Proceedings of the 2nd International Conference of Continental Ichnology (ICCI 2017), Nuy Valley (Western Cape Winelands), 1–8 October 2017

Table of Contents

Introduction and a brief history of ichnological research in southern Africa

The 2nd International Conference of Continental Ichnology (ICCI 2017) was held in Nuy Valley (Western Cape Winelands) and followed by a field trip across South Africa to Lesotho from 1st to 8th of October 2017. The conference was dedicated to the study of continental trace fossils, and delegates presented research that focused on investigating various ichnofossils such as burrows, nests, tracks and trails. These are important not only for detailed characterization of past depositional environments, recognition of unconformities, prospecting for hydrocarbon resources, and biostratigraphic subdivisions, but also for the direct link they provide to ancient animal behaviour.

The conference was organized by Dr Emese M. Bordy and the postgraduate students of her Sedimentology–Palaeontology Group at University of Cape Town (UCT), and was attended by 50 international delegates from Canada, U.S.A., Uruguay, Argentina, France, Germany, Sweden, Switzerland, Russia, Spain, U.K., Italy, Poland, South Africa and Lesotho (Fig. 1). This proceedings volume reflects the calibre and experience of the ICCI 2017 attendees, who appeared to be an ideal mix of senior and junior scientists. One third of the delegates were postgraduate students, and about of quarter of them were international students.

We hope that all of you will enjoy the scientific content of this proceedings volume, which, among others, aims to showcase some of the best continental ichnological work globally and demonstrate why southern Africa is not only an exquisite geological and palaeontological wonder but also a world class ichnological research destination.

The abundance and often uniqueness of the continental trace fossils in southern Africa are in stark contrast with the slow and punctuated development of ichnology in the region, even though the recognition and utilization of animal traces have been actively practiced here since prehistoric times. Cave paintings from the pre-1800s indicate that the indigenous hunter-gatherer San people, who have legendary neoichnological expertise, developed an early interest in the rich palaeoichnological record of the region and attempted to interpret ancient trace-making organisms (Ellenberger *et al.* 2005). Fascination with trace fossils and the identification of the producers by layman have also been recorded, among others, in the Western Cape (South Africa), where local farmers interpreted some Ordovician eurypterid tracks as footprints of ancient tortoises (Fig. 2A – Braddy & Almond 1999). The incorrect identification of trace fossils, which seems to be one of the most persistent traits of ichnology, is also associated with the first written record of a southern African trace fossil (later named *Plagiogmus*, a vermiform metazoan trace – Fig. 2B) originally reported as impressions of fossil eels by H. Lichtenstein in his diary in 1803 (Macrae 1999; Master 2010).

Figure 1. Delegates at the ICCI 2017 during the conference dinner in Nuy Valley.
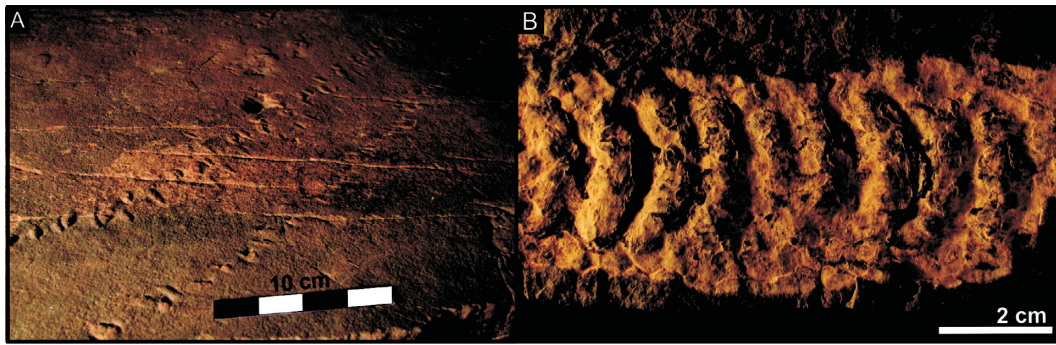
Figure 2. **A**, *Palmichnium* isp. was interpreted by the local farmers as tracksways of ancient tortoises (Skilpadsklip) (SAM-PT-K8667; Upper Ordovician Graafwater Formation, Table Mountain Group, Cape Supergroup, Brandenburg 239, Clanwilliam, South Africa). **B**, *Plagiogmus* isp., a vermiform metazoan trace that was first reported as an impression of a fossil eel in 1803. The original sample was destroyed, but new findings of the same trace fossil are held, among others, in the Iziko Museum (SAM-PT-K8496; Lower Permian Whitehill Formation, Ecca Group, Karoo Supergroup, Onwetende Fontein 743, Calvinia, South Africa).

The first published record of invertebrate ichnofossils appeared in press nearly 70 years later as 'trails of worms and tracks of Crustacea' found in the Permian Ecca Group on Schietfontein farm (near Carnarvon) (Dunn 1872). Although vertebrate tracks were recorded in southern Africa in the late 19th century (?*Dicynodon* tracks in South Africa by Holub 1881; bird or lizard trackways in Lesotho by Dieterlen 1885 and Christol 1897), the first mention of invertebrate ichnofossils (*Spirophyton*) as fairly reliable stratigraphic markers has only been published in southern Africa in the early 20th century (Rogers 1905), after the 'Age of Fucoids' and well into the 'Period of Reaction' in European history of trace fossil studies. In these early days, *Spirophyton* was attributed to fucoids (remains of marine algae) or inorganic processes (Rogers 1905; Hatch & Corstorphine 1905) and impressions of seaweed of screw-like form (Schwarz 1912). Its first acceptable interpretation was given almost half of a century later as fossil traces of burrowing worms (Du Toit 1954).

Following a slow start, ichnology in southern Africa only developed into an established discipline that links geology, sedimentology and palaeontology during the early 1970s and 1980s. This period is marked by the publication of the first detailed ichnofossil descriptions, ichnotaxonomic treatments and ichnologically based biostratigraphic and palaeoecological reconstructions. This golden era of southern African ichnology is primarily featured in internationally acclaimed contributions by Ann Anderson (Palaeozoic invertebrate ichnofossils, South Africa), Paul Ellenberger (Mesozoic vertebrate tracks, Lesotho), and Gerald Germs (Precambrian and Cambrian invertebrate ichnofossils, Namibia and South Africa). These active years also led to pioneering application of ichnofossils (in conjunction with lithofacies assemblages) to sedimentary facies analysis and interpretation (e.g. palaeobathymetry, marine *vs* non-marine settings) and incorporation of neoichnological studies in trace fossil interpretations (see works by D.K. Hobday, T.R. Mason, R. Shone, R.M.H. Smith, I.G. Stanistreet, I. Rust, B.R. Turner).

The sluggish progress of ichnology in southern Africa, possibly due to geoscientific preoccupation with Karoo vertebrates and economically important Archaean rocks (Mason 1985), appears to be transformed by renewed interest in ichnological research in recent decades. We trust that the transformation has been spurred on by ICCI 2017, which injected even more rigour and enthusiasm into our local research community and offered all attendees opportunities to share and exchange ideas and to foster networking among potential collaborators.

Once again, enjoy reading this proceedings volume of *Palaeontologia africana*!

On behalf of the organizing committee:
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[signature]

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References

Braddy, S.J. & Almond, J.E. 1999. Eurypterid trackways from the Table Mountain Group (Ordovician) of South Africa. *Journal of African Earth Sciences* 29, 165–177.

Christol, F., 1897. *Au sud de l'Afrique*. Nancy, Berger-Levrault, 308 pp.

Dieterlen, H., 1885. Nonyana ea Makhuarane. Leselinyana la Lesotho, (1 July 1885), 2–3.

Du Toit, A. 1954. *The Geology of South Africa*. Edinburgh, Oliver and Boys, 611 pp.

Dunn, E.J., 1872. Through Bushmanland, Part 1. *Cape Monthly Magazine* 5(30), 375–376.

Ellenberger, P., Mossman, D.J., Mossman, A.D. & Lockley, M.G. 2005. Bushman cave paintings of ornithopod dinosaurs: paleolithic trackers interpret Early Jurassic footprints. *Ichnos* 12, 223–226.

Hatch, F.H. & Corstorphine, G.S. 1905. *The Geology of South Africa*. London, Macmillan, 348 pp.

Holub, E., 1881. *Sieben Jahre in Sud-Afrika. Erlebnisse, Forschungen und Jagden 1872–1879*. Bd. 11. Wien, Alfred Holder, 532 pp.

Huene, F. von 1925. Die sudafrikanische Karroo-Formation als geologisches und faunistisches *Lebensbild. Fortschr. Geol. Palaont*. 12: (iii) 124 pp.

MacRae, C. S. 1999. *Life Etched in Stone. Fossils of South Africa*. Johannesburg, The Geological Society of South Africa, 305 pp.

Mason, T.R. 1985. Trace fossils: records of ancient life. *South African Journal of Science* 81, 441–445.

Master, Sh. 2010. Hinrich Lichtenstein's fossil "fish" at the Cape in 1803: Discovery of a new Early Triassic marine ichnofossil *Pseudoplagiogmus ichnogenus* novum) from the Ecca Group, Karoo Basin, South Africa. Abstract, 4th Workshop on Ichnotaxonomy, 21–23 June 2010, Moscow, Russia.

Rogers, A. W. 1905. *An Introduction to the Geology of the Cape Colony*. London, Longmans, Green and Co., 463 pp.

Schwarz, E.H.L. 1912. *South African Geology.* London, Blackie and Son, 200 pp.

Painting title: Karoo Life in the Middle Permian. To acknowledge and promote the amazing work of renowned geo-paleo-wildlife artist, Maggie Newman, we used her work to generate the cover of our book of abstracts distributed at the conference in 2017. For more see: https://www.facebook.com/MaggieNewmanArtist

Keynote Address

Experimental continental neoichnology: the lessons animals can teach us in the laboratory and the field

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Interpretation of continental ichnofossils is often impeded by our limited knowledge of traces produced by many modern continental animals. This makes the interpretation of continental ichnofossils difficult and inhibits our understanding of ancient continental ecosystems. Actualistic studies of living animals in the laboratory and field provide the data that make trace fossils invaluable to palaeoecological and palaeoenvironmental reconstructions. These studies allow for the interpretation of tracemakers, associated behaviours, and the environmental factors that influenced burrow production. Laboratory based experiments have been undertaken to understand the burrow morphologies of terrestrial myriapods, arachnids, salamanders, toads, lizards, and snakes. By using multiple properties of burrow morphology to compare the burrows statistically, many of the burrows were separated according to different behaviours and tracemakers. Field experiments in desert scrublands, mountain conifer forests, and temperate woodlands have provided additional insight into continental ichnocoenoses. These studies reveal the complex array of trace assemblages and the effect of environmental conditions, both biotic and abiotic, on their morphology. Results from these studies provide an assessment of our ability to reconstruct ancient continental ecosystems based on trace fossil morphology. They also provide insight into understanding the ecological interactions between continental animals and how these may be recorded by the morphology of trace fossils. By assembling a comprehensive analysis of the burrows and other biogenic structures of modern continental animals, trace fossils may be described in a similar manner and compared directly to these modern analogs. This will be invaluable to improving the interpretation of tracemakers, behaviours, and environmental conditions.
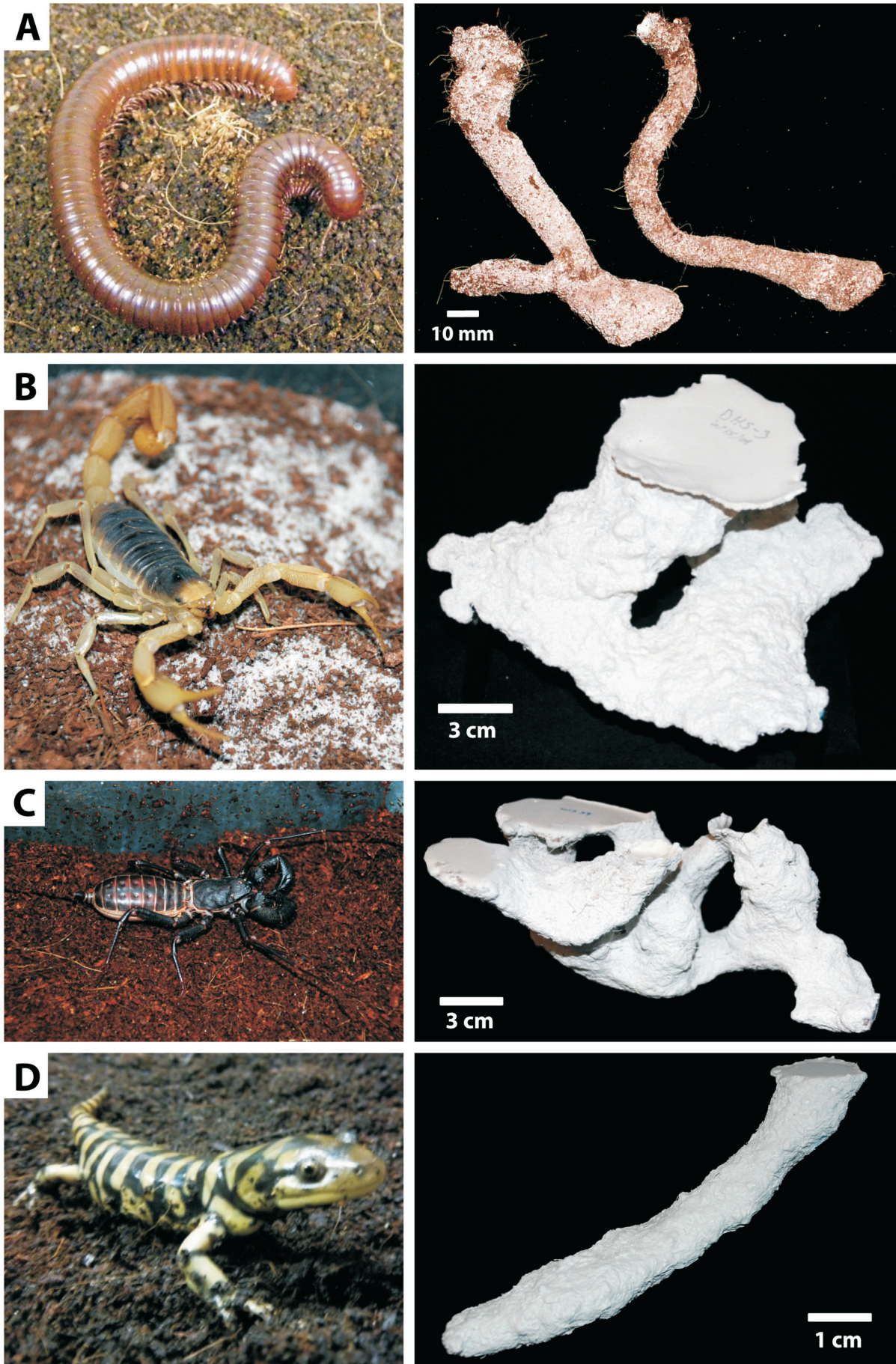
Figure 1. Modern terrestrial burrowing animals and casts of their common burrow morphologies. **A**, Millipede and subvertical shafts with chambers. **B**, Scorpion and a helical burrow. **C**, Whip scorpion and a branching burrow network. **D**, Salamander and a subvertical tunnel.

Keynote Address

Let's make ichnotaxonomy a repeatable science

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If ichnotaxonomy is to be scientific, then it must be repeatable. While some ichnotaxa are identified consistently, others are not, suggesting a failure of the scientific method. For example, when researchers identify a specimen presented on social media as *Palaeophycus*, *Trichophycus* and *Teichichnus*, it suggests that closer examination is needed: an intermediate stage in the scientific method. But when ichnologists publish different names for the same trace fossils, as with Pennsylvanian trackways from Alabama, multiple trials of classification have yielded different results.

A more complex case is provided by crustacean burrows *Ophiomorpha*, *Thalassinoides* and *Spongeliomorpha*. One researcher distinguishes them based on short segments of burrows, while another uses all the information from complete burrow systems. The first approach is easily learned and applied by nonspecialists in cores as well as outcrops. The second is much more difficult to learn and requires favourable exposures. Both taxonomic systems are repeatable, but the second is more natural and yields more information for analysis. Custom has not served us well in this case.

A uniform approach to ichnotaxonomy has been emphasized by previous works. To create a more repeatable approach to the taxonomy of trace fossils, ichnologists should take inspiration from the taxonomy of body fossils. Observation should be detailed; description, uniform. The most constant diagnostic features should be used: those that relate to behaviour and anatomy of the tracemaker. The whole trace fossil must be studied in as many specimens as possible. Type material can be reinvestigated; where it is inadequate, topotypes may be sought. Incomplete or poorly preserved material should be avoided as types. Taphonomic effects should be filtered out rather than used as criteria. This approach should result in a firm basis for the science of ichnotaxonomy.

Figure 1. Can a hundred ichnologists agree on the names of ichnospecies from a single exposure? Or even the number of ichnotaxa? Ordovician, Bell Island, Newfoundland (Canada), on an excursion during the Ichnia conference, 16 August 2012.

Keynote Address

Neoichnology in a fluvial environment of the moderate climatic zone: examples from the Vistula River catchment in Poland

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During summer and autumn, traces of invertebrate and vertebrate animals are abundant in sandy bars with local muddy drapes and pools in rivers of the Vistula catchment. On wet surfaces, earthworms produce straight or slightly winding surface grooves (Fig. 1A), locally with side probes and spreite-like surface structures in places of rapid turns. Crane fly larvae (Tipulidae) surface trails and subsurface mines are very common (Fig. 1B). They can lead to total bioturbation of sediment. Subsurface mines with side probes produced by Chironomidae are less common. In mud, fly larvae of the Rhagonidae family and nematodes produce sinusoidal trails (*Cochlichnus*) (Fig. 1C). Mud-loving beetles *Heteroceras* are tracemakers of shallow, branched mining galleries with fine scratch marks and pellets (Fig. 1D). Mole crickets (*Gryllotalpa*) mine subsurface branched galleries with characteristic scratch marks (Fig. 1E).

Under water and on wet surfaces, bivalves (*Unio*, *Anodonta*, *Pisidium*) produce v-shaped, winding and looping grooves with levees (Fig. 1G). They may dig under surface waiting for higher water, but they always come on the surface when dying because of dehydration. Gastropods leave v-shaped, shallow u-shaped or flat-bottom winding trails with levees. The *Limnoria* trails display chevron marks on the bottom, and the *Galba* trails show longitudinal corrugations. *Limnoria* can dig shallow, vertical depression in drying mud. In softened wood logs, deep U-shaped burrows with limbs and scratch marks are produced by mayfly (Ephemeroptera) larvae or nymphs, while smaller and shallower u-shaped burrows (*Asthenopodichnium*) are produced by gammarid amphipods (Fig. 1F). In fluvial plains, mainly in organic-rich recent or shallowly buried soils, small, variable oriented burrows, commonly filled with mud are made by earthworms; some of them follow roots. European mole (*Talpa europaea*) produces shallow and deep branched burrows and shallow subsurface mines in sand bars. The preservational potential of the surface traces is very low, but it increases when conserved by microbial mats or buried slowly by migrating dunes or wind-blown sand.
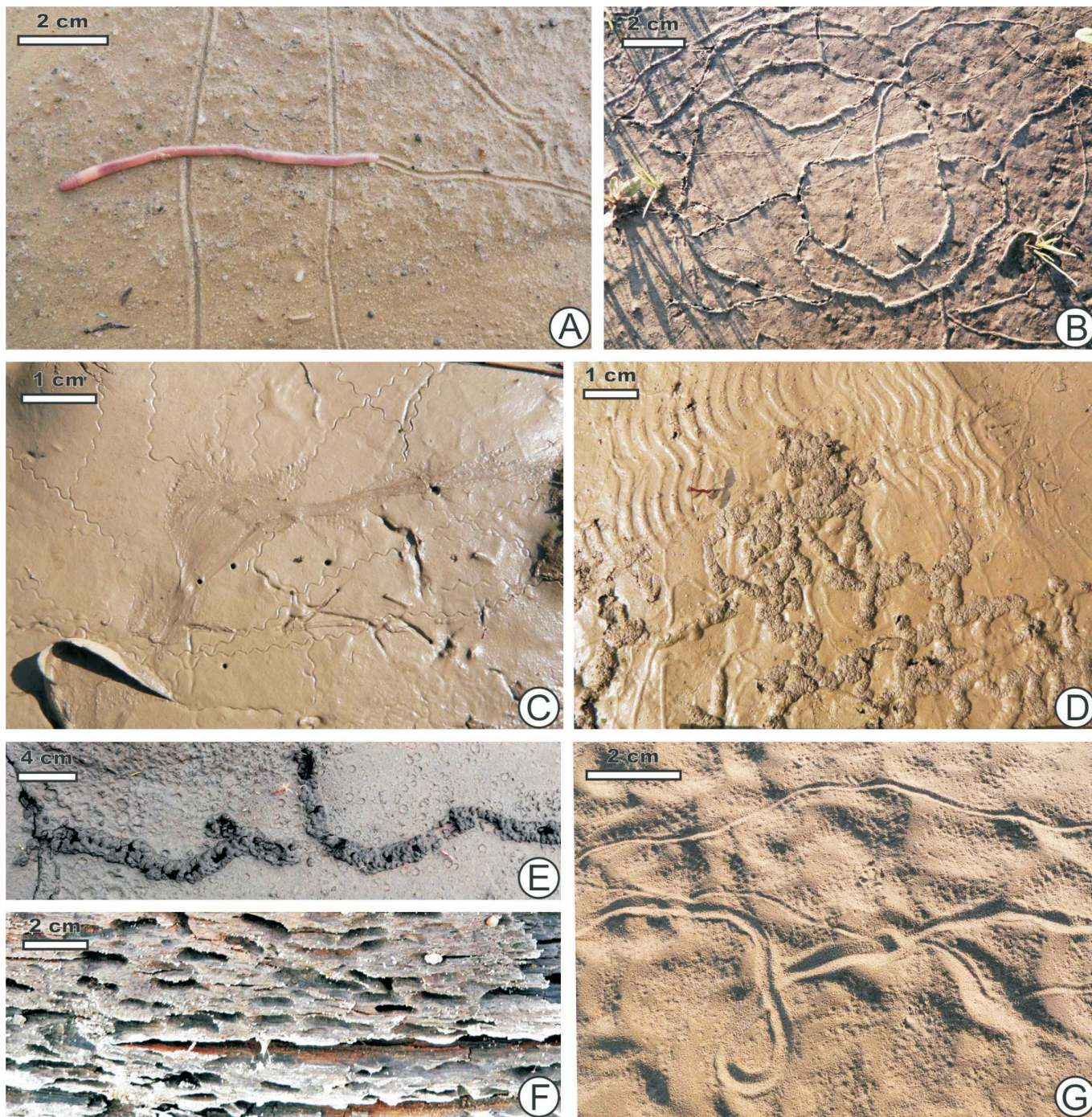
Figure 1. Examples of recent invertebrate traces in the Vistula catchment, Poland. **A**, Surface earthworm trails and their tracemaker. **B**, Crane fly larvae (Tipulidae) subsurface mines. **C**, Incipient *Cochlichnus* produced by nematodes. **D**, Mud-loving beetle *Heteroceras* subsurface mines. **E**, Mole cricket (*Gryllotalpa*) subsurface mines. **F**, Incipient *Asthenopodichnium* in decaying wood log. **G**, Surface trail produced by the bivalve *Unio* sp.

Conference Abstracts

Sedimentological context of Early Jurassic dinosaur tracksites (Elliot Formation, Karoo Supergroup) in the Roma Valley, Lesotho

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Dinosaur tracksites in the Lower Jurassic part of the Elliot Formation within the Roma Valley of Lesotho were studied, with the aid of high resolution sedimentological assessments of the host rocks, to better understand the palaeoenvironmental and ichnite preservation conditions (Fig. 1A,B). Moreover, the geochronology of the tracksites, using the U-Pb LA-ICPMS method on detrital zircons separated from the host rock, is currently underway to refine their temporal relationship (Fig. 1C). The ichnogenus present at three sites are tridactyl tracks and trackways on the *Grallator–Eubrontes* spectrum. Additionally, the Lephoto and Matobo sites preserve ichnites that belong to the ichnogenus *Trisauropodiscus* and *Kayentapus*, respectively. Sedimentologically all the track-bearing palaeosurfaces are preserved atop of tabular sandstone beds that are fine-grained, horizontally laminated, low-angle cross-laminated or massive. The sandstones are interbedded with pedogenically altered mudstones with *in situ* carbonate nodules, calcretizied root traces, invertebrate burrows, etc. The track-bearing palaeosurfaces also preserve current ripple marks and desiccation cracks. The upper Elliot Formation has been interpreted as a fluvio-lacustrine depositional system that experienced repeated periods of high energy, flash flooding and drying in the Early Jurassic. Under the semi-arid climatic conditions, pedogenic alteration of the floodplain sediments led, amongst others, to the bioturbation of sediments and precipitation of carbonate nodules in the palaeosols.

While the large-scale sedimentology of the three Roma Valley tracksites is similar, localized sedimentary features associated with the tracks vary within and amongst the tracksites. Footprint morphology is a function of dynamic trackmaker-substrate interaction; thus, the preserved tracks provide insights into the substrate conditions at the time of track formation. This is most simply illustrated by deep, undefined tracks with expulsion rims being interpreted to have formed in a saturated medium, whereas defined tracks with distinct morphological detail such as claw marks and digital pads being interpreted to have formed in a firmer medium. Some tracks show evidence of acting as microenvironments indicated by the preservation of pitted textures due to algal matting and invertebrate traces within the foot impressions. This suggests that the epirelief tracks formed on the wet sediment surface in small pools where microorganisms and invertebrates could temporarily flourish, and ultimately assist in the footprint preservation.
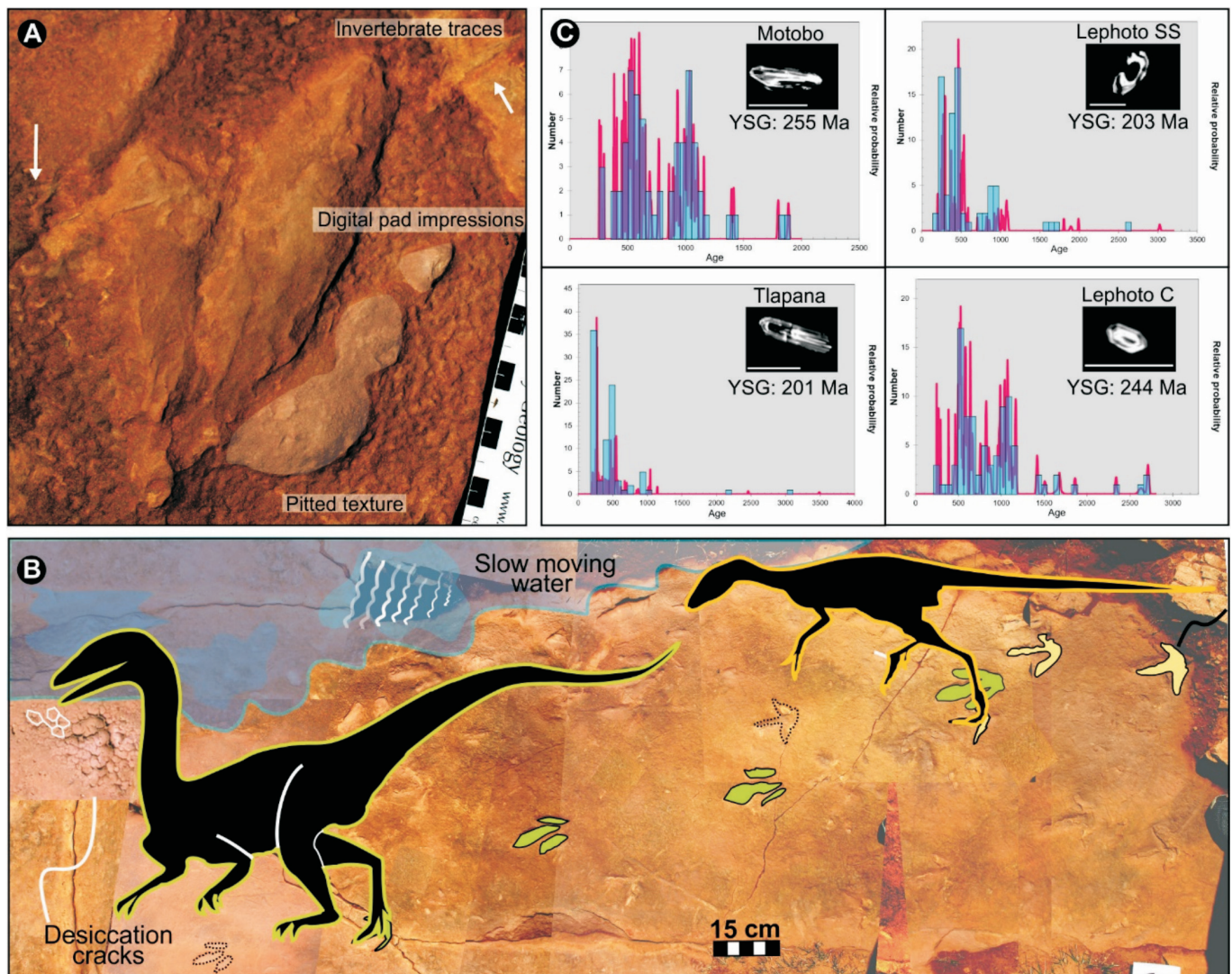
Figure 1. Overview of the Roma Valley tracksites. **A**, Fine-scale sedimentological features, including invertebrate traces and pitted textures possibly created by microbial activity, associated with a *Grallator* track with digital pad impressions in digit II. **B**, Palaeoenvironmental interpretation of the Lephoto tracksite, which preserves *Grallator* and *Trisauropodiscus* tracks. **C**, Detrital zircon probability density diagrams for three tracksites in the Roma Valley, where YSG is the youngest single grain age obtained. Scales represent 100 μm.

An exceptional coprolite assemblage from Las Hoyas fossil site (La Huérguina Formation, Cuenca, Spain)

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Las Hoyas is an Upper Barremian continental Konservat-Lagerstätte, located in Cuenca (Spain), and has yielded a vast diversity of plant and animal body fossils as well as ichnofossils. Coprolites are one of the most abundant remains, with more than 2000 coprolites having been collected. Twelve different morphotypes have been described: spiral, circular, irregular, elongated, rosary, ellipsoidal, cylinder, bump-head lace, Christmas-tree, cone, straight lace and thin lace coprolites. The differences among morphotypes have been established considering some features such as the external shape, the outlines and the shape of the ends. A dichotomous key was built to test and facilitate their identification. Differences on the relative abundance denote that two morphotypes, thin lace and cylinder are the most dominant. Thin lace morphotypes have dense intrusions, and also contain several tiny vertebrae. The preservation and abundance of the bone remains suggest either poor digestion, or a short retention time of food. Cylinder morphotypes show scales and bone remains, but not in as much abundance as in the thin lace morphotype. Most of Las Hoyas coprolites are from carnivores, as is possible to infer from EDX analysis: the elemental composition shows high levels of phosphorous and calcium, which suggests a predominant calcium-phosphate composition, typical from carnivorous scats. The quality of the Las Hoyas coprolites, their wide variety of sizes and their multiplicity of shapes, strongly suggest that coprolites should be considered autochthonous fossils deposited in aquatic ecosystems.
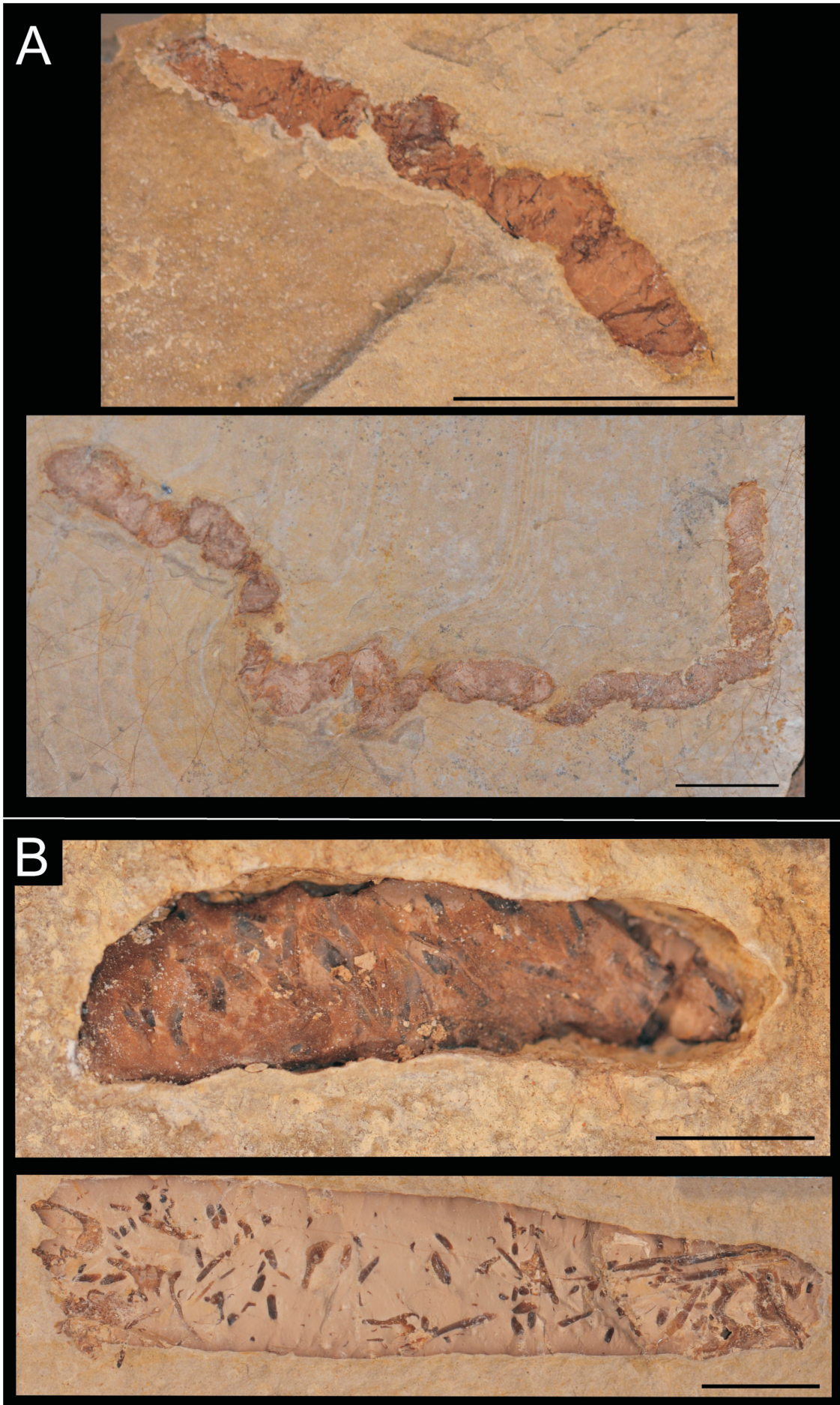
Figure 1. Thin lace (**A**) and cylinder (**B**) morphotypes from Las Hoyas. The cylinder morphotypes show well-preserved bone remains. Scale bar = 0.5 cm.

The Ntumbe dinosaur tracksite, Chewore Safari area, Zimbabwe: a place for new discoveries

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The Ntumbe dinosaur tracksite lies in the Ntumbe Valley within the Chewore Safari area of northern Zimbabwe. Numerous dinosaur footprints have been described from this area since the first tridactyl trackway was reported by Broderick. The sedimentary sequence is preserved within the Chenje Sub-basin, which is sandwiched between the rifted Zambezi Escarpment and gneissic blocks comprising the Chewore Inliers. The Sub-basin reflects a transition between the Karoo and post-Karoo sedimentary infill to the Zambezi Rift that is proposed to represent a Mid- to Late-Jurassic deposition. The 'Ntumbe beds', which host the footprint site, form a distinct unit within thick-bedded red sandstones of the post-Karoo Dande Sandstone Formation, interpreted as an alluvial fan deposit. This Ntumbe unit is interpreted as a distal facies of the alluvial fan, reflecting the presence of meandering rivers and lakes. It comprises cross-laminated, fine- to medium-grained sandstones preserving ripple-marks and desiccation cracks intercalated with green mudstone layers containing freshwater conchostracans and a flood sequence entombing the bones and scales of Lepidote fish. Two dinosaur footprint varieties have been found: A) Tridactyl theropod footprints, which are 25–50 cm long and 10–30 cm wide. In excess of 140 of these prints, some defining distinct trackways, have now been mapped. A few small tridactyl footprints, <5 cm in length, may reflect a nursery site. B) Circular pes (diameter: ~90 cm) with toe impressions and crescent-shaped manus impressions of sauropodomorphs, which were first discovered by Ait-Kaci Ahmed in 2001. The Ntumbe River area is far from being fully described, but it does represent a world-class tracksite location, protected in a national park setting.

Figure 1. Diverging trackway directions across a rippled sandstone surface exposed in a left bank tributary to the Ntumbe River (bottom left print is 45 cm long). Photograph Sally Wynne, 2000

The trace fossils of Iziko Museum, with special reference to Ann Anderson's collection

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Iziko Museums of South Africa (formerly the South African Museum) currently houses 382 ichnological specimens of which 9 are holotypes, 11 are syntypes and 15 are paratypes. Amongst these specimens are coprolites, eggs, invertebrate traces, vertebrate tracks and burrow casts, which range in age from the Ordovician to the Neogene. Trace fossils collected initially by Norman Savage and later by Ann Anderson are mainly from the Carboniferous and Permian sedimentary rocks of the Dwyka and Ecca Groups (Karoo Supergroup) and form a valuable part of the Iziko collection. Among these are the ichnofossils described in Anderson's Ph.D., which focuses on trace fossils from the Lower Permian in South Africa. Her detailed work on arthropod trackways as well as fish fin traces led to the establishment of two, by now well-known, ichnogenera: *Umfolozia* and *Undichna*, respectively. Among others, she worked on Ordovician arthropods trackways (*Petalichnus capensis*) and associated burrows (*Metaichna rustica*) from the Cape Supergroup as well as limulid trackways in the Late Palaeozoic of the South Africa. Anderson pioneered multi-disciplinary studies, and combined ichnological evidence with sedimentological and palaeontological findings to refine the palaeoenvironmental conditions during the early history of the Karoo Basin. Specifically, where a paucity of body fossils made it difficult to reconstruct the ancient sedimentary conditions, Anderson's work on limulid tracks in the upper Ecca provided evidence of a marine depositional setting for the basin. Her collaborative work with her husband, Ian McLachlan, on the Dwyka Group demonstrated that the Karoo Basin was flooded by the sea during the final melting of the ice in the Late Carboniferous. Anderson, affectionately known as the 'mother of South African ichnology', made significant contributions to the study of trace fossils, which was an emerging field of earth sciences in the 1970s.
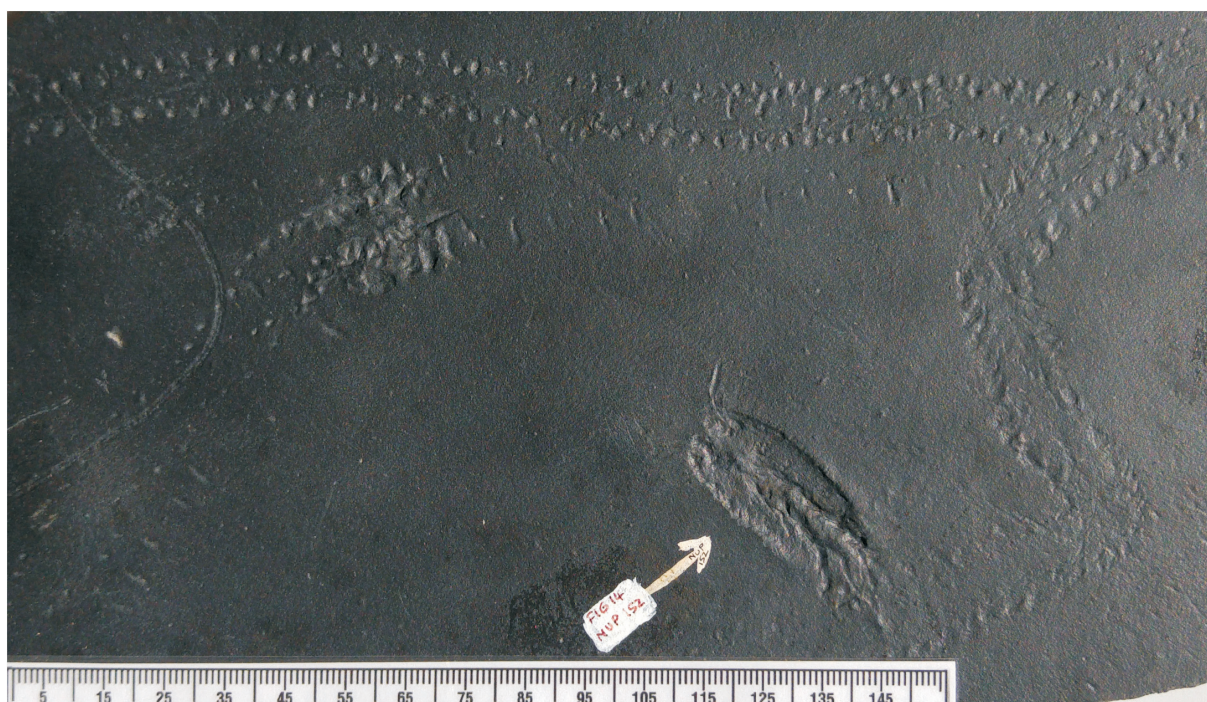
Figure 1. Carboniferous mudstone with trace fossils (Dwyka Group) from the Swart Umfolozi site in Kwazulu Natal. The resting trace (white arrow) is the type specimen of *Kingella natalensis* that was first described by Savage (1971). The slab also contains various arthropod trackways including *Protichnites* isp. Scale is in millimetres.

Ichnology of lacustrine basins

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Lacustrine ichnology has experienced a significant development during the last two decades. In particular, the classification into overfilled, balanced-fill and underfilled lakes has allowed framing ichnological observations within palaeoenvironmental and stratigraphic settings (Fig. 1). Overfilled lake basins typically contain well-developed softground associations (*Mermia* and *Skolithos* ichnofacies and the softground suite of the *Scoyenia* ichnofacies), whose recognition helps in delineation of parasequences and parasequence sets. A relatively diverse benthos is typically present as a result of freshwater conditions. Firmground suites are rare because overfilled lakes usually do not experience desiccation. In contrast, balanced-fill lakes are characterized by abundant and widespread firmground suites of the *Scoyenia* ichnofacies. Softground assemblages are usually of low diversity. The combination of hypersalinity during lowstands and oxygen depletion during transgressions and highstands imparts high stress on the lake biota and, as a result, softground ichnofaunas are depauperate. In underfilled lakes, the *Scoyenia* ichnofacies is associated with lowstand desiccated substrates. Arthropod trackways are extremely abundant, forming tracked omission surfaces that may represent sequence boundaries expressed by co-planar surfaces of lowstand and subsequent flooding. Composite ichnofabrics occur as result of rapid changes in depositional conditions reflecting desiccation during vertical aggradation. A checklist approach is of limited value because none of these lake-basin types is characterized by specific ichnotaxa. In contrast, a combined ichnofacies and ichnofabric approach to the study of overfilled, balanced-fill, and underfilled lakes may represent the best strategy to characterize lacustrine basins. Information from modern lakes is particularly useful to further enhance our understanding of the complexities of lakes.
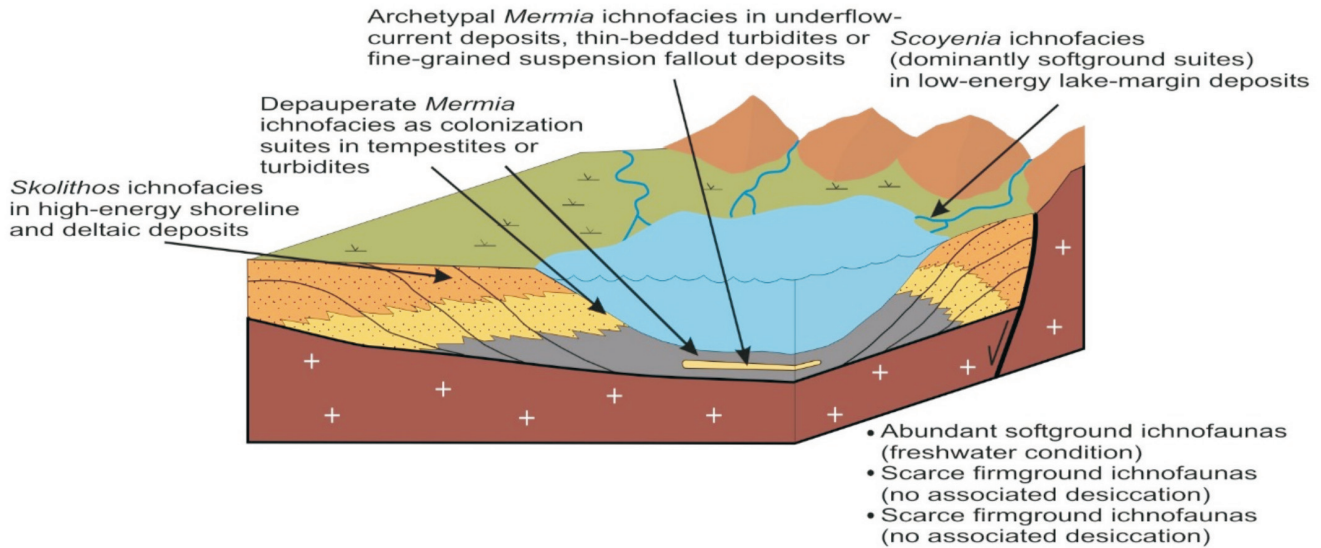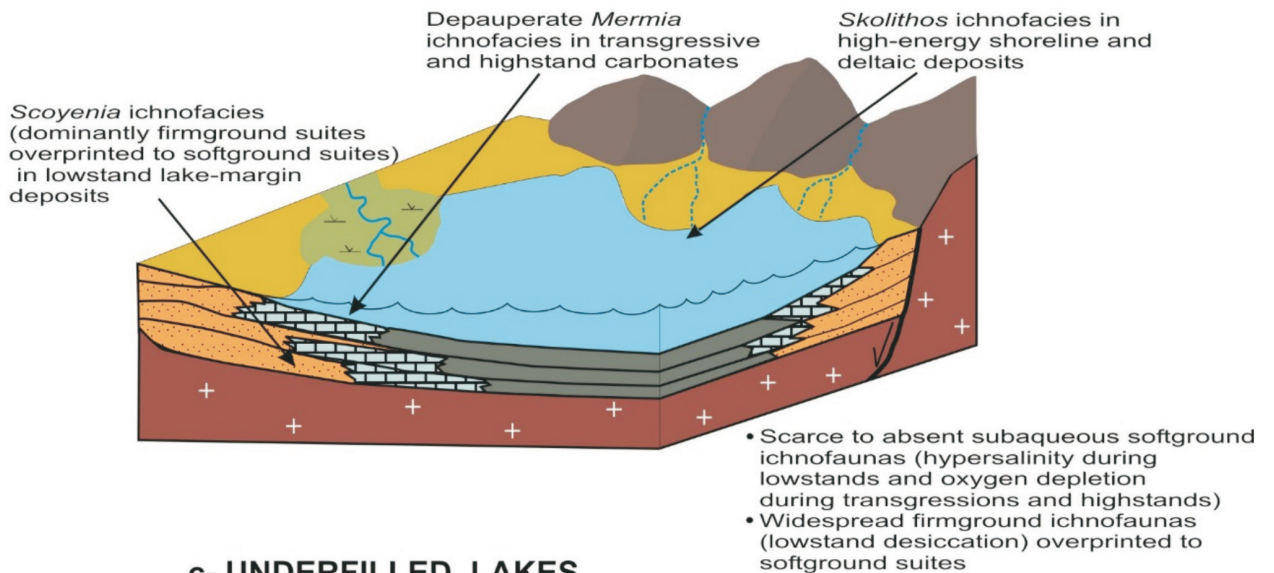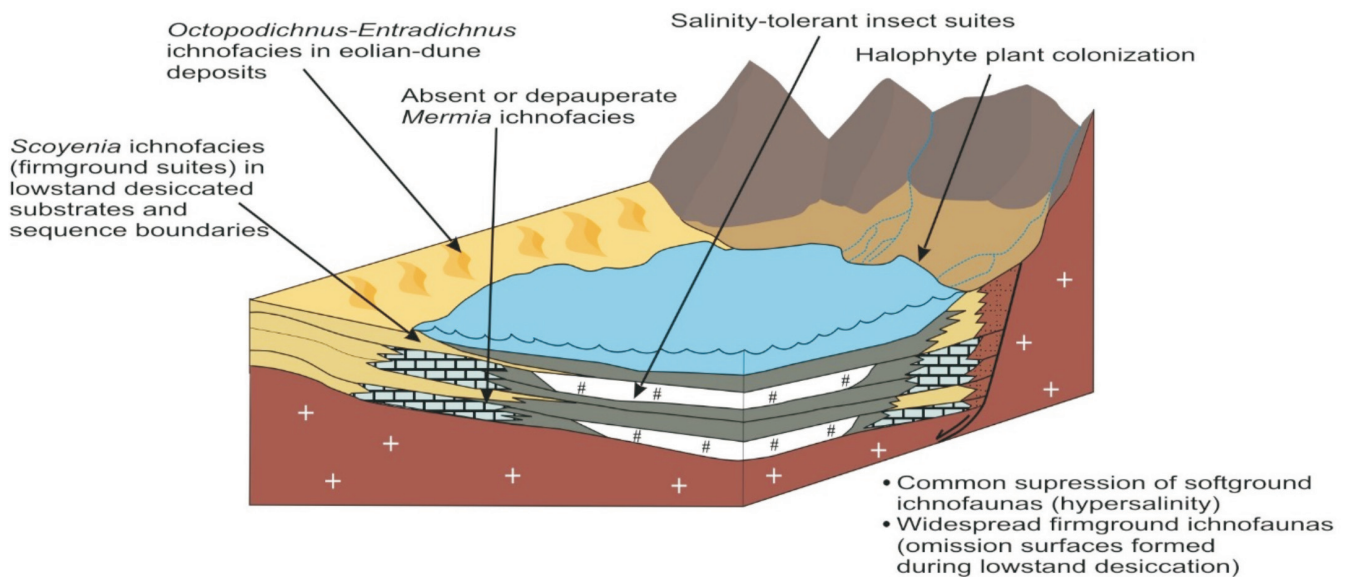
Figure 1. Trace fossil assemblages, environmental controls, and lacustrine sequence stratigraphy in overfilled (**a**), balanced-fill (**b**) and underfilled (**c**) lakes.

A Middle to Late Permian tetrapod tracksite from northern Germany

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We report a new assemblage of continental trace fossils from the Flechtingen High area in Saxony-Anhalt, northern Germany. In the Mammendorf andesite quarry, Upper Carboniferous to Lower Permian volcanic and subvolcanic rocks are unconformably overlain by a non-marine succession of interbedded conglomerates, sandstones and siltstones, which have been preliminarily referred to as the Upper Rotliegend. Most of the newly discovered vertebrate tracks and invertebrate burrows come from a 1.5-metre-thick unit of grey-white sandstones that are intercalated with thin horizons of siltstone. Apart from trace fossils, these layers contain ripple marks and mud cracks of varying size and shape. The most fossiliferous track horizon was documented and partly excavated by the Museum für Naturkunde Magdeburg in July and August 2016. Apart from invertebrate burrows, tetrapod scratches are the most abundant ichnofossils within this horizon and occur either as (a) isolated or footprint-related subparallel scratch marks or (b) about 25 cm wide, roundish structures composed of consecutive overlapping left- and right groups of (five) scratches. At least five different types of tetrapod tracks with imprint sizes ranging from 1.5 to 14 cm can be distinguished: (1) numerous imprints and one trackway of a small reptilian trackmaker, *Erpetopus*; (2) one small reptilian trackway, cf. *Procolophonichnium*; (3) medium- to large-sized paw-like therapsid tracks, cf. *Dicynodontipus*; (4) one larger individual reptile imprint, cf. *Paradoxichnium*; (5) large roundish imprints including possible *Pachypes* undertracks. The poorly constrained ranges of these ichnotaxa suggest a Middle to Late Permian age of the track-bearing strata. Within this time interval, the Mammendorf assemblage may turn out to be the most diverse tetrapod ichnofauna reported from any German locality, probably exceeding that of the Cornberg Sandstone, Hesse (which is in need of revision).
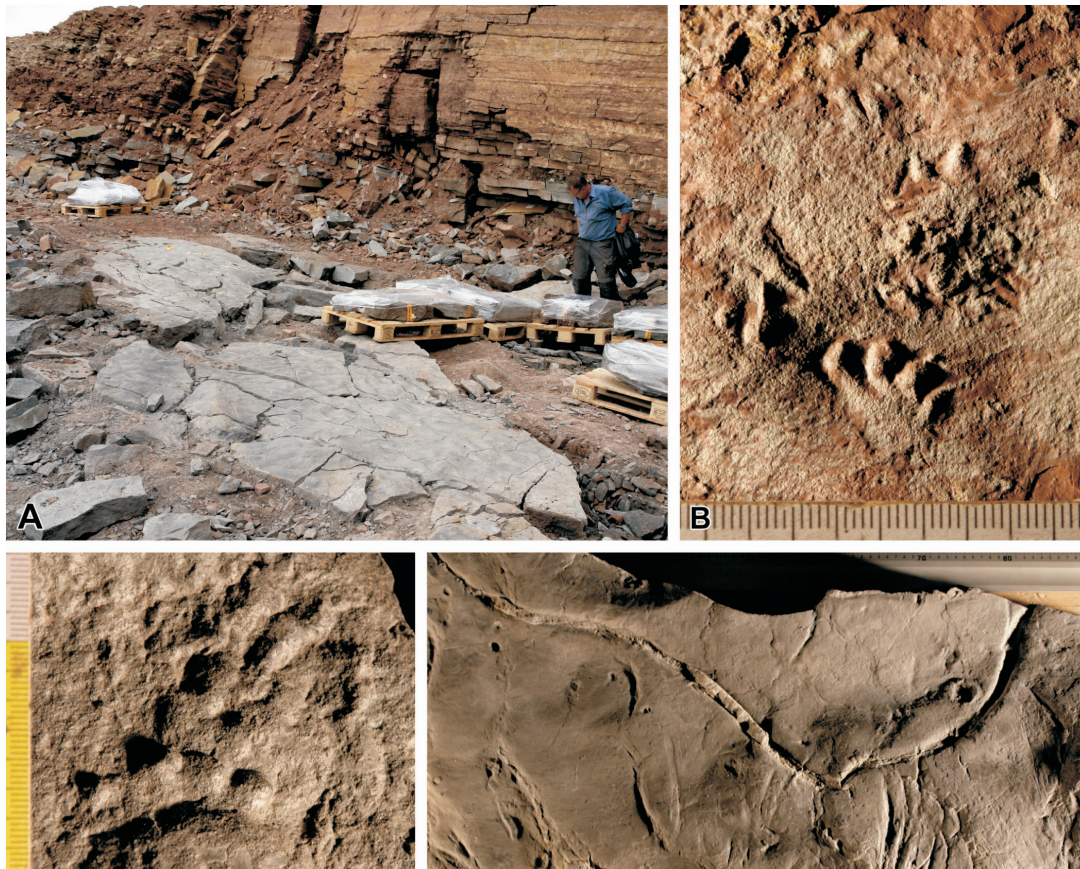
Figure 1. Mammendorf trackway locality. **A**, Fieldwork at the excavation site in August 2016. **B**, Imprints of *Erpetopus*; small scale unit is 1 mm. **C**, Imprint couple of cf. *Dicynodontipus*; small scale unit is 1 mm. **D**, Tetrapod scratches; scale bar (upper right) is ~27 cm long.

Burrow systems of the extant South American fossorial rodent *Ctenomys*: key to its recognition in the fossil record

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Burrow systems of *Ctenomys azarae* (Ctenomidae) were studied in central Argentina. The area has a temperate continental climate and the vegetation includes the pampean steppe and the caldenal (*Prosopis* forest). *Ctenomys azarae* is a small (average body mass of 138 g), fossorial, scratch-digging and solitary rodent. The genus *Ctenomys* has been recorded since the Pliocene (3.5 Ma). The burrow systems are complex (Fig. 1A), large (covering 13.2 to 49 m^2), dominantly subhorizontal (dip up to 27°), and shallow (15–60 cm deep). The systems include a main tunnel and secondary tunnels, and have several entrances plugged by sediment. Tunnel segments are connected by T- or Y-junctions to short blind tunnels, grass-stuffed tunnels and rare chambers. Tunnels exhibit an elliptical cross-section with a larger vertical diameter (average vertical diameter: 77.3 mm, average horizontal diameter: 67.7 mm). The grass-stuffed tunnels are filled by compacted grass and separated from the main tunnel by a sediment plug (Fig. 1B). Elevated organic content enhances the preservation potential of these structures. The ceiling and lateral walls of the burrow contain a surface ornamentation in the form of 12 mm-wide sets of three parallel scratch marks (Fig. 1C) that are oblique to the tunnel axis (average 53°). The diagnostic features for recognition of fossil Ctenomydae burrows are: (1) subhorizontal burrows with massive fill, (2) size and elliptical cross-section (vertical to horizontal diameter ratio ≥1), (3) sets of three parallel scratch marks forming an acute angle with burrow axis, and (4) presence of grass-stuffed tunnels.
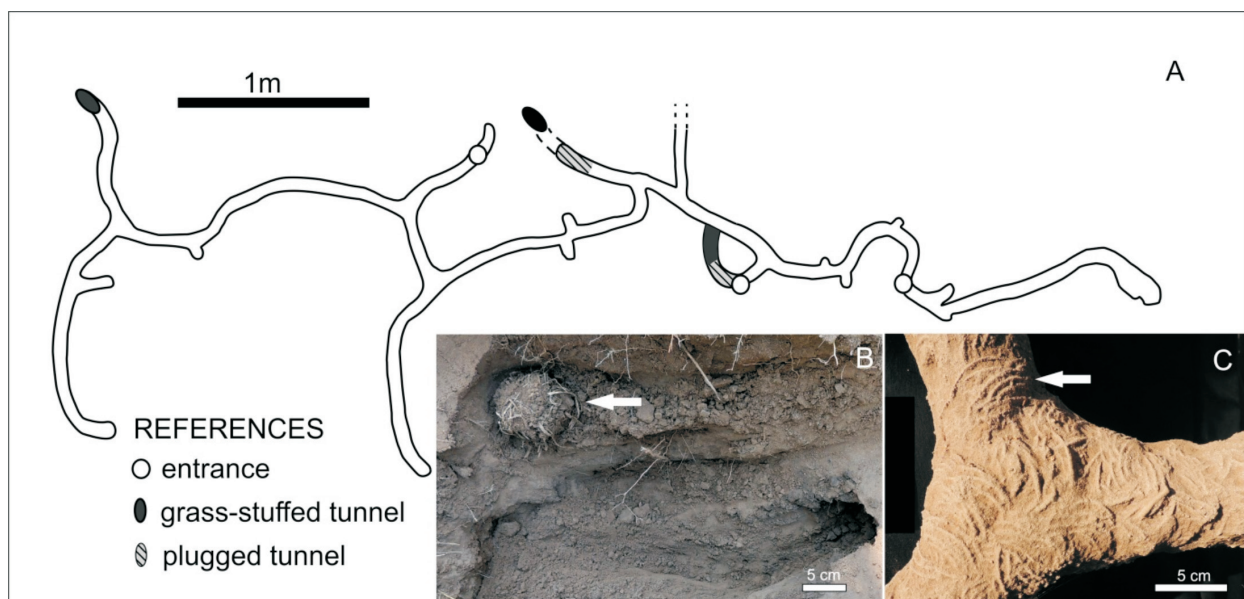
Figure 1. **A**, Example of the architecture of the burrow system of *Ctenomys azarae*. **B**, Grass-stuffed tunnel (arrowed). **C**, Detail of surface ornamentation on cast, note sets of three parallel ridges (arrow).

Tracking the Jurassic–Cretaceous tetrapod faunal turnover in Spain: a comparison between the Lastres (Kimmeridgian) and Huérteles (Berriasian) Formations

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   The Jurassic-Cretaceous interval is characterized by a significant biotic change in the tetrapod assemblages. One way to analyse this faunal turnover is by comparing the tetrapod footprint record from the Upper Jurassic of Asturias and the Lower Cretaceous of Soria in Spain. The Lastres Formation (Kimmeridgian) from Asturias was deposited in a fluvial-dominated deltaic system. On the other hand, the Huérteles Formation (Berriasian) from Soria was deposited in a tide-influenced fluvial-deltaic setting. Both of them represent the two formations with highest tetrapod ichnodiversity for their respective ages in Europe. A total of 14–16 ichnotaxa have been identified in the Lastres Formation: theropods (4), ornithopods/ornithischians (2), sauropods (2), stegosaurs (1), crocodylomorphs (2/3), pterosaurs (1/2), quelonians (1) and squamatans (1). In the Huérteles Formation the same groups (with the exception of squamatan tracks) have been identified, the total number of ichnotaxa being around 11–13: theropods (2/3), ornithopods (1), sauropods (1/2), stegosaurs (1), crocodylomorphs (1), pterosaurs (4), and quelonians (1). Both formations have some similarities in the ichnoassemblages and share some ichnotaxa (Fig. 1) such as: *Pteraichnus*, *Deltapodus*, *Crocodylopodus* or *Emydhipus* but also show some differences (e.g. theropod, ornithopod/ornitischian tracks). It is noteworthy that some of these differences suggest a slight change in the ichnoassemblages and that there is a small decrease in the ichnodiversity across the Jurassic–Cretaceous transition in Spain. Further work is needed in order to understand if these changes might represent a sample/preservational bias or whether they represent the biotic change described on the basis of the osteological record.
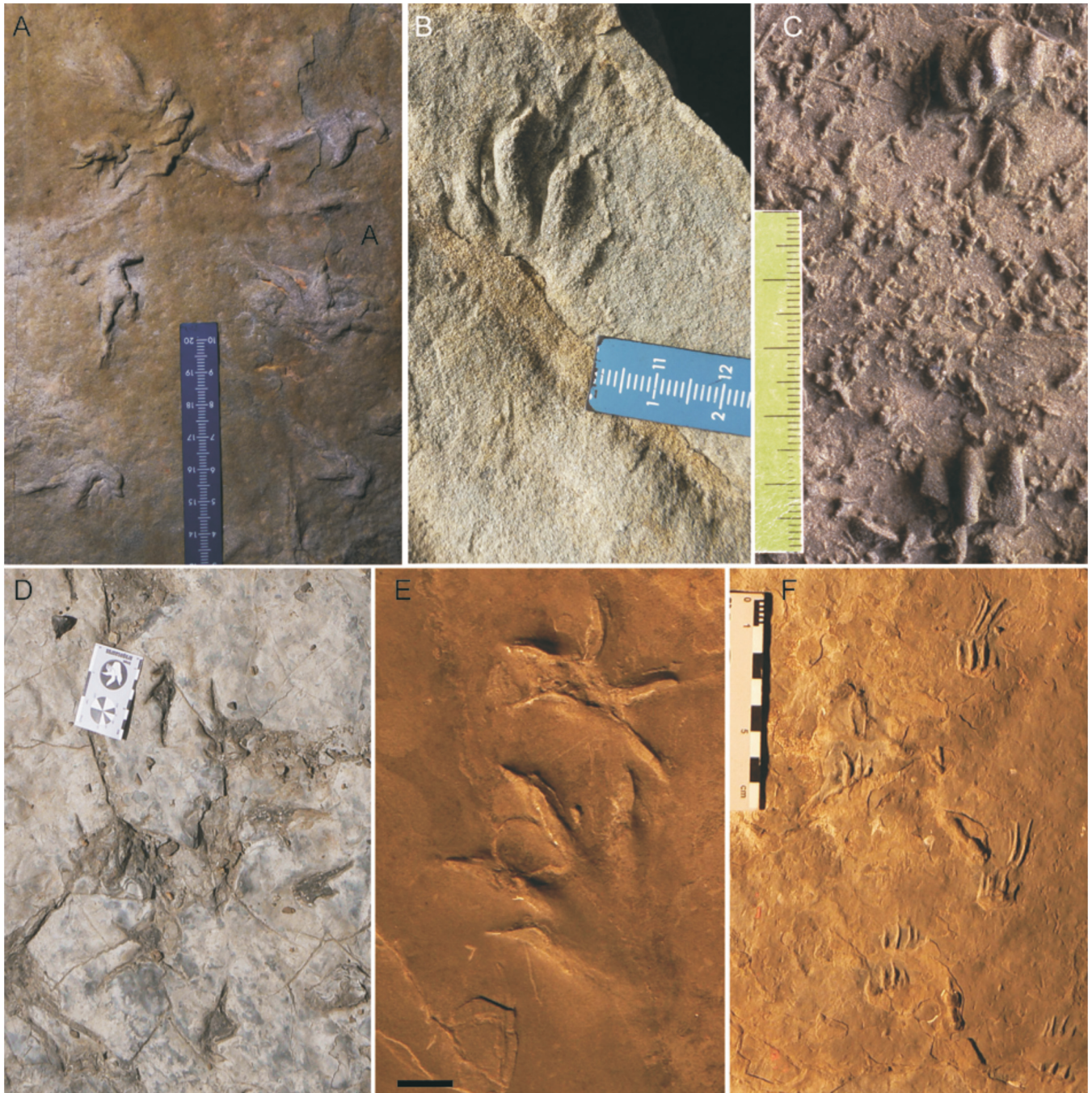
Figure 1. Shared ichnotaxa within the Lastres Formation (Asturias) and Huérteles Formation (Soria). **A**, Isolated manus prints of *Pteraichnus* from Quintueles (Villaviciosa, Lastres Formation). **B**, Pes print of *Crocodylopodus meijidei* from Playa de España (Villaviciosa, Lastres Formation). **C**, *Emydhipus* from Luces (Colunga, Lastres Formation). **D**, Isolated manus prints of *Pteraichnus* from Valdelavilla (Huérteles Formation). **E**, Manus-pes set of *Crocodylopodus meijidei* from El Frontal (Bretún, Huérteles Formation). Scale bar = 1 cm. **F**, *Emydhipus cameroi* from Valduérteles (Huérteles Formation).

La Sagarreta: a new avian and mammalian tracksite from the Early Oligocene in the Northern Ebro Basin (Aragón, Spain)

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The tetrapod ichnological record of the Oligocene is scarce worldwide but northeastern Spain hosts a considerable number of important tracksites. The first Cenozoic tracksite reported in Spain was the 'La Playa Fósil' tracksite, located in Peralta de la Sal where hundreds of avian footprints were found. The beds containing the tracks belong to the Lower Oligocene Peralta Formation and were deposited in an alluvial system in the Ebro Basin. A recent survey of the Peralta Formation unveiled a new tracksite named 'La Sagarreta', which is composed of several ichnological levels (Fig. 1), each preserved in very fine sandstone beds deposited in a fluvial floodplain environment. The exact number of vertebrate tracks at the site is currently under evaluation, but 22 slabs have been recovered thus far and are housed in the Natural Science Museum of the University of Zaragoza. The analysis of the slabs has allowed the identification of tracks and related them with five different morphotypes, of which two have avian (Fig. 1) and three have mammalian affinity. The avian morphotypes can be assigned to the ichnofamily Gruipedidae. The mammal tracks can be tentatively classified as *Plagiolophustipus*-like (an ichnotaxon related with perisodactyl trackmakers), *Canipeda*-like (an ichnotaxon related with canids) and *Pecoripeda*-like, an ichnotaxon related with artiodactyls. The discovery of this tracksite adds to the ichnodiversity of the Peralta de la Sal area and emphasizes its importance for the Oligocene ichnological record of Spain and worldwide.
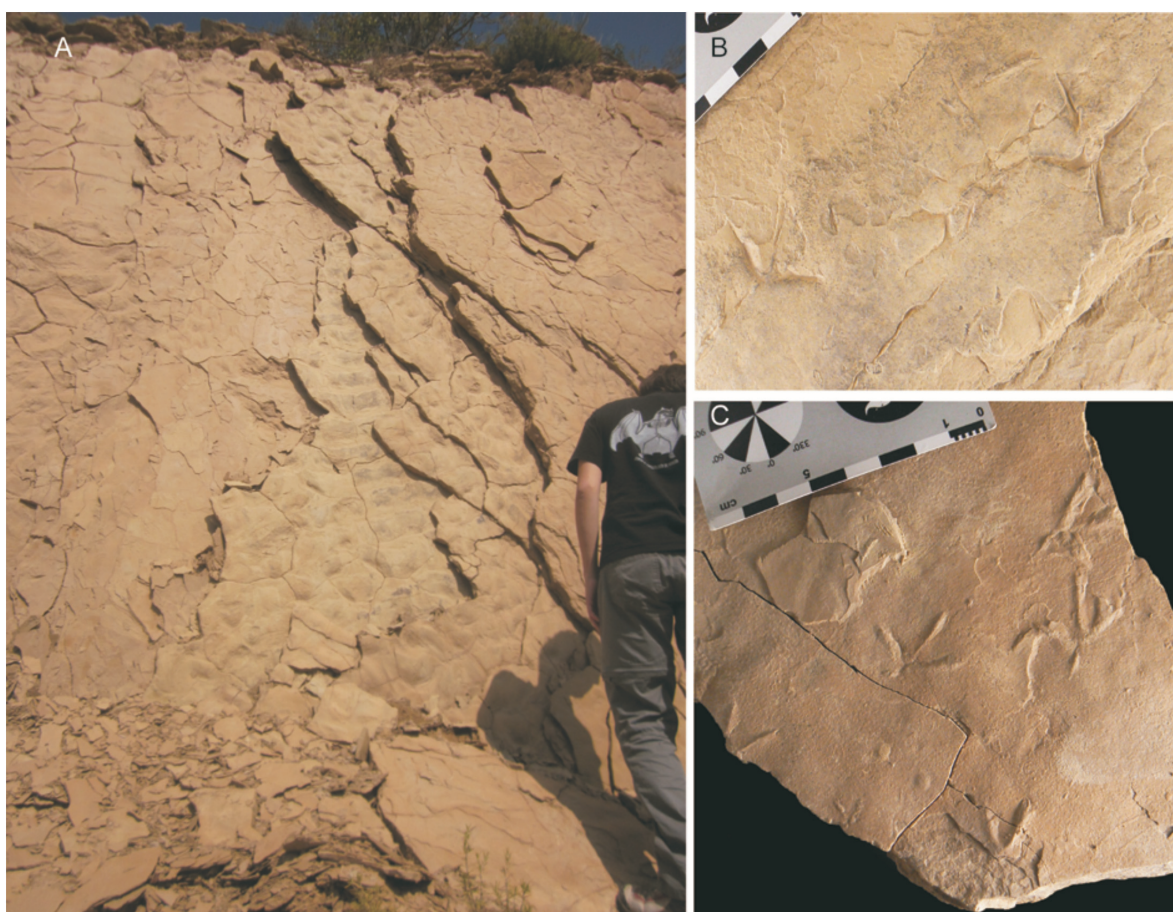
Figure 1. **A**, Various discrete ichnological levels at the La Sagarreta tracksite. **B**, **C**, The two different avian morphotypes identified. Morphotype 1 (**B**) is characterized by a larger size, higher divarication and a more prominent hallux mark than Morphotype 2 (**C**).

The ichnofauna of a singular Middle to Late Permian playa lake in Europe (Upper Hornburg Fm., Saxony-Anhalt, Germany)

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The Hornburg Formation of East Germany was deposited in a small playa basin close to the southern border of the mega-playa system of the Southern Permian Basin. It is one of the rarely preserved Middle to Late Permian fan and playa environments in Europe. Nevertheless, the bio-, magneto- and lithostratigraphic data are sparse. The playa basin is filled with conglomerates and sandstones of an alluvial fan to braid plain system, laterally and vertically followed by braid plain and evaporitic sand flat deposits. Aeolian transport is indicated by bimodal, coarse- to fine-grained sandstones and by well-sorted, fine- to medium-grained fluvially reworked and redeposited aeolian sandstones. They are overlain by fossiliferous, lacustrine strata that comprise laminated silty claystones, pure claystones and intercalated, decimetre thick, channel sandstones. The fossils consist of conchostracans (*Pseudestheria graciliformis*) and hydromeduses (*Medusina limnica*) in the lacustrine beds. Tracks and swimming trails of tetrapods (e.g. *Dromopus*, cf. *Amphisauropus*) are preserved at the bottom of the small fluvial channel sandstones as well as in the lacustrine claystones. Locally, mass occurrences of arthropod (mainly insect) tracks are associated with claystones, fluvial siltstones and silty sandstones. The following genera have been reported previously: *Lineatichnus, Multipodichnus, Acripes, Euproopichnus, Heteropodichnus, Permichnium, Lithographus, Secundumichnus, Heterotripodichnus, Etterwindichnus, Tarsichnus, Striatichnium, ?Tripodichnus, ?Taslerella* and *Avolatichnus.* Plant remains are extremely rare (one coniferan cone). Litho- and biofacies patterns indicate that the red beds formed in a semiarid to arid environment that was associated with a microbial mat based ecosystem. Further excavations will examine the stratigraphic utility of ichnofossils as age markers in the Hornburg Formation.
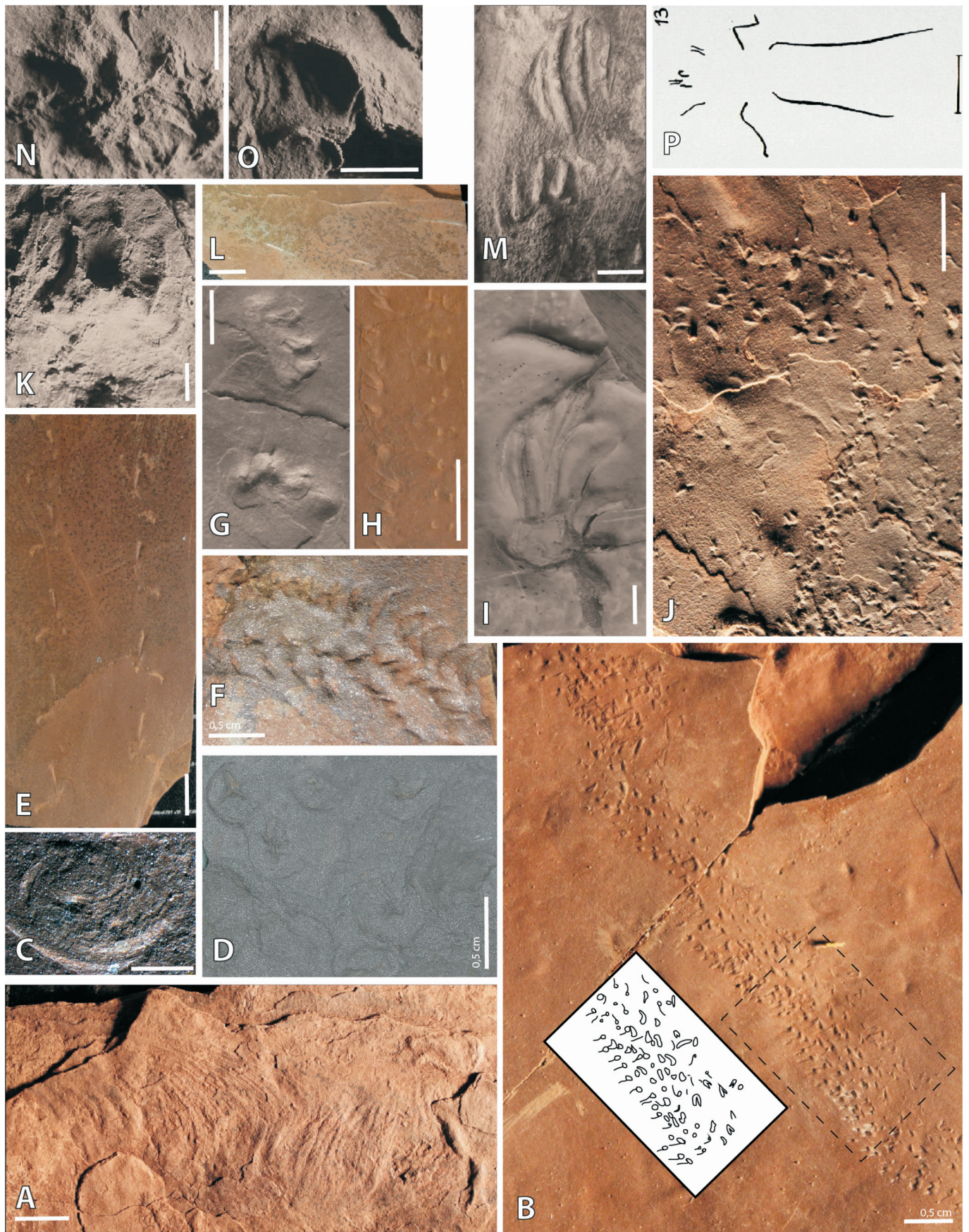
Figure 1. Ichofauna of the Late to Middle Permian Upper Hornburg Formation (Saxony-Anhalt, Germany); **A**, microbial mat; **B**, *Heterotripodichnus divaricatus*; **C**, *Pseudesteria graciliformis*; **D**, several *Medusina limnica*; **E**, *Lithographus niersteinensis*; **F**, *Multipodichnus reptatis*; **G, I, K, M, N, O**, tetrapod tracks ind.; **H**, *Permichnium unistriatum*; **J**, *Permichnium unistriatum* and other traces; **L**, potential 'Natichnia' (swimming traces); **P**, 'Volichnia', sketch from from Gebhardt and Lützner 2012. Scale = 1 cm, unless otherwise noted.

Tracks on a Permo-Triassic desert surface in southern Brazil and their therapsid affinities

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Aeolian, cross-stratified sandstones, informally named the 'Pirambóia' Formation, occur along the southern border of the Paraná Basin (Brazil), and are stratigraphically located between the Guadalupian–Lopingian Rio do Rasto Formation and the Induan–Olenekian Sanga do Cabral Formation (Fig. 1A). Body fossils were never discovered in this unit, but vertebrate trackways and burrows were recently found at the Ibicuí d'Armada locality (Santana do Livramento municipality, Rio Grande do Sul State, southern Brazil; Fig. 1B). The best preserved of these trackways (SLIA-1; Fig. 1C) comprises a sequence of 14 manus and pes tracks, preserved as concave epireliefs. Using the morphological features of the SLIA-1 trackway, we identified heteropod quadrupedal trackmakers, being that the feet are about 50% larger than the hand impressions (Fig. 1D–F). Both autopodia impressions are pentadactyl, mesaxonic and palmigrade/plantigrade (Fig. 1D–G). The manus tracks are rotated inward (~30°) in relation to the trackway main axis. The feet have a well-marked heel and, in some footprints, the plantar pads are visible. Body and tail drag traces are absent and claw impressions are subtle in the pes tracks (Fig. 1E–F). The comparison of the SLIA-1 with another ichnotaxa allowed the recognition of morphological affinities with *Chelichnus* (=*Laoporus*), a common ichnogenus in the Permian aeolian deposits worldwide, and with trackways attributed to dicynodonts, mainly those from the Teekloof and Vera formations from the Lopingian of South Africa and Norian of Argentina, respectively. The complete description of the SLIA-1 trackway is in progress, and so is the dating of the detrital zircons recovered from the ancient aeolian dunes at the Ibicuí d'Armada locality. Finally, the presence of possible therapsid tracks in the 'Pirambóia' Formation in southern Brazil can fill the knowledge gap about the biodiversity in the deserts of western Gondwana during the end-Permian biotic crisis and the faunal recovery after that.
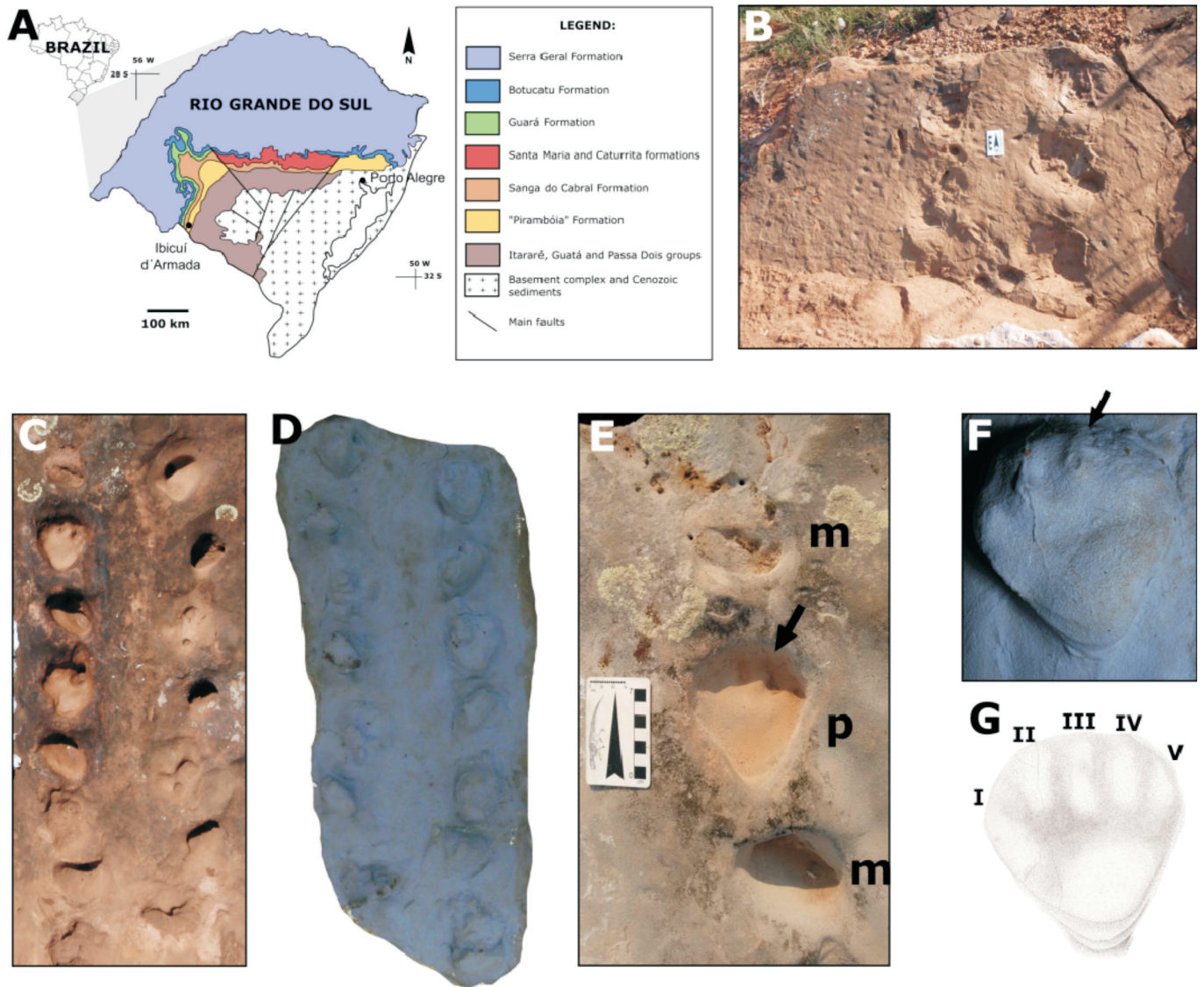
Figure 1. Tracks in the aeolian 'Pirambóia' Formation of southern Brazil. **A**, Geological context of the track site near Ibicuí d'Armada (Santana do Livramento municipality, Rio Grande do Sul State, southern Brazil). **B**, General view of the tracks in the outcrop. **C**, The trackway SLIA-1. **D**, The silicon cast of the SLIA-1 trackway. **E**, Detail of the trackway SLIA-1, showing two left manus (m) and one left pes (p). Black arrow points to the claw imprints. **F**, Detail of the silicon cast of a left footprint in the SLIA-1 trackway, showing the claw imprints (arrow) and the triangular shape of the pes with a well-defined heel. **G**, Interpretative drawing of F (digits are numbered from I to V). Scales in B and E are 8 cm long.

Tetrapod trackways and the Permian Ecca-Beaufort contact in the Estcourt District, Kwazulu Natal Province, South Africa

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The contact between the Permian Ecca and Beaufort Groups (Karoo Supergroup) is diachronous in South Africa and has been the subject of much debate, with different criteria having been used to define it in the past. It is currently accepted that the lithological contact between the Ecca and Beaufort Groups is a palaeoshoreline that marks the transition from aqueous to continental environments. In the Estcourt district of KwaZulu-Natal Province, below the Ecca-Beaufort contact, a remarkable palaeosurface exposes a number of unique trace fossils of medium to large tetrapods, fish and invertebrates. Among these trace fossils are at least six body impressions that are thought to have been formed by a large rhinesuchid temnospondyl. Rhinesuchidae is the only temnospondyl family present in the Permian Beaufort Group of the main Karoo Basin, and are thought to have been the dominant predators in fluviatile, lacustrine and possibly some shallow marine ecosystems. These body impressions are preserved along with associated swimming traces, which provide unique insights into the behaviour of rhinesuchid temnospondyls. These traces show that the animals swam using an undulatory motion of the tail and held their legs tucked in next to the body, similar to extant crocodiles. Careful documentation of the sedimentary facies in the study area shows the presence of the Waterford Formation at the ichnofossil site, which has implications for the placement of the Ecca-Beaufort contact in this part of the main Karoo Basin.
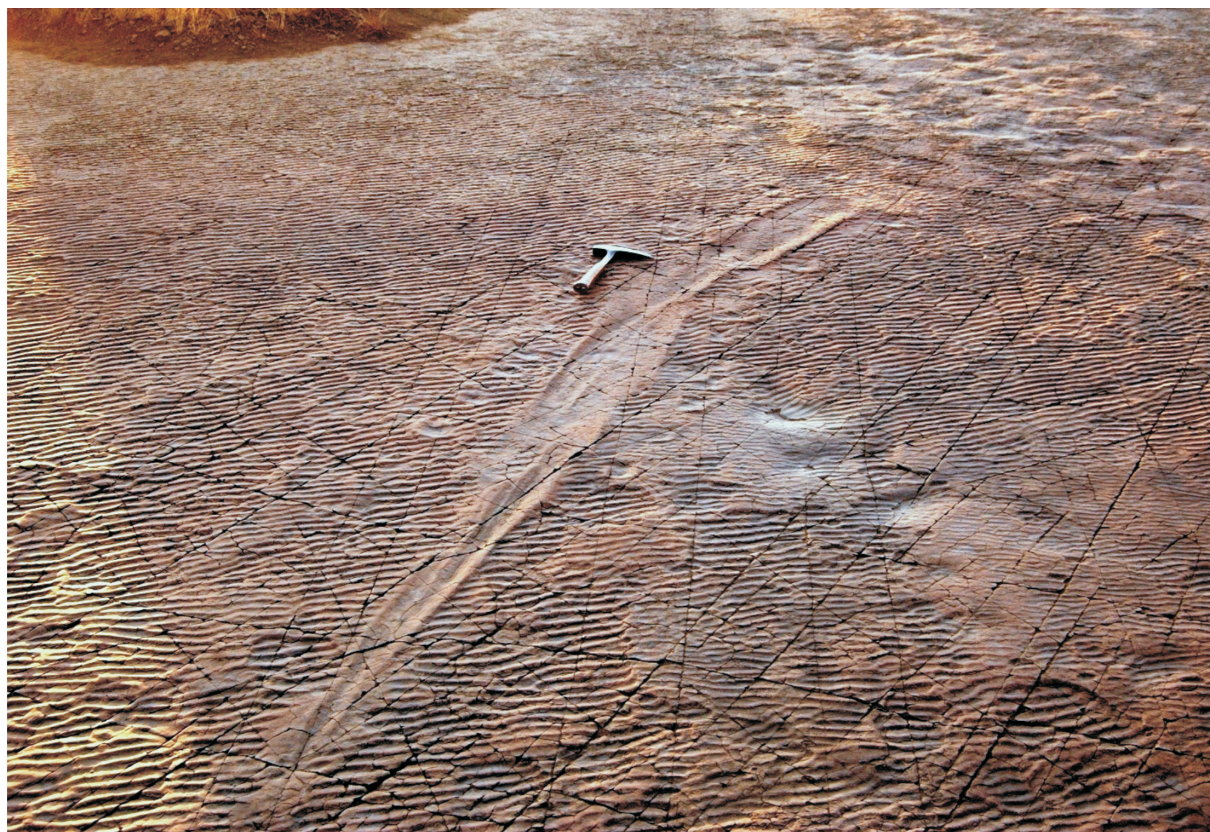
Figure 1. Ripple-marked palaeosurface exposed in the Rensburgspruit, with one of the better-preserved tail and body impressions, which are interpreted as having been made by a rhinesuchid amphibian.

Burrowing as a necessity for survival: ichnological lessons from burrows of *Smaug giganteus* in South Africa

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Casts of vertebrate burrows date back to the Permian in the Karoo Basin in South Africa. Although mammals are amongst the greatest architects of burrow design, the best modern burrowing architects are the sungazer lizards (*Smaug giganteus*, formerly *Cordylus giganteus)* that dig highly advanced tunnel systems in specific soil types in the northeastern Free State and Highveld regions (eastern Mpumalanga) of South Africa. During an elaborate relocation experiment, we excavated 1050 burrows to move the occupants to safety, and observed not only the architecture of the burrows, but also the behaviour of the burrow-makers.

The *Smaug giganteus* burrows are nearly straight to slightly curved (no spiralling), range in length from 2 to 5 m and terminate in a chamber that is slightly elevated from the rest of the burrow. Few burrow entrances face south, and most burrows have a preferred orientation towards the northwest or setting sun. In cross-sectional view, the burrows are kidney-shaped (average diameters: ~15–20 cm) and invariably show a clearly defined 'middelmannetjie', an elevated longitudinal ridge on the burrow floor (Fig. 1). The burrows are often made close to termite mounds, and are dug only in Westleigh or Avalon soils with high water tables and a prominent soft plinthic B horizon.

Data gathered in this study show, among others, that: a) *Smaug giganteus* live in separate colonies in burrow clusters of up to 20 burrows; b) the lizards are extremely good at house-keeping, never foul their 'homes', and use a communal toilet facility at least 20 m away from the closest burrow cluster; c) the lizards are opportunistic and only forage a few metres away from their burrows; d) the burrow chamber may be shared with specific amphibians; e) cross-gender burrow sharing is unusual, but 'family burrows', occupied by a male, a female, and two juveniles, were occasionally noted; f) females may share their burrows with up to two juveniles in winter; g) juveniles are never found alone in a burrow.

Relocation of 1050 lizards to man-made burrows in the Golden Gate Highlands National Park saved only 60 animals from predation and, although the relocated groups were kept in their original colonial groups, the destruction of the natural social system led to the demise of hundreds of lizards. After 20 years, the 60 surviving individuals have established a new social structure and their burrow numbers reached the maximum carrying capacity of the area with suitable soil types. This study shows that the survival of this opportunistic feeder species depends not only on the stability of the social structure, but also on the availability of the 'burrowable' substrates (soil types), food resources (mostly dung beetles) and fire. The latter is needed for keeping the *Themeda triandra* grassland short enough for the lizards to move efficiently between the communal toilet sites and burrows, where they return very quickly if warned of the presence of predators. The results also indicate that the burrows are permanent dwelling structures that are constructed for survival and shelter. The carefully chosen soil types, in areas with high groundwater tables and relatively stable temperatures, possibly allow the survival of the burrow occupants in both extreme summer and winter temperatures.
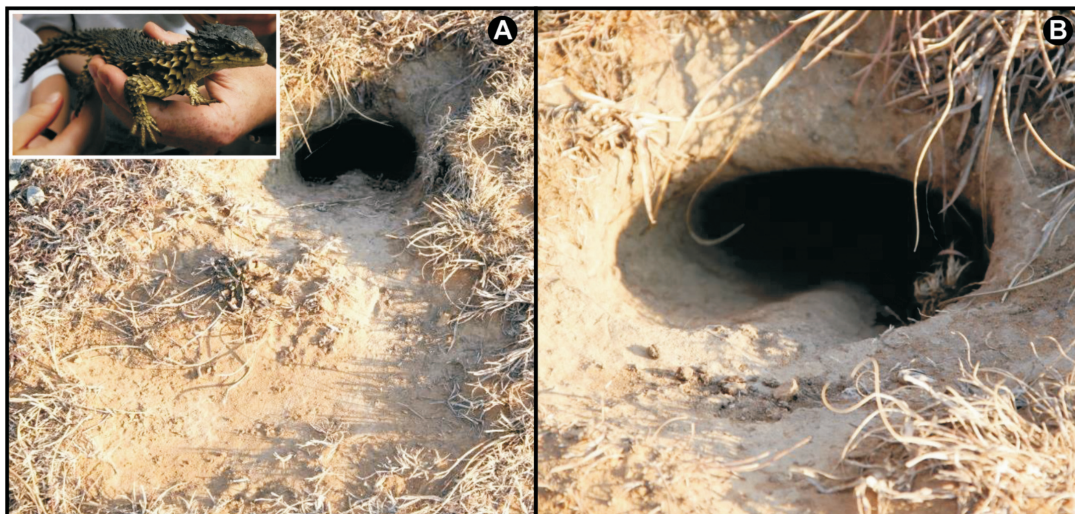
Figure 1. Sungazer lizard (*Smaug giganteus* – inset) and burrows with distinct, kidney-shaped cross-sections; well-defined, central ridges (~3 cm wide) as well as a 'plaza', a bare patch of ground near the burrow entrance, which is used by the burrow occupants for foraging and basking in the sun. Photographs courtesy of S. Parusnath and Science Dump.

A trace fossil assemblage from 'lingulid mud beds' in the Upper Devonian Witpoort Formation, Witteberg Group, South Africa

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Trace fossils associated with an occurrence of lingulid brachiopods from the Upper Devonian Witpoort Formation (Witeberg Group, Cape Supergroup) of South Africa. Lingulids (*Dignomia* cf. *lepta*) occur in great abundance in an up to 12 m thick mudstone unit, which extends for at least 3 km along strike on Governor's Kop ridge to the east of Grahamstown (Eastern Cape). The taphonomy of lingulid shells suggests autochthonous burial. Other shelly faunas are absent from these deposits. The bioturbated mudstone contains cylindrical vertical and horizontal burrows, feeding traces (*Spirophyton*) as well as spiral coprolites. A laminated, fine-grained sandstone interbed preserves vertical walled elliptical burrows (*Lingulichnus*), vertical crater-shaped burrows connected by horizontal back filled burrows (?*Diplocraterion*), epichnial, bisearially lobate trails (?*Nereites*) and miniature *Phycodes*-like galleries. The underlying ~30 m thick arenaceous unit records a progression from trough and planar cross-bedded sandstones with *Altichnus* and *Selenichnites*, to low angle cross-bedded and planar laminated tabular sandstone sheets with cylindrical vertical burrows (*Skolithos*). These sandstones indicate a shallowing from shoreface to foreshore; the overlying lingulid mudstone bed represents a backshore lagoon. A shallow water, low-energy depositional setting is suggested by *Kinneya*-like wrinkle structures. Numerous plant fragments indicate fluvial input, which may have contributed freshwater to the lagoon. The laminated sandstone interbed is interpreted as a washover fan deposit. Given the monospecific brachiopods and associated ichnofossils, we propose that the lagoonal environment was inhabited by an opportunistic fauna, tolerant of stressful local conditions including fluctuating salinity. This mudstone horizon represents a more marine influenced backshore setting compared to the proximal fresh-to-brackish water palaeoenvironments indicated by the other mudstone units of the Witpoort Formation.
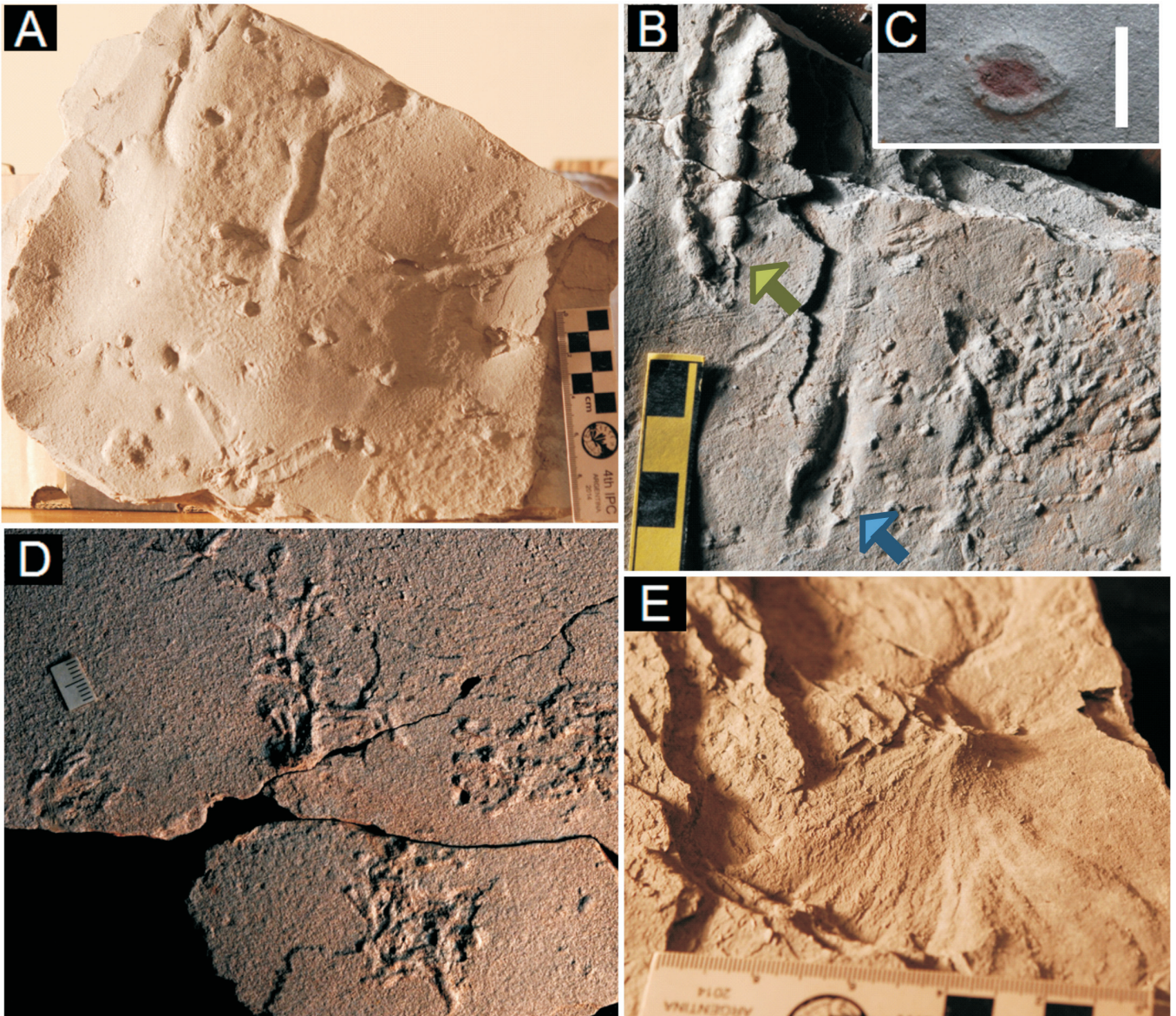
Figure 1. **A–D**, Traces from a fine-grained sandstone unit. **A**, Trace fossils on the rippled palaeosurface include funnel-shaped verti-
cal burrows interconnected by horizontal back-filled burrows (?*Diplocraterion*). Scale bar = 10 cm. **B**, Slab with numerous horizontal
trackways including a biserially lobate trail superficially resembling *Nereites* (green arrow) and preservational variant thereof (blue
arrow). Scale in cm. **C**, Walled burrow (*Lingulichnus*) with oxidized central tunnel. Scale bar = 1 cm. **D**, *Phycodes*-like galleries. Scale
bar = 1 cm. **E**, *Spirophyton* in mudstone Scale bar = 1 cm.

Ichnopedofacies of the Upper Triassic Chinle Formation, southeastern Utah: Implications for pedogenesis, sediment accumulation rate, valley formation, and palaeoclimate

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We systematically integrate ichnological and pedological features of the Upper Triassic Chinle Formation into ichnopedofacies (IPF) to interpret stratigraphic variations in palaeoenvironments, physicochemical conditions, and palaeoclimate in the NE Chinle Basin. The Chinle Formation in the Stevens Canyon area, SE Utah, represents fluvial, palustrine, and lacustrine strata deposited in a continental back-arc basin on the western edge of Pangea under a megamonsoonal climate with increasing aridity towards the end of the Late Triassic. Seventeen ichnofossil morphotypes and six palaeosol orders were combined to form 12 IPF, whose development was controlled by autocyclic and allocyclic processes, and hydrology. IPF in the NE Chinle Basin indicate both long-term drying of climate and short-term, wet–dry fluctuations. Lateral distribution of IPF indicate depositional energy, sedimentation rate, and height of the water table decrease with increasing distance from fluvial systems, and indicate the presence of incised palaeovalleys. Landscape degradation, basin subsidence, and salt tectonics influenced palaeovalley formation. Valley incision was additionally controlled by the shifting from wetter to drier climates, while valley fill likely occurred during shifts back to wetter intervals. Sedimentation varied during Chinle Formation deposition: (1) high, nonsteady in the Moss Back Member; (2) low, nonsteady in the Petrified Forest and lower Owl Rock members; (3) high, nonsteady in the middle Owl Rock Member; (4) high, steady in the upper Owl Rock Member; (5) high nonsteady in the Church Rock Mbr. The water table was controlled by precipitation levels and increases in depth up section. High water tables in the upper Chinle Formation are present in proximal fluvial deposits from losing rivers. Lacustrine deposits were uplifted by salt tectonism and reworked by fluvial systems. The only evidence of lake systems in Stevens Canyon area are oncoid clasts in laterally accreted conglomerate beds. IPF indicate megamonsoonal circulation continued until the end of the Triassic Period. IPF enable higher resolution reconstructions of palaeoenvironments and physiochemical conditions, and can aid identification of sand-in-sand and silt-in-sand palaeovalleys. IPF are valuable tools for evaluating lateral and vertical fluid conductivity, subsurface facies architecture, and reservoir characterization in continental settings which contain hydrocarbons.

Figure 1. Distribution of trace fossils, pedogenic features, and palaeosols in the members of the Upper Triassic Chinle Formation in southeastern Utah near Canyonlands National Park, with interpretation of palaeoprecipitation throughout the formation.

Vertebrate burrows of the Lower Triassic Fremouw Formation, Beardmore and Shackleton Glaciers, Central Transantarctic Mountains, Antarctica: Comparisons to other Gondwanan and Laurentian examples

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Vertebrate burrows have been reported from Early Triassic continental deposits from the Central Transantarctic Mountains of Antarctica, but most descriptions have been based on few examples. Recent discoveries at several localities in the Beardmore Glacier area, however, provide more detailed information on the architectural and surficial burrow morphologies and their occurrences in relation to the Permian-Triassic boundary (PTB), which represents the greatest mass extinction (ME) of all time. The Lower Triassic Fremouw Formation contains fluvial and floodplain deposits that record braided rivers and well drained, weak to moderately developed palaeosols. The lowest interval of burrows is at Coalsack Bluff and is ~2 m above the PTB. These are open helical burrows ~10–15 cm in diameter, and eliptical in cross-section; two whorls are visible in outcrop but more are possible. In a similar stratigraphic position at Graphite Peak (GP) are burrows preserved at the base of the first large fluvial sandstone of the Fremouw Formation that cuts into the underlying green to grey mudrock. These burrows exhibit the W cross-section pattern and range from ~60–70 cm in diameter with scratch patterns along the based of the burrow wall; they are subhorizontal in orientation. Burrows of similar size and morphology are found slightly higher at Wahl Glacier and contain terminal chambers with wall scratches. The smallest helical burrows, 2 cm in diameter and expressing ~3 whorls, occur in the upper part of the lower Fremouw Formation at GP. In the same stratigraphic position are weathered remains of silicified burrow remnants that are 5–7 cm in diameter with the W-shaped cross-section and scratch marks on all surfaces. These burrows represent a hydroclimate shift to better drained conditions with no dead zone associated with the ME. Antarctic burrows compare well to the more simple architectures in Lower Triassic deposits of the Karoo Basin, but less so to more open helical and penetrative vertebrate burrows in the Upper Triassic Chinle Formation. Antarctic burrows have similar architectural and surficial morphologies compared to the simple vertebrate burrows in the Lower Jurassic Navajo Sandstone in southeastern Utah.
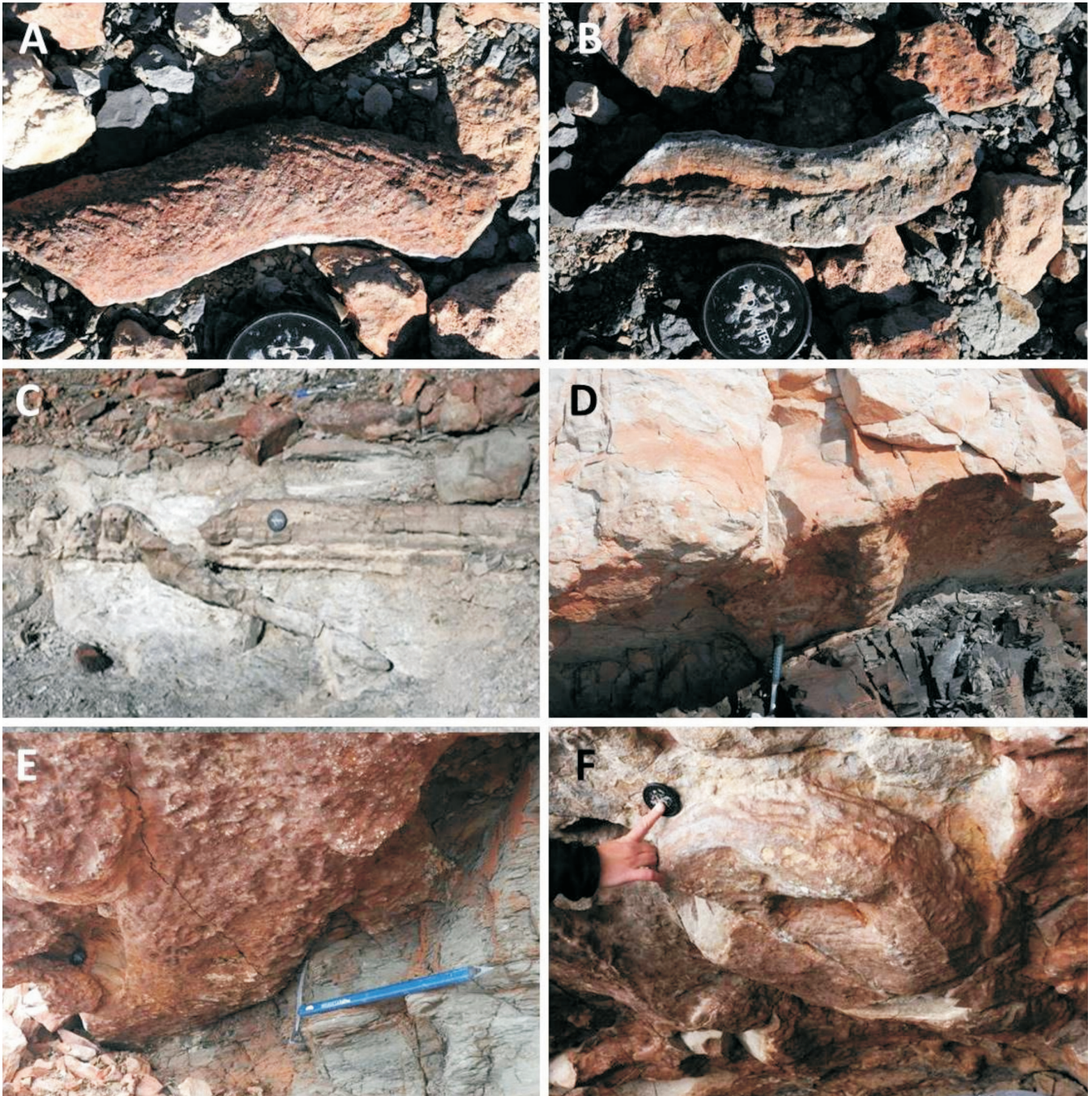
Figure 1. Vertebrate burrows from the Lower Triassic Fremouw Formation, Beardmore Glacier region, Antarctica. Lens cap is 6 cm; ice axe is ~70 cm long. **A & B**, Small-diameter burrow as viewed from top (**A**) and bottom (**B**), revealing the W-shaped and longitudinal, crossing scratch marks. Graphite Peak locality. **C**, Large-diameter burrow showing entrance and two downward whorls to a subhorizontal tunnel; surfaces with scratch patterns similar to images A and B. **D**, **E** & **F**, Mega-diameter burrows showing W-shaped cross-section, scratch patterns, and terminal chamber (F).

Understanding the distribution of ichnofossils in eolian deposits: examples from the Lower Jurassic Navajo Sandstone

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Ichnofossil distribution in eolian deposits has been discussed in many papers, with emphasis placed on comparisons to modern eolian systems. The *Entradichnus* ichnofacies was proposed for eolian deposits, with palaeoclimate and moisture as the driving mechanisms behind ichnofossil distribution, however, it is for all lithofacies that represent all subenvironments and physicochemical conditions, which is over-generalized. Study of ichnofossil diversity, distribution, abundance, and lithofacies associations in the Lower Jurassic Navajo Sandstone in SE Utah illustrates how the activity of microbes, plants, invertebrates, and vertebrates reflect environmental, ecological, pedogenic (soil formation), and hydroclimatic settings. These associations also reflect degrees of landscape stability and pedogenesis, from local and very short term to regional and very long term, based on the modification of bounding surfaces. Eolian bounding surfaces are defined as 3rd order (reactivation), 2nd order (superposition), 1st order (interdune migration), and super surfaces (regional nondeposition, or erosional), in order generally of increasing degree of bioturbation, diversity, abundance, and pedogenesis. Third and 2nd order surfaces are of shortest duration and typically display little to no bioturbation or pedogenesis. When preserved, it is shallow, low abundance, low to high diversity, and short-lived, representing mist-moistened surfaces. First order surfaces are local to regional, with weak to strong pedogensis, reflecting greater amounts of moisture; regional surfaces are more likely stabilized by a change in hydroclimate with increased influence of groundwater and precipitation. Greater landscape stability is generaly reflected by more penetrative, tiered, and diverse traces. The shortest duration surfaces contain mostly invertebrate trace fossils; vertebrate footprints are typical of moist dune surfaces and lacustrine margin deposits. Vertebrate burrows are found originating from short- to long-term dune and interdune surfaces, with greater numbers reflecting several generations. Lacustrine deposits represent short- to long-term duration of water table levels above the ground surface, dominated by microbial traces that represent phototactic and chemotactic behaviours. Lacustrine surfaces represent flooding and maximum lake extent, which has been traced to over 2 km in lateral extent. These deposits grade laterally into and interfinger with dune and pedogenically modified interdune deposits, which contain plant, invertebrate, and vertebrate traces.
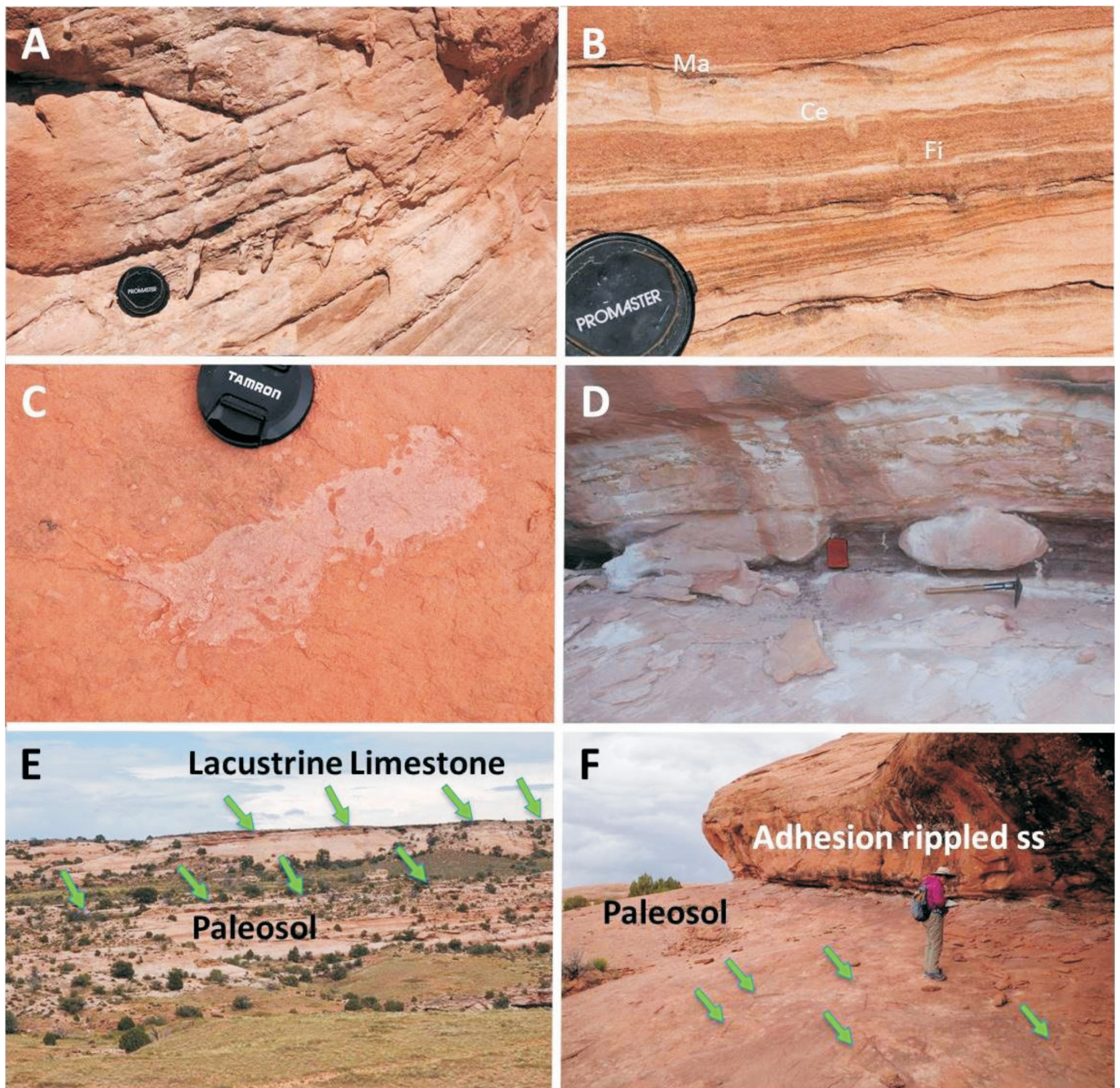
Figure 1. Trace fossils from the Lower Jurassic Navajo Sandstone, Utah. **A**, *Cylindrichum* isp. along 3rd order surfaces. **B**, *Maconopsis* (Ma), *Celliforma* (Ce), and *Fictovichnus* (Fi) in thin-bedded, planar laminated beds of interdune deposits. **C**, Rhizohaloe with *Naktodemasis bowni*, reflecting arthropod–plant interactions. **D**, Megadiameter burrows terminating in interdune deposits, likely originating from a stabilized 3rd order surface. **E & F**, First-order surfaces that are likely super surfaces defined by a high water table producing a lake (**E**) and a palaeosol with extensive trace fossils and pedogenic features that exhibit lateral variability (**F**).

Early Jurassic palaeoenvironmental change in Moyeni, SW Lesotho: from Hettangian dinosaur-trampled surfaces to Toarcian flood basalts

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The Stormberg Group in the main Karoo Basin of southern Africa encompasses the geological history of the Late Triassic-Early Jurassic in southern Gondwana and is associated with the end-Triassic mass extinction event. The depositional environment over this period shifted from a semi-arid fluvio-lacustrine to an aeolian system before the outpouring of the Lower Toarcian continental flood basalts (Drakensberg Group). We integrated geological methods (e.g. field mapping, sedimentary and ichnofacies analysis) for a high-resolution documentation of the palaeoenvironmental changes in Moyeni (SW Lesotho). Here, the fluvio-lacustrine upper Elliot Formation boasts two major ichnosites, which are ~65 m apart vertically. The lower site is well known, but the upper Moyeni ichnosite has been newly discovered at Mampoboleng (Fig. 1). It preserves more than 50 tridactyl footprints, some of which are up to 48 cm in length and form trackways. These tridactyl theropod tracks are found on a ripple marked surface at the top of a 17 m thick, interbedded mudstone and sandstone succession, the last of which thins and fines upward (Fig. 1). In the immediate vicinity of Moyeni, the upper Elliot Formation is a succession of mainly very fine to fine-grained sandstone (either massive or with ripple cross-lamination, low-angle cross-bedding) and sandy siltstone with *in situ* carbonate nodules, desiccation cracks, various bone fossils and ichnofossils (e.g. adhesive meniscate burrows). These collectively suggest that the depositional environment, which was prone to flash flooding, was part of a low energy system of rivers and shallow lakes in the earliest Jurassic. However, ongoing aridification gave rise to a wet aeolian system that was dominated by large, windblown sand dunes in the Sinemurian. Finally, as shown by the overlying pillow lavas and sedimentary interbeds with ephemeral stream and lake affinities, the climate became again seasonally wet during the early stages of the Toarcian Karoo volcanism (Karoo-Ferrar Large Igneous Province).
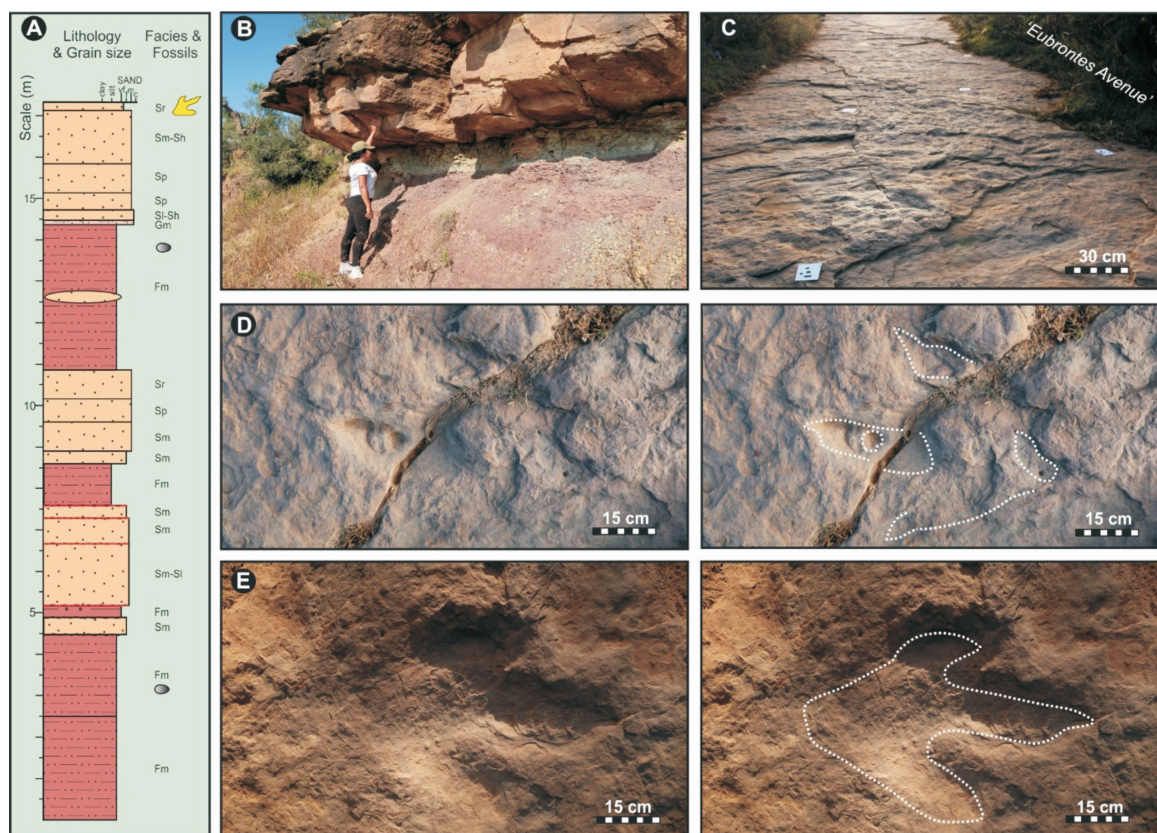
Figure 1. **A**, Sedimentary log of the upper Elliot Formation near Mampoboleng, at upper Moyeni, showing sedimentary features and trace fossils. Facies codes: G – gravel; S – sandstone; F – mudstone; m – massive; l – low-angle cross-bedded; h – horizontally laminated; p – planar cross-bedded; r – ripple cross-laminated. **B**, Overlying the sandy siltstones with *in situ* carbonate nodules, the medium- to coarse-grained sandstones show upward thinning and fining, and terminate in the track-bearing, ripple marked surface. **C**, Overview of the upper Moyeni tracksite, a busy suburban road, aka the 'Eubrontes Avenue' of Mampoboleng. **D & E**, Two representative large tridactyl tracks (and their outlines) showing digital pad impressions (**D**) and claw marks (**D and E**).

Southern Cape Pleistocene trackways in coastal aeolianites

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Pleistocene aeolianites, the consolidated remains of ancient sand dunes and inter-dune areas, extend intermittently along much of South African coastline, where they are exposed in embayments on the coastal plain. Exposed bedding planes are common, and may contain ichnofossils (Fig. 1). Over one hundred Late Pleistocene ichnofossil sites have been identified in aeolianites or foreshore deposits along a 275 km stretch of the southern Cape coastline between Witsand and Robberg. These are in the 60 000–140 000 year age range. Many are ephemeral, being eroded by wind and wave action or collapsing into the sea soon after exposure. Some sites provide the southernmost known occurrence or first documented trackways of extant or locally extirpated mammal species such as elephant, bovids and carnivores. Three reptile track sites and sixteen avian track sites have been recorded. Such sites provide an opportunity for comparison with the tracks of the current fauna. Other sites indicate significant range differences compared with historic records or the skeletal fossil record, and have implications for palaeoclimate and palaeovegetation. Others can be attributed to extinct species or subspecies, representing the first ichnofossils of species that are known from the body fossil record. Humans inhabited the area at the time that these tracks were made. Information on fossil trackways may help in understanding the environment in which these early humans existed, can be directly compared to archaeological remains preserved in caves, and can buttress and strengthen other related areas of interdisciplinary research.
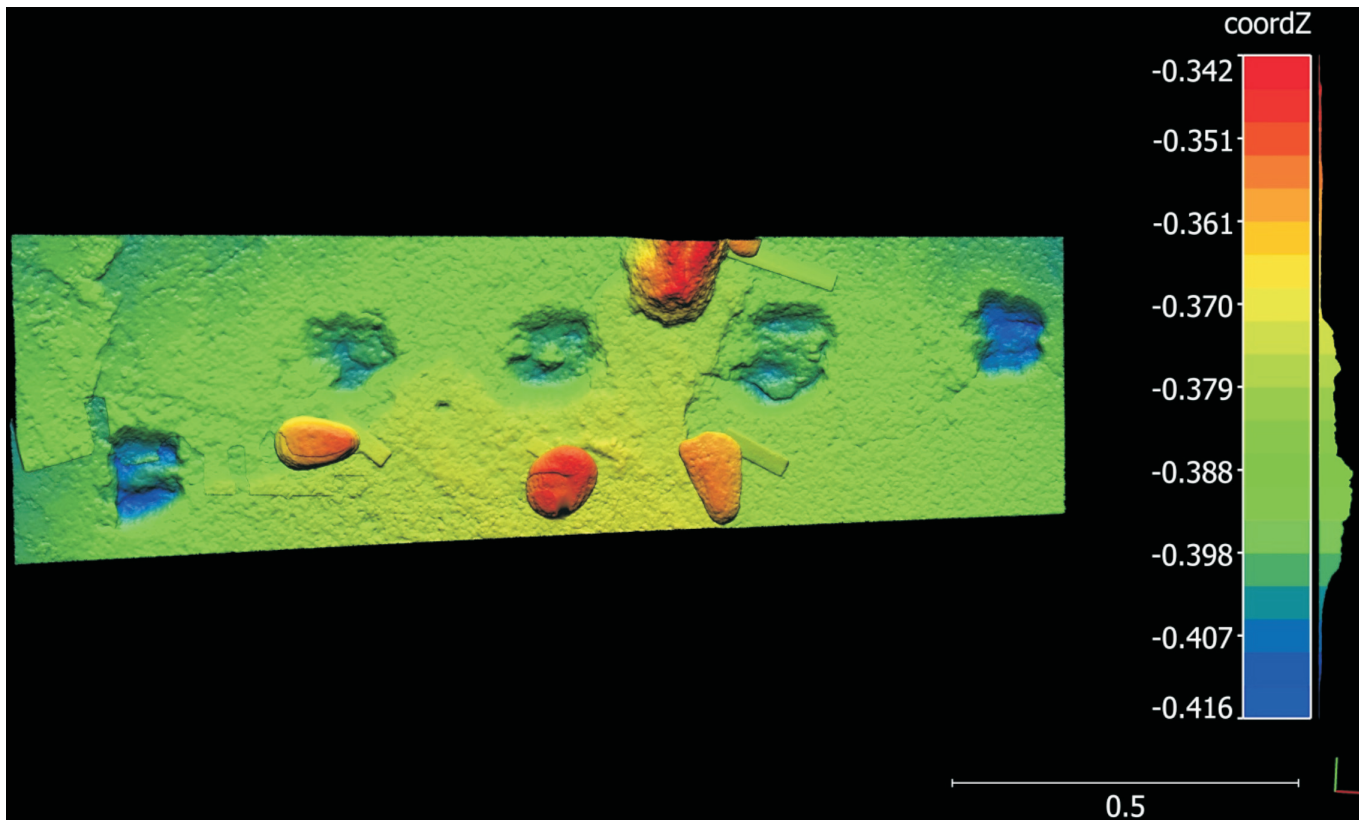
Figure 1. False-colour depth map, based on a photogrammetric model, of a portion of a probable *Syncerus antiquus* (long-horned buffalo) trackway from the southern Cape coast (courtesy of Richard T. McCrea, Peace Region Palaeontology Research Centre).

Figure 2. A slab of sandstone with elephant and artiodactyl trackways in the southern Cape coast. The slab has slid into the ocean since this photograph was taken. The largest elephant track was ~25 cm in diameter.

Crocodylomorph and turtle footprints in dinosaur-dominated Middle Jurassic and ?Lower-mid-Cretaceous ichnoassemblages of the Central High Atlas and High Moulouya regions, Morocco – ichnotaxonomy, trackmakers and implications for palaeoecology

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Footprints of Crocodylomorpha (Archosauria, Pseudosuchia) are rare in Mesozoic ichnoassemblages. However, those of small terrestrial forms (*Batrachopus*) occur in the Late Triassic-Early Jurassic. *Crocodylopodus* trackways of semi-aquatic crocodylomorphs have been found in the Jurassic-Cretaceous. We discovered tetradactyl pes (8 cm long) and associated outwards rotated pentadactyl manus imprints, similar to *Crocodylopodus*, in continental red-beds of the Isli Formation (Middle Jurassic, Bathonian-?Callovian) in the Central High Atlas of Morocco. These ichnites co-occur with small theropod tracks of *Carmelopodus* as well as with sauropod, ornithischian and pterosaur footprints. Large crocodylomorph scratch marks similar to *Hatcherichnus*, well known from the Jurassic-Cretaceous, are part of a diverse dinosaur-dominated ichnoassemblage with theropod, ornithopod, pterosaur, turtle, mammal and invertebrate ichnofossils in the lower Midelt Formation of the High Moulouya region. From this unit, fish and ostracod fossils have also been reported, however the exact age remains unknown (?Lower-mid-Cretaceous, ?Aptian-Cenomanian). The locality, originally called the Mibladen tracksite, was misinterpreted as Jurassic in age. The turtle footprints (5 cm long) occur in trackways, are similar to Jurassic-Cretaceous *Emydhipus* and represent a semi-aquatic animal that frequented the channels and riverbanks in a floodplain to brackish-deltaic environment. Turtles possibly fed on plants, invertebrates and fishes, themselves being a potential prey of crocodylomorphs and theropods. The ichnofauna lacks avian and thyreophoran tracks. Potential sauropod footprints, present in other Lower-mid-Cretaceous assemblages, need further confirmation. The co-occurrence of crocodylomorph and mammal tracks at this Moroccan site is similar to an Angolan Lower Cretaceous site. This is one of very few Early and mid-Cretaceous footprint sites in Africa and the first record of turtle tracks from this epoch on the continent.
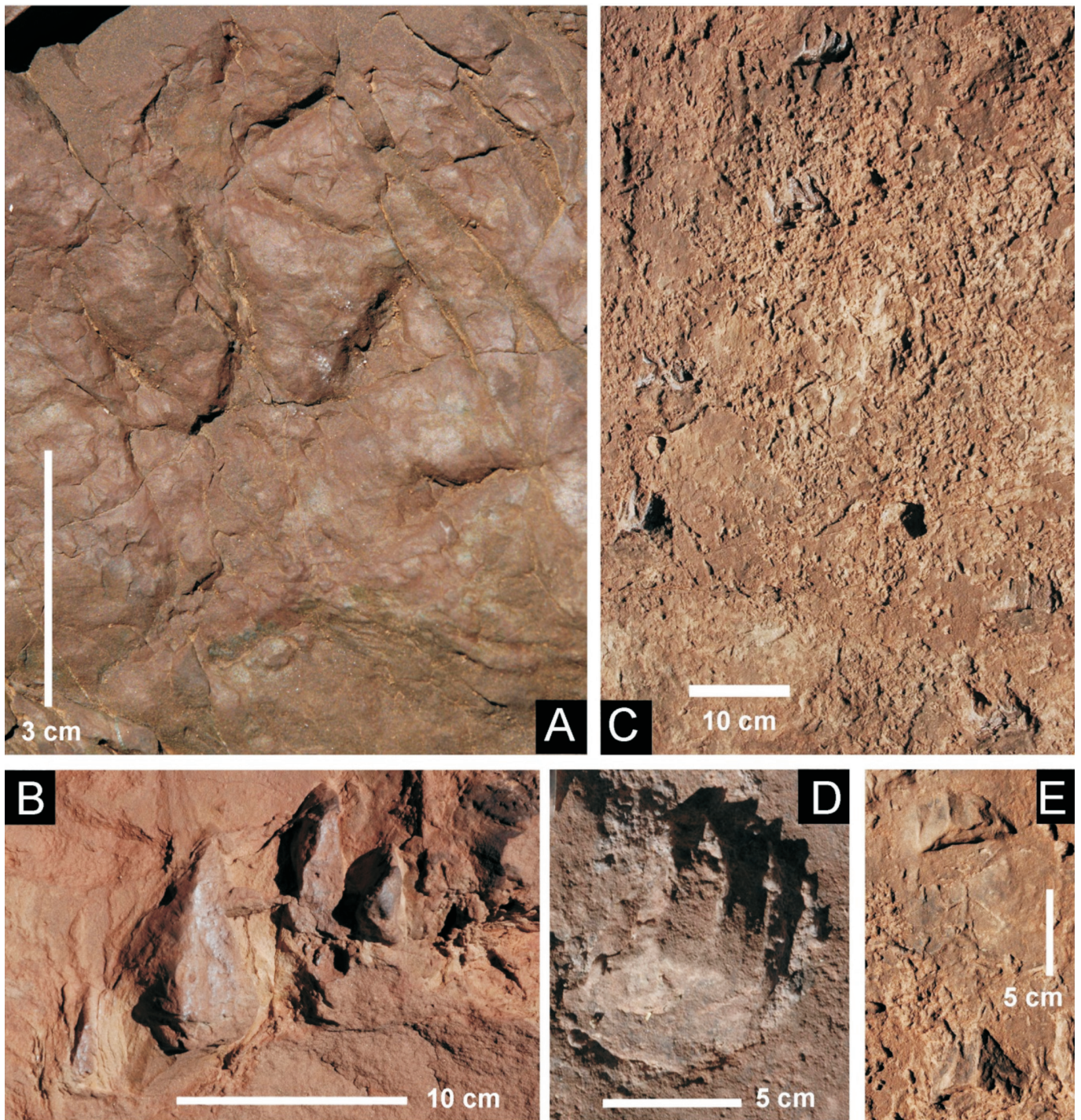
Figure 1. **A**, *Crocodylopodus meijidei* right pes-manus couple (Isli Formation, Middle Jurassic, Bathonian-?Callovian). **B**, *Hatcherichnus* isp. **C–E**, cf. *Emydhipus* isp. **C**, Trackway with pes-manus couples. **D**, Isolated imprint. **E**, Pes-manus couple. B–E are from the lower Midelt Formation, ?Lower-mid-Cretaceous, ?Aptian-Cenomanian.

Desert ichnofaunas: spatial and temporal perspectives

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   Although deserts are commonly regarded as having a poor ichnological record, analysis of trace fossils in space and time may provide valuable insights into secular changes in biotic composition and colonization patterns. Deserts encompass a wide variety of mosaics of habitats or physical units associated reflecting variable patterns of organism activity. Trace-fossil distribution may help to understand the partitioning of desert settings in a mosaic of landscape units through geological time. Five main phases of colonization of desert environments through the Phanerozoic are reconstructed (Fig. 1). The first phase (Cambrian–Silurian) involved animal incursions into coastal dune fields directly from the sea, although it is unlikely that these animals would have remained for long periods of time in coastal deserts. The second phase (Devonian) reflects pioneer invasion of eolian dunes by organisms that left their fluvial habitat to enter temporary or permanently into inland deserts. The third phase (Carboniferous–Permian) involved the colonization of deserts by tetrapods. The fourth phase (Triassic–Cretaceous) consists of a major exploitation of the infaunal ecospace as revealed by the appearance of more varied behavioural patterns in infaunal structures. The fifth phase (Palaeogene–Recent) signals the appearance of modern desert communities. Landscape units, such as eolian sand seas, salt flat and playa lake systems, ephemeral rivers and alluvial fans, provide local spatial heterogeneity and interact in response to regional-scale climate variations in hyper-arid, arid, and semiarid climatic settings. The invertebrate ichnofacies for eolian dunes is renamed as the '*Octopodichnus-Entradichnus* Ichnofacies', whereas the *Chelichnus* ichnofacies is retained for vertebrate trace-fossil assemblages in eolian settings.
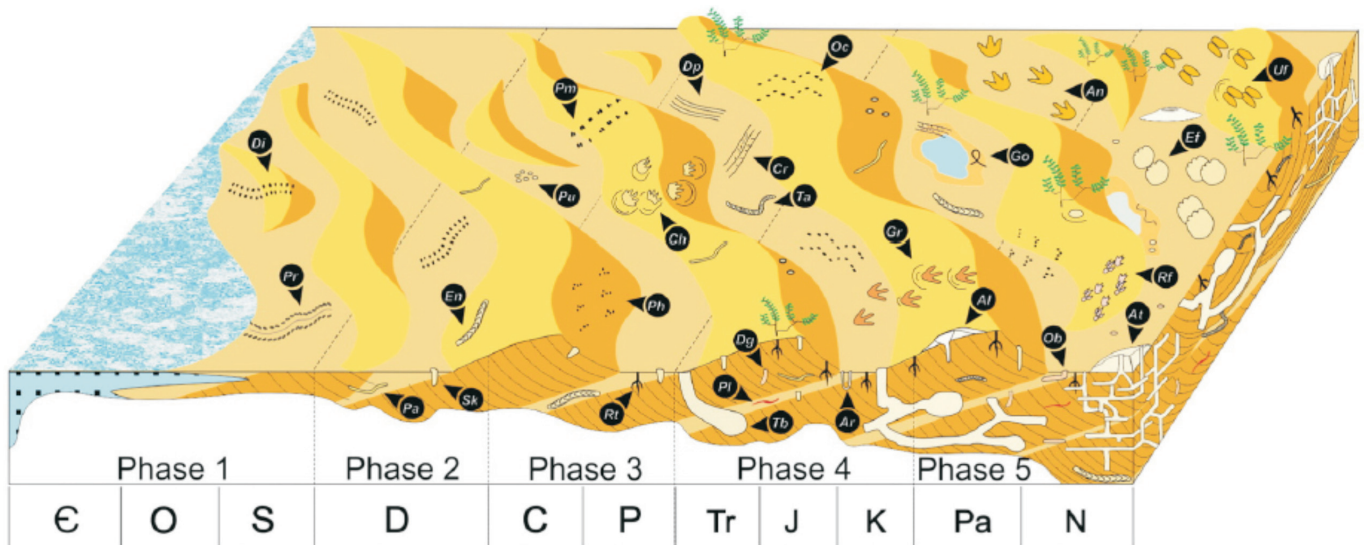
Figure 1. Desert megatrends: five main phases of colonization of desert environments through the Phanerozoic. Al: Antlion burrow, An: *Anchisauripus*, Ar: *Arenicolites*, At: ant's nest, Ch: *Chelichnus*, Cr: *Cruziana*, Dg: *Digitichnus*, Di: *Diplichnites*, Dp: *Diplopodichnus*, Ef: elephant footprints, En: *Entradichnus*, Go: *Gordia*, Gr: *Grallator*, Ob: open burrow, Oc: *Octopodichnus*, Pa: *Palaeophycus*, Pm: *Palmichnium*, Pr: *Protichnites*, Pu: *Pustulichnus*, Rf: rodent footprints, Rt: root traces, Sk: *Skolithos*, Ta: *Taenidium*, Tb: tetrapod burrow, Uf: ungulate footprints.

Cretaceous 'nest scrape display' traces indicate courtship behaviour by large non-avian theropods

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Nest scrape display behaviour, well known among extant ground-nesting birds, may take place in well-defined 'display arenas' or 'leks.' Most such 'play' or 'display' nests are created before actual nests are established and occupied nearby. Although no such traces were known from the ancient track record prior to 2016, discoveries in the track-rich Cretaceous Dakota Sandstone (Early Cenomanian ~97 Mya) of Colorado, have yielded five sites with diagnostic scrapes, formally named as *Ostendichnus bilobatus*. These consist of two parallel troughs, astride a central ridge, with multiple, elongate, narrow, claw traces, and associated theropod tracks (Fig. 1B). Three sites, each with between 10 and 60 scrapes, occur within a narrow stratigraphic zone (~5.0 m) in an area only 6 km in diameter. These indicate heavily-used display arenas in coastal plain settings. Although evolutionary avian/non-avian theropod relationships are based on tangible morphological evidence, palaeontologists also speculate on behavioural similarities between both groups based on intangibles: i.e. potential use of colourful crests, feathers and energetic display for courtship. All such inference was *purely speculative* until theropod scrapes provided actual *physical evidence* of this bird-like behaviour. Isolated *Ostendichnus*-like traces, also known from the Cretaceous (Albian) of Canada and South Korea, suggest this behaviour was widespread. The Cretaceous evidence suggests avian courtship display behaviour originated with non-avian theropods at least 100 million years ago. The traces likely represent early, or Spring-time, breeding season behaviour taking place near future nest sites (representing physical evidence of later phases in the breeding cycle). Thus display arenas point to nearby nest sites, which may be unknown or not preserved.
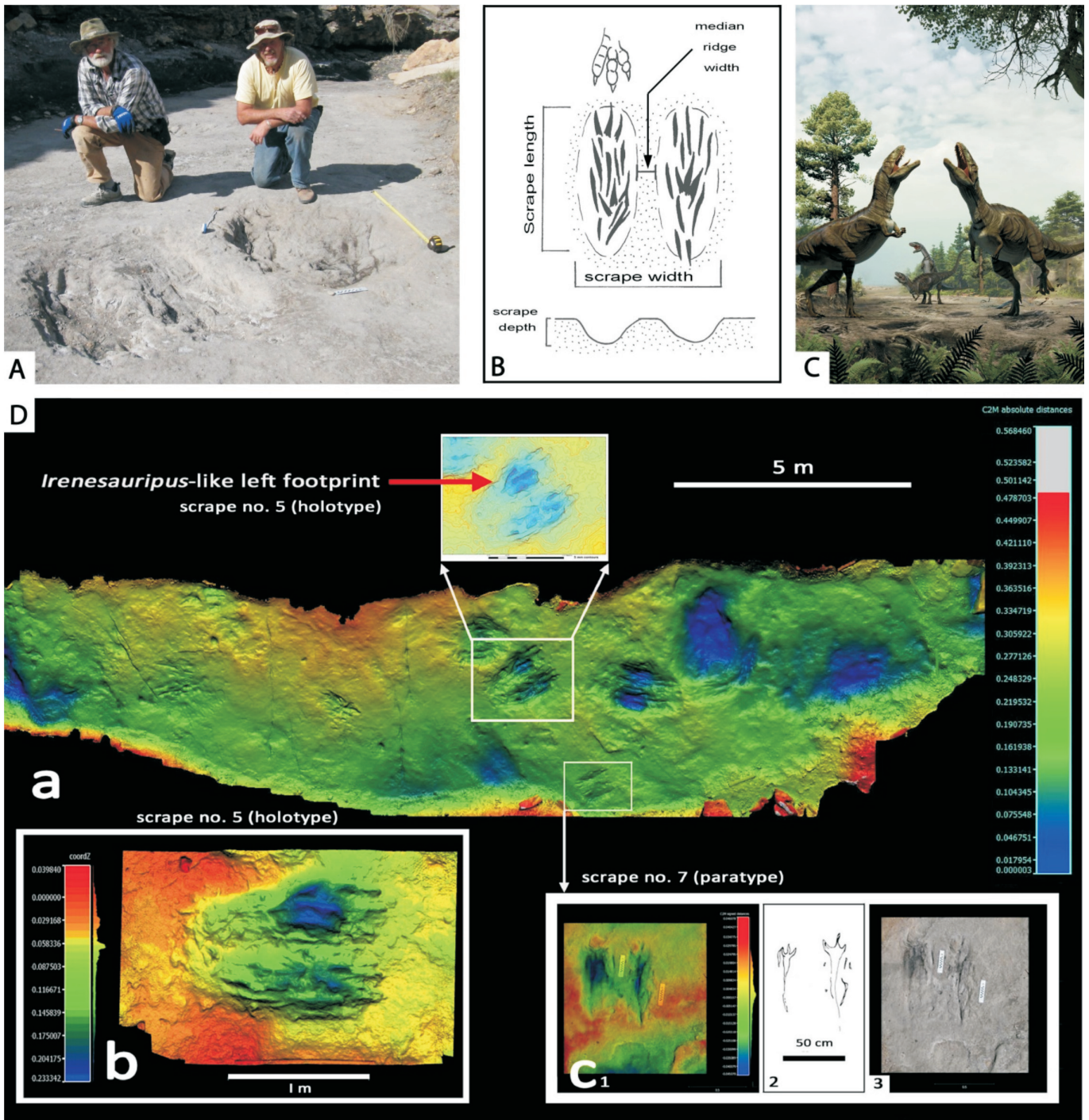
Figure 1. A, Field photograph of Cretaceous theropod display traces, Dakota Sandstone, western Colorado, showing holotype scrape of *Ostendichnus bilobatus* (left). **B**, Schematic plan and cross-section of *O. bilobatus* trace made by functionally tridactyl theropod track. **C**, Reconstruction of *Acrocanthosaurus*-like theropods making *O. bilobatus* display traces. (Da) 3D image of Dakota Sandstone display arena site with detail of *Irenesauripus*-like tridactyl theropod track associate with holotype scrape (Db), and paratype scrape (Dc) made by smaller tridactyl theropod.

Tetrapod ichnofaunas across the Permian–Triassic boundary (PTB): potential and perspective for biostratigraphy, palaeobiogeography and palaeoecology

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Recent research on Late Permian (Lopingian) tetrapod ichnofaunas from Europe and North Africa significantly augmented our knowledge of end-Palaeozoic low-latitude biotas. In these ichnofaunas, typical Permian ichnogenera, including *Batrachichnus*, *Dromopus*, *Erpetopus*, *Hyloidichnus*, *Pachypes*, and *Paradoxichnium*, occur together with typical Triassic ichnogenera, including *Capitosauroides*, *Dicynodontipus*, *Procolophonichnium*, *Protochirotherium*, and *Rhynchosauroides*. The footprints are attributed to small temnospondyl amphibians (*Batrachichnus*), non-mammalian therapsids (*Dicynodontipus*), parareptiles (*Erpetopus*, *Procolophonichnium*, *cf. Capitosauroides*), pareiasaurid parareptiles (*Pachypes*), captorhinids (*Hyloidichnus*), lacertoid neodiapsids (cf. *Dromopus*, *Rhynchosauroides*), and archosauromorphs (*Paradoxichnium*, cf. *Protochirotherium*). The Lopingian ichnofaunas are dominated by parareptilian, captorhinid, and neodiapsid tracks, with rare therapsid and temnospondyl tracks, known from a wide range of depositional environments, suggesting a tetrapod ichnofauna of fairly uniform taxonomic composition and biostratigraphic value. Exceptions concern an apparently lower tetrapod ichnodiversity in eolian substrates and an apparently greater abundance of non-mammalian therapsid tracks in high-latitude tetrapod ichnofaunas of Gondwana. Low-latitude Early Triassic (Olenekian) tetrapod ichnofaunas are characterized by archosauromorph (*Protochirotherium*, *Synaptichnium*, *Isochirotherium*, *Chirotherium*, *Rotodactylus*), lacertoid neodiapsid (*Rhynchosauroides*, *Prorotodactylus*), stem-turtle (*Chelonipus*), procolophonid parareptile (*Procolophonichnium*, *Capitosauroides*), non-mammalian therapsid (*Dicynodontipus*, cf. *Therapsipus*) and temnospondyl tracks (*Batrachichnus*). The most striking differences from the Lopingian ichnofaunas are the abundance and diversity of archosauromorph tracks, the first occurrence of stem-turtle tracks, and the disappearance of captorhinid, and of some parareptile and archosauromorph tracks. The scarcity of non-mammalian therapsid tracks in both Late Permian and Early Triassic assemblages could be due to taphonomic, palaeoecological or ichnotaxonomic reasons. Importantly, the stratigraphic range of several ichnogenera that first occur during the Permian or earlier (*Batrachichnus*, *Capitosauroides*, *Dicynodontipus*, *Procolophonichnium*, *Protochirotherium*, *Rhynchosauroides*) is extended into the Triassic. We cannot determine if the PTB and the boundary between the *Paradoxichnium* biochron and the *Protochirotherium* biochron really coincide, because the latest Permian ichnofaunas lack stratigraphic density. Also, Induan ichnofaunas comprise a few Gondwana sites only, with small reptilian footprints that have partly been assigned to *Dicynodontipus* but are of uncertain affinity. Beginning during the Olenekian, the increasing diversity of archosauromorph ichnoassemblages matches the early rise of this tetrapod group reflected in the body fossil record. Additional records and careful track-trackmaker analyses are needed in order to understand the effects of the PTB extinctions and the relationship of contemporaneous low-latitude and high-latitude tetrapod ichnofaunas.
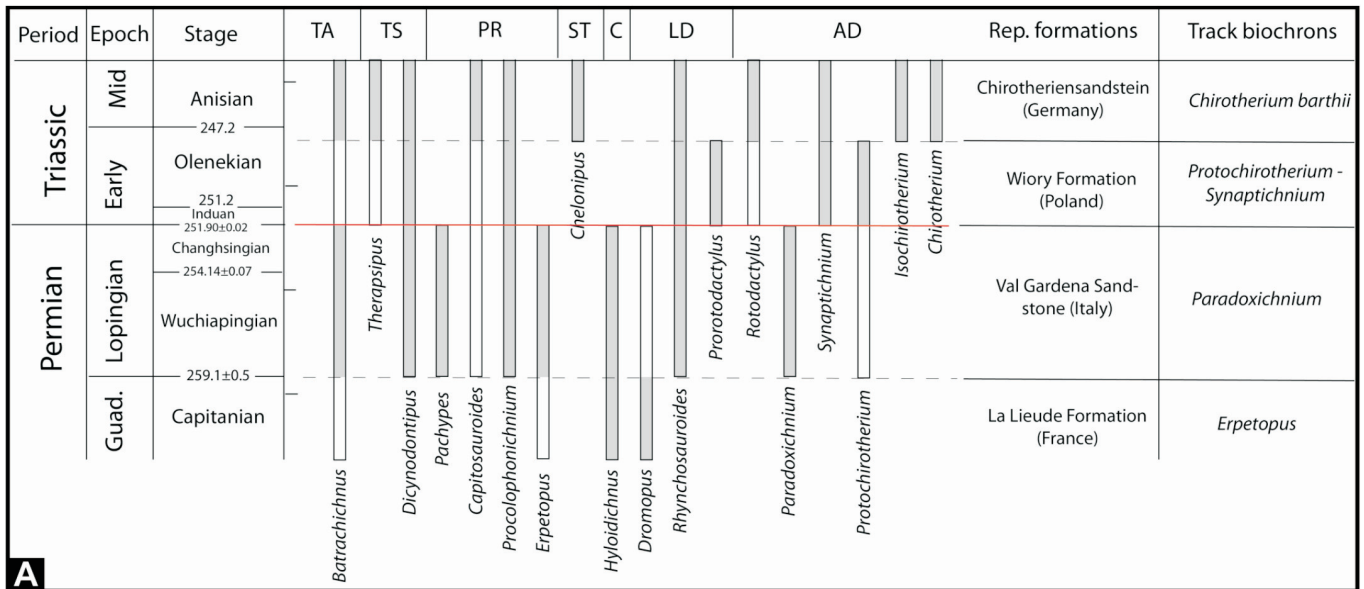
Figure 1. **A**, Biostratigraphic range of Late Permian (Lopingian) and Early Triassic tetrapod ichnotaxa. Grey bars are ichnotaxa occurrences, white bars uncertain or supposed occurrences. Note that the bars cover the entire stratigraphic interval in which the ichnotaxa are found. TA = temnospondyl amphibians; TS = therapsid synapsids; PR = parareptiles; ST = stem turtles; C = captorhinids; LD = lacertoid diapsids; AD = archosauromorph diapsids. (B) Palaeogeographic map after Blackey (2008) with position of Late Permian (1–12, red stars) and Early Triassic tetrapod ichnosites (A–N, blue dots).
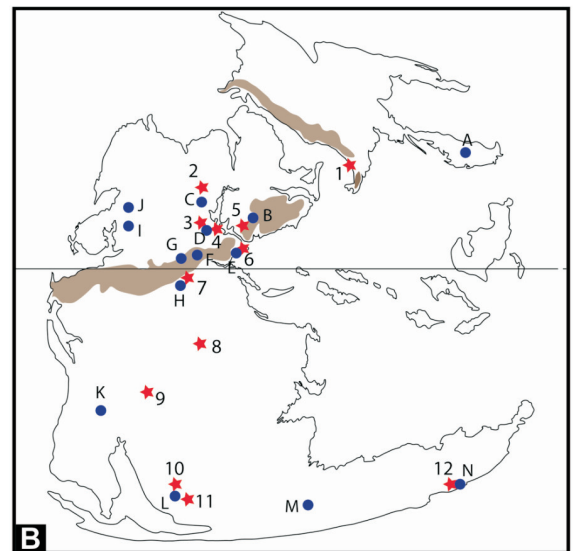
Late Silurian–Early Devonian terrestrialization: ichnology of Lower Old Red Sandstone alluvial deposits, Anglo-Welsh Basin, U.K.

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The Old Red Sandstone comprises predominantly continental redbed deposits of Late Silurian to Early Carboniferous age. Terrestrial faunas from the Late Silurian/Early Devonian are poorly preserved and often fragmentary. However, a diverse assemblage of trace fossils is preserved in the Lower Old Red Sandstone of the Anglo-Welsh Basin, U.K., giving an insight into faunal behaviours in the absence of body fossils. From sedimentological studies, the terrestrial environments represented are perennial and ephemeral rivers, floodplain lakes, alluvial fans and marginal marine environments and the trace fossils are preserved mainly in the fine-grained components of these environments. The associated ichnocoenoses reflect the activities of aquatic and semi-aquatic fauna and include meniscate backfilled burrows and arthropod trackways, resting and foraging traces (Fig. 1). Most of the ichnocoenoses can be classified within the *Scoyenia* ichnofacies. The stratigraphic distribution indicates an increase in diversity from the Late Silurian into the Early Devonian. Ludlow-age deposits are dominated by vertical burrows and in the Pridoli, the basal deposits include foraging and resting traces linked to marginal marine deposits so there was probably not a major faunal change. However, from the mid-Pridoli, backfilled burrows and arthropod trackways are widespread, with the appearance of *Beaconites barretti* and *Diplichnites gouldi* Type B at the Pridoli/Lochkovian boundary. At that boundary, there was also a major change in alluvial architecture and provenance. The Lochkovian ichnocoenoses are the most diverse in the Lower Old Red Sandstone.
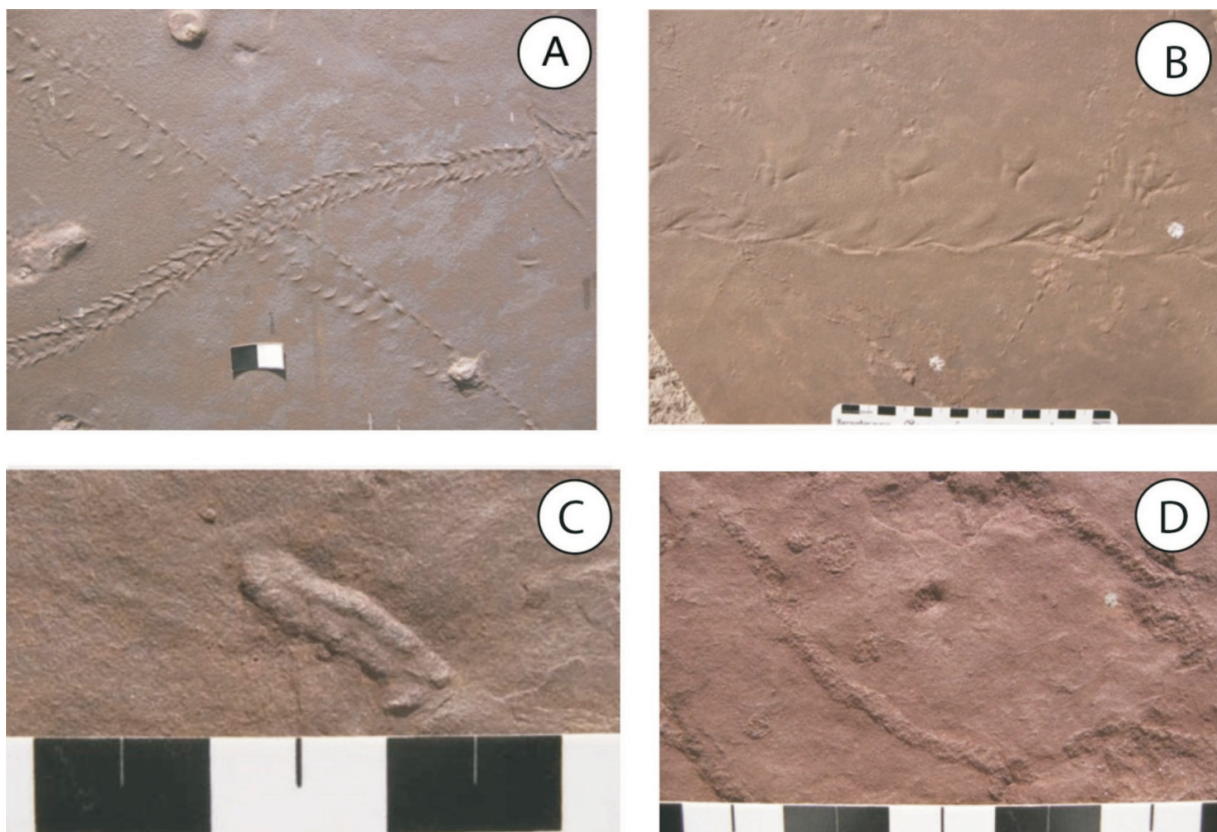
Figure 1. Selected traces from Old Red Sandstone inclined heterolithic strata. **A**, *Diplichnites gouldi* type A. **B**, *Palmichnium* isp. **C**, *Cruziana*. **D**, *Beaconites antarcticus*.

Wolf spider burrows from a modern saline mudflat: morphology and potential of preservation

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We describe burrows excavated by the wolf spider *Pavocosa* sp. (Lycosidae) from the Gran Salitral saline lake, La Pampa province, Argentina. The burrows were only found in the sparsely vegetated siliciclastic-evaporitic mudflat on the edge of the saline lake. The general morphology is a simple, nearly vertical (66–88°) and cylindrical burrow, with a slight widening in the lower half, roughly comparable with the ichnogenus *Skolithos* (Fig. 1A). Entrance is circular, slightly narrower than the burrow, and displays silk and some sediment pellets. During a wet period, the burrow entrance was surrounded by small sediment pellets. Active burrows were occupied by an individual and contained an egg sac. Burrow casts are about 10.4–12.3 cm long, the maximum diameter is 1.9–2.9 cm, and the diameter at the entrance is 1.1–1.3 cm. The burrow wall was covered with silk (Fig. 1B) and displayed a surface ornamentation in the form of sets of two linear parallel grooves about 2.8–4 mm long and 2.8–3 mm wide (Fig. 1C), matching the size and shape of the wolf spider fangs. Predation by armadillos makes the entrance funnel-shaped, similar to the ichnogenus *Monocraterion*. *Pavocosa* burrows show a particular environmental distribution (sparsely vegetated saline mudflat) and moderate potential of preservation due to the presence of silk. Although the fossil record of Lycosidae dates back to the Neogene (probably to the Late Cretaceous), until now no fossil Lycosidae burrow has been recognized. Distinctive features of these burrows are a cylindrical shape with a slight widening and a characteristic surface ornamentation.
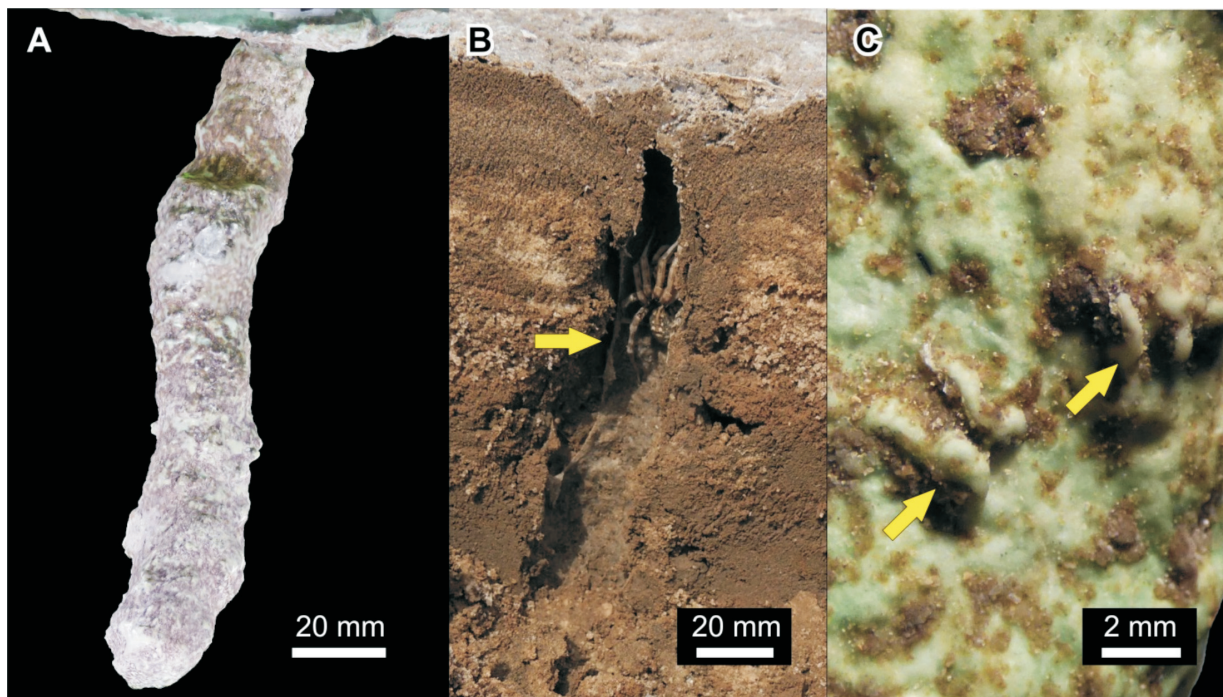

Figure 1. **A**, Plaster cast of *Pavocosa* sp., enlargement on top marks the ground surface. **B**, Occupied burrow (arrow) cut vertically. Note silk on burrow wall. **C**, Detail of burrow cast showing surface ornamentation (arrows).

Titanosaurid trackways from the El Molino Formation (Maastrichtian) of Bolivia (Cal Orck'o, Sucre, Dep. Chuquisaca)

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The Cal Orck'o tracksite lies in a quarry approximately 4.4 km to the northeast of the centre of Sucre (Dep. Chuquisaca, Bolivia) at an altitude of 3028 m.a.s.l. in the Altiplano/Cordillera Oriental. The El Molino Formation (Middle Maastrichtian, Upper Cretaceous) is composed of sandy limestones and claystones. Fossiliferous oolitic limestones, associated with large freshwater stromatolites and nine levels with dinosaur tracks, document an open lacustrine environment. The documented main track level comprises approximately 64 968 m^2 and its surface is almost vertical. A continuous mapping of the site from 1998 until 2015 revealed a total of 12 092 individual dinosaur footprints in 465 trackways. Nine different morphotypes of dinosaur tracks have been documented. Amongst those are several theropods, ornithopods, ankylosaurs and sauropods. A good 26% were left by sauropod dinosaurs. Morphotype E presents coupled oval-shaped manus and large pes imprints (length: 70 cm) with few details, which include characteristic overall slender shape of the tracks, the outward position of the manus and the narrow-gauge configuration. The second morphotype (Morphotype F) has more rounded and axially compressed pes imprints (length 50 cm), but more horseshoe-like manus impressions. The manus shows clear impressions of digit I and V and the trackways are more wide-gauge in appearance. Titanosaurid origin is confirmed by the morphology and configuration of type E, while it is not unambiguous for type F, whose features are obliterated by a peculiar gait and/or by substrate influence. The presence of narrow-gauge sauropod trackways is in contrast to previous studies, which noted a complete absence of this pattern in the Late Cretaceous. As titanosaurids are the only sauropods present during that time period, our observation suggests that trackway width is not an osteological correlate.

Figure 1. Left: Manus-pes couple of titanosaurid sauropod (Morphotype E; scale 10 cm) Right: Manus-pes couple of titanosaurid sauropod (Morphotype F; scale 1 m).

Tetrapod track assemblages from the Upper Triassic Fleming Fjord Formation, East Greenland

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Although the ichnorecord of tetrapods during the Triassic has been the focus of extensive research, the unevenly sampled Late Triassic record leaves many open-ended questions about the composition of tetrapod ichnoassemblages of Norian and Rhaetian age. One of the most diverse records of the Upper Triassic tetrapod tracks comes from the Fleming Fjord Formation of the East Greenland. A detailed analysis of ichnoassemblages, including previous accounts and new material recently discovered, suggest the presence of diversified track assemblages in the Fleming Fjord Formation. Tetrapod tracks have been recorded from two members: Malmros Klint Member and the Ørsted Dal Member. Most of tracks were found in lacustrine succession of the upper part of the Ørsted Dal Member (Tait Bjerg Beds). At least four Upper Triassic tetrapod ichnoassemblages can be recognized in the East Greenland succession. The most interesting ichnoassemblage is in the lower part of the Malmros Klint Member, which is characterized by the highest ichnodiversity and the presence of small to medium-sized tridactyl dinosaur footprints in association with therapsid and pseudosuchian tracks. The track assemblage from the Tait Bjerg Beds displays the dominance of dinosaur ichnotaxa. The known track types from the Fleming Fjord Formation include: *Rhynchosauroides* isp., cf. *Apatopus* isp., cf. *Brachychirotherium* isp. A and B, *Chirotherium* isp., cf. *Batrachopus* isp., *Dicynodontipus* isp., unamaed therapsid track, *Parachirotherium* isp., cf. *Atreipus* isp., *Grallator* isp., *Anchisauripus* isp., *Eubrontes* isp., cf. *Tetrasauropus* isp., cf. *Evazoum* isp., *Eosauropus* isp., large oval-shaped sauropodomorph tracks, *Anomoepus* isp., large Chirotheriidae indet., and large tridactyl footprints (possibly left by theropod dinosaur). These new finds suggest that the diversity, distribution and frequency of tetrapod tracks within the Fleming Fjord Formation are much wider than previously assumed.

Figure 1. **a**, Exposure of the Upper Triassic red beds of the Fleming Fjord Formation, northern margin of Macknight Bjerg, East Greenland. **b**, Slab with a small *Grallator* isp., Malmros Klint Member, Liasryggen (Norian). **c**, Large tridactyl footprint, *Eubrontes* isp., rsted Dal Member, Liasryggen (late Norian-Rhaetian). **d**, Surface with numerous dinosaur footprints, Ørsted Dal Member, Liasryggen tracksite.

Tetrapod tracks form the latest Olenekian–early Anisian of the Holy Cross Mountains, Poland

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More than four hundred specimens of tetrapod traces (footprints, scratches, swim traces) have been discovered on several bedding planes in the six sandstone and claystone quarries/clay-pits and other temporary outcrops of the Baranów Formation exposed in the northern margin of the Holy Cross Mountains, Poland. About 300 traces were studied in detail. The other specimens were too obscure or fragmentarily preserved for meaningful analysis. A relatively diverse ichnoassociation, in which various ichnogenera can be recognized, comes from a siliciclastic, red bed unit of latest Olenekian (latest Smithian; Early Triassic) and Aegetian–Bithynian (early Anisian; Middle Triassic) age. The collected material is referred to eleven tetrapod ichnotaxa: *Rhynchosauroides* isp., cf. *Procolophonichnium* isp., cf. *Synaptichnium* isp., *Chirotherium barthii*, *Isochirotherium* isp. A and B, cf. *Rigalites* isp., *Rotodactylus* isp., *Sphingopus/ Parachirotherium* isp., *Brontopus* isp. and *Dicynodontipus* isp. Most of the footprint specimens pertain to small lizard-like diapsid reptiles referable to ichnogenus *Rhynchosauroides* and, subordinately, to archosauromorph reptiles. The newly discovered ichnofauna represents one of the richest late Early–early Middle Triassic record of terrestrial tetrapod described from Europe, and provides important information to better appreciate the process of the early archosaurs radiation.
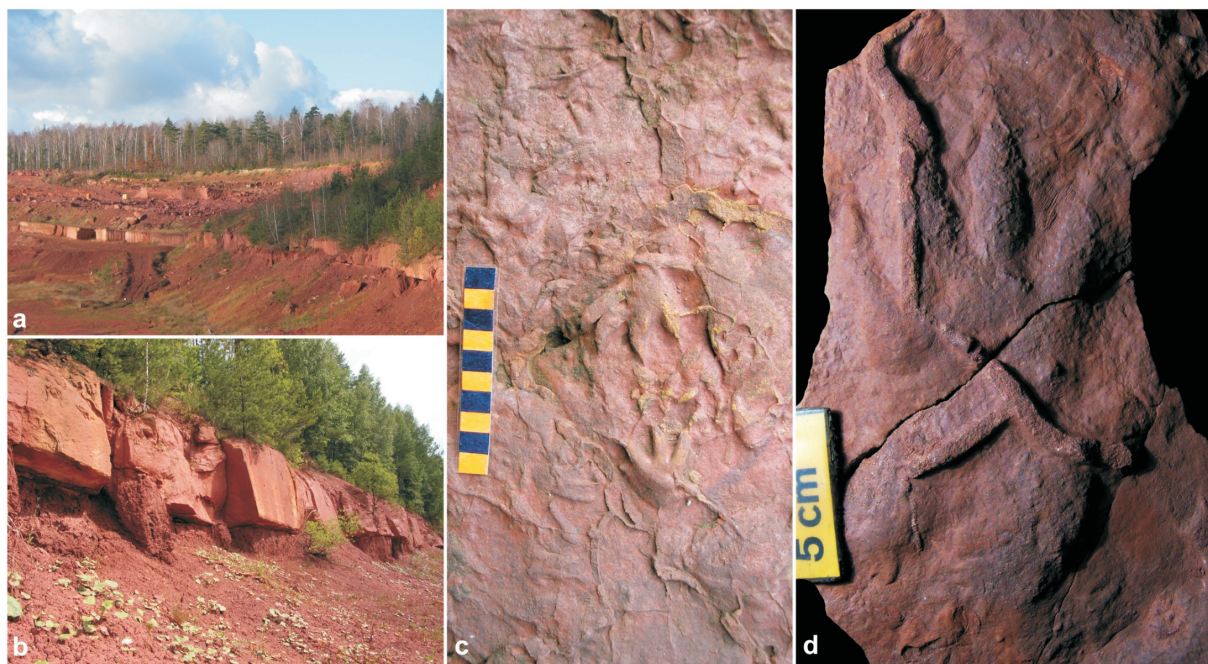
Figure 1. A sedimentological and ichnological overview of the Baranów Quarry, which is the largest exposure of the Baranów Formation in the Holy Cross Mountains, Poland. **a**, **b**, Thick sandstone body exposed in lower part of the section, which separates the sandstone-rich interval from the mudrock dominated units. **c**, Small tetrapod manus and pes tracks, *Rhynchosauroides* isp. **d**, Medium tetrapod pes track, *Isochirotherium* isp.

Lizard trackways from the Late Jurassic of Asturias, northern Spain

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The Dinosaur Coast, in Asturias (northern Spain), is well-known for its abundant vertebrate (dinosaur, pterosaur, crocodile and turtle) prints. However, the lizard tracks are very rare in the Asturian Jurassic record at present, only represented by one isolated manus print attributed to *Rhynchosauroides*. Two additional trackways (T1 and T2) were recovered by the authors in 2016 on the seacliffs close to Villaverde (Villaviciosa). The tracks are preserved as natural casts (hyporeliefs) on the bottom of an isolated sandstone block from the Lastres Formation, which is deltaic in origin and Kimmeridgian in age. The manus impressions, smaller than the pes, are located closer to the midline than the pes tracks and anteromedially to them. The pes trackway width is larger than the manus trackway width. The digit length increases from I to IV in manus and in pes prints. T1 consists of seven tracks: four manus and three pes impressions. Manus and pes tracks, are tetradactyl to pentadactyl, and show digital pad impressions and large medially or anteromedially rotated claw marks in same tracks. The manus prints are digitigrade, while the pes prints are digitigrade to semiplantigrade. Tail trace is also observed. T2 comprises six tracks: three manus and three pes impressions. The manus prints are tridactyl to pentadactyl, whereas the pes tracks are tetradactyl. Both, manus and pes prints, are digitigrade. The trackmaker was smaller than the T1 trackmaker. These characteristics let us attribute the trackways to lizards, being the first well-authenticated record of lizard trackways in the Upper Jurassic.

Figure 1. Sandstone block with two lizard trackways from the Upper Jurassic of Asturias (northern Spain); currently this sample is housed in the Jurassic Museum of Asturias (MUJA-4698). Arrows labelled T1 and T2 refer to individual trackways mentioned in the text.

Contents of coprolites reveal feeding habits of the Late Triassic archosaur *Smok wawelski* (Lisowice, Poland)

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Large coprolites (>16 cm long) were found in the Lipie Śląskie clay-pit at Lisowice (Poland) within bone-bearing strata, and in close association to sandstones with large tridactyl footprints. Initial studies of the coprolite contents showed that they contain various bone fragments, fish scales and a serrated tooth from *Smok wawelski* with signs of digestion. The shape, large size and contents of the specimens suggest that they were produced by *Smok wawelski*, a large predatory archosaur whose systematic position is still poorly resolved. Propagation phase-contrast synchrotron microtomography (PPPC-SRμCT) has shown to be an invaluable method to non-destructively study coprolite contents in three dimensions. Three coprolites from *Smok wawelski* were scanned using PPC-SRμCT at the European Synchrotron Radiation Facility in France. Our results show that all three coprolites contain large amounts of bone fragments (>30% of the total volume), including those from dicynodonts and a temnospondyl. The bones show various stages of digestive alteration and some of the bones exhibit bite marks, which are also commonly found on isolated bones from the locality. Multiple fragments from, in total, three crushed serrated teeth were found in the coprolites along with invertebrate borings, microbial structures and other small inclusions. The presence of several teeth in different coprolites demonstrates that ingesting teeth was not a rare phenomenon among these archosaurs. Our findings show that *Smok wawelski* was a top predator with a diverse menu, including frequent exploitation of bones.

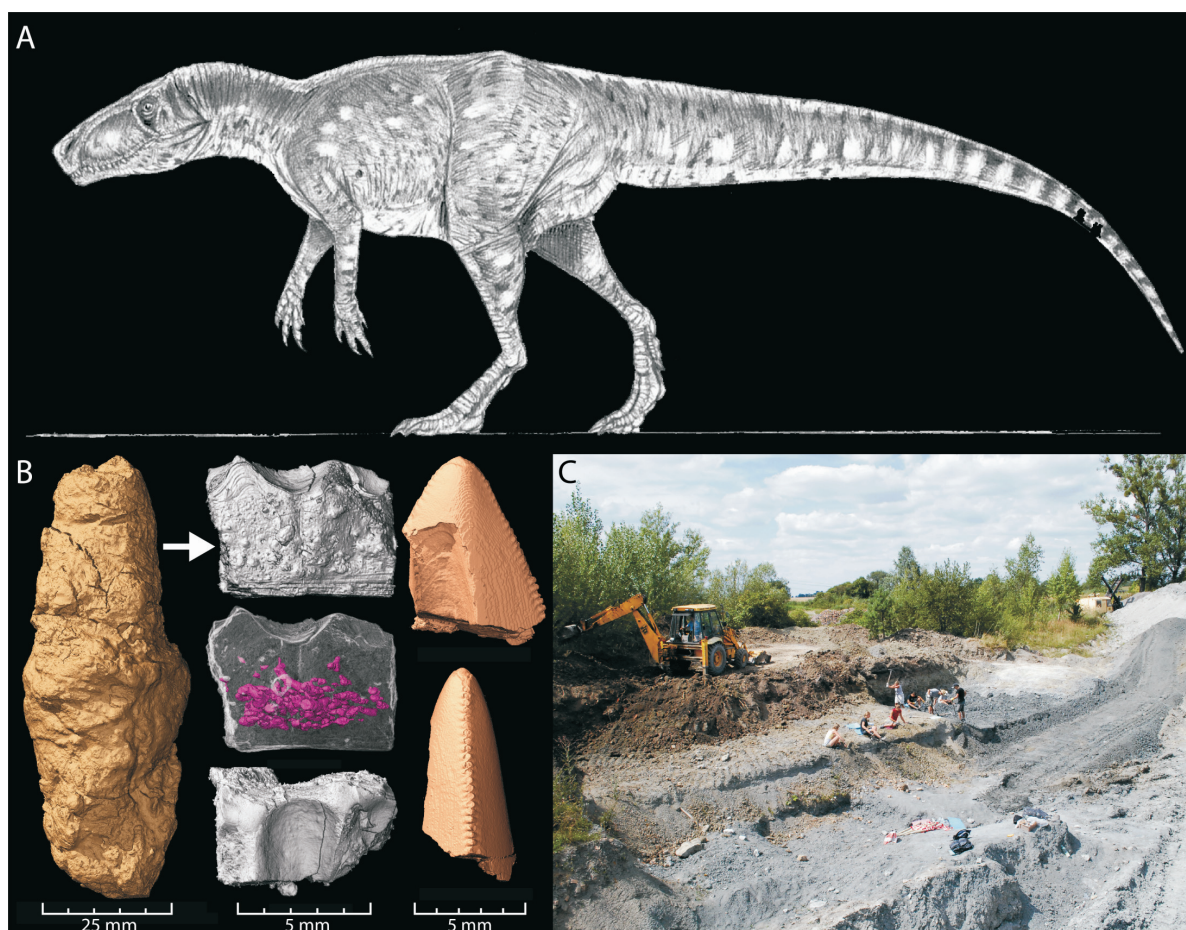**Figure 1**. **A**, Artistic life reconstruction of *Smok wawelski* made by Jakub Kowalski (Poland). **B**, Virtual 3D-reconstruction of: a coprolite assigned to *S. wawelski*, a temnospondyl bone fragment, and a fragmented piece of a serrated tooth (the latter two are food residues found as inclusions within the coprolite). **C**, The locality Lisowice (Silesia, Poland) from which the fossils derive.

Radiometric age dating of key ichnological surfaces within the Elliot Formation at Maphutseng and Quthing (Moyeni), Kingdom of Lesotho, southern Africa

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A plethora of trace fossil assemblages have been described in the Upper Triassic and Lower Jurassic Elliot and Clarens formations, including those at Maphutseng and Quthing (Moyeni), in western and south-western parts of Lesotho, respectively (Fig. 1). To date, the most extensive work on the vertebrate tracks of Lesotho was carried out by Ellenberger, and more recently by Marsicano, Smith and Wilson. The Maphutseng and Moyeni trackway sites host a remarkable abundance of well-preserved footprints, which include tracks by dinosaurs (e.g. *Neotrisauropus* (=*Grallator*), *Moyenisauropus*), chirotheroid-type basal crurotarsal archosaurs and tetrapods. Dinosaur tracksites exist throughout the Elliot Formation, which also excitingly hosts the Triassic–Jurassic Boundary (TJB). Several past and recent studies focused on resolving temporal placement of the TJB within the Elliot Formation via correlative work based on bio- and magnetostratigraphic investigations. Yet, temporal placement for these significant vertebrate ichnofossil assemblages and that of the TJB remains tentative. Therefore, this project seeks to couple historically constructed biostratigraphic records with revised lithostratigraphic context and newly acquired radiometric age dates. Initial results to be discussed include the newly acquired and rigorously assessed radiometric age dates via LA-ICPMS of detrital zircons from samples taken at the Maphutseng and Moyeni tracksites (Fig. 1). Ultimately this project aims to provide greater temporal resolution to these and other well-preserved ichnite assemblages within the Karoo Basin of southern Africa, which in turn will impact on our understanding of the TJB, evolutionary patterns, faunal diversity and turnover rates in the early Mesozoic of southern Gondwana.

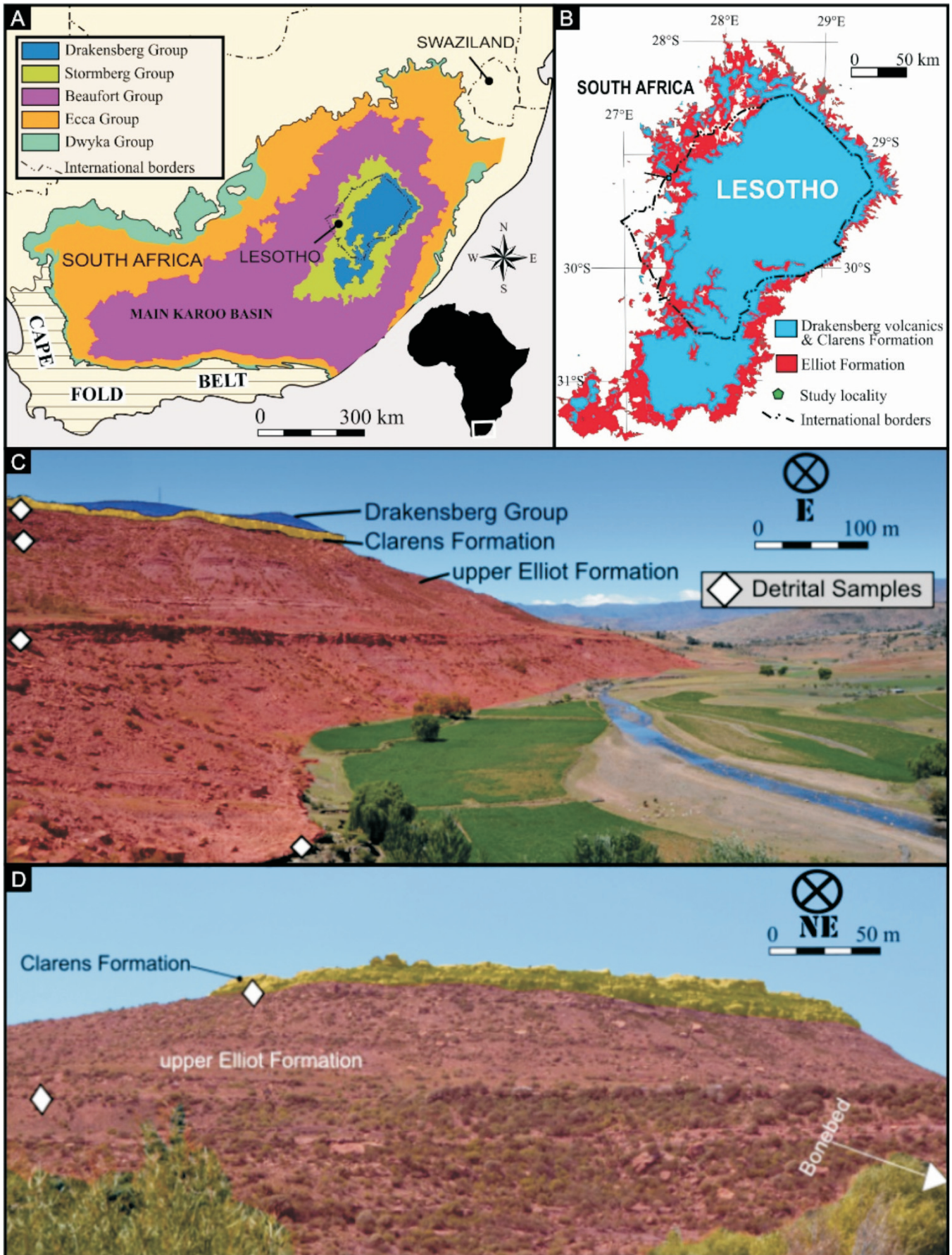**Figure 1**. **A**, Simplified geological map of the Karoo Basin of southern Africa showing Lesotho; **B**, Study localities at Quthing (Moyeni) and Maphutseng within the outcrop area of the Elliot Formation in Lesotho. **C** & **D**, Examples of the 7 traverses mapped during this study; diamonds mark the sites where detrital zircon geochronology samples were collected (C – Moyeni, Quthing; D – Maphutseng).

Dynamics of Early Jurassic lacustrine palaeo-ecosystem: sedimentology and ichnology of the uppermost Elliot Formation in Lesotho

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The continental red beds of Elliot Formation of Lesotho and South Africa were deposited during a dynamically changing climate in southern Gondwana. They preserve a rich history of life before and after the end-Triassic mass extinction event and across the boundary of the Triassic and Jurassic. The facies variations in the lowermost Jurassic upper Elliot Formation (UEF) have been linked to an increasingly arid climate during the Early Jurassic of this region. More specifically, aridification triggered the environmental shift from ephemeral rivers and playa lakes with some aeolian influence in the UEF to a well-established desert system in the overlying Clarens Formation. The geology of the richly fossiliferous, continental rocks in UEF are well-documented. However, further investigation of these deposits, most importantly the playa lakes and their ichnology, may be a key for advancing palaeoclimatic and palaeoenvironmental reconstructions in the region, as well as for refining the lake facies models in general. In this study, we present the sedimentology and ichnology of two UEF lake sites from southern and northern Lesotho, at Ha Nohana and Cana, respectively. Both sites expose an interbedded succession of dark-grey to black, organic matter-rich mudstone and laterally persistent, <50 cm thick, tabular sandstone layers. Our high-resolution, cm-scale analysis of the fossiliferous, playa lake sedimentary rocks at both sites reveal sedimentological evidence for perturbations in the lake ecosystem that ranged from drying out, recurring stormy conditions with flash flooding, seasonality in sediment supply and lake water stratification leading to anoxia (Fig. 1A,B,C,D). These events, which typify large, but relatively shallow lakes under semi-arid climatic conditions (e.g., desiccation cracks in Fig. 1D,H,I), are also supported by the associated fossil assemblages, which range from conchostracans (bivalved branchiopod crustaceans with fossil carapaces up to 12 mm in diameter; Fig. 1E,F) to trace fossils of invertebrates (Fig. 1G) as well as vertebrates (Fig. 1J,K).
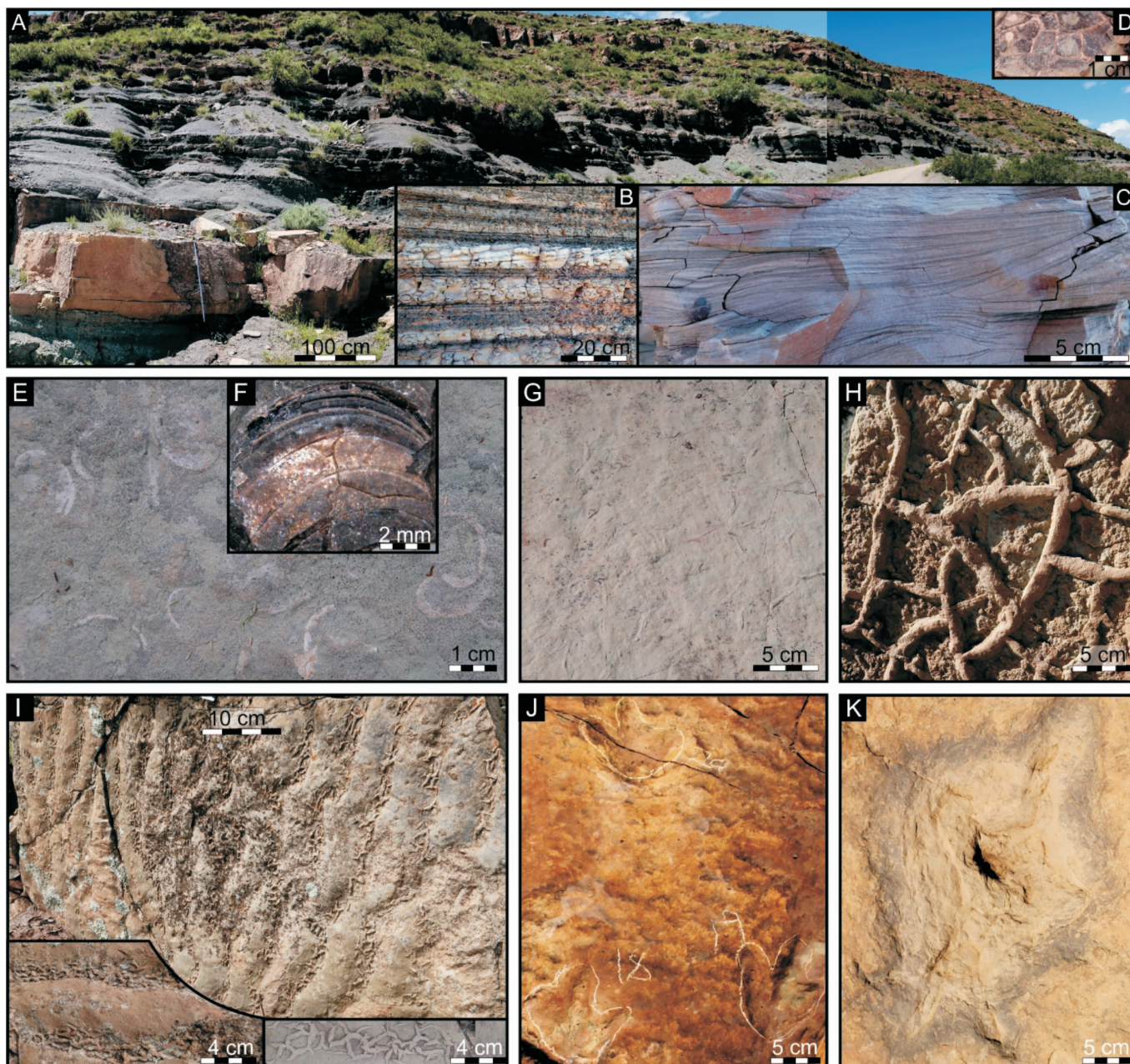
Figure 1. Sedimentary features and trace fossils from two Lower Jurassic lake deposits of Lesotho: Ha Nohana (**A**, **B**, **C**, **D**, **H**, **I**, **J**) and Cana (**E**, **F**, **G**, **I**). **A**, Rhythmical bedding in dark-grey to black lacustrine mudstones. **B**, Close-up of rhythmical bedding and climbing ripple cross-lamination. **C**, Hummocky cross-stratification in very fine-grained, tabular sandstone. **D**, Casts of desiccation cracks in dark-grey to black mudstone. **E**, Cream-white coloured impressions of fossil conchostracan (clam shrimps) carapaces. **F**, Close-up of the growth rings on the conchostracan carapace. **G**, Isolated invertebrate burrows are either parallel (**G**) or perpendicular (**H**) to the bedding planes. Note the well-developed network of desiccation cracks (**H** & **I**) with stockwork pattern are confined to the troughs of ripple marks in very fine-grained sandstone. **I** (**J** & **K**) Theropod tracks on the upper bedding plane of sandstone layers, which are directly underlying the extensive lake sediments in A. Note the ripple marks in I and the digit I impression of the pes in K.

Swimming across the PT boundary: first indirect proof of fish activity in the Late Permian and Early Triassic of the Dolomites, Italy

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In the Upper Permian continental succession of the Southern Alps (Dolomites, North Italy), the ichnological record of the Val Gardena Sandstone consists of vertebrates footprints and invertebrate trace fossils, which are mainly documented in the well-known 'Butterloch-Bletterbach ichnoassociation'. After the end-Permian extinction event, vertebrate ichnoassociations are scarce until the Middle Triassic (Anisian), while the latest Permian-Early Triassic Werfen Formation preserves a rich invertebrate trace fossil record. To date, findings of *Undichna* in the pre- and post-extinction deposits of Dolomites are very rare; only Todesco and Avanzini identified *Undichna gosiutensis* (De Gibert, 2001) in the outcrops of the 'Voltago Conglomerate' (Upper Anisian) and some unpublished specimens have been discovered in the slightly younger 'Richtofen Conglomerate' by some of us. Recently, for the first time, some fish trails (Fig. 1) have been discovered in strata both below and above the PT boundary, i.e. in the Val Gardena Sandstone (Lopingian) and in the Werfen Formation (Campil Member, Lower Triassic, Lower? Olenekian), respectively. In the former deposit *Undichna quina* (Trewin, 2000) and *U. bina* (Anderson, 1976) have been identified; at present they represent the oldest fish trails found in the Southern Alps. Conversely, the specimens found in the Werfen Formation can be assigned to *Undichna cfr. britannica* (Higgs, 1988) and represent the oldest Mesozoic record of fish activity of northern Italy.

Figure 1. **A**, *Undichna* cf. *britannica* Higgs, 1988, Werfen Formation (Campil Member, Olenekian). **B**, *Undichna quina*, Trewin, 2000, Val Gardena Sandstone (Lopingian). **C**, *Undichna bina* Anderson, 1976, Val Gardena Sandstone (Lopingian).

Early Triassic invertebrate trace fossils from the Ma'in Formation of the eastern Dead Sea region in Jordan: New data on the ichnofaunal diversity and interregional comparison

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Permian continental deposits of the Umm Irna Formation and discordantly overlying Early Triassic mixed continental/marine deposits of the Ma'in Formation in Jordan are often studied for micro- and macrofloras, conchostracans, and shark egg capsules. Here we present new results on the invertebrate ichnia from the Himaraand Nimra Members (Ma'in Formation), collected in February 2017 during a joint German–Jordan field work in the eastern Dead Sea region of Jordan (Fig. 1). *Fuersichnus communis*, *Lockeia siliquaria*, *Cruziana problematica*, and *Rusophycus eutendorfensis* were recorded in the Himara Member. Towards the overlying Nimra Member the ichnofauna becomes increasingly dominated by bivalve traces resembling *Palaeophycus* isp. This ichnofaunal transition is interpreted to reflect a gradual facies change from continental coastal to nearshore brackish-marine conditions. Ichnofaunal elements of the Ma'in Formation are similar to Late Permian–Early Triassic invertebrate traces known from other regions, such as the Gröden Sandstone/Val Gardena Formation in northern Italy and the Bernburg Formation in central Germany. This demonstrates the potential of further studies on interregional comparisons of ichnofaunas of this crucial stratigraphic interval.
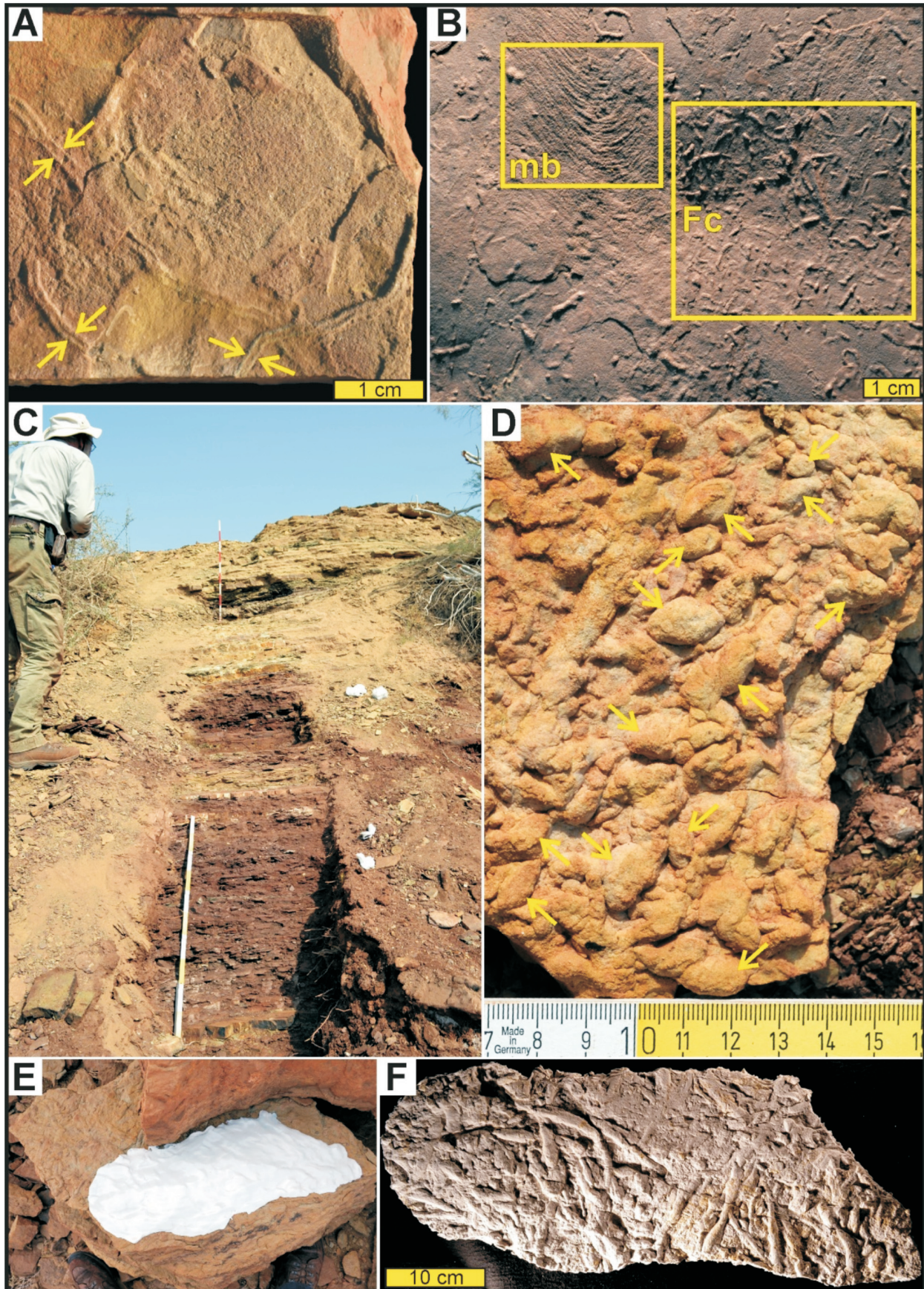
Figure 1. Invertebrate trace fossils from the Early Triassic Ma'in Formation in the eastern Dead Sea region of Jordan. **A**, *Cruziana problematica* showing two parallel ridges separated by a furrow (marked by yellow arrows), locality FS-J4c (31°37′34.3″N, 035°34′46.4″E), Himara Member. **B**, *Fuersichnus communis* ('Fc') and microbial mats ('mb'), Wadi Dardur, Himara Member. **C**, Outcrop conditions at the excavation site 'Bivalve Wadi' (31°32′13.3″N, 035°33′25.9″E) exposing a transition from the Himara Member to the overlying Nimra Member; scale bars 1 m. **D**, Bivalve steinkerns (marked by yellow arrows), 'Bivalve Wadi', Nimra Member; scale bar 9 cm. **E**, Intensive bioturbated surface of a block (31°30′47.6″N, 035°33′58.2″E) used for the production of a silicone cast, outcrop area at Al Mamalih, Nimra Member. **F**, Replica resulting from the silicone cast showing horizontal burrows similar to *Palaeophycus* isp.

Burrows of mayflies (Ephemeroptera) in fresh water ecosystems – general comments and examples from recent rivers of the Czech Republic and Poland

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Burrowing larvae and nymphs of several mayflies are ecosystem engineers in rivers and lakes. They increase surface of the sediment-water interface, bio-irrigate and mix the sediment, causing an exchange of elements, solutes, a release of methane and CO_2 from the sediment and an improvement of oxygenation in sediments. They produce U-shaped burrows (Fig. 1), the fossil record of which is still poorly documented. Burrowing taxa range since the Middle Triassic, but Mesozoic–Palaeogene mayfly burrows are problematic.

Recent mayfly burrows are rarely a target of neoichnological research. U-shaped, pouch-like burrows with parallel limbs, covered with short scratches arranged in sets, occur in the thalweg of the Ohře River in NW Czech Republic. Similar, but smaller burrows with rare scratches, not arranged in sets, occur in the thalweg of the Drwęca River in northern Poland (Uchman *et al.*, in press). Probably, they are produced by larvae and/or nymphs of *Palingenia* and *Polymitarcis* (*Ephoron*), respectively. In both localities, they burrowed in firmground surfaces at shallow water depths. A review of recent mayfly burrows include: 1) U-shaped pouches with parallel limbs and septum, which may be covered with short scratches and are oriented perpendicular to the bottom, irrespective of its inclination, or 2) wide U-shaped burrows with divergent limbs, which may be branched. In the fossil record, the ichnogenera *Fuersichnus*, *Asthenopodichnium* and *Rhizocorallium* recorded in freshwater sediments are partly ascribed to mayfly burrows, but their comparison to the recent burrows shows that such interpretations are somewhat problematic. The mayfly burrows are potentially good indicators of aquatic, non-marine, well-oxygenated, clean waters.
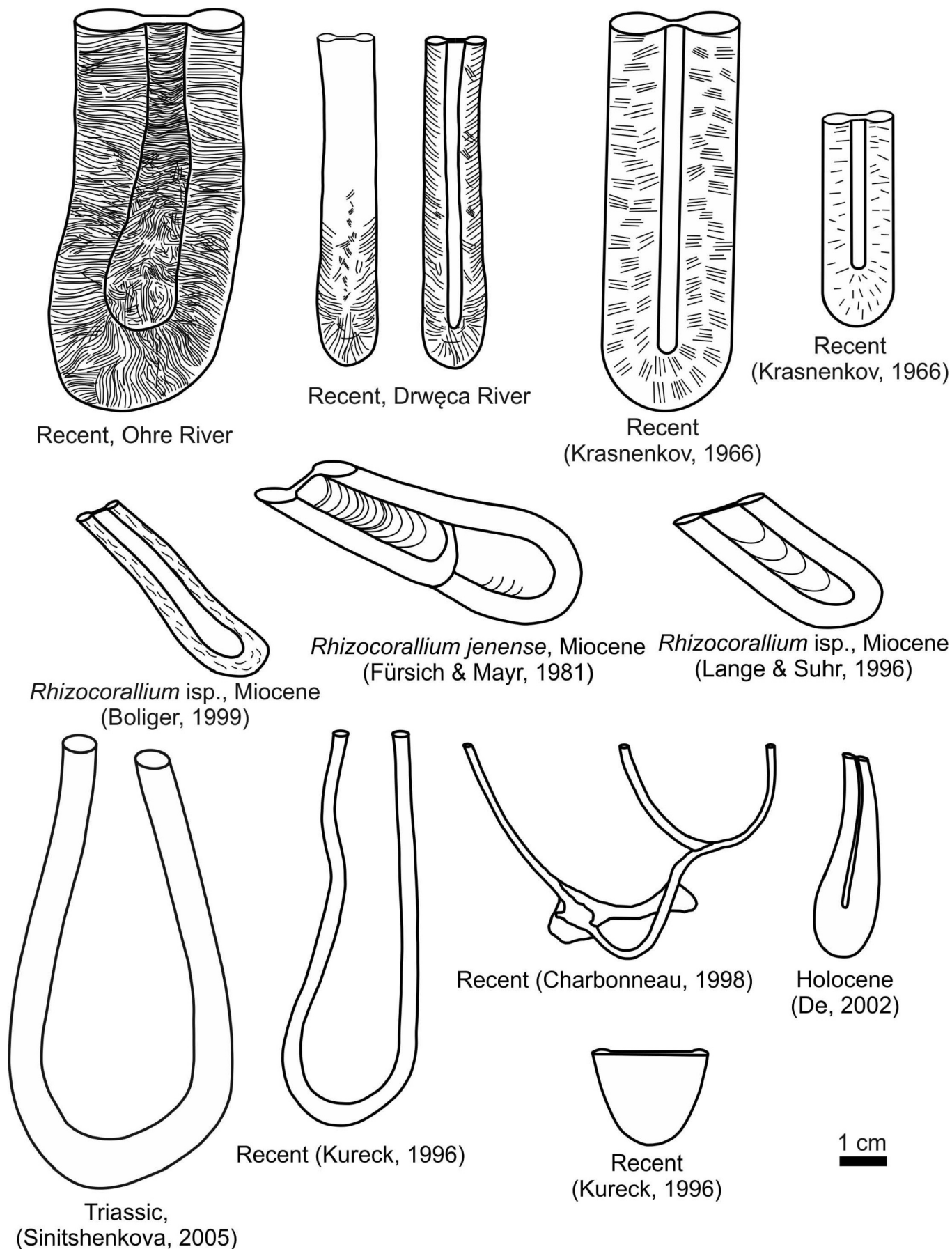
Figure 1. Different mayfly burrows, fossil and recent
(modified after Uchman *et al*., 2017, Ichnos http://dx.doi.org/10.1080/10420940.2016.1257488).

The Early Permian ichnofossil assemblage of Bromacker Quarry (Thuringia, Germany)

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Since 1887, the Bromacker locality in the Thuringian Forest in central Germany is a well-known fossil site for different trace and body fossils with high abundance and exquisite preservation. Stratigraphically situated in the Lower Permian Tambach Formation, Bromacker sedimentary rocks consist mainly of red-coloured silt- and sandstones, deposited in an inland and upland semi-arid environment, which was dominated by low-energy sheet floods and low-relief-landscape sedimentation. The site has produced spectacular articulated skeletons of a variety of tetrapods, including early amphibians, early sauropsids, and synapsids. Some ichnotaxa can even be linked to their producers: the two species of the ichnogenus *Ichniotherium*, *I. cottae* and *I. sphaerodactylum*, can be assigned to body fossils of the diadectids *Diadectes absitus* and *Orobates pabsti*, respectively. Other vertebrate ichnotaxa at Bromacker include the common *Dimetropus leisnerianus*, and the rare *Tambachichnium schmidti*, *Varanopus microdactylus*, and *Amphisauropus kablikae*. Skin impressions are known from well-preserved footprints and from body resting traces. Invertebrate trace fossils include *Tambia spiralis*, small spirally-arranged traces with a typical diameter of ~20 mm and *Striatichnium bromackerense*, fan-arranged striae distally bifurcated and 1 mm wide. Systems of parallel to crossing smooth impressions 1 cm wide and 10 cm long, arranged in rows or spiral structures of about 30–40 cm in diameter, were variably interpreted as claw marks in tetrapod burrows or nests, but an invertebrate origin cannot be excluded. Imprints of bones with a length of up to 45 cm indicate much larger tetrapods than what has been found in the Bromacker bone record, yet. A new research project about the Bromacker site aims for detailed studies of the sedimentology of the area, the taphonomy, taxonomy, and palaeoecology of its fossils; answering the many open questions of this unique Permian palaeoenvironment.
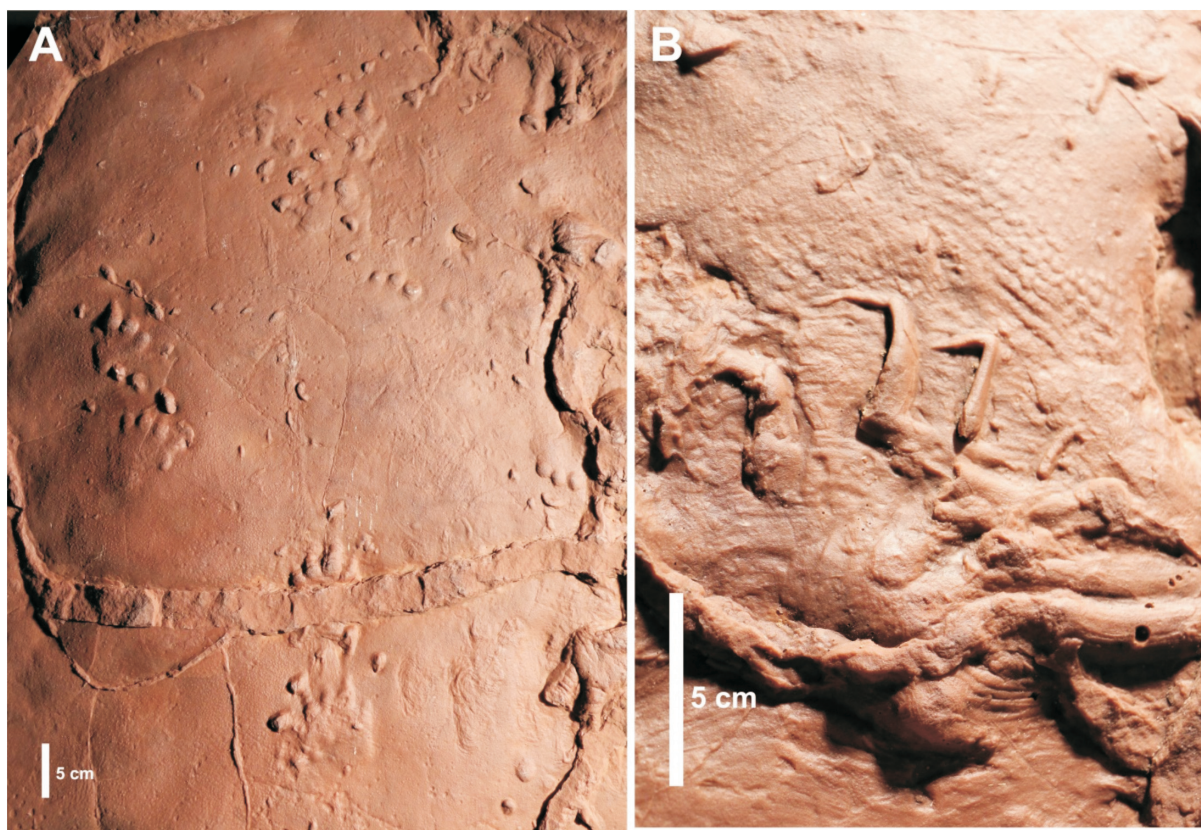

Figure 1. Details of the cast of a large track-bearing sandstone slab from Bromacker (collection no.: MNG 13490). **A**, An exceptionally well-preserved trackway of *Dimetropus leisnerianus* with partial tail trace, cut by large mud cracks. Note *Tambia spiralis* traces and *Ichniotherium* tracks on the right. **B**, Skin impressions and claw marks.