A highly diverse Pennsylvanian tetrapod ichnoassemblage from the Semily Formation (Krkonoše Piedmont Basin, Czechia) (#122838)

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A highly diverse Pennsylvanian tetrapod ichnoassemblage from the Semily Formation (Krkonoše Piedmont Basin, Czechia)

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The Krkonoše Piedmont Basin (KPB) is one of the Late Paleozoic continental basins in Bohemia, Czechia, comprising a sedimentary sequence from the Late Pennsylvanian to the early Cisuralian. The Pennsylvanian in the KPB consist of alluvial-fluvial to lacustrine deposits with a relatively rich fossil record, comprising mainly ray-finned fishes, freshwater sharks, and invertebrates. Although no physical remains of terrestrial vertebrates have been discovered in the Late Pennsylvanian deposits of the KPB, recent studies of tetrapod footprints provide the first direct evidence of pre-Permian terrestrial tetrapod diversity within this basin. Furthermore, the abundant ichnofauna, including ichnotaxa such as *Amphisauropus* isp., *Batrachichnus salamandroides*, *Dimetropus* isp., *Dromopus lacertoides*, *Ichniotherium cottae*, and *Limnopus heterodactylus* represents the most diverse tetrapod ichnoassemblage described to date from the Pennsylvanian. Among these, the *Amphisauropus* tracks from the KPB represent the first globally recognised occurrence of this ichnotaxon from the Gzhelian. Furthermore, the *Ichniotherium cottae* tracks described here complement the still rare Pennsylvanian occurrences of this ichnospecies in the European part of Pangea. This ichnofauna is associated with alluvial to lacustrine nearshore deposits , suggesting the ecological importance of the lacustrine environment and its adjacent areas for the occurrence of terrestrial vertebrates and the preservation of their footprints.

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Abstract

The Krkonoše Piedmont Basin (KPB) is one of the Late Paleozoic continental basins in Bohemia, Czechia, comprising a sedimentary sequence from the Late Pennsylvanian to the early Cisuralian. The Pennsylvanian in the KPB consist of alluvial-fluvial to lacustrine deposits with a relatively rich fossil record, comprising mainly ray-finned fishes, freshwater sharks, and invertebrates. Although no ~~physical~~ remains of terrestrial vertebrates have been discovered in the Late Pennsylvanian deposits of the KPB, recent studies of tetrapod footprints provide the first direct evidence of pre-Permian terrestrial tetrapod diversity within this basin. Furthermore, the abundant ichnofauna, including ichnotaxa such as *Amphisauropus* isp., *Batrachichnus salamandroides*, *Dimetropus* isp., *Dromopus lacertoides*, *Ichniotherium cottae*, and *Limnopus heterodactylus* represents the most diverse tetrapod ichnoassemblage described to date from the Pennsylvanian. Among these, the *Amphisauropus* tracks from the KPB represent the first globally recognised occurrence of this ichnotaxon from the Gzhelian. Furthermore, the *Ichniotherium cottae* tracks described here complement the still rare Pennsylvanian occurrences of this ichnospecies in the European part of Pangea. This ichnofauna is associated with alluvial

to lacustrine nearshore deposits, suggesting the ecological importance of the lacustrine environment and its adjacent areas for the occurrence of terrestrial vertebrates and the preservation of their footprints.

Introduction

The Krkonoše Piedmont Basin (KPB) preserves the most abundant Pennsylvanian tetrapod footprint assemblage in Czechia, offering invaluable insights into the early tetrapod diversity of a landlocked basin that formed part of equatorial Pangea. Fossil sites with tetrapod footprints in the KBP have been known since the 19th century and are significant from a historical perspective ~~mainly~~ due to early Permian locality Horní Kalná (Prosečné Formation) which became the type locality for three typical ichnospecies of the Late Paleozoic (see Geinitz 1961, Geinitz & Deichmüller, 1882). Finds of Pennsylvanian tetrapod tracks have until recently been described much less frequently in this area. Frič (1912a, 1912b) was the first who reported the occurrences of *Saurichnites calcaratus*, a junior synonym of *Dromopus lacertoides* (Geinitz, 1861) in the railway cut Kyje–Ploužnice (Ploužnice Horizon, Ghzelian) in the KPB. Later, Haubold & Katzung (1975) expanded the ichnotaxonomic list from the same locality with *Anthichnium salamandroides*, a junior synonym of *Batrachichnus salamandroides*, (Geinitz, 1861), *Amphisauropus latus*, a junior synonym of *Amphisauropus kablikae*, (Geinitz & Deichmüller, 1882), *Dromopus lacertoides* (Geinitz, 1861), and *Ichniotherium cottae* (Pohlig, 1885). However, these early studies lacked descriptions or depictions of the listed ichnotaxa. Despite this, the relatively diverse tetrapod ichnoassemblage contrasts sharply with the extremely rare tetrapod body fossils in the Pennsylvanian of the KPB, which are limited to a few bones of branchiosaurid temnospondyl (Frič 1912a, 1912b).

This study presents the first comprehensive description of Pennsylvanian tetrapod tracks from the KPB, based on both new fossil finds – including the first documentation of tracks in the stratigraphic profile of the lacustrine Ploužnice Horizon of the Semily Formation (Gzhelian; Stephanian C–lower Autunian) and the newly discovered locality Štikov – as well as on a complete revision of all historical collections of tetrapod tracks from the Semily Formation stored in Czech institutions. The tetrapod ichnofossil record now includes six ichnotaxa: *Amphisauropus* isp., *Batrachichnus salamandroides*, *Dimetropus* isp., *Dromopus lacertoides*, *Ichniotherium cottae*, and *Limnopus heterodactylus.* Special attention is given to the palaeoecological assessment of track localities and spatiotemporal distribution of track producers in the KPB. Our study provides unique evidence of terrestrial life during the latest Pennsylvanian, associated with a lakeshore environment. This, in turn, enriches our view on the diversity of terrestrial palaeoecosystems within the intra-Variscan basins of equatorial Pangea.

Geological setting

The Krkonoše Piedmont Basin (KPB) is ~1100 km^2 large W–E elongated basin, a part of an extensive Pennsylvanian–Permian Bohemian basin system (Fig. 1), also termed as the Pilsen–Trutnov Basin Complex (PTBC – Cháb et al., 2008; Opluštil et al., 2016a).

Palaeogeographically, the PTBC was located within the tropical belt, between ca. 2° and 4° north of the palaeoequator (Krs and Pruner, 1995: fig. 2). The KPB is located in northeastern Bohemia in the southern foothills of the Krkonoše Mountains (Fig. 1B) and is formed by several separate sub-basins altogether deformed into a set of synclinoria and anticlinoria (Fig. 1C). The infill of the PTBC contains up to ~1400 m (cf. Pešek, 2001) of the Middle Moscovian (lower Bolsovian) to the lower Permian (Asselian; cf. Opluštil et al., 2016a) strata predominantly red, coal- and fossil-barren/poor formations: Kumburk, Semily (except for its middle part), Vrchlabí, Prosečné and Chotěvice formations (Fig. 2). Compared to the central and western part of the PTBC, the basin fill of the KPB contains substantially less of grey, coal-bearing deposits. Coal seams are preserved within the Syřenov Fm., and within the middle part of the Semily Fm. Several unconformities in the basin fill (Fig. 2) record ~1–4 Myr hiatuses reflecting late orogenic to intraplate tectonic processes that resulted in reactivation of Variscan faults, inversion of older basin fill and rearrangement of basin geometry (Opluštil et al., 2016b; Nádaskay et al., 2024, 2025). Therefore, the infill of the KPB records several tectonosedimentary cycles (Nádaskay, 2021). The Semily Fm., ~~on~~ which this paper ~~is focussing,~~ represents the basal part of the Late Pennsylvanian–early Permian tectonosedimentary cycle, generated by widespread extension within the Variscan Belt, in places interfering with transtension (Nádaskay et al., 2024, 2025). Based on the rich fossil plant assemblages from individual stratigraphic levels of the KPB, the increasing seasonality is traceable from Pennsylvanian towards the Permian (Opluštil et al. 2022a).

Semily Formation with focus on the Ploužnice Horizon

The Semily Fm. represents a ~500 m thick sequence of predominantly reddish conglomerates, sandstones, siltstones and claystones (Pešek, 2001; Opluštil et al. 2016). In its typical development, the formation is divided into three parts – lower, middle and upper (Fig. 2; cf. Pešek, 2001), each with ~~a~~ distinct lithofacies development. The lower part of the formation is dominated by coarse clastic deposits that are particularly concentrated along the northern, tectonically-driven basin margin. These are represented by up to ca. 120 m thick (cf. Pešek, 2001) often poorly-sorted coarse-grained conglomerates or even breccias containing mostly phyllite and quartz clasts from the nearby Krkonoše–Jizera Crystalline Complex (Fig. 1B). In the south, the basal part of the Semily Fm. is formed by conglomerates up to ~40 m thick (cf. Pešek, 2001) with good sorting and clast rounding and coarse-grained sandstones.

The middle part of the formation is dominated by fine-grained deposits and is ~130 m thick in the south and ~100 m thick in the north. In the south, the middle part of the formation contains a succession formed by varicoloured siltstones, claystones with subordinate limestones, and ~~containing~~ distinctive lenses of cherts, interpreted as lacustrine deposits grouped into the so-called Ploužnice Horizon. This unit is formed by two lacustrine intervals (lower and upper Ploužnice Horizons), each ~10–60 m thick, separated by alluvial deposits – brownish-reddish interval of predominantly mudstones and fine-grained sandstones, ~10–30 m thick (Pešek, 2001). The lacustrine deposits are also represented by the Štepanice–Čikvásky Horizon, a presumed continuation of the Ploužnice Horizon to the northern part of the Central sub-basin (Fig. 1C). Both units are traditionally termed as 'horizons', although their greater thickness and varied lithology contradict the concept of 'stratigraphic horizon' as a thin marker of distinctive lithology (cf. Courel et al., 2008), and should be defined as a member of the Semily Fm.

The Ploužnice Horizon reportedly contains numerous flora remains of lycopsids, Equisetids (Calamites, Sphenophylls), Ferns (Marattiales, Zygopteridales, Filicales), Pteridosperms (Medullosales, Lyginopteridales, Callistophytales, Peltaspermales) and Gymnosperms (Cordaitopsids, Coniferopsids) as well as a rich fauna of bivalves, ostracodes, conchostracans, blattoid insect, arachnids, elasmobranchs, actinopterygians, and tetrapod footprints (Fig. 2; Fritsch, 1901; Frič, 1912a, 1912b; Kamarád, 1951, 1959; Rieger, 1958, 1968; Pešek, 2001; Zajíc, 2007; Štamberg 2001, 2018, 2023, 2024; Štamberg and Zajíc, 2008; Mencl et al. 2013; Opluštil et al., 2016, 2022; Schneider et al.; 2020). These horizons are represented by intervals of 10–60 m thick lacustrine sequence of grey, red to purple mudstones, claystones, and ripple bedded sandstones with intercalated red cherts and redeposited or in situ volcaniclastics (Pešek, 2001). Lacustrine intervals are separated by a 10–30 m thick layer of fluvial redish aleuropelites and sandstones (Pešek, 2001).

The Late Pennsylvanian fossil fauna of the KPB has been known since the beginning of the 20th century based on the discoveries in the railway cut between Ploužnice and Kyje (Figs. 3A, 3C) and the Krsmol locality (Fritsch, 1901; Frič, 1912a, 1912b) representing the localities of the Ploužnice Horizon (Stephanian C). Above the Ploužnice Horizon, alluvial-lacustrine deposits of the upper part of the Semily Fm. pass into the Vrchlabí Fm. whose basal part of is lithologically similar but devoid of cherts and features monotonous colours (brownish/reddish and/or greyish). This interval contains the Carboniferous-Permian boundary (Opluštil et al., 2013, 2022a). Based on the litho- and biostratigraphic correlation of the Ploužnice Horizon with the Klobuky Horizon (Líně Fm.) in central Bohemia, dated at 298.97 ± 0.09 Ma (Opluštil et al., 2016a), and unpublished dating of the base of the Vrchlabí Fm. at 298.72 Ma (cf. Nádaskay et al., 2024), the uppermost part of the Semily Fm. is decidedly early Permian in age.

Railway cut Kyje–Ploužnice (Ploužnice Horizon)

~~This palaeontological site has~~ been known since the beginning of the 20th century (1912a, 1912b). The railway cut created several outcrops in the Ploužnice Horizon between Kyje and Ploužnice railway stops (Fig. 3A) and was depicted in detail already by Fřič (1912a: ~~figs.~~ 12, 13; 1912b: figs. 12, 13) and Purkyně (1929; Fig. 3C). The series of railcuts were studied sedimentologically by Blecha et al. (1997) – out of several exposures described by these authors, this paper focusses on the section closest to the Kyje railway stop where the Ploužnice Horizon is well-exposed on both sides of the railway (Fig. 4A). The Kyje section (Fig. 5A) displays two fining-upward cycles. The lower cycle is formed by mudstones at the base, overlain by fine-grained sandstones with ripple- (Fig. 4B) or low-angle cross-bedding, often with sharp bases and sometimes with conspicuous channelization (Fig. 4B). The alternation of mudstones and sandstones is topped by silty-sandy limestone overlain by pedogenic horizon (Fig. 4B) with conspicuous vertic slickensides and abundant carbonate nodules. The lower cycle (Fig. 5) is predominantly brown- or red-brown coloured. The middle cycle (Fig. 5) starts at the base with very fine- to fine-grained sandstones, often silty or argillaceous, with mud drapes or even thin interbeds of mudstones (Fig. 4C). Mud drapes are occasionally with rain rills and rain-drop impressions (Fig. 4D), sometimes with wrinkle structures (Fig. 4E) possibly left by microbial mats and with invertebrate burrows (Fig. 4F). Mudcracks (Fig. 4G) are present both in red- and violet/grey-coloured deposits.

These sandstones pass upward into ~7–8 m thick sequence of predominantly violet and grey mudstones with cm to first dm thick interbeds of greyish sandstones (Fig. 4A). The upper part of this sequence is apparently finer, mudstone-dominated, and contains nodular interbeds of reddish cherts and cm thick volcaniclastic layers. The top of the section, inclined towards the Kyje railway stop, is represented by alternation of violet to brownish mudstones and brownish sandstones. These deposits represent a lower part of an upper, incompletely exposed cycle.

Concerning fossil finds, the flora is represented by Lycopsids (*Asolanus camptotaenia*, *Halonia* (*Ulodendron*), *Stigmaria ficoides, Lepidostrobus variablis, Lepidophyllum* sp.), Equisetales (*Sphenophyllum oblongifolium, Asterophyllites equisetiformis, Annularia spinulosa*, *Calamites gigas, C. cruciatus, C. undulates*, *C. suckowii*, *C. cistii, Calamostachys tuberculata* etc.), ferns (*Cyathocarpus arboreus, Pecopteris arborescens*, *Scolecopteris cyathea*, *Acitheca polymorpha* etc.), Pteridosperms (*Odontopteris subcrenulata, O. schlotheimii, Callipteridium pteridium, Ca. costei, Neuropteris zeilleri, N. cordata, Neurodontopteris auriculata* etc.) and Gymnosperms

(*Culmitzschia* cf. *speciosa, Walchia piniformis, Ernestiodendron filiciforme*, *Cordaites borassifolius*) (Purkyně, 1929; Němejc, 1932; Štamberg & Lapacík, 2018; Šimůnek et al., 2022; Opluštil et al., 2022a). Fossil fauna comes from thin layer (~ 0.5m) of dark red claystone originally called "bonebeds" by Frič (1912a, 1912b) and from the lower part of varicoloured tuffitic claystones (Štamberg, 2023). Fossils are represented by wings of the blattoid insect *Spiloblattina lawrenceana*, *Sysciophlebia rubida*, *Neorthroblattina* cf. *multineuria* and *Anthracoblattina* sp., scales of elasmobranchs Xenacanthidae and *Sphenacanthus* sp., scales and fin spines of *Acanthodes* sp., scales and bones of actinopterygians *Elonichthys* sp*., Sphaerolepis kounoviensis*, *Spinarichthys disperses, Progyrolepis speciosus* and *Zaborichthys fragmentalis* and bones of branchiosaurid (Frič, 1912a,b; Schneider, 1983; Zajíc, 2007, Štamberg & Lapacík, 2018; Štamberg, 2023). As mentioned above, Frič (1912a, 1912b) described a tetrapod ichnotaxon *Saurichnites calcaratus*= *Dromopus lacertoides* (Geinitz, 1861) in a "dark" shale (the layer corresponds to a red mudstone containing ichnofossils of *Dromopus*; e.g. MZM Ge34179) in an outcrop near the railway milestone marking the distance 60.5 km. Later Haubold & Katzung (1975) expanded the list of ichnotaxa from the railway cut Kyje–Ploužnice with *Anthichnium salamandroides* = *Batrachichnis salamandroides* (Geinitz, 1861), *Amphisauropus latus* = *Amphisauropus kablikae* (Geinitz and Deichmüller, 1882), *Dromopus lacertoides* and *Ichniotherium cottae,* which are revised in this study and described and depicted for the first time.

Krsmol – locality "Hluboká rokle" (Ploužnice Horizon)

The locality Krsmol is well known from the beginning of the paleontological research in the KPB (Frič 1901, 1912a, 1912b). The outcrop is located in the upper part of a deep erosional gorge. Its current condition is described in detail by Štamberg (2024). From the base of profile, he described 30 cm thick chert, 5 cm thick massive red sandstone, well bedded 10 cm thick grey siltstone, with fauna on the base and 100 cm thick purplish siltstone with fauna. According to Štamberg (2024), these layers are comparable to the "bonebed" at the Kyje–Ploužnice railway cut. Flora is represented by Lycopsids (*Sigillaria brardi, Lepidodendron* sp. etc.), Equisetales *Calamites gigas* and Pteridosperms *Odontopteris schlotheimii, Neurodontopteris auriculata* and *Callipteridium pteridium* (Purkyně, 1929; Němejc, 1932; Opluštil et al., 2022). The fauna is represented by bivalves *Carbonicola bohemica*, arachnids *Anthracolysa* sp., wings of blattoid insect *Sysciophlebia rubida*, fin spines, scales, teeth, and fin spin of elasmobranchs *Turnovichthys magnus*, *Lissodus* sp., *Orthacanthus* sp. and *Bohemiacanthus* sp., scales of acanthods and scales and teeth of the actinopterygians *Elonichthys* sp. and *Sphaerolepis kounoviensis* (Frič, 1901, 1912a, 1912b; Štamberg, 2001, 2024; Zajíc, 2007).

Štikov – roadcut Nová Paka–Vidochov

This locality displayed a temporary outcrop (e.g., Fig. 4H) created by construction of a new road from Nová Paka to Vidochov (Fig. 3B) that was exposed during the years 2023–2024. The approximately 700 m long outcrop displays a NE dipping sequence (Fig. 3D) of conglomerates and sandstones alternating with siltstones (ca. 5 m thick; Fig. 4I) that forms the lower part of the Semily Fm., i.e., beneath the Ploužnice Horizon (Fig. 5B). This sequence is underlain by whitish arkoses (Fig. 4H) and further downward by a sequence of grey mudstones with thin interbeds of violet-grey sandstones, which belong to the Syřenov Fm. (Fig. 5B). Upsection, the conglomerates of the basal part of the Semily Fm., typically clast-supported, poorly-sorted with pebbles of quartz and micaschists (Fig. 4J) pass into alternating sandstones and siltstones (~5 m thick), and the exposed part of the sequence ends with red mudstones. In the upward direction, a colour of the sediments changes from grey-violet to red. The fossil tracks of *Ichniotherium* come from the sequence of conglomerates alternating with ~30 cm thick siltstones interbeds containing *Dromopus* isp. (MZM Ge34182), cf. *Batrachichnus* (MZM Ge34182) and cf. *Ichniotherium* (MZM Ge34183) footprints (M. Stárková, pers. comm., 2023). This sequence is overlain by predominantly red mudstones.

Materials & Methods

Material

The study is based on tetrapod track specimens from several localities falling into the Semily Fm., Krkonoše Piedmont Basin: Kyje, Ploužnice = (Railway cut Kyje–Ploužnice) Krsmol, and Štikov (Figs. 6-10). The tracks consist of isolated tracks, manus-pes couples, and trackways, and are preserved as both concave epirelief and convex hyporelief. The specimens are housed at the Czech Geological Survey in Prague (CGS), the Moravian Museum in Brno (MZM), the National Museum in Prague (NM), and the Nová Paka City Museum (NMP).

The stratigraphically oldest specimen (Figs. 9A–7B) MZM Ge34184 (convex hyporelief) includes a manus–pes couple and three isolated tracks that were discovered in 2024 by the authors (GC, JB) in the excavated material from the temporary outcrop that was created during the construction of the road from Nová Paka to Vidochov (Fig. 3B). The outcrop was buried during construction in 2025 and consequently no longer exists. Due to limited access, the sedimentary profile at this location could not be thoroughly studied and is thus only indicative (Fig. 5B). The specimen is preserved in violet sandy conglomerate. The conglomerate layers are located in the lower part of the Semily Fm. (Stephanian C).

In 2024 and 2025, the authors (GC, JB, RN) discovered track specimens in the railway cut Kyje–Ploužnice including MZM Ge34174–Ge34184, most of which were excavated directly from the reddish and purplish coloured layers and marked in the profile (Fig. 5A). From the same localities also come the specimens CGS JZ626 and JZ632 discovered in the 1990s by Z.

Šimůnek (ČGS), and the specimens CGS XA736, XA737, XA738, XA739, XA740, XA741, XA742, XA743, XA744, XA746 discovered by K. Havlata most probably in the 1930s. The Havlata's collection was most likely mentioned in the study by Haubold & Katzung (1975), although their ichnotaxa list is not accompanied by any description or registration numbers. The historical collections of track specimens from the railway cut Kyje–Ploužnice always lack localization in the profile and probably represent collections from the talus. However, they are preserved in a fine sandstone to claystones of reddish or purplish colours, which suggests at least two fossil layers.

Some collection from the 20th century housed in the Czech museums marked separately under the localities Kyje (MZM Ge 31124, NMP P103, NMP P104) and Ploužnice (NMP P307, NM M4949a) most probably come from the same railway cut, which are well known and often cited from the beginning of palaeontological research in this basin (see Fritsch 1901, Frič 1912a, 1912b). Specimens NMP P103, NMP P104 and NMP P307 were donated to the Nová Paka City Museum by V. Fejfar in 1926 in the first case and by K. Tuček in 1971 in the other cases. NM M4949a housed at the National Museum Prague was donated most probably in the turn of the 19th and 20th centuries.

The specimen NMP P3573 from the locality Krsmol was donated to the Nová Paka City Museum by K. Tuček in the 1970s.

Anatomical terminology and measurements

The anatomical terminology used to describe fossil footprints follows Leonardi (1987). Measurements were obtained using a digital calliper and ImageJ.

Systematic palaeoichnology

Amphisauropus, Haubold, 1970

***Amphisauropus* isp. (Figs. 6A–6D)**

Referred material. CGS JZ626 – convex hyporelief; CGS JZ632 – concave epirelief. The specimens are convex hyporelief and concave epirelief of the same specimens.

Description:

The manus imprints are pentadactyl and plantigrade whereas the pes imprints are incomplete semidigitigrade to digitigrade. The footprints are up to ~9 mm in long (Material SI). The manus imprints are smaller than the pes imprints. The manus are slightly wider than longer. The palm impressions show a rectangular shape. The length of the manual digit impressions increases from I to IV. The digit V is shorter than digit II. Manual digits I have the typical basal pad. The digits show a round termination. The manus imprint is turned inward compared to the pes imprint. The trackway shows an alternating arrangement of successive manus and pes imprints. There is no overstepping within the manus-pes couple.

Discussion:

The specimens described above show all the diagnostic features of *Amphisauropus*, including pentadactyl wide manus imprint with relatively thick digits with rounded termination, the longest manual digit IV is similar size as digit III, the palm is well impressed in the proximal portion, strongly inwards oriented manus imprint in relation to the pes imprint.

Amphisauropus tracks have been known from the Pennsylvanian to the Cisuralian (early Permian), while the vast majority specimens have been discovered in the Cisuralian of Europe (e.g. Frič, 1901; Pabst, 1905; Haubold, 1971, 1996; Voigt, 2005, Gand & Durand, 2006; Avanzini et al., 2008; Voigt et al., 2012; Marchetti et al., 2015a, 2015b, 2016, 2018; Mujal et al., 2016; Santi et al., 2020; Calábková et al., 2022), North America (Haubold et al., 1995; Lucas et al., 2001, 2009; van Allen et al., 2005; Voigt & Lucas, 2015, 2017; Marchetti et al., 2019, 2020), and Africa (Voigt et al., 2011). The *Amphisauropus* tracks from the Ploužnice Horizon represent the only evidence about this ichnotaxa from the Ghzelian. The older occurrence of *Amphisauropus* was designated by Lucas & Stimson (2025), which comes from the Keota Sandstone Member of Middle Pennsylvanian in Oklahoma (an isolated manus imprint).

***Batrachichnus* Woodworth, 1900**

***Batrachichnus salamandroides* (Geinitz, 1861)**

Referred material. CGS XA738 – convex hyporelief, trackway consists of four manus-pes couples; MZM Ge31124 – convex hyporelief, isolated three tracks **(Figs. 7A–7D)**

Description:

Manus imprints are tetradactyl and plantigrade, and pes imprints are pentadactyl to digitigrade. The footprints are up to 24 mm in long (Material SI). The manus imprints are smaller than the pes imprints. The manus imprints are slightly longer, whereas the pes imprints are slightly longer than widee. The manual digits imprints are relatively short with rounded terminations. The length of the manual digits increases from I to III, and the digit IV is about as long as the digits I or II. The length of the pedal digits increases from I to IV, and V is shorter than III. The manual digit I has often distinctly impressed the basal pad. The palm and sole impressions are most often wider than longer. The manus imprints are slightly turned inward, whereas the pes imprints are parallel or slightly outward orientated to the midline. The trackway shows an alternating arrangement of successive manus and pes imprints. Overstepping does not occur.

Discussion

The small-sized tetradactyl manus imprints with short digits with rounded termination are clearly assignable to the ichnospecies *Batrachichnus salamandroides*.

The *Batrachichnus* have been reliably documented from the Mississippian to the Middle Triassic of Europe (Makowsky & Rzehak, 1884; Frič, 1901; Pabst, 1908a, 1908b; Haubold, 1970, 1971;

Haubold & Katzung, 1975; Gand, 1987; Voigt, 2005, Mujal et al., 2016; Marchetti et al., 2022) North America (Stimson et al., 2012; Klein & Lucas, 2021; Allen et al., 2022), South America (Melchor & Serjant, 2005), and Africa (Voigt et al., 2011a, 2011b, Cisneros et al., 2020).

***Limnopus* Marsh, 1894**

***Limnopus heterodactylus* (King 1845) (Figs. 8A–8D)**

Referred material. NMP P3573 – convex hyporelief, manus-pes couple; CGS XA741 – convex hyporelief, manus-pes couple

Description

The manus imprints are tetradactyl and plantigrade, whereas the pes imprints are pentadactyl plantigrade to semiplatigrade. The footprints are up to ~30 mm long (Material SI). The manus imprints are wider than longer are strongly inwardly rotated compared with the pes imprint. The sole and palm impressions are wider than longer. Manual digit imprints are relatively short, thick, and most often straight. The manual and pedal digits show rounded terminations. The lengths of the manual digit imprints are similar and slightly increases from I to III, whereas digits IV are about as long as the digits II. Further, digits IV are often separated from digits I-III and rotated outwards. The length of the pedal digits increases from I to IV, and V is shorter than III. The pedal digit impressions are in close vicinity to the manus imprint. The trackway shows an alternating arrangement of successive manus and pes imprints. The manus imprints show medial-median functional prevalence. Specimen ČGS XA741 (Figs. 8C–8D) shows distinct pads of digit I.

Discussion

The specimens NMP P3573 and CGS XA741 have manus imprint distinctly wider than longer, the length of manual digits IV is as long as digit II in contract with a very similar ichnotaxon

Batrachichnus, which has commonly manus imprint as long as wide or slightly wider than longer and the manual digit IV is often shorter than digit II (Voigt 2005). In addition, *Batrachichnus* pes imprints are typically of length up to 20 mm. However, the strict differences of digit proportions are not always be clearly present. For this reason, some authors presented the *Batrachichnus*-*Limnopus* plexus (see Voigt et al., 2011).

The specimen CGS XA741 (Figs. 8C–8D) was labelled as *Amphisauropus latus* = *A. kablikae* with the initial of H. Haubold, and this determination was used in the study by Haubold & Katzung (1975). ~~Apparently,~~ the distinct pad impression of digit I was mistaken for the digit I impression itself. The manual digits V of the *Amphisauropus* tracks are only slightly longer than the digits I (see Voigt, 2005, 2015; Calábková et al., 2022), which is inconsistent with the specimen CGS XA741. These facts most ~~probably also~~ explained why the *Amphisauropus* tracks from the Ploužnice Horizon have never been described in followed studies. The morphology of the CGS XA741 is almost identical to that of *Limnopus* from the study of Voigt (2015, fig.2). *Limnopus* is well known from the Pennsylvanian to the Cisuralian of Europe (Tucker & Smith, 2004; Marchetti et al., 2013, 2015a, 2015b; Niedźwiedzki, 2015; Meade et al., 2016; Mujal et al., 2016), Greenland (Milàn et al., 2016), North America (Martino, 1991; van Allen, 2005; Voigt & Lucas, 2016), Morocco (Voigt et al., 2011a; Lagnaoui et al., 2018).

***Limnopus* isp.** (Figs. 8E–8F)

Referred material. MZM Ge34174 – convex hyporelief, incomplete manus-pes couple

Description

The large tetradactyl plantigrade manus imprint is ~72 mm long (Material SI). The manus and palm imprints are distinctly wider than longer. The digits are straight, thick, and short with rounded termination. The IV digit is turned outward. The manual digits show almost the same length but increase slightly from I to III, while digit IV is almost the same length as digit II. The pes imprint is not completely preserved. The pedal digit imprints are thick, relatively long with rounded termination.

Discussion: The large tetradactyl manus imprints with short thick digits well correspond to the large *Limnopus* tracks. Regarding the incomplete pes impression, we assign the specimen MZM Ge34174 to *Limnopus* isp.

***Ichniotherium* Pohlig, 1892**

***Ichniotherium cottae* (Pohlig, 1885) (Figs. 9A– 9H)**

Referred material. MZM Ge34184– convex hyporelief, manus-pes couple with two isolated tracks; CGS XA737 – concave epirelief, manus-pes couple; CGS XA739 – convex hyporelief, isolated pes imprint; NMP P103 – concave epirelief, isolated pes imprint,; NMP P307 – concave epirelief, isolated pes imprint

Description

The manus and pes imprints are plantigrade and pentadactyl. The footprints are up to ~135 mm long (Material SI). The pes imprints are larger than the manus imprints (Figs. 9A–9B). The pes imprints are most often as wide as long, whereas the manus imprints are as wide as long or wider than long. The palm and sole impressions are deeply impressed with subcircular to elliptical shapes. The pedal digit imprints are rather straight and the manual digits III–V are slightly bent inward. The digit terminations are the deepest impressed parts of the tracks and show an extended, round termination. In the manus and pes imprints, the lengths of the digits increase from I to IV. The digits V are slightly shorter than the digits II or are of the same length. The pedal digits V reach approximately half the length of digit IV. The tracks show the medial-median functional prevalence. The trackway shows an alternating arrangement of successive manus and pes imprints. No overstepping occurs within the manus-pes couple. *Ichniotherium* track of PM P307 (Figs. 9G–9H) accompanied also *Dimetropus* manus-pes couple (Fig. 9I; see bellow for description) and small *Batrachichnus* tracks with tetradactyl manus impression.

Discussion

The specimen MZM Ge34184, NMP P103, NMP P307, CGS XA737 and CGS XA 739 ~~show all~~ diagnostic features of *Ichniotherium cottae*, such relatively short pedal digit V with pV/pIV ratio < 0.60 (in average value), deeply impressed elliptical to circular palm and sole and distal parts of the digits. MZM Ge34184 (Figs 9A–9B) shows doubled sole impression, which was described in sole impressions of early Permian *I. cottae* from the Tambach Formation, Thuringian Forrest, (see e.g. Voigt et al. 2007, fig. 3) ~~or also~~ in palm impression of *I. cottae* from the Boskovice Basin, Czechia, in lowermost Permian deposits (Calábková et al. 2023b, fig. 2). The *I. cottae* differs from *I. sphaerodactylum* ~~and the~~ significantly shorter short pedal digit V in contrast to the longer digit V in I. *sphaerodactylus*, which can reach about 80% of the pedal digit IV (see e.g. Voigt et al., 2007; Calábková et al., 2022). The CGS XA737 (Figs. 9E–9F) has well visible transverse segmentation on footprints often present on *Ichniotherium cottae* tracks (e.g Voigt, 2005; Marchetti et al., 2018; Calábková et al., 2023).

The first occurrence of *I. cottae* comes from the Alveley locality, Birmingham, UK (Moscovian–Kasimovian) (Haubold & Sarjeant, 1973; Buchwitz & Voigt, 2018). Further Pennsylvanian occurrences come from the Gzhelian of Saar-Nahe Basin (Voigt 2007) and Ohio (Baird 1952). However, most of the *I. cottae* come from the Cisuralian of Europe (Hochstetter, 1868; Frič, 1887, 1901; Haubold & Katzung, 1975; Voigt & Haubold, 2000; Voigt, 2005; Haubold & Sarjeant, 1974; Voigt et al., 2012, 2024; Mujal & Marchetti, 2020; Calábková et al., 2023b), USA (Voigt et al., 2005; Voigt & Lucas, 2015) and North Africa (Lagnaoui et al., 2018).

***Dimetropus* Romer & Price, 1940**

***Dimetropus* isp. (Fig. 9I)**

Material. NMP P307 – concave epirelief, manus-pes couple

Description

The pes imprint is plantigrade, longer than wide, and proximo-distally elongated. The manus are preserved only laterally. The pes imprint is 95 mm long (Material SI). The manus imprint is shorter than the pes imprint. The pes imprint is longer than wider. The manual and pedal digits are short, straight with a sharp clawed termination. The pedal digit impressions show a continuous increase in the length from I to IV. The digit V is not clearly identified. The impression of pedal digit I is orientated inwards. The manus-pes distance is relatively high.

Disscusion

The elongated proximal part of the footprints, and relatively short and sharp terminated digit impressions are typical features for the ichnotaxon *Dimetropus leisnerianus*. However, given the poorly preserved tracks and uncompletely impressed manus, we assigned the track to *Dimetropus* isp., which shows great similarities with *Dimetropus* specimens from Morocco (Voigt et al., 2011b, fig. 5; Lagnaoui et al. 2014, fig. 5; Lagnaoui et al. 2018, fig.6-7) and France (Gand, 1987, fig. 58A, planche 6B).

Dimetropus are known from the Pennsylvanian and the Cisuralian of North America (Tilton, 1931; Haubold et al., 1995; Van Allen et al., 2005; Sacchi et al., 2014; Voigt & Lucas, 2015; Lucas et al., 2016) Europe (Haubold, 1971; Gand & Haubold, 1984; Gand, 1987; Voigt, 2005; Niedźwiedzki & Bojanowski, 2012; Voigt et al., 2012; Marchetti, 2016; Meade et al., 2016; Mujal et al., 2016; Matamales-Andreu et al., 2021, 2022) and North Africa (Voigt et al., 2011a, 2011b; Lagnaoui et al., 2018). Except for the most common *Dimetropus leisnerianus,* the ichnospecies *Dimetropus osageorum* has been described from the Kungurian (lower Permian) of Oklahoma, USA (Sacchi et al., 2014), which differs from *D. leisnerianus* in that it shows a high degree of heteropody, short, subcircular manus imprint separated into two portions, short digit impressions which are subequal in length, and the pes imprint with a subelliptical to subcircular pad impression in the proximal central part of the sole.

***Dromopus* Marsh, 1894**

***Dromopus lacertoides* (Geinitz 1861) (Figs. 10A–10F)**

Referred material. NM M4949a – concave epirelief, CGS XA735 – convex hyporelief, three manus-pes couples and two isolated tracks; CGS XA742 – convex hyporelief, two tracks; CGS XA743 – convex hyporelief, three manus-pes couples; CGS XA744 – convex hyporelief, at least 8 tracks; NMP P104 – convex hyporelief, manus-pes couple; NMP P3608 – convex hyporelief, pes imprint; MZM Ge34176 – convex hyporelief, manus-pes couples and two isolated tracks; MZM Ge34177 – convex hyporelief and concave epirelief, at least 15 tracks; MZM Ge34178 – convex hyporelief and concave epirelief, manus-pes couple; MZM Ge34179 – concave epirelief, isolated track; MZM Ge34180 – convex hyporelief and concave epirelief, incomplete manus-pes couple; MZM Ge 34180 – convex hyporelief, manus-pes couple; MZM Ge34182 – convex hyporelief, manus-pes couple

Description

Pentadactyl plantigrade to digitigrade manus and pes imprints of similar size and shape. The pes footprints are up to ~ 70 mm long (Material SI). The manus imprints are slightly shorter than the pes imprints. The manus and pes imprints are longer than wide. The manus imprints often show a slightly inward orientation to the midline, whereas the pes imprints show a parallel or slightly outward rotation to the midline. The impressions of the digits are long and slender with tapered terminations. Palm and sole impressions are short and often not impressed. The length of the digits increases from I to IV, and the digit V is about as long as the digits II or III. Overstepping the manus imprints by the pes imprints is common. The specimen NM M4949a (Figs. 10A–10B) shows also a several circular structures with a diameter between 3–5 cm.

Discussion

The manus and pes imprints of similar shape and size with long and slender digits well correspond to the ichnospecies *Dromopus lacerdoides*. The CGS X742 footprints are among the largest *Dromopus lacertoides* which have been described to date. The *Dromopus* tracks are known from late Pennsylvanian to late Permian deposits of North America (Van Allen et al., 2005; Lucas et al., 2011; Voigt & Lucas, 2015; Voigt & Lucas, 2017), Europe (Makowsky & Rzehak, 1884; Frič, 1901; Pabst, 1908a, 1908b; Gand, 1987; Voigt, 2005; Voigt et al., 2012, Gand & Durand, 2006; Avanzini et al., 2011; Marchetti et al., 2015a, 2015b; Mujal et al., 2016), and North Africa (Voigt et al., 2011a, 2011b). The circular structure on NM M4949a (Figs. 10A–10B) likely formed as a result of gas escaping from the sediment after it was compressed by passing tetrapods.

Discussion

Spatiotemporal significance of vertebrate ichnoassemblage

The tetrapod ichnofauna is generally much more widespread than the body fossils of their trackmakers. Therefore ichnological record plays a crucial role for tracing the spatiotemporal distribution of specific tetrapod groups, especially where the body fossils of terrestrial fauna are missing (Fig. 2). The tetrapod ichnoassemblage from the Semily Fm. revealed the very early occurrences of *Amphisauropus* tracks (ČGS JZ 626, 632) from the Ploužnice Horizon, which represents the second oldest occurrence of these ichnotaxon worldwide and at the same time the first occurrence from the Late Pennsylvanian. Although *Amphisauropus* was mentioned by

Haubold & Katzung (1975) as originating from the Ploužnice Horizon (material stored at the Czech Geological Survey), this specimen has never been described or figured in their study and most probably corresponds to the *Limnopus* track (Ge CGS XA741) in our present study. The identification of *Amphisauropus* tracks in the Late Pennsylvanian deposits of the KPB carries significant implications for understanding the spatiotemporal distribution of Seymouriamorpha. While skeletal remains of this group are predominantly known from the lower Permian strata across North America, Europe, and around the Urals (Amalitzky, 1921; White, 1939; Tchudinov & Vjuschkov, 1956; Tatarinov, 1968; Ivakhnenko, 1981; Berman et al., 1987; Berman & Martens, 1993; Klembara, 1995, 2005, 2009a, 2009b; Sullivan & Reisz, 1999; Klembara & Bartík, 2000; Bulanov, 2003, Klembara et al. 2020, 2013, Calábková et al., 2022), our ichnofossil record, together with the *Amphisauropus* find from the Middle Pennsylvanian of the USA (Lucas & Stimson, 2025) fundamentally support their earlier presence in the Pennsylvanian.

Ichniotherium cottae (MZM Ge34184; Figs.9A–9B) from the Štikov, which falls into the lower part of the Semily Fm. (Stephanian C; Fig. 2) represents a rare occurrence of this ichnospecies from the European part of Pangaea in the Pennsylvanian. The morphology of *I. cottae* tracks and trackways is well comparable to the autopodia and body posture of representatives of Diadectomorpha (see Voigt et al., 2007; Buchwitz & Voigt, 2018). Although *Ichniotherium* is widespread from the Permian deposits of the KPB (Frič, 1887, 1912) and the nearby Intra-Sudetic Basin (Voigt et al., 2012; Voigt et al., 2024) and the Boskovice Basin (Calábková et al. 2023; Fig. 1A), these tracks still provide the only evidence about the presence of diadectomorphs in the Pennsylvanian of Czechia. Since diadectomorphs belong to one of the oldest lineages of herbivorous tetrapods that evolved the ability to consume and process plant matter with a high fiber content (e.g., Beerbower, Olson & Hotton, 1992; Hotton, Olson & Beerbower, 1997; Sues, 2000) their occurrence in a lake ecosystem extremely rich in flora (Fig. 2) is ~~more than~~ expected. The discovery of *Limnopus* (Fig. 8), published for the first time in Czechia, significantly expands our understanding of Pennsylvanian large temnospondyl distribution in basins of the Central European Variscan Belt. While *Limnopus* trackmakers are generally accepted as medium to large-sized temnospondyls, particularly members of the Eryopidae clade (Baird, 1965; Gand, 1987; Haubold, 2000; Voigt, 2005), skeletal fossil record of such large temnospondyls in the KPB ~~is~~ rare and restricted only to younger Asselian strata (Fig. 2). These include eryopid and archegosaurid temnospondyls from the Vrchlabí Fm. (Steen, 1938; Milner, 1981; Zajíc & Štamberg, 2008) and an unspecified eryopid from the Prosečné Fm. (Štamberg 2014). The occurrence of tracks (MZM Ge34174, Figs. 8E–8F) left by large temnospondyl in the Semily Fm. corresponds well with the abundant fish fossils (Fig. 2), because representatives of eryopids or stereospondylomorphs were mostly piscivorous (Boy 2003; Schoch 2021).

Similarly, smaller *Batrachichnus* tracks point to the presence of small-sized temnospondyls (Haubold 1996; Voigt 2005; Stimson et al. 2012) or even lepospondyls (Stimson et al. 2012; Allen et al. 2022). To date, no body fossils of lepospondyls have been discovered in the KPB, whereas Frič (1912a, 1912b) provided limited skeletal evidence of temnospondyls in his description of scarce remains of unspecified branchiosaurids from the Kyje–Ploužnice railway cut.

Dimetropus tracks are typically attributed to various non-therapsid synapsid groups, such as mostly carnivorous sphenacodontians, piscivorous ophiacodotids, or herbivorous edaphosaurids, and casesaurs (Tilton, 1931; Romer & Price, 1940; Haubold, 1971, 2000; Fichter, 1979; Voigt, 2005; Niedźwiedzki & Bojanowski, 2012; Voigt & Ganzelewski, 2010; Sacchi et al., 2014;

Romano et al., 2016). Skeletal evidence for early-diverging synapsids in Czechia is extremely rare and includes only *Macromerion schwarzenbergii*, discovered by Fritsch (1875) in the Pennsylvanian deposits of the Kounov locality (Gzhelian, Stephanian B) within the Slaný Fm., Kladno–Rakovník Basin (Fig. 1A). This locality also yielded an isolated dorsal vertebra of edaphosaurid *Bohemiclavulus mirabilis* (Fritsch, 1895). Additionally, an element of the dorsal spine of the edaphosaurid *Ramodendron obvispinosum* was discovered in the Gzhelian strata (Stephanian C) of the nearby Boskovice Basin (Švestka, 1944). Studied ichnofossils of *Dimetropus* (Fig. 9I) demonstrates the earlier presence of synapsids in the Pennsylvanian of KPB. The fossil record of the Ploužnice Horizon suggests that the Pennsylvanian ecosystem of the Krkonoše Piedmont Basin provided adequate food resources for both herbivorous and carnivorous synapsids (Fig. 2).

Dromopus is undoubtedly the most abundant vertebrate ichnofossil in Gzelian deposits of the KBP. These tracks are referred to bolosaurid parareptile, aeroscelid diapsid or non-varanodontine varanopid trackmakers (e.g., Haubold, 1971, 2000; Voigt, 2005; Marchetti et al., 2021). Notably, no skeletal remains of provable early sauropsids or varanopid synapsids have been reported directly from this area (Fig. 2). Only the unrevised material of potential sauropsids, tentatively assigned to "?*Macromerion*", was figured by Fritsch (1885) from the Kounov locality (Gzhelian, Stephanian B) in the Kladno–Rakovník Basin. Additionally, the unrevised *Sphenocaurus sternbergii*, figured by Fritsch (1885), comes from unknown locality in Bohemia, which Štamberg and Zajíc (2008) described as an "unknown Lower Permian locality (the red sandstone probably comes from the Krkonoše Piedmont Basin or from the Intra-Sudetic Basin)". The extremely rich discoveries of *Dromopus* footprints from the KPB (Fig. 10) contribute significantly to our understanding of the initial diversification of amniotes, especially in areas where the fossil record of bodies is very limited. The abundant fossil insect finds in the Ploužnice Horizon may also indicate good food availability for these early sauropsids.

Beyond the KPB, the only other Carboniferous tetrapod traces documented in Czechia come from the Radnice Member (Westphalian C, Pennsylvanian) of the Pilsen Basin including *Gracilichnium* (?) *chlupaci* and *Lunichnium gracile*, interpreted as temnospondyl swimming, walking, and resting traces (Turek, 1989) and tetrapod footprints not described in more detail from the Žacléř Fm. (upper part of the Lampertice Member, Westphalian A, Pennsylvanian) (Opluštil et al. 2022b). Therefore, the tetrapod ichnoassemblage of the KPB is exceptionally crucial for understanding the diversity and evolution of terrestrial tetrapods in this intra-Variscan part of equatorial Pangea.

Palaeoecological implications

The Štikov section is interpreted as deposits of a river mouth, possibly a braided delta, where individual gravel- or sand-filled distributary channels incised into violet-grey mudstones – i.e., lacustrine nearshore deposits. The lacustrine deposits are interpreted here as a result of the expansion of the Ploužnice Lake during a more humid period in the latest Pennsylvanian (Fig. 11) – a trend recorded by the contemporary Líně Fm. in central and western Bohemia (Nádaskay et al., 2025). Upsection, the colour change into red indicates lake-shore retreat and formation of a nearshore mudflat, accessible to the diadectomorph as well as eventually sauropsid and temnospondyl trackmakers.

The Kyje section can be interpreted in terms of cyclic alternation of fluvial–alluvial and lacustrine environment of the so-called Ploužnice Lake (Fig. 11). The lowest of three identified cycles (cf. Blecha et al., 1997), with predominant reddish-brownish sediments, represents a vertical transition from lacustrine nearshore with intense clastic supply, probably close to a river mouth (Fig. 11) as evidenced by numerous sandstone bodies interpreted as mouth bars or alluvial bars, and one possibly incised alluvial or delta-plain channel. These are overlain by deposits of lacustrine coastal mudflat topped by a pedogenic horizon (Fig. 4B) that could be interpreted as a vertic calcisol, which indicates emergence of the lake coast for a longer period of time under predominantly dry climate with seasonal precipitation (Fig. 11; cf. Mack and James, 1994). The overlying cycle is interpreted as a transition from the nearshore to the more distal portion of the lake. The tetrapod footprints were found in fine-grained sandstones in the lowermost part of this cycle, and were accompanied by mud drapes (sometimes with wrinkled surface possibly left by microbial mats), mudcracks and occasional rain-drop impressions and invertebrate burrows (Fig. 5, Fig. 11). These features point to a sandy lake nearshore that repeatedly emerged for a relatively short period of time (cf. Melchor & Sarjeant, 2004; Minter et al., 2007; Mujal et al., 2016), because no significant rooting or pedogenic features are present. Similar environment can be interpreted from the topmost part of the section above the more distal lacustrine deposits. The footprints were left by early sauropsids, non-therapsid synapsids, diadectomorphs, seymouriamorphs as well as temnospondyls, which roamed these areas during periods of low water level (up to only a few cm). The abundance of footprints suggests that the lake ecosystem was a sought-after habitat for terrestrial and semi-terrestrial tetrapods, whether as a source of water, food, or a place for reproduction.

Concentric structures (Figs. 10A–10 B) associated with *Dromopus* tracks, some of which are overlain by these concentric structures, are the most likely eroded subaerial parts of sand volcanoes that formed after the footprints. Formation of sand volcanoes is most commonly driven by dewatering related to earthquakes (e.g., Montenat et al., 2007; van Loon & Maulik, 2011), it is possible that in this case they were generated by liquefaction of unconsolidated sand underlying the surface on which the trackmaker roamed. Build-up of pressure within the sandbed that preceded the "explosion" of a sand volcano (Owen, 1996) could have been ensured by sealing mud layer covering the sandbed. Although sand volcanoes are among frequently-occurring structures of inorganic origin at vertebrate footprint sites (e.g., Thulborn, 1990), their direct relationship to footprints – i.e., by loading of sandbed by passing trackmaker, has not been discussed, and other soft-sediment deformation structures were interpreted to be produced by trackmakers (e.g., Plint et al., 2025). The formation of sand volcanoes has also been attributed to the accumulation of gases from microbial mats (e.g., Smith et al., 2009; Taj et al., 2014), which were likely present at the margins of the Ploužnice Lake, as indicated by wrinkle structures on mud drapes.

In contrast, fossil-rich "bonebeds" are found within decidedly distal deposits of open lake, since they contain bone fragments of predominantly aquatic (nektonic) vertebrates such as sharks, fishes and acantodes (Fig. 2). Sparse body fossils found in grey or violet–grey mudstones also evidence relatively open-lake environment, probably shallow and well-oxygenated (Blecha et al., 1997).

The sedimentary record of both studied localities allows for the interpretation of the lacustrine environment (Ploužnice Lake) that occupies the central part of the basin, fed by fluvial systems entering the basin from south, forming fan deltas (Štikov) or more widely distributed fluvial deltas on a flatter basin margin (Kyje). The evolution of the Ploužnice Lake (Fig. 11) was strongly influenced by relatively short-term (100–400 Kyr) climate fluctuations reflected by the decrease and increase in precipitation, as suggested by the evolution of a coeval depositional system of the Líně Fm. (with Klobuky Lake) in central Bohemia (Nádaskay et al., 2025). The Pennsylvanian taxonomic diversity probably outlasted the Carboniferous-Permian boundary as palaeodiversity of Semily Fm. seems to be comparable to that of Vrchlabí Fm. (Fig. 2). During the deposition of fossiliferous horizons such as the Ploužnice, Rudník, and others (Fig. 2), conditions were more favourable for the preservation of fossils. This suggests that the apparent scarcity of the fossil record in the KPB prior to the deposition of the Ploužnice Horizon in the Gzhelian or after deposition of the Kalná Horizon during Asselian is more likely a result of taphonomic bias than an actual decrease in biodiversity in the KPB.

Conclusions

The uppermost Carboniferous deposits of the Semily Fm. (Gzhelian, Stephanian C) in the KBP have revealed the presence of six ichnotaxa, assigned to the ichnogenera *Amphisauropus isp.*, *Batrachichnus salamandroides*, *Dimetropus* isp., *Dromopus lacertoides*, *Ichniotherium cottae*, and *Limnopus heterodactylus*. These ichnotaxa are attributed to seymourimorphs, temnospondyls, diadectomorphs, early sauropsids and non-therapsid synapsids, which fills critical gaps given by the extremely sparse body fossil record, providing invaluable insights into the faunal composition and ecological dynamics of early tetrapod ecosystems during this pivotal period in terrestrial evolution.

Late Paleozoic limnic basins such as the KPB were likely crucial for the survival of terrestrial and semi-terrestrial tetrapods in the continental interior environment of the Variscan Belt. Fluctuations in the lake water level played a key role in preserving their footprints, which often represent the only direct evidence of their presence in this area. The diversity of ichnotaxa makes this site the richest locality for Upper Pennsylvanian tetrapod footprints. Taxonomic diversity in the KPB appears to have persisted without major changes until the beginning of the early Permian.

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Institutional abbreviations

CGS; Czech Geological Survey, Prague, Czechia**, MZM**; Moravian Museum, Brno, Czechia, **NM**; National Museum, Prague, Czechia, **NPM**; Nova Paka City Museum, Nová Paka, Czechia.

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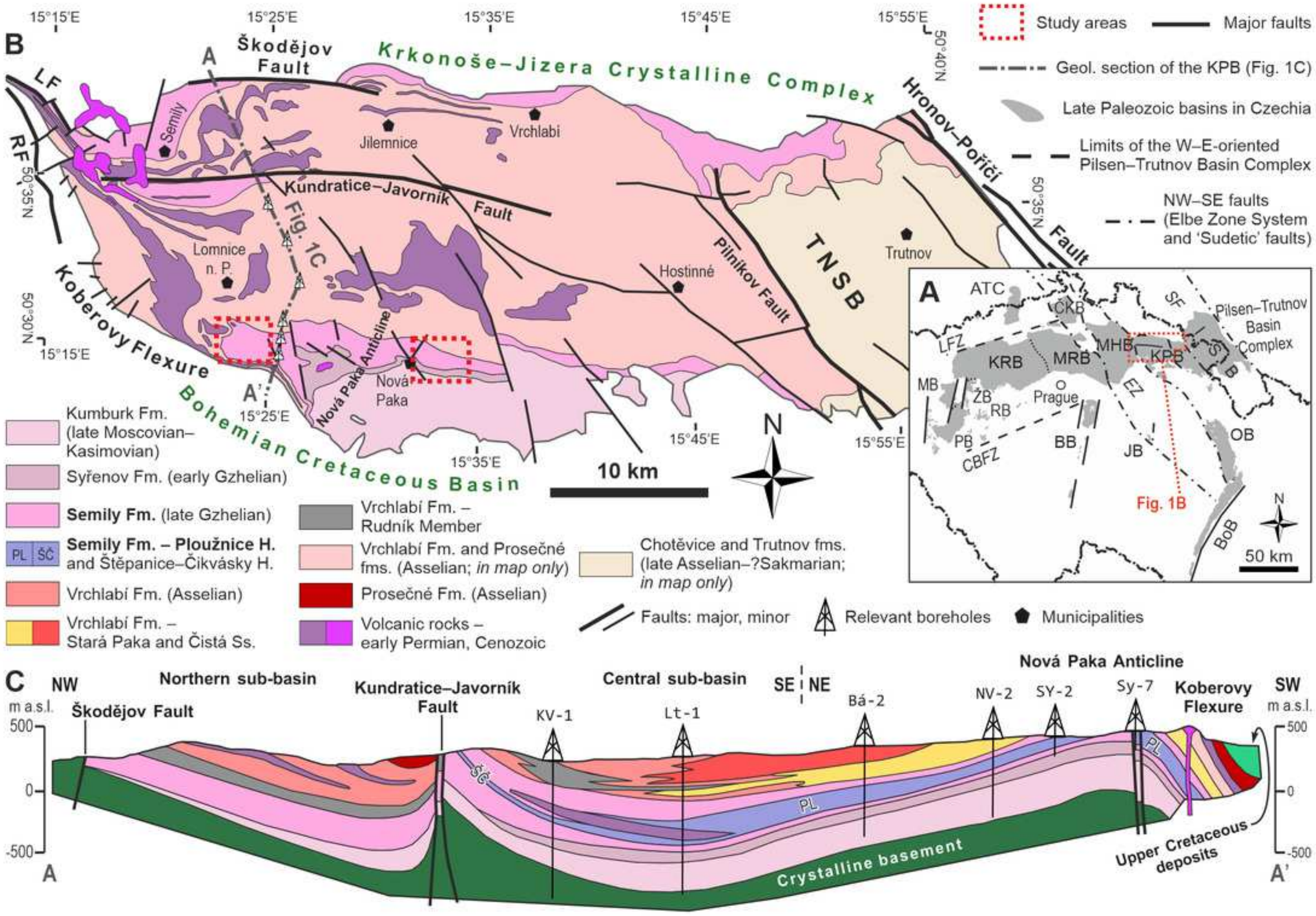
Figure 1

Location of the studied area.

(A) Present-day situation of the Late Paleozoic continental basins of the Bohemian Massif (Opluštil et al., 2013a, amended). Abbreviations: ATC – Altenberg–Teplice Caldera, BB – Blanice Graben, BoB – Boskovice Graben, CBFZ – Central Bohemian Fault Zone, ČKB – Česká Kamenice Basin, EZ – Elbe Zone, ISB – Intra-Sudetic Basin, JB – Jihlava Graben, KPB – Krkonoše Piedmont Basin, KRB – Kladno–Rakovník Basin, LFZ – Litoměřice Fault Zone, MB – Manětín Basin, MHB – Mnichovo Hradiště Basin, MRB – Mšeno–Roudnice Basin, OB – Orlice Basin, PB – Pilsen Basin, RB – Radnice Basin, SF – Sudetic faults, ŽB – Žihle Basin. (B) A detailed map of the KPB (compiled after Martínek et al., 2006; Stárková et al., 2010, 2017, and Prouza et al., 2013). Study areas indicated. Abbreviations: LF – Lusatian Fault; RF – Rovensko Fault; TNSB – Trutnov–Náchod sub-basin. (C) Geological section of the western part of the KPB (amended after V. Prouza in Pešek, 2001, and Stárková et al., 2010). Location of the section indicated in Fig. 1B.



Study areas
Major faults
Geol. section of the KPB (Fig. 1C)
Late Paleozoic basins in Czechia
Limits of the W–E-oriented Pilsen–Trutnov Basin Complex
NW–SE faults (Elbe Zone System and 'Sudetic' faults)
Krkonoše–Jizera Crystalline Complex
Bohemian Cretaceous Basin
Škodějov Fault
Kundratice–Javorník Fault
Koberovy Flexure
Pilníkov Fault
Hronov–Poříčí Fault
Nová Paka Anticline
TNSB
Kumburk Fm. (late Moscovian–Kasimovian)
Syřenov Fm. (early Gzhelian)
Semily Fm. (late Gzhelian)
Semily Fm. – Ploužnice H. and Štěpanice–Čikvásky H.
Vrchlabí Fm. (Asselian)
Vrchlabí Fm. – Stará Paka and Čistá Ss.
Vrchlabí Fm. – Rudník Member
Vrchlabí Fm. and Prosečné fms. (Asselian; in map only)
Prosečné Fm. (Asselian)
Volcanic rocks – early Permian, Cenozoic
Chotěvice and Trutnov fms. (late Asselian–?Sakmarian; in map only)
Faults: major, minor
Relevant boreholes
Municipalities
10 km
50 km
Pilsen–Trutnov Basin Complex
Fig. 1B
Northern sub-basin
Central sub-basin
Crystalline basement
Upper Cretaceous deposits

Figure 2

Interpretation of palaeodiversity in the Krkonoše Piedmont Basin based on the fossil record.

Taxa highlighted in red represent those known only from ichnological evidence. Stratigraphy follows Opluštil et al. (2016). Lithologic column modified after Stárková et al. (2015). Fossil record data are compiled from Fritsch (1895, 1901), Frič (1912a, 1912b), Kamarád (1951, 1959), Rieger (1958, 1968), Pešek et al. (2001), Zajíc (2007, 2014), Štamberg & Zajíc (2008), Opluštil et al. (2016, 2022), Mencl et al. (2013), Schneider et al. (2020), and Štamberg (2018, 2023).

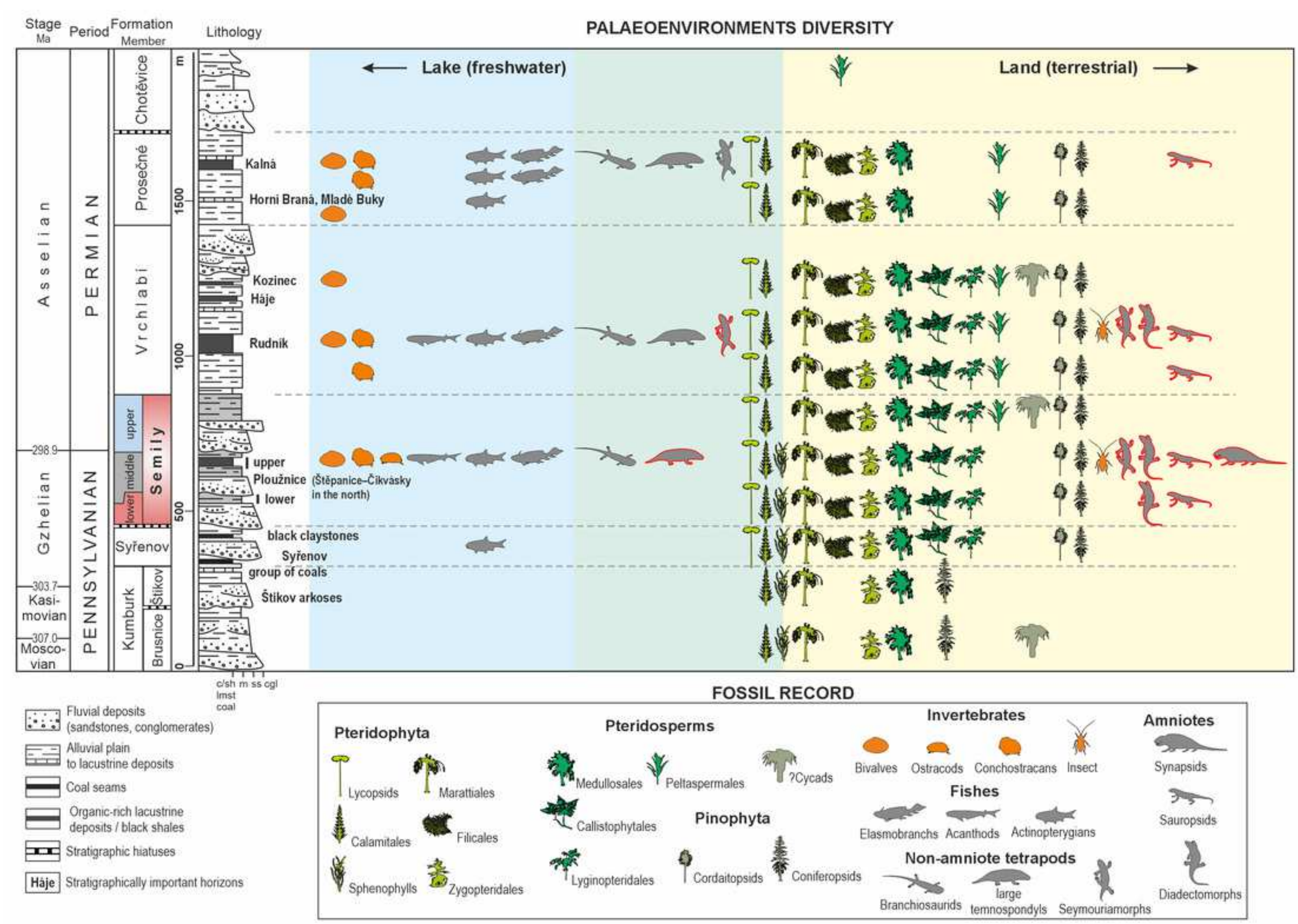


Figure 3

Geological conditions of the studied area.

(A) A geological map of the vicinity of the studied locality Kyje–Ploužnice railway cut. Amended after Stárková et al. (2013). (B) A geological map of the vicinity of the studied locality Štikov roadcut, on a road construction site east of Nová Paka. Amended after Stárková et al. (2017). The entire railway cut (C) with lithological variability and tectonic deformation of the Ploužnice Horizon was first depicted by Purkyně (1929). The schematic lithological profile of road cut Nová Paka–Vidochov (D) under Ploužnice Horizon.

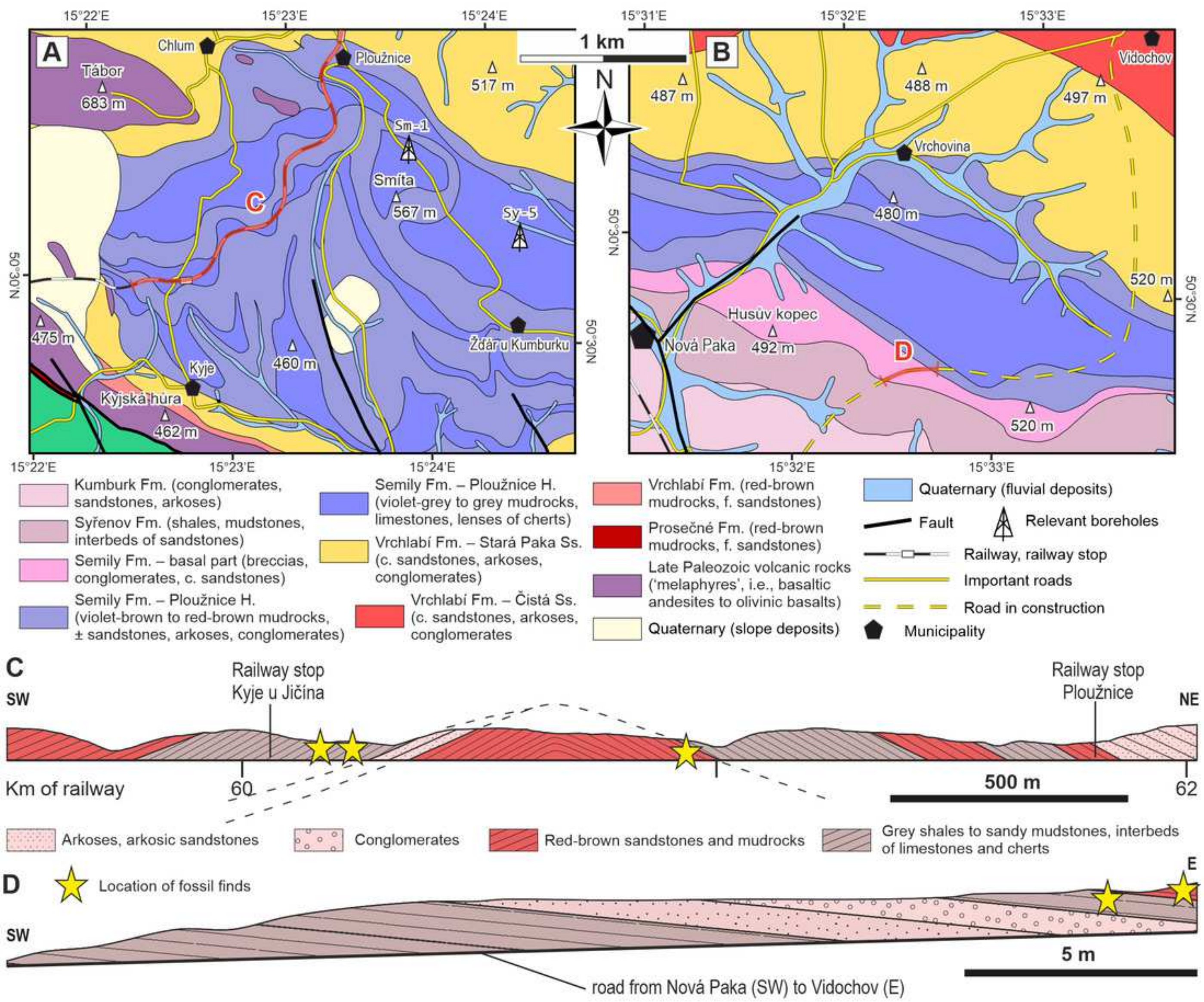

A
B
1 km
N
15°22'E
15°23'E
15°24'E
15°31'E
15°32'E
15°33'E
50°30'N
Chlum
Tábor
683 m
Ploužnice
517 m
Sm-1
Smíta
567 m
Sy-5
C
475 m
460 m
Žďár u Kumburku
Kyje
Kyjská hůra
462 m
Vidochov
487 m
488 m
497 m
Vrchovina
480 m
520 m
Husův kopec
Nová Paka
492 m
D
520 m
Kumburk Fm. (conglomerates, sandstones, arkoses)
Syřenov Fm. (shales, mudstones, interbeds of sandstones)
Semily Fm. – basal part (breccias, conglomerates, c. sandstones)
Semily Fm. – Ploužnice H. (violet-brown to red-brown mudrocks, ± sandstones, arkoses, conglomerates)
Semily Fm. – Ploužnice H. (violet-grey to grey mudrocks, limestones, lenses of cherts)
Vrchlabí Fm. – Stará Paka Ss. (c. sandstones, arkoses, conglomerates)
Vrchlabí Fm. – Čistá Ss. (c. sandstones, arkoses, conglomerates
Vrchlabí Fm. (red-brown mudrocks, f. sandstones)
Prosečné Fm. (red-brown mudrocks, f. sandstones)
Late Paleozoic volcanic rocks ('melaphyres', i.e., basaltic andesites to olivinic basalts)
Quaternary (slope deposits)
Quaternary (fluvial deposits)
Fault
Relevant boreholes
Railway, railway stop
Important roads
Road in construction
Municipality
C
SW
Railway stop Kyje u Jičína
Railway stop Ploužnice
NE
Km of railway
60
62
500 m
Arkoses, arkosic sandstones
Conglomerates
Red-brown sandstones and mudrocks
Grey shales to sandy mudstones, interbeds of limestones and cherts
D
Location of fossil finds
E
SW
5 m
road from Nová Paka (SW) to Vidochov (E)

Figure 4

Photographs of the studied localities.

(A) The western end of the locality Kyje – railway cut with predominantly violet–grey-coloured mudstones with interbeds of very fine- to fine-grained sandstones (occasionally with volcaniclastic layers and cherts) exposed on both sides of the railcut. Railcut walls are up to 10 m high in places. Red-beds are visible in the background. (B) Red-beds in the middle part of the locality Kyje – railway cut. The palaeosol with abundant carbonate nodules and conspicuous vertic structures is overlain by a succession of reddish–brownish very fine- to fine-grained sandstones with thin interbeds of mudstones. A hammer for scale. (C) A slab of reddish sandstone with 3D ripples covered by a thin mud drape. Kyje – railway cut , middle part of the section (red-beds). (D) An example of raindrop impressions (negative) accompanied by rills produced by surface runoff. These features indicate that at the time, the mudflat was emerged. Kyje – railway cut , middle part of the section (red-beds). (E) Irregular structures, possibly a form of wrinkle structures (cf. Porada & Bouougri, 2007) possibly formed by bacteria colonizing the sediment surface in the shallow-water pool on the mudflat. Kyje – railway cut , middle part of the section (red-beds).(F) Fine-grained sandstone with intense invertebrate burrows.[Roland Ná1] Kyje – railway cut , middle part of the section (red-beds). (G) An example of mud cracks (filled with fine sand) preserved in a slab of pale grey mudstone from the upper part of the section Kyje – railway cut . (H) Conglomerates of the basal part of the Semily Fm. Conglomerates are clast-supported, relatively poorly-sorted, with rounded clasts of predominantly vein quartz and micaschists. Locality Štikov – roadcut. (I) A boundary between Syřenov and Semily formations at the locality Štikov – roadcut. Syřenov Fm. is represented here by whitish arkoses overlain by incised reddish conglomerates (Fig. 4H) of the Semily Fm. Note the bed inclination in conglomerates. A hammer for scale. (J) Upper part of the section at the locality Štikov – roadcut displaying grey mudstones overlain by reddish conglomerate. A hammer for scale.

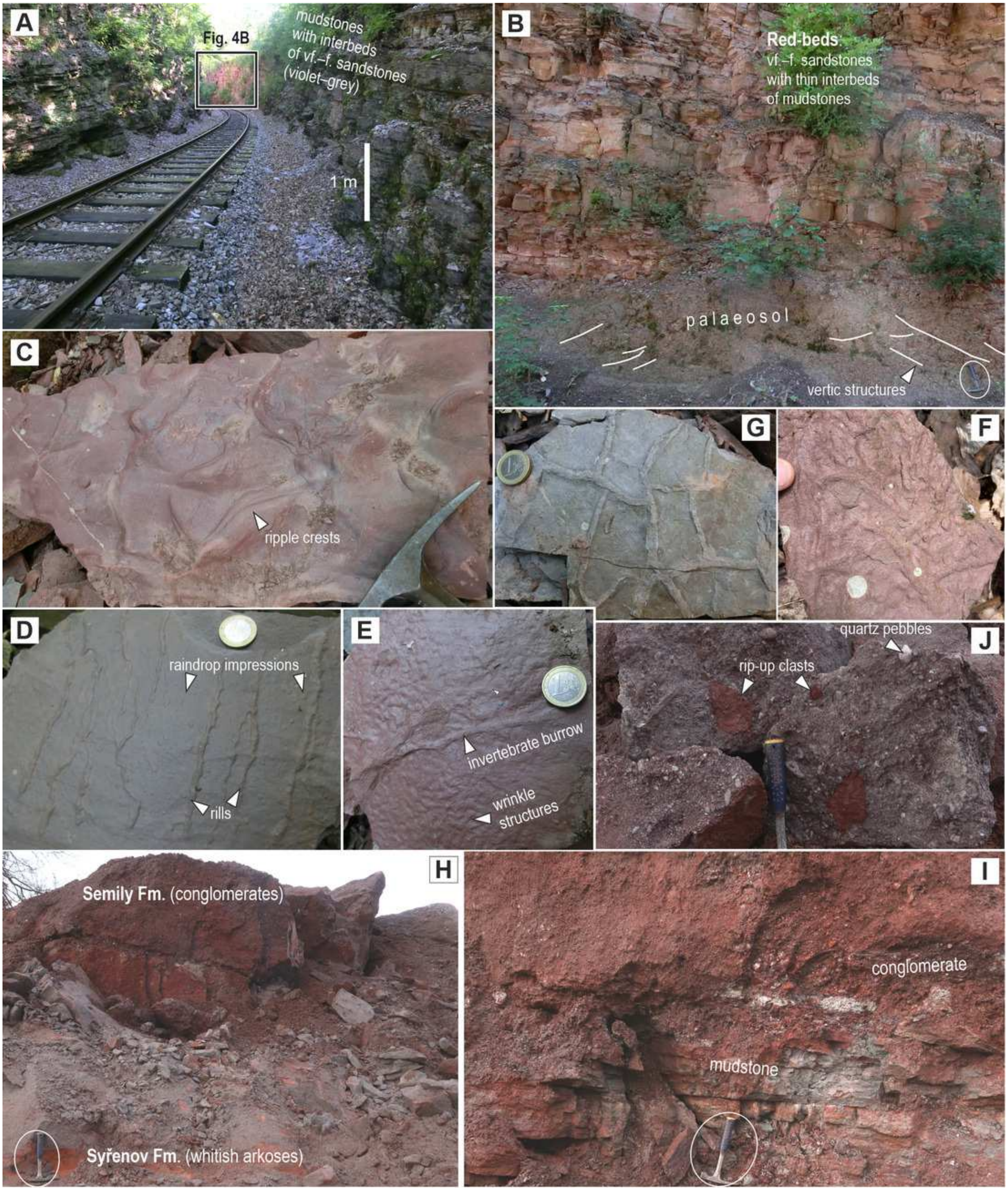


Figure 5

Sedimentary logs of studied localities.

(A) Kyje – railway cut; (B) Štikov – roadcut Nová Paka–Vidochov. Position of tetrapod footprints excavated in 2024 and 2025 is indicated.

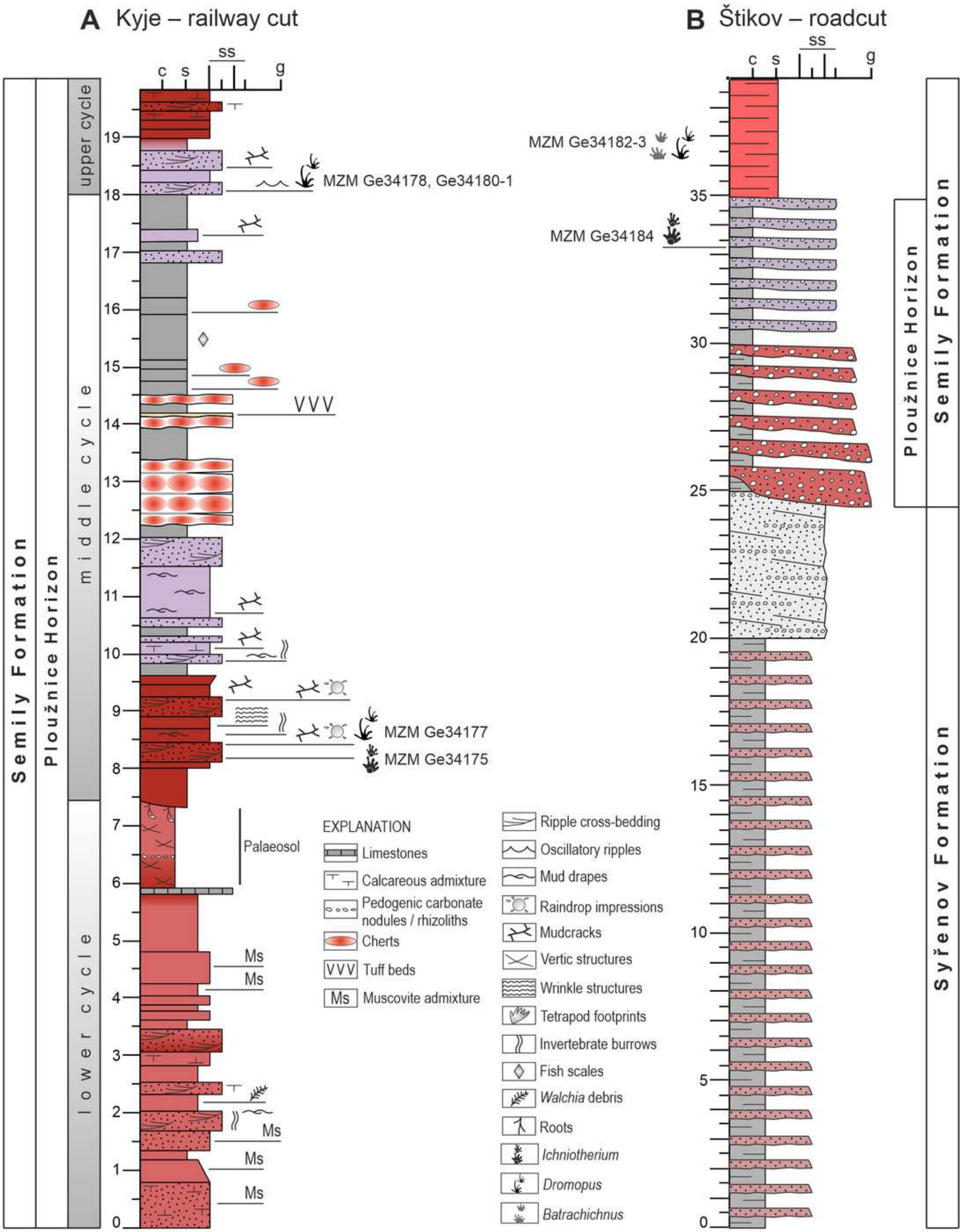

A Kyje – railway cut
B Štikov – roadcut
Semily Formation
Ploužnice Horizon
upper cycle
middle cycle
lower cycle
Syřenov Formation
c s ss g
MZM Ge34178, Ge34180-1
MZM Ge34177
MZM Ge34175
MZM Ge34182-3
MZM Ge34184
VVV
Palaeosol
Ms
EXPLANATION
Limestones
Calcareous admixture
Pedogenic carbonate nodules / rhizoliths
Cherts
Tuff beds
Muscovite admixture
Ripple cross-bedding
Oscillatory ripples
Mud drapes
Raindrop impressions
Mudcracks
Vertic structures
Wrinkle structures
Tetrapod footprints
Invertebrate burrows
Fish scales
Walchia debris
Roots
Ichniotherium
Dromopus
Batrachichnus

Figure 6

Amphisauropus isp.

(A) CGS JZ626, incomplete trackway, convex hyporelief, (B) magnified manus imprint, (C) and manus imprint accompanied by incomplete preserved pes imprint, (D) Outline drawing of the trackway.

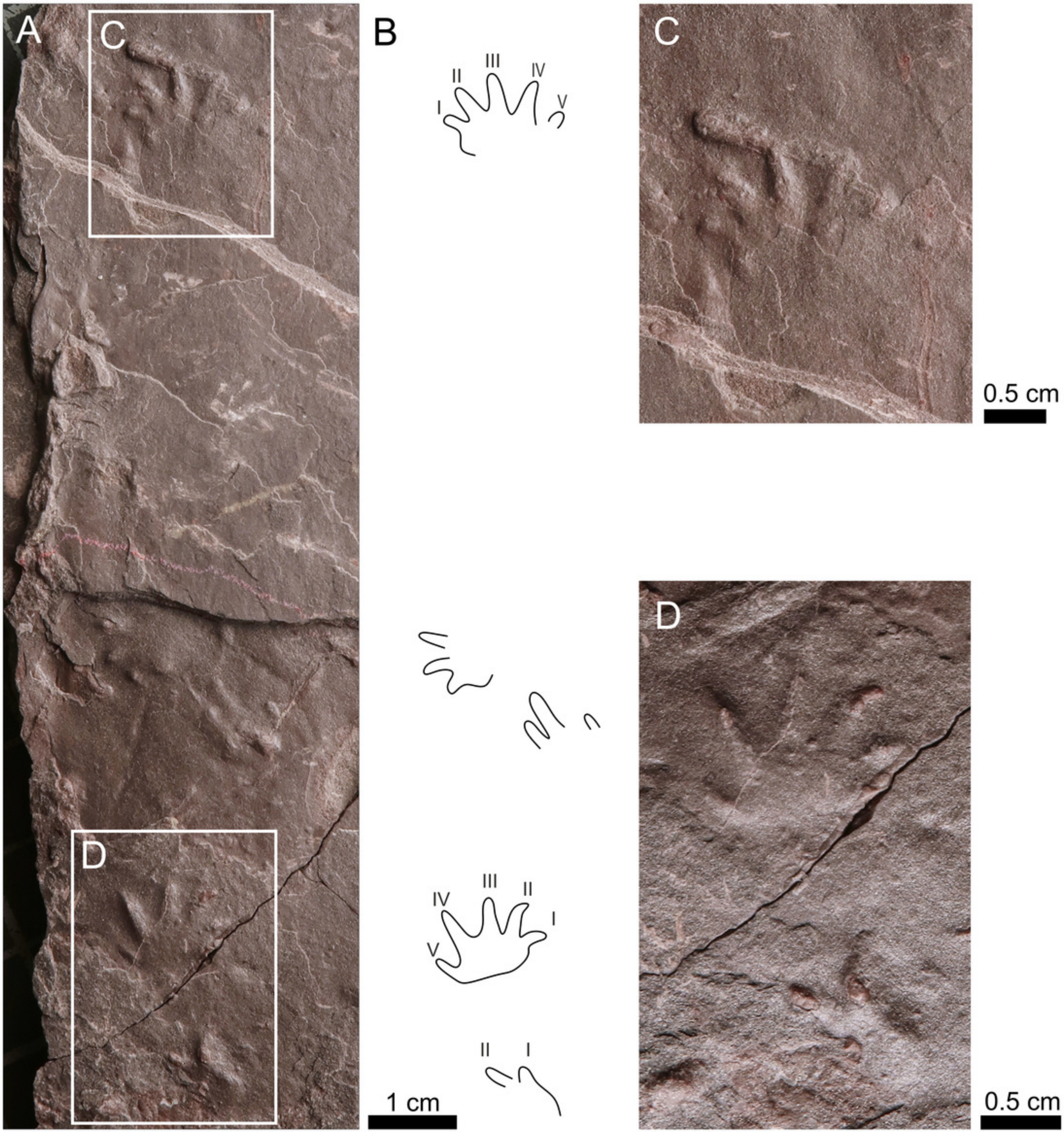

A
C
B
II
III
IV
I
V
IV
III
II
I
V
II
I
1 cm
C
0.5 cm
D
D
0.5 cm

Figure 7

Batrachichnus salamandroides

(A) CGS XA738, trackway , convex hyporelief; (B) outline drawing of CGS XA738; (C) MZM Ge31124, isolated three tracks (tetradactyl manus and two pentadactyl pes imprints), convex hyporelief, (D) outline drawing of MZM Ge31124.

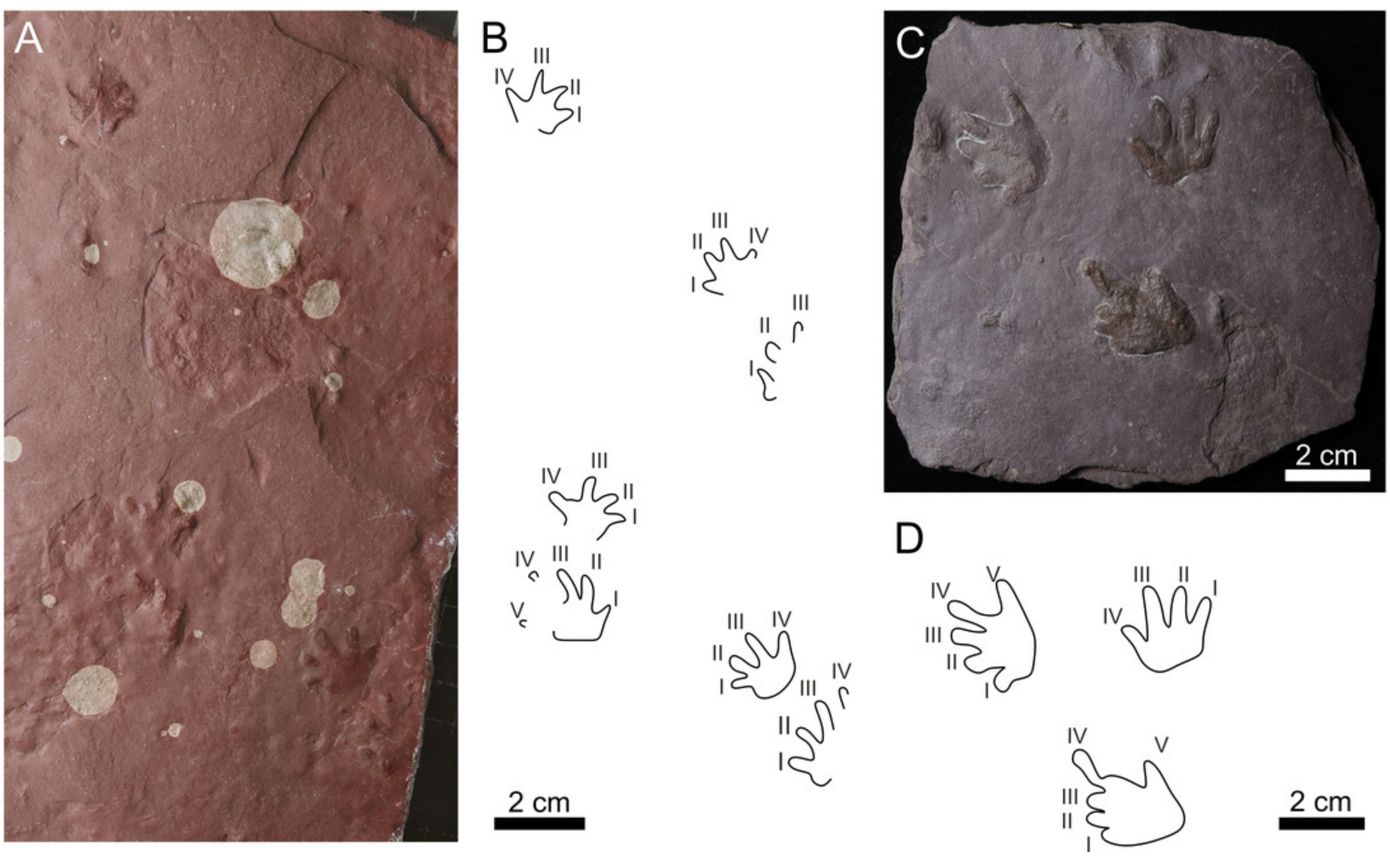


Figure 8

Limnopus heterodactylus

(A) NMP P3573, manus-pes couple, convex hyporelief, (B) outline drawing of NMP P3573; (C) CGS XA741, manus-pes couple, convex hyporelief; (D) outline drawing of CGS XA741; (E) *Limnopus* isp., MZM Ge34174, incomplete manus-pes couple, convex hyporelief.

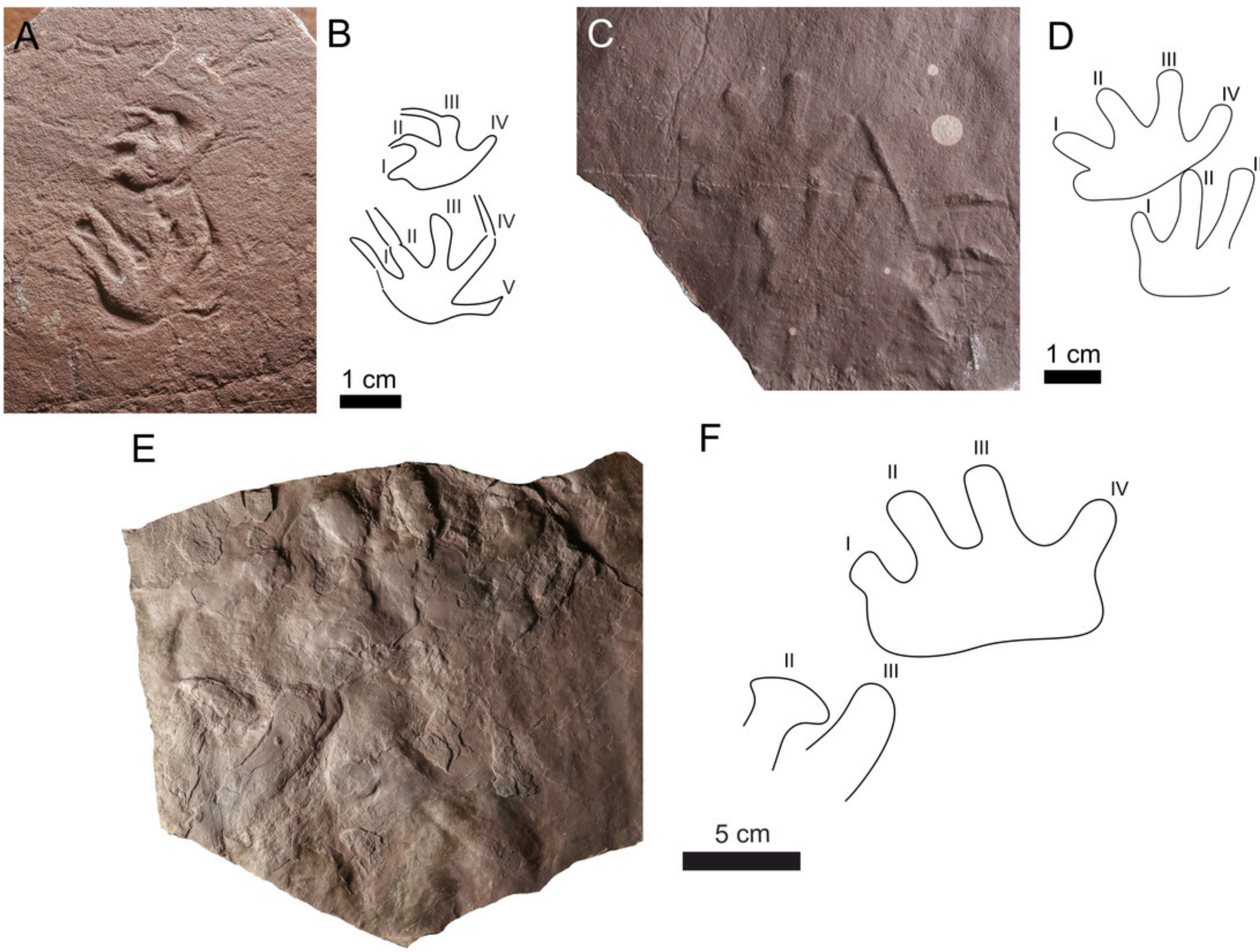


Figure 9

Ichniotherium and *Dimetropus* tracks.

(A) MZM Ge34184, *Ichniotherium cottae*, manus-pes couple with two isolated tracks, convex hyporelief,; (B) outline drawing of MZM Ge34184; (C) NMP P103, *Ichniotherium cottae*, isolated pes imprint, concave epirelief (D) outline drawing of NMP P103; (E) CGS XA 737, *Ichniotherium cottae*, manus-pes couple, convex hyporelief, (F) outline drawing of CGS XA 737; (G) NMP P307, *Ichniotherium cottae*, manus imprint, concave epirelief,; (H) outline drawing of NMP P307, (I) NMP P103, *Dimetropus* isp., manus-pes couple, concave epirelief.

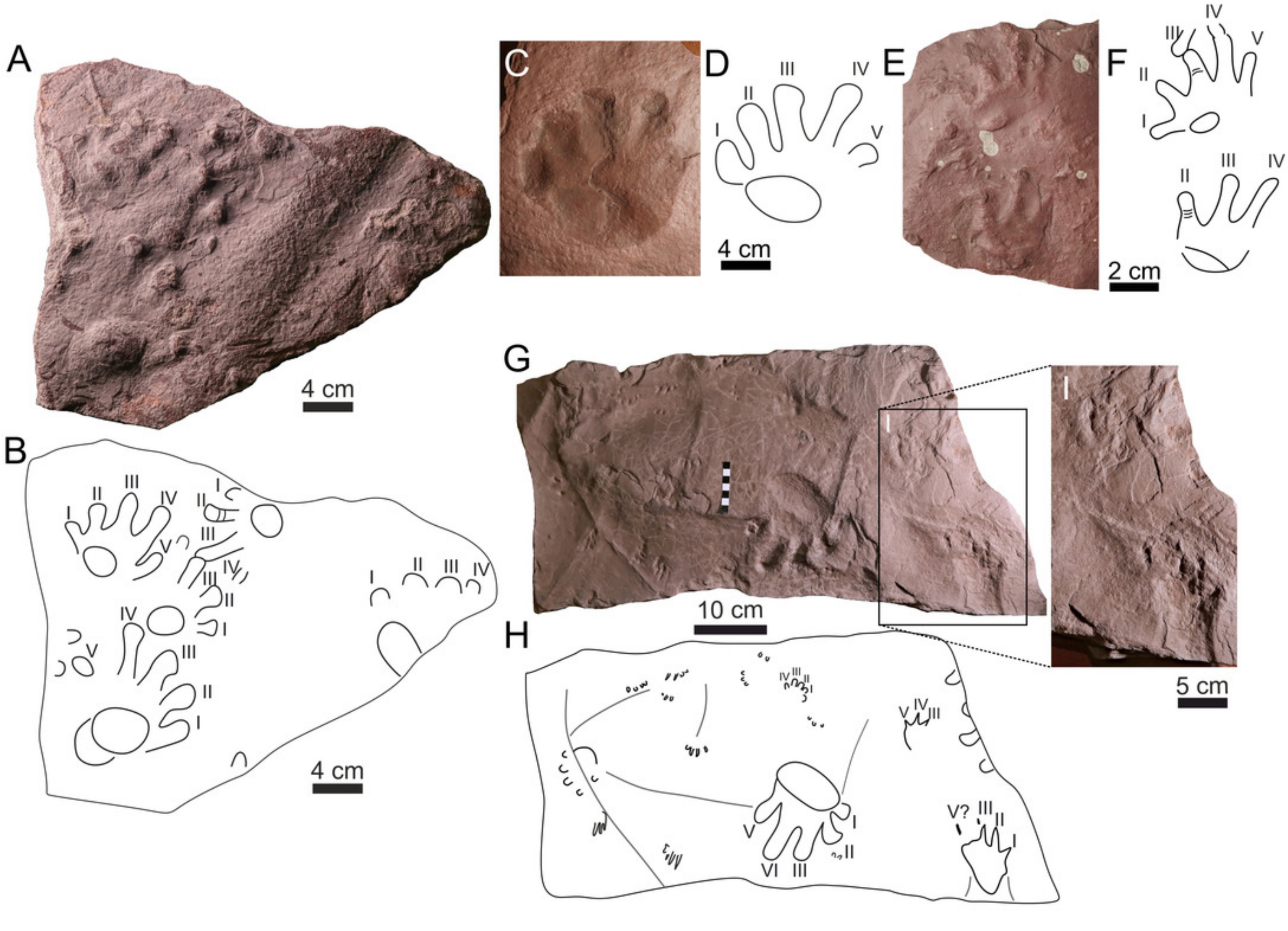


Figure 10

Dromopus lacertoides

(A) NM M4949a, several trackways, concave epirelief; (B) outline drawing of NM M4949a; (C) MZM Ge34176, manus-pes couple and two isolated track, convex hyporelief; (D) outline drawing of MZM Ge34176; (E) ČGS XA742, two tracks, convex hyporelief (F) outline drawing of ČGS XA742.

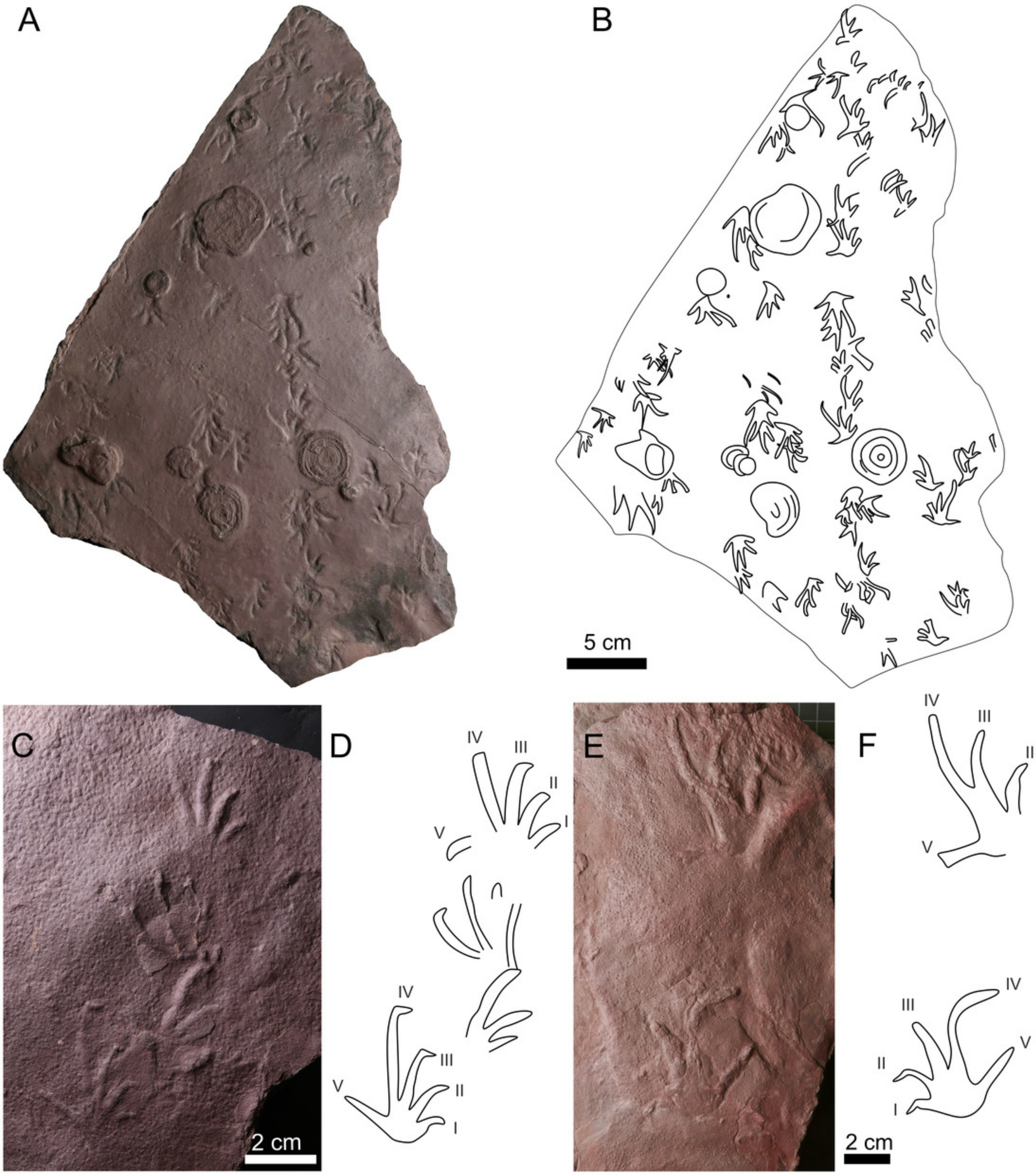
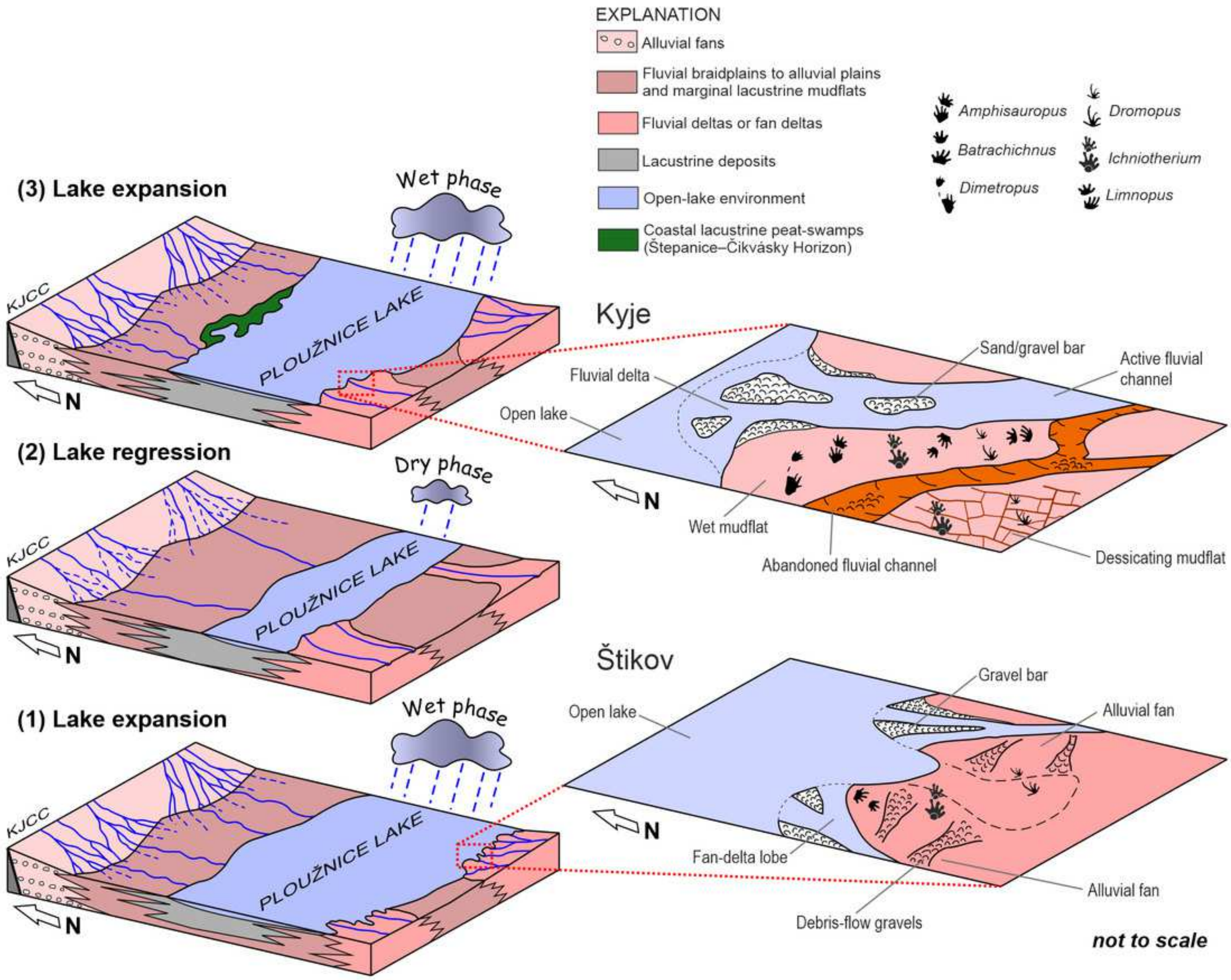

A
B
5 cm
C
2 cm
D
IV
III
II
I
V
IV
III
V
II
I
E
F
IV
III
II
V
IV
III
V
II
I
2 cm

Figure 11

Blockdiagrams.

A series of blockdiagrams illustrating a development of Ploužnice Lake as interpreted from studied sections (Kyje, Štikov) and data to Ploužnice Horizon by Blecha et al. (1997). Alternation of wet and dry climate phases that controlled the extent of the Ploužnice Lake has already been interpreted from contemporaneous deposits of the Líně Fm. in central Bohemia (Nádaskay et al., 2025). Close-ups display a detailed interpretation of depositional environment in which the trackmakers roamed and left their traces.


EXPLANATION
Alluvial fans
Fluvial braidplains to alluvial plains and marginal lacustrine mudflats
Fluvial deltas or fan deltas
Lacustrine deposits
Open-lake environment
Coastal lacustrine peat-swamps (Štepanice–Čikvásky Horizon)
Amphisauropus
Dromopus
Batrachichnus
Ichniotherium
Dimetropus
Limnopus
(3) Lake expansion
Wet phase
KJCC
PLOUŽNICE LAKE
N
(2) Lake regression
Dry phase
KJCC
PLOUŽNICE LAKE
N
(1) Lake expansion
Wet phase
KJCC
PLOUŽNICE LAKE
N
Kyje
Sand/gravel bar
Active fluvial channel
Fluvial delta
Open lake
N
Wet mudflat
Abandoned fluvial channel
Dessicating mudflat
Štikov
Gravel bar
Open lake
Alluvial fan
N
Fan-delta lobe
Alluvial fan
Debris-flow gravels
not to scale