

TRACE FOSSILS FROM THE CONTINENTAL UPPER TRIASSIC KÅGERÖD FORMATION OF BORNHOLM, DENMARK

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Abstract: The Upper Triassic Kågeröd Formation of Bornholm consists of clays, sandstones and conglomerates of floodplain and fluvial origin, but details of the depositional environment are poorly understood. Trace fossils are described for the first time from the red and green clays (floodplain with lake deposits) and cross-stratified sandstones (fluvial channel deposits) of the Upper Triassic Kågeröd Formation on Bornholm, Denmark. The sparse ichnofauna consists of large, mud-filled shafts and tunnels in caliche-bearing conglomerate, determined as *Camborygma* and attributed to the burrowing activity of crayfish. The sandstones preserve vertical U-shaped burrows passively filled with sand, assigned to *Arenicolites* and probably produced by insects. Furthermore, they contain winding, horizontal, oblique and vertical unbranched burrows with an active meniscate sand fill, referable to *Taenidium* and supposedly produced by burrowing beetles. The clays and the sandstones contain numerous caliche nodules of centimetre to decimetre size, some of which contain root traces in the form of rhizoliths. This trace-fossil association reflects deposition on a vast floodplain with shallow lakes and fluvial channels, under semiarid conditions.

Key words: Trace fossils, Upper Triassic, Norian, Keuper, Kågeröd Formation, fluvial, Bornholm.

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INTRODUCTION

The Danish island Bornholm in the Baltic Sea defines the border zone between the old and stable Fennoscandian-Baltic Shield in the north and the younger and subsiding Danish Basin, German Basin and Polish Trough in the south. It has been investigated by Danish, German and Swedish geologists for more than a century, because of its fascinating and complex geology. Most parts of Bornholm consist of crystalline basement (e.g., gneiss and granite), while other parts contain Palaeozoic sedimentary rocks. Only some down-faulted areas, such as the Rønne Graben and the Arnager-Sose Block, preserve Mesozoic sedimentary deposits of Triassic to Cretaceous age, which are partly exposed in low-lying cliff sections along the southern and western coast of Bornholm.

The oldest Mesozoic unit of this succession is made up of late Triassic deposits and crops out on the south coast, near the mouth of the Risebæk Stream. These deposits belong to the Kågeröd Formation, named after time-equivalent and similar deposits in Scania, southern Sweden (Erlström and Sivhed, 2012); the name of the unit is also spelled Kågerød in some of the Danish literature. The facies of the Swedish and Danish Kågeröd Formation shows parallels to the time-equivalent Norian Steinmergelkeuper (Arnstadt Formation) in Germany (e.g., Shukla *et al.*, 2006) and reflects a marginal position within the German Basin facies province.

Since the 19th century, sporadic investigations of the Triassic Kågeröd Formation on Bornholm have been dependent on the outcrop situation, because landslides and vegetation might have covered them for decades (Forchhammer, 1838; Grönwall and Milthers, 1916; Höhne, 1933; Gry, 1969; Bertelsen, 1980; Gravesen *et al.*, 1982; Hamann, 1989; Knaust, 1997; Clemmensen *et al.*, 2011). Therefore, the Triassic of Bornholm remains poorly understood as based on only a few stratigraphical and lithological studies, performed so far, compared with the extensively examined, adjacent deposits of Jurassic and Cretaceous age (see Gravesen, 1996). The Kågeröd Formation has a scarce fossil content (such as ostracods; Christensen, 1972), and its trace-fossil content is presented here for the first time. Together with sedimentological evidence, the ichnological data add some information that is useful for palaeoenvironmental interpretation (see Knaust and Bromley, 2012).

GEOLOGICAL SETTING

Upper Triassic (late Ladinian to Carnian) deposits of the Risebæk Member (Kågeröd Formation; Gravesen *et al.*, 1982) are exposed in several cliff sections on the coast, near the mouth of the Risebæk Stream (between coordinates 55°02 05.6 N, 14°52 26.2 E and 55°02 10.0 N, 14°52 10.0 E; Fig. 1). The outcrop area is reached by walking

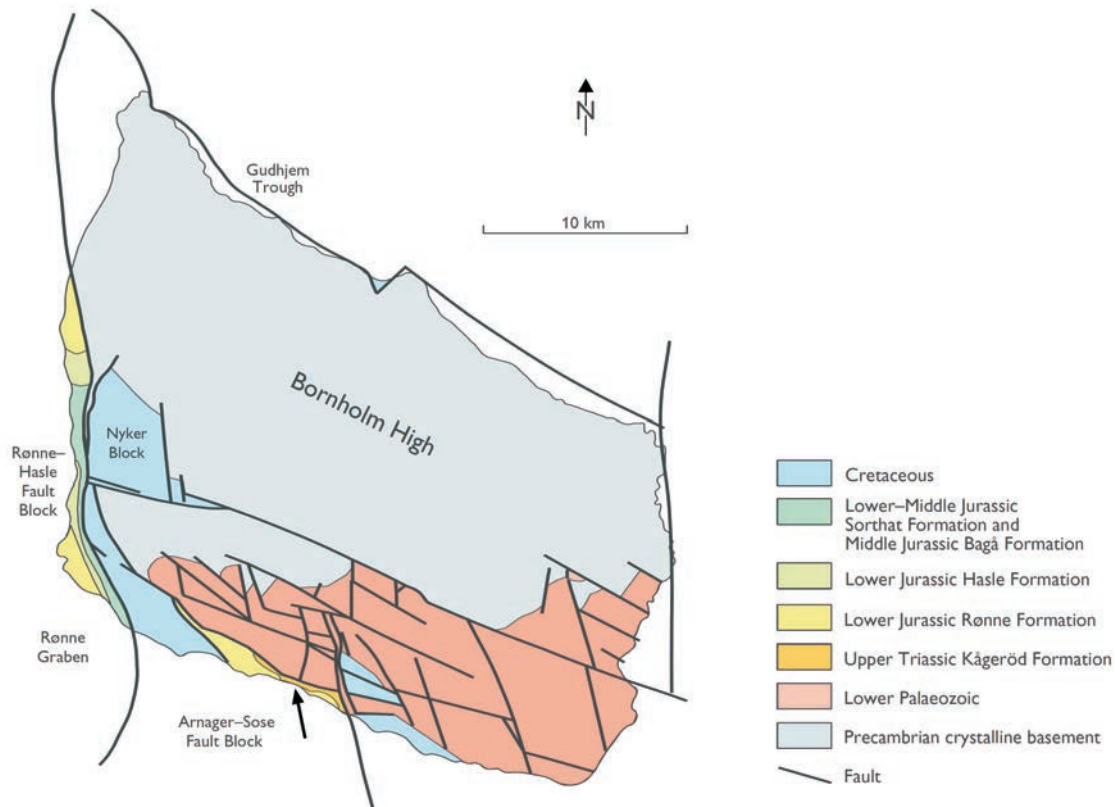


Fig. 1. Simplified geological map of Bornholm (based on Petersen *et al.*, 2003), with the Triassic outcrops on the south coast indicated by an arrow.

along the field and the Risegård farm and is entered through a large landslide, about 60×60 m in size. Cliff instability is obvious and is related to the clay-rich substrate and the steep dip of strata towards the south due to faulting. The cliff sections are part of a narrow fault block, trending east-west and bounded in the north (about 150 m from the cliff edge) by the hanging-wall fault block with Upper Ordovician *Dicellograptus* Shale exposed with a little waterfall in the Risebæk valley (Hamann, 1989). The total thickness of the Triassic succession is estimated to be between 60 and 70 m, but it could be more (Gravesen, 1996).

SEDIMENTARY FACIES

Depending on the outcrop situation, clay dominates the cliff exposures, in which isolated sandstone bodies occur. Three lithofacies types can be discriminated: clay, conglomerate and sandstone (Figs 2–4). Individual conglomerate-sandstone-clay cycles show a general fining-upward trend, but coarsening-upward cycles also occur. These three lithofacies types are described in detail below:

(1) Clay with a brownish red and greyish green colour, and a massive appearance. The red colour of the clay originates from the ferric oxide (hematite), while the green colour is related to a reduced state of iron. The clay contains abundant caliche nodules with a mixed carbonate-siliciclastic composition. *In-situ* brecciation is common and has led to the formation of lithoclasts. The nodules frequently are dissected by tangential cracks filled with sparry calcite

cement (Knaust, 1997). Caliche nodules are often washed out and have accumulated at the beach.

(2) Conglomerate and pebble-bearing sandstone of grey, red and yellow-brown colour and with weak stratification, containing rock fragments and caliche nodules. Some conglomerates are clast-supported and originated from the *in-situ* brecciation of caliche crusts. More mature conglomerates have a matrix- or grain-supported fabric. Point counting ($n = 500$) of four randomly selected sandstone samples resulted in recognition of the predominance of rock fragments (e.g., caliche fragments and sandstone clasts) in addition to detrital minerals (e.g., quartz and feldspar) as well as matrix or cement (Knaust, 1997).

(3) Sandstone varieties with a yellow to grey colour, including pebble-bearing sandstone and coarse- and fine-grained sandstone with reworked rock fragments, parallel and cross-stratification, and ripple lamination. Erosion and syn-sedimentary deformation structures are common. The sandstone is composed of rock fragments (e.g., reworked caliche nodules and sandstone clasts) commonly corroded and superficially stained with limonite. Reworked fossils (mainly fish remains) and plant fragments are present.

SYSTEMATIC ICHNOLOGY

Camborygma eumekenomos Hasiotis and Mitchell, 1993

Description: Multiply branched, cylindrical burrow systems occurring in the conglomeratic facies (Fig. 5). The burrow systems

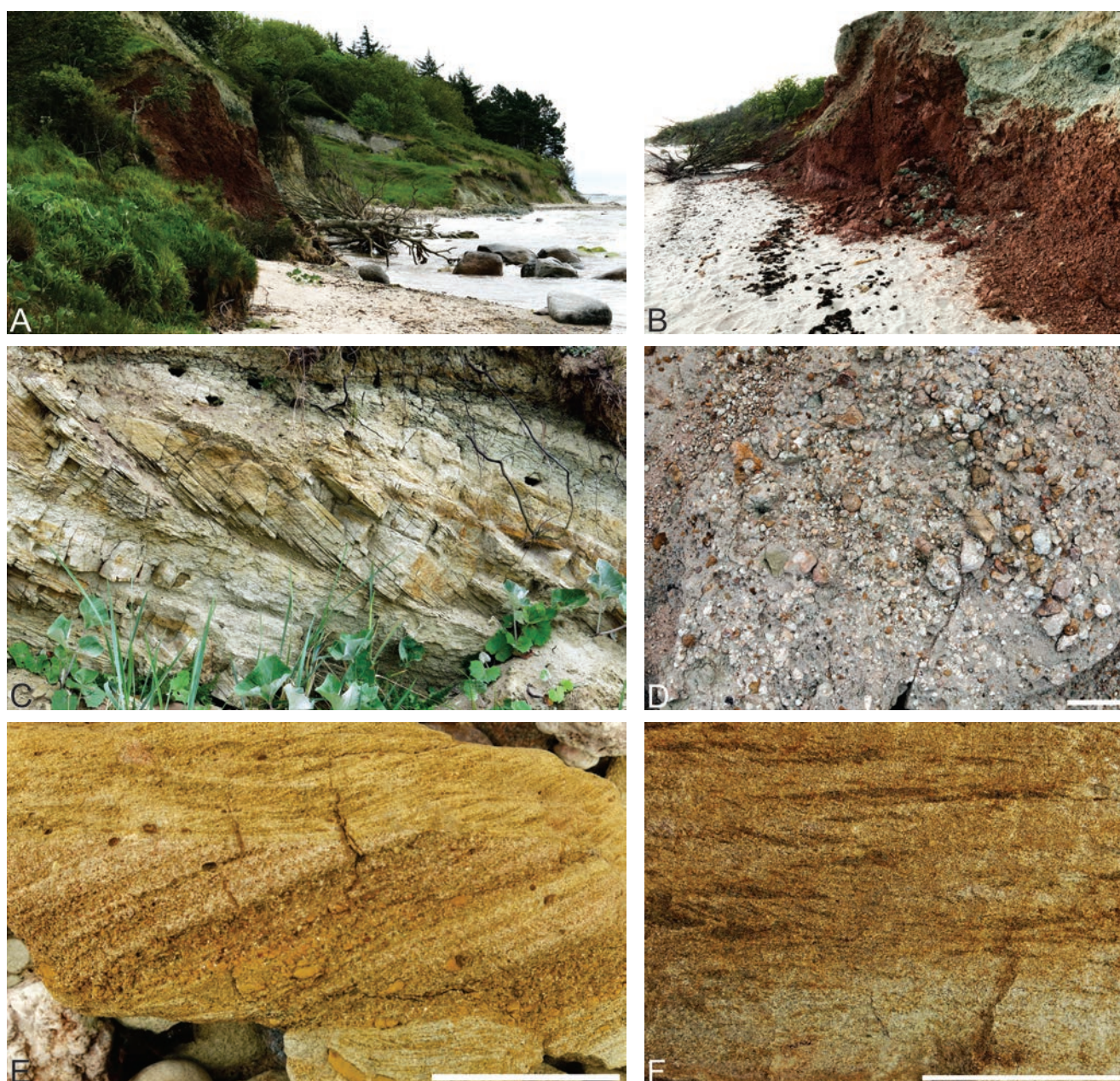


Fig. 2. Outcrop overview and facies of the Kägeröd Formation at the Risebæk cliff section. **A.** Downslid blocks of clay with red (foreground) and green (background) colour. **B.** Red and green clay cropping out in a downslid block at the beach. **C.** Ca. 1 m thick sandstone unit with cross-stratification. **D.** Conglomeratic sandstone with rock fragments and reworked caliche nodules. Scale bar = 5 cm. **E.** Sandstone slab with angular cross stratification (lower part) and ripple cross-bedding (upper part). Note the reworked pebbles at some laminae. Scale bar = 5 cm. **F.** Ripple-laminated sandstone. Scale bar = 5 cm.

include sub-vertical and oblique shafts, from which sub-horizontal tunnels arise. Individual burrow elements are up to 40 cm long and have a diameter of 2–3 cm. Burrow terminations and intervals between them may be enlarged with chambers up to 5 cm wide. The burrow systems are passively filled with green clay. No ornamentation (e.g., scratches, striations) is developed or preserved along the burrow margins.

Ichnotaxonomy: Because of its complex burrow architecture, individual occurrences of *Camborygma* may be confused with morphologically similar crustacean burrows and thus not permit a clear distinction. *Loloichnus* is another crayfish burrow in continental deposits, which differs from *Camborygma* in the absence of chambers, common tunnels and multiple shafts (Bedatou *et al.*,

2008). Other decapod crustacean burrows (e.g., *Ophiomorpha*, *Thalassinoides*, *Spongiomorpha*, *Psilonichnus*, *Pholeus* and others) may partly resemble crayfish burrows (e.g., Martin *et al.*, 2008), but are restricted to marine environments. Four ichnospecies have been distinguished by Hasiotis and Mitchell (1993), on the basis of the manner and complexity of burrow branching, the development of chambers, and size: *C. eumekenomos*, *C. symplokonomos*, *C. araioklados* and *C. lironomos*.

Producers and ethology: *Camborygma* is the burrow of crayfish (continental decapod crustaceans) and can be compared directly with modern analogues (e.g. Hobbs, 1981). It is a trace that served the purposes of dwelling and reproduction (domichnion; Hasiotis, 2010).

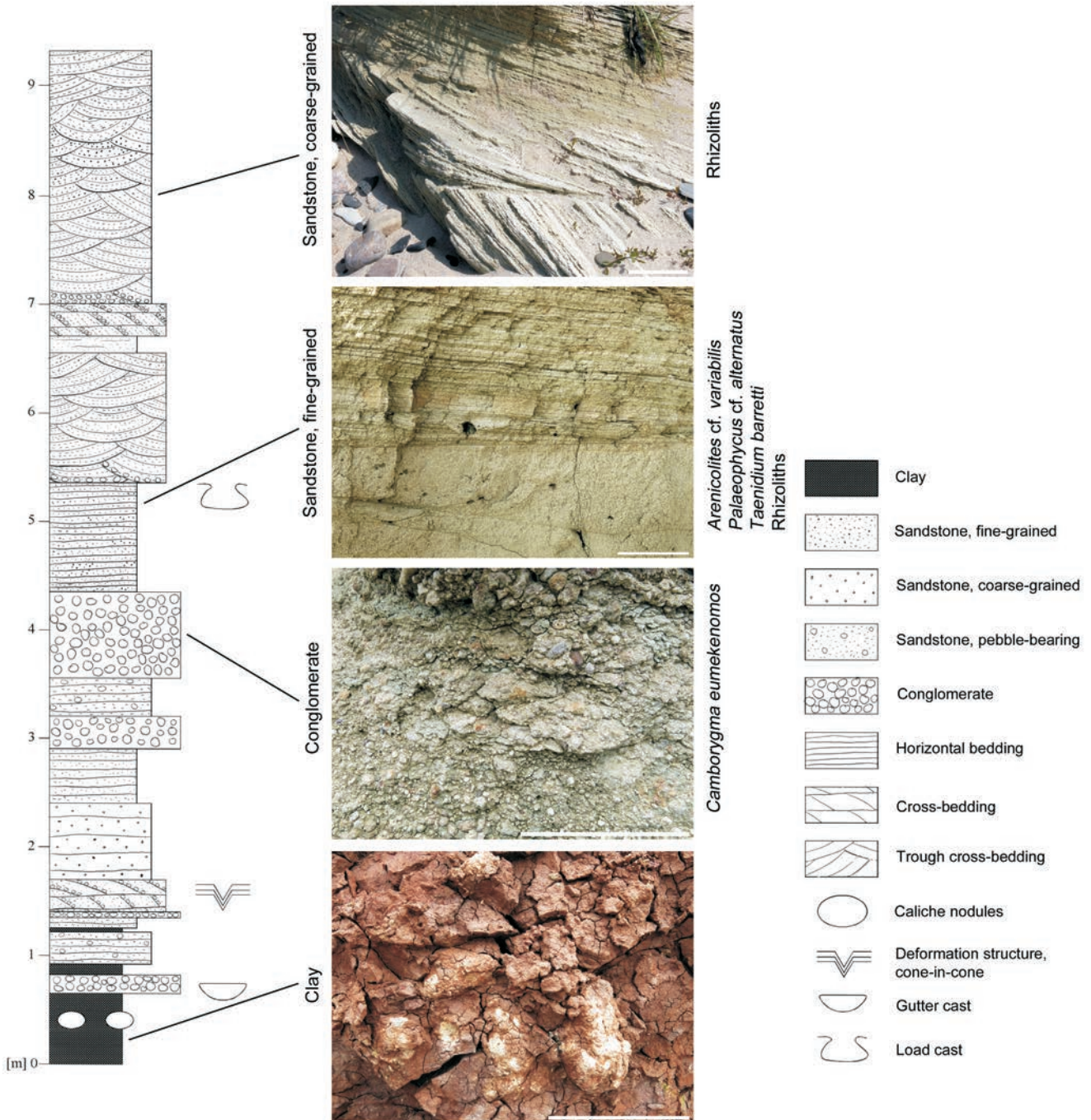


Fig. 3. Part of the section of the Kågeröd Formation at Risebæk with representative lithofacies in photographs (scale bars = 10 cm) and their associated trace fossils. Modified after Knaust (1997).

Palaeoenvironment and stratigraphy: *Camborygma* is a common constituent of continental ichnofacies. Crayfish evolved in the Permian and crayfish burrows such as *Camborygma* are recorded from continental deposits of Permian to Holocene age (Hasiotis, 2010; Baucon *et al.*, 2014). *Camborygma* is a continental trace fossil, typically associated with weakly- to well-developed palaeosols, formed in proximal to distal, alluvial and marginal-lacustrine environments (channels, levees and overbanks, floodplains). A high abundance of burrowing crayfish occurs in humid to hot, wet seasonal climates, although it also occurs under continental and semiarid conditions (Hasiotis and Mitchell, 1993;

Hasiotis, 2010; Fiorillo *et al.*, 2015). Starting from a discontinuity surface at the top, the burrow shafts penetrate the vadose zone and typically branch below the water table with the chamber situated in the phreatic zone. The architecture and depth of the hydrophilic burrows reflect the depth and fluctuation of the ancient water table (Hasiotis and Mitchell, 1993). Burrow density and size variation are other aspects in the reconstruction of palaeoenvironments. Lateral variation in burrow density may reflect spatial heterogeneity in the water table and soil moisture levels, while crayfish size increases from the fluvial channel towards the overbank (Kowalewski *et al.*, 1998).

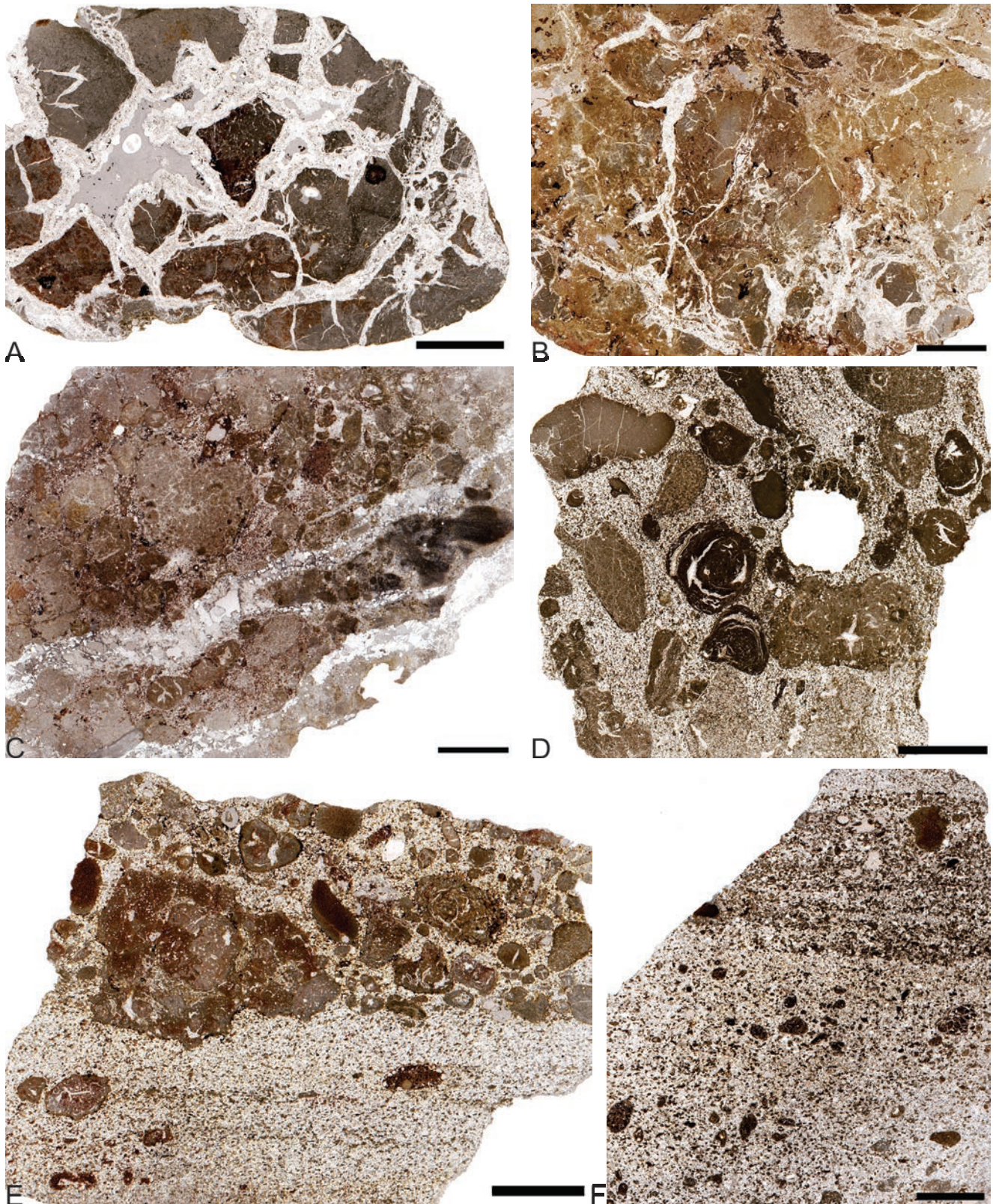


Fig. 4. Microfacies of common rock types of the Kågeröd Formation at Risebæk. Scale bars = 1 cm. **A.** Drusy caliche nodule with micritic matrix, which is frequently dissected by fractures filled with sparry calcite. This fracturing led to the formation of an *in-situ* breccia with angular lithoclasts in a sparry matrix. **B.** *In-situ* brecciation of a large caliche nodule, the micritic matrix of which is stained with limonite (brownish colour) and dissected by fractures filled with sparry calcite. **C.** Incipient conglomerate originated from an *in-situ* brecciated caliche crust. **D.** Conglomerate consisting of caliche nodules, sandstone and mud clasts, quartz and feldspar grains. The caliche nodules show tangential and radial cracks filled with calcite. **E.** Bedded sandstone with lithoclast pebbles and abundant fish remains (lower part) and conglomerate with caliche nodules and sandstone clasts (upper part). **F.** Bedded sandstone bearing pebbles of sandstone and caliche nodules.



Fig. 5. *Camborygma eumekenomos* in caliche-pebble bearing sandstone to conglomerate (alluvial deposits on a floodplain). Scale bars in A–C = 5 cm, in D = 1 cm. The burrows were passively filled with green mud, which is cracked, owing to desiccation. **A.** Oblique shaft associated with horizontal tunnels in longitudinal section (left) and cross section (right). **B.** Vertical shaft. **C.** Oblique shaft with Y-shaped branching (upper part) and chamber-like extension (lower part). **D.** Burrow cross-section.

Arenicolites cf. *variabilis* Fürsich, 1974

Description: A bedding plane of a white-grey, partly pinkish and brownish, fine-grained ripple-laminated sandstone bed is disrupted by numerous vertical burrows, the empty apertures of which are arranged in pairs (Fig. 6A–D). The paired burrow apertures reach a density as great as approximately 100 per square metre, and the burrow diameter of most apertures varies between 0.2 and 0.5 cm, although some may be slightly funnel-shaped and enlarged. The distance between the paired apertures is mostly in the range of 0.7 to 2.5 cm, while patches with a higher burrow density make an identification of individual pairs challenging. Removal of the uppermost layer of the weathered sandstone bed (which is ca. 2–3 cm thick) revealed the same paired burrows passively filled with sand, which contrasts in its lighter colour from the surrounding brownish, iron-stained rock. Furthermore, the burrows show a thin but significant lining of mud. On the same bedding plane, *A.* cf. *variabilis* is accompanied by sparse *Palaeophycus* cf. *alternatus*. The total length of the burrows and their basal U-shaped turn remains indefinite in most cases because of

the lack of exposure. In the deeper tier, *A.* cf. *variabilis* co-occurs with *Taenidium barretti*.

Ichnotaxonomy: Although a basal bend of the burrows could only rarely be verified, the paired occurrence of the vertical burrows together with their appearance leaves no doubt about their U-shaped morphology (*Arenicolites*), instead of simple vertical shafts (*Skolithos*). It is likely that those burrows were already observed by Gry (1969, p. 72), who mentioned “...skolithos-like burrows occur in the sandstone”. On the basis of their overall morphology, the occurrence of a mud lining as well as their similar size, the described burrows are most akin to *A. variabilis* and are provisionally assigned to that ichnospecies, until a thorough review of the ichnogenus *Arenicolites* has consolidated all its ichnospecies. About 15 ichnospecies of *Arenicolites* have been described in the literature, many of them pending a critical review. Differentiation criteria include secondary branching (*A. carbonarius*) and orientation of the limbs (vertical in *A. sparsus*, the most characteristic *Arenicolites* ichnospecies; inclined in *A. curvatus*; variable in *A. variabilis*; subhorizontal in *A. longistriatus*), and the presence or absence of a lining (Rindsberg and Kopaska-Merkel, 2005). The

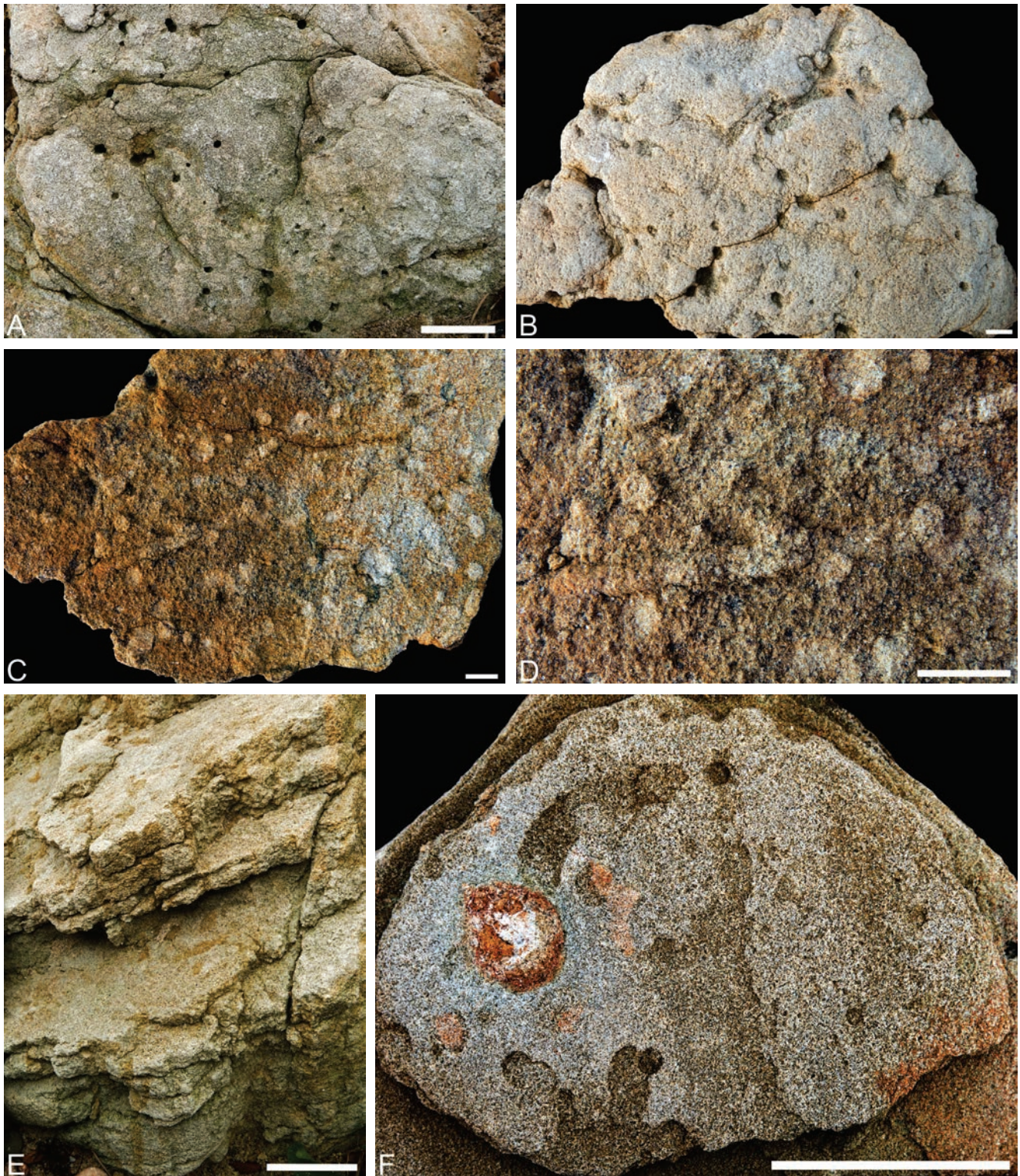


Fig. 6. Cross-stratified, fine-grained sandstone bed, containing various burrows. Scale bars in A, E and F = 5 cm, in B–D = 1 cm. **A.** Bedding surface with numerous paired burrow apertures, belonging to *Arenicolites cf. variabilis*. **B.** Slab of bedding surface with *Arenicolites cf. variabilis* burrow apertures and weathered horizontal burrows, probably belonging to *Palaeophycus* isp. **C.** Same slab as in B (ca. 2–3 cm thick), lower surface with *A. cf. variabilis* (vertical burrows) and *Palaeophycus cf. alternatus* (horizontal burrows). **D.** Close-up view from C, showing thin burrow lining in *A. cf. variabilis* and *P. cf. alternatus*, and the sculptured surface of *P. cf. alternatus*. **E.** Deeper tier of the same bed as in A–D (ca. 10–30 cm below surface) with actively filled brownish burrows, belonging to *Taenidium barretti*. **F.** Loose slab of sandstone collected from the beach with a reworked caliche nodule and winding *T. barretti* burrows with pronounced backfill.

ichnogenus *Arenicolites* is restricted to vertical U-tubes without spreite and should not include broad, arc-like burrows, such as those described and figured by Bjerstedt (1987), Mángano *et al.* (2002) and Baucon *et al.* (2014). The latter are better accommodated in *Catenarichnus* Bradshaw, 2002 (if thinly lined or unlined), or in *Cylindrichnus* Toots in Howard, 1966 (if thickly lined).

Producers and ethology: The lining of the relative large burrows indicates that they were occupied over a longer time by a suspension-feeding animal (domichnion) that benefited from the infrequent current action, associated with this channel-overbank deposit. Potential producers of continental *Arenicolites* may include bivalves, oligochaetes, amphipod crustaceans and insects (e.g., Smith and Hein, 1971; Hasiotis, 2010).

Palaeoenvironment and stratigraphy: Opportunistic colonisation of event beds (e.g., storm deposits) was originally referred to the *Arenicolites* ichnofacies by Bromley and Asgaard (1991), but now is included in the *Skolithos* ichnofacies, occurring both in marine and continental settings. *Arenicolites* is known from a wide range of continental to deep-marine environments and often occurs in association with other trace fossils. Mass occurrences of *Arenicolites* in low diversity (such as the one reported from Bornholm) are indicative of stressed environments, such as infrequent current activity, and reflect opportunistic colonisation of open niches. *Arenicolites* is commonly associated with high- and moderate-energy deposition, for instance, fluvial channel-overbank deposits. *Arenicolites* is known from the Lower Cambrian to the Holocene.

***Palaeophycus* cf. *alternatus* Pemberton and Frey, 1982**

Description: *Arenicolites* cf. *variabilis* from the bed described above is accompanied by a few horizontal, unbranched and cylindrical burrows with a thin mud lining, passive fill and sculptured margin, which can be assigned to *Palaeophycus* cf. *alternatus* (Fig. 6C, D). On the upper bedding surface, the straight to slightly winded burrows are weathered and their outline is weakly discernible, while on deeper bedding planes better preserved specimens occur. The burrows are 0.3–0.4 cm in diameter and 4–5 cm long, slightly annulated and bear robust scratches oblique to the burrow long axes.

Ichnotaxonomy: The ichnogenus *Palaeophycus* includes about 20 ichnospecies, of which the thin-walled *P. tubularis* and thick-walled *P. heberti* are the most relevant. Other ichnospecies are very thinly lined and differ from each other by varying kinds of striae (Pemberton and Frey, 1982). The characteristics of the material described meets the diagnostic features of *Palaeophycus* (cf. Keighley and Pickerill, 1995) and the development of annulation and oblique striae makes an assignment to *P. alternatus* most likely (cf. Buckman, 1995).

Producers and ethology: Various kinds of vermiform organisms (e.g., annelids) are generally assumed to produce *Palaeophycus*. In the present case, the robust striae may probably result from scratching with strong appendices, as it is common for arthropods. The similar appearance and burrow diameter compared with co-occurring *Arenicolites* cf. *variabilis* indicates the same producer for both burrow types, probably an insect. *Palaeophycus* is commonly interpreted as the dwelling (domichnion) of a predaceous or suspension-feeding animal (Pemberton and Frey, 1982).

Palaeoenvironment and stratigraphy: *Palaeophycus* occurs in a wide range of palaeoenvironments in marine and continental settings. Continental *Palaeophycus* occur in different ichnofacies (Melchor *et al.*, 2012), of which the *Mermia* and *Scoyenia* ichnofacies are probably most relevant, and is common in (but not restricted to) fluvial and lacustrine deposits. *Palaeophycus* is known from the Proterozoic to the Holocene.

***Taenidium barretti* (Bradshaw, 1981)**

Description: The same fine-grained ripple-laminated sandstone bed, hosting *Arenicolites* cf. *variabilis* and *Palaeophycus* cf. *alternatus* at the top (as well as other beds, partly with reworked caliche nodules), also contains *Taenidium barretti* in a deeper tier (ca. 10–30 cm below surface). The cylindrical, unlined and unbranched burrows are winding in a (predominantly) sub-horizontal to sub-vertical direction (Fig. 6E, F). The diameter of the burrows varies between 0.3 and 1.2 cm. Burrows are actively filled with sand, slightly darker in colour than the host rock, and the fill shows a meniscate structure. The backfill menisci are often tightly spaced and, although discernible, with little contrast in lithology, grain size or colour.

Ichnotaxonomy: About seven *Taenidium* ichnospecies are currently distinguished, although this number may change after a thorough review of *Taenidium* and related meniscate trace fossils. The distinction of *Taenidium* from the similar trace fossil *Beaconites* is still debated and finally may show that *Beaconites* must be regarded as junior synonym of *Taenidium* (see discussion in D'Alessandro and Bromley, 1987; Goldring and Pollard, 1995). Likewise, *Naktodemasis* ichnospecies probably also can be accommodated in this ichnogenus (Krapovickas *et al.*, 2009). Ichnospecies of *Taenidium* are differentiated by the style of meniscate backfill, and *T. serpentinum*, *T. diesingi*, *T. cameronensis*, *T. barretti*, *T. irregulare* (= *T. crassum*), *T. planicostatum* and *T. boweni* can currently be regarded as valid ichnospecies.

Producers and ethology: By comparison with modern analogues and experimental studies, there is good confidence that continental *T. barretti* (like the material from the Kågeröd Formation of Bornholm) is produced by the activity of beetles, soil bugs, cicada nymphs, or other insects, but also earthworms (Brussaard and Runia, 1984; Hembree and Hasiotis, 2008; Smith *et al.*, 2008; Counts and Hasiotis, 2009). *Taenidium* is interpreted as burrows produced by a combination of detritus-feeding, locomotion and dwelling behaviours (domichnion, repichnion; Hembree and Hasiotis, 2008). It is likely that the trace makers fed on organic matter and roots within the soil profile (fodinichnion; Smith *et al.*, 2008).

Palaeoenvironment and stratigraphy: *T. barretti* is a typical continental trace fossil of the *Scoyenia* ichnofacies, where it is commonly found in alluvial, fluvial and marginal-lacustrine environments (e.g., Keighley and Pickerill, 1994; Bedatou *et al.*, 2009; Hasiotis, 2010; Melchor *et al.*, 2012) of Lower Ordovician to Pleistocene age (Keighley and Pickerill, 1994). It is part of many soil deposits, particularly those with a higher amount of moisture, but above the water table (A and upper B horizons of soil; Hembree and Hasiotis, 2008).

Root traces (rhizoliths)

Description: Root traces occur in form of rhizoliths (i.e. organo-sedimentary structures resulting in the preservation of plant roots in mineral matter; Klappa, 1980) preferably in the fine-grained, but occasionally also in the coarser-grained sandstone. Fragments of rhizoliths can be found on the beach in front of the outcrop, where they resist fast breakup compared to sandstone without roots because of their preferential cementation in friable host sand. Several kinds of preservation can be recognised and reflect different stages in the decay and diagenetic alteration of the roots (Fig. 7): (1) in some cases, the carbonaceous material of the decayed root is partly preserved with a dark-brown to black colour and a crust of incipient carbonate cement is developed around the root. The root leads to a concretionary growth with diffuse calcite cementation around it (rhizoconcretion); (2) the most common preservation is in the form of amorphous or crystalline dolomite, which has re-

placed the root itself and filled the root cast. Such preservation results in a beige to light-brown colour of the root cast, which is surrounded by a nebulous calcite rim; (3) the third style of preservation is related to the previous one, but shows a more advanced and complex cementation pattern within the root cast in the form of calichification. Cross-sections of such pedodiagenetic accumulations within decaying roots resemble caliche nodules, which are common in the conglomerate and sandstone facies (Fig. 4), with features such as radial and circular voids and fractures cemented with calcite. Carbonaceous material is partly preserved and incorporated in the carbonate cement.

The style of preservation also may be dependent on the types of plant, which originally produced the root traces. Although purely based on fragmentary material and therefore potentially concerning parts of one and the same type of plant, four basic morphotypes of root traces can be recognised: (1) horizontal rootlets, a few millimetres in diameter, without preserved branching and with numerous short root hairs more or less perpendicular to the main root; (2) vertical, cylindrical parts of roots, commonly between 1 and 2 cm in diameter, without preserved branching and a rugose outer surface; (3) vertical, cylindrical parts of roots, commonly between 1 and 2 cm in diameter, with frequent branching, so that off-branches radiating from the central axis, are a few millimetres in diameter, a few centimetres in length, and distally tapering; and (4) horizontal networks of bifurcated rootlets with a diameter of a few millimetres and length of individual segments of several centimetres.

Ichnotaxonomy: Fossil plant roots are covered by the International Code of Nomenclature for algae, fungi, and plants (McNeill *et al.*, 2012) and can be named independent from other parts of the plant. There is a transition between fossil plant roots (body fossils) and their traces (trace fossils). Attempts to classify fossil root plants and their traces have been made by Klappa (1980), Pfefferkorn and Fuchs (1991), Bockelie (1994) and Wright *et al.* (1995).

Producers and ethology: Unknown kinds of higher plants originally colonised floodplain deposits (such as riverbanks) in a continental environment and produced the root traces.

Palaeoenvironment and stratigraphy: The different types of root traces preserved in the section studied indicate a relatively diverse flora of higher plants colonising the sandy substrate on emerging overbank deposits, adjacent to the river channels. Furthermore, different stages of preservation indicate pedogenetic processes and the development of incipient palaeosols. In turn, these data indicate higher humidity during deposition of the sandy sediments of the Kågeröd Formation than previously was understood and support an interpretation of semiarid, rather than arid conditions (e.g., Gravesen *et al.*, 1982, p. 45).

INTERPRETATION AND CONCLUSION

The thick, brownish-red and greyish-green mud deposits of the Bornholm Kågeröd Formation originated from sedimentation on a floodplain with shallow lakes, under semiarid conditions. The conglomeratic and sandy facies in the upper part of the exposed succession indicate seasonal, monsoonal rain, in an overall semiarid climate. The conglomerates were probably deposited as lag deposits on the beds of river channels. The sandstone represents the deposits of fluvial channels, the meandering courses of which produced widespread levee and overbank deposits, with sparse vegetation and pedogenic modifications. Incipient palaeosols with caliche nodules developed within the clay, but also on top of alluvial fan deposits, the conglomeratic

facies of which contains reworked caliche nodules and crayfish burrows (*Camborygma eumekenomos*) down to below the water table in the phreatic zone. The top surfaces of abandoned fluvial channel deposits and their lateral levee and overbank deposits were rapidly colonised, probably by insects (e.g., beetles) and other invertebrates, resulting in a relatively low-diversity trace-fossil assemblage with a high abundance of *Arenicolites cf. variabilis* and *Taenidium barretti*, as well as rare *Palaeophycus cf. alternatus*. All members of this trace-fossil assemblage are characteristic for fluvial channel belts and the continental *Skolithos* ichnofacies (Melchor *et al.*, 2012). Further pedogenisation of the floodplain and overbank deposits allowed the growth of plants in a partly vegetated fluvial environment, with root structures preserved in diagenetically modified (cemented) variants (rhizoliths).

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Fig. 7. Root traces (rhizoliths) in fine- to medium-grained sandstone. Scale bars = 1 cm. **A.** Sandstone slab containing numerous vertical and horizontal rhizoliths (branched and unbranched) with brownish colour due to dolomitisation. Note the different size of the diagenetic halo around the root traces, which consists of calcite. **B.** Close-up view of A, showing a network of small horizontal root traces. **C.** Close-up view of A, showing a large, cylindrical, vertical rhizolith with smaller and tapering rootlets branching off from the central axis in a radial manner. **D.** Bedding plane, showing a small horizontal rootlet with numerous short root hairs and preserved in carbonaceous material. **E.** Large, cylindrical, vertical rhizolith in calichified (pedogenised) dolomite preservation and subsequent cementation around the root structure with calcite (rhizoconcretion). **F.** Cross-section of an intensely calichified root structure embedded in sandstone. Black carbonaceous material is preserved in a central axis and in some thin, tangential drapes.

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