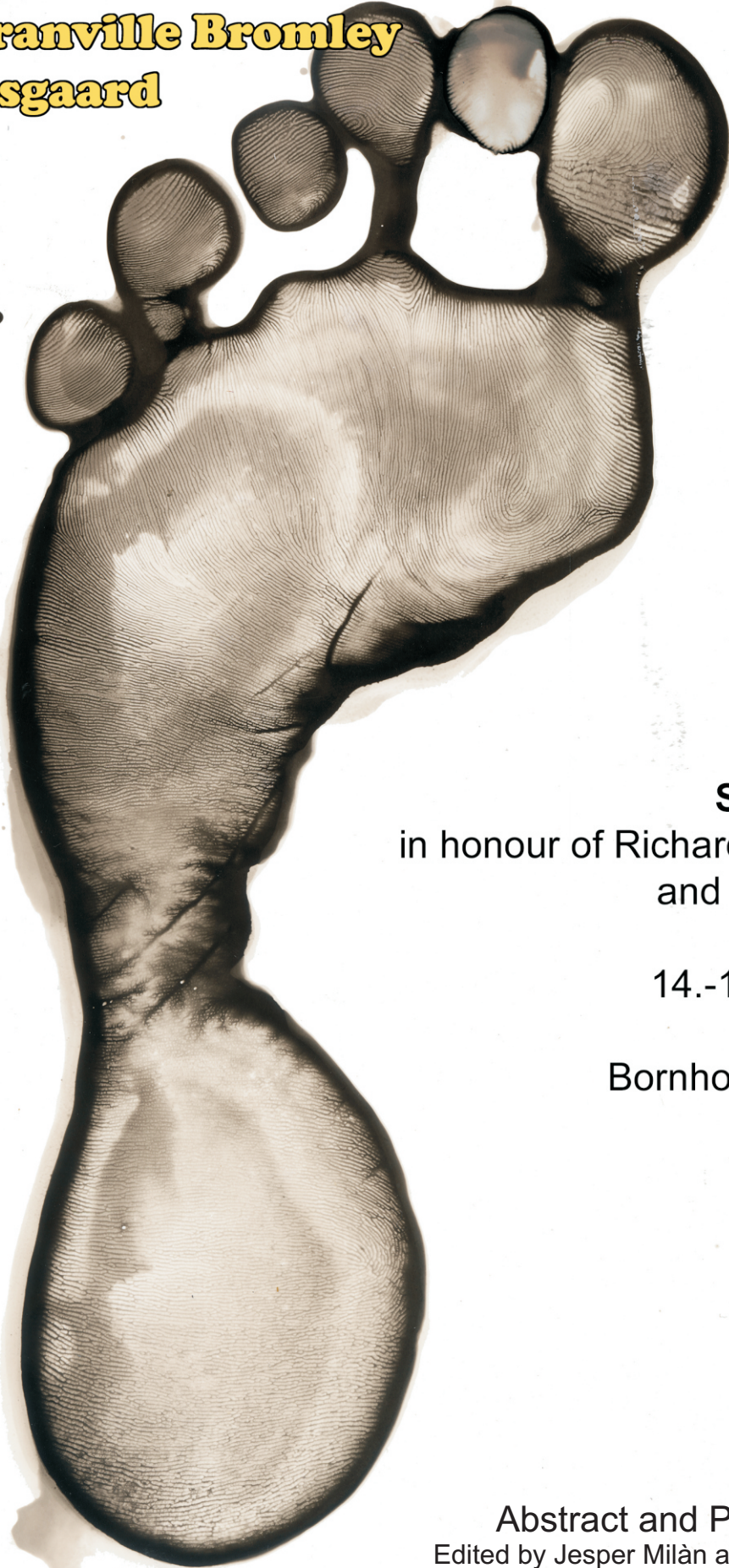


ONE ICHNOLOGY

**Honouring the contribution of
Richard Granville Bromley
and Ulla Asgaard
to science**



SYMPOSIUM

in honour of Richard G. Bromley
and Ulla Asgaard

14.-16. May 2014
Egilsholm
Bornholm, Denmark

*Detailed imprint
of Richard Bromley's
left foot, c. 1990.*

Abstract and Programme
Edited by Jesper Milàn and Lothar H. Vallon

ONE ICHNOLOGY
Symposium in honour of Richard G. Bromley and Ulla Asgaard
14 -16th May, Egilsholm, Bornholm, Denmark
Scientific program

ONE ICHNOLOGY – Honouring the contributions of Richard G. Bromley and Ulla Asgaard to science

14-16th of May 2014, Egilsholm, Bornholm, Denmark

Organized by Kurt S.S. Nielsen, Lothar H. Vallon, Noelia Carmona and Jesper Milàn

May 14th.

	Arrival of participants
From 12:00	We can move into Egilsholm from 12:00 (This also means that the organisational committee cannot move in before! So if you arrive with us, there will be total chaos... ☺ But you might be able to help us setting things up)
21:00-22:00	Late Dinner
22:00	Icebreaker Party (including an oral presentation by Jesper MILÀN: Fossils rock, rock-fossils!)

May 15th.

07:00-08:00	Breakfast
08:30-09:20	EKDALE, A.A. (Keynote): The Ontogeny of Ichnofabric: A Parental Perspective
09:20-09:40	NEUMANN, C.: The role of birds in marine bioerosion
09:40-10:00	WISSHAK, M., NEUMANN, C., ABERHAN, M., GIROD, P., RÖSNER, T. & BROMLEY, R.G.: <i>Centrichnus eccentricus</i> revisited: A new view on anomiid bivalve bioerosion
10:00-10:20	RODRÍGUEZ-TOVAR, F.J., UCHMAN, A. & PUGA-BERNABÉU, Á: Miocene macroborings in gneiss boulders: a case from SE Spain
10:20-11:00	Coffee break and poster presentation
11:00-11:20	MILÀN, J., THEODOROU, G., LOOPE, D.B. & PANNAYIDES, I.: Vertebrate tracks in Late Pleistocene – Early Holocene? Aeolian carbonate deposits in Pafos, Cyprus
11:20-11:40	DAVID, A.: Activity of bioeroding worms in different Miocene Formations of Hungary
11:40-12:00	KNAUST, D.: Bioturbation and reservoir quality: towards a genetic approach
12:00-12:20	JACOBSEN, A. R.: Ichnotaxa for tetrapod bite traces: Has it been a useful tool?

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12:30-14:00	Lunch
14:00-14:20	BUATOIS, L.: In defense of the ichnoguild concept
14:20-14:40	MÁNGANO, M. G.: A whole new world: Cryptic ecosystems in a Copenhagen basement?
14:40-15:00	RINDSBERG, A.K.: Where is ichnotaxonomy heading?
15:00-15:20	BROMLEY, R. G., WETZEL, A. & UCHMAN, A.: Earthworm trails - What are underground miners doing on the surface?
15:20-16:00	Coffee break and poster presentation
16:00-16:20	WERVER, O.: Ichnofossil markerbeds in between extremely arid deposits in the Northern Pangaea Interior, Lower Triassic, Netherlands subsurface
16:20-16:40	NARA, M.: A <i>Hillichnus</i> -like trace fossil from Jurassic tidal deposits of the Sakamoto Formation, Southwest Japan, and its evolutionary significance
16:40-17:00	EKDALE, E.: The evolution of hearing in baleen whales
18:30	Dinner
Thereafter	Ichnocommunity (= Ichnologists' get-together)

May 16th.

07:00-08:00	Breakfast
Latest 12:00 (probably much earlier!)	Departure from Egitsholm As we came, we have to go. Everything needs to be packed down at 12:00 when we have to hand over Egitsholm again to the owners or the next group staying there.
	Fieldtrip (Museum NaturBornholm, Strøby Quarry (Cambrian sandstone with jellyfish and trace fossils)

The Ontogeny of Ichnofabric: A Parental Perspective

by A. A. EKDALE

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The ichnofabric concept was conceived in 1981 in the Cretaceous chalk of Denmark, and the word “ichnofabric” was born on the island of Bornholm shortly thereafter. In 1982 ichnofabric was officially baptized into the family of ichnology by means of several technical abstracts submitted for presentations at international meetings in Denmark, Canada and the United States (BROMLEY & EKDALE 1982A, 1982B; EKDALE & BROMLEY 1982). In 1983 the term “ichnofabric” was formally introduced to the world at large in a peer-reviewed paper published by the *Bulletin of the Geological Society of Denmark* (EKDALE & BROMLEY 1983; see fig. 1). During its early childhood in the 1980's, ichnofabric was nourished and nurtured by different workers in different countries on different continents. Ichnofabric entered adolescence at its grand “coming out” during the first internationally oriented symposium on “Ichnofabric and Ichnofacies” at the IAS Sedimentological Congress in Nottingham in 1990, which spawned the publication of a special theme issue of *Palaios* on the topic of ichnofabrics and ichnofacies in the following year (e.g., EKDALE & BROMLEY 1991).

During its somewhat tumultuous teenage years that followed, ichnofabric faced challenges and even engaged in a public brawl with attackers who challenged its very existence (FREY & PEMBERTON 1990). Ichnofabric prevailed (EKDALE et al. 1991), and it entered adulthood with the staging of the First International Ichnofabric Workshop in Norway in 1991, which was sponsored by Norsk Hydro Oil Company. In the following years, ichnofabric has grown and matured via the continuation of the ever-expanding International Ichnofabric Workshops in the United States (1993), Denmark (1995), Bahamas (1997), England (1999), Venezuela (2001), Switzerland (2003), New Zealand (2005), Canada (2007), China (2009), Spain (2011), and Turkey (2013). These very lively meetings live on – the 13th International Ichnofabric Workshop will occur in Japan next year (2015).

Ichnology has been widely recognized as the link between paleobiology and sedimentology, and ichnofabric in particular represents the direct interface between organisms and the sediment that they inhabit (EKDALE et al. 2012). Ichnofabric studies take us far beyond mere trace fossil descriptions to contribute insights in such areas as paleoethological interpretations, habitat partitioning of the sedimentary substrate, sedimentary processes, paleoenvironmental reconstructions, diagenetic modification of sedimentary rocks, and stratigraphic correlation of sedimentary units. Happily, ichnofabric research continues to thrive and mature with the growing number of contributions accomplished by new generations of energetic young geoscientists. As the parents and godparents of ichnofabric advance into their senior years, ichnofabric research remains vibrant and appears to be unstoppable, as it continues to progress towards new (and unpredictable) horizons!

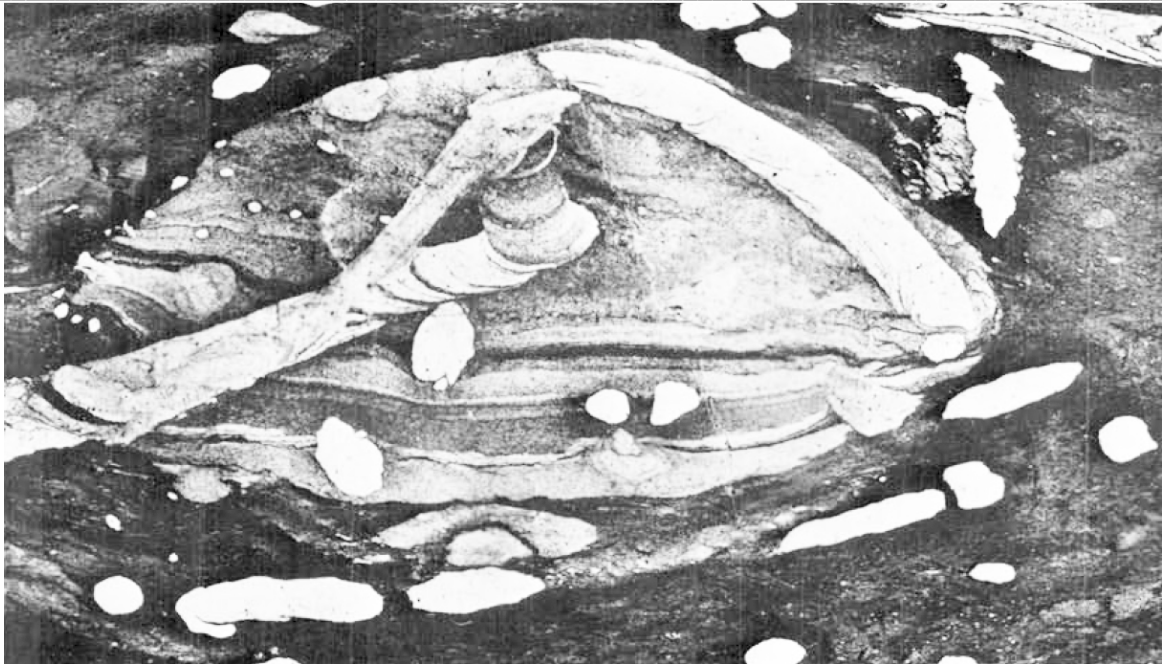


Figure 1. Example of the complex ichnofabric displayed in the uppermost Cretaceous Kjølby Gaard Marl in Jylland, Denmark. A totally bioturbated and compacted background ichnofabric was penetrated by a large *Thalassinoides*, whose sediment fill was parallel-laminated in the bottom and bioturbated in the top, and then that *Thalassinoides* subsequently was cross-cut by several generations of later burrows, including *Zoophycos*, *Teichichmus* and *Chondrites* (EKDALE & BROMLEY 1983, fig. 12).

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The role of birds in marine bioerosion

By Christian NEUMANN

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Birds, which evolved from dinosaurs at the end of the Jurassic period, today form two major clades (Passerines and Non-passerines) with about 10 000 known species. Among the Non-passerines, about 16 families can be ecologically considered as “seabirds”. These are birds adapted to spend a large part of their life cycle on the sea where they exploit the rich food resources the oceans offer. Whereas most sea birds rely on fish as the main food source, at least members of six families (Diomedidae, Procellariidae, Anatidae, Charadriiformes, Lariidae, Alcidae) also feed upon invertebrates which possess mineralized hard-parts and thus, play an active role as marine bioeroders. Main prey organisms are bivalves, gastropods, crustaceans and echinoderms. Whereas most birds feed on exposed tidal flats and along the shoreline, eiders (*Somateria* ssp.) and scoters (*Melanitta* ssp.) are excellent divers and forage in depths up to 15 metres. From the Thick-billed Murre (*Uria lomvia*), a maximum diving depth of 250 metres (!) has been recorded. Albatrosses and shearwaters are pelagic birds of the open ocean. Some of these, e.g., the Sepia shearwater (*Calonectris diomedea*) are specialized cephalopod predators and leave diagnostic peck marks on aragonitic cuttlebones.

Charadriiform birds (e.g. Oystercatchers, *Haematopus* ssp.) and gulls manipulate the prey with their bill and produce significant traces. Ducks and geese (especially eiders and shelducks) swallow their prey organisms completely. Shells are crushed in the stomach and regurgitated and/or shed out with faeces.

Bird bioerosion is most significant where large concentrations of sea birds occur such as breeding colonies and roosting sites. The Wadden Sea, for instance, is a migration hot spot along the East Atlantic Flyway, where two times each year, millions of seabirds stop to rest, molt and refuel during their migrations from and to their breeding grounds in the Eurasian arctic. For instance, between July and September, the complete northwest-European population (about 250 000 birds) of the Ruddy shelduck (*Tadorna tadorna*) gathers in the mouth of the Elbe estuary for molting. Estimating a residence time of 60 days for each individual bird and a production of 30 g of shell fragments per day, a rate of 450 tons of fragmented shells per molting season can be calculated for this restricted area of the Wadden Sea. This simple calculation emphasizes the significance of birds as bioeroders in marine habitats, which has long been neglected and/or underestimated.

In summary, bird bioerosion is most significant in the high-productive sandy/muddy intertidal zone and seems to be less important in the rocky intertidal. The subtidal zone is only available for diving birds. In the pelagic realm, bioerosion is restricted to specialized cephalopod-predating birds. There is no information available for coral reef and mangrove habitats.

Centrichnus eccentricus revisited: **A new view on anomiid bivalve bioerosion**

By Max WISSHAK¹⁾, Christian NEUMANN²⁾, Martin ABERHAN²⁾, Peter GIROD³⁾, Thomas RÖSNER⁴⁾ and
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Saddle oysters (Anomiidae) attach themselves to calcareous hard substrates by means of a calcified byssus that etches an attachment scar, referred to as ichnospecies *Centrichnus eccentricus* BROMLEY & MARTINELL, 1991. Examination of rich material from the Late Cretaceous of central Europe extend the fossil record of this ichnotaxon and revealed a set of previously unrecognised morphological features which appear to be typical for this time period and the respective anomiid trace maker. Excellent preservation of a large number of trace fossil specimens with a complete set of morphological characters allowed a biometrical analysis and additional observations indicating a distinct substrate preference for belemnite rostra, a strong intra- and interspecific competition for settlement space, as well as interactions with durophagous predators. Further implications for anomiid palaeobiology and palaeoecology arise from allometric growth, development of a ‘pseudo-hinge’ between anterior valve margin and an etched hinge groove, and an etched outline suture along the lateral and posterior shell margin. All of these features enhanced a firm attachment and increased shear resistance, and is thus interpreted as an effective defence mechanism against shell-crushing enemies under the intensified predation pressure in marine environments in the late Cretaceous.

Miocene macroborings in gneiss boulders: a case from SE Spain

by Francisco J. RODRÍGUEZ-TOVAR ¹⁾, Alfred UCHMAN ²⁾ & Ángel PUGA-BERNABÉU ¹⁾

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Macroborings are commonest in carbonate substrate and very rare in crystalline rocks (e.g. WARME 1975; BROMLEY 1978; BROMLEY & ASGAARD 1993; JOHNSON 2006). In the latter, they are most frequent in weathered basaltoids and only a few cases are noted in hard metamorphic or igneous rocks (e.g., MASUDA & MATSUSHIMA 1969; FISHER 1981; ALLOUC et al. 1996; BUATOIS & ENCINAS 2011; SANTOS et al. 2012). Therefore, the occurrence of marine macroborings in augen gneiss boulders in the Miocene (Upper Tortonian) of the Sorbas Basin in SE Spain is exceptional. The borings occur in a few metres thick transgressive conglomerate that rests on a crystalline basement of the Internal Zone of the Betic Cordillera and is covered by sandstones followed by coralline floatstones and rudstones (Azagador Member of the Turre Formation). The borings are mentioned by WOOD (1996) and DOYLE et al. (1998) but they are not studied in detail. A new field research in vicinity of Los Castaños has allowed distinguishing two types of macroborings. The most abundant are regular, hemispherical depressions. They represent probably the basal part of the mostly bivalve boring *Gastrochaenolites* which was truncated by erosion. The second, less common type is a pouch-like depression, tapering downward, elliptical in outline, clearly different to other non-circular in outline macroborings of similar shape. Therefore, this is considered to be a new ichnogenus and ichnospecies. The possible *Gastrochaenolites* and the pouch-shaped boring can be produced by bivalves. The tracemaker of the latter, due to non-circular outline, might be an endolithic or semi-endolithic bivalve, which used chemical means to boring in weathered feldspar blasts and mechanically removed quartz blasts. Only some (no more than a few percent) largest boulders at the top of the conglomerate are bored. They provided a stabilized substrate in a nutrient-rich environment and decreasing energy during advancing transgression, allowing colonization by boring organisms. The further decreasing energy and increasing amount of fine-grained sediment suspension in the water might kill the borers. The borings were abraded before final burial under the overlying sediments.

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Vertebrate tracks in Late Pleistocene – Early Holocene? Aeolian carbonate deposits in Pafos, Cyprus.

By Jesper MILÀN^{1,2}, Georgios THEODOROU³, David B LOOPE⁴ and Ioannis PANAYIDES⁵

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In 2005 numerous tracks were discovered in Aeolian deposits in and around the town of Pafos in the south-western part of Cyprus. The main trackbearing exposure is located in the protected archaeological site near Ayia Solomoni church inside the city of Pafos, where cross-sections through tracks are abundant in the vertical exposures of the aeolianite. Some exposures show as many as 10 tracks per m² in vertical exposure. Several additional tracks were found in the extensive subterranean tomb complex, Tombs of the Kings, just outside Pafos. The aeolianite was formed when westerly to south-westerly winds drove fine- to medium-grained calcareous sand onshore from the beach, generating 1 – 2 meter-thick eolian crossbed sets composed of both grainflow and wind-ripple strata, and sand sheets composed entirely of wind-ripple strata. The sediment does not have yet an absolute date, but is expected to be of similar age to other coastal aeolianites from the Mediterranean area, which is Late Pleistocene to Early Holocene. The Late Pleistocene endemic fauna in Cyprus were limited to dwarf hippopotamus *Phanourios minor*, dwarf elephants *Elephas Cypriotes*, a small carnivore *Genetta plesictoides*, and possibly humans. The tracks are 5 – 15 cm in diameter, with few tracks up to 23 cm. This range of size correlates well with the estimated foot size of dwarf hippopotamus and dwarf elephants. This limited endemic island fauna gives a unique opportunity to correlate tracks with trackmakers.

Activity of Bioeroding Worms in Different Miocene Formations of Hungary

By Arpad DAVID

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Traces of Polychaete and Sipunculid worms have been investigated at six different Miocene age localities (Nagyvisnyó, abandoned gravel quarry; Lénárdaróc, Szodonka valley; Dédestapolcsány, abandoned gravel quarry; Bánhorváti, cemetery hill; Sajólászlófalva, Bocsonya Hill; Hetvehely, rail road cut) in Hungary.

The following ichnotaxa occurred in the examined material: *Caulostrepsis taeniola* CLARKE, 1908; *Caulostrepsis contorta* BROMLEY - D'ALESSANDRO 1983; *Caulostrepsis cretacea* (VOIGHT 1971); *Maeandropolydora decipiens* VOIGHT, 1965; *Maeandropolydora sulcans* VOIGHT, 1965; *Maeandropolydora elegans* BROMLEY - D'ALESSANDRO, 1983; *Maeandropolydora barocca* BROMLEY - D'ALESSANDRO, 1983; *Trypanites solitarius* (HAGENOW) 1840; *Trypanites weisei* MÄGDEFRAU 1939; *Trypanites* isp.

Abrasion pebbles and *Ostrea* valves served as hard substrate for the bioeroding organisms. The shape of the worm borings is determined by the structure of the substrate primarily. The morphology is influenced by the presence of other borings (eg.: clionids, bivalves, other worms).

	Nagyvisnyó	Lénárdaróc	Dédestapolcsány	Bánhorváti	Sajólászlófalva	Hetvehely
<i>Caulostrepsis taeniola</i>	+	++	++	++	++	
<i>C. contorta</i>	++	++	+++		+	++
<i>C. cretacea</i>	++	+++			+	
<i>Maeandropolydora decipiens</i>	+++	+	++		++	
<i>M. sulcans</i>	+	+			+++	
<i>M. elegans</i>	+++	++	++	+++	+++	+++
<i>M. barocca</i>	++		+			
<i>Trypanites solitarius</i>		++	+	+	+	+
<i>T. weisei</i>					+	
<i>Trypanites</i> isp.					++	

Table 1.: Distribution of trace fossils produced by different worms at the examined localities
Legend: + rare; ++ frequent; +++ abundant

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Bioturbation and reservoir quality: towards a genetic approach

By Dirk KNAUST

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The process of bioturbation, or the organism/sediment interaction, has a strong impact on reservoir quality and its flow behaviour and is capable to either enhance or diminish it. Despite this fact, existing classifications of porosity in carbonates and siliciclastics do not really consider

ichnological components as a part, while existing bioturbation-focused classifications are based on the final appearance of burrow-related heterogeneities in the sedimentary rock (GINGRAS et al. 2012). A novel approach is made classifying bioturbation-influenced porosity on the basis of the size as well as morphological and compositional features of bioturbate textures and discrete trace fossils (KNAUST 2013, 2014). Given the diverse appearance of trace fossils and, consequently, their highly variable influence on the fluid-flow within the sediment, an attempt is made to classify bioturbation-influenced porosity (both, enhancement and diminishing) at different scales and by appreciating the specific burrow nature as a function of the overall behaviour of their tracemaker. This newly proposed key aims for a better predictability of reservoir quality as an integral part of the reservoir-characterization workflow together with sedimentological and diagenetic analysis. Selected examples of bioturbation-related modifications of rock properties are presented from platform carbonates of the Permian/Triassic Khuff Formation from the South Pars gas field in the Persian Gulf (KNAUST 2009a), from shallow-marine Jurassic siliciclastics of the Norwegian North Sea, and from Late Cretaceous deep-marine fan deposits of the Norwegian Sea (KNAUST 2009b). These case studies show that the porosity in these reservoirs is significantly impacted by diverse bioturbation, which either results in an enhancement or a diminishing of the reservoir quality. Given a solid understanding of the conditions, burrow-related porosity and permeability are predictable to a certain degree.

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"Ichnotaxa for thetrapod bite traces: Has it been a useful tool?"

By Aase Roland JACOBSEN

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Serrated predation traces have the opportunity to provide important information on predator-prey relations and interaction in ancient environments. Therefore, in 2009 two new ichnotaxa *Linichnus serratus* and *Knethichnus parallelum* (Jacobsen and Bromley, 2009) were introduced to get focus on the significance of bite traces as an ichnological tool. At that time, only Mikulas et al. (2006) had provided ichnotaxa used for bite traces on bones and teeth. So today, has ichnotaxa for thetrapod bite traces been a useful tool?

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	Bioturbation-influenced porosity															
Producer size	Microfauna				Meiofauna				Macrofauna				Macroflora			
Process	Microbioturbation				Meioturbation				Macroturbation							
Pore size	< 0.0625 mm (micropores)				0.0625 - 4 mm (mesopores)				> 4 mm (megapores)							
Rock texture / trace-fossil group	Interstitial modification				Cryptic bioturbate texture, small burrows				Bioturbate texture		Burrows		Borings		Root traces	

In defense of the ichnoguild concept

By Luis A. BUATOIS

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Almost 25 years ago, while Gabriela and I were PhD students in Argentina, we attended our first trace-fossil meeting, an Ichnology session organized by Tony Ekdale and John Pollard within the framework of the International Sedimentological Congress (Nottingham, 1990). It was a memorable experience. Richard was the keynote speaker and gave a fascinating talk, essentially outlining some of the topics covered in his recently published book. After the talk, I approached and asked him one single question: Which is the difference between the concepts of ichnocoenose and the concept of ichnoguild? After the talk, we bought his book, and I still remember the feeling of reading it while travelling on the train across Europe. The incorporation of the ichnofabric approach to the conceptual and methodological toolbox of the science of animal-substrate interactions resulted in a more careful evaluation of the taphonomic controls that filter the biogenic signal through the fossilization barrier. However, in our view this concept has not been extensively used yet. An ichnoguild reflects three parameters: (1) bauplan; (2) food source, and (3) use of space. With respect to bauplan, biogenic structures are categorized as permanent to semi-permanent burrows produced by stationary organisms, or transitory structures made by vagile animals. Food source includes categories, such as detritus feeding, deposit feeding, suspension feeding, gardening, and chemosymbiosis. Use of space is essentially equivalent to the vertical position within substrate recorded by the tiering structure. The ichnoguild concept is of wide applicability in evolutionary paleoecology and macroevolution. In particular, the ichnoguild concept yields valuable insights to understand patterns of colonization in specific environments through geologic time, behavioral innovations as a result of evolutionary radiations, and ecosystem performance during mass extinctions. Ichnologists are lucky to have this wonderful concept that allows us to frame our ideas within the broader picture of evolutionary paleoecology and macroevolution.

A whole new world: Cryptic ecosystems in a Copenhagen basement?

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This is the story of an unusual discovery, in a wet, dark basement in Copenhagen, and the excitement and ideas that followed it up. In 2009, I contacted Richard to find some elusive specimens from the Lower Cambrian Sirius Passet of Greenland. These specimens showing minute trace fossils were mostly undescribed and illustrated in a paper focused on the invertebrate fauna. Richard replied and kindly offered not only to serve as my link (i.e. locate the specimens, get my

access to the collections), but also to stay with him and Ulla in their cozy downtown flat. As an additional note, he wrote “and this is to help you Gab, I cannot get involved in this adventure. I have too many interesting projects I am working on...”. He found the specimens, with the help of David Harper, but they were deposited in a safety box at the Museum of Natural History in Copenhagen, and the key, somehow, was not available at the time of my visit! That morning, while regretting the unlucky situation, we paid a visit to Dave Harper, who was leading with Paul Smith a new comprehensive research effort at the Sirius Passet. To Richard’s and my surprise, they invited us to browse through some, still unclassified, “fresh *in situ* collected material”. And in fact, they had noticed some intriguing structures in them. Unfortunately, torrents of rain had got into the basement, some areas were under water and some floors had no access, but luckily the material was in a safe spot. We spent less than one hour unwrapping material, when the first *Tegopelte*-like specimens (now assigned to a new genus *Arthroaspis*) showed up in the dim light of our lamp....and what incredible excitement! I still vividly remember Richard’s bright eyes and the “Woww!” There were many delicate structures associated to the carapace! They certainly looked like trace fossils, but they were doing many weird things...We spent several hours in a mix of silence and admiration, followed by frantic discussion...He was hooked...Richard was part of the team!

This discovery led to a larger and more ambitious, still in progress, collaboration with Dave Harper (Durham University), Arne Thorshøj Nielsen (Natural History Museum), Paul Smith (Oxford Museum) and Jakob Vinther (University of Bristol). In particular, we focused on several *Arthroaspis* carapaces directly associated to trace fossils (recording essentially one stratigraphic horizon). We were able to recognize a variety of structures most of them apparently below the carapace (i.e. simple trails, annulated tubes, interconnected burrow systems, narrow-caliber structures with dendritic terminations and pellet-filled burrows). Although taphonomic control was instrumental, the confined distribution and variety of burrows within the carapace were strongly suggestive of an ecologic control. A variety of feeding strategies were recorded, including not only scavenging and deposit feeding, but also grazing (or farming) of bacteria. Disregarding the “boneless nature of *Arthroaspis*”, we came to the realization that large carapaces were to some degree comparable to whale carcasses in modern seas. On Cambrian sea floors carcasses and molds delivered to the sediment-water interface may have acted as attractors, supporting a relatively diverse community of small invertebrates. Mat-dominated homogenous seascapes were changed to more complex, heterogeneous ones. These hidden treasures in a museum basement opened a new window on the study of Burgess Shale-type communities revealing the presence of cryptic ecosystems on the Cambrian sea floor.

Where is ichnotaxonomy heading?

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Trace fossils are fossils without DNA and with no imprint of the body that made them: How can they be classified other than arbitrarily? Arbitrary morphologic classifications have indeed been tried, e.g., by counting the numbers of repeating foot impressions and digits per foot in vertebrate trackways, but often with misleading results (e.g., ALDRICH 1931; FAUL 1951). Biologically better informed classifications tend to generate more meaningful predictions, e.g., the prediction that three-toed, bipedal trackways were made by giant “birds” (dinosaurs; HITCHCOCK 1858). Over the course of the twentieth century, ichnologists developed ethologically based, but still morphologic classifications that have turned out to have much greater predictive power (e.g., KREJCI-GRAF 1932; SEILACHER 1953). However, it is striking that biologists uniformly reject arbitrarily and ethologically based morphologic classifications of modern traces in favor of identifying living tracemakers (morphologic classification based on biological clues), and do so with impressive accuracy (e.g., ELBROCH 2003). Historically, vertebrate ichnologists have had considerably greater success in identifying makers than invertebrate ichnologists, and this has colored their taxonomy (e.g. HAUBOLD et al. 2005).

In invertebrate ichnotaxonomy, the ethologic method championed by SEILACHER (1953) has been utilized with much greater success than biologically based methods. At one point, most invertebrate ichnologists rejected the idea that the makers of most trace fossils could ever be known (e.g., SIMPSON 1975), but the thought remained alive that if we just knew enough about trace fossils, we could deduce their makers and discover a more rational classification based upon them. For example, SEILACHER never gave up the effort to relate ichnospecies of *Cruziana* to their makers (SEILACHER 1955, 1970, 2007; FORTEY & SEILACHER 1997). The characters that allow these deductions have variously been referred to as the tracemaker’s *fingerprint* (SEILACHER 2007), *bioglyphs* (BROMLEY et al. 1984), or *bioprint* (RINDSBERG & KOPASKA-MERKEL 2005).

But the clash between ethologically based morphologic systems and biologically based morphologic systems may be more apparent than real. Most burrowing or boring invertebrates possess a relatively low number of standard behaviors involving interaction with the substrate. If higher ichnotaxa are based on the most important morphologic differences with regard to tracemaker biology and ethology, then they should be based on the bioprint of higher taxonomic and ethologic groupings, such as symmetry, general proportions, evidence of open versus filled traces, and so on. Some of these criteria were promoted by the report of the first two Workshops on

Ichnotaxonomy (WIT; BERTLING et al. 2005). Although bioprint was not emphasized in this report, it was the minority opinion of several attendees and has been gaining in usage since then.

KNAUST (2012) took up the challenge of constructing a key based on WIT criteria. For better or for worse, this is a classification of invertebrate trace fossils based on a consensus of ichnotaxonomists, and it should generate new patterns on which predictions of relationship may be based. Accordingly, it is being used, with modifications as they become necessary, as the basis of classification for the trace-fossil volume of the *Treatise on Invertebrate Paleontology*. In effect, this is a massive test by many ichnotaxonomists of the WIT hypotheses (BERTLING et al. 2005).

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Earthworm trails – what are underground miners doing on the surface?

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At three different localities in southern, western and central Europe surface trails of earthworms exhibit a similar pattern and geometrical arrangement and hence, document distinct behavioural modes of the producers. Straight to slightly winding trails (gutters bounded by levees) are a record of normal behaviour to move to a new habitat; earthworms tend to use at least for some distance trails of other earthworms. To explore a new habitat earthworms made blind ending probings at an acute to sharp angle to one or the other side of their course. When deviating from the main direction at a sharp angle, a pseudospreiten is produced while the posterior part of the body is obliquely dragged producing a shortcut. When earthworms leave subsurface tunnels they sometimes produce stellate probing structures. If the substrate is very soft earthworms may use the anterior or posterior

body part as anchor by bent it away from the direction of movement; also the body may be twisted to form meanders. Circular overcrossing, looping trails record the death throes of earthworms and often dead producers are found at the end of the trails. If the substrate is muddy and soft, subtle details can be preserved such as parapodia or body segmentation imprints. The fossilization potential of earthworm trails is like that of rain drop imprints. Their occurrence characterizes temporarily wet surfaces in an environment wherein the substrate contains some organic matter.

Ichnofossil markerbeds in between extremely arid deposits in the Northern Pangaea Interior, Lower Triassic, Netherlands subsurface.

By Onno WERVER

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This is a work in progress, consisting of an inventarisation of ichnofossils. They are present in cores of the Triassic era in the core shed of the Dutch Geological Survey in Zeist, the Netherlands. The studied interval is almost completely devoid of any fossil. Interestingly, about 95% of the gas reserves of the Netherlands are in these deposits. Why was this a barren area? Firstly, this area was a super hot and bone dry desert plain with alluvial outwashes from the nearby Hercynian mountain range. Secondly there was no or very little life in the rainshadow of the Hercynian mountains. Thirdly any organic remains such as spores, shell material or bone was soon oxydized or desintegrated in the harsh climate. As a consequence, stratigraphic correlations and subdivision has always been an issue since drilling for gas began. Some progress was made recently by means of gamma-ray correlation, providing a crude sort of stratigraphy of which the origin remained unclear. However ichnofossils do not suffer from oxidation once in place, so chances are that they may be preserved in less inhospitable places in the area or as transitional phenomena towards more favourable areas. This became my a priori hypothesis.

My original aim in this study therefore was to make an inventory of all ichnofossils present and evaluate if they could be used as environmental indicators of such transitional areas. Two years later, after logging several hundreths of meters of core and many photos I have come to the conclusion that my original hypothesis is completely wrong and has to be replaced by an alternative one. Ichnofossils, if present at all, are extremely sparse and of low diversity, except for a small number of systematically arranged decimetre to metre thick beds with wide regional distribution. Such beds were never before described in the Netherlands geological literature. I will show you

some key examples of such beds. These beds show ample signs of life, as traces, burrows or root casts. Moreover, pedogenic structures and the beginning of laterization in one of the examples point to abundant seasonal rainfall. When traced laterally, these beds change into marine influenced or completely marine beds. Such beds were found several times in the stratigraphy.

My results using ichnology therefore point to an alternative hypothesis: Climatic conditions fluctuating strongly between an arid mode and a humid mode. The first mode is a super hot, bone dry climate on a huge interior desert plain which prevailed during very long intervals, the second mode is a shortlived tropical humid climate in areas bordering an inland sea, with intermittent connections to either the Tethys ocean or the Boreal Ocean. These connections were formed during highstands of the Panthalassa ocean.

A *Hillichnus*-like trace fossil from Jurassic tidal deposits of the Sakamoto Formation, Southwest Japan, and its evolutionary significance

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Well-preserved specimens of a morphologically complex trace fossil showing affinity to *Hillichnus* are found from cross-bedded sandstones of tidal sand flat to tidal channel deposits of the Upper Jurassic Sakamoto Formation in Uminoura, Kumamoto Prefecture, SW Japan. The trace fossil consists of a lower faintly meniscate burrow, and the upper numerous tubes radiating upward from the burrow. It is similar to the ichnogenus *Hillichnus* Bromley *et al.*, 2003, which was established based on Palaeogene deep-sea specimens, but can be distinguished from the ichnogenus because it lacks distinctly vertical tubes and lateral lamellae showing a feather-like (*Lophoctenium*-like) appearance. Instead, the upward radiating tubes of the trace fossils treated here locally show such a feather-like arrangement, especially in a mud drape intercalated in trough cross-bedded sandstones. The mode of the tube occurrence strongly suggests that the tracemaker systematically probed along the subsurface mud drape in which nutrition was concentrated.

The vertical tubes of the type ichnospecies *Hillichnus lobosensis* Bromley *et al.*, 2003 are interpreted to have functioned as irrigation canals for tracemaker's respiration and chemosymbiotic bacterial culture (Bromley, *et al.*, 2003). The lack of the distinct vertical tubes in the Sakamoto trace fossils thus suggests that the tracemaker, living in a relatively nutrient-rich tidal flat environment, was not a chemosymbiont but a mere deposit feeder.

Another ichnospecies of *Hillichmus*, *H. agrioensis* Pazos and Fernández, 2010, reported from the Lower Cretaceous shallow marine deposits of Argentina, is characterised by an intermediate form between *H. lobosensis* and the Sakamoto trace fossil treated here, and is composed of distinct vertical tubes and radiating tubes that are oriented diagonally upward. The Jurassic Sakamoto trace fossil therefore might represent an ancestral form of *Hillichmus* in its early evolutionary stage before the tracemakers acquired to construct vertical tubes and chemosymbiotic life.

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The Evolution Of Hearing In Baleen Whales

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The ear bones of whales provide tangible evidence for understanding the evolution of a specialized sense of hearing under water by cetaceans (EKDALE 2012, 2013; EKDALE et al. 2011). Late Oligocene marine deposits of the southeastern United States have yielded baleen whale (mysticete) fossils that play a critical role in the interpretation of whale evolution. In particular are the earliest toothless mysticetes and also some mysticetes that retained teeth into adulthood from an earlier ancestor. Cochlear (inner ear) anatomy of those taxa provides information regarding the sensory physiologies of extinct whales, and in particular the evolution of low frequency auditory sensitivity in mysticetes – a major physiological difference between extant toothed (odontocete) and baleen (mysticete) whales. The link between frequency sensitivity and cochlear morphology is complex, especially given the uncertainty of extant mysticete hearing ranges, but knowledge of early mysticete anatomy elucidates the evolution of hearing in whales. Taxa with sensitivity to lower frequencies tend to have cochleae with a greater number of turns, less extensive bony supports for the organ of hearing (which sits upon a membrane within the cochlea), and thinner walls between the basal and apical turns. Using CT (computed tomography) data, those features that are thought to relate to hearing are explored in important Oligocene mysticetes, including the toothless taxa *Eomysticetus whitmorei* and *Micromysticetus rothauseni*, as well as an earlier diverging toothed mysticete.

In general, the inner ear morphology of the Oligocene cetacean taxa is consistent with that described for stratigraphically younger mysticetes rather than for contemporaneous and later odontocetes. The cochleae of *Eomysticetus* and *Micromysticetus* complete over 2.5 turns, similar to what is seen in extant rorqual mysticetes, but the cochlea of the toothed mysticete completes only a little over 2 turns, which is similar to that seen in extant bowhead whales but more than the extant odontocete dolphin (fig. 1). Although outer bony support for the organ of hearing is restricted to the basal turn in *Eomysticetus* and the toothed taxon (similar to extant mysticetes), the lamina extends well into the second turn in *Micromysticetus*, but to a lesser extent than observed in extant odontocetes. The wall separating the basal and apical turns in all of the mysticetes examined for this study is half as thick as that in odontocetes. Together, these observations

suggest that extant baleen whale auditory physiology (low frequency sensitivity) is the ancestral condition for the mysticete clade. In addition, the cochlea of the Eocene archaeocete *Zygorhiza kochii* (2.5 turns, bony support for the organ of hearing restricted to basal turn, thin wall separating basal and apical turns) implies further that low frequency hearing may be ancestral for the crown group Cetacea and therefore was retained across the mysticete lineage with a shift towards higher frequency auditory sensitivity in odontocetes.

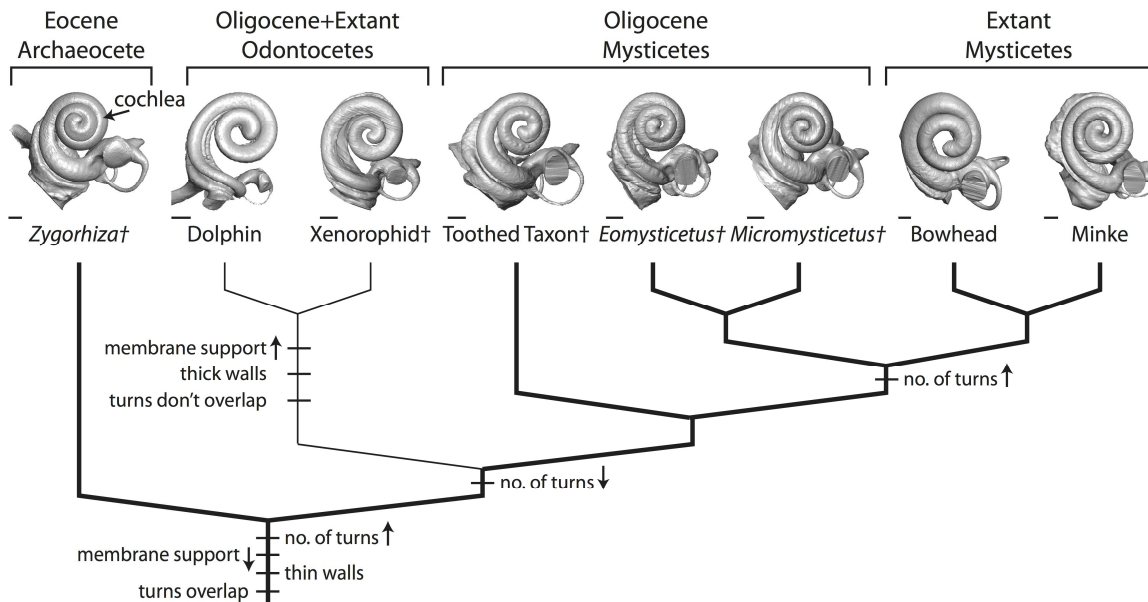


Figure 1. Cetacean cladogram with select fossil and recent cochleae generated from CT images. Thick branches on the cladogram indicate hypothesized low frequency sensitivity, and thin branches indicate sensitivity to high frequency noises. Scale bars equal 2 mm.

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Poster presentation

Integrating short- and long-term bioerosion patterns in the Eastern Mediterranean Sea

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Many bioerosion experiments have been conducted in the past decades addressing bioerosion rates and patterns. Most of these, however, were limited to short-term periods recording mainly microbial bioerosion, while the succession of macrobioerosion communities is considered to require generally longer exposure times to reach mature stages. In order to investigate the succession of bioerosion communities on carbonate substrates, a long-term settlement experiment has been conducted deploying marble test blocks in 3-17 m water depth around Rhodes island, Greece from 1982-1996. Preliminary results after 1-2 years revealed a first colonisation of boring sponges, but even after 6 years, equilibrium had not been established (Bromley et al. 1990). The complete assessment of the 1-14 year deployments is currently being carried out in the framework of a project dealing with the integration of short- and long-term bioerosion patterns in the Eastern Mediterranean Sea. Additional data on the temporal, bathymetrical, and latitudinal variability of bioerosion patterns are provided by a seasonal experiment that had been carried out in 15-250 m water depth in the SW-Peloponnese area, and an ongoing 1-2 year experiment in the inter-/supratidal zone at Rhodes.

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Poster presentation

Trace fossils from the Eocene Lillebælt Clay Formation, Røsnæs (Denmark)

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The Eocene strata of Denmark comprise mainly very fine-grained deposits. These became accumulated in an offshore environment far from the palaeocoastline in North Germany, South Sweden and South Norway (e.g., GRAVESEN 1998). This resulted in the Lillebælt Clay Formation, which consists mostly of greyish to greenish, non-calcareous clay. The formation has been biostratigraphically assigned to ?Early – Middle Eocene. It exists widespread in the Danish area of Eocene deposits, except in northern Jutland (HEILMANN-CLAUSEN et al. 1985). The Røsnæs peninsula in the western part of Zealand contains glacio-tectonically disturbed intervals of the Lillebælt Clay Formation (BERTHELSEN 1975). The lithological units L2, L3 and L4 have been recognised in coastal sea cliffs and clay pits. They are presently poorly exposed and, therefore, observations of trace fossils are difficult in the field. The trace fossils, which are preserved as concretions in certain intervals, can be subdivided into morphological groups. PETERSEN (1969) provided preliminary notes about the trace fossils, but any formal description and determination have not yet been done. From a coastal section, we recognise the groups: (A) Branching burrow systems with tiny pellets; (B) Disc-shaped burrows; (C) Irregular thin burrows being closely spaced in lumps; (C) Meniscate backfill burrows; (D) Nodular wall lined burrows; (E) Spreite structures. Comments and discussion about these trace fossils are welcome.

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Poster presentation

Preservational Impact of Dolomitization on Ichnofabrics in the Carboniferous Black Crag Beds, Spitsbergen

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The Black Crag Beds of the Wordiekammen Formation are well exposed on the peninsula Brøggerhalvøya, NW Spitsbergen. The deposition took place on a broad warm-water carbonate platform. The Black Crag Beds comprise a succession of well-bedded wackestones and packstones interbedded by dark grey to black carbonate mudstone units. Each of the five mudstones units is up to four metres in thickness. The units are partially dolomitized and have an unusual colour pattern similar to leopard fur, yellowish with black spots.

The ichnofabrics of the mudstones are mainly composed of mottled background with diffuse trace fossil margins. The background is occasionally cross-cut by specimens of *Planolites* that commonly is less dolomitized than the lighter background. The differential dolomitization appear related to the substrate consistency. The background is interpreted as been mottled as a soupground, whereas it was a softground during the formation of distinctive burrows.

The wackestones and packstones between the five mudstone units have a mottled to structureless, light background cross-cut by dark grey *Planolites* and *Thalassinoides*. These show mutual cross-cutting relationships and were formed mainly as horizontal burrows. *Diplocraterion* occurs only rarely. The background is much more dolomitized than specimens of *Planolites* and *Thalassinoides*. The ichnofabric has in some intervals been entirely destroyed by dolomitization.

Stylolitization has also contributed the visual characteristics of the Black Crag Beds. Amplitudes of the stylolites range from millimetres to centimetres in scale. Dolomite is abundant close to the stylolites, decreasing the preservation potential of trace fossils. The differential dolomitization of the Black Crag Beds is related to both bioturbation and stylolitization.

Poster presentation

Trace fossils in source rocks of Permian age: Evidence of anoxicity in the Norwegian Barents Sea

By Jan Kresten NIELSEN¹⁾, Jesper Kresten NIELSEN²⁾ & Nils-Martin HANKEN³⁾

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The formation of source rocks may be controlled by factors such as anoxicity, sedimentation rates, the original chemical composition of the organic matter, and biological activity such as bioturbation. Bioturbation, which extent may be controlled by anoxicity and substrate properties, is regarded to facilitate diffusion of oxidants (e.g., oxygen and sulfate) into the sediment. An early degradation of the organic matter is thereby introduced in the sediment.

Late Permian dark shales from East Greenland (Ravnefjeld, Schuchert Dal and Wordie Creek formations), Spitsbergen (Kapp Starostin Formation) and the Norwegian Barents Sea (Ørn Formation) have been investigated; they can be regarded as good to excellent source rocks. These may have sourced adjacent reservoir rocks such as carbonates and porous spiculites. The dark shales, which occur regionally, are particularly enriched in organic matter. They are mainly finely laminated and may contain scattered trace fossils. The presence of these small trace fossils indicates oxygen-deficiency during deposition. However, intercalated sediments, such as organic-poor carbonates, sandstones and spiculites, contain trace fossil assemblages typically indicative of more oxygenated waters.

Framboidal pyrite (spherical aggregates of micro-crystallites) is finely disseminated in the organic-rich dark shales and is often associated with burrows in the organic-poor, light-coloured sediments. Size distribution of the framboidal pyrite is used as an unambiguous anoxia indicator of the bottom-water conditions. Relatively small framboids occur in the dark shales, which indicate that the deposition occurred in anoxic and sulfidic waters. In contrast, relatively large framboids occur in the bioturbated sediments, indicating oxic to dysoxic bottom-water conditions. This is consistent with the evidence we have obtained from sedimentary structures, trace fossil assemblages and major and trace element geochemistry. We thus conclude that oxygen-deficient bottom-water conditions were usually present when organic-rich sediments and thereby potential source rocks were deposited.

Poster presentation

Improving ichnofabric analysis in cores: A novel method on digital image treatment

By Francisco J. RODRÍGUEZ-TOVAR & Javier DORADOR

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Ichnofabric analysis, as a relatively young ichnological approach, has experimented from the earlier studies a rapid growth, showing its usefulness in basin analysis, with special attention to palaeoecological aspects (i.e., from EKDALE & BROMLEY 1983 and BROMLEY & EKDALE 1984, 1986; to the recent revisions in BUATOIS & MÁNGANO 2011 and EKDALE et al. 2012). During these three decades, ichnofabric approach has evolved from the near exclusive description of the trace composition and the whole intensity of bioturbation, to include information on cross-cutting relationships, tiering structure, and dimension of ichnotaxa, among other data (from REINECK 1963, and DROSER & BOTTJER, 1986 to BROMLEY 1990, 1990 and TAYLOR & GOLDRING 1973).

The development of the ichnofabric approach practically occurred in parallel with the study of the deep-sea sediments, mainly based on the explosion of information supported by the deep-sea drilling programs, such as the ODP, DSDP and IODP explorations. However, the application of the ichnofabric approach to cores is not an easy matter, considering the well-known disadvantages of the ichnological analysis of cores, as were pointed early by BROMLEY (1990, 1996), as the limited size and restricted surface (narrowness) of the sample, the almost exclusive availability of two-dimensional core slabs perpendicular or oblique to bedding, or the absence of 3D structures, among others. The difficulty of ichnological studies cores increases when working with modern marine sediments, being, in cases, even difficult the differentiation between biodeformational structures and trace fossils (UCHMAN & WETZEL 2011; WETZEL & UCHMAN 2012). To solve some of these limitations, since the second half of the 20th century particular techniques to core analysis have been applied, as X-radiography, ultra-violet radiation, computed tomography, magnetic resonance, or high-resolution core images (BROMLEY 1996; KNAUST 2012). However, in most cases they are expensive and the necessary instruments may be inaccessible.

The aim of this research is to present a novel, inexpensive and easy to use, method for ichnological analysis of modern marine cores based on the digital treatment of high-resolution images (DORADOR et al. 2014a, b; RODRÍGUEZ-TOVAR et al. in press), especially useful to ichnofabric approach. Ichnofabric analyses using visual representations as the Ichnofabric Constituent Diagram of TAYLOR & GOLDRING (1993) and that of BROMLEY (1996) can be potentially benefited to the proposed methodology.

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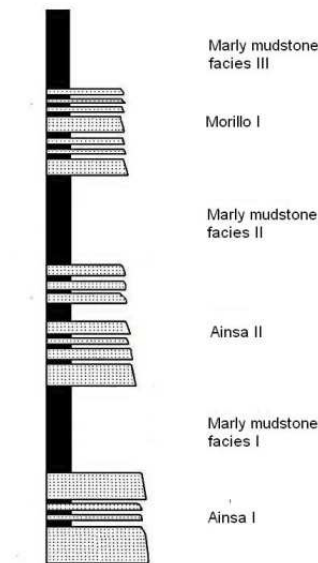
Poster presentation

New findings of trace fossils at the Ainsa Slope Complex, South-Central Pyrenees, Spain

By Nadine BALK

NOTE BY EDITORS: Private address removed

The Ainsa Slope Complex belonging to the Campodarbe Group is part of the Ainsa Basin, which is an Eocene-age foreland basin in the southern part of the Central Pyrenees. The studied area of the Ainsa Slope Complex crops out in a stripe from c. 1 km to the north of the town of Ainsa and extending to Morillo de Tou in the south and contains three of six sandstonebodies belonging to the slope complex (i.e. Ainsa I, Ainsa II, Morillo I), which are imbedded in marly mudstones. The sandstonebodies are formed by sandy and silty turbidites which are interpreted as channel-systems while marly mudstones represent the background sedimentation and interchannel-facies.



Simplified stratigraphy of the studied area

The trace fossils are predominantly confined to the turbidite units, while the marly mudstones contain no bioturbation except of intercalated thin-bedded turbidites. In previous studies (Uchman 2001; Heard & Pickering 2008) 25 ichnogenera and 44 ichnospecies were described for this area. The ichnofaunal assemblage which were found at this study belongs to the Nereites ichnofacies and includes 20 ichnogenera and 32 ichnospecies (*Chondrites*, *Circulichnis*, *Cochlichnus*, *Cosmorhapse*, *?Glockerichnus*, *Gordia*, *Halopoa*, *Helminthopsis*, *Helminthorhapse*, *Nereites*,

Ophiomorpha, *Palaeophycus*, *Paleodictyon*, *Planolites*, *Protopaleodictyon*, *Rotundusichnium*, *Scolicia*, *Skolithos*, *Spirorhaphe*, *Thalassinoides*).

For the first time the ichnospecies of *Chondrites patulus*, *Chondrites targionii*, *Circulichnis montanus*, *Cochlichnus anguineus*, *Cosmoraphe sinuosa*, *Helminthopsis abeli*, *Helminthopsis hieroglyphica*, *Palaeophycus striatus*, *Palaeophycus sulcatus*, *Paleodictyon goetzingeri*, *Palaeodictyon tectifforme*, *Protopaleodictyon incompositum*, *Protopaleodictyon minutum*, *Protopaleodictyon spinata*, “*Rotundusichnium*” *zumayenses*, *Scolicia plana* and *Skolithos linearis* are described for this area.

The Ainsa I and Ainsa II channel and the interchannel-facies of Ainsa II contain the most diverse assemblages. The outcrop conditions of the Morillo I channel was bad in the studied area, whereas Heard & Pickering (2008) found 15 ichnogenera including 24 ichnospecies in the Morillo I unit. The vertical and lateral variation of the ichnofauna is studied focusing in its ichnotaxonomic composition and intensity of bioturbation. The vertical variation is controlled by changes in the lithofacies, which are represented by facies A to E after the classification-model for sediments of Pickering et al (1986). Pre-depositional ichnotaxa occur mainly and graphoglyptids only in sediments of facies C 2 (organized sand-mud couplets) and it can be suggested that the preservation-potential is dependent on the grain-size and the energy of the sediment-flow of the turbidites. The post-depositional forms are not bound to any facies, they occur in every lithofacies. The lateral variation shows that the bioturbation rate is highest in the channel axis (ca. 80 %) of the Ainsa I channel and lowest in intercalated turbidites in the marly mudstones (5-10 %). The ratio of pre- and post-depositional ichnotaxa reflect that the common conditions were oligotroph with high oxygen content, so that the high bioturbation-rate of the channel axis expresses a nutrient supply by the turbiditic events, which led to a colonization of opportunistic animals.

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