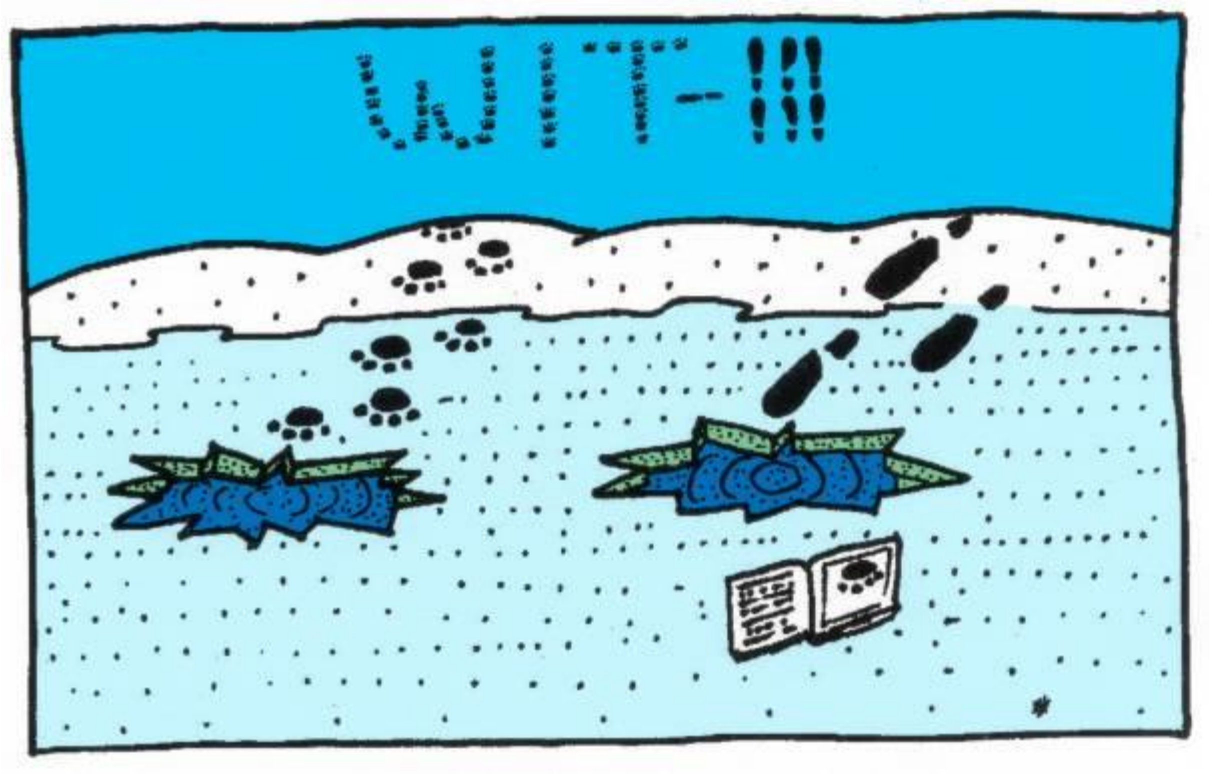
3rd Workshop on Ichnotaxonomy

Prague and Jevíčko (Czech Republic)
September 4 – 9, 2006



Objectives of the Workshop

The two previous workshops on ichnotaxonomy (Bornholm and Kraków) convened by Markus Bertling & Richard Bromley and Alfred Uchman, respectively, definitely contributed to the recognition and solution of many basic ichnotaxonomic questions. This, however, does not make ichnotaxonomy a closed book. The ideas expressed at WIT-1 and WIT-2 (and finally published in a coherent form) have to be confronted with ichnotaxonomic studies based on different lines of fossil and modern evidence. We have felt the need to open this workshop to all specialists who wish to come to discuss particular ichnotaxonomic problems. May this Abstract Book bring new inputs to the general consensus on how to classify and name traces of past life!

Discussions and presentations

Monday, 4th September (National Museum, Prague)

9.00-9.30
Opening session

9.30-10.00
Andrew K. Rindsberg: Fixing types in ichnotaxonomy

10.00-10.30
Coffee break

10.30-11.00
Richard G. Bromley and Kurt S. S. Nielsen: When is a trace fossil not a trace fossil?

11.00-11.30
Radek Mikuláš and Alfred Uchman: Some bivalve trace fossils in the Miroslav Plička collection

Tuesday, 5th September (National Museum, Prague)

9.00-9.30
Bárbara Sánchez-Hernández: Lower Cretaceous dinosaur nests in the Cameros Basin of Soria Province (Spain)

9.30-10.00
Andrey G. Sennikov: The plantigrade dinosaurs – evidence from segnosaurian trackways

10.00-10.30
Ricardo Néstor Melchor and Silvina de Valais: Ichnotaxobases for bird-like footprints: towards a uniform approach

10.30-11.00
Coffee break

11.00-11.30

Jorge F. Genise: Inadvertent advances in the ichnotaxonomy of non-animal traces: a contribution to the *status quo*

11.30-12.00
Marilyn E. Zorn, Murray K. Gingras and S. George Pemberton:
Burrow wall microstructure of modern brackish water fauna: a valid ichnotaxobase?

Thursday, 7th September (Hotel Morava, Jevíčko)

9.00-9.30
Veronica B. Kushlina: Biting traces on echinoderms from the Ordovician of the St. Petersburg Region (Russia)

9.30-10.00
Jozef Michalík and Vladimír Šimo: A new type of trace fossil from Lower Cretaceous "spotted" limestone from Western Carpathians (Slovakia)

10.00-10.30
Andrei V. Dronov, R. Mikuláš, M. Savitskaya: *Gastrochaenolites oelandicus* and similar borings and/or burrows in the Ordovician of Baltoscandia

10.30-11.00
Coffee break

11.00-11.30
Nicholas J. Minter and Simon J. Braddy: Arthropod trackways and ichnotaxonomy

11.30-12.00
Ricardo Néstor Melchor, Emilio Bedatou and Richard Bromley:
***Spongeliomorpha* in continental settings**

12.00-12.30
Radek Mikuláš: Problematic points in ichnotaxonomy: taphoseries, „photoseries“ and „graphoseries“

14.00-16.30 (approx.)
Small celebration to the issue of the "WIT 1-2 paper" (Bertling et al. 2006, Lethaia); discussion on various topics

Friday, 8th September (Hotel Morava, Jevíčko)

9.00-10.00
A. K. Rindsberg: The Treatise Session

10.00-10.30
Coffee break

10.30-12.00
Decision on the future of WITs, WIT-III publications, closing session.

When is a trace fossil not a trace fossil?

Richard G. Bromley and Kurt S. S. Nielsen

Geological Institute, University of Copenhagen, Denmark

Trace fossil names must be based on fossilized material. Before we can publish a trace fossil name, therefore, we must be quite clear about the definition of the concept “fossilized”. We have therefore made a search of the literature. Palaeontology textbooks are not helpful, telling us about the process but not the definition. Dictionaries make an effort, but are clearly not written by geologists. Here are some “better” examples of the definition of “Fossil”.

Concise Oxford English Dictionary, 1964: “Found buried, dug up…. Thing preserved in strata of earth with more or less *chemical or other change of texture* and recognizable as remains or impressions of plant or animal of past (*usually prehistoric*) ages.”

Dictionary of Geological Terms, American Geological Institute, 1976. “The remains or *traces* of animals or plants which [sic] have been preserved by natural causes in the earth’s crust exclusive of organisms which [sic] have been buried *since the beginning of historical time*”.

Chambers Dictionary of Science and Technology, 1971. “A relic of some former living thing – plant or animal – embedded in, or dug out of, the *superficial deposits* of past geological periods.”

Dictionary of Applied Geology, Elsevier, 1967. “The remains or traces of an animal or plant naturally preserved in the rocks, whether they be *consolidated or not*.”

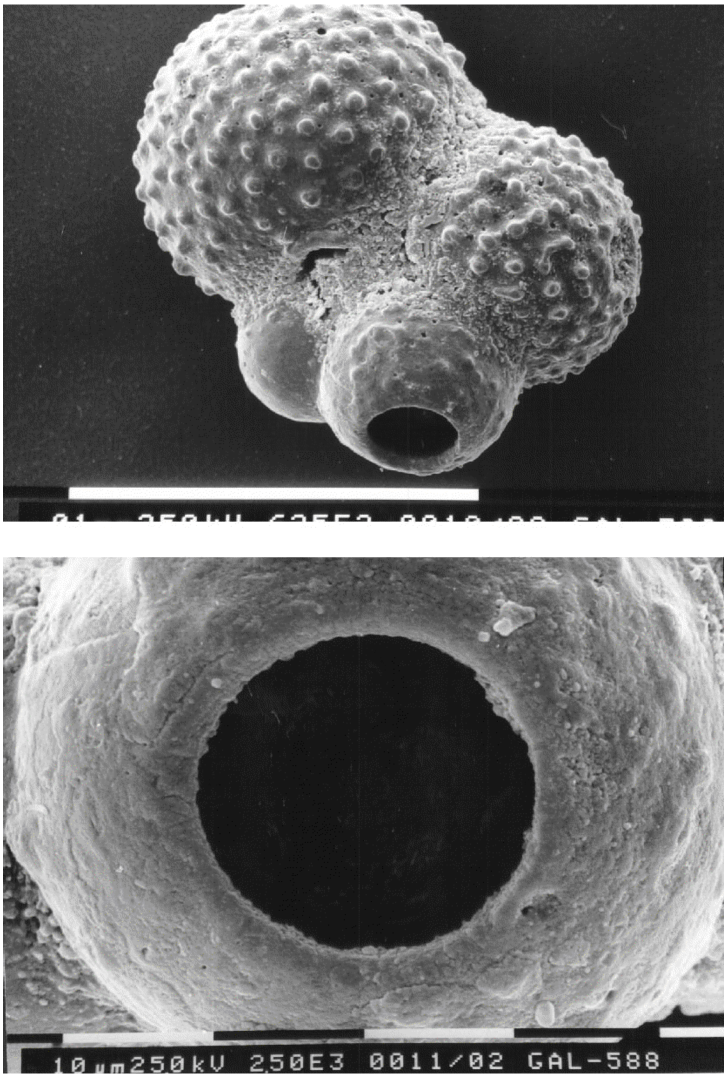
(All these definitions seem to exclude mammoths in ice; and definitely no fungi or bacteria or protists.)

Bertling et al. (in press in Lethaia), in the WIT 1+2 report, acknowledge that “fossilized” is indefinable. They ask “Does it mean ‘found in lithified sediment’, ‘found in pre-Holocene strata’, or ‘found below the taphonomically active zone’?”

One of the reasons for ICZN excluding the use of unfossilized type material for establishing ichnotaxa is that this would cause chaos. There is a plethora of traces today that have no chance of preservation, of crossing the fossilization barrier: tracks in snow, biogenic ripples in water, turbulence around a bird’s wing, etc. Naming these would be of no service to science; they should rather be referred directly to their tracemaker. However, as we are unable to define the onset of fossilization, this prevents modern traces that *do have* a good chance of preservation from being named. It also casts doubt on much named material in the “grey zone”. Our colleagues describing microborings in foraminiferans dredged from the seafloor do not know whether they are truly fossils or not. When does a modern sponge boring become a nameable fossil? We are prevented from naming borings in modern shells (even live shells), although these borings have high preservation potential.

We are therefore tempted to create our own definition of the fossilization barrier. Trace fossils mostly are produced in non-living substrates. A corpse can be eaten, microbially degraded, reworked and is chemically a diagenetic time bomb. Here the fossilization barrier plays an important role. In contrast, however, most trace fossils are a rearranging of the grains of the substrate or holes in rock. They are ready-made fossils. There is no fossilization barrier. An echinoid, passing through the sediment as it rearranges the grains, poses no ichnotaxonomic problems. As the tip of its spine places the grain in its final position, the grain, the backfill meniscus, the whole structure is fossilized. Microbial loss of grain-binding mucus is all that will happen during early diagenesis. Likewise, a sponge boring is a ready-made fossil as soon as the tracemaker dies, and an incipient one before it dies. A Jurassic and a modern sponge boring can be hard to tell apart.

Owing to the variable nature of sediment and xylic substrates (and other “modern” substrates such as snow, cement, unburnt bricks), the possibility of unpreservable modern traces is sufficiently important that the ban on “unfossilized” type material is sustainable here. However, we propose that the ban be lifted for the lithic borings (in rock and skeletal material) or alternatively, that these structures be considered fossilized on the death of the tracemaker.



Dredged from the seafloor, is this planktonic foraminiferan fossilized? Can the *Oichnus* isp. be named, for instance, *Oichnus radeki*? The borer is probably dead. Maybe it just moved on. Upper scale 100 µm, lower 10 µm.

Gastrochaenolites oelandicus and similar borings and/or burrows in the Ordovician of Baltoscandia

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Omission surfaces at the base of the Volkhovian Regional Stage (base of the Middle Ordovician Series) in Baltoscandia contain abundant, well-developed amphora- or vase-shaped structures, which ichnotaxonomic affinities have been much debated. Hecker (1960) and Männil (1966) described them as burrows while Orviku (1940; 1960), Dronov et al., (1996; 2002) and Mikuláš & Dronov (2004; 2005) attributed them to borings. These structures, usually filled with glauconite grains, can be traced over vast area (1000 ×1000 km) from the Oslo graben in Norway on the west to the Syas River in Russia in the east, and from Siljan Lake in Sweden in the north to Poland in the south. The shape of the structures differs slightly in various facies depending on substrate characteristics and depositional environments. Some observations allow them to be regarded as burrows, while in other places they are clearly attributable to borings. It is obvious, however, that they were made by the same tracemaker.

Ekdale and Bromley (2001) pointed out that it is quite possible that the producer of the "amphora-like" structures was an organism that was adapted for penetrating substrates with varying degrees of firmness and hardness and therefore could have produced burrows in firmgrounds and borings in hardgrounds. They included the trace fossils under discussion within the ichnogenus *Gastrochaenolites* based on the consideration that, even though it is not always possible to be certain whether individuals of *G. oelandicus* are borings or burrows (or a combination of both), the tracemaking organism was fully equipped for boring. This approach seems to be useable when dealing with closely spaced trace fossils from one bed, which is the case of the sequence boundary surface at the base of the Volkhovian ("Steklo" surface in Russia, "Pystakkiht" in Estonia and "Blommiga Bladet" in Sweden). But it creates uncertainty when we try to use it for other beds even within the same stratigraphic unit.

For example, vertical burrows of similar shape and size filled with glauconite grains have been reported from the topmost beds of the Volkhovian succession in St. Petersburg Region. There are no hardgrounds at that level and we do not know if the organism were equally equipped for boring or not. Vertical finger-shaped, vase-like or amphora-like phosphatized burrows have been reported also from the basal sandstone layer of the Leetse Formation about 1,5 m below the "Steklo" surface with prominent amphora-like borings (Fedorov & Ershova, 2004). It cannot be excluded that the same animal was responsible for producing amphora-like burrows and borings in all three cases.

Basically, all possible ways of ichnotaxonomic treatment of the situation are highly subjective. All these trace fossils can be placed within *Gastrochaenolites* considering their similar morphology. Another possibility is to use the maximum data from the presumed substrate consistency. In practice, burrows in sandstones can be classified as *Skolithos*, burrows in limestone as *Amphorichnus* and borings in limestone as *Gastrochaenolites*. Both approaches have their advantages and disadvantages.

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“Steklo” hardground surface with openings of *Gastrochaenolites*-like trace fossils. Sablino, right bank of Tosna River. Size of the view is 20 ×30 cm.

Ichnology of the Upper Cretaceous (Cenomanian – Coniacian) sequence of west-central Sinai (Egypt)

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The Upper Cretaceous (Cenomanian - Coniacian) sequence of west-central Sinai (Egypt) contains a relatively abundant and moderately diverse ichnofauna. The recorded ichnofossils represent domichnial, praedichnial and fixichnial structures. The sequence includes *Caulostrepsis spiralis* Pickerill *et al*., 2001; *C. cretacea* (Voigt, 1971); *Arachnostega gastrochaenae* Bertling, 1992; *Entobia ovula* Bromley & D'Alessandro, 1984; *Entobia* isp., *Gastrochaenolites* isp. *Talpina ramosa* von Hagenow, 1840; *Maeandropolydora sulcans* Voigt, 1965; *Maeandropolydora* isp; *Oichnus simplex* Bromley, 1981; *Rogerella* isp., *Trypanites* isp., and *Renichnus arcuatus* Mayoral 1987. Nearly all these ichnotaxa are formally documented in Egypt for the first time.

Moreover, the record herein of *Renichnus arcuatus* in the Upper Cretaceous (middle Coniacian) of Egypt has the following implications: 1) It extends the stratigraphic range of this ichnotaxon from the Maastrichtian down to the middle Coniacian, and 2) it expands its known geographic distribution during this period from southern and central Europe (Spain, Greece and Netherlands) to North Africa (Egypt). The ichnogenus *Entobia* displays different successive ontogenetic stages that allow detailed study of its formation. Paleoecologically, the studied ichnofossils characterize the shallower marine biofacies in the Cenomanian – Coniacian of Sinai and reflect the principal shallowing events in that region during the Cretaceous.

Inadvertent advances in the ichnotaxonomy of non-animal traces: a contribution to the *status quo*

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Ichnotaxa of plant and fungal origin had no legal standing under any of the nomenclatorial codes until 2000. The extension of the regulations of the ICZN to all trace fossils resulted in protistan, plant, and fungal trace fossils included in “animals” for the purposes of the code (Bertling et al., in press). However, non-animal trace fossils have no available ichnotaxonomy up to now, and some problems in giving them formal names have been pointed out (Mikuláš, 1999). The principal concern is that, according to purely morphological criteria as is usual in ichnotaxonomy, some non-animal traces would have to be placed in ichnogenera of animal burrows (Mikuláš, 1999). It was proposed therefore to include root traces in a separate category, while recognizing the danger of possible misinterpretations.

Herein, real and potential cases of misinterpretation are outlined. Paleosols and plant remains contain insect and non-animal trace fossils as well, which in many cases are hard to distinguish. As a result, non-animal traces can be included under formal ichnotaxonomy almost inadvertently.

Syntermesichnus fontanae was described as a possible termite nest by Bown and Laza (1990) from the Miocene Pinturas Formation of Argentina. Very similar structures composed of a boxwork of tunnels of different diameter occur in central Patagonia (Argentina) in volcaniclastic formations ranging from the Lower Cretaceous to the Miocene. One working hypothesis suggests that at least some of these boxworks may be root systems. In that case, we would have root systems named after a termite genus. Along with this trace fossil, another, still unnamed but informally called “thick-walled tubes”, occurs in the same formation, which covers **hundreds of thousands of square kilometers in Patagonia. Fragments of thick-walled tubes, ranging from 1 to 2 cm in diameter** and 10 to 20 cm in length, occur at many stratigraphic levels within these formations. Judging by the most complete specimens occurring in the Bajo Tigre Formation (Early Cretaceous), they are probably invertebrate (crayfish) burrows. However, in the remaining formations, which bear only fragments of these tubes, a root origin is also possible. The first rhizoconcretions were described by Kindle (1925) from living roots. Intriguingly**,** this author noted that rhizoconcretions did not form along the whole root, but only where microorganisms provided suitable conditions for their development. These rhizoconcretions are similar to the fragmentary taphonomical variant of these thick-walled tubes.

Fungal traces provide other examples for possible misinterpretations. Fungal trace fossils **in wood (Genise, 2004) can be confused with insect pupation chambers. This**

bioerosional trace has been mostly overlooked until now, but fungal traces are known from different ages and formations in Africa, Europe and America, and its paleoenvironmental value would be very great. This is another trace fossil that deserves a formal ichnotaxonomical treatment, currently in preparation (Genise et al., in prep.) whose origin involves organisms other than animals, but which can be easily confused with them. Galls, leaf spots and ringspots, which may be produced by invertebrates, plants, fungi, bacteria, or viruses pose a similar problem. Herein is presented an Oligocene leaf ringspot, which at the moment has unknown affinities (Sarzetti et al., in prep.), and whose ichnotaxonomical treatment would result indistinctly in a name for an invertebrate, fungi, bacteria, or more probably, a virus trace fossil.

These cases show that it will be not easy to avoid the present *status quo*, **namely to avoid neither the inclusion of non-animal traces in animal ichnotaxa, nor to create at once a different category to a**void its inclusion. In both cases, the problem is the same: to recognize with confidence the affinities of the trace fossil before naming it. In any case, this procedure, or any other conceivable method, must go beyond the **usual** and exclusively morphological approach used in ichnotaxonomy.

References

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Biting traces on echinoderms from the Ordovician of the St. Petersburg Region (Russia)

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The Ordovician deposits of the St. Petersburg Region are rich in echinoderm remains. Among them, traces of active predation have been reported only on skeletons of specific eocrinids – the genus *Bolboporites*. According to the latest interpretation (Rozhnov & Kushlina, 1994), *Bolboporites* are highly specialized benthic echinoderms with conical body partly sunk into the substrate and a single brachiole rising above the flat upper surface (Fig. 1). Most of the soft tissue of the animal, including digestive system, coelomic cavities, and so on, was located on its upper surface and probably was covered with a thin film of skin. The skeleton was relatively thick and uniform. This situation was probably favorable for preservation of traces left by the attacks of predators.

The traces can be characterized as 1.5-3 mm long, curved chains of little pits on the upper surface of *Bolboporites* (Fig. 2-3). The pits are 0.15-0.5 mm in diameter and increase in size from one end of the chain to another. Series of subhorizontal thin sections made for one of the trace-bearing skeletons demonstrates that the pits could be entirely healed by the surviving animal. Where the depth of the pit is equal to its diameter, its bottom is smooth and rounded. The pits may deepen to become connected in a curved groove. This groove is V-shaped in vertical section, with obliquely hatched asymmetrical walls. The pairs of symmetrical grooves are rarely found on the surface of *Bolboporites*. The paired grooves are not connected and diverge at an angle about 40°. The length of each groove is 4-6 mm. The traces belong to the ethological group of mordichnia (Müller, 1962; biting traces) – or, as much more frequently cited, praedichnia (Ekdale, 1985; predation traces).

The described traces were possibly made by a tool that consisted of two hard, curved, and denticulated protuberances, directed toward each other and connected by a mechanism that enabled the work resembling the function of claws. The whole construction [reword: trace?] was about 7 mm in size.

The traces under consideration are possibly biting traces of an unknown arthropod. Arthropods were abundant in all Ordovician seas but their potential preservation was extremely low. In the Ordovician of Baltoscandia, only arthropods with a carbonate exoskeleton were preserved. The other cases are exceptional. A single phosphatized part of an arthropod's mandibula (superorder Phyllocarida) is known from the kukersite oil shale (Kukruse Regional Stage) of Eastern Estonia, but its size and shape does not match the biting traces on *Bolboporites*.

The trace requires ichnotaxonomic treatment. In the given case, the palaeobiological constraints of the trace are very strong, and they should be kept in mind when defining the ichnotaxon. The trace should not be synonymized with morphologically similar Mesozoic and Cainozoic reptilian or mammalian biting traces.

Figure 1. Reconstruction of *Bolboporites Pander,* showing its mode of life.

Figures 2 and 3. *Bolboporites mitralis* Pander,1830; specimen PIN, no. 4125/728:
(2) scheme of arrangement of biting traces: (2a) side view, (2b) from above; P1, P2 - pairs of symmetrical grooves; Ch - chains of pits;
(3) different views

Middle Ordovician, Volkhov regional stage, Babino Quarry.

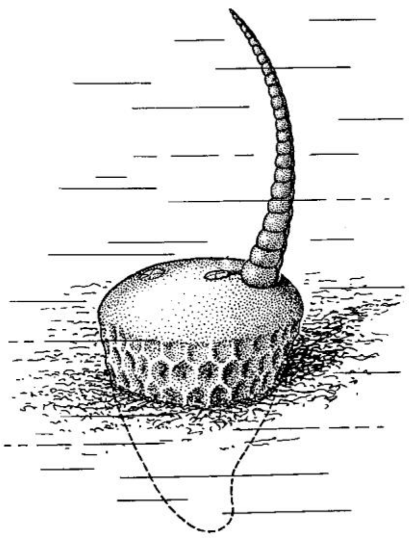

Fig. 1

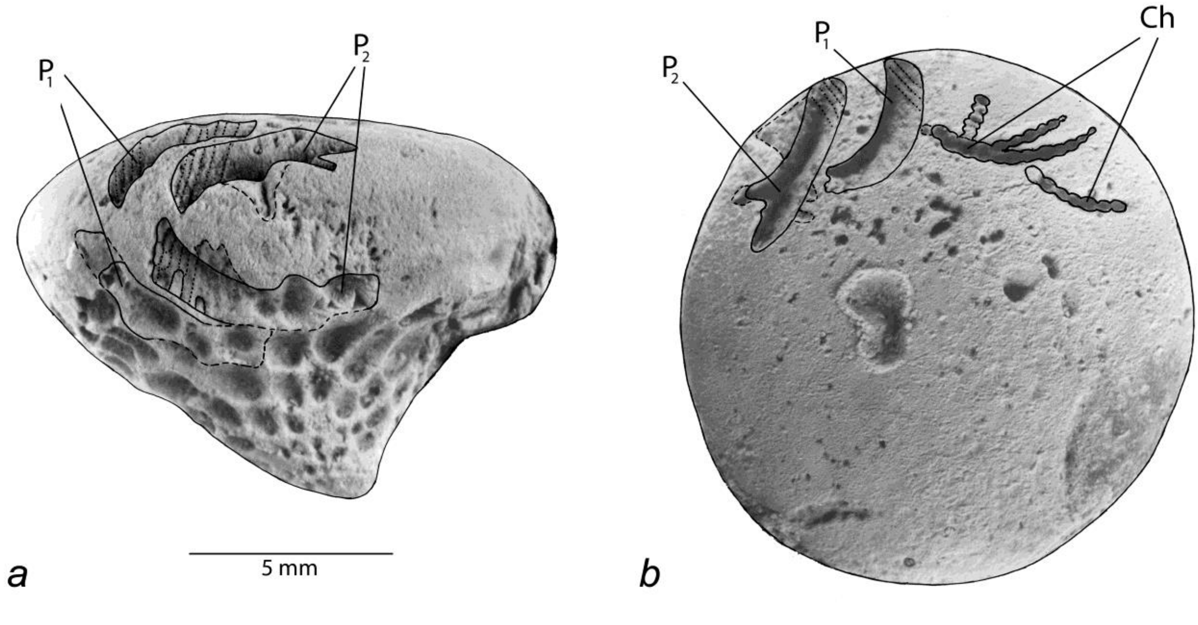

Fig. 2

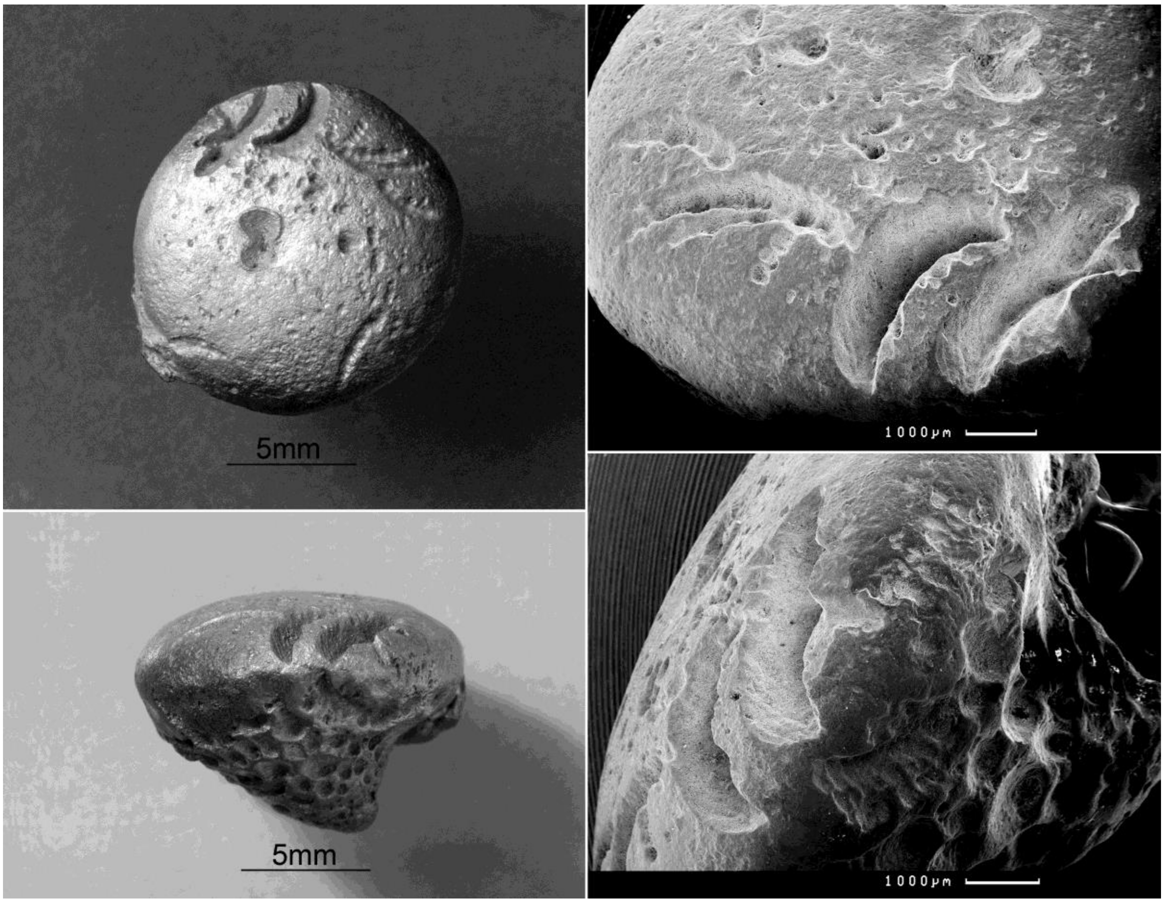

Fig. 3

Spongeliomorpha in continental settings

Ricardo Néstor Melchor[1], Emilio Bedatou[1] and Richard Bromley[2]

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The main characteristics of the ichnogenus *Spongeliomorpha* de Saporta are a dominantly horizontal, unlined burrow system showing Y- and T-branching, and ornamented with scratches of different orientation. *Spongeliomorpha* is herein considered as an ichnogenus distinct from *Ophiomorpha* Lundgren and *Thalassinoides* Ehrenberg, because of its scratch-ornamented walls. Another character of ichnotaxonomic value for *Spongeliomorpha* is the angle of bifurcation of the burrow system. The synonymy of *Steinichnus* Bromley & Asgaard, 1979 under *Spongeliomorpha* was advanced more than two decades ago, although no formal proposal has been published to date. Subsequently, different authors have used both ichnogenera to refer to burrow systems with striae transversal or oblique to the burrow axis.

The specimens of *Spongeliomorpha* commonly found in continental settings display a pattern of striation that is consistently oblique to transverse to the burrow axis. There are two named ichnospecies of *Spongeliomorpha* with this feature: *S. carlsbergi* Bromley & Asgaard, 1979 and *S. milfordensis* Metz, 1993. Metz (1993) recognized the morphological similarity between *S. carlsbergi* and *S. milfordensis* and indicated that the main differences are thicker striae and striae that form an average oblique angle with the axis of the burrow in the latter, while *S. carlsbergi* displays transversal striation. For this study, we compared the angle of striations with the axis of the burrow for the holotype and paratype material of *Spongelomorpha (Steinichnus) carlsbergi* (Bromley & Asgaard, 1979) and the paratypes and photographs of the holotype of *Spongeliomorpha milfordensis* (Metz, 1993). The histogram of the orientation of the scratch ornament (Figure 1) suggests that both ichnospecies show a marked overlap in the range 30-90°, although *S. milfordensis* has more readings than *S. carlsbergi* for acute angles (30-60°), whereas the latter shows more readings at higher angles (60-90°). In addition, the average orientation of scratches is fairly similar (Figure 2).

A hypothesis test performed to compare the average orientation of scratch ornament between the type series of *S. carlsbergi* and *S. milfordensis* suggest that both values are different with a confidence of 99.99%, although the difference in average orientation is only 10 degrees (Figure 2). The apparent variability in the distribution of scratch ornament is easily accommodated if the type series of *Steinichnus carlsbergi* (specimen GGU 146315, housed at the Geological Museum, Copenhagen; paratype of *Steinichnus carlsbergi*, illustrated in Bromley & Asgaard 1979, fig. 11B) is considered (Figure 2). This comparison indicates that the striation angles in one part of a burrow can be dominantly transversal ("*carlsbergi* type") and dominantly oblique in another adjacent portion ("*milfordensis* type"). However, to compare both ichnospecies the holotype material must be contrasted. A visual comparison suggests that both ichnospecies are similar. This subjective impression is further supported by a hypothesis test for the mean of the two populations, performed to compare the average orientation of scratch ornament between the holotype material of *S. carlsbergi* and *S. milfordensis*. This test suggests ($p = 0.22$) that both values are statistically similar (Figure 2). In consequence, it is considered that the morphological differences between both type specimens are minor and they should be included under a single ichnospecies. In this case, *S. milfordensis* is proposed as junior synonym of *S. carlsbergi*. Further micromorphological characterization of *Spongeliomorpha (Steinichnus) carlsbergi* is obtained by study of a longitudinal thin section of a specimen of the type locality and unit. The burrow displays structureless fill composed of calcareous siltstone and microsparite, similar to the host rock, with micritic, darker rip-up clasts, up to 5 mm long. Similarly, paratype material of *S. milfordensis* shows structureless fill in thin section, although in this case it is composed of siltstone devoid of rip-up clasts, which is identical to the host rock.

It is proposed that *Spongeliomorpha carlsbergi* should be restricted to burrow systems with deeply striated walls, striation ranging from transverse to oblique to the burrow axis, with occasional T- or Y-bifurcation; showing no lining, and having structureless fill. The published records of *S. carlsbergi* are restricted to Late Triassic – Early Jurassic continental deposits, although recent accounts of the ichnospecies from Miocene and modern deposits of Argentina considerably extend its stratigraphic range.

As a corollary of this ichnotaxonomic analysis, the distinction of ichnospecies should be based on clear morphologic differences that can be easily observed and measured and not on subtle morphological contrasts that require statistical studies to define the assignment of new material.

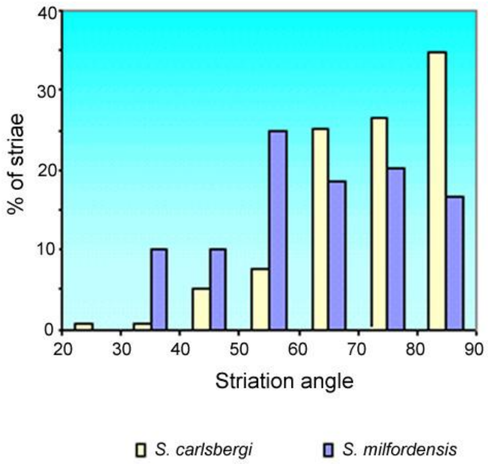

Figure 1. Histogram of the orientation of striations in the type series of *Steinichnus carlsbergi* and *Spongeliomorpha milfordensis.*

	Average angle (degrees)	Standard Deviation
Steichnichnus carlsbergi holotype	70.9	1.9
Spongeliomorpha milfordensis holotype	68.2	3.7
Steichnichnus carlsbergi type series	70.6	12.9
Spongeliomorpha milfordensis type series	60.1	13.6
Steichnichnus carlsbergi type series "*carlsbergi* type" portion	74.8	9.6
Steichnichnus carlsbergi type series "*milfordensis* type" portion	65.6	15.5

Figure 2. Summary of the average orientation and standard deviation for the type material of *Steinichnus carlsbergi* and *Spongeliomorpha milfordensis.*

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Ichnotaxobases for bird-like footprints: towards a uniform approach

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The conceptual and working approach to the ichnotaxonomy of vertebrate footprints, including that of bird-like footprints, is far from uniform. Ichnologists have recognised ichnofamilies, ichnogenera and ichnospecies of bird-like footprints on different grounds. As examples of the current inconsistency of criteria, some ichnofamilies are defined with greater detail than some ichnogenera, and commonly the geologic age of the track-bearing lithostratigraphic unit and the supposed trackmaker are considered as first-order criteria for ichnotaxonomy. The aims of this paper are to revise and discuss the ichnotaxobases used for the classification of avian footprints, and to suggest those considered as most appropriate for this kind of footprints. The proposed procedures are applied to the ichnotaxonomic analysis of the Santo Domingo Formation (Late Triassic, northwest Argentina) avian-like footprints.

Ichnogeneric taxobases that are used by most authors to classify tracks with avian affinities include the number, morphology, relative length, orientation of the impressions of the digits or the total divarication, and trackway parameters. Certain features are regarded as ichnogeneric taxobases by some authors, such as the footprint length/width ratio, divarication between the impressions of the digits II-III and III-IV, presence or absence of the sole impression, heel, and webbing, and the correspondence of the axis of the impression the digit I with that of the III. Other characters have been used indistinctly to name ichnogenera or ichnospecies by different authors, including presence of claw marks, number of phalangeal pads, and size of the footprint.

Most authors consider the details of the morphology, outline, and range and absolute length of the digit impressions, especially of the hallux, as ichnospecific taxobases. Other features often regarded in an secondary level are the morphology of the impressions of claws, phalangeal pads, sole, and heels; the range of the divarication between the impressions of the digits II-III, III-IV, and II-IV; and the distance between the tips of the middle and the inner and outer digit imprints and projection of the impression of the III beyond the external digit imprints.

Ichnofamilies should be erected to include ichnogenera that share key morphological features. In this respect, it is suggested that the number, relative position and proportionate length of digits, as well as the presence or absence of webbing impressions, are useful taxobases to define ichnofamilies of bird-like footprints. Similarly, the proposed ichnogeneric taxobases to be used with bird-like footprints are: the number, morphology, relative length, and orientation of the digit imprints (especially that of digit I), length/width ratio of footprints, number of phalangeal pad marks, divarication between the impressions of digits, and presence or absence of webbing. The ichnospecific taxobases used in this study are range of length/width ratio of footprints, proportion of digit length I:II:III:IV, range of the angles among the impressions of the digits, morphology of the sole, footprint size, pace angulation, stride length, and departure of tracks from the midline. Regarding size of footprints, an arbitrary position is considered necessary. It is proposed that a representative (modal or average) size value for the holotype series be estimated (using a number of readings no lower than 30) and a relative or absolute range of variability be defined for each ichnospecies.

The listed criteria are potentially useful for distinguishing new ichnotaxa, although the importance given to each will vary depending on the features of the track population under study. Erection of new ichnotaxa should always be based on a large sample size and considering the full variability of the footprint population. The material selected as type should preferentially be a trackway instead of individual footprints. Diagnosis of ichnotaxa must be as concise as possible, highlighting the key features of the ichnotaxa and avoiding interpretative terms like “shorebird footprint”, “charadriform footprint”, etc. If the only material available are a few specimens of footprints of potentially distinctive morphology that cannot be compared with known ichnotaxa, it is considered desirable to leave them in open nomenclature instead of creating a new ichnotaxon.

A new type of trace fossil from Lower Cretaceous “spotted” limestone from Western Carpathians (Slovakia)

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A rich association of trace fossils occurs in the Lower Cretaceous pelagic limestones of the Butkov Quarry. The exposed Lower to Middle Cretaceous succession encompasses the Ladce Formation, the Mráznica Formation, the Kališčo Formation and the Lúčkovská Formation (Michalík et al. 2005), which were analysed paleoichnologically. Trace fossils on fresh surfaces of the pelagic limestone are preserved as dark spots. The most abundant [or: richest?] assemblages of trace fossils occur in the Hauterivian Mráznica Formation, in which *Planolites*, *Thalassinoides*, *Chondrites*, *Zoophycos* and cylindrical trace fossils in the surfaces of ammonites were distinguished.

Typically, more or less spiral cross sections are sometimes C, G, S or U-shaped (Fig.1). Three-dimensional images of its shape were reconstructed by the method of serial cross-sections, each slice being 0,2 mm to 0,5 mm thick. The trace fossil is thus enlarged from an apparently simple, linear trace spreading from a broadly folded or scroll-like form and attenuates to a linear trace again (Fig.2).

This type of trace fossil represents an element of a typical lithofacies of the Lower Cretaceous Mráznica Formation bioturbated limestone, characteristic of the Valanginian – Aptian sequence in the frontal parts of the Krížna Nappe (Michalík and Vašíček 1980) and of the Upper Valanginian interval in the Manín Unit (Borza et al. 1987).

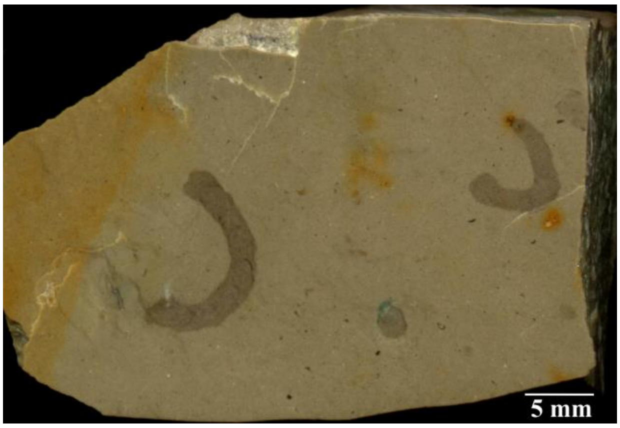

Figure1. Cross section of trace fossil studied. Butkov Quarry, Mráznica Formation

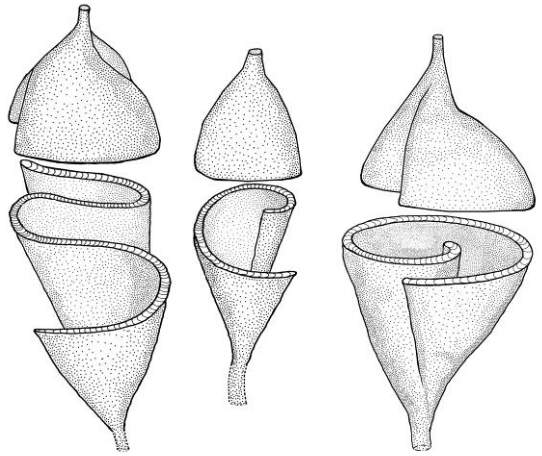

Figure 2. Idealized trace fossil reconstruction

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Problematic points in ichnotaxonomy: taphoseries, „photoseries“ and „graphoseries“

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MacNaughton and Pickerill (1995) erected the term **taphoseries** for a group of trace fossils that result from the same biogenic sedimentary structure but pass through different taphonomic (stratinomic and diagenetic) conditions. As a result, decrease of quality of preservation may selectively remove features important for ichnotaxonomic determination of the structure (e.g., wall lining, backfill). Determined according to the preserved features, the originally identical traces may form a series such as *Ancorichnus coronus* – *Ancorichnus ancorichnus* – *Taenidium* isp. – *Planolites* isp. The authors emphasize that such misidentifications of the original biogenic structures are not necessary, and that "taphoseries are of greatest use following initial ichnotaxonomic assessment and consideration of taphonomic effects, and prior to final assignment of material".

Though the term taphoseries is not used frequently, it represents so far the only consistent theoretical attitude to the problem. Many ichnotaxonomists are aware of it and they carefully consider not only the effects of diagenesis and weathering on the studied structures, but also changes made by erosion (cf. Uchman 1998 and the *Scolicia* – *Taphrhelminthopsis* dilemma). The recognition of taphoseries is, however, much more difficult if the material is not studied in the field but only in museum collections (where terminal members of the series tend to prevail). The chance to recognize a taphoseries is even lower if the revision is made only on published photographs and drawings.

A taphoseries resulting from bottom erosion has been documented from tempestites of the Kosov Formation (Late Ordovician, Czech Republic; Fig. 1A). Here, annulate tunnels attributable to the ichnogenus *Fustiglyphus* Vialov, 1971 according to the proposal by Stanley and Pickerill (1993) occur frequently. They were originally described by Fritsch (1908) as *Spongolithus annulatus* Fr. Stanley and Pickerill synonymised this homonymous ichnospecies with *Fustiglyphus annulatus* Vyalov, 1971 and proposed to use the latter ispecies for maintaining nomenclatural stability. Stanley and Pickerill (*op. cit.*) distinguished *Fustiglyphus* Vyalov, 1971 and *Rhabdoglyphus* Vassoevich, 1951, in the following way: *Rhabdoglyphus* is composed of invaginated segments, and *Fustiglyphus* is a tunnel-like form with well-defined rings or knots and no invagination.

Observations of several large soles of tempestite beds from the Praha-Běchovice and Praha-Michle localities showed that "invaginated segments" can be "modeled" by erosion of annulate tunnels in/on the muddy bottom, which is proved by additional erosional features on the same slabs. This creates the taphoseries *Fustiglyphus* – *Rhabdoglyphus* (Fig. 1B-C). Eventually, the rings may be eroded completely, which adds the ichnogenus *Planolites* as the terminal member of the series.

Notably, this taphoseries may not necessarily be unidirectional, despite the fact that the unidirectional character is postulated as a principle of taphoseries by Stanley and Pickerill (*op. cit.*). Invaginated segments may be, in the first stage, eroded into the form of an annulated tunnel/furrow, subsequently – by further erosion – certain annulae may be deepened as individual segments.

The existence of the above-mentioned taphoseries was not recognized by Stanley and Pickerill (1993), who assigned the material from the Kosov Formation partly to the ichnogenus *Fustiglyphus*~~,~~ and partly to *Rhabdoglyphus*. The probability of misidentification was increased by the fact that the authors did not see the original material but used only published photographs. Clearly, it is impracticable to visit all the collections containing the revised material and impossible to visit all type localities, but further caution against the use of photos or drawings must be done here. Photographed material can result in the effect named here “**photoseries**”: just the method of illumination of the object can make it classifiable as two different ichnotaxa. Diffuse light enables an annulate tunnel to be featured as *Rhabdoglyphus*, but raking light depicts instead “invaginated segments” of *Fustiglyphus* (Fig. 1D-E). Similar “photoseries” was created by Mikuláš (1992) who used very different illumination of figured specimens, leaving a puzzle for readers of the paper.

Use of idealized drawings is obviously even more problematic, as shown by nice “**graphoseries**” if we consider the original specimen, the method of its preparation, and the published figure (Fig. 2A-C). The example shown is *Spongolithus spinosus* Fritsch, 1908.

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Tempestite sole, Late Ordovician, Czech Republic

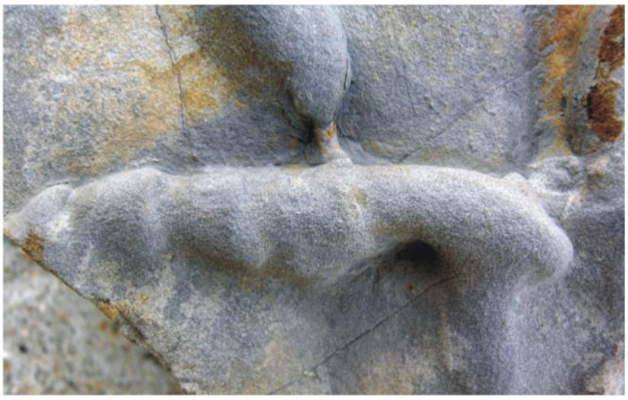
TAPHOSERIES

Fustiglyphus

“Rhabdoglyphus”

PHOTOSERIES

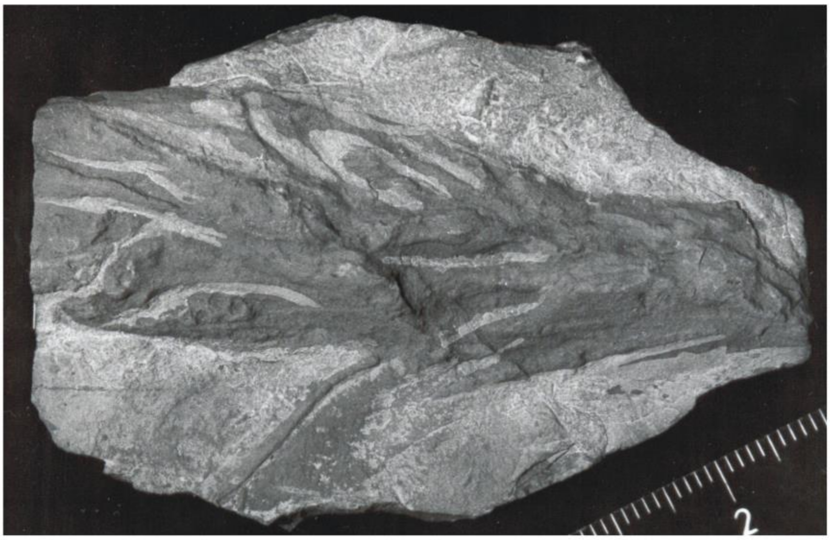
“Rhabdoglyphus”



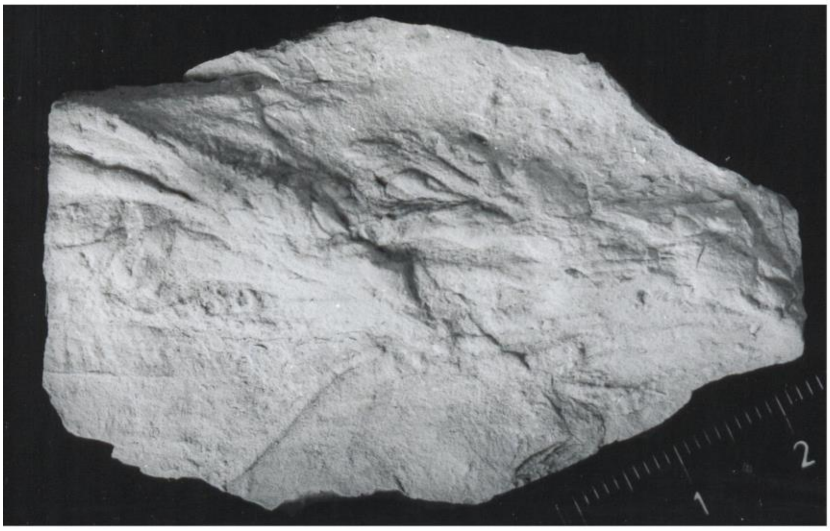
Fustiglyphus

GRAPHOSERIES

“Alga”



“Phycodes”



Mechanic structure

Some bivalve trace fossils in the Miroslav Plička collection

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Miroslav Plička (1920-1989) (for memorial see Novák, 1990) collected more than 2,000 trace fossil specimens, mostly from the Cretaceous-Paleogene flysch of the Czech and Slovak Carpathians. They are described in more than 30 publications by Plička and coauthors, wherein 26 new ichnogenera and 30 ichnospecies are distinguished. A large part of the ichnotaxa requires a revision.

Some of trace fossils from the Plička collection can be attributed to bivalves. They include *Hostynichnium duplex* Plička & Siráňova (1989), *Tuberculichnus vagans* Książkiewicz (1977) (only in the collection [meaning not clear]), and *Oravichnium hrabei* Plička & Uhrová (1990). They display common features: the hypichnial, smooth ridge that is subquadrate in cross-section and winding, irregularly meandering or looping in course. In the case of *Hostynichnium* and *Tuberculichnus*, the ridge is undulating and in *Oravichnium* it is even. Most probably, these trace fossils were produced by periodically or continuously ploughing bivalves, respectively. Plička & Siráňova (1989) noticed the similarity of *Hostynichnium duplex* to *Tuberculichnus meandrinus* Książkiewicz (1977), but argued that the former trace fossil is distinguished by its parallel to subparallel (double) course. This feature, however, can be incidental and can result from incomplete preservation of a meander whose turning segment is missing. Therefore, these two trace fossils are conspecific. Uchman (1998) included *Tuberculichnus vagans* Książkiewicz and *T. meandrinus* Książkiewicz (including its holotype) in *Protovirgularia* M^c^Coy as *Protovirgularia vagans* Książkiewicz and recommended to *Tuberculichnus* as useless ichnogenus. It seems, however, that *Protovirgularia* M^c^Coy should be restricted to forms that display signs of work of a cleft foot, such as chevron ribs (Seilacher & Seilacher, 1994). The discussed trace fossils are smooth and can be attributed to work of a wedgelike foot. Therefore, *Hostynichnium duplex* and *Tuberculichnus meandrinus* Książkiewicz are included in *Tuberculichnus vagans*. The ichnogenus *Tuberculichnus* Książkiewicz (1977) is conserved, but its diagnosis should be emended. Some trace fossils described as *Tuberculichnus meandrinus* Książkiewicz (but not the holotype) and complete [?] type material of *Tuberculichnus bulbosus* Książkiewicz should be involved [meaning unclear] in other ichnogenera (Uchman, 1998). *Lockeia serialis* Seilacher & Seilacher (1994), judging from the description, resembles *Tuberculichnus vagans* but is poorly documented. Therefore, it is difficult to decide if it is a younger synonym of *T. vagans* or a separate ichnotaxon. *Oravichnium hrabei* Plička & Uhrová should be kept as is, or the diagnosis of *Tuberculichnus* should be broadened in order to include this trace fossil.

A large trace fossil, *Radhostium carpathicum* Plička & Říha (1989) from the Upper Cretaceous flysch of the Czech Carpathians, can be considered with reservation as a bivalve trace fossil produced by a cleft foot. The challenge here is the very large size (up to 80 mm wide) of this trace fossil. It is also known from the Upper Cretaceous Rhenodanubian Flysch of Austria as the so-called “Pinsdorfer Versteinerung” (Abel, 1935). Vialov (1989) provided an ichnogenus and ichnospecies name for this trace fossil as *Pinsdorfichnus abeli*. Uchman (1998) called it cf. *Protovirgularia* isp.

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Figure 1. Holotype of *Tuberculichnus vagans* (TF UJ 1036)

Arthropod trackways and ichnotaxonomy

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Ichnology may be perceived as a rather esoteric subject by the general scientific community and this is probably belied by the "dark arts" of ichnotaxonomy clouding the wealth of potential applications. Ichnotaxonomy is a means to an end, and differences in ichnotaxonomic methodology are hindering potential applications. Only through a unified approach will it be possible to evaluate ichnofacies models, assess biostratigraphic schemes, understand sequences of ecospace utilisation and colonisation, and investigate the evolution of behaviour.

Two main problems exist in ichnotaxonomy: how to rationalise the plethora of ichnotaxa we already have and what to do when diagnosing new ichnotaxa. The following priciples have been developed with arthropod trackways in mind, but it is hoped that they will be of more general application to other types of trace fossils. The key to rationalising existing ichnotaxa and justifying their synonymy is the recognition of intergrading specimens. However, this is only the case for minor behavioural (i.e. differences resulting from variation in placement of limbs or gait parameters) or preservational variants (i.e. differences resulting from undertrack fallout or slight variations in substrate), regardless of ichnotaxonomic rank. Intergrading specimens should not be used to justify synonymy between major behavioural variants (i.e. separate ethological categories) and can be treated as hybrids e.g. *Cruziana* × *Rusophycus*. The distinction between minor and major preservational variation is somewhat of a grey area, but intergradations between major preservational variants could be related to differences in morphology resulting from substrate consistency e.g. *Diplichnites* × *Diplopodichnus* × *Dendroidichnites*, and there is some merit to retaining these as distinct ichnogenera. New ichnotaxa should ideally be based on observations of large samples of material, so that recurrence is demonstrable, and morphological continuums representing minor behavioural or preservational variants are identified. Ichnotaxa may only be erected on the basis of limited material if they truly represent a unique morphology that cannot be reconciled as a minor behavioural or preservational variant of existing ichnotaxa.

Fixing types in ichnotaxonomy

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More than one thousand invertebrate ichnogenera have been named so far, and probably about as many vertebrate ichnogenera. Until 2000, the International Code of Zoological Nomenclature did not require type specimens or type ichnospecies for ichnotaxa, but nearly all ichnotaxa were assigned types regardless. In cases where types are lacking, the first reviser is allowed to designate them.

Problems arise when ichnologists practice taxonomy without paying close attention to types, or when inappropriate types are designated at the start. As a result, ichnotaxa can drift away from their original meanings and more careful taxonomists are left to clean up the mess.

The situation is acute for common ichnotaxa, many of which were named more than one hundred years ago with very different interpretations. As pointed out by Michael Schlirf, the lectotype of *Skolithos linearis* is a vertical U-burrow with a spreite, which throws the concept of *Skolithos* as a simple vertical shaft into confusion (Fig. 1). The type specimen of *Diplocraterion parallelum* has deep funnels, which are scarcely ever preserved in other specimens of *Diplocraterion,* most of which probably never had funnels. *Monocraterion tentaculatum* has an atypical funnel that is filled with smaller tubes reminiscent of those of *Parahaentzschelinia,* but not seen in other *Monocraterion*. The typical form of *Chondrites* was probably intended by its author to be *C. targionii,* whose morphology is relatively well understood, but the first reviser chose the poorly understood and unusual *C. antiquus* instead. The author of *Trichophycus* chose a form, *T. lanosus*, that was represented by only two specimens as its monotype, and only later named the more common form as *T. venosus,* throwing into question for more than a century whether the two were conspecific (they are, but it was not obvious). An ichnotaxonomy in which the type species of *Skolithos, Monocraterion, Diplocraterion, Chondrites,* and *Trichophycus* (and *Arenicolites* and *Rhizocorallium* and *Zoophycos*) are all "atypical" is not a stable system, but hasty revision would only make things worse.

Early Cambrian ichnotaxa present especially challenging problems. At first glance, many seem to be similar to younger trace fossils and therefore are congeneric with them. However, we know from body fossils that the makers of Early Cambrian traces were dominated by a fauna whose members are now few or extinct, such as trilobites and priapulids. It makes sense, at some ichnotaxonomic rank, to search for subtle morphologic differences that distinguish, for example, burrows made perhaps by Early Cambrian marine worms ("*Treptichnus*" *pedum*) from burrows made by Pennsylvanian insect larvae (*Treptichnus bifurcus*). Let us be informed by biology rather than ignore it.

What should be done? No single solution can be applied to every case, but general principles can be proposed. To be scientific, ichnotaxonomy must be based on principles that use repeatable procedures and that allow patterns to emerge from the data. The most useful taxonomy of trace fossils is based on biologic principles rather than sedimentologic ones. It is based on specimens rather than conceptual constructs, and on whole specimens rather than fragments. Close observation is used to determine which morphologic features are significant clues to the biology of the tracemaker and which are more general clues to its ecology. Similar forms, and forms made by similar organisms, should be investigated for comparison.

Types can then be selected that truly represent their ichnotaxa, and ecologic and other patterns should emerge from the classification.

Reference

Howell, B.F. 1943. Burrows of *Skolithos* and *Planolites* in the Cambrian Hardyston sandstone at Reading, Pennsylvania. Bulletin of the Wagner Free Institute of Science of Philadelphia, **3**: 3-33, pl. 1-8.

Fig. 1.—What was Howell thinking when, after carefully studying topotypes of *Skolithos linearis* from the Lower Cambrian of Pennsylvania, he designated this indistinct example of *Diplocraterion* as his neotype? By doing so, he made the taxonomy of two “problematica” even more problematic. In this case, the ichnotaxonomist must reject the neotype in favor of a specimen that matches the search image of a simple vertical shaft, because stability in nomenclature is more important than following a poor decision regardless of priority. This will require a petition to the International Commission for Zoological Nomenclature.

Lower Cretaceous dinosaur nests in the Cameros Basin of Soria Province (Spain)

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Clusters of hollows have been found in the Berriasian (Lower Cretaceous) sediments of Soria (Spain), emplaced in a basin where direct and indirect evidence of dinosaurs and other reptiles is quite common. These curious concentrations of hollows are interpreted as remains of nests. Considering their size (the diameter ranging from 8 to 16 cm), the producer of these possible nests is inferred to have been a titanosaurid dinosaur, whose footprints have been found in different beds within the same outcrop. The hollows (each presumably made for one egg) are arranged in imaginary parallel lines inside the nest, as described for titanosaurid nests from Romania by Dughi and Sirugue (1966). Also, the number of eggs per nest (not more than twelve) is closer to those of titanosaurid nests rather than theropod nests. Distance between different clusters (1.48-2.0 m) is low for a sauropod nest. In Auca Mahuevo, Argentina, they are separated about 43 m, according to Chiappe et al. (1998), but in Rahioli (India) titanosaurid nests have a separation between nests of less than a meter (Jain, 1989). Also in Asifabad (India), other titanosaurid nests separated 2.6 m have been described.

Thus, the great variation in size noted in Soria for the presumed nests studied here could be explained by the interment of the nests by the dinosaurs to aid the proper development of embryos within the eggs (Coombs, 1990; Dodson, 1990), by a specific treatment on each egg. Post-sedimentary acidic conditions (in diagenetic phases) could have dissolved the calcium of the eggshells, preserving only the hollows made by the eggs. This could also account for the lack of *Lepidotes* and *Unio* remains in these beds.

Figure 1- Detail of one of the possible dinosaur nests from the Valdelavilla outcrop (Soria province, Spain)


Figure 2- Theropod and sauropod footprints from Los Campos outcrop (Soria province, Spain)

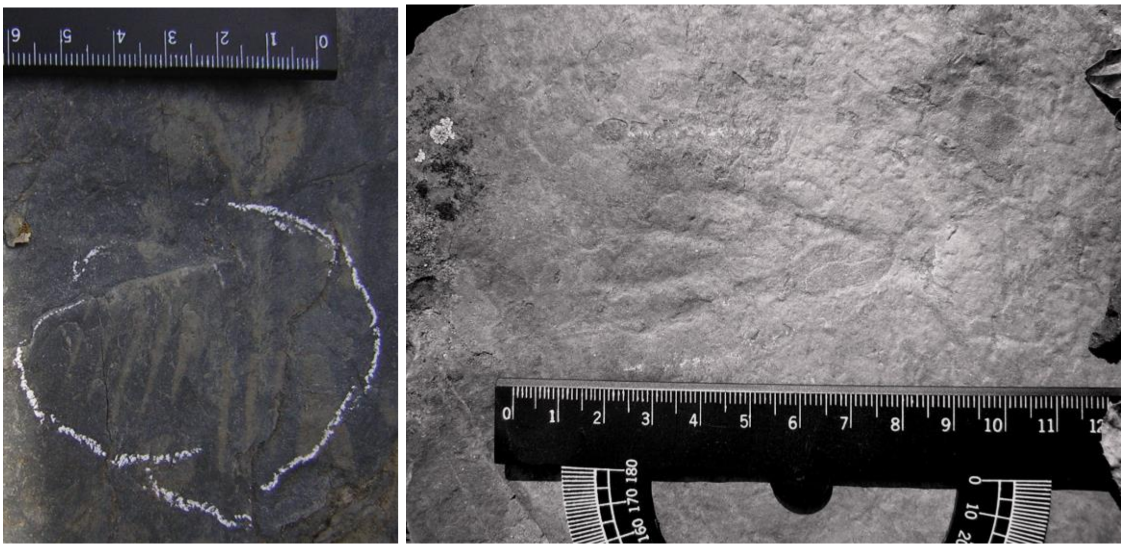

Figure 3- Turtle and pterosaur footprints from the Los Tolmos outcrop (Soria province, Spain).

The plantigrade dinosaurs – evidence from segnosaurian trackways

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Many previous authors (Charig, 1972; Parrish, 1989, etc.) analyzed the evolution of the pes and appearance of digitigrady in archosauromorphs. Digitigrady usually has been accepted as common apomorphic character of dinosaurs (Gauthier, 1986). Very rare exceptions from this principle have been confirmed in trackways (Haubold, 1971; Kuban, 1989), but all these were the evidence only for facultative plantigrady in the typical digitigrade dinosaurs.

Enigmatic trackways of the bipedal dinosaur *Macropodosaurus gravis* were found in the Lower Cretaceous (Albian) locality Shirkent-1 in Tajikistan (Zagharov, 1964). Even then, S.A. Zagharov suggested that *Macropodosaurus* was a plantigrade theropod of unknown group. Most of the authors (Haubold, 1971, etc.) identified *Macropodosaurus* as megalosauroid footprints, and McCrea and others (2001) as ankylosaur ones. Only L.A. Nesov (1995) refered *Macropodosaurus* to segnosaurs.

Restudy of these trackways during my fieldwork in Central Asia in 1987 demonstrated these traces to be the first known segnosaurian trackways and clear evidence of obligate plantigrady of its makers.

The main trackway of *Macropodosaurus* consists of 7 footprints, and another of 2 footprints (fig. 1). The trackways belonged to bipedal animals, being represented only by hindlimb footprints. The footprints of the right and left foot with toes are oriented forwards and situated close to the midline. Pace angulation is approximately 160°. Pace length is 72-75 cm, stride 146 cm. Footprints are evenly deep, wide-oval, 50-56 cm long. Such correlation of the short length of pace to long footprint suggests the slow walking gait of this graviportal animal. Clear, deep imprints of four toes with long, narrow and straight claws and wide metatarsal division of the foot are well exhibited by the footprints. This implies that *Macropodosaurus* stepped on the whole plantar surface of the foot including the metatarsals. Thus this dinosaur was an obligate plantigrade. The toes are disposed in a subparallel manner. Toes II-IV are equal in length; toe I is shortest.

Macropodosaurus footprints are quite unlike tridactyl footprints of typical theropods, as well as of ankylosaurs. *Macropodosaurus* footprints are somewhat similar to footprints of a large prosauropod *Otozoum*, but differ in certain morphological details. The morphology and size of *Macropodosaurus* footprints best resemble the form of the segnosaurian foot and reconstructed habitat of the trackmakers (Zagharov, 1964) resembles the appearance of these graviportal dinosaurs. The feet of the largest segnosaurs, *Erlikosaurus* and *Therizinosaurus,* match *Macropodosaurus* footprints best of all (fig. 2). However, all previous authors reconstructed segnosaurs (like other dinosaurs) as digitigrade animals. I suggest that such a reconstruction may be incorrect. Segnosaurs have the most primitive pes within the dinosaurs, with toes I-IV and rudimentary metatarsal V, also with short, unconsolidated metatarsal elements I-IV. Therefore, metatarsals of segnosaurs probably did not form an additional free segment in the hindlimb (tarsometatarsus); these graviportal dinosaurs walked [or: pressed] on the whole foot and were probably [or, if certain: must have been] obligately plantigrade. Such reconstruction seems natural (fig. 3) and corresponds well to *Macropodosaurus* footprints.

Segnosaurs are most probably closely related to maniraptors. The common ancestors of segnosaurs, maniraptors and birds probably passed through an arboreal phase in their history (Chatterjee, 1991, 1999). Subsequently, segnosaurs first returned to a terrestrial mode of life and increased in size. These heavy animals with short tail and long neck could not walk using [?] their massive forelimb with huge claws, and attained obligate plantigrady by increasing the area of hindfoot support. So a strange mixture of avian characters and specialized characters (including plantigrady) appeared in segnosaurs.

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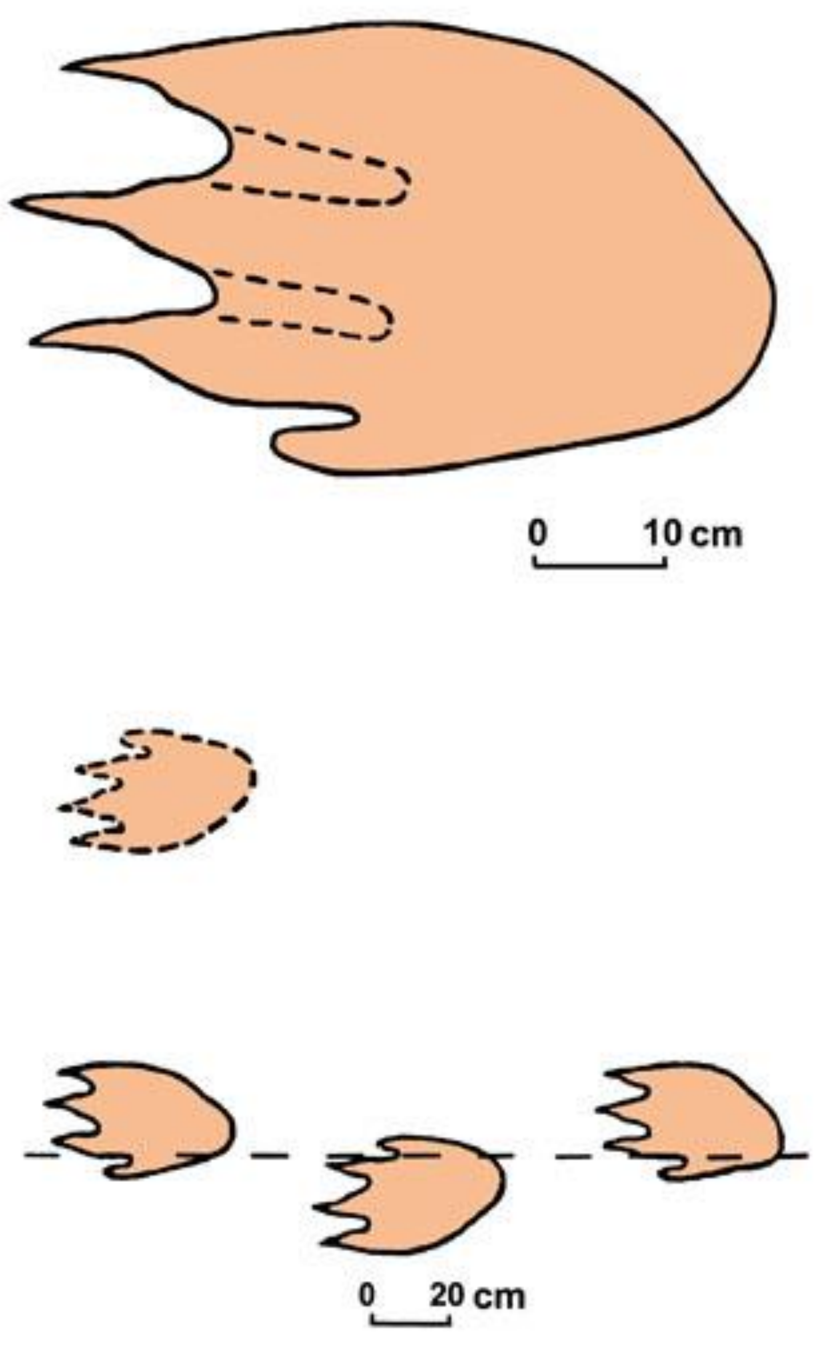

Figure 1. *Macropodosaurus* trackways and footprint of the right hindlimb. Locality Shirkent-1, Tajikistan, Early Cretaceous (Albian) (after Zagharov, 1964).

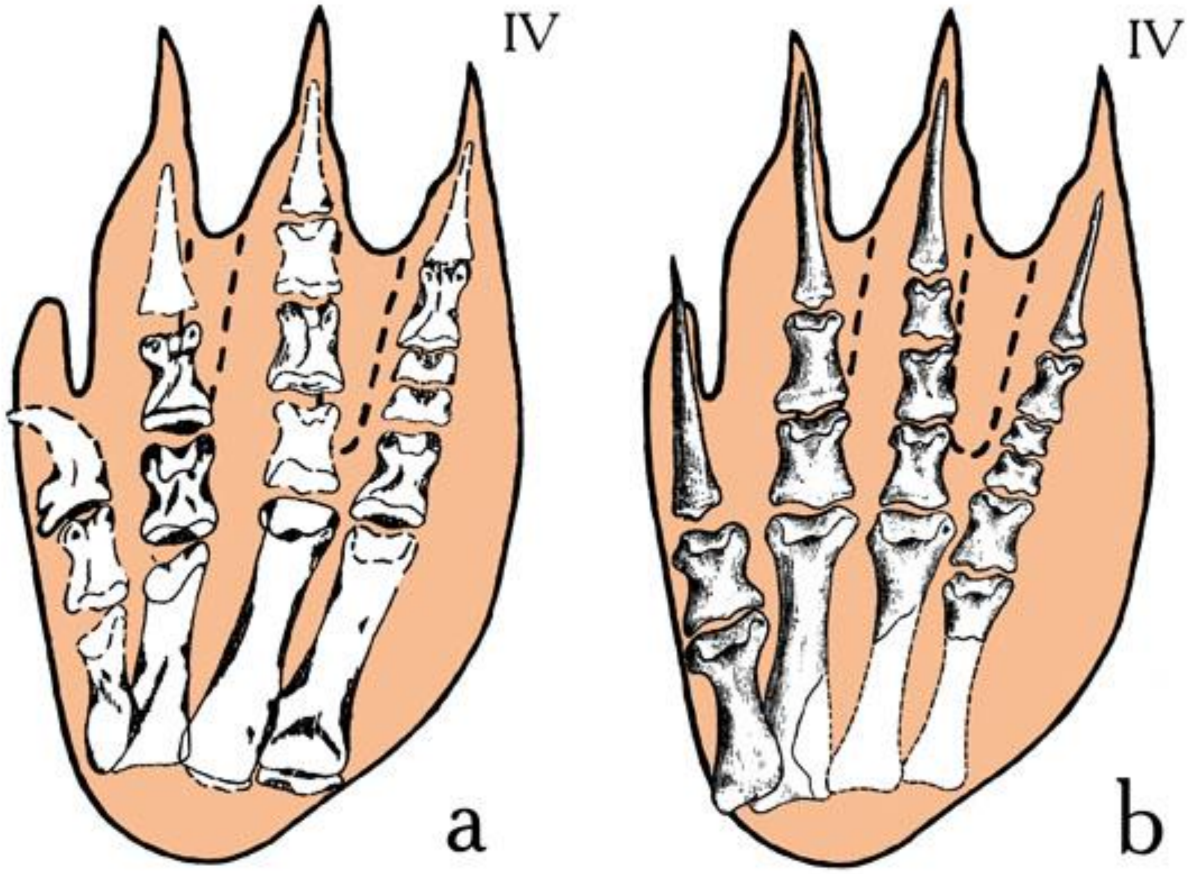

Figure 2. *Macropodosaurus* footprint of the right hindlimb (shaded) compared to a) *Therizinosaurus* and b) *Erlikosaurus* pes.

Figure 3. Skeleton of *Therizinosaurus,* Late Cretaceous, Mongolia (reconstruction after Lambert et al., 2001, modified).

Burrow wall microstructure of modern brackish water fauna: a valid ichnotaxobase?

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Modern burrows often have served as analogues for trace fossils, but their distinctive attributes are commonly overlooked in ichnotaxonomic discussions. As plaster/resin casting is a prevalent collection method, previous descriptions of modern burrows have focused on the general form of the burrow structure and infrequently detail either the burrow fill or burrow boundaries. However, in the course of burrow construction and dwelling, the inhabitants of these modern burrows produce numerous sedimentary characteristics on a scale that is better observed with scanning electron microscopy (SEM) than standard resin casting techniques.

Burrow structures of nine infanual invertebrates, collected from the west coast of Washington, Oregon and California (USA), were examined using SEM imagery. Burrows studied included those of *Corophium volutator, Heteromastus filiformis, Arenicola marina, Saccoglossus bromophenolosus, Clymenella sp*., *Cirriformia luxuriosa, Upogebia pugettensis, Nereis virens* and *Phoronopsis viridis*. SEM data indicate that, at a microscopic scale, the burrow morphology is best characterized by the properties of the burrow-sediment boundary. Three characteristics appear significant in defining the microscale burrow morphology including grain orientation and size distribution, nature of the mucous lining, and wall sculpture.

In several burrow types, the burrow structure was distinguishable from the ambient sediment by changes in the modal grain size and the range of particle diameters present. Variations in the degree of packing (i.e. loose vs. tight packing) between the burrow and sediment often accompanied these differences in grain size. Some burrows, such as *Phoronopsis viridis,* displayed a high degree of particle manipulation resulting in burrow walls with preferred grain orientation and imbrication.

In addition to the alterations to grain size distribution and orientation, most burrows surveyed displayed mucus-stabilized walls. These mucous linings can be separated by the form of the original mucous secretion and the resultant structure used to stabilize the burrow wall. Mucous secretions appear to be produced in one of three ways, forming globules, threads or ribbons. Secretions are incorporated into the burrow wall in the form of smooth blankets or woven mats. Some species (e.g. *Cirriformia luxuriosa*) use multiple mucous linings throughout the wall, whereas others employ only one layer at the burrow-water interface (e.g. *Saccoglossus bromophenolosus*).

Wall sculpture was observed only in burrows belonging to *Corophium volutator*. Though the feature occurs less commonly than the particle manipulation or mucous linings, when present it is highly distinctive.

At a microscopic level, the burrow morphology of modern infaunal invertebrates can be described within the existing framework of ichnotaxonomy. The characteristics used to describe these burrows – grain orientation and size distribution, nature of the mucous lining, and wall sculpture – are an elaboration of the burrow boundary ichnotaxobase defined by Bromley (1990) and are a necessity at this scale.