

An ornithischian-theropod ichnoassemblage from the Norian-Rhaetian transition of Poland

Grzegorz Niedźwiedzki^{a,b,*}, Krzysztof Owocki^c, Martin Qvarnström^a, Gerard D. Gierliński^{b,d}

^a Department of Organismal Biology, Uppsala University, Norbyvägen 18A, 752 36 Uppsala, Sweden

^b Polish Geological Institute – National Research Institute, Rakowiecka 4, 00-975 Warszawa, Poland

^c Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, 00-818 Warsaw, Poland

^d JuraPark, Bałtów 8a, 27-423 Bałtów, Poland

ARTICLE INFO

Editor Name: Dr. Howard Falcon-Lang

Keywords:

Dinosauria
Trace fossils
Keuper
Norian
Rhaetian
Silesia

ABSTRACT

In this paper, we describe a dinosaur track assemblage from an Upper Triassic fluvial succession at the Lisowice-Lipie Śląskie site in Silesia, southern Poland. The tetrapod tracks were identified in two studied intervals (A and C), each comprising several track-bearing beds, and representing the deposits of meandering fluvial systems. The stratigraphically higher interval C (track-bearing beds a to e) contains *Anomoepus* isp., attributed to an early ornithischian, as well as *Grallator* isp., *Anchisauripus* isp., *Apatichnus minor* Lull 1915, *Apatichnus* isp., *Eubrontes* isp., and cf. *Eubrontes* isp., attributed to at least six different theropods. As such, the site is one of the richest dinosaur ichnoassemblages from the entire Upper Triassic of the Central European Basin. The track-bearing beds are separated by a bone-bearing succession with skeletal remains of temnospondyls, therapsids and dinosaurs and also contain tracks of non-dinosaurian tetrapods, mainly therapsid tracks. Dinosaur tracks are the most common, representing ~70 % of the total number of recorded ichnotaxa. *Grallator*, *Anchisauripus* and *Apatichnus* are the most ubiquitous track ichnogenera, and the fauna represents a rather diverse ornithischian-theropod dinosaur community, without any early dinosauriforms (*Atreipus*) or sauropodomorphs (*Evazoum*, *Eosauropus*, *Tetrasauropus*), which is also reflected in the skeletal record of the site. Stratigraphical data support a late Norian-earliest Rhaetian age for the tracks. The presence of ornithischian tracks in Lisowice-Lipie Śląskie and anomoeopoid-like tracks from a few other Triassic sites suggests that the origin of the ornithischian clade predates the late Norian-early Rhaetian. Moreover, the presence of large eubrontid tracks (*Eubrontes* and cf. *Eubrontes*) demonstrates the early presence of large theropods in the region. The new finds offer unique insights into a previously poorly known early dinosaur community from the Late Triassic of northern Pangaea.

1. Introduction

Tetrapod trace fossils are used in addition to skeletal records for estimating biodiversities in Late Triassic and Jurassic terrestrial and marginal-marine ecosystems (e.g., Olsen and Galton, 1984; Lockley et al., 1996; Olsen et al., 2002; Whyte et al., 2007; Milàn, 2011; Zatoń et al., 2015), and they can be used as an excellent tool for reconstructing overall ecological structures (e.g., Qvarnström et al., 2024). Unlike skeletal remains, which are subject to transportation, redeposition, and other taphonomic processes, in-situ preserved tracks represent a record of animals in the biotopes they visited and at least temporally lived in. The comparison of the ichnological record with skeletal finds from the same site is therefore particularly valuable.

Skeletal remains are extremely rare in the Lower Jurassic of Poland, restricted only to a few narrow lithostratigraphical intervals in the early Hettangian and late Pliensbachian fluvial sequences (e.g., Gierliński et al., 2004). Therefore, the dinosaur fauna of this time interval is mainly reconstructed based on track assemblages (Gierliński et al., 2004; Niedźwiedzki and Pieńkowski, 2016; Pacyna et al., 2022; Qvarnström et al., 2024). The Upper Triassic fossil record of the Central European Basin yields more well-preserved body fossils (see Sues and Fraser, 2010; Mujal et al., 2025), but the taxonomic diversity in these assemblages typically also increases due to the presence of tetrapod tracks (e.g., Haubold and Klein, 2000, 2002; Wagensommer et al., 2022). Thus, tracks and trackways provide crucial information on the faunal diversity of this period, give insight into the evolution and ecology of their

* Corresponding author at: Department of Organismal Biology, Uppsala University, Norbyvägen 18A, 752 36 Uppsala, Sweden.

E-mail address: grzegorz.niedzwiedzki@ebc.uu.se (G. Niedźwiedzki).

<https://doi.org/10.1016/j.palaeo.2025.113312>

Received 19 August 2025; Received in revised form 26 September 2025; Accepted 26 September 2025

Available online 29 September 2025

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producers, and complement our understanding of the rise of dinosaurs in these ecosystems. This study presents a detailed documentation of the dinosaur tracks from the Lisowice-Lipie Śląskie site (Fig. 1) (previously also referred to as the Lipie Śląskie clay pit) that, besides the dominance of grallatorid theropod tracks (*Grallator* and *Anchisauripus*), appears to be different in composition from other Upper Triassic ichnoassemblages from the Central European Basin in that it includes a medium-sized anomoepoid (*Anomoepus*), a large-sized eubrontid (*Eubrontes* and cf. *Eubrontes*) and a medium-sized theropod (*Apatichnus*).

1.1. Upper Triassic tetrapod tracks from the Central European Basin

Studies on Upper Triassic tetrapod tracks from the Central European Basin have a long history. The most important localities with tracks are located in Franconia in northern Bavaria (Haarländer, 1938; Beurlen, 1950; Rehne, 1950, 1952, 1960, 1983; Heller, 1952, 1956, 1958; Kuhn, 1955, 1956, 1958, 1967; Aumann, 1957, 1960; Warth, 1972; Karl and Haubold, 1998; Haubold and Klein, 2000; Hofbauer and Klein,

2013; Klein and Lucas, 2013, 2015, 2025a, 2025b; Klein and Kneidl, 2015; Mujal et al., 2025) and the Stuttgart area in Baden-Württemberg (Plieninger, 1838; Huene, 1935, 1943; Haderer, 1988, 1990, 1991, 1992, 1994, 1996, 2012, 2017, 2020; Wagensommer et al., 2022; Mujal et al., 2025). An Upper Triassic (lower Carnian) ichnoassemblage from the Central European Basin has yielded a low-diversity ichnofauna with *Chirotherium* (“*Parachirotherium*”) *postchirotherioides* and *Rhynchosaur-oides* isp. (Klein and Kneidl, 2015). A much richer, and slightly older, late Ladinian tetrapod ichnofauna with “*Parachirotherium*” (= *Chirotherium*), “*Parachirotherium*”-*Atreipus*-*Grallator* plexus, as well as “*Brachychirotherium*”-like chirotheriids have been reported from the Benk Formation (Haubold and Klein, 2002; Klein and Haubold, 2004). The mid-Carnian Stuttgart Formation has yielded an enigmatic ichnotaxon, *Chelonipus*, which has traditionally been attributed to stem-turtles (Lichtig et al., 2018), but such traces could also potentially have been produced by temnospondyl amphibians (Klein, 2021; Mujal and Schoch, 2020). However, the arc-like broad and short manus impression of *Chelonipus* shows a strong similarity to other post Triassic (Jurassic-

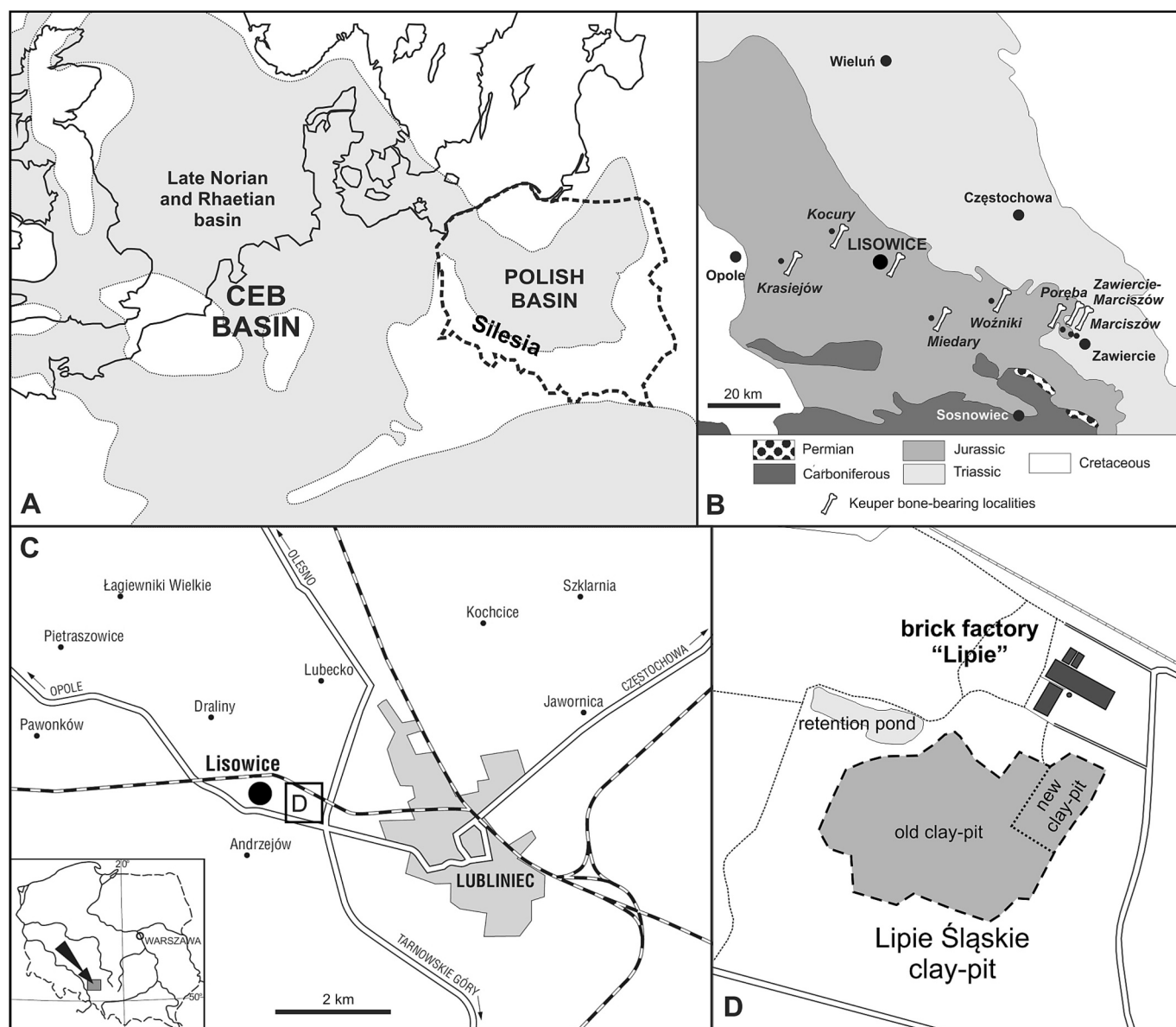


Fig. 1. Location of the Lisowice-Lipie Śląskie site. A. A simplified palaeogeographic map of the Central European Basin, the Polish Basin and the location of Silesia. B. Bone-bearing sites from the Upper Triassic of Poland and location of the Lisowice-Lipie Śląskie site. C. Location of the Lisowice-Lipie Śląskie site near Lubliniec. D. Simplified map of the Lipie Śląskie clay-pit. See text for details.

Cretaceous) turtle tracks (H. Klein, pers. comm.). Tracks probably produced by phytosaurs (*Apatopus lineatus*) have been reported from the Steigerwald Formation, the so-called Ansbacher Sandstein and in the Hassberge Formation of northern Bavaria (Hofbauer and Klein, 2013; Klein and Lucas, 2013, 2015). Numerous lacertoid tracks (*Rhynchosauroides* and other *Rhynchosauroides*-like tracks) occur in the Stuttgart Formation and other age-equivalent rock units (Haubold and Klein, 2002; G.N. – pers. obser.). The tetrapod ichnoassemblages from the late Carnian in the Central European Basin include chirotheriid tracks (“*Chirotherium*” *wondrai*, *Brachychirotherium hasfurtense*, *B. thuringiacum* and *Brachychirotherium* isp.), *Apatopus lineatus*, *Rhynchosauroides* isp., *Procolophonichnium lockleyi* and *Atreipus-Grallator* plexus (e.g., *Atreipus* isp., *Atreipus metzneri*, *Grallator* isp., *Grallator cursorius*) and *Evazoum* isp. (see Haubold and Klein, 2002; Haderer, 2012, 2015, 2017; Klein et al., 2015; Klein, 2021; Klein and Lucas, 2013, 2015, 2021, 2025a, 2025b; Mujal et al., 2025). The early to mid Norian of the Central European Basin yielded a more diverse ichnoassemblage with cf. *Ischirotherium* isp. (small and slender), *Ischirotherium* isp. (large and wide), small crocodylomorph tracks, the small *Rhynchosauroides*, the probable sauropodomorph ichnotaxon *Evazoum*, the tridactyl (dinosauriform and/or theropod) ichnotaxa *Grallator* and *Atreipus*, and the pseudosuchian ichnotaxon *Brachychirotherium* (Haderer, 1991, 2012, 2015; Klein, 2021; Klein and Lucas, 2021; Haderer and Schwarzkopf, 2023).

In a recently published summary of data on Triassic tetrapods from the Central European Basin, several ichnotaxa for the late Norian (e.g. *Pseudotetrasauropus*, *Evazoum*) and Rhaetian (cf. *Grallator*) are listed (see Mujal et al., 2025; Fig. 3), but the provided description lacks information on the provenance of these finds. These are probably the traces from the Late Triassic of Poland, which were mentioned in numerous conference abstracts, and are summarised below.

The ichnological record of tetrapods from the late Norian and Rhaetian in the Central European Basin is relatively poor. It is represented by sites in Sweden, Germany, and Poland, including the Lisowice-Lipie Śląskie assemblage described here. The record is richer from the Carpathians and the Alps, areas located outside of the Central European Basin. In the Slovak and Polish parts of the Tatra Mts. there are sites from the late Norian or Rhaetian that yielded a rich dinosaur ichnofauna (Niedźwiedzki, 2011b).

Rather poorly-preserved dinosaur tracks (cf. *Grallator* isp., *Anchisauripus* isp., cf. *Eubrontes* isp., and Theropoda track indet.) were found in the middle-upper Rhaetian deposits exposed in the Seebergen quarry located near Kammerbruch in the Thuringia Basin (Niedźwiedzki, 2008a). This site is particularly interesting due to its latest Triassic age, and further exploration is therefore planned.

Numerous theropod dinosaur tracks (cf. *Eubrontes giganteus*; *Kayentapus soltykovensis*) from the Triassic-Jurassic transition are known from Skåne in southern Sweden (Gierliński and Ahlberg, 1994), an area that, like the Holy Cross Mts. (=Świętokrzyskie) or Silesia region in Poland, represented a marginal part of the Central European Basin in the Late Triassic. Recently, several new sites with dinosaur and other tetrapod tracks have been discovered in Skåne, which are currently under study.

1.2. Upper Triassic tetrapod tracks in Poland

A growing interest in the Upper Triassic of Poland has led to several new discoveries of tetrapod fossils, including spectacular finds of dinosaur precursors, early dinosaurs, large therapsids and mammalian ancestors (e.g., Dzik, 2001, 2003; Niedźwiedzki et al., 2012, 2014; Sulej and Niedźwiedzki, 2019; Sulej et al., 2012). However, the reconstructions of these new Upper Triassic faunas have only occasionally included footprint data (e.g., Sulej et al., 2011; Sadlok and Wawrzyniak, 2013). Hereto, the Upper Triassic trackway record from Silesia, Holy Cross Mts. and Tatra Mts. has resulted in a series of conference presentations, short reports, preliminary illustrations of discoveries, some of which await detailed study (see Gierliński, 2007; fig. 1, 2009; fig. 2; Dzik et al., 2008a; p. 736; Dzik et al., 2008b; pp. 14–16 and two figures;

Niedźwiedzki and Sulej, 2007, 2008; fig. 5; Niedźwiedzki, 2005, 2008a; fig. 6c,d, 2008b, 2009, 2011a, 2011b; Gierliński et al., 2009; fig. 4; Sulej et al., 2011; fig. 7; Niedźwiedzki et al., 2012; p. 269; Sadlok and Wawrzyniak, 2013; Niedźwiedzki and Pieńkowski, 2014; Pieńkowski et al., 2014; fig. 6; Gierliński et al., 2014; p. 38, 40–42; Gierliński and Lichota, 2018; fig. 1).

The first Upper Triassic tetrapod tracks from Poland were found in the natural outcrops of the Tomanová Formation (?late Norian–Rhaetian) in the western part of the Tatra Mts. (Niedźwiedzki, 2005, 2008a; fig. 6 e, f, 2008b, 2011b). Seven more or less distinct morphotypes of dinosaur tracks have been recognized in the Tomanová Formation (exposed in Slovakia and Poland), some of which are preserved well enough to be assigned to cf. *Grallator*, *Anchisauripus*, *Kayentapus*, and cf. *Eubrontes*, cf. *Anomoepus* or/and *Eoanomoepus*, cf. *Moyenisauropus* and?Sauropodomorpha tracks indet. (see Niedźwiedzki, 2011a; Lockley et al., 2018).

Two fossil-bearing intervals recognized in the Upper Triassic fluvial succession at the Lisowice-Lipie Śląskie site (Fig. 1) have recently become globally famous for the unique tetrapod skeletal findings of the gigantic dicynodont *Lisowicia bojani* and the large predatory theropod-like archosaur *Smok wawelski* (Sulej and Niedźwiedzki, 2019). At the same site, numerous and well-preserved tetrapod tracks (more than 100 specimens) were found in two trace fossil-bearing sections (Dzik et al., 2008a, 2008b; Niedźwiedzki and Sulej, 2007, 2008; Niedźwiedzki, 2008a, 2011a; Niedźwiedzki et al., 2012; Pieńkowski et al., 2014). This material has not been described in detail thus far, but the dinosaur tracks of the assemblage from the section C (Fig. 2) is the subject of this paper.

A few slabs with isolated small to large pentadactyl-, tetradactyl- and tridactyl tetrapod tracks preserved in a sandy and coarse clastic succession exposed along a small creek (probably representing late Carnian-early-mid Norian transition), at the Skarszyny site near the larger village of Broniszowice (Niedźwiedzki and Sulej, 2007; Gierliński, 2007, 2009; Pieńkowski et al., 2014). The material collected from this site comprises 9 specimens, of which small (?*Evazoum*) and large tetradactyl (*Pseudotetrasauropus*) footprints of sauropodomorph affinity have been described in detail (Nicosia and Loi, 2003; Lockley and Gierliński, 2006; Porchetti and Nicosia, 2007; Gierliński, 2007, 2009; but see Rainforth, 2003 or Klein and Haubold, 2007 for different view). Niedźwiedzki and Sulej (2007) expands the inventory of finds from this site by reporting tracks of Chirotheriidae, tracks of predatory dinosaurs (*Grallator* isp. and *Anchisauripus* isp.), and problematic specimens (fragmentarily or poorly preserved tracks), probably of early dinosaurs.

A few small theropod dinosaur tracks, *Grallator* isp. (mid Carnian to early Norian), have been reported by Niedźwiedzki and Sulej (2007) from the Chelsty Clay-pit near Żarnów. Recently, a few additional slabs with *Grallator*-like and *Atreipus*-like tracks and non-dinosaur tetrapod ichnites were discovered at this site (on-going study). The in-situ preserved bed with tetrapod tracks, observed there in 2021 and exposed in the northern part of the mine, was unfortunately destroyed during mining operation.

Interesting material was documented at the still poorly explored Southern Gromadzice locality (re-named as Gromadzice-Rzuchów site by Qvarnström et al., 2024), which corresponds to the uppermost Triassic sections in the Kaminonka River Valley. Niedźwiedzki and Sulej (2007) previously described dinosaur tracks from there and a few additional sandstone blocks with tetrapod tracks were recently found in a series of small outcrops in ephemeral stream valleys, representing very similar sedimentological sequences (Qvarnström et al., 2024). The two track-bearing levels recognized in the Gromadzice-Rzuchów section yield large sauropodomorph tracks (*Evazoum* and *Tetrasauropus*-like tracks), archosauromorph or crocodylomorph tracks (*Chirotherium*-like), small ornithischian dinosaur tracks (cf. *Anomoepus*) and small to large-sized tridactyl theropod dinosaur tracks (*Grallator*, *Anchisauripus*, *Kayentapus* and *Eubrontes*).

Several isolated archosaur tracks (cf. *Grallator* isp. or cf. *Atreipus* isp., cf. *Brachychirotherium* isp., cf. *Apatopus* isp., Chirotheriidae indet.), a

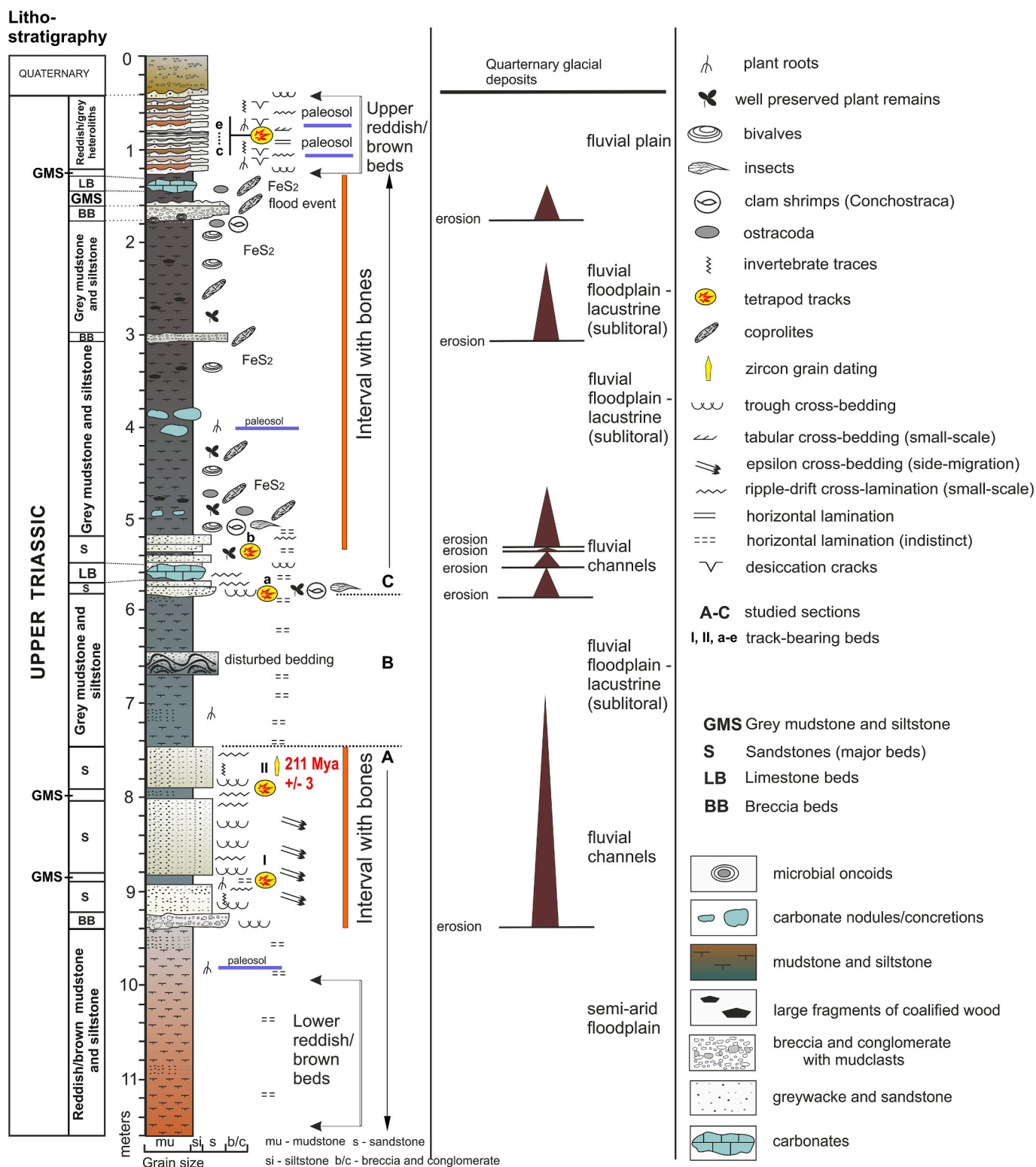


Fig. 2. Stratigraphical and sedimentological section of the main exposure in the Lisowice-Lipie Śląskie site, with position of the bone-bearing intervals, tetrapod trace fossils, other faunal and floral remains, and intervals with red-bed deposits (modified from Pieńkowski et al., 2014). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

poorly preserved tetra- or pentadactyl lacertoid-like track (Rhynchosauroidae indet.), large tracks with short and wide digit impressions probably made by therapsids, and traces made by swimming animals were found at Woźniki Clay-pit near Częstochowa (Niedźwiedzki and Sulej, 2007; Gierliński et al., 2009; Sulej et al., 2011). These tracks were

initially studied by Sulej et al. (2011) but new material has been found since this study was published. The Woźniki biota (Sulej et al., 2011, 2020; Qvarnström et al., 2024) is structurally very similar to that of Krasiejów and represents a mix of terrestrial and lacustrine mid-to late Carnian ecological communities (e.g., Dzik and Sulej, 2007). Sulej et al.

(2011) considered the Woźniki locality to be of mid-late Carnian age based on the presence of the conchostracan *Laxitextella* cf. *laxitexta* (see Olempska, 2004), and freshwater bivalves similar to *Silesunio parvus* (see Skawina and Dzik, 2011) from Krasiejów. The currently recognized temporal range of *Laxitextella laxitexta* covers major parts of the Carnian in the Germanic Basin and not stretch into post-Carnian strata (see Geyer and Kelber, 2018).

The tetrapod track material was described from the Marciszów site (Sadlok and Wawrzyniak, 2013) located near Zawiercie in the easternmost part of the Upper Silesian subbasin, close to the margin of the Kraków-Częstochowa Upland. This locality has yielded isolated, and rather poorly preserved tracks of archosaurs and dicynodonts. An additional isolated pes imprint (*Anchisauripus*) was found at this site and will be described in future. The section at Marciszów has an equivalent age to the upper bone-bearing levels exposed at Lisowice-Lipie Śląskie site (Niedźwiedzki and Budziszewska-Karwowska, 2018).

The presented short overview does not include the latest finds (2018–2023) of tetrapod tracks from the Upper Triassic of Poland, which were not taken into account because they are still poorly set in the local stratigraphical schemes or are the subject of separate studies. These are in total five new sites (e.g., Pałegi II, Szkucin-Hucisko, Wyszyna Machorowska), which will be included in a broader palaeoecological study, where a revision and detailed description of new materials from the Woźniki Clay-pit, Skarszyny site, Chełsty Clay-pit, Marciszów and Gromadzice-Rzuchów sites will also be presented.

1.3. Upper Triassic tetrapod tracks from the Lisowice-Lipie Śląskie site

The Lipie Śląskie clay-pit is located in the village of Lisowice near Lubliniec (Fig. 1). It has been well-sampled and documented during several seasons of fieldwork. It offers important insights into the trace fossil record of the Upper Triassic terrestrial deposits of the eastern part of the Central European Basin. The first tetrapod tracks from the site were discovered in 2006 and first mentioned by Niedźwiedzki and Sulej (2007, 2008) and Dzik et al. (2008a, 2008b). This fossiliferous locality has been reported on with the primary focus on the body fossil vertebrate fauna, the stratigraphy and the environment of deposition (e.g., Szulc et al., 2006; Dzik et al., 2008a, 2008b; Niedźwiedzki and Sulej, 2008, 2010; Niedźwiedzki et al., 2011, 2012; Pieńkowski et al., 2014; Jewuła et al., 2019; Sulej and Niedźwiedzki, 2019; Sulej, 2024; Qvarnström et al., 2024). Vertebrate ichnological finds from the Lisowice-Lipie Śląskie site such as bromalites and bite marks have been studied in more detail (Niedźwiedzki et al., 2011; Bajdek et al., 2014; Zatoń et al., 2015; Qvarnström et al., 2019, 2024), but the tetrapod tracks have not been properly explored to date.

In a conference abstract, Niedźwiedzki and Sulej (2007) reported, the presence of tracks of small predatory dinosaurs (*Grallator* isp., *Anchisauripus* isp.), large tridactyl tracks with a length of 40–45 cm and Chirotheriidae tracks (similar to *Brachychirotherium* isp. and *Chirotherium* isp.) from this site. Subsequently, Niedźwiedzki et al. (2012) briefly described large tridactyl tracks (about 35–50 cm long) associated with body fossils of *Smok wawelski* Niedźwiedzki et al., 2011, a large theropod-like archosaur. All these tracks were found in sandstone layers located below (track-bearing beds a-b) and above the upper bone-bearing interval (track-bearing beds c-e) and mudstone-sandstone intercalations associated with the lower bone interval (track-bearing beds I and II), (Fig. 2). During field work (2009–2010, 2012–2014, 2017) further specimens (in total 89 specimens) were found in the track-bearing beds a to e, complementing the picture of the diversity, stratigraphical occurrence and state of preservation of tetrapod tracks at this site. We focus on 42 specimens of the dinosaur tracks from the track-bearing beds a-e (Fig. 2) that are directly associated with the upper bone-bearing interval (Fig. 2; see Table 1). The remaining non-dinosaurian tracks, mainly therapsid tracks and non-dinosaur archosaur ichnites from the track-bearing beds a-e and therapsid, dinosaur and other archosaur tracks from the track-bearing beds I and II, will be

the subject of separate studies.

The Lisowice-Lipie Śląskie site is unique as it preserves different trace fossils of vertebrates, e.g. signs of predation (Gorzela et al., 2009; Niedźwiedzki et al., 2011), coprolites of herbivores and predators (Niedźwiedzki, 2013; Bajdek et al., 2014; Zatoń et al., 2015; Qvarnström et al., 2019, 2024), as well as gastric pellets produced by an osteophagous predator (Niedźwiedzki, 2013; Qvarnström et al., 2019, 2024). The site provided the most abundant tetrapod track record from the Upper Triassic of Poland.

2. Geological setting

In the Late Triassic, the Lisowice-Lipie Śląskie site was located in the south-western part of the Polish Basin (in the central part of the Silesian sub-basin), which was part of the widespread epicontinental Central European Basin located at around 30–35°N (Pieńkowski et al., 2014). Following the retreat of the Middle Triassic Muschelkalk Sea, terrestrial environments established in the Silesian sub-basin for longer durations, reflected in the upper Middle to Upper Triassic Keuper facies, and were not replaced by brackish or marine facies until the Early Jurassic transgression (Pieńkowski, 2004; Pieńkowski et al., 2014).

The sedimentary sequence of the Upper Triassic in the general Lubliniec area was determined based on observations in outcrops (clay-pits, gravel-pits, limestone quarries; see Fuglewicz and Śniezek, 1980; Haisig et al., 1983; Szulc et al., 2006) and nearby boreholes, the deepest of which (Solarnia IG-1; Lubliniec IG-1) provide key data on the Upper Triassic succession in the region.

The studied section at the Lisowice-Lipie Śląskie site (Fig. 2) is approximately 12 m thick and was visible in a series of up to 5-m-high temporary exposures in the northern (today largely covered by water), southern and eastern parts of the clay-pit (Fuglewicz and Śniezek, 1980; Haisig et al., 1983; Szulc et al., 2006; Szulc, 2007; Dzik et al., 2008a, 2008b; Niedźwiedzki and Sulej, 2008, 2010; Pieńkowski et al., 2014; Jewuła et al., 2019). The section shows deposits of meandering-river system with six major lithofacies: 1) breccia-like strata with fragments of plants and bones; 2) poorly sorted conglomerates (mud clast or oncoids/carbonate nodule supported); 3) trough cross-, tabular-, epsilon cross-bedded well to poorly sorted sandstones (greywackes); 4) low angle cross-bedded or horizontal-bedded sandstone-mudstone-siltstone intercalations (heteroliths); 5) horizontal and thin-bedded sandstone-claystone intercalations with well sorted sandstones; and 6) poorly laminated or blocky mudstone-siltstone-claystone subsets with preserved organic matter (see also Pieńkowski et al., 2014; Jewuła et al., 2019). The strata dip about 4–7° north. Some tectonic deformations have been observed, and there are also local fault zones and Pleistocene glacial structures preserved in the highly weathered topmost Triassic rocks.

The lowermost exposed part of the section represents middle to upper Norian red to brown, yellowish mudstone and siltstone intercalations with indistinct horizontal lamination and with thin sandy layers and locally breccia-like deposits composed of red and green clasts of the mudstone or claystone. No fossils, including palynomorphs, were found in this part of the section. The lithology and colour of these rocks indicate that they can be related to the locally distinguished and informal “Lisów Beds”, described from the nearby Solarnia IG-1 and Lubliniec IG-1 boreholes. Above this red/brown sequence there is a short, only 40 cm thick sequence of greenish mudstone/siltstone (the boundary is without a distinct change in lithology), somewhat sandy, in which a distinct palaeosol horizon is recorded.

These beds, which show indistinct horizontal lamination, are sharply terminated at the top by distinct channel infill with basal conglomerate. Above this characteristic conglomerate, the major part of the section is represented by grey to greenish (in the top-most part also red and brown) mudstone-siltstone-claystone intercalations and cross-bedded sandstones (greywackes), mainly with trough cross-bedded and ripple-drift cross lamination, including climbing ripples (lower sandstones).

Table 1

Field or collection measurements and data of dinosaur track specimens collected or documented (casts, 3D optical scans, photographs) from the Lisowice-Lipie Śląskie site.

Specimen no.	Field data	DN	TL (cm)	TW (cm)	TL/ TW	II (cm)	III (cm)	IV (cm)	Preservation	Footprint depth (cm)	Angle between digits	Ichnotaxonomy	Trackmaker identification
ZPAL 33.V.T1(plaster cast); Figs. 3A; 4A; 5D	Field observation, cast in 2009; upper ichnoassemblage	3	14.3	12.6	1.13	5.2	7.5	9.5	concave epirelief true footprint	0.1–1.3	II/III = 35; III/IV = 32	<i>Anomoepus</i> isp.	Small ornithischian
ZPAL 33.V.T2 (plaster cast); Figs. 3B; 4B; 5B	Field observation, cast in 2010; upper ichnoassemblage	3	11.2	9.5	1.18	?	?	?	concave epirelief: true footprint	0.1–0.8	II/III = 28; III/IV = 24	<i>Anomoepus</i> isp.	Small ornithischian
ZPAL 33.V.T3 (original slab); Figs. 3C; 4C; 5A	coll. 2007; upper ichnoassemblage	3	19.2	18.3	1.05	8.3	11.8	15.5	convex hyporelief: natural cast	0.1–1.4	II/III = 34; III/IV = 37	<i>Anomoepus</i> isp.	Medium ornithischian
ZPAL 33.V.T4(original slab); Figs. 3D; 4D	coll. 2008; upper ichnoassemblage	3	14.7	16.2	1.09	?	?	?	convex hyporelief: natural cast	0.1–1.3	II/III = 29; III/IV = 33	<i>Anomoepus</i> isp.	Small ornithischian
Specimen FM (not collected); Figs. 3E; 4E	Field observation, 2009; upper ichnoassemblage	3	17	15	1.13	?	?	?	convex hyporelief: natural cast	0.1–2.4	II/III = 27; III/IV = 30	<i>Anomoepus</i> isp.	Medium ornithischian
ZPAL 33.V.T5 (plaster cast); Figs. 3F; 4F; 5C; 12E	Field observation, cast in 2010; upper ichnoassemblage	3	10.2	9.1	1.12	?	?	?	concave epirelief: true footprint	0.1–0.7	II/III = 25; III/IV = 26	<i>Anomoepus</i> isp.	Small ornithischian
ZPAL 33.V.240a (original slab); Figs. 9A; 10A,F; 12A	coll. 2007; upper ichnoassemblage	3	13.2	10.8	1.22	5.2	8.3	6.5	concave epirelief: true footprint	0.1–1.1	II/III = 19; III/IV = 37	<i>Apatichnus minor</i>	Medium theropod
ZPAL 33.V.240b1, b2 (original slab); Figs. 9B,C,D; 10C,D, F; 12B,C	coll. 2007; upper ichnoassemblage	3	13.3/ 13.6	11/ 10.5	1.21/ 1.29	5.1	8.1	6.8	concave epirelief: true footprint	0.1–0.7/ 0.1–0.5	II/III = 17/ 19; III/IV = 39/37	<i>Apatichnus minor</i>	Medium theropod
ZPAL 33.V.240c (original slab); Figs. 9E; 10B,F; 12D	coll. 2007; upper ichnoassemblage	3	10.2	9.3	?	?	?	?	concave epirelief: true footprint	0.1–0.6	II/III = ?; III/IV = ?	<i>Apatichnus minor</i>	Medium theropod
ZPAL 33.V.240d (original slab); Fig. 10E	coll. 2007; upper ichnoassemblage	3	?	?	?	?	?	?	concave epirelief: true footprint	0.1–0.3	II/III = ?; III/IV = ?	<i>Apatichnus minor</i>	Medium theropod
Specimen FI (not collected); Figs. 9F; 11B	Field observation, 2007; upper ichnoassemblage	3	11	8.4	1.31	?	?	?	concave epirelief: true footprint	0.1–2.8	II/III = 16; III/IV = 34	<i>Apatichnus</i> isp.	Medium theropod
Specimen FJ (not collected); Figs. 9G; 11D	Field observation, 2008; lower ichnoassemblage	3	11.3	8.2	1.38	?	?	?	convex hyporelief: natural cast	0.1–3.4	II/III = 27; III/IV = 19	<i>Apatichnus</i> isp.	Medium theropod
Specimen FK (collected by Piotr Menducki); Figs. 9H; 11C	Field observation, 2007; upper ichnoassemblage	3	13.2	?	?	?	?	?	concave epirelief: true footprint	0.1–4.9	II/III = ?; III/IV = ?	? <i>Apatichnus</i> isp.	Medium theropod
ZPAL 33.V.T6 (plaster cast); Figs. 9I; 11A; 12E	Field observation, cast in 2009; lower ichnoassemblage	3	11.2	9.5	1.18	?	?	?	concave epirelief: true footprint	0.1–0.7	II/III = 26; III/IV = 35	<i>Apatichnus minor</i>	Medium theropod
ZPAL 33.V.241 (original slab); Figs. 6A; 7A; 8B	coll. 2007; upper ichnoassemblage	3	18.5	10.5	1.76	?	?	?	convex hyporelief: natural cast	0.1–1.2	II/III = 12; III/IV = 17	<i>Anchisauripus</i> isp.	Medium theropod
ZPAL 33.V.T8 (plaster cast); Figs. 6B; 7B	Field observation, cast in 2008; upper ichnoassemblage	3	19	12	1.58	?	?	?	concave epirelief: true footprint	0.1–1.1	II/III = 15; III/IV = 21	<i>Anchisauripus</i> isp.	Medium theropod
Specimen FL (not collected); Figs. 6C; 7C	Field observation, 2010; lower ichnoassemblage	3	16.5	10.2	1.62	?	?	?	convex hyporelief: natural cast	0.1–1.6	II/III = 13; III/IV = 26	<i>Anchisauripus</i> isp.	Medium theropod
Specimen FN (not collected); Figs. 6D; 7D	Field observation, 2007; upper ichnoassemblage	3	16	9	1.78	?	?	?	convex hyporelief: natural cast	?	II/III = ?; III/IV = ?	<i>Anchisauripus</i> isp.	Medium theropod
Specimen FO (not collected); Figs. 6E; 7E	Field observation, 2008; upper ichnoassemblage	3	16.3	?	?	?	?	?	concave epirelief: true footprint	0.1–2.9	II/III = ?; III/IV = ?	? <i>Anchisauripus</i> isp.	Medium theropod
Specimen FP (not collected); Figs. 6F; 7F	Field observation, 2010; lower ichnoassemblage	3	16.5	11.4	1.44	?	?	?	convex hyporelief: natural cast	0.1–1.5	II/III = ?22; III/IV = ?27	<i>Anchisauripus</i> isp.	Medium theropod
Specimen FQ (not collected); Figs. 6G; 7G	Field observation, 2009; lower ichnoassemblage	3	16.5	10.5	1.57	?	?	?	convex hyporelief: natural cast	0.1–1.1	II/III = 24; III/IV = 28	<i>Anchisauripus</i> isp.	Medium theropod
ZPAL V.33.T9 (plaster cast); Figs. 6H; 7H; 8A	Field observation, cast in 2009; upper ichnoassemblage	3	16.2	10.1	1.6	6.5	10.2	10.1	concave epirelief: true footprint	0.1–1.2	II/III = 14; III/IV = 18	<i>Anchisauripus</i> isp.	Medium theropod
Specimen FR (not collected); Figs. 6I; 7I	Field observation, 2008; upper ichnoassemblage	3	10	5.5	1.82	?	?	?	convex hyporelief: natural cast	?	II/III = 12; III/IV = 14	<i>Grallator</i> isp.	Small theropod

(continued on next page)

Table 1 (continued)

Specimen no.	Field data	DN	TL (cm)	TW (cm)	TL/ TW	II (cm)	III (cm)	IV (cm)	Preservation	Footprint depth (cm)	Angle between digits	Ichnotaxonomy	Trackmaker identification
Specimen FS (not collected); Figs. 6J; 7J	Field observation, 2008; upper ichnoassemblage	3	13.2	7.5	1.76	?	?	?	convex hyporelief: natural cast	?	II/III = 13; III/IV = ?20	<i>Grallator</i> isp.	Small theropod
ZPAL V.33.T10 (original slab); Figs. 6K; 7K	coll. 2009; upper ichnoassemblage	3	13	8	1.62	?	?	?	convex hyporelief: natural cast	0.1–0.5	II/III = ?; III/IV = ?	<i>Grallator</i> isp.	Small theropod
Specimen FT (not collected); Figs. 6O; 7O	Field observation, 2008; upper ichnoassemblage	3	14	7.5	1.87	?	?	?	convex hyporelief: natural cast	0.1–2.5	II/III = ?; III/IV = ?	<i>Grallator</i> isp.	Small theropod
ZPAL V.33.T11 (plaster cast); Figs. 6L; 7L; 8E	Field observation, cast in 2009; upper ichnoassemblage	3	12.5	7.1	1.76	3.9	6.7	6.3	epirelief: true footprint	0.1–0.9	II/III = 11; III/IV = 15	<i>Grallator</i> isp.	Small theropod
ZPAL V.33.T12 (plaster cast); Figs. 6M; 7M; 8D	Field observation, cast in 2009; upper ichnoassemblage	3	13.7	9	1.52	?	?	?	concave epirelief: true footprint	0.1–0.9	II/III = ?29; III/IV = ?36	<i>Grallator</i> isp.	Small theropod
Specimen FU (not collected); Figs. 6N; 7N	Field observation, 2009; lower ichnoassemblage	3	11.2	7	1.6	?	?	?	concave epirelief: natural cast	?	II/III = ?; III/IV = ?	<i>Grallator</i> isp.	Small theropod
ZPAL V.33.T13 (original slab); Figs. 6P; 7P; 8C	coll. 2009; upper ichnoassemblage	3	13.5	8.2	1.65	4.5	7.8	8	convex hyporelief: true footprint	0.1–0.7	II/III = 14; III/IV = 19	<i>Grallator</i> isp.	Small theropod
ZPAL 33.V.219 (original slab); Figs. 14B; 15B; 16B	coll. 2006; upper ichnoassemblage	3	41	37	1.1	?	?	?	convex hyporelief: underprint, natural cast	3 to 6	II/III = 22; III/IV = 32	cf. <i>Eubrontes</i> isp.	Large theropod
ZPAL 33.V.508 (original slab); Figs. 14A; 15A; 16	coll. 2006; lower ichnoassemblage	3	55	42	1.29	?	?	?	convex hyporelief: deep underprint, natural cast	6 to 12	II/III = 25; III/IV = 27	cf. <i>Eubrontes</i> isp.	Large theropod
ZPAL 33.V.509 (plaster cast); Figs. 14C; 15C; 16C	Field observation, cast in 2009; upper ichnoassemblage	3	38	26	1.46	?	?	?	concave epirelief: true footprint	3 to 4	II/III = 25; III/IV = 18	<i>Eubrontes</i> isp.	Large theropod
ZPAL 33.V.510 (plaster cast); Figs. 14E; 15E	Field observation, cast in 2010; lower ichnoassemblage	3	43	39	1.1	?	?	?	concave epirelief: true footprint	2 to 3	II/III = 29; III/IV = 33	<i>Eubrontes</i> isp.	Large theropod
Specimen FA; Figs. 14D; 15D	Field observation, 2009; upper ichnoassemblage	3	39	31	1.26	?	?	?	convex hyporelief: natural cast	3 to 5	II/III = 23; III/IV = 42	<i>Eubrontes</i> isp.	Large theropod
Specimen FB (plaster cast; unregistered); Figs. 14G; 15G	Field observation, cast in 2010; upper ichnoassemblage	3	37	28	1.32	?	?	?	convex hyporelief: underprint, natural cast	2 to 3	II/III = 23; III/IV = 24	<i>Eubrontes</i> isp.	Large theropod
Specimen FC; Figs. 14F; 15F	Field observation, 2010; upper ichnoassemblage	3	43	40	1.07	?	?	?	convex hyporelief: natural cast	2 to 5	II/III = 28; III/IV = 27	<i>Eubrontes</i> isp.	Large theropod
Specimen FD; Figs. 14H; 15H	Field observation, 2007; lower ichnoassemblage	3	42	38	1.1	?	?	?	concave epirelief: true footprint	1 to 2	II/III = 28; III/IV = 36	<i>Eubrontes</i> isp.	Large theropod
Specimen FE; Figs. 14I; 15I	Field observation, 2008; upper ichnoassemblage	3	39	29	1.34	?	?	?	concave epirelief: true footprint	1 to 3	II/III = 18; III/IV = 33	<i>Eubrontes</i> isp.	Large theropod
Specimen FF (not illustrated)	Field observation, 2010; lower ichnoassemblage	3	38	30	1.27	?	?	?	concave epirelief: true footprint	1 to 3	II/III = 21; III/IV = 37	<i>Eubrontes</i> isp.	Large theropod
Specimen FG (not illustrated)	Field observation, 2010; upper ichnoassemblage	3	56	43	1.31	?	?	?	concave epirelief: true footprint	2 to 4	II/III = 23; III/IV = 28	cf. <i>Eubrontes</i> isp.	Large theropod
Specimen FH (plaster cast; unregistered), (not illustrated)	Field observation, cast in 2010; upper ichnoassemblage	3	54	41	1.32	?	?	?	concave epirelief: true footprint	3 to 8	II/III = 24; III/IV = 31	cf. <i>Eubrontes</i> isp.	Large theropod
Trackway ZPAL 33.V.240a, b1, b2, c, d (original slabs)	TwL = 153 cm TwW = 7 cm–5 cm P (41, 32, 31, 32) λ (76, 65, 64) mean 68 Pα = 145–170 H = 13.4 × 4; 53.6 G = 68/53.6; G = 1.27 Absolute speed = 8 mph												

This part of the section has been divided into three parts (A–C) according to the character of sediments and fossil content (Fig. 2). The lowest part A is definitely dominated by sandstone deposits. The general transport of material in part A was to NE and N (see Pieńkowski et al., 2014). The epsilon cross-bedding produced by lateral migration of channels is common in this part of the section (Fig. 2), where also plant remains and bones are preserved. The largest number of bone fragments was discovered in the basal conglomerate, but bones were also found in the local lenses of conglomerates in sandstones. The entire part A has been designated as the lower bone-bearing interval, because it is characterized by clear differences from the bone record from the fossiliferous beds identified in part C. In part A, two surfaces with tetrapod tracks (named I and II) were recognized, but these traces are not included in this publication. The lower bone-bearing interval, which is characterized by a much poorer fossil record and preservation of bones (abrasion), cannot be divided into sublevels.

The sequence dominated by sandstones passes without a clear erosional boundary into olive-green to grey clayey and mudstone deposits (approx. 1.5 m thick) in which no organic remains occur, and the only fossils that could be recognized are traces of plant roots. This unfossiliferous sequence (part B) also contains a sandstone layer with strongly disturbed bedding (Fig. 2) that has been interpreted as a tectonic shake effect (Pieńkowski et al., 2014). It is probably the record of a local seismite. The layer is observed at three locations in the clay-pit and in the same lithostratigraphic position, which indicates its isochronous character.

The part C in the section begins with a distinct erosional boundary (after which there are several additional erosion boundaries), and the deposits developed above this boundary are very fossiliferous. All breccia/conglomerate, sandstone and mudstone-siltstone-claystone lithofacies contain numerous drifted plant remains, bone fragments, vertebrate bromalites and bivalve fragments. In some sandstone and mudstone-siltstone-claystone beds, pedogenesis is also well-developed and remains after plant roots and pedogenic nodules are present.

The mudstones-siltstones and sandstones in the C part are enriched in carbonates, likely because of redeposition and destruction of older carbonate rocks (Pieńkowski et al., 2014), but it is also probable that these carbonates were formed by the precipitation of carbonates from groundwaters, surface or groundwater-fed rivers/streams/ponds with a high content of carbonates. Layers of palustrine and crenogenic carbonates and dolomitic sandstones-mudstones-siltstones, as well as beds with accumulations of oncoids and stromatolites, occur in the section (Tałańda et al., 2017). This unit is called regionally the “Woźniki Limestone”, a diachronous and genetically inhomogeneous lithological unit; see Szulc et al., 2006). At the Lisowice-Lipie Śląskie site, their formation can be seen in the genetical association with the “Woźniki Limestone” deposits, which are known several hundred meters to the north of the clay pit. There are four discrete bone-bearing beds in the upper bone-bearing interval in the part C of the section. All are separated by bone-barren mudstone-siltstone-claystone levels with numerous plant remains and casts of bivalve shells.

Conglomerates and breccia-like coarse sediments appear mostly at the bottoms of sandstone layers (=bottoms of fluvial cycles) and are composed of reworked carbonate nodules, clasts of carbonate mudstones, mud- or clay-clasts from older Upper Triassic sediments and fragments of quartzites (probably of a Palaeozoic age). These conglomerates or breccias are traditionally known as the “Lisów breccia” Bed (in Polish, *brekcja lisowska*; diachronous lithological unit), described from the Upper Triassic outcrops and boreholes in Silesia. These beds often contain vertebrate bones and bivalve remains, often forming local outcrops observed on weathered Triassic surfaces.

A red-greenish-brownish heterolithic unit (interbedded mudstone, siltstone, claystone and sandstone beds) occurs at the top of the outcrop. It contains carbonate nodules and infilled plant roots. Pieńkowski et al. (2014) suggested that both red bed units at the bottom and at the top of the outcrop were deposited on an alluvial plain under semi-arid climate

conditions. The origin of these upper red beds is not entirely clear, but additional observations and studies of collected samples indicate local redeposition as an important factor in the formation of these deposits. A more detailed discussion of this problem will be presented in a coming publication.

Lithological characteristics, geometry of the lithic units, and sedimentary structures suggest that bone accumulations in the so-called upper bone-bearing interval was formed in a mosaic of alluvial plain environments – oxbows, swamps with ephemeral ponds and laterally shifting river channels (Pieńkowski et al., 2014; Jewuła et al., 2019). In particular, texturally immature sediments (greywackes), lack of stable channels and presence of climbing ripples point to an increased rainfall and runoff, combined with fast deposition (Pieńkowski et al., 2014). The presence of kaolinite and smectite-rich beds, the presence of complex floral assemblages (macro- and microfossils), and changes in vertebrate faunas recorded in the Lisowice-Lipie Śląskie section, point to a gradual onset of a more humid climate across the late Norian/earliest Rhaetian interval in the Polish Basin (see Pieńkowski et al., 2014; Qvarnström et al., 2024).

The dinosaur and other tetrapod tracks in the Lisowice-Lipie Śląskie section occur at multiple beds (I, II; a–e), in the lower bone-bearing interval and just above and below the upper bone-bearing interval (Fig. 2). No tetrapod traces were found in the middle to late Norian red beds (part of the section A), in the section B located between lower and upper bone-bearing intervals or sandstone-mudstone layers directly associated with the upper bone-bearing interval. The lithologies of track-bearing beds from the part C section (lower beds: a–b, upper beds c–e; see Fig. 2) are grey, yellowish moderate-fine sandstones, grey siltstones, and grey silty mudstone. The overall sedimentological character of these facies is indicative of floodplain deposits of a meandering river system (Pieńkowski et al., 2014).

3. Stratigraphy and age

Determining the stratigraphic age of the fossil accumulations in the Lisowice-Lipie Śląskie section has given rise to much discussion (see Dzik et al., 2008a, 2008b; Świło et al., 2014; Pieńkowski et al., 2014; Szulc et al., 2015), mainly generated by conflicting evidence in determining the age of the fossil-bearing intervals (biostratigraphy/palaeontology vs. lithostratigraphy/chemostratigraphy). According to the stratigraphical interpretations, the lower and upper bone-bearing intervals exposed at the section (A and C in Fig. 2) represent the Norian Woźniki Limestone (Szulc et al., 2006) or the middle Norian part of the Grabowa Formation (Szulc et al., 2015). In another proposed interpretation of the age of these deposits (Pieńkowski et al., 2014), the upper bone-bearing interval (part C) and grey, mudstone deposits located below (part B) were correlated with the lowermost Rhaetian part of the Wielichowo Beds. The lower interval with bones (part A) was placed between the Wielichowo Beds and the Zbąszynek Beds, without indicating affiliation to one or another lithoformation (Pieńkowski et al., 2014). The lower redbeds (lower part of the section A; red to brown mudstones and siltstones) were assigned to the uppermost Norian part of the Zbąszynek Beds. In the interpretation of Pieńkowski et al. (2014), the Lisowice-Lipie Śląskie section therefore represents a transition between two informal lithostratigraphic units described from the Polish Lowlands: 1) the Zbąszynek Beds (lower red/brown mudstone and siltstone) and Wielichowo Beds (grey sandstone-mudstone, upper bone-bearing interval plus heterolith unit) (see also Deczkowski, 1997; Franz et al., 2007a, 2007b; Franz, 2008; Franz et al., 2021).

The occurrence of plant fossils in this site was first noted in the early 1980s (Fuglewicz and Śniezek, 1980; Marcinkiewicz, 1981), but only megaspores were initially described (Fuglewicz, 1977). Recent studies have yielded many new important finds (Stanecko, 2007; Ociepa et al., 2008; Dzik et al., 2008a, 2008b; Marynowski and Simoneit, 2009; Wawrzyniak and Ziąja, 2009, 2010; Wawrzyniak, 2010a, 2010b, 2010c, 2010d, 2011; Jarzynka and Wawrzyniak, 2012; Świło et al., 2014;

Pieńkowski et al., 2014; Zatoń et al., 2015; Wawrzyniak and Filipiak, 2023). These are mostly represented by palynomorphs, dispersed plant cuticles, but also include more well-preserved plant macrofossils and numerous plant remains preserved in bromalites. Further materials are being developed, and the comparison of palynological data from the upper and lower bone-bearing intervals and bromalites seems particularly interesting from a stratigraphical point of view.

There are noticeable taxonomic differences between the floral assemblages of the lower and upper bone-bearing intervals (on-going study). Comparable floras are known from other middle-late Norian, Rhaetian and Early Jurassic floral assemblages of the region (Pacyna, 2014). The flora from Lisowice-Lipie Śląskie is surprisingly diverse, including many conifers and cycads similar to younger Jurassic taxa (cf. Harris, 1932, 1935, 1937). Some fossils, especially of conifers, show apparent affinity to taxa described from other Late Triassic Silesian floras (Pacyna, 2014). Its transitional, Norian-Rhaetian character emphasizes its unique importance for biostratigraphic and palaeoecological studies.

A latest Norian-earliest Rhaetian age of the upper fossil assemblage in the Lisowice-Lipie Śląskie section is indicated by the presence of: 1) the conchostracan *Gregoriusella polonica* Kozur, Niedźwiedzki and Sulej, 2010 (see Kozur and Weems, 2010); 2) the occurrence of isoëtelean macrospores *Trileites* cf. *pinguis* (Harris, 1935) and *Horstisporites bertelsenii* Fuglewicz, 1977 (see Fuglewicz, 1977; Fuglewicz and Śniezek, 1980); 3) the occurrence of *Rhaetipollis germanicus* pollen (Świło et al., 2014; and on-going study); 4) finds of numerous cuticle and leaf fragments or fructifications (*Peltaspermum rotula*) of the seed-fern *Lepidopteris ottonis* (Stanecko, 2007; Ociepa et al., 2008; Dzik et al., 2008a, 2008b; Wawrzyniak and Ziaja, 2009; Wawrzyniak, 2010a, 2010b; Świło et al., 2014; Zatoń et al., 2015; Pieńkowski et al., 2014; Wawrzyniak and Filipiak, 2023; Qvarnström et al., 2024); 5) the presence of a highly diversified dinosaur fauna, skeletal (Qvarnström et al., 2019, 2024; and on-going study) and footprint records (this study); 6) teeth of rhomphaiodon sharks (Zalewski et al., in prep.); 7) as well as the record of double-rooted, early mammaliaform *Hallautherium* teeth (Świło et al., 2014).

Based on palynomorph studies, the upper bone-bearing strata were assigned to the *Corollina meyeriana* Subzone IVb (see Stanecko, 2007; Szulc et al., 2006; Fijałkowska-Mader et al., 2015) or *Corollina meyeriana* Subzone IVc/*Ricciisporites tuberculatus* Zone (Dzik et al., 2008a, 2008b; Świło et al., 2014; Pieńkowski et al., 2014; Qvarnström et al., 2019, 2024). The identification of the *Corollina meyeriana* IVc subzone in the Lisowice-Lipie Śląskie section (Świło et al., 2014; Pieńkowski et al., 2014, and on-going study), defined by the first appearance of *Rhaetipollis germanicus* (see Orłowska-Zwolińska, 1983, 1985; Herngreen, 2005; Fijałkowska-Mader, 2015) and new U—Pb dating of detrital zircon crystals from the upper bone-bearing strata have important implications for regional stratigraphic interpretation.

The problem of the absence or presence of a *Ricciisporites tuberculatus* zone in this section remains to be solved (see Świło et al., 2014; Pieńkowski et al., 2014). The numerous and well-preserved palynomorphs recovered from bromalites will probably be helpful here. The *Ricciisporites tuberculatus* zone (Orłowska-Zwolińska, 1983, 1985), which was later incorporated into the Rhaetian *Rhaetipollis germanicus* zone in the Central European Basin (Lund, 1977; Herngreen, 2005; Kürschner and Herngreen, 2010), probably refers to the earliest Rhaetian. However, to precisely correlate terrestrial sequences from the Central European Basin (based on palynomorphs and radiometric datings) with the marine standard, the Norian-Rhaetian boundary stratotype (GSSP) must be defined and the numerical age of the boundary precisely determined and ratified by the stratigraphic commission.

A published U—Pb dating of a single detrital zircon crystal (Ion Microprobe SHRIMP IIe/MC), recovered from the conglomeritic bed (positioned below the upper fossil-bearing interval, but in the upper part of the lower bone-bearing interval; see Fig. 2), yielded an absolute age of 211 ± 3 Ma (Kowal-Linka et al., 2019). The boundary between the

Norian and Rhaetian stages is currently defined at the age of ~ 208.5 or ~ 205.5 million years. The zircon date falls within the 208–214 Ma range, thus suggests not older than 1) late Norian or 2) latest Norian age for the lower bone-bearing interval. This is in agreement with the palaeontological material collected from the lower fossil-bearing interval and suggests a time difference between the deposition of the two fossiliferous intervals (see Sulej and Niedźwiedzki, 2019; Qvarnström et al., 2024, on-going study). Alternatively, if the Norian-Rhaetian boundary age were to be taken as ~ 205.5 Ma, then the age of the youngest zircon, would point to 1) the middle Norian (Alaunian–Sevatian boundary at ~ 209 –210 Ma) or 2) late Norian (Alaunian–Sevatian boundary at ~ 214 –216 Ma) as the maximum depositional age of the lower bone-bearing interval (Kowal-Linka et al., 2019). Finally, it is worth noting that the late Norian-earliest Rhaetian transitional character of this sedimentary succession is reflected in the subsequent results obtained from several zircon datings, as well as from comprehensive biostratigraphic studies (palynomorphs, plant macrofossils, conchostracans and vertebrate remains), which will be presented in the coming stratigraphic study. In this publication, we therefore use the late Norian-earliest Rhaetian age interpretation of the upper bone-bearing interval (part C in the section, Fig. 2).

4. Vertebrate fauna

The ichnological material from Lisowice-Lipie Śląskie is associated with numerous bones of a gigantic dicynodont (*Lisowicia bojani*), a theropod-like archosaur (*Smok wawelski*) and many isolated or fragmentary preserved bones of temnospondyls (*Cyclotosaurus* sp. and *Gerrhotorax* sp.), early anurans (Salientia indet.), small diapsids (Diapsida indet. and a pachystropheus-like reptile), lepidosauromorphs (Sphenodontia indet.), archosauromorphs (?Pterosauria indet., ?Sharovipterygidae indet. and Crocodylomorpha indet.), early dinosaurs (several forms of Saurischia and ?Ornithischia), remains of bony fish (actinopterygians and sarcopterygians), fin spines and teeth of hybodont sharks and other vertebrates (Dzik et al., 2008a, 2008b; Niedźwiedzki et al., 2012; Niedźwiedzki, 2013; Niedźwiedzki et al., 2015; Sulej and Niedźwiedzki, 2019; Qvarnström et al., 2024). There are also remains of small therapsids, in the form of isolated teeth and postcranial elements of a mammaliaform (*Hallautherium* sp.; see Świło et al., 2014) and a eucynodont (Cynodontia indet.).

The fossil assemblage from the upper bone-bearing interval, which consists of four sub-levels, differs from that recognized below, the so-called lower bone-bearing interval. This lower level will not be considered here because it is not directly associated with the studied tracks (track-bearing beds a–e). Numerous bromalites (coprolites and gastric pellets) were found in several fossiliferous horizons in the section C (Bajdek et al., 2014; Zatoń et al., 2015; Qvarnström et al., 2019, 2024).

5. Material and methods

Around 100 tetrapod tracks (42 described in this paper) were collected or documented during more than 20 field campaigns led by the first author between 2006 and 2017. Old or newly uncovered surfaces with potential ichnological record were cleaned and studied in detail (photographs, drawings, plaster casts, 3D scans). Between 2006 and 2007, a generalized lithostratigraphic section was measured (see Dzik et al., 2008a, 2008b) and photographs of the distinctive tetrapod tracks were taken for preliminary analysis and identification. Due to the uniqueness of some observed tracks, such as the large tridactyl *Eubrontes*-like tracks, more focus was put on finding high-quality ichnofossil material between 2008 and 2017. In 2010 and 2012, the section was again measured in detail, and a new generalized profile was published by Pieńkowski et al. (2014), which is reproduced in this study (Fig. 2). The entire ichnological collection has not yet been studied or catalogued, but we illustrate the most diagnostic dinosaur track specimens and provide useful morphometric parameters (Table 1).

The dinosaur track specimens described here come from two ichnoassemblages (upper and lower), which in turn consist of several beds (a-e) with tetrapod trace fossils (Fig. 2). All were found near their source beds in loose blocks/slabs that were excavated during mining. Several specimens were found in the old part of the clay-pit (see Table 1), and their origin was determined based on lithological features and slab thickness. Each track presented herein was traced using clear acetate film to produce schematic drawings (all were later digitized). The best-preserved tracks were collected, and in some cases, replicas were made using plaster. Due to the large sizes of some slabs or the difficulty of accessing certain parts of the clay-pit with vehicles, some of the blocks were left in the field. Plaster casts or 3D scans were made from these specimens. All original specimens or replicas are identified with appropriate field and collection numbers in the text and data table (Table 1). The existing dinosaur track collection (originals and replicas) is housed in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw and Paleontological Museum at Lisowice, which includes 21 specimens (Table 1). They represent the most diagnostic material from this site. The format adopted below is to categorize tracks according to their general affinity within standard classification schemes (e.g., small to large theropod, ornithischian), present line drawings (interpretive drawings) and photographs to standard scales, 3D scan data (visualizations and false-colour depth maps) and tabulate basic morphometric parameters. Only well-preserved tracks have been considered relevant to a more detailed study. These specimens record the anatomy-consistent features of trackmaker pes (e.g., claws, sizes and shapes of digital pads or metatarsal pads), which are used as diagnostic characters. The track-trackmaker correlations were based on morphofunctional features that tracks and pes skeletons (Fig. 17B) of the potential trackmakers have in common (see Olsen et al., 1998). The large *Eubrontes* tracks from the Lisowice-Lipie Śląskie site were subjected to simple morphometric analyses to check their similarity or dissimilarity to other finds of this type from the Late Triassic–Early Jurassic sites in the region (Fig. 18D).

Specimens were photographed with a digital camera perpendicular to the tracks surface, under oblique artificial or natural light to emphasize the track morphology. We have strictly avoided any specimen painting or touch-up of track images. Rather, filtering allows for enhancement purely through changing the contrast of the unmodified original image. Most of the specimens were imaged using Nikon Digital Camera D5300 and Canon EOS 2000D. Optical scans were undertaken with Range Vision Spectrum and Calibri Thor 3D and were processed in Range Vision 3D studio 2022.1 and Calibri Nest software. The resulting STL files were rendered for greyscale images or false-colour depth maps in ParaView 5.10.1.

The tracks are preserved in siltstones, sandy mudstones and sandstones, both as natural impressions /natural molds (concave epirelief; see Fig. 9A) and as natural casts (convex hyporelief; see Fig. 3C), some with high relief and others with very little relief (Table 1). Despite the diversity and size range of specimens (Table 1; Figs. 3–12, 14, 15), most tracks are isolated specimens, and there is only one example of a trackway, which was produced by a medium theropod dinosaur (*Apatichtnus minor*) (Fig. 10). This bias against trackway segments is a consequence of the breakup of track-bearing beds by digging machines operating in the clay-pit and limited access to larger palaeosurfaces.

Non-metric parameters (general outline, size and shape of claw imprints, digital pad and metatarsalphalangeal pad imprints shape) were recorded to distinguish the track's general morphology. Forty-two individual, tridactyl, mesaxonic tracks are found in the Lisowice-Lipie Śląskie site and they can be grouped into three major (anomoepoid, grallatorid and eubrontid) morphotypes based on: (a) track morphology; (b) total digit divarication; and (c) length to width ratios (Table 1). Then, quantitative parameters (Table 1) to describe and characterize morphotypes tracks were used based on Leonardi (1987), Farlow and Lockley (1993) and Olsen et al. (1998): number of digit impressions (DN), total footprint length = total length of phalangeal part of foot

skeleton (TL), total track width (TW), ratio length/width (TL/TW), II – length of phalanges II2 + II3; III – length of phalanges III2 + III3 + III4; IV – total length of phalanges IV1 through IV5, digit divarication angle between digits II and III (II/III) and between digits III and IV (III/IV). The conventions for obtaining parameters from tracks are shown in Fig. 18A, B. The trackmaker identifications are based on the analyses presented by Olsen et al. (1998) and Olsen and Rainforth (2003) who studied three-toed dinosaur tracks from Early Jurassic sites in the Hartford and Deerfield basins. The parameters used to describe trackways also follow Leonardi (1987): trackway length (TwL), trackway width (TwW), stride (λ), pace (P), and pace angulation ($P\alpha$). Measurements were obtained from the tracks in the field and later, from casts and acetate film line drawings.

Three-dimensional reconstructions of selected tracks were performed through optical 3D scanning. Grey-scale models and depth false colour maps with contours for additional imaging of specimens were created with the open-source software Paraview 5.10.1 (www.paraview.org).

Body size was estimated in terms of body length and isolated tracks can be used to estimate the size of the trackmaker (Table 1). Total body lengths (TBL) for the theropod and ornithischian dinosaur trackmakers were calculated using modified equation of Thulborn's (1990): $TBL_{(TL < 25-35 \text{ cm})} = 4 \times (3.06 \times TL^{1.14})$ and $TBL_{(TL > 35 \text{ cm})} = 2 \times (8.6 \times TL^{0.85}) + 3.5$. In order to determine the gait and speed from the only preserved trackway (Fig. 10), it is important to get a good estimate of hip height of the trackmaker. After Henderson (2003) we used the simple formula for the hip height estimations, $H = 4 \times TL$ (four times the foot length). The equation used to calculate the absolute speed of a trackmaker depends on the gait determined for the trackmaker, i.e. walking vs. running. The trackmakers' gait (G) was determined by the relative stride ratio λ/H where λ is the stride length (see Alexander, 1976; Thulborn, 1989, 1990; Thulborn and Wade, 1984). We used the formula $\text{Absolute speed} = 0.25 g^{0.5} \times \lambda^{1.67} \times h^{-1.17}$ (Alexander, 1976), because the results for the trackmaker gait ($\lambda/H < 2.0$) indicated that the animal was walking (Table 1).

Abbreviations of cited repositories: AC – Pratt Museum of Natural History, Amherst College, Amherst, Massachusetts, USA; MGUH – Geological Museum, University of Copenhagen, Copenhagen, Denmark; ZPAL – Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland

6. Systematic ichnology

6.1. Ichnofamily Anomoepodidae (Lull, 1904) Gierliński, 1991

6.2. Ichnogenus *Anomoepus* (Hitchcock, 1848) Gierliński, 1991
Anomoepus isp. (Figs. 3–5)

Material. Six pes tracks (Table 1), isolated specimens collected or documented from different beds in the upper (c-e) ichnoassemblage in the section C (Figs. 2 and 17). Three specimens preserved as concave epirelief (Fig. 3A, B, and F) and three as convex hyporelief (Fig. 3C, D and E), (Table 1).

Description. Pes imprints are mesaxonic, tridactyl, digitigrade, slightly longer than wide. They average 15 cm in length and 12 cm in width with a length/width ratio between 1.05 and 1.18. Digits III and IV are similar in length, digit II is clearly shorter than III or IV (digit formula $II < III < IV$). The digits are narrow, with oval-shaped pads and preserve evidence of short triangular claws. The digits are highly divergent: the total divergence between digits II and IV is more than 50° (Table 1). The characteristic feature of these tracks is the prominent metatarsalphalangeal pad of digit IV, set below the axis of digit III (Figs. 3A; 4A; 5). This makes these specimens similar to the classic *Anomoepus scambus* Hitchcock, 1848 from the Lower Jurassic of North America (Olsen and Rainforth, 2003). These tracks show digit length ratios more typical for ichnogenus *Anomoepus* (see Fig. 18C) than for theropod tracks.

Comments. *Anomoepus* is a classical Early Jurassic ichnogenus

produced by a relatively small to medium, gracile ornithischian dinosaur (Olsen and Rainforth, 2003). It has a tetradactyl pes, but only three pedal digits are impressed while the animal was walking. Specimens from Lisowice-Lipie Śląskie have proportionally shorter digit III, and widely positioned outer digits (II and IV) than grallatorid tracks collected from the site, which indicates that this is not the state of preservation of *Anchisauripus*, *Apatichnus* or *Grallator* tracks. The ichnogenus is cosmopolitan, known from eastern and western North America, many sites in Europe, Africa, Asia and Australia (Lockley and Gierliński, 2006). The first unequivocal occurrence of *Anomoepus* 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). The occurrence of this ichnogenus in the late Norian–earliest Rhaetian of Lisowice-Lipie Śląskie is quite surprising. It is believed that *Anomoepus* is an indicator of the earliest Jurassic, but there are a few finds reported from the Upper Triassic sections that were classified as *Anomoepus* (e.g., Niedźwiedzki, 2011b; cf. *Anomoepus* isp.; Weems, 2018; *Anomoepus* aff. *A. isodactylus*). Recently described Late Triassic anomoepoid-like tracks from the Chinle Group of western North America were named *Eoanomoepus* (Lockley et al., 2018). However, they differ from *Anomoepus* by widely spread digits not connected posteriorly, these tracks can be ?four-digitated and show unusually wide trackways, which may question its dinosaurian affinity. *Eoanomoepus* resembles a subdigitigrade, tridactyl (or tetradactyl) version of *Crocodylopodus* (see Castarena et al., 2021), possibly produced by a bipedal crocodile-line archosaur. The revision and broader description of the Upper Triassic occurrences of the *Anomoepus* ichnogenus is a topic for a separate publication (see also discussion part). New data from sections in Poland, Sweden, East Greenland and Western USA suggest that *Anomoepus* and *Anomoepus*-like tracks have a wider stratigraphic distribution in the Late Triassic and are associated with a specific dinosaur-dominated track assemblage. The appearance of the *Anomoepus* ichnogenus in the Late Triassic corresponds to when the first ornithischian dinosaurs appeared in tetrapod faunas (Müller and García, 2020; Norman et al., 2022; Fonseca et al., 2024; Yao et al., 2025).

6.3. Ichnofamily Grallatoridae Lull, 1904

6.4. Ichnogenus *Grallator* Hitchcock, 1858

Grallator isp. (Figs. 6I–P; 7I–P; 8C–E)

Material. Eight pes tracks (Table 1), isolated specimens collected or documented from different beds in the lower (a–b) and upper (c–e) ichnoassemblages in the section C (Figs. 2 and 17). Three specimens preserved as concave epirelief (Fig. 6L, M, P) and five as convex hyporelief (Fig. 6I–K, N, O), (Table 1).

Description. Small, tridactyl, gracile grallatorid pes imprints, 11.2–14 cm long. The total length to total width ratio is between 1.62 and 1.87. These tracks show digit length ratios: III/II = 1.72–1.73, III/IV = 0.97–1.06 (see Fig. 18C).

Comments. Specimens show features typical for the ichnogenus *Grallator* Hitchcock, 1858, such as slender, slightly divaricated digits with the third toe highly projecting. The digit length ratios of these specimens are close to those given by Olsen et al. (1998) for *Grallator parallelus* Hitchcock, 1858, the type ichnospecies of *Grallator* (see Fig. 18C), but the size of these traces is much larger. Therefore, we name all discussed specimens as *Grallator* isp., according to the ichnotaxonomic interpretations presented by Lockley and Hunt (1995) and following the ichnotaxonomy concept of Olsen et al. (1998). The ichnogenus *Grallator* is quite widespread in Late Triassic and Early Jurassic sedimentary sequences globally. There is currently a tendency to designate as *Grallator* small theropod tracks from Late Jurassic and Cretaceous formations, which is probably incorrect. However, a further discussion of this issue requires additional studies and is beyond the scope of this publication. Here we only want to signal this problem and emphasize that the identification of this ichnogenus should be related to the type ichnospecies of *Grallator* (see Olsen et al., 1998) and perhaps

limited to occurrences of small-sized grallatorid traces in Middle-Late Triassic and Early Jurassic ichnoassemblages.

Most researchers agree that *Grallator* represents a small theropod, possibly *Coelophysis* and related forms (e.g. Olsen et al., 1998; Lockley and Gierliński, 2009). Tracks in the Lisowice-Lipie Śląskie assemblage have a mean foot length around 12 cm and foot width around 7 cm. This size corresponds to early theropods such as *Coelophysis* (Colbert, 1989; Thulborn, 1990). However, the mean sizes in the Lisowice-Lipie Śląskie *Grallator* specimens are about 20 % larger than those recorded for *Grallator* from the numerous Upper Triassic sites from North America (Lockley and Gierliński, 2009). *Grallator* tracks from Lisowice-Lipie Śląskie represent large forms, and perhaps the lack of smaller tracks (in the length range = 6–8 cm) is due to a taphonomical or sampling bias. There are not many finds of small tracks of tetrapods at the site. However, there are changes in the median and maximum size of different theropod tracks in the Late Triassic and Early Jurassic (Lockley and Gierliński, 2009). Haubold (1984, 1986) noted the increase in the size of theropod ichnotaxa (*Grallator*, *Anchisauripus* and *Eubrontes*) across the Late Triassic–Early Jurassic interval (see Lockley and Hunt, 1995; Olsen et al., 2002). The *Grallator* from Lisowice-Lipie Śląskie may fit into this trend, representing a rather large form of this ichnogenus, distinctly larger than the typical Carnian or Norian ones, known from many localities in North America, Africa, Australia and Asia. *Grallator* is a long-ranging ichnogenus and therefore of little biostratigraphic utility.

6.5 Ichnogenus *Anchisauripus* Lull, 1904

Anchisauripus isp. (Figs. 6A–H; 7A–H, 8A, B)

Material. Eight pes tracks (Table 1), isolated specimens collected or documented from different beds in the lower (a–b) and upper (c–e) ichnoassemblages in the section C (Figs. 2 and 17). Three specimens preserved as concave epirelief (Fig. 6B, E, H) and five as convex hyporelief (Fig. 6A, C, D, F, G), (Table 1).

Description. Medium-sized, tridactyl, gracile grallatorid pes specimens, 16–19 cm long that show features typical for the ichnogenus *Anchisauripus* Hitchcock, 1858, such as slender, slightly divaricated digits with the third toe moderately projecting (digit III projection ratio averages about 1.3–1.5). The total length to total width ratio is between 1.57 and 1.78, but this is probably a slightly distorted range due to the state of preservation of the specimens. These tracks show digit length ratios: III/II = 1.72 and 1.73; III/IV = 0.97 and 1.06 (see Fig. 18C).

Comments. A noticeable and quite interesting feature of these tracks is the rather wide spacing of the outer digits (TD), which is greater than in classic *Anchisauripus* tracks from the Early Jurassic. Perhaps it is related to the state of preservation of the specimens from Lisowice-Lipie Śląskie. This of course also affects the calculated TL/TW ratios. Nevertheless, it cannot be ruled out that this is an anatomically controlled feature, but the ichnological material obtained does not allow for more detailed observations. One can imagine that the wider positioning of the metatarsal bones in the trackmaker foot (e.g. lower degree of their fusion) determined the wider positioning of digit II and IV. The digit length ratios of these specimens are close to those given by Olsen et al. (1998) for *Anchisauripus sillimani* (Hitchcock, 1841), the type ichnospecies of *Anchisauripus* (see Fig. 18).

6.6. Ichnogenus *Apatichnus* (Hitchcock, 1858) Lull, 1915, emended herein

1858 *Gigantitherium* Hitchcock, in part, p. 93.

1858 *Apatichnus* Hitchcock, in part, p. 99.

1904 *Apatichnus* Hitchcock, Lull, p. 508.

1992 *Kayentapus* Welles, Weems, p. 126.

Emended diagnosis. Functionally tridactyl footprints of facultative small and often medium-sized bipeds. Very small oval manus traces with no defined digits is present occasionally. Pes is mesaxonic and highly asymmetrical with the angle between digit III and IV usually two times wider than that between digit II and III. Pedal tracks have spur-shaped metatarsophalangeal pads of digit IV and elongate egg-shaped phalangeal pads.

Comments. Hitchcock (1858) erected the ichnogenus

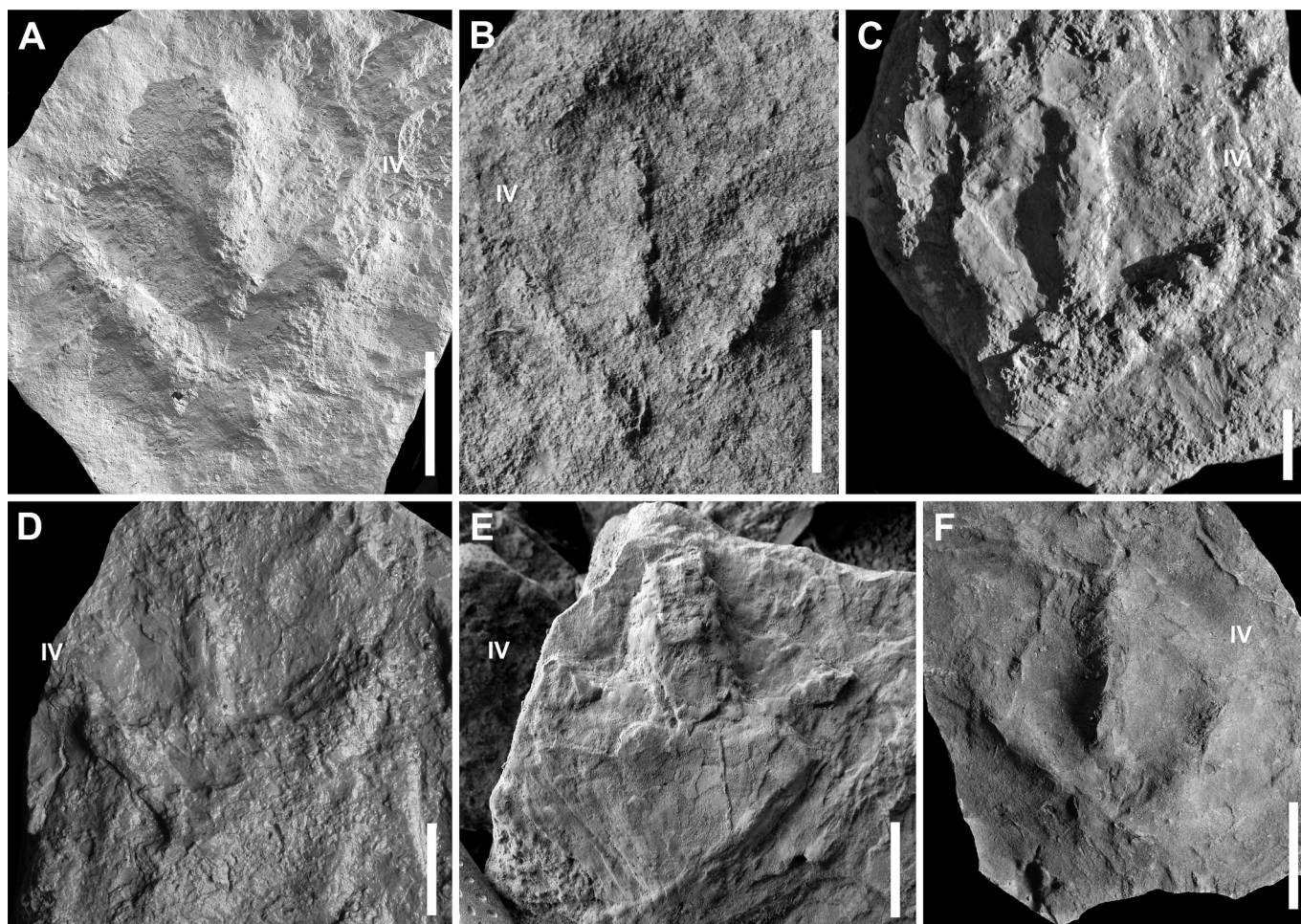


Fig. 3. Photographs of ornithischian tracks, *Anomoepus* isp., from the Lisowice-Lipie Śląskie site. A. ZPAL V.33.T1 (plaster cast), upper ichnoassemblage. B. ZPAL V.33.T2 (plaster cast), upper ichnoassemblage. C. ZPAL V.33.T3 (original slab), upper ichnoassemblage. D. ZPAL V.33.T4 (original slab), upper ichnoassemblage. E. Specimen FM (not collected, field observation), upper ichnoassemblage. F. ZPAL V.33.T5 (plaster cast), upper ichnoassemblage. Explanations: IV – digit number four. See Table 1 for details. The scale bar is 5 cm.

Gigantitherium and *Apatichnus*. His concept of establishing *Gigantitherium* based on *G. caudatum* – a giant theropod track with a large clawed hallux. This large track was originally named *Gigandipus caudatum* by Hitchcock (1855, 1856) and later that name has been applied to this morphotype again by Lull (1904). In 1858, Hitchcock added also to *Gigantitherium* a much smaller and gracile morphotype labelled by him as *Gigantitherium minus*. This form, which is very different from *Gigantitherium caudatum* was later revised as *Apatichnus minus* by Lull (1904) and *A. minor* by Lull (1915). Originally, Hitchcock (1858) referred to the ichnogenus *Apatichnus* two ichnospecies - *A. circumagens* (seen by him on the same slab AC 1/3 as *G. minus*) and *A. bellus*. *A. bellus* was later assigned to *Batrachopus* by Lull (1904) and finally Lull (1915, 1953) recognized two *Apatichnus* ichnospecies - *A. minor* with the designated holotype from the slab AC 1/3 (Fig. 13A) and *A. circumagens* with the holotype AC 21/2 (with not clearly designated possible paratype AC 23/8 and without mention AC 1/3 listed originally by Hitchcock). As we know recently the holotype specimen AC 21/2 as well as the possible lectotype 23/8 are missing and then *A. circumagens* is a *nomen nudum*. Consequently, *Apatichnus* seemingly disappeared since Weems (1992) transferred informally the only valid *Apatichnus* ichnospecies (i.e. *A. minor*) to *Kayentapus* and Olsen and Rainforth (2003) transferred invalid *A. circumagens* to *Anomoepus scambus* based on its illustrated anomoeopoid-like manus. Nevertheless, the specimen is lost and the associated manus could not be proved especially considering the fact that the Hitchcock's specimens are the strongly bioturbated and several

different tracks occur there very closely on the slab. Usually this is the mix of grallatorid and anomoeopoid tracks. On the other hand, Weems (2006) indeed reported occasional presence of a small oval manus traces in this morphotype from the Upper Triassic of Virginia. However, their shape does not match anomoeopoid manus at all. These are the toe-lacked circular prints slightly elongated and four times smaller from the pedal prints. In contrast, anomoeopoid manus is pentadactyl, chirotheriid-like in shape, relatively wide with clearly defined digits and the three or just two times smaller from the pes.

In our opinion there is no reason to reject formally still existing *Apatichnus*, or other words we see the reason to emend *Apatichnus* as the still valid ichnogenus represented by the very distinctive morphotype of *A. minor*. Firstly, as shown by Lull (1904, 1915, 1953) *A. minor* (formerly *A. minus*) demonstrates identical pedal morphology to the missing *A. circumagens*, which even questions their separation on the ichnospecies level. Secondly, this distinctive morphotype is recently found in several regions of Northern Hemisphere and horizons near the Triassic-Jurassic boundary (Fig. 13) and interestingly these tracks are usually at the same size of about 10-20 cm in length. *Apatichnus* is usually twice smaller from typical *Kayentapus* (i.e. *Kayentapus* tracks with (fl-te)/fw value lower than 0.82 and te/fw value lower than 0.50 - see, fig. 6 in Lockley et al., 2011) and usually twice larger from *Anomoepus scambus* type material. Thirdly, *Apatichnus* clearly differentiates from *Kayentapus* and *Anomoepus* by the very wide angle between digit III and IV, usually two times greater than that between digit II and III. This feature is

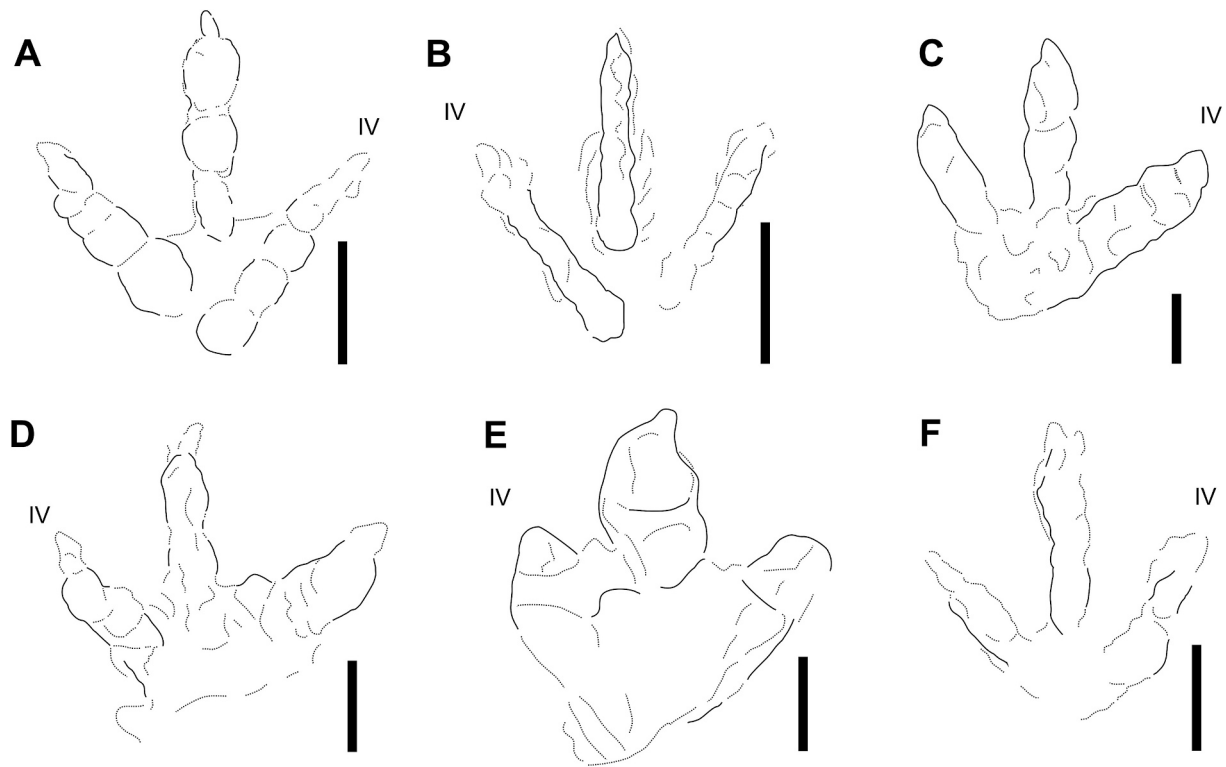


Fig. 4. Schematic drawings of ornithischian tracks, *Anomoepus* isp., from the Lisowice-Lipie Śląskie site. A. ZPAL V.33.T1 (plaster cast), upper ichnoassemblage. B. ZPAL V.33.T2 (plaster cast), upper ichnoassemblage. C. ZPAL V.33.T3 (original slab), upper ichnoassemblage. D. ZPAL V.33.T4 (original slab), upper ichnoassemblage. E. Specimen FM (not collected, field observation), upper ichnoassemblage. F. ZPAL V.33.T5 (plaster cast), upper ichnoassemblage. Explanations: IV – digit number four. See [Table 1](#) for details. The scale bar is 5 cm.

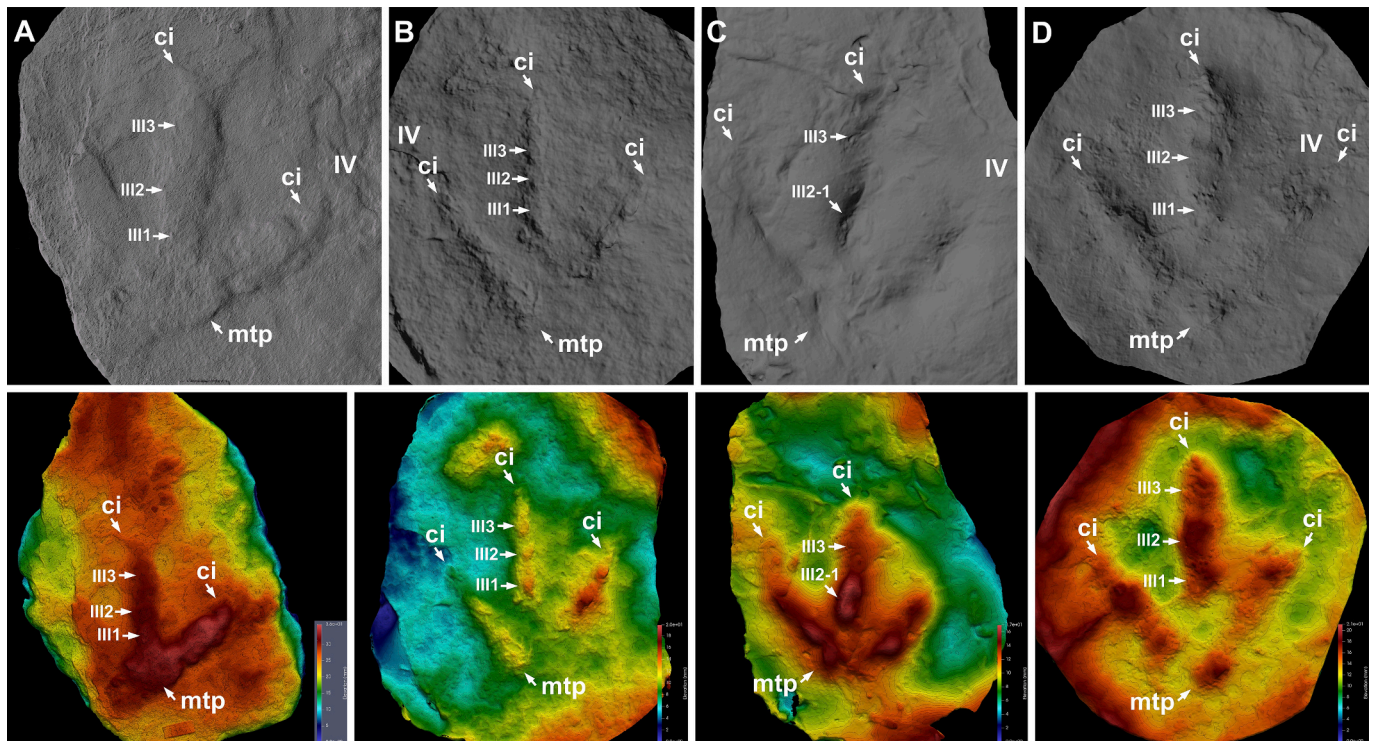


Fig. 5. 3D visualizations (grey scale images and false colour depth maps) of ornithischian tracks, *Anomoepus* isp., from the Lisowice-Lipie Śląskie site. A. ZPAL V.33.T3 (original slab), upper ichnoassemblage. B. ZPAL V.33.T2 (plaster cast), upper ichnoassemblage. C. ZPAL V.33.T5 (plaster cast), upper ichnoassemblage. D. ZPAL V.33.T1 (plaster cast), upper ichnoassemblage. Explanations: ci – claw impressions, mtp – metatarsalphalangeal pad, III1–3 – digital pads no. 1 to 3, IV – digit number four. See [Table 1](#) for details.

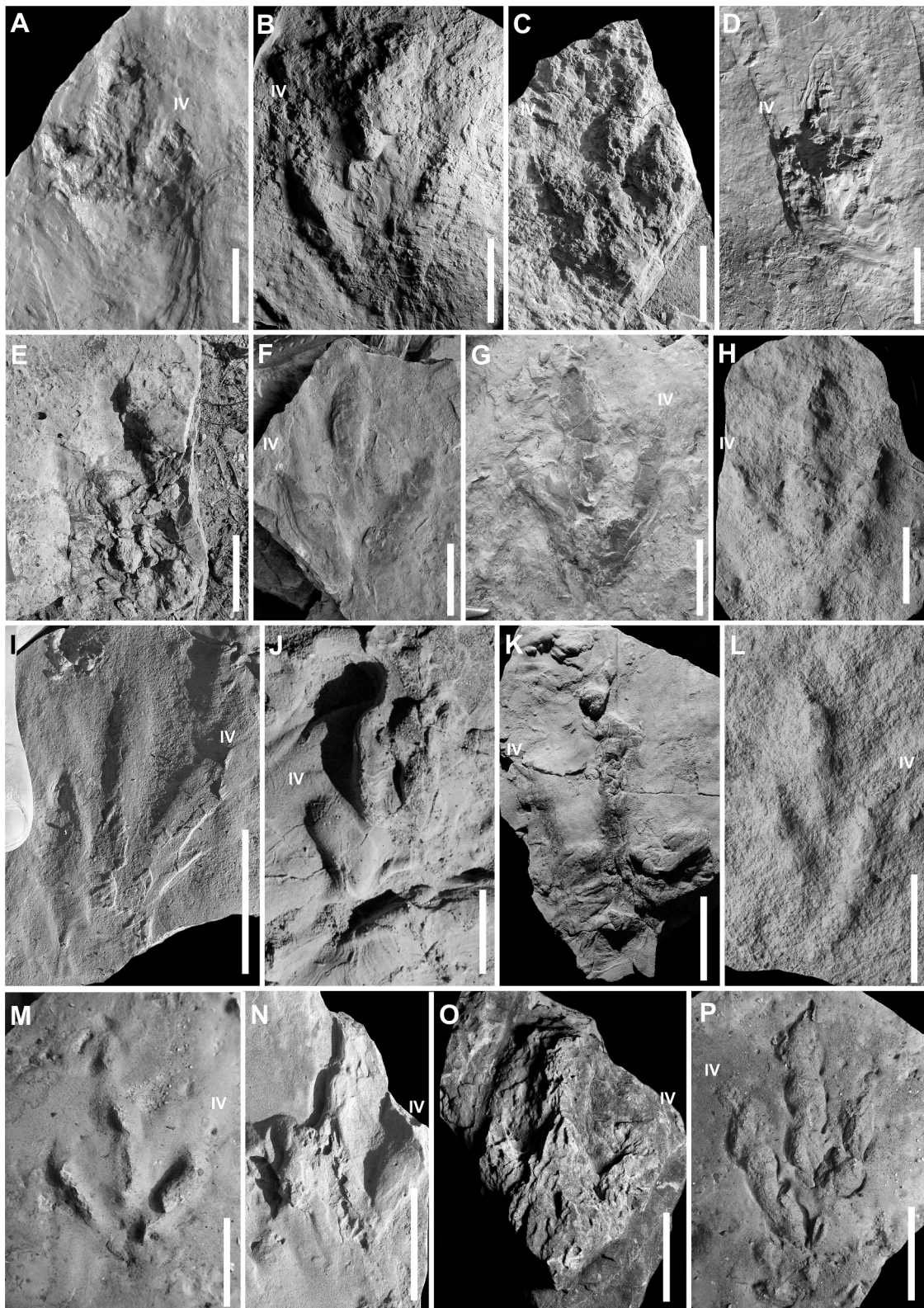


Fig. 6. Photographs of theropod tracks, *Anchisauripus* isp. (A–H) and *Gallator* isp. (I–P) from the Lisowice-Lipie Śląskie site. A. ZPAL V.33.241 (original slab), upper ichnoassemblage. B. ZPAL V.33.T8 (plaster cast), upper ichnoassemblage. C. Specimen FL (not collected, field observation), lower ichnoassemblage. D. Specimen FN (not collected, field observation), upper ichnoassemblage. E. Specimen FO (not collected, field observation), upper ichnoassemblage. F. Specimen FP (not collected, field observation), lower ichnoassemblage. G. Specimen FQ (not collected, field observation), lower ichnoassemblage. H. ZPAL V.33.T9 (plaster cast), upper ichnoassemblage. I. Specimen FR (not collected, field observation), upper ichnoassemblage. J. Specimen FS (not collected, field observation), upper ichnoassemblage. K. ZPAL V.33.T10 (original slab), upper ichnoassemblage. L. ZPAL V.33.T11 (plaster cast), upper ichnoassemblage. M. ZPAL V.33.T12 (plaster cast), upper ichnoassemblage. N. Specimen FU (not collected, field observation), lower ichnoassemblage. O. Specimen FT (not collected, field observation), upper ichnoassemblage. P. ZPAL V.33.T13 (original slab), upper ichnoassemblage. Explanations: IV – digit number four. See Table 1 for details. Scale bar is 5 cm.

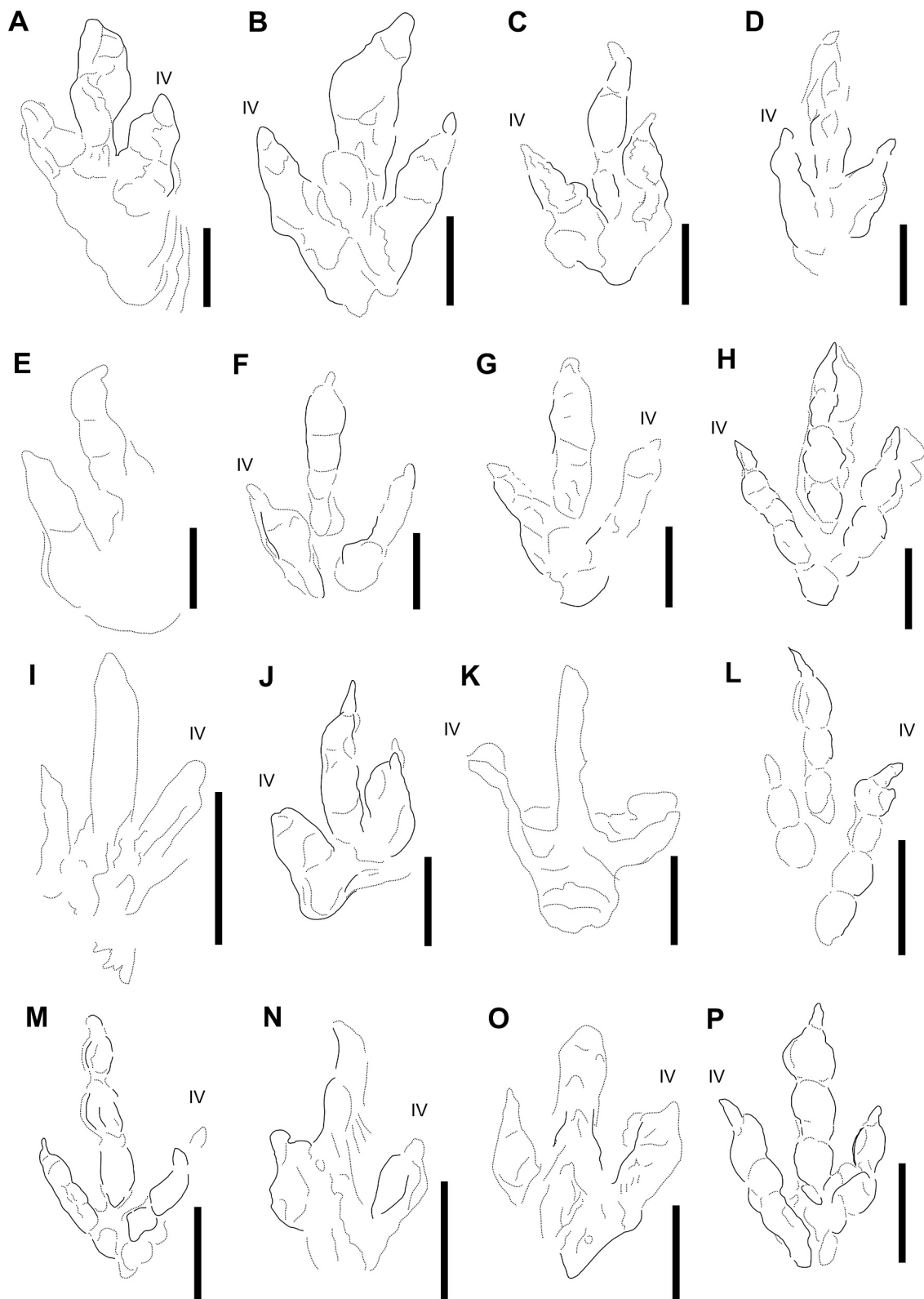


Fig. 7. Schematic drawings of theropod tracks, *Anchisauripus* isp. (A–H) and *Gallator* isp. (I–P) from the Lisowice-Lipie Śląskie site. A. ZPAL V.33.241 (original slab), upper ichnoassemblage. B. ZPAL V.33.T8 (plaster cast), upper ichnoassemblage. C. Specimen FL (not collected, field observation), lower ichnoassemblage. D. Specimen FN (not collected, field observation), upper ichnoassemblage. E. Specimen FO (not collected, field observation), upper ichnoassemblage. F. Specimen FP (not collected, field observation), lower ichnoassemblage. G. Specimen FQ (not collected, field observation), lower ichnoassemblage. H. ZPAL V.33.T9 (plaster cast), upper ichnoassemblage. I. Specimen FR (not collected, field observation), upper ichnoassemblage. J. Specimen FS (not collected, field observation), upper ichnoassemblage. K. ZPAL V.33.T10 (original slab), upper ichnoassemblage. L. ZPAL V.33.T11 (plaster cast), upper ichnoassemblage. M. ZPAL V.33.T12 (plaster cast), upper ichnoassemblage. N. Specimen FU (not collected, field observation), lower ichnoassemblage. O. Specimen FT (not collected, field observation), upper ichnoassemblage. P. ZPAL V.33.T13 (original slab), upper ichnoassemblage. Explanations: IV – digit number four. See [Table 1](#) for details. Scale bar is 5 cm.

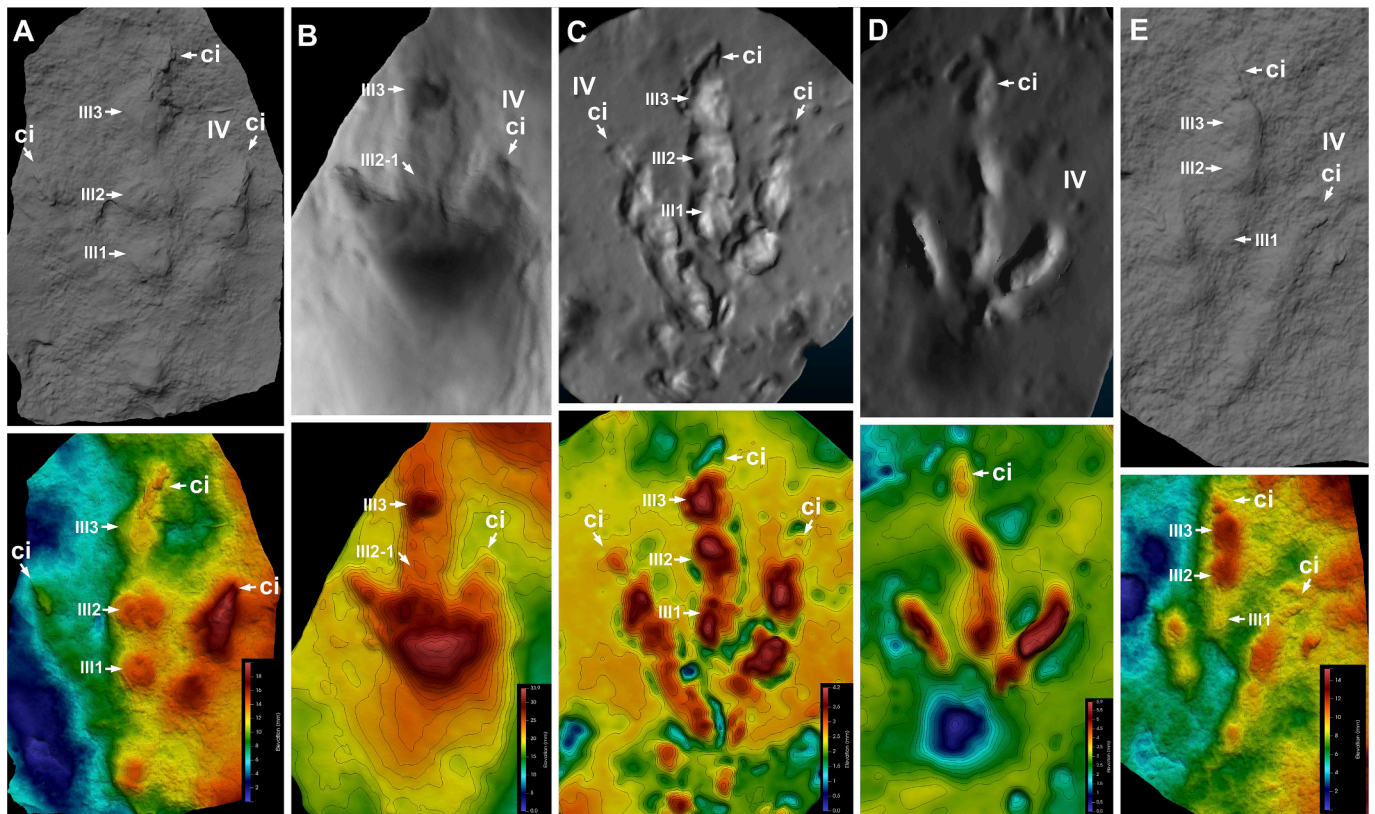


Fig. 8. 3D visualizations (grey scale images and false colour depth maps) of theropod tracks, *Anchisauripus* isp. (A, B) and *Grallator* isp. (C–E), from the Lisowice-Lipie Śląskie site. A. ZPAL V.33.T9 (plaster cast), upper ichnoassemblage. B. ZPAL V.33.241 (original slab), upper ichnoassemblage. C. ZPAL V.33.T13 (original slab), upper ichnoassemblage. D. ZPAL V.33.T12 (plaster cast), upper ichnoassemblage. E. ZPAL V.33.T11 (plaster cast), upper ichnoassemblage. Explanations: ci – claw impressions, mtp – metatarsalphalangeal pad, III1–3 – digital pads no. 1 to 3, IV – digit number four. See Table 1 for details.

constant along the trackways, which clearly speaks of being the feature anatomically controlled. Fourthly, *Apatichnus* has the very characteristic spur-shaped fourth digit metatarsalphalangeal pad not seen in *Anomoepus* nor *Kayentapus*. *Apatichnus* differs also from *Kayentapus* by its high asymmetry (see Welles, 1971) and distinguishes from *Anomoepus* by the elongate egg-shaped phalangeal pads. The only so far known ichnogenus, which is the relatively similar to *Apatichnus* but much larger is *Zizhoupus* Li and Zhang, 2017 from the Middle Jurassic Yan'an Formation of China.

Occurrence. Late Triassic to Early Jurassic of eastern North America and Europe.

Type ichnospecies *Apatichnus minor* Lull, 1915, emended herein.

Apatichnus minor Lull, 1915, emended herein

1858 *Gigantitherium minus* Hitchcock, p. 95.

1858 *Apatichnus circumagens* Hitchcock, in part, p. 100.

1904 *Apatichnus minus* Hitchcock, Lull p. 508.

1915 *Apatichnus minor* Lull p. 508.

1992 *Kayentapus minor* Lull, p. 508.

1992 *Kayentapus* Welles, Weems, p. 126.

Holotype. AC 1/3 (housed at Pratt Museum of Natural History, Amherst College, Amherst, Massachusetts, USA).

Type horizon. Turners Falls Formation.

Type locality. Lily Pond, Massachusetts, USA.

Distribution. As for ichnogenus.

Diagnosis. As for ichnogenus.

Apatichnus minor Lull, 1915 (Figs. 9A–E, I; 10; 11A; 12) and *Apatichnus* isp. (Figs. 9F–H; 11B–D).

Material. Five pes imprints (Fig. 9A–E), from the same trackway (see Fig. 10) and four isolated specimens collected or documented from different beds in the lower (a–b) and upper (c–e) ichnoassemblages in the section C (Figs. 2 and 17). Specimens preserved as concave epirelief

(Figs. 9A–E, H, I; 10) and convex hyporelief (Fig. 9F–G), (Table 1).

Description. Medium-sized, tridactyl, gracile grallatorid pes specimens, 10–13 cm long that show features typical for the ichnogenus *Apatichnus minor* Lull, 1915, emended herein, such as slender, highly divaricated digit IV from digit III and third toe moderately projecting (digit III projection ratio averages about 1.2–1.3). The total length to total width ratio is between 1.18 and 1.38. These tracks show digit length ratios (III/II = 1.6 and 1.59, III/IV = 1.28 and 1.12; see Fig. 18). In all studied specimens, the claw traces of digit II and III are somewhat curved inward toward the midline, oriented anteromedially. The trace of digit II shows two, well defined phalangeal pad impressions (Fig. 10A, C). The digit IV, which shows four pads (Fig. 9A), is slightly shorter than digit III. The best preserved specimen from the trackway (Fig. 10A) allows us to unequivocally determine the 2–3–4 phalangeal formula corresponding to digits II–III–IV. The trackway is narrow (pace angulation about 145–170°) and characterized by a relatively long step (about 68 cm).

Comments. The trackmaker of *Apatichnus minor* from Lisowice-Lipie Śląskie can be confidently identified as a predatory dinosaur based on the tridactyl morphology and the presence on the tips of the pedal digits of sharp, robust, and elongate claw imprints (e.g. Fig. 9A, I). High asymmetry due to the great angle between digit III and VI is a distinctive feature among all tridactylous ichnotaxa found in Lisowice-Lipie Śląskie. *Apatichnus* resembles tracks from the ichnogenus *Kayentapus*, which in some localities co-occurs with *Apatichnus*. The ichnogenus *Kayentapus* shows a different position and shape of digit II and sizes of metatarsal pads, anatomically controlled features and is seen in both small (about 15 cm) and large tracks longer than 30 cm. The status of *Kayentapus* has recently been thoroughly reviewed and confirmed to be a clearly distinguishable ichnotaxon (Lockley et al., 2011; Sciscio et al., 2017). Some authors, notably Rainforth (2005) and Lucas et al. (2006) consider

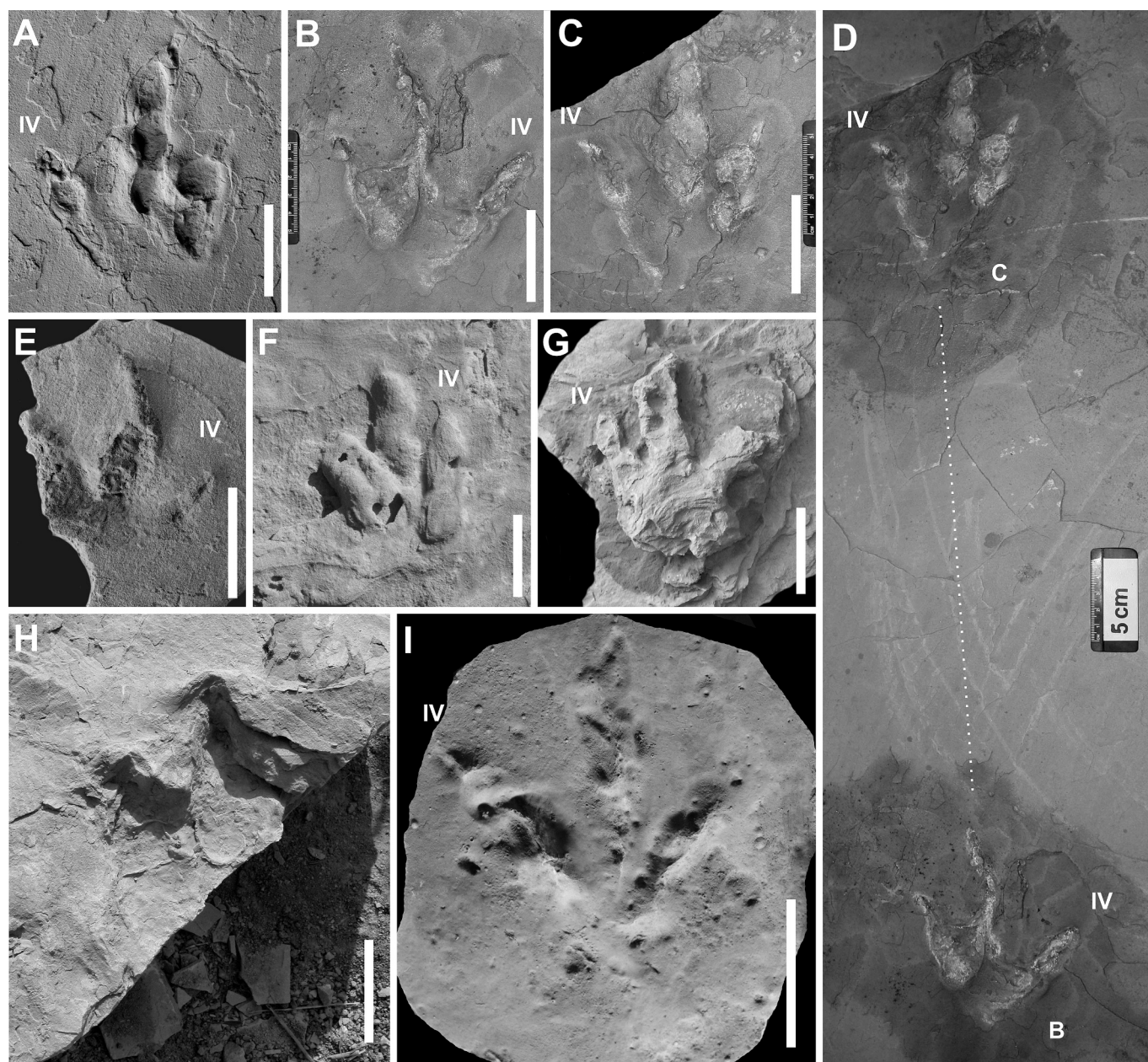


Fig. 9. Photographs of theropod tracks, *Apatichnus minor* (A–E, I) and *Apatichnus* isp. (F–H) from the Lisowice-Lipie Śląskie site. A. ZPAL V.33/240a (original slab), part of the trackway, upper ichnoassemblage. B. ZPAL V.33/240b1 (original slab), part of the trackway, upper ichnoassemblage. C. ZPAL V.33/240b2 (original slab), part of the trackway, upper ichnoassemblage. D. ZPAL V.33/240b1–2 (original slab), part of the trackway, upper ichnoassemblage. E. ZPAL V.33/240c (original slab), part of the trackway, upper ichnoassemblage. F. Specimen FI (not collected, field observation), upper ichnoassemblage. G. Specimen FJ (not collected, field observation), lower ichnoassemblage. H. Specimen FK (not collected, field observation; collected by Piotr Menducki), upper ichnoassemblage. I. F. ZPAL V.33.T6 (plaster cast), lower ichnoassemblage. Explanations: IV – digit number four. See Table 1 for details. Scale bar is 5 cm.

or suspect that *Kayentapus* may be a synonym of *Eubrontes*. *Kayentapus* was described from many locations in North America, Africa and Europe, in the Late Triassic and Early Jurassic, numerous authors regard *Kayentapus* as a valid and important ichnogenus distinct from *Grallator*, *Anchisauripus* and *Eubrontes* (Weems, 1987, 1992, 2006, 2018, 2021; Lockley and Hunt, 1995; Gierliński, 1996; Piubelli et al., 2005; Lockley, 2009; Sciscio et al., 2017).

6.7. Ichnofamily Eubrontidae Lull, 1904

6.8. Ichnogenus *Eubrontes* Hitchcock, 1845

Eubrontes isp. (Figs. 14C–I; 15C–I; 16C).

Material. Eight pes tracks (Table 1), isolated specimens collected or documented from different beds in the lower (a–b) and upper (c–e) ichnoassemblages in the section C (Figs. 2 and 17). Five specimens

preserved as concave epirelief (Fig. 14C, E, H, I) and three as convex hyporelief (Fig. 14D, F, G), (Table 1).

Description. Large, tridactyl, robust eubrontid specimens, 37–43 cm long that show features typical for the ichnogenus *Eubrontes* Hitchcock, 1858, such as a relatively short digit III, a broad pes. The total length to total width ratio is between 1.07 and 1.46. These tracks show digit length ratios: III/II = 1.42 and 1.44; III/IV = 0.76 and 0.79 (see Fig. 18C).

Comments. Tracks of *Eubrontes* are known from the Late Triassic record (Lucas et al., 2005, 2006), although it has been proposed that the first large eubrontid traces (e.g. *Eubrontes*) appear in the ichnological record at the Triassic–Jurassic boundary (Olsen et al., 2002; see also comments for cf. *Eubrontes* isp.). Tracks identified as *Eubrontes* were

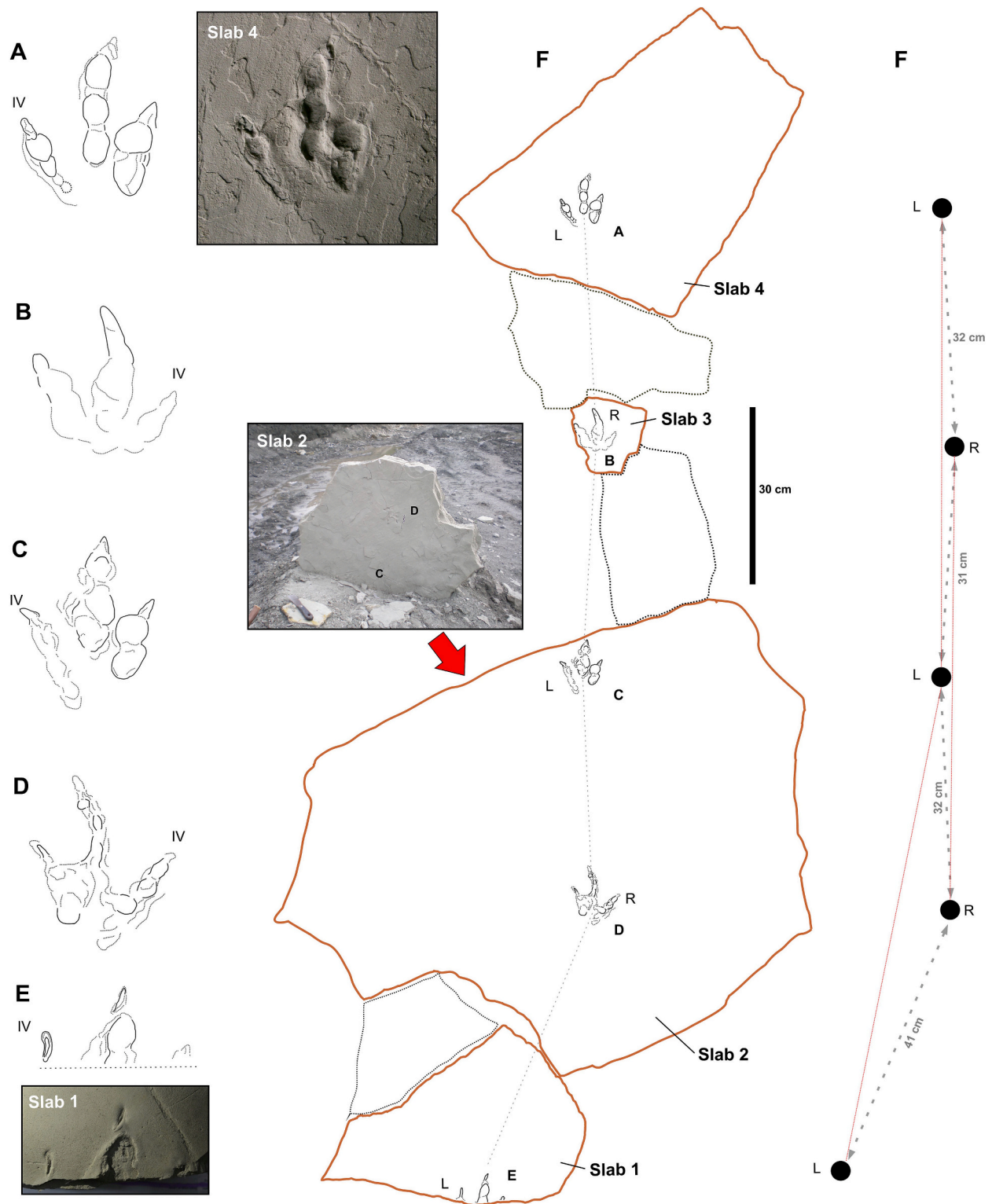


Fig. 10. Photographs, schematic drawings and measurements of theropod trackway, *Apatichnus minor* (original slab), ZPAL V.33/240, from the Lisowice-Lipie Śląskie site. A. ZPAL V.33/240a. B. ZPAL V.33/240c. C. ZPAL V.33/240b2. D. ZPAL V.33/240b1. E. ZPAL V.33/240d. F. Schematic drawing of the surface with trackway. G. Measurements taken on the trackway specimen. Explanations: IV – digit number four, L, R – left and right track. See Table 1 for details.

reported from the late Carnian of Morocco (Lagnaoui et al., 2012; Zouheir et al., 2020). However, it seems that illustrated specimens (Lagnaoui et al., 2012: fig. 5C; Zouheir et al., 2020: fig. 7F–H) cannot be classified as *Eubrontes*, because they are poorly preserved or represent pentadactyl tracks, and are not related to theropod dinosaurs. *Eubrontes* isp. specimens found at Lisowice-Lipie Śląskie are not the best preserved,

e.g. it is difficult to directly refer them to *Eubrontes giganteus*, but all specimens clearly show that these are three-toed tracks. The best preserved specimen (Figs. 14C–I; 15C–I; 16C) shows a rather moderately-imprinted digit III, on which three digital pads are visible; also, the general shape and size of this specimen strongly resemble *E. giganteus*. These tracks show digit length ratios close to those given by Olsen et al.

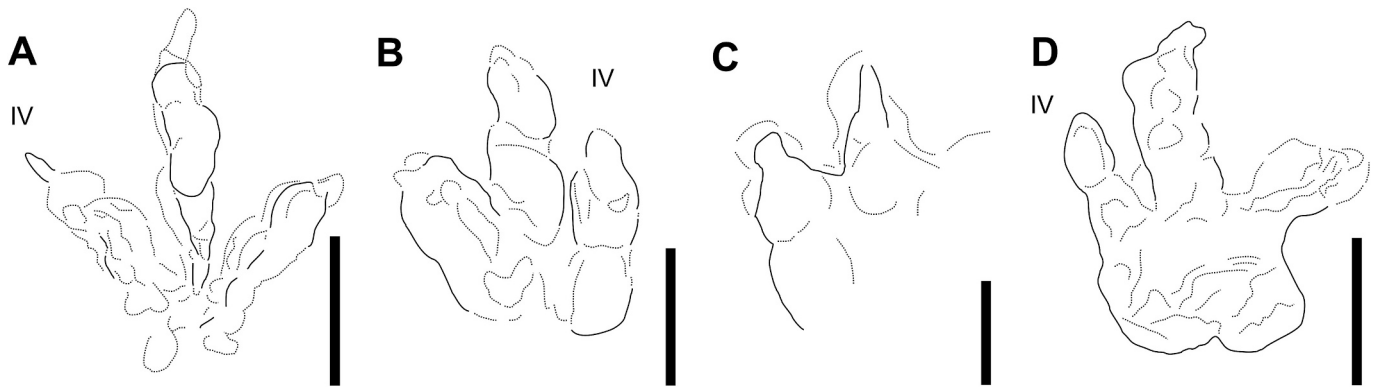


Fig. 11. Schematic drawings of theropod tracks, *Apatichnus minor* (A), *Apatichnus* isp. (B, D) and? *Apatichnus* isp. (C) from the Lisowice-Lipie Śląskie site. A. ZPAL V.33.T6 (plaster cast), lower ichnoassemblage. B. Specimen FI (not collected, field observation), upper ichnoassemblage. C. Specimen FK (not collected, field observation; collected by Piotr Menducki), upper ichnoassemblage. D. Specimen FJ (not collected, field observation), lower ichnoassemblage. Explanations: IV – digit number four. See Table 1 for details. Scale bar is 5 cm.

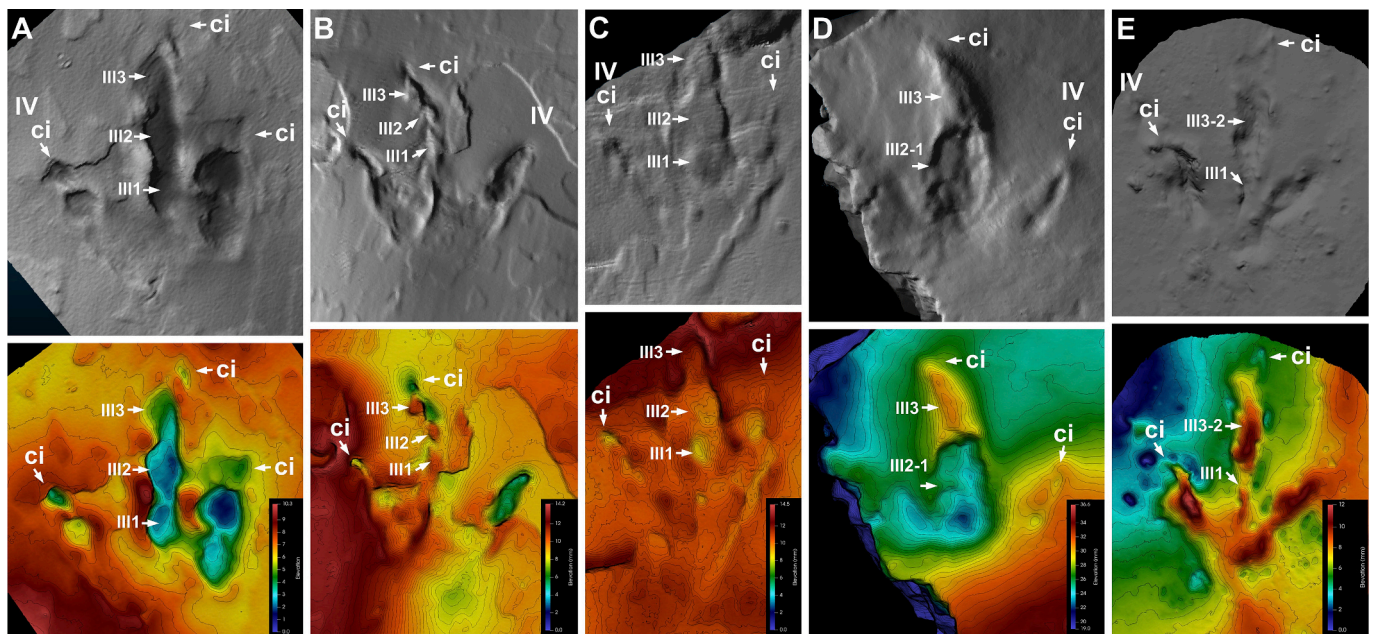


Fig. 12. 3D visualizations (grey scale images and false colour depth maps) of theropod tracks, *Apatichnus minor*, from the Lisowice-Lipie Śląskie site. A. ZPAL V.33/240a (original slab), part of the trackway, upper ichnoassemblage. B. ZPAL V.33/240b2 (original slab), part of the trackway, upper ichnoassemblage. C. ZPAL V.33/240b1 (original slab), part of the trackway, upper ichnoassemblage. D. ZPAL V.33/240c (original slab), part of the trackway, upper ichnoassemblage. E. ZPAL V.33/T6 (plaster cast), lower ichnoassemblage. Explanations: ci – claw impressions, mtp – metatarsalphalangeal pad, III1–3 – digital pads no. 1 to 3, IV – digit number four. See Table 1 for details.

(1998) for *Eubrontes giganteus* Hitchcock, 1845, the type ichnospecies of *Eubrontes* (see Fig. 18C). The only feature that clearly distinguishes this specimen from *E. giganteus* is the strongly protruding digit IV. Similar geometry of the eubrontid tracks was observed by Gierliński and Ahlberg (1994) in the material from the middle-late Rhaetian of Sweden.

cf. *Eubrontes* isp. (Figs. 14A, B; 15A, B; 16A, B)

Material. Four pes tracks (Table 1), isolated specimen collected or documented from different beds in the lower (a-b) and upper (c-e) ichnoassemblages in the section C (Figs. 2 and 17). All specimens are preserved as convex hyporelief (Fig. 14A, B), (Table 1).

Description. Very large, tridactyl, robust eubrontid specimens, 41–56 cm long that show features typical for the ichnogenus *Eubrontes* Hitchcock, 1845, such as a relatively short digit III, a broad pes and divarication of outer digits between 35°–50°. The total length to total width ratio is between 1.10 and 1.32. The state of preservation of all four specimens (two illustrated in this publication) makes it impossible to

determine digit length ratios, so more detailed comparisons of these parameters to those given by Olsen et al. (1998) for *Eubrontes giganteus* Hitchcock, 1845, the type ichnospecies of *Eubrontes* (see Fig. 18C), is impossible.

Comments. The finds of large tridactyl cf. *Eubrontes* isp. tracks at Lisowice-Lipie Śląskie are surprising. These intriguing specimens are more similar to the large tracks from the Middle-Late Jurassic theropods than to those from the Late Triassic and Early Jurassic. Despite great sizes, they are mainly distinctive by having large metatarsophalangeal areas (see Gierliński et al., 2001, 2004) and very robust and wide digit impressions; they look like giant *Eubrontes* tracks inflated like a balloon. The state of preservation of these specimens (they contain visible claw marks and digital pads) does not indicate any deformation, e.g. an increase of track surface as a result of plasticity or hydration of the sediment during their formation. It is difficult to find a potential trackmaker of these specimens in the known Late Triassic theropod skeletal record.

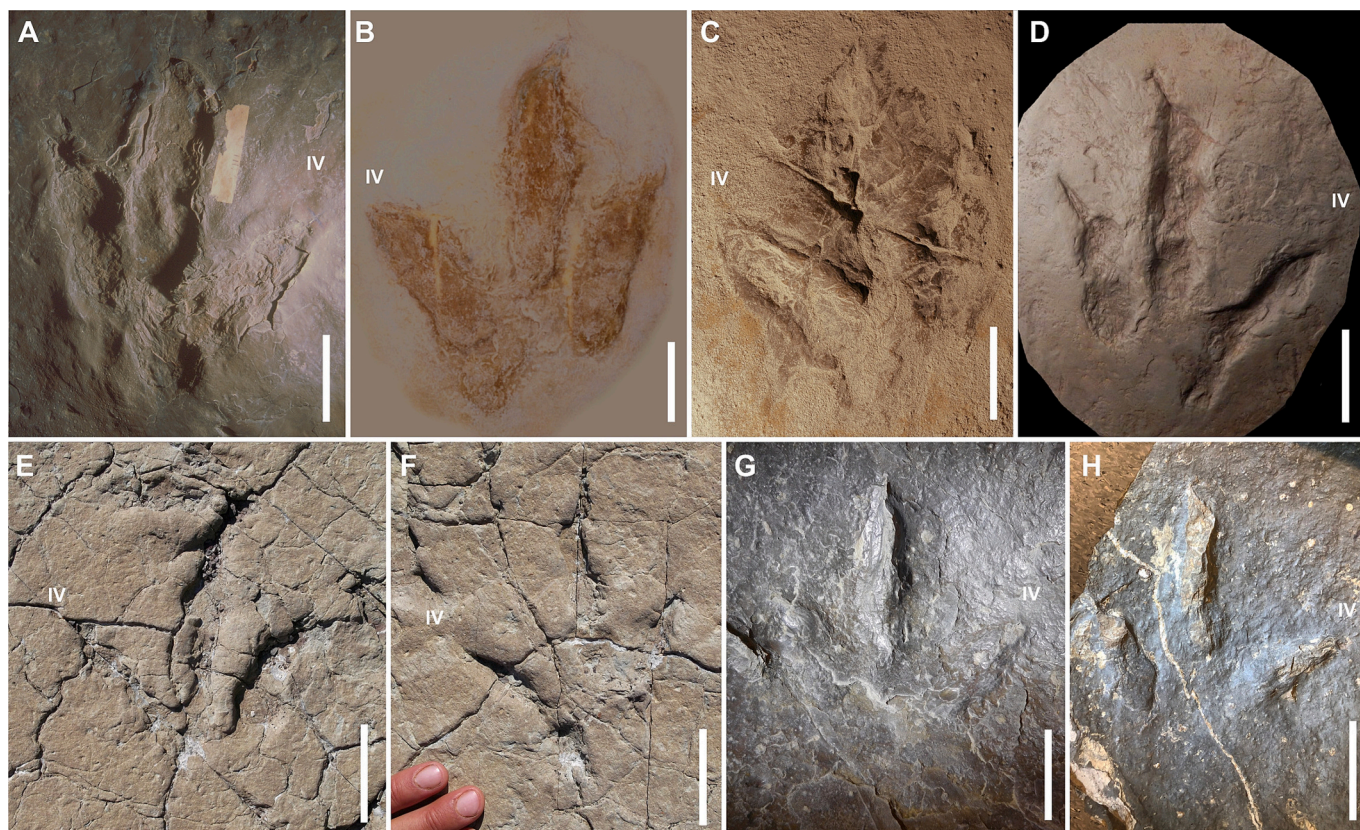


Fig. 13. Examples of *Apatichnus minor* Lull, 1915 from the Lower Jurassic (A, G, H) and Upper Triassic (B–F) of North America and Europe. A. *A. minor* holotype AC 1/3 from Turners Falls Formation of Massachusetts (USA). B. Part of the trackway B3 from Bull Run Formation of Virginia (USA). D. The specimen from Balls Bluff Formation of Virginia (USA). C, E, F. Specimen from Fleming Fjord Formation of Greenland (C, MGUH 27814). G, H. Specimens from Helsingborg Member (Höganäs Formation) of Skåne (Sweden). Explanations: IV – digit number four. Scale bar is 5 cm.

The length of these tracks indicates that it was an animal about 7–8 m long or larger, as large as the largest Early-Middle Jurassic theropods (e.g. *Cryolophosaurus*, *Torvosaurus*, *Megalosaurus*). The claims that large tracks (*Eubrontes*) only occur above the Triassic-Jurassic boundary in the earliest Hettangian (Olsen et al., 2002) were disputed previously (Lucas et al., 2005, 2006). The ichnological finds from Lisowice-Lipie Śląskie support the earlier, late Norian-earliest Rhaetian appearance of very large theropods, and also indicate that theropods reached considerable sizes (>7 m) before the Early Jurassic, which is supported by the latest skeletal finds of ontogenetically more adult individuals of *Liliensternus* (with an estimated body length of 7–9 m) from the Trossingen Formation (late Norian-early Rhaetian) of Bavaria, Germany (Kirmse et al., 2024). Tracks of large theropods are also known from the Early Jurassic record in this region (e.g., Gierliński et al., 2001, 2004; Niedźwiedzki, 2011c). At the Sołtyków tracksite, in a section dated to the early Hettangian, numerous 50–60 cm long eubrontid-like tracks were identified, suggesting the presence of 8-m-long theropods at the beginning of the Early Jurassic.

7. Discussion

Upper Triassic outcrops from the Central European Basin have yielded impressive skeletal remains of numerous early sauropodomorphs (e.g. *Plateosaurus*) and rare theropods, e.g. *Liliensternus* (e.g. Huene, 1934; Sander, 1992; Rauhut and Hungerbühler, 1998; Yates, 2003; Sues and Fraser, 2010; Rauhut et al., 2020). However, despite almost 200 years of effort, findings of Upper Triassic dinosaur tracks from the Central European Basin have mainly been represented by numerous small grallatorid tracks, poorly preserved material, or single slabs (see Wagensommer et al., 2022). Dinosaur tracks with abundant and diverse

trace fossils have instead been restricted to the lowermost Jurassic (e.g., Gierliński and Pieńkowski, 1999; Gierliński et al., 2004; Niedźwiedzki, 2011c; Niedźwiedzki and Pieńkowski, 2016; Pacyna et al., 2022) or Triassic-Jurassic transitional interval (Gierliński and Ahlberg, 1994). The Lisowice-Lipie Śląskie ichnoassemblage changes this and greatly enhances our knowledge about the dinosaur-rich ichnofaunas of the Late Triassic. The tracksite is of exceptional value because of the following points.

- (1) **The precise dating:** The collected material is obtained from a well-studied palaeontologically section (Dzik et al., 2008a, 2008b; Niedźwiedzki et al., 2012; Świło et al., 2014; Pieńkowski et al., 2014; Sulej and Niedźwiedzki, 2019; Qvarnström et al., 2024). The maximum depositional age of the beds is determined by radiometric dating of strata below a-e track-bearing beds (211 ± 3 Mya, see Kowal-Linka et al., 2019), which supports a late Norian to earliest Rhaetian age of the dinosaur ichnoassemblage (Fig. 2). The Norian-Rhaetian transitional character of the flora and fauna, as well as biostratigraphical data (palynomorphs, plant macrofossils, conchostracans, and vertebrate skeletal remains) further support such interpretation (Świło et al., 2014; Pieńkowski et al., 2014; Sulej and Niedźwiedzki, 2019; Qvarnström et al., 2024; on-going study).
- (2) **The abundance and diversity of dinosaur tracks:** The 42 tri-dactyl pes tracks (Figs. 3–12, 14–16) represent a total of at least five ichnogenera, of which one, *Anomoepus* isp., is attributed to early ornithischians, and *Grallator* isp., *Anchisauripus* isp., *Apatichnus minor*, *Apatichnus* isp., *Eubrontes* isp., cf. *Eubrontes* isp. are ichnites of theropods (Fig. 17B). There are only a few other Upper Triassic-Lower Jurassic track sites in the region that have yielded

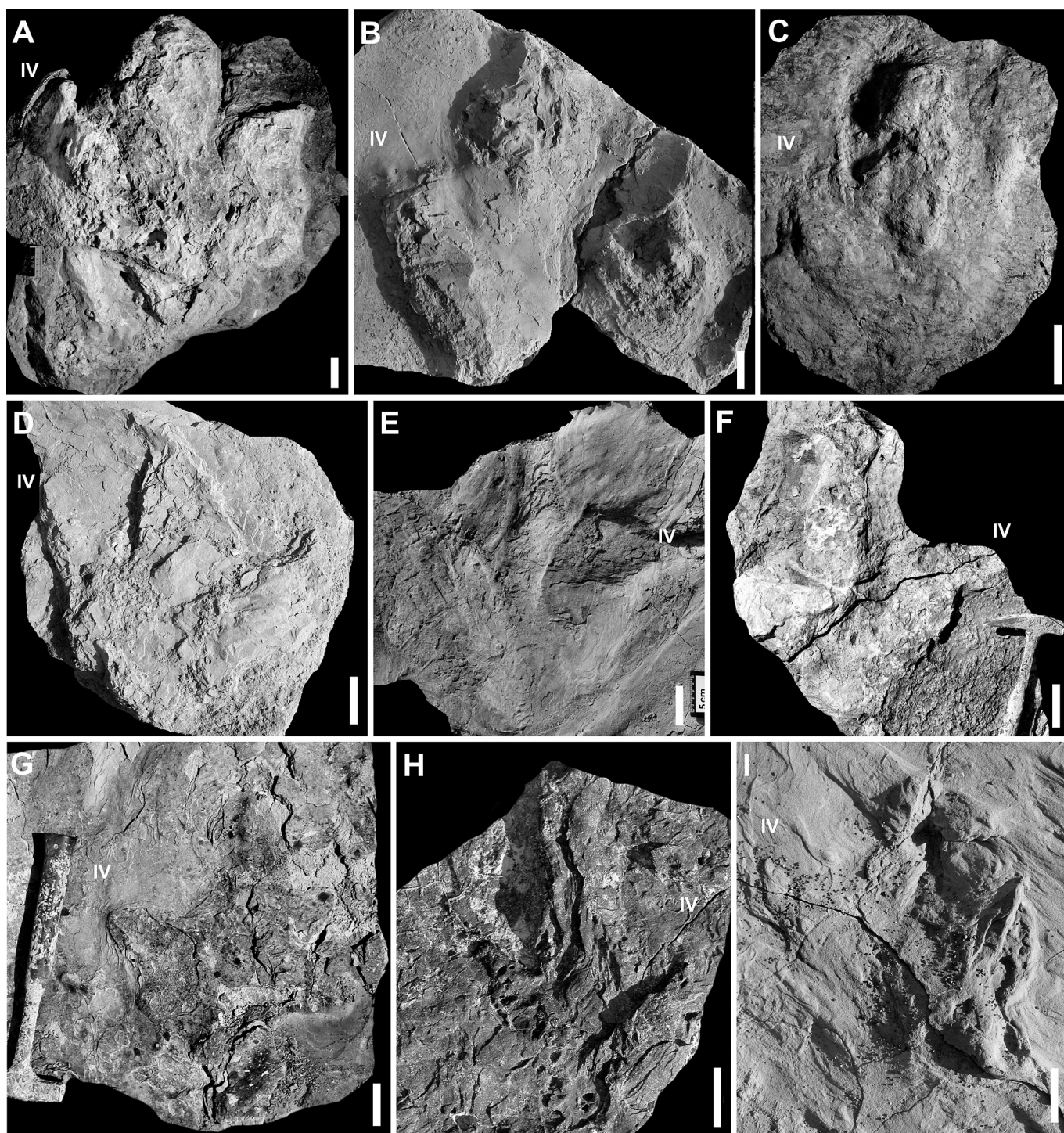


Fig. 14. Photographs of theropod tracks, *Eubrontes* isp. (C–I) and cf. *Eubrontes* isp. (A, B), from the Lisowice-Lipie Śląskie site. A. ZPAL 33.V.508 (original slab), lower ichnoassemblage. B. ZPAL 33.V.219 (original slab), upper ichnoassemblage. C. ZPAL 33.V.509 (plaster cast), upper ichnoassemblage. D. Specimen FA (not collected, field observation), upper ichnoassemblage. E. ZPAL 33.V.510 (plaster cast), lower ichnoassemblage. F. Specimen FC (not collected, field observation), upper ichnoassemblage. G. Specimen FB (plaster cast; unregistered), upper ichnoassemblage. H. Specimen FD (not collected, field observation), lower ichnoassemblage. I. Specimen FE (not collected, field observation), upper ichnoassemblage. Explanations: IV – digit number four. See [Table 1](#) for details. Scale bar is 5 cm.

so many dinosaur track ichnotaxa (e.g. [Gierliński et al., 2004](#); [Niedźwiedzki, 2011c](#)). The diversity of theropod tracks at the Lisowice-Lipie Śląskie indicates that small to large dinosaurs were the key predators at that time.

- (3) **The presence of a dinosaur-therapsid track assemblage:** The Lisowice-Lipie Śląskie ichnofauna from the section C ([Fig. 2](#)) is dominated by dinosaur tracks representing ~50 % ($n = 42$) of the

total recorded specimens ($n = 89$), and ~70 % of the total recorded ichnotaxa, with theropod ichnogenera (*Grallator*, *Anchisauripus* and *Apatichnus*) being the most common ([Fig. 17A, B](#)). This result is probably distorted by the limitations of the sampling and the nature of the ichnological record at this site, but the material obtained shows that there was a large variety of theropod trackmakers in the Lisowice-Lipie Śląskie ecosystem.

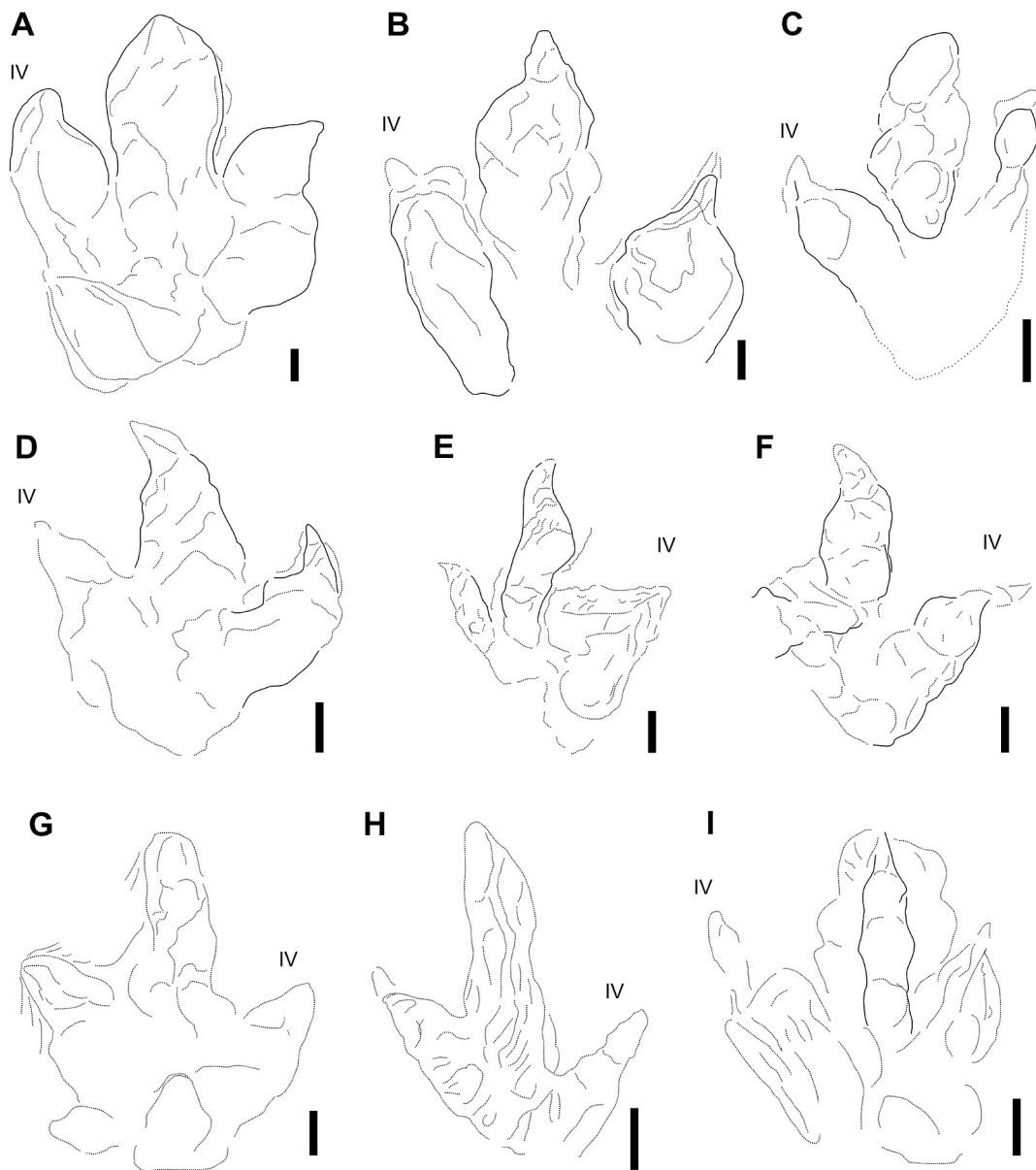


Fig. 15. Schematic drawings of theropod tracks, *Eubrontes* isp. (C–I) and cf. *Eubrontes* isp. (A, B), from the Lisowice-Lipie Śląskie site. A. ZPAL 33.V.508 (original slab), lower ichnoassemblage. B. ZPAL 33.V.219 (original slab), upper ichnoassemblage. C. ZPAL 33.V.509 (plaster cast), upper ichnoassemblage. D. Specimen FA (not collected, field observation), upper ichnoassemblage. E. ZPAL 33.V.510 (plaster cast), lower ichnoassemblage. F. Specimen FC (not collected, field observation), upper ichnoassemblage. G. Specimen FB (plaster cast; unregistered), upper ichnoassemblage. H. Specimen FD (not collected, field observation), lower ichnoassemblage. I. Specimen FE (not collected, field observation), upper ichnoassemblage. Explanations: IV – digit number four. See Table 1 for details. Scale bar is 5 cm.

The tracks of other tetrapods from the section C were mainly made by small to large therapsids. This is also exceptional, because therapsid tracks are poorly known from the Late Triassic of the Central European Basin. These therapsid tracks will be described in a separate study.

- (4) **The absence of sauropodomorph and non-dinosaur archosaur tracks:** The composition of the Lisowice-Lipie Śląskie ichnofauna from a-e beds (Fig. 17A) is significant because it reflects a dinosaur-rich tetrapod community, but without traces of sauropodomorphs (e.g., *Evazoum*, *Eosauropus*, *Tetrasauropus*) or typical Upper Triassic archosaurian ichnotaxa (e.g. *Apatopus*, *Atreipus*, *Brachychirotherium*). The Lisowice-Lipie Śląskie ichnoassemblage, together with new finds from the Gromadzice-Rzuchów site (Qvarnström et al., 2024; on-going study), shows an important stage in the evolution of dinosaur faunas in the late Norian to mid-Rhaetian time interval (Fig. 19), which highlights

the complexity of the dinosaur faunas that developed in the northern part of Pangaea, several million years before the end-Triassic faunal turnover.

- (5) **The Late Triassic occurrence of otherwise typical Early Jurassic ichnogenera:** The track assemblage from the section C at Lisowice-Lipie Śląskie contains the ichnotaxa *Anomoepus* and *Eubrontes*, which are very characteristic of Lower Jurassic ichnoassemblages in the region (e.g. Gierliński et al., 2004). These are globally distributed dinosaurian ichnotaxa in the basal Hettangian and younger intervals of the Early Jurassic (e.g. Olsen and Galton, 1984; Olsen et al., 2002; Olsen and Rainforth, 2003; Lockley and Gierliński, 2006). Although their presence, sometimes problematic, was already reported from Late Triassic locations. Of particular note are the finds of potential Late Triassic *Anomoepus* records; such traces had already been noted from the Late Triassic of Europe, but were wrongly described as ichnites of

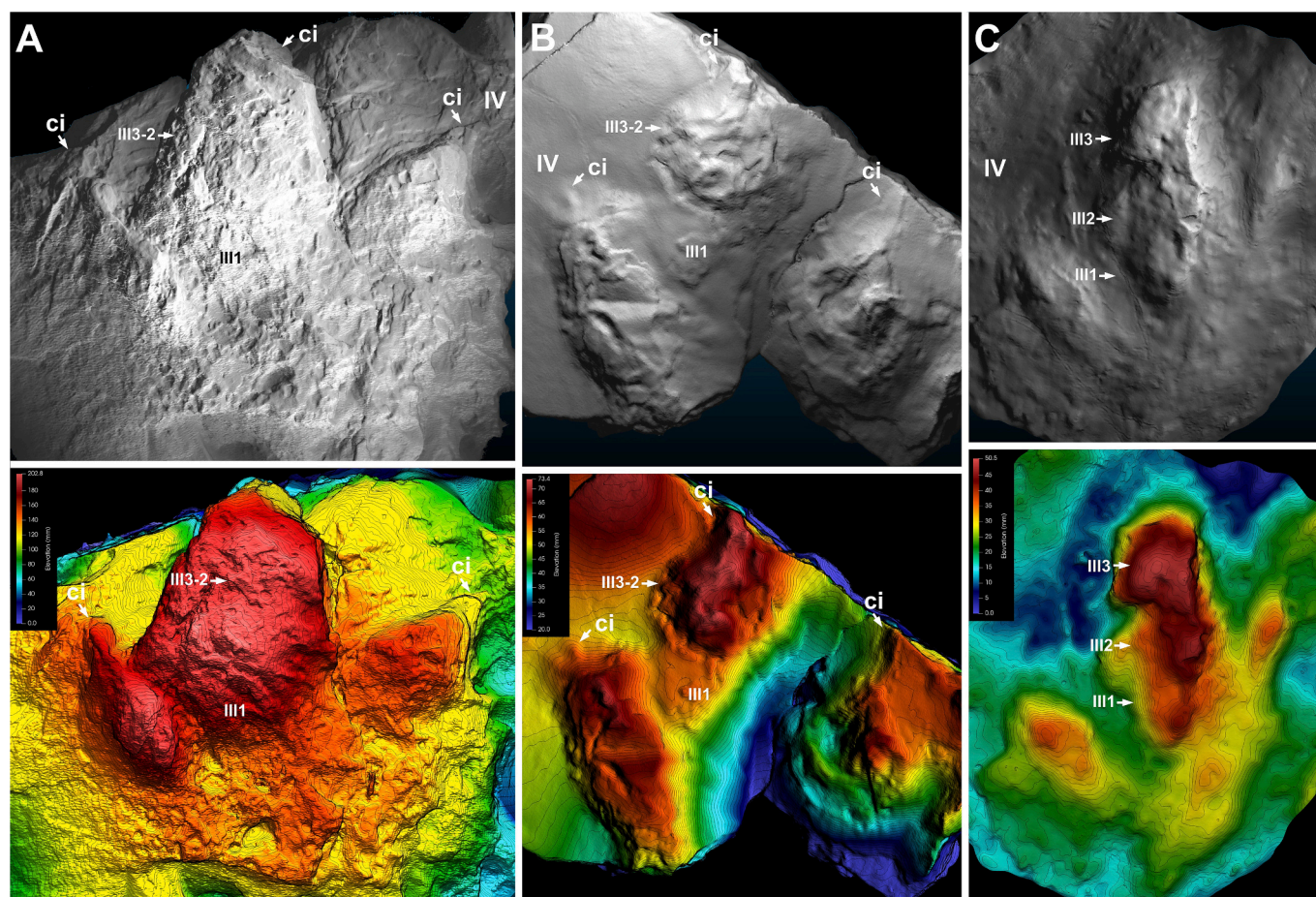


Fig. 16. 3D visualizations (grey scale images and false colour depth maps) of theropod tracks, *Eubrontes* isp. (C) and cf. *Eubrontes* isp. (A, B), from the Lisowice-Lipie Śląskie site. A. ZPAL 33.V.508 (original slab), lower ichnoassemblage. B. ZPAL 33.V.219 (original slab), upper ichnoassemblage. C. ZPAL 33.V.509 (plaster cast), upper ichnoassemblage. Explanations: ci – claw impressions, mtp – metatarsalphalangeal pad, III1–3 – digital pads no. 1 to 3, IV – digit number four. See Table 1 for details.

predatory dinosaurs (Haderer, 1990) or defined as *Anomoepus*-like tracks (Niedźwiedzki, 2011b). Anomoepoid tracks, designated as *Trisauropodiscus*, a bird-like track, have been described from the Late Triassic of Lesotho (Ellenberger, 1970, 1972; see also Abrahams and Bordy, 2023: fig. 5A, morphotype 1). The ornithischian interpretation of these bird-like tracks and their similarities to *Anomoepus* was discussed by Gierliński et al. (2017).

Enigmatic, *Anomoepus*-like tracks (*Anomoepus* aff. *A. isodactylus*) have also been described from the Late Triassic Passaic Formation, USA (Weems, 2018). Other, *Anomoepus*-like tracks (*Pengxianpus*) have also been discovered from Xujiawe Formation (Norian-Rhaetian) of Sichuan Province, China, although these tracks are also attributed to a theropod (Yang and Yang, 1987; Xing et al., 2013; Peng et al., 2023). Finally, it is worth mentioning that the occurrence of *Anomoepus* tracks in the mid-Rhaetian of Gromadnice-Rzuchów (Poland), anomoepoid tracks in the late Rhaetian of Norra Albert (Sweden) and the late Norian-early Rhaetian of Jameson Land (Greenland), (Qvarnström et al., 2024; on-going study). These examples show the need for re-description and substantial revision of anomoepoid specimens from Late Triassic sites as well as the importance of these new finds from Lisowice-Lipie Śląskie. The Silesian ichnoassemblage therefore can be potentially useful in future for more detailed biostratigraphic correlation and palaeogeographic studies. We still lack a high-resolution interpretation for the Norian and Rhaetian dinosaur ichnofaunas, their composition and changes over time.

(6) **The co-occurrence of bones and tracks:** In Lisowice-Lipie Śląskie, tridactyl dinosaur tracks co-occur with numerous dinosaur bones and a theropod-like *Smok wawelski* (see Niedźwiedzki et al., 2012; Sulej and Niedźwiedzki, 2019; Qvarnström et al., 2024; on-going study), which creates unique opportunities for their direct comparison or even identification of some recorded ichnotaxa with osteological finds. The bone-bearing beds, where the remains of at least four different dinosaurs have been found (Sulej and Niedźwiedzki, 2019; Qvarnström et al., 2024; on-going study), occur both below (lower bone-bearing interval) and between (upper bone-bearing interval) the track-bearing beds (Fig. 2). Preliminary studies of these skeletal remains indicate they are the remains of dinosaurs of various sizes and distinct morphologies. These indicate that it will be possible to directly compare the ichnological with the osteological record, based on the estimated sizes and taxonomic identifications. There are very few sites in the world where dinosaur bones (potential track-makers) directly co-occur (same site, same exposed section) with their tracks. Sedimentological observations indicate that the mudstone-siltstone interval with the skeletal remains (upper bone-bearing interval) is a local oxbow lake that accumulated organic remains, transported there during floods or runoff after heavy rains. The correlation of the ichnological and osteological records from the Lisowice-Lipie Śląskie section is very justified here and may constitute an important comparison for future paleoecological studies of early dinosaurs.

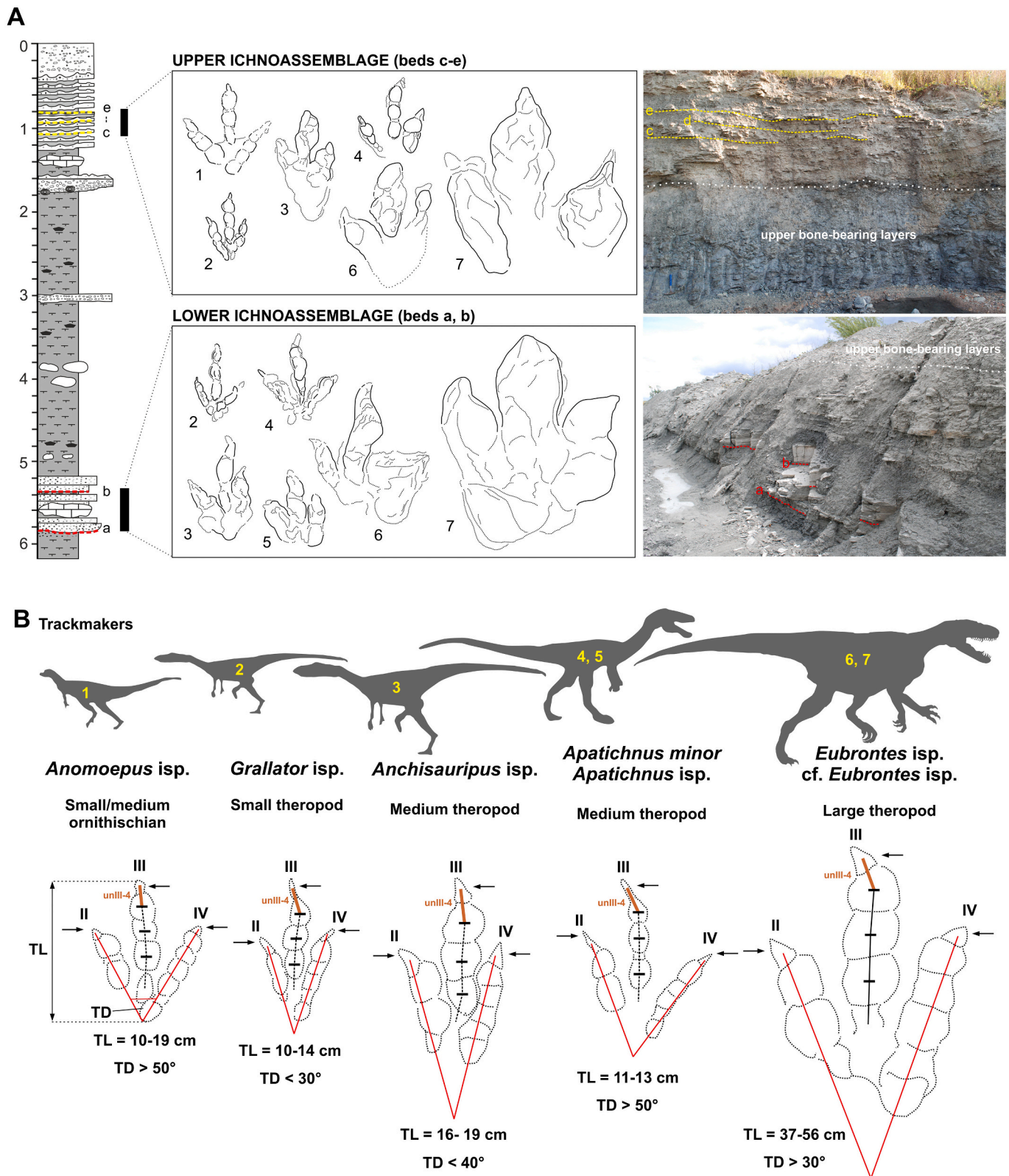


Fig. 17. A. Location and composition of dinosaur track assemblages (lower, a–b and upper c–e ichnoassemblage) in the sedimentologic section of the main exposure at the Lisowice-Lipie Śląskie site. Track assemblages are similar to each other, and their location in section, both below and above the upper bone-bearing layers (see photographs), suggests they can be correlated with the osteological record from this site. However, no tracks of *Anomoepus* isp. (no. 1) were identified in the lower assemblage. B. Identification of trackmakers and basic characteristics of individual track types. Explanations: 1 – *Anomoepus* isp.; 2 – *Grallator* isp.; 3 – *Anchisauripus* isp.; 4, 5 – *Apatichnus minor*/*Apatichnus* isp.; 6, 7 – *Eubrontes* isp./cf. *Eubrontes* isp.

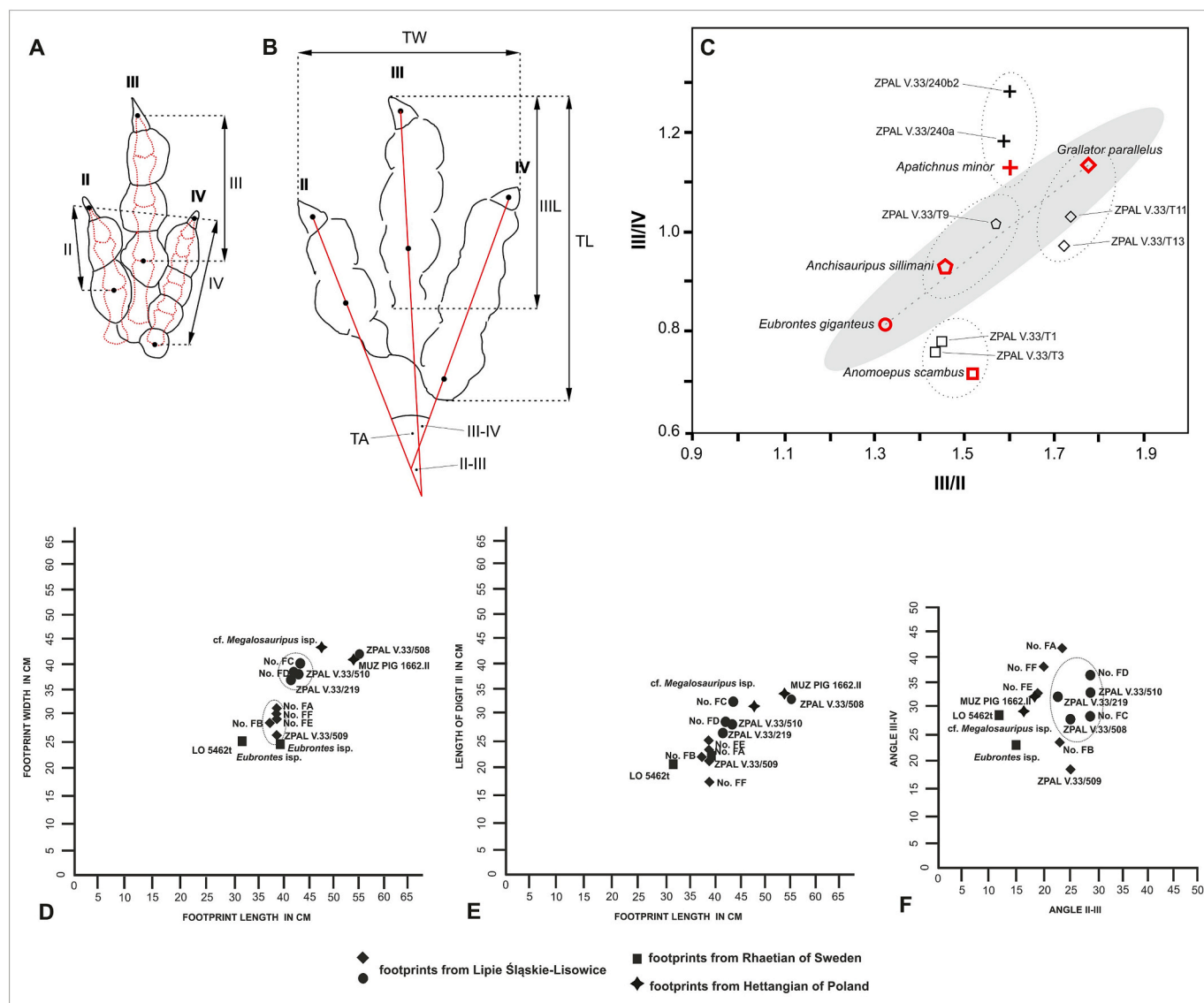


Fig. 18. A, B. Conventions of track and skeletal measurements used in this study (modified from Leonardi, 1987; Olsen et al., 1998; see also Track description and Table 1 for details). C. Graph comparing the proportions (the relative length of the digits) of tracks described in the paper with holotypes/paratypes of ornithischian (*Anomoepus scambus*) and theropod (*Grallator parallelus*, *Anchisauripus sillimani*, *Eubrontes giganteus*) tracks (see Track description and Table 1 for details). The grey area shows the extent of *grallatorid*-type tracks. Data from Olsen et al. (1998). D–F. Comparisons of the morphology of the *Eubrontes* isp. and *cf. Eubrontes* isp., with large and gigantic theropod dinosaur tracks from the Rhaetian of Sweden and Hettangian of Poland based on measurement of track length and width (D), track length and length of digit III (E), and angles between digits II–III and III–IV (F). Data from (Böla, 1952; Gierliński and Ahlberg, 1994; Gierliński et al., 2001, 2004).

These points stress that the Lisowice-Lipie Śląskie ichnorecord is one of the most important Upper Triassic dinosaur tracksites in the Central European Basin and adjacent areas. It can be compared to that of more or less contemporary dinosaur track assemblages from the upper Norian-lower Rhaetian Ørsted Dal Formation of East Greenland (Jenkins et al., 1994; Sulej et al., 2014; Clemmensen et al., 2016; Lallensack et al., 2017), the upper Norian to Rhaetian part of the Mercia Mudstone Group of South Wales (Lockley et al., 1996), the mid-Rhaetian Parszów Beds at Gromadzice-Rzuchów (Qvarnström et al., 2024; on-going study), the ? upper Norian–Rhaetian of Tomanova Formation in the Tatra Mountains, Slovakia and Poland (Niedźwiedzki, 2011b), the mid to upper Rhaetian Bjuv Member and Boserup Beds of the Höganäs Formation, Sweden (see Gierliński and Ahlberg, 1994; Milàn and Gierliński, 2004) or the upper Rhaetian-lower Hettangian Zagaje Formation, Poland (Gierliński et al., 2004; Niedźwiedzki, 2011c) which represent similar dinosaur-rich track assemblages.

8. Conclusions

The dinosaur tracks from the Lisowice-Lipie Śląskie site represent the hereto most thoroughly analysed track assemblage in the Upper Triassic of Poland, providing a welcome window into the otherwise still poorly known Late Triassic dinosaur faunas of Silesia (e.g., Niedźwiedzki et al., 2014; Skawiński et al., 2017; Sulej and Niedźwiedzki, 2019; Qvarnström et al., 2024). It highlights the presence of a diversified dinosaur fauna in the Polish Basin that pre-dates the big evolutionary expansion that marked the rise of dinosaurs to ecological dominance in the latest Triassic and Early Jurassic (see Qvarnström et al., 2024).

The studied material consists of 42 tridactyl pes imprints. The most common tracks belong to *Grallator* isp., *Anchisauripus* isp., *Apatichnus minor*, and *Apatichnus* isp., indicating a relatively large diversity of small to medium theropods in the Lisowice-Lipie Śląskie ecosystem. Tridactyl tracks assigned to *Eubrontes* isp. are relatively large (>30 cm) for the Late Triassic, but they are still not the largest in the assemblage. Another

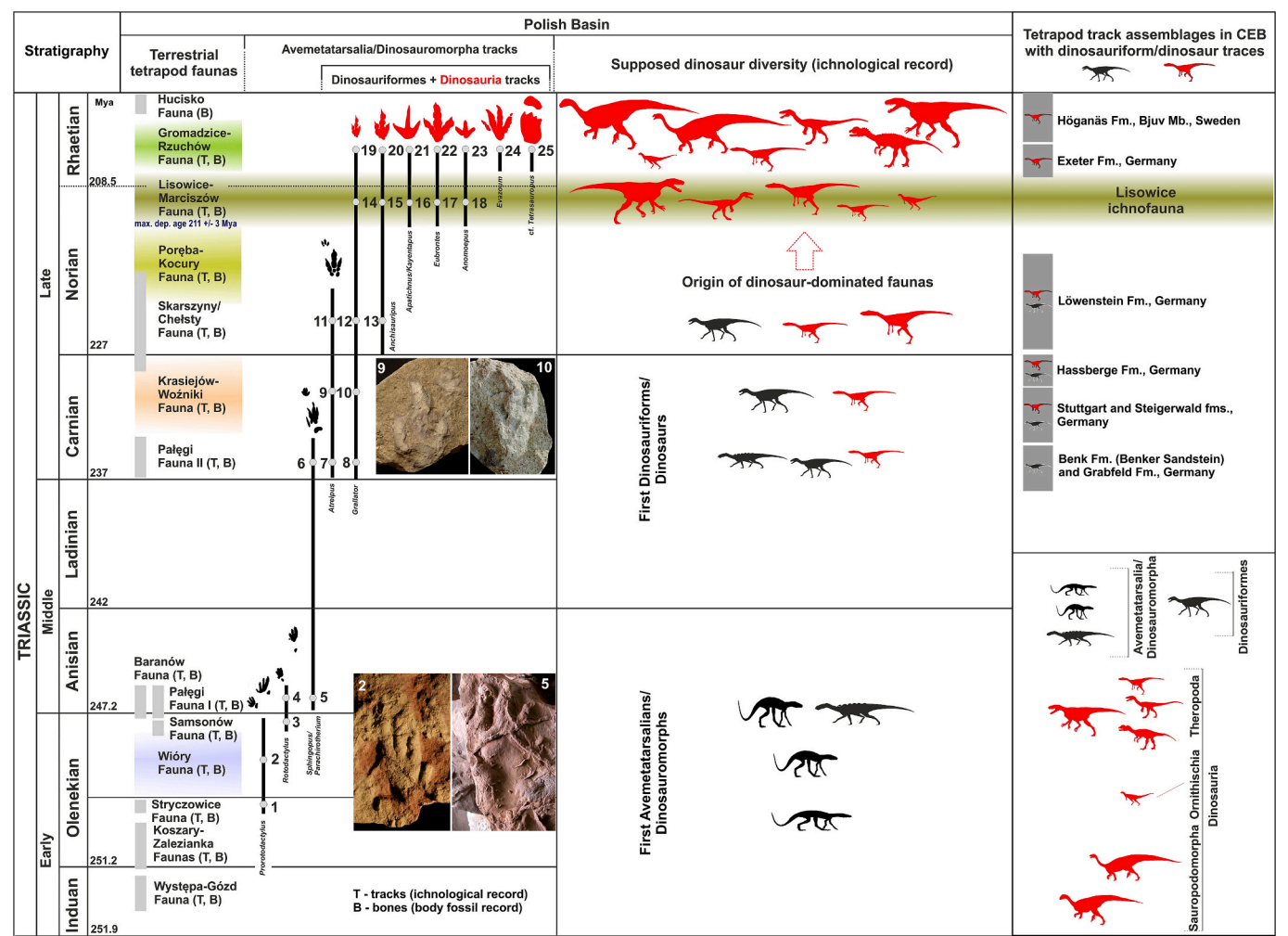


Fig. 19. The ichnological record of avemetatarsalian/dinosauromorph/dinosaur and described terrestrial tetrapod faunas in the Early-Late Triassic of Poland and Central European Basin (based on Gierliński and Ahlberg, 1994; Ptaszyński, 2000; Haubold and Klein, 2002; Moser, 2003; Niedźwiedzki and Ptaszyński, 2007; Brusatte et al., 2011; Niedźwiedzki et al., 2013; Wagensommer et al., 2022; Qvarnström et al., 2024; Klein and Lucas, 2025a, 2025b; Mujal et al., 2025 and unpublished data). Silhouettes represent different trackmakers, with an explanation in the lower right-hand corner. Explanations: 1 – *Prorotodactylus* isp., 2 – *Prorotodactylus mirus* (see also photo no. 2), 3 – cf. *Rotodactylus* isp., 4 – *Rotodactylus matthewsi*, 5 – *Sphingopus* isp. (see also photo no. 5), 6 – *Parachirotherium* isp.; 7 – *Atreipus* isp., 8 – cf. *Grallator* isp.; 9 – cf. *Atreipus* isp. (see also photo 9); 10 – *Grallator* isp. (see also photo 10), 11 – *Atreipus acadianus*; 12 – *Grallator* isp.; 13 – *Anchisauripus* isp.; 14 – *Grallator* isp.; 15 – *Anchisauripus* isp.; 16 – *Apatichnus minor*/*Apatichnus* isp.; 17 – *Eubrontes* isp./cf. *Eubrontes* isp.; 18 – *Anomoepus* isp.; 19 – *Grallator* isp.; 20 – *Anchisauripus* isp.; 21 – *Kayentapus soltykovensis*/*Kayentapus* isp.; 22 – *Eubrontes giganteus*; 23 – cf. *Anomoepus* isp., 24 – *Evazoum* isp.; 25 – cf. *Tetrasauropus* isp.

type of eubrontid tracks (cf. *Eubrontes* isp.) shows broad and massive digit imprints and is enormous in size (>40–50 cm) – no similar large tridactyl tracks have been described from the Late Triassic record in the Central European Basin. Moreover, early ornithischian tracks, represented by anomoeopid pes traces without hallux impressions, are assigned to *Anomoepus* isp., which is a widely known ichnogenus from the Early Jurassic (Olsen and Rainforth, 2003). The presence of this ichnogenus in this late Norian-earliest Rhaetian provides further evidence for an earlier appearance of the ornithischian clade in the area. Interestingly, the Lisowice-Lipie Śląskie track assemblage also comprises the first record of *Apatichnus* – an ichnogenus that can be confidently identified as a small predatory dinosaur – from the Late Triassic-Early Jurassic of Europe and North America.

The ichnofauna reflects a rich presence of dinosaurs and is reminiscent of the latest Triassic and Early Jurassic dinosaur-dominated ichnoassemblages from the Central European Basin. Still, the lack of sauropodomorph tracks in the Lisowice-Lipie Śląskie stands out. Numerous localities with sauropodomorph tracks are known from the

middle Norian-late Rhaetian tracksites in the northern part of Pangaea (Lockley et al., 1996; Lockley and Meyer, 2000; Nicosia and Loi, 2003; Clemmensen et al., 2016; Lallensack et al., 2017), but the absence in contemporaneous Polish strata is probably due to palaeoecological factors that controlled both the faunal composition and its distribution in this region during the Late Triassic (see Qvarnström et al., 2024).

CRediT authorship contribution statement

Grzegorz Niedźwiedzki: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Krzysztof Owoc:** Writing – original draft, Formal analysis, Data curation. **Martin Qvarnström:** Writing – original draft, Investigation, Formal analysis. **Gerard D. Gierliński:** Writing – original draft, Investigation, Formal analysis, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This project was financed by the Polish Ministry of Science and Informationisation as the project No. 3941/B/P01/2009/36 (2009–2014, study grant of G.N., Faculty of Biology, University of Warsaw). They were also supported by the Swedish Research Council (2017-05248) awarded to G.N., and from resources of the National Fund of Environmental Protection and Water Management (Polish Geological Survey financing, project no. 22.9611.2303.00.1). M.Q. acknowledges support from the European Research Council (ERC), starting grant ERC-2025-STG “DINO-DIGEST” (project no. 101222665). Wojciech Lewenstam is acknowledged for obtaining and processing optical surface scan data.

Data availability

The authors confirm that all data necessary for supporting the scientific findings of this paper have been provided.

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