OS-220/27: 139–144 trackway. **B**. Muz. PIG OS-220/39: 13–18 trackway. Scale bars: A, 20 cm, B, 10 cm.

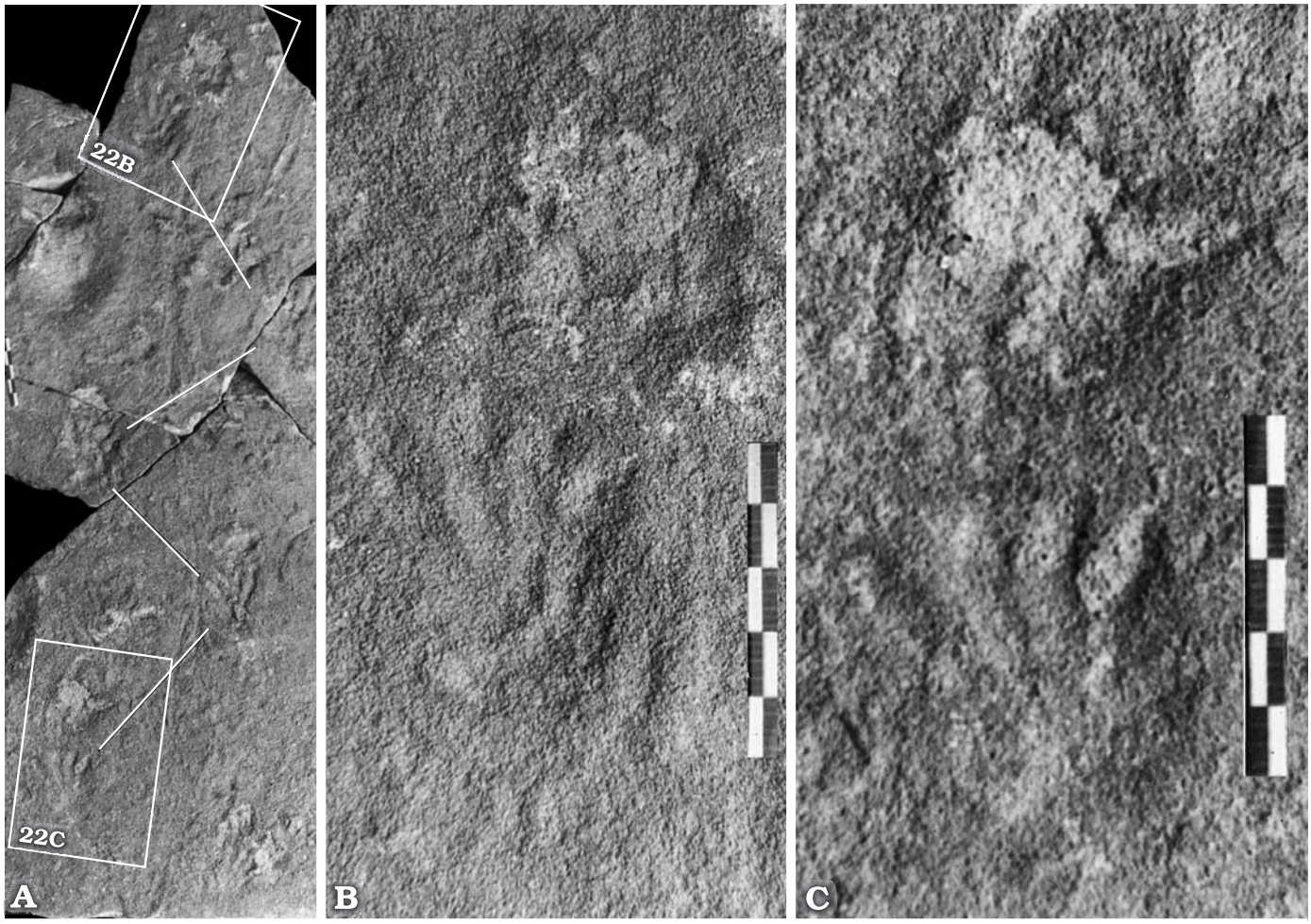

Fig. 22. *Phalangichnus gradzinskii* ichnosp. nov. **A**. Muz. PIG OS-220/30A: 1–12 trackway consist of six consecutive sets of imprints. **B**. Muz. PIG OS-220/30A: 11, 12 set of left pedal and manual imprints. **C**. Muz. PIG OS-220/30A: 3, 4 set of left pedal and manual imprints. Scale bars 5 cm.

scribed as representing *Phalangichnus simulans* by Schmidt (1959: figs. 3, 11) and *Phalangichnus perwangeri* by Conti et al. 1977 (fig. 10, pl. 2: 1, 2) have been left by not one, but at least two animals leaving their trackways along almost the same line overstepping manual imprints by pedal ones. This interpretation explains well the "strange" arrangement of pedal and manual imprints of the *Phalangichnus simulans* holotype (Schmidt 1959: figs. 3, 11; Haubold 1984: fig. 68. 1; Haubold 1996: fig. 35A), and remarkable irregularities in the trackway of *Phalangichnus perwangeri* (Conti et al. 1977: fig. 10; Haubold 1984: fig. 77). This pattern of trackways left by animals walking along the same line was also observed in specimens from the Tumlin beds (Figs. 25A, 27B). Possible erroneous interpretation of the trackways makes the real track features uncertain.

Phalangichnus gradzinskii ichnosp. nov.

Figs. 22A–C, 23A–C, 24A–D, $34C_2$.

Holotype: Set of right pedal and manual imprints, Muz. PIG OS-220/30B: 5, 6 (Figs. 23C, $24B_1$).

Type locality: Tumlin Gród quarry, 11 km NW of Kielce, Holy Cross Mts., Poland.

Type horizon: Tumlin beds, Lower Buntsandstein, uppermost Permian.

Derivation of the name: In honour of Ryszard Gradziński, who studied the Tumlin beds sedimentary environment and discovered vertebrate tracks there for the first time.

Material.—Muz. PIG OS-220/30A: 1–12 six consecutive sets of pedal and manual imprints, Muz. PIG OS-220/30B: 1–6 natural casts of the same trackway as Muz. PIG OS-220/30A: 1–12, showing the consecutive sixth, seventh (partly preserved) and eighth set of imprints, from which the eighth one, right pedal and manual imprints, Muz. PIG OS-220/30B: 5, 6 are designed as the holotype (Figs. 22A–C, 23C, 24A, B); Muz. PIG OS-220/27: 92–97 three consecutive sets of imprints, Muz. PIG OS-220/27: 86–91 three consecutive sets of imprints. Isolated imprints: Muz. PIG OS-220/38: 1 left pedal imprint (Figs. 23B, 24C); Muz. PIG OS-220/53: 1 left pedal imprint (Figs. 23A, 24D); Muz. PIG OS-220/39: 28–33 three consecutive sets of imprints (Fig. $34C_2$).

Diagnosis.—Medium-sized *Phalangichnus* having manual axes inclined to the midline at +13.5°; pedal imprints slightly diverging out from the midline at –4°. Pedal pace angulation varies from somewhat less than 90° up to 115°. The manual pace width is only a slightly less than the pedal pace width.

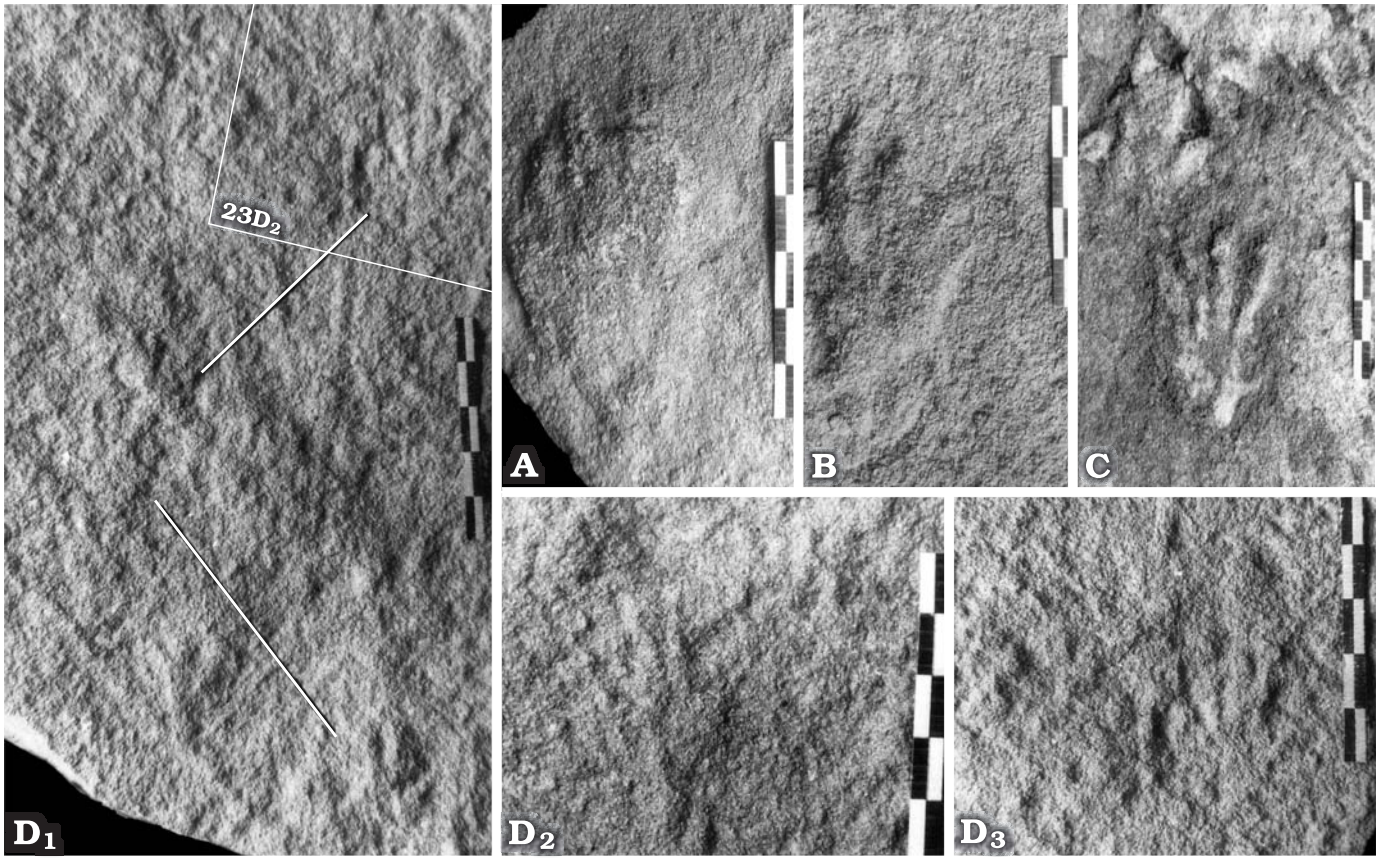

Fig. 23. **A**–**C**. *Phalangichnus gradzinskii* ichnosp. nov. **A**. Muz. PIG OS-220/53: 1 isolated left pedal imprint. **B**. Muz. PIG OS-220/38: 1 right pedal imprint. **C**. Muz. PIG OS-220/30B: 5, 6 set of left pedal and manual imprints, holotype. **D**. *Varanopus* aff. *microdactylus* (Pabst, 1896). **D_1**. Muz. PIG OS-220/61A: 1–4 three consecutive pedal imprints with fragmentary manual imprint accompanied the second pes; **D_2**. Muz. PIG OS-220/61A: 4 fully preserved, left pedal imprint; **D_3**. Muz. PIG OS-220/61A two not numbered fragmentary imprints with good visible claw marks. Scale bars 5 cm.

Description.—Trackways. The manual pace width is somewhat smaller than the pedal one, which connects with similar pace angulation in the trackway containing the holotype, Muz. PIG OS-220/30A: 1–12 and Muz. PIG OS-220/30B: 1–6 (Figs. 22A–C, 23C, 24A, B) close to 90°. Pedal imprints diverge from the midline at about –4°, while manual axes are inclined to the midline at +13.5° on average. The stride/pedal length ratio is only 4.6. The average manual width of pace, 104 mm is very close to the pedal one, 122 mm. The trackway with the holotype is somewhat irregular. In the more regular part of the trackway, the average manual pace angulation, 88°, somewhat exceeds the pedal one, 85°. In other trackways enclosed to the material, Muz. PIG OS-220/27: 92–97 and Muz. PIG OS-220/27: 86–91 the pedal pace angulation exceeds 90°, ranging from 97 to 115°. The pedal pace width exceeds 1.3–1.6 times the manual one. Pedal axes are almost parallel to the midline attaining the average angle of –4°. The manual inclination to the midline is +13.5°. Manual imprints are situated more or less before pedal ones, but have never been observed overstepped by them. In the trackway containing the holotype and also the trackway Muz. PIG OS-220/39: 28–33 (Fig. 34C_2), the tail mark is present, although poorly visible.

Pes.—The pedal length in the type trackway, 50 mm, distinctly exceeds its width, 38 mm. The group of digits I–IV is almost as long as it is wide, 37 and 38 mm, respectively. The length of digits I–IV equals average values 24, 28, 30, and 31 mm. All those digits have distinct claw marks. The digit V is relatively short, long as like as the II, situated backward from the digit group I–IV. Pedal digits II/IV, l/IV and I/V diverge of. 25.5, 37, and 54°, respectively.

Manus.—Manual imprints are 33 mm long and 31 mm wide. From the digit group I–IV, of which length somewhat exceeds the width (33 and 31 mm) first four digits increase in length from I to IV: 16, 19, 24.5, and 25.5 mm on average. The digit V length is comparable with that of II, 20.5 mm. Digits II/IV, I/IV and I/V diverge of 36.5, 48, and 88.5°, respectively.

Discussion.—The small number of fully preserved trackways under description is caused by the similarity of mostly incompletely preserved imprints to other Rhynchosauroidae ichnospecies present in the Tumlin Sandstone. Many tracks found at Tumlin Gród and Sosnowica Hill quarries may represent this ichnospecies, but appear usually as only digit tips imprints, and therefore are hardly distinguishable from other Rhynchosauroidae representatives (Fig. 34A, B). Their main characteristic features are close pedal and manual values for

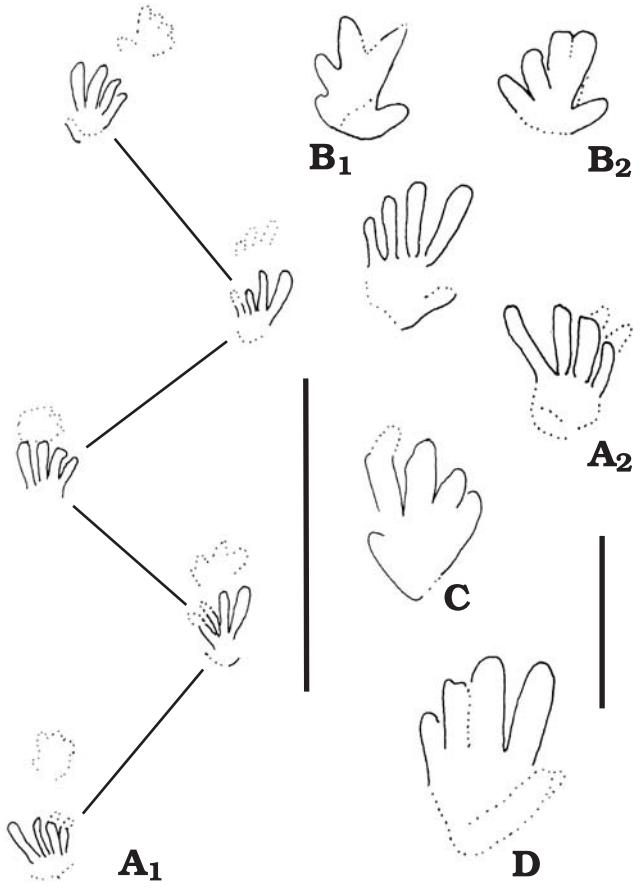

Fig. 24. *Phalangichnus gradzinskii* ichnosp. nov. **A_1**. Muz. PIG OS-220/30A: 3–12 five consecutive sets of imprints; **A_2**. Muz. PIG OS-220/30A: 3 left pedal imprint. **B_1**. Muz. PIG OS-220/30B: 5, 6 set of left pedal and manual imprints, holotype. **B_2**. Muz. PIG OS-220/30B: 2 left manual imprint, natural cast of the mould Muz. PIG OS-220/30A: 12. **C**. Muz. PIG OS-220/38: 1 right pedal imprint. **D**. Muz. PIG OS220/53: 1 left pedal imprint. Scale bars: A_1, 20 cm, A_2–D, 5 cm.

pace width and low pace angulation angle. Also characteristic is the arrangement of digits I–IV tip imprints along a straight line, a feature stated by Schmidt (1959) as characteristic of the ichnogenus, not found by authors in *Rhynchosauroides* imprints. The characteristic arrangement of digit tips may result from dragging on the substrate causing elongation of imprints of the first two digits (Figs. 22B, C, 23B, $24A_2$). Trackways with such incomplete imprints (Figs. 34A, B) have not been included in this ichnospecies but are treated in this paper as determinable only to the ichnogeneric level. *Phalangichnus gradzinskii* ichnosp. nov. shows similarity to *Phalangichnus alternans* Schmidt, 1959, having a higher stride/pedal length ratio and a distinct, big manual digit V imprint, being much more similar to *Rhynchosauroides* manual imprints (see Schmidt 1959: fig. 10). Pedal imprints of *Phalangichnus alternans*, although similar in size, are narrower and distinctly directed outward from the midline. The exact comparison of those two similar ichnospecies is difficult because of incomplete preservation of *Phalangichnus alternans* specimens, this being the reason for doubts of the authors of revision works (see below). From *Rhynchosauroides kuletae* ichnosp. nov., *Phalangichnus gradzinskii* ichnosp. nov. differs clearly in size and arrangement of digit V (if visible), and much more close values of the pedal and manual width of pace. The overstepping of manual imprints by pedal ones have not been observed. In fragmentary or poor trackways both ichnospecies are not always easy distinguishable.

Phalangichnus gagoli ichnosp. nov.

Figs. 25A–D, 26A–F, 27A–D, 28A–H.

Palmichnus sp. Ptaszyński, 2000b: fig. 4 (right part of the photograph), fragmentary trackway described in this paper as Muz. PIG OS-220/33: 1–4.

Holotype: Set of pedal and manual imprints Muz. PIG OS-222/1: 3, 4 (Figs. 25C, 26F, 27C, 28A).

Type locality: Tumlin Gród quarry, 11 km NW of Kielce, Holy Cross Mts., Poland.

Type horizon: Tumlin beds, Lower Buntsandstein, uppermost Permian.

Derivation of the name: In honour of Jerzy Gągol, researcher of the Holy Cross Mountains Buntsandstein lithostratigraphy.

Material.—Tumlin quarry: Muz. PIG OS-222/1: 1–6 three consecutive sets of pedal and manual imprints (Figs. 25C, 27C); the second set of them, Muz. PIG OS-222/1: 3 (left pedal imprint) and Muz. PIG OS-222/1: 4 (left manual imprint) are designated as the holotype (Figs. 26F, 28A); Muz. PIG OS-222/1: 7–18 six consecutive pedal and manual imprints (Figs. 25C, 26E, 27D, 28B); Muz. PIG OS-222/1: 19–26 four sets of imprints; Muz. PIG OS-222/1: 29–44 trackway, somewhat irregular composed of at least eight sets (Figs. 25A, 26B–D, 27B, 28C, F, H); Muz. PIG OS-222/1: 45–56 six sets of imprints (Figs. 25B, 27A, 28D); Muz. PIG OS-222/1: 57, 58 isolated set of left pedal and manual imprints (Figs. 26A, 28G); Muz. PIG OS-222/1: 27, 28 isolated imprints from the poorly preserved trackway being parallel to that of Muz. PIG OS-222/1: 29–44 (Fig. 25A); Muz. PIG OS-222/1: 59–64 four sets of consecutive pedal and manual imprints (Fig. 25D); Muz. PIG OS-220/33: 1–4 two sets of right pedal and manual imprints; Muz. PIG OS-220/73: 42, 43 isolated set of pedal and manual imprints; Muz. PIG OS-220/73: 44–49 three consecutive pedal and manual imprints; Muz. PIG OS-220/40: 1–4 two consecutive sets of pedal and manual imprints.

Diagnosis.—Small *Phalangichnus* with differentiated trackway features: pedal pace angulation ranging from 83° up to 120°; respective manual values vary from 110° up to 147°. Manus may be situated before the pes, on the same line, or may be overstepped by the latter, which is interpreted as connected with a differentiated kind of the gait. Pedal digit V small, long as like as the II. Divarication of pedal digits I–IV attains 42°. The stride/pedal length ratio ranges from 4.6 up to 8.3.

Description.—Trackway. Most of trackways described were obtained from the Tumlin beds and came mainly from the large slab exhibited in front of the building of the Holy Cross Branch of the Polish Geological Institute, Kielce. The most characteristic feature of these trackways is the varied degree of overstepping of pes imprints by those of manus. On the same

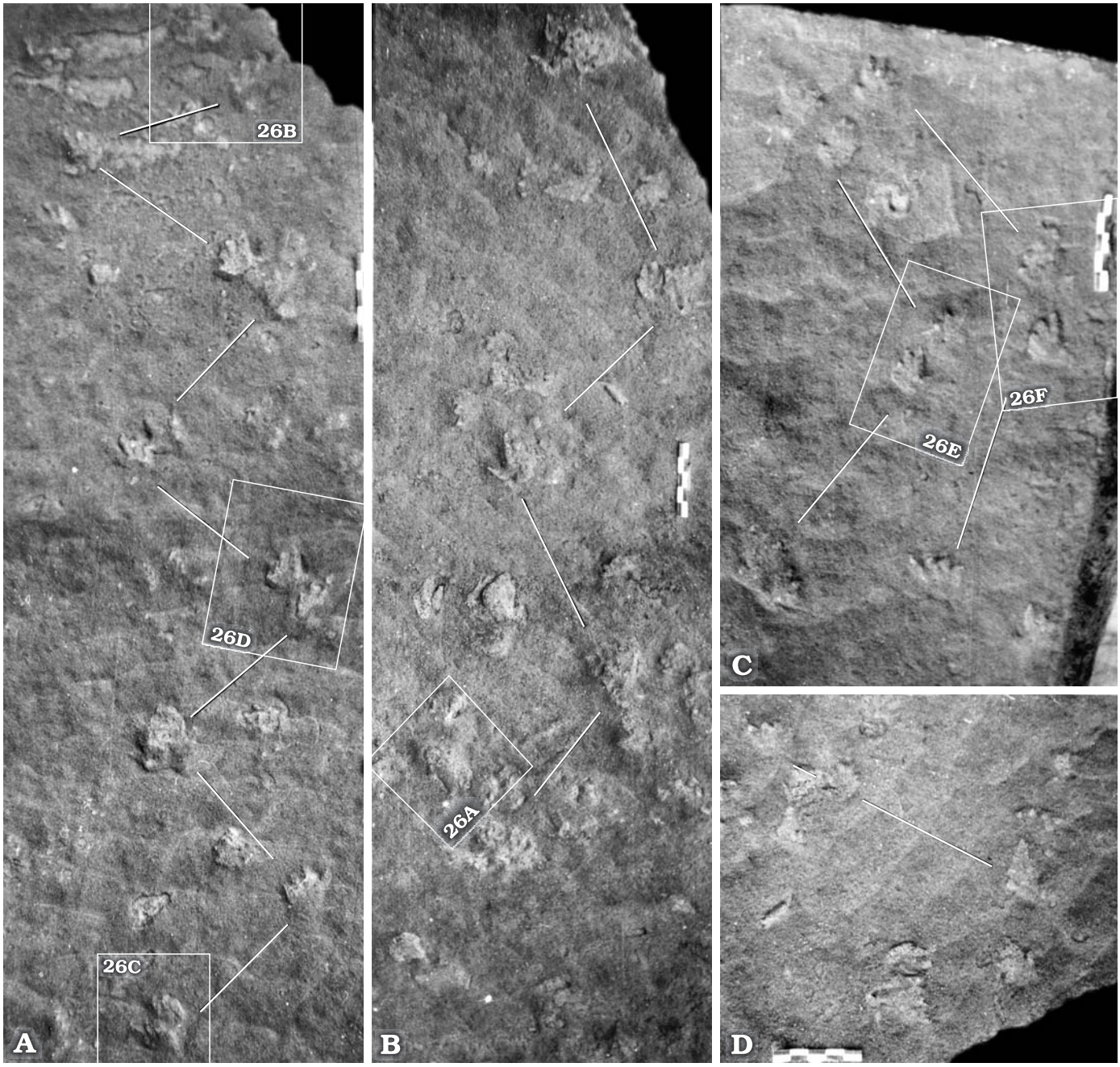

Fig. 25. *Phalangichnus gagoli* ichnosp. nov. **A**. Muz. PIG OS-222/1: 29–41 long, somewhat irregular trackway composed of at least seven sets of imprints, specimens Muz. PIG OS-222/1: 42–44 are also visible. **B**. Muz. PIG OS-222/1: 47–56 five consecutive pedal and manual imprints. **C**. Two trackways, Muz. PIG OS-222/1: 1–6 three consecutive sets of pedal and manual imprints, the second set of imprints is designed as the holotype, Muz. PIG OS-222/1: 3, 4 and Muz. PIG OS-222/1: 13–18 three consecutive sets of imprints. **D**. Muz. PIG OS-222/1: 59–62 two consecutive sets of imprints. Scale bars 5 cm.

slab, different trackways show manus imprints situated before pes ones (Muz. PIG OS-222/1: 57, 58; Muz. PIG OS-222/1: 27–44; Muz. PIG OS-222/1: 19–26, Figs. 25A, 26A–C, 27B, 28C, F–H); more or less on the same line (Muz. PIG OS-222/1: 45–56; Muz. PIG OS-220/33: 1–4, Figs. 25B, 26D, 27A, 28D) and show manual imprints overstepped by those of pes (Muz. PIG OS-222/1: 1–6; Muz. PIG OS-222/1: 59–64, Figs. 25C, D, 26E, F, 27C, D, 28A, B). Those features are interpreted as results of differentiated speed (walking and running gait) of animals. Pedal imprints diverge out from the midline at –3° up to –23°; those of manus are inclined to the midline from 0° up to +32°. The pedal stride is strongly variable, as is the pace angulation, ranging from 150 mm up to 290 mm. The pedal pace width ranges from 85–105 mm, while the pedal one is 47–65 mm. The stride/pedal length ratio ranges from 4.6 up to 8.3.

Pes.—All five digits have claw marks. The digit group I–IV is triangular in outline. The average length and width of the

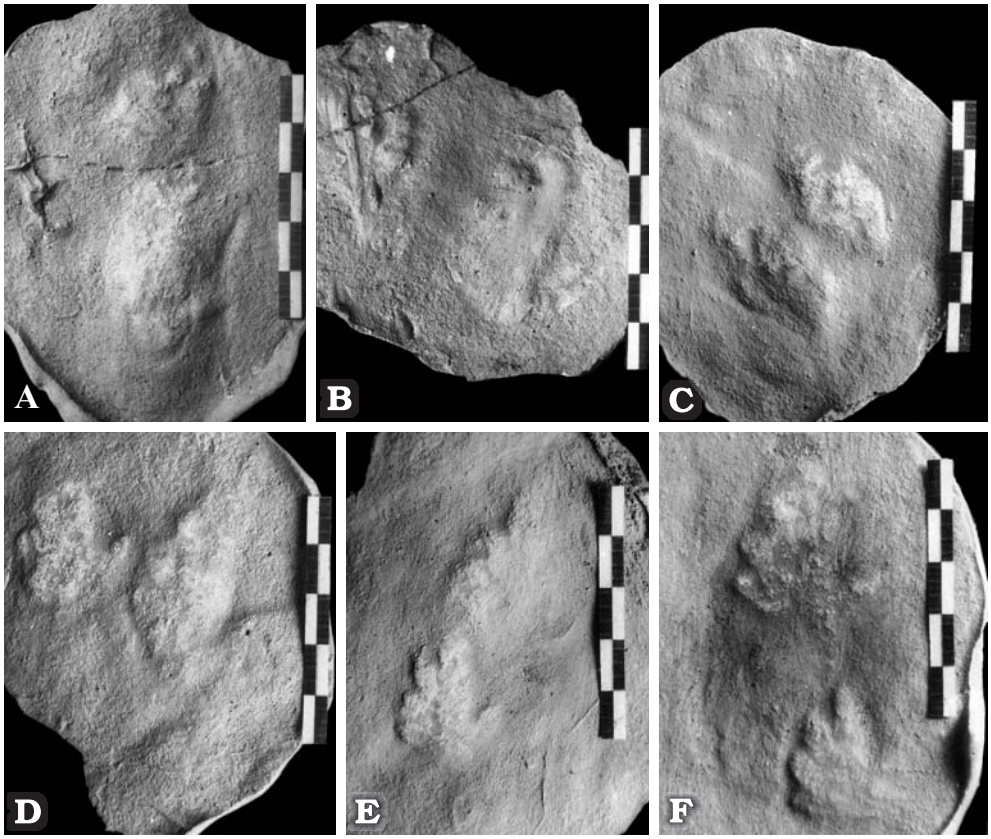

Fig. 26. *Phalangichnus gagoli* ichnosp. nov. **A**. Muz. PIG OS-222/1: 57, 58 set of pedal and manual imprints. **B**. Muz. PIG OS-222/1: 43, 44 set of pedal and manual imprints. **C**. Muz. PIG OS-222/1: 29, 30 set of pedal and manual imprints. **D**. Muz. PIG OS-222/1: 35, 36 set of pedal and manual imprints. **E**. Muz. PIG OS-222/1: 15, 16 set of pedal and manual imprints. **F**. Muz. PIG OS-222/1: 3, 4 set of pedal and manual imprints, holotype. Scale bars 5 cm.

digit group I–IV of many specimens from the slab Muz. PIG OS-222/1 is 29 mm and 24 mm, respectively. The maximum known length of this group is up to 40 mm (specimens Muz. PIG OS-220/73: 44, 46). Digits are closely arranged, with typical length proportions: IV>III>II>I, showing average values: 13, 17, 21, 25 mm, respectively with total divarication of digits II–IV of 25°, and I–IV of 42°. Digit V is long as like as digit II, situated somewhat posteriorly and laterally to the digit group I–IV; in many footprints well visible.

Manus.—Manus imprints smaller than pes ones. The length of manus imprints only somewhat exceeds their width, attaining average values 25 and 24 mm. All digits from group I–IV have claw marks and increase in length from I to IV: 11, 16, 18, and 20 mm, respectively. Average divarications of digits I–IV, II–IV, and I–V are 38, 22, and 80°, respectively. Digit V is about 13.5 mm long.

Discussion.—*Phalangichnus gagoli* ichnosp. nov. differs from *Phalangichnus alternans* in smaller manual pace width than that of pes, which are almost equal in *Phalangichnus alternans*. *Phalangichnus gagoli* ichnosp. nov. is somewhat smaller in size. Manual imprints of *P. gagoli* ichnosp. nov. are distinctly narrower than those of *P. alternans*, having relatively smaller pedal imprints in relation to manual ones than in the latter. All known trackways of *P. gagoli* show pace angulation bigger than *P. alternans*. The comparison of *Phalangichnus gagoli* ichnosp. nov. with *P. simulans* is difficult because of the unsatisfactory state of preservation of the latter and means that track features might be erroneously interpreted (see discussion above).

Phalangichnus gagoli ichnosp. nov. shows a pace angulation greater than 90°, much more than that of *Phalangichnus simulans,* if the interpretation of its trackway given by Schmidt (1959) and Haubold (1971b, 1984) is correct. It shows axes of pedal imprints more closely situated to the midline and manual axes are distinctly inclined to it. It is somewhat difficult to compare the track features of *Phalangichnus gagoli* ichnosp. nov. with *Phalangichnus perwangeri* Conti et al., 1977 because of the lack of exactly specified determined trackway features of the latter. In this case there is also a possibility of erroneous interpretation of material from Val Gardena. It is possible that specimens visible on the slab with the holotype of *Phalangichnus perwangeri* (Conti et al. 1977: fig. 10, pl. 2) have been made by at least two animals walking along almost the same line. *Phalangichnus gagoli* ichnosp. nov. shows pedal axes less diverged from the midline; less differentiated pedal digits lengths and quite different outline of manual imprints, being narrower and showing in opposition to those of pes, greater differences of digits lengths. Trackway features of *Phalangichnus gagoli* ichnosp. nov. differ greatly from those of *Phalangichnus perwangeri* interpreted by Conti et al. (1977). In comparison with *Phalangichnus perwangeri*, *Phalangichnus gagoli* ichnosp. nov. is smaller and shows lesser divarication of digits I–V, about 90°. If the trackway interpretation by Conti et al. (1977) is correct, *Phalangichnus gagoli* ichnosp. nov. shows much

bigger pace angulation in trackways with manual imprints situated in similar position to those of pes as in *P. perwangeri*. *P. gagoli* ichnosp. nov. can be compared with problematic ichnospecies *P. simulans* interpreted as trackways of two individuals with manual imprints overstepped by pedal ones, similarly as in specimens Muz. PIG OS-222/1: 29–44 and Muz. PIG OS-222/1: 27, 28 (Figs. 25A, 27B).

In connection with the possible narrower manual width of pace in relation to the pedal one, and existence of overstepping, *P. simulans* is not a synonym of *P. alternans* (see Fichter 1983b).

In our opinion *P. simulans* and *P. alternans* represent different ichnospecies, but both need re-examination. All five ichnospecies together with *P. perwangeri, P. gagoli* ichnosp. nov. and *P. gradzinskii* ichnosp. nov. represent a branch of reptiles that show track features developed in the Triassic in *Rhynchosauroides* representatives. There are two main morphological types of *Phalangichnus*: the smaller, with manual width of pace much narrower than the pedal one, with manual imprints overstepped by pedal ones during speed gait, represented by *P. simulans, P. perwangeri*, and *P. gagoli* ichnosp. nov. and the bigger one, with manual and pedal width of pace close one to another, have never observed with manual imprints overstepped by pedal ones, represented by *P. alternans* and *P. gradzinskii* ichnosp. nov.

Ichnogenus *Varanopus* Moodie, 1929

Varanopus aff. *microdactylus* (Pabst, 1896)

Figs. 23D, 29A.

?*Eumekichnium gampsodactylum* (Pabst, 1896); Mietto 1975: figs. 1, 2.
?*Rhynchosauroides palmatus* (Lull, 1942); Conti et al. 1977: fig. 17, pl. 5: 1.
?*Varanopus microdactylus* (Pabst, 1896); Fichter and Kowalczyk 1983: fig. 21.
?Lepidosauria indet. Ceoloni et al. 1987: fig. 10, pl. 4: 4.

Material.—Tumlin Gród quarry: Muz. PIG OS-220/61A: 1–7 fragmentary trackway composed of six consecutive pedal imprints, with only one fragmentary manual imprint (Figs. 23D, 29A); many other fragmentary imprints occur on this slab, but no trackway can be distinguished; Muz. PIG OS-220/61B other part of the same slab with mass occurrence of mostly poorly preserved, not numbered imprints. Sosnowica Hill quarry: Muz. PIG OS-220/2A; Muz. PIG OS-220/2B; Muz. PIG OS-220/2C plaster casts of parts of the surface with mass occurred imprints.

Description.—Only one known fragmentary trackway Muz. PIG OS-220/61A: 1–7 shows six consecutive pedal imprints associated with poorly visible manual imprints. The oblique pedal pace in this trackway varies from 85 to 105 mm, attaining 93 mm as an average value. The stride is 125–145 mm; pace angulation 95° up to 112°. The width of pace varies from 55 mm up to 72 mm varies because the trackway is not straight, but turning slightly left. Pedal axes are slightly (about +4°) inclined to the midline. The trackway shows the presence of a tail drag mark, 3–4 mm wide and situated somewhat asymmetrically in relation to pedal imprints.

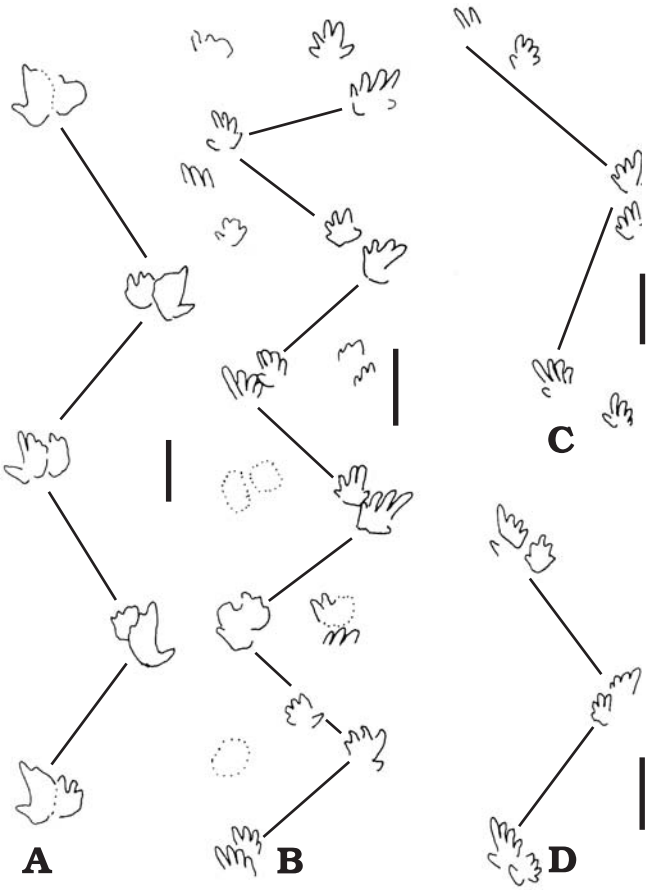

Fig. 27. *Phalangichnus gagoli* ichnosp. nov. **A**. Muz. PIG OS-222/1: 47–56 five consecutive pedal and manual imprints. **B**. Muz. PIG OS-222/1: 29–43 eight consecutive sets of imprints; among them imprints (not numbered) of other fragmentary trackways made almost along the same line. **C**. Muz. PIG OS-222/1: 1–6 three consecutive sets of pedal and manual imprints; the second set of imprints is designed as the holotype. **D**. Muz. PIG OS-222/1: 13–18 three consecutive sets of imprints. Scale bars 5 cm.

Pes.—Pedal imprints are lacertoid in shape, about 24 mm long and 22 mm wide. All five digits have distinct, narrow claw marks; digits I–IV increase in length from I to IV, exceeding 10, 14, 18, and 20 mm, respectively. The fifth digit is 17 mm long. Digits I–IV diverge at 35°; divarications between digits I–V and II–IV are 65 and 20°, respectively.

Manus.—In the trackway described only one, poorly preserved manus imprint is visible. In other, isolated and incompletely preserved sets, manus imprints are distinguishable from those of pes, being somewhat smaller in size and possibly slightly more inclined to the midline.

Remarks.—Footprints at Sosnowica Hill quarry are abundant, but no trackway has been determined. Imprints from Tumlin Gród and Sosnowica Hill show no differences in shape, digit proportions, size of imprints and angles to *Varanopus microdactylus* (Pabst, 1896). The trackway of *Varanopus* aff. *microdactylus* (Pabst, 1896) known from Tumlin Gród shows one difference in comparison with type specimens, namely the relatively high stride to pedal length ratio (smaller size of im-

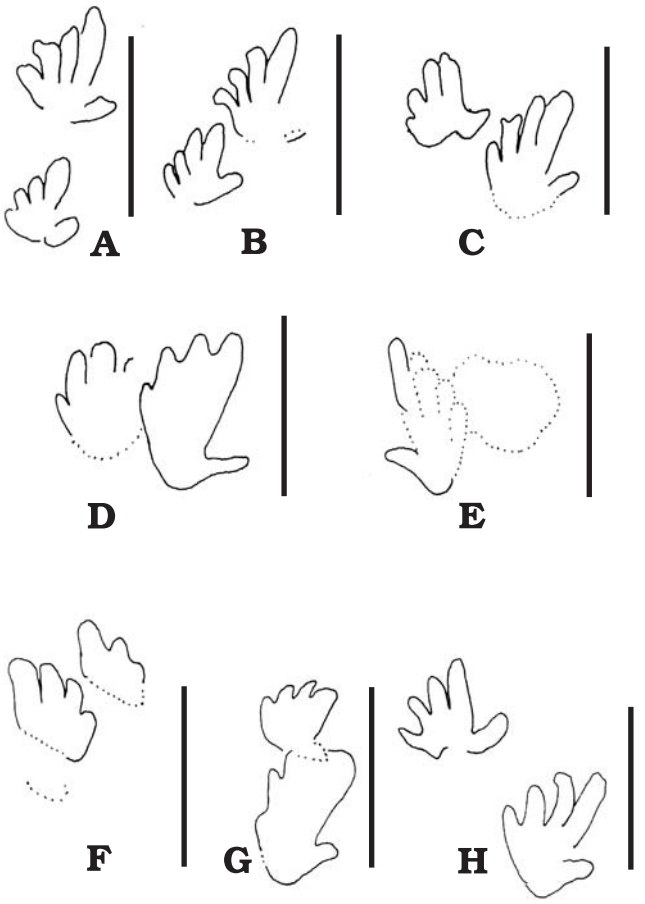

Fig. 28. *Phalangichnus gagoli* ichnosp. nov. **A**. Muz. PIG OS-222/1: 3, 4 set of pedal and manual imprints, holotype. **B**. Muz. PIG OS-222/1: 15, 16 set of pedal and manual imprints. **C**. Muz. PIG OS-222/1: 35, 36 set of pedal and manual imprints. **D**. Muz. PIG OS-222/1: 53, 54 set of pedal and manual imprints. **E**. Muz. PIG OS-222/1: 55, 56 set of pedal and manual imprints. **F**. Muz. PIG OS-222/1: 29, 30 set of pedal and manual imprints. **G**. Muz. PIG OS-222/1: 57, 58 set of pedal and manual imprints. **H**. Muz. PIG OS-222/1: 43, 44 set of pedal and manual imprints. Scale bars 5 cm.

prints in relation to the trackway patterns) attaining 5–6, as compared to only about 4 in *Varanopus microdactylus* (see Haubold 1971b). On the other hand, it shows a great degree of similarity to specimens described by Mietto (1975) as *Eumekichnium gampsodactylum* Pabst, by Ceoloni et al. 1987 as Lepidosauria indet. by Conti et al. (1977) as *Rhynchosauroides palmatus*, except for the pedal digit V is not visible in that trackway (Conti et al. 1977: fig. 17, pl. 5: 1), and possibly to one of the specimens of *Varanopus microdactylus* (Pabst, 1896) described by Fichter and Kowalczyk (1983).

Ichnogenus *Dimetropus* Romer and Price, 1940

Dimetropus sp.

Figs. 29B, 30A, 31D, 32A, E, 33D, E.

Material.—Muz. PIG OS-220/39: 1–6 short trackway with three sets of imprints (Figs. 29B, 30A). Other specimens, representing ?*Dimetropus* sp.: Muz. PIG OS-220/64 small slab with fragmentary imprint of four digits (Figs. 32E, 33E); Muz. PIG OS-220/69 slab with scratches of claws (Figs. 32A, 33D). Not determined specimens possibly representing this ichnogenus include also: Muz. PIG OS-220/70 (Fig. 31B), Muz. PIG OS-220/71 (Fig. 32B) and not collected slab shown in Fig. 31D.

Description.—The material obtained from Tumlin Gród quarry contains mostly poorly preserved trackways and only fragmentary imprints. A small poorly impressed short trackway Muz. PIG OS-220/39: 1–6 (Figs. 29B, 30A) shows a stride length of about 280 mm; pedal oblique pace 180 mm and 190 mm; relatively narrow pedal and manual pace width of 80 mm; pace angulation 110°. Pedal imprints, from which specimen Muz. PIG OS-220/39: 3 of the second set is the most completely preserved, 55 mm long and 46 mm wide, diverge from the midline at about –8°. Its digits are 21–29 mm long and narrow, not regularly arranged; exact measurements are impossible. From them, digits I and V are the shortest; digits III and IV seem to be equally long. The divarication of digits

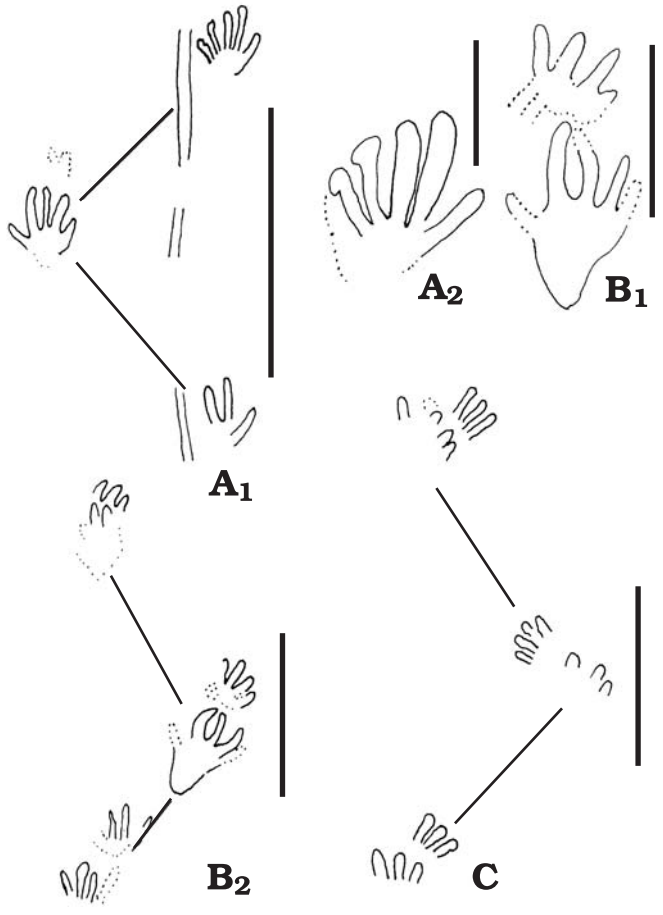

Fig. 29. **A**. *Varanopus* aff. *microdactylus* (Pabst, 1896). **A_1**. Muz. PIG OS-220/61A: 1– 4 three consecutive pedal imprints with the problematic manual one; **A_2**. Muz. PIG OS-220/61A: 4 fully preserved left pedal imprint. **B**. *Dimetropus* sp. **B_1**. Muz. PIG OS-220/39: 3, 4 set of left pedal and manual imprints. **B_2**. Muz. PIG OS-220/39: 1–6 trackway composed of three consecutive but poorly preserved imprints. **C**. *Paradoxichnium tumlinense* ichnosp. nov.; Muz. PIG OS-220/27: 173–178 three consecutive sets of pedal and manual imprints representing slow gait. Scale bars: A_1, B_2, C, 10 cm; A_2, 2 cm; B_1, 5 cm.

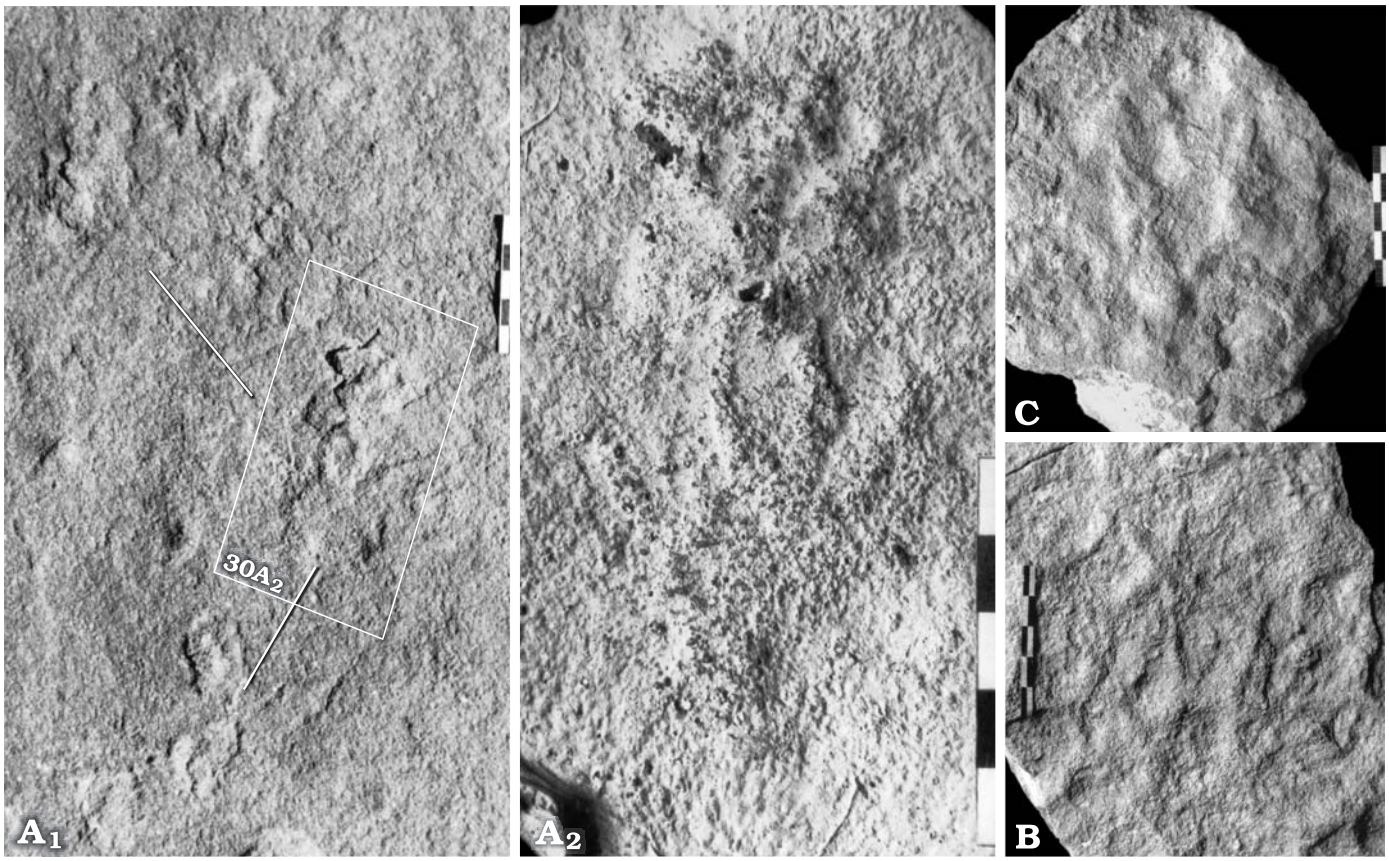

Fig. 30. **A**. *Dimetropus* sp. $\mathbf{A_1}$. Muz. PIG OS-220/39: 1–6 trackway. $\mathbf{A_2}$. Muz. PIG OS-220/39: 3, 4 set of pedal and manual imprints. **B**, **C**. *Chelichnus* cf. *duncani* (Owen, 1842). **B**. Muz. PIG OS-220/68: 1, 2 poorly preserved set of imprints. **C**. Muz. PIG OS-220/63: 1 isolated imprint. Scale bars 5 cm.

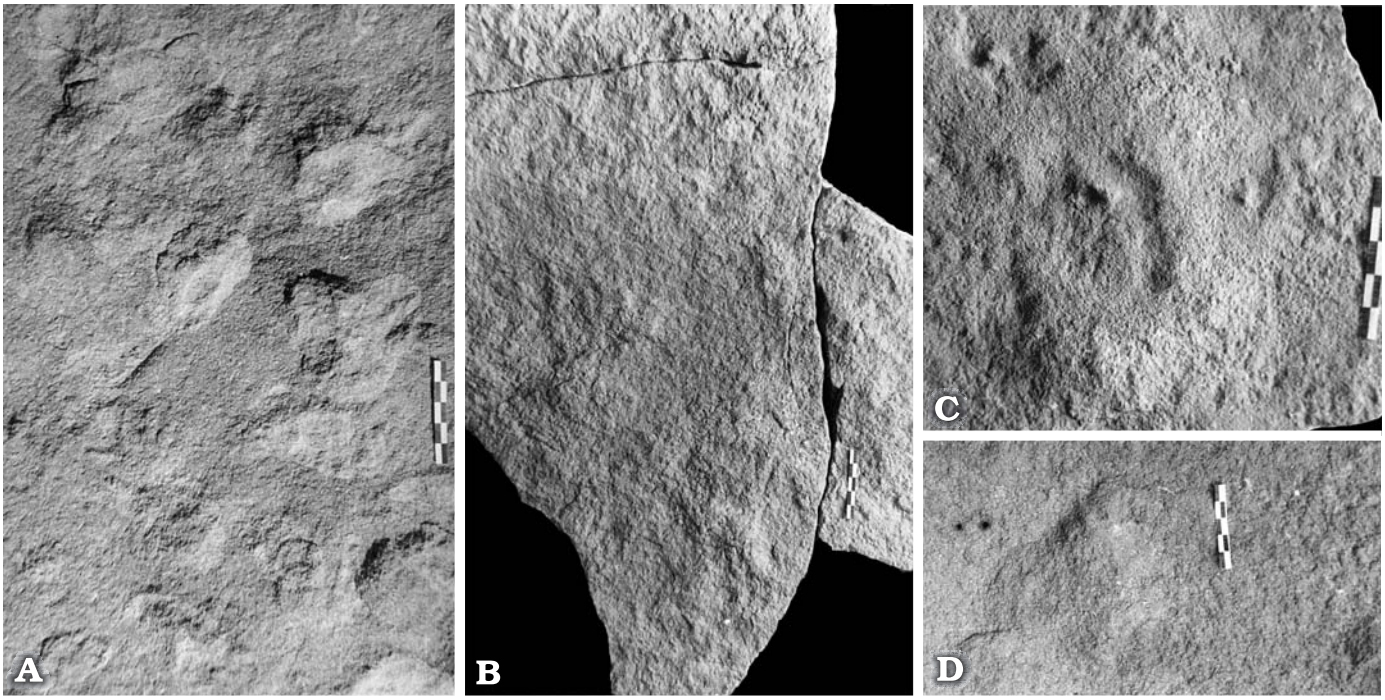

Fig. 31. **A**–**C**. *Chelichnus* cf. *duncani* (Owen, 1842). **A**. Muz. PIG OS-220/39: 20–27 the best distinguishable part of the trackway. **B**. Muz. PIG OS-220/70 association of poorly preserved tracks. **C**. Muz. PIG OS-220/62: 1, 2 poorly preserved imprint with claw marks visible on all five digits. **D**. *Dimetropus* sp. Poorly preserved imprint (specimen not collected). Scale bars 5 cm.

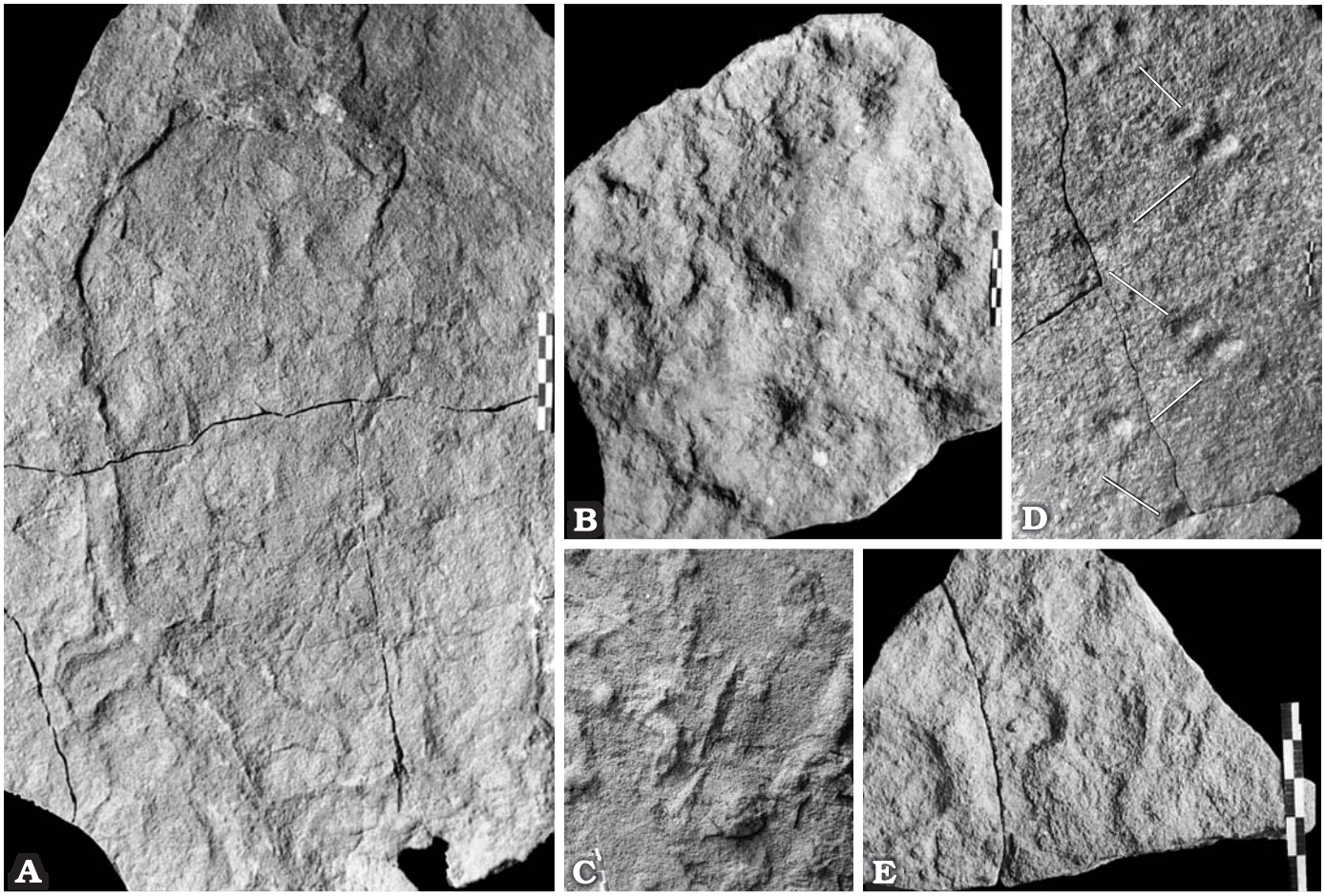

Fig. 32. **A**, **E**. ?*Dimetropus* sp. **A**. Muz. PIG OS-220/69 surface showing only claw scratches. **E**. Muz. PIG OS-220/64: 1 broken slab with a part of imprint showing four digits with claw marks. **B**, **C**, **D**. Not determinable imprints. **B**. Muz. PIG OS-220/71 two big, indeterminable footprints might represent *Dimetropus* sp. or *Chelichnus* sp. **C**. Claw marks (natural casts) of very big animal on the surface with Rhynchosauroidae imprints (specimen not collected). **D**. Muz. PIG OS-220/32 a part of trackway showing no details of pedal and manual imprints. Scale bars in cm.

I–V attains 50°. All five digits occur in front of a big sole (30 mm long) relatively narrow and asymmetrical in shape. Manual imprints are smaller in size, about 40 mm long and 40 mm wide. Their axes seem to be approximately parallel to axes of pedal imprints. Digits I–IV diverge of about 50°; of them, III and IV are about 26 mm long. Digit V imprint is not preserved.

Remarks.—Specimen Muz. PIG OS-220/39: 1–6 clearly resembles *Dimetropus* (= *Gonfaronipes*) *latus* Heyler and Montenat, 1980 (see Gand 1987: fig. 58A, B) and specimen described as *Chelichnus incurvus* Gand et al., 1995 (see Gand et al. 1995: fig. 11, pl. 4.1). The exact comparison of relatively small in size *Dimetropus* sp. from Tumlin Gród (Muz. PIG OS-220/39: 1–6) with those ichnospecies is now, unfortunately, impossible and needs new, more complete materials.

In Tumlin Gród much larger imprints of ?*Dimetropus* sp. occur, to date only found as indeterminable, poorly and fragmentarily preserved specimens, comparable in the size and shape to those of *Dimetropus leisnerianus* (Geinitz, 1863). Specimen Muz. PIG OS-220/64 shows palm part of imprint with four digits showing distinct, big claw marks (Figs. 32E, 33E). The width of digit group I–IV, which length increases from I to IV, is 70 mm. Digit IV is the longest but slightly narrower than III and II. The divarication of digits I–IV is low, although not exactly determinable. On the slab Muz. PIG OS-220/69 (Figs. 32A, 33D) only claw scratches made by several big animals are present, accompanying mud cracks. They have been left by large sized trackmakers; with footprints up to 130 mm wide. A similar state of preservation of big footprints *Dimetropus leisnerianus* was observed by Gand (1987: fig. 50).

Uncollected slabs with poorly preserved, indeterminable, although numerous, imprints were observed in the upper part of the Tumlin Gród quarry (Fig. 31D); Muz. PIG OS-220/70 (Fig. 31B). Specimen Muz. PIG OS-220/71 (Fig. 32B) show presence of similar, big imprints with digit length increasing from I to IV. Its width of the digit group I–IV attains 85 mm. Unfortunately, the shape of whole imprints and trackway features are impossible to determine. The material obtained from Tumlin Gród also contains indeterminable claw scratches or problematic imprints showing the width of digit group I–IV exceeding 150 mm (Fig. 32C), made by very large animals. The length of the largest footprint-like structure exceeds even

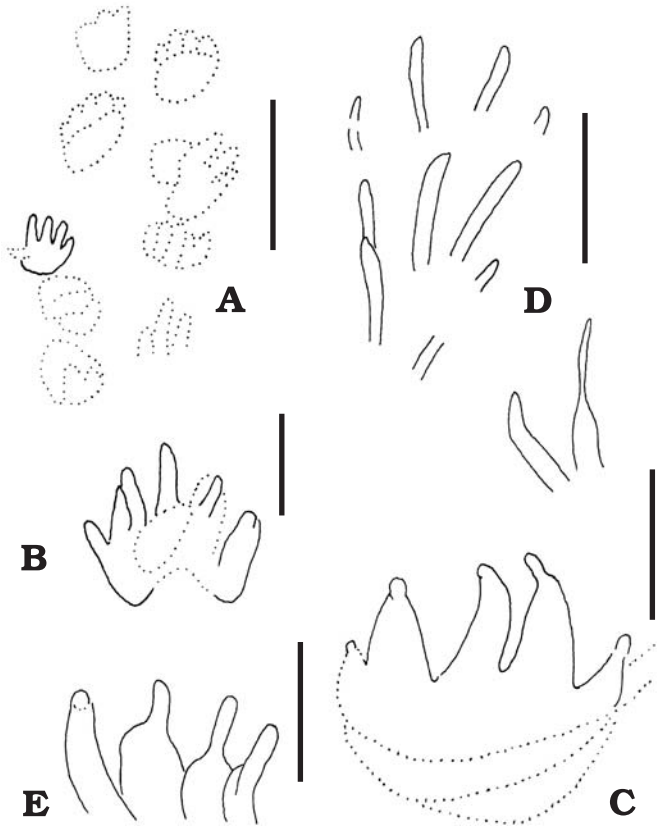

Fig. 33. **A**–**C**. *Chelichnus* cf. *duncani* (Owen, 1842). **A**. Muz. PIG OS-220/39: 20–27 somewhat irregular trackway. **B**. Muz. PIG OS-220/63: 1 isolated imprint. **C**. Muz. PIG OS-220/62: 1 left pedal imprint. **D**, **E**. ?*Dimetropus* sp. **D**. Muz. PIG OS-220/69 slab with claw scratches. **E**. Muz. PIG OS-220/64: 1 specimen with four digits imprints. Scale bars: A, D, 10 cm; B, C, E, 5 cm.

200 mm. They testify the possible presence of very large animals leaving footprints comparable in size with the largest ichnospecies of *Dimetropus* or *Pachypes*. Such poorly documented and problematic imprints deserve future research.

Ichnogenus *Chelichnus* Jardine, 1850

Chelichnus cf. *duncani* (Owen, 1842)

Figs. 30B, C, 31A–C, 33A–C.

"Protorosuchia indet." Ptaszyński 2000b: fig. 5, specimen described in this paper as Muz. PIG OS-220/68: 1, 2 (Fig. 30B).

Material.—Muz. PIG OS-220/39: 20–27 the best visible part of the trackway from the slab Muz. PIG OS-220/39 (Figs. 31A, 33A); Muz. PIG OS-220/62: 1, 2 set of left pedal and manual (poorly preserved) imprints (Figs. 31C, 33C); Muz. PIG OS-220/68: 1, 2 set of poorly and shallowly impressed left pedal and manual imprints (Fig. 30B).

Description.—Trackway Muz. PIG OS-220/39: 20–27 (Figs. 31A, 33A) is the most completely preserved part of the larger association of poorly preserved imprints. Manual and pedal imprints are not distinguishable. Imprints are about five centimetres in diameter. Their axes are approximately parallel to the trackway. The width of pace can be determined at about 7 cm; pace angulation attains about 90°. The best preserved footprint, specimen Muz. PIG OS-220/39: 23 is 47 mm wide and 39 mm long. Digits I–IV diverge of 30°, while the divarication of digits I–V attains 75°. At least first four digits end sharply and possibly had claw marks.

Digits I and II are 20 and 23 mm long. Digits III and IV are equal in length, attaining 25 mm. Digit V is somewhat shorter, 23 mm. The separation of pedal digit II and IV bases is 13 mm. In the set of left imprints Muz. PIG OS-220/62: 1, 2 both imprints are wide and relatively short. The second one, interpreted as manual imprint is poorly visible. The first one, Muz. PIG OS-220/62: 1 (Figs. 31C, 33C) has five digits. Possibly all digits have claw marks, distinctly visible on tips of II, III, IV and V. The width of the footprint is 85 mm, while its length attains about 75 mm. The length of digits, which may be slightly deformed by the sliding movement, increase from I to IV: 20, 40, 50, 50 mm (the III and IV are equal in length). The length of digit V attains approximately 40 mm. Digits I–V, I–IV, II–IV diverge of relatively low angles: 55, 25, and 15°, respectively. The separation of pedal digit II and IV bases is 35 mm.

Specimen Muz. PIG OS-220/68: 1, 2 (Fig. 30B) shows set of left pedal and manual imprints. The shape of footprints, except for pedal digits II–IV, is not clearly visible. Pedal imprint is about 80 mm long and 75 mm wide. Digits I–V diverge of 75°. The separation of pedal digit II and IV bases is 30 mm. In the specimen Muz. PIG OS-220/68: 2 interpreted as somewhat smaller, manual imprint, the distance between externally situated digits, possibly I–IV attains 50 mm; their divarication attains 84°. Indeterminable, rounded, imprints with a diameter of 50–80 mm imprints, with no visible details of the foot, occurring on upper sides of layers, sometimes with sand crescents around (Muz. PIG OS-220/65, Muz. PIG OS-220/66, Muz. PIG OS-220/67). Although not determinable, they possibly represent *Chelichnus*.

Remarks.—Because no clear trackway known, and presence of specimens mainly as isolated, poorly preserved imprints, their exact determination is difficult. According to the newest revision (McKeever and Haubold 1996) they may be regarded as relatively small (Muz. PIG OS-220/39: 20–27) and relatively large (Muz. PIG OS-220/62: 1) representatives of *Chelichnus* cf. *duncani* (Owen, 1842). Among footprints from Tumlin Gród, there are observed atypically and not completely impressed, deformed by the sliding movement, attributed to *Rhynchosauroides kuletae* ichnosp. nov. (Fig. $35A_4$), ? *Phalangichnus gradzinskii* ichnosp. nov. (Fig. 34A, B) and *Palmichnus lacertoides* ichnosp. nov. (Fig. 35C), which if found as isolated imprints, could be erroneously determined as *Chelichnus* representatives.

We believe, that vertebrate ichnotaxa should be uniform class of objects. It means, that all should be described as objects with comparable and compared features. Only under this condition vertebrate tracks can be treated as fully valuable systematic (parataxonomic) group. It should be accepted, that considerable part of specimens can not be exactly determined rather, than create a different parataxonomical category of poorly preserved tracks originated in the Late Permian dune environment (see McKeever and Haubold 1996). Erecting not

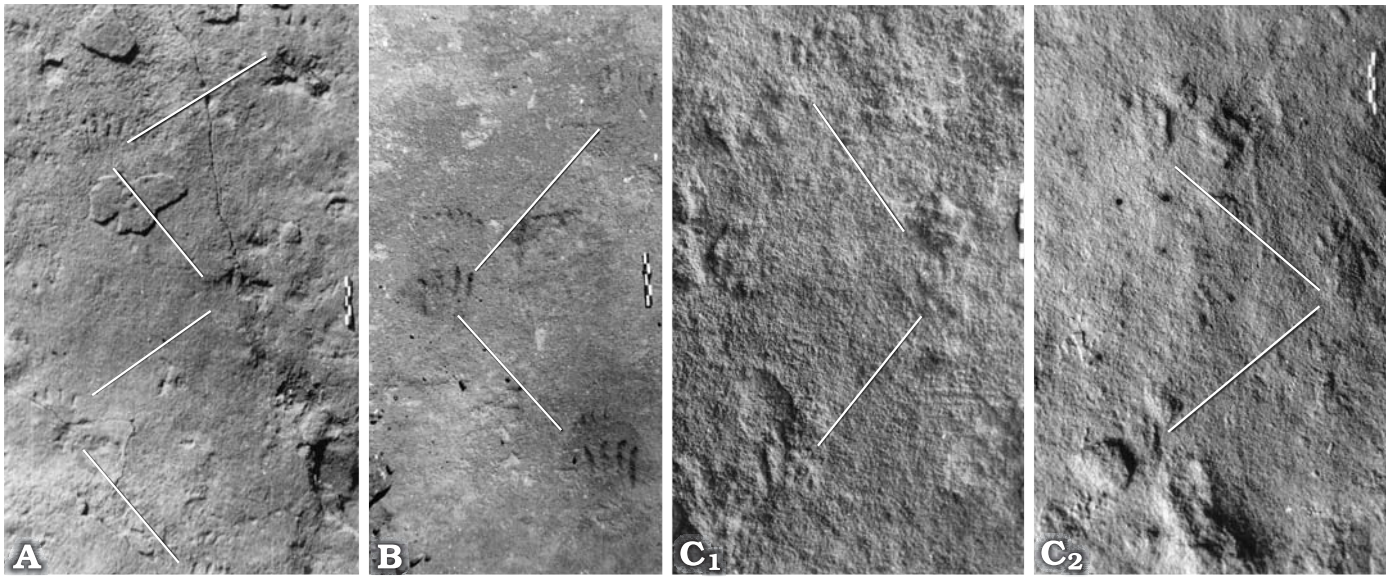

Fig. 34. **A**. Muz. PIG OS-220/27: 98–102 five consecutive pedal, partly with accompanying manual imprints preserved in the state characteristic of *Phalangichnus*. **B**. Muz. PIG OS-220/73: 76–81 three consecutive pedal and manual imprints preserved in the state characteristic of *Phalangichnus*. **C_1**. *Palmichnus lacertoides* ichnosp. nov.; Muz. PIG OS-220/39: 7–12 three consecutive sets of imprints. **C_2**. *Phalangichnus gradzinskii* ichnosp. nov.; Muz. PIG OS-220/39: 28–33 three consecutive sets of imprints. Scale bars 5 cm.

fully comparable categories of ichnotaxonomic objects, with diagnostic criteria not uniform, but depending on facies, age and kind of taxon, is not a recommendable practice, making different ichnofaunas incomparatible (not described with uniform criteria). The data derived from Tumlin Sandstone show that it may lead to erroneous conclusions concerning poor diversity of the Late Permian vertebrate ichnofaunas (see McKeever and Haubold 1996).

The problem of *Anhomoiichnium* and tracks not exactly determined. The problem of unsatisfactory preservation is connected with the formal existence of the questionable (see Haubold et al. 1995; Haubold 1996; Haubold and Stapf 1998) ichnogenus *Anhomoiichnium* Dozy, 1935 with the ichnospecies *A. diversum* (Schmidt, 1959). We found no trackways or isolated imprints unequivocally attributable to this ichnospecies. Some poorly preserved or deformed specimens representing possibly *Paradoxichnium tumlinense* ichnosp. nov. (Muz. PIG OS-220/47: 1 isolated pedal imprint; not numbered set of right imprints on the slab Muz. PIG OS-220/27, Fig. 35A$_1$) and some imprints of *Palmichnus lacertoides* ichnosp. nov. (Fig. 35C) exhibit shape and characteristic deformations very similar to those of *Anhomoiichnium* (see Fichter 1983b: figs. 27–29). At present, the existence of *Anhomoiichnium* representatives in Tumlin Sandstone cannot be confirmed.

During field investigations we found many trackways and isolated imprints not preserved well enough for detailed determination. Some of them show only digit tips imprints situated characteristic as in *Phalangichnus* trackways (Fig. 34A, B). Others show mostly manual imprints visible (Fig. 35A$_1$, A$_3$). Many tracks are too poorly preserved to account them to any ichnogenus or ichnospecies (Fig. 32C, D), but their presence supplements the knowledge concerning this ichnocoenose and is of big meaning to the whole concept of the assemblage. Systematic position of those problematic specimens may be explained in future but their presence can be here already pointed out.

Conclusions

The vertebrate track assemblage from the Tumlin Sandstone is the youngest known from the Permian vertebrate ichnofaunal succession of the Buntsandstein.

This assemblage contains three ichnogenera attributable to amphibian trackmakers (for *Amphisauropus* see Gand and Haubold 1988). Their presence indirectly confirms a Permian age for the assemblage because all post-Permian temnospondyl amphibians are considered to be of Gondwana origin, whereas most of those present in the Late Permian were exclusively Laurasian (Kozur 1998a after Milner 1990). Indeed, the Early Triassic assemblages contain a quite different ichnofauna, with imprints made by amphibian trackmakers having five digits in both pes and manus, *Capitosauroides* Haubold, 1971a (Fuglewicz et al. 1990; Ptaszyński 2000a; Kuleta et al. 2001).

Among Late Permian track assemblages, the ichnoassemblage from the Tumlin Sandstone most closely resembles that from the Val Gardena Sandstone (Conti et al. 1977; Ceoloni et al. 1988), sharing the presence of *Rhynchosauroides* tracks. It is possible that both assemblages are even more similar than appear from their ichnofaunal lists, as the same tracks might be ascribed to different ichnotaxa by different authors (see Gand 1987; Gand and Haubold 1988). The Val Gardena ichnofauna also shows the presence of ichnogenera characteristic of the Rotliegendes such as *Ichniotherium*,

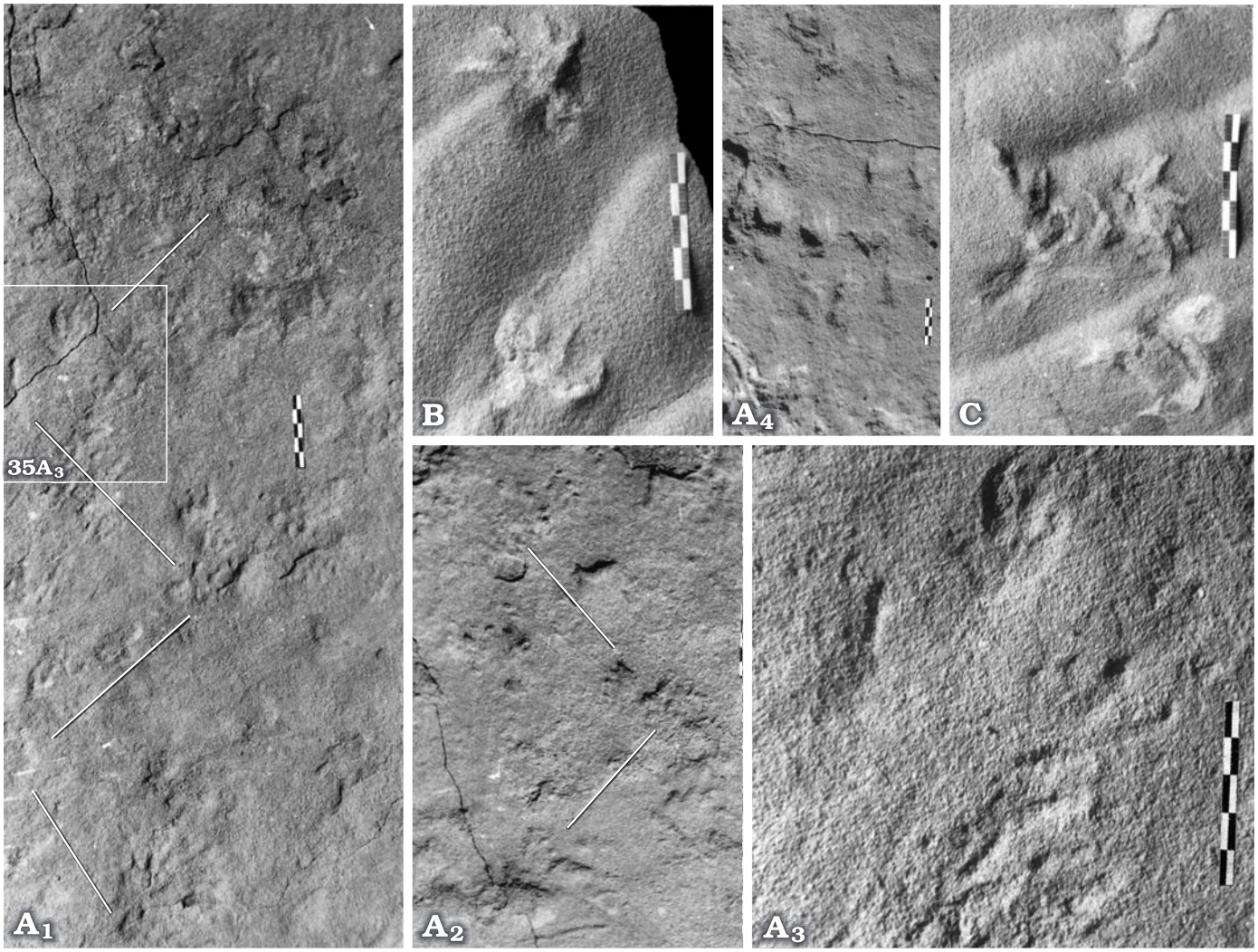

Fig. 35. **A$_1$**. Muz. PIG OS-220/27: 56–62 not determined trackway showing mostly manual imprints (possibly representing *Phalangichnus gradzinskii* ichnosp. nov.). **A$_2$**. *Paradoxichnium tumlinense* ichnosp. nov.; Muz. PIG OS-220/27: 173–178 three consecutive sets of pedal and manual imprints. **A$_3$**. Two sets of imprints, Muz. PIG OS-220/27: 60, 61 set of left poorly preserved pedal and manual imprints, accompanying not numbered, just visible set of right pedal and manual imprints of *Paradoxichnium tumlinense* ichnosp. nov. preserved in state could be erroneously interpreted as set of *Anhomoiichnium*. **A$_4$**. *Rhynchosauroides kuletae* ichnosp. nov.; Muz. PIG OS-220/27: 73 left manual imprint (in the center of the photograph) deformed by the sliding movement could be erroneously interpreted as *Chelichnus*. **B**, **C**. *Palmichnus lacertoides* ichnosp. nov. **B**. Muz. PIG OS-220/57: 1, 2 set of left pedal and manual impressed in state could be erroneously interpreted as *Chelichnus.***C**. Muz. PIG OS-220/55: 30, 31 set of right pedal and manual in state of preservation could be erroneously interpreted as *Anhomoiichnium*. Scale bars 5 cm.

Hyloidichnus and *Dromopus* (Conti et al. 1977; Ceoloni et al. 1986), whose presence in the Tumlin ichnoassemblage has not been confirmed. In both ichnoassemblages *Paradoxichnium*, *Palmichnus* and *Phalangichnus* have been found, together with other ichnogenera (*Varanopus*, *Chelichnus*, *Dimetropus*) widely known from the Rotliegendesbut absent in younger Early Triassic ichnoassemblages.

The most characteristic feature of the Tumlin ichnoassemblage is the presence of numerous Rhynchosauroidae footprints attributed to lacertoid trackmakers. They are seldom present in other Late Permian deposits. This may be an artifact due to misidentification resulting from the resemblance of poorly preserved Rhynchosauroidae tracks to *Chelichnus*. For example, Hunt et al. (1995), warned that *Gilmoreichnus hermitanus* tracks may be erroneously identified as *Chelichnus* or *Laoporus*, while *Amphisauropus* imprints may be also misidentified as *Chelichnus* (Haubold and Stapf 1998). Indeed, atypical footprints of *Palmichnus*, *Paradoxichnium* and *Phalangichnus* show great resemblance to *Chelichnus*, and such poorly preserved tracks might be erroneously determinated as representatives of this ichnogenus (see above). The recent papers of Haubold et al. (1995), Haubold (1996, 1998), McKeever and Haubold (1996) and Haubold and Stapf (1998) contain comprehensive revisions. Type specimens of previously described *Phalangichnus simulans*, *Phalangichnus alternans*, *Palmichnus renisus* and *Palmichnus tambachensis* were recognised as *Chelichnus*, *Dromopus*, and *Varanopus* or indeterminable specimens. These ichnogenera should thus be

treated as "phantom taxa". On the other hand, tracks compatible with definitions of the ichnogenera *Phalangichnus* and *Palmichnus* by Schmidt (1959) do exist, as confirmed by their occurrence in the Upper Permian Val Gardena Formation (*Phalangichnus perwangeri*) and newly discovered material from the Tumlin Sandstone. We agree with Haubold et al. (1995), Haubold (1996, 1998) and Haubold and Stapf (1998) that the type specimens of these ichnospecies are poorly or incompletely impressed, but cannot be recognised as belonging to *Chelichnus*, *Dromopus* or *Varanopus*.

Many specimens described as *Chelichnus* from Saxonian and Thuringian localities (McKeever 1994; Haubold et al. 1995; Haubold 1996, 1998; McKeever and Haubold 1996; Haubold and Stapf 1998), possibly made by Rhynchosauroidae trackmakers, need ichnotaxonomic revision. Modern, systematic revision is also required for *Amphisauropus latus*, possibly a junior synonym of *"Ichnium" pachydactylum* Pabst, 1900 and *"Saurichnites" intermedius* Fritsch, 1895 (see above), and also for small, differentiated imprints not always sufficiently well preserved, that have been attributed by different authors to *Saurichnites* Geinitz, 1861, *Batrachichnus* Woodworth, 1900, *Anthichnium* Nopcsa, 1923, *Amphisauroides* Haubold, 1970 and many other different ichnogenera.

There is no reason to assume reduced vertebrate diversity during the latest Permian (see McKeever and Haubold 1996). The Tumlin Sandstone Member, containing almost exclusively dune and interdune sandstone deposits, contains diverse and abundant vertebrate and invertebrate ichnocoenoses (Gradziński et al. 1979, Gradziński and Uchman 1994, Ptaszyński 2000b, Ptaszyński and Niedźwiedzki 2002). A high diversity of vertebrate tracks is also known from other Late Permian localities (Conti et al. 1977; Fichter 1983b; Gand et al. 1995; Gand et al. 2000).

Representatives of the Chirotheriidae are absent from the Tumlin ichnoassemblage, although some poorly preserved, isolated and dubious imprints were found in the Val Gardena Formation (Conti et al. 1977; Ceoloni et al. 1986). In the somewhat younger Early Triassic Labyrinthodontidae Beds of the Holy Cross Mountains at Wióry (Fuglewicz et al. 1990; Ptaszyński 2000a), as in many other Early Triassic tracksites of the world, Chirotheriidae became a significant element.

Large tracks from the Tumlin Sandstone that cannot be precisely determined have equivalents in Permian and Triassic tracks from other localities that are attributed to pelycosaurs, pareiasaurs and therapsids (see Gand and Haubold 1988; Ceoloni et al. 1988; Hunt et al. 1993; Gand et al. 2000).

In the Late Permian, the development of efficiently running representatives of the ichnofamily Rhynchosauroidae is observed (ichnogenera: *Rhynchosauroides*, *Phalangichnus*, *Paradoxichnium*, and *Palmichnus*). The trackmakers could overstep manus by pes, and this indicates their ability to run quickly. Except for *Phalangichnus*, all of these ichnogenera have a characteristic feature: a long and often preserved digit V imprint. Only the *Rhynchosauroides* trackmakers survived into the Triassic. Among Lower and Middle Triassic small ichnogenera with relatively long and usually fully impressed digit V is *Procolophonichnium* Nopcsa, 1923 (Demathieu and Müller 1978; Demathieu and Oosterink 1983; Haubold 1971b, 1984; Fuglewicz et al. 1990; Ptaszyński 2000a).

In the Early Triassic Wióry ichnoassemblage *Prorotodactylus* Ptaszyński, 2000 appears. This has features (close to *Rhynchosauroides* and *Rotodactylus* Peabody, 1948) expected of a dinosaurs ancestor (Ptaszyński 2000a). Possibly as early as the Late Permian there was selection for efficient running, though not necessarily for large size. This could be related to the fact that some groups of vertebrates in both synapsid and archosaur lineages acquired better running adaptations through modified stance (Ptaszyński 2000a) and physiological developments, leading to endothermy. These phenomena might have accelerated the evolutionary rates of terrestrial vertebrates in the Late Permian.

The transitional character of Late Permian vertebrate ichnofaunas provides no indication of a catastrophic mass extinction of terrestrial vertebrate faunas (compare the discussion in Kozur 1998a, b). Instead, changes seem to be gradual, although rapid and consistent, throughout the whole of the Late Permian (see Kozur 1998a: 256; Ptaszyński and Niedźwiedzki 2002). While it is difficult to prove this evolutionary scenario, investigations of vertebrate body fossil assemblages seem to be compatible with it (Lozovsky 1997).

Thus, further studies of vertebrate tracks may be of great importance not only for enhancing palaeontological knowledge, but also for the biostratigraphy of terrestrial deposits, and models of mass extinctions.

Acknowledgements

The authors are grateful to Maria Kuleta, Stanisława Zbroja, Jolanta Studencka, and Jerzy Gągol, Holy Cross Branch of the Polish Geological Institute at Kielce, for their friendly help in field investigations, kind remarks, and suggestions. Thanks are also due to Sławomir Ptaszyński and Łukasz Ptaszyński, discoverers of many valuable specimens, for their help and field assistance. Thanks are offered also to Heinz Kozur for remarks and discussions especially concerning stratigraphic aspects of Fig. 2.

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