A Late Triassic Dinosaur-Dominated Ichnofauna from the Tomanová Formation of the Tatra Mountains, Central Europe

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A Late Triassic dinosaur-dominated ichnofauna from the Tomanová Formation of the Tatra Mountains, Central Europe

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Osteological fossils of dinosaurs are relatively rare in the Late Triassic and Early Jurassic. Thus, ichnofossils are a critical source of information on Late Triassic terrestrial vertebrate communities. The outcrops of the Tomanová Formation (?late Norian–Rhaetian) in the Tatra Mountains of Poland and Slovakia have yielded a diverse ichnofauna. Seven more or less distinct morphotypes of dinosaur tracks have been recognized and are discussed. Most tracks are partly eroded or deformed, but are preserved well enough to be assigned to a range of trackmakers, including early ornithischians, small and large theropods (coelophysoids and/or possibly early tetanurans), and probably basal sauropodomorphs ("prosauropods") or first true sauropods.

Key words: dinosaur tracks, paleoichnology, Triassic, Tatra Mountains, Poland, Slovakia.

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Introduction

Trackways, footprints and coprolites are the most common vertebrate fossils and provide unparalleled information about the behavior of terrestrial vertebrates in the environments in which they lived (Lockley 1998). One of the aims of ichnological research is the reconstruction of the animal communities represented by the trace fossils. However, in the case of vertebrates in particular, such reconstruction can be fraught with difficulties, mostly due to problems with identifying the trackmakers and their relative abundance.

Studies of the Late Triassic ichnofauna illustrate some of these difficulties (see Olsen et al. 1998, 2002), but these are also critical fossils to consider when studying faunal change during the Late Triassic, an interval marked by evolutionary radiations, climate change, and supposed mass extinctions (see Brusatte et al. 2008). The information that can be inferred from Late Triassic ichnofaunas is particularly vital for our understanding of dinosaur ecology because of the scarcity of skeletal remains of Late Triassic members of this iconic group (see Langer and Benton 2006; Nesbitt et al. 2007; Brusatte et al. 2008; Langer et al. 2010).

This paper presents a description of the Late Triassic dinosaur track assemblages from the Tatra Mountains of Poland and Slovakia (Fig. 1). This overview includes the revision of published and previously unpublished material (housed in the Museum of the Tatra Mountains National Park in Tatranská Lomnica, Slovakia; Slovak National Museum, Bratislava, Slovakia and Nature Museum of the Tatra Mountains National Park, Zakopane, Poland), and is based upon both data generated from existing collections and in situ measurements of additional material that has recently been discovered during new fieldwork (Figs. 2A, B, 3A, B–E, 4B, C, 5, 6). This fieldwork was part of the revision of Carboniferous–Cretaceous tetrapod tracks in Poland by a group of researchers from the Department of Paleobiology and Evolution of the University of Warsaw (Warsaw, Poland), the Institute of Paleobiology, Polish Academy of Sciences (Warsaw, Poland) and the Geological Museum, Polish Geological Institute (Warsaw, Poland).

The first dinosaur tracks reported from the Tatra Mountains were discovered in the Tomanová Formation, on the southern slope of Czerwone Wierchy in Cicha Valley, in the Červený Ŭplaz region of Slovakia (Fig. 1). These tracks were found by Jozef Michalík and described by Michalík et al. (1976). Those authors proposed a new ichnospecies, *Coelurosaurichnus tatricus*, for three tridactyl ichnites preserved on one sandstone slab (specimen numbers Z 14 296—paratype and Z 14 297—holotype, Slovak National Museum, Bratislava). Later, Michalík and Kundrát (1998) redescribed these ichnites and suggested that they could be referred to the ichnogenus *Eubrontes* Hitchcock, 1845, an ichnotaxon that is characteristic of the Early Jurassic dinosaur ichnoassemblages from North America, Europe and South Africa (Olsen

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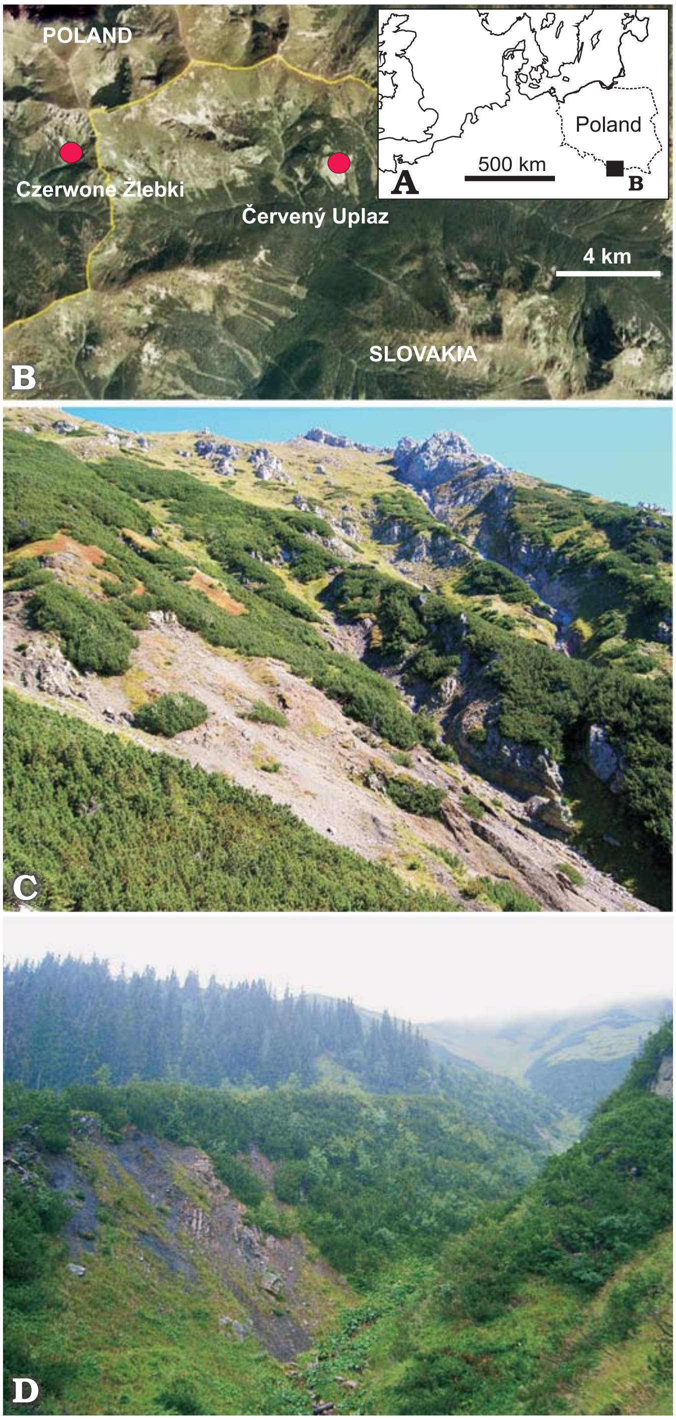

Fig. 1. **A**. The location of this area in Poland. **B**. Satellite map of the Western Tatra Mountains showing positions of sites at which dinosaur tracks have been recorded. **C**. Czerwone Żlebki tracksite, Poland. **D**. Červený Ŭplaz tracksite, Slovakia.

and Galton 1984; Olsen et al. 1998; Lockley and Meyer 2000). Large tridactyl theropod tracks discovered in Cicha Valley were also revised by Gierliński and Sabath (2005) and Lucas et al. (2006). According to Gierliński and Sabath (2005) these tracks are assignable to *Eubrontes* and are associated in the Tatra Mountains tetrapod ichnoassemblage with characteristic Triassic ichnogenera: "*Tetrasauropus*" (= *Eosauropus*, Lockley et al. 2006) and "*Pseudotetrasauropus*" (= *Evazoum*, Nicosia and Loi, 2003; = *Brachychirotherium*, Klein et al. 2006). Both proposals have not been confirmed by the study presented here.

Nearly thirty years later, new footprints were discovered in the Late Triassic fluvial deposits of the Tatra Mountains (Niedźwiedzki 2005, 2008; Niedźwiedzki and Sulej 2007). In September 2004, three dinosaur footprints were found at Czerwone Żlebki, in the Polish Western Tatra Mountains (Fig. 1). Two specimens were found in the talus slope (Fig. 2C, D) and the third (Fig. 4E) was found in situ in the middle part of an exposed lithological profile. Other material was discovered in 2006 and 2007 during short field investigations in the Polish and Slovakian parts of the Tatra Mountains. These tracks came from two sites (Czerwone Żlebki and Červený Ŭplaz, Western Tatra Mountains; Fig. 1) where the strata of the Tomanová Formation are well exposed.

The new footprints represent pedal ichnites of theropod dinosaurs (cf. *Kayentapus* isp., *Anchisauripus* isp., cf. *Grallator* isp.; Figs. 3–5) and possible ornithischian dinosaurs (cf. *Anomoepus* isp., ?cf. *Moyenisauropus* isp.; Fig. 2). There are also enigmatic large circular and oval structures, probably made by an early sauropodomorphs (Fig. 6), and a large tridactyl ichnite (described in this paper as cf. *Eubrontes* isp.), probably theropod in origin (Fig. 5). These new paleoichnological finds are important for understanding the ichnodiversity and ichnotaxonomy of latest Triassic (?Norian– Rhaetian) vertebrate assemblages (especially dinosaur assemblages), and may bear on the patterns of faunal change associated with the radiation and early evolution of dinosaurs.

Geological setting

Near the end of the Triassic period, following the depositions of the characteristic Alpine Keuper facies, typical continental conditions developed in the High-Tatric Basin, resulting in the formation of fresh-water organic-rich black shales with macrofloral remains (Raciborski 1890) and sphaerolitic iron-ore nodules (Radwański 1968; Nejbert and Jurewicz 2004). These strata, which include the Tomanová Formation, have been studied for more than 100 years; important works include Raciborski (1890), Uhlig (1897), Kuźniar (1913), Rabowski (1925, 1959), Turnau-Morawska (1953), Kotański (1956, 1959a–c, 1961), Gorek (1958), Radwański (1968), Michalík (1978, 1980), and Michalík et al. (1976, 1988). The Tomanová Formation is usually assigned a Rhaetian age (Jurewicz 2005). Under the lithostratigraphic scheme of Raciborski (1890), the "Tomanová layers" included the whole clastic complex of diverse sediments of various colors. Uhlig (1897) divided this complex into lower-beds (so-called "varicolored") classified as Keuper, and upper dark brown/black-colored beds of Rhaetian age. According to Uhling (1897), only the upper, dark brown part of the complex was designated as the "Tomanová layer".

Plant fossils from the upper part of the assemblage, described by Raciborski (1890), were interpreted as Rhaetian in age (*Lepidopteris* floral assemblage). Macrofloral fossils from the Tomanová Formation were unfortunately not the subject of detailed research by Reymanówna (1984) and Michalík et al. (1988).

A similar division of the clastic complex of the "Tomanová layer" was proposed by Kotański (1959b, c, 1961). The lower complex ("varicolored"), distinguished and classified by Uhlig (1897) as Keuper strata, was referred to as Rhaetian by Kotański (1956).

In addition, on the basis of the continuity of sedimentation between the Norian/Rhaetian complexes (noticed previously by Uhlig 1897), it was assumed that the "Tomanová layers" (sensu Uhlig 1897) may partially represent Norian deposits (Kotański 1959b, c, 1961). This assumption is not in contradiction to the macrofloral record. A Rhaetian macroflora, described by Raciborski (1890), originates from the upper part of the deposits of the Tomanová Formation. Slovakian researchers consider these deposits as Norian–Rhaetian. Michalík et al. (1976, 1988), on the basis of results of palynological studies, divided the Tomanová Formation into a lower part with a Norian–Rhaetian microflora and an upper sequence with a typical Rhaetian palynoassemblage. Similar palynological observations of the uppermost Triassic strata of the Tatra Mountains were presented by Fijałkowska and Uchman (1993). These researchers identified the palynoassemblage in the "Tomanová beds" as typical for the latest Norian–Rhaetian deposits of the Germanic Basin, and suggested its correlation with the upper part of the *Corollina meyeriana* Zone of Orłowska-Zwolińska's (1983) palynological scheme for the Polish Keuper. In this paper, the stratigraphic position and age interpretations of these Upper Triassic strata are based on the published analyses of macro- and microflora discussed above, together with lithostratigraphic data.

Systematic ichnology

This section contains the identified ichnotaxa in systematic ichnology, followed by forms that are left in open nomenclature. Material of uncertain designation is also referred to here. Dinosaur tracks from the Tomanová Formation are generally preserved as natural casts. Two ichnites preserved as true tracks (natural moulds) were also found. A total of twenty specimens were found. I identify seven kinds of track morphotypes and briefly summarize here my ichnotaxonomic concepts.

Ornithischia Seeley, 1887

Ichnogenus *Anomoepus* Hitchcock, 1848

Type species: *Anomoepus scambus* Hitchcock, 1848, Massachusetts, USA; Portland Formation, Lower Jurassic.

cf. *Anomoepus* isp.

Fig. 2A, D.

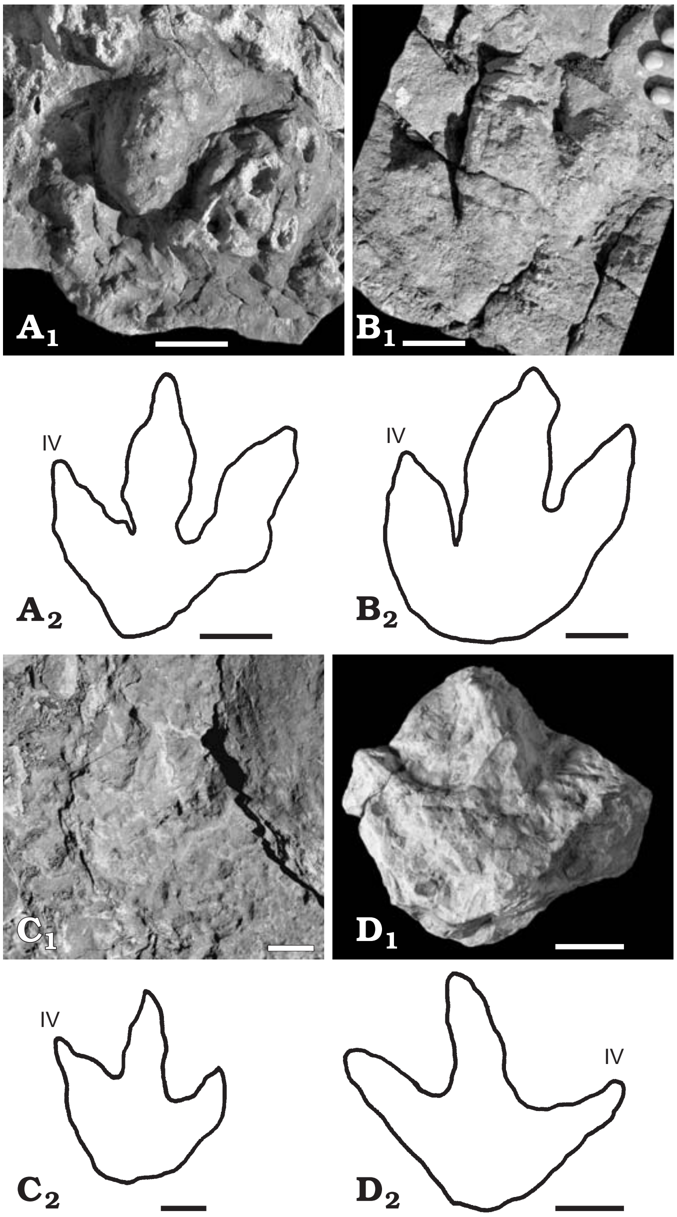

Fig. 2. Tridactyl tracks (pes prints) of possibly early ornithischian dinosaurs from the Czerwone Żlebki site, Tomanová Formation (?late Norian–Rhaetian), Poland. **A**, **B**. cf. *Moyenisauropus* isp. **C**, **D**. cf. *Anomoepus* isp. **A**–**C**. Specimens left in field. **D**. Specimen deposited at Tatra Mountains National Park, Zakopane, Poland. Photographs (A_1–D_1) and drawings (A_2–D_2). Scale bars 5 cm.

Description.—Two specimens (field observation from Czerwone Żlebki—specimen from Fig. 2A and specimen collected from Czerwone Żlebki and deposited at Tatra Mountains National Park, Zakopane, Poland; Fig. 2D) of tridactyl *Anomoepus*-like footprints were discovered at Czerwone Żlebki. Both tracks are preserved as natural moulds and are partly eroded and slightly deformed but their morphology (with short digit III which is also separated from the other digits) and size (both are about 15 cm long) are characteristic for the ichnogenus *Anomoepus* (Olsen and Rainforth 2003). The angle between the digits II and III varies from 25° to 42°,

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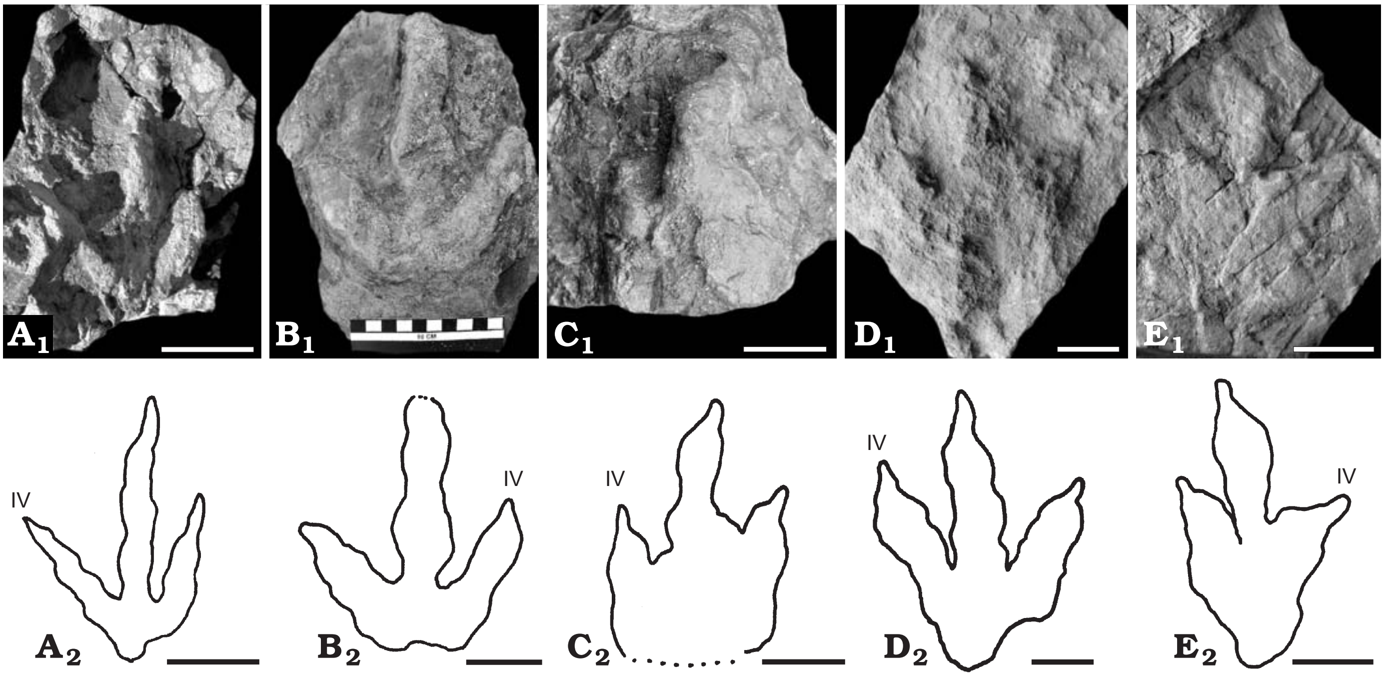

Fig. 3. Tridactyl tracks (pes prints) of small to medium sized theropod dinosaurs. **A**. cf. *Grallator* isp. **B**–**E** *Anchisauripus* isp. **A**, **E**. Specimens from Czerwone Żlebki site, Tomanová Formation (?late Norian–Rhaetian), Poland. **B**–**D**. Specimens from Červený Ŭplaz site, Tomanová Formation (?late Norian–Rhaetian), Slovakia. **A**, **C**, **E**. Specimens left in field. B. Specimen Z 14 297 housed at Slovak National Museum, Bratislava, Slovakia. **D**. Specimen deposited at Tatra Mountains National Park, Zakopane, Poland. Photographs (A_1–E_1) and drawings (A_2–E_2). Scale bars 5 cm.

while the angle between the digits III and IV varies from 26° to 57°.

Remarks.—*Anomoepus*, a purported ornithischian footprint, is a significant component of several diverse ichnofaunas from the Early Jurassic (Olsen and Rainforth 2003). The first unequivocal occurrence of this ichnogenus was reported from the basalmost Hettangian of the Newark Supergroup, eastern USA (Olsen et al. 2002) and from the earliest Jurassic of the Wingate-Kayenta transition zone at Lisbon Valley Oilfield in the western USA (Lockley and Gierliński 2006). *Anomoepus* tracks were also found in the earliest Hettangian of Poland (Gierliński et al. 2004). Therefore, the two specimens from the Tomanová Formation represent probably the oldest known occurrence of this characteristic ichnogenus.

Ichnogenus *Moyenisauropus* Ellenberger, 1974

Type species: *Moyenisauropus natator* Ellenberger, 1974, Lesotho, Africa; Upper Red Beds, Lower Hettangian.

cf. *Moyenisauropus* isp.

Fig. 2B, C.

Description.—Two specimens (field observations from Czerwone Żlebki) of tridactyl, 20–25 cm long, blunt-toed, and generally robust footprints with *Anomoepus*-like morphology were found at the Czerwone Żlebki site. Their morphology and size are strongly similar to the Early Jurassic *Moyenisauropus* ichnogenus (Gierliński 1999; Lockley and Gierliński 2006). Both discovered specimens show imprints of only two phalangeal pads of digit III (see Fig. 2). The angle between the digits II and III varies from 20° to 31°, while the angle between the digits III and IV varies from 29° to 45°.

Remarks.—The ichnogenus *Moyenisauropus* Ellenberger, 1974 is an intriguing ichnogenus first ilustrated by Ellenberger (1970, 1972, 1974) from the Late Triassic and Early Jurassic ichnofaunas of southern Africa (see also Smith et al. 2009). Ellenberger (1974) named eight ichnospecies of this ichnogenus, which later authors have regarded as a junior synonym of *Anomoepus* (Olsen and Galton 1984; Haubold 1984; Thulborn 1994; Olsen and Rainforth 2003). New observations suggest that most of the Ellenberger's (1974) material represents typical *Anomoepus* footprints (Gierliński 1991; Olsen and Rainforth 2003). There are indeed no morphological differences between *Anomoepus* and most ichnospecies of *Moyenisauropus* to distinguish them at the ichnogeneric level. However, *Moyenisauropus natator* (the type ichnospecies of *Moyenisauropus*) is different from any anomoepodid tracks. *Moyenisauropus* is distinguished from other tridactyl ornitischian ichnogenera from the Jurassic in having only two phalangeal pads on pedal digit III (Gierliński 1991, 1999; Lockley and Gierliński 2006). In *Moyenisauropus* the angle between pedal digits II and III, in comparison to that between digits III and IV, is usually larger than in the pes of *Anomoepus* (Lockley and Gierliński 2006). A new important occurrence of *Moyenisauropus* tracks was reported from the Early Jurassic of western United States (Lockley and Gierliński 2006) and there is also some diagnostic *Moyenisauropus*-like tracks from the Late Triassic of Sweden (Milán and Gierliński 2004).

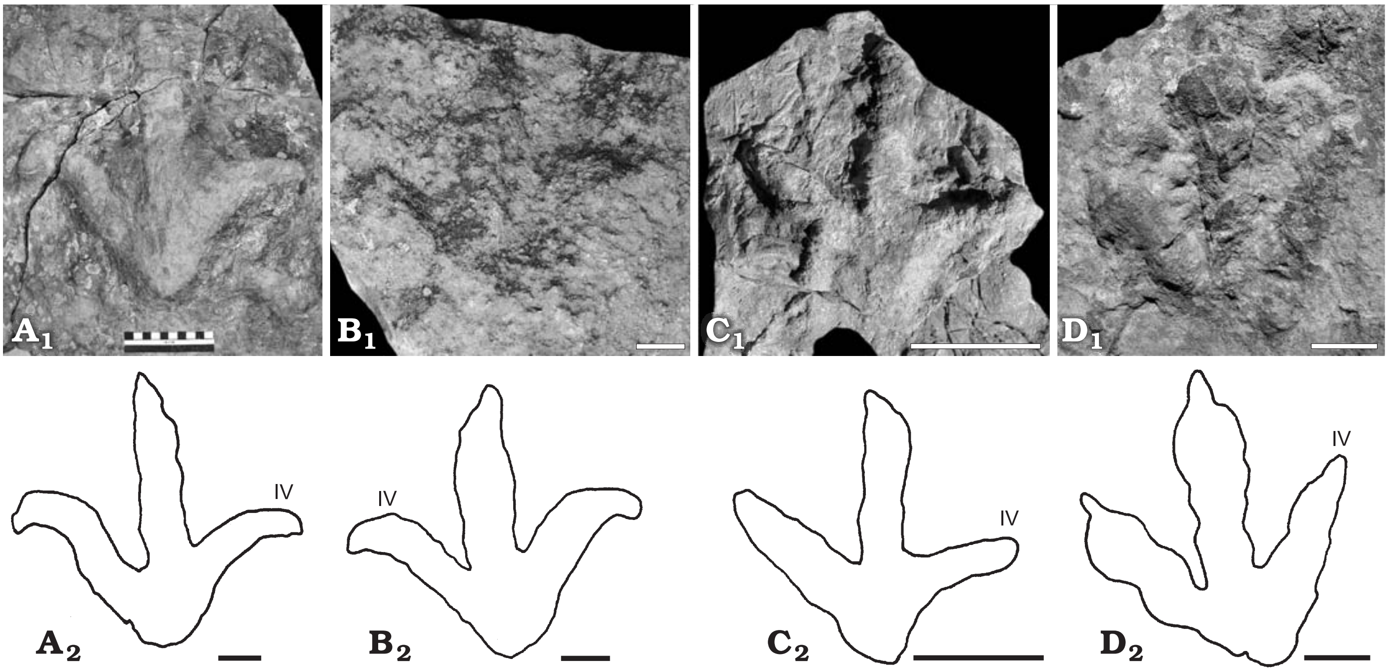

Fig. 4. Tridactyl tracks (pes prints) of small to large theropod dinosaurs. cf. *Kayentapus* isp. **A**, **B**. Specimens from Červený Ŭplaz site, Tomanová Formation (?late Norian–Rhaetian), Slovakia. **C**, **D**. Specimens from Czerwone Żlebki site, Tomanová Formation (?late Norian–Rhaetian), Poland. **A**. Specimen Z 14 296 housed at Slovak National Museum, Bratislava, Slovakia. **B**, **D**. Specimens left in field. **C**. Specimen deposited at Tatra Mountains National Park, Zakopane, Poland. Photographs (A_1–D_1) and drawings (A_2–D_2). Scale bars 5 cm.

Saurischia Seeley, 1887

Theropoda Marsh, 1881

Ichnogenus *Grallator* Hitchcock, 1858

Type species: *Grallator parallelus* Hitchcock, 1858; South Hadley, Massachusetts, USA, Portland Formation, Lower Jurassic.

cf. *Grallator* isp.

Fig. 3A.

Description.—One specimen of this ichnogenus preserved as natural cast was found (field observation from Czerwone Żlebki). *Grallator* is the ichnogeneric name applied to relatively small (generally <15 cm long pes) tridactyl tracks of functionally bipedal dinosaurs from the Late Triassic and Early–Middle Jurassic (Olsen et al. 1998; Clark et al. 2004). The pes is narrow, tulip-shaped and digit III projects far anteriorly relative to digits II and IV, which are rather sub-equal in length. The single specimen shows all these characteristics. The angle between the digits II and III is 9°, while the angle between the digits III and IV is 18°.

Remarks.—*Grallator* tracks are very common in Upper Triassic and Lower Jurassic strata (e.g., Lockley and Hunt 1995; Olsen et al. 1998; Gaston et al. 2003). They are found in the United States, Canada, Europe, Australia and China but are most abundant on the east coast of North America, especially the Upper Triassic and lowermost Jurassic formations of the northern part of the Newark Supergroup (Haubold 1984; Olsen et al. 1998).

Ichnogenus *Anchisauripus* Lull, 1904

Type species: *Anchisauripus sillimani* Hitchcock, 1865; Chicopee Falls, Massachusetts, USA, Portland Formation, Lower Jurassic.

Anchisauripus isp.

Fig. 3B–E.

Description.—Four specimens of this ichnogenus were found in the Tatra Mountains tracksites (field observations from Czerwone Żlebki and Červený Ŭplaz; specimens from Fig. 3C, E and two specimens collected from Červený Ŭplaz deposited at Slovak National Museum, Bratislava, Slovakia; Fig. 3B and Tatra Mountains National Park, Zakopane, Poland; Fig. 3D). All are partially eroded and deformed, but all specimens possess the characteristic size and morphology for this ichnogenus (Olsen et al. 1998). It is a medium sized functionally tidactyl ichnite (about 17–23 cm long) with relativelly low divarication of outer digits (about 25–30°). All discovered tracks are preserved as natural casts.

Remarks.—As has been discussed by several authors, there are various subtle differences between the type specimens of *Grallator parallelus* and *Anchisauripus sillimani.* For example, Olsen (1980) noted that the projection of digit III beyond the two lateral digits (II and IV) decreases rapidly throughout the *Grallator–Anchisauripus* ichnite assemblages (see Olsen et al. 1998). In addition, the whole footprint size, shape, and the position of the proximal pads are distinguishing features of both ichnotaxa. Although these differences are evident in the type specimens (e.g., Olsen et al. 1998), some authors avoid the use of the ichnogenus *Anchisauripus* because it is often

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difficult if not impossible to distinguish this morphotype from large *Grallator* and small *Eubrontes* (see Milner and Kirkland 2006).

Ichnogenus *Kayentapus* Welles, 1971

Type species: *Kayentapus hopii* Welles, 1971; Moenave Road Tracksite, Arizona, USA, Kayenta Formation, Lower Jurassic.

cf. *Kayentapus* isp.

Fig. 4A–D.

Description.—Four specimens (field observations from Červený Ŭplaz and Czerwone Żlebki; specimens from Fig. 4B, D and one specimen collected from Červený Ŭplaz deposited at Slovak National Museum, Bratislava, Slovakia; Fig. 4A and one specimen collected from Czerwone Żlebki and deposited at Tatra Mountains National Park, Zakopane, Poland; Fig. 4C). Those tracks represent a distinguished variant of grallatorid morphology with highly divaricated, elongate digits. The first specimen of that kind (Fig. 4A) was found in Slovakia and described by Michalík et al. (1976) and Michalík and Kundrát (1998). According to the diagnosis based on the method of Weems (1992) and the descriptions presented by Gierliński (1994, 1996), these specimens show characters of the ichnogenus *Kayentapus* Welles, 1971 (see Gierliński 1996). However, poor preservation of the Polish and Slovakian specimens does not allow ichnospecies-level assignment and precise comparison with known forms of this ichnogenus (see Gierliński 1996). These footprints are also slightly similar to footprints of early ornitchishian dinosaurs such as *Anomoepus* Hitchcock, 1848 and *Moyenisauropus* Ellenberger, 1974. However, the projection of digit III beyond the two lateral digits (II and IV) is much greater in *Kayentapus* than it is in ornithischian tracks (but see specimen of *Anomoepus* from Fig. 2D). The angle between the digits II and III varies from 34° to 53°, while the angle between the digits III and IV varies from 32° to 57°.

Remarks.—Footprints of *Kayentapus* are known from deposits of the Norian, Hettangian, Sinemurian, and Pliensbachian of Europe and North America (Weems 1987, 1992; Gierliński 1991, 1996; Gierliński and Ahlberg 1994; Lockley and Hunt 1995; Lockley and Meyer 2000; Gierliński et al. 2004, 2009). According to an osteological restoration presented by Gierliński and Ahlberg (1994), footprints belonging to *Kayentapus* were made by an Early Jurassic (Hettangian–Sinemurian) early theropod dinosaur similar in pedal anatomy to *Dilophosaurus wetherilli* Welles, 1970.

Ichnogenus *Eubrontes* Hitchcock, 1845

Type species: *Eubrontes giganteus* Hitchcock, 1845; Holyoke, Massachusetts, USA, Portland Formation, Lower Jurassic.

cf. *Eubrontes* isp.

Fig. 5.

Description.—A single specimen of a *Eubrontes*-like footprint was found in Cicha Valley, Červený Ŭplaz, Slovakia (field observation). This specimen is partially eroded but its size (~ 45 cm long) and morphology support referral to *Eubrontes*. *Eubrontes* is the ichnogeneric name applied to relatively large (pes length greater than 25 cm) tridactyl tracks of bipedal dinosaurs (Olsen et al. 1998). Digit III is usually relatively shorter than in *Grallator* and *Anchisauripus*, but essentially corresponds with grallatorid pattern and looks generally like a robust version of *Anchisauripus.* The angle between the digits II and III is 18°, while the angle between the digits III and IV is 36°.

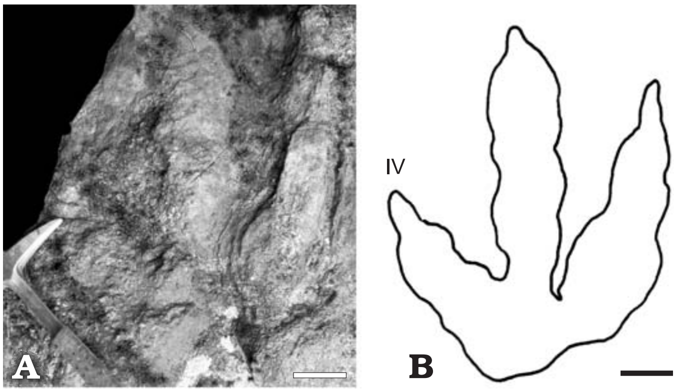

Fig. 5. Tridactyl track (pes print) cf. *Eubrontes* isp. from Červený Ŭplaz site, Tomanová Formation (?late Norian–Rhaetian), Slovakia. Specimen left in field. Photograph (**A**) and drawing (**B**). Scale bars 5 cm.

Remarks.—A theropod dinosaur is widely-agreed to be the *Eubrontes* trackmaker (Lockley and Hunt 1995; Olsen et al. 1998; Lockley and Meyer 2000) but some authors have suggested a sauropodomorph affinity for these tracks (e.g., Weems 2003). Since the 1980s, some workers have argued that the earliest occurrence of *Eubrontes* coincides with the Triassic–Jurassic boundary (see Olsen et al. 1998, 2002). However, other authors suggest that the earliest occurrence of *Eubrontes* does not coincide with the base of the Jurassic, as there are various well-documented *Eubrontes* records from the Late Triassic (Gierliński and Ahlberg 1994; Lucas et al. 2006). New occurrences of Late Triassic *Eubrontes*-like tracks have been reported (Lucas et al. 2006; Dzik et al. 2008), but it is outside the scope of this paper to discuss ichnotaxonomy, morphological variation and stratigraphic positions of those tracks. Preliminary observations, however, suggest that the Late Triassic record of large tridactyl tracks (with pes length greater than 25 cm) may represent rather two or even three different ichnomorphotypes and that the classical ichnospecies *Eubrontes giganteus* Hitchcock, 1845 is known only from the latest Rhaetian or in Rhaetian–Hettangian transitional beds (Gierliński and Ahlberg 1994; Gierliński et al. 2001, 2004; Dzik et al. 2008).

Sauropodomorpha von Huene, 1932

? Sauropodomorpha indet.

Fig. 6.

Description.—Two large (about 30–40 cm long), oval-shaped structures similar to earliest Jurassic sauropodomorph dinosaur tracks were found (see Gierliński et al. 2004) in both

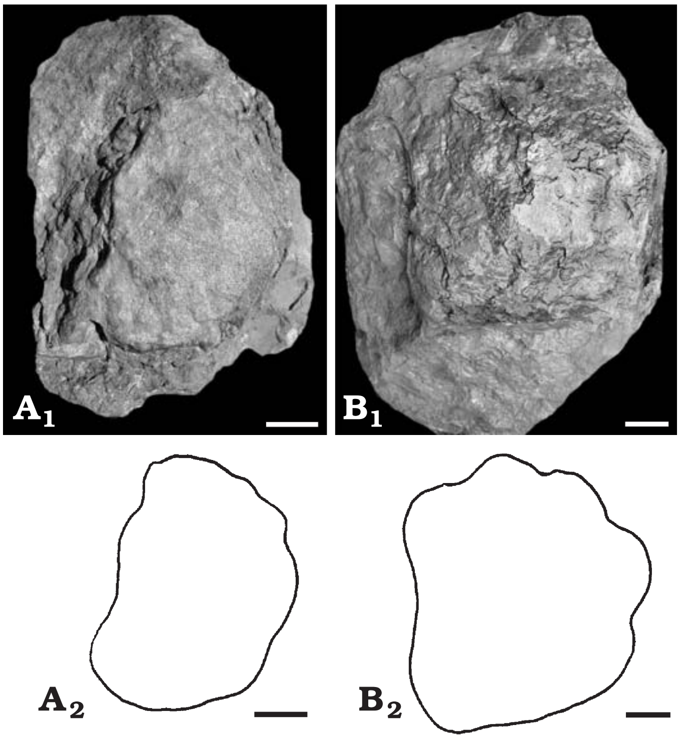

Fig. 6. ?Sauropodomorph tracks indet. **A**. Specimen from the Czerwone Żlebki found in 2004, Tomanová Formation (?late Norian– Rhaetian), Poland. **B**. Specimen from the Červený Ŭplaz found in 2007, Tomanová Formation (?late Norian–Rhaetian), Slovakia. Both specimens left in field. Photographs (A$_1$, B$_1$) and drawings (A$_2$,B$_2$). Scale bars 5 cm.

localities (Czerwone Żlebki, Poland and Červený Ŭplaz, Slovakia; field observations). Similar structures, but organized in a narrow-gauge trackway indicative of a large quadruped animal with strong heteropody (pes larger than manus), have been described from the Late Triassic of Europe, South Africa, and North America (*Eosauropus*, Lockley et al. 2006).

Remarks.—In all described Late Triassic specimens, the pedal imprints are oval and elongate, tetradactyl to pentadactyl, and possess a long axis and distal claw impressions that are rotated outwards. These features are not clearly visible in the specimens from the Tatra Mountains. The Tatra Mountains specimens are also similar to the Early Jurassic sauropodomorph footrpint *Parabrontopodus* because both are large in size (Lockley et al. 2006).

Comparison with other Late Triassic ichnofaunas

It is generally accepted that Late Triassic tetrapod footprint assemblages are dominated by archosaurs. The most common are tracks of *Brachychirotherium* (probable trackmakers are crurotarsans) and tridactyl dinosaur imprints of the *Grallator–Anchisauripus–Eubrontes* type (Klein and Lucas 2010). There is some controversy among tetrapod ichnologists concerning the presence and validity of other ichnogenera used for Late Triassic tracks, especially *Pseudotetrasauropus*, *Tetrasauropus*, *Evazoum*, *Eosauropus*, *Otozoum* (see Klein and Lucas 2010), but also *Moyenisauropus* (Milán and Gierliński 2004) and *Anomoepus* (Niedźwiedzki 2005; Gierliński 2009).

Theropod ichnogenera recorded from the Late Triassic of the Tatra Mountains are generally similar to those recorded in successions of the same or similar age in eastern North America (Weems 1987, 1992; Lockley and Hunt 1995), Europe (Haubold 1984; Lockley and Meyer 2000), South Africa (Ellenberger 1972; Olsen and Galton 1984) and South America (Melchor and de Valais 2006). However, some significant differences are apparent. (1) The dinosaur track assemblage from the Tatra Mountains is more diverse. This may be a reflection of either a different degree of study or preservational potential, or perhaps the current age determination of the Tomanová Formation is incorrect and it cannot be considered coeval with these other sites. However, further detailed studies may reveal a possible relationship with Late Triassic tracks described as the ichnogenus *Eubrontes*. (2) An intriguing single large footprint similar to the Early Jurassic *Eubrontes giganteus* was identified. *Eubrontes* tracks are well known from Lower Jurassic strata, especially in southern Africa, Western Europe, eastern North America and the southwestern USA, and some have advocated that the earliest occurrence of *Eubrontes* corresponds to the Triassic–Jurassic boundary. However, there are well documented Late Triassic records of *Eubrontes*-like footprints in Australia,

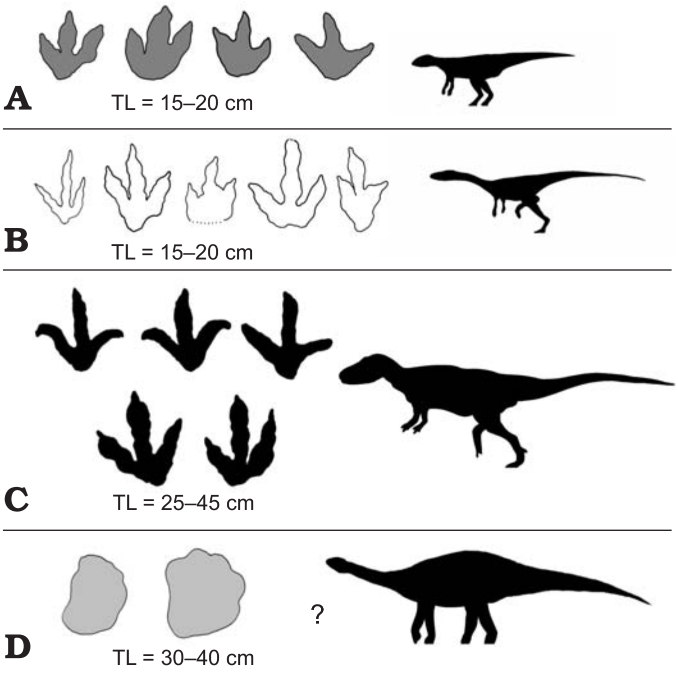

Fig. 7. Dinosaur ichnofauna of the Late Triassic of the Tatra Mountains, Poland and Slovakia. **A**. cf. *Anomoepus* isp. and cf. *Moyenisauropus* isp. Trackmakers: possibly early ornithischian dinosaurs. **B**. cf. *Grallator* isp. and *Anchisauripus* isp. Trackmakers: theropod dinosaurs. **C**. cf. *Kayentapus* isp. and cf. *Eubrontes* isp. Trackmakers: theropod dinosaurs. **D**. ?Sauropodomorpha tracks indet. Trackmakers: "prosauropod" or sauropod dinosaurs. Abbreviation: TL, track length.

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southern Africa, Western Europe, Greenland, and North America (Lucas et al. 2006). (3) The presence of possibly ornithischian footprints in the the Upper Triassic Tomanová Formation is remarkable. The morphologically most similar tracks are some of the footprints referred to *Anomoepus* and *Moyenisauropus* from Lower Jurassic strata.

Conclusions

The ichnotaxonomic descriptions presented in this paper indicate that many ichnotaxa from the Upper Triassic strata of the Tatra Mountains are comparable to well-known Triassic dinosaur track types (*Grallator*, *Anchisauripus*, *Kayentapus*, and *Eubrontes*), but also with typical Early Jurassic ichnomorphotypes (*Anomoepus*, *Moyenisauropus*). In comparison to other Late Triassic ichnofaunas, this newly recognized ichnoassemblage is the most diverse and includes six, or possibly seven, dinosaur track types (Fig. 7). The most common track types are tridactyl footprints, which are very similar to the *Kayentapus,* which so far was only recognized in one Late Triassic site of Virginia but is very common in several Early Jurassic tracksites over the world.

Well-preserved *Anomoepus*-like (*Anomoepus–Moyenisauropus* group) tracks are widely known from Lower Jurassic strata of Poland (Gierliński 1991, 1999). *Anomoepus* and *Moyenisauropus* tracks from the Late Triassic of the Tatra Mountains show considerable morphologic variation in pedal morphology and cannot be accommodated in a single ichnotaxon. The stratigraphic and geographic distribution of *Anomoepus–Moyenisauropus* tracks offer promise of an improved understanding of early ornithischian evolution, paleoecology and the establishment of palichnostratigraphic zones that may ultimately facilitate correlation of Late Triassic and Early Jurassic vertebrate terrestrial successions.

It is clear from the current study which ichnomorphotypes are present in the Tomanová Formation. However, some tracks require more detailed study, which may require additional material (e.g., cf. *Eubrontes* isp.). For example, further study of the large and oval-shaped tracks could provide new information about the morphology of the manus and pes of Late Triassic sauropodomorphs, as well as information about the size and ecological behavior of these dinosaurs. Similarly, it remains unclear whether the Late Triassic tracksites of the Tatra Mountains include a truly great taxonomic diversity of tridactyl tracks or preserves many tracks that appear different but actually represent preservational and/or behavioral variations in the tracks of one or two trackmakers.

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References

Brusatte, S.L., Benton, M.J., Ruta, M., and Lloyd, G.T. 2008. Superiority, competition, and opportunism in the evolutionary radiation of dinosaurs. *Science* 321: 1485–1488.

Clark, N.D.L., Booth, P., Booth, C., and Ross, D.A. 2004. Dinosaur footprints from the Duntulum Formation (Bathonian, Jurassic) of the Isle of Skye. *Scotish Journal of Geology* 40: 13–21.

Dzik, J., Sulej, T., and Niedźwiedzki, G. 2008. A dicynodont-theropod association in the latest Triassic of Poland. *Acta Palaeontologica Polonica* 53: 733–738.

Ellenberger, P. 1970. Les niveaux paleontologiques de première apparition des mammifères primordiaux en Afrique du Sud et leur ichnologie. *In*: *Second Gondwana Symposium, South Africa, July to August 1970, Proceedings and Papers*, 343–370. Council for Scientific and Industrial Research, Pretoria.

Ellenberger, P. 1972. Contribution à la classification des pistes de vertébrés du Trias: les types du Stormberg d'Afrique du Sud (I Partie). *Palaeovertebrata, Mémoire Extraordinaire* 1972: 1–152.

Ellenberger, P. 1974. Contribution à la classification des pistes de vertébrés du Trias: les types du Stormberg d'Afrique du Sud (II^{ème} partie: le Stormberg Superieur – I. Le biome de la zone B/1 ou niveau de Moyeni: ses biocénoses). *Palaeovertebrata, Mémoire Extraordinaire* 1974: 1–143.

Fijałkowska, A. and Uchman, A. 1993. New data on palynology of the Triassic of the Polish Tatra Mts. *Przegląd Geologiczny* 41: 373–375.

Gaston, R., Lockley, M.G., Lucas, S.G., and Hunt, A.P. 2003. *Grallator*-dominated fossil footprint assemblages and associated enigmatic footprints from the Chinle Group (Upper Triassic), Gateway area, Colorado. *Ichnos* 10: 153–163.

Gierliński, G. 1991. New dinosaur ichnotaxa from the Early Jurassic of the Holy Cross Mountains, Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 85: 137–148.

Gierliński, G. 1994. Early Jurassic theropod tracks with the metatarsal impressions. *Przegląd Geologiczny* 42: 280–284.

Gierliński, G. 1996. Dinosaur ichnotaxa from the Lower Jurassic of Hungary. *Geological Quarterly* 40: 119–128.

Gierliński, G. 1999. Tracks of a large thyreophoran dinosaur from the Early Jurassic of Poland. *Acta Palaeontologica Polonica* 44: 231–234.

Gierliński, G. 2009. A preliminary report on new dinosaur tracks in the Triassic, Jurassic and Cretaceous of Poland. *Actas de las IV Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno Salas de los Infantes, Burgos*, 75–90. Colectivo Arqueológico Paleontológico de Salas, C.A.S.

Gierliński, G. and Ahlberg, A. 1994. Late Triassic and Early Jurassic dinosaur footprints in the Höganas Formation of southern Sweden. *Ichnos* 3: 99–105.

Gierliński, G. and Sabath, K. 2005. Dinosaur tracks in the Upper Triassic and Lower Jurassic of Central Europe. *In*: *Tracking Dinosaur Origins. St. George, Utah, 15–6.03.2005, Abstracts Volume*, 5. Utah.

Gierliński, G., Niedźwiedzki, G., and Pieńkowski, G. 2001. Gigantic footprint of a theropod dinosaur in the Early Jurassic of Poland. *Acta Palaeontologica Polonica* 46: 441–446.

Gierliński, G., Niedźwiedzki, G., and Pieńkowski, G. 2004. Tetrapod track assemblage in the Hettangian of Sołtyków, Poland, and its paleoenvironmental background. *Ichnos* 11: 195–213.

Gierliński, G.D., Lockley, M.G., and Niedźwiedzki, G. 2009. A distinctive crouching theropod trace from the Lower Jurassic of Poland. *Geological Quarterly* 53: 471–476.

Gorek, A. 1958. Geologické pomery skupiny Červených vrchov, Tomanovej a Tichej doliny. *Geologický Sbornik Slovenskej Akadémie, Vied* 9: 203–240.

Haubold, H. 1984. *Saurierfährten*. 231 pp. Wittenberg, Ziemsen.

Jurewicz, E. 2005. Geodynamic evolution of the Tatra Mts. and the Pieniny Klippen Belt (Western Carpathians): problems and comments. *Acta Geologica Polonica* 55: 295–338.

Klein, H. and Lucas, S.G. 2010. Tetrapod footprints—their use in biostratigraphy and biochronology of the Triassic. *In*: S.G. Lucas (ed.), The Triassic Timescale. *Geological Society, London, Special Publications* 334: 419–446.

Klein, H., Lucas, S.G., and Haubold, H. 2006. Tetrapod track assemblage of the Redonda Formation (Upper Triassic, Chinle Group) in east-central New Mexico—re-evaluation of ichnofaunal diversity from studies of new material. *In*: J.D. Harris, S.G. Lucas, J.A. Spielmann, M.G. Lockley, A.R.C. Milner, and J.I. Kirkland (eds.), The Triassic–Jurassic Terrestrial Transition. *New Mexico Museum of Natural History and Science, Bulletin* 37: 241–250.

Kotański, Z. 1956. O stratygrafii i paleografii kajpru wierchowego w Tatrach. *Acta Geologica Polonica* 6: 273–286.

Kotański, Z. 1959a. Profile stratygraficzne serii wierchowej Tatr Polskich. *Biuletyn Instytutu Geologicznego* 139: 1–139.

Kotański, Z. 1959b. Stratigraphy, sedimentology and palaeogeography of the high-tatric Triassic in the Tatra Mts. *Acta Geologica Polonica* 9: 113–145.

Kotański, Z. 1959c. Trias wierchowy. Z badań geologicznych wykonanych w Tatrach i na Podhalu. *Biuletyn Instytutu Geologicznego* 149: 143–157.

Kotański, Z. 1961. Tektogeneza i rekonstrukcja paleogeografii pasma wierchowego w Tatrach. *Acta Geologica Polonica* 11: 187–476.

Kuźniar, C. 1913. Skały osadowe tatrzańskie. *Rozprawy Wydziału Matematyczno-Przyrodniczego Polskiej Akademii Umiejętności, Kraków* 13: 3–48.

Langer, M.C. and Benton, M.J. 2006. Early dinosaurs: a phylogenetic study. *Journal of Systematic Palaeontology* 4: 309–358.

Langer, M.C., Ezcurra, M.D., Bittencourt, J.S., and Novas, F.E. 2010. The origin and early evolution of dinosaurs. *Biological Reviews* 85: 55–110.

Lockley, M.G. 1998. The vertebrate track record. *Nature* 396: 429–432.

Lockley, M.G. and Hunt, A.P. 1995. *Dinosaur Tracks and Other Fossil Footprints of the Western United States*. 338 pp. Columbia University Press, New York.

Lockley, M.G. and Meyer, C.A. 2000. *Dinosaur Tracks and Other Fossil Footprints of Europe*. 360 pp. Columbia University Press, New York.

Lockley, M.G. and Gierlinski, G.D. 2006. Diverse vertebrate ichnofaunas containing *Anomoepus* and other unusual trace fossils from the Lower Jurassic of the western United States: implications for paleoecology palichnostratigraphy. *In:* J.D. Harris, S.G. Lucas, J.A. Spielmann, M.G. Lockley, A.R.C. Milner, and J.I. Kirkland (eds.), The Triassic–Jurassic Terrestrial Transition. *New Mexico Museum of Natural History and Science, Bulletin* 37: 176–191.

Lockley, M.G., Lucas, S.G., and Hunt, A.P. 2006. *Evazoum* and the renaming of northern hemisphere "*Pseudotetrasauropus*": implications for tetrapod ichnotaxonomy at the Triassic–Jurassic boundary. *In*: J.D. Harris, S.G. Lucas, J.A. Spielmann, M.G. Lockley, A.R.C. Milner, and J.I. Kirkland (eds.), The Triassic–Jurassic Terrestrial Transition. *New Mexico Museum of Natural History and Science, Bulletin* 37: 199–206.

Lucas, S.G., Klein, H., Lockley, M.G., Spielmann, J.A., Gierliński, G.D., Hunt, A.P., and Tanner, L.H. 2006. Triassic–Jurassic stratigraphic distribution of the theropod footprint ichnogenus *Eubrontes*. *In*: J.D. Harris, S.G. Lucas, J.A. Spielmann, M.G. Lockley, A.R.C. Milner, and J.I. Kirkland (eds.), The Triassic–Jurassic Terrestrial Transition. *New Mexico Museum of Natural History and Science, Bulletin* 37: 86–93.

Melchor, R.N. and de Valais, S. 2006. A review of Triassic tetrapod track assemblages from Argentina. *Palaeontology* 49: 355–379.

Michalík, J. 1978. To the paleogeography, paleotectonics and paleoclimatology of the uppermost Triassic of the West Carpathians. *In*: J. Vozár (ed.), *Paleogeographic Development of the Western Carpathians*, 189–211. GÚDŠ, Bratislava.

Michalík, J. 1980. A paleoenvironmental and paleoecological analysis of the West Carpathian part of the northern Tethyan nearshore region in the latest Triassic time. *Rivista Italiana di Paleontologia e Stratigrafia* 85: 1047–1064.

Michalík, J. and Kundrát, M. 1998. Uppermost Triassic dinosaur ichnoparataxa from Slovakia. *Journal of Vertebrate Paleontology* 3 (Supplement 18): 63A.

Michalík, J., Plenderová, E., and Sýkora, M. 1976. To the stratigraphic and paleogeographic position of the Tomanová-Formation in the Uppermost Triassic of the West Carpathians. *Geologický Zbiorník, Geologica Carpathica* 27: 299–318.

Michalík, J., Kátlovský, V., and Hluštík, A. 1988. Plant remains in the Tomanová Formation (Uppermost Triassic, West Carpathians): their origin, composition and diagenetic alteration. *Geologický Zbiorník, Geologica Carpathica* 39: 523–537.

Milán, J. and Gierliński, G. 2004. A probable thyreophoran (Dinosauria, Ornithischia) footprint from the Upper Triassic of southern Sweden. *Bulletin of the Geological Society of Denmark* 51: 71–75.

Milner, A.R.C. and Kirkland, J.I. (eds.) 2006. The Triassic–Jurassic Terrestrial Transition. *New Mexico Museum of Natural History and Science, Bulletin* 37: 86–93.

Nejbert, K. and Jurewicz, E. 2004. Mineralogy and petrography of the ferruginous concretions from siliciclastic Rhaetian deposits, Tatra Mountains, Poland. *Mineralogical Society of Poland Special Papers* 24: 299–302.

Nesbitt, S.J., Irmis, R.B., and Parker, W.G. 2007. A critical re-evaluation of the Late Triassic dinosaur taxa of North America. *Journal of Systematic Palaeontology* 5: 209–243.

Nicosia, U. and Loi, M. 2003. Triassic footprints from Lerici (La Spezia, northern Italy). *Ichnos* 10: 127–140.

Niedźwiedzki, G. 2005. Nowe znalezisko śladów dinozaurów w górnym triasie Tatr. *Przegląd Geologiczny* 53: 410–413.

Niedźwiedzki, G. 2008. Dinosaur tracks in the Late Triassic of the Tatra Mountains. *9th Paleontological Conference, Warszawa, 10–11 October, 2008, Abstracts*, 62–63. Polish Academy of Sciences, Institute of Paleobiology, Warszawa.

Niedźwiedzki, G. and Sulej, T. 2007. Tropy kręgowców w górnym triasie Polski. *Granice Paleontologii, XX Konferencja Naukowa Paleobiologów i Biostratygrafów PTG, Św. Katarzyna pod Łysicą, 10–13 września 2007*, 93–94. Polskie Towarzystwo Geologiczne, Kielce-Warszawa.

Olsen, P.E. 1980. Fossil great: lakes of the Newark Supergroup in New Jersey: *In*: W. Manspeizer (ed.), *Field Studies in New Jersey Geology and Guide to Field Trips, 52nd Annual Meeting of New York State Geological Association*, 352–398. NJ Rutgers University, Newark College of Arts and Sciences, Newark.

Olsen, P.E. and Galton, P. 1984. A review of the reptile and amphibian assemblages from the Stromberg of southern Africa, with special emphasis on the footprints and the age of the Stromberg. *Paleontologia Africana* 25: 87–110.

Olsen, P.E. and Rainforth, E.C. 2003. The Early Jurassic ornithischian dinosaurian ichnogenus *Anomoepus*. *In*: P.M. Le Tourneau and P.E. Olsen (eds.), *The Great Rift Valleys of Pangea in Eastern North America, vol. 2: Sedimentology, Stratigraphy, and Paleontology*, 314–367. Columbia University Press, New York.

Olsen, P.E., Smith, J.B., and McDonald, N.G. 1998. The material of the species of the classic theropod footprint genera *Eubrontes*, *Anchisauripus* and *Grallator* (Early Jurassic, Hartford and Deerfield basins, Connecticut and Massachusetts, U.S.A.). *Journal of VertebratePaleontology* 18: 586–601.

Olsen, P.E., Kent, D.V., Sues, H.-D., Koeberl, C., Huber, H., Montanari, A., Rainforth, E.C., Fowell, S.J., Szajna, M.J., and Hartline, W. 2002. As-

doi:10.4202/app.2010.0027

cent of dinosaurs linked to an iridium anomaly at the Triassic–Jurassic boundary. *Science* 296: 1305–1307.

Orłowska-Zwolińska, T. 1983. Palinostratygrafia epikontynentalnych osadów wyższego triasu w Polsce. *Prace Instytutu Geologicznego* 104: 1–88.

Rabowski, F. 1925. Budowa Tatr. Pasmo wierchowe. *Sprawozdania Państwowego Instytutu Geologicznego* 3: 169–177.

Rabowski, F. 1959. Serie wierchowe w Tatrach zachodnich. *Prace Instytutu Geologicznego* 27: 5–178.

Raciborski, M. 1890. Flora retycka w Tatrach. *Rozprawy Wydziału Matematyczno-Przyrodniczego Polskiej Akademii Umiejętności, Kraków* 21: 243–260.

Radwański, A. 1968. Studium petrograficzne i sedymentologiczne retyku wierchowego Tatr. *Studia Geologica Polonica* 25: 1–146.

Reymanówna, M. 1984. Flora retycka z Czerwonych Żlebków. *Paleontologia mezozoiku Tatr. Materiały VIII Konferencji Paleontologów PTG, Zakopane 1984*, 12–13. Polskie Towarzystwo Geologiczne, Zakopane.

Smith, R.M.H., Marsicano, C.A., and Wilson, J.A. 2009. Sedimentology and paleoecology of a diverse Early Jurassic tetrapod tracksite in Lesotho, Southern Africa. *Palaios* 24: 672–684.

Thulborn, R.A. 1994. Ornithopod dinosaur tracks from the Lower Jurassic of Queensland. *Alcheringa* 18: 247–258.

Turnau-Morawska, M. 1953. Kajper tatrzański, jego petrografia i sedymentologia. *Acta Geologica Polonica* 3: 212–234.

Weems, R.E. 1987. A Late Triassic footprint fauna from the Culpeper basin, northern Virginia (U.S.A.). *Transactions of the American Philosophical Society* 77: 1–79.

Weems, R.E. 1992. A re-evaluation of the taxonomy of Newark Supergroup saurischian dinosaur tracks, using extensive statistical data from a recently exposed tracksite near Culpeper, Virginia. *In*: P.C. Sweet (ed.), Proceedings 26th Forum on the Geology of Industrial Minerals. *Virginia Division of Mineral Resources Publication* 119: 113–127.

Weems, R. 2003. *Plateosaurus* foot structure suggests a single trackmaker for Eubrontes and Gigandipus footprints. *In*: P.M. Le Tourneau and P.E. Olsen (eds), *The Great Rift Valleys of Pangea in Eastern North America, vol. 2*, 293–313. Columbia University Press, New York.

Uhlig, V. 1897. Geologie der Tatragebirges I: Einleitung und der stratigraphischer Theil. *Anzeiger Akademie der Wissenschaften, Mathematish-Naturwissenschaftliche Klasse* 64: 643–684.